Record and description of *Anandrodasys agadasys* (Gastrotricha: Redudasyidae) from Lee Stocking Island (Bahamas), with remarks on populations from different geographic areas

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Abstract

We here report the occurrence of a marine gastrotrich species, *Anandrodasys agadasys,* from sublittoral calcareous sands of Lee Stocking Island, Bahamas. This is the first record of this species from the Bahamas ecoregion; three other records include the South Florida (Florida Keys), Lesser Antilles (St. John Island) and Central Caribbean ecoregions (Panama). *A. agadasys* is also known from Australia and Egypt (Red Sea). Based on a detailed description of the specimens of Lee Stocking Island and data from the literature, a pattern of slight morphological differences between Caribbean, Pacific and Red Sea specimens were found. This might either indicate a geographic structure of this parthenogenic species with distinct regional forms or even a complex of different, independent evolutionary species.

Key words: meiofauna, biogeography, taxonomy, Caribbean Sea

Introduction

Gastrotricha is a phylum that solely comprises microscopic aquatic animals (standard body lengths between 120 and 1000 µm, with a few larger species to 3 mm), which live in benthic or periphytic microhabitats and feed on a microscopic diet (microalgae, flagellates, bacteria). Members of the subtaxon Macrodasyida are mainly worm- or strap-shaped animals and can be found in marine and brackish environments. They predominantly live in the interstitial spaces of medium to coarse grain-sized sands (Todaro & Hummon 2008) and hence belong to the community of the so-called marine meiofauna (aka the mesopsammon). Here, they can occupy the second or third place in total abundance behind nematodes and copepods (Todaro et al. 1995, Hochberg 1999).

Due to their minuscule size, difficult preparation, and a global undersupply of experts, the global to regional knowledge on the diversity patterns and biogeography of Gastrotricha is still extremely heterogeneous. Marine regions such as the Mediterranean or the NE Atlantic

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shelf (e.g. the North Sea) are well-known areas with regards to the gastrotrich fauna (see, e.g., Todaro et al. 2000, 2003; Gerlach 2004). However, even in these regions, there still is a continuous discovery of new taxa (e.g. Dal Zotto et al. 2010, Hummon 2008). The tropical and subtropical regions of the world including the ecoregions of the Caribbean Sea (Tropical Northwestern Atlantic, TNWA) are particularly poorly studied with regards to the diversity and distribution of marine meiofauna (Miloslavich et al. 2010). Recently, a collaborative international effort has been made to inventory the marine Gastrotricha of the TNWA with a focus on four of the five ecoregions, i.e. South Florida, Bahamian, Lesser Antilles, and the Central Caribbean; the fifth ecoregion – the Gulf of Mexico – had until recently received the most attention (see Hummon 2010a, Todaro et al. 1995). With these new efforts, several new records and descriptions of gastrotrichs from the TNWA have become available. In some cases, studies have revealed species new to science (Atherton & Hochberg 2012a,b; Hochberg 2008, 2010; Hochberg & Atherton 2010, 2011; Hummon 2010a; Todaro et al. 2012), while in other cases, they have extended the geographic distributions of known species and provided additional information on morphological variation within species (Hummon 2010a). All of this data is important for understanding Caribbean biodiversity and appreciating zoogeographical patterns throughout the TNWA. With this in mind, we report here additional morphological data and a range extension for *Anandrodasys agadasys* (Hochberg, 2003) in the TNWA, i.e. Lee Stocking Island. This data is intended to extend our understanding of intraspecific variation, which is often underreported for many species and may lead to taxonomic confusion when conspecifics are found outside their type locality (see Hummon 2011). Also, it may be of significance that *A. agadasys* is purportedly a strict asexual (Hummon 2011), which is rare in marine Gastrotricha; there are in fact no reports that focus on variation in asexual macrodasyidan species.

