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# A New Species of *Condyloderes* (Cyclorhagida, Kinorhyncha) from Korea

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A new kinorhynch species, *Condyloderes megastigma* sp. nov., is described from the Korea Strait. The new species is characterized by the presence of 16 placids with either eight, four, or two knobby projections, middorsal and lateroventral acicular spines on segments 1 to 9, lateroventral cuspidate spines on segment 2 in females only, but otherwise lateroventral cuspidate spines on segments 4 and 5, and 8 and 9 in both sexes. Unique for the new species is furthermore the presence of paired ventromedial appendages on segments 7 and 8, giant ventromedial sensory spots on segment 9, and a terminal segment consisting of one tergal and one sternal plate. The mouth cone and introvert armature are described in detail for the first time for the genus *Condyloderes* Higgins, 1969. This study reveals similarities in several morphological characters between this genus and species of *Campyloderes* Zelinka, 1913.

**Key words:** *Condyloderes megastigma*, kinorhynch, phylogeny, taxonomy

## INTRODUCTION

*Condyloderes* Higgins, 1969 is one of the sixteen kinorhynch genera with only five or fewer described species (see Sørensen and Pardos [2008] for the most recent summary of kinorhynch taxonomy). Currently, we have a fair idea about the morphological disparity among species of the three diverse genera *Echinoderes*, *Kinorhynchus*, and *Pycnophyes*; however, for the minor genera where only a smaller fraction of the diversity may have been discovered, our knowledge about potential variability is much more restricted. It is well known that an extensive taxon sampling provides improved explanation of data in phylogenetic studies based on molecular sequence data (e.g., Graybeal, 1998), and this general rule can also be applied to phylogenetic analysis with a morphological approach. It will, for example, affect the result if a genus is represented solely by a single exemplar with characters that are highly derived within the genus, opposed to a situation where the genus is represented by several species that display a mix of both derived and more ancestral traits (Hillis and Wiens, 2000). Hence, for future studies of kinorhynch relationships, discovery of species belonging to the minor genera may provide particularly significant information.

In the present contribution, we describe a new species of *Condyloderes*, collected from the Korea Strait. The genus currently consists of four species, of which only *Condyloderes multispinosus* (McIntyre, 1962) occurs in Europe (McIntyre, 1962; Higgins 1969a). It was originally assigned to

*Centroderes* Zelinka, 1907 by McIntyre (1962), but was subsequently allocated to *Condyloderes* when Higgins (1969a) erected the genus and described a second species,



**Fig. 1.** Map showing collecting localities for the holotype (Station 2), allotype (Station 3), and additional specimens (Stations 1–3) of *Condyloderes megastigma* sp. nov. in the Korea Strait.

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*C. paradoxus* Higgins, 1969, from the Indian part of the Bay of Bengal. The description of the third species, *C. setoensis* Adrianov et al., 2002, provided for the first time information on *Condyloderes* revealed through both light and scanning electron microscopy. This species was described from Tanabe Bay near Osaka, Japan, and is hence from an area that is closely situated to the localities examined in the present study. The fourth and most recently described species, *C. storchi* Martorelli and Higgins, 2004 is based on a single specimen found in the stomach contents of a shrimp from the coast of Argentina. The genus is currently assigned to the family Centroderidae, and thus is considered as closely related to *Centroderes* and *Campyloderes* Zelinka, 1913 (Higgins, 1969a; Adrianov and Malakhov, 1999).

## MATERIAL AND METHODS

The specimens here described as a new species of *Condyloderes* were collected during an extensive sampling of meiobenthic animals under the KORDI (Korea Ocean Research and Development Institute) cruise of the research vessel RV *Onnuri* within the framework of the research program Pacific Ocean Study on Environment and Interactions Between Deep Ocean and National Seas. Marine benthic sediments, yielding specimens for the present study, were taken with a box corer from the subtidal zone of the Korea Strait in the Northwest Pacific Ocean (Fig. 1). Specimens were collected at three stations: St. 1, 34°47'19"N, 129°05'58"E, 109 m in depth, on 6 Oct. 2008; St. 2, 34°10'24"N, 128°25'90"E, 90 m in depth, on 6 Sept. 2006; and St. 3, 33°40'33"N, 126°04'33"E, 103 m in depth, on 8 Oct. 2008. At all three stations, the sediment consisted of coarse mud mixed with tiny shell fragments.

