An interesting new gastrotrich from littoral meiohobos (Long Beach Island, USA), with a key to species of *Tetranchyroderma* (Gastrotricha: Macrodasyida)

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Marine representatives of the phylum Gastrotricha are reported for the first time from the State of New Jersey, USA. Littoral and shallow sublittoral sediment collected at Ship Bottom on Long Beach Island, near Atlantic City, yielded 11 species belonging to eight genera in six families in the orders Macrodasyida (four genera in three families) and Chaetonotida (four genera in three families). Littoral samples were richer than the one sublittoral sample (7 vs 4 spp.). Among the taxa was a large, undescribed species of *Tetranchyroderma* characterized by the following key traits: total body length up to 605 μm; cuticular covering complete, made up of pentancres; a pair of cephalic tentacles; dorsal adhesive tubes arranged in dorsal and dorsolateral columns; a pair of ventral adhesive tubes arising from a common base, near the perigenital area only on the right side; peculiar cuticular openings ‘stomata’ along the ventrolateral margins of the body; protogynous hermaphroditism. *Tetranchyroderma weissi* sp. nov. is, at least in the investigated location, restricted to the sediment layers below 20 cm of the intertidal zone, and is able to live in thiobiotic sediment. A key to the described species of the world based on easily discernible traits, visible in both living and formalin-fixed specimens is provided.

**INTRODUCTION**

In July 2001, several collecting trips were made along the Atlantic and Gulf coasts of the USA in search of gastrotrich species suitable for ongoing molecular and ultrastructural studies aimed to shed light on the ingroup phylogenetic relationships of these lower metazoans (cf. Balsamo et al., 2001a,b). Samples collected at Long Beach Island in the State of New Jersey yielded, among others, several specimens of an undescribed thiaustodermatid gastrotrich belonging to the genus *Tetranchyroderma*.

This exclusively marine genus is the second-most species-rich of the entire phylum Gastrotricha, and the most specious in the order Macrodasyida. Thus far the genus *Tetranchyroderma* includes more than 55 species (all biodetritus feeders), 280 to 650 μm in total body length, recorded from the Atlantic, the Pacific, and the Indian Oceans and their satellite seas (e.g. Thane-Fenchel, 1970; Valbonesi & Luporini, 1984; Rao, 1991; Todaro et al., 1995, 2001; Hummon et al., 1996; Chang et al., 1998; Clausen, 2000). Nearly ubiquitous in shallow sublittoral medium-grained sediments, where up to 5–6 co-occurring species frequently may be found, populations of these worms may reach high density also in the littoral zone of unpoluted sandy beaches (e.g. Hummon, 1975; Nixon, 1976; Ruppert, 1977; Todaro, 1998; Todaro et al., 2000).

Species of *Tetranchyroderma* are easily discernible by virtue of their characteristic dorsal and lateral cuticular covering of three-, four-, or five-pronged anchor-like hooks, called triancres, tetrancres and pentancres respectively. In contrast to the ease of generic identification, species identification is difficult. For this reason in addition to describing the new species, I provide here a working key to the identification of all known species of *Tetranchyroderma* worldwide. The key is based on easily discernible (mostly meristic) traits of the external anatomy, visible in both living and formalin-fixed specimens. It will hopefully prove useful not only to gastrotrich specialists but also to marine ecologists who find these abundant metazoans in the course of research on interstitial meiohobos.

