



## *Macellomenia profundorum* n. sp. (Mollusca, Solenogastres, Pholidoskepia) a new abyssal species from the South Atlantic Ocean (Angola Basin)

## *Macellomenia profundorum* n. sp. (Mollusca, Solenogastres, Pholidoskepia) una nueva especie abisal del Océano Atlántico Sur (Cuenca de Angola)

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### ABSTRACT

A new species of solenogaster (Mollusca, Aplacophora) from the Angola Basin is described: *Macellomenia profundorum* n. sp. The studied specimen was collected during the DIVA 1 expedition (Latitudinal Gradients of Deep-Sea BioDiversity in the Atlantic Ocean). The description is based primarily on the sclerites and the internal anatomy (histological study). *Macellomenia profundorum* n. sp. is the first species of the family to be described from the southern hemisphere and constitutes its deepest record (5400 m deep). Even though only anterior anatomical characters are known, these and especially the radula and mantle sclerites are enough to justify that it is a new species. Amended diagnoses are also provided for the family and genus.

### RESUMEN

Se describe una nueva especie de solenogastro (Mollusca, Aplacophora) de la Cuenca Abisal de Angola: *Macellomenia profundorum* n. sp. El ejemplar estudiado fue recolectado durante la expedición DIVA 1 (Latitudinal Gradients of Deep-Sea BioDiversity in the Atlantic Ocean). La descripción está basada en los escleritos y la anatomía interna (estudio histológico). Es la primera especie de la familia procedente del hemisferio sur y la más profunda (5400 m de profundidad). A pesar de que solo se tiene información sobre las características anatómicas internas de la región anterior del cuerpo, éstas y sobre todo el tipo de rádula y los escleritos del manto son suficientes para justificar que se trata de una especie nueva. Se aportan además diagnosis corregidas para la familia y el género.

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KEY WORDS: Aplacophora, biodiversity, new taxa, DIVA-project.

PALABRAS CLAVE: Aplacophora, biodiversidad, nuevo taxón, proyecto DIVA.

### INTRODUCTION

The traditional classification of the aplacophoran molluscs recognizes Solenogastres as a class consisting of four main orders (SALVINI-PLAWEN, 1978).

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Morphology-based studies have already suggested that several of the traditional groups within Solenogastres might not be monophyletic (SCHELTEMA AND SCHANDER, 2000; SALVINI-PLAWEN, 2003a; SCHELTEMA, SCHANDER AND KOCOT, 2012). This was further corroborated by two recent molecular-based studies (BERGMEIER ET AL., 2019; KOCOT ET AL., 2019), therefore major revisions are now needed. In addition, according to the available phylogenomic analyses the placement of Solenogastres (=Neomeniamorpha) and Caudofoveata (=Chaetodermomorpha) in a clade (Aplacophora) that, along with Polyplacophora, forms the sister group to all remaining Mollusca is strongly supported (KOCOT ET AL., 2011, 2020; SMITH ET AL., 2011). However, the relations between all the groups have not yet been clarified and therefore a new classification has not been stabilized.

Pholidoskepia Salvini-Plawen, 1978, one of the four traditional orders of Solenogastres, was retrieved by KOCOT ET AL. (2019) as monophyletic. This order is characterized by thin cuticles with sclerites as scales inserted in one layer (GARCÍA-ÁLVAREZ AND SALVINI-PLAWEN, 2007). While the distinction between species to family group taxa based on sclerites is generally complex (and usually requires additional anatomical characters), in Pholidoskepia scales are sometimes helpful to determine the family or even the genus. Macellomeniidae Simroth, 1893 has sclerites as nail-shaped bodies formed by a basal plate with a pointed needle (claviform sclerites) as an exclusive character. This family consists of a single genus (*Macellomenia* Simroth, 1893) of which five species have been described so far: *Macellomenia palifera* (Pruvot, 1890) (Mediterranean Sea, 80 m depth); *M. aciculata* Scheltema, 1999 (European Basin, Atlantic Ocean, 2498 m); *M. adenota* Salvini-Plawen, 2003 (Gibraltar, Atlantic Ocean, 25-40 m); *M. schanderi* Kocot & Todt, 2014 and *M. morseae* Kocot & Todt, 2014 (San Juan Channel, Pacific Ocean, 59 m). *Macellomenia profundorum* n. sp. is the first described species of the family

from the abyss (3500 - 6000 m) (COBO AND KOCOT, 2019). Nonetheless, one more species, non-identified, was collected in the Northwest Pacific at 5000 m depth (Bergmeier, *personal communication*).