Meiofaunal organisms were extracted from the samples in the field by freshwater shocking (Kristensen and Higgins, 1984; Sørensen
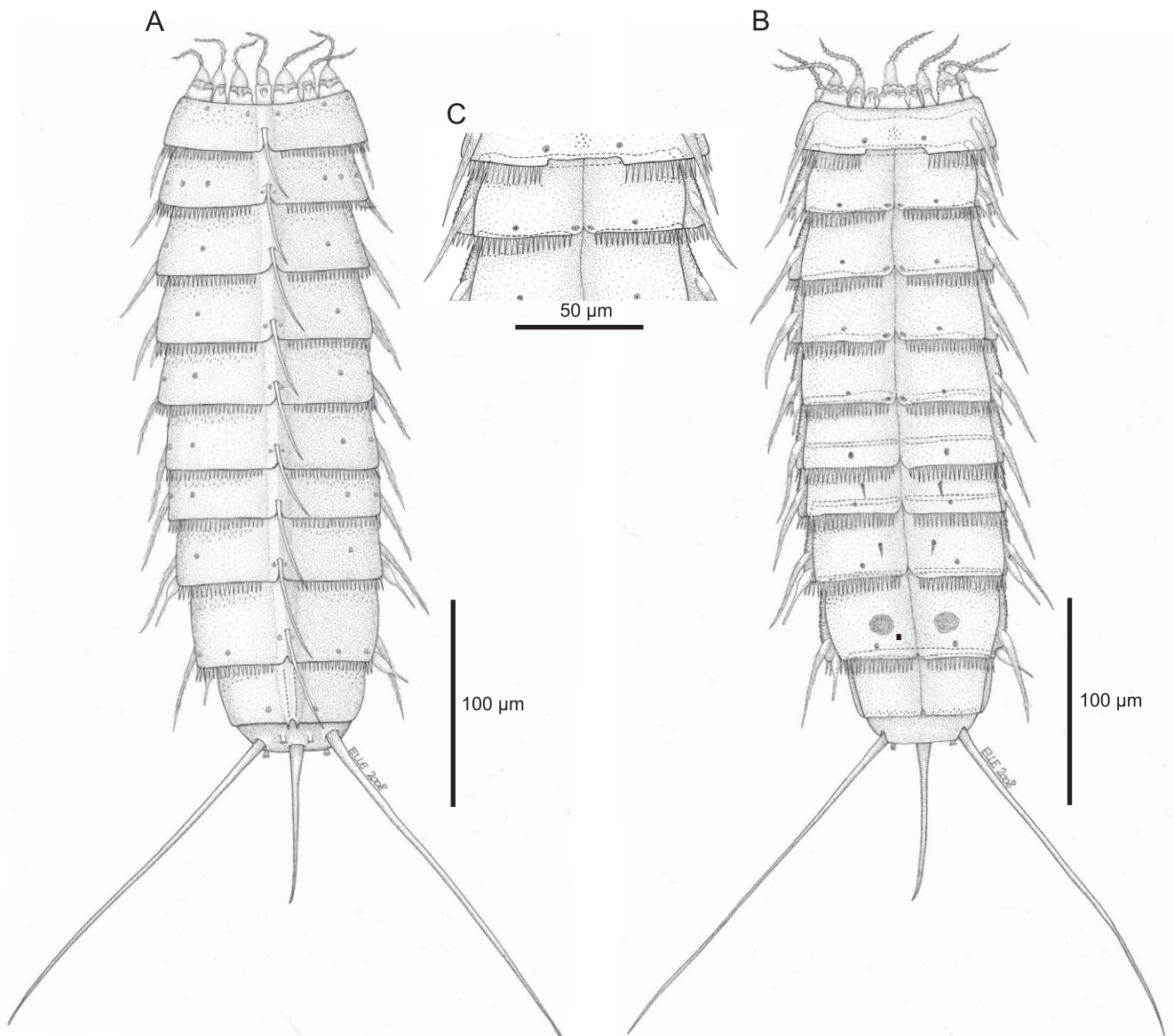


**Fig. 2.**  Line art illustrations of *Condyloderes megastigma* sp. nov. **(A)** Female, dorsal view. **(B)** Female, ventral view. **(C)** Male, segments 2 and 3, ventral view.

and Pardos, 2008) and sieving through a 63 μm mesh sieve. The concentrated samples were subsequently fixed in either 4% forma-lin buffered with sea water for morphological studies, or stored in 99% molecular-grade ethanol for future molecular analysis. The kinorhynch specimens were picked out from the mixed meiobenthos under a high magnification LEICA MZ 8 stereomicroscope with differential interference contrast.

Specimens for scanning electron microscopy (SEM) were dehydrated through a graded series of ethanol, transferred to acetone, and critical-point dried. The dried specimens were mounted on aluminum stubs, sputter coated, and examined with a JEOL JSM-6335F field emission scanning electron microscope. Specimens for light microscopy (LM) were transferred to distilled water, dehydrated through a graded series of glycerin, and mounted in Fluoromount G. The mounted specimens were examined and photographed by using Nomarski differential interference contrast with an Olympus BX60 microscope equipped with an Olympus DP20 camera. Measurements were taken with Cell^D software for analysis of light microscopical photos.

The terminology adopted for the taxonomic account follows Pardos et al. (1998), Neuhaus and Higgins (2002), and Sørensen and Pardos (2008). The morphology of the species examined prompted the introduction of a novel trunk segment position, which we refer to as paraventral, i.e., the location imidiately next to the midventral position or, eventually, the midsternal junction.

## TAXONOMY

### Cyclorhagida Zelinka, 1896
### Centroderidae Zelinka, 1896
### *Condyloderes* Higgins, 1969
### *Condyloderes megastigma* sp. nov.
(Figs. 2–6)

### Type material

HOLOTYPE. Adult female, collected on 6 September 2006 in the Korea Strait at Station 2, mounted in Fluoro-mount G, deposited in the Zoological Museum, Natural History Museum of Denmark, under accession number ZMUC KIN-250.

ALLOTYPE. Adult male, collected on 8 October 2008 in the Korea Strait at Station 3, mounted in Fluoromount G, deposited in the Zoological Museum, Natural History Museum of Denmark, under accession number ZMUC KIN-251. Additional material, all collected in the Korea Strait, include one female collected on 6 October 2008 from Station 1, one male bearing the same sampling data as the holotype, and one male bearing the same sampling data as the allotype. All additional material was mounted for SEM and is stored in the first author's personal collection. Fresh raw samples of sediment from these localities are further-more stored at –80°C for future molecular studies.

### Diagnosis

Mouth cone with nine poorly developed outer oral styles and a single ring with 10 inner oral styles. Sixteen placids with knobby projections; broad, midventral placid with eight projections; other broader placids with four projections, narrower ones with two projections. Segment 1 consisting of one closed cuticular ring, segments 2 to 10 of one tergal and two sternal plates, and segment 11 of one tergal and one sternal plate. Middorsal and lateroventral acicular spines on segments 1 to 9; lateroventral cuspidate spines on segment 2 in females only, otherwise lateroventral cuspidate spines

on segments 4 and 5, and 8 and 9 in both sexes; segment 11 with midterminal and lateral terminal accessory spines. Paired ventromedial appendages present on segments 7 and 8. Tergal plates of segment 9 each with one giant ventromedial sensory spot, measuring about $10 \times 7$ μm.

### Etymology

The species name is derived from ancient Greek *mega* meaning big and *stigma* meaning mark or spot, and refers to the extraordinarily large ventromedial sensory spots on segment 9.

