



ORIGINAL ARTICLE

Two new species of *Waldo* Nicol, 1966 from sub-Antarctic waters (Bivalvia: Galeommatoidea)

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Abstract

Two new sub-Antarctic *Waldo* species (Bivalvia) are described: *Waldo digitatus* and *W. paucitentaculatus*. *Waldo digitatus* has a large, elongate–oval shell, with a short, horizontal dorsal margin, the valves showing a wide ventral gape, well separated from the anterior gape, and faint radial sculpture, fading toward shell margin. In addition, in this species the inhalant-pedal aperture is flanked by 5–15 pairs of tentacles. *Waldo paucitentaculatus* has a small, triangular–oval shell, with anterior and posterior half of dorsal margin long, sloping gently at similar angles, the anterior and ventral shell gapes coalesce to form a single, narrow and elongated gape, and radial sculpture well-marked and visible from beaks to ventral margin. Another distinctive character is the presence of only 1 or 2 pairs of tentacles bordering the siphonal-pedal aperture. Both species were found living as epibionts on the heart sea urchin *Abatus cavernosus*: *W. digitatus* is restricted to the perioral area and *W. paucitentaculatus* is more widely distributed, mainly on the oral surface.

Key words: *Bivalvia*, *Galeommatoidea*, *Waldo*

Introduction

The genus *Waldo* (Bivalvia) was proposed by Nicol (1966) to reallocate *Lepton parasiticum* Dall, 1876. Zelaya & Ituarte (2002) redescribed the type species and, after describing a second species, *Waldo trapezialis*, enlarged the generic diagnosis. According to the authors, *Waldo* is characterized by having a fragile shell, gaping at the margins, with an edentulous hinge both in adults and juveniles. In addition, the mantle extends beyond the shell margin, partially covering the shell surface, and forming a temporary anterior inhalant ‘siphon’. Another distinctive character is the presence of a variable number of tentacles along the mantle border. *Waldo* is an epibiont on irregular echinoids (Zelaya & Ituarte 2002). Zaixso et al. (2003) reported *Waldo parasiticus* as living on *Abatus cavernosus* (Philippi, 1845) from Puerto Deseado, Santa Cruz, Argentina, giving details on its ecology and behaviour. Other bivalves reported from the southern tip of South America also living in association with echinoids are *Scioberetia australis*

Bernard, 1895 (Bernard 1895a,b,c) and *Tellimya tehuelcha* Zelaya & Ituarte, 1912.

This article describes two new species of *Waldo* from sub-Antarctic waters. Aspects of their ecology, reproduction and habits are also given.

Materials and methods

Specimens of the irregular sea urchin *Abatus cavernosus* (Philippi, 1845), the host of *Waldo* species, were hand-collected from Puerto Deseado, Santa Cruz Province, Argentina. Between March 2009 and October 2011 more than 100 sea urchins were collected during maximum low tides from sandy flats at the lower intertidal and shallow subtidal zone. They were transported to the laboratory where the spatial distribution of the bivalves on the echinoid surface was documented. Bivalves were then removed from their hosts and maintained in aquaria to observe behavioural and biological information.

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Specimens were analysed by scanning electron microscopy (SEM). In the formal descriptions, shell length (L) refers to the maximum anterior–posterior distance, parallel to the anterior–posterior axis, and height (H) to the maximum dorso–ventral distance perpendicular to L. Mean value and standard deviation (SD) for the H/L ratio were calculated. For comparative purposes, the type specimens of *W. parasiticum* deposited as *Lepton parasiticum* at the United States National Museum (USNM 11907) were examined.

The anatomy was studied by dissecting specimens under a stereo microscope and by histological serial sections. Specimens for histology were fixed in Bouin's solution, dehydrated, embedded in Historesin (Leica®) and sectioned (3.5 µm thick). Sections were stained with haematoxylin and eosin.

Voucher specimens were deposited at Museo de La Plata (MLP) and Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN).

TAXONOMY

Superfamily Galeommatoidea Gray, 1840

Genus *Waldo* Nicol, 1966

Type species: *Lepton parasiticum* Dall, 1876 (OD)

***Waldo digitatus* sp. nov.**

Figures 1, 2, 3C–F

Types

Holotype (MACN-In 38620) and 17 paratypes (10 paratypes MACN-In 38621; 7 paratypes MLP 13585), all preserved in ethanol.

Type locality

47°45'S, 65°52'W, Puerto Deseado, Santa Cruz, Argentina.

Other material examined

Sixteen specimens from the type locality (MACN-In 38622).

Diagnosis

Shell large for the genus, elongate–oval, with a short, horizontally projecting dorsal margin. In ventral view, the posterior half of the right and left valves show a slight lateral depression. A wide ventral shell gape is well-separated from the anterior gape. Radial sculp-

ture faint, more evident near beaks, fading toward shell margin. Ventral margin smooth. Inhalant–pedal aperture flanked by 5–15 pairs of tentacles. Exhalant siphon short, with the upper border of the aperture slightly expanded and bent upwards.

