UNIVERSIDADE DE SÃO PAULO

MUSEU DE ZOOLOGIA

Hilton de Castro Galvão Filho

Taxonomy and Cladistic Analysis of Plakobranchidae (Gastropoda: Sacoglossa)

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Taxonomy and Cladistic Analysis of Plakobranchidae (Gastropoda: Sacoglossa)

Taxonomia e Análise Cladística de Plakobranchidae (Gastropoda: Sacoglossa)

Original Version

Thesis presented to the Post-Graduate Program of the Museu de Zoologia da Universidade de São Paulo, to obtain the degree of Doctor of Sciences in Systematics, Animal Taxonomy, and Biodiversity

Advisor: Luiz Ricardo Lopes de Simone, PhD.

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Nome: GALVÃO FILHO, Hilton de Castro

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Dedico este trabalho a todos as pessoas LGBT+
que escolheram a ciência como profissão.

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‘If you wish to make an apple pie from scratch,
you must first invent the universe.’

Carl Sagan

ABSTRACT

The comprehension of the evolutionary history of the order Sacoglossa is fundamental to understand the adaptive radiation of Heterobranchia, the most morphologically heterogeneous group in Gastropoda. Sacoglossans form a well-supported monophyletic group, but the relationship of its internal clades is still confused. Plakobranchidae is the most diverse family and the main systematic problem of Sacoglossa since the lack of detailed descriptions provided many synonyms and invalid taxa from genus to species level. The family Plakobranchidae resulted in a monophyletic group only in few phylogenetic hypotheses of Sacoglossa. However, either molecular or morphological data were usually analyzed to reconstruct Sacoglossa phylogeny, while an integrative approach has never been applied for such purpose. A total 42 species, including 30 species of Plakobranchidae, 10 related species in Sacoglossa and other two heterobranchs, was analyzed to test the monophyly of Plakobanchidae and the relationship of its internal clades. A parsimonious phylogenetic analysis was performed in TNT considering 109 characters of external morphology, internal anatomy and ecology data. Molecular partial sequences of two mitochondrial (COI, 16S) and three nuclear (H3, 18S and 28S) genes were used to build a phylogenetic hypothesis under Bayesian Inference and Maximum Likelihood criteria. One final BI analysis was performed with a combined matrix with molecular, morphological and ecological data of all analyzed taxa. Plakobranchidae resulted as monophyletic only in morphological and combined data, but the monophyletic status of the genera *Plakobranchus* van Hasselt, *Thuridilla* Bergh and *Elysia* Risso, 1818 was fully supported by all analyses. Species within the multi-diverse *Elysia* form similar clades in all different analysis matching with prior synonymized names, meaning that old names might be resurrected for a better explanation of the natural history of this genus.

Keywords: Sea slugs; Heterobranchia; phylogeny; total evidence; morphology.

RESUMO

Compreender a evolução da ordem Sacoglossa é de fundamental importância para o entendimento da irradiação adaptativa de Heterobranchia, o grupo de Gastropoda mais morfologicamente diverso. Os sacoglossos formam um grupo monofilético bem suportado, mas as relações dos seus clados internos ainda é confusa. Plakobranchidae é a família mais diversa e com os principais problemas sistemáticos de Sacoglossa, uma vez que a ausência de descrições detalhadas contribuiu para muitas sinonimizações e invalidações de táxons em níveis de gênero e de espécie. A família Plakobranchidae resultou em um grupo monofilético apenas em poucas hipóteses filogenéticas de Sacoglossa. Entretanto, apenas dados moleculares ou morfológicos foram analisados para reconstruir a filogenia de Sacoglossa, enquanto que uma abordagem integrativa nunca foi feita para esse propósito. Um total de 42 espécies, incluidon 30 espécies de Plakobranhida, 10 de espécies próximas em Sacoglossa e dois outros heterobrâqnuios, foram analisados para testar a monofilia de Plakobranchidae e as relações entre seus grupos internos. Uma análise filogenética de parcimônia foi realizada no TNT considerando 109 caracteres da morfologia externa, anatomia interna e dados ecológicos. Sequências moleculares dois genes mitocondriais (COI, 16S) e três nucleares (H3, 18S e 28S) foram usados para construir hipóteses filogenéticas sob os critérios de Inferência Bayesiana e Máxima Verossimilhança. Uma última análise bayesiana foi feita com os dados moleculares, morfológicos e col. ógicos combinados em uma matriz. Plakobanchidae resultou como um grupo monofilético apenas nas análises com dados morfológicos e dados combinados, mas a monofilia dos gêneros *Plakobranchus*, *Thurudilla* e *Elysia* foram bem suportados em todas as análises. Espécies do multi-diverso *Elysia* formam clados similares nas diferentes análises que coincidem com nomes sinonimizados do gênero, o que significa que nomes antigos do grupo podem ser reerguidos para explicar melhor a história evolutiva do grupo.

Palavras-chave: Lesmas-do-mar; Heterobranchia; filogenia; evidência total; morfologia.

LIST OF TABLES

LIST OF FIGURES

system, dorsal view; C) detail of cerebro-pleural ganglia, dorsal view; D) detail of pedal ganglia, ventral view. Scales: 1 mm.

Figure 13. *Ascobulla ulla* live animal. A) dorsal view; B) lateral left view; C) ventral view; D) shell apex.

Figure 14. *Ascobulla ulla* anatomy, shell removed, focusing pallial cavity structures: A) Whole dorsal view; B) ventral view; C) lateral view. Scales= 1 mm.

Figure 15. *Ascobulla ulla* anatomy: A) Whole dorsal view, shell and dorsal mantle removed, focusing pallial cavity structures; B) pallial cavity organs. Scales= 1 mm.

Figure 16. *Ascobulla ulla* anatomy of digestive system: A) Whole dorsal view; B) whole left view (scales= 1 mm). C-E) Buccal mass anatomy: C) dorsal; D) ventral; E) right view (scales: 0.5 mm).

Figure 17. *Ascobulla ulla* radula. A) Whole view; B) detail of leading tooth.

Figure 18. *Ascobulla ulla* anatomy of reproductive and nervous systems: A) schematic drawing of the reproductive system, dorsal view; B) whole dorsal view of central nervous system; C) detail of cerebro-pleural ganglia and pedal ganglia, anterior view. Scales: 1 mm (A, B); 0.5 mm (C).

Figure 19. *Oxynoe antillarum* live animal. A) dorsal view; B) ventral view. Length: 18 mm.

Figure 20. *Oxynoe antillarum* anatomy, shell removed, focusing pallial cavity structures: A) Whole dorsal view; B) ventral view; C) lateral view, dorsal mantle removed. Scales= 1 mm.

Figure 21. *Oxynoe antillarum* anatomy: A) Whole dorsal view, shell and dorsal mantle removed, focusing pallial cavity structures; B) pallial cavity organs. Scales= 1 mm.

Figure 22. *Oxynoe antillarum* anatomy of digestive system: A) Whole dorsal view; B) whole left view. C-E) Buccal mass anatomy: C) dorsal; D) ventral; E) lateral right view. Scales: 1 mm.

Figure 23. *Oxynoe antillarum* radula. A and C) Whole view; B and D) detail of leading tooth.

Figure 24. *Oxynoe antillarum* anatomy of reproductive and nervous systems: A) schematic drawing of the reproductive system, dorsal view; B-C) whole view of central nervous system; B) anterior view; C) posterior view. Scales: 1 mm.

Figure 25. Live specimen of *Caliphylla mediterranea*. A) 18 mm length; B) 33 mm length.

Figure 26. External morphology of *Caliphylla mediterranea*. A) dorsal view with cerata; B) ventral view; C) lateral right view with no cerata. Scale: 1 mm.

Figure 27. Digestive system of *Caliphylla mediterranea*. A) Dorsal view; B) Lateral left view; Detail of buccal mass: C) dorsal view; D) ventral view side; E) lateral right view. Scales: 1 mm.

Figure 28. Scan electron microscope images of radula of *Caliphylla mediterranea.* A and C) general view; B and D) detail of the leading tooth.

Figure 29. Reproductive system of *Caliphylla mediterranea*. A) Dorsal view of whole system; B) schematic drawing, dorsal view. Scales = 1 mm.

Figure 30. *Caliphylla mediterranea* anatomy. A) Circulatory and excretory systems, renopericardial cavity. B-C) Central nervous system; B) anterior view; D) posterior view. Scales= 0.5 mm.

Figure 31. Live specimen of *Olea* n. sp.

Figure 32. External morphology of *Olea* n. sp. (A) Dorsal, (B) lateral, and (C) ventral view of a 1,5mm specimen with cerata. (D) Dorsal and (E) lateral view of a 2 mm specimen with no cerata.

Figure 33. Digestive system of *Olea* n. sp. A) Lateral view. B) Dorsal view. C) Radula. D) Internal view.

Figure 34. Internal morphology of *Olea* n. sp. A) Dorsal view of hemocoel organs disposition. B) Ventral view of kidney and pericardium. C) Reproductive system. D) Anterior and posterior (E) view of central nervous system.

Figure 35. Scanning electron microscope image of penis of *Olea* n. sp.

Figure 36. Live specimen of *Stiliger vossi*.

Figure 37. External morphology of *Stiliger vossi*. A) dorsal view with cerata; B) ventral; C) dorsal view with no cerata; D) lateral view with cerata; E) lateral view with no cerata.

Figure 38. *Stiliger vossi* anatomy, circulatory and excretory systems. A) dorsal view of boy withtou the dorsal mantle; B) ventral view of renopericardial organs. Scales: A = 1 mm; B = 0.2 mm.

Figure 38. Digestive system of *Stiliger vossi*. A) Dorsal view; B) Lateral view; Buccal mass: C) left side; D) right side. E) Posterior portion of digestive system.

Figure 39. Scan electron microscope images of radula of *Stiliger vossi* (scale: 10 µm): A-B) general view; C-D) detail of the leading tooth; E-F detail of ascus.

Figure 40. Visceral mass and reproductive system of *Stiliger vossi*. A) Dorsal view of visceral mass; B) Ventral view of visceral mass; C) Overview of reproductive system; D) schematic drawing of reproductive system.

Figure 41. *Stiliger vossi* anatomy, central nervous system: A) anterior view; B) posterior view. Scale = 0.2 mm.

Figure 42. Live specimen of *Bosellia mimetica*. A, B = 7 mm length; C = 5 mm length.

Figure 43. External morphology of *Bosellia mimetica*. A) dorsal view; B) ventral view. Scales: 0.5 mm

Figure 44. Digestive system of *Bosellia mimetica*. A) Dorsal view; B) Lateral view; Buccal mass: C) dorsal view side; D) ventral side. E) lateral right view.

Figure 45. Scan electron microscope images of radula of *Bosellia mimetica* : A) general view; B) detail of the leading tooth; C) detail of ascus.

Figure 46. Scan electron microscope images of penis of *Bosellia mimetica*: A) general view; B) detail of the stylet.

Figure 47. Anatomy of *Bosellia mimetica*. A) whole reproductive system, dorsal view; B) schematic reproductive system; C) renopericardial cavity, ventral view; D) nervous system, aneterior view; E) nervous system, posterior view. Scales A-C= 0.5 mm; D-E = 0.25 mm.

Figure 48. External morphology of *Plakobranchus ocellatus*. A) dorsal view; B) lateral view; C) ventral view; D) dorsal view of parapodia opened.

Figure 49. External morphology of *Plakobranchus ocellatus*. A) dorsal view; B) ventral view; C) lateral view.

Figure 50. Digestive system of *Plakobranchus ocellatus*. A) Dorsal view; B) lateral view. Buccal mass: C) Dorsal view; D) Ventral view; E) Right side.

Figure 51. Scan electron microscope images of radula of *Plakobranchus ocellatus.* A) descending limb; B & D) detail of some teeth; C) overview.

Figure 52. Scan electron microscope image of penis of *Plakobranchus ocellatus.*

Figure 53. Reproductive system of *Plakobranchus ocellatus*. A) Schematic drawing; B) overview.

Figure 54. Circulatory and nervous systems of *Plakobranchus ocellatus*; A) Renopericardial cavity. B) anterior view of nervous system. C) posterior view of nervous system.

Figure 55. External morphology of *Plakobranchus ianthobapsus*. A) dorsal view; B) lateral view; C) dorsal view with parapodia oppened; D) ventral view.

Figure 56. *Plakobranchus ianthobapsus* internal morphology. Digestive system. A) dorsal view. B) Lateral view. C-E) Buccal mass, dorsal (C), ventral (D) and lateral view (E). F) Internal surface of digestive system.

Figure 57. Scan electron microscope images of radula of *Plakobranchus ocellatus.* A) overview; B) detail of leading tooth; C) discarded teeth.

Figure 58. Scan electron microscope image of penis of *Plakobranchus ianthobapsus.*

Figure 59. Internal morphology of *Plakobranchus ianthobapsus*. A-B) Reproductive system, overview (A) and schematic arrangement (B). C) Circulatory and excretory systems. D-E) Nervous system, anterior (D) and posterior (E) view.

Figure 60. External morphology of *Plakobranchus papua*. A-B) Dorsal view; C) ventral view; C) ventral view; D) dorsal view with parapodia oppend.

Figure 61. Internal morphology of *Plakobranchus papua*. Digestive system. A) dorsal view. B) Lateral view. C-E) Buccal mass, dorsal (C), ventral (D) and lateral view (E). F) Internal surface of digestive system.

Figure 62. Radula of *Plakobranchus papua*. A) overview; B) leading tooth; C) discarded tooth.

Figure 63. Penis of *Plakobranchus papua*.

Figure 64. Internal morphology of *Plakobranchus papua*. A-B) Reproductive system, overview (A) and schematic arrangement (B). C) Circulatory and excretory systems. D-E) Nervous system, anterior (D) and posterior (E) view.

Figure 65. External morphology of *Plakobranchus* sp. 1. A) Dorsal view; B) dorsal view with parapodia opened; C) ventral view; D) lateral view.

Figure 66. Internal morphology of *Plakobranchus* sp. 1. Digestive system. A) dorsal view. B) Lateral view. C-E) Buccal mass, dorsal (C), ventral (D) and lateral view (E). F) Internal surface of digestive system.

Figure 67. Radula of *Plakobranchus* sp. 1. A) overview; B) leading tooth; C) old teeth; D) discarded teeth.

Figure 68. Penis of *Plakobranchus* sp. 1. A) overview; B) detail of penial stylet.

Figure 69. Internal morphology of *Plakobranchus* sp. 1. A-B) Reproductive system, overview (A) and schematic arrangement (B). C) Circulatory and excretory systems. D-E) Nervous system, anterior (D) and posterior (E) view.

Figure 70. Photos of preserved specimens of *Plakobranchus* sp. 2 Africa. A) Dorsal view with closed parapodia; B) ventral view; C) dorsal view with opened parapodia; D) lateral left view.

Figure 71. External morphology of *Plakobranchus* sp. 2 Africa. A) Dorsal view. B) Ventral view. C) Lateral view.

Figure 72. Internal morphology of *Plakobranchus* sp. 2 africa. Digestive system. A) dorsal view. B) Lateral view. C-E) Buccal mass, dorsal (C), ventral (D) and lateral view (E). F) Internal surface of digestive system.

Figure 73. Radula of *Plakobranchus* sp. 2. A) overview; B) leading tooth; C) old teeth; D) discarded teeth.

Figure 74. Penis of *Plakobranchus* sp. 2.

Figure 75. Internal morphology of *Plakobranchus* sp. 1 aff. purple. A-B) Reproductive system, overview (A) and schematic arrangement (B). C) Circulatory and excretory systems.

Figure 76. External morphology of *Thuridiila hopei*. A) dorsal view; B) ventral view; C) lateral right view. Scales: 0.5 mm

Figure 77. Digestive system of *Thuridilla hopei*. A) Dorsal view; B) Lateral view; Buccal mass: C) dorsal view side; D) ventral side. E) lateral right view. Scales: 0.5mm

Figure 78. Scan electron microscope images of radula *Thuridilla hopei* : A) general view; B) detail of the leading tooth; C) detail of older tooth; D) Ascus.

Figure 79. Anatomy of *Thuridilla hopei*. A) whole reproductive system, dorsal view; B) schematic reproductive system; C) renopericardial cavity, ventral view; D) nervous system, aneterior view; E) nervous system, posterior view. Scales A-C= 0.5 mm; D-E = 0.25 mm.

Figure 80. Live specimens of *Thuridiila picta*. A) dorsal view with closed parapodia; B) dorsal view with oppend parapodia. Body length: 18 mm.

Figure 81. External morphology of *Thuridiila picta*. A) dorsal view; B) ventral view; C) lateral right view. Scales: 0.5 mm.

Figure 82. Digestive system of *Thuridilla picta*. A) Dorsal view; B) Lateral view; Buccal mass: C) dorsal view side; D) ventral side. E) lateral right view. Scales: 0.5mm

Figure 83. Scan electron microscope images of radula *Thuridilla picta*: A) general view; B) detail of the leading tooth; C) detail of older tooth; D) Ascus.

Figure 84. Anatomy of *Thuridilla picta*. A) whole reproductive system, dorsal view; B) schematic reproductive system; C) renopericardial cavity, ventral view; D) nervous system, aneterior view; E) nervous system, posterior view. Scales A-C= 0.5 mm; D-E = 0.25 mm.

Figure 85. Live specimens of *Thuridiila mazda*. A) dorsal view with closed parapodia; B) lateral. Body length: 5 mm.

Figure 86. External morphology of *Thuridiila mazda*. A) dorsal view; B) ventral view; C) lateral right view. Scales: 0.5 mm

Figure 87. Digestive system of *Thuridilla mazda*. A) Dorsal view; B) Lateral view; Buccal mass: C) dorsal view side; D) ventral side. E) lateral right view. Scales: 0.5mm

Figure 88. Scan electron microscope images of radula *Thuridilla mazda*: A) general view; B) detail of the leading tooth; C) detail of older tooth.

Figure 89. Anatomy of *Thuridilla mazda*. A) whole reproductive system, dorsal view; B) schematic reproductive system; C) renopericardial cavity, ventral view; D) nervous system, aneterior view; E) nervous system, posterior view. Scales A-C= 0.5 mm; D-E = 0.25 mm.

Figure 90. External morphology of *Elysia timida*. A) dorsal view; B) ventral view.

Figure 91. Digestive system of *Elysia timida*. A) Dorsal view. Buccal mass**:** B) dorsal; C) ventral; D) lateral.

Figure 92. Scan electron microscope images of radula *Elysia timida*: A) general view; B) detail of the leading tooth; C) detail of older tooth.

Figure 93. Reproductive system of *Elysia timida*.

Figure 94. Circulatory and nervous systems of *Elysia timida*. A) Renopericardial cavity. B) anterior view of nervous system.

Figure 95. External morphology of *Elysia viridis*. A) dorsal; B) ventral; C) lateral.

Figure 96. Digestive system of *Elysia viridis*. A) Dorsal view; B) Lateral view; Buccal mass: C) dorsal; Buccal mass: D) ventral; E) left side; F) right side.

Figure 97. Scan electron microscope images of radula *Elysia viridis*: A-C) general view; B-D) detail of the leading tooth.

Figure 98. Reproductive system of *Elysia viridis*. A) Schematic drawing; B) Overview.

Figure 99. Circulatory and nervous systems of *Elysia viridis*. A) Renopericardial cavity. B) anterior view of nervous system.

Figure 100. External morphology of *Elysia australis*. A) dorsal; B) ventral; C) lateral.

Figure 101. Digestive system of *Elysia australis*. A) Dorsal view; B) Lateral view; Buccal mass: C) lateral; D) dorsal; E) ventral.

Figure 102. Scan electron microscope images of radula of *Elysia australis* (scale: 10 µm): A-B) general view; C-D) detail of the leading tooth.

Figure 103. Reproductive system of *Elysia australis* - Schematic drawing.

Figure 104. Circulatory and nervous systems of *Elysia australis*. A) Renopericardial cavity. B) anterior view of nervous system.

Figure 105. External morphology of live *Elysia ornata* live animal: A) dorsal view (length: 22 mm) parapodia opened; B) ventral view of same animal; C) lateral left view (length: 31 mm).

Figure 106. External morphology of *Elysia ornata* (scale: 1 mm): A) dorsal view; B) ventral view; C) lateral view.

Figure 107. Digestive system of *Elysia ornata*: A) dorsal view and B) lateral view of the whole system. Buccal mass: C) dorsal; D) ventral and E) lateral right view.

Figure 108. Scan electron microscope images of radula of *Elysia ornata*: A) general view; B-C) detail of the leading tooth; D) detail of old tooth.

Figure 109. Reproductive, circulatory, excretory and nervous systems of *Elysia ornata*: A) general view of reproductive system; B) schematic view of reproductive system; C) ventral view of renopericaldial cavity in 4mm specimen; D) ventral view of renopericaldial cavity in 6mm specimen; E) posterior view of the nervous system; F) anterior of the nervous system. (scales: A-C = 1 mm; D-E = 0,5 mm).

Figure 110. External morphology of live *Elysia crispata* live animal: A) dorsal view (length: 28 mm) parapodia opened; B) ventral view of same animal; C) dorsal view (length: 37 mm); D) ventral view of same animal.

Figure 111. External morphology of *Elysia crispata* (scale: 1 mm): A) dorsal view; B) ventral view; C) lateral view.

Figure 112. Digestive system of *Elysia crispata*: A) dorsal view and B) lateral view of the whole system. Buccal mass: C) dorsal; D) ventral and E) lateral right view.

Figure 113. Scan electron microscope images of radula of *Elysia crispata*: A and C) general view; B and D) detail of the leading tooth.

Figure 114. Reproductive, circulatory, excretory and nervous systems of *Elysia crispata*: A) general view of reproductive system; B) schematic view of reproductive system; C) ventral view of renopericaldial cavity in 4mm specimen; D) ventral view of renopericaldial cavity in 6mm specimen; E) posterior view of the nervous system; F) anterior of the nervous system. (scales: A-C = 1 mm; D-E = 0,5 mm).

Figure 115. External morphology of live *Elysia diomedea* live animal: A) dorsal view (length: 33 mm) parapodia opened; lateral right view of same animal.

Figure 116. External morphology of *Elysia diomedea* (scale: 1 mm): A) dorsal view; B) ventral view; C) lateral view.

Figure 117. Digestive system of *Elysia diomedea*: A) dorsal view and B) lateral view of the whole system. Buccal mass: C) dorsal; D) ventral and E) lateral right view.

Figure 118. Scan electron microscope images of radula of *Elysia diomedea*: A) general view; B) detail of the leading tooth.

Figure 119. Reproductive, circulatory, excretory and nervous systems of *Elysia diomedea*: A) general view of reproductive system; B) schematic view of reproductive system; C) ventral view of renopericaldial cavity in 4mm specimen; D) ventral view of renopericaldial cavity in 6mm specimen; E) posterior view of the nervous system; F) anterior of the nervous system. (scales: A-C = 1 mm; D-E = 0,5 mm).

Figure 120. External morphology of live *Elysia papillosa*: A) dorsal view (length: 12 mm); B) ventral view (length 12 mm); C) dorsal view open parapodia (length: 11 mm); D) dorsal view juvenile (length: 4 mm).

Figure 121. External morphology of *Elysia papillosa* (scale: 1 mm): A) dorsal view; B) ventral view; C) lateral view.

Figure 122. Digestive system of *Elysia papillosa* (scale: 0,5 mm): A) dorsal view of digestive system; B) lateral view of digestive system; C-F) buccal mass: C) dorsal; D); ventral; E) right side; F) left side; G) detail morphology of posterior digestive system; H) Detail morphology of buccal mass.

Figure 123. Scan electron microscope images of radula of *Elysia papillosa* (scale: 10 µm): A) general view; B) detail of the leading tooth.

Figure 124. Reproductive, circulatory, excretory and nervous systems of *Elysia papillosa* (scale: 0,5 mm): A) general view of reproductive system; B) schematic view of reproductive system; C) ventral view of renopericaldial cavity in 4mm specimen; D) ventral view of renopericaldial cavity in 6mm specimen; E) posterior view of the nervous system; F) anterior of the nervous system.

Figure 125. Live specimen of *Elysia cornigera*. A) dorsal; B) ventral.

Figure 126. External morphology of *Elysia cornigera*. A) dorsal; B) ventral.

Figure 127. Digestive system of *Elysia cornigera*. A) Dorsal view. Buccal mass: B) dorsal; C) lateral; D) ventral.

Figura 128. Reproductive, circulatory and nervous systems of *Elysia cornigera*. A) Renopericardial cavity. B) anterior view of nervous system.

Figure 129. External morphology of live *Elysia zuleicae*: A-B) dorsal view (length: 11 mm); B) ventral view (length 11 mm); C) dorsal view juvenile (length: 4 mm); E) lateral view (length: 10 mm).

Figure 130. External morphology of *Elysia zuleicae* (scale: 1 mm): A) dorsal view; B) ventral view; C) lateral view.

Figure 131. Digestive system of *Elysia papillosa* (scale: 0,5 mm): A) dorsal view of digestive system; B) lateral view of digestive system; C-E) zuleicae mass: C) dorsal; D); ventral; E) right side; F) detail morphology of posterior digestive system; G) Detail morphology of buccal mass.

Figure 132. Scan electron microscope images of radula of *Elysia zuleicae* (scale: 10 µm): A) general view; B) detail of the leading tooth.

Figure 133. Reproductive, circulatory, excretory and nervous systems of *Elysia zuleicae* (scale: 0,5 mm): A) general view of reproductive system; B) schematic view of reproductive system; C) ventral view of renopericaldial cavity in 4mm specimen; D) ventral view of renopericaldial cavity in 6mm specimen; E) posterior view of the nervous system; F) anterior of the nervous system.

Figure 134. External morphology of live *Elysia orientalis*: A) dorsal view (length: 6 mm); B) dorsal view (length 4 mm); C) ventral view (length: 4 mm); D) lateral view (length: 6 mm).

Figure 135. Drawings of the external morphology of *Elysia orientalis* (scale: 1 mm): A) dorsal view; B) ventral view; C) lateral view.

Figure 136. Digestive system of *Elysia orientalis* (scale: 0,5 mm): A) dorsal view of digestive system; B) lateral view of digestive system; C) detailed morphology of posterior digestive system; D-G) buccal mass: D) dorsal; E); ventral; F) right side; G) left side.

Figure 137. Scan electron microscope images of radula of *Elysia orientalis* BMSM 59035 (scale: 10 µm): A) general view; B) detail of the leading tooth; C) detail of teeth on ascus.

Figure 138. Reproductive, circulatory, excretory and nervous systems of *Elysia orientalis* (scale: 0,5 mm): A) general view of reproductive system; B) schematic view of reproductive system; C) ventral view of renopericaldial cavity in 4mm specimen; D) ventral view of renopericaldial cavity in 6mm specimen; E) anterior view of the nervous system; F) posterior of the nervous system.

Figure 139. External morphology of live *Elysia pawliki*: A-B) dorsal view of juveniles specimens (length 11 mm (A); 8 mm (B)); C) lateral view; D) lateral view juvenile (length: 9 mm); E-F) dorsal view (length: 22 mm); G) ventral view (length: 22 mm).

Figure 140. External morphology of *Elysia pawliki* (scale: 1 mm): A) dorsal view; B) ventral view; C) lateral view.

Figure 141. Digestive system of *Elysia papillosa* (scale: 0,5 mm): A) dorsal view of digestive system; B) lateral view of digestive system; C-E) zuleicae mass: C) dorsal; D); ventral; E) right side; F) detail morphology of posterior digestive system; G) Detail morphology of buccal mass.

Figure 142. Scan electron microscope images of radula of *Elysia orientalis* BMSM 59035 (scale: 10 µm): A) general view; B) detail of the leading tooth; C) detail of teeth on ascus.

Figure 143. Reproductive, circulatory, excretory and nervous systems of *Elysia orientalis* (scale: 0,5 mm): A) general view of reproductive system; B) schematic view of reproductive system; C) ventral view of renopericaldial cavity in 4mm specimen; D) ventral view of renopericaldial cavity in 6mm specimen; E) anterior view of the nervous system; F) posterior of the nervous system.

Figure 144. Consensus tree of Plakobranchidae and outgroup species obtained through parsimonious analysis in TNT with prior weight. Nodes are named with letters and numbers bellow branches matching with the nodes with the implied weight final tree (Fig. 85). Relative Bremer support is on top of branches.

Figure 145. Consensus tree of Plakobranchidae obtained through parsimonious analysis in TNT with prior weight. Nodes are named with letters and numbers bellow branches matching with the nodes in the implied weight final tree (Fig. 3). Relative Bremer support is on top of branches.

Figure 146. Phylogenetic tree obtained through parsimonious analysis in TNT with implied weight (K=8). A-G nodes with outgroup taxa and 1-19 with ingroup taxa.

Figure 147. Section of the phylogenetic tree obtained through parsimonious analysis in TNT with implied weight (K=8) with *Elysia* matching nodes with previous synonyms.

Figure 148. Phylogenetic tree obtained through parsimonious analysis in TNT with implied weight (K=8) and character optimization. A-G nodes with outgroup taxa and 1-18 with ingroup taxa.

Figure 149. Phylogenetic tree (part 1) with the characters that suport each node. Nodes: A) unamed; B) Sacoglossa; C) Oxynoacea; D) Plakobranchacea.

Figure 150. Phylogenetic tree (part 2) with the characters that suport each node. Nodes: D) Plakobranchacea; E) Limapontioidea+ Plakobranchoidea; F) Limapontioidea; G) Plakobranchoidea.

Figure 151. Phylogenetic tree (part 3) with the characters that suport each node. Nodes: G) Plakobranchoidea; 1) Plakobranchidae; 2) *Thuridilla* + *Plakobranchus*; 3) *Thuridilla*; 4) *Plakobranchus*; 5) *Elysia*.

Figure 152. Phylogenetic tree (part 4) with the characters that suport each node. Nodes are unamed subdivision of *Elysia* (Node 5).

Figure 153. Phylogenetic tree obtained through Maximum Likelihood of concatenated DNA sequences of two mitochondrial (COI, 16S) and three nuclear (H3, 18S and 28S) genes. Support values as ML bootstrap percentages on each node.

Figure 154. Phylogenetic tree obtained through Bayesian analysis of concatenated DNA sequences of two mitochondrial (COI, 16S) and three nuclear (H3, 18S and 28S) genes. Support values as BI posterior probabilities on each node.

Figure 155. Section of phylogenetic tree obtained through Maximum Likelihood (Fig. 93) with *Elysia* matching nodes with previous synonyms.

Figure 156. Section of phylogenetic tree obtained through Bayesian Inference (Fig. 7) with *Elysia* matching nodes with previous synonyms.

Figure 157. Phylogenetic tree obtained through Bayesian analysis of combined data of 109 morphological characters and concatenated DNA sequences of two mitochondrial (COI, 16S) and three nuclear (H3, 18S and 28S) genes. Support values as BI posterior probabilities on each node.

Figure 158. Section of phylogenetic tree obtained through Bayesian Inference (Fig. 97) with *Elysia* matching nodes with previous synonyms.

Figure 159. Phylogenetic tree obtained through Maximum Likelihood of concatenated DNA sequences of two mitochondrial (COI, 16S) genes. Support values as ML bootstrap percentages on branch.

Figure 160. Phylogenetic tree obtained through Maximum Likelihood of partial DNA sequences of the nuclear gene H3. Support values as ML bootstrap percentages on branch.

ABBREVIATIONS

ab – abdominal ganglion;

ac – accessory ganglion;

ad – ampulla duct

ag - albumen gland;

am - ampulla;

an - anus;

ao – aorta;

as - *ascus*;

au – auricle;

ba- bulb armature

bc – bursa copulatrix;

bg – buccal gland

bm – buccal mass;

bp – bucal pouch

bu – buccal ganglia;

ca – capsule gland

cb – cerebro-bucal connective;

cb – ciliary band;

cc – cerebral commissure

cg – cerebral ganglia;

cp – cerebropleral ganglia;

cr - crop;

cs – cephalic shield;

ct – cerata;

dg – digestive gland;

dl – dorsal lamellae;

dv – dorsal vessels;

ep – esophageal pouch;

es - esophagus;

ey – eye

fc – fertilization chamber

fd - female duct

fl – mesopodial groove

fo – foot

fp – female pore;

gg – genital ganglion;

gi – gill;

go – gonad;

gp – gizzard plates;

gr – genital receptacle;

gv – gametolitic vesicles

hd – hermaphrodite duct;

hf – hermaphrodite folicule;

hg - hermaphrodite groove;

hy – hypobranchial gland;

in - intestine;

ja – jaw;

ki – kidney;

ko – kidney opening;

lb – labial lobe

lg – lateral groove

ma – ascus musculature

md - male duct

me – membrane gland

mg – mucus gland;

mo – mouth;

mp – male pore;

ms – metapodial sole – mudar para propodium

ns – nervous system;

od – odontophore;

on – optical nerve;

or – odontophore region

os - oral sphincter;

ot – oral tube;

ov - oviduct;

pa – parapodial sole;

pb – penile bulb

pc – pericardium

pd – pedal ganglia

pe - penis;

pe –posterior esophagus;

pg – pedal ganglia;

pl – pleural ganglia;

po - propodium

pp – parapodia

pr – prostate gland

ps –penis sheath;

ra – radulae;

rc – renopericardial cavity;

rh – rhinophore;

rp – renal papilla;

rr – renal ridge;

sb – subintestinal ganglion;

sg – salivary gland;

sm – dorsal septate muscle;

sp – supraintestinal ganglion;

st – stomach;

tl - tail;

to – oral tentacles;

vc - visceral connective;

vd – vas deferens;

vg – vagina;

vt – ventricle;

SUMÁRIO

1. INTRODUCTION

1.1. GENERAL CLASSIFICATION

Phylum Mollusca is a highly diverse animal group with about 200.000 extant and 30.000 extinct species (PONDER & LINDBERG, 2008). Being the second most species animal group, Mollusca comprises 8 living classes with distinct body organizations, comprising interstitial worm-like specimens, chitons, bivalves, octopuses, snails, limpets and terrestrial slugs. The diversity of body plans allowed the mollusks to explore different habitats in marine, aquatic and terrestrial environments (PONDER & LINDBERG, 2008).

The class Gastropoda is the one with more successful adaption in distinct environments and represents the richest class in Mollusca (BIELER, 1992). Gastropods are usually the most common mollusks in all marine ecosystems. In addition, they are the only group to have invaded the land and freshwater habitats on all continents (AKTIPIS *et al*., 2008).

The traditional division of Gastropoda in Prosobranchia, Opisthobranchia and Pulmonata has changed drastically since phylogenetic analyses indicated the paraphyly of these groups (PONDER & LINDBERG, 1997, ZAPATA *et al*., 2014). After the first work to use cladistic methods, the groups Opisthobranchia, Pulmonata and some prosobranchs were included in the clade Heterobranchia, and the remaining prosobranchs were grouped in the clades Patellogastropoda, Cocculiniformia, Neritimorpha, Vetigastropoda and Caenogastropoda (PONDER & LINDBERG, 1997; BOUCHET & ROCCOI, 2005; SIMONE, 2011).

Within the gastropods, Heterobranchia is the most morphologically diverse clade, represented by up to 40.000 species inhabiting pelagic, benthic, terrestrial and freshwater habitats (WÄGELE *et al*., 2008; MORDAN & WADE, 2008). The synapomorphies of Heterobranchia includes the sinistral larval shell, absence of ctenidium, simple esophagus and lack of odontophoral cartilages (PONDER & LINDBERG, 1997). Both morphological (PONDER & LINDBERG, 1997; DAYRAT & TILLIER, 2002; SIMONE, 2011) and molecular phylogenies (GRANDE *et al*., 2004; DINAPOLI & KLUSSMANN-KOLB, 2010) have recovered Heterobranchia as monophyletic as proposed by Hazsprunar (1985).

Heterobranchia presents the internal clade Euthyneura, which is composed mostly by previous opisthobranch and pulmonate groups and is characterized by different degrees of detorsion on nervous system and nerve concentration (HASPRUNAR, 1985). The monophyly of Euthyneura was largely corroborated by morphological based phylogenies (PONDER & LIINDBERG, 1997; DAYRAT & TILLIER, 2002; WÄGELE & KLUSSMANN-KOLB, 2005), but was changed after the inclusion of Glacidorboidea and Pyramidelloidea in molecular based analyses (GRANDE *et al.*, 2008; DINAPOLI & KLUSSMANN-KOLB, 2009; JÖRGER *et al.*, 2010).

Relationships among opisthobranch and pulmonate groups has changed after the inclusion of more “lower heterobranchs” groups in phylogenetic analysis of Heterobranchia. A new classification of Euthyneura was proposed by Jörger *et al*. (2010) as following: Nudipleura (Nudibranchia and Pleurobranchomorpha), Euopisthobranchia (Umbraculida, Cephalaspidea *s.s.*, Aplysiomorpha and Pteropoda), and Panpulmonata. The latter is composed by the former opisthobranch clades Sacoglossa and Acochlidiacea, lower heterobranch groups (Pyramidelloidea e Glacidorboidea) and all former pulmonated groups. A monophyletic group was named as Eupulmonata including the pulmonate clades Stylommatophora, Systellomatophora, Ellobioidea, Otiinoidea and Trimusculoidea. Other authors found similar relationship among opisthobranch clades, but not for pulmonates (GOBBELER & KLUSSMANN-KOLB, 2010; SCHRÖDL *et al*., 2011; DAYRAT *et al*., 2011). Medina *et al*., (2011) was the only analysis that recovered Opisthobranchia as monophyletic.

One of the most intriguing findings with new molecular framework in Heterobranchia was the relationship between the opisthobranch group Sacoglossa and Siphonarioidea. Both groups were recovered as a clade (JÖRGER *et al*., 2010) or separated (GOBBELLER & KLUSSMANN-KOLB, 2011) at the base of Panpulmonata, or forming a clade related to other opisthobranch groups (MEDINA *et al*., 2011). Sacoglossans have small size, generally ranging from 5 to 40 mm, and body characteristics resembling other marine (e. g., Cephalaspidea and Nudibranchia) and terrestrial groups (Pulmonata) (JENSEN, 1996, 1997). Thus, the order occupies a strategic position for understanding the evolutionary history of Heterobranchia.

1.2. THE ORDER SACOGLOSSA: GENERAL FEATURES

There are up to 300 described species of Sacoglossa, but many undescribed ones have been reported in sea slugs field guides and website forums from different parts of the world (COLEMAN, 2001; YONOW, 2008; VALDÉS, HAMANN & BEHRENS, 2006; GOSLINER, BEHRENS & VALDÉS, 2008; GOSLINER, VALDÉS & BEHRENS, 2015). Some groups present a small and fragile shell, varying in shape from slightly elongated to bulloid and bivalve forms, but in the more diverse groups the shell is completely lacking in adults (JENSEN, 1996).

Sacoglossans are highly specific herbivores with body size reaching up to 4 cm, living cryptically associated to marine plants (JENSEN, 1996). Many species feed on siphonalean green algae (Caulerpales, Codiales and Dasycladales), few specialized on brown algae, diatoms and sea grasses (JENSEN, 1997), and three non-herbivorous species feed on egg masses of other opisthobranchs (JENSEN, 1986, 1997; COELHO *et al*., 2006).

Most genera of Sacoglossa are restricted to feed on one green algal group, and a wide variety of diets among different species is apparently an evidence that the speciation process in sacoglossans has been strongly driven by diet changes (JENSEN, 1997). This high specific diet has also limited the species distributions to the oceanic photic zone (down to 100m depth), with the highest number of sacoglossans occurring on tropical areas of the globe, such as Central Pacific and Caribbean Sea (JENSEN, 2007).

As one of few specialized herbivores in marine environment, the sacoglossans have developed a digestive system morphologically and physiologically adapted to feed on this group of algae (MARÍN & ROS, 2004). The buccal apparatus is equipped with an uniseriate radula that pierce the marine plants' cells, while a muscular and modified buccal mass suck the algal cytoplasm, that is later absorbed by the large internal surface of the digestive tract (JENSEN, 1997).

In general, the algae that sacoglossans feed on are rich of secondary metabolites capable of keep generalist herbivores away (MARÍN & ROS, 2004). However, sacoglossans can sequester the algal secondary metabolites and use them for their own defense, either by bioaccumulation or even modifying them in new compounds (biotransformation) (GAVAGNIN *et al*., 2000). Those chemical defense strategies are commonly observed in shelled sacoglossans, while shell-less sacoglossans produce their own deterrent chemicals (usually polypropionates) by *de novo* bio-synthesis (MARÍN & ROS, 2004). This can be an evidence of a parallel evolutionary pathway between morphological change from a shell to shell-less body types, and a switch on chemical defense strategy from bioaccumulation and biotransformation to bio-synthesis of new compounds (CIMINO, FONTANA & GHISELIN, 1999).

The evolution of Sacoglossa is also related to the ability of members of the clade to keep functional plastids from the algae they consume within their digestive gland cells, a biological phenomenon known as kleptoplasty (RUMPHO *et al.*, 2007). This physiological adaptation is common in ciliate and foraminifera protists. The order Sacoglossa, however, is the only metazoan group known to retain chloroplasts intracellularly for different amount of time (RUMPHO, SUMMER & MANHART, 2010).

The species of shelled sacoglossans in the genera *Volvatella* Pease, 1860 and *Ascobulla* Ev. Marcus, 1972 are incapable to keep chloroplasts alive in their digestive tract. However, other shelled genera such as *Oxynoe* Rafinesque, 1814 and *Lobiger* Krohn, 1847, retain functional chloroplasts intact for up to four days, although with no carbon fixation (see RUMPHO *et al*., 2007). On the other hand, functional kleptoplasty has evolved in two lineages of shell-less sacoglossans, the cerata-bearing genus *Costasiella* Pruvot-Fol, 1951 and the highly diverse clade Plakobranchoidea, which comprises all parapodia-bearing species (CHRISTA *et al*., 2014).

Functional kleptoplasty is considered like short-term in the great majority of species, in which the chloroplast is functional up for 14 days (HÄNDELER *et al*., 2009). When kleptoplasty is considered as long-term, intact chloroplasts might last few weeks to months without being digested by the sea slug. Only few species of different independent lineages are capable of such rates of intracellular plastid survival, which is an evidence that long-term retention might have evolved independently at least five times in Sacoglossa (CHRISTA *et al*., 2013; 2014).

1.3. THE ORDER SACOGLOSSA: THE EARLY CLASSIFICATION AND PHYLOGENETIC FRAMEWORK

The taxon Sacoglossa was erected by von Ihering (1876) to group shelled and non-shelled sea slugs by sharing a modified gill, a central nervous system with seven closely spaced ganglia and an uniseriate radula, which part of it is stored at a ventral pouch on buccal mass. After that, the status of natural group of Sacoglossa was rarely debated, but the hypotheses of relationship among internal groups were quite different in the first classifications (see JENSEN, 1996).

Major taxonomic changes in Sacoglossa include the insertion of other groups of gastropods after further morphological investigations. The former cephalaspidean group

Volvatellidae, the bivalve gastropods group Juliidae and the worm-like group Platyhedylidae were transferred to Sacoglossa based on radula and buccal mass morphology (EVANS, 1950; BABA, 1961; WAWRA, 1979; MARCUS, 1982).

Sacoglossa is subdivided in two major morphological groups: the shelled suborder Oxynoacea and the shell-less suborder Plakobranchacea (JENSEN, 1996). Both groups have the monophyly well-supported, although the relation of the genus *Cylindrobulla* P. Fischer, 1857 with the other sacoglossans is still widely debated (MIKKELSEN, 1998; LAETZ *et al*., 2014). This former cephalaspidean genus was considered as sister to all Sacoglossa in the first phylogenetic analysis of the order (JENSEN, 1996) and some molecular based phylogenies (HÄNDELER & WÄGELE, 2007; HÄNDELER *et al*., 2009), but also placed in a more derived position within Sacoglossa as sister to all shelled groups by both morphological and molecular phylogenetic hypothesis (MIKKELSEN, 1998; LAETZ *et al*., 2014).

The suborder Oxynoacea is represented by headshielded species (Cylindrobullidae and Volvatellidae), bivalve shelled species (Juliidae) and species with bulloid shell and autotomic body parts (Oxynoidea). Plakobranchacea is subdivided in two shell-less groups, the cerata-bearing superfamily Limapontioidea and the parapodia-bearing superfamily Plakobranchoidea (JENSEN, 1996).

The superfamily Limapontioidea is a cerata-bearing group in Sacoglossa with a large variety of morphological traits and food habits. The rhinophore can be simple, rolled, grooved or absent in different genera, while the radular shape, anus position and food preference can be variable in the same genus (JENSEN, 1997b). The morph diversity made the Limapontioidea unsatisfactory classified for many authors in the past (PRUVOT-FOL, 1954, BABA & HAMATANI, 1970, GASCOIGNE, 1976). Furthermore, phylogenetic reconstructions based on morphological (Jensen, 1996) and molecular evidences (HÄNDELER & WÄGELE, 2007, CHRISTA *et al*., 2014) have not recovered Limapontioidea as monophyletic.

The family Platyhedylidae, later synonymized with Gascoignellidae by Jensen (1996), has only two genera, both with characters that resemble less derived Sacoglossa. *Platyhedyle* Salvini-Plawén, 1973 and *Gascoignella* Jensen, 1985 are interstitial worm-like animals with a highly flattened body and no parapodia or rhinophores. The group were placed in Limapontioidea in early classifications and transferred later to Plakobranchoidea by morphological phylogenetic analysis (JENSEN, 1996; MIKKELSEN, 1998). However, molecular based analysis placed Platyhedylidae back to Limapontioidea (KRUG *et al.*, 2015) or sister to all other shell-less Sacoglossa (CHRISTA *et al*., 2014).

The superfamily Plakobranchoidea is represented by the monogeneric family Bosellidae and the hyper diverse family Plakobranchidae. The genus *Bosellia* Trinchese, 1891 was previously classified as Polybranchidae (a cerata-bearing group) and Plakobranchidae, but later Marcus (1982) erected the family Bosellidae due to absence of parapodia and lower number of chromosome (n=7) comparing to other sacoglossans (JESNEN, 1997a). The family was later considered paraphyletic by a molecular phylogenetic hypothesis, because *Bosellia marcusi* Marcus, 1972 was recovered in Plakobranchidae (BASS & KARL, 2006), and later considered as a derived *Elysia* Risso, 1818 with reduced parapodia (see CARMONA *et al*., 2011).

Plakobranchidae is the most diverse family by far, covering almost half of the Sacoglossa richness (JENSEN, 2007). This group encompasses the genus *Elysia* Risso, 1818, which includes 90 valid species and a list of synonymies with nearly 20 names (KRUG *et al*., 2016). This vast synonymic list is mainly due to the large number of taxa created based on one specific morphological character of one single species, such as in the genera *Tridachia* Deshayes, 1857 and *Tridachiella* MacFarland, 1924 (KRUG *et al*., *op. cit.*), which were created to place species with highly undulated parapodial margins.

The members of the Plakobranchidae family are especially notable by the presence of many lineages that display short and long-term kleptoplasty, as well as a wide variety of diets (RUMPHO *et al*., 2000; EVERTSEN *et al*., 2007; JENSEN, 1996, 1997). Moreover, species within Plakobranchidae have been subjects of pharmaceutical studies (CIMINO & GAVAGNIN, 2007) and proposed as potential bioinvasion control models (THIBAUT *et al*., 2001).

In one of the main systematic considerations of Plakobranchidae Jensen (1992) proposed the validity of the genera *Plakobranchus* van Hasselt, 1824, *Pattyclaya* Ev. Marcus, 1982, *Elysiella* Bergh, 1871, *Thuridilla* Bergh, 1872 and *Elysia*, inserting *Tridachia* and *Tridachiella* in *Elysia*. However, the first cladistic analyses of the group proposed the monophyly of *Elysia* after insertion of *Pattyclaya* and *Elysiella* or subdivision of the genus into smaller groups (GOSLINER, 1995; JENSEN, 1996).

Molecular-based analyses suggest that *Elysia* could be monophyletic after the inclusion of *Pattyclaya*, *Elysiella*, *Tridachia* and *Tridachiella* (BASS & KARL, 2006; HÄNDELER & WÄGELE, 2007; CHRISTA *et al*., 2014, 2015; KRUG *et al*., 2016). Furthermore, the paraphyletic status of the family Plakobranchidae has also been proposed (MAEDA *et al*., 2010; CHRISTA *et al*., 2014, 2015).

Species description of Plakobranchidae are almost exclusively restricted to external morphology and few details of reproductive system. Hence, diagnoses of the genera, even when based on phylogenetic systematics, are incomplete. Despite the efforts of the aforementioned authors, there is a large gap in the knowledge of morphological diversity in Plakobranchidae. Also, patterns of evolution and diversification in different lineages. Therefore, clarifying some of these gaps can help elucidate more of the poorly known internal relationship of Plakobranchidae.

2. OBJECTIVES

1. To provide a phylogenetic hypothesis of the family Plakobranchidae based on morphological characters and molecular data of representatives;
2. To test the monophyly of Plakobranchidae and the genera *Plakobranchus*, *Thuridilla*, and *Elysia*;
3. To propose a phylogenetic classification of the family Plakobranchidae based on the putative phylogenies;
4. To describe the morphological diversity in Plakobranchidae.

3. MATERIAL AND METHODS

3.1. TAXON SAMPLING

A scenario with 42 species was chosen to obtain representative taxa sample of Plakobranchidae and related taxa (Table 1). A total of 30 species representing the three valid genera in Plakobranchidae (*Plakobranchus, Thuridilla* and *Elysia*) was included as ingroup. Also, other families of Sacoglossa were included in the analysis as outgroup to test the monophyly of Plakobranchidae: Bosellidae, Platyhedylidae, Stiligeridae, Caliphylidae, Costasiellidae, Oxynoidae, Juliidae, Volvatellidae and Cylindrobulidae. In addition to outgroup, other Heterobranchia taxa related to Sacoglossa were considered in this survey: Siphonarioidea (*Siphonaria pectinata* (Linnaeus, 1758)) and Cephalaspidea (*Haminoea* sp.)

Specimens conserved in 70-95% EtOH were obtained from the following zoological collections: California State University – Los Angeles (CSULA), Bailey-Matthews Shell Museum (BMSM); Museu de Zoologia da Universidade de São Paulo (MZSP) and Malacological Mollection Professor Henry Ramos Matthews (CMPHRM) – Federal University of Ceará.

3.2. MORPHOLOGICAL ANALYSIS

Different specimens from each taxon on Table 1 were dissected under a stereomicroscope immerse in fixative. External morphology was illustrated by photographs of live animals, and drawings were done with the aid of a camera lucida. Specimens were dissected immersed in EtOH 70%, and the digestive, reproductive, circulatory, excretory, and nervous systems were also drawn. Blue methylene was used to contrast the structures during the dissections. The buccal mass was dissected and dissolved in 10% sodium hypochlorite (NaClO) until the radula was totally cleaned, and subsequently rinsed in water and mounted for examination in scanning electron microscope (SEM). The penises of some species were removed and placed in 1 mL of hexamethyldisilazane until all the liquid evaporated and then mounted for SEM examination of penial stylet.

Morphological characters and character states were obtained from the morphological analysis to build a morphological matrix. Also, characters from previous phylogenetic analysis based on morphology (GOSLINER, 1995; JENSEN, 1996; MIKKELSEN, 1998) were incremented and included in this analysis. Three species were included based on data published in previous work: 1) S*iphonaria pectinata* was recently and completely described by Simone & Seabra (2017); 2) *Platyhedyle denudata* Salvini-Plawen, 1973 has its morphology reconstructed in 3D by Rückert *et al*. (2008); and 3) *Pattyclaya arena* Marcus, 1982. Other two species were analyzed to compliment previous works: 1) *Berthelinia caribbaea* Edmunds, 1963 (EDMUNDS, 1963); and 2) *Costasiella ocellifera* (Simroth, 1895) as the original description of *Costasiella lilianae* (Ev. Marcus & Er. Marcus, 1969). Also, *Elysia subornata* Verrill, 1901 and *Elysia* sp. (as *Elysia* sp. 2) were previously studied by Galvão Filho (2013).

Table 1. List of species analyzed for acquisition of morphological characters.

	Taxon	Voucher	#	Locality
Haminoeidae	*Haminoea* sp.	CMPHRM 3077B	6	Brazil
Siphonaroidea	*Siphonaria pectinata*	Simone & Seabra, 2017	-	Portugal
Cylindrobullidae	*Cilindrobulla beauii*	CMPHRM 2444B	1	Brazil
		CMPHRM 2413B	1	Brazil
		MZSP 132648	1	Brazil
Volvatellidae	*Ascobulla ulla*	MZSP 97049	2	Brazil
		MZSP 132649	1	Brazil
		CMPHRM 3086B	1	Brazil
Juliidae	*Berthelinia caribbaea*	Edmunds, 1963	-	Jamaica
		MZSP 132019	1	Brazil
		MZSP 132048	2	Brazil
Oxynoidae	*Oxynoe antillarum*	CMPHRM 4089B	2	Brazil
		MZSP 121856	6	Panama
		MZSP 121857	8	Panama
Platyhedylidae	*Platyhedyle denudata*	Rückert *et al*., 2008	-	Italy
Costasiellidae	*Costasiella ocellifera*	Marcus & Marcus, 1969	-	Brazil
		MZSP 122693	4	Brazil
Caliphyllidae	*Caliphylla mediterranea*	CMPHRM 3089B	4	Brazil
		CMPHRM 3014B	3	Brazil
Stiligeridae	*Olea* sp.	BMSM 1640	6	USA
Stiligeridae	*Stiliger vossi*	MZSP 121850	8	Panama
Bosellidae	*Bosellia mimetica*	MZSP 41942	1	Brazil
		CMPHRM 4237B	4	Brazil
		CMPHRM 4259B	2	Brazil
Plakobranchidae	*Plakobranchus ocellatus*	MZSP 122699	5	Philippines
Plakobranchidae	*Plakobranchus ianthobapsus*	CSULA 16Haw01-06	6	EUA, Hawaii
		CSULA 17Haw01-05	5	EUA, Hawaii
Plakobranchidae	*Plakobranchus papua*	CSULA	1	Indonesia
		CSULA	1	Philippines
		CSULA	1	Indonesia

Plakobranchidae	*Plakobranchus* sp. 1	CSLULA 08Mor01-02 09Gua01-02	2 2	French Polynesia Guam
Plakobranchidae	*Plakobranchus* sp. 2	MZSP 99892	3	Djibouti
Plakobranchidae	*Thurilla hopei*	MZSP 132634	2	Greece
Plakobranchidae	*Thuridilla picta*	MZSP 97355 CMPHRM 2990B CMPHRM 2991B	2 2 4	Portugal Brazil Brazil
Plakobranchidae	*Thuridlla mazda*	CMPHRM 4250B BMSM 59104 BMSM 59107 BMSM 59114	1 1 1 1	Brazil Bahamas Bahamas Bahams
Plakobranchidae	*Elysia timida*	MZSP 132627B MZSP 132626B	1 1	Spain Spain
Plakobranchidae	*Elysia cornigera*	MZSP 131252 BMSM 59034 BMSM 59036	1 1 1	Panama Bahamas Bahamas
Plakobranchidae	*Elysia orientalis*	BMSM 59035 BMSM 59037	1 1	Bahamas Bahamas
Plakobranchidae	*Elysia marcusi*	CMPHRM 3144B BMSM 59051 BMSM 59052	6 1 1	Brazil Bahamas Bahamas
Plakobranchidae	*Elysia pusilla*	MZSP 122702	2	Singapore
Plakobranchidae	*Elysia vellutinus*	CMPHRM 3141B MZSP 103412 MZSP 121849	4 1 8	Brazil Brazil Panama
Plakobranchidae	*Elysia papillosa*	MZSP 121852	10	Panama
Plakobranchidae	*Elysia zuleicae*	MZSP 121853	6	Panama
Plakobranchidae	*Elysia canguzua*	CMPHRM 3658B MZSP 107977 MZSP 121846	2 4 1	Brazil Brazil Panama
Plakobranchidae	*Elysia evelinae*	CMPHRM 3140B CMPHRM 3775B MZSP 75271	1 1 6	Brazil Brazil Brazil
Plakobranchidae	*Elysia viridis*	MZSP 122698	8	Denmark
Plakobranchidae	*Elysia serca*	MZSP 75269 MZSP 122692	10 2	Brazil Brazil
Plakobranchidae	*Elysia australis*	MZSP 122696	9	Australia
Plakobranchidae	*Elysia diomedea*	MZSP 132624 MZSP 64257	5 1	Peru Panama
Plakobranchidae	*Elysia crispata*	MZSP 108711 MZSP 121855	2 5	Grenada Panama
Plakobranchidae	*Elysia marginata*	MZSP	1	Japan
Plakobranchidae	*Elysia ornata*	CMPHRM 4245B MZSP 104106 MZSP 121854	3 1 1	Brazil Brazil Panama
Plakobranchidae	*Elysia subornata*	Galvão Filho (2013) MZSP 121848	- 1	Brazil Panama
Plakobranchidae	*Elysia pawliki*	CMPHRM 2989B	1	Brazil

		CMPHRM 3783B MZSP 97061	1 4	Brazil Brazil
Plakobranchidae	*Elysia tomentosa*	MZSP 122697 CSULA	1 2	Australia Australia
Plakobranchidae	*Pattyclaya arena*	Marcus, 1982	-	Guam
Plakobranchidae	*Elysia* sp.	Galvão Filho (2013) CMPHRM 2988B CMPHRM 3018B	 1 1	Brazil Brazil Brazil

3.3. MOLECULAR DATA

Muscle tissue was dissected from foot of preserved specimens. The DNA then was extracted using the Blood Tissue Kit (Qiagen) with minimal modifications. Partial sequences from mitochondrial cytochrome *c* oxidase subunit I (COI), mitochondrial large ribosomal subunit rRNA (16S), nuclear histone III (H3), nuclear large ribosomal subunit rRNA (28S), and nuclear small ribosomal subunit rRNA (18S), were amplified and sequenced for at least two specimens per species for phylogenetic analyses. The partial sequence for COI, 16S and H3 genes were sequenced from all available specimens of *Plakobranchus* for species delimitation studies.

PCR products were purified and amplified in both directions by Retrogen, Inc. (San Diego, CA). Chromatograms were edited, and primer sequences removed using Geneious version 6.1.6 (http://www.geneious.com, Kearse *et al*., 2012). Resulting sequences were blasted in GenBank and compared with the available data assemble. The new sequences will be deposited at GenBank during manuscript preparation. In addition, some sequences obtained from GenBank were included in the analysis. Sequences were initially aligned using MUSCLE with default settings in Geneious v6.1.6, refined by hand using secondary structure models for 16S and 28S, and sequence blocks masked by the least stringent criteria in Gblocks v.0.91b were removed (CASTRESANA, 2000) as performed by Krug *et al*. (2016).

Table 2. List of species used in molecular phylogenetic analysis with voucher name for tissue sample from California State University – Los Angeles. X – partition included in the analysis. Asterix means partial sequence and dash means the sequence was not included.

Taxon	Voucher	GENE PARTITION				
		16S	COI	28S	H3	18S
Haminoea hydatis	-	KJ022796	KK615841	KF615802	KJ022925	AY427504
Siphonaria pectinata	Siph_pectinata	X	X*	X	X	-
Cylindrobulla beaui	Cylin_bea_09FL01	X	X	X	X	X
Ascobulla ulla	As_ull_10Swe02	X	X*	X	X	X
Oxynoe antillarum	Oxy_ant_04PanA1	X	X*	X	X	X
Berthelinia caribbea	Ber_car_10Swe01	X	X	X	X	X
Costasiella ocellifera	Coce_06LKey02L	X	X	X	X	X
Olea sp.	Ol_han_10FHL01	X	X	X	X	X
*Caliphylla mediterane*a	Ca_med_09Cur01	X	X	X	X	X
Stiliger vossi	H_vos_15Pan01	-	X*	-	X	X
Bosellia mimetica	Bmim_06Ber01	X	X	X	X	X
Plakobranchus occelatus	Pk_wht_Jap01	X	X	X	X	X
Plakobranchus sp.	Pk_aff_pur_08Mor01	X	X	X	X	X
Plakobranchus papua	Pk_aff_sp1_PNG01	X	X	X	X	X
Plakobranchus ianthobapsus	Pk_sp2_Phi02	X	X	X	X	X
Thuridilla hopeii	Thop_07Ity01	X	X	X	X	X
Thurilla picta	Tpic_10Nex01	X	X	X	X	X
Thuridilla mazda	Tmaz_NCBI	X	X	-	X	-
Elysia pusilla	Epus_04Jap01	X	X	X	X	X
Elysia velutinus (=tuca)	Evel_04Boc01	JN819133	KM086402	KM230538	KM040853	X
Elysia papillosa	Epap_06Tar01	KP187840	KP187843	KP187837	KP187834	-
Elysia zuleicae	Ezul_07Swe01	JN81946	JN819105	KM230541	JN819178	-
Elysia marcusi	Emar_06Jam01	KM204234	KM086384	KM230512	KM040837	-
Elysia canguzua	Ecan_10Dry01	KM204225	KM086376	KM230499	KM040827	-
Elysia serca	Eser_06MUS03	X	X*	X	X	-
Elysia viridis	Evir_05Ire01	KM204254	KM086403	KM230539	KM040854	-
Elysia evelinae	Eeve_08Bra01	-	X	KM230505	KM040831	-
Elysia crispata	Ecri_04Swe02	X	X	X*	X	-
Elysia diomedea	Edio_07BLR03	KM204228	KM086379	KM230504	KM040830	X
Elysia timida	Etim_07Fra01	EU140857	KM086400	KM230536	JN819155	-
Elysia cornigera	Ecor_06Jam01	JN819125	JN819084	KM230501	JN819154	X
Elysia ornata	Eorn_06Jam01	JN819132	JN819093	KM230516	JN819157	-
Elysia marginata	E_cf_mar_sp3_08Jap01	KM204206	KC573752	KM230475	KM040810	-
Elysia tomentosa	E_cf_tom_sp1_05Jap01	KM204204	KC573749	KM230473	KC597175	X
Elysia subornata	Esub_06Jam01	JN819135	JN819111	KM230533	KM040849	X
Elysia pawliki	Epaw_03Swe01	KM204205	KC573751	KM230474	KC597176	X
Elysia orientalis	Eori_13FL01	KP187839	KP187842	KP187836	KP187833	X*
Elysia australis	Eaus_07Aus03	JN819142	JN819109	KM230497	JN819176	-
Elysia pratensis	Epra_07Pla04	KM204237	JN819112	KM230518	JN819169	X
TOTAL		37	39	37	39	25

3.4. PHYLOGENETIC ANALYSES

The morphological matrix was analyzed in TNT (GOLOBOFF *et al.*, 2007) to infer phylogenetic trees under maximum parsimony principles. The search for topologies was performed by traditional search through TBR with replication of 1000 trees and retention of 90 trees with prior and implied weights. A strict consensus tree was generated from the resulting trees with prior weight and relative Bremmer support was performed for this analysis. For implied weight was adopted different values of K (3, 5, 6, 8, 10, 12, 15, 20, 40, 60, 80, 100) to assess topological changes under distinct weights. The character optimization was performed using the tree from implied weight analysis on Winclada, version 0.9.9 (NIXON 1999).

The best nucleotide substitution model was selected using JMODELTEST 2.1.10 with the Bayesian Information Criterion (BIC) for each gene partition, resulting on the evolutionary models GTR + I + G for 16S, 28S, COI and H3 partitions and SYM + I + G for 18S. Phylogenetic relationships were estimated using Maximum Likelihood (ML) implemented in RAxML v7.6.6 (STAMATAKIS, 2006) and Bayesian Inference (BI) implemented in BEAST 1.8.3 (DRUMMOND *et al*., 2012). Both analyses were performed on CIPRES web platform (MILLER *et al*., 2015), using the RAxML-HPC BlackBox tool with default parameters for ML analysis and BEAST on XSEDE for BI analysis. For BI analyses was used Markov Chain Monte Carlo (MCMC) sampling 20 million generations, saving trees every 20.000 steps. In addition, a combined matrix with morphological and molecular characters was analyzed by BI with the same evolutionary models and parameters.

4. RESULTS

4.1. SPECIES DESCRIPTION

TAXONOMY

SYSTEMATICS

***Order* Cephalaspidea P. Fischer, 1883**

***Superfamily* Haminoeoidea Pilsbry, 1895**

***Family* Haminoeidae Pilsbry, 1895**

Genus *Haminoea* Turton & Kingston [in Carrington], 1830

Type species: *Bulla hydatis* Linnaeus, 1758, type by monotypy

***Haminoea* sp.** (Gould, 1952)

(Figures 1-6)

Haminoea elegans (Gray, 1825): Marcus, Er., 1957: 395; 1958: 35; Ev. Marcus & Er. Marcus, 1963: 6; 1967: 24, fig. 13; Redfern, 2001: 156, fig. 651, pl. 69, fig. 651D, pl. 114; Valdés *et al*., 2006: 24; Rios, 2009: 403, fig. 1091; Redfern *et al*., 2013: 267, figs. 471A-C. Goodheart *et al.,* 2016: 17, fig. 9A.

Description

External morphology: (Figs. 1-2)**:** Cephalic shield (cs) trapezoidal, developed posteriorly into one tapered cephalic lobe, reaching most anterior part of shell. Hancock's organ (ho) with multiple lamellae. Parapodial lobes (pp) extended from foot sole to anterior dorsal side of shell. Plicate gill (Fig. 2A: g) internal to mantle cavity. Posterior and anterior border of foot rounded. Shape bulloid and globose, mainly formed by body whorl. Spire involuted. Lip thin, sharp. Growth lines conspicuous forming grid pattern. Spiral striae thin, present all over shell. Periostracum thin, orange-brown in color.

Circulatory and excretory systems (Fig. 2): Pericardial cavity dorsally positioned over anterior region of digestive gland. Auricle (au) elongated thin-walled tissue anterior to gill and lateral to ventricle, with two main connections. Kidney glandular-shape positioned between gill and heart.

Digestive system (Fig. 3-4): Buccal mass (bm) elongated, 3x longer than wider with no dorsal septate muscles. Oral sphincter bit elongated. Radular composed of rachidian tooth and multiple lateral teeth (formula 28 x 22.1.22). Rachidian tooth curved, with three cusps and smooth cutting edge. Lateral teeth elongated and curved towards central region. Jaws (Fig. 4C-D) with rhomboidal shape and irregular surface and positioned on posterior portion of buccal mass. Anterior esophagus thinner and elongated, length bit longer than buccal mass length, with inner surface with one pair of tiny folds. Salivary glands paired, thin and elongated, connected to most anterior part with three gizzard plates attached and posterior part very muscular and thicker. Gizzard plates composed of many V-shaped crests with irregular surface. Stomach thin walled and positioned inside digestive gland. Digestive gland like huge homogeneous mass and fused with gonad, occupying most part of posterior region of body. Intestine elongated, thick, surrounding digestive gland and finishing on posterior dorsal anus.

Genital system (Fig. 5): Gonad fused with digestive gland. One main hermaphrodite duct runs anteriorly from central part of gonad to right side of body, internally expanded forming one tubular ampulla (am). Ampulla occupies more than half of hermaphrodite duct. Hermaphrodite duct connects to seminal receptacle (sr), right before mucus gland (mg). Bursa copulatrix (bc) absent. Mucus gland granulose, positioned on posterior part of oviduct and not fused with oviduct. Albumen gland (ag) forming one big compact mass positioned near to mucus gland. Genital receptacle as larger genital structure, size ~4x mucus gland size, connecter to oviduct in anterior position near to female opening (fp). Oviduct not glandular, elongated and anteriorly curved and opening on female bulb on side of body. Male organs positioned anteriorly on animal, inside right portion of cephalic shield and near to buccal mass. Prostate gland formed by bilobed rounded gland. Vas deferens absent. Seminal groove running from male aperture to female bulb on right side of body. Penis (pe) curved and elongated, size bit smaller than prostate gland larger as longer, with a terminal slightly curved stylet.

Nervous system (Fig. 6): Cerebral ganglia connected by short simple commissure, each ganglion with more than 10 innervations, with larger one directly branching and connecting to Hancock's organ. Optic nerve ~4x longer than cerebral length. Pleural ganglia partially fused with cerebral ganglia and not innervated. Pedal ganglia highly innervated and connected to each other by one single and short pedal commissure. Buccal ganglia short, connected to cerebral ganglia through elongated connective, united with single short buccal commissure. Visceral loop very elongated. Subintestinal and visceral ganglia slightly fused, size large as half of cerebral ganglion size. Supraintestinal ganglia size as larger as abdominal ganglia, connected to abdominal ganglia by elongated connective.

Distribution: Florida to Brazil (Sao Paulo).

Habitat: Estuarine species, muddy bottoms (Rios, 2009).

Material examined: BRAZIL, Estuarine area in Ceara river, Caucaia, Ceará, CMPHRM 3077B, 100 specimens (H. Galvão Filho *et al*., 12/xii/2009).

Remarks: *Haminoea elegans* was described from Mediterranean Sea and was widely reported in shell and sea slug guides (*e. g.* RIOS, 1994, 2009; VALDÉS *et al.,* 2006; REDFERN, 2013) from West Atlantic Ocean. However, Malaquias & Cervera (2006) stated that *H. elegans* is probably a synonym of the Mediterranean species *Haminoea navicula* (da Costa, 1778) due to similar shell morphology. Specimens previously identified as *H. elegans* from Brazil have differences on penial and radular morphology from the description of *H. navicula* made by Malaquias & Cervera (2006). In this regard, its considered that *H. elegans* from West Atlantic is probably a previous synonymized name, and further taxonomic investigation must be done soon.

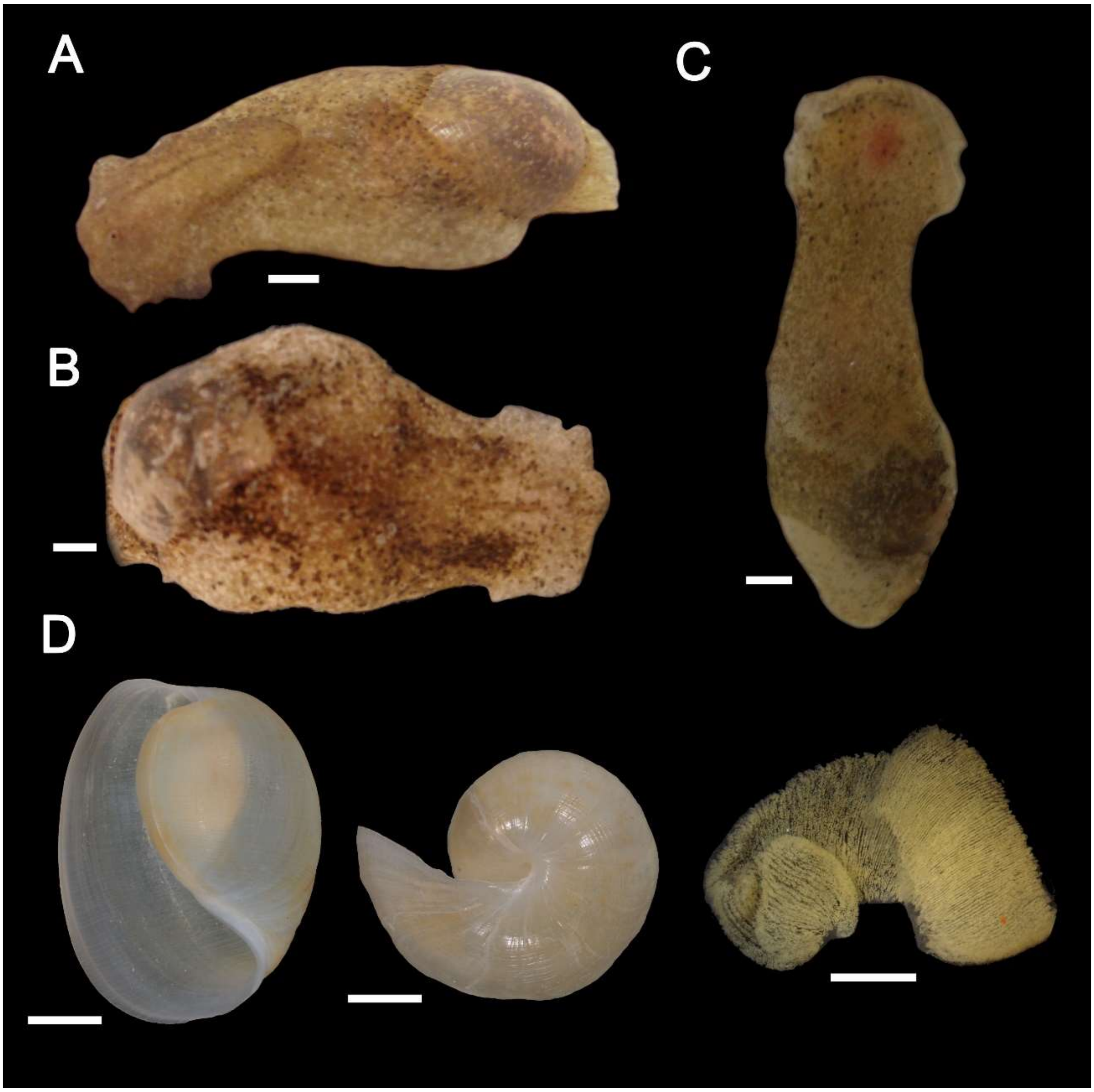

Figure 1. *Haminoea* sp. live animal. A-B) Dorsal view; C) ventral view; D) shell aperture; E) shell apex; F) egg mass.

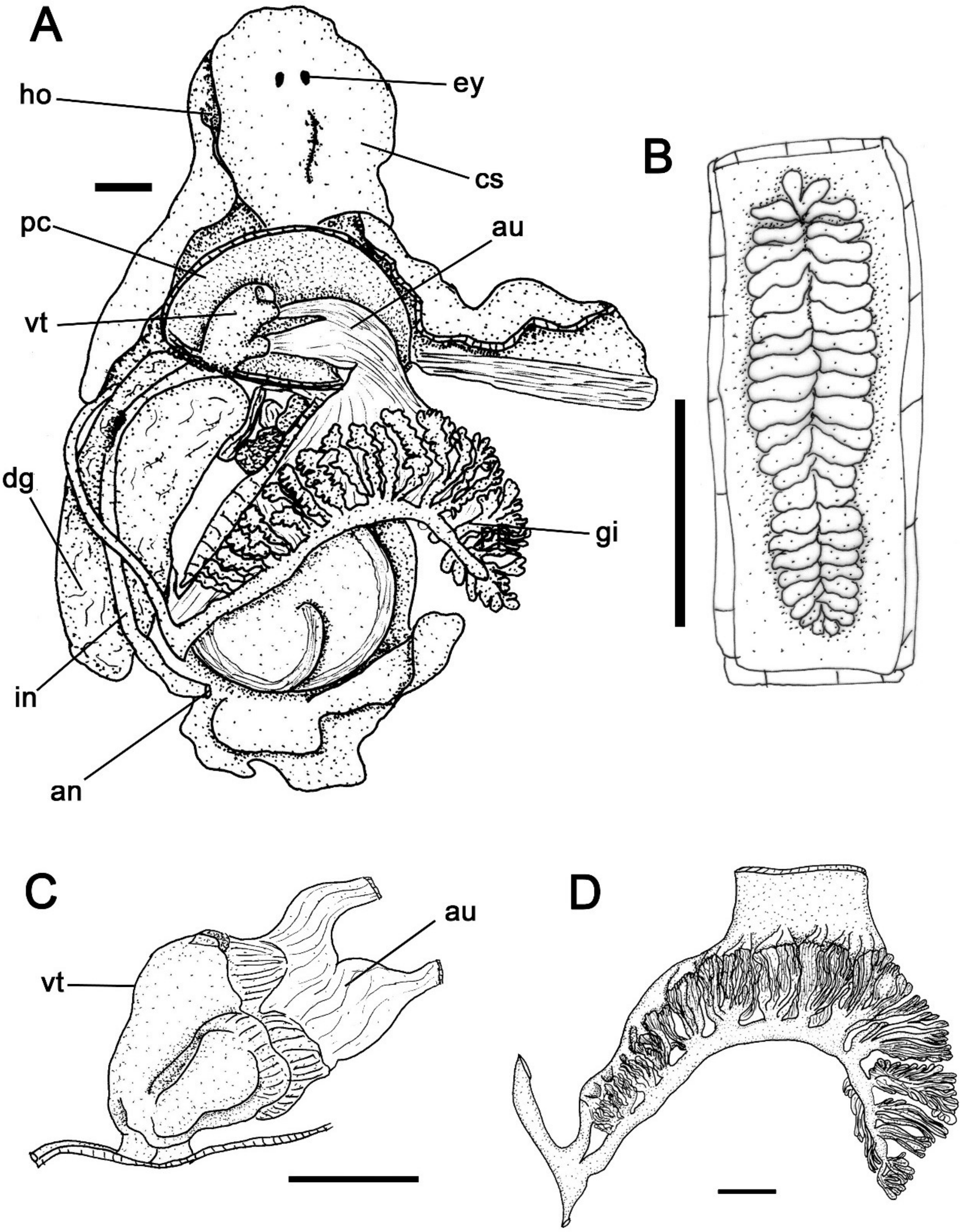

Figure 2. *Haminoea* sp. anatomy: A) Whole dorsal view, shell and dorsal mantle removed, focusing pallial cavity structures; B) hancock's organ; C) heart, dorsal view; D) gill, dorsal view, some adjavent structures also shown. Scales= 1 mm.

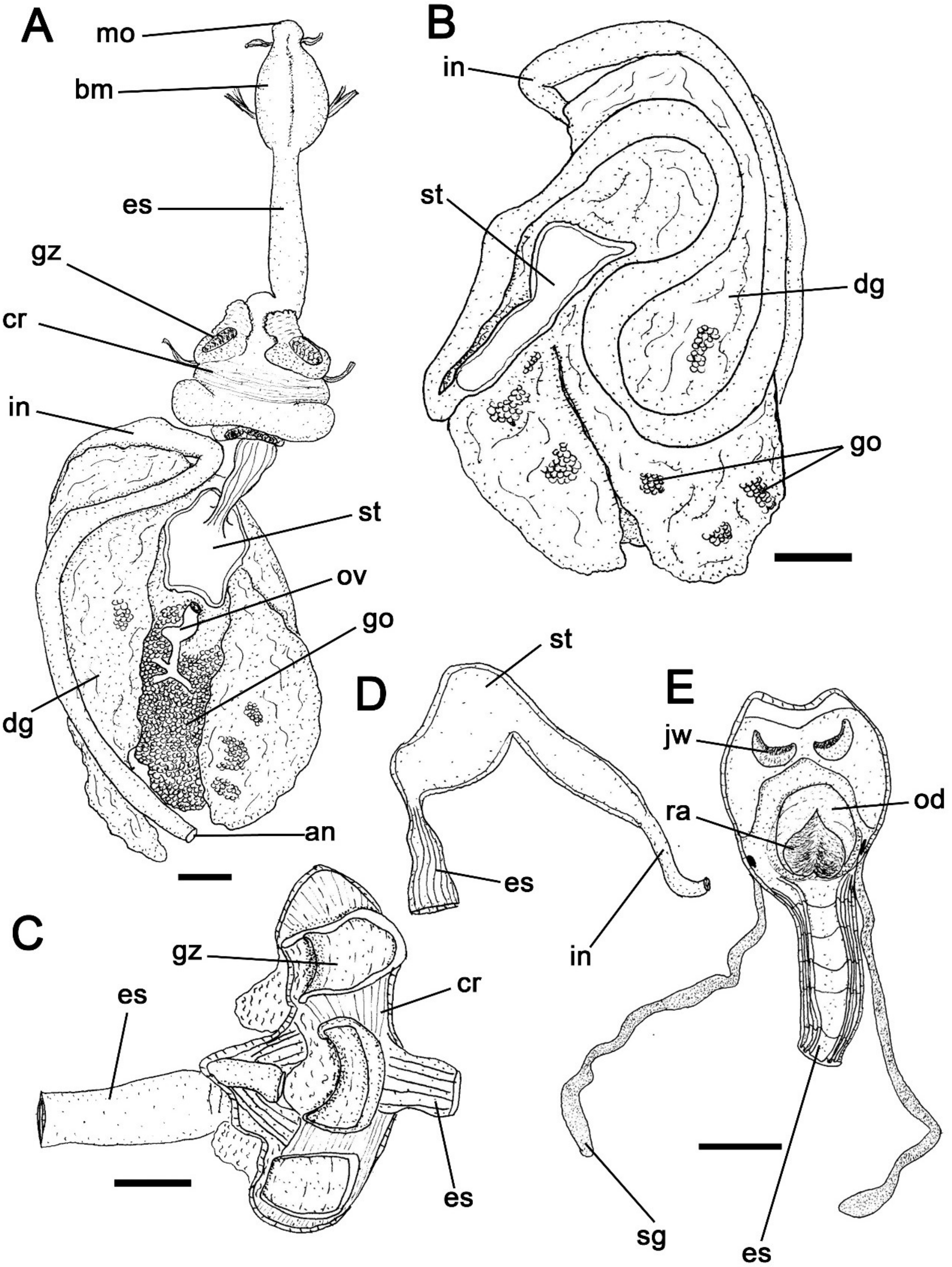

Figure 3. Digestive system of *Haminoea* sp. A) Dorsal view; B) ventral view of digestive gland; C) internal surface of crop; D) detail of stomach; E) internal view of buccal mass.

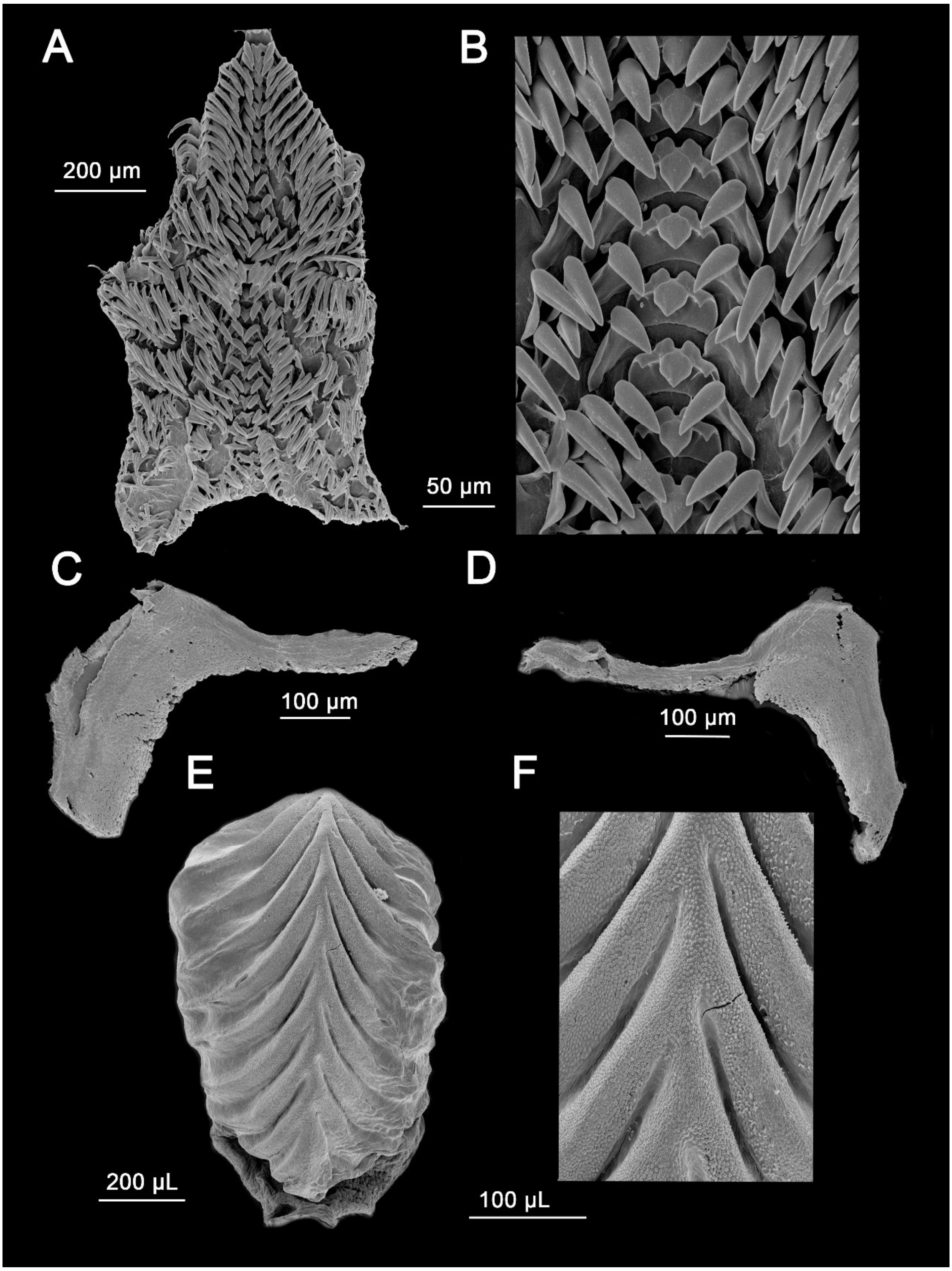

Figure 4. Buccal hard parts of *Haminoea* sp. A-B) Radula; C-D) Jaws; E-F) Gizzard plate.

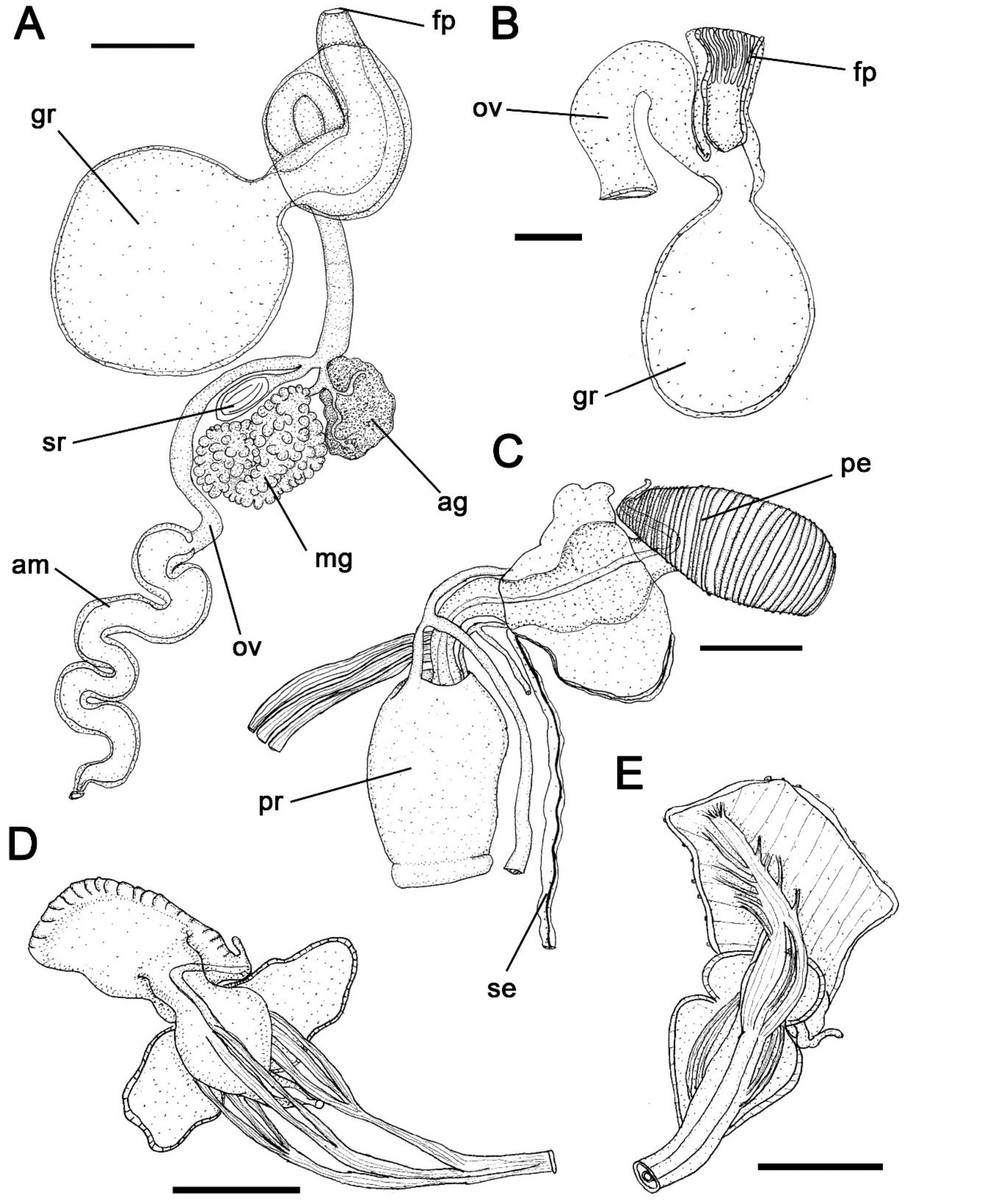

Figure 5. Reproductive system of *Haminoea* sp. A) posterior portion of reproductive system with female and hermaphrodite parts; B) detail of female opening; C) anterior portion of reproductive system; D-E) detail view of penis.

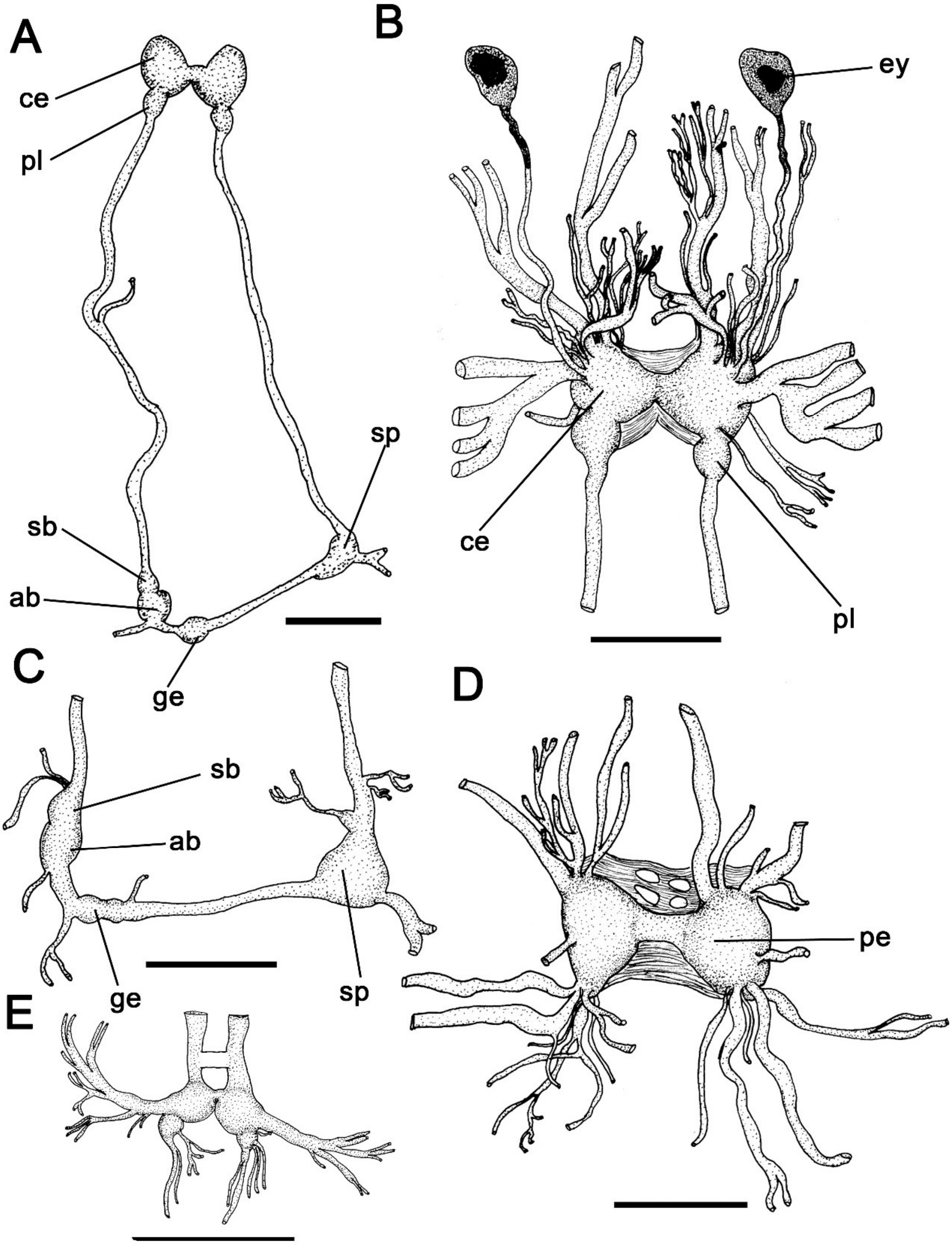

Figure 6. Nervous system of *Haminoea* sp. A) Overview; B) detail of cerebro-pleural ganglia; C) visceral ganglia; D) pedal ganglia; E) buccal ganglia.

***Order* Sacoglossa Ihering, 1876**

***Superfamily* Oxynooidea Stoliczka, 1847**

***Family* Cylindrobullidae Thiele, 1931**

Genus *Cylindrobulla* P. Fischer, 1857

Type species: *Cylindrobulla beauii* P. Fischer, 1857, type by monotypy

***Cylindrobulla beauii* P. Fischer, 1857**

(Figures 7-12)

Complemented from Mikkelsen, 1998.

Cylindrobulla beauii P. Fischer, 1857. Valdés *et al.*, 2006: 46; Redfern, 2013: 281, fig. 782A-B; Laetz *et al.,* 2014: 348, figs. 1 and 4; Galvão-Filho, 2015: 7, fig. 2H; Caballer *et al*. 2015: 225, fig. 3O.

Description

External morphology: (Figs. 7-8)**:** Cephalic shield shape square, elongated, ~3x longer than wider, not covering shell. Hancock's organ or rhinophores absent. Parapodia absent. Lamellate gill (gi) internal to mantle cavity. Posterior and anterior border of foot rounded. Shell shape bulloid and elongated, mainly formed by body whorl. Spire involuted with protoconch completely immerse. Lip thin, sharp. Growth lines inconspicuous. Periostracum thick, brownish.

Circulatory and excretory systems (Fig. 8-9): Mantle cavity on dorsal and right sides of body. Mantle edge with multiple digitiform expansions. Gill (gi) composed of multiple regular filaments. Hypobranchial gland (hy) right posterior to gill. Secondary glandular layer (gl) more posterior, apical and wider than hypobranchial gland. Pericardial cavity anterior to gill and posterior to adductor muscle (ac) insertion on shell. Auricle (au) shape rounded with thin-walled tissue, positioned lateral to ventricle. Ventricle (vt) smaller than auricle and more muscular, rounded shaped. Kidney rod-like shaped, positioned on left side of pericardium and anterior to gill.

Digestive system (Fig. 10-11): Buccal mass (bm) elongated, 3x longer than wider with 16 dorsal inconspicuous septate muscles (sm). Oral sphincter (os) elongated with 1/3 of buccal mass length. Uniseriate radula composed of 80 rhomboid-shaped teeth with similar size, each tooth with 11 smooth cusps decreasing on size laterally. Ascending and descending limbs not well-delimited. Descending limb surrounded by thinner elongated ascus muscle (ma) on ventral part of buccal mass and finishing inside of ventral part of buccal mass near to odontophore. Odontophore region (or) rounded. Pharyngeal pouch (pp) on most posterior part of buccal mass, width wider as buccal mass width. Jaws (Fig. 4C-D) absent. Esophagus (es) thinner on anterior part before central nervous system and expanding and forming huge sack through almost all its extension. Salivary glands (sg) paired, thick, elongated, not attached to esophagus. Gizzard plates absent. Stomach inconspicuous, thin walled and positioned anterior to digestive gland. Digestive gland (dg) like huge homogeneous mass and fused with gonad, occupying most part of posterior region of body. Intestine (in) elongated, thick, running inside digestive gland and finishing on posterior dorsal anus.

Reproductive system (Fig. 12): Gonad fused with digestive gland. One main hermaphrodite duct runs anteriorly from central part of gonad to mucus gland (mg). Mucus gland granulose, positioned on posterior part of oviduct and not fused with oviduct. Albumen gland (ag) forming one big compact mass positioned near to mucus gland. Male duct (md) running from hermaphrodite duct expands forming one tubular ampulla (am). Ampulla occupies half of male duct length. Prostate gland anteriorly attached to male duct, just before the connection of male duct to oviduct (ov). Bursa copulatrix (bc) connected to genital receptacle (gr) in one duct that connects with oviduct near to female opening (fp). Penis elongated, straight, positioned anteriorly on animal, inside right portion of cephalic shield, near to esophageal expansion. Vas deferens absent. Seminal groove running from male aperture to female oppening on right side of body.

Nervous system (Fig. 12): Cerebral and pleural ganglia fused. Cerebro-pleural (cp) connected to each other by one slightly elongated commissure. Each cerebro-pleural ganglion with 6 main innervations highly branching toward cephalic shield borders. Optic nerve ~5x longer than cerebral length and branching from or fused with cerebral innervation. Cerebro-pleural ganglia connected to pedal ganglia (pd) by doubled short connective tissue. Pedal ganglion with two paired innervations and connected by reduced connective tissue. Buccal ganglia (bu) size small, connected to cerebral ganglia through elongated connective. Visceral loop very elongated. Subintestinal (sb) ganglia inconspicuous and connected to abdominal ganglia (ab) by very elongated connective tissue. Supraintestinal ganglia (sp) size as larger as abdominal ganglia, connected to abdominal ganglia by elongated connective, but ~3x smaller than sb-ab connective.

Distribution: Florida to Brazil (Sao Paulo) (MIKKELSEN, 1998).

Habitat and diet: Shallow waters associated with the calcareous algae *Halimeda* spp. (MIKKELSEN, 1988).

Material examined: BRAZIL, Ceara, CMPHRM 2413B, 1 specimen (xii/2003), CMPHRM 2444B, 1 specimen (xii/2003), Pirangi do Norte, Rio Grande do Norte, MZSP 132648, 1 specimen (01/viii/2007).

Remarks: The relationship between *Cylindrobulla* and the remain Sacoglossa was widely debated (see MIKKELSEN, 1998; LAETZ, *et al.,* 2014), specially because of its radular shape, questionable presence of ascus and food habits. In a morphological based phylogeny Jensen (1996) recovered *Cylindrobulla* as sister to Sacoglossa, while Mikkelsen (1998) included *Cylindrobulla* in Sacoglossa as sister to all other shelled families. This same result was supported later by molecular phylogenetic analysis (LAETZ *et al.*, 2014). The present phylogenic analysis also placed *Cylindrobulla* within Sacoglossa and sister to *Ascobulla*.

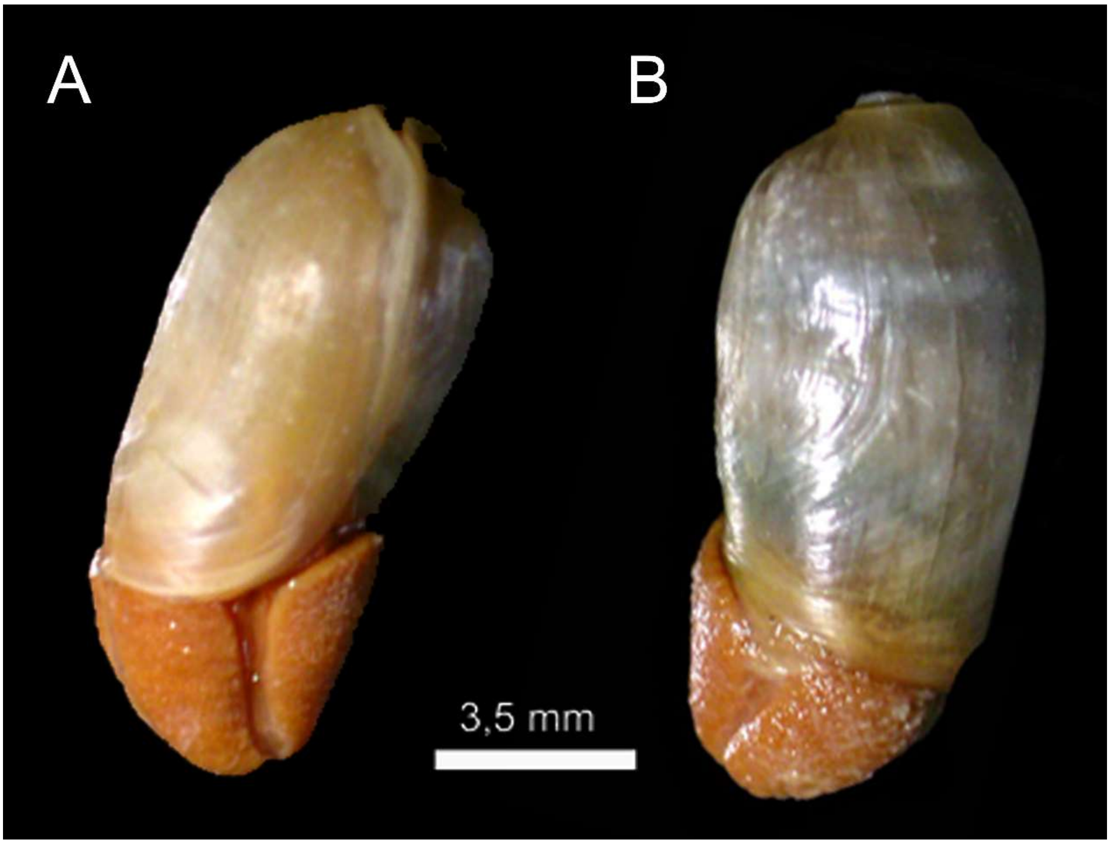

Figure 7. *Cylindrobulla beauii* live animal. A) lateral view; B) dorsal view. (Photo credit: C.A.O. Meirelles).

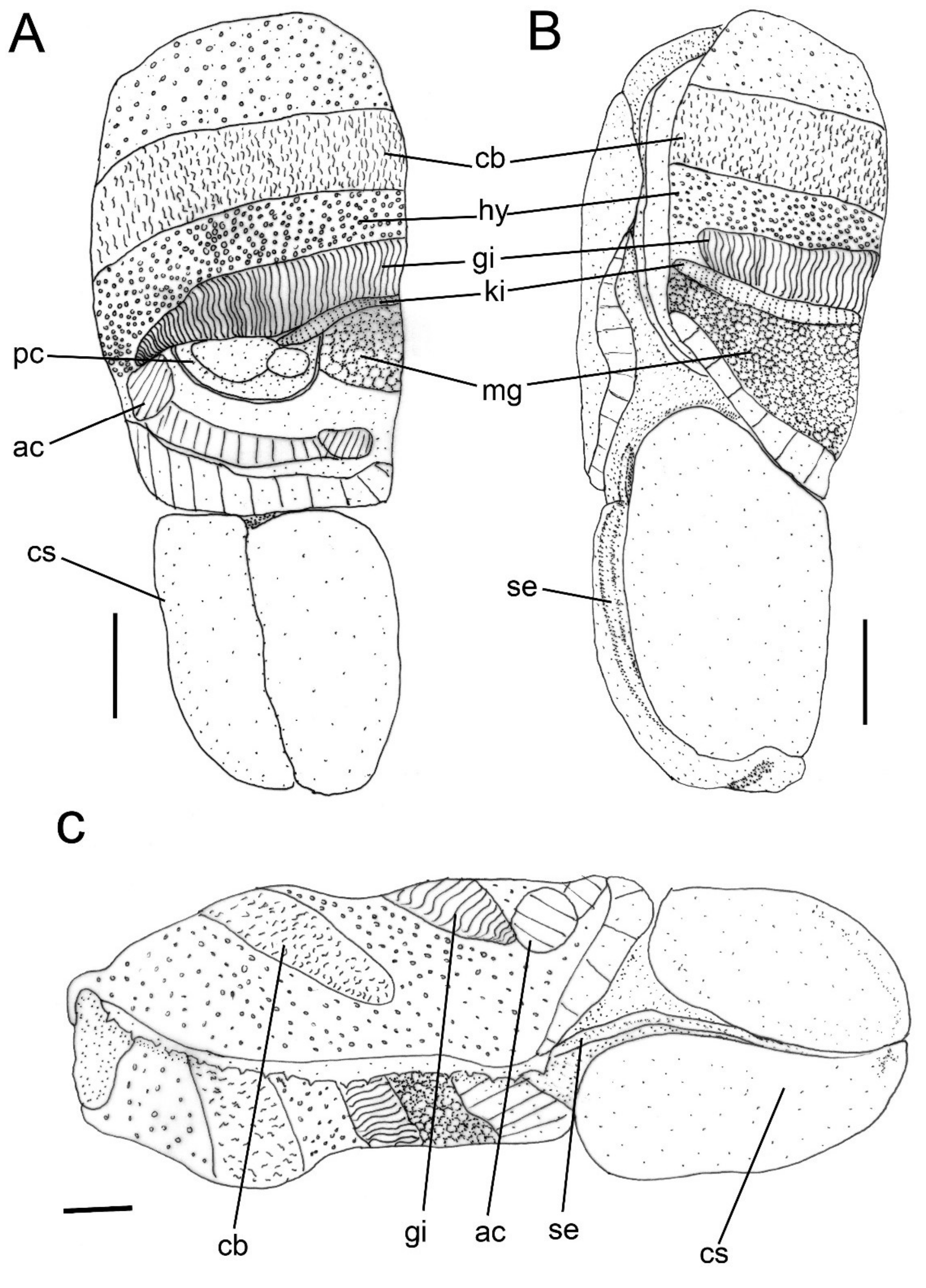

Figure 8. *Cylindrobulla beauii* anatomy, shell removed, focusing pallial cavity structures: A) Whole dorsal view; B) ventral view; C) lateral view. Scales= 1 mm.