### Habitat and species associations

Subtidal mud with tiny mollusk shell particles. *Condyloderes megastigma* sp. nov. co-occurred with other kinorhynchs (*Echinoderes* spp., *Sphenoderes* sp., *Paracentrophyes* sp., and *Pycnophyes* sp., all undescribed species), as well as other meiobenthic taxa, such as nematodes (*Desmoscolex* sp., *Tricoma* sp., *T.* (*Quadricoma*) sp., *Dracograllus* sp., *Richtersia* sp., *Sphaerolaimus* sp., and *Ceramonema* sp.), loriciferans (*Rugiloricus* sp.), isopods, harpacticoids, halacarids, polychaetes, and sipunculans.

### Description

Adult specimens consist of head, neck, and eleven trunk segments (Figs. 2A, 2B, 4A–E, 5A). See Table 1 for mea-
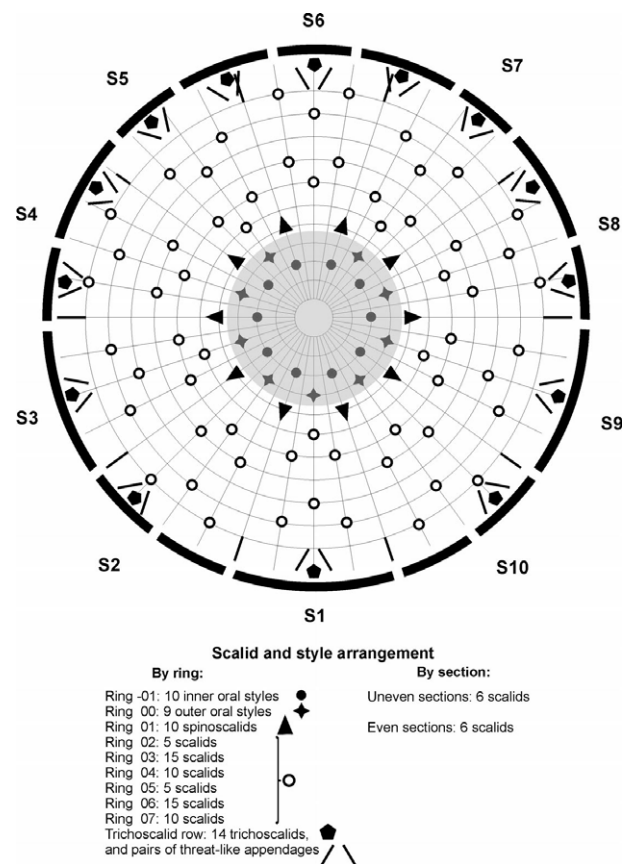


**Fig. 3.** Diagram of the mouth cone (grey shaded area), introvert, and placids in *Condyloderes megastigma* sp. nov., indicating the distribution of the inner and outer oral styles, scalids, and placids. Placids are symbolized by the bent bars around the introvert diagram.
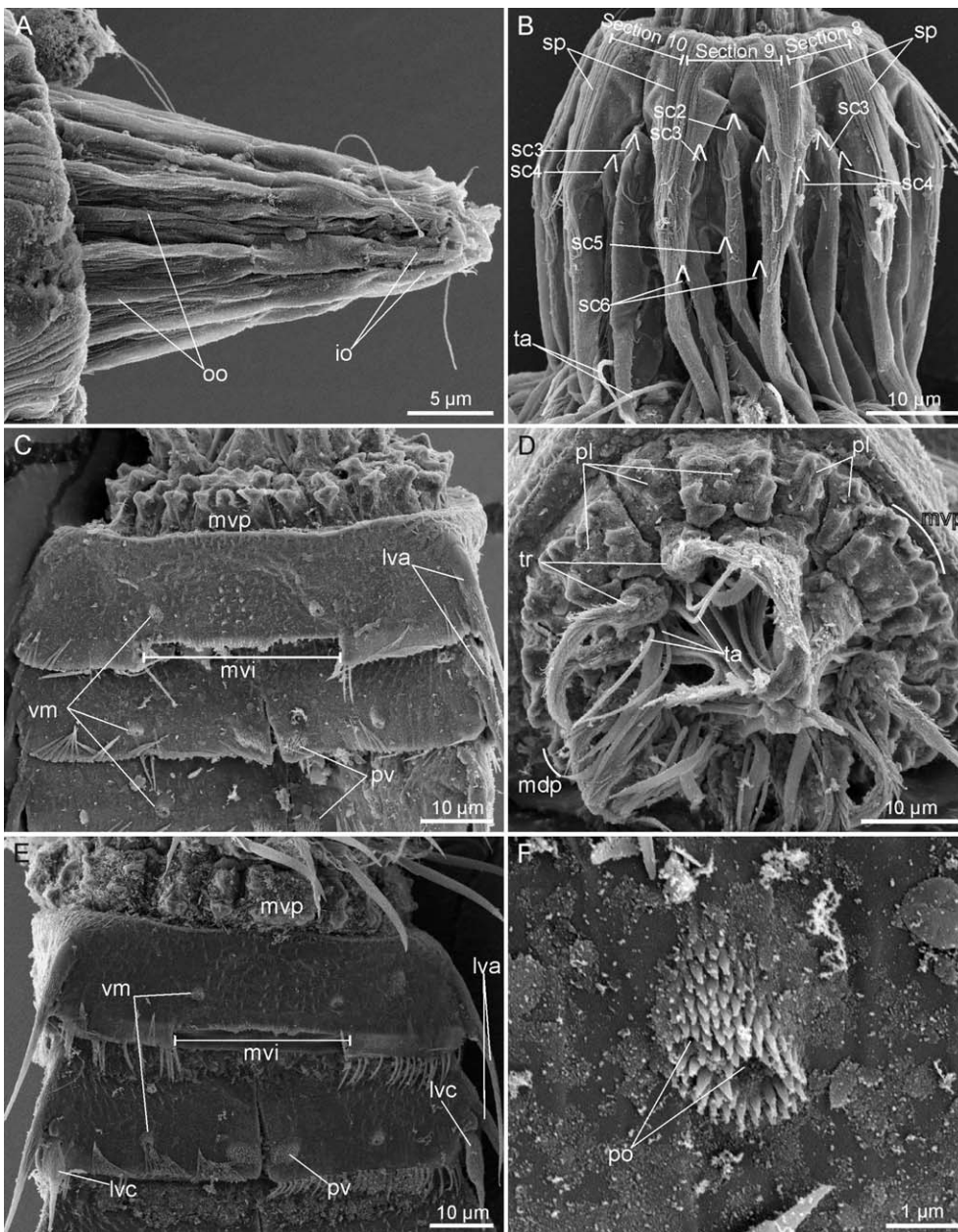
**Fig. 4.** Scanning electron micrographs showing details of the head, neck, and anterior trunk segments of *Condyloderes megastigma* sp. nov. **(A)** Extended mouth cone. **(B)** Introvert section 9 in the center, with section 10 to the left and section 8 to the right. **(C)** Neck region and segments 1 to 3 in a male specimen, ventral view (note the absence of cuspidate spines on segment 2). **(D)** Neck and head opening with the introvert retracted. **(E)** Neck region and segments 1 to 3 in a female specimen, ventral view. **(F)** Close-up of ventromedial sensory spot on segment 2. Abbreviations: io, inner oral styles; lva, lateroventral acicular spine; lvc, lateroventral cuspidate spine; mdp, middorsal placid; mvi, midventral indentation; mvp, midventral placid; oo, outer oral styles; pl, placid; po, pore; pv, paraventral sensory spots; sc, scalid; sp, spinoscalid; ta, thread-like appendages; tr, trichoscalid; vm, ventromedial sensory spots. Digits after the labels are the introvert ring numbers. Lambda symbols (Λ) mark the attachment points of scalids.