Description

Shell extremely thin, large for the genus (maximum observed L = 4.0 mm), elongate–oval (H/L ratio = 0.69 ± 0.04 ; $n = 15$), slightly inequivalve, moderately inflated. Anterior end high, relatively widely rounded. Posterior end lower and slightly longer, somewhat triangular in profile (Figure 1A–H). Dorsal margin short, nearly straight, horizontal with respect to the anterior–posterior axis, forming well-marked angles at the junction with anterior and posterior margins (Figure 1A–H). Anterior part of dorsal margin longer than posterior one. Anterior margin with a nearly straight, sloping upper portion and an arcuate lower half. Ventral margin slightly crenulate, widely and unevenly curved, pronounced at anterior half. Upper portion of posterior margin long, straight, rapidly sloping, lower end shorter (Figure 1A–H). In ventral view, the posterior half of both valves show a slight lateral depression (Figure 1L,M). Anterior, ventral, and posterior gapes present, the ventral one more accentuated and well separated from the anterior (Figure 1L,M). Beaks low, subcentral, posteriorly directed. Prodissoconch ovate, inflated, about 380 µm in diameter, with fine, irregular commarginal lines. Prodissoconch boundary sharply marked (Figure 1K). Shell translucent, surface whitish, glossy, with visible growth lines and weak radial sculpture, most discernible near beaks, fading toward shell margin (Figure 1A–F). Hinge edentulous (Figure 1G,H,J). Shell margin anterior and posterior to beaks with irregular calcareous concretions (Figure 1J). Larval hinge edentulous, only minute rugosities present (Figure 1I).

Anatomy

Mantle thin, middle mantle fold (Figure 2C) extending beyond shell margin covering, most of the outer shell surface in live specimens (Figures 1A,B, 3C). External surface uneven, with granular aspect. Histologically, this corresponds to small papillae or warts formed by two or three swollen cells of the outer mantle epithelium (Figure 2H). Mantle opens widely in an antero–ventral inhalant–pedal aperture, extending for two-thirds of the total mantle margin length. At the anterior end, the mantle expands forming a large, forward- and upward-directed cowl (the so-called inhalant 'siphon') (Figures 1A,B, 2E,

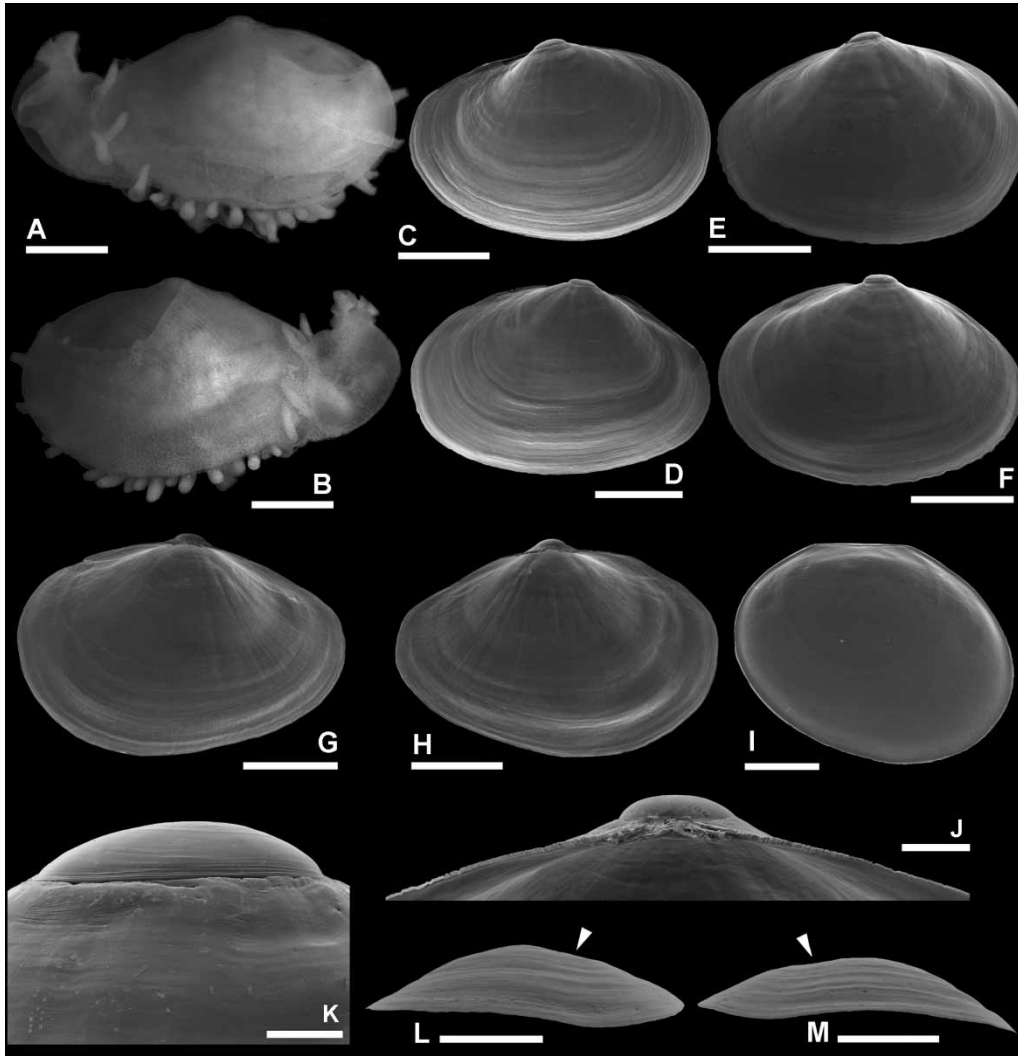


Figure 1. *Waldo digitatus* sp. nov. A,B: Holotype (A: Left view, B: Right view). C–M: Shell morphology. C–F: Outer view; C,E: right valve; D,F: left valve. G–I: Inner views; G: right valve adult specimen; H: left valve adult specimen; I: left valve of a larva. J: Detail of hinge plate. K: Prodissoconch. L,M: Ventral view of valves (arrows show the lateral depression). Scale bars: A–H,L,M = 1 mm; I,K = 100 μ m; J = 200 μ m.

