691

Cah. Biol. Mar. (2007) 48 : 155-168

A new species of *Antygomonas* (Kinorhyncha: Cyclorhagida) from the Atlantic coast of Florida, USA

Martin V. SØRENSEN
Ancient DNA and Evolution Group, Biological Institute, University of Copenhagen, Juliane Maries Vej 30, 2100 Copenhagen, Denmark. Email: mvsorensen@bi.ku.dk

Abstract: A new kinorhynch species, *Antygomonas paulae* sp. nov., is described from the West Atlantic coast off Fort Pierce, Florida, USA. The new species is characterized by the presence of a first trunk segment consisting of one complete ring with concavities in the anterior middorsal and midventral margins, and the following 10 segments consisting of a tergal and two sternal plates. Middorsal spines are present on all segments, whereas lateroventral/lateral accessory cuspidate and acicular spines are present on trunk segments 2 through 9. *Antygomonas paulae* sp. nov. is distinguished from the two currently described species of *Antygomonas* by the combination of absence of cuspidate spines on trunk segment 6 and the presence of lateroventral cuspidate spines and lateral accessory acicular spines on trunk segment 9. The diagnostic characters and the general morphology of the new species are discussed with special emphasis on the introvert and appearance and distribution of sensory spots.

Résumé : *Une nouvelle espèce du genre* Antygomonas *(Kinorhyncha : Cyclorhagida) de la côte atlantique de Floride, USA.* Une nouvelle espèce de kinorhynque, *Antygomonas paulae* sp. nov., est décrite sur la côte ouest atlantique au large de Fort Pierce, Floride, USA. La nouvelle espèce est caractérisée par la présence d'un premier segment du tronc constitué d'un anneau complet et de concavités sur les marges antérieures médiodorsales et médioventrales et des 10 segments suivants constitués d'une plaque tergale et de deux plaques sternales. Des épines médiodorsales sont présentes sur tous les segments alors que des épines accessoires latéroventrales/latérales cuspides et aciculaires sont présentes sur les segments 2 à 9 du tronc. *Antygomonas paulae* sp. nov. se distingue des deux espèces déjà décrites dans le genre *Antygomonas* par la combinaison de l'absence d'épines cuspides sur le segment 6 du tronc et la présence d'épines cuspides latéroventrales et d'épines accessoires latérales aciculaires sur le segment 9 du tronc. Les caractères diagnostiques et la morphologie générale de la nouvelle espèce sont discutés avec une attention particulière sur l'introvert et l'apparence ainsi que la distribution de tâches sensorielles.

Keywords: Kinorhyncha • *Antygomonas paulae* sp. nov. • Florida • New species • Marine meiofauna • Phylogeny

Reçu le 16 octobre 2006 ; accepté après révision le 27 mars 2007.
Received 16 October 2006; accepted in revised form 27 March 2007.

Introduction

Kinorhynchs are marine, psammobiontic microscopic animals. They are found throughout the world, but reports on their distribution are rather patchy (see Adrianov & Malakhov, 1999 for review). However, some well investigated regions exist and especially the Mediterranean, the coast off Washington State and the West Atlantic have been investigated more intensively. Most kinorhynch reports from the Mediterranean date back to the first part of the last century or earlier (Metschnikoff, 1869; Pagenstecher, 1875; Panceri, 1876; Zelinka, 1928), but more recent contributions exist as well (Marcotte & Coull, 1974; Dinet, 1976; Higgins, 1978; Nebelsick, 1990 & 1992). The kinorhynch fauna from the Northwest American coast has mostly been examined in Puget Sound around Friday Harbor (Higgins, 1960 & 1961; Adrianov & Higgins, 1996), whereas the Atlantic coast of North America has been sampled from Maine to Florida (Blake, 1930; Higgins, 1964a, 1964b, 1965, 1972, 1977 & 1990; Horn, 1978). Especially the calcareous sediments in the subtropical waters off the Floridian west coast support a high biodiversity of meiofaunal organisms, and through four decades the Smithsonian Marine Station at Fort Pierce has facilitated research of various meiofaunal groups in this area (Reiger & Ruppert, 1978; Kristensen & Higgins, 1984 & 1989; Higgins & Kristensen, 1986; Norenburg, 1988; Higgins, 1990; Thomas et al., 1995; Newman et al., 2000; Hochberg, 2004). Robert P. Higgins collected kinorhynchs in the psammon off Fort Pierce through the 1980's and one of his most significant achievements was the description of the new family Zelinkaderidae (see Higgins, 1990). More recently I have had the opportunity to collect in the area at several occasions, and this work has until now resulted in the description of three new species, inclusive one new genus (Sørensen et al., 2006; Sørensen et al., in press). The present study presents the description of the fourth new species from this area, and should hereby finalize the series of contributions about kinorhynchs from the Fort Pierce area on the Floridian East coast.

The phylum Kinorhyncha currently consists of 157 species based on the description of adult stages and 17 genera, inclusive the new genus from the Floridian East coast. Of these, 121 species, however, are distributed on three genera only, which means that each the remaining 13 genera consist of one to five species only. It remains uncertain why these particular three genera have been that successful in terms of species diversity, whereas other genera apparently contain relatively few species. Hence, the species-poor genera have for obvious reasons attracted special attention in systematic and phylogenetic works. The species described herein belongs to the genus *Antygomonas* Nebelsick, 1990 that currently consists of two species only, *A. incomitata* Nebelsick, 1990 and *A. oreas* Bauer-Nebelsick, 1996. The new species, *A. paulae* sp. nov., is described using light- and scanning electron microscopical techniques, and special emphasis is put on the morphology of the introvert and neck region, and the shape and distribution of sensory spots and spines.

Materials and Methods

The specimens were sampled with a meiofauna dredge from the research vessel R/V Sunburst, belonging to the Smithsonian Marine Station at Fort Pierce. They were collected from sandy sediments (*Dentalium* sand) on July 22, 2003 at 15.1 m in the Atlantic Ocean, on the locality Inlet Sand Spoil off Fort Pierce, Florida (27°29.56'N, 080°12.23'W). The water temperature was 15.3°C and the salinity was 35. Additional material was collected in April 2004 and May 2006 on the same, and nearby localities (5 mile station: 27°29.96'N, 080°12.67'W; 6 mile station: 27°29.11'N, 080°11.02'W). The sediment on the two latter localities consisted of fine shell gravel. The specimens in the samples were either freshwater-shocked or anesthetized with a 30‰ solution of magnesium sulphate and decanted through a net with 63 µm mesh width.

Animals were sorted under an Olympus SZX12 dissecting microscope. Specimens for light microscopy were dehydrated through a graded series of glycerine and mounted in Fluoromount G®. The mounted specimens were examined and photographed using Nomarski differential interference contrast with an Olympus BX51 microscope equipped with Colorview I digital camera. Habitus drawings were made with a camera lucida.

Specimens for SEM were dehydrated through a graded series of ethanol, transferred to acetone and critical point dried. The dried specimens were mounted on aluminium stubs, sputter coated and examined with a JEOL JSM-6335F field emission scanning electron microscope.

From the Natural History Museum in Vienna and Dr. Monika Bright's personal collection, specimens of *Antygomonas oreas* were borrowed for comparison with *Antygomonas paulae* sp. nov.

Results

Order Cyclorhagida Zelinka, 1896

Suborder Cyclorhagae Zelinka, 1896

Family Antygomonidae* Adrianov & Malakhov, 1994

Antygomonas paulae sp. nov.

Diagnosis

Neck consisting of 16 placids, articulating with trunk segment 1. First trunk segment consisting of one complete

*Adrianov & Malakhov (1994) published the family-group name Antigomonidae, based on the incorrect spelling *Antigomonas* of *Antygomonas* Nebelsick, 1990. The correct family group name is Antygomonidae (see ICZN Article 35.4).

ring; anterior margin with dorsal and ventral concavities. Internal markings of partly differentiated sternal plate visible. Trunk segments 3-10 more triangular in cross-section, consisting of one tergal plate and two sternal plates; sternal plates completely separated at midventral line, tergal and sternal plates separated by intracuticular articulations only. Middorsal spines present on trunk segments 1 through 11, located near posterior margins of segments; posterior margins with small notch at base of middorsal spine. Segment 2 with pair of thick, lateroventral cuspidate spines located close to pair of much smaller, flexible spines. Segments 3 through 9 with lateroventral/lateral accessory acicular spines; segments 5, 8 and 9 additionally with pair of lateroventral/lateral accessory cuspidate spines. Cuspidate spines in lateroventral position on segments 5 and 9; cuspidate spines on segment 8 in lateral accessory position. Segment 10 with laterodorsal acicular spines. Terminal trunk segment with middorsal spine, midterminal spine, lateral terminal spines and lateral terminal accessory spines; lateral terminal spines and lateral terminal accessory spines of same lengths.

Etymology

The species is named after Dr. Valerie Paul, scientific director of the Smithsonian Marine Station at Fort Pierce, in recognition of her help and kind hospitality during my visits at the station.

