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Aspects of the Postembryonic Development of *Campyloderes* cf. *vanhoeffeni* and *Ryuguderes casarrubiosi* (Kinorhyncha, Campyloderidae)

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Seven late juvenile stages or young males, two late juvenile stages or males fixed in the process of moulting, three stage-1 and seven stage-2 females, and 17 juvenile specimens of *Campyloderes* cf. *vanhoeffeni* Zelinka, 1913 from various locations as well as a late juvenile or male and a juvenile specimen of *Ryuguderes casarrubiosi* Cepeda et al., 2022 were studied by light microscopy. The investigation yielded important insights into the life history of mainly the former species, viz, (1) establishment of clear distinctive characters between late juvenile and female as well as more maturated male life history stages, (2) the principal developmental series of juvenile stages, (3) development of spines via anlagen and modified spines, and (4) dissolution of septa in the primary spinoscalids of the head during moulting.

Keywords: Meiofauna, Kinorhyncha, Postembryonic development, Deep sea

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BACKGROUND

Kinorhyncha comprise some 353 species based on the description of adult life history stages and 9 species based on the description of juvenile stages (Neuhaus 2025). These species are mainly identified by the presence and arrangement of placids, spines, setae, sensory spots, and gland cell outlets. However, more recent publications described variation of such characters partly challenging previous species delimitations (Neuhaus and Sørensen 2013; Neuhaus et al. 2013 2014 2019; Yamasaki and Dal Zotto 2019; Sørensen and Herranz 2022; Sørensen et al. 2025). The situation is further complicated by reports of adults moulting to another adult life history stage, often with a slightly differing morphology (Higgins 1990; Bauer-Nebelsick 1996; Neuhaus and Sørensen 2013; Neuhaus and Kegel 2015; Neuhaus 2017; Sørensen et al. 2019; Sørensen and Herranz 2022). These results prompted a re-investigation of several life history stages of *Tubulideres seminoli* Sørensen et al., 2007 and of *Wollunquaderes majkenae* Sørensen and Thormar, 2010 in order to clarify the morphological distinction between early juvenile stages, late juvenile stages, and potential stage-1 and stage-2 adults (Neuhaus 2017).

Among the species with probably at least two adult life history stages, two female stages morphologically differing in few characters were reported for *Campyloderes* cf. *vanhoeffeni* Zelinka, 1913, one with a middorsal spine each on segments 10 and 11and the other without these spines (Neuhaus and Sørensen 2013). No moulting adult specimens were available at that time. The species showed also intraspecific variation among adult specimens regarding the presence and absence of spines, sensory spots, papillae, and gland cell outlets. Two additional species of *Campyloderes* were described, viz, *C. vanhoeffeni* var. *kerguelensis* Zelinka, 1928 and *C. macquariae* Johnston, 1938 (see Zelinka 1928; Johnston 1938), but Neuhaus (2004) suggested that these three species formed an "almost indistinguishable species complex of *Campyloderes vanhoeffeni*–*C. vanhoeffeni* var. *kerguelensis*–*C. macquariae*". However, it cannot be ruled out that the complex harbours cryptic species (Neuhaus and Sørensen 2013).

One of the most obvious recognisable characters to distinguish any specimen of the two genera of Campyloderidae, viz, *Campyloderes* and *Ryuguderes*, from a specimen of any other genus were the presence of primary spinoscalids with internal septa, which could be usually observed, even if the head was withdrawn into the trunk. Species of *Campyloderes* and *Ryuguderes* also possessed a midterminal spine considerably shorter in length than the lateral terminal accessory spines but longer than the lateral terminal spines (Zelinka 1913; Johnston 1938; Moore 1973; Neuhaus 2004; Neuhaus and Sørensen 2013; Cepeda et al. 2022).

In recently studied samples from the Clarion Clipperton Fracture Zone in the Pacific Ocean deep sea, we found one late juvenile or male specimen resembling *Campyloderes* cf. *vanhoeffeni* but lacking internal septa in the spinoscalids and possessing a midterminal spine slightly exceeding the lateral terminal accessory spines in length. In addition, the pattern of sensory spots and gland cell outlets differed to some degree from that of previously reported specimens (Neuhaus and Sørensen 2013). This was a very tempting combination of characters possibly indicating a new species of Campyloderidae. However, a more detailed investigation of the specimen revealed that it was moulting from a late juvenile stage or from a young male to another life history stage, a situation not directly observed before for this species. Therefore, we also re-studied the juvenile and adult specimens of *Campyloderes* cf. *vanhoeffeni* peviously investigated by Neuhaus and Sørensen (2013). This comparison revealed that several adult specimens identified as juvenile might represent either late juvenile stages or young males, one late juvenile stage or young male was moulting, and different life history stages showed different length ratios of the midterminal spine to the lateral terminal accessory spine. At the same time, the re-examination allowed to provide some general conclusions about the postembryonic development of *Campyloderes* cf. *vanhoeffeni*. In addition, a specimen of the recently described species *Ryuguderes casarrubiosi* Cepeda et al., 2022 from the same family Campyloderidae caught our attention, because it was labelled as a “pre-adult male” (Cepeda et al. 2022), which might actually represent a late juvenile or male specimen.

The aim of the present contribution is (1) to describe two late juvenile stages or young males of *Campyloderes* cf. *vanhoeffeni*, both specimens fixed in the process of moulting, and (2) to compare characters of juvenile and adult ontogenetic stages of *Campyloderes* cf. *vanhoeffeni* in order to broaden the knowledge about the postembryonic development of this species and of Kinorhyncha in general and to document distinctive characters of different life history stages of the species. We included a late juvenile or male and the only known juvenile specimen of *Ryuguderes casarrubiosi* in order to possibly widen the perspective.

MATERIALS AND METHODS

Meiofauna samples were collected by several deep-sea expeditions with R/V Sonne and R/V Polarstern in the Atlantic and Pacific Ocean (Table 1). Alltogether, 26 specimens of *Campyloderes* cf. *vanhoeffeni* were investigated, viz, seven males, two males moulting to another male, 16 juveniles, and one juvenile exuvia. In addition, a male and a juvenile specimen of *Ryuguderes casarrubiosi* were received on loan from the Natural History Museum of Denmark, Copenhagen, and re-investigated (Tables 1, 3). New specimens of this study were deposited at the Museum für Naturkunde Berlin in the collection “Vermes” and catalogued in the Generalkatalog Free-living Worms (ZMB numbers, see Table 1).

Table 1. Location data of *Campyloderes* cf. *vanhoeffeni* and *Ryuguderes casarrubiosi*

Species: station data (location, georeferences, field station #, depth)	Collection date; gear	Collectors; ship	Specimens; remarks	Reference
C. cf. *vanhoeffeni*: North East Atlantic Ocean, southeast of Canary Islands, cruise PS 40 (ANT XIII-5), station 122, 23°10.9’N, 024°26.2’W, 5,102 m	11.06.1996; MIC	N. J. Debenham, T. J. Ferrero, P. Martínez Arbizu, G. Silveira Moura; R/V Polarstern	ZMB 5986a–c: 1 late juvenile stage or young male, 2 juveniles; Hoyer’s Mounting Medium	Neuhaus and Sørensen 2013
C. cf. *vanhoeffeni*: North East Atlantic Ocean, southeast of Canary Islands, cruise PS 40 (ANT XIII-5), station 122, 23°10.9’N, 024°26.3’W, 5,055 m	12.06.1996; MUC	N. J. Debenham, T. J. Ferrero, P. Martínez Arbizu, G. Silveira Moura; R/V Polarstern	ZMB 5966: 1 stage-1 female; Hoyer’s Mounting Medium	Neuhaus and Sørensen 2013
C. cf. *vanhoeffeni*: South West Atlantic Ocean, Antarctica, King George Island, cruise PS 48 (ANT XV-3)**,** station 306, 62°21.9’S, 058°43.0’W, 801 m	15.03.1998; MUC	H. J. Lee, J. Van de Velde; R/V Polarstern	ZMB 5967b–d, f: 3 stage-2 females, 1 late juvenile stage or young adult; glycerol-paraffin mount	Neuhaus and Sørensen 2013
C. cf. *vanhoeffeni*: South West Atlantic Ocean, Antarctica, east of South Shetland Islands, cruise PS 61 (ANT XIX-3–4), station 46-1, 60°38.12’S, 053°57.67’W, 2,893 m	30.01.2002; MUC	P. Martínez Arbizu; R/V Polarstern	ZMB 5981: 1 juvenile; Fluoromount G™, re-mounted as glycerol-paraffin slide	Neuhaus and Sørensen 2013
C. cf. *vanhoeffeni*: equatorial East Pacific Ocean, Carnegie Ridge, cruise SO 144-3, station 14, from 01°10.92’S, 082°15’W to 01°10.46’S, 082°15’W, 1,408–1,333 m	15.11.1999; gDR	B. Neuhaus, P. Götz; R/V Sonne	ZMB 5985: 1 juvenile; mounted in Euparal green	this paper
C. cf. *vanhoeffeni*: equatorial East Pacific Ocean, Cocos Ridge, cruise SO 144-3, station 49b, 07°00.29’N, 083°54.17’W, 1,048 m	29.11.1999; TVG	B. Neuhaus, P. Götz; R/V Sonne	ZMB 5969c: 1 juvenile; mounted in Euparal green	Neuhaus and Sørensen 2013
C. cf. *vanhoeffeni*: equatorial East Pacific Ocean, transform fault of Galápagos spreading centre, cruise SO 158, station 67b, from 00°51.80’N, 0910°8.70’W to 00°51.80’N, 091°08.56’W, 2,121–2,119 m	10.8.2001; MDR	B. Neuhaus, P. Götz; R/V Sonne	ZMB 11174e–l: 3 late juvenile stages or young males, 4 juveniles, 1 juvenile exuvia; glycerol-paraffin mount	Neuhaus and Sørensen 2013
C. cf. *vanhoeffeni*: equatorial East Pacific Ocean, near Galápagos spreading centre, cruise SO 208, station 19, 08°43.31’N, 090°44.14’W, 2,426 m	21.07.2010; MUC	B. Neuhaus, C. Lüter; R/V Sonne	ZMB 5983a–e: 1 late juvenile stage or male moulting, 2 late juvenile stages or males, 2 juveniles; glycerol-paraffin mounts	Neuhaus and Sørensen 2013
C. cf. *vanhoeffeni*: equatorial East Pacific Ocean, near Galápagos spreading centre, cruise SO 208, station 26, from 10°41.12’N, 87°45.52’W to 10°40.91’N, 87°45.28’W; 2,995–2,680 m	21.07.2010; gDR	B. Neuhaus, C. Lüter; R/V Sonne	ZMB 5984a, b: 2 stage-1 females; glycerol-paraffin mounts	Neuhaus and Sørensen 2013
C. cf. *vanhoeffeni*: equatorial East Pacific Ocean, near Galápagos spreading centre, cruise SO 208, station 26, from 10°41.12’N, 87°45.52’W to 10°40.91’N, 87°45.28’W, 2995–2680 m	23.07.2010; gDR	B. Neuhaus, C. Lüter; R/V Sonne	ZMB 5984a, b: 2 stage-2 females; glycerol-paraffin mounts	Neuhaus and Sørensen 2013
C. cf. *vanhoeffeni*: South West Pacific Ocean, Hikurangi Plateau, cruise SO 168, station 11, from 41º7.03’S, 179º45.25’W to 41º7.10’S, 179º45.55’W; 1,940–1,817 m	18.12.2002; gDR	B. Neuhaus, C. Lüter; R/V Sonne	ZMB 5971: 1 stage-2 female; glycerol-paraffin mount	Neuhaus and Sørensen 2013