3C,D). Posterior to the inhalant-pedal aperture, left and right middle mantle folds fuse for a short distance (the presiphonal suture), leaving posteriorly a small aperture: the exhalant siphon. Exhalant siphon short, obliquely truncated in lateral view, with dorsal margin of the opening slightly elongated and bent upward and slightly recurved (Figure 3D). Along shell margin, the mantle border projects in long cylindrical tentacles (Figures 1A,B, 3C,D): a latero-dorsal pair at base of inhalant siphon, 5–15 pairs along the border of the inhalant-pedal aperture, 1–3 pairs at the level of the presiphonal suture, and a single tentacle dorsal to the exhalant siphon. Tentacles along the inhalant-pedal aperture arranged in one or sometimes two alternate rows at each side (Figure 1A,B). The number of tentacles along the inhalant-pedal aperture is related to size: specimens of 1.4–2.2 mm length bear 5–7 pairs of tentacles,

specimens of 2.3–3.0 mm length bear 6–10 pairs, and specimens larger than 3.1 mm in length bear 11–15 pairs. Foot cylindrical, highly mobile, able to function as a creeping sole. A well-marked posterior heel and byssus gland is present (Figure 2A). A ciliated byssus groove runs mid-ventrally from the heel to just behind anterior tip of foot. Byssus composed of a single strong thread that arises from a bilobed byssus gland (Figure 2A,G). Only one demibranch, the inner, present (Figure 2B), high and long. Ascending lamellae three-quarters of the length of descending lamellae. Posterior ends of left and right ascending lamellae fused. Suprabranchial gland well-developed at the posterior end of suprabranchial chamber (Figure 2A,F). Labial palps large, club-shaped, comprising 5 sorting ridges. Transverse section of anterior and posterior adductor muscles small, ovate, the anterior one larger.

