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Neodiplopeltula gen. nov. from the west coast of Sweden and reappraisal of the genus *Diplopeltula* Gerlach, 1950 (Nematoda, Diplopeltidae)

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Abstract. The new genus *Neodiplopeltula* gen. nov. is proposed to accommodate those species from the genus *Diplopeltula* Gerlach, 1950 that possess the following morphological characters: amphids in the shape of an elongated loop, a well-developed subcylindrical stoma and outstretched ovaries. The genus *Diplopeltula* is considered *genus inquirendum et incertae sedis*. Four species placed in *Neodiplopeltula* gen. nov. are redescribed. The following taxonomic changes are proposed: *Neodiplopeltula asymmetrica* (Allgén, 1935) gen. et comb. nov.; *Neodiplopeltula barentsi* (Steiner, 1916) gen. et comb. nov.; *Neodiplopeltula bathmanni* (Jensen, 1991) gen. et comb. nov.; *Neodiplopeltula cuspidiboja* (Leduc, 2017) gen. et comb. nov.; *Neodiplopeltula indica* (Gerlach, 1962) gen. et comb. nov.; *Neodiplopeltula intermedia* (Gerlach, 1954) gen. et comb. nov.; *Neodiplopeltula obesa* (Nguyen Vu Thahn, Nguyen Thahn Hien & Gagarin, 2012) gen. et comb. nov.; *Neodiplopeltula onusta* (Wieser, 1956) gen. et comb. nov.; *Neodiplopeltula ovalis* (Ditlevsen, 1928) gen. et comb. nov. and *Neodiplopeltula tchesunovi* (Fadeeva & Mordukhovich, 2013) gen. et comb. nov. New synonyms include: *Diplopeltis asymmetricus* Allgén, 1935 and *Diplopeltis ovalis* Ditlevsen, 1928 are synonimised with *Neodiplopeltula barentsi* (Steiner, 1916) gen. et comb. nov.; *Diplopeltula tchesunovi* Fadeeva & Mordukhovich, 2013 is synonimised with *Neodiplopeltula onusta* (Wieser, 1956) gen. et comb. nov.; the male of *Diplopeltula cuspidiboja* Leduc, 2017 is synonimised with *Neodiplopeltula barentsi* gen. et comb. nov. and the female with *N. bathmanni* gen. et comb. nov. A key to the species of *Neodiplopeltula* gen. nov. is provided.

Keywords. Identification key, morphology, revision, SEM, taxonomy.

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Introduction

The genus *Diplopeltula* Gerlach, 1950 was proposed for two new and one known species, but without an explicit generic diagnosis. Diagnostic characters of this genus mentioned in the identification key from the original publication (amphid is loop shaped, with equally long ventral and dorsal branches; amphid not located on the shield-like cuticular plate) match a number of genera currently included in the family Diplopeltidae, such as *Morlaxia* Vincx & Gourbault, 1988; *Mudwigglus* Leduc, 2013; *Pararaeolaimus* Timm, 1961; *Pseudaraeolaimus* Chitwood, 1951 and even *Araeolaimus* de Man, 1888. Taxonomic instability of the genus is further sustained by the fact that the original description of the type species *Diplopeltula breviceps* Gerlach, 1950 does not include clear descriptions of characters currently considered diagnostic at the genus and family level, such as the exact structure of the pharynx or of the female reproductive system (Table 1), and because the type material was not preserved by S.A. Gerlach. As a result, the genus *Diplopeltula* recently underwent several taxonomic revisions, with more and more species being moved to other known and newly proposed genera (Holovachov *et al*. 2009; Leduc 2013; Holovachov 2017; Holovachov & Boström 2017). In this manuscript we propose to move all the remaining properly described species from the genus *Diplopeltula* to a new genus *Neodiplopeltula* gen. nov., treat both *Diplopeltula breviceps* and *D. longiceps* Gerlach, 1950 as *species inquirenda et incertae sedis*, treat *Diplopeltula ostrita* Boucher & Helléouët, 1977 and *D. striolata* Vincx & Gourbault 1992 as *species incertae sedis*, and consider *Diplopeltula* a *genus inquirendum et incertae sedis*.

Material and methods

Bottom sediment samples were collected in several locations in the southern part of the Skagerrak and in the Gullmarn Fjord off the west coast of Sweden. All samples were collected with a bottom dredge or box corer and further sieved in the laboratory before fixation. Nematodes were extracted from samples using a decanting and sieving method (smallest mesh sizes: 45 µm or 70 µm). Freshwater was used during sieving to induce an osmotic shock in nematodes inducing their detachment from the substrate. Material retained on the sieves was immediately fixed in a 4% formaldehyde solution in freshwater.

For light microscopy, formaldehyde-preserved specimens were transferred to pure glycerine using Seinhorst's (1959) rapid method as modified by De Grisse (1969). Permanent nematode mounts on glass slides were prepared using the paraffin wax ring method. After observations, six females and five males of *N. incisa* (Southern, 1914) gen. et comb. nov. from the sample #S053 (SWEDEN: Skagerrak, 58°17′32″ N, 11°11′24″ E, coarse sediment with algae at a deep of 45–55 m, 9 Aug. 2011, O. Holovachov leg.) were removed from slides and rehydrated by first gradually adding drops of S2 (5% glycerine, 95% ethanol) to glycerine in an embryo-dish, starting with a 1:4 ratio of S2 to glycerine, until the volume tripled, then gradually adding distilled water until the volume tripled again. The specimens were then washed in distilled water before resuspension in formaldehyde. For SEM, specimens were post-fixed in 1% osmium tetroxide (OsO_4) and transferred to pure acetone through an acetone/distilled water series. Specimens were critical point dried in liquid CO_2, mounted on stubs, gold-plated under vacuum to a thickness of 200 Å in an Agar High Resolution Sputter Coater Model 20, and examined in a Hitachi S-4300 SEM at an accelerating voltage of 10 kV.

All curved structures were measured along the curved median line. Measurements in all tables are presented in µm as mean and (range) where appropriate. Terminology follows Maggenti (2005). Specimens are deposited in the invertebrate collection of the Department of Zoology, Swedish Museum of Natural History, Stockholm, Sweden (SMNH). Type specimens of *Diplopeltis asymmetricus* Allgén, 1935 deposited in the Swedish Museum of Natural History in Stockholm, *Diplopeltis ovalis* Ditlevsen, 1928 deposited in the Natural History Museum of Denmark in Copenhagen and *Diplopeltula ostrita* Boucher & Helléouët, 1977 deposited in the National Museum of Natural History in Paris were also examined.

Table 1. Comparison of diagnostic characters between the genera *Neodiplopeltula* gen. nov., based on the type species *N. incisa* (Southern, 1914) gen. et comb. nov. and generic diagnosis (this publication), *Diplopeltula* Gerlach, 1950 based on the type species *D. breviceps* Gerlach, 1950, and *Diplopeltoides* Gerlach, 1962 based on the type species *D. ornatus* (Gerlach, 1950) and emended generic diagnosis in Holovachov & Boström (2017).

Family	Diplopeltidae	*incertae sedis*	Diplopeltoididae
Genus	*Neodiplopeltula* gen. nov.	*Diplopeltula*	*Diplopeltoides*
Stoma	subcylindrical	absent	small funnel-shaped
Pharynx	uniformly cylindrical, gradually widening posteriorly, with evenly distributed myofilaments	not described	subdivided in anterior muscular corpus with evenly distributed myofilaments and posterior glandular postcorpus, consisting of narrow isthmus and basal swelling
Female gonads	ovaries outstretched	not described	ovaries antidromously reflexed

Results

Phylum Nematoda Potts, 1932
Class Chromadorea Inglis, 1983
Order Araeolaimida De Coninck & Schuurmans Stekhoven, 1933
Family Diplopeltidae Filipjev, 1918

Genus ***Neodiplopeltula*** gen. nov.
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Type species

Neodiplopeltula incisa (Southern, 1914) gen. et comb. nov.
= *Diplopeltis incisus* Southern, 1914
= *Diplopeltula incisa* (Southern, 1914)
= *Diplopeltis incisus* sensu Gerlach, 1950 partim (note #1)
= *Diplopeltula incisa* sensu Voronov, 1982 partim (note #2)

Diagnosis

Cuticle transversely striated; striae visibly smooth under light microscope, may have fine longitudinal incisures visible under SEM. Lateral alae absent. Body pores and epidermal glands absent. Somatic sensilla present, most prominent along anterior part of pharyngeal region and on tail. Labial region bluntly rounded; lips fused. Six inner labial sensilla small, pore-like, located on anterior surface of lips, discernible under SEM only. Six outer labial sensilla papilliform, located on anterior surface of lips. Four cephalic sensilla setiform; their bases located at base of labial region, at level with anteriormost part of amphid. Bases of dorsosublateral setae often located more posteriorly than bases of ventrosublateral setae. Subcephalic sensilla absent. Cervical sensilla present in some species, setiform or papilliform, arranged in dorsosublateral and ventrosublateral rows at level with amphid and subcuticular periamphideal plates. Deirid and ocelli absent. Amphids in some species on strongly refractive lateral subcuticular periamphideal plates that can be connected together on ventral and dorsal sides forming a 'cephalic framework'. Amphidial fovea loop-shaped (inverted U-shaped), dorsal branch often longer than ventral branch; both branches of amphideal fovea closely adjacent. Secretory-

excretory system present; renette cell located opposite to posterior part of pharynx or anterior part of intestine. Secretory-excretory ampulla present, located at level of pharynx. Cuticularised secretory-excretory duct very short, opens to exterior either anterior or posterior to nerve ring level. Oral opening apical or shifted towards dorsal side of body. Buccal cavity usually well developed, subcylindrical and often asymmetrical: cheilostom usually broad, flexible; gymnostom subcylindrical, with weakly cuticularised walls; stegostom short conoid, its lining is uniform with lining of pharynx. Pharyngeal tubes absent. Pharynx subcylindrical, muscular, with evenly distributed myofilaments, gradually expanding towards posterior end; not subdivided into distinct sections; pharyngeal lumen uniform in thickness along entire pharynx length; valves absent. Cardia glandular, variable in shape and size, its posterior part embedded in intestinal tissue. Female reproductive system didelphic-amphidelphic, with equally developed branches, ovaries outstretched. Spermatheca present. Vulva equatorial or postquatorial. Vagina straight; *pars proximalis vaginae* encircled by large sphincter muscle; *pars refringens vaginae* absent, epiptygmata present or absent. Male reproductive system diorchic, testes opposed (anterior testis outstretched and posterior testis reflexed). Spicules symmetrical, arcuate; gubernaculum present, usually with strongly developed apophyses. Supplements, precloacal and postcloacal sensilla absent. Three caudal glands present, open via three separate openings, their cells and nuclei incaudal. Spinneret absent.

Etymology

The genus name is composed of a prefix 'neo–', meaning 'new' and *Diplopeltula*, and defines a new taxon proposed to accommodate species formerly placed in the genus *Diplopeltula*.

Relationships

The new genus differs from all other taxa currently included in the family Diplopeltidae (Holovachov 2017) in having amphids in the shape of an elongated loop, a well-developed subcylindrical stoma and outstretched ovaries. It is proposed in order to accommodate a number of species previously placed in the genus *Diplopeltula* and to solve a long lasting taxonomic conundrum (Vincx & Gourbault 1992; Holovachov *et al*. 2009; Holovachov 2017; Holovachov & Boström 2017). The description of *Diplopeltula breviceps*, type species of the genus *Diplopeltula,* does not include clear descriptions of several important taxonomic characters (see Table 1) and the absence of such data prevents an unequivocal placement of the species *D. breviceps* and the genus *Diplopeltula* in the classification system of Nematoda. As a result, *D. breviceps* is considered *species inquirenda et incertae sedis* and the genus *Diplopeltula* is accordingly considered *genus inquirendum et incertae sedis*. The second species, *D. longiceps,* is also considered *species inquirenda et incertae sedis* for the same reasons (incomplete description and unclear systematic position).

Valid species

Neodiplopeltula barentsi (Steiner, 1916) gen. et comb. nov.
= *Diplopeltis barentsi* Steiner, 1916
= *Diplopeltis ovalis* Ditlevsen, 1928 syn. nov. (note #3)
= *Neodiplopeltula ovalis* (Ditlevsen, 1928) gen. et comb. nov., syn. nov.
= *Diplopeltis asymmetricus* Allgén, 1935 syn. nov. (note #4)
= *Neodiplopeltula asymmetrica* (Allgén, 1935) gen. et comb. nov., syn. nov.
= *Diplopeltis incisus* sensu Gerlach, 1950 partim (note #1)
= *Diplopeltula incisa* sensu Voronov, 1982 partim (note #2)
= *Diplopeltis ovalis* sensu Sergeeva, 1977 (note #5)
= *Diplopeltula cuspidiboja* Leduc, 2017 partim syn. nov. (note #6)
= *Neodiplopeltula cuspidiboja* (Leduc, 2017) gen. et comb. nov., syn. nov.

Neodiplopeltula bathmanni (Jensen, 1991) gen. et comb. nov.
= *Diplopeltis bathmanni* Jensen, 1991
= *Diplopeltula bathmanni* (Jensen, 1991)
= *Diplopeltula incisa* sensu Vitiello, 1972 (note #7)
= *Diplopeltula incisa* sensu Voronov, 1982 partim (note #2)
= *Diplopeltula cuspidiboja* Leduc, 2017 partim syn. nov. (note #8)
= *Neodiplopeltula cuspidiboja* (Leduc, 2017) gen. et comb. nov., syn. nov.

Neodiplopeltula indica (Gerlach, 1962) gen. et comb. nov. (note #9)
= *Diplopeltula indica* Gerlach, 1962

Neodiplopeltula intermedia (Gerlach, 1954) gen. et comb. nov. (note #9)
= *Diplopeltula intermedia* Gerlach, 1954

Neodiplopeltula obesa (Nguyen Vu Thahn, Nguyen Thahn Hien & Gagarin, 2012) gen. et comb. nov.
= *Diplopeltula obesa* Nguyen Vu Thahn, Nguyen Thahn Hien & Gagarin, 2012 (note #9)

Neodiplopeltula onusta (Wieser, 1956) gen. et comb. nov.
= *Diplopeltis onustus* Wieser, 1956
= *Diplopeltula onusta* (Wieser, 1956)
= *Diplopeltula incisa* sensu Voronov, 1982 partim (note #2)
= *Diplopeltula tchesunovi* Fadeeva & Mordukhovich, 2013 syn. nov. (note #10)
= *Neodiplopeltula tchesunovi* (Fadeeva & Mordukhovich, 2013) gen. et comb. nov., syn. nov.

