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Revision of *Condyloderes* (Kinorhyncha, Cyclorhagida) including description of *Condyloderes shirleyi* sp. nov.

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Abstract

The description of a new representative of the species-poor genus *Condyloderes* Higgins, 1969 from the Northeast Pacific (Alaska) is reported. The analyzed specimens of *Condyloderes shirleyi* **sp. nov.** showed a significant variation of numerous morphological characters, along with female-specific traits known also from other congeneric species. These findings stimulated the re-investigation of the type material of the six species of *Condyloderes* described so far, i.e., *C. kurilensis* Adrianov & Maiorova, 2016, *C. megastigma* Sørensen, Rho & Kim, 2010b, *C. multispinosus* (McIntyre, 1962) Higgins, 1969, *C. paradoxus* Higgins, 1969, *C. setoensis* Adrianov, Murakami & Shirayama, 2002, and *C. storchi* Higgins, 2004 in Martorelli & Higgins, 2004. Our study allowed to reveal various morphological novelties and to emend the diagnosis of these species and of the genus *Condyloderes*. Furthermore, our analysis led to synonymize *C. megastigma* with *C. setoensis*. The results of our investigation about the significant variation in *C. shirleyi* **sp. nov.** raise a wider question on species identity within Kinorhyncha, underscoring the necessity, if possible, to describe new species from a higher number of specimens and to concentrate on the morphological variation of the going-to-be-described species.

Key words: Centroderidae, intraspecific variation, meiofauna, new species, taxonomy

Introduction

The phylum Kinorhyncha comprises to date over 260 species of microscopic metazoans inhabiting marine environments, from the intertidal to abyssal depths (Neuhaus 2013; Sørensen *et al.* 2018; Yamasaki *et al.* 2018). The majority of the studies on this group have dealt with taxonomical issues, leading to a constant increase of the discovery of new species, particularly marked over the last decades, and characterized also by the description of new higher taxonomic ranks (Neuhaus & Blasche 2006; Dal Zotto *et al.* 2013; Sánchez *et al.* 2014; Yamasaki 2016). Within this context which highlights the necessity of further basic taxonomic research, a particular consideration is evidently directed to the species-poor genera, far more numerous than the two richest ones, i.e., *Echinoderes* and *Pycnophyes*, accounting for nearly half of the total number of known species. Among these genera, *Condyloderes* Higgins, 1969 is currently represented by six species only, distributed worldwide. The first of these was originally found in the North Sea off Scotland and described by McIntyre (1962) as *Centroderes multispinosus*. Higgins (1969) re-described this species as *Condyloderes multispinosus* (McIntyre, 1962) Higgins, 1969, contextually erecting the new genus and describing a second species from the Bay of Bengal (*C. paradoxus* Higgins, 1969). More recently, *C. setoensis* Adrianov, Murakami & Shirayama, 2002 was described from Honshu Island (Adrianov *et al*. 2002) and *C. storchi* Higgins, 2004 in Martorelli & Higgins 2004 was recovered and described from the stomach of the shrimp *Pleoticus muelleri* (Bate, 1888) found off the coast of Patagonia (Martorelli & Higgins 2004). The latest two known species are *C. megastigma* Sørensen, Rho & Kim, 2010, occurring in the Korea Strait (Sørensen *et al*. 2010b) and *C. kurilensis* Adrianov & Maiorova, 2016 discovered at abyssal depths near the Kuril-Kamchatka Trench (Adrianov & Maiorova 2016).

In the present study, we report the description of a new species of *Condyloderes* from the Northeast Pacific (Alaska). The analyzed specimens showed a marked variation of some diagnostic morphological characters. Actually, the degree of variation reached would have normally allowed the erection of more than a single new species. The new taxon also exhibited female-specific characters in line with those recently described for *C. kurilensis* (Adrianov & Maiorova 2016). Furthermore, numerous specimens of some undescribed congeneric species from different areas of the world which we had the opportunity to examine (information on part of this material is reported by: Sørensen *et al*. 2012a: East China Sea; Neuhaus 2013: East Pacific; Dal Zotto & Todaro 2016: Mediterranean Sea; Yamasaki 2017: Japanese waters; Dal Zotto, Neuhaus & Yamasaki, unpubl. obs.) suggested similarly sexually dimorphic characters for species of *Condyloderes*. All these findings prompted us to re-investigate the type and non-type material of the six species described so far. The examination allowed to extensively document the morphology of the known species of *Condyloderes* and to reveal several morphological novelties, emending the diagnosis of the genus and of its known species and synonymizing *C. megastigma* with *C. setoensis*.

Other recent investigations on the morphology of a taxon closely related to *Condyloderes*, *viz Centroderes* (see Sørensen *et al*. 2015), along with the description of new species of this latter genus (Neuhaus *et al*. 2013, 2014), revealed a series of features that stimulated a new outlook on the whole class Cyclorhagida, i.e., some sexually-dimorphic characters, the presence of spermatophores, and the existence of two (*Centroderes barbanigra* Neuhaus *et al*., 2014, *C. bonnyae* Neuhaus *et al*., 2014, *C. readae* Neuhaus *et al*., 2014, and *C. spinosus* (Reinhard, 1881)) or more (*C. drakei* Neuhaus *et al*., 2014) adult life history stages during the postembryonic development. Furthermore, the analysis of specimens of *Campyloderes*, another genus formerly considered to be closely related to *Condyloderes* (see Higgins 1969; Adrianov & Malakhov 1999; Neuhaus 2013; Sørensen *et al*. 2015), from different areas of the world showed again the existence of two adult stages and a significant variation of some morphological traits, which did not allow a clear species identification, stimulating to hypothesize the presence of an ongoing species formation process (Neuhaus & Sørensen 2013).

The data reported herein extend the considerations of this recently developed taxonomical context and raise a wider question on the diagnostic characters and hence the species identity within Kinorhyncha, underscoring the necessity to describe new species from a higher number of specimens, if available, and to focus on the morphological variation of the going-to-be-described species.

We also document deterioration of mounting media of microscope slides because of ageing over years or initiated by handling. This issue is important, since specimens turned out to become unavailable for future studies within few weeks after mechanical stress impact.

Materials and methods

Concerning *Condyloderes shirleyi* **sp. nov.**, sediment was collected with a meiofauna dredge at Glacier Bay in Alaska from 33 m depth by R.P. Higgins and L. McNutt (Fig. 1; see Table 1 for details). The meiofauna was extracted from sediment samples with the bubble and blot method developed by Müller (1894) and emended by Higgins (1964, 1988). For further details about processing and about the location of *Condyloderes shirleyi* **sp. nov.** see Table 1. The type material was deposited both at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM) and at the Museum für Naturkunde Berlin (ZMB; Table 1).

TABLE 1. Location and processing data of all known species of *Condyloderes*. Abbreviations: BMNH, British Museum of Natural History, London; ICHUM, Invertebrate Collection at the Hokkaido University; MIMB, Museum of A.V. Zhirmunsky Institute of Marine Biology, Vladivostok; NHMUK, Natural History Museum of the United Kingdom, London; USNM, Museum of Natural History, Smithsonian Institution, Washington, D.C. (previously United States National Museum); ZMB, collection “Vermes” of Museum für Naturkunde Berlin (previously Zoological Museum Berlin); ZMUC-KIN, Natural History Museum of Denmark, Copenhagen (previously Zoological Museum of Copenhagen - collection Kinorhyncha).

Species	**Station data** (location, georeferences, field station #; depth)	**Collection date; gear**	**Collector, ship**	**Processing of specimens for light microscopy**	**Specimens; remarks**	**Reference**
Condyloderes kurilensis	Northwest Pacific Ocean, plain at south border of Kuril-Kamchatka Trench, 43°02.3230’ N, 152°59.0997’ E, Station 7-4, mud; 5,222 m depth	17.VIII.2012; box corer	R/V Sonne, cruise SO 250	extracted from water above box corer by sieving, fixed in 4% formaldehyde buffered with sea water, transferred to ethanol and glycerol, mounted in Vectashield on H-S plastic slides	holotypic ♂: MIMB 32339; paratypic ♀: MIMB 32340, specimen mounted too close to margin of coverslip for observation with oil immersion lens	Adrianov & Maiorova 2016
C. multispinosus	North Atlantic Ocean, west Scotland, Loch Ness, 56°59’35’’ N, 005°40’45’’ W, mud; 101 m depth	15.VII.1960 [on label]; core sampler	A.D. McIntyre	stored in ethanol, mounted as glycerol-paraffin slide on Cobb aluminium frame and sealed with Glyceel (recipe according to Bates 1997) by B. Neuhaus	holotypic ♂: BMNH 1962.82 (= NHMUK ecatalogue 7046691), previously identified as adult (McIntyre 1962; Higgins 1969)	McIntyre 1962
	North Atlantic Ocean, west Scotland, Loch Torridon, 57°34’48’’ N, 005°45’48’’ W; 137 m depth	1959–1962; core sampler	A.D. McIntyre	unknown	1 specimen (not studied here; unknown if deposited in a collection)	
	North Atlantic Ocean, North Sea, east off Scotland, Fladen, 58°20’ N, 000°30’ E; 140 m depth	1959–1962; core sampler	A.D. McIntyre	unknown	8 specimens (not studied here; unknown if deposited in a collection)	
	North Atlantic Ocean, Scotland, Loch Nevis	7.II.1963 [from Access database]	A.D. McIntyre	unknown	1 ♂: USNM 1209820 (= K-80.2 from RH-2334), previously identified as adult; 1 juvenile: USNM 1209819 (= K-80.1 from RH-2334)	Higgins 1969
	North Atlantic Ocean, Scotland, Loch Nevis; 101 m depth	1962 [on label]	A.D. McIntyre	unknown	1 ♂: USNM W37459 (= K-81.1 from RH-2335), previously identified as ♀	
	North Atlantic Ocean, Scotland, Loch Nevis; 101 m depth [on label]	unknown	A.D. McIntyre	unknown	1 ♂: USNM 1209821 (= K-81.2 = RH-2335), previously identified as ♀	
	North Atlantic Ocean, southern North Sea, The Netherlands, north of mouth of Westerscheldt estuary, 51°28'25" N, 03°28'10" E; depth 7.5 m, fine sand	1983 or 1984; Reineck box corer	unknown	fixed in 7% neutralised formaldehyde, extracted by decantation or centrifugation with Ludox, transferred to 7% formaldehyde and later to glycerol, mounted in Hoyer’s medium on Cobb aluminum slides, coverslip sealed with Glyceel	3 adult specimens (not studied here; not deposited at Royal Belgian Institute of Natural Sciences, Brussels, material probably lost)	Huys et al. 1986; Huys & Coomans 1989

… …continued on the next page

TABLE 1. (Continued)

Species	**Station data** (location, georeferences, field station #; depth)	**Collection date; gear**	**Collector, ship**	**Processing of specimens for light microscopy**	**Specimens; remarks**	**Reference**
C. paradoxus	Indian Ocean, India, Bay of Bengal, about 10 km off shore east of Visakhapatam, brown sandy mud; 40 m depth	26.III.1964; meiobenthic dredge	R.P. Higgins	extracted with bubble & blot, fixed in 7% formaldehyde; 6 specimens unstained, transferred to ethanol-glycerol, mounted from glycerol in Hoyer's medium on Cobb aluminium slides; 6 specimens stained with Semichon's, mounted in Permount on Cobb aluminium slides	holotypic ♂: USNM 37460 (= RH-37.81); 3 paratypic ♀: USNM 37461 (= RH-37.78; = allotype), 1209809 (= RH-37.79), 1209812 (= RH-37.83, previously identified as ♂, stained); 3 paratypic ♂: USNM 1209810 (= RH-37.80), 1209813 (= RH-37.84, stained), 1209814 (= RH-37.85, stained); 1 paratypic juvenile moulting: USNM 1209811 (= RH-37.82, stained)	Higgins 1969
	Indian Ocean, India, Bay of Bengal, about 5 km southeast of Kakinada Bay, soft brown mud; 40 m depth	23.III.1964; meiobenthic dredge	R.P. Higgins		3 paratypic ♂: USNM 1209804 (= RH-36.9, stained), 1209805 (= RH-36.10, stained), 1209807 (= RH-36.29); 1 paratypic ♀ : 1209808 (= RH-36.30, previously identified as ♂)	
	Northwest Pacific Ocean, south of Singapore Island, between Bedok Jetty and Sungai Bedok, 01°18.387' N, 103°57.591' E, stations SI-03 and SI-04, sand with mud; 9 m depth	16.V.2014; dredge	R.C. Neves, R/V Galaxea	extracted with bubble & blot, fixed in 4% paraformaldehyde overnight, rinsed in 0.1 mol/l phosphate buffer, dehydrated via glycerol, mounted in Fluoromount G™ on Higgins-Shirayama plastic slides	1 ♀: ZMUC-KIN-848 (station SI-04 according to label on slide); SEM images of 2 uncatalogued specimens: ♀ (station SI-03) and late juvenile stage (station SI-04), provided by M.V. Sørensen	Sørensen *et al.* 2016
C. paradoxus or *C. setoensis*	Northwest Pacific Ocean, Korea Strait, 33°18.91' N, 127°40.96' E, MAP-07, mud; 132 m depth	30.IX.2006; box corer	H.S. Rho	fixed in 4% formaldehyde, extracted by centrifugation with Ludox	SEM images of 1 uncatalogued late juvenile stage, previously identified as *C.* cf. *paradoxus*, provided by M.V. Sørensen	Sørensen *et al.* 2012a; this paper
C. setoensis	Northwest Pacific Ocean, Japan, Honshu Island, Kii-Peninsula, Tanabe Bay, near Seto Marine Biological laboratory, 33°42.2' N, 135°22.9' E, mud; 15–27 m depth	2000; meiobenthic dredge	R/V Janthina II	extracted with bubble & blot, fixed in 10% buffered formaldehyde in seawater, transferred to ethanol-glycerol, mounted in modified Hoyer's 125 medium on Higgins-Shirayama plastic slides	holotypic ♂: AVA-CM-JAP-01, not studied here; 3 paratypic ♂: AVA-CM-JAP-02, AVA-CM-JAP-03, AVA-CM-JAP-04 [information from labels]; paratypic ♀ CM-A-JAP-04.C + paratypic ♂ CM-A-JAP-01.C + juvenile CM-A-JAP.04.C [sic!] + 3 adults mounted for SEM, not studied here	Adrianov *et al.* 2002

… …*continued on the next page*

TABLE 1. (continued)

Species	**Station data** (location, georeferences, field station #; depth)	**Collection date; gear**	**Collector, ship**	**Processing of specimens for light microscopy**	**Specimens; remarks**	**Reference**
C. setoensis	Northwest Pacific Ocean, Japan, off south coast of Honshu Island, Shirahama, 33°42'02'' N, 135°22'32'' E, mud; 30 m depth	19.IV.1986; meiobenthic dredge	R.P. Higgins & Y. Shirayama	all specimens stained, probably with Rose Bengal; mounted as paraffin-glycerol slides on Cobb aluminium frames, coverslip sealed with Glyceel	♀: USNM 1490850 (= RH-2092.01); 3 juveniles: USNM 1490851–1490853 (= RH-2092.02–RH-2092.04)	this paper
C. setoensis (specimens with lateral accessory cuspidate spine on segment 4)	Northwest Pacific Ocean, Japan, off south coast of Honshu Island, Shirahama; 33°42'06'' N, 135°21'06'' E, mud; 20 m depth	19.IV.1986; meiobenthic dredge	R.P. Higgins & Y. Shirayama	mounted on Cobb aluminium slide	♂: USNM 1490844 (= RH-2074.01); database erroneously reports 133° E which is on land, location description fits 135° E	this paper
	Northwest Pacific Ocean, Japan, Honshu Island, off Sanriku, off Ohtsuchi Bay, station SK 1-2, 39°20'12'' N, 142°01'36'' E, muddy sand; 124 m depth	15.VIII.1985; unknown	Y. Shirayama, R/V Tansei-maru, cruise KT 85-11	mounted on Cobb aluminium slide	♂: USNM 1490845 (= RH-2076.01)	this paper
	Northwest Pacific Ocean, Sea of Japan, off Kyushu Island, station 11-1, 34°11'34.56'' N, 130°37'30.24'' E; 91 m depth	27.V.2014; dredge	H. Yamasaki, R/V Toyoshio-maru	mounted in Fluoromount G™ on Higgins-Shirayama plastic slide with rectangular hole, coverslip sealed with Canada balsam	♂: ICHUM 5836 (hologenophore after DNA extraction)	this paper
	Northwest Pacific Ocean, East China Sea, 33°30' N, 123°59' E; 66 m depth	10.VIII.1981; unknown	T. Zhican	mounted on Cobb aluminium slide, coverslip sealed with an (epoxy) paint	♂: USNM 1491399 (= RH-1608.1 = G8135.1)	this paper
	Indian Ocean, Andaman Sea, Thailand, south of Phuket between Marine Station and Ko Lon, 07°47'30'' N, 098°24'18'' E, silty coarse sand and shells; depth 11 m	28.III.1988; meiobenthic dredge	R.P. Higgins	mounted as paraffin-glycerol slide on Cobb aluminium frame, coverslip sealed with Glyceel	♂: USNM 1490857 (= RH-2210)	this paper

… …*continued on the next page*

TABLE 1. (continued)

Species	**Station data** (location, georeferences, field station #; depth)	Collection date; gear	Collector, ship	Processing of specimens for light microscopy	Specimens; remarks	Reference
C. setoensis (previously *C. megastigma*)	Northwest Pacific Ocean, Korea Strait, 34°10.24' N, 128°25.90' E, Station 2 (= MAP-06), mud; 76 m depth	6.IX.2006; box corer	H.S. Rho, R/V Onnuri	extracted with freshwater shock and sieving through 63 µm sieve or by Ludox centrifugation, fixed in 4% formaldehyde buffered with sea water, transferred to distilled water and later to glycerol, mounted in Fluoromount G™ on glass slides	holotypic ♀: ZMUC-KIN-250; SEM images of 1 uncatalogued ♀, previously identified as ♂, provided by M.V. Sørensen	Sørensen *et al.* 2010b, 2012a, pers. comm.
	Northwest Pacific Ocean, Korea Strait, 33°40.33' N, 126°04.33' E, Station 3 (= MAP-31), mud; 103 m depth	8.X.2008; box corer			paratypic ♀: ZMUC-KIN-251, previously identified as ♂; SEM images of 1 uncatalogued ♀, previously identified as ♂, provided by M.V. Sørensen	
	Northwest Pacific Ocean, Korea Strait, 34°47.19' N, 129°05.58' E, Station 1 (= MAP-32), mud with tiny shells; 109 m depth	6.X.2008; box corer			SEM images of 1 uncatalogued ♀ with introvert more or less withdrawn, provided by M.V. Sørensen	
C. shirleyi **sp. nov.**	North Pacific Ocean, Alaska, Glacier Bay, Berg Bay, North Element, brown mud, 58°32'48'' N, 136°09'00'' W, Higgins's station RH-2707; 33 m depth	17.VII.1990;meiofauna dredge	R.P. Higgins and L. McNutt	extracted with bubble & blot, fixed in 5% formaldehyde, transferred to 70% ethanol and later to glycerol, mounted in modified Hoyer's medium on Higgins-Shirayama plastic and Cobb aluminium slides in 1992 and 1993, coverslip sealed with an epoxy paint (see Higgins 1983)	holotypic ♂: USNM 1480999; 44 paratypic ♂: USNM 1480980–1480998, 1481000–1481019, ZMB 11598–11602; 28 paratypic ♀:1481020–1481042, ZMB 11603–11607; SEM: USNM 1481164 & 1481166 (specimens lost after study), 1481167, 1481168 (stub 46 with RH-2707.04SEM, .05SEM), 1481169 (with 1481164 on same stub), 1481170 (stub 45 with RH-2707.06SEM, .07SEM, .08SEM), 1481171 (stub 43), 1481172 (stub 42)	this paper
C. storchi	Southwest Atlantic Ocean, Argentina, San Jorge Gulf, Chubut, Comodoro Rivadavia, 46°47' S, 67°31' W, from stomach of shrimp *Pleoticus muelleri*	V.1993	cruise EH 05-03	fixed in 5% formaldehyde, transferred to ethanol-glycerol, mounted in Hoyer's 150 medium on Higgins-Shirayama plastic slide	holotypic ♂: USNM 1025879 (= RH-3000.3), specimen mounted too close to margin of coverslip for observation of reverse side with oil immersion lens	Martorelli & Higgins 2004
Condyloderes sp. 1	Indian Ocean, India, Bay of Bengal, about 5 km southeast of Kakinada Bay, soft brown mud; 40 m depth	23.III.1964; meiobenthic dredge	R.P. Higgins	extracted with bubble & blot, fixed in 7% formaldehyde, stained with Semichon's, mounted in Permount on Cobb aluminium slide	1 ♂: USNM 1209806 (= RH-36.11, stained, previously identified as paratypic juvenile stage of *C. paradoxus*)	Higgins 1969
Condyloderes sp. 2	Northwest Pacific Ocean, East China Sea, 30°31.66' N, 125°55.86' E, MAP-05, mud; 79 m depth	28.IX.2006; box corer	H.S. Rho	fixed in 4% formaldehyde, extracted by centrifugation with Ludox	1 SEM image of 1 uncatalogued male, previously identified as *C.* cf. *setoensis*, provided by M.V. Sørensen	Sørensen et al. 2012a; this paper

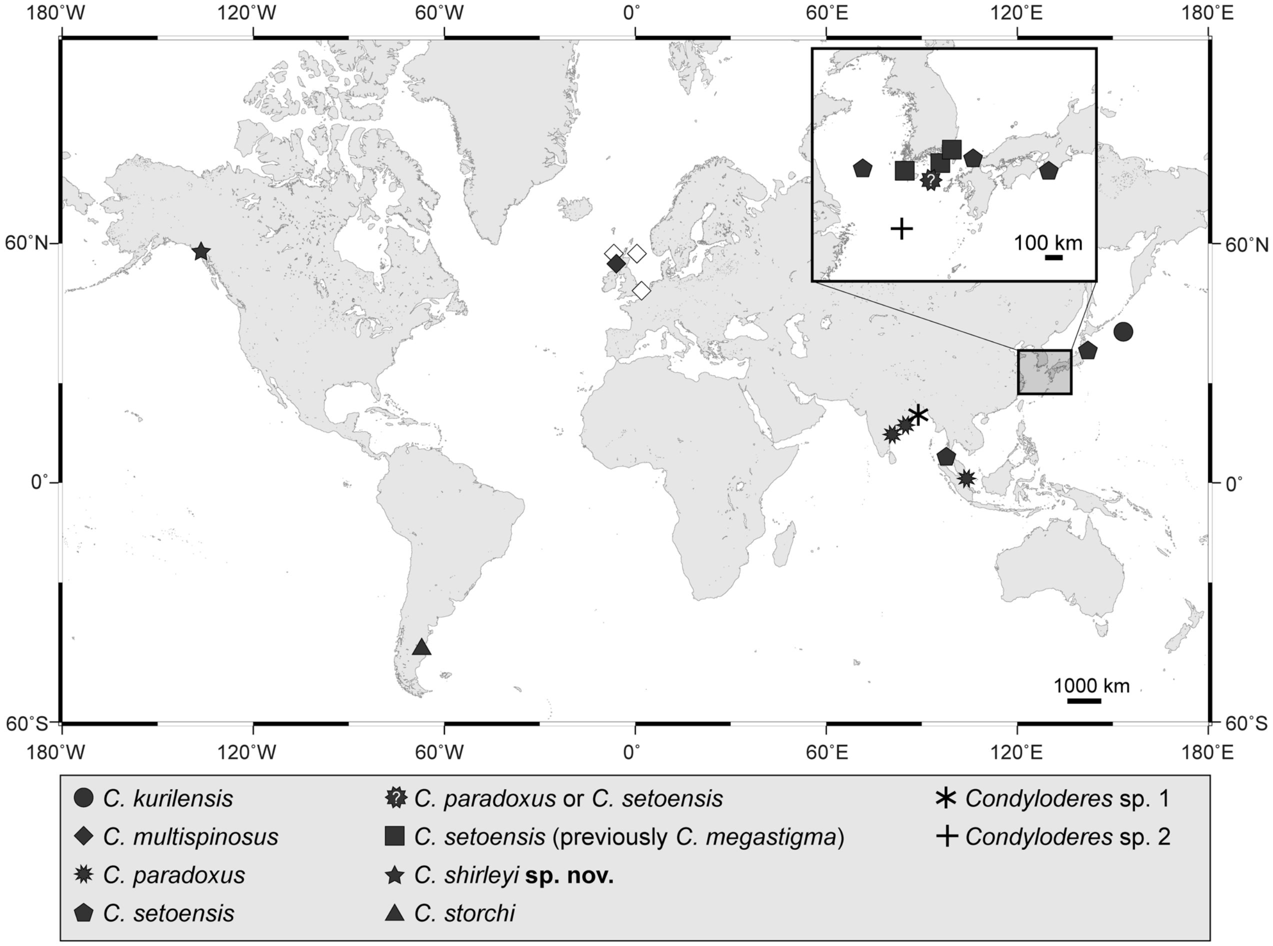


FIGURE 1. Map of locations of all known species of *Condyloderes* identified to species level; see Table 1 for location data. Filled symbols indicate specimens studied in this article, open symbols refer to specimens not investigated here.

All type and voucher material mounted for light microscopy of all described species of *Condyloderes* (with few exceptions, see Table 1) was given on loan by the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (*Condyloderes multispinosus*, *C. paradoxus*, *C. setoensis*, *C. storchi*), by the Natural History Museum, London (*C. multispinosus*), by the Natural History Museum of Denmark, Copenhagen (*C. megastigma*), and by the A. V. Zhirmunsky Institute of Marine Biology, Russian Academy of Sciences, Vladivostok (*C. kurilensis*, *C. setoensis*). In addition, we received SEM images of several uncatalogued specimens from the private collection of M.V. Sørensen (see Table 1). The holotypic male of *C. setoensis* was not available to us but three paratypic males were. The only paratypic female of the original type series, a paratypic male, and a juvenile were supposed to be deposited at Seto Marine Biological Laboratory, Japan (Adrianov *et al.* 2002) but could not be recovered. One specimen of *C. setoensis* collected by H.Y. was deposited at the Invertebrate Collection at the Hokkaido University Museum, Sapporo, Japan (Table 1).

The holotype of *C. multispinosus* was provided to us in ethanol and had not been squeezed for microscopic investigation at high magnification before, because it still revealed its more or less triangular cross-section. In addition to this observation, both the text of a previous re-description of this species by Higgins (1969) and the text and illustration in the original description by McIntyre (1962) do not indicate that the holotype of *C. multispinosus* was studied in detail at any time. The first author of this paper mounted the specimen with permission of the museum in London in order to obtain more detailed morphological data (Table 1; Figs 9, 10). Sample information about the voucher material of *C. multispinosus* is confusing. The holotype of the species was collected at Loch Nevis at 101 m depth on 15.VII.1960 according to the label in the jar accompanying the holotype, whereas no information about the date was given in the original description (McIntyre 1962); additional specimens were mentioned by McIntyre (1962) from Loch Torridon (1 specimen) and from Fladen (8 specimens) but no information is available about their deposition in a museum collection. Higgins (1969) noted that four voucher specimens were given to him by A.D. McIntyre without data, and so states the Microsoft Access database at the National Museum of Natural History containing Higgins's field stations. However, the labels of the specimens read "Topotype" and "1962, Loch Nevis, Scotland, depth 101 m". It remains open whether the voucher material was collected at Loch Nevis after 1960 or whether the voucher material is part of the originally collected series of specimens, but several specimens were only sampled at Fladen and not at Loch Nevis (see McIntyre 1962). Specimens of *C. multispinosus* were also reported from Westerscheldt estuary, The Netherlands (Huys & Coomans 1989) but could not be recovered (see Table 1).

Higgins (1969) stated that specimens of *C. paradoxus* were stained with Semichon's, transferred to ethanol-glycerol, and mounted from glycerol in Hoyer's medium. According to Gray (1954, p. 302), Semichon's stain is an acid carmine stain consisting of glacial acetic acid and carmine. Our re-investigations revealed that some specimens appeared deeply red stained but others were not at all (Figs 2, 15–17; Table 1). Also, the mounting media differed in appearance suggesting that the un-stained specimens were mounted in Hoyer's, whereas the stained specimens were mounted in a different medium (see paragraph below about Deterioration of slides). Raman spectroscopy (Schmid *et al.* 2016) of two slides each with an unstained and with a stained specimen of *C. paradoxus* confirmed the light microscope observations and yielded that the stained specimens of that species were mounted in Permount™.

Kinorhynchs were observed with a microscope Zeiss Universal equipped with an Optovar 1.25x/1.6x/2.0x magnification changer and objectives Planachromat 40/0.65 and 100/1,25 Oil and with a Zeiss Axioskop 50 equipped with differential interference contrast after Nomarski, an Optovar 1.25x/1.6x, and objectives Plan-Neofluar LD 63x/0.75 Ph2 Korr. and 100x/1.30 Oil. A Plan-Apochromat 100x/1.4 Oil and an oil immersion condenser were used in order to get the highest possible resolution for study of hard-to-observe specimens like those of *C. paradoxus*. Specimens were measured and drawn with pencil with the help of a drawing tube mounted on a Zeiss Axioskop 50 using a Plan-Neofluar LD 63x/0.75 Ph2 Korr. and a 100x/1.30 Oil. The scanned drawings served as a basis for the final illustration with the vector graphic programmes Adobe Illustrator CS6 and Corel Draw V.16.4. Specimens were photographed either with a Leitz MPS camera mounted to a Zeiss Universal on Kodak T-max 100, or with a digital Zeiss AxioCam MRc5 and objectives Plan-Apochromat 20x/0.60, 63x/1.40 DIC Oil, and 100x/1.40 Oil as well as Plan-Neofluar 40x/0.75 and 40x/1.30 Oil attached to a Zeiss Axioplan 2 mot, or with a Zeiss AxioCam MRc5 attached to a Zeiss AxioScope A1 with a Plan-Neofluar 1.25x/0.03. Extended focus images were created either with Syncroscopy Auto-Montage Essentials V.5.03.0061 ES or with Combine ZP from 28.06.2008 using the parameter "all methods". Negatives were scanned with an Epson Perfection 1200 Photo. Both digitized negatives and primarily digital images were improved with Corel Photo Paint V.16.4 and mounted with Corel Draw V.16.4.

The maps were drawn with the Generic Mapping Tools (GMT 5.4.1, https://www.soest.hawaii.edu/gmt/) by using the bathymetric data from the database of the National Center for Environmental Information.

The preparation for scanning electron microscopy followed the procedure described by Neuhaus (1995). In short, some specimens were treated by means of an ultrasonic cleaner for several seconds in either Carosafe or in a mixture of the detergent Contrad 70 and KOH (comp. Kornicker 1976). Unfortunately, such processing revealed only limited success, specimens could not always be cleaned sufficiently or lost many of their spines. Treatment with the detergents 409 and terg-a-zyme, proteinases (Adolph's meat tenderizer), bleaching agents (Clorox), acetone, chloroform, or toluene in combination with an ultrasonic cleaner did not yield better results. After postfixation in 1% OsO_4 for about 2.5 hours, the material was dehydrated via an ethanol series, critical point-dried, mounted on top of minutia needles on aluminium stubs, and coated with carbon and gold-palladium in a CVE 301T sputter coater, Cooke Vacuum Prod. Specimens were viewed with a Cambridge Stereoscan 250 MK 2 scanning electron microscope at 10 kV and photographed on Kodak Tri-X pan professional 4164 film at a size of 10.2 cm x 12.7 cm (= 4 inch x 5 inch).

Remarks about the descriptions. The (re-)descriptions are based on the holotype and specimens of the same sex except for *C. setoensis*, because only paratypes were available for loan. Several images of additional specimens demonstrate the described anatomical situation better than images of the holotype alone would. Also in order to avoid unnecessary duplication of text, such images are, therefore, included in the description of the holotype. Not all structures are documented by images, because most Higgins-Shirayama plastic slides bent upwards and did not allow oil immersion observation or photography from the reverse side, e. g., in *C. storchi*. Photography became especially difficult sometimes, because the plan-apochromatic lenses possessed a considerably larger front diameter than the plan-neofluar lenses. Also, some specimens were occasionally mounted too close to the margin for oil immersion study, e. g., in the paratypic female of *C. kurilensis*. The descriptive text partly repeats for the different species, because each description of a species stands for itself. Considering the variation in the new species, *Condyloderes shirleyi* **sp. nov.**, the holotype was chosen to reveal all characters, which the majority of specimens possessed. Almost all specimens of this species mounted for light microscopy suffered from a variable amount of detritus on the specimens.

The terminology of the description follows Higgins (1983) as emended by Neuhaus and Higgins (2002), Sørensen and Pardos (2008), Herranz *et al*. (2012), Neuhaus (2013), and Yamasaki *et al.* (2018). Opposite to Herranz *et al*. (2012), the term “pectinate fringe tips” is replaced here by “pectinate fringe teeth” (see Yamasaki *et al.* 2018 for argumentation).

We herewith introduce the new term type-6 sensory spots for sensory spots in Kinorhyncha elevated above the trunk cuticle and giving the impression of being half-drowned in the cuticle (for comparison see *Condyloderes shirleyi* **sp. nov.**, Fig. 43D, E). The current paper shows that these spots occur in all species of *Condyloderes*.

Deterioration of slides. The holo- and paratype of *Condyloderes megastigma* were mounted in Fluoromount G™ and suffered from crystals near and on the specimens (Figs 3E, 25, 26A, B) as well as from formation of cavities. One slide of *C. setoensis* mounted in Hoyer’s medium showed clear spherical bodies throughout the mounting medium (Fig. 3C). A second slide revealed bar-like crystals often appearing clustered (Fig. 3D). Also, the specimens of *C. multispinosus* and some specimens *C. shirleyi* **sp. nov.** as well as those of *C. paradoxus* mounted in Hoyer’s medium were difficult to study and to measure now because of formation of cavities, precipitations, and brown spherical bodies (possibly containing iodine) at the specimens and continuing maceration of specimens due to the chloral hydrate contained in Hoyer’s (Figs 2E, F, 3A, B, F, G, 11, 12, 15, 16C, D, F).

Stained specimens of *Condyloderes paradoxus* and *Condyloderes* sp. revealed a clear surrounding mounting medium without precipitations and brown spherical bodies (comp. Fig. 2A–D with Fig. 2E, F). Two stained specimens of the latter species (USNM 1209804, 1209813) and the stained specimen of *Condyloderes* sp. (USNM 1209806) developed after our study cracks in the mounting medium and rainbow-coloured discolouration (Fig. 2A, D), and in one specimen in addition the peripheral medium yellowed and cracked totally. All these characters are typical of Permount™ (Neuhaus *et al*. 2017). Most probably, the damage was initiated by mechanical stress during investigation with an oil immersion lens and an oil immersion condenser as well as during cleaning from the oil with a laboratory tissue. The cracks started from the periphery of the coverslip and reached the specimen of *C. paradoxus* within less than two weeks (Fig. 2A).

The problems described above are well known for the mounting media Fluoromount G™, Hoyer’s medium, and Permount™, so these media should be avoided under all circumstances for taxonomically important material (Neuhaus *et al.* 2017). Also, Higgins-Shirayama plastic slides with a circular hole bend upwards in their central area over time, so observation from the reverse side becomes extremely difficult.

List of abbreviations

BMNH	British Museum of Natural History, London (now Natural History Museum of the United Kingdom)
comp.	compare
H-S slide	Higgins-Shirayama slide
ICHUM	Invertebrate Collection at the Hokkaido University
MIMB	Museum of A.V. Zhirmunsky Institute of Marine Biology, Vladivostok Museum, Sapporo, Japan
NHMUK	Natural History Museum of the United Kingdom, London (previously British Museum of Natural History)
pers. comm.	personal communication
R/V	research vessel
unpubl. obs.	unpublished observations
USNM	Museum of Natural History, Smithsonian Institution, Washington, D.C. (previously United States National Museum)
ZMB	Collection “Vermes” of Museum für Naturkunde Berlin (previously Zoological Museum Berlin)
ZMUC-KIN	Natural History Museum of Denmark, Copenhagen (previously Zoological Museum of Copenhagen—collection Kinorhyncha)

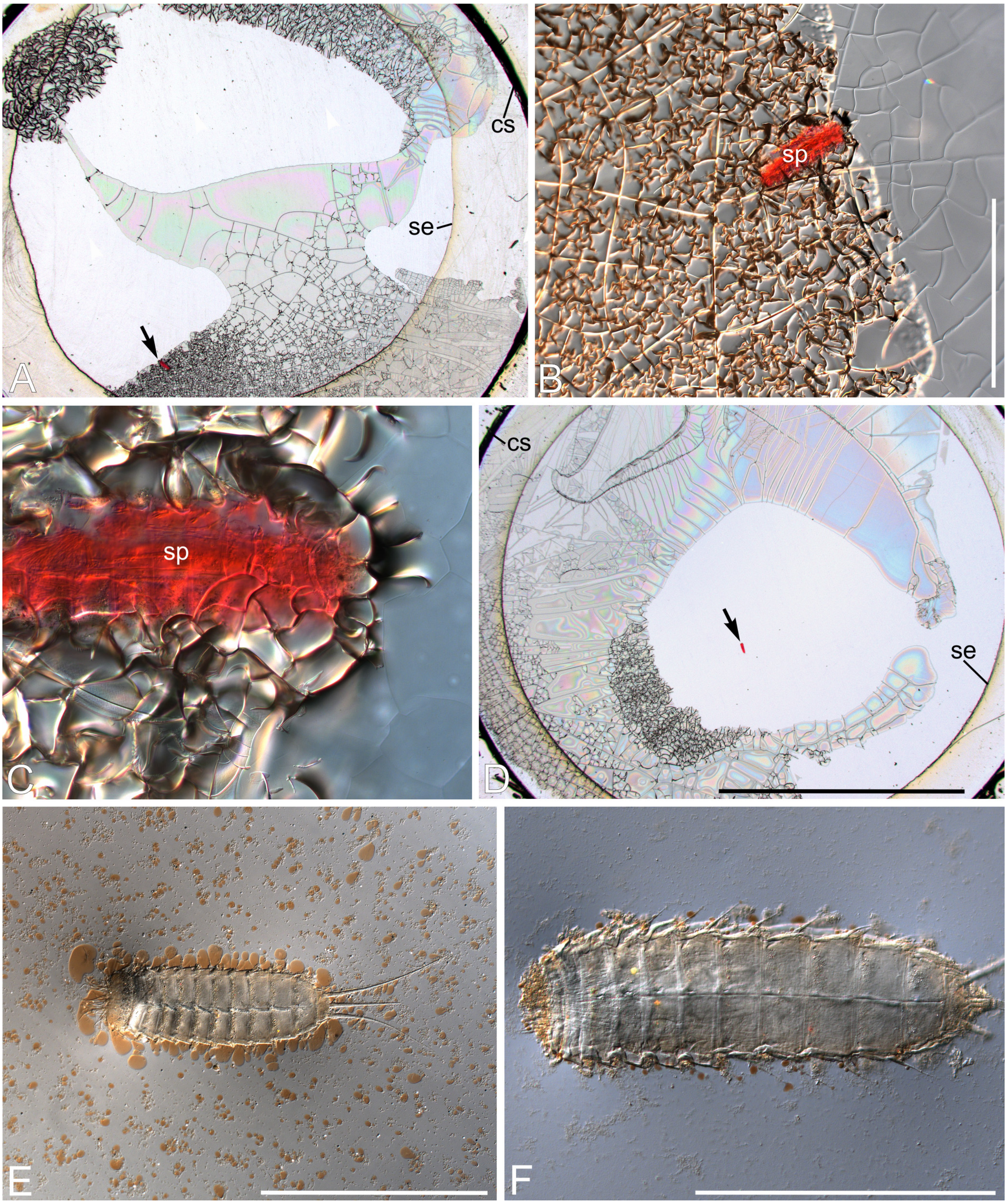


FIGURE 2. Holotypic (**E**) and paratypic (**A–C**, **F**) males of *Condyloderes paradoxus* (**A–C**, **E**, **F**) and *Condyloderes* sp. (**D**), deterioration of mounting media, DIC. **A–D**. Specimens mounted in Permount with cracks developing within two weeks after initial study (USNM 1209804, **A–C**; 1209806, **D**). **E, F.** Specimens (USNM W37460, **E**; 1209807, **F**) mounted in Hoyer's medium with brown spherical bodies (**E**, **F**) and precipitations (**F**). Arrows in **A** and **D** mark specimens. Scale bar in **B** 500 µm. Scale bar in **D** 5 mm, valid for **A** and **D**. Scale bar in **E** 300 µm. Scale bar in **F** 200 µm, valid for **C** and **F**. Abbreviations: cs, margin of coverslip; se, margin of coverslip seal; sp, specimen.

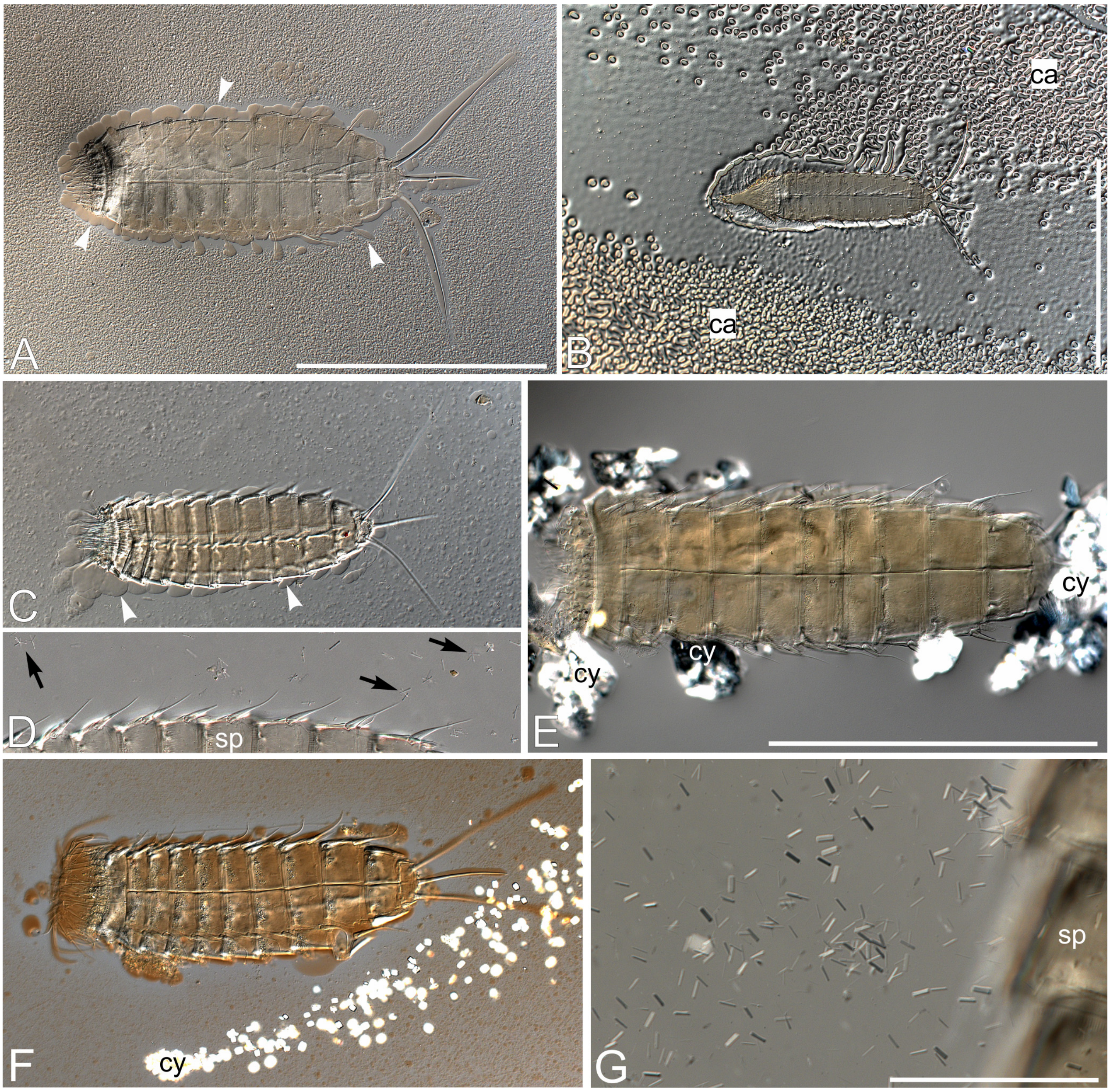


FIGURE 3. *Condyloderes multispinosus* (**A**, **B**), paratypic males of *C. setoensis* (**C**, **D**), holotypic female of *C. megastigma* (**E**), and paratypic female of *C. shirleyi* **sp. nov.** (**F**, **G**), deterioration of mounting media, DIC. **A, B**. Specimens probably mounted in Hoyer's medium with brown spherical bodies (**A**) and cavities (**B**) (USNM W37459, **A**; 1209821, **B**). **C, D.** Specimens (AVA-CM-JAP-02, **C**; AVA-CM-JAP-04, **D**) mounted in Hoyer's medium with spherical bodies (**C**) and bar-like crystals (**D**, arrows). **E.** Specimen mounted in Fluoromount G™ with radially growing crystals (ZMUC-KIN-250). **F, G.** Specimens mounted in Hoyer's medium with brown spherical bodies and different kinds of crystals (USNM 1481021, **F**; ZMB 11598, **G**). Arrowheads in **A** and **C** mark spherical bodies at specimens. Scale bar in **A** 300 µm, valid for **A**, **C**, and **F**. Scale bar in **B** 500 µm. Scale bar in **E** 100 µm, valid for **D** and **E**. Scale bar in **G** 50 µm. Abbreviations: ca, cavity in mounting medium; cy, crystals in mounting medium; sp, specimen.

Results

Condyloderes Higgins, 1969

Included species. *Condyloderes kurilensis* Adrianov & Maiorova, 2016; *C. multispinosus* (McIntyre, 1962) Higgins, 1969; *C. paradoxus* Higgins, 1969; *C. setoensis* Adrianov, Murakami & Shirayama, 2002; *C. shirleyi* **sp. nov.** Neuhaus & Higgins; *C. storchi* Higgins, 2004 in Martorelli & Higgins, 2004.

Emended diagnosis. Mouth cone with 9 individual outer oral styles with broader base and thin and flexible anterior part; 14 trichoscalids each originating from trichoscalid plate and accompanied anteriorly by two pointed filamentous appendages; 16 placids with broader midventral placid, neighboured by two narrower placids and alternatingly a broader and a narrower placid; all placids with knobby projections (= condyles) in one or two rows in narrower placids and two or three rows in broader placids; midventral placid with three apical condyles, two in intermediate row, and 3–6 in basal row; ventromedial to midventral free flap and primary pectinate fringe of segment 1 at least partly reduced; acicular spine middorsally on segments 1–9, midterminally on segment 11 (= midterminal spine), lateroventrally on segments 1–9, laterodorsally on segment 10 (male only in species with irregularly distributed or almost no cuticular hairs), and lateral accessorily on segment 11 (= lateral terminal accessory spine); cuspidate spines present; type-3 sensory spot ventrolaterally next to lateral terminal accessory spine and subdorsally on segment 11; type-6 sensory spot elevated above trunk surface giving the impression to be half-drowned in the trunk cuticle; ventromedial appendage at least on two segments of segments 5–8 in female; area of micropapillae ventromedially on segment 9 in female of species with irregularly distributed or almost no cuticular hairs.

Re-description of *Condyloderes kurilensis* Adrianov & Maiorova, 2016

(Figs 4–7; Tables 1, 2, 7)

Condyloderes kurilensis Adrianov & Maiorova, 2016: pp. 13–18, figs 1–4, table 1.
Condyloderes kurilensis —Zeppilli *et al.* 2018: p. 56.

Diagnosis. Neck placids with condyles in two rows in narrower placids and 2–3 rows in broader placids; each narrower placid with one apical and one basal condyle; primary pectinate fringe of all segments reduced, free flap with numerous short spinose or broad extensions on most parts of a segment; acicular spine middorsally on segments 1–9 (and on segment 10 in male only), midterminally on segment 11, laterodorsally on segment 10 (in male only), and lateroventrally on segments 1–9; cuspidate spine ventrolaterally on segment 5 and lateral accessorily on segment 8; type-6 sensory spot ventromedially on segments 1 (slightly more paraventrally), 2, 4, 6, 8 and 9, lateroventrally on segment 10, sublaterally on segments 3, 5–7 and 9, midlaterally on segments 1 and 2, laterodorsally on segments 2, 3 and 7–9, and paradorsally on segments 1 (almost subdorsally), 4–6, 8 and 9; ventromedial appendage on segments 7 and 8 and area of micropapillae ventromedially on segment 9 in female only.

Material examined. Holotypic male (MIMB 32339) and paratypic female (MIMB 32340) mounted for light microscopy (Fig. 1; Table 1).

Description

Head. Information on the head is sparse, because this organ is not well preserved in both specimens. Inner oral styles are recognizable as long and tubular styles.

The introvert bears one ring of primary spinoscalids, several rings of spinoscalids, and one ring of trichoscalids. The 10 primary spinoscalids (ring 01) divide the introvert into 10 sectors. The primary spinoscalids are finger-like, with a broad basis showing a proximal, flat tuft of longer spinose processes projecting outwards, and a second slightly more distal bundle of shorter spinose processes. The distal part ends bluntly.