**MATERIALS AND METHODS**

Sand samples were taken on 22 June 2001 on the ocean front of Ship Bottom, a small town on Long Beach Island, a longshore island, located a few miles north-east of Atlantic City, New Jersey, USA. Littoral samples were taken during low tide, by digging three 30 cm-deep holes, ~5 m apart, at mid-water mark, and collecting the sand from the wall using a 50 ml plastic syringe with the end cut off. Sediment from the top 20 cm and the bottom 10 cm of each hole was kept separate in two distinct 200 ml plastic bags (six bags in total). Sublittoral sand, 500 ml in total, was taken at 1.5 m water depth by scooping the top sediment layers with a plastic jar. The sublittoral sand and the sediment from the top 20 cm layer of the littoral zone were analysed within a week at Louisiana State University (USA), while sand from the bottom 10 cm layer of the littoral area was brought to Italy and analysed two weeks after collection in the author’s laboratory. Specimens were extracted by the narcotization–decantation technique using a 7% magnesium chloride solution (Pfannkuche & Thiel, 1988). Gastrotrichs were observed *in vivo* with phase contrast optics using a Leitz Ortholux microscope (Louisiana) or with Nomarski differential interference contrast (DIC) optics using a...
Leitz Dialux 20 microscope (Italy). Several specimens of the new species were fixed overnight in a 1.0 M phosphate buffered (pH 7.3) solution of paraformaldehyde, glutaraldehyde and picric acid, following Ermak & Eakin (1976) and prepared for scanning electron microscopy (SEM) analysis. To this end, worms were rinsed in 0.2 M cacodylate buffer, dehydrated through a graded ethanol series, critical point-dried using CO₂, mounted on aluminium stubs, sputter coated with gold-palladium, and observed with a Philips XL 30 Scanning Electron Microscope. Measurements were taken using an ocular micrometer or derived from SEM micrographs. In the description, locations of some morphological characteristics along the body are given in percentage units (U) of total body length measured from anterior to posterior. Since the term *Tetranchyroderma* is neuter in gender, the feminine endings of the following species: *Tetranchyroderma indica* Rao & Ganapati, 1968, *Tetranchyroderma vera* Wilke, 1958, *Tetranchyroderma suecica* Boaden, 1960 and *Tetranchyroderma enallosa* Hummon, 1977, are adjusted accordingly in the key reported herein.

Granulometric analysis of the substrata was carried out according to Giere et al. (1988). Mean grain size, sorting coefficient, kurtosis, and skewness were calculated by a computerized program based on the equation of Seward-Thompson & Hail (1973). The organic content of the sediment was determined by per cent weight loss after combustion of 100 g of sediment at 480°C for 4 h; sediment was previously oven-dried at 60°C for 24 hours.

**Abbreviations and terminology**

CT, cephalic tentacles (in the literature these organs are also reported as antennae): rod-like organs inserted dorsally on head (Figures 1A & 2A);

SO, sensorial organs (also called pestle organs or lateral tentacles): knob-like, crescent-shaped, or elongate organs inserted bilaterally on head posterior to ventral margin of mouth (Figure 4A–C);

PhJIn, junction between pharynx and intestine;

TbA, anterior adhesive tubes: elements inserted ventrally along the posterior margins of the mouth (Figures 1C & 4D);

TbL, lateral adhesive tubes: elements inserted laterally or ventrolaterally along both sides of body (Figures 1C & 4D);

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**Figure 1.** *Tetranchyroderma weissi* sp. nov. (A) Habitus drawing, dorsal view, showing the opening of the epidermal glands (pentancrous armature omitted); (B) internal structures seen as from above; (C) habitus drawing, ventral view, showing the adhesive apparatus, locomotor ciliary band, and anal opening. CO, caudal organ; CT, cephalic tentacles; E, egg; FO, frontal organ; GO, gland opening; PP, pharyngeal pores; T, testicle; TbA, dorsal adhesive tubes; TbDL, dorsolateral adhesive tubes; TbL, ventrolateral adhesive tubes; TbV, ventral adhesive tubes.
TbD, dorsal adhesive tubes: elements inserted dorsally or dorsolaterally (TbDL) on trunk, including also the tubes of cirrata type (Figures 1A & 3A);

TbV, ventral adhesive tubes: elements inserted ventrally under the trunk (Figures 1C & 4D);

TbP, posterior adhesive tubes: elements posterior to the anus, inserted on, between, and lateral to the caudal pedicles;

CF, caudal pedicles (they are also called caudal feet): two posterior elongate extensions of body ending with two
or three adhesive tubes and delimiting a caudal indentation; 
CL, caudal lobes: two posterior, rounded extensions of body bearing marginal adhesive tubes.

RESULTS

Abiotic factors
Granulometric analysis of the sediments indicates that in both cases particles were siliceous in nature. The sublittoral substratum comprised very fine, moderately sorted sand, while the littoral was made of fine to medium, moderately well-sorted sand. The amount of organic matter in the sediment ranged from 0.5% (dry weight) to 2.0%, being higher at the sublittoral site. Salinity was 33 psu and temperature 21.5°C (Table 1).

