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A NEW SPECIES OF *URODASYS* (GASTROTRICHA, MACRODASYIDA) FROM DYSOXIC SEDIMENTS OF THE SANTA BARBARA BASIN (CALIFORNIA, U.S.A.)

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ABSTRACT

Numerous specimens belonging to an undescribed macrodasyid gastrotrich species were recovered during a survey of the biota associated with the severely dysoxic sediments of the Santa Barbara Basin, off California, U.S.A. Densities of this species reach 10 specimens cm^{-2}. *Urodasys anorektoxys* sp. nov. is described and figured. Specimens of this taxon attain the largest size within the genus; body, excluding the motile tail, is up to 1100 μm in length. Adults are protandric, then simultaneous hermaphrodites and lack a stylet-like sexual structure; the main morphological traits include (1) a unitary ventral ciliary field, and (2) a pharyngeal region that bears a total of 14 pairs of adhesive tubes, 12 pairs ventrolaterally and two pairs dorsolaterally. The systematic position of the new species is discussed.

The sediments of the bathyal Santa Barbara Basin (SBB), California, U.S.A., are bathed in severely dysoxic to anoxic water (i.e., typically <5 μM or <0.1 mL L^{-1}; Reimers et al., 1996; Bernhard et al., 1997) and sulfide concentrations in the surface cm of sediment can be ~1 μM (Kuwabara et al., 1999). A mat of the filamentous sulfide oxidizing bacterium *Beggiatoa* is the most notable biological feature of this sediment, which additionally hosts a fairly diverse eukaryotic meiofaunal assemblage (Bernhard et al., 2000). Many constituents of the eukaryotic community are apparently undescribed species, among which is a rather large macrodasyid gastrotrich. This species is characterized by an elongate motile tail and is taxonomically assigned to the genus *Urodasys*. To date, this genus groups 12 fully described species (Remane, 1926; Wilke, 1954; Renaud-Mornant, 1969; Schoepfer-Sterrer, 1974; Kisielewski, 1987; Fregni et al., 1999a,b), plus two described, but not named (Schoepfer-Sterrer, 1974, Valbonesi and Luporini, 1984), species. None of the previously described species has been reported from poorly oxygenated, sulfidic habitats.

METHODS

The specimens described and figured herein were obtained from the top 1–2 cm of sediment collected by a Soutar box-core during September 1998 (hereafter denoted SBB998) and February 1999 (hereafter denoted SBB299) between 588–592 m depth in the Santa Barbara Basin (Table 1). After collection, and during transport to South Carolina, sediments were maintained at ambient temperature (~5°C). In the laboratory, sediments were sieved briefly over a 63-μm screen with chilled artificial seawater (ASW) and the coarser fraction was observed with an Olympus SZH10 stereomicroscope. Individual specimens were removed with a small-bore pipette, rinsed in 0.2-μm filtered ASW (FASW), relaxed in 8% $MgCl_2$, rinsed quickly in FASW, and fixed in either 10% neutralized formalin or 3% glutaraldehyde / 0.1 M cacodylate buffer. For taxonomic analysis, 24 specimens were transferred to glycerol, individually whole-mounted on glass slides, and surveyed under a Leitz Dialux 20 microscope equipped with Nomarski optics. Twelve additional specimens were dehydrated through a graded ethanol series, critical point-dried using CO_2, mounted on alumi-

Table 1. List of site information, including bottom water oxygen concentrations (O_2) and number of *Urodasys anorektoxys* specimens per square cm (#/cm^2). Sample designations are coded with month and year information (e.g., 998G was collected in September 1998). SL = north of Shipping Lanes. * denotes type locality.

Sample	Site	Coordinates (° N, ° W)	Water depth (m)	O_2 (μM)	#/cm^2
998G	Center	34° 13.522, 120° 02.285	589	1.4	5.3
299L	Center	34° 13.423, 120° 02.065	592	2.4	10.2
299C*	SL	34° 15.939, 120° 01.990	588	3.8	8.6
299P	Northern	34° 17.476, 120° 01.896	581	ND	1.6
299X	Edge3	34° 16.845, 119° 58.561	555	5.1	1.8
299U	Edge2	34° 17.817, 119° 56.886	521	5.1	0

num stubs, sputter coated with gold-palladium and observed with a Philips XL 40 Scanning Electron Microscope (SEM). Measurements were taken using an ocular micrometer or derived from photomicrographs. The location of some morphological characteristics along the body are given in percentage units (U) of total body length measured from anterior to posterior, but excluding the tail.