C. cf. *vanhoeffeni*: South West Pacific Ocean, Hikurangi Plateau, cruise SO 168, station 13, from 40º25.202'S, 179º26.816'W to 40º 25.425'S, 179º27.216'W; 1,865–1,605 m	18.12.2002; gDR	B. Neuhaus, C. Lüter; R/V Sonne	ZMB 5972: 1 stage-2 female; glycerol-paraffin mount	Neuhaus and Sørensen 2013
C. cf. *vanhoeffeni*: South West Pacific Ocean, Hikurangi Plateau, cruise SO 168, station 28, from 39°02.08'S, 177°15.881'W to 39°02.18'S, 177°16.354'W, 3,102–2.922 m	23.12.2002; gDR	B. Neuhaus, C. Lüter; R/V Sonne	ZMB 5987: 1 juvenile; glycerol-paraffin mount	Neuhaus and Sørensen 2013
C. cf. *vanhoeffeni*: South West Pacific Ocean, Chatham Rise, cruise SO 168, station 98, from 44º24.135'S, 175°55.220'E to 44°24.18'S, 175°55.10'E, 490-420 m	13.01.2003; gDR	B. Neuhaus, C. Lüter; R/V Sonne	ZMB 5874b: 1 juvenile; glycerol-paraffin mount	Neuhaus and Sørensen 2013
C. cf. *vanhoeffeni*: central Pacific Ocean, Manihiki Plateau, Danger Islands Troughs, cruise SO 193, station 30, 08°39.19'S, 164°19.99'W, 4,925 m	06.06.2007; MUC	B. Neuhaus, C. Lüter; R/V Sonne	ZMB 5977b: 1 early juvenile; glycerol-paraffin mount	Neuhaus and Sørensen 2013
C. cf. *vanhoeffeni*: equatorial Pacific Ocean, Clarion-Clipperton Fracture Zone, BGR contract area, cruise SO 240, station 70, 12°39.857'N, 119°13.385'W, 4,270 m	27.05.2015; MUC	A. Janssen, K. Uhlenkott; R/V Sonne	ZMB 13068: 1 late juvenile stage or male moulting; mounted in DMHF	Kuhn 2015; this paper
C. cf. *vanhoeffeni*: equatorial Central Pacific Ocean, Clarion-Clipperton Fracture Zone, BGR contract area, cruise SO 240, station 116, 13°11.098'N, 118°06.003'W, 4,270 m	10.06.2015; MUC	A. Janssen, K. Uhlenkott; R/V Sonne	ZMB 13069: 1 juvenile; mounted in DMHF	Kuhn 2015; this paper
C. cf. *vanhoeffeni*: equatorial Central Pacific Ocean, DISCOL area, reference area west, cruise SO 242-1, station 91/ MUC 24, 07°04.583'S, 088°31.558'W, 4,127 m	15.08.2015; MUC	R.l Singh, G. Egho, T.Y. Patel, G. De Smet, P. Martínez Arbizu; R/V Sonne	ZMB 13104: 1 juvenile; glycerol-paraffin mount	Greinert 2015; this paper
R. casarrubiosi: South West Indian Ocean, Mozambique Channel, Betsiboka slope, station 01MTB03, 15°23.23'S, 45°59., 528 m (data from label; data in publication erroneous)	7.10.2014; MUC	K. Olu; R/V L'Atalante	NHMD 672703, NHMD 672704: 1 juvenile, 1 late juvenile or young male; mounted in Fluoromount G™	Cepeda et al. 2022

Abbreviations: DMHF, dimethyl hydantoin formaldehyde resin; gDR, geological dredge; L'Atalante, cruise of R/V L'Atalante; MDR, meifauna dredge; MIC, minicorer; MUC, multicorer; NHMD, The Natural History Museum of Denmark; PS, cruise of R/V Polarstern; R/V, Research Vessel; SO, cruise of R/V Sonne; ZMB, collection "Vermes" of Museum für Naturkunde Berlin (previously Zoological Museum Berlin).

Specimens were mounted either in dimethyl hydantoin formaldehyde resin (DMHF), Euparal green, Hoyer’s Mounting Medium, Fluoromount G™, or as glycerol-paraffin slides on Cobb aluminum frames or on glass slides (Table 1). It turned out that DMHF deteriorated quickly and formed smaller and very large crystals of irregular shape and larger spheroid bodies. It also emerged that the refractive index of this mounting medium masked fine details and, therefore, cannot be favoured for meiofauna studies. Hoyer’s Mounting Medium had dissolved all inner organs of the specimens, and only the cuticle remained. A slide of *Campyloderes* cf. *vanhoeffeni* mounted in Fluoromount™ G showed large cavities at the specimen impacting light microscopical investigation, so the specimen was re-mounted as glycerol-paraffin slide. The slides of *Ryuguderes casarrubiosi* mounted in Fluoromount™ G exhibited large rainbow-coloured cavities, different complex crystal patterns, small bright spherical precipitations, and light-refracting bodies making the detection of sensory spots and gland cell outlets extremely difficult in the thin cuticle of the specimens. Furthermore, both specimens of *Campyloderes* cf. *vanhoeffeni* in DMHF and *R. casarrubiosi* in Fluoromount™ G were mounted on glass slides, so the side of the specimen further away from the coverslip was considerably more difficult to observe. One specimen mounted in glycerol was partly contaminated with paraffin crystals.

Kinorhynch specimens were identified to species level using light microscopes equipped with differential interference contrast optics, inter alia with the help of an Olympus BX51 microscope. In addition, a microscope Zeiss Axioplan 2 mot. with objectives Plan-Apochromat 10x/0.32, 20x/0.60, 63x/1.40 Oil DIC, 100x/1.40 Oil DIC, and a Plan-Neofluar 40x/1.30 Oil DIC, and a camera Zeiss AxioCam MRc5 were used for photography. Images were improved and photographic plates mounted with the help of CorelDraw® Graphics Suite 2019 V 21.3.0.755.

RESULTS

Late juvenile stages or males of *Campyloderes* cf. *vanhoeffeni* with 11 segments separated and pectinate fringes

Two late juvenile stages or males, specimen ZMB 5983a with a trunk length of 373 µm (Fig. 1L) and specimen ZMB 13068 (Fig. 1A) with a trunk length of 675 µm (for measurements of this largest specimen known for *Campyloderes* cf. *vanhoeffeni* see Table 2), were fixed in the process of moulting. In both specimens, the head was withdrawn and no septa were found in the primary spinoscalids, although such septa are usually traceable in adult and juvenile specimens either by the chambers in the scalids or by the cuticular thickenings, where the septa meet the cuticle of the scalids. Specimen ZMB 13068 revealed only 13 trichoscalids instead of the usual 14, each associated with one of the 14 placids except for the middorsal placid. The neck region consisted of a broad midventral placid neighboured by 13 alternating narrower and broader placids and a narrow middorsal placid (Fig. 1B, C).

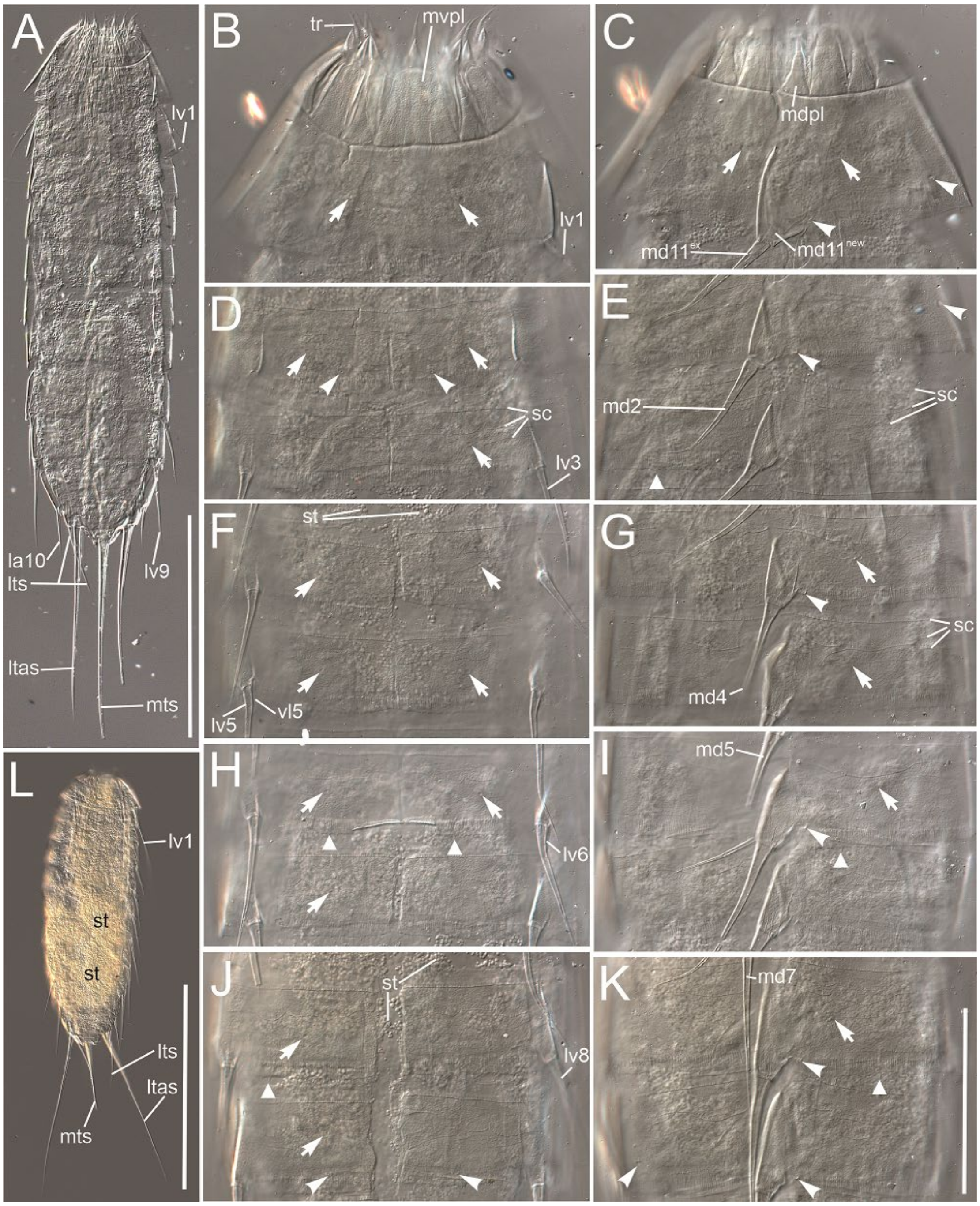

Fig. 1. *Campyloderes* cf. *vanhoeffeni*, late juvenile stage (potential juvenile stage group H) or male moulting(A–L), ZMB 13068 (A–K) and ZMB 5983a (L), ventral (A, B, D, F, H, J, L) and dorsal view (C, E, G, I, K). A, overview. B, C. Segment 1. D, E. Segments 2–3. F, G. Segments 4–5. H, I. Segments 6–7. J, K. Segments 8–9. L. overview, specimen filled with storage vesicles. Scale bar in A and L 300 µm, in K 200 µm, valid for B–K. Abbreviations: ex, refers to structure of exuvial cuticle in moulting specimen; la, lateral accessory spine; ltas, lateral terminal accessory spine; lts,

lateral terminal spine; lv, lateroventral spine; md, middorsal spine or placid; mts, midterminal spine; mv, midventral; new, refers to structure of newly formed cuticle in moulting specimen; pl, placid; sc, secondary fringe; st, storage vesicles; tr, trichoscalid; vl, ventrolateral tube. Number after abbreviation refers to segment. Sensory spots marked by arrowheads, gland cell outlets by arrows, and short spinose processes of free flap with triangles.

Table 2. Measurements and proportions of a late juvenile stage or a male moulting of *Campyloderes* cf. *vanhoeffeni*, specimen ZMB 13068. The numbers following the abbreviations indicate the corresponding segment

Specimen	ZMB 13068, late juvenile stage or ♂ moulting
Character	
tl	675 µm
cl	671 µm
cl/tl	99%
sw10	136 µm
s1	79 µm
s2	70 µm
s3	47 µm
s4	46 µm
s5	50 µm
s6	54 µm
s7	67 µm
s8	69 µm
s9	59 µm
s10	62 µm
s11	68 µm
md1 (ac)	63 µm
md2 (ac)	60 µm
md3 (ac)	66 µm
md4 (ac)	80 µm
md5 (ac)	84 µm
md6 (ac)	93 µm
md7 (ac)	96 µm
md8 (ac)	113 µm
md9 (ac)	139 µm
md10 (ac)	86 µm
md11 (ac)	92 µm
mts (ac)	broken, > 271 µm
lv1 (ac)	113 µm
lv2 (tu)	16 µm
lv3 (ac)	54 µm
lv4 (ac)	65 µm
lv5 (ac)	66 µm
vl5 (tu)	17 µm
lv6 (ac)	78 µm
lv7 (ac)	81 µm
lv8 (ac)	98 µm
lv9 (ac)	108 µm
la10 (ac)	58 µm
lts (ac)	107 µm
ltas (ac)	261 µm
mts/tl	> 40%
lts/tl	16%
ltas/tl	39%
mts/ltas	> 104%
mts/lts	> 253%
ltas/lts	41%

Abbreviations: ac, acicular; cl, cumulative length of lengths of segments 1–11; la, lateral accessory spine; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lv, lateroventral spine; md, middorsal spine; mts, midterminal spine; s, segment length; sw, standard width, measured on segment 10; tl, total trunk length; tu, tube; vl, ventrolateral spine.