this single ring, no other inner oral styles are present. Nine outer oral styles are present in ring 00. The outer oral styles are thin and poorly developed, consisting of a single unit; inner surfaces are fused with the mouth cone (Fig. 4A).

The introvert has seven rings of scalids and one additional ring of trichoscalids that are closely associated with the placids (Fig. 3). Ring 01 has 10 spinoscalids consisting of a proximal sheath-like basis and an elongate end piece. The basis has a transverse row of conspicuously long fringes extending from the distal edge of the basis, and a median, longitudinal fringed area that extends over the proximal part of the end piece (Fig. 4B). The end piece shows no complete pseudosegmentation, but constrictions extending halfway around the spinoscalid are present in the distal third of the end piece. The latitude of the scalids attaching medially in each section between the spinoscalids alternates between the sections so that the anteriormost medial scalids are located in ring 02 in odd numbered sections, and in ring 03 in even numbered ones (Figs. 3, 4B). Also these scalids consist of a sheath-like basis and an end piece. The basis has a proximal fringe, and its distal edge terminates in a fringe as well (Fig. 4B). The end pieces are covered with minute scales and are laterally flattened. The anteriormost medial scalid in each section is flanked by two additional scalids that, corresponding to the alternation of the medial scalids, are located in either ring 03 (odd numbered sections) or ring 04 (even numbered sections) (Figs. 3, 4B). These scalids resemble the medial ones in rings 02/03 but have in addition a thin longitudinal fringe that extends along their bases. This pattern with one medial scalid flanked by two further and slightly more posterior scalids is repeated again in the posteriormost part of the introvert (Fig. 3). One ring is always left open between the anterior

surements and dimensions, and Table 2 for a summary of spine and sensory spot locations.

*Head.* The head consists of a retractable mouth cone and an introvert (Figs. 3, 4A, 4B). The mouth cone has numerous longitudinal wrinkles and 10 more prominent longitudinal lamellae that articulate with 10 inner oral styles near the terminal tip of the mouth cone (Fig. 4A). Besides
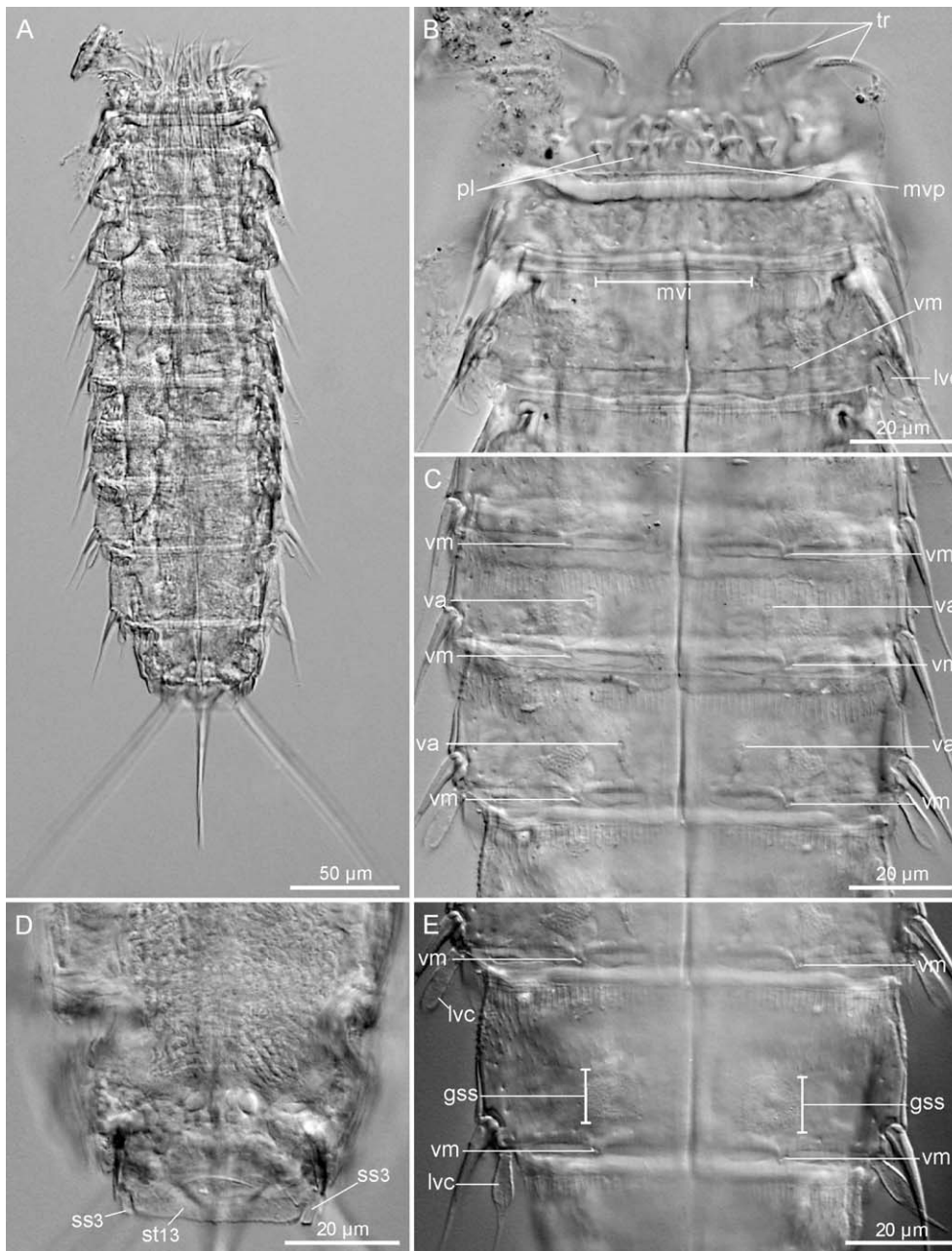
**Fig. 5.** Light micrographs showing the female holotype of *Condyloderes megastigma* sp. nov. **(A)** Overview of holotype, ventral view. **(B)** Neck region and segments 1 to 3, ventral view. **(C)** Segments 6 to 9, ventral view. **(D)** Segments 9 to 11, ventral view (note the absence of a midsternal junction on segment 11). **(E)** Segment 9, ventral view. Abbreviations: gss, giant sensory spot; lvc, lateroventral cuspidate spine; mvi, midventral indentation; mvp, midventral placid; pl, placid; ss3, sensory spot type 3 (modified sensory spot); st13, sternal plate of segment 13; tr, trichoscalid; va, ventromedial appendage; vm, ventromedial sensory spots.

