

A new genus of marine chaetonotids (Gastrotricha), with a description of two new species from Greenland and Denmark

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Two new marine species of Gastrotricha: Chaetonotidae are described from West Greenland and Denmark. Some peculiar features suggest the affiliation of the two species to a new genus, for which the name *Diuronotus* is proposed. The affinity of these gastrotrichs with species of *Musellifer*, the only genus entirely marine and hermaphroditic, and possibly the most basal one along the Chaetonotidae evolutionary line, is discussed from a morphological point of view. The span of the geographical distribution of *Diuronotus* is discussed in the light of a record of an additional co-generic, undescribed species from the USA. The relationships of this genus will be important in reconstructing the evolutionary pathways within Gastrotricha: Chaetonotida.

INTRODUCTION

The phylum Gastrotricha includes about 690 meiobenthic-sized species grouped into two orders: Macrodasysida, with 240 strap-shaped species, all but two (i.e. *Marinellina flagellata* Ruttner-Kolisko, 1955 and *Redudasys forneris* Kisielowski, 1987; see Kisielowski, 1987 for discussion) of which are marine or estuarine, and Chaetonotida with 450 tenpin-shaped species (except *Neodasys*) living in both marine and freshwater habitats. Among Chaetonotida, four families, Dasydytidae, Dichaeturidae, Neogosseidae and Proichthyidiidae, include only fresh water species, two families, Neodasyidae and Xenotrichulidae have only marine representatives, whereas the remaining seventh family, the Chaetonotidae, includes both marine and fresh water forms. The latter family is the most species-rich of the entire phylum and consists of 12 genera, two of which (i.e. *Musellifer* Hummon, 1969 and *Halichaetonotus* Remane, 1936), include only marine species, five other (i.e. *Arenotus* Kisielowski, 1987, *Fluxiderma* d'Hondt, 1974, *Lepidochaetus* Kisielowski, 1991, *Polymerurus* Remane, 1927 and *Undula* Kisielowski, 1991) are found only in fresh water ecosystems, whereas the remaining five genera (*Aspidiophorus* Voigt, 1907, *Chaetonotus* Ehrenberg, 1830, *Heterolepidoderma* Remane, 1927, *Ichthyidium* Ehrenberg, 1830, and perhaps *Lepidodermella* Blake, 1933) include both marine and fresh water species.

The rare species of *Musellifer* bear particular relevance within an evolutionary framework since their primary habitat (i.e. the sea), coupled with the display of characteristics perceived to be plesiomorphic, at least from a morpho-functional point of view (i.e. presence of well structured spermatozoa and accessory reproductive structures, cf. Guidi et al., 2003), make them the likely candidates for the most basal position in the Chaetonotidae

hypothetical evolutionary tree (however, see Hochberg & Litvaitis, 2000 for a different conclusion). Herein we provide the description of some specimens belonging to two undescribed species that in many respects recall the characteristics of the three known *Musellifer* species, yet the peculiarity of other morphological traits suggests their affiliation to a newly established genus, for which the name *Diuronotus* is proposed.

MATERIALS AND METHODS

The description of the new species follows mostly the convention of Hummon et al. (1992) whereas the locations of some morphological characteristics along the body are given in percentage units (U) of total body length measured from anterior to posterior. Details about sampling sites, collection and specimens processing are given in the sections below (i.e. type locality and type material).

SYSTEMATICS

Order CHAETONOTIDA Remane, 1925
[Rao & Clausen, 1970]

Family CHAETONOTIDAE Zelinka, 1889
[sensu Kisielowski, 1991]

Subfamily CHAETONOTINAE Zelinka, 1889
[sensu Kisielowski, 1991]

Diuronotus gen. nov.

Diagnosis

Chaetonotidae with weakly marked head, drawn out into a muzzle; muzzle surrounded by a ciliary band; head plates absent; caudal furca less than $\frac{1}{7}$ of total body length, showing a secondary adhesive tube on the dorso-medial side of each branch; secondary adhesive tube

reduced or lacking (?) in juvenile; cuticle thickened into elongate scales, having a concave posterior edge; scales bear an obvious keel, which generally extends to form a short spine; ventral locomotory cilia as a continuous field under the head and the first third of the pharyngeal region, then splitting into two longitudinal bands; simultaneous hermaphrodite, with paired anterior testes and posterior ovaries; thread-like sperm; oocytes maturing anteriorly; accessory reproductive structures unknown.

Etymology

From the latin 'di'—double, 'uro'—tail, and 'notus'—known, referring to the double sets of furcal adhesive tubes.

Diuronotus aspetos sp. nov.

(Figures 1 & 2)

Type material

The holotype: an adult hermaphroditic specimen, formalin–glycerin wholemount, deposited at the Zoological Museum, University of Copenhagen, Copenhagen, Denmark (ZMUC-GAT-13) collected on 10 January 1979 at 2.5 m water depth near Skansen, Disko Island, West Greenland.

Additional material: one paratypic adult specimen, formalin–glycerin wholemount (ZMUC-GAT-14), one juvenile stage, formalin–glycerin wholemount (ZMUC-GAT-15) and one large specimen (ZMUC-GAT-16) in polyvinyl–lactophenol. These paratypes were collected in the same sandy sediment as the holotype. The other specimen: an adult animal with diatoms in the midgut was collected through a seal hole (30 January 1979) close to the type locality (polyvinyl–lactophenol wholemount, ZMUC-GAT-17). All specimens were collected by R.M. Kristensen when he was the scientific leader of Danish Arctic Station, Disko Island, West Greenland.