Material and Methods

Samples of medium to coarse biogenic calcareous sand were taken on April 11, 2010 at the shallow sublittoral station LSI 8 (N 23°46.816'; W 76°06.720') on the north-western tip of Lee Stocking Island, Bahamas. Sand was collected by snorkeling and using 750 ml polyethylene jars that were plowed through the upper 5 to 10 cm layer of sediment at a bottom depth of 4 m. Living meiofauna was either extracted immediately from the sediment samples or were kept for a few days before extraction at the Perry Institute for Marine Sciences. Extraction used the anesthetization-decantation method (e.g. Giere 2009, see also Todaro & Hummon 2008): ca. 100 ml of sediment was combined with 7 % (w/v) aqueous solution of $MgCl_2$ and the supernatant decanted into a sieve with a mesh size of 40 µm. Concentrated meiofauna was rinsed into petri dishes with seawater and viewed under a Leica EZ4 stereomicroscope. Individual gastrotrich specimens were removed using capillary glass pipettes, transferred to a drop of $MgCl_2$ solution on a glass slide, covered with a cover slip, and observed alive under a Zeiss Axio Scope A1 equipped with differential interference contrast (DIC). One specimen of *Ananadrodasys agadasys* was documented with a Sony Handycam digital video camera mounted at the camera interface of the microscope; video files and photographs were captured. Three video sequences of the specimen from LSI will be deposited on the Gastrotricha Global Database server (Hummon et al. 2005, Humon 2010b) and can be obtained from the first author on request. Printouts of these digital data served as the basis for the original line drawings on parchment paper. Different positions and size ranges of internal and external structures are referred to as percentage body units (U), where the total body length represents 100 units.

Two further specimens were fixed with 5 % formaldehyde solution in 0.1 M PBS (pH 7.4) after short relaxation in 7 % $MgCl_2$ (fixation at ambient temperature and storage within fixative for several months). A single recovered specimen was prepared as a whole mount in glycerol after dehydration for several days in a glycerol-PBS mixture of 1:10 ratio. The coverslip was mounted with a beeswax-paraffin mixture of 1:2 ratio and sealed with clear nail varnish. This specimen (F-100411-2C) was observed with a Leica DM2500 microscope equipped with DIC and is kept in the collection of A.K.
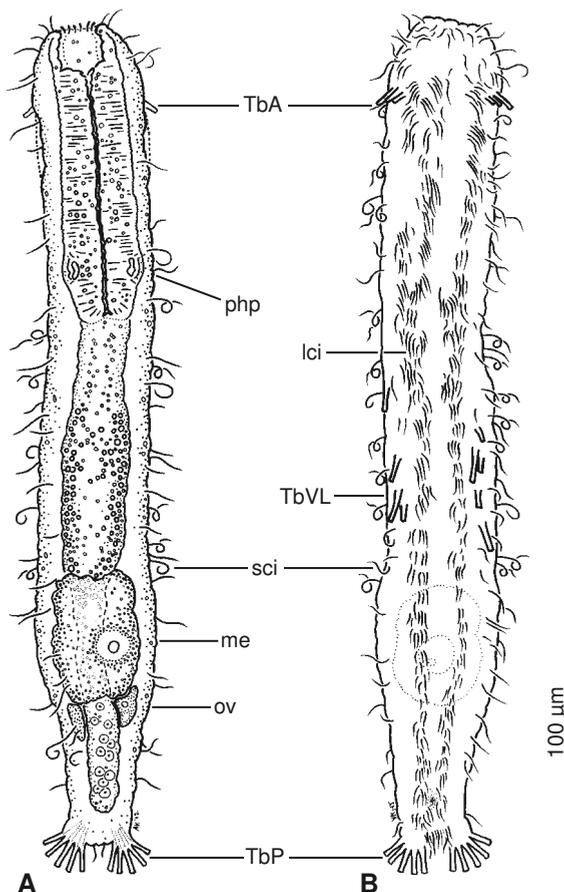
Fig. 1. Schematic drawings of *Anandrodasys agadasys* from Lee Stocking Island (LSI), Bahamas. **A.** Internal view. **B.** Ventral view with adhesive tubes and cilia. Abbreviations: lci, locomotory cilia; me, mature egg; ov, ovary; php, pharyngeal pores; sci, sensory cilia; TbA, TbP, TbVL, anterior, posterior, ventrolateral adhesive tubes.