Density data were obtained from 2.5 cm diameter subcores of the box core. The surface cm was fixed in either 3.7% formaldehyde / Phosphate Buffered Saline (PBS) or 3% glutaraldehyde / 0.1 M cacodylate buffer (pH 7.1). In the laboratory, a solution of rose Bengal (~2 g L^{-1} aqueous) was introduced to the sample for at least 12 h after which the entire sample was sieved with appropriate buffer over a 63-μm screen. All gastrotrichs (and other metazoans) were enumerated from the >63 μm fraction.

SYSTEMATICS

Order Macrodasyida Remane, 1925
[Rao and Clausen, 1970]
Family Macrodasyidae Remane, 1926
Genus *Urodasys* Remane, 1926
Urodasys anorektoxys new species
(Figs. 1–4)

Type material.—The holotype, which is the illustrated SEM-prepared adult of 735-μm length (Fig. 3A), is retained in the collection of the senior author (MAT; URO-CA-99/1). Four formalin-glycerin whole mounts have been submitted as paratypes to the National Museum of Natural History, Washington, D.C. (USNM 186541, USNM 186542, USNM 186543, USNM 186544).

Type locality.—Santa Barbara Basin, California (34°16′N; 120°02′W); bathyal muddy sediment, ~590 m water depth, February 1999.

Diagnosis.—A long and slender *Urodasys*, up to 1100 μm in length (tail excluded) and up to 150 μm in width; pharynx, which is up to 432 μm in length, bears pores near its posterior end; intestine is elliptically trapezoidal and lacks any apparent anus. Ventral locomotor ciliary field is unitary, covering the pharyngeal and anterior half of the trunk region. Adhesive apparatus consists of up to 16 pairs of ventrolateral adhesive tubes (of which 12 occur along the pharyngeal region) plus 4–5 pairs of dorsolateral tubes. Two pairs of the latter occur in the pharyngeal region and three pairs occur near the trunk posterior. Animals are protandric to simultaneous hermaphrodites, with paired testes but lacking a cuticularized stylet-like sexual organ. The left testis tends to be larger than the

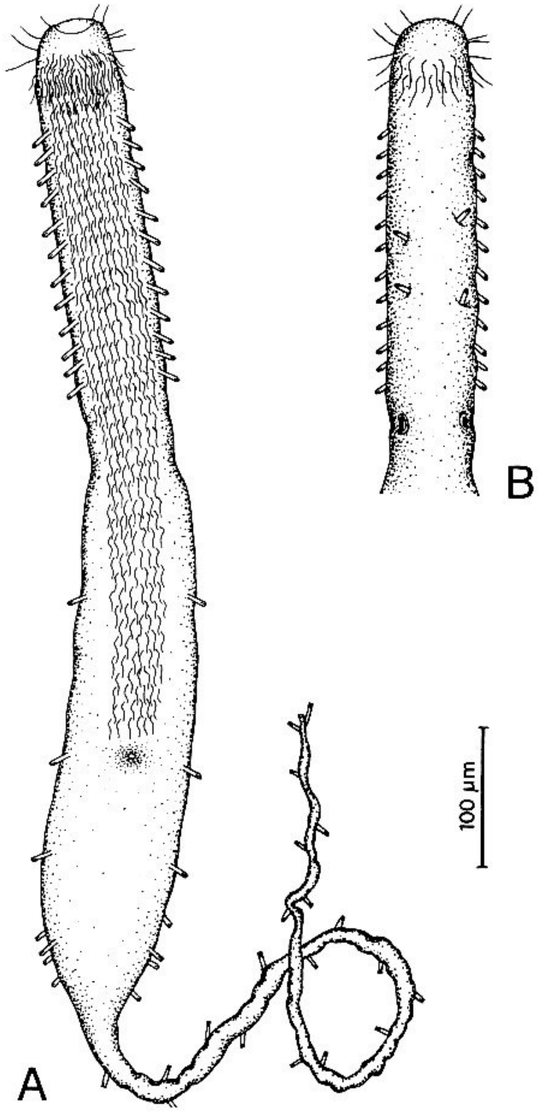

Figure 1. *Urodasys anorektoxys* new species. A, ventral view showing the adhesive apparatus, the locomotor ciliary band, and the male pore; B, dorsal view of the pharyngeal region, showing the pharyngeal pores. Drawings were made from a 731-µm long adult specimen.

one on the right. The male genital pore is ventral, slightly posterior to the end of the ventral ciliary field.