The 14 trichoscalids are associated with the placids except for the narrow paraventral placid on either side, where no trichoscalid occurs. Each trichoscalid originates from a cuticular trichoscalid plate, which shows about the same size as the base of a trichoscalid. Each trichoscalid is accompanied anteriorly by two filamentous, pointed appendages, which are much thinner than the trichoscalid. The trichoscalids are covered by numerous cuticular hairs.

Neck. The 16 placids of the neck are arranged in a specific way. The broader midventral placid (18–19 µm width at base; measurement based on one specimen) is neighboured by two narrower placids (710 µm width x 13–19 µm height), and alternatingly a broader (15–18 µm width) and a narrower placid (8–11 µm width x 15–21 µm height; measurements based on two specimens). All placids reveal cone-like condyles arranged in two rows in the narrower placids and most probably in three rows in the broader placids. Each narrower placid shows one apical and one or two basal condyles (Table 7). The anterior condyles are difficult to see on the broader placids because of dirt and tilting of the placids. For these reasons, the height of the broader placids was not measured.

Trunk. The trunk is divided into 11 segments. Whereas the cuticle of the first trunk segment is ring-like without any articulation, the cuticle of segments 2–10 possesses both a midventral and a lateral articulation resulting in a tergal and two sternal plates (Figs 4–7). In segment 11, a tergal and a single sternal plate exist (Figs 4B, 5A, 7B).

The anterior margin of the first trunk segment is smooth (Fig. 6A, D). At the anterior margin of all segments and at the midventral margin of the sternal plates of segments 2–10, the cuticle thickens slightly towards the interior of the animal and forms a pachycyclus (Figs 6, 7). Ventrally, the tergal plate and sternal plates of each segment form a more sclerotized peg and socket articulation. A variable number of irregularly arranged, small canals extends from the epidermis into each cuticular trunk plate and does not seem to be connected with gland cells. At the posterior end of most parts of segments 1–9, the free flap overlapping the subsequent segment terminates in numerous, irregularly distributed spinose or broad extensions of the free flap giving the free flap a deeply and irregularly indented appearance (Figs 4–7). The free flap is almost completely missing in the ventromedial to midventral area of segment 1, in the paraventral area of segments 2–9, ventrally on segments 10, and all around segment 11 (Figs 4B, 5A, 6A, 7B–D). The basal part of the free flap reveals fine, regularly arranged, longitudinal bars inside the flap (Figs 4–6, 7A–D). The bars also continue into the spinose or broad extensions of the free flap thus indicating that the extensions indeed derive from the free flap (Figs 6A, D, 7C, D). The free flap is missing where the spines originate. A primary pectinate fringe does not exist.

The surface of the cuticle of segments 2–10 is covered in the anterior third with little elevated, irregularly arranged longitudinal ridges and with numerous, irregularly distributed, cuticular scale-like hairs in the remaining part of all segments (Figs 6A–D, 7AD). The secondary fringe, a single row of short cuticular scales, separates the anterior third of a segment from the posterior third (Fig. 6). Cuticular hairs occur middorsally and laterally on the trunk cuticle anterior to the middorsal and lateroventral spines of segments 2–11 in a narrow area (Figs 6, 7A–D).

All sensory spots elevate above the surface of the trunk cuticle and display on the outside cuticular micropapillae surrounding one or two pores. Whereas two spots on segment 11 belong to type-3 sensory spots, the remaining spots are identified as type-6 sensory spots. The distribution of sensory spots is bilateral symmetrical. Type-3 sensory spots occur ventrolaterally next to the lateral terminal accessory spine and subdorsally on segment 11 (Fig. 7B, D). A type-6 sensory spot occurs ventromedially on segment 1 (slightly more paraventrally) and on segments 2, 4, 6, 8 and 9, lateroventrally on segment 10, sublaterally on segments 3, 5–7 and 9, midlaterally on segments 1 and 2, laterodorsally on segments 2, 3 and 7–9, subdorsally on segment 10, and paradorsally on segments 1 (almost subdorsally), 46, 8 and 9 (Figs 4–7; Tables 2, 7). The sublateral sensory spot on segment 1 could not be observed in the holotypic male and on segments 1 and 3 and in the paratypic female, but they are very likely to occur based on the documentation of the spots in the non-type male in the original publication (Adrianov & Maiorova 2016); therefore, these spots are indicated by dotted lines in Figures 4 and 5.

The nephropore is located slightly dorsally of the sublateral sensory spot at the posterior margin of segment 9 (Figs 4A, 7C, D; Table 2).

Segments 1–10 bear a middorsal and segments 1–9 on each side a lateroventral spine and segment 11 such a spine in a lateral accessory position (= lateral terminal accessory spine) and as the midterminal spine (Figs 4–7; Table 2); the spines are hirsute and acicular. A short hirsute cuspidate spine with a basal thickened and an apical thinner part appears ventrolaterally on segment 5 and in a lateral accessory position on segment 8 (Figs 4, 5, 6B, C; Tables 2, 7). Whereas the acicular spines appear clearly sclerotized, the cuspidate spines are almost translucent in light microscopy.

Female. In the following, only those characters are mentioned that distinguish females from males. The female can be distinguished from the male in the existence of the ventromedial appendage on the sternal plates of segments 7 and 8 (Fig. 7E; Tables 2, 7) *versus* its lack in the male, in the existence of a more or less rectangular area with prominent cuticular micropapillae on each sternal plate of segment 9 (Fig. 7E; Tables 2, 7) *versus* its lack in the male, the lack of a middorsal and laterodorsal acicular spine on segment 10 (Fig. 5B; Tables 2, 7) *versus* the possession of these spines in the male, and in the existence of large circular gonopores with a sclerotized edge at their anterior and posterior margin on each sternal plate of segment 11 (Figs 5A, 7E) *versus* their lack in the male.

On each sternal plate of segments 7 and 8, the paratypic female's ventromedial appendage gives the impression of an extremely elongated sensory spot covered by numerous cuticular micropapillae (Figs 5A, 7E). At its base, each structure shows a sclerotized cuticular duct penetrating the trunk cuticle. The duct seems to be surrounded by a cavity. The structures occur ventromedially on segment 7 and slightly more paraventrally on segment 8 (Figs 5A, 7E). The structure is termed ventromedial appendage here because of its uncertain nature that may be sensorial or glandular (see also Sørensen *et al*. 2010b, p. 240).

Each sternal plate of segment 9 possesses a more or less rectangular area with prominent cuticular micropapillae (Figs 5A, 7E; Table 2). Pores and ducts penetrating the trunk cuticle do not seem to exist in this area.

Comparison with previous description

Information in the original description of *C. kurilensis* is partly confusing. The authors state that the female reveals more sensory spots in a slightly different arrangement than the male (Adrianov & Maiorova 2016, p. 18) but this is not corroborated by our study. According to their illustration of the paratypic female mounted for light microscopy (Adrianov & Maiorova 2016, fig. 2) and of the female SEM specimen (Adrianov & Maiorova 2016, fig. 4), a sublateral sensory spot exists on segments 1 and 3 (Adrianov & Maiorova 2016, figs 2a, 4b) and on segment 9 (Adrianov & Maiorova 2016, figs 2b, 4c). However, these spots on segments 1 and 3 cannot be confirmed by us for the paratypic female specimen, because it is not observable with an oil immersion lens, and the resolution of a long distance objective is too low to see these spots. Probably, information from the paratypic female light microscope specimen was mixed with data from the female SEM specimen in the drawing of the female light microscope specimen (Adrianov & Maiorova 2016, fig. 2). The holotypic male mounted for light microscopy reveals the sublateral sensory spots on segments 3 and 9, and possibly on segment 1 as well (see also below). Therefore, we indicate the probable existence of the latter spot in our drawings of the holotype (Fig. 4A) and of the female paratype (Fig. 5B).

Whereas Adrianov & Maiorova (2016, fig. 4a, white arrowhead) pointed to a paraventral supposed sensory spot on the sternal plates of segment 2 of a female specimen mounted for SEM, we found in the holotypic male specimen mounted for light microscopy very small cuticular processes (micropapillae?) but did not recognize pores or ducts indicative of a sensory spot in that position and on subsequent segments. We also compared the female of *C. kurilensis* with the females of *C. megastigma*, for which paraventral sensory spots were first described (Sørensen *et al*. 2010b). However, we cannot confirm the existence of paraventral sensory spots for *C. kurilensis* at this stage, also because we could not use an oil immersion lens for the female specimen.

Our light microscope findings differ from the original descriptive text (Adrianov & Maiorova 2016) in that in both the male and female (1) two narrower neck placids are located next to the broader midventral placid and the 11 remaining placids alternate in width instead of placids alternate between 7 broader and 9 narrower placids, (2) a ventrolateral cuspidate spine exists on segment 5 of both the holotypic male and the paratypic female instead of its lack on that segment (but recognizable in Adrianov & Maiorova 2016, fig. 4a), (3) type-6 sensory spots exist midlaterally and paradorsally (almost subdorsally) on segment 1 (also recognizable in Adrianov & Maiorova 2016, fig. 4b) rather than laterodorsally and subdorsally, (4) type-6 sensory spots exist midlaterally and laterodorsally on segment 2 (also recognizable in Adrianov & Maiorova 2016, fig. 4b) rather than laterodorsally and subdorsally, (5) a type-6 sensory spot exists sublaterally but not paradorsally on segment 3 (also recognizable in Adrianov & Maiorova 2016, fig. 4b) instead of its lack sublaterally and its existence paradorsally, (6) a type-6 sensory spot exists sublaterally on segment 5 (also recognizable in Adrianov & Maiorova 2016, fig. 4c) rather than laterodorsally, (7) a type-6 sensory spot is present sublaterally on segment 6 (also recognizable in Adrianov & Maiorova 2016, fig. 4c) instead of its lack in that position, (8) type-6 sensory spots exist sublaterally and laterodorsally on segment 7 (also recognizable in Adrianov & Maiorova 2016, fig. 4c) instead of subdorsally and paradorsally, (9) a type-6 sensory spot exists laterodorsally on segment 8 (also recognizable in Adrianov & Maiorova 2016, fig. 4c, d) rather than subdorsally, (10) type-6 sensory spots exist sublaterally and laterodorsally on segment 9 (also recognizable in Adrianov & Maiorova 2016, fig. 4c) instead of subdorsally and its lack sublaterally, (11) a protonephridial opening exists sublaterally on segment 9 instead of its non-mentioning in that position (but recognizable in Adrianov & Maiorova 2016, fig. 4c), (12) a type-6 sensory spot exists lateroventrally on segment 10 (also recognizable in Adrianov & Maiorova 2016, fig. 4a) instead of its lack in that position, (13) two type-3 sensory spots exist ventrolaterally and subdorsally on segment 11 instead two dorsal and one ventral sensory papilla, (14) segment 11 reveals a single sternal plate rather than a sternal plate "with underdeveloped midventral articulation" (Adrianov & Maiorova 2016, p. 15), (15) segment 11 possesses a lateral terminal accessory spine rather than a lateral terminal spine, and (16) the lateral terminal accessory spine displays at its base two thin areas instead of their lack. Concerning the female only, no "minute tubular-like scars" can be recognized by light microscopy ventromedially on segment 9 (but recognizable in Adrianov & Maiorova 2016, fig. 4a, g) instead of their existence in this position.

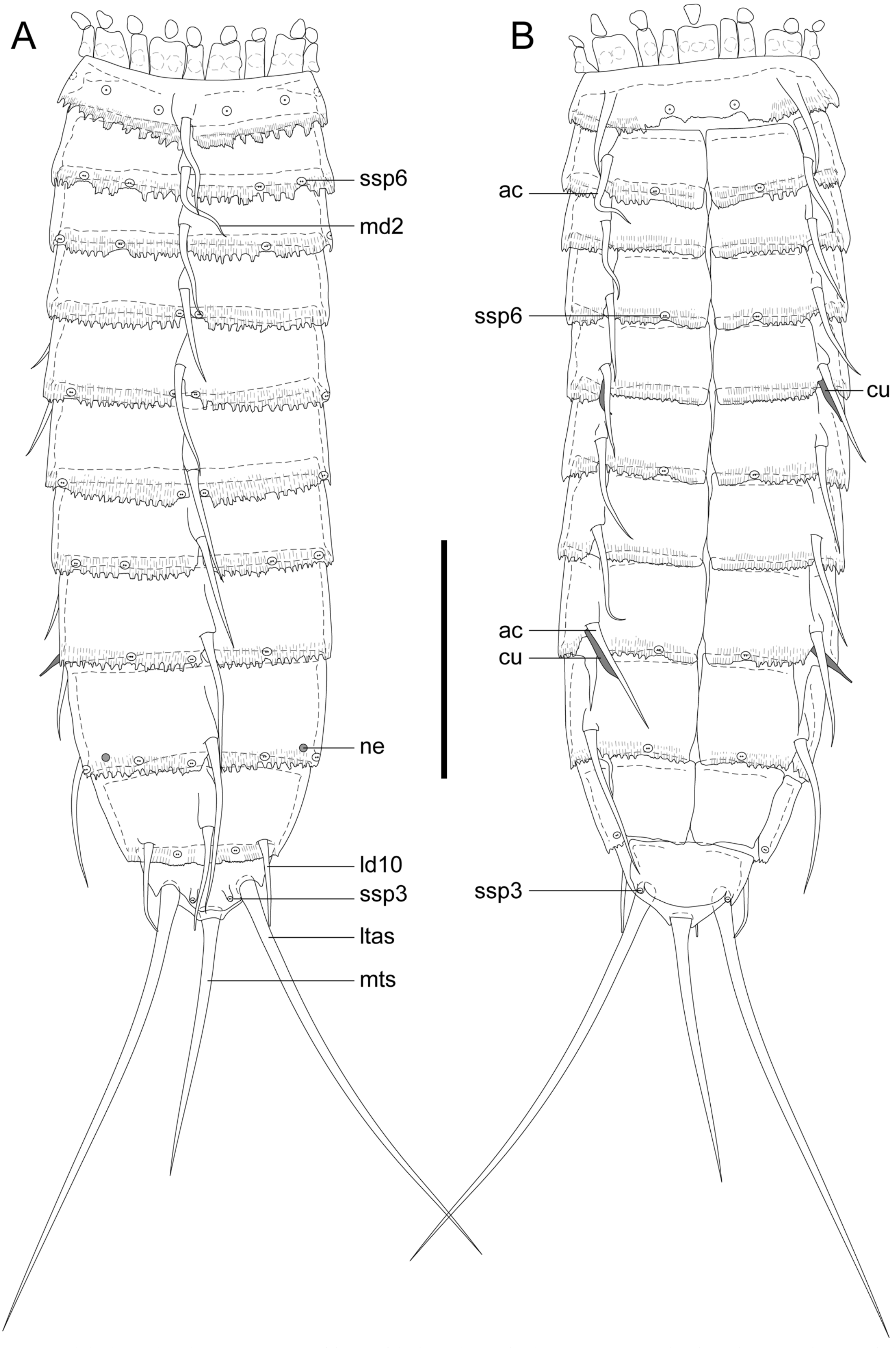


FIGURE 4. *Condyloderes kurilensis*. **A, B**. Habitus of holotypic male (MIMB 32339) in dorsal (**A**) and ventral (**B**) view. Sublateral sensory spot on segment 1 indicated by dotted lines not observed in holotype but very likely based on documentation of spot in non-type male in original publication (Adrianov & Maiorova 2016). Cuspidate spines highlighted by grey colour. Scale bar 100 µm, valid for **A** and **B**. Abbreviations: ac, acicular spine; cu, cuspidate spine; ld10, laterodorsal spine of segment 10; ltas, lateral terminal accessory spine; md2, middorsal spines of segment 2; mts, midterminal spine; ne, protonephridial openings; ssp3, type-3 sensory spot.

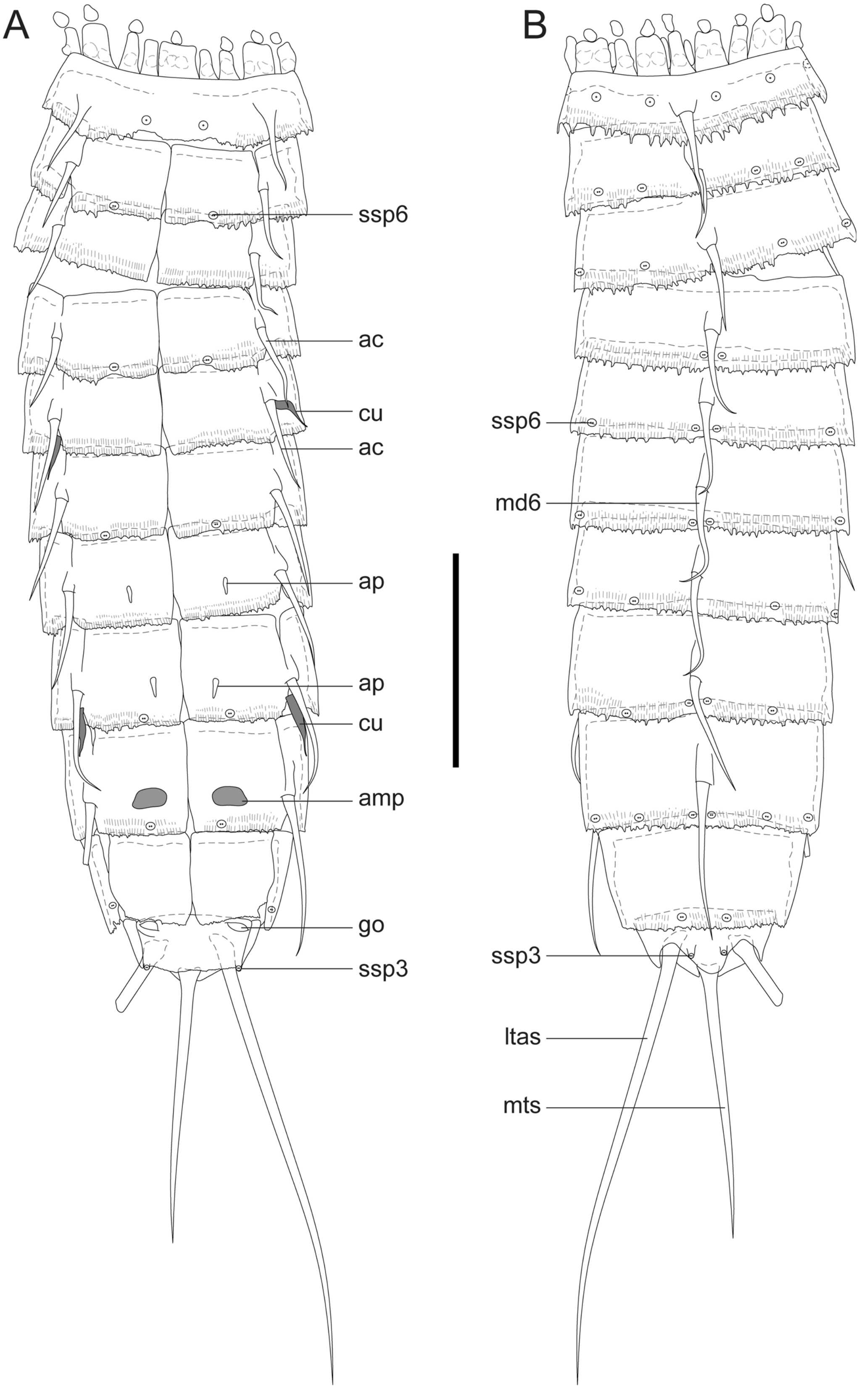


FIGURE 5. *Condyloderes kurilensis*. **A, B**. Habitus of paratypic female (MIMB 32340) in ventral (**A**) and dorsal (**B**) view. Sublateral sensory spot on segments 1 and 3 indicated by dotted lines not observed in paratype but very likely based on documentation of spot in non-type male in original publication (Adrianov & Maiorova 2016; see also text). Cuspidate spines highlighted by grey colour. Scale bar 100 µm, valid for **A** and **B**. Abbreviations: ac, acicular spine; amp, female-specific area of micropapillae; ap, female-specific appendage; cu, cuspidate spine; gp, gonopore; ltas, lateral terminal accessory spine; md6, middorsal spines of segment 6; mts, midterminal spine; ssp3, type-3 sensory spot.

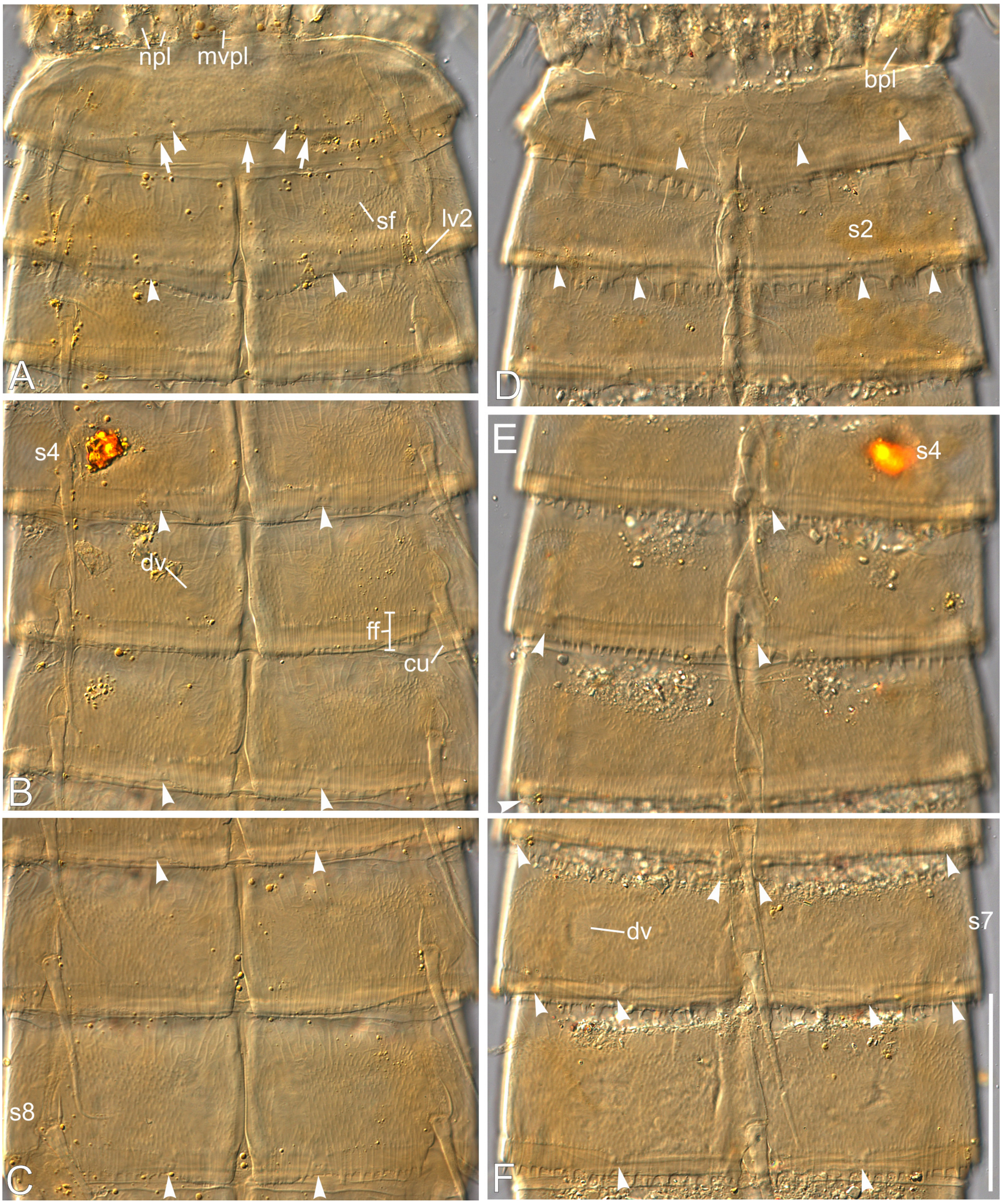


FIGURE 6. *Condyloderes kurilensis*, holotypic male (MIMB 32339) in ventral (**A–C**) and dorsal view (**D–F**), DIC. **A.** Segments 1–3; arrows point to reduced free flap. **B**. Segments 4–6. **C.** Segments 7 and 8. **D.** Segments 1–3. **E.** Segments 4–6. **F.** Segments 7 and 8. White arrowheads in **A–F** mark type-6 sensory spots. Notice fused and reduced pectinate fringe of free flap with irregular outline on all segments. Scale bar in **F** 50 µm, valid for **A–F**. Abbreviations: cu, cuspidate spine; dv, attachment area of dorsoventral muscle; ff, free flap; lv2, lateroventral spine of segment 2; s2, segment 2; sf, secondary fringe.

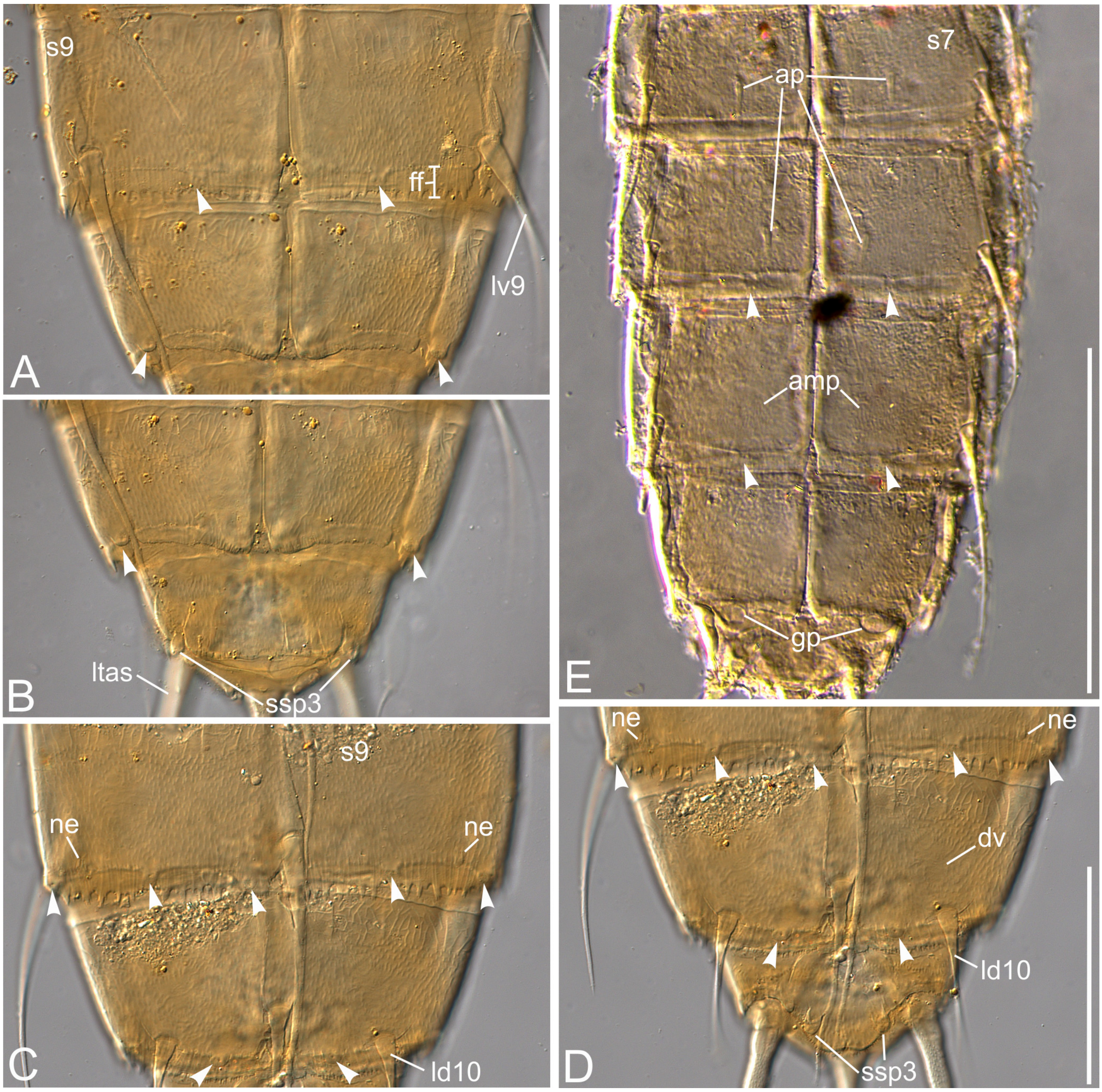


FIGURE 7. *Condyloderes kurilensis*, holotypic male (MIMB 32339) in ventral (**A**, **B**) and dorsal view (**C**, **D**) and paratypic female (MIMB 32340) in ventral view (**E**), DIC. **A.** Segments 9 and 10. **B**. Segments 10 and 11. **C.** Segments 9 and 10. **D.** Segments 10 and 11. **E.** Segments 7–11. White arrowheads in **A–E** mark type-6 sensory spots. Notice fused and reduced pectinate fringe of free flap with irregular outline on all segments. Scale bar in **D** 50 µm, valid for **A–D**. Scale bar in **E** 100 µm. Abbreviations: amp, female-specific area of micropapillae of female; ap, female-specific appendage; dv, attachment area of dorsoventral muscle; ff, free flap; ld10, laterodorsal spine of segment 10; ltas, lateral terminal accessory spine; lv9, lateroventral spine of segment 9; ne, protonephridial openings; s7, segment 7; ssp3, type-3 sensory spot.

Condyloderes multispinosus (McIntyre, 1962) Higgins, 1969

Centroderes multispinosus McIntyre, 1962: p. 505, fig. 1.

Condyloderes multispinosus comb. nov.—Higgins, 1969: pp. 3–6, figs 1–9, table 1.

Condyloderes multispinosus—Higgins 1971: p. 26.—Moore 1973: p. 341, 350.—Brown 1985: p. 93.—Higgins 1986: p. 115.—Higgins 1988: fig. 28.1d.—Huys & Coomans 1989: pp. 211, 213, fig. 1.—Nebelsick 1993: p. 221, 226.—Adrianov & Malakhov 1994: p. 229, fig. 130b.—— Bamber 1997: pp. 65, 424.—Adrianov & Malakhov 1999: pp. 114, 253, 254, fig. 5.10B, C.—Adrianov *et al*. 2002: p. 205, 206, 214, 215.—Martorelli & Higgins 2004: pp. 88–90, tables 1, 2.—Sørensen & Pardos 2008: pp. 52, 53.—Sørensen *et al*. 2010b: pp. 234, 241, [not *Centroderes*].—Neuhaus 2013: pp. 291, 326, tables 6, 11 [not *Centroderes multispinosus*].—Neuhaus & Sørensen 2013: p. 73.—Adrianov & Maiorova 2016: pp. 11, 18.—Dal Zotto & Todaro 2016: p. 99.

Re-description of *Condyloderes multispinosus* based on type material

(Figs 8–10; Tables 1–3, 7)

Diagnosis. Neck placids with condyles in one row in narrower placids and three rows in broader placids; each narrower placid with one basal condyle; each broader placid with two condyles both in apical, intermediate, and basal row; midventral placid with three apical and basal condyles and two in intermediate row; acicular spine middorsally on segments 1–10, midterminally on segment 11, lateroventrally on segments 1–9, and laterodorsally on segment 10; cuspidate spine ventrolaterally on segments 2, 5 and 9 and lateral accessorily on segment 8; type-6 sensory spot ventromedially on segments 1 (slightly more paraventrally), 2–4 and 6–9, lateroventrally on segment 10, sublaterally on segments 1–3 and 5–9, midlaterally on segments 1 and 2, laterodorsally on segments 1–9, subdorsally on segment 10, and paradorsally on segments 1 (almost subdorsally), 2 and 49; gland cell outlet ventromedially on segment 10.

Material examined. Holotypic male (ZOO 1962.82, previously identified as adult by McIntyre (1962) and Higgins (1969)) mounted for light microscopy (Fig. 1; Table 1).

Description

For data and morphological measurements see Tables 1–3.

Head. Information on the head is incomplete. The mouth cone reveals longitudinal cuticular bars, which are interpreted as a mouth cone weir (Fig. 9B, C). At its anterior margin, the mouth cone carries individual outer oral styles, which are broader at the base and taper to a filamentous apical part (Fig. 9B, C). Three rings of inner oral styles are recognizable outside of the protruded foregut structures of the holotype (Fig. 9B, C): the five styles of each of the posterior rings are long and tubular, whereas the anteriormost styles are hook-like.

Head sectors 5–7 of the holotype seem to possess the same arrangement of spinoscalids as described for *C. shirleyi* **sp. nov.** (comp. Fig. 34). The introvert bears one ring of primary spinoscalids (Fig. 9D), five rings of spinoscalids, and one ring of trichoscalids (comp. Fig. 34 for *C. shirleyi* **sp. nov.**). The 10 primary spinoscalids (ring 01) divide the introvert into 10 sectors. The primary spinoscalids are finger-like, with a broad basis showing a proximal, flat tuft of longer spinose processes projecting outwards, and a second slightly more distal bundle of shorter spinose processes. The spinoscalids of rings 02–06 are formed by two parts as well: a proximal basis, and a distal, needle-like, pointed shaft (Fig. 9D).

The 14 trichoscalids are associated with the placids except for the narrow paraventral placid on either side, where no trichoscalid occurs. Each trichoscalid originates from a cuticular trichoscalid plate, which shows about the same size as the base of a trichoscalid (Fig. 9E). Each trichoscalid is accompanied anteriorly by two pointed filamentous appendages, which are much thinner than the trichoscalid (Fig. 9D). Possibly, the filamentous appendages possess inner septa. The trichoscalids are covered by numerous cuticular hairs.

Neck. The 16 placids of the neck are arranged in a specific way. The broader midventral placid (14 µm width at base x 16 µm height; measurements based on one specimen) is neighboured by two narrower placids (6–9 µm width x 9–11 µm height), and alternatingly a broader (13–15 µm width x 15–17 µm height) and a narrower placid (8–9 µm width x 13–14 µm height). All placids reveal cone-like condyles arranged in one basal row in the narrower placids and in three rows in the broader placids (Table 7). Each narrower placid shows one basal condyle. Each broader placid displays two condyles both in the apical, intermediate, and basal row (Table 7). The midventral placid possesses three apical condyles, two in the intermediate row and four in the basal row. The two central condyles originate from a common base in the holotype.

Trunk. The trunk is divided into 11 segments (Figs 8, 9A), which appear triangular in cross-section when observed from anteriorly like in the previously unmounted holotype. Whereas the cuticle of the first trunk segment is ring-like without any articulation, the cuticle of segments 2–10 possesses both a midventral and a lateral articulation resulting in a tergal and two sternal plates (Figs 8, 9A, F, G, 10, for non-type male see 11A–D, F). In segment 11, a tergal and a single sternal plate exist (Figs 8A, 10B, for non-type males see 11D, F) and show paraventral folds in two non-type males (see Fig. 11D, F).

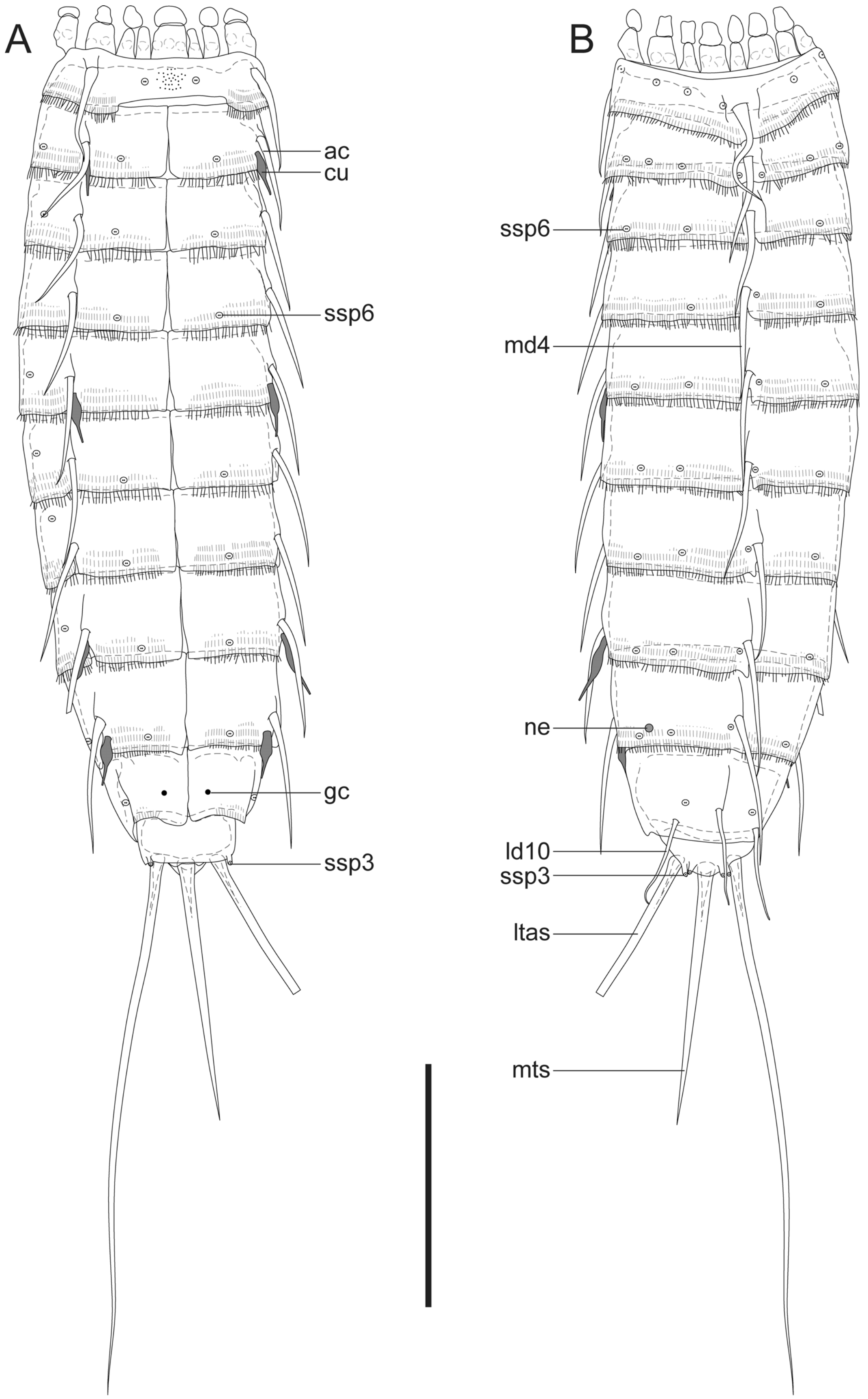


FIGURE 8. *Condyloderes multispinosus*. **A, B**. Habitus of holotypic male (ZOO 1961.82) in ventral (**A**) and dorsal (**B**) view. Cuspidate spines highlighted by grey colour. Scale bar 100 µm, valid for **A** and **B**. Abbreviations: ac, acicular spine; cu, cuspidate spine; gc, gland cell outlet; ld10, laterodorsal spine of segment 10; ltas, lateral terminal accessory spine; md4, middorsal spine of segment 4; mts, midterminal spine; ne, protonephridial openings; ssp3, type-3 sensory spot.

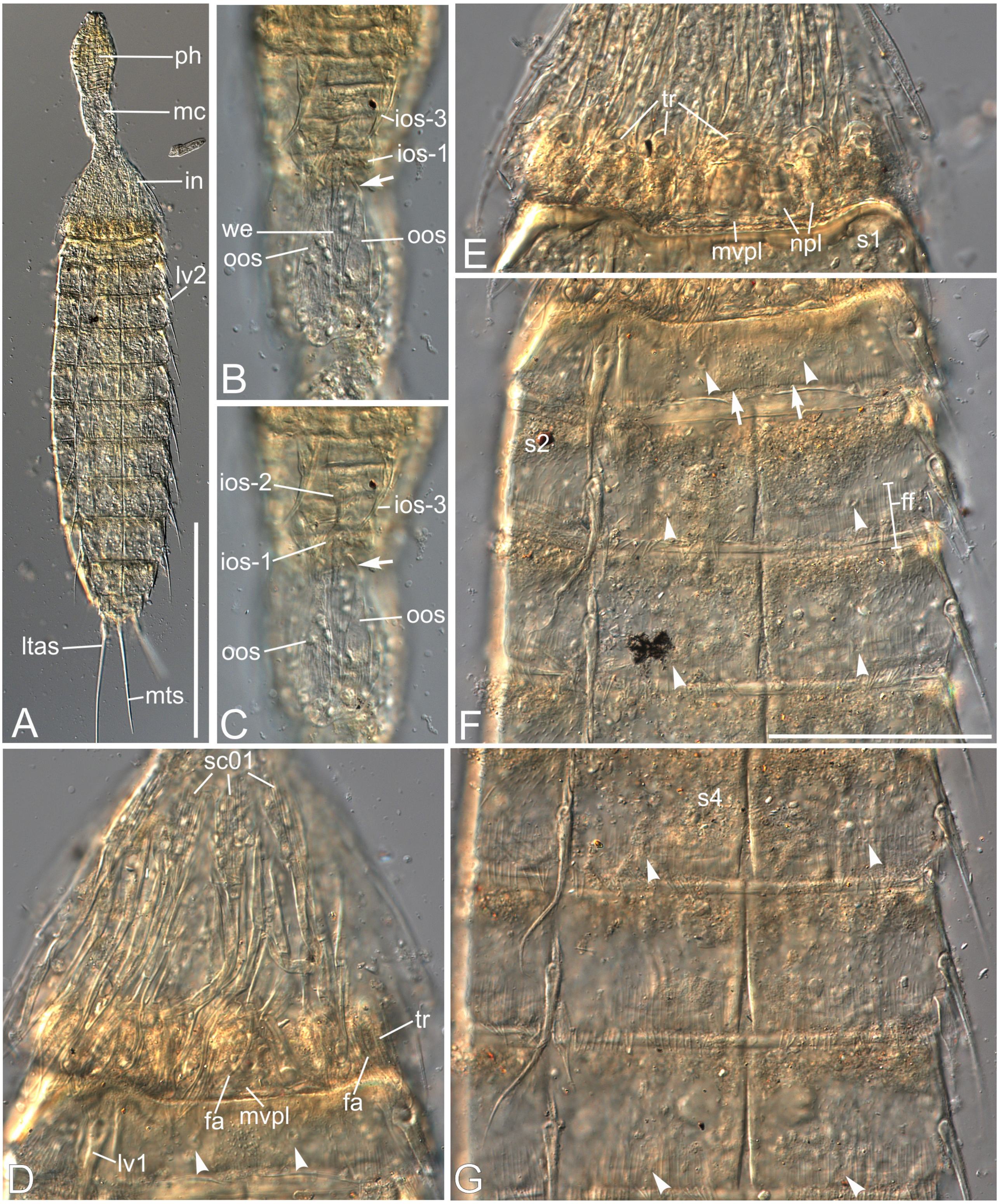


FIGURE 9. *Condyloderes multispinosus*, holotypic male (ZOO 1961.82) in ventral (**A–G**) view, DIC. **A.** Habitus with extremely protruded pharynx. **B, C**. Outer and inner oral styles and cuticular weir at different focal levels; arrows mark thin terminal part of outer oral styles. **D.** Head and neck. **E.** Placids. **F.** Segments 1–3; extended focus image of four images; arrows mark reduced free flap. **G.** Segments 4–6; extended focus image of four images. White arrowheads in **D**, **F** and **G** mark type-6 sensory spots. Scale bar in **A** 200 µm. Scale bar in **F** 50 µm, valid for **B–G**. Abbreviations: fa, filamentous appendage of trichoscalid; ff, free flap; in, introvert; ios-1, inner oral style of ring -1; ltas, lateral terminal accessory spine; lv1, lateroventral spine of segment 1; mc, mouth cone; md7, middorsal spine of segment 7; mts, midterminal spine; mvpl, midventral placid; npl, narrow placid; oos, outer oral styles; ph, pharynx; s1, segment 1; sc01, primary spinoscalids of ring 01; tr, trichoscalid (**D**) or its basal plate (**E**); we, cuticular weir.

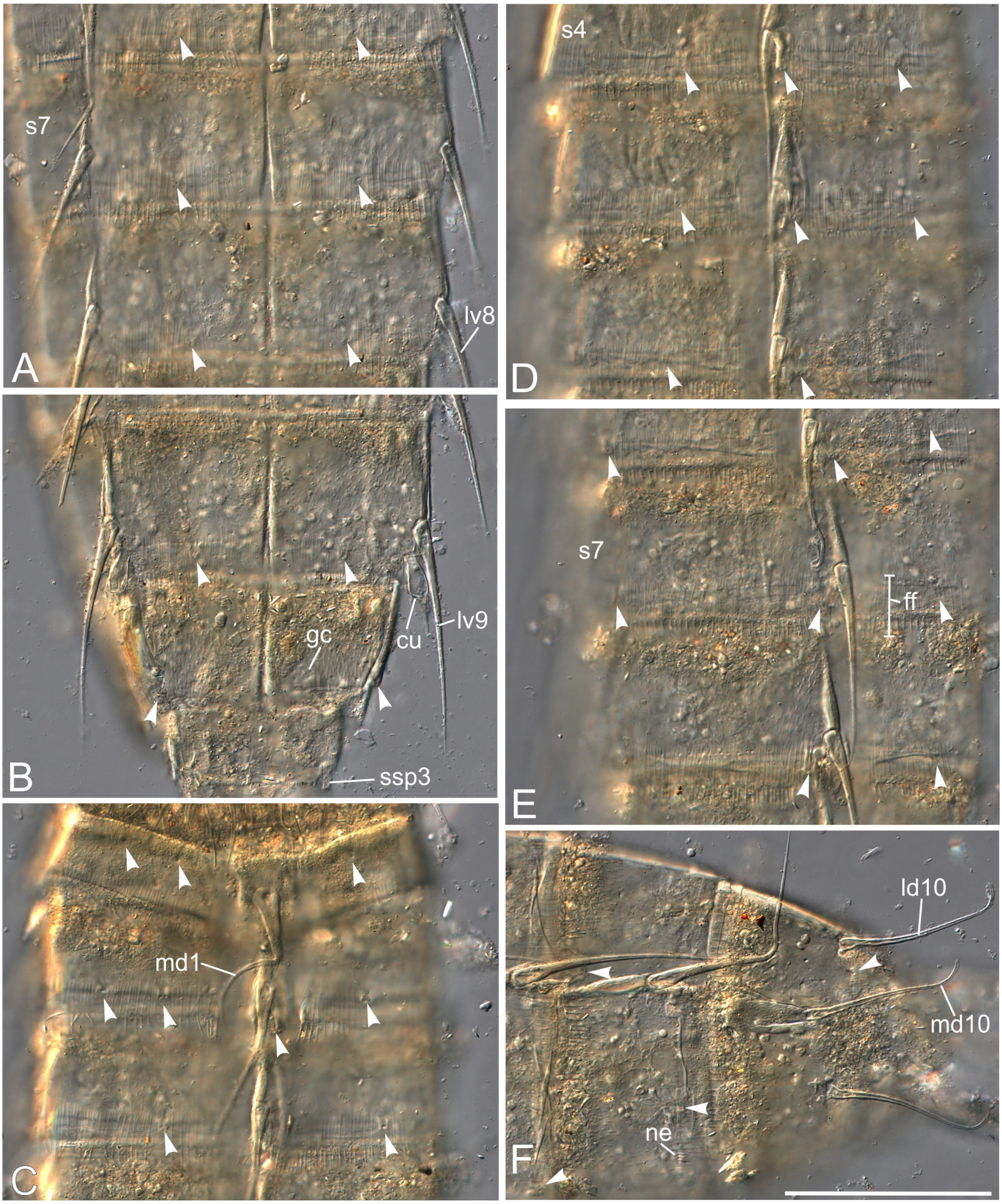


FIGURE 10. *Condyloderes multispinosus*, holotypic male (ZOO 1961.82) in ventral (**A**, **B**) and dorsal (**CF**) view, DIC. **A.** Segments 7 and 8; extended focus image of two images. **B.** Segments 9–11; extended focus image of four images. **C**. Segments 1–3; extended focus image of three images. **D.** Segments 4–6; extended focus image of three images. **E.** Segments 7 and 8; extended focus image of five images. **F.** Segments 9–11; extended focus image of nine images. White arrowheads in **A–F** mark type-6 sensory spots. Scale bar in **F** 50 µm, valid for **A–F**. Abbreviations: cu, cuspidate spine; ff, free flap; ld10, laterodorsal spine of segment 10; lv8, lateroventral spine of segment 8; md1, middorsal spine of segment 1; ne, protonephridial openings; s4, segment 4; ssp3, type-3 sensory spot.

TABLE 2. Characters of known species of *Condyloderes* present in the majority of specimens of a given species. Number of studied specimens mounted for light microscopy provided in ( ) after species name. Features appearing anteriorly on a segment do not show any background, features located centrally on a segment are indicated by a grey background, and characters occurring posteriorly on a segment are marked in black. Characters found in one gender only are indicated. Characters occupying an intermediate position to two reference positions are arranged right or left in a column (on segment 1: paradorsally to subdorsally, subdorsally to laterodorsally, laterodorsally to midlaterally, and ventromedially to paraventrally; on segment 10: ventromedially to paraventrally). Abbreviations: ?, character questionable but probable (comp. text for respective species); [ ], indicates variation in some specimens; ac, acicular spine; amp, area of micropapillae; ap, appendage; gc, gland cell outlet; la, lateral accessory; ld, laterodorsal; ltas, lateral terminal accessory spine; lv, lateroventral; md, middorsal; ml, midlateral; mts, midterminal spine; ne, nephridial openings; pd, paradorsal; pv, paraventral; sd, subdorsal; sl, sublateral; ssp3, type-3 sensory spot; vl, ventrolateral; vm, ventromedial.