Results

Description of the Bahamian specimens. Gross morphology. *Ananadrodasys agadasys* has a slender, belt-shaped body of 378 µm length (Fig. 1). There is no distinctly separated head section, but an inconspicuous constriction of the trunk posterior to the position of the anterior adhesive tubes (TbA) ranging from approximately U10–20. The anterior end is blunt with slightly rounded edges (seen from dorsal); at the likewise blunt caudal end of the trunk there is a pair of inconspicuous lobes that bear the posterior adhesive tubes (TbP). The trunk width is almost equal in most body regions and only tapers slightly posterior to the mature egg from U85 on. Trunk width (Wt) at U0/10/40/60/85/95

is 31/51/49/49/56/36/28 µm respectively. The body is covered with a smooth cuticle that does not form any armament but has a fine granular texture (see below). The slightly undulating contours of the trunk indicate some irregular folds and depressions of the integument. Epidermal glands were not observed. Measurements of the second specimen are as follows: Total length approximately 270 µm, Wt at U10/18/52/88 is 38/35/42/27 µm, respectively. The length value could be erroneous due to contraction of the animal during fixation.

Adhesive tubes. At U10, there is a paired group of ventrolaterally inserting anterior adhesive tubes (TbA) that successively lengthen from median to lateral. Per group, there are three tubes that are directed caudo-laterally, forming an

angle of approximately 45° with the longitudinal body axis (Fig. 2B,E). The most lateral tubes are the longest while the most median tubes are the shortest. They possess a length of 12.5, 7.5, and 5 µm, respectively. TbA directly insert on the ventral body surface. Between U45 and U65 there is a paired group of ventrolateral adhesive tubes (TbVL). The tubes of this group are asymmetric in arrangement, number, and length of each single tube. There are five tubes in the left group of TbVL whereas only four tubes in the right one (Fig. 2D). In the second specimen, there are seven tubes in the right group but only five in the left. The lengths of the tubes range from 7.7 to 15.4 µm. On each side of the caudal trunk end at U100, there is a group of five posterior adhesive tubes (TbP) inserting at the inconspicuous paired lobes and arranged in an arc-like manner, thus

Tab. 1. Overview of published records of *Anandrodasys agadasys* (Hochberg, 2003) and some morphological characters if available. The "specimen ID" refers to, e.g. video-file numbers (see Hummon 2010b), or figure plate numbers of the source literature. In the column 'pattern of TbVL' '2×2' means 2 adhesive tubes per side in a paired group while '2&1' means two grouped tubes on the one side and a single tube on the opposite side etc. Abbreviations: LPh, length of pharynx, Lt, total body length, TbA, anterior adhesive tubes, TbP, posterior adhesive tubes, TbVL, ventrolateral adhesive tubes, U, percentage body units, Wt, trunk width at different body regions (U). According to Hummon (2011) the species is present also in the following localities (but no morphological data of the specimens are available): Sharm el-Arab, Sharm el-Naga, Na'ama Bay, Ras Nasrani (all Egypt, Red Sea), and Crandon Park, Florida, Atlantic

specimen ID, source and locality	latitude/ longitude	adult	Lt (µm)	LPh (µm)	LPh (% of Lt)	Wt U10 (µm)	Wt U18 (µm)
Fig. 5 of Hochberg (2003) Macleay Island, Australia, **Pacific**	S 27°35' E 153°21'	*	438	170	39	48	41
Fig. 6 of Hochberg (2003) Macleay Island, Australia, **Pacific**	S 27°35' E 153°21'		307	94	30	43	40
#770 & Fig. 4 of Hummon (2011) Nabq South, Egypt, **Red Sea**	N 28°04' E34°25'	*	389 390	121 126	31 32	30 33	24 28
#769 of Hummon (2011) Nabq South, Egypt, **Red Sea**	N 28°04'N E34°25'	*	369	127	34	41	33
#772 of Hummon (2011) Nabq South, Egypt, **Red Sea**	N 28°04' E 34°25'		362	120	33	50	44
#773 of Hummon (2011) Nabq South, Egypt, **Red Sea**	N 28°04' E 34°25'		322	103	32	46	41
Fig. 2A of Hochberg (2008) Isla Colón, Bocas del Torro, Panama, **Caribbean**	N 9°22.974' W 82°14.176'		137	47	34	19	19
Photo 01 (1) of Todaro 2/14/10 St. John Island, USA, **Caribbean**	N 18°19'11" W 64°43'34"		304	103	34	49	45
#920 of Hummon (2011) Bahia Honda SW, Florida, USA, **Caribbean**	N 24°39' W 81°16'		270	90	33	32	28
Figs. 3A–B and 3D–E of Todaro et al. (2012) St. John Island, USA, **Caribbean**	N 18°19'11" W 64°43'34"	*	357	114	32	43	41
Fig. 3C of Todaro et al. (2012) St. John Island, USA, **Caribbean**	N 18°19'11" W 64°43'34"		n.a.	n.a.	n.a.	n.a.	n.a.
Figs. 1A–B and 2A–G of this study, Lee Stocking Island, Bahamas, **Caribbean**	N 23°46.816' W 76°06.720'	*	378	135	35.5	51	47
F-100411-2C of this study Lee Stocking Island, Bahamas, **Caribbean**	N 23°46.816' W 76°06.720'	*	270	103	38	38	35