The present description of *M. profundorum* n. sp. provides useful information about the diagnostic characters of Macellomeniidae. Based on this, and on the available descriptions, amended diagnoses for the family and genus are provided.

## MATERIAL AND METHODS

The specimen was collected during DIVA 1 expedition (Me 48/1, 2000) (DIVA project: Latitudinal Gradients of Deep-Sea BioDiversity in the Atlantic Ocean) in the Angola Basin (16°16.18'S - 005°24.24'E, 5430 m depth) with an epibenthic sled and fixed and preserved in 70 % ethanol.

Sclerites were obtained by digesting a small piece of the medial body with 10 % sodium hypochlorite solution (6 h), they were then cleaned with distilled water, air dried and mounted (Canada balsam). They were studied and photographed under a light optical microscope with Nomarski optics (Olympus BX51 optical microscope; Olympus DP71 camera) and on an Environmental Scanning Electron Microscope (ZEISS EVO LS 15). For histology the anterior and posterior region were decalcified with EDTA solution (5.5 % EDTA in 10 % formaldehyde; overnight), dehydrated in an increasing graded ethanol series (20 minutes for each soak), followed by two xylene soaks (15 minutes for each soak) and embedded in paraffin (GIL-MANSILLA ET AL., 2008). Then they were sectioned (5 µm serial transverse sections, Leica RM2235 rotary microtome) and stained with Mallory's Trichromic stain. During the staining process sections of the posterior region were lost. The internal anatomy of the anterior body was manually reconstructed and drawn using Corel Draw X7.

## RESULTS

Order PHOLIDOSKEPIA Salvini-Plawen, 1978  
Family MACELLOMENIIDAE Salvini-Plawen, 1978  
Genus *Macellomenia* Simroth, 1893

### *Macellomenia profundorum* n. sp. (Figures 1, 2)

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**Type material:** Holotype: • 1 specimen, serial sections of the anterior region (5  $\mu\text{m}$ ; two slides), sclerites (one SEM stub and two slides); Angola Basin; 16°16.18'S, 005°24.24'E – 16°19.28'S, 005°27.20'E; 5430 m depth; DIVA1 Me 48/1, station 348 (Area 6); Zoologische Staatssammlung München (ZSM Mol20171255).

**Derivatio nominis:** Plural genitive of *profundum*, i (meaning “from the depths”)

**Diagnosis:** Small animal with five different claviform sclerites, distinguished by their basal plates. One type of scales restricted to the pedal groove. Pedal groove containing a single triangular fold. Mouth separated from the atrium. Atrium with several, simple (unbranched) and voluminous oval papillae. Ventrolateral foregut glands of type A. Monoserial radula with straight radula plate and five equally-sized denticles. Antero-ventral radular sac. Midgut with a bilobed antero-dorsal caecum. Posterior organs unknown.

**Description:** Habitus. small animal (1.38 mm long, 0.2; 0.24; 0.18 mm thick in the anterior, middle, and posterior region) with truncated anterior end and rounded posterior end. The pedal pit and groove are externally evident. White and velvety appearance in 70 % ethanol (Figure 1A).