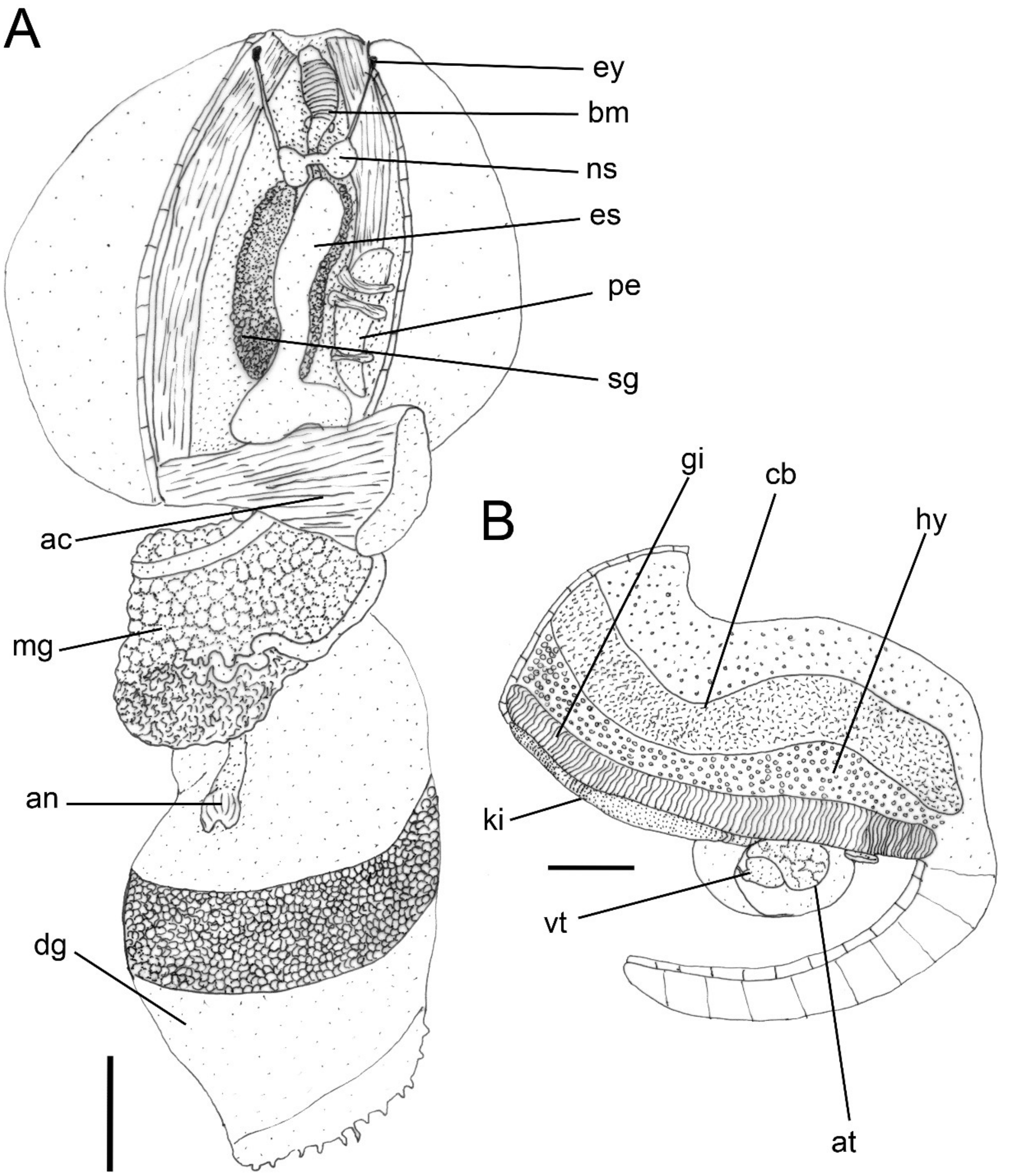

Figure 9. *Cylindrobulla beauii* anatomy: A) Whole dorsal view, shell and dorsal mantle removed, focusing pallial cavity structures; B) pallial cavity organs. Scales= 1 mm.

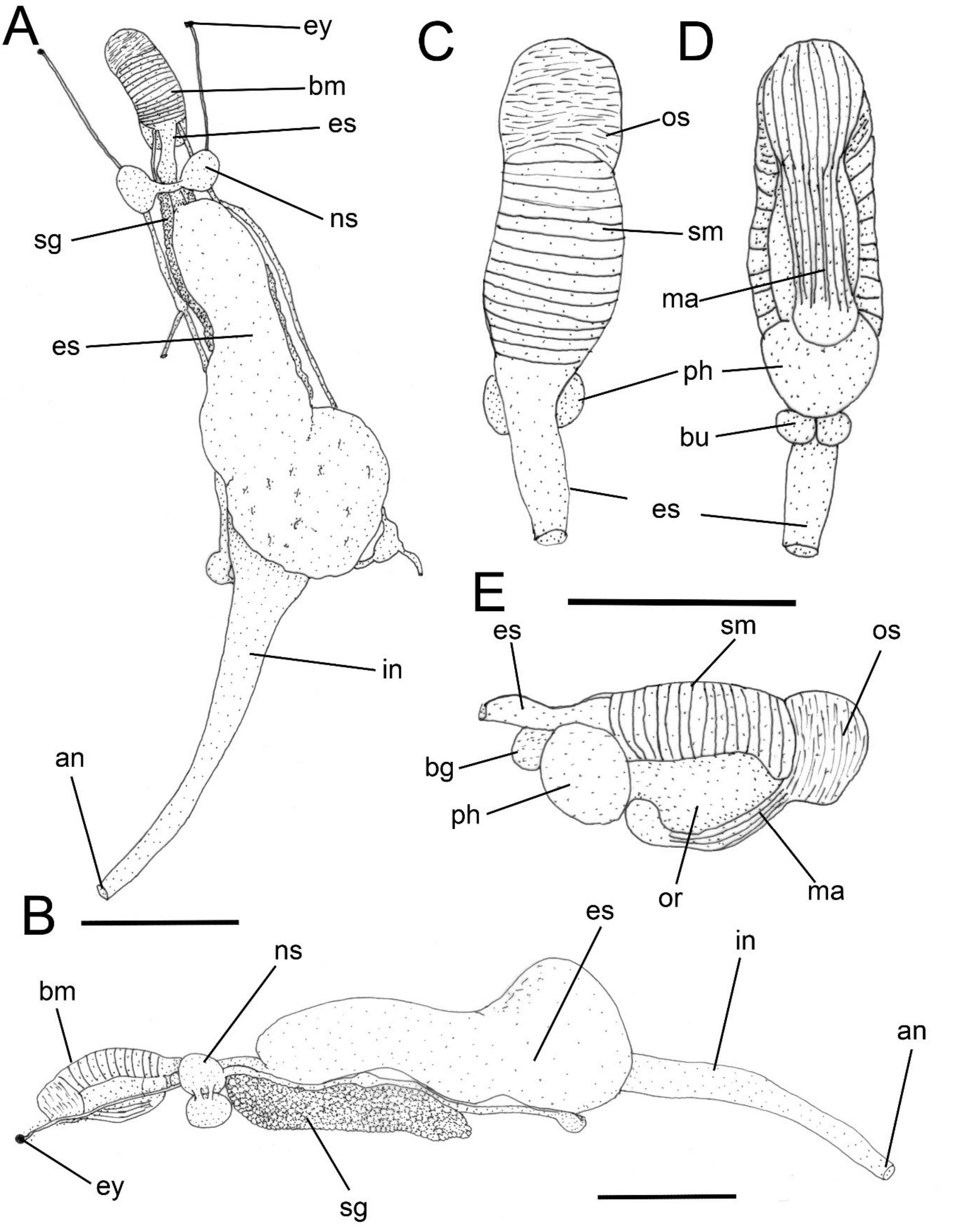

Figure 10. *Cylindrobulla beauii* anatomy of digestive system: A) Whole dorsal view; B) whole left view (scales= 1 mm). C-E) Buccal mass anatomy: C) dorsal; D) ventral; E) right view (scales: 0.5 mm).

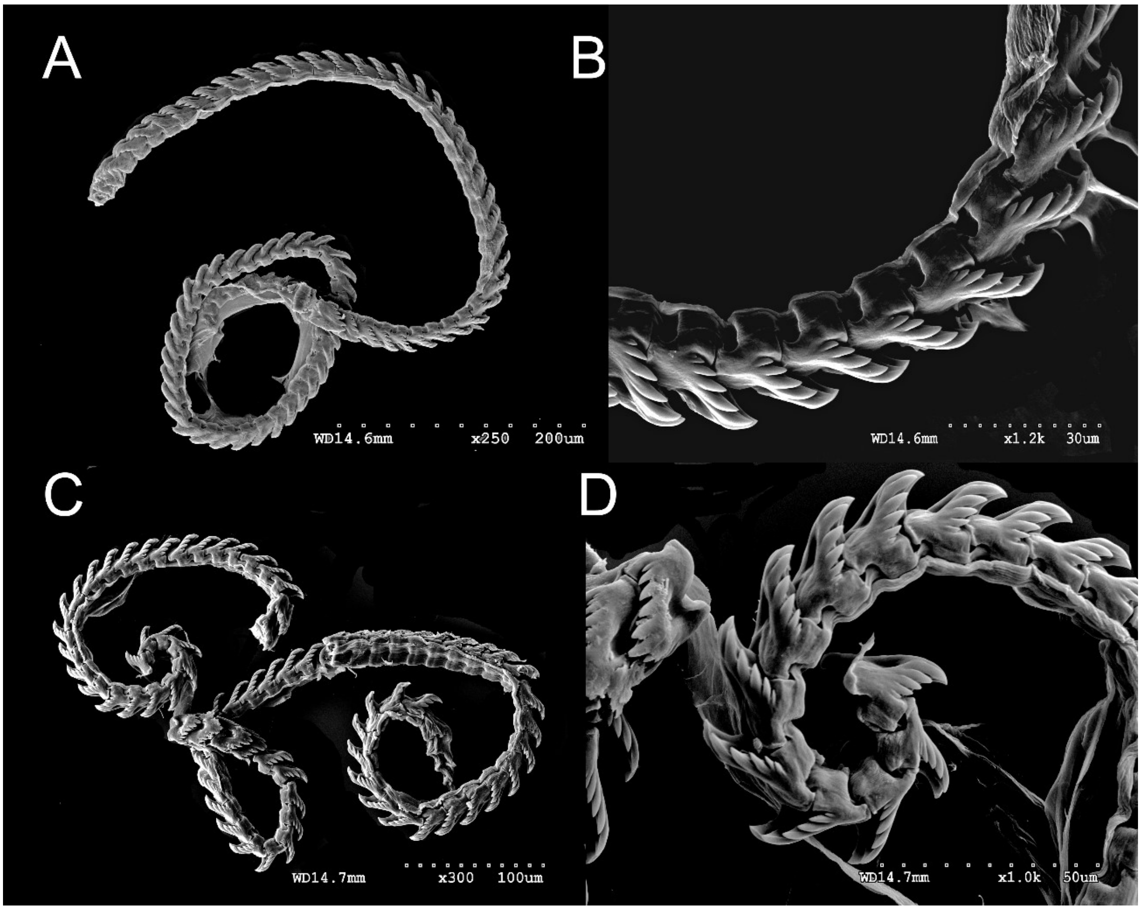

Figure 11. *Cylindrobulla beauii* radula. A and C) Whole view; B and D) detail of teeth.

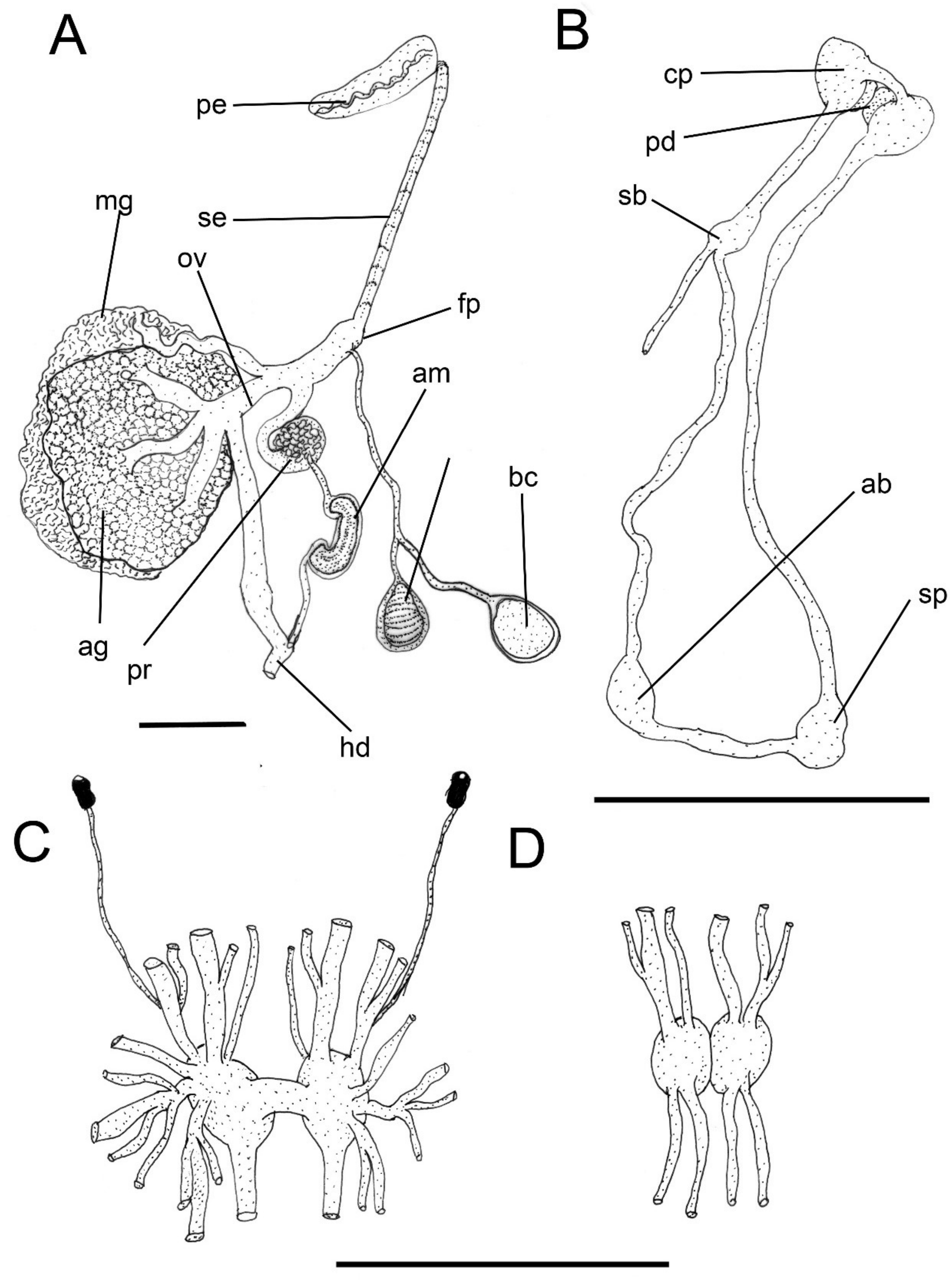

Figure 12. *Cylindrobulla beauii* anatomy of reproductive and nervous systems: A) schematic drawing of the reproductive system, dorsal view; B) whole dorsal view of central nervous system, dorsal view; C) detail of cerebro-pleural ganglia, dorsal view; D) detail of pedal ganglia, ventral view. Scales: 1 mm.

***Family* Volvatellidae Pilsbry, 1895**

Genus *Ascobulla* Ev. Marcus, 1972

Type species: *Cylindrobulla ulla* Marcus & Marcus, 1970, type by original designation.

***Ascobulla ulla* (Er. Marcus & Ev. Marcus, 1970)**

(Figures 13-17)

Complemented from Mikkelsen, 1998.

Ascobulla ulla (Er. Marcus & Ev. Marcus, 1970). Valdés *et al*., 2006: 50; Redfern, 2013: 281, fig. 781A-B; Galvão-Filho, 2015: 7, fig. 2I; Goodheart *et al*., 2116: 21, 11a.

Description

External morphology: (Figs. 13-14)**:** Cephalic shield shape square, short, as longer as wider, not covering shell. Hancock's organ or rhinophores absent. Parapodia absent. Lamellate gill (gi) internal to mantle cavity. Posterior and anterior border of foot rounded. Shell shape bulloid and elongated, mainly formed by body whorl. Spire involuted with protoconch partially immerse. Lip thin, sharp. Growth lines inconspicuous. Periostracum thin, translucent.

Circulatory and excretory systems (Fig. 14-15): Mantle cavity on dorsal and right sides of body. Mantle edge with multiple digitiform expansions. Gill (gi) composed of multiple regular filaments. Hypobranchial gland (hy) right posterior to gill. Secondary glandular band (cb) more posterior, apical and wider than hypobranchial gland. Pericardial cavity anterior to gill and posterior to adductor muscle (ac) insertion on shell. Auricle (au) shape rounded with thin-walled tissue, positioned lateral to ventricle, size twice as larger as ventricle (vt). Ventricle (vt) smaller than auricle and more muscular, rounded shaped. Kidney rod-like shaped, length half of gill length, positioned on left side of pericardium and anterior to gill.

Digestive system (Fig. 16-17): Buccal mass (bm) elongated, twice longer as wider with 16 dorsal inconspicuous septate muscles. Oral sphincter (as) short with 1/6 of buccal mass length. Uniseriate radula composed of 38 blade-shaped teeth decreasing in size towards ascus, each tooth with two lateral cusps forming cutting edges with 40 elongated denticles, central cusp smooth. Ascending limb with 5 well-formed teeth and 3 in formation. Descending limb with 30 teeth, which last 10 are organized in spiral inside ascus near to odontophore. Odontophore region (or) rounded. Pharyngeal pouch (pp) on most posterior part of buccal mass, width wider as buccal mass width, size ~3x smaller than buccal mass. Esophagus (es) anteriorly expanded and curved to left side of animal, on anterior portion to central nervous system, extending posteriorly and forming elongated esophageal pouch (ep). Esophageal pouch positioned on ventrally to adductor muscle (ac), without internal folds. Salivary glands paired, thick, elongated, not attached to esophagus. Stomach inconspicuous, thin walled and positioned anterior to digestive gland. Digestive gland like huge homogeneous mass and fused with gonad, occupying most part of posterior region of body. Intestine elongated, thick, running inside digestive gland and finishing on posterior dorsal anus.

Reproductive system (Fig. 18): Gonad fused with digestive gland. One main hermaphrodite duct (hd) runs anteriorly from central part of gonad to mucus gland (mg). Mucus gland granulose, positioned on left side of animal, posterior and not fused to oviduct. Albumen gland (ag) forming one big compact mass positioned near to mucus gland. Male duct (md) running from hermaphrodite duct expands forming one tubular ampulla (am). Ampulla occupies 1/5 of male duct length. Prostate gland anteriorly attached to male duct, just before the connection of male duct to oviduct (ov). Bursa copulatrix (bc) connected to genital receptacle (gr) in one duct that connects with oviduct near to female opening (fp). Penis (pe) elongated, coiled, positioned anteriorly on animal, inside right portion of cephalic shield, near to esophageal. Vas deferens absent. Seminal groove (se) running from male aperture to female opening on right side of body.

Nervous system (Fig. 18): Cerebral and pleural ganglia fused. Cerebro-pleural (cp) connected to each other by one elongated commissure. Each cerebro-pleural ganglion with 3 main innervations highly branching toward cephalic shield borders. Optic nerve ~4x longer than cerebral length and branching from or fused with cerebral innervation. Cerebro-pleural ganglia connected to pedal ganglia (pd) by doubled short connective tissue. Pedal ganglion with 4 paired innervations and connected by reduced connective tissue. Buccal ganglia (bu) size small, bit smaller than subintestinal ganglion (sb), connected to each other by long commissure, connected to cerebral ganglia through elongated connective. Visceral loop very elongated. Subintestinal (sb) ganglia inconspicuous and connected to abdominal ganglia (ab) by very elongated connective tissue. Supraintestinal ganglia (sp) size as half as abdominal ganglia size, connected to abdominal ganglia by elongated connective, but ~3x smaller than sb-ab connective.

Distribution: Florida to Brazil (Sao Paulo) (MIKKELSEN, 1998).

Habitat and diet: Shallow waters associated with the green algae *Caulerpa* spp..

Material examined: BRAZIL, Praia dos Dois Coqueiros, Caucaia, Ceara, MZSP 132649, 1 specimen (H. Galvão Filho, 02/ii/2014), Taíba beach, São Gonçalo do Amarante, Ceara, CMPHRM 3086B, 1 specimen (H. Galvão Filho, 02/ii/2010); Rita beach, Entremoz, Rio Grande do Norte, MZSP 97049, 2 specimens (M. Delgado, 24/vi/2009).

Remarks: *Ascobulla ulla* has many morphological similarities with *Cylindrobulla* on external and internal morphology. Externally, *Ascobulla* can be distinguished by a short cephalic shield, smaller and more fragile shell, and the protoconch is not immerse in the spire as in *Cylindrobulla*. The reproductive system is very similar, but *A. ulla* has smaller ampulla and the penis is much more elongated than *C. beauii*. In addition, the visceral loop in *A. ulla* is shorter and the ganglia are less innervated. The most differences among them are in the digestive system. Th buccal mass of *Ascobulla* has a very short oral sphincter and the pharyngeal pouch is proportionally larger. The radula is formed by elongated aciculiform teeth in *Ascobulla*, which is adapted to feed on siphonaleous green algae *Caulerpa* spp.. Instead, *Cylindrobulla* has very modified short teeth with multiple cusps, which allow the species on this genera feed on calcareous green algae *Halimeda*. Also, *Ascobulla* has a well-formed esophageal pouch, which is absent in *Cylindrobulla*.

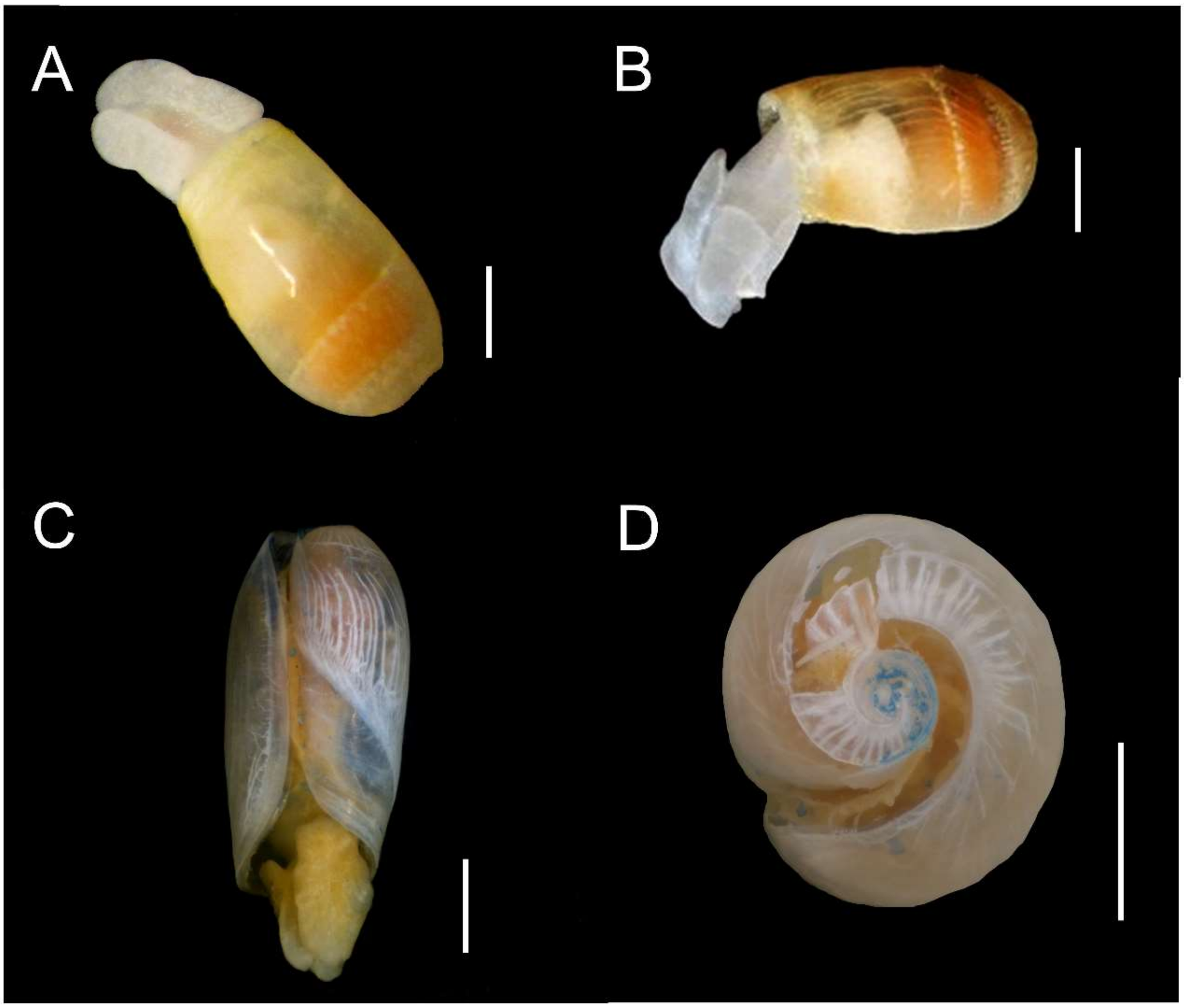

Figure 13. *Ascobulla ulla* live animal. A) dorsal view; B) lateral left view; C) ventral view; D) shell apex.

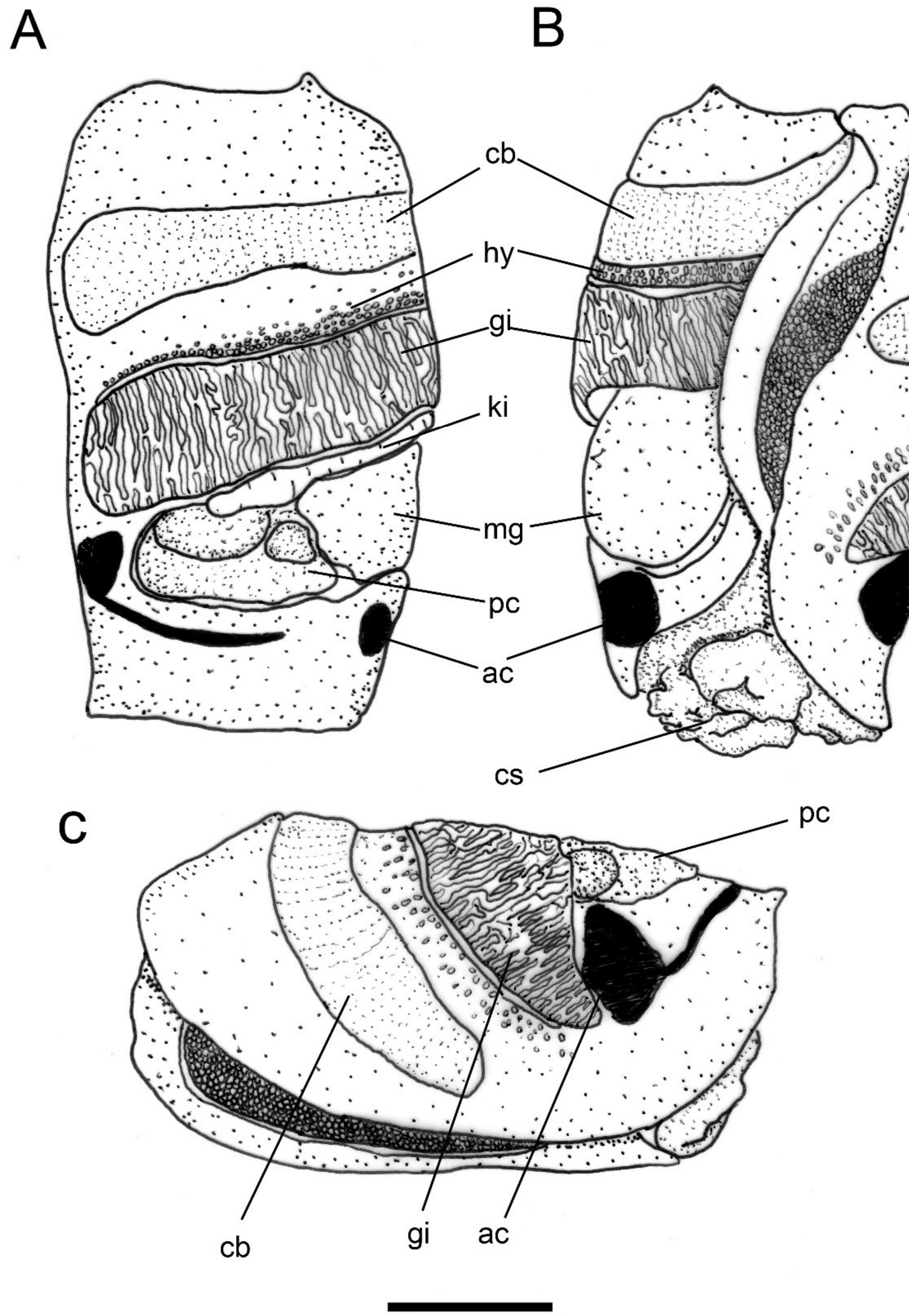

Figure 14. *Ascobulla ulla* anatomy, shell removed, focusing pallial cavity structures: A) Whole dorsal view; B) ventral view; C) lateral view. Scales= 1 mm.

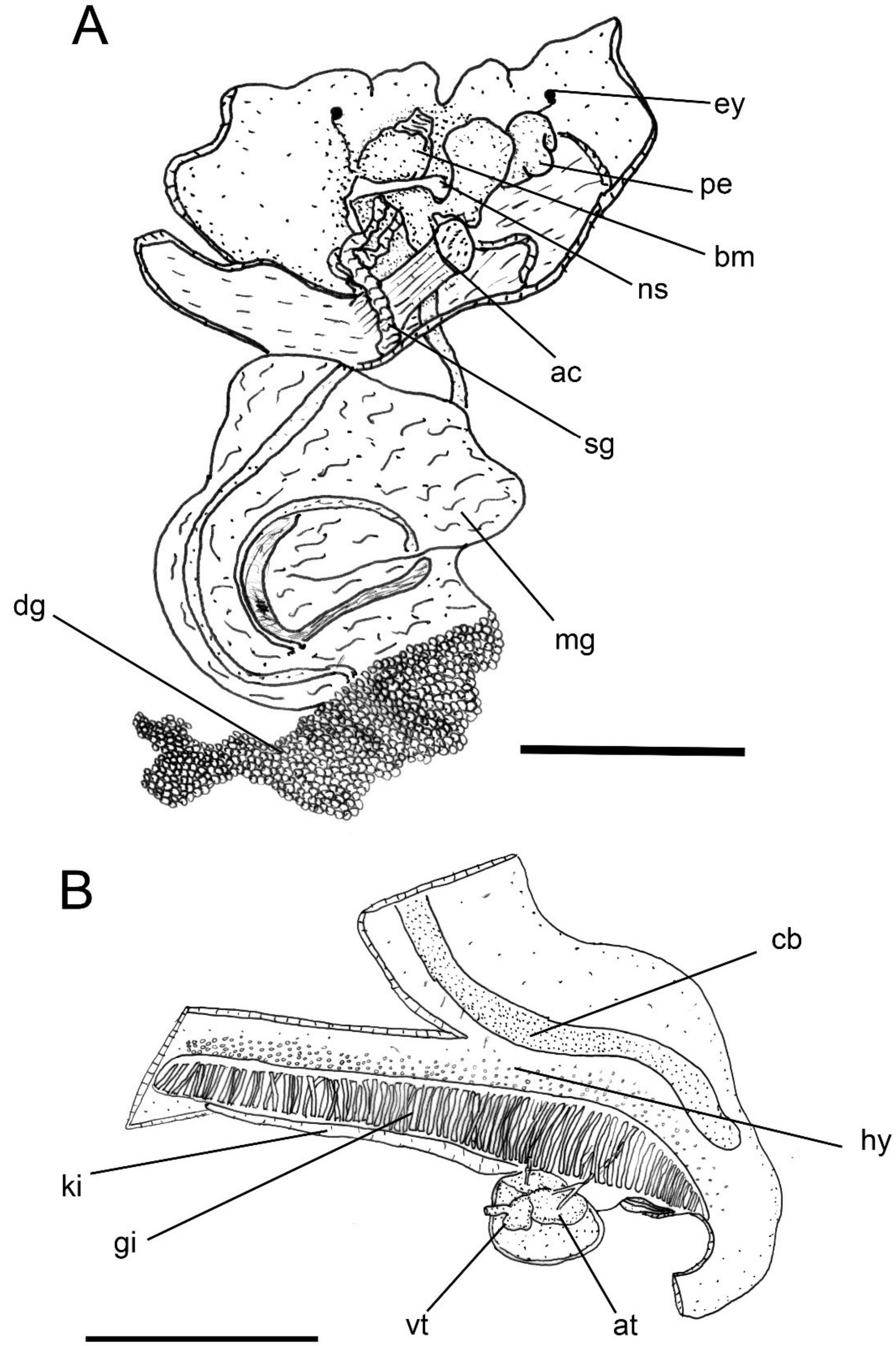

Figure 15. *Ascobulla ulla* anatomy: A) Whole dorsal view, shell and dorsal mantle removed, focusing pallial cavity structures; B) pallial cavity organs. Scales= 1 mm.

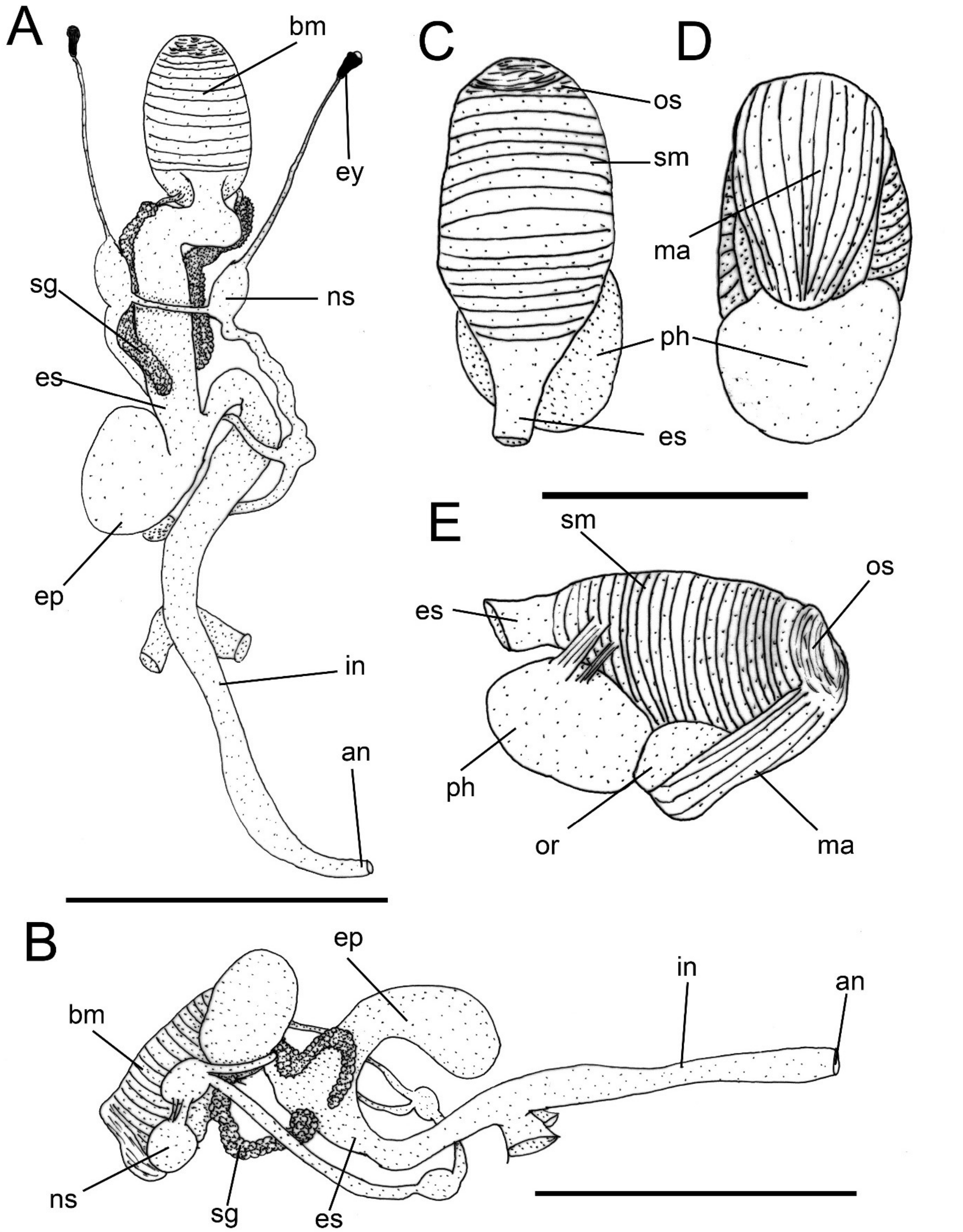

Figure 16. *Ascobulla ulla* anatomy of digestive system: A) Whole dorsal view; B) whole left view (scales= 1 mm). C-E) Buccal mass anatomy: C) dorsal; D) ventral; E) right view (scales: 0.5 mm).

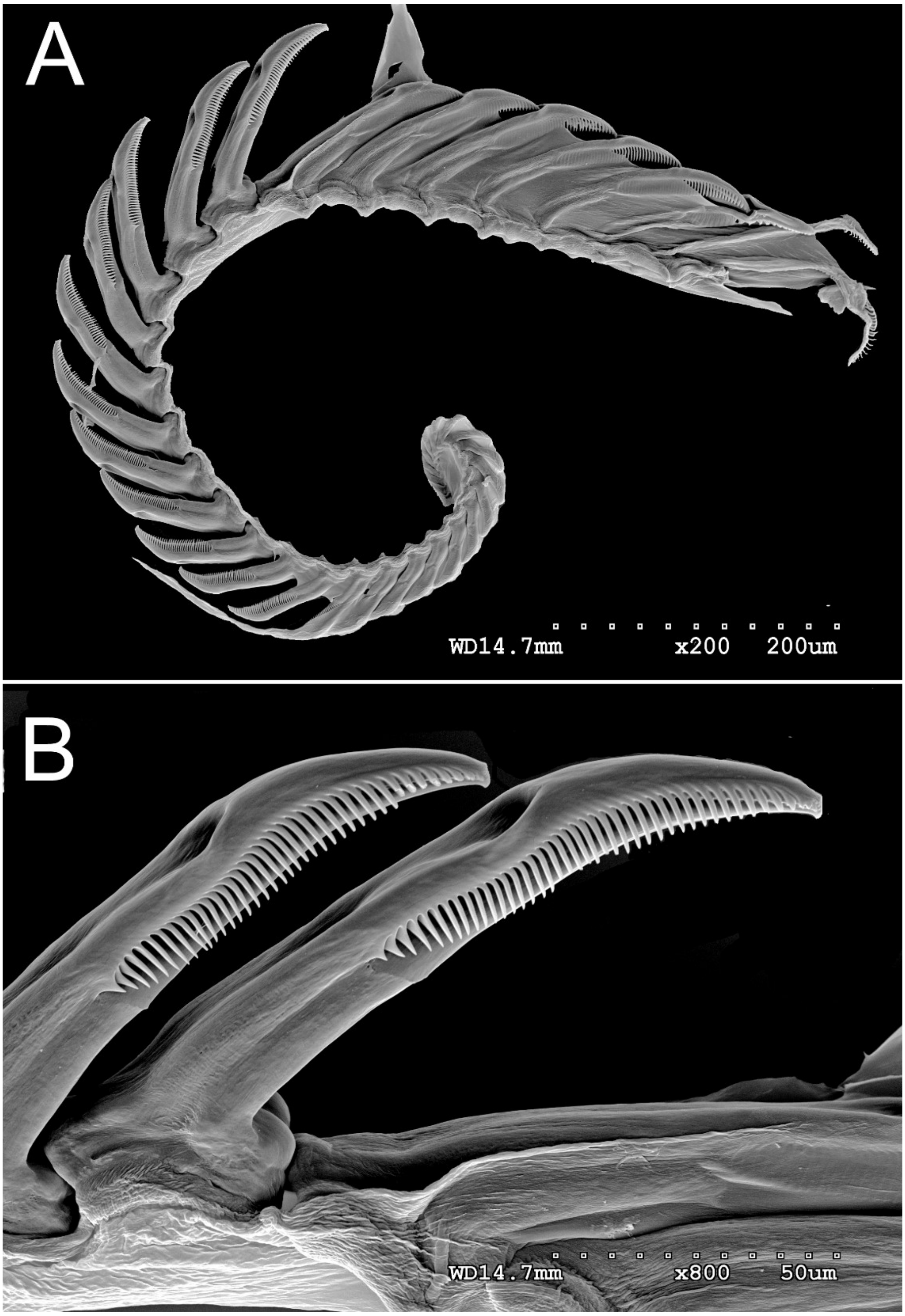

Figure 17. *Ascobulla ulla* radula. A) Whole view; B) detail of leading tooth.

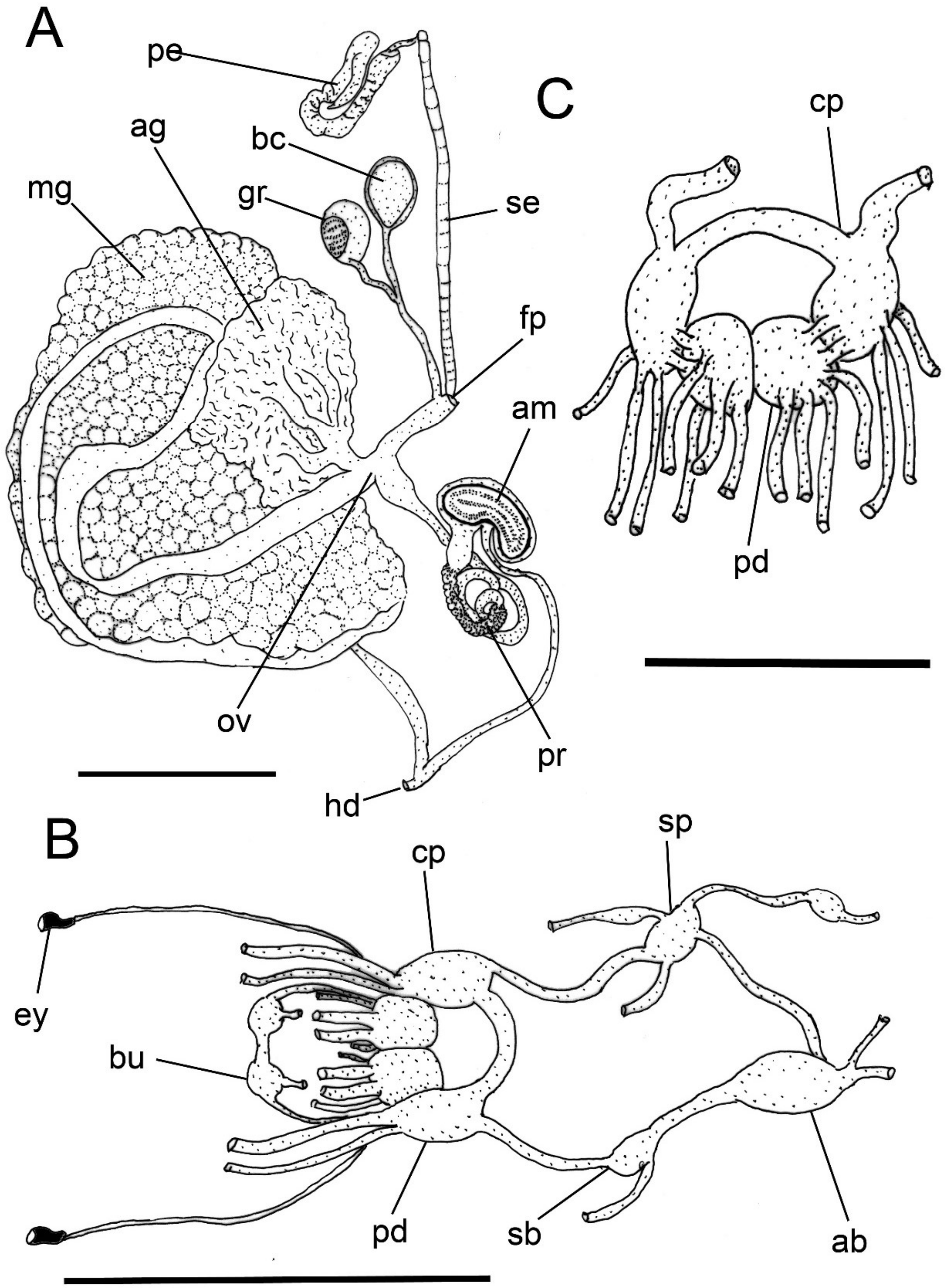

Figure 18. *Ascobulla ulla* anatomy of reproductive and nervous systems: A) schematic drawing of the reproductive system, dorsal view; B) whole dorsal view of central nervous system; C) detail of cerebro-pleural ganglia and pedal ganglia, anterior view. Scales: 1 mm (A, B); 0.5 mm (C).

***Family* Oxynoidae G. & H. Nevill, 1869**

Genus *Oxynoe* Rafinesque, 1819

Type species: *Oxynoe olivacea* Rafinesque, 1819 type by monotypy.

***Oxynoe antillarum* Mörch, 1863**

(Figures 19-24)

Oxynoe antillarum Mörch, 1836: 27; Ev. Marcus & Er. Marcus, 1963: 16; 1967: 25, fig. 20; Marcus & Hughes, 1974: 502, figs. 5-6; Thompson, 1977: 120, figs. 22b, 23; Jensen & Clark, 1983: 3; Clark, 1984: 87, fig. 9; Valdés *et al*., 2006: 54; Padula, 2008: 22, figs. 3, 4, 6, 9, 10, 12, 13; Meirelles *et al.,* 2010: 45, figs. 1-2; Redfern, 2013: 278, fig. 775A-C; Caballer *et al.*, 2015: 220, fig. 3E; Goodheart *et al*., 2116: 21, 11b.

Oxynoe aguayoi Jaume, 1945: 22; Caballer *et al.,* 2015: 220.

Description

External morphology: (Figs. 19-20)**:** Head very distinguishable from rest of body, retractable to under shell, elongated, length ~1/3 of animal body length. Rhinophores rolled, with no papillae, elongated, length bit smaller than head length, pointed forwards. Parapodial lobes extended from foot sole to dorsal side of animal and covering shell almost entirely. Lamellate gill (gi) internal to mantle cavity. Anterior border of foot rounded. Posterior end of foot very elongated forming long autotomized tail with almost half of total animal length. Small conic papillae present on external face of parapodia and dorsal region of tail. Shell shape bulloid and rounded, mainly formed by body whorl and wide aperture. Spire involuted with protoconch immerse. Lip thin, sharp. Growth lines inconspicuous. Periostracum thin, translucent.

Circulatory and excretory systems (Fig. 20-21): Mantle cavity on dorsal of body. Mantle edge smooth. Gill (gi) composed of multiple regular filaments. Hypobranchial gland (hy) right posterior to gill but concentrated only on left side of gill. Secondary glandular ciliated band (cb) more posterior, apical and wider than hypobranchial gland, length as half as gill length. Pericardial cavity very large, occupying 1/3 of mantle cavity, anterior to gill. Auricle (au) shape triangular an elongated, size twice as larger as ventricle (vt), in contact with gill through all its extension. Ventricle (vt) smaller than auricle and more muscular, rounded shaped. Kidney rod-like shaped, reduced, positioned near to auricle and gill.

Digestive system (Fig. 22-23): Buccal mass (bm) with posterior part bit elongated, twice longer as wider with 14 dorsal inconspicuous septate muscles. Oral sphincter (as) very muscular and lar, size twice as larger as rest of buccal mass, composed of complex muscles in many directions and forming huge cavity. Mouth (mo) opens almost ventrally. Uniseriate radula composed of 34 blade-shaped teeth decreasing in size towards ascus, each tooth with two lateral cusps forming cutting edges with multiple elongated and thin denticles, central cusp smooth. Ascending limb with 9 well-formed teeth and other 2 in formation. Descending limb with 23 teeth, finishing straight inside ascus near to odontophore. Odontophore region (or) rounded. Pharyngeal pouch (pp) on most posterior part of buccal mass, rounded, width bit wider than buccal mass width. Esophagus (es) with same width through all its extension. Esophageal pouch (ep) on most posterior part of esophagus, shape very elongated, length as longer as esophagus length, and curled on apex, internally folded. Salivary glands paired, thick club-shaped, not attached to esophagus, with many hairy prolongations. Stomach inconspicuous, thin walled and positioned anterior in digestive gland. Digestive gland like huge homogeneous mass and fused with gonad, occupying most part of posterior region of body. Intestine elongated, thick, running inside digestive gland and finishing on posterior dorsal anus.

Reproductive system (Fig. 24): Gonad fused with digestive gland. One main hermaphrodite duct (hd) runs anteriorly from central part of gonad to mucus gland (mg). Mucus gland granulose, positioned on left side of animal, posterior and not fused to oviduct. Albumen gland (ag) forming one big compact mass positioned near to mucus gland. Male duct (md) running from hermaphrodite duct expands forming one tubular ampulla (am). Ampulla occupies half of male duct length. Prostate gland (pr) anteriorly attached to male duct, just before the connection of male duct to oviduct (ov). Bursa copulatrix (bc) connected to genital receptacle (gr) in one duct that connects with oviduct near to female opening (fp). Penis (pe) elongated, folded at base, with multiple papillae near top, positioned anteriorly on animal, on right side to buccal mass. Vas deferens (vd) very elongated and curled near to penis, length ~3x penis length. Seminal groove absent.

Nervous system (Fig. 24): Cerebral and pleural ganglia fused. Cerebro-pleural (cp) connected to each other by one short commissure. Each cerebro-pleural ganglion with 3 main innervations highly branching toward cephalic shield borders. Optic nerve ~4x longer than cerebral length and branching from or fused with cerebral innervation. Cerebro-pleural ganglia connected to pedal ganglia (pd) by doubled short connective tissue. Pedal ganglion with 5 innervations and connected by reduced connective tissue. Buccal ganglia (bu) size large, size as twice as subintestinal ganglion (sb) size, connected to each other by long commissure, connected to cerebral ganglia through elongated connective. Visceral loop reduced. Subintestinal (sb) ganglia inconspicuous and connected to abdominal ganglia (ab) by reduced connective tissue. Supraintestinal ganglia (sp) size as twice as abdominal ganglia size, connected to abdominal ganglia by short connective.

Distribution: Florida to Brazil (Sao Paulo) (RIOS, 2009).

Habitat and diet: Shallow waters associated with the green algae *Caulerpa* spp..

Material examined: PANAMA, Isla Colón, Bocas del Toro, MZSP 121856, 6 specimens (P. Krug; R. Ellingson; H. Galvão Filho, 07/viii/2015); MZSP 121857, 8 specimens (P. Krug; R. Ellingson; H. Galvão Filho, 07/viii/2015); BRAZIL, Farol do Trapiá beach, Camocim, Ceara, CMPHRM 4089B, 2 specimens (H. Galvão Filho, 08/iv/2012).

Remarks: *Oxynoe antillarum* presents many morphological variations on its external characters. Some populations may present a bluish pattern on rhinophores and parapodia margins, more numerous and elongated papillae on parapodia and variation on shell shape. For this reason, *Oxynoe aguayoi* Jaume, 1945 was synonymized with *O. antillarum* by Marcus & Marcus (1967) and largely accepted by other authors (THOMPSON, 1977, MARCUS & HUGHES, 1974, CLARK, 1984). Although other authors considerer the possibility of *O.*

antillarum be a complex of species or the validity of *O. aguayoi* (VALDÉS *et al*., 2006; CABALLER *et al*., 2015), neither morphological or molecular investigation was done for such purpose.

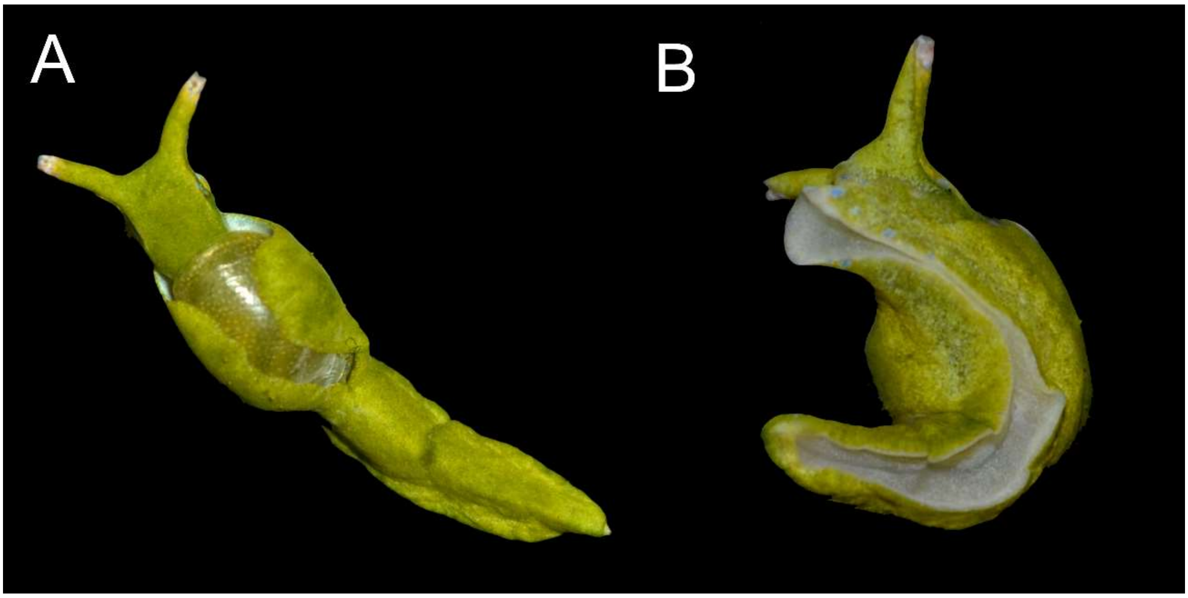

Figure 19. *Oxynoe antillarum* live animal. A) dorsal view; B) ventral view. Length: 18 mm.

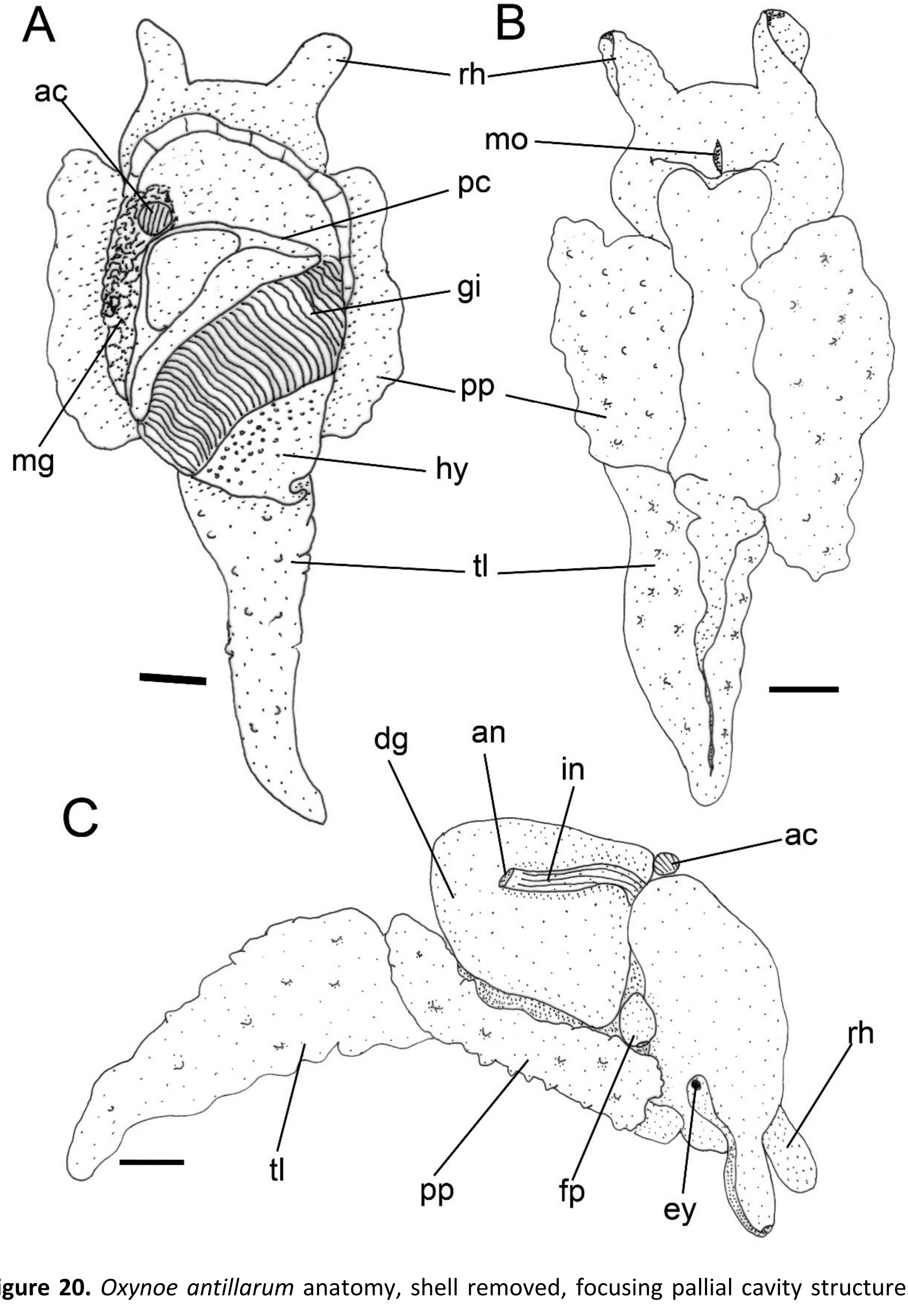

Figure 20. *Oxynoe antillarum* anatomy, shell removed, focusing pallial cavity structures: A) Whole dorsal view; B) ventral view; C) lateral view, dorsal mantle removed. Scales= 1 mm.

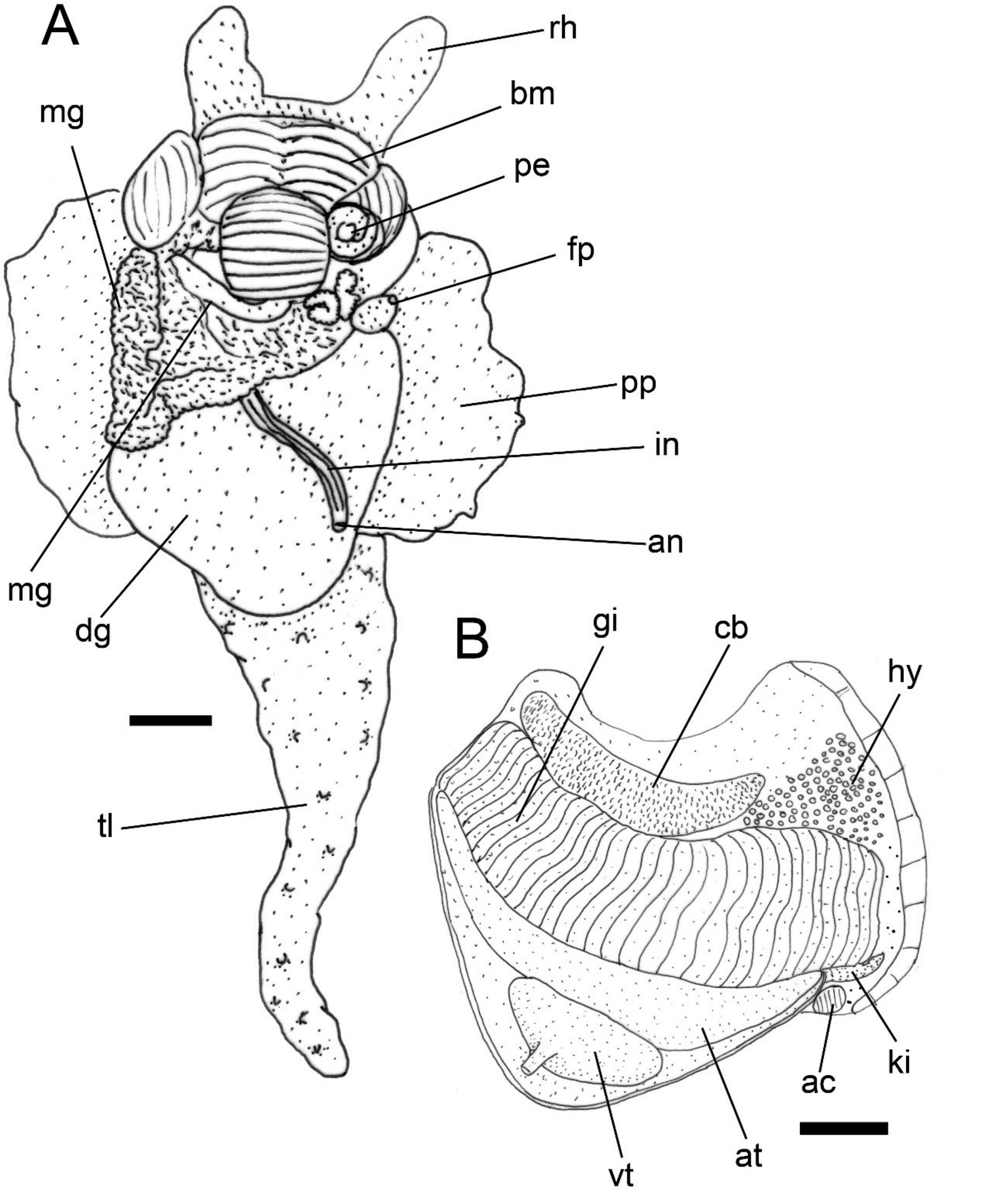

Figure 21. *Oxynoe antillarum* anatomy: A) Whole dorsal view, shell and dorsal mantle removed, focusing pallial cavity structures; B) pallial cavity organs. Scales= 1 mm.

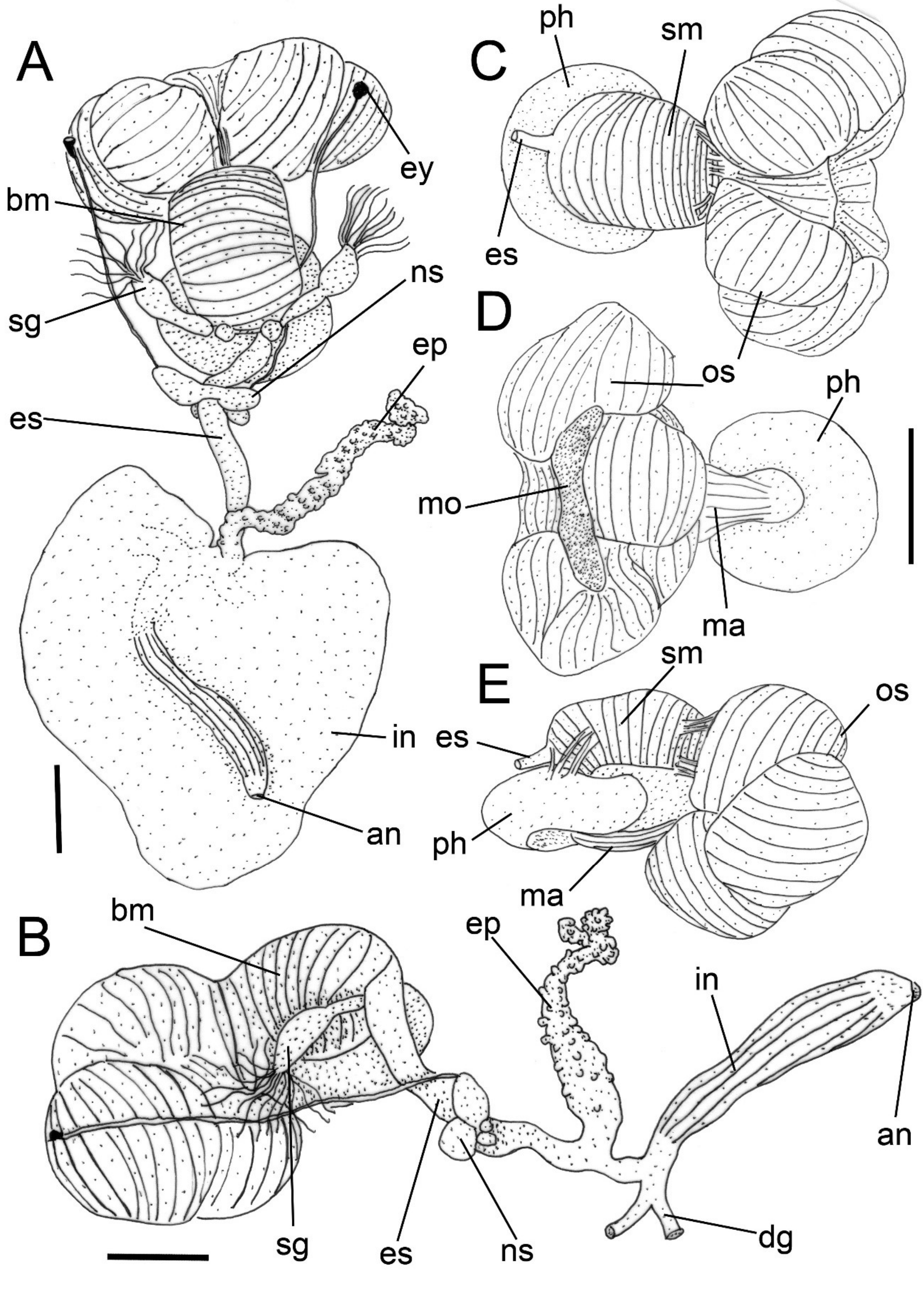

Figure 22. *Oxynoe antillarum* anatomy of digestive system: A) Whole dorsal view; B) whole left view. C-E) Buccal mass anatomy: C) dorsal; D) ventral; E) lateral right view. Scales: 1 mm.

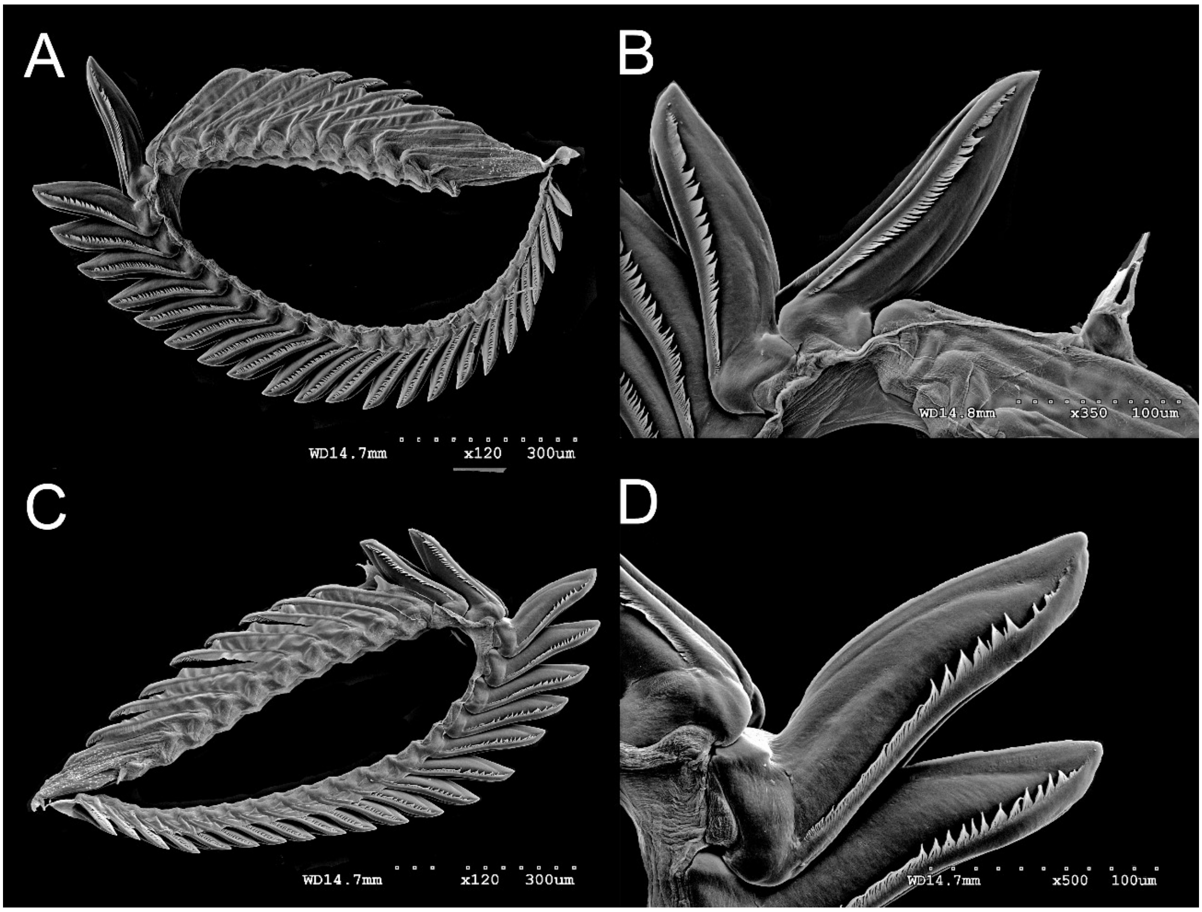

Figure 23. *Oxynoe antillarum* radula. A and C) Whole view; B and D) detail of leading tooth.

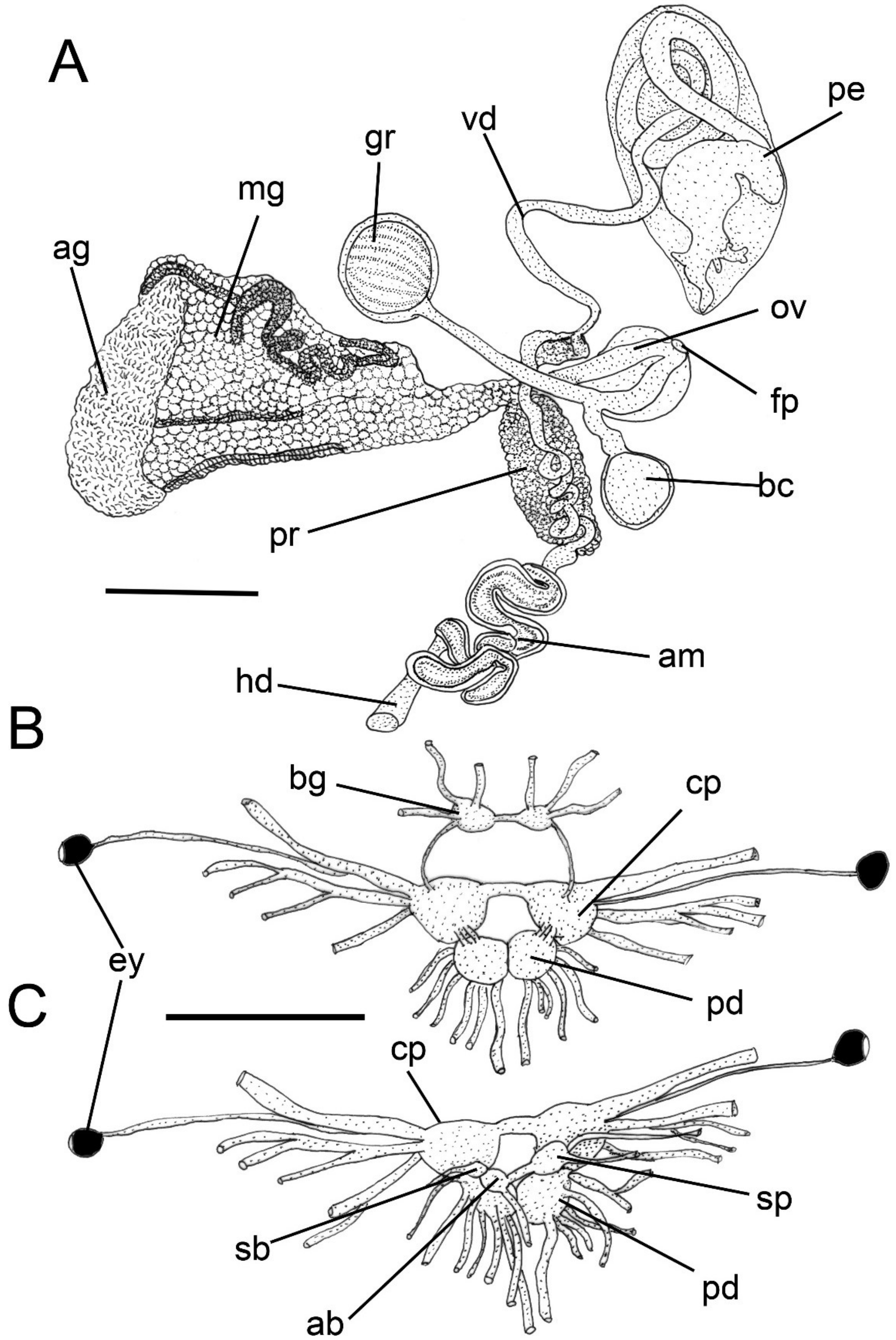

Figure 24. *Oxynoe antillarum* anatomy of reproductive and nervous systems: A) schematic drawing of the reproductive system, dorsal view; B-C) whole view of central nervous system; B) anterior view; C) posterior view. Scales: 1 mm.

***Superfamily* Limapontioidea Gray, 1847**

***Family* Polybranchiidae O'Donogue, 1949**

Genus *Caliphylla* A. Costa, 1867

Type species: *Caliphylla mediterranea* A. Costa, 1867 type by monotypy.

***Caliphylla mediterranea* A. Costa, 1867**

(Figures 25-30)

Caliphylla mediterranea A. Costa, 1867: 17; Engel, 1927: 116, fig. 37; Pruvot-Fol, 1954: 177, fig. 69; Marcus, 1958: 11, fig. 19-24; Gascoigne, 1979: 300, figs. 1-5; Valdés *et al*., 2006: 90; Padula *et al*., 2012: 4: 4B; Jensen, 2014: 118, figs. 1ª, 2-5; Galvão-Filho *et al*., 2015: 8, fig. 3C; Goodheart *et al*., 2016: 24, 12e; Padula, Wirtz & Schrödl, 2017: 750: 3D.

Description

External morphology (Fig. 25-26). Live animals reaching p 35 mm. Body smooth, elongated and tapering posteriorly as pointed tail. Head rounded, hardly distinguishable from rest of body, as longer as wider, length ~1/7 of animal length. Rhinophores (rh) bifid, with more dorsal branch twice longer than ventral one ventral short, length bit smaller than head length, smooth, tip rounded. Eyes (ey) big and positioned on posterior end of head on dorsolateral position. Foot (fo) with mesopodial groove absent. Pericardial (pc) hump well-developed, positioned on middle of body, right after head. Dorsal vessels absent. Cerata (ct) organized in four longitudinal rows, each row with multiple flat leaf-like cerata. Male aperture positioned on right side near to rhinophore. Female aperture on right side, posterior to male aperture ate same level as anus. Vaginal opening absent. Anus positioned laterally on anterior part of body on top of anal papilla.

Coloration (Fig. 25)**.** Translucent body with dark green to brownish digestive ducts branching internally through all animal body. Tiny and numerous opaque white spots spread through all body. Preserved specimens completely yellowish.

Circulatory and excretory systems (Fig. 30A)**.** Pericardium large, occupying almost half of renopericardial cavity. Ventricle spherical and muscular, size bit larger than auricle. Auricle thin-walled and folded. Kidney as thin elongated rounded gland, not branched, positioned posteriorly to pericardium, near the base of auricle. Nephrostome not observed.

Digestive system (Fig. 27-28)**.** Buccal mass (bm) barrel-shaped, elongated. Dorsal septate muscle (sm) with about 20 thick muscular transversal bundles close to each other. Oral sphincter (os) reduced, hardly distinguishable. Ascus musculature (ma) running ventrally from oral sphincter to middle part of buccal mass, straight. Ascus external and very short. Radula with ascending limb composed of 5 well-formed teeth and 2 other in formation. Descending limb length as longer ascending limb, with long series of well-formed teeth plus uncountable teeth in coiled ascus. Leading tooth blade-shaped, elongated, length ~3x longer than base length, edge smooth and lateral cutting edges weakly marked. Esophagus (es) very elongated, length twice as longer as buccal mass length. Salivary glands (sg) paired, attached on most anterior part of esophagus, short, length less than half of esophageal length. Esophageal pouch (ep) muscular, elongated, size twice as small as buccal mass size. Stomach (st) flat, short, wide, positioned on middle of body under reproductive system; internally folded. Two elongated digestive gland ducts (dg) run towards posterior and anterior end of body highly branching through all animal including inside all cerata. Intestine (in) elongated, length as longer as esophagus lentgh thick, with winner surface covered with irregular ridges.

Reproductive system (Fig. 29)**.** Gonad composed of multiple hermaphrodite follicles (hf) with rounded shape and similar size. Small ducts connect all follicles to one main hermaphrodite duct (hd) that expands forming one tubular ampulla (am). Ampulla occupies ~1/3 of hermaphrodite duct. Hermaphrodite duct connects to male duct (md) proximally to ampulla expansion and runs to oviduct. Bursa copulatrix (bc) connected to handled formed by hermaphrodite duct right after connection with male duct, sizebit larger the hermaphrodite follicles. Genital receptacle (gr) connected to oviduct near to mucus gland (mg), close to female aperture (fp). Mucus glande very elongated and not fused with oviduct. Albumen gland (ag) highly branched lateral and ventral to hermaphrodite follicles and with and connected to hermaphrodite duct before ampulla. Oviduct (ov) not glandular. Prostate gland as one curved thick gland, positioned anteriorly in animal body under intestine and over esophagus. Vas deferens (vd) very elongated, coiled near to penis (pe). Penis short and conical, length as wider as longer

Nervous system (Fig. 30)**.** Central nervous system composed by six ganglia and positioned posterior to buccal mass around most anterior part of esophagus. Cerebro-pleural ganglia (cp) size bit larger than pedal ganglia (pd), each ganglion with 5 main innervations. Optic nerve length bit longer than cerebro-pleural ganglion length. Cerebral commissure reduced. Buccal ganglia (bg) size large, size bit larger as subintestinal ganglion (sb), connected to each other by short buccal commissure. Pedal ganglia with 4 main innervations running towards posterior end of body attached to foot under all organs. Pedal commissure long, length as longer as pedal ganglion length. Visceral loop reduced. Abdominal ganglion (ab) very large, size as larger as cerebral ganglion size and with 4 main innervations. Supraintestinal ganglion twice smaller than abdominal ganglia and with one innervation. Subintestinal ganglion small, ~5x smaller than supraintestinal ganglion. Abdominal ganglion connected to supraintestinal and subintestinal ganglia by reduced connective tissue.

Distribution. Amphi-Atlantic. Mediterranean Sea and tropical West Atlantic from Florida to Brazil.

Material examined: BRAZIL, Pedra Rachada beach, Paracuru, Ceará, CMPHRM 3089B, 4 specimens (H. Galvão Filho, 17/x/2009); Barretinha, Atol das Rocas, Rio Grande do Norte, CMPHRM 3014B, 3 specimens (03/ix/2009).

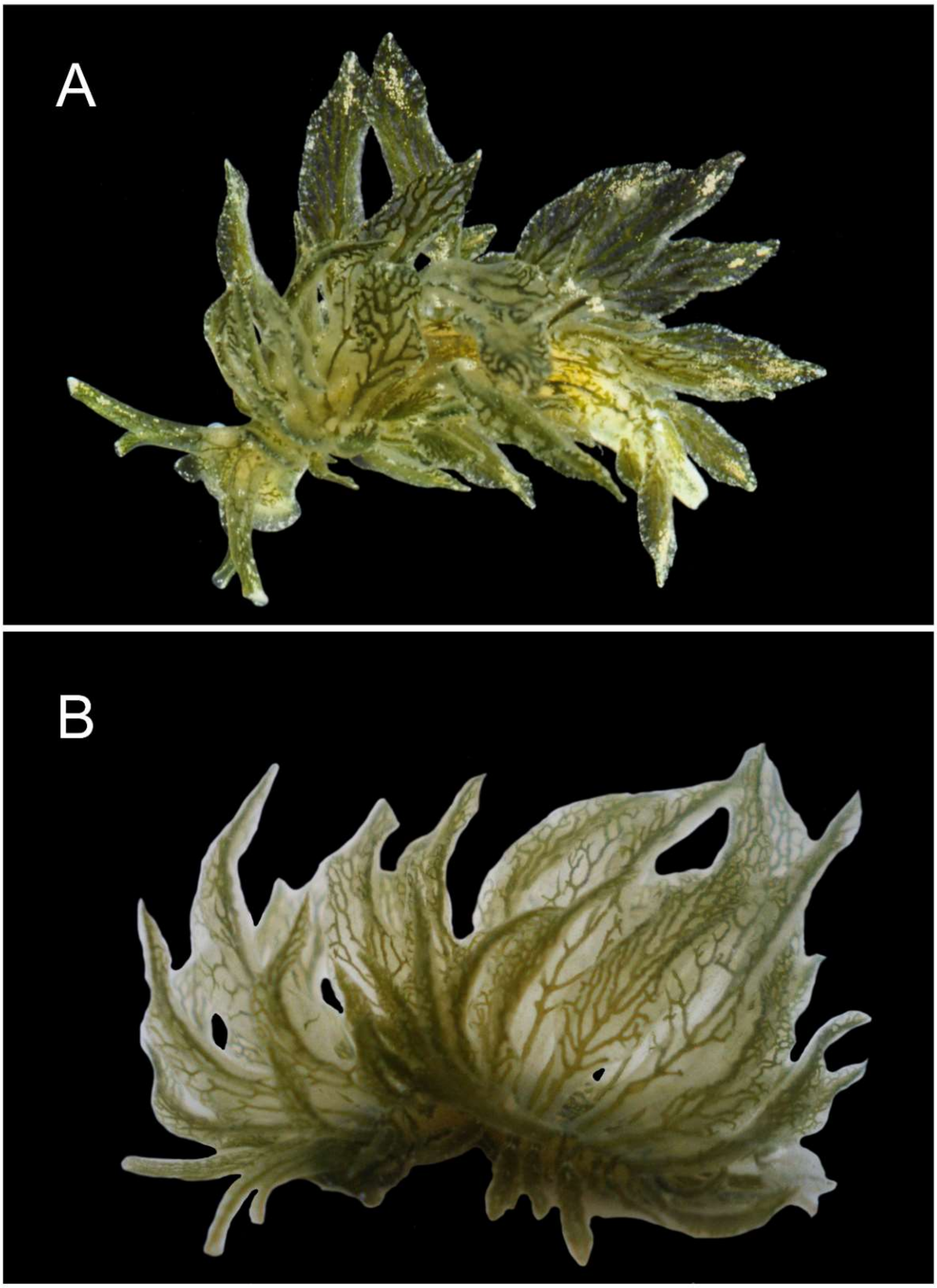

Figure 25. Live specimen of *Caliphylla mediterranea*. A) 18 mm length; B) 33 mm length.

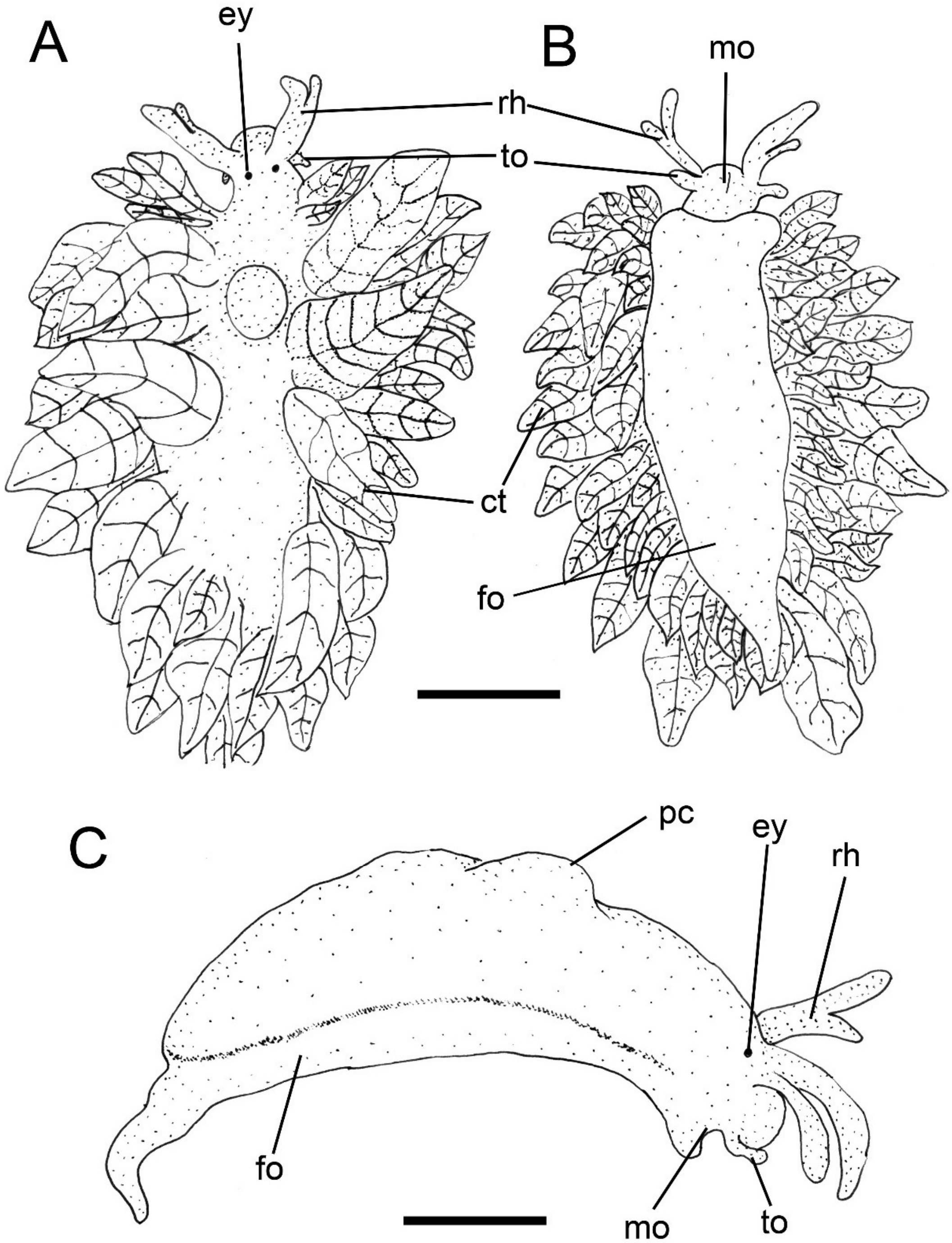

Figure 26. External morphology of *Caliphylla mediterranea*. A) dorsal view with cerata; B) ventral view; C) lateral right view with no cerata. Scale: 1 mm.

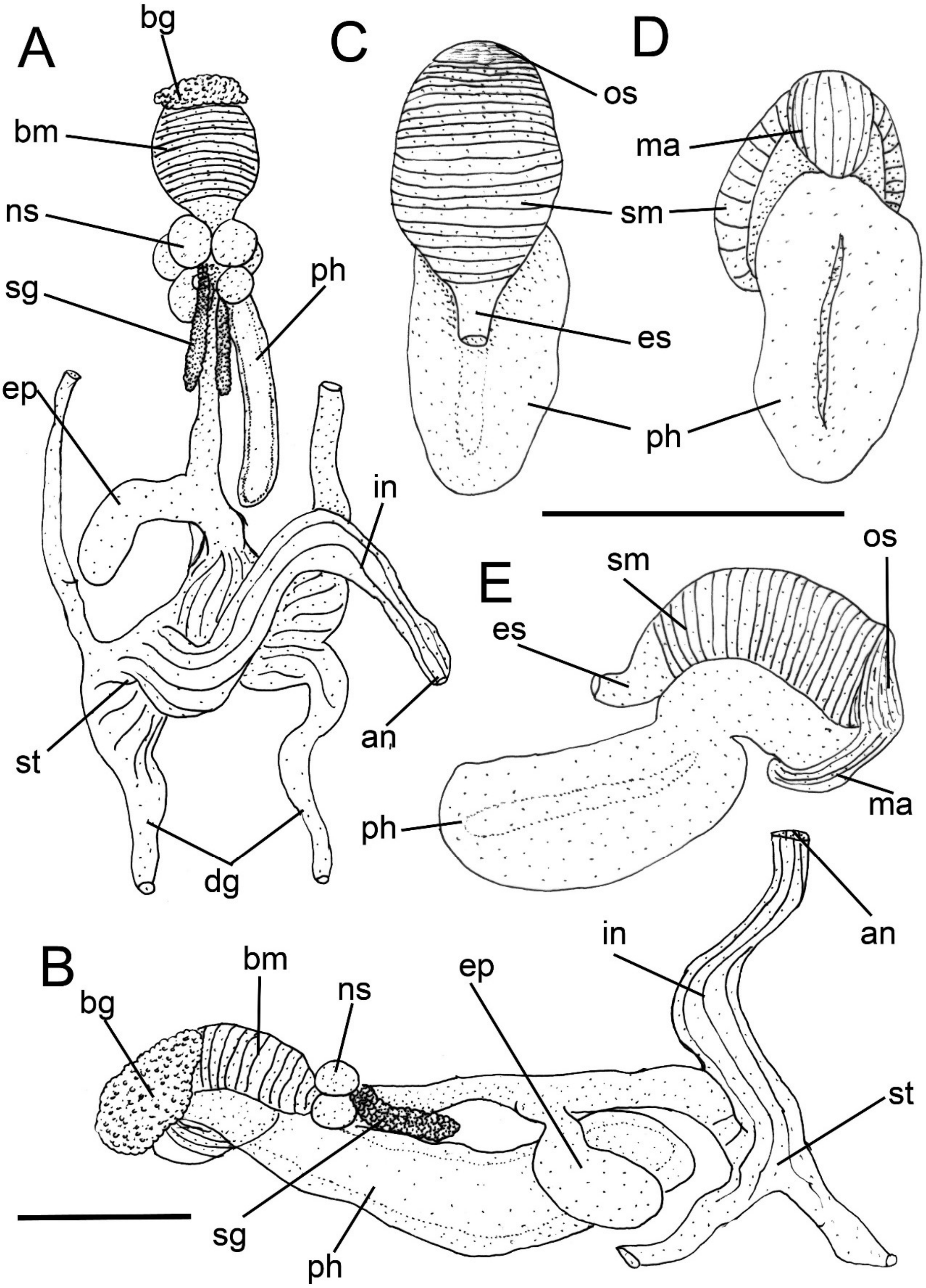

Figure 27. Digestive system of *Caliphylla mediterranea*. A) Dorsal view; B) Lateral left view; Detail of buccal mass: C) dorsal view; D) ventral view side; E) lateral right view. Scales: 1 mm.

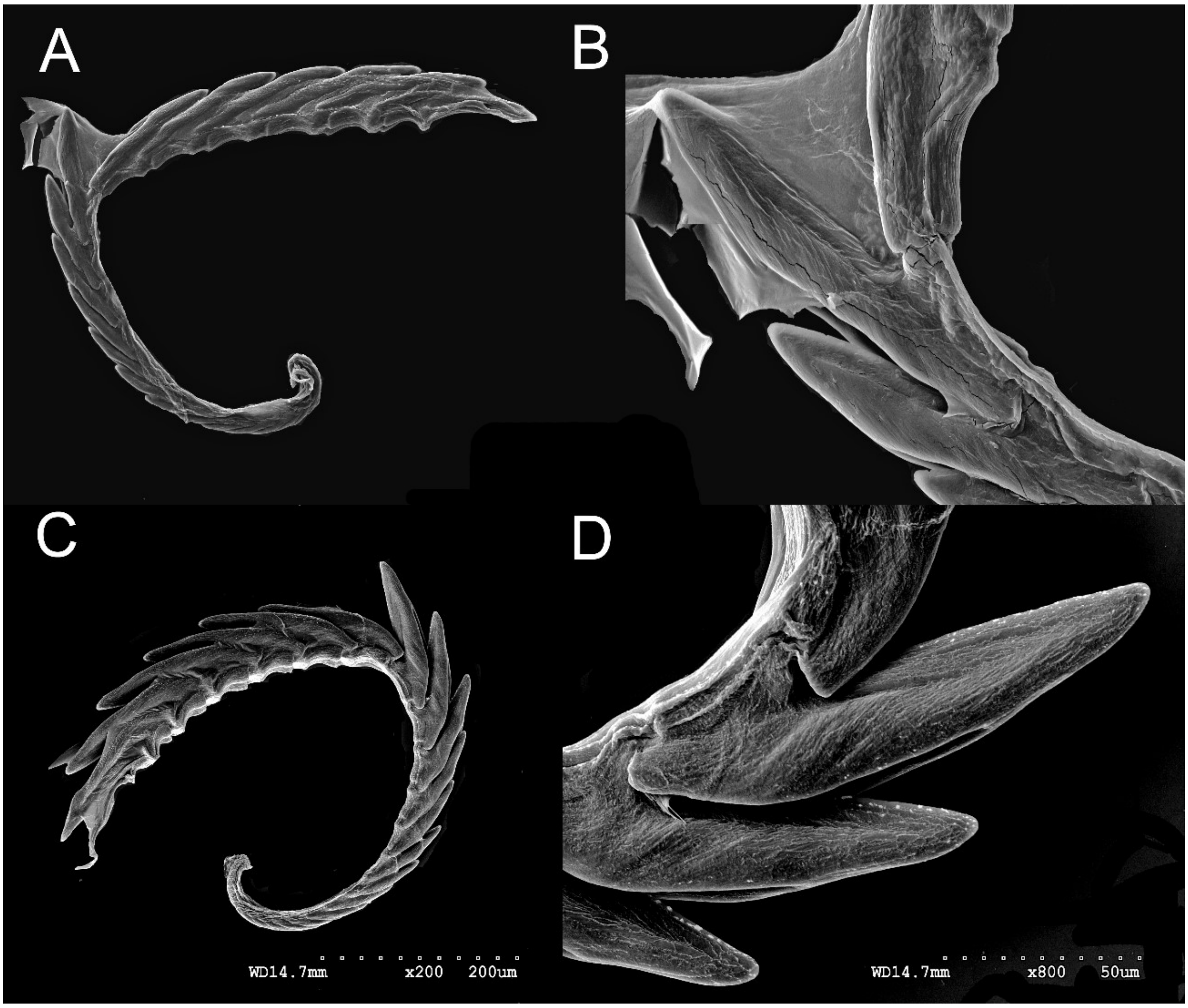

Figure 28. Scan electron microscope images of radula of *Caliphylla mediterranea.* A and C) general view; B and D) detail of the leading tooth.

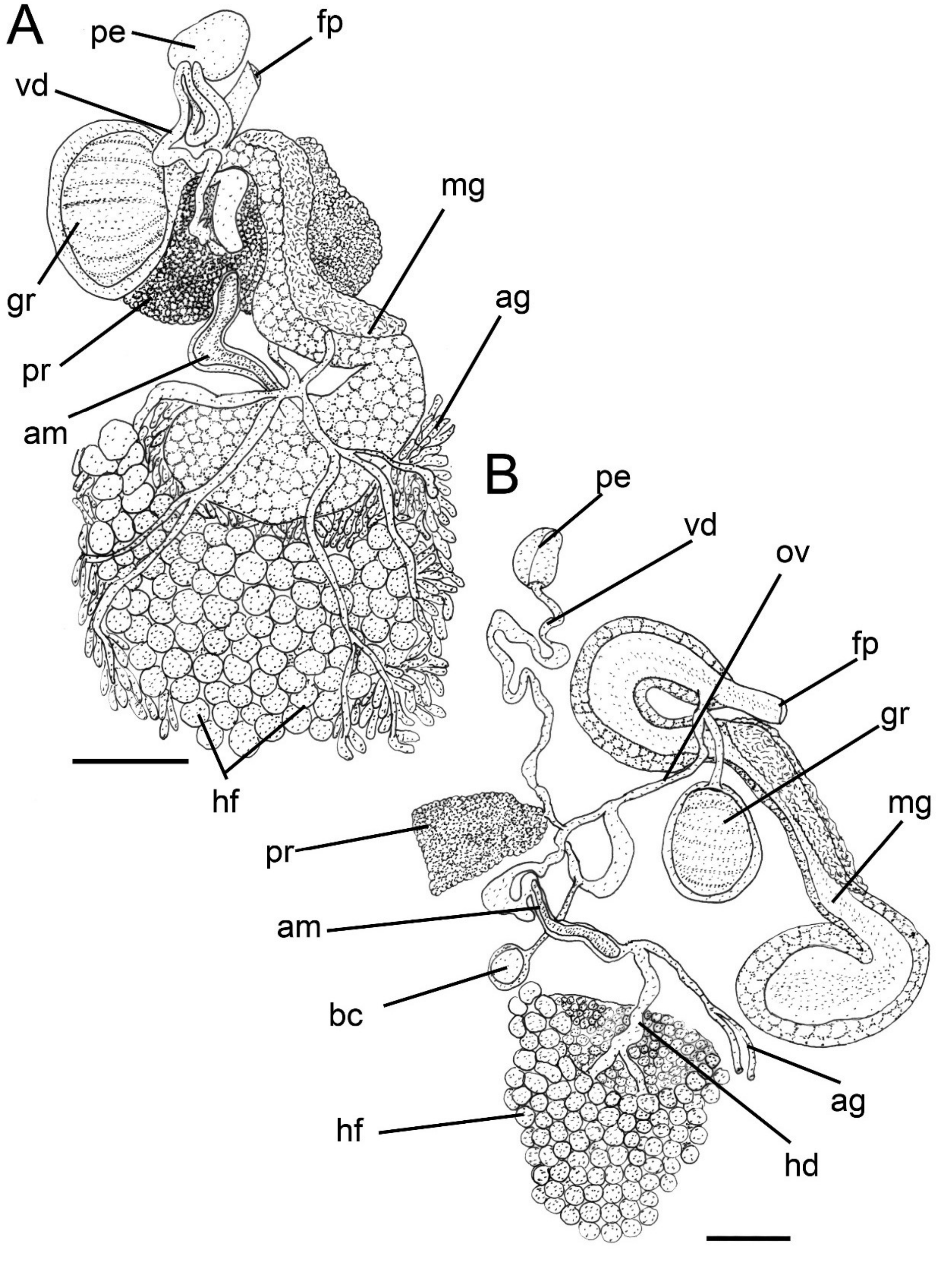

Figure 29. Reproductive system of *Caliphylla mediterranea*. A) Dorsal view of whole system; B) schematic drawing, dorsal view. Scales = 1 mm.

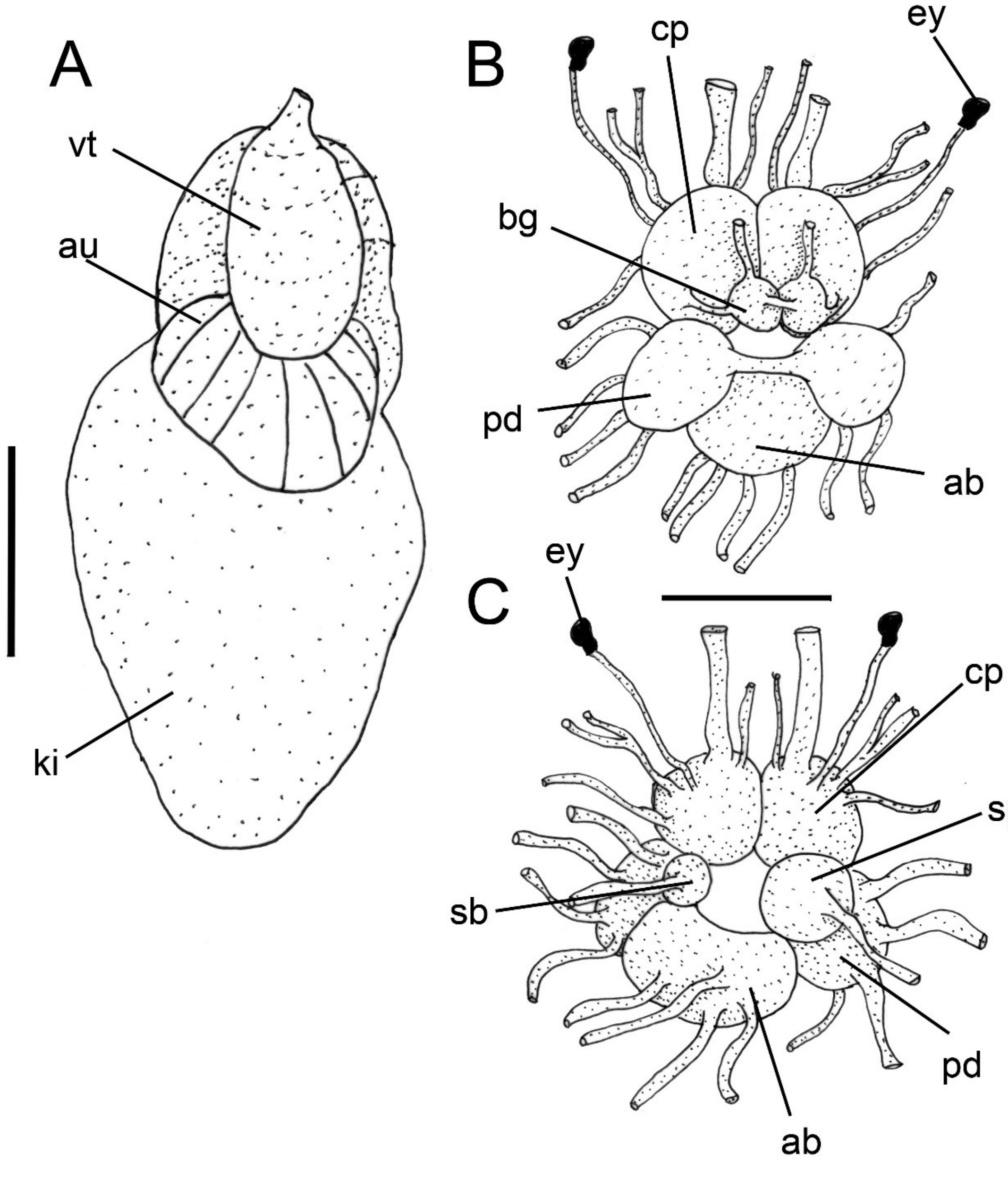

Figure 30. *Caliphylla mediterranea* anatomy. A) Circulatory and excretory systems, renopericardial cavity. B-C) Central nervous system; B) anterior view; D) posterior view. Scales= 0.5 mm.

***Family* Limapontiidae Gray, 1847**

Genus *Olea* Agersborg, 1923

Type species: *Olea hansineensis* Agersborg, 1923 type by monotypy.

***Olea* sp.**

(Figs. 31-35)

Description

External morphology (Fig. 31-32)**.** Live animals reach up 2.5 mm. Body smooth, elongated and tapering posteriorly as pointed tail. Head square shaped, width as wider as body width, ~2x wider than longer, length ~1/8 of animal length. Rhinophores extremely reduced to short expansions on posterior end of head. Eyes big and positioned on posterior end of head on dorsolateral position. Foot with a longitudinal groove and mesopodial groove absent. Pericardial hump inconspicuous, positioned mid-centrally on body, right before cerata. Dorsal vessels absent. Cerata organized in two longitudinal rows, each row with 3 fusiform cerata. Male aperture positioned on right side of body laterally to right eye. Female aperture posteriorly and close to male aperture. Vaginal opening centrally positioned on right side of body, at same level as pericardium, and far from female aperture. Anus positioned mid dorsally on body, just posterior to eyes.