giving the TbP an appearance of a pair of small feet (Fig. 2B). The ten TbP are almost equal in length and measure 12.8 μm. The angle between the innermost and the outermost tube per group ranges between 55° (right group) and 68° (left group). There are no adhesive tubes in a ventral (TbV), lateral (TbL), dorsolateral (TbDL), or dorsal (TbD) group.

Cilia. *A. agadasys* possesses two ventral, longitudinal columns of locomotory cilia (Figs. 1B, 2B,D). The width of each column of cilia slightly decreases toward the caudal trunk end (approximately 15 μm at U30, and 8 μm at U80). Posterior to the anus (at U95), both columns of locomotory cilia fuse into a median field that reaches the caudal trunk end (Fig. 2B). Around the region of the TbA (at U10) both longitudinal columns of cilia approach and form a loose field

of cilia on the ventral surface of the "head". The cilia of the ventral columns have a length around 10 μm. Furthermore, there are cilia (sensory and/or locomotory) surrounding the terminal mouth opening ventrally, laterally, and dorsally. On the dorsal surface of the "head" there are four additional paired patches of cilia (Fig. 2G). In a ventrolateral, lateral and dorsolateral position, there are six loosely arranged longitudinal columns of probably sensory cilia (2B,D). These cilia are much longer (around 20 μm) than the locomotory cilia. Many cilia of these groups are distally curved or even curled.

Digestive tract. The digestive tract is subdivided into a straight muscular pharynx (U00 to U35) and a slightly curved intestine (U35 to U95). Hence, the pharyngeo-intestinal junction (PhJIn) is situated at U35 (Figs. 1A, 2A). *A. agadasys* has

Wt U52 (μm)	Wt U88 (μm)	#TbA	#TbVL	#TbP	pattern of TbVL (anterior to posterior)	incision between caudal lobes	remarks
52	43	2×3	2×5	2×5	2×1, 2×1, 2×1, 2×1, 2×1	shallow	measurements taken from scale bars of Fig. 5 (photo adult)
53	33	2×3	2×5	2×5	2×1, 2×1, 2×1, 2×1, 2×1	medium	measurements taken from scale bars of Fig. 6 (drawing subadult)
36	25	2×3	2×6	2×6	2×3, 2×2, 2×1	deep	measurements taken from #770 (video adult)
39	30	2×3	2×6	2×6	2×4, 2×2, 2×1		and scale bar of Fig. 4 (drawing same adult)
40	30	2×3	2×3	2×6	2×1, 2×1, 2×1	medium	data reanalysed by WDH Nov 2012; adult; large egg
46	41	2×3	2×4	2×5	2×2, 2×1, 2×1	shallow	data reanalysed by WDH Nov 2012; barely mature; small egg
39	31	2×3	3&2	2×5	1&1, 1&0, 0&1, 1&0	shallow	data reanalysed by WDH Nov 2012; barely mature; medium egg
20	13	n.a.	n.a.	n.a.	n.a.	shallow	measurements taken from scale bar of Fig. 2A (photo subadult)
49	35	2×3	2&1	2×4	2×1	medium	subadult specimen
36	23	2×3	4&3	2×5	1&0, 0&1, 1&0, 0&1, 1&0, 0&1, 1&0,	shallow	data reanalysed by WDH Nov 2012; barely mature; medium egg
41	27	2×3	4&5	2×5	1&2, 2×1, 2×1, 2×1	shallow	adult specimen
n.a.	n.a.	n.a.	6&5	n.a.	1&0, 2×1, 2×1, 2×2, 2×1	n.a.	only one image of the ventral mid trunk with TbVL is available
53	32	2×3	4&5	2×5	1&0, 0&1, 1&2, 2&1, 0&1	shallow	adult specimen
42	27	2×3	7&5	2×5	n.a.	shallow	pattern of TbVL could not be determined since animal is twisted; adult specimen