Type material

All type material was obtained from a sample taken on July 22, 2003 in the Atlantic Ocean, at the locality Inlet Sand Spoil off Fort Pierce, Florida. Position: 27°29.559'N 080°12.233'W. Holotype: Adult male, mounted in Fluoromount G® (ZMUC KIN-191). Allotype: Adult female, mounted in Fluoromount G® (ZMUC KIN-192). Paratypes: 6 adult females and 6 adult males, mounted in Fluoromount G® (ZMUC KIN-193 to KIN-204). Additional material was collected at the same and nearby localities (5 and 6 miles from the Station) in April 2004 and May 2006. All types are stored at the Zoological Museum, University of Copenhagen. Additional material is stored in MVS's personal collection.

Description

The adult specimen consists of a head, a neck and eleven trunk segments (Figs 1A-B, 3 & 5A-C). Measurements and dimensions are given in Table 1. A summary of spine, tubule and sensory spot locations is given in Table 2.

The head consists of a narrow mouth cone with helioscalids, two rings of inner oral styles and one ring with outer oral styles, and an introvert with seven rings of scalids (Figs 2 & 4A-C). In the following description the ring with

Table 1. *Antygomonas paulae* sp. nov. Measurements of adults including number of measured specimens (n) and standard deviation (S.D.). Abbreviations: ac, acicular spine; cu, cuspidate spine; LD, laterodorsal; LTAS, lateral terminal accessory spine; LTS, lateral terminal spine; LV, lateroventral; MD, middorsal; MTS, midterminal spine; S1-11, lengths of trunk segments 1-11; TL, trunk length; f, female; m, male.

Tableau 1. *Antygomonas paulae* sp. nov. Mesures réalisées sur des individus adultes. Nombre de spécimens (n) et écart-types (S.D.). Abréviations : ac, épine aciculaire ; cu, épine cuspide ; LD, latérodorsal ; LTAS, épine accessoire latérale terminale ; LTS, épine terminale latérale ; LV, latéroventral ; MD, médiodorsal ; MTS, épine médioterminale ; S1-S11, longueurs des segments 1-11 du tronc ; TL, longueur du tronc ; f, femelle ; m, mâle.

Character	n	Range	Mean	S.D.
TL	6	423 – 495 µm	455 µm	29.2
S1	7	38 – 50 µm	45 µm	4.0
S2	7	38 – 48 µm	42 µm	3.7
S3	7	34 – 42 µm	38 µm	3.1
S4	7	33 – 42 µm	38 µm	3.1
S5	7	38 – 45 µm	41 µm	2.2
S6	7	41 – 48 µm	45 µm	2.3
S7	7	43 – 53 µm	48 µm	3.7
S8	7	47 - 55 µm	50 µm	2.8
S9	7	44 – 53 µm	50 µm	3.2
S10	7	46 – 52 µm	49 µm	2.0
S11	7	32 – 42 µm	37 µm	4.1
MD 1	7	34 – 42 µm	39 µm	2.4
MD 2	7	47 – 56 µm	50 µm	3.5
MD 3	7	54 – 64 µm	59 µm	3.7
MD 4	7	69 – 89 µm	81 µm	6.7
MD 5	7	78 – 90 µm	85 µm	4.8
MD 6	6	72 – 90 µm	84 µm	6.3
MD 7	7	74 – 92 µm	83 µm	6.6
MD 8	7	79 – 91 µm	86 µm	3.7
MD 9	7	72 – 87 µm	81 µm	5.5
MD 10	6	68 – 79 µm	73 µm	3.9
LD 10 (f)	3	53 – 78 µm	58 µm	8.7
LD 10 (m)	4	57 – 70 µm	64 µm	5.6
MD 11	7	218 – 280 µm	246 µm	22.3
LV 2 (cu)	7	32 – 38 µm	36 µm	2.3
LV 2 (ac)	2	12 – 14 µm	13 µm	1.4
LV 3	7	33 – 38 µm	35 µm	2.0
LV 4	7	41 – 51 µm	45 µm	3.8
LV 5 (cu)	7	35 – 39 µm	37 µm	1.6
LV 5 (ac)	7	48 – 57 µm	54 µm	3.4
LV 6	7	42 – 61 µm	55 µm	6.6
LV 7	7	57 – 66 µm	61 µm	3.5
LV 8 (cu)	7	34 – 46 µm	41 µm	3.7
LV 8 (ac)	6	62 – 78 µm	72 µm	6.3
LV 9 (cu)	7	37 – 45 µm	40 µm	2.5
LV 9 (ac)	6	70 – 85 µm	75 µm	5.6
LTS	7	114 – 147 µm	131 µm	12.3
LTAS	7	115 – 144 µm	134 µm	9.9
LTAS/LTS	7	89% – 118%	103%	11.0
MTS	4	364 – 506 µm	458 µm	65.6
MTS/TL	4	85% – 119%	104%	14.9

Table 2. *Antygomonas paulae* sp. nov. Summary of nature and location of spines and sensory spots arranged by segments. Abbreviations: MD, middorsal; PD, paradorsal; SD, subdorsal; LD, laterodorsal; ML, midlateral; LA, lateral accessory; LV, lateroventral; VL, ventrolateral; VM, ventromedial; ac, acicular spine; cu, cuspidate spine; ltas, lateral terminal accessory spine; lts, lateral terminal spine; mt, midterminal spine; ss, sensory spot.

Tableau 2. *Antygomonas paulae* sp. nov. Synthèse de la nature et de la localisation des épines et des tâches sensorielles arrangées en séries. Abréviations : MD, médiodorsal ; PD, paradorsal ; SD, sudorsal ; LD, latérodorsal ; ML, médiolatéral ; LA, accessoire latéral ; LV, latéroventral ; VL, ventrolatéral ; VM, médioventral ; ac, épine aciculaire ; cu, épine cuspide ; ltas, épine accessoire latérale terminale ; lts, épine terminale latérale ; mt, épine médioterminale ; ss, tâche sensorielle.

Segment	MD	PD	SD	LD	ML	LA	LV	VL	VM
1	ac	ss		ss					ss
2	ac	ss			ss		cu, ac		
3	ac	ss					ac	ss	
	ac	ss				ss	ac	ss	
5	ac	ss				ac	cu		
6	ac	ss			ss		ac	ss	
7	ac	ss			ss, ss	ss	ac	ss	
8	ac	ss				cu	ac	ss	
9	ac	ss		ss		ac	cu		
10	ac	ss	ss	ss, ac		ss			
11	ac, mt	ss, ss				ltas	ss, lts		

the outer oral styles will define ring 0, hence rings in the internal introvert will be numbered -1, -2, and -3 for the innermost ring, whereas rings in the introvert will be referred to as ring 1 (spinoscalids) to ring 7 (trichoscalids). The internal introvert shows one ring (ring -3) with 5 helioscalids, followed by two rings with 5 (ring -2) and 10 (ring -1) inner oral styles, respectively. The following ring (ring 0) consists of nine outer oral styles with two segments and pointed tips (Figs 2 & 4C). The first ring in the introvert consists of 10 spinoscalids, with monoliform tips consisting of two short segments. The base of each spinoscalid is equipped with a dense row of long fringes (Fig. 4A). Rings 2 to 6 consist of 10, 20, 5, 15 and 15 scalids, respectively, and the outermost 7th ring has 14 spinoscalids (Fig. 2). Instead of describing the introvert armature ringwise, the introvert can also be divided into 10 sections defined by radii drawn through each spinoscalid. The midventral section will be section 1, followed in clockwise direction by section 2, etc (Fig. 2). All sections (except the middorsal section 6) would contain 1 oral style, and section 1 would furthermore have seven scalids and one trichoscalid; sections 2, 4, 8, 10 (Figs 2 & 4B): six scalids and one trichoscalid; sections 3, 5, 7, 9 (Figs 2 & 4A): seven scalids and two trichoscalids, and the middorsal section 6: six scalids and one trichoscalid. This division of the introvert may be more convenient for comparison of interspecific variation (see discussion below).

The neck consists of sixteen placids (11-15 µm in length) that alternate with another sixteen pairs of interstitial placids. The midventral placid is broadest (14 µm), and flanked to each side by two pairs of relatively narrow placids (7 µm). The remaining placids are more uniform in size (10-13 µm). The placids are separated from the first trunk segment, but appear to be fused with the cuticle that forms the head and introvert. SEM examinations of the interstitial placids revealed that they are not isolated elements, but rather flexible connections between the main scalids. The interstitial placids are somewhat wedge- or elongate diamond shaped, with a medial, longitudinal fold (Fig. 4D). The surface is densely plicate, like the cuticle of the head, and anteriorly they fuse with the head cuticle.