Species *inquirenda et incertae sedis*

Diplopeltula breviceps Gerlach, 1950
Diplopeltula longiceps Gerlach, 1950

Species *incertae sedis*

Diplopeltula striolata Vincx & Gourbault, 1992 (note #11)
Diplopeltula ostrita Boucher & Helléouët, 1977 (note #12)

Nomenclatorial changes and notes

1) The description of *Diplopeltis incisus* sensu Gerlach, 1950 is based on specimens collected in several localities in the Kiel Bay and is likely to be a mixture of at least two different species: based on the oval shape and relatively small size of the periamphideal refractive plate, the position of cephalic setae posterior to the oral opening, and the position of the oral opening close to the anterior end, *N. barentsi* gen. et comb. nov. can be identified on fig. 3h, 3k & 3m in Gerlach (1950), while fig. 3b likely depicts *N. incisa* sensu stricto, based on the irregular shape and relatively large size of the periamphideal refractive plate, the position of cephalic setae posterior to the oral opening, and the position of the oral opening close to the anterior end. Unfortunately, exact measurements of morphological characters cannot be attained from the figures in Gerlach's publication due to the absence of proper scale bars. Thus, our hypothesis on the taxonomic identity of specimens studied by Gerlach (1950) must solely rely on illustrations and cannot be verified any further.

2) The description of *Diplopeltula incisa* sensu Voronov, 1982 is based on specimens collected in six different locations from the White Sea, within an area of more than 100 × 200 km in size and ranging in depth from 50 to 250 meters. Many measurements given by Voronov vary within 2×–4× range. Morphological features of the anterior end also show a considerable variability (noted by Voronov himself) suggesting that his description is based on more than one morphospecies. Here

we suggest that there are four different species of *Neodiplopeltula* gen. nov. illustrated in Voronov's publication: fig. 1a likely depicts *N. bathmanni* gen. et comb. nov. with very narrow periamphideal plates and an oral opening located at level with the cephalic setae bases; both specimens depicted on fig. 1б and 1в match our concept of *N. barentsi* gen. et comb. nov. with relatively broad oval periamphideal plates and an oral opening located close to the anterior terminus, anterior to the cephalic setae bases; the presence of irregularly shaped periamphideal plates and an oral opening located close to the anterior terminus, anterior to cephalic setae bases in specimen depicted on 1г suggest it to belong to *N. incisa* gen. et comb. nov.; while the anterior end shown on fig. 1д completely matches with *N. onusta* gen. et comb. nov. (and confirmed by Voronov in his figure caption) in having periamphideal plates merging on the dorsal and ventral body sides and an oral opening located at level with the cephalic setae bases.

3) The holotype of *Diplopeltis ovalis* described by Ditlevsen (1928) from Greenland is available in the collection of the Natural History Museum of Denmark in Copenhagen and is in rather acceptable shape. Some morphological features, such as cephalic setae and the spinneret cannot be seen due to deterioration, while the vagina and rectum are difficult to observe since the specimen is not in perfect lateral position on the slide. Morphological and morphometric features that are visible and measurable, show no differences from *N. barentsi* gen. et comb. nov. – in particular, the position of the oral opening and morphology of refractive plates underlying the amphids are identical (Figs 14A, 15A–B). Consequently, *Diplopeltis ovalis* is being transferred to the genus *Neodiplopeltula* gen. nov. and synonimised with *N. barentsi* gen. et comb. nov.

4) The lectotype of *Diplopeltis asymmetricus* described by Allgén (1935) from Öresund was found in the collection and is in poor shape. The specimen is partly dried, thus making it impossible to observe and measure smaller features such as cephalic setae, spinneret and rectum. It is also slightly flattened, which affects a- and c'-ratios. Morphological features that are visible, show no differences from *N. barentsi* gen. et comb. nov. – in particular, the position of the oral opening and the morphology of refractive plates underlying the amphids are identical (Figs 14B, 15C). Consequently, *Diplopeltis asymmetricus* is being transferred to the genus *Neodiplopeltula* gen. nov. and synonimised with *N. barentsi* gen. et comb. nov.

5) *Diplopeltis ovalis* sensu Sergeeva, 1977 is similar to *N. barentsi* gen. et comb. nov. in the position of the oral opening on the dorsal side of the body but close to the anterior end, length and arrangement of the cephalic setae (7.5 µm vs 3.5–7.5 µm in present specimens), and the shape of refractive plates (elongated ovoid, not connected).

6) The male of *Diplopeltula cuspidiboja* gen. et comb. nov. is identical to *N. barentsi* gen. et comb. nov. in the position of the oral opening, size and shape of refractive plates and the great majority of quantitative characters (see Table 3), except for a slightly longer amphid (32 µm vs 21–25.5 µm) and gubernaculum (20 µm vs 10–11.5 µm).

7) *Diplopeltula incisa* sensu Vitiello, 1972 is similar to *D. bathmanni* in the position of the oral opening, length and the arrangement of the cephalic setae, the size and position of the periamphideal refractive plate, length of the tail and position of the caudal gland openings.

8) The female of *Diplopeltula cuspidiboja* gen. et comb. nov. is identical to *N. bathmanni* gen. et comb. nov. in the position of the oral opening, the position of the cephalic sensilla, the size and shape of the refractive plates (Leduc 2017); as a result of having a larger body (2076 µm vs 1270–1673 µm), many morphometric characters of the female of *D. cuspidiboja* are also outside

the measurement range of both Nordic populations, which can be attributed to geographic variability.

9) *Diplopeltula indica* and *Diplopeltula intermedia* both match the diagnostic characters of the genus *Neodiplopeltula* gen. nov.: amphids in the shape of an elongated loop, a well-developed subcylindrical stoma and outstretched ovaries. *Diplopeltula obesa* also has amphids in the shape of an elongated loop and outstretched ovaries, however, the structure of the stoma in this species is described as "not expressed", leaving some doubts as to its exact morphology.

10) *Diplopeltula tchesunovi* is identical to *D. onusta* in all qualitative and quantitative characters (Table 4), with the exception of longer refractive plates (41–48 μm vs 32–38 μm), which can be attributed to geographic variability.

11) *Diplopeltula striolata* is described based only on one male, thus the structure of the female reproductive system remains unknown, questioning its systematic affinities. It is similar to the genus *Neodiplopeltula* gen. nov. in the morphology of the amphid (in the shape of an elongated loop) and stoma (small but well developed, subcylindrical). The morphology of the pharynx (uniformly cylindrical) also matches that of *Neodiplopeltula* gen. nov. However, *D. striolata* strongly differs from *Neodiplopeltula* gen. nov. in having a strongly annulated cuticle, the position of the excretory pore at the level with the anterior part of the intestine, the presence of a spinneret, the absence of a gubernaculum. Although this species can easily be identified, and its validity is unquestionable, its taxonomic position remains unresolved as it cannot be assigned to any of the existing genera with confidence (*species incertae sedis*).

12) All available type specimens of *Diplopeltula ostrita* were examined, but not all morphological characters can be observed. That includes the female reproductive system and the structure of the ovaries. However, *D. ostrita* strongly differs from *Neodiplopeltula* gen. nov. in having a strongly annulated cuticle, a minute buccal cavity, weak spicules and gubernaculum. Similar to *Diplopletula striolata*, *D. ostrita* is here considered to be a valid species, which, however, cannot be assigned to any existing genus with confidence and must be considered *species incertae sedis*.

Neodiplopeltula incisa (Southern, 1914) gen et. comb. nov.
Figs 1–4; Table 2

Diagnosis (based on combined data)

Neodiplopeltula incisa gen. et comb. nov. is characterised by a 1.52–2.24 mm long body; refractive plates underlying cephalic cuticle around amphids present, irregular in shape, not joined, 28–33 μm long and 21–25 μm wide; cephalic setae 8–14 μm long; amphidial fovea 22–28 μm long and 5.5–7 μm wide; oral opening 1–3 μm from anterior end, posterior to cephalic setae bases; secretory-excretory pore located opposite to posterior part of pharynx; tail 2.5–3.9 anal body diameters long; vagina with epiptygmata; spicules 66–79 μm long.

Material examined

SWEDEN: 4 ♀♀, 3 ♂♂, Skagerrak, 58°12′37″ N, 11°18′53″ E, shells and sand at a deep of 15–22 m, 10 Oct. 2012, O. Holovachov leg. (SMNH-169255); 1 ♀, 1 ♂, Skagerrak, 58°20′21″ N, 11°12′42″ E, coarse shell sand at a deep of 14–17 m, 19 Aug. 2014, O. Holovachov leg. (SMNH-169258).

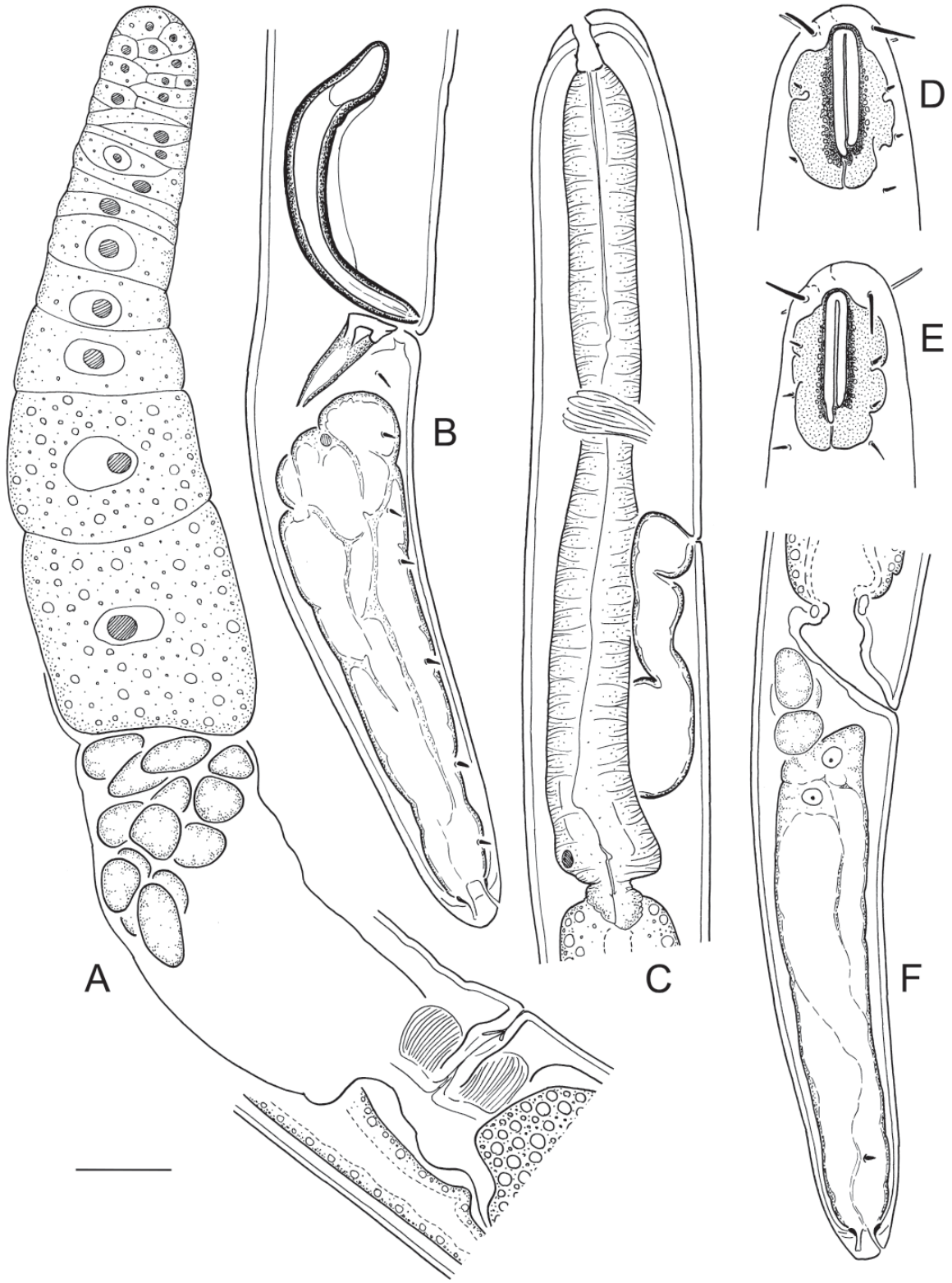

Fig. 1. *Neodiplopeltula incisa* (Southern, 1914) gen. et comb. nov. (SMNH-169255). **A**. Anterior part of female reproductive system. **B**. Male tail. **C**. Female pharyngeal region, optical median section. **D**. Female anterior end, surface view. **E**. Male anterior end, surface view. **F**. Female tail. Scale bar = 20 µm.

Description

Adult

Body cylindrical, posteriorly tapering in tail region, straight or weakly ventrally curved upon fixation. Cuticle finely transversely striated along entire body as seen under SEM (striation can be observed under LM but very fine and shallow and cannot be measured with confidence), except for visually smooth labial region and terminal part of tail; longitudinal striation not observed under the light

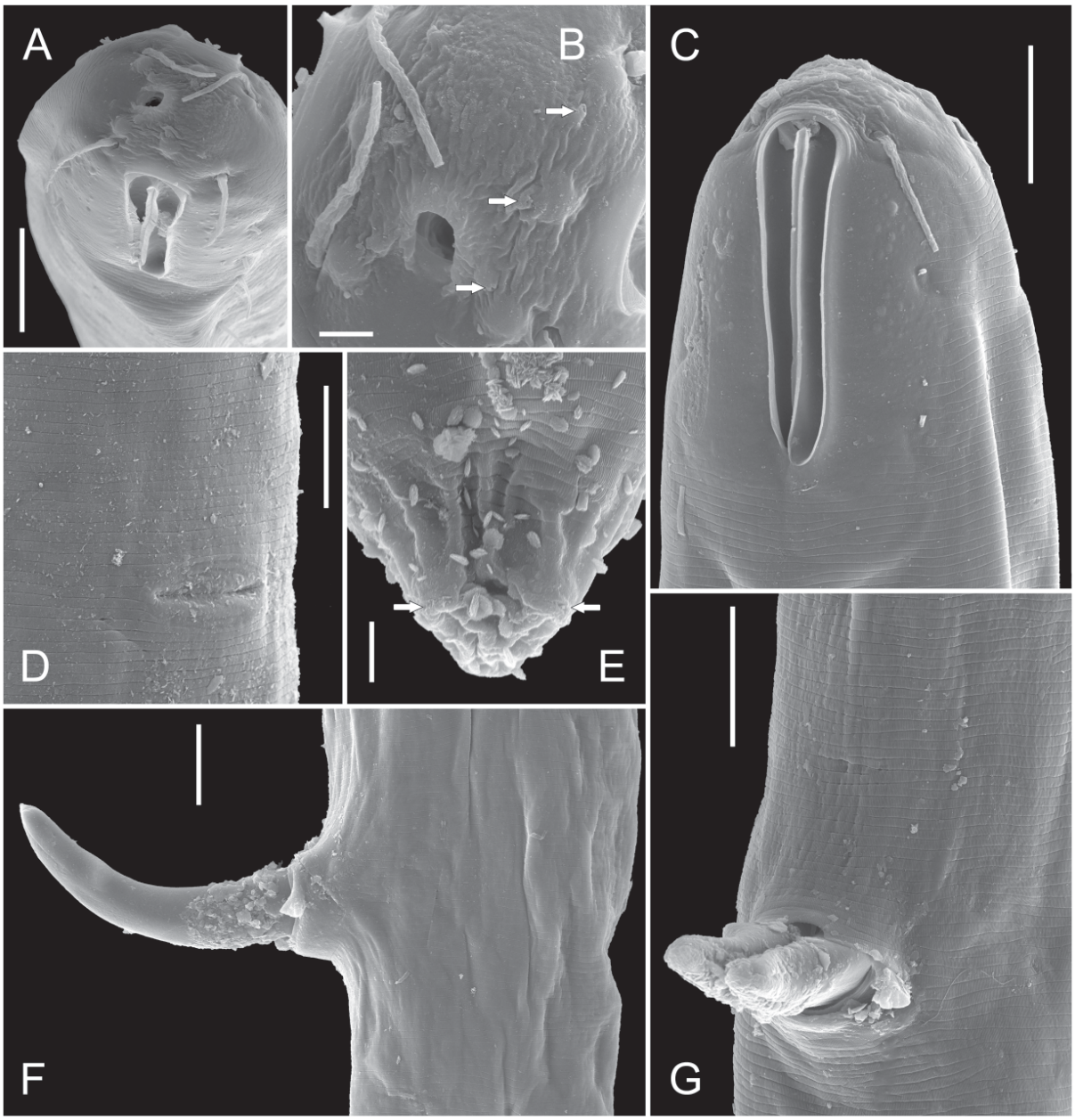

Fig. 2. *Neodiplopeltula incisa* (Southern, 1914) gen. et comb. nov., SEM micrographs. **A–C**, **F–G**. ♂. **D–E**. ♀. **A**. Male anterior end, semi-apical view, dorsal side to the left. **B**. Male labial region, semi-apical view, dorsal side down (arrows point at inner labial sensilla). **C**. Male anterior end, right lateral view. **D**. Vulval region. **E**. Tail terminus. **F**. Male cloacal region, lateral view. **G**. Male cloacal region, ventrosubventral view. Scale bars: A, C–D, F–G = 10 μm; B, E = 2 μm.