a terminal mouth opening of 15.5 µm width and an inconspicuous ventral anus at U95. The 135 µm long pharynx (including the oral cavity) has an almost constant width around 33 µm and only slightly swells toward the region of the pharyngeal pores at U30. The pharyngeal pores open dorso-laterally. The oral cavity of *A. agadasys* is cylindrical to club-shaped and measures approximately 20×20 µm (Fig. 2F). The terminal mouth opening has a diameter of 15–18 µm; the outer mouth rim is slightly undulated. There are short (5 µm), hook-shaped enforcements that project out of the oral cavity and surround the mouth rim in a regular manner (approximately 10 hooks, see Fig. 2F). The intestine is 226 µm long, has a regional swelling from approximately U45–U70, and then tapers again toward the anus. The width at U40/50/60/70/80/90 is 23/31/31/15/13/13 µm, respectively. There is a slight curve to the left side in the region of the mature egg (U65–U85). Apart from the different width pattern (narrow – wide – narrow), the content of the gut cells seems to support a kind of regionalisation of the intestine: there is a high density of big and less transparent granules in the 'middle region' (U45–U70, see Fig. 2A, B). In the fixed specimen, the position of the PhJIn seems to be placed slightly more caudal at U38. This difference could be due to fixation artefacts.

Reproductive organs. Both Bahamian specimens of *A. agadasys* are obviously mature animals that possess a mature egg (between U68 and U83 in the drawn specimen) in a dorsal to dorso-lateral position with respect to the intestine (Figs. 1A, 2A, C). The mature egg has a roughly rectangular shape (seen from dorsal) and measures 59×38 µm (31×27 µm in the fixed animal). It is densely filled with globular yolk vesicles and has a large nucleus (15 µm in diameter) with a rather big nucleolus inside (7 µm in diameter). Posterior to the mature egg there is a paired ovary (around U85) with few oocytes (Fig. 2C). There was no trace of a male gonad or further accessory reproductive organs (frontal- and caudal organs).

Muscular components. In the ventral part of the animal, one can observe several longitudinal muscle strands in a ventral to ventro-lateral position. The muscle strands show a distinct pattern of cross-striation (Fig. 2E). Anteriorly, there is a pair of muscle strands that branch from the rest (between U10 and 15) and run diagonally to the bases of the TbA.

Additional observations. Although *A. agadasys* does not have cuticular differentiations such as scales or spines, there is a dense layer of small globular particles on the body surface in different regions of the animal (see, e. g., Fig. 2G). We interpret this as epizooic, coccus-shaped bacteria.