Segment 1 consists of one complete cuticular ring. Indistinct ventrolateral lines on the ventral side (Figs 1B & 3C) could indicate a partial division of the segment into a tergal and a sternal plate, but this is uncertain. The cuticle on this and the following segments appears to be relatively thin and flexible. In cross-section the segment (as well as the following) appears conspicuously triangular. A middorsal spine, flanked by paradorsal sensory spots is present on this and the following trunk segments (Figs 1A, 3A-B & 5A, E). The sensory spots belong to type 1, i.e. consist of small cuticular papillae and pores (see Fig. 4H for corresponding sensory spot on segment 7). Only one pore was visible in the paradorsal sensory spots. The tergal plate is slightly elevated anterior to the insertion point of the spine (Fig. 5E). Paired sensory spots are furthermore present in a laterodorsal (closest to anterior segment margin) and a ventromedial (closest to posterior segment margin) position (Fig. 4E-F and inset). Both the laterodorsal and ventromedial sensory spots are rounded and belong to type 2, i.e., consisting of short papillae and pores, but with one of the pores elevated on the tip of a short tube. Both the laterodorsal and ventromedial sensory spots have two central pores, whereas the third one is more laterally positioned and forms a small tube (Figs 4E-F). The anterior margin of the segment is slightly concave on the dorsal and ventral sides (Figs 1A-B & 3A), whereas the posterior margin is straight. The margin of the actual segment is covered externally, however, by a thin, overlapping cuticular extension that extends posteriorly and exceeds the segment margin (Fig. 5D-E). The margin of the

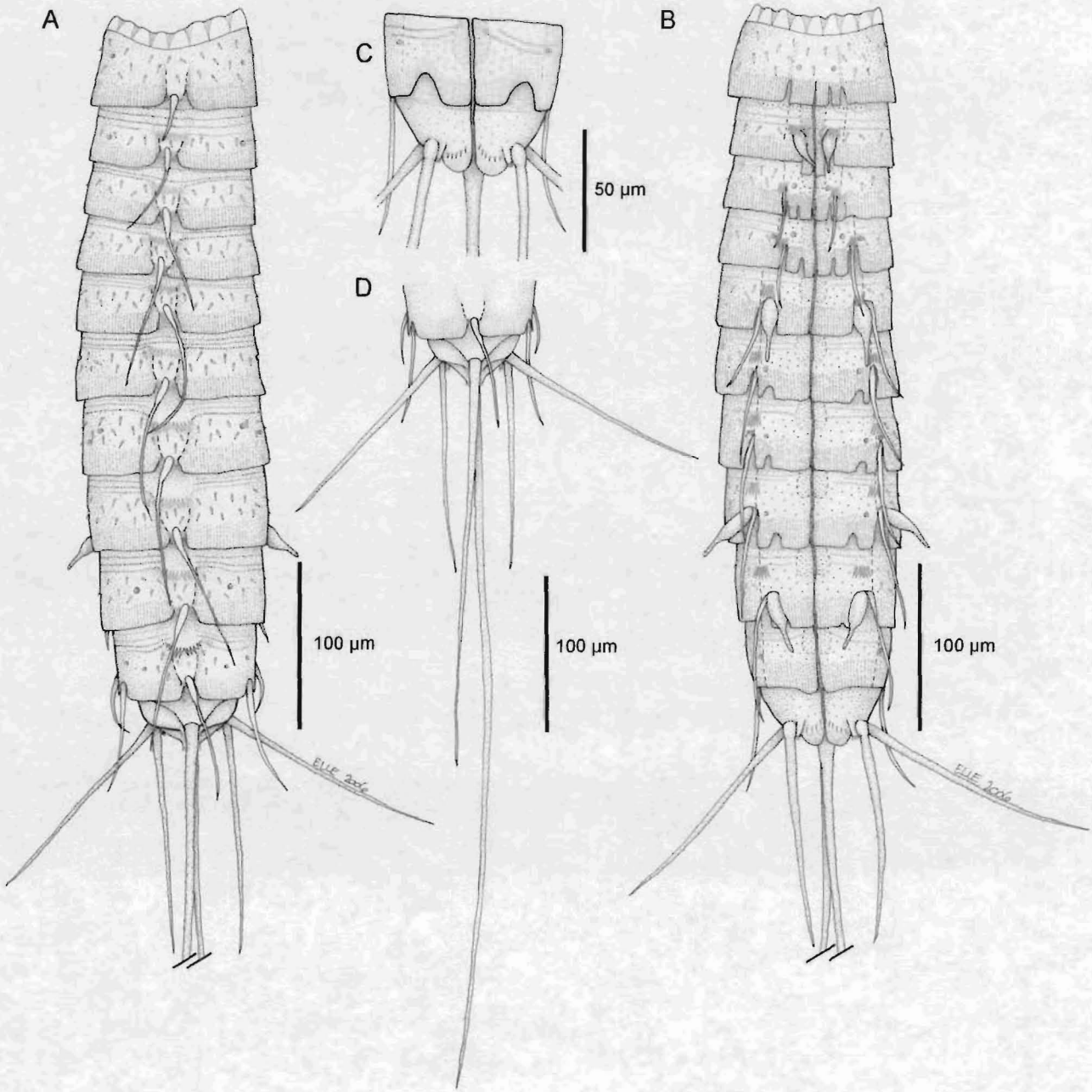


Figure 1. *Antygomonas paulae* sp. nov. **A.** Male, dorsal view. **B.** Male, ventral view. **C.** Female, Trunk segments 10-11, ventral view. **D.** Female, terminal segments and spines, dorsal view.

Figure 1. *Antygomonas paulae* sp. nov. **A.** Mâle, vue dorsale. **B.** Mâle, vue ventrale. **C.** Femelle, segments 10-11 du tronc, vue ventrale. **D.** Femelle, épines et segments terminaux, vue dorsale.

segmental extension is straight on the dorsal and lateral sides, except for the notch around the middorsal spine (Fig. 5E). On the ventral side, it forms a thin but broad, caudally extending lobe with deep indentions (Fig. 5D). Cuticular hairs are scattered over the segment. The hairs resemble small leaves that attach with a narrow stalk in a cuticular depression (Fig. 4G). The distal part of the hair is much broader, with bent lateral sides that give each hair a crescentic appearance in cross-section. Cuticular hairs in juvenile specimens are spiniform, pointed and much thinner.

Segment 2 and the following 9 segments consist of one tergal plate and two sternal plates (Figs 1A-B & 3C-D). The

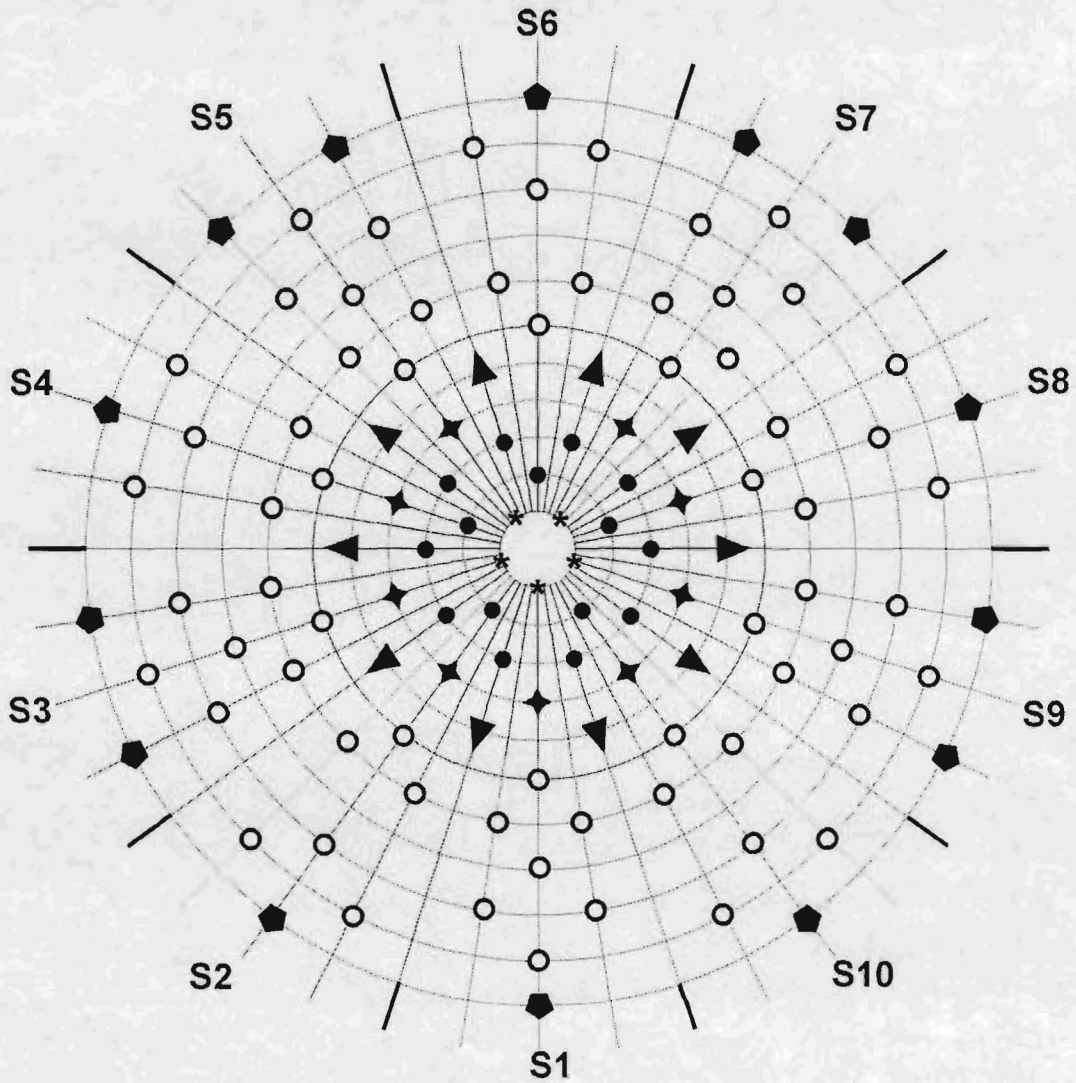


Figure 2. *Antygomonas paulae* sp. nov. Diagram of mouth cone and introvert showing distribution of oral styles and scalids.