Type locality

The samples were taken by a mini van Veen grab (225 cm²) from a long-shore sandy barrier (2–5 m water depth), Kigdlugssaitut (69°29'N 52°11'W) near the abounded settlement of Skansen, Disko Island, West Greenland. All specimens were collected during the Arctic mid-winter in 1979 through streamholes or seal-holes in the sea ice. The temperature in the medium–coarse well sorted sandy sediment was –1.7°C, that of the surrounding sea ice was –10°C. The interstitial fauna was very rich. Further information can be found in Kristensen & Niilonen (1982) and Kristensen & Nørrevang (1982).

Etymology

The name of the new species comes from the Greek 'aspetos', unspeakably big, alluding to the large size of these chaetonotids.

Diagnosis

A large *Diuronotus* with total length up to 533.5 µm; pharyngo-intestinal junction (PhIJ) at U34.5; furca short, indenting to U93, with secondary tubes much longer than the primary ones (ratio 3:1). Body enveloped

by 65 columns of keeled, elongate scales; ventral ciliation forming a continuous field from the posterior edge of the mouth to the second third of the pharynx (U24.3) then splitting into two bands that run through the trunk region, ending at U90. Protogynous, then simultaneous hermaphrodite with paired, round to sac-like testes lateral to the intestine, at U63; thread-like spermatozoa; maturing oocytes in the posterior trunk region.

Description

The description is based on an adult specimen 533.5 µm in total body length, when the animal is measured from the anterior edge of the mouth to the tip of the primary tube of the caudal furca. Pharynx is 174.0 µm in length, from the posterior edge of the mouth to the junction with the intestine; PhIJ at U34.5. Head unilobed, bearing a tapering muzzle without cephalion, pleuria and hypostomion. The muzzle is surrounded by a ciliary band, 24.4 µm wide on the dorsal side, that connects with the ventral locomotory ciliature; on either side of the anterior region of the head are scattered sensory cilia of widely varying length. Body elongate, robust, with short neck, extended trunk and distinct furcal base; widths of head/neck/trunk/caudal base are as follows: 69/64/97/58 µm at U09/U28/U55/U91, respectively. Caudum relatively short, less than 1/8 of total body length, with a distal furca that indents medially to U93 and has exterior borders that diverge obliquely to the rear; each furcal branch is peculiarly shaped because beside comprising a larger fleshy portion proximally (57.1 µm in length) and a shorter adhesive tube distally (19.5 µm in length), it bears an additional, longer, adhesive tube (the secondary tube) that arises more proximally from the dorso-medial side of the fleshy portion; the secondary tube is 59.5 µm in length.

Sensory organs: four to six isolated cephalic sensory cilia on either side of the head, generally ranging from 20–25 µm, but some reaching 50–55 µm; neither sensory cilia nor tactile bristles were observed in other anatomical districts; eye spots were also lacking.

Cuticular armature: the body is enveloped by 41–43 alternating columns (25–27 dorsal and 8+8 ventrolateral) of about 50 scales each. Scales are relatively small and elongate; they overlap anterolaterally, and are hemi-elliptic in shape but with a concave posterior edge; each scale bears a median keel, which in most scales extends to form a short, single spine (up to 1/4 the length of the keel). Scales are smaller on the head and on the furcal branches (1.5×4.0 µm), and larger on the mid-trunk region (up to 4× up to 12.0 µm), whereas the keel is somewhat higher in the scales of the lateral columns. Armature extends over the whole fleshy portion of the furcal branches, and it is worth noting that scales also cover the entire shaft of the secondary adhesive tubes. The ventral interciliary field, which extends from U24.3 to U90, has up to 23 alternating columns of scales similar in shape, size and arrangement to the dorsal ones, yet, no differently shaped scales can be seen neither near the peri-anal region nor on the ventral side of the furcal base.

Ventral ciliature: a continuous field of densely packed cilia from the posterior edge of the mouth (U02) to the second third of the pharynx (U24.3), then splitting into two bands that run through most of the trunk region, and ending at U90. The anterior continuous field is wider at its