Specimens ZMB 5967f, 5983a–c, 5986a, 11174e–g, and 13068 showed a thin, non-sclerotised trunk cuticle without recognisable pachycycli, which are interior cuticular thickenings at the anterior margin of a segment (Figs. 1A–K, 2A–D). The cuticle surface revealed scales and secondary pectinate fringes (Figs. 1B–K, 2A–C, F–I, 3A–D; Table 3). Postmarginal spicula at the posterior margin of a segment were absent; a free flap was present instead (Figs. 1B–K, 2A–I, 3A–D; Table 3). The flap was reinforced internally by regularly arranged longitudinal cuticular bars, which appeared in light microscopy as a regular striation pattern. Some variation in the expression of the free flap was observed concerning the width of the striation, the extension of the striation pattern limited to the anterior part of the flap or over its entire length, and the posteriormost ending of the free flap appearing more or less smoothly or with shorter or slightly longer, irregularly distributed spinose processes (Figs. 1B–K, 2A–C, F–I, 3A–D). Several specimens showed only a weak internal striation pattern (Fig. 2H). The free flap of each segment terminated in the primary pectinate fringe consisting of either few individual spinose processes (ZMB 5967f: Fig. 3A, 11174f, 11174g), a higher amount of very short spinose processes (ZMB 5983b: Fig 3B), or short spinose processes (ZMB 5983a, c, 5986a, 11174e, 13068; Figs. 1E, H–K, 2A–C, 3C, D).

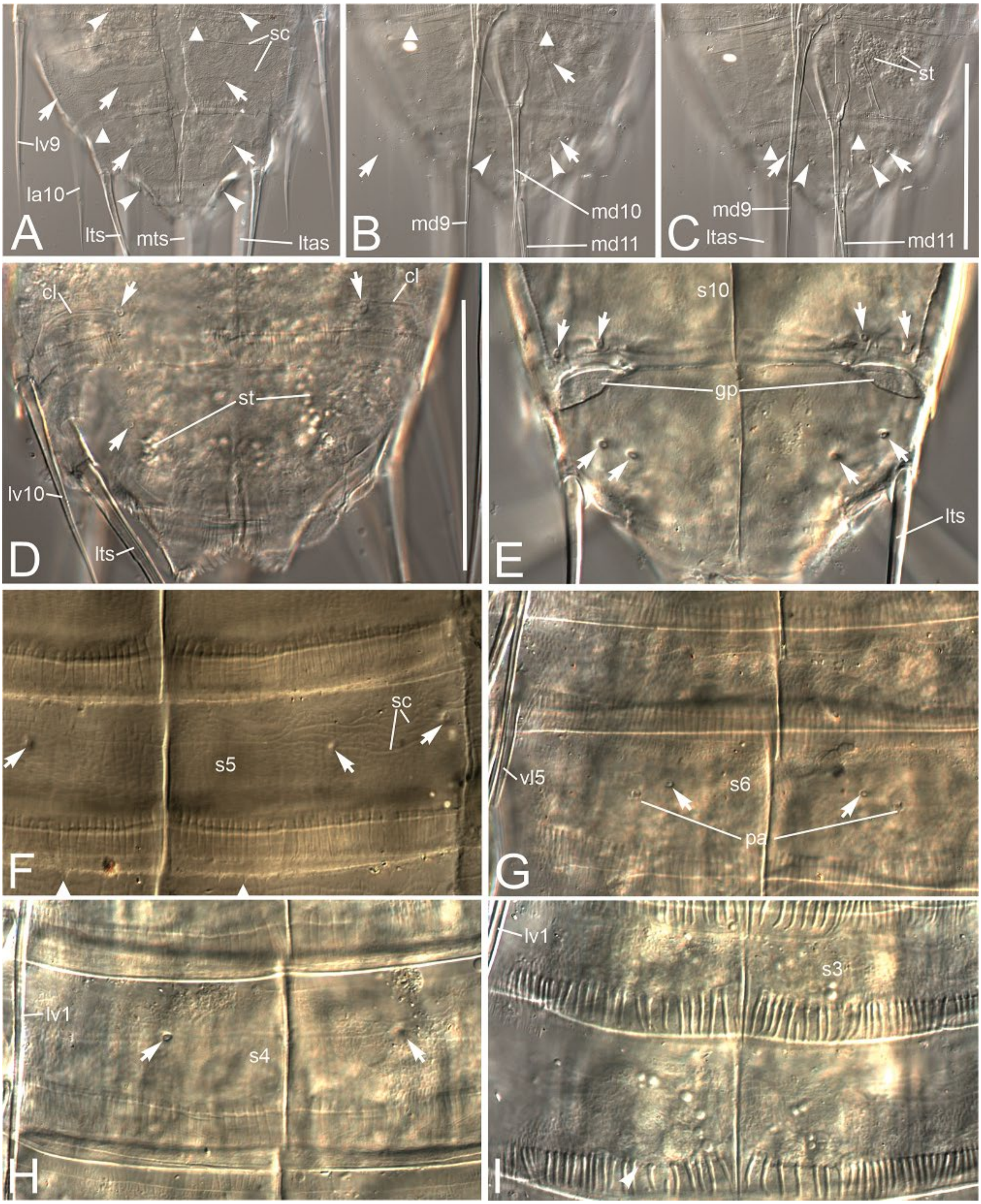

Fig. 2. *Campyloderes* cf. *vanhoeffeni*, late juvenile stage (potential juvenile stage group H) or male moulting (A–D) and female (E–I), ventral (A, D–I) and dorsal view (B, C). A–C, ZMB 13068, segments 10–11. D, ZMB 5983a. E, ZMB 5984a, segments 10–11. F–I, internal striation pattern of free flap. F, ZMB 5966, segment 5. G, ZMB 5967c, segments 5–6. H, ZMB 5984a, segment 4. I, ZMB 5984b, segments 3–4. Scale bar in C 200 µm, valid for A–C, in D 50 µm, valid for D–I. Abbreviations: cl, clasp; gp, gonopore; la, lateral accessory spine; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lv, lateroventral spine; md, middorsal spine; mts, midterminal spine; pa, papilla; s, segment; sc, secondary fringe; st, storage vesicles; vl, ventrolateral tube. Number after

abbreviation refers to segment. Sensory spots marked by arrowheads, gland cell outlets by arrows, and short spinose processes of free flap with triangles.

In both specimens ZMB 5983a and ZMB 13068, an acicular spine occurred lateroventrally on segments 1 (elongate spine), 3–9 and as lateral terminal spine on segment 11, in a lateral accessory position on segment 10 (only on left side of specimen ZMB 5983a, lateroventrally on right side) and as lateral terminal accessory spine on segment 11, middorsally on segments 1–11, and as midterminal spine on segment 11 (Figs. 1A–L, 2A–D). A short tube was found lateroventrally on segment 2 and ventrolaterally on segment 5 in both specimens (Fig. 1F) as well as ventrolaterally on segment 1 only in specimen ZMB 5983a. Whereas the proportion of the length of the midterminal spine to the lateral terminal accessory spine was 41% in the old cuticle of specimen ZMB 5983a, this relation was >103% in specimen ZMB 13068 (Table 3). All spines and tubes of the moulting specimens were expressed both in the old and new cuticle.

Table 3. Characters of different life history stages of *Campyloderes* cf. *vanhoeffeni* and *Ryuguderes casarrubiosi*. Horizontal lines grouping specimens of assumed same life history stages A–G and possibly H

Group	Specimen, status	Middorsal spines on segments[1]; notes	Lateral appendages on segments[1, 2]; notes	Relative length of md11 and/ or mts to ltas	% of length of md11 and/ or mts to ltas
	Campyloderes cf. *vanhoeffeni*				
Specimen with segments 1–8 separated and 9+10+11 still fused; postmarginal spicula in continuous row dorsally (ventrally n. a.)					
A	ZMB 5977b, early juvenile	md4, md6, md 8, very long md11	lv8, spinose anlagen of lts and ltas, vl5	md11 >>>> anlage ltas	2,169%
Specimens with segments 1–9 separated and 10+11 still fused and with weak border; postmarginal spicula in continuous row dorsally					
B	ZMB 13104, early juvenile	md1–10, very long md11	lv1–10, short basally bulbous lts, vl5	md11 >>> lts	1,025%
C	ZMB 11174i, juvenile, advanced stage of moulting	md1–10, very long md11, spinose anlage of mts; md11 & anlage of mts with common base	lv1–9, la10, short basally bulbous lts, ltas, vl1, vl5	md11 >> ltas; mts < ltas	222%; 40%
	ZMB 11174l, juvenile exuvia	md1–10, very long md11, spinose anlage of mts; md11 & anlage of mts with common base	lv1–9, la10, short basally bulbous lts, ltas, vl1, vl5	md11 >> ltas; mts < ltas	223%; 45%
D	ZMB 5969c, juvenile, recently moulted	md1–10, very long md11, anlage of mts elongated; md11 & anlage of mts with common base	lv1–9, la10, short thickened lts, ltas, vl5	md11 > ltas; mts ≈ ltas	119%; 103%
E	ZMB 11174j, juvenile, very early stage of moulting	md1–11, mts; md11 & mts separated	lv1–9, la10, lts, ltas, vl1, vl5	mts ≈ ltas	101%
	ZMB 5974b, juvenile, moulting	md1–11, mts; md11 & mts separated	lv1–9, la10, lts, ltas, vl1, vl5	mts ≈ ltas	92%
F	ZMB 5986b, juvenile	md1–11, mts	lv1–9, la10, lts, ltas, vl1 n. a., vl5	mts >> ltas	175%
	ZMB 5986c, juvenile	md1–11, mts	lv1–9, la10, lts, ltas, vl1, vl5	mts >> ltas	157%
G	ZMB 5981, juvenile	md1–11, mts	lv1–9, la10, lts, ltas, vl1, vl5	mts < ltas	78%
	ZMB 5983d, juvenile, early stage of moulting	md1–11, mts	lv1–9, lv10 (ri), la10 (le), lts, ltas, vl1, vl5	mts < ltas	61%
	ZMB 5983e, juvenile	md1–11, mts	lv1–9, la10, lts, ltas, vl1, vl5	mts < ltas	66%
	ZMB 5985, juvenile	md1–11, mts	lv1–9, lv10 (ri), la10 (le), lts, ltas, vl1, vl5	mts < ltas	61%
	ZMB 5987, juvenile	md1–11, mts	lv1–9, la10, lts, ltas, vl5	mts < ltas	60%
	ZMB 11174h, juvenile	md1–11, mts	lv1–9, la10, lts, ltas, vl1, vl5	mts < ltas	53%
	ZMB 11174k, juvenile	md1–11, mts	lv1–9, la10, lts, ltas, vl1, vl5	mts < ltas	63%
	ZMB 13069, juvenile	md1–8, md9–11 and mts lost	lv1–9, la10, lts, ltas, vl5	n. a.	n. a.
Specimens with segments 1–11 separated; free-flap with internal striation					
(H)	ZMB 5967f, late juvenile or young ♂	md1–11, mts	lv1–9, sl10, lts, ltas, vl1, vl5	mts < ltas	41%
	ZMB 5983b, late juvenile or young ♂	md1–11, mts	lv1–9, la10, lts, ltas, vl1, vl5	mts < ltas	49%

	ZMB 5983c, late juvenile or young ♂	md1–11, mts	lv1–9, la10, lts, ltas, vl1, vl5	mts < ltas	38%
	ZMB 5986a, late juvenile or young ♂	md1–11, mts	lv1–9, la10, lts, ltas, vl spines n. a.	mts < ltas	68%
	ZMB 11174e, late juvenile young or ♂	md1–11, mts	lv1–9, la10, lts, ltas, vl1, vl5	mts < ltas	47%
	ZMB 11174f, late juvenile or young ♂	md1–11, mts	lv1–9, la10, lts, ltas, vl1, vl5	mts < ltas	32%
	ZMB 11174g, late juvenile or young ♂	md1–11, mts	lv1–9, la10, lts, ltas, vl1, vl5	mts < ltas	42%
	ZMB 5983a, late juvenile or young ♂, moulting	md1–11, mts; old and new cuticle	lv1–9, la10, lts, ltas, vl1, vl5; old and new cuticle	mts < ltas	41%
	ZMB 13068, late juvenile or young ♂, moulting	md1–11, mts (broken); old and new cuticle	lv1–9, la10, lts, ltas, vl5	mts > ltas	>103%
Ryuguderes casarrubiosi					
Specimen with segments 1–8 separated and 9+10+11 still fused; postmarginal spicula in continuous row dorsally					
	NHMD 672703: juvenile	md2–4, 6, very short 7 (triangular), 8, 9, 11, spinose anlage of mts; md11 & anlage of mts with common base	lv 2, 4, 6, 8, 10, lts & ltas as very short spinose anlagen, vl5	md11 >>>> anlage ltas; mts >> anlage ltas	2,525%; 550%
Specimen with segments 1–11 separated; free-flap with internal striation					
	NHMD 672704, late juvenile or young ♂	md1–11, mts	lv3–9, sl10, lts, ltas, vl5	mts < ltas	53%

Abbreviations: [1], all appendages acicular spines except lateroventral tube of segment 2 in *Campyloderes* and ventrolateral tube of segments 1 and 5 of both species; [2], lateroventral spine of segment 1 elongate in *Campyloderes*; +, character present; –, character not present; <, spine shorter; >, spine longer; ≈, spines of about equal length; la, lateral accessory spine; ld, laterodorsal spine; le, left side; ltas, lateral terminal accessory spine; lts, lateral terminal spine; md, middorsal spine; mts, midterminal spine; n. a., not available; ri, right side; vl, ventrolateral spine. Number after abbreviation refers to segment.