Position Segment	md	pd	sd	ld	ml	sl	la	lv	vl	vm	pv
Condyloderes kurilensis (1 ♀, 1 ♂)											
1	ac	ssp6			ssp6	[ssp6]		ac		ssp6	
2	ac			ssp6	ssp6			ac		ssp6	
3	ac			ssp6		ssp6		ac			
4	ac	ssp6						ac		ssp6	
5	ac	ssp6				ssp6		ac	cu		
6	ac	ssp6				ssp6		ac		ssp6	
7	ac			ssp6		ssp6		ac		♀: ap	
8	ac	ssp6		ssp6			cu	ac		ssp6 ; ♀: ap	
9	ac	ssp6		ssp6		ne ; ssp6		ac		ssp6 ; ♀: amp	
10	♂: ac		ssp6	♂: ac				ssp6			
11	mts		ssp3				ltas		ssp3		
C. multispinosus (4 ♂)											
1	ac	ssp6		ssp6	ssp6	ssp6		ac		ssp6	
2	ac	ssp6		ssp6	ssp6	ssp6		ac	cu	ssp6	
3	ac			ssp6		ssp6		ac		ssp6	
4	ac	ssp6		ssp6				ac		ssp6	
5	ac	ssp6		ssp6		ssp6		ac	cu		
6	ac	ssp6		ssp6		ssp6		ac		ssp6	
7	ac	ssp6		ssp6		ssp6		ac		ssp6	
8	ac	ssp6		ssp6		ssp6	cu	ac		ssp6	
9	ac	ssp6		ssp6		ne ; ssp6		ac	cu	ssp6	
10	♂: ac		ssp6	♂: ac				ssp6		♂: gc	
11	mts		ssp3				ltas		ssp3		
C. paradoxus (5 ♀, 7 ♂)											
1	ac	ssp6		ssp6 [–]	ssp6	ssp6		ac		ssp6	
2	ac	ssp6?		ssp6	ssp6	ssp6		ac	cu	ssp6	n. a.
3	ac			ssp6		ssp6		ac		ssp6	n. a.
4	ac	ssp6		ssp6			cu	ac		ssp6	n. a.
5	ac	ssp6		ssp6		ssp6		ac	cu	ssp6	n. a.
6	ac	ssp6		ssp6		ssp6		ac		ssp6	
7	ac	ssp6 [–]		ssp6		ssp6		ac		ssp6 ; ♀: ap	
8	ac	ssp6		ssp6		ssp6	cu	ac		ssp6 ; ♀: ap	
9	ac	ssp6		ssp6		ne ; ssp6		ac	cu [–]	ssp6 ; ♀: amp	
10	ac		ssp6	♂: ac		ssp6		♂: ssp6 ; ♀: ac			
11	mts		ssp3				ltas		ssp3		

TABLE 2. (continued)

Position Segment	md	pd	sd	ld	ml	sl	la	lv	vl	vm	pv
C. setoensis (1 ♀, 4 ♂)											
1	ac	ssp6			ssp6	ssp6		ac		ssp6	
2	ac	ssp6		ssp6	ssp6	ssp6		ac	cu [–]	ssp6	♀: ssp1?
3	ac			ssp6		ssp6		ac		ssp6	♀: ssp1?
4	ac	ssp6		ssp6			– [cu]	ac		ssp6	♀: ssp1?
5	ac	ssp6		ssp6		ssp6		ac	cu	ssp6	♀: ssp1?
6	ac	ssp6		ssp6		ssp6		ac		ssp6	
7	ac			ssp6		ssp6		ac		ssp6 ; ♀: ap	
8	ac	ssp6		ssp6			cu	ac		ssp6 ; ♀: ap	
9	ac	ssp6		ssp6		ne ; ssp6		ac	cu	ssp6 ; ♀: amp	
10	♂: ac		ssp6	♂: ac				ssp6		♂: gc	
11	mts		ssp3				ltas		ssp3	ssp(6?)	
C. setoensis (previously ***C. megastigma***) (2 ♀, 5 ♂)											
1	ac	ssp6			ssp6	ssp6		ac		ssp6	
2	ac	ssp6		ssp6	ssp6	ssp6		ac	cu [–]	ssp6	♀: ssp1?
3	ac			ssp6		ssp6		ac		ssp6	♀: ssp1?
4	ac	ssp6		ssp6			cu	ac		ssp6	♀: ssp1?
5	ac	ssp6		ssp6		ssp6		ac	cu	ssp6	♀: ssp1?
6	ac	ssp6		ssp6		ssp6		ac		ssp6 [–]	
7	ac			ssp6		ssp6		ac		ssp6 ; ♀: ap	
8	ac	ssp6		ssp6			cu	ac		ssp6 ; ♀: ap	
9	ac	ssp6		ssp6		ne ; ssp6		ac	cu	ssp6 ; ♀: amp	
10	♂: ac		ssp6	♂: ac				ssp6		♂: gc	
11	mts		ssp3				ltas		ssp3	ssp(6?)	
C. storchi (1 ♂)											
1	ac	ssp6		ssp6	ssp6	ssp6	cu	ac		ssp6	
2	ac	ssp6		ssp6	ssp6	ssp6		ac		ssp6	
3	ac			ssp6		ssp6		ac		ssp6	
4	ac	ssp6		ssp6			cu	ac		ssp6	
5	ac ; cu			ssp6		ssp6		ac	cu	ssp6	
6	ac	ssp6		ssp6		ssp6		ac		ssp6	
7	ac ; cu			ssp6		ssp6		ac		ssp6	
8	ac	ssp6		ssp6			cu	ac		ssp6	
9	ac	ssp6		ssp6		ne ; ssp6		ac	cu	ssp6	
10	♂: ac		ssp6	♂: ac				ssp6			
11	mts		ssp3				ltas		ssp3	ssp(6?)	

TABLE 3. *Condyloderes multispinosus*, males and *C. paradoxus*, female, morphological data (length in μm; data given for left/right side if applicable). Abbreviations: [1] middorsal spine possibly broken at tip; [2] segment length measured on right side; [3] standard width calculated from single sternal plate; ac, acicular spine; cu, cuspidate spine; ld10, length of laterodorsal spine of segment 10; lost, spine missing but anchoring pit existing; ltas, length of lateral terminal accessory spine; lv1, length of lateroventral spine of segment 1; md1, length of middorsal spine on segment 1; mts, midterminal spine; n. a., data not available; s1, length of segment 1; sw8, standard width of segment 8; TL, trunk length; USNM, catalogue number of United States National Museum; vl2, length of ventrolateral spine of segment 2; ZOO, catalogue number of Natural History Museum London.

Species	*C. multispinosus*		*C. paradoxus*
Specimen Character	holotypic ♂ ZOO 1962.82	♂ USNM W37459	♀ ZMUC-KIN-848
TL	356	350	277
s1	16	20	19[2]
s2	35	30	28[2]
s3	35	31	23[2]
s4	36	33	29[2]
s5	38	33	29[2]
s6	38	37	29[2]
s7	39	39	31[2]
s8	42	39	34[2]
s9	43	40	36[2]
s10	31	31	29[2]
s11	20	18	21[2]
sw8	77	77	68 (sw7)[3]
sw10	58	59	54[3]
md1	46	broken	31
md2	44	35	31
md3	45	38[1]	29
md4	54	40[1]	32
md5	45	40	36
md6	46	44	33
md7	54	48	34
md8	58	51	35
md9	63	65	36
md10	40	34	44
ld10	39/40	38/n. a.	–
mts	105	107	94
lv1 (ac)	43/43	38/39	36/34
vl2 (cu)	18/n. a.	n. a./n. a.	n. a./16
lv2(ac)	44/44	41/42	29/29
lv3 (ac)	44/44	40/41	31/31
lv4 (ac)	43/44	40/40	35/34
la4 (cu)	–	–	16/16
vl5 (cu)	23/21	lost/18	18/23
lv5 (ac)	51/49	39/39	34/34
lv6 (ac)	45/48	43/40	n. a./34
lv7 (ac)	43/50	42/46	32/34
lv8 (ac)	54/broken	46/47	32/30
la8 (cu)	25/29	27/26	24/22
vl9 (cu)	21/21	n. a./20	n. a./n. a.
lv9 (ac)	62/60	55/55	32/34
lv 10 (ac)	–	–	40/39
ltas (ac)	broken/223	193/198	152/154

The anterior margin of the first trunk segment is smooth (Figs 8, 9D, 10C). At the anterior margin of all segments and at the midventral margin of the sternal plates of segments 2–10, the cuticle thickens towards the interior of the animal and forms a pachycyclus (Figs 9F, G, 10, for non-type males see 11A–F). A variable number of easily recognizable, irregularly arranged, small canals extend from the epidermis into each cuticular trunk plate and do not seem to be connected with gland cells. At the posterior end of all segments, the free flap overlapping the subsequent segment terminates in a primary pectinate fringe. The basal part of the free flap reveals fine, regularly arranged, longitudinal bars inside the flap (Figs 8, 9F, G, 10, for non-type males see 11A–D, F). The free flap is missing where the spines originate. In the midventral to ventromedial area of segment 1, the posterior margin of the segment shows a considerably shorter free flap with a reduced primary fringe and ends more anteriorly than the ventrolateral margin resulting in a peculiar outline (Figs 8A, 9F). The free flap of the tergal plate of segment 1 is shorter than on the succeeding segments and terminates in a short spinose extension of the free flap at least laterodorsally (Fig. 10C). The teeth of the primary pectinate fringe are well expressed on this and all following segments except for the considerably shorter teeth ventrally on segments 10 and all around segment 11 (for non-type males see Fig. 11D, F).

The surface of the cuticle of segments 2–10 is covered in the anterior fourth with little elevated, irregularly arranged longitudinal ridges (for non-type males see Fig. 11C, D, F) and with numerous, irregularly distributed, cuticular scale-like hairs in the remaining part of all segments (Fig. 9D, F, G, 10, for non-type males see 11A–D, F). Their number is lower on segment 1 than on the remaining segments. The hairs are stronger anteriorly on segments 2–10 than posteriorly. Segment 1 reveals a paraventral area of knobby cuticular projections (Figs 8A, 9F). Numerous cuticular hairs and triangular scale-like hairs occur middorsally and laterally on the trunk cuticle anterior to the middorsal and lateroventral spines of segments 2–9 in a narrow area. Here, the anteriormost hairs are stronger sclerotized than those in the more central area of a segment (for non-type male see Fig. 11A–C).

All sensory spots elevate clearly above the surface of the trunk cuticle and display on the outside cuticular micropapillae surrounding one or two pores. The distribution of sensory spots is bilateral symmetrical. Type-3 sensory spots occur ventrolaterally next to the lateral terminal accessory spine and subdorsally on segment 11 (Figs 8, 10B, for non-type male see 11C, D; Table 2). A type-6 sensory spot occurs ventromedially on segments 1 (slightly more paraventrally), segments 2–4 and 6–9, lateroventrally on segment 10, sublaterally on segments 1–3 and 5–9, midlaterally on segments 1 and 2, laterodorsally on segments 1–9, subdorsally on segment 10, and paradorsally on segments 1 (almost subdorsally), 2 and 4–9 (Figs 8, 9D, F, G, 10, for non-type males see 11A–D, F; Tables 2, 7).

A gland cell outlet with a short sclerotized cuticular duct and an intra- and subcuticular cuticle-lined cavity is located ventromedially on segment 10 (Figs 10B, for non-type male see 11D).

The nephropore occurs slightly dorsally of the sublateral sensory spot at the posterior margin of segment 9 (Figs 10F, for non-type male see 11C; Table 2).

Segments 1–9 bear a middorsal and on each side a lateroventral spine; segment 11 possesses a spine in a lateral accessory position (= lateral terminal accessory spine) and as the long midterminal spine (Figs 8, 9A, F, G, 10, for non-type male see 11A–D; Tables 2, 7); the spines are hirsute and acicular. Each middorsal and lateroventral acicular spine reveals a strongly sclerotized thick base and a considerably thinner and more flexible apical part. The lateral terminal accessory spine displays at its base two thin areas (for non-type male see Fig. 11E). The middorsal and laterodorsal acicular spine on segment 10 are thinner and less sclerotized than the lateroventral and middorsal spines of other segments (Figs 8B, 10F, for non-type male see 11C). A short cuspidate spine with a basal thickened and an apical thinner part appears ventrolaterally on segments 2, 5 and 9 and in a lateral accessory position on segment 8 (Figs 8, 9F, G, 10A, B; Table 2). Whereas the acicular spines appear clearly sclerotized, the cuspidate spines are almost translucent in light microscope mounts. All acicular and cuspidate spines are covered almost completely by cuticular microthreads, which give the spines their hirsute appearance.

Comparison with previous description

The species was originally described as *Centroderes multispinosus* by McIntyre (1962) and subsequently placed in a new genus and combined as *Condyloderes multispinosus* (McIntyre, 1962) by Higgins (1969). In comparison with McIntyre (1962) and Higgins (1969), we identify the sex of the holotype as male. Our findings differ from the original description (McIntyre 1962) in that we describe, measure (Table 3), and photographically document (Figs 8–10) in detail characters of the head, neck, and cuticular surface structures of the trunk including sensory spots and a gland cell outlet, none of which were reported or illustrated before. Especially the total length is corrected from 580 µm (McIntyre 1962) to 356 µm (Table 3), because head structures are generally not included in measurements of what is nowadays called trunk length (Higgins 1983; Neuhaus & Higgins 2002; Sørensen & Pardos 2008; Neuhaus 2013). The new data for the holotype is in agreement with measurements of the non-type material (Table 3; Higgins 1969, table 1).

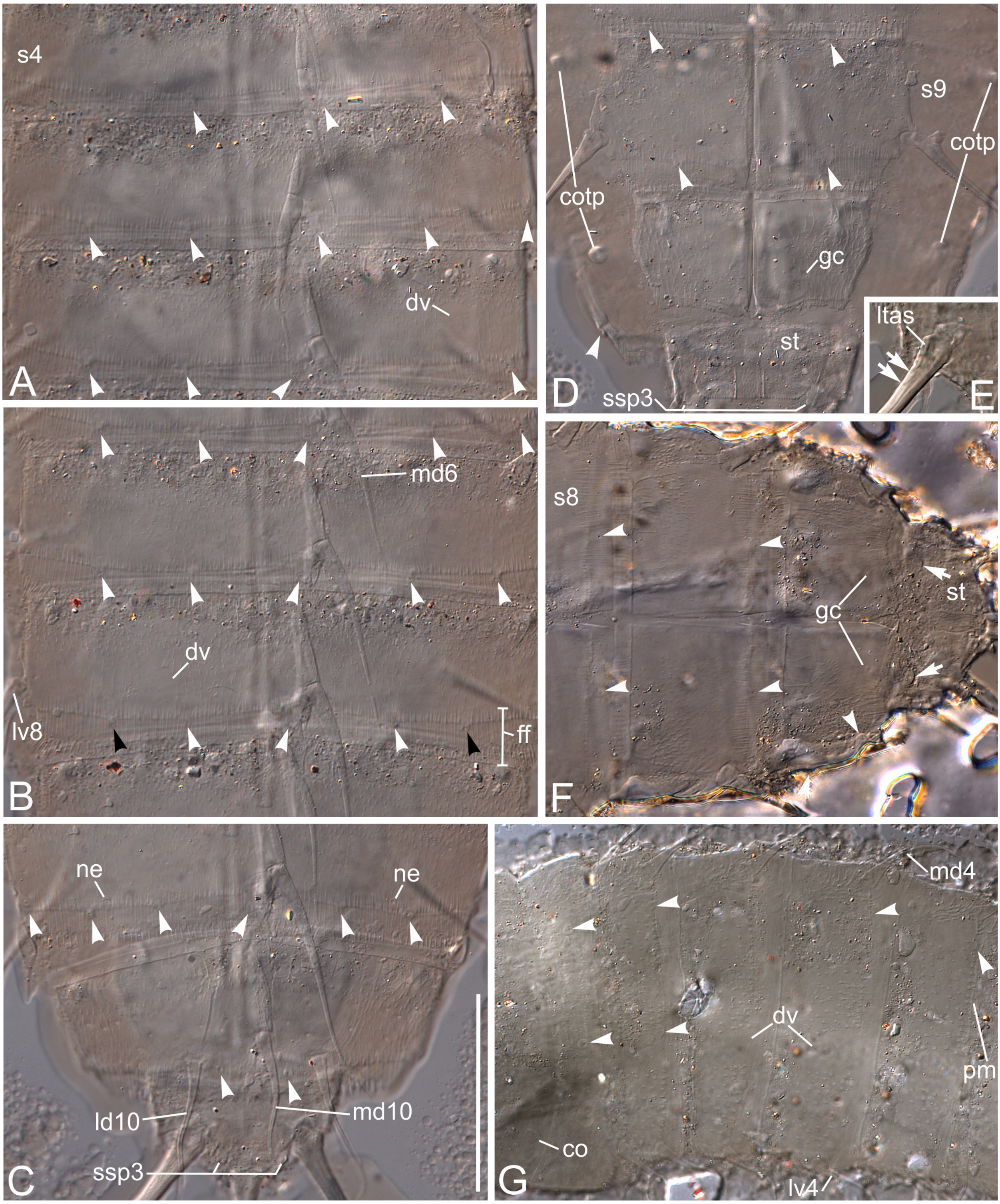


FIGURE 11. *Condyloderes multispinosus*, paratypic males (USNM W37459, **A–E**; 1209821, **F**) and juvenile (USNM 1209819, **G**) in dorsal (**A–C**) and ventral (**D**, **F**) view, as optical section (**E**), and from left side (**G**), DIC. **A.** Segments 4–6. **B.** Segments 7 and 8; note sublateral type-6 sensory spots on segment 8 (black arrowheads). **C**, **D**, **F**. Segments 9–11; extended focus image of six images (**F**); arrows in **F** point to curved sclerotized structures anteriorly and ventrolaterally on segment 11. **E.** Right lateral terminal accessory spine with two thin areas (arrows). **G.** Segments 1–5. Arrowheads in **A–D**, **F**, and **G** mark type-6 sensory spots. Scale bar in **C** 50 µm, valid for **A–G**. Abbreviations: co, condyle of placid; cotp, condyle of tergal plate; dv, attachment area of dorsoventral muscle; ff, free flap; gc, gland cell outlet; ld10, laterodorsal spine of segment 10; lv4, lateroventral spine of segment 4; md4, middorsal spine of segment 4; ne, protonephridial openings; pm, postmarginal spicula; s4, segment 4; ssp3, type-3 sensory spot; sternal plate.

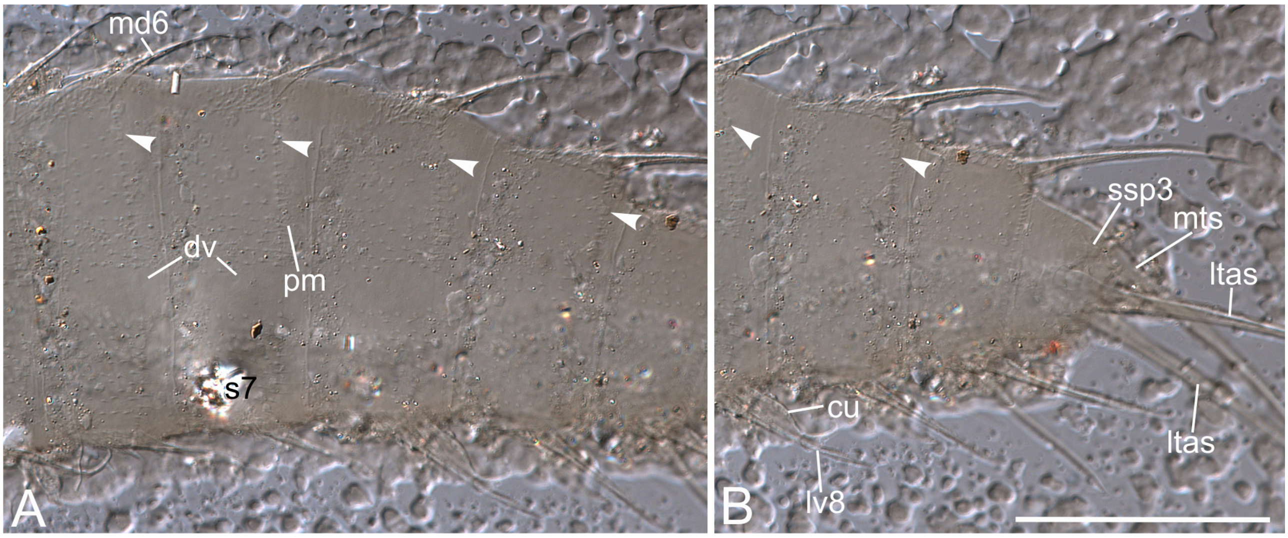


FIGURE 12. *Condyloderes multispinosus*, juvenile (USNM 1209819) from left side, DIC. **A.** Segments 6–9. **B.** Segments 8–11. Arrowheads mark type-6 sensory spots. Scale bar in **B** 50 µm, valid for **A** and **B**. Abbreviations: cu, cuspidate spine; dv, attachment area of dorsoventral muscle; ltas, lateral terminal accessory spine; lv8, lateroventral spine of segment 8; md6, middorsal spine of segment 6; mts, midterminal spine; pm, postmarginal spicula; s7, segment 7; ssp3, type-3 sensory spot.

Additional material of *Condyloderes multispinosus*

(Figs 11, 12; Tables 1–3, 7)

Material examined. Three males (USNM W37459, 1209821, previously identified as females; USNM 1209820, previously identified as adult), and one juvenile (USNM 1209819) mounted for light microscopy (Fig. 1; Table 1).

Description

Males. The adult specimens agree with the description of the holotype. In two specimens (USNM W37459, USNM 1209821: Fig. 11F), segment 11 reveals in its anterior third ventrolaterally a curved sclerotized structure of unknown function (see also *C. shirleyi* **sp. nov.**).

Variation. In one male (USNM 1209821), the cuspidate spine of segment 2 seems to appear in a lateral accessory position on the right side instead of a ventrolateral position. In one male (USNM W37459), a ventromedial gland cell outlet can be traced only on the left side of segment 10.

Intermediate or late juvenile stage. Many characters are not available for study because of the advanced stage of maceration, dirt particles, and lateral mount. Placids with condyles exist but are difficult to separate from each other. The trunk is composed of 11 segments (Figs 11G, 12). Segment 1 reveals a single cuticular plate, whereas segments 2–10 probably possess one tergal and two sternal plates. The situation cannot be evaluated for segment 11 in the laterally mounted specimen. Segments do not possess a free flap but a series of postmarginal spicula with a stronger base (Figs 11G, 12). All segments are covered by short cuticular hairs with a stronger base except midlaterally, where the dorsoventral muscles originate. A type-3 sensory spot occurs ventrolaterally and subdorsally on segment 11 (Fig. 12B). Type-6 sensory spots appear at least ventromedially on segment 1, midlaterally on segments 1 and 2, laterodorsally on segments 2 and 7, subdorsally on segment 10, and paradorsally on segments 1 (almost subdorsally), 2 and 4–9 (Figs 11G, 12). Acicular spines are found lateroventrally and middorsally on segments 1–10 as well as in a lateral accessory position and midterminally on segment 11 (Figs 11G, 12). Cuspidate spines are located ventrolaterally on segments 2, 5 and 9 and in a lateral accessory position on segment 8 (Figs 11G, 12).

Comparison with previous description

In comparison with Higgins (1969), we regard two specimens (USNM W37459, 1209820) previously identified as females and one specimen (USNM 1209821) previously identified as adult now as males (see chapter Discussion). In addition, one specimen (USNM 1209806) previously identified as a juvenile is now assumed to represent the recently moulted male of a new undescribed species *Condyloderes* (see chapter Description of *Condyloderes* sp.). Our findings further differ from the re-description of *C. multispinosus* based on non-type specimens by Higgins (1969) in that (1) two narrower neck placids are located next to the broader midventral placid and the 11 remaining placids alternate in width instead of "placids adjacent to midventral placid slightly narrower than others", (2) broader placids display three rows each with two condyles and the midventral placid three rows with three, two, and three condyles per row instead of just two rows each with two condyles in broader placids and two rows each with three condyles in midventral placid, (3) narrower placids show single condyle basally instead of two rows with anterior and basal condyle, (4) cuspidate spines are located ventrolaterally on segments 2, 5 and 9 instead of in a lateral accessory position on these segments, (5) a single sternal plate exists in segment 11 rather than two sternal plates, (6) type-3 and type-6 sensory spot are now recognized as such and their distribution is described for the species, and (7) morphological characters are documented extensively by photography.

Condyloderes paradoxus **Higgins, 1969**

Condyloderes paradoxus Higgins, 1969: pp. 6–9, figs 10–20, table 2.

Condyloderes paradoxus—Moore 1973: p. 350. Higgins & Rao 1979: p. 76.—Higgins 1983: p. 2. Higgins 1986: p. 115.—Adrianov & Malakhov 1994: p. 229, fig. 130c.—Rao 1998: p. 82.—Adrianov & Malakhov 1999: pp. 114, 253, 254, fig. 5.10D, E.—Adrianov *et al*. 2002: p. 205, 206, 214, 215.—Martorelli & Higgins 2004: pp. 88–90, tables 1, 2.—Sørensen 2007: pp. 165, 166, table 3.—Sørensen & Pardos 2008: p. 53.—Sørensen *et al*. 2010b: pp. 235, 241.—Neuhaus 2013, pp. 329, 292, 329, figs 5.5.2C, 5.8.2A, table 6.—Neuhaus & Sørensen 2013: p. 73.—Venkataraman *et al*. 2015: p. 3.—Sørensen *et al*. 2016: pp. 3, 4, 12, 13, fig. 6, table 1.—Adrianov & Maiorova 2016: pp. 11, 18.—Jeeva & Mohan 2016: p. 251.

Condyloderes cf. *paradoxus*—Sørensen *et al*. 2012a: p. 163, table 1.—this paper: Late juvenile stage of *Condyloderes paradoxus* or *C. setoensis* [either *C. paradoxus* or *C. setoensis*].

Re-description of *Condyloderes paradoxus* based on type material

(Figs 13–17; Tables 1, 2, 7)

Diagnosis. Neck placids with condyles in two rows in narrower placids and three rows in broader placids; narrower placids with one apical and one basal condyle; broader placids with two condyles both in apical, intermediate, and basal row; midventral placid with three apical and basal condyles and two in intermediate row; acicular spine middorsally on segments 1–10, midterminally on segment 11, lateroventrally on segments 1–9 (and on segment 10 in female only), and laterodorsally on segment 10 (male only); cuspidate spine ventrolaterally on segments 2, 5 and 9 and lateral accessorily on segments 4 and 8; type-6 sensory spot ventromedially on segments 1 (slightly more paraventrally) and 2–9, lateroventrally on segment 10 (male only), sublaterally on segments 1–3 and 5–9, midlaterally on segments 1 and 2, laterodorsally on segments 1–9, subdorsally on segment 10, and paradorsally on segments 1 (almost subdorsally), 2 and 4–9; ventromedial appendage on segments 7 and 8 and area of micropapillae ventromedially on segment 9 in female only.

Material examined. Holotypic male (USNM 37460), four paratypic females (USNM 37461, 1209809; USNM 1209808 and 1209812, previously identified as males), six paratypic males (USNM 1209804, 1209805, 1209807, 1209810, 1209813, 1209814), and one juvenile moulting (USNM 1209811) (Fig. 1; Table 1).

Description

Observation of sensory spots was hampered by abundant detritus particles covering all specimens and deeply red stain in some specimens. The sublateral sensory spot on segment 1 was not observed in the holotypic male but is likely to occur based on the observation of the spot in other paratypic adults; therefore, the spot is indicated by dotted lines in Figure 13. The description refers to males.

Head. A single specimen (USNM 1209813) had its introvert protruded, but spinoscalids appeared collapsed around the head. Outer oral styles were not traceable around the extremely protruded pharynx. In other specimens, at least one ring of long, tubular inner oral styles was recognizable.

The 14 trichoscalids are associated with the placids except for the narrow paraventral placid on either side, where no trichoscalid occurs. Each trichoscalid originates from a cuticular trichoscalid plate, which shows about the same size as the base of a trichoscalid. Each trichoscalid is accompanied anteriorly by two filamentous, pointed appendages, which are much thinner than the trichoscalid.

Neck. The 16 placids of the neck are arranged as follows. The broader midventral placid (12 µm width at base x 10 µm height; measurements based on one specimen) is neighboured by two narrower placids (5–7 µm width x 9–11 µm height), and alternatingly a broader (10–12 µm width x 12–13 µm height) and a narrower placid (7 µm width x 11 µm height) (Figs 13, 14, 17D). All placids reveal cone-like condyles arranged in two rows in the narrower placids and in three rows in the broader placids (Table 7). Each narrower placid shows one apical and one basal condyle. Each broader placid displays two condyles in the apical, intermediate, and basal row (Table 7). The midventral placid possesses three condyles in the apical and basal row and two in the intermediate row. Sometimes, a condyle is only partly split into two apical cones. Interstitial placids are located between placids (Fig. 17D). Specimens stained with Semichon's stain indicate that all placids are connected by circular muscles.

Trunk. The trunk is divided into 11 segments (Figs 13–15). Whereas the cuticle of the first trunk segment is ring-like without any articulation, the cuticle of segments 2–10 possesses both a midventral and a lateral articulation resulting in a tergal and two sternal plates. In segment 11, a tergal and a single sternal plate exist (Figs 13A, 14A, 15C, 16F).

The anterior margin of the first trunk segment is smooth (Figs 13, 14, 15A). At the anterior margin of all segments and at the midventral margin of the sternal plates of segments 2–10, the cuticle thickens towards the interior of the animal and forms a pachycyclus (Fig. 17A, B) to which the longitudinal muscles attach. These muscles seem to be continuous over segments 58 on the ventral side. Ventrally, the tergal and sternal plate form a more sclerotized peg and socket articulation. A variable number of irregularly arranged, small canals exists, which extend from the epidermis into each cuticular trunk plate and do not seem to be connected with gland cells. At the posterior end of all segments, the free flap overlapping the subsequent segment terminates in a primary pectinate fringe consisting of narrow teeth. The basal part of the free flap reveals fine, regularly arranged, longitudinal bars inside the flap. The free flap is missing where the spines originate. In the midventral to ventromedial area of segment 1, the posterior margin of the segment shows a considerably shorter free flap but a regular-sized primary pectinate fringe and ends more anteriorly than the ventrolateral margin resulting in a peculiar outline (Figs 13A, 14A).

The surface of the cuticle of all segments is covered with irregularly distributed, triangular cuticular scale-like hairs (Fig. 16C, D, F). The latter are more numerous anteriorly on a segment. Numerous cuticular hairs and triangular scale-like hairs occur middorsally and laterally on the trunk cuticle anterior to the middorsal and lateroventral spines of all segments in a narrow area. Anterior longitudinal ridges on segments 2–10 cannot be traced because of the detritus on the specimens and the unsatisfying conservation status.

All sensory spots elevate above the surface of the trunk cuticle and display on the outside a smooth area surrounding two pores. The distribution of sensory spots is bilateral symmetrical. Type-3 sensory spots occur ventrolaterally next to the lateral terminal accessory spine and subdorsally on segment 11 (Figs 13B, 14, 16B; Table 2). A type-6 sensory spot occurs ventromedially on segments 1 (slightly more paraventrally) and on segments 2–9, lateroventrally on segment l0, sublaterally on segments 1–3 and 5–9, midlaterally on segments 1 and 2, laterodorsally on segments 1–9, subdorsally on segment 10, and paradorsally at least on segments 1 (almost subdorsally) and 4–6 as well as on segment 2 at least in 6 out of 11 specimens (Figs 13–15, 16C, D, F; Table 2). Observation of Semichon's stained specimens indicates that each type-6 sensory spot possesses two cuticular ducts extending through the trunk cuticle and probably connecting with a gland cell.

The nephropore is located slightly dorsally of the sublateral sensory spot at the posterior margin of segment 9 (Table 2; for a female see Fig. 18D).

Segments 1–10 bear a middorsal and on each side a lateroventral spine and segment 11 such a spine in a lateral accessory position (= lateral terminal accessory spine) and as the midterminal spine (Figs 13–15, 16C–F; Tables 2, 7); the spines are hirsute and acicular. Each middorsal and lateroventral acicular spine reveals a strongly sclerotized thick base and a considerably thinner and more flexible apical part. The basal part of the sclerotized lateroventral and middorsal spines shows a strong proximal cuticle around a central cellular cavity. The lateral terminal accessory spine displays at its base two thin areas. The anterolateral part of each lateral terminal accessory spine extends far into the interior of segment 11 and possesses two attachment sites for longitudinal muscles projecting posteriorly. One of these muscles terminates at the sternal plate of segment 11, whereas the other muscle ends lateral to the midterminal spine (Fig. 17C). A transversal muscle extends more dorsally in segment 11 (Fig. 17C). The middorsal and laterodorsal acicular spine on segment 10 are considerably thinner, more flexible, and less sclerotized basally than the lateroventral and middorsal spines of other segments (Figs 13B, 15F). A short hirsute cuspidate spine with a basal thickened and an apical thinner part appears ventrolaterally on segments 2, 5 and 9 and in a lateral accessory position on segments 4 and 8 (Figs 13, 14, 15A–C, 16C–F; Table 2). Whereas the acicular spines appear clearly sclerotized, the cuspidate spines are almost translucent in light microscope mounts.

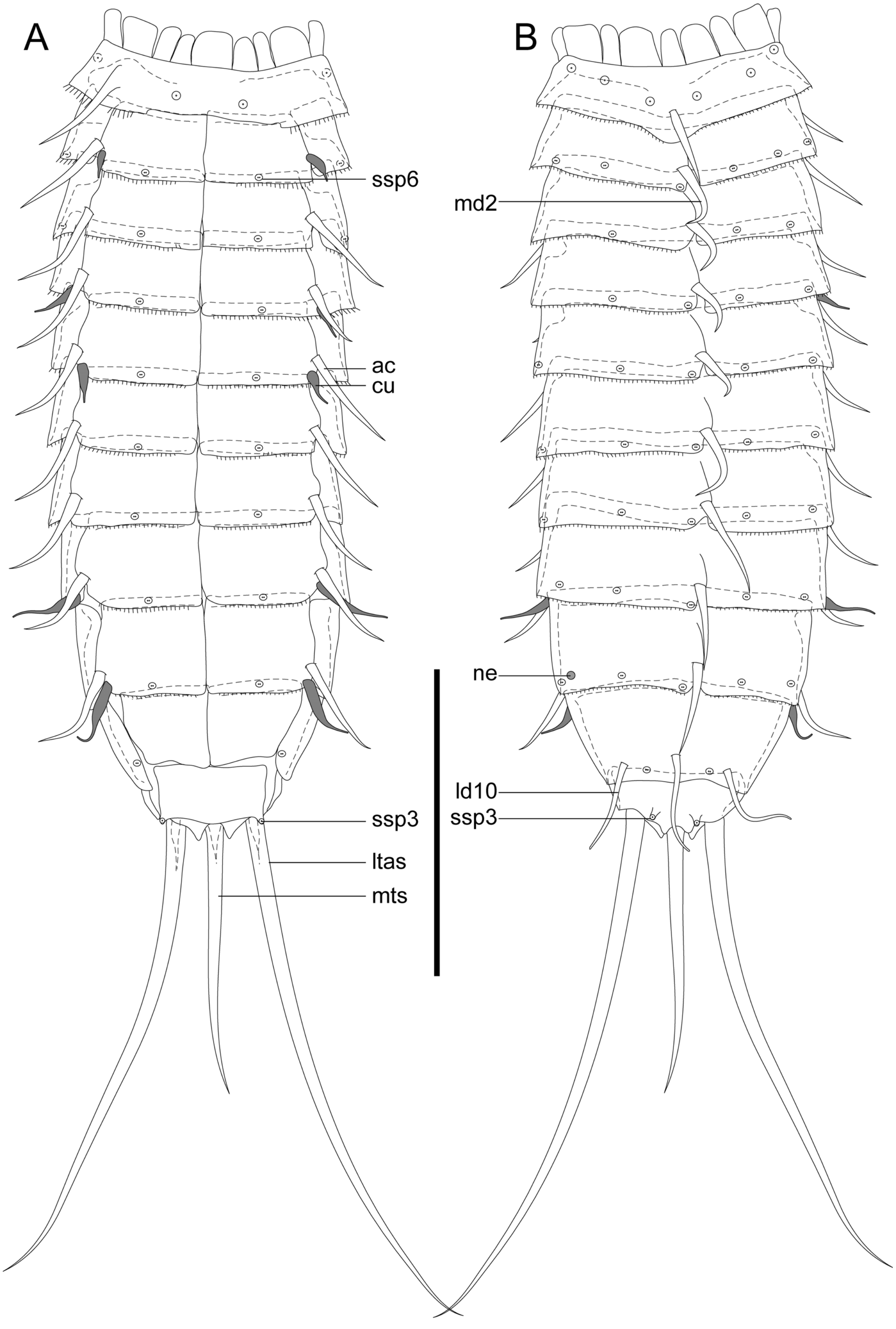


FIGURE 13. *Condyloderes paradoxus*. **A, B**. Habitus of holotypic male (USNM 37460) in ventral (**A**) and dorsal (**B**) view. Sublateral sensory spot on segment 1 indicated by dotted lines not observed in holotype but very likely based on observation of spots in other paratypic adults (see text). Cuspidate spines highlighted by grey colour. Scale bar 100 µm, valid for **A** and **B**. Abbreviations: ac, acicular spine; cu, cuspidate spine; ld10, laterodorsal spine of segment 10; ltas, lateral terminal accessory spine; md2, middorsal spines of segment 2; mts, midterminal spine; ne, protonephridial openings; ssp3, type-3 sensory spot.

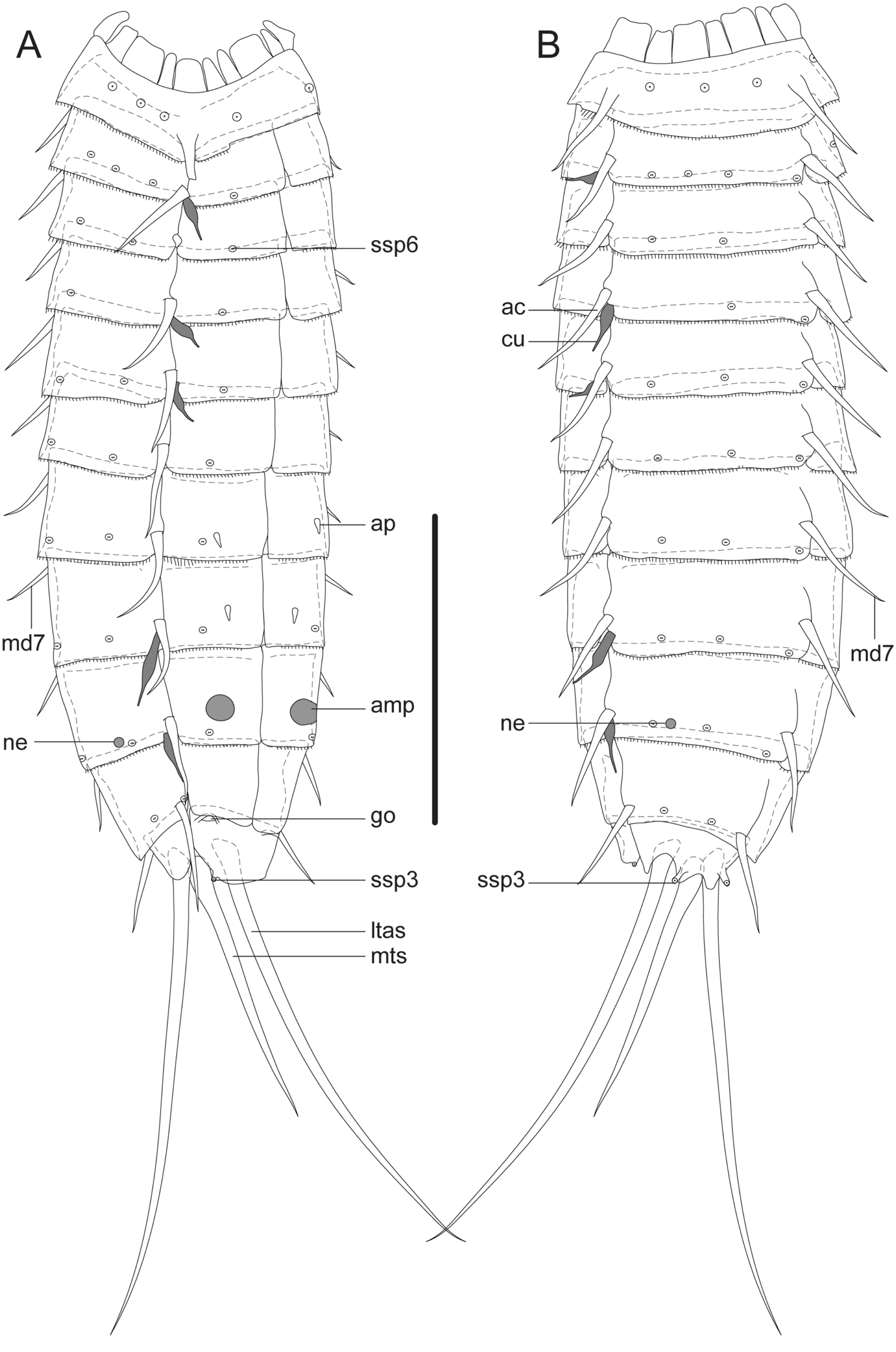


FIGURE 14. *Condyloderes paradoxus*. **A, B**. Habitus of paratypic female (USNM 37461, allotype) from ventrolateral-right (**A**) and left side (**B**). Notice cuspidate spine on segment 9 in lateral accessory instead of ventrolateral position representing variation. Cuspidate spines highlighted by grey colour. Scale bar 100 µm, valid for **A** and **B**. Abbreviations: ac, acicular spine; amp, female-specific area of micropapillae; ap, female-specific appendage; cu, cuspidate spine; gp, gonopore; ltas, lateral terminal accessory spine; md7, middorsal spines of segment 7; mts, midterminal spine; ne, protonephridial openings; ssp3, type-3 sensory spot.

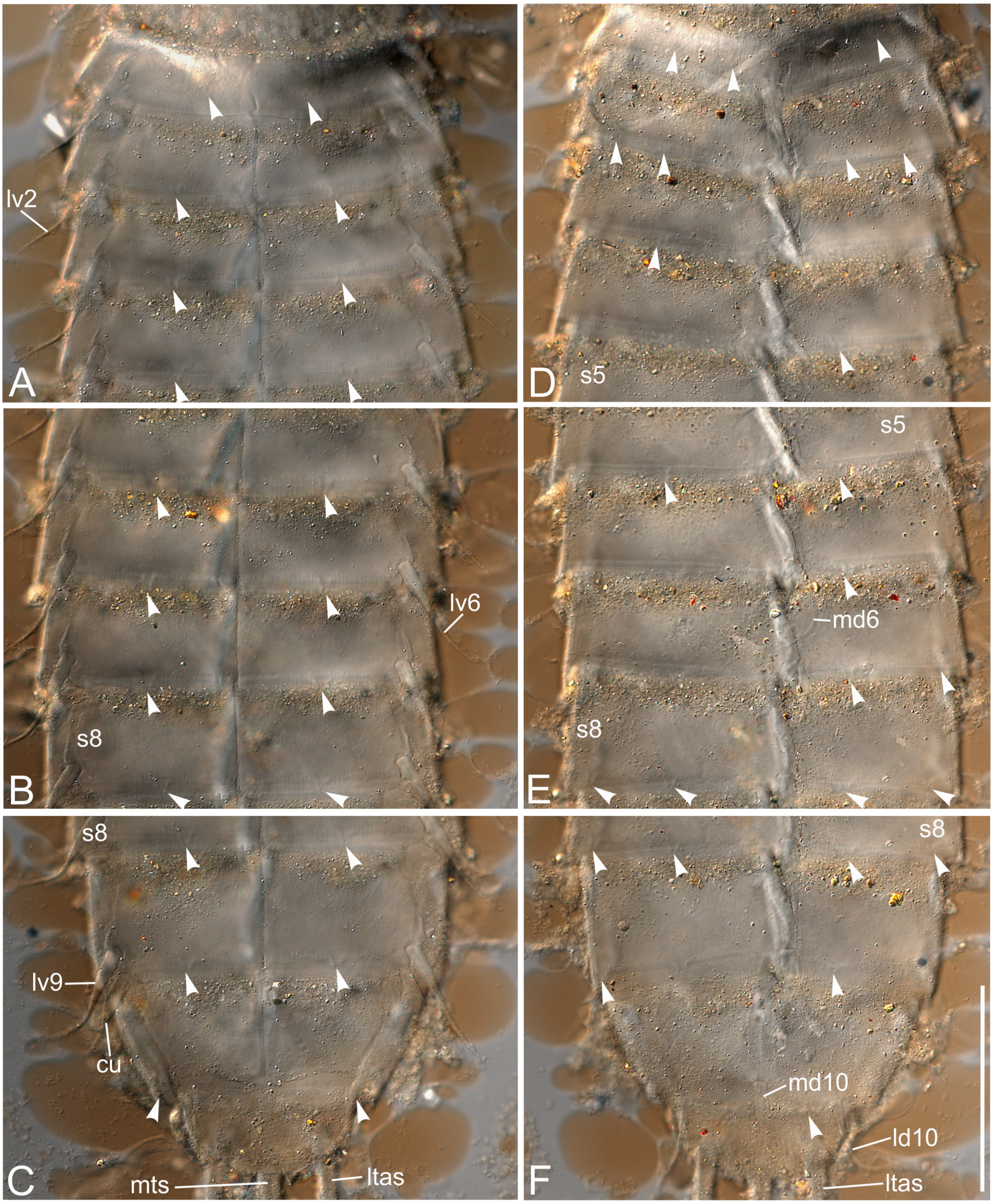


FIGURE 15. *Condyloderes paradoxus*, holotypic male (USNM 37460) in ventral (**A–C**) and dorsal (**D–F**) view, DIC. **A, D.** Segments 1–4. **B, E**. Segments 5–8. **C, F.** Segments 9–11. Arrowheads in **A–F** mark type-6 sensory spots. Scale bar in **F** 50 µm, valid for **A–F**. Abbreviations: cu, cuspidate spine; ld10, laterodorsal spine of segment 10; ltas, lateral terminal accessory spine; lv2, lateroventral spine of segment 2; md6, middorsal spines of segment 6; mts, midterminal spine; s5, segment 5.