except at the paraventral pair, which has no associated trichoscalids (Fig. 3). The trichoscalids are relatively long and densely fringed throughout their lengths (Figs 4D, 5B). A pair of thread-like appendages is attached anteriorly to each trichoscalid. The appendages are pointed and much thinner than the scalids, and do not exhibit any structures or sculpturing externally (Fig. 4B, D).

*Neck.* The neck consists of 16 placids (Figs. 3, 4C–E, 5B). The placids have irregular, knobby surfaces that resemble mammalian molars (e.g., Fig. 4D). The midventral placid is broadest (12 µm), whereas the two next pairs are much narrower (5 µm) (Figs. 4C, 4D, 5B). From the lateroventral placid to the middorsal one, the placids alternate in width between 10 µm and 6 µm. The midventral placid has six knobby projections arranged in two lateral rows with three in each, plus one antero- and one posteromedial projection. Other broad placids have two posterior projections and two larger anterior projections, whereas the narrower ones have one antero- and one posteromedial projection only (Fig. 4C, D). All placids join segment 1 at a distinct articulation line.

*Trunk.* The trunk has 11 segments (Figs. 2A, 2B, 5A). Segment 1 consists of one closed cuticular ring, segments 2 to 10 of one tergal and two sternal plates, and segment 11 of one tergal and one sternal plate (Fig. 5D). The trunk is conspicuously triangular in cross-section, with the tergosternal junctions located along two of the lateroventral angles. The cuticle is of medium thickness and the pachycycli are well developed.

Segment 1 with middorsal and lateroventral acicular spines (Figs. 2A, 2B, 4C, 4E, 5B, 6A). The middorsal spine on this and the following eight segments emerge through a rounded cuticular perforation medially on the segment. The posterior segment margin is straight, carrying long, flexible spicular extensions that form a fringe. The fringe is inter-

and posterior scalid-trio, and hence the three posteriormost scalids in odd numbered sections are located in rings 05 and 06, whereas those in even numbered ones attach in rings 06 and 07. The scalids in these rings resemble those in ring 04, and are not conspicuously smaller.

