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Populations of *Campyloderes* sp. (Kinorhyncha, Cyclorhagida): One global species with significant morphological variation?

Birger Neuhaus [a,*], Martin Vinther Sørensen [b]

[a] *Museum für Naturkunde Berlin, Invalidenstr. 43, D-10115 Berlin, Germany*
[b] *Natural History Museum of Denmark, Universitetsparken 15, DK-2100 Copenhagen, Denmark*

ARTICLE INFO

ABSTRACT

Altogether, 103 adult and 23 juvenile specimens of *Campyloderes* from 33 locations both in the deep sea and on the continental shelf all over the world were studied by light microscopy (97 specimens) and scanning electron microscopy (28 specimens). Especially from the Faroe Island, the Central American East Pacific Ocean and from the area east and northeast of New Zealand, enough specimens are available to study the regional variation of characters. Specimens both from these regional areas and worldwide reveal a significant morphological variation, especially in the distribution of sensory spots, gland cell outlets, and papillae, whereas characters conventionally used for species identification, such as spine pattern do not vary much. Overlapping character patterns do not allow identification of different species and to discriminate the current populations from previously described species. We conclude that the morphological variation results from ongoing species formation processes. We also report observations that two adult life history stages may exist in *Campyloderes*. The character set in the ground pattern of *Campyloderes* is presented.

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1. Introduction

The microscopic Kinorhyncha comprise some 177 species based on descriptions of the adult stage, 48 species described from a juvenile stage and 3 indeterminable species. The animals live in muddy, coralline or sandy sediments from intertidal mud flats to the deep sea until at least 7800 m depth (Zelinka, 1928; Bauer-Nebelsick, 1995; Danovaro et al., 2002; Neuhaus and Higgins, 2002). Little is known about Kinorhyncha from the deep sea at species level (Bauer-Nebelsick, 1996; Neuhaus, 2004; Neuhaus and Blasche, 2006), but during the past years, several deep-sea expeditions with RV Sonne and RV Polarstern revealed plenty of material of Kinorhyncha (Fahrbach and Gerdes, 1997; Arntz and Gutt, 1999; Hoernle et al., 2003; Werner et al., 2000, 2009, 2010; Werner, 2002; Werner and Hauff, 2007; Sørensen, 2008).

New species and genera of Kinorhyncha have been described in recent years with the aim of searching for characters for a phylogenetic analysis of Kinorhyncha (Neuhaus, 2004; Neuhaus and Blasche, 2006; Sørensen et al., 2007, 2010a,b; Sørensen, 2008; Sørensen and Rho, 2009; Sørensen and Thormar, 2010; Herranz et al., in press). Among the genera studied, *Campyloderes* seemed to represent an easy target, because it consists of three
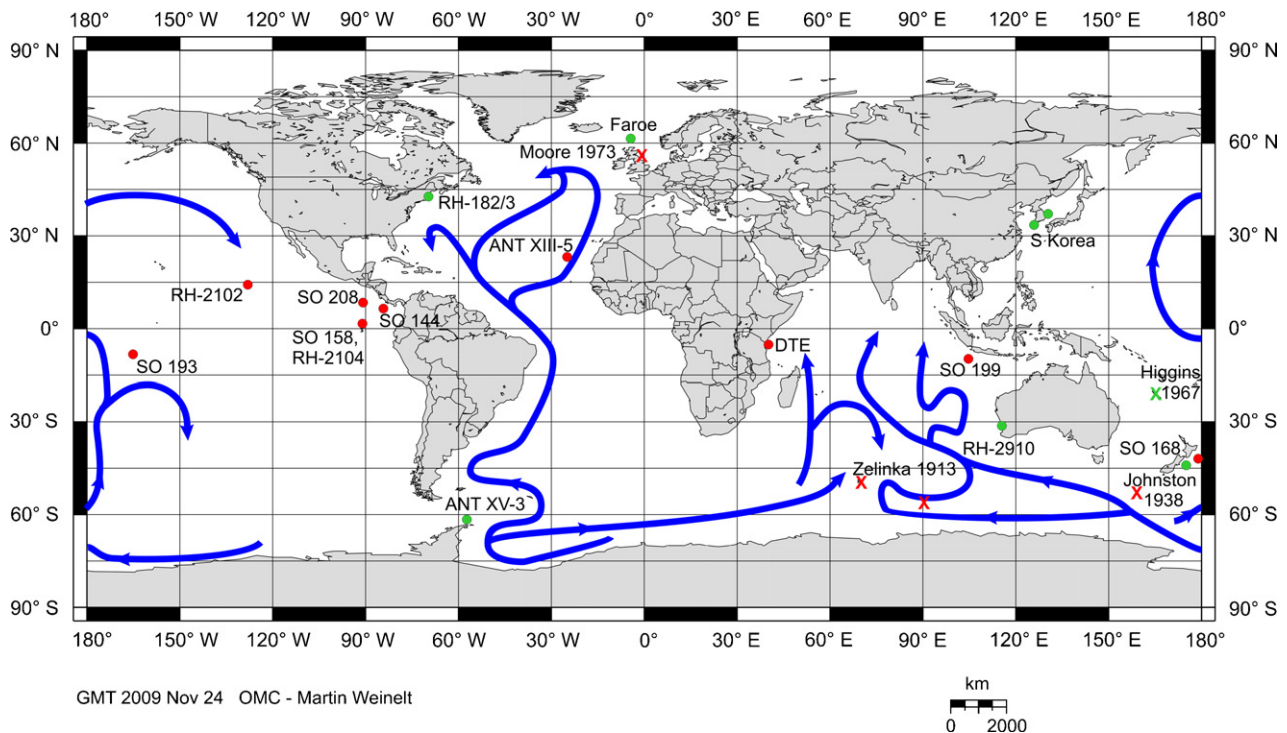
Fig. 1. Map with locations of specimens of *Campyloderes* based on study material (circles) and reports from the literature (crosses). Stations revealing specimens with lateroventral papillae marked in green (Faroe, RH-182/3, ANT XV-3, S-Korea, RH-2910, Higgins, 1967, partly SO 168), all other stations in red. Arrows indicate global thermohaline bottom current system according to Schmitz (1996a: Fig. 1–10) but without the upper level compensation flows. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

species and one subspecies only, namely *C. vanhoeffeni* Zelinka, 1913, *C. vanhoeffeni* var. *kerguelensis* Zelinka, 1928, *C. macquariae* Johnston, 1938, and *C. adherens* Nyholm, 1947 (see Zelinka, 1913, 1928; Johnston, 1938; Nyholm, 1947; Moore, 1973). However, in his review Neuhaus (2004, pp. 13, 17, 18) concluded that these species form an "almost indistinguishable species complex of *Campyloderes vanhoeffeni*–*C. vanhoeffeni* var. *kerguelensis*–*C. macquariae*" and that *Campyloderes adherens* may represent a species of *Centroderes*. Also, species of *Campyloderes* are currently discriminated from each other by minor details such as a spinose versus a blunt tip of the midterminal spine, a rounded versus a pointed terminal end of segment 11, and a proximal cuticle of the lateral terminal spine with thin areas versus an evenly thick cuticle (Zelinka, 1913, 1928; Johnston, 1938; Nyholm, 1947; Higgins, 1967; Moore, 1973; Neuhaus, 2004). All previous investigations of specimens of *Campyloderes* were based on few specimens available at that time, and a limited amount of morphological measurements are available. Meanwhile, the inclusion of material from several different expeditions and collections in connection with the finding of many more specimens offering the possibility to conduct SEM investigations and to study both dorsoventral and lateral mounts on slides allow to shed a different light on populations of *Campyloderes*. Now it becomes possible to recognize variation of characters, to correct former interpretations, and to establish the characters in the ground pattern of *Campyloderes*.

This study is part of a series on species of Kinorhyncha from the deep sea collected mainly by the German research vessels RV Sonne, RV Meteor and RV Polarstern. These papers intend to describe new species, compare the fauna of the deep sea with that of the continental shelves and elucidate the phylogenetic relationships both within the Kinorhyncha and of the Kinorhyncha to their closest relatives Loricifera and Priapulida.

2. Materials and methods

Specimens were collected during several expeditions and by different scientists (Fig. 1 and Table 1). Table 1 provides detailed information about the sampling sites, processing of specimens, deposition of material and references. Specimens were mounted in Hoyer's mounting medium, Euparal green, Fluoromount-G or as glycerin–paraffin slides on Cobb-aluminium slides or on glass slides (Table 1). Two media turned out to be less recommendable for mounting, namely Hoyer's and Euparal. The former inevitably clears specimens over years to a degree where they are no longer recognizable. During the process of complete dehydration of specimens for embedding in Euparal the specimens harden so much that they usually break into pieces. Specimens mounted by these authors are sealed with glyceel according to the recipee of Bates (1997).

Specimens for scanning electron microscopy were dehydrated through a graded series of ethanol, transferred to acetone (Martin V. Sørensen = MVS only) and critical point dried. The dried specimens were mounted on aluminum stubs, sputter coated (BN: with gold–palladium) and examined with a JEOL JSM-6335F field emission (MVS) or with a Zeiss EVO LS 10 (BN) scanning electron microscope.

Kinorhynchs were observed with microscopes equipped for differential interference contrast after Nomarski, namely either with an Olympus BX51 (MVS) or with a Zeiss Axioskop 50 (BN). Specimens were documented with a camera lucida. Photographs were taken with a digital camera ColorView I (MVS) or with a Zeiss Axio-Cam MRc5 attached to a Zeiss Axioplan 2 mot. (BN). The images were digitally improved with Corel Photo Paint V.11, and mounted with the help of Corel Draw. Measurements were made either with CellÔ software for analysis of light microscopical photos (MVS) or with a camera lucida (BN).

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Table 1
Location data of studied specimens.

Expedition, collector	Station #	Station data (location, georeferences; depth)	Collection date; gear	Processing (LM, SEM); specimens (SEM)	Specimens (LM)	Remarks
DTE, E. Vanhöffen	245	West Indian Ocean, Tansania, Zanzibar canal, 5°27′9″S, 39°18′8″E; 463 m	22.3.1899; trawl net	Mounted in Canada balsam (?) by E. Vanhöffen	ZMB Q.2757: 1♀ + 2♂, poor condition	
ANT XIII-5, N. J. Debenham, T. J. Ferrero, P. Martínez Arbizu, G. Silveira Moura	5, PS 40/122	Atlantic Ocean, southeast of Canary Islands, 23°10.9′N, 24°26.2′W; 5102 m	11.6.1996; MIC	Fixed in seawater-buffered 4% formalin; extraction by centrifugation with Levasil 200 A/40% (Bayer); mounted in Hoyer's mounting medium by BN	ZMB 5965: 1 ♀	Fahrbach and Gerdes, 1997 (expedition report); donation by P. Martínez Arbizu
		Atlantic Ocean, southeast of Canary Islands, 23°10.9′N, 24°26.3′W; 5055 m	12.6.1996; MUC		ZMB 5966: 1 ♀	
		Atlantic Ocean, southeast of Canary Islands, 23°11′N, 24°26.3′W; 5118 m	12.6.1996; MG corer		ZMB 5986: 3 juveniles	
ANT XV-3, H. J. Lee, J. Van de Velde	PS 48/306	South Atlantic Ocean, Antarctica, King George Island, 62°21.9′S, 58°43.0′W; 801 m	15.3.1998; MUC	Fixed in 4% formalin; 48/306: 7 specimens mounted as glycerin–paraffin slides by BN; 2 ♀ + 2 ♂ + 3 adults mounted for SEM by BN (ZMB 5967); 48/340: originally mounted in Hoyer's mounting medium & re-embedded in glycerin by BN	ZMB 5967: 3 ♀ + 2 ♂ + 1 young ♂ + 1 juvenile	Arntz and Gutt, 1999 (expedition report); donated by P. Martínez Arbizu
	PS 48/340	South Atlantic Ocean, Antarctica, Drake Passage, north of King George Island, 61°34.3′S, 58°7.6′W; 411 m	19.3.1998; MUC		ZMB 5968: 1 ♀	
ANT XIX-3–4, P. Martínez Arbizu	PS 61/46–4	South Atlantic Ocean, Antarctica, east of South Shetland Islands, 60°38.12′S, 53°57.67′W; 2893 m	30.1.2002; MUC	Fixed in 4–6% formalin; extraction by centrifugation with Levasil 200 A/40% (Bayer); mounted in Fluoromount G by MVS	ZMB 5981: 1 juvenile	Fütterer et al., 2003 (expedition report); donated by P. M. Arbizu
Me 63/2, P. Martínez Arbizu	Me 60	East Atlantic Ocean, East Guinea Basin, 0°0.001′S, 2°25.005′W; 5064 m	15.3.2005; MUC	Fixed in 4–6% formalin; extraction by centrifugation with Levasil 200 A/40% (Bayer); mounted in Fluoromount G by MVS	ZMB 5982: 1 ♀	Türkay and Pätzold, 2009 (expedition report); donated by P. M. Arbizu
SO 144-3, B. Neuhaus, P. Götz	TVG 49b	Central American East Pacific Ocean, Cocos Ridge, 7°0.29′N, 83°54.17′W; 1048 m	29.11.1999; TVG	Extraction by bubble & blot technique; fixed in 4% buffered formalin (see SO 158); mounted in Euparal green (Chroma 3C 240) by BN	ZMB 5969: 1 ♀ + 1 ♂ + 1 juvenile	Werner et al., 2000; Neuhaus, 2002 (extraction), 2004 (specimens)
SO 158, B. Neuhaus, P. Götz	MDR 20b	Central American East Pacific Ocean, near Galápagos spreading centre, from 0°57.277′N, 88°18.463′W to 0°57.285′N, 88°18.307′W; 2493–2496 m	31.7.2001; MDR	Fixed in 6–8% formalin buffered with buffer tablets for haematology at pH = 7.0 (Merck 109468); extraction by centrifugation with Levasil 200 A/40% (Bayer); mounted as glycerin–paraffin slides modified from Hooper (1970) by BN; MDR 67b: 1 ♀ + 1 ♂ mounted for SEM by BN (ZMB 11173)	ZMB 5970: 1 young ♂	Hooper, 1970 (mounting light microscopy); Werner, 2002 (expedition report); Neuhaus, 2004 (specimens 11173a–c, 11174a)
	MDR 67b	Central American East Pacific Ocean, transform fault of Galápagos spreading centre, from 0°51.80′N, 91°8.70′W to 0°51.80′N, 91°8.56′W; 2121–2119 m	10.8.2001; MDR		ZMB 11173: 7 ♀, ZMB 11174: 4 ♂ + 3 young ♂ + 4 juveniles + 1 exuvia	
SO 168, B. Neuhaus, C. Lüter	DR 11	Pacific Ocean, Hikurangi Plateau, from 41°7.03′S, 179°45.25′W to 41°7.10′S, 179°45.55′W; 1940–1817 m	18.12.2002; DR	See above: SO 158	ZMB 5971: 1 ♀	Hoernle et al., 2003 (expedition report)

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Table 1 (*Continued*)

Expedition, collector	Station #	Station data (location, georeferences; depth)	Collection date; gear	Processing (LM, SEM); specimens (SEM)	Specimens (LM)	Remarks
	DR 13	Pacific Ocean, Hikurangi Plateau, from 40°25.202′S, 179°26.816′W to 40° 25.425′S, 179°27.216′W; 1865–1605 m	18.12.2002; DR		ZMB 5972: 1 ♀	
	DR 87	Pacific Ocean, Chatham Rise, from 44°38.581′S, 176°49.498′W to 44° 38.376′S, 176°49.121′W; 684–511 m	9.1.2003; DR		ZMB 5973: 3 ♂	
	DR 98	Pacific Ocean, Chatham Rise, from 44°24.135′S, 175°55.220′E to 44°24.18′S, 175°55.10′E; 490–420 m	13.1.2003; DR		ZMB 5974: 1 young ♂ + 1 juvenile	
	TVG 103	Pacific Ocean, Chatham Rise, 44°45.211′S, 174°49.065′E; 885 m	14.1.2003; TVG		ZMB 5975: 1 ♀	
	DR 104	Pacific Ocean, Chatham Rise, from 44°45.90′S, 174°23.907′E to 44°46.24′S, 174°23.902′E; 594-770m	14.1.2003; DR		ZMB 5976: 1 ♂	
SO 193, B. Neuhaus, C. Lüter	MUC 30	Central Pacific Ocean, Manihiki Plateau, Danger Islands Troughs, 8°39.19′S, 164°19.99′W; 4925 m	6.6.2007; MUC	See above: SO 158	ZMB 5977: 1 ♂ + 1 juvenile	Werner and Hauff, 2007 (expedition report)
SO 199, B. Neuhaus, C. Lüter	DR 55	Indian Ocean, Christmas Island, from 10°30.85′S, 105°28.42′E to 10°30.93′S, 105°28.82′E; 1891–1427 m	28.8.2008; DR	See above: SO 158	ZMB 5978: 1 ♂	Werner et al., 2009 (expedition report)
SO 208, B. Neuhaus, C. Lüter	MUC 19	Central American East Pacific Ocean, near Galápagos spreading centre, 8°43,31′N, 90°44,14′W; 2426 m	21.7.2010; MUC	See above: SO 158	ZMB 5983: 5 juveniles	Werner et al., 2010 (expedition report)
	DR 26	Central American East Pacific Ocean, near Galápagos spreading centre, from 10°41.12′N, 87°45.52′W to 10°40.91′N, 87°45.28′W; 2995–2680 m	23.7.2010; DR		ZMB 5984: 2 ♀	
W. Coffin	26	West Atlantic Ocean, USA, New Hampshire, Seabrook; from *Corallina* holdfasts	16.1.1976; by hand	n.a.; mounted in Hoyer's mounting medium by R. P. Higgins	USNM 1170803, 20089, RH-182.1: 1 ♂	collection of R. P. Higgins at NMNH
W. Coffin	–	(See above)	10.7.1975; by hand	(See above)	USNM 1170804, 16502, RH-183.1: 1 ♂	(See above)
LGL Ecological Research Association	–	West Atlantic Ocean, Gulf of Mexico, 27°35′N, 93°33′W; 344 m	4.4.1984; box corer	n.a.; 1 juv. + 1 ♀ mounted for SEM by MVS, very dirty; NMNH RH-1975	–	Collection of R. P. Higgins at NMNH
	–	West Atlantic Ocean, Gulf of Mexico, 27°28.18′N, 89°46.48′W; 1386 m	13.4.1984; box corer	n.a.; 1 ♂ mounted for SEM by MVS, very dirty; NMNH RH-1983	–	
CENTOB, R. Le Suave	NIXO 47 + T47031	Central Pacific Ocean, Clarion-Clipperton fraction zone, 14°40′17″N, 130°40′50″W; 5050 m	11.6.1986; ?	n.a.; mounted as glycerin-paraffin slide by BN	USNM 1170805, RH-2102: 1 young ♂	