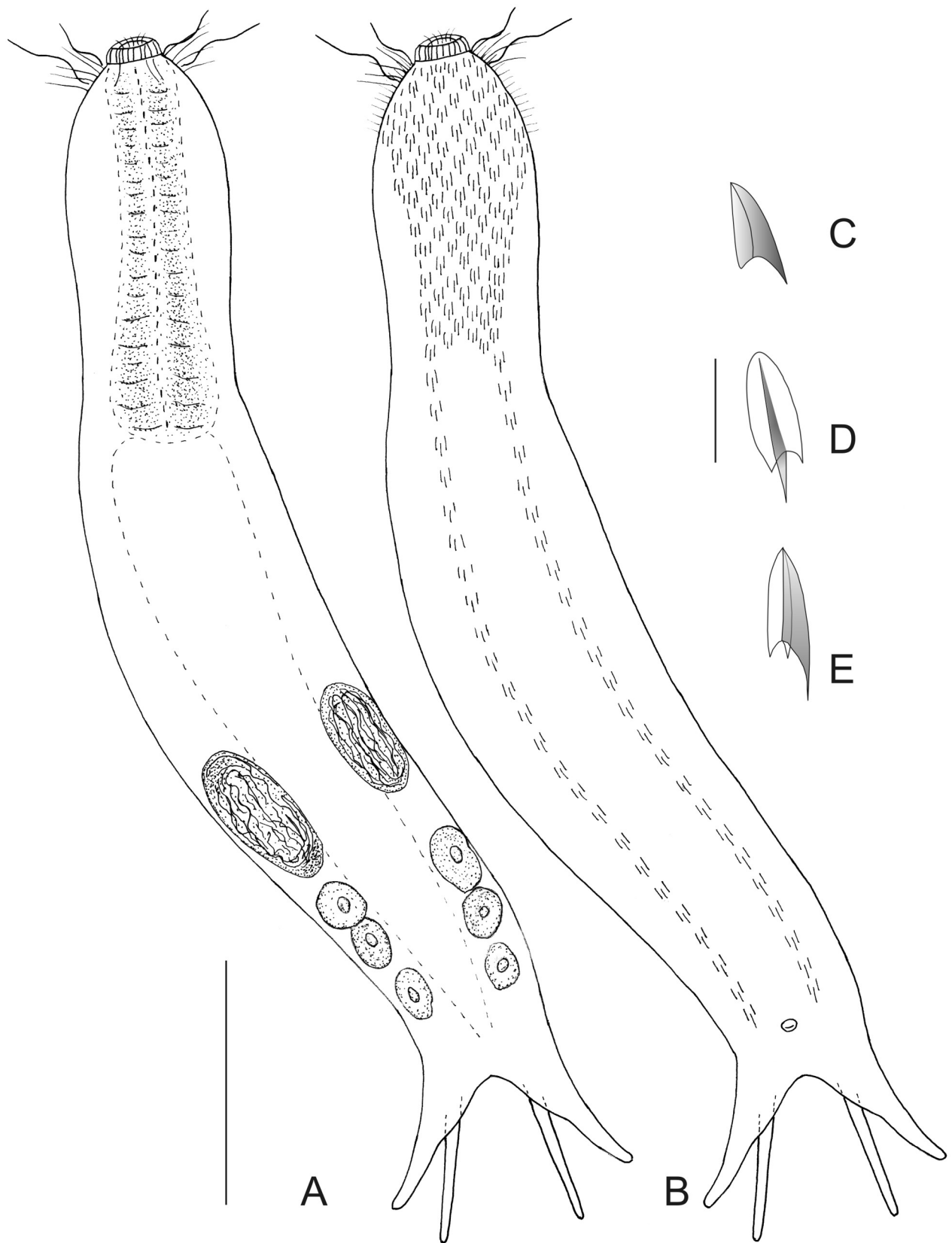


Figure 1. *Diuronotus aspetos* sp. nov.—drawing of the habitus—(A) internal anatomy; (B) ventral side; (C) scale of the head; (D) scale of the trunk; and (E) scale of the rear trunk. Scale bars: A, B, 100 μ m; C–E, 10 μ m.

