



Biodiversity of the genus *Hemimenia* (Mollusca, Solenogastres, Neomeniamorpha) in Galician waters (NW Spain) with the description of three new species

Biodiversidad del género *Hemimenia* (Mollusca, Solenogastres, Neomeniamorpha) en aguas de Galicia (NO España) con la descripción de tres nuevas especies

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ABSTRACT

Solenogastres belong to the genus *Hemimenia* Nierstrasz, 1902 collected from the Galician upper slope (NW Spain) during the DIVA-ARTABRIA I (2002 and 2003) expeditions are treated herein. To date, the genus *Hemimenia* was represented by five species, three of them present in Galicia. The investigation on these specimens resulted in new material of the Iberian species *Hemimenia cyclomyata* Salvini-Plawen, 2006 and the discovery of three new species: *Hemimenia rugosa* n. sp., *Hemimenia nanodoryata* n. sp. and *Hemimenia tripla* n. sp. The species are described and illustrated and taxonomically compared with the other taxa of the genus.

RESUMEN

Se estudian los Solenogastres del género *Hemimenia* Nierstrasz, 1902 recolectados en la parte superior del talud continental de Galicia (NO España) durante las expediciones DIVA-ARTABRIA I (2002 y 2003). El género *Hemimenia* estaba representado por cinco especies, tres de ellas presentes en Galicia. La investigación de los especímenes dio como resultado nuevos datos sobre la especie ibérica *Hemimenia cyclomyata* Salvini-Plawen, 2006 y el descubrimiento de tres nuevas especies: *Hemimenia rugosa* n. sp., *Hemimenia nanodoryata* n. sp. y *Hemimenia tripla* n. sp. Las especies se describen e ilustran y se comparan taxonómicamente con los otros taxa del género.

INTRODUCTION

Solenogastres Gegenbaur, 1878 is a small class of the Mollusca that comprises around 280 marine species, inhabiting a variety of ecosystems, ranging from coastal to abyssal depths as benthic or epibenthic fauna. Solenogastres exhibit many unique characteristics that distinguish them from other mol-

luscs such as: worm-like body, mantle consisting of cuticle with aragonitic sclerites, small reduced terminal or subterminal pallial cavity and a vestigial foot reduced to a ventral pedal groove.

Among Solenogastres, the order Neomeniamorpha Salvini-Plawen, 1978 is characterized by a stout body with a

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thick or moderately thick cuticle bearing several types of sclerites (scales; acicular spicules; groove-like elements with or without lanceolate distal end; short harpoon-shaped bodies), by the presence of a complex copulatory apparatus including glands and by the absence of ventrolateral foregut glands. Neomeniomorpha includes two families: Neomeniidae Ihering, 1876 and Hemimeniidae Salvini-Plawen, 1978. Neomeniidae lack both harpoon-shaped bodies and radula and contains only the genus *Neomenia* Tullberg, 1875. Hemimeniidae is a small family distributed in two genera, *Archaeomenia* Thiele, 1906 and *Hemimienia* Nierstrasz, 1902, characterized by the presence of short harpoon-shaped bodies and generally showing a thin cuticle and epidermal papillae. *Hemimienia* can be easily differentiated from *Archaeomenia* by the absence of radula, among other characters. (GARCÍA-ÁLVAREZ AND SALVINI-PLAWEN, 2007).

So far, *Hemimienia* comprises five species: the type species *Hemimienia intermedia* Nierstrasz, 1902 described from Celebes Islands, Indonesia (NIERSTRASZ, 1902); *Hemimienia dorsosulcata*, 1978 from the Pacific subantarctic (SALVINI-PLAWEN, 1978); and three species in the Atlantic, *Hemimienia atlantica*, Salvini-Plawen 2006 (Azores and Banco "A Quiniela" of Galicia/NW Spain), *Hemimienia glandulosa* Salvini-Plawen 2006 (Banco de Galicia/NW Spain) and *Hemimienia cyclomyata* Salvini-Plawen 2006 (Banco de Galicia/NW Spain) (SALVINI-PLAWEN, 2006; GARCÍA-ÁLVAREZ ET AL., 2014).

Although in recent years the Solenogastres fauna of Europe has been intensively studied and several new species have been described (e.g. GARCÍA-ÁLVAREZ & URGORRI, 2001; GARCÍA-ÁLVAREZ ET AL., 2001; SALVINI-PLAWEN, 2008, 2009; ZAMARRO ET AL., 2013, 2015; PEDROUZO ET AL., 2014) our present knowledge about biodiversity and distribution is quite incomplete. The Spanish research project DIVA-ARTABRIA I "Diversidad latitudinal en los fondos profundos del Océano Atlán-

tico (DIVA): Biodiversidad y distribución batimétrica (100–2000 m) en el NW de las costas de Galicia" (Latitudinal diversity in the deep sea of the Atlantic Ocean: Biodiversity and bathymetric distribution in the north western Galician coasts) is targeted to provide baseline data on diversity, composition and distribution of benthic assemblages on this Iberian area, including Solenogastres. The present paper is based on new samples and data of the genus *Hemimienia* obtained from those expeditions and provides new records of *H. cyclomyata* and the description of three new species: *Hemimienia rugosa* n. sp., *Hemimienia nanodoryata* n. sp. and *Hemimienia tripla* n. sp.

MATERIAL AND METHODS

Eleven specimens of Mollusca Solenogastres have been studied. All of them were collected in two stations sampled during the DIVA-ARTABRIA I 2002 and 2003 cruises with an Agassiz trawl close to 1000 m depth. Specimens were fixed and preserved in 70% ethanol. The specimens were photographed and measured and their external anatomy was described. The sclerites were studied directly on the surface of the animals and by separating small pieces of the mantle from the dorsal and ventral areas of the body. These pieces were treated with 5% sodium hypochlorite for 12 h in order to isolate the sclerites; they were later rinsed with water, dried in a heater at 40°C and mounted using Eukitt or Araldite for their study with a Light Microscope (Olympus) and a Differential Interference Contrast (DIC) Microscope (Olympus) or sputter-coated with gold-palladium for those studies with a Scanning Electron Microscope (SEM).

For the histology examination, the specimens were decalcified with an EDTA solution and the anterior and posterior region of the specimens were embedded in paraffin or araldite. The paraffin blocks were cut in 5 µm cross-sections and stained with Mallory's

trichromic; the araldite blocks were cut in ribbons of semithin serial sections (cross-sections 2 µm) with glass knives and stained with Richardson's solution (GIL-MANSILLA ET AL., 2008). Histological examination and reconstruction were done under an Olympus microscope. The internal anatomy was manually reconstructed.

Type material of the new species described herein are housed at the Museo de Historia Natural da Universidade de Santiago de Compostela (MHNUSC). Specimens of *Hemimenia cyclomyata* Salvini-Plawen, 2006 are part of the collection of the Departamento de Zooloxía e Antropoloxía Física, Universidade de Santiago de Compostela.

RESULTS

(Systematics following GARCÍA-ÁLVAREZ AND SALVINI-PLAWEN, 2007)

Order NEOMENIAMORPHA Salvini-Plawen, 1978

Family HEMIMENIIDAE Salvini-Plawen, 1978

Genus *Hemimenia* Nierstrasz, 1902

Type Species: *Hemimenia intermedia* Nierstrasz, 1902, by monotypy.

(Amended) Sclerites mainly of scales and solid spicules; short harpoon-shaped bodies present. With common atrio-buccal opening. Radula miss-

ing. Secondary genital openings separate or fused. With/without dorsoterminal sense organ. With respiratory organs.

Hemimenia cyclomyata Salvini-Plawen, 2006 (Fig. 1)

Material examined: Seven specimens (1.5–7.6 mm long; 0.6–1.2 mm wide in the middle body region, 0.4–0.65 mm wide posteriorly) cut in 5 µm serial cross-sections. Collected in the DIVA-ARTABRIA I (2002 and 2003) expeditions in NW Galician waters (NW Spain): two specimens from the station DIVA-ARTABRIA I/2002 AT-1000 (43°57.00'N; 08°54.79'W – 43°57.25'N; 08°54.13'W), on a bottom of stones and dead corals, at 1132–1191 m; five specimens from the station DIVA-ARTABRIA I/2003 AT-1000 (43°53.85'N; 08°57.32'W – 43°54.62'N; 08°57.36'W), on a bottom of dead and live corals at 993–1004 m depth.

Distribution: Galicia (NW Spain).
Type locality: Banco de Galicia, 760–769 m (Salvini-Plawen 2006). Further records: Artabro Gulf, 993–1004 and 1132–1191 m (this report).

Taxonomic remarks: The specimens of *Hemimenia cyclomyata* studied herein were collected in the same geographic area as those previously known (SALVINI-PLAWEN, 2006; GARCÍA-ÁLVAREZ ET AL., 2014). The organization of the present specimens is almost identical with the holotype of *H. cyclomyata*: with a mid-dorsal keel of an irregular structure, that in the animal at hand is present with the structure of a single lump or as a more complex structure

provided with a medial groove, also absent in some body regions; thin matrix; pharynx with three regions, the medial one provided with a strong muscular ring; without seminal vesicles; with seminal receptacles; spawning duct paired throughout and opening by means of a common short cone; with two copulatory stylets and 4–6 prepallial spines on each body side; copulatory stylet gland with double connection; without suprappallial and pallial glands. However, some unknown features were observed and are herein described to complement the description of the species. There are large specimens, up to 7.6 mm long (holotype: 3.5 mm;

paratype: 2.1 mm, juvenile). They present six types of mantle sclerites (instead of four), including one type of excavate scales (75 μm long; 15–20 μm maximum wide) of pointed apex, basal and lateral uniformly rimmed and provided with a pair of laminar expansion and one type of blade scale-shaped scales on both beside of the pedal groove (40–50 μm long; 10–12 μm maximum wide) (Fig. 1B–D). Examined specimens

have a proboscis. The gutter-like stylets are located from laterally to ventrally to the acicular stylets (instead of just laterally); the gutter-like stylets can rotate around the acicular ones, probably by the action of the associated muscular fibers (Fig. 1E). It present up to 24 respiratory folds. The studied animals have a dorsoterminal sense organ placed dorsally to the posterior region of the pallial cavity instead of terminally.

Hemimenia rugosa n. sp. (Figs. 2-5)

Type material: Holotype from NW Galicia (NW Spain). Station DIVA-ARTABRIA I/2003 AT-1000 (43°53.85'N; 08°57.32'W – 43°54.62'N; 08°57.36'W); on a bottom of stones and dead corals at 993–1004 m depth, adult of 18 mm length (Fig. 2A); sectioned in 5 μm thickness cross-sections and mounted on slides (twenty slides) and three slides of sclerites. The holotype is deposited in the Museo de Historia Natural da Universidade de Santiago de Compostela (Spain), number MHNUSC 10052.

Etymology: From Latin: *ruga*, wrinkle, *-osus*, abundant presence of. With reference to the numerous and marked wrinkle-like cuticular folds on the body surface.

Diagnosis: Body with cuticular wrinkles and mid-dorsal keel. Thin cuticle (10–15 μm). Without epidermal papillae. Mantle sclerites of seven types of mantle sclerites, including one type of excavated scales distally pointed with a pair of laminar lateral expansion towards the concave face. Matrix thin. Pedal fold extending into ventroanterior pouch of pallial cavity. Anterior pedal glands voluminous. Atrial papillae simple. With narrow proboscis. Pharynx with three regions: anterior region with thick muscular and glandular wall; medial region with thick muscular ring; posterior region with broad coating of extraepithelial pharyngeal glands. Oesophagus with thin sphincter. Without anterodorsal midgut caecum. Midgut without constrictions. With pair of long ventroposterior midgut sacs surrounding the copulatory stylets. Without seminal vesicles. Seminal receptacles at spawning ducts. Spawning ducts paired throughout, opening into pallial cavity by means of common glandular genital cone. Two pairs of copulatory stylets with associated glands; glands with two outlets. Ten respiratory folds. Pallial glands on the genital cone and around the anterior

region of the ventroanterior pouch of the pallial cavity. Without suprapallial glands. Four prepallial spines at each body side. Without dorsoterminal sense organ.

Description: *Habitus:* The single animal is adult, 18 mm long and 2 mm wide on the body ends. With abundant and deep cuticular wrinkles giving them a characteristic creased appearance. Furthermore, it presents a mid-dorsal keel (0.4 mm high) that does not reach to the body ends. On the mid-dorsal keel the sclerites clearly protrude on the body surface and are inserted almost at right angles. With sclerites obliquely and radially inserted and protruding slightly from the cuticle. Pallial cavity has subterminal opening. The body colour is brown-yellow colour after fixation and preservation in 70° ethanol (Fig. 2A–C).

Mantle: The cuticle is 10–15 μm thick. The epidermis is monostratified (30–50 μm thick) and lacks epidermal papillae, but shows glandular cells with granule of basic secretion. There is a well marked mid-dorsal keel; in cross-section it is present as a triangular to oval dorsal bulge provided with a mid-longitudinal groove bearing a circular

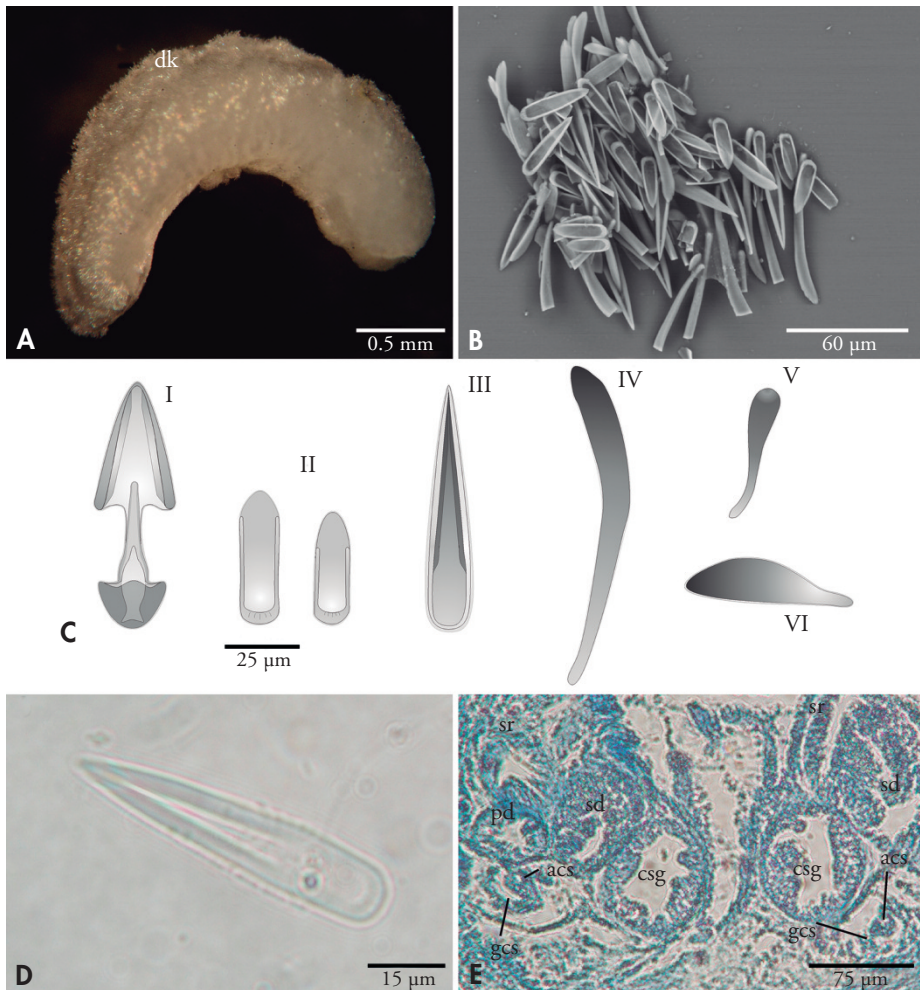


Figure 1. *Hemimenia cyclomyata* Salvini-Plawen, 2006. A: habitus; B: SEM micrographs of some types of sclerites; C: drawing of the mantle sclerites (I: short harpoon-shaped sclerite; II: small elongate and excavate scale with the basal and lateral rims reinforced; III: excavate scale distally pointed, basally and laterally reinforced and with a pair of laminar extension; IV: large paddle-shaped scale; V: small paddle-shaped scale; VI: foot-groove scale); D: optical microscope photograph of the excavate scales distally pointed and with a pair of lateral extensions (type III); E: cross-section through the posterior body, showing the organization of the copulatory apparatus. Abbreviations, acs: acicular copulatory stylet; csg: gland of the copulatory stylets; dk: mid-dorsal keel; gcs: gutter-like copulatory stylet; pd: pericardioduct; sd: spawning duct; sr: seminal receptacle.

