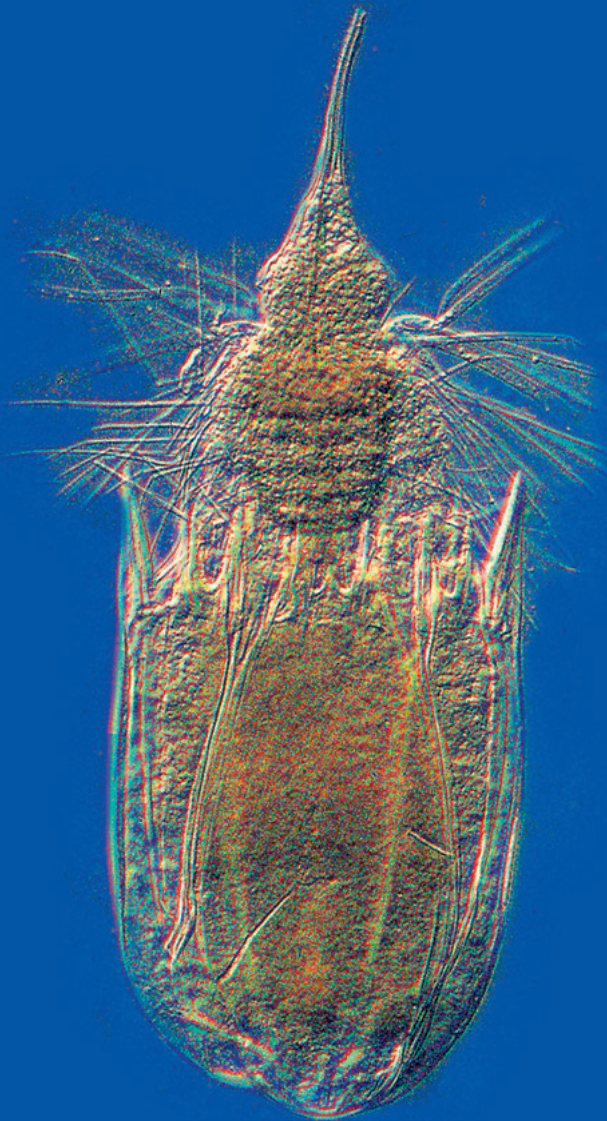


# MEIOFAUNA MARINA

Biodiversity, morphology and ecology  
of small benthic organisms

17



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***Tetranchyroderma parapapii* n. sp.**  
**(Gastrotricha, Thaumastodermatidae),**  
**a North American analog to the European *T. papii*,**  
**with a redescription of the latter**

William D. Hummon\*

**Abstract**

A mistaken case of amphi-Atlantic distribution is rectified. The North American species of *Tetranchyroderma*, having pentancreas and elongate lateral cephalic tentacles has been referred to as *T. papii* since I first published its occurrence in Massachusetts (Hummon 1967). Subsequently, my identification has universally been accepted in this region. In light of further morphological information on both the European and the North American forms, that identification has to be recinded. There follows a description of a new species from North America, *Tetranchyroderma parapapii*, followed by a redescription of the European species, *T. papii* Gerlach, 1953. Both have pentancreas armature, and also have rod-like tentacles atop the oral hood and elongate spathiform tentacles on either side of the mouth; both lack dorsal adhesive tubes. As an adult, *T. parapapii* has a shorter pharynx length relative to total body length and a shorter oral hood length relative to head width than comparably sized *T. papii*. *T. parapapii* has 4-5 TbA and 33-34 TbL per side, along with 1-2 TbV per side, which are difficult to see because they are only somewhat more ventral than tubes of the lateral column, and also has hip-like prominences, while *T. papii* has but 4 TbA and 25-28 TbVL per side and lacks both TbV and hips.

Key words: benthic, meiofauna, cosmopolitanism, Macrodasyida

**Introduction**

*Tetranchyroderma papii* Gerlach, 1953 was described from San Rossore, Tuscany, Italy. It was mentioned again (Gerlach 1955) and recorded once more (Fize 1963) in Europe before I reported it from North America (Hummon 1967 abstract), and more recently in Europe by Luporini et al. (1971), Westheide (1972), Todaro & Balsamo (1990), Balsamo et al. (1995, 1996), Todaro et al. (2002), and Todaro et al. (2003). It has also been

reported in faunal lists by Balsamo & Tongiorgi (1995) and Todaro et al. (2006); a key by Todaro (2002), with greater faunistic and distributional detail by Todaro et al. (2000); and in a study of molecular genetics by Todaro et al. (2003). Videos of this species are included in the list of Hummon et al. (2005) and on the server of Hummon (2008). The North American species of *Tetranchyroderma*, having pentancreas, rod-like tentacles on the oral hood, and elongate spathiform tentacles on either side of the mouth, has been universally accepted

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as *T. papii* since I first published it for this region (Hummon 1967 abstract). Additional citations of this species as *T. papii* include: systematics (Hummon 1969), geography (Hummon 1968, 1974; Ruppert & Hogue 1978), ecology and tolerance physiology (Hummon 1969, 1975; Ruppert 1977), morphology (McGeary 1974), hybridization (Hummon 1977), and anatomy (Gagne 1980: palps, Tyler & Reiger 1980: adhesive organs, and Hochberg & Litvaitis 2001a,b: musculature). This mistaken case of an amphi-Atlantic distribution is here rectified. In light of further morphological information on both the European and the North American forms, the identification of the North American species as *T. papii* has to be recinded.