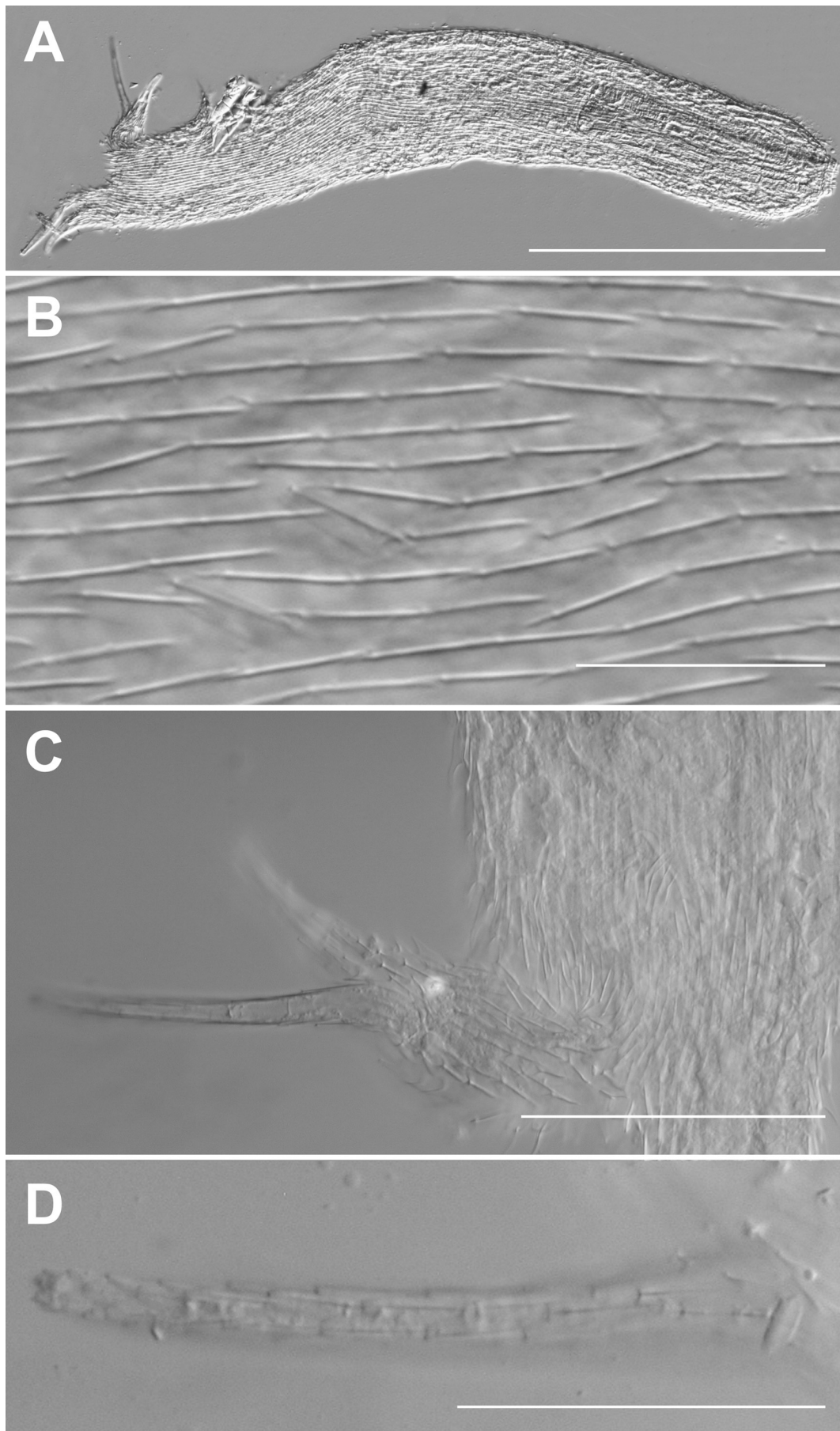


Figure 2. *Diuronotus aspetos* sp. nov.—differential interference contrast optics —(A) habitus; (B) arrangement of the dorsal scales; (C) posterior end, showing the secondary adhesive tube of the left furcal branch; and (D) close-up of the secondary adhesive tubes, showing the scales along its shaft. Scale bars: A, 200 μm ; B, 20 μm ; C, 30 μm ; D, 50 μm .

first third, from U02 to U10.5, where it connects with the dorsal band, then tapers rearward before definitively splitting.

Digestive tract: the mouth apparatus is of relatively large width; the external muzzle rim measures $14\ \mu\text{m}$ in diameter and is characterized by a very thick wall; the mouth opening measures $7.8\ \mu\text{m}$ in diameter and continues into a $14\ \mu\text{m}$ long buccal cavity, slightly enlarging toward the rear; 19–20 teeth-like cuticular ridges strengthen the mouth wall: they are arranged radially and can be everted, so forming a spiny basket placed in front, and surrounding the muzzle/mouth. The pharynx has a swelling at each end, the anterior being less obvious ($32\ \mu\text{m}$) than the posterior ($47.5\ \mu\text{m}$), whereas its central portion has a fairly constant width ($30\ \mu\text{m}$); the intestine is broadest anteriorly ($56\ \mu\text{m}$) and narrows gradually over its length (to $8\ \mu\text{m}$); the anus opens ventrally at U90.

Reproductive tract: simultaneous hermaphrodite with paired, round to sac-like testes, lateral to the intestine at U63. Thread-like spermatozoa. No information regarding ovaries *per se*, however, several oocytes at different stages of maturation were seen in the posterior trunk region, dorso-laterally to the intestine.

Remarks

It seems that the shape of the scales undergoes some sort of change during ontogenetic growth; in fact, in the smallest juvenile specimen studied, $301\ \mu\text{m}$ in total length, the scales, particularly on the head and on the furcal base, are shorter, rather narrow, show a deeply concave posterior edge, and bear a much higher keel, which continues into a comparatively longer spiny process, up to the same length as the scale. Juvenile specimen (ZMUC-GAT-15) has reduced secondary adhesive tubes. One specimen (ZMUC-GAT-17), has the intestine totally filled with diatoms. All specimens were only found during the Arctic winter. The type locality has been visited several times since 1979 during the summer, but the species has never been found again (see Ehrhardt & Svendsen, 1994). This may indicate that the species is a 'High Arctic species', which can be found in Low Arctic (Disko Island) only during the wintertime. All the other genera of gastrotrichs found together with *Diuronotus aspetos* sp. nov. such as *Tetranchyroderma*, *Thaumastoderma*, *Paradasys*, *Mesodasys*, *Turbanella*, *Chaetonotus* and *Halichaetonotus* were also found during the summer time.

Diuronotus rupperti sp. nov. (Figures 3–5)

Type material

The holotype: an adult hermaphroditic specimen (ZMUC-GAT-18), formalin–glycerin wholemount, deposited at the ZMUC. Collected by R.M. Kristensen on 6 April 1993.

Additional material: eight adult paratypic specimens, formalin–glycerin wholemount (ZMUC-GAT-19–26), and four paratypic juvenile stages, formalin–glycerin wholemount (ZMUC-GAT-27–30). Three other specimens mounted on scanning electron microscopy stubs are kept in the meiofauna collection of R.M. Kristensen (ZMUC-GAT-31–33).

Type locality

The samples were taken by a meiofauna corer ($25\ \text{cm}^2$) intertidally at low water mark in a sandy beach, ($57^{\circ}19'N$ $11^{\circ}19'E$) near Bansten Beach, Læsø, Denmark. All specimens were collected on 6 April 1993. The sediment was made of fine, moderately sorted sand. The interstitial fauna was very rich.

Etymology

The species is dedicated to Professor Edward E. Ruppert of Clemson University, North Carolina, USA, in recognition of his outstanding contribution to the knowledge of Gastrotricha.