Figura 1. *Hemimenia cyclomyata* Salvini-Plawen, 2006. A: habitus; B: micrografías al MEB de algunos tipos de escleritos; C: dibujo de los escleritos del manto (I: esclerito en forma de arpón corto; II: escama excavada y alargada pequeña, con el borde basal y lateral reforzado; III: escama excavada apuntada distalmente, con refuerzo basal y lateral y con un par de extensiones laminares; IV: paletas grandes; V: paletas pequeñas; VI: escama del surco pedio); D: fotografía al microscopio óptico de escamas excavadas apuntadas distalmente y con un par de extensiones laminares (tipo III); E: corte en sección de la parte posterior del cuerpo donde se observa la organización del aparato copulador. Abreviaturas, acs: estilete copulador acicular; csg: glándula del estilete copulador; dk: quilla mediodorsal; gcs: estilete copulador acanalado; pd: pericardioducto; sd: conducto de desove; sr: receptáculo seminal.

mass of epidermal gland cells surrounded by a cuticular layer (Fig. 2J). Under the epidermis there is a matrix (55 μm thick, reaching 100–150 μm under the mid-dorsal keel) as a pale-staining layer of background substance traversed by muscle fibres and by numerous lacunae containing hemocytes. The dorsoventral bundles of musculature are weak and not related to the external body folds, which are exclusively cuticular. Calcareous mantle sclerites comprise seven different types (Fig. 2D–I) having an oblique insertion in one cuticular layer. Short harpoon-shaped bodies (65–75 μm long) are present along the mid-dorsal keel, leaning 70° a 90°, pointing in all directions. There are three different types of excavate scales, including two types of striated excavate scales with blunt apex and rimmed basal and lateral edges: predominant small and wide scales (20–31 μm long; 10–12 μm wide), a rim which is broad at base, narrow on both sides, and not extending in the distal region of the scale; a second type of large, straight and narrow scales (30–45 μm long; 7–11 wide) with a rim of constant width. The third type of excavate scales have a pointed apex, a rim along their entire edge and a pair of lateral laminar expansions towards the concave part of the scale (50–60 μm long; 10–13 μm wide); they are inserted along the mid-dorsal keel at right angles or slightly inclined and directed in all directions. With two types of paddle-shaped scales: small (35–40 μm long), thin and curved paddle-shaped scales present in the ventral and lateral walls of the body; large paddle-shaped

scales (70–80 μm long) with wide distal part and irregular outline, distributed in dorsal and lateral parts of the body and quite abundant close to the mid-dorsal keel. Finally, one type of blade scale-shaped scales (32–38 μm high; 10–13 μm wide) inserted at both sides of the pedal groove.

Pedal pit and pedal groove: The single pedal fold starts in a long pedal pit (300 μm long; 150 μm high; 150 μm wide) which has numerous long cilia; is connected with the outside of the body by a wide opening. Pedal groove (175 μm high; 100 μm wide) with a single ciliated fold (150 μm high; 100 μm wide) extending to the ventroanterior pouch of the pallial cavity. Voluminous and follicular anterior pedal glands open frontally and laterally into the pedal pit; the glands occupy anteriorly the entire visceral space between the digestive system and the matrix, up to the cerebral ganglia (Figs. 3A, 4A–C). Small posterior pedal glands dorsally opening into the pedal pit as well as laterally along the entire pedal groove.

Pallial cavity: Pallial cavity (780 μm long; 650 μm high; 550 μm wide) with a broad subterminal opening. In their posterior region, ten respiratory folds are radially arranged (Figs. 3B). Anteriorly, the pallial cavity is divided by a glandular genital cone into two areas: a dorsal one into which the rectum opens, and a ventral one that forms a ventroanterior pouch which receives the opening of the sheaths of the copulatory stylets (Fig. 5G–I). The spawning ducts open pairwise through the genital cone. It shows pallial glands on the genital cone and around the anterior region of the ven-

(Right page) Figure 2. *Hemimienia rugosa* n. sp. A: *habitus*, lateral view; B: detail of dorsal body region, showing the well-developed mid-dorsal keel and the deep cuticular wrinkles; C: detail of the mid-dorsal keel showing the disposition of the short harpoon-shaped sclerites; D: drawing of the sclerite types (I: short harpoon-shaped sclerite; II: small and excavate scale with the basal and lateral rims reinforced; III: narrow and slender excavate scale the basal and lateral rims reinforced; IV: excavate scales distally pointed, basally and laterally reinforced and with a pair of laminar extension; V: large paddle-shaped scale; VI: small paddle-shaped scale; VII: foot-groove scales); E–I: SEM micrographs of different sclerite types (E: type I; F: type II; G: type III; H: type V; I: type VI); J: cross-section through the mid-dorsal keel. Abbreviations, cu: cuticle; gl: glandular mass of the mid-dorsal keel; gk: groove of the mid-dorsal keel.

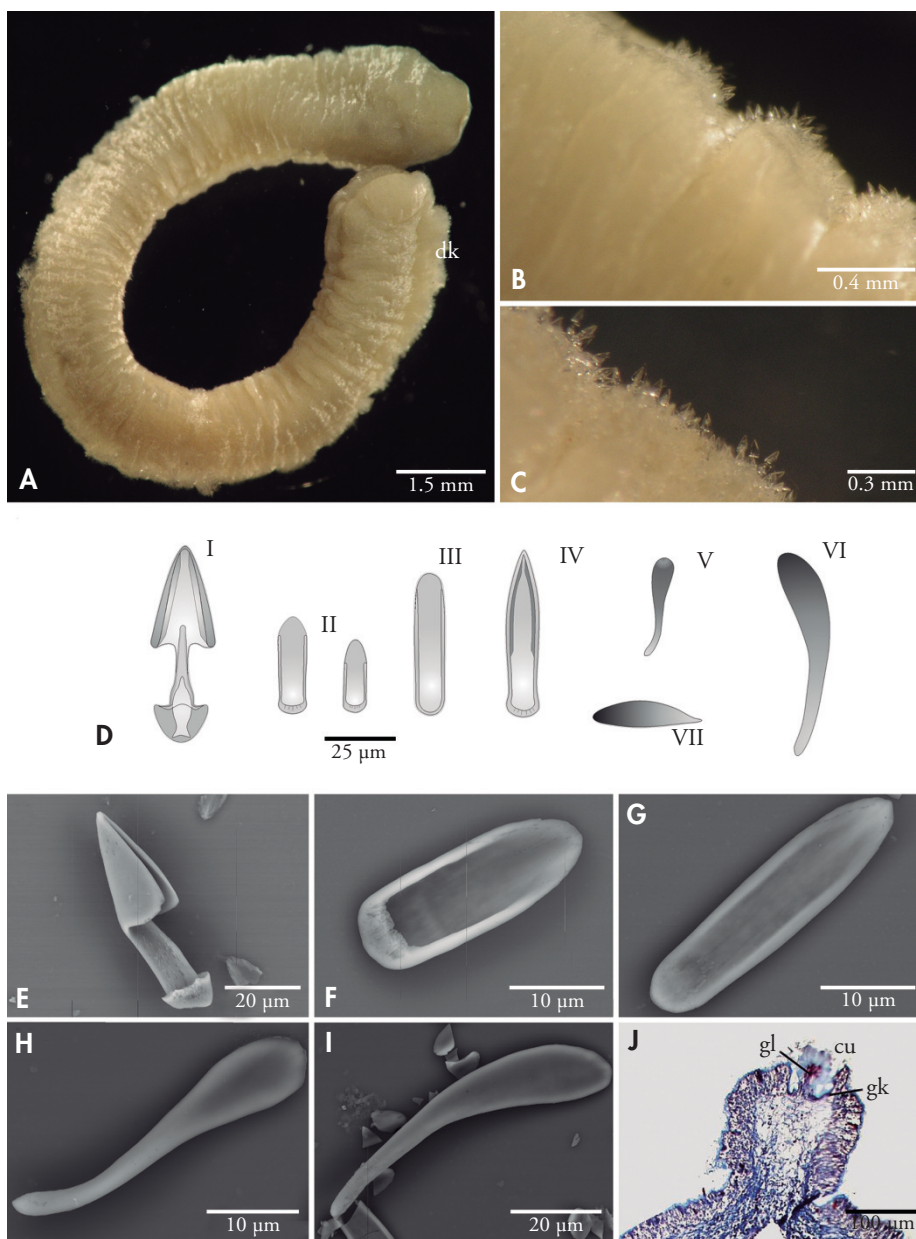


Figura 2. *Hemimenia rugosa* n. sp. A: habitus, vista lateral; B: detalle de la región dorsal donde se observa la quilla mediodorsal bien desarrollada y los profundos pliegues cuticulares; C: detalle de la disposición de los escleritos en forma de arpón sobre la quilla mediodorsal; D: dibujo de los tipos de escleritos (I: esclerito en forma de arpón corto; II: escama excavada pequeña con el borde basal y lateral reforzado; III: escama excavada estrecha y alargada con el borde basal y lateral reforzado; IV: escama excavada, apuntada distalmente, con refuerzo basal y lateral y un par de extensiones laminares; V: paletas grandes; VI: paletas pequeñas; VII: escama del surco pedio); E-I: micrografía al MEB de diferentes tipos de escleritos (E: tipo I; F: tipo II; G: tipo III; H: tipo V; I: tipo VI); J: corte en sección de la quilla medio dorsal. Abreviaturas, cu: cutícula; gl: masa glandular de la quilla medio dorsal; gk: de la quilla medio dorsal.

troanterior pouch of the pallial cavity. There is also one bundle of four pre-pallial spines (200 μm long; 30 μm high; 60 μm wide) into a shallow ventroanterior pouch on both sides of the pedal groove (Figs. 3B, 5K).

Nervous system and sense organs: Unpaired cerebral ganglion (185 μm long; 110 μm high; 300 μm wide) placed above the anterior region of the pharynx. Several pairs of atrial nerves emerging from anterior region of the cerebral ganglion. Main connectives with separate origin. Short cerebro-lateral connectives leave ventrolaterally from the posterior region of the cerebral ganglion to connect with the first lateral ganglia (90 μm long; 115 μm high; 50 μm wide). The lateral nerve cords (25 μm diameter) run medially and are regularly provided with ganglia of 100 μm diameter; the last pair or lateral ganglia are voluminous (200 μm long; 125 μm high; 65 μm wide) and connected by a short and wide supra-rectal loop (80 μm long; 250 μm wide). Cerebro-buccal connectives 17 μm in diameter; buccal ganglia laterally placed to the anterior region of the pharynx and interconnected by a slender commissure. Ventral ganglia (150 μm long; 100 μm high; 80 μm wide) are located ventrolaterally to the middle region of the pharynx, connected each other by a thin commissure (2.5 μm in diameter). The ventral nerve cords (25 μm diameter) originate in the ventral ganglia and run to the posterior body, where they end shortly anterior to the terminal end of the foot without forming a distinct terminal ganglia. The atrial sense organ occupies the posterior region of the

atrio-buccal cavity, has an internal cuticular layer (7 μm thick) and is delimited anteriorly by a horseshoe-shaped ciliary tract that does not extend posteriorly. It shows numerous long and wide simple atrial papillae (70 μm long; 10 μm wide) (Fig. 4A). No dorso-terminal sense organ could be discerned.

Digestive system: The atrio-buccal cavity opens terminally. The mouth lies in the atrio-buccal cavity and leads into the foregut. Pharyngeal epithelium is cuticularized and longitudinally folded throughout. There are three pharyngeal regions of markedly different dimensions and features (Fig. 4). Anterior region has a thick wall which is more developed latero-dorsally and latero-ventrally, generating a pharyngeal lumen cruciform (Fig. 4D). This wall includes a thin epithelium enveloped by a broad layer of circular and longitudinal muscular fibres (250 μm max. thick) and extraepithelial glandular cells (with granules of basic and acid secretion) that open into the lumen of the pharynx (Fig. 4B–C). Medial pharyngeal region has an oblique and wide ring of circular fibres (150 μm thick) which are compressing laterally the lumen of the pharynx (13 μm wide), a thin epithelium and a dense thick envelope of extraepithelial gland cells (125 μm wide) filled of granules of basic secretion (Fig. 4D–G). Posterior pharyngeal region has an oval and wide lumen (70 μm high; 60 μm wide), a thin epithelium (35 μm wide) and a moderate layer of both circular musculature and bottle-shaped extraepithelial gland cells (100 μm wide) less dense than in ante-

(Right page) Figure 3. *Hemimenia rugosa* n. sp., organization of the anterior (A) and posterior body (B). Abbreviations, ac: atrio-buccal cavity; acs: acicular copulatory stylet; ago: anterior gonadal sack; ap: atrial papillae; apg: anterior pedal gland; aph: anterior pharyngeal region; cg: cerebral ganglion; csg: copulatory stylet gland; gcs: gutter-like copulatory stylet; gp: gonopericardioduct; he: heart; lg: lateral ganglion; ma: matrix; mg: midgut; mgs: midgut sack; mn: mantle; mo: mouth; mph: medial pharyngeal region; mr: muscular ring; oe: oesophagus; pa: pallial cavity; pb: proboscis; pc: pericardium; pd: pericardioduct; pg: pharyngeal glands; pgo: posterior gonadal sack; pp: pedal pit; ppg: posterior pedal glands; pph: posterior pharyngeal region; ps: pre-pallial spines; re: rectum; rf: respiratory fold; sc: supra-rectal commissure; sd: spawning duct; so: oesophageal sphincter; sr: seminal receptacle; vp: ventroanterior pouch of the pallial cavity.