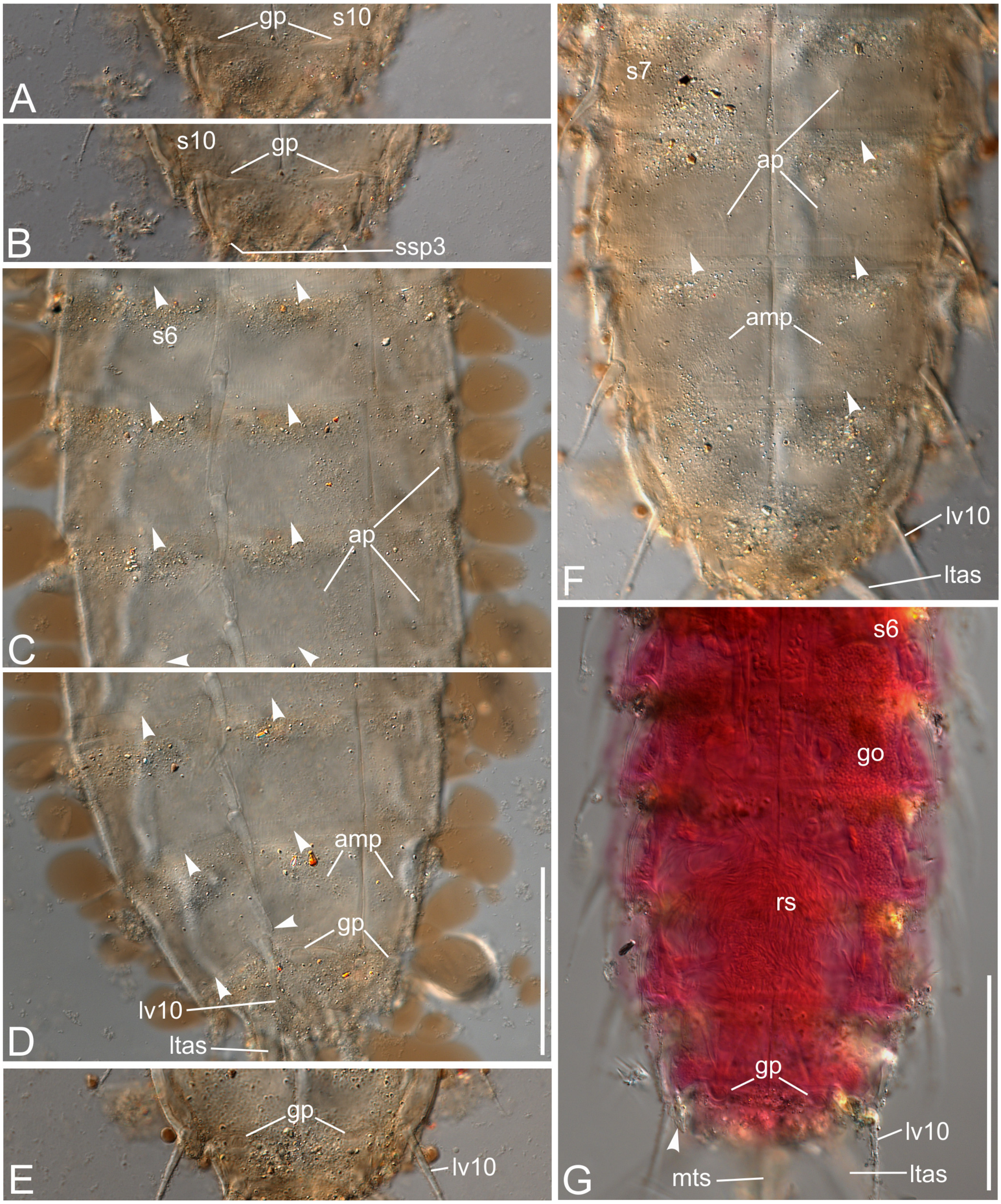


FIGURE 16. *Condyloderes paradoxus*, paratypic male (USNM 1209807, **A**, **B**) and paratypic females (USNM 37461, **C**, **D**; 1209808, **E**, **F**; 1209812, **G**) from ventral (**A**, **B**, **E–G**) and ventrolateral-right side (**C**, **D**), DIC. **A, B.** Male gonopores at border of segments 10 and 11, different focal levels, same specimen. **C, D.** Segments 6–8 (**C**) and 8–11 (**D**). **E–G.** Sex-specific characters of two specimens previously identified as males; segments 10 and 11 with female gonopores (**E**, same specimen as in **F**), segments 7–11 with appendages and area of micropapillae (**F**), and segments 6–11 with female gonopores, receptaculum seminis, and female gonad (**G**). Arrowheads in **C**, **D**, **F**, and **G** mark type-6 sensory spots. Scale bar in **D** 50 µm, valid for **A–E**. Scale bar in **G** 50 µm, valid for **F** and **G**. Abbreviations: amp, female-specific area of micropapillae; ap, female-specific appendage; go, female gonad; gp, gonopore; ltas, lateral terminal accessory spine; lv10, lateroventral spine of segment 10; mts, midterminal spine; rs, receptaculum seminis; s6, segment 6; ssp3, type-3 sensory spot.

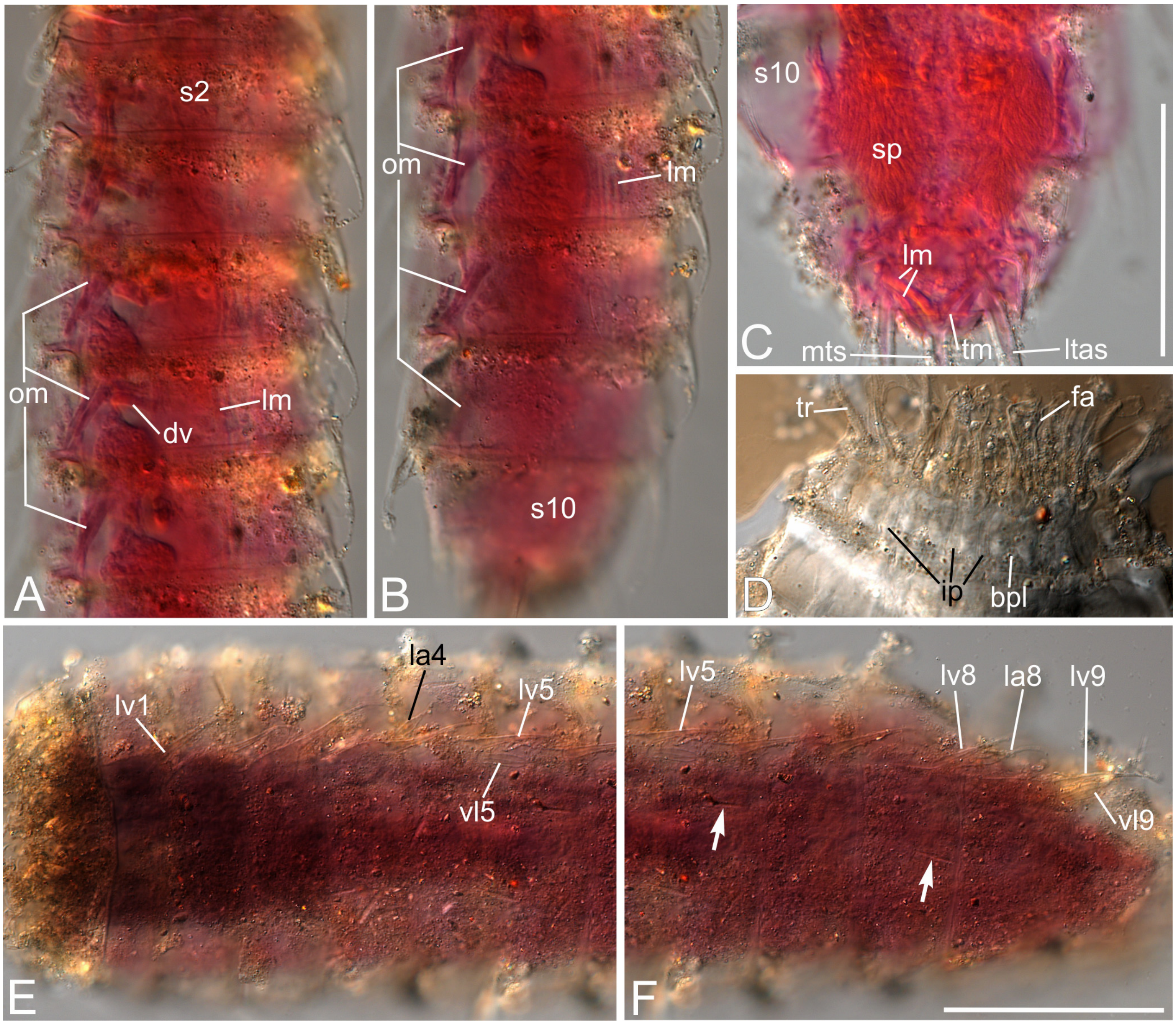


FIGURE 17. *Condyloderes paradoxus*, paratypic males (USNM 1209813, **A**, **B**; 1209805, **C**; 1209810, **D**) and paratypic juvenile ready for moulting (USNM 1209811, **E**, **F**) from left (**A**, **B**), ventrolateral-right (**C**, **D**), and ventral (**E–G**) side, DIC. **A, B.** Segments 1–6 (**A**) and 6–10 (**B**), oblique muscles, parasagittal optical section, same specimen. **C.** Segments 10 and 11, horizontal section. **D**. Neck with interstitial placids, dorsal view. **E, F.** Segments 1–6 (**E**) and 5–11 (**F**), ventral view, same specimen; arrows in **F** mark midventral articulation of sternal plates. Scale bar in **C** 50 µm, valid for **C** and **D**. Scale bar in **F** 50 µm, valid for **A**, **B**, **E**, and **F**. Abbreviations: bpl, broader placid; dv, dorsoventral muscle; fa, filamentous appendage of trichoscalid; ip, interstitial placid; la4, lateral accessory cuspidate spine of segment 4; lm, longitudinal muscle; ltas, lateral terminal accessory spine; lv1, lateroventral acicular spine of segment 1; mts, midterminal spine; om, oblique muscle; s2, segment 2; sp, sperm; tm, transversal muscle; tr, trichoscalid; vl5, ventrolateral cuspidate spine of segment 5.

The anterior ventrolateral cuticle of segment 11 slightly curves posteriorly and is more thickened than in other areas. This is the region where male gonopores would be expected (Fig. 16A, B). Oblique muscles occur in segments 4–9 (Fig. 17A, B).

Female. In the following, only those characters are mentioned for the female that differ from the male. The female can be distinguished from the male in the existence of the ventromedial appendage on the sternal plates of segments 7 and 8 (Figs 14A, 16C, D, F; Table 2) *versus* its lack in the male, in the existence of a more or less rectangular area with prominent cuticular micropapillae on each sternal plate of segment 9 (Figs 14A, 16D, F; Table 2) *versus* its lack in the male, the lack of a laterodorsal acicular spine on segment 10 (Fig. 14; Table 2) *versus* the existence of this spine in the male, the existence of a lateroventral acicular spine on segment 10 and the lack of a type-6 sensory spot in this position (Figs 14, 16E–G; Table 2) *versus* the lack of this spine in the male and the existence of a type-6 sensory spot in this position, and in the existence of the large oval gonopores with a sclerotized edge at the anterior margin of the sternal plate of segment 11 (Figs 14A, 16D, E, G) *versus* its different appearance in the male.

The paraventral area of all four specimens was too dirty to check for potential type-1 sensory spots.

On each sternal plate of segments 7 and 8, the females reveal a (sensory? glandular?) ventromedial appendage, which gives the impression of an extremely elongated sensory spot covered by numerous cuticular micropapillae (Figs 14A, 16C, D, F). At its base, each structure shows a cuticular duct penetrating the trunk cuticle.

Each sternal plate of segment 9 possesses a more or less rectangular area with prominent cuticular micropapillae. Pores and ducts penetrating the trunk cuticle do not seem to exist in this area. At the anterior margin of the sternal plate of segment 11, a pair of oval gonopores with a sclerotized anterior margin and a short cuticular canal is located (Figs 14A, 16D, F).

Intermediate or late juvenile stage. One specimen in the process of moulting (USNM 1209811) possesses 11 trunk segments. Sternal plates are recognizable only in few segments (Fig. 17 F). A free flap is missing (Fig. 17E, F). The specimen reveals an acicular middorsal spine on segments 1–10, an acicular midterminal spine on segment 11, an acicular lateroventral spine on segments 1–10, an acicular lateral terminal accessory spine on segment 11, and a cuspidate spine ventrolaterally on segments 2, 5 and 9 as well as in a lateral accessory position on segments 4 and 8. All spines show a thin cuticle without sclerotization (Fig. 17E, F). Sensory spots are not visible on any segment except the ventrolateral type-3 sensory spot on segment 11 because of the abundant dirt particles on the surface.

Variation. The allotypic female (USNM 37461) does not seem to possess naturally a ventrolateral cuspidate spine at least on the right side of segment 9 (Fig. 16D) but a cuspidate spine does exist on the left side. Variation in the distribution of sensory spots is not considered here because of insufficient data resulting from coverage of specimens with detritus, staining, and deterioration of mounting medium.

Comparison with previous description

We regard two paratypic specimens previously identified as males (USNM 1209808: Fig. 16F, 1209812: Fig. 16G) now as females (see chapter Discussion) and one specimen previously identified as a juvenile as a different species (see chapter *Condyloderes* sp.). In the single specimen with its introvert protruded, outer oral styles could not be observed at all despite their specific mentioning by Higgins (1969). Also, more detailed spinoscalid characters beyond general characters shared by most kinorhynch species were almost impossible to recognize.

Our findings differ further from the original description (Higgins 1969) in that (1) two narrower neck placids are located next to the broader midventral placid and the 11 remaining placids alternate in width instead of "placids adjacent to midventral placid slightly narrower than others", (2) broader placids display three rows each with two condyles and the midventral placid three rows with three, two, and three condyles per row instead of just two rows each with one condyle in broader placids and two rows each with three condyles in midventral placid, (3) cuspidate spines are located ventrolaterally on segments 2, 5 and 9 instead of being in a lateral accessory position on these segments, (4) a single sternal plate exists in segment 11 rather than two sternal plates, (5) type-3 and type-6 sensory spot are now recognized as such and their distribution is described for the species, and (6) morphological characters are documented extensively by photography.

Additional material of *Condyloderes paradoxus* (females and juvenile)

(Fig. 18; Table 3)

Material examined. One female mounted for light microscopy (ZMUC-KIN-848) as well as SEM images of one uncatalogued female from Singapore (Table 1).

Description.

For morphological measurements of female mounted for light microscopy see Table 3.

The females agree basically with the description of the original material of *C. paradoxus*. However, the female mounted for light microscopy (ZMUC-KIN-848) lacks a type-6 sensory spot laterodorsally on segment 1 (Fig. 18B) and paradorsally on segment 7 (Fig. 18C). The mouth cone of this specimen carries at its anterior margin individual outer oral styles, which are broader at the base and taper to a filamentous apical part (Fig. 18A). The specimen was previously identified as an adult (Sørensen *et al.* 2016) and represents clearly a female based on the gonopores, ventromedial appendage on the sternal plates of segments 7 and 8, and area with prominent cuticular micropapillae on each sternal plate of segment 9 (Fig. 18E).

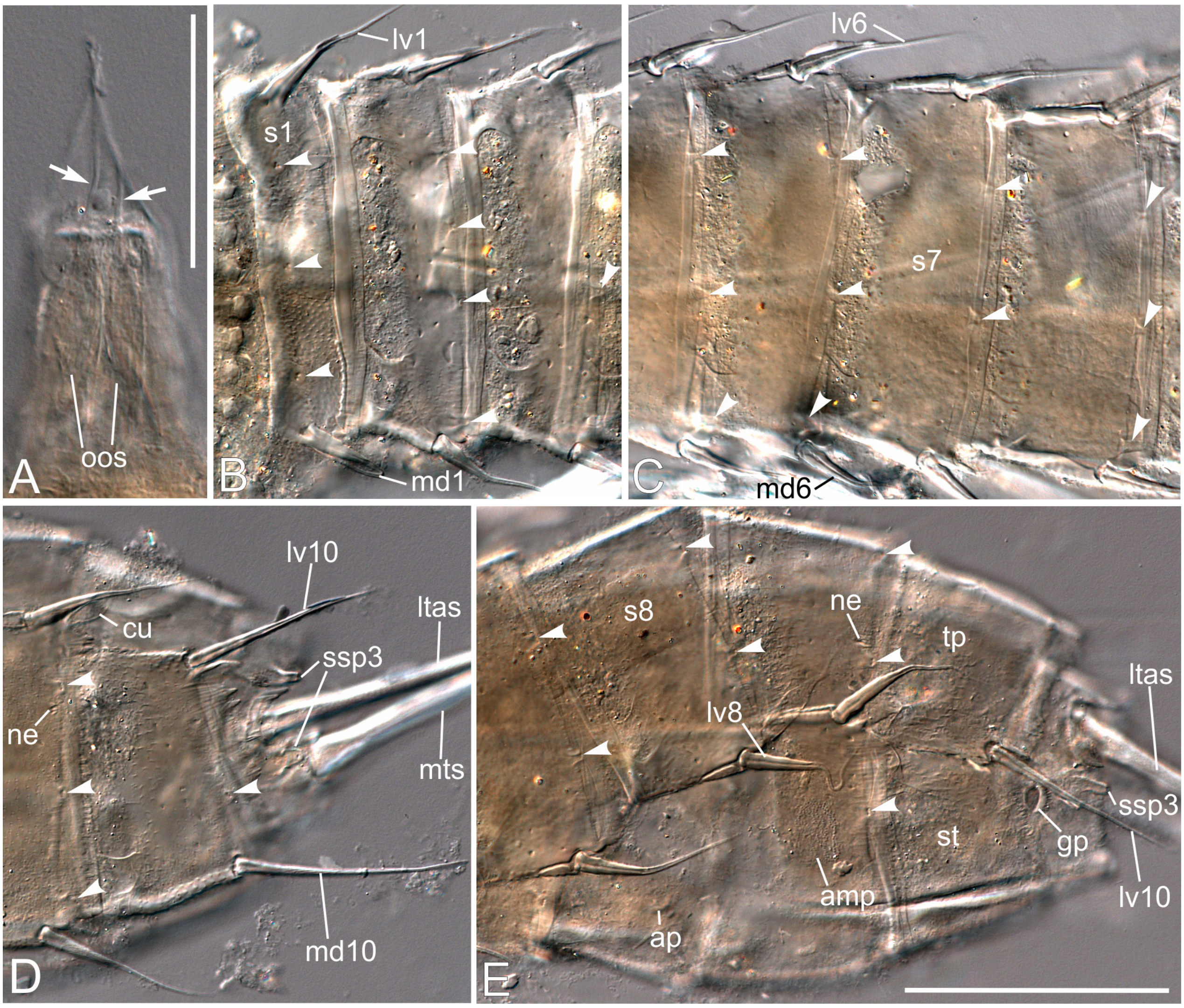


FIGURE 18. *Condyloderes paradoxus*, female (ZMUC-KIN-848) from right (**A–D**) and ventrolateral-left side (**E**), DIC. **A.** Outer oral styles of mouth cone with broad base and narrow tip (arrows). **B, C.** Segments 1–3 (**B**) and 6–8 (**C**), ventral side up. Note that type-6 sensory spot is missing laterodorsally on segment 1 (**B**) and paradorsally on segment 7 (**C**). **D.** Segments 10 and 11, ventral side up. **E.** Segments 8–11. Scale bar in **A** 30 µm. Scale bar in **E** 50 µm, valid for **B–E**. Arrowheads in **B–E** point to type-6 sensory spots. Abbreviations: amp, female-specific area of micropapillae; ap, female-specific appendage; cu, cuspidate spine; gp, gonopore; ltas, lateral terminal accessory spine; lv1, lateroventral spine of segment 1; md1, middorsal spine of segment 1; mts, midterminal spine; ne, protonephridial openings; oos, outer oral style; s1, segment 1; ssp3, type-3 sensory spot; st, sternal plate; tp, tergal plate.

Condyloderes setoensis Adrianov, Murakami & Shirayama, 2002

Condyloderes setoensis Adrianov, Murakami & Shirayama, 2002: pp. 208–215, figs 2–6.

Condyloderes setoensis—Martorelli & Higgins 2004: pp. 88–90, tables 1, 2.—Sørensen & Pardos 2008: p. 53, fig. 14.—Sørensen *et al*. 2010b: pp. 235, 241.—Yamasaki *et al*. 2012: p. 23.—Yamasaki & Kajihara 2012: p. 109.—Adrianov & Maiorova 2016: pp. 11, 18.—Yamasaki 2017: pp. 549, 552, table 21.1.

Condyloderes megastigma Sørensen, Rho & Kim, 2010b: pp. 236–241, figs 2–6, tables 1, 2.—this paper: not *Condyloderes megastigma* Sørensen, Rho & Kim, 2010b but *Condyloderes setoensis* Adrianov, Murakami & Shirayama, 2002. *Condyloderes megastigma*—Sørensen *et al*. 2010a: p. 53.—Sørensen *et al*. 2012b: p. 231.—Sørensen & Thormar 2010: p. 273.—Neuhaus 2013: p. 232, 254, 291, table 6.—Neuhaus *et al*. 2013: p. 129.—Neuhaus *et al*. 2014: pp. 57, 64.—Neuhaus & Sørensen 2013: p. 73.—Adrianov & Maiorova 2016: pp. 11, 18.—Yamasaki 2016: p. 79.—Neuhaus 2017: p. 147, table 5.

Condyloderes cf. *megastigma*—Sørensen *et al*. 2012a: p. 163, table 1.—this paper: not *Condyloderes* cf. *setoensis* but *Condyloderes* sp. 2.

Re-description of *Condyloderes setoensis* based on type material

(Figs 19–21; Tables 1, 2, 7)

Diagnosis. Neck placids with condyles in one basal row in narrower placids and in three rows in broader placids; each narrower placid with one basal condyle; each broader placid with two condyles each in apical, intermediate, and basal row; midventral placid with three condyles in apical and basal row and two in intermediate row; acicular spine middorsally on segments 1–10, midterminally on segment 11, lateroventrally on segments 1–9, midterminally on segment 11, and laterodorsally on segment 10; cuspidate spine ventrolaterally on segments 2, 5 and 9, and lateral accessorily on segment 8 and sometimes on segment 4; type-5 (?) sensory spot ventromedially on segment 11; type-6 sensory spot ventromedially on segments 1 (slightly more paraventrally) and 2–9, lateroventrally on segment 10, sublaterally on segments 1–3, 5–7 and 9, midlaterally on segments 1 and 2, laterodorsally on segments 2–9, subdorsally on segment 10, and paradorsally on segments 1 (almost subdorsally), 2–9; gland cell outlet ventromedially on segment 10.

Material examined. Three paratypic males (MIMB AVA-CM-JAP-02, AVA-CM-JAP-03, AVA-CM-JAP-04) mounted for light microscopy (Fig. 1; Table 1).

Description

The description is based on the three paratypic males available to us. The drawing is based on the specimen (AVA-CM-JAP-03) closest in morphology to the original description (Adrianov *et al*. 2002).

Head. The 14 trichoscalids are associated with the placids except for the narrow paraventral placid on either side, where no trichoscalid occurs. Each trichoscalid originates from a cuticular trichoscalid plate, which shows about the same size as the base of a trichoscalid. Each trichoscalid is accompanied anteriorly by two filamentous, pointed appendages, which are much thinner than the trichoscalid (Fig. 20A). Each trichoscalids is covered by numerous cuticular hairs (Fig. 20A, C). Inner septa are not recognizable in the filamentous appendages.

Neck. The 16 placids of the neck are arranged as follows. The broader midventral placid (13–15 µm width at base x 13–14 µm height; all measurements based on three specimens) is neighboured by two narrower placids (6–7 µm width x 10–13 µm height), and alternatingly a broader (12–13 µm width x 13–17 µm height) and a narrower placid (7–8 µm width x 10–13 µm height) (Figs 19, 20A–C, I; for female see Fig. 22B). All placids reveal cone-like condyles arranged in one basal row in the narrower placids and in three rows in the broader placids (Figs 19, 20A, C, E, I; Table 7). Each narrower placid shows one basal condyle. Each broader placid displays two condyles each in the apical, intermediate, and basal row (Figs 19, 20A, C, E, I; Table 7). The midventral placid possesses three apical condyles, two in the intermediate row, and three in the basal row (for female see Fig. 22B). A small, narrow interstitial placid of irregular size can be observed between each two neighbouring regular placids in light microscopy (Fig. 20B) and is interpreted as cuticular folds (see also Adrianov *et al*. 2002, p. 213).

Trunk. The trunk is divided into 11 segments (Fig. 19). Whereas the cuticle of the first trunk segment is ring-like without any articulation, the cuticle of segments 2–10 possesses both a midventral and a lateral articulation resulting in a tergal and two sternal plates (Figs 19, 20E–I, 24; for female see Fig. 22B, D). In segment 11, a tergal and a single sternal plate exist. Two specimens reveal a paraventral area of thinner cuticle (Fig. 20H).

The anterior margin of the first trunk segment is smooth but reveals short cuticular hairs (Figs 19, 20A–C, E, I). At the anterior margin of all segments and at the midventral margin of the sternal plates of segments 2–10, the cuticle thickens towards the interior of the animal and forms a pachycyclus (Figs 20E–I, 21; for female see Fig. 22E). Ventrally, the tergal and sternal plate form a strongly sclerotized peg and socket articulation. A variable number of easily recognizable, irregularly arranged, small canals occurs, which extend from the epidermis into each cuticular trunk plate (Fig. 20H, I) and do not seem to be connected with gland cells. At the posterior end of all segments, the free flap overlapping the subsequent segment terminates in a primary pectinate fringe of cuticular teeth (for female see Fig. 22C). The basal part of the free flap reveals fine, regularly arranged, longitudinal bars inside the flap (Figs 20E–I, 21). The free flap is missing where the spines originate. In the midventral to ventromedial area of segment 1, the posterior margin of the segment shows a considerably shorter free flap without a pectinate fringe and ends more anteriorly than the ventrolateral margin resulting in a peculiar outline (Figs 19A, 20E; for female see Fig. 22B).The teeth of the primary pectinate fringe are considerably shorter ventrally on segment 10 and all around segment 11 (Figs 19A, 20H).

The surface of the cuticle of segments 2–10 reveals in the anteriormost one fourth little elevated cuticular ridges (Fig. 20G, H). The remaining part of these segments is covered with numerous, irregularly distributed, cuticular scale-like hairs, which are more numerous and stronger in the anterior area (Figs 20E–I, 21; for female see Fig. 22B, D). Such hairs are also more numerous and stronger in a midventral to paraventral area on segment 1. Numerous cuticular hairs occur middorsally and laterally on the trunk cuticle anterior to the middorsal and lateroventral spines of segments 2–11 in a narrow area (Fig. 21A–C).

All sensory spots except the ventromedial and the subdorsal ones on segment 11 elevate above the surface of the trunk cuticle and display on the outside cuticular micropapillae surrounding one or two pores. The distribution of sensory spots is bilateral symmetrical. Type-3 sensory spots occur ventrolaterally next to the lateral terminal accessory spine and subdorsally on segment 11 (Figs 19, 20H; Table 2). A sensory spot ventromedially on segment 11 may represent a type-6 spot. A type-6 sensory spot occurs ventromedially on segments 1 (slightly more paraventrally) and on segments 2–9, lateroventrally on segment 10, sublaterally on segments 1–3, 5–7 and 9, midlaterally on segments 1 and 2, laterodorsally on segments 2–9, subdorsally on segment 10, and paradorsally on segments 1 (almost subdorsally), 2, 4–6, 8 and 9 (Figs 19, 20E–I, 21; for female see Fig. 22B D; Tables 2, 7).

A small structure with cuticular micropapillae elevates above the surface of the trunk cuticle slightly dorsally of the sublateral sensory spot at the posterior margin of segment 9. It is regarded as the nephropore.

A gland cell outlet ventromedially on segment 10 reveals a short sclerotized cuticular tube and an intra- and subcuticular cuticle-lined cavity (Figs 19A, 24H; Table 2).

Segments 1–9 bear a middorsal (also on segment 10) and on each side a lateroventral spine and segment 11 such a spine in a lateral accessory position (= lateral terminal accessory spine) and as the long midterminal spine (Figs 19, 20E–I, 21; Tables 2, 7); the spines are hirsute and acicular. Each middorsal and lateroventral acicular spine reveals a strongly sclerotized thick base and a considerably thinner and more flexible apical part. The basal part of the lateroventral and middorsal spines shows a strong proximal cuticle around a central cellular cavity and tapers towards its tip. The lateral terminal accessory spine displays at its base two thin areas (Fig. 20D). The middorsal and laterodorsal acicular spine on segment 10 are considerably thinner, more flexible, and less sclerotized basally than the lateroventral and middorsal spines of other segments (Figs 19B, 21C). A short hirsute cuspidate spine with a basal thickened and an apical thinner part appears ventrolaterally on segments 2, 5 and 9, in a lateral accessory position on segment 8 (Figs 19, 20E–H, 21D; for female see Fig. 22D; Tables 2, 7). Whereas the acicular spines appear clearly sclerotized, the cuspidate spines are almost translucent in light microscope mounts.

The anterior ventrolateral cuticle of segment 11 slightly curves posteriorly and is more thickened than in other areas. This is the region where male gonopores would be expected (Fig. 20H).

Variation. One male (AVA-CM-JAP-02) reveals a lateral accessory cuspidate spine only on the right side of segment 4 (Fig. 20F). Such a spine is lacking in the other specimens (Fig. 21D).

Comparison with previous description

Text and illustrations of the original description of the species are partly confusing. A cuspidate spine is supposed to be located lateroventrally on segments 2, 5 and 9 (Adrianov *et al.* 2002, p. 213), but the illustrations show the spine in a ventrolateral position (their figs 2A, 3A). We agree with the illustrations. The authors also claim that the female differs in the arrangement of sensory spots on segments 1–3 (Adrianov *et al.* 2002, p. 214). Comparing their figures for the male (Adrianov *et al.* 2002, fig. 2) and female (Adrianov *et al.* 2002, fig. 3) with each other and with the three paratypic males available to us, we suggest that sublateral type-6 sensory spots on segments 1–3 were not recognizable in the female, because the specimen was not squeezed sufficiently to see that character. Also, we never noticed a sex-specific difference in the existence and lack of sublateral sensory spots on segments 1–3 in any of the known and undescribed species of *Condyloderes* we studied.

Our observations differ from the original description (Adrianov *et al.* 2002) in that (1) two narrower neck placids are located next to the broader midventral placid and the 11 remaining placids alternate in width instead of placids alternating between 7 broader and 9 narrower, (2) broader placids display three rows each with two condyles and the broad midventral placid three rows with three, two, and three condyles per row instead of just two rows of condyles, (3) a type-6 sensory spot exists laterodorsally on segment 4 rather than sublaterally, (4) a type-6 sensory spot exists lateroventrally on segment 10 instead of its lack, (5) a ventromedial gland cell outlet exists on segment 10 instead of its lack, (6) one specimen (AVA-CM-JAP-02) possesses a lateral accessory cuspidate spine on the right side of segment 4 only and this was not mentioned before, (7) an acicular spine is located laterodorsally on segment 10 rather than subdorsally, (8) the sternal plate of segment 11 consists of a single plate and does not possess an "underdeveloped" midventral articulation (Adrianov *et al.* 2002, p. 214), and (9) morphological characters are documented now extensively by photography.

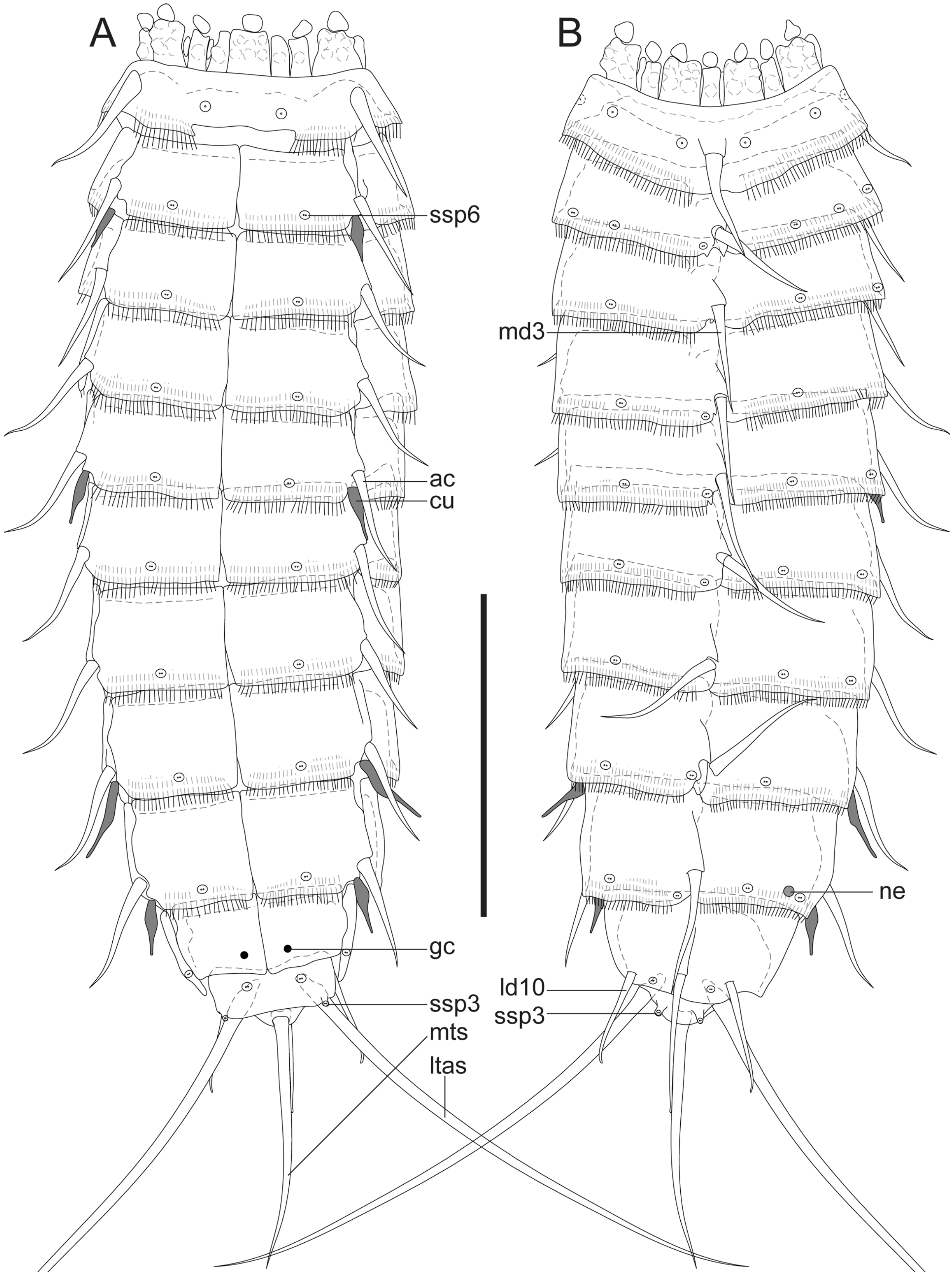


FIGURE 19. *Condyloderes setoensis*. **A, B**. Habitus of paratypic male (AVA-CM-JAP-03) in ventral (**A**) and dorsal (**B**) view. Cuspidate spines highlighted by grey colour. Scale bar 100 µm, valid for **A** and **B**. Abbreviations: ac, acicular spine; cu, cuspidate spine; gc, gland cell outlet; ld10, laterodorsal spine of segment 10; ltas, lateral terminal accessory spine; md3, middorsal spines of segment 3; mts, midterminal spine; ne, protonephridial openings; ssp3, type-3 sensory spot.

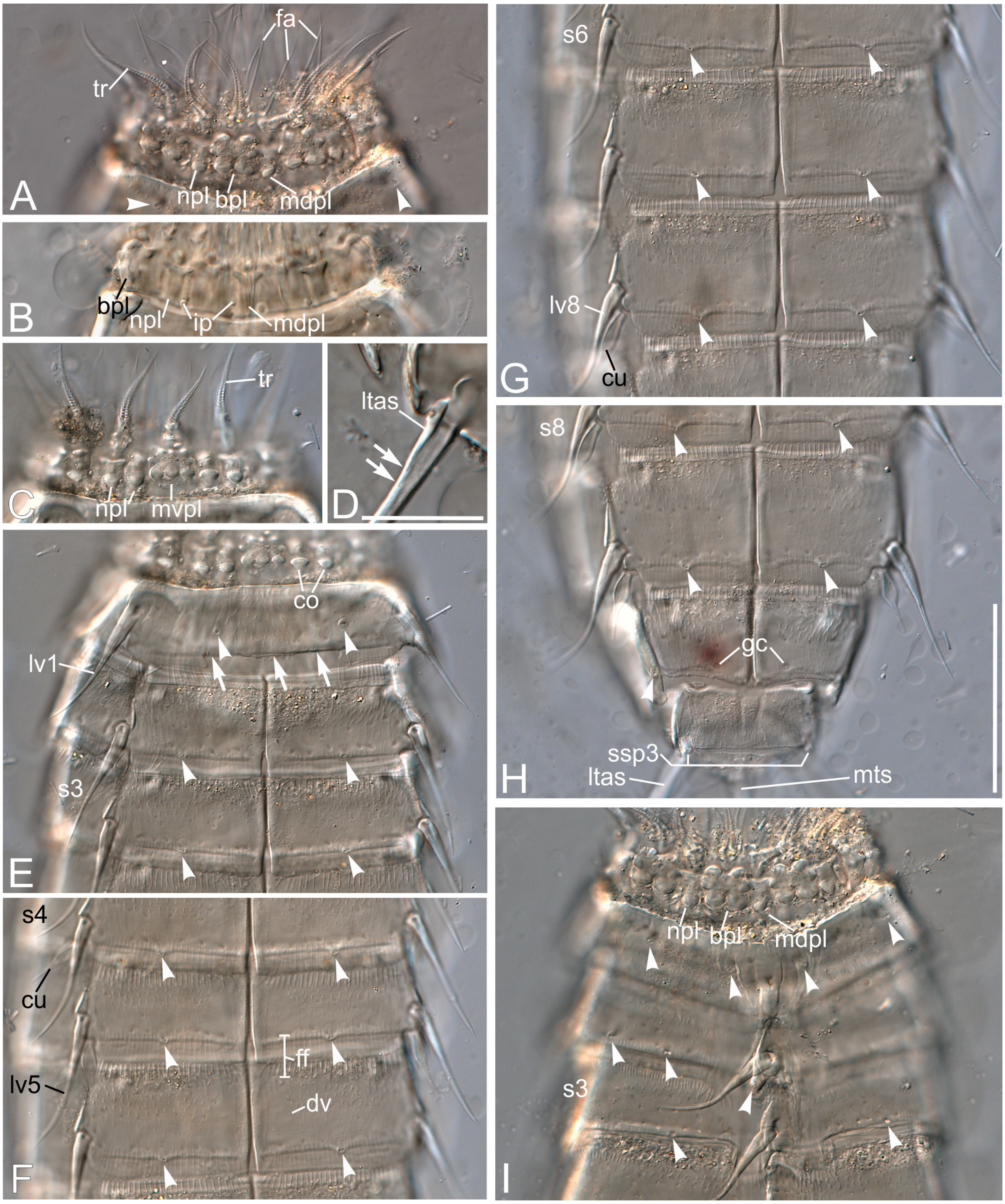


FIGURE 20. *Condyloderes setoensis*, paratypic males (AVA-CM-JAP-02, **A**, **C–I**; AVA-CM-JAP-03, **B**) in dorsal (**A**, **B**, **I**) and ventral (**C–H**) view, DIC. **A–C**. Neck showing placids and interstitial placids (**B**). **D.** Lateral terminal accessory spine with two thin areas (arrows). **E.** Segments 1–3; arrows mark reduced free flap. **F.** Segments 4–6; note existence of lateral accessory cuspidate spine on right side of segment 4 only. **G.** Segments 7 and 8. **H.** Segments 9–11. **I.** Segments 1–3. Arrowheads in **A** and **E–I** mark type-6 sensory spots. Scale bar in **D** 20 µm. Scale bar in **H** 50 µm, valid for **A–C** and **E–I**. Abbreviations: bpl, broader placid; co, condyle of placid; cu, cuspidate spine; dv, attachment area of dorsoventral muscle; fa, filamentous appendage of trichoscalid; ff, free flap; gc, gland cell outlet; ip, interstitial placid; ltas, lateral terminal accessory spine; lv1, lateroventral spine of segment 1; mdpl, middorsal placid; mts, midterminal spine; mvpl, midventral placid; npl, narrower placid; s3, segment 3; ssp3, type-3 sensory spot; tr, trichoscalid.

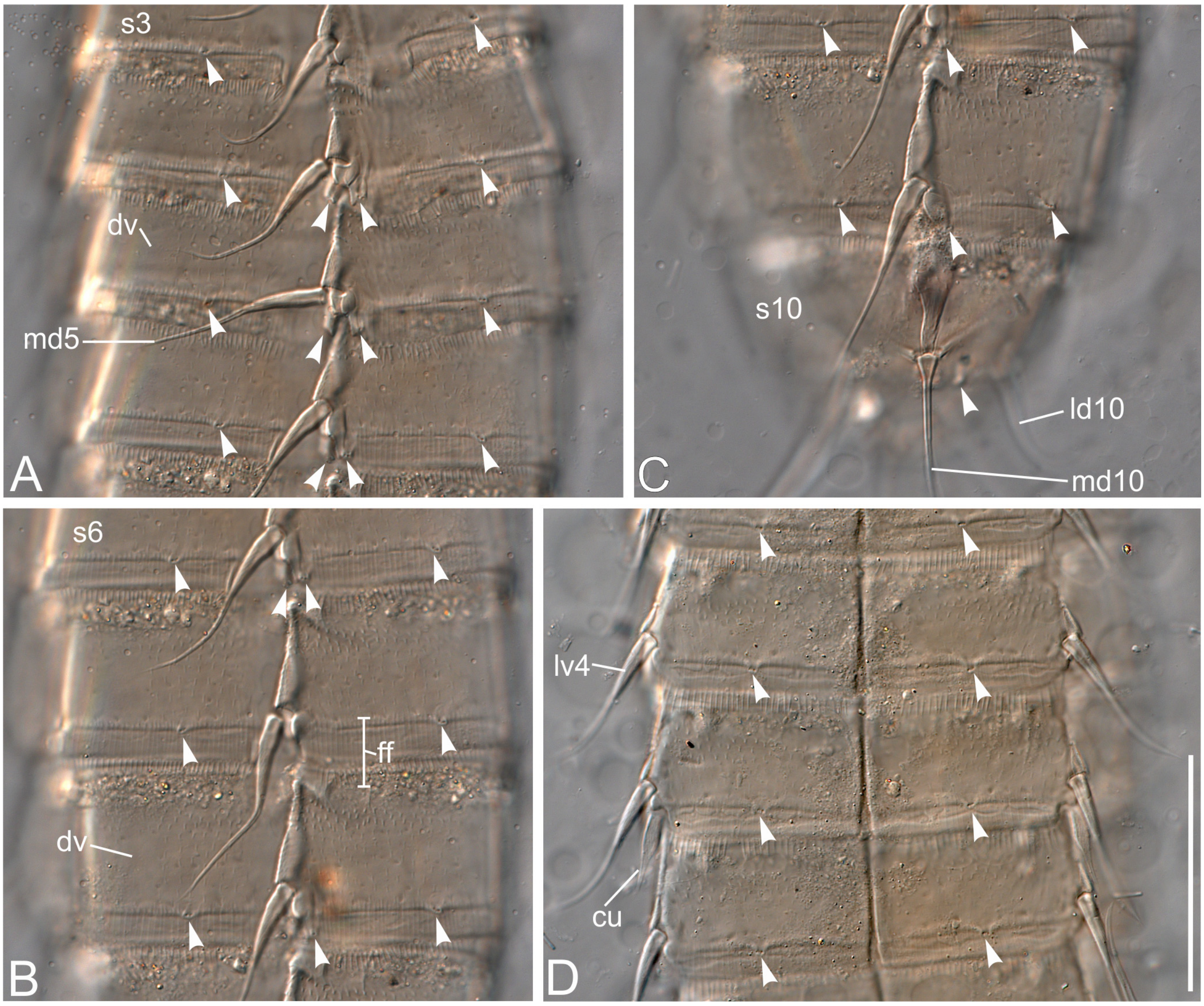


FIGURE 21. *Condyloderes setoensis*, paratypic males (AVA-CM-JAP-02, **A**–**C**; AVA-CM-JAP-03, **D**) in dorsal (**A–C**) and ventral (**D**) view, DIC. **A**. Segments 4–6. **B.** Segments 7 and 8. **C.** Segments 9–11. **D.** Segments 4–6; note lack of lateral accessory cuspidate spine on segment 4. Arrowheads in **A–D** mark type-6 sensory spots. Scale bar in **D** 50 µm, valid for **A–D**. Abbreviations: cu, cuspidate spine; dv, attachment area of dorsoventral muscle; ff, free flap; ld10, laterodorsal spine of segment 10; lv4, lateroventral spine of segment 4; md5, middorsal spine of segment 5; s3, segment 3.

Additional material of *Condyloderes setoensis* (female and juveniles)

(Figs 22, 23; Tables 4, 7)

Material examined. One female specimen (USNM 14908450) and three juveniles (USNM 1490851-1409853) from a station almost at the type locality of *C. megastigma* at the coast of Honshu Island, Japan (Fig. 1; Table 1).

Description

For morphological measurements and data see Tables 2, 4, and 7.

Female. One adult agrees in almost all characters with the males of *C. setoensis* but is a female with eggs in the ovaries (Fig. 22A). The latter differs from the males in the existence of ventromedial appendages on segments 7 and 8 (Fig. 22D) *versus* their lack in the males, the existence of a ventromedial area of micropapillae on segment 9 (Fig. 22D) *versus* its lack in the males, the lack of a ventromedial gland cell outlet on segment 10 *versus* its existence in the males, the existence of gonopores anteriorly on segment 11 (Fig. 22E) *versus* their lack in the males, and the lack of a thin middorsal and laterodorsal spine on segment 10 *versus* their existence in the males. A paraventral area of micropapillae on segments 2–5 possibly representing a type-1 sensory spot is only barely recognizable with a plan-apochromatic 100x objective (Fig. 22C), because the specimen was stained with Rose Bengal (see also chapter Original material of "*Condyloderes megastigma* Sørensen, Rho & Kim, 2010b"). Pores and ducts penetrating the cuticle were not observed.

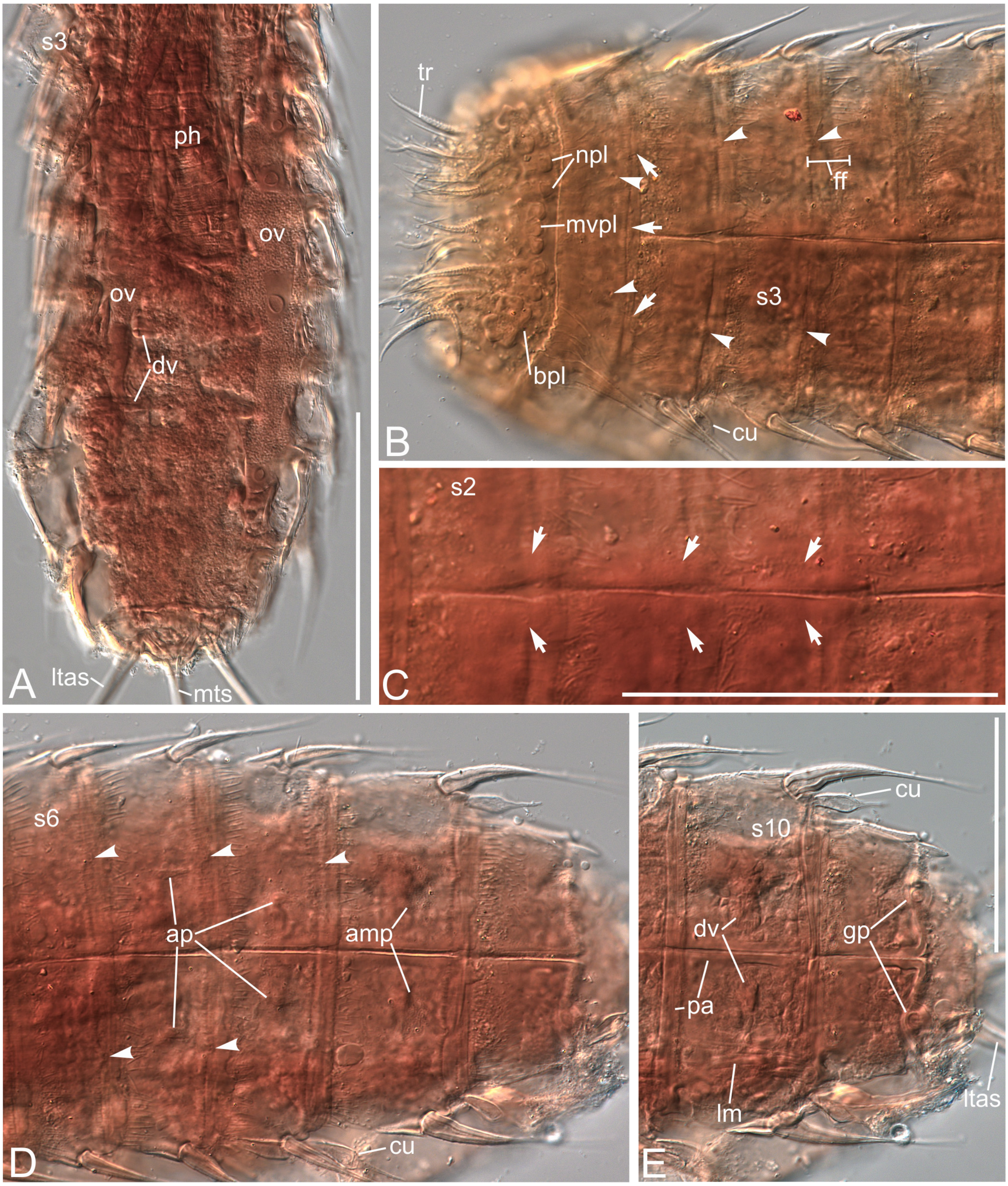


FIGURE 22. *Condyloderes setoensis*, female (USNM 1490850) in optical section (**A**) and ventral view (**B–E**), DIC. **A**. Segments 3–1 with ovaries. **B.** Segments 1–5; arrows mark area of reduced free flap on segment 1. **C.** Segments 2–5; arrows mark potential type-1 (?) sensory spots. **D.** Segments 6–11; note appendages and area of micropapillae. Arrowheads in **B** and **D** mark type-6 sensory spots. Scale bar in **A** 100 µm. Scale bar in **C** 50 µm. Scale bar in **E** 50 µm, valid for **B**, **D**, and **E**. Abbreviations: amp, female-specific area of micropapillae; ap, female-specific appendage; bpl, broader placid; cu, cuspidate spine; dv, dorsoventral muscle; ff, free flap; gp, gonopore; lm, longitudinal muscle; ltas, lateral terminal accessory spine; mts, midterminal spine; mvpl, midventral placid; npl, narrower placid; ov, ovary; pa, pachycyclus; ph, pharynx; s2, segment 2; tr, trichoscalid.