Coloration (Fig. 31)**.** Translucent body with dark brown and yellowish patches dorsally and laterally on body. White rounded glands spread all over the body, head and cerata, bigger bluish ones closer to posterior border of head and forming one centrally longitudinal row of glands on tail. Kidney opaque white with renal aperture marked by one black dot. Digestive gland yellowish. Preserved specimens still present all dorsolateral brown patches and white glands, while digestive gland become whitish.

Circulatory and excretory systems (Fig. 34B)**.** Pericardium extremely small. Ventricle spherical and muscular, size ~5X bigger than auricle. Auricle thin-walled with smooth surface. Kidney as thin elongated flat gland, not branched, positioned posteriorly to pericardium, near the base of auricle. Nephrostome readily visible and marked as a dark spot near to pericardium.

Digestive system (Fig. 33). Buccal mass (bm) barrel-shaped, short, elongated, 3x longer than wider. Dorsal septate muscle (ds) with tiny muscular transversal bundles close to each other and hardly distinguishable. Oral sphincter reduced. Ascus musculature running ventrally from oral sphincter to middle part of buccal mass, composed of tiny longitudinal muscles holding the descending limb of buccal mass. Ascus apparently absent or extremely reduced. Radula with ascending limb composed of 11 teeth in formation and barely recognizable. Descending limb twice shorter than ascending limb, with leading tooth well-formed plus three rod-like teeth. Leading tooth blade-shaped, short, length longer as base length, edge smooth and lateral flanges absent. Esophagus thin and elongated, length ~3x longer than buccal mass length and bit longer than intestine length. Esophageal inner surface with one pair of tiny folds. Salivary glands paired, attached on most anterior part of esophagus, cover first 1/5 of esophagus length. Esophageal pouch absent. Stomach flat, wide, positioned on middle of body under albumen gland and some dorsal follicles; thin-walled with inner surface with no folds. Two elongated digestive gland ducts run towards posterior end of body. Each duct branches in three straight non-ramified ducts inside all cerata. Intestine elongated, thick, with winner surface covered with irregular ridges.

Reproductive system (Fig 34A and C, 35)**.** Gonad composed of multiple hermaphrodite follicles (hf) with irregular shape and slightly variable in size. Multiple small ducts connect all follicles to one main hermaphrodite duct (hd), that expands forming one tubular ampulla (am). Ampulla occupies more than half of hermaphrodite duct. Hermaphrodite duct connects to male duct (md) proximally to ampulla expansion, running to oviduct on fertilization chamber (fc). Bursa copulatrix (bc) with its own aperture and one main duct connected to fertilization chamber. Albumen gland (ag) highly branched over hermaphrodite follicles and with one connection to fertilization chamber at the same point as hermaphrodite ducts and one distal connection on bursa copulatrix duct. Genital receptacle size as larger as bursa copulatrix, also connected to fertilization chamber, closer to glandular oviduct. Glandular oviduct with two distinct glands. Mucus gland most distally one, larger, thicker and flimsy. Capsule gland proximal to female opening on right side of animal body, less translucent and firmer than mucus gland. Prostate gland formed by bilobed short gland, positioned anteriorly in animal body under intestine and over esophagus. Vas deferens (vd) long, length ~3x longer than penis length. Penis (pe) short and conical, size as larger as longer, with a terminal slightly curved stylet. Stylet length as half as penis length.

Nervous system (Fig. 34D-E)**.** Central nervous system composed of six ganglia and positioned posterior to buccal mass around most anterior part of esophagus. Cerebro-pleural ganglia (cp) size as large as pedal ganglia (pg), each ganglion with 5 main innervations. One innervation highly ramified close to ganglion and runs towards posterior end of head to reduced rhinophore region. Optical nerve length twice as longer as cerebro-pleural ganglion length. Cerebral commissure external, short and thin. Buccal ganglia (bg) size large, as half as supraintestinal ganglion size, with one main innervation running from each ganglion to anterior part of buccal mass. Buccal commissure internal. Pedal ganglia with for main innervation running towards posterior end of body attached to foot under all organs. Pedal commissure internal. Visceral ganglia composed by one large abdominal ganglion, size half of cerebral ganglion size and with two innervations, and one supraintestinal ganglion bit smaller than abdominal ganglia and with one innervation. Abdominal ganglion connected to supraintestinal ganglion by one short connective and connected to cerebro-pleural by one longer innervated connective, length as longer as cerebro-pleural commissure length.

Distribution. Florida.

Remarks

Both molecular and morphological evidence have suggested the position of the new egg-feeder sacoglossan belonging to the genus *Olea*. The probably new species *Olea* sp. was recovered as sister to *Olea hansineensis* Agersborg, 1923 with a strong support for Bayesian and maximum likelihood trees.

Although the phylogenetic relationship among the genera traditionally placed in Limapontiidae is still debatable, the genera *Calliopaea* d'Orbigny, 1837 and *Olea* were resulted as sister groups in both scenarios they were included in (JENSEN, 1996; KRUG *et al*., 2015). Our results support this relationship, also placing *Caliopaea belulla* d'Orbigny, 1837 as sister to *O. hansineensis* and *Olea* sp. This relationship suggests that the change of food habits from herbivory to oophagy has happened only once in Sacoglossa evolutionary history.

Externally, the genera *Olea* and *Calliopaea* are quite similar, but *Olea* sp. looks more like to *O. hansineensis* than *Calliopaea* spp. due to less number of cerata and reduced rhinophore. However, similar external features have been reported to smaller *Caliopaea oophaga* Lemche in Gascoigne & Sartory, 1974 specimen (GASCOIGNE & SIGURDSSON, 1977, fig. 1c). The radular teeth in *Olea* n. sp. are quite unusual as in *O. hansineensis*, with the ascending limb mostly with teeth in formation and descending limb with same number of teeth and some rod-like shaped ones (GASCOIGNE, 1975). Although Gascoigne (1975) has reported intraspecific variations on the number of fully formed teeth on *O. hansieensis*, it represents more teeth of this type as in *Olea* sp., which it was reported only with one fully formed in all specimens analyzed. Differently from *Olea* spp., *Calliopaea* spp. present a longer radula with many fully formed teeth in both ascending and descending limbs (GASCOIGNE & SIGURDSSON, 1977; GASCOIGNE & TODD, 1977). Also, the ascus in *Olea* is extremely reduced, while is still remarkable.

Figure 31. Live specimen of *Olea* n. sp.

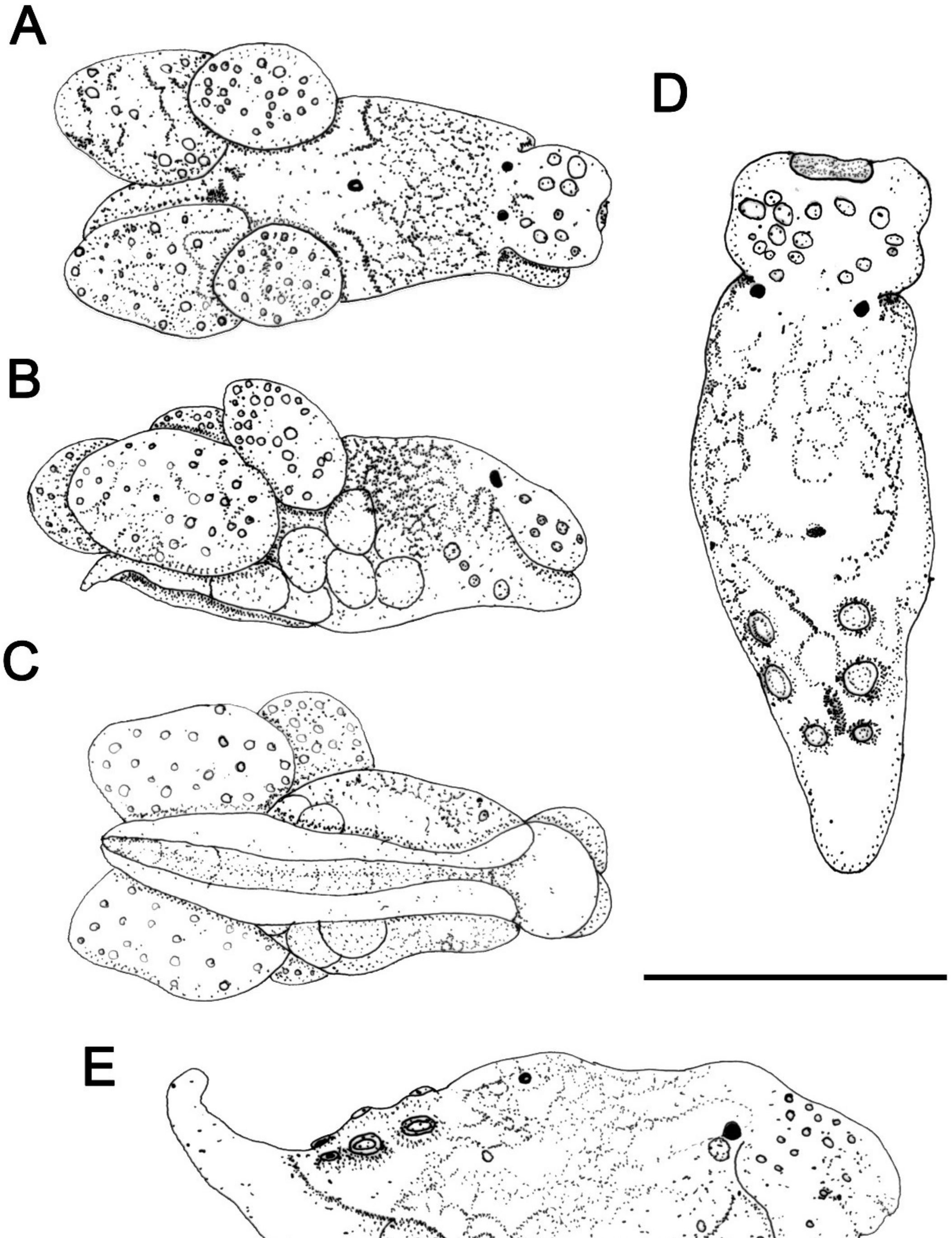

Figure 32. External morphology of *Olea* n. sp. (A) Dorsal, (B) lateral, and (C) ventral view of a 1,5mm specimen with cerata. (D) Dorsal and (E) lateral view of a 2 mm specimen with no cerata.

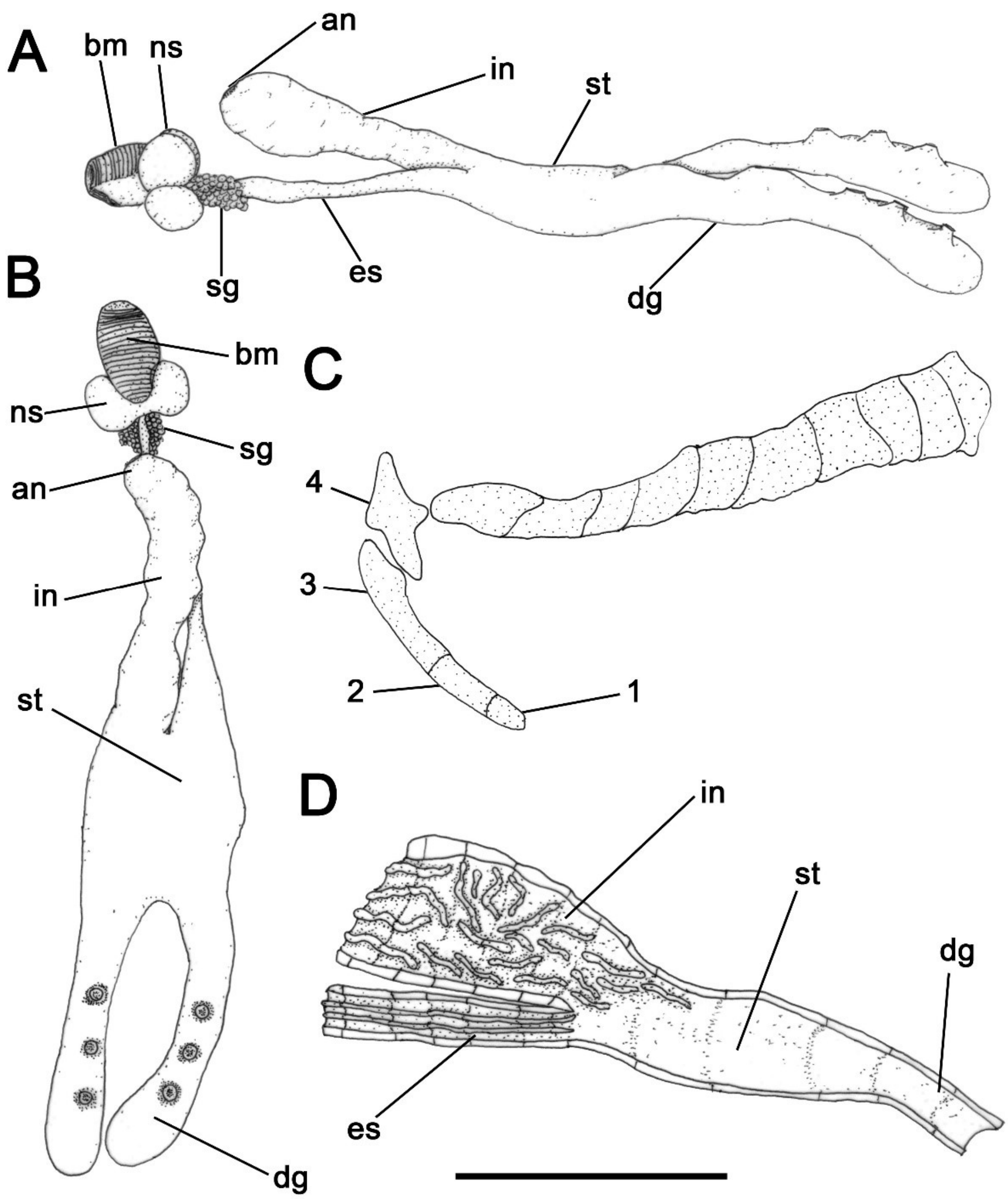

Figure 33. Digestive system of *Olea* n. sp. A) Lateral view. B) Dorsal view. C) Radula. D) Internal view.

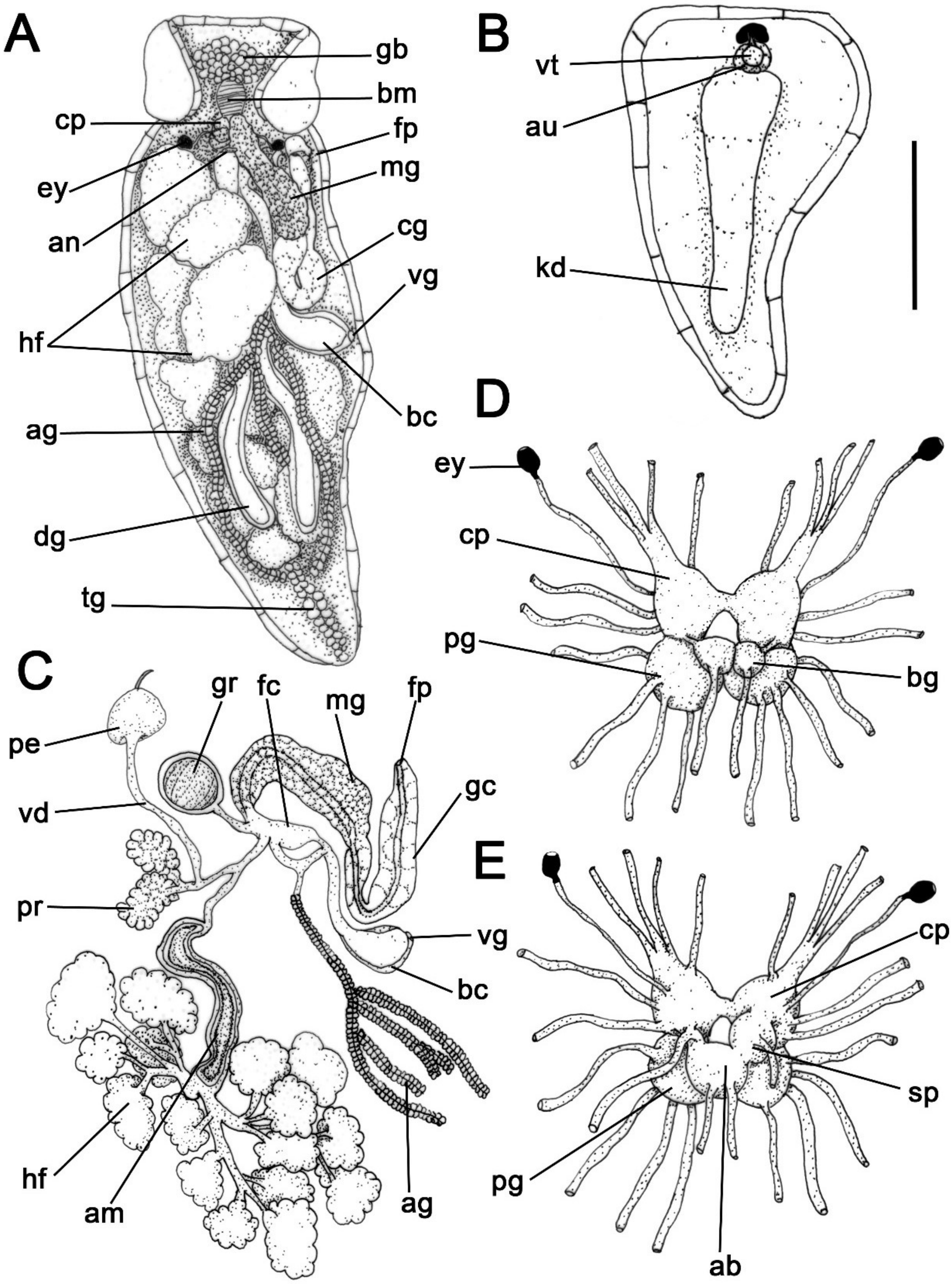

Figure 34. Internal morphology of *Olea* n. sp. A) Dorsal view of hemocoel organs disposition. B) Ventral view of kidney and pericardium. C) Reproductive system. D) Anterior and posterior (E) view of central nervous system.

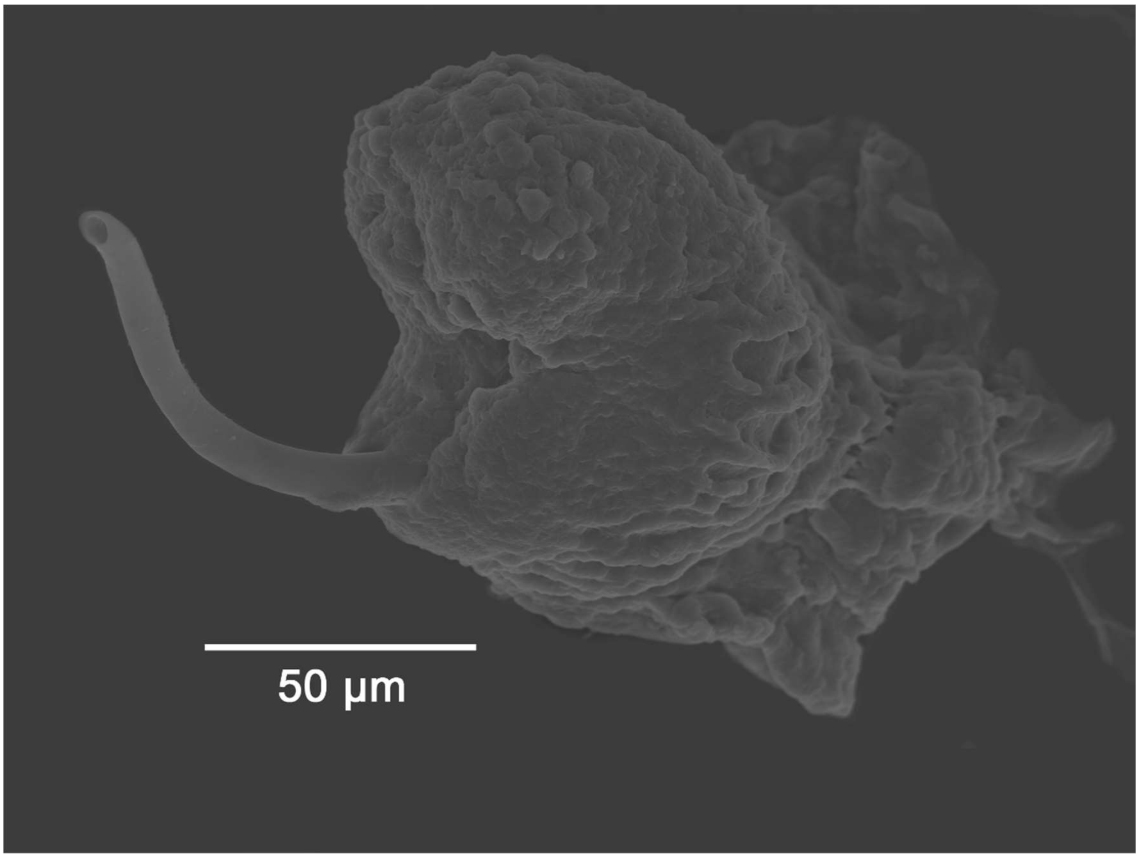

Figure 35. Scanning electron microscope image of penis of *Olea* n. sp.

Family Stiligeridae

Genus *Stiliger* Ehrenberg, 1828

Type species: *Stiliger ornatus* Ehrenberg, 1828 type by monotypy.

***Stiliger vossi* Ev. Marcus & Er. Marcus, 1960**

(Figs. 36-41)

Stiliger vossi Ev. Marcus & Er. Marcus, 1960: 144, figs. 18-21.

Description

External morphology (Fig. 36-37). Live animals reaching 5 mm. Body smooth, elongated and tapering posteriorly as pointed tail. Head rounded, bit longer than, length ~1/5 of animal length. Rhinophores simple shape, short, length smaller than head length, smooth, tip rounded. Eyes big and positioned on posterior end of head on dorsolateral position. Foot with a longitudinal groove and mesopodial groove absent. Pericardial hump well-developed, positioned anteriorly on body, right after head. Dorsal vessels absent. Cerata organized in two longitudinal rows, each row with up to 9 fusiform cerata. Male aperture positioned on top of penial bulb on right side of animal body. Female aperture at base of penial bulb, close to male aperture. Vaginal opening absent. Anus positioned mid dorsally on body, just posterior to eyes.

Coloration (Fig. 36)**.** Translucent body with dark brown patches dorsally and laterally on body. White rounded glands spread all over the body, head and cerata. Digestive gland yellowish. Preserved specimens still present all dorsolateral brown patches and white glands, while digestive gland become whitish.

Circulatory and excretory systems (Fig. 38)**.** Pericardium extremely small. Ventricle spherical and muscular, size ~3X bigger than auricle. Auricle thin-walled with smooth surface. Kidney as thin elongated flat gland, not branched, positioned posteriorly to pericardium, near the base of auricle. Nephrostome not observed.

Digestive system (Fig. 38-39)**.** Buccal mass (bm) barrel-shaped, short, elongated, 2x longer than wider. Dorsal septate muscle (ds) with tiny muscular transversal bundles close to each other and hardly distinguishable. Oral sphincter reduced. Ascus musculature running ventrally from oral sphincter to middle part of buccal mass in spiral shape. Ascus as same size as odontophore region. Radula with ascending limb composed of 9 teeth. Descending limb ~9x longer than ascending limb, with long series of well-formed teeth plus 6 rod-like teeth in ascus. Leading tooth blade-shaped, elongated, length ~5x longer than base length, edge smooth and lateral flanges absent. Esophagus thin and short, length ~5x shorter than buccal mass length and bit smaller than intestine length. Salivary glands paired, attached on most anterior part of esophagus, cover all esophagus length and anterior most part of stomach. Esophageal pouch muscular, size bit smaller than buccal mass, internally folded. Stomach flat, elongated, wide, positioned on middle of body under albumen gland and some dorsal follicles; thin-walled with inner surface with no folds. Two elongated digestive gland ducts run towards posterior end of body. Each duct branches in 9 straight non-ramified ducts inside cerata. Intestine short, thick, with winner surface covered with irregular ridges.

Reproductive system (Fig. 40)**.** Gonad composed of 2 hermaphrodite follicles (hf) with rounded shape and similar size. Small ducts connect both follicles to one main hermaphrodite duct (hd), that expands forming one tubular ampulla (am). Ampulla occupies less than half 1/5 of hermaphrodite duct. Hermaphrodite duct connects to male duct (md) proximally to ampulla expansion and runs to oviduct. Bursa copulatrix (bc) absent. Genital receptacle (gr) connected to oviduct after male duct. Albumen gland (ag) highly branched over hermaphrodite follicles and with and connected to oviduct after genital receptacle. Glandular oviduct as a big rounded gland. Prostate gland as one curved thick gland, positioned anteriorly in animal body under intestine and over esophagus. Vas deferens (vd) short, length as longer as penis length. Penis (pe) short and conical, size as larger as longer, positioned inside a penial bulb.

Nervous system (Fig. 41)**.** Central nervous system composed by six ganglia and positioned posterior to buccal mass around most anterior part of esophagus. Cerebro-pleural ganglia (cp) size as large as pedal ganglia (pg), each ganglion with 6 main innervations. Optical nerve length bit longer than cerebro-pleural ganglion length. Cerebral commissure external, short and thin. Buccal ganglia (bg) size large, as half as supraintestinal ganglion size, with one main innervation running from each ganglion to anterior part of buccal mass. Buccal commissure internal. Pedal ganglia with 2 main innervations running towards posterior end of body attached to foot under all organs. Pedal commissure external, long, length as longer as pedal ganglion length. Visceral ganglia composed by one large abdominal ganglion, size half of cerebral ganglion size and with one main innervation, and one supraintestinal ganglion twice smaller than abdominal ganglia and with one innervation. Abdominal ganglion connected to supraintestinal ganglion by one short connective and connected to cerebro-pleural by one longer innervated connective, length as longer as cerebro-pleural commissure length.

Distribution. Florida (type-locality); Panamá (present study).

Material examined: PANAMA, Isla Colón, Bocas del Toro, MZSP 121850, 8 specimens (P. Krug; R. Ellingson; H. Galvão Filho, 07/viii/2015).

Remarks: This is the first finding of *Stiliger vossi* after its original description. The species was placed in the genus *Stiliger* due to its general morphology, but some morphological characters are similar to other species from other genera and family in Sacoglossa (MARCUS & MARCUS, 1960). The radula of *S. vossi* is quite different in shape and presence of serrate cutting edge from species at the same genus, but similar to *Hermaea* (MARCUS & MARCUS, 1960).

Preliminary barcoding and phylogeny with other cerata-bearing genera have place *S. vossi* with species previously named in *Hermaea* (KRUG, *pers. com.*). However, a more complete revision must be done soon with the genera in Limapontiidae.

Figure 36. Live specimen of *Stiliger vossi*.

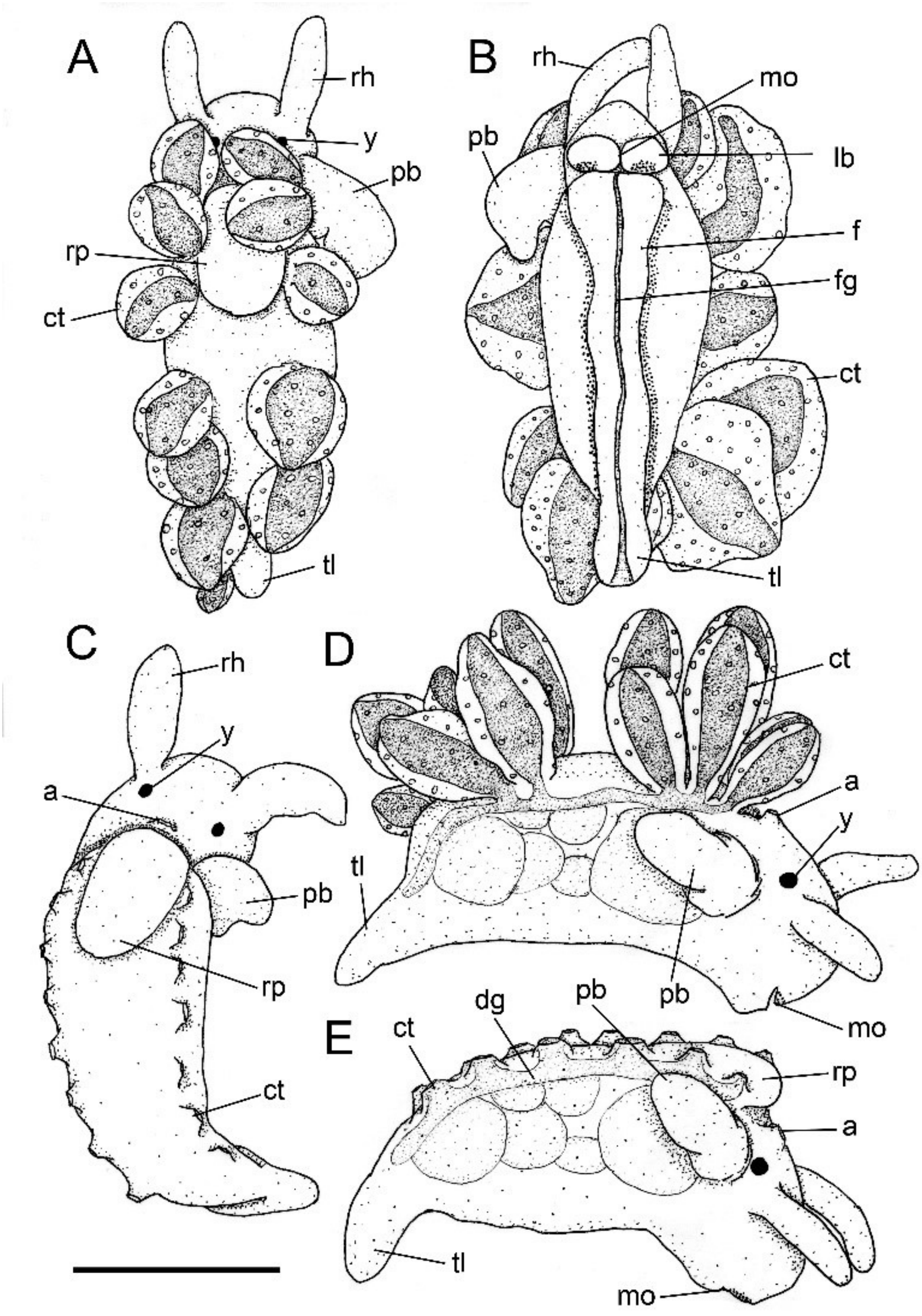

Figure 37. External morphology of *Stiliger vossi*. A) dorsal view with cerata; B) ventral; C) dorsal view with no cerata; D) lateral view with cerata; E) lateral view with no cerata.

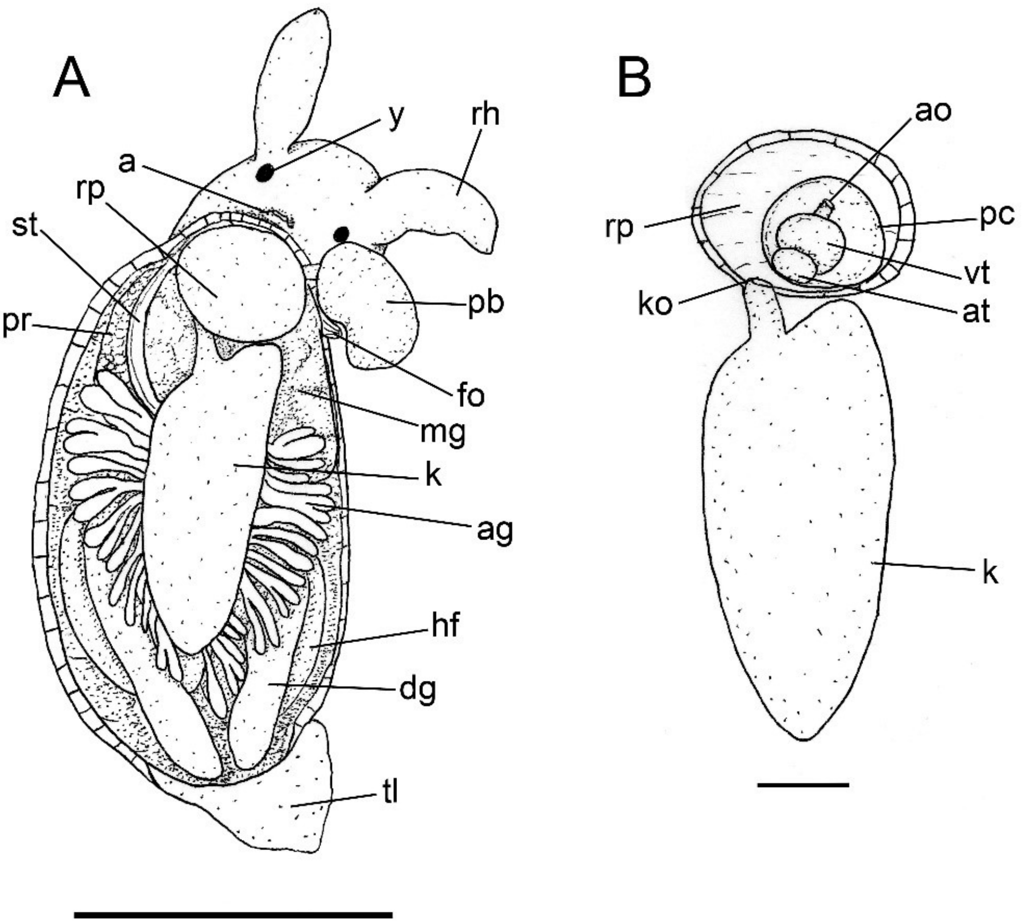

Figure 38. *Stiliger vossi* anatomy, circulatory and excretory systems. A) dorsal view of boy withtou the dorsal mantle; B) ventral view of renopericardial organs. Scales: A = 1 mm; B = 0.2 mm.

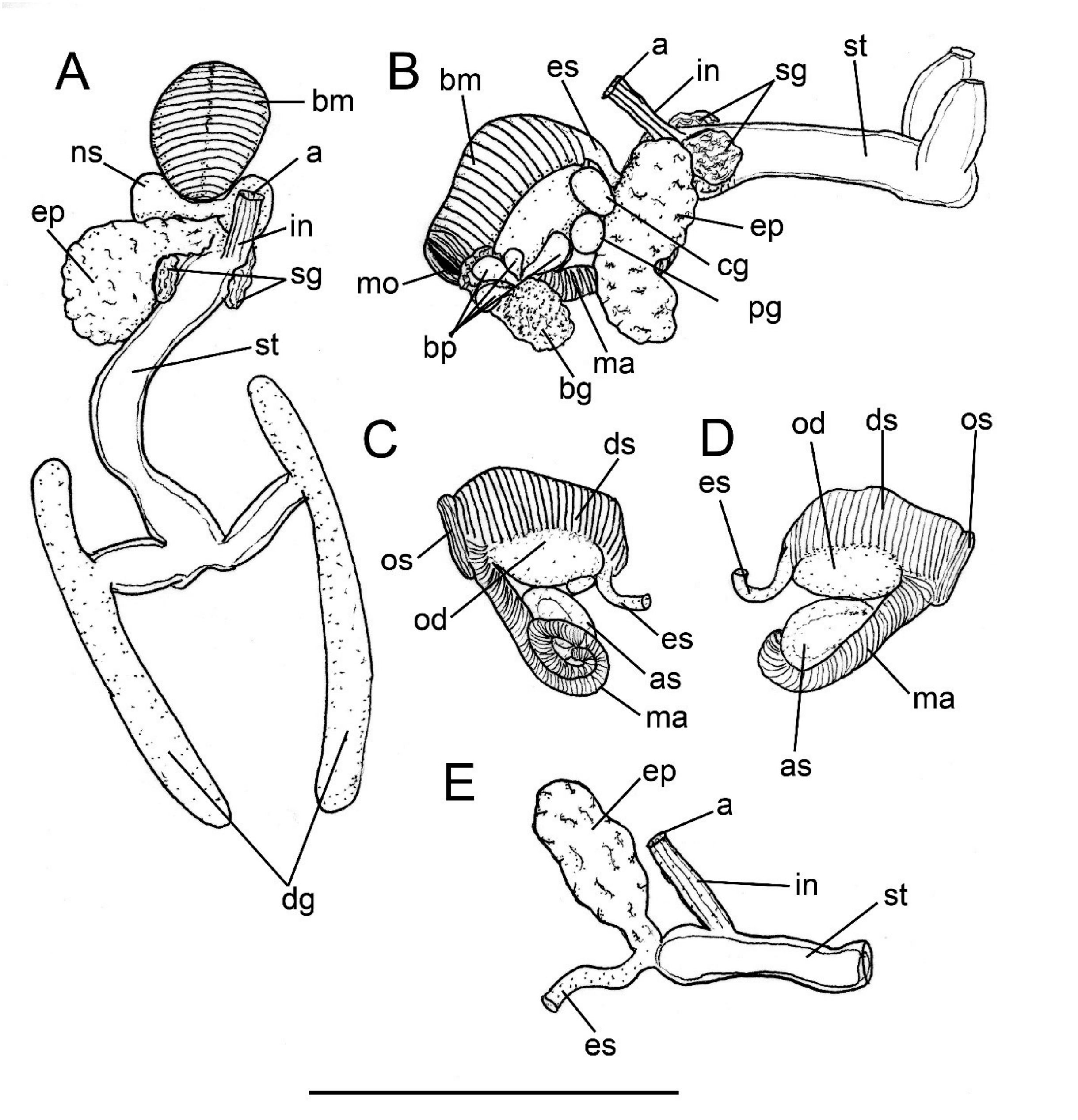

Figure 38. Digestive system of *Stiliger vossi*. A) Dorsal view; B) Lateral view; Buccal mass: C) left side; D) right side. E) Posterior portion of digestive system.

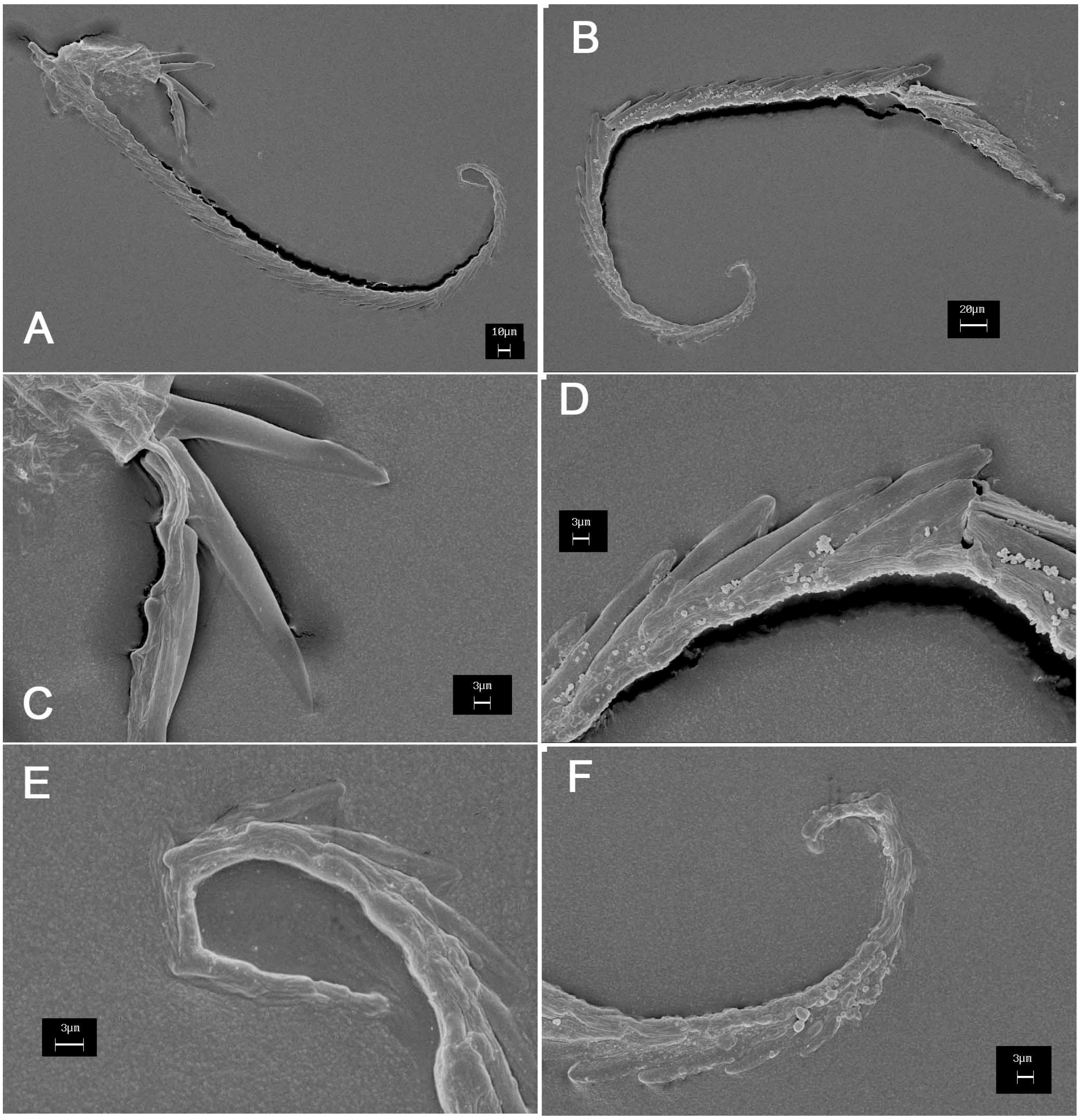

Figure 39. Scan electron microscope images of radula of *Stiliger vossi* (scale: 10 µm): A-B) general view; C-D) detail of the leading tooth; E-F detail of ascus.

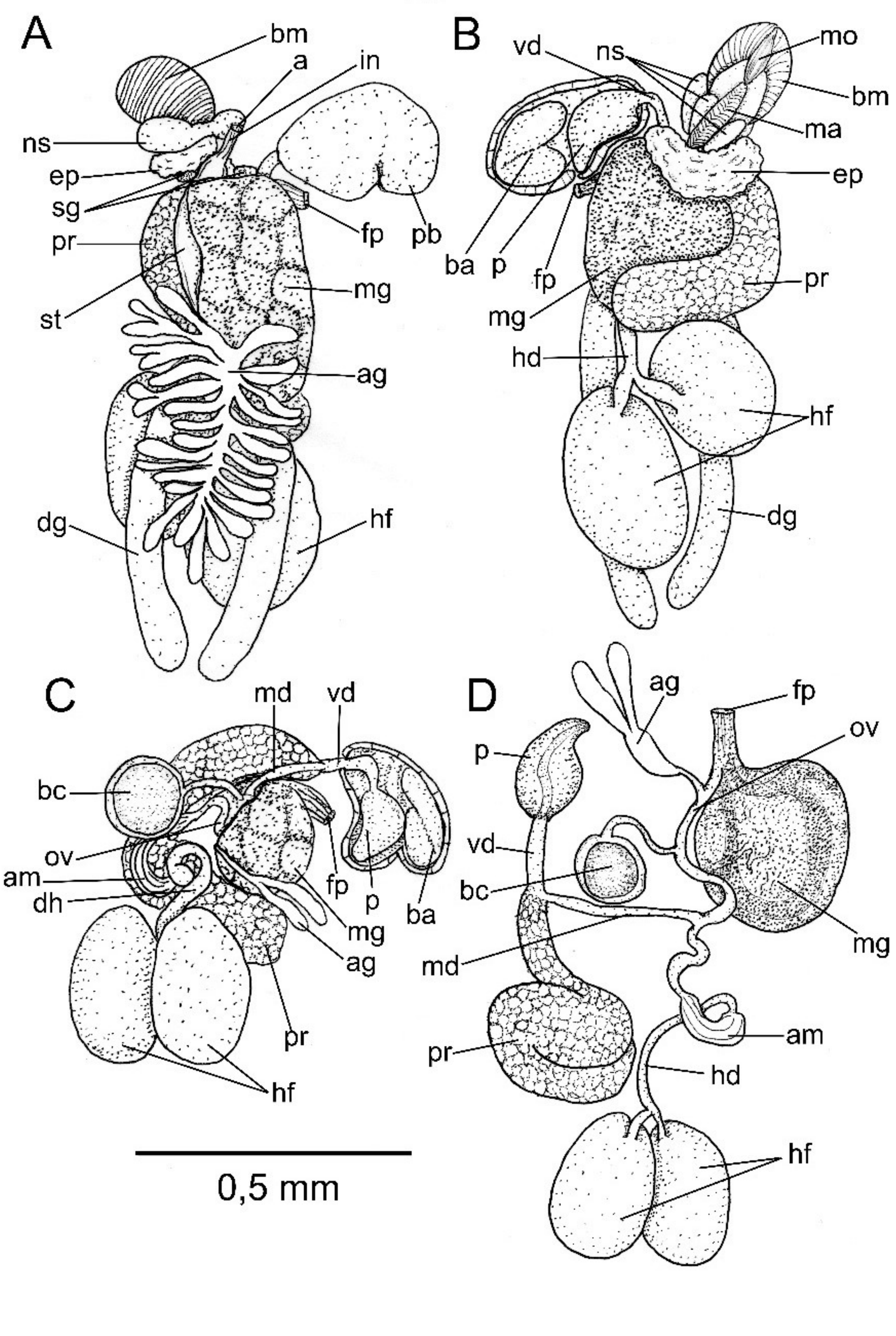

Figure 40. Visceral mass and reproductive system of *Stiliger vossi*. A) Dorsal view of visceral mass; B) Ventral view of visceral mass; C) Overview of reproductive system; D) schematic drawing of reproductive system.

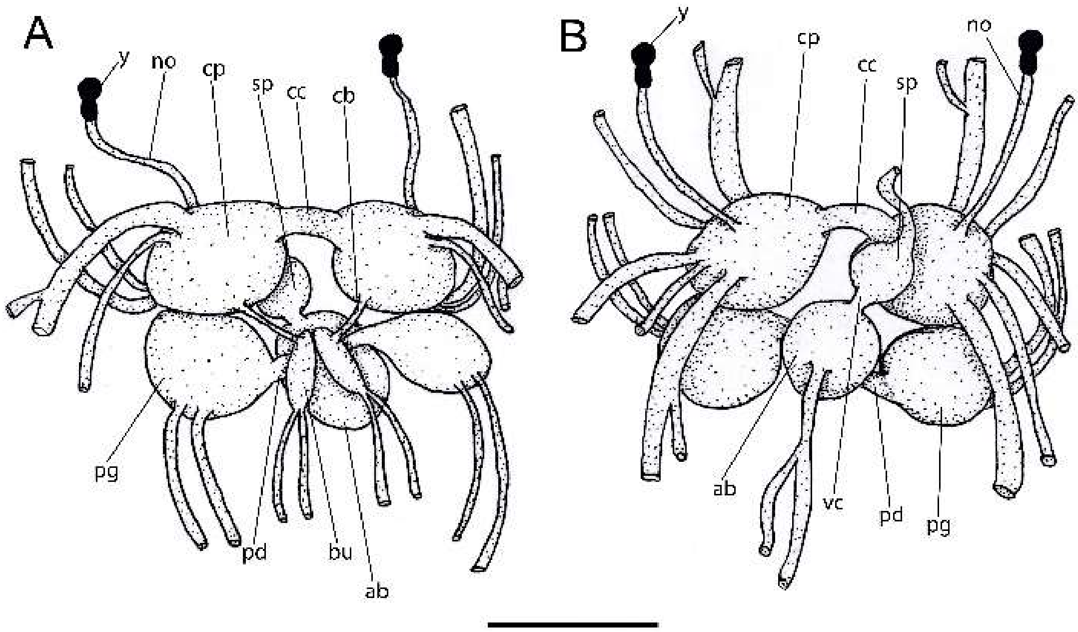

Figure 41. *Stiliger vossi* anatomy, central nervous system: A) anterior view; B) posterior view. Scale = 0.2 mm.

Superfamily **Plakobranchoidea Gray, 1847**

Family **Bosellidae Marcus, 1982**

Genus *Bosellia* Trinchese, 1891

Type species: *Bosellia mimetica* Trinchese, 1891 type by monotypy.

Bosellia mimetica **Trinchese, 1891**

(Figs. 42-47)

Bosellia mimetica Trinchese, 1891: 119, figs. 1-12; Pruvot-Fol, 1954: 179, fig. 70a-d; Ballesteros, 1979: 13, fig. 1; Clark, 1984: 91, fig. 25; Thompson & Jaklin, 1988: 67, fig. 6; Valdés *et al*., 2006: 56;

Bosellia mimetica curasoae Er. Marcus & Ev. Marcus, 1970: 50, figs. 91-98.; Marcus, 1973: 813, fig. 2.

Description

External morphology (fig. 42-43): Body rounded when animal is relaxed, but it can be posteriorly tapered after starts crawling. Body smooth Reaching up to 15 mm in live animals. Head evident, short, length ~1/6 of total body length, 2x longer than wider. Rhinophores (rh) short, length as half as head length, rolled, smooth, and with tip blunt. Eyes (ey) located dorsolaterally behind rhinophores. Foot (fo) broad and muscular. Parapodial sole ~4x larger than propodium (po) in live animals; anterior part of propodium rounded; mesopodial groove (fl) evident. Renopericardial cavity prominent, but only pericardium (pc) form hump. Pericardium small, size slightly smaller than head, muscular, globose. Dorsal vessels (dv) organized in 3 pairs disposed radially on dorsum, arrangement symmetric. All vessels branch few times, near to body margins. Parapodia absent. Female opening (fp) located on extreme dorsal point of lateral groove (lg). Male opening (mp) below right rhinophore. Anus (a) positioned dorsolaterally on posterior right side of head, close to lateral groove, above female pore.

Coloration (Fig. 42): background color live green. Dorsal surface of body darker than foot. Multiples white small dots spread through animal body, concentrated on body margin and rhinhophores. Foot olive green. Some species might be extremely covered with white dots.

Circulatory and excretory system (Fig. 47C): Pericardium (pc) evident, globose, occupying 1/4 of renopericardial cavity; auricle (au) size ~6x smaller than ventricle (vt) size, auricle wall smooth. Ventricle size large, occupying almost all pericardium, pear-shaped. Kidney slightly branched in few thick renal ridges (rr). Renal opening (rp) on topo of elongated duct near to most anterior part of pericardium.

Digestive system (Fig. 44-45): Buccal mass (bm) remarkable, very large, rounded. Dorsal septate muscle (sm) composed of 14 large bundles. Oral sphincter (os) elongated, length ~4x smaller than dorsal septate muscle length. Ascus musculature (ma) wide and short, occupying almost all width and half-length of ventral side of buccal mass; ascus internal in buccal mass. Odontophore region rounded. Radula with 16 teeth in ascending limb. Leading tooth triangular shaped, very short, total length as longer as base length. Central cusp serrated only on half near to tip. Ascus containing old teeth organized in spiral, last ones rod-like shape. Salivary glands (sg) very elongated, positioned ventrally and laterally on all esophagus extension. Esophagus length twice as longer as buccal mass length, width not variable. Esophageal pouch (ep) elongated and coiled on top positioned on anterior part of esophagus. Stomach (st) flatten, wide, width ~4x wider than intestine (in), not internally folded. Digestive gland (dg) paired in each side of stomach; anterior ducts shorter than posterior ducts, runs laterally and anteriorly inside head; posterior duct runs towards parapodial region. Intestine (in), length bit shorter than esophagus length, width twice as wider as esophagus, internally folded through all its extension, finishes in dorsolateral anus (a) positioned near to lateral groove.

Reproductive system (Fig. 46-47A-B): Gonad composed of few hermaphrodite follicles (hf) forming continuous area on central region of body. Follicles size few variable, size bit bigger than genital receptacle (gr). Hermaphrodite ducts (hd) connect all follicles and and expands forming one thick tubular ampulla (am). Hermaphrodite ampulla positioned on left side of mucus gland (mg), occupies almost all hermaphrodite duct. Bursa copulatrix (bc) absent. Male duct (md) connects prostate gland (pr) and vas deferens (vd) to hermaphrodite duct before albumen gland (ag) connection. Prostate gland slightly branched in few lobes over most central follicles, composed of one main glandular duct. Penis (p) size as half as mucus gland size, shape conic and short, total length as longer as base length. Penial stylet straight, short, length ~4x smaller than penis length. Vas deferens ~4x longer than penis length, slightly undulated near to penis. Oviduct (ov) starts from hermaphrodite duct after connection with male duct and forms 3 well delimited chambers completely evolved by mucus gland and finishes on female lateral (fp) in lateral groove. First chamber of mucus gland smaller one, rounded, albumen gland and male duct connect to oviduct in this area; middle chamber of mucus gland bigger one, formed by a curved expansion of glandular oviduct; distal chamber elongated. Genital receptacle connected to oviduct on posterior position, near to hermaphrodite duct. Albumen gland (ag) composed of many dorsal thin branches ventrally to follicles.

Nervous system (Fig. 47D-E): Cerebro-pleural ganglia (cp) size as larger as pedal ganglia (pd); each one has 7 innervations; commissure cerebro-pleural not evident. Optic nerve length short, bit longer than half of cerebro-pleural ganglion length. Buccal ganglia (bu) remarkable, size larger than sub-intestinal ganglion (sb), with accessory ganglion ~3x smaller than buccal ganglion; each buccal ganglion has 3 innervations. Buccal commissure simple, short, bit smaller than buccal ganglion length. Pedal ganglia present 4 innervations by ganglion. Pedal commissure reduced. Visceral loop very short. Abdominal ganglion (ab) size ~3x smaller than pedal ganglion size, has 1 innervation. Sub-intestinal ganglion size ~5x as small as supra-intestinal ganglion (sp), has 1 innervation. Supra-intestinal ganglion size as large as abdominal ganglion and has 1 innervation. Connective tissue among visceral ganglia reduced.

Distribution: Amphi-Atlantic. Mediterranea Sea and West Atlantic Ocean from Florida to Brazil.

Material examined: BRAZIL, Atol das Rocas, Rio Grande do Norte, CMPHRM 4237B, 4 specimens (H. Galvão Filho; C. Meirelles, 26/viii/2014). CMPHRM 4259B, 2 specimens (H. Galvão Filho; C. Meirelles, 06/ix/2014); Ubatuba, São Paulo, 23º56' S, 45º28' W, MZSP 41942, 1 specimen (10/vi/2001).

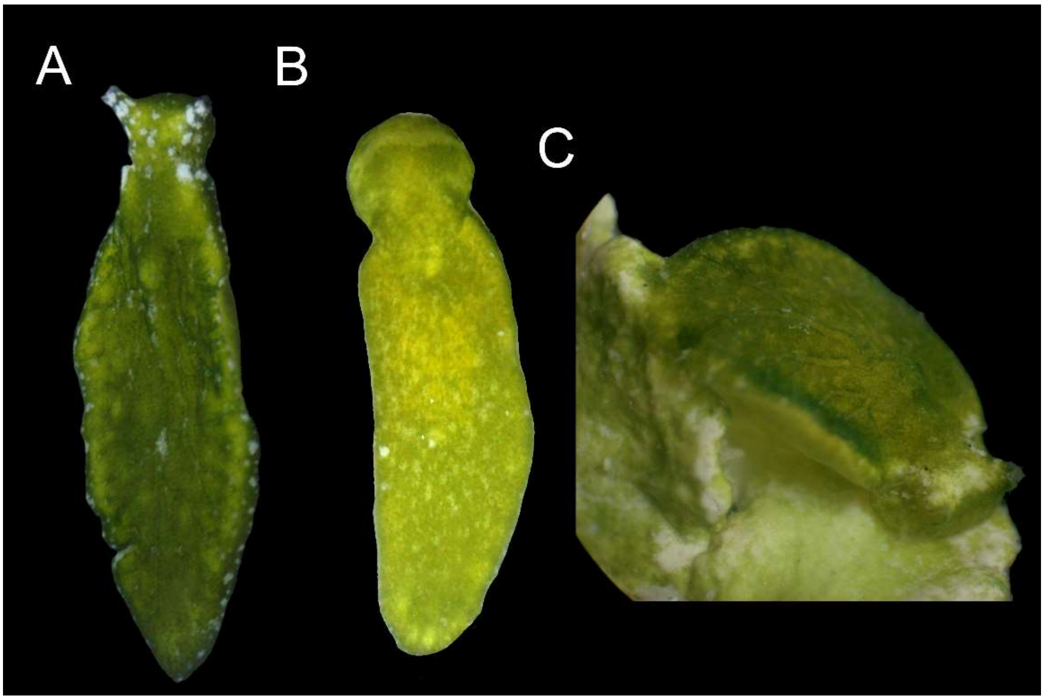

Figure 42. Live specimen of *Bosellia mimetica*. A, B = 7 mm length; C = 5 mm length.

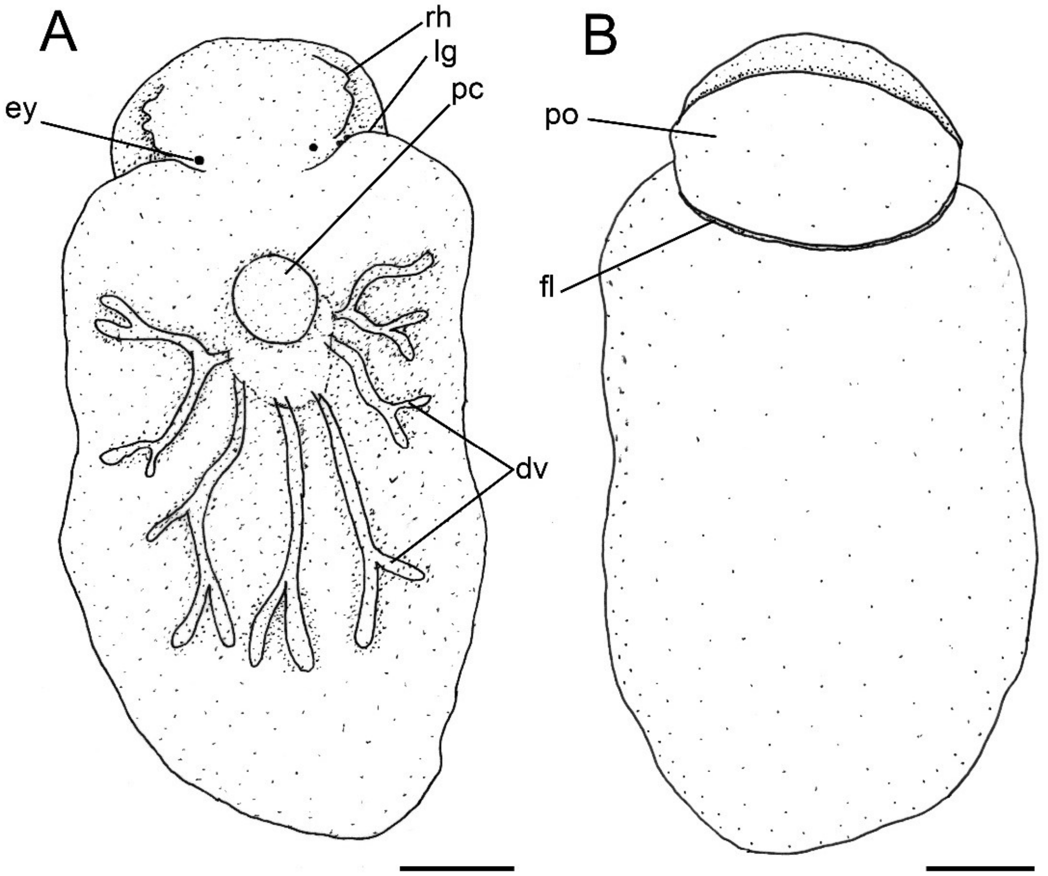

Figure 43. External morphology of *Bosellia mimetica*. A) dorsal view; B) ventral view. Scales: 0.5 mm

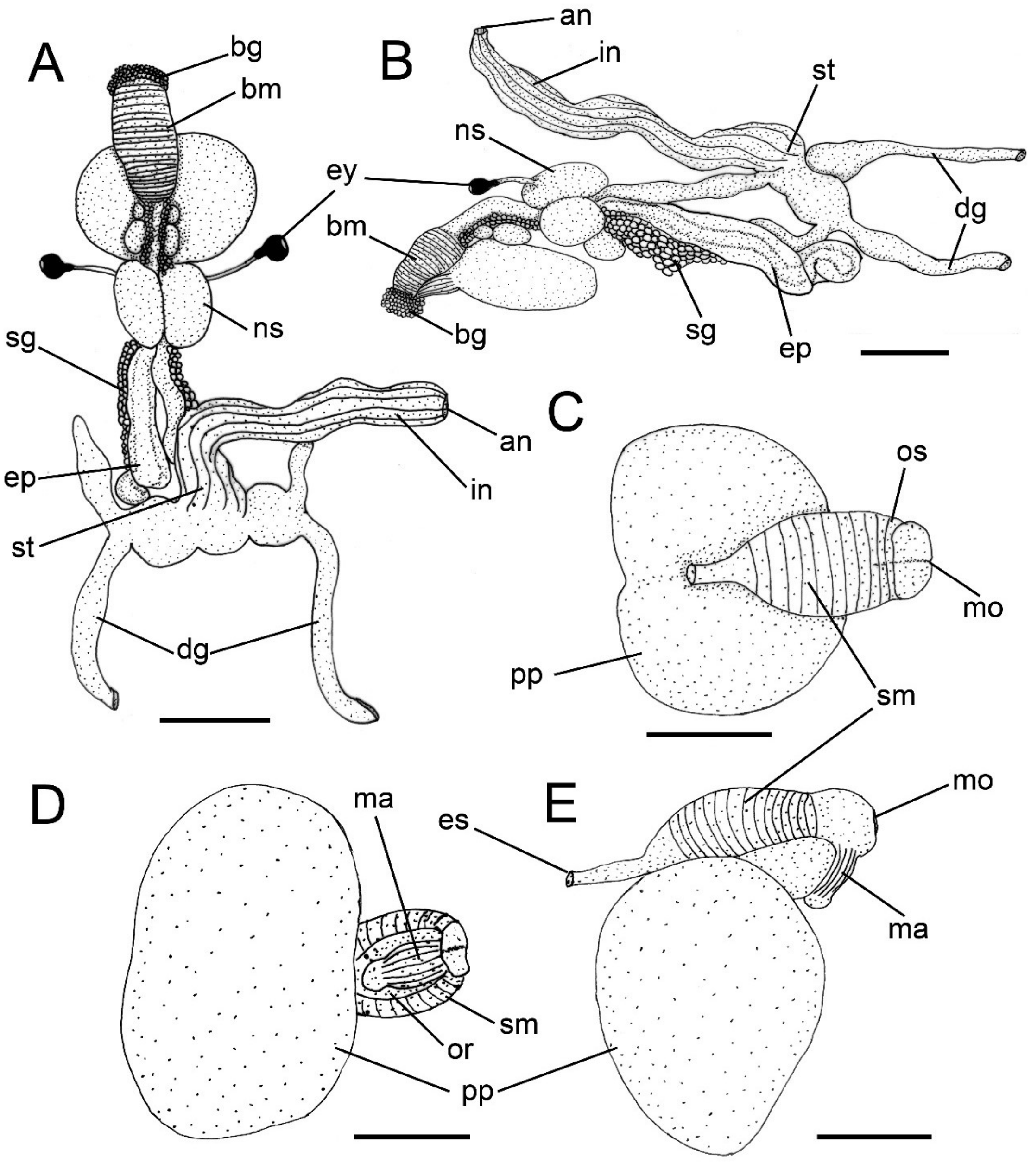

Figure 44. Digestive system of *Bosellia mimetica*. A) Dorsal view; B) Lateral view; Buccal mass: C) dorsal view side; D) ventral side. E) lateral right view.

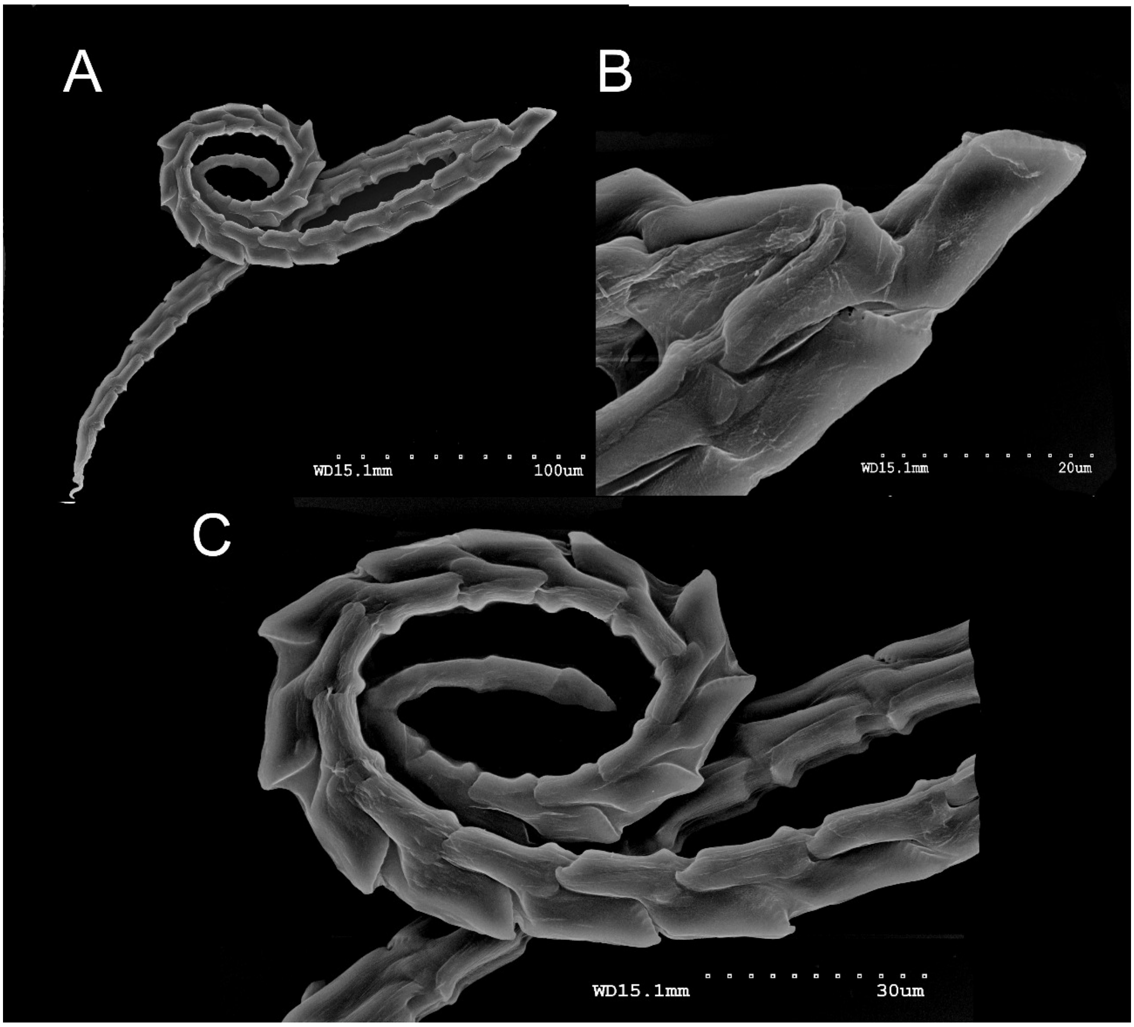

Figure 45. Scan electron microscope images of radula of *Bosellia mimetica* : A) general view; B) detail of the leading tooth; C) detail of ascus.

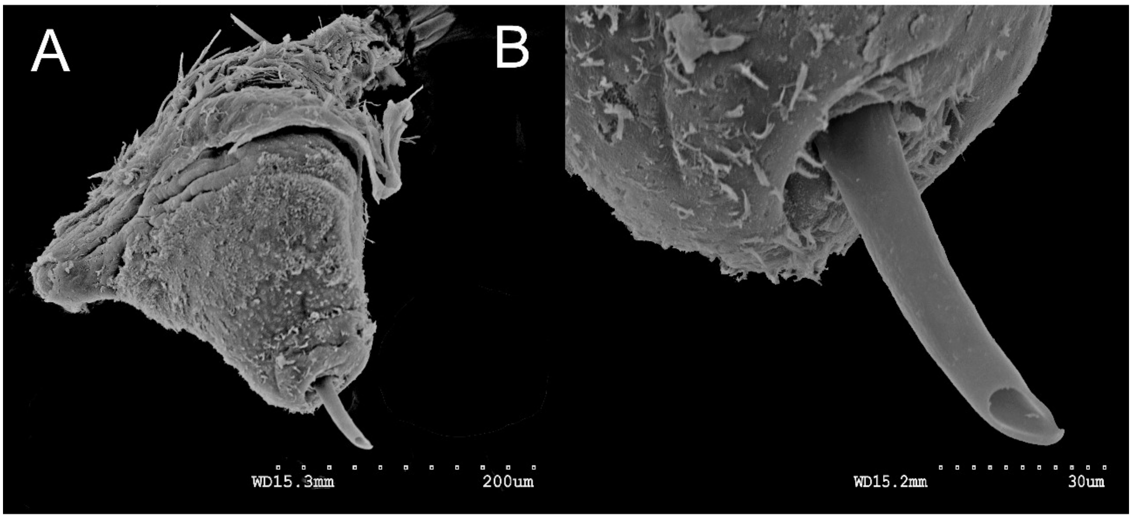

Figure 46. Scan electron microscope images of penis of *Bosellia mimetica*: A) general view; B) detail of the stylet.

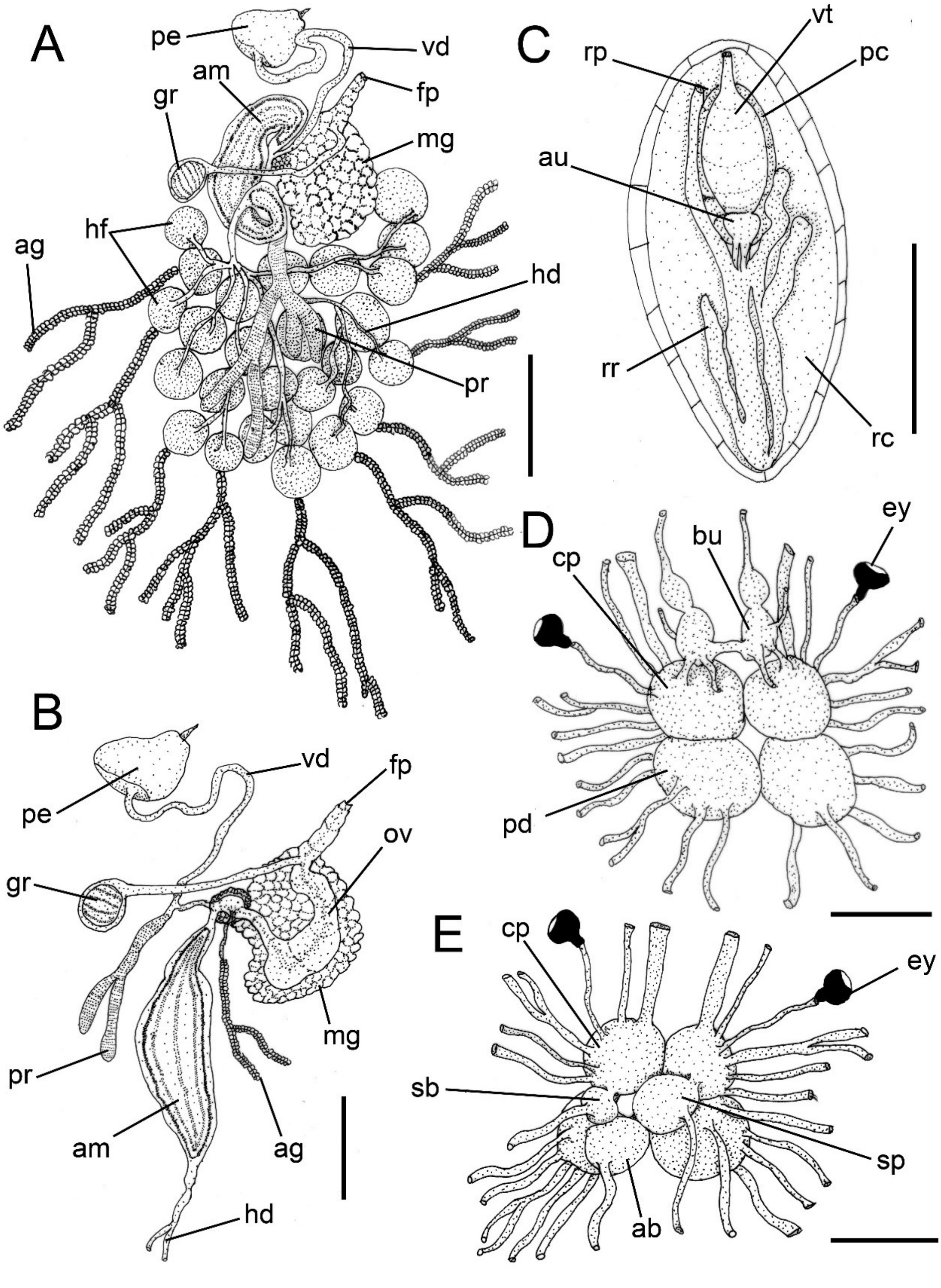

Figure 47. Anatomy of *Bosellia mimetica*. A) whole reproductive system, dorsal view; B) schematic reproductive system; C) renopericardial cavity, ventral view; D) nervous system, aneterior view; E) nervous system, posterior view. Scales A-C= 0.5 mm; D-E = 0.25 mm.

Family Plakobranchidae Gray, 1840

Genus *Plakobranchus* van Hasselt, 1824

Type species: *Plakobranchus ocellatus*, van Hasselt, 1824, by monotypy.

***Plakobranchus ocellatus* van Hasselt, 1824**

(Figs. 48-54)

See Meyers-Muñoz *et al*. (2016)

External morphology and Coloration (Fig. 48-49): Body elongated, reaching up to 45 mm in live animals. Body surface smooth with no papillae. Head flatten, anteriorly cordiform, length ~1/5 of total body length, ~2x wider than longer. Rhinophores (rh) laterally inserted on head corners, rolled, smooth, long, length as longer as head length, tip bit tapered. Eyes (ey) located middle dorsally on a retractile cephalic protuberance. Foot (f) with parapodial sole (pa) ~4x larger than metapodium (ms). Mouth slightly bilobed and with one long transversal black line on upper lip. Anterior part of propodium rounded, with tapered corners forming small pedal tentacles. Posterior end of parapodial sole truncated. Tail absent. Pericardium(pc) fused with kidney prominence forming pericardial hump globose, slightly elongated, short, length ~6x smaller than parapodia length. 12 dorsal vessels (dv) running radially from kidney to posterior end of body or parapodial margins, located on top of digestive gland projections forming lamellae (dl). Lamellae tall, numerous, multiple branching in bifurcations, but some can anastomose, and covering almost all inner surface of parapodia except for extreme posterior part of body. Dark green digestive gland branches inside lamellae but can get light green or yellow in starving animals. Parapodia (pp) wide, covering all body when folded up, with irregular edge and no papillae. Parapodia do not form a parapodial siphon, and stay almost completely folded up on midline, except for anterior slightly opening on pericardial area to water flows inward internal parapodial surface. Yellow glands on parapodial margins where parapodium touch each other. Female aperture (fp) located on extreme dorsal level of lateral groove (lg). Male aperture (mp) below right rhinophore. Anus (an) positioned laterodorsally on posterior part of head near to pericardium.

Excretory and circulatory systems (Fig. 54): Pericardium (pc) large, occupying 1/3 of renopericardial cavity. Auricle (au) thin walled, folded, voluminous, size bit smaller than ventricle (vt). Ventricle size large, occupying almost half of pericardium, shape piriform. Kidney posterior on renopericardial cavity where dorsal vessels open, composed of many longitudinal tubules arranged on compact mass. Nephrostome (np) tubular running anteriorly from kidney and opening on right side of renopericardium prominence.

Digestive system (Fig. 50-51): Buccal mass (bm) elongated, ~2x longer than wider, positioned right after mouth opening, size ~3x larger as esophageal pouch (ep). Dorsal wall of buccal mass composed of 10 dorsal septate muscle (sm), most anterior and posterior ones thinner than middle ones; occupies half dorsal part of buccal mass. Oral sphincter (os) composed of small circular muscles, size ~5x smaller than dorsal septate muscle length. Radula composed of triangular shaped teeth with long base, length twice as small as tooth length, central cusp reduced, lateral cutting edged with multiple short square projections. Ascending limb with 9 well-formed teeth and 3 others in formation, bit longer than descending limb. Ascus musculature (ma) covering descending limb of radula, running ventrally from oral sphincter to middle part of buccal mass, anteriorly wide and posteriorly tapered, short, finishing before reaching pharyngeal pouch (ph). Ascus (as) internal too buccal mass, positioned under odontophore muscles, occupying 1/3 of the buccal mass. Odontophore region (or) ventral, rounded and occupies half of ventral part pf buccal mass. Pharyngeal pouch (ph) with lumen connected with posterior part of oral tube, size as larger as odontophore region, long, as longer as wider. Jaws absent. Esophagus long, length as longer as buccal mass length. Esophageal pouch (ep) globose and muscular, positioned on middle part of esophagus. Stomach (st) flat and wide, internally presenting multiples thin folds running toward intestine and digestive gland ducts. Stomach can expand its volume and form pouches on posterior region. Digestive gland (dg) with anterior ducts shorter than posterior one, running laterally and anteriorly in head; posterior ducts running toward parapodial area and posterior end of body, branching in many smaller ducts ventrally and among gonadal follicles and running in multiple directions. Intestine (in) running from dorsal portion of stomach and opening in laterodorsal anus on right side near to pericardium, length as longer as esophagus length. Intestinal inner surface with multiple longitudinal folds through all its extension.

Reproductive system (Fig. 52-53): Gonad composed of innumerous spherical hermaphrodite follicles (hf) forming one big group on central part of body, from posterior end of pericardium to almost posterior end of body and expanding laterally at most basal part of parapodia. Hermaphrodite follicles large, size as large as hermaphrodite ampulla (am). Multiple hermaphrodite ducts (hd) connect all hermaphrodite follicles to one main middle-lateral hermaphrodite duct. Hermaphrodite ampulla positioned on left side of mucus gland (mg), large, ~3x smaller than genital receptacle (gr). Paired gametolytic vesicles positioned laterally to posterior part pf mucus gland, right under renoperdicardial cavity; kidney-shaped bag with granulose texture, yellowish color, easily breakable during manipulation and involved by fine membrane; size ~2x bigger than penis size and ~2x smaller than second chamber of mucus gland; connected to each other by one straight main tube, positioned on middle of dorsal part of mucus gland, connected first to hermaphrodite ampulla duct and then to hermaphrodite duct. Prostate gland (pr) and vas deferens (vd) connected to hermaphrodite duct after connection with gametolytic vesicles and ampulla. Prostate gland as highly branched tubular gland on both sides of mucus gland and over most anterior follicles. Vas deferens (vd) length twice as longer as penis length, almost completely straight though all its extension. Penis (pe) shape conic and short, as longer as wider. Penile stylet slightly curved, short, length ~4x smaller than penis length, and centrally inserted on top of penis. Male opening posterior to right rhinophore. Oviduct (ov) starting from hermaphrodite duct after connection with male duct, forming 3 well delimited chambers completely evolved by mucus gland, finishing on female apperture (fp) in lateral groove. Proximal chamber of mucus gland smallest one, bit smaller than hermaphrodite ampulla, where hermaphrodite duct, genital receptacle and albumen duct connect to oviduct. Middle chamber of mucus gland biggest one, where oviduct is arranged as one big spiral involved by mucus gland and forming one big rounded gland, positioned on midline of body. Distal chamber bit elongated, size ~2x smaller than remaining mucus gland, darker glandular part of mucus gland, with one simple flatten lumen, and forming one distal small duct opening on female bye. Albumen gland (ag) shaped and branched as and mixed with prostate gland. Duct of albumen gland not glandular, running posteriorly from oviduct and branching into smaller ducts dorsally to prostate gland duct. Genital receptacle positioned anteriorly on right side of mucus gland, connected to oviduct in proximal position after hermaphrodite and male ducts connections and on proximal chamber of mucus gland, size bit smaller than gametolytic vesicles.

Nervous system (Fig. 54): Nervous ring located anteriorly on esophagus, covering most anterior part of esophagus, just posterior to buccal mass. Cerebral and pleural ganglia fused. Cerebro-pleural ganglia (cp) size as larger as pedal ganglia (pg), each ganglion with 6 nerves. Cerebro-pleural ganglia commissure reduced. Optic nerve very short, with eyes very close to cerebro-pleural ganglia. Each pedal ganglion innervated with 7 highly branched nerves running ventral-posteriorly on body. Pedal commissure elongated, positioned ventrally between pedal ganglia, short, length ~5x smaller than pedal ganglion length. Visceral loop composed of 3 ganglia, positioned very close to nervous ring and ventrally to esophagus; connected among them and to base of cerebro-pleural ganglia by reduced connectives. Abdominal ganglion (ab) size bit smaller than pedal ganglia, with one main innervation. Sub-intestinal ganglion size ~3x smaller than supra-intestinal ganglion (sp), with 1 nerve. Supra-intestinal ganglion bit smaller than abdominal ganglion, with 1 nerve. Buccal ganglia (bu) very small, size ~10x smaller than sub-intestinal ganglion (sb); each ganglion with 1 main innervation; buccal commissure reduced.

Material examined: THAILAND, Puket, MZSP 122699, K. R. Jensen col., [5 specimens], 31/viii/1987.

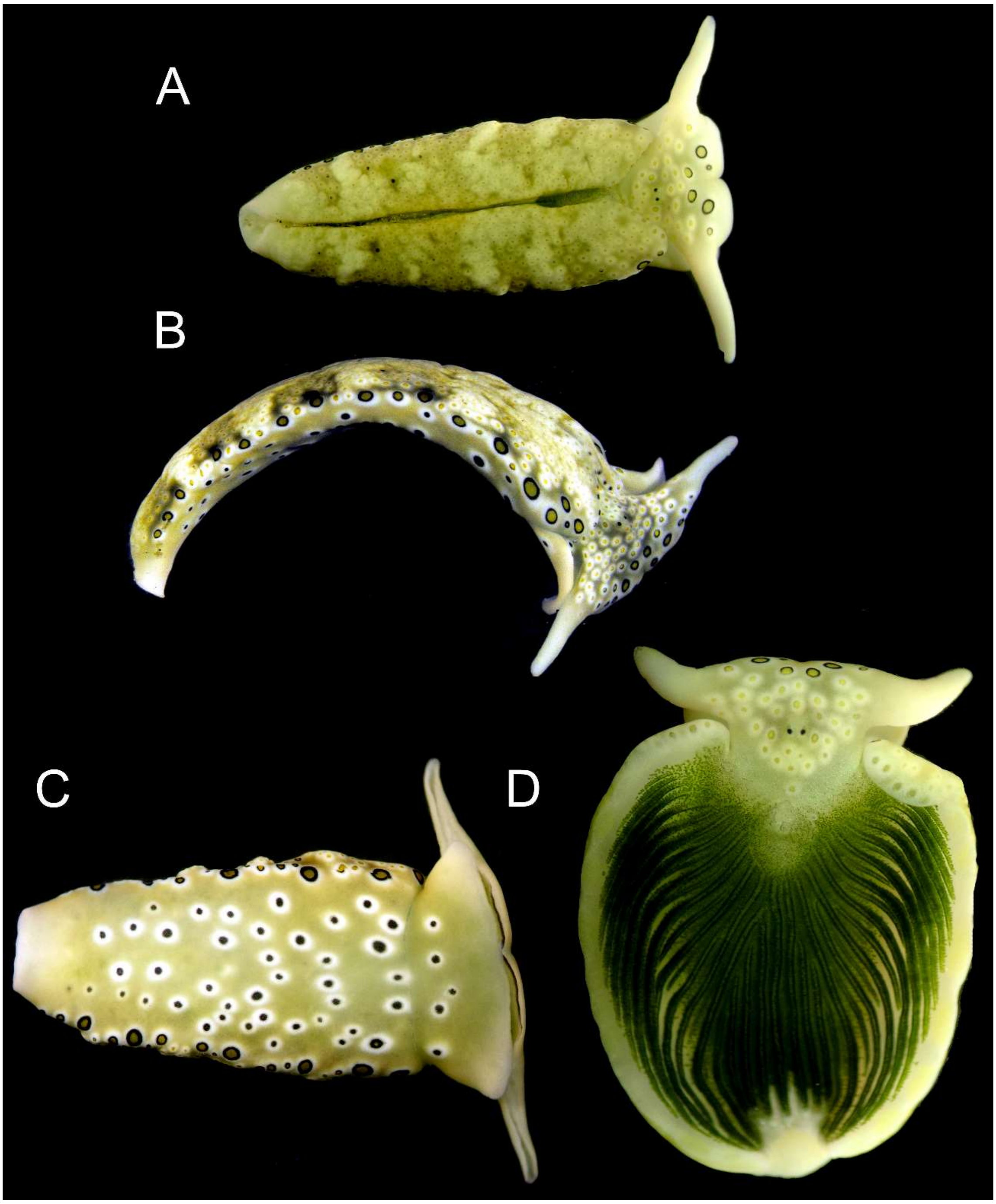

Figure 48. External morphology of *Plakobranchus ocellatus*. A) dorsal view; B) lateral view; C) ventral view; D) dorsal view of parapodia opened.

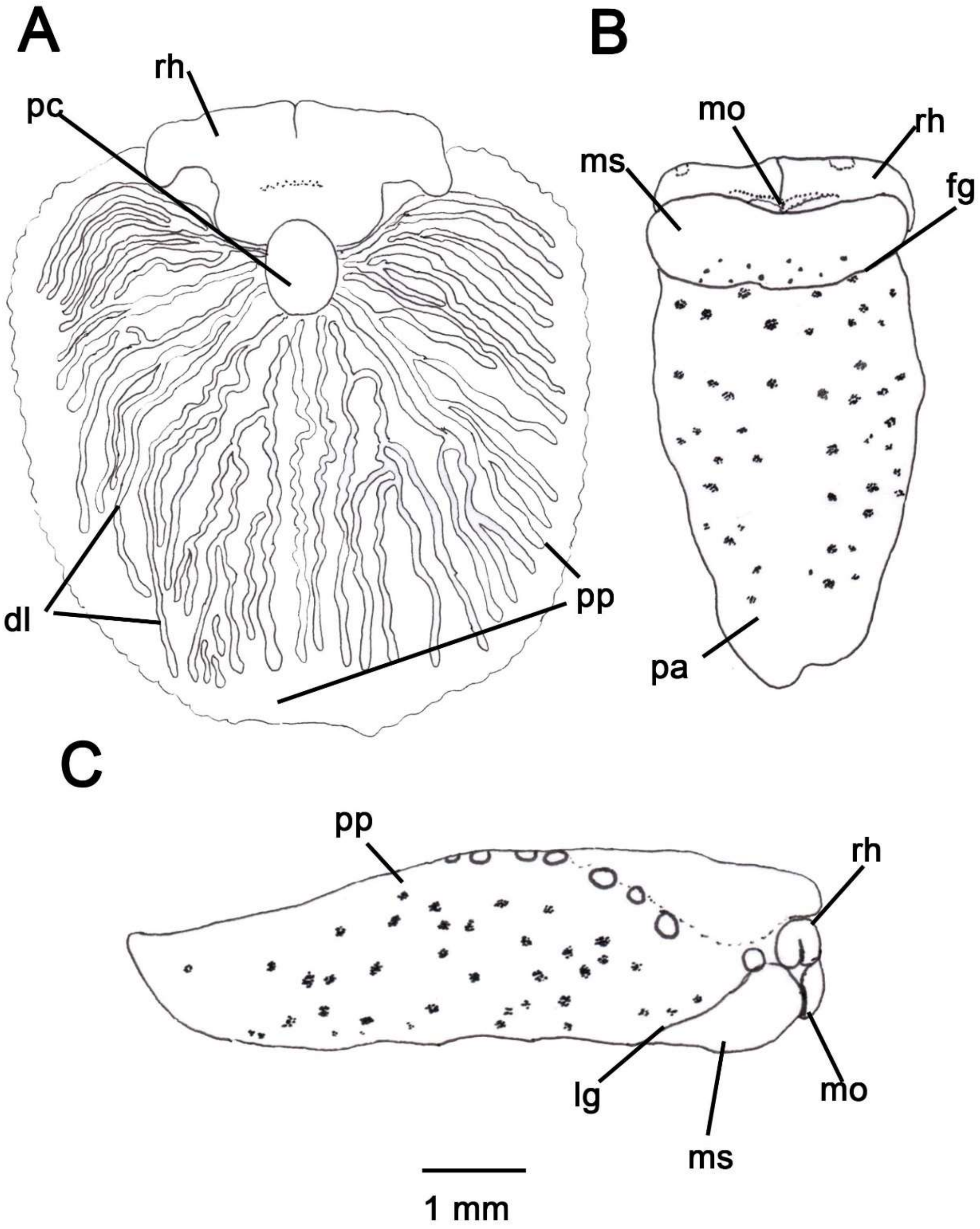

Figure 49. External morphology of *Plakobranchus ocellatus*. A) dorsal view; B) ventral view; C) lateral view.

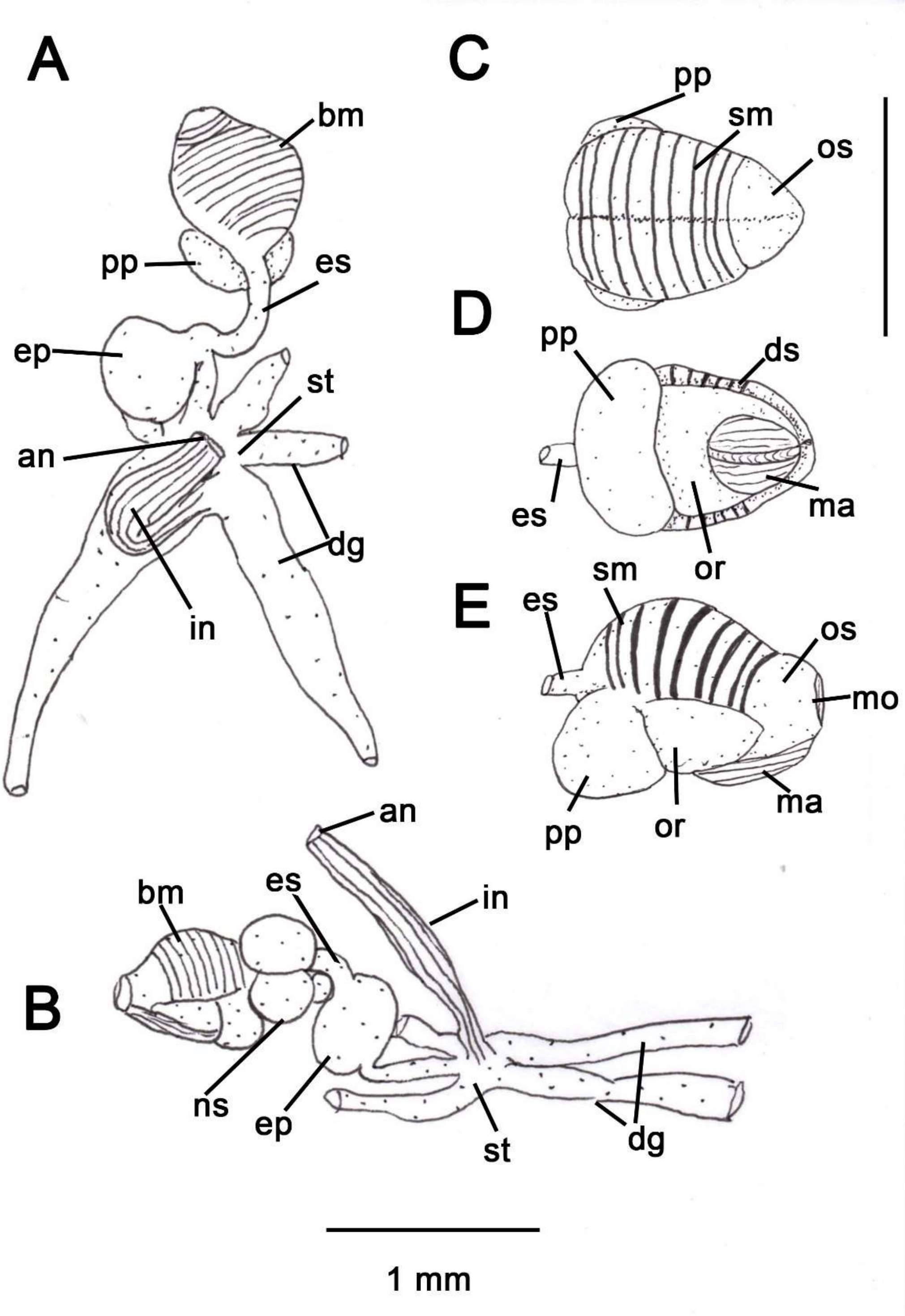

Figure 50. Digestive system of *Plakobranchus ocellatus*. A) Dorsal view; B) lateral view. Buccal mass: C) Dorsal view; D) Ventral view; E) Right side.

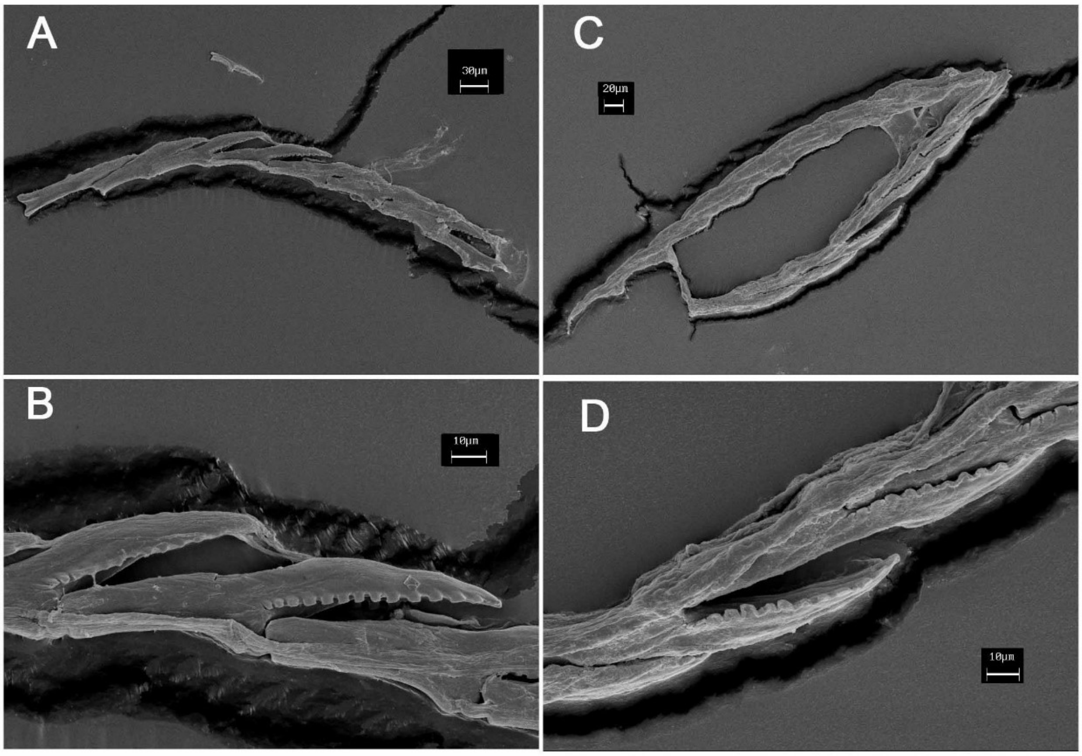

Figure 51. Scan electron microscope images of radula of *Plakobranchus ocellatus.* A) descending limb; B & D) detail of some teeth; C) overview.

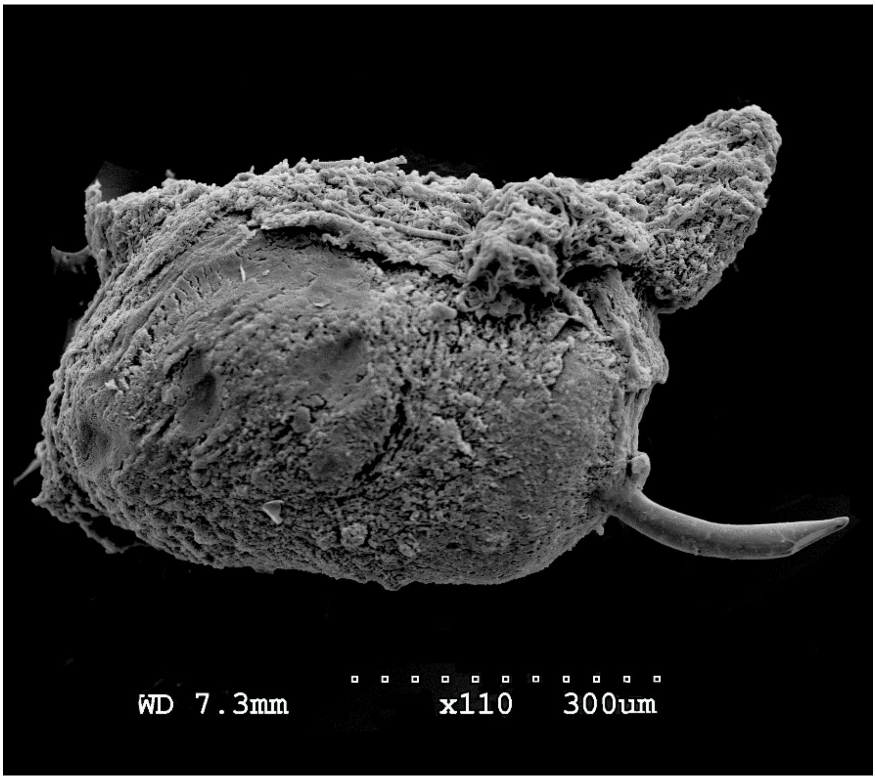

Figure 52. Scan electron microscope image of penis of *Plakobranchus ocellatus.*

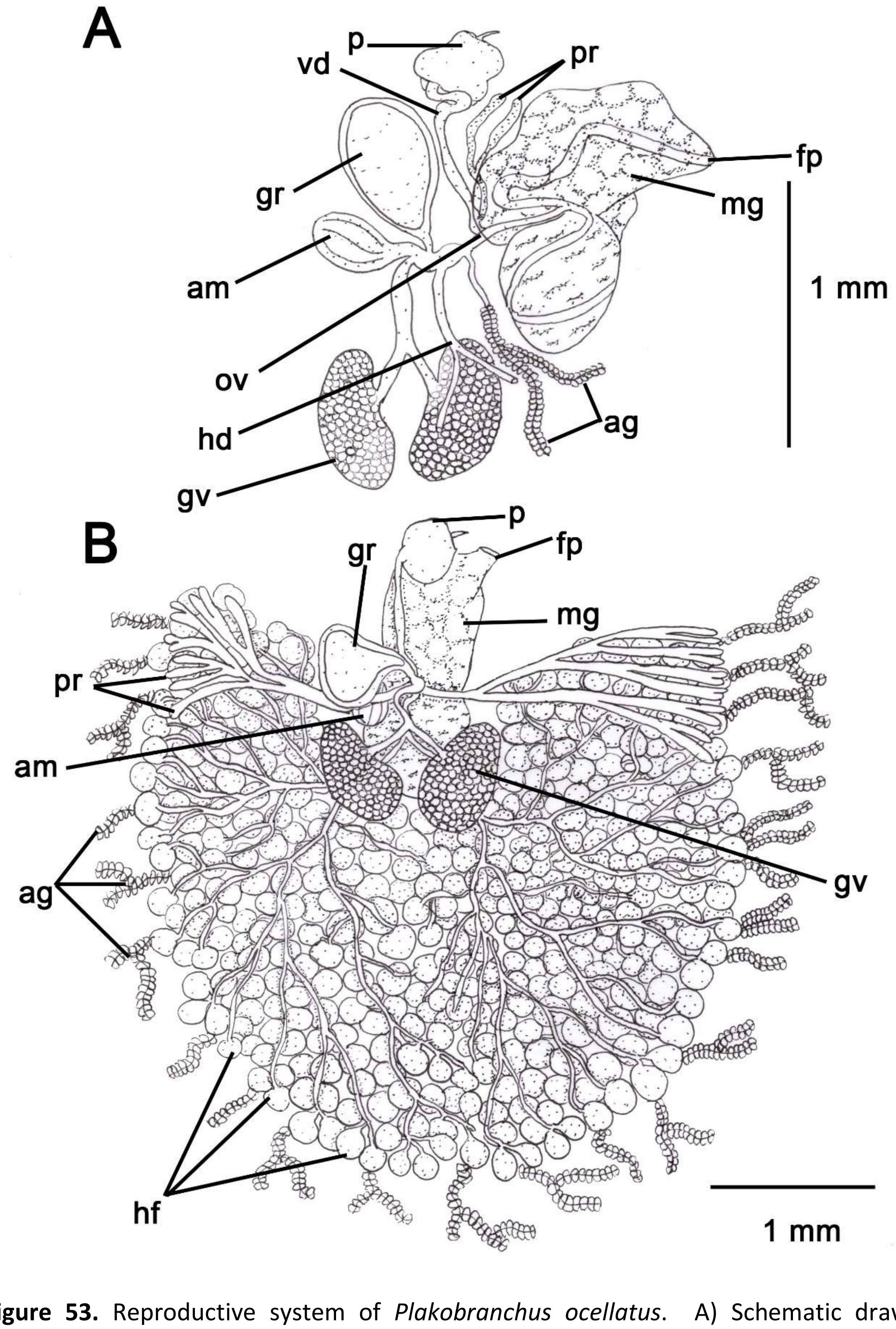

Figure 53. Reproductive system of *Plakobranchus ocellatus*. A) Schematic drawing; B) overview.

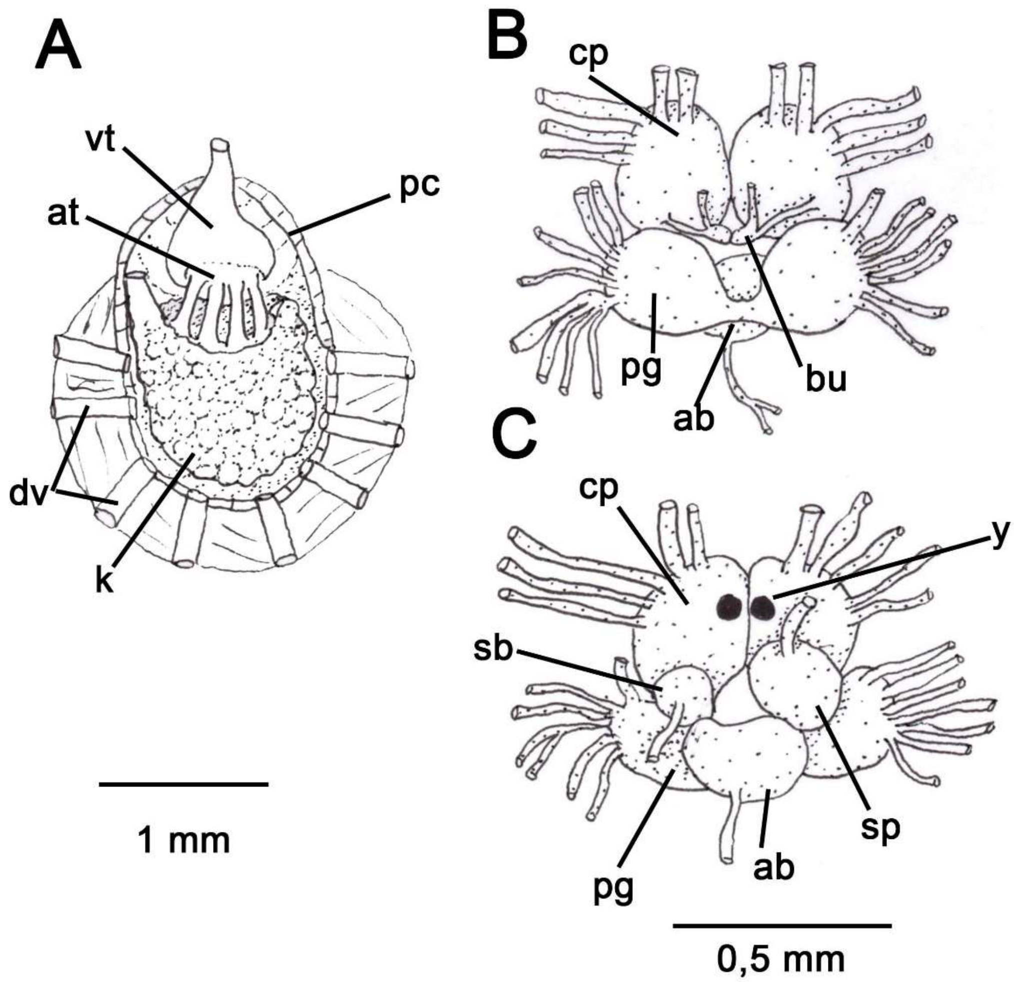

Figure 54. Circulatory and nervous systems of *Plakobranchus ocellatus*; A) Renopericardial cavity. B) anterior view of nervous system. C) posterior view of nervous system.