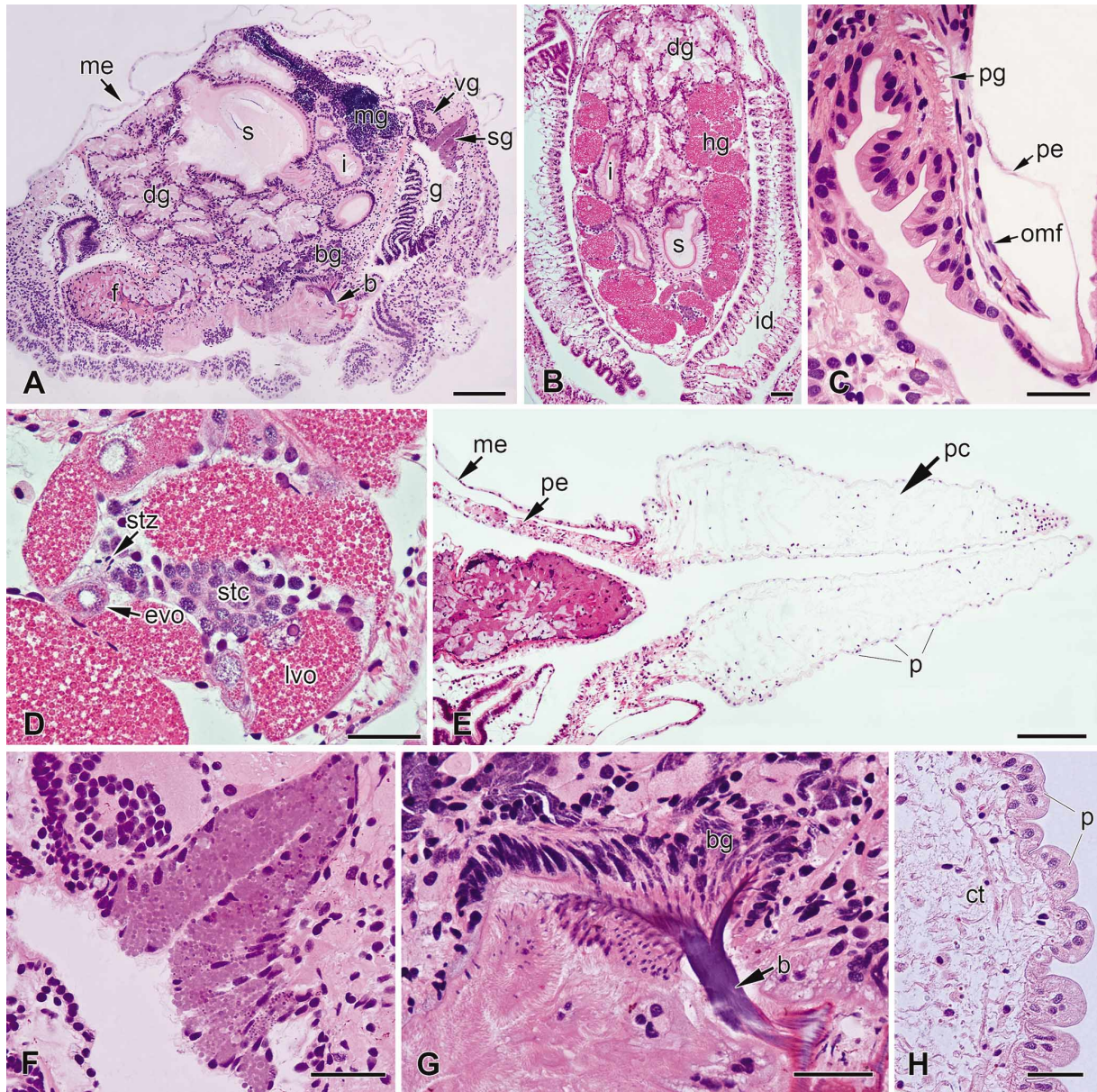


Figure 2. *Waldo digitatus* sp. nov. Anatomy of a 2.7-mm long specimen. A: Sagittal section showing the general internal anatomy. B: Transverse section of the anterior half of the visceral mass and gills. C: Detail of the free mantle margin. D: Detail of an acinus of the gonad. E: Anterior projection of the medium mantle fold to form the 'inhalant siphon'. F: Detail of the suprabranchial gland. G: Detail of the byssus gland. H: Detail of mantle papillae. b, byssus; bg, byssus gland; ct, connective tissue; dg, digestive gland; evo, early vitellogenic oocyte; f, foot; g, gill; hg, hermaphrodite gonad; i, intestine; id, inner demibranch; lvo, late vitellogenic oocyte; me, mantle extension; mg, male gonad; omf, outer mantle fold; p, papillae; pc, protruded cowl; pe, periostracum; pg, periostracal groove; s, stomach; sg, suprabranchial gland; stc, spermatocytes; stz, spermatozoids; vg, visceral ganglion. Scale bars A,E = 200 μ m; B = 100 μ m; C,D,F-H = 50 μ m.

Biological observations

Waldo digitatus was found living on the heart sea urchin *Abatus cavernosus*. Specimens live at the oral side, exclusively on the peristomial area. No more than two or three adult specimens were found on each sea urchin.

Waldo digitatus is simultaneously hermaphroditic and specimens are usually functional males or females, depending on the predominance of male or female tissues (Figure 2A,B,D). Eggs, of about 200 μ m in diameter, and embryos are brooded within

maternal gills up to an advanced developmental stage, being released as minute juveniles (Figure 3F); thus a free larval stage is completely suppressed. Up to 165 embryos per maternal individual were observed.

Gravid specimens maintained in laboratory conditions for a few hours spontaneously released their embryos: the maternal individual remained in a standing position (using the foot as a creeping sole) and started spasmodic rocking movements, while embryos were released through the exhalant siphon, remaining in a circle around the parental specimen