**Mantle.** Thin epidermis consists of simple cells (stained in blue) intercalated by numerous oval, brown-orange staining, glandular cells (2 to 4  $\mu\text{m}$  in diameter). Thin cuticle (7.5 to 10 to 12.5  $\mu\text{m}$  thick) with solid claviform sclerites arranged in a single layer. According to the shape of the basal plate five different sclerites can be distinguished (Fig 1 B-F). Basal plates are as follows:

a) Tongue-shaped basal plate (Figure 1B, H-1): Base with numerous grooves and a rim at the proximal end that extends along the plate sides to the distal end. Size of the basal plate: 18 to 24  $\mu\text{m}$  long; 14 to 9  $\mu\text{m}$  wide in the distal end; 6 to 4  $\mu\text{m}$  wide in the proximal end.

b) Trapezoidal (Figure 1C\*, H-2): Striated base (covered with grooves) with a thicken proximal rim. Variable in size: 9 to 24  $\mu\text{m}$  long; 6 to 20  $\mu\text{m}$  wide at the distal end; 4 to 10  $\mu\text{m}$  wide in the proximal end.

c) Triangular (Figure 1D, F\*, H-3): The third most abundant type. The grooves that run along the bases are mostly longitudinal. With a rim in the proximal end of the base. Size: 17 to 23  $\mu\text{m}$  long; 9 to 10  $\mu\text{m}$  wide at the distal end; 3.5 to 6  $\mu\text{m}$  wide at the proximal end.

e) Oval (Figure 1H-4): They are slightly striated. Most of them are small, although there are exceptions. Size: 9 to 18  $\mu\text{m}$  long; 5 to 9  $\mu\text{m}$  wide.

d) Rounded (Figure 1E, H-5): Scarce. With a wide rim at the proximal end of the base that extends along the plate sides to the distal end. Size: 12 to 19  $\mu\text{m}$  long; 10 to 14  $\mu\text{m}$  wide.

The sclerites are very fragile and in almost all the obtained slides the needles are broken, something that has already been pointed out by CAUDWELL, JONES AND KILLEEN (1995) in the redescription of *M. palifera* and by SCHELTEMA (1999) in the description of *M. aciculata*. This hampers the measurement of the total length (base + needle) of the sclerites. Numerous needles were measured without the base, most between 30 and 40  $\mu\text{m}$  in length and some up to 87  $\mu\text{m}$ . The needles are between 1.5 to 4  $\mu\text{m}$  wide. A correlation between the basal plate size and the needle length cannot be confirmed (see also SCHELTEMA, 1999) nor

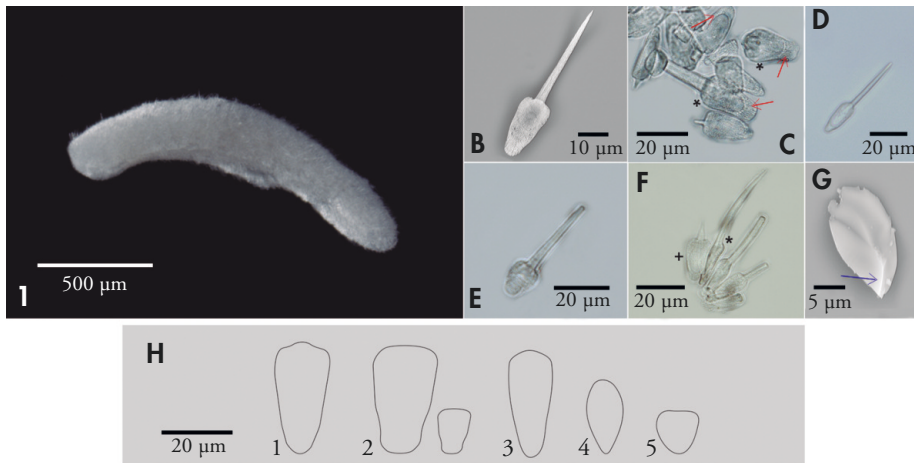


Figure 1. A. Habitus of *Macellomenia profundorum* n. sp. (holotype). B, H-1. Sclerites with tongue-shaped base. C, H-2 Sclerites with trapezoidal base (arrows indicate rims in the sclerites bases). D, H-3. Sclerites with triangular base. E, H-5 Sclerites with rounded base. F. Sclerite with trapezoidal base (+), lateral view of a sclerite with triangular base (\*), sclerite with an ovoid base. G. Scale of the pedal groove (arrow indicates the keel). H-4 Oval base.