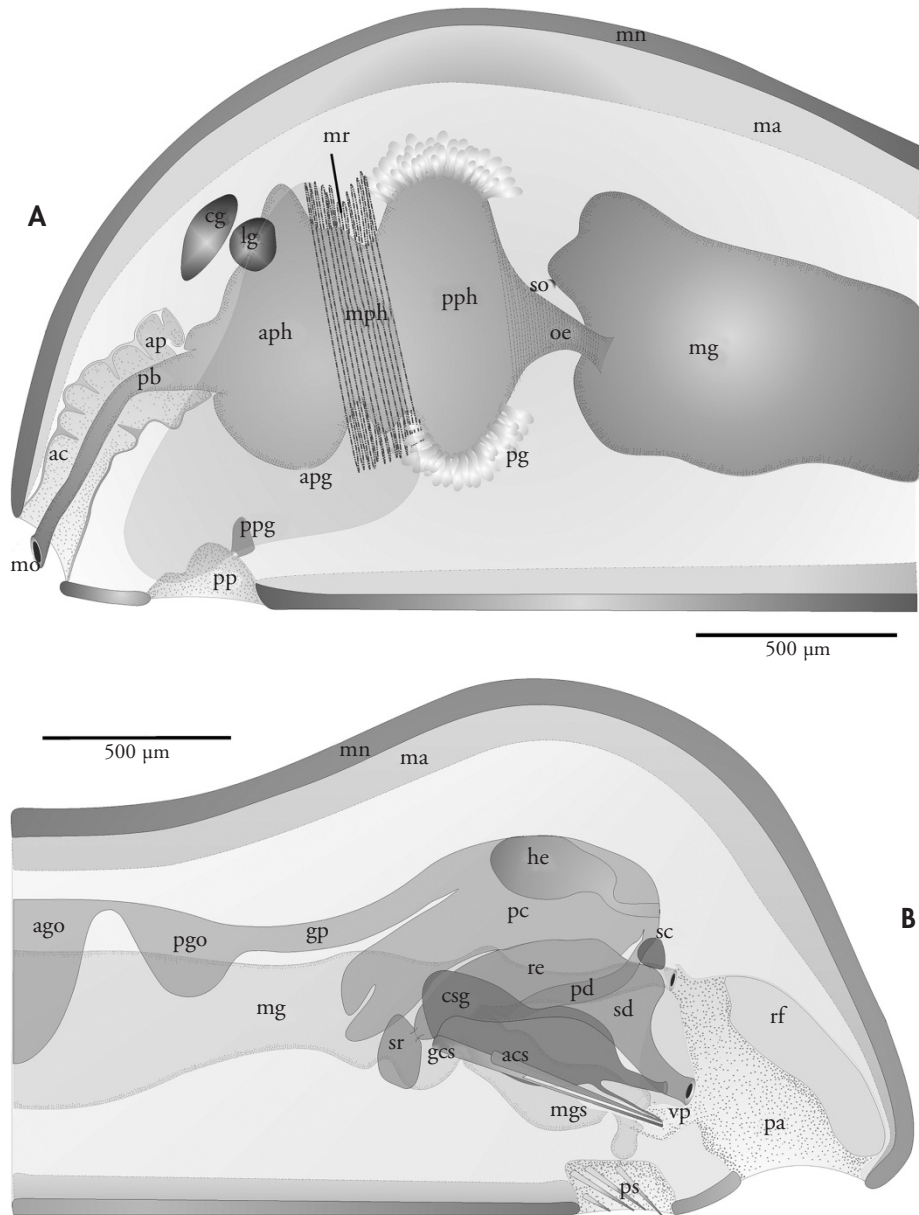


Figura 3. *Hemimenia rugosa* n. sp., organización de la parte anterior (A) y posterior (B) del cuerpo. Abreviaturas, ac: cavidad atriobucal; acs: estilete copulador acicular; ago: saco gonadal anterior; ap: papilas atriales; apg: glándula pedia anterior; aph: región faríngea anterior; cg: ganglio cerebral; csg: glándula del estilete copulador; gcs: estilete copulador acanalado; gp: gonopericardioducto; he: corazón; lg: ganglio lateral; ma: matriz; mg: intestino; mgs: saco intestinal; mn: manto; mo: boca; mph: región faríngea media; mr: anillo muscular; oe: esfago; pa: cavidad paleal; pb: probóscide; pc: pericardio; pd: pericardioducto; pg: glándulas faríngea; pgo: saco gonadal posterior; pp: foseta pedia; ppg: glándulas pedias posteriores; pph: región faríngea posterior; ps: espinas prepaliales; re: recto; rf: pliegues respiratorios; sc: comisura suprarrectal; sd: conducto de desove; so: esfínter esofágico; sr: receptáculo seminal; vp: bolsa ventroanterior de la cavidad paleal.

rior region. Here there are two types of extraepithelial pharyngeal glands: of mucus acidic secretion (in blue) and of basic secretion (in red) (Fig. 4H). There is no vestige of radular apparatus. The oesophagus is long and narrow with a strong sphincter (Fig. 4I); it also shows extraepithelial glands of basic secretion. The oesophagus opens frontally into a voluminous midgut (600 μm high; 300 μm wide) that shows a mid-dorsal ciliated tract. The midgut lacks anterodorsal caecal and serial constrictions but posteriorly gives rise to a pair of ventroposterior sacs that reach the anterior region of the pallial cavity; the sacs are ventrolaterally located to the spawning ducts and partially wrapping the copulatory stylets, except distal parts (Figs. 3B, 5D–F). A narrow ciliated rectum opens through the anus into the short dorsoanterior region of the pallial cavity (Fig. 3B).

Circulatory system: The ventricle (200 μm high; 180 μm wide) is attached to the dorsal wall of the anterior pericardium. The auricle is narrow (80 μm diameter) and unpaired, extends freely through pericardium and continues with the posterior sinuses related to the respiratory folds. The dorsal sinus (60 μm high; 90 μm wide) runs, in continuation of the ventricle, above the gonopericardioducts, gonads and midgut. There are numerous small sanguineous sinuses through the matrix.

Reproductive system: Gonads divided into two longitudinal sacs (Fig. 3B): a large anterior one contains oocytes in different stages of development (Figs. 3B, 5A–B) and a short and narrow posterior one with oocytes in the lateromedial walls and spermatozooids in the rest of the spaces. Size of oocytes in gonads up to 75 μm in diameter and showing a nucleus of 30 μm in diameter, a small nucleolus and many granules of vitellus in the cytoplasm. Sperm have a medium size of 60 μm in length. Gonads connecting to frontal pericardium via pair of gonopericardioducts (120 μm high; 60 μm wide) which are filled with spermatozooids. Voluminous pericardium (900 μm long; 380 μm

high; 300 μm wide) is also containing spermatozooids. The anterior region of the pericardium forms two pairs of frontal pouches (Figs. 3B, 5C). The pericardioducts have an oval outline in transverse section, slightly compressed laterally, and are provided mid-dorsally with a ciliary epithelium. They leave the pericardium posterolaterally and run anterolaterally to connect with the distal region of the spawning ducts. At this position, a seminal receptacle is located on each side as a prolongation of the spawning ducts; each seminal receptacle consists on a globular-shaped body (150 μm long; 170 μm high; 230 μm wide) filled with spermatozooids and a short, narrow and curved stalk (Figs. 3B, 5C). The voluminous spawning ducts (260 μm high; 240 μm wide) are paired throughout and open ventrally into the pallial cavity through a common glandular cone, posterior to the beginning of ventroanterior pouch of the pallial cavity. The spawning ducts have a columnar and glandular epithelium of basic secretion (Figs. 3B, 5E–H). The copulatory apparatus consist of two pairs of copulatory stylets with glands. They are located ventrolaterally to the spawning ducts and open into the ventroanterior pouch of the pallial cavity (Fig. 5B). Each pair of stylets includes: a dorsal acicular element; and a ventral element, that is gutter-shaped distally and acicular proximally (Figs. 3B, 5F–I). Styles provided throughout with their own sheath, and distally with a common sheath for each pair that is composed by epithelium of the pallial cavity. Furthermore, each pair of copulatory stylets has associated a voluminous and globular gland (300 μm high; 200 μm wide) with a columnar and glandular epithelium of acidic secretions (Fig. 5D–I). The copulatory stylet glands run ventrolaterally to the spawning ducts and show a double connection: opening into the posterior region of the spawning ducts, just before the opening of the secondary genital orifices into the pallial cavity; and also connecting with the distal part of the sheath of the copu-

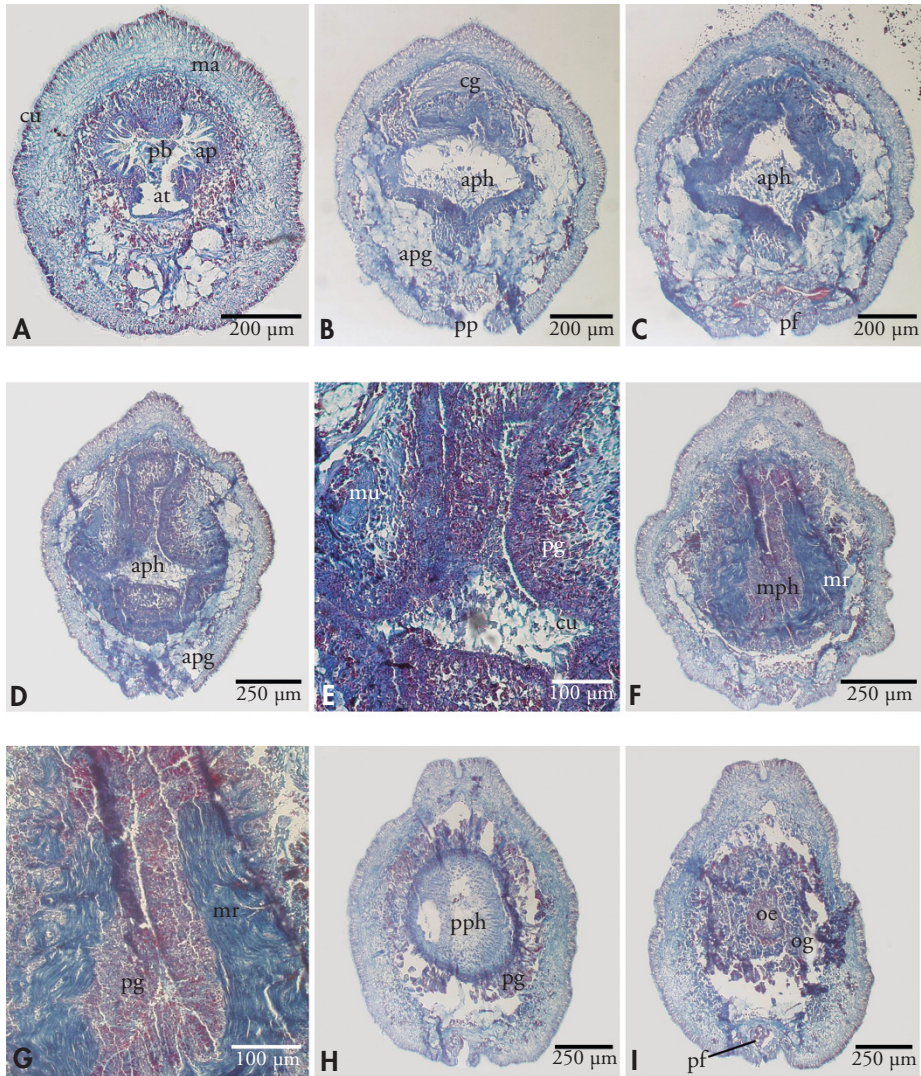


Figure 4. *Hemimenia rugosa* n. sp., body cross-sections. A: atribuccal cavity; B, C: beginning of the anterior region of the pharynx; D, E: details of the structure of the anterior region of the pharynx; F, G: middle region of the pharynx; H: posterior pharynx; I: oesophageal region. Abbreviations, ap: atrial papillae; apg: anterior pedal gland; aph: anterior pharyngeal region; at: atrium; cg: cerebral ganglion; cu: cuticle; ma: matrix; mph: medial pharyngeal region; mr: muscular ring; mu: musculature; oe: oesophagus; og: oesophagus glands; pb: proboscide; pf: pliegue pedio; fold; pg: pharyngeal glands; pp: pedal pit; pph: posterior pharyngeal region.

Figura 4. *Hemimenia rugosa* n. sp., cortes transversales. A: cavidad atribuccal; B, C: comienzo de la región anterior de la faringe; D, E: detalles de la estructura de la región anterior de la faringe; F, G: región media de la faringe; H: faringe posterior; I: región del esófago. Abreviaturas: ap: papilas atriales; apg: glándula pedia anterior; aph: región faríngea anterior; at: atrio; cg: ganglio cerebral; cu: cutícula; ma: matriz; mph: región faríngea media; mr: anillo muscular; mu: musculatura; oe: esófago; og: glándulas esofágicas; pb: proboscide; pf: pliegue pedio; pg: glándulas faríngeas; pp: foseta pedia; pph: región faríngea posterior.

latory stylets by means of a narrow duct (Figs. 3B, 5H).