Figure 2. *Antygomonas paulae* sp. nov. Diagramme du cône de la bouche et de l'introvert montrant la distribution des stylets oraux et des scalides.

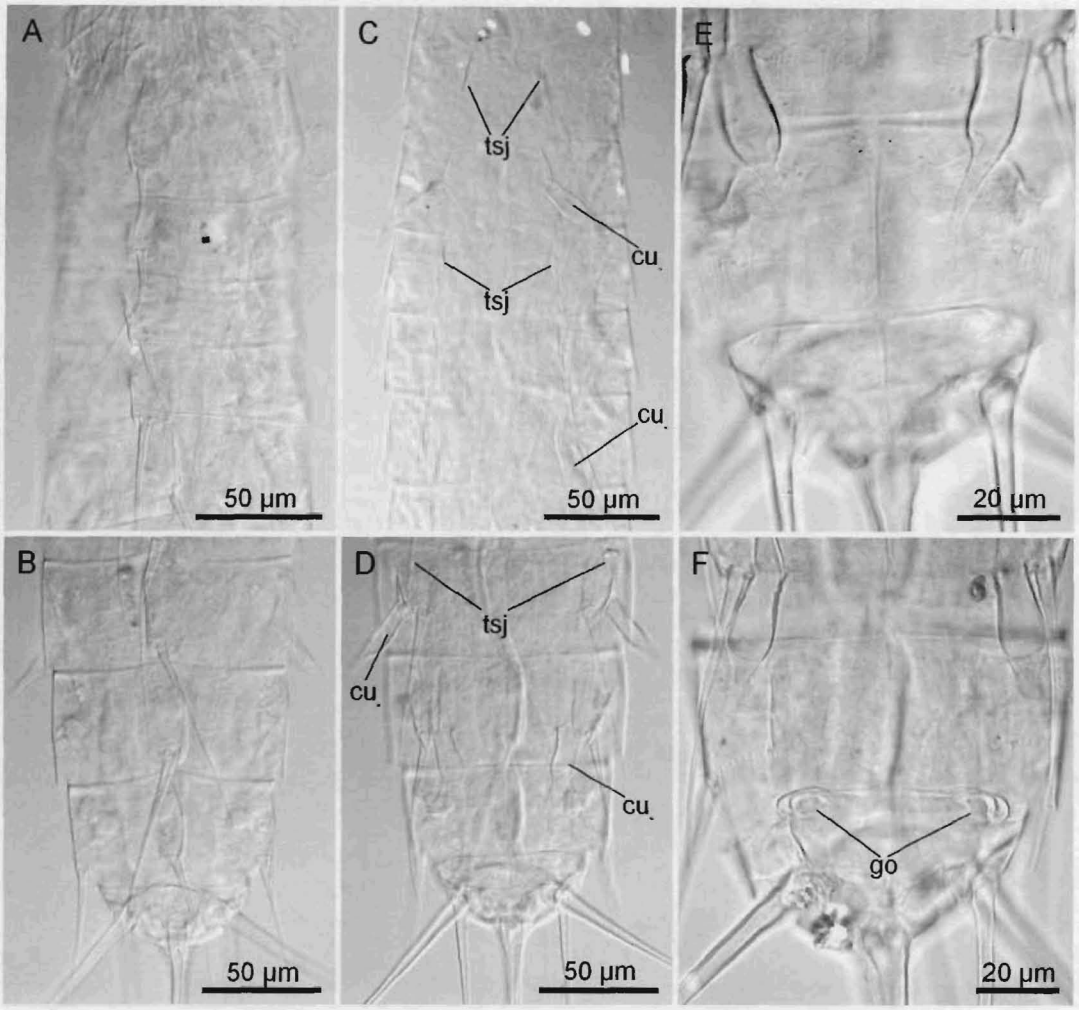


Figure 3. *Antygomonas paulae* sp. nov. Light microscope photos. **A.** Anterior segments, dorsal view. **B.** Posterior segments, dorsal view. **C.** Anterior segments, ventral view. **D.** Posterior segments, ventral view. **E.** Trunk segments 10 to 11 in male, ventral view. **F.** Trunk segments 10 to 11 in female, ventral view. Abbreviations: cu, cuspidate spines; go, female gonopores; tsj, tergal-sternal junctions.

Figure 3. *Antygomonas paulae* sp. nov. Photos au microscope photonique. **A.** Segments antérieurs, vue dorsale. **B.** Segments postérieurs, vue dorsale. **C.** Segments antérieurs, vue ventrale. **D.** Segments postérieurs, vue ventrale. **E.** Segments 10 et 11 du tronc chez le mâle, vue ventrale. **F.** Segments 10 et 11 du tronc chez la femelle, vue ventrale. Abréviations : cu, épines cuspides ; go, gonopores femelles ; tsj, jonctions tergo-sternales.

lateral tergal-sternal junctions are indistinct, whereas the midventral junction is more conspicuous. A middorsal spine with paradorsal sensory spots is present. The spine and its base resemble the one on the previous segment, but in addition the middorsal spine on segment 2 and the following 8 segments has a conspicuous fringe on the elevation right behind the base of the spine (Figs 1A & 5E). A pair of large cuspidate spines is located in a lateroventral position, and a pair of much smaller, flexible spines is located at the bases of the cuspidate spines, at the side facing the midventral line (Figs 1B & 5F). Sensory spots belong to type 2, have two central pores and a lateral one on a tube, and are located in a midlateral position. Leaf like cuticular hairs are lightly scattered over the segment, except on the posterior segmental extensions. The anterior part of the tergal plate has two to three secondary fringes (Fig. 5E). The fringes are rather small, but the most posterior one becomes more prominent middorsally, where it forms the fringe behind the base of the spine. The sternal plates have fringed areas as well, but here the fringes are more curved and form patches, rather than lines (Fig. 5D, F). A conspicuously large, oval patch is present close to the midventral line. A large fringe is located anterior to the lateroventral cuspidate spines. The posterior margin of the