All specimens ZMB 5967f, 5983a–c, 5986a, 11174e–g, and 13068 exhibited numerous light-refracting storage vesicles (Fig. 1A–L, 2A–D) thus impeding observation of sensory spots, gland cell outlets, and papillae. In specimens ZMB 5983a and 13068, sensory spots were found ventromedially on segments 2 and 9, ventrolaterally on segment 11 (ZMB 13068 only), midlaterally on segments 1, 2 (ZMB 13068 only), 5 (ZMB 13068 only), 7 (ZMB 13068 only), 9 (ZMB 13068 only), and 10 (ZMB 13068 only), subdorsally on segment 11, paradorsally on segments 1, 2, 4, and 6 in specimen ZMB 5983a and on segments 1–9 in specimen ZMB 13068 (Fig. 1A–L, 2A–D). Gland cell outlets appeared ventromedially on segments 1 (ZMB 13068 only), 2–10, and 11 (ZMB 13068 only), ventrolaterally on segment 10 (ZMB 13068 only), and subdorsally on segments 1–11 (Fig. 1A–L, 2A–D). Papillae were observed lateroventrally on segments 2–10 of specimen ZMB 5983a only. Light-refracting storage vesicles were also observed in other adult specimens.

None of specimens ZMB 5983a–c, 5986a, 11174e–g, and 13068 revealed any developing or mature gonad, whereas specimen ZMB 5967f possessed a developing gonad on the right side. It could not be decided, whether this gonad would result in the production of eggs or sperm. Specimen ZMB 5983a revealed below the old cuticle surface on each side of segment 10 a posterior lateral cuticular clasp (?) curving to the ventromedial gland cell outlet (Fig. 2D). This structure was not regarded as a gonopore, because the latter appeared in more mature females with gonads as a more or less triangular area of thinner cuticle with rounded edges located anteriorly on segment 11 (Fig. 2E).

Females of *Campyloderes* cf. *vanhoeffeni* with 11 segments separated and pectinate fringes

Ten specimens were undoubtedly identified as females based on the existence of papillae on segments 6 and 7 and of gonopores at the anterior margin of segment 11 (Fig. 2E). Three of these specimens were stage-1 females (ZMB 5966, 5984a, b), because they possessed a middorsal spine both on segments 10 and 11 but missed lateral spines on segment 10. The remaining females were assigned to stage-2 females, because they lacked spines on segment 10 and a middorsal spine on segment 11 (comp. Neuhaus & Sørensen 2013). Four specimens showed developing gonads or eggs (ZMB 5967b, 5971, 5984a, b). Whereas nine females possessed a sclerotised cuticle with well developed pachycycli, only specimen ZMB 5984b had a thin cuticle. Three females without gonads and one female with eggs (ZMB 5984a) exhibited storage vesicles.

Juvenile specimens of *Campyloderes* cf. *vanhoeffeni* with up to 9 segments separated and postmarginal spicula

In this paper, 17 obviously recognisable juvenile specimens of *Campyloderes* cf. *vanhoeffeni* from 11 stations were studied, including four specimens in the process of moulting (ZMB 5974b, 5983d, 11174i, 11174j), one recently moulted specimen (ZMB 5969c), and one exuvia (ZMB 11174l) (Figs 3E–H, 4A–I, 5A–G; Tables 1, 3). In two specimens, the ventral side was not fully available for study, because they were mounted in a lateral position (ZMB 5977b: Fig. 3E, F; ZMB 13104: Fig. 3G, H). Although specimen ZMB 5977b missed the characteristic elongate lateroventral spine on segment 1, it was assigned to *Campyloderes* cf. *vanhoeffeni* based on its arrangement of tubes and spines, its very large midventral placid, and its cuticular scales. The lack of an incomplete series of middorsal spines in juvenile stages contrasting a middorsal spine on all segments in adults was reported for juveniles of other cyclorhagid species before and probably represented an ontogenetic pattern for at least some species (Sørensen et al. 2010; Neuhaus 2017; this paper; comp. Discussion, chapter Aspects of postembryonic development of *Campyloderes* cf. *vanhoeffeni* (4)). All remaining specimens did show the spines characteristic of the species. It cannot be totally excluded that specimen ZMB 5977b represented a juvenile stage of an unknown cyclorhagid species of Kinorhyncha because of its short instead of long lateroventral spines on segment 1. However, three males were previously reported to possess exactly such a short spine in this position (Neuhaus and Sørensen 2013, p. 71). Therefore, we assigned specimen ZMB 5977b to a juvenile stage of *Campyloderes* cf. *vanhoeffeni* (see also chapter Aspects of postembryonic development of *Campyloderes* cf. *vanhoeffeni*).

Segments 1–8 or 1–9 appeared clearly separated in all juvenile specimens (Figs. 3E–H, 4A, C, H, I, 5A–C, E–G). The border between the prospective segments 10+11 and between the prospective segments 9+10+11, respectively, were indicated by an incomplete row of postmarginal spicula much shorter in length and more indistinct than between the borders of more anterior segments (Figs 3H inset, 5G; Table 3).

All juvenile specimens possessed a ring-like cuticle without recognisable cuticular plates in each segment (Figs 4A, C, H, I, 5A–C, F, G), but this character was undeterminable for the laterally mounted specimens ZMB 5977b and ZMB 13104. All specimens lacked a cuticular interior thickening of the trunk cuticle (= pachycyclus) at the anterior margin of a segment. The cuticle showed scales and secondary pectinate fringes on the surface from the second group of juveniles on (Figs. 3G, 4A, C, H, I, 5A–C, E–G; Table 3).

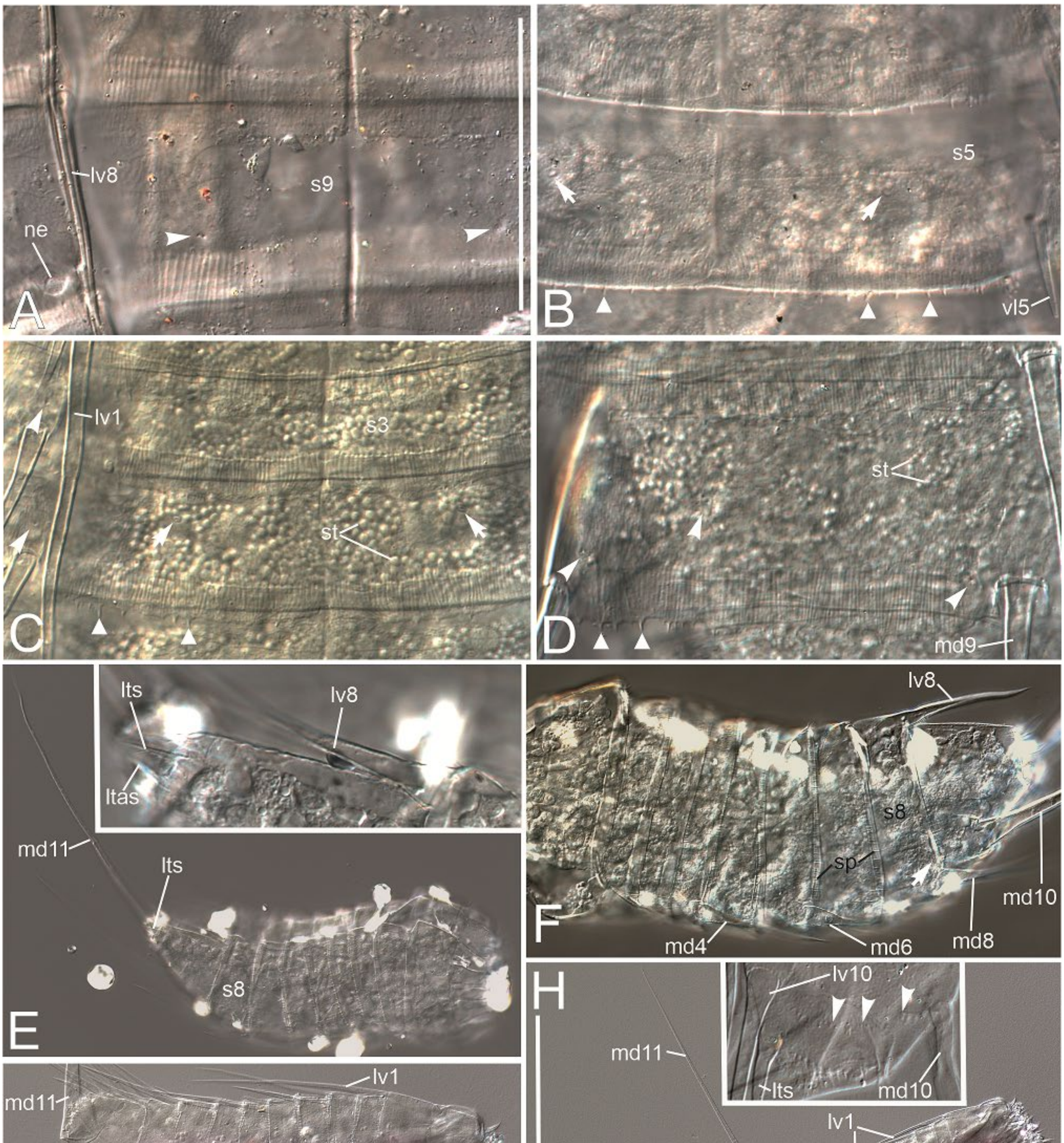

Fig. 3. *Campyloderes* cf. *vanhoeffeni*, late juvenile stage (potential juvenile stage group H) or male (A–D) and juvenile stages (E–H), ventral (A–C), dorsal (D), and lateral view (E–H). A–D, internal striation pattern of free flap. A, ZMB 5967f, segment 9. B, ZMB 5983b, segment 5. C, ZMB 5983c, segments 3–4. D, ZMB 11174e, segment 9. E–F, ZMB 5977b (juvenile stage group A), segments 1–8 and prospective segments 9+10+11; partly contaminated with paraffin. G–H, ZMB 13104 (juvenile stage group B), segments 1–9 and prospective segments 10+11. Insets in E and H: posterior end of specimens with spinose anlagen of terminal spines (E) and bulbous lateral terminal spine (H). Scale bar in A 50 µm, valid for A–D and insets in E and H, in H 100 µm, valid for E–H. Abbreviations: ltas, lateral terminal accessory spine; lts, lateral terminal spine; lv, lateroventral

spine; md, middorsal spine; ne, nephropore; s, segment; sp, spicula; st, storage vesicles; vl, ventrolateral tube. Number after abbreviation refers to segment. Sensory spots marked by arrowheads in A, C and D, gland cell outlets by arrows in B and C, short spinose processes of free flap with triangles in B–D, and spicula at weak border between segments 10 and 11 by arrowheads in H inset.

All juvenile specimens were characterised by postmarginal spicula at the posterior end of segments 1–9 or 1–10. Each spiculum showed a very small basal spherical cuticular thickening and extended as a short spine-like process from the cuticle. The spicula varied slightly in length and were distributed in a more or less continuous row both ventrally and dorsally (Fig. 5B, C, E–G) except in specimens ZMB 5969c, 11174i, 11174j, and 11174l (Figs. 4C, H, 5A), where the ventral spicula appeared discontinually in a lateral and a paraventral to midventral cluster (Table 3). Paraventral to midventral spicula were often slightly thicker than the remaining spicula (Figs. 4C, 5A). The paraventral to midventral cuticular area also yielded a slightly more prominent patch of scales.