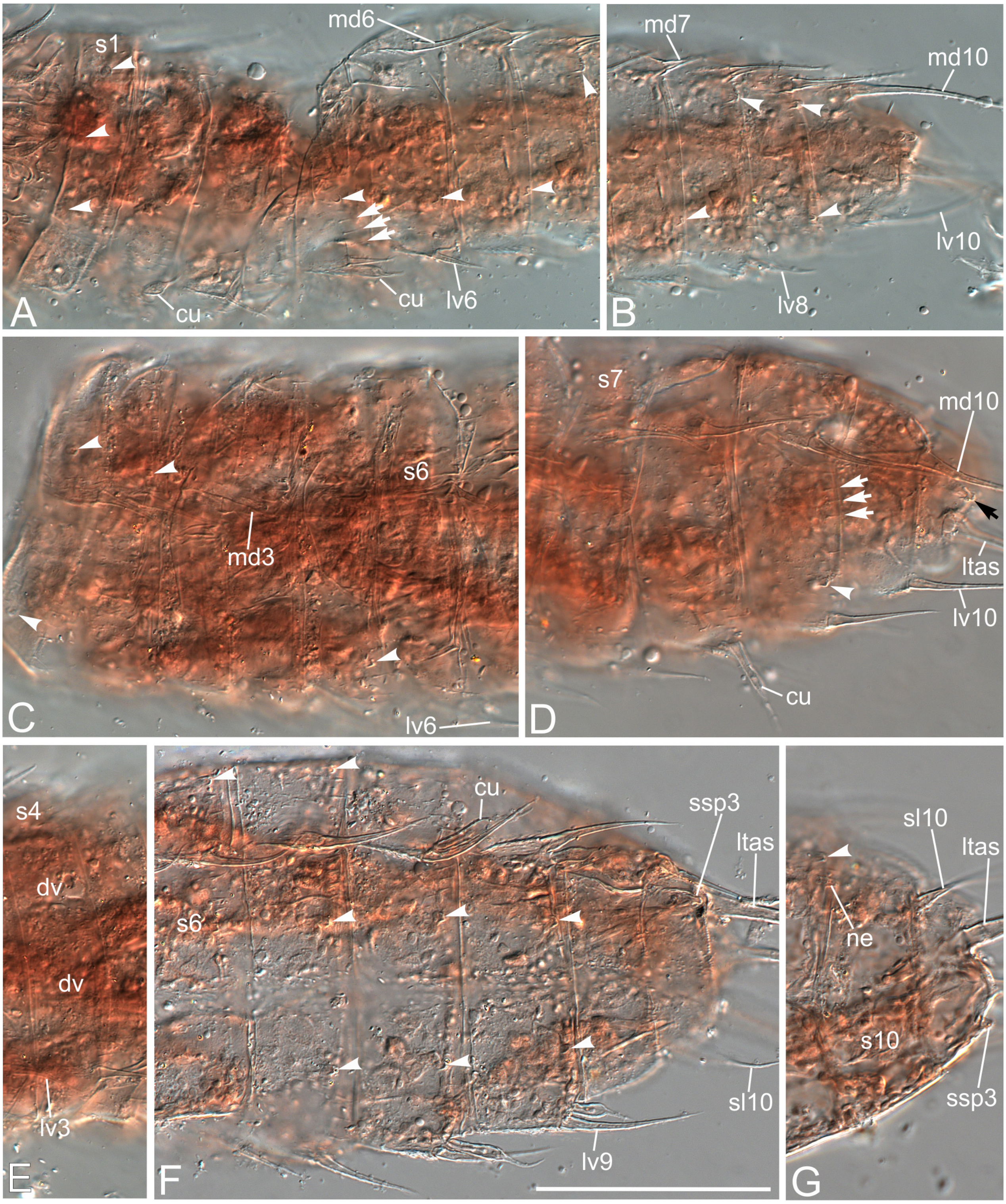


FIGURE 23. *Condyloderes setoensis*, juveniles (USNM 1490851, **A**, **B**; 1490852, **C–E**, 1490853, **F**, **G**) from left side (**A**, **B**), in dorsal (**C**, **D**, **G**) and ventral (**E**, **F**) view, DIC. **A.** Segments 1–8. **B.** Segments 7–11. **C.** Segments 1–7. **D.** Segments 7–11; black arrow points to type-3 sensory spot. **E.** Segment 4 with single sternal plate. **F.** Segments 6–11. **G.** Segments 10 and 11; note sublateral acicular spine on segment 10. White arrows in **A** and **D** mark spicula. Arrowheads in **A–D**, **F**, and **G** mark type-6 sensory spots. Scale bar in **F** 50 µm, valid for **A–G**. Abbreviations: cu, cuspidate spine; dv, attachment area of dorsoventral muscle; ltas, lateral terminal accessory spine; lv6, lateroventral spine of segment 6; md3, middorsal spine of segment 3; ne, protonephridial openings; s1, segment 1; sl10, sublateral spine on segemnt 10; ssp3, type-3 sensory spot.

TABLE 4. *Condyloderes setoensis*, morphological data of additional adult specimens (length in µm; data given for left/right side if applicable). Abbreviations: ac, acicular spine; cu, cuspidate spine; ICHUM, Invertebrate Collection at the Hokkaido University Museum, Sapporo, Japan; ld10, length of laterodorsal spine of segment 10; lost, spine missing but anchoring pit existing; ltas, length of lateral terminal accessory spine; lv1, length of lateroventral spine of segment 1; md1, length of middorsal spine on segment 1; mts, midterminal spine; n. a., data not available; s1, length of segment 1; sw8, standard width of segment 8; TL, trunk length; USNM, catalogue number of United States National Museum; vl2, length of ventrolateral spine of segment 2.

Species	*C. setoensis*	*C. setoensis* (specimens with cuspidate spine on segment 4)				
Specimen	USNM 1490850	USNM 1491399	USNM 1490844	USNM 1490845	USNM 1490857	ICHUM 5836
Sex	♀	♂	♂	♂	♂	♂
Character/location	Japan	East China Sea	Japan	Japan	Thailand	Japan
TL	234	324	343	281	271	321
s1	19	19	17	21	31	18
s2	28	30	30	33	25	31
s3	31	31	31	33	29	30
s4	33	34	34	36	29	32
s5	34	35	36	36	30	34
s6	34	34	39	38	32	36
s7	34	35	38	41	33	38
s8	36	37	39	43	35	39
s9	39	39	39	41	34	44
s10	26	27	25	29	28	29
s11	13	19	16	16	21	19
sw8	79	74	76	81	75	69
sw10	55	56	54	61	58	57
md1 (ac)	28	36	34	45	30	35
md2 (ac)	32	28	36	n. a.	27	broken
md3 (ac)	31	31	37	49	32	broken
md4 (ac)	30	30	40	48	30	34
md5 (ac)	34	33	41	51	29	36
md6 (ac)	37	32	39	56	33	39
md7 (ac)	37	32	42	54	34	36
md8 (ac)	36	36	44	55	32	38
md9 (ac)	50	34	48	broken	36	43
md10 (ac)	no spine	34	51	65	31	51
ld10 (ac)	no spine	28/29	46/broken	broken/59	35/37	49/48
mts (ac)	88	77	82	broken	111	86
lv1 (ac)	35/33	34/31	39/n. a.	48/46	37/35	34/33
vl2 (cu)	14/14	no spine	15/n. a.	n. a./18	15/n. a.	16/lost
lv2(ac)	31/36	29/31	26/34	42/46	37/31	31/32
lv3 (ac)	31/31	32/30	37/n. a.	n. a./44	34/36	32/30
lv4 (ac)	32/34	30/29	39/broken	46/51	38/32	33/32
la4 (cu)	no spine	14/14	16/n. a.	21/20	16/18	15/n. a.
vl5 (cu)	17/lost	16/18	21/n. a.	20/24	18/18	17/n. a.
lv5 (ac)	35/34	31/30	43/34	44/44	37/37	33/broken
lv6 (ac)	31/34	31/29	41/42	50/49	37/38	broken/33
lv7 (ac)	34/34	30/30	39/34	49/50	34/39	34/32
lv8 (ac)	34/34	27/29	38/broken	49/broken	31/31	34/32
la8 (cu)	23/24	31/24	28/lost	26/28	18/21	29/29
vl9 (cu)	16/15	19/19	18/16	21/21	16/21	21/n. a.
lv9 (ac)	41/41	29/30	42/broken	56/56	34/37	37/39
ltas (ac)	181/184	broken/169	178/176	221/216	197/198	179/177

Juveniles. Three specimens mounted for light microscopy represent three different juvenile stages recognizable by their thin cuticle without a cuticular flap but with postmarginal spicula (Fig. 23A, D; Table 1). Short cuticular hairs are distributed irregularly on the cuticle. An acicular spine occurs at least middorsally on segments 1–10, midterminally on segment 11, lateroventrally on segments 1–9, and lateral accessorily on segment 11 (= lateral accessory terminal spine). A cuspidate spine exists ventrolaterally on segments 2, 5 and 9 and lateral accessorily on segment 8. The protonephridial opening is located sublaterally on segment 9 (Fig. 23G).

In the earliest stage (USNM 1490851, trunk length 152 µm, length lateral terminal accessory spine 72 µm, length midterminal spine 53 µm), segments 1–9 are separated from each other and from a still fused segment 10 + 11 (Fig. 23A, B). A sensory spot elevated above the cuticular surface is found at least ventromedially on segment 1, ventrolaterally on segment 11, sublaterally on segments 5–7, midlaterally on segments 1 and 2, laterodorsally on segment 2, subdorsally on segment 11 (twice, behind each other), and paradorsally on segments 1 (almost subdorsally), 4–6, 8 and 9 (Fig. 23A, B). In addition to the spines mentioned before, a lateroventral acicular spine occurs on segment 10 (Fig. 23B).

A later juvenile stage (USNM 1490852, trunk length 191 µm, length lateral terminal accessory spine 106/104 µm, length midterminal spine 60 µm, standard width on segment 7 49 µm) shows 11 segments separated from each other (Fig. 23D). Segments reveal a single sternal plate (Fig. 23D, E). Each segment reveals a midventral area with thicker short cuticular hairs bordered by the attachment area of the dorsoventral muscles which is devoid of hairs (Fig. 23E). A sensory spot elevated above the cuticular surface is found at least ventromedially on segments 1, 4 and 69, ventrolaterally on segment 11, sublaterally on segments 5–7 and 9, midlaterally on segments 1 and 2, laterodorsally on segments 2 and 5, subdorsally on segments 10 and 11, and paradorsally on segments 1 (almost subdorsally), 2, 46, 8 and 9. In addition to the spines mentioned above, a lateroventral acicular spine occurs on segment 10 (Fig. 23D).

The latest juvenile stage (USNM 1490853, trunk length 245 µm, length lateral terminal accessory spine 129/132 µm, length midterminal spine 73 µm, standard width on segment 7 69 µm) reveals sternal plates on segments 2–10 (Fig. 23F). A sensory spot elevated above the cuticular surface is found at least ventromedially on segments 1–9, ventrolaterally on segment 11, lateroventrally on segment 10, sublaterally on segments 1–3, 5–7 and 9, midlaterally on segments 1 and 2, laterodorsally on segments 2–9, subdorsally on segments 10 and 11, and paradorsally on segments 1 (almost subdorsally), 2, 4–6, 8 and 9. In addition to the spines mentioned for the other specimens, a sublateral acicular spine occurs on segment 10 (Fig. 23F, G). The position of the latter two spines on segment 10 probably indicates that the juvenile stage would have moulted to a male with a middorsal and a laterodorsal spine on segment 10 based on unpublished information about several late juvenile stages of *C. shirleyi* **sp. nov.** moulting to a female or to a male (Neuhaus unpubl. obs.).

Original material of "*Condyloderes megastigma* Sørensen, Rho & Kim, 2010b"

(Figs 24–27; Tables 1, 2, 7)

Material examined. Holotypic female (ZMUC-KIN-250) and paratypic female (ZMUC-KIN-251; previously identified as male) mounted for light microscopy as well as SEM images of three females, one of them with protruded introvert, two specimens previously identified as males (Fig. 1; Table 1).

Description

Head. The mouth cone reveals longitudinal structures between outer and inner oral styles, which most certainly represent a mouth cone weir. At its anterior end, the mouth cone reveals 9 outer oral styles, which appear to be collapsed around the partly protruded inner foregut structures, but each style is separated from its neighbouring style. Each style is broader over about three quarters of its length and appears filamentous in the apical part (for comparison see Sørensen *et al.* 2010b, fig. 4A). Neighbouring outer oral styles do not seem to alternate in length. The basal third of an outer oral style shows numerous spinose processes, which appear as longitudinal ridges, because most processes are collapsed on the style, probably an artefact from SEM preparation. Inner oral styles are not clearly visible in the SEM specimen with its mouth cone protruded but exist in the specimens mounted for light microscopy.

The introvert bears one ring of primary spinoscalids, five rings of spinoscalids, and one ring of trichoscalids. The 10 primary spinoscalids (ring 01) divide the introvert into 10 sectors. The primary spinoscalids are finger-like, with a broad basis showing a proximal, flat tuft of longer spinose processes projecting outwards, and a second slightly more distal bundle of shorter spinose processes. The distal part of the primary spinoscalid exhibits several transverse lines near its blunt end and is densely covered with regularly arranged, tiny cuticular hairs. The spinoscalids of rings 02–06 are formed by two parts as well: a proximal basis with fringes at its margin, and a distal, needle-like, pointed shaft covered with short hairs. Ring 02–06 spinoscalids are shorter than the primary ones. The spinoscalids are in principal arranged as reported earlier (Sørensen *et al.* 2010b, fig. 3), but we are not sure whether or not a gap exists between subsequent rings of spinoscalids in ring 4 of odd sectors and in ring 5 of even sectors as reported previously. The cuticle between spinoscalids shows numerous tiny cuticular knobs.

The 14 trichoscalids are associated with the placids except for the narrow paraventral placid on either side, where no trichoscalid occurs (Figs 25A, B, 26A). Each trichoscalid originates from a cuticular trichoscalid plate, which shows about the same size as the base of a trichoscalid. Each trichoscalid is accompanied anteriorly by two filamentous, pointed appendages, which are much thinner than the trichoscalid (Fig. 25B). The trichoscalids are covered by numerous cuticular hairs. Inner septa are not recognizable in the appendages.

Neck. The 16 placids of the neck are arranged in a specific way, based on observations of two specimens mounted for SEM and two specimens mounted for light microscopy. The broader midventral placid (12–14 µm width at base x 12–13 µm height; measurements based on two specimens) is neighboured by two narrower placids (6–7 µm width x 10–13 µm height), and alternatingly a broader (12–13 µm width x 12–15 µm height) and a narrower placid (7 µm width x 12–13 µm height) (Figs 24, 25A, B, 26A, C). All placids reveal cone-like condyles arranged in two rows in the narrower placids and in three rows in the broader placids. Each narrower placid shows one apical and one basal condyle. Each broader placid displays two condyles each in the apical, in the intermediate, and in the basal row (Figs 24,25A, B, 26A, C). The midventral placid possesses three condyles in the apical and in the basal row as well as two in the intermediate row (Figs 24A, 25A; Table 7). The condyles display often an irregular surface and sometimes seem to be partly split into two apical cones, especially in specimens mounted for SEM. This may represent a preparation artefact resulting in a partly collapsed cuticular condyle. A small and narrow interstitial placid of irregular size can be observed between every two neighbouring regular placids in light microscopy (Fig. 25B). SEM images reveal that these interstitial placids are in fact cuticular folds and, therefore, represent different structures than the placids, which consist of a thickened cuticular plate with cuticular condyles or cones on the surface.

Trunk. The trunk is divided into 11 segments, which appear triangular in cross-section when observed from anteriorly by SEM. Whereas the cuticle of the first trunk segment is ring-like without any articulation, the cuticle of segments 2–10 possesses both a midventral and a lateral articulation resulting in a tergal and two sternal plates (Figs 24A, 25, 26C–E, 27); the lateral articulation becomes clearly recognizable only in light microscopy (Figs 25E, F, 27; for male see Fig. 28A–D). In segment 11, a tergal and a single sternal plate exist (Fig. 27B, C; for male see Fig. 28B).

The anterior margin of the first trunk segment is smooth but reveals short cuticular hairs (Figs 24, 25A, 26A, C). At the anterior margin of all segments and at the midventral margin of the sternal plates of segments 2–10, the cuticle thickens towards the interior of the animal and forms a pachycyclus (Figs 24–27). Ventrally, the tergal and sternal plate form a strongly sclerotized peg and socket articulation (Fig. 27A). Light microscope observations reveal a variable number of easily recognizable, irregularly arranged, small canals, which extend from the epidermis into each cuticular trunk plate (Figs 25E, 26A, B) and do not seem to be connected with gland cells. A comparison with SEM images does not indicate that the canals penetrate the trunk cuticle completely. At the posterior end of all segments, the free flap overlapping the subsequent segment terminates in a primary pectinate fringe. The basal part of the free flap reveals fine, regularly arranged, longitudinal bars inside the flap (Figs 24, 25A, C, D, 26C–E; for male see Fig. 28A–D, F). These bars elevate slightly above the surface in favourite SEM images. The free flap is missing where the spines originate. In the midventral to ventromedial area of segment 1, the posterior margin of the segment shows a considerably shorter free flap with a reduced primary fringe and ends more anteriorly than the ventrolateral margin resulting in a peculiar outline (Figs 24A, 25A, 26C; for male see Fig. 28A). The teeth of the primary pectinate fringe are considerably shorter ventrally on segments 10 and all around segment 11 (Figs 24, 25E).

Segment 1 reveals little elevated, irregularly arranged cuticular ridges especially at the anterior margin of the segment as well as a midventral to ventromedial area with short, stronger sclerotized triangular scale-like hairs (Figs 25A, 26C). The surface of the cuticle of segments 2–10 reveals in the anteriormost one fourth little elevated cuticular ridges (Fig. 25D–F; for male see Fig. 28C). The remaining part of segments 2–10 as well as in segment 11 are covered with irregularly distributed, triangular cuticular scale-like hairs, especially the second fourth of the cuticle of each segment (Figs 25A, C, D, 26C–E, 27B). Stronger scale-like hairs appear in a middorsal area on segment 10. Numerous short cuticular hairs occur middorsally and laterally on the trunk cuticle anterior to the middorsal and lateroventral spines of segments 2–9 in a narrow area (Fig. 26C, D; for male see Fig. 28F).

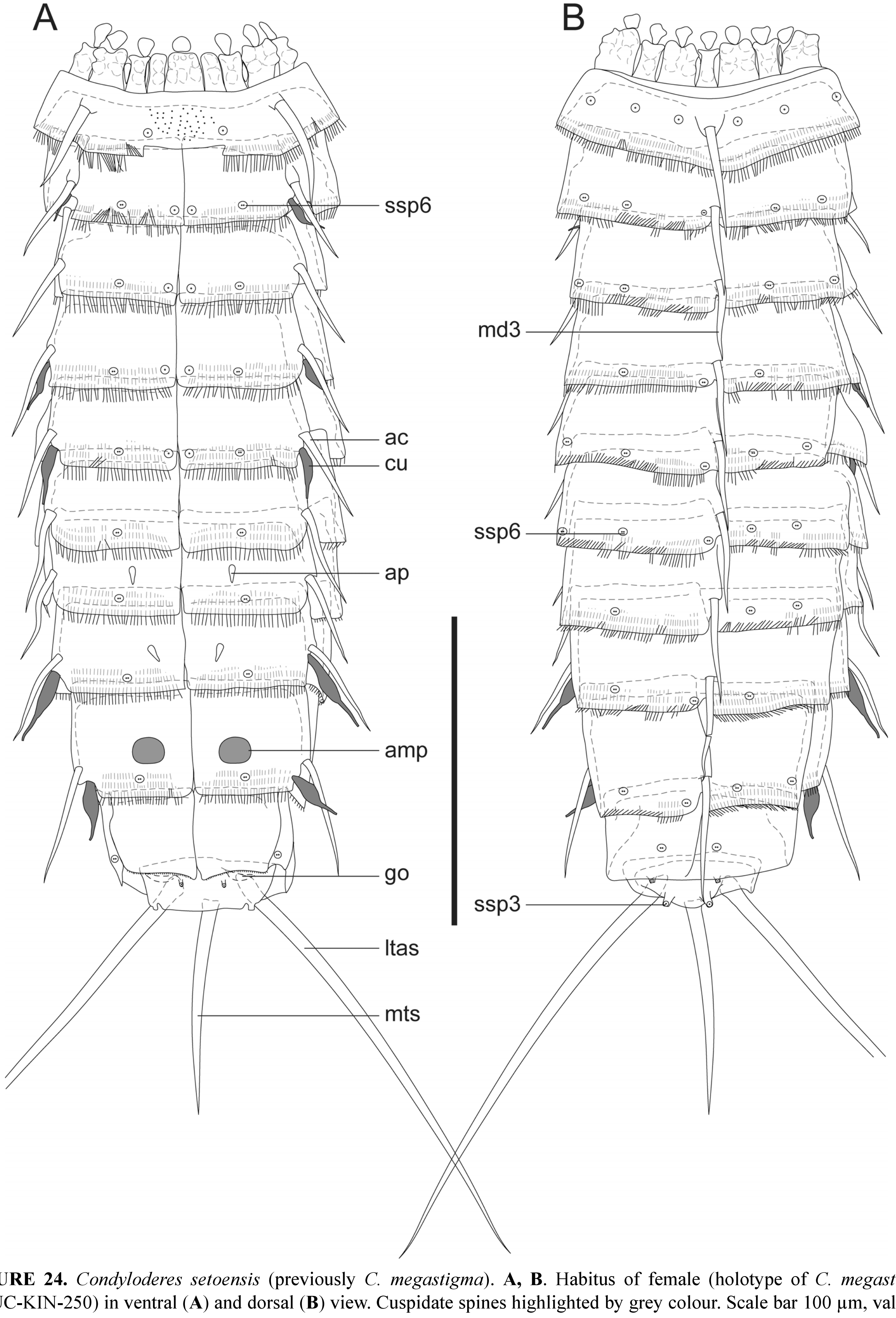


FIGURE 24. *Condyloderes setoensis* (previously *C. megastigma*). **A, B**. Habitus of female (holotype of *C. megastigma*, ZMUC-KIN-250) in ventral (**A**) and dorsal (**B**) view. Cuspidate spines highlighted by grey colour. Scale bar 100 µm, valid for **A** and **B**. Abbreviations: ac, acicular spine; amp, female-specific area of micropapillae; ap, female-specific appendage; cu, cuspidate spine; gp, gonopore; ltas, lateral terminal accessory spine; md3, middorsal spines of segment 3; mts, midterminal spine; ssp3, type-3 sensory spot.

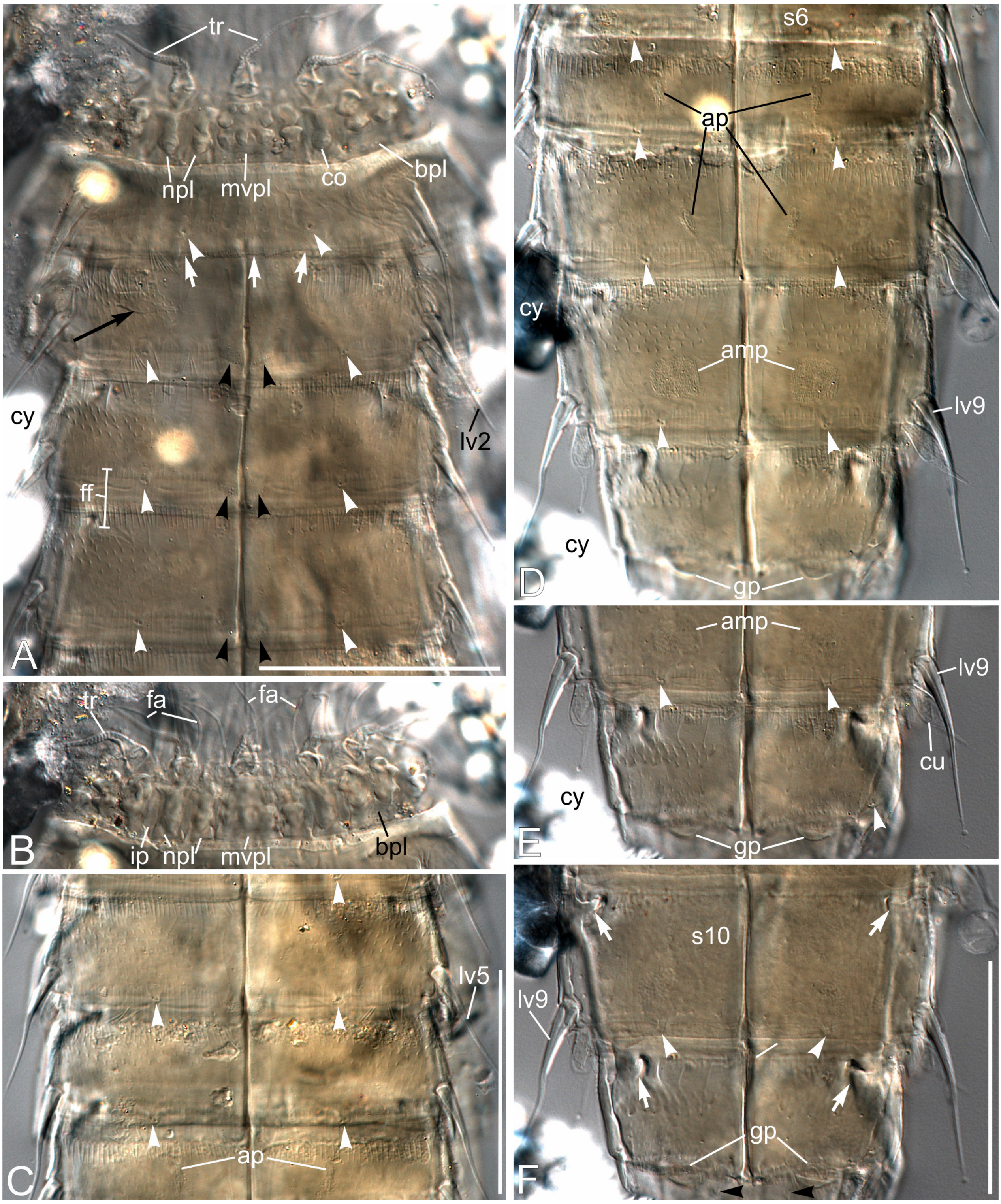


FIGURE 25. *Condyloderes setoensis* (previously *C. megastigma*), female (holotype of *C. megastigma*, ZMUC-KIN-250), ventral view, DIC. **A.** Neck and segments 1–4, right ventrolateral spine of segment 2 dislocated from attachment site (black arrow); white arrows point to reduced pectinate fringe of free flap; black arrowheads mark potential type-1 sensory spots. **B.** Neck with placids and interstitial placids. **C.** Segments 5 and 6. **D.** Segments 7–10. **E.** Segment 10. **F.** Segments 9 and 10; arrows mark processes of tergal plates articulating with sockets of sternal plates; black arrowheads indicate potential type-5 sensory spots. Note gonopores at different focal levels in **DF**. White arrowheads in **A** and **C–F** mark type-6 sensory spots. Scale bar in **A** 50 µm, valid for **A** and **B**. Scale bar in **C** 50 µm. Scale bar in **F** 50 µm, valid for **D–F**. Abbreviations: amp, female-specific area of micropapillae; ap, female-specific appendage; bpl, broader placid; co, condyle of placid; cu, cuspidate spine; cy, crystal in mounting medium; fa, filamentous appendage at trichoscalid; ff, free flap; gp, gonopore; ip, interstitial placid; mvpl, midventral placid; lv2, lateroventral spine of segment 2; npl, narrower placid; s6, segment 6; tr, trichoscalid.

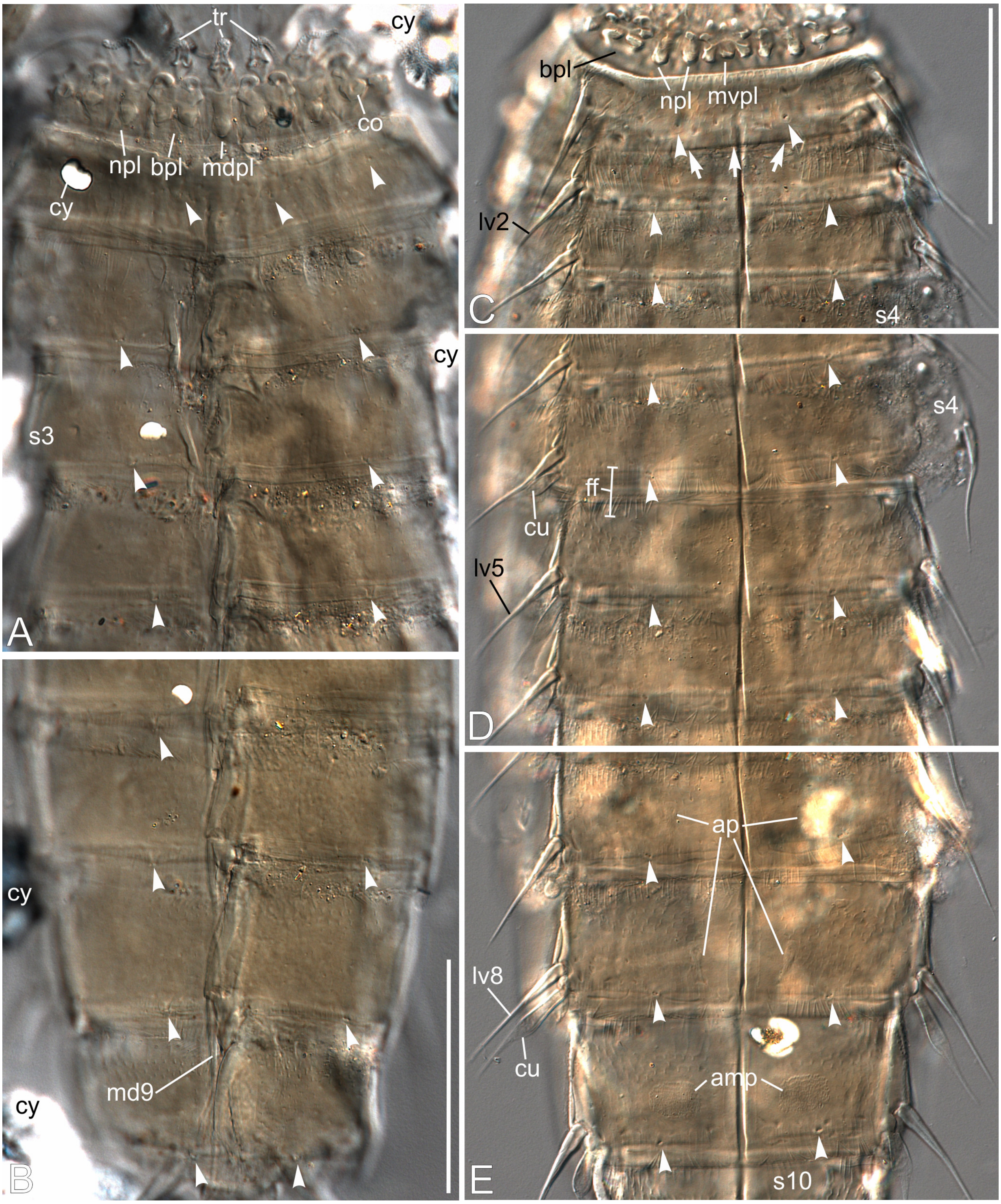


FIGURE 26. *Condyloderes setoensis* (previously *C. megastigma*), female (holotype of *C. megastigma*, ZMUC-KIN-250, **A**, **B**) in dorsal view and female (paratype of *C. megastigma*, ZMUC-KIN-251, **C–E**) in ventral view, DIC. **A.** Neck and segments 1–4. **B**. Segments 8–10. **C.** Neck and segments 1–3; arrows mark reduced pectinate fringe of free flap. **D.** Segments 4–6. **E.** Segments 7–9. White arrowheads in **A–E** mark type-6 sensory spots. Scale bar in **B** 50 µm, valid for **A** and **B**. Scale bar in **C** 50 µm, valid for **C–E**. Abbreviations: amp, female-specific area of micropapillae; ap, female-specific appendage; bpl, broader placid; co, condyle of placid; cu, cuspidate spine; cy, crystal in mounting medium; fa, filamentous appendage at trichoscalid; ff, free flap; gp, gonopore; md9, middorsal spine of segment 9; mdpl, middorsal placid; mvpl, midventral placid; lv2, lateroventral spine of segment 2; npl, narrower placid; s3, segment 3; tr, trichoscalid.

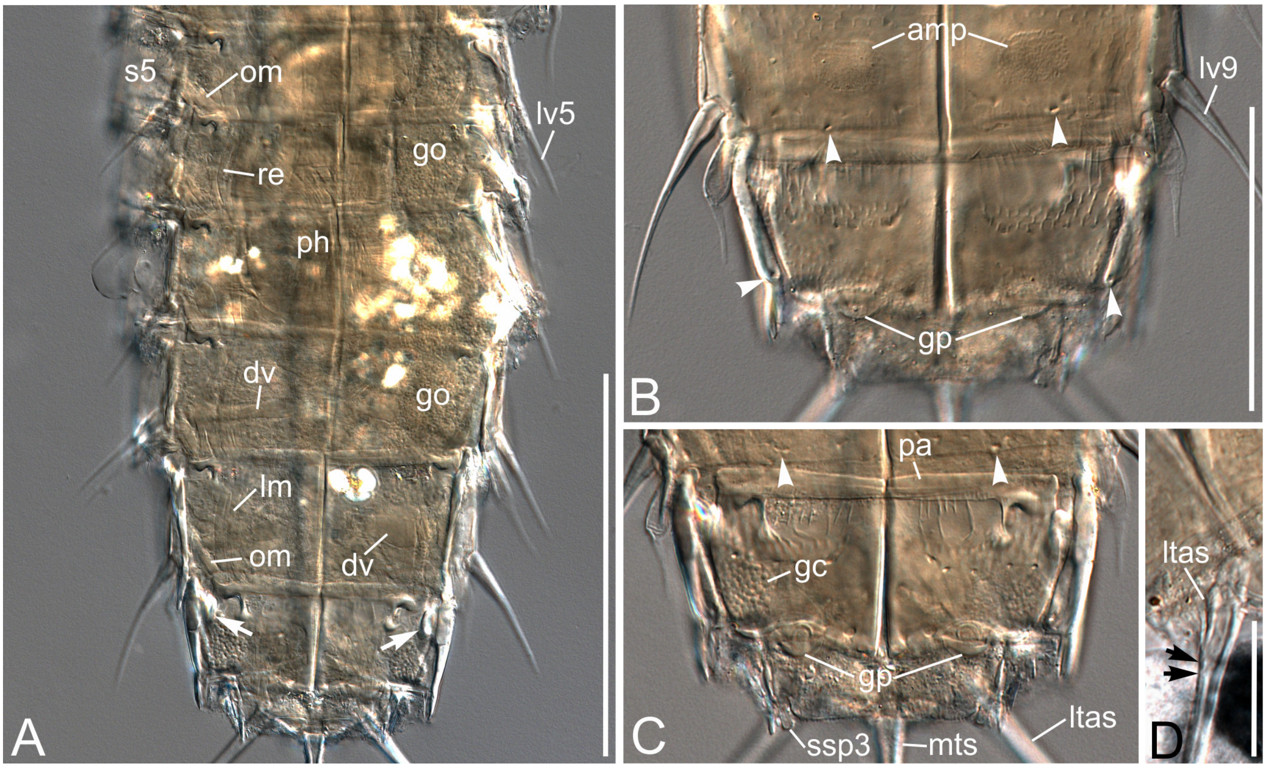


FIGURE 27. *Condyloderes setoensis* (previously *C. megastigma*), female (paratype of *C. megastigma*, ZMUC-KIN-251, **A–C**) and female (holotype of *C. megastigma*, ZMUC-KIN-250, **D**), in optical section (**A**) and ventral view (**B**–D), DIC. **A.** Segments 5–11; arrows mark processes of tergal plate articulating with socket of sternal plate. **B, C**. Segments 10 and 11; note gonopores at different focal levels; arrowheads mark type-6 sensory spots. **D.** Lateral terminal accessory spine with two thin areas (arrows). Scale bar in **A** 100 µm. Scale bar in **B** 50 µm, valid for **B** and **C**. Scale bar in **D** 20 µm. Abbreviations: amp, female-specific area of micropapillae; dv, dorsoventral muscle; gc, gland cell; go, gonad; gp, gonopore; lm, longitudinal muscle; ltas, lateral terminal accessory spine; lv5, lateroventral spine of segment 5; mts, midterminal spine; om, oblique muscle; pa, pachycyclus; ph, pharynx; re, retractor muscle; s5, segment 5; ssp3, type-3 sensory spot.

All sensory spots elevate clearly above the surface of the trunk cuticle and display on the outside cuticular micropapillae surrounding one or two pores. The distribution of sensory spots is bilateral symmetrical. Type-3 sensory spots occur ventrolaterally next to the lateral terminal accessory spine and subdorsally on segment 11 (Figs 24, 27C; for male see Fig. 28B, F; Table 2). A sensory spot ventromedially on segment 11 may represent a type-6 spot (Fig. 24A). A type-6 sensory spot occurs ventromedially on segments 1 (slightly more paraventrally) and on segments 2–9, lateroventrally on segment 10, sublaterally on segments 1–3, 5–7 and 9, midlaterally on segments 1 and 2, laterodorsally on segments 2–9, subdorsally on segment 10, and paradorsally on segments 1 (almost subdorsally), 2, 4–6, 8 and 9 (Figs 24–26; for male see Fig. 28A–F; Tables 2, 7). Possibly, the paraventral micropapillate area on the sternal plates of segments 2–5 represent sensory spots as well. They do not elevate above the surface of the cuticle like the type-6 sensory spots, pores and ducts could be traced on some segments (Figs 24A, 25A; Tables 2, 7). We assign the potential sensory spots to type-1 with a question mark.

The nephropore is located slightly dorsally of the sublateral sensory spot at the posterior margin of segment 9 (Table 2).

On each sternal plate of segments 7 and 8, each specimen reveals a cone-like (sensory? glandular?) ventromedial appendage, which gives the impression of an extremely elongated sensory spot covered by numerous cuticular micropapillae (Figs 24A, 25C, D, 26E; Table 2). At its base, each structure shows a sclerotized cuticular duct penetrating the trunk cuticle. The duct seems to end in a cavity. The structures occur ventromedially on segment 7 and slightly more paraventrally on segment 8 (Figs 24A, 25D, 26E).

Each sternal plate of segment 9 possesses a more or less circular area with prominent cuticular micropapillae. Pores and ducts penetrating the trunk cuticle do not seem to exist in this area (Table 2). The holotypic female reveals a gland cell at the outer margin of the area of micropapillae.

Segments 1–9 bear a middorsal and on each side a lateroventral spine, and segment 11 shows such a spine in a lateral accessory position (= lateral terminal accessory spine) and as the midterminal spine (Figs 24, 25A, C–F, 26, 27;

Table 2); these spines are hirsute and acicular. Each middorsal and lateroventral spine reveals a sclerotized thicker base and tapers apically. The lateral terminal accessory spine displays at its base two thin areas (Fig. 27D; for male see Fig. 28G). A lateroventral spinose process on segment 11 may represent the anlage of the lateral terminal spine. A short hirsute cuspidate spine with a basal thickened and an apical thinner part appears ventrolaterally on segments 2, 5 and 9, in a lateral accessory position on segments 4 and 8 (Figs 24, 25A, C–E, 26C–E, 27; Table 2). Whereas the acicular spines appear clearly sclerotized, the cuspidate spines are almost translucent in light microscope mounts.

At the anterior margin of each sternal plate of segment 11 of both the holotypic and paratypic female, a large circular gonopore with a sclerotized anterior margin, a short strongly sclerotized cuticular canal, and a posterior flap-like elevation of cuticle shaped like a half-disc is located (Figs 24A, 25E, F, 26B, C). Gonads can be recognized in both specimens mounted for light microscopy, but eggs could not be identified (Fig. 27A).

Variation. The paratypic female and two specimens mounted for SEM lack the ventrolateral cuspidate spine on segment 2 (Fig. 26C). There is no indication that the spine was lost during preparation, because no modified attachment area was found (see chapter Discussion).

Comparison with previous description

We regard all specimens of the original description of this species as females instead of females and males (see chapter Discussion). Our findings further differ from the original description (Sørensen *et al*. 2010b) in that (1) all sensory spots are assigned to type 6 rather than to type 1except the ones subdorsally and ventrolaterally on segment 11 (type-3 sensory spot) and paraventrally on segments 2–5 (type-1 sensory spot?), (2) the area with micropapillae paraventrally on segments 2–5 may or may not represent a sensory spot, (3) a sensory spot on segment 1 is regarded as paradorsal (almost subdorsally) in position instead of subdorsal, (4) a type-6 (?) sensory spot is located ventromedially on segment 11 instead that it is absent, (5) cuspidate spines occur ventrolaterally on segments 2, 5 and 9 and in lateral accessory position on segments 4 and 8 instead of lateroventrally on the respective segments, (6) the lack of a ventrolateral cuspidate spine on segment 2 in two specimens (including the paratype) out of five specimens is interpreted as variation within the species rather than as a sex-specific character (see chapter Discussion), (7) a protonephridial opening exists on segment 9 sublaterally instead of its lack in that position, (8) the ventromedial “giant sensory spot” on segment 9 is here termed more neutrally as “area of micropapillae”, because no pores or ducts penetrating the cuticle were found which are typical of sensory spots, and (9) the lateral terminal accessory spine displays at its base two thin areas instead of the lack of these thin areas. We are not sure whether or not a gap exists between subsequent rings of head spinoscalids in ring 4 of odd sectors and in ring 5 of even sectors as reported previously.

Additional material of “*Condyloderes megastigma*” (males and juvenile)

(Fig. 28; Tables 4, 7)

Material examined. Three male specimens from three stations around Japan (USNM 1490844, 1490845; ICHUM 5836), one male specimen from the East China Sea (USNM 1491399), one male specimen from Thailand (USNM 1490857), and SEM images of one uncatalogued late juvenile stage from the Korea Strait, the latter previously identified as *C*. cf. *paradoxus* (Fig. 1; Table 1).

Description

This chapter refers to specimens with a lateral accessory spine on segment 4, which represented one of the major characters to distinguish *C. megastigma* from *C. setoensis* in previous publications. For morphological measurements and data see Tables 2, 4, and 7.

Males. The five specimens agree in almost all characters with the female holotype of “*C. megastigma*” but are males. However, a paraventral area of micropapillae on segments 2–5 possibly representing a type-1 sensory spot was not found. Data about the size of placids are available for the specimen from the East China Sea (midventral placid: 14 µm width x 14 µm height, narrower placid: 5–9 µm width x 11 µm height, broader placid: 12–14 µm width x 14 µm height). The male differs from the female in the lack of ventromedial appendages on segments 7 (Fig. 28D) and 8 *versus* their existence in the female, the lack of the ventromedial area of micropapillae on segment 9 *versus* its existence in the female, the existence of a ventromedial gland cell outlet on segment 10 (Fig. 28B) *versus* its lack in the female, a ventrolateral, curved, sclerotized anterior margin of segment 11 where the male gonopores are expected to occur (Fig. 28B) *versus* the existence of gonopores with a strongly sclerotized duct anteriorly on segment 11 in the female, and the existence of a thin middorsal and laterodorsal spine on segment 10 (Fig. 28F) *versus* their lack in the female. In one male (ICHUM 5836), at least some filiform appendages anterior of the trichoscalids show inner septa.

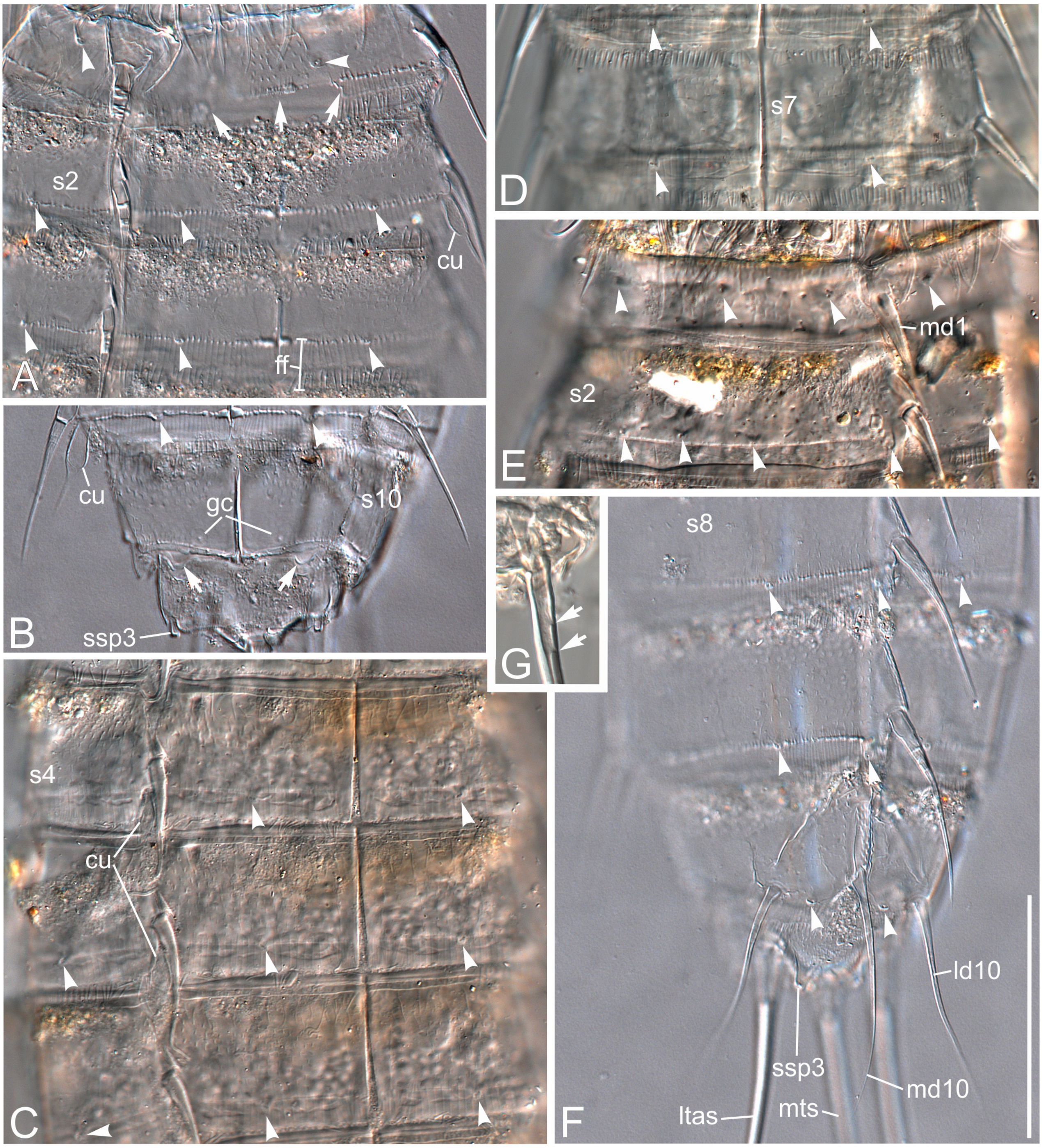


FIGURE 28. *Condyloderes setoensis*, males with lateral accessory cuspidate spine on segment 4, (ICHUM 5836, exuvia after DNA extraction, **A**, **B**, **F**; USNM 1490844, **C**, **E**; USNM 1490845, **D**, **G**), ventral view (**A–D**), dorsal view (**E**, **F**), and optical section (**G**), DIC. **A.** Segments 13; arrows mark area of reduced free flap on segment 1. **B.** Segments 10 and 11; arrows point to the sclerotized anterior margin of segment 11 where male gonopores are expected to occur. **C.** Segments 4–6; note little elevated longitudinal ridges anteriorly on segments. **D.** Segment 7; note lack of ventromedial appendage. **E.** Segments 1 and 2. **F.** Segments 9–11. **G.** Lateral terminal accessory spine with two thin areas (arrows). Arrowheads in **A–F** mark type-6 sensory spots. Scale bar in **F** 50 µm, valid for **A–G**. Abbreviations: ff, free flap; gc, gland cell outlet with intracuticular cavity; ld10, laterodorsal spine on segment 10; ltas, lateral terminal accessory spine; md1, middorsal spine on segment 1; mts, midterminal spine; s2, segment 2; ssp3, type-3 sensory spot.

Variation. One male form the East China Sea (USNM 1491399) lacks the ventrolateral cuspidate spine on segment 2. Another male (USNM 1490845) misses the ventromedial sensory spot on segment 5 and lacks the left lateral accessory cuspidate spine on segment 8 but possesses a left ventrolateral cuspidate spine on that segment instead.

Juvenile. A juvenile specimen from the Korea Strait mounted for SEM possesses 11 segments separated from each other. Segments 1 and 11 consist of a single plate, segments 2–10 reveal two sternal plates. A free flap is missing and postmarginal spicula exist. The pattern of sensory spots and spines agrees with that of a female but in addition an acicular spine occurs middorsally and lateroventrally on segment 10. The position of the latter two spines on segment 10 probably indicates that the juvenile stage would have moulted to a female with no spines on segment 10 based on unpublished information about several late juvenile stages of *C. shirleyi* **sp. nov.** moulting to a female or to a male (Neuhaus unpubl. obs.).