Faunistic and taxonomic account
In total 11 species were recovered belonging to 8 genera in 6 families in the orders Macrodasyida (4 genera in 3 families) and Chaetonotida (4 genera in 3 families); littoral samples were richer than the single sublittoral sample (7 vs 4 spp.; Table 2). For the 10 positively identified species, all of which have previously been reported from the Atlantic coast of the United States, the metric and meristic characteristics are in substantial accordance with data reported in recent literature. For one species, Cephalodasys sp., full identification was not possible because in the single specimen recovered the posterior body region was damaged. Discovery of several specimens of a previously undescribed species of Tetranchyroderma leads to establishment of the following new taxon:

Order MACRODASYIDA Remane, 1925
[Dao & Clausen, 1970]
Family THAUMASTODERMATIDAE Remane, 1926
Subfamily THAUMASTODERMATINA Ruppert, 1978
Genus Tetranchyroderma Remane, 1926
Tetranchyroderma weissi sp. nov. (Figures 1 & 2A–E)

Diagnosis
A Tetranchyroderma with an adult length to 605 μm; pharynx length to 195 μm, with pharyngeal pores at base. PgJn at U3; head single-lobed, with cephalic tentacles at U03; body with parallel sides and short, bilobed caudum. Sensory hairs scarce, forming lateral columns along the body and a fringe around the oral opening; epidermal glands few (seven per side, plus one at the posterior end), mixed in size, and scattered along the length of the body. Well recognizable lenticular gland openings on the dorsal surface of the body. Paired cuticular openings ‘stomata’ of unknown function, along the ventrolateral sides of the body. Cuticular armature complete, made up of pentances, small at the anterior and posterior ends of the body but medium-sized elsewhere. Adhesive tubes: TbA, five per side, one slightly larger in the middle at U08 and four lateral of equal size at U06–U08; TbB, 14 per side, a small isolated one implanted laterally at U13, and 13 of the same size more or less evenly spaced, implanted ventrolaterally from U32 to U72; TbD, seven per side in two longitudinal columns, four dorsolateral, robust, at U32, U60, U75, and U92, and three dorsal at U45, U56, and U67; TbV, two arising from a common base, only on the right side, at U86; TbP, 16 in all, two medial, four per side laterally behind the anus, and two þ one on each of two paired pedicles. Ventral locomotor cilia: a continuous field of transverse rows covering the entire surface except the ano-genital area. Reproductive system: testis on the right body side, caudal organ, frontal organ, and egg on the left as seen from above.

Holotype
An adult specimen 474 μm long, formalin–glycerine wholemount, deposited at the Museo Civico di Storia Naturale di Verona, Lungadige Porta Vittoria 9, I-37129 Verona, Italy. Additional material: four specimens on SEM

Table 1. Microhabitat characteristics in the littoral and sublittoral sites at Long Beach Island, New Jersey.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Littoral (top 20 cm layer)</th>
<th>Littoral (bottom 10 cm layer)</th>
<th>Sublittoral</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grain size (ϕ)</td>
<td>1.05</td>
<td>1.18</td>
<td>2.79</td>
</tr>
<tr>
<td>Size-class</td>
<td>0.72</td>
<td>0.70</td>
<td>0.83</td>
</tr>
<tr>
<td>Skewness</td>
<td>−0.03</td>
<td>−0.01</td>
<td>−0.80</td>
</tr>
<tr>
<td>Kurtosis</td>
<td>3.80</td>
<td>3.26</td>
<td>3.56</td>
</tr>
<tr>
<td>Organic matter (% d.w.)</td>
<td>0.5</td>
<td>0.8</td>
<td>2.0</td>
</tr>
<tr>
<td>Temperature (°C)</td>
<td>21.5</td>
<td>21.5</td>
<td>21.5</td>
</tr>
<tr>
<td>Salinity (psu)</td>
<td>33.0</td>
<td>33.0</td>
<td>33.0</td>
</tr>
</tbody>
</table>