*Habitus de Macellomenia profundorum n. sp. (holotipo). B, H-1. Escleritos con base en forma de lengua. C, H-2 Escleritos con base trapezoidal (las flechas indican el reborde del extremo proximal, que puede extenderse a los laterales). D, H-3. Escleritos con base triangular. E, H-5 Escleritos con base redondeada. F. Escleritos con base trapezoidal (+), Escleritos con base triangular e vista lateral (\*), escleritos con base ovoide. G. Escamas del surco pedio (la flecha indica la quilla dorsal). H-4 Base oval.*

between the thickness of the plates and their length, but it was observed that, in general, sclerites with trapezoidal plates have thicker needles.

With one type of scales of the pedal groove (15 to 37.5 µm long, 8 to 12.5 µm wide), leaf-shaped with the distal end slightly pointed and with a short keel (Figure 1G).

**Pedal pit and groove.** The pedal pit (20 µm long, 100 µm wide, 45 µm high) has a small antero-ventral extension (5 µm long, 5 µm wide, 2.5 µm high). In its posterior region the ciliated cells increase in size and become rectangular (9 µm high, 3 µm wide) (Figure 2A-5). The pedal groove contains a single triangular fold (17.5 to 20 µm high, 14 to 27.5 µm wide in the middle region). The anterior follicular pedal glands, paired and bulky, are constituted by a single cellular type (Figure 2A-4).

**Nervous system and sensory organs.** The cerebral ganglion has an oval shape

(17.5 µm long, 60 µm wide, 10 to 35 µm high) (Figure 2A-3). The pair of buccal ganglia (16.5 µm long, 3 to 7.5 µm wide, 3 to 7.5 µm high) are located between the foregut and the radular sac, remains of a ventral commissure were observed. The pedal ganglia are joined by a large commissure (25 µm long, 17 µm wide, 15 µm high).

The opening of the atrium is antero-ventral (50 µm long, 52.5 µm wide, 65 µm high) (Figure 2A-1). The oval and non-pedunculated atrial papillae (12 - 14 papillae), are bulky (12.5 to 2 µm wide, 10 to 15 µm high) and they are mostly concentrated in the middle and posterior regions of the atrium (Figure 2A-1).

**Digestive system.** The mouth is separated from the atrium and opens to the exterior as a narrow ventral channel (42.5 µm high, 5 µm long and wide) (Figure 2A-3). The foregut is wider than high (30 µm long, 37.5 to 45 µm wide, 10 to 17.5 µm) and it is surrounded by a thin layer of cir-