***Plakobranchus ianthobapsus* (Gould, 1852)**

(**Figs. 55-59**)

Plakobranchus ianthobapsus (Gould, 1852)

Placobranchus ianthobapsus Gould, 1852: 307, pl.26, figs.407a-c (Honolulu, Hawaii); Bergh, 1872: 166; Ostergaard, 1955: 120-122, fig. 8a-f

Placobranchus gracilis Pease, 1871:303, pl.21 fig.1a-b (Tahiti, French Polynesia). Eliot, 1899: 521 (Apia, Samoa)

Placobranchus argus Bergh, 1872: 151–165, pls. IX figs 6–9, XVII, XVIII (Honolulu, Hawaii);

Placobranchus sp.; Ostegaard, 1950: 107-108, fig. 34a-d;

Placobranchus ocellatus Eliot, 1904: 294-295, pl. XVII, fig 13-13a

Plakobranchus ocellatus Meyers-Muñoz *et al*., 2016:79-80, fig. 7b-e.

External morphology and Coloration (Fig. 55): Body elongated, reaching up to 60 mm in live animals. Body surface smooth with no papillae. Head flattened, anteriorly cordiform, length ~1/5 of total body length, ~2x wider than longer. Rhinophores (rh) laterally inserted on head corners, rolled, smooth, long, length as longer as head length, tip bit tapered. Eyes (ey) located middle dorsally on a retractile cephalic protuberance. Foot (f) with metapodium (mt) ~4x larger than propodium (po). Mouth slightly bilobed and with one long transversal black line on upper lip. Anterior part of propodium rounded, with tapered corners forming small pedal tentacles. Posterior end of parapodial sole truncated. Tail absent. Renopericardial prominence (rp) uniform with kidney area very similar to heart region, globose, slightly longitudinally elongated, short, length ~5x smaller than parapodia length. 10 dorsal vessels (dv) running longitudinally from kidney region to posterior end of body or parapodial margins on inner side of parapodia, located on top of digestive gland projections forming lamellae, first anterior pair highly branched before fuse to lamellae. Lamellae tall, numerous, multiple branching in bifurcations, but can distally anastomose sometimes, and covering almost all inner surface of parapodia except for extreme posterior part of body. Dark green digestive gland branches inside lamellae but can get light green or yellow in starving animals. Parapodia (pp) wide, covering all body when folded up, with irregular edge and no papillae. Parapodia do not form a parapodial siphon, and stay almost completely folded up on midline, except for anterior slightly opening on pericardial area to water flows inward internal parapodial surface. Parapodial yellow glands on all area where parapodium touch each other, varying on size, and rod-like or round shaped. Female pore (fp) located on extreme dorsal level of lateral groove (lg). Male pore (mp) below right rhinophore. Anus (an) positioned laterodorsally on posterior part of head near to pericardium.

Overall color pale yellow to dark brown varying among specimens. Some specimens also can present dark brown or pale white regions dorsally on head and body. Ocellated spots varying on size and spread all over the body except for the inner face of parapodia, rhinophores and kidney region on renopericardial prominence, and only few on pericardial region and propodium. Ocellated spots as orange circles surrounded by white ring; few of them with orange circle darker on margin and light yellow, dark brown or bluish on central, and fewer with darker orange margin turning to black forming either incomplete or complete black rings; foot only with orange ocellated spots surrounded by white circle. Some specimens can present few ocellated spots completely black on dorsal surface. Ocellated spots with black ring usually bigger than others, more common close to foot on head and parapodia, less numerous close to parapodial margins and absent on foot, inner surface of parapodia and perdicadium. General foot color lighter than dorsal surface. Violet band present on anterior end of head, rhinophore tips and posterior end of foot, fading to light violet or white on rhinophore tips; violet color turns to black in preserved specimens. Retractile cephalic protuberance colored as same as body background coloration.

Excretory and circulatory system (Fig. 59): Renopericardial area position mid dorsally posteriorly to head. Pericardium (pc) large, occupying 1/3 of renopericardial cavity. Heart of large size occupying 2/3 of pericardium. Auricle (au) thin walled, ventrally flatten, dorsally like loose wrinkled bag, voluminous, size ~3x smaller than ventricle (vt). Ventricle size large, occupying almost all pericardium, shape piriform. Kidney posterior on renopericardial cavity where dorsal vessels open, composed of many longitudinal tubules arranged on compact mass. Multiples crystals were observed in many different specimens from Hawaii. Nephrostome (np) tubular running anteriorly from kidney and opening on right side of renopericardium prominence.

Digestive system (Figs. 56-57): Mouth with elongated upper lip and shorter lower lip; mouth opening centrally positioned. Buccal mass (bm) elongated, ~2x longer than wider, positioned right after mouth opening, size twice as larger as esophageal pouch (ep). Dorsal wall of buccal mass composed of 10 dorsal septate muscle (sm), most anterior and posterior ones thinner than middle ones; occupies half of buccal mass. Oral sphincter (os) composed of small circular muscles, size ~6x smaller than dorsal septate muscle length. Ascus musculature (ma) running ventrally from oral sphincter to middle part of buccal mass, anteriorly wide and posteriorly tapered, short, finishing before reaching pharyngeal pouch (ph). Ascus (as) internal too buccal mass, positioned under odontophore muscles, occupying 1\4 of the buccal mass. Odontophore region (or) ventral, rounded and occupies half of buccal mass. Pharyngeal pouch (ph) present a lumen connected with posterior part of oral tube, size as larger as odontophore region, long, as longer as wider. Jaws absent. One pair of salivary glands (sg) as elongated thing layer positioned lateroventrally along all esophagus length, more concentrated on posterior end of esophagus, open on posterior end of buccal mass dorsally to esophagus. Esophagus long, length ~2x longer than buccal mass length, width similar to intestine width. Esophageal inner surface with 2 longitudinal low folds running from buccal mass to stomach. Esophageal pouch (ep) globose and muscular, positioned on posterior part of esophagus, size ~3x smaller than buccal mass; inner surface with many thin folds, which can be either complete from base to top or incomplete. Stomach (st) flat and wide, internally presenting multiples thin folds running toward intestine and digestive gland ducts. Stomach can expand its volume and form pouches on posterior region. Digestive gland (dg) with anterior ducts shorter than posterior one, running laterally and anteriorly in head; posterior ducts running toward parapodial area and posterior end of body, branching in many smaller ducts ventrally and among gonadal follicles and running in multiple directions. Intestine (in) running from dorsal portion of stomach and opening in laterodorsal anus on right side near to pericardium, length as longer as esophagus length. Intestinal inner surface with multiple longitudinal folds through all its extension.

Reproductive system (Fig. 58-59): Gonad composed of innumerous rounded hermaphrodite follicles (hf) forming one big group on central part of body, from posterior end of pericardium to almost posterior end of body and expanding laterally to proximal part of parapodia.

Hermaphrodite follicles size really small, as large as hermaphrodite ampulla (am), weakly variable in all specimens analyzed. Multiple hermaphrodite ducts (hd) connect all hermaphrodite follicles to one main middle-lateral hermaphrodite duct. Hermaphrodite ampulla positioned on left side of mucus gland (mg), really small, size ~12x smaller than genital receptacle (gr). Paired gametolytic vesicles positioned lateroposterior on mucus gland, right under renoperdicardial cavity; kidney-shaped bag with granulose texture, yellowish color, easily breakable during manipulation and involved by fine membrane; size large as penis size, and 5x smaller than second chamber of mucus gland; connected to each other by one dorsal-lateral highly undulating main tube, positioned on left side of mucus gland, connects first to hermaphrodite ampulla duct and then to hermaphrodite duct. One specimen presented one of its gametolytic vesicles with doubled small duct connected to main one. Male duct (md) connects prostate gland (pr) and vas deferens (vd) to hermaphrodite duct after its connection with gametolytic vesicles and ampulla. Prostate gland composed of multiple acinous-shaped glands, located on both sides of mucus gland, on region anterior to follicles and under gametolytic vesicles and few anterior follicles; all braches connected to one dorsal transversal glandular duct on each side of mucus gland and fused to each other on one main duct over mucus gland. Vas deferens (vd) length bit longer than penis length, almost completely straight though all its extension. Penis (pe) shape bit conic and elongated, twice longer than large, size ~2x smaller than distal chamber of mucus gland, positioned dorsally to distal` chamber of mucus gland, involved by a penile sheath. Penile stylet curved, short, length ~5x smaller than penis length, and centrally inserted on top of penis. Male opening lateroposterior to right rhinophore. Oviduct (ov) starting from hermaphrodite duct after connection with male duct, forming 3 well delimited chambers completely evolved by mucus gland, finishing on female pore (fp) in lateral groove. Proximal chamber of mucus gland smallest one, size twice bigger than hermaphrodite ampulla, where hermaphrodite duct, genital receptacle and albumen duct connect to oviduct. Middle chamber of mucus gland biggest one, where oviduct is arranged as one big spiral involved by mucus gland and forming one big rounded gland, positioned on midline of body. Distal chamber bit elongated, size ~2x smaller than remaining mucus gland, darker glandular part of mucus gland, with one simple flatten lumen, and forming one distal small duct opening on female pore. Albumen gland (ag) shaped and branched similar to prostate gland, but thinner, positioned mixed with prostate gland, but only anteriorly to follicles. Duct of albumen gland not glandular, running posteriorly from oviduct and branching into smaller ducts dorsally to prostate gland duct. Genital receptacle positioned anteriorly on right side of mucus gland, connected to oviduct in proximal position after hermaphrodite and male ducts connections and on proximal chamber of mucus gland, size ~3x smaller than gametolytic vesicles.

Nervous system (Fig. 59): Nervous ring located anteriorly on esophagus, covering 1/3 of esophagus, and just posteriorly to buccal mass. Cerebral and pleural ganglia fused. Cerebro-pleural ganglia (cp) size as larger as pedal ganglia (pg). About 10 nerves innervating from each cerebro-pleural ganglion to buccal mass, rhinophores and eye. Cerebro-pleural ganglia commissure internal. Optic nerve long, length as twice as longer as cerebro-pleural ganglion length. Each pedal ganglion innervated with 6 highly branched nerves running ventral-posteriorly on body. Pedal commissure external, positioned centrally between pedal ganglia, very short, length ~5x smaller than pedal ganglion length. Visceral ganglia composed of 3 ganglia, positioned very close to nervous ring and ventrally to esophagus; connected among them and to base of cerebro-pleural ganglia by reduced connectives. Abdominal ganglion (ab) size larger than half of pedal ganglia size, with one main bifurcated nerve. Sub-intestinal ganglion size twice as small as supra-intestinal ganglion (sp), with 1 nerve. Supra-intestinal ganglion bit smaller than abdominal ganglion, with 1 nerve. Visceral ganglia connective reduced. Buccal ganglia (bg) small, size ~8x smaller than sub-intestinal ganglion (sb); each ganglion with 1 main innervation; buccal commissure reduced.

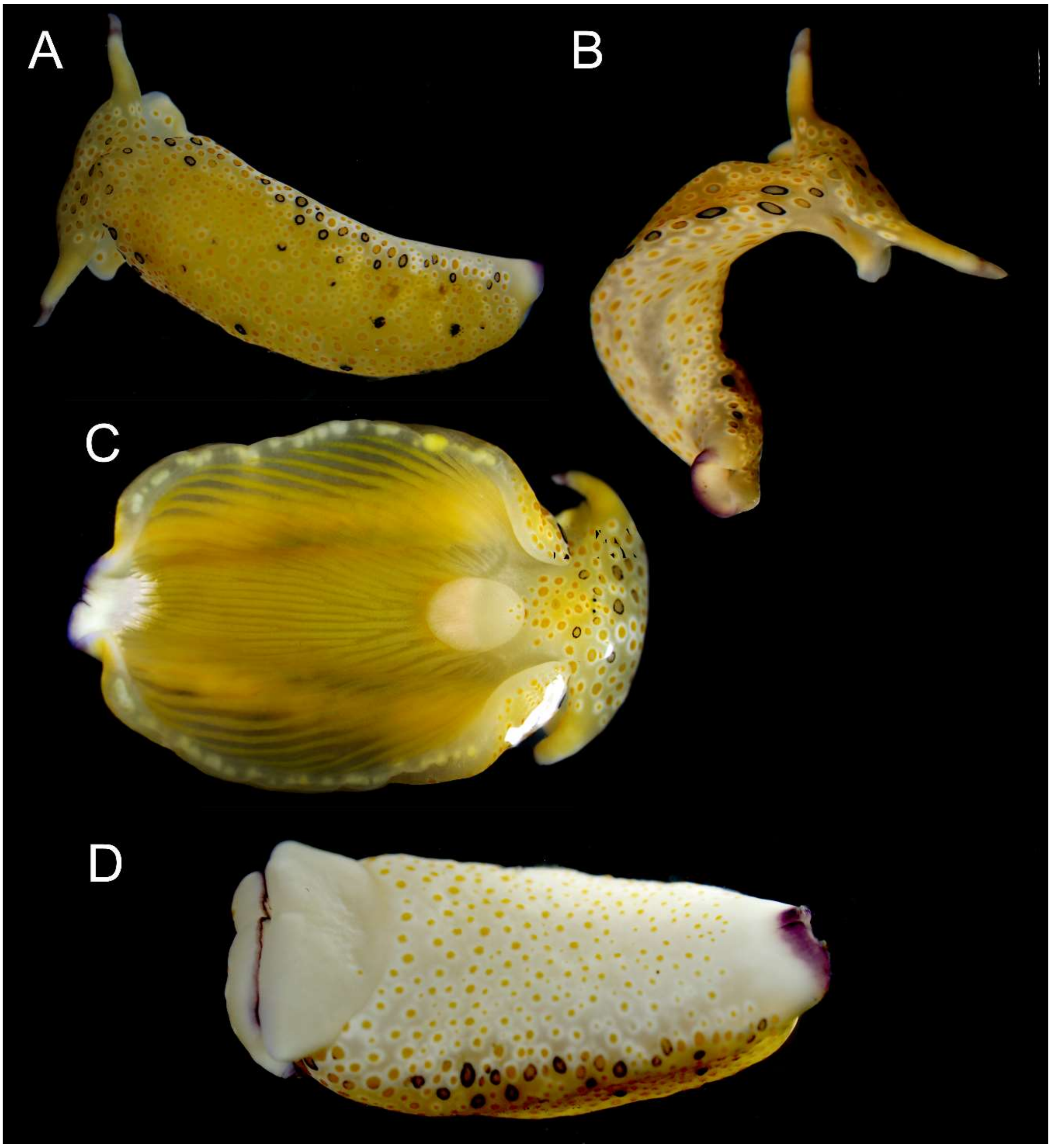

Figure 55. External morphology of *Plakobranchus ianthobapsus*. A) dorsal view; B) lateral view; C) dorsal view with parapodia oppened; D) ventral view.

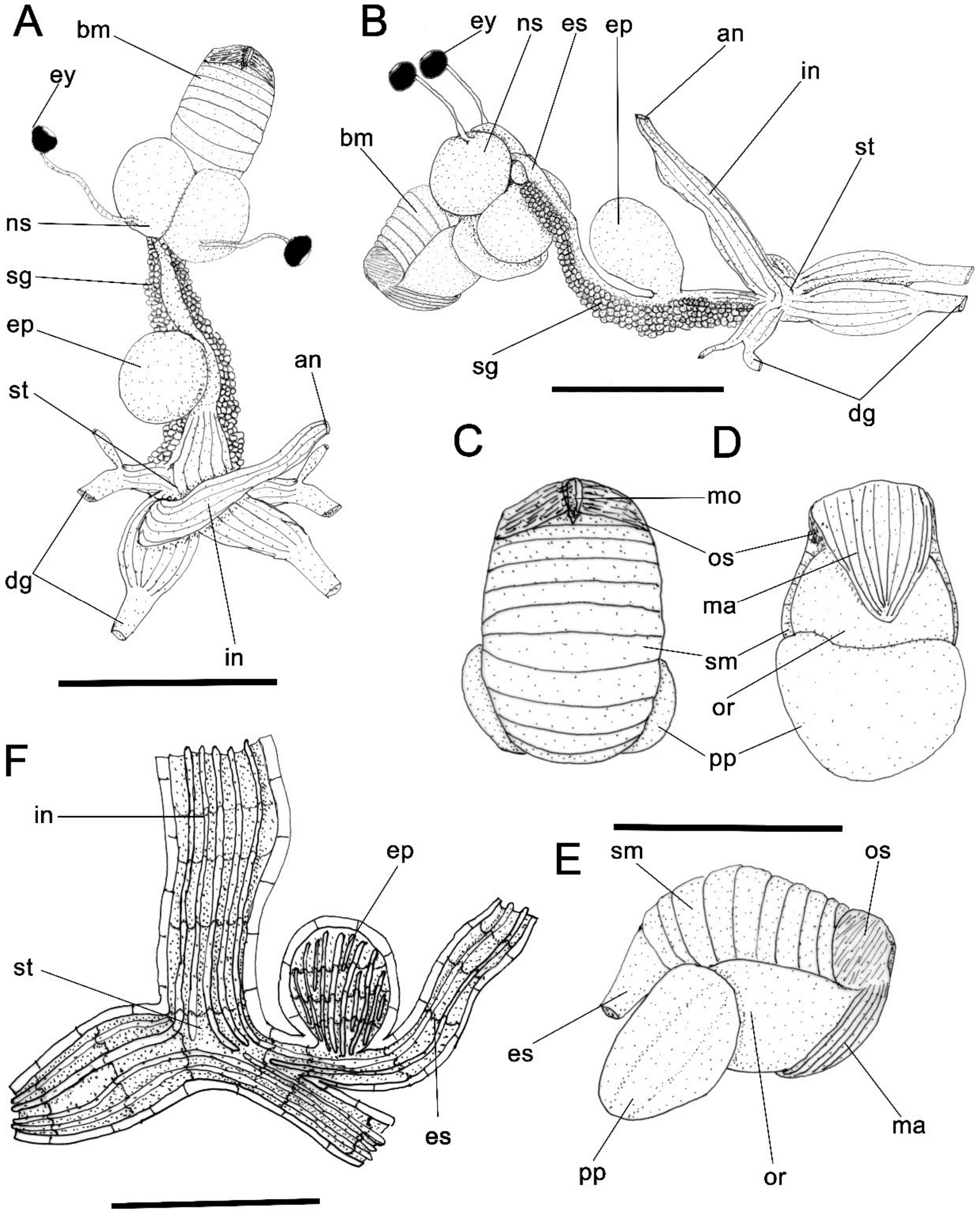

Figure 56. *Plakobranchus ianthobapsus* internal morphology. Digestive system. A) dorsal view. B) Lateral view. C-E) Buccal mass, dorsal (C), ventral (D) and lateral view (E). F) Internal surface of digestive system.

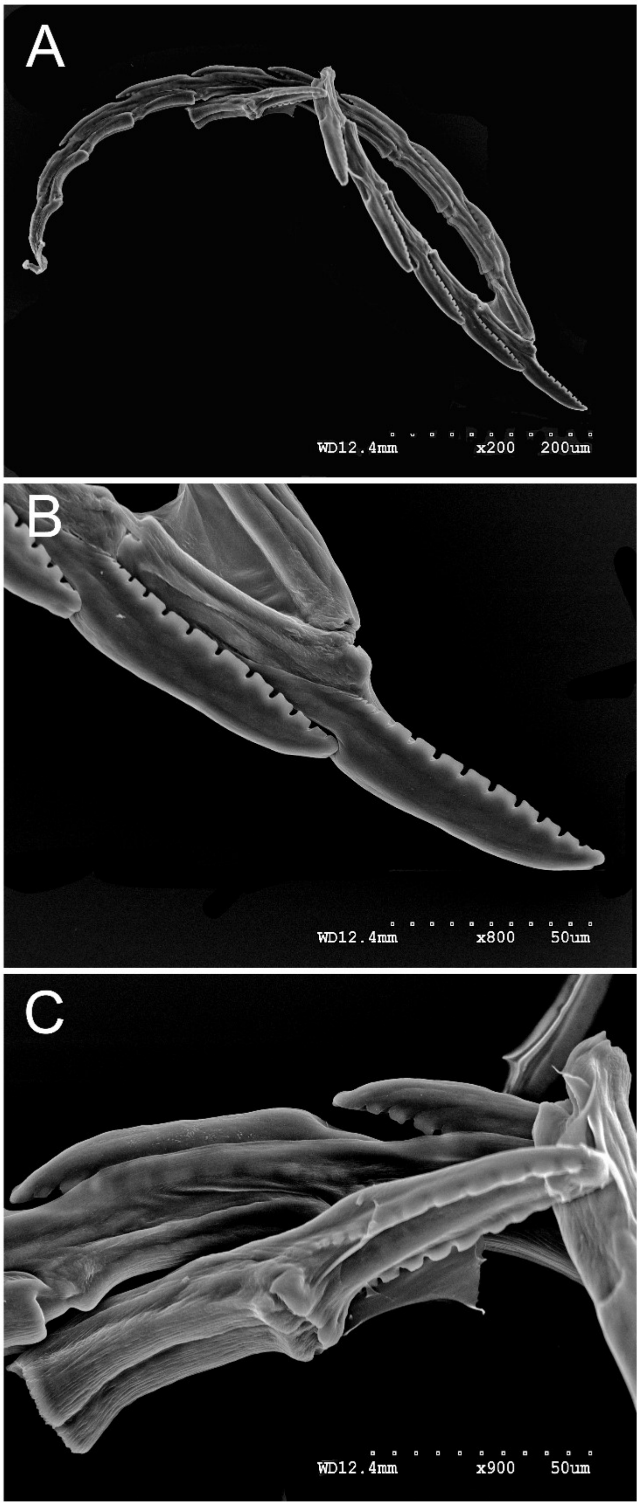

Figure 57. Scan electron microscope images of radula of *Plakobranchus ocellatus.* A) overview; B) detail of leading tooth; C) discarded teeth.

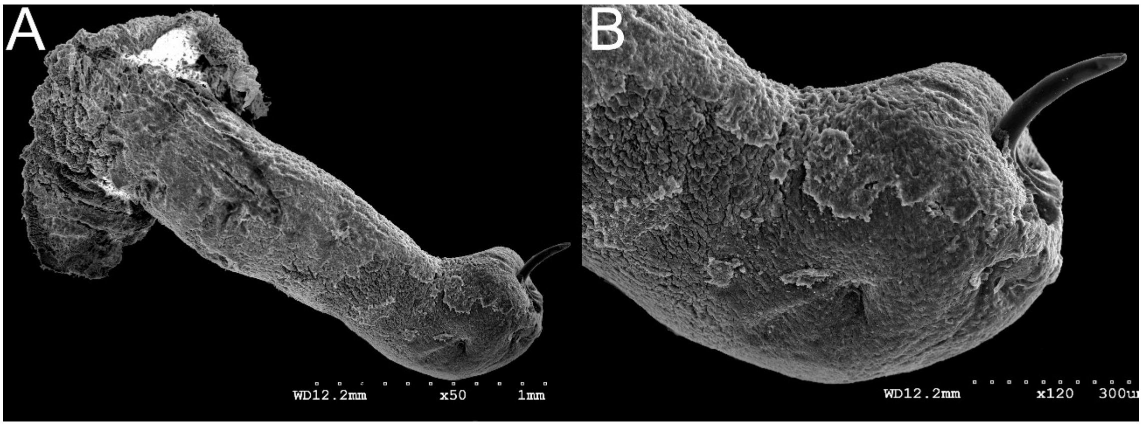

Figure 58. Scan electron microscope image of penis of *Plakobranchus ianthobapsus.*

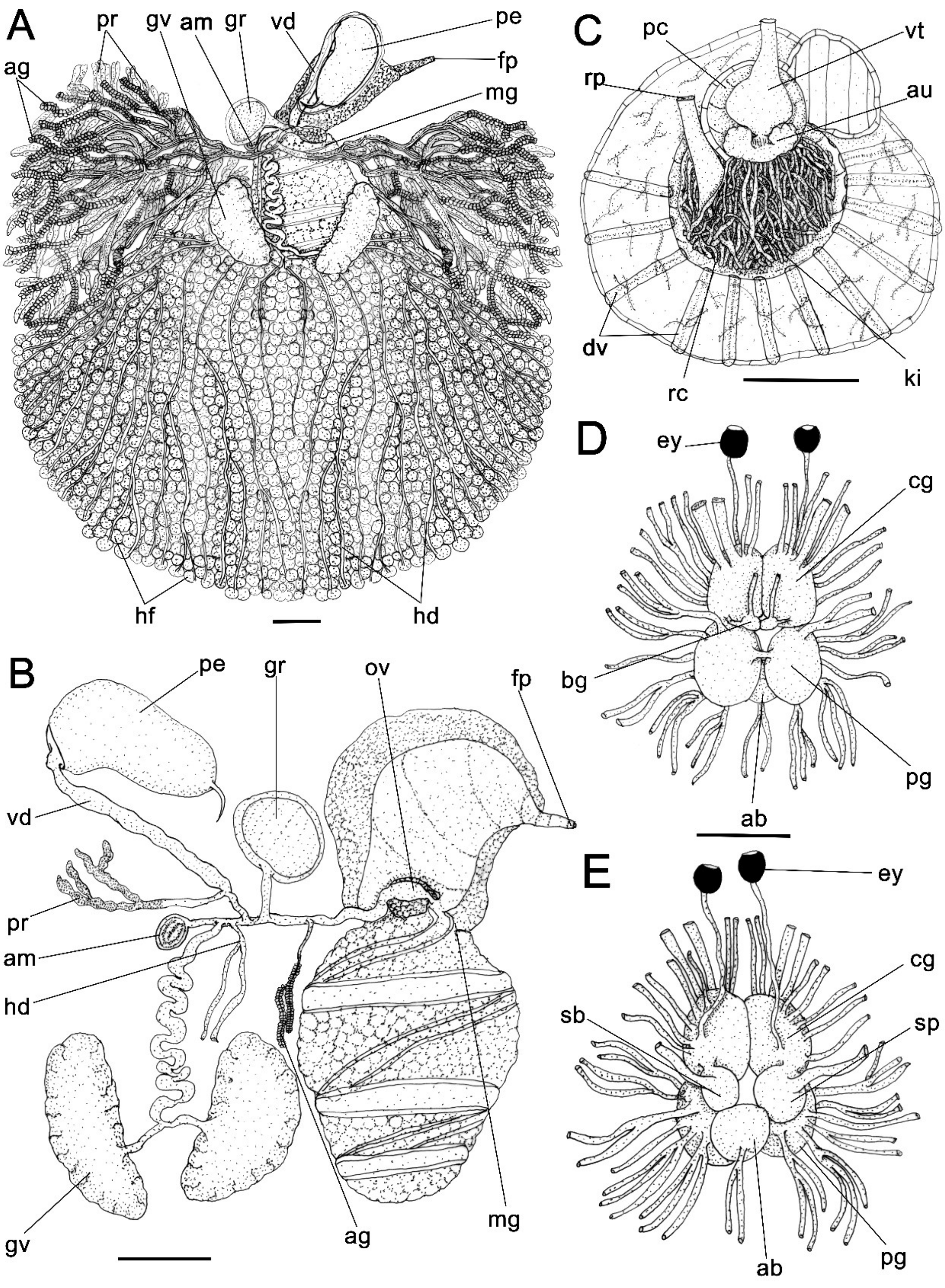

Figure 59. Internal morphology of *Plakobranchus ianthobapsus*. A-B) Reproductive system, overview (A) and schematic arrangement (B). C) Circulatory and excretory systems. D-E) Nervous system, anterior (D) and posterior (E) view.

Plakobranchus papua Meyers-Munoz & van der Velde, 2016

(Figs. 60-64)

Plakobranchus papua Meyers-Muñoz & van der Velde, 2016: 80-88, fig. 2-7a.

External morphology and coloration (Fig. 60)**:** Body reaching up to 70 mm in live animals. General body shape similar to *P. ianthobapsus* except for the following. Head proportionally bit smaller, length ~1/6 of total body length Rhinophores (rh) length bit longer than head length, tip blunt. Foot (fo) with metapodium (mt) ~5x larger than propodium (po). Anterior part of propodium with pedal tentacles bit more tapered. Renopericardial very short, length ~11x smaller than parapodia length. 8 dorsal vessels (dv) running longitudinally from kidney. Lamellae shorter, showing inner parapodial surface, multiple branching in bifurcations, not distally anastomosing. Body overall color olive green to ochre yellow varying among specimens. Some parts of external face of parapodia with yellowish patches. Foot color white, but some specimens with fading blue on margins and usually more intense on posterior end. Large black band present on middle of rhinophores, fading to bluish tone upwards top and brownish downwards base. Black band present on posterior end of body. Retractile cephalic protuberance completely white. Rounded white spots varying on size, covering almost all dorsal surface of head and external side of parapodia, completely absent on inner side of parapodia, renopericardial prominence, rhinophores and foot; bigger and less numerous close to foot; smaller and in large quantity closer to parapodial margins. Ocellated spots completely absent.

Digestive system (Fig. 61-62): Very similar to *P. ianthobapsus*, with following exceptions. Buccal mass (bm) proportionally larger, posteriorly rounded and anteriorly tapered, size ~5x larger than esophageal pouch (ep). Dorsal wall of buccal mass composed of 10 dorsal septate muscle (sm) with similar width, occupies more than half of buccal mass. Ascus musculature (ma) bit shorter. Ascus (as) occupying 1\3 of ventral side of buccal mass. Odontophore region (or) occupies less than half of buccal mass. Pharyngeal pouch (ph), short, ~2x wider than longer, length as half as dorsal septate muscles length. Salivary glands (sg) short, finishing before posterior end of esophagus under esophageal pouch, equally distributed through its extension. Esophagus short, as longer as buccal mass length, width ~3x smaller than intestine width. Esophageal pouch (ep) size ~5x smaller than buccal mass, with inner surface with multiple longitudinal thick folds, running from base to top. Intestine (in) longer, lenth bit longer than esophagus length.

Excretory and circulatory system (Fig. 64C): Heart and kidney characters similar to *P. ianthobapsus.*

Reproductive system (Figs. 63, 64A-B): The arrangement and characters are similar to *P. ianthobapsus* with the following exceptions. Hermaphrodite ampulla proportionally larger, size ~8x smaller than genital receptacle (gr) and ~3x bigger than hermaphrodite follicles. Gametolytic vesicles (gv) elliptical shaped, size large as penis size and ~3x smaller than second chamber of mucus gland, connected to each other by one middle-dorsal straight duct. Duct of gametolytic vesicles bit expanded where bifurcates. Prostate glands (pr) more spread under follicles and expanded through proximal part of parapodia. Vas deferens (vd) length twice as longer as penis length. Penis (pe) shorter, bit longer than larger. Penile stylet less curved, length ~3x smaller than penis length. Proximal chamber of mucus gland size as larger as hermaphrodite ampulla size. Middle chamber of mucus gland proportionally smaller than in *P. ianthobapsus*. Distal chamber size ~3x smaller than second one.

Nervous system (Fig. 64): Cerebro-pleural ganglia with about 8 innervations. Optic nerve long, length as longer as cerebro-pleural ganglion length. Pedal commissure positioned ventrally, longer and thicker, length ~3x smaller than pedal ganglion length. Abdominal ganglion (ab) with two innervations. Sub-intestinal ganglion size ~4x smaller than supra-intestinal ganglion (sp). Buccal ganglia (bg) proportionally larger, size twice as small as sub-intestinal ganglion (sb).

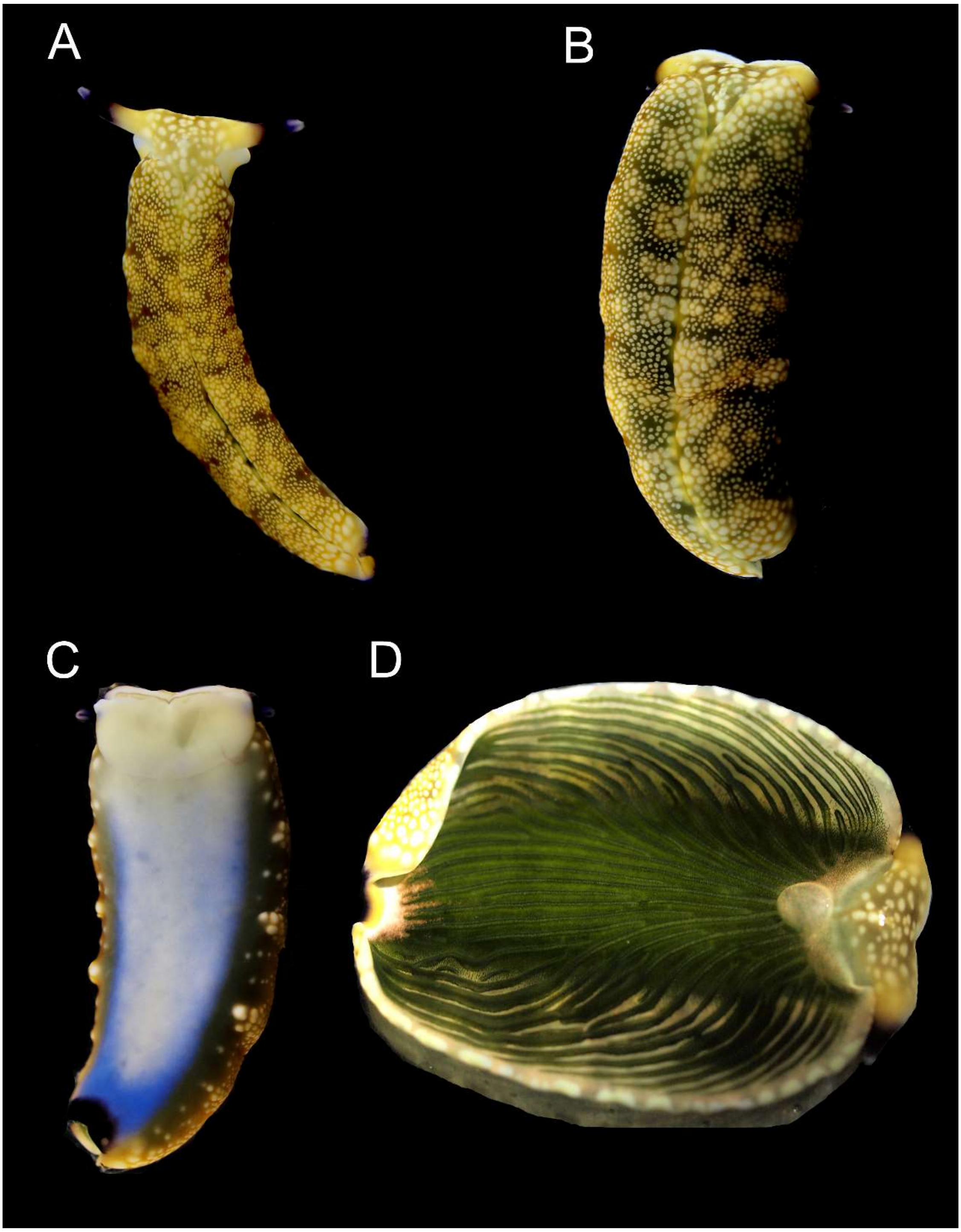

Figure 60. External morphology of *Plakobranchus papua*. A-B) Dorsal view; C) ventral view; C) ventral view; D) dorsal view with parapodia oppend.

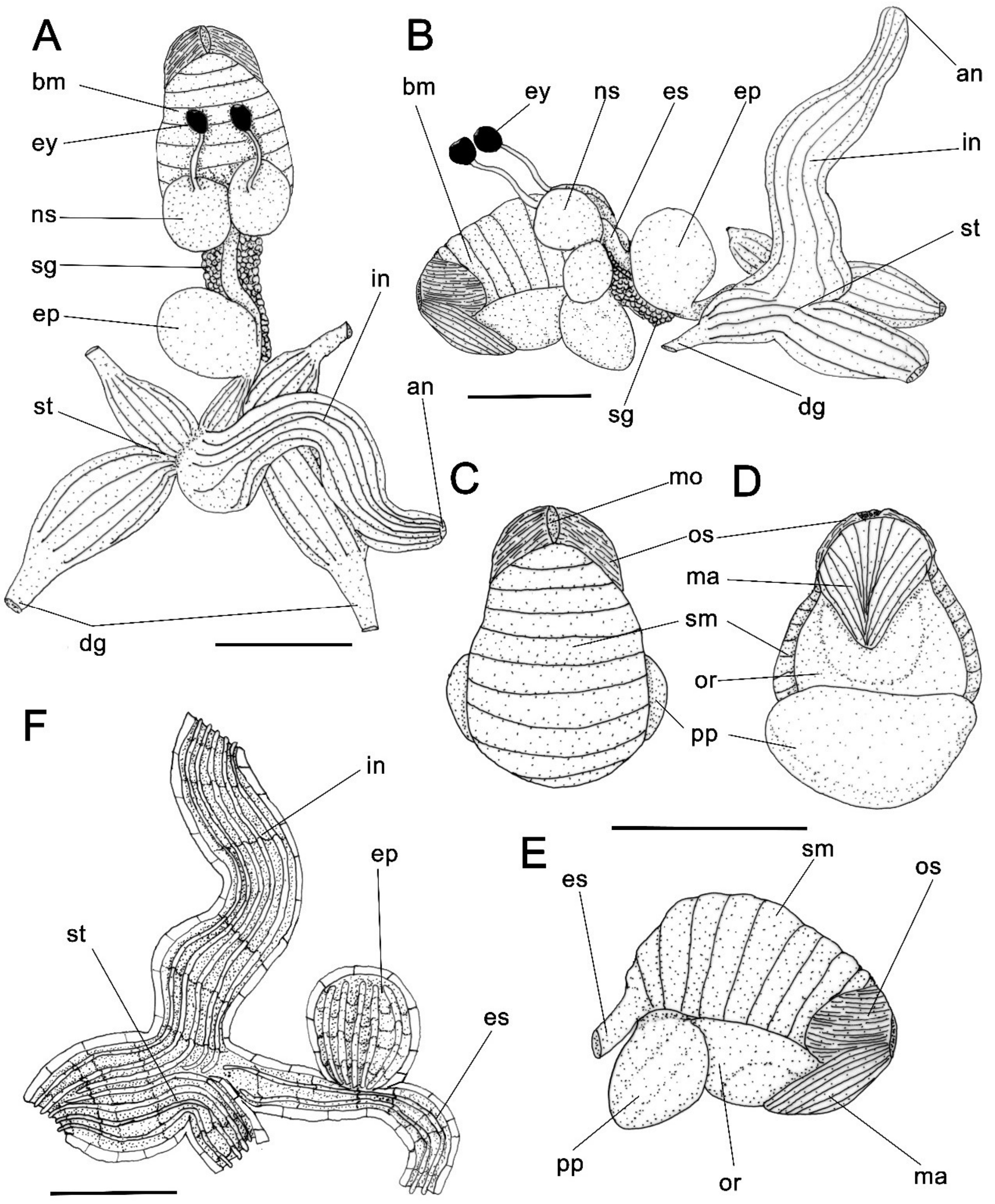

Figure 61. Internal morphology of *Plakobranchus papua*. Digestive system. A) dorsal view. B) Lateral view. C-E) Buccal mass, dorsal (C), ventral (D) and lateral view (E). F) Internal surface of digestive system.

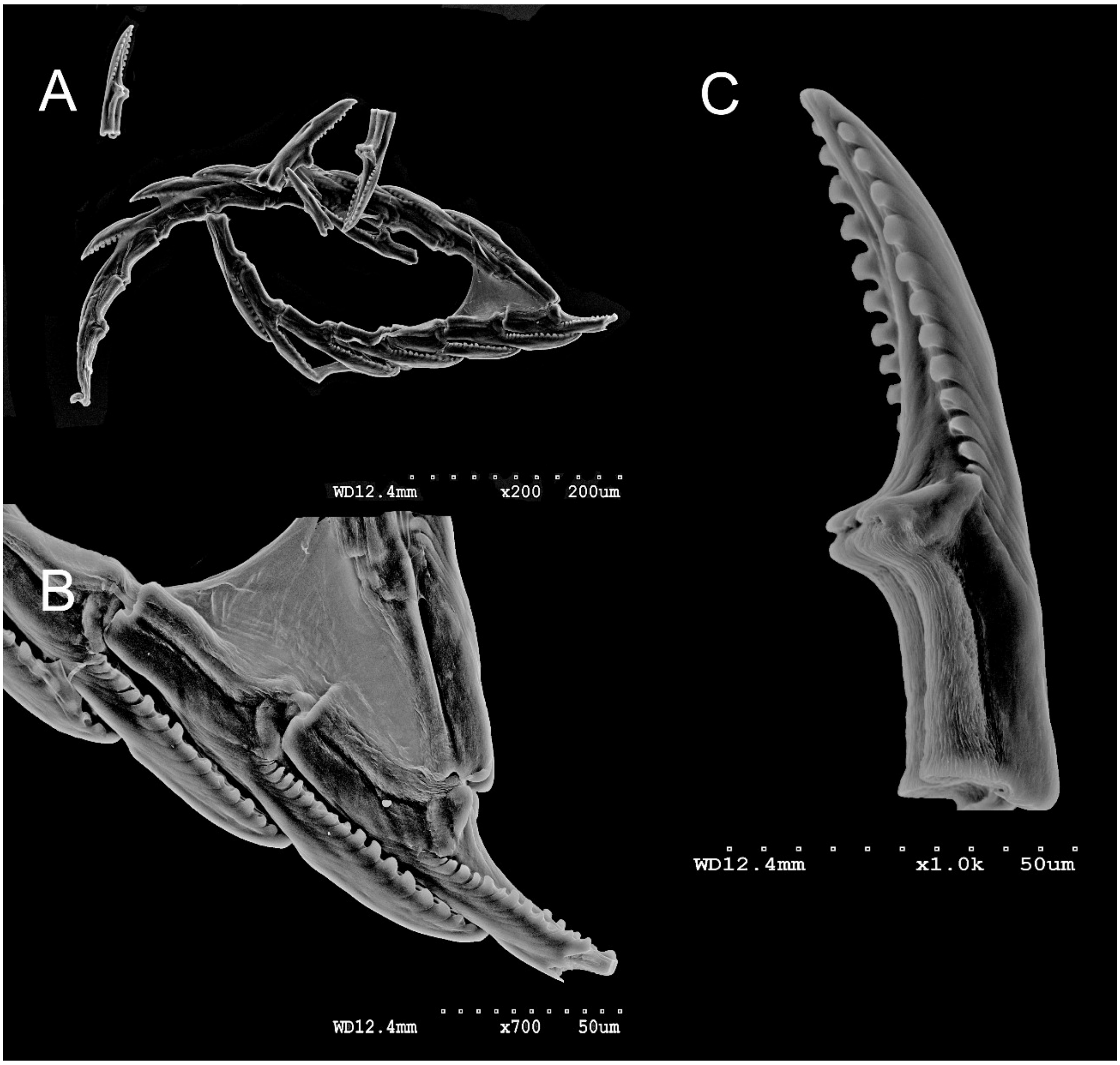

Figure 62. Radula of *Plakobranchus papua*. A) overview; B) leading tooth; C) discarded tooth.

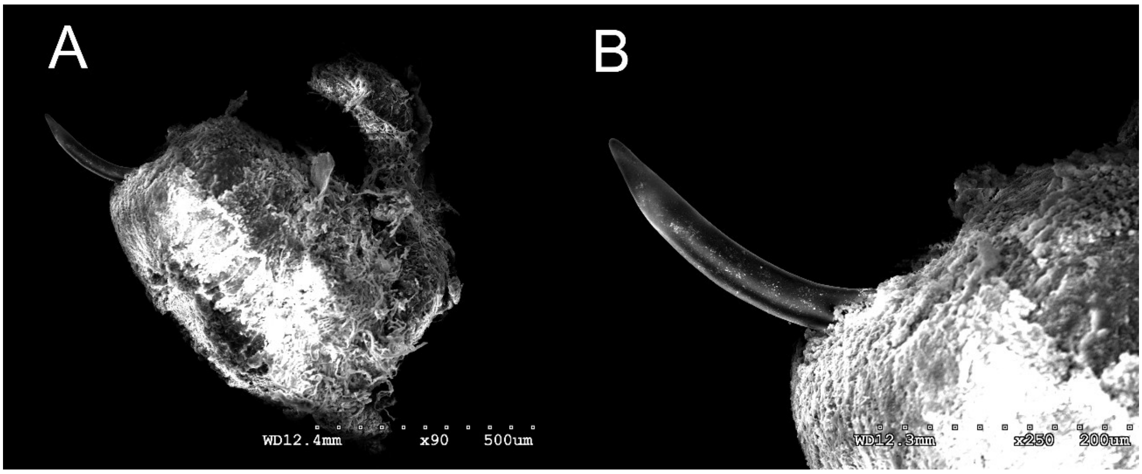

Figure 63. Penis of *Plakobranchus papua*.

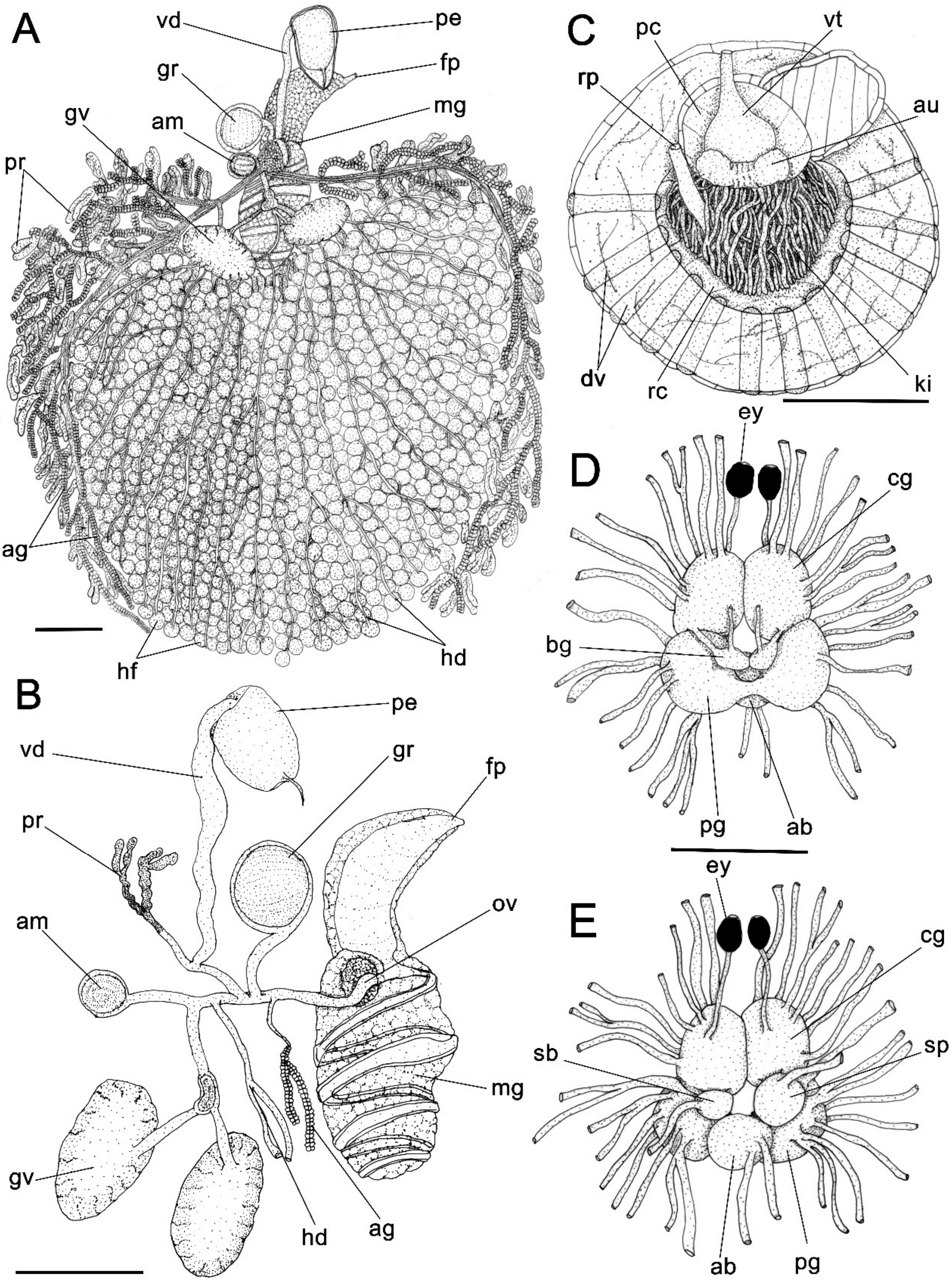

Figure 64. Internal morphology of *Plakobranchus papua*. A-B) Reproductive system, overview (A) and schematic arrangement (B). C) Circulatory and excretory systems. D-E) Nervous system, anterior (D) and posterior (E) view.

***Plakobranchus* sp. 1 (aff. Purple)**

(Figs. 65-69)

Plakobranchus sp. 5 Gosliner *et al*., 2015: 99.

External morphology and coloration (Fig. 65)**:** Body reaching up to 30 mm in live animals. General body shape similar to *P. ianthobapsus* except for the following. Foot (f) with metapodium (mt) ~5x larger than propodium (po). 8 dorsal vessels (dv) running longitudinally from kidney. Lamellae shorter, showing inner parapodial surface, multiple branching in bifurcations, not distally anastomosing. Body with overall color creamy or pale white, varying in darkness among specimens. Dark grey reticulated pattern on head, rhinophores and lateral of body close to foot. Green digestive gland visible on mouth region and forming large patches on external surface of parapodia. Ocellated spots as iridescent dots between pink and orange in color either darker orange border or surrounded by one complete or incomplete black ring, spread over external face of parapodia, head and rhinophores, and completely absent on inner face of parapodia, renopericardium prominence and foot. Smaller and more numerous black dots spread among iridescent spots. Foot white, densely dotted with black spots variable in size from tiny to large; each surrounded by diffuse ring of faint greyish purple; no spots on anterior and posterior end of foot. Rhinophores with same color pattern as head on dorsum side, and no color on ventral side. No colored band on rhinophores and posterior end of body. Retractile cephalic protuberance colored as same as body background coloration.

Excretory and circulatory system (Fig. 69): Heart and kidney characters similar to *P. ianthobapsus.*

Digestive system (Fig. 66-67): Very similar to *P. ianthobapsus*, with following exceptions. Buccal mass (bm) less elongated, as longer as wider, with posterior part rounded and anterior part bit tapered, length ~3x longer than cerebro-pleural ganglia length. Dorsal wall of buccal mass composed of 10 dorsal septate muscle (sm) with similar width; short, occupies less than half of buccal mass. Ascus musculature (ma) shorter, finishing before middle part of odontophore region. Odontophore region larger, occupying more than half of buccal mass.

Pharyngeal pouch (ph) size half as larger as odontophore region size, length as half as dorsal buccal mass length, short, ~2x wider than longer. Ascus occupying 1/5 of ventral part of buccal mass. Esophagus short, length as longer as buccal mass length, width as half as intestine width. Inner surface of esophageal pouch (ep) with two thick longitudinal fold running from base to almost top portion.

Reproductive system (Fig. 68-69): The arrangement and characters are similar to *P. ianthobapsus* with the following exceptions. Gonad shorter, do not expand to posterior end of body. Hermaphrodite follicles larger, size twice as large as hermaphrodite ampulla (am). Hermaphrodite ampulla small as in *P. ianthobapsus*, size ~3x smaller than genital receptacle (gr). Paired gametolytic elliptical shaped, longer, size twice as large as penis size, and large as second chamber of mucus gland; connected to each other by one highly curled dorsolateral main duct. Prostate gland (pr) as in *P. papua*. Vas deferens (vd) length ~3x longer than penis length, bit curled close to penis. Penis (pe) shorter as in *P. papua*, twice longer than larger, size ~3x smaller than distal chamber of mucus gland. Penile stylet longer, length big longer than penis length, and laterally inserted on top of penis. Mucus gland similar to *P.* papua, but distal chamber bit larger. Genital receptacle smaller, size ~10x smaller than gametolytic vesicles.

Nervous system (Fig. 69): Nervous ring covering almost half of esophagus length. Cerebro-pleural (cp) with about 8 innervations. Optic nerve shorter, length bit smaller than cerebro-pleural ganglion length. Each pedal ganglion innervated with 4 highly branched nerves. Supra-intestinal ganglion smaller than half of abdominal ganglion size, with 2 nerves. Buccal ganglia (bg) proportionally larger as in *P. papua*, size twice as small as sub-intestinal ganglion (sb).

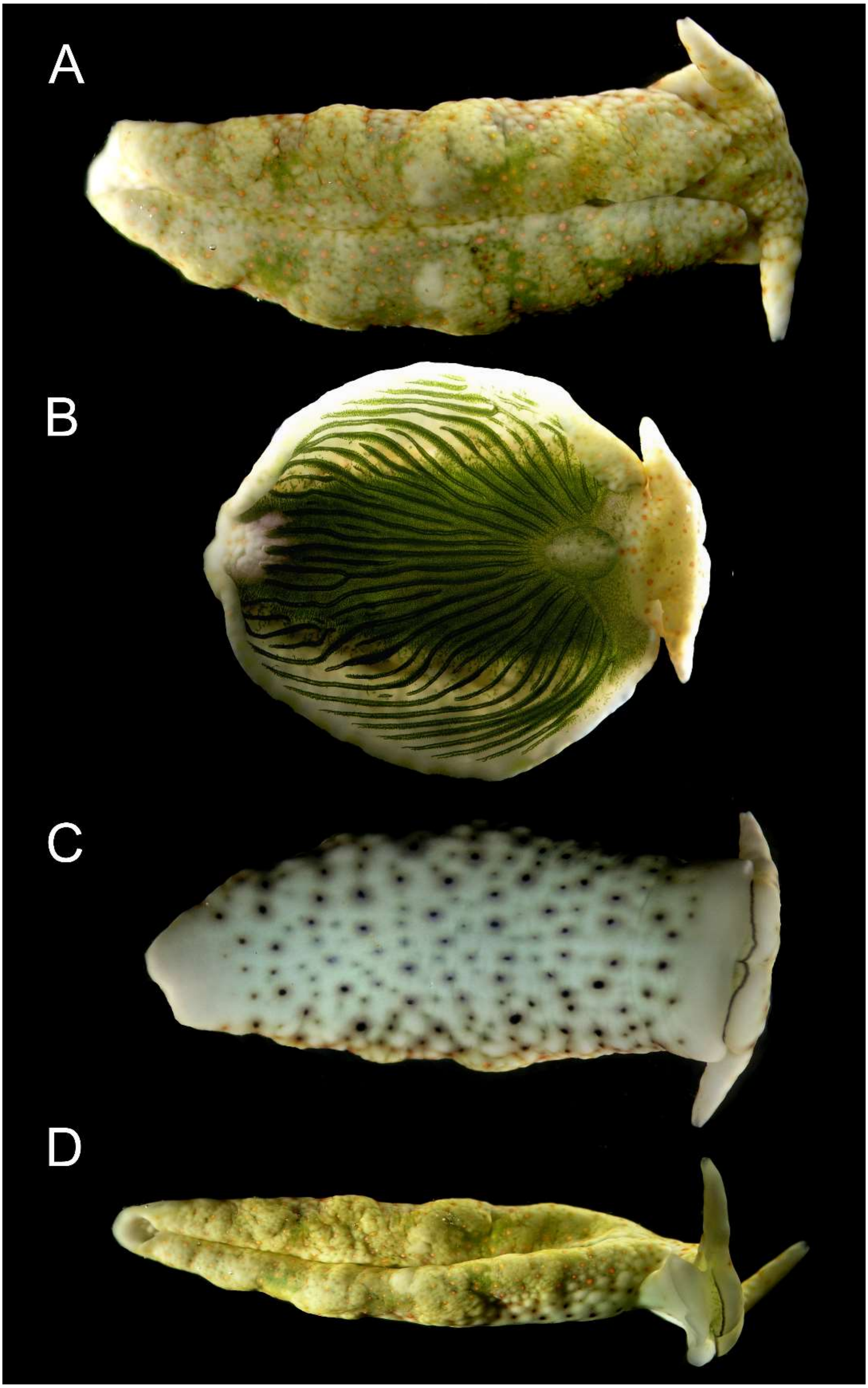

Figure 65. External morphology of *Plakobranchus* sp. 1. A) Dorsal view; B) dorsal view with parapodia opened; C) ventral view; D) lateral view.

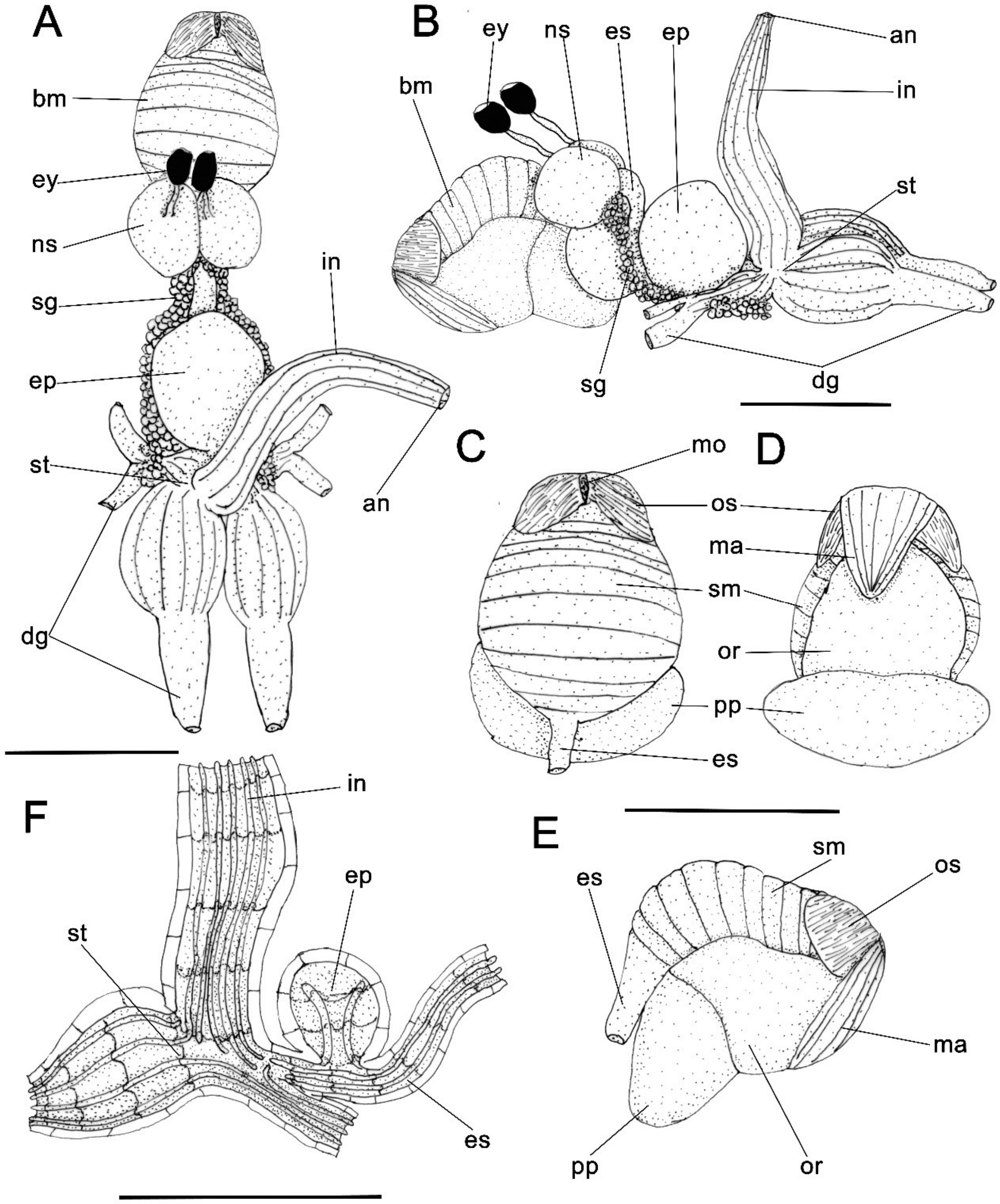

Figure 66. Internal morphology of *Plakobranchus* sp. 1. Digestive system. A) dorsal view. B) Lateral view. C-E) Buccal mass, dorsal (C), ventral (D) and lateral view (E). F) Internal surface of digestive system.

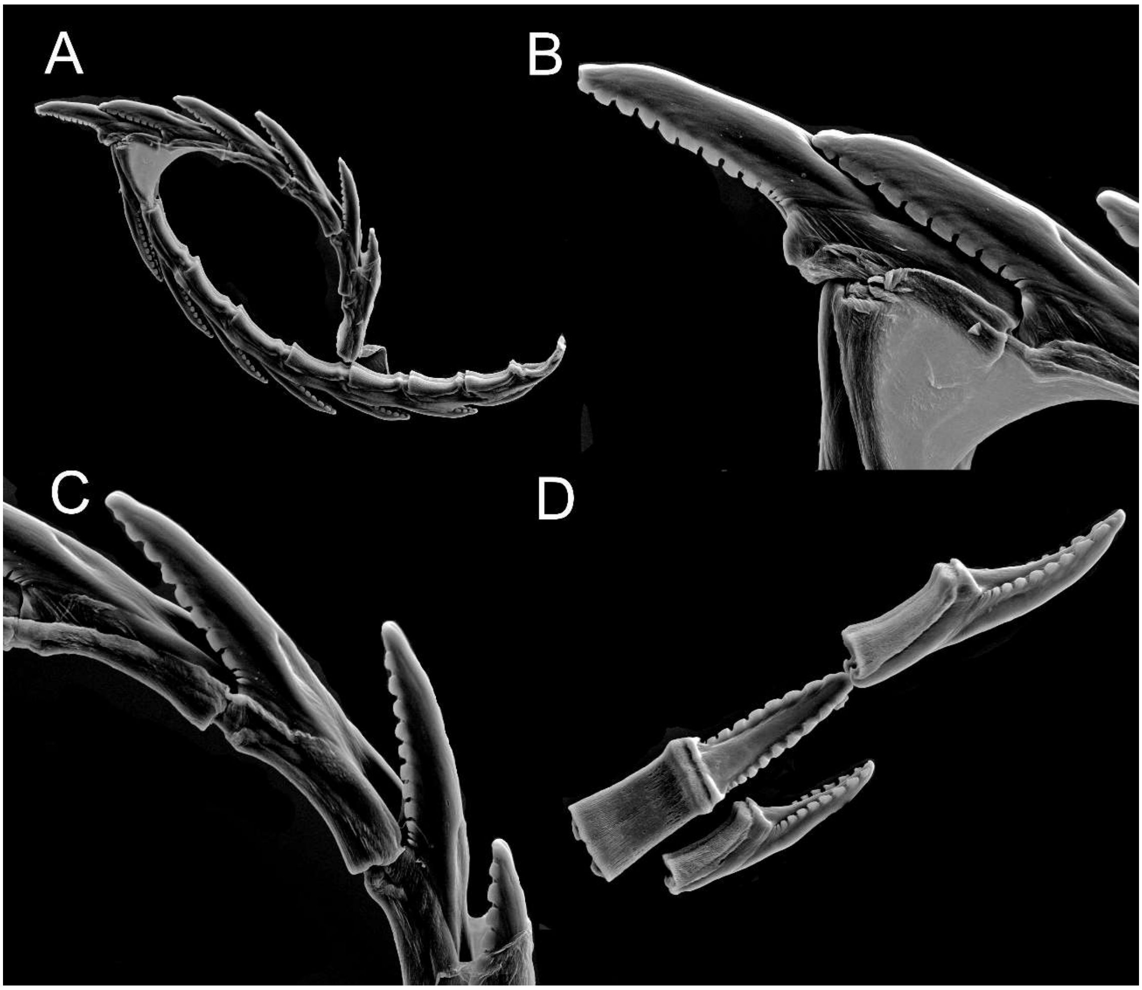

Figure 67. Radula of *Plakobranchus* sp. 1. A) overview; B) leading tooth; C) old teeth; D) discarded teeth.

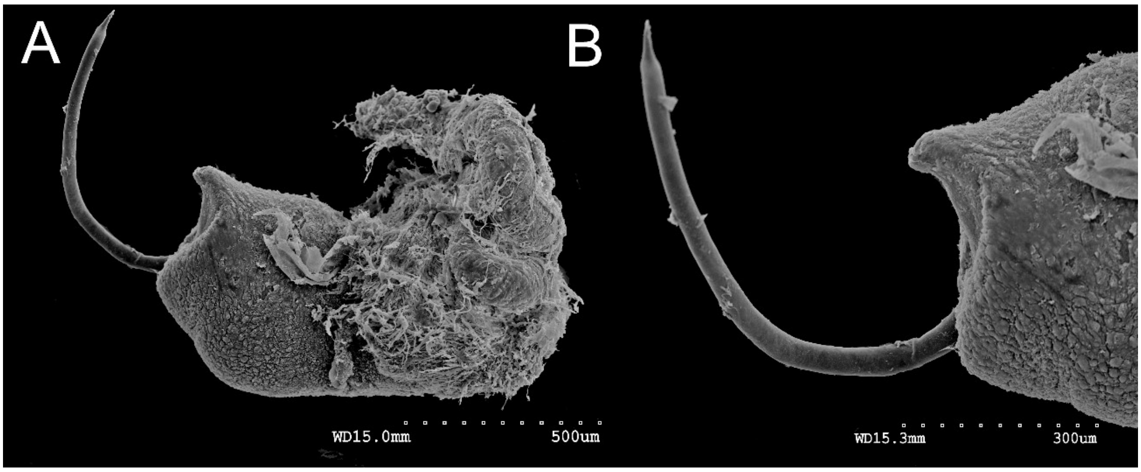

Figure 68. Penis of *Plakobranchus* sp. 1. A) overview; B) detail of penial stylet.

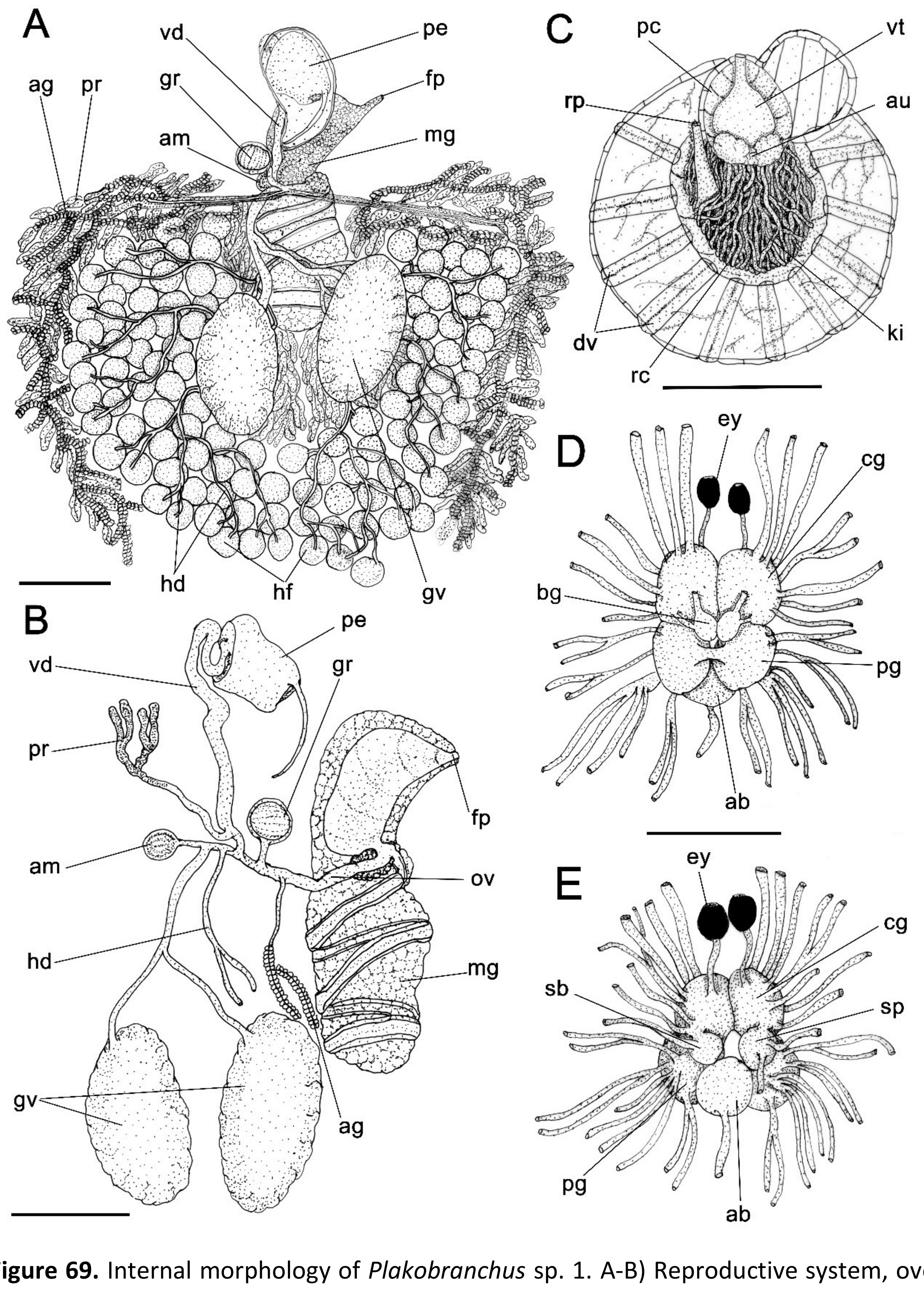

Figure 69. Internal morphology of *Plakobranchus* sp. 1. A-B) Reproductive system, overview (A) and schematic arrangement (B). C) Circulatory and excretory systems. D-E) Nervous system, anterior (D) and posterior (E) view.

***Plakobranchus* sp. 2**

(Figs. 70-74)

External morphology (Figs. 70-71): Body reaching up to 18 mm in preserved specimens. Head proportionally bit larger, length ~1/4 of total body length. Number of dorsal vessel not observed. Dorsal lamellae less tall and less branched. Coloration on specimens preserved in ethanol very similar to *P. ianthobapsus* except for the following. Head dark brown on middle dorsal part. Ocellated spots with bluish inner potion seem to be absent. Foot with no orange ocellated spots; densely dotted with black spots variable in size from medium to large; each black spot surrounded by pale white ring; no spots on anterior and posterior end of foot. Anterior end of head, posterior end of body and rhinophore tips with black band.

Excretory and circulatory system (Fig. 45): Heart and kidney characters similar to *P. ianthobapsus* except for the following. Pericardium larger, occupying less than half of renopericardial cavity. Heart occupying more than half of pericardium space. Ventricle larger, size ~5x auricle size.

Digestive system (Fig. 42-43): Very similar to *P. ianthobapsus*, with following exceptions. Buccal mass (bm) shorter, bit longer than wider, posteriorly rounded and anteriorly tapered. Dorsal wall of buccal mass composed of 10 dorsal septate muscle (sm) with similar width. Oral sphincter (os) as longer as half dorsal septate muscle (sm) length. Ascus musculature (ma) posteriorly rounded, large, covering more than half of odontophore region. Ascus (as) occupying almost half of ventral side of buccal mass. Buccal pouch (bp), short, ~2x wider than longer, length as half as dorsal septate muscles length. Salivary glands (sg) short, finishing before posterior end of esophagus under esophageal pouch, equally distributed through its extension. Esophageal pouch (ep) size as larger as buccal mass size, with muscular top portion occupying half of lumen, and inner surface with no folds. Intestine (in) longer, length ~2x longer than esophagus length.

Reproductive system (Fig. 44-45): Very similar to *P. iathobapsus* with the following exceptions. Hermaphrodite follicles size proportionally bit larger, size ~3x smaller than hermaphrodite ampulla (am). Hermaphrodite ampulla larger as in *P. papua*, size ~6x smaller than genital receptacle (gr). Gametolytic vesicles connected to each other by one dorsal-lateral straight duct. Prostate gland arranged as is *P. papua*. Vas deferens (vd) length ~2x longer as penis length, half proximally to penis highly curled and other half straight. Penis (pe) shape bit longer than larger. Penile more curved, longer, length bit smaller than penis length. Secondary genital receptacle positioned under the penis, and connected on oviduct right after other genital receptacle.

Nervous system (Fig. 45): Nervous covering almost half esophagus length. Cerebro-pleural ganglia (cp) with about 8 innervations. Optic nerve short, length bit smaller than cerebro-pleural ganglion length. Pedal commissure as in *P. papua*. Abdominal ganglia (ab) elongated, twice wider than longer. Sub-intestinal ganglion size ~3 smaller than supra-intestinal ganglion (sp). Supra-intestinal ganglion ~3x smaller than abdominal ganglion. Buccal ganglia (bg) size as small as sub-intestinal ganglion (sb). Buccal commissure exposed and short.

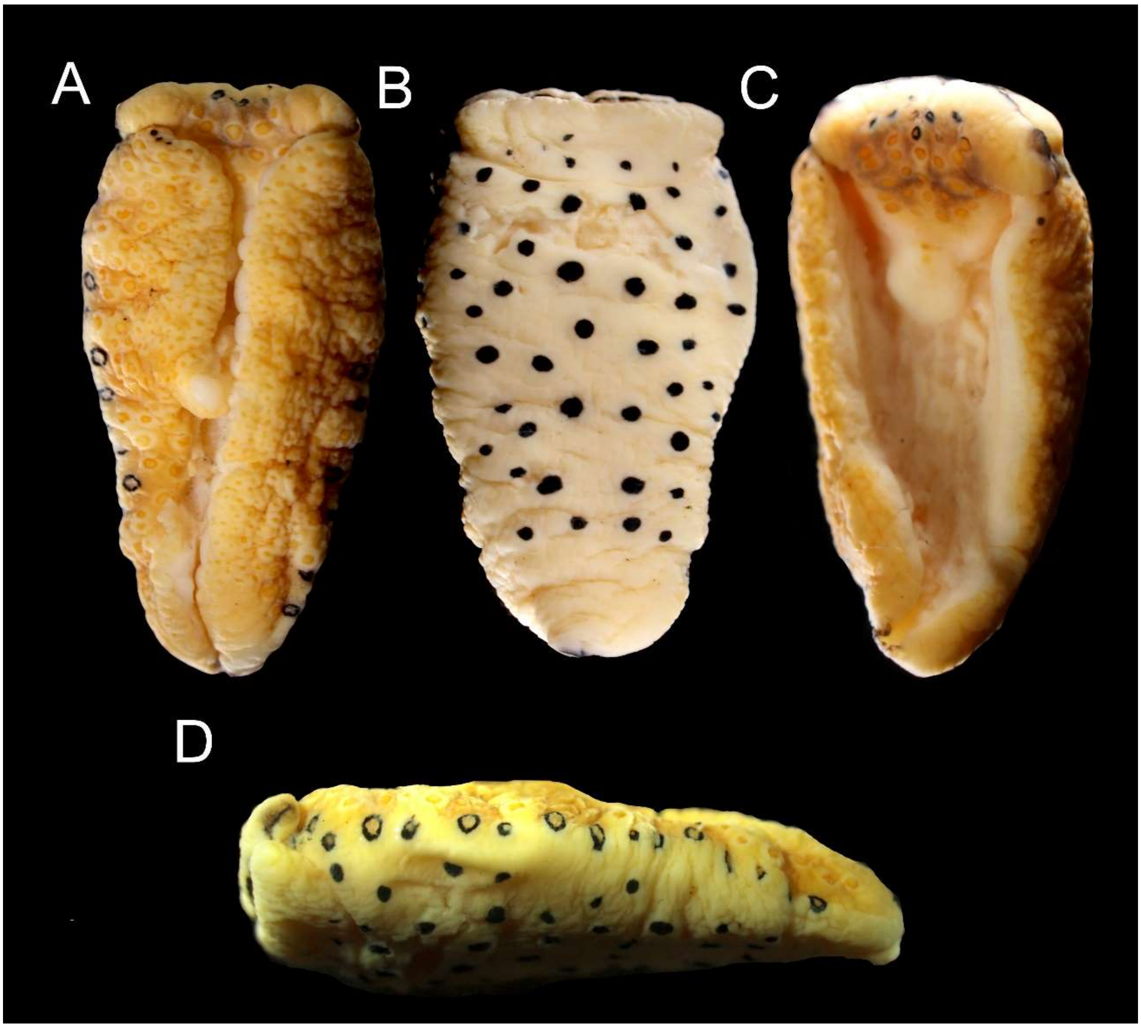

Figure 70. Photos of preserved specimens of *Plakobranchus* sp. 2 Africa. A) Dorsal view with closed parapodia; B) ventral view; C) dorsal view with opened parapodia; D) lateral left view.

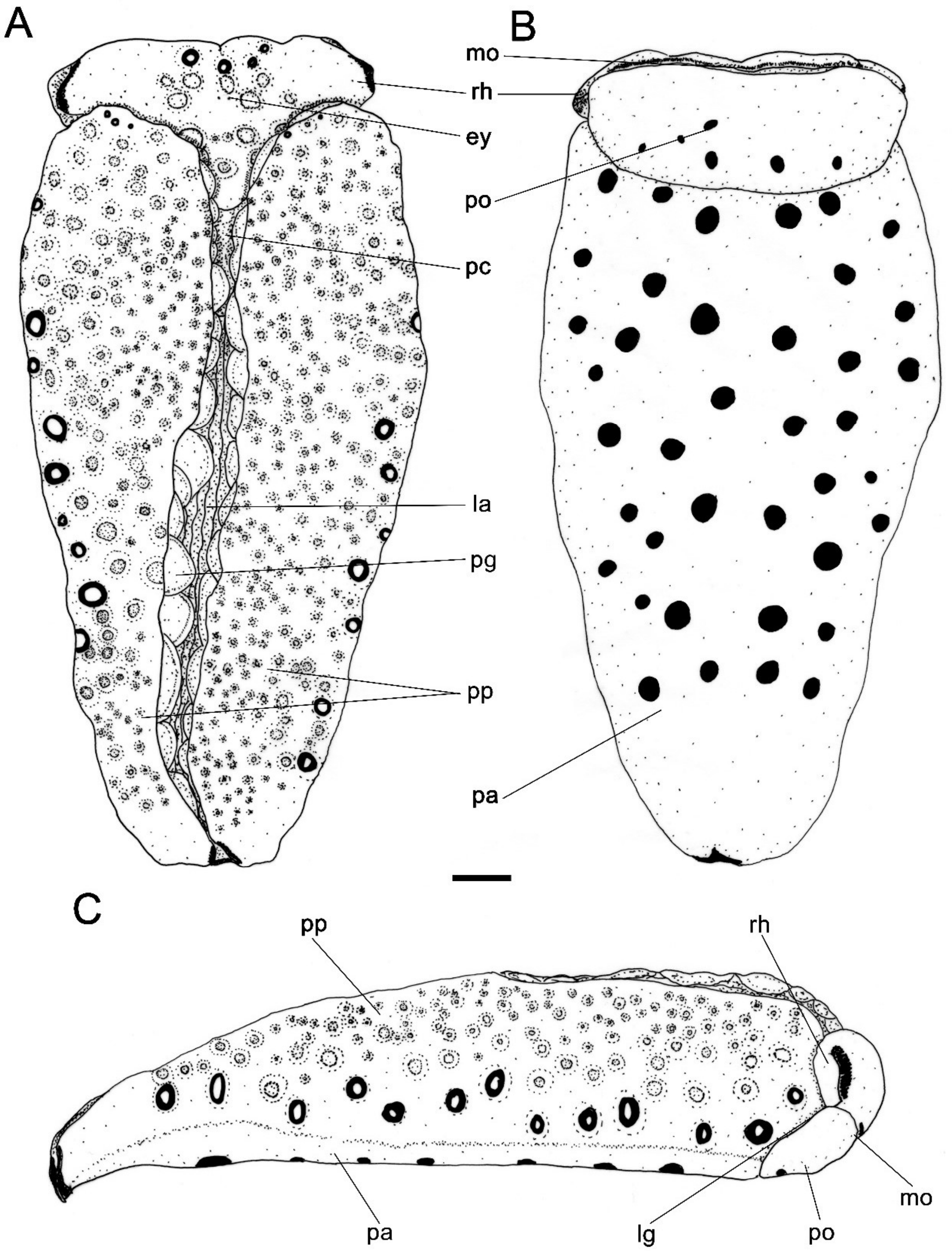

Figure 71. External morphology of *Plakobranchus* sp. 2 Africa. A) Dorsal view. B) Ventral view. C) Lateral view.

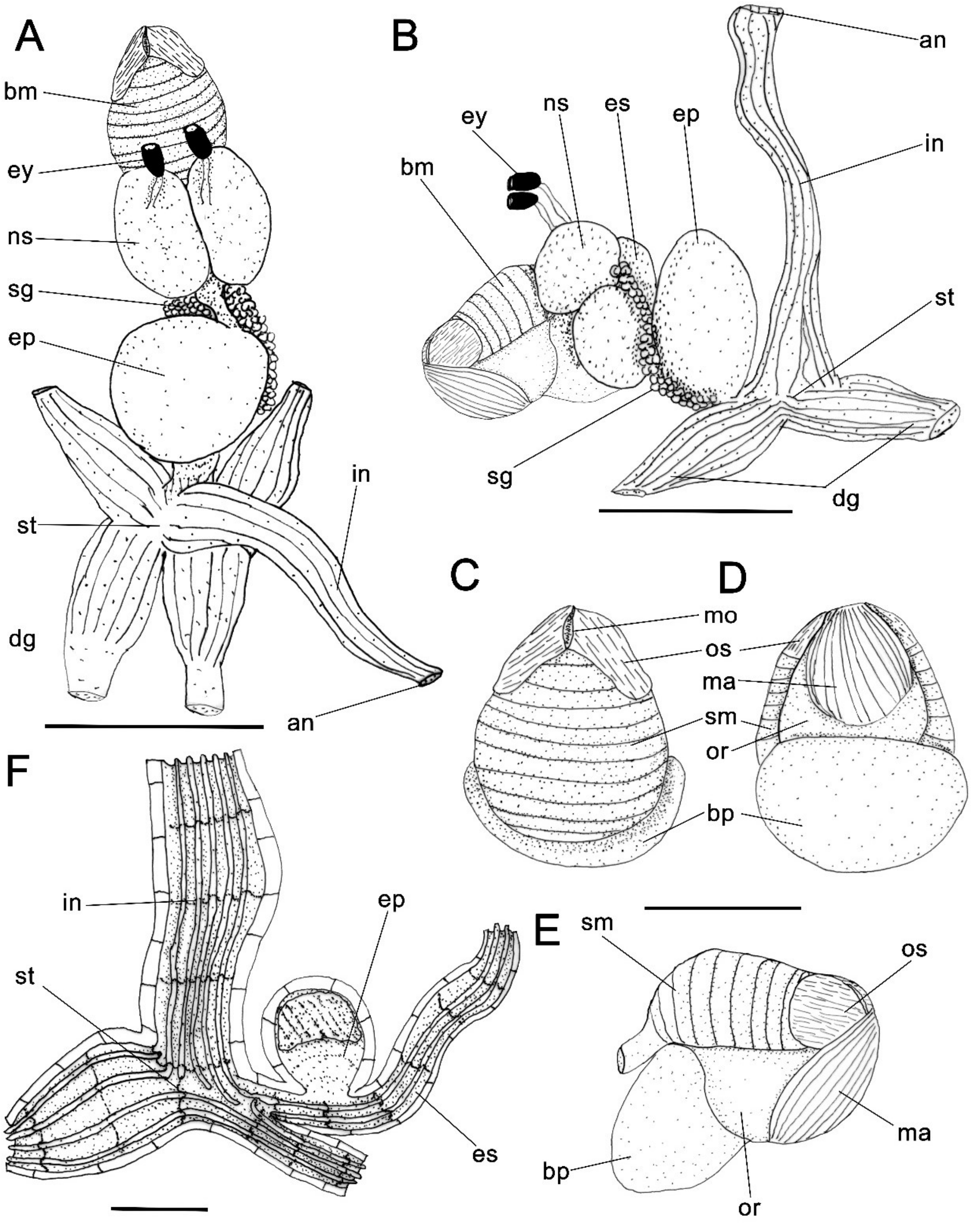

Figure 72. Internal morphology of *Plakobranchus* sp. 2 africa. Digestive system. A) dorsal view. B) Lateral view. C-E) Buccal mass, dorsal (C), ventral (D) and lateral view (E). F) Internal surface of digestive system.

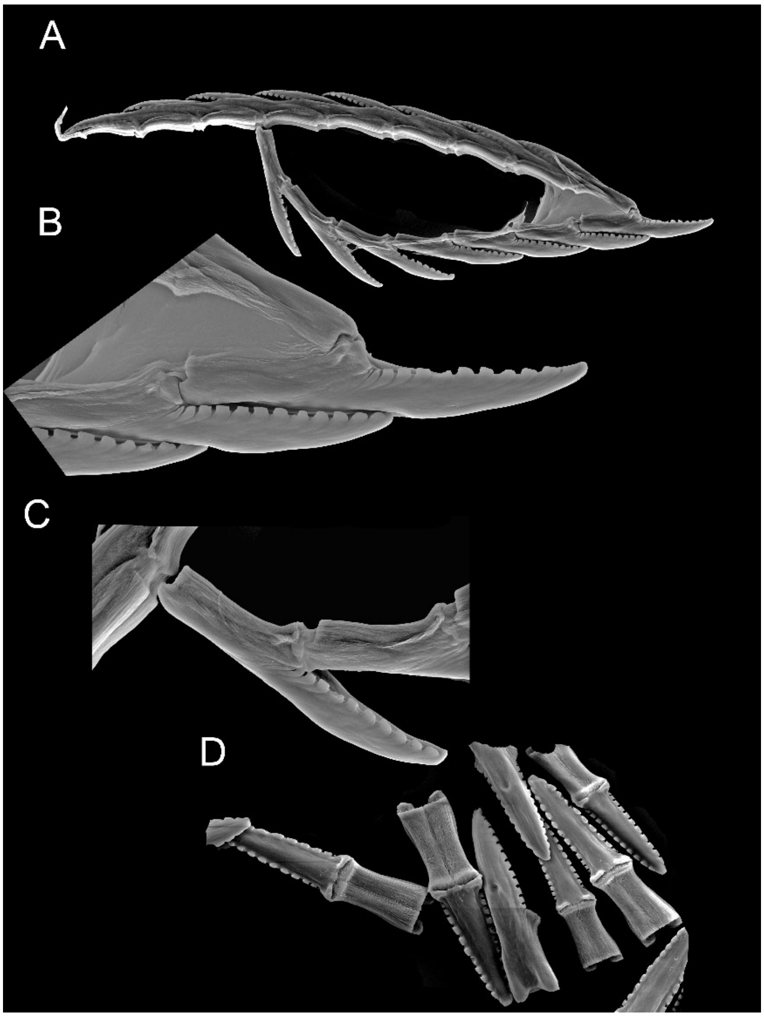

Figure 73. Radula of *Plakobranchus* sp. 2. A) overview; B) leading tooth; C) old teeth; D) discarded teeth.

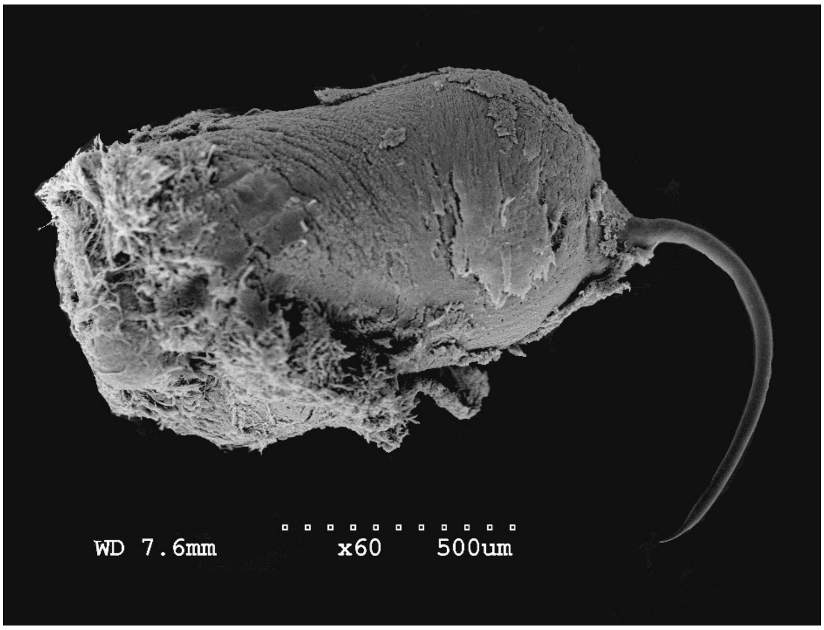

Figure 74. Penis of *Plakobranchus* sp. 2.

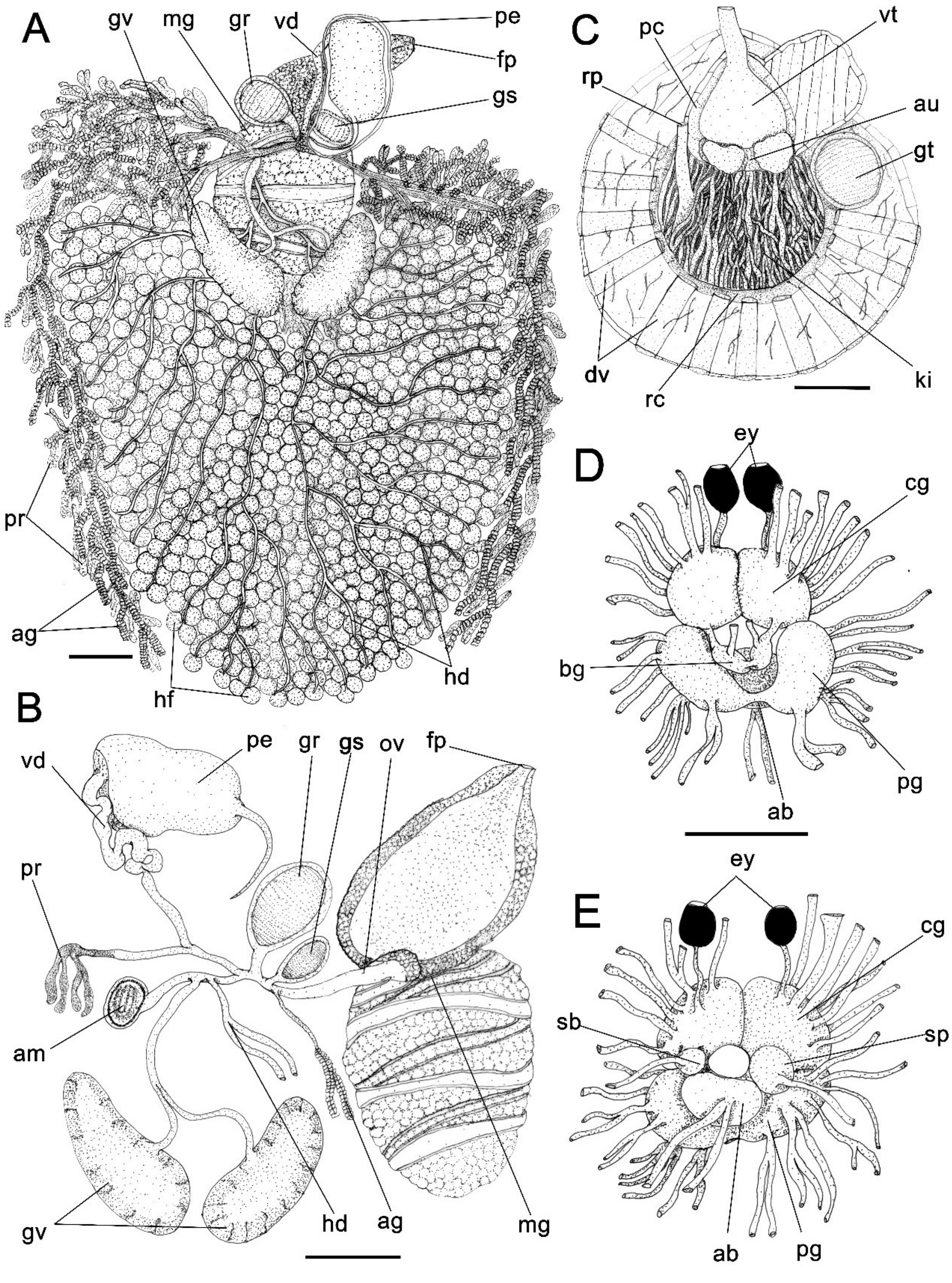

Figure 75. Internal morphology of *Plakobranchus* sp. 1 aff. purple. A-B) Reproductive system, overview (A) and schematic arrangement (B). C) Circulatory and excretory systems. D-E) Nervous system, anterior (D) and posterior (E) view.

Genus *Thuridilla* van Hasselt, 1824

Type species: *Elysia splendida* Grube, 1861 type by monotypy.

***Thuridilla hopei* (Vérany, 1853)**

(Figs. 76-79)

Actaeon hopei Vérany, 1853: 392.

Elisia splendida Grube, 1861: 86, 133, pl. 1 figs. 1-3.

Thuridilla picta Malaquias *et al*., 2014:5, fig. 2F

Elysia hopei (Vérrany, 1853). Thompson, 1981: 77, fig. 5.

Thuridilla hopei (Vérrany, 1853). Pruvot-Fol, 1954: 203; Bouchet, 1984: 26, figs. 6, 11.

Description

External morphology (Fig. 76): Body elongated with 12 mm length in preserved animals. Head evident, large, size ~1/3 of total body size, 2x longer than wider. Rhinophores (rh) short in preserved specimens, length as half as head length, rolled, smooth, and with tip rounded. Eyes (ey) located dorsolaterally behind rhinophores. Foot (fo) elongated and muscular. Parapodial sole (pa) ~3x larger than propodium (po) in live animals; anterior part of propodium bit expanded; mesopodial groove (fl) evident. Pericardium (pc) and renal prominence (rp) fused forming short globose renopericardial hump. Dorsal vessels (dv) organized in one single pair, branching multiple times only in central part of body. Parapodium (pp) large, with regular margin and do not form closure pattern or parapodial tail. Female pore (fp) located on extreme dorsal point of lateral groove (lg). Male pore (mp) below right rhinophore. Anus (a) positioned dorsolaterally on posterior right side of head, near to pericardium.

Circulatory and excretory system (Fig. 79C): Pericardium (pc) evident, globose, occupying half of renopericardial cavity. Auricle (au) size ~3x smaller than ventricle (vt) size, folded. Ventricle size large, occupying almost all pericardium, pear-shaped. Kidney highly branched with renal ridges forming a huge compact mass. Renal opening (rp) on top of elongated duct near to most anterior part of pericardium.

Digestive system (Fig. 77-78): Buccal mass (bm) remarkable, very large, rounded. Dorsal septate muscle (sm) composed of 8 large bundles. Oral sphincter (os) short, length ~6x smaller than dorsal septate muscle length. Ascus musculature (ma) thin and elongated, occupying only 1/3 of ventral side of buccal mass; ascus internal in buccal mass. Odontophore region rounded. Radula with 5 well-formed teeth in ascending limb and one in formation. Leading tooth triangular shaped, short, total length twice as longer as base length. Central cusp reduced and lateral cutting edges with small denticles. Ascus containing old teeth organized in spiral. Salivary glands (sg) very thick and concentrated on anterior part of esophagus between nervous ring (ns) and esophageal pouch (ep). Esophagus length twice as longer as buccal mass length, width not variable. Esophageal pouch (ep) spherical, voluminous, size as half as buccal mass size, positioned on middle of esophagus. Stomach (st) flatten, short, width similar to intestine (in) width, internally folded. Digestive gland (dg) paired in each side of stomach; anterior ducts shorter than posterior ducts, runs laterally and anteriorly inside head; posterior duct runs towards parapodial region. Intestine (in), length bit longer than esophagus length, width twice as wider as esophagus, internally folded through all its extension, finishes in dorsolateral anus (a) positioned near to pericardium.

Reproductive system (Fig. 79A-B): Gonad composed of multiple hermaphrodite follicles (hf) forming continuous area on central region of body. Follicles size few variable, size ~4x smaller than genital receptacle (gr). Hermaphrodite ducts (hd) connect all follicles at one main central duct, which runs toward ampulla (am). Hermaphrodite ampulla separated from hermaphrodite duct, positioned centrally on body, posterior to mucus gland (mg), size bit larger than genital receptacle. Bursa copulatrix (bc) with its own aperture near to female opening, positioned on right side of mucus glang, size twice as larger as genital receptacle; connected to genital receptacle and then to glandular oviduct at first chamber. Male duct (md) connects prostate gland (pr) and vas deferens (vd) to hermaphrodite duct before albumen gland (ag) connection at first chamber. Prostate gland highly branched over all follicles, composed of one main glandular duct. Penis (p) size ~3x smaller than mucus gland size, shape conic and short, total length as longer as base length. Penial stylet absent. Vas deferens ~3x longer than penis length, slightly undulated near to penis. Oviduct (ov) starts from hermaphrodite duct after connection with male duct and forms 3 well delimited chambers completely evolved by mucus gland and finishes on female aperture (fp) in lateral groove. First chamber of mucus gland very small, rounded, darker, where albumen gland and male duct connect to oviduct. Middle chamber of mucus gland bigger one, formed by a curved expansion of glandular oviduct; last chamber elongated. Albumen gland (ag) composed of many dorsal thin branches mixed with prostate gland.

Nervous system (Fig. 79D-E): Cerebro-pleural ganglia (cp) size as larger as pedal ganglia (pd); each one has 4 innervations; commissure cerebro-pleural reduced. Optic nerve length bit shorter than cerebro-pleural ganglion length. Buccal ganglia (bu) large, size ~2x larger than sub-intestinal ganglion (sb), with accessory ganglion ~4x smaller than buccal ganglion. Buccal commissure simple, short, bit smaller than buccal ganglion length. Pedal ganglia present 4 innervations by ganglion. Pedal commissure very short. Visceral loop very short. Abdominal ganglion (ab) size twice as small as pedal ganglion size, with 2 innervations. Sub-intestinal ganglion size ~3x as small as supra-intestinal ganglion (sp), has 1 innervation. Supra-intestinal ganglion size bit smaller than abdominal ganglion, with 1 innervation. Connective tissue between supraintestinal ganglia ~3x longer than connective between subintestinal and abdominal ganglia.

Distribution: Mediterranean Sea.

Material examined: PORTUGAL, Azores, São Jorge, Fajã de Santo Cristo, Lisboa, MASP 97355, 2 specimens (V. Padula, 30/viii/2007); GREECE, Agia Pelagia, Crete, MZSP 162634, 2 specimens.

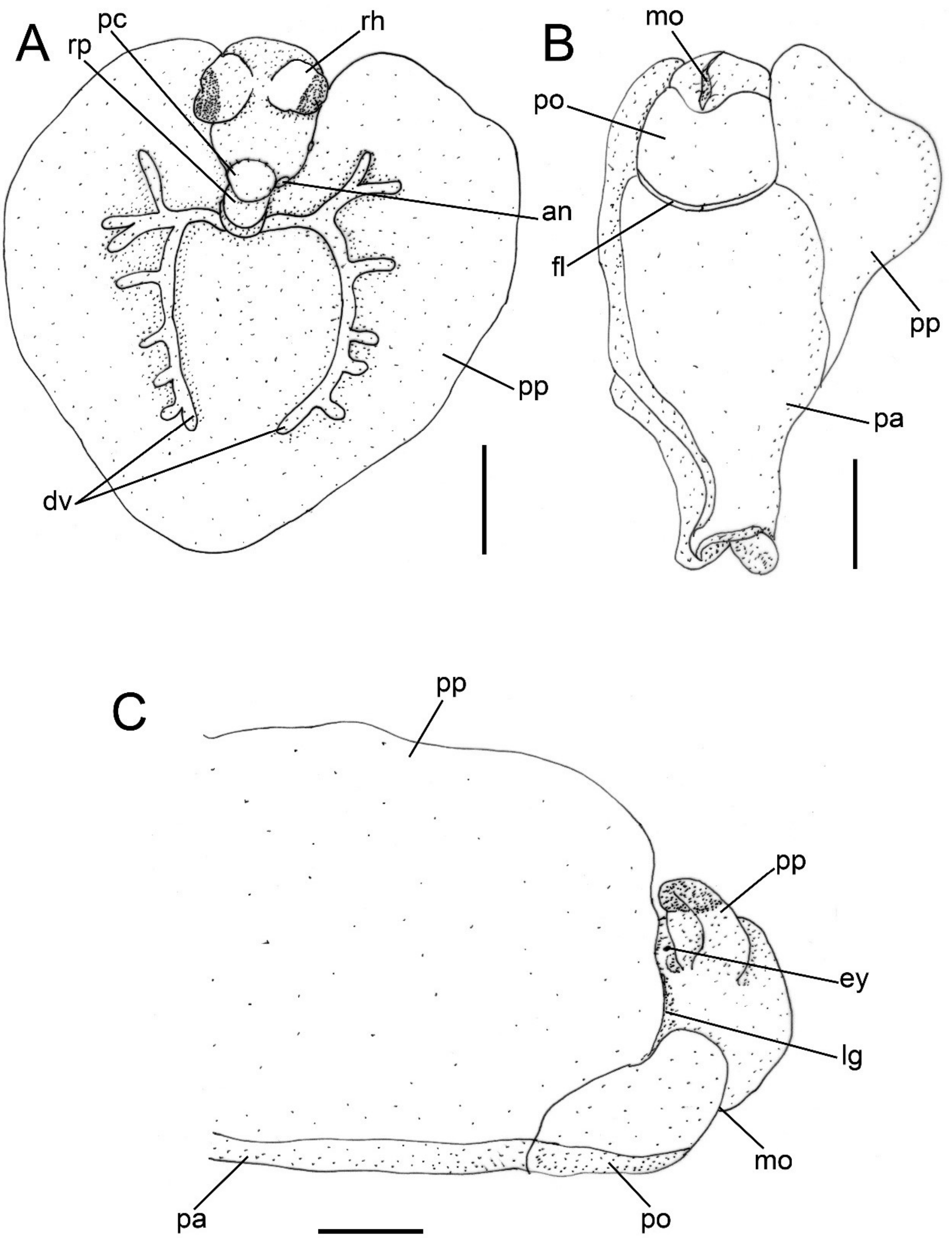

Figure 76. External morphology of *Thuridiila hopei*. A) dorsal view; B) ventral view; C) lateral right view. Scales: 0.5 mm

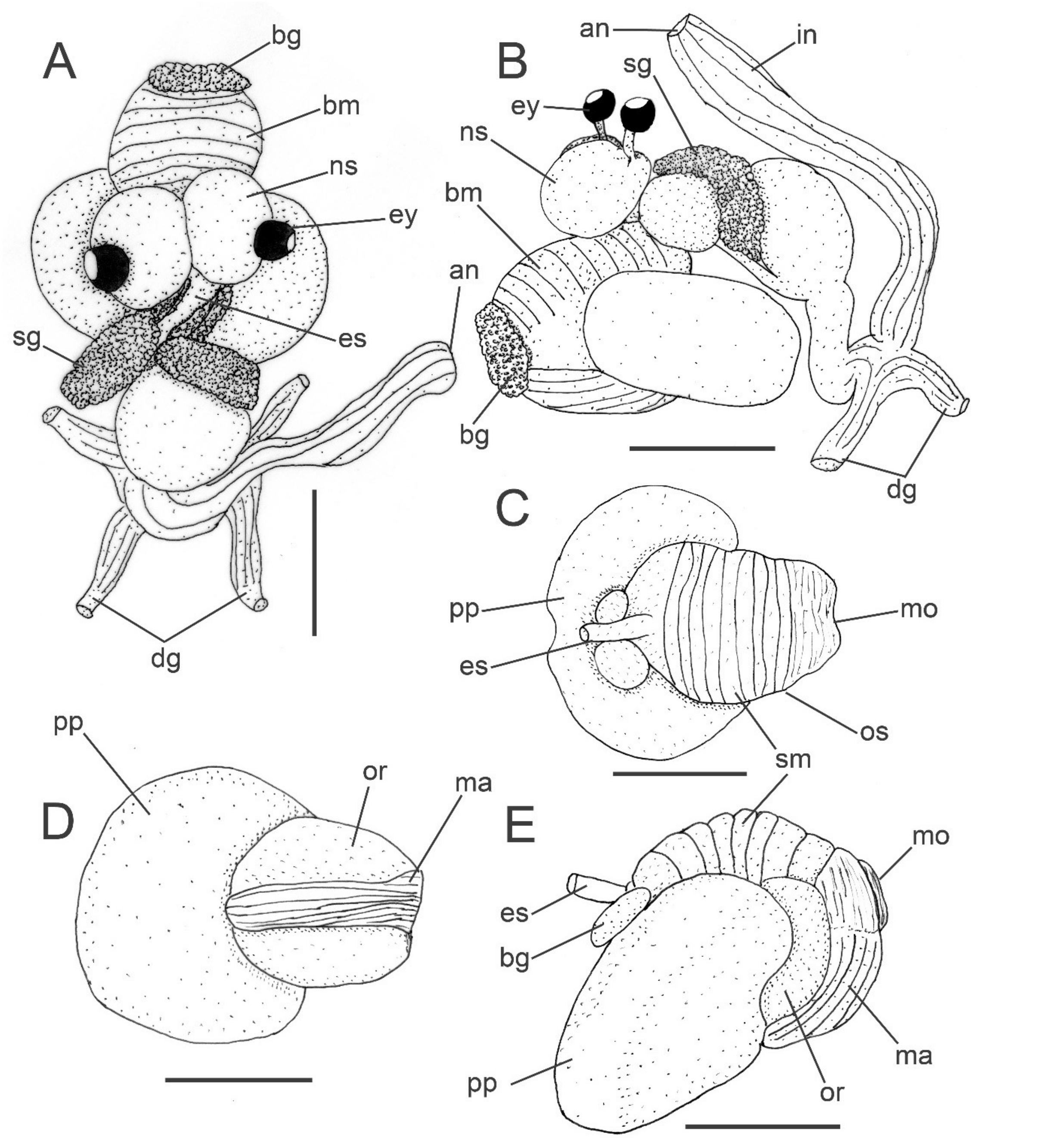

Figure 77. Digestive system of *Thuridilla hopei*. A) Dorsal view; B) Lateral view; Buccal mass: C) dorsal view side; D) ventral side. E) lateral right view. Scales: 0.5mm

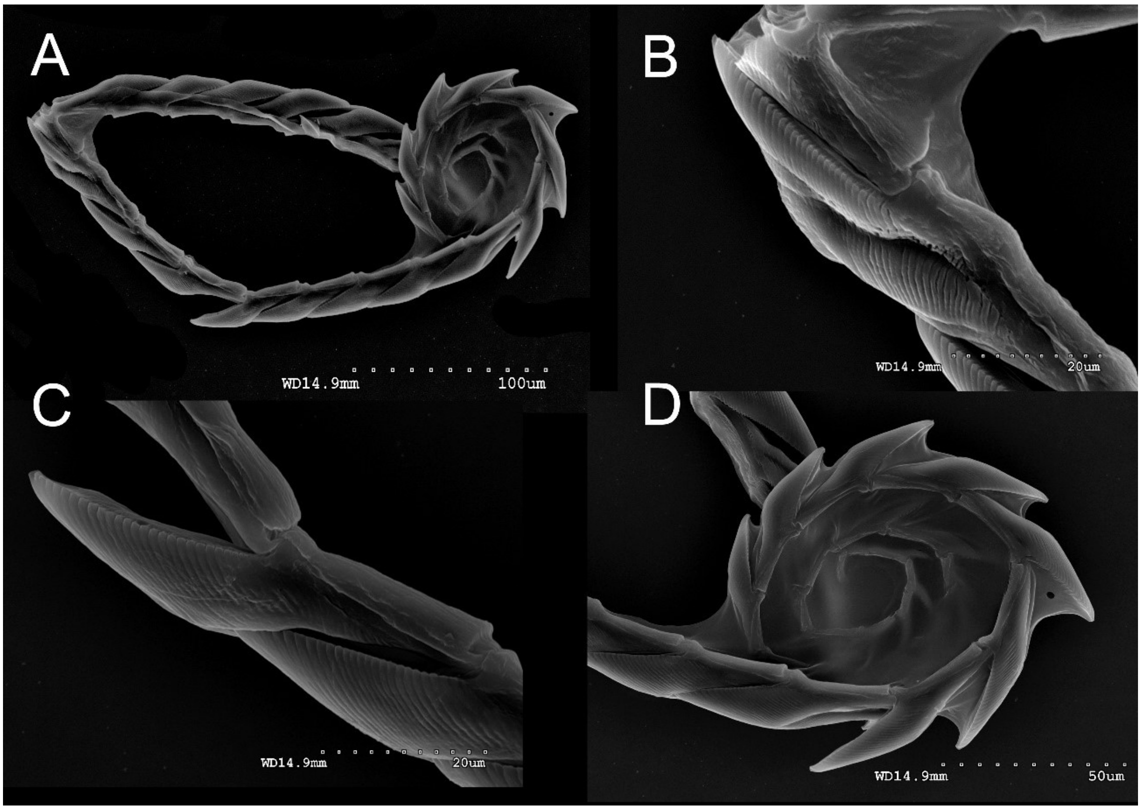

Figure 78. Scan electron microscope images of radula *Thuridilla hopei* : A) general view; B) detail of the leading tooth; C) detail of older tooth; D) Ascus.