Discussion

Systematic remarks. *Anandrodasys agadasys* was first described as a species of the genus *Dactylopodola*, *D. agadasys*, from fine or even muddy sand at the mid to low tide level of the western shore of Macleay Island, northeast Australia (Hochberg 2003). Shortly after, Hummon (2011) presented a redescription of *D. agadasys* based on material collected at different sites of the Egypt coast of the Red Sea. The redescription was legitimized by Hummon (2011) due to some discrepancies between the original drawing of *Dactylopodola agadasys* and the presented light micrographs in the original description (Hochberg 2003: cf. his Fig. 5 with Fig. 6). Recently, the systematic placement of "*Dactylopodola agadasys*" was challenged by a molecular phylogenetic analysis of several Macrodasyida based on the 18S rRNA gene that was focusing on the position of the enigmatic gastrotrich *Redudasys fornerise* (Todaro et al. 2012). The sequence of *D. agadasys* that was used turned out to be unrelated to any member of the taxon *Dactylopodola* included in the analysis, but rather formed a well-supported sister group relationship with *R. fornerise*. Some shared characters of these two species (i. e. similar size and general appearance, anterior adhesive tubes distributed in two groups, a bilobed caudum, three pairs of protonephridia, clearly visible striated longitudinal muscles) were regarded as homologies that might give support to the *R. fornerise – D. agadasys*-relationship (see Todaro et al. 2012). However, the mentioned similarities can be found in other species of Gastrotricha, too, and are therefore not necessarily synapomorphies. But there is at least one synapomorphic similarity in both species (see Todaro et al. 2012): they are probably parthenogens that only develop a female gonad. Within Macrodasyda, this character is only present in few more species of the non-related genera *Urodasys* and perhaps *Paradasys*. However, it has to be stressed that both taxa, *Urodasys* and *Paradasys* are placed into a common clade comprising *Anan-*
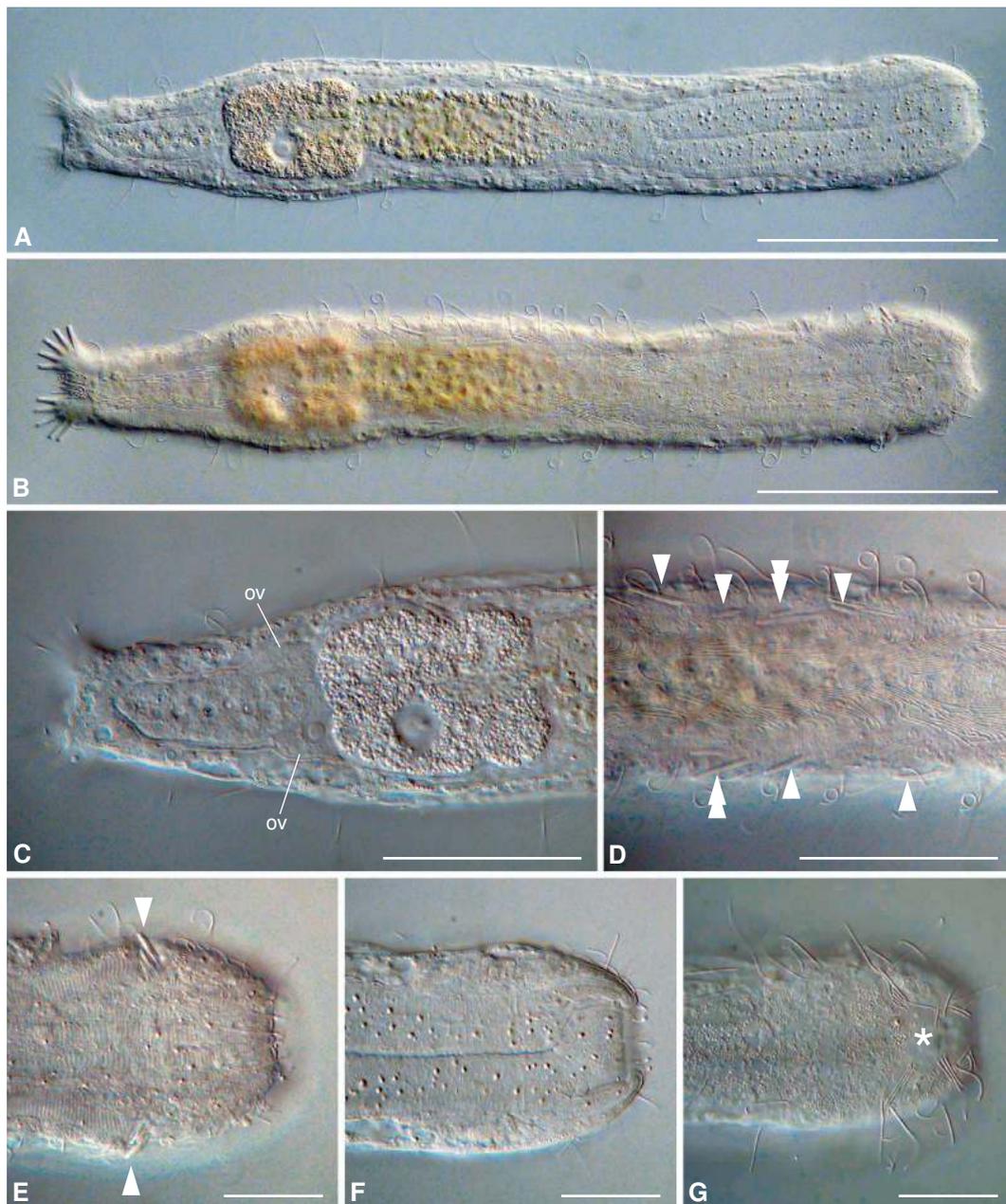
Fig. 2. Light micrographs (DIC) of *Anandrodasys agadasys* from LSI. **A, B.** Habitus at different focal plains. **C.** Detail of the posterior trunk end with ovary (ov) and mature egg. **D.** Detail of mid ventral side with ventrolateral adhesive tubes (white triangles). **E- G.** Anterior end at different focal depths showing anterior adhesive tubes (white triangles), buccal cavity, and paired patches of cilia on the dorsal surface (asterisk). Scale bars in A–B: 100 µm, in C–D: 50 µm, in E–G: 25 µm.

drodasys, *Redudasys* and further genera (Todaro et al. 2012). The results of the mentioned phylogenetic analysis led to the erection of the genus *Anandrodasys* Todaro et al., 2012 which so far is monotypic. In the following section, we perform a comparison of the basic morphological traits of all published records of *A. agadasys* in order to test if their affiliation with records of the former *D. agadasys* is appropriate.