Etymology.—*anorektos* (Gr.), without appetite for, and *oxys* (Gr.), oxygen; the trivial name alludes to the poorly oxygenated microhabitat in which the species lives.

Description.—Length of adult specimens, excluding the tail, ranging from 654 to 1100 µm (mean = 844 ± 144 µm, n = 20). Body ribbon-shaped, 70–100 µm in width along the

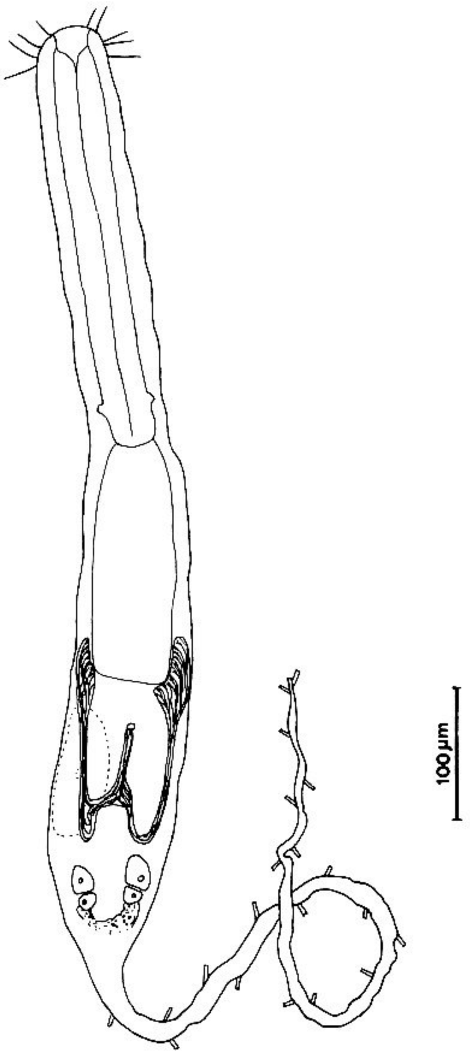

Figure 2. *Urodasys anorektoxys* new species, internal structures as seen from below, showing from anterior to posterior: buccal cavity, pharynx with pharyngeal pores near the base, the elliptical trapezoidal gut, left (dwarfed) and right testis, the male ventral pore, a maturing egg on the left side dorsal to the testis, and the posterio ovaries. Drawing was based mainly on a 731-µm long adult specimen.

pharyngeal region, often distinctly broadening to the rear of the pharyngeo-intestinal junction, reaching a width of 100–150 µm at mid-trunk and then tapering again toward the caudum; the skin of fixed specimens usually appears wrinkled, although that is likely a fixation artifact because live specimens appear turgid. The slender tail attains a length of at least 1 mm, but is often truncated because of mechanical damage. Anterior end is blunt, with head region 38–43 µm long and 68–93 µm wide (mean = 78 ± 8 µm; n = 9), lacking pestle organs, demarcated posteriorly by two broad rings of 18–22 µm long cilia; head

