

This article was downloaded by: [University of Massachusetts Lowell], [Rick Hochberg]

On: 15 August 2012, At: 03:51

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



## Marine Biology Research

Publication details, including instructions for authors and subscription information:  
<http://www.tandfonline.com/loi/smar20>

### Tetranchyroderma bronhostylus sp. nov., the first known gastrotrich (Gastrotricha) with a sclerotic canal in the caudal organ

Sarah Atherton<sup>a</sup> & Rick Hochberg<sup>a</sup>

<sup>a</sup> University of Massachusetts Lowell, Lowell, Massachusetts, USA

Version of record first published: 15 Aug 2012

To cite this article: Sarah Atherton & Rick Hochberg (2012): Tetranchyroderma bronhostylus sp. nov., the first known gastrotrich (Gastrotricha) with a sclerotic canal in the caudal organ, Marine Biology Research, 8:9, 885-892

To link to this article: <http://dx.doi.org/10.1080/17451000.2012.676187>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.



ORIGINAL ARTICLE

## ***Tetranchyroderma bronhostylus* sp. nov., the first known gastrotrich (Gastrotricha) with a sclerotic canal in the caudal organ**

SARAH ATHERTON & RICK HOCHBERG\*

University of Massachusetts Lowell, Lowell, Massachusetts, USA

### **Abstract**

A new species of *Tetranchyroderma* (Macrodasysida: Gastrotricha) is described from coarse sediments at 9 m depth at Capron Shoals, Florida. *Tetranchyroderma bronhostylus* sp. nov. is distinguished primarily by the presence of a sclerotic canal within the accessory caudal organ, and represents the first species of *Tetranchyroderma* described with such a feature. The following combination of characters further distinguish this species from its congeners: an oral hood with a scalloped margin, paired cephalic tentacles, paired sensorial organs, a pentancrous cuticle, three pairs of dorsolateral adhesive tubes, one pair of ventrolateral adhesive tubes in the pharyngeal region and up to 11 pairs of ventrolateral tubes in the trunk region, and one pair of lateral adhesive tubes close to the paired caudal pedicles.

**Key words:** *Gastrotricha*, *interstitial*, *hermaphrodite*, *meiofauna*, *taxonomy*

### **Introduction**

Thaumastodermatidae is the most speciose family of marine Gastrotricha and accounts for the majority of Macrodasysida with elaborate cuticular features. The cuticle, which is bilayered and surrounds the entire body, is ornamentally complex in most species and often consists of various spines and scales (Rieger & Rieger 1977). Few described species of Gastrotricha also bear cuticular/sclerotic structures within their reproductive systems, e.g. hardened canals or protrusible stylets (e.g. Schoepfer-Sterrer 1974; Ruppert 1991), although such features are regularly found in other hermaphroditic meiofauna such as species of Gnathostomulida (Mainitz 1977) and Platyhelminthes (Rieger 1977).

The first observations of cuticular reproductive structures in Gastrotricha were made on species of *Macrodasys* (e.g. Remane 1950; Wilke 1954), which appeared to bear a cuticular nozzle on the tip of a sperm-bearing accessory organ (see Schoepfer-Sterrer 1974), later determined to be part of a broken stylet from a copulating partner (see Ruppert 1991 for terminology and explanations). Currently, most

descriptions of stylets in Gastrotricha come from studies of *Urodasys*, which includes several species that bear a stylet bulb (Schoepfer-Sterrer 1974; Fregni et al. 1999). Stylets are presumably derived from secretions of the bulb lumen (Ruppert 1991). Although no ultrastructural or functional accounts of stylets exist for any species, stylet shape appears to have high taxonomic value (see Schoepfer-Sterrer 1974), especially considering its rarity within Gastrotricha. Within Thaumastodermatidae, stylet-bearing accessory organs are only known from *Oregodasys styliferus* (Boaden, 1965), although sclerotic reproductive canals may be common throughout the family but not easily recognizable. Ruppert (1991) presented details on sclerotic canals in species of *Tetranchyroderma* (two canals lead to paired caudal glands) and *Acanthodasys* (singular canal that connects the oviduct and rosette gland), but the functional significance of these canals and their utility in taxonomic investigations remains unknown. To date, there are no descriptions of sclerotized canals within the accessory reproductive organs of any species of *Tetranchyroderma* – the largest genus of Thaumastodermatidae.

\*Correspondence: Rick Hochberg, University of Massachusetts Lowell, One University Avenue, Lowell, MA 01854, USA. E-mail: rick\_hochberg@uml.edu

Published in collaboration with the University of Bergen and the Institute of Marine Research, Norway, and the Marine Biological Laboratory, University of Copenhagen, Denmark

During a recent survey of the marine Gastrotricha of Capron Shoal, Florida, we discovered an undescribed species of *Tetranchyroderma* with a sclerotic canal in its caudal organ. The structure bears superficial resemblance to the stylets of species of *Urodasys* (Schoepfer-Sterrer 1974) and *Oregodasys* (Boaden 1965), and constitutes the first report of a species of *Tetranchyroderma* with a sclerotic canal in the caudal organ.