Table 1 (*Continued*)

Expedition, collector	Station #	Station data (location, georeferences; depth)	Collection date; gear	Processing (LM, SEM); specimens (SEM)	Specimens (LM)	Remarks
RV S. Johnson + Johnson Sea Link I, S. Cairns	24-XI-86.1	Central American East Pacific Ocean, Galápagos, 0°10′18″S, 91°24′40′W; 539 m	24.11.1986; dive # 1931	n.a.; mounted as glycerin-paraffin slides by BN	USNM 1170825–9, RH-2104: 2 ♀ + 3 ♂	
I. Bortsch	–	East Indian Ocean, West Australia, Rottnest Island, 32°1′S, 115°28′E; 1–2 m, from *Amphibolis antarctica*	17.1.1991; by hand	n.a.; mounted as glycerin-paraffin slides by BN; ♀ without head & segment 1	USNM 1170830–31, RH-2910: 1 ♂ + 1 ♀	
C. Y. Chang, J. M. Lee, Y. H. Song	–	South Korea, south coast, Jeju Island, Beomseom Island off Seogwipo, 33°13′29″N, 126°34′14″E; subtidal	3.3.2000; rinsing grasses	Extraction by rinsing grasses or benthic invertebrates; fixed in buffered 5% formalin; mounted in Hoyer's mounting medium 125 by C. Y. Chang; 1 ♀ + 1 ♂ from Gangreung mounted for SEM by BN (ZMB 5980)	ZMB 5979: 1 ♀	Song and Chang, 2001 (location details); donation by C. Y. Chang
C. Y. Chang, Y. H. Song	–	South Korea, east coast, Namae, Gangreung, 37°56′37″N, 128°47′17″E; 30–50 m	6.10.2000; fishing nets		ZMB 5980: 1 ♂	
Galathea 3, J. Thormar	–	Solomon Islands, near Ghizo Island, 8°0.817′S, 156°45.429′E; 14 m; coral sand from small ledges on rocky walls	4.1.2007; SCUBA diving	Extraction by decantation; 1 ♀ mounted for SEM by J. T. (ZMUC KIN-458)	–	Thormar, 2010 (location details)
M. V. Sørensen	–	North Atlantic Ocean, Denmark, Northern Kattegat, Hirsholmene; 57°29.280′N, 10°38.020′E; 10 m	29.1.2001; van Veen grab	Extraction from shell gravel by freshwater shocking; fixed in borax-buffered 4% formalin; mounted in Hoyer's mounting medium	ZMUC KIN-535: 1 young ♂	
M. V. Sørensen	–	North Atlantic Ocean, Faroe Islands, Kaldbak Fjord, 62°3′28.3″N, 6°49′40.7″W; 0–0.4 m	6.7.2001; by hand	Extraction from *Corallina officinalis* by freshwater shocking; fixed in borax-buffered 4% formalin; mounted in Hoyer's (KIN-83–104)/ Fluoromount-G (KIN-306–309) on glass slides by MVS; 8 ♀ + 5 ♂ (from 2001) mounted for SEM by MVS	ZMUC KIN-83–104: 6 ♀ + 9 ♂ + 3 young ad. + 4 juv.	Higgins, 1988; Sørensen and Pardos, 2008; this paper
B. Trygvadóttir	–	North Atlantic Ocean, Faroe Islands, Kaldbak Fjord, off Kaldbak laboratory, 62°3′28″N, 6°49′41″W; 0.2 m	2004		ZMUC KIN-306–309: 2 ♀ + 2 ♂	

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Table 2
Selected characters of adult specimens studied by light microscopy. Additional sensory spots and gland cell outlets occurring on one side only are not mentioned. Several characters appearing in one or several specimens only are marked (grey background, underlined, bold, in italics). Catalogue numbers refer to museum collections in Berlin (plain number), Copenhagen (ZMUC KIN-), and Washington (NMNH, RH-).

source, station #	DTE, station 245			SO 199, DR 55	I. Bortsch, RH-2910		C. Y. Chang		SO 193, MUC 30
location; depth	West Indian Ocean, Tanzania, Zanzibar canal; 463 m			Indian Ocean, Australia, Christmas Island; 1,891-1,427 m	East Indian Ocean, West Australia, Rottnest Island; 1-2 m		South Korea		Central Pacific Ocean, Manihiki Plateau; 4,925 m
							south coast; subtidal	east coast; 30-50 m	
catalogue #,gender	Q.2757a, ♀	Q.2757b, ♂	Q.2757c, ♂	5978, ♂	RH-2910.1, ♂	RH-2910.2, ♀	5979, ♀	5980, ♂	5977a, ♂
TL	325 µm	317 µm	391 µm	**513 µm**	391 µm	n.a.	321 µm	332 µm	**610 µm**
segments bulging lat.	-	-	-	+	n.a.	n.a.	-	-	+
scalids: # septa	+, # n.a.	n.a.	n.a.	18-23	+, # n.a.	n.a.	11-14	12-13	21-23
spines: thin	-	-	-	+	-	-	-	-	-
flexible	-	-	-	-	-	-	-	-	+
length lv1	119 µm /n.a.	105 µm /n.a.	n.a./n.a.	183/156 µm	95/95 µm	n.a./n.a.	84/88 µm	84/88 µm	78/66 µm
length ltas	172 µm /n.a.	n.a./192 µm	152 µm/n.a.	371/364 µm	n.a/n.a.	108/107 µm	100/89 µm	122/116 µm	341/326 µm
length mts	n.a.	93 µm	n.a.	197 µm	51 µm	50 µm	48 µm	56 µm	264 µm
cuticle: scales	small	small	small	broader	small	small	small	small	small
longitudinal ridges	-	-	-	+	-	-	-	-	+
posterior processes	-	-	short, ~ 8	large: many s1-3/10, ~8 in s4-9	-	-	-	-	large, ~ 8
papillae: lv	-	-	-	-	s3-10	s4-7/9/10	s3-10 (long)	s4-11	-
vm/pv	s6/7	-	-	-	-	s6/7	s5/6/7	-	-
sensory spots: pd	s1-9	s1-9	s4-9	s1-9	s1-9	s1n.a./2-9	s1-9	s1-9	s1/2/4/6/8/9
la in s8	-	-	-	2x	?	2x(pa or ssp?)	1x	-	1x
lv	s3-7/9/10	s3/4?/5?/6/7?/8?/9/10	s2-4/5?/6/7/9/10	s3-7/9/10	see remarks	-	-	-	s3/5/6/7/9
vm	s2/9	s2/9	s2n.a./9	s2/4/6/9/11	s2/9	s2/9/11	s2/9	s2/9	s2/5/7/9
gland cell outlets: ld	s2-10	s2-10	s2-9	s1/2/4-9	s1-10	s1n.a./2-10	s1-9	s1-9	s1-10 (partly ml)
vm	s2-9/11	s2-9/11	s2n.a./3-9/11	s2-9/11	s1-11	s1n.a./2-11	s2-9/11	s2-9/11	s1-11
remarks		short spine vl1: −		mts: 2 dorsal thin areas	spine: in s10 lv instead sl; lv3-10: pa or ssp?; add. gc: md in s4	head and segment 1 missing	additional pa: la s11 (elongate)		spines: short vl1: −, short vl5 replaced by elongate pa, short lv2: long & acicular

Table 2 (*continued*)

source, station #	SO 168								SO 144-3, TVG 49b	
	DR 11	DR 13	DR 87			DR 98	TVG 103	DR 104		
location; depth	NZ, Hikurangi Plateau;		Pacific Ocean, New Zealand (NZ), Chatham Rise;						Central American East Pacific Ocean, Cocos Ridge; 1,048m	
	1,940-1,340m	1,865-1,605m	684-511 m			490-420 m	885 m	594-770 m		
catalogue #, gender	5971, ♀	5972, ♀	5973a, ♂	5973b, ♂	5973c, ♂	5974a, ♂	5975, ♀	5976, ♂	5969a, ♂	5969b, ♀
TL	402 μm	362 μm	353 μm	**499 μm**	454 μm	237 μm	520 μm	253 μm	**540 μm**	**603 μm**
segments bulging lat.	-	-	-	+	-	-	+	-	+	(+)
scalids: # septa	8-11	+, # n.a.	+, # n.a.	n.a.	+, # n.a.	n.a.	+, # n.a.	~ 12	~ 20	26-31
spines: thin	-	-	-	+	-	-	+	-	+	+
flexible	-	-	-	+	-	-	+	-	-	+
length lv1	98/97 μm	102/78 μm	n.a./43 μm	56/55 μm	34/31 μm	89/82 μm	n.a./63 μm	n.a./n.a.	156 μm/n.a.	n.a./82 μm
length ltas	269/246 μm	255/246 μm	n.a./194 μm	216/220 μm	192/179 μm	116/115 μm	255/253 μm	128/134 μm	289/289 μm	337/342 μm
length mts	77 μm	88 μm	51 μm	135 μm	75 μm	68 μm	155 μm	61 μm	176 μm	189 μm
cuticle: scales	small	small	small	broader	small	small	broader	small	broader	broader
longitudinal ridges	-	-	-	+	-	-	+	-	+	+
posterior processes	-	-	-	short, ~ 8	-	-	short, ~8	s1-6: short, many	short, ~ 8	short, ~ 8
papillae: lv	-	see remarks	-	-	-	-	-	s3-10	-	-
vm/pv	s6/7	s6/7	-	-	-	-	s6/7	-	-	s6/7
ensory spots: pd	*s2/4/6-9*	*s2/4/6-9*	*s2/4/6-9*	s1-9	s2/4/6/9	*s2/4/6-9*	s1-9	s1-9	s1-9	s1-9
la in s8	-	-	2x	2x	-	2x	2x	-	1x	1x
lv	s3-10	s2-10	s3-7/9/10	s2-7/9/10	s2-10	s3-7/9/10	s2-7/9/10	see remarks	s3-7/9/10	s2-7/9/10
vm	s2/9/11	s2/9/11?	s2/4/6/9/11?	s2/5/7/9	s2/4/6/9/11?	s2/9	s2/5/7/9/11?	s2/9/11?	s2/9/11?	s2/5/7/9
gland cell outlets: ld	s1-9	s2-10	s2-10 (partly ml)	s1-10	s1-11	n.a.	s1-10	s1-9	s1-9	s1-9 in ±ml position
vm	s2-9/11	s2-9	s2-9/11	s1-9/11	s1-11	s2/9	s1-9	s2-11	s1-9/11	s1-9/11
remarks	short spine vl1: right side only	short spine vl1: –; lv9/10: pa or ssp?	spines: lv1: –, vl1: long, short vl1: –; additional gc: la1; additional ssp: sl5, 7	short spine vl1: –; additional gc: pd1-10, ml3-9, sl2, vl10, vm7-9	short spines vl1/lv2: –; additional gc: vm8, 9	young specimen; lts with only 1 thin area	short spine vl1: –; additional gc: pd1-9, sd4, ld1, sl2-10, vl1, vm2/6/8/9; additional ssp: vl11	pa lv(2)-8: pa or ssp?		short spine vl1: –; additional gc: sd7, la8

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Table 2 (*continued*)

source, station #	SO 158, MDR 67b									
location; depth	Central American East Pacific Ocean, transform fault of Galápagos spreading centre; 2,121-2,119 m									
catalogue #, gender	11173a, ♀	11173b, ♀	11173c, ♀	11173d, ♀	11173e, ♀	11173f, ♀	11173g, ♀	11174a, ♂	11174b, ♂	11174c, ♂
TL	418 μm	488 μm	466 μm	309 μm	402 μm	321 μm	378 μm	369 μm	371 μm	350 μm
segments bulging lat.	-	-	-	-	-	-	-	-	-	-
scalids: # septa	8-10	+, # n.a.	9-12	n.a.	+, # n.a.	+, # n.a.	+, # n.a.	9-10	+, # n.a.	+, # n.a.
spines: thin	-	-	-	-	-	-	-	-	-	-
flexible	-	-	-	-	-	-	-	-	-	-
length lv1	108/102 μm	130/124 μm	117/126 μm	126/122 μm	128/116 μm	130/130 μm	118 μm/n.a.	133/138 μm	139/125 μm	130/128 μm
length ltas	248/239 μm	251/278 μm	258/248 μm	260/249 μm	247/245 μm	276/268 μm	264/269 μm	260/262 μm	257 μm/n.a.	n.a./259 μm
length mts	90 μm	95 μm	91 μm	84 μm	80 μm	91 μm	100 μm	88 μm	98 μm	102 μm
cuticle: scales	small	small	small	small	small	small	broader	small	small	small
longitudinal ridges	-	-	-	-	-	-	-	-	-	-
posterior processes	-	-	-	-	-	-	-	-	-	-
papillae: lv	-	-	-	-	-	-	-	-	-	-
vm/pv	s6/7	s6/7	s6/7	s6/7	s6/7	s6/7	s6/7	-	-	-
sensory spots: pd	s2/4/6/8/9	*s*1/*2/4/6-9*	s2/4/6/8/9	s2/4/6/8/9	*s*1/*2/4/6-9*	s2/4/6/8/9	s1-4/6/8/9	s2/4/6/8/9	s2/4/6/8/9	s2/4/6/8/9
la in s8	-	2x	-	-	3x?	-	2x	-	-	-
lv	s3/9-11	s3/4?/5-7/9?/10	s3/4/5-8?/9-11	s3-10	s3-7/9/10	s3/4?/5-10	s2-10	s3-6/7?/8/10	s3/4?/5-10	s3-9
vm	s2/9/11	s2/9/11?	s2/9/11	s2/9/11	s2/9/11	s2/9/11	s2/9/11	s2/9/11	s2/9/11?	s2/9/11
gland cell outlets: ld	s1-9	s1-10 (in s2 more ml)	s1-9	s1-9	s1-9	s1-9	s1-9	s1-9	s1/3-10	s1-9
vm	s2-9/11	s1-9/11	s2-9/11	s2-9/11	s2-9/11	s2-9/11	s2-9/11	s1-9/11	s2-9/11	s2-9/11
remarks	additional gc: sd6 2x; ssp also lv2/4-8 ?	additional gc: vm11		spine md 4: with 5 incomplete septa	**short thin spinose process: lv10 on right side**	short spine vl1: right side only		additional gc: ml9	lts with only 1 thin area	additional short spine right side vl1; right lts with 5 thin areas

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Table 2 (*continued*)

source, station #	**SO 208**, DR 26		RV S. Johnson + **Johnson Sea Link I**, **RH-2104**				
location; depth	Central American East Pacific Ocean, near Galápagos spreading centre; 2,995-2,680 m		Central American East Pacific Ocean, Galápagos; 539 m				
catalogue #, gender	5984a, ♀	5984b, ♀	RH-2104.1, ♀	RH-2104.3, ♀	RH-2104.2, ♂	RH-2104.4, ♂	RH-2104.5, ♂
TL	444 µm	378 µm	**590 µm**	389 µm	**538 µm**	362 µm	382 µm
segments bulging lat.	-	-	+	(+)	+	(+)	-
scalids: # septa	+, # n.a.	+, # n.a.	23-29	~ 20	n.a.	11-13	+, # n.a.
spines: thin	-	-	+	-	+	-	-
flexible	-	-	-	-	-	-	-
length lv1	182/179 µm	167/177 µm	97/93 µm	151/145 µm	147/135 µm	143/152 µm	152 µm/n.a.
length ltas	276/264 µm	274/261 µm	267/262 µm	164/169 µm	290/280 µm	176/183 µm	190/181 µm
length mts	79 µm	86 µm	151 µm	74 µm	148 µm	n.a.	81 µm
cuticle: scales	small	small	small	small	broader	small	small
longitudinal ridges	-	-	weak, anterior segments only	-	+	-	-
posterior processes	-	-	large, ~ 8	short, ~ 8	large, ~ 8	short, # n.a.	-
papillae: lv	s2-7/9-11	s2-11	-	-	-	-	-
vm/pv	s6/7	s6/7	s6/7	s6/7	-	-	-
sensory spots: pd	s1/2/4-9	s1/2/4-9	s1-9	s1-9	s1-9	s1-9	s1-9
la in s8	2x	2x	1x	1x	2x	1x	1x
lv	-	-	s2-7/9/10	s2-7/9/10	s3/4/6/7/9/10	s2-4/6/7/9/10	s2-4/6/7/9/10
vm	s2/9	s2/9	s2/5/7/9/11	s2/9/11	s2/9/11	s2/9/11	s2/9/11
gland cell outlets: ld	s1-9	s1-11	s1-10	s1-10	s1-9	s1-10	s1-10
vm	s1-11	s1-11	s1-9/11	s1-11 (in s10 more vl)	s2-9/11	s1-9/11	s1-9/11
remarks	additional gc: sd1; spines: **md10/11**	spines: **md10/11**	additional gc: vl10, vm4/6/8; additional ssp: vl10	additional gc: vl10; additional ssp: vl10; spines: **md10/11**		additional gc: vl10	