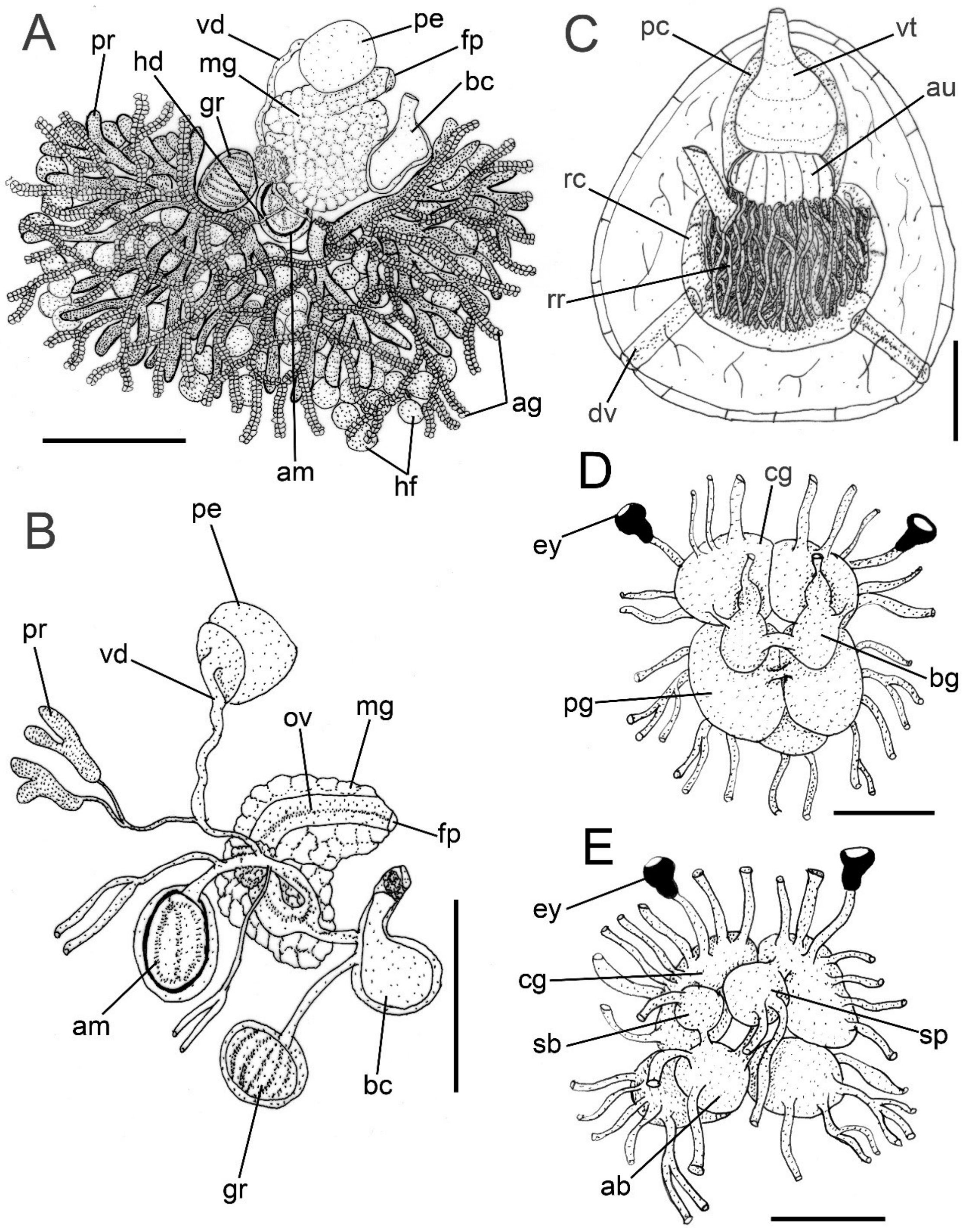

Figure 79. Anatomy of *Thuridilla hopei*. A) whole reproductive system, dorsal view; B) schematic reproductive system; C) renopericardial cavity, ventral view; D) nervous system, aneterior view; E) nervous system, posterior view. Scales A-C= 0.5 mm; D-E = 0.25 mm.

***Thuridilla picta* (Verrill, 1901)**

(Figs. 80-84)

Elysia picta Verrill, 1901: 30-31, pl. 4, fig. 2; Thompson, 1977a: 217-218, fig. 1; Thompson, 1977b: 129, pl. 1f, fig. 26g, 27c-e; Marcus, 1980: 66-67, fig. 13, 33, 34, 54; Ortea, Luque & Templado, 1988: 243, fig. 1-2.

Elysia duis Marcus & Marcus, 1967: 31-32, fig. 33-37; 1970:47, fig. 4 f.

Thuridilla picta Valdés et al., 2006: 58-59; Malaquias *et al*., 2009: 5, fig 2F; Carmona *et al*., 2011: 9, fig. 3 D-F; Redfern, 2013: 287, fig. 296; Camacho-Gacía et al., 2014: 114.

Description

External morphology (Fig. 80-81): Body elongated with 18 mm length in live animals. Head evident, large, size ~1/3 of total body size, 2x longer than wider. Rhinophores (rh) long, length as long as head length, rolled, smooth, and with tip rounded. Eyes (ey) located dorsolaterally behind rhinophores. Parapodial sole (pa) ~3x larger than propodium (po) in live animals; anterior part of propodium bit expanded; mesopodial groove (fl) evident. Pericardium (pc) and renal prominence (rp) fused forming short globose renopericardial hump. Dorsal vessels (dv) organized in one single pair, highly branched and anastomosed multiples times, running towards parapodia edge. Parapodium (pp) large, with regular margin and do not form closure pattern or parapodial tail. Female pore (fp) located on extreme dorsal point of lateral groove (lg). Male pore (mp) below right rhinophore. Anus (a) positioned dorsolaterally on posterior right side of head, near to pericardium.

Circulatory and excretory system (Fig. 84C): similar to *T. hopei*, but with auricle (au) proportionally smaller than ventricle (vt).

Digestive system (Fig. 82-83): Similar to *T. hopei* except for the following. Buccal mass (bm) with pharyngeal pouch (ph) and oral sphincter (os) larger. Radula with 9 well-formed teeth in ascending limb and 2 others in formation. Salivary glands (sg) less thick and more elongated, trespassing esophageal pouch (ep).

Reproductive system (Fig. 84A-B): Similar to *T. hopei* with the following exceptions. Hermaphrodite ampulla (am) and bursa copullatrix with similar size and ~2x smaller than genital receptacle (gr). Prostate gland (pr) branched only over more central follicles. Penis (pe) more elongated than *T. hopei*, total length twice as longer as base length. Vas deferens ~2x longer than penis length. First chamber of mucus gland (mg) proportially larger.

Nervous system (Fig. 84D-E): Similar to *T. hopei* with the following exceptions. Cerebro-pleural ganglia (cp) 6 innervations. Optic nerve length much shorter than cerebropleural ganglion. Buccal ganglia (bu), size ~2x smaller than sub-intestinal ganglion (sb), with accessory ganglion ~3x smaller than buccal ganglion. Pedal ganglia (pg) with pedal commissure bit longer and more evident than in *T. hopei*. Sub-intestinal (sb) ganglion size ~2x as small as supra-intestinal ganglion (sp). Supra-intestinal with 2 innervations. Connective tissue between supraintestinal ganglia and abdominal ganglia (ab) reduced.

Distribution: Caribbean to Brazil.

Remarks:

Thuridilla picta was originally described as belonging to the genus *Elysia* by Verrill (1901). Later Marcus & Marcus (1967) described *Elysia duis* with a similar coloration but synonymized with *Elysia picta* by Thompson (1977a) after a study of a topotype specimen and confirmed by Thompson (1977b) and Marcus (1980). Jensen (1992) in a bigger review of the genera in the family Elysiidae (=Plakobranchidae), placed *Elysia picta* and other twelve species into the genus *Thuridilla*, arguing that external and internal features unite them, and proved phylogenetically later by Gosliner (1995).

Thuridilla picta was previously considered amphiatlantic by some authors (ORTEA, LUQUE & TEMPLADO, 1988; CERVERA *et al*., 2004; VALDÉS *et al.*, 2006; MALAQUIAS *et al*., 2009) and conspecific with *Thuridilla hopei* in Eastern Atlantic. Later Carmona *et al.* (2011) point it out that *T. picta* exclusive occurs in Western Atlantic, while the Eastern specimens are molecular distinct and then they really are *T. hopei* with various color patterns. A pattern color of *T. hopei* similar to *T. picta* were found in Azores (MALAQUIAS *et al.*, 2009; CARMONA *et al.*, 2012), the same place where *Thuridilla mazda* were found for the first time in Eastern Atlantic

(MALAQUIAS *et al*., 2011). As *T. picta* is poorly known in relation to biology and morphology, a larger study is needed to confirm an exclusive Western Atlantic distribution. Possibly *T. picta* occurs in Cape Verde and Canary Islands too, as recorded by Ortea, Luque & Templado (1988).

Material examined: BRAZIL, Atol das Rocas, Rio Grande do Norte, CMPHRM 2990B, 2 specimens (14/ii/2009); CMPHRM 2998B, 4 specimens (15/ii/2009).

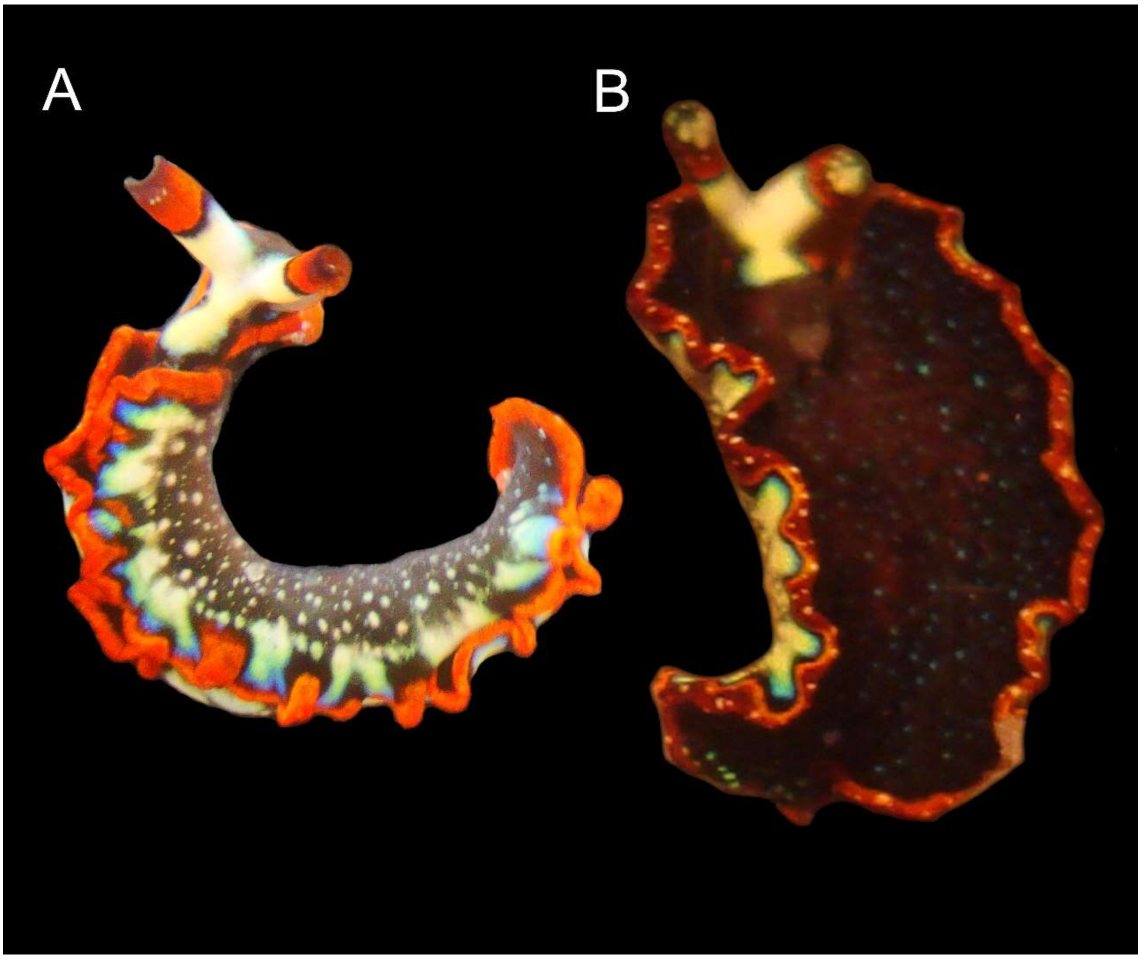

Figure 80. Live specimens of *Thuridiila picta*. A) dorsal view with closed parapodia; B) dorsal view with oppend parapodia. Body length: 18 mm.

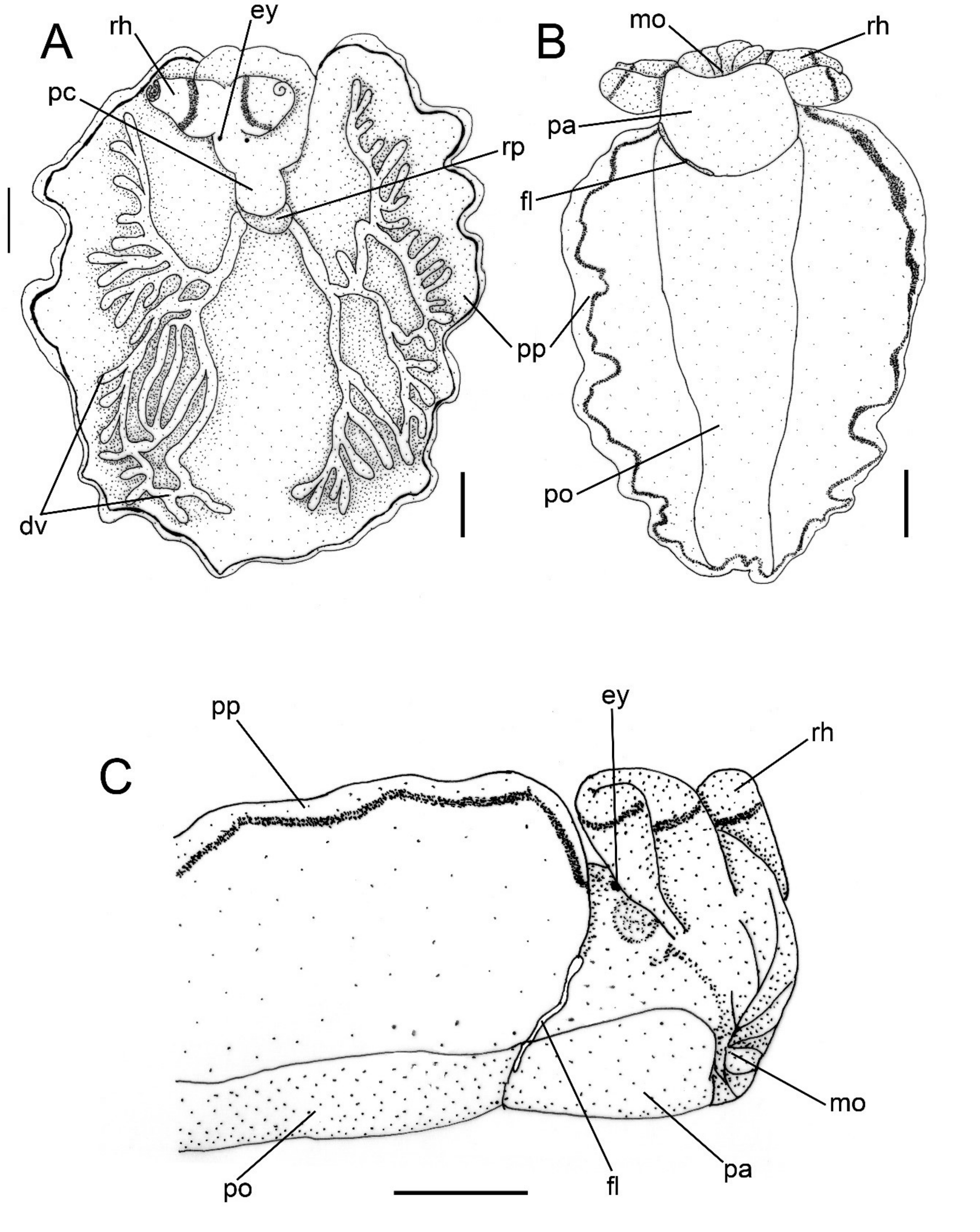

Figure 81. External morphology of *Thuridiila picta*. A) dorsal view; B) ventral view; C) lateral right view. Scales: 0.5 mm.

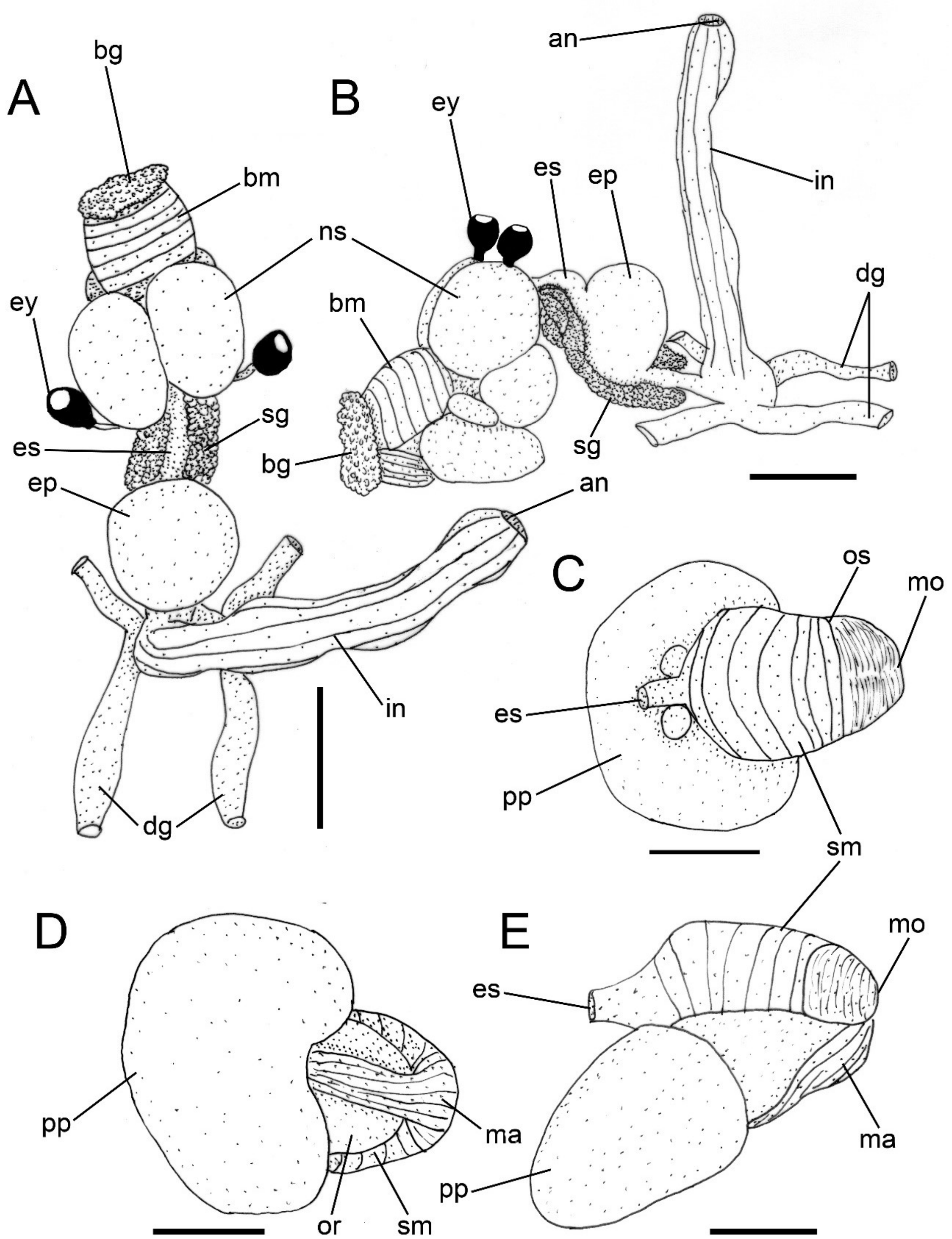

Figure 82. Digestive system of *Thuridilla picta*. A) Dorsal view; B) Lateral view; Buccal mass: C) dorsal view side; D) ventral side. E) lateral right view. Scales: 0.5mm

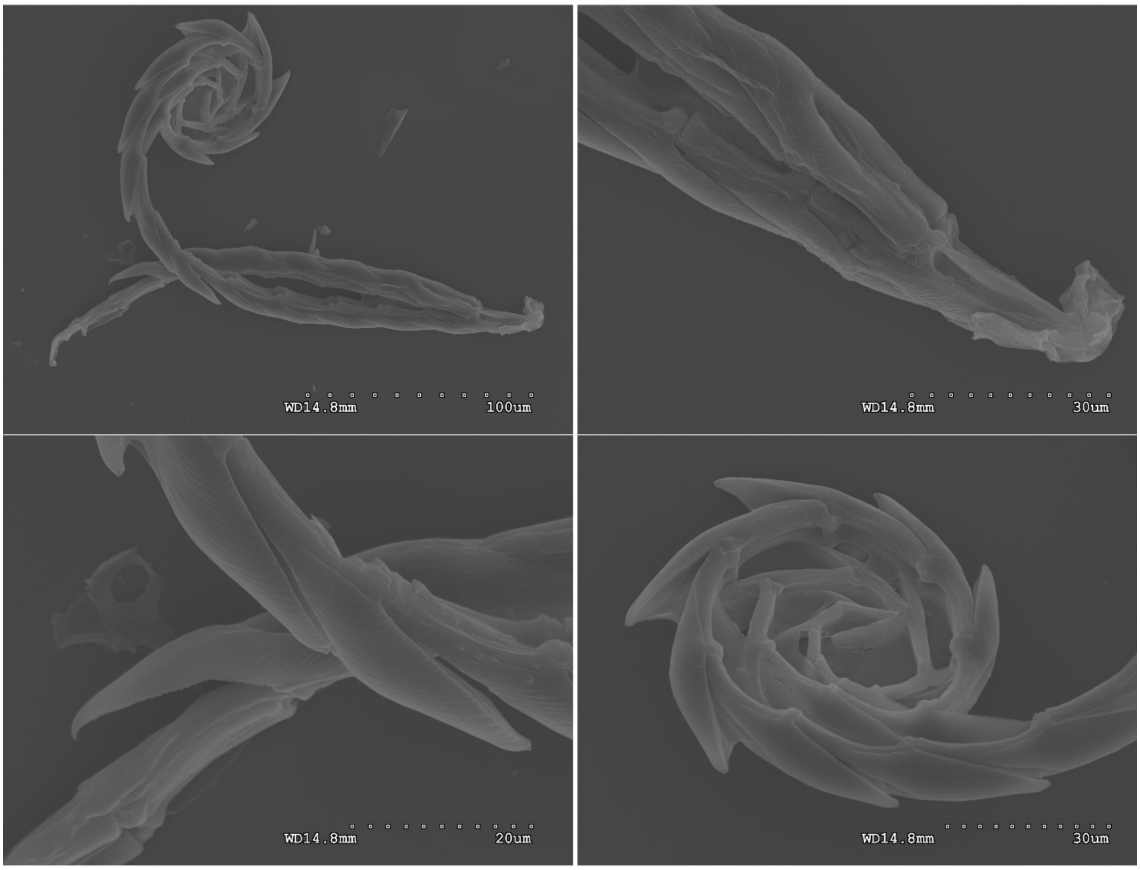

Figure 83. Scan electron microscope images of radula *Thuridilla picta*: A) general view; B) detail of the leading tooth; C) detail of older tooth; D) Ascus.

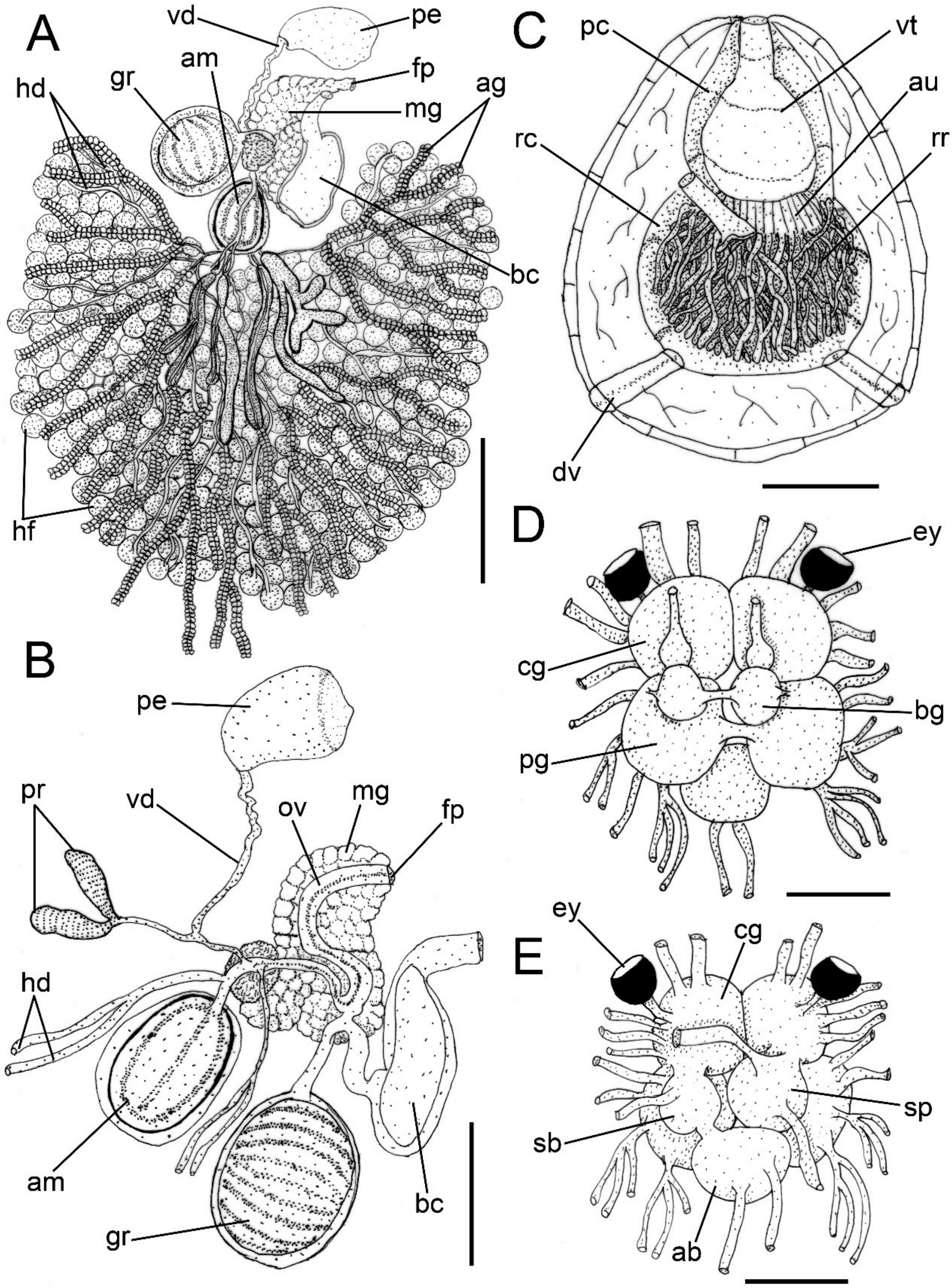

Figure 84. Anatomy of *Thuridilla picta*. A) whole reproductive system, dorsal view; B) schematic reproductive system; C) renopericardial cavity, ventral view; D) nervous system, aneterior view; E) nervous system, posterior view. Scales A-C= 0.5 mm; D-E = 0.25 mm.

***Thuridilla mazda* Ortea & Espinosa, 2000**

(Figs. 85-89)

Thuridilla mazda Ortea & Espinosa, 2000: 88-90 (Pl. 1); Malaquias *et al*., 2011: 1-3 p. (Fig. 1); Redfern, 2013: 287 (Fig. 795 A-B); Camacho-Gacía *et al*., 2014: 114.

Description

External morphology (Fig. 85-86): Body elongated with 5 mm length in live animals. Head evident, large, size ~1/3 of total body size, 2x longer than wider. Rhinophores (rh) long, length as long as head length, rolled, smooth, and with tip bit tapered. Eyes (ey) located dorsolaterally behind rhinophores. Parapodial sole (pa) ~3x larger than propodium (po) in live animals; anterior part of propodium bit expanded; mesopodial groove (fl) evident. Pericardium (pc) and renal prominence (rp) fused forming short globose renopericardial hump. Dorsal vessels (dv) organized in one single pair, not branched. Parapodium (pp) large, with regular margin and do not form closure pattern or parapodial tail. Female pore (fp) located on extreme dorsal point of lateral groove (lg). Male pore (mp) below right rhinophore. Anus (a) positioned dorsolaterally on posterior right side of head, near to pericardium.

Circulatory and excretory system (Fig. 89C): similar to *T. hopei*, but kidney is proportionally smaller than pericardium.

Digestive system (Fig. 87-88): Similar to *T. hopei* except for the following. Buccal mass (bm) with pharyngeal pouch (ph) smaller and oral sphincter (os) larger. Radula tooth more elongated and poited, with lateral cutting edge well-marked, ascus not in spiral. Ascending limb with 5 well-formed teeth and 2 others in formation. Salivary glands (sg) less thick as in *T. picta*, but longer. Esophageal pouch (ep) proportionally smaller than buccal mass.

Reproductive system (Fig. 89A-B): Similar to *T. hopei* with the following exceptions. Hermaphrodite ampulla (am) much bigger, bit smaller than mucus gland (mg) size and ~6x bigger than genital receptacle (gr). Penis (pe) very elongated, total length ~4x longer than base length. Vas deferens ~2x longer than penis length. First chamber of mucus gland (mg) proportially larger. Bursa copulatrix absent and genital receptacle is directly connected to oviduct at first chamber.

Nervous system (Fig. 89D-E): Similar to *T. hopei* with the following exceptions. Cerebro-pleural ganglia (cp) with 6 innervations. Buccal ganglia (bu) with accessory ganglion ~4x smaller than buccal ganglion. Pedal ganglia (pg) with pedal commissure bit longer and more evident than in *T. hopei*. Abdominal ganglion (ab) size as half as pedal ganglion size. Sub-intestinal (sb) ganglion size ~2x as small as supra-intestinal ganglion (sp). Connective tissue between supraintestinal ganglia and abdominal ganglia reduced.

Distribution: Amphi-Atlantic: Azores; Caribbean to Brazil.

Remarks: The most remarkable features of *T. mazda* were present in original description. The authors distinguish the only two Western Atlantic *Thuridilla* species by color pattern of the body, shape and length of rhinophores (triangle and shortest in *T. mazda*) and radulae length. Malaquias *et al*. (2011) report this species to the Eastern Atlantic Ocean, in Azores Island. The specimens found were compared only by color pattern, which match almost exactly except by the lighter colors. Another difference is the body length, the eastern specimen has 17 mm while the western specimens were commonly reported with 5-8 mm (VALDÉS & ESPINOSA, 2000; REDFERN, 2013) (ORTIGOSSA *et al*., 2013 found one with 13 mm). Malaquias *et al*. (2011) mentioned the importance of a molecular distinction test between Caribbean and Azorean population, but we reinforce that the morphology of this species is almost unknown, and this is also necessary. *Thuridilla mazda* was found for the first time in Brasil in Rocas Atoll, where the occurrence of *T. picta* was reported too.

Material examined: BRAZIL, Atol das Rocas, Rio Grande do Norte, CMPHRM 4250B, 1 specimen (H. Galvão Filho; C. Meirelles, 31/viii/2014).

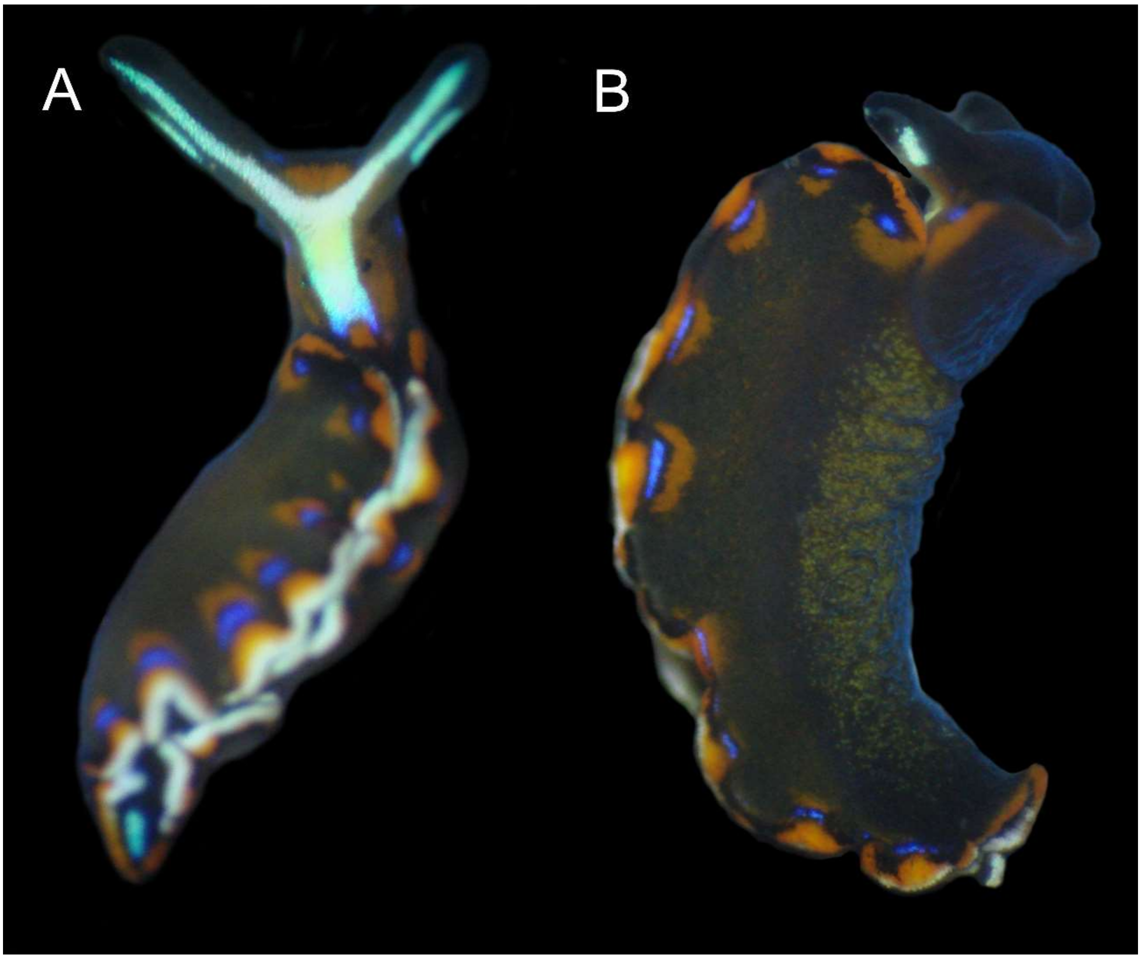

Figure 85. Live specimens of *Thuridiila mazda*. A) dorsal view with closed parapodia; B) lateral. Body length: 5 mm.

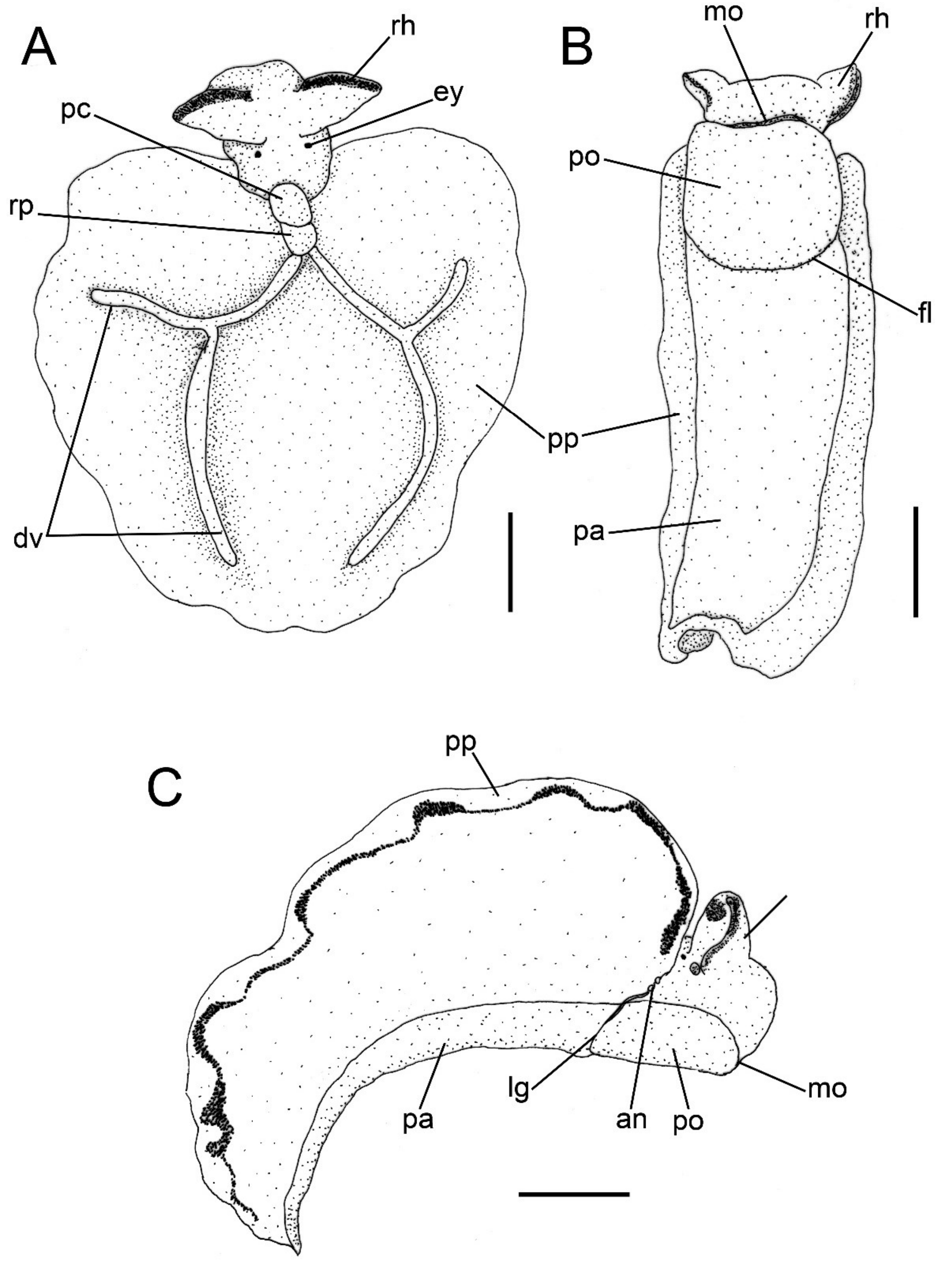

Figure 86. External morphology of *Thuridiila mazda*. A) dorsal view; B) ventral view; C) lateral right view. Scales: 0.5 mm

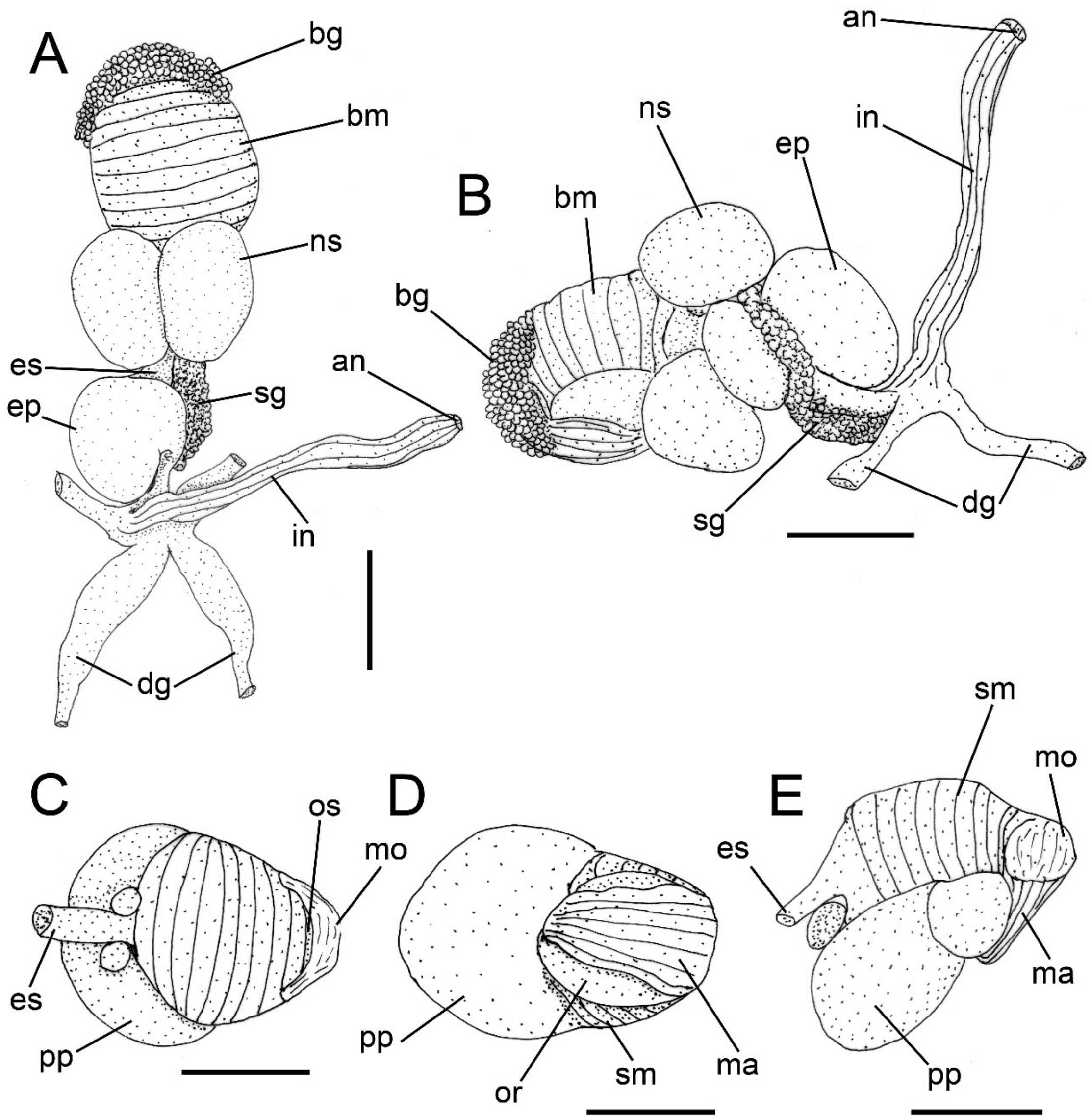

Figure 87. Digestive system of *Thuridilla mazda*. A) Dorsal view; B) Lateral view; Buccal mass: C) dorsal view side; D) ventral side. E) lateral right view. Scales: 0.5mm

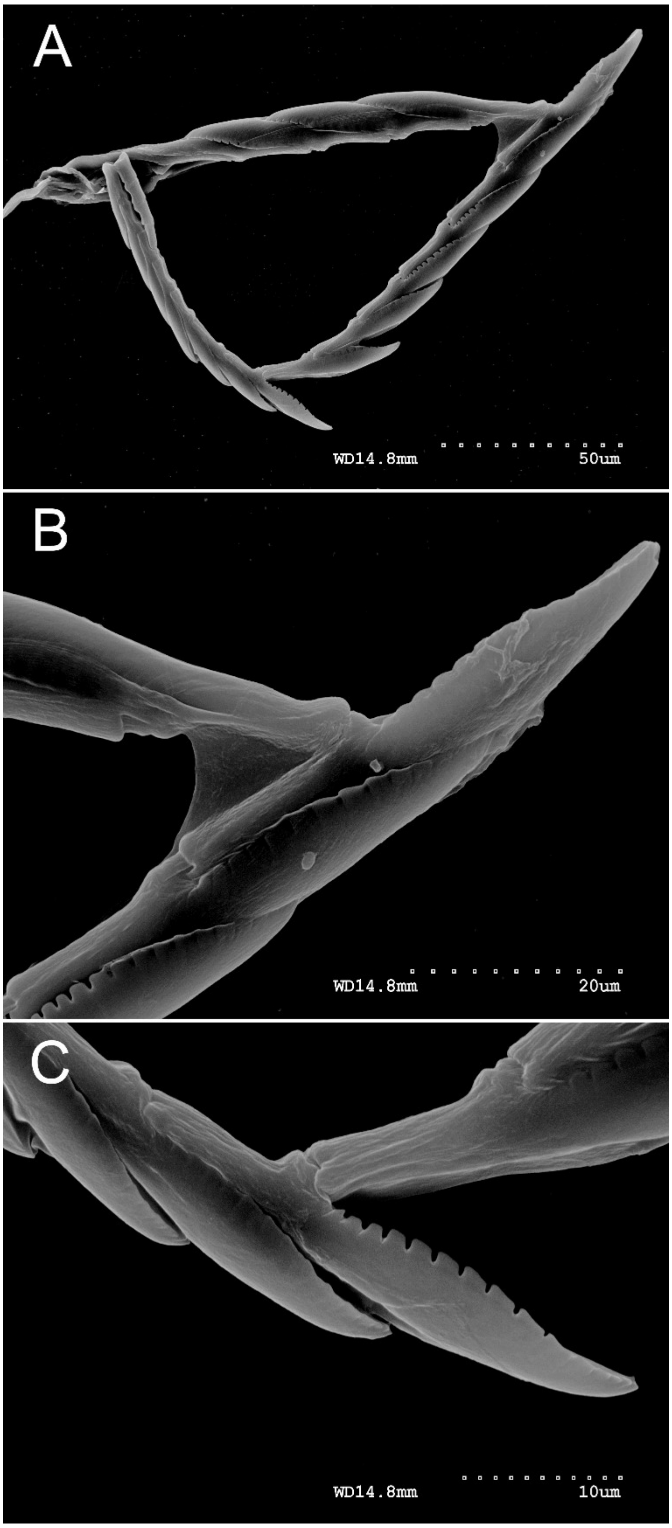

Figure 88. Scan electron microscope images of radula *Thuridilla mazda*: A) general view; B) detail of the leading tooth; C) detail of older tooth.

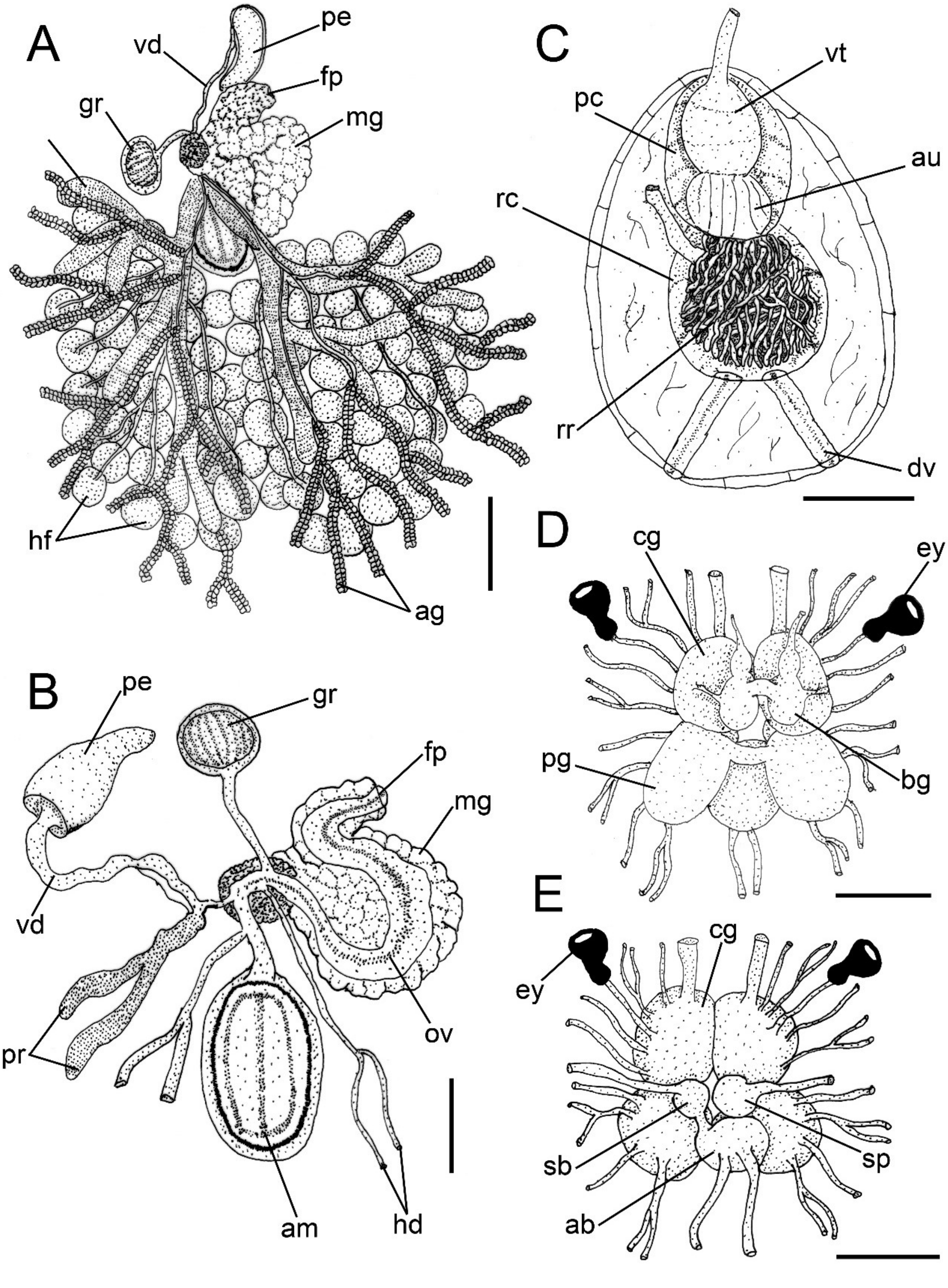

Figure 89. Anatomy of *Thuridilla mazda*. A) whole reproductive system, dorsal view; B) schematic reproductive system; C) renopericardial cavity, ventral view; D) nervous system, aneterior view; E) nervous system, posterior view. Scales A-C= 0.5 mm; D-E = 0.25 mm.

Genus *Elysia* Risso, 1818

Elysia Risso, 1818. Tyoe species *Elysia timida* Risso, 1818 by monotypy

Laplysia Montagu, 1840. Type species *Laplysia viridis* Montagu, 1840 by monotypy

Actaeon Ferrusac, 1819. Type species *Laplysia viridis* Montagu, 1840

Aplysiopterus Delle Chiaje, 1830. Type species *Aplysiopterus neapoliatanus* Delle Chiaje, 1830 by monotypy

Rhyzobranchus Contraine, 1835. Type species *Laplysia viridis* Montagu, 1840 by designação original.

Thallepus Swainson, 1840. Type species *Thallepus ornatos* Swainson, 1840 by monotypy

? *Pterogasteron* Pease, 1860. Type species *Pterogasteron ornatum* Pease, 1860 by monotypy

Elysiella Verrill, 1872. Type species *Plakobranchus catulus* Gould, 1870 by original designation.

? *Elysiobranchus* Pruvot-Fol, 1930. Type species *Elysiobranchus mercieri* Pruvot-Fol, 1930 by monotypy

? *Elysiopterus* Pruvot-Fol, 1946. Type species not designed.

Checholysia Ortea *et al*., 2005. Type species not designed.

***Elysia timida* Risso, 1818**

(Figs. 90-94)

External morphology (Figs. 90): Body elongated, smooth, reaching up to 10 mm in live animals. Head evident, with scattered small papillae, length as half as body length, 2x longer than wider. Rhinophores (rh) rolled, smooth, long, length as longer as head length, and with rounded tip; papillae small through all rhinophore length. Eyes (e) dorsolateral behind rhinophores. Foot (f) easily distinguished from parapodia. Mesopodial groove (fl) conspicuous. Parapodial sole (ps) length bit longer than propodium (po) length in live animals; anterior part of propodium rounded. Renopericardial cavity (rc) remarkable, well subdivide into pericardium (pc) and renal pad (rp), length ~5x smaller as parapodial length. Pericardium (pc) muscular, globose, bit elongated longitudinally, with small papillae. Renal pad very short, attached to pericardium. Dorsal vessels (dv) organized in one symmetric pair, branching anteriorly and posteriorly several times Parapodium (pp) large, with irregular edge and papillae on external surface. Tail absent. Lateral groove (lg) starts on anterior extreme of right parapodia, where female bye (fp) is positioned, and finishes left to middle point of foot line. Male bye (mp) positioned below to right rhinophore. Anus (a) positioned dorsolaterally on posterior right side of head, close to anus.

Circulatory and excretory system (Fig. 94): Pericardium (pc) evident, globose, occupying half of renopericardial cavity. Auricle (au) large, size as half as ventricle (vt) size and with wall smooth. Ventricle occupying almost all pericardium, shape rounded. Kidney branched, composed of many renal ridges (rr) connected in lacunar shape. Nephrostome not observed.

Digestive system (Fig. 91-92): Buccal mass (bm) remarkable, size ~20x larger than esophageal pouch (ep), elongated, 3x longer than wider. Dorsal septate muscle (ds) composed of 10 thin bundles. Oral sphincter (os) reduced, compose of many circular muscles, size ~10x smaller than dorsal septate muscle length. Ascus musculature (ma) wide and long, occupying half of wide and all length of ventral side of buccal mass. Ascus (as) as narrowest as ascus musculature, short and rounded. Odontophore (od) rounded, parallel to oral cavity. Buccal pouch absent. Ascus containing discarded teeth not organized. Salivary glands (sg) positioned dorsal and lateral to esophagus between nervous system and stomach (st). Esophagus (es) length ~5x shorter than buccal mass length. Esophageal pouch (ep) globose and muscular, positioned on posterior part of esophagus. Stomach (st) short, flat, width as wider as intestine (in) width. Digestive gland (dg) with anterior ducts shorter than posterior ducts, run laterally and anteriorly inside head; posterior ducts run towards parapodial region. Intestine (in) internally folded through all its extension, finishes in dorsolateral anus (a) positioned near to lateral groove.

Reproductive system (Fig. 93):

Gonad composed of numerous hermaphrodite follicles (hf) forming two separated areas, each area in one side of parapodia. Follicles size few variable, size up to 5x smaller than hermaphrodite ampulla (am). Gametholitic vesicle (gv) absent. Hermaphrodite ducts (hd) connect all follicles to one central duct which connects to hermaphrodite ampullas duct, width univariable. Hermaphrodite ampulla paired, each one in each side of parapodia. Male duct (md) connects prostate gland (pr) and vas deferens (vd) to hermaphrodite duct same as preceding species. Prostate gland composed of many small clustered glands positioned among follicles. Penis (p) shape conic, curved and elongated, ~8x longer than wider. Penial stylet absent. Vas deferens (vd) curled through all its length. Oviduct (ov) starts from hermaphrodite duct after connection with male duct and forms 3 well delimited chambers completely evolved by mucus gland and finishes on female bye (fp) in lateral groove. Proximal chamber of mucus gland smallest one, rounded, albumen duct and male duct connect to oviduct in it. Second chamber of mucus gland biggest one, formed by a curved expansion of glandular oviduct, where bursa copulatrix connects with oviduct. Distally chamber short and with folds. Albumen gland (ag) composed of many dorsal thin branches over prostate gland; main duct of albumen gland runs from hermaphrodite duct, more proximal than male duct connection with hermaphrodite duct, then branches into many ducts in parapodial area dorsally to prostate gland. Genital receptacle absent. Bursa copulatrix (bc) absent.

Nervous system (Fig. 94): Cerebro-pleural ganglia (cp) bit larger than pedal ganglia (pg) size; each ganglion has 6 innervations; commissure cerebro-pleural short. Optic nerve long, bit longer than cerebro-pleural ganglion length. Buccal ganglia (bg) remarkable, size bit larger than sub-intestinal ganglion (sb); accessory ganglion absent; each ganglion has 2 innervations; buccal commissure internal. Pedal ganglia with 5 innervations by ganglion; pedal commissure simple and short, length bit smaller than pedal ganglion length. Visceral ganglia well developed. Abdominal ganglion (ab) size as half as pedal ganglion size, with 2 innervations. Sub-intestinal ganglion size ~4x as small as supra-intestinal ganglion (sp), with 1 innervation. Supra-intestinal ganglion size 3x smaller than abdominal ganglion size, with 2 innervation; connective between abdominal ganglion and sub-intestinal ganglion evident and long, length as longer as sub-intestinal ganglion; connective between abdominal ganglion and supra-intestinal long, as long as supra-intestinal ganglion length.

Distribution. Mediterranean Sea (THOMPSON & JAKLIN, 1988)

Material examined: SPAIN, Fornells, Menorca, MZSP 132627B, 1 specimen (27/v/2008), Cala Galdana, Menorca, MZSP 132626B, 1 specimen (26/v/2008).

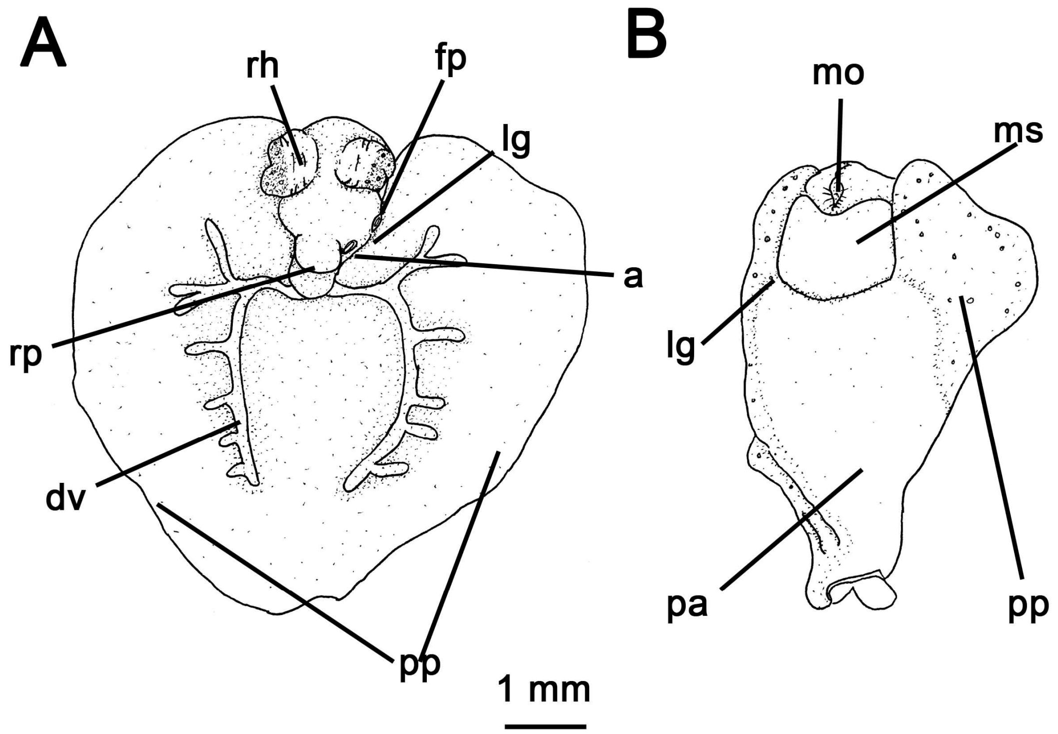

Figure 90. External morphology of *Elysia timida*. A) dorsal view; B) ventral view.

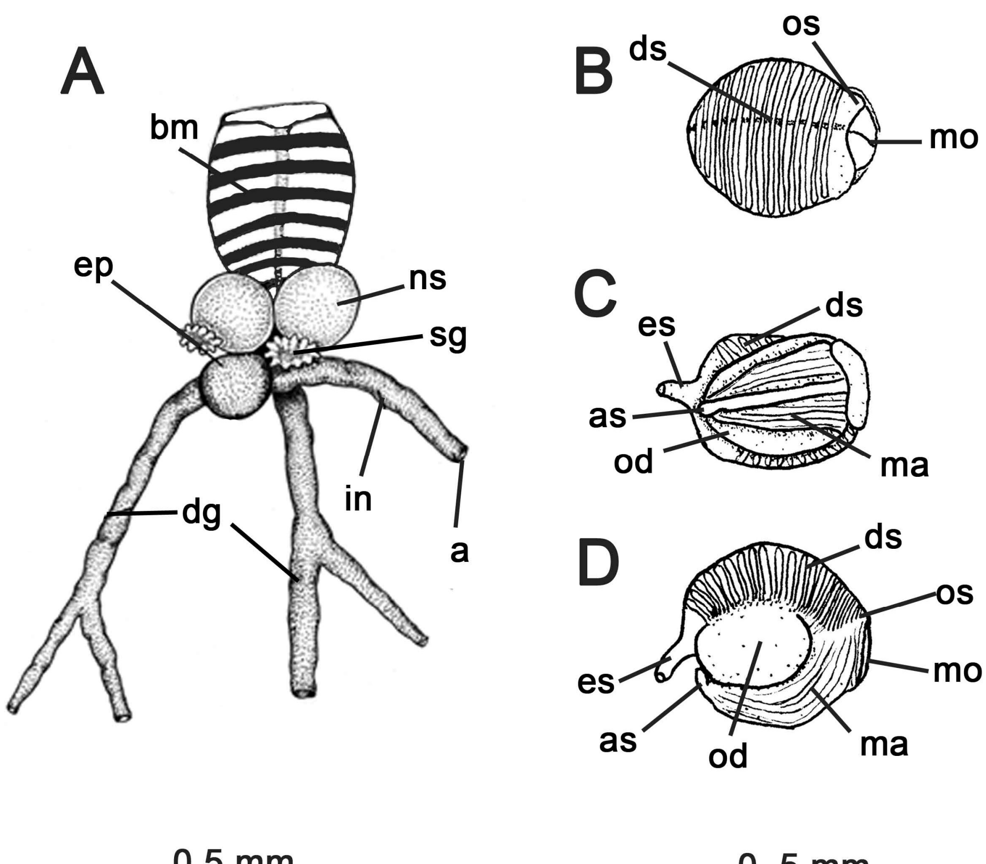

Figure 91. Digestive system of *Elysia timida*. A) Dorsal view. Buccal mass**:** B) dorsal; C) ventral; D) lateral.

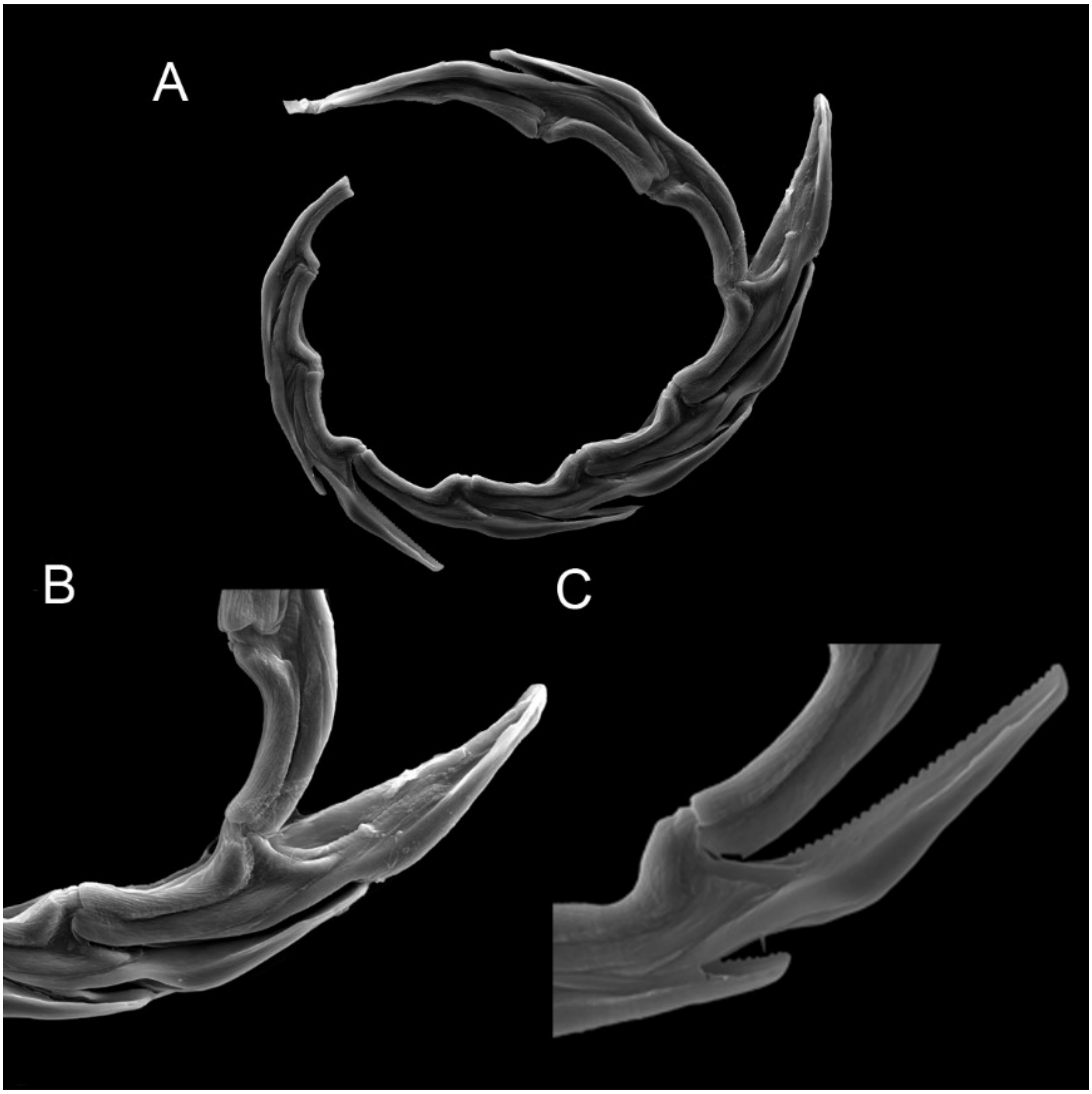

Figure 92. Scan electron microscope images of radula *Elysia timida*: A) general view; B) detail of the leading tooth; C) detail of older tooth.

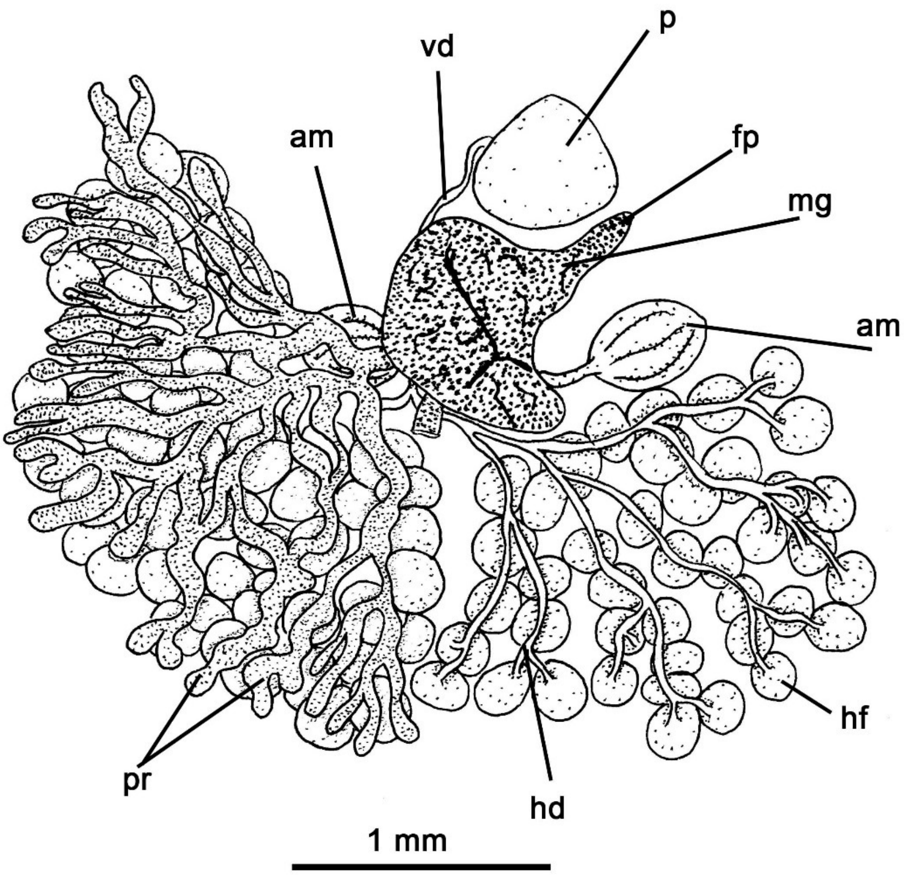

Figure 93. Reproductive system of *Elysia timida*.

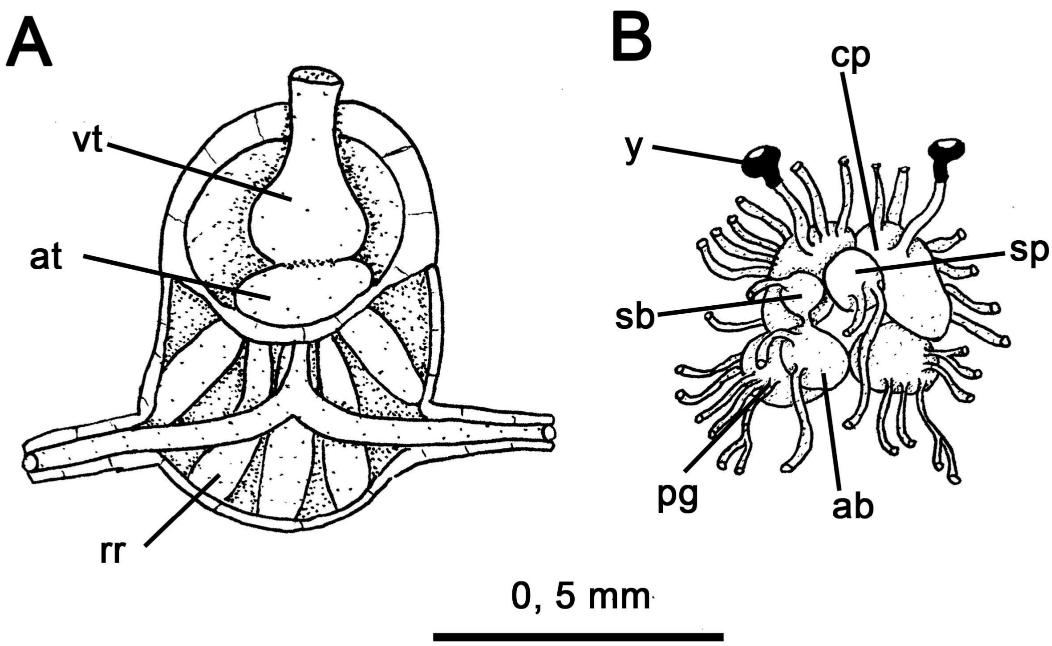

Figure 94. Circulatory and nervous systems of *Elysia timida*. A) Renopericardial cavity. B) anterior view of nervous system.

***Elysia viridis* (Montagu, 1804)**

(Figs. 95-99)

External morphology (Fig. 95): Body elongated, smooth, no papillae, reaching up to 12 mm in live animals. Head evident, length up to 1/3 of total body length, 2x longer than wider. Rhinophores (rh) rolled, smooth, short, length twice as smaller as head length, and with rounded tip; papillae absent. Eyes (e) dorsolateral behind rhinophores. Foot (f) inconspicuous and hard to distinguish from parapodia. Mesopodial groove (fl) inconspicuous. Parapodial sole (ps) length 3x longer than propodium (po) length in live animals; anterior part of propodium rounded. Renopericardial cavity (rc) remarkable, well subdivide into pericardium (pc) and renal pad (rp), length 1/6 as longer as parapodial length. Pericardium (pc) muscular, globose, bit elongated longitudinally, with no papillae. Renal pad very short, attached to pericardium. Dorsal vessels (dv) organized in 4 symmetric pairs, three anterior pairs run parallel to parapodia margin and most posterior pair runs posteriorly and branching several times Parapodium (pp) large, with irregular edge and no papillae. Tail short. Lateral groove (lg) starts on anterior extreme of right parapodia, where female bye (fp) is positioned, and finishes left to middle point of foot line. Male bye (mp) positioned below to right rhinophore. Anus (a) positioned dorsolateral on posterior right side of head, close to pericardium.

Circulatory and excretory system (Fig. 99): Pericardium (pc) evident, globose, occupying half of renopericardial cavity. Auricle (au) size ~4x smaller than ventricle (vt) size and with wall folded. Ventricle occupying half of pericardium, shape rounded. Kidney branched, composed of many renal ridges (rr) connected in trabecular shape. Nephrostome not observed.

Digestive system (Fig. 96-97): Buccal mass (bm) remarkable, size ~20x larger than esophageal pouch (ep), elongated, 2x longer than wider. Dorsal septate muscle (ds) composed of 26 thin bundles. Oral sphincter (os) reduced, compose of many circular muscles, size ~10x smaller than dorsal septate muscle length. Ascus musculature (ma) thin and long, occupying all length of ventral side of buccal mass. Ascus (as) as narrowest as ascus musculature, short and rounded. Odontophore (od) pointed, parallel to oral cavity. Buccal pouch absent. Ascus containing discarded teeth not organized. Salivary glands (sg) positioned ventrally to esophagus and stomach (st). Esophagus (es) length twice shorter than buccal mass length. Esophageal pouch (ep) globose and muscular, positioned on posterior part of esophagus. Stomach (st) short, flat, width as wider as intestine (in) width. Digestive gland (dg) with anterior ducts shorter than posterior ducts, run laterally and anteriorly inside head; posterior ducts run towards parapodial region. Intestine (in) internally folded through all its extension, finishes in dorsolateral anus (a) positioned near to lateral groove.

Reproductive system (Fig. 98): Gonad composed of numerous hermaphrodite follicles (hf) forming two separated areas, each area in one side of parapodia. Follicles size few variable, size up to 10x smaller than hermaphrodite ampulla (am). Gametholitic vesicle (gv) absent. Hermaphrodite ducts (hd) connect all follicles to one central duct which connects to hermaphrodite ampullas duct, width univariable. Hermaphrodite ampulla positioned in middle of body. Male duct (md) connects prostate gland (pr) and vas deferens (vd) to hermaphrodite duct same as preceding species. Prostate gland composed of one highly branched duct positioned on top and among follicles. Penis (p) shape conic and short, bit longer than wider. Penial stylet absent. Vas deferens (vd) curled through all its length. Oviduct (ov) starts from hermaphrodite duct after connection with male duct and forms 3 well delimited chambers completely evolved by mucus gland and finishes on female bye (fp) in lateral groove. Proximal chamber of mucus gland smallest one, rounded, albumen duct and male duct connect to oviduct in it. Second chamber of mucus gland biggest one, formed by a curved expansion of glandular oviduct, where bursa copulatrix connects with oviduct. Distally chamber short and with folds. Albumen gland (ag) composed of many dorsal thin branches over prostate gland; main duct of albumen gland runs from hermaphrodite duct, more proximal than male duct connection with hermaphrodite duct, then branches into many ducts in parapodial area dorsally to prostate gland. Genital receptacle absent. Bursa copulatrix (bc) with its own aperture.

Nervous system (Fig. 99): Cerebro-pleural ganglia (cp) size as larger as pedal ganglia (pg) size; each ganglion has 6 innervations; commissure cerebro-pleural short. Optic nerve long, length twice as longer as cerebro-pleural ganglion length. Buccal ganglia (bg) remarkable, size bit larger than sub-intestinal ganglion (sb); accessory ganglion absent; each ganglion has 2 innervations; buccal commissure internal. Pedal ganglia with 4 innervations by ganglion; pedal commissure simple and long, length as longer as pedal ganglion length. Visceral ganglia well developed. Abdominal ganglion (ab) size as half as pedal ganglion size, has 3 innervations. Sub-intestinal ganglion size ~5x as small as supra-intestinal ganglion (sp), with 1 innervation. Supra-intestinal ganglion size 4x smaller than abdominal ganglion size, with 1 innervation; connective between abdominal ganglion and sub-intestinal ganglion evident and long, length as longer as sub-intestinal ganglion; connective between abdominal ganglion and supra-intestinal short.

Distribution: Baltic Sea and Mediterranean Sea (THOMPSON, 1988).

Material examined: DENMARK, Roskilde Fjord, MZSP 122698, 8 specimens (K. Jensen, ix/2013).

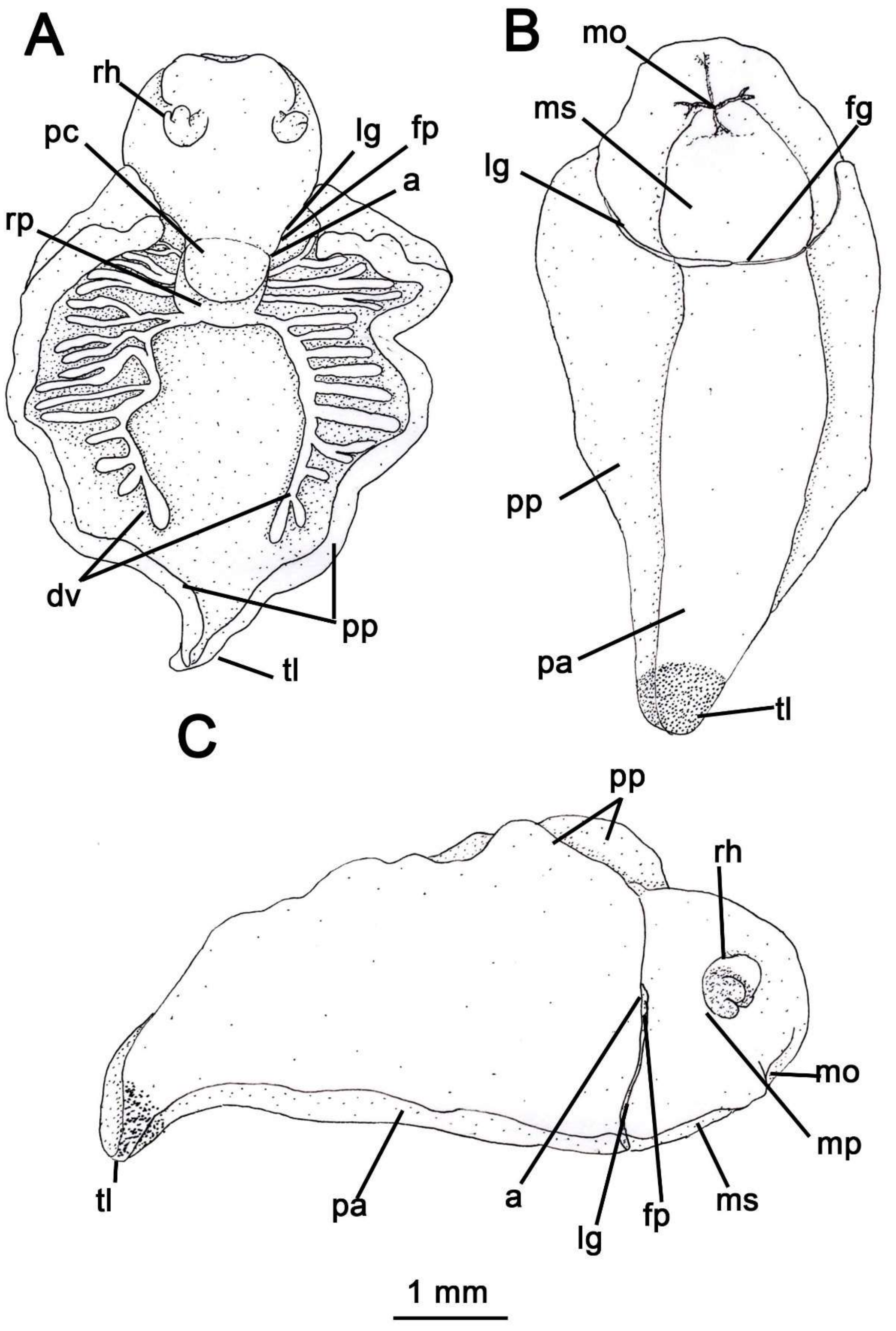

Figure 95. External morphology of *Elysia viridis*. A) dorsal; B) ventral; C) lateral.

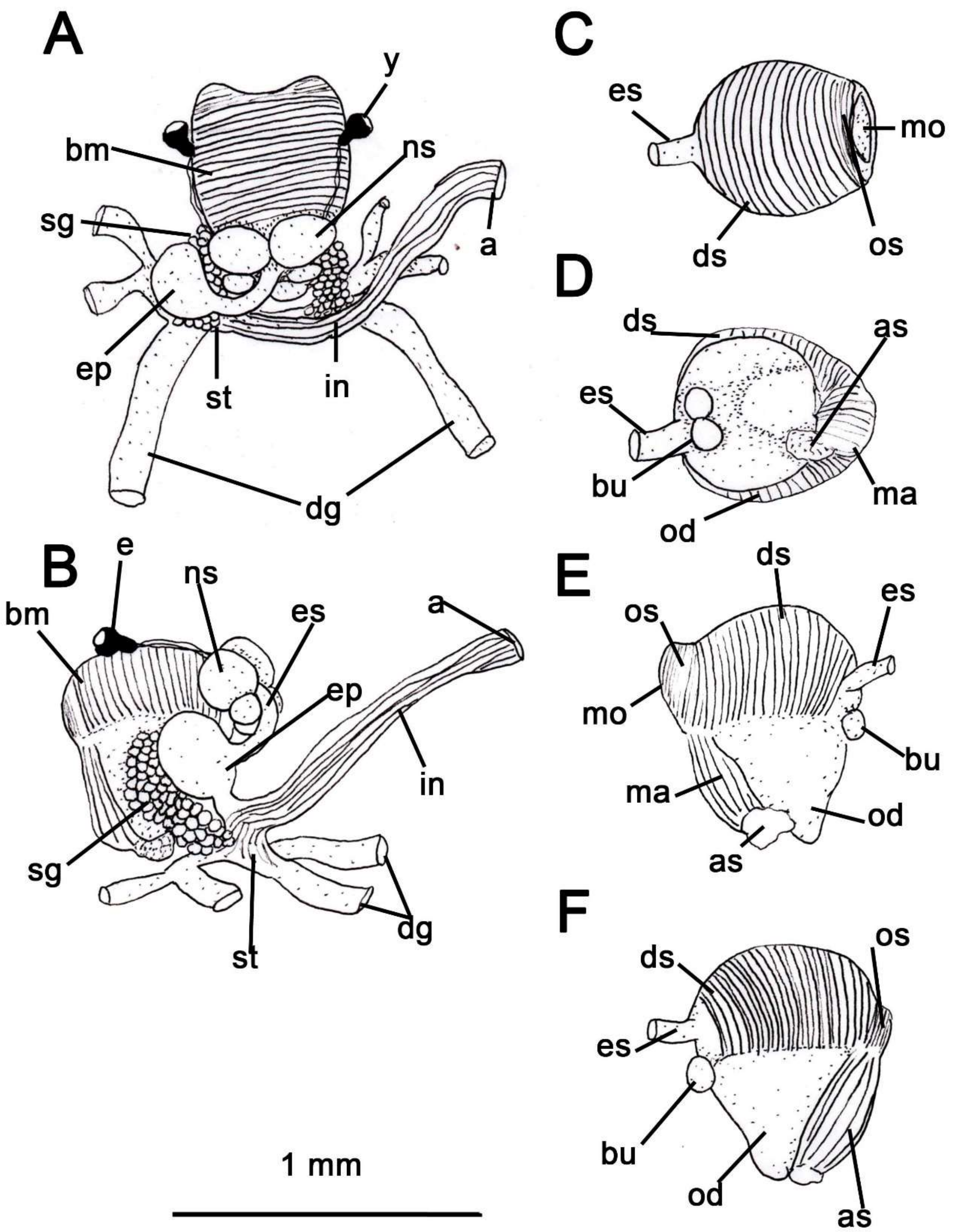

Figure 96. Digestive system of *Elysia viridis*. A) Dorsal view; B) Lateral view; Buccal mass: C) dorsal; Buccal mass: D) ventral; E) left side; F) right side.

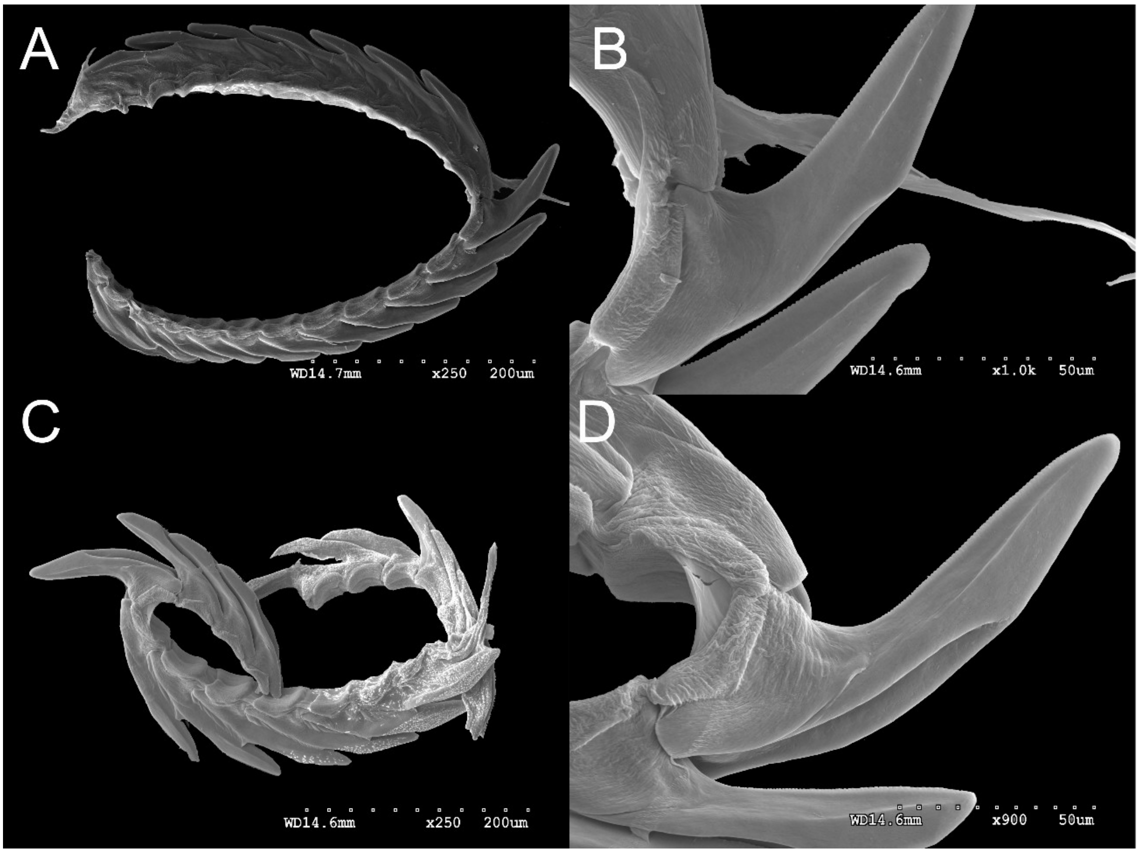

Figure 97. Scan electron microscope images of radula *Elysia viridis*: A-C) general view; B-D) detail of the leading tooth.

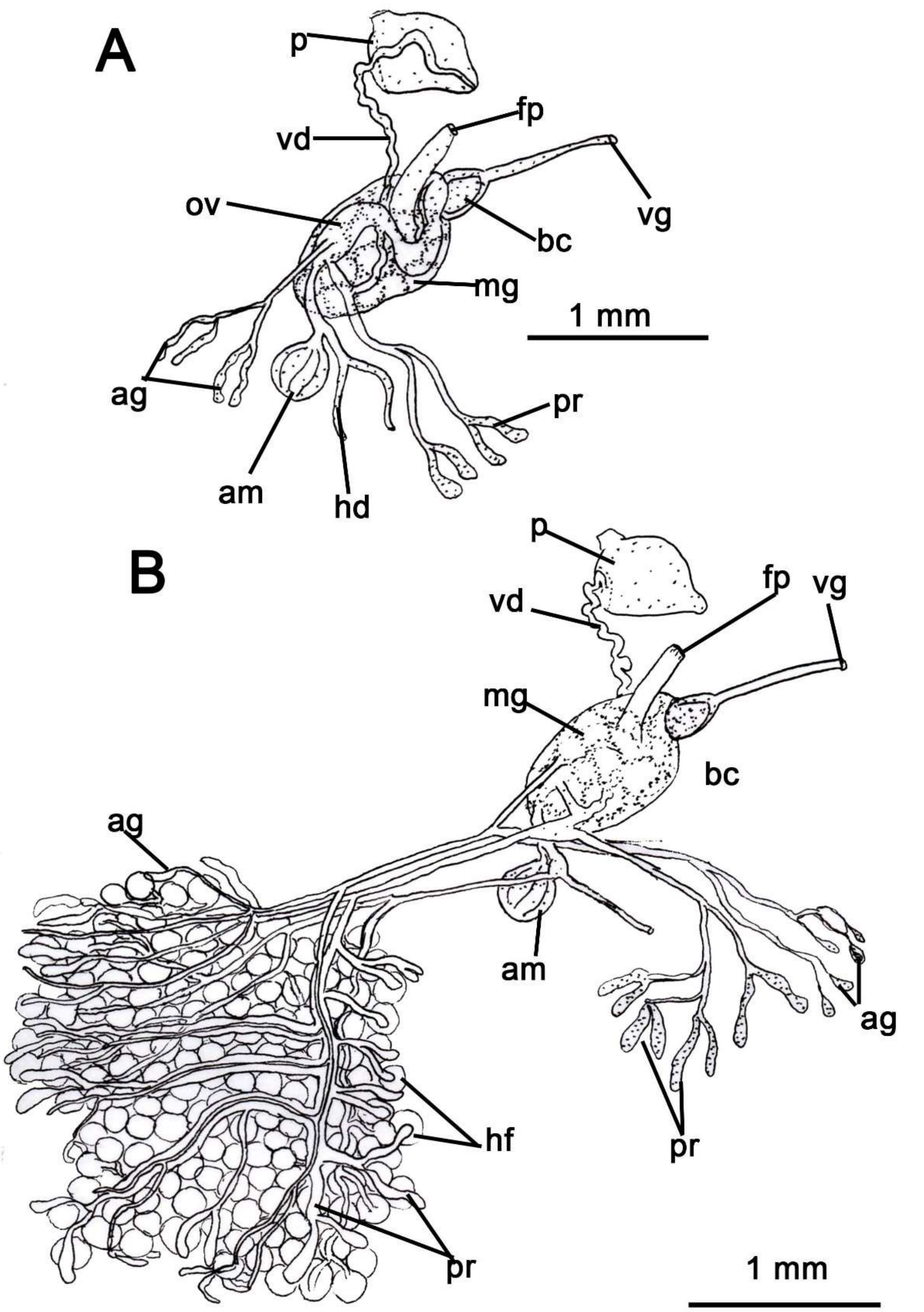

Figure 98. Reproductive system of *Elysia viridis*. A) Schematic drawing; B) Overview.

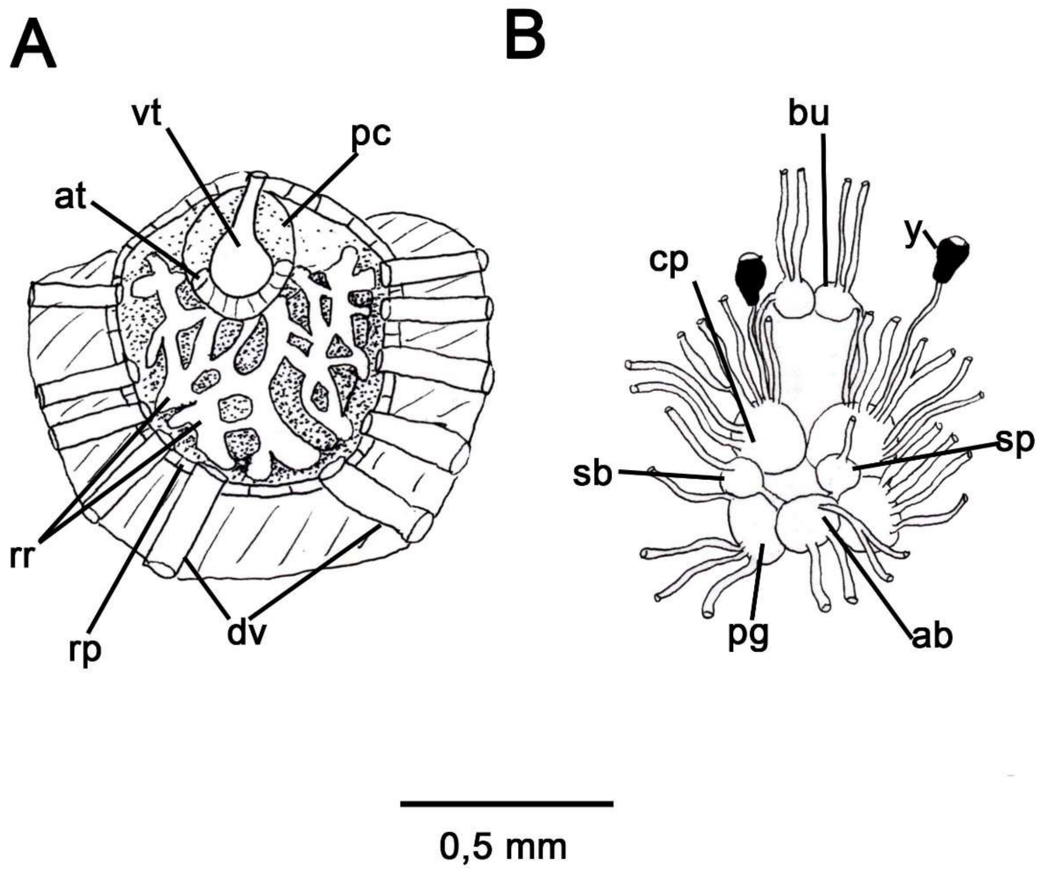

Figure 99. Circulatory and nervous systems of *Elysia viridis*. A) Renopericardial cavity. B) anterior view of nervous system.

Elysia australis **(Quoy & Gaimard, 1832)**

(Figs. 100-104)

External morphology (Fig. 100): Body elongated, smooth, no papillae, reaching up to 8 mm in live animals. Head evident, length up to 1/4 of total body length, 2x longer than wider. Rhinophores (rh) rolled, smooth, short, length twice as smaller as head length, and with rounded tip; papillae absent. Eyes (e) dorsolateral behind rhinophores. Foot (f) inconspicuous and hard to distinguish from parapodia. Mesopodial groove (fl) inconspicuous. Parapodial sole (ps) length 6x longer than propodium (po) length in live animals; anterior part of propodium rounded. Renopericardial cavity (rc) remarkable, well subdivide into pericardium (pc) and renal pad (rp), length 1/6 as longer as parapodial length. Pericardium (pc) muscular, globose, bit elongated longitudinally, with no papillae. Renal pad very short, attached to pericardium. Dorsal vessels (dv) organized in 3 symmetric pairs, two anterior pairs run parallel to parapodia margin and most posterior pair runs posteriorly and branching several times Parapodium (pp) large, with irregular edge and no papillae. Tail absent. Lateral groove (lg) starts on anterior extreme of right parapodia, where female pore (fp) is positioned, and finishes left to middle point of foot line. Male pore (mp) positioned below to right rhinophore. Anus (a) positioned dorsolaterally on posterior right side of head, close to pericardium.

Circulatory and excretory system (Fig. 104): Pericardium (pc) evident, globose, occupying half of renopericardial cavity. Auricle (au) size as large as ventricle (vt) size, auricle smooth. Ventricle occupying half of pericardium, shape rounded. Kidney branched, composed of many renal ridges (rr) connected in trabecular shape. Nephrostome not observed.

Digestive system (Fig. 101-102): Buccal mass (bm) remarkable, size ~5x larger than esophageal pouch (ep), elongated, 2x longer than wider. Dorsal septate muscle (ds) composed of 24 large bundles. Oral sphincter (os) evident, compose of many circular muscles, size ~3x smaller than dorsal septate muscle length. Ascus musculature (ma) wide and long, occupying almost all width and length of ventral side of buccal mass. Ascus (as) twice narrowest than ascus musculature, short and straight. Odontophore (od) pointed, parallel to oral cavity. Buccal pouch absent. Radula with 12 teeth in ascending limb; leading tooth elongated, total length

5x longer than base length; cusp bearing numerous small denticles through all extension; lateral cutting absent. Ascus containing discarded teeth not organized. Salivary glands (sg) positioned ventrally to esophagus and stomach (st). Esophagus (es) length twice shorter than buccal mass length. Esophageal pouch (ep) globose and muscular, positioned on posterior part of esophagus. Stomach (st) short, flat, width as wider as intestine (in) width. Digestive gland (dg) with anterior ducts shorter than posterior ducts, run laterally and anteriorly inside head; posterior ducts run towards parapodial region. Intestine (in) internally folded through all its extension, finishes in dorsolateral anus (a) positioned near to lateral groove.

Reproductive system (Fig. 103): Gonad composed of numerous hermaphrodite follicles (hf) forming a continuous area through all parapodia with central region of body, under the renopericardial cavity, with no follicles. Follicles size few variable, size up to 10x smaller than biggest hermaphrodite ampulla (am). Gametholitic vesicle (gv) absent. Hermaphrodite ducts (hd) connect all follicles to one central duct which connects to hermaphrodite ampullas duct, width univariable. Hermaphrodite ampulla absent. Male duct (md) connects prostate gland (pr) and vas deferens (vd) to hermaphrodite duct same as preceding species. Prostate gland composed of one highly branched duct positioned on top and among follicles. Penis (p) shape conic and short, bit longer than wider. Penial stylet absent. Vas deferens (vd) curled near to penis, length as longer as penis length. Oviduct (ov) starts from hermaphrodite duct after connection with male duct and forms 3 well delimited chambers completely evolved by mucus gland and finishes on female bye (fp) in lateral groove. Proximal chamber of mucus gland smallest one, rounded, albumen duct and male duct connect to oviduct in it. Second chamber of mucus gland biggest one, formed by a curved expansion of glandular oviduct, where bursa copulatrix connects with oviduct. Distally chamber short and with folds. Albumen gland (ag) composed of many dorsal thin branches over prostate gland; main duct of albumen gland runs from hermaphrodite duct, more proximal than male duct connection with hermaphrodite duct, then branches into many ducts in parapodial area dorsally to prostate gland. Genital receptacle absent. Bursa copulatrix (bc) with its own aperture.

Nervous system (Fig. 104): Cerebro-pleural ganglia (cp) size bit smaller than pedal ganglia (pg) size; each ganglion has 5 innervations; commissure cerebro-pleural short. Optic nerve short, much smaller than cerebro-pleural ganglion length. Buccal ganglia (bg) remarkable, size bit larger than sub-intestinal ganglion (sb); accessory ganglion absent; each ganglion has 2 innervations; buccal commissure simple and short, length 5x smaller than buccal ganglion length. Pedal ganglia with 3 innervations by ganglion; pedal commissure simple and long, length as longer as pedal ganglion length. Visceral ganglia well developed. Abdominal ganglion (ab) size as half as pedal ganglion size, has 2 innervations. Sub-intestinal ganglion size ~5x as small as supra-intestinal ganglion (sp), with 1 innervation. Supra-intestinal ganglion bit smaller than abdominal ganglion size, with 1 innervation; connective between abdominal ganglion and sub-intestinal ganglion evident and long, length as longer as sub-intestinal ganglion; connective between abdominal ganglion and supra-intestinal short.

Distribution: Australia (JENSEN, 2007).

Material examined: Albany, Austrália: MZSP 122696, K. R. Jensen col., [9 espécimes], 10/i/1988.