Table 2 (continued on next page). Measurements (in µm) of *Neodiplopeltula incisa* (Southern, 1914) gen. et comb. nov.

	original description		recent specimens	
	♀	2 ♂♂	5 ♀♀	4 ♂♂
Body length	2020	2100–2240	1740 ± 176 (1515–2001)	1748 ± 131 (1591–1908)
Body diameter (BD)	62	53–58	48 ± 7 (42–59)	45 ± 9 (34–53)
Pharynx length	270	250–270	204 ± 24 (186–245)	216 ± 31 (178–254)
Tail length	124	124–136	122 ± 10 (106–135)	133 ± 13 (116–147)
Anal body diameter (ABD)	45	50	35 ± 3 (32–39)	37 ± 1 (37–39.0)
a	36.7	38.6–39.6	36.9 ± 4.3 (30.0–40.8)	39.9 ± 6.1 (32.8–46.5)
b	7.5	8.3–8.4	8.6 ± 0.7 (7.7–9.6)	8.2 ± 0.6 (7.5–8.9)
c	16.3	16.5–17	14.4 ± 1.6 (12.4–16.8)	13.1 ± 0.4 (12.9–13.7)
c’	2.8	2.5	3.5 ± 0.3 (2.9–3.8)	3.6 ± 0.3 (3.2–3.9)
V(%) / T(%)	61	?	62.7 ± 0.4 (62.1–62.9)	45.8 ± 5.1 (40.4–51.6)
Labial region diameter	?	?	19.6 ± 1.6 (18.0–22.0)	20.9 ± 1.1 (20.0–22.0)
Cephalic setae length	?	?	10.6 ± 2.2 (8.0–14.0)	11.0 ± 1.0 (10.5–12.0)
Subdorsal cephalic setae from anterior end	?	?	7.2 ± 2.0 (5.5–10.5)	6.4 ± 0.8 (5.5–7.0)
Subventral cephalic setae from anterior end	?	?	7.2 ± 2.0 (5.5–10.5)	6.4 ± 0.8 (5.5–7.0)
Cephalic setae length / labial region diam.	?	?	0.5 ± 0.1 (0.4–0.8)	0.5
Anterior end of plate from anterior end	?	?	9.5 ± 1.0 (8.0–10.5)	10.0
Refractive plate length	?	?	31.4 ± 2.1 (28.0–33.0)	32.0 ± 1.1 (31.0–33.0)
Refractive plate width	?	?	23.6 ± 2.0 (21.0–25.0)	23.2 ± 0.8 (23.0–24.0)
Anterior end of amphid from anterior end	?	?	6.2 ± 1.2 (4.0–7.0)	6.4 ± 0.8 (5.5–7.0)
Dorsal amphid branch length	?	?	27.3 ± 1.8 (25.5–30.0)	28.5 ± 1.6 (27.6–30.4)
Ventral amphid branch length	?	?	25.4 ± 2.3 (22.0–27.0)	27.6 ± 0.7 (26.9–28.3)
Amphid width	?	?	5.7 ± 0.3 (5.5–6.0)	6.2 ± 0.7 (5.5–6.9)
Amphid length / width	?	?	4.8 ± 0.2 (4.6–5.0)	4.6 ± 0.3 (4.4–5.0)

Table 2 (continued).

	original description		recent specimens	
Stoma length	?	?	14.4 ± 1.8 (12.5–17.0)	16.3 ± 0.8 (16.0–17.0)
Stoma width	?	?	5.7 ± 0.3 (5.5–6.0)	6.0 ± 0.4 (5.5–6.0)
Nerve ring from anterior end	?	111–115	102 ± 10 (94–114)	106 ± 12 (91–120)
Nerve ring from anterior end (% pharynx)	?	42.6–44.4	49.7 ± 3.1 (46.5–53.8)	49.4 ± 1.7 (47.1–51.3)
Secretory-excretory pore from ant. end	?	?	118 ± 13 (108–140)	125 ± 19 (99–143)
Secr.-excr. pore from ant. end (% pharynx)	?	?	58.2 ± 1.4 (57.0–60.6)	57.8 ± 2.2 (55.8–60.4)
Vagina or spicules length	?	66	24.8 ± 3.3 (23.0–29.5)	77.5 ± 1.6 (75.0–79.0)
Vagina / BD or spicules / ABD	?	1.3	0.5	2.1 ± 0.1 (1.9–2.2)
Rectum or gubernaculum length	?	?	29.6 ± 3.2 (27.5–35.0)	12.3 ± 0.6 (11.5–12.5)
Rectum / ABD or apophysis length	?	?	0.8 ± 0.1 (0.8–0.9)	27.4 ± 1.3 (26.0–28.5)
Caudal gland openings from tail terminus	?	?	2.9 ± 0.7 (2.0–3.5)	2.0

microscope, but distinct under the scanning electron microscope, covers cuticle over entire body length. Somatic sensilla visible along pharyngeal region (cervical setae, see below) and on tail. Labial region bluntly rounded, lips fused. Refractive plates underlying cephalic cuticle around amphids present (periamphideal), extending from level of anteriormost edge of amphid posteriorly some distance behind posteriormost edge of amphid; refractive plates irregular in shape (with incised edges), not connected with each other on ventral and dorsal sides. Inner labial sensilla small pore-like, located on anterior surface of lips, discernible under SEM only. Outer labial sensilla papilliform, located on anterior surface of lips, clearly visible under SEM only. Cephalic sensilla setiform, bases of dorsosublateral setae located posterior to oral opening. Cervical sensilla papilliform, arranged in four sublateral rows starting at level with middle of amphid and ending at level with posterior edge of refractive plate, two or three per row. Amphids similar in shape and size between sexes: amphidial fovea inverted U-shape with dorsal branch 0.5–3.5 µm longer than ventral branch. Oral opening shifted towards dorsal side of body. Stoma barrel-shaped: cheilostom broad; gymnostom barrel-shaped, with weakly cuticularised walls; stegostom short conoid, its lining uniform with lining of pharynx. Pharyngeal tubes absent. Pharynx subcylindrical, muscular, with evenly distributed myofilaments, gradually expanding towards posterior end; not subdivided in distinct sections; pharyngeal lumen uniform in thickness along entire pharynx length; valves absent. Cardia ovoid, almost entirely embedded into intestinal tissue. Secretory-excretory system present; secretory-excretory pore located along ventral body line opposite to posterior $^{3}/_{5}^{th}$ of pharynx; secretory-excretory duct very short, leading from pore to ampulla; renette cell small, its body adjacent and ventral to posterior part of pharynx. Tail cylindro-conical with bluntly rounded terminus. Caudal glands opening via three separate subterminal openings, spinneret absent.

Female

Reproductive system didelphic, amphidelphic, ovary branches outstretched and symmetrical, on opposite sides of intestine. Anterior genital tube 248–280 µm long, situated to either right (n = 1) or left (n = 4) of intestine; posterior genital tube 224–259 µm long, situated to either left (n = 1) or right

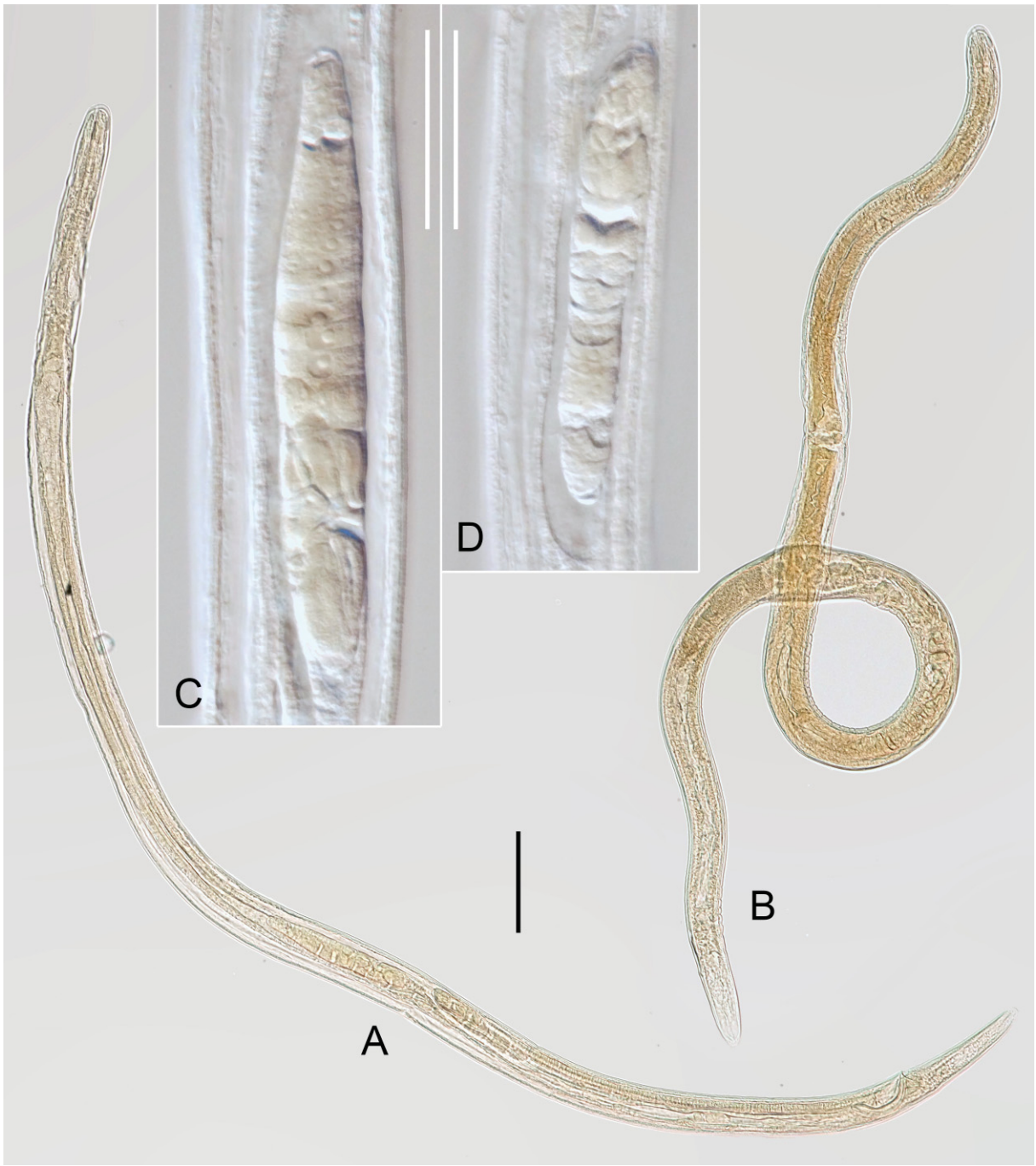

Fig. 3. *Neodiplopeltula incisa* (Southern, 1914) gen. et comb. nov. (SMNH-169255). **A**. ♂, entire specimen. **B**. ♀, entire specimen. **C**. Anterior testis. **D**. Posterior testis. Scale bars: A–B = 100 µm; C–D = 50 µm.

(n = 4) of intestine. Vulva a transverse slit, located posterior to midbody. Vagina straight, with developed sphincter muscle surrounding proximal part and distinct epiptygmata in distal part; *pars refringens vaginae* absent. Sack-like spermatheca present, filled with oval spermatozoa in fertilized specimens. Rectum short.

Male

Reproductive system diorchic, testes opposed; anterior testis 162–286 µm long, outstretched and posterior testis 117–162 µm long, reflexed. Spicules paired and symmetrical, strongly curved, with ovoid manubrium and subcylindrical shaft. Gubernaculum plate-like, with pair of strong, closely set caudal apophyses variable in shape (Fig. 4C–E). Caudal setae present, several ventrosublateral and dorsosublateral pairs arranged in rows along entire tail length (often difficult to observe).

Remarks

Despite the fact that the original description by Southern (1914) is rather brief, the present population closely resembles the type specimens in most morphological and morphometric features, including the shape of the refractive plates underlying the amphids (described as "shield shaped" with "front and lateral walls are notched"). Spicules are slightly shorter in the type specimens (66 µm vs 75–79 µm in recent specimens).