Fourteen trichoscalids are present in the most posterior part of the introvert, and their occurrence is strictly correlated with the placids of the neck region (Figs. 3, 4D, 5B). Hence, one trichoscalid is present anterior to each placid,
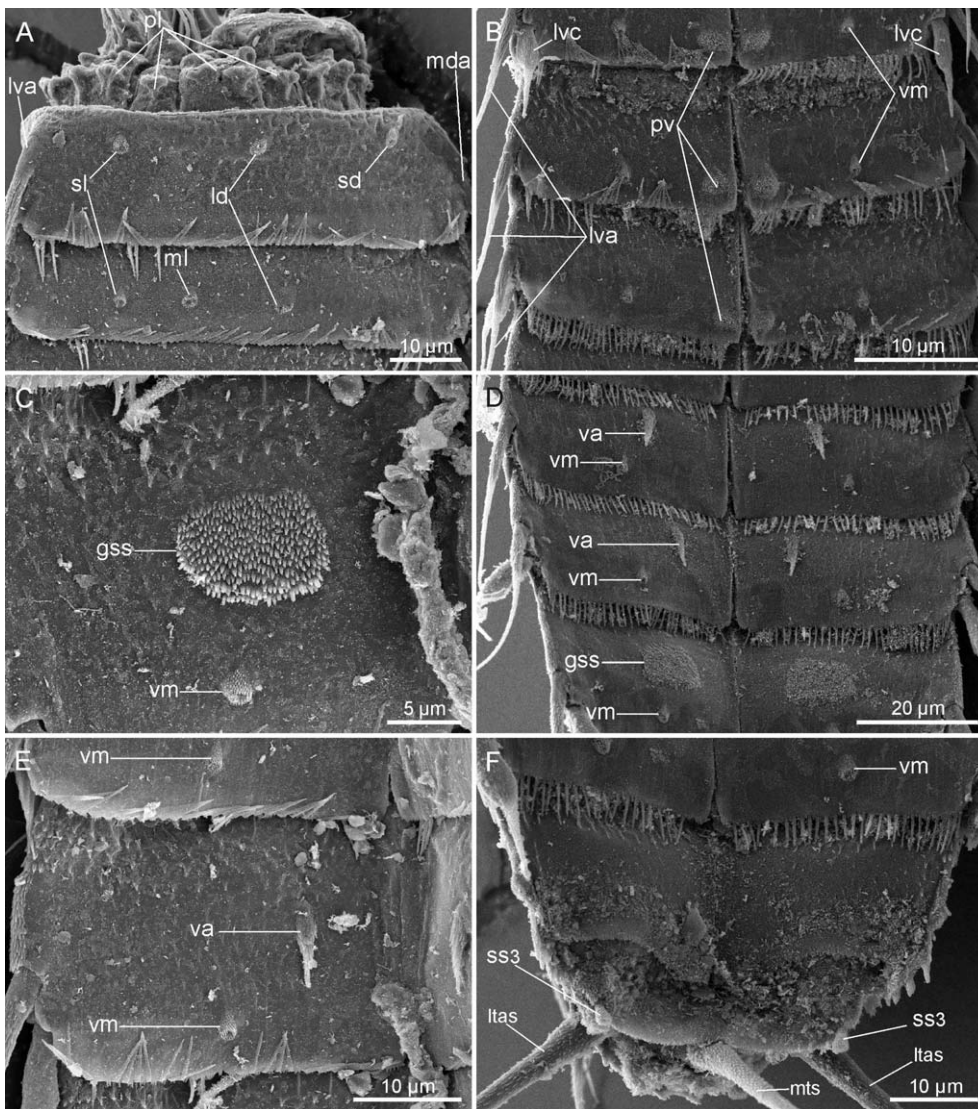
**Fig. 6.** Scanning electron micrographs showing an overview and details of the trunk morphology of *Condyloderes megastigma* sp. nov. **(A)** Segments 1 and 2, lateral view. **(B)** Segments 3 and 4 in female specimen, ventral view. **(C)** Giant ventromedial sensory spot on segment 9. **(D)** Segments 7 to 9, ventral view. **(E)** Right sternal plate of segment 8. **(F)** Segments 9 to 11 in a female specimen (note the shape of the posterior segment margin of segment 10), ventral view. Abbreviations: gss, giant sensory spot; ld, laterodorsal sensory spot; ltas, lateral terminal accessory spine; lva, lateroventral acicular spine; lvc, lateroventral cuspidate spine; mda, middorsal acicular spine; ml, midlateral sensory spot; mts, midterminal spine; pl, placid; pv, paraventral sensory spots; sd, subdorsal sensory spot; sl, sublateral sensory spot; ss3, sensory spot type 3 (modified sensory spot); va, ventromedial appendage; vm, ventromedial sensory spots.

Segment 2 with middorsal and lateroventral acicular spines, females furthermore with a pair of lateroventral cuspidate spines, located posterior to the lateroventral acicular ones (Figs. 2A, 2B, 4E, 5B; for male condition, see Figs. 2C, 4C). A pair of minute, non-elevated paradorsal sensory spots is present. Elevated sensory spots, similar to those on the previous segment, are present in the laterodorsal, midlateral, sublateral, and ventromedial positions (Figs. 2A, 2B, 4C, 4E, 4F, 5B, 6A). In addition, a pair of putative sensory spots is located in a paraventral position close to the posterior margin of the segment (Fig. 4C, E). These sensory spots are not elevated and the papillae make up a more diffuse shape, opposed to the more rounded shape of the elevated sensory spots. Pores are obscure in shape but may be present. A few scale-like cuticular hairs are scattered sporadically on the anterior half of the tergal plate and on the anterolateral parts of the sternal plates. The posterior segment margin has a fringe formed by spicular extensions, as those on the previous segment.

Segment 3 with middorsal and lateroventral acicular spines (Figs. 2A, 2B, 6B). Cuspidate spines and paradorsal sensory spots are not present. Elevated sensory spots are present in the laterodorsal, sublateral, and ventromedial positions. Paraventral sensory spots, similar to those in the corresponding position on the previous segment, are present. Cuticular hairs and posterior segment margin appear as on the previous segment.

Segment 4 with middorsal and lateroventral acicular spines, and lateroventral cuspidate spines (Figs. 2A, 2B, 6B). A pair of non-elevated paradorsal sensory spots is present. Elevated sensory spots are present in the laterodorsal and ventromedial positions. Paraventral sensory spots, similar to those in the corresponding positions on the previous segment, are present. Cuticular hairs and posterior segment margin appear as on the previous segment.

Segment 5 is identical to the previous segment, but with

rupted by a small middorsal notch and a much broader, rectangular midventral indentation (Figs. 4C, 4E, 5B). Paired sensory spots are present in the subdorsal, laterodorsal, sublateral and ventromedial positions. The sensory spots are rounded and slightly elevated on small, posteriorly directed bases (see Fig. 4F for similar sensory spot on segment 2). They consist of numerous short papillae that are also orientated in the posterior direction. Each sensory spot has a distinct central pore, and, in some instances, a smaller lateral pore is visible as well. The segment has minute, acicular cuticular hairs on its anterior part. Otherwise it has only short, scattered scale-like hairs.