In the following, specimens will be described in more detail on the basis of shared group characters. This does not mean that each group of specimens separated by horizontal lines in Table 3 will necessarily represent a well-defined juvenile stage from which the next stage will moult, because some inconsistencies were noticed. Generally, only differences in comparison with the presumed earlier stage are described.

Juvenile stage group A. Specimen ZMB 5977b represented a very early juvenile stage with segments 1–8 separated and the prospective segments 9+10+11 still fused. It revealed a set of middorsal spines on segments 4, 6, 8, and the prospective segment 11 and a short ventrolateral tube on segment 5, a lateroventral spine on segment 8, as well as the short spinose anlagen of the lateral terminal and the lateral terminal accessory spine; these anlagen did not show any articulation (Fig. 3E, E inset). The middorsal spine of the prospective segment 11 was considerably longer than the anlagen of the lateral terminal and lateral terminal accessory spine (Fig. 3E, F; Table 3). The surface of the cuticle showed short triangular scales.

Juvenile stage group B. Specimen ZMB 13104 was regarded as an early juvenile stage revealing segments 1–9 clearly separated and the prospective segments 10+11 still more or less fused. A middorsal and a lateroventral spine on segments 1–9 and the prospective segment 10, a very long middorsal spine on the prospective segment 11, a short ventrolateral tube on segment 5, and a short, basally bulbous lateral terminal spine were traced (Fig. 3G, H, H inset; Table 3). The primary spinoscalids possessed septa. The postmarginal spicula were arranged in a continuous row dorsally.

Juvenile stage group C. Deviating from the situation described just before, specimens ZMB 11174i and ZMB 11174l had developed a lateral terminal accessory spine and a very long middorsal on the prospective segment 11 with a large base, from which the spinose anlage of the midterminal spine extended ventrally; the anlage did not show any articulation (Fig. 4F; Table 3). A basally bulbous lateral terminal spine still occurred (Fig. 4E). On segment 10, a spine appeared in these and in all remaining specimens in a lateral accessory instead of a lateroventral position (Fig. 4A, C). The ventral cuticle showed postmarginal spicula grouped in a lateral and a paraventral to midventral area (Fig. 4A, C, E, F; Table 3). The middorsal spine emerging from the prospective segment 11 was about double as long as the lateral terminal accessory spine, whereas the midterminal spine was less than half as long as the lateral terminal accessory spine (Fig. 4A; Table 3). Specimen ZMB 11174i in the process of moulting exhibited partly incomplete septa in the primary spinoscalids of the old head cuticle (Fig. 4B) and complete septa in the newly formed cuticle (Fig. 4 D). The surface of the cuticle revealed from this stage on weak secondary fringes. The ventral postmarginal spicula appeared as an interrupted row in three areas. The outer oral styles appeared fused.

Juvenile stage group D. Specimen ZMB 5969c still exhibited a common base of the middorsal spine and the midterminal spine of the prospective segment 11, but the length ratios of these spines to the lateral terminal accessory spine changed to ratios of 119% and 103%, respectively (Fig. 4G–I; Table 3). The lateral terminal spine lost its bulbous base, elongated, but appeared still thickened (Fig. 4H). From this stage on, primary spinoscalids with septa could be traced in almost all specimens.

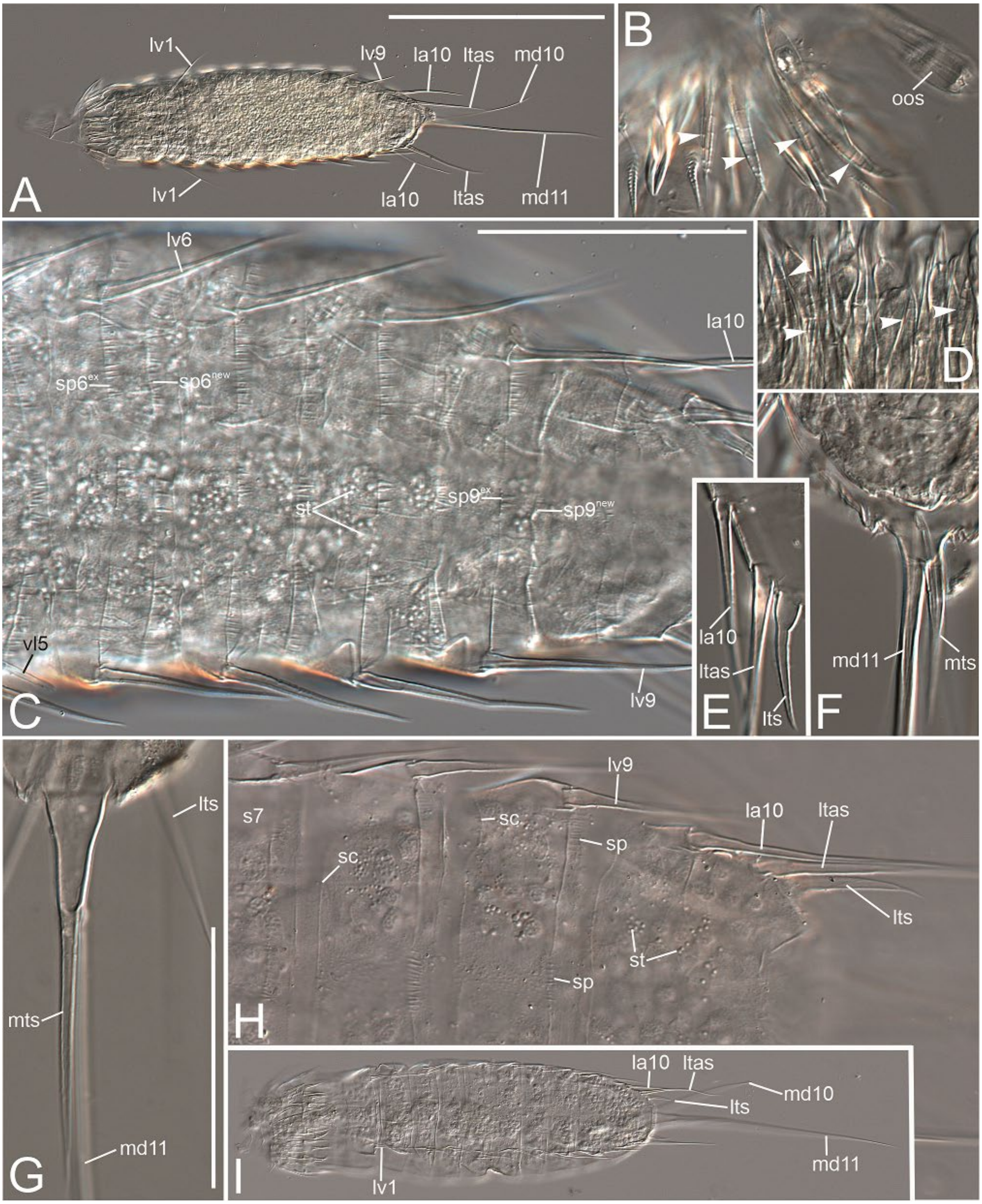

Fig. 4. *Campyloderes* cf. *vanhoeffeni*, juvenile stages, ventral view (A, B, C, G–I) and optical section (D–F). A, C, D, F, ZMB 11174i (juvenile stage group C), moulting; overview (A), segments 6–11 (C), scalids with septa (arroweads) in new cuticle (D), spinose anlage of midterminal spine (F). B, E, ZMB 11174l (juvenile stage group C), exuvia, scalids with septa (arroweads) and fused outer oral styles (B) and terminal spines (E). G–I, ZMB 5969c (juvenile stage group D), prospective segment 11 with shared base of spinose anlage of midterminal and middorsal spine of segment 11 (G), segments 8–9 and prospective segments 10+11 (H), and entire specimen (I). Scale bar in A 200 µm, valid for A and I, in C 50 µm, valid for B–F and H, in G 50 µm. Abbreviations: ex, refers to structure of exuvial cuticle in moulting specimen; la, lateral accessory spine; ltas, lateral terminal

accessory spine; lts, lateral terminal spine; lv, lateroventral spine; md, middorsal spine; new, refers to structure of newly formed cuticle in moulting specimen; oos, outer oral styles; sc, secondary fringe; sp, spicula; st, storage vesicles; vl, ventrolateral tube. Number after abbreviation refers to segment.

Juvenile stage group E. Specimen ZMB 5974b and ZMB 11174j showed clearly separated origins of the middorsal spine and the midterminal spine on the prospective segment 11. Whereas the former became much shorter, the latter reached about the length of the lateral terminal accessory spine (Fig. 5B; Table 3). Postmarginal spicula were arranged in three ventral areas in specimen ZMB 11174j (Fig. 5A) but not in specimen ZMB 5974b, which showed a continuous row of spicula (Fig. 5C).

Juvenile stage group F. Specimens ZMB 5986b and ZMB 5986c differed from the remaining juvenile specimens in a much longer midterminal spine than the lateral terminal accessory spine with ratios of 157–175% versus ratios of 53–78% (Fig. 5E; Table 3). From this stage on, postmarginal spicula appeared as a continuous row both dorsally and ventrally.

Juvenile stage group G. The latest available juvenile stage in the series of stages with postmarginal spicula showed still fused segments 10+11 with a more distinct border between these segments (Fig. 5G). The lateral terminal spine had elongated further to a regular acicular spine (Fig. 5F). The midterminal spine was considerably shorter than the lateral terminal accessory spine (Fig. 5F; Table 3).

Potential juvenile stage potential group H. It could not be decided whether specimens with segments 1–11 separated and primary pectinate fringes represented late juvenile stages or young males with still not expressed gonads. These specimens were labelled as potential group H in the series of the assumed developmental stages (Table 3; see chapter Late juvenile stages or males of *Campyloderes* cf. *vanhoeffeni* with 11 segments separated and pectinate fringes).