### Materials and Methods

Sediments were collected from Capron Shoal, Florida (USA) on 9 August 2011 using a small anchor dredge (29 × 12 cm opening) suspended from Smithsonian Marine Station's R/V *Sunburst*. The dredge was trawled for 6 min along the shoals (Dredge in: 27° 29.78' N, 80° 13.73' W; Dredge out: 27° 29.99' N, 80° 13.72' W). Extraction and grain size analysis of the sediments took place at the Smithsonian Marine Station in Fort Pierce, Florida.

Gastrotrichs were extracted using the anesthetization-decantation technique with 7.5% MgCl<sub>2</sub> and a 63 µm mesh. Animals were sorted in Petri dishes using a Leica EZ4 stereomicroscope and examined at higher magnification with a Zeiss A1 compound microscope equipped with DIC optics and a Sony Handycam digital video camera. Measurements were taken with an ocular micrometer. Position of individual structures and organs is reported in terms of percentage body units, with total body length measured as 100 units (anterior is U00, posterior tip is U100). Abbreviations used in the text and figures follow the style of Hummon (2008).

Video records of holotype and paratype specimens were submitted to the Smithsonian Institution's National Museum of Natural History (NMNH) for archiving through their Licence Agreement. All records may be made available through the NMNH's electronic on-line catalogue.

Grain size analysis was performed on ~500 cm<sup>3</sup> of sediment by drying the sediments in a 100°C oven for 24 h prior to fractionation on a mechanical Gilson SS-15 Sieve Shaker with mesh sizes 2 mm, 1 mm, 500 µm, 250 µm, 125 µm and 63 µm. The program GRANPLOTS with line segment (Balsillie et al. 2002) was used to calculate the phi values for the different sediment fractions.

### Taxonomy

**Phylum Gastrotricha** Metschnikoff, 1865

**Order Macrodasyida** Remane, 1925 [Rao & Clausen, 1970]

**Family Thaumastodermatidae** Remane, 1927

**Subfamily Thaumastodermatinae** Remane, 1927

**Genus *Tetranchyroderma*** Remane, 1926

***Tetranchyroderma bronchostylus* sp. nov.**

Figures 1–4

*Materials examined.* Three adult specimens observed with DIC optics; two of the specimens (holotype and paratype) were sacrificed for molecular sequencing at a future date; one specimen was accidentally destroyed during photography.

*Holotype.* Video record of one adult specimen, 288 µm long. Smithsonian Cat. No. 1172360.

*Paratype.* Video record of one adult specimen, 240 µm long, Smithsonian Cat. No. 1172361.

### Diagnosis

A *Tetranchyroderma* with an adult body length to 288 µm; body narrows to 38 µm at U29 before slightly widening at the pharyngeointestinal junction (PIJ) at U36 and reaching 58 µm width at U50; body then narrows toward caudal lobes. Oral hood scalloped, with sensory hairs, and cephalic tentacles at U03; mouth to 53 µm wide with ventral margin bearing numerous sensory papillae and cilia, leads into pharynx to 79 µm long; pharyngeal pores at base. Sensory hairs numerous to 15 µm long and form lateral columns along margin of body. Epidermal glands to 10 µm diameter, with up to 10 glands per side. Cuticular armature consists of pentaneres of small to medium size with tines of equal length. Adhesive tubes: TbA, 3 per side forming a row, the medial tube short, the second tube robust and elongate, the lateral tube short and directed laterally; TbL, one per side at U84; TbVL, one small pair at U16 and up to 11 per side beginning just posterior of PIJ and extending to U83; TbDL, 3 per side, to 17 µm long at U23, U40 and U59; 3 terminal TbP, all on pedicle, with one additional pair of tubes on inner margin of pedicle. Ventral locomotory cilia continuous from U09 to the caudal end. Reproductive system: single testis on right side of body, leads to muscular caudal organ containing a sclerotic canal; caudal organ is invested with circular and spiral muscles. Ovoid frontal organ anterior to caudal organ; large egg present at mid-body region.

### Description

The description is based on the largest adult specimen (holotype), 288 µm in total length (Figures 1–4).

Pharynx to 79  $\mu\text{m}$  in length as measured from the ventral mouth margin to the pharyngo-intestinal junction (PIJ) at U36. Head highly scalloped; body short with pharyngeal region that narrows to 38  $\mu\text{m}$  at U29 before widening toward midpoint of body (53  $\mu\text{m}$ ) and narrowing again gradually to the base of the caudum. Widths of mouth/midpharynx/PIJ/mid-trunk/caudal base are as follows: 53/36/40/53/21  $\mu\text{m}$  at U09/U25/U36/U50/U90, respectively. Oral hood with undulating border bearing two pairs of stiff sensory cilia to 14  $\mu\text{m}$  long and several mobile cilia to 10  $\mu\text{m}$  long; the anterior 18  $\mu\text{m}$  of hood is free of cuticular ornaments but bears a pair of 10  $\mu\text{m}$  long rod-like, cephalic tentacles at U03, several whip-like cilia to 15  $\mu\text{m}$  long, and stiff cilia to 10  $\mu\text{m}$  long at  $\sim$ U09. The mouth of 53  $\mu\text{m}$  width has numerous papillae with sensory hairs to 5  $\mu\text{m}$  long; shorter sensory cilia to 3  $\mu\text{m}$  dispersed between papillae. A tuft of sensory cilia to 15  $\mu\text{m}$  long, some stiff and

others limp, project out from the lateral mouth margin  $\sim$ U08. A pair of anteriorly directed, 10  $\mu\text{m}$  long spatulate, sensorial organs insert just behind lateral mouth margin at U09. Numerous stiff cilia to 15  $\mu\text{m}$  long project from either side of lateral body wall and form a column down to the caudal pedicles. Glands of varying size, from 5 to 10  $\mu\text{m}$  diameter, oval in shape, distributed from U21 to U82.