Re-description of *Condyloderes storchi* Higgins, 2004 in Martorelli & Higgins, 2004

(Figs 29–31; Tables 1, 2, 7)

Condyloderes storchi Higgins, 2004 in Martorelli & Higgins, 2004: pp. 86–88, figs 2–5, tables 1, 2.

Condyloderes storchi—Sørensen & Pardos 2008: pp. 53, 54 [species erroneously cited as *C. storchi* Martorelli & Higgins, 2004].—Shirley 2009: p. 1129 [species erroneously cited as *C. storchi* Martorelli & Higgins, 2004].—Neuhaus *et al*. 2010: p. 468.—Sørensen *et al*. 2010b: pp. 235, 241 [species erroneously cited as *C. storchi* Martorelli & Higgins, 2004].—Neuhaus 2013, pp. 297, 332, tables 6, 12.—Adrianov & Maiorova 2016: pp. 11, 18 [species erroneously cited as *C. storchi* Martorelli & Higgins, 2004].

Diagnosis. Neck placids with condyles in one basal row in narrower placids and three rows in broader placids; narrower placids with one basal condyle; broader placids with two condyles each in apical, intermediate, and basal row; midventral placid with three apical and basal condyles and two in intermediate row; acicular spine middorsally on segments 1–10, midterminally on segment 11, lateroventrally on segments 1–9, and laterodorsally on segment 10; cuspidate spine ventrolaterally on segments 5 and 9, lateral accessorily on segments 1, 4 and 8, and middorsally on segments 5 and 7; type-5 (?) sensory spot ventromedially on segment 11; type-6 sensory spot ventromedially on segments 1 (slightly more paraventrally) and 2–9, lateroventrally on segment 10, sublaterally on segments 1–3, 5–7 and 9, midlaterally on segments 1 and 2, laterodorsally on segments 1–9, subdorsally on segment 10, and paradorsally on segments 1 (almost subdorsally), 2, 4–6, 8 and 9.

Material examined. Holotypic male (USNM 1025879) mounted laterally (Fig. 1; Table 1).

Description

The specimen is covered by numerous droplets and particles of variable size making observations tedious. In addition, cuticular structures are weak and the micropapillae of the type-6 sensory spots not resolvable with light microscopy, probably both because of partial digestion in the stomach of the shrimp and because of the macerating power of chloral hydrate in Hoyer's mounting medium.

Head. At its anterior margin, the mouth cone carries outer oral styles with a thin cuticle. The outer oral styles appear to be collapsed around the partly protruded inner foregut structures (Fig. 30A). Inner oral styles were recognizable (Fig. 30A Inset).

The introvert bears one ring of primary spinoscalids, several rings of spinoscalids, and one ring of trichoscalids (Fig. 30A). The primary spinoscalids are finger-like, with a broad basis showing a proximal, flat tuft of longer spinose processes projecting outwards, and a second slightly more distal bundle of shorter spinose processes (Fig. 30A). Information about the remaining spinoscalids is too sparse to be mentioned here.

The 14 trichoscalids are associated with the placids (Fig. 30B) except for the narrow paraventral placid on either side, where no trichoscalid occurs. Each trichoscalid originates from a cuticular trichoscalid plate (Fig. 30B), which shows about the same size as the base of a trichoscalid. Each trichoscalid is accompanied anteriorly by two filamentous, pointed appendages, which are much thinner than the trichoscalid (Figs 30A, C, 31A).

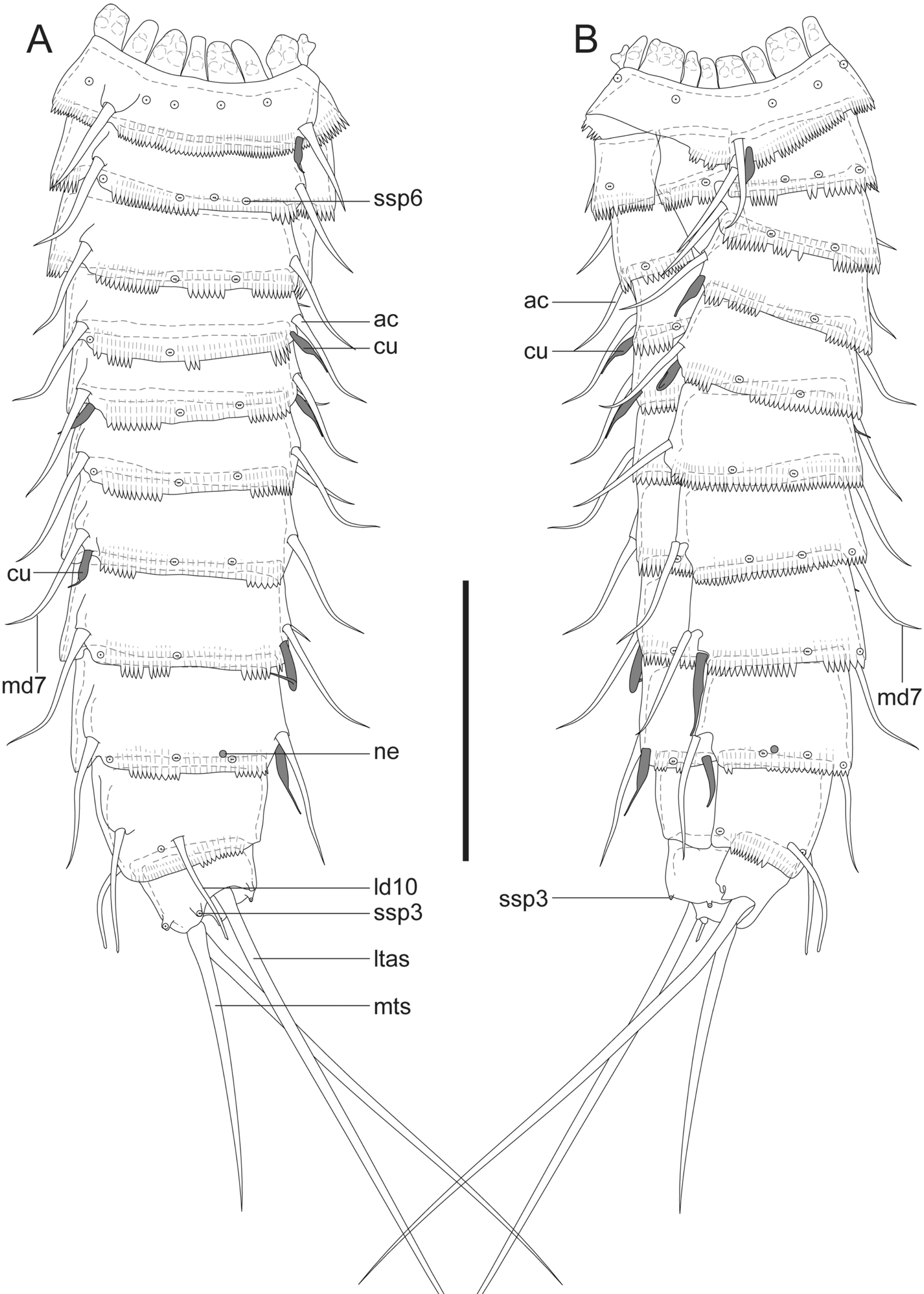


FIGURE 29. *Condyloderes storchi*. **A, B**. Habitus of holotypic male (USNM 1025879) from right (**A**) and ventrolateral-left side (**B**). Cuspidate spines highlighted by grey colour. Scale bar 100 µm, valid for **A** and **B**. Abbreviations: ac, acicular spine; cu, cuspidate spine; lf10, laterodorsal spine of segment 10; ltas, lateral terminal accessory spine; md7, middorsal spines of segment 7; mts, midterminal spine; ne, protonephridial openings; ssp3, type-3 sensory spot.

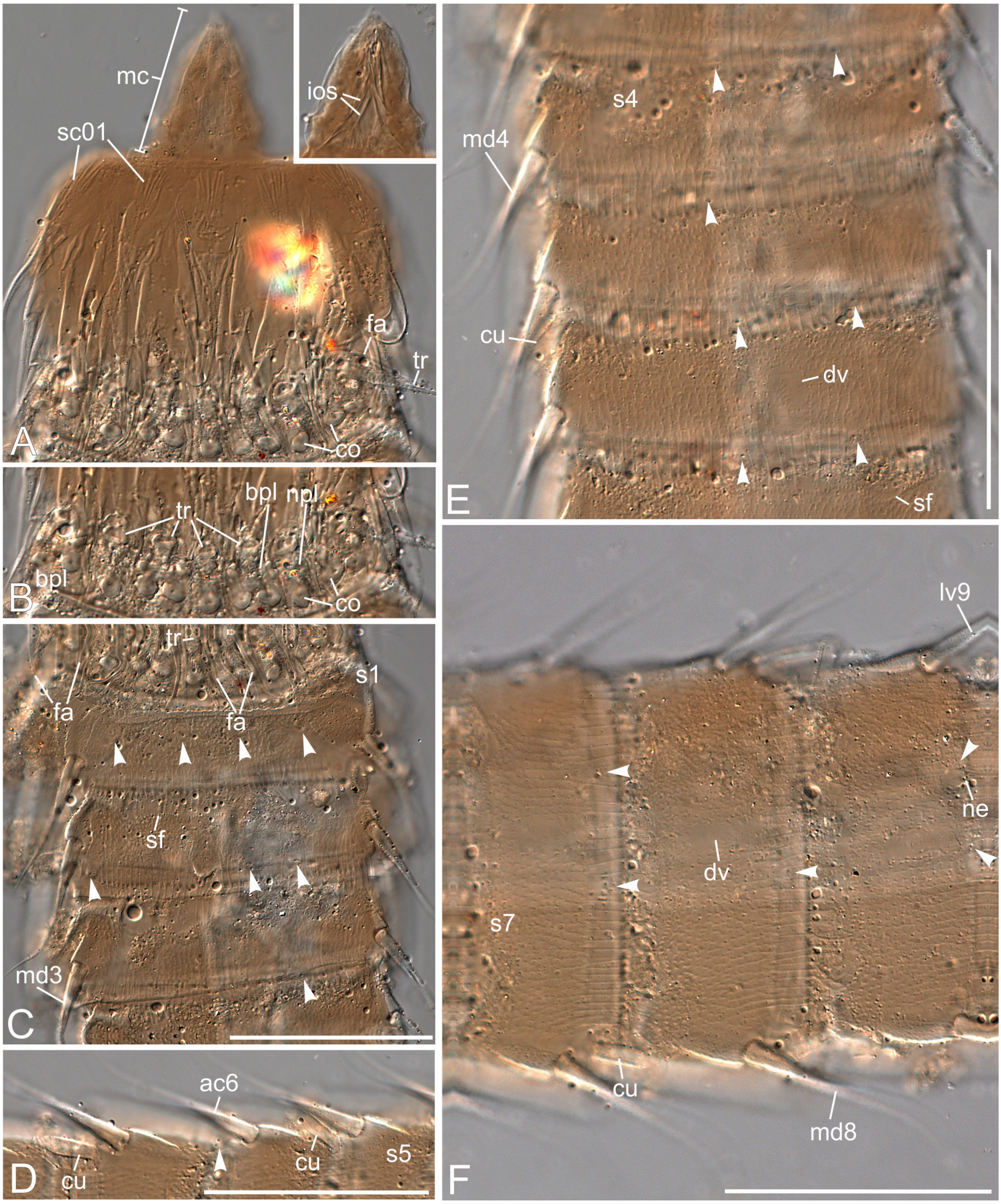


FIGURE 30. *Condyloderes storchi*, holotypic male (USNM 1025879) from right side, DIC. **A.** Head and neck with placids; note condyles of placids. Inset with inner oral styles. **B.** Neck, placids and basal plate of trichoscalids. **C.** Segments 1–3; extended focus image of four images. **D.** Dorsal part of segments 5–7. **E.** Segments 4–6; extended focus image of two images. **F.** Segments 7–9; extended focus image of five images. Notice middorsal cuspidate spine on segments 5 and/or 7 in **D–F**. Arrowheads in **C–F** mark type-6 sensory spots. Scale bar in **C**, **E**, and **F** 50 µm. Scale bar in **D** 50 µm, valid for **A**, **B**, and **D**. Abbreviations: ac6, acicular spine of segment 6; bpl, broader placid; co, condyle of placid; cu, cuspidate spine; dv, attachment area of dorsoventral muscle; ios, inner oral style; mc, mouth cone; md3, middorsal spine of segment 3; ne, protonephridial openings; npl, narrower placid; s1, segment 1; sc01, spinoscalid of ring 01; sf, secondary fringe; tr, trichoscalid or its basal plate.

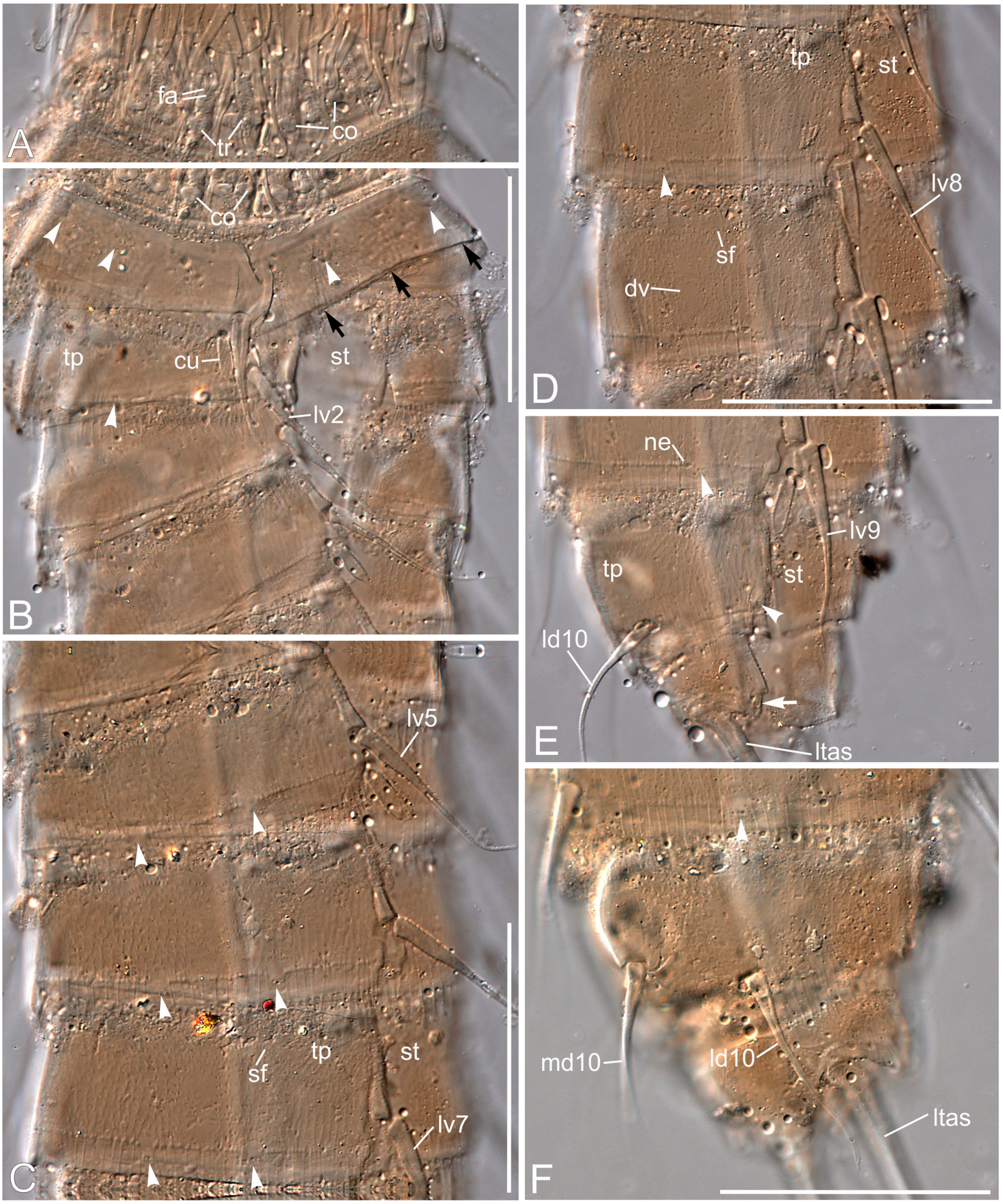


FIGURE 31. *Condyloderes storchi*, holotypic male (USNM 1025879) from ventrolateral-left (**A–E**) and right (**F**) side, DIC. **A.** Placids; note appendages of trichoscalids. **B.** Segments 1–4; arrows mark lack of free flap ventromedially on segment 1. **C.** Segments 5–7; extended focus image of two images. **D.** Segments 8 and 9; extended focus image of two images. **E, F.** Segments 10 and 11; arrow in **E** points to type-3 sensory spot. Arrowheads in **B–F** mark type-6 sensory spots. Scale bar in **B** 50 µm, valid for **A**, **B**, and **E**. Scale bar in **C**, **D**, and **F** 50 µm. Abbreviations: co, condyle of placid; cu, cuspidate spine; dv, attachment area of dorsoventral muscle; fa, appendage at trichoscalid; ld10, laterodorsal spine of segment 10; ltas, lateral terminal accessory spine; lv2, lateroventral spine of segment 2; md10, middorsal spine of segment 10; ne, protonephridial openings; sf, secondary fringe; st, sternal plate; tp, tergal plate; tr, trichoscalid.

Neck. The 16 placids of the neck are arranged in a specific way. The broader midventral placid (15 µm width at base x 14 µm height; measurements based on one specimen) is neighboured by two narrower placids (5–7 µm width x 10 µm height), and alternatingly a broader (13–14 µm width x 14–15 µm height) and a narrower placid (8–10 µm width x 9–12 µm height) (Figs 29, 30B). All placids reveal cone-like condyles arranged in one (?) or two rows in the narrower placids and in three rows in the broader placids (Figs 29, 30A–C; Table 7). Each narrower placid shows one basal condyle. One apical condyle is recognizable at least in the two narrower placids next to the midventral placid and possibly in the remaining narrower placids, too. Each broader placid displays two condyles each in the apical, intermediate, and basal row (Table 7). The midventral placid possesses three apical condyles, two in the intermediate row, and three in the basal row. A small and narrow interstitial placid of irregular size can be observed between each two neighbouring regular placids.

Trunk. The trunk is divided into 11 segments (Fig. 29). Whereas the cuticle of the first trunk segment is ring-like without any articulation, the cuticle of segments 2–10 possesses both a midventral and a lateral articulation resulting in a tergal and two sternal plates (Figs 29, 31B–E). In segment 11, a tergal and a single sternal plate exists (Fig. 30E).

The anterior margin of the first trunk segment is smooth (Figs 29, 30B, 31A). At the anterior margin of all segments and at the midventral margin of the sternal plates of segments 2–10, the cuticle thickens slightly towards the interior of the animal and forms a pachycyclus. A variable number of easily recognizable, irregularly arranged, small canals exist, which extend from the epidermis into each cuticular trunk plate (Fig. 31B, C) and do not seem to be connected with gland cells. At the posterior end of all segments, the free flap overlapping the subsequent segment terminates in a primary pectinate fringe consisting of short, broad cuticular teeth. These teeth are missing in many irregularly distributed positions (Fig. 29), most probably because they were lost either in the stomach of the shrimp or during preparation. The basal part of the free flap reveals fine, regularly arranged, longitudinal bars inside the flap (Figs 29, 30C, E, F, 31B–F). The free flap is missing where the spines originate. In the midventral to ventromedial area of segment 1, the posterior margin of the segment shows a considerably shorter free flap and ends more anteriorly than the ventrolateral margin resulting in a peculiar outline (Figs 29B, 31B).

The surface of the cuticle of all segments reveals anteriorly weak, longitudinal cuticular ridges. This area is bordered by short cuticular hairs arranged in a wavy line, the secondary fringe (Figs 30C, E, 31C, D. Subsequently, the cuticle is covered with irregularly distributed, cuticular hairs, which appear more densely arranged in the anterior rather than the posterior area (Figs 30C, E, F, 31B–F). More densely arranged, slightly longer cuticular hairs occur middorsally and laterally on the trunk cuticle anterior to the middorsal and lateroventral spines of all segments in a narrow area. Short cuticular hairs are missing in the midlateral attachment area of the dorsoventral muscles (Fig. 30E, F, 31C, D).

All sensory spots display on the outside an area appearing smooth in light microscopy surrounding one or two pores. The distribution of sensory spots is bilateral symmetrical. Type-3 sensory spots occur ventrolaterally next to the lateral terminal accessory spine and subdorsally on segment 11 (Fig. 29; Table 2). A sensory spot ventromedially on segment 11 may represent a type-6 spot. A type-6 sensory spot is located ventromedially on segments 1 (slightly more paraventrally) and on segments 2–9, lateroventrally on segment 10, sublaterally on segments 1–3, 5–7 and 9, midlaterally on segments 1 and 2, laterodorsally on segments 1–9, subdorsally on segment 10, and paradorsally on segments 1 (almost subdorsally), 2, 4, 6, 8 and 9 (Figs 29, 30C–F, 31B–F; Tables 2, 7).

The nephropore occurs slightly dorsally of the sublateral sensory spot at the posterior margin of segment 9 (Fig. 31E; Table 2).

Segments 1–9 bear a middorsal (also on segment 10) and on each side a lateroventral spine, and segment 11 shows such a spine in a lateral accessory position (= lateral terminal accessory spine) and as the long midterminal spine (Figs 29, 30C–F, 31B–F; Table 2); the spines are hirsute and acicular. Each middorsal and lateroventral acicular spine reveals a sclerotized thick base and a considerably thinner apical part. The lateral terminal accessory spine displays at its base at least one thin area. The middorsal and laterodorsal acicular spine on segment 10 are considerably thinner, more flexible, and less sclerotized basally than the lateroventral and middorsal spines of other segments (Figs 29A, 31E, F). A short hirsute cuspidate spine with a basal thickened and an apical thinner part appears ventrolaterally on segments 5 and 9, in a lateral accessory position on segments 1, 4 and 8 as well as middorsally on segments 5 and 7 (Figs 29, 30D, 31B–E; Table 2). Whereas the acicular spines appear clearly sclerotized, the cuspidate spines are almost translucent.

Comparison with previous description

The specimen is mounted laterally, and its cuticle displays signs of beginning digestion in the shrimp's gut and maceration by Hoyer's mounting medium. Therefore, observation of the sensory spots is extremely difficult. Our observations differ from the original description (Martorelli & Higgins 2004) in that (1) two narrower neck placids are located next to the broader midventral placid and the 11 remaining placids alternate in width instead of being "placids of unequal width", (2) broader placids display three rows each with two condyles and the broad midventral placid three rows with three, two, and three condyles per row instead of just two rows with one and two condyles, respectively, (3) narrower placids show single condyle basally instead of two rows with anterior and basal condyle, (4) a cuspidate spine exists on segments 4 and 8 in a lateral accessory rather than in a ventrolateral position, (5) cuspidate spines exist middorsally on segments 5 and 7 rather than paradorsally, (6) a thin acicular spine exists laterodorsally on segment 10 rather than subdorsally, (7) a single sternal plate exists in segment 11 rather than two sternal plates, (8) the distribution of type-3 and type-6 sensory spot is now described for the specimen, (9) cuticular characters of the surface cuticle and of the free flap are now reported, and (10) morphological characters are now documented extensively by photography.

Condyloderes sp. 1

(Fig. 32; Tables 1, 7)

Material examined. One recently moulted male (USNM 1209806) mounted for light microscopy and previously identified as a juvenile stage of *Condyloderes paradoxus* from the Bay of Bengal, India (Fig. 1; Table 1).

Description. For some basic measurements see Table 7.

Trunk. The trunk is divided into 11 segments. Whereas the cuticle of the first trunk segment is ring-like without any articulation, the cuticle of segments 2–10 possesses both a midventral and a lateral articulation resulting in a tergal and two sternal plates (Fig. 32A). In segment 11, a single sternal and tergal plate exist although the sternal plate reveals a paraventral fold on both sides (Fig. 32A).

The anterior margin of the first trunk segment is smooth (Fig. 32A). The trunk cuticle and the pachycyclus are only very weakly developed (Fig. 32A). At the posterior end of all segments, the free flap overlapping the subsequent segment terminates in a primary pectinate fringe. The free flap is missing where the spines originate.

Surface characters of the cuticle like hairs were not recognizable. Also, type-6 sensory spots were extremely difficult to trace if at all because of the thin cuticle. Type-3 sensory spots occur ventrolaterally next to the lateral terminal accessory spine and subdorsally on segment 11.

Segments 1–10 bear a middorsal, segments 1–9 on each side a lateroventral spine, segment 10 also possesses a subdorsal to laterodorsal spine, and segment 11 has a spine in a lateral accessory position (= lateral terminal accessory spine) and as the midterminal spine (Fig. 32A, C; Table 7); the spines are hirsute and acicular. A short hirsute cuspidate spine with a basally thickened and an apically thinner part appears ventrolaterally on segment 5 but displaced towards the ventromedial position (Fig. 32A), in a lateral accessory position on segment 8, as well as sublaterally on segments 3, possibly 4 and 9 (Fig. 32A; Table 7).

Gonads are well developed and extend until the middle of the trunk revealing sperm in the posterior segments (Fig. 32B).

Comparison with previous description. Opposite to Higgins (1969) who identified the single specimen as a juvenile of *Condyloderes paradoxus*, we regard the specimen as a recently moulted male of a new species. The specimen reveals a thin cuticle typical for a juvenile or a recently moulted adult, a free flap only occurring in adults but not in juveniles, and a well developed gonad with sperm characteristic of a male. The specimen is assumed to belong to a new species, because it lacks the cuspidate spine ventrolaterally on segments 2 and 9 and in a lateral accessory position on segment 4, whereas *C. paradoxus* possesses a cuspidate spine in these positions. In addition, the specimen reveals a sublateral cuspidate on segments 3, possibly 4 and 9 lacking in *C. paradoxus*, and the ventrolateral cuspidate spine on segment 5 is displaced towards the ventromedial position in comparison with *C. paradoxus*. Sublateral cuspidate spines do not occur in any other known species of *Condyloderes* (Table 7; Higgins 1969; Adrianov *et al*. 2002; Martorelli & Higgins 2004; Sørensen *et al*. 2010b; Adrianov & Maiorova 2016). The specimen is not described formally as a new species, because only a single specimen is available, many cuticular characters are hard to recognize if at all also because of the thin cuticle, the specimen is covered with detritus hampering observation, and the preparation is not too satisfying.

Late juvenile stage of *Condyloderes paradoxus* or *C. setoensis*

Material examined. SEM images of one uncatalogued late juvenile stage from Singapore (Table 1).

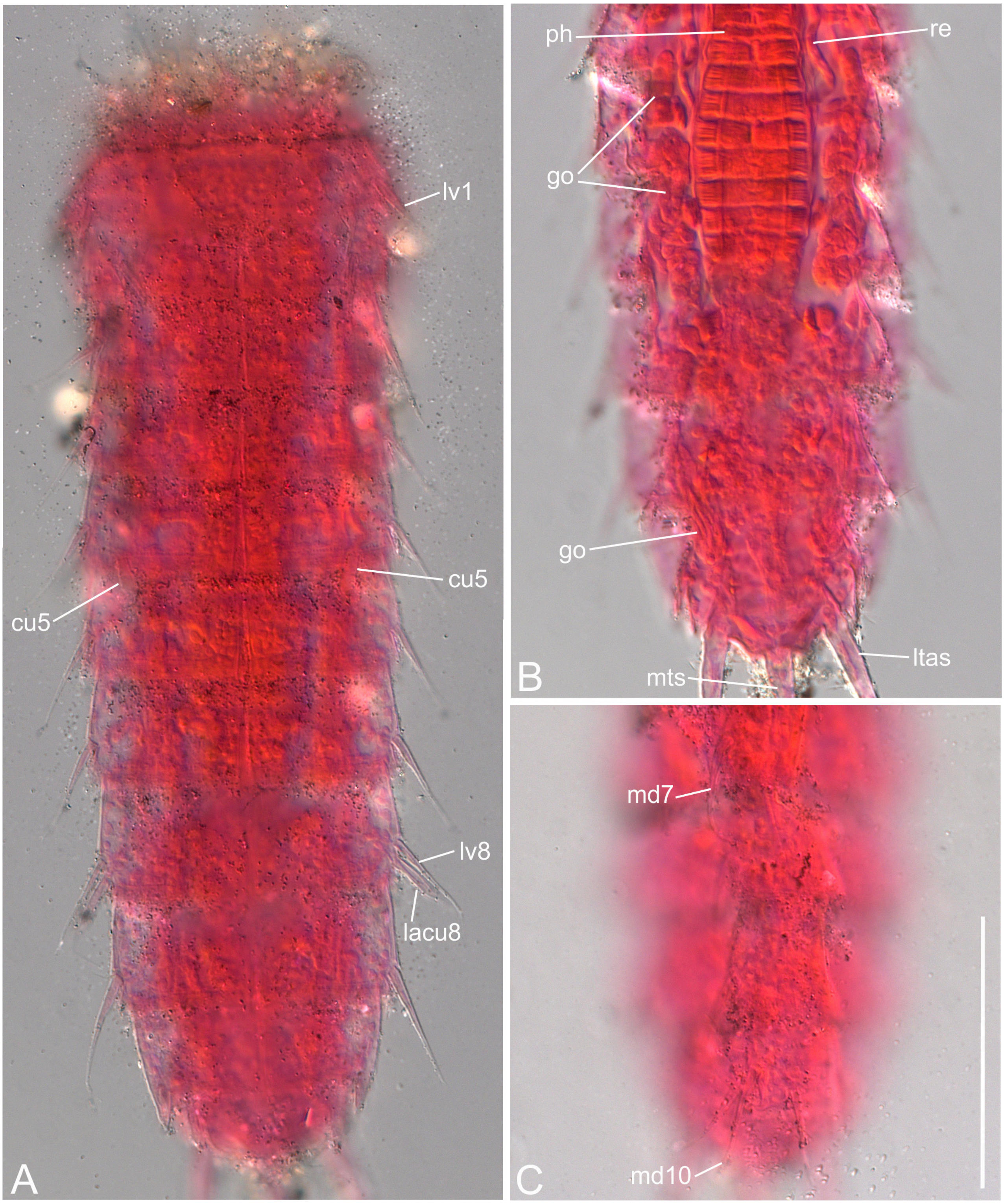


FIGURE 32. *Condyloderes* sp. 1, recently moulted male (USNM 1209806), DIC. **A.** Segments 1–11, ventral view. **B.** Segments 6–11, optical section. **C.** Segments 7–11, dorsal view. Scale bar in **C** 50 µm, valid for **A–C**. Abbreviations: cu5, ventromedially displaced cuspidate spine of segment 5; go, gonad; lacu8, lateral accessory cuspidate spine of segment 8; ltas, lateral terminal accessory spine; lv1, lateroventral spine of segment 1; md7, middorsal spine of segment 7; mts, midterminal spine; ph, pharynx; re, retractor muscle.

Description. The late juvenile stage possesses 11 segments separated from each other. A free flap is missing and postmarginal spicula exist. Many characters like sensory spots are difficult to trace because of the dirt covering the specimen. An acicular spine occurs middorsally and midlaterally on segment 10. The position of the latter two spines probably indicates that the juvenile stage would have moulted to a male with a middorsal and a laterodorsal spine on segment 10 based on unpublished information about several late juvenile stages of *C. shirleyi* **sp. nov.** moulting to a female or to a male (Neuhaus unpubl. obs.).

Comments. The specimen is not illustrated here, because it is covered with some mucous-like substance and little detail about the specimen could be observed. Therefore, no information could be obtained about the single character that distinguishes *Condyloderes paradoxus* from *C. setoensis*, *viz* the type-6 sensory spot sublaterally on segment 8 (for discussion about spines on segment 10 see also chapter Differential diagnosis).

Description of *Condyloderes shirleyi* sp. nov. Neuhaus & Higgins

(Figs 33–44; Tables 1, 5–7)
http://zoobank.org/urn:lsid:zoobank.org:act:0A136401-7882-45BA-A92C-9D1FA76E08EA

Condyloderes sp.—Neuhaus 2013: pp. 232, 239, 267, figs 5.1.14, 5.1.15.—Neuhaus 2017: p. 146.

Diagnosis. Neck placids with condyles in two rows in narrower placids and three rows in broader placids; each narrower placid with one apical and two basal condyles except paraventral placid next to midventral placid revealing in majority of specimens one apical and one basal condyle; each broader placid usually with two apical condyles, two condyles in intermediate row, and four basal condyles; midventral placid always with three apical condyles and usually two in intermediate row and four in basal row; acicular spine middorsally on segments 1–9 (and on segment 10 in male only), midterminally on segment 11, lateroventrally on segments 1–9, and laterodorsally on segment 10 (in male only); cuspidate spine ventrolaterally on segments 2, 5, 7 and 9, lateral accessorily on segments 2, 4, 6 and 8, and middorsally on segments 5 and 7; type-5 (?) sensory spot ventromedially on segment 11; type-6 sensory spot ventromedially on segments 1 (slightly more paraventrally) and 29, lateroventrally on segment 10, sublaterally on segments 1–3, 5-7 and 9, midlaterally on segments 1 and 2, laterodorsally on segments 1–9, subdorsally on segment 10, and paradorsally on segments 1 (almost subdorsally), 2 and 4–9; gland cell outlet ventromedially on segment 10 in male only; ventromedial appendage on segments 6–8 and area of micropapillae ventromedially on segment 9 in female only.

Material examined. Holotypic male (USNM 1480999), 44 paratypic males (USNM 1480980-1480998, 1481000-1481019; ZMB 11598-11602), 27 paratypic females (USNM 1481020-1481029, 1481031-1481042; ZMB 11603-11607), and one paratypic female exuvia (USNM 1481030), mounted for light microscope study; 6 males and 5 females, mounted for examination with the SEM (USNM 1481164, 1481166-1481172). All specimens originate from the same sample in Alaska (Fig. 1; Table 1).

Deposition of material. The holotype and 62 paratypes are deposited at the National Museum of Natural History, Smithsonian Institution, Washington D.C., catalogued under the numbers USNM 1480999 (holotype) and USNM 1480980-1480998, 1481000-1481042 (Table 1). Also, all specimens mounted for SEM investigation are kept at the Smithsonian Institution (USNM 1481164, 1481166-1481172). Ten additional paratypes are located in the “worm” collection of the Museum für Naturkunde, Berlin and catalogued in the “Generalkatalog freilebende Würmer” under the numbers ZMB 11598-11607 (Table 1).

Type locality. North Pacific Ocean, Alaska, Glacier Bay, Berg Bay, North Element, 58°32’48” N, 136°09’00” W.

Etymology. The species is named in honour of Prof. Dr Thomas Shirley, who supported sampling in Alaska.

Description.

The description refers to males. For morphological measurements and data see Tables 5–7.

Head. Information on the head is based on 10 specimens mounted for light microscopy and on five specimens mounted for SEM (e. g., Figs 37A, 41A, E). The mouth cone reveals longitudinal cuticular bar-like structures between the outer and inner oral styles, which most certainly represent a mouth cone weir (Figs 37E, 41C, D). At its anterior margin, the mouth cone carries 9 individual outer oral styles with a thin cuticle (Figs 34, 37BE, 41C, D). Light microscope observations suggest a very weak articulation (if at all) located between a deeply folded basal part and a central part (Fig. 37B), whereas the apical part of a style appears filamentous (Figs 37A–E, 41C, D). No articulation can be recognized at all between the filamentous and the central part. Therefore, the outer oral styles are regarded as consisting of a single element. No information is available, whether or not neighbouring outer oral styles alternate in length. The basal third of an outer oral styles shows numerous spinose processes (Figs 37B, 41D), which appear often as longitudinal ridges, because most processes are collapsed on the style, probably an artefact from SEM preparation. In adult specimens, the outer oral styles appear often to be collapsed around the partly protruded inner foregut structures, but each style is clearly separated from its neighbouring style (Figs 37A–E, 41A, C, D).

The inner oral styles were only recognizable in specimens mounted for light microscopy. There are 10 long and tubular basal styles and 10 spinose shorter styles (Figs 34, 37D, E).

The introvert bears one ring of primary spinoscalids, five rings of spinoscalids, and one ring of trichoscalids (Fig. 34). The 10 primary spinoscalids (ring 01) divide the introvert into 10 sectors. The primary spinoscalids are finger-like, with a broad basis showing a proximal, flat tuft of longer spinose processes projecting outwards, and a second slightly more distal bundle of shorter spinose processes. The distal part of the primary spinoscalid is densely covered with tiny cuticular hairs at its proximal outer part, but is devoid of hairs more distally (Fig. 41E), with up to 10 transverse lines near its blunt end. The spinoscalids of rings 02–06 are formed by two parts as well: a proximal basis with fringes at its margin, and a distal, needle-like, pointed shaft covered with short hairs. Ring 02–06 spinoscalids are shorter than the primary ones and appear as 15 per ring (Figs 34, 41E). The second ring (ring 02) consists of five spinoscalids positioned centrally in odd-numbered sectors. In even-numbered sectors, a single centrally located spinoscalid is found in ring 03, because its attachment point is shifted to a slightly more posterior position in comparison with a ring 02 spinoscalid of odd-numbered sectors. A central spinoscalid occurs in rings 04 and 06 in odd-numbered sectors and in ring 05 in even-numbered sectors. Paired spinoscalids appear in rings 03 and 05 in odd-numbered sectors, and in rings 04 and 06 in even-numbered ones (Figs 34, 41E).

Hence, summarized sector-wise, all odd-numbered sectors consist of one anterior (ring 02) and one posterior spinoscalid (ring 06), with five spinoscalids arranged as a quincunx (rings 03−05) in between; even-numbered sectors contain only one anterior spinoscalid (ring 03) and five posterior spinoscalids arranged as a quincunx (rings 04−06) (Fig. 34).

The 14 trichoscalids are associated with the placids except for the narrow paraventral placid on either side, where no trichoscalid occurs (Figs 34, 35C, 37G–J, 41B, F, H). Each trichoscalid originates from a cuticular trichoscalid plate (Figs 34, 37I). Each trichoscalid is accompanied anteriorly by two pointed filamentous appendages, which are much thinner than the trichoscalid (Figs 37I, 41E, G). Both the trichoscalids and the filamentous appendages are covered by numerous cuticular hairs, which are stronger on the trichoscalids (Figs 37G–J, 41G, H, 42E). Each filamentous appendage reveals inner septa, which are only recognizable by light microscopy (Fig. 37G–J).

Neck. The 16 placids of the neck are arranged in a specific way, based on observations of three specimens mounted for SEM and 17 specimens mounted for light microscopy revealing at least 8 placids for recognition of placids. The broader midventral placid (14–16 µm width at base x 14–17 µm height; measurements based on 12 specimens) is neighboured by two narrower placids (6–9 µm width x 10–15 µm height), and alternatingly a broader (12–16 µm width x 12–20 µm height) and a narrower placid (7–11 µm width x 13–16 µm height). Each placid reveals cone-like condyles arranged in two rows in the narrower placids and in three rows in the broader placids (Figs 34, 35D, 37G–K, 41B, F, H; Table 7). Each narrower placid shows one apical and two basal condyles except the paraventral placid next to the midventral placid revealing in the majority of specimens one apical and one basal cone. Each broader placid displays in most specimens two apical condyles, two condyles in the intermediate row, and four basal condyles (Figs 35C, 37G–K, 41B, F, H; Table 7). The midventral placid possesses always three apical condyles and in the majority of specimens two in the intermediate row and four in the basal row (Figs 37J, 41B, F, 42E). Sometimes, a condyle is only partly split into two apical cones. A small and narrow interstitial placid of irregular size can be observed between each of the two neighbouring regular placids in light microscopy (Fig. 37F, H). SEM images reveal that these interstitial placids are in fact cuticular folds (Figs 41B, F, H, 42E) and, therefore, represent different structures than the placids, which consist of a thickened cuticular plate with cuticular condyles or cones on the surface.

Trunk. The trunk is divided into 11 segments (Figs 33, 35A, 37A, 41A, 44A, B, D), which appear triangular in cross-section when observed from anteriorly (Fig. 41B). Whereas the cuticle of the first trunk segment is ring-like without any articulation, the cuticle of segments 2–10 possesses both a midventral and a lateral articulation resulting in a tergal and two sternal plates; the lateral articulation becomes clearly recognizable only in light microscopy, because the upper layer of the cuticle covers the thickened cuticular plates (Figs 33, 35D–G, 38, 42A–C, G, 43A, B, E). In segment 11, a single sternal and tergal plate exist (Figs 33A, 35G, 38G, H, 42C, F, 43B, F).

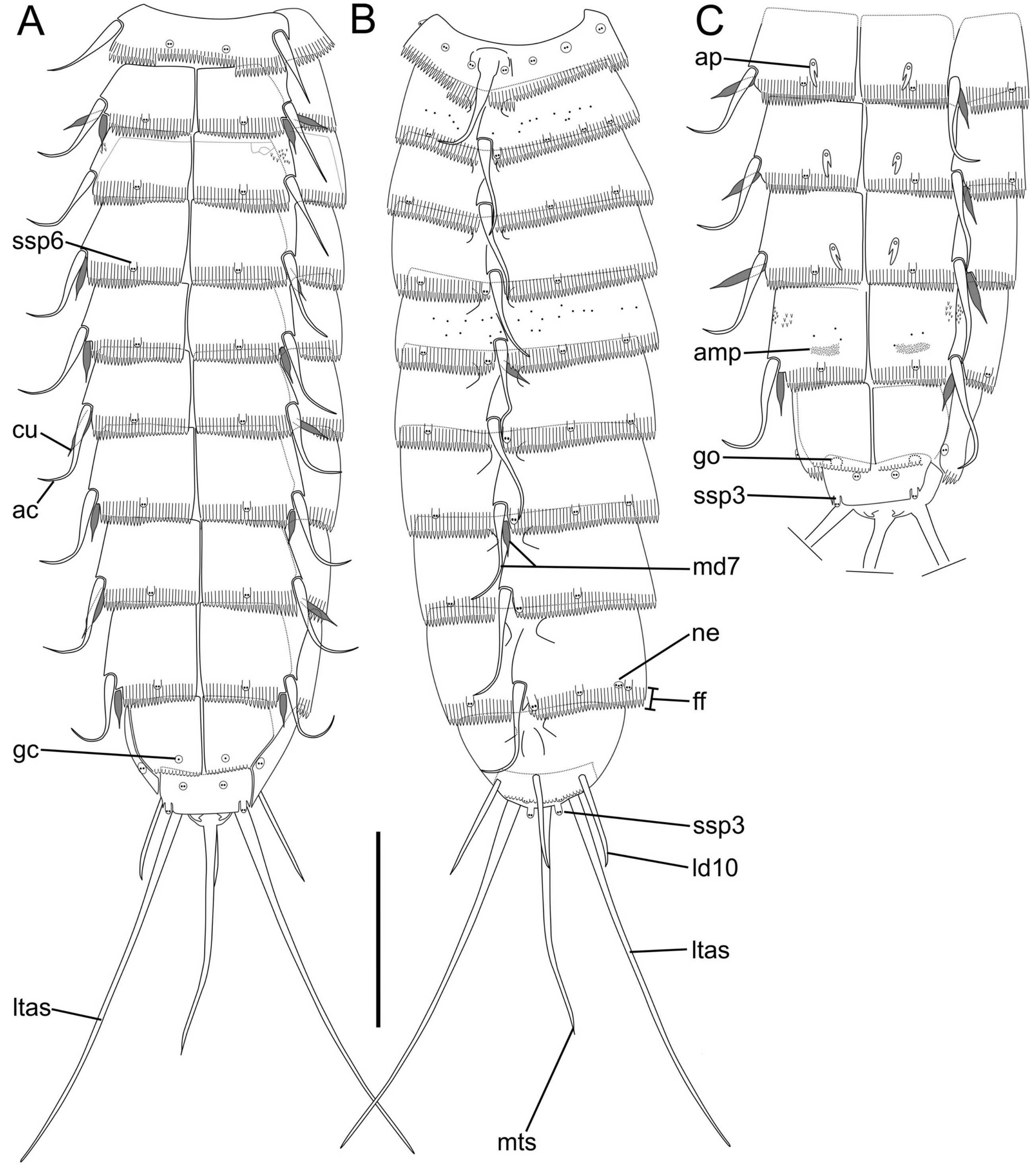
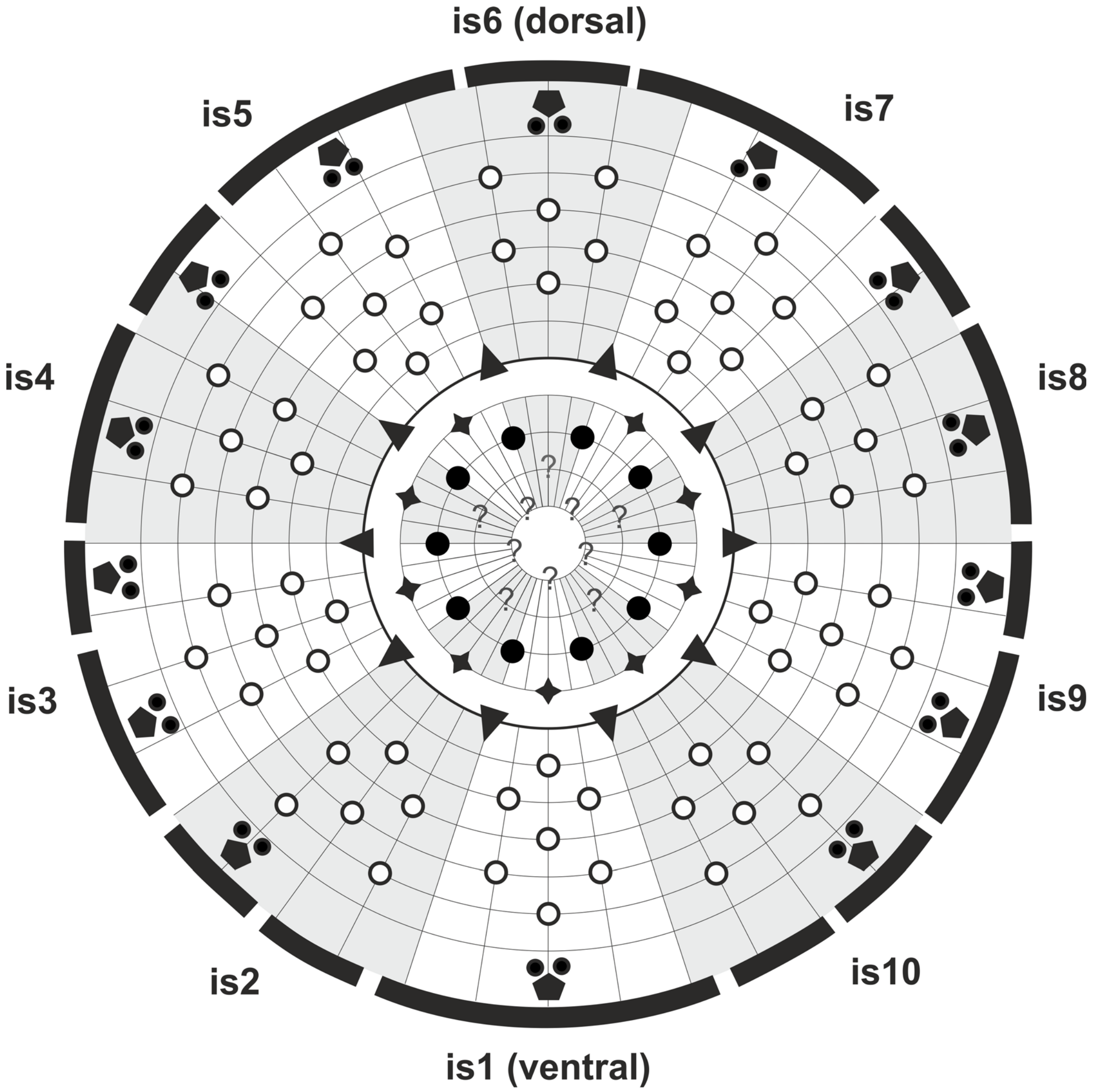


FIGURE 33. *Condyloderes shirleyi* **sp. nov. A, B**. Habitus of holotypic male (USNM 1480999). Placids not illustrated because of dirt particles hiding details. **A**. Ventral view. Sternal and tergal plate slightly separated on left side during mounting but still covered by interplate cuticle. Pachycyclus and cuticular hairs on surface indicated on segment 3. **B.** Dorsal view. Pores shown in segments 2 and 5. **C.** Segments 6–11 of paratypic female (USNM 1481025), ventral view. Variation of cuspidate spine of segment 7 in lateral accessory instead of ventrolateral position. Pores and cuticular hairs indicated on segment 9. Cuspidate spines highlighted by grey colour. Scale bar 100 µm, valid for **A–C**. Abbreviations: ac, acicular spine; amp, female-specific area of micropapillae; ap, female-specific appendage; cu, cuspidate spine; ff, free flap; gc, gland cell outlet of male; ltas, lateral terminal accessory spine; md7, middorsal spines of segment 7; mts, midterminal spine; ne, protonephridial openings; ssp3, type-3 sensory spot.