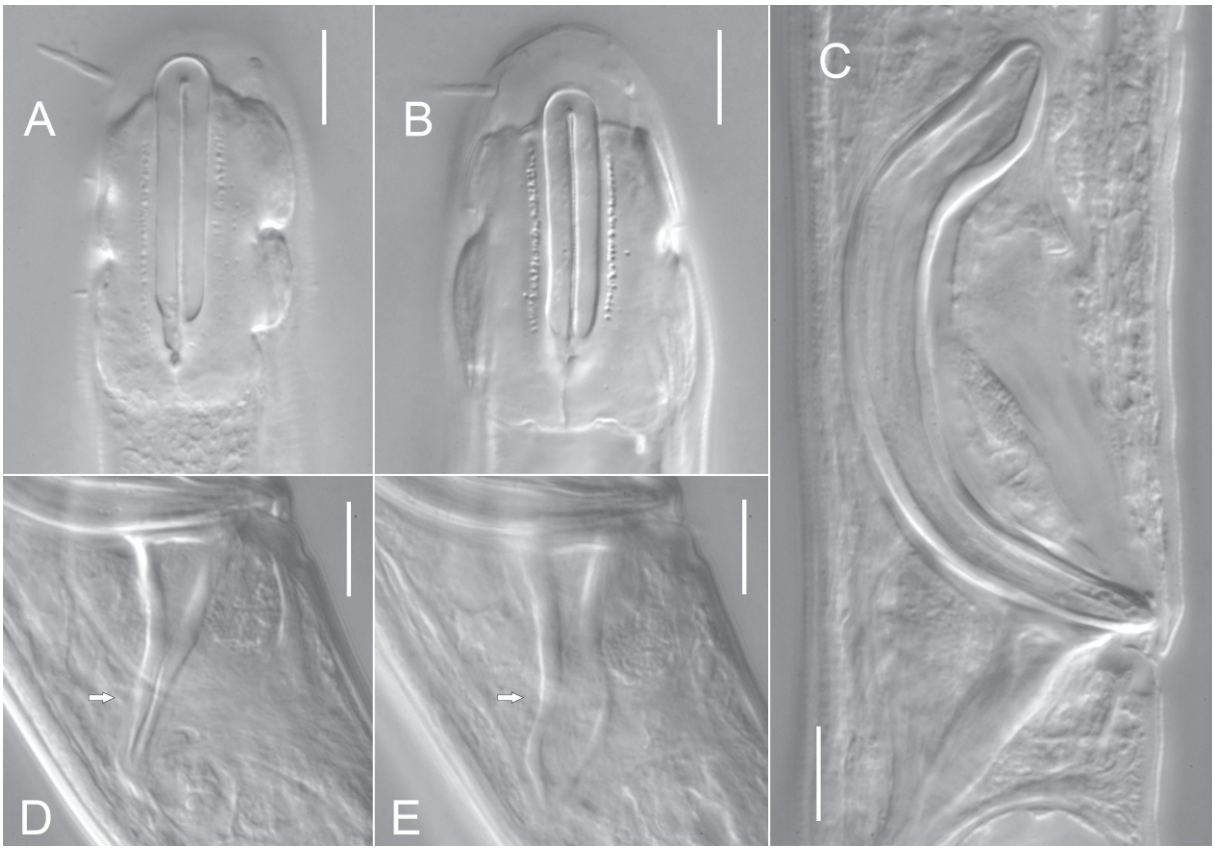

Fig. 4. *Neodiplopeltula incisa* (Southern, 1914) gen. et comb. nov. (SMNH-169255). **A**. Male anterior end, lateral view. **B**. Female anterior end, lateral view. **C**. Spicules and gubernaculum. **D–E**. Variability in the shape of gubernaculum apophyses in the same specimen (arrows). Scale bars = 10 µm.

Neodiplopeltula barentsi (Steiner, 1916) gen. et comb. nov.
Figs 5–7, 14–15; Table 3

Diagnosis (based on combined data)

Neodiplopeltula barentsi gen. et comb. nov. is characterised by a 0.94–1.67 mm long body; refractive plates underlying cephalic cuticle around amphids present, elongated ovoid in shape, not joined, 23.5–32 µm long and 12–16 µm wide; cephalic setae 3.5–7.5 µm long; amphidial fovea 21–32 µm long and 4–7 µm wide; oral opening 1–2 from anterior end, posterior to cephalic setae bases; secretory-excretory

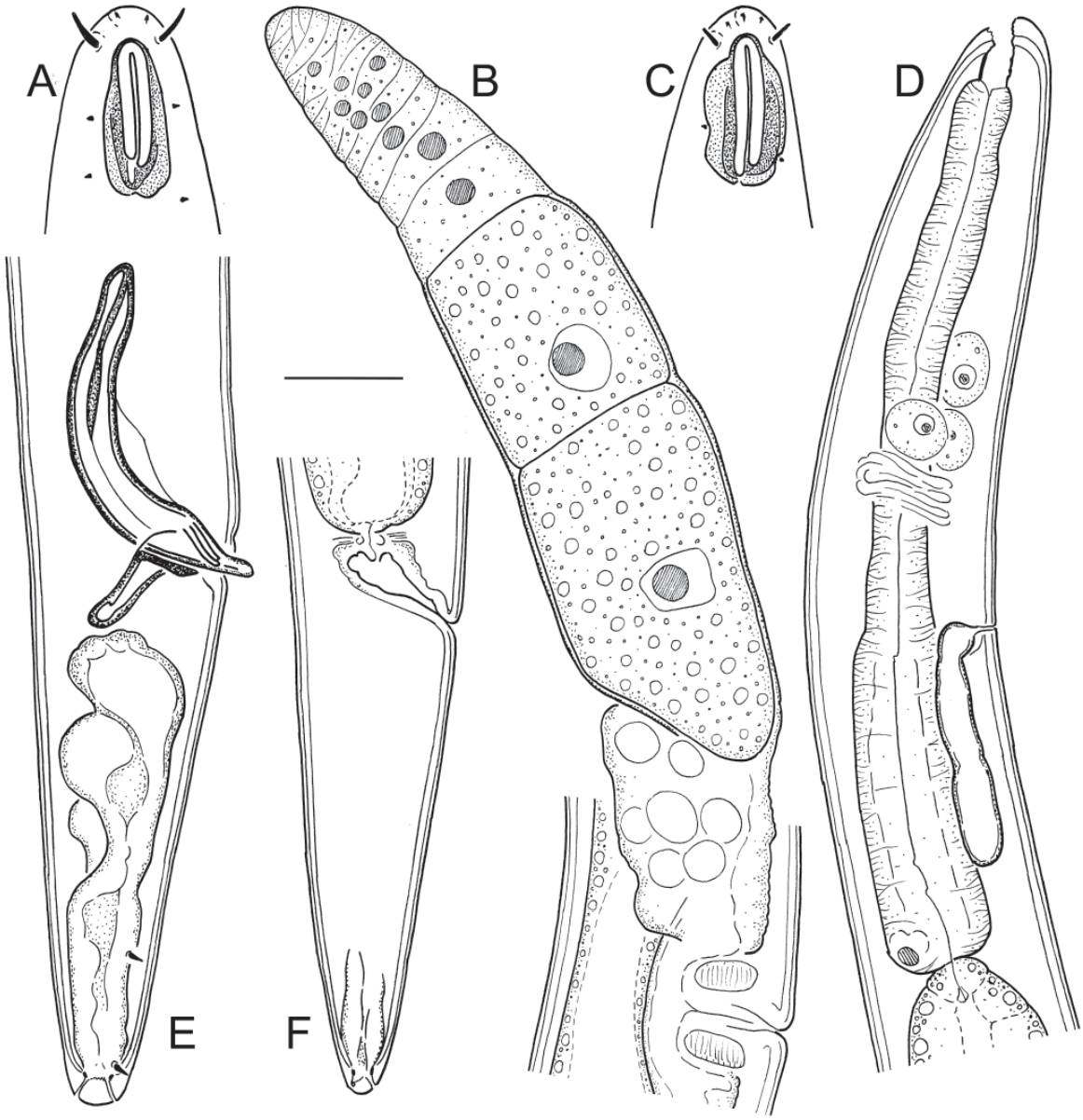

Fig. 5. *Neodiplopeltula barentsi* (Steiner, 1916) gen. et comb. nov. (SMNH-169268). **A**. Male anterior end, surface view. **B**. Anterior part of female reproductive system. **C**. Female anterior end, surface view. **D**. Female pharyngeal region, optical median section. **E**. Male tail. **F**. Female tail. Scale bar = 20 µm.

pore located opposite to posterior part of pharynx; tail 1.6–3.3 anal body diameters long; vagina with epiptygmata; spicules 45–73 µm long.

Material examined

SWEDEN: 1 ♀, 1 ♂, Skagerrak, 58°20′06″ N, 11°09′24″ E, muddy sediment at a deep of 53 m, 9 Aug. 2011, O. Holovachov leg. (SMNH-169264); 1 ♀, 1 ♂, Skagerrak, 58°22′19″ N, 11°04′55″ E, muddy sediment at a deep of 55–70 m, 9 Aug. 2011, O. Holovachov leg. (SMNH-169266); 3 ♀♀, 1 ♂, Gullmarn Fjord near Östersidan, 58°15′09″ N, 11°27′54″ E, shells, gravel sand and mud, 14 Aug. 2014, O. Holovachov leg. (SMNH-169268); 1 ♀ lectotype of *Diplopeltis asymmetricus*, Öresund, west of Valgrundet, at a deep of 30–36 m, *Zostera* and *Echinocardium*, 7 Aug. 1926 (SMNH Type-9015).

GREENLAND: 1 ♀, holotype of *Diplopeltis ovalis*, Godhavn, mud, 17 Aug. 1926, Reisinger and Steinböck leg. (NHMD 102171).

Description

Adult

Body cylindrical, posteriorly tapering in tail region, straight or weakly ventrally curved upon fixation. Cuticle finely transversely striated along entire body, except for visually smooth labial region and terminal

Fig. 6. *Neodiplopeltula barentsi* (Steiner, 1916) gen. et comb. nov. (SMNH-169268). **A**. ♂, entire specimen. **B**. ♀, entire specimen. **C**. Anterior testis. **D**. Posterior testis. Scale bars: A–B = 100 µm; C–D = 50 µm.

Table 3 (continued on next page). Measurements (in µm) of *Neodiplopeltula barentsi* (Steiner, 1916) gen. et comb. nov.

	original description	*D. ovalis*	*D. asymmetricus*	*D. onustus* sensu Sergeeva (1974)		data for *D. cuspidiboja*	recent specimens	
	♂	♀ holotype	♀ lectotype	♀	♂	♂	5 ♀♀	3 ♂♂
Body length	1526	1228	970	1057	1147	1147	1207 ± 258 (935–1532)	1487 ± 285 (1159–1670)
Body diameter (BD)	?	61	65	39	45	44	52 ± 13 (41–74)	55 ± 15 (38–65)
Pharynx length	205	197	159	169	180	175	176 ± 11 (168–193)	182 ± 15 (165–195)
Tail length	122	95	64	73	79	67	84 ± 8 (76–96)	98 ± 9 (91–108)
Anal body diameter (ABD)	?	38	40	22	34	32	35 ± 6 (29–43)	41 ± 6 (34–46)
a	?	20.1	14.9	26.8	25.5	26	23.3 ± 4.0 (19.1–29.6)	27.7 ± 2.9 (25.1–30.8)
b	7.4	6.2	6.1	6.3	6.4	7	6.8 ± 1.1 (5.5–8.0)	8.1 ± 1.0 (7.0–8.9)
c	12.5	12.9	15.2	14.5	13.6	17	14.3 ± 2.0 (12.0–16.0)	15.2 ± 2.6 (12.7–17.9)
c’	?	2.5	1.6	3.3	2.3	2.1	2.4 ± 0.3 (2.2–2.8)	2.4 ± 0.3 (2.1–2.7)
V(%) / T(%)	?	60.7	64.2	62.3	?	?	61.5 ± 1.9 (59.6–63.5)	48.1 ± 4.7 (43.6–53.1)
Labial region diameter	?	16	18	12	17	17	14.9 ± 0.8 (14.0–16.0)	15.0 ± 1.1 (14.0–16.0)
Cephalic setae length	?	?	?	7.5	7.5	4	5.5 ± 1.7 (3.5–7.5)	7.4 ± 0.4 (7.0–7.5)
Subdorsal cephalic setae from anterior end	?	?	?	?	?	11	6.6 ± 0.6 (5.5–7.0)	7.6 ± 0.7 (7.0–8.0)
Subventral cephalic setae from anterior end	?	?	?	?	?	9	6.5 ± 0.6 (5.5–7.0)	7.1 ± 0.4 (7.0–7.5)
Cephalic setae length / labial region diam.	?	?	?	?	?	?	0.4 ± 0.1 (0.2–0.5)	0.5
Anterior end of shield from anterior end	?	10	?	?	?	?	7.5 ± 0.6 (7.0–8.0)	10.0 ± 1.5 (9.0–11.0)
Refractive plate length	?	25	?	?	?	32	25.7 ± 1.5 (23.5–27.0)	24.5 ± 0.5 (24.0–25.0)
Refractive plate width	?	12	?	?	?	12.5	13.9 ± 1.3 (12.5–16.0)	15.2 ± 1.0 (14.5–16.0)
Anterior end of amphid from anterior end	?	7	6	?	?	6	5.5 ± 0.7 (5.0–6.0)	6.4 ± 1.1 (5.5–7.5)
Dorsal amphid branch length	?	26	26	29	29	32	23.3 ± 2.4 (21.0–25.5)	22.5 ± 1.1 (21.5–23.5)
Ventral amphid branch length	?	23	24	?	?	30	22.6 ± 1.6 (21.0–24.0)	21.9 ± 0.4 (21.5–22.0)
Amphid width	?	6	7	6	6	7	5.1 ± 0.6 (4.0–5.5)	5.8 ± 0.4 (5.5–6.0)
Amphid length / width	?	4.3	3.7	4.8	4.8	4.6	4.6 ± 0.9 (3.8–6.2)	3.9 ± 0.3 (3.7–4.3)
Anterior edge of stoma from anterior end	?	1	1	?	?	?	1.1 ± 0.4 (1.0–1.5)	1.4 ± 0.7 (1.0–2.0)

Table 3 (continued).

	original description	*D. ovalis*	*D. asymmetricus*	*D. onustus* sensu Sergeeva (1974)		data for *D. cuspidiboja*	recent specimens	
Stoma width	?	?	?	?	?	?	5.4 ± 0.6 (5.0–6.0)	5.3 ± 0.4 (5.0–5.5)
Nerve ring from anterior end	?	?	?	84	96	72	90 ± 5 (84–97)	96 ± 10 (86–104)
Nerve ring from anterior end (% pharynx)	?	?	?	?	?	41	51.1 ± 1.0 (50.3–52.7)	52.7 ± 0.8 (51.7–53.2)
Secretory-excretory pore from ant. end	?	115	?	?	?	104	109 ± 3 (106–112)	110 ± 7 (103–115)
Secr.-excr. pore from ant. end (% pharynx)	?	58.4	?	?	?	60	62.2 ± 2.8 (58.0–65.5)	60.3 ± 1.6 (59.1–62.1)
Vagina or spicules length	?	?	?	?	45	58	18.2 ± 1.1 (17.0–19.5)	63.8 ± 8.2 (57.0–73.0)
Vagina / BD or spicules / ABD	?	?	?	?	1.1	?	0.4 ± 0.1 (0.3–0.5)	1.6 ± 0.3 (1.3–1.8)
Rectum or gubernaculum length	?	?	?	?	?	20	23.7 ± 5.0 (20.5–32.0)	11.0 ± 0.7 (10.0–11.5)
Rectum / ABD or apophysis length	?	?	?	?	?	?	0.7 ± 0.1 (0.6–0.7)	18.6 ± 2.4 (16.0–20.5)
Caudal gland openings from tail terminus	?	?	?	?	?	3	2.0 ± 0.6 (1.0–2.0)	1.9 ± 0.7 (1.0–2.0)

part of tail (striation can be observed under LM but very fine and shallow and cannot be measured with confidence); longitudinal striation not observed. Somatic sensilla visible along pharyngeal region (cervical sensilla, see below) and on tail. Labial region bluntly rounded, lips fused. Refractive plates underlying cephalic cuticle around amphids present (periamphideal), extending from level of anteriormost edge of amphid posteriorly some distance behind posteriormost edge of amphid; refractive plates elongated ovoid in shape (plate edges not incised), not connected with each other on ventral and on dorsal sides. Inner labial sensilla indistinct. Outer labial sensilla papilliform, located on anterior surface of lips. Cephalic sensilla setiform, bases of dorsosublateral setae located posterior to oral opening. Cervical sensilla papilliform, arranged in four sublateral rows starting at level with middle of amphid and ending at level with posterior edge of refractive plate, one or two per row. Amphids similar in shape and size between sexes: amphidial fovea inverted U-shape with dorsal branch usually 0.5–2.0 µm longer than ventral branch (in two specimens ventral branch 0.5–1.0 µm longer than dorsal branch). Oral opening shifted towards dorsal side of body. Stoma barrel-shaped: cheilostom broad; gymnostom subcylindrical, with weakly cuticularised walls; stegostom short conoid, its lining uniform with lining of pharynx. Pharyngeal tubes absent. Pharynx subcylindrical, muscular, with evenly distributed myofilaments, gradually expanding towards posterior end; not subdivided in distinct sections; pharyngeal lumen uniform in thickness along entire pharynx length; valves absent. Cardia ovoid, entirely embedded into intestinal tissue. Secretory-excretory system present; secretory-excretory pore along ventral body line opposite to $^{3}/_{5^{th}}$ of pharynx; secretory-excretory duct very short, leading from pore to ampulla; renette cell small, its body adjacent and ventral to posterior part of pharynx. Tail conoid with bluntly rounded terminus. Caudal glands opening via three separate subterminal openings, spinneret absent.

