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A new species of *Cephalodasys* (Gastrotricha, Macrodasyida) from the Caribbean Sea with a determination key to species of the genus

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Abstract

A new marine gastrotrich species of the genus *Cephalodasys* is described from shallow sublittoral coralline sand sampled between Lee Stocking Island and Norman's Pond Cay (Exuma Cays), Bahamas. *Cephalodasys interinsularis* **n. sp.** reaches a body length of 471 µm and is characterized by a new combination of characters including six total anterior adhesive tubes and five pairs of ventrolateral adhesive tubes. The new species is morphologically similar to *C. swedmarki* but can be distinguished by the different number of anterior adhesive tubes, the spatial arrangement of the ventrolateral adhesive tubes, and a shorter pharynx. We provide an updated diagnosis of the genus and a determination key to all known species of *Cephalodasys*. *C. interinsularis* **n. sp.** is the third known species of *Cephalodasys* from the Caribbean marine province.

Key words: biodiversity, marine meiofauna, taxonomy, species description, Bahamian ecoregion

Introduction

Lee Stocking Island (LSI) is one of a series of small islands on the eastern margin of the Great Bahama Bank in the Caribbean Sea. The geology of the island is well characterized (reviewed in Kindler 1995), and as a research site for the Perry Institute for Marine Science, is host to numerous biodiversity and ecology studies devoted to macroscopic organisms (e.g. Albins & Hixon 2008, Lapointe *et al.* 2004, Sánchez *et al.* 2003, Stoner 2003). However, marine meiofauna is poorly characterized from the island (for some individual records of nematodes and naidids see, e.g., Musat *et al.* 2007 and Kvist *et al.* 2010), and this is especially true for the taxon Gastrotricha, where only a few species have been described and/or recorded so far (Kieneke et al 2013a, 2013b, von und zu Gilsa *et al.* 2014). During our studies of the marine meiofauna of LSI in 2010, we encountered numerous gastrotrichs (see Schmidt–Rhaesa *et al.* 2010) that we are still in the process of analyzing. Among these are specimens of *Cephalodasys* Remane, 1926, a relatively common marine taxon of Macrodasyida but one that only comprises 12 described species to date (see Hummon & Todaro 2010, Hummon 2011, Kieneke & Schmidt–Rhaesa 2015, Todaro 2015). Our examinations of the few specimens we encountered revealed a consistent combination of characters that is unique among the currently known species. Here, we describe a new species of *Cephalodasys* from LSI based on live and fixed material and provide an updated taxonomic key to the genus.

Material and methods

The sediment sample LSI09 (rather fine calcareous biogenous sand) containing four specimens of *Cephalodasys* was collected from a sublittoral shoal between Lee Stocking Island and Norman's Pond Cay on April 13, 2010 (N 23°45.972′; W 76°06.897′, Fig. 1). The sample was taken at a water depth of approximately 2m via skin-diving deployed from a small research boat of the Caribbean Marine Research Center (CMRC) of the Perry Institute for Marine Science (PIMS). The sand was qualitatively collected from the sea floor with wide-necked PE bottles (1000