In 1968, Ruppert Riedl and Anna Thane-Fenchel visited Woods Hole from Chapel Hill. Riedl asked how I knew that species which I listed as cosmopolitans were really so. I answered that the question must be reviewed on a case by case basis using available evidence. While there, Thane-Fenchel showed me her new tetrancrous species of *Thaumastoderma* from Miami. Though I told her it was a *Tetranchyroderma*, she followed Riedl's advice and published it as *Thaumastoderma bunti* Thane-Fenchel, 1970. d'Hondt subsequently (1974) corrected her genus designation, but considered the species to be a junior synonym of the pentancrous *Tetranchyroderma papii*. Hummon (1977) rejected the synonymy, though none of us then realized that the North American species we were calling *T. papii* was in fact different from the European species. The point is that fallible judgments can only be corrected with additional evidence, and then a roadmap must be constructed to help us to see how we proceeded from there to here.

There follows a description of the species from North America as a new species, *Tetranchyroderma parapapii*, followed by a redescription of the European species, *T. papii* Gerlach, 1953. Each of the two species actually has a fairly restricted range, *T. parapapii*: North America from Maine to South Carolina; *T. papii*: through out the Mediterranean Sea, with but one Atlantic Ocean record in southern Portugal.

### Materials and Methods

Collections were made from whole-beach transects of temperate beaches, with 8-10 sites spaced more or less equally from lowest water level to high

spring tide level (Hummon 2008). Sampling depths in the sand were from 0-10 cm (low tide levels) to 0-50 or more cm (high tide levels), usually reaching ground water levels. Sand was placed in 250 ml whirl-pak bags, kept at 15-20 °C and returned to the laboratory in 1 to 5 days (ranging from day trips to expeditions) for analysis. Samples were kept at 5 to 10 °C in the lab, where they will keep for up to 10 days with little loss of gastrotrichs. Analysis was carried out as soon as possible, beginning with earliest collected samples or samples with heavy organic loads.

About 20 ml of sand was placed in a 125 ml plastic cup, 20 ml of 6 to 7 % MgCl<sub>2</sub> added, and after swirling, left for 10 minutes. After relaxation, ~20 ml of sea-water was added, the contents swirled, and the supernatant poured into a 60 ml plastic Petri dish. A second 20 ml of sea-water and another decantation filled the Petri dish, its contents then being split between that and another similar Petri dish. After contents settled to the bottom, the dish was inspected for now-revived gastrotrichs using a Wild M8 stereo-microscope at 18 to 20× magnification. Specimens were transferred to a drop of MgCl<sub>2</sub> on a microscope slide, oriented, covered with a 16 mm square coverslip with posts of non-toxic modeling clay at its corners. Excess water was carefully wicked from the glass sandwich using a piece of filter paper until the relaxed animal stopped without compression. After marking the specimen's location, the slide was transferred to the stage of the Olympus Lab-Phot II compound microscope. A numerical aperture (n.a.) of 1.00 to 1.25 at higher magnifications was as important for viewing as having a differential interference contrast (DIC) optical system. Scanning electron micrographs were captured by WDH, MAT and WAE, during a visit to the Marine Biology Laboratory, Woods Hole, MA in October 1988; after critical point drying, sputtering was done using a Tousimis Samsputter 2a and scanning electron microscopy using a JEOL JSM-840.

Drawings were made using a drawing tube on the microscope or by transferring ocular micrometer units (millimeter ruler off a video display) onto graph paper. In my illustrations, dorsal and ventral views are mirror images of one another; other illustrators may do dorsal and ventral views as if focusing down through the specimen. Videotaping began in 1990 (using SVHS, then Hi8) starting at the highest magnification that could show the entire specimen (4× objective

for very long animals to 40× for short animals), working one's way up to higher magnifications. Videos have been (are being) digitized, edited, and rendered into MPEG 2 and WMV (= MPEG 4) versions, to be placed on my server for read-only downloading by other workers (Hummon et al. 2005, Hummon 2008).

Morphological symbols and conventions are as follows: **Lt**, Length, total: from anterior tip of head to posterior tip of caudum and its adhesive tubes; **LPh**, Length, pharynx from anterior tip of head to PhJIn; **PhJIn**, Junction between pharynx and intestine; **WHd/WNk/WTr/WFrBs**, Width of head, neck, trunk, furcal base and furcal tips; **TbA/TbL/TbD/TbV/TbP**, adhesive tubes of the anterior, lateral, dorsal, ventral, and posterior (caudal) series; **U**, Percentage units of Lt from anterior to posterior; **Columns**: longitudinal in orientation; **Rows**: transverse in orientation. The caret (^) indicates a type locality.

### Systematics

Order Macrodasysida Remane, 1929  
(Rao & Clausen, 1970)

Family Thaumastodermatidae Remane, 1927  
Subfamily Thaumastodermatinae Ruppert, 1978