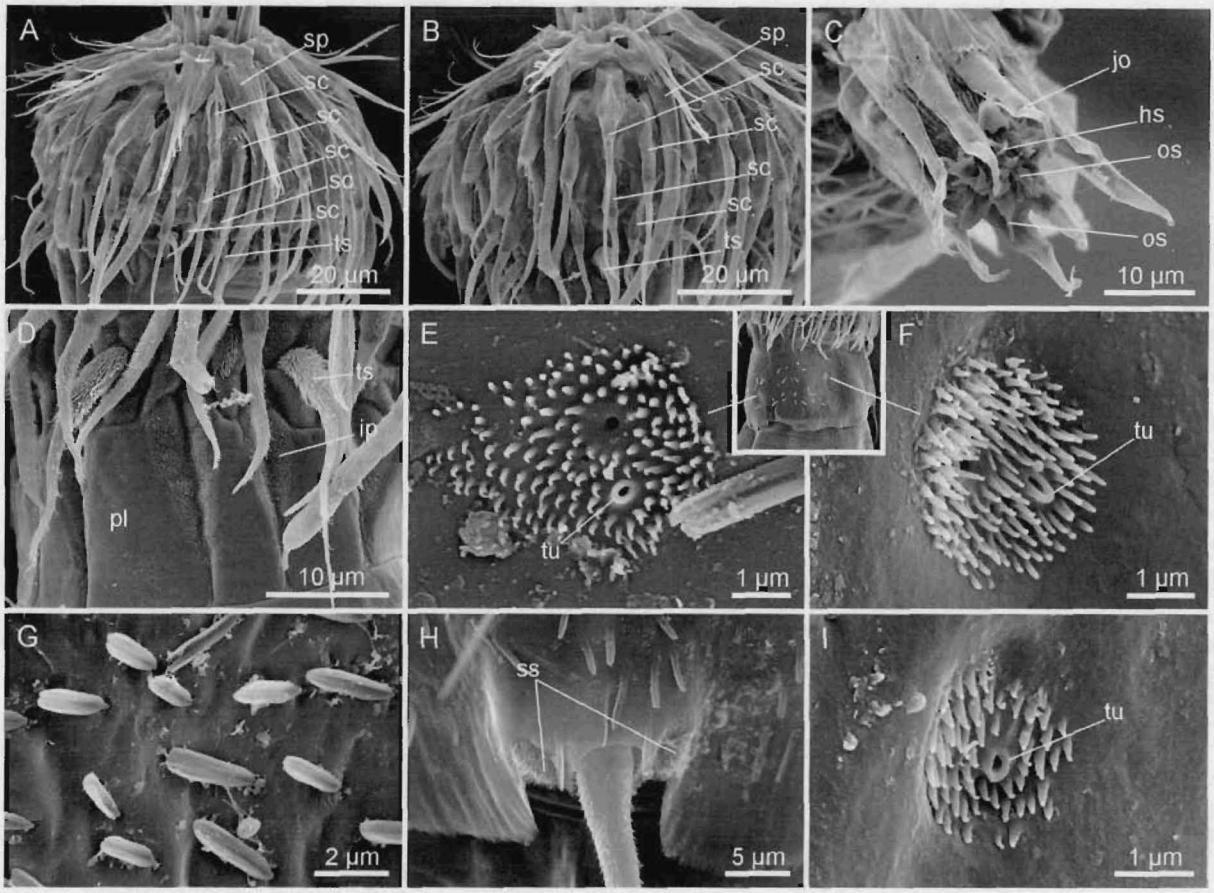
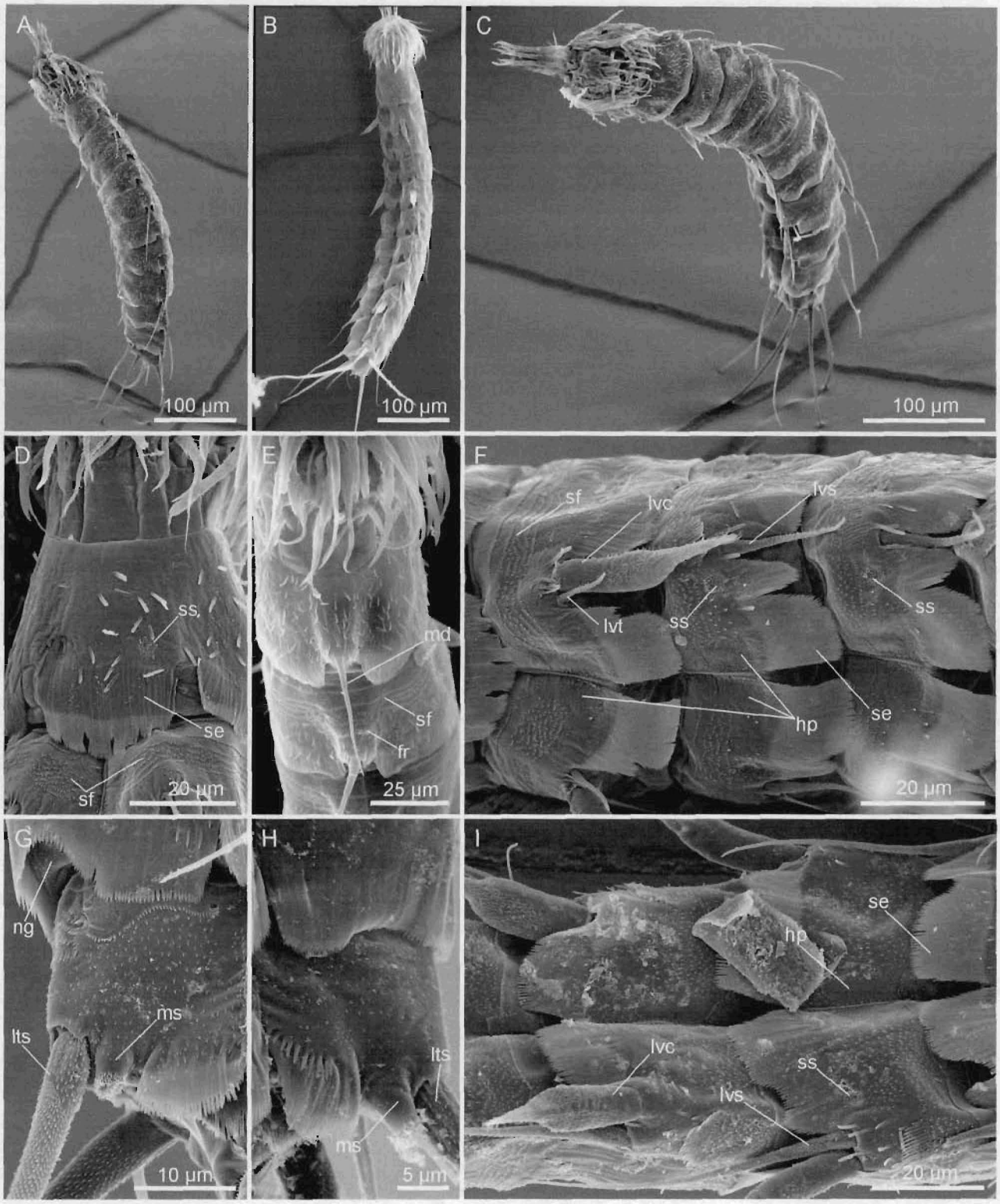


Figure 4. *Antygomonas paulae* sp. nov. Scanning electron micrographs of introvert and cuticular details. **A.** Arrangement of scalids in introvert section 9. **B.** Arrangement of scalids in introvert section 10 (compare with diagram in Fig. 2). **C.** Inner and outer oral styles. **D.** Neck region showing placids and interstitial placids. **E.** Ventromedial sensory spot on segment 1. **F.** Laterodorsal sensory spot on segment 1. Inset: Segment 1, lateroventral view. **G.** Cuticular hairs on segment 1. **H.** Base of middorsal spine on segment 7. **I.** Laterodorsal sensory spot on segment 9. Abbreviations: hs, helioscalid in ring -1; ip, interstitial placid; jo, joint in outer oral style; os, inner oral style; pl, placid; sc, scalid; sp, spinoscalid; ss, sensory spot; ts, trichosclid; tu, tube.

Figure 4. *Antygomonas paulae* sp. nov. Micrographies au MEB de l'introvert et détails de la cuticule. **A.** Arrangement des scalides sur l'introvert de la section 9. **B.** Arrangement des scalides de l'introvert de la section 10 (comparer avec le diagramme de la Fig. 2). **C.** Stylets oraux internes et externes. **D.** Région du cou montrant les placides et placides intertitiels. **E.** Tâche sensorielle médioventrale sur le segment 1. **F.** Tâche sensorielle latérodorsale sur le segment 1. **G.** Poils cuticulaires sur le segment 1. **H.** Base de l'épine médiodorsale sur le segment 7. **I.** Tâche sensorielle sur le segment 9. Abréviations : hs, helioscalide sur l'anneau -1 ; ip, placide interstitiel ; jo, junction du stylet oral externe ; os, stylet oral interne ; pl, placide ; sc, scalide ; sp, spinoscalide ; ss, tâche sensorielle ; ts, trichosclide; tu, tube.

Figure 5. *Antygomonas paulae* sp. nov. Scanning electron micrographs. **A.** Male, dorsolateral view. **B.** Female, ventrolateral view. **C.** Male, lateroventral view. **D.** Neck and first trunk segment, ventral view. **E.** Trunk segments 1 to 2, dorsal view. **F.** Trunk segments 2 to 4, ventral view. **G.** Trunk segments 10 to 11 in female, ventral view. **H.** Trunk segments 10 to 11 in male, ventral view. **I.** Trunk segments 8 to 9, ventral view. Abbreviations: fr, fringe; hp, hairless patch; lts, lateral terminal spine; lvc, lateroventral cuspidate spines; lvs, lateroventral spine; lvt, lateroventral tubule; md, middorsal spine; ms, modified sensory spot; ng, notch at female gonopore opening; se, posterior cuticular segment extension; sf, secondary fringe; ss, sensory spot.

Figure 5. *Antygomonas paulae* sp. nov. Micrographies au MEB. **A.** Mâle, vue dorsolatérale. **B.** Femelle, vue ventrolatérale. **C.** Mâle, vue ventrolatérale. **D.** Cou et premier segment du tronc, vue ventrale. **E.** Segments 1 et 2 du tronc, vue dorsale. **F.** Segments 2 à 4 du tronc, vue ventrale. **G.** Segments 10 et 11 du tronc chez la femelle, vue ventrale. **H.** Segments 10 et 11 du tronc chez le mâle, vue ventrale. **I.** Segments 8 et 9 du tronc, vue ventrale. Abréviations : fr, frange ; hp, zone sans poil ; lts, épine latérale terminale ; lvc, épines cuspides latéroventrales ; lvs, épine latéroventrale ; lvt, tubule latéroventral ; md, épine médiodorsale ; ms, tâche sensorielle modifiée ; ng, encoche sur l'ouverture du gonopore femelle ; se, extension cuticulaire postérieure du segment ; sf, frange secondaire ; ss, tâche sensorielle.