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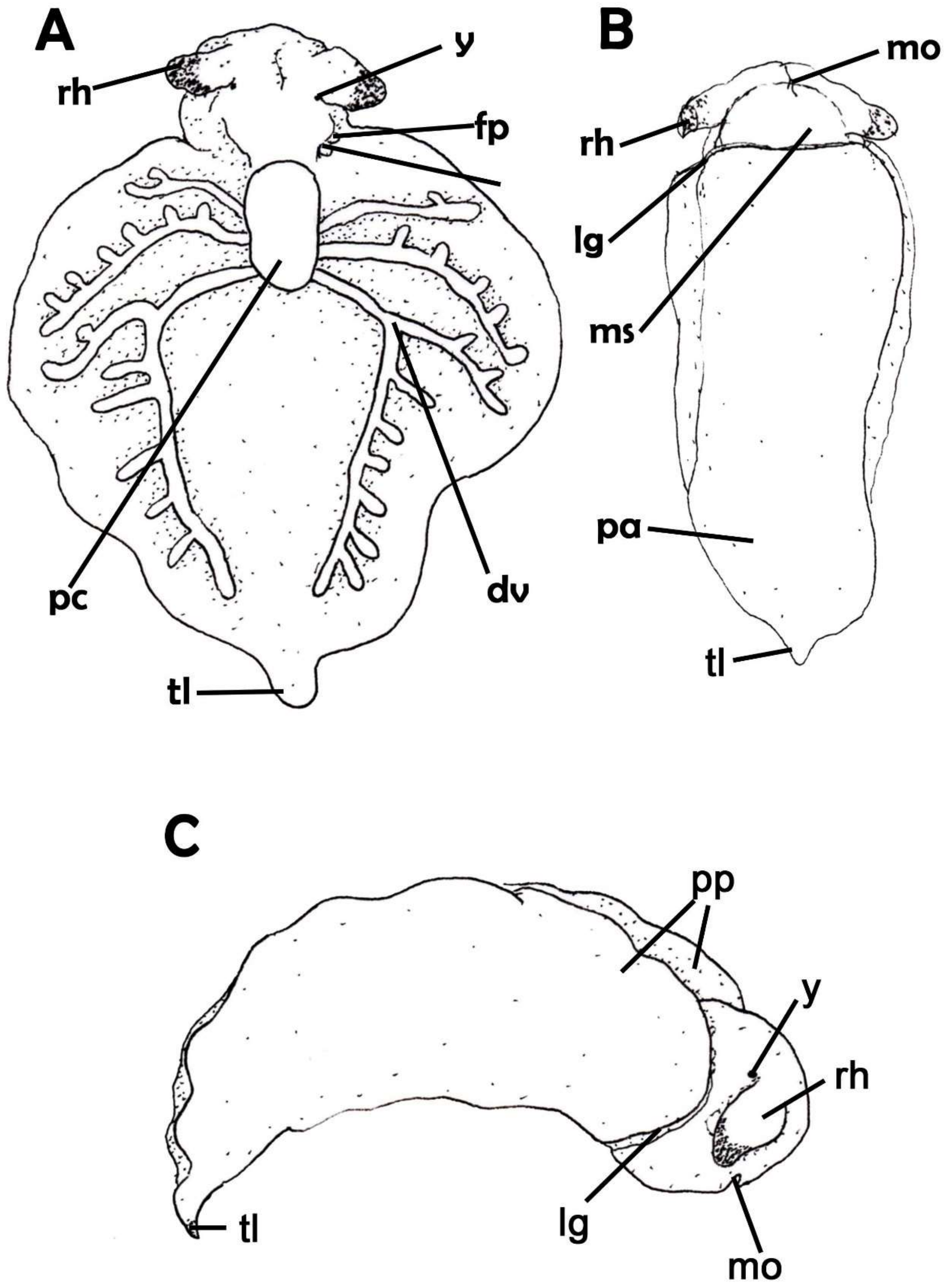

Figure 100. External morphology of *Elysia australis*. A) dorsal; B) ventral; C) lateral.

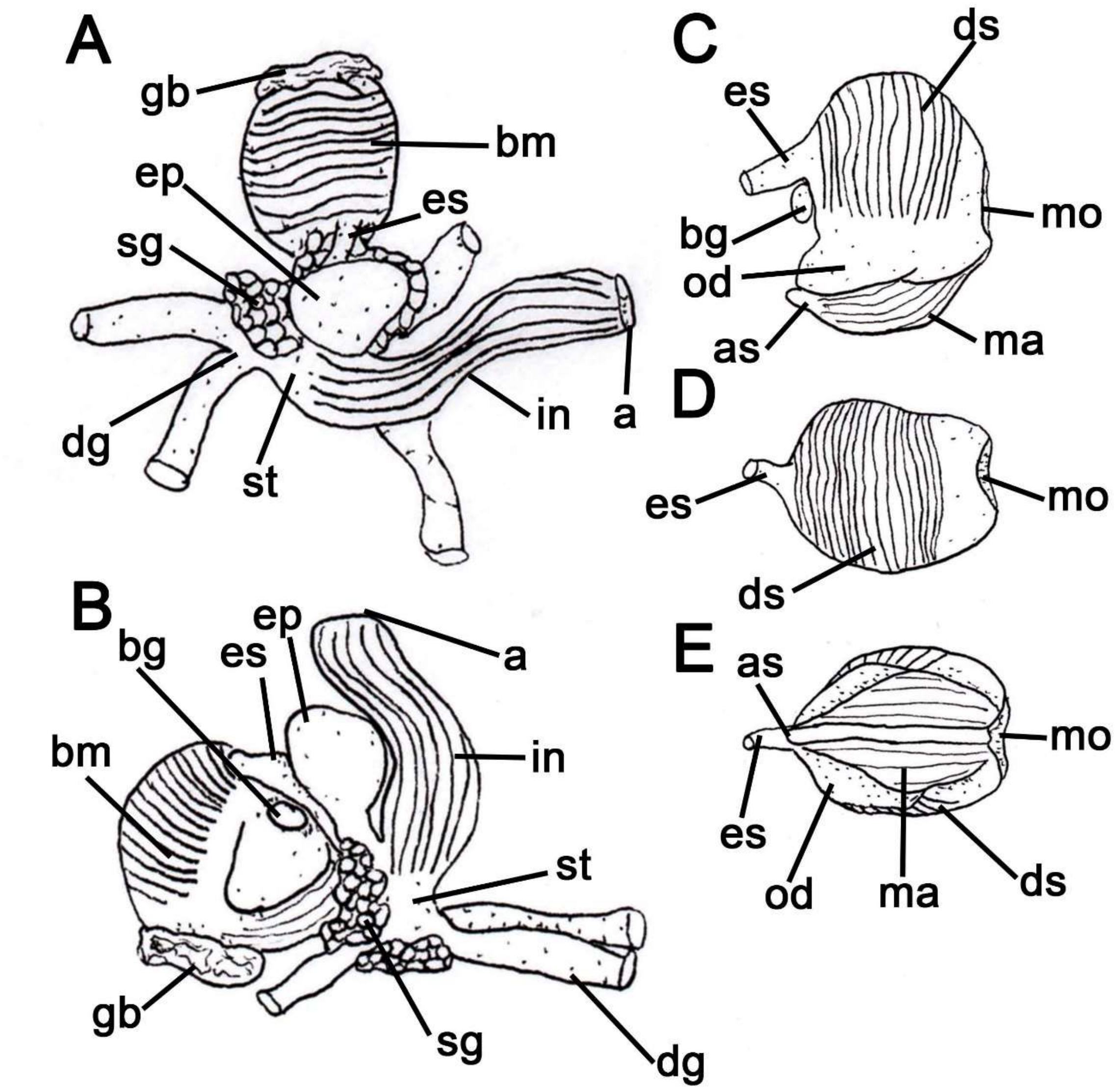

Figure 101. Digestive system of *Elysia australis*. A) Dorsal view; B) Lateral view; Buccal mass: C) lateral; D) dorsal; E) ventral.

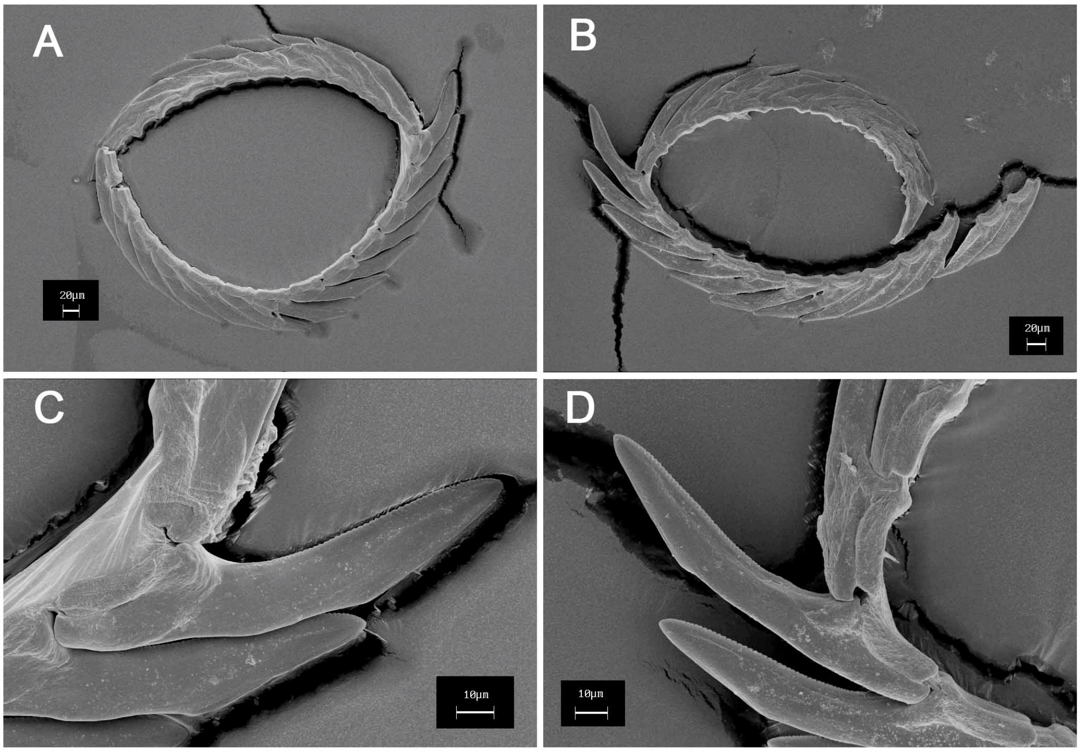

Figure 102. Scan electron microscope images of radula of *Elysia australis* (scale: 10 µm): A-B) general view; C-D) detail of the leading tooth.

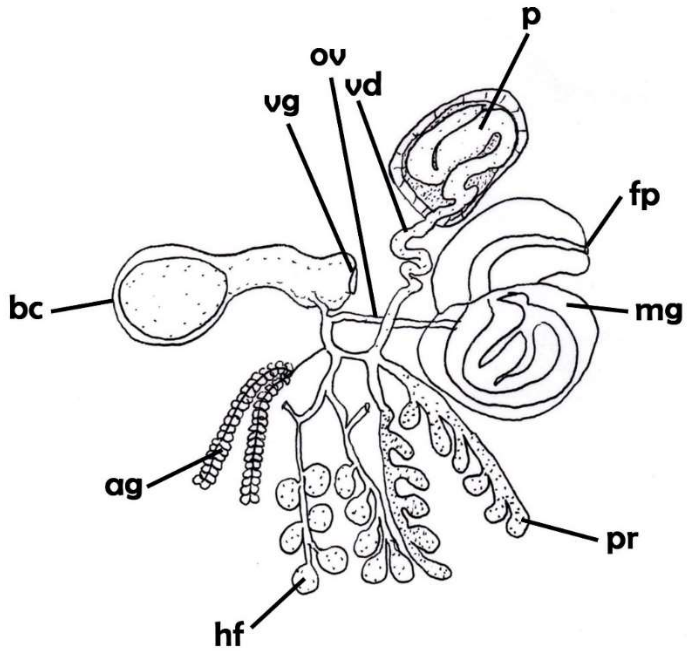

Figure 103. Reproductive system of *Elysia australis* - Schematic drawing.

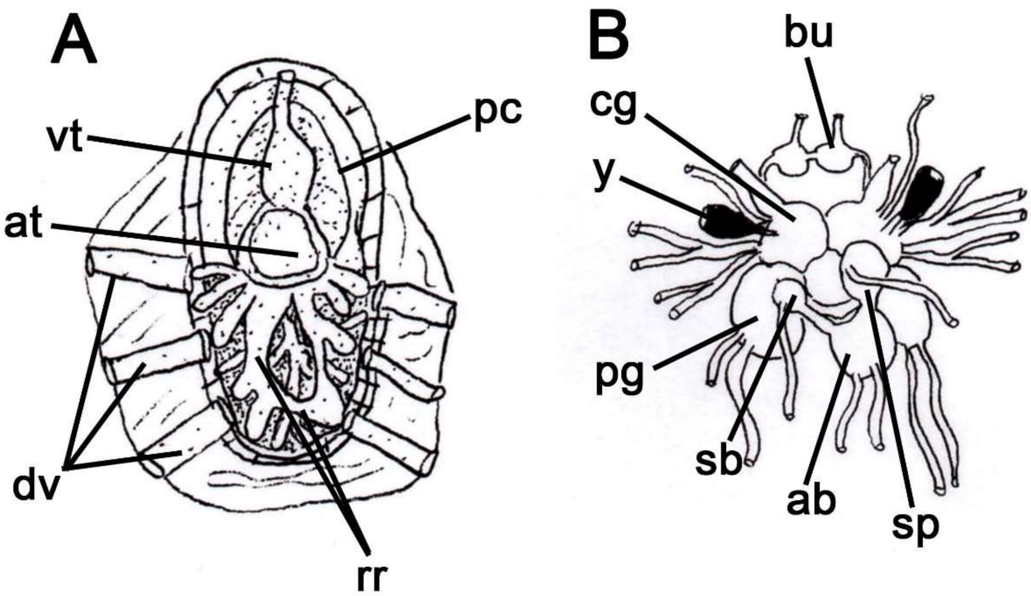

Figure 104. Circulatory and nervous systems of *Elysia australis*. A) Renopericardial cavity. B) anterior view of nervous system.

***Elysia ornata* (Swainson, 1840)**

Figs. 105-109

See Krug, Vendetti & Valdés, 2016.

External morphology (Figs. 105-106): Body elongated, smooth, reaching up to 32 mm in live animals. Head evident, length up to 1/4 of total body length, 3x longer than wider. Rhinophores (rh) rolled, short, ~3x smaller than head length, and with bit tapered tip; papillae absent. Foot sole (fo) similar to parapodial external surface. Foot line (fl) well evident. Parapodial sole (ps) 5x larger than propodium (po) in live animals. Anterior part of propodium rounded. Renopericardial cavity (rc) external, rounded, with renal pad (rp) partially fused with pericardium (pc), length ~8x smaller than parapodial length; pericardium (pc) muscular, globose, smooth. Dorsal vessels (dv) in symmetric arrangement, three pairs running through all parapodia and anastomosing in some parts Parapodium (pp) large, with regular and with no closure pattern. External face of parapodia smooth with similar ornamentation as rest of body. Tail absent. Gametholitic vesicles absent.

Coloration (Fig. 105): in agreement with *Krug* et al., 2016.

Circulatory and excretory system (Fig. 109): Pericardium (pc) evident, globose, occupying 1/4 of renopericardial cavity. Auricle (au) size as half as ventricle (vt) size, auricle wall furrowed. Ventricle occupying 1/3 or pericardium, shape rounded. Kidney branched, composed of many renal ridges (rr) connected in trabecular shape. Nephrostome positioned on right side of renal cavity near to pericardium.

Digestive system (Fig. 107-108): Buccal mass (bm) remarkable, size ~5x larger than esophageal pouch (ep), elongated, 3x longer than wider; dorsal septate muscle (ds) composed of 24 large bundles; oral sphincter (os) evident, compose of many circular muscles, size ~5x smaller than dorsal septate muscle length; ascus musculature (ma) wide and long, occupying half width and 1/3 length of ventral side of buccal mass. Ascus (as) covered by ascus musculature and straight. Odontophore (od) rounded, parallel to oral cavity. pharyngeal pouch absent. Radula with 5 teeth in ascending limb; leading tooth elongated, total length ~5x longer than base length; cusp bearing numerous small denticles through all extension; lateral cutting absent; ascus containing discarded teeth not organized. Salivary glands (sg) positioned ventrally to esophagus and stomach (st). Esophagus (es) bit bigger than buccal mass length, width ~5x thinner than intestine width; internal surface with two longitudinal folds through all its extension. Esophageal pouch (ep) globose and muscular, positioned on posterior part of esophagus. Stomach (st) bulky, rounded, wide, width as twice as wider intestine (in); folds internally present on dorsal portion. Digestive gland (dg) dilated forming stomach pouches well developed, elongated, voluminous and with internal wall folded; anterior ducts shorter than posterior ducts, run laterally and anteriorly inside head; posterior ducts run towards parapodial region. Intestine (in) internally folded through all its extension, finishes in dorsolateral anus (a) positioned near to lateral groove.

Reproductive system (Fig. 109): Gonad composed of numerous hermaphrodite follicles (hf) forming a continuous area through all parapodia with central region of body, under the renopericardial cavity, with no follicles. Follicles size few variable, size up to 5x smaller than biggest hermaphrodite ampulla (am). Gametholitic vesicle (gv) absent. Hermaphrodite ducts (hd) connect all follicles to one central duct which connects to hermaphrodite ampullas duct, width univariable. Hermaphrodite ampulla variable in number from 10 to 22 on each side of body, positioned on parapodia anteriorly to hermaphrodite follicles, size variable, biggest one bit smaller than genital receptacle (gr) and 1/5 of mucus gland (mg) size. All ampulla on each side of animal are united for one main duct which joins in a single duct that connects to hermaphrodite duct. Male duct (md) connects prostate gland (pr) and vas deferens (vd) to hermaphrodite duct same as preceding species. Prostate gland composed of ona main glandular duct branching over ampulla and most anterior follicles. Penis (p) shape conic and short, size bit smaller than mucus gland size, total length as longer as base diameter; stylet absent. Vas deferens (vd) highly curled posteriorly and straight near to penial base, length ~4x longer than penis length when outstretched. Oviduct (ov) starts from hermaphrodite duct after connection with male duct and forms 3 well delimited chambers completely evolved by mucus gland and finishes on female pore (fp) in lateral groove. Proximal chamber of mucus gland smallest one, rounded, albumen duct and male duct connect to oviduct in it. Second chamber of mucus gland biggest one, formed by a curved expansion of glandular oviduct, where bursa copulatrix connects with oviduct. Distally chamber short and with folds. Albumen gland (ag) composed of many dorsal thin branches over prostate gland; main duct of albumen gland runs from hermaphrodite duct, more proximal than male duct connection with hermaphrodite duct, then branches into many ducts in parapodial area dorsally to prostate gland. Genital receptacle connected to oviduct in anterior position.

Nervous system (Fig. 109): Cerebro-pleural ganglia (cg) size as larger as pedal ganglia (pg); each ganglion has 6 innervations; commissure cerebro-pleural absent. Optic nerve length long, bit longer than cerebro-pleural ganglion length. Buccal ganglia (bg) remarkable, size bit larger than sub-intestinal ganglion (sb); accessory ganglion size ~3x smaller as buccal ganglion; each ganglion has 2 innervations; buccal commissure simple and long, length as longer as buccal ganglion length. Pedal ganglia present 3 innervations by ganglion; pedal commissure reduced. Visceral ganglia well developed; abdominal ganglion (ab) size bit smaller than pedal ganglion size, has 2 innervations; sub-intestinal ganglion as half as supra-intestinal ganglion (sp), has 2 innervation; supra-intestinal ganglion bit smaller than abdominal ganglion size, has 1 innervation. Connective among visceral ganglia reduced.

Material examined: PANAMA, Isla Colón, Bocas del Toro, MZSP 121848, 1 specimen; BRAZIL, Arquipélago de São Pedro e São Paulo, Pernambuco, MZSP 104106, 1 specimen; Arquipélago de São Pedro e São Paulo, Pernambuco, MZSP 104106, 1 specimen.

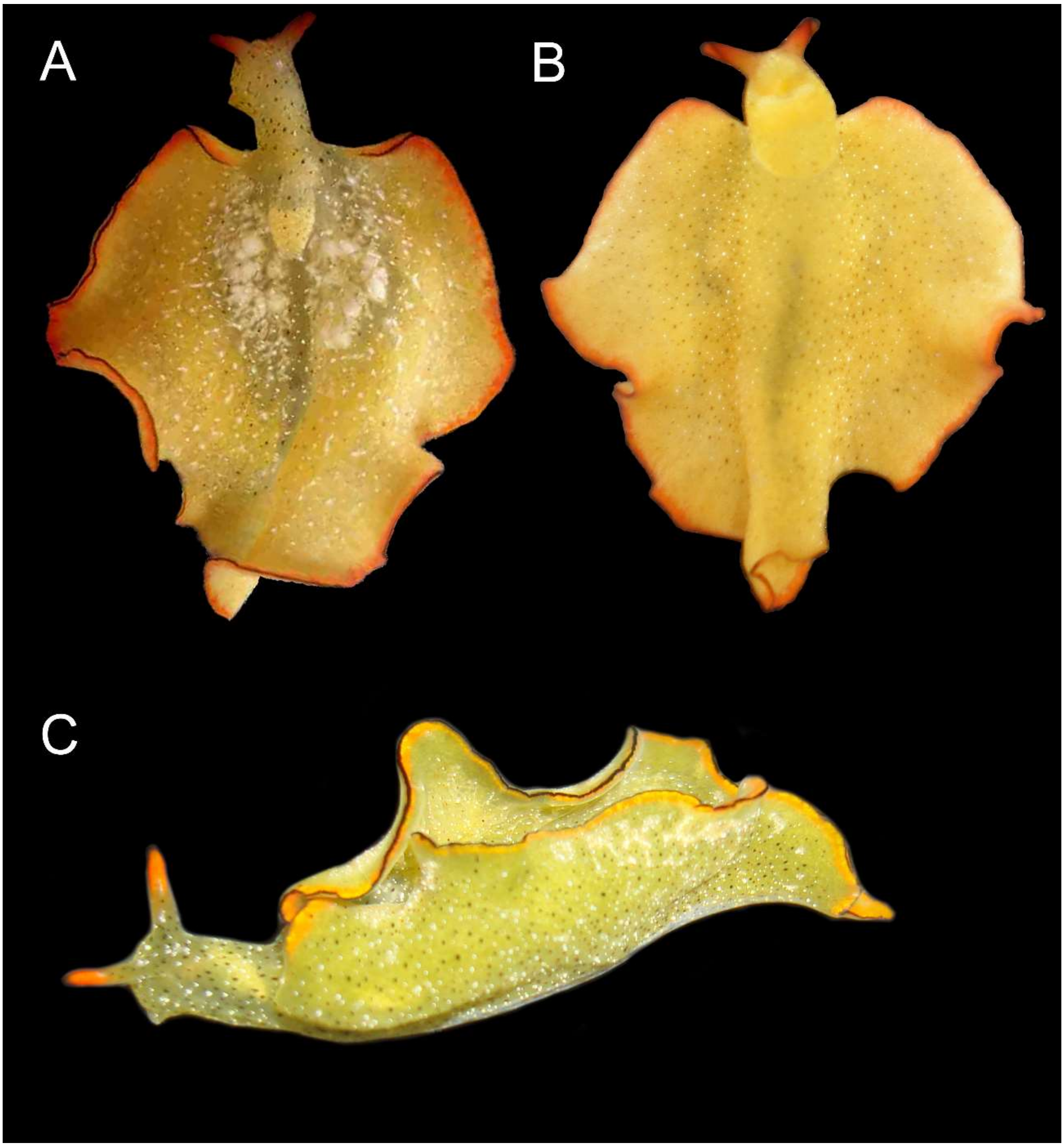

Figure 105. External morphology of live *Elysia ornata* live animal: A) dorsal view (length: 22 mm) parapodia opened; B) ventral view of same animal; C) lateral left view (length: 31 mm).

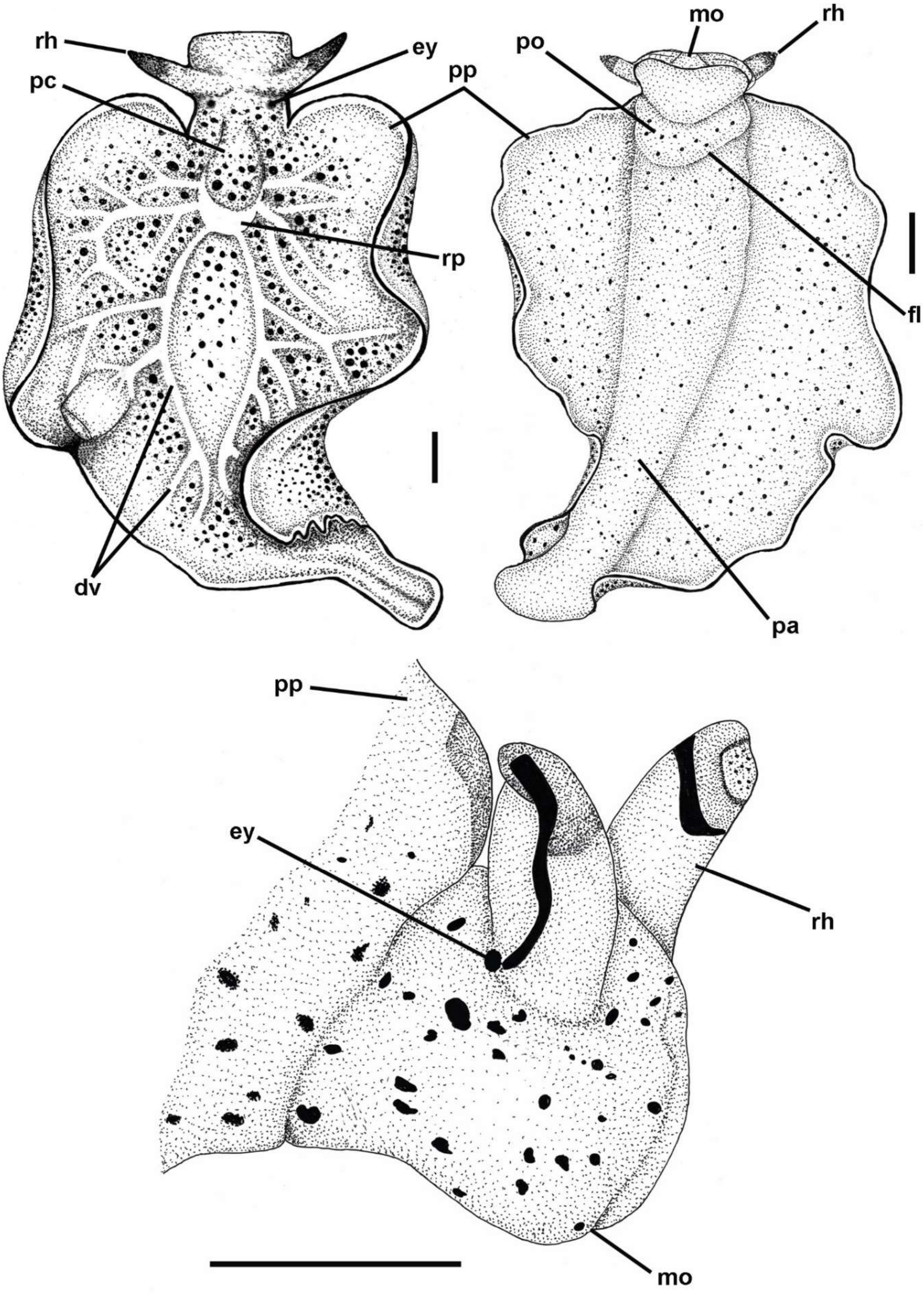

Figure 106. External morphology of *Elysia ornata* (scale: 1 mm): A) dorsal view; B) ventral view; C) lateral view.

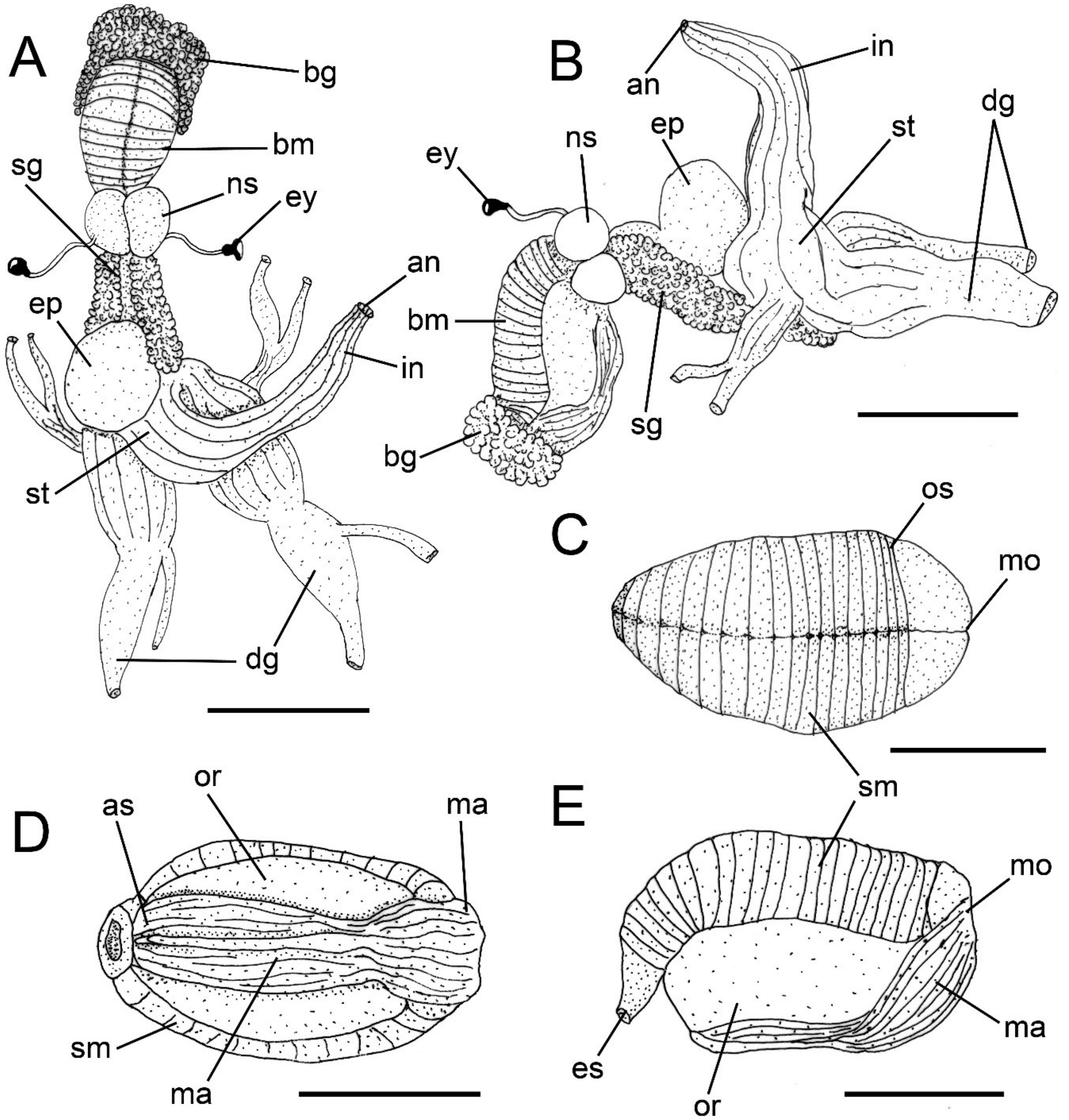

Figure 107. Digestive system of *Elysia ornata*: A) dorsal view and B) lateral view of the whole system. Buccal mass: C) dorsal; D) ventral and E) lateral right view.

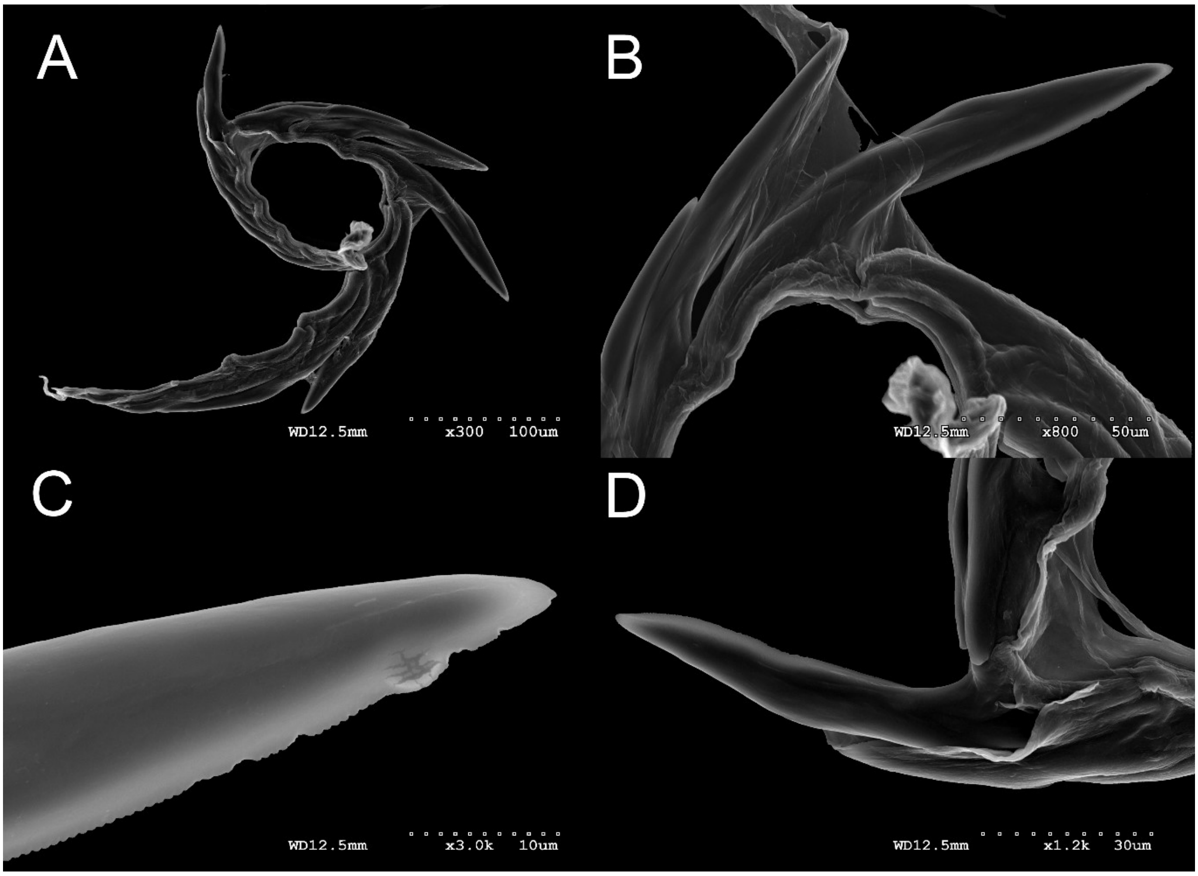

Figure 108. Scan electron microscope images of radula of *Elysia ornata*: A) general view; B-C) detail of the leading tooth; D) detail of old tooth.

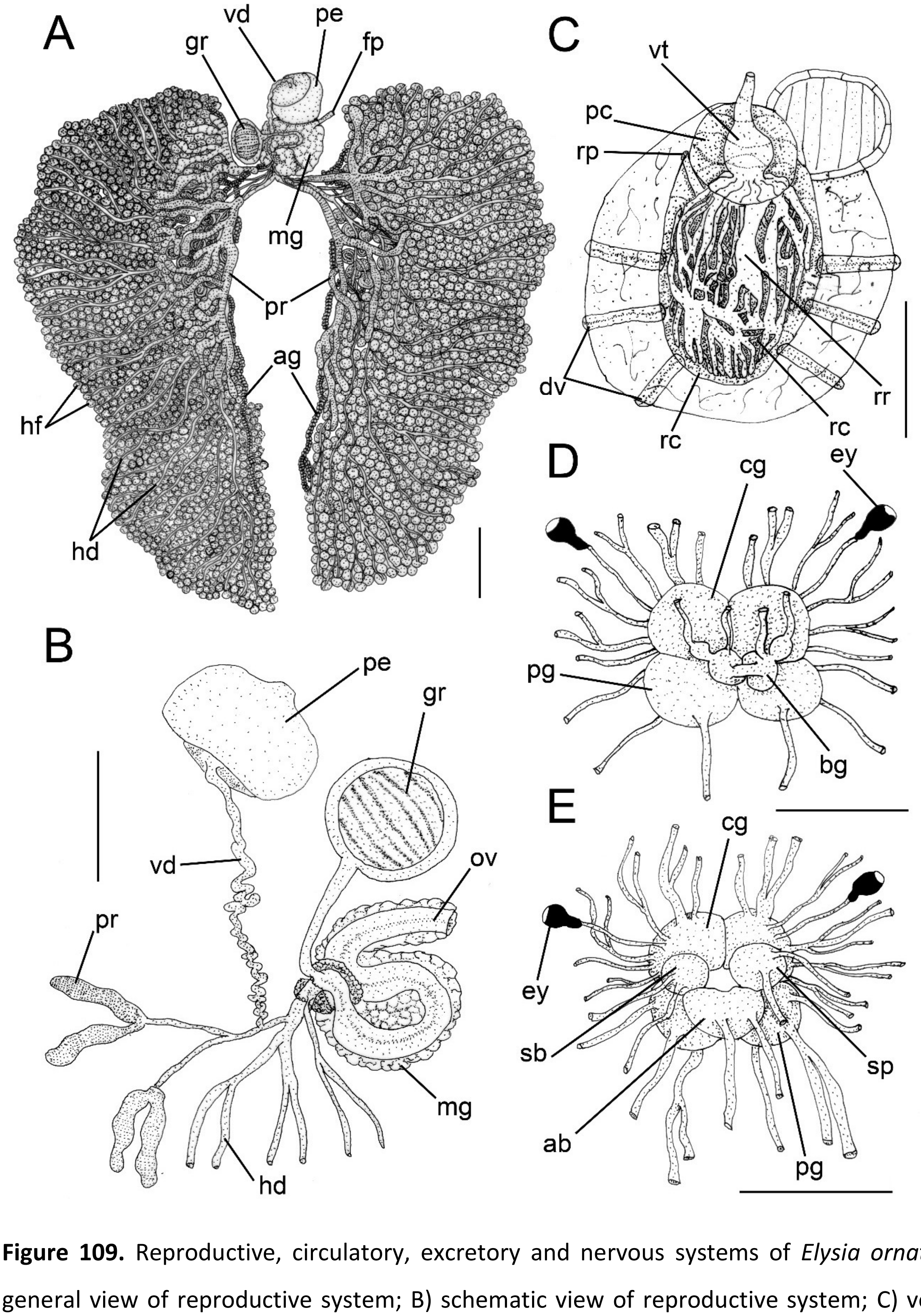

Figure 109. Reproductive, circulatory, excretory and nervous systems of *Elysia ornata*: A) general view of reproductive system; B) schematic view of reproductive system; C) ventral view of renopericaldial cavity in 4mm specimen; D) ventral view of renopericaldial cavity in 6mm specimen; E) posterior view of the nervous system; F) anterior of the nervous system. (scales: A-C = 1 mm; D-E = 0,5 mm).

Elysia crispata Mörch, 1863

Figs. 110-114

See Krug, Vendetti & Valdés, 2016.

External morphology (Figs. 110-111): Body elongated, smooth, reaching up to 48 mm in live animals. Head evident, length up to 1/5 of total body length, 3x longer than wider. Rhinophores (rh) rolled, smooth, long, bit longer than head length, and slightly opened near tip. Foot sole (fo) very muscular and quite different from parapodial musculature. Foot line (fl) well evident. Parapodial sole (ps) 5x larger than propodium (po) in live animals. Anterior part of propodium slightly expanded. Renopericardial cavity (rc) external, rounded, with renal pad (rp) partially fused with pericardium (pc), length ~6x smaller than parapodial length; pericardium (pc) muscular, globose, smooth. Dorsal vessels (dv) in symmetric arrangement, two pairs running through all parapodia, with anterior most pair anastomosing with anterior branching of posterior one. Parapodium (pp) large with the edge highly frilled and with no closure pattern. External face of parapodia smooth with similar ornamentation as rest of body. Tail absent. Gametholitic vesicles absent.

Coloration (Fig. 110): in agreement with Krug, Vendetti and Valdés, 2016.

Circulatory and excretory system (Fig. 114): Similar with the previous species with the following exceptions. Pericardium (pc) as half as renal cavity (rc). Auricle (au) size ~4x smaller than ventricle (vt) size and smooth. Ventricle occupying almost all pericardium.

Digestive system (Fig. 112-113): Similar to *E. ornata* except for the following. Buccal mass (bm) quite small comparing animal body, size twice as larger as esophageal pouch (ep), bit rounded, bit longer than wider; dorsal septate muscle (ds) composed of 12 large bundles; oral sphincter (os) evident, compose of many circular muscles, size ~4x smaller than dorsal septate muscle length; ascus musculature (ma) wide but short, finishing at half length of ventral side of buccal mass. Odontophore region (or) bit elongated. Pharyngeal pouch absent. Radula with 8 well-formed teeth and two others in formation in ascending limb; leading tooth elongated, total length ~3x longer than base length; cusp bearing numerous small denticles through all extension; lateral cutting reduced; ascus containing discarded teeth not organized. Stomach (st) flatten, rounded, wide, width as twice as wider intestine (in); folds internally present on dorsal portion.

Reproductive system (Fig. 113): Similar to *E. ornata* with the following exceptions. Gonad composed of numerous hermaphrodite follicles (hf) on central part of body and absent on frilled area of parapodia. forming a continuous area through all parapodia. Hermaphrodite ampulla most numerous and smaller, size bit larger than follicles size. Prostate gland composed of one main glandular duct branching over all ampulla and follicles area, concentrating after follicles where parapodia get frilled. Penis (pe) more elongated, ~3x longer than wider, but proportionally smaller, size bit smaller than genital receptacle (gr) size. Vas deferens (vd) highly curled near to penial base, length twice as longer as penis length when outstretched. Mucus gland (mg) as larger and well-developed.

Nervous system (Fig. 113): Similar to *E. ornata* except for the following. Cerebro-pleural ganglia (cg) with 5 innervations. Optic nerve shorter than cerebro-pleural ganglion length. Buccal ganglia (bg) bit smaller than sub-intestinal ganglion (sb); accessory ganglion size ~5x smaller as buccal ganglion. Buccal commissure short, length ~3x shorter than buccal ganglion length. Connective between sub-intestinal and abdominal ganglia external and short.

Material examined: PANAMA, Isla Colón, Bocas del Toro, MZSP 121855, 5 specimens. GRENADA, Anse la Roche beach, L'Appelle, Carriacou, MZSP 108711 2 specimens.

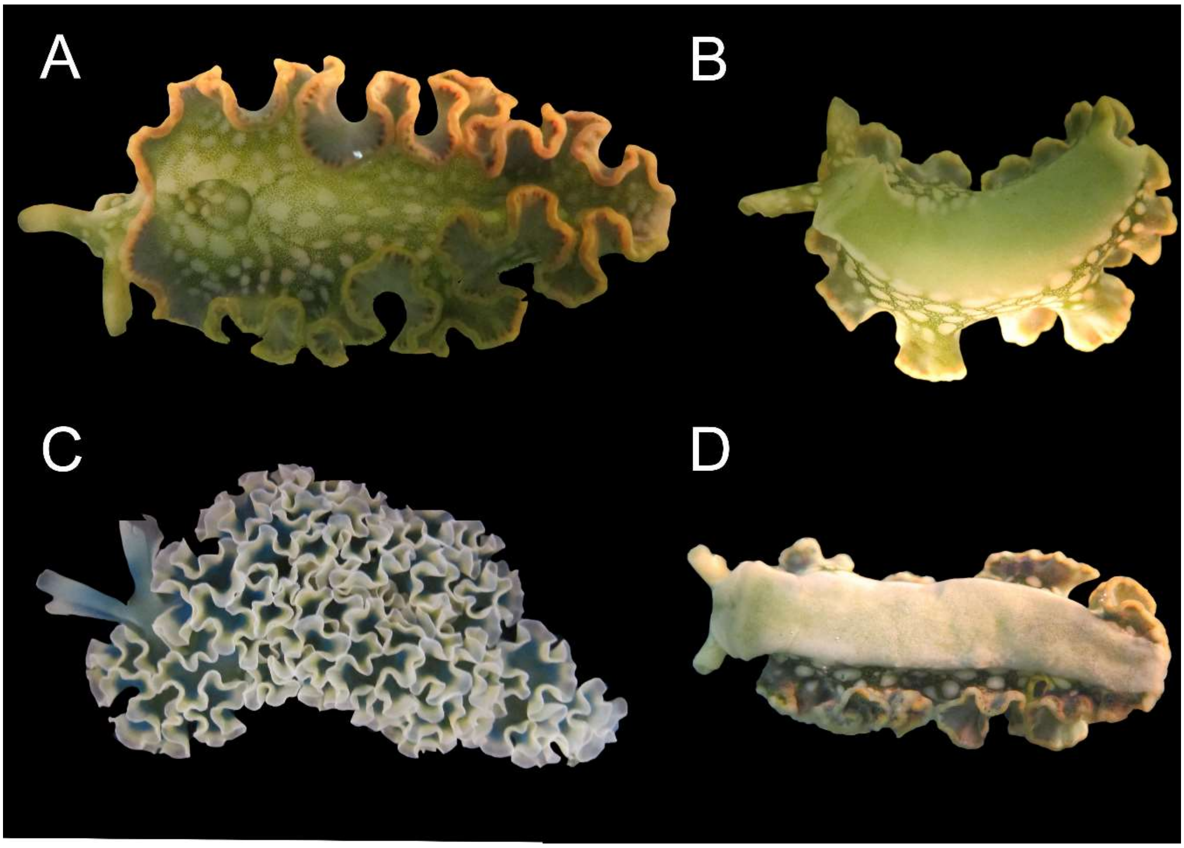

Figure 110. External morphology of live *Elysia crispata* live animal: A) dorsal view (length: 28 mm) parapodia opened; B) ventral view of same animal; C) dorsal view (length: 37 mm); D) ventral view of same animal.

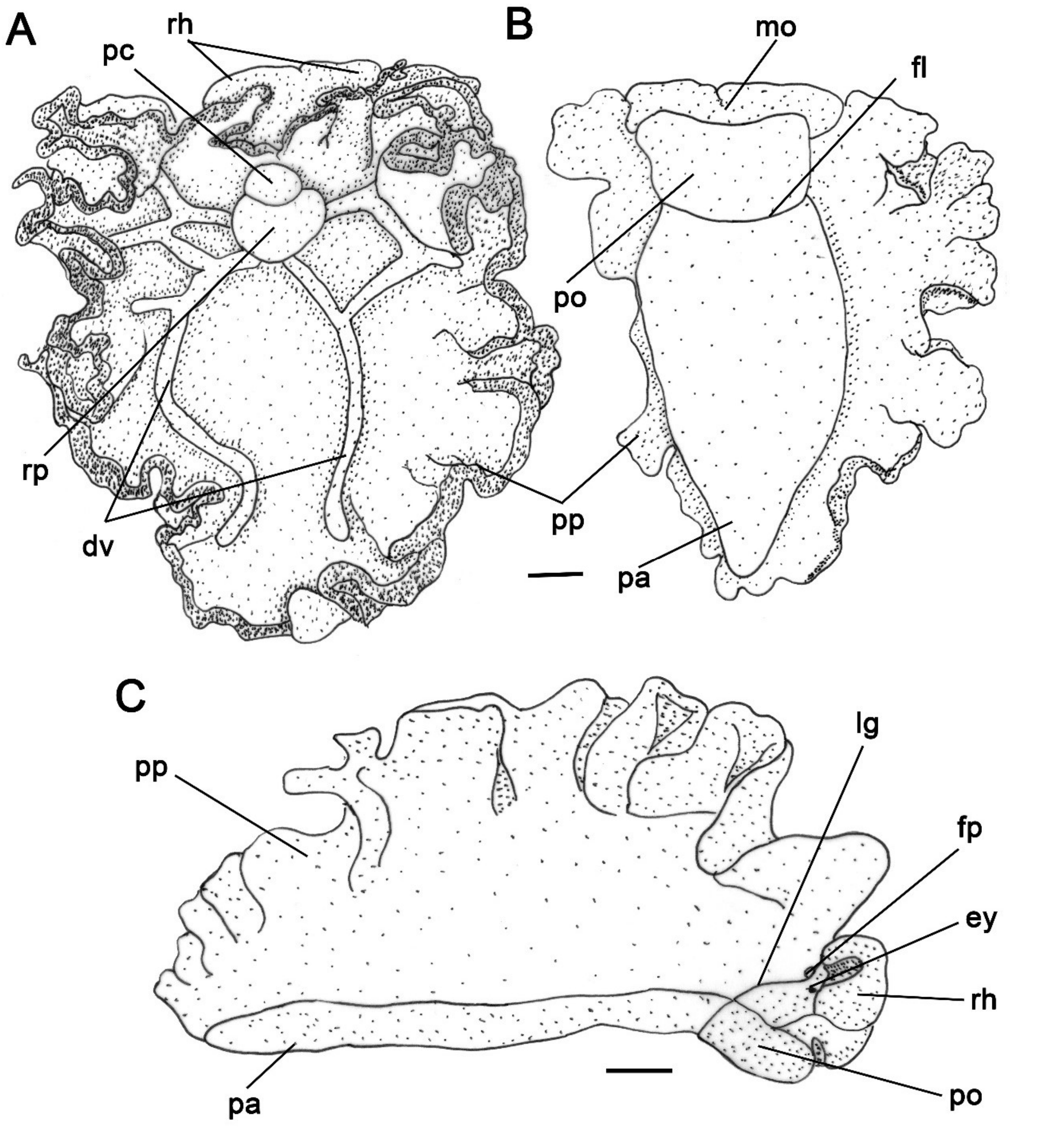

Figure 111. External morphology of *Elysia crispata* (scale: 1 mm): A) dorsal view; B) ventral view; C) lateral view.

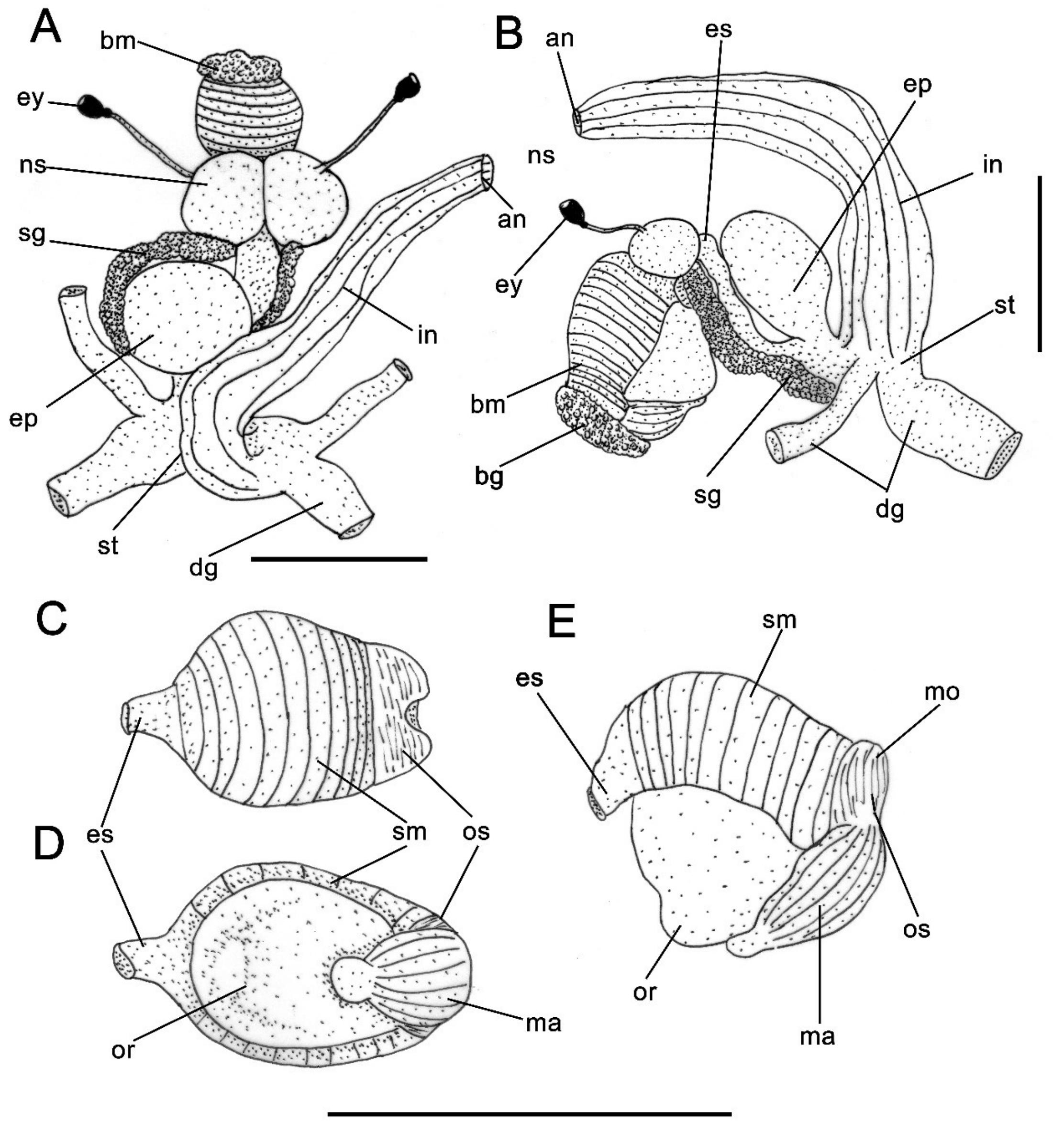

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Figure 112. Digestive system of *Elysia crispata*: A) dorsal view and B) lateral view of the whole system. Buccal mass: C) dorsal; D) ventral and E) lateral right view.

Figure 113. Scan electron microscope images of radula of *Elysia crispata*: A and C) general view; B and D) detail of the leading tooth.

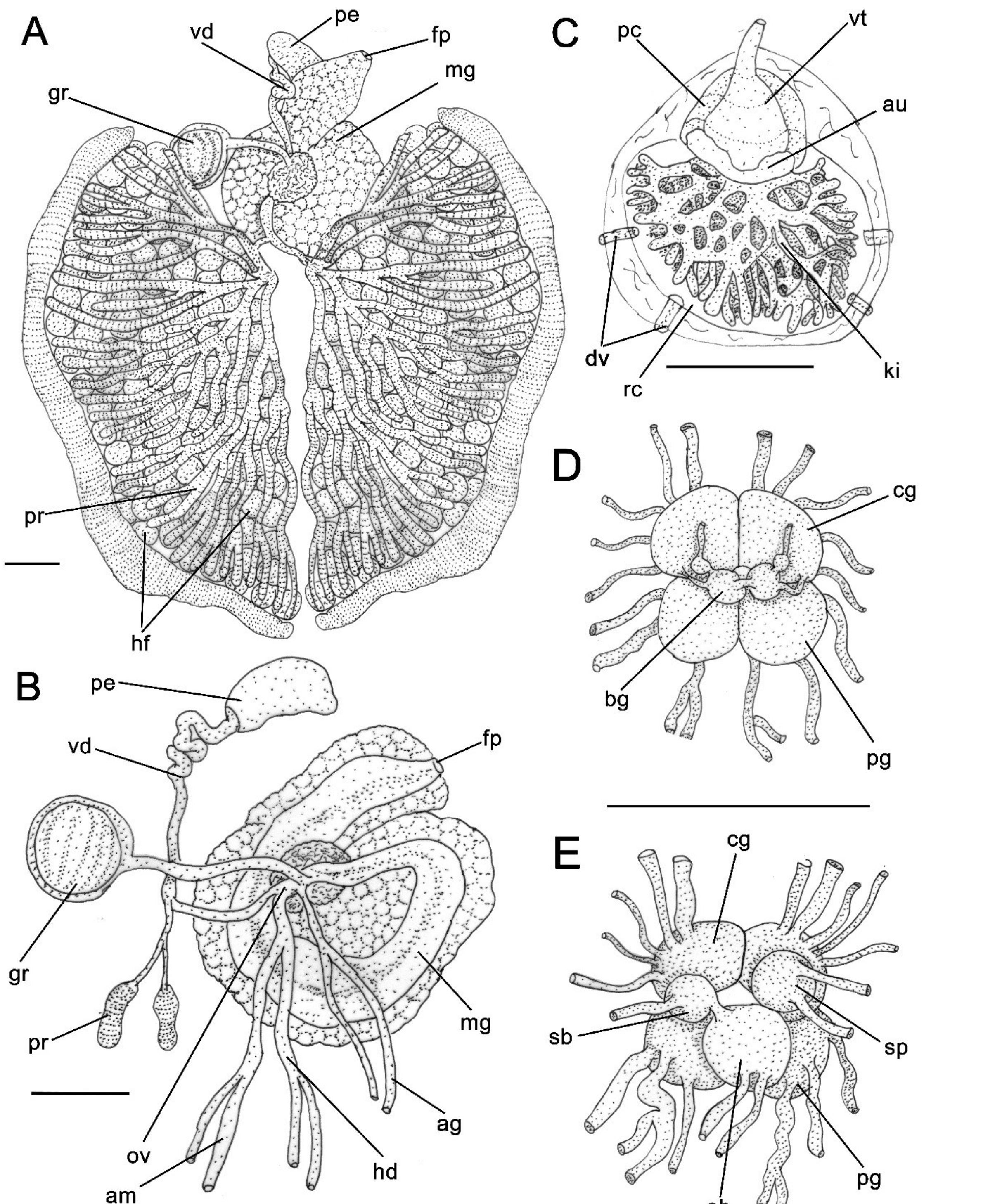

Figure 114. Reproductive, circulatory, excretory and nervous systems of *Elysia crispata*: A) general view of reproductive system; B) schematic view of reproductive system; C) ventral view of renopericaldial cavity in 4mm specimen; D) ventral view of renopericaldial cavity in 6mm specimen; E) posterior view of the nervous system; F) anterior of the nervous system. (scales: A-C = 1 mm; D-E = 0,5 mm).

***Elysia diomedea* Mörch, 1863**

Figs. 115-119

External morphology (Figs. 115-116): Body elongated, smooth, reaching up to 40 mm in live animals. Head evident, length up to 1/5 of total body length, 3x longer than wider. Rhinophores (rh) rolled, smooth, long, bit longer than head length, and slightly opened near tip. Foot sole (fo) very muscular and quite different from parapodial musculature. Foot line (fl) well evident. Parapodial sole (ps) 5x larger than propodium (po) in live animals. Anterior part of propodium slightly expanded. Renopericardial cavity (rc) external, rounded, with renal pad (rp) partially fused with pericardium (pc), length ~6x smaller than parapodial length; pericardium (pc) muscular, globose, smooth. Dorsal vessels (dv) in symmetric arrangement, two pairs running through all parapodia, with anterior most pair anastomosing with anterior branching of posterior one. Parapodium (pp) large with the edge highly frilled and with no closure pattern. External face of parapodia smooth with similar ornamentation as rest of body. Tail absent. Gametholitic vesicles absent.

Coloration (Fig. 115): in agreement with Krug, Vendetti and Valdés, 2016.

Circulatory and excretory system (Fig. 119): Similar with the previous species with the following exceptions. Pericardium (pc) as half as renal cavity (rc). Auricle (au) size ~4x smaller than ventricle (vt) size and smooth. Ventricle occupying almost all pericardium.

Digestive system (Fig. 117-118): Similar to *E. ornata* except for the following. Buccal mass (bm) quite small comparing animal body, size twice as larger as esophageal pouch (ep), bit rounded, bit longer than wider; dorsal septate muscle (ds) composed of 12 large bundles; oral sphincter (os) evident, compose of many circular muscles, size ~4x smaller than dorsal septate muscle length; ascus musculature (ma) wide but short, finishing at half length of ventral side of buccal mass. Odontophore region (or) bit elongated. Pharyngeal pouch absent. Radula with 8 well-formed teeth and two others in formation in ascending limb; leading tooth elongated, total length ~3x longer than base length; cusp bearing numerous small denticles through all extension; lateral cutting reduced; ascus containing discarded teeth not organized. Stomach (st) flatten, rounded, wide, width as twice as wider intestine (in); folds internally present on dorsal portion.

Reproductive system (Fig. 119): Similar to *E. ornata* with the following exceptions. Gonad composed of numerous hermaphrodite follicles (hf) on central part of body and absent on frilled area of parapodia. forming a continuous area through all parapodia. Hermaphrodite ampulla most numerous and smaller, size bit larger than follicles size. Prostate gland composed of one main glandular duct branching over all ampulla and follicles area, concentrating after follicles where parapodia get frilled. Penis (pe) more elongated, ~3x longer than wider, but proportionally smaller, size bit smaller than genital receptacle (gr) size. Vas deferens (vd) highly curled near to penial base, length twice as longer as penis length when outstretched. Mucus gland (mg) as larger and well-developed.

Nervous system (Fig. 119): Similar to *E. ornata* except for the following. Cerebro-pleural ganglia (cg) with 5 innervations. Optic nerve shorter than cerebro-pleural ganglion length. Buccal ganglia (bg) bit smaller than sub-intestinal ganglion (sb); accessory ganglion size ~5x smaller as buccal ganglion. Buccal commissure short, length ~3x shorter than buccal ganglion length. Connective between sub-intestinal and abdominal ganglia external and short.

Material examined: PANAMA, Isla Colón, Bocas del Toro, MZSP 121855, 5 specimens. GRENADA, Anse la Roche beach, L'Appelle, Carriacou, MZSP 108711 2 specimens.

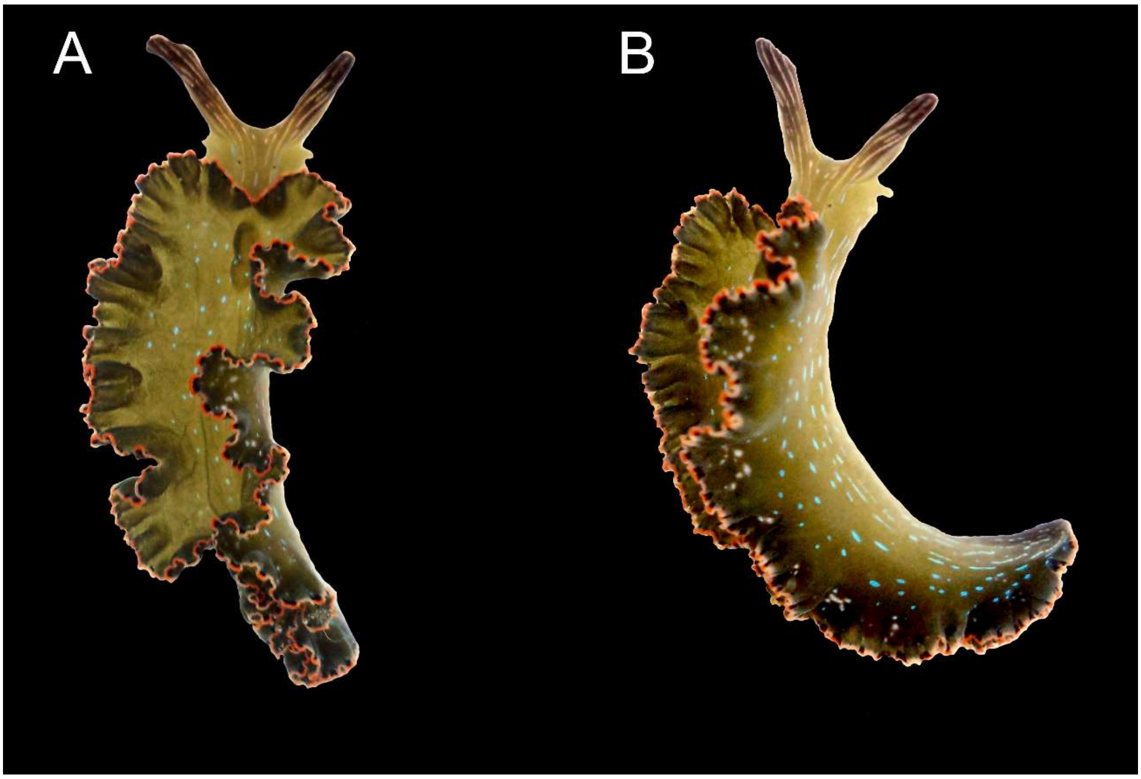

Figure 115. External morphology of live *Elysia diomedea* live animal: A) dorsal view (length: 33 mm) parapodia opened; lateral right view of same animal.

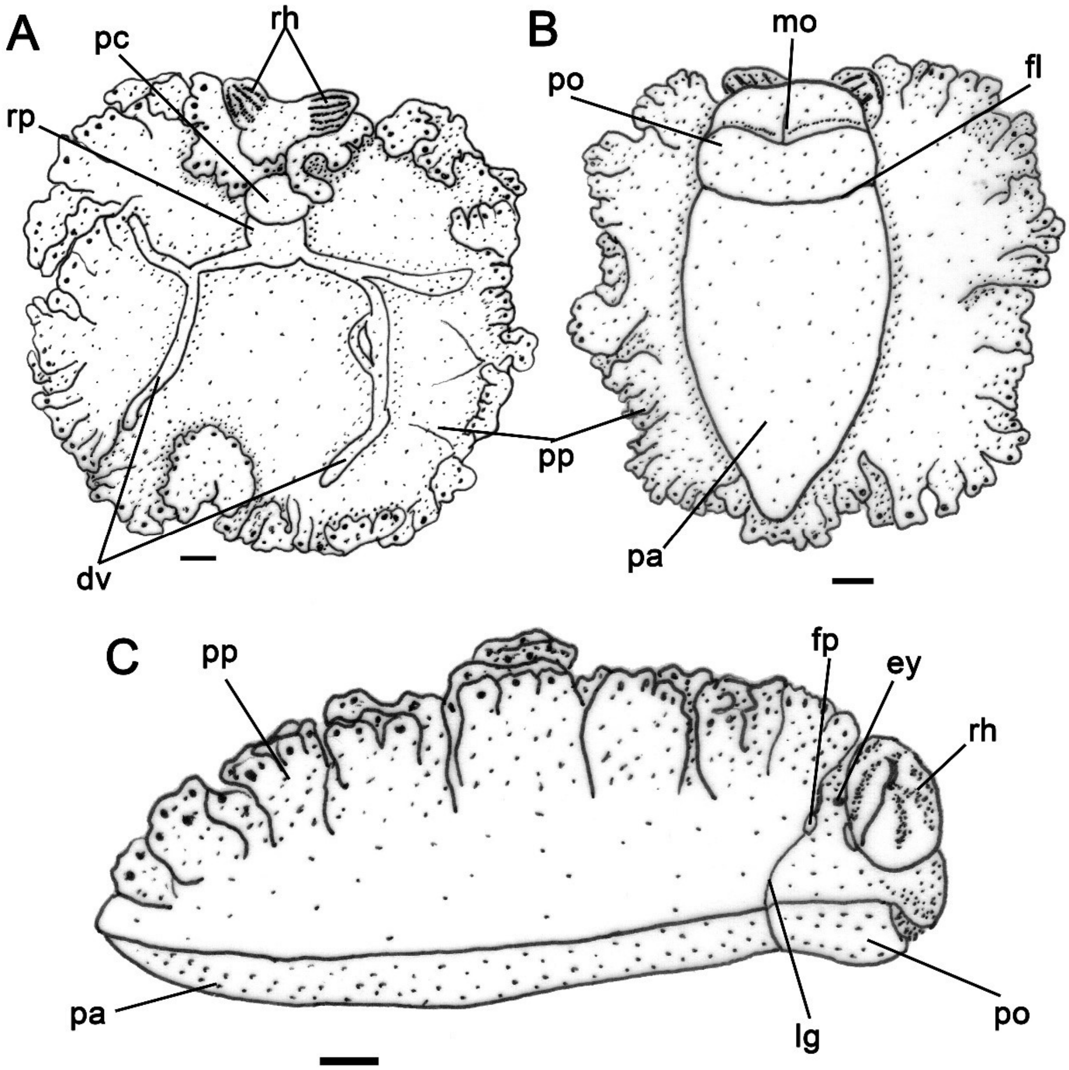

Figure 116. External morphology of *Elysia diomedea* (scale: 1 mm): A) dorsal view; B) ventral view; C) lateral view.

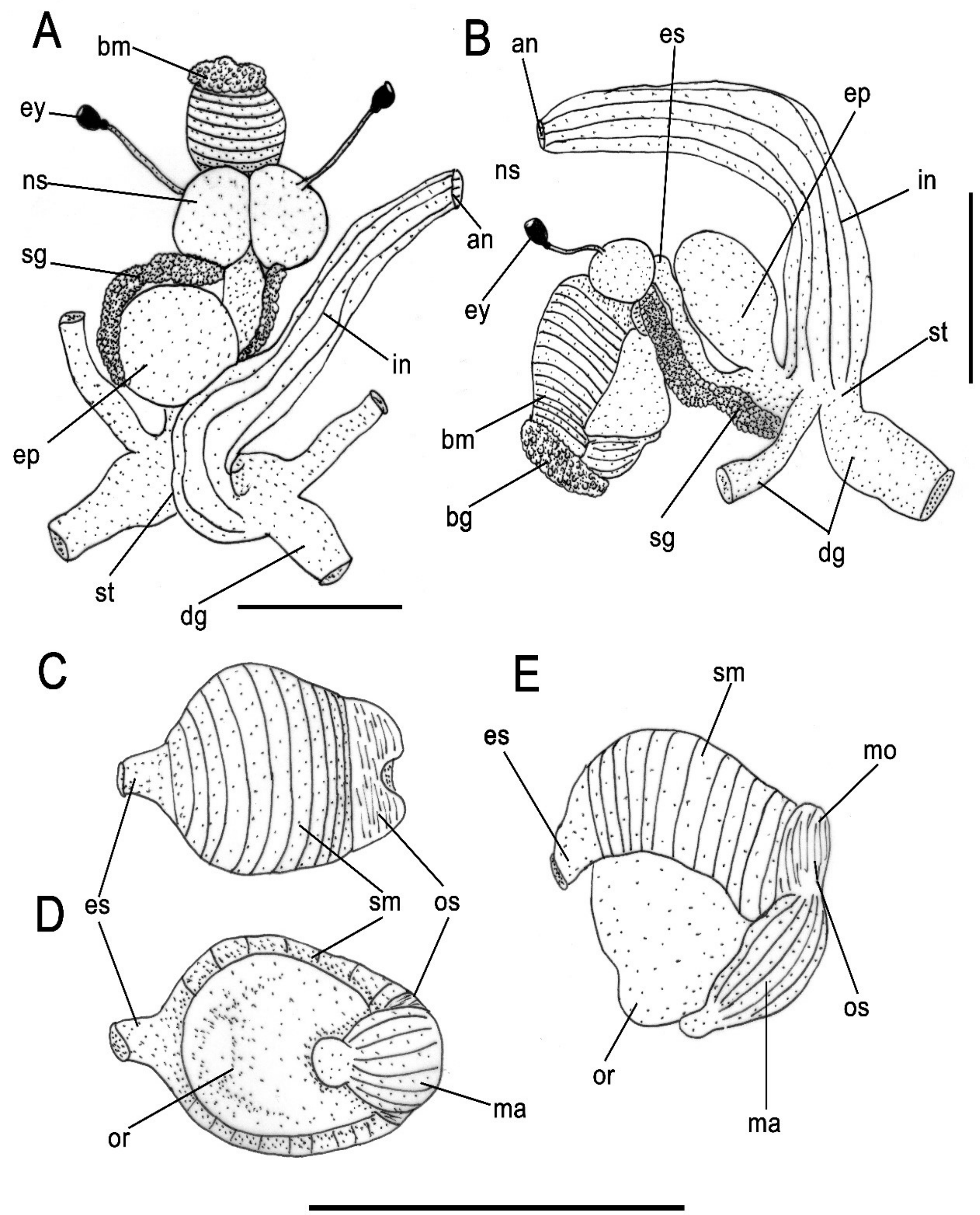

Figure 117. Digestive system of *Elysia diomedea*: A) dorsal view and B) lateral view of the whole system. Buccal mass: C) dorsal; D) ventral and E) lateral right view.

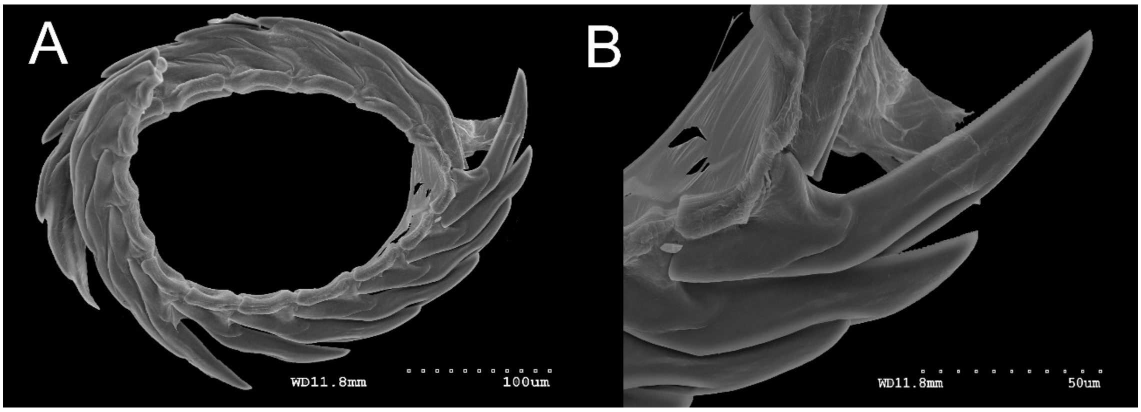

Figure 118. Scan electron microscope images of radula of *Elysia diomedea*: A) general view; B) detail of the leading tooth.

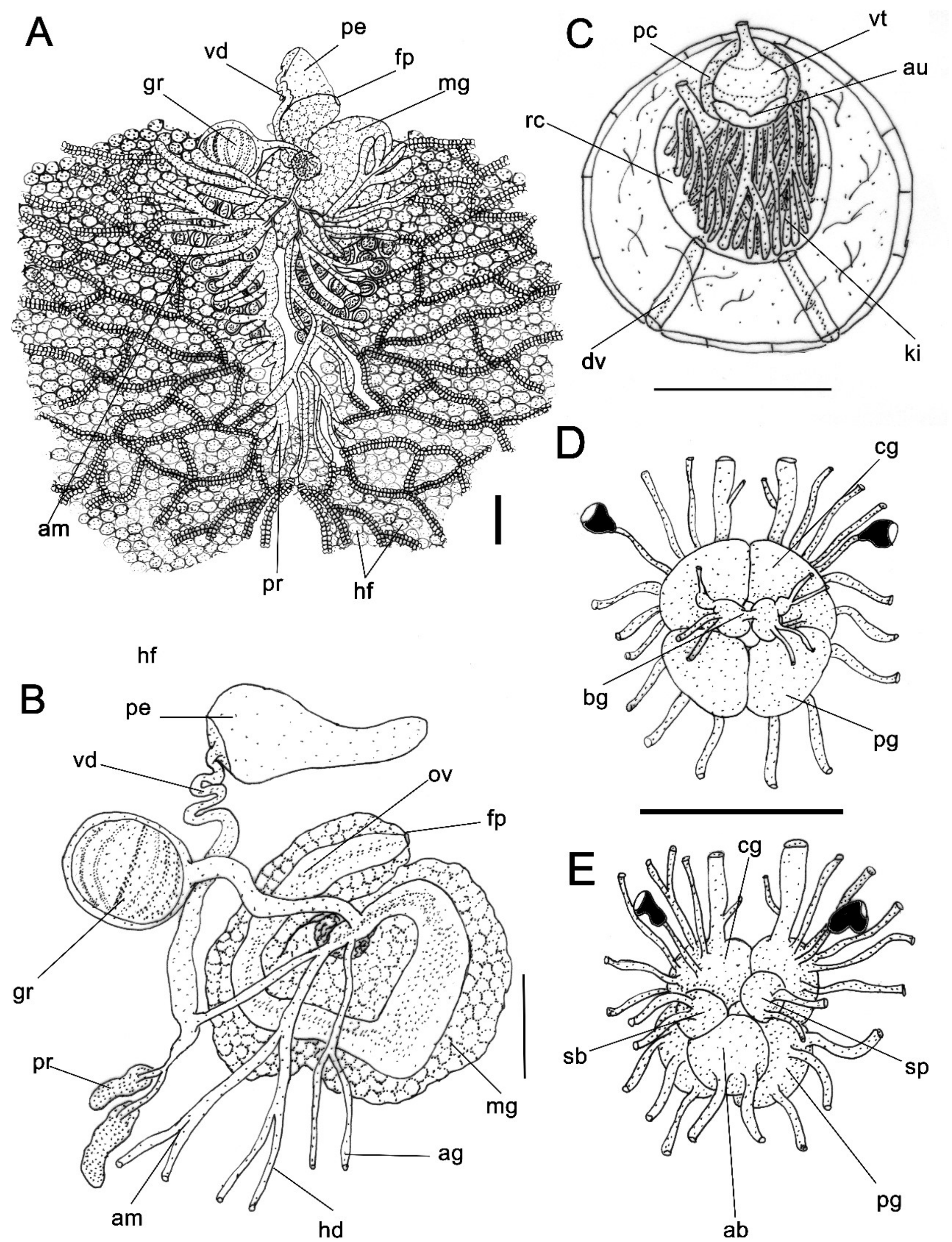

Figure 119. Reproductive, circulatory, excretory and nervous systems of *Elysia diomedea*: A) general view of reproductive system; B) schematic view of reproductive system; C) ventral view of renopericaldial cavity in 4mm specimen; D) ventral view of renopericaldial cavity in 6mm specimen; E) posterior view of the nervous system; F) anterior of the nervous system. (scales: A-C = 1 mm; D-E = 0,5 mm).

***Elysia papillosa* Verrill, 1901**

Figs. 120-124

See Krug, Vendetti & Valdés, 2016.

External morphology (Fig. 120-121): Body elongated, reaching up to 12 mm in live animals; ornamented with innumerous papillae scattered through external side of parapodia, head, pericardium and rhinophores. Head evident, length ~1/4 of total body length, 2x longer than wider. Rhinophores (rh) short, length as half as head length, rolled, papillose, and with tip blunt; papillae size small, spread through all rhinophore extension. Eyes (ey) located dorsolaterally behind rhinophores. Foot (f) with remarkable limit near to parapodia; parapodial sole (ps) 3x larger than propodium (po) in live animals; anterior part of propodium laterally expanded; foot line (fl) well evident. Renopericardial cavity (rc) prominent, well subdivided into pericardium (pc) and renal pad (rp); total length slightly smaller than half of parapodial length; pericardium (pc) muscular, globose, slight longitudinally elongated, papillose, size as half as head size; renal pad (rp) smooth, thin-walled, length 3x longer than pericardium length; dorsal vessels (dv) organized in 6 pairs, arrangement asymmetric; most posterior pair of vessels runs posteriorly and branching several times, while other pairs branch towards parapodia edge laterally. Parapodium (pp) large, with irregular edge in scalloped shape; parapodial closure pattern forming many siphons through all parapodial extension; each parapodium presents three papillae where siphons are formed. External face of parapodia with many short papillae with similar size, while inner surface has few smaller and scattered papillae. Tail (tl) very short, length ~5x smaller than head length, can be proportionally larger in smaller specimens. Gametic vesicles (gv) remarkable in bigger specimens, visible through parapodial surface, positioned on half-length of parapodia on same length position than posterior end of renal pad. Female pore (fp) located on extreme dorsal point of lateral groove (lg). Male pore (mp) below right rhinophore. Anus (a) positioned dorsolaterally on posterior right side of head, close to lateral groove, above female pore.

Coloration (Fig. 120): in agreement with *Krug* et al., 2016.

Circulatory and excretory system (Fig. 124): Pericardium (pc) evident, globose, occupying 1/3 of renopericardial cavity; auricle (au) size as large as half of ventricle (vt) size, auricle wall smooth; ventricle size large, occupying almost all pericardium, shape rounded. Kidney branched, rounded, composed of many renal ridges (rr) connected in trabecular shape. Nephrostome not observed.

Digestive system (Fig. 122-123): Buccal mass (bm) remarkable, size ~10x larger than esophageal pouch (ep), rounded, as longer as wider; dorsal septate muscle (ds) composed of 14 large bundles; oral sphincter (os) evident, composed of small circular muscles, short, length ~4x smaller than dorsal septate muscle length; ascus musculature (ma) wide and short, occupying almost all width and half-length of ventral side of buccal mass; ascus (as) ~4x narrowest than ascus musculature, short, length twice as small as buccal mass length, curved to right side of buccal mass; odontophore (od) elongated, voluminous, not parallel to oral cavity, prominent, forming evident elongated protuberance ventrally on posterior side of buccal mass; buccal pouch absent. Radula with 6 teeth in ascending limb; leading tooth elongated, total length twice as longer as base length; cusp bearing numerous remarkable denticles through all extension; lateral cutting edges inconspicuous and smooth; ascus containing discarded teeth not organized. Salivary glands (sg) positioned ventrally and laterally to esophagus between central nervous system (ns) and esophageal pouch. Esophagus length as longer as buccal mass length, width as large as intestine width; internal surface with two folds. Esophageal pouch (ep) globose and muscular, positioned on posterior part of esophagus; internal surface with many thin complete folds. Stomach (st) flatten, wide, width ~4x wider than intestine (in); folds internally present on dorsal portion; stomach pouches absent. Digestive gland (dg) paired in each side of stomach; anterior ducts shorter than posterior ducts, runs laterally and anteriorly inside head; posterior duct runs towards parapodial region. Intestine (in) width as wider as esophagus, internally folded through all its extension, finishes in dorsolateral anus (a) positioned near to lateral groove.

Reproductive system (Fig. 124): Gonad composed of numerous hermaphrodite follicles (hf) forming a continuous area through all parapodia and central region of body; follicles size few variable, size ~8x smaller than hermaphrodite ampulla (am); one gametic vesicle (gv) occur on each side of body, size up to ~10x larger than follicles and twice as larger as bursa copulatrix; hermaphrodite ducts (hd) connect all follicles and gamethic vessicles to one central duct which connects to hermaphrodite ampulla, width wider in branch where connects gametic vesicles with remaining follicles. Hermaphrodite ampulla positioned mid-centrally in reproductive system, size bit larger than bursa copulatrix (bc) and 1/3 of mucus gland (mg) size. Male duct (md) connects prostate gland (pr) and vas deferens (vd) to hermaphrodite duct before albumen gland (ag) connection; prostate gland ramified in net shape dorsally to follicles through all parapodial area, composed of one main glandular duct; penis (p) size bit smaller than ampulla and ~3x smaller than mucus gland size, shape conic and short, total length 3x bigger as base diameter; stylet present; vas deferens twice longer than penis length, proximally few undulated and not curled; distally curved and proximally bit straight inside penis. Oviduct (ov) starts from hermaphrodite duct after connection with male duct and forms 3 well delimited chambers completely evolved by mucus gland, and finishes on female pore (fp) in lateral groove. Proximal chamber of mucus gland smaller one, elongated, albumen duct and male duct connect to oviduct connected before it; middle chamber of mucus gland bigger one, formed by a curved expansion of glandular oviduct; distal chamber elongated and unfolded. Bursa copulatrix connected to oviduct in distal chamber near to female pore. Albumen gland (ag) composed of many dorsal thin branches over prostate gland; main duct of albumen gland runs from hermaphrodite duct, more proximal than male duct connection with hermaphrodite duct, then branches into many ducts in parapodial area dorsally to prostate gland.

Nervous system (Fig. 124): Cerebro-pleural ganglia (cp) size as larger as pedal ganglia (pg); each one has 7 innervations; commissure cerebro-pleural not evident. Optic nerve length short, bit longer than half of cerebro-pleural ganglion length. Buccal ganglia (bg) remarkable, size larger than sub-intestinal ganglion (sb); accessory ganglion (ac) present, size ~3x smaller than buccal ganglion; each ganglion has 3 innervations, which one of them runs from accessory ganglion; buccal commissure simple, length ~4x smaller than buccal ganglion length. Pedal ganglia present 3 innervations by ganglion; pedal commissure present, simple and short, smaller as half as pedal ganglia length. Visceral ganglia well developed; abdominal ganglion (ab) size bit smaller than pedal ganglion size, has 2 innervations; sub-intestinal ganglion size ~6x as small as supra-intestinal ganglion (sp), has 1 innervation; supra-intestinal ganglion size ~3x smaller than abdominal ganglion, has 2 innervations; connective between abdominal ganglion and sub-intestinal ganglion evident, length as longer as sub-intestinal ganglion; connective between abdominal ganglion and supra-intestinal ganglion absent.

Distribution: Florida (Krug *et al*., 2016), Bahamas (present study) e Cuba [Havana – type locality (Ortea *et al*., 2011)].

Material examined: PANAMA, Isla Colón, Bocas del Toro, MZSP 121852, 10 specimens (P. Krug; R. Ellingson; H. Galvão Filho, 07/viii/2015).

Remarks: Verrill (1901) was one of first to describe species of *Elysia* from Caribbean Sea. His contribution brought information about the external morphology of three species collected in Bermuda, including *Elysia papillosa*. Marcus & Marcus (1963) wrongly reported *E. papillosa* for the first time after Verrill (1901). Later, this specimen was described as a new species, *Elysia tuca* Marcus & Marcus, 1967 after the authors find another specimen from Florida that fits in the original description of *E. papillosa* (Marcus & Marcus, 1967).

Marcus & Marcus (1967) described new morphological characters of *E. papillosa*, such as the form of pericardial hump, dorsal vessels pattern, radula and penial shape, which has a long stylet with triangular base. After the Marcuses, Clark (1984) assessed the taxonomic status of Sacoglossa's species from Bermuda, including *E. papillosa*. Although Clark (1984) has not added morphological information about *E. papillosa*, his work was important to confirm the characteristics described by Marcus & Marcus (1967) from a specimen collected in type locality.

More recently, Ortea *et al*. (2005) claimed that *E. papillosa* was described based on two specimens belonging to distinct species. The original illustration of *E. papillosa* would comprises the head of one species and the body of another one, being impossible to determine the identity of *E. papillosa*, since data on the internal anatomy and external characteristics were not well described (Ortea *et al*. 2005). Then, the authors proposed the new species *Elysia annedupontae* Ortea, Espinosa & Caballer, 2015 and a redescription of *E* *papillosa.* A similar *E. papillosa* was described first by Thompson (1977), which illustrated a drawing of the dorsal view with closed parapodia and a smooth radula.

Redfern (2013) was the first to report that *E. papillosa* of Thompson (1977) and Ortea *et al.* (2005) was not the same species described by Verrill (1901). Redfern (2013) noticed that the specimens collected and named as *Elysia* sp. A did not swim as mentioned by Verrill (1901) in the original description of *E. papillosa*. After his observation, other authors considered that *Elysia papillosa sensu* Ortea *et al*. (2005) was an undescribed species (Camacho-García *et al*., 2014; Galvão-Filho *et al*., 2015).

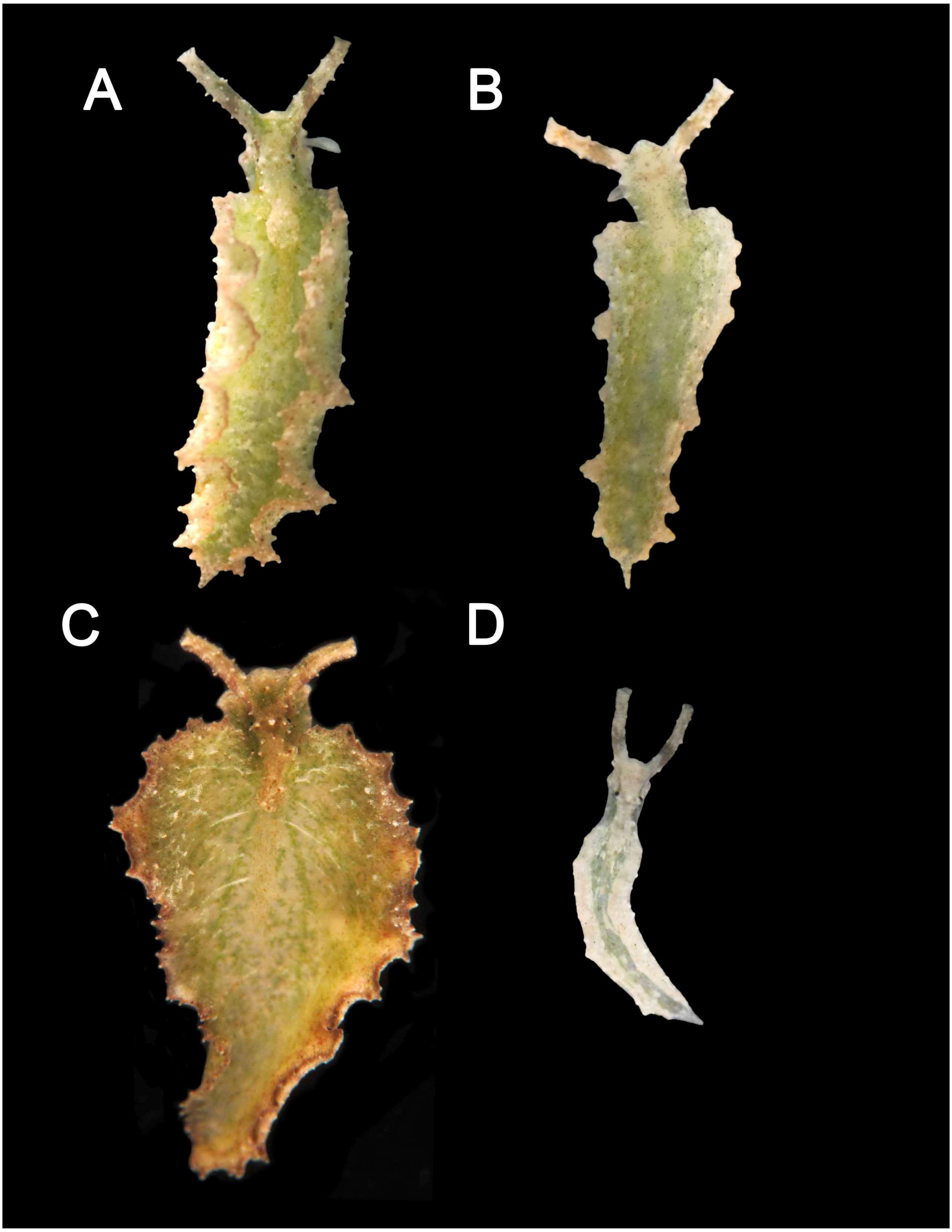

Figure 120. External morphology of live *Elysia papillosa*: A) dorsal view (length: 12 mm); B) ventral view (length 12 mm); C) dorsal view open parapodia (length: 11 mm); D) dorsal view juvenile (length: 4 mm).

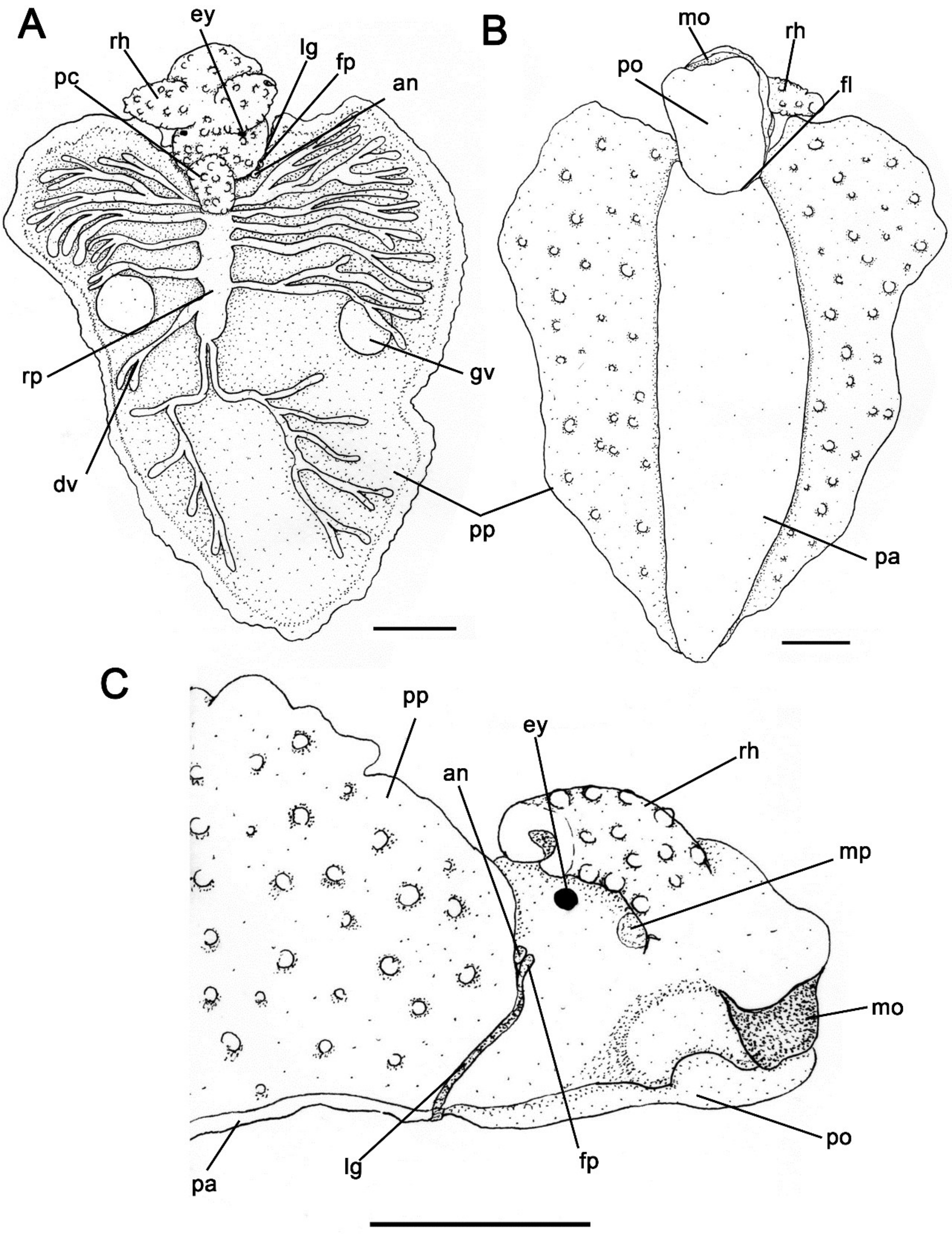

Figure 121. External morphology of *Elysia papillosa* (scale: 1 mm): A) dorsal view; B) ventral view; C) lateral view.

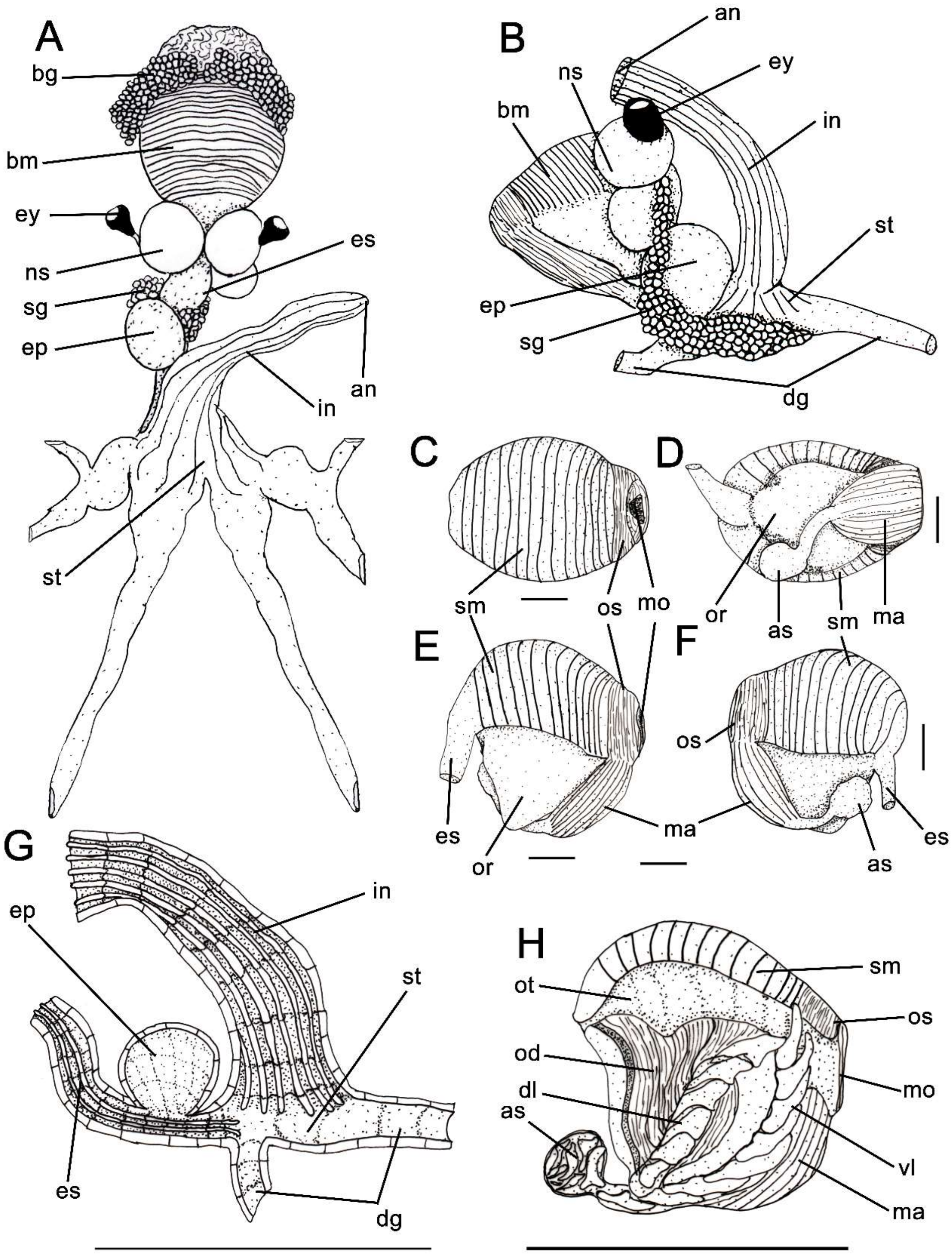

Figure 122. Digestive system of *Elysia papillosa* (scale: 0,5 mm): A) dorsal view of digestive system; B) lateral view of digestive system; C-F) buccal mass: C) dorsal; D); ventral; E) right side; F) left side; G) detail morphology of posterior digestive system; H) Detail morphology of buccal mass.

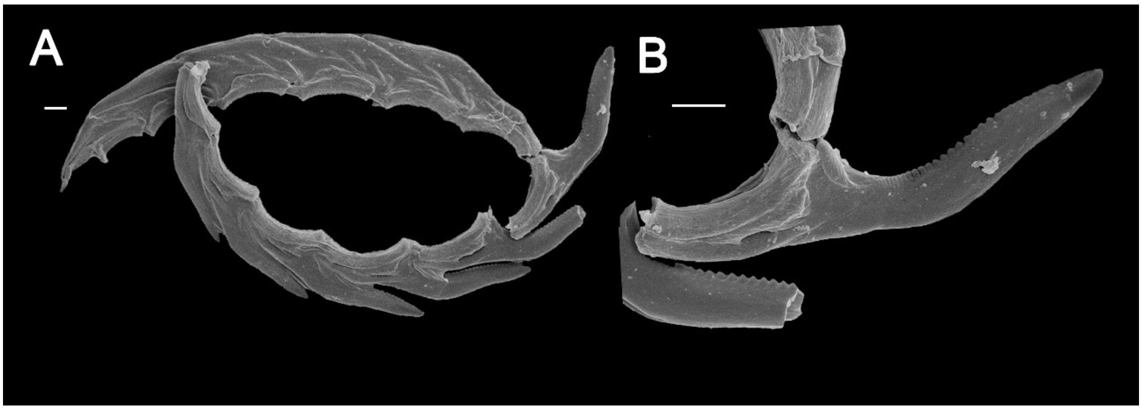

Figure 123. Scan electron microscope images of radula of *Elysia papillosa* (scale: 10 µm): A) general view; B) detail of the leading tooth.

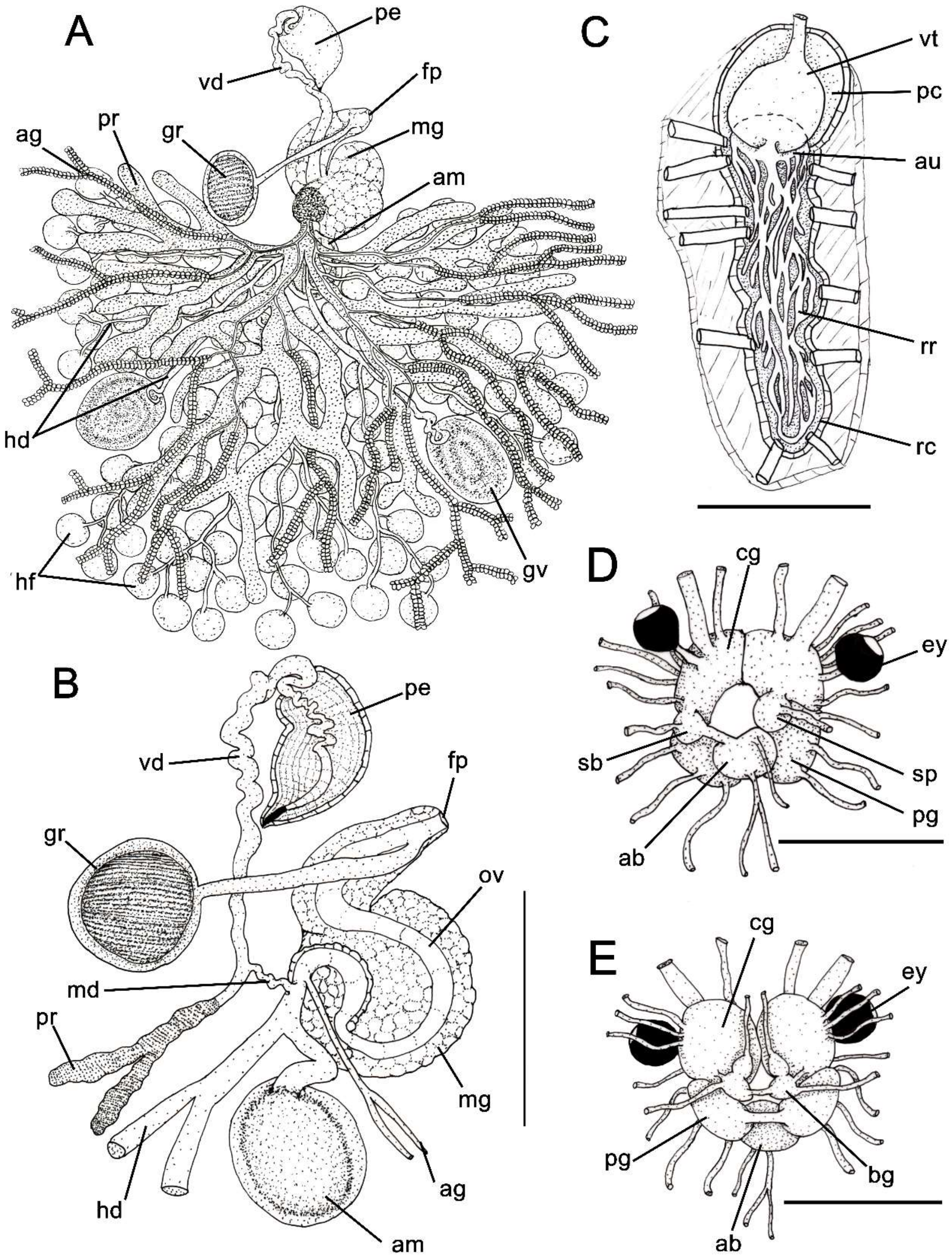

Figure 124. Reproductive, circulatory, excretory and nervous systems of *Elysia papillosa* (scale: 0,5 mm): A) general view of reproductive system; B) schematic view of reproductive system; C) ventral view of renopericaldial cavity in 4mm specimen; D) ventral view of renopericaldial cavity in 6mm specimen; E) posterior view of the nervous system; F) anterior of the nervous system.