#### Genus *Tetranchyroderma* Remane, 1927

##### *Tetranchyroderma parapapii* new species

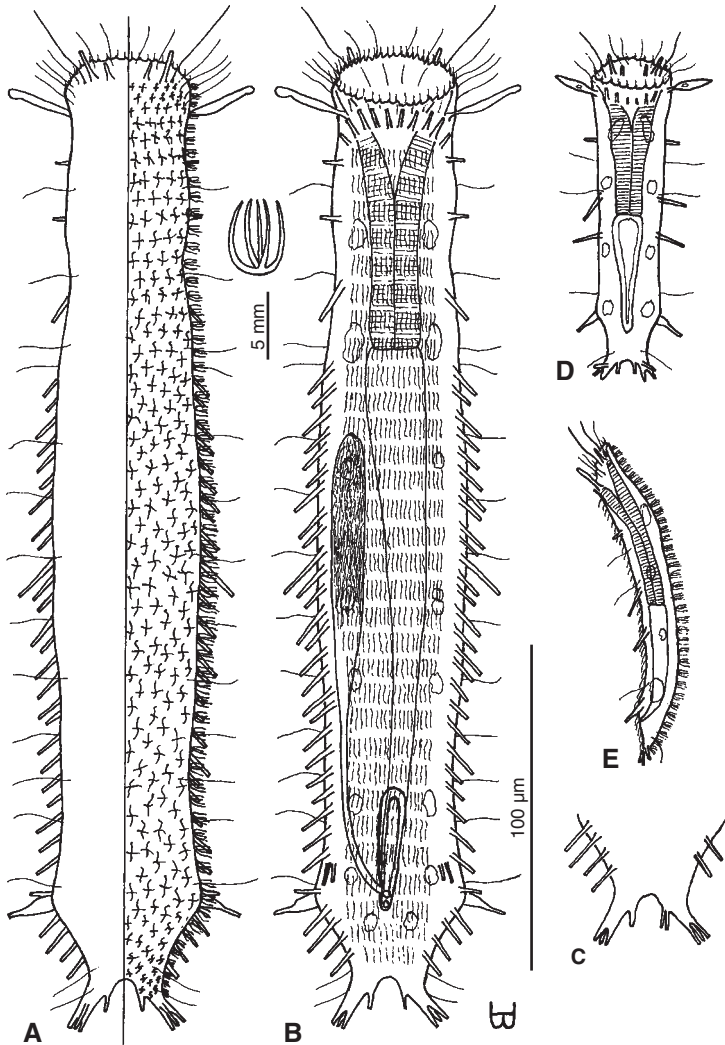
[Tet ppap]  
(Figs. 1-3)

*Tetranchyroderma papii* Hummon (1967: p. 452 abstract); Hummon (1968: p. 423 abstract); Hummon (1969: pp. 51, 89); Hummon (1974: p. 212); McGeary (1974: p. 13, fig. 3, tab. III); Hummon (1975: p. 503 ff.); Hummon (1977: p. 114, fig. 1d-f, tab. 1); Ruppert (1977: p. 241, fig. 1f., 12, 13E); Ruppert & Hogue (1978: p. 99); Gagne (1980: p. 116); Tyler & Rieger (1980: p. 2 ff., fig. 1B,C); Hochberg & Litvaitis (2001a: p. 37); Hochberg & Litvaitis (2001b: p. 62); Hummon (2008: N. Amer. database).

**Diagnosis.** Adult Lt 288-416 µm; PhJIn at U34-U32. Oral opening scalloped; body undulating in width along its length, with hip-like prominences at the level of the anus; short bilobed caudum incises to U95. Rod-like tentacles (L = 10 µm) arise forward on the oral hood; spathiform palps

(L = 24 µm) insert laterally on each side just behind the mouth; cirrata absent from head and trunk. Glands 8-10 per side, from U17 to U90, the largest being at the PhJIn. Dorsal/lateral covering of pentancreas is complete, with 19 longitudinal columns of ~55 ancreas each, reaching from the oral hood onto the caudal lobes; ancreas, as long as wide, have tines of equal length, those on both ends being smaller. TbA 4-5 per side inserting on the body surface in a shallow arc at U07-U08, 1 medially and 3-4 laterally. TbL 33-34 per side, with 1 along the fore and 2 the rear pharynx at U11, U17 and U24, 24-25 regularly spaced along the gut at U33-U80, 1 at U87, 1 having a heavy conical base on the lateral prominence at U86, and 4 along the narrowing part of the rear trunk behind the anus. TbD absent. TbV 1-2 insert more ventrally than the TbL, and occur just before the lateral prominence at U83-U84. TbP 7 per side; 3 per side form the caudal pedicles with the fused 'two fingers and a thumb' typical of the family, being supplemented by a cirrata-like structure projecting posteriodorsally from between the 'fingers', with no additional tubes between the pedicles, but with 4 tubes per side laterally behind the anus that continues the TbL series past the lateral prominence. Ventral locomotor cilia in transverse rows that cover the entire ventral surface from the TbA to the caudal base. Mouth subterminal, broad; length of oral hood is 30 % of mouth width; basal pharyngeal pores are inconspicuous; intestine narrows fore to aft, ventral anus opens at U87. Hermaphroditic; testis on right side as seen from above; vas deferens opens into the rear of the caudal organ, in front of the anus; eggs develop back to front, lying above the mid-gut; caudal organ elongate, tubular; frontal organ hyaline, bladder-like.

**Description.** Mature adult Lt 288-416 µm (Fig. 1A,B, 2A,B); LPh 108-127 from the ventral border of the oral opening to the PhJIn at U34-U30, mature specimens being drawn from throughout the species distribution. Oral hood scalloped in front (Fig. 3A), undulating in width along the pharynx; trunk swelling in fore-gut region, continuing with parallel or slightly convex sides back to lateral hip-like prominences at the level of the anus (U86), then quickly narrowing to a short bilobed caudum (Fig. 3F) that incises medially to U95. Rod-like tentacles (L = 10 µm) arise forward on the oral hood (Fig. 3C) at U02; spathiform palps (L = 24 µm) insert laterally on each side just behind the



**Fig. 1.** Dorsal view (A), and ventral view (B) of a mature *Tetranchyroderma parapapii* n. sp. Lt=304 µm (pentancre drawn to a different scale); a developmentally anomalous caudum of the same species (C); composite dorso-ventral view (D), and lateral view of a juvenile of the same species (E), all collected from Crane's Beach, Woods Hole, MA and drawn with DIC optics.

mouth (Fig. 3A) at U05. Dorsal cirrata are absent from neck and trunk. Widths of/at oral opening, pharynx/trunk, prominence/caudal base are as follows: 39,35-38/50,47/23 µm at U03,U09-U25/U58,U86/U94, respectively. Glands 8-10 per side (3 µm diameter to <math>5 \times 11 \mu\text{m}</math>), run dorsolaterally at regular intervals from U17 to U90, the largest being sited adjacent to the PhJIn.