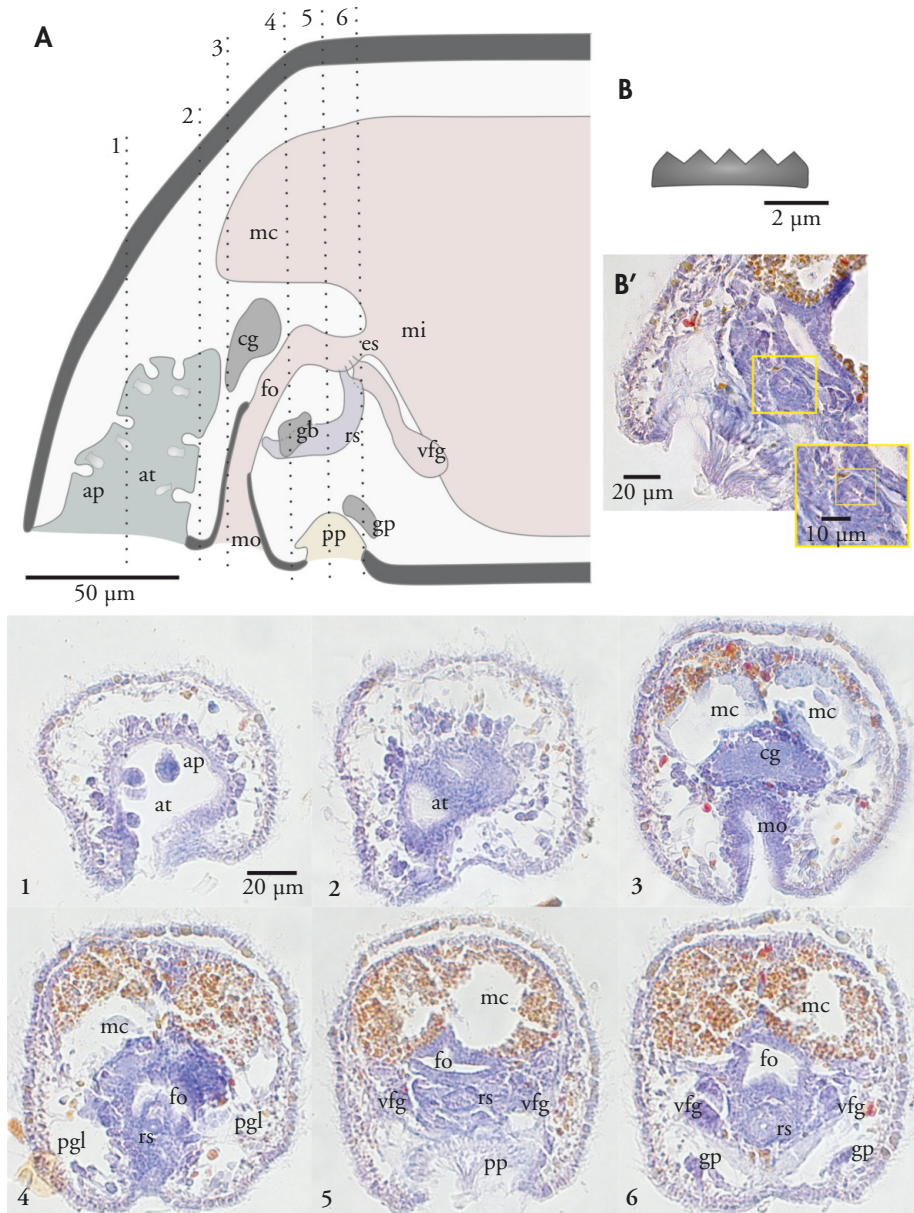


Figure 2. A. Reconstruction of the anterior body region of *Macellomenia profundorum* n. sp. B. Reconstruction of the radula. B' Section of the radula (in yellow square). 1-6. Serial sections of the anterior body region as indicated in A. at - atrium; ap - atrium papillae; bg - buccal ganglia; cg - cerebral ganglia; es - esophagus; fo - foregut; mc - midgut caecum; mi - midgut; mo - mouth; pp - pedal pit; rs - radular sac; vfg - ventrolateral foregut glands. *Reconstrucción interna de la región anterior de Macellomenia profundorum* n. sp. B. *Rádula*: reconstrucción y corte (rádula encuadrada en amarillo) 1-6 Cortes seriados de la región anterior según indicado en A. at - atrio; ap - papilas atriales; bg - ganglio bucal; cg - ganglio cerebroide; es - esófago; fo - faringe; mc - ciego intestinal; mi - intestino medio; mo - boca; pp - ganglios pedios; pgl - glándula pedia; pp - foseta pedia; ra - rádula; rs - saco radular; vfg - glándulas ventrolaterales de la faringe.