*Cuticular armature.* The dorsal and lateral covering of pentaneres is complete (without bare patches), forming 13–16 columns (Figure 1A, B and 3A). Pentaneres begin at the base of the oral hood (U09) and form staggered rows made up of the smallest aneres on the body, to 2  $\mu\text{m}$  diameter (tine to tine) (Figure 2B). Pentaneres double in size immediately posterior of the smallest aneres and reach a maximum diameter of 8  $\mu\text{m}$  at  $\sim$ U30. Tines are only slightly curved and have approximately equal length.

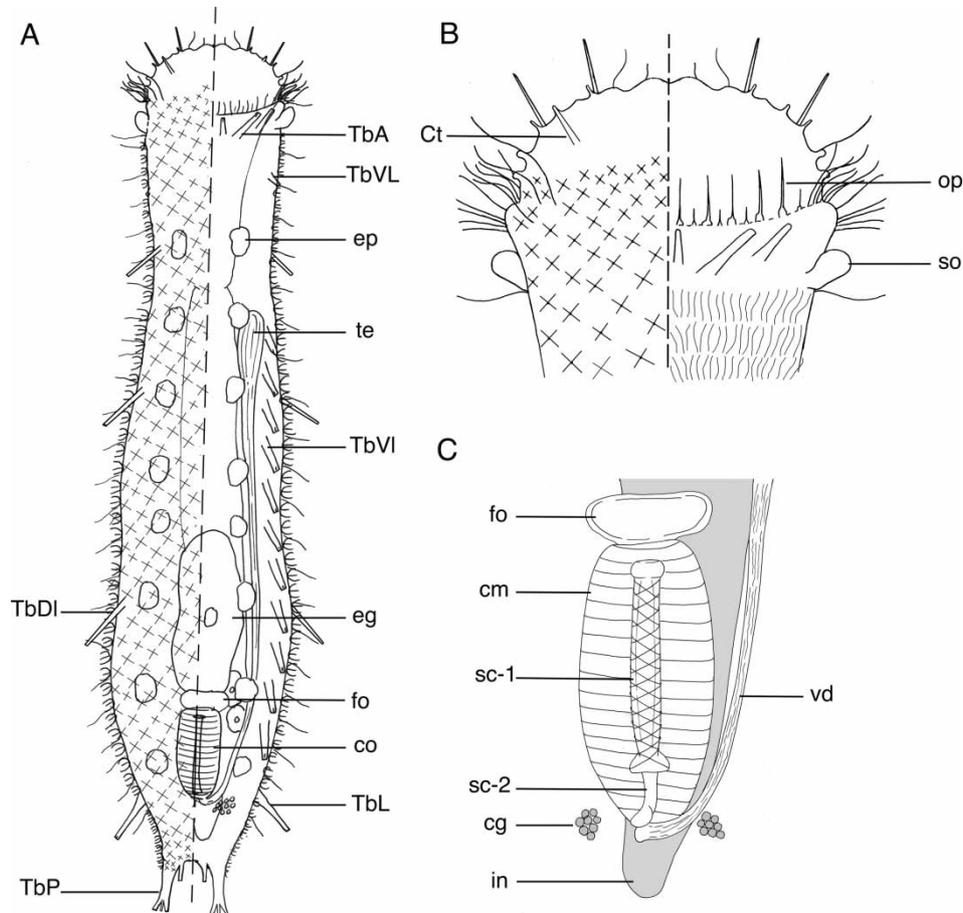


Figure 1. *Tetranchyroderma bronchostylus* sp. nov. (A) Composite sketch of dorsal (left) and ventral (right) sides as viewed from above (scale bar = 50  $\mu\text{m}$ ); (B) composite sketch of head showing dorsal (left) and ventral (right) views (scale bar = 15  $\mu\text{m}$ ); (C) schematic of a portion of the reproductive system (scale bar = 25  $\mu\text{m}$ ). Abbreviations: co, caudal organ; cg, caudal glands; cm, circular muscles of the caudal organ; ct, cephalic tentacle; eg, mature egg; ep, epidermal gland; fo, frontal organ; in, intestine; op, oral papillae of ventral mouth margin; so, spatulate sensory organ; sc-1, columnar portion of the sclerotic canal; sc-2, arm portion of the sclerotic canal; TbA, anterior adhesive tubes; TbDI, dorsolateral adhesive tubes; TbL, lateral adhesive tubes; TbP, posterior adhesive tubes; TbVI, ventrolateral adhesive tubes; te, right testis; vd, vas deferens.