**Cuticular armature.** Dorsal/lateral covering of pentancre is complete, with 19 longitudinal columns of ca. 55 ancre each, reaching from the

beginning of the oral hood at U01 onto the caudal lobes; ancre robust, having tines of equal length that recurve toward the center; ancre are as long as wide (7-8 µm), with those on the fore and hind ends being smaller (3 µm).

**Adhesive tubes.** TbA 4-5 per side insert directly on the body surface in a shallow arc at U07-U08, 1 medially (L=4 µm) and 3-4 laterally (L=5-8 µm) that point obliquely forward and outward. TbL 33-34 per side (L=5-16 µm), with 1 along the fore and 2 the rear of the pharynx at



Fig. 2. Dorsal habitus view of a *Tetranchyroderma parapapii* n. sp. (Lt=264  $\mu$ m), showing spathiform palps, 'hips', and caudum (A); ventral view of the same species (Lt=307  $\mu$ m), showing the same features as well as the oral opening (B); ventral oblique view of the same species (Lt=247  $\mu$ m), showing ventrolateral adhesive tubes (C); and lateral view of the same species (Lt=289  $\mu$ m), showing oral hood covering the oral opening dorsally (D). All views photographed by SEM. Scale bars = 100  $\mu$ m.

U11, U17 and U24, 24-25 regularly spaced along the gut at U33-U80, 1 at U87, 1 having a heavy conical base (L = 13  $\mu$ m) that inserts on the lateral prominence at U88, and 4 along the narrowing part of the rear trunk behind the anus. TbD absent. TbV 1-2 (L=8-9  $\mu$ m), inserting more ventrally than the TbL, are located just before the lateral prominence at U83-U84. TbP 7 per side; 3 per side (L = 4  $\mu$ m), form the caudal pedicles each with the fused 'two fingers and a thumb' typical of the family, being supplemented by a cirrata-like structure projecting posteriodorsally from between the 'fingers', with no additional tubes between the pedicles, but with 4 tubes per side (L=8-9  $\mu$ m) laterally behind the anus that continues the TbL series past the hip-like prominences.

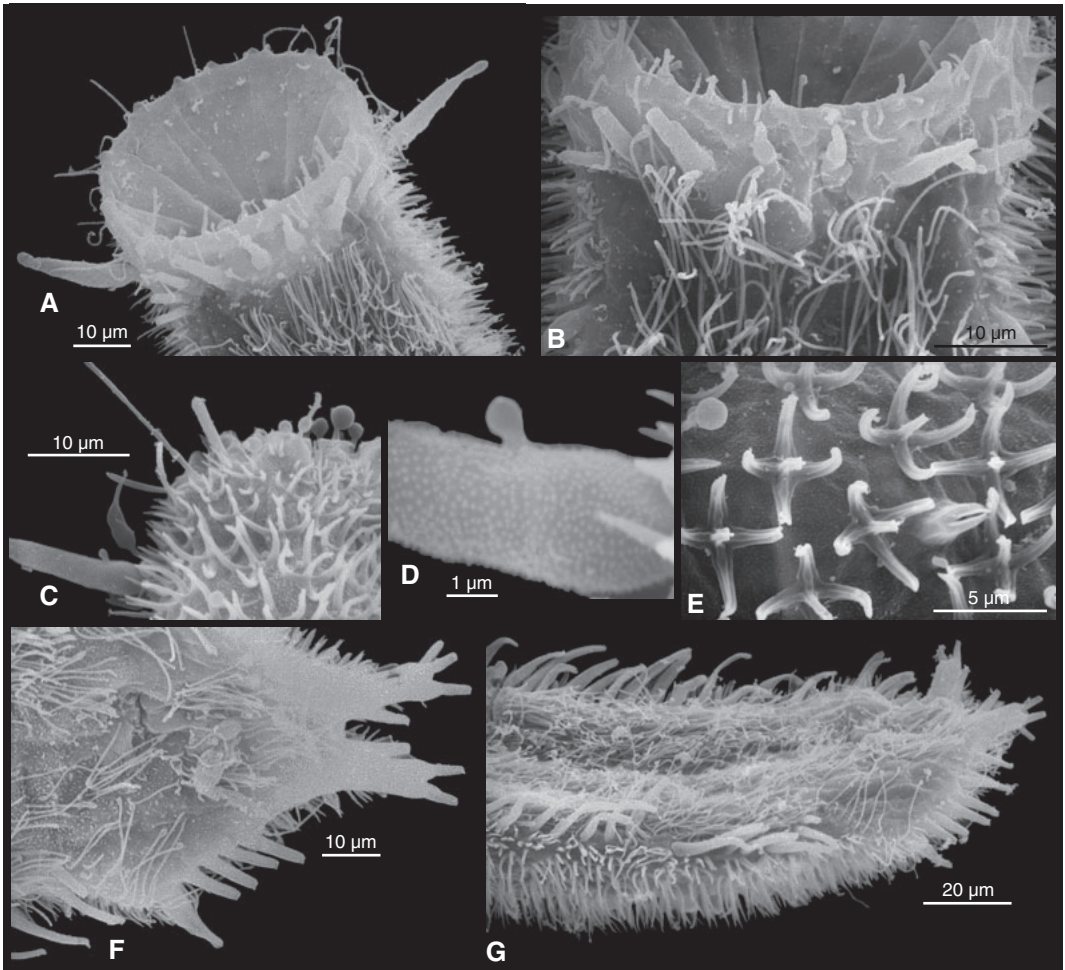
**Ciliation.** Sensory cilia surround the mouth, (L=3  $\mu$ m below, 3 & 12-15  $\mu$ m atop), with one elongate pair (L=42  $\mu$ m) at U02; other cilia (L=10-14  $\mu$ m) ca. 15 per side occur more or less regularly along the body from U13 to U93, with

1 per side inserting on each caudal lobe. Ventral locomotor cilia occur in 30 transverse rows that cover the entire ventral surface from the TbA to the caudal base; lengths of cilia are ca. 6  $\mu$ m.