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ml volume). Samples were brought to the marine lab and processed as soon as possible. Unused sand was kept for few days in flow-through basins of the wet laboratory of CMRC. Extraction of living meiofauna was achieved by the anaesthetization-decantation method (Pfannkuche & Thiel 1988, Todaro & Hummon 2008) using an aqueous solution of $MgCl_2$ (7% w/v) and sieves with mesh sizes of 40–60 µm. Meiofauna was rinsed from the sieves into petri dishes with filtered sea water and inspected under a Leica EZ4 stereo microscope. Single specimens were sucked out of the sample by means of a capillary glass pipette attached to a silicon hose. For proper microscopic investigation, specimens were anaesthetized again with a drop of $MgCl_2$ solution, mounted on a glass slide and covered with a cover slip. Three specimens were viewed and digitally documented under a Zeiss Axioscope A1 equipped with differential interference contrast (DIC) and a Sony Handycam digital video camera. Line art drawings were made from printouts of different focal planes of one adult specimen. Drawings were digitized with the software Adobe® Illustrator® CS5. A semi-automated workflow for adding a dotting to the drawings was used (see Bober & Riehl 2014). A fourth specimen was fixed with 4% (w/v) formaldehyde in 0.1M phosphate buffered saline (pH 7.4). That specimen was stored within the fixative at 4°C until November 20th 2014 for subsequent preparation for scanning electron microscopy (SEM). Before, the specimen was transferred to glycerol via a dehydration medium consisting of 1 part glycerol to 4 parts H_2O to 5 parts ethanol (1:4:5). Light microscopic images and video files have been compiled at different magnifications using an Olympus BX53 microscope equipped with DIC and an Olympus PEN E-PL5 digital camera. The specimen was then post-fixed with 1% (v/v) OsO_4 in 0.1M sodium-cacodylate buffer (pH 7.25) for 1h at 4° C. Dehydration with a graded ethanol series (starting with 5%) was followed by critical point drying performed with a Leica CPD 300 manual critical point drier. The specimen was glued to a round cover glass with Tempfix mounting resin (Plano GmbH, Wetzlar, Germany), which was then placed on an aluminum stub and coated with gold-palladium using a Bal-Tec SCD 050 sputter-coater (150 seconds at 40 mA). Microscopic investigation and documentation was performed with a Tescan VEGA3 SEM operated at 10 kV. Unfortunately, the specimen was partly damaged but still provided relevant taxonomic information. Measurements of all investigated specimens were carried out using the digital images and the open source software ImageJ 1.48v (Rasband 1997–2014).

The description of the new species of *Cephalodasys* follows the convention of Hummon *et al.* (1992, 1993), whereby the position of most morphological characteristics along the body are given in percentage units (U) of total body length measured from anterior to posterior ends, not including the posterior adhesive tubes.

Results

Taxonomic account

Phylum Gastrotricha Mečnikow, 1865

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

Family Cephalodasyidae Hummon & Todaro, 2010

Genus *Cephalodasys* Remane, 1926

Hummon (1974a) provided the first diagnosis of the genus beyond Remane's (1926) original description of *Cephalodasys maximus*. Since then, *Cephalodasys* was reclassified from the Lepidodasyidae to the Cephalodasyidae (see Hummon & Todaro 2010) but a rediagnosis of the genus was not provided. Below, we present an emended version of Hummon's (1974a) original classification. Primarily, information concerning the reproductive system and the external cilia has been added.

Emended diagnosis. Cephalodasyidae with head delineated from trunk by means of a constriction; posterior end broadly expanded, often rounded or truncated, or tapered into a medial process. Anterior adhesive tubes (TbA) 2–7 per side, located posterior to buccal cavity in vicinity of neck constriction and often borne on extensible feet; ventrolateral adhesive tubes (TbVL) present, with several to many pairs occurring along pharyngeal and intestinal regions, but may be absent from pharyngeal region; dorsal adhesive tubes (TbD) mostly absent, so far only known from one species; posterior adhesive tubes (TbP) 10–20, rarely fewer, located on lateral and posterior borders of caudal end, and may be separated into groups on either side of midline or may merge almost indistinguishably with TbVL. Cuticle thin, without armament, but often with granular appearance, epidermal glands are mostly absent but exist in two species. Pharyngeal length in adults about one-third total body length; intestine more or less divisible into broad anterior secretory region and narrower posterior absorptive region. An unpaired dorsal ovary is located posterior to U50, eggs mature in a caudal direction, one or few eggs mature at a time; paired testes at both sides of the intestine in the anterior part of the trunk (approximately U25–U50), caudally directed sperm ducts often fuse into a ventral unpaired gonopore; frontal organ present, caudal organ only known in some species. Locomotory cilia cover entire ventral region of head and then extend posteriorly as two longitudinal columns along the neck and trunk; both columns fuse into a narrow field of cilia at the posterior end. Ring-shaped field of sensory cilia on the dorsal side of the head. Stiff sensory cilia evenly spaced along the trunk in lateral and/or dorsolateral rows.