Table 2 (*continued*)

	M. V. Sørensen, B. Trygvadóttir		M. V. Sørensen	ANT XIII-5, PS 40/122		RH-182	RH-183
source, station #							
location; depth	North Atlantic Ocean, Faroe Islands; intertidal		North Atlantic Ocean, Northern Kattegat, Hirsholmene; 10 m	Atlantic Ocean, southeast of Canary Islands;		West Atlantic Ocean, USA, New Hampshire; ?	
				5,055 m	5,102 m		
catalogue #, gender	ZMUC KIN-83-86, -89-91, -95, -96, -306, -308, ♂	ZMUC KIN-87, -88, -92-94, -97, -307, -309, ♀	ZMUC KIN-535, ♂	5966, ♀	5965, ♀	20089, ♂	16502, ♂
TL	350-433 μm		230 μm	400 μm	457 μm	362 μm	303 μm
segments bulging lat.	-	-	-	-	-	-	-
scalids: # septa	12-17	12-17	11-12	~ 9	~ 8	13-18	n.a.
spines: thin	-	-	-	-	-	-	-
flexible	-	-	-	-	-	-	-
length lv1	84-110 μm		68/71 μm	159/157 μm	166/176 μm	89/88 μm	n.a./100 μm
length ltas	103-138 μm		97/93 μm	179/181 μm	235/248 μm	114/114 μm	128/128 μm
length mts	56-68 μm		57 μm	124 μm	126 μm	55 μm	60 μm
cuticle: scales	small	small	small	small	small	small	small
longitudinal ridges	-	-	-	-	-	-	-
posterior processes	-	-	-	short, ~ 8	-	-	-
papillae: lv	s2-11 (in s11 elongate)	s2-11 (in s11 elongate)	s6-9/11	-	-	s3-9	s2-11
vm/pv	-	s6/7 + **vl5**	-	s6/7	s6/7	-	-
sensory spots: pd	s1-9	s1-9	s1-9	*s*1/*2*/*4*/*6-9*	*s*1/*2*/*4*/*6-9*	s1-9	s1-9
la in s8	-	-	-	1x	1x	-	1x
lv	-	-		s2/3?/4-7/9/10	s3-7/9?/10	see remarks	-
vm	s2/9/11	s2/9/11	s2/9	s2/9	s2/9/11?	s2/9	s2/9
gland cell outlets: ld	s1-9	s1-9	n. a.	s1-10	s1-10	s1-9	s1-9
vm	s2-9/11 (KIN-91 in s11: vl)	s2-9/11	n. a.	s1-9/11	s2-9/11	s2-9/11	s1-9/11
remarks	s1: ssp ld instead of ml; KIN-83-85 additional gc: vm1; KIN-86 ssp pd7: –, additional gc: md7 3x, spine md7: –; KIN-90 additional gc: sd10; KIN-91 additional gc: ld8, left lts with 3 thin areas; KIN-95 short spine vl5: right side only; KIN-96 add. gc: vl11	s1: ssp ld instead of ml; additional ssp: lv 10, **short thin spinose process: lv10**; KIN-87 gc sd11: –; KIN-93 additional gc: sd10; KIN-94 additional gc: sd4, ld4; KIN-97 additional gc: sd10, short spine vl5: left side only	young ♂; additional pa: sl10?	additional gc: vl10, vm11; additional ssp: sd1; spines: **md10/11**, short vl5: –	spines: **md10/11**	lv3-8: pa or ssp?	

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Table 2 (*continued*)

source, station #	Me 63/2	ANT XV 3, PS 48/306					ANT XV-3, PS 48/340
location; depth	East Atlantic Ocean, East Guinea Basin; 5,064 m	South Atlantic Ocean, Antarctica, near King George Island; 801 m					South Atlantic Ocean, Antarctica, Drake Passage; 411 m
catalogue #, gender	5982, ♀	5967b, ♀	5967c, ♀	5967d, ♀	5967a, ♂	5967f, ♂	5968, ♀
TL	499 µm	353 µm	321 µm	382 µm	330 µm	303 µm	364 µm
segments bulging lat.	-	-	-	-	-	-	-
scalids: # septa	14-17	+, # n.a.	+, # n.a.	+, # n.a.	+, # n.a.	10-14	~ 10
spines: thin	-	-	-	-	-	-	-
flexible	-	-	-	-	-	-	-
length lv1	212/215 µm	118/109 µm	88/117 µm	78/124 µm	119/119 µm	127/123 µm	122/124 µm
length ltas	325/334 µm	136/132 µm	133/135 µm	143 µm/n.a.	150/158 µm	159/167 µm	136/138 µm
length mts	150 µm	58 µm	56 µm	n.a.	61 µm	67 µm	54 µm
cuticle: scales	small	small	small	small	small	small	small
longitudinal ridges	-	-	-	-	-	-	-
posterior processes	-	-	-	-	-	-	-
papillae: lv	-	s3-10	s3-10	s2?/3-10	s2-10	s3-9	s2-10
vm/pv	s6/7	s6/7	s6/7	s6/7	-	-	s6/7
sensory spots: pd	s1-9	s1-9	s1-9	s1-9	s1-9	s1-9	s1-9
la in s8	1x	-	-	-	1x	-	-
lv	s2-10	see remarks	-	see remarks	-	see remarks	-
vm	s2/9	s2/9/11?	s2/9/11	s2/9/11	s2/9/11	s2/9/11	s2/9/11?
gland cell outlets: ld	s1-9	s1-9	s1-9	s1-9	s1-9	s1-9	s1-9
vm	s2-11	s2-9/11	s2-9/11	s2-9/11	s2-9/11	s2-9/11	s2-9/11
remarks	additional gc: vm in s10; lts with only 1 thin area	add. spine: left side vl5; add. gc: vm6; lv3-10: pa or ssp?; s9-11: sternal plates oblique		lv9/10: pa or ssp?		lv3-9: pa or ssp?	**short, thin spinose processes: vl8, lv10**

Segment borders of recently moulted animals are difficult to observe because of the thin cuticle. Therefore, segment lengths are in such cases measured laterally in that optical longitudinal section of a specimen where the cuticle appears best focused laterally. Otherwise, the terminology of the description and the way measurements are conducted follow Higgins (1983) as emended by Bauer-Nebelsick (1996), Pardos et al. (1998) and Sørensen and Pardos (2008). Numbering of trunk segments follows Neuhaus and Higgins (2002, p. 621) for the reasons stated there.

In order to recover the type material of *Campyloderes vanhoeffeni*, *C. vanhoeffeni* var. *kerguelensis*, *C. macquariae* and *C. adherens*, BN searched the collection of the Berlin museum where most material of the German South Polar Expedition 1901–1903 was deposited and requested information from the Natural History Museum Senckenberg, Frankfurt (also holder of material from the German South Polar Expedition), from the Natural History Museum, Vienna (Carl Zelinka was Austrian), from the Australian Museum, Sydney (Johnston deposited his type material here according to his article in 1938), from the Gothenburg Museum of Natural History, the Swedish Museum of Natural History, Stockholm and the Museum of Evolution, Uppsala (Karl-Georg Nyholm worked at the university of Uppsala, his specimens originate from the Swedish west coast). All efforts were in vain, not a single specimen of the type material turned up.

3. Results

In all specimens of *Campyloderes* studied here, the arrangement of spines, sensory spots, gland cell outlets and papillae follows a basic pattern summarized in Table 4. Characters listed in Table 2 concentrate on those traits that show variation among the examined specimens. It includes information from all specimens where characters can be identified with some certainty; therefore, recently molted specimens are often excluded. "Additional" characters in Table 2 refer to characters in addition to characters of the ground pattern (comp. Table 4).

Often, it is difficult to assign the position of a character to the general reference schedule developed for Kinorhyncha by Higgins and coworkers (Pardos et al., 1998; Sørensen and Pardos, 2008). Segments also possess different diameters, so it may become demanding to identify the same reference position on different segments. In addition, specimens are mounted in different views between perfectly dorsoventral and lateral, obscuring certain positions to some degree. We avoid creating a bunch of intermediate positions and choose to assign the position of a given character to the nearest general reference position (comp. Table 3, female).

Other characters may be difficult to recognize, because the specimen is mounted laterally, because the preservation condition is suboptimal, or because spines cover the area of interest; e.g., in segment 2, lateroventral sensory spots or papillae are often not traceable, because the long lateroventral spine of the first segment is located just above this area. This character may very well exist in those specimens where it is not mentioned in Table 2.

The following description is based on observations of all specimens except for the head where information originates mainly from specimens from the Faroe Islands.

3.1. Head

The head consists of a mouth cone and an introvert (Fig. 2A). Unlike all other kinorhynchs, specimens of *Campyloderes* do not possess any separated outer oral styles (Fig. 2C, F and G). Hence, the outer visible part of the mouth cone appears as a soft, densely plicated tube with about 9–10 main longitudinal lamellae or ribs (Fig. 2C–G) which run from the base of the mouth cone to a point very close to its tip (Fig. 2F). At this point, they form short, 3–5 μm long fibrillate appendages (Fig. 2D and F). Between two main ribs, two smaller lamellae or ribs begin at the base of the mouth cone and terminate well below the tip. Between two smaller lamellae, a central lamella extends from the middle of the mouth cone to the tip (Fig. 2F and G). These features can also be recognized by light microscopy and are confirmed for all specimens with their head protruded.

Inner oral styles exist (Fig. 2E) but are difficult to observe in most specimens (Fig. 2D), because the fused outer oral styles cover the eventual presence of inner oral styles, or the pharynx is protruded artificially to an extent that inner oral styles cannot be separated from the pharyngeal crown.

The introvert exhibits six rings of scalids and one additional ring of trichoscalids that are associated with the placids (Figs. 2A, J, K, 3, and 4A, B). The first scalid ring (ring 01) contains 10 primary spinoscalids. Each spinoscalid consists of a square socket and a long end piece with internal septa and a pointed tip (Figs. 2J, K and 4A). The end piece is densely fringed along its whole length, whereas the socket has a strong medial fringe. The number of internal septa in the end piece appears to vary from 8 to 31 between different adult specimens (Table 2). Each septum consists of a thin cuticular lamella in the scalid's lumen and forms a ring-like cuticular thickening where it meets the scalid wall. Traces of the septa can hardly be observed with SEM (Fig. 4A), and they are most clearly visualized by light microscopy (Fig. 2J and K). Unfortunately, the head is withdrawn in many specimens, so information about the number of septa is limited.

Ring 02 has 10 scalids located in between the sockets of the primary scalids (Figs. 2J, K, 3, and 4A). The scalids in this particular ring are conspicuously short (length about 1/3 of the regular scalids in the following two rings) and have an acicular appearance. Each scalid consists of a proximal sheath and an end piece with a pointed tip. Both the sheath and the proximal half of the end piece are densely fringed. This kind of scalids is present in all specimens with protruded introvert studied by light microscopy or SEM.

The following rings carry 20 (ring 03), 10 (ring 04), 10 (ring 05), and 15 (ring 06) scalids (Figs. 2J, K, 3, and 4A). The scalids in these rings are generally uniform in shape, whereas their lengths change gradually from relatively long scalids in the anterior ring towards shorter ones in the more posterior rings. Each scalid consists of a sheath with a broad, medial fringe, and a fringed and pointed end piece. However, scalids of ring 06 end with a blunt tip and are more hook-like shaped in several specimens (ZMB 5967f, j, k, 5971: Fig. 4B, 11173a, I, 11174a, j) but more straight with a pointed tip in other specimens (ZMB 5969b, 5976, 5977a, 5982, 11173h, specimens from Faroe Islands: Figs. 2J, K, and 4A).

The posteriormost ring (ring 07) carries 14 trichoscalids (Figs. 2J, K, 3, and 4A, B). Unlike the scalids in the rings 01–06, the position of the trichoscalids does not follow a strict radial symmetrical pattern around the introvert. Instead, their positions relate to the 14 placids in the neck, so that a trichoscalid and a placid go together pair-wise (Figs. 2J, K, 3, and 4B). Each trichoscalid consists of a short, fringed sheath and a fringed end piece and is basally associated with a sclerotized trichoscalid plate (Figs. 2J, K and 4A, B).

The location of scalids in rings 01–06 follows a strict pattern around the introvert. Described section-wise, the midventral section (section 1) and all odd numbered sections possess 7 scalids, whereas the middorsal section (section 6) and all even numbered sections have 6 scalids (Fig. 3). Trichoscalids are, as stated above, not a part of this pattern.

3.2. Neck

The neck consists of 14 placids (Figs. 2B, H and 3). The midventral placid is significantly broader (30 μm) than all other placids.
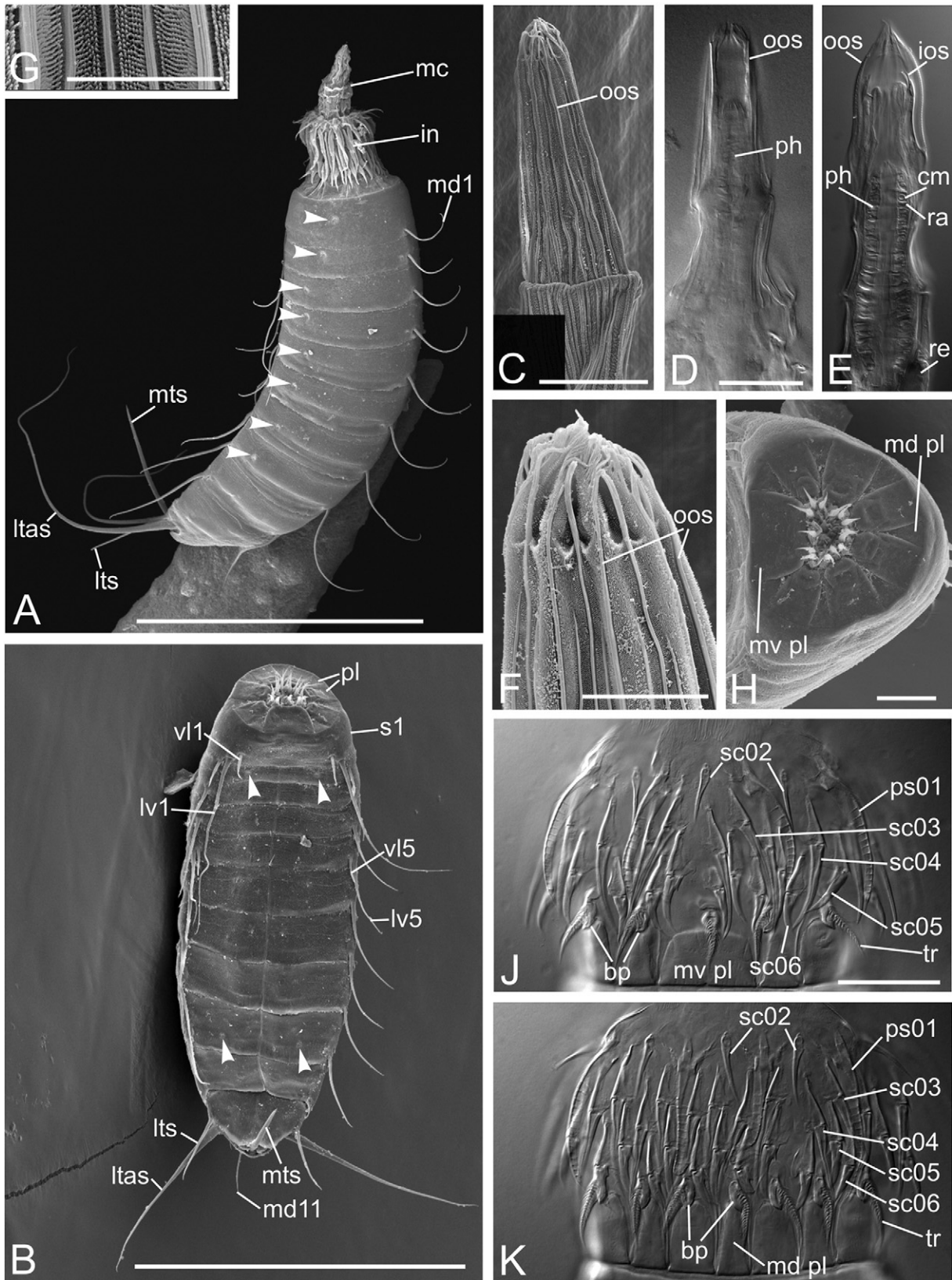
Fig. 2. (A–K). SEM (A–C, F–H) and DIC images (D, E, J, K) of male (C, J) and female (A, B, D–H, K) *Campyloderes* cf. *vanhoeffeni* from the Galápagos area (A, E), Antarctica (B, H) and the Faroe Islands (C, D, F, G, J, K). (A, B) Habitus from left side (A) and ventral side (B). Arrow heads mark sensory spots. (C) Mouth cone in surface view, individual outer oral styles absent. (D, E) Optical section of mouth cone of specimens ZMUC KIN-87 (D) and ZMB 5967i (E). Inner oral styles recognizable in specimen from Galápagos area (E) but not in Faroe specimen (D). Pharynx with alternating circular and radial muscle cells in (E). (F, G). Tip of mouth cone (F) and detail of fused outer oral styles (G). (H) Frontal view of placids. (J, K) Head and placids of specimens ZMUC KIN-95 (J) and KIN-94 (K) in ventral (J) and dorsal view (K). Scale bar in A and B 200 μm, in C and H 20 μm, in D 30 μm (valid for D, E), in F 5 μm, in G 2 μm, in J 30 μm (valid for J, K).