***Elysia cornigera* Nutall, 1989**

See Krug, Vendetti & Valdés, 2016

(Figs. 125-128)

External morphology (Figs. 125-126): Body elongated, papillose, reaching up to 12 mm in live animals. Head evident, with scattered small papillae, length as half as body length, 2x longer than wider. Rhinophores (rh) rolled, papillose, long, length as longer as head length, and with rounded tip; papillae small through all rhinophore length. Eyes (e) dorsolateral behind rhinophores. Foot (f) easily distinguished from parapodia. Mesopodial groove (fl) conspicuous. Parapodial sole (ps) length bit longer than propodium (po) length in live animals; anterior part of propodium rounded. Renopericardial cavity (rc) remarkable, well subdivide into pericardium (pc) and renal pad (rp), length ~5x smaller as parapodial length. Pericardium (pc) muscular, globose, bit elongated longitudinally, with small papillae. Renal pad very short, attached to pericardium. Dorsal vessels (dv) organized in one symmetric pair, branching anteriorly and posteriorly several times Parapodium (pp) large, with irregular edge and papillae on external surface. Tail absent. Lateral groove (lg) starts on anterior extreme of right parapodia, where female bye (fp) is positioned, and finishes left to middle point of foot line. Male bye (mp) positioned below to right rhinophore. Anus (a) positioned dorsolaterally on posterior right side of head, close to anus.

Coloration (Fig. 125)**:** Body with yellowish general color in live animals. Intense green coloration on the foot and on the inside of the parapodia. Staining pattern formed by numerous white dots close to the renopericardial and inner surface of parapodia. Orange spots scattered over head and outer surface of parapodia. Renopericardial cavity yellowish on anterior bytion and whitish posteriorly and orange dots through all its extension. Parapodial margin colored as rest of body. Rhinophores yellowish and with some red dots scattered along its length.

Circulatory and excretory system (Fig. 128): Pericardium (pc) evident, globose, occupying half of renopericardial cavity. Auricle (au) very short, size ~12x smaller than ventricle (vt) size and with wall smooth. Ventricle occupying almost all pericardium, shape rounded. Kidney branched, composed of many renal ridges (rr) connected in lacunar shape. Nephrostome not observed.

Digestive system (Fig. 127): Buccal mass (bm) remarkable, size ~20x larger than esophageal pouch (ep), elongated, 3x longer than wider. Dorsal septate muscle (ds) composed of 10 thin bundles. Oral sphincter (os) reduced, compose of many circular muscles, size ~10x smaller than dorsal septate muscle length. Ascus musculature (ma) wide and long, occupying half of wide and all length of ventral side of buccal mass. Ascus (as) as narrowest as ascus musculature, short and rounded. Odontophore (od) rounded, parallel to oral cavity. Buccal pouch absent. Ascus containing discarded teeth not organized. Salivary glands (sg) positioned dorsal and lateral to esophagus between nervous system and stomach (st). Esophagus (es) length ~5x shorter than buccal mass length. Esophageal pouch (ep) globose and muscular, positioned on posterior part of esophagus. Stomach (st) short, flat, width as wider as intestine (in) width. Digestive gland (dg) with anterior ducts shorter than posterior ducts, run laterally and anteriorly inside head; posterior ducts run towards parapodial region. Intestine (in) internally folded through all its extension, finishes in dorsolateral anus (a) positioned near to lateral groove.

Reproductive system (Fig. 128): Gonad composed of numerous hermaphrodite follicles (hf) forming two separated areas, each area in one side of parapodia. Follicles size few variable, size up to 5x smaller than hermaphrodite ampulla (am). Gametholitic vesicle (gv) absent. Hermaphrodite ducts (hd) connect all follicles to one central duct which connects to hermaphrodite ampullas duct, width univariable. Hermaphrodite ampulla paired, each one in each side of parapodia. Male duct (md) connects prostate gland (pr) and vas deferens (vd) to hermaphrodite duct same as preceding species. Prostate gland composed of many small clustered glands positioned among follicles. Penis (p) shape conic, curved and elongated, ~8x longer than wider. Penial stylet absent. Vas deferens (vd) curled through all its length. Oviduct (ov) starts from hermaphrodite duct after connection with male duct and forms 3 well delimited chambers completely evolved by mucus gland and finishes on female bye (fp) in lateral groove. Proximal chamber of mucus gland smallest one, rounded, albumen duct and male duct connect to oviduct in it. Second chamber of mucus gland biggest one, formed by a curved expansion of glandular oviduct, where bursa copulatrix connects with oviduct. Distally chamber short and with folds. Albumen gland (ag) composed of many dorsal thin branches over prostate gland; main duct of albumen gland runs from hermaphrodite duct, more proximal than male duct connection with hermaphrodite duct, then branches into many ducts in parapodial area dorsally to prostate gland. Genital receptacle absent. Bursa copulatrix (bc) absent.

Nervous system (fig. 128): Cerebro-pleural ganglia (cp) bit larger than pedal ganglia (pg) size; each ganglion has 6 innervations; commissure cerebro-pleural short. Optic nerve long, bit longer than cerebro-pleural ganglion length. Buccal ganglia (bg) remarkable, size bit larger than sub-intestinal ganglion (sb); accessory ganglion absent; each ganglion has 2 innervations; buccal commissure internal. Pedal ganglia with 5 innervations by ganglion; pedal commissure simple and short, length bit smaller than pedal ganglion length. Visceral ganglia well developed. Abdominal ganglion (ab) size as half as pedal ganglion size, with 2 innervations. Sub-intestinal ganglion size ~4x as small as supra-intestinal ganglion (sp), with 1 innervation. Supra-intestinal ganglion size 3x smaller than abdominal ganglion size, with 2 innervation; connective between abdominal ganglion and sub-intestinal ganglion evident and long, length as longer as sub-intestinal ganglion; connective between abdominal ganglion and supra-intestinal long, as long as supra-intestinal ganglion length.

Distribution: Caribbean Sea (VALDÉS *et al.*, 2006).

Material examined: PANAMA, Isla Colón, Bocas del Toro, MZSP 131252, 1 specimens (P. Krug; R. Ellingson; H. Galvão Filho, 07/viii/2015).

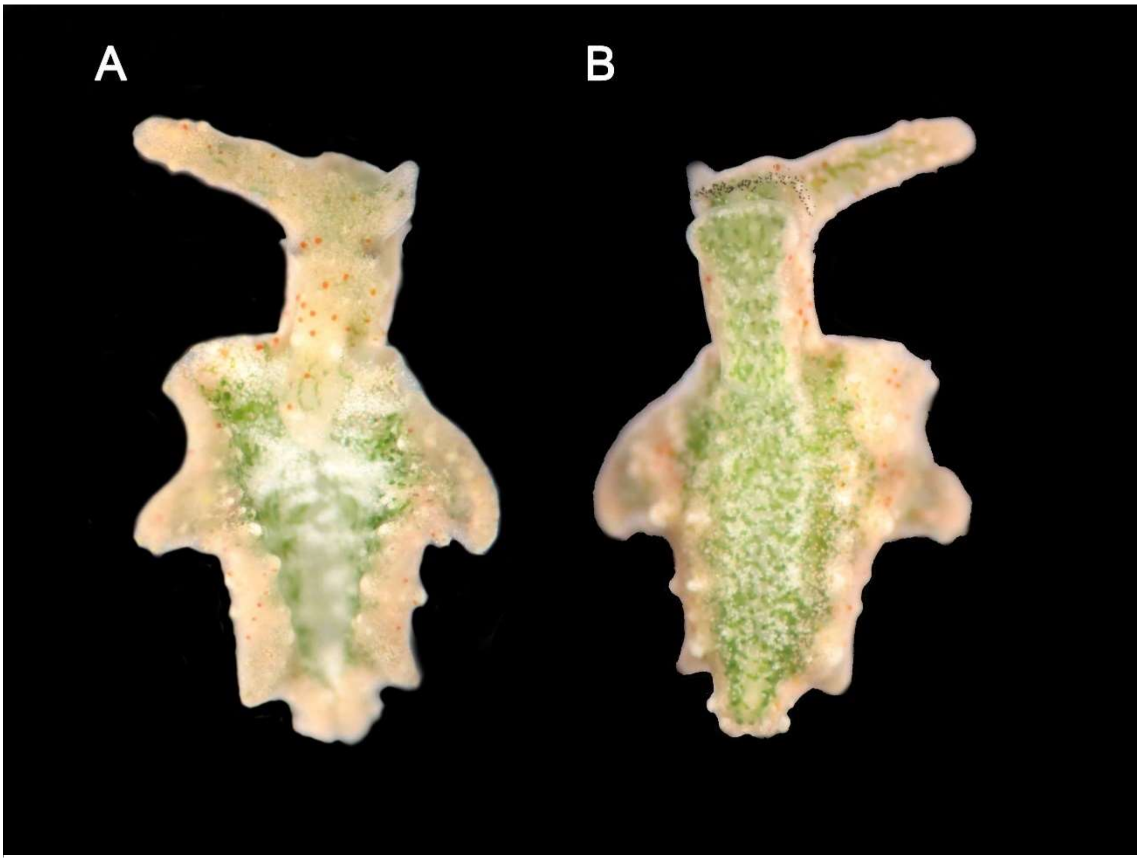

Figure 125. Live specimen of *Elysia cornigera*. A) dorsal; B) ventral.

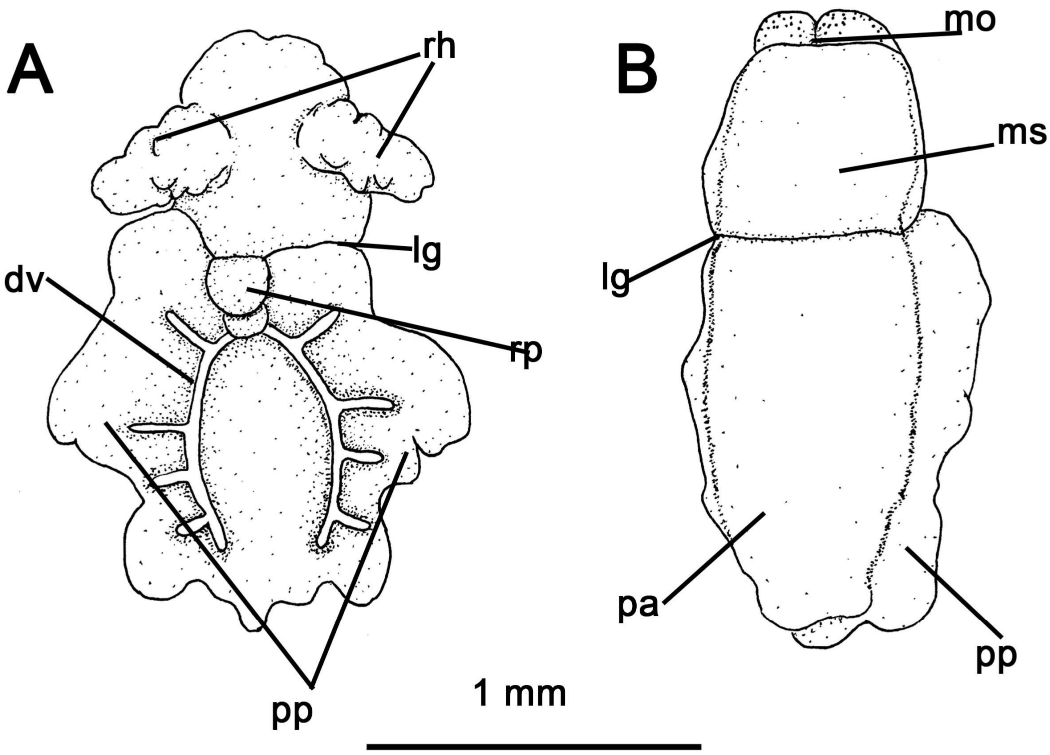

Figure 126. External morphology of *Elysia cornigera*. A) dorsal; B) ventral.

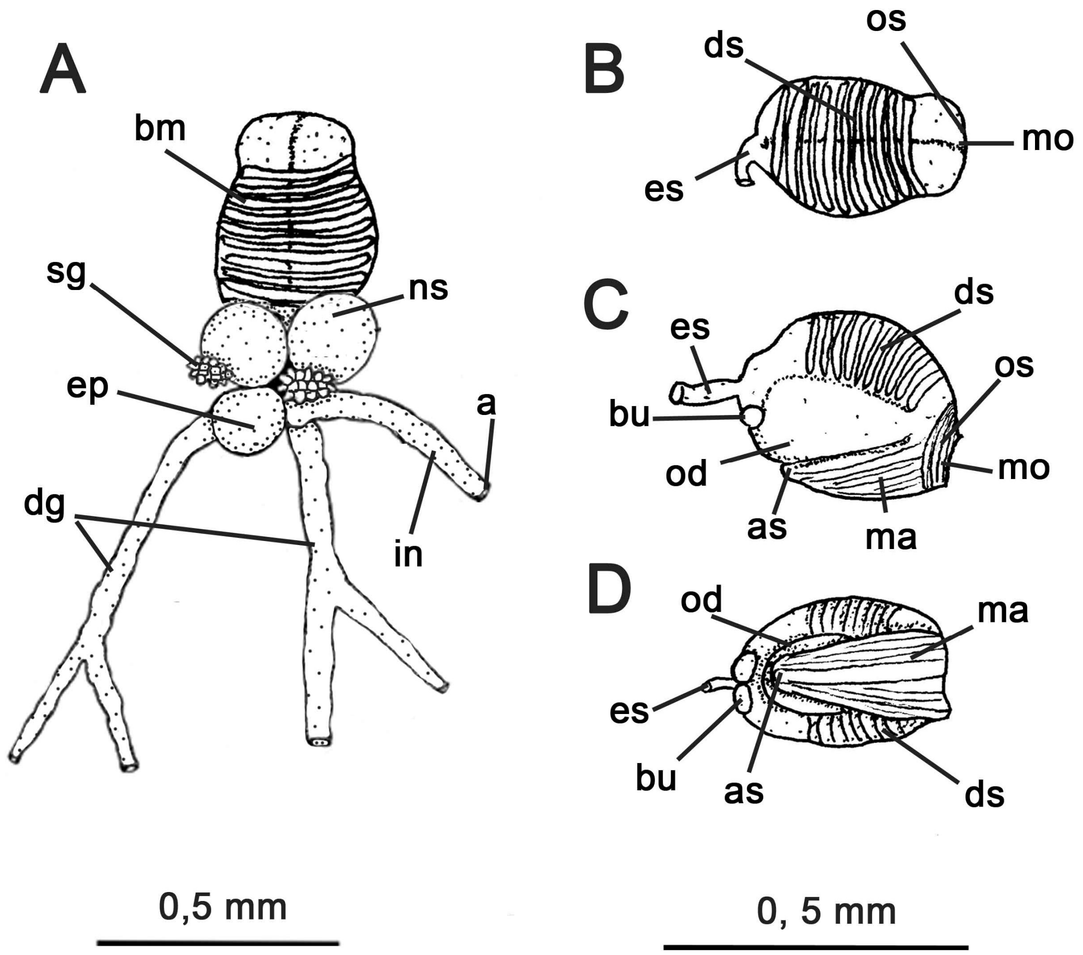

Figure 127. Digestive system of *Elysia cornigera*. A) Dorsal view. Buccal mass: B) dorsal; C) lateral; D) ventral.

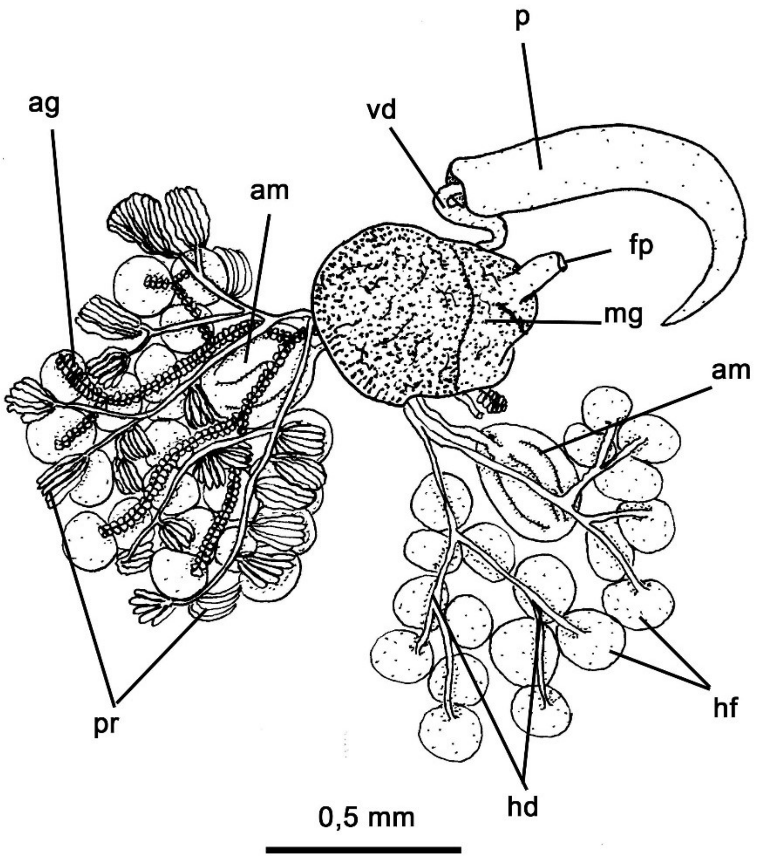

Figura 128. Reproductive system of *Elysia cornigera*.

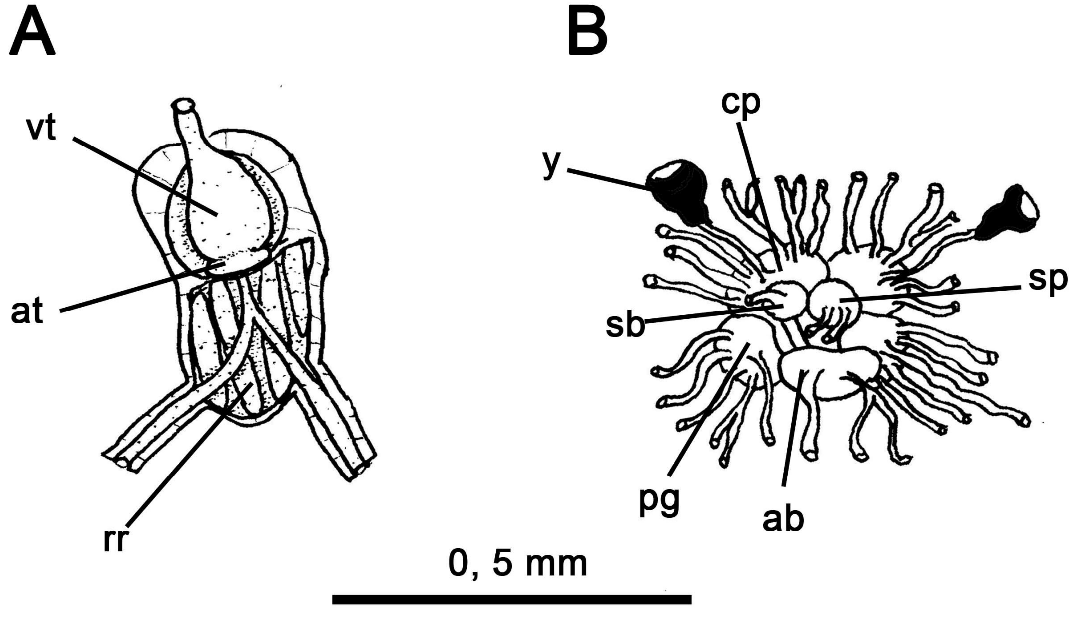

Figure 129. Circulatory and nervous systems of *Elysia cornigera*. A) Renopericardial cavity. B) anterior view of nervous system.

Elysia zuleicae Ortea & Espinosa, 2002

(Figs. 129-133)

See. Krug, Vendetii & Valdés, 2016

External morphology (Figs. 129-130): Body elongated, reaching up to 12 mm in live animals; ornamented with small papillae scattered through external side of parapodia, head, pericardium and rhinophores. Head evident, length ~1/5 of total body length, 2x longer than wider. Rhinophores (rh) folded, long, length as longer as head length, and with tip and base unfolded; papillae size small, spread through all rhinophore extension, but more concentrated on tip half. Eyes (e) dorsolateral behind rhinophores. Foot (f) remarkable distinct from parapodia; foot line (fl) well evident; parapodial sole (ps) 3x larger than propodium (po) in live animals; anterior part of propodium expanded laterally. Renopericardial cavity (rc) remarkable, well subdivide into pericardium (pc) and renal pad (rp), length ~4x smaller than parapodial length; pericardium (pc) muscular, globose, slight longitudinally elongated, papillose, length ~3x smaller than head length; renal pad smooth, thin-walled, length twice as longer as pericardium length; dorsal vessels (dv) organized in 2 symmetric pairs; most posterior pair of vessels runs posteriorly and branching several times, while anterior pair branch towards parapodia edge laterally. Parapodium (pp) large, with irregular edge and papillae; parapodia closure pattern regular, with six apertures, do not form parapodial siphon. External face of parapodia with dispersed small papillae, while inner surface has no ornamentation. Tail (tl) short, length ~3x smaller than head length. Gametholitic vesicles (gv) remarkable in bigger specimens, visible though parapodial surface, positioned on half-length of parapodia or posteriorly after renal pad. Lateral groove (lg) starts where right parapodia meets neck line, which female pore (fp) is located on, and finishes left to middle point of foot line. Male pore (mp) positioned below to right rhinophore. Anus (a) positioned dorsolaterally on posterior right side of head, really close to lateral groove, above female pore.

Coloration (Fig. 129): in agreement with *Krug* et al., 2016.

Circulatory and excretory system (Fig. 133): Pericardium (pc) evident, globose, occupying 1/4 of renopericardial cavity; auricle (au) size as large ventricle (vt) size, auricle wall furrowed; ventricle size occupying 1/3 or pericardium, shape rounded. Kidney branched, composed of many renal ridges (rr) connected in trabecular shape. Nephrostome not observed.

Digestive system (Fig. 131-132): Buccal mass (bm) remarkable, size ~10x larger than esophageal pouch (ep), elongated, more longer than wider; dorsal septate muscle (ds) composed of 11 large bundles; oral sphincter (os) evident, compose of a pair of large muscles, size ~5x smaller than dorsal septate muscle length; ascus musculature (ma) narrow and long, occupying almost all width and 1/3 length of ventral side of buccal mass; ascus (as) twice narrowest than ascus musculature, elongated, length trespassing ventral length of buccal mass, straight; odontophore (od) short, parallel to oral cavity, inconspicuous; buccal pouch (bp) connected near to oral sphincter, size half of buccal mass size. Radula with 9 teeth in ascending limb; leading tooth elongated, total length twice as longer as base length; cusp bearing numerous small denticles through all extension; lateral cutting edges inconspicuous and smooth; ascus containing discarded teeth not organized. Salivary glands (sg) positioned ventrally and laterally to esophagus between central nervous system (ns) and esophageal pouch. Esophagus (es) length as longer as buccal mass length, width as large as intestine width; internal surface with two longitudinal folds through all its extension. Esophageal pouch (ep) globose and muscular, positioned on posterior part of esophagus; internal surface with two complete large folds. Stomach (st) flatten, wide, width ~4x wider than intestine (in); folds internally present on dorsal portion; stomach pouches absent. Digestive gland (dg) paired in each side of stomach; anterior ducts shorter than posterior ducts, run laterally and anteriorly inside head; posterior ducts run towards parapodial region. Intestine (in) internally folded through all its extension, finishes in dorsolateral anus (a) positioned near to lateral groove.

Reproductive system (Fig. 133): Similar to *E. papillosa* except for: hermaphrodite ampulla larger than other reproductive structures, almost twice as larger as mucus gland (mg) size, and ~20x bigger than follicles; penis (p) length as longer as mucus length, shape conic and elongated, total length 4x bigger as base diameter, stylet absent; vas deferens bit longer than penis length, few undulated and not curled.

Nervous system (Fig. 133): Cerebro-pleural ganglia (cp) size bit larger than pedal ganglia (pg); each ganglion has 7 innervations; commissure cerebro-pleural not evident. Optic nerve length short, bit longer than half of cerebro-pleural ganglion length. Buccal ganglia (bg) remarkable, size larger than sub-intestinal ganglion (sb); accessory ganglion present, size ~3x smaller than buccal ganglion; each ganglion has 2 innervations, which one of them runs from accessory ganglion; buccal commissure simple. Pedal ganglia present 2 innervations by ganglion; pedal commissure short, much smaller than pedal ganglion length and ~3x longer than buccal commissure. Visceral ganglia well developed; abdominal ganglion (ab) size bit smaller than pedal ganglion size, has 3 innervations; sub-intestinal ganglion size ~6x as small as supra-intestinal ganglion (sp), has 1 innervation; supra-intestinal ganglion bit larger than half of abdominal ganglion size, has 1 innervations; connective between abdominal ganglion and sub-intestinal ganglion evident and short; connective between abdominal ganglion and supra-intestinal ganglion absent.

Distribution: Florida (Krug *et al*., 2016), Bahamas (present study) e Cuba [Havana – type locality (Ortea *et al*., 2011)].

Material examined: PANAMA, Isla Colón, Bocas del Toro, MZSP 121853, 6 specimens (P. Krug; R. Ellingson; H. Galvão Filho, 07/viii/2015).

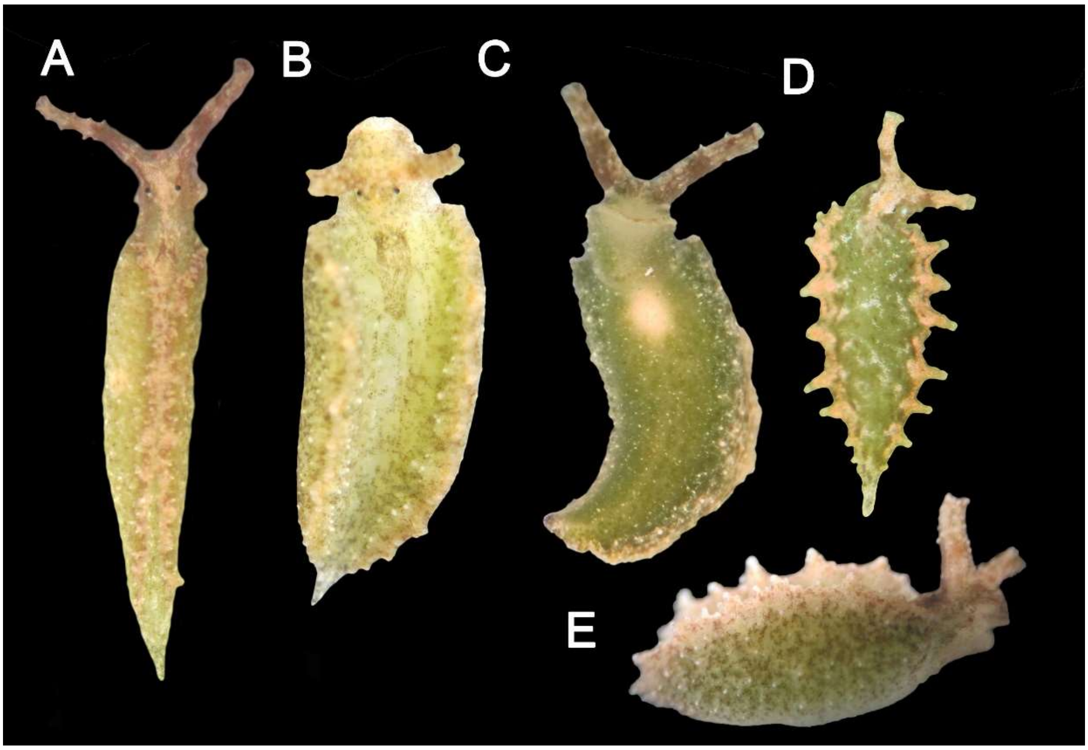

Figure 129. External morphology of live *Elysia zuleicae*: A-B) dorsal view (length: 11 mm); B) ventral view (length 11 mm); C) dorsal view juvenile (length: 4 mm); E) lateral view (length: 10 mm).

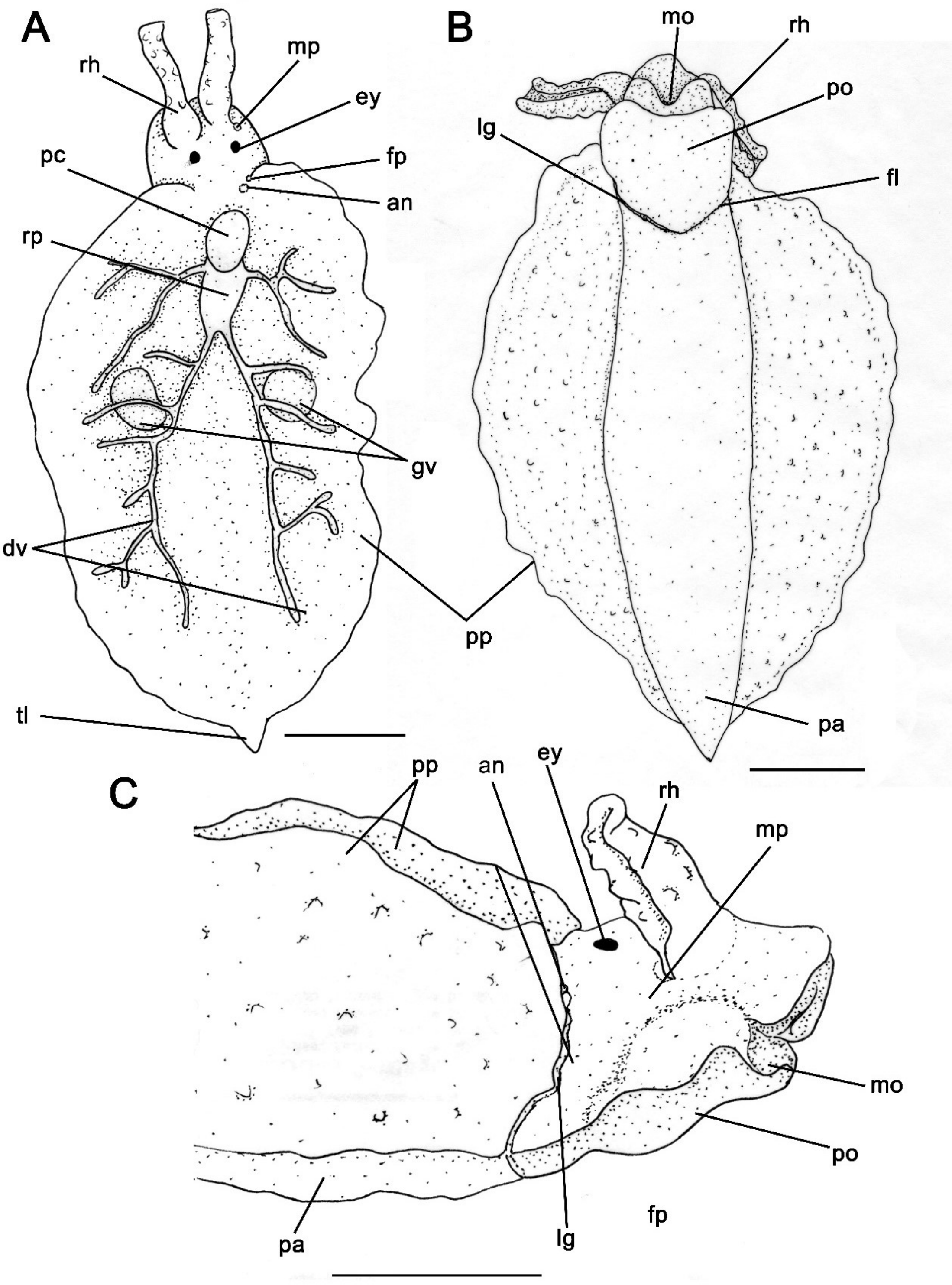

Figure 130. External morphology of *Elysia zuleicae* (scale: 1 mm): A) dorsal view; B) ventral view; C) lateral view.

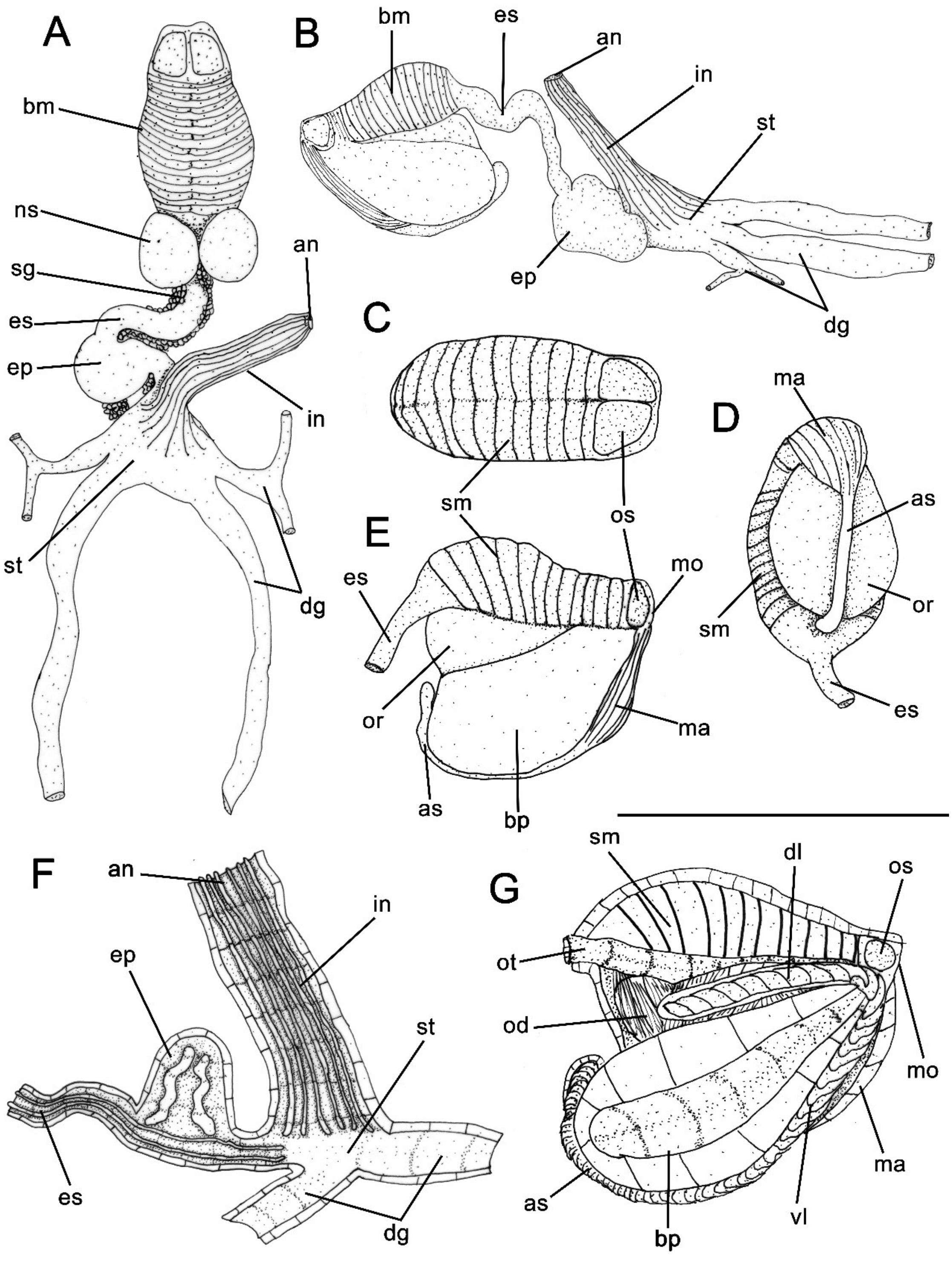

Figure 131. Digestive system of *Elysia papillosa* (scale: 0,5 mm): A) dorsal view of digestive system; B) lateral view of digestive system; C-E) zuleicae mass: C) dorsal; D); ventral; E) right side; F) detail morphology of posterior digestive system; G) Detail morphology of buccal mass.

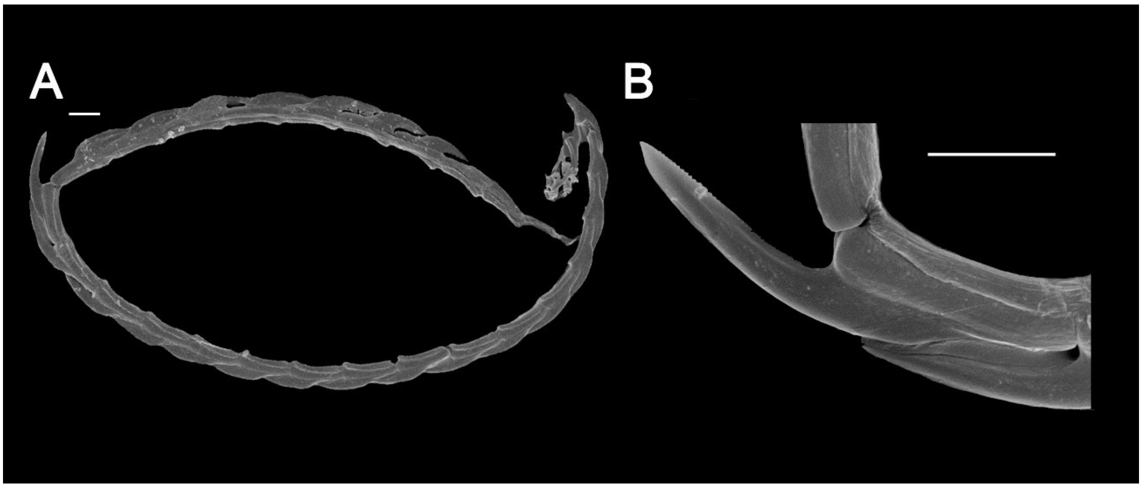

Figure 132. Scan electron microscope images of radula of *Elysia zuleicae* (scale: 10 µm): A) general view; B) detail of the leading tooth.

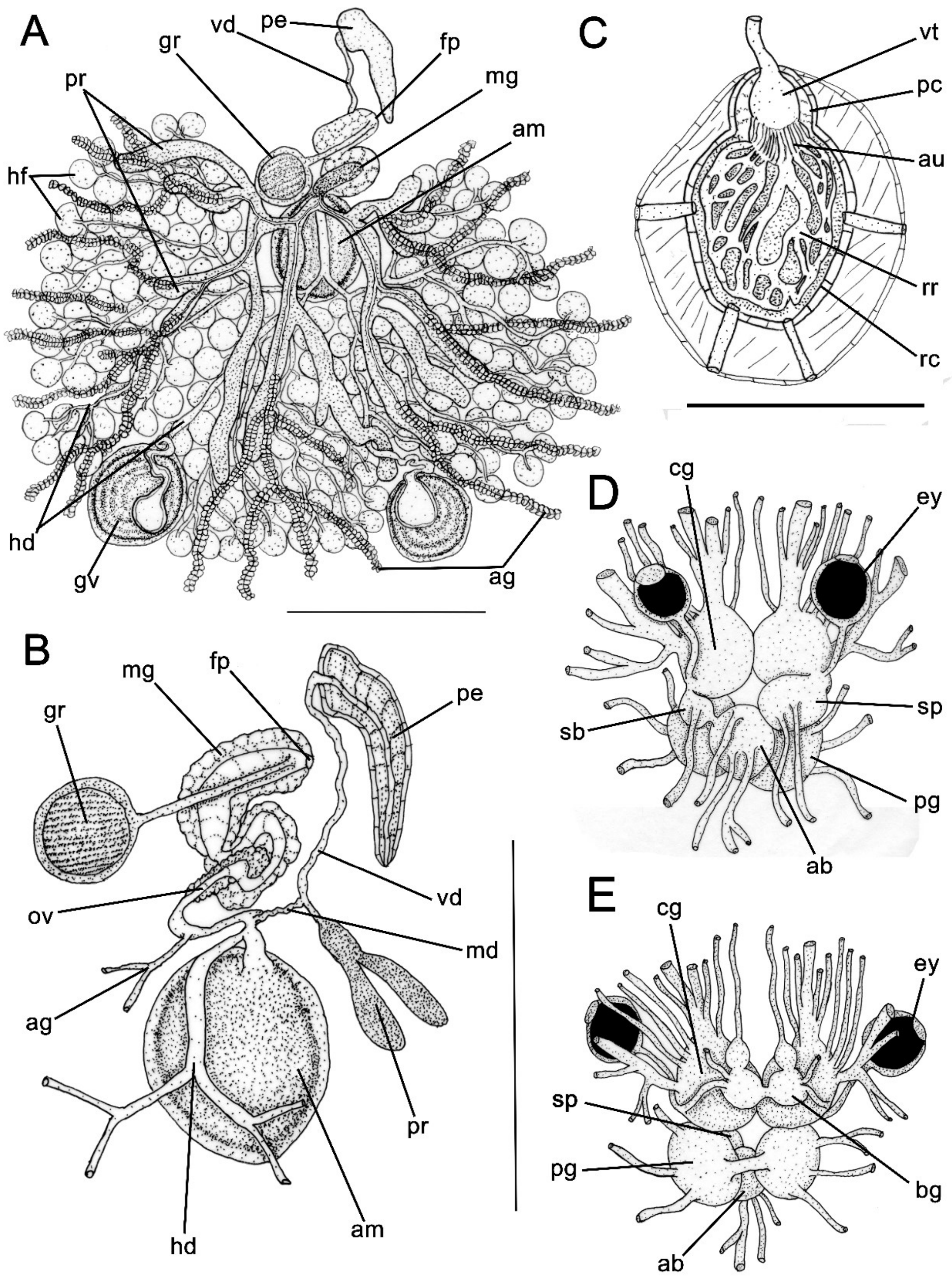

Figure 133. Reproductive, circulatory, excretory and nervous systems of *Elysia zuleicae* (scale: 0,5 mm): A) general view of reproductive system; B) schematic view of reproductive system; C) ventral view of renopericaldial cavity in 4mm specimen; D) ventral view of renopericaldial cavity in 6mm specimen; E) posterior view of the nervous system; F) anterior of the nervous system.

Elysia orientalis Ortea, Moro, Caballer & Espinosa, 2011
(Fig. 134-1388)

Elysia orientalis Ortea, Moro, Caballer & Espinosa, 2011:205, fig. 5; Krug *et al*., 2016:94, fig. 56B.

External morphology (Fig. 134-135): Body smooth, elongated, reaching up to 6 mm in live animals. Head evident, length ~1/3 of total body length, 2x longer than wider. Rhinophores (rh) very short, rolled, smooth, length ~1/5 of head length, and with tip rounded. Eyes (y) located dorsolaterally behind rhinophores. Foot (f) with remarkable limit near to parapodia; parapodial sole (ps) twice as large as propodium (po) in live animals; anterior part of propodium rounded. Renopericardial cavity (rc) inconspicuous, slightly globose, twice as small as parapodia length. Dorsal vessels absent. Parapodia(pp) short, with irregular edge and no papillae, begin after lateral groove and end at third part of body length; parapodia pattern totally opened and do not form parapodial siphon. Tail (tl) long as head length. Female pore (fp) located on extreme dorsal point of lateral groove (lg). Male pore (mp) below right rhinophore. Anus (an) positioned dorsolaterally on posterior part of head, above lateral groove and near to pericardium.

Coloration (Fig. 134): Body of live animals translucent yellowish. Dorsal and lateral body portion covered by innumerous white and few orange dots; greenish transversal pattern between eyes and posteriorly to parapodia. Foot intense green with scattered colorful bright orange, blue, green and white dots. Tip of tail translucent with fewer white dots than rest of body. Rhinophores translucent, white dots through all extension, orange dots mainly on tips, and green longitudinal line from digestive gland branch.

Digestive system (Fig. 136-137): Buccal mass (bm) size ~4x larger than esophageal pouch (ep), rounded, as longer as wider; dorsal septate muscle (ds) composed of 16 thin bundles; oral sphincter (os) inconspicuous, compose of small circular muscles, size ~6x smaller than dorsal septate muscle length; ascus musculature (ma) wide and short, occupying almost all width and half-length of ventral side of buccal mass; ascus (as) external, ~5x narrowest than ascus musculature, long, curled twice to left of buccal mass; odontophore (od) rounded and parallel to oral cavity. Radula with 6 teeth on ascending limb; leading tooth elongated, total length twice as longer as base length; cusp bearing numerous very small denticles through all extension; lateral cutting edges remarkable, partially serrated, small denticles present only in first third near to tooth tip. Ascus containing discarded teeth organized in curled row following ascus length. Salivary glands (sg) positioned dorsally and laterally to esophagus between central nervous system (ns) and esophageal pouch. Esophagus length bit shorter than buccal mass length, width ~3x thinner than intestine width; internal surface with no folds. Esophageal pouch (ep) globose and muscular, positioned on posterior part of esophagus, size 6x smaller than buccal mass; internal surface with no folds. Stomach (st) size similar to esophageal pouch, globose shape, internally presents one big fold coming from intestine (in); stomach pouches (sc) size bit smaller than stomach and not subdivided. Digestive gland (dg) paired in each stomach pouch; anterior ducts shorter than posterior ducts, run laterally and anteriorly in head; posterior duct run toward parapodial area and tail. Intestine (in) twice as wider as esophagus, bit thinner than stomach, and folded through all extension, finishes in dorsolateral anus (a) positioned near to pericardium.

Reproductive system (Fig. 138): Gonad composed of 9-12 hermaphrodite follicles (hf) on each side of body and forming two isolated groups; follicles size few variable and large as hermaphrodite ampulla (am), distributed through parapodial area; gametolytic vesicles absent; hermaphrodite ducts (hd) connect all follicles to one central duct which connects to hermaphrodite ampulla. Hermaphrodite ampulla positioned laterally in reproductive system, on left side under mucus gland (mg), size bit small than genital receptacle (gr). Male duct (md) connects prostate gland (pr) and vas deferens (vd) to hermaphrodite duct after hermaphrodite ampulla connection; prostate gland dorsally ramified over follicles through all parapodial area, composed of one main glandular duct; vas deferens twice as longer as penis length, few undulated though all extension, not curled; penis (pn) size 3x bigger than ampulla and 4x smaller than mucus gland (mg), shape conic and short, total length twice as longer as base diameter, stylet absent. Oviduct (ov) starts from hermaphrodite duct after connection with male duct and forms 3 well delimited chambers completely evolved by mucus gland, and finishes on female pore (fp) in lateral groove; proximal chamber of mucus gland smallest one, where male duct and albumen duct connect to oviduct; second chamber of mucus gland biggest one, where oviduct forms a circular handle and connects to genital receptacle; distally chamber rounded, size ~3x smaller than remaining mucus gland, form a dorsal darker glandular area with simple lumen connected distally to oviduct after genital receptacle connection. Albumen gland (ag) composed of many thin branches ventrally to follicles; main duct of albumen gland runs from oviduct next to hermaphrodite duct, branching into smaller ducts in parapodial area dorsally to prostate gland. Genital receptacle connected to oviduct in distally position near to female pore, size bit larger than hermaphrodite ampulla.

Circulatory and excretory system (Fig. 138): Pericardium (pc) very small, occupying 1/4 of renopericardial cavity; auricle (au) inconspicuous, size more than 10x smaller than ventricle (vt); auricle wall smooth; ventricle size large, occupying almost all pericardium, shape piriform. Kidney short, branched, composed of 3 (in 4mm specimen) or 5 (in 6 mm specimen) renal ridges (rr) arranged radially, bisected posteriorly where they connect to each other in short network. Nephrostome not observed.

Nervous system (Fig. 138): Cerebro-pleural ganglia (cp) size bit larger than pedal ganglia (pg); each ganglion has 6 innervations; commissure cerebro-pleural absent. Optic nerve length short, half of cerebro-pleural ganglion length. Buccal ganglia (bg) remarkable, size larger than sub-intestinal ganglion (sb); each ganglion has three innervations; buccal commissure absent. Pedal ganglia present 3 innervations by ganglion; pedal commissure inconspicuous. Visceral ganglia well developed; abdominal ganglion (ab) size larger than half of pedal ganglia size, has 2 innervations; sub-intestinal ganglion size 3x as small as supra-intestinal ganglion (sp), has 1 innervation; supra-intestinal ganglion size twice as small as abdominal ganglion, has 1 innervation; connective between abdominal ganglion and sub-intestinal ganglion ~3x smaller than connective between abdominal ganglion and supra-intestinal ganglion.

Distribution: Florida (KRUG, VENDETII & VALDÉS, 2016), Bahamas (present study) e Cuba [Havana – type locality (ORTEA *et al*., 2011)].

Remarks

The two specimens analyzed herein have similar color pattern as the original description, except for blue dots are exclusively on foot instead through dorsal surface. Also, lateral body color was original described as pinkish, while Bahamian specimens have opaque whitish color. The oblique eyes are diagnostic character in original description, nevertheless this character is only evident in the smallest specimen. Rhinophores were not described regarding their size, but the original illustration shows the rhinophores as longer as head length, whereas the specimens analyzed present a really short rhinophore, almost 1/5 of head length.

Elysia orientalis is easily identifiable due to its external characters, such as remarkable oblique parapodial shape, long tail and absence of dorsal vessels. *Elysia chitwa* Marcus, 1955 is another western Atlantic *Elysia* species without dorsal vessels as compared by Ortea *et al*. (2011). According to Krug *et al.* (2016) original description of *E. chitwa* is not much detailed, then the status of *nomen dubium* was attributed to it. However, morphological traits of external and internal morphology described by Marcus (1955, 1957) still allows comparison.

Other similarities between *E. orientalis* and *E. chitwa* are on the reproductive system, including the anterior connection of genital receptacle, oviduct forming a handle surrounded by mucus gland and the single hermaphrodite ampulla (see Marcus, 1955). Apart from differences on body coloration, *E. chitwa* has a different parapodial shape and tail absent, which externally distinguishes it from *E. orientalis*. Internally, *E. chitwa* has the kidney as a simple sac (Marcus, 1957, p. 414), while *E. orientalis* has a branched kidney type. Although not specified on the original description, the Marcus' drawings of *E. chitwa* reveals that ascus is not spiral (Marcus, 1957, p. 409, fig. 45), radula tooth does not have denticulate lateral edges (Marcus, 1955, p.6 fig. 57) and proximal chamber of mucus gland is not evident as in *E. orientalis* (Marcus, 1955, pl. 7, fig. 58).

Phylogenetically, *Elysia orientalis* is related to *Elysia tomentosa* complex, which comprises large *Caulerpa* feeder species (Krug *et al*., 2016). The species on this clade present papillose body, large parapodia, long renopericaridal prominence and no tail (Krug *et al*., 2016), whereas *E. orientalis* has a smooth body, short parapodia and kidney and a long tail. Except for *Elysia pratensis* Ortea & Espinosa, 1996, the radulae among the Caribbean species on *E. tomentosa* complex are very similar. The leading tooth is elongate with curved cusp bearing very fine, blunt denticles, pointed tip on club-shaped apex, and lateral edges inconspicuous (see *Elysia subornata* Verrill, 1901, *Elysia pawliki* Krug, Vendetti & Valdés, 2016 and *Elysia zemi* Krug, Vendetti & Valdés, 2016 in Krug *et al*., 2016). On the other hand, *E.*

orientalis presents an elongated leading tooth with straight denticulate cusp, a very pointed teeth apex, and remarkable lateral edges with denticles.

Regarding the morphological comparison of this study, we are aware about the difficulties to infer similarities among species in the genus *Elysia* due to lacking detailed information other than on radular, penis and external morphology. Besides the morphological description of the rare *E. orientalis*, the goal of this study is to support the morphological study of the genus *Elysia* as a resource for future taxonomy and phylogenetic study of the genus *Elysia*.

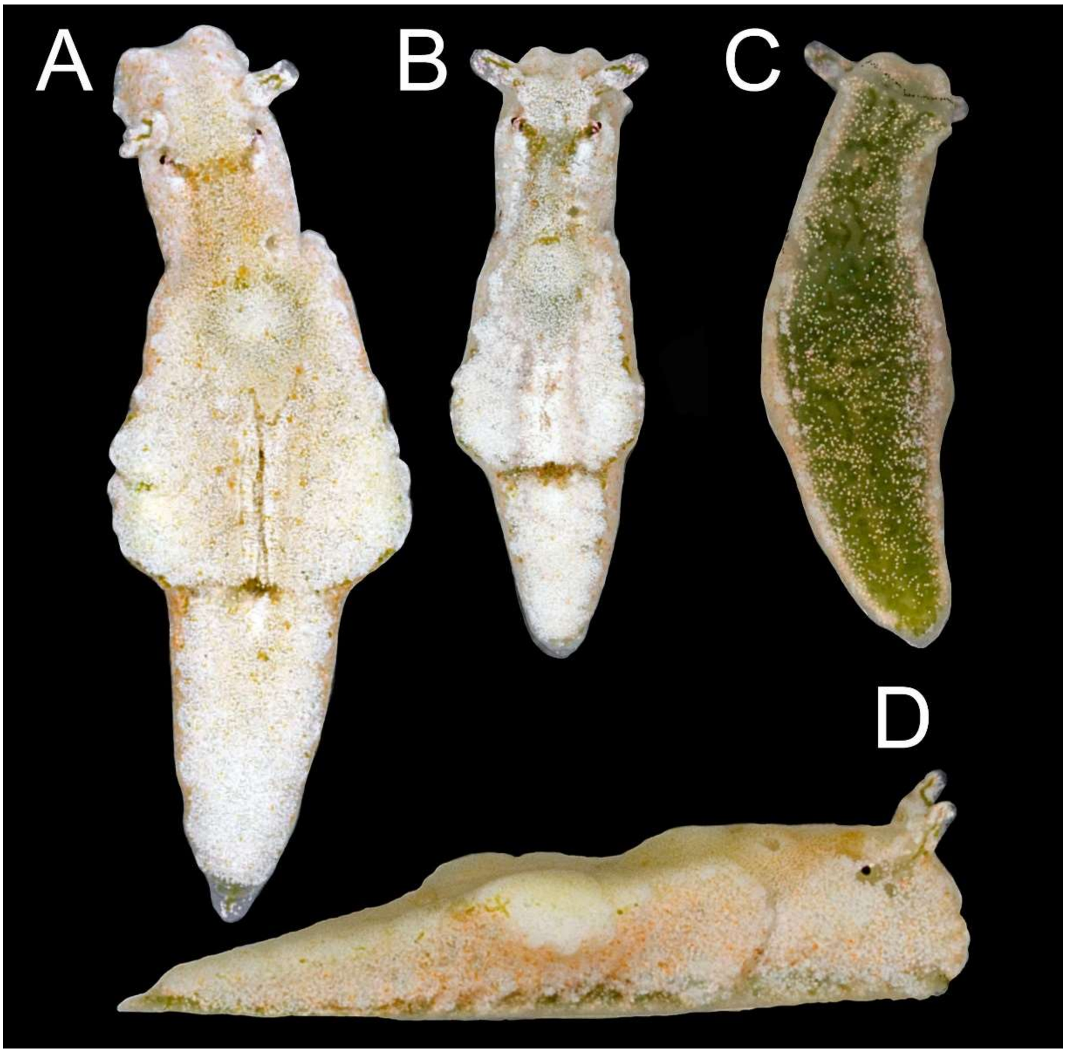

Figure 134. External morphology of live *Elysia orientalis*: A) dorsal view (length: 6 mm); B) dorsal view (length 4 mm); C) ventral view (length: 4 mm); D) lateral view (length: 6 mm).

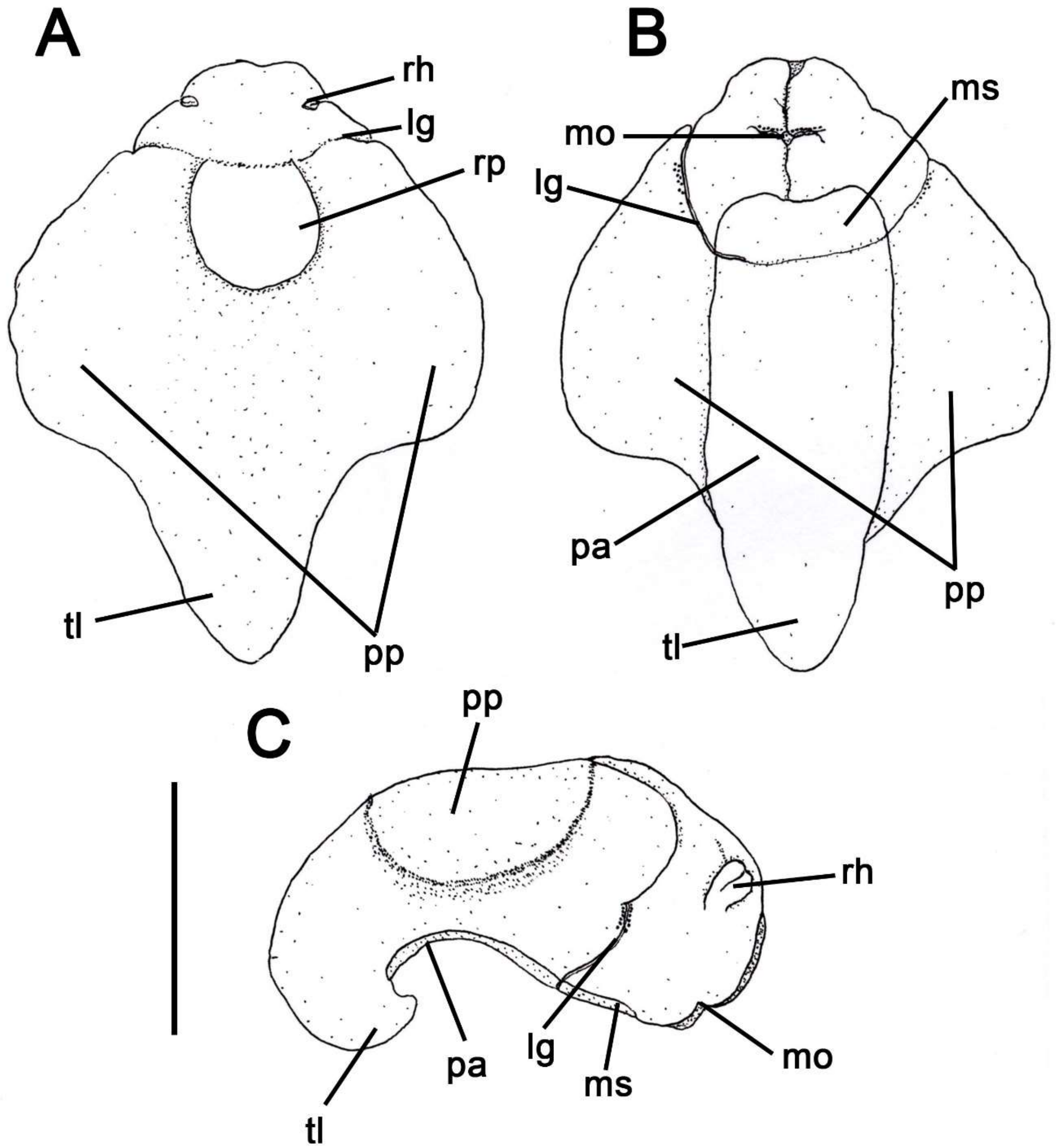

Figure 135. Drawings of the external morphology of *Elysia orientalis* (scale: 1 mm): A) dorsal view; B) ventral view; C) lateral view.

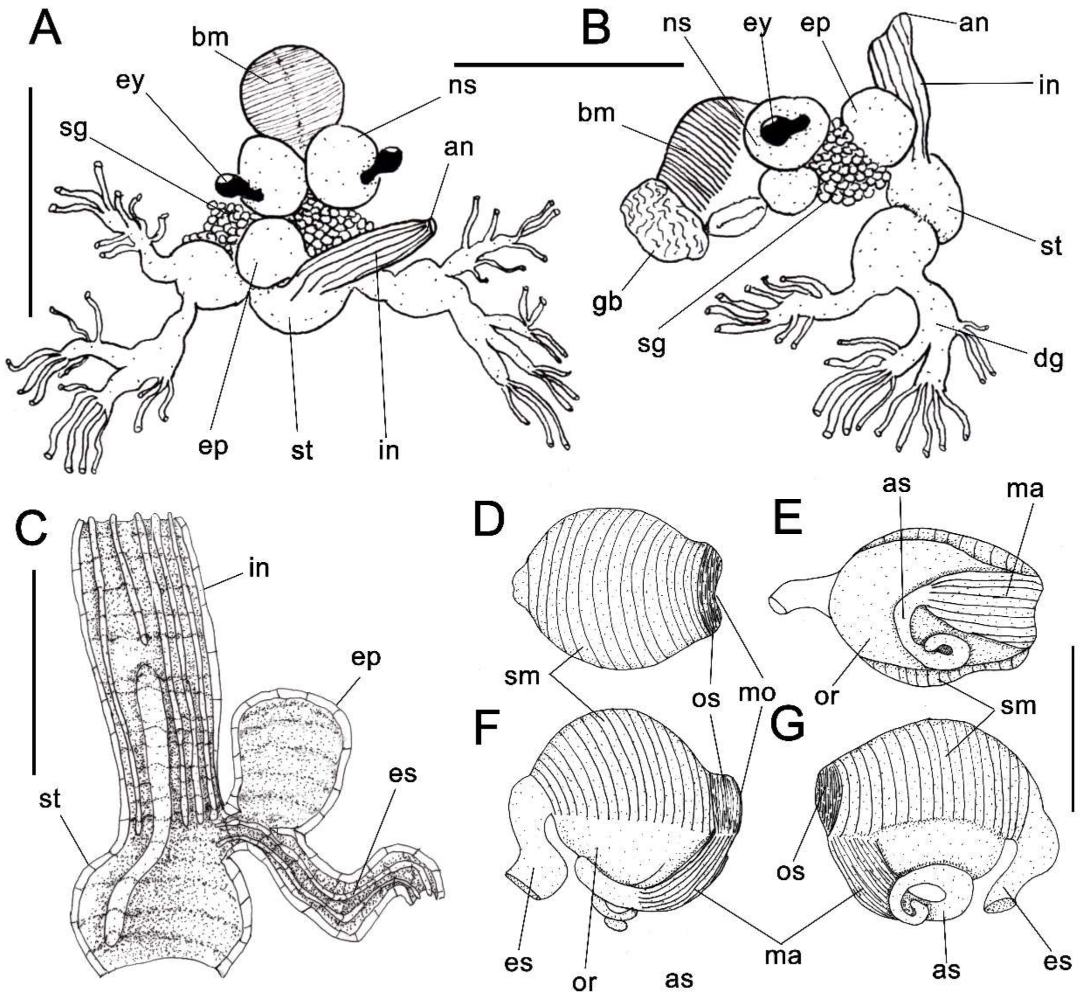

Figure 136. Digestive system of *Elysia orientalis* (scale: 0,5 mm): A) dorsal view of digestive system; B) lateral view of digestive system; C) detailed morphology of posterior digestive system; D-G) buccal mass: D) dorsal; E); ventral; F) right side; G) left side.

Figure 137. Scan electron microscope images of radula of *Elysia orientalis* BMSM 59035 (scale: 10 µm): A) general view; B) detail of the leading tooth; C) detail of teeth on ascus.

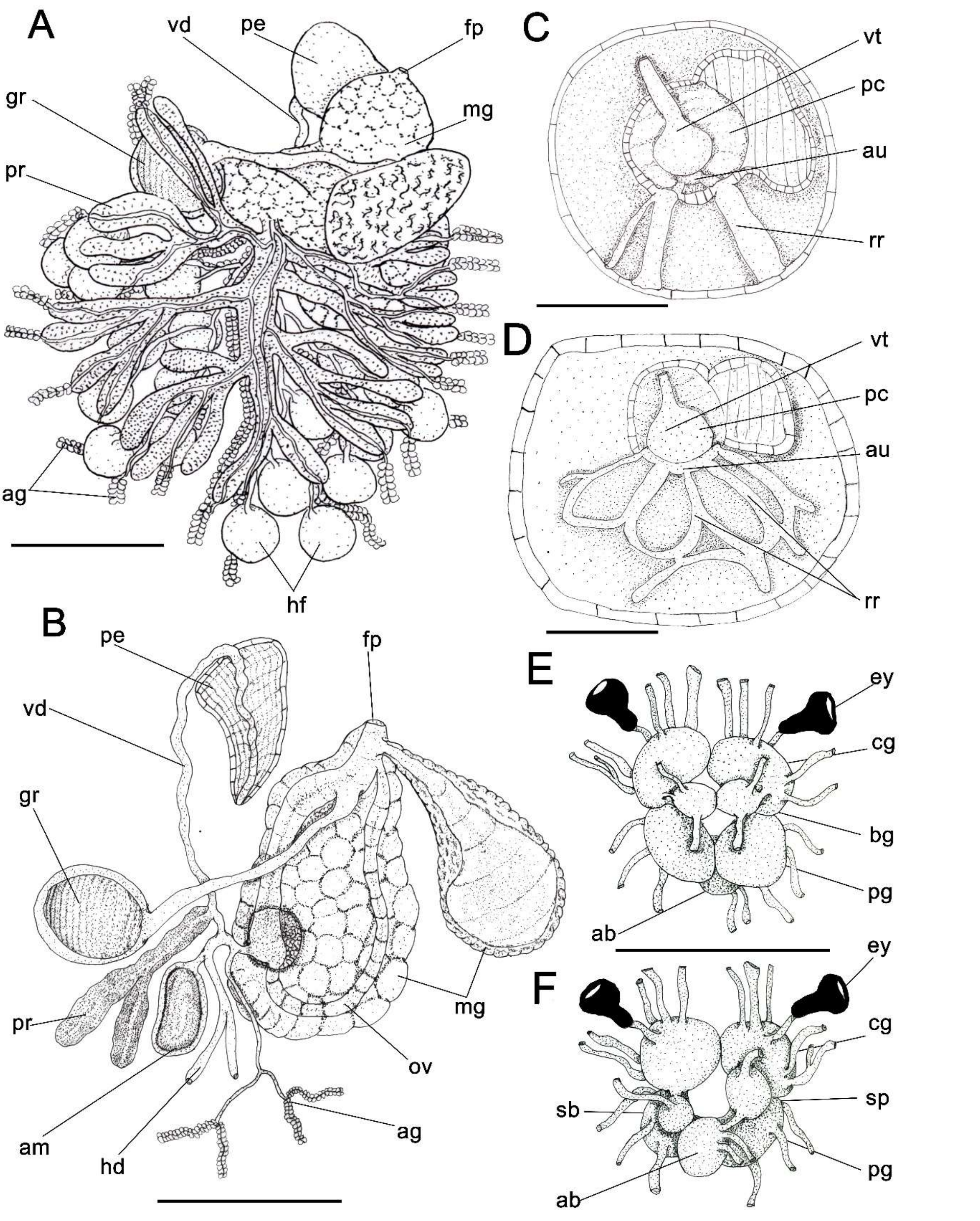

Figure 138. Reproductive, circulatory, excretory and nervous systems of *Elysia orientalis* (scale: 0,5 mm): A) general view of reproductive system; B) schematic view of reproductive system; C) ventral view of renopericaldial cavity in 4mm specimen; D) ventral view of renopericaldial cavity in 6mm specimen; E) anterior view of the nervous system; F) posterior of the nervous system.

Elysia pawliki Krug, Vendetti & Valdés, 2016
(Figs. 139-144)

External morphology (Figs. 139-140): Body elongated, reaching up to 30 mm in live animals; ornamented with irregular papillae scattered through both sides of parapodia, head, pericardium, renal pad and rhinophores. Head evident, length up to 1/5 of total body length, 2x longer than wider. Rhinophores (rh) rolled, short, bit smaller than head length, and with rounded tip; papillae size variable, spread through all rhinophore extension. Eyes (e) dorsolateral behind rhinophores. Foot (f) remarkable distinct from parapodia; foot line (fl) well evident; parapodial sole (ps) 3x larger than propodium (po) in live animals; anterior part of propodium rounded. Renopericardial cavity (rc) remarkable, well subdivide into pericardium (pc) and renal pad (rp), length half as longer as parapodial length; pericardium (pc) muscular, globose, papillose, length ~6x smaller than head length; renal pad few papillose, thin-walled, length 4x longer than pericardium length; dorsal vessels (dv) in asymmetric arrangement, five vessels in one side of parapodia and six in another one, which right/left variation among specimens, most posterior pair of vessels runs posteriorly and branching several times, while anterior pair branch towards parapodia edge. Parapodium (pp) large, with irregular edge and papillae; parapodia closure pattern regular, with two apertures, most anterior aperture bit bigger than posterior one, one big rounded glandular structure (gs) present on each extreme point of both aperture. External face of parapodia with elongated papillae varying in size, while inner surface has few small and scattered papillae. Tail absent. Gametholitic vesicles absent. Lateral groove (lg) starts on anterior extreme of right parapodia, where female pore (fp) is positioned, and finishes left to middle point of foot line. Male pore (mp) positioned below to right rhinophore. Anus (a) positioned dorsolaterally on posterior right side of head, close to lateral groove, above female pore.

Coloration (Fig. 139): in agreement with *Krug* et al., 2016.

Circulatory and excretory system (Fig. 144): Pericardium (pc) evident, globose, occupying 1/5 of renopericardial cavity. Auricle (au) size 3x smaller than ventricle (vt) size, auricle wall furrowed. Ventricle occupying 1/3 or pericardium, shape rounded. Kidney branched, composed of many renal ridges (rr) connected in trabecular shape, surrounded by a compacted U-shaped gland; many digitiform papillae near close to dorsal vessels aperture on renal cavity. Nephrostome positioned on right side of renal cavity near to pericardium.

Digestive system (Fig. 141-142): Buccal mass (bm) remarkable, size ~8x larger than esophageal pouch (ep), elongated, 3x longer than wider; dorsal septate muscle (ds) composed of 22 large bundles; oral sphincter (os) evident, compose of many circular muscles, size ~6x smaller than dorsal septate muscle length; ascus musculature (ma) narrow and long, occupying almost all width and 1/3 length of ventral side of buccal mass; ascus (as) twice narrowest than ascus musculature, elongated, length trespassing ventral length of buccal mass, coiled only on posterior region; odontophore (od) rounded, parallel to oral cavity; buccal pouch absent. Radula with 6 teeth in ascending limb; leading tooth elongated, total length 3x longer than base length; cusp bearing numerous small denticles through all extension; lateral cutting absent; ascus containing discarded teeth not organized. Salivary glands (sg) positioned ventrally to esophagus and stomach (st). Esophagus (es) bit bigger than buccal mass length, width ~5x thinner than intestine width; internal surface with two longitudinal folds through all its extension. Esophageal pouch (ep) globose and muscular, positioned on posterior part of esophagus; internal surface with up to 8 incomplete large folds. Stomach (st) bulky, rounded, wide, width as twice as wider intestine (in); folds internally present on dorsal portion. Digestive gland (dg) dilated forming stomach pouches well developed, elongated, voluminous and with internal wall folded; anterior ducts shorter than posterior ducts, run laterally and anteriorly inside head; posterior ducts run towards parapodial region. Intestine (in) internally folded through all its extension, finishes in dorsolateral anus (a) positioned near to lateral groove.

Reproductive system (Fig. 143): Gonad composed of numerous hermaphrodite follicles (hf) forming a continuous area through all parapodia with central region of body, under the renopericardial cavity, with no follicles. Follicles size few variable, size up to 10x smaller than biggest hermaphrodite ampulla (am). Gametholitic vesicle (gv) absent. Hermaphrodite ducts (hd) connect all follicles to one central duct which connects to hermaphrodite ampullas duct, width univariable. Hermaphrodite ampulla variable in number from 10 to 16 on each side of body, positioned on parapodia anteriorly to hermaphrodite follicles, size variable, biggest one bit smaller than genital receptacle (gr) and 1/5 of mucus gland (mg) size. All ampulla on each side of animal are united for one main duct which joins in a single duct that connects to hermaphrodite duct. Male duct (md) connects prostate gland (pr) and vas deferens (vd) to hermaphrodite duct same as preceding species. Prostate gland composed of many glandular sacs positioned among and under hermaphrodite ampullae and anterior follicles, one non-glandular duct connects all glandular sacs on each side of animal which is joined in a single duct that connects to vas deferens. Penis (p) shape conic and elongated, length ~3x longer than biggest ampulla length and ~2x longer than mucus gland length, total length 3x bigger as base diameter; stylet absent. Vas deferens (vd) completely curled, length ~2x longer than penis length when outstretched. Oviduct (ov) starts from hermaphrodite duct after connection with male duct and forms 3 well delimited chambers completely evolved by mucus gland and finishes on female pore (fp) in lateral groove. Proximal chamber of mucus gland smallest one, rounded, albumen duct and male duct connect to oviduct in it. Second chamber of mucus gland biggest one, formed by a curved expansion of glandular oviduct, where bursa copulatrix connects with oviduct. Distally chamber short and with folds. Albumen gland (ag) composed of many dorsal thin branches over prostate gland; main duct of albumen gland runs from hermaphrodite duct, more proximal than male duct connection with hermaphrodite duct, then branches into many ducts in parapodial area dorsally to prostate gland. Genital receptacle connected to oviduct in anterior position.

Nervous system (Fig. 144): Cerebro-pleural ganglia (cp) size bit larger than pedal ganglia (pg); each ganglion has 6 innervations; commissure cerebro-pleural absent. Optic nerve length long, bit longer than cerebro-pleural ganglion length. Buccal ganglia (bg) remarkable, size bit larger than sub-intestinal ganglion (sb); accessory ganglion absent; each ganglion has 2 innervations; buccal commissure simple and short, length 5x smaller than buccal ganglion length. Pedal ganglia present 4 innervations by ganglion; pedal commissure simple and long, length as longer as pedal ganglion length. Visceral ganglia well developed; abdominal ganglion (ab) size bit smaller than pedal ganglion size, has 2 innervations; sub-intestinal ganglion size ~5x as small as supra-intestinal ganglion (sp), has 2 innervation; supra-intestinal ganglion bit smaller than abdominal ganglion size, has 1 innervation; connective between abdominal ganglion and sub-intestinal ganglion evident and long, length as longer as sub-intestinal ganglion; connective between abdominal ganglion and supra-intestinal ganglion absent.

Distribution: Florida (Krug *et al*., 2016), Bahamas (present study) e Cuba [Havana – type locality (Ortea *et al*., 2011)].

Material examined: BRAZIL, Parrachos do Rio Pirangí, Parnamirim, Rio Grande do Norte, CMPHRM 3783B, 1 specimen (H. Galvão Filho, 19/ix/2007); Praia de Búzios, Pirangi, Rio Grande do Norte, MZSP 97061, 4 specimens (M. Delgado, 13/iii/2009); Atol das Rocas, Rio Grande do Norte, CMPHRM 2989B, 1 specimen (14/ii/2009).

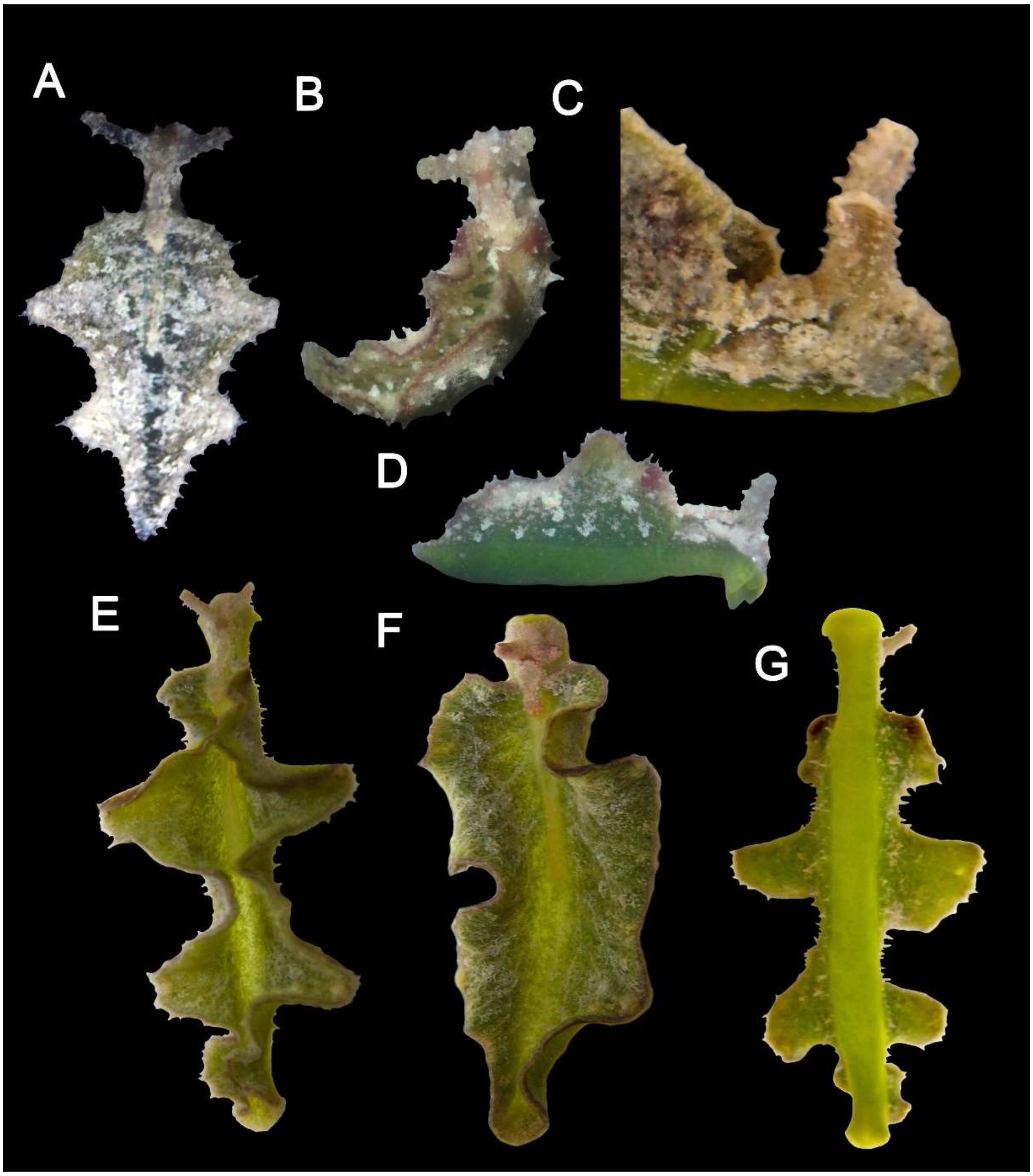

Figure 139. External morphology of live *Elysia pawliki*: A-B) dorsal view of juveniles specimens (length 11 mm (A); 8 mm (B)); C) lateral view; D) lateral view juvenile (length: 9 mm); E-F) dorsal view (length: 22 mm); G) ventral view (length: 22 mm).

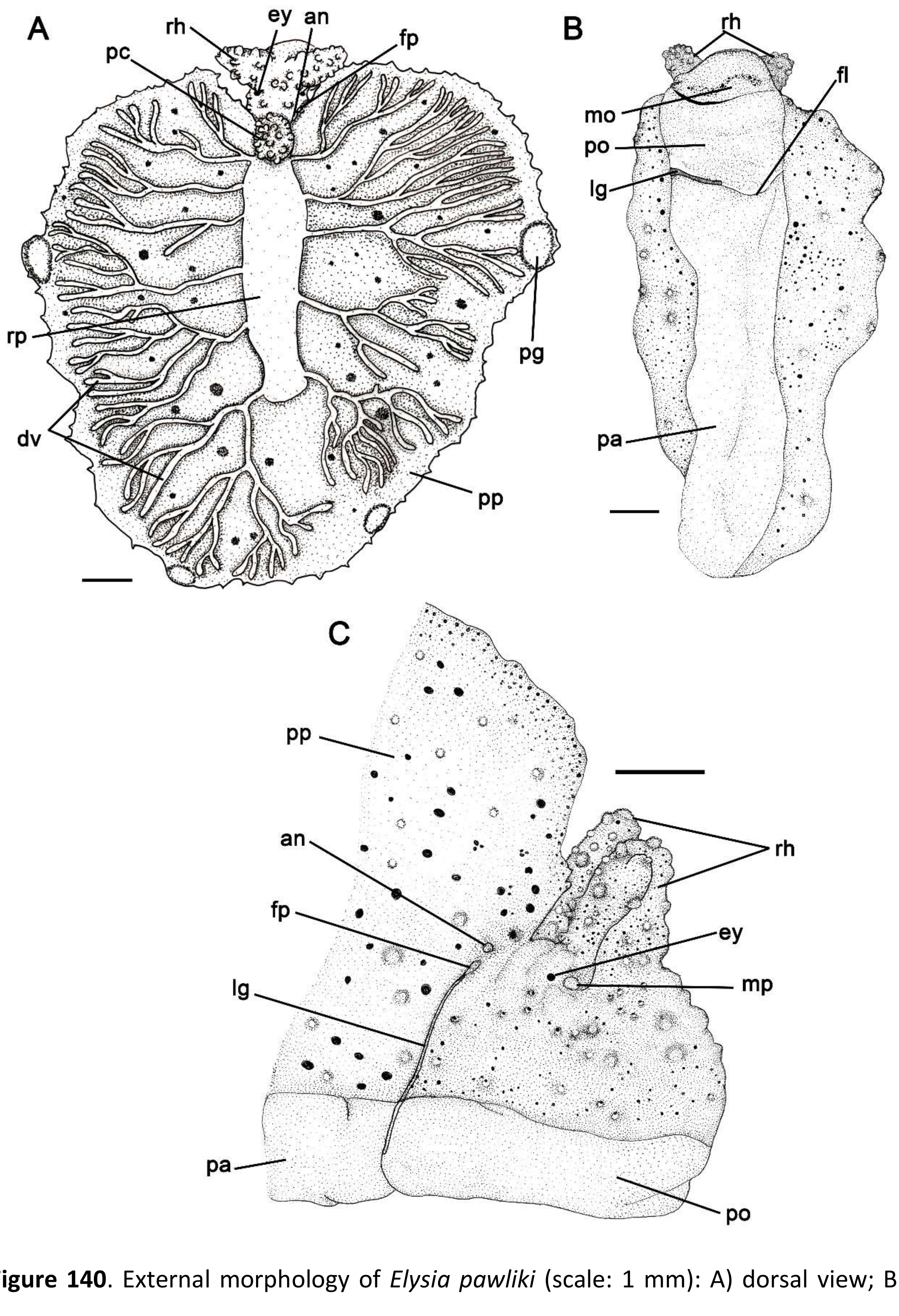

Figure 140. External morphology of *Elysia pawliki* (scale: 1 mm): A) dorsal view; B) ventral view; C) lateral view.

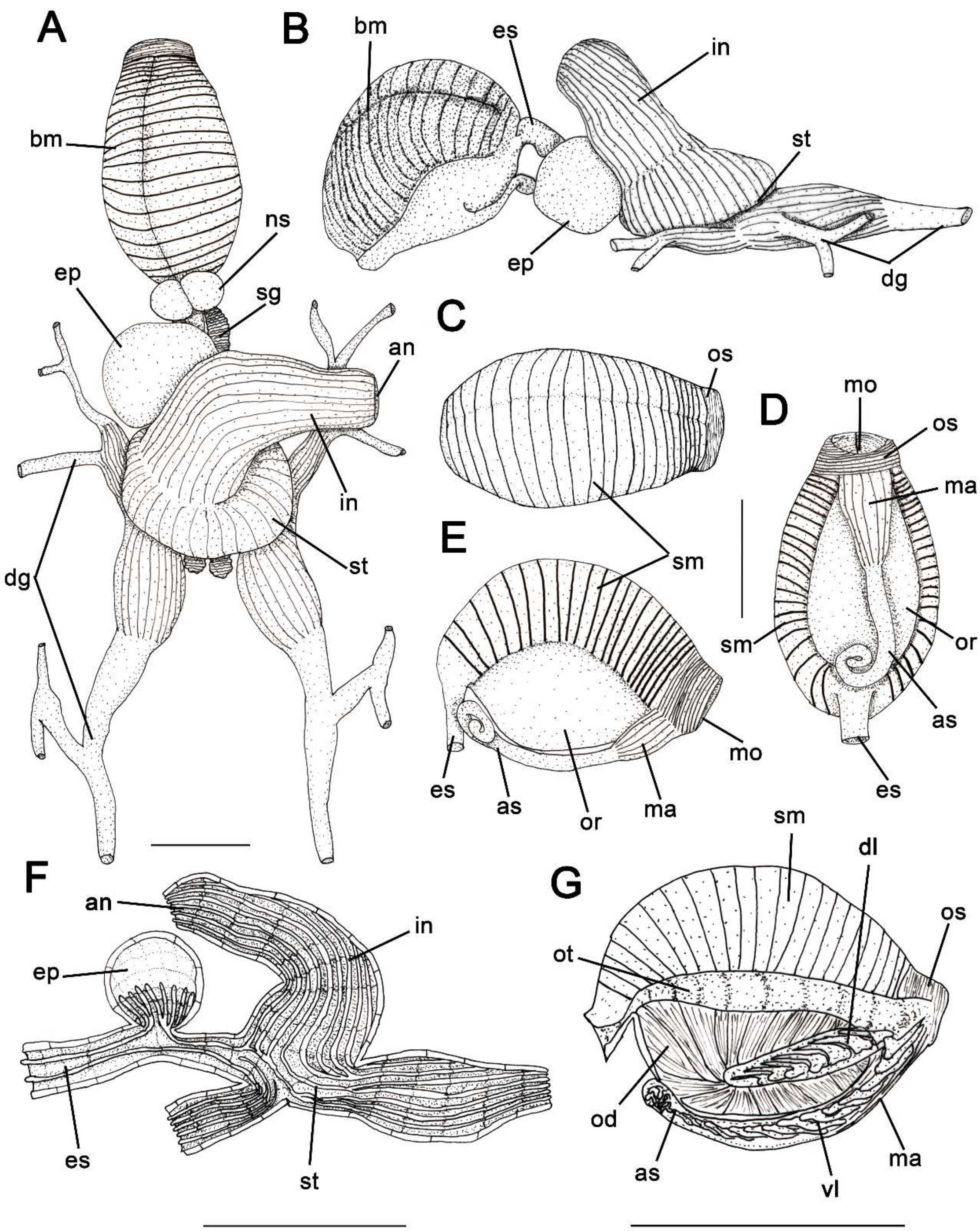

Figure 141. Digestive system of *Elysia papillosa* (scale: 0,5 mm): A) dorsal view of digestive system; B) lateral view of digestive system; C-E) zuleicae mass: C) dorsal; D); ventral; E) right side; F) detail morphology of posterior digestive system; G) Detail morphology of buccal mass.

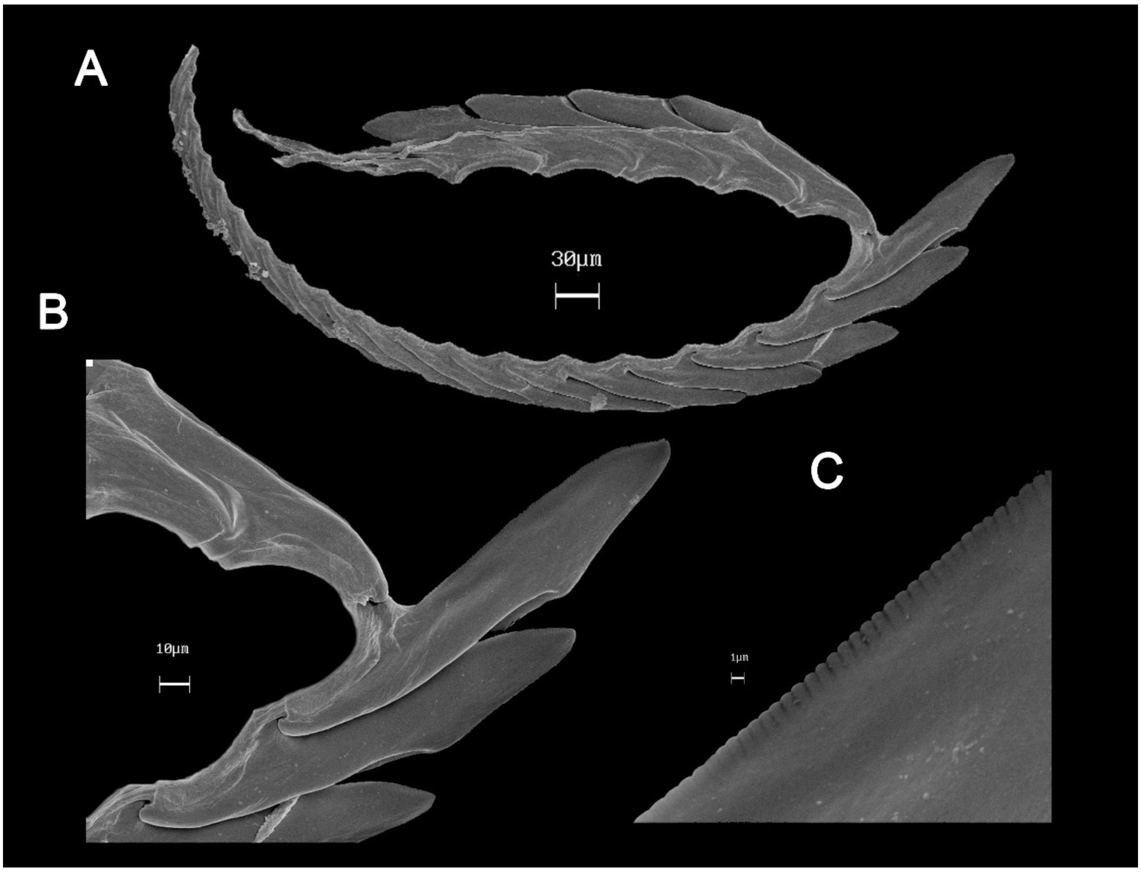

Figure 142. Scan electron microscope images of radula of *Elysia orientalis* BMSM 59035 (scale: 10 µm): A) general view; B) detail of the leading tooth; C) detail of teeth on ascus.

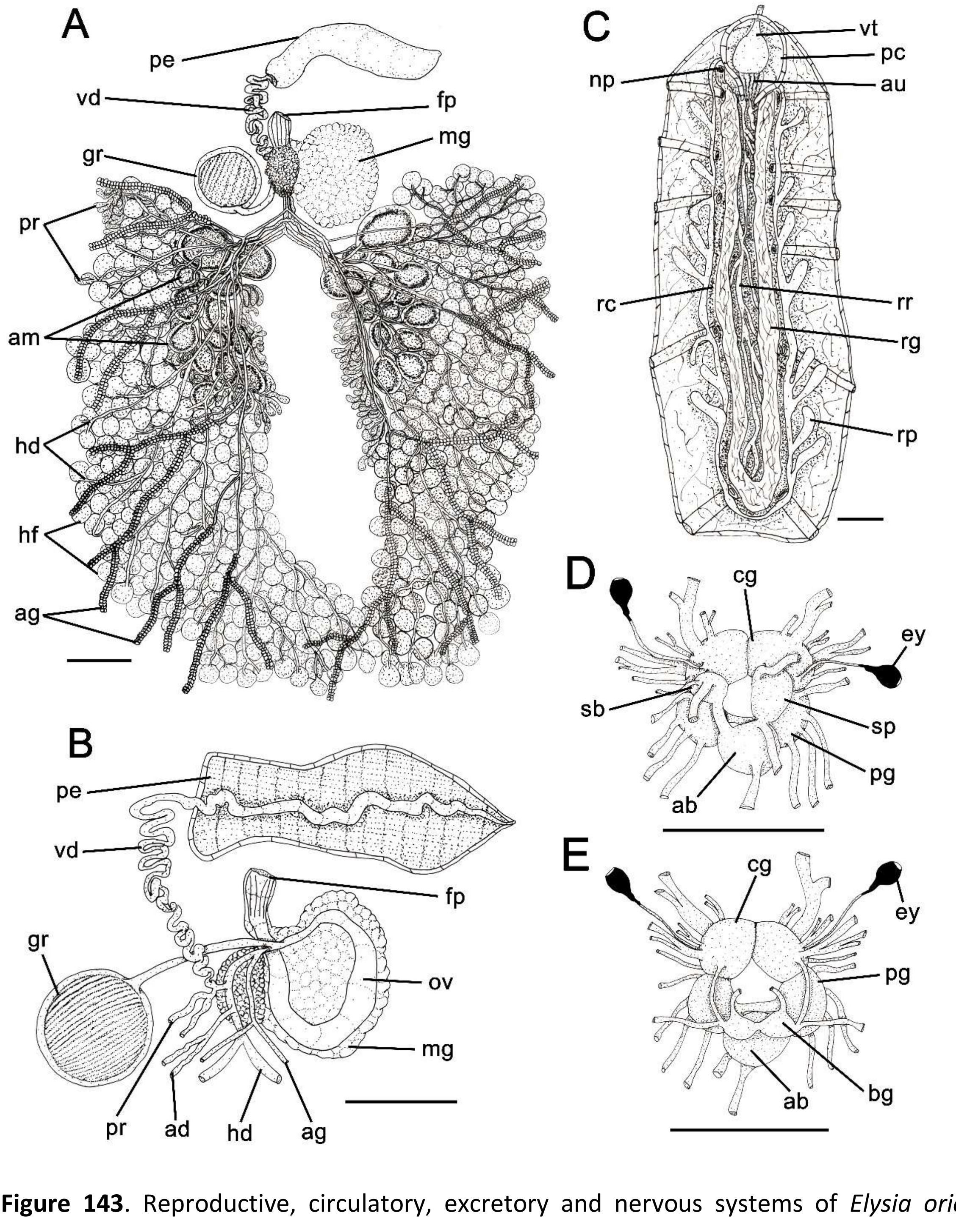

Figure 143. Reproductive, circulatory, excretory and nervous systems of *Elysia orientalis* (scale: 0,5 mm): A) general view of reproductive system; B) schematic view of reproductive system; C) ventral view of renopericaldial cavity in 4mm specimen; D) ventral view of renopericaldial cavity in 6mm specimen; E) anterior view of the nervous system; F) posterior of the nervous system.

4.2. CHARACTER ANALYSIS

4.2.1. External Morphology

1. Shell: 0 = present; 1 = absent. (L= 1; CI= 100; RI= 100).
2. Shell type: 0 = bulloid; 1= limpet; 2= bivalve. (L= 3; CI= 66; RI= 0).
3. Shell size: 0 = reduced; 1 = covering the whole body. (L= 2; CI= 50; RI= 0).
4. Shell aperture: 0 = wide; 1 = narrow. (L= 1; CI= 100; RI= 100).
5. Shell columellar muscle: 0= short; 1= horseshoe shaped; 2= simple adductor muscle; 3= double adductor muscle . (L= 3; CI= 100; RI= 100). Optimization: AccTran.
6. Gill: 0 = present; 1 = absent. (L= 1; CI= 100; RI= 100).
7. Type of gill: 0 = plicate; 1 = lamellar. (L= 2; CI= 100; RI= 100). Optimization: AccTran.
8. Cephalic shield: 0 = present; 1 = absent. (L= 2; CI= 50; RI= 50).
9. Rhinophores: 0 = absent; 1 = present. (L= 2; CI= 50; RI= 75).
10. Shape of rhinophores: 0 = rolled; 1 = simple; 2= bifid. (L= 2; CI= 100; RI= 100).
11. Rhinophores length: 0 = shorter than head; 1 = longer than head. (L= 9; CI= 11; RI= 52). Optimization: AccTran.
12. Rhinophore position: 0 = dorsal; 1 = anterior. (L= 1; CI= 100; RI= 100).
13. Papilla on rhinophores: 0 = absence; 1 = presence. (L= 4; CI= 25; RI= 66).
14. Oral tentacle: 0 = absent; 1 = present. (L= 2; CI= 50; RI= 0). Optimization: AccTran
15. Oral black dots: 0 = absent; 1 = present. (L= 1; CI= 100; RI= 100).
16. Eyes position: 0 = mid-line; 1 = lateral. (L= 4; CI= 25; RI= 57).
17. Ocular tubercle: 0 = absent; 1 = present. (L= 2; CI= 50; RI= 50).
18. Ciliated groove: 0 = present; 1 = absent. (L= 4; CI= 25; RI= 50). Optimization: DelTran.
19. Ciliated groove orientation: 0= longitudinal; 1=transversal. (L= 1; CI= 100; RI= 100). Optimization: DelTran.
20. Mesopodial groove: 0 = absent; 1 = present. (L= 1; CI= 100; RI= 100).
21. Anterior border of foot: 0 = rounded; 1 = expanded. (L= 2; CI= 50; RI= 91).
22. Posterior border of foot: 0 = rounded; 1 = pointed; 2 = truncate. (L= 4; CI= 50; RI= 77).
23. Pigmentation on foot sole: 0 = absent; 1 = present. (L= 3; CI= 33; RI= 66).
24. Parapodia – foot extensions: 0 = absent; 1 = present. (L= 2; CI= 50; RI= 0).
25. Parapodia – body flap: 0 = absent; 1 = present. (L= 1; CI= 100; RI= 100).

26. Parapodial tail: 0 = absent; 1 = present. (L= 4; CI= 25; RI= 70).
27. Parapodial margins frilled: 0 = absence; 1 = presence. (L= 1; CI= 100; RI= 100).
28. Orange parapodial margin: 0 = absent; 1 = present. (L= 1; CI= 100; RI= 100).
29. Pigmentation of inner surface of parapodia: 0 = absence; 1 = as same as body pigmentation. (L= 2; CI= 50; RI= 50). Optimization: AccTran.
30. Ocellated spots: 0 = absent; 1 = present. (L= 1; CI= 100; RI= 100).
31. Body papillae: 0 = absent; 1 = present. (L= 4; CI= 25; RI= 70).
32. Cerata: 0 = absent; 1 = present. (L= 1; CI= 100; RI= 100).
33. Pericardium: 0 = in mantle cavity; 1 = exposed. (L= 1; CI= 100; RI= 100).
34. Position of pericardium: 0 = middle of body; 1 = anterior position. (L= 2; CI= 50; RI= 0.
35. Dorsal vessels: 0 = absent; 1 = present. (L= 3; CI= 33; RI= 81).
36. Dorsal vessel type: 0 = simple; 1 = fused with digestive lamellae; 2 = mixed. (L= 3; CI= 66; RI= 80).
37. Dorsal vessels arrangements: 0 = single paired; 1 = radial; 2= multiple paired. (L= 6; CI= 33; RI= 69).
38. Kidney prominence: 0 = absent; 1 = present. (L= 1; CI= 100; RI= 100).
39. Kidney prominence length: 0 = short; 1 = up to middle of body; 2 = after middle of body. (L= 3; CI= 66; RI= 88).
40. Anus position: 0 = posterior; 1 = anterior-lateral; 2 = anterior-dorsal. (L= 7; CI= 28; RI= 77). Optimization: AccTran.

4.2.2. Circulatory and Excretory Systems

41. Auricle wall: 0 = smooth; 1 = folded. (L= 2; CI= 50; RI= 50).
42. Kidney: 0 = solid; 1 = ramified. (L= 5; CI= 20; RI= 76).
43. Type of ramification: 0 = trabecular; 1 = compact; 2 = radial; 3 = semi-trabecular. (L= 3; CI= 66; RI= 90).
44. Renal papilla: 0 = absent; 1 = present. (L= 1; CI= 100; RI= 100).

4.2.3. Digestive System

45. Pharyngeal pouch: 0 = absent; 1 = present. (L= 1; CI= 100; RI= 100).
46. Shape of pharyngeal pouch: 0 = short collar; 1 = single; 2 = paired. (L= 4; CI= 50; RI= 0).

47. epithelium-lined ascus-sac: 0 = absent; 1 = present. (L= 1; CI= 100; RI= 100).
48. length of ascus muscle: 0 = short; 1 = long. (L= 7; CI= 14; RI= 66).
49. attachment of ascus muscles: 0 = attached; 1 = posteriorly freely. (L= 3; CI= 33; RI= 33).
50. position of ascus: 0 = internal; 1 = external. (L= 3; CI= 33; RI= 33).
51. shape of ascus: 0 = straight; 1 = spiral; 2 = heap. (L= 7; CI= 28; RI= 58).
52. oral tube: 0 = non-eversible; 1 = eversible. (L= 1; CI= 100; RI= 100).
53. radula type. 0 = multiple teeth; 1 = uniseriate teeth. (L= 1; CI= 100; RI= 100).
54. rachidian teeth shape: 0 = rhomboid; 1 = blade; 2 = triangular. (L= 3; CI= 33; RI= 85).
55. Number of cusps on rachidian tooh: 0 = more than three; 1 = three; 2 = 1. (L= 9; CI= 22; RI= 53).
56. serrated central cusp: 0 = absent; 1 = present. (L= 3; CI= 33; RI= 89).
57. serrated on lateral cusp: 0 = present; 1 = absent. (L= 5; CI= 20; RI= 55).
58. Type of lateral denticulation: 0 = short; 1 = ellongated. (L= 1; CI= 100; RI= 100).
59. storage area: 0 = elongated; 1 = short. (L= 1; CI= 100; RI= 100).
60. first preradular: 0 = very short; 1 = long rod. (L= 1; CI= 100; RI= 100).
61. esophageal pouch: 0 = absent; 1 = present. (L= 3; CI= 33; RI= 33).
62. esophageal pouch shape: 0 = short; 1 = elongated; 2 = rounded; 3 = conic. (L= 2; CI= 50; RI= 66).
63. digestive gland: 0 = solid; 1 = shortly branched; 2 = highly branched. (L= 2; CI= 100; RI= 100).
64. Salivary glands: 0 = free from esophagus; 1 = attached to esophagus. (L= 6; CI= 16; RI= 37).
65. salivary glands length: 0 = longer than esophagus; 1 = shorter than esophagus. (L= 6; CI= 16; RI= 37).
66. esophagus length: 0 = longer than intestine; 1 = shorter than intestine. (L= 3; CI= 33; RI= 66).
67. Odontophore size: 0 = smaller than radula; 1 = bigger than radula. (L= 3; CI= 33; RI= 81).
68. digestive system organization: 0 = spread; 1 = compact. (L= 1; CI= 100; RI= 100).

4.2.4. Reproductive System

69. penis: 0 = long; 1 = short. (L= 8; CI= 12; RI= 22).

70. penial stylet: 0 = absent; 1 = present. (L= 8; CI= 12; RI= 53).
71. shape of penial stylet: 0 = straight; 1 = curved. (L= 2; CI= 50; RI= 80).
72. length of penial stylet: 0 = smaller than penis; 1 = equal or longer than penis. (L= 1; CI= 100; RI= 100).
73. vas deferens: 0 = imbedded in body wall; 1 = free. (L= 2; CI= 50; RI= 50).
74. female genital papilla: 0 = present; 1 = absent. (L= 3; CI= 33; RI= 33).
75. prostate position: 0 = part of vas deferens; 1 = separate. (L= 1; CI= 100; RI= 100).
76. prostate type: 0 = short lobes; 1 = highly branched; 2 = clustered. (L= 1; CI= 100; RI= 100).
77. ampulla: 0 = part of duct; 1 = separate. (L= 3; CI= 66; RI= 91).
78. Ampulla pigmentation: 0 = absent; 1 = present. (L= 8; CI= 12; RI= 50).
79. Number of ampulla: 0 = one; 1 = two; 2 = more than two. (L= 5; CI= 40; RI= 80).
80. position of ampulla: 0 = central; 1 = lateral on mucus gland; 2 = on parapodia. (L= 5; CI= 40; RI= 84).
81. genital receptacle: 0 = present; 1 = absent. (L= 3; CI= 33; RI= 60).
82. Position of Genital receptacle: 0 = proximal; 1 = distal. (L= 7; CI= 14; RI= 53).
83. Bursa copulatrix: 0 = absent; 1 = present. (L= 6; CI= 16; RI= 61).
84. bursa copulatrix aperture: 0 on female duct; 1 = own aperture. (L= 2; CI= 50; RI= 80).
85. Gametholitic vesicle on ganad: 0 = absent; 1 = present. (L= 1; CI= 100; RI= 100).
86. Gametholitic vesicles on hermaphrodite duct: 0 = absent; 1 = present. (L= 1; CI= 100; RI= 100).
87. albumen gland: 0 = solid; 1 = branched. (L= 1; CI= 100; RI= 100).
88. gonad: 0 = solid; 1 = follicles. (L= 1; CI= 100; RI= 100).
89. follicles: 0 = clustered; 1 = partially divided; 2 = completely divided. (L= 11; CI= 18; RI= 62).
90. follicle shape: 0 = spherical; 1 = amorph. (L= 2; CI= 50; RI= 0).
91. gonad distribution: 0 = central; 1 = partially on parapodia; 2 = through all parapodia. (L= 4; CI= 50; RI= 88).

4.2.5. Nervous System

92. visceral loop: 0 = long; 1 = short. (L= 2; CI= 50; RI= 75).