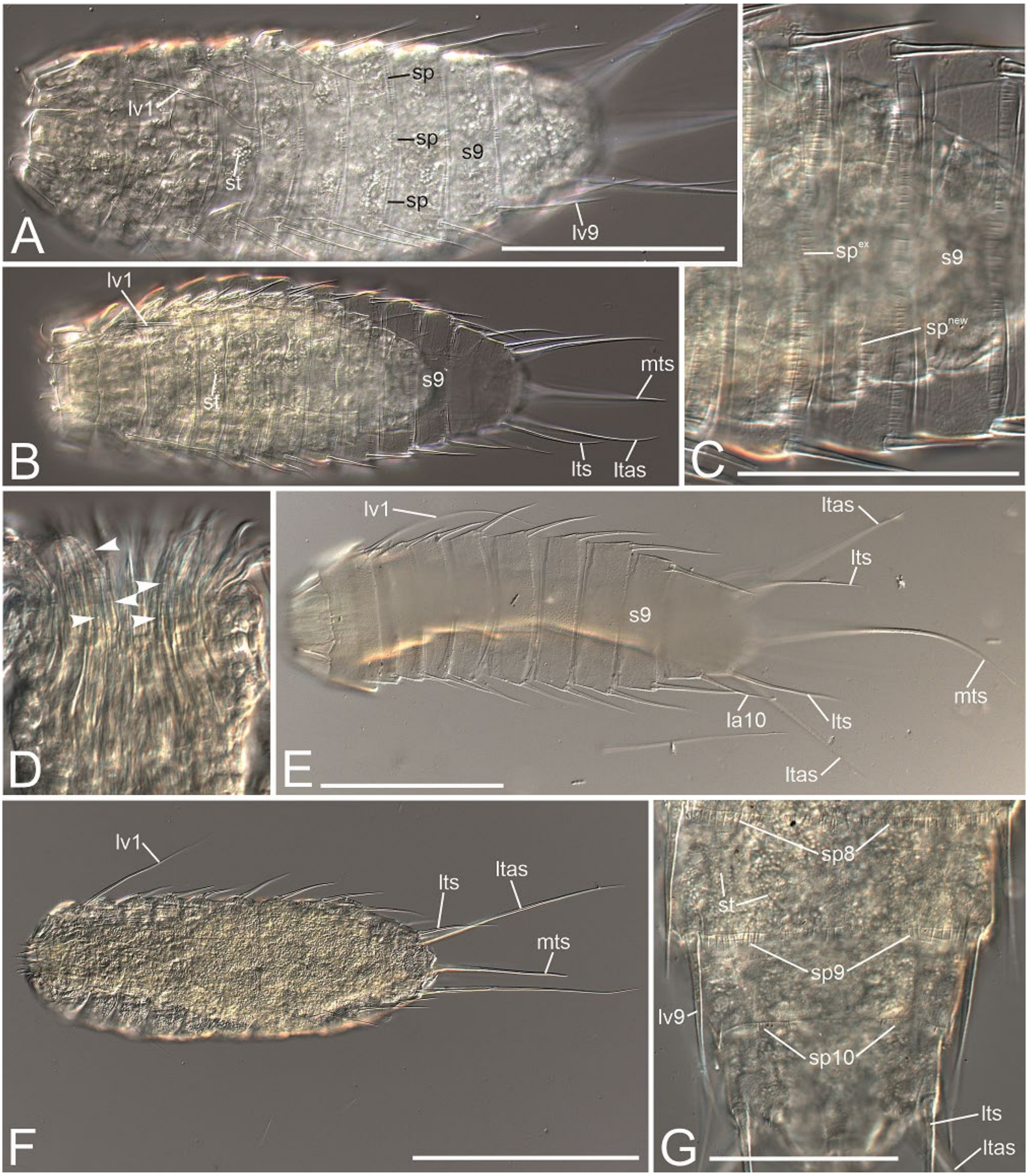

Fig. 5. *Campyloderes* cf. *vanhoeffeni*, juvenile stages, ventral view (A–C, E–G) and optical section (D). A, ZMB 11174j (juvenile stage group E), segments 1–9 and prospective segments 10+11 with discontinuous row of spicula. B–D, ZMB 5974b, (juvenile stage group E) moulting, segments 1–9 and prospective segments 10+11 (B), segments 7–9 with continuous row of spicula (C), and segment 1 with septa (arrowheads) in scalids (D). E, ZMB 5986c (juvenile stage group F), segments 1–11. F, ZMB 5983d (juvenile stage group G), segments 1–9 and prospective segments 10+11. G, ZMB 5987 (juvenile stage group G), segments 9 and prospective segments 10+11 with weak border of segment 10. Scale bar in A 100 µm, valid for A and B, in C 50 µm, valid for C and D, in E 100 µm, in F 200 µm, and in G 50 µm. Abbreviations: ex, refers to structure of exuvial cuticle in moulting specimen; la, lateral accessory spine; ltas, lateral terminal accessory spine; lts, lateral terminal spine; lv, lateroventral spine; new, refers to structure of newly formed cuticle in moulting specimen; sp, spicula; st, storage vesicles. Number after abbreviation refers to segment.

Late juvenile or male of *Ryuguderes casarrubiosi*

Specimen NHMB 672704 with a trunk length of 377 µm represented probably a late juvenile stage or, less probably, a recently moulted male, because it showed a thin cuticle and no pachycyli. The head was withdrawn and septa were found in the primary spinoscalids. The neck region consisted of a broad midventral placid neighboured by 13 alternating narrower and broader placids, each associated with one of the 14 trichoscalids.

The cuticle of segment 1 was ring-like, whereas the cuticle of segments 2–11 appeared ring-like but with a midventral fissure where both ends met; lateroventral junctions or separated sternal cuticular plates could not be detected (Fig. 6A, B). The cuticle revealed scales and secondary pectinate fringes on the surface (Fig. 6A–D; Table 3). Postmarginal spicula at the posterior margin of a segment did not occur but a free flap with a pectinated fringe instead with short spinose processes (Fig. 6A–D). The flap was reinforced internally by regularly arranged longitudinal cuticular bars, which appeared in light microscopy as a regular striation pattern (Fig. 6A–D).

An acicular spine occurred lateroventrally on segments 3–9 and as lateral terminal spine, as lateral terminal accessory spine on segment 11 (Fig. 6A, B), sublaterally on segment 10, middorsally on segments 1–11 and as midterminal spine (Fig. 6C, D). A short tube was found ventrolaterally on segment 5 (Fig. 6A).

The specimen exhibited light-refracting storage vesicles (Fig. 6A–D). Type-1 sensory spots were found ventromedially on segments 4, 6–9 and possibly on segment 11, sublaterally on segment 8, midlaterally on segments 1–4, 6, 9 and 10, and paradorsally on segments 2, 4, 6, 8, 9, 11 and possibly on segment 7 (Fig. 6A–D). Type-1 gland cell outlets appeared ventromedially on segments 6, ventrolaterally on segments 1 and 9, and lateroventrally on segment 10, in lateral accessory position on segments 7 and 8, and subdorsally on segment 11 (Fig. 6A–D). Papillae were not observed on segments 6–8.

Gonads were not developed, yet.

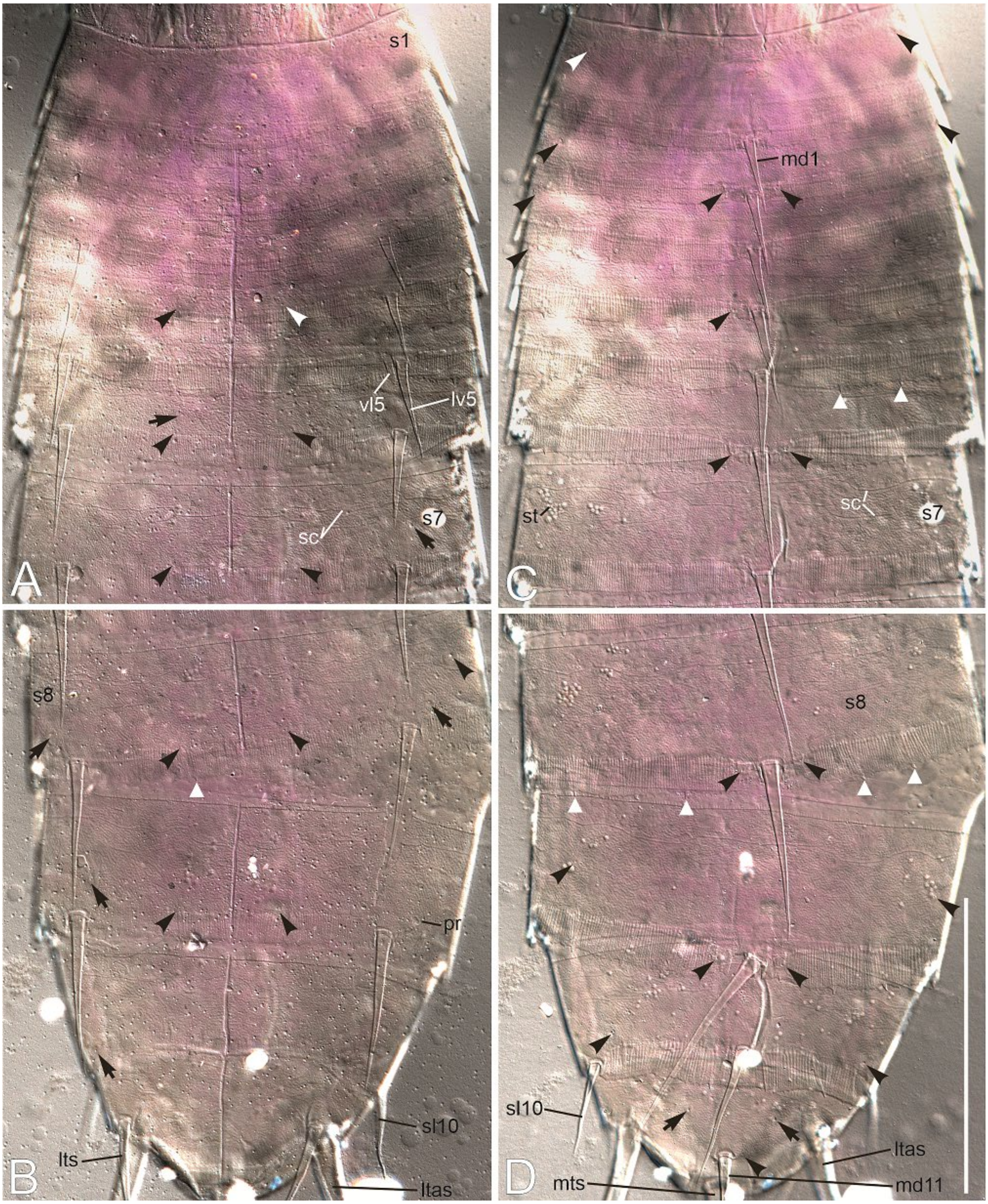

Fig. 6. *Ryuguderes casarrubiosi*, late juvenile or young male NHMD 672704, ventral (A, B) and dorsal view (C, D). A, C, segments 1–7. B, D, segments 8–11. Scale bar in D 100 µm, valid for A–D. Abbreviations: ltas, lateral terminal accessory spine; lts, lateral terminal spine; lv, lateroventral spine; md, middorsal spine; pr, protonephridial outlet; s, segment; sc, secondary fringe; st, storage vesicles; vl, ventrolateral tube. Sensory spots marked by arrowheads, gland cell outlets by arrows, and short spinose processes of free flap with triangles. Number after abbreviation refers to segment.

Juvenile of *Ryuguderes casarrubiosi* with 8 segments separated and postmarginal spicula

A single juvenile specimen of *Ryuguderes casarrubiosi* with a trunk length of 192 µm was available for study, viz, specimen NHMD 672703. The primary spinoscalids of the head possessed septa. Segments 1–8 appeared clearly separated from a still fused posterior trunk part consisting of segments 9+10+11 (Fig. 7A, B, D, E; Table 3). The weak borders between segments 9+10+11 were indicated dorsally by incomplete lines of very short postmarginal spicula (Fig. 7E). The juvenile specimen possessed a ring-like cuticle without recognisable cuticular plates in each segment. The midventral to paraventral area appeared a bit separated from the remaining ventral cuticle on segments 2–8 (Fig. 7A, B). At the anterior margin of a segment, the specimen lacked a cuticular interior thickening of the trunk cuticle (= pachycyclus). The surface cuticle showed short scales and one secondary pectinate fringe on each segment. At the posterior margin of segments 1–8, postmarginal spicula occurred (Fig. 7A, D; Table 3). The spicula varied slightly in length and were distributed in a more or less continuous row dorsally but an interrupted row ventrally (Fig. 7A, B, D, E; Table 3). The 4–5 paraventral to midventral spicula of segments 2–8 were much thicker than the remaining spicula (Fig. 7A, B; Table 3). Each spiculum showed basally a very small spherical cuticular thickening and extended as a short spine-like process from the cuticle.

An acicular spine occurred lateroventrally on segments 2, 4, 6, 8, and in the region which will develeop into segment 10 (Fig. 7A–C), as very short spinose anlagen of a lateral terminal spine and a lateral terminal accessory spine on segment 11 (Fig. 7C), middorsally on segments 2–4, 6, 8, 9, 11 and as spinose anlage of the midterminal spine (Fig. 7 B, C). The latter and the middorsal spine of segment 11 shared a common base. Spinose anlagen of spines did not reveal an articulation site. A short tube was found ventrolaterally on segment 5 (Fig. 7A; Table 3). Sensory spots occurred subdorsally (left side) and laterodorsally (right side) on the prospective segment 10, respectively, as well as paradorsally on the prospective segment 11 (Fig. 7D).