Table 2. Species of gastrotrichs found in the littoral and sublittoral sites at Long Beach Island, New Jersey.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Littoral (top 20 cm layer)</th>
<th>Littoral (bottom 10 cm layer)</th>
<th>Sublittoral</th>
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</thead>
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<tr>
<td>MACRODASYIDA</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>TURBANELLIDAE</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Turbanella ambronensis</td>
<td>+</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Turbanella ocellata</td>
<td>+</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>LEPIDODASYIDAE</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cephalodasys sp.</td>
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<td>−</td>
<td>+</td>
</tr>
<tr>
<td>Mesodasys laticaudatus</td>
<td>−</td>
<td>−</td>
<td>+</td>
</tr>
<tr>
<td>THAUMASTODERMATIDAE</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tetranchyroderma weissi</td>
<td>−</td>
<td>+</td>
<td>−</td>
</tr>
<tr>
<td>Tetranchyroderma bunti</td>
<td>+</td>
<td>+</td>
<td>−</td>
</tr>
<tr>
<td>Tetranchyroderma swedmarkii</td>
<td>−</td>
<td>−</td>
<td>+</td>
</tr>
<tr>
<td>CHAETONOTIDA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NEODASYIDAE</td>
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<td></td>
</tr>
<tr>
<td>Neodasys cirtus</td>
<td>+</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>XENOTRICHULIDAE</td>
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<tr>
<td>Xenotrichula intermedia</td>
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<td>−</td>
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</tr>
<tr>
<td>CHAETONOTIDAE</td>
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</tr>
<tr>
<td>Chaetonotus atrox</td>
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<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Halichaetonotus aculifer</td>
<td>+</td>
<td>−</td>
<td>−</td>
</tr>
</tbody>
</table>

+, species present; −, species not present.
stub kept in meiofauna collection of the author (ref. no. NJ-6-2001).

Type locality
Ship Bottom, Long Beach Island, New Jersey, USA (Latitude 39°38'N; Longitude 74°11'W). Mid-water mark zone, in medium clean sand at 20–30 cm depth.

Etymology
The new species is dedicated to Dr Mitchell J. Weiss of the State of New Jersey in recognition of his meaningful studies on the reproductive biology of Gastrotricha.

Description
The description is based mostly on an adult specimen of 570 μm total body length. Pharynx reaches 184 μm in length (measured from the ventral border of the oral opening to the pharyngeo-intestinal junction) and bears a pair of pores near its base. PfPhIn at U31. Oral opening flared, with smooth border. Body of large size, elongate, somewhat swollen in the trunk region, with relatively short caudal pedicles; widths of oral opening/PfPhIn/trunk/caudal base are as follows: 74/62/89/29 at U04/U21/U60/U96 respectively. A pair of cephalic tentacles (12.5 μm in length) arising atop the oral hood at U03. Lateral sensorial organs absent. Sensorial bristles include a fringe around the oral opening ventrally (~6 μm long) and around the leading edge of the oral hood dorsally (~12 μm in length); other hairs form a lateral, evenly spaced column of 7–10 each per side; individual hairs are 19–20 μm in length. Few (seven per side) large (up to 13 μm in diameter), round viscid glands arranged in two dorsolateral columns in the pharyngeo-intestinal region from U07 to U84. Externally emptying glands with elliptic opening (10 × 4 μm), which are readily discernible dorsally amid the elements of the cuticular armature. An additional gland of similar size occurs medially on the rear end at U94. Peculiar openings with strongly cuticularized lips (hereafter referred to as 'stomata'), are discernible bilaterally along the ventrolateral margins of the body; they are tenticular in shape and about 2 μm in length; their function is unknown.

Cuticular armature: dense, made up of delicate pentancres with nearly straight tines, as tall as wide; they are lenticular in shape and about 2 μm in length; other hairs form a lateral, evenly spaced column of 7–10 each per side; individual hairs are 19–20 μm in length. Few (seven per side) large (up to 13 μm in diameter), round viscid glands arranged in two dorsolateral columns in the pharyngeo-intestinal region from U07 to U84. Externally emptying glands with elliptic opening (10 × 4 μm), which are readily discernible dorsally amid the elements of the cuticular armature. An additional gland of similar size occurs medially on the rear end at U94. Peculiar openings with strongly cuticularized lips (hereafter referred to as 'stomata'), are discernible bilaterally along the ventrolateral margins of the body; they are tenticular in shape and about 2 μm in length; their function is unknown.