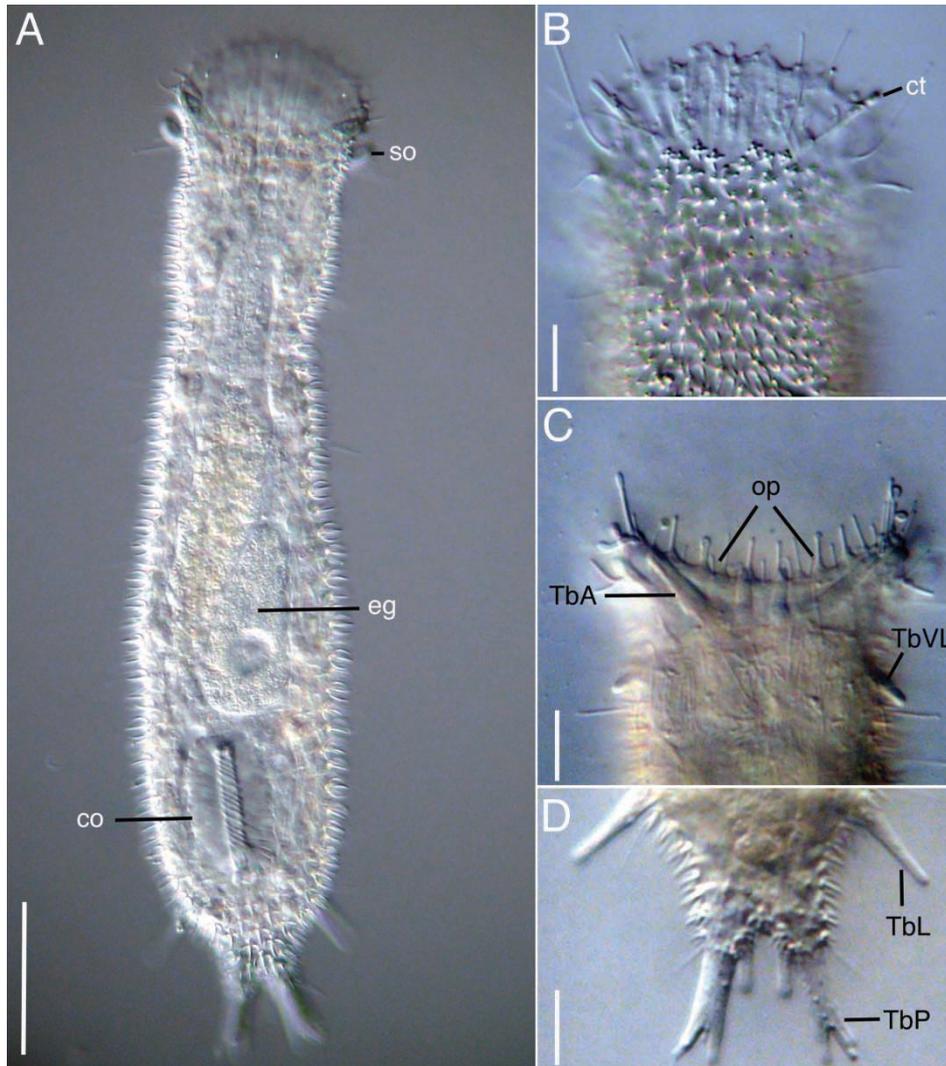


Figure 2. *Tetranchyroderma bronchostylus* sp. nov., DIC photomicrographs. (A) Adult specimen, holotype (scale bar = 40  $\mu$ m); (B) dorsal view of the head of the holotype (scale bar = 10  $\mu$ m); (C) ventral view of the head of the holotype (scale bar = 10  $\mu$ m); (D) posterior end (scale bar = 8  $\mu$ m). Abbreviations: co, caudal organ; ct, cephalic tentacles; eg, mature egg; op, oral papillae; so, cephalic sensory organ; TbA, anterior adhesive tubes; TbL, lateral adhesive tubes; TbP, posterior adhesive tubes.

Pentacres extend to the base of the caudal pedicles and are  $\sim 3$   $\mu$ m in diameter.

**Adhesive tubes.** Three anterior adhesive tubes (TbA) per side arise directly from body surface: one medial tube is directed anteriorly and  $\sim 7$   $\mu$ m in length; the second tube is 15  $\mu$ m long, robust and directed anterolaterally; the third tube is 10  $\mu$ m long and also directed anterolaterally (Figure 1B). One pair of robust lateral adhesive tubes (TbL) on each side of the body at U84; each tube is directed posterolaterally and about 15  $\mu$ m long. One pair of small (3  $\mu$ m) ventrolateral adhesive tubes (TbVL) at U16. Up to 11 TbVL begin at U38, all approximately 5–7  $\mu$ m long, and extend to U82. Three dorsolateral adhesive tubes (TbDL), each relatively thin, present at U23 (12  $\mu$ m), U40 (16  $\mu$ m) and U59 (17  $\mu$ m)

(Figure 1). Paired caudal pedicles at posterior end, each bearing three terminal adhesive tubes about 6–7  $\mu$ m long; the middle tube is thinner and projects dorsally. A single robust adhesive tube to 8  $\mu$ m long arises off the inner margin of each pedicle.

**Cilia.** Ventral locomotory cilia continuous down the length of the body, extending from approximately U09 to the caudal pedicles. A bare patch is present in around U88–90.