Table 3
Variation of spines, sensory spots, gland cell outlets and papillae in one male and female specimen from Chatham Rise, New Zealand. Several characters occur only on the left (**le**) or right (**ri**) side of the specimen. Other characters with an intermediate position between reference positions (female: positions sd/ld and sl/la) are marked in bold and underlined.

position segment	md	pd	sd	ld	ml	sl	la	lv	vl	vm
Male – specimen ZMB 5973b										
1	ac	ssp; gc	gc	2× gc	ssp			elongate ac	gc; **le: gc**	**ri: gc**
2	ac	ssp; gc	**le: gc**	gc	ssp	gc		blunt; ssp	gc	ssp; gc; **le: gc**
3	ac	ssp; gc	**le: gc**	gc	ssp; gc			ac; ssp	gc	gc
4	ac	ssp; gc	gc; **ri: gc**	gc; **le: 2× gc**	gc	ssp		ac; ssp	gc	gc
5	ac	ssp; gc	gc	gc	ssp; gc			ac; ssp	gc	**ri: ssp**; gc
6	ac	ssp; gc	**le: gc**	gc; **ri: gc**	ssp; gc			ac; ssp	gc	gc
7	ac	ssp; gc	**ri: gc**	gc; **le: gc**	ssp; gc			ac; ssp	gc	ssp; 2× gc
8	ac	ssp; gc	gc	gc	gc		2× ssp	ac	gc	2× gc
9	ac	ssp; gc	gc	gc	ssp; gc			ac; ssp	gc	ssp; 2× gc
10	ac	gc	gc	gc		ac; ssp		ssp	2× gc	
11	ac + mts		2× gc; 2× ssp				ac	ac		gc
Female – specimen ZMB 5975										
1	ac	ssp; gc	gc	2× gc	ssp			elongate ac	2× gc	gc
2	ac	ssp; gc	**gc**		ssp	gc		blunt; ssp	gc	ssp; 2× gc
3	ac	ssp; gc	gc; **ri: gc**	gc		gc; **ssp**		ac; ssp	gc	**ri: gc**
4	ac	ssp; gc	2× gc	gc		ssp; gc		ac; ssp	gc	gc
5	ac	ssp; gc	**gc**	gc		gc; **ssp**		ac; ssp	gc	blunt; ssp; **le: gc**
6	ac	ssp; gc	**gc**	gc		ssp; gc		ac; ssp	gc	2× gc; pa
7	ac	ssp; gc	**gc**	gc		ssp; gc		ac; ssp	gc	gc; ssp; **ri: gc**; pa
8	ac	ssp; gc	**gc**	**ri: gc**		gc	2× ssp	ac	gc	gc; **le: 2× gc**
9	ac	ssp; gc	gc; **ri: gc**	gc		ssp; gc		ac; ssp	gc	ssp; 2× gc
10			gc	gc		ssp gc		ac; ssp	gc; **le: gc**	
11	mts		gc; 2× ssp				ac	ac; ssp	gc; **ri: gc**	

It is neighbored by almost triangular narrow placids (9–11 μm) which alternate with broader placids (16 μm) showing parallel lateral margins and a rounded anterior margin (Figs. 2B, H and 3). Circular musculature (Fig. 5H) connects the placids and serves in closing the neck region when the head is retracted (Fig. 2B and H).

3.3. Trunk

The trunk contains 11 segments which consist of a single, ring-like cuticle in segment 1 and a cuticle divided into one dorsal tergal plate and two ventral sternal plates in the remaining segments (Fig. 2A and B). In SEM, the sternal plates appear separated from each other midventrally but not from the tergal plates (Figs. 5N, 6C, F, and 7A, C, G, J). In few specimens, the lateral segmental cuticle bulges slightly out in its posterior part (Figs. 4J and 5A), whereas in most specimens the cuticle appears straight.

At the anterior margin, each segmental cuticular plate thickens towards the interior of the body and forms a pachycyclus to which the segmentally arranged ventral and dorsal longitudinal muscles attach (Figs. 4L, 5H, 6L, and 7E, F). The surface of the cuticle is arranged into an anterior secondary fringe with an anterior, straight line of minute, cuticular, spine-like processes followed by two wave-like lines of small, cuticular, spine-like processes, a central area with cuticular scales and a posterior primary fringe which extends over the subsequent segment (Figs. 4D, E, H, K, 5J, N, 6A, B, and 7A). Usually, the latter shows in all segments (but occasionally in the posterior segments only) an internal, short, longitudinal striation pattern (Figs. 4D, E, K, 5D, L, O, 6A, and 7A). At the posterior margin of the tergal plates, some specimens reveal generally 8 but sometimes numerous cuticular, triangular, tooth-like processes which may be short or large (Table 2). The scales of the central area of the cuticular plates may be small and shaped triangular to column-like (Figs. 4D–G, K, 5L, N, 6A–C, F, and 7A–D), or they may be broader and in light microscopy give the appearance of rice-terraces in an aerial view (Figs. 4J and 5A, E, F; Table 2). At its posterior margin, each scale possesses a minute hair-like cuticular process only visible in SEM. In the first segments, scales often reveal two to few such processes (Fig. 4G). Scales are not associated with perforation

sites of the trunk cuticle. In general, perforation sites as well as cuticular hairs as known from other Kinorhyncha are lacking completely. The attachment sites of the dorsoventral muscles appear as two neighboring, circular, slightly crumpled cuticular areas without scales (Figs. 6C, F and 7A). Few specimens exhibit in the central area clearly recognizable, longitudinal, cuticular ridges which may appear on all segments or on the anterior segments only (Figs. 4J and 5A, E, F; Table 2). These cuticular ridges appear only in those specimens which also reveal broader scales.

Sensory spots consist of 1–3 cuticular tubes extending through the body cuticle from a more or less conical atrium with few subcuticular cells. On the surface, the pores of the tubes are surrounded by a circular to oval area of small cuticular micropapillae (Figs. 2A, B, 4H, 6C, F, and 7A–D and G–J), which cannot be resolved in more detail in light microscopy. The paradorsal sensory spots possess a more flask-shaped atrium with one to two necks and much shorter tubes than found in all other sensory organs (Figs. 4C and 5B–D, G). In dorsoventral mounts of specimens with a well developed cuticle, a lateral sensory spot can be recognized by its conical atrium, which extends partly into the cuticle (Figs. 4J and 5E, F). A sensory spot in this position may also be traced by its cuticular tubes extending from the body tissue to the cuticle in specimens where the tissue has partly withdrawn from the cuticle during the process of fixation and subsequent preparation.

The distribution of sensory spots follows the ground pattern of *Campyloderes* shown in Table 4 but varies between specimens from different locations (Table 2; e.g., comp. Fig. 4C with Fig. 5B–D). Often, a sensory spot can be noticed by light microscopy or SEM at the border of the tergal and the sternal plate of segment 11 (Fig. 6C), on the tergal plate of one side and on the sternal plate of the other side (Fig. 6D), or on the tergal plate of both sides (Fig. 6E). This character is not recognizable in all specimens.

A **gland cell outlet** appears as a circular depression of the surface with a central, conical "plug" and an egg-shaped, sub- and intra-cuticular atrium in the light microscope (Figs. 4C–F, J–L, 5A–G, L–O, and 6A, D), whereas its outlet is feebly visible or not recognizable at all in SEM (Figs. 6C and 7A). Also, the posterior margin of a segment may cover a gland cell outlet of the subsequent segment. Hence, it is not possible to identify the outlets

Table 4

Position (not in brackets!) of spines, sensory spots, gland cell outlets and papillae occurring in all specimens of *Campyloderes*. The ground pattern of the taxon *Campyloderes* comprises all characters in the table, including positions in brackets which are derived from the outgroup comparison within Kinorhyncha. Characters only occurring in females are marked in bold and underlined. Characters appearing (almost) exclusively in males are highlighted in italics and bold. It remains uncertain for the lateroventral position in segments 2–10 whether sensory spots or papillae belong to the ground pattern (marked as ssp/pa). In segment 8, a sensory spot may appear in a sublateral or in a lateral accessory position or in both positions.

Position segment	md	pd	sd	ld	ml	sl	la	lv	vl	vm
1	ac	(ssp)	gc		ssp			elongate ac	bl; gc	
2	ac	ssp	gc	gc	ssp			bl; ssp/pa	gc	ssp; gc
3	ac	(ssp)	gc	gc		ssp		ac; ssp/pa	gc	gc
4	ac	ssp	gc	gc		ssp		ac; ssp/pa	gc	gc
5	ac	(ssp)	gc	gc		ssp		ac; ssp/pa	bl; gc	gc
6	ac	ssp	gc	gc		ssp		ac; ssp/pa	gc	gc; **pa**
7	ac	(ssp)	gc	gc		ssp		ac; ssp/pa	gc	gc; **pa**
8	ac	(ssp)	gc	gc		ssp	ac; ssp/pa	gc	gc	
9	ac	ssp	gc	gc		ssp		ac; ssp/pa	gc	ssp; gc
10	*ac*		gc			ssp; *ac*		ssp/pa	gc	
11	*ac* + mts		gc; 2× ssp				ac	ac		gc
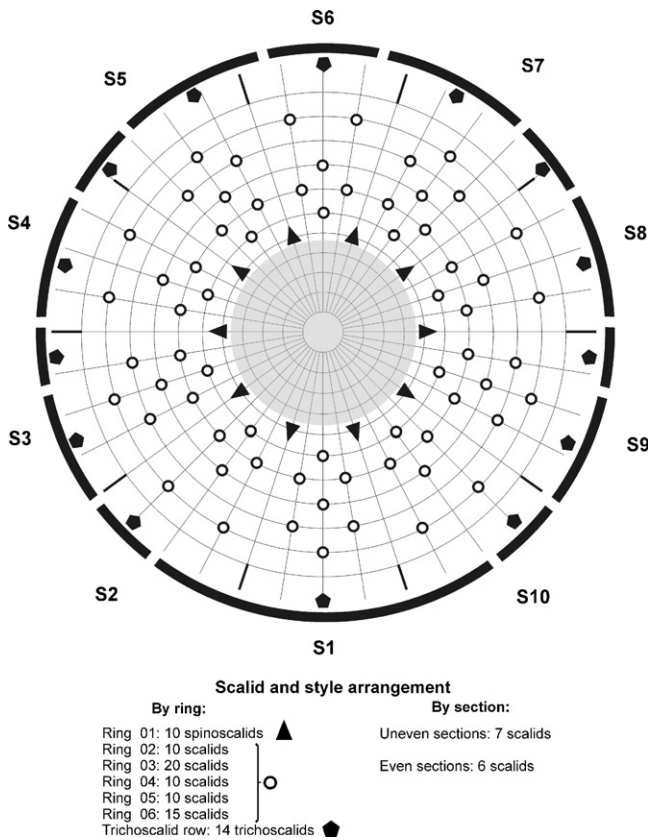
Fig. 3. Diagram of mouth cone, introvert and placids of *Campyloderes* cf. *vanhoeffeni* from the Faroe Islands with indication of scalid and placid distribution. Placids are symbolized by the bold bent bars around the introvert diagram. Inner oral styles in grey area not illustrated.

Scalid and style arrangement

By ring:

Ring 01: 10 spinoscalids ▲
Ring 02: 10 scalids
Ring 03: 20 scalids
Ring 04: 10 scalids ○
Ring 05: 10 scalids
Ring 06: 15 scalids
Trichoscalid row: 14 trichoscalids ⬠

By section:

Uneven sections: 7 scalids

Even sections: 6 scalids

of the glandular cells on tergal and most sternal plates with SEM. On the sternal plates, ventromedial outlets can be at least in the posterior segments identified as inconspicuous notches or interruptions in the posteriormost secondary fringe. The outlet is covered by several small hair-like cuticular processes (Figs. 6C and 7A). However, openings such as a porous area or an actual hole are apparently not present.

Papillae are in most cases very short (ca. 0.6–0.8 μm), conical, covered with cuticular micropapillae and often reveal a terminal pore (Figs. 4D, F, 5E, K–O, 6A–C, and 7B–D, G, J). Papillae are considerably elongate lateroventrally in segments 3–11 of one female specimen from South Korea (ZMB 5979) and lateroventrally in segment 11 just above the lateral terminal spine of all specimens from the Faroe and Solomon Islands (ZMUC

KIN-83–97, -306–309; ZMUC KIN-458), become progressively longer from segment 8 to 11 in one male South Korean specimen (ZMB 5980) and are more elongate ventrolaterally in segment 5 of a male from the Manihiki Plateau (ZMB 5977; here, papillae replace the ventrolateral short spines). In several specimens, a papilla may occur anterior to the lateroventral spines in segments 2–11 (Figs. 4D, F, K, L, N, 6C, 7C, D, and G and Table 2). Sometimes the lateroventral papillae are difficult to discriminate from sensory spots (Table 2 and Fig. 6A and D). Females always possess a ventromedial papilla in segment 6 and 7, in segment 7 in an almost paraventral position (Figs. 5E, M, O and 6A, B). Females from South Korea also exhibit a ventromedial papilla in segment 5 (Fig. 5L), whereas females from the Faroe Islands show the papilla in the ventrolateral position in segment 5 (Fig. 5N). A papilla can be identified both by SEM and light microscopy. However in the latter, it only appears as a weak marking (Figs. 5E, L, M, O and 6A), whereas in SEM its appearance becomes more clear (Figs. 5K, N and 6B).

Acicular **spines** are covered by small cuticular scales and terminate in a spinose tip (Figs. 4G and 5K). Generally, they occur lateroventrally in segments 1–9 and 11, in an accessory position in segment 11, middorsally in segments 1–9 and 11, ventrolaterally in segments 1 and 5, and midterminally in segment 11 (Fig. 2A, B and Table 4; see also below, sexual dimorphism). The lateroventral spine of segment 1 is in almost all specimens elongated (to the extreme of up to 210 μm) and extends over two to several segments with the exception of three male specimens from Chatham Rise, New Zealand (ZMB 5973a–c), which exhibit a short spine, 30–55 μm long. The elongated spine of segment 1 may occur in a ventrolateral instead of a lateroventral position (ZMB 5973a).

The midterminal spine may terminate in a spinose tip, especially in recently moulted specimens, or in a more blunt tip. The distinction between spinose and blunt appears fluid. The midterminal spine shows a thick proximal cuticle around a central cellular cavity and one dorsal thin area in the cuticle where possibly sensory receptors are located. In one specimen, two such thin areas are noticed (ZMB 5978). Each lateral terminal accessory spine reveals a similar morphology but with two such thin areas, and occasionally only one, three or five on one side (ZMB 5974, 11174b, c; ZMUC KIN-91; Table 2). Lateroventral spines may also exhibit one thin area near their bases, but this was not checked in all specimens.

Short, more tubular spines with a thinner cuticle, a smooth surface and a blunt tip occur in segments 1 and 5 in a ventrolateral position and in segment 2 in a lateroventral position (Figs. 4D–G, J, 5A, K, N, and 6B).