**Table 1.** Measurements for the female holotype and male allotype of *Condyloderes megastigma* sp. nov. from the Korea Strait. Abbreviations: ac, acicular spine; ap, appendage; cu, cuspidate spine; f, female condition of sexually dimorphic character; LTAS, lateral terminal accessory spine; LV, lateroventral; MD, middorsal spine; NB, middorsal spines (present on segments 1 to 9 in both sexes, though it was not possible measure them accurately in the female holotype); MSW-7, maximum sternal width (measured on segment 7 in this species); MTS, midterminal spine; S, segment; SD-10, standard width of sternal plates, always measured on segment 10; TL, trunk length; question marks (?) indicate that an exact measurement could not be obtained.

| Character | Female holotype | Male allotype |
|---|---|---|
| TL | 279 μm | 265 μm |
| MSW-7 | 81 μm | 81 μm |
| MSW-7/TL | 29.0% | 30.6% |
| SD-10 | 56 μm | 59 μm |
| SD-10/TL | 20.1% | 22.3% |
| S1 | 21 μm | 21 μm |
| S2 | 28 μm | 27 μm |
| S3 | 29 μm | 58 μm |
| S4 | 31 μm | 34 μm |
| S5 | 32 μm | 35 μm |
| S6 | 33 μm | 37 μm |
| S7 | 35 μm | 38 μm |
| S8 | 35 μm | 38 μm |
| S9 | 38 μm | 40 μm |
| S10 | 31 μm | 31 μm |
| S11 | 18 μm | 17 μm |
| MD 1 (ac) | ? | 23 μm |
| MD 2 (ac) | ? | 28 μm |
| MD 3 (ac) | ? | 28 μm |
| MD 4 (ac) | ? | 26 μm |
| MD 5 (ac) | ? | 31 μm |
| MD 6 (ac) | ? | 32 μm |
| MD 7 (ac) | ? | 33 μm |
| MD 8 (ac) | ? | 36 μm |
| MD 9 (ac) | ? | 39 μm |
| LV 1 (ac) | 33 μm | 24 μm |
| LV 2 (ac) | 29 μm | 25 μm |
| LV 2 (cu) (f) | 15 μm | – |
| LV 3 (ac) | 30 μm | 27 μm |
| LV 4 (ac) | 30 μm | 29 μm |
| LV 4 (cu) | 15 μm | ? |
| LV 5 (ac) | 31 μm | 29 μm |
| LV 5 (cu) | 18 μm | 20 μm |
| LV 6 (ac) | 33 μm | 30 μm |
| LV 7 (ac) | 33 μm | 32 μm |
| LV 8 (ac) | 34 μm | 34 μm |
| LV 8 (cu) | 19 μm | 27 μm |
| LV 9 (ac) | 39 μm | 40 μm |
| LV 9 (cu) | 19 μm | 22 μm |
| MV 7 (ap) | 8 μm | 8 μm |
| MV 8 (ap) | 9 μm | 9 μm |
| LTAS | 165 μm | 154 μm |
| MTS | 67 μm | 70 μm |
| MTS/LTAS | 40.6% | 45.5% |

the addition of a pair of elevated sublateral sensory spots as the only difference.

Segment 6 with middorsal and lateroventral acicular spines. Cuspidate spines and paraventral sensory spots are not present. Otherwise, the segment is identical with the previous one.

Segment 7 with middorsal and lateroventral acicular spines (Figs. 2A, 2B, 5C, 6D). Paradorsal sensory spots are not present. Elevated sensory spots are present in the laterodorsal, sublateral and ventromedial positions. A pair of unusual structures is present in the ventromedial positions (Figs. 2B, 5C, 6D, 6E). The structures are cone-shaped, approximately 8 μm long, and densely fringed throughout their length (see Fig. 6E for similar structure on segment 8). They may possibly be regarded enlarged tubules or papillae, but appear more like the distal part of a cuspidate spine. Due to the uncertainty in the nature of this new structure, we refer to them here with the neutral term "appendages". The ventromedial appendages are present in both sexes. Cuticular hairs and posterior segment margin appear as on the previous segment.

Segment 8 with middorsal and lateroventral acicular spines, and lateroventral cuspidate spines (Figs. 2A, 2B, 5C, 6D). A pair of non-elevated paradorsal sensory spots is present. Elevated sensory spots are also present in the laterodorsal and ventromedial positions. A pair of ventromedial appendages is present (Fig. 6E). Compared to those on the previous segment, these appendages are slightly longer, and are located slightly closer to the midsternal junction (Figs. 2B, 5C, 6D). Cuticular hairs and posterior segment margin appear as on the previous segment.

Segment 9 with middorsal and lateroventral acicular spines, and lateroventral cuspidate spines (Figs. 2A, 2B, 5E). A pair of non-elevated paradorsal sensory spots is present. Elevated sensory spots are also present in the laterodorsal, sublateral and ventromedial positions. In addition, a pair of giant sensory spots is located in the ventromedial position, anterior to the much smaller elevated sensory

**Table 2.** Summary of the nature and location of sensory spots, spines, and appendages arranged by series in *Condyloderes megastigma* sp. nov. from the Korea Strait. Abbreviations: ac, acicular spine; cu, cuspidate spine; f, female condition of sexually dimorphic character; ltas, lateral terminal accessory spine; mts, midterminal spine; ss1/3, sensory spot type 1/3 (giant sensory spot marked with an exclamation mark [!]); LA, lateral accessory; LD, laterodorsal; LV, lateroventral; MD, middorsal; ML, midlateral; PD, paradorsal; PV, paraventral; SD, subdorsal; SL, sublateral; VM, ventromedial.

| Position Segment | MD | PD | SD | LD | ML | SL | LA | LV | VM | PV |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | ac | | ss1 | ss1 | | ss1 | | ac | ss1 | |
| 2 | ac | ss1 | | ss1 | ss1 | ss1 | | ac, cu (f) | ss1 | ss1 |
| 3 | ac | | | ss1 | | ss1 | | ac | ss1 | ss1 |
| 4 | ac | ss1 | | ss1 | | | | ac, cu | ss1 | ss1 |
| 5 | ac | ss1 | | ss1 | | ss1 | | ac, cu | ss1 | ss1 |
| 6 | ac | ss1 | | ss1 | | ss1 | | ac | ss1 | |
| 7 | ac | | | ss1 | | ss1 | | ac | ap, ss1 | |
| 8 | ac | ss1 | | ss1 | | | | ac, cu | ap, ss1 | |
| 9 | ac | ss1 | | ss1 | | ss1 | | ac, cu | ss1 (!), ss1 | |
| 10 | | | ss1 | | | | | ss1 | | |
| 11 | mts | | ss3 | | | | ltas | ss3 | | |

spots (Figs. 2B, 5E, 6C, 6D). The giant sensory spots consist of numerous minute papillae that cover an area of 10 × 7 µm (Fig. 6C). Pores are not clearly visible. Cuticular hairs and posterior segment margin appear as on the previous segment.