A
100 µm
B
100 µm
C
100 µm
D
ss
se
sf
20 µm
E
md
sf
fr
25 µm
F
sf
lvc
lvs
lvt
ss
ss
hp
se
20 µm
G
ng
ms
lts
10 µm
H
lts
ms
5 µm
I
se
hp
lvc
ss
lvs
20 µm

segment is covered by the overlapping cuticular extension. On the dorsal and lateral sides it looks like the extension on the previous segment, whereas it becomes very thin on the ventral side and forms two deep notches around the bases of the lateroventral spines (Fig. 5F).

Segment 3 has a middorsal spine with paradorsal type 1 sensory spots like the one on the previous segment. A pair of lateroventral acicular spines with conspicuous fringes at their bases is present (Figs 1B, 3C & 5F). The spine is composed of a short basis and a long distal tip. Both the basis and tip are covered with minute hairs. A pair of ventrolateral type 2 sensory spots is present (Fig. 5F). The sensory spots have two or three pores. The posterior margin of the segment is like on the previous segment on the dorsal and lateral sides. On the ventral side, the posterior segmental extension is very thin with deep notches at the bases of the lateroventral spines. A pair of notches is furthermore present in a more ventromedial position (Fig. 5F). Cuticular hairs and fringes are like on the previous segment.

Segment 4 has a middorsal spine with paradorsal type 1 sensory spots and a pair of lateroventral acicular spines with basal fringes. A pair of type 2 sensory spots is located in the lateral accessory and ventrolateral positions, respectively. Both pairs have 2 central pores and a lateral one on a tube. Posterior segmental extension, hair and fringe patterns are generally like on the previous segment.

Segment 5 has a middorsal spine with paradorsal type 1 sensory spots, a pair of lateroventral cuspidate spines, and lateral accessory acicular spines (Figs 1B & 3C). Lateral accessory and ventrolateral sensory spots are not present. Posterior segmental extension, hair and fringe patterns are generally like on the previous segment.

Segment 6 has a middorsal spine with paradorsal type 1 sensory spots and a pair of lateroventral acicular spines. Also on this segment, a conspicuous lateroventral fringe is present, but on this and the following four segments, the fringes are moved to a more anterior position, and are not located particularly at the bases of the spines. A pair of type 2 sensory spots with three pores is present in a midlateral position. Type 2 sensory spots are also present ventrolaterally, but the number of pores is uncertain. Posterior segmental extension, hair and fringe patterns are generally like on the previous segment.

Segment 7 has a middorsal spine with paradorsal type 1 sensory spots and a pair of lateroventral acicular spines. Two pairs of type 2 sensory spots are present midlaterally, one pair is present in a lateral accessory position, and an additional pair is present in the ventrolateral series. The sensory spots have two or three pores and the lateral one is elevated. Posterior segmental extension, hair and fringe patterns are generally like on the previous segment.

Segment 8 has a middorsal spine with paradorsal type 1 sensory spots, a pair of lateroventral acicular spines, and lateral accessory cuspidate spines (Figs 1B, 3D & 5I). A pair of ventrolateral type 2 sensory spots with three pores is present. Posterior segmental extension, hair and fringe patterns are generally like on the previous segment.

Segment 9 has a middorsal spine with paradorsal type 1 sensory spots, a pair of lateroventral cuspidate spines, and lateral accessory acicular spines (Figs 1B, 3D-F & 5I). A pair of laterodorsal sensory spots is present. The spots probably belong to type 2, but have only one central pore which is elevated on the tip of a tube (Fig. 4I). Hair and fringe patterns are generally like on the previous segment.

Segment 10 has a middorsal spine with paradorsal type 1 sensory spots and a pair of laterodorsal acicular spines (Figs 1A & 3B). A pair of subdorsal, laterodorsal and lateral accessory type 2 sensory spots with two or three pores is present. The anterior margin of the segment has two to three secondary fringes, as the previous segments. The posterior margin of the segmental extension on the tergal plate has deep notches around the middorsal and laterodorsal spines. Otherwise, it is straight. Its posterior margins on the sternal plates are straight in males (Figs 1B, 3E & 5H), whereas it has rounded notches around the female gonopores (Figs 1C, 3F & 5G). In SEM, the sexes can only be discriminated by the shape of the posterior sternal plate margin (Fig. 5G-H). In addition, the female gonopores are easily recognized in LM as two strongly cuticularized areas at the intersegmental junction between segment 10 and 11 (Fig. 3F). The differences in length of the laterodorsal spines do not appear to be sexually dimorphic.

Segment 11 has a middorsal spine with paradorsal type 1 sensory spots, one midterminal spine, and paired lateral terminal and lateral terminal accessory spines (Fig. 1D). The middorsal spine is considerably longer (250-500 %) than the middorsal spines on any other segment. The conspicuous fringe anterior to the base of the middorsal spine is missing. Paired modified sensory spots (type 3) are located at the base of the middorsal spine, the midterminal spine and at the bases of the lateral terminal spines (Fig. 5G-H). The sensory spots consist of a collar of fringes that encircle a central tuft of scale-like hairs. The tergal and sternal plates have only one anterior secondary fringe. The leaf-like cuticular hairs and posterior segmental extension are lacking. Instead the segmental plates are equipped with small triangular hairs. The sternal plates terminate posteriorly into well-developed pectinate fringes.

Discussion

Taxonomic remarks

The presence of sixteen placids, first trunk segment consisting of a closed ring and middorsal spines on several trunk segments clearly places the new species in the order

Cyclorhagida and suborder Cyclorhagae (for order and suborder diagnoses see Higgins, 1990). Several characters point towards a relationship with *Antygomonas*, inclusive: the presence of interstitial placids (see further discussion below), middorsal and midventral concavities in the anterior margin of the first trunk segment in combination with the lack of a middorsal and midventral wedge-shaped cuticular plate in trunk segment 1, mixed presence of cuspidate and acicular spines, the thickness of the cuticle and its surface structures, and the characteristic notches in the posterior margins of the trunk segment. Hence, based on these similarities the species is assigned to *Antygomonas*.

Currently *Antygomonas* consists of two species, *A. incomitata* and *A. oreas*. *Antygomonas paulae* sp. nov. is distinguished from *A. incomitata* by its lack of lateral accessory cuspidate spines on segment 6 and lateroventral cuspidate spines on segment 8. The new species is most easily distinguished from *A. oreas* from the relative position of the lateral spines on segment 9. In *A. oreas* the acicular spines sit in a lateroventral position and the cuspidate spines in a lateral accessory position, whereas the position of these spines have shifted in *A. paulae* sp. nov. so that the cuspidate spines are lateroventral and the acicular ones occupy a lateral accessory position. *Antygomonas paulae* sp. nov. can furthermore be discriminated from *A. oreas* by the presence of midlateral sensory spots on segments 2, 6 and 7, lateral accessory sensory spots on segments 4, 7 and 10 and ventrolateral sensory spots on segment 3, 4 and 7.

The species of *Antygomonas* are most easily distinguished by the spine formula, or more precisely, the distribution of lateroventral cuspidate spines. As listed above, *A. paulae* sp. nov. generally fits into the genus diagnosis of *Antygomonas*, but it also differs in some crucial points. According to the emended diagnosis given by Bauer-Nebelsick (1996) the genus is characterized by a first trunk segment consisting of a completely closed ring, whereas the following nine segments consist of a tergal plate with a midventral articulation only. Contrarily, trunk segments 2 through 11 in *A. paulae* sp. nov. consist of a tergal plate and two sternal plates, with a distinct midventral line and much more indistinct articulations between the tergal and sternal plates. Based on this difference solely, one would have to reject assignment of the new species to *Antygomonas*, but re-examination of *A. oreas* paratypes revealed that segments 2 through 11 in this species also displays very indistinct lateroventral junctions, hence consisting of a tergal and two sternal plates. As these lines are very inconspicuous, and even invisible in some specimens, it is very likely that they are present in *A. incomitata* as well. Thus, with this correction to the diagnosis, *A. paulae* sp. nov. would fit into the genus.

A more consistent difference, however, can be observed in the first trunk segment. On the ventral side of this segment, *Antygomonas paulae* sp. nov. possesses two incomplete, but still distinct articulation lines (Figs 1B & 3C), which implies the anlage of an unpaired sternal plate. Such lines are not reported from any of the previously described species (Nebelsick, 1990; Bauer-Nebelsick, 1996), and they were not found in the *A. oreas* paratypes. However, this single trait is insufficient to justify the erection of a new genus; in particular because an unpaired sternal plate in segment 1 is also found in species of *Sphenoderes* and *Cateria* (Higgins, 1968 & 1969), which implies that the trait could be considered plesiomorphic for *Antygomonas paulae* sp. nov.