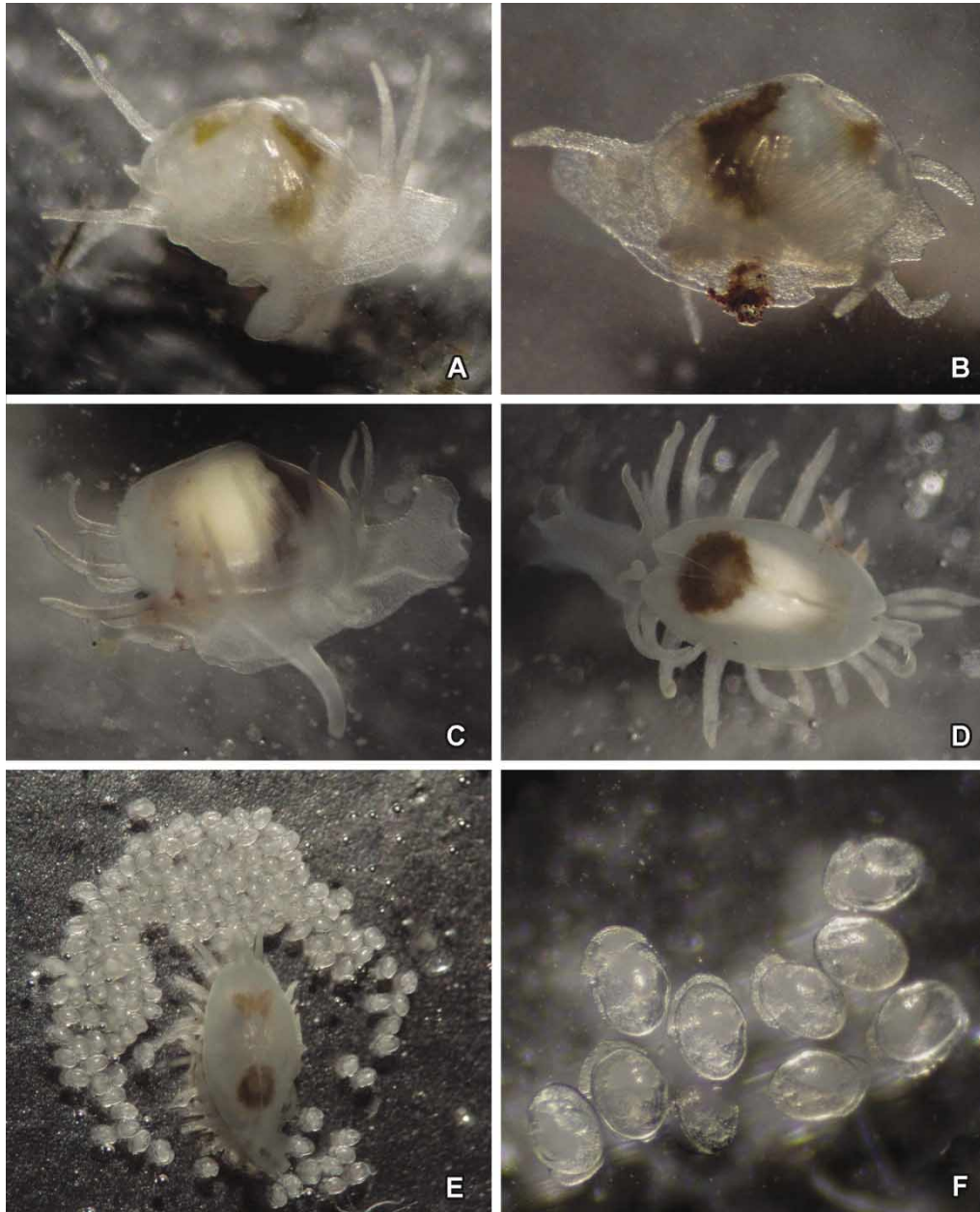


Figure 3. *Waldo paucitentaculatus* sp. nov. and *Waldo digitatus* sp. nov. Living specimens. A,B: *Waldo paucitentaculatus*, right and left lateral views. C-F: *Waldo digitatus*. C: Lateral view; D: dorsal view; E: adult specimen releasing larvae; F: detail of larvae.

(Figure 3E). In 2011, reproductive activity showed a peak of brooding in August.

Etymology

The species name refers to the large number of tentacles along the mantle border.

Remarks

In general, *Waldo digitatus* resembles *W. parasiticus* in its shell outline. Type specimens of *W. parasiticus* are poorly preserved and mostly destroyed. The species

was redescribed by Zelaya & Ituarte (2002) based mainly on specimens from South Georgia. Compared with the South Georgia specimens, *W. digitatus* differs by having a shorter dorsal margin and straight and sloping upper portions of anterior and posterior shell margins. In addition, the radial sculpture in *W. digitatus* is more clearly marked near the beaks, fading and almost disappearing toward the shell margin, whereas in *W. parasiticus*, the radial sculpture is marked and reaches the shell margin, which is distinctly crenulate.

Waldo digitatus differs from *W. trapezialis* Zelaya & Ituarte, 2002 in having more projecting anterior and

posterior ends, resulting in a more elongate shell outline, whereas *W. trapezialis* is shorter and higher, having a characteristic subtrapezoidal shell outline. The shell surface in *W. trapezialis* is completely smooth, whereas in *W. digitatus* the radial sculpture is faint but visible, particularly near the beaks. Both *W. parasiticus* and *W. trapezialis* lack the lateral shell depression shown by *W. digitatus* in ventral view.

The *W. digitatus* prodissoconch is about 380 µm in diameter, smaller than in *W. parasiticus* (470 µm) and in *W. trapezialis* (590 µm). Another difference between these species is the number of tentacles along the inhalant-pedal aperture. *W. digitatus* has up to 15 pairs of tentacles, whereas *W. parasiticus* has 5 pairs and *W. trapezialis* only 3 pairs.

***Waldo paucitentaculatus* sp. nov.**

Figures 3A,B, 4, 5

Types

Holotype (MACN-In 38617) and 20 paratypes (10 paratypes MACN-In 38618; 10 paratypes MLP 13586), all preserved in ethanol.

Type locality

47°45'S, 65°52'W, Puerto Deseado, Santa Cruz, Argentina.

Other material examined

Thirty-five specimens from the type locality (MACN-In 38619). Sixty loose valves (4 mounted for SEM), Puerto Basil Hall, Isla de los Estados (MACN-In-34938-1).

Diagnosis

Shell small for the genus, triangular-oval. Anterior and posterior halves of dorsal margin long, sloping gently at similar angles. In ventral view, right and left valves uniformly convex. Anterior and ventral gap coalescent, forming a single, narrow and elongated gap. Radial sculpture well-marked and visible from beaks to ventral margin, which is irregularly wavy. One or two pairs of tentacles along the border of the siphonal-pedal aperture. Exhalant siphon with evenly rounded distal edge.

Description

Shell small for the genus (maximum observed L = 2.2 mm), extremely thin, triangular-oval (H/L ratio = 0.71 ± 0.03; n = 15), slightly inequivalve,

moderately inflated. Dorsal margin long, angular, with anterior and posterior halves straight, sloping uniformly, forming an open angle (Figure 4A–E). Anterior margin evenly arcuate, continuous with ventral margin. Lower part of posterior margin flattened (Figure 4A–E). In ventral view, shell is uniformly convex (Figure 4I,J). Anterior and ventral gap coalescent, forming a continuous, narrow and elongated gap (Figure 4I,J). Posterior gap small. Beaks low, subcentrally located. Prodissoconch ovate, about 360 µm in diameter, with irregular commarginal lines, particularly evident at the boundary, which is clearly marked (Figure 4F). Shell translucent, whitish, glossy, sculptured with slightly marked growth lines, and well-marked radial sculpture, usually visible from beaks to shell margin, which is crenulate (Figure 4A–E). Hinge edentulous. Anterior and posterior to beaks, inner dorsal margin with irregular calcareous concretions (Figure 4K,L). Larval hinge edentulous (Figure 4M).