Diagnosis

A *Diuronotus* with total length up to $472.5\ \mu\text{m}$; PhIJ at U22; furca short, indenting to U88, with secondary tubes shorter than the primary ones (ratio 1:2). Body enveloped by 63–65 columns of elongate, keeled scales; ventral locomotory ciliature forming a continuous field from the posterior edge of the mouth to over the second third of the pharynx (U18.3), then splitting into two bands that extend along the whole trunk, ending at U85. Protogynous, then simultaneous hermaphrodite with paired, round to sac-like testes, lateral to the intestine at U63; thread-like sperm; maturing oocytes in the posterior trunk region.

Description

The description is based on an adult specimen, $472.5\ \mu\text{m}$ in total body length, when the animal is measured from the anterior edge of the mouth to the tip of the primary tube of the caudal furca. Pharynx is $96.0\ \mu\text{m}$ in length, from the posterior edge of the mouth to the junction with the intestine; PhIJ at U22. Head unilobed, bearing a tapering muzzle but lacking cephalion, pleuria and hypos-tomion. The muzzle is surrounded by a ciliary band ($23.5\ \mu\text{m}$ wide on the dorsal side) that connects with the ventral locomotory ciliature; on either side of the anterior region of the head are scattered sensory cilia of widely varying length. Body elongate, robust, with ill-defined neck, extended trunk and distinct furcal base; widths of head/neck/trunk/caudal base are as follows: $58/63/73/60\ \mu\text{m}$ at U09/U28/U55/U91, respectively. Caudum relatively short, less than $\frac{1}{7}$ of total body length, with a distal furca that indents medially to U88 and has exterior borders that diverge obliquely to the rear; each furcal branch comprises an extended fleshy portion ($40\ \mu\text{m}$ in length), a conical primary adhesive tube ($16.8\ \mu\text{m}$ in length) and a secondary tube implanted more proximally on the dorso-medial side of the fleshy portion; the secondary tube is rather short, measuring only $8.5\ \mu\text{m}$ in length.

Sensory organs: four to six scattered cephalic sensory cilia on either side of the head, ranging from 15 to $25\ \mu\text{m}$ in length; neither sensory cilia nor tactile bristles were observed in other anatomical districts; eye spots were also lacking.

Cuticular armature: the body is enveloped by 41–43 alternating columns (25–27 dorsal and 8+8 ventrolateral) of about 50 overlapping scales each. Scales are relatively small, generally elongate with a concave posterior edge and bear a median keel, generally extending into a short