Female

Reproductive system didelphic, amphidelphic, ovary branches outstretched and symmetrical, on opposite sides of intestine. Anterior genital tube 179–269 µm long, situated to either right (n = 3) or left (n = 2) of

intestine; posterior genital tube 173–286 µm long, situated to either left (n = 3) or right (n = 2) of intestine. Vulva transverse slit, located posterior to midbody. Vagina straight, with developed sphincter muscle surrounding proximal part and distinct epiptygmata in distal part; *pars refringens vaginae* absent. Sack-like spermatheca present, filled with oval spermatozoa in fertilized specimens. Rectum short.

Male

Reproductive system diorchic, testes opposed; anterior testis 145–314 µm long, outstretched and posterior testis 117–207 µm long, reflexed. Spicules paired and symmetrical, strongly curved, with weakly defined elongated manubrium and shaft, cylindrical along most of its length. Gubernaculum plate-like, with pair of strong, closely set caudal apophyses variable in shape (Fig. 7C–E). Caudal setae present, several ventrosublateral and dorsosublateral pairs arranged in rows along entire tail length (often difficult to observe).

Remarks

The original description of this species by Steiner (1916) is rather short, with a few measurements given. The present population has a shorter pharynx and tail compared to the type specimen, but in all other respects both match very well, including the position of the oral opening and the shape of the underlying refractive plates.

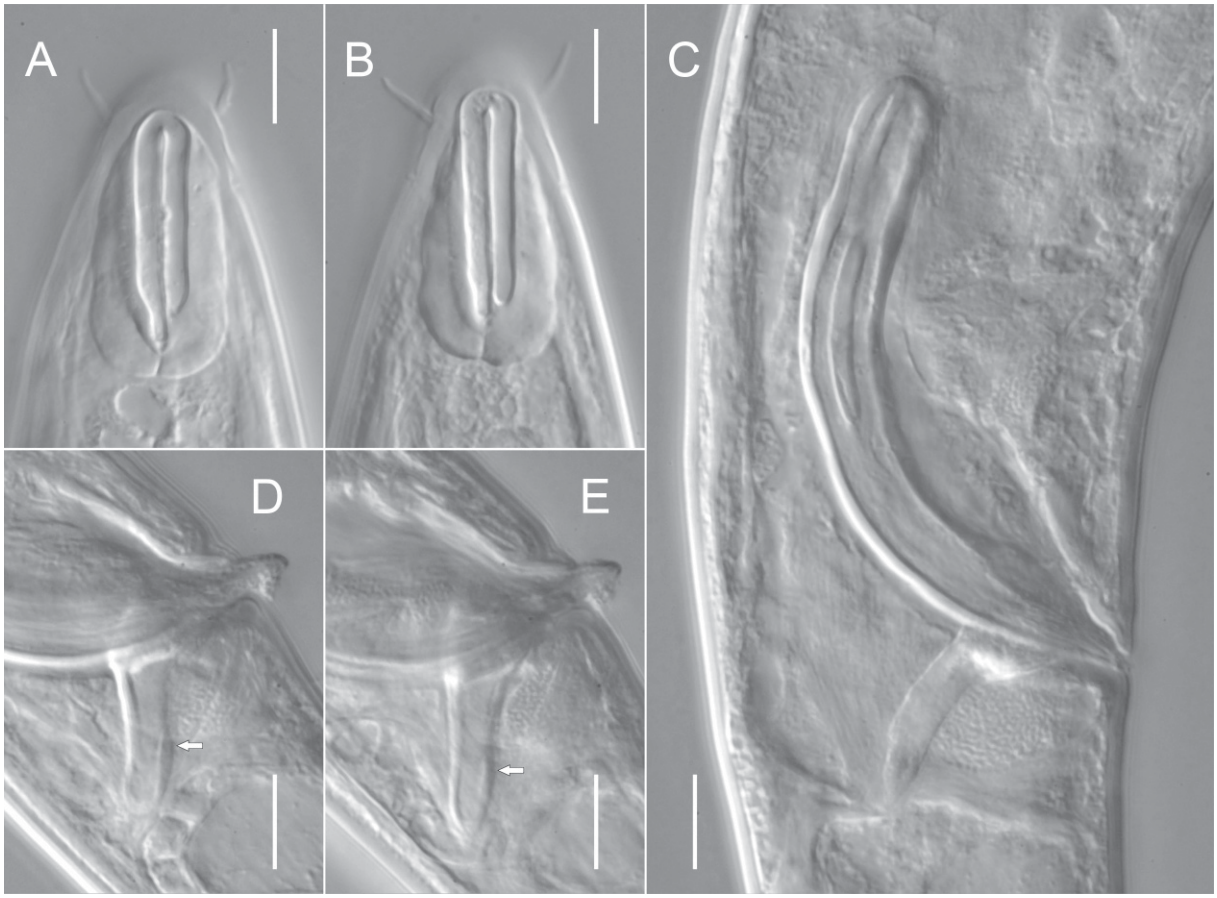

Fig. 7. *Neodiplopeltula barentsi* (Steiner, 1916) gen. et comb. nov. (SMNH-169266 and SMNH-169268). **A**. Female anterior end, lateral view. **B**. Male anterior end, lateral view. **C**. Spicules and gubernaculum. **D–E**. Variability in the shape of thegubernaculum apophyses in the same specimen (arrows). Scale bars = 10 µm.

Neodiplopeltula onusta (Wieser, 1956) gen. et comb. nov.
Figs 8–10; Table 4

Diagnosis (based on combined data)

Neodiplopeltula onusta gen. et comb. nov. is characterised by a 0.99–1.48 mm long body; refractive plates underlying cephalic cuticle around amphids present and joined, 32.5–48 µm long and 18.5–24 µm wide; cephalic setae 3–6.5 µm long; amphidial fovea 32–44 µm long and 5–8 µm wide; oral opening

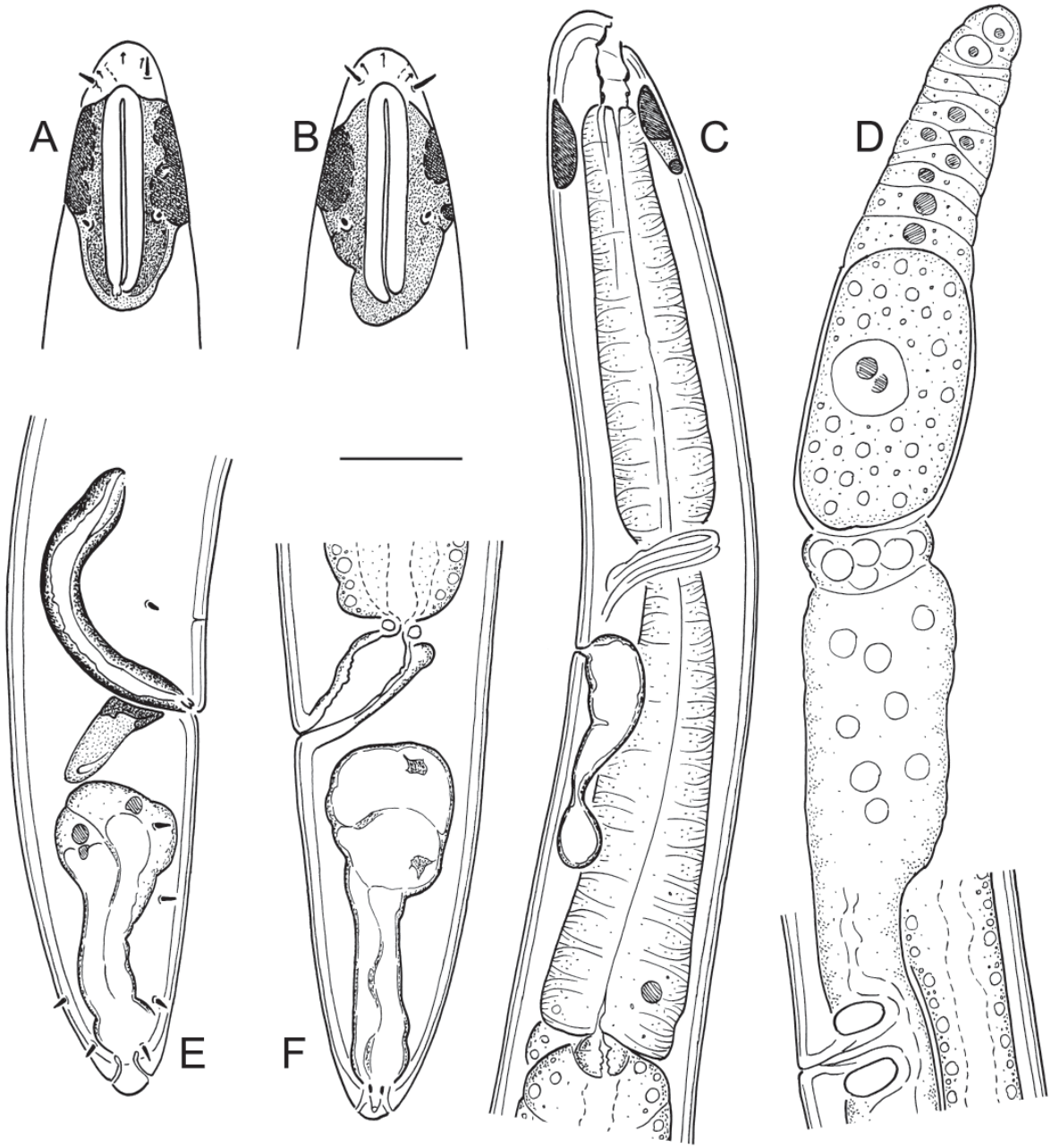

Fig. 8. *Neodiplopeltula onusta* (Wieser, 1956) gen. et comb. nov. (SMNH-169282). **A**. Male anterior end, surface view. **B**. Female anterior end, surface view. **C**. Female pharyngeal region, optical median section. **D**. Anterior part of female reproductive system. **E**. Male tail. **F**. Female tail. Scale bar = 20 µm.

Table 4 (continued on next page). Measurements (in µm) of *Neodiplopeltula onusta* (Wieser, 1956) gen. et comb. nov.

	original description	data for *Diplopeltula tchesunovi*		recent specimens	
	♀	4 ♀♀	3 ♂♂	4 ♀♀	3 ♂♂
Body length	990	1348–1481	1003–1323	1064 ± 104 (947–1199)	1056 ± 50 (999–1094)
Body diameter (BD)	?	65–88	48–58	47 ± 9 (38–55)	46 ± 7 (39–53)
Pharynx length	?	201–223	172–212	170 ± 17 (149–187)	174 ± 15 (159–189)
Tail length	?	75–77	65–81	58 ± 7 (51–68)	74 ± 12 (65–88)
Anal body diameter (ABD)	?	44–52	37–41	34 ± 3 (32–37)	37 ± 3 (34–39)
a	26	17–23	21–23	23.6 ± 5.9 (19.3–31.9)	23.4 ± 4.4 (20.5–28.4)
b	5.1	6.3–7.3	5.9–6.3	6.3 ± 0.8 (5.3–7.2)	6.1 ± 0.3 (5.8–6.3)
c	14.2	17.5–19.2	12.5–17.4	18.7 ± 3.1 (15.2–21.4)	14.6 ± 2.8 (11.4–16.9)
c’	1.7	?	?	1.7 ± 0.3 (1.4–2.2)	2.0 ± 0.2 (1.8–2.3)
V(%) / T(%)	65.4	65.1–67.6	?	66.1 ± 1.5 (64.7–68.0)	41.0 ± 7.9 (35.4–46.6)
Labial region diameter	15	12–16.5	14–15	11.2 ± 1.7 (9.0–13.0)	12.0 ± 0.8 (11.0–12.5)
Cephalic setae length	6.5	3.5–5.4	3.5–4.5	4.0 ± 1.2 (3.0–5.5)	3.9 ± 0.8 (3.5–5.0)
Subdorsal cephalic setae from anterior end	8	?	?	6.4 ± 0.7 (5.5–7.0)	7.4 ± 1.1 (6.0–8.0)
Subventral cephalic setae from anterior end	?	?	?	5.9 ± 0.7 (5.0–6.0)	6.2 ± 0.7 (5.5–7.0)
Cephalic setae length / labial region diam.	?	?	?	0.4 ± 0.1 (0.3–0.5)	0.3 ± 0.1 (0.3–0.4)
Anterior end of shield from anterior end	?	?	?	9.2 ± 0.4 (9.0–10.0)	10.1 ± 0.4 (10.0–10.5)
Refractive plate length	?	45–48	41–47	36.1 ± 3.2 (32.5–38.0)	35.0 ± 1.1 (34.0–36.0)
Refractive plate width	?	20–24	19–20	21.6 ± 1.5 (19.0–23.0)	20.0 ± 1.4 (18.5–21.5)
Anterior end of amphid from anterior end	?	4–7	5–7	5.9 ± 0.9 (5.0–7.0)	7.4 ± 0.8 (7.0–8.0)
Dorsal amphid branch length	40	41–44	36–43	36.2 ± 2.6 (32.5–38.0)	35.9 ± 0.7 (35.0–36.5)
Ventral amphid branch length	40	39–43	34–41	35.0 ± 2.5 (32.0–37.0)	34.3 ± 1.1 (33.0–35.0)
Amphid width	8	5–7	5–6	6.6 ± 0.9 (5.5–7.5)	6.7 ± 0.4 (6.0–7.0)