**Digestive tract.** Mouth subterminal, of medium breadth (39  $\mu$ m); oral hood is 30 % of mouth width; pharynx narrows to 14  $\mu$ m, basal pharyngeal pores inconspicuous at U28; intestine broadest in front (18  $\mu$ m), narrowing posteriorly (4  $\mu$ m) to the ventral anus, which opens at U87.

**Reproductive tract.** Hermaphroditic; single elongate testis on the right (viewed from above, left when viewed from below), testis beginning well behind the PhJIn; vas deferens opens near the anus; egg (ca. 100  $\times$  40  $\mu$ m) left of the gut at U50-U75; caudal organ elongate, tubular (34  $\times$  8  $\mu$ m); frontal organ hyaline, bladder-like.

**Ecology.** Occasional to common in frequency of occurrence (10-60 % of samples); scarce to prevalent in abundance (3-5 % to greater than 30 % of a sample, often co-dominant [cdom] or



**Fig. 3.** Ventral view of the head of a fully mature specimen of *Tetranchyroderma parapapii* n. sp., showing lateral spathiform tentacles and TbA 5 per side (A); ventral view of the rear oral rim of a less mature specimen of the same species, showing TbA 4 per side (B); dorsal view of the oral hood of the same species, showing a rod-like tentacle, pentancre and the base of a spathiform tentacle, bearing a small sensory knob (C); magnified view of the sensory knob seen in Fig. 3C (D); dorsal view of several pentancre and an epidermal gland of the same species (E); ventral view of the caudum of the same species, showing pedicles, the prominent 'hip' tubule of the TbL series along with the 4 tubules that insert laterally behind the anus, and the TbV that lies in front of the hip (F); and a ventral oblique view of the rear trunk region, showing TbL, TbV, caudum, pentancre and locomotor cilia (G). All views photographed by SEM. Scale bars = 20 µm for G, 10 µm for A,B,C,F, and 1 µm for D and E.

dominant [**dom**], though not often reported by others); maximum densities of 148/cm<sup>3</sup> have been recorded, though densities of 5-10 and often 20/cm<sup>3</sup> are routinely found in early and late summer seasons (Hummon 1975); *littoral* in medium-fine to coarse, well to poorly sorted sand at extreme high water spring (EHWS), 10-100 cm sand depth, to extreme low water spring (ELWS), 0-20 cm sand depth; *sublittoral* in very fine-fine,

well-medium well sorted to very fine-very coarse, poorly sorted sand at 4-10 m water depth.

**Geographical distribution.** Note: **Cap** indicates how to look up such locations in a data base.

**Atlantic NW – North America:**

Delaware {Gordon's Pond, Cape **H**enlopen North Outside, Roosevelt Inlet In/Out [2-videos]/Tip};

Massachusetts {Crane's Beach^ [dom] [video], Duxbury B In, Egypt B, Gurnet Point Out [cdom] [video], Mattakeset B Out/In, MBL B [2-videos], Nantasket B [dom], Nauset B Out/In, Nobska B Mid [dom]/W [dom], Plum Island South [2-videos]/Southeast [dom]/Southwest, Quissett B [2-videos], Salisbury B [video], Saquish Neck In, Singing B [dom] [video], Situate, Woodneck B};  
 Maine {L Cranberry, Old Orchard North [video], Seal Harbor};  
 North Carolina {Beaufort Green Buoy In [dom]/Green Buoy Out [dom], Bogue Inlet, Fort Macon [video], Shackleford East};  
 New Hampshire {Hampton Harbor, Seabrook B};  
 New York {Shinnecock B Out/In};  
 South Carolina {North Inlet In};  
 Virginia {Community B [video], First Landing [dom] [video]}

**Type material.** The holotype (USNM 1121843, Lt=301, LPh=99) and three paratypes (USNM 1121844; a lateral mount of Lt=320, LPh=106; USNM 1121845, Lt=298, LPh=96; and USNM 1121846, Lt=288, LPh=93), all formalin-glycerin whole mounts of mature adult specimens, have been submitted to the National Museum of Natural History, Smithsonian Institution, Washington, DC. All were collected by W. D. Hummon in July 2000 from Crane's Beach (just west of MBL or 'Stony' Beach) on the Buzzard's Bay side of Penzance Point, Woods Hole, Cape Cod, Massachusetts, USA (Lat. 41°32'N, Long. 70°41'W). Other materials measured include 179 individuals from the same beach location collected in by the same person during the summer of 1970 (see Hummon 1977: Tab. 1). It should be noted that introgression is now present in the previously 'pure' population of *T. parapapii* from Crane's Beach, often evidenced by the presence of one or more dorsal cirrata on the body.

**Etymology.** *Parapapii* is named to distinguish the new species from its long confusing sister species, *Tetranchyroderma papii*.