Adhesive tubes: there are five anterior tubes (ThA) per side arising directly from the body surface one medial, slightly larger than the others, 8 μm in length, at U08, and four somewhat more lateral at U06–U08, 6–7 μm in length. There are 14 adhesive tubes of the ThB series per side; a small lateral one, 8 μm in length, in the pharyngeal region, at U14, and 13 larger ventrolateral tubes, 12–18 μm in length, evenly spaced in the intestinal region from U32 to U72. There are seven tubes of the ThD series, arranged in two columns per side; four dorsolateral, robust (19.5–28.0 μm in length), at U32, U60, U73, and U92 respectively, and three dorsal (up to 18 μm in length), at U43, U56, and U67 respectively. There are two ventral adhesive tubes (ThV), 12–15 μm in length, present only on the right side at U86, arising from a common base. The caudum is medially indented at U95 and formed from two pedicles, each with a proximal fleshy lobes and two distal adhesive tubes (TbP), 7 μm long and fused at their bases, together with a thinner mid-dorsal tube, 10 μm long, which projects beyond them; up to six additional posterior tubes, 10–12.5 μm in length, flank each foot, three–five laterally and one medially.

Ventral ciliation: a continuous field of cilia arranged in transverse rows that extends from the ventral border of the oral opening to the base of the caudal feet, leaving bare only the ano-genital area. Individual cilia are ~12 μm long.

Digestive tract: the oral opening is broad (71 μm in width), with oral hood extending forward above the mouth from U00 to U06; the pharynx is narrow over its anterior half, up to 22–25 μm in width, its pores opening basally at U27; the intestine is broad (30–35 μm in width) over most of its length, narrowing somewhat to the rear (14 μm); the anus opens ventrally at U91.

Reproductive tract: protogynous then simultaneous hermaphrodites; a single elongate testis occurs on the animal's right side as seen from above, starting at U39; vas deferens opens into the rear of the caudal organ, which is pear-shaped (53 μm long × 23 μm wide) and oriented from left rear to forward midline; frontal organ sac-like (39 × 28 μm), connected to the caudal organ and containing motile sperm; ovary not seen; a large egg (102 × 47 μm) is located dorsally in the mid-intestinal region.

Remarks
Fifteen specimens ranging from 335 μm to 605 μm in length were observed with DIC optics. Eight specimens with total body length up to 450 μm were in the female phase, in that all were carrying a large egg; one specimen 445 μm long had egg and caudal organ but no testis; six specimens ranging from 525 μm to 605 μm showed both the female and the male sexual apparatus. On these grounds, it is reasonable to assume that *Tetranchyroderma weissi* is protogynous. This represents the first example of protogynous hermaphroditism among Thaumastodermatidae and one of the few cases (e.g. *Cephalodasyss hadrosum* Hummon et al., 1993) in the entire order Macrodasyida. If the large egg visible in female phase animals is fertilized and how this could happen in the absence of accessory sexual structures (i.e. frontal—caudal organ system) remains an open question.

Cuticular openings along the ventrolateral sides of the body as the 'stomata' described in *T. weissi* were thus far unreported within gastrotrichs in general and in *Tetranchyroderma* in particular, however, while surveying the gastrotrich fauna of the Meloria shoals, Tuscany (cf. Todaro, 1998), I had the chance to observe (M.A.T., unpublished data), similar structures in *Platydasyis ruber* Swedmark, 1956 (Figure 2F), a bulky thaumastodermatid exceeding 700 μm in total body length; a that time two hypothesis came to my mind about the possible function of these organs: (i) stomata can facilitate respiration in large species characterized by a thick cuticle; or (ii) they may just be the openings of some kind of glands, these two alternative hypotheses still are not resolved.