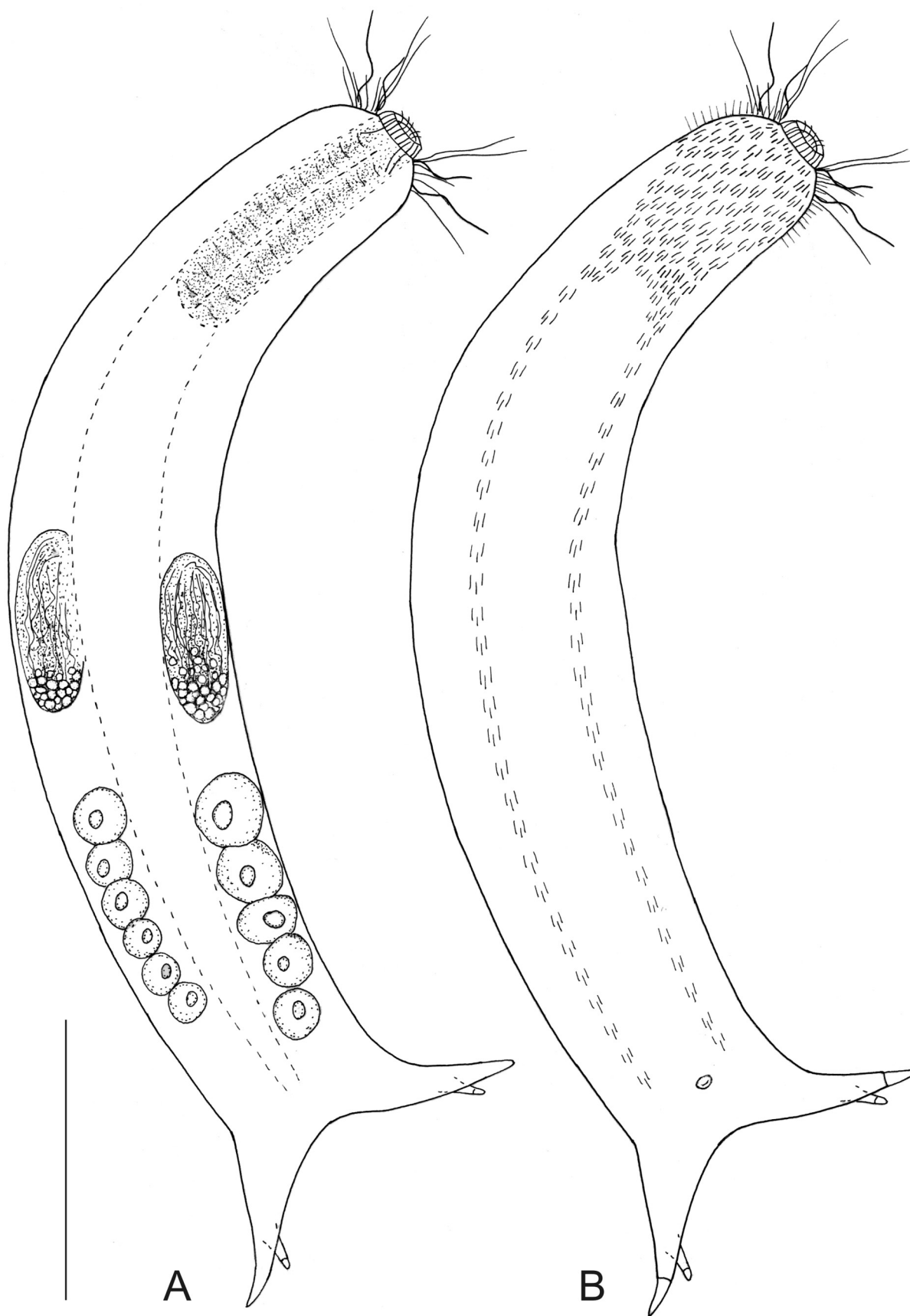


Figure 3. *Diuronotus rupperti* sp. nov.—drawing of the habitus—(A) internal anatomy; (B) ventral side. Scale bar: 100 μ m.

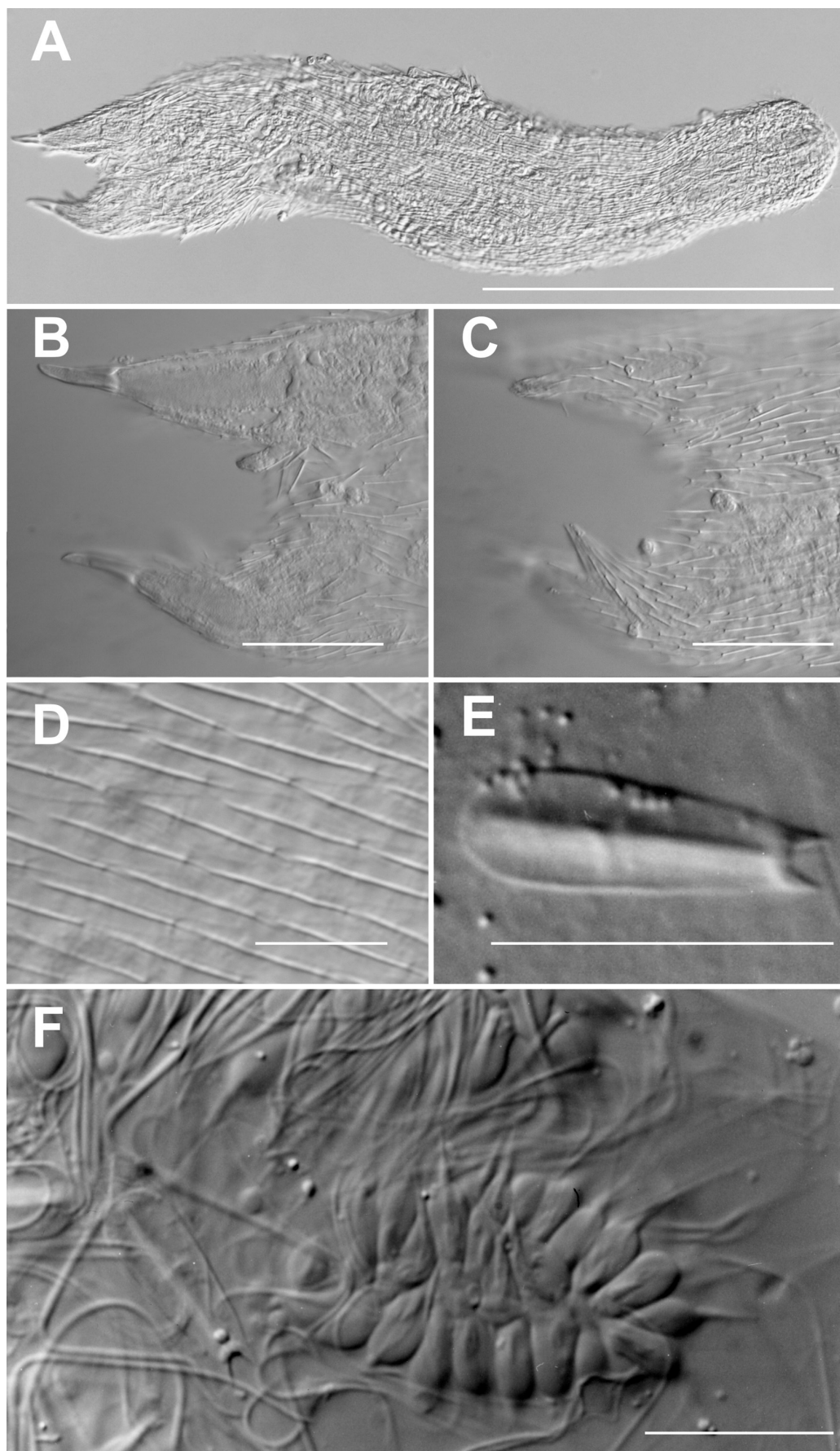


Figure 4. *Diuronotus rupperti* sp. nov.—differential interference contrast optics—(A) habitus; (B) posterior end, showing the primary tube of the furcal branches; (C) posterior end showing the secondary tubes of the furcal branches; (D) arrangement of the scales on the dorsal side; (E) scale on the dorsal side, lacking spiny process; and (F) maturing spermatids. Scale bars: A, 200 μm ; B, C, 25 μm ; D–F, 10 μm .