cular musculature (4 to 6  $\mu\text{m}$  thick). The ventrolateral foregut glands consist on two long, simple ducts (75  $\mu\text{m}$  long, 7–12.5  $\mu\text{m}$  wide and high) with inner musculature and extraepithelial gland cells opening into the ducts along the entire length of the gland (type A; GARCÍA-ÁLVAREZ AND SALVINI-PLAWEN, 2007) (Figure 2A: 5, 6), no posteriorly bent necks of the glandular cells were observed (*Pararrhopalia*-type; HANDL AND TODT, 2005). The monoserial radula is formed by a straight radular plate (4.8  $\mu\text{m}$  long) and five equally-sized triangular denticles (<0.5  $\mu\text{m}$  high, 0.8  $\mu\text{m}$  wide) (Figure 2B, B'). A single row of teeth was observed, just at the junction of the radular sac and the foregut (Figure 2B'). The radular sac is narrow and long (35  $\mu\text{m}$  long, 1.5 to 2.5  $\mu\text{m}$  wide, 2.5 to 5  $\mu\text{m}$  high) and is directed anteriorly (Figure 2A: 4,5,6). The esophagus is short and slightly wider than the foregut (5.5  $\mu\text{m}$  long, 45 to 50  $\mu\text{m}$  wide) and leads into the middle region of the midgut. No esophageal glands were observed. Midgut with a dorso-anterior caecum which is paired in its anterior end (47.5  $\mu\text{m}$  long, 65 to 130  $\mu\text{m}$  wide, 15 to 45.5  $\mu\text{m}$  high) (Figure 2 A: 3,4,5,6).

**Comparisons:** Currently, the family Macellomeniidae, includes five species (Table I). The new species described here, *Macellomenia profundorum* n. sp., was easily placed in Macellomeniidae due to the characteristic claviform sclerites. Although there is no anatomical information on the posterior region of the body, the anatomy of the anterior region and most notably the radula and sclerites allow to determine that it represents a new species. This is also supported by other morphological differences between the new species and the existing ones and also by its distribution (Table I).

The major difference between *M. profundorum* n. sp. and *M. palifera* is the number of denticles of the monoserial radulae: five in *M. profundorum* and seven in *M. palifera* (NIESTRASZ, 1905). The morphology of the claviform sclerites of both species is also different: in *M. profundorum* n. sp. there are five different sclerite types according to the shape of their bases, whereas for *M. pali-*

*fera* only one, with oval base, was described (PRUVOT, 1890; NIESTRASZ, 1905; THIELE, 1913; HOFFMAN, 1949; SALVINI-PLAWEN, 1986; CAUDWELL ET AL., 1995; KOCOT AND TODT, 2014). In addition, *M. profundorum* n. sp. has a paired midgut caecum, absent in *M. palifera*, and the mouth and atrium separated, while *M. palifera* presumably has a common atrio-buccal cavity, although this should be reviewed (SALVINI-PLAWEN, 2003b; KOCOT AND TODT, 2014). In *M. profundorum* n. sp. one type of scale of the pedal groove was found, while in *M. palifera* Simroth (1893) mentions spicules of different length along the pedal groove.

The radula of *M. profundorum* n. sp. and *M. aciculata* are similar, both with five equal teeth, however, they are clearly distinguished: in *M. profundorum* n. sp. the radular plate is smaller (Table I) and the denticles are closer, not as far apart as those of *M. aciculata* (SCHELTEMA, 1999). The new species also differs from *M. aciculata* in the shape of the bases of the sclerites (SCHELTEMA, 1999). In addition, *M. profundorum* n. sp. has a single type of scale of the pedal groove, while two types were described in *M. aciculata* (SCHELTEMA, 1999). *M. profundorum* n. sp. and *M. aciculata* also differ in the atrial papillae and because the new species has the atrium and mouth are separated.

*M. profundorum* n. sp. and *M. adenota* share several characters: the size, the mouth separated from the atrium (with similar papillae), the anterior bilobate midgut caecum and also some of the claviform sclerites are similar (SALVINI-PLAWEN, 2003b). However, *M. profundorum* sp. has five different claviform sclerites, whereas only two were described for *M. adenota* (SALVINI-PLAWEN, 2003b). In addition, there are important differences between the two species (Table I). *Macellomenia profundorum* n. sp. has a straight radular plate with five denticles of the same size, in *M. adenota* the plate is curved with seven denticles of which the central denticle is prominent (SALVINI-PLAWEN, 2003b).