**Digestive tract.** Mouth subterminal to 53  $\mu$ m wide beneath oral hood (Figure 2C). Pharynx to 79  $\mu$ m long  $\times$  25  $\mu$ m wide. Pharyngeal pores near base of pharynx, around U40–41. Intestine narrow and tapering at posterior. Anus around U93.

*Reproductive system.* Hermaphroditic, with a single right testis (as viewed from above) at the pharyngo-intestinal junction (Figures 1–4). The vas deferens extends posteriorly to the distal region of the caudal organ at about U91 (Figure 1A, C). No muscles were observed around the distal portion of the vas deferens. The caudal organ is approximately 43  $\mu\text{m}$  long and heavily ensheathed in an external coat of circular muscles (Figures 3 and 4). Dextrally coiled spiral muscles form an internal layer that wraps around a sclerotized canal. The canal appears to be divided into two sections (Figures 1C and 4). The section that forms the main body of the canal is columnar, 38  $\mu\text{m}$  long, and with an anterior rim and a posterior swelling near the distal end of the caudal organ. The column appears hollow. At the distal end of the canal is a second section that appears to form a

‘c-shaped’ arm. This portion of the canal does not appear to be wrapped in spiral muscles and appears to extend out the distal end of the caudal organ. A possible frontal organ (seminal receptacle), which appears as a flattened sac atop the caudal organ, was devoid of sperm; the paratype had no distinguishable frontal organ. A single ovary is present on the right side of the animal; eggs mature from a posterior position close to the distal end of the vas deferens and the caudal organ, with the most mature ova in proximity to the frontal organ on the dorsal side of the midgut.

*Etymology.* This species is named for the windpipe-like appearance of the sclerotized canal (Gr, *branch*, windpipe; Gr, *stylus*).

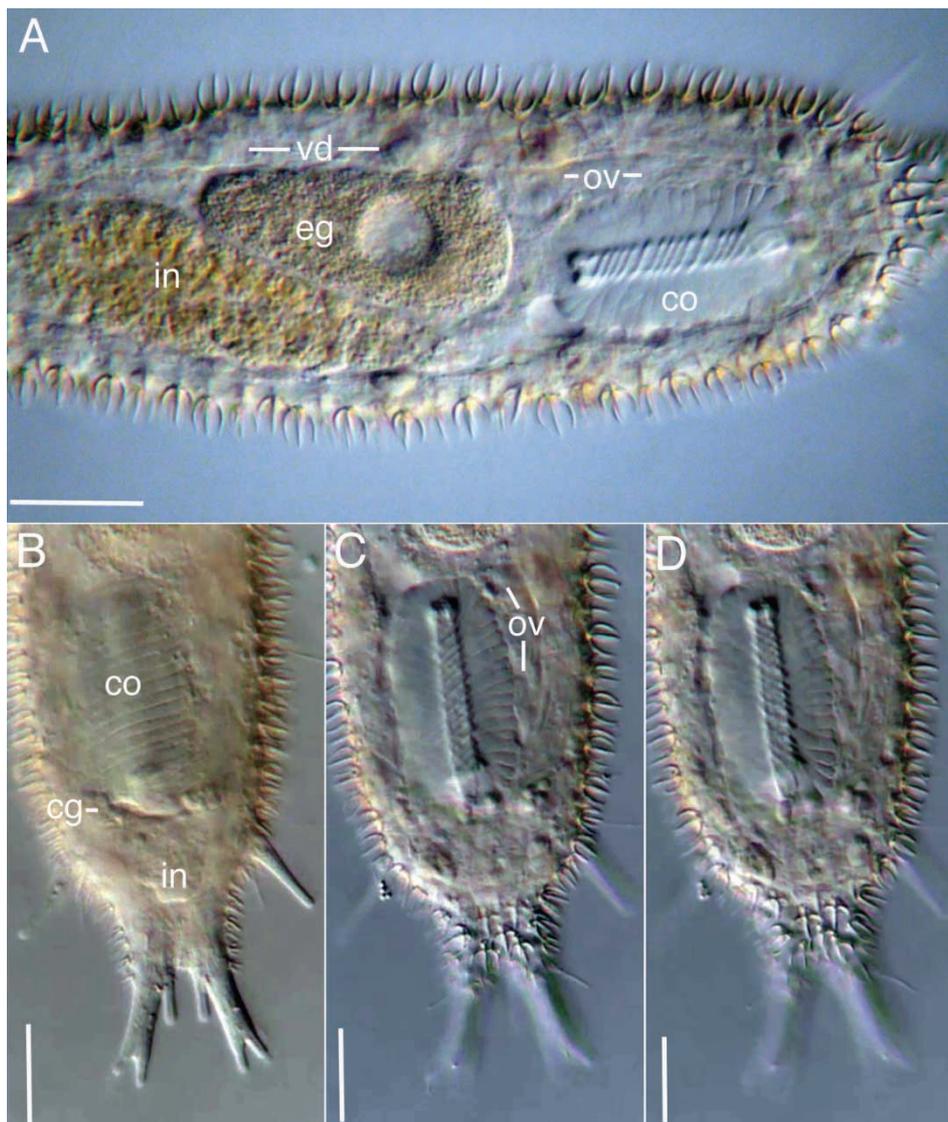


Figure 3. *Tetranychoderma bronchostylus* sp. nov. (A) Focus on reproductive anatomy in posterior trunk (scale bar = 12  $\mu\text{m}$ ); (B–D) different focal planes (ventral to dorsal) through the caudal organ (scale bars = 12  $\mu\text{m}$ ). Abbreviations: cg, caudal glands; co, caudal organ; eg, mature egg; in, intestine; ov, immature ova; vd, vas deferens.