**Taxonomic affinities**

In its general body shape and size as well as the presence of cephalic tentacles, *Tetranchyroderma weissi* resembles...
A new gastrotrich from the Atlantic US water depth. These data suggest that the top 10 cm layer of sublittoral sediment collected at 1.5 m sediment of the littoral zone, or in the jar filled with those containing exclusively more superficial (0–20 cm) sediment of the sublittoral zone. In this respect it is probably not a coincidence that the specimens were able to cope well with the thio-biotic conditions (\textit{in situ} Boaden, 1977) that are shared by these species. The cuticular covering made up of pentancres. \textit{Tetranchyroderma weissi} is distinguishable by its larger size (605 \( \mu \)m vs 350 \( \mu \)m in total body length) as well as its cephalic tentacles and dorsal adhesive tubes, absent in \textit{T. inaequitubulatum}. Further, in the Mediterranean species the number of ventral adhesive tubes (two) does not change with age or size, while in the American species the number increases from two tubes in 250 \( \mu \)m long specimens to five tubes in a fully grown worm, 350 \( \mu \)m in total body length.

Ecological comments

Up to 50 specimens of \textit{T. weissi} were extracted from bags containing littoral sediment from the 20–30 cm deep layer. Extraction was performed more than ten days after collection, and at that time sand had a slight, yet distinct, smell of sulphur; except for one specimen of \textit{Tetranchyroderma bunti} (Thane-Fenchel, 1970), no other gastrotrich species were found in these bags. \textit{Tetranchyroderma weissi} was not found in either the top third sediment layer of these bags, in those containing exclusively more superficial (0–20 cm) sediment of the littoral zone, or in the jar filled with the top 10 cm layer of sublittoral sediment collected at 1.5 m water depth. These data suggest that \textit{T. weissi} is a meio-benthic organism typical of the littoral zone, and yet its vertical distribution within this zone appears more a deliberate choice (\textit{preference}) than a consequence due to active interspecific competition. In this respect it is probably not a coincident that the specimens were able to cope well with the thio-biotic conditions \textit{(in situ) Boaden, 1977} that had developed in the collecting bags by ten days after collection.

Key to the species of \textit{Tetranchyroderma}

<table>
<thead>
<tr>
<th>1. Cuticular armature made of triancres only</th>
<th>\textit{T. tribolatum} Clausen, 1965</th>
</tr>
</thead>
<tbody>
<tr>
<td>— Other</td>
<td>2</td>
</tr>
<tr>
<td>2. Cuticular armature made of tetrancre only</td>
<td>3</td>
</tr>
<tr>
<td>— Other</td>
<td>28</td>
</tr>
<tr>
<td>3. Full dorsal covering (Figure 3A)</td>
<td>4</td>
</tr>
<tr>
<td>— Dorsal covering scanty (Figure 3B)</td>
<td>26</td>
</tr>
<tr>
<td>4. Cephalic tentacles and/or sensorial organs present</td>
<td>5</td>
</tr>
<tr>
<td>— Cephalic tentacles and/or sensorial absent</td>
<td>13</td>
</tr>
<tr>
<td>5. Cephalic tentacles only</td>
<td>6</td>
</tr>
<tr>
<td>— Other</td>
<td>8</td>
</tr>
</tbody>
</table>

6. Caudal feet present ........................................ 7
— Caudal feet absent ........................................... 8
7. TbD present (~9 pairs) ............ \textit{T. aphenthosigmum} Hummon, Todaro, Tongiorgi & Balsamo, 1998
— TbD absent ........................................... \textit{T. apum} Remane, 1927
8. Sensorial organs only.................. 9
— Sensorial organs and cephalic tentacles ......... 12
9. TbV present ............................................ 10
— TbV absent ........................................... 11
10. TbD present ........................................... \textit{T. schizocirratum} Chang, Kubota & Shirayama, 2002
— TbD absent ........................................... \textit{T. sanctaeaterinae} Todaro, Balsamo & Tongiorgi, 1992
11. One pair of TbP between the caudal feet ................. \textit{T. massiliense} Swedmark, 1956
— Two pairs of TbP between the caudal feet ................. \textit{T. gracilium} Chang, Lee & Clausen, 1998
12. At most 20 TbL ................................ \textit{T. bunti} (Thane-Fenchel, 1970)
— More than 20 TbL ................................ \textit{T. hoomsoui} Chang & Lee, 2001
13. TbD and/or TbV present .................... 14
— TbD and/or TbV absent .............................. 23
14. TbD only ............................................... 15
— Other .................................................. 19
15. Head single-lobed ......................................... 16
— Head double-lobed ................................. \textit{T. heterovulabulatum} Hummon, Todaro & Tongiorgi, 1993
16. Two pairs of TbD .............................. 17
— More than two pairs of TbD .......................... 18