One female from Antarctica (ZMB 5968) shows a very thin, bent spinose process or appendage ventrolaterally on the right side of segment 8 and about lateroventrally on both sides of segment 10. The appendage does not seem to be articulated and may be retractable (see discussion). A similar, about 12 μm long
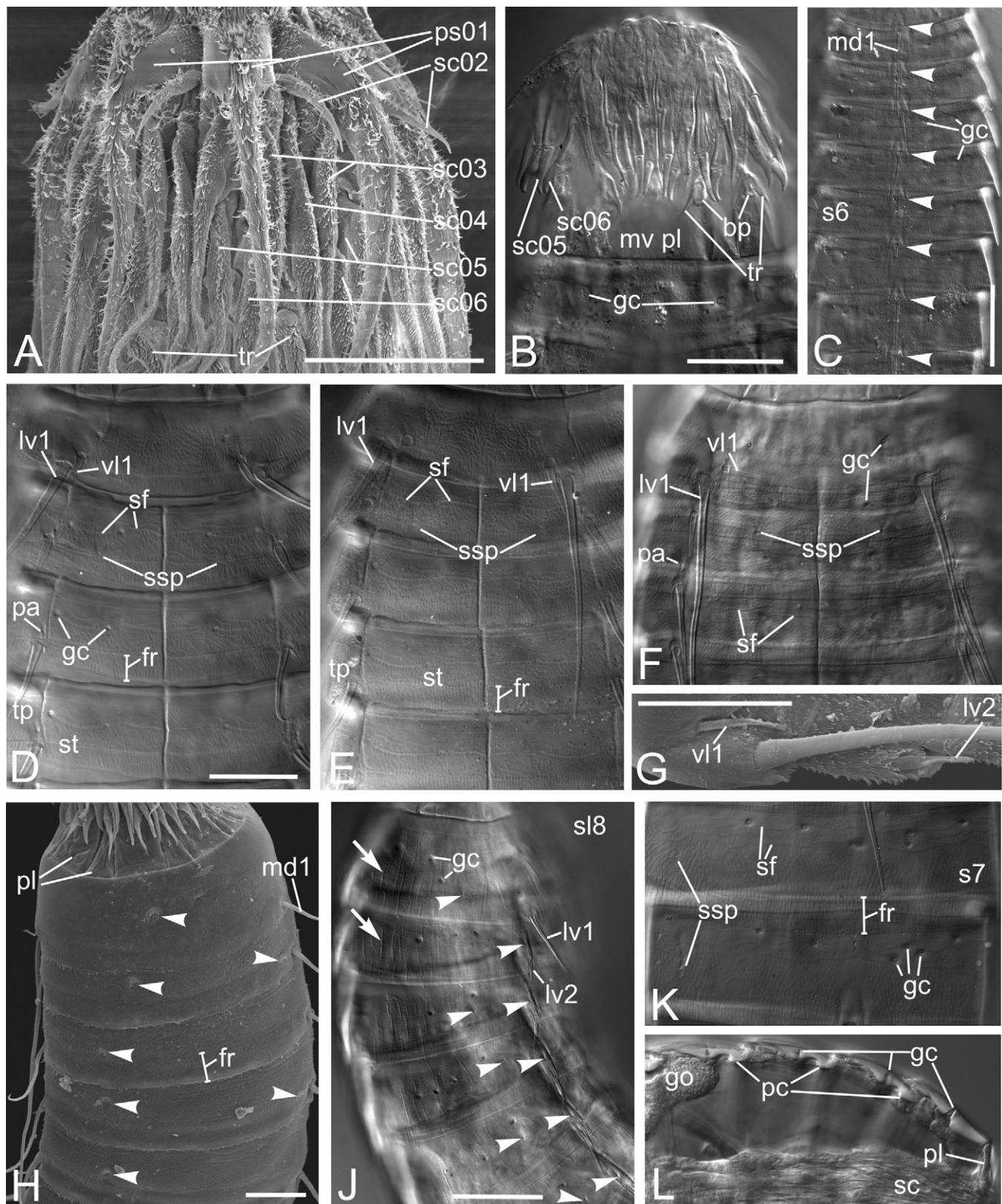
Fig. 4. (A–L). SEM (A, G, H) and DIC images (B–F, J–L) of male (A, E, G, J–L) and female (B–D, F, H) *Campyloderes* cf. *vanhoeffeni* from the Galápagos area (F–H), New Zealand (B, J, L), South Korea (C), American East coast (E) and the Faroe Islands (A, D, K). (A) Head, left side, sections 8 and 9. (B) Specimen ZMB 5971, head, placids and segment 1, ventral view. Note blunt tip of scalids of rings 05 and 06. (C) Specimen ZMB 5979, segments 2–8, dorsal view. (D) Specimen ZMUC KIN-92, segments 1–4, ventral view. (E) Specimen RH-182.1, segments 1–5, ventral view. (F) Specimen ZMB 11173f, segments 1–4, ventral view. Ventrolateral spine of segment 1 missing on left side. (G) Lateral spines of segments 1 and 2, ventral view. (H) Segments 1–5, left side. (J) Specimen ZMB 5973b, segments 1–5, right side. Note longitudinal cuticular ridges (arrows). Comp. with Table 3 for distribution of sensory spots and gland cell outlets. (K) Specimen ZMUC KIN-86, irregular distribution of gland cell outlets in segments 7 and 8, dorsal view. (L) Specimen ZMB 5973b, transversal section of tergal plates of segments 1–4. Sensory spots marked by arrowheads in (C), (H) and (J). Scale bar in (A), (G) and (H) 20 μm, in B 30 μm, in C 50 μm, in D 30 μm (valid for D–F, K), in J 50 μm (valid for J, L).

appendage is found in all females from the Faroe Islands about lateroventrally in segment 10 (Fig. 6F–K). The lateroventral spinose appendage may become visible on one (ZMUC KIN-87, -88, -92–94, -97) or both sides (ZMUC KIN-307, -309), and may be unbranched (ZMUC KIN-92, -307; Fig. 6F, G), bifurcated (ZMUC KIN-87, -88, -94, -97, -309; Fig. 6J, K) or even trifurcated near its tip (ZMUC KIN-93; Fig. 6H). The spinose appendage also appears on one side in a female from the Galápagos area (ZMB 11173e). Towards the interior of the specimens, a strongly sclerotized cuticular area can be recognized as an interior extension of the spinose appendage (Fig. 6G–J).

Longitudinal **muscles** attach to the pachycycli of subsequent segments on the left and right side dorsally and ventrally in all segments (Figs. 5H and 7E). Their number diminishes from six on one side dorsally and ventrally in segments 2–7 via four in segment 9 and two in segment 10 to a single ventral and dorsal muscle in segment 11 (ZMB 5973c). In segments 1–7, 2–3 oblique muscle strands connect the tergal plates of subsequent segments and the tergal plate with the sternal plate of the subsequent segment (Fig. 5H). In segment 8, a single muscle extends from the tergal plate of segment 8 to the sternal plate of segment 9. Oblique muscles do not seem to occur in segments 9–11. One pair of dorsoventral muscles each consisting of two strands stretches between the tergal and sternal plate of each segment (ZMB 5973a–c; Fig. 5H). In segment 11, two muscle strands connect the apodeme of the lateral terminal spine with the posterior margin of the tergal plate and one strand with the midterminal spine (ZMB 5973c; Fig. 6L–N). The left and right dorsal longitudinal muscle attach to the midterminal spine.

The pharynx seems to possess about 20 circular muscle cells alternating with about 20 radial muscle cells (Fig. 2E).

3.4. Variation of characters

Generally, characters such as sensory spots, gland cell outlets, and papillae are arranged bilateralsymmetrically. However, 48 out of 81 specimens studied do reveal 1–13 characters only on one side (e.g., Table 3; Figs. 4J, K and 5A, G); in 6 out of these 48 specimens, the asymmetry refers to only one character, in 16 specimens to two characters, and in 7 specimens to three characters.

Characters may appear in an intermediate position between reference positions (see also remarks above). Especially sensory spots may be found in a laterodorsal, intermediate, or midlateral position in segments 1 and 2. Table 3 lists other characters as an example.

Paradorsal and ventromedial sensory spots are especially conspicuous for variation (Table 2). They appear both on the left and right side paradorsally in segments 1–9 (most specimens), or in segments (1), 2, 4 and 6–9 (ZMB 5965, 5966, 5971, 5972, 5973a, 5974a, 11173e), or in segments 1, 2, 4–9 (ZMB 5984a, b), or in segments (1), 2, 4, 6 and 9 (ZMB 5973c, 11173b), or in segments (1), 2, 4, 6, 8 and 9 (ZMB 5970, 5977a, 11173a, c, d, f, 11174a–c), or in segments 1–4, 6, 8 and 9 (ZMB 11173g). Ventromedial sensory spots may occur both on the left and right side in segments 2 and 9 (most specimens), or in segments 2, 4, 6, 9 and (11) (ZMB 5973a, c, 5978), or in segments 2, 5, 7 and 9 (ZMB 5969b, 5973b, 5975, 5977a; RH-2104.1).

A sensory spot is regularly found inter alia in a sublateral and lateroventral position (here in certain specimens replaced by a papilla) at least in segments 3–10 (Table 4 and Figs. 2A, 3H, J, 5A, and 7B, D). However in segment 8, a sensory spot is often found both on the left and right side in the lateral accessory position instead of the sublateral and/or lateroventral position. This results in either one or two lateral accessory spots (Table 2 and Fig. 5F) and a corresponding gap sublaterally and lateroventrally. In two females from the Galápagos area (ZMB 11173e, g) an additional sensory spot without a corresponding gap seems to occur both on the left and right side in the lateral accessory position of segment 8.

Seven male and 8 female specimens of *Campyloderes* of this study lack a spine primarily on the left or right side (no preference)

or on both sides (Table 2), no articulation site is found indicating a secondary loss of a spine. In 11 cases this refers to the ventrolateral short spine in segment 1 (missing on one side: ZMB 5971, 11173f: Fig. 4F, ZMUC KIN-97; missing on both sides: ZMB Q.2757b, 5969b, 5972, 5973a-c, 5975, 5977), one specimen does not possess a middorsal spine in segment 2 (ZMB 5967k: Fig. 6H), one lacks it in segment 7 (ZMUC KIN-86), one specimen does not exhibit a ventrolateral short spine in segment 5 (ZMB 5966), and one specimen (ZMUC KIN-534a) lacks a lateral terminal spine on both sides (Table 2 and Fig. 7J). One male misses a lateroventral short spine in segment 2 in addition to the ventrolateral short spine in segment 1 (ZMB 5973c). In a second male the ventrolateral short spine in segment 5 is modified to an elongated papilla, and the more tubular, short lateroventral spine in segment 2 appears as a much longer acicular spine (ZMB 5977). An additional short, more tubular spine occurs on one side ventrolaterally in segment 1 (ZMB 11174c: Fig. 8 A) and in segment 5 (ZMB 5967a), respectively. Segment 10 generally lacks a lateroventral spine and in females also a middorsal spine (but see Fig. 5G), but males always show a spine sublaterally on both sides. However, one male (RH-2910.1) and two juvenile specimens (ZMB 5983a, d) do posses a lateroventral instead of a sublateral spine, and two juvenile specimens show a spine in a lateral accessory position (ZMB 5983b, c).

Developmental artifacts are rare in the specimens studied. One female (ZMB 5967a) reveals displaced sternal plates but regular tergal plates in segments 9–11 (Fig. 7E, F). One female (ZMUC KIN-534a) shows a very short bifurcate middorsal spine in segment 11 (Fig. 7J), and one young adult from the Galápagos area reveals a short, thickened, bifurcate lateroventral spine on one side in segment 8 (ZMB 5983b: Fig. 8B). The middorsal spine in segment 4 of one specimen (ZMB 11174d) appears incompletely chambered by 5 thin septa similar to the primary scalids.

3.5. Sexual dimorphism

Males are distinguished from females by their testes, the lack of the characteristic ventrolateral female gonopores at the border between the 10th and 11th trunk segment (Figs. 6C–F, K and 7G), the lack of a ventromedial papilla in segments 6 and 7 (plus ventromedially and ventrolaterally in segment 5 of the South Korean and Faroese specimens, respectively), an acicular sublateral spine in segment 10, and an acicular middorsal spine in segments 10 and 11. However, three female specimens from the Atlantic Ocean and three females from the East Pacific area do possess a middorsal spine in segments 10 and 11, although they are clearly identified as females by their gonopores and ventromedial papilla in segments 6 and 7 (ZMB 5965, 5966, 5984b: Fig. 5G; ZMUC KIN-534a) and by gonopores, ventromedial papilla in segments 6 and 7 and eggs (ZMB 5984a; RH-2104.3). A specimen from the Solomon Islands (ZMUC KIN-458), recognizable as a female by its gonopores and its ventromedial papillae in segments 6 and 7, seems to possess a very short or broken middorsal spine in segment 10.

3.6. Recently molted adult stage

In recently molted adults, the body cuticle is much thinner than in the more matured specimens and lacks the yellowish appearance of the more sclerotized cuticle in light microscopy. The pachycycli are weakly developed (Fig. 8B, J). The posterior margin of tergal and sternal plates shows a primary fringe but no spinose processes like in juvenile stages. Gland cell outlets and lateral sensory spots are extremely difficult to recognize (Fig. 8B, J) and often not traceable, because the thin cuticle lacks the characteristic cavities of gland cell outlets and sensory spots, and because the light refracting storage
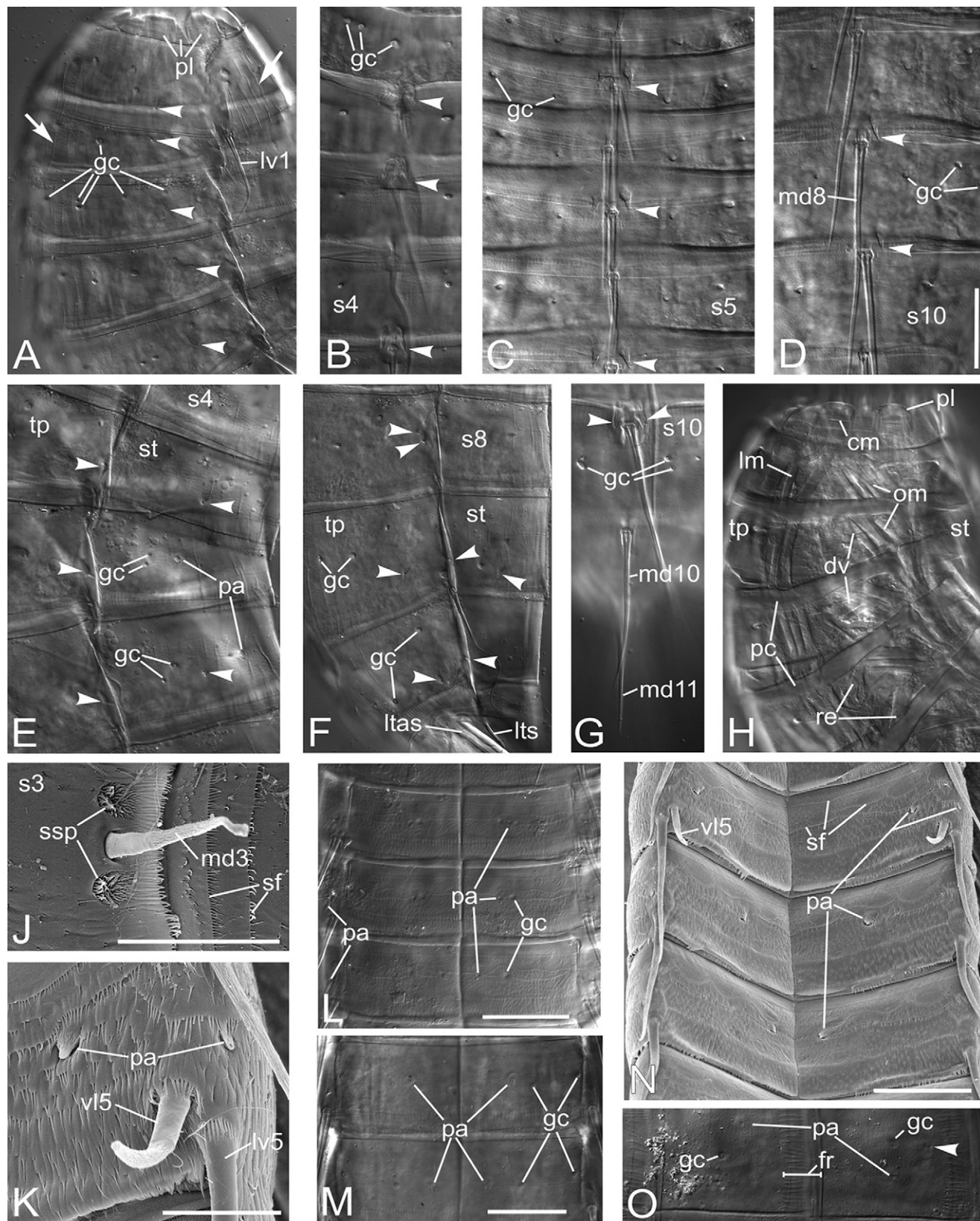
Fig. 5. (A–O). DIC (A–H, L, M, O) and SEM images (J, K, N) of female (A, B, E–G, J–O) and male (C, D, H) *Campyloderes* cf. *vanhoeffeni* from New Zealand (A, E, F, H), the Galápagos area (B–D, G, M, O), South Korea (L) and the Faroe Islands (J, K, N). (A) Specimen ZMB 5975, segments 1–5, right and ventral side; cuticular longitudinal ridges (arrows) and short lateroventral spine in segment 1. Comp. with Table 3. (B) Specimen ZMB 5984a, segments 1–4, middorsal view; paradorsal sensory spots in segments 1, 2 and 4 and additional middorsal and subdorsal gland cell outlets in segment 1. (C, D) Specimen ZMB 11174a, segments 1–5 (C) and 8–10 (D), middorsal view; paradorsal sensory spots in segments 2, 4, 6, 8 and 9. (E, F) Specimen ZMB 5975, segments 5–7 (E) and 8–11 (F), right and ventral view. Note sensory spots: ventromedially in segments 5 and 7 (E) and 9 and 10 (F), lateroventrally in segments 5–7 (E), two times in lateral accessory position in segment 8 (F). (G) Specimen ZMB 5984a, segments 10–11, middorsal view; middorsal spines in segment 10 and 11 of female (!). (H) Specimen ZMB 5973a, muscular system of segments 1–5, transversal section. (J) Middorsal spine and paradorsal

(?) vesicles and cells do not allow examination of cuticular details properly.