Table 4 (continued).

	original description	data for *Diplopeltula tchesunovi*		recent specimens	
Amphid length / width	?	?	?	5.6 ± 0.7 (5.0–6.6)	5.4 ± 0.2 (5.2–5.7)
Anterior edge of stoma from anterior end	?	5	5	2.8 ± 0.8 (2.0–3.5)	3.7 ± 1.1 (3.0–5.0)
Stoma length	?	?	?	13.6 ± 0.7 (13.0–14.5)	13.6 ± 0.4 (13.0–14.0)
Stoma width	?	?	?	4.8 ± 0.6 (4.0–5.5)	5.0
Nerve ring from anterior end	?	96–106	90–103	92 ± 6 (84–96)	95 ± 6 (91–102)
Nerve ring from anterior end (% pharynx)	?	?	?	54.4 ± 2.9 (50.5–56.8)	54.3 ± 2.6 (52.0–57.1)
Secretory-excretory pore from ant. end	115	110–125	85–87	104 ± 8 (95–112)	107 ± 4 (103–112)
Secr.-excr. pore from ant. end (% pharynx)	66	?	?	61.1 ± 2.9 (57.0–63.5)	61.7 ± 2.9 (59.3–64.8)
Vagina or spicules length	?	35–40	62–72	19.7 ± 2.7 (16.5–23.0)	63.7 ± 11.8 (56.5–77.0)
Vagina / BD or spicules / ABD	?	?	1.3–1.5	0.4 ± 0.1 (0.3–0.6)	1.7 ± 0.3 (1.5–2.0)
Rectum or gubernaculum length	?	?	15–20	24.1 ± 3.6 (21.0–28.0)	10.0 ± 0.5 (10.0–10.5)
Rectum / ABD or apophysis length	?	?	?	0.7 ± 0.1 (0.6–0.9)	16.1 ± 1.1 (15.0–17.0)
Caudal gland openings from tail terminus	?	?	?	terminal	terminal

2–5 from anterior end, at level with cephalic setae bases; secretory-excretory pore located opposite to posterior part of pharynx; tail 1.4–2.3 anal body diameters long; vagina with epiptygmata; spicules 52–77 μm long.

Material examined

SWEDEN: 1 ♀, Skagerrak, 58°19′15.6″–20.9″ N, 10°29′33.5″–34.0″ E, soft bottom at a deep of 352–374 m, 10 Sep. 2012, "Inventering Bratten" leg. (SMNH-169284); 1 ♂, Skagerrak, 58°23′00.8″–22′00.8″ N, 10°20′28.8″–38.3″ E, soft bottom at a deep of 390–428 m, 10 Sep. 2012, "Inventering Bratten" leg. (SMNH-169280); 1 ♂, Skagerrak, 58°28′21.2″–19.2″ N, 10°29′35.6″–43.6″ E, soft bottom at a deep of 248–316 m, 11 Sep. 2012, "Inventering Bratten" leg. (SMNH-169281); 3 ♀♀, 1 ♂, Skagerrak, 58°27′36.7″–43.3″ N, 10°32′52.0″–59.4″ E, soft bottom at a deep of 232–240 m, 12 Sep. 2012, "Inventering Bratten" leg. (SMNH-169282 – SMNH-169283).

Description

Adult

Body cylindrical, posteriorly tapering in tail region, straight or weakly ventrally curved upon fixation. Cuticle finely transversely striated along entire body, except for visually smooth labial region and terminal part of tail (striation can be observed under LM but very fine and shallow and cannot be measured with

confidence); longitudinal striation not observed. Somatic sensilla visible along pharyngeal region (cervical setae, see below) and on tail. Labial region bluntly rounded, lips fused. Refractive plates underlying cephalic cuticle around amphids present (periamphideal), extending from level of anteriormost edge of amphid posteriorly some distance behind posteriormost edge of amphid; refractive plates connected with each other on ventral and on dorsal sides. Inner labial sensilla indistinct. Outer labial sensilla papilliform, located on anterior surface of lips. Cephalic sensilla setiform, bases of dorsosublateral setae located at level with oral opening. Cervical sensilla papilliform, arranged in four sublateral rows at level with amphid, one or two per row. Amphids similar in shape and size between sexes: amphidial fovea inverted U-shape with dorsal branch 1.0–2.0 µm longer than ventral branch. Oral opening shifted towards dorsal side of body. Stoma subcylindrical: cheilostom broad; gymnostom barrel-shaped, with weakly cuticularised walls; stegostom short conoid, its lining uniform with lining of pharynx. Pharyngeal tubes absent. Pharynx subcylindrical, muscular, with evenly distributed myofilaments, gradually expanding towards posterior end; not subdivided in distinct sections; pharyngeal lumen uniform in thickness along

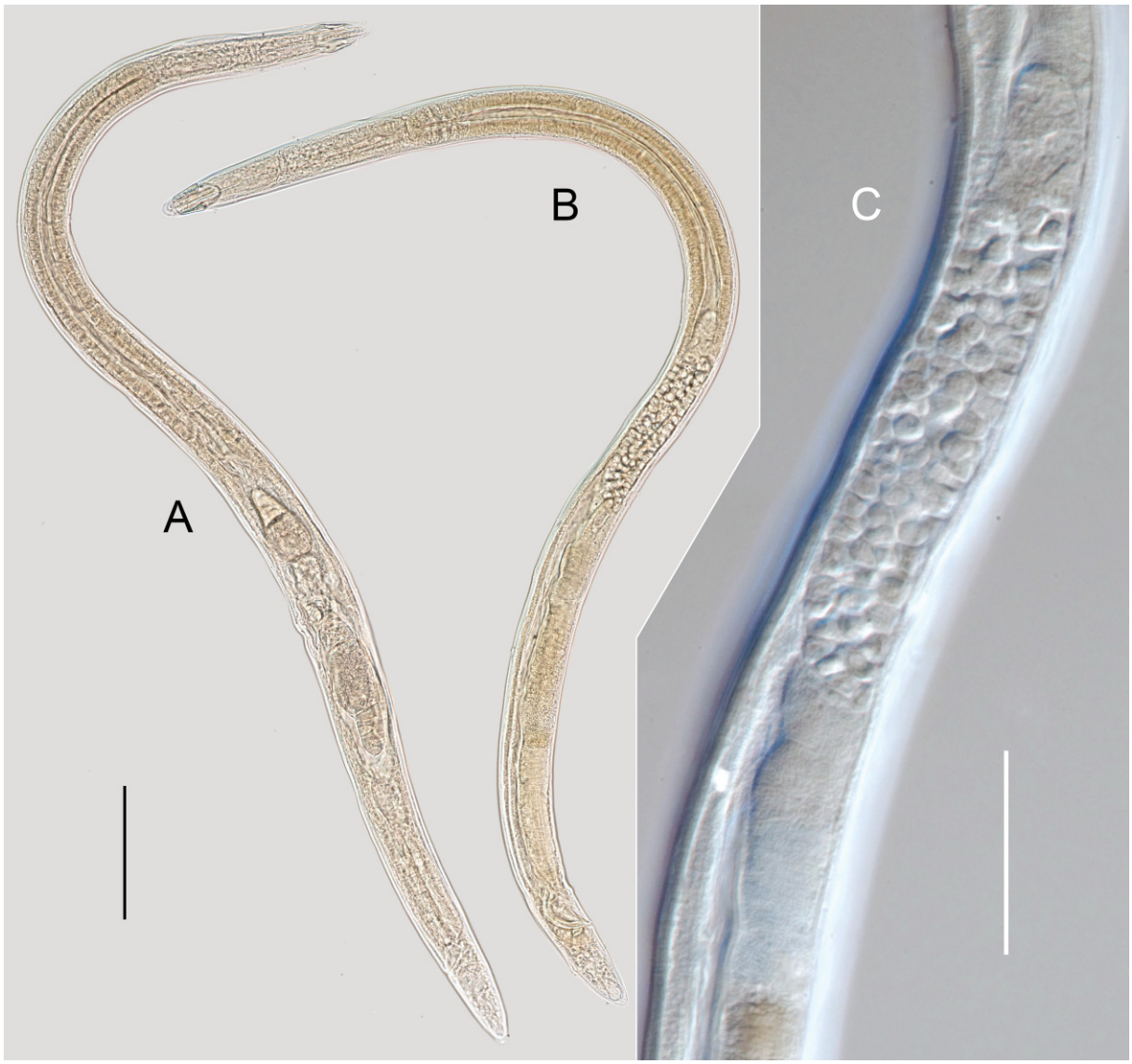

Fig. 9. *Neodiplopeltula onusta* (Wieser, 1956) gen. et comb. nov. (SMNH-169282). **A**. ♀, entire specimen. **B**. ♂, entire specimen. **C**. Testes. Scale bars: A–B = 100 µm; C = 50 µm.

entire pharynx length; valves absent. Secretory-excretory system present; secretory-excretory pore located along ventral body line opposite to $^{3}/_{5}^{th}$ of pharynx; secretory-excretory duct very short, leading from pore to ampulla; renette cell small, its body adjacent and ventral to posterior part of pharynx. Tail conoid with bluntly rounded terminus. Caudal glands opening via three separate subterminal openings, spinneret absent.

Female

Reproductive system didelphic, amphidelphic, ovary branches outstretched and symmetrical, on opposite sides of intestine. Anterior genital tube 109–180 μm long, situated to either right (n = 3) or left (n = 1) of intestine; posterior genital tube 109–145 μm long, situated to either left (n = 3) or right (n = 1) of intestine. Vulva transverse slit, located posterior to midbody. Vagina straight, with developed sphincter muscle surrounding proximal part and distinct epiptygmata in distal part; *pars refringens vaginae* absent. Sack-like spermatheca present, filled with oval spermatozoa in fertilized specimens. Rectum short.

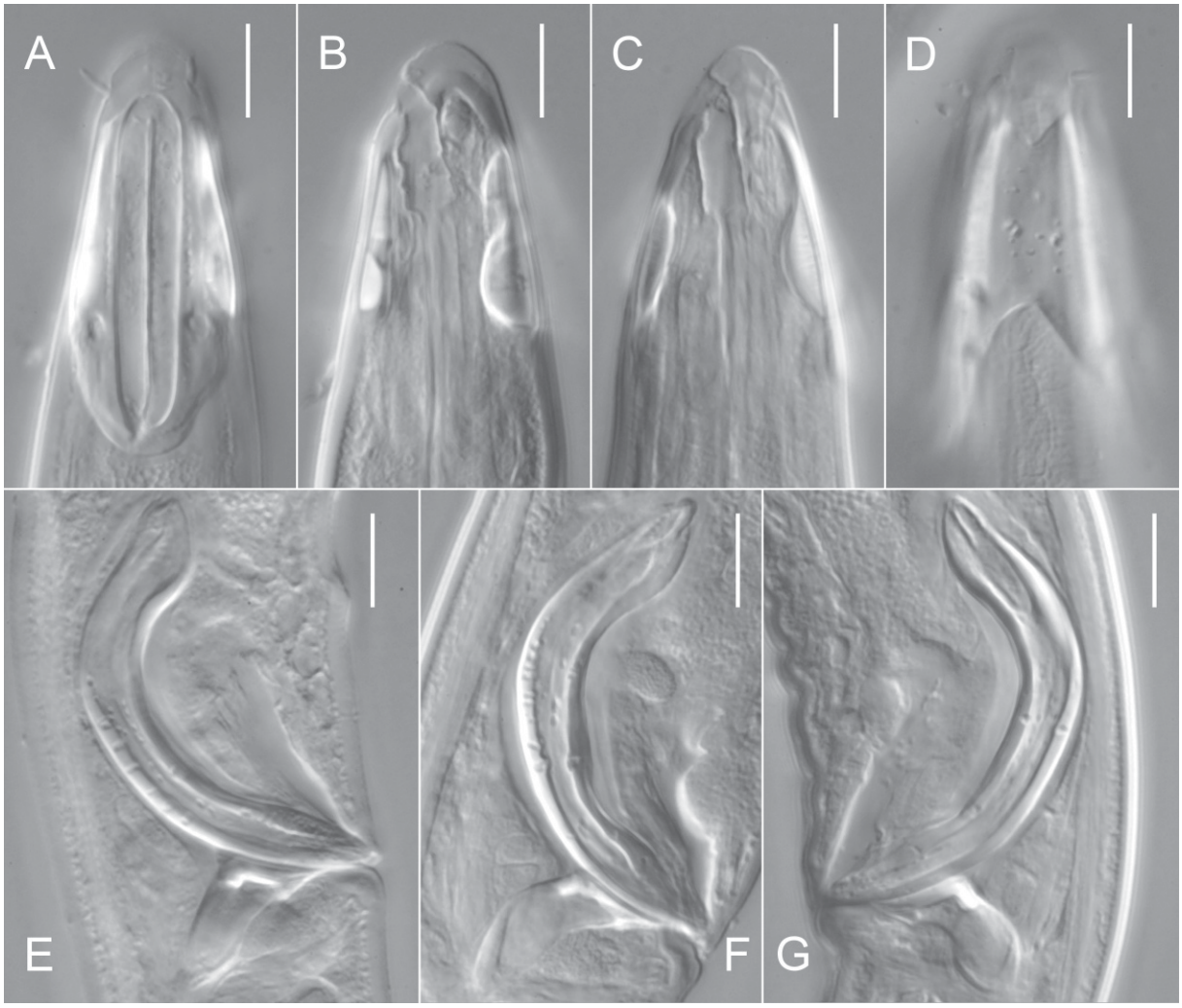

Fig. 10. *Neodiplopeltula onusta* (Wieser, 1956) gen. et comb. nov. (SMNH-169282). **A**. Male anterior end, lateral view. **B**. Male stoma, lateral view. **C**. Female stoma, lateral view. **D**. Male anterior end, dorsal view. **E–G**. Variability in the shape of spicules and gubernaculum in different specimens. Scale bars = 10 μm.

Male

Reproductive system diorchic, testes opposed; anterior testis outstretched and posterior testis reflexed (poorly discernible in most specimens due to highly granular and dark content of overlapping intestine and cannot be measured). Spicules paired and symmetrical, strongly curved, with elongated ovoid manubrium and subcylindrical shaft. Gubernaculum plate-like, with pair of strong closely set caudal apophyses variable in shape (Fig. 10E–G). Caudal setae present, several ventrosublateral and dorsosublateral pairs arranged in rows along entire tail length.

Remarks

The single female used by Wieser (1956) to describe this species has a slightly broader labial region and longer cephalic setae than the population from Sweden, but the specimens described under the name *Diplopeltula tchesunovi* fill this gap. The position of the oral opening is at level with the cephalic setae bases and the shape of the refractive plates underlying the cephalic cuticle around the amphids (joined along the dorsal and ventral body sides) in both type female and recent specimens are identical and confirm the conspecificity.