93. number of visceral ganglia: 0 = > three; 1 = three; 2 = two. (L= 4; CI= 150; RI= 50).
94. cerebral commissure: 0 = shorter than cp; 1 = reduced; 2 = longer than cp. (L= 3; CI= 33; RI= 77).
95. optic innervation: 0 = from cerebral ganglia; 1 = from cerebral innervation. (L= 1; CI= 100; RI= 100).
96. optic nerve – length: 0 = very long; 1 = long; 2 = short. (L= 6; CI= 33; RI= 77).
97. connective cerebro-pedal: 0 = present; 1 = absent. (L= 1; CI= 100; RI= 100).
98. pedal commissure: 0 = shorter than pd; 1 = longer than pd; 2 = reduced. (L= 8; CI= 12; RI= 46).
99. size of ab-sp connective: 0 = bigger than supraintestinal ganglion; 1 =reduced; 2 = equal or smaller than supraintestinal ganglion. (L= 2; CI= 50; RI= 75).
100. size of sb-ab connective: 0 = equal or bigger than sb ganglion; 1 = reduced; 2 = smaller than sb ganglion. (L= 2; CI= 50; RI= 83).
101. proximity of sp-sb: 0 = far; 1 = close. (L= 3; CI= 33; RI= 66).
102. buccal commissure length: 0 = shorter than bu; 1 = longer than bu; 2= reduced. (L= 3; CI= 33; RI= 0).
103. accessory buccal ganglia: 0 = absent; 1 = present. (L= 4; CI= 25; RI= 72).

4.2.6. Ecology and Behavior

104. spawn: 0 = clump; 1 = spiral; 2 = sausage. (L= 8; CI= 25; RI= 33).
105. extra-capsular yolk: 0 = absent; 1 = present. (L= 4; CI= 25; RI= 76).
106. swimming behavior: 0 = absent; 1 = present. (L= 1; CI= 100; RI= 100).
107. burrow behavior: 0 = present; 1 = absent. (L= 5; CI= 20; RI= 55).
108. algae food: 0 = halimeda; 1 = caulerpa; 2 = ulvophycea; 3 = udotacea 4 = red/brown algae; 5 = dasycladales; 6 = seagrass. (L= 22; CI= 22; RI= 51).
109. Chloroplast retention: 0 = non-rentention; 1= retention.

4.3. PHYLOGENETIC ANALYSIS

4.3.1. Morphology Based Analysis

The morphological analysis was based on 109 characters, which 40 were related to external morphology, 4 to excretory and circulatory systems, 28 to digestive system, 23 to reproductive system and 17 to nervous system (see topic 4.2). Another six characters related to behavior and reproduction were also included in this analysis. A total of 49 characters were adapted from Gosliner (1995), Jensen (1996) and Mikkelsen (1998), while 60 were proposed herein.

The traditional search through TBR (replication of 1000 trees and retention of 90 trees) and prior weights resulted in 36 equally most parsimonious trees with 338 steps (best hit scored 896 times out of 1000; IC= 38; IR=73), with the strict consensus resulting in one tree with 424 steps (IC= 34; IR= 68) (Figs. 1 and 2).

The implied weigh comparative analysis with different values of K resulted in one tree with 386 steps (IC=37; IR= 72) (Fig. 4). The following phylogenetic discussion and character optimization are based on the implied weight tree, in which the characters (upper region) and states (below) are represented for each node and terminal taxa. The homologous synapomorphies are presented as a dark square and the homoplasies (reversions or convergences) by an empty circle. The nodes are tagged with letters for outgroups and numbers for the ingroup.

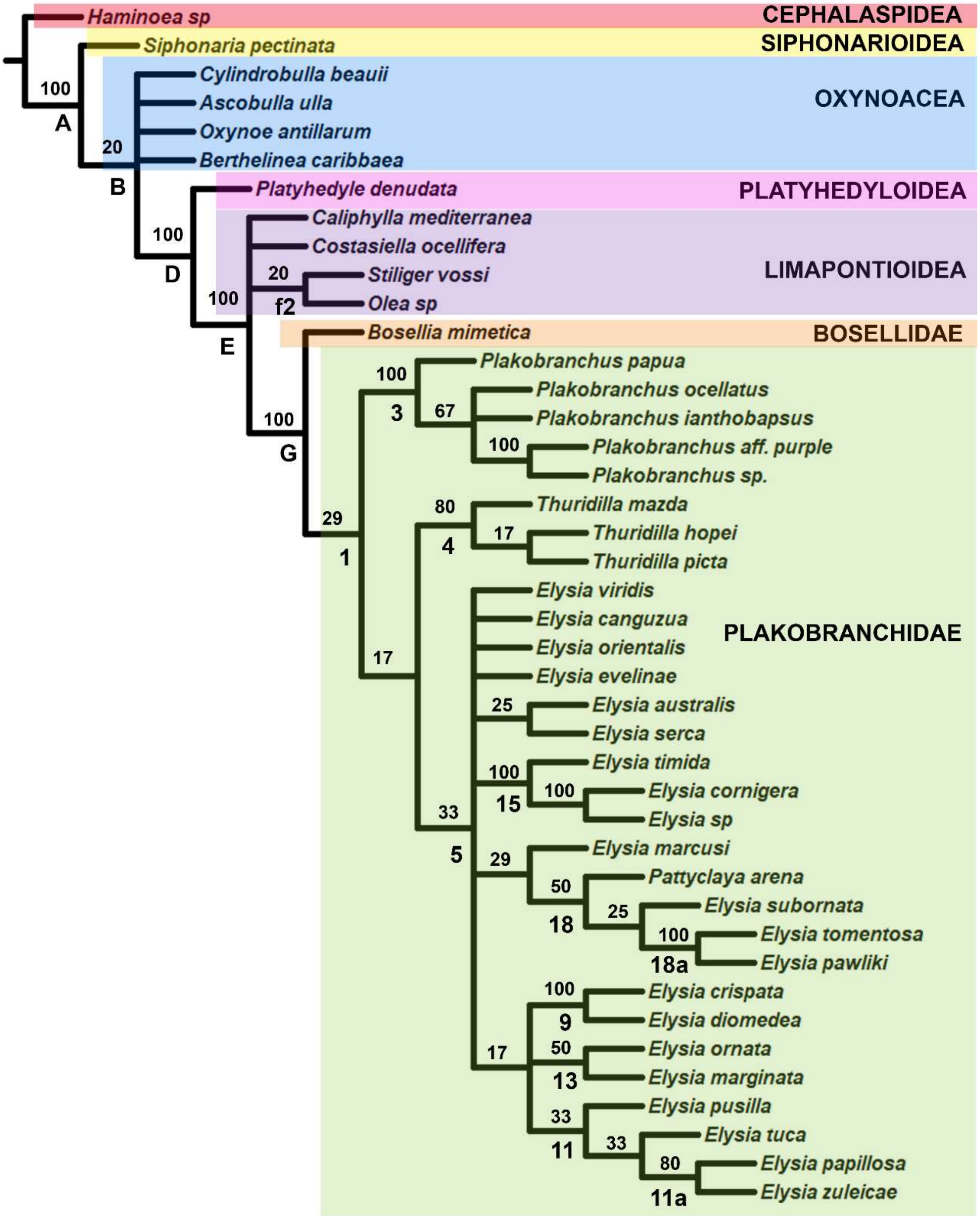

Figure 144. Consensus tree of Plakobranchidae and outgroup species obtained through parsimonious analysis in TNT with prior weight. Nodes are named with letters and numbers bellow branches matching with the nodes with the implied weight final tree (Fig. 85). Relative Bremer support is on top of branches.

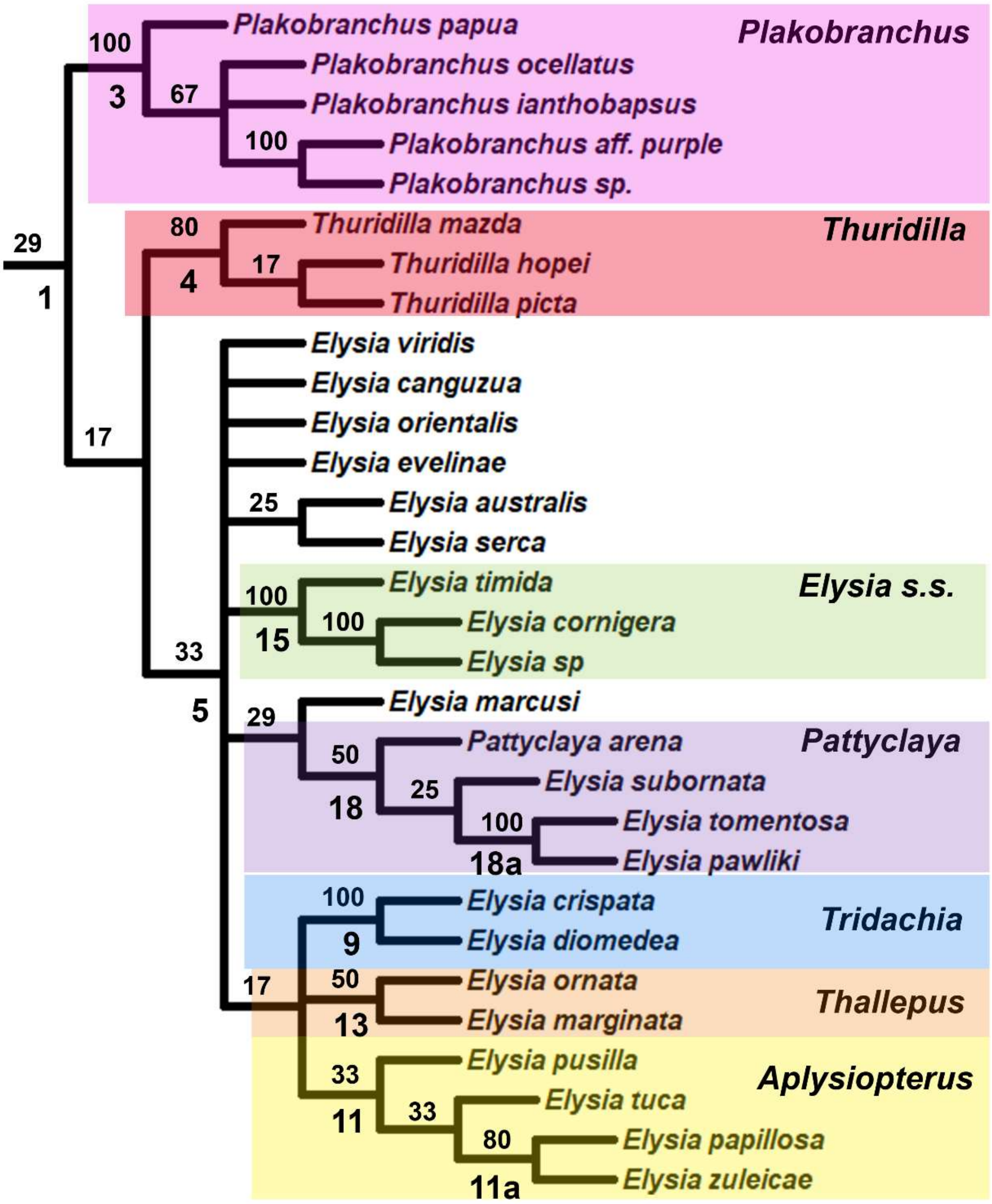

Figure 145. Consensus tree of Plakobranchidae obtained through parsimonious analysis in TNT with prior weight. Nodes are named with letters and numbers bellow branches matching with the nodes in the implied weight final tree (Fig. 3). Relative Bremer support is on top of branches.

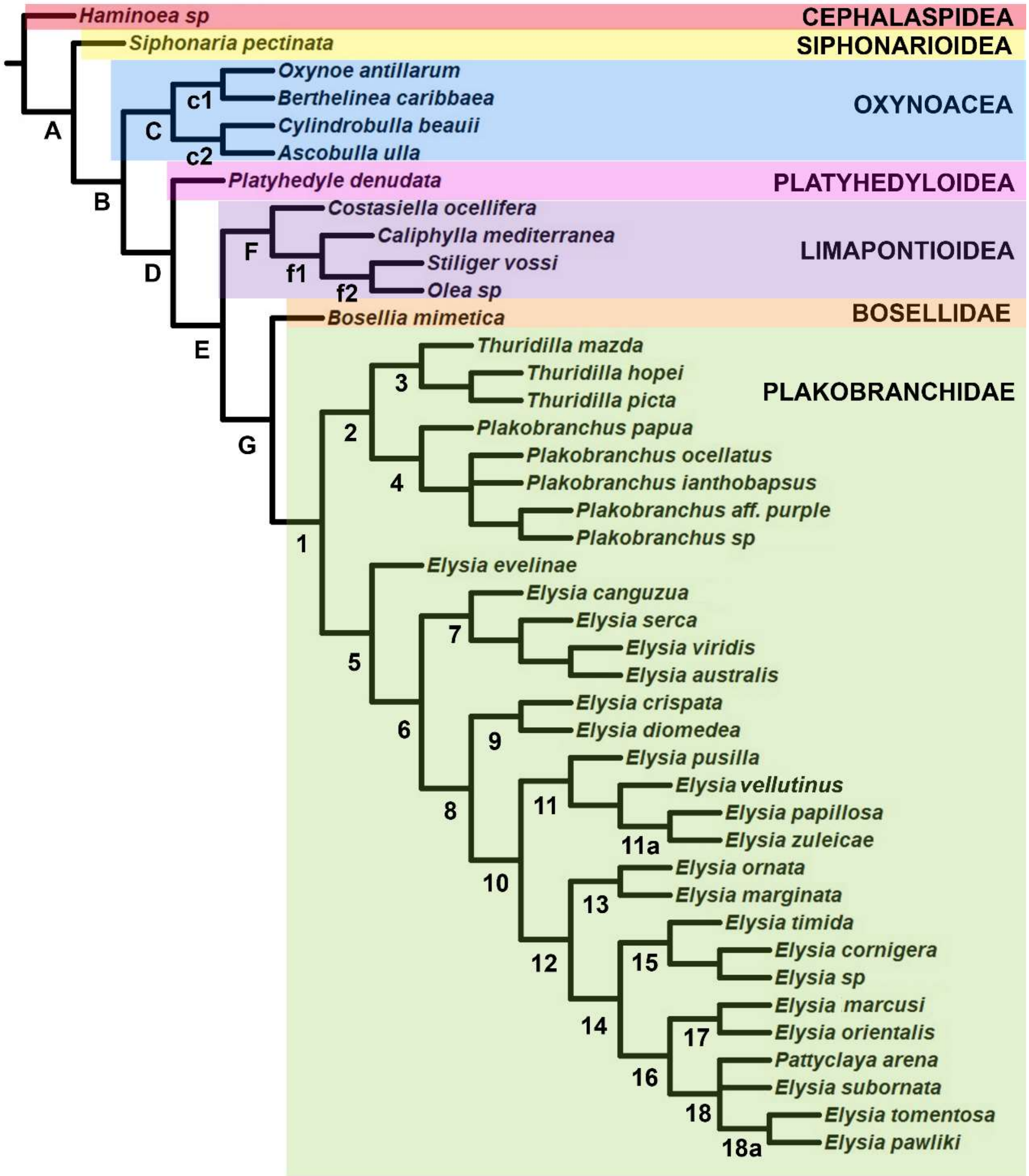

Figure 146. Phylogenetic tree obtained through parsimonious analysis in TNT with implied weight (K=8). A-G nodes with outgroup taxa and 1-19 with ingroup taxa.

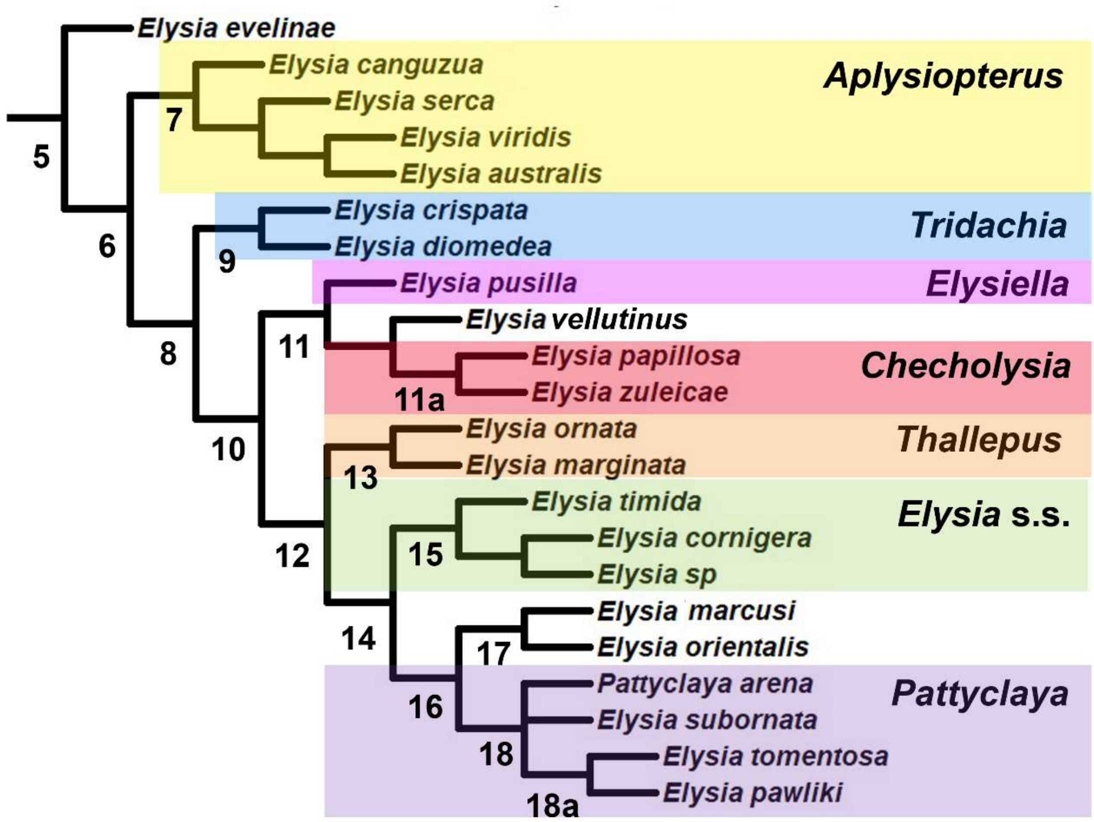

Figure 147. Section of the phylogenetic tree obtained through parsimonious analysis in TNT with implied weight (K=8) with *Elysia* matching nodes with previous synonyms.

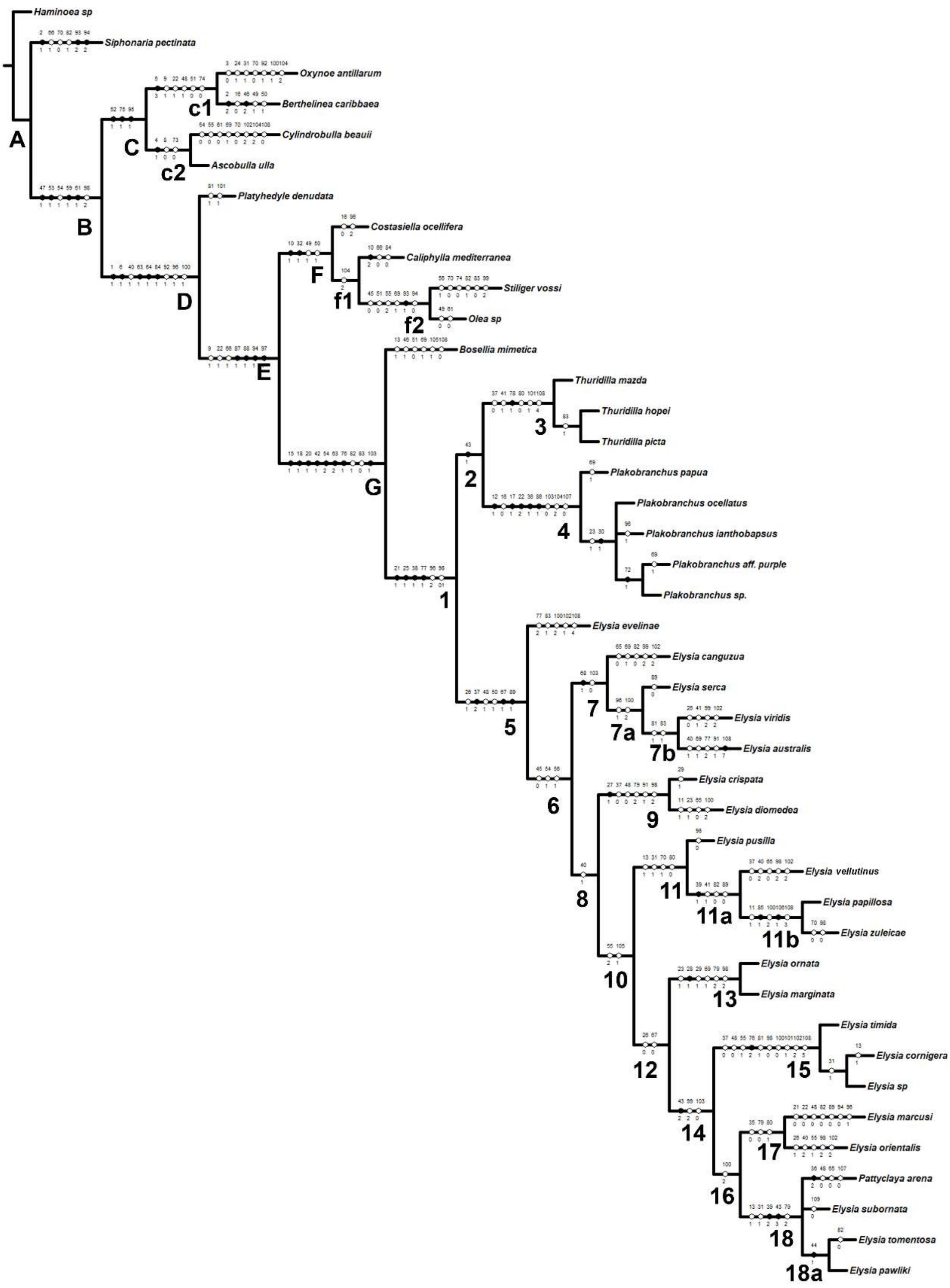

Figure 148. Phylogenetic tree obtained through parsimonious analysis in TNT with implied weight (K=8) and character optimization. A-G nodes with outgroup taxa and 1-18 with ingroup taxa.

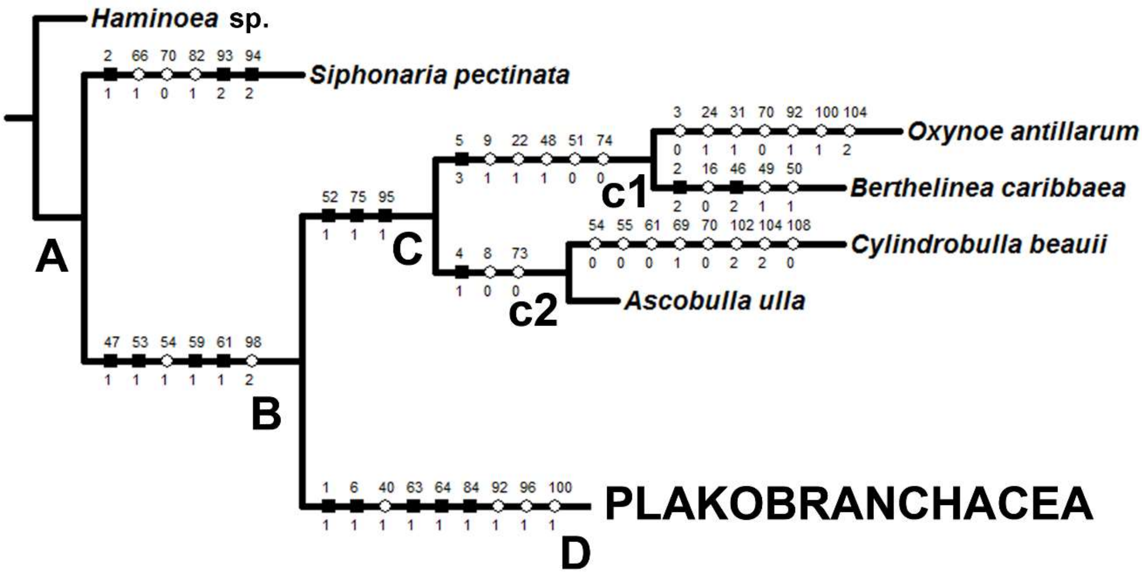

Figure 149. Phylogenetic tree (part 1) with the characters that suport each node. Nodes: A) unamed; B) Sacoglossa; C) Oxynoacea; D) Plakobranchacea.

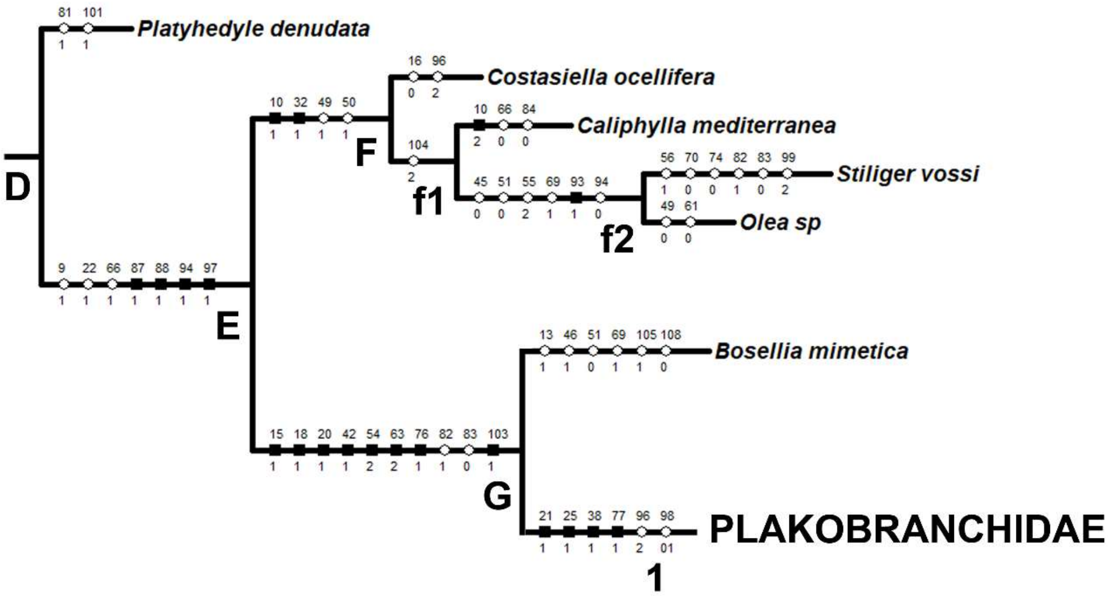

Figure 150. Phylogenetic tree (part 2) with the characters that suport each node. Nodes: D) Plakobranchacea; E) Limapontioidea+ Plakobranchoidea; F) Limapontioidea; G) Plakobranchoidea.

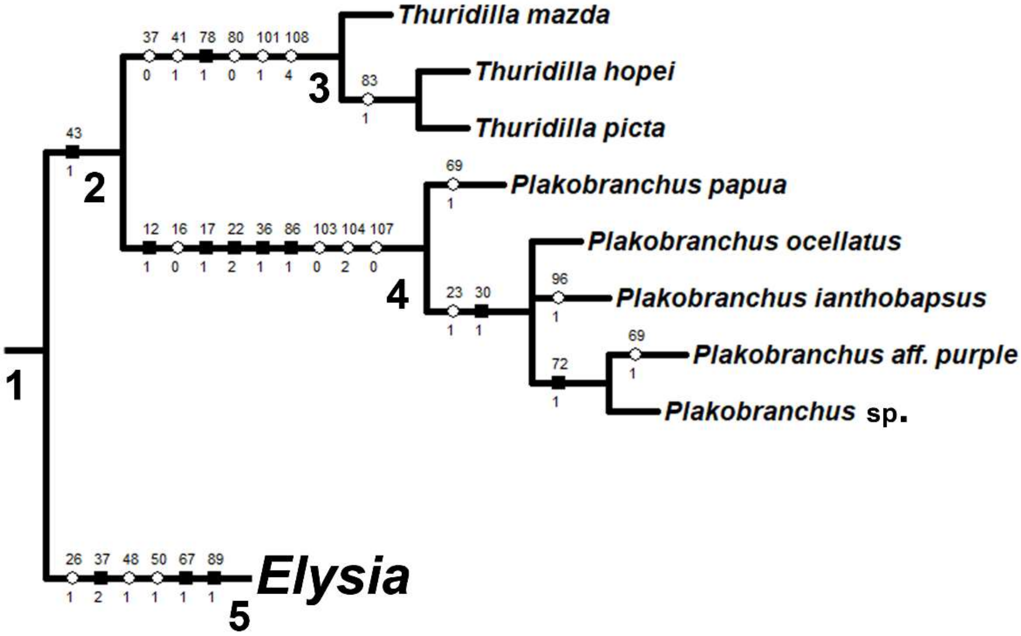

Figure 151. Phylogenetic tree (part 3) with the characters that suport each node. Nodes: G) Plakobranchoidea; 1) Plakobranchidae; 2) *Thuridilla* + *Plakobranchus*; 3) *Thuridilla*; 4) *Plakobranchus*; 5) *Elysia*.

Figure 152. Phylogenetic tree (part 4) with the characters that suport each node. Nodes are unamed subdivision of *Elysia* (Node 5).

4.3.1.1. Monophyly of Sacoglossa and internal clades

With the advances of molecular phylogenetic studies, the position of the order Sacoglossa within Heterobranchia has changed drastically (see WÄGELE *et al*., 2014). Many of these studies have placed Sacoglossa in a close relationship with Siphonarioidea at the base of Panpulmonata, a clade with previous pulmonate, opisthobranch and lower heterobranch taxa (GRANDE *et al*., 2008; DINAPOLI & KLUSSMANN-KOLB, 2010; JÖRGER et al., 2010; GOBBELLER & KLUSSMANN-KOLB, 2011).

Indeed, Siphonaria and Sacoglossa present many morphological similarities on pallial organs and shell muscles, but they might be convergent adaptations to a shallow water habitat (JENSEN, 2011; SIMONE & SEABRA, 2017). In the present analysis the clade Siphonarioidea + Sacoglossa (Node A) is not supported by any synapomorphies and form a trichotomy with Cephalaspidea.

Sacoglossa has 6 synapomorphies, being two homoplastic. The group is supported by the presence of epithelium-lined ascus-sac (47:1), an uniseriate radula (53:1), a short storage area for the radula (59:1) and an esophageal pouch (61:1), and the convergence for a blade shaped tooth (54:1) and reduced pedal commissure (76:1). The monophyly of the order Sacoglossa was almost never debated and has always been recovered as monophyletic group in all previous phylogenetic analysis (JENSEN, 1996; MIKKELSEN, 1998; HÄNDELER & WÄGELE, 2006).

The order Sacoglossa is subdivided in two major groups, the shelled group Oxynoacea (clade C) and the shell-less group Plakobranchacea (Clade D). Oxynoacea is supported by the presence of eversible oral tube (52:1), the prostate gland as part of vas deferens (75:1) and optic nerve innervating from a cerebral nerve (95:1). Jensen (1996) has not recovered *Cylindrobulla* in Oxynoacea, but as sister to Sacoglossa. However, a reanalysis of Jensen's morphological data by Mikkelsen (1998), which increased and modified the data for *Cylindrobulla,* also included more outgroups, placed the genus within Oxynoacea. This same hypothesis was corroborated by molecular analyses (LAETZ *et al*., 2014; KRUG *et al*., 2015). Our results also corroborated *Cylindrobulla* in Oxynoacea, as sister to *Ascobulla* instead of early branching in Sacoglossa.

Plakobranchacea (node D) is supported by the following non-homoplastic synapomorphies: absence of shell (1: 1) and gill (6: 1) and presence of branched digestive gland (63: 1), vaginal opening for bursa copulatrix (84: 1), salivary glands attached to esophagus (64: 1). Also, four homoplastic characters support Plakobranchacea: anterior-lateral anus (40:1), short visceral loop (92: 1), long optical nerve (96: 1) and reduced commissure between abdominal and subintestinal ganglion (100: 1).

In morphology-based phylogenies Plakobranchacea was subdivided in two major groups: Limapontioidea (cerata bearing group) and Plakobranchoidea (parapodia bearing group) (JENSEN, 1996; MIKKELSEN, 1988). The interstitial group Platyhedylidae was recovered as Plakobranchoidea in those analysis, whereas it was positioned as sister group to all shell-less sacoglossans in molecular phylogenies (CHRISTA *et al*., 2014; KRUG *et al*., 2015). Our morphological analysis is congruent with the molecular hypothesis, with Platyhedylidae less derived in Plakobranchacea.

The sister relationship between Limapontioidea and Plakobranchoidea (node D) is supported by secondary appearance of rhinophores (9:1), a pointed posterior end of foot (22:1) and esophagus shorter than intestine (66:1). Also, this group presents highly branched reproductive structures, such as albumen gland (87:1) and gonad (88:1), and a more compact nervous system, with the reduction of cerebral commissure (94:1) and loss of cerebro-pedal connective (97:2).

The monophyly of Limapontioidea (node F) was recovered by the presence of simple rhinophores (10:1) and cerata (32: 1) as exclusive synapomorphy. In addition, the group is characterized by the ascus muscles posteriorly free (49: 1) and external ascus (49: 1). Although this group is monophyletic in larger morphological analyses (JENSEN, 1996; MIKKELSEN, 1998), molecular phylogenies have proposed that the cerata-bearing sacoglossans do not form a natural group (HÄNDELER & WÄGELE, 2007; MAEDA *et al*., 2010; CHRISTA *et al*., 2014d; KRUG *et al*., 2015).

The clade Plakobranchoidea (node G) was recovered without Platyhedilidae and supported by the acquisition of the following novel characters: presence of oral dots on upper lip (15: 1), lateral ciliated groove (19: 1), mesopodial groove (20:1), ramified kidney (42: 1), triangular tooth (54: 2), digestive gland branched in multiple short tubules (63: 2), and accessory buccal ganglion (103: 1). The group is also supported by the posterior genital receptacle (82: 1) and loss of of bursa copulatrix (83: 0) by reversion.

4.3.1.2. The family Plakobranchidae

Plakobranchoidea is represented by the families Bosellidae and Plakobranchidae (node 1). Bosellidae is a monogeneric family erected by Marcus (1982) and characterized by the absence of parapodia, three ganglia on short visceral loop and small number of chromosomes (n =7) comparing with other sacoglossans (n= 17). Two species of *Bosellia* were included in this analysis to test the monophyly of Plakobranchidae. *Bosellia mimetica* was recovered as sister group to Plakobranchidae, while *Bosellia marcusi* was recovered within Plakobranchidae.

Previous works have already suggested the insertion of *B. marcusi* in Plakobranchidae (HANDELER & WÄGELE, 2007; CHRISTA *et al*., 2014; KRUG *et al*., 2015) and officially transferred to *Elysia* later (KRUG *et al*., 2016). Krug *et al*. (2016) have discussed that Marcus (1972) misplaced *E. marcusi* in *Bosellia* because of the reduced parapodia and secondary loss of dorsal vessels. The analysis of anatomical characters revealed that *E. marcusi* has no pharyngeal pouch and presents a short spherical esophageal pouch, blade-shaped tooth and external hermaphrodite ampulla, which are common characters found in *Elysia* spp.. On the other hand, *B. mimetica* has a large pharyngeal pouch, elongated esophageal pouch, triangular shaped teeth and ampulla internal to hermaphrodite duct. In the present phylogenetic analysis, *E. marcusi* was also placed within *Elysia*.

The family Plakobranchidae has four exclusive synapomorphies: anterior border of foot expanded (21: 1), parapodia formed by body flap (25:1), external kidney housed in a prominence (38) and ampulla separated from hermaphrodite duct (71: 1). In addition, Plakobranchidae is also supported by short optic nerve (96: 2) and elongated pedal commissure (98: 0, 1).

The monophyletic status of Plakobranchidae resulted from this analysis is congruent with some morphological and molecular analysis (JENSEN, 1996; BASS & KARL, 2006; HÄNDELER & WÄGELE, 2007; HÄNDELER *et al*., 2009; KRUG *et al*., 2015). Other scenarios, however, have been proposed. In Mikkelsen's (1998) morphological analysis *Plakobranchus* branches earlier in Plakobranchoidea and is sister to a group formed by Bosellidae and *Elysia* + *Thuridilla*. Christa *et al*. (2014) recovered Bosellidae sister to *Plakobranchus* + *Thuridilla* and forming the sister clade to *Elysia*. In this case, the family Plakobranchidae would be represented only by *Plakobranchus* and *Thuridilla*, while *Elysia* would be part of the monogeneric family Elysiidae.

The phylogenetic tree with implied weight supports the clade *Thuridilla* + *Plakobranchus* (node 2) only by one synapomorphy, which is the central distribution of gonadal follicles (98: 0). This relationship is strongly support by many molecular analysis (BASS & KARLS, 2006; CHRISTA *et al*., 2014d; KRUG *et al.,* 2015; KRUG, VENDETTI & VALDÉS, 2016), but with one exception in which *Thuridilla* branches earlier in Plakobranchidae (HANDELER & WÄGELE, 2007).

Morphologically, the clade *Thuridilla* + *Plakobranchus* was only recovered by Gosliner (2005) with five synapommorphies, but those characters are very homoplastic and do not support the clade in analysis with more taxa (JENSEN, 1996; MIKKELSEN, 1998; present study). The consensus tree with prior weight also recovered the monophyly of Plakobranchidae (Figs. 1 and 2) with *Plakobranchus* sister to *Thuridilla* + *Elysia*. This topology is similar to the one proposed by Jensen (1996).

4.3.1.3. The genus *Plakobranchus*

The genus *Plakobranchus* was considered monospecific for a long time (see KRUG *et al*., 2015), and for this reason only one species was included in most analysis (GOSLINER, 1995; JENSEN, 1996; MIKKELSEN, 1998; BASS & KARL, 2006; MAEDA *et al*., 2010). However, Jensen (1997a, 2007) considered that *Plakobranchus* could be represented by a complex with up to 14 species under the name *P. ocellatus*, which was subsequently proved by molecular analysis (HÄNDELER & WÄGELE, 2007; CHIRSTA *et al*., 2014d; KRUG *et al.*, 2013, 2015; KRUG, VENDETTI & VALDÉS, 2016; MEYERS-MUÑOZ *et al*., 2016).

The present analysis considered five species of *Plakobranchus* with distinct morphological characters, also recovered as independent lineages by molecular analysis (see topic 4.5). In both topologies with prior and implied weight *Plakobranchus* resulted as monophyletic and supported by nine synapomorphies, being 4 homoplastic. The genus is characterized by the rhinophores on anterior position (12:1), secondary median eyes (16: 1->0) on top of ocular tubercle (17:1), posterior end of foot truncate (22:2), dorsal vessels on top of lamellae (36:1), gametolytic vesicles connected on hermaphrodite ducts (86:1), loss of accessory buccal ganglia (103:1->0), reversion of egg mass shape for a clump format (104:1->0) and the burrow behavior (107:1->0).

4.3.1.4. The genus *Thuridilla*

The node 3 represents the monophyletic genus *Thuridilla* and is supported by six synapomorphies, which the presence of a pigmented ampulla (78:1) is the only non-homoplastic. The group is also characterized by single paired dorsal vessels (37:0), folded auricle (41:1), central ampulla (80:0) the visceral ganglia very close to each other (101:1) and feeds on brown algae (4).

Gosliner (1995) described the morphology of 16 species of *Thuridilla* from the Indo-Pacific Ocean and proposed a phylogenetic relationship within the genus based on 23 characters of 19 taxa. He recovered a sister relationship between *T. hopei* and *T. picta* as in previous molecular analyses that included both species (CHRISTA *et al*., 2014d; KRUG *et al*., 2015; KRUG, VENDETTI & VALDÉS, 2016) and the present analysis. Indeed, those species are morphologically similar and were considered sympatric in East Atlantic Ocean until later molecular study considered them allopatric (CARMONA *et al*., 2011).

Comparing the morphological descriptions made by Gosliner (1995) and the present morphological analysis, is possible to assume that *Thuridilla* are quite similar on internal and external morphological features, but varying in coloration, dorsal vessels pattern and size of internal organs. In this way, *T. mazda* stands out for the absence of bursa copulatrix.

4.3.1.5. The genus *Elysia*

The genus *Elysia* (node 5) resulted as monophyletic after the inclusion of *B. marcusi* (discussed above) and *Pattyclaya arena*. The clade is supported by three non-homoplastic synapomorphies, multi-paired dorsal vessels (37:2), odontophore larger than radula (67:1) and the gonad forming one group of follicles in each parapodia (89: 1). The following homoplasies support *Elysia* as well: presence of parapodial tail (26:1), long ascus muscles (48: 1) and external ascus (50: 1).

Pattyclaya arena was originally described as *Elysia* (CARLSON & HOFF, 1977) and then designed as type-species of the genus *Pattyclaya* erected by Marcus (1982). The genus

Pattyclaya was characterized by presence of parallel transverse lamellae on upper surface of parapodia connected with the long renopericardial prominence by dorsal vessels. After the first phylogenetic analysis, the validity of the genus has been questioned, and *Pattyclaya* was placed in the genus *Elysia* in all analysis (GOSLINER, 1995; JENSEN, 1996; MIKKELSEN, 1998). The results of present analysis also positioned *Pattyclaya* in *Elysia* (node 18).

The monophyly of *Elysia* has been widely debated with the first phylogenetic hypotheses for Plakobranchidae. Thus, the insertion of other previous genera (*Pattyclaya*, *Elysiella*, *Tridachia, Tridachiella* and *Checholysia*) in *Elysia* was proposed by morphological and molecular phylogenetic hypothesis (GOSLINER, 1995; JENSEN, 1996; MIKKELSEN, 1998; BASS & KARL, 2006; KRUG *et al*., 2016) to recovery its monophyletic status. Gosliner (1995) and Jensen (1996) also suggested that *Elysia* might be subdivided.

The present morphological analysis recovered some clades within *Elysia* that matches with synonymized names (Fig. 6). Although, they have low Bremmer values in the consensus topology with prior weight, almost all of them still form monophyletic groups. The node 7 includes the type species of *Aplysiopterus*, *Elysia viridis*. This clade is supported by non-homoplastic synapomorphy for a compact digestive system (68:1) and the secondary loss of accessory buccal ganglia (103: 0).

The synonymized genera *Tridachia* (type species: *E. crispata*) and *Tridachiella* (type species: *E. diomedea*) were grouped together in node 9, which presents the non-homoplastic synapomorphy for frilled parapodial margins (27: 1), and the homoplastic character states for single paired dorsal vessels (37:0), short ascus muscle (48: 0), multiple ampulla (79:2), gonad partially spread through parapodia (91: 1) and reduced pedal commissure (98:2).

The node 11 is represented by *E. pusilla* (type-species of *Elysiella*) plus the node 11a, which includes *E. papillosa* previously placed in *Checholysia*. The clade *Elysiella* + *Checholysia* is supported by four homoplastic synapomorphies: the presence of papillae on rhinophores (13:1) and body (31:1), penial stylet (70:1) and ampulla on central position (80:0). *Checholysia* (node 11a) presents two non-homoplastic synapomorphies for the presence of gametolytic vesicles on gonad (85:1) and the capability to swim (106:1). Three other homoplastic character supports the node: rhinophores smaller than head (11:1), longer commissure between abdominal and subintestinal ganglia (100:0) and the change on diet for the calcareous algae Udotacea (108:3).

The node 13 groups *E. ornata* (type-species for *Thallepus*) *E. marginata* (type species for *Pterogasteron*) and is supported by the non-homoplastic synapomorphy for presence of an orange band on parapodial margin (28: 1) and the following homoplastic characters: pigmentation on foot sole (23: 1) and inner surface of parapodia (29: 1), short penis (69: 1), multiple ampullae (79:2) and reduced pedal commissure (98:2).

The node 16 presents the type species of *Elysia*, *Elysia timida*, and is the only group to have clustered prostate gland (76:2) and feed on Dasycladales algae (118: 5). The group also presents the homoplastic synapomorphies for single paired dorsal vessels (37:0), short ascus muscles (48: 0), seminal receptacle absent (81: 1), short pedal commissure (98:0), big connective between subintestinal and abdominal ganglia (100: 0), short distance between supraintestinal and subintestinal ganglia (101: 1) and reduced buccal commissure (102: 2).

Finally, the node 18 presents *Pattyclaya arena* and is supported by five synapomorphies, which the kidney prominence very long (39: 2) and semi-trabecular kidney ramification (43:3) are non-homoplastic. This clade is also characterized by the presence of papillae on rhinophores (13:1) and body (31:1) and multiple ampullae (79:2).

4.3.2. Molecular Based Analysis

The molecular analysis was based on five partial genes of 49 species. Three species included in the morphological analysis were excluded in both molecular analyses since no gene sequence were obtained: *Platyhedyle denudata*, *Elysia* sp. and *Pattyclaya arena.* From the total of 39 species used in this analysis, we obtained 37 16S sequences (~404 bp), 39 COI sequences (~1271 bp), 28S sequences for 25 specimens (~1391 bp), 38 H3 sequences (328 bp) and 36 18S sequences (~1781 bp). Some partial sequences were used according to Table 2. The final alignment dataset was ~5175 bp long for each taxon.

Both topologies are quite similar on major groups relationship (Figs. 93 and 94), being Oxynoacea and Plakobranchacea monophyletic groups. On the other hand, Limapontioidea resulted as non-monophyletic, with *Costasiella* placed as sister to all shell-less sacoglossans with high ML and BI values. This result is similar to previous molecular works and corroborates the multiple independent origins of kleptoplasty proposed by Christa *et al*. (2014).

In both analysis *Plakobranchus* and *Thuridilla* are well-supported monophyletic groups and form a clade, the family Plakobranchidae, however, resulted as paraphyletic. In this scenario, Bosellidae is placed as sister to *Thuridilla* + *Plakobranchus* with higher value for BI posterior probability. Similar result was found by Christa *et al*. (2014) for BI analysis, but Krug *et al*. (2015) recovered Plakobranchidae as monophyletic and sister to Bosellidae although with low BI value and no ML support.

The genus *Elysia* is highly supported by the present analyses after the inclusion of *Bosellia marcusi* (as *E. marcusi*) and other species previously placed in synonymic genera of *Elysia*. Although some internal nodes were not well resolved, many clades were recovered as in previous molecular analysis with more species of *Elysia* (CHRISTA *et al*., 2014; KRUG *et al*., 2015, 2016). The phylogenetic analysis performed by Krug *et al*. (2016) for 76 terminals and four genes (16S, 28S, COI and H3) is the most similar, with the same relation among the internal nodes.

The morpho groups comprising *Elysiella* and *Checholysia* is likely to form a trichotomy with the other *Elysia* spp.. In this trichotomy, *Elysia vellutinus* was placed as sister to *E. pusilla* or forming a clade with *Checholysia*. In both analysis the clade that groups the type species for *Tridachia* and *Aplysiopterus* comprises the same species and similar topology, except for *E. canguzua* branching earlier in BI analysis. The two topologies are completely similar on the other branches and present high values supporting the nodes with the morpho groups *Thallepus*, *Elysia* s.s. and *Pattyclaya.*

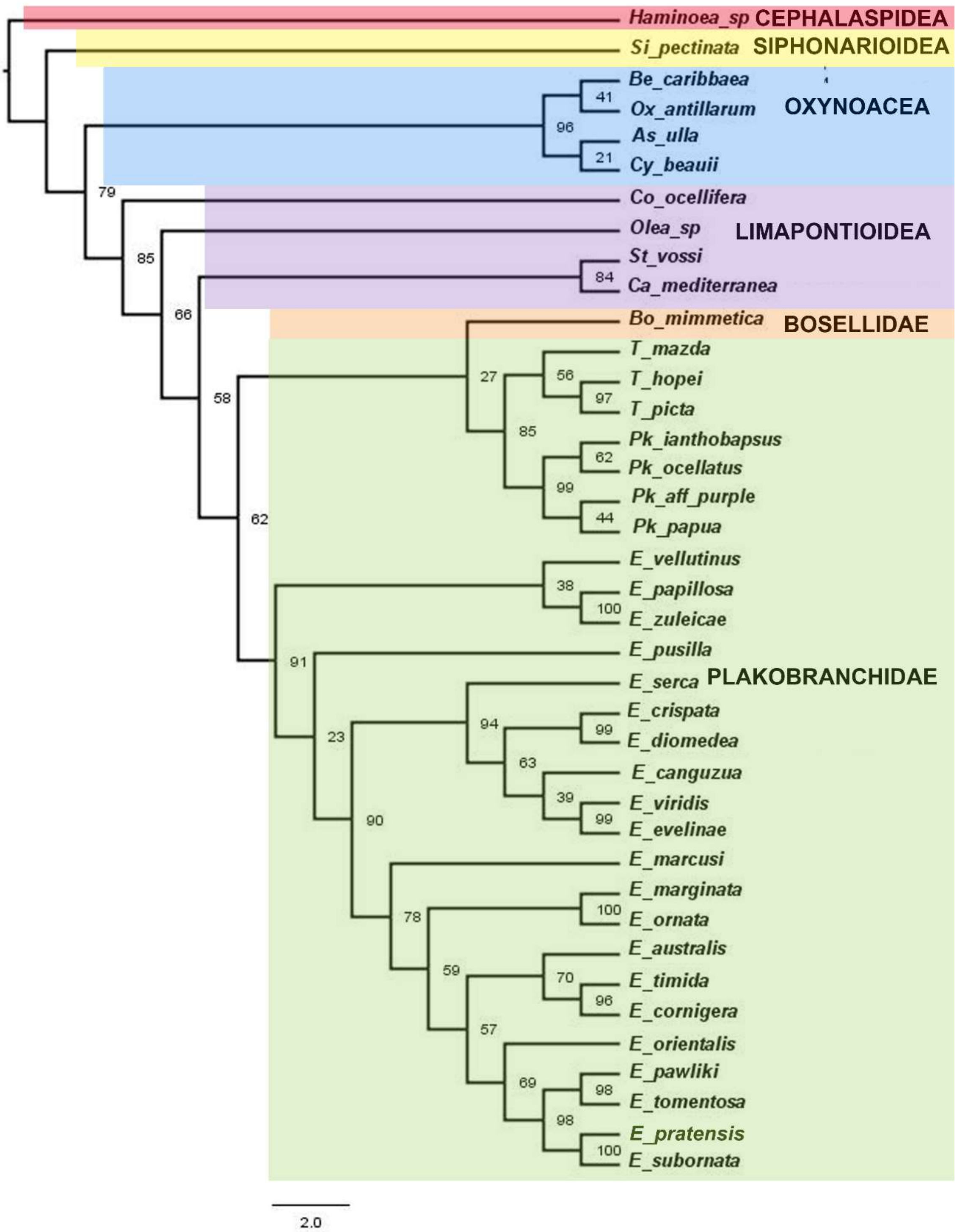

Figure 153. Phylogenetic tree obtained through Maximum Likelihood of concatenated DNA sequences of two mitochondrial (COI, 16S) and three nuclear (H3, 18S and 28S) genes. Support values as ML bootstrap percentages on each node.

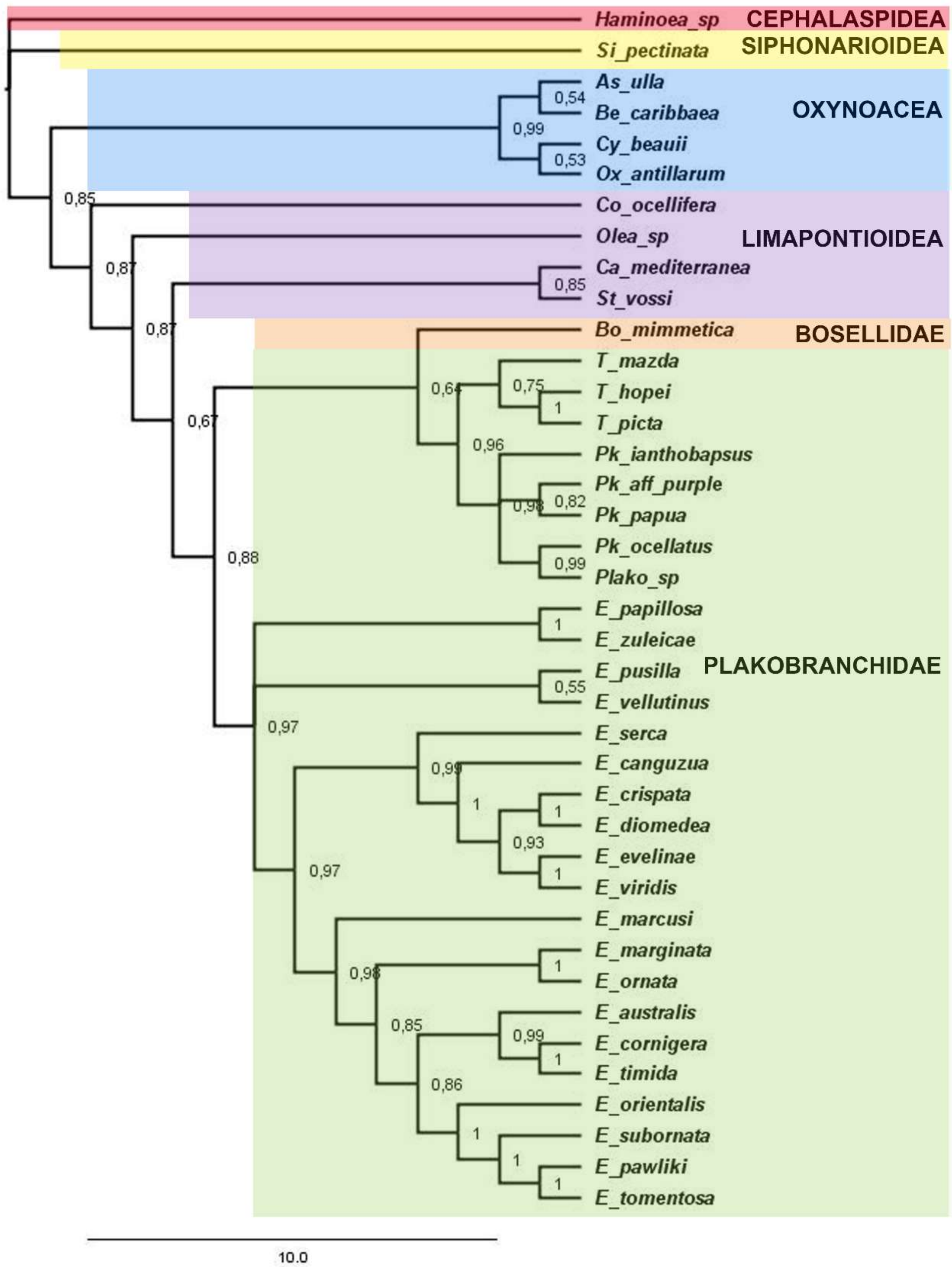

Figure 154. Phylogenetic tree obtained through Bayesian analysis of concatenated DNA sequences of two mitochondrial (COI, 16S) and three nuclear (H3, 18S and 28S) genes. Support values as BI posterior probabilities on each node.

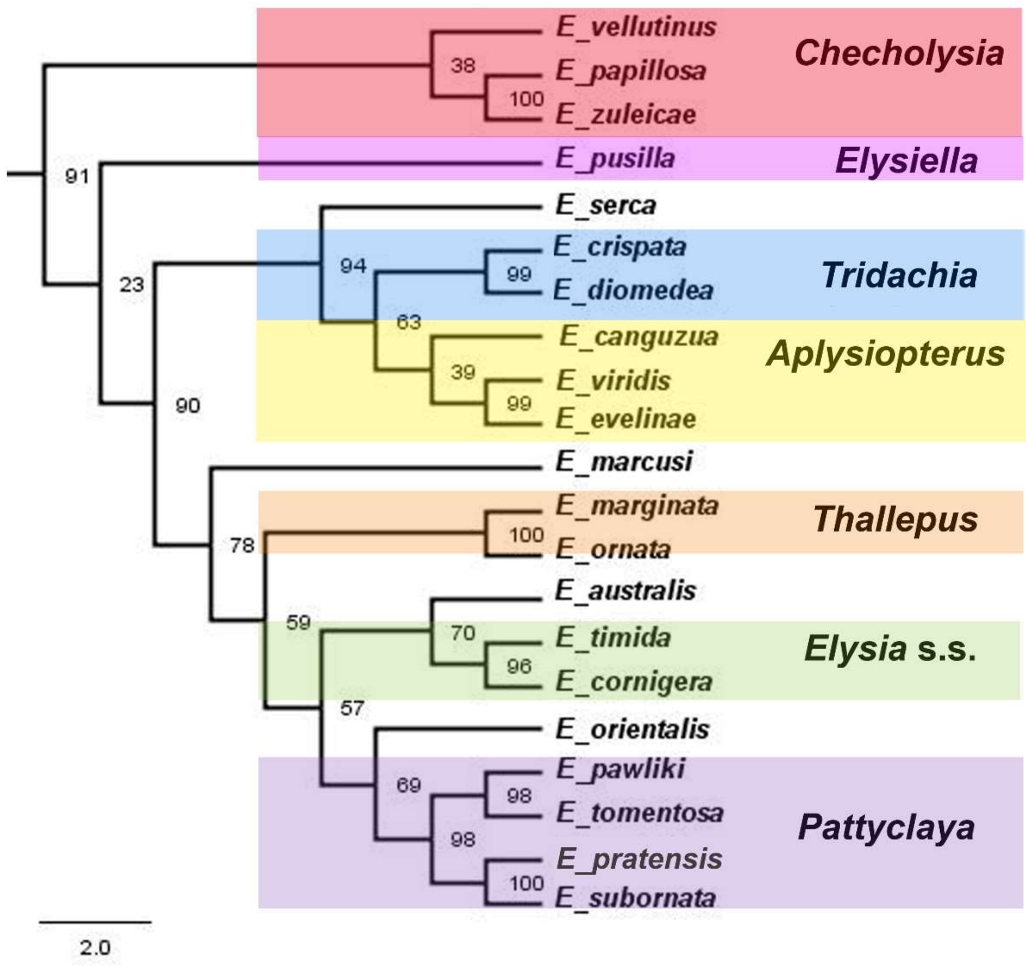

Figure 155. Section of phylogenetic tree obtained through Maximum Likelihood (Fig. 93) with *Elysia* matching nodes with previous synonyms.

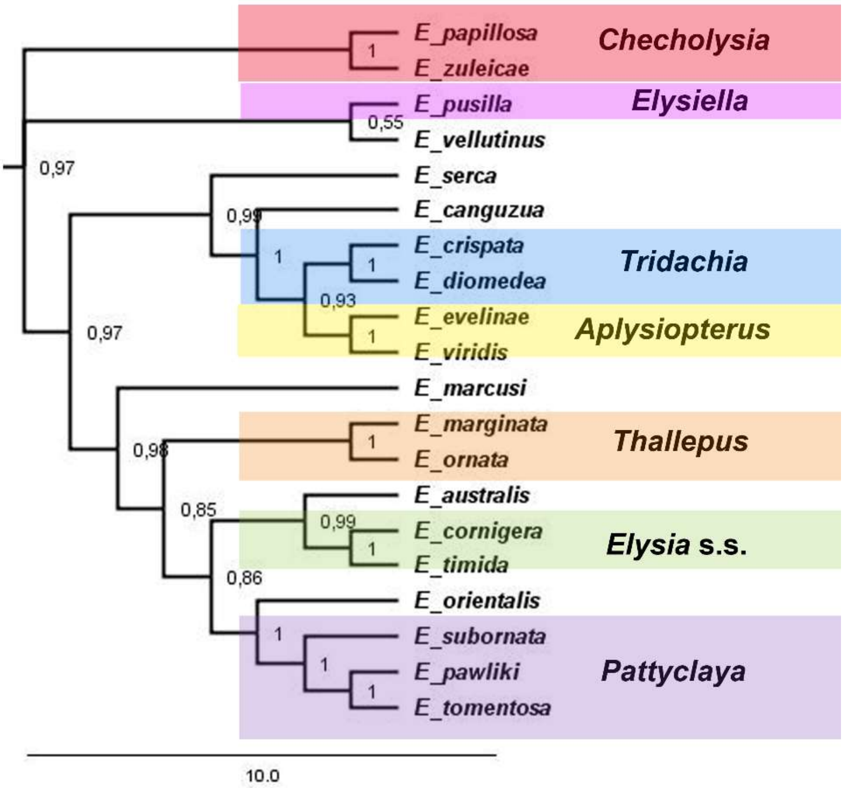

Figure 156. Section of phylogenetic tree obtained through Bayesian Inference (Fig. 7) with *Elysia* matching nodes with previous synonyms.

4.3.3. Total Evidence Analysis

This is the first phylogenetic analysis with species of Sacoglossa that includes both molecular and morphological data sets. The resulted topology (Fig. 97 and 98) presents similarities and differences with the ones resulted from each type of data set, and comparison will be made among bayesian trees and morphological tree resulted from MP analysis.

Sacoglossa resulted as monophyletic in the analyses with one type of data, resulted as polyphyletic in the combined analysis. The shelled species were clustered together and forming the monophyletic Oxynoacea, but sister to Siphonarioidea, whereas the shell-less Plakobranchacea resulted as highly polyphyletic. This polyatomic topology with the outgroup species might be a consequence of a low representation.

In the combined analysis the family Plakobranchidae resulted as monophyletic, although with a low BI value. The valid genera of Plakobranchidae have also their monophyly well-supported, and the sister relationship between *Plakobranchus* and *Thuridilla* is also congruent with the results from analyses with one data set.

The internal clades in *Elysia* of both morphological and molecular topologies are quite similar, with old names of *Elysia* matching similar nodes. However, the combined tree is identical with the molecular one, but with lower BI values. The main differences between morphological and molecular (= combined) are on the arrangement of the internal nodes in *Elysia*.

On the morphological topology *E. evelinae* is sister to all *Elysia*, but it is grouped with *E. viridis* in the combined tree. The clade matching the synonym *Checholysia* is sister to all other *Elysia* in the molecular and combined trees, but more derived in the morphological topology. Another well supported node in molecular tree groups the morpho group for *Aplysiopterus* with *Tridachia*, while in the morpho tree *Aplysiopterus* is sister to all other groups of *Elsyia* (except for *E. evelinae*). The node 12 on morphological tree (Fig. 86 and 87) groups almost the same species in similar arrangement of molecular trees. The differences are the inclusion of *E. australis* and *E. marcusi* branching earlier on the molecular tree. The previous phylogenetic studies (CHRISTA *et al*., 2014; KRUG *et al*., 2015, 2016) also recovered the same major groups.

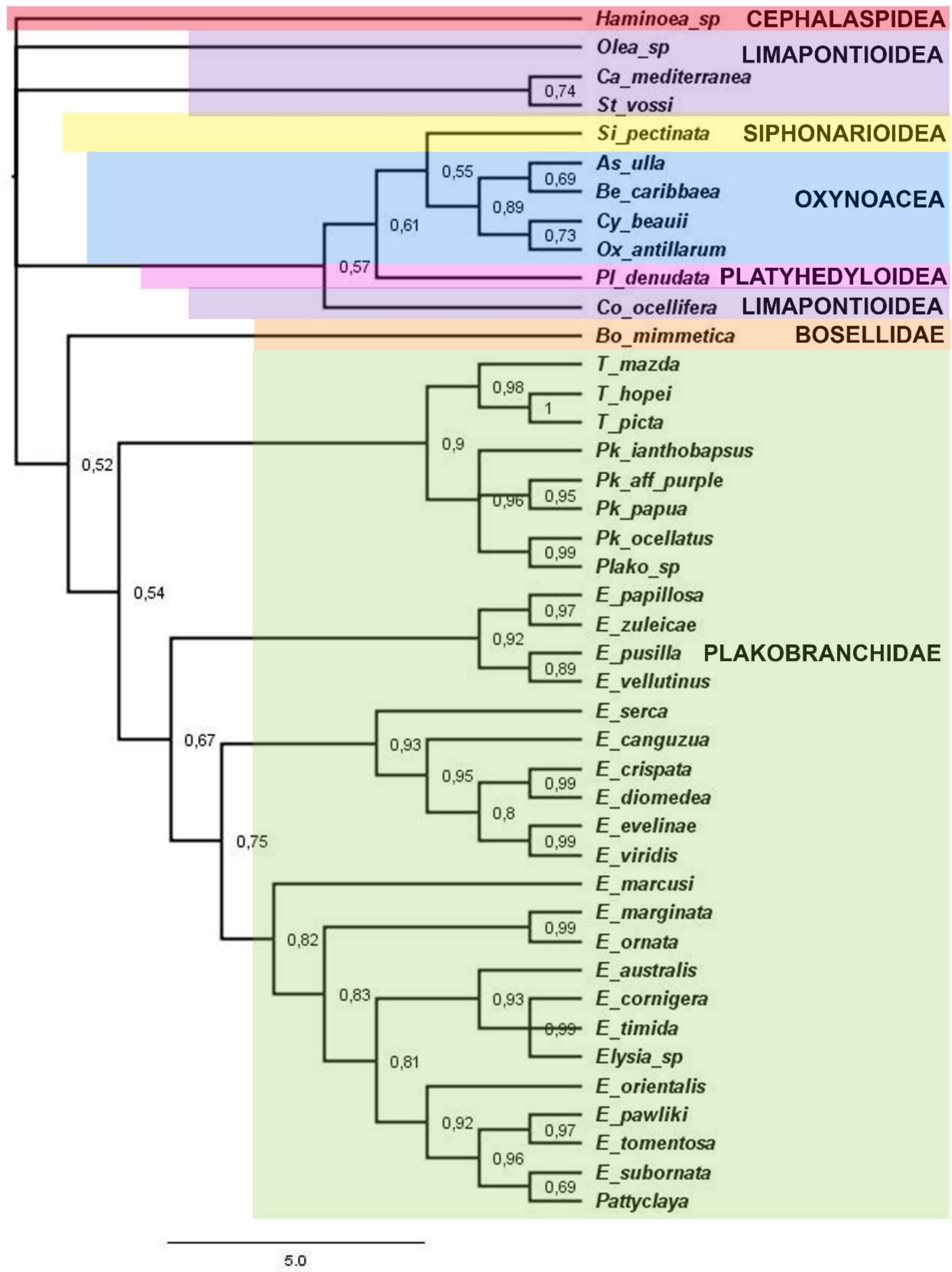

Figure 157. Phylogenetic tree obtained through Bayesian analysis of combined data of 109 morphological characters and concatenated DNA sequences of two mitochondrial (COI, 16S) and three nuclear (H3, 18S and 28S) genes. Support values as BI posterior probabilities on each node.

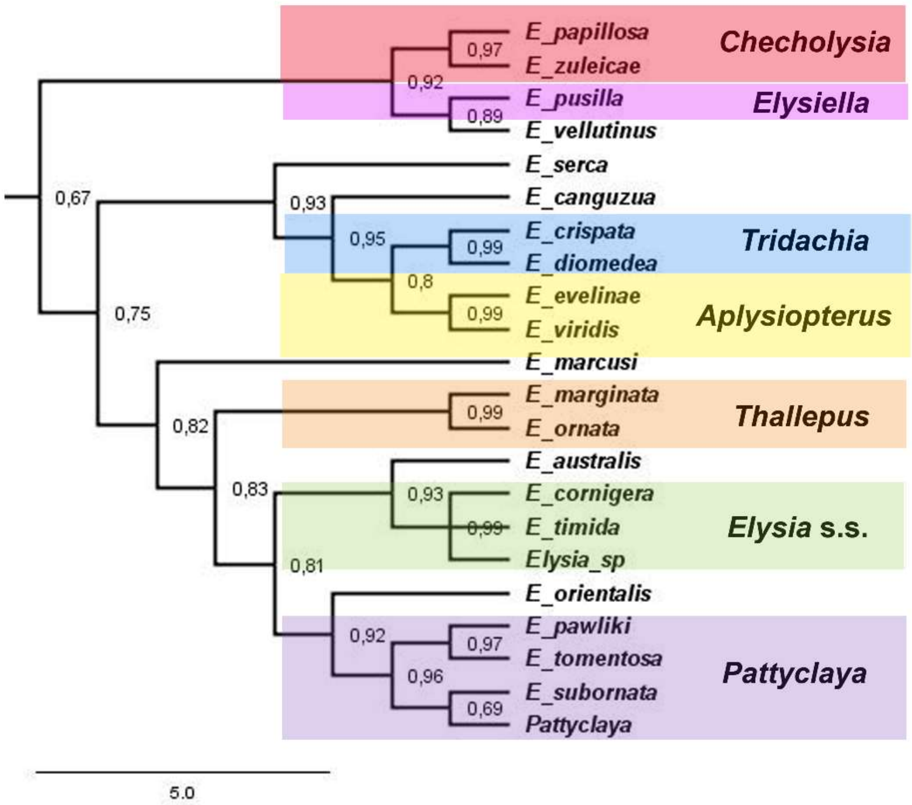

Figure 158. Section of phylogenetic tree obtained through Bayesian Inference (Fig. 97) with *Elysia* matching nodes with previous synonyms.

4.4. MOLECULAR EVIDENCE OF MULTIPLE SPECIES UNDER THE NAME *PLAKOBRANCHUS OCELLATUS* (GASTROPODA: SACOGLOSSA)

The genus *Plakobranchus* was described from Indonesia, and the type species (*Plakobranchus occelatus*) was considered the only valid member for a long time. Other species were later described from Hawaii (GOULD, 1852; BERGH, 1872), French Polynesia (PEASE, 1871, BERGH, 1873), Japan (STIMPSON, 1855) and Philippines (BERGH, 1872), but synonymized afterwards (BERGH, 1887; RISBEC, 1953; JENSEN, 1992). Including the type species of *Plakobranchus*, many of these species were shortly described based only on external features and color patterns. Bergh (1872, 1873) provided information on internal morphology of some species, but later considered them as intraspecific variations of *P. ocellatus* (BERGH, 1887).

However, distinct color morphs of *Plakobranchus* were reported in different localities on Indo-Pacificic (see KRUG *et al*., 2013; GOSLINER *et al*., 2015). Later, molecular evidence has found 10 candidate species under the name *Plakobranchus ocellatus* with distinct color patterns (KRUG *et al*., 2013), and a new species were described based on molecular and morphological evidence (MEYERS-MUÑOZ *et al*., 2016).

We analyzed COI and 16S partial sequences of 62 specimens of *Plakobranchus* spp.. Also, we included the sequences already published (total of 54 COI sequences and 58 16S sequences) to check which species was used for different works (BASS & KARL, 2006; KLUSSMANN-KOLB & DINAPOLI, 2006; MAEDA *et al*., 2010; HÄNDELER & WÄGELE, 2012; TAKANO *et al*., 2013; LERAY *et al*., 2013; MEYER-MUÑOZ *et al*., 2016).

The phylogenetic data of concatenate analysis of COI and 16S resulted in 11 candidate species. Krug *et al*. (2013) found 10 candidate species, and one of them was later described as *Plakobranchus papua.* Our analysis found the same 10 species plus another new one from Djibouti, Africa (Pk_saf_99829A-C) from the malacological collection of Zoological Museum of Sao Paulo University.

We propose the resurrection of *Plakobranchus ianthobapsus* as a valid species, which is the only species to occur in Hawaii. Also, we provide the redescription of *Plkobranchus papua* and the description of two new species, Plakobranchus sp. 1 aff purple and *Plakobranchus* sp. 2 Africa.

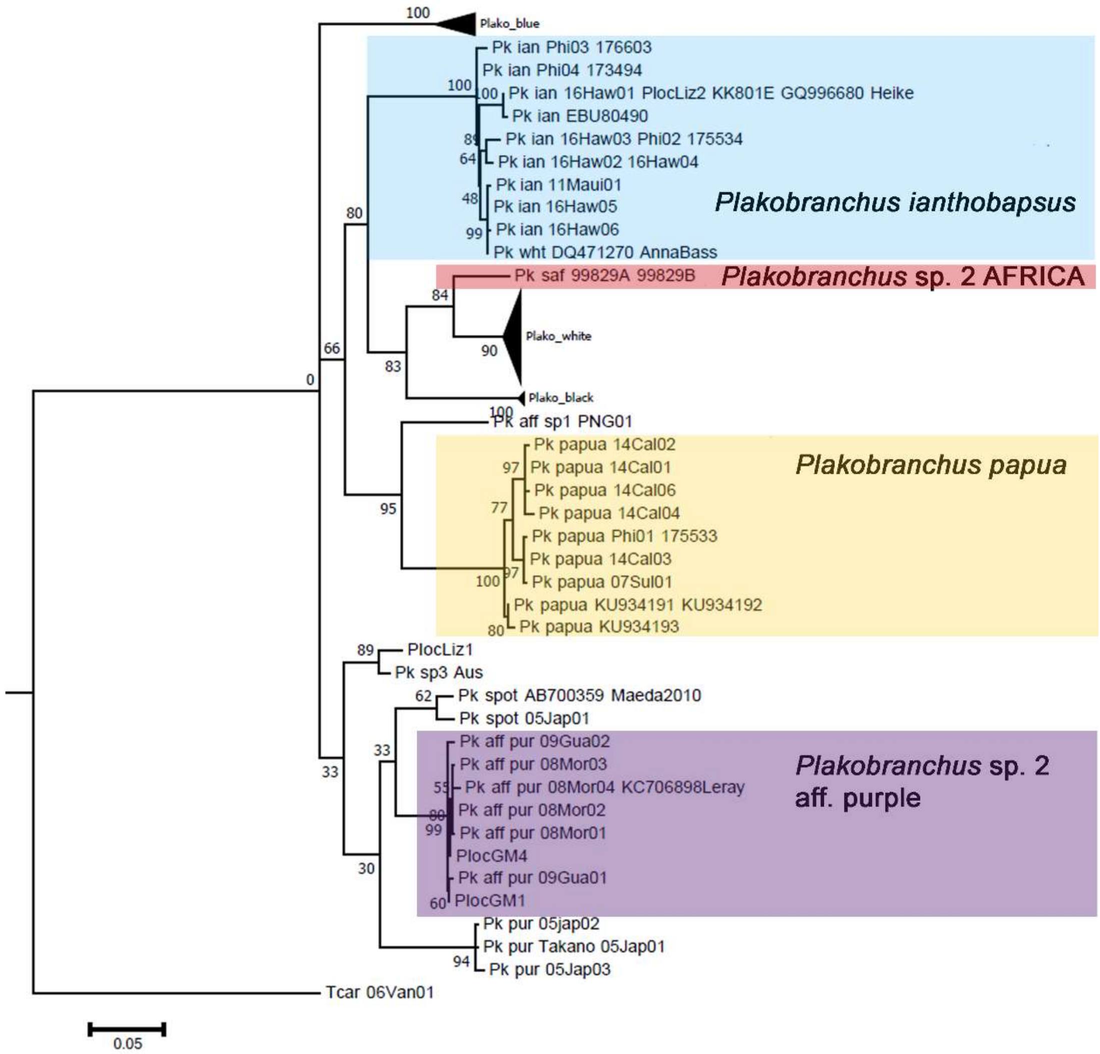

Figure 159. Phylogenetic tree obtained through Maximum Likelihood of concatenated DNA sequences of two mitochondrial (COI, 16S) genes. Support values as ML bootstrap percentages on branch.

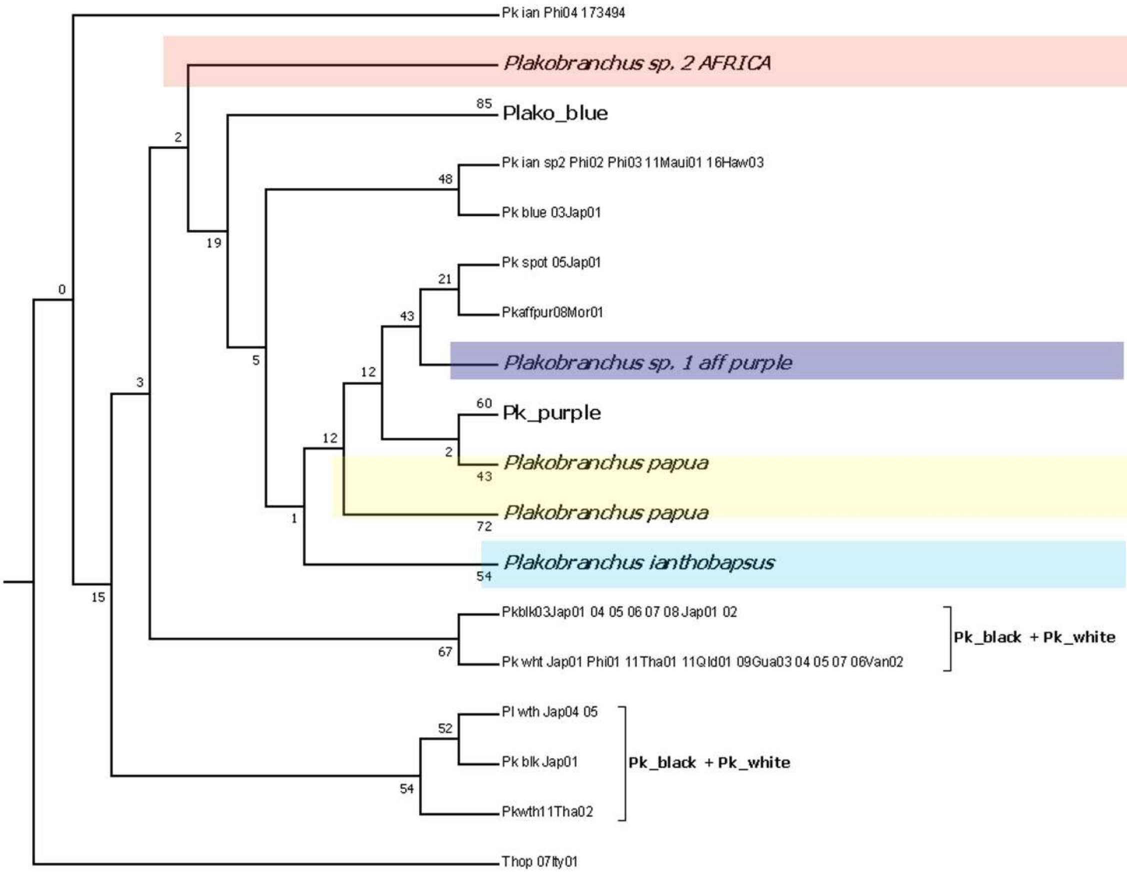

Figure 160. Phylogenetic tree obtained through Maximum Likelihood of partial DNA sequences of the nuclear gene H3. Support values as ML bootstrap percentages on branch.

5. CONCLUSIONS

1. The family Plakobranchidae resulted as a well-supported monophyletic group in all morphological analysis;
2. Plakobranchidae has not resulted as a natural group in molecular phylogenies, but its monophyletic status was recovered in total evidence analysis;
3. All the three valid genera within Plakobranchidae are monophyletic in analyses with distinct criteria and data set;
4. *Thuridilla* and *Plakobranchus* are well-supported in all scenarios and, except for the consensus topology with prior weights, resulted as sister groups;
5. The genus *Elysia* are low supported in all analysis, and its internal clades are grouped slightly different among analyses;
6. Morpho groups in *Elysia* has been recovered as clades in most analyses, which clearly reflects distinct evolutionary pathways, and meaning that a future subdivision of the genus is necessary for a better understanding of their natural history;
7. Despite similar external morphology, plakobranchids present a large variation on their internal morphology in all systems studied herein;

6. REFERENCES

Aktipis, S. W.; Giribet, G.; Lindberg, D. R., & Ponder, W. F. (2008). Gastropoda: an overview and analysis. *Phylogeny and Evolution of the Mollusca*, 201-237.

Baba, K. (1961). On the identification and the affinity of Tamanovalva limax, a bivalved sacoglossan mollusc in Japan. *Publications of the Seto Marine Biological Laboratory, 9*(1): 37-62.

Baba, K., & Hamatani, I. (1970). Occurrences of specimens presumably identifiable with Stiliger ornatus Ehrenberg, 1831, at Seto, Kii, middle Japan (Opisthobranchia: Sacoglossa).

Ballesteros, M. (1979). *Bosellia mimetica* Trinchese, 1891 y *Elysia timida* Risso, 1818, dos ascoglosos nuevos para la fauna ibérica. *Publicaciones Dpto. Zoología Barcelona*, *4*, 13-17.

Bass, A. L., & Karl, S. A. (2006). Molecular phylogenetic analysis of genera in the family Plakobranchidae (Mollusca: Opisthobranchia: Sacoglossa). *Records of the Western Australian Museum*, 69: 61-68.

Bieler, R. (1992). Gastropod phylogeny and systematics. *Annual Review of Ecology and Systematics*, 23(1), 311-338.

Bouchet, P., Rocroi, J. P., Frýda, J., Hausdorf, B., Ponder, W., Valdés, Á., & Warén, A. (2005). Classification and nomenclator of gastropod families. *Malacologia*, 47(1-2), 1-368

Brace, R. C. (1977). The functional anatomy of the mantle complex and columellar muscle of tectibranch molluscs (Gastropoda: Opisthobranchia), and its bearing on the evolution of opisthobranch organization. *Phil. Trans. R. Soc. Lond. B*, *277*(951), 1-56.

Caballer, M. G., Ortea, J., Rivero, N., Tucker, G. C., Malaquías, M. A. E., & Narciso, S. (2015). The opisthobranch gastropods (Mollusca: Heterobranchia) from Venezuela: an annotated and illustrated inventory of species. *Zootaxa*, *4034*(2), 201-256.

Carmona, L., Malaquias, M. A. E., Gosliner, T. M., Pola, M., & Cervera, J. L. (2011). Amphi-Atlantic distributions and cryptic species in sacoglossan sea slugs. *Journal of Molluscan Studies*, *77*(4), 401-412.

Christa, G., Händeler, K., Kück, P., Vleugels, M., Franken, J., Karmeinski, D., & Wägele, H. (2014). Phylogenetic evidence for multiple independent origins of functional kleptoplasty in Sacoglossa (Heterobranchia, Gastropoda). *Organisms Diversity & Evolution*, *15*(1), 23-36.

Christa, G., Wescott, L., Schäberle, T. F., König, G. M., & Wägele, H. (2013). What remains after 2 months of starvation? Analysis of sequestered algae in a photosynthetic slug, Plakobranchus ocellatus (Sacoglossa, Opisthobranchia), by barcoding. *Planta*, *237*(2), 559-572.

Cimino, G. & Gavagnin, M. (2007). *Molluscs: from chemo-ecological study to biotechnological application.* Springer Science & Business Media, p. 397.

Cimino, G., Fontana, A., & Gavagnin, M. (1999). Marine opisthobranch molluscs: chemistry and ecology in sacoglossans and dorids. *Curr Org Chem*, *3*(4), 327-72.

Clark, K. B. (1984). New records and synonymies of Bermuda opisthobranchs (Gastropoda). *The Nautilus*, 98(2): 85-97.

Coelho, R., Malaquias, M., & Calado, G. (2006). Calliopaea bellula feeding upon egg-masses of Haminoea orbignyana: oophagy among opisthobranch molluscs. *Journal of the Marine Biological Association of the United Kingdom*, *86*(2), 423-424.

Coleman, N. (2001). *1001 Nudibranchs: catalogue of Indo-Pacific sea slugs*. Neville Coleman's Underwater Geographic Pty Ltd.

Costa, A. (1867). Saggio sui molluschi eolididei del Golfo di Napoli. *Annuario del Museo Zoologico della Reale Università di Napoli*, *4*: 26-37.

Cruz, S., Calado, R., Serôdio, J., & Cartaxana, P. (2013). Crawling leaves: photosynthesis in sacoglossan sea slugs. *Journal of experimental botany*, *64*(13), 3999-4009.

Dayrat, B., & Tillier, S. (2002). Evolutionary relationships of euthyneuran gastropods (Mollusca): a cladistic re-evaluation of morphological characters. *Zoological Journal of the Linnean Society*, *135*(4), 403-470.

Dayrat, B., Conrad, M., Balayan, S., White, T. R., Albrecht, C., Golding, R., ... & de Frias Martins, A. M. (2011). Phylogenetic relationships and evolution of pulmonate gastropods (Mollusca): new insights from increased taxon sampling. *Molecular Phylogenetics and Evolution*, *59*(2), 425-437.

Dinapoli, A., & Klussmann-Kolb, A. (2010). The long way to diversity–phylogeny and evolution of the Heterobranchia (Mollusca: Gastropoda). *Molecular Phylogenetics and Evolution*, *55*(1), 60-76.

Drummond, A.J., Suchard, M.A., Xie, D. and Rambaut, A. (2012). Bayesian phylogenetics with BEAUTi and the Beast 1.7. *Molecular Biology and Evolution* 29(8)**,** 1969–1973.

Engel, H. (1927). Westindische Opisthobranchiate Mollusken. II. Aplysiidae, Pleurobranchidae, Oxynoidae, Elysiidae, Phyllobranchidae. *Bijdragen tot de Dierkunde*, 25: 83-122.

Evans, T. J. (1950). A review of Pease's genus Volvatella, together with a preliminary report on a new sacoglossan genus. *Journal of Molluscan Studies*, *28*(2-3), 102-106.

Evertsen, J., Burghardt, I., Johnsen, G., & Wägele, H. 2007. Retention of functional chloroplasts in some sacoglossans from the Indo-Pacific and Mediterranean. *Marine Biology*, 151(6): 2159-2166.

Fahrner, A., & Haszprunar, G. (2001). Anatomy and ultrastructure of the excretory system of a heart-bearing and a heart-less sacoglossan gastropod (Opisthobranchia, Sacoglossa). *Zoomorphology*, *121*(2), 85-93.

GALVÃO FILHO, H. C. (2013). Taxonomia de espécies do gênero *Elysia* Risso 1818 (Mollusca: Gastropoda: Sacoglossa) do Brasil. Universidade Federal do Ceará, Fortaleza, 127 p.

Galvão Filho, H. C., Araújo, A. K., Silva, F. V., Azevedo, V. M., Meirelles, C. A., & Matthews-Cascon, H. (2015). Sea slugs (Gastropoda: Heterobranchia) from a poorly known area in North-east Brazil: filling gaps in Atlantic distributions. *Marine Biodiversity Records*, *8*.

Gascoigne, T. (1975). The radula and reproductive system of Olea hansineensis Agersborg, 1923. *Veliger*, *17*, 313-317.

Gascoigne, T. (1976). The reproductive systems and classification of the Stiligeridae (Opisthobranchia: Sacoglossa). *Journal of the Malacological Society of Australia*, *3*(3-4), 157-172.

Gascoigne, T. (1979). A redescription of Caliphylla mediterranea Costa, 1867 (Opisthobranchia: Ascoglossa). *Journal of Molluscan Studies*, *45*(3), 300-311.

Gascoigne, T., & Sigurdsson, J. B. (1977). Calliopaea oophaga Lemche, 1974, a species new to the British fauna (Opisthobranchia: Sacoglossa). *Journal of Molluscan Studies*, *43*(3), 286-289.

Gascoigne, T., & Todd, C. D. (1977). A description of a specimen of Calliopaea bellula D'Orbigny, 1857 found at Robin Hood's Bay, North Yorkshire (Opisthobranchia: Sacoglossa). *Journal of Molluscan Studies*, *43*(3), 290-295.

Gavagnin, M., Mollo, E., Montanaro, D., Ortea, J., & Cimino, G. (2000). Chemical studies of Caribbean sacoglossans: dietary relationships with green algae and ecological implications. *Journal of chemical ecology*, *26*(7), 1563-1578.

Göbbeler, K., & Klussmann-Kolb, A. (2011). Molecular phylogeny of the Euthyneura (Mollusca, Gastropoda) with special focus on Opisthobranchia as a framework for reconstruction of evolution of diet. *Thalassas*, *27*(2), 121-154.

Goodheart, J. A., Ellingson, R. A., Vital, X. G., Galvão Filho, H. C., McCarthy, J. B., Medrano, S. M., ... & Hoover, C. A. (2016). Identification guide to the heterobranch sea slugs (Mollusca: Gastropoda) from Bocas del Toro, Panama. *Marine Biodiversity Records*, *9*(1), 56.

Gosliner, T. M. (1994). Gastropoda. Opisthobranchia. In *Microscopic Anatomy of Invertebrates*. Vol. 5. *Mollusca I*, Edited by F. W. Harrison and A. J. Kohn. New York: Wiley-Liss, pp. 253-355.

Gosliner, T. M. (1995). The genus *Thuridilla* (Opisthobranchia: Elysiidae) from the tropical Indo-Pacific, with a revision of the phylogeny and systematics of the Elysiidae. *Proceedings of the California Academy of Sciences*, 49(1): 1-54.

Gosliner, T. M., Behrens, D. W., & Valdés, Á. (2008). *Indo-Pacific nudibranchs and sea slugs: a field guide to the world's most diverse fauna*. Sea Challengers Natural History Books; California Academy of Sciences.

Gosliner, T. M., Valdés, A. & Behrens, D. W. (2015). *Nudibranch & sea slug identification: Indo-Pacific*. New World Publications.

Gosliner, T. M., Valdés, A. & Behrens, D. W. (2015). *Nudibranch & sea slug identification: Indo-Pacific*. New World Publications.

Grande, C., Templado, J., Cervera, J. L., & Zardoya, R. (2004). Phylogenetic relationships among Opisthobranchia (Mollusca: Gastropoda) based on mitochondrial cox 1, trnV, and rrnL genes. *Molecular phylogenetics and evolution*, *33*(2), 378-388.

Händeler, K., & Wägele, H. (2007). Preliminary study on molecular phylogeny of Sacoglossa and a compilation of their food organisms. *Bonn Zool Beitr*, *55*, 231-254.

Händeler, K., Grzymbowski, Y. P., Krug, P. J., & Wägele, H. (2009). Functional chloroplasts in metazoan cells-a unique evolutionary strategy in animal life. *Frontiers in Zoology*, *6*(1), 28.

Ihering, H. v. (1876). Versuch eines natiirlichen Systems der Mollusken. J b , dt. Malakozool. Ges. 3**,** 97-174.

Jaume, M. L. (1945). El genero *Oxynoe* en Cuba occidental. *Revista de la Sociedad Malacologia*, *3*:18-25.

Jensen, K. R. (1986). Observations on feeding, copulation and spawning of the Ascoglossan Opisthobranch Calliopaea oophaga lemche. *Ophelia*, *25*(2), 97-106.

Jensen, K. R. (1991). Comparison of Alimentary Systems in Shelled and Non-shelled Sacoglossa (Mollusca, Opisthobranchia). *Acta Zoologica*, *72*(3), 143-150.

Jensen, K. R. (1993). Morphological adaptations and plasticity of radular teeth of the Sacoglossa (= Ascoglossa) (Mollusca: Opisthobranchia) in relation to their food plants. *Biological Journal of the Linnean Society*, *48*(2), 135-155.

Jensen, K. R. (1996). Phylogenetic systematics and classification of the Sacoglossa (Mollusca, Gastropoda, Opisthobranchia). *Phil. Trans. R. Soc. Lond. B*, *351*(1335), 91-122.

Jensen, K. R. (1997a). Evolution of the Sacoglossa (Mollusca, Opisthobranchia) and the ecological associations with their food plants. *Evolutionary Ecology 11*: 301–335.

Jensen, K. R. (1997b). Sacoglossernes systematik, fylogeni og evolution (Mollusca, Opisthobranchia). (Systematics, phylogeny and evolution of the Sacoglossa (Mollusca, Opisthobranchia). *Vestjydsk Forlag*, Copenhagen, 94 pp.

Jensen, K. R. (2007). Biogeography of the Sacoglossa (Mollusca, Opisthobranchia). *Bonner Zoologische Beiträge*, *55*(3/4), 255-281.

Jensen, K. R. (2014). Anatomy of three sacoglossans (Mollusca," Opisthobranchia") newly recorded from São Miguel, Azores. *Açoreana, Suplemento*, *10*, 117-138.

Jörger, K. M., Stöger, I., Kano, Y., Fukuda, H., Knebelsberger, T., & Schrödl, M. (2010). On the origin of Acochlidia and other enigmatic euthyneuran gastropods, with implications for the systematics of Heterobranchia. *BMC Evolutionary Biology*, *10*(1), 323.

Klussmann-Kolb, A. (2004). Phylogeny of the Aplysiidae (Gastropoda, Opisthobranchia) with new aspects of the evolution of seahares. *Zoologica Scripta*, *33*(5), 439-462.

Krug, P. J., Vendetti, J. E., & Valdés, Á. (2016). Molecular and morphological systematics of Elysia Risso, 1818 (Heterobranchia: Sacoglossa) from the Caribbean region. *Zootaxa*, *4148*(1), 1-137.

Laetz, E., Christa, G., Haendeler, K., & Waegele, H. (2014). The *Cylindrobulla/Ascobulla* complex—unraveling problems in identification and adding to Cylindrobulla diversity (Gastropoda, Heterobranchia, Sacoglossa) by describing a new species. *Zootaxa*, *3893*(3), 339-362.

Laetz, E., Christa, G., Haendeler, K., & Waegele, H. (2014). The Cylindrobulla/Ascobulla complex—unraveling problems in identification and adding to Cylindrobulla diversity (Gastropoda, Heterobranchia, Sacoglossa) by describing a new species. *Zootaxa*, *3893*(3), 339-362.

Lewin, R. A. (1970). Toxin secretion and tail autotomy by irritated *Oxynoe panamensis* (Opisthobranchiata; Sacoglossa). *Pacific Science*, 24(3), 356-358.

Maeda, T., Kajita, T., Maruyama, T., & Hirano, Y. (2010). Molecular phylogeny of the Sacoglossa, with a discussion of gain and loss of kleptoplasty in the evolution of the group. *The Biological Bulletin*, *219*(1), 17-26.

Malaquias, M. A. E., & Cervera, J. L. (2005). The genus *Haminoea* (Gastropoda: Cephalaspidea) in Portugal, with a review of the European species. *Journal of Molluscan Studies*, *72*(1), 89-103.

Marcus, Er. (1957). On Opisthobranchia from Brazil (2). *Journal of the Linnean Society*, *London* 34: 390-486.

Marcus, Er. & Marcus, Ev. (1970). Opisthobranchs from Curaçao and faunistically related regions. *Studies on the Fauna of Curaçao and other Caribbean Islands 33*(122): 1-129.

Marcus, Er. (1958). On Western Atlantic opisthobranchiate gastropods. *American Museum Novitates* 1906: 1-82.

Marcus, Ev. & Marcus, Er. (1963). Opisthobranchs from the Lesser Antilles. *Studies on the fauna of Curaçao and other Carribbean Islands* 19: 1-76.

Marcus, Ev. & Marcus, Er. (1967). Opisthobranchs from the southwestern Caribbean Sea. Biological Investigations of the Deep Sea, 33. *Bulletin of Marine Science* 17: 597- 628.

Marcus, Ev. (1973). On the genus *Bosellia* (Mollusca: Gastropoda; Ascoglossa). *Bulletin of Marine Science*, *23*(4), 811-823.

Marcus, Ev. (1982). Systematics of the genera of the order Ascoglossa (Gastropoda). *Journal of Molluscan Studies*, *48*(supp10), 1-31.

Marcus, Ev., & Hughes, H. P. (1974). Opisthobranch mollusks from Barbados. *Bulletin of Marine Science*, *24*(3), 498-532.

Marcus, Ev., & Marcus, Er. (1960). Opisthobranchs from American Atlantic warm waters. *Bulletin of Marine Science*, *10*(2), 129-203.

Marín, A., & Ros, J. (2004). Chemical defenses in Sacoglossan Opisthobranchs: Taxonomic trends and evolutionary implications. *Scientia Marina,* 67(1), 227-241.

Medina, M., Lal, S., Vallès, Y., Takaoka, T. L., Dayrat, B. A., Boore, J. L., & Gosliner, T. (2011). Crawling through time: transition of snails to slugs dating back to the Paleozoic, based on mitochondrial phylogenomics. *Marine Genomics*, *4*(1), 51-59.

Meirelles, C. A., Galvão Filho, H. C., Scramosin, K. A., & Matthews-Cascon, H. (2010). Oxynoe antillarum (Mollusca, Oxynoidae) no estado do Ceará, Nordeste do Brasil. *Revista Nordestina de Zoologia*, *4*, 42-47.

Meyers-Muñoz, M. A., van der Velde, G., van der Meij, S. E., Stoffels, B. E., van Alen, T., Tuti, Y., & Hoeksema, B. W. (2016). The phylogenetic position of a new species of Plakobranchus from West Papua, Indonesia (Mollusca, Opisthobranchia, Sacoglossa). *ZooKeys*, (594), 73.

Mikkelsen, P. M. (1996). The evolutionary relationships of Cephalaspidea sl (Gastropoda: Opisthobranchia): a phylogenetic analysis. *Malacologia*, *37*(2), 375-442.

Mikkelsen, P. M. (1998). *Cylindrobulla* and *Ascobulla* in the western Atlantic (Gastropoda, Opisthobranchia, Sacoglossa): systematic review, description of a new species, and phylogenetic reanalysis. *Zoologica Scripta*, *27*(1), 49-71.

Mikkelsen, P. M. (2002). Shelled opisthobranchs. *Advances in Marine Biology*, *42*, 67-136.

Millen, S. V. (1980). Range extensions, new distribution sites, and notes on the biology of sacoglossan opisthobranchs (Mollusca: Gastropoda) in British Columbia. *Canadian Journal of Zoology*, *58*(6), 1207-1209.

Miller, M.A., Schwartz, T., Pickett, B.E., He, S., Klem, E.B., Scheuermann, R.H., Passarotti, M. and Kaufman, S. (2015). A RESTful API for access to phylogenetic tools via the CIPRES Science Gateway. *Evolutionary Bioinformatics* 11*,* 43–48.

Mordan, P., & Wade, C. (2008). Heterobranchia II: The Pulmonata *in* W. F. Ponder. & D. R. Lindberg (eds.). *Phylogeny and Evolution of the Mollusca*, 409-426.

Nixon, K. C. (1999). *Winclada (BETA) ver 0.9.9*

Ortea, J., Espinosa, J., Buske, Y., & Caballer, M. (2013). Additions to the inventory of the sea slugs (Opisthobranchia and Sacoglossa) from Guadeloupe (Lesser Antilles, Caribbean Sea). *Revista de la Academia Canaria de Ciencias*, *25*, 163-194.

Padula, V. (2008). Notes on the morphology of *Elysia subornata* and *Oxynoe antillarum* (Mollusca, Opisthobranchia, Sacoglossa) from the state of Rio de Janeiro, Brazil. *Strombus*, *15*(2), 19.

Padula, V., Bahia, J., Correia, M. D., & Sovierzoski, H. H. (2012). New records of opisthobranchs (Mollusca: Gastropoda) from Alagoas, northeastern Brazil. *Marine Biodiversity Records*, *5*.

Padula, V., Wirtz, P., & Schrödl, M. (2017). Heterobranch sea slugs (Mollusca: Gastropoda) from Ascension Island, South Atlantic Ocean. *Journal of the Marine Biological Association of the United Kingdom*, *97*(4), 743-752.

Ponder, W. F., & Lindberg, D. R. (1997). Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of the Linnean society*, *119*(2), 83-265.

Pruvot-Fol, A. (1954). Mollusques opisthobranches. *Faune de France* 58, 1-460. Lechevalier.

Puillandre, N., Lambert, A., Brouillet, S. & Achaz, G. 2012. ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Molecular Ecology*, 21: 1864–1877.

Redfern, C. (2001). Bahamian Seashells – A Thousand Species from Abaco, Bahamas, 280 pp. *Bahamianseashells.com*, Boca Ratón.

Redfern, C. (2013*).* Bahamian seashells: 1161 species from Abaco, Bahamas. *Bahamianseashells.com*, Incorporated.

Rios, E. (2009). Compendium of Brazilian Sea Shells. Rio Grande: Ed. Evangraf. 668p.

Rückert, I. M., Altnöder, A., & Schrödl, M. (2008). Computer-based 3D anatomical reconstruction and systematic placement of the mesopsammic gastropod Platyhedyle denudata Salvini-Plawen, 1973 (Opisthobranchia, Sacoglossa). *Organisms Diversity & Evolution*, *8*(5), 358-367.

Rumpho, M. E., Dastoor, F. P., Manhart, J. R., & Lee, J. (2007). The kleptoplast. In *The structure and function of plastids* (pp. 451-473). Springer Netherlands.

Rumpho, M. E.; Summer, E. J.; Manhart, J. R. 2010. Solar-powered sea slugs. Mollusc/algal chloroplast symbiosis. *Plant Physiology*, 123(1), 29-38.

Schrödl, M., Jörger, K. M., Klussmann-Kolb, A., & Wilson, N. G. (2011). Bye bye "Opisthobranchia"! A review on the contribution of mesopsammic sea slugs to euthyneuran systematics. *Thalassas*, *27*(2), 101-112.

Simone, L. R. L. (2011). Phylogeny of the Caenogastropoda (Mollusca), based on comparative morphology. *Arquivos de Zoologia (São Paulo)*, *42*(4), 161-323.

Simone, L. R. L., & Seabra, M. I G. L. (2017). Shell and body structure of the plesiomorphic pulmonate marine limpet Siphonaria pectinata (Linnaeus, 1758) from Portugal (Gastropoda: Heterobranchia: Siphonariidae). *Folia Malacologica*, *25*(3), 147-164.

Stamatakis, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22: 2688-90.

Stirts, H. M., & Clark, K. B. (1980). Effects of temperature on products of symbiotic chloroplasts in Elysia tuca Marcus (Opisthobranchia: Ascoglossa). *Journal of Experimental Marine Biology and Ecology*, *43*(1), 39-47.

Thibaut, T.; Meinesz, A.; Amade, P.; Charrier, S.; De Angelis, K.; Ierardi, S.; Mangialajo, K.; Melnick, J. & Vidal, V. 2001. *Elysia subornata* (Mollusca) a potential control agent of the alga *Caulerpa taxifolia* (Chlorophyta) in the Mediterranean Sea. *Journal of the Marine Biological Association of the UK*, 81(03): 497-504.

Thompson, T. E. (1977). Jamaican opisthobranch molluscs I. *Journal of Molluscan Studies*, *43*(2), 93-140.

Thompson, T. E. (1988). Eastern Mediterranean Opisthobranchia: Oxynoidae, Polybranchhdae, Stiligeridae (Sacoglossa). *Journal of Molluscan Studies*, *54*(2), 157-172.

Thompson, T. E., & Jaklin, A. (1988). Eastern Mediterranean Opisthobranchia: Elysiidae (Sacoglossa= Ascoglossa). *Journal of Molluscan Studies*, *54*(1), 59-69.

Trinchese, S. (1891). Descrizione del nuovo genere *Bosellia. Memorie della Regia Accademia delle Scienze dell'Istituto di Bologna* (5), 1, 773-8.

Valdés, A., & Camacho-García, Y. E. (2000). A new species of Cyerce Bergh, 1871 (Mollusca, Sacoglossa, Polybranchiidae) from the Pacific coast of Costa Rica. Una especie nueva de

Cyerce Bergh, 1871 (Mollusca, Sacoglossa, Polybranchiidae) de la costa Pacífica de Costa Rica. *Bulletin of Marine Science.*, *66*(2), 445-456.

Valdés, Á., Hamann, J., & Behrens, D. W. (2006). *Caribbean Sea Slugs: A Field Guide to the Opisthobranch Mollusks from the Tropical Nortwestern Atlantic*. Sea Challengers Natural History Books.

Wägele, H., & Klussmann-Kolb, A. (2005). Opisthobranchia (Mollusca, Gastropoda)–more than just slimy slugs. Shell reduction and its implications on defence and foraging. *Frontiers in Zoology*, *2*(1), 3.

Wägele, H., & Martin, W. F. (2014). Endosymbioses in sacoglossan seaslugs: plastid-bearing animals that keep photosynthetic organelles without borrowing genes. In *Endosymbiosis* (pp. 291-324). Vienna: Springer.

Wägele, H., Klussmann-Kolb, A., Verbeek, E., & Schrödl, M. (2014). Flashback and foreshadowing—a review of the taxon Opisthobranchia. *Organisms Diversity & Evolution*, *14*(1), 133-149.

Wägele, H., Klussmann-Kolb, A., Vonnemann, V., & Medina, M. (2008). Heterobranchia I: the opisthobranchia. In W. F. Ponder. & D. R. Lindberg (eds.). *Phylogeny and Evolution of the Mollusca*. Oakland: University of California Press, 385-408.

Wawra, E. (1979). Zur systematischen Stellung von *Platyhedyle denudata* Salvini-Plawen, 1973 (Opisthobranchia, Gastropoda). *Journal of Zoological Systematics and Evolutionary Research*, *17*(3), 221-225.

Wilson, N. G., Howison, M., Andrade, S. C., Jörger, K. M., Schrödl, M., ... & Dunn, C. W. (2014). Phylogenomic analyses of deep gastropod relationships reject Orthogastropoda. *Proc. R. Soc. B*, *281*(1794), 20141739.

Yonow, N. (2008). *Sea slugs of the Red Sea* (Vol. 74). Pensoft Pub.

Zapata, F., Wilson, N. G., Howison, M., Andrade, S. C., Jörger, K. M., Schrödl, M., ... & Dunn, C. W. (2014). Phylogenomic analyses of deep gastropod relationships reject Orthogastropoda. *Proc. R. Soc. B*, 281(1794), 20141739.