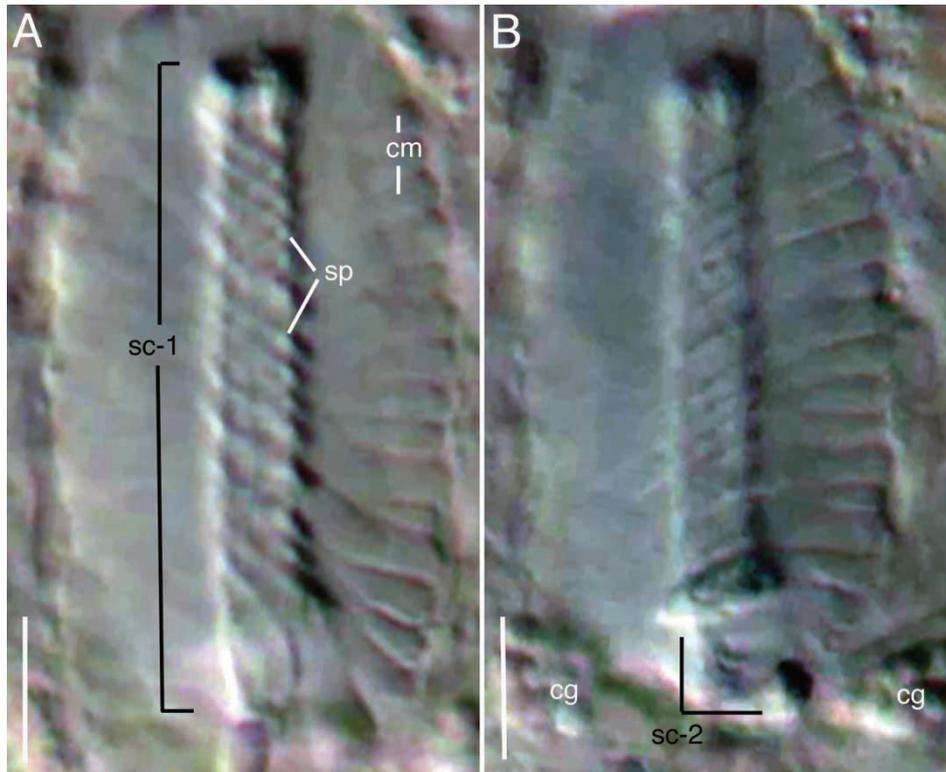


Figure 4. *Tetranchyroderma bronchostylus* sp. nov. (A,B) Close-ups of the sclerotic canal (sc) within the caudal organ as seen through different focal planes (dorsal to ventral). The sclerotic canal is made up of an anterior column (sc-1) and a posterior arm (sc-2). Circular muscles (cm) wrap around the entire caudal organ, while spiral muscles (sp) ensheath the internal canal. Scale bars = 10  $\mu\text{m}$ .

**Locality.** Capron Shoal, Florida ( $27^{\circ}26.52' \text{ N}$ ,  $80^{\circ}13.81' \text{ W}$ ), 9 m depth, coarse sand (mean 1.66 phi; standard deviation 0.72 phi units; skewness  $-0.95$ ; and kurtosis 5.11). Sediments collected via anchor dredge.

#### Taxonomic affinities

To date, there are approximately 69 species of *Tetranchyroderma* described from marine sediments across the globe, including both temperate and tropical waters (Hummon 2009; Hummon & Todaro 2010). Most species of *Tetranchyroderma* are easily identified based on the ornamentation of their cuticle, which bears either 3-, 4- or 5-pronged spines called triances, tetranques or pentanques, respectively (Todaro 2002). Some species may possess more than one type of ancre (e.g. *T. paradoxum* Thane-Fenchel, 1970), and some anques may form feather-shaped scales (e.g. *T. adela* Hochberg, 2008).

Approximately half the described species of *Tetranchyroderma* possess pentanques, which is the case with *T. bronchostylus* sp. nov. Among the species with a full dorsal covering of only pentanques, five species also possess head appendages similar to those of the new species: *T. antenniphorum* Hummon & Todaro, 2010 (= *T. antennatum* Luporini, Maganini

& Tongiorgi, 1973; see Hummon & Todaro 2010), *T. enalosum* Hummon, 1977, *T. esarabdophorum* Tongiorgi & Balsamo, 1984, *T. papii* Gerlach, 1953 and *T. sardum* Todaro, Balsamo & Tongiorgi, 1988. Within this group of five species, only *T. esarabdophorum* also possesses three pairs of dorsal cirrata-like adhesive tubes similar to those of the new species. However, these two species can be easily distinguished by the larger number of ventrolateral adhesive tubes (22/side) in *T. esarabdophorum* and by the structure of their reproductive systems. In particular, the caudal organ of the new species contains a well-developed sclerotized canal that has yet to be recorded from any other species in the genus.