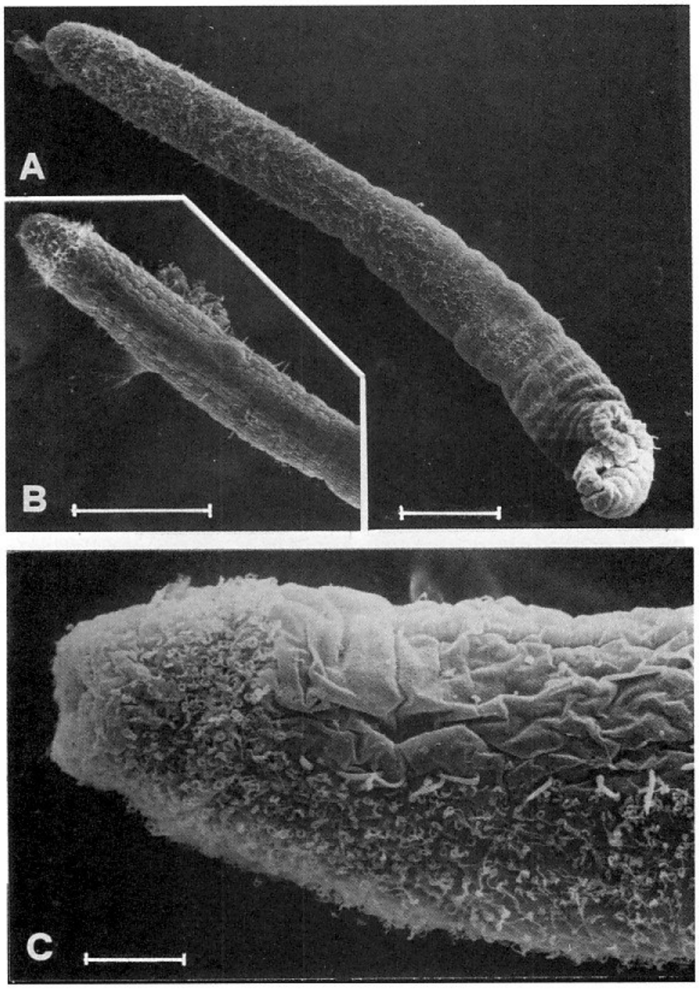

Figure 3. *Urodasys anorektoxys* new species, SEM micrographs of holotype. A, total ventral view; B, dorsal view of the head and of the pharyngeal region; C, close up of the lateral side of the head, showing the distribution of the cilia and the implant of some adhesive tubes. Scale bars: A, B = 100 μm, C = 20 μm.

bears additional scattered tactile cilia, including 4–6 laterally directed hairs per side. Sensory hairs along the body margin are few or absent altogether.

Ventral locomotor ciliation begins just behind the tactile cilia that encircle the head and extends over the first half of the trunk, consisting of individual cilia, 12–18 μm in length. These cilia are arranged in a single band that completely covers the surface beneath the pharynx and most of the first half of the trunk region. Cilia are more abundant and densely packed in the pharyngeal region and become more sparse posteriorly.

Body adhesive apparatus consists of up to 32 tubes arranged in two ventrolateral columns or longitudinal series, and up to 10 tubes organized in dorsolateral columns. Ventrolateral tubes, which occur up to 12 per side along the pharyngeal region, are about 15

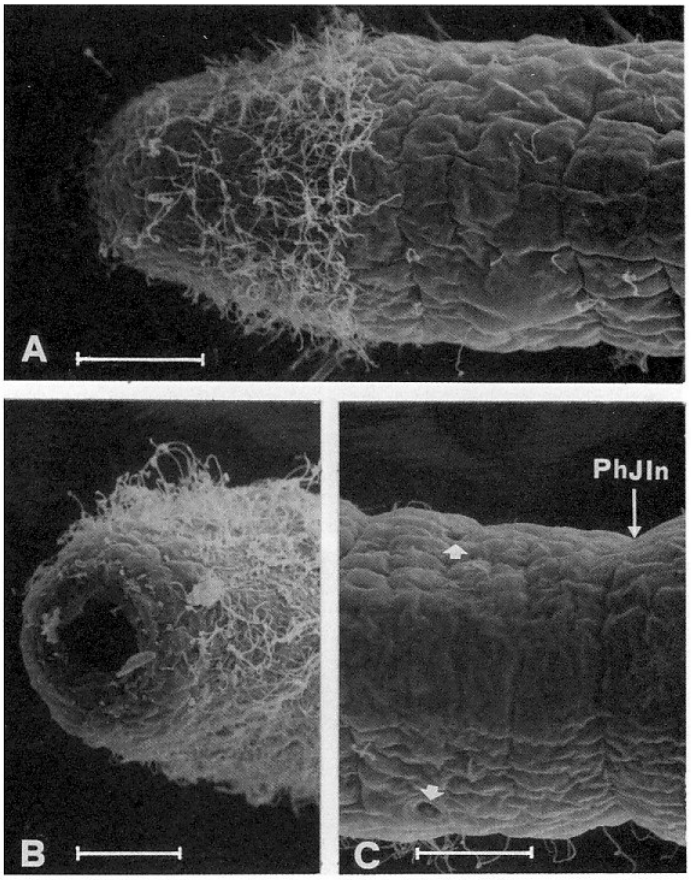

Figure 4. *Urodasys anorektoxys* new species, SEM micrographs. A, dorsal view of the anterior end showing the head ciliary ring; B, anterior end showing the mouth opening and the cephalic ciliature; C, dorsal view at the pharyngeo-intestinal junction (PhJIn) level, showing the pharyngeal pores (arrows). Scale bars: A–C = 20 µm.