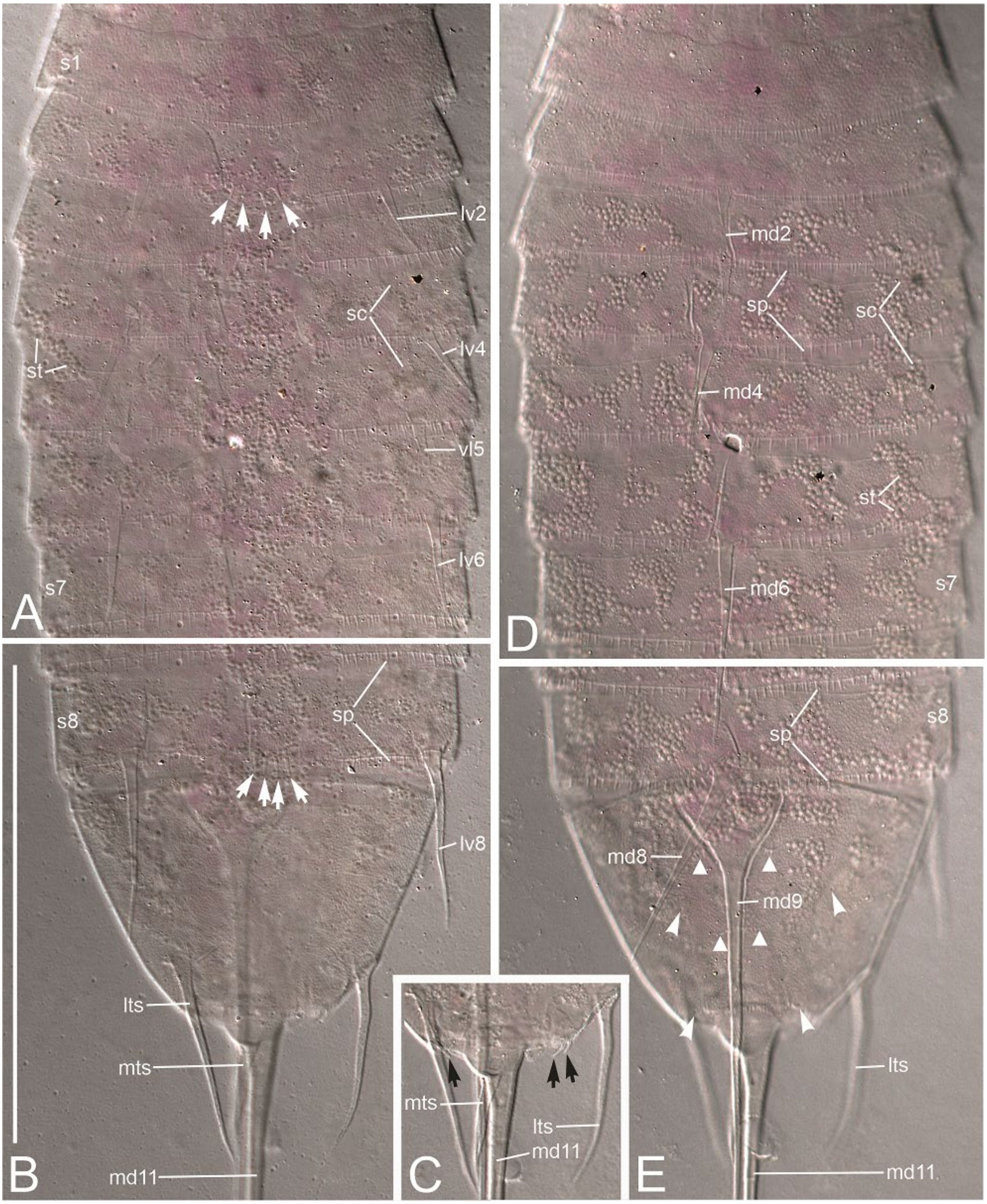

Fig. 7. *Ryuguderes casarrubiosi*, juvenile NHMD 672703, ventral (A–C) and dorsal view (D, E). A, D, segments 1–7. B, E, segment 8 and prospective segments 10+11. C, segment 11 with spinose anlagen of lateral terminal and lateral terminal accessory spines (black arrows). Scale bar in B 100 µm, valid for A–E. Abbreviations: lts, lateral terminal spine; lv, lateroventral spine; md, middorsal spine; sc, secondary fringe; sp, spicula; st, storage vesicles; vl, ventrolateral tube. Strong midventral spicula marked by white arrows, sensory spots by arrowheads, and weak border between terminal segments by triangles. Number after abbreviation refers to segment.

DISCUSSION

Variation within adult specimens of *Campyloderes* cf. *vanhoeffeni*

Quite some morphological variation was reported for 103 adult specimens of *Campyloderes* cf. *vanhoeffeni* from 24 locations worldwide in the Atlantic, Indian, and Pacific Ocean; variation concerned the presence or absence of a short tube ventrolaterally on segment 1 and lateroventrally on segment 2 on one or both sides, the short ventrolateral tube on segment 5 replaced by an elongate papilla, the short lateroventral tube on segment 2 replaced by a long acicular spine, additional and variable positions of sensory spots, papillae, and gland cell outlets on several segments, the relative length of the midterminal spine compared to the lateral terminal accessory spine (29–79%), the expression of cuticular surface structures of the trunk like scales and ridges, and the body size ranging from 237–610 µm; tubes were termed previously "short spine with thin cuticle and blunt tip" (Neuhaus 2004; Neuhaus and Sørensen 2013). The specimens studied in this paper fitted well into the documented pattern of variation (but see also chapter Moulting of late juvenile or adult life history stage in Campyloderidae).

Discrimination of females from males of *Campyloderes* cf. *vanhoeffeni*

A previous study suggested that males of *Campyloderes* cf. *vanhoeffeni* were distinguished from females by the presence of a middorsal spine each on segments 10 and 11 and a sublateral spine on segment 10 in males, and these spines were supposed to be lacking in 27 out of 33 females; all females revealed in addition gonopores and female-specific ventromedial papillae on segments 6 and 7, which were both absent in males (Neuhaus and Sørensen 2013, table 4). However, these authors also discussed that probably two adult life history stages existed based on the observation of a middorsal spine each on segments 10 and 11 and the lack of a sublateral spine on segment 10 in 6 out of 33 females. Later juvenile stages possessed a middorsal spine each on segments 10 and 11 and a lateral accessory to sublateral spine on segment 10 (see also Table 3). Therefore, it was concluded that stage-1 females lost the lateral spines on segment 10 but still possessed the middorsal spine each on segments 10 and 11, whereas stage-2 females lost also these middorsal spines. Later on, this hypothesis was confirmed for *Campyloderes* cf. *vanhoeffeni* because of more observations having become available for other species of Kinorhyncha but was only noted in a table of an article about two different species (Neuhaus 2017, table 7). This ontogenetic concept is followed here as well.

Discrimination of late juvenile from adult stages of *Campyloderes* cf. *vanhoeffeni* and *Ryuguderes casarrubiosi*

Stage-1 females of *Campyloderes* cf. *vanhoeffeni* differed from late juvenile stages (potential juvenile stage group H) in the possession of gonopores and ventral papillae on segments 6 and 7 and in the lack of lateral spines on segment 10 in females *versus* the lack of gonopores and ventral papillae and the existence of lateral spines on segment 10 in juveniles (potential juvenile stage group H). Stage-2 females of *Campyloderes* cf. *vanhoeffeni* were discriminated from late juveniles (potential juvenile stage group H) by their possession of gonopores and ventral papillae on segments 6 and 7 and their lack of all spines on segment 10 and of the middorsal spines on segment 11 *versus* the lack of gonopores and ventral papillae and the existence of lateral and a middorsal spine on segment 10 and of a middorsal spines on segment 11 in juveniles (potential juvenile stage group H). Gonads or eggs occurred both in stage-1 and stage-2 females, but had not developed in all females with a sclerotised cuticle at the time of fixation. These findings also indicated that both female stages seemed to reproduce.

The situation was more problematic for males of *Campyloderes* cf. *vanhoeffeni*, because they shared the same arrangement of spines, tubes, sensory spots, and gland cell outlets and cuticular characters with late juvenile stages and lacked specific characters or obvious gonopores. More maturated males possessed developing gonads or sperm and a sclerotised cuticle lacking in late juveniles. As reported for the females of *C.* cf. *vanhoeffeni* in this paper, gonads would not necessarily become visible directly after moulting from the last juvenile stage and from the stage-1 female. The same would be assumed for males, so recently moulted males could not be distinguished from late juvenile stages (potential juvenile stage group H).

Specimen ZMB 5967f did not show female characters, but a gonad developed on one side. This specimen might represent either the last juvenile stage expressing already a female or male developing gonad or alternatively a young male. With the limited amount of specimens at hand, it cannot be totally excluded that some specimens of the last juvenile stage might start developing a gonad, which would maturate in the stage-1 adult. Therefore, the postembryonic development of *C.* cf. *vanhoeffeni* might be more flexible that can be concluded from existing information.

For *Ryuguderes casarrubiosi*, only one adult life history stage is known from two females and one male; a single juvenile specimen with postmarginal spicula was described, so no information is available about late juvenile stages of this species (Cepeda et al. 2022). Possibly, the lack of lateroventral junctions or separated sternal cuticular plates in segments 2–11 of specimen NHMD 672704 indicated a late but not the last juvenile stage of this species, because an adult with sternal plates in segments 2–11 would moult from a last juvenile stage specimen with separated sternal plates in exactly these segments in other species of Kinorhyncha (Neuhaus 2017, table 6 and references therein).

Light-refracting storage vesicles occupied small parts of the trunk or filled it to a large degree. Such vesicles did occur both in earlier juvenile, late juvenile or adult stages, and some females of various degrees of maturation (Figs. 1A–L, 2A–D, I, 3B–D, 4A, C, H, 5A, B, F, G, 6A–D, 7A–D) and, therefore, seemed to reflect more the situation of food supply than the developmental stage of a specimen.

At the anterior margin of more maturated adult life history stages of *Campyloderes* cf. *vanhoeffeni* and of *Ryuguderes casarrubiosi*, a cuticular interior thickening of the trunk cuticle (= pachycyclus) appeared (Figs. 2H, 3A; Cepeda et al. 2022). This structure was always missing in recently hatched adults or late juvenile stages, which includes the two late juvenile stage or male specimens moulting ZMB 5983a and ZMB 13068, and in juvenile stages, which also yielded a thinner cuticle than adults (Figs. 3E–H, 4A, C, H, I, 5A–C, E–G, 7A–D).

During the ontogeny of many cyclorhagid Kinorhyncha, at least earlier juvenile stages with up to 9 separated segments possessed postmarginal spicula at the posterior margin of a segment and no free flap, which was in fact a cuticular fold partly overlapping the subsequent segment; this free flap only appeared in late juvenile and in adult life history stages (Neuhaus 2017, table 6). The same situation applied to late juvenile stages and the adult of *Campyloderes* cf. *vanhoeffeni* and most probably also of *R. casarrubiosi*, which revealed a free flap as found by previous studies and confirmed here (Figs. 1B–K, 2A–I, 3A–D, 6A–D; Zelinka 1913, p. 433, plate 39, figs. 1, 2, 11; Neuhaus 2004; Neuhaus and Sørensen 2013; Cepeda et al. 2022).

Most certainly, the cuticular bars connected the upper and the lower part of the free flap cuticle and prevented the flap from inflating during locomotion, which was facilitated by contraction of the dorsoventral muscles increasing the body pressure and leading to protrusion of the head (Neuhaus and Higgins 2002). It is assumed that in those adult specimens without a recognisable internal striation pattern, cuticle was deposited between the longitudinal cuticular bars and filled the free flap entirely. A similar phenomenon was reported for species of Pycnophyidae and Echinoderidae, which showed cuticular button-like structures representing actually pillars between the upper and lower cuticle of the free flap instead of a longitudinal striation pattern (Neuhaus 2013, p. 245, fig. 5.1.40D). The free flap ended more or less smoothly or in short, irregularly distributed spinose processes (Figs. 1B–K, 2A–I, 3A–D, 6A–D).

Aspects of postembryonic development of *Campyloderes* cf. *vanhoeffeni*

The previously mentioned juvenile specimens of *Campyloderes* cf. *vanhoeffeni* as well as new material were investigated to establish some basic aspects of the postembryonic development of this species (Table 1; Neuhaus and Sørensen 2013). The current study was hampered by the limited amount of 16 available juvenile specimens plus one juvenile exuvia as well as 9 specimens assigned here either to a late juvenile stage of young male, most of them collected from different locations (Tables 1, 3). Although a considerable variation was reported for adult specimens of the species from numerous locations in the Atlantic, Indian, and Pacific Ocean and even between more closely related geographic areas, it was not possible to identify distinct species based on morphological characters; also, ongoing species formation was considered (see chapter Variation within adult specimens; Neuhaus 2004; Neuhaus and Sørensen 2013, p. 72). Therefore, we tentatively treated the juvenile specimens as belonging to a single species in this study.

For *Campyloderes* cf. *vanhoeffeni*, a series of juvenile stage groups A–G and potentially H could be established (Table 3), not all of them necessarily representing subsequent stages, which would moult directly from each other. The postembryonic development of this species revealed the following characters (Table 3), which are compared with those of other cyclorhagid species:

(1) The earliest juvenile stage of *Campyloderes* cf. *vanhoeffeni* (juvenile stage group A) had segments 1–8 clearly separated and segments 9+10+11 still fused, whereas segments 1–9 appeared distinctly and segments 10+11 weakly separated in all remaining juvenile specimens with postmarginal spicula (juvenile stage groups B–G). Late juvenile stages with segments 1–11 separated most certainly revealed a free flap (potential juvenile stage group H).