Anatomy

Animal whitish, translucent. Mantle thin, extending beyond shell margin, covering most of outer shell surface, bearing shallow warts or papillae (Figures 3A,B, 5A,C,F). A wide anterior inhalant-pedal aperture from which an extension of the mantle border forms a moderately large and protrusible cowl (the inhalant 'siphon') (Figure 3A). Posterior to inhalant-pedal aperture, left and right middle mantle folds fused in a relatively short presiphonal suture (Figure 5B). Exhalant siphon short with evenly rounded distal edge (Figure 3B). Long, cylindrical, and stout tentacles distributed on the mantle border along the shell margin (Figures 3A,B, 4A,B): one pair dorsolateral at the base of the cowl, one or two pairs at level of inhalant-pedal aperture, one (exceptionally two) pairs at the level of presiphonal suture, and a single tentacle dorsal, at the base of exhalant siphon. Foot cylindrical, highly mobile, able to function as a creeping sole, with well-marked posterior heel. Byssus gland present (Figure 5C,D) and well-developed. Byssus groove long, ciliated, running mid-ventrally, from the heel to just behind anterior tip of foot (Figure 5C,D). Only one, the inner, demibranch present, high and long. Ascending lamellae one-third the length of descending lamellae. Posterior ends of left and right ascending lamellae fused. Suprabranchial gland well-developed (Figure 5B). Labial palps club-shaped, comprising four sorting ridges. Transverse section of anterior and posterior adductor muscles small, ovate, the anterior slightly larger.