3.7. Juvenile stages

The juvenile stages available for this study probably belong to the last 3–4 of presumably 6 life history stages, J-1 through J-6. They differ from adult specimens by (1) a thinner cuticle including barely developed pachycycli, gland cell outlets and cuticular scales (Fig. 8D–H, L), (2) a clear separation of anterior segments but a less obvious border between segments 10 and 11 until J-4 or J-5 (Fig. 8E), (3) numerous, thin spinose processes of different length at the posterior border of sternal and tergal plates in earlier stages (Fig. 8D–G), (4) numerous light refracting vesicles in most of the trunk obscuring partly cuticular characters (Fig. 8F, G, K), and (5) gonads not becoming visible before the late juvenile stage(s) (Fig. 8K). Gland cell outlets can be observed subdorsally and ventromedially but seem to be lacking in all other positions. Sensory spots appear clearly ventromedially in segments 2 and 9, subdorsally in segment 11, midlaterally in segment 2 and sublaterally in segments 4 (Fig. 8D), 6 and occasionally 9 (Fig. 8F, H). Papillae are more easily traceable lateroventrally in segments 9 and 10. Juvenile stages always seem to possess a spine middorsally in segments 10 and 11 as well as in a sublateral to almost lateroventral position in segment 10.

However, the characteristic elongate ventrolateral spines of segment 1, the broader midventral placid, and the chambered primary scalids (5–12 septa) are already expressed in earlier stages (Fig. 8C). The cuticular scales, the secondary fringe on the anterior tergal and sternal plates (Fig. 8H), and the thin areas in the midterminal as well as in the lateral terminal accessory spines are detectable in late juvenile stages. The cuticular surface of the trunk cuticle of molting specimens appears crumpled because of its low thickness (Fig. 8L). The cuticular tubes of sensory spots and the cuticular lining of the hind gut are molted together with the head and body cuticle (Fig. 8C). Stages until J-4 or J-5 possess a single sternal plate in all segments (Fig. 8E–G, H) except segment 1 which is ring-like. The scales and the thin spinose processes at the posterior border of each sternal plate are more pronounced in the midventral area than in more lateral parts (Fig. 8F, G). Late juvenile stages develop sternal plates in segments 2–10. It remains open whether the last juvenile stage or just the adult stage develops a separation into two sternal plates in segment 11 as in the adult stage. Some of what is identified as young adult stage in this study may turn out to represent in fact the last juvenile stage once more specimens will become available for an investigation of the postembryonic development of *Campyloderes*.

3.8. Campyloderes Zelinka, 1907

Included species. *Campyloderes vanhoeffeni* Zelinka, 1913; *Campyloderes vanhoeffeni* var. *kerguelensis* Zelinka, 1913 [regarded as species *C. kerguelensis* (Zelinka, 1928) by Johnston (1938) but not by Moore (1973)]; *Campyloderes macquariae* Johnston, 1938; *Campyloderes adherens* Nyholm, 1947 [probably belonging to *Centroderes*, see discussion below].

Emended diagnosis. Neck with 14 placids; midventral placid significantly broader than remaining placids, neighbored by smaller placid alternating with broader placid. Cuticle of 1st trunk segment ring-like; cuticle of all subsequent segments with midventral and lateral articulation resulting in two sternal and one tergal plate. 1st trunk segment with elongated lateroventral acicular spine; short spine with blunt tip lateroventrally in 2nd and ventrolaterally in 1st and 5th segment; one acicular, middorsal spine at least in trunk segments 1–9 in females and in segments 1–11 in males; regular, acicular lateroventral spine in segments 3–9 and 11 in females and additionally sublaterally in segment 10 in males; midterminal spine significantly shorter than lateral terminal accessory spine. Outer oral styles connected by thin cuticle appearing fused. Primary scalids with septa in ring 01, ring 02 scalids short and acicular.

4. Discussion

4.1. Morphological comparison

Several previous studies mention the unusual appearance of the primary scalids in specimens of *Campyloderes* which is not known from any other kinorhynch (Johnston, 1938; Moore, 1973; Song and Chang, 2001; Neuhaus, 2004). Johnston (1938, p. 8) describes these scalids as bearing "numerous minute hairs arranged in transverse bands". He illustrates 17 such bands in his Fig. 6 and 13 bands in his Fig. 7a (Johnston, 1938). Moore (1973, p. 346, Fig. 3A) notices a "spiral of setae" with "10–12 whorls". Song and Chang (2001: pp. 209–210) characterize the primary scalids as "banded with minute setules (usually 10–13 rings)". The reinvestigation of two specimens of their material in this paper leads to the conclusion that the "banded setules" are in fact internal septa inside the scalids, giving the impression of chambered scalids like in all other specimens studied (Table 2 and Fig. 2J, K). Based on this reinvestigation and on the material studied here, the authors of this paper suggest that chambered primary scalids are present in all specimens of *Campyloderes*.

The short acicular 02 ring scalid found in all specimens of *Campyloderes* with a protruded introvert in this study have been illustrated previously but not interpreted as a scalid (Zelinka, 1913, pp. 426–427, Tafel XXXIX, Fig. 4, 1928, pp. 286–287, Figs. 51, 54; Johnston, 1938, pp. 8–9, Figs. 6, 7; Moore, 1973, pp. 346, 349, Fig. 3A, B; Song and Chang, 2001, pp. 209–210, Figs. 1C, 2B, C). Neuhaus (1995, Tab. IV) first proposes that this spinose head appendage in fact represents a scalid in *C. vanhoeffeni*, a view that is followed here throughout.

Provided that the short acicular ring 02 scalids are included as scalids in the spine formula of previous studies, the arrangement of scalids in rings given in this paper agrees in the anterior 5 rings (Zelinka, 1928) or even in all rings except in ring 06 for which Moore (1973) and Song and Chang (2001) report only 14 scalids instead of 15 (this paper).

The spine pattern of the specimens studied in this paper agrees with previous reports (Zelinka, 1913, 1928; Johnston, 1938; Higgins, 1967; Moore, 1973; Song and Chang, 2001; Neuhaus, 2004) except that the actual sublateral position of the male acicular spine in segment 10 as found in all male specimens of this study was not recognized and illustrated instead in a lateroventral position in the literature (Zelinka, 1913, 1928; Johnston, 1938; Higgins, 1967). Also, Adrianov and Malakhov (1999) and Neuhaus (2004) mislabeled the lateral terminal spine and the lateral terminal accessory spine.

Fig. 5. (*Continued*). sensory spots of segment 3. (K) Segment 5, ventrolateral view. (L) Specimen ZMB 5979, segments 5–7, ventral papillae in segments 5(!)–7. (M) Specimen RH-2104.3, segments 6–7, ventral papillae in segments 6–7. (N) Segments 5–7, ventral papillae in segments 5(!)–7. (O) Specimen ZMB 5969b, segments 6–7, ventral papillae on left sternal plates of segments 6–7. Arrowheads mark sensory spots in A–G and O. Scale bar in D 30 μm (valid for B–E, G, H, O) μm, in L 50 μm (valid for A, F, L), in J and K 10 μm, in N 20 μm, in M 30 μm.
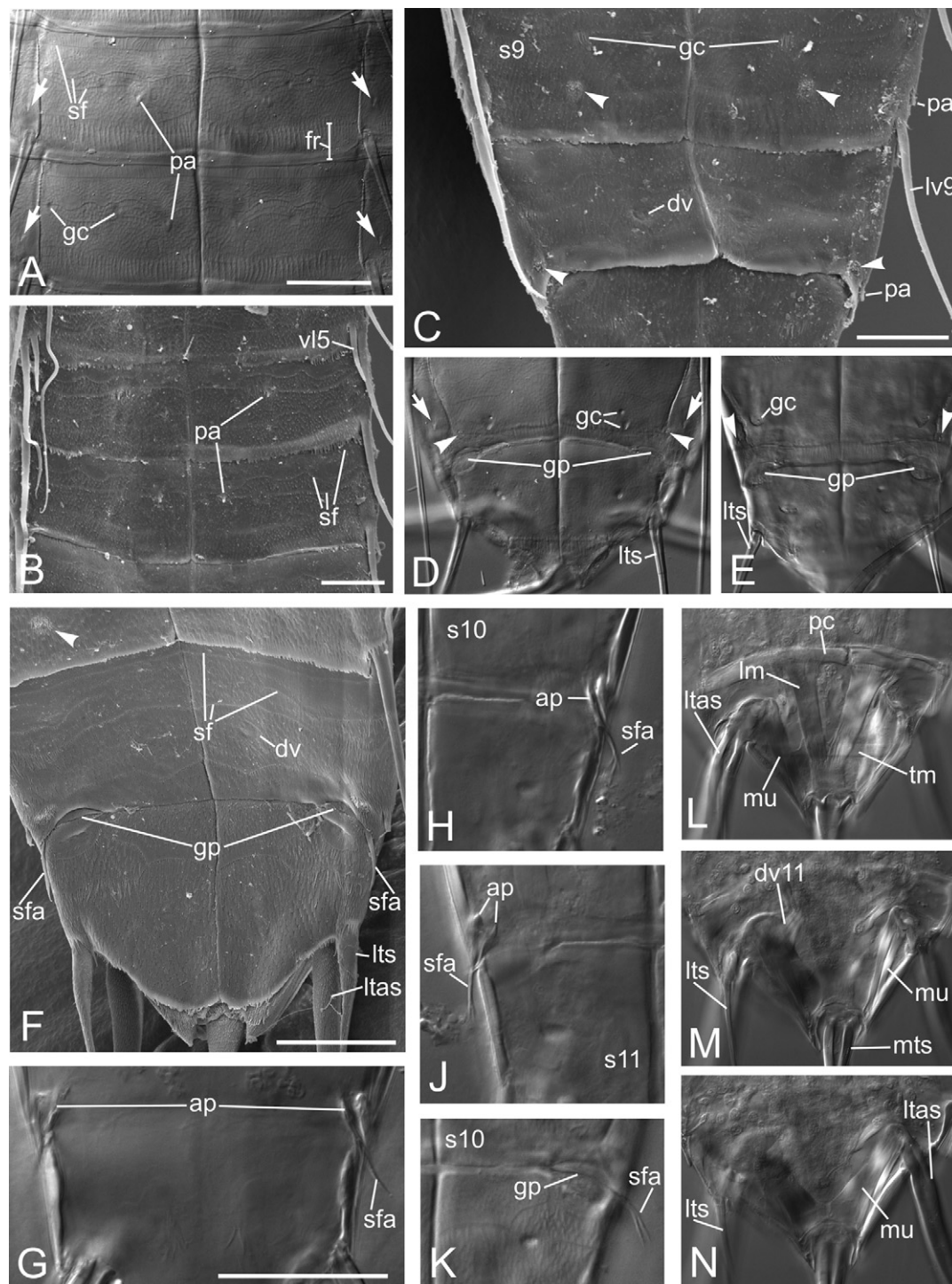
Fig. 6. (A–N). DIC (A, D, E, G–N) and SEM images (B, C, F) of female *Campyloderes* cf. *vanhoeffeni* from the East (A, C) and South Atlantic Ocean (B, E), the Galápagos area (D, L–N), and the Faroe Islands (F–K). (A) Specimen ZMB 5982, ventral papillae in segments 6–7. (B, C) Segments 5–7 with ventral papillae (B) and segments 10 and 11 (C). No gland cell outlets recognizable in (B) but in (C). (D, E) Specimens ZMB 5982 and 11173e, segments 10–11 with gonopores, ventral view. Sensory spots (arrowheads) in segment 10 ventrolaterally on left side but lateroventrally on right side (D) or lateroventrally on both sides (E). F-K. Specimens ZMUC KIN-307 (G), KIN-93 (H), KIN-87 (J) and KIN-94 (K), segment 10 with single (F, G), trifurcate (H) or bifurcate (J, K) lateroventral spinose appendage protruding from gonopore area, ventral view. (L–N) Specimen ZMB 5969b, segment 11, muscular system at different optical sections from dorsal (L) to ventral (N) side. Lateroventral structures (arrows in A, D) may represent sensory spots or papillae. Arrowheads in C–F mark sensory spots. Scale bar in A 30 μm (valid for A, D, E, L–N), in B, C and F 20 μm, in G 30 μm (valid for G–K).

Sensory spots, gland cell outlets, and papillae have always been very difficult to identify and to discriminate from each other, especially at the time when light microscopes equipped with differential interference contrast were not available. Zelinka (1913, p. 433, Tafel XXXIX, Fig. 1, 1928, p. 286, Fig. 52) recognizes paradorsal "helle Flecke" [= brighter spots] and illustrates these in segments 1–9; the authors of this paper interpret the spots as sensory spots. The same situation is mentioned by Johnston (1938, p. 11) as "highly refracting depressions" and by Moore (1973, p. 346) as "flask-shaped bodies". Zelinka's ventrolateral, subdorsal and laterodorsal circles
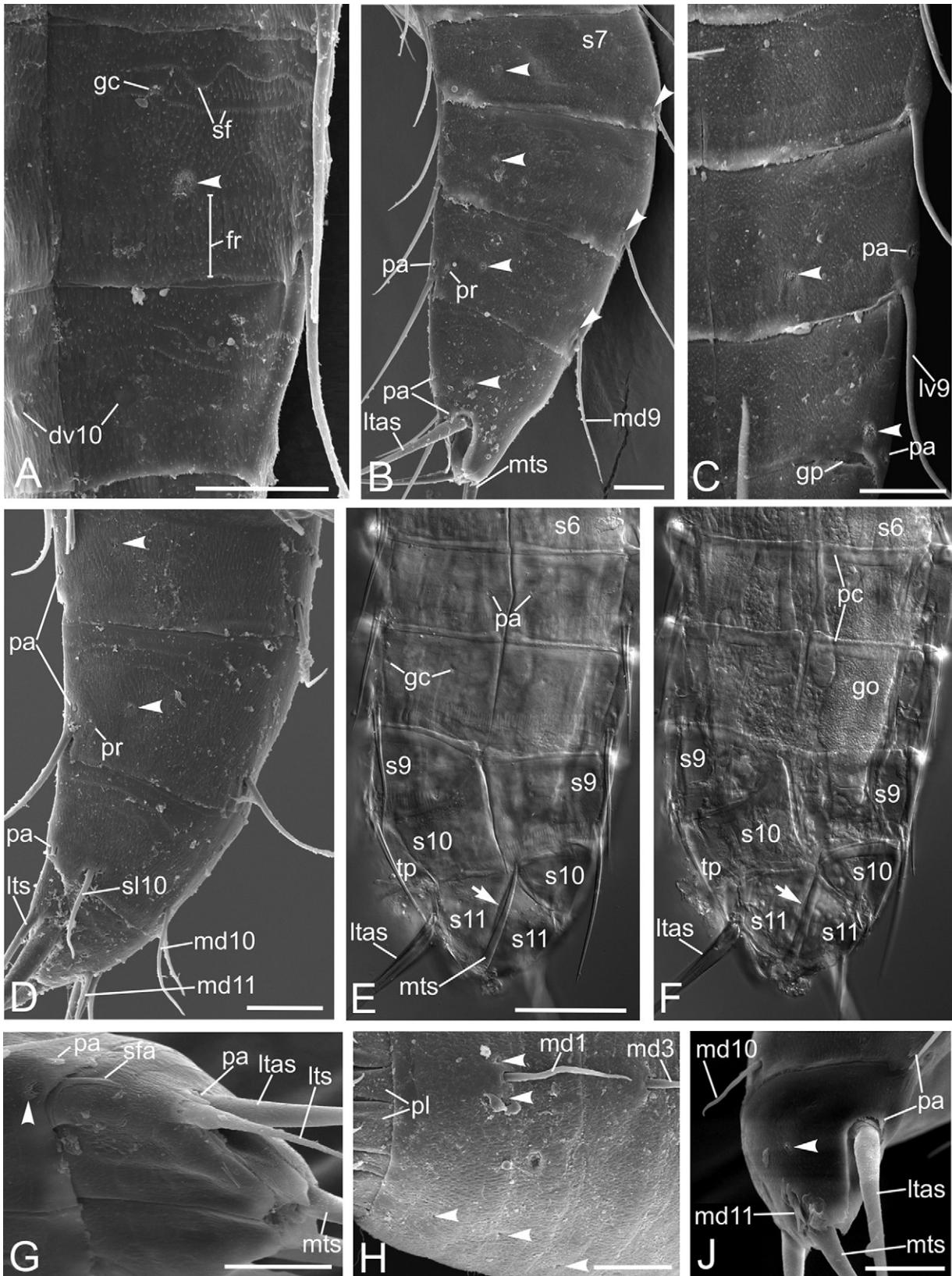
Fig. 7. (A–J). SEM (A–D, G–J) and DIC images (E, F) of male (A, D) and female (B, C, E–J) *Campyloderes* cf. *vanhoeffeni* from the South Atlantic Ocean (A, B, E, F, H), Galápagos area (C), South Korea (D) and the Faroe Islands (G, J). (A) Segments 9–10, ventral view. (B) Segments 7–11, left side. (C) Left sternal plates of segments 8–10, ventral view. (D) Segments 8–11, left side. (E and F) Specimen ZMB 5967b, segments 7–11 with distorted sternal plates in segments 9–11 at different optical sections, ventral view. Arrows mark midventral border between sternal plates of segment 11. (G) Segment 13, ventrolateral view. (H) Segments 1–3 without middorsal spine in segment 2, middorsal view. (J) Segment 13 lacking lateral terminal spines and with bifurcate middorsal spine, dorsolateral view. Arrowheads in A–D and G–J mark sensory spots. Scale bar in A–D and G–J 20 μm, in (E) 30 μm (valid for E, F).