Figure 3. Examples of cuticular coverings in dorsal view; scanning electron micrographs; (A) \textit{Tetranchyroderma cirro-phorum}, covering complete; (B) \textit{T. hypopsilancrum} T. heterotubulatum

— TbD present (~9 pairs) ............ \textit{T. aphenthosigmum} Hummon, Todaro, Tongiorgi & Balsamo, 1998
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14. TbD only ............................................... 15
— Other .................................................. 19
15. Head single-lobed ......................................... 16
— Head double-lobed ................................. \textit{T. heterovulabulatum} Hummon, Todaro & Tongiorgi, 1993
16. Two pairs of TbD .............................. 17
— More than two pairs of TbD .......................... 18
17. One pair of TbD in the mid-trunk and one pair in the posterior trunk region .......... *T. borealis* Clausen 2000
   — Both pairs of TbD in the mid-trunk region .......... *Tetranchyroderma* sp. II of Schrom, 1972

18. Five-six pairs of TbD spread sparsely along the body .......... *T. cirrophorum* Levi, 1950
   — Four pairs of TbD restricted to intestinal region .......... *T. verum* Wilke, 1954

19. TbV only ........................................ 20
   — Both TbD and TbV .................................. 22

20. One group of TbV per side ................................ 21
   — Two groups of TbV per side .......... *T. littoralis* Rao, 1981

21. At most 15 TbL per side ................................
   — More than 15 TbL per side .................. *T. thysanogaster* Boaden, 1965

22. One pair of TbD, located in the anterior body region ...
   — One pair of TbD, located in the posterior body region ...
   — More than 1 pair of TbD, located in the anterior or posterior body region .......... *Tetranchyroderma* sp. 4 Valbonesi & Luporini, 1984

23. Body ending with caudal pedicles ............... 24
   — Body ending with caudal lobes ............. *T. dragescoi* Swedmark, 1967