Morphological remarks: The introvert

Available information on the detailed morphology of the introvert armature in different kinorhynch species is currently rather sporadic, and much of it relies on reports from the older literature and is based on light microscopical observations only. Summaries of our current knowledge of scalid arrangements in various kinorhynch species have been given by Nebelsick (1993) and Neuhaus (1995). A comparison between the investigated species quickly reveals that the number of scalids in each ring varies greatly between the different taxa, and a distinct pattern is not readily observed. Neither does the scalid arrangement in *Antygomonas paulae* sp. nov. fit any other investigated species. Instead of comparing the scalid arrangement ring-by-ring, it might however be an advantage to use another comparative approach, and focus on the arrangement in radial sections (sections are illustrated on Fig. 2). First, we do not know whether the exact position of a specific scalid is fixed or whether it can be radially displaced in closely related species, so that two homologues scalids appear in different, neighboring rings. Furthermore, we have to be aware that the introvert morphology is rather complex, and that the exact location of each scalid may depend on the eye that sees it. It is not unlikely that different authors have reported homologous scalids as appearing in different rings. Thus, by comparing the scalid arrangement sectionvise instead of ringvise we might be able to overcome problems with radial displacement and bias from incongruent interpretations. Sectionvise comparison, however, requires a complete diagram of the introvert armature and currently this is available from eight species only, of which just seven descriptions are based on examinations with SEM: *Kinorhynchus phyllotropis* Brown & Higgins, 1983 (see Brown, 1989), *Paracentrophyes praedictus* Higgins, 1983 (see Neuhaus, 1995), *Zelinkaderes floridensis* Higgins, 1990 (see Higgins, 1990), *Z. klepali* Bauer-Nebelsick, 1995 (see Bauer-Nebelsick, 1995), *Antygomonas oreas* Bauer-Nebelsick, 1996 (see Bauer-Nebelsick, 1996) *Condyloderes paradoxus* Higgins, 1969 (see Higgins,

1969), *Echinoderes capitatus* Zelinka, 1928 (see Nebelsick, 1993) and *Tubulideres seminoli* (Sørensen et al., in press). Available information on scalid arrangements compared sectionvise is presented in Table 3.

A sectionvise comparison between the scalid arrangement in *A. paulae* sp. nov. and other species reveals that the outer introvert armature follows an identical pattern as present in *A. oreas*, *K. phyllotropis*, *P. praedictus*, and *T. seminoli*. An almost corresponding pattern is found in *E. capitatus* as well, even though some of the trichoscalids in the outermost ring apparently have been transformed to, or replaced by, regular scalids (Nebelsick, 1993).

Sensory spots

In her review of kinorhynch sensory spots, Nebelsick (1992) distinguishes between three types namely type 1, consisting of numerous cuticular papillae and a central and a lateral pore. This type is found in various taxa of both Cyclorhagida as well as Homalorhagida. Even though all type 1 sensory spots probably can be considered homologous, they tend to display a quite heterogeneous morphology, and the disparity can be significant, even on suprageneric levels (Sørensen, 2006). Type 2 sensory spots resemble type 1, but the lateral pore is elevated at the tip of a small tube. This type has only been reported from homalorhagid species (e.g. Brown & Higgins, 1983; Higgins, 1983; Higgins & Kristensen, 1988; Lemburg, 2002). Type 3, also referred to as modified sensory spots, is always located on the terminal trunk segment and consists of a conus like basal part with terminal papillae. This type was first reported from homalorhagids (Higgins, 1983; Higgins & Kristensen, 1988; Neuhaus, 1995), but has later been recorded from cyclorhagids as well, inclusive species of *Antygomonas* (see Nebelsick, 1990; Bauer-Nebelsick, 1996), *Zelinkaderes* (see Bauer-Nebelsick, 1995), *Semnoderes* (Sørensen, pers. obs.), and *Tubulideres* (Sørensen et al., in press). The absence of modified sensory spots in species of Echinoderidae and *Dracoderes* appears to be consistent (e.g. Higgins & Shirayama, 1990; Nebelsick, 1992; Sørensen, 2006) and unpublished SEM observations on species of *Centroderes* and *Campyloderes* (Sørensen, pers. obs.) support that this is the case in Centroderidae as well.

In relation to the morphological disparity of sensory spots and their distribution among taxa *A. paulae* sp. nov. is interesting, as this is the first example of a kinorhynch species where all three types of sensory spots co-occur. Especially the occurrence of type 2 sensory spots is interesting because this type until now has been reported from homalorhagids only. Their presence in both kinorhynch classes suggests that type 2 sensory spots were present in the kinorhynch ground pattern. As stated above, the presence type 3 sensory spots, or modified sensory spots appears to be restricted to Antygomonidae, Zelinkaderidae and Semnoderidae, which could indicate a closer relationship between the three families. Alternatively, type 3 sensory spots most have either evolved independently more than ones or be considered a plesiomorphic condition.

Acknowledgements

I wish to thank Valerie Paul and the staff on the Smithsonian Marine Station at Fort Pierce for providing excellent research facilities during my stays at the station. Special thanks go to the crew on R/V Sunburst, Hugh

Table 3. *Antygomonas paulae* sp. nov. Arrangement of outer introvert armature in selected kinorhynch species, compared section vise. Note that *E. capitatus* has 9 scalids and 0 trichoscalids in sections 3 and 9, whereas sections 5 and 7 have 8 scalids and 1 trichoscalid. *Condyloderes paradoxus* has 7 scalids in sections 3 and 9, and 8 scalids in sections 5 and 7.

Tableau 3. *Antygomonas paulae* sp. nov. Arrangement de l'armature de la partie externe de l'introvert des espèces de kynorhynques sélectionnées, comparées par section. Notez que *E. capitatus* possède 9 scalides et 0 trichoscalides sur les sections 3 et 9, alors que les sections 5 et 7 ont 8 scalides et 1 trichoscalide. *Condyloderes paradoxus* possède 7 scalides sur les sections 3 et 9, et 8 scalides sur les sections 5 et 7.

Species / Section	Section 1	Sections 2, 4, 8, 10	Sections 3, 5, 7, 9	Section 6
Antygomonas paulae n. sp.	1 os, 7 sc, 1tr	1 os, 6 sc, 1 tr	1 os, 7 sc, 2 tr	0 os, 6 sc, 1 tr
A. oreas	1 os, 7 sc, 1 tr	1 os, 6 sc, 1 tr	1 os, 7 sc, 2 tr	0 os, 6 sc, 1 tr
Tubulideres seminoli	1 os, 7 sc, 1 tr	1 os, 6 sc, 1 tr	1 os, 7 sc, 2 tr	0 os, 6 sc, 1 tr
Kinorhynchus phyllotropis	1 os, 7 sc, 1 tr	1 os, 6 sc, 1 tr	1 os, 7 sc, 2 tr	0 os, 6 sc, 1 tr
Paracentrophyes praedictus	1 os, 7 sc, 1 tr	1 os, 6 sc, 1 tr	1 os, 7 sc, 2 tr	0 os, 6 sc, 1 tr
Echinoderes capitatus	1 os, 8 sc, 0 tr	1 os, 6 sc, 1 tr	1 os, 9(8) sc, 0(1) tr	0 os, 7 sc, 0 tr
Zelinkaderes floridensis	1 os, 3 sc, 1 tr	1 os, 3 sc, 1 tr	1 os, 3 sc, 2 tr	0 os, 3 sc, 1 tr
Z. klepali	1 os, 4 sc, 1 tr	1 os, 5 sc, 1 tr	1 os, 4 sc, 2 tr	0 os, 5 sc, 1 tr
Condyloderes paradoxus	1 os, 6 sc, 1 tr	1 os, 5 sc, 1 tr	1 os, 7 (8) sc, 2 tr	0 os, 5 sc, 1 tr

Reichardt and Woody Lee. I also thank Iben Heiner, Ole Ziemer, Reinhardt M. Kristensen, Jesper G. Hansen and Thomas M. Jespersen for their help collecting or processing the samples, Birger Neuhaus for valuable discussions about the affinities of the new species, Stine Elle for providing line art illustrations, and the Zoological Museum, University of Copenhagen, for providing access to scanning electron microscopical facilities. I thank Dr. Monika Bright and Dr. Helmut Sattmann from the Museum of Natural History in Vienna for providing type specimens and supplementary material of *Antygomonas oreas*. This is contribution n° 691 from the Smithsonian Marine Station at Fort Pierce. Funding was provided by the Danish Natural Science Research Council (Grants No. 21-04-0331 and 21-04-0047). The compound microscope, camera lucida and imaging software were funded by the Carlsberg Foundation (Grant No. 2005-1-545) and the Novo Nordic Foundation.

References

Adrianov A.V. & Higgins R.P. 1996. *Pycnophyes parasanjuanensis*, a new kinorhynch (Kinorhyncha: Homalorhagida: Pycnophyidae) from San Juan Island, Washington, USA. *Proceedings of the Biological Society of Washington*, **109**: 236-247.