Scalid and style arrangement

by ring:

ring -03:	? 5 spinose styles	?
ring -02:	? 5 spinose styles	?
ring -01:	10 inner oral styles	●
ring 00:	9 outer oral styles	✦
ring 01:	10 primary spinoscalids	▼
ring 02:	5 spinoscalids	○
ring 03:	15 spinoscalids	○
ring 04:	15 spinoscalids	○
ring 05:	15 spinoscalids	○
ring 06:	15 spinoscalids	○
ring 07:	14 trichoscalids with 2 filamentous appendages	●● ⬟

by sector:

odd sector: 7 spinoscalids
even sector: 6 spinoscalids

total amount of scalids:

75 spinoscalids
14 trichoscalids

FIGURE 34. Diagram of mouth cone, introvert, and placids of adult *Condyloderes shirleyi* **sp. nov.** with indication of inner and outer oral styles as well as scalid and placid distribution. Placids symbolized by bold, bent bars around the introvert diagram. Abbreviation: is, introvert sector.

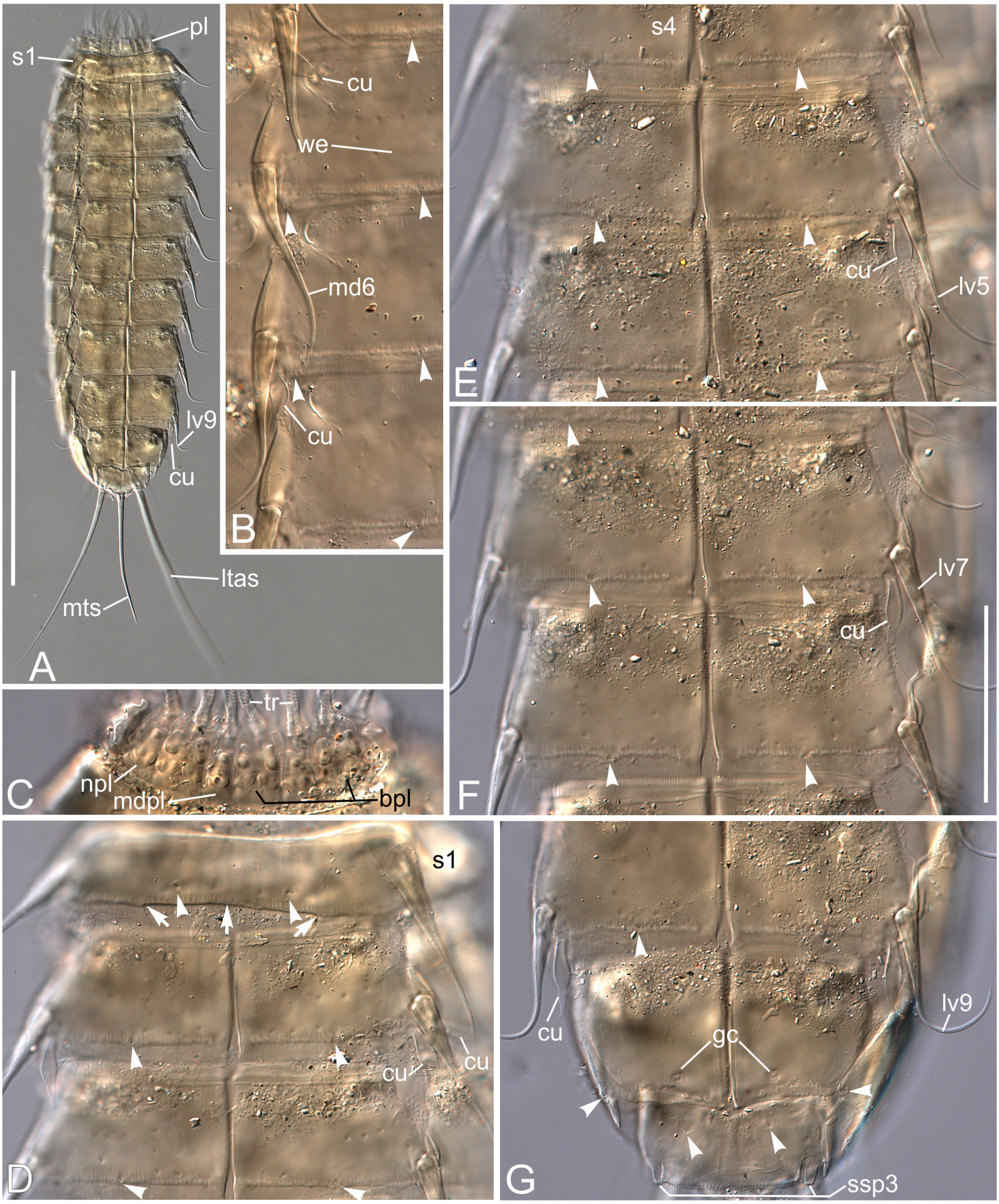


FIGURE 35. *Condyloderes shirleyi* **sp. nov.**, holotypic male (USNM 1480999) in ventral (**A**, **D–G**) and dorsal view (**B**, **C**), DIC. **A.** Habitus, mouth cone and introvert withdrawn. **B.** Segments 6–8; notice middorsal cuspidate spines. **C.** Placids. **D.** Segments 1–3; arrows point to reduced free flap. **E.** Segments 4–6. **F.** Segments 7 and 8. **G** Segments 9–11; extended focus image of five images. Arrowheads in **B** and **D–G** mark type-6 sensory spots. Scale bar in **A** 200 µm. Scale bar in **F** 50 µm, valid for **B–G**. Abbreviations: bpl, broader placid; cu, cuspidate spine; gc, gland cell outlet of male; ltas, lateral terminal accessory spine; lv5, lateroventral spine of segment 5; md6, middorsal spine of segment 6; npl, narrower placid; pl, placid; s1, segment 1; ssp3, type-3 sensory spot; tr, trichoscalid.

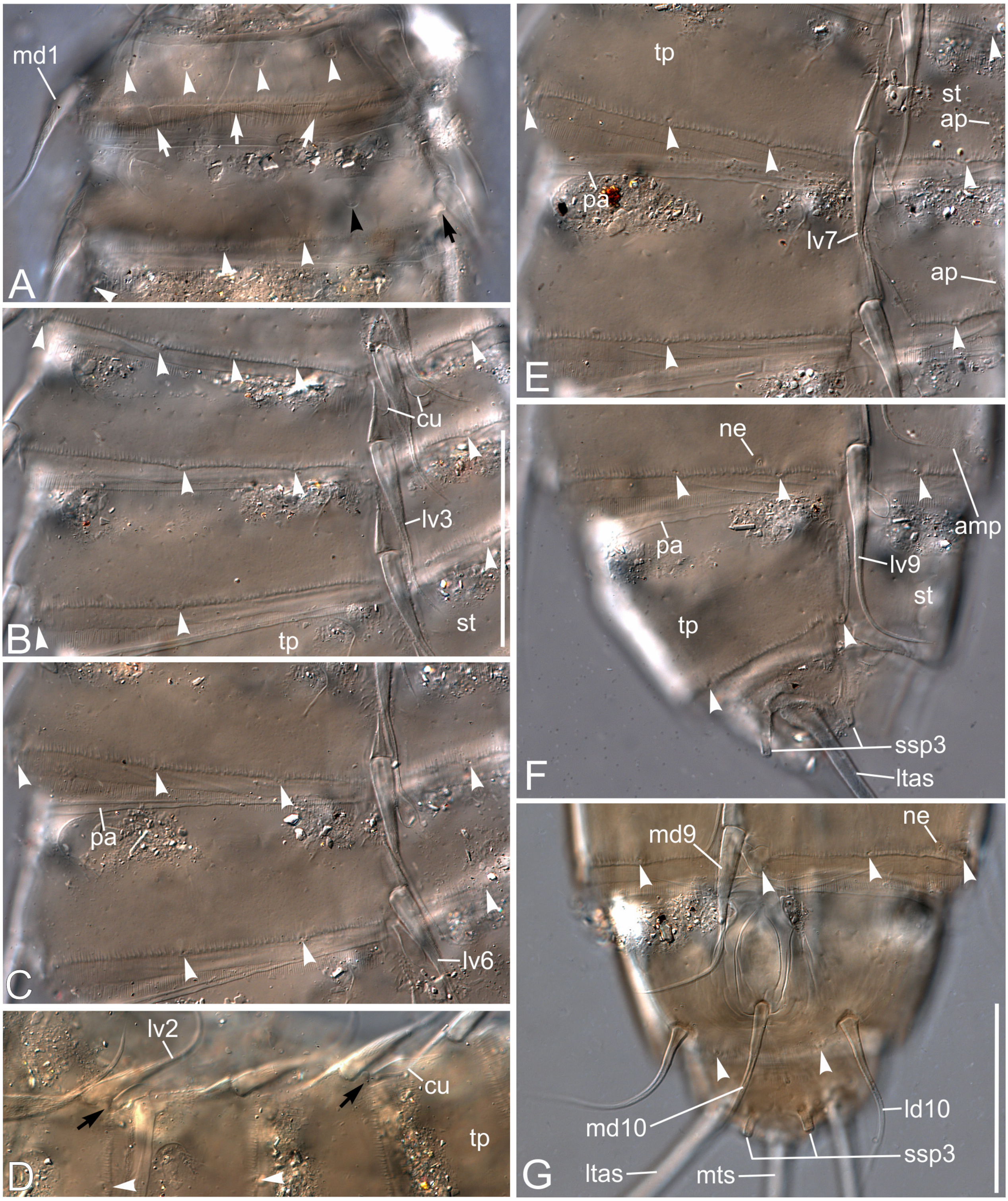


FIGURE 36. *Condyloderes shirleyi* **sp. nov.**, paratypic females (ZMB 11603, **A**; USNM 1481022, **B**, **C**, **E**, **F**; USNM 1481040, **D**) and paratypic male (USNM 1480983, **G**) from right (**A–F**) and dorsal side (**G**), DIC. **A–G.** Segments 1 and 2 (**A**), 3 and 4 (**B**), 5 and 6 (**C**), 2–5 (**D**), 7 and 8 (**E**), 10 and 11 (**F**, **G**). White arrows mark reduced free flap (**A**). Black arrows indicate modified attachment sites of tergal plates for lateral accessory cuspidate spines (**A**, **D**), spine lost in **A**. Arrowheads in **A–G** mark type-6 sensory spots. Black arrowhead in **A** points to type-6 sensory spot located centrally on segment instead of posteriorly. Scale bar in **G** 50 µm, valid for **A–G**. Abbreviations: amp, female-specific area of micropapillae; ap, female-specific appendage; cu, cuspidate spine; ld10, laterodorsal spine of segment 10; ltas, lateral terminal accessory spine; lv3, lateroventral spine of segment 3; md1, middorsal spine of segment 1; mts, midterminal spine; ne, protonephridial openings; pa, pachycyclus; ssp3, type-3 sensory spot; st, sternal plate; tp, tergal plate.

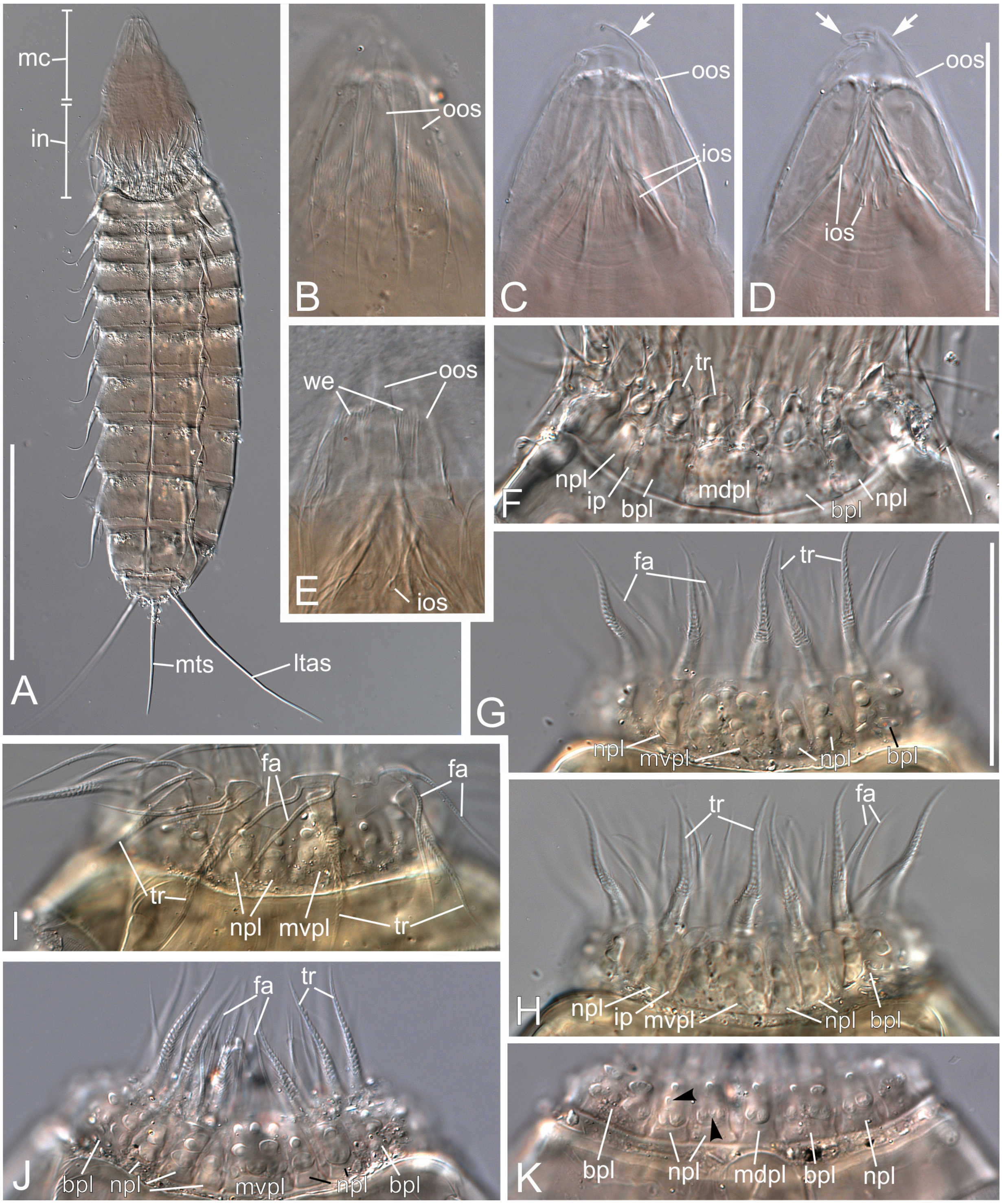


FIGURE 37. *Condyloderes shirleyi* **sp. nov.**, paratypic females (ZMB 11606, **A**, **C**, **D**; USNM 1481025, **B**, **F**) and paratypic males (USNM 1480986, **E**; 1481000, **G**, **H**; 1481012, **I**; 1481003, **J**, **K**) in ventral (**A–E**, **G–J**) and dorsal view (**F**, **K**), DIC. **A.** Habitus, introvert and mouth cone protruded. **B–E.** Mouth cone; notice tapering tips of outer oral styles (**C**, **D**, arrows) and mouth cone weir (**E**). **F–H, J, K.** Variation of placids; notice broad instead of narrow middorsal placid (**F**), midventral placid fused with neighbouring right placid (**G**, **H**, same specimen at different focal levels), midventral placid neighboured by three instead of two narrow placids on right side (**J**), and middorsal placid neighboured by two narrow placids instead of a broad placid (**K**, arrowheads point to additional condyles). **I.** Trichoscalid plates and filamentous appendages. Notice association of a trichoscalid with a placid except for narrow placids neighbouring midventral placid (**G–K**). Scale bar in **A** 200 µm. Scale bar in **D** 50 µm, valid for **B–E**. Scale bar in **G** 50 µm, valid for **F–K**. Abbreviations: bpl, broader placid; fa, filamentous appendage; in, introvert; ios, inner oral style; ip, interstitial placid; ltas, lateral terminal accessory spine; mc, mouth cone; mdpl, middorsal placid; mts, midterminal spine; mvpl, midventral placid; npl, narrower placid; oos, outer oral style; tr, trichoscalid or its basal plate; we, mouth cone weir.

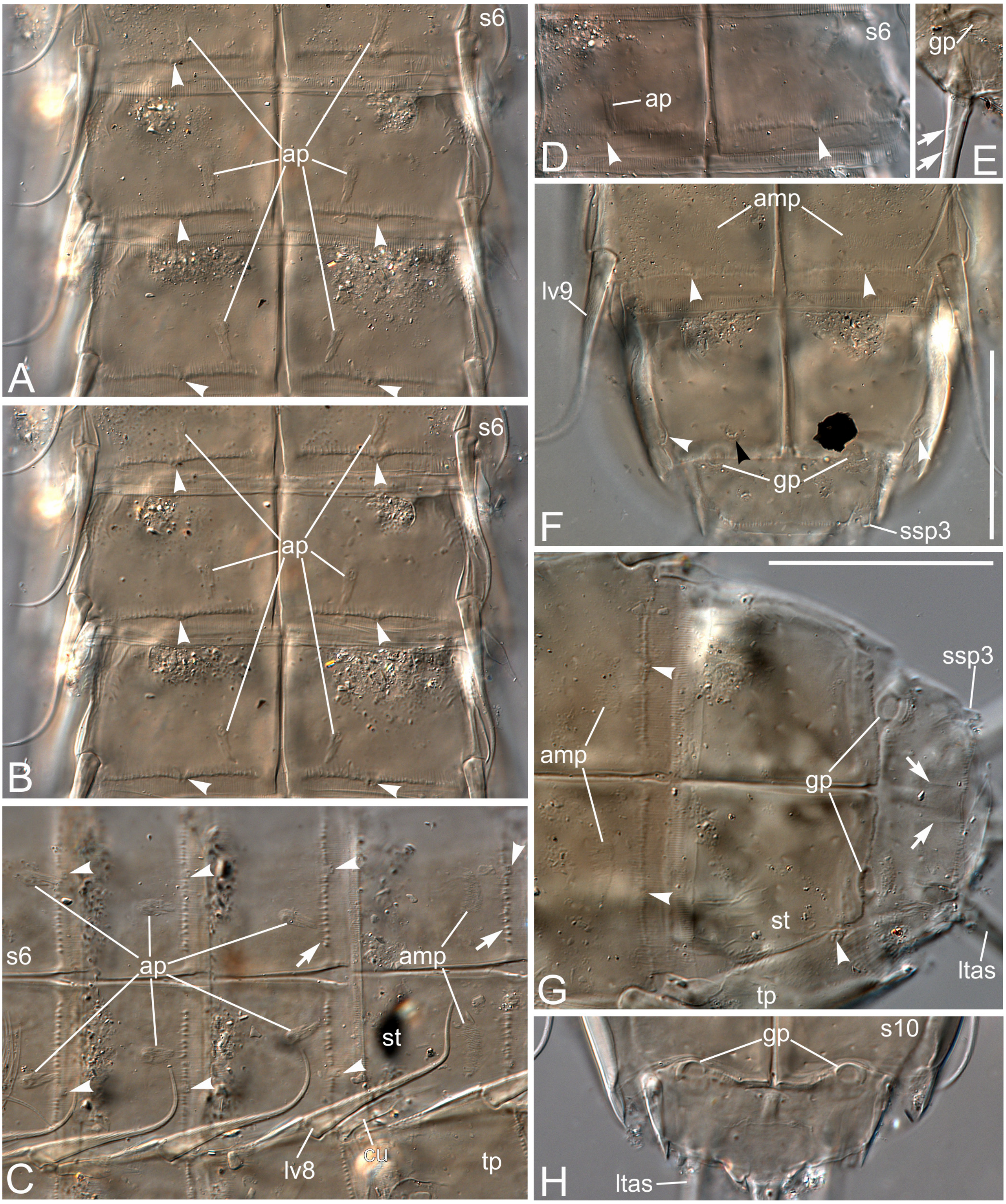


FIGURE 38. *Condyloderes shirleyi* **sp. nov.**, paratypic females (ZMB 11604, **A**, **B**, **H**; ZMB 11607, **C**, **E**; USNM 1481038, **D**; 1481026, **F**; 1481032, **G**) in ventral view, DIC. **A, B.** Segments 6–8, same specimen, showing surface (**A**) and pores through trunk cuticle (**B**) of female-specific appendages. **C.** Segments 7–9 of recently moulted specimen with thickened cuticular structures anterior to free flap (arrows). **D.** Segment 6, appendage on right sternal plate only. **E.** Lateral terminal accessory spine with two thin areas (arrows). **F, G.** Segments 9–11, different extension of area of micropapillae; black arrowhead points to unusual type-6 sensory spot (**F**), arrows mark paraventral folds (**G**). **H.** Segment 11, sclerotization of gonopores. Arrowheads in **A–D**, **F**, and **G** mark type-6 sensory spots. Scale bar in **F** 50 µm, valid for **A–F**. Scale bar in **G** 50 µm, valid for **G** and **H**. Abbreviations: amp, female-specific area of micropapillae; ap, female-specific appendage; cu, cuspidate spine; gp, gonopore; ltas, lateral terminal accessory spine; lv8, lateroventral spine of segment 3; s6, segment 6; ssp3, type-3 sensory spot; st, sternal plate; tp, tergal plate.

The anterior margin of the first trunk segment is smooth (Figs 33, 35D, 37F, H–K, 41B, E–H, 42E, 44A). The cuticle bulges outwards in a half-circle about paradorsally, sublaterally, and ventrolaterally at the anterior margin of segments 2–10 (Figs 41A, 42A–C, 43I, 44A, B, D). At the anterior margin of all segments and at the midventral margin of the sternal plates of segments 2–10, the cuticle thickens towards the interior of the animal and forms a pachycyclus (Figs 36C, E, F, 40A, I, N). Ventrally, the tergal and sternal plate form a strongly sclerotized peg and socket articulation in more maturated adult specimens (Fig. 39A). Light microscope observations reveal a variable number of easily recognizable, irregularly arranged, small canals, which extend as "pores" from the epidermis into each cuticular trunk plate (Figs 33B, 35D–F) and do not seem to be connected with gland cells. Examination with the SEM shows that the canals do not penetrate the trunk cuticle completely. The function of these canals remains unknown. At the posterior end of all segments, the free flap overlapping the subsequent segment terminates in a primary pectinate fringe. The basal part of the free flap reveals fine, regularly arranged, longitudinal bars inside the flap. These bars elevate slightly above the surface (Figs 35D–G, 36, 38D–G). Under SEM, the internal striation shows an alternating pattern of darker and brighter striation on the surface, because the SEM beam penetrates the cuticle to a variable amount depending on the amount of underlying cuticular mass (Fig. 43H). The free flap is missing where the spines originate. On the ventral and dorsal side of segment 1, the central posterior margin of the segment shows a considerably shorter free flap but a regular-sized primary pectinate fringe and ends more anteriorly than the subdorsal, sublateral, and ventrolateral margin resulting in a peculiar outline (Figs 35D, 36A, 42A, 44A). On segments 1–9, the teeth of the primary pectinate fringe are shorter and slightly smaller in the ventromedial to midventral area than more laterally; the teeth are considerably shorter all around segments 10 and 11 (Figs 42A–C, 44D, E).

The smooth surface of the cuticle of all segments is covered with few, irregularly distributed, triangular cuticular scale-like hairs (Figs 35DG, 36, 38A, 42A–C, 44). The hairs are more numerous on the sternal and tergal plate of segment 11. Numerous acicular cuticular hairs and broader triangular scale-like hairs occur middorsally and laterally on the trunk cuticle anterior to the middorsal and lateroventral spines of all segments in a narrow area. Here, the anteriormost hairs are more sclerotized than those in the more central area of a segment and are also found ventrolaterally (Figs 42A–C, 44). Anterior little elevated longitudinal ridges could not be detected in this species.

All sensory spots except the ventromedial one on segment 11 elevate clearly above the surface of the trunk cuticle and display on the outside cuticular micropapillae surrounding 1–3 pores. The distribution of sensory spots is bilateral symmetrical. A type-3 sensory spot occurs ventrolaterally next to the lateral terminal accessory spine and subdorsally on segment 11 (Figs 33, 35G, 36F, G, 38F, G, 39D, 42I, F, 43F, 44D, E; Table 5). A sensory spot ventromedially on segment 11 may represent a type-6 spot (Figs 35G, 42D, F, 43F). A type-6 sensory spot occurs ventromedially on segments 1 (slightly more paraventrally) and on segments 2–9, lateroventrally on segment 10, sublaterally on segments 1–3, 5–7 and 9, midlaterally on segments 1 and 2, laterodorsally on segments 1–9, subdorsally on segment 10, and paradorsally on segments 1 (almost subdorsally), 2 and 49 (Figs 33, 35B, D–G, 36, 42A–D, F, G, 44; Table 5).

A small structure with cuticular micropapillae elevates above the surface of the trunk cuticle slightly dorsally of the sublateral sensory spot at the posterior margin of segment 9. We assume that this structure represents the nephropore (Table 5) because of the smaller size in comparison with a sensory spot (Figs 36F, G, 40M, 43E, 44D, E), the presence of several cuticular ducts penetrating the apical trunk cuticle more obliquely than in the "regular" sensory spots (Fig. 43E), and the origin from a cavity in the basal trunk cuticle (Fig. 39B).

A gland cell outlet ventromedially on segment 10 is inconspicuous under SEM but reveals a short sclerotized cuticular duct and a spherical cavity in the basal trunk cuticle in light microscopy (Figs 33A, 35G; Table 5). Recently moulted males lack the cavity in the basal trunk cuticle, because their cuticle is much thinner than in the more maturated male.

Segments 1–10 bear a middorsal, segments 1–9 on each side a lateroventral spine, and segment 11 possesses an acicular spine in a lateral accessory (= lateral terminal accessory spine) and in a midterminal position (Figs 33, 35A, B, D–G, 36, 42A–D, F, G, 44; Table 5); the spines are hirsute and acicular. Each middorsal and lateroventral acicular spine reveals a strongly sclerotized thick base and a considerably thinner and more flexible apical part. The basal part of the sclerotized lateroventral and middorsal spines shows a strong proximal cuticle around a central cellular cavity and one or two thin areas in the cuticle (Fig. 39H). The lateral terminal accessory spine displays at its base two such thin areas (Fig. 38E). The middorsal and lateroventral spines of the trunk bend outwards in light microscope preparations but inwards in SEM mounts (comp. Figs 33, 35A, E–G, 37A, 39M with Figs 41A, 42A–C, 44). The middorsal and laterodorsal acicular spine on segment 10 are considerably thinner, more flexible, and less

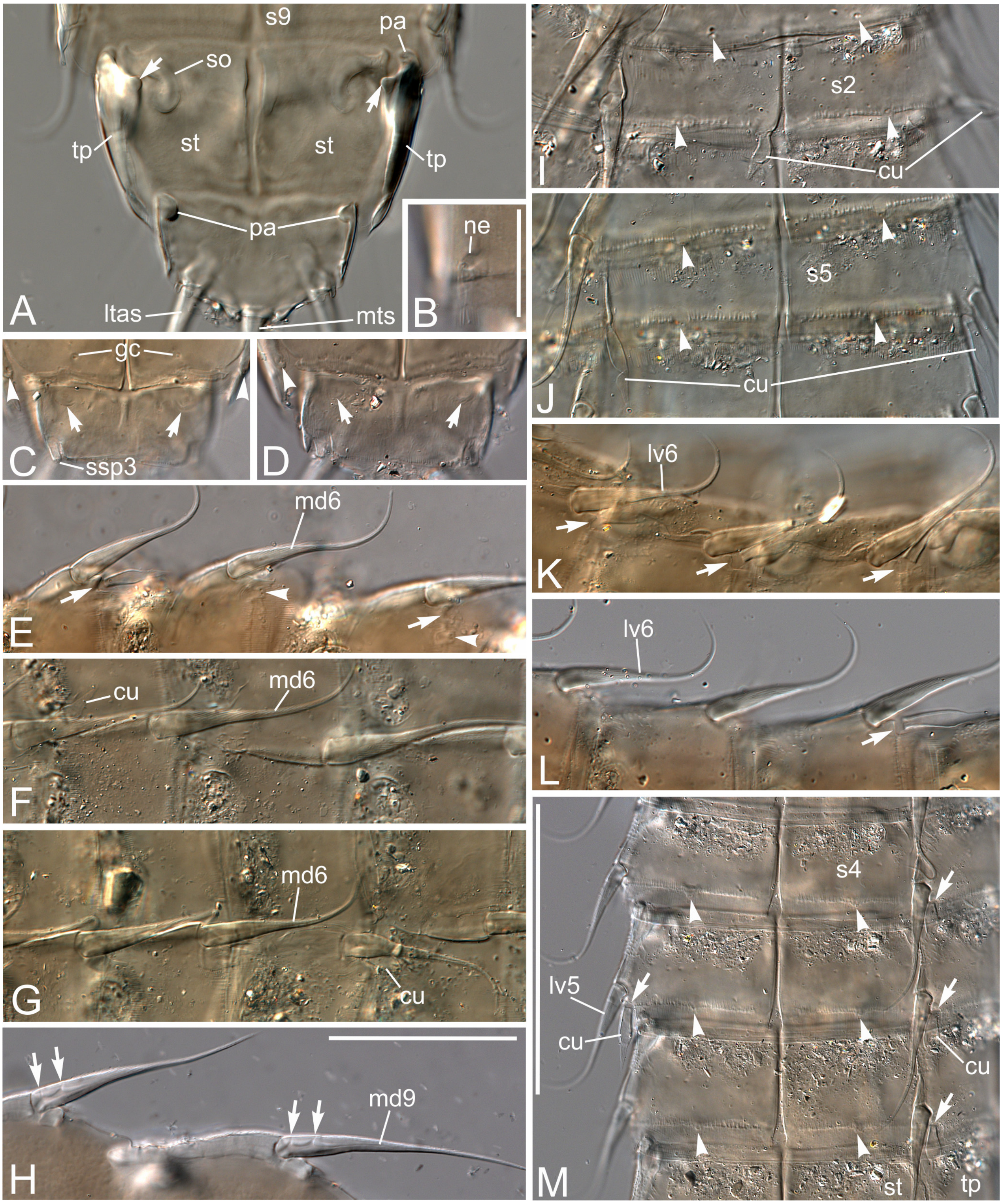


FIGURE 39. *Condyloderes shirleyi* **sp. nov.**, paratypic males (ZMB 11598, **A**; 11600, **B**, **D**; USNM 1481006, **C**; 1481008, **J**; 1480993, **M**) and paratypic females (USNM 1481041, **E**; ZMB 11606, **F**; USNM 1481036, **G**; 1481022, **H**; 1481042, **I**; 1481040, **K**, **L**) in optical section (**A**, **B**, **H**), from ventral (**C**, **D**, **I**, **J**, **M**), dorsal (**F**, **G**), left (**E**, **K**), and right side (**L**), DIC. **A.** Segments 10 and 11, condyle (arrows) and socket articulation. **B.** Intracuticular cavity of protonephridial openings. **C, D.** Segment 11, anterior ventrolateral sclerotizations (arrows). **E.** Segments 5–7, attachments of cuspidate spines (arrows). **F, G.** Segments 6–8 (**F**) and 5–8 (**G**), specimen without middorsal cuspidate spine on segment 7 (**F**) or on segment 5 (**G**). **H.** Middorsal spines of segments 8 and 9 with two thin areas (arrows). **I.** Segment 2, right cuspidate spine paraventrally instead of ventrolaterally. **J.** Segment 5, no indication of right lateroventral spine. **K, L.** Right cuspidate spine on segment 7 in lateral accessory instead of ventrolateral position (**K**) and lack of right lateral accessory cuspidate spine on segment 6 (**L**), same specimen; arrows (**K**) mark attachment areas of cuspidate spines. **M.** Segments 4–6, left cuspidate spine of segment 5 lateral accessorily instead of ventrolaterally; arrows point to attachment areas of cuspidate spines. Arrowheads in **C–E**, **I**, **J**, and **M** mark type-6 sensory spots. Scale bar in **B** 20 µm. Scale bar in **H** 50 µm, valid for **A** and **C–L**. Scale bar in **M** 100 µm. Abbreviations: cu, cuspidate spine; gc, gland cell outlet of male; ltas, lateral terminal accessory spine; lv5, lateroventral spine of segment 5; md6, middorsal spine of segment 6; mts, midterminal spine; ne, protonephridial openings; pa, pachycyclus; s2, segment 2; so, socket; ssp3, type-3 sensory spot; st, sternal plate; tp, tergal plate.

sclerotized basally than the lateroventral and middorsal spines of other segments (Figs 33B, 36G, 44D). A short hirsute cuspidate spine with a basally thickened and an apically thinner part appears ventrolaterally on segments 2, 5, 7 and 9, in a lateral accessory position on segments 2, 4, 6 and 8 as well as middorsally on segments 5 and 7 (Figs 33, 35A, D–G, 36, 37A, 42A–C, 44; Table 5). All acicular and cuspidate spines originate from a modified attachment area of the trunk cuticle (for cuspidate spines: Figs 36D, 39E, K–M, 43H, 44C). Therefore, it can be elucidated whether an acicular or cuspidate spine is missing primarily or secondarily. Whereas the acicular spines appear clearly sclerotized, the cuspidate spines are almost translucent in light microscope mounts.

The anterior ventrolateral cuticle of segment 11 slightly curves posteriorly and is more thickened than in other areas. This is the region where male gonopores would be expected (Fig. 39D).

Several males reveal ventrolaterally on segment 11in its anterior third a circular or curved depressed structure of unknown function (Figs 39C, D, 42D, F).

Female. In the following, only those characters are reported for the female, which differ from the male. The female can be distinguished from the male by the existence of a row of short cuticular projections in the ventromedial area of each sternal plate of segments 2–5 and less pronounced on segment 6 just anterior to the free flap (only recognizable under SEM; Figs 42G, 43A) *versus* its lack in the male (Fig. 42A, B), the existence of the ventromedial appendage on the sternal plates of segments 6–8 (Figs 33C, 38A–D, 43B–D; Table 5) *versus* its lack in the male (Figs 33A, 35E, F, 42B), in the existence of a more or less rectangular area with prominent cuticular micropapillae but without pores on each sternal plate of segment 9 (Figs 33C, 38C, F, G, 43B, C; Table 5) *versus* its lack in the male (Figs 33A, 35G, 42A), the lack of a gland cell outlet ventromedially on segment 10 (Figs 32C, 37G, H; Table 5) *versus* its existence in the male (Figs 33A, 35G), the lack of a middorsal and laterodorsal acicular spine on segment 10 (Fig. 44E; Table 5) *versus* the possession of these spines in the male (Figs 33A, B, 36G, 42C, D, 44D), and in the existence of the large circular gonopores with a sclerotized edge, a short cuticular canal, and a posterior serrated, curved rim of cuticle at the anterior margin of the sternal plate of segment 11 (Figs 33C, 38F–H, 43F) *versus* the lack of such structures in the male (Figs 35G, 39C, D).

On each sternal plate of segments 6–8, the females reveal a (sensory? glandular?) ventromedial appendage, which gives the impression of an extremely elongated sensory spot covered by numerous cuticular micropapillae. The structure may be split into two parts at its tip (Figs 33C, 38A–D, 43B–D). At its base, each structure shows a sclerotized cuticular duct penetrating the trunk cuticle. The duct seems to be surrounded by a cavity (Fig. 38B). The structures occur ventromedially on segment 6 and progressively more paraventrally on segments 7 and 8 (Figs 33C, 38A–C).

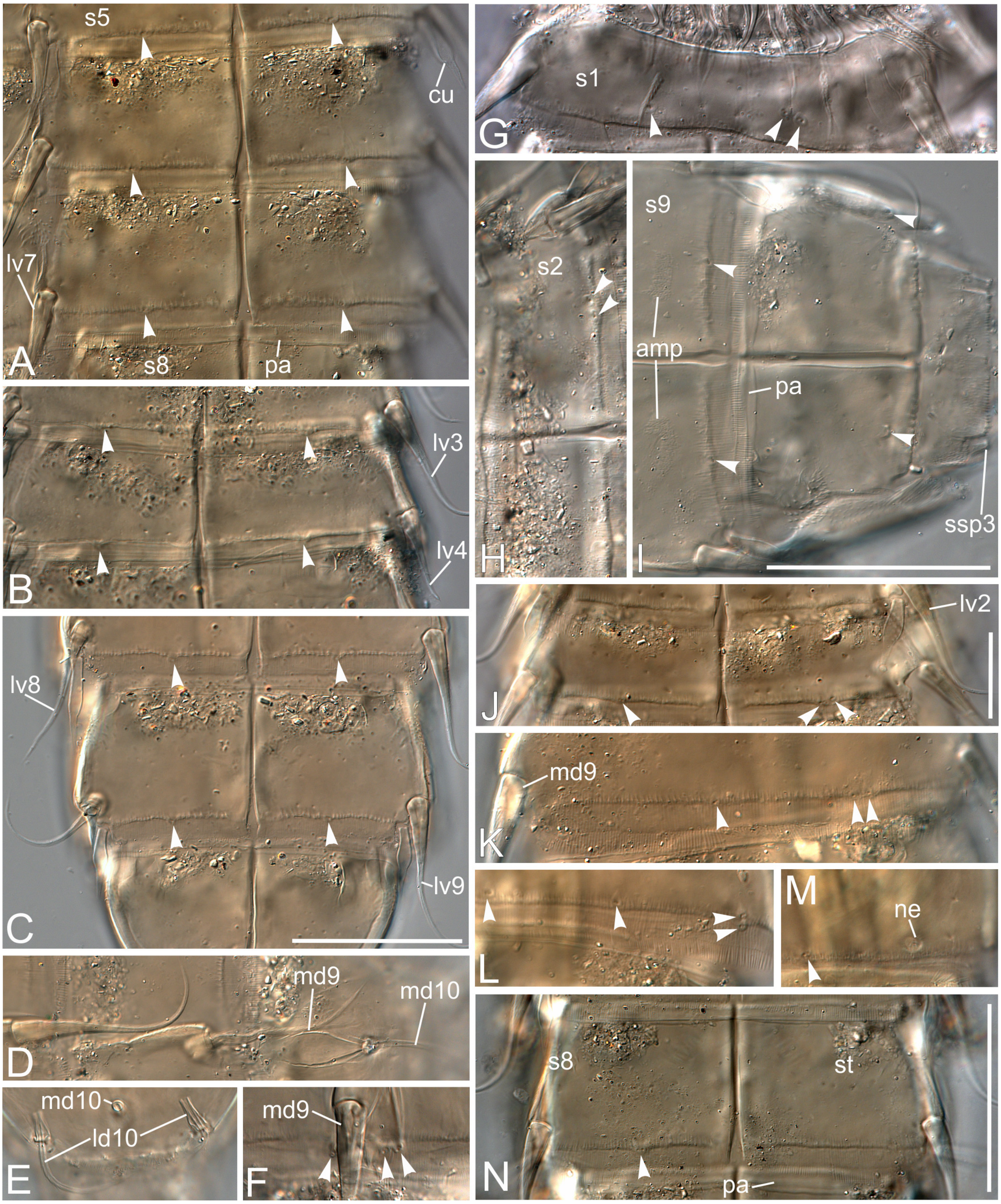

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FIGURE 40. *Condyloderes shirleyi* **sp. nov.**, paratypic males (USNM 1481012, **A**; ZMB 11600, **B**; USNM 1481005, **C–E**; 1480981, **F**; 1481013, **J**; 1481014, **M**; 1480984, **N**) and paratypic females (ZMB 11605, **G**; USNM 1481028, **H**; ZMB 11604, **I**; USNM 1481040, **K**; 1481041, **L**) from ventral (**A–C**, **G–J**, **N**), dorsal (**D–F**), right (**K**, **M**), and left side (**L**), DIC. **A.** Segments 6 and 7 lacking any cuspidate spine. **B.** Segment 4, left lateroventral spine small. **C–E.** Small spines lateroventrally on segments 8 and 9 (**C**, spines on right side) and middorsally on segment 9 (**D**) as well as laterodorsal spines of segment 10 not fully extended (**E**), same specimen. **F.** Right paradorsal sensory spot doubled. **G, H.** Segments 1 (**G**) and 2 (**H**), left ventromedial sensory spot doubled. **I.** Segments 9–11, right sensory spot ventromedially instead of lateroventrally. **J.** Segment 3, left ventromedial sensory spot doubled. **K.** Segment 6, sublateral sensory spot doubled on right side. **L.** Segment 9, left paradorsal sensory spot doubled, right organ missing. **M.** Segment 9, right side, laterodorsal sensory spot and nephridial openings, sublateral sensory spot missing. **N.** Segment 8, ventromedial sensory spot missing on left sternal plate. Arrowheads in **A–N** mark type-6 sensory spots. Scale bar in **C** 50 µm. Scale bar in **I** 50 µm, valid for **F–I** and **K–M**. Scale bar in **J** 20 µm. Scale bar in **N** 50 µm, valid for **A**, **B**, **D**, **E**, and **N**. Abbreviations: amp, area of micropapillae; cu, cuspidate spine; ld10, laterodorsal spine of segment 10; lv2, lateroventral spine of segment 2; md9, middorsal spine of segment 9; ne, protonephridial openings; pa, pachycyclus; s1, segment 1; ssp3, type-3 sensory spot; st, sternal plate.

Recently moulted adults. Eight specimens seem to have moulted recently to the adult stage, because they possess in comparison to more maturated specimens a considerably thinner cuticle (Fig. 39I, J), which folds easily in light microscope preparations. The surface does not reveal the numerous, small cuticular hairs typical of the juvenile stages. The cuticular hairs are less sclerotized than in more maturated adult specimens. The trunk cuticle does not display the canals found in older specimens with a thicker cuticle. At the anterior margin of the free flap, a row of intracuticular small knobs or bar-like sclerotizations occurs (Figs 38C, 39I, J). The pachycycli and the posterior pectinate fringe exist but are not fully developed. The type-6 sensory spots are barely visible in some specimens. However, the female gonopores, the female-specific appendages on segments 6–8, the female-specific area of cuticular micropapillae on segment 9, and the male-specific laterodorsal and middorsal spines, exist as in the more aged specimens.

Variation. The number of cuticular condyles on the placids varies to some degree. In the midventral placid, the intermediate row may reveal two or four condyles and the basal row 4–6 condyles (comp. Figs 35C, 37I, J, 41B, F, H). In one male (USNM 1481000: Fig. 37G, H), the midventral placid is fused with the right narrow placid. Broader placids may possess in the intermediate row two or three condyles, the basal row 3–6 condyles (comp. Figs 35C, 41F, H). One male (USNM 1481003: Fig. 37J) displays on one side ventrally three narrower placids instead of two next to the midventral placid and two narrower placids with an unusual arrangement of condyles instead of a broader placid next to the narrower middorsal placid (Fig. 37K). Each of these variations exists in one or two, rarely three specimens out of 20 specimens investigated for these characters, and a variation may apply only to one broader placid of a specimen.

Out of 72 adults and one female exuvia mounted for light microscopy, 68 specimens are in a condition to check variation of trunk characters. Of these, 64 specimens (= 94 %) reveal some variation of spines, female appendages on segment 6–8, and sensory spots in one character (14 specimens), two characters (17 specimens), three characters (14 specimens), four characters (11 specimens), five characters (5 specimens), six characters (1 specimen), or seven characters (2 specimens) in a total of 37 positions (comp. Table 5). Most variation results from the lack of a cuspidate spine middorsally on segments 5 and/or 7 (comp. Figs 33B, 35B, 39E–G, 43I, 44C, D), on one or both sides in a lateral accessory position on segment 6, and ventrolaterally on segment 7 (Table 5). Frequently, a cuspidate spine is missing middorsally both on segments 5 and 7 (17 specimens) or both middorsally on segments 5 and 7 plus ventrolaterally on segment 7 on one or both sides (11 specimens). A cuspidate spine may appear on one or both sides in a ventrolateral instead of a lateral accessory position or *vice versa*, especially on segments 7–9 (Fig. 39J, M, comp. Fig. 39K with Fig. 39L; Table 5). A cuspidate spine may also occur in an unusual position and be lacking at its normal position, e. g., paraventrally instead of ventrolaterally on one side of segment 2 (USNM 1481042: Fig. 39I). In one male, the right lateroventral acicular spine on segments 8 and 9 and the middorsal acicular spine on segments 9 and 10 are considerably thinner than the same kind of spines on other segments; also the laterodorsal spine of both sides on segment 10 is not fully extended (Fig. 40C–E). Another male reveals a much thinner acicular spine lateroventrally on segment 4 (Fig. 40B). In two females and one mounted for SEM, the ventromedial appendage is missing on one side of segment 6 or 7 (Fig. 40A). The female-specific appendage may be missing on one sternal plate (Figs 38D, 43B). The extension of the female-specific area of micropapillae may

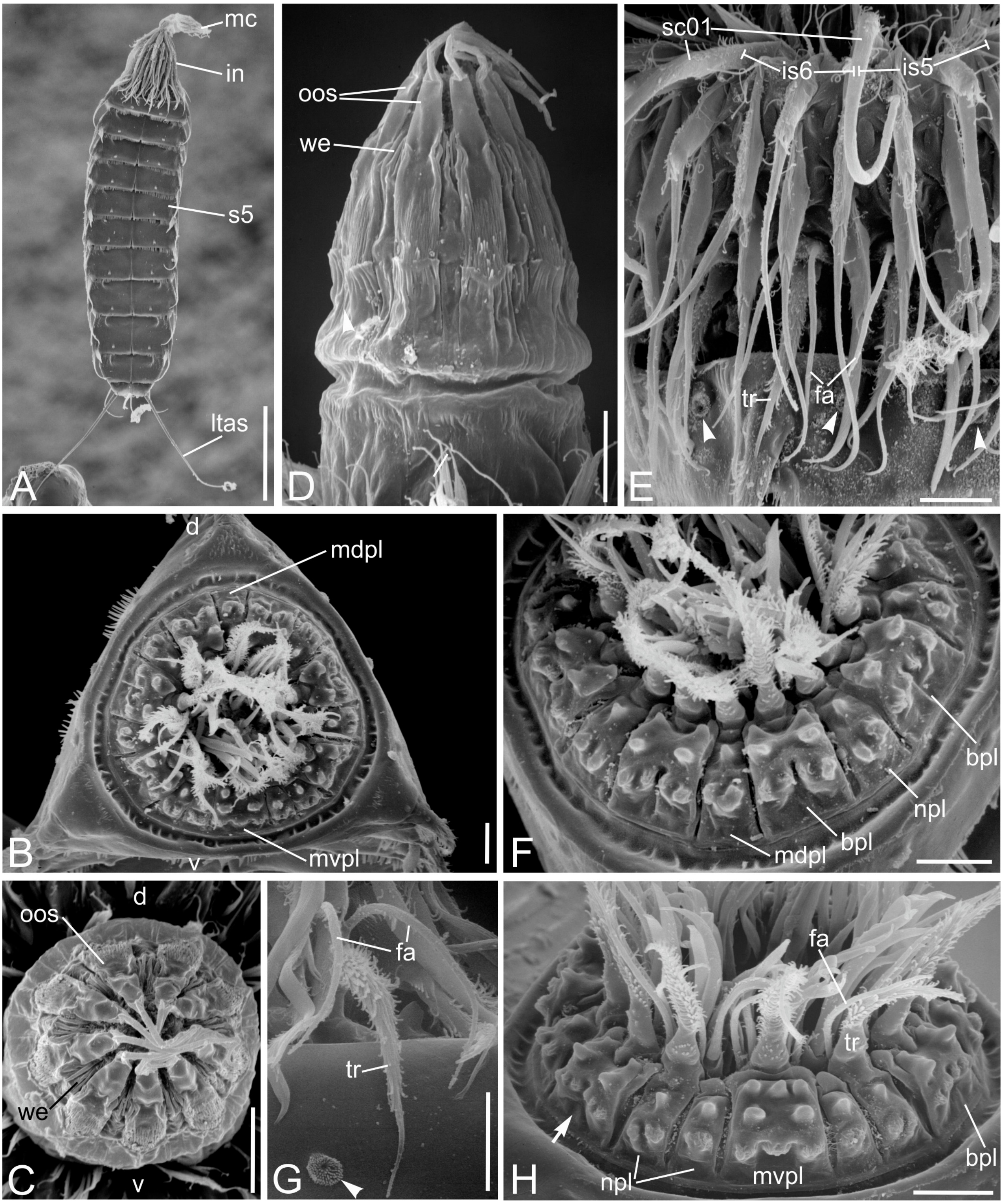

FIGURE 41. *Condyloderes shirleyi* **sp. nov.**, males (USNM 1481164, **A**, **G**; 1481168—RH-2707.04SEM, **B**, **F**; 1481170—RH-2707.08SEM, **H**) and female (USNM 1481170—RH-2707.07SEM, **C–E**) from ventral (**A**, **D**, **G**, **H**), frontal (**B**, **C**), dorsolateral-right (**E**), and dorsal (**F**) side, SEM. **A.** Habitus, head and mouth cone protruded. **B.** Trunk triangular in cross-section; (after Neuhaus 2013, fig. 5.1.14B, © Walter de Gruyter). **C, D.** Mouth cone; note thin tips of outer oral styles. **E.** Introvert sectors 5 and 6. **F, H.** Neck; arrow in **H** marks broad placid with six condyles in basal row; (**H** after Neuhaus 2013, fig. 51.14C, © Walter de Gruyter). **G.** Trichoscalid with filamentous appendages. Arrowheads in **E** and **G** mark type-6 sensory spots. Scale bar in **A** 100 µm. Scale bars in **B–H** 10 µm. Abbreviations: bpl, broader placid; d, dorsal side; fa, filamentous appendage; in, introvert; is5, introvert sector 5; ltas, lateral terminal accessory spine; mc, mouth cone; md1, middorsal spine of segment 1; mdpl, middorsal placid; mvpl, midventral placid; npl, narrower placid; oos, outer oral style; s5, segment 5; sc01, ring 01 primary spinoscalid; tr, trichoscalid; v, ventral side; we, cuticular weir.