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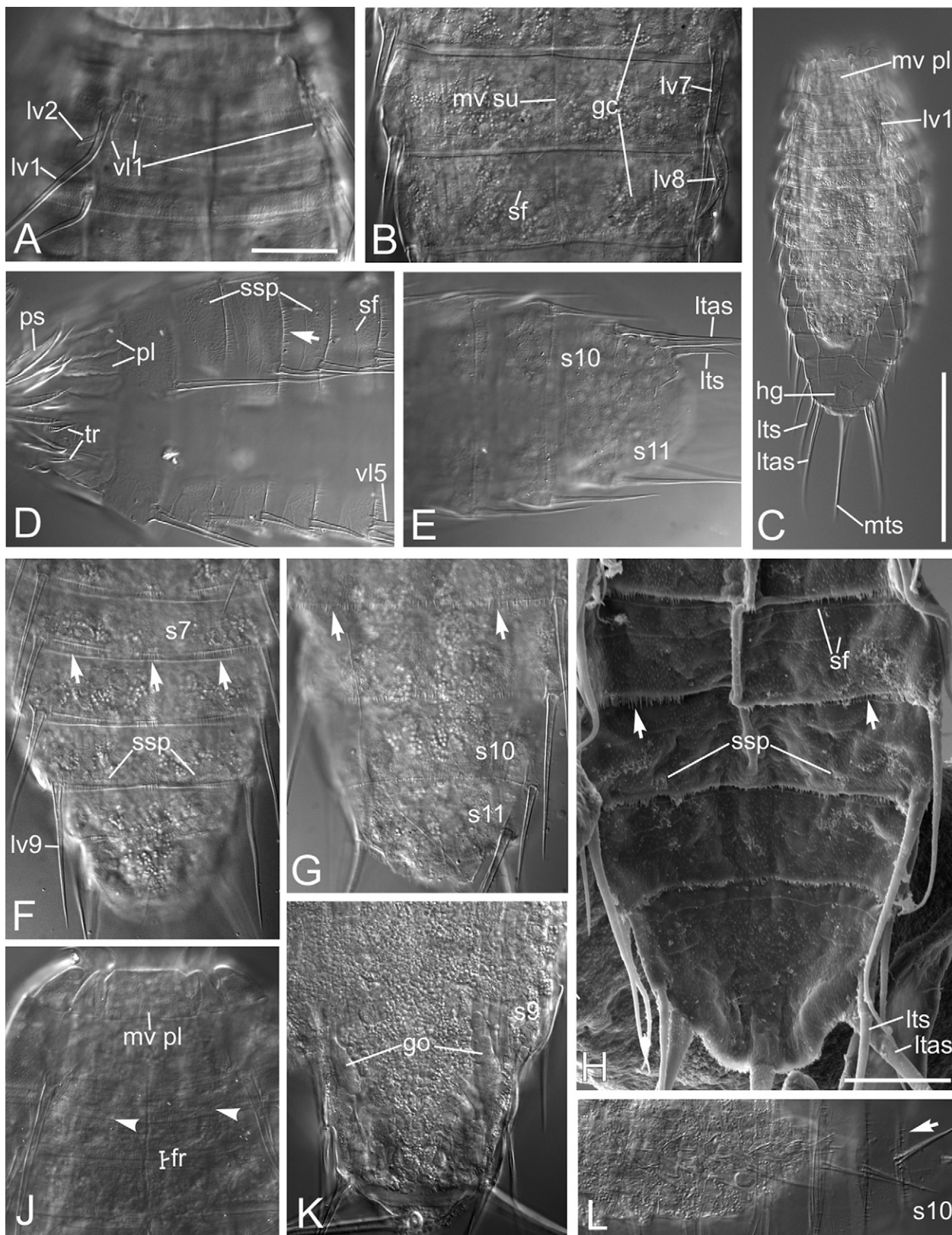
Fig. 8. (A–L). DIC (A–G, J–L) and SEM images (H) of male (A), young adult (B, J), juvenile (C, E–H, K, L) and exuvia (D) of *Campyloderes* cf. *vanhoeffeni* from the Galápagos area (A, B, D–G, K), South Atlantic Ocean (H, J) and New Zealand (C, L), ventral (A-K) or dorsal view (L). A. Segments 1–4 with double ventrolateral spine on right side of segment 1. (B) Segment 8–9 with left bifurcate lateroventral spine in segment 8. (C) Juvenile stage moulting inside exuvia. (D) Segments 1–5. (E) Segments 8–11 without midventral suture between sternal plates and without clear separation of posteriormost two segments. (F) Segments 7–11 with lateral and midventral area of spines. (G) Segments 9–11 with barely visible separation of segments 10 and 11. (H) Segments 8–11 without midventral separation of sternal plates. (J) Segments 1–4. Arrowheads mark sensory spots. (K) Segments 8–11 of late juvenile stage with anlagen of gonads. (L) Segments 4–10 of juvenile stage moulting inside exuvia with crumpled cuticle. Thin spines at posterior margin of cuticular plates marked with arrow in (D), (F–H) and (L). Scale bar in (A) 30 μm (valid for A, B, D–G, J–L), in (C) 100 μm, in (H) 20 μm.

in segments 1 and 2 (Zelinka, 1913, Tafel XXXIX, Figs. 1, 2, 1928, Figs. 52, 53) are regarded here as gland cell outlets. Similarly, Moore (1973, p. 346) is not sure whether the subdorsal, laterodorsal, ventrolateral and ventromedian structures in segment (1), 2–9 should be interpreted as sensory spots or not. We suggest that what Moore (1973) observed were in fact gland cell outlets.

Song and Chang (2001, Fig. 1) illustrate the positions of sensory spots, gland cell outlets, and papillae but take gland cell outlets for sensory spots ventromedially, subdorsally, and laterodorsally in segments (1), 2–10, (11) in the text description. Neuhaus (2004, p. 12) distinguishes between sensory spots type 1 and type 2. This reinvestigation of his specimens suggests that his "sensory spots type 1" are in fact gland cell outlets and only the "sensory spots type 2" represent sensory spots that are also found in other species of Kinorhyncha (Neuhaus, 1995; Sørensen and Pardos, 2008). To complicate matters further, his paradorsal "sensory spots type 1" in segments (1), 2, 4, 6, 8, and 9 are not gland cell outlets according to the previous statement but sensory spots. Also, he does not report the midlateral, sublateral, and lateroventral sensory spots. Ventromedial sensory spots in segments 3 and 6–8 are not confirmed in this paper.

Papillae have not been recognized as such before but were labelled "lateral tube", photographed, and illustrated by Song and Chang (2001, Figs. 1B and 2E, F), illustrated but not labeled by Higgins (1967) and mistaken for "sensory spots type 1" by Neuhaus (2004, Figs. 2A and 4C). Papillae vary slightly in shape and size within the South Korean specimens and in comparison with specimens from other regions. They appear either more elongate and tubular (Song and Chang, 2001, Fig. 2F) or shorter and a kind of "collapsed" (Song and Chang, 2001, Fig. 2E; this paper: Figs. 5K, L, N, 6C, and 7B–D, G).

4.2. Regional and global variation of characters

Conventional identification of kinorhynch species uses body shape, number and arrangement of cuticular trunk plates, shape and arrangement of cuticular placids, shape, number and arrangement of spines, and cuticular structures (Zelinka, 1928; Higgins, 1983, 1988; Adrianov and Malakhov, 1999; Neuhaus, 2002; Sørensen and Pardos, 2008). Promising additional characters such as sensory spots and gland cell outlets have always been difficult to recognize and to discriminate from each other, if sufficient material for SEM studies was lacking (Zelinka, 1928; Higgins, 1983; Neuhaus, 2004). Therefore, these characters have virtually not been available for species identification. In more recent publications, Pardos, Higgins, Sørensen, Neuhaus and coworkers summarize data about the arrangement of spines, sensory spots, gland cell outlets, and papillae in a table with reference positions introduced by Pardos et al. (1998) (see also Neuhaus and Blasche, 2006; Sørensen, 2006; Sørensen et al., 2000, 2007, 2009, 2010a,b; Sørensen and Thormar, 2010).

Information about intraspecific variation of characters in Kinorhyncha such as asymmetrical distribution of sensory spots is available for very few species, namely for juvenile and adult Pycnophyes kielensis Zelinka, 1928 and P. dentatus Reinhard, 1881 and for juvenile Paracentrophyes praedictus Higgins, 1983 (see Neuhaus, 1993, 1995). Furthermore, the holotype of Antygomonas incomitata Nebelsick, 1990 reveals two spines on the right side of segment 10 but only one spine on the other side without having any indication of a cuticular insertion scar on the left side (Nebelsick, 1990).

In this study, 19 adult specimens from the Faroe Islands (collected by MVS and B. Trygvadóttir), 25 specimens from the Central American East Pacific Ocean (collected by R/V Sonne: SO 144-3, SO 158, SO 208, and Johnson Sea Link I) and 8 specimens from the area east and northeast of New Zealand (collected by SO168) are available for investigation of regional variation of morphological

characters. On the Faroe Islands, specimens originate from two localities within a distance of 100 m whereas specimens from the East Pacific Ocean and from around New Zealand have been collected in an area of several hundred kilometers apart from each other. None of the characters mentioned below are gender-specific.

On the Faroe Islands, specimens harmonize well regarding their size and general pattern of sensory spots, gland cell outlets and papillae (Table 2). However, 16 out of 19 specimens in comparison with the general pattern of Faroe specimens express 1–8 additional gland cell outlets on one or both sides of 1–5 individual segments (e.g., Fig. 4K) whereas 7 out of 19 specimens have lost a sensory spot or a gland cell outlet on one side (Table 2). In segment 1 of all Faroese specimens, a sensory spot is found laterodorsally whereas this sensory spot appears almost consistently in a more midlateral position in all other specimens (Table 2).

In the East Pacific Ocean, groups with varying composition of specimens agree in different character sets (Table 2), such as large size (ZMB 5969a, b, RH-2104.1-2), high number of septa (20–30) in the primary scalids (ZMB 5969a, b; RH-2104.1), broader cuticular scales (ZMB 5969a, b, 11173g; RH-2104.2), ventromedial sensory spots in segments 2, 5, 7, and 9 (ZMB 5969b; RH-2104.1) or in segments 1 and 9 (remaining specimens), paradorsal sensory spots in segments 1–4, 6, 8, and 9 (ZMB 11173g), in segments 1, 2, 4, and 6–9 (ZMB 11173b, e), in segments 2, 4, 6, 8, and 9 (ZMB 5970, 11173a, c, d, f, 11174a–d; Fig. 5C and D), or in segments 1–9 (ZMB 5969a, b; RH-2104.1-5; Fig. 4C).

Similarly, the New Zealand specimens can also be assigned to groups of different character sets but with varying members (Table 2), such as large size, broader cuticular scales, ventromedial sensory spots in segments 2, 5, 7, and 9 (Fig. 5E), additional gland cell outlets paradorsally in segments 1–9 and in a midlateral to sublateral position at least in segments 3–9 (ZMB 5973b, 5975: Fig. 5A, F), paradorsal sensory spots in segments 2, 4, 6–9 (ZMB 5971, 5972, 5973a, 5974), and ventromedial sensory spots in segments 2, 4, 6, and 9 (ZMB 5973a, c). However, the character sets mentioned above show a considerable overlap between groups of specimens both from the New Zealand area and from the East Pacific Ocean, and appear as well in specimens from different regions of the world. This, e.g., regards characters such as large body size (ZMB 5977, 5978) and broader cuticular scales (ZMB 5978) (Table 2). It is therefore not possible to identify morphologically different species among the populations studied.

It is conspicuous that out of the 11 specimens of Campyloderes of this study lacking one or both ventrolateral short spines in segment 1, six are found among the only 8 specimens from the New Zealand area (Table 2). Also, variation of morphological characters among the specimens from the Central American East Pacific Ocean and among the New Zealand area is considerably higher than between specimens from the remaining locations of the world (Table 2). Possibly, evolutionary processes which will finally lead to the formation of new species in the New Zealand and East Pacific Ocean areas are responsible for this finding.

Amazingly, lateroventral papillae seem to occur only in specimens from quite distant locations, namely the North Atlantic Ocean (Faroe Islands: ZMUC KIN-83–97, -306–309), West Atlantic Ocean (New Hampshire, USA: RH-182, RH-183), South Atlantic Ocean (Antarctica: ZMB 5967a–e, 5968), East Indian Ocean (West Australia: RH-2910.1, RH-2910.2) and Pacific Ocean (New Caledonia: Higgins, 1967; South Korea: ZMB 5979, 5980, Song and Chang, 2001; New Zealand: 5976) (Table 2 and Fig. 1). It would not be too astonishing, if specimens from the Atlantic Ocean and Antarctica would agree in this character, because the Antarctic bottom water current may move the holobenthic kinorhynch specimens of Campyloderes across the Atlantic Ocean towards the North and West (Schmitz, 1996b, Figs. II-8 and II-156). The Antarctic circumpolar current system may distribute kinorhynch specimens

around Antarctica from where Antarctic bottom currents separate, and head in a northern direction east of the African East coast, west of Australia and east of New Zealand (Fig. 1 and Schmitz, 1996a, Fig. I-10, 1996b, Figs. II-8 and II-156). Such a global bottom current system may facilitate the exchange of specimens between the Atlantic, East Indian and Pacific Ocean.

Similarly, the female from South Korea and the Faroe Islands reveals in segment 5 a ventromedial and ventrolateral papilla, respectively. Such a papilla does not occur in segment 5 of any other female *Campyloderes* studied here (Table 2). These characters may have evolved independently. Or possibly, specimens from South Korea and the Faroe Islands share a common ancestor distributed from a common location by bottom current systems. The scenario would include the circumpolar Antarctic bottom current from which one branch of the bottom current system, the Antarctic Bottom Water, heads North in the Atlantic Ocean and reaches as far as the British Isles; in the Pacific Ocean, one branch of the bottom current system heads North east of New Zealand, than East until it reaches 20°N at about 165°W, and bends Northeast until 40°N at 160°E (Fig. 1 and Schmitz, 1996a,b, Fig. I-10, 1996b, Figs II-8 and II-156). Both the Atlantic and Pacific bottom water currents end not too far fom the Faroe Islands and South Korea, respectively, so further distribution does not seem impossible.

Among the larger specimens a tendency shows up for (1) a segmental cuticle bulging out laterally, (2) thin and/or flexible middorsal and lateroventral acicular spines, (3) more septa (20–30) in the primary scalids, (4) cuticular longitudinal ridges, (5) broader cuticular scales, and (6) generally 8 but sometimes numerous cuticular, triangular, tooth-like, cuticular, short or larger processes at the posterior margin of the tergal plates (ZMB 5969a, b, 5973b, 5975, 5977, 5978, RH-2104.1-2; Table 2). Again, short posterior cuticular processes and broader cuticular scales also occur in other specimens (Table 2). The specimens show quite a large distributional range in the Pacific Ocean from Manihiki Plateau (Central Pacific Ocean), to Christmas Island (East Indian Ocean, Australia, south of Java), Chatham Rise (New Zealand, Southern Pacific Ocean), and the Central American East Pacific Ocean. The authors of this study do not regard it very likely that the specimens mentioned above belong to one single population with an origin shared only by them.

In almost all specimens studied here, the acicular lateroventral spine of segment 1 is significantly longer than the lateroventral spine in segments 3–9 except in three males from Chatham Rise, New Zealand and one male from the Manihiki Plateau (ZMB 5973a–c, 5977; Table 2) where the spines in segments 1 and 3–9 show a similar length. Although the elongated lateroventral spine of segment 1 is regarded as one of the key characters of species of *Campyloderes* (e.g., Zelinka, 1913, 1928; Adrianov and Malakhov, 1999; Song and Chang, 2001; Neuhaus, 2004; Sørensen and Pardos, 2008), the three males with the short lateroventral spine in segment 1 clearly belong to the taxon *Campyloderes*, because they possess other key characters not known from any other kinorhynch genus such as the chambered primary scalids, a broad midventral placid neighbored by one small placid alternating with a broader placid, and a midterminal spine significantly shorter than the lateral terminal accessory spines (Neuhaus, 2004; Sørensen and Pardos, 2008; Table 2). Also, the specimens agree largely with the remaining specimens of *Campyloderes* in the cuticular structures and in the arrangement of sensory spots and gland cell outlets.

4.3. Sexual dimorphism

The male of *C.* cf. *vanhoeffeni* differs from the female inter alia in the possession of an acicular middorsal spine in segments 10 and 11 (Table 2). Sexual dimorphism has not been recognized by some older studies (Zelinka, 1913, 1928; Higgins, 1967; Song and Chang, 2001). Johnston (1938, p. 11) notices the lack of the "lateral

spines on segment 12 [= 10 according to the counting of body segments used in this paper] – perhaps a sexual character" but does not mention the situation of middorsal spines in segments 10 and 11 in females. Moore (1973, p. 350) reports that "the dorsal displacement of the 12th lateral spine [= spine of segment 10 in this paper] was consistent in all specimens possessing this spine" but rejects the idea of a gender-specific character. Song and Chang (2001, p. 213) annotate that in 9 out of 28 adults the middorsal spines on segments 10 and 11 and the sublateral spine of segment 10 are lacking. Neuhaus (2004) first suggests sexual dimorphism in specimens of *Campyloderes* which is corroborated by this paper.

However, five specimens from the Atlantic Ocean and from the Central American East Pacific Ocean (ZMB 5965, 5966, 5984a; RH-2104.3; ZMUC KIN-534a) can be clearly identified as female life history stages even though they <u>do</u> possess a middorsal spine in segments 10 and 11 (Fig. 5G) but no sublateral spine in segment 10. Two hypothess seem possible. First, the five females may represent exceptions from the general scheme of females not showing middorsal spines on the two posteriormost segments. However regarding other morphological characters, the five females fall well in the range of character variation observed for the remaining specimens studied (Table 2).