µm in length and are evenly spaced from U10 to U36, with four more, 12 µm in length, inserting along the trunk at U57, U74, U84 and U93, respectively. Dorsolateral tubes: two per side arise in the mid-pharyngeal region, between U20 and U28, and three pairs on the posterior end of the trunk originating at U89, U94 and U96, respectively; left and right tubes of a pair may not insert symmetrically. Caudal tubes: 50 or more on a 1 mm-long tail, 12–18 µm in length, often alternate sides.

Mouth terminal, 14–16 µm in diameter. Pharynx is 300–432 µm long (mean = 373 ± 44 µm, n = 16), with pores opening dorsolaterally near the base, at U40. The gut is typical of the genus, resembling a blind sac, elliptically trapezoidal in shape, often filled with white-yellowish digesting material, and lacking any apparent anus.

Reproductive apparatus consist of paired testes and paired ovaries, without either caudal or frontal organs. The left testis appears slightly larger than the right one. Vasa deferentia extend backward and then recurve forward, joining at about U82, the common duct continuing forward to open ventrally just behind the ciliary field at U74. Spermatozoa are filiform with a corkscrew-like anterior part. Eggs mature rostrally, a large ovum often being seen on one side in front of the ovaries.

Taxonomic Affinities.—The cosmopolitan genus *Urodasys* includes 13 known species that, on the basis of the morphology of the sexual structures and reproductive strategy, seem the result of two distinct evolutionary avenues undertaken by the early representative of this taxon. As envisioned, one branch of the hypothetical evolutionary tree includes species displaying a somewhat reduced male reproductive apparatus that is characterized by one testis only, located on the left side, and by a strongly cuticularized accessory penial stylet-like organ (i.e., *U. acanthostylis, U. bucinostylis, U. calicostylis, U. cornustylis, U. nodostylis, U. remostylis, U. spirostylis, U. uncinostylis, Urodasys* sp. I Schoepfer-Sterrer, 1974, *Urodasys* sp. 1 Valbonesi and Luporini, 1984). In another species on this branch, *U. viviparus*, the testes and penial structure are lacking altogether (cf Wilke, 1954; Schoepfer-Sterrer, 1974; Valbonesi and Luporini, 1984; Fregni et al., 1999a,b; for function of accessory reproductive structures in *Urodasys* see also Ruppert, 1991: 89). The second branch comprises species whose male reproductive system includes two testes but lacks a penial structure (i.e., *U. apuliensis, U. elongatus, U. mirabilis, U. roscoffensis*). The species described herein, because of its reproductive features, obviously falls within the latter branch. *Urodasys anorektoxys* differs from the Mediterranean *U. apuliensis* Fregni, Faienza, De Zio-Grimaldi, Tongiorgi, and Balsamo, 1999 principally because it is of a larger size (up to 1100 vs 670 μm) and it bears dorsal adhesive tubes that are lacking in *U. apuliensis*. In addition, *U. anorektoxys* has fewer ventrolateral adhesive tubes (≤16 per side vs ≤23). *U. anorektoxys* can easily be separated from *U. elongatus* Renaud Mornant, 1969, which were collected in the Tuamoto Archipelago, because of its larger size (844 vs 350 μm, respectively), the extent of the ciliary field, which in *U. elongatus* is confined within the pharyngeal region, as well as the number and arrangement of adhesive tubes. The new SBB species is discernible from *U. roscoffensis* Kisielewki, 1987, which were collected along the Atlantic coast of France, mainly by its larger size (654–1100 vs 400–630 μm, respectively) and by its unitary ciliary band. By contrast, the locomotor ciliation in *U. roscoffensis* consists of a uniform area along the pharyngeal region and two separate bands along the first half of the trunk.