**Remarks.** There are 16 video sequences of *Tetranchyroderma parapapii* n. sp. available from 12 locations in eastern North America. Three of these are available in Hummon (2008): #1978 a mature adult of Lt=371 µm (LPh=112 µm) from

Crane's Beach, MA; #2078 a barely mature adult of Lt=288 µm (LPh=108 µm) from Salisbury, MA; and #2522 a juvenile of Lt=140 (LPh=67 µm) from Indian River, DE. These are listed on the server as Tet spMA until publication and thereafter as Tet ppap so as to make them available in the interim and yet not to contravene the international code with respect to *nomen nudum* publication. The juvenile here illustrated (Fig. 1D,E) is: Lt=96, LPh=51, LCfTn=11 µm; WMu=24, WNK=23, WTr=21, WCdBs=11 µm; No./side: TbA=1, TbL=5; TbP=2+1+1m+0l. Tabular data on morphology for this species are presented in McGeary (1974: tab. III), based on analysis of 35 specimens, and in Hummon (1977: tab. 1), based on analysis of 179 specimens.

While based on different length classes (50 µm in McGeary and 25 µm in Hummon), individuals from the New Hampshire (NH) and Massachusetts (MA) populations differ in length of pharynx (LPh) and length of intestine (LIn), but not in length of tentacle (LT) or width of head (WHd). Note that NH specimens did not include individuals shorter than 150 µm or longer than 350 µm; specimens from MA had LPh about 8 % longer than those from NH, both sets being measured in the same manner (i.e. from tip of oral hood to beginning of intestine); McGeary's measurements of LIn are somehow bogus, as is illustrated in his Fig. 3B, where he shows the intestine ceasing at the level of the ovum, rather than near the level of the caudal organ, where it actually ends. Other measurements are not comparable from one study to the other. Note as well that McGeary's Fig. 3AB shows a mature specimen of 278 µm, the same minimum length that Hummon found in southern Maine, not far distant.

Hybridization with other species of the genus is not uncommon, though seldom reported; it has been demonstrated to occur with *Tetranchyroderma enalosum* (Hummon 1977), the most readily indicated character being the presence of dorsal cirrata. Occasionally an anomalous caudum has an extra 'thumb' tube or fewer than 4 TbL posterior to the anus (Fig. 1C). Two morphological features in the SEM images should be noted: a) a small structure on the proximal portion of the spathiform palp (Fig. 3C,D) appears to be sensory, perhaps a modified chemosensory cilium, as in Gagné (1980: p. 118, Fig. 1d), and b) the opening of a dorsal epidermal gland as figured by Todaro (2002: p. 559, Figs. 1A, 2A,B).

**Taxonomic affinities.** *Tetranchyroderma parapapii* n. sp. is the only mid-sized species in the genus completely covered with pentancreas, that also has rod-like tentacles on the oral hood and spathiform tentacles of medium length on either side of the mouth, has a PhJIn at ca. U34-U30, has 5 TbA and 33-34 TbVL per side, along with 1-2 TbV per side (at U86), which are difficult to see because they are only somewhat more ventral than tubes of the ventrolateral column, and has hip-like prominences at U88, while lacking dorsal cirrata and TbD. As an adult, *T. parapapii* has a shorter pharynx relative to total body length and a shorter oral hood length relative to mouth width than *T. papii*.

***Tetranchyroderma papii* Gerlach, 1953**

[*Tet papii*]  
(Fig. 4)

*Tetranchyroderma papii* Gerlach, 1953: p. 205, f. 2. – **new species.** Gerlach (1955: p. 61); Fize (1963: p. 715); Luporini, Magagnini & Tongiorgi (1971: p. 438, fig. 2, pl. I[1]); Westheide (1972: p. 24); Hummon (1977: p. 134, fig. 1c); Tongiorgi & Balsamo (1984: p. 338); Todaro & Balsamo (1990: 39 abstract); Balsamo, Fregni & Tongiorgi (1995: p. 277); Balsamo & Tongiorgi (1995: p. 4); Balsamo, Fregni & Tongiorgi (1996: p. 176); Todaro, Hummon, Fregni, Balsamo & Tongiorgi (2000: p. 126); Todaro (2002: p. 562); Todaro, Balsamo & Tongiorgi (2002: p. 252); Todaro, Matinato, Balsamo & Tongiorgi (2003: Tab. III, Appx. I); Todaro, Littlewood, Balsamo, Herniou, Cassanelli, Manicardi, Wirz & Tongiorgi (2003: Tab. 1 ff.). Hummon, Todaro & Evans (2005: p. 24); Todaro, Balsamo & Tongiorgi. (2006: Checklist p. 2) Hummon (2008: N. Europe, W. Med., E. Med. & Red).

*Tetranchyroderma bunti* d'Hondt (1974 for the year 1972-73: p. 232); **junior synonym** of *T. papii*; Rejected by Hummon (1977: p. 117).

**Diagnosis.** Adult Lt 290-402  $\mu\text{m}$ ; PhJIn at U35-U34. Oral opening scalloped, narrowing along the pharynx, swelling along the gut, then narrowing gently without hip-like prominences to a bilobed caudum that incises medially to U94. Rod-like tentacles ( $L=10\ \mu\text{m}$ ) arise forward on the oral hood; spathiform palps ( $L=36\ \mu\text{m}$ ) insert laterally on each side just behind the mouth; cirrata 2 per

side on the trunk. Glands 6-7 per side, from U18 to U86. Dorsal/lateral covering of pentancreas is complete, with 19 longitudinal columns of 40-45 ancreas each, reaching from the oral hood onto the caudal lobes; ancreas, as long as wide, have tines of equal length, those on both ends being smaller. TbA 4 per side inserting on the body surface in a transverse row at U10-U11, 1 medially and 3 laterally that point obliquely forward and outward. TbL 25-28 per side, with 1 along the fore and 2 the rear pharynx at U11, U17 and U24, 1 at the PhJIn and the others more or less regularly spaced along the gut at U38-U86, with 2 of them along the narrowing part of the rear trunk behind the anus. TbD/TbV absent. TbP 5 per side; 3 per side form the caudal pedicles with the fused 'two fingers and a thumb' typical of the family, being supplemented by a cirrata-like structure projecting posteriodorsally from between the 'fingers', with no additional tubes between the pedicles, but with 2 tubes per side laterally that continues the TbL series behind the anus. Ventral locomotor cilia in transverse rows that cover the entire ventral surface from the TbA to the caudal base. Mouth subterminal, broad; length of the oral hood is 50 % of mouth width; basal pharyngeal pores are inconspicuous; intestine narrows fore to aft, ventral anus opens at U87. Hermaphroditic; testis on right side as seen from above; vas deferens opens into the rear of the caudal organ, near the anus; eggs develop back to front, lying above the mid-gut; caudal organ elongate, tubular; frontal organ hyaline, bladder-like.