The sclerites of *M. profundorum* are different from those of the Pacific *Macellomenia* species, which are hugely diffe-

Table I. Main diagnostic characters for the *Macellomenia* species (modified from KOCOT AND TODT, 2014).Tabla I. Principales caracteres diagnósticos para especies de *Macellomenia* (modificado de KOCOT AND TODT, 2014).

	<i>M. palifera</i> (Pruvot, 1890)	<i>M. aciculata</i> Scheltema, 1999	<i>M. morseae</i> Kocot & Todt, 2014	<i>M. adenota</i> Salvini-Plawen, 2003	<i>M. schanderi</i> Kocot & Todt, 2014	<i>M. profundorum</i> n. sp.
Distribution	Mediterranean Sea 80 m Irish Sea 120 m	European Basin 2498 m	San Juan Channel 59 m	Gibraltar 60 m	San Juan Channel 59 m	Angola Basin 5430 m
Size (mm)	4 - 8 x 0.7	3 x 1	2 x 0.2	1.65 - 2 x 0.75	2 x 0.2	1.38 x 0.2
Habitus	Rounded body ends	Rounded body ends	Rounded body ends	Rounded body ends	Rounded body ends	Truncated anterior end and rounded posterior end
	Dorsal line of scales	Spiny				
	White-yellowish	White-yellowish	White-yellowish	White-yellowish	White-yellowish	White
Shape of the bases of the sclerites	Oval	Rectangular and trapezoidal	Oval (spiny sclerites)	Oval and trapezoidal	Oval (spiny sclerites)	5 types
Maximum length of the sclerites	80 µm	47 µm	90 µm	25 µm	50 µm	87 µm
Needles of the sclerites with spicules	-	-	+	-	+	-
Atrio-buccal cavity	+	+	+	-	-	-
Atrium papillae (number)	?	Long ciliated (18-20)	Short papillae (5)	Simple and robust (few)	Simple papillae (20)	Voluminous simple papillae (14)
N denticles	7	5	8	7	7	5
Length of the radular plate		15 µm	15 µm	25 µm	16.5 µm	4.8 µm
Intestinal caecum	-	+	+ paired	+ paired	+ paired	+ paired
Seminal receptacles	+	+	?	?	+	?
Seminal vesicles	-	-	?	?	-	?
Abdominal spicules	-	-	-	+	+	?
Abdominal gland	-	-	-	+	-	?
Copulatory stylets	-	-	-	-	-	?
Respiratory folds	+	+	-	?	-	?
Dorsoterminal sensory organ	+	+	-	?	+	?

rent from the remaining species of the genus: spiny needles (KOCOT AND TODT, 2014). The radula of *M. profundorum* n. sp., with five denticles, is also different: *M. morseae* has radula with eight denticles and *M. schanderi* with seven. In addition, in *M. profundorum* n. sp. the mouth is separated from the atrium, while *M. morseae* has common atrio-buccal cavity. The esophagus of *M. palifera* n. sp. is very

short, compared with the foregut (Figure 2A) as in *M. morseae* but in *M. schanderi* foregut and esophagus are of same length (KOCOT AND TODT, 2014). The new species lacks dorsal esophageal glands, observed in *M. schanderi* and the pre-atrial organ characteristic of *M. morseae* (KOCOT AND TODT, 2014). The number and shape of the atrial papillae of the three species are also different (Table I).

## DISCUSSION

Macellomeniidae is well defined by the presence of claviform sclerites as an exclusive character. All species in the family are currently grouped into a single genus, *Macellomenia*, even though some characters usually considered diagnostic at genus level (common or separate atrio-buccal cavity, presence/absence of abdominal spicules, dorsoterminal sensory organ or respiratory folds) appear with different states. SALVINI-PLAWEN (2003b) expressed his concern about this in the discussion of the original description of *M. adenota*, but also about the difficulty of a requalification or rearrangement of the species within the family, due to the limited data and specimens and to the fact that the diagnostic validity of some characters should be questioned (SALVINI-PLAWEN 1967, 1978, 2003).