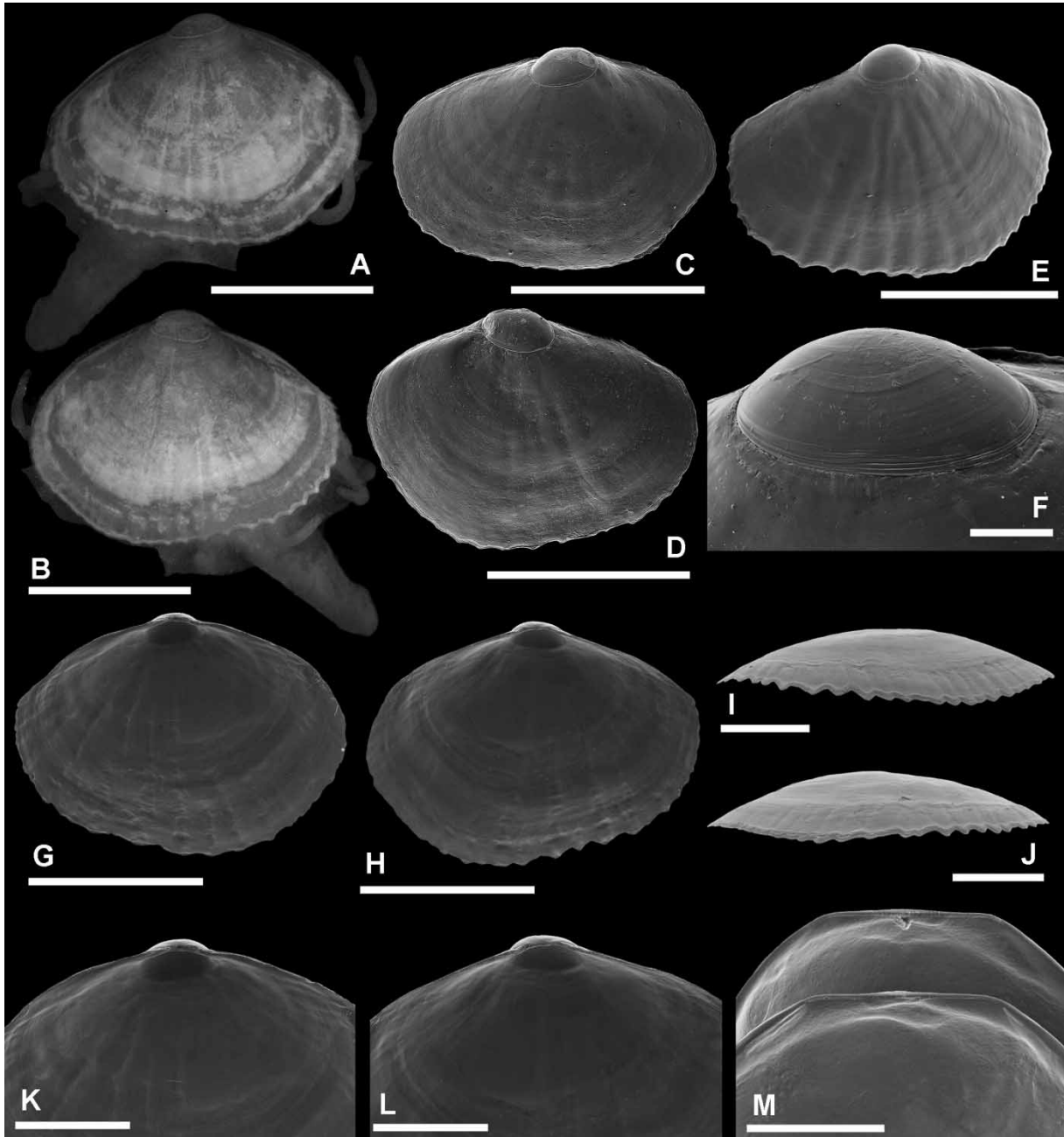


Figure 4. *Waldo paucitentaculatus* sp. nov. A,B: Holotype (A: left view, B: right view). C–M: Shell morphology. C–E: Outer view; C,E: left valve; D: right valve. F: Prodissoconch. G,H: Inner views, adult specimen; G: left valve; H: right valve. I,J: Ventral view of valves. K–M: Detail of hinge plate; K: left valve, adult specimen; L: right valve, adult specimen; M: left (upper) and right (lower) valves of a larva. Scale bars: A–E,G,H = 1 mm; F,M = 100 μ m; I–L = 500 μ m.

Biological observations

Waldo paucitentaculatus was found living on the irregular sea urchin *Abatus cavernosus*, coexisting with *W. digitatus*, being always more abundant than the latter. *W. paucitentaculatus* appears to be distributed mainly on the oral surface, being also present on the aboral surface, never on the periproct or the peristomial area.

Waldo paucitentaculatus is a simultaneous hermaphroditic, brooding species (Figure 5A,C,E). Eggs and embryos are incubated in the suprabranchial and

branchial spaces. The maximum number of embryos observed was 67 in a 1.9-mm length specimen. Brooding was observed in specimens larger than 1.4 mm length. The reproductive activity showed a peak in the number of brooding eggs and embryos in May.

Etymology

The species name refers to the reduced number of mantle tentacles.