Neodiplopeltula bathmanni (Jensen, 1991) gen. et comb. nov.
Figs 11–13; Table 5

Diagnosis (based on combined data)

Neodiplopeltula bathmanni gen. et comb. nov. is characterised by a 0.85–2.08 mm long body; refractive plates underlying cephalic cuticle around amphids present, not joined, 19–29 µm long and 12–16.5 µm wide; cephalic sensilla 2–3.5 µm long; amphidial fovea 20–32 µm long and 4–7 µm wide; oral opening 6–16 µm from anterior end, at level with or posterior to cephalic setae bases; secretory-excretory pore located opposite to posterior part of pharynx; tail 1.5–2.2 anal body diameters long; vagina with epiptygmata; spicules 52–66 µm long.

Material examined

SWEDEN: 1 ♀, 4 ♂♂, Skagerrak, 58°19′15.6″–20.9″ N, 10°29′33.5″–34.0″ E, soft bottom at a deep of 352–374 m, 10 Sep. 2012, "Inventering Bratten" leg. (SMNH-169274 and SMNH-169284); 1 ♀, Skagerrak, 58°22′17.8″–19.4″ N, 10°23′50.8″–24′03.2″ E, soft bottom at a deep of 351–387 m, 10 Sep. 2012, "Inventering Bratten" leg. (SMNH-169275); 1 ♀, 1 ♂, Skagerrak, 58°34′21.3″–16.6″ N, 10°38′11.2″–29.4″ E, soft bottom at a deep of 139–153 m, 12 Sep. 2012, "Inventering Bratten" leg. (SMNH-169277).

Description

Adult

Body cylindrical, posteriorly tapering in tail region, straight or weakly ventrally curved upon fixation. Cuticle finely transversely striated along entire body, except for visually smooth labial region and terminal part of tail (striation can be observed under LM but very fine and shallow and cannot be measured with confidence); longitudinal striation not observed. Somatic sensilla visible along pharyngeal region (cervical setae, see below) and on tail. Labial region bluntly rounded, lips fused. Refractive plates underlying cephalic cuticle around amphids present (periamphideal), extending from level of anteriormost edge of amphid posteriorly some distance behind the posteriormost edge of amphid; refractive plates are elongated ovoid in shape (plate edges not incised), not connected with each other on ventral and on dorsal sides. Inner labial sensilla indistinct. Outer labial sensilla papilliform, located on anterior surface of lips. Cephalic sensilla setiform, bases of dorsosublateral setae located at level with or anterior to oral opening. Cervical sensilla absent; small papilliform somatic sensilla visible posterior to amphid and refractive plate. Amphids similar in shape and size between sexes: amphidial

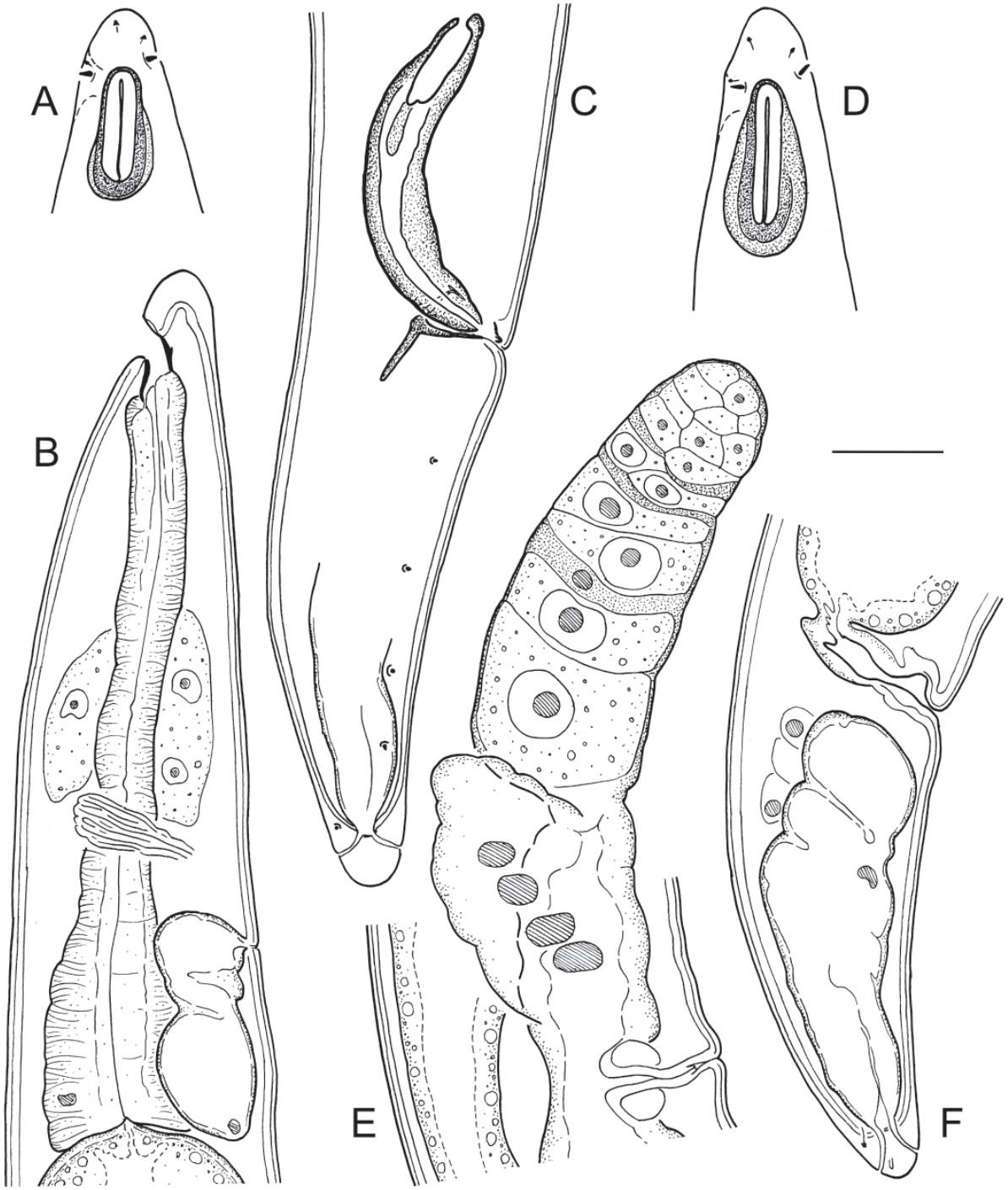

Fig. 11. *Neodiplopeltula bathmanni* (Jensen, 1991) gen. et comb. nov. (♂ SMNH-169274 and ♀ SMNH-169277). **A**. Female anterior end, surface view. **B**. Female pharyngeal region, optical median section. **C**. Male tail. **D**. Male anterior end, surface view. **E**. Anterior part of female reproductive system. **F**. Female tail. Scale bar = 20 μm.

fovea inverted U-shape branches unequal in length with either dorsal or ventral branch 1.0–2.0 µm longer than opposite branch. Oral opening shifted towards dorsal side of body. Stoma subcylindrical: cheilostom broad; gymnostom barrel-shaped, with weakly cuticularised walls; stegostom short conoid, its lining uniform with lining of pharynx. Pharyngeal tubes absent. Pharynx subcylindrical, muscular, with evenly distributed myofilaments, gradually expanding towards posterior end; not subdivided in distinct sections; pharyngeal lumen uniform in thickness along entire pharynx length; valves absent. Secretory-excretory system present; secretory-excretory pore located along ventral body line opposite to $^{4}/_{5}^{th}$ of pharynx; secretory-excretory duct very short, leading from pore to ampulla; renette cell small, its body adjacent and ventral to posterior part of pharynx. Tail conoid with bluntly rounded terminus. Caudal glands opening via three separate subterminal openings, spinneret absent.

Female

Reproductive system didelphic, amphidelphic, ovary branches outstretched and symmetrical, on opposite sides of intestine. Anterior genital tube 97–242 µm long, situated to either right (n = 2) or left (n = 1) of

Fig. 12. *Neodiplopeltula bathmanni* (Jensen, 1991) gen. et comb. nov. (♂ SMNH-169274 and ♀ SMNH-169277). **A**. ♂, entire specimen. **B**. ♀, entire specimen. **C**. Anterior testis. **D**. Posterior testis. Scale bars: A–B = 100 µm: C–D = 50 µm.

intestine; posterior genital tube 103–245 µm long situated to either left (n = 2) or right (n = 1) of intestine. Vulva transverse slit, located posterior to midbody. Vagina straight, with developed sphincter muscle surrounding proximal part and distinct epiptygmata in distal part; *pars refringens vaginae* absent. Sack-like spermatheca present, filled with oval spermatozoa in fertilized specimens. Rectum short.

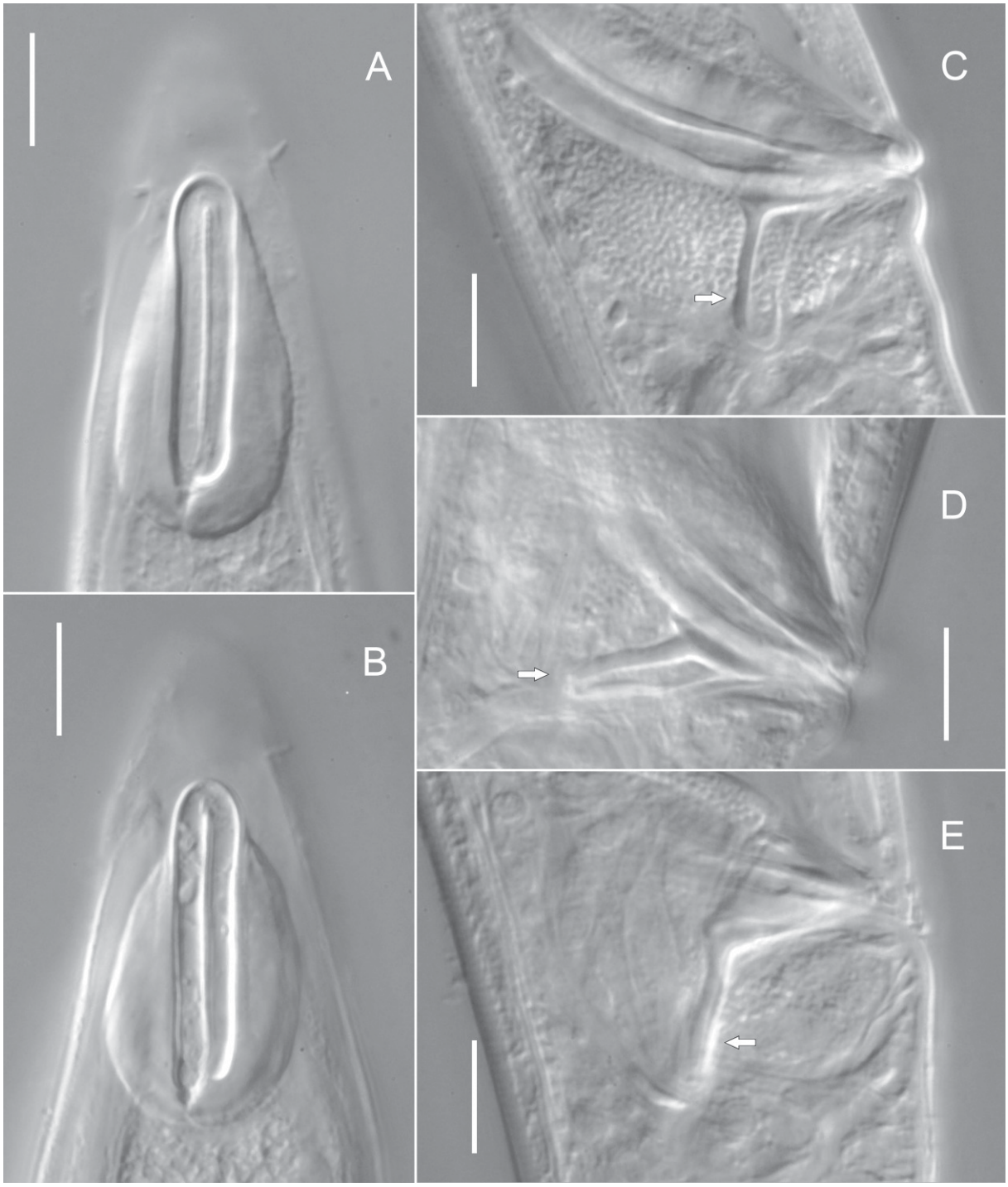

Fig. 13. *Neodiplopeltula bathmanni* (Jensen, 1991) gen. et comb. nov. (SMNH-169274 and SMNH-169277). **A**. Male anterior end, lateral view. **B**. Female anterior end, lateral view. **C–E**. Variability in the shape of gubernaculum apophyses in different specimens (arrows). Scale bars = 10 µm.