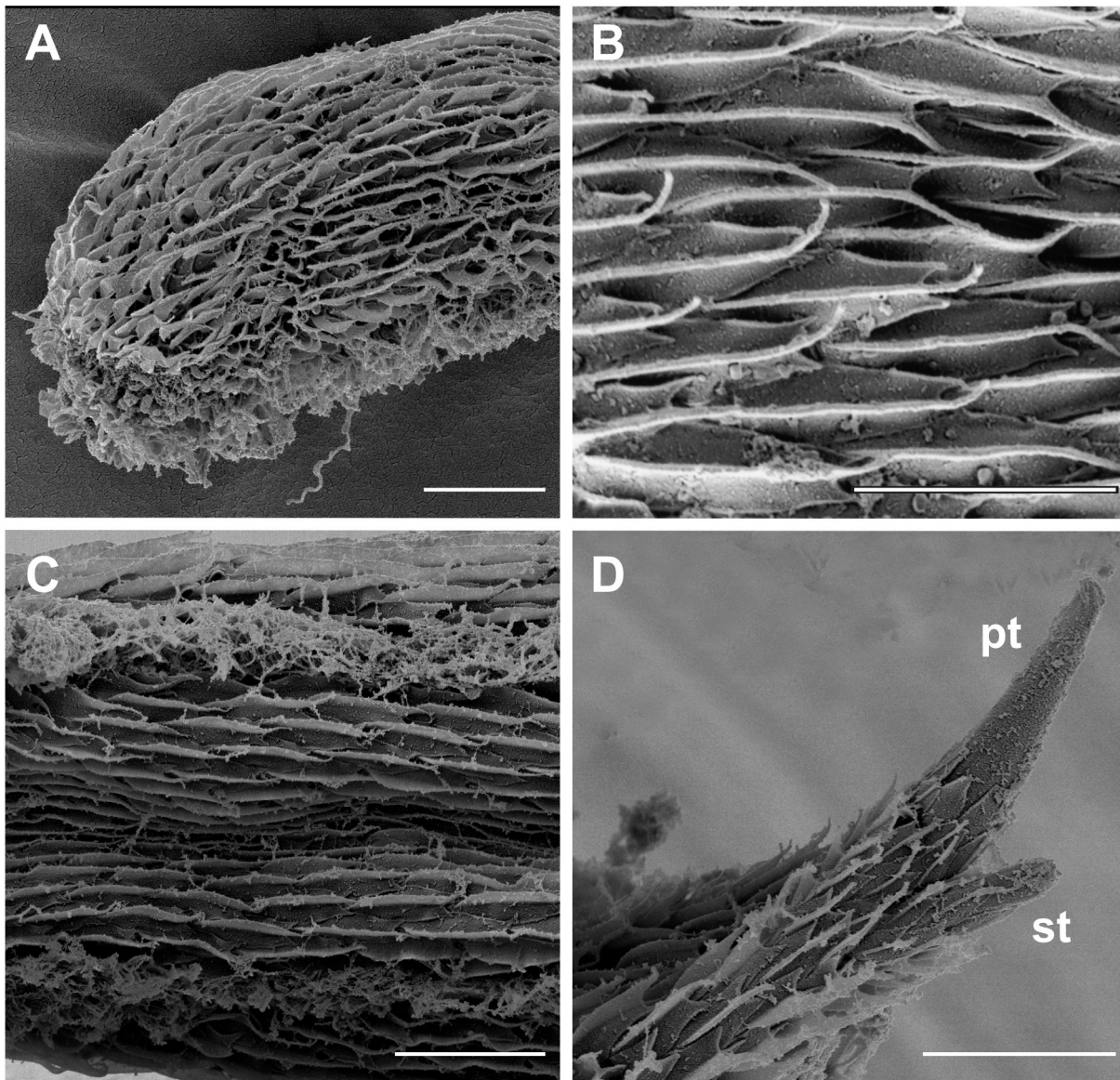


Figure 5. *Diuronotus rupperti* sp. nov.—scanning electron microscope micrographs—(A) dorsolateral view of the anterior end, showing an unilobate scale with high keel extending into a crescent-shaped spiny process; (B) scales on the dorsal side; (C) ventral ciliary bands and scales of the interciliary field; and (D) close-up of the posterior end showing the primary (pt) and secondary (st) tube of the left furcal branch. Scale bars: 10 μm .

spine (up to $\frac{1}{4}$ the length of the keel). Scales are smaller and shorter on the head and on the furcal branches ($1.5 \times 3.0 \mu\text{m}$), and larger on the mid-trunk region (up to $3 \times$ up to $10.0 \mu\text{m}$), whereas the keel is somewhat higher on the head and the lateral scales. The armature extends over the whole fleshy portion of the furcal branches, and also covers most of the shaft of the secondary adhesive tubes. The ventral interciliary field, which extends from U24.3 to U85, has up to 25 alternating columns of scales similar in shape, size and arrangement to the dorsal ones, yet, no differently shaped scales can be seen near the perianal region nor under the furcal base.

Ventral ciliature: a continuous field of densely packed cilia from the posterior edge of the mouth (U02) to over the second third of the pharynx (U18.3), then splitting into two bands that run through the whole trunk region, ending at U85. The anterior continuous field is wider at its first third, from U02 to U15, where it connects with

the dorsal band, then tapers rearward before definitively splitting.