#### Discussion

Hypodermic impregnation is hypothesized to be the plesiomorphic form of copulation among gastrotrichs, yet the presence of sclerotic/cuticular canals and/or stylets that might function in impregnation are rare in the Gastrotricha (Ruppert 1991). Cuticular stylets in various shapes and sizes occur in several species of *Urodasya* (Macrodasyidae; see Schoepfer-Sterrer 1974; Fregni et al. 1999), where they probably form as secretions (intra- or extra-

cellular is unknown; Ruppert 1991) in the lumen of the stylet bulb. In most species, the vas deferens does not appear to transport autosperm directly to the stylet bulb but instead to a male pore at midbody where sperm are picked up by the bulb via a twisting of the body (as in *Macrodasyus*; see Ruppert 1978a). Alternatively, most species of Thaumastodermatinae (*Pseudostomella*, *Ptychostomella*, *Tetranchyroderma*, *Thaumastoderma*) possess a vas deferens that terminates close to the posterior end of the body near the distal end of the caudal organ, where they may share a common pore. In some species, this region of the vas deferens is heavily invested with muscles, which led Ruppert (1978b, 1991) to speculate that the distal portion of the vas deferens originated from a splitting of the ancestral caudal organ, and hence, took on the 'male' function of what was originally a dual function (bipartite male and female) caudal organ. The remaining portion of the caudal organ, which is also muscular but contains a canal and is anatomically connected to the frontal organ (= seminal receptacle), is the 'female' portion. The fact that the caudal organ and frontal organ share a continuous lumen hints at their shared 'female' function in sperm reception. However, there is not sufficient anatomical or functional evidence to support this hypothesis, and so the evolution of the caudal organ/frontal organ system and their anatomical and functional diversity among species of Thaumastodermatidae remains unknown.

To date, the only known species of Thaumastodermatinae to possess a cuticular/sclerotic stylet in any portion of the reproductive system is *Oregodasyus styliferus* (Boaden 1965). In this species, a funnel-shaped stylet is present in the distal end of the vas deferens (= 'male' portion of the caudal organ *sensu* Ruppert 1978b), while the caudal organ *sensu strictu* contains a cuticular mouthpiece (which may be a broken piece of stylet from a copulating partner). Further details on this species, including photographic and structural accounts of the stylet, are lacking, and so the ultimate function of the stylet remains to be determined.

Interestingly, in *T. bronchostylus* sp. nov., the sclerotic canal is not present in the vas deferens as in *O. styliferus*, but instead, in the caudal organ body. The caudal organ of the new species is a large muscular cylinder with a distal opening to a gonopore (shared with the vas deferens) and a proximal opening to the frontal organ; this is similar to what has been observed in other species of Thaumastodermatinae (Ruppert 1978b, 1991). Based purely on light microscope observations, the caudal organ's sclerotic canal appears to be a hollow cylinder with thickened walls and a proximal opening. Circular muscles form an external sheath around the caudal

organ, and spiral muscles wrap around the main body of the canal. Neither group of muscles appears to contain the distal c-shaped arm of the canal, which protrudes from the distal end of the caudal organ (see Figure 4). Based on the orientation of the canal, the presence of spiral muscles around its main axis, and its proximity to the vas deferens, one might speculate that the sclerotic canal functions as an intromittent organ for copulation. Contraction of the spiral muscles, from anterior to posterior would result in canal protrusion, thereby 'paving' the way for sperm entry into the partner. However, such a functional hypothesis will require further evidence prior to acceptance, generally in the form of ultrastructural data on the canal and behavioral observations of mating. A recent phylogeny of the Thaumastodermatidae by Todaro et al. (2011) should provide the necessary background for understanding the evolution of this unique reproductive feature in species of *Tetranchyroderma*.

### Acknowledgements

The authors gratefully acknowledge Dr M. Antonio Todaro and Dr Alexander Kieneke for their helpful comments on an earlier version of this manuscript. We thank Hugh Reichardt and the staff and scientists of the Smithsonian Marine Station in Fort Pierce, Florida for their assistance in sample collection and their hospitality. This is Smithsonian Marine Station contribution number # 873. This material is based upon work supported by the National Science Foundation under Grant No. DEB 0918499 to R. Hochberg.

### References

- Balsillie JH, Donoghue JF, Butler KM, Koch JL. 2002. Plotting equation for Gaussian percentiles and a spreadsheet program for generating probability plots. *Journal of Sedimentary Research* 72:929–33.
- Boaden PJS. 1965. Two new interstitial Gastrotricha of the family Thaumastodermatidae. *Pubblicazioni della Stazione Zoologica di Napoli* 34:219–25.
- Fregni E, Faienza MG, Grimaldi SDZ, Tongiorgi P, Balsamo M. 1999. Marine gastrotrichs from the Tremiti archipelago in the southern Adriatic Sea, with the description of two new species of *Urodasyus*. *Italian Journal of Zoology* 66:183–94.
- Gerlach SA. 1953. Gastrotrichen aus dem Kuestengrundwasser des Mittelmeeres. *Zoologischer Anzeiger* 150:203–11.
- Hochberg R. 2008. Ultrastructure of feathered trianeres in the Thaumastodermatidae and the description of a new species of *Tetranchyroderma* (Gastrotricha: Macrodasyida) from Australia. *Journal of the Marine Biological Association of the UK* 88:729–37.
- Hummon WD. 1977. Introgressive hybridization between two intertidal species of *Tetranchyroderma* (Gastrotricha, Thaumastodermatidae) with the description of a new species. *Mikrofauna Meeresboden* 61:113–36.