The Californian *Urodasys anorektoxys* differs from *U. mirabilis* Remane, 1926 chiefly in that it bears ventrolateral and dorsolateral adhesive tubes along the pharyngeal region (absent in *U. mirabilis* as described by Remane), in a much lower number of ventrolateral tubes along the trunk (three on each side in *U. anorektoxys* vs 10 in *U. mirabilis*), and in carrying dorsolateral tubes on the trunk (absent in *U. mirabilis*). The body length, excluding the tail, could also be a distinctive characteristic between the two species (≤1100 μm in *U. anorektoxys* vs ≤800 μm in *U. mirabilis*). For *U. mirabilis*, however, literature data concerning this trait are puzzling. Remane (1926) and Forneris (1961) report the body length of exclusively male specimens to range from 600 to 800 μm whereas Teuchert (1968) and Schmidt and Teuchert (1969) note the body of simultaneous hermaphroditic specimens to be 450–500 μm in length. Assuming that in *Urodasys*, like most other macrodasyidans, male gonads mature first (e.g., Balsamo et al., 1999) and the body continues to grow until female gonads mature, it is evident that the specimens referred to above fall within two distinct size classes. Recently, body size coupled with an individual's sexual state allowed discrimination of the proper identity of sympatric specimens of otherwise remarkably similar species (i.e., *Dactylopodola typhle* vs *D. mesotyphle*; cf. Hummon et al., 1998). If the same phenomenon also occurs in populations of *Urodasys* *mirabilis* found along the northern coast of Europe, then specimens of the two groups would in fact represent two reproductively separate populations and would by inference belong to two species. Similarly, *U. anorektoxys* is indeed of a much longer body size compared to the specimens referred to by Teuchert (1968) and Schmidt and Teuchert (1969) while the same may not be true for the specimens of Remane and Forneris.

Although *Urodasys* have been reported from different regions of the world, single species seem to have limited geographic ranges. An exception to this generality is the cosmopolitan *U. viviparus*, whose near ubiquity is perhaps a prerogative derived from its characteristic reproductive strategy, in which parthenogenesis is coupled with viviparity.

Ecology.—As noted, depths below about 550 m in the Santa Barbara Basin have waters that are severely depleted in dissolved oxygen and sediments support the filamentous sulfide oxidizing bacterium *Beggiatoa*. Although megafauna and most macrofauna are absent from these depths of the SBB, there are extremely high abundances of protists, including foraminifera, flagellates, and ciliates (Bernhard et al., 2000). The only metazoan taxa in the *Beggiatoa*-laden sediments of the SBB are *Urodasys anorektoxys*, the nematode *Desmodora masira*, a rare species of the nematode genus *Daptonema*, and a previously undescribed nerillid polychaete, possibly a new genus. Occasionally, the epifaunal gastropod *Astryx permodesta* occurs in some box cores, although not when the oxygen levels are extremely low. The majority of eukaryotic taxa in the SBB sediments have putative symbionts, including either or both epibionts and endobionts (Bernhard et al., 2000). SEM and transmission electron microscopic studies of *U. anorektoxys* have not yielded any evidence of such bacterial associations to date. However, we infer the existence of some adaptation to allow inhabitation of this environment because specimens die within about 15 min after isolation from oxygen-depleted sediments. Because temperature and salinity were maintained near ambient values, presumably the *U. anorektoxys* die because they are exposed to too much oxygen or too little sulfide.

Although no other *Urodasys* species have been found in oxygen-depleted, sulfidic environments, a few other gastrotrich species are known from such seemingly hostile conditions (e.g., Powell et al., 1983; Meyers et al., 1988; see also Kraus and Colacino, 1983; Fox and Powell, 1986). In fact, in an experiment that produced a mat of *Beggiatoa*, abundant gastrotrichs of the species *Turbanella ocellata* (Meyers et al., 1988) occurred in the bacterial mat. The abundance of *U. anorektoxys* in SBB exceeds previous abundance data on gastrotrichs from oxygen-depleted environments (Table 1). For example, *U. anorektoxys* reached maximum densities of 10.2 specimens per cm^{-2}, but the maximum density of *Turbanella ocellata* in Corpus Christi Bay, Texas was only ~2.2 cm^{-2} (Meyers et al., 1987) and that of an unidentified gastrotrich in the East Flower Garden Brine Seep was only ~1.3 cm^{-2} (Powell et al., 1983). The abundance of *U. anorektoxys* was higher in samples with low oxygen levels (i.e., <4 μM) and were lowest in samples with higher oxygen concentrations (>5 μM; Table 1).

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