The relation between atrium and mouth opening traditionally serves as a diagnostic character on genus level. Of the six *Macellomenia* species three have a common atrio-buccal cavity (*M. palifera*, *M. aciculata* and *M. morseae*) and the other three have a separate mouth and atrium (*M. adenota*, *M. schanderi* and *M. profundorum* n. sp.). Even though ZAMARRO ET AL. (2013) pointed out the ambiguity of this character in some genera of the family Pruvotinidae ('Cavibelonia'), where the division of the atrium and the mouth is sometimes not clearly defined (i.e. "partially separated"; ZAMARRO ET AL., 2013) in the *Macellomenia* species the division, if present, is evident. Other characters, such as the existence or absence of the dorsoterminal sensory organ, abdomi-

nal spicules or respiratory folds, should be taken into account, considering the current lower solenogaster classification (SALVINI-PLAWEN, 1967, 1978; GARCÍA-ÁLVAREZ AND SALVINI-PLAWEN, 2007).

The three species with a common atrio-buccal cavity (*M. palifera*, *M. aciculata* and *M. morseae*) share the lack of abdominal spicules, and two of them have dorsoterminal sensory organs and respiratory folds (*M. palifera* and *M. aciculata*). Nevertheless, *M. morseae* was described from an immature specimen (KOCOT AND TODT, 2014), so the presence of these characters cannot be ruled out.

*M. adenota* and *M. schanderi* (species with separated atrium and mouth) have abdominal spicules. *M. schanderi* has also dorsoterminal sensory organ like the species with a common atrio-buccal opening, although it differs from these species as lacks respiratory folds. The presence or absence of dorsoterminal sensory organ and respiratory folds is unknown for *M. adenota*, for which data of the posterior region is not available. If additional material of both species (*M. adenota* and *M. profundorum* n. sp.) can be investigated in the future, respiratory folds together with abdominal spicules, dorsoterminal sensory organ, and a separated atrium and mouth might provide diagnostic criteria. The possibility of creating a new genus within the family, including the two Atlantic species (*M. adenota* and *M. profundorum* sp.nov.) and the northeast Pacific interstitial species (*M. schanderi*) could then be considered. Although the proximity of



the two Pacific species, already pointed out by the authors (KOCOT & TODT, 2014) and confirmed by Bergmeier *et al.* (2019), should not be underestimated. There is still agreement with SALVINI-PLAWEN (2003b), on that the lack of information currently impedes to rearrange the internal classification of Macellomeniidae.

While the claviform sclerites seem a consistent character for the family, the real, intraspecific, and even developmental variation of most of the other characters is unknown. In fact, this is a problem that concerns most of the solenogaster classification (BERGMEIER *ET AL.*, 2016). Undoubtedly, genetic information could bring out more about the monophyletic nature of Macellomeniidae or about its relation within solenogasters. Future integrative taxonomic studies would also be desirable to address the real classification and to decide on valid diagnostic characters. To date, two molecular-based studies included Macellomeniidae. According to the phylogenomic analysis in KOCOT *ET AL.* (2019), it is retrieved in a sister group relationship with Dondersiidae Simroth, 1893, which is consistent with the multi-marker analyses of BERGMEIER *ET AL.* (2019), even though in the latter with low support and polyphyletic Dondersiidae. In addition, in the COI single-gene maximum-likelihood tree of BERGMEIER *ET AL.* (2019; supplement) the included Macellomeniidae (*M. schanderi* and *M. morseae*) are monophyletic.

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Based on the current criteria, and after comparing the available diagnoses with the formal descriptions of the now six known species, updated diagnoses for the family and genus are proposed:

*Macellomeniidae*: Claviform sclerites (formed by a basal plate from which a solid needle emerges) arranged in a single layer. Serrated monoserial radula. Ventrolateral foregut glands of type A. With or without respiratory folds.

*Macellomenia*: Claviform sclerites. Common atrio-buccal cavity or mouth and atrium separated Unpair secondary genital opening. With or without dorso-terminal sensory organ. Without copulatory stylets. With or without abdominal spicules. With seminal receptacles.

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