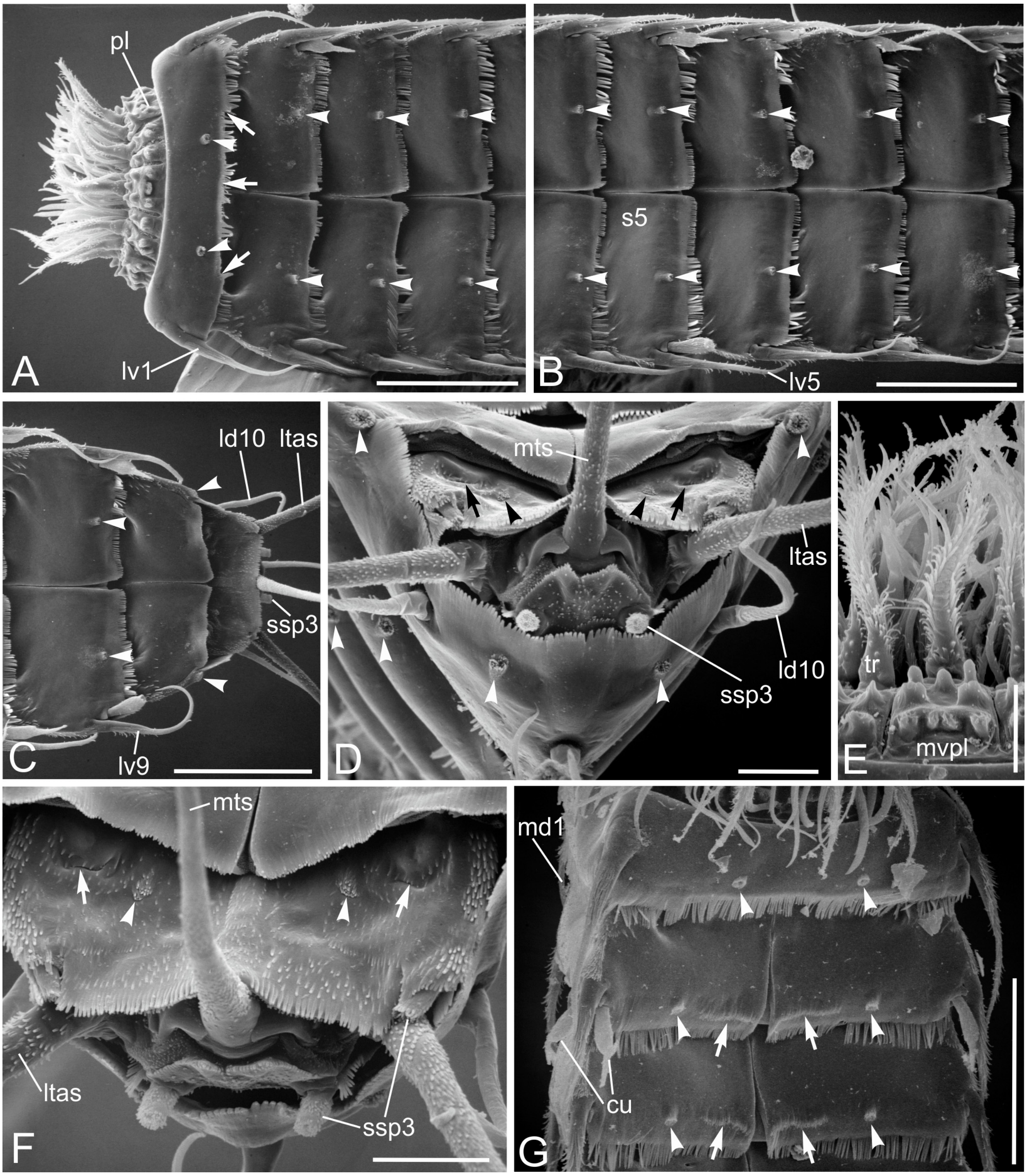

FIGURE 42. *Condyloderes shirleyi* **sp. nov.**, males (USNM 1481170—RH-2707.08SEM, **A–D**, **F**; 1481168—RH-2707.04SEM, **E**) and female (USNM 1481166, **G**) in ventral (**A–C**, **E–H**) and ventrocaudal view (**D**, **F**), SEM. **A.** Segments 1–4; arrows mark reduced free flap. **B.** Segments 5–8. **C.** Segments 9–11. **D, F.** Segments 10 and 11, ventral side up; arrows mark anterior ventrolateral unknown structures on segment 11. **E.** Placids and trichoscalids. **G.** Segments 1–3; arrows mark row of short cuticular projections on sternal plates. Arrowheads in **A–D, F,** and **G** mark type-6 sensory spots. Scale bars in **A–C** and **G** 40 µm. Scale bars in **D–F** 10 µm. Abbreviations: cu, cuspidate spine; ld10, laterodorsal spine of segment 10; ltas, lateral terminal spine; lv1, lateroventral spine of segment 1; md1, middorsal spine of segment 1; mts, midterminal spine; mvpl, midventral placid; pl, placid; s5, segment 5; ssp3, type-3 sensory spot; tr, trichoscalid.

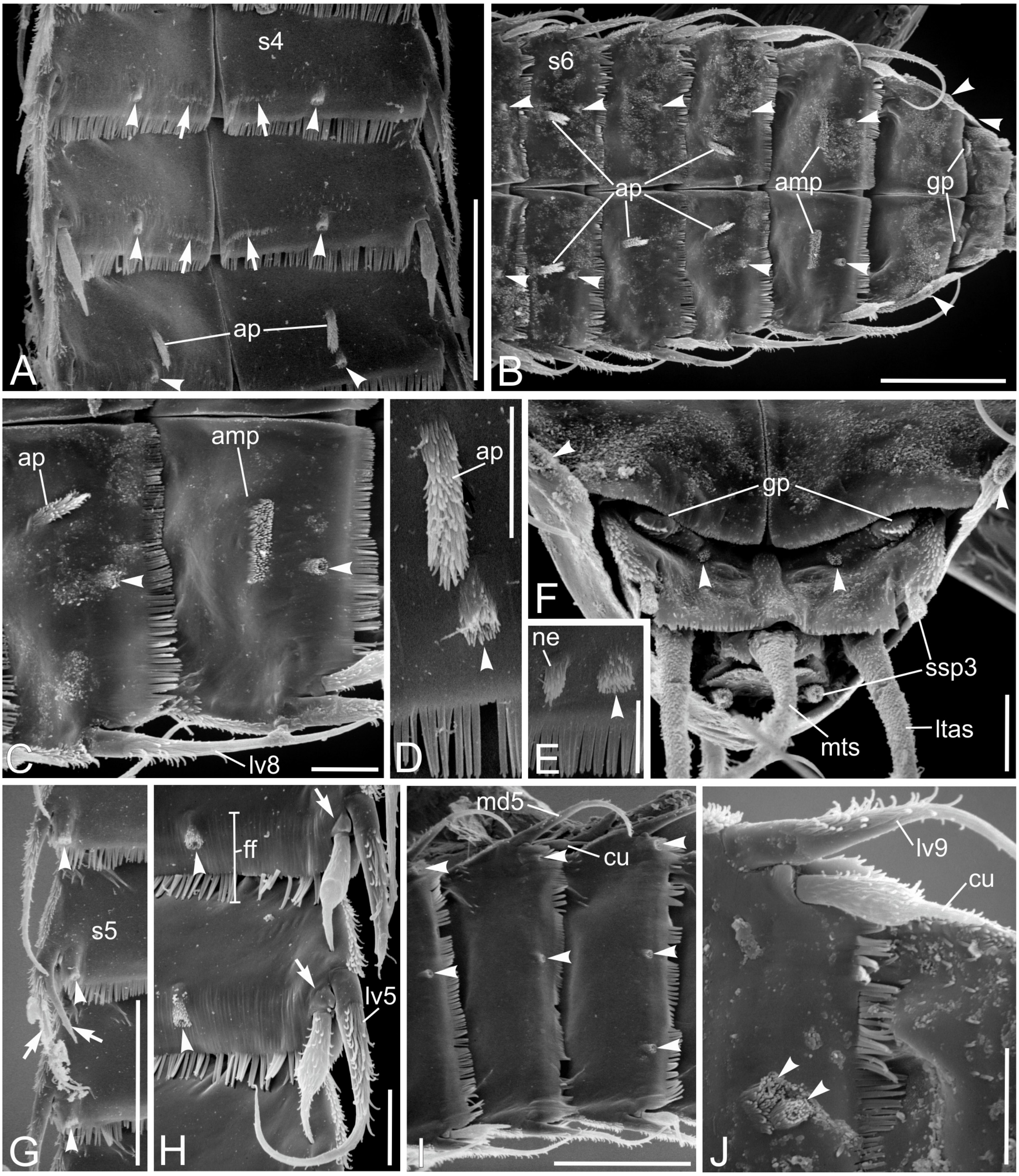

FIGURE 43. *Condyloderes shirleyi* **sp. nov.**, females (USNM 1481166, **A**, **D**, **E**, **G**; 1481170—RH-2707.07SEM, **B**, **C**, **F**) and males (USNM 1481168—RH-2707.04SEM, **H**; 1481168—RH-2707.05SEM, **I**; 1481171, **J**) from ventral (**A–D**, **H**, **J**), ventrocaudal (**F**), right (**E**, **G**), and left side (**I**), SEM. **A.** Segments 4–6; arrows mark row of short cuticular projections on sternal plates. **B.** Segments 6–11; note lack of appendage on left sternal plate of segment 7. **C.** Segments 8 and 9. **D.** Segment 6, female-specific appendage. **E.** Segment 9, sublateral protonephridial openings and sensory spot. **F.** Segments 10 and 11, gonopores. **G.** Segments 4 and 5, bifid middorsal acicular spine of segment 5 (arrows). **H.** Segments 4 and 5, cuspidate spine on segment 4 in ventrolateral instead of lateral accessory position; arrows mark attachment sites of cuspidate spines; (after Neuhaus 2013, fig. 5.1.14D, © Walter de Gruyter). **I.** Segments 4–6; note lack of sublateral spine on segment 5 **J.** Segment 9, sensory spot doubled. Arrowheads in **A–I** mark type-6 sensory spots. Scale bars in **A**, **B**, **G**, and **I** 40 µm. Scale bars in **C–D**, **H**, and **J** 10 µm. Scale bar in **E** 4 µm. Abbreviations: amp, female-specific area of micropapillae; ap, female-specific appendage; cu, cuspidate spine; ff, free flap; gp, gonopore; ltas, lateral terminal accessory spine; lv5, lateroventral spine of segment 5; md5, middorsal spine of segment 5; mts, midterminal spine; ne, protonephridial openings; s4, segment 4; ssp3, type-3 sensory spot.

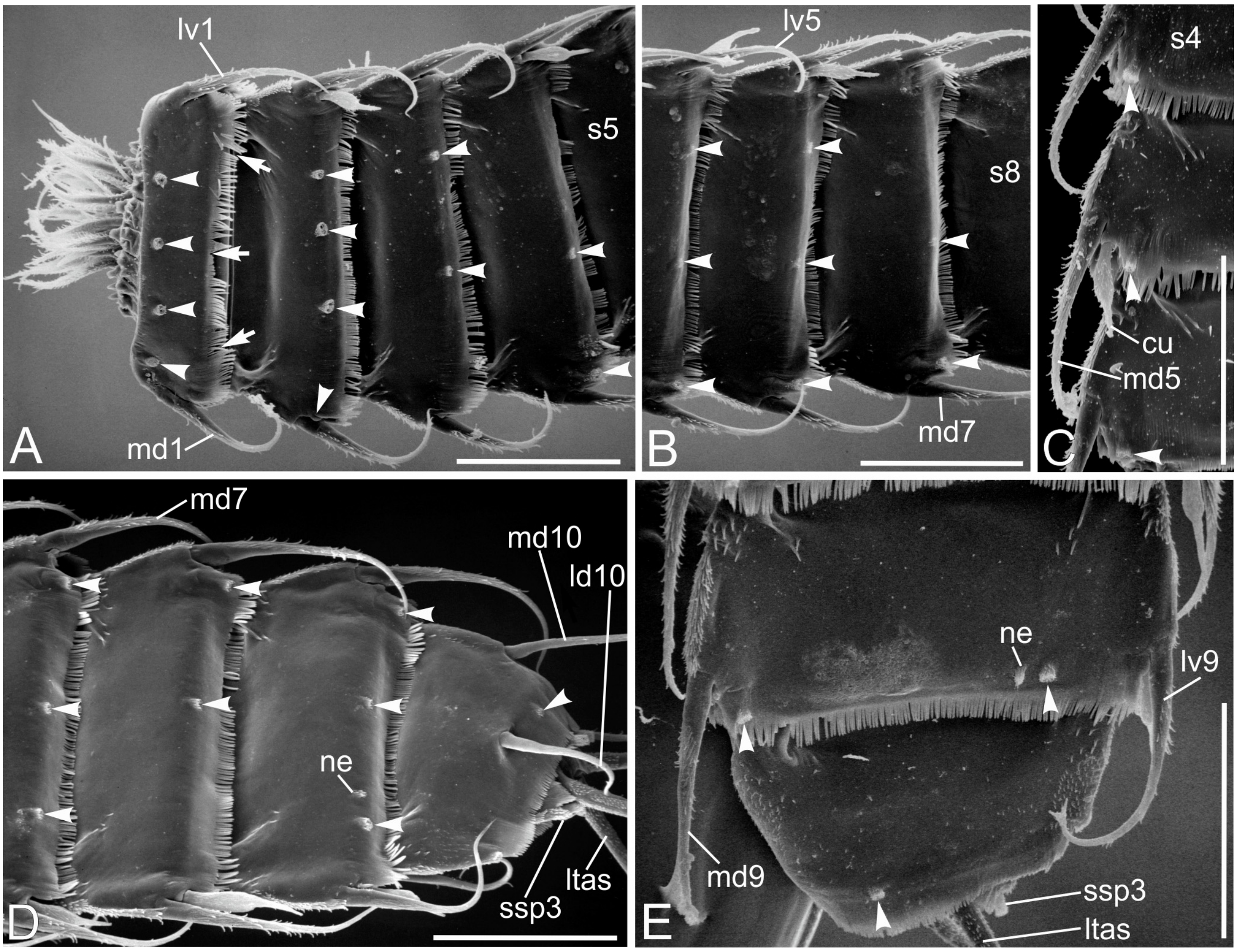

FIGURE 44. *Condyloderes shirleyi* **sp. nov.**, males (USNM 1481168—RH-2707.04SEM, **A**, **B**;1481167, **C**; 1481170—RH-2707.08SEM, **D**) and female (USNM 1481166, **E**;) from right (**AC**, **E**), and left side (**D**), SEM. **A.** Segments 1–4; arrows mark reduced free flap. **B.** Segments 6 and 7; notice lack of sublateral sensory spot on segment 7. **C.** Segments 4–6, middorsal cuspidate spine of segment 5. **D.** Segments 8–11, middorsal and laterodorsal spine on segment 10 of male and sublateral sensory spot on segment 7. **E.** Segments 9 and 10, lack of middorsal and laterodorsal spine on segment 10 of female. Arrowheads in **A–E** mark type-6 sensory spots. Scale bars in **A–E** 40 µm. Abbreviations: cu, cuspidate spine; ltas, lateral terminal accessory spine; lv1, lateroventral spine of segment 1; md1, middorsal spine of segment 1; ne, protonephridial openings; s4, segment 4; ssp3, type-3 sensory spot.

vary (comp. Figs 33C, 38F, G, 43B, C). A sensory spot may be missing or added on one (more frequently) or both sides (rarely) of a specimen, mainly ventromedially (Figs 38F, 40F–H, J–N, 43I, J; Table 5). A sensory spot may be missing in its regular position and appear in an unusual position (Fig. 40I). In addition, one female mounted for SEM reveals a bifid middorsal acicular spine on segment 5 (Fig. 43G). The variation of characters is probably higher than described here, but may not have been observed because of detritus particles on and under the free flap at the posterior margin of segments of almost all specimens.

Species identity of *Condyloderes shirleyi* sp. nov.

Specimens of *C. shirleyi* **sp. nov.** show a considerable amount of variation in the arrangement of spines, female appendages, and sensory spots (Table 5). Whereas variation in the latter two characters has not been considered as critical for taxonomic purposes, the spine formula is usually used as one of the key characters for identifying species of Kinorhyncha (Neuhaus 1993, 2013; Dal Zotto *et al.* 2013; Sørensen & Pardos 2008; Neuhaus & Sørensen 2013; Neuhaus *et al.* 2013, 2014; Neuhaus & Kegel 2015; Yamasaki 2016, 2017). Most variation in *C. shirleyi* **sp. nov.** refers to the cuspidate spines, *viz*, their presence or absence middorsally on segments 5 and 7 and

TABLE 5. Characters of 28 female and 45 male *Condyloderes shirleyi* **sp. nov.** present in the majority of specimens mounted for light microscopy (upper part of table) and variation of characters (lower part of table). Digits in brackets refer to number of specimens showing a variable character. Features appearing anteriorly on a segment do not show any background, features located centrally on a segment are indicated by a grey background, and characters occurring posteriorly on a segment are marked in black. Characters found in one gender only are indicated. Characters occupying an intermediate position to two reference positions are arranged right or left in a column (on segment 1: paradorsally to sublaterally, subdorsally to laterodorsally, and ventromedially to paraventrally). Positions of more frequent variation of organ (n ≥ 5) are highlighted by oblique hatching. Abbreviations: + or −, additional or lacking character in comparison with most frequent occurrence; ac, acicular spine; amp, area of micropapillae; ap, appendage; gc, gland cell outlet; la, lateral accessory; ld, laterodorsal; ltas, lateral terminal accessory spine; lv, lateroventral; md, middorsal; ml, midlateral; mts, midterminal spine; ne, nephridial openings; pd, paradorsal; sd, subdorsal; sl, sublateral; ssp3, type-3 sensory spot; vl, ventrolateral; vm, ventromedial.

Position Segment	md	pd	sd	ld	ml	sl	la	lv	vl	vm	pv
Character distribution in majority of specimens											
1	ac		ssp6	ssp6	ssp6	ssp6		ac		ssp6	
2	ac	ssp6		ssp6	ssp6	ssp6	cu	ac	cu	ssp6	
3	ac			ssp6		ssp6		ac		ssp6	
4	ac	ssp6		ssp6			cu	ac		ssp6	
5	ac ; cu	ssp6		ssp6		ssp6		ac	cu	ssp6	
6	ac	ssp6		ssp6		ssp6	cu	ac		ssp6 ; ♀: ap	
7	ac ; cu	ssp6		ssp6		ssp6		ac	cu	ssp6 ; ♀: ap	
8	ac	ssp6		ssp6			cu	ac		ssp6 ; ♀: ap	
9	ac	ssp6		ssp6		ne ; ssp6		ac	cu	ssp6 ; ♀: amp	
10	♂: ac		ssp6	♂: ac				ssp6		♂: gc	
11	mts		ssp3				ltas		ssp3	ssp(6?)	
Variation of characters											
1										+ssp6 (le) (1)	
2						ssp6 (ri) (le: n. a.) (1)	−cu (le/ri) (3)		−cu (le/ri) (4)	+ssp6 (le) (1)	+cu (ri) (1)
3				+ssp6 (le) (1)						+ssp6 (le/ri) (2)	
4							−cu (le/ri) (3)	ac (le) thin (1)			
5	−cu (24)						+cu (le) (1)	−ac (ri) (1)	−cu (le/ri) (3)	−ssp6 (le/ri) (2)	
6				−ssp6 (le) (1)		+ssp6 (ri) (1)	−cu (le/ri) (7) −cu (5)			−♀: ap (le) (1)	
7	−cu (33)			−ssp6 (le) (1)			+cu (le/ri) (9) +cu (2)		−cu (le/ri) (15) −cu (24)	−♀: ap (ri) (1) −ssp6 (ri) (1) +ssp6 (le) (1)	
8							−cu (le/ri) (4)	ac (ri) thin (1)	+cu (le) (2)	+ssp6 (le/ri) (2)	
9	ac thin (1)	+ssp6 (le) anterior to 2nd ssp6 (ri n. a.) (1) +ssp6 (ri) (1)				−ssp6 (1) −ssp6 (le) (1)	+cu (le/ri) (2) +cu (1)	ac (ri) thin (1) −ac (le) (1)	−cu (le/ri) (5) −cu (1)	−ssp6 (1)	
10								−ssp6 (ri) (1)		+ssp6 (2) +ssp6 (ri) (1)	

on one or both sides ventrolaterally or in a lateral accessory position on segments 4, 6, 7 and 9 or in a switch of their position between ventrolateral and lateral accessory (Table 5). Absence of a tube on one side only in 7 out of 11specimens of *Centroderes barbanigra* Neuhaus, Pardos, Sørensen & Higgins, 2014 and in 3 out of 10 specimens of *Centroderes bonnyae* Neuhaus, Pardos, Sørensen & Higgins, 2014 has been treated as if the specimens possessed this spine on both sides of the respective segment, because the specimens agreed otherwise with specimens with bilateral symmetrical arrangement of tubes (Neuhaus *et al.* 2014). A similar situation is found in *C. shirleyi* **sp. nov.**, all specimens agree in their morphology except for the variation mentioned (Table 5).

However, specimens of *Centroderes barbanigra*, *C. bonnyae*, and *C. drakei* Neuhaus, Pardos, Sørensen & Higgins, 2014 differ from specimens of *Condyloderes shirleyi* **sp. nov.** by a discontinuous *versus* a continuous character distribution. The three species of *Centroderes* co-occur at the same locality but can be discriminated from each other by several characters (Neuhaus *et al.* 2014, table 5). It is not possible to separate the specimens of *C. shirleyi* **sp. nov.** from one and the same sample into populations with distinct characters, because character distribution appears continuous among different specimens. Therefore, we regard all specimens of *C. shirleyi* **sp. nov.** as belonging to just one species with a high morphological plasticity in certain segments.

TABLE 6. *Condyloderes shirleyi* **sp. nov.**, morphological data of the holotype, 10 additional males, and 10 females (length in µm). Holotype indicated by bold catalogue number; data given for left/right side if applicable. Abbreviations: ac, acicular spine; cu, cuspidate spine; ld10, length of laterodorsal spine of segment 10; ltas, length of lateral terminal accessory spine; lv1, length of lateroventral spine of segment 1; md1, length of middorsal spine on segment 1; mts, midterminal spine; n, number of specimens measured; s1, length of segment 1; sw8, standard width of segment 8; TL, trunk length; USNM, catalogue number of United States National Museum; vl2, length of ventrolateral spine of segment 2.

Character	USNM 1480999 (♂)	range (♂)	mean (♂)	standard deviation (♂)	n (♂)	range (♀)	mean (♀)	standard deviation (♀)	n (♀)
TL	413	360–413	386	±15	11	328–436	381	±27	10
s1	23	23–37	30	±4	11	26–37	32	±4	10
s2	38	30–38	35	±2	11	30–40	35	±3	10
s3	40	34–42	37	±2	11	32–40	36	±3	10
s4	40	34–44	40	±3	11	33–42	39	±3	10
s5	41	36–44	40	±3	11	36–45	40	±3	10
s6	44	40–48	45	±2	11	38–48	43	±3	10
s7	47	44–50	47	±2	11	43–53	47	±3	10
s8	47	46–52	50	±2	11	50–54	52	±1	10
s9	51	44–55	51	±3	11	51–56	53	±2	10
s10	43	36–46	39	±3	11	44–50	47	±2	10
s11	22	20–27	23	±2	11	23–30	26	±2	10
sw8	90	84–90	87	±2	11	80–96	88	±4	10
sw10	70	68–72	70	±1	11	70–76	73	±2	10
md1 (ac)	57	46–57	50	±4	11	32–54	43	±7	10
md2 (ac)	50	42–56	47	±4	11	34–54	45	±6	10
md3 (ac)	57	45–57	50	±3	11	36–54	47	±6	10
md4 (ac)	50	44–53	49	±3	11	42–61	51	±5	10
md5 (ac)	54	48–54	51	±2	10	45–57	52	±3	10
md5 (cu)	n. a.	18–20	19	±1	5	19–22	20	±1	3
md6 (ac)	54	46–56	52	±3	11	47–58	52	±4	10
md7 (ac)	57	50–57	53	±3	11	49–64	55	±5	10

......*continued on the next page*

TABLE 6. (Continued)

Character	USNM 1480999 (♂)	range (♂)	mean (♂)	standard deviation (♂)	n (♂)	range (♀)	mean (♀)	standard deviation (♀)	n (♀)
md7 (cu)	19	18–21	19	±1	3	16–20	18	±2	2
md8 (ac)	63	48–63	56	±4	11	50–66	59	±4	10
md9 (ac)	60	54–63	60	±3	11	63–76	67	±4	9
md10 (ac)	60	42–60	54	±5	10	-	-	-	-
ld10 (ac)	57/54	40–58	52	±5	12	-	-	-	-
mts (ac)	125	90–139	111	±12	11	100–108	104	±3	10
lv1 (ac)	48/45	42–52	48	±3	12	35–50	44	±4	10
vl2 (cu)	n. a./19	16–20	18	±1	10	14–20	17	±2	10
lv2(ac)	45/48	40–48	45	±2	12	43–53	47	±3	10
la2 (cu)	19/19	16–19	18	±1	12	16–24	18	±3	10
lv3 (ac)	45/50	38–52	45	±4	12	38–54	47	±4	10
lv4 (ac)	49/49	44–52	47	±3	12	46–54	50	±2	10
la4 (cu)	17/18	17–21	19	±1	12	16–26	20	±3	10
vl5 (cu)	19/19	18–23	21	±2	12	17–21	20	±1	10
lv5 (ac)	53/54	46–54	50	±3	12	50–56	51	±2	10
lv6 (ac)	50/53	44–54	50	±3	12	50–56	53	±2	10
la6 (cu)	20/21	19–23	21	±1	12	14–24	19	±3	8
vl7 (cu)	19/18	18–22	20	±1	9	16–22	19	±2	6
lv7 (ac)	54/54	46–55	51	±3	12	52–56	54	±1	10
lv8 (ac)	55/54	46–58	52	±4	12	52–61	57	±3	10
la8 (cu)	25/25	19–28	25	±3	12	18–28	24	±3	10
vl9 (cu)	17/21	17–22	20	±1	12	18–24	20	±2	10
lv9 (ac)	54/51	48–57	53	±3	12	56–66	62	±3	10
ltas (ac)	199/208	180–208	192	±8	12	166–200	186	±9	10

Condyloderes shirleyi **sp. nov.** also shows cuspidate spines on segments 5 and 7–9 frequently in a lateral accessory instead of a ventrolateral position or *vice versa* (Table 5). A similar phenomenon has been reported from species of *Centroderes* in the Northwest Atlantic for the occurrence of tubes on segments 2, 5, and 7 and was attributed to the "quality of preparation" (Neuhaus *et al*. 2014, p. 6). However, in *C. barbanigra* the tube on segment 7 may appear either lateroventrally or ventrolaterally (Neuhaus *et al*. 2014, p. 17). These are to our knowledge the first records of the variation of a spine displaying a switched position on a segment, sometimes only on one side, sometimes on both sides.

Discussion

Synonymy of *C. megastigma* with *C. setoensis*

Condyloderes megastigma differs from *C. setoensis* in the possession of a lateral accessory cuspidate spine on segment 4 *versus* the lack of this character in *C. setoensis* (Tables 2, 7). Female *C. megastigma* display a paraventral type-1 (?) sensory spot on segments 2–5 (Figs 24A, 25A), but this character is only barely visible in the single female of *C. setoensis* because of its staining (Fig. 22C). One paratypic male of *C. setoensis* (AVA-CM-Jap02) exhibits a lateral accessory cuspidate spine on segment 4 on one side only, so the specimen shows a character intermediate between *C. megastigma* and *C. setoensis*. This finding means that characters to distinguish

C. megastigma from *C. setoensis* are lacking. Therefore, we herewith conclude that *C. megastigma* is conspecific with *C. setoensis* and represents a junior synonym of this species. We also interpret the minor differences in sensory spot and spine occurrence between the populations recorded from relatively close areas in the Korea Strait as variation (comp. also chapters Original material of "*Condyloderes megastigma* Sørensen, Rho & Kim, 2010b" and Additional material of "*Condyloderes megastigma*"; Tables 2, 4, 7).

Differential diagnosis

Spines on segment 10 are not used here for the discrimination of species of *Condyloderes* for the reasons given in the following chapter (see Discrimination of female and male in species of *Condyloderes*).

Condyloderes kurilensis differs from all other species of the genus by a reduced primary pectinate fringe on all segments and a free flap with numerous short spinose or broader extensions on most parts of a segment *versus* a well developed pectinate fringe in all other species, the lack of a type-6 sensory spot ventromedially on segments 3 and 7, sublaterally on segment 2, laterodorsally on segments 4–6, and paradorsally on segment 2 *versus* the existence of these spots in all other species (Tables 2, 7). *Condyloderes shirleyi* **sp. nov.** differs from all other species of the genus by four condyles in the basal row of all broader placids *versus* only three such condyles in all other species, two condyles in the basal row of all narrower placids except the paraventral one *versus* only one such condyle in all other species, a partly reduced laterodorsal to midlateral free flap of segment 1 *versus* its existence in all other species, a reduced number of irregularly arranged cuticular hairs on segments 210 *versus* numerous such hairs in all other species, the existence of a ventrolateral cuspidate spine on segment 7 (but missing in many specimens) *versus* the lack of this spine in all other species, the existence of a lateral accessory spine on segments 2 and 6 (but missing in many specimens on segment 6) *versus* the lack of this spine in all other species, the existence of a ventromedial to paraventral row of cuticular projections anterior to the free flap on segments 2–5 of females *versus* the lack of this character in all other species, and the existence of a ventromedial appendage on segment 6 of females *versus* the lack of this character in all other species (Tables 2, 5, 7). *Condyloderes storchi* differs from all other species by the existence of a lateral accessory spine on segment 1 *versus* the lack of this spine in all other species (Tables 2, 7).

Condyloderes multispinosus, *C. paradoxus*, and *C. setoensis* are not identified by unique characters but each by a combination of characters shared with other species or discriminating them from other species. Whereas *C. multispinosus* agrees with *C. kurilensis* in the lack of a lateral accessory cuspidate spine on segment 4, it differs from this species by the existence of a ventrolateral cuspidate spine on segments 2 and 9 as well as by the existence of a type-6 sensory spot ventrolaterally on segments 3 and 7, sublaterally on segments 2 and 8, and paradorsally on segment 7 (Tables 2, 7). *Condyloderes multispinosus* differs from both *C. paradoxus* and *C. setoensis* by the lack of a lateral accessory cuspidate spine on segment 4, the lack of a ventromedial type-6 sensory spot on segment 5 (but this character also missing in one male of *C. setoensis*), as well as by the existence of a type-6 sensory spot laterodorsally on segment 1 and paradorsally on segment 7 (but these characters also exist in several specimens of *C. paradoxus*).

Condyloderes paradoxus differs from *C. setoensis* in the possession of a type-6 sensory spot laterodorsally on segment 1, paradorsally on segment 7, and sublaterally on segment 8 *versus* the lack of these characters in the latter species (Tables 2, 7). However, one female *C. paradoxus* from Singapore (ZMUC-KIN-848) lacks a type-6 sensory spot laterodorsally on segment 1 and paradorsally on segment 7. This leaves a sublateral sensory spot on segment 8 as the single distinguishing character between *C. paradoxus* and *C. setoensis* (for spines on segment 10 see before). In view of the significant variation in *C. shirleyi* **sp. nov.** (Table 5) and the few specimens of *C. paradoxus* and *C. setoensis* studied, the minor difference(s) between the latter two species concerning the occurrence of a sensory spot in a single position, *viz* sublaterally on segment 8 (and two spines on segment 10 of females, but see before and subsequent chapter Discrimination of female and male in species of *Condyloderes*), indicate a very close relationship between these species if not species identity with minor variation. We only refrain from synonomizing the two species at this stage because of the lack of specimens moulting to a second adult life history stage or of a specimen with a sublateral type-6 sensory spot on only one side of segment 8.

TABLE 7. Comparison of selected characters of species of *Condyloderes* present in the majority of specimens mounted for light microscopy. + / –, character present / not present; [ ], indicates variation in few specimens. Characters unique within genus are underlain with grey background. Measurements taken from Higgins (1969), Adrianov *et al*. (2002), Martorelli & Higgins (2004), Sørensen *et al*. (2010b), Adrianov & Maiorova (2016), and this paper (Tables 2–6).

Species	*C. kurilensis*	*C. multispinosus*	*C. paradoxus*	*C. setoensis*		*C. shirleyi* **sp. nov.**	*C. storchi*	*Condyloderes* sp. 1
Character					(previously *C. megastigma*)			
specimens studied as ♀ / ♂ (light microscopy)	1 ♀, 1 ♂	4 ♂	5 ♀, 7 ♂	1 ♀, 4 ♂	2 ♀, 5 ♂	28 ♀, 46 ♂	1 ♂	1 ♂
trunk length	370–402 µm	336–356 µm	216–282 µm	226–296 µm	265–343 µm	356–436 µm	320 µm	185 µm
length of lateral terminal accessory spine	188–190 µm	193–223 µm	148–170 µm	131–188 µm	154–221 µm	166–200 µm	200 µm	103 µm
length of midterminal spine	114 µm	80–107 µm	85–96 µm	77–93 µm	67–111 µm	90–139 µm	100 µm	79 µm
trichoscalids with trichoscalid plate	+	+	+	+	+	+	+	n. a.
filiform appendages anterior to trichoscalids	+	+	+	+	+	+	+	n. a.
broad midventral placid neighboured by 2 narrow placids and alternatingly a broader and narrower placid	+	+	+	+	+	+	+	+
arrangement of condyles on broader placids	n. a.	o o o o o o	o o o o o o	o o o o o o	o o o o o o	o o o o oooo	o o o o o o	n. a.
arrangement of condyles on midventral placid	n. a.	ooo o o o o o	ooo o o o o o	ooo o o o o o	ooo o o o o o	ooo o o oooo	ooo o o o o o	n. a.
arrangement of condyles on narrower placids	o o	o	o o	o	o	o o o	o? o	n. a.
arrangement of condyles on paraventral narrow placid	o	o	o o	o	o	o o	o o	n. a.
segment 1 with partly reduced ventromedial to midventral free flap (including primary pectinate fringe)	+	+	+	+	+	+	+	n. a.
segment 1 with partly reduced laterodorsal to midlateral free flap (including primary pectinate fringe)	–	–	–	–	–	+	–	–
primary pectinate fringe of all segments reduced, free flap with numerous short spinose or broader extensions on most parts of a segment	+	–	–	–	–	–	–	–
irregularly arranged cuticular hairs on segments 2–10	many	many	many	many	many	few	many	many
middorsal cuspidate spine on segments	–	–	–	–	–	5 [–], 7 [–]	5, 7	–
ventrolateral cuspidate spine on segments	5	2, 5, 9	2, 5, 9	2, 5, 9	2 [–], 5, 9	2, 5, 7 [–], 9	5, 9	5 (displaced ventromedially)
lateral accessory cuspidate spine on segments	8	8	4, 8	[4], 8	4, 8	2, 4, 6 [–], 8	1, 4, 8	8
sublateral cuspidate spine on segments	–	–	–	–	–	–	–	3, 4?, 9
lateral terminal accessory spine with two thin areas	+	+	+	+	+	+	+	n. a.
♀: middorsal & lateroventral acicular spine on segment 10	–	n. a.	+	–	–	–	n. a.	n. a.
♂: middorsal & laterodorsal acicular spine on segment 10	+	+	+	+	+	+	+	(± subdorsally?)

… …continued on the next page

TABLE 7. (continued)

Species	*C. kurilensis*	*C. multispinosus*	*C. paradoxus*	*C. setoensis*		*C. shirleyi* **sp. nov.**	*C. storchi*	*Condyloderes* sp. 1
Character					(previously *C. megastigma*)			
specimens studied as ♀ / ♂ (light microscopy)	1 ♀, 1 ♂	4 ♂	5 ♀, 7 ♂	1 ♀, 4 ♂	2 ♀, 5 ♂	28 ♀, 46 ♂	1 ♂	1 ♂
♀: paraventral type-1 (?) sensory spot on segments	2?	n. a.	n. a. (dirt)	2–5	2–5	–	n. a.	n. a.
♀: ventromedial to paraventral row of cuticular projections anterior to free flap (SEM only) on segments	n. a.	n. a.	n. a. (dirt)	–	–	2–5	n. a.	n. a.
ventromedial type-6 sensory spot not on segments	3, 5, 7, 10, 11	5, 10, 11	10, 11	10	[5], 10	10	10	n. a.
sublateral type-6 sensory spot not on segments	2, 4, 8, 10, 11	4, 10, 11	4, 10, 11	4, 8, 10, 11	4, 8, 10, 11	4, 8, 10, 11	4, 8, 10, 11	n. a.
laterodorsal type-6 sensory spot not on segments	1, 4–6, 11	10, 11	[1],10, 11	1, 10, 11	1, 10, 11	10, 11	10, 11	n. a.
paradorsal type-6 sensory spot not on segments	2 , 3, 7, 10, 11	3, 10, 11	3, [7], 10, 11	3, 7, 10, 11	3, 7, 10, 11	3, 10, 11	3, 7, 10, 11	n. a.
♀: ventromedial appendage on segment 6	–	n. a.	–	–	–	+	n. a.	n. a.
♀: ventromedial appendage on segment 7	+	n. a.	+	+	+	+	n. a.	n. a.
♀: ventromedial appendage on segment 8	+	n. a.	+	+	+	+	n. a.	n. a.
♀: ventromedial area of micropapillae on segment 9	+	n. a.	+	+	+	+	n. a.	n. a.
segment 11 with 1 tergal and 1 sternal plate	+	+	+	+	+	+	+	+

Discrimination of female and male in species of *Condyloderes*

The sex of species of *Condyloderes* has been misidentified in at least some specimens of almost all described species except *C. kurilensis* and *C. storchi* (for which only a single male is known; Table 1). The key characters to distinguish the female from the male, *viz*, the ventromedial appendage at least on segments 7 and 8 as well as the ventromedial area of micropapillae on segment 9, were not recognized in several studies (McIntyre 1962; Higgins 1969; Adrianov *et al*. 2002; Sørensen *et al*. 2016). Sørensen *et al*. (2010b) recognized and described these characters for the first time for a species of *Condyloderes* and regarded them as species-specific characters, also because they mistook several females as males (see also chapter Comments about selected morphological characters). Adrianov and Maiorova (2016) were the first to correctly address the appendages and the area of micropapillae as a sex-specific character in *C. kurilensis*. Since they did not re-investigate *C. megastigma*, the only other known species with these characters at that time, they did not realize that their interpretation was true for all already described species of the genus *Condyloderes* in general. The latter interpretation became reasonable only in this paper by the re-study of all known species of *Condyloderes*, description of a new species based on numerous specimens, and examination of several more undescribed species of *Condyloderes* in the current authors' hands (Dal Zotto, Neuhaus, and Yamasaki, unpubl. obs.). The latter material and the hint of an anonymous reviewer suggest however, that there seem to be different evolutionary lines within *Condyloderes*. In species with irregularly distributed or almost no cuticular hairs on the segments' surface, the female does possess a ventromedial area of micropapillae on segment 9 and lacks both a middorsal and a lateral acicular spine on segment 10. In species with a different arrangement of cuticular hairs, the female lacks the area of micropapillae on segment 9 but reveals a middorsal and a lateral acicular spine on segment 10.

Male specimens of all species of *Condyloderes* reveal a middorsal and a laterodorsal acicular spine on segment 10, whereas females of all species except *C. paradoxus* (females unknown for *C. multispinosus*) lack spines on segment 10 (Table 2). The middorsal and lateroventral acicular spine on segment 10 of female *C. paradoxus* (Tables 2, 7) may not represent species-specific but developmental characters. Few adult specimens of almost all species of *Condyloderes* were studied (Tables 1, 7), and reports of adult specimens moulting to a second adult life history stage are missing yet. However, it has been documented for several species of *Campyloderes* and *Centroderes* that an adult life history stage may moult from a stage with spines on segment 10 to another adult life history stage without any spine on this segment (Neuhaus & Sørensen 2013; Neuhaus *et al*. 2014). It cannot be excluded that more than one adult life history stage exists also in species of *Condyloderes*, especially in the light of the suggested close phylogenetic relationship between this genus and *Centroderes* (see Sørensen *et al*. 2015).

Comments about selected morphological characters

During our ongoing study about a number of new species of *Condyloderes* we realized that we had to re-evaluate several characters of species of *Condyloderes*. The current paper certainly benefits both from a considerably higher number of specimens available to us (up to 84 adults for one species opposed by only 1–12 specimens available for any species in previous studies), a re-investigation of all known species of *Condyloderes*, and from a wide range of several undescribed new species one of which is described in this paper, *viz*, *C. shirleyi* **sp. nov.**, and another is noted briefly. This broad amount of information also provided us with new insights into character distribution. In the following we discuss selected characters.

Position of cuspidate spines and sensory spots. Mature specimens of species of *Condyloderes* reveal a strongly sclerotized cuticle and an almost triangular cross-section with prominent middorsal and lateral edges resulting in kinds of "keels" (Fig. 41B). During the dorsoventral preparation of a specimen for light microscopy, the edges may be simply pressed in dorsoventral direction or may "fall" to one side (Figs 35B, 39F, G), especially if a specimen ends up with both the ventral and sublateral area in one focal plane. If the middorsal keel falls to one side, a middorsal cuspidate spine may appear to originate slightly paradorsal of the middorsal acicular spine of these segments (*C. shirleyi* **sp. nov.**: Figs 35B, 39F, G; for *C. storchi* see Martorelli & Higgins 2004, p. 87, fig. 3). In fact, these cuspidate spines emerge from below the associated acicular middorsal spine in *Condyloderes shirleyi* **sp. nov.** (Figs 39E, 43I, 44C) and in *C. storchi* (Fig. 30D). Similarly, the ventrolateral and lateral accessory cuspidate spine of a given segment seem to attach from below the neighbouring lateroventral acicular spine in some specimens. In favourite mounts however, it turns out that the ventrolateral and lateral accessory cuspidate spine originate from a modified attachment area slightly anterior to the neighbouring free flap (Figs 36A, D, 39E, K–M, 43H). The result of preparation of a specimen may also lead to problems in identifying the reference position of a sensory spot properly, especially with respect to the paradorsal sensory spot on segment 1 appearing almost in a subdorsal position in all species.

Sternal plate on segment 11. Segment 11 of all species of *Condyloderes* studied reveals a single sternal plate rather than a sternal plate with an "underdeveloped" midventral articulation (Adrianov *et al*. 2002, p. 214; Adrianov & Maiorova 2016, p. 15) or two sternal plates (Higgins 1969; Martorelli & Higgins 2004). However, we noticed in several specimens of different species that the sternal plate revealed a midventral to paraventral area, which appeared optically separated from the remaining plate because of a paraventral fold in the cuticle (*C. multispinosus*: Fig. 11D, F, *C. setoensis*: Fig. 20H, *C. shirleyi* **sp. nov.**: Figs 35G, 38G, 39C, D, 40I, 42F, 43F). Because the insertion area of the dorsoventral muscles of segment 11 is located in a paraventral position, we suggest that contraction of these dorsoventral muscles during fixation caused the midventral to paraventral area to stand out slightly against the remaining sternal plate and that a midsternal articulation of whatever degree does not exist on segment 11 in the species studied here.

Lateral terminal accessory spine. Segment 11 of all species of *Condyloderes* reveals a single lateral spine, whereas all species of Cyclorhagida except the males of most Echinoderidae reveal two such spines on the segment, *viz*, a lateral terminal spine in the lateroventral position and a lateral terminal accessory spine in the lateral accessory position (comp. Neuhaus 2013, table 8). The spine of species of *Condyloderes* has been reported as a lateral terminal spine for almost all species but as a lateral terminal accessory spine for *C. setoensis* (previously *C. megastigma*) (see McIntyre 1962; Higgins 1969; Adrianov *et al*. 2002; Martorelli & Higgins 2004; Sørensen *et al*. 2010b; Adrianov & Maiorova 2016). We fully agree with the interpretation of Sørensen *et al*. (2010b), because in fact the spine is located in a lateral accessory rather than a lateroventral position, i. e., in a more dorsal than lateroventral position (*C. kurilensis*: Fig. 7B, *C. multispinosus*: Fig. 11C, *C. paradoxus*: Fig. 16D, *C. setoensis*: Fig. 20H, *C. setoensis* (previously *C. megastigma*): Fig. 27B, *C. storchi*: Fig. 31E, *C. shirleyi* **sp. nov.**: Figs 36F, 44D, E). Further evidence may come from the two thin areas in the spine (*C. multispinosus*: Fig. 11E, *C. setoensis*: Fig. 20D, *C. setoensis* (previously *C. megastigma*): Fig. 27D, *C. shirleyi* **sp. nov.**: Fig. 38E). Exactly two such thin areas have been noted for the lateral terminal accessory spine but not for the lateral terminal spine of *Campyloderes* cf. *vanhoeffeni* by Neuhaus and Sørensen (2013) and are now known for *Ryuguderes iejimaensis* Yamasaki, 2016 as well (Neuhaus, unpubl. obs.), whereas this character is unknown for species of *Centroderes* (Neuhaus *et al.* 2013, 2014). Species of *Campyloderes*, *Centroderes*, and *Condyloderes* have been included in a taxon Centroderidae previously (see summary in Neuhaus 2013, tables 5, 9), but this grouping has been rejected more recently (Sørensen *et al*. 2015).

Sex. In all described species of *Condyloderes* except *C. kurilensis* and *C. storchi* (for which only a single male is known), the sex has been identified incorrectly in at least some specimens (see chapter Discrimination of female and male in species of *Condyloderes*; McIntyre 1962; Higgins 1969; Adrianov *et al*. 2002; Sørensen *et al*. 2010b, 2016; Adrianov & Maiorova 2016). Two specimens of *C. multispinosus* studied by Higgins (1969; USNM W37459, 1209821) reveal ventrolaterally in the anterior third of segment 11 a weak curved sclerotization (Fig. 11F). Probably, these structures of unknown function were mistaken as female gonopores. Similar structures are reported here for several male *C. shirleyi* **sp. nov.** (Figs 39C, D, 42D, F). However, gonopores would be expected directly at the border of segments 10 and 11. Possibly, a longitudinal (?) muscle may attach in this area and may have contracted. Alternatively, a gland cell may deliver its contents through what appears like a slit-like opening in one specimen mounted for SEM (Fig. 42F). However, no cuticular ducts or gland cells could be traced in any specimen mounted for light microscopy, which also may be because of the macerating activity of Hoyer's mounting medium. The nature of the structures remains unclear.

In *C. setoensis* (previously *C. megastigma*), two out of five specimens lacked the ventrolateral cuspidate spine on segment 2, and this character was attributed to the female sex whereas specimens with a ventrolateral cuspidate spine on segment 2 were regarded as male (Sørensen *et al*. 2010b, p. 239, figs 2C, 4C) despite the presence of female gonopores in one specimen mounted for light microscopy (Fig. 27B, C). Presence and absence of the cuspidate spine on segment 2 is regarded merely as variation within the species in the current paper, also based on the observation of considerable variation described for *C. shirleyi* **sp. nov.** in this paper and known for a range of undescribed species of *Condyloderes* (Dal Zotto, Neuhaus & Yamasaki, unpubl. obs.). Spine pattern was and still is regarded as taxonomically important for Kinorhyncha (Sørensen & Pardos 2008; Neuhaus 2013; Dal Zotto *et al.* 2013; Yamasaki 2016, 2017), but at the time of the original description of *C. setoensis* (previously *C. megastigma*) in 2010 no information was available about the variation of the spine pattern of kinorhynch species described subsequently (Neuhaus & Sørensen 2013; Neuhaus *et al.* 2013, 2014; Neuhaus & Kegel 2015; this paper). Also, Sørensen *et al.* (2010b) were the first to describe the ventromedial appendages on segments 7 and 8 and the ventromedial large area of micropapillae on segment 9. These characters were discussed in a taxonomic content in their study in 2010 but are now known to discriminate in all currently described species the female from the male which lack these characters (see previous chapter).

Outlook

Until this study, variation was rarely mentioned for kinorhynch species (e. g., Neuhaus & Sørensen 2013; Neuhaus *et al.* 2013, 2014; Neuhaus & Kegel 2015) and was not even thought to be of any importance for kinorhynch taxonomy (Sørensen & Pardos 2008; Neuhaus 2013; Dal Zotto *et al*. 2013; Yamasaki 2016, 2017). Our current observation of an enormous amount of variation in *C. shirleyi* **sp. nov.** from a single location changes the situation entirely. This finding and our re-descriptions emphasize that individual specimens should be checked more carefully for variation and this variation should be documented.

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