**Description.** Mature adult Lt 290-402  $\mu\text{m}$  (Fig. 4A,B); LPh 98-142 from the ventral border of the oral opening to the PhJIn at U34-U35, mature specimens being drawn from throughout the species distribution; there are no tabular data on morphology for this species. Oral hood scalloped in front, narrowing a bit along the pharynx; trunk swelling somewhat, then narrowing gently without hip-like prominences to a bilobed caudum that incises medially to U94. Rod-like tentacles ( $L=10\ \mu\text{m}$ ) arise forward on the oral hood at U04; spathiform palps ( $L=36\ \mu\text{m}$ ) insert laterally on each side of the mouth at U09; dorsal cirrata 2 per side ( $L=10-12\ \mu\text{m}$ ) on the trunk at U38 and U61. Widths of /at oral opening, mid-pharynx/PhJIn/trunk/caudal base are as follows: 49,41/44/50/16  $\mu\text{m}$  at U04,U16/U36/U53/U95, respectively. Glands 6-7 per side (6  $\mu\text{m}$  diameter to  $14 \times 7\ \mu\text{m}$  oblong), run dorsolaterally at irregular intervals,

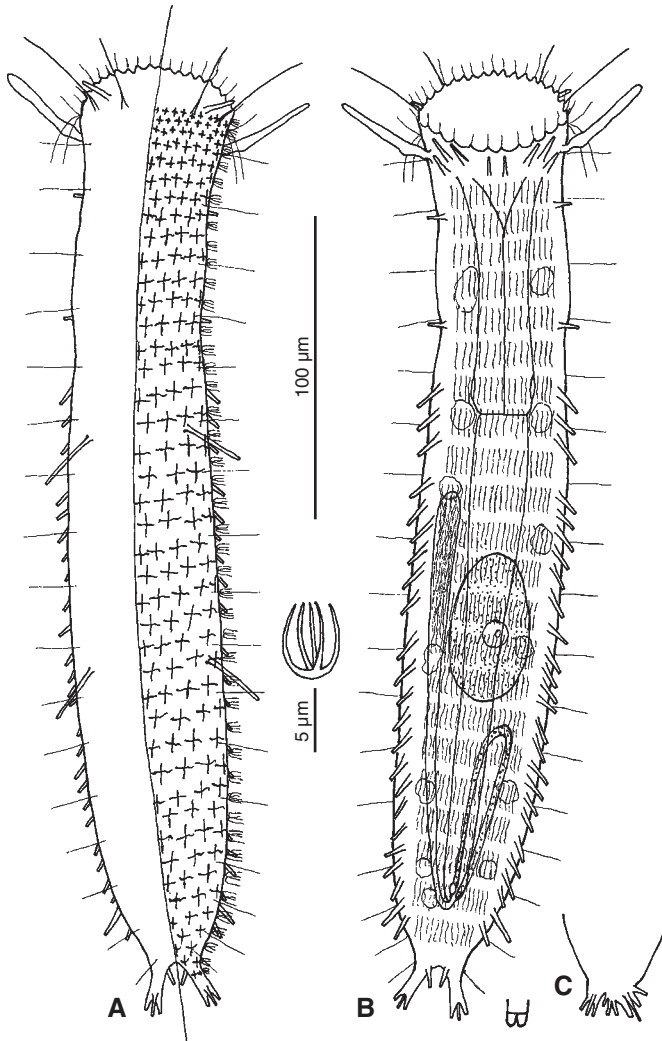


Fig. 4. Dorsal view (A), and ventral view of a mature *Tetranchyroderma papii* Papi, 1957 Lt=312 µm (pentancre drawn to a different scale) (B); view of a developmentally anomalous caudum of the same species, both collected from Belliche, Portugal and drawn from DIC optics (C).

often with some asymmetry, from U18 to U86.

**Cuticular armature.** Dorsal/lateral covering of pentancre is complete, with 19 longitudinal columns, of 40-45 ancre each, beginning mid way down the oral hood at U04 and continuing onto the caudal lobes; ancre have tines of medium heft that are of equal length and recurve toward the center; ancre are as long as wide (7 µm), with those on the fore and hind ends being smaller (2 µm).

**Adhesive tubes.** TbA 4 per side insert directly on the body surface in a transverse row at U10-U11, 1 medially (L=6 µm) and 3 laterally

(L=7-9 µm) in a triangular formation pointing anteriolaterally; TbL 25-28 per side (L=6-10 µm), with 1 in the fore, 2 in the rear pharynx at U15, U27 and U33, and 1 at the PhJIn at U36, the others showing nearly regular spacing in the intestinal region at U38-U86, down to the level of the anus, and 2 along the narrowing part of the rear trunk behind the anus. TbD/TbV absent. TbP 5 per side; 3 per side (L=3-5 µm), form the caudal pedicles each with the fused 'two fingers and a thumb' typical of the family, being supplemented by a cirrate-like structure projecting posteriodorsally from

between the 'fingers', with no additional tubes between the pedicles, but with 2 tubes per side (L=6-10  $\mu\text{m}$ ) laterally that continues the TbL series past the anus.