Taxonomic remarks: The examined specimen is classified within the order Neomeniomorpha Salvini-Plawen, 1978, on the basis of having several types of solid sclerites and a copulatory apparatus that includes two pair of copulatory stylets and associated glands, but lacking ventrolateral foregut glands (SALVINI-PLAWEN, 1978; GARCÍA-ÁLVAREZ AND SALVINI-PLAWEN, 2007). It shows the main diagnostic characters of *Hemimenia* Nierstrasz, 1902: sclerites mainly of scales and solid spicules, including short harpoon-shaped bodies; common atriobuccal cavity; without radula; and presence of respiratory folds (NIERSTRASZ, 1902; SALVINI-PLAWEN, 1978, 2006; GARCÍA-ÁLVAREZ AND SALVINI-PLAWEN, 2007). So far, five species of the genus *Hemimenia* are known (GARCÍA-ÁLVAREZ AND SALVINI-PLAWEN, 2007). Three of these species inhabit east-Atlantic bottoms and were originally described in the Galician waters: *Hemimenia atlantica* Salvini-Plawen, 2006 from Azores Islands to A Quiniela Bank off Galicia (Galicia, NW Spain) at 752–1240 m; *Hemimenia glandulosa* Salvini-Plawen, 2006 from Galicia Bank (NW Spain) at 760–769 m; and *Hemimenia cyclomyata* Salvini-Plawen, 2006, from Galicia Bank and Artabro Gulf (Galicia, NW Spain) at 760–1191 m (SALVINI-PLAWEN, 2006; GARCÍA-ÁLVAREZ ET AL., 2014; this report). *Hemimenia rugosa* n. sp. differs from all of them by its unique *habitus*, its large body size (Table I), its sclerites, by the presence of simple atrial papillae instead of grou-

ped, by the absence of a dorsoterminal sense organ and by the configuration of its midgut, lacking serial constrictions but showing a pair of ventroposterior sacs that envelope the copulatory stylets. We report herein, for the first time, the presence of ventroposterior midgut sacs in *Hemimenia*, previously known in other taxa of Neomeniomorpha (*Archaeomenia prisca* Thiele, 1906 and three species of *Neomenia* Tullberg, 1875) and in the species *Imeroherpia laubieri* Handl, 2002 of the Order Sterrofustia (THIELE, 1906; HANDL, 2002; SALVINI-PLAWEN, 2004, 2006).

With respect to *H. cyclomyata*, *Hemimenia rugosa* n. sp. differs also by having an oesophageal sphincter, pallial glands and a ventroanterior pouch in the pallial cavity (SALVINI-PLAWEN, 2006; GARCÍA-ÁLVAREZ ET AL., 2014; present report). From *H. glandulosa* and *H. atlantica*, the new species differs by having the peculiar structure of the mid-dorsal keel, a thinner matrix, a long proboscis, the pharynx with three regions (two in *H. glandulosa* and *H. atlantica*), an oesophagus, a genital cone, two genital orifices instead of one, and a great number of respiratory folds, and by the absence of suprapallial glands and seminal vesicles. In addition, *H. atlantica* shows a special configuration of the final region of the spawning duct forming an unpaired duct which is absent in *Hemimenia rugosa* n. sp. (SALVINI-PLAWEN, 2006; GARCÍA-ÁLVAREZ ET AL., 2014). For more comparative details with other taxa of the genus see Table I, where the main characteristics of the species of *Hemimenia* are summarized.

(Right page) Figure 5. *Hemimenia rugosa* n. sp., body cross sections. A, B: anterior bags of the gonads with oocytes; C: seminal receptacles and gonopericardioducts, both with spermatozoa; D: beginning of the midgut sacks; E: middle region of the spawning ducts and copulatory stylet glands; F: copulatory stylets enveloped by the midgut sacks; G: posterior region of the spawning ducts; H, I: connexion of the copulatory stylets glands with the posterior region of the spawning ducts. Abbreviations, acs: acicular copulatory stylet; ago: anterior gonadal sacks; cs: copulatory stylets; csg: copulatory stylet gland; gcs: gutter-like copulatory stylet; gp: gonopericardioduct; he: heart; mg: midgut; mgs: midgut sack; oc: oocyte; pc: pericardium; pd: pericardioduct; pe/ps: pre-pallial spines; re: rectum; sd: spawning duct; sr: seminal receptacle; vp: ventroanterior pouch of the pallial cavity.

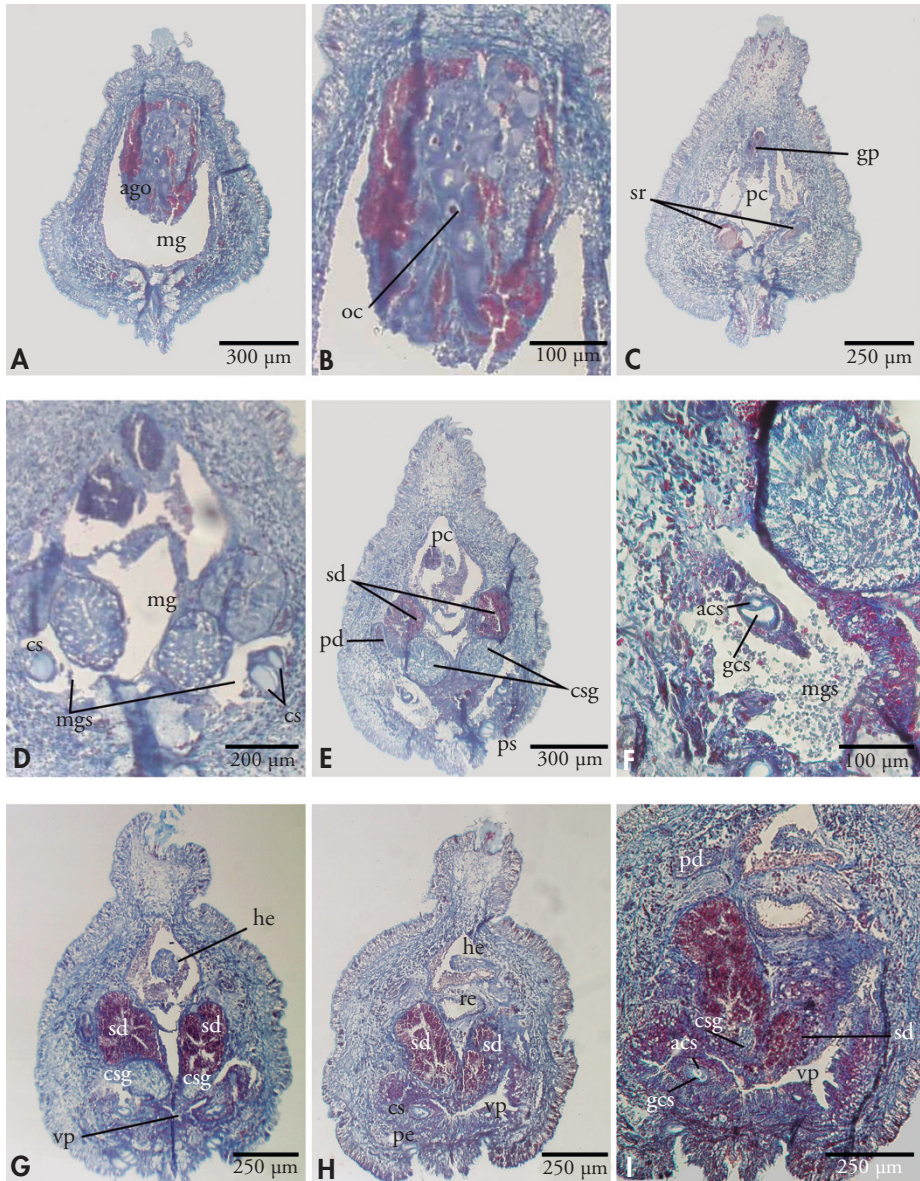


Figura 5. *Hemimenia rugosa* n. sp., cortes transversales. A, B: bolsas de la gónada anterior con oocitos; C: receptáculos seminales y gonopericardioductos, con espermatozoides; D: comienzo de los sacos intestinales; E: región media de los conductos de desove y glándulas de los estiletes copuladores; F: sacos intestinales envuelven a los estiletes copuladores; G: región posterior de los conductos de desove; H, I: conexión de las glándulas de los estiletes copuladores con la región posterior de los conductos de desove. Abreviaturas, acs: estilete copulador acicular; ago: saco gonadal anterior; cs: estiletes copuladores; csg: glándula del estilete copulador; gcs: estilete copulador acanalado; gp: gonopericardioducto; he: corazón; mg: intestino; mgs: saco intestinal; oc: oocito; pc: pericardio; pd: pericardioducto; pels: espinas prepaliales; re: recto; sd: conducto de desove; sr: receptáculo seminal; vp: bolsa ventroanterior de la cavidad paleal.

Table I. Comparison of the species of de genus *Hemimenia* Nierstrasz, 1902. (+ present; - absent; ? unknown; 1 according to SALVINI-PLAWEN, 2006).

	<i>H. intermedia</i>	<i>H. dorsosulcata</i>	<i>H. cyclomyata</i>
Distribution	Indonesia	Subantarctic Pacific	Galicia (NW Spain)
Maximum length	14 mm	30 mm	7.6 mm
Sclerite types	3	3	6
Mid-dorsal keel	+ with pouches	-	+ complex
Latero-ventral keels	-	-	-
Matrix	?	+	+
Atrial papillae	in groups	paired	in groups
Pedal fold	20	10-14	10-24
Pedal fold into pallial cavity	-	-	+
Proboscis	-	-	+
Pharyngeal regions	1	2	3
Epithelial pharyngeal glands	-	+	-
Subepithelial pharyngeal glands	+	+	+
Oesophagus	-	-	+
Sphincter oesophagus	-	-	-
Anterodorsal midgut caecum	+ long	+ short	-
Constriction midgut	+	+	+
Ventroposterior midgut sacs	-	-	-
Seminal vesicles	+	-	-
Seminal receptacles	+	+	+
Genital cone	-	-	+
Genital orifice	1	2	2
Genital orifice position in the pallial cavity	ventroanterior pouch	ventroanterior pouch	ventral
Length copulatory stylets regarding spawning duct	long	long	long
Length copulatory stylet glands regarding spawning duct	wide and long	wide and long	wide and long
Connection copulatory stylet glands	double	double	double
Pallial glands	-	-	-
Suprapallial glands	+	-	-
Prepallial spines	6-10 pairs	7 pairs	6 pairs
Dorsoterminal sense organ	-	+	+

Hemimenia tripla n. sp. (Figs. 6–8)

Type material: Holotype from NW Galicia (NW Spain). Station DIVA-ARTABRIA I/2002 AT-1000 (43°57.00'N; 08°54.79'W – 43°57.25'N; 08°54.13'W), on a bottom of stones and dead corals, at 1132–1191 m, adult, 7.6 mm long (Fig. 6A–B) sectioned in 2 µm wide cross-sections and mounted on slides (sixty slides), two slides of sclerites. Paratype, collected with holotype, adult, 8 mm long, sectioned in 5 µm wide cross-sections and mounted on slides (seven slides), sclerites on two slides. The holotype and paratype are deposited in the Museo de Historia Natural da Universidade de Santiago de Compostela (Spain), numbers MHNUSC 10053 and MHNUSC 10054 respectively.

Etyymology: The specific epithet, “*tripla*”, is a Latin adjective referred to the triple connection of the copulatory stylet glands.

Diagnosis: With mid-dorsal keel of complex structure and each side latero-ventral keels of simple structure. Cuticle

thin (8–10 µm). Without epidermal papillae. Matrix thin (50–150 µm). Mantle sclerites of seven types, includ-

Tabla I. Comparación de las especies del género *Hemimenia* Nierstrasz, 1902. (+ presente; - ausente; ? desconocido; ¹según SALVINI-PLAWEN, 2006).

<i>H. atlantica</i>	<i>H. glandulosa</i>	<i>H. rugosa</i> n. sp.	<i>H. tripla</i> n. sp.	<i>H. nanodoryata</i> n. sp.
Azores Island and Galicia (NW Spain)	Galicia (NW Spain)	Galicia (NW Spain)	Galicia (NW Spain)	Galicia (NW Spain)
3-5 mm	3 mm	18 mm	8 mm	6.4 mm
5	4	7	7	9
+ simple	+ simple	+ complex	+ complex	+ complex
-	-	-	+	-
+	+	+	+	+
in groups	in groups	simple	in groups	in groups
6-7	4	10	9-10	9
+1	-	+	-	-
+	-	+	+	+
2	2	3	3	3
-	-	-	-	-
+	+	+	+	+
-	-	+	-	+
-	-	-	-	+ short
+	+	-	-	+
-	-	+	+	+ short
+	+	-	-	-
+	+	+	+	-
-	-	+	+	-
1	1	2	2	2
ventroanterior pouch ¹ long	ventroanterior pouch long	ventral long	ventroanterior pouch long	ventroanterior pouch shorts
wide and long double	wide and long double	wide and long double	narrow and short triple	very narrow and very short double
+	+	+	+	-
+	+	-	-	-
5-10 pairs	7 pairs	4 pairs	4 pairs	-
+	+	-	+	-

ing two types of distally pointed excavated scales and with pair of laminar lateral expansions through the concave face. Anterior pedal glands voluminous. Single pedal fold not entering mantle cavity. Cerebral connectives separate. Atrial papillae bundled in groups up to five with same base. With narrow proboscis. Pharynx with three regions: a long anterior region; middle region with an oblique and strong muscular ring; posterior region short. Without oesophagus. Anterodorsal midgut caecum and midgut sacculations absent. With a pair of long ventroposterior midgut sacs sur-

rounding partially the copulatory stylets. Without seminal vesicles. Seminal receptacles at spawning ducts. Secondary genital opening pairwise into the ventroanterior pouch of the pallial cavity through a common genital cone. With pairs of two copulatory stylets with glands; copulatory stylets glands with three outlets. With nine to ten respiratory folds. Pallial glands around the ventroanterior pouch of the pallial cavity and the distal region of the spawning ducts. Without suprapallial glands. Paired bundle of four prepallial spines. With dorsoterminal sense organ.

Description: *Habitus*: The body is 7.6 to 8 mm long, by 1.2 to 1.4 mm wide at mid-body, 1 to 1.2 mm wide at posterior body. Both specimens have a strong mid-dorsal keel (0.2 mm high) and two small latero-ventral keels. The combination of these three keels determines a characteristic triangular cross-section of the body which is well marked on the anterior region, but becomes more circular in the body ends, where the keels do not reach. There are slightly marked cuticular wrinkles caused by the dorsoventral musculature. The body surface looks smooth except in the dorsal body region, where the sclerites protrude from the mid-dorsal keel; sclerites on the mid-dorsal keel is inserted at right angles or slightly leaning toward the posterior body region. The pedal pit and the pedal groove externally marked. The pallial cavity has sub-terminal opening. The body colour is iridescent white after fixation and preservation in 70° ethanol (Fig. 6A–B).