- Hummon WD. 2008. Gastrotricha of the North Atlantic Ocean: 1. Twenty four new and two redescribed species of Macrodasys. *Meiofauna Marina* 16:117–74.
- Hummon WD. 2009. Global database for marine Gastrotricha (Taxonomic, Geographic, Bibliographic and Video). <http://hummon-nas.biosci.ohiou.edu> (accessed on 2 August 2012).
- Hummon WD, Todaro MA. 2010. Analytic taxonomy and notes on marine, brackish-water and estuarine Gastrotricha. *Zootaxa* 2392:1–32.
- Luporini P, Magagnini G, Tongiorgi P. 1973. Gastrotrichi macrodasioidei delle coste della Toscana. *Pubblicazioni della Stazione Zoologica di Napoli* 38:267–88.
- Mainitz M. 1977. The fine structure of the stylet apparatus in Gnathostomulida Scleroperalia and its relationship to turbellarian stylets. *Acta Zoologica Fennica* 154:163–74.
- Metschnikoff E. 1865. Ueber einige wenig bekannte niedere Thierformen. *Zeitschrift für Wissenschaftliche Zoologie* 15:450–63.
- Rao CG, Clausen C. 1970. *Planodasys marginalis* gen et. sp. nov. and *Planodasyidae* fam. nov. (Gastrotricha Macrodasyoidea). *Sarsia* 42:73–82.
- Remane A. 1925. Organisation und systematische Stellung der aberranten Gastrotrichen. *Zoologischer Anzeiger Supplementband* 1:121–28.
- Remane A. 1926. Morphologie und Verwandtschaftsbeziehungen der aberranten Gastrotrichen I. *Zeitschrift für Morphologie und Ökologie der Tiere* 5:625–754.
- Remane A. 1927. Neue Gastrotricha Macrodasyoidea. *Zoologische Jahrbücher (Abteilung für Systematik, Ökologie, und Geographie der Tiere)* 53:269–320.
- Remane A. 1950. *Macrodasys africanus* nov. spec., ein Gastrotrich von der Kueste Suedwest-Afrikas. *Kieler Meeresforschung* 7:35–37.
- Rieger RM. 1977. Morphology of the Turbellaria at the ultrastructural level. *Hydrobiologia* 84:213–29.
- Rieger GE, Rieger RM. 1977. Comparative fine structure study of the gastrotrich cuticle and aspects of cuticle evolution within the Aschelminthes. *Zeitschrift für Zoologie Systematik und Evolutionsforschung* 15:81–124.
- Ruppert EE. 1978a. The reproductive system of gastrotrichs. II. Insemination in Macrodasys: A unique mode of sperm transfer in Metazoa. *Zoomorphologie* 89:207–28.
- Ruppert EE. 1978b. The reproductive system of gastrotrichs. III. Genital organs of Thaumastodermatinae subfam. n. and Diplodasyinae subfam. n. with discussion of reproduction in Macrodasyoidea. *Zoologica Scripta* 7:93–114.
- Ruppert EE. 1991. Gastrotricha. In: Harrison FW, Ruppert EE, editors. *Microscopic Anatomy of Invertebrates* Vol. 4, Aschelminthes. New York, NY: Wiley-Liss, p 41–109.
- Schoepfer-Sterrer C. 1974. Five new species of *Urodasys* and remarks on the terminology of the genital organs in Macrodasyoidea (Gastrotricha). *Cahiers de Biologie Marine* 15:229–54.
- Thane-Fenchel A. 1970. Interstitial gastrotrichs in some south Florida beaches. *Ophelia* 7:113–38.
- Todaro MA. 2002. An interesting new gastrotrich from littoral meiobenthos (Long Beach Island, USA), with a key to species of *Tetranchyroderma* (Gastrotricha: Macrodasyoidea). *Journal of the Marine Biological Association of the United Kingdom* 82:555–63.
- Todaro MA, Balsamo M, Tongiorgi P. 1988. *Tetranchyroderma sardum*, a new species of the family Thaumastodermatidae (Gastrotricha, Macrodasyoidea). *Bollettino di Zoologia* 55:69–72.
- Todaro MA, Kanneby T, Dal Zotto M, Jondelius U. 2011. Phylogeny of Thaumastodermatidae (Gastrotricha: Macrodasyoidea) inferred from nuclear and mitochondrial sequence data. *PLoS One* 6:e17892. 13 pages.
- Tongiorgi P, Balsamo M. 1984. A new *Tetranchyroderma* species (Gastrotricha, Macrodasyoidea) from the Adriatic coast. *Bollettino di Zoologia* 51:335–38.
- Wilke U. 1954. *Mediterrane Gastrotrichen*. *Zoologische Jahrbücher Systematik (Jena)* 82:497–550.

*Editorial responsibility: Tomas Cedhagen*