Adrianov A.V. & Malakhov V.V. 1994. Kinorhynchs (structure, development, phylogeny and systematics). Nauka Publishers: Moscow, 260 pp.

Adrianov A.V. & Malakhov V.V. 1999. *Cephalorhyncha of the World Ocean*. KMK LTD.: Moscow, 328 pp.

Bauer-Nebelsick M. 1995. *Zelinkaderes klepali* sp.n., from shallow water sands of the Red Sea. *Annalen des Naturhistorischen Museum in Wien*, **97B**: 57-74.

Bauer-Nebelsick M. 1996. *Antygomonas oreas* sp.n., a new deep sea kinorhynch from the Pacific Ocean. *Annalen des Naturhistorischen Museum in Wien*, **98B**: 5-22.

Blake C.H. 1930. Three new species of worms belonging to the order Echinodera. *Biological Survey of the Mount Desert Region*, **4**: 3-10.

Brown R. 1989. Morphology and ultrastructure of the sensory appendages of a kinorhynch introvert. *Zoologica Scripta*, **18**: 471-482.

Brown R. & Higgins R.P. 1983. A new species of *Kinorhynchus* (Homalorhagida, Pycnophyidae) from Australia with a redescription and range extension of other Kinorhyncha from the South Pacific. *Zoologica Scripta*, **12**: 161-169.

Dinet A. 1976. Étude quantitative du méiobenthos dans le secteur nord de la Mer Egée. *Acta Adriatica*, **18**: 81-88.

Higgins R.P. 1960. A new species of *Echinoderes* (Kinorhyncha) from Puget Sound. *Transactions of the American Microscopical Society*, **79**: 85-91.

Higgins R.P. 1961. Three new homalorhagid kinorhynchs from the San Juan Archipelago, Washington. *Journal of the Elisha Mitchell Scientific Society*, **77**: 81-88.

Higgins R.P. 1964a. Redescription of the kinorynch *Echinoderes remanei* (Blake, 1930) Karling 1954. *Transactions of the American Microscopical Society*, **83**: 243-247.

Higgins R.P. 1964b. Three new Kinorhynchs from the North Carolina coast. *Bulletin of Marine Sciences of the Gulf and Caribbean*, **14**: 479-493.

Higgins R.P. 1965. The homalorhagid Kinorhyncha of Northeastern US coastal waters. *Transactions of the American Microscopical Society*, **84**: 65-72.

Higgins R.P. 1968. Taxonomy and postembryonic development of the Cryptorhagae, a new suborder for the mesopsammic kinorhynch genus *Cateria*. *Transactions of the American Microscopical Society*, **87**: 21-39.

Higgins R.P. 1969. Indian Ocean Kinorhyncha: 1, *Condyloderes* and *Sphenoderes*, new cyclorhagid genera. *Smithsonian Contributions to Zoology*, **14**: 1-13.

Higgins R.P. 1972. Kinorhyncha of the Chesapeake Bay. *Chesapeake Science, Supplement*, **13**: 105-106.

Higgins R.P. 1977. Two new species of *Echinoderes* (Kinorhyncha) from South Carolina. *Transactions of the American Microscopical Society*, **96**: 340-354.

Higgins R.P. 1978. *Echinoderes gerardi* n. sp. and *E. riedli* (Kinorhyncha) with descriptions of closely related species. *Transactions of the American Microscopical Society*, **97**: 171-180.

Higgins R.P. 1983. The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, II: Kinorhyncha. *Smithsonian Contributions to Marine Science*, **18**: 1-131.

Higgins R.P. 1990. Zelinkaderidae, a new family of Cyclorhagid Kinorhyncha. *Smithsonian Contributions to Zoology*, **500**: 1-26.

Higgins R.P. & Kristensen R.M. 1986. New Loricifera from Southeastern United States coastal waters. *Smithsonian Contributions to Zoology*, **438**: 1-70.

Higgins R.P. & Kristensen R.M. 1988. Kinorhyncha from Disko Island, West Greenland. *Smithsonian Contributions to Zoology*, **458**: 1-56.

Higgins R. P. & Shirayama Y. 1990. Dracoderidae, a new family of the cyclorhagid Kinorhyncha from the Island Sea of Japan. *Zoological Science*, **7**: 1-13

Hochberg R. 2004. *Smithsoniarhynches*, a New Genus of Interstitial Gnathorhynchidae (Platyhelminthes, Kalyptorhynchia) from Mosquito Lagoon and Indian River Lagoon, Florida. *Journal of the Marine Biological Association of the United Kingdom*, **84**: 1143-1149.

Horn T.D. 1978. The distribution of *Echinoderes coulli* Kinorhyncha along an interstitial salinity gradient. *Transactions of the American Microscopical Society*, **97**: 586-589.

Kristensen R.M. & Higgins R.P. 1984. A New Family of Arthrotardigrada (Tardigrada: Heterotardigrada) from the Atlantic Coast of Florida, U.S.A. *Transactions of the American Microscopical Society*, **103**: 295-311.

Kristensen R.M. & Higgins R.P. 1989. Marine Tardigrada from the Southeastern United States Coastal Waters. I. *Paradoxipus orzeliscoides* n. gen. n. sp. (Athrotardigrada: Halechiniscidae). *Transactions of the American Microscopical Society*, **108**: 262-282.

Lemburg C. 2002. A new kinorhynch *Pycnophyes australensis* sp. n. (Kinorhyncha: Homalorhagida: Pycnophyidae) from Magnetic Island, Australia. *Zoologischer Anzeiger*, **241**: 173-189.

Metschnikoff E. 1869. Bemerkungen über *Echinoderes*. *Bulletin de l'Académie des Sciences de Saint Pétersbourg*, **4**: 190-194.

Marcotte B.M. & Coull B.C. 1974. Pollution, diversity and meiobenthic communities in the North Adriatic (Bay of Piran, Yugoslavia). *Vie et Milieu*, **24**: 281-300.

Nebelsick M. 1990. *Antygomonas incomitata* gen. et sp. n. (Cyclorhagida, Kinorhyncha) and its phylogenetic relationships. *Zoologica Scripta*, **19:**143-152

Nebelsick M. 1992. Sensory spots of *Echinoderes capitatus* (Zelinka, 1928) (Kinorhyncha, Cyclorhagida). *Acta Zoologica*, **73**: 185-195.

Nebelsick M. 1993. Introvert, mouth cone, and nervous system of *Echinoderes capitatus* (Kinorhyncha, Cyclorhagida) and implications for the phylogenetic relationships of Kinorhyncha. *Zoomorphology*, **113**: 211-232.

Neuhaus B. 1995. Postembryonic development of *Paracentrophyes praedictus* (Homalorhagida): neoteny questionable among the Kinorhyncha. *Zoologica Scripta*, **24**: 179-192.

Newman L.J., Norenburg J.L. & Reed S. 2000. Taxonomic and biological observations on the tiger flatworm, *Maritigrella crozieri* (Hyman, 1939), new combination (Platyhelminthes, Polycladida, Euryleptidae) from Florida waters. *Journal of Natural History*, **34**: 799-808.

Norenburg J. L. 1988. Remarks on marine interstitial nemertines and key to the species. *Hydrobiologia*, **156**: 87-92.

Pagenstecher H.A. 1875. *Echinoderes Sieboldii*. *Zeitschrift für wissenschaftliche Zoologie, Supplement*, **25**: 117-123.

Panceri P. 1876. Osservazioni intorno a nuove forme di Vermi Nematodi marini. *Atti della Reale Accademia delle Scienze Fisiche e Matematiche*, **7**: 1-9.

Reiger R. & Ruppert E. 1978. Resin embedments of quantitative meiofauna samples for ecological and structural studies - Description and Application. *Marine Biology*, **46**: 223-235.

Sørensen M.V. 2006. New kinorhynchs from Panama, with a discussion of some phylogenetically significant cuticular structures. *Meiofauna Marina*, **15**: 51-77.

Sørensen M.V., Heiner I. & Ziemer O. 2006. A new species of *Echinoderes* from Florida (Kinorhyncha: Cyclorhagida). *Proceedings of the Biological Society of Washington*, **118**: 499–508.

Sørensen M.V., Heiner I., Ziemer O. & Neuhaus, B. 2007. *Tubulideres seminoli* gen. et sp. nov. and *Zelinkaderes brightae* sp. nov. (Kinorhyncha, Cyclorhagida) from Florida. *Helgoland Marine Research*, in press.

Thomas M.B., Edwards N.C. & Higgins R.P. 1995. *Cryptohydra thieli* n. gen., n. sp.: a meiofaunal marine hydroid (Hydroida, Athecata, Capitata). *Invertebrate Biology*, **114**: 107-118.

Zelinka C. 1928. *Monographie der Echinodera*. Verlag Wilhelm Engelmann: Leipzig, 360 p.