Ciliation. Sensory cilia surround the mouth, (L=5  $\mu\text{m}$  below, 5-7  $\mu\text{m}$  atop); 2 vibratile cilia (L=35 and 34  $\mu\text{m}$ ) per side insert on the oral hood at U04; other cilia, (L=10-14  $\mu\text{m}$ ) ca. 17 per side occur at regular intervals along the body from U09 to U90. Ventral locomotor cilia occur in 22 transverse rows that cover the entire ventral surface from the TbA to the caudal base; lengths of cilia are ca. 9  $\mu\text{m}$ .

Digestive tract. Mouth subterminal, broad; oral hood is 50 % of mouth width; pharynx narrows in the middle to 16  $\mu\text{m}$ , basal pharyngeal pores inconspicuous at U34; intestine broadest in front (18  $\mu\text{m}$ ), narrowing (7  $\mu\text{m}$ ) to the ventral anus, which opens at U87.

Reproductive tract. Hermaphroditic; single elongate testis on the right (viewed from above, left when viewed from below), testis beginning well behind the PhJn; vas deferens opens near the anus; ovum (50  $\times$  27  $\mu\text{m}$  or more) above the gut at U51-U66; caudal organ elongate, tubular (60  $\times$  10  $\mu\text{m}$ ); frontal organ ovate, hyaline and sac-like (23  $\times$  13  $\mu\text{m}$ ), often containing mobile sperm.

Ecology. Occasional to common in frequency of occurrence (10-60 % of samples); scarce to prevalent in abundance (3-5 % to greater than 30 % of a sample, often sub-dominant [**sdom**], co-dominant [**cdom**] or dominant [**dom**]); *littoral* in fine to medium sand from mid-water level (MWL), 0-40 cm sand depth, to below extreme low water (ELW), 0-15 cm sand depth; *sublittoral* in fine, well sorted to very fine-very coarse, poorly sorted sand at 1.5 m water depth.

**Geographical Distribution.** {Note: **Cap** indicates how to look up such locations in a data base.}

**Atlantic NE – Europe:**

Portugal (Belliche).

**Mediterranean – Europe:**

France (Russillon: Canet Plage, **F**autea, Moriani P, **P**adulone; Languedoc: **C**orniche, Palavas, **P**etit Travers, Sete);

Greece (Aegean: Krassa, Loutsia [**dom**], Monolithos, Perissa [**dom**], Psakoudia, Salanikos [2-videos], Sani, Stomion, Varkiza [**dom**]; Mediterranean: Glystra [**dom**], Makryalos [**dom**], Tsambika);

Italy (Adriatic: Alimini, T. Fortore, F. Isonzo [video], Peschici [2-videos], S. Cataldo; Ionian:

T. **L**apillo, T. **S**. Giovanni, T. **V**ado; Ligurian: B. **G**orgona, S. Rossore<sup>^</sup>, C. **Z**urletto; Mediterranean: Bosa, Calasetta, T. **C**orsari, P. **P**alo, S. Teodoro; Tyrrhenian: P. **A**la, Bagnara, **C**aletta, M. **C**amerota, Castiglione, M. **C**uringa, **F**eniglia, Fiumicino, **F**ondi, **G**iannella, C. **L**iberotto, Licola, Montalto, Mortelliccio, **N**infeo, Paestum, Palinuro, T. **P**aola, Sabaudia, S. Severa, T. **S**cissura, **S**erapo, Simius, Torregaveta).

**Middle East:**

Cyprus (Dhekelia [**sdom**] [video]);

Egypt (Mediterranean: Aghiba [**sdom**], Aida [**dom**], **A**rish E, **A**rish EO, Boghoush E, Boghoush W, Marakia, Markaz [**dom**], Marsa **M**atruh [**dom**] [2-videos], **R**ahman);

Israel (Mediterranean: Ahziv [video], Nitzanim [3-videos]).

**North Africa:**

Algeria (**A**ndalouses, Beni-Saf, C. **B**lanc, Bomo, C. **F**alcon, **P**oules);

Tunisia (Amilcar, Raoud).

**Remarks.** There are 12 video sequences of *Tetranychroderma papii* available from seven locations in the mouth and interior of the Mediterranean Sea. Two of these are available in Hummon (2007): #1022 a mature adult of demonstration quality, Lt=335  $\mu\text{m}$  (LPh=129) from Nizanim, Israel and #1478 a sub-adult of Lt=226  $\mu\text{m}$  (LPh=108) from Dhelelia, Cyprus. *T. papii* is considered to be a species typical of the "Küstengrundwasser" in non-tidal locations; it was often a prevalent member of the gastrotrich community, though such data were as often not recorded. Hybridization with other species of the genus is likely, possibly with *T. esarhabdophorum* Tongiorgi & Balsamo (1984), being most readily indicated by the presence of dorsal cirrata. In one specimen from Belliche, Portugal a developmental anomaly was seen with respect to one of the caudal pedicles (Fig. 4C).

**Taxonomic affinities.** *Tetranychroderma papii* is the only mid-sized species in the genus completely covered with pentancreas, that also has rod-like tentacles on the oral hood, long spathiform tentacles on either side of the mouth, and 2 cirrata per side on the trunk, has a PhJn at ca. U35, has 4 TbA and 25-28 TbVL per side, but lacks hip-like prominences and TbD/TbV. As an adult, *T. papii* has a longer pharynx relative to total body length and a longer oral hood length relative to mouth width than *T. parapapii*.

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