A similar situation for the earlier stages was observed in the postembryonic stages of the cyclorhagids *Antygomonas incomitata* Nebelsick, 1990, *Cateria gerlachi* Higgins, 1968, *Cateria styx* Gerlach, 1956, *Ryuguderes casarrubiosi* (Fig. 7A–D), *Tubulideres seminoli*, *Wollunquaderes majkenae*, and *Zelinkaderes floridensis* Higgins, 1990 (see Higgins 1990; Sørensen et al. 2010; Neuhaus and Kegel 2015; Neuhaus 2017; this paper).

(2) The cuticle of all segments of all juvenile specimens of *Campyloderes* cf. *vanhoeffeni* with postmarginal spicula (juvenile stage groups A–G) was ring-like without any cuticular plates identifyable by light microscopy. The latest juvenile stages or at least the last stage possessed most certainly a free flap as well as sternal plates in segments 2–11 (potential juvenile stage group H). These stages might not be distinguishable from young males (Table 3).

A ring-like cuticle was noted for *A. incomitata*, *R. casarrubiosi* (Fig. 7A–D), and *T. seminoli* and might also exist in early juvenile stages of species of *Centroderes*, whereas later stages expressed three ventral plates (Sørensen et al. 2010; Neuhaus et al. 2014, figs 5A, B, 16D, F, G; Neuhaus 2017; this paper). The slightly separated midventral to paraventral area of *R. casarrubiosi* might have been caused either by a slight contraction of the dorsoventral muscles or by a preservation artefact during mounting.

Among the cyclorhagid species with sternal plates in the adult stage, the supposedly last juvenile stage of only one species of *Echinoderes* revealed a ring-like cuticle and no sternal plates, but only an incomplete series of juvenile stages was available and assignment to the stages can be considered as questionable (Higgins 1977, Fig. 7).

(3) All earlier juvenile specimens of *Campyloderes* cf. *vanhoeffeni* (juvenile stage groups A–G) possessed postmarginal spicula at the posterior margin of all segments except the terminal one or of fused segments. Weak secondary fringes on the cuticle surface appeared from juvenile stage group C on.

Postmarginal spicula were reported as a continuous ventral and dorsal row at least for earlier juvenile stages of *A. incomitata*, *Cateria gerlachi*, *Cateria styx*, *T. seminoli*, and *W. majkenae*. Ventral spicula occurred as an interrupted row from a lateroventral to paraventral area and from a paraventral to midventral area only in some stages of *A. incomitata*, *Campyloderes* cf. *vanhoeffeni*, *Centroderes readae* Neuhaus et al., 2014, *T. seminoli*, *W. majkenae*, and in the single known juvenile specimen of *R. casarrubiosi* (Fig. 7A–D; Table 3; Sørensen et al. 2010; Neuhaus et al. 2014; Neuhaus 2017; this paper).

Later juvenile stages revealed secondary pectinate fringes in the cyclorhagids *A. incomitata*, *Campyloderes* cf. *vanhoeffeni, Centroderes barbanigra* Neuhaus et al., 2014, and *Centroderes drakei* Neuhaus et al., 2014 (see Sørensen et al. 2010; Neuhaus et al. 2014).

(4) The earliest known juvenile stage of *Campyloderes* cf. *vanhoeffeni* (juvenile stage group A) did not show the full set of lateral and dorsal spines, only each second segment bore a middorsal spine.

Middorsal spines of alternating length or lateral and middorsal spines missing on neighbouring segments were also described for *A. incomitata*, *R. casarrubiosi* (Fig. 7A–D), and *W. majkenae* (see Sørensen et al. 2010; Neuhaus 2017; this paper).

(5) The lateral terminal and the lateral terminal accessory spine of *Campyloderes* cf. *vanhoeffeni* appeared as short spinose anlagen without an articulation in the earliest known juvenile stage (juvenile stage group A). The lateral terminal spine subsequently elongated slightly and became bulbous at its base (juvenile stage group B), lost the bulbous part in a subsequent stage (juvenile stage groups B and C), and finally elongated to a regular acicular spine (from juvenile stage group D on). Confusingly, specimen ZMB 13104 (juvenile stage group B) missed a lateral terminal accessory spine or its anlage although the specimen seemed to represent a more advanced stage with more spines than specimen ZMB 5977b (juvenile stage group A).

Anlagen of the lateral terminal and the lateral terminal accessory spine without an articulation were mentioned for *Cateria gerlachi*, *R. casarrubiosi*, *T. seminoli*, *Z. floridensis*, and possibly for *A. incomitata* (see Higgins 1990; Sørensen et al. 2010; Neuhaus and Kegel 2015; Neuhaus 2017; this paper: Fig. 7C).

(6) A lateral spine on segment 10 appeared lateroventrally in one early juvenile stage of *Campyloderes* cf. *vanhoeffeni* (juvenile stage group B) but was expressed in a lateral accessory position in later juvenile stages (juvenile stage groups C–G) and in a sublateral position in the last juvenile stage or male (potential juvenile stage group H).

A change in position of the lateral spine on segment 10 from lateroventral to more dorsally is unknown within Kinorhyncha.

(7) A middorsal spine on segment 11 existed from the earliest known juvenile stage on in *Campyloderes* cf. *vanhoeffeni* (juvenile stage groups A and B). Ventrally of the large base of this spine, the spinose anlage of the short midterminal spine without an articulation occurred at a later stage (juvenile stage groups C and D), which subsequently elongated to a regular acicular midterminal spine (juvenile stage group E). This developmental pattern of dorsal spines on the terminal segment suggested that the dorsal terminal spine of early juvenile stage groups A and B had to be interpreted as a middorsal spine of segment 11 and not as a midterminal spine.

A common base of a very long middorsal spine of segment 11 and the spinose anlage of the ventral short midterminal spine without an articulation was found in *Echinoderes prior* González-Casarrubios et al., submitted, *R. casarrubiosi* (Fig. 7B), and *W. majkenae* (see Neuhaus 2017, p. 144, fig. 14E; González-Casarrubios et al. submitted; this paper).

(8) The ratio of the length of the midterminal spine to the lateral terminal accessory spine showed a confusing pattern among the juvenile specimens of *Campyloderes* cf. *vanhoeffeni*. Initially, the former spine was shorter than the latter. However, specimens were found either with an equally long or an even longer midterminal spine than a lateral terminal accessory spine. In a later stage and the adult, the former spine was shorter than the latter except for a male moulting to a male, which had a longer midterminal spine (ZMB 13068). Similarly, the development of the lateral terminal spine and the lateral terminal accessory spine appeared to be inconsistent (see (5) above). Currently, we conclude that possibly different populations of *Campyloderes* cf. *vanhoeffeni* may exist with different developmental patterns. It can also not be ruled out that more than six juvenile stages may exist for this species.

This situation is unknown within Kinorhyncha.

In summary (Table 3), the postembryonic developments of *Campyloderes* cf. *vanhoeffeni* started probably with a stage showing segments 1–8 separated and 9+10+11 still fused possessing postmarginal spicula at the posterior margin of a segment, a long middorsal spine on segment 11, and spinose anlagen of the lateral terminal spine and lateral terminal accessory spine (juvenile stage group A). In a subsequent stage, segments 1–9 appeared separated and segments still 10+11 fused, and the specimens revealed a short basally bulbous lateral terminal spine and the spinose anlage of a midterminal spine at the base of the middorsal spine of segment 11 (juvenile stage group B). During the ongoing ontogeny, the lateral terminal spine first thickened (juvenile stage groups B–D) and turned later into a regular acicular spine (juvenile stage group E). Similarly, the short anlage of the midterminal spine below the middorsal spine of the prospective segment 11 of juvenile stage group C elongated to a regular acicular spine in the juvenile stage group D and separated from the middorsal spine of the prospective segment 11 in juvenile stage group E. Late juvenile stages of the potential juvenile stage group H had segments 1–11 separated and a free flap at the posterior margin of a segment; these stages were indistinguishable from young males. Confusingly, the relative length of the midterminal spine to the lateral terminal accessory spine varied considerably and inconsistently between specimens of several juvenile stages with postmarginal spicula both between the different groups C–G and within group D. This observation might be related either to considerable variation within the currently indistinguishable *Campyloderes vanhoeffeni–C. vanhoeffeni* var. *kerguelensis–C. macquariae* species complex or to the existence of additional unrecognised species within this potential species complex (Neuhaus 2004; Neuhaus and Sørensen 2013). For these reasons, we neither presented a list of diagnostic characters of the groups of juvenile stages nor drawings of the groups.

Moulting of late juvenile or adult life history stage in *Campyloderes* cf. *vanhoeffeni*

Two late juvenile stages (potential juvenile stage group H) or young males of *Campyloderes* cf. *vanhoeffeni* were fixed in the process of moulting (ZMB 5983a, ZMB 13068). Both specimens agreed in their morphology with adult *Campyloderes* cf. *vanhoeffeni* in the existence of a broad midventral placid and 13 alternating narrower and broader placids, an elongate lateroventral spine on segment 1, lateroventral acicular spines on segments 3–11, a short lateroventral tube on segment 2, a short ventrolateral tube on segment 5, middorsal acicular spines on segments 1–11, a midterminal spine, and the cuticular scales and secondary fringe pattern. In addition, a short ventrolateral tube on segment 1 was found in specimen ZMB 5983a but was missing in specimen ZMB 13068, which was reported as intraspecific variation for this species before (Zelinka 1913; Neuhaus 2004; Neuhaus and Sørensen 2013). Whereas specimen ZMB 5983a with a trunk length of 373 µm fell well in the body length range previously reported for *Campyloderes* cf. *vanhoeffeni* (237–610 µm), specimen ZMB 13068 exceeded this range with a size of 675 µm.

The length ratio of the midterminal spine to the lateral terminal accessory spine of adult *Campyloderes* cf. *vanhoeffeni* was 29–79% as calculated here from the data provided by Neuhaus and Sørensen (2013, table 2). The morphology of specimen ZMB 13068 was a bit confusing, because the midterminal spine, although broken near the end, was slightly longer than the lateral terminal accessory spine with a length relation of >103% (Table 3). However, given the considerable variation mentioned by the latter authors (see above chapter Variation within adult specimens), we did not consider it justified to describe a new species based on this character alone.

Both specimen ZMB 5983a and ZMB 13068 did not show septa in the primary spinoscalids, which were characteristic for all known species of Campyloderidae, viz, *Campyloderes* cf. *vanhoeffeni*, *Ryuguderes casarrubiosi*, and *R. iejimaensis* Yamasaki, 2016 (see Neuhaus 2004; Neuhaus and Sørensen 2013; Yamasaki 2016; Cepeda et al. 2022). It is suggested here that the septa were dissolved in the old cuticle and not established in the new cuticle yet, because new scalids have to form within the old cuticle of the moulting animal. Development of a new scalid would not become possible without at least partial dissolution of septa in the old cuticle, since septa spanned the entire cross-section of a scalid. The finding of septa in the primary spinoscalids of four moulting juvenile specimens (ZMB 5974b, 5983d, 11174i, 11174j) did not contradict the aforementioned hypothesis, because dissolution of septa in the old cuticle and formation of septa in the new cuticle would happen subsequently with an intermediate period lacking recognisable septa. The juvenile specimen ZMB 11174i showed partly incomplete septa in the old cuticle and complete septa in the newly formed cuticle.Our finding of two late juvenile or young male specimens of *Campyloderes* cf. *vanhoeffeni* moulting (ZMB 5983a, ZMB 13068) could be interpreted either as a late juvenile moulting to another late juvenile or to a male or alternatively as a male moulting to another male; gonads were not developed in the two specimens, yet. Late juvenile stages could not be distinguished from young males in *Campyloderes* cf. *vanhoeffeni* (see chapter Discrimination of late juvenile from adult stages of *Campyloderes* cf. *vanhoeffeni* and *Ryuguderes casarrubiosi*), so no decision could be taken at this stage.

During the current re-investigation, the adult specimen of *Ryuguderes casarrubiosi*, confusingly termed “pre-adult male” in the original species description (Cepeda et al. 2022, p. 99, fig. 3H), proved to be either a late but possibly not the last juvenile stage or, less probably, a male, which had probably moulted recently. The number and arrangement of sensory spots and gland cell outlets differed from the pattern of the original description but was not further evaluated here because of the unsatisfying preservation status of the specimen studied and the lack of additional specimens.

CONCLUSIONS

This paper provided first insights into the postembryonic development and characters to distinguish late juvenile from stage-1 and stage-2 female and from more maturated male life history stages for one species of Campyloderidae, viz, *Campyloderes* cf. *vanhoeffeni* and to some degree also for a second species of the family, *Ryuguderes casarrubiosi*. This data will become most valuable for future descriptions of new species, which may get into conflict with the recognition of juvenile and adult life history stages and variation within a species.

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