Mantle: The cuticle is 8–10 μm in thick. The epidermis is monostratified (10–15 μm thick) and lacks epidermal papillae but shows numerous glandular cells, especially on the mid-dorsal keel. There is a strong mid-dorsal keel and a mid-longitudinal groove with a circular epidermal gland mass wrap up by a cuticular layer. Latero-ventral keels small, narrow and of simple structure. Below the epidermis, there is a matrix of variable thickness which reaches up to 150 μm dorsally, 40 to 75 μm in average on the ventral and lateral areas of the anterior body, 75 to 125 μm on the posterior body. There are seven different types of sclerites arranged in two cuticular layers (Fig. 6C–H). Short harpoon-shaped bodies (45–60 μm long) restricted to the mid-dorsal keel, with a vertical insertion or slightly inclined toward the posterior body end. There are two types of excavate scales with a blunt apex and a basal and lateral rim, that are distributed on the lateral and ventral walls with an oblique arrangement, leaning on small angles and pointing posteriorly: predominant type, small and wide scales (31–40 μm long;

5–7 μm wide) with a blunt apex, and a rim which is thick at the base but thin laterally, not extending latero-distally; the second type including narrow and elongated scales (55–60 μm long; 7–10 μm wide) with a blunt apex and a rim of constant width; the third type, excavated scales, but with a pointed apex, a rim around the entire perimeter and a pair of laminar lateral expansions projected towards the concave side of the scale (50–70 μm long; 12–15 μm wide); they are inserted at right angles or slightly pointing towards the posterior body and restricted to the dorsal body region (especially over the mid-dorsal keel). It also show two types of paddle-shaped scales: small paddle-shaped scales (30–35 μm long; 5–7 μm wide) with a narrow recurved tail, that are located in the ventral and lateral body; and large paddle-shaped scales of irregular outline (90–105 μm long; width proximally 3–4 μm , distally 7.5–10 μm) are numerous dorsally, also present laterally and ventrally, pointing their distal ends towards the posterior body region. Furthermore, adjacent to the foot there are knife-blade scales (32–40 μm long; 10–11 μm wide).

Pedal pit and pedal groove: The pedal pit is long and wide (180 μm long; 110 μm high; 150 μm wide) with a ciliated dorsal wall that originates three ciliated folds: two wide and short lateral folds and a middle narrow fold that continues into the pedal groove, where they attain up to 80 μm height and 50 μm width. The dimension of the pedal groove increases toward the posterior part of the body (150 μm high; 90 μm wide); pedal fold ends before the opening of the pallial cavity. The anterior pedal glands are a pair of voluminous bunching follicles that open frontally and laterally into the pedal pit and extend dorsally up to the sides of the cerebral ganglion (Fig. 8B). There are also small epithelial posterior pedal glands along the lateral walls of the pedal groove (Fig. 8D).

Pallial cavity: The pallial cavity is spacious, of 450 μm long, 400 μm high and 300 μm wide. Large opening of

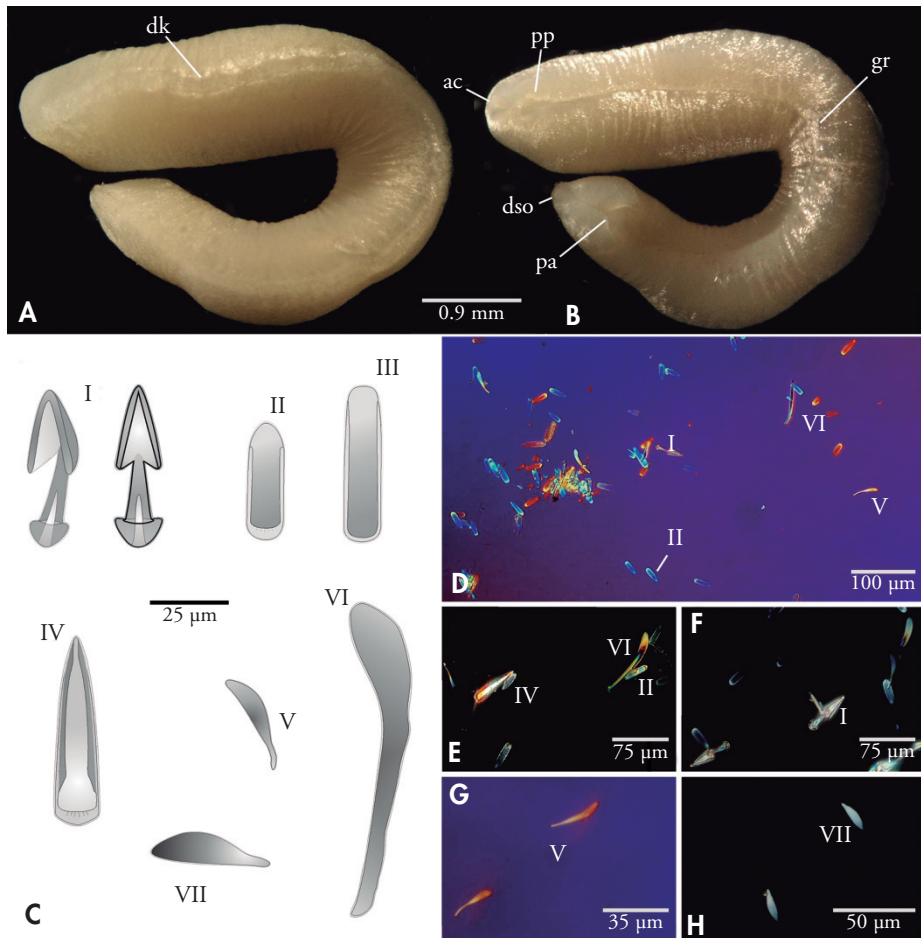


Figure 6. *Hemimenia tripla* n. sp. A-B. Habitus. A: dorsal view; B: ventral view; C: drawing of the sclerite types; D-H: optical microscope photographs of the sclerite types (I: short harpoon-shaped sclerite; II: small and excavate scale with the basal and lateral rims reinforced; III: narrow and slender excavate scale the basal and lateral rims reinforced; IV: excavate scales distally pointed, basally and laterally reinforced and with a pair of laminar extension; V: small paddle-shaped scale; VI: large paddle-shaped scale; VII: foot-groove scales). Abbreviations, ac: atrio Buccal cavity; dk: mid-dorsal keel; dso: dorsoterminal sense organ; gr: pedal groove; pa: pallial cavity; pp: pedal pit.

Figura 6. *Hemimenia tripla* n. sp. A-B. Habitus. A: vista dorsal view; B: vista ventral; C: dibujo de los tipos de escleritos; D-H: fotografías al microscopio óptico de los tipos de escleritos (I: esclerito en forma de arpón corto; II: escama excavada pequeña, con el borde basal y lateral reforzado; III: escama escavada estrecha y alargada con los bordes basal y lateral reforzados; IV: escama excavada distalmente, con refuerzo basal y lateral y con un par de extensiones laminares; V: paletas pequeñas; VI: paletas grandes; VII: escama del surco pedio). Abreviaturas, ac: cavidad atrio bucal; dk: quilla mediodorsal; dso: órgano sensitivo dorsoterminal; gr: surco pedio; pa: cavidad paleal; pp: foseta pedia.

pallial cavity ventrally placed, just anterior to posterior body end. The pallial cavity shows 9–10 respiratory folds in

the lateral and dorsal walls of its posterior region. Anterior region the pallial cavity is divided by a transverse septum

into two pouches: a short dorsal pouch where the rectum opens and a long ventroanterior pouch extending anteriorly up to the middle region of the spawning ducts (Fig. 7B). The ventroanterior pouch receives dorsally the opening of the spawning ducts and one of the ducts of each copulatory stylet gland and is latero-frontally continuous with the paired sheath of copulatory stylets. There are pallial glands around the ventroanterior pouch of the pallial cavity and the distal region of the spawning ducts but there are not suprapallial glands. At both sides of the posterior-most region of the pedal groove, before the opening of the pallial cavity, there are four prepallial spines (Figs. 7B, 8E–F).

Nervous system and sense organs: The cerebral ganglion unpaired (150 μm long; 130 μm high; 240 μm wide) located above the anterior region of the pharynx (Figs. 7A, 8B). Several atrial nerves are emerging from anterior region of the cerebral ganglion and running anteriorly. The cerebro-buccal connectives emerge laterally from the mid-ventral region of the cerebral ganglion and extending to the middle pharynx region, forming there the buccal ganglia (65 μm diameter), which are located laterally to the muscle ring of the pharynx (Fig. 7A). Long cerebro-lateral connectives leave ventrolaterally from the posterior region of the cerebral ganglion to connect with the first lateral ganglia (100 μm long; 80 μm high; 50 μm wide). The lateral cords (45 μm diameter) are running latero-dorsally below the matrix. The posteriormost lateral ganglia (150 μm long; 90 μm high; 55 μm wide) are connected by a thick suprarectal loop (20 μm wide) bellow the beginning of the pericardiioducts (Fig. 6B). The cerebro-ventral connectives emerging close to the cerebro-lateral connectives, but separated. The first ventral ganglia (120 μm long; 90 μm high; 60 μm wide) are located dorsally to the anterior region of the pedal groove and interconnected by two commissures (10 μm diameter). The ventral nervous cords are 30 μm thick. The atrial sense organ is delimited by a

horseshoe-shaped ciliated tract and bears numerous slender papillae (50–65 μm long; 10–12 μm wide) basally united in groups of up to five (Figs. 7A, 8A). A dorsoterminal sense organ is located in terminal position (Fig. 7B).

Digestive system: Narrow mouth with a thin sphincter opening into the common atriobuccal cavity; it leads to a narrow proboscis which is also provided by a narrow sphincter (Fig. 8A). Pharyngeal epithelium cuticularized and surrounded by a moderate layer of circular muscles. The pharynx is divided into three regions. A long anterior region (300 μm long) with a thin and folded epithelium which delimited a lumen that varies from strait and oval anteriorly (220 μm high; 200 μm wide) to X-shaped and high posteriorly (400 μm high). The middle pharyngeal region is characterized by the presence of an oblique and strong ring (110 μm width) of muscle fibres that constrict markedly the lumen of the pharynx (90–100 μm diameter) (Fig. 8C). The posterior pharyngeal region is short (50 μm long), has a thin epithelium of digitiform cells and a large lumen which is circular in cross-section (350 μm diameter). There is a thick coating of extraepithelial pharyngeal gland cells along the entire foregut; glands of spherical somata containing the nucleus and granules of secretion, and a narrow neck going through the muscular coat of the pharyngeal epithelium to open into the lumen of the pharynx. The glandular coat is more densely packed in the anterior pharynx, whereas posteriorly the glands increase in size and in number of secretion granules. The foregut opens frontally into the midgut, slightly narrowed (250 μm diameter). The midgut is lacking anterodorsal caecum and serial constrictions but posteriorly forming a pair of long ventroposterior sacs surrounding partially the copulatory stylets (Fig. 8D–I). The epithelium of the midgut is composed of digitiform digestive cells throughout and a mid-dorsal tract of ciliary cells posteriorly. The midgut was confluent with the ciliated rectum that is ventral to the pericardium

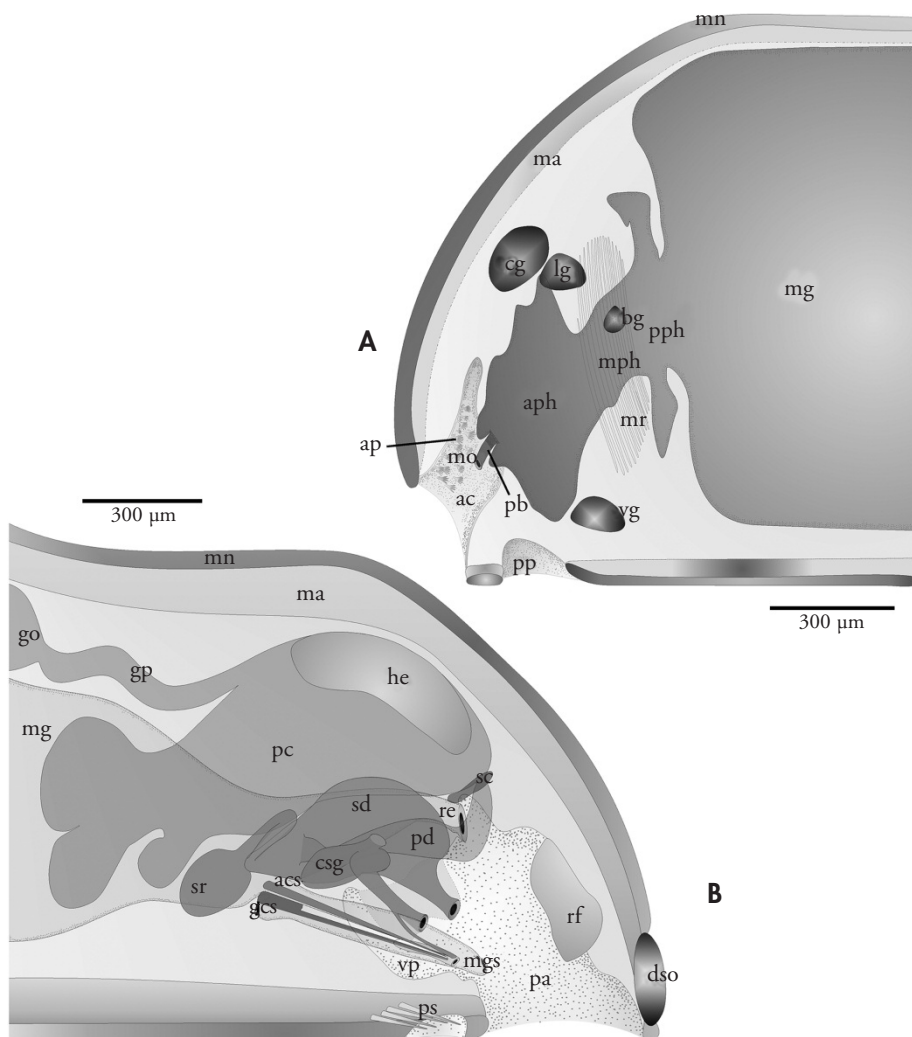


Figure 7. *Hemimenia tripla* n. sp., organization of the anterior (A) and posterior region (B). Abbreviations, ac: atriobuccal cavity; acs: acicular copulatory stylet; ap: atrial papillae; aph: anterior pharyngeal region; bg: buccal ganglion; cg: cerebral ganglion; csg: copulatory stylet gland; dso: dorsoterminal sense organ; gcs: gutter-like copulatory stylet; go: gonad; gp: gonopericardioduct; he: heart; lg: lateral ganglion; ma: matrix; mg: midgut; mgs: midgut sack; mn: mantle; mo: mouth; mph: medial pharyngeal region; mr: muscular ring; pa: pallial cavity; pb: proboscis; pc: pericardium; pd: pericardioduct; pp: pedal pit; ps: pre-pallial spines; pph: posterior pharyngeal region; re: rectum; rf: respiratory fold; sc: suprarectal commissure; sd: spawning duct; sr: seminal receptacle; vg: ventral ganglion; vp: ventroanterior pouch of the pallial cavity.