Segment 10 without spines or paradorsal sensory spots (Fig. 2A, B). Elevated sensory spots are present in the subdorsal and lateroventral positions. The middorsal line is marked by a serrated ridge (Fig. 2A). The posterior segment margin is serrated as well and has no spicular fringe. The posterior margins of the sternal plates are straight in males, whereas they are broadly concave in females (Fig. 6F). Female gonopores are indistinct.

Segment 11 has midterminal and lateral terminal accessory spines (Figs. 2A, 2B, 5A, 6F), of which the latter are more than double the length of the midterminal spine. Stalked, modified sensory spots (type 3 sensu Nebelsick, 1992) are present in the subdorsal and lateroventral positions (Figs. 5D, 6F). Cuticular hairs are scale-like and scattered over the segment.

## DISCUSSION

### Notes on diagnostic features

*Condyloderes megastigma* sp. nov. can be distinguished from all other species in the genus by the presence of ventromedial appendages on segments 7 and 8 (Figs. 2B, 5C, 6D, 6E), the presence of giant ventromedial sensory spots on segment 9 (Figs. 2B, 5E, 6C, 6D), and the absence of middorsal and laterodorsal spines on segment 10 (Fig. 2A). The new species furthermore possesses a unique distribution of knobby projections on the placids. Of the species recognized for *Condyloderes*, only *C. megastigma* sp. nov. has eight projections on the midventral placid, opposed to six in *C. multispinosus* and *C. paradoxus* (Higgins, 1969a), four in *C. setoensis* (Adrianov et al., 2002), and three in *C. storchi* (Martorelli and Higgins, 2004). On the other placids, *C. megastigma* sp. nov. has either two or four projections, opposed to two or six in *C. multispinosus* and *C. paradoxus*, one or four in *C. setoensis*, and one or three in *C. storchi*.

Opposed to *C. megastigma* sp. nov., which possesses lateral terminal accessory spines, all other previously described species in the genus are reported to have lateral terminal spines, viz. terminal spines belonging to the lateroventral series sensu Pardos et al. (1998). From the illustrations in the original descriptions of these species, however, the paired terminal spines are obviously more dorsally displaced and should be considered as lateral terminal accessory spines as well (see McIntyre, 1962; Higgins, 1969a; Adrianov et al., 2002; Martorelli and Higgins, 2004). Hence, this feature cannot be used to distinguish the five species of *Condyloderes*.

The pattern of the lateral series of spines in female *C. megastigma* sp. nov. (see Table 2) is identical with the pattern in *C. paradoxus*, whereas the presence of lateroventral cuspidate spines on segment 4 (present in both male and female of *C. megastigma* sp. nov.) differentiates the new species from *C. multispinosus* and *C. setoensis*. In *C. storchi*, lateral accessory cuspidate spines occur on segment 1, whereas they are found neither in *C. megastigma* sp. nov. nor any other known species. Also, the paradorsal cuspidate spines on segments 5 and 7 are unique to *C. storchi*.

Another discriminative trait is found in the tegumental composition of the terminal segment. In *C. multispinosus*, *C. paradoxus*, and *C. storchi* the terminal segment is composed of a tergal plate and two completely separated sternal plates. In *C. setoensis*, however, the midsternal articulation is only partly developed, and in *C. megastigma* sp. nov. the ventral side of the segment is composed of only a single sternal plate (Figs. 2B, 5D).

### Systematic and phylogenetic considerations

The description of *C. megastigma* sp. nov. is accompanied by the first detailed SEM observations and descriptions of the mouth cone and introvert appendages for the genus *Condyloderes* (Figs. 3, 4A, 4B). In most other well-examined kinorhynch species, the inner armature of the mouth cone includes two rings with inner oral styles and an innermost ring with helioscalids (e.g., Brown, 1989; Nebelsick, 1993; Bauer-Nebelsick, 1995, 1996; Sørensen, 2007; Sørensen and Pardos, 2008). The only hitherto known deviation from this pattern occurs in the genus *Campyloderes*, in which both helioscalids, plus outer and inner oral styles are absent (Neuhaus, 2004; Sørensen and Neuhaus, unpubl. obs.). With a mouth cone armature consisting of only a single ring of inner oral styles and poorly developed outer oral styles that are partly fused with the mouth cone (Fig. 4A), *C. megastigma* sp. nov. seems to represent an intermediate state between the conditions found in species of *Campyloderes* and all other kinorhynch species. The polarity of this character transformation needs appropriate evaluation in a future phylogenetic analysis, but the missing mouth cone armature in species of *Campyloderes*, and the poorly developed armature in *C. megastigma* sp. nov., could provide further support for a close relationship between these two genera.

Another feature in the new species that attracts our special attention is the composition of the terminal segment. The segment consists of one single tergal and one single sternal plate (Figs. 2A, 2B, 5D). Besides in *C. megastigma* sp. nov., a single, undivided sternal plate on segment 11 is found only in species of the homalorhagid genus *Paracentrophyes* Higgins, 1983 (Higgins, 1983). The recorded difference is interesting, because the segmental composition usually carries much weight in the kinorhynch classification, and it is typically used to recognize larger clades at the generic or familial level (e.g., Higgins, 1968, 1969a, 1969b, 1990; Adrianov and Malakhov, 1999; Sørensen and Pardos, 2008). However, species of *Condyloderes*, the new one included, share several putative synapomorphies, and monophyly of the genus is thus highly likely, despite the varying composition of segment 11. Instead, the observation suggests that some segments show more morphological plasticity than others, and that the composition of the terminal segment may show substantial variability at the intrageneric level. An analogous example of this can be observed among species of *Fissuroderes* Neuhaus and Blasche, 2006, where closely related species vary between having either a single or two paired tergal plates on the terminal segment (Neuhaus and Blasche, 2006).

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