Table 5 (continued on next page). Measurements (in µm) of *Neodiplopeltula bathmanni* (Jensen, 1991) gen. et comb. nov.

	original description		**data for *D. cuspidiboja***	***D. incisa* sensu Vitiello, 1972**		**recent specimens**	
	2 ♀♀	2 ♂♂	1 ♀	♀	♂	3 ♀♀	5 ♂♂
Body length	1300–1420	1150–1240	2076	853	1138	1467 ± 92 (1366–1546)	1442 ± 193 (1270–1673)
Body diameter (BD)	52–57	43–47	98	?	?	71 ± 10 (60–78)	51 ± 8 (43–60)
Pharynx length	150–189	154–170	165	?	?	154 ± 5 (148–157)	151 ± 14 (139–171)
Tail length	82–88	77–91	98	60	72	84 ± 4 (81–89)	84 ± 8 (76–96)
Anal body diameter (ABD)	40	43	67	?	?	46 ± 5 (40–50)	42 ± 6 (35–48)
a	25	24–29	21	21.8	27.3	20.7 ± 1.7 (19.2–22.6)	28.6 ± 2.4 (25.3–30.6)
b	7.5–8.7	7.3–7.4	13	6.3	9.1	9.5 ± 0.9 (8.7–10.4)	9.6 ± 0.8 (8.6–10.6)
c	14.2–17.3	13.6–15.7	21	14.2	18.5	17.5 ± 1.8 (15.4–18.6)	17.1 ± 1.0 (15.7–18.1)
c’	?	?	1.5	1.9	1.8	1.9 ± 0.3 (1.7–2.2)	2.0 ± 0.2 (1.8–2.2)
V(%) / T(%)	71–73	?	74	64	?	69.5 ± 0.6 (69.0–70.2)	39.8 ± 2.0 (37.6–41.4)
Labial region diameter	?	?	23	?	?	14.7 ± 0.8 (14.0–15.0)	14.0 ± 1.3 (13.0–16.0)
Cephalic setae length	?	2	3	2.6	2.6	3.0	2.9 ± 0.3 (2.5–3.5)
Subdorsal cephalic setae from anterior end	?	13	23	?	?	14.1 ± 3.4 (12.0–16.5)	12.9 ± 0.7 (12.5–14.0)
Subventral cephalic setae from anterior end	?	10	18	?	?	11.0 ± 1.2 (10.0–12.0)	10.5 ± 1.3 (10.0–12.5)
Cephalic setae length / labial region diam.	?	?	?	?	?	0.2	0.2 (0.2–0.3)
Anterior end of shield from anterior end	?	?	?	?	?	17.3 ± 1.4 (16.0–18.5)	14.3 ± 0.9 (13.0–15.0)
Refractive plate length	?	23	27	28	29	22.8 ± 3.2 (19.0–25.5)	23.1 ± 3.3 (20.0–27.5)
Refractive plate width	?	13	16	11.7	13.6	14.3 ± 2.4 (12.0–16.5)	14.3 ± 1.0 (13.0–15.0)
Anterior end of amphid from anterior end	?	?	19	?	?	12.9 ± 2.2 (10.5–14.5)	11.0 ± 1.1 (10.0–12.5)
Dorsal amphid branch length	?	20	32	?	?	23.7 ± 2.8 (21.0–26.0)	22.9 ± 2.5 (21.0–26.0)
Ventral amphid branch length	?	20	28	?	?	24.4 ± 3.3 (21.0–27.0)	24.0 ± 3.2 (21.0–28.0)
Amphid width	?	4	7	?	?	5.8 ± 0.4 (5.5–6.0)	5.2 ± 0.4 (5.5–5.5)

Table 5 (continued).

	original description		data for *D. cuspidiboja*	*D. incisa* sensu Vitiello, 1972		recent specimens	
Amphid length / width	?	?	4.6	?	?	4.2 ± 0.7 (3.3–4.8)	4.5 ± 0.7 (3.8–5.4)
Anterior edge of stoma from anterior end	?	13	16	6.5	10	12.0 ± 1.7 (10.5–14.0)	10.9 ± 1.7 (9.0–13.0)
Stoma length	?	?	?	?	?	15.5 ± 1.5 (14.5–16.5)	14.7 ± 0.9 (14.0–16.0)
Stoma width	?	?	?	?	?	3.9 ± 0.4 (3.5–4.0)	3.8 ± 0.4 (3.5–4.0)
Nerve ring from anterior end	?	?	122	?	?	103 ± 2 (102–105)	98 ± 10 (91–112)
Nerve ring from anterior end (% pharynx)	?	?	74	?	?	66.8 ± 2.4 (64.5–69.2)	64.9 ± 2.3 (61.5–66.4)
Secretory-excretory pore from ant. end	?	?	148	?	?	123 ± 5 (117–127)	119 ± 14 (111–139)
Secr.-excr. pore from ant. end (% pharynx)	?	?	90	?	?	79.6 ± 0.8 (79.0–80.4)	78.7 ± 2.5 (76.4–81.3)
Vagina or spicules length	?	63	?	?	52	21.7 ± 2.0 (19.5–23.0)	61.8 ± 4.0 (57.0–66.0)
Vagina / BD or spicules / ABD	?	?	?	?	1.3	0.3 ± 0.1 (0.3–0.4)	1.5 ± 0.1 (1.4–1.6)
Rectum or gubernaculum length	?	?	?	?	?	31.5 ± 4.0 (27.5–35.0)	9.7 ± 1.1 (9.0–11.5)
Rectum / ABD or apophysis length	?	10	?	?	?	0.7 ± 0.1 (0.6–0.8)	12.8 ± 1.7 (11.5–15.0)
Caudal gland openings from tail terminus	?	?	3.5	?	?	5.3 ± 1.7 (3.5–7.0)	6.0 ± 0.6 (5.5–7.0)

Male

Reproductive system diorchic, testes opposed; anterior testis outstretched and posterior testis reflexed (cannot be measured). Spicules paired and symmetrical, strongly curved, with ovoid manubrium and fusiform shaft. Gubernaculum plate-like, with pair of strong closely set caudal apophyses variable in shape (Fig. 13C–E). Caudal setae present, several ventrosublateral pairs arranged in rows along entire tail length, one dorsosublateral pair located close to tail terminus (not always visible).

Remarks

No morphological or morphometric differences can be found between the recent specimens and the original description of this species (Jensen 1991).

Key to species of the genus* Neodiplopeltula *gen. nov. (see Table 6 for additional diagnostic characters)

1. Refractive periamphideal plates absent ..... ***N. intermedia*** (Gerlach, 1954) gen. et comb. nov.
– Refractive periamphideal plates present 2

2. Refractive periamphideal plates connect on dorsal and ventral body sides 3
– Refractive periamphideal plates do not connect 4

3. Oral opening subdorsal; amphid 32–44 µm long ..... ***N. onusta*** (Wieser, 1956) gen. et comb. nov.
– Oral opening terminal; amphid 16–17 µm long ..... ***N. obesa*** (Nguyen Vu Thahn, Nguyen Thahn Hien & Gagarin, 2012) gen. et comb. nov.

4. Oral opening terminal .....***N. indica*** (Gerlach 1962) gen. et comb. nov.
– Oral opening subdorsal 5

5. Oral opening at level with or posterior to cephalic setae bases, 6–16 µm from anterior end ....***N. bathmanni*** (Jensen, 1991) gen. et comb. nov.
– Oral opening anterior to cephalic setae bases, 1–3 µm from anterior end 6

6. Refractive periamphideal plates with incised margins; cephalic setae more than 8 µm long .... ***N. incisa*** (Southern, 1914) gen. et comb. nov.
– Refractive periamphideal plates oval in shape; cephalic setae less than 8 µm long ....***N. barentsi*** (Steiner, 1916) gen. et comb. nov.

Amendment to the key to the genera of Diplopeltidae (from Holovachov 2017)

10. Stoma subcylindrical; caudal glands open via three separate pores .....***Neodiplopeltula*** gen. nov.
– Stoma small and undifferentiated; caudal glands open via common spinneret 11

11. Amphid located on a well-developed refractive subcuticular plate .... ***Diplopeltis*** Cobb in Stiles & Hassal, 1905
– Refractive subcuticular plate absent ..... ***Pseudaraeolaimus*** Chitwood, 1951

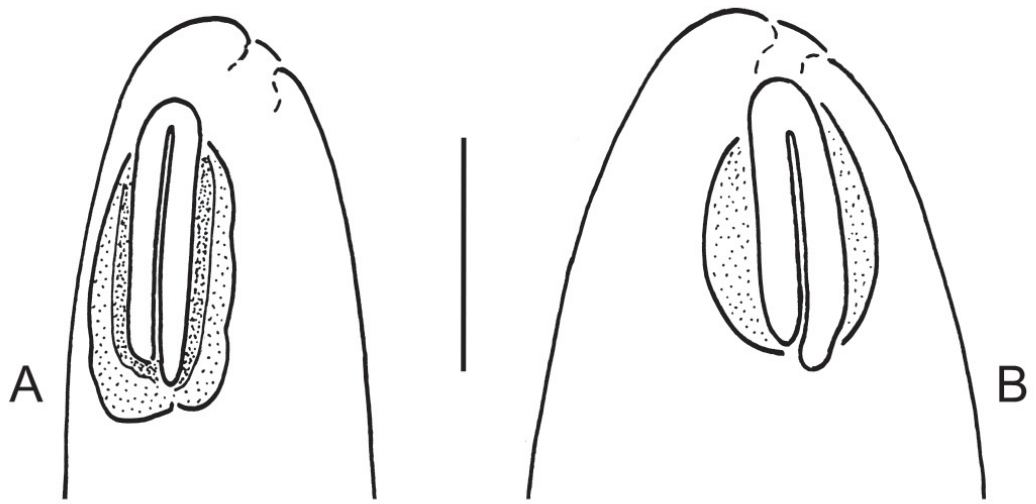

Fig. 14. A. Anterior end of holotype of *Diplopeltis ovalis* Ditlevsen, 1928. **B**. Anterior end of lectotype of *Diplopeltis asymmetricus* Allgén, 1935. Scale bar = 20 µm.

Table 6. Selected diagnostic characters of species of the genus *Neodiplopeltula* gen. nov. based on literature data supplemented with recent observations, all measurements in µm except for the body length (mm) (NA = data not available; * = data supplemented with measurements from original illustrations). Data for *N. barentsi* gen. et comb. nov. is based on the original description, new measurements of the types of *D. ovalis* and *D. asymmetricus*, *D. onustus* sensu Sergeeva (1977), the male description of *D. cuspidiboja* (Leduc 2017) and recent data; for *N. bathmanni* gen. et comb. nov. on the original description (Vitiello 1972), recent data and female description of *D. cuspidiboja* (Leduc 2017) gen. et comb. nov.; for *N. incisa* gen. et comb. nov. on the original description and recent data; for *N. indica* (Gerlach 1962) gen. et comb. nov. – original description and Vincx & Gourbault (1992); and for *N. onusta* gen. et comb. nov. on the original description, recent data and the description of *D. tchesunovi* (Fadeeva & Mordukhovich 2013).

	Body length	Cephalic setae length	Cephalic setae position from anterior end	Amphid size	Refractive plate shape	Refractive plate size	Oral opening position from anterior end	V (%)	Spicules length	c'	Caudal gland openings position from posterior end	Secr.-excr. pore from anterior end (% pharynx)	Distribution
N. barentsi	0.94–1.67	3.5–7.5	subdorsal: 5.5–11 subventral: 7–9	length: 21–32 width: 4–7	oval	length: 23.5–32 width: 12.5–16	subdorsal 1–2 µm	60–64	45–73	1.6–3.3	1–2	58–66	White Sea; Barents Sea; Skagerrak; Black Sea; Davis Strait; Kiel Bay; New Zealand continental slope
N. bathmanni	0.85–2.08	2–3.5	subdorsal: 12–23 subventral: 10–18	length: 20–32 width: 4–7	oval	length: 19–29 width: 12–16.5	dorsal 6–16 µm	64–74	52–66	1.5–2.2	subterminal 3.5–7 µm	76–90	White Sea; Norwegian Sea; Skagerrak; Gulf of Lion; New Zealand continental slope
N. incisa	1.52–2.24	8–14	subdorsal: 5.5–10.5 subventral: 5.5–10.5	length: 22–28 width: 5.5–7	irregular	length: 28–33 width: 21–25	subdorsal 1–3 µm	61–63	66–79	2.5–3.9	subterminal 2–3.5 µm	56–61	North East Atlantic; Skagerrak; Kiel Bay; White Sea
N. indica	0.98–1.40	9–12	subdorsal: 5 subventral: 6*	length: 15–18 width: 8*	oval	length: 17 width: 10–12	terminal	59	40–50	2.6–3.4	terminal	?	Maldives; Southern Caribbean
N. intermedia	1.69	10	6*	length: 15 width: 6	absent	NA	terminal	60	NA	3.5	?	21	Balearic Sea
N. obesa	0.47–0.50	1.2	?	length: 16–17 width: ?	circumferal	?	terminal	49–52	NA	3.3–3.5	terminal	?	West Sea of Vietnam
N. onusta	0.99–1.48	3–6.5	subdorsal: 5.5–8 subventral: 5–7	length: 32–44 width: 5–8	circumferal	length: 32.5–48 width: 18.5–24	subdorsal 2–5 µm	65–68	52–77	1.4–2.3	terminal	57–66	Salish Sea; White Sea; Sea of Japan; Skagerrak

Discussion

The genus *Diplopeltula* exhibits two pertinent problems in the systematics of marine nematodes: ignorance of the female morphology in descriptions of new taxa and the absence of type material. The 'Traditional' focus lies on male characters in species descriptions and diagnoses of genera, and the partial or complete ignorance towards the morphology of female reproductive system causes taxonomic and nomenclatorial problems in those cases where higher classification of taxa relies on female-specific characters. The genus *Diplopeltula* is but one example (see detailed discussions in Holovachov *et al*. 2009; Leduc 2013; Holovachov 2017; Holovachov & Boström 2017). Of course, it would not be such an issue if the type material for such 'troublesome' taxa were preserved and available for restudy. Unfortunately, S. Gerlach, being one of the most prolific nematode taxonomists, did not preserve any type specimens and did not make any permanent slides until 1964, thus preventing any future taxonomic revisions and corrections. Regrettably, he was not alone in this practice. As it turned out, W. Wieser did not leave any trace of the enormous and taxonomically important collection of marine nematodes from Chile, consequences of which are yet to be dealt with.

Acknowledgments

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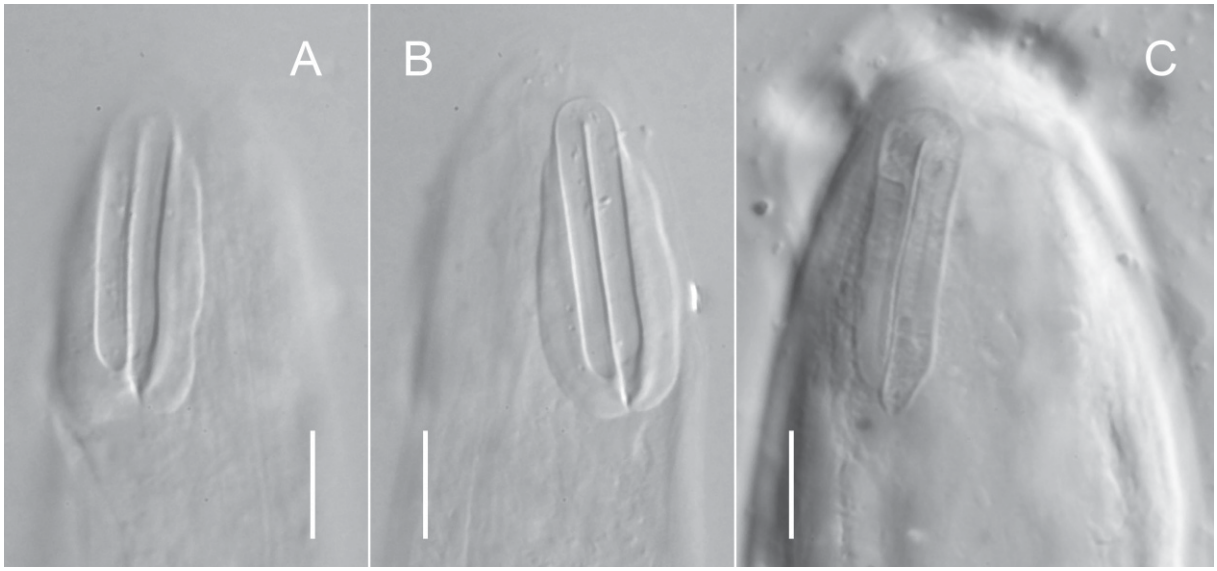

Fig. 15. A–B. Anterior end of the holotype of *Diplopeltis ovalis* Ditlevsen, 1928. **C**. Anterior end of the lectotype of *Diplopeltis asymmetricus* Allgén, 1935. Scale bar = 10 µm.

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