Figura 7. *Hemimenia tripla* n. sp., organización de la parte anterior (A) y posterior (B). Abreviaturas, ac: cavidad atriobuccal; acs: estilete copulador acicular; ap: papilas atriales; aph: región faríngea anterior; bg: ganglio bucal; cg: ganglio cerebral; csg: glándula del estilete copulador; dso: órgano sensitivo dorsoterminal; gcs: estilete copulador acanalado; go: gónada; gp: gonopericardioducto; he: corazón; lg: ganglio lateral; ma: matriz; mg: intestino; mgs: saco intestinal; mn: manto; mo: boca; mph: región faríngea media; mr: anillo muscular; pa: cavidad paleal; pb: proboscide; pc: pericardio; pd: pericardioducto; pp: foseta pedia; ps: espinas prepalliales; pph: región faríngea posterior; re: recto rf: pliegues respiratorios; sc: comisura suprarrrectal; sd: conducto de desove; sr: receptáculo seminal; vg: ganglio ventral; vp: bolsa ventroanterior de la cavidad paleal.

and the pericardioducts; rectum opens dorsally through the anus into the anterior pouch of the pallial cavity (Fig. 7B).

Circulatory system: The heart is consisting of ventricle and paired auricle. Muscularised ventricle (150 μm high, 50 μm wide) as an invagination of the pericardial roof; the auricles (80 μm high, 30 μm wide), partially fused, run free into the pericardium, connected with roof of pericardium only in posterior portion. The dorsal sinus (50 μm high; 70 μm wide) runs anteriorly in continuation of the heart, above the gonopericardioducts and gonads up to the pharynx. The ventral sinus (60 μm high; 100 μm wide) dorsally and laterally delimited by a muscular layer; it runs between the ventral nervous cords to arrive anteriorly up to the beginning of the pedal groove.

Reproductive system: The gonad is paired (100 μm long; 150 μm wide) not extending into anterior body; some spermatozoa (4–5 μm long) are in the lateral walls whereas the ova are in the lateral ones. The oocytes show a nucleus and a dense wrap, and increase in size posteriorly (up to 13 μm of diameter). Ciliated gonopericardioducts are narrow and oval in cross-section (340 μm long; 65 μm high; 55 μm wide), open dorsally into pericardium. Voluminous pericardium (780 μm long; 300 μm high; 420 μm wide) has three pairs of anterior pouches: dorsal, middle and ventral pouches (Fig. 7B). The posterior region of the pericardium narrows and continues in the pericardioducts (300 μm long; 75 μm high; 50 μm wide) which run antero-laterally to open laterally into the anterior region of the spawning ducts. No seminal vesicles are recognised, but pericardioducts have aggregations of sperm. A globular-shaped seminal receptacle (100 μm long; 85 μm high; 65 μm wide) opens into the anteriormost end of each spawning ducts through a narrow curved duct (Figs. 7B, 8D). Spawning ducts separated throughout, with high glandular epithelium and an oval cross-section (125 μm high; 150 μm wide); they are large anteriorly, becoming narrow towards the posterior end to open pairwise into the ventroanterior

pouch of the pallial cavity through a common genital cone (Figs. 7B, 8F–I). Two pair of copulatory stylets, each pair has a dorsal acicular element narrow distally (7.5 μm diameter medially) and a ventral stylet of gutter-shape distally to acicular proximally (19 μm high; 20 μm wide) (Figs. 7B, 8E–I). Each stylet is provided by a thin individual sheath throughout; furthermore there is a distal common sheath for each pair of stylets. The stylets are laterally placed to the ventroanterior pouch of the pallial cavity where they open (posterior to the genital cone) and extend up to the proximal region of the spawning ducts. The copulatory stylet glands are globular, shorter and narrower than the spawning ducts (100 μm long; 60 μm high; 85 μm wide). These glands are located ventrally to the spawning ducts and have a triple connection: with the spawning duct, with the copulatory stylets and with the pallial cavity. They open laterally into the middle region of the spawning duct and, via a ventroposterior duct distally bifurcated, lead into the ventroanterior pouch of the pallial cavity and connect distally with the copulatory stylets (Figs. 7B, 8E–I).

Taxonomic remarks: The organizations of the specimens at hand are characteristic for the genus *Hemimenia* (NIERSTRASZ, 1902; SALVINI-PLAWEN, 1978, 2006; GARCÍA-ÁLVAREZ AND SALVINI-PLAWEN, 2007). The triple connection of the stylets glands (with an extra duct that opens into the pallial cavity) is a relevant specific character that, together with the presence of a pair of latero-ventral keels, makes the proposed new species, *Hemimenia tripla* n. sp., easily distinguishable from the other species of the genus (Table I). A closer relationship between *H. rugosa* and *Hemimenia tripla* n. sp. is suggested because they share a similar set of sclerites, thin matrix, structure of the mid-dorsal keel, pharynx with three regions, ventroposterior midgut sacs and so on. In respect to *H. cyclomyata*, it differs by having an oesophagus, pallial glands and a ventroanterior pouch of the pallial cavity. From *H. glandulosa* and *H. atlantica* the

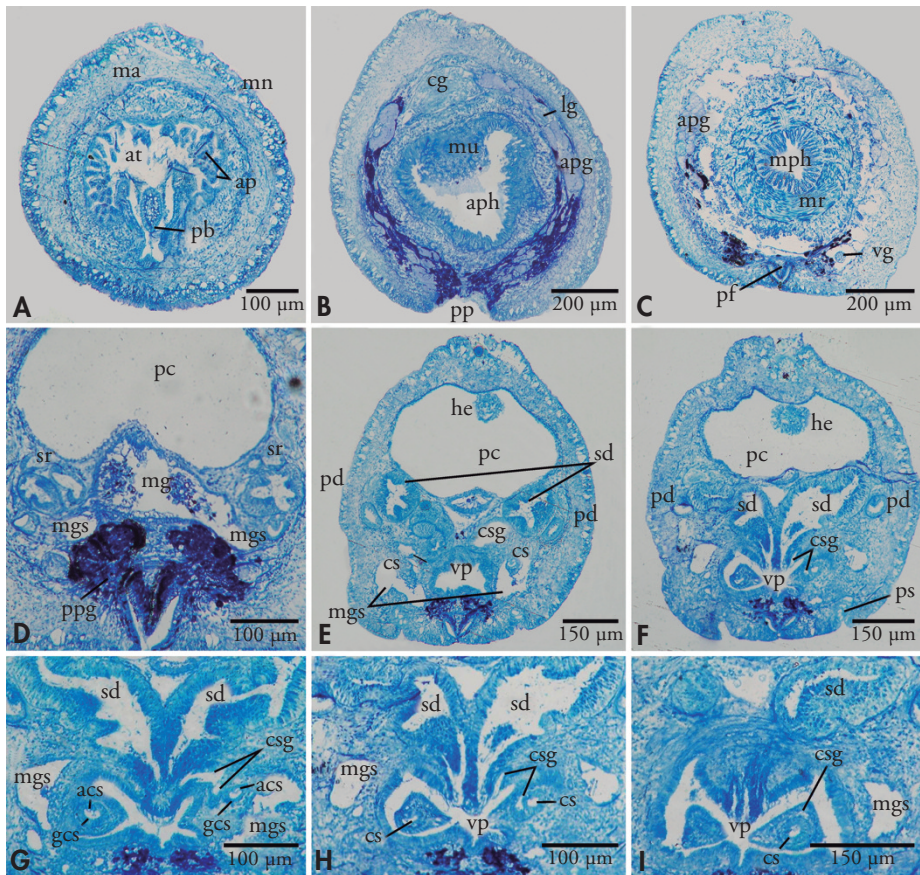


Figure 8. *Hemimenia tripla* sp. nov., body cross-sections. A: posterior region of the atriobuccal cavity showing the atrial papillae and the proboscis; B: anterior region of the pharynx; C: middle region of the pharynx with a strong muscle ring; D: beginning of the ventroposterior midgut sacks; E: section through the middle region of the spawning ducts; F: organization of the copulatory apparatus; G-I: connexion of the copulatory stylet glands with the ventroanterior pouch of the pallial cavity and with the distal part of the copulatory stylets. Abbreviations, acs: acicular copulatory stylet; ap: atrial papillae; apg: anterior pedal gland; aph: anterior pharyngeal region; at: atrium; cg: cerebral ganglion; cs: copulatory stylets; csg: copulatory stylet gland; gcs: gutter-like copulatory stylet; he: heart; lg: lateral ganglion; ma: matrix; mg: midgut; mgs: midgut sack; mph: pharyngeal middle region; mn: mantle; mr: muscular ring; mu: musculature; pb: proboscis; pc: pericardium; pd: pericardioduct; pf: pedal fold; pp: pedal pit; ps: pre-pallial spines; ppg: posterior pedal gland; sd: spawning duct; sr: seminal receptacle; vg: ventral ganglion; vp: ventroanterior pouch of the pallial cavity.

Figura 8. *Hemimenia tripla* sp. nov., cortes transversales. A: región posterior de la cavidad paleal mostrando las papilas atriales y la probóscide; B: región anterior de la faringe; C: región media de la faringe con un fuerte anillo muscular; D: comienzo de los sacos ventroposteriores intestinales; E: corte a través de la región media de los conductos de desove; F: organización del aparato copulador; G-I: conexión de las glándulas del estiletes copulador con la bolsa ventroanterior de la cavidad paleal y con la parte distal de los estiletes copuladores. Abreviaturas, acs: estilete copulador acicular; ap: papilas atriales; apg: glándula pedia anterior; aph: región faríngea anterior; at: atrio; cg: ganglio cerebral; cs: estiletes copuladores; csg: glándula del estilete copulador; gcs: estilete copulador acanalado; he: corazón; lg: ganglio lateral; ma: matriz; mg: intestino; mgs: saco intestinal; mph: región faríngea media; mn: manto; mr: anillo muscular; mu: musculatura; pb: probóscide; pc: pericardio; pd: pericardioducto; pf: pliegue pedio; pp: foseeta pedia; ps: espinas prepalliales; ppg: glándula pedia posterior; sd: conducto de desove; sr: receptáculo seminal; vg: ganglio ventral; vp: bolsa ventroanterior de la cavidad paleal.

present species differs in the structure of the mid-dorsal keel, by having a proboscis, a pharynx divided in three regions, a thinner matrix, a genital cone, two genital orifices instead of one, more respiratory folds, less abdominal

spicules and by lacking both suprapallial glands and seminal vesicles. Other specific difference with *H. atlantica* is the absence of a terminal unpaired duct of the spawning duct (SALVINI-PLAWEN, 2006; GARCÍA-ÁLVAREZ *ET AL.*, 2014).

Hemimenia nanodoryata n. sp. (Figs. 9–12)

Type material: Holotype from NW Galicia (NW Spain). Station DIVA-ARTABRIA I/2003 Cruise, station AT-1000 (43°53.847'N; 08°57.324'W – 43°54.621'N; 08°57.361'W), on a bottom of live and dead corals at 993–1004 m depth, adult (Fig. 9A–B) of 6.4 mm long. sectioned in 5 μ m wide cross-sections and mounted on slides (thirteen slides) and two slides of sclerites. The holotype is deposited in the Museo de Historia Natural da Universidade de Santiago de Compostela (Spain), number MHNUSC 10055.

Etymology: From greek: *nanus-*, very small; *dory*, spear; latin: *-ata*, provided with. Referring to the small size of the copulatory stylets.

Diagnosis: With mid-dorsal keel of complex structure, thin cuticle (7 μ m) and matrix, and lacking epidermal papillae. Mantle sclerites of nine types, including two types of pointed and excavated scales with a pair of lateral laminar expansions. Pedal fold ending before the opening of the pallial cavity. Cerebral connectives separated. Atrial papillae paired or bundled basally into up to four organs. Proboscis narrow. Pharynx with three regions: anterior region with a large lumen; middle pharyngeal region with an oblique and strong muscular ring; posterior pharynx with a thick coating of extraepithelial gland cells. Oesophagus with a thin anterior sphincter. With anterodorsal midgut caecum. The midgut has constrictions. With a pair of short ventro-posterior midgut sacs that is not surrounding the copulatory stylets. Without seminal vesicles. Without seminal receptacles. Spawning duct paired throughout opening pairwise into the ventroanterior pouch of the pallial cavity. Copulatory apparatus (glands and stylets) small; copulatory stylets gland with two outlets. With nine respiratory folds. Pallial and suprapallial glands absent. Without prepallial spines. Without dorsoterminal sense organ.

Description: *Habitus:* Bodies measure of 5.3 and 6.4 mm long by 0.75 and 0.88 mm wide at mid-body; 0.5 and 1.15 mm

wide anteriorly; 0.4 and 0.5 mm wide posteriorly (Fig. 10A), with a mid-dorsal keel (0.1 mm high) of trapezoid outline and many shallow cuticular wrinkles originated by the dorsoventral muscle bundles. The cross-section of the body is round anteriorly, becoming triangular posteriorly. The sclerites are obliquely inserted protruding slightly from the cuticle in the dorsal body region; lateral walls seem smooth. The pedal pit and pedal groove are externally marked. The pallial cavity has subterminal opening. The body colour is white after fixation and preservation in 70° ethanol (Fig. 9).

Mantle: The cuticle is thin (5–7 μ m thick). The epidermis (5–10 μ m wide) lacks papillae. Under the epidermis there is a relatively thin matrix (37–90 μ m) which reaches up to 150 μ m thickness under the mid-dorsal keel. The matrix is an unstructured layer stained in blue-grey where circular and longitudinal muscular fibres and blood sinuses and cells were recognized (SALVINI-PLAWEN 2006). The mid-dorsal keel is circular to trapezoidal in cross-section; the keel has a longitudinal groove that houses a circular mass of epidermal glandular cells of basic secretions enveloped by a cuticular layer. Nine types of sclerites are arranged in one cuticular layer (Fig. 10). Short harpoon-shaped bodies (40–65 μ m long) are restricted to the mid-dorsal keel and

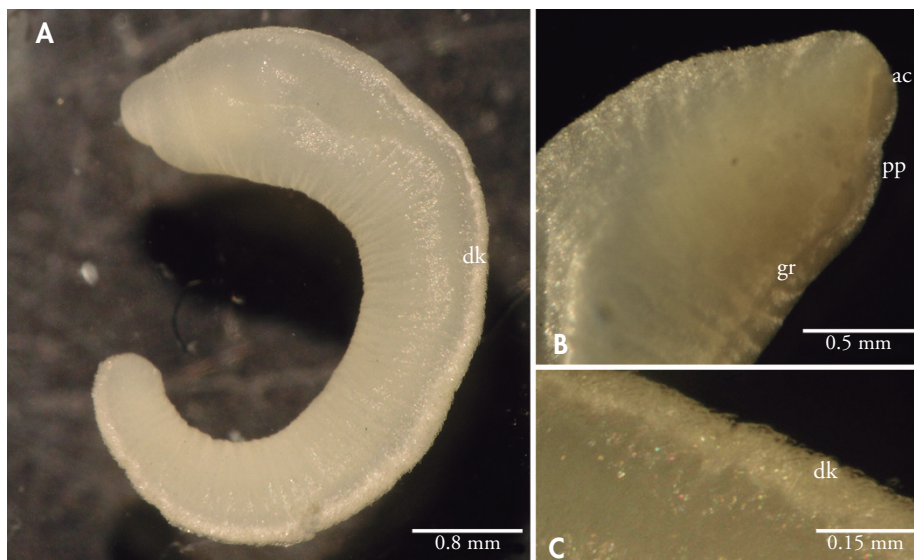


Figure 9. *Hemimenia nanodoryata* n. sp., habitus. A: lateral view; B: detail of anterior body region; C: detail of the mid-dorsal keel. Abbreviations, ac: atriobuccal cavity; dk: mid-dorsal keel; gr: pedal groove; pp: pedal pit.