Digestive tract: the mouth apparatus is of relatively large width; the external muzzle rim measures $14 \mu\text{m}$ in diameter and is characterized by a very thick wall; the mouth opening is $7.5 \mu\text{m}$ in diameter and continues into a $12 \mu\text{m}$ long buccal cavity, slightly enlarging toward the rear; 19–21 teeth-like cuticular ridges strengthen the mouth wall, they are arranged radially and can be everted, forming a spiny basket placed in front, and surrounding the muzzle/mouth. The pharynx is of fairly constant width ($22 \mu\text{m}$); the intestine is broader over its anterior third ($23 \mu\text{m}$) and narrows gradually over its length (to $6 \mu\text{m}$); the anus opens ventrally at U85.

Reproductive tract: simultaneous hermaphrodite with paired, round to sac-like testes, lateral to the intestine at U47. Anterior portion of the testes filled with thread-like spermatozoa maturing from round cellular elements

(spermatocytes?) located in the posterior half of each gonad. No information regarding ovaries *per se*, however, several oocytes at different stages of maturation were seen in the posterior trunk region, dorsolaterally to the intestine.

Remarks

It seems that the size of the secondary adhesive tubes undergoes some sort of change during ontogenetic growth; in fact, in the smallest juvenile specimen (ZMUC-GAT-30) studied, 221 μm in total length, these tubes are totally lacking. There are no signs of these tubes in animals from 253 to 311 μm in length (ZMUC-GAT-27-29); however, when the ovaries begin to develop specimens of 372–402 μm in length (ZMUC-GAT-20-22), the secondary adhesive tubes can be observed. *Diuronotus rupperti* sp. nov. appears so similar in its traits to the undescribed, North American, species drawn in figure 24.3g by Ruppert (1988), to suggest a close relationship (sister species?) between the two taxa.

Taxonomic remarks

At gross anatomy level the examined specimens can be easily affiliated to the order Chaetonotida based on the absence of anterior adhesive tubes, and to the suborder Paucitubulatina because of the absence of lateral adhesive tubes. The most striking feature of these gastrotrichs from Greenland and Denmark are the two supernumerary (secondary) adhesive tubes present on the furcal branches that gives a furcate appearance to each caudal ramus. Within Chaetonotida: Paucitubulatina, the latter characteristic is known to occur only in members of the genus *Dichaetura* Lauterborn, 1910, which to date counts only two species, both described from freshwater habitats, i.e. *D. capricornia* (Metschnikoff, 1865) and *D. piscator* (Murray, 1913). Observations of these small gastrotrichs, up to 150 μm in total length, are mostly old dated and their descriptions are largely incomplete (e.g. Murray, 1913). For instance, the real structure of the secondary caudal ramus is not yet clearly explained. It is very likely, however, that the innermost caudal branch in both these species is made up by a stout spine or a cuticular hook, as reported in the most recent descriptions of *D. capricornia* (i.e. Martin, 1981), and thus it is not an additional adhesive tube as it appears to be in the specimens under study.

The head drawn out into a muzzle surrounded by a ciliary band, along with the uniform cuticular covering (i.e. absence of scales of distinctly different shape around the peri-anal area and/or on the furcal branches), a primary hermaphroditic condition and the habitat they live in (i.e. marine settings) approach the specimens under study to the species of the genus *Musellifer*. However, *Diuronotus aspetos* sp. nov. and *D. rupperti* sp. nov. cannot be assigned to *Musellifer* without grossly extending its generic boundaries. This is primarily due to the presence of the supernumerary adhesive tubes on the furcal branches that makes the new species unique amidst Chaetonotidae, and the presence of scales along the shaft of these adhesive tubes which appears to be an autoapomorphy of these taxa. The much smaller furca/total body length ratio (less than $\frac{1}{7}$ in *Diuronotus* versus up to $\frac{1}{3}$ in *Musellifer*), the different shape of the scales (elongate, with a strong keel ending with a spiny process in *Diuronotus*

versus sub-rounded to rhomboidal, with or without a week keel ending into a tiny filament or a seta in *Musellifer*) should further contribute to differentiate the species of the two genera. The greatly different length of the secondary adhesive tubes shown in specimens of the two new species (up to 59.9 μm in *D. aspetos* versus up to 8.5 μm in *D. rupperti*) should easily allow their discrimination. Furthermore, juvenile specimens of *D. rupperti* totally lack the secondary adhesive tubes.

CONCLUSION

Ruppert (1988) figured a chaetonotid gastrotrich belonging to a new genus and species, of which he later on provided ultrastructural data concerning the muscle organization (Ruppert 1991). None of the recent papers on Gastrotricha phylogeny has taken this taxon into account (e.g. Hochberg & Litvaitis, 2000; Todaro et al., 2003; Zrzavy, 2003), likely due to the fact that the specimens found by Ruppert were not formally described. Since we regard Ruppert's species to be at least congeneric with the present ones, it is hoped that, in a larger framework, the formal systematization of these animals may contribute to future debate on the reconstruction of the evolutionary pathways within Gastrotricha and especially Chaetonotida. From a biogeographical point of view, Ruppert's record is illuminating; even though the author did not provide indications about the sampling sites of the new genus and species, it is very likely that his specimens were from the Atlantic coast of the USA, therefore making the geographical range of *Diuronotus* much wider than it appears from our data. Only future research can reveal a possible cosmopolitan distribution of the new genus, as it is in the case of most gastrotrich genera.

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