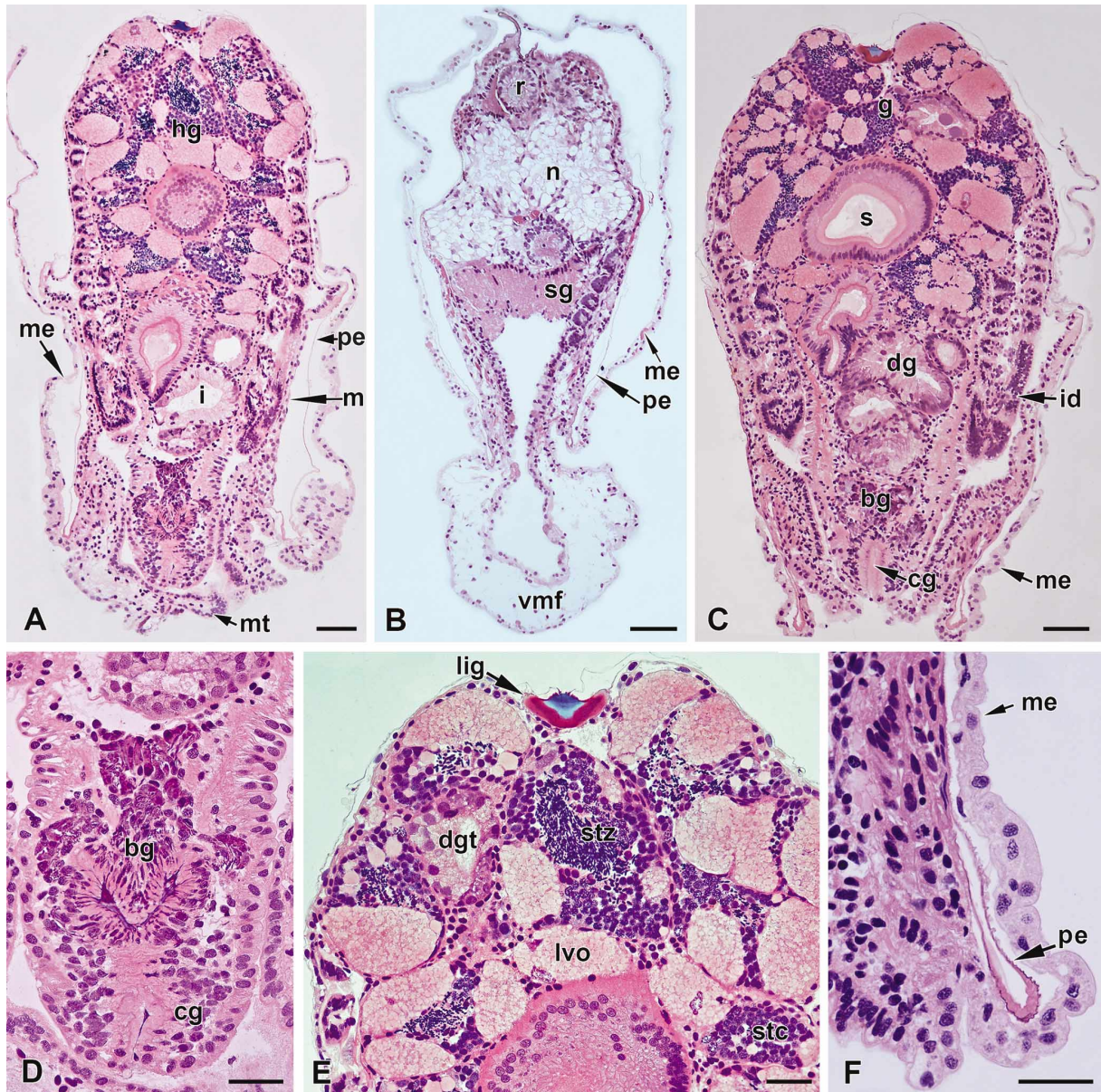


Figure 5. *Waldo paucitentaculatus* sp. nov. Anatomy. A: Transverse section of the anterior visceral mass of a 1.7-mm long specimen. B: Transverse section of the posterior visceral mass (same specimen as A). C: Transverse section of the mid visceral mass. D: Detail of byssus gland. E: Detail of gonad. F: Detail of mantle border. bg, byssus gland; cg, ciliated groove; dg, digestive gland; dgt, digestive gland tubule; g, gonad; hg, hermaphrodite gonad; i, intestine; id, inner demibranch; lig, ligament; lvo, late vitellogenic oocyte; m, mantle; me, mantle extension; mt, mantle tentacle; n, nephridium; pe, periostracum; r, rectum; s, stomach; sg, suprabranchial gland; stc, spermatocytes; stz, spermatozooids; vmf, ventral mantle fusion. Scale bars: A–C = 100 μ m; D–F = 50 μ m.

Remarks

Waldo paucitentaculatus resembles in general shell shape *W. parasiticus* and *W. digitatus*, from which it differs in having a longer dorsal margin, with the anterior and posterior parts clearly sloping, whereas in *W. parasiticus* and *W. digitatus* this margin is shorter and horizontal. In addition, the lower part of the posterior shell margin is straight in *W. paucitentaculatus*, whereas in *W. parasiticus* and *W. digitatus* it is evenly curved. *Waldo trapezialis*, another sub-Antarctic species, differs from *W. paucitentaculatus*

in having a trapezoidal shell outline. Furthermore, the anterior and ventral shell gapes are well separated in *W. parasiticus*, *W. digitatus* and *W. trapezialis*, whereas in *W. paucitentaculatus* they are coalescent, forming a single narrow and elongated gape. Prodisoconch size is similar in *W. paucitentaculatus* and *W. digitatus* (360 and 380 μ m diameter, respectively), but smaller than those of *W. parasiticus* (470 μ m) and *W. trapezialis* (590 μ m). *Waldo paucitentaculatus* is similar to *W. parasiticus* in having a well-developed radial sculpture and crenulate shell margin, differing from *W. digitatus*,

which has a weak shell sculpture only visible near the beaks, and *W. trapezialis*, which lacks radial sculpture. The two latter species have smooth shell margins. *Waldo paucitentaculatus* has only 1 or 2 pairs of tentacles along the inhalant-pedal aperture, *W. trapezialis* has 3 pairs, *W. parasiticus* 5 pairs, and *W. digitatus* up to 15 pairs of tentacles. Although the number of tentacles varies with size in *W. digitatus*, even smaller specimens have a greater number of tentacles than *W. paucitentaculatus*: specimens of 1.4–2.2 mm length of *W. digitatus* have 5–7 pairs of tentacles, whereas specimens of the same size of *W. paucitentaculatus* have 1 or at most 2 pairs.

Discussion

Since Nicol (1966) erected the genus *Waldo*, and for almost 40 years afterwards, only one species – *W. parasiticus* – was reported within this genus. That species was regarded as widespread in Antarctic and sub-Antarctic (Magellanic) waters (Soot-Ryen 1959; Zelaya & Ituarte 2002; and references therein). Based on a number of morphological and anatomical characters, Zelaya & Ituarte (2002) described a second species: *Waldo trapezialis*. However, no previous authors examined the conspecificity of the Magellanic and Antarctic records of ‘*Waldo parasiticus*’. The present study describes two new *Waldo* species from sub-Antarctic (Magellanic) waters, which closely resemble *W. parasiticus* in shell morphology (see the differences listed in the Remarks section). Based on the two new species described here, the occurrence of ‘*Waldo parasiticus*’ in the sub-Antarctic (Magellanic) waters is regarded as doubtful. Soot-Ryen (1959) reported *Lepton* cf. *parasiticum* from Southern Chile, but the specimen described by the author in his plate 2, figure 19 seems to correspond to *W. digitatus*. Zelaya & Ituarte (2002) reported and illustrated specimens from Isla de los Estados (MACN 22219) as *W. parasiticus*. The re-examination of this material allowed us to conclude that some of these specimens actually correspond to *W. paucitentaculatus* (now under MACN-In 34938-1). On the other hand, the two species here described were obtained at the same locality from where Zaixso et al. (2003) reported *W. parasiticus* as epibiont on *Abatus cavernosus*. The authors described a sort of space selectivity on the host according to the size of bivalves: the larger specimens restricted to the buccal area and the smaller specimens widely distributed on the oral and aboral surfaces. The specimens reported by Zaixso et al. (2003) as *W. parasiticus* actually correspond to *W. digitatus* (the ‘larger’ specimens) and *W. paucitentaculatus* (the ‘smaller’ specimens).

The two species described in this study proved to be common, being present on nearly all specimens of *Abatus cavernosus* at the study site.

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