Second, the five specimens of *Campyloderes* may represent females molting into a second form of females thus suggesting two morphologically slightly different adult stages for *Campyloderes*. This idea is supported by the observation that all 11 specimens of late juvenile stages and all young adults of *Campyloderes* available in this study (collected by SO 144-3, SO 158, SO 168, ANT XIII-5, on the Faroe Islands) possess a male spine pattern, i.e., a middorsal spine in segments 10 and 11 and a sublateral spine in segment 10. It is supposed that stage-1 females molt from the last juvenile stage still possessing the middorsal spine in the posteriormost segments but lacking the sublateral spine in segment 10. From these females, stage-2 females molt loosing the middorsal spine in segments 10 and 11. This idea is somewhat contradicted by an illustration of Zelinka who draws a specimen of *Campyloderes vanhoeffeni* in lateral view with eggs, middorsal spines in segments 10 and 11, and a lateral spine in segment 10 (!) (original drawing: Zelinka, 1913, Tafel XXXIX, Fig. 4; reproduced illustration: Zelinka, 1928, Fig. 54).

It is known for other species of Kinorhyncha that adult specimens may molt into a second adult stage, namely for one female *Antygomonas oreas* Bauer-Nebelsick, 1996 (see Bauer-Nebelsick, 1996, Fig. 25) and for two female and one male *Zelinkaderes floridensis* Higgins, 1990 (see Higgins, 1990, Fig. 65). One male *Centroderes spinosus* (Reinhard, 1881) from the Black Sea and two female *Centroderes* sp. from Newfoundland have been found molting into a second adult stage (Neuhaus, Higgins, Pardos and Sørensen, unpublished results). Observations on a new species of *Semnoderes* from the deep sea around Christmas Island (Australia) indicate the possibility that the last juvenile stage molts into a subadult stage without clear male or female characters, and that this stage subsequently molts into the final adult stage (Neuhaus unpublished observation). *Echinoderes coulli* Higgins, 1977 reveals two morphologically slightly different female stages which both seem to develop gonads with eggs (Higgins, 1977). A study of the population structure of this species and of its morphology does not support the hypothesis that one female stage may molt from the other female stage (Higgins, 1977; Higgins and Fleeger, 1980). In summary of the observations before, it is suggested that molting of an adult (or subadult) stage into a second adult stage may be more widespread at least among Cyclorhagida than assumed previously.

One female from Antarctica (ZMB 5968), one female from the Galápagos area (ZMB 11173e) and all 8 females from the Faroe Island reveal a very thin, acicular spinose appendage lateroventrally in segment 10 visible on one side (ZMB 11173e, ZMUC KIN-87,

-88, -92–94, -97; Fig. 6H–K) or on both sides (ZMB 5968, ZMUC KIN-307, -309; Fig. 6F, G). Since the appendage on one side of the female from Antarctica is much shorter than on the other side, the appendages may be retractable. This hypothesis may be further supported by the presence of inner sclerotized cuticular apodemes (Fig. 6G–J) which may serve as a guiding structure. The function of the spinose appendages is unknown but involvement in copulation is likely. The spinose appendage is tentatively termed as such and not as a spine, because a regular spine is articulated and not potentially retractable. Appendages with this morphology have not been reported for any kinorhynch specimen before.

4.4. Identification of previously described species

So far three and four species of *Campyloderes* have been described, respectively, namely *C. vanhoeffeni*, *C. vanhoeffeni* var. *kerguelensis* which is regarded as *C. kerguelensis* (Zelinka, 1928) by Johnston (1938) but not by Moore (1973), *C. macquariae*, and *C. adherens* (see Zelinka, 1913; Johnston, 1938; Nyholm, 1947). For the argumentation given by Neuhaus (2004), the authors of this paper regard *Campyloderes adherens* as a member of the taxon *Centroderes*. This hypothesis is further supported by Nyholm's photograph of the mouth cone of *C. adherens* (see Nyholm, 1947, Plate 1, Fig. 2) which clearly shows individual outer oral styles whereas no specimen of *Campyloderes* possesses such separated outer oral styles (Zelinka, 1913, 1928; Moore, 1973; Song and Chang, 2001; Neuhaus, 2004; this paper). Therefore, *C. adherens* is excluded from the following discussion.

The older literature suggests that species of *Campyloderes* are distinguished from each other by minute details such as different body lengths, spinose versus blunt tip of midterminal spine, rounded versus pointed terminal end of segment 11, proximal cuticle of the lateral terminal spine with two thin areas versus evenly thick cuticle (Higgins, 1967; Johnston, 1938; Moore, 1973; Zelinka, 1913, 1928). This study reveals that body length varies widely between specimens even from the same location (Table 2). In addition, considerable subjective judgement is involved in identifying the tip of the midterminal spine as spinose or blunt; only recently moulted adult specimens possess a midterminal spine with an undoubtedly spinose tip. Also, the authors of this paper do not notice much difference between the terminal end of segment 11 in the 101 adult specimens investigated by light microscopy; some very minor differences result from manipulating and mounting specimens on the slides in different positions. Similar differences in specimens from the North Sea are also mentioned and illustrated by Moore (1973, Figs. 2 and 4A, B). Neuhaus (2004) already demonstrates that *C. vanhoeffeni* does possess two thin areas in the proximal cuticle of the lateral terminal accessory spine (comp. Zelinka, 1913, Tafel XXXIX, Fig. 4, 1928, Fig. 54 in the text) as does *C. macquariae* (see Johnston, 1938; Higgins, 1967; Moore, 1973). He concludes that "this character can no longer be used to identify different species of *Campyloderes*" and that "this situation leads to an almost indistinguishable species complex of *Campyloderes vanhoeffeni–C. vanhoeffeni* var. *kerguelensis–C. macquariae*" (Neuhaus, 2004, pp. 13, 17). In this study, we confirm that all specimens investigated reveal the thin areas in the lateral terminal accessory spines making this character entirely obsolete for a comparison within the taxon *Campyloderes*.

In 2004, Neuhaus (2004) suggests that the morphology of the primary scalids may represent one of the more promising characters to discriminate species of *Campyloderes* from each other. This study does not corroborate this expectation, because the number of septa in the scalids varies widely among the specimens studied and shows a tendency towards being correlated with body size and other characters (see above; Table 2).

Morphological measurements of many characters, detailed description and photographic documentation of cuticular surface structure, arrangement of sensory spots, and scalid morphology are missing widely for the described species (Zelinka, 1913, 1928; Johnston, 1938; Higgins, 1967; Moore, 1973). With this situation, overlapping character patterns of the specimens investigated here, and no type material at hand, the specimens of this study cannot be assigned clearly to any of the known species of *Campyloderes* with good argumentation. Therefore, the specimens described in this paper are tentatively assigned to *Campyloderes* cf. *vanhoeffeni*, the first species of *Campyloderes* described.

It is not very likely that one and the same species occupies an almost worldwide distribution from Atlantic Antarctica to the North and West Atlantic Ocean, from the Indian Ocean to the Central American East Pacific Ocean and to the North Pacific Ocean with a depth range from intertidal to more than 5100 m. Specimens may very well represent different species and possibly even new species. We also conclude that the observed morphological variation results from ongoing species formation processes.

4.5. Ground pattern of Campyloderes

Comparison within *Campyloderes*. The ground pattern of *Campyloderes* is established here mainly on the basis of the specimens available for this paper because of insufficient data about the described species (see before). Table 4 summarizes characters occurring in given reference positions in <u>all</u> specimens studied here (=characters not in brackets). For the reasons given in the introductory remarks of the Results section, positions in Table 4 should be regarded as an approximation of reality.

Comparison within Kinorhyncha. In the following, several characters will be discussed which offer the potential to belong to the ground pattern of *Campyloderes* and to represent even autapomorphies of this taxon. Most Kinorhyncha possess three rings of inner oral styles (5 + 5 + 10 individual styles) and one ring with 9 individual outer oral styles (Higgins, 1983, 1990; Brown, 1989; Nebelsick, 1993; Neuhaus, 1995; Bauer-Nebelsick, 1995, 1996; Sørensen, 2007; Sørensen et al., 2007, 2009; Sørensen and Rho, 2009; Sørensen and Thormar, 2010; Herranz et al., in press). A single ring of inner oral styles and poorly developed, partly fused outer oral styles have been reported for *Condyloderes poseidon* (see Sørensen et al., 2010a). Specimens of *Campyloderes* cf. *vanhoeffeni* do exhibit at least one ring of inner oral styles. Separated outer oral styles are not recognizable. However, a comparison of longitudinal optical sections through the mouth cone of *Campyloderes* (Fig. 2E), *Echinoderes capitatus* (Zelinka, 1928) (see Nebelsick, 1993, Fig. 1), and *Zelinkaderes floridensis* (see Neuhaus, 1994, Fig. 2) reveals that in *Campyloderes* the 9–10 main lamellae or ribs (Fig. 2F, labelled as oos) are located in the very same position as outer oral styles in *E. capitatus* and *Z. floridensis*. Therefore, the plicated tube with the 9–10 main lamellae or ribs is interpreted as modified outer oral styles fused laterally over their entire length. The finding of outer oral styles partly fused laterally in *Condyloderes poseidon* (see Sørensen et al., 2010a, Fig. 4A) supports this hypothesis, which may be confirmed or rejected by ontogenetic studies of *Campyloderes*. We evaluate separated outer oral styles as plesiomorphic character within Kinorhyncha. The partly fused outer oral styles of *C. poseidon* may represent a step in the transformation towards complete loss of separated outer oral styles, which could indicate a closer phylogenetic relationship of species of *Condyloderes* and *Campyloderes*. Consequently, the proposed complete fusion of outer oral styles has to be regarded as an autapomorphic character of *Campyloderes*.

Primary scalids with internal septa are not known for any kinorhynch except specimens of *Campyloderes* (Higgins, 1969, 1983, 1990; Brown, 1989; Neuhaus, 1993, 1995, 2004; Bauer-Nebelsick, 1995, 1996; Adrianov and Malakhov, 1999; Sørensen,

2007; Sørensen et al., 2007, 2009, 2010a; Sørensen and Rho, 2009; this paper). The chambering of scalids is regarded as an autapomorphy of species of *Campyloderes*.

Short and acicular ring 02 scalids have not been reported for any kinorhynch species except species of *Campyloderes* (see Zelinka, 1913, 1928; Johnston, 1938; Higgins, 1969, 1983, 1990; Moore, 1973; Brown, 1989; Neuhaus, 1993, 1995, 2004; Bauer-Nebelsick, 1995, 1996; Adrianov and Malakhov, 1999; Song and Chang, 2001; Sørensen, 2007; Sørensen et al., 2007, 2009, 2010a; Sørensen and Rho, 2009, this paper) and is therefore suggested to represent an autapomorphy of *Campyloderes*.

A midventral placid being wider than the remaining placids is common in *Centroderes spinosus*, *Tubulideres seminoli* Sørensen et al., 2007, species of *Echinoderes*, and is found also in specimens of *Campyloderes* (see Zelinka, 1913, 1928; Johnston, 1938; Moore, 1973; Higgins, 1983; Neuhaus, 2004; Sørensen et al., 2007). However, specimens of *Campyloderes* reveal a special arrangement, namely a considerably broad midventral placid neighbored by a small, triangular placid alternating a with broader, rounded placid (Fig. 2H); this contrasts the situation in *Tubulideres seminoli* and species of *Echinoderes* which possess equally wide placids, and the situation in *Centroderes spinosus* which shows two small placids neighboring the midventral placid and then alternating a broader and a smaller placid (comp. discussion in Zelinka, 1928; Higgins, 1983; Neuhaus, 2004). The condition in specimens of *Campyloderes* is part of the ground pattern of this taxon but not evaluated here, because a phylogenetic analysis of Kinorhyncha is still impossible due to insufficient information.

A significantly elongated acicular spine in segment 1 is known for *Centroderes spinosus*, *Campyloderes vanhoeffeni* and *Campyloderes macquarie* (see Zelinka, 1913, 1928; Johnston, 1938; this paper). However, these spines are in a lateroventral position in *Campyloderes* and in a ventromedial position in *Centroderes* (Pardos, Sørensen, Neuhaus, and Higgins, unpubl. obs.). Therefore, an elongated lateroventral spine in segment 1 is considered as an autapomorphic character of *Campyloderes*.

Among the cyclorhagid species possessing a lateral spine in a lateroventral to laterodorsal position in segment 10, this spine has also been reported for both sexes of *Antygomonas incomitata*, *A. paulae* Sørensen, 2007, *Condyloderes multispinosus* (McIntyre, 1962), *C. paradoxus* Higgins, 1969, *Sphenoderes poseidon* Sørensen et al., 2010, *Triodontoderes anulap* Sørensen and Rho, 2009, *Tubulideres seminoli*, *Zelinkaderes floridensis*, *Z. klepali* Bauer-Nebelsick, 1995, *Z. submersus* (Gerlach, 1969), *Wollunquaderes majkenae* Sørensen and Thormar, 2010, and probably *Sphenoderes indicus* Higgins, 1969 (see Zelinka, 1928; Nyholm, 1947; Higgins, 1969, 1990; Bauer-Nebelsick, 1995; Sørensen, 2007; Sørensen et al., 2007, 2009, 2010b; Sørensen and Rho, 2009; Sørensen and Thormar, 2010). Male specimens of *Campyloderes* and *Centroderes* reveal a sublateral spine in segment 10 whereas females do not except in some specimens of *Centroderes* (comp. chapter Sexual dimorphism above; Pardos, Sørensen, Neuhaus and Higgins, unpublished results). We assume that the lack of a lateral spine on the tergal plate of segment 10 of females may indicate a closer relationship of species of *Centroderes* and *Campyloderes*.

Thin areas in the basal cuticle of the midterminal (one spot) and of the lateral terminal accessory (two spots) spine are not known for any kinorhynch (Higgins, 1969, 1983; Nebelsick, 1990; Neuhaus, 1993, 1995; Bauer-Nebelsick, 1996; Adrianov and Malakhov, 1999; Lemburg, 2002; Sørensen et al., 2007, 2009, 2010a,b; Sørensen and Rho, 2009) except specimens of *Campyloderes*, so we suggest this characters as autapomorphies of *Campyloderes*.

Paradorsal sensory spots occur at least in segments 1–9 in the cyclorhagids *Antygomonas incomitata*, *A. oreas*, *A. paulae*, *Semnoderes armiger*, *Sphenoderes poseidon*, *Triodontoderes anulap*, and *Tubulideres seminoli*, in the homalorhagid *Paracentrophyes*

praedictus, and in most segments of segments 1–9 in the cyclorhagid *Wollunquaderes majkenae* and in the homalorhagids *Pycnophyes australensis* Lemburg, 2002, *P. dentatus*, and *P. kielensis* (see Higgins, 1983; Nebelsick, 1990; Neuhaus, 1993, 1995; Bauer-Nebelsick, 1996; Lemburg, 2002; Sørensen, 2007; Sørensen et al., 2007, 2009, 2010a; Sørensen and Rho, 2009; Sørensen and Thormar, 2010). Furthermore, the perispinal subdorsal sensory spots in segments 3–8 in species of *Dracoderes* are believed to be laterally displaced paradorsal sensory spots (Sørensen et al., in press). We therefore conclude that paradorsal sensory spots in segments 1–9 belong to the ground pattern of *Campyloderes*, and that specimens showing this character possess the plesiomorphic condition for *Campyloderes*.

A papilla on each of the sternal plates occurs in all females of *Campyloderes* cf. *vanhöffeni* (ventromedially in segment 6 and 7; South Korean specimens: also ventromedially in segment 5; Faroese specimens: also ventrolaterally in segment 5), *Semnoderes armiger* and *Wollunquaderes majkenae* (ventrolaterally in segment 8, ventromedially in segment 9), *Triodontoderes anulap* (ventrolaterally in segments 7 and 8, ventromedially in segment 9), *Condyloderes megastigma* (ventromedially in segments 7 and 8), *C. multispinosus* (McIntyre, 1962) (ventromedially in segments 6–8), two undescribed species of *Condyloderes* (ventromedially in segments 7 and 8) and probably in *Sphenoderes indicus* (lateroventrally in segment 8, ventromedially in segment 9) (Higgins, 1969; Sørensen and Rho, 2009; Sørensen et al., 2009, 2010a; Sørensen and Thormar, 2010; unpubl. obs. B. Neuhaus & R. P. Higgins; this study). These papillae show a tendency from being located in a more ventrolateral position in anterior segments to having a more paraventral position towards posterior segments. Such papillae on sternal plates are not known for other Kinorhyncha and may indicate a closer relationship of the above mentioned species. The answer to this question must remain open until a more detailed phylogenetic analysis will have been done.

In the following, a list of characters that are not mentioned in Table 4 is given for the ground pattern of *Campyloderes*. Based on the discussion above, these characters are postulated as **autapomorphic characters** of a taxon *Campyloderes*:

- outer oral styles fused over entire length,
- primary scalids (=ring 01) of adult stage with at least 8 internal septa,
- ring 02 scalids short and acicular,
- considerably broad midventral placid neighbored by a small, triangular placid alternating with a broader, rounded placid,
- lateroventral acicular spine in segment 1 significantly elongated,
- midterminal spine with thick proximal cuticle around central cellular cavity and one dorsal thin area in the cuticle,
- lateral terminal accessory spine with thick proximal cuticle around central cellular cavity and two dorsal thin areas in the cuticle.

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