Figura 9. *Hemimenia nanodoryata* n. sp., habitus. A: vista lateral; B: detalle de la región anterior del cuerpo; C: detalle de la quilla mediodorsal. Abreviaturas, ac: cavidad atriobuccal; dk: quilla mediodorsal; gr: surco pedio; pp: fosea pedia.

obliquely inserted forming angles of 45–70° with the surface of the body. There are two types of excavated and striated scales of blunt apex, rimmed basal and laterally and inserted on small angles with the body surface to nearly tangential: predominant, short and wide scales (25–45 μm long; 9–14 μm wide) with a broad basal rim but narrow laterally and variable in shape and size appearing in the lateral and ventral surface of the body; and long and narrow scales with a uniform rim reaching the distal end of the scales (40–50 μm long; 7.5–13 μm wide), abundant ventrally. With two types of excavate scales distally pointed, rimmed around their entire outline and with a pair of lateral laminar expansions towards the concave face of the scales, present in the mid-dorsal keel with oblique insertion forming angles of 45–70°: predominant, scales with a low-cut near to the base (50–65 μm long); and slightly larger scales (60–70 μm long), distally wider

than proximally and with a pair of broad and prominent laminar expansions. It also presents two types of paddle-shaped scales: small ones (38–50 μm long; 7.5–9 μm wide) present along the sides of the body, variable in shape, with a short blade and curved base, or with a long blade and a short and straight base; and paddle-shaped scales (80–150 μm long; 10–15 μm wide) inserted in the mid-dorsal keel forming angles close to 90°, less abundant laterally. There is one type of slender solid sclerites (55–60 μm long), and blade-shaped scales (75–88 μm long; 22–24 μm wide) in the margins of pedal groove, atriobuccal cavity and pedal pit.

Pedal pit and pedal groove: The ciliated pedal pit is large (300 μm long; 90 μm high; 60 μm wide) oval in cross section, with the small anterior and posterior pedal glands open in its dorsal part. The single pedal fold is originated in the longitudinal midline of the pedal pit, is oval in cross-section and ends before the

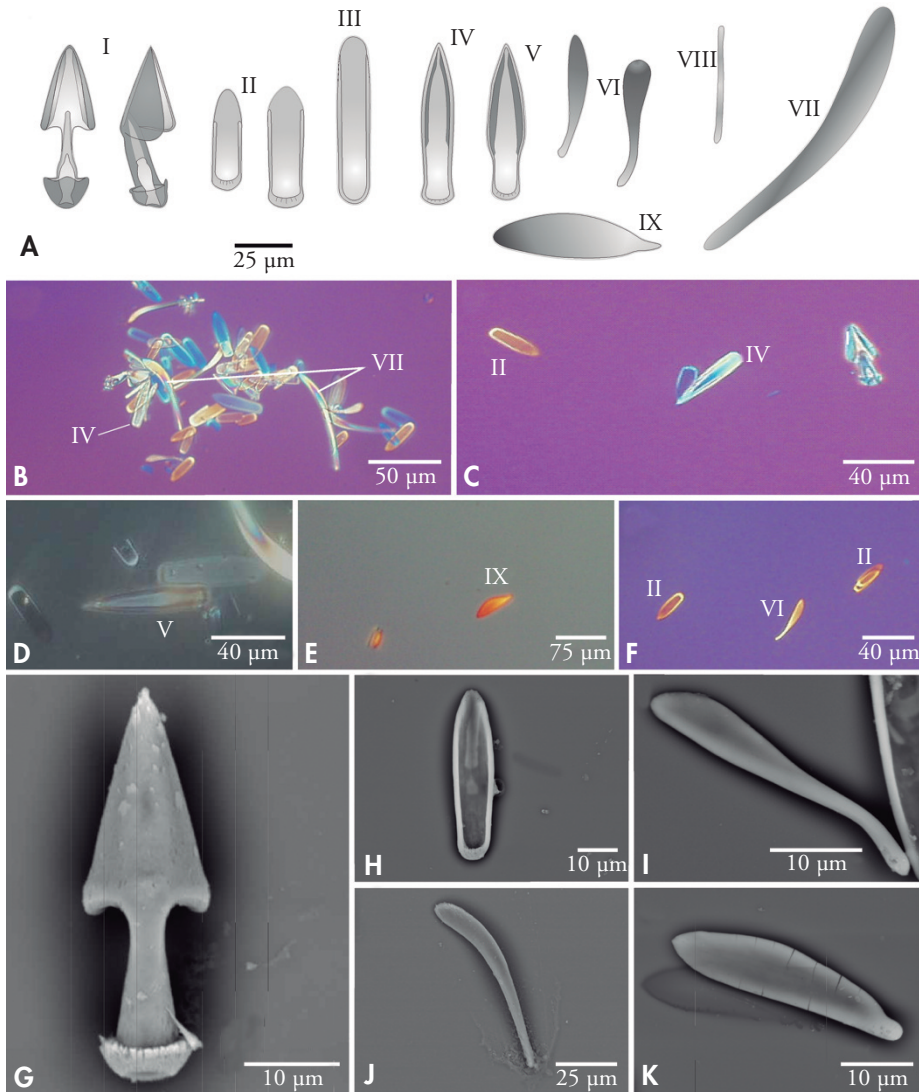


Figure 10. *Hemimienia nanodoryata* n. sp., mantle sclerites. A: drawings of the different types of sclerites (I: short harpoon-shaped sclerite; II: small and excavate scale with the basal and lateral rims reinforced; III: narrow and slender excavate scale the basal and lateral rims reinforced; IV: excavate scales distally pointed, basally and laterally reinforced and with a pair of laminar extensions; V: excavate scales distally pointed, basally and laterally reinforced and with a pair of laminar extensions; VI: large paddle-shaped scale; VII: small paddle-shaped scale; VIII: slender solid sclerites; IX: foot-groove scales); B-F: optical microscope photographs; G-K: SEM micrographs.

Figura 10. *Hemimienia nanodoryata* n. sp., escleritos del manto. A: dibujo de los diferentes tipos de escleritos (I: esclerito en forma de arpón corto; II: escama excavada y alargada pequeña, con el borde basal y lateral reforzado; III: escama excavada estrecha y delgada con el borde basal y lateral reforzado; IV: escama excavada apuntada distalmente, con refuerzo basal y lateral y con un par de extensiones laminares; V: escama excavada apuntada distalmente, con refuerzo basal y lateral y con un par de extensiones laminares; VI: paletas grandes; VII: paletas pequeñas; VIII: esclerito macizo delgado; IX: escama del surco pedio); B-F: fotografías al microscopio óptico; G-K: micrografías al MEB.

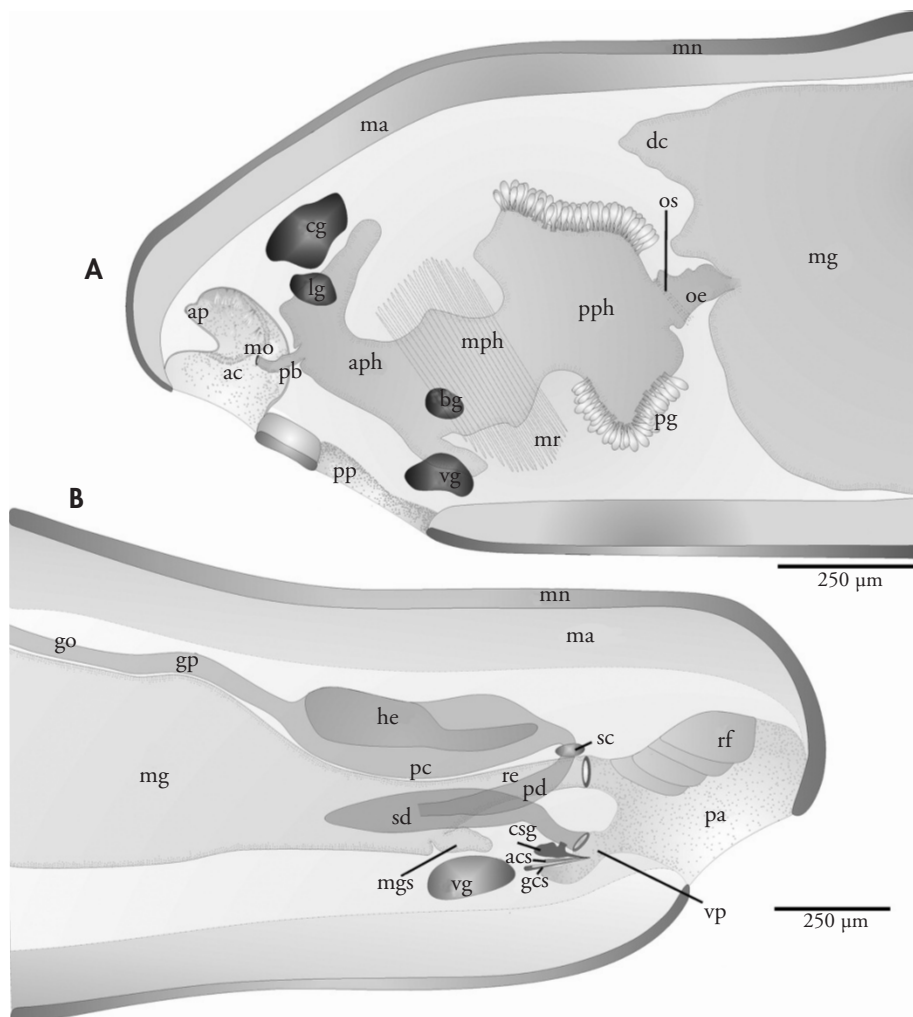


Figure 11. *Hemimenia nanodoryata* n. sp., organization of the anterior (A) and posterior region (B). Abbreviations, ac: atrio buccal cavity; acs: acicular copulatory stylet; ap: atrial papillae; aph: anterior pharyngeal region; bg: buccal ganglion; cg: cerebral ganglion; csg: copulatory stylet gland; dc: anterodorsal midgut caecum; gcs: gutter-like copulatory stylet; go: gonad; gp: gonopericardioduct; he: heart; lg: lateral ganglion; ma: matrix; mg: midgut; mgs: midgut sack; mn: mantle; mo: mouth; mph: medial pharyngeal region; mr: muscular ring; oe: oesophagus; os: oesophageal sphincter; pa: pallial cavity; pb: proboscis; pc: pericardium; pd: pericardioduct; pg: pharyngeal glands; pp: pedal pit; pph: posterior pharyngeal region; re: rectum; rf: respiratory fold; sc: suprarectal commissure; sd: spawning duct; vg: ventral ganglion; vp: ventroanterior pouch of the pallial cavity.

Figura 11. *Hemimenia nanodoryata* n. sp., organización de la región anterior (A) y posterior (B). Abreviaturas, ac: cavidad atrio bucal; acs: estilete copulador acicular; ap: papilas atriales; aph: región faríngea anterior; bg: ganglio bucal; cg: ganglio cerebral; csg: glándula del estilete copulador; dc: ciego anterodorsal del intestino; gcs: estilete copulador acanalado; go: gónada; gp: gonopericardioducto; he: corazón; lg: ganglio lateral; ma: matriz; mg: intestino; mgs: saco intestinal; mn: manto; mo: boca; mph: región faríngea media; mr: anillo muscular; oe: esófago; os: esfínter esofágico; pa: cavidad paleal; pb: probóscide; pc: pericardio; pd: pericardioducto; pg: glándulas faríngeas; pp: foseta pedia; pph: región faríngea posterior; re: recto; rf: pliegues respiratorios; sc: comisura suprarectal; sd: conducto de desove; vg: ganglio ventral; vp: bolsa ventroanterior de la cavidad paleal.

opening of the pallial cavity. The pedal groove and its pedal fold are small in the anterior body region (pedal groove 50 μm high and 55 μm wide; pedal fold 40 μm high and 40 μm wide), becoming wide posteriorly (pedal groove 120 μm high and 100 μm wide; pedal fold 80 μm high and 80 μm wide).

Pallial cavity: Large pallial cavity opens subterminally by a narrow opening. Dorsoposterior region of the pallial cavity has nine respiratory folds arranged radially (Figs. 11B, 12J). Anteriorly, the pallial cavity is subdivided by a transverse septum in two pouches: a dorsal pouch where the rectum opens; and a ventral pouch that receives mid-dorsally the paired opening of the spawning ducts (Fig. 12H–I). There are two pairs of small copulatory stylets laterally to the ventroanterior pouch of the pallial cavity and included into the body wall. It lacks pallial and suprapallial glands. There are no prepallial spines, but two small pouches in similar positions (laterally to the pedal groove) are present.

Nervous system and sense organs: Unpaired cerebral ganglion with trapezoidal cross-section (160 long; 120 μm high; 190 μm wide), is located dorsally to the anterior region of the pharynx (Figs. 11A, 12A). At least, a pair of nerves arises anteriorly from the cerebral ganglion to the atrio-buccal cavity. The cerebral connectives with separated origin: cerebro-lateral connectives (80 μm long; 15 μm wide) and cerebro-ventral connectives leave from the

medial region of the cerebral ganglion, laterodorsally and lateroventrally respectively. The first lateral ganglia (85 μm long; 80 μm high; 35 μm wide) are located lateral to the anterior pharyngeal region. The ventral ganglia are large (130 μm long; 65 μm high; 60 μm wide) and are located dorsally to the posterior region of the pedal pit; they are interconnected by two commissures (3 μm wide). The ventral nerve cords (40 μm diameter) are originated in the ventral ganglia and run to the posterior body. The buccal ganglia (85 μm long; 50 μm high; 60 μm wide) are located lateral to the muscle ring of the middle pharyngeal region. The posterior most lateral ganglia are large (150 μm long; 65 μm de high; 60 wide) (Fig. 12H) connected by a wide suprarectal loop (50 μm long; 60 μm high; 25 μm wide), positioned ventrally to the posterior pericardium. The atrial sense organ takes the dorsal region of the atrio-buccal cavity and their lateral and dorsal walls are covered by numerous papillae paired or bundled basally into groups up to four (Fig. 11A). No dorsoterminal sense organ was observed.