*Figure 4.* Examples of sensorial organs (A–C) and distribution of adhesive tubes (D); scanning electron micrographs. (A) *Tetranchyroderma* sp. (= *Tetranchyroderma* sp. I Todaro, Fleeger & Hummon, 1995), anterior end, dorsal view showing knob-like sensorial organs; (B) *T. swedmarki*, anterior end, dorsal view showing rod-like sensorial organs; (C) *T. bunti*, anterior end, ventral view showing elongate sensorial organs; (D) *T. pachysomum*, whole animal, showing ventral adhesive tubes in bilateral clusters (arrows). Scale bars: A–C, 20 μm; D, 50 μm.
24. TbP between the caudal feet present ........................................... 25
   — TbP between the caudal feet absent ........................................ 25
   — T. dendricum Saito, 1937
25. Eight TbP between the caudal feet ........................................... 26
   — Fewer than eight adhesive tubes between the caudal feet .............. 26
   — T. pugetensis Wieser, 1957
26. TbL in the pharyngeal region present .......................................... 27
   — TbL in the pharyngeal region absent ........................................ 27
   — T. pugetensis Wieser, 1957
27. One TbP per side in the pharyngeal region .................................... 28
   — T. hypobalanum Hummon, Todaro & Tongiorgi, 1993
   — More than one TbP per side in the pharyngeal region ................. 28
   — T. boadeni Schrom, 1972
28. Cuticular armature made up of pentancres only ................................ 29
   — Cuticular armature made up of mixed types of ancres .................. 29
   — T. bulbosum
29. Full dorsal covering ........................................................................ 30
   — Scanty dorsal covering .................................................................. 30
30. Cephalic tentacles and/or sensorial organs present .......................... 31
   — Cephalic tentacles and/or sensorial organs absent ....................... 31
31. Cephalic tentacles only .................................................................... 32
   — Other ......................................................................................... 32
32. One pair of cephalic tentacle ............................................................ 33
   — Two pairs of cephalic tentacles .................................................... 33
   — T. antennatum
33. Sensorial organs only ....................................................................... 34
   — Cephalic tentacles and sensorial organs ........................................ 34
   — T. quadritentaculatum Todaro, Balsamo & Tongiorgi, 1992
34. Sensorial organ knob-like .................................................................. 35
   — Sensorial organ shaped otherwise ............................................... 35
35. TbD and/or TbV present .................................................................... 36
   — TbD and/or TbV absent ...... T. hystricis Remane, 1926
36. TbD only .......................................................................................... 37
   — T. polyprobolostomum Hummon, Todaro, Balsamo & Tongiorgi, 1996
   — Other ......................................................................................... 37
37. TbV only.......................................................................................... 38
   — T. bulbosum Clausen, 2000
   — TbD and TbV ...... T. norvegicum Clausen, 1996
38. Sensorial organ rod-like ..................................................................... 39
   — Sensory organ elongate ................................................................. 40
   — T. scweinarki Rao & Ganapati, 1968
   — T. heterotentaculatum Chang & Lee, 2001
39. TbD present ...................................................................................... 40
   — TbD absent .................................................................................. 40
40. Three pairs of TbD ................................................................. 41
   — T. esarabdophorum Tongiorgi & Balsamo, 1984
   — More than three pairs of TbD ....................................................... 41
   — T. eraspeophorum Hummon, 1977
41. Sensorial organ knob-like .................................................................. 42
   — Sensorial organ elongate ............................................................... 42
   — T. papii Gerlach, 1953
42. TbV present, one pair........................................................................ 43
   — T. antennatum
   — T. dendricum Saito, 1937
43. TbV and/or TbV present .................................................................... 44
   — TbV and/or TbV absent .................................................................. 44
44. TbD only .......................................................................................... 45
   — Other ......................................................................................... 45
45. One pair of TbD ............................................................................... 46
   — More than one pair of TbD .......................................................... 46
   — T. hystrix Lupinori, Magagnini & Tongiorgi, 1973
46. TbV only .......................................................................................... 47
   — Both TbD and TbV ...... T. weissi sp. nov. Todaro, 2002
47. TbV arranged bilaterally .................................................................... 48
   — TbV forming a group of 4–5 tubes on the right side only .............. 48
   — T. inequitubulatum Todaro, Balsamo & Tongiorgi, 2002
48. One group of TbV per side ................................................................ 49
   — One single TbV per side .............................................................. 49
   — T. thyssanophorum
49. Eight TbA per side ................................................................. T. pacificum Schmidt, 1974
   — Three TbA per side ...... T. coelopodium Boaden, 1963
50. Pentancres bearing tines of roughly the same length ......................... 51
   — Pentancres with the central tine longer than the others ............... 51
51. Body elongate, TL more than 300 μm ............................................ 52
   — Body short, TL less than 300 μm ................................................ 52
52. Ten TbP between the caudal feet, and eight TBA per side .................. 53
   — T. polydonium Lupinori, Magagnini & Tongiorgi, 1971
   — Six TbP between the caudal feet and fewer than eight TbA per side T. megastoma (Remane, 1927)
53. Ten TbA per side ............................................................................... 54
   — T. insulare Balsamo, Fregni & Tongiorgi, 1994
   — Fewer than 10 TbA per side ....................................................... 54
   — T. kontosorum Hummon, Todaro, Balsamo & Tongiorgi, 1996
54. Central tine 4–5 times longer than the others .................................. 55
   — T. polyacanthus (Remane, 1926)
   — Central tine 2–3 times longer than the others ............................... 55
   — T. tanymesatherum Hummon, Todaro, Balsamo & Tongiorgi, 1996
55. Eight TbP between the caudal feet, and 5 TbA per side, forming an arc T. psiloporum
   — Hummon, Todaro, Tongiorgi & Balsamo, 1998
   — Six TbP between caudal feet, and six TbA per side, 5 of which form a fan-like arc .................................................. T. anomalopsum
   — Hummon, Todaro, Balsamo & Tongiorgi, 1996
56. Cuticular armature made up of tetrancres and pentancres ................. T. paradoxum Thane-Fenchel, 1970
   — Cuticular armature made up of triancres, tetrancres and pentancres T. paratilis Rao, 1991
   — T. paratilis Rao, 1991
   — T. paratilis Rao, 1991
   — T. paratilis Rao, 1991
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REFERENCES