Biogeography and character variation. *Anandrodasys agadasys* is so far recorded from three different biogeographic regions. There is one record from the Pacific east coast of Australia (Hochberg 2003), several records from the Red Sea coast of Egypt (Hummon 2011) and several records from the wider Caribbean or TNWA: Panama (Hochberg 2008), Florida (Hummon 2011), Virgin Islands (Todaro et al. 2012), and recently the Bahamas (this study, see Tab. 1). These records would imply a cosmopolitan distribution at least in the tropical and subtropical zone, if *A. agadasys* represents a single evolutionary unit. In order to shed some initial insights into this topic, we carried out a comparison of some morphometric/meristic characters of geographically distant populations of *A. agadasys*. We gathered some basic measurements and counts from specimens in Australia, Egypt, Virgin Islands, and the Bahamas since suitable descriptions and/or images of these records are available. William D. Hummon kindly provided further unpublished measurements of specimens from the Red Sea (see Tab. 1). Characters that may be useful to detect intraspecific or possibly interspecific variation are the total body length and the length of the pharynx, trunk widths at different regions (but trunk width in soft-bodied gastrotrichs is a problematic measure since it may be strongly influenced by pressure of the cover slip), number and arrangement of adhesive tubes, and finally the shape of the caudal end (Tab. 1). In terms of comparability, we will only regard fully mature animals. While the total body length (Lt) predominantly overlaps across most geographic regions (most adult specimens range from 357 to 390 µm, a single one is with 270 µm clearly smaller), the specimen from Australia is obviously larger (Lt: 438 µm). The relative length of the pharynx supports this pattern: in adult Caribbean and Red Sea specimens this measure has a range of 31 to 35 %, while the Australian *A. agadasys* has a pharynx measuring 39 % of the total body

length. Meristic characters such as the number of adhesive tubes are less problematic and in terms of *A. agadasys*, there is a slight geographic pattern: adult Red Sea specimens have 12 TbP (Hummon 2011) while all other populations are characterised by possessing a maximum of 10 TbP (Hochberg 2003, Todaro et al. 2012, this study). Subadults from the Red Sea as well have a number of 10 TbP but it is difficult to assess whether this number will rise to 12 tubes in fully mature animals. The TbVL in the Red Sea and the Australian animals show a strict bilateral symmetric arrangement, while there is a certain degree of asymmetry in the distribution of TbVL in the Caribbean specimens. However, there is one record of a subadult specimen from the Red Sea that also shows this kind of asymmetry (Tab. 1).

Conclusion

At least with the different number of TbP, the pattern of asymmetric arrangement of TbVL, and the size disparity, subtle morphological differences may exist between distant geographic populations of *Anandrodasys agadasys*. It is possible, though hard to assess, that records of *A. agadasys* from such distant localities – SW Pacific, Red Sea, Caribbean Sea – already represent different evolutionary units. Minor but consistent morphological differences have been used to split a formerly widespread species into more but geographically restricted ones like, e. g. in the case of *Turbanella wieseri* Hummon, 2010 (see Hummon 2010c). We also know that widespread (cosmopolitan) species may represent complexes of several cryptic genetic species. Examples have already been discovered in microscopic benthic marine animals such as nematodes (Derycke et al. 2008), flatworms (Sanna et al. 2009), and also gastrotrichs (Todaro et al. 1996, Kieneke et al. 2012). It would be favourable to test whether such subtle phenotypic differences are in congruence with observable genetic divergence. Before we have no such supportive molecular analyses and more satisfying sampling sizes for morphometrics, it is hard to assess the evolutionary nature of taxa like *Anandrodasys agadasys* – a single cosmopolitan species with a certain degree of morphological variability or several evolutionary entities with more restricted distributions?

Acknowledgements

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