Digestive system: The mouth opens into the posterior region of the common atrio-buccal cavity and leads into a narrow protruding proboscis that opens ventrally into the pharynx. The pharynx has three regions (Fig. 11A). The anterior region of large lumen (380 μm high; 340 μm wide), a thin cuticularized epithelium and a moderate peripheral layer of circular muscle fibres and

(Right page) Figure 12. *Hemimenia nanodoryata* n. sp., body cross-sections. A: anterior region of the pharynx and cerebral ganglion; B–D: middle region of the pharynx showing the oblique muscular ring; E: posterior region of the pharynx; F: oesophageal region; G: anterior region of the spawning ducts; H, I: opening of the copulatory stylets glands into the distal region of the spawning ducts; copulatory stylets laterally located to the spawning ducts; J: opening of the spawning ducts into the ventroanterior pouch of the pallial cavity. Abbreviations, acs: acicular copulatory stylet; aph: anterior pharyngeal region; au: auricle; cg: cerebral ganglion; csg: copulatory stylet gland; cu: cuticle; dc: anterodorsal midgut caecum; ds: dorsal sinus; gcs: gutter-like copulatory stylet; lc: cerebro-lateral connective; lg: lateral ganglion; ma: matrix; mph: middle pharyngeal region; mr: muscular ring; oe: oesophagus; og: oesophageal glands; pa: pallial cavity; pc: pericardium; pd: pericardioduct; pf: pedal fold; pg: pharyngeal glands; pph: posterior pharyngeal region; re: rectum; rf: respiratory fold; sd: spawning duct; vg: ventral ganglion; vp: ventroanterior pouch of the pallial cavity; vs: ventral sinus.

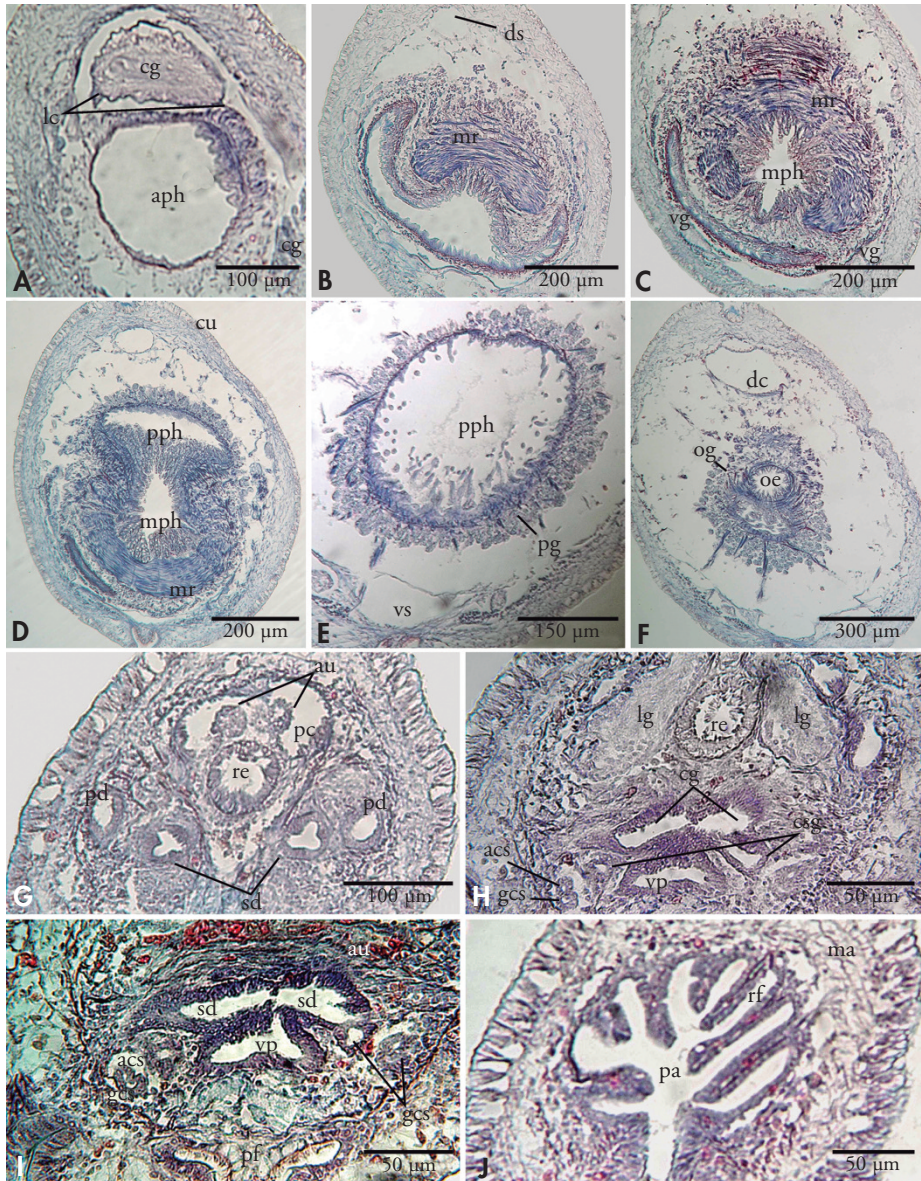


Figura 12. *Hemimenia nanodoryata* sp. nov., cortes transversales. A: región anterior de la farínge y ganglio cerebral; B-D: región media de la farínge mostrando el anillo musculoso oblicuo; E: región posterior de la farínge; F: región del esófago; G: región anterior de los conductos de desove; H, I: apertura de las glándulas de los conductos de desove en la región distal de los conductos de desove; situación lateral de los estiletes copuladores a los conductos de desove; J: apertura de los conductos de desove en la bolsa ventroanterior de la cavidad paleal. Abreviaturas, acs: estilete copulador acicular; aph: región faríngea anterior; au: aurícula; cg: ganglio cerebral; csg: glándula del estilete copulador; cu: cutícula; dc: ciego intestinal anterodorsal; ds: seno dorsal; gcs: estilete copulador acanalado; lc: conectivo cerebro-lateral; lg: ganglio lateral; ma: matriz; mph: región faríngea media; mr: anillo musculoso; oe: esófago; og: glándulas del esófago; pa: cavidad paleal; pc: pericardio; pd: pericardioducto; pf: pliegue pedio; pg: glándulas faríngeas; pph: región posterior de la faríngea; re: recto; rf: pliegues respiratorios; sd: conducto de desove; vg: ganglio ventral; vp: bolsa ventroanterior de la cavidad paleal; vs: seno ventral.

extraepithelial gland cells of small size containing granules of acidic secretion (Fig. 12A). The middle pharyngeal region characterized by a strong, obliquely running and wide muscle ring that narrows the lumen of the pharynx (170 μm diameter); this region has a folded epithelium and extraepithelial gland cells of the same features as those of the anterior region, associated with the muscle fibres (Figs. 11A, 12B–D). The posterior pharynx region has a large lumen (390 μm high; 340 μm wide) and a thin epithelium; with a narrow muscular layer of circular fibres and a dense and thick coating of extraepithelial bottle-shape gland cells containing granular vesicles of acidic nature (Figs. 11A, 12E). The pharynx leads into a narrow oesophagus (90 μm diameter) which opens frontally into the midgut; oesophagus with an oblique and thin muscle ring and extraepithelial gland cells as same quality as those of the middle and anterior pharyngeal regions. The anterodorsal caecum of the midgut is short, extending above the oesophagus only. Serial dorsoventral muscle bundles cause ventrolateral pouches of midgut every 100 to 150 μm . Posteriorly, the midgut gives rise a pair of small and short ventroposterior sacs which run ventrolaterally to the spawning ducts; these short sac are not related to the copulatory stylets (Fig. 11B). The midgut leads into a ciliated rectum that opens dorsally into the anterodorsal pouch of the pallial cavity (Fig. 11B).

Circulatory system: The heart consisting of ventricle and paired auricle. Muscularised ventricle (150 μm high, 50 μm wide) appears as an invagination of the pericardial roof; the auricles (80 μm high, 30 μm wide), partially fused, run free into the pericardium, connected with roof of pericardium only in posterior portion. The dorsal sinus (50 μm high; 70 μm wide) runs anteriorly in continuation of the heart, above the gonopericardioducts and gonads up to the pharynx. The ventral sinus (60 μm high; 100 μm wide) dorsally and laterally delimited by a muscular layer; it runs between the ventral nervous cords

to arrive anteriorly up to the beginning of the pedal groove.

Reproductive system: The gonads are narrow (35 μm high; 25 μm wide) and run above the midgut, showing oocytes at the medial walls and spermatozooids in the ventrolateral ones (simultaneous hermaphrodite). The gonopericardioducts with the same diameter than the gonads, opening dorsofrontally into the voluminous pericardium (600 μm long; 90 μm de high; 150 μm de wide). Each pericardioduct emerges laterotermally from the pericardium, immediately bends and runs anteriorly along the lateral body wall; they open ventrolaterally into the proximal region of the spawning ducts (Fig. 11B). Although there are no seminal receptacles, the proximal region of the spawning ducts which runs anteriorly to the pericardioducts could serve for the alosperm storage. The spawning ducts (45 μm high; 60 μm wide) are paired throughout and they narrow posteriorly (30 μm high; 45 μm wide) to open pairwise into the ventroanterior pouch of the pallial cavity (Figs. 11B, 12H–I). Small copulatory apparatus consists of two short pairs of copulatory stylets with associated glands (Figs. 11B, 12H–I). The copulatory stylets are located lateroventrally to the ventroanterior pouch of the pallial cavity but no direct connection with this could be discerned. On each body side, there is an acicular stylet (100 μm long) and ventrally to this, a gutter-like stylet (150 μm long) that becomes proximally acicular. Each stylet has its own sheath of cubical epithelium, but there is no common sheath for each pair. There are two small and tubular copulatory stylet glands which open into the spawning ducts, anteriorly to the opening of the gonopores into the pallial cavity; the glands also connect distally with the copulatory stylets through a narrow duct (Figs. 11B, 12H–I).

Taxonomic remarks: *Hemimenia nanodoryata* n. sp. shares relevant features with *H. rugosa* and *H. tripla* (described above), such as the mantle sclerites, the structure of the pharynx with three regions and the presence of a pair of ven-

troposterior midgut sacs; also in part with *Hemimenia cyclomyata* (the latter without ventroposterior midgut sacs). All these species have been reported from the same geographical area as *Hemimenia nanodoryata* n. sp., however, in detail, specific differences emerge (Table I). These include the small size of both the copulatory apparatus (glands and stylets) and the ventroanterior midgut sacs, together with the presence of a second type of excavate scales with laminar extensions and the absence of seminal receptacles and prepallial spines. Other differences with *H. rugosa* are its small body size, the slightly marked cuticular wrinkles, the types of sclerites (including slender solid sclerites and two types of excavated scales with lateral extension) and the presence of paired and grouped atrial papillae rather than simple. Regarded the organization of the digestive system, main specific

differences are the configuration of the pharyngeal region and the structure of the midgut that has midgut constrictions but lacks an anterodorsal caecum. Moreover, *Hemimenia nanodoryata* n. sp. lacks seminal receptacles, prepallial spines and suprapallial glands. *Hemimenia tripla* has two lateroventral keels, absent in *Hemimenia nanodoryata* n. sp., stylets glands with three connection rather than with two, a genital cone, and pallial glands. Otherwise, *Hemimenia nanodoryata* n. sp. has an oesophagus, a midgut caecum and midgut constrictions, all of them absent in *H. tripla*. With respect to *H. cyclomyata*, it also differs by: the presence of an anterodorsal midgut caecum, an oesophageal sphincter and a ventroanterior pouch of the pallial cavity; and by the absence of a genital cone and dorsoterminal sense organ (SALVINI-PLAWEN, 2006; GARCÍA-ÁLVAREZ ET AL., 2014; this report).

DISCUSSION

Although the Solenogastres fauna of the Galician waters was one of the better studied of the Iberian Península (GARCÍA-ÁLVAREZ ET AL., 2014), the continuous new findings of undescribed species and their relative high abundance suggests that its biodiversity on these area is vastly underestimated. The results of only two researches carried out in the coast of Galicia recorded the presence of nine taxa of Neomeniomorpha (SALVINI-PLAWEN, 2006; present report), three species of *Neomenia* and six species of *Hemimenia* (including the three new species presented herein).

Apart from the external appearance and sclerites, the present study shows that the main specific differences among the taxa of *Hemimenia* are related to the organization of the foregut and the accessory genital organs. The present work reveals that in *Hemimenia*, the anatomy of the foregut differentiated into diverse regions (including proboscis, different pharyngeal regions and oesophagus) provides relevant specific characters, like previously indicated for

other genera without radula such as *Neomenia* (SALVINI-PLAWEN, 2006). Solenogastres feed mainly on various groups of Cnidaria, also in polychaetes (SALVINI-PLAWEN, 1981, 1988, 2008b; TODT AND SALVINI-PLAWEN, 2005); species without radula suck the prey tissue by means of the action of the sphincter (s) of the foregut, then digesting it chemically by enzymatic secretion from the unicellular glands of the foregut (SALVINI-PLAWEN, 1985, 1988). Therefore, in species lacking a radula, the anatomical features of the foregut (mainly those of the pharyngeal regions) may be considered as features of high taxonomic value, probably reflecting the prey-specificity.

With regard to the accessory genital organs, species of *Hemimenia* have a paired copulatory apparatus and can include prepallial spines. The copulatory apparatus always comprises paired copulatory stylets and associated glands, both of variable size, together with a powerful set of musculature. That musculature permits the extrusion

of the stylets and, as indicated in this report for *H. cyclomyata*, probably allows the rotation of the gutter-like stylets around the acicular ones. The stylet glands in *Hemimenia* connect with both, the copulatory stylets and the spawning ducts, showing in *H. tripla* one extra connection directly with the pallial cavity. The outlet of the stylet glands into the pallial cavity was previously known just in *Imeroherpia* Salvini-Plawen, 1978 (HANDL, 2002). However, the triple connection of the stylet glands presented in *H. tripla* is herein observed at first time in Solenogastres.

Finally, NIERSTRASZ (1902) described *H. intermedia* without a dorsoterminal sense organ, but years later, SALVINI-PLAWEN (1978) pointed out that Nierstrasz probably overlooked the organ due to its ventroposterior position, concluding that the presence of a dorsoterminal sense organ should be considered

as a generic character of *Hemimenia*. However, its absence in *H. rugosa* and *H. nanodoryata* confirms that is a variable character and therefore, the diagnosis of *Hemimenia* is herein emended considering the possibility of presence or absence of a dorsoterminal sense organ.

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