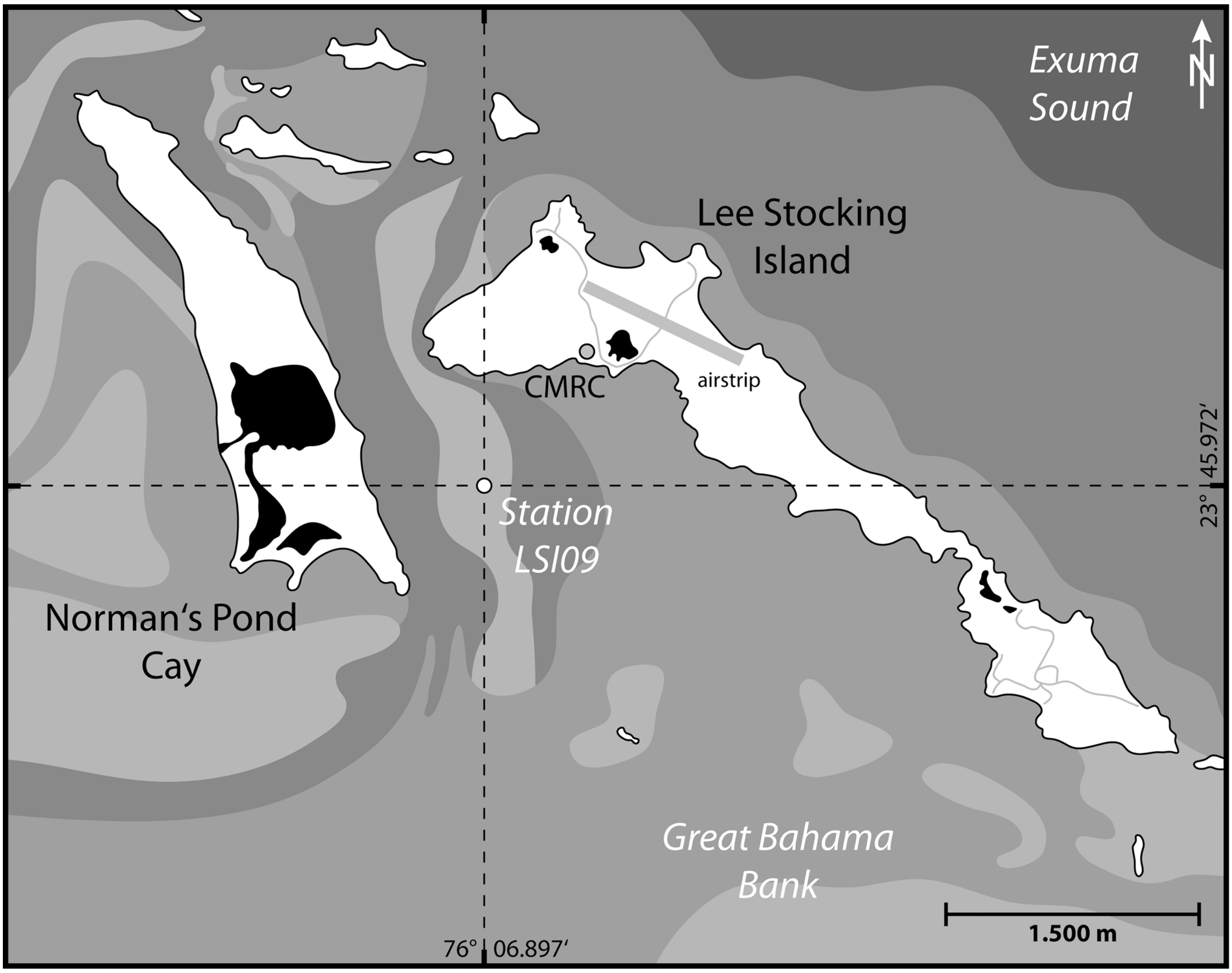

FIGURE 1. Lee Stocking Island (Bahamas) at the southwestern edge of the Exuma Sound, Caribbean Sea with the *locus typicus* of *Cephalodasys interinsularis* **n. sp.** (station LSI09). Areas around the islands marked with different shades of grey indicate major sublittoral sandbars. Black areas on the islands are lagoons or ponds. The Caribbean Marine Research Center (CMRC) is the field station of the Perry Institute for Marine Science. Map modified from White and Curran (1993) and emended with information from satellite images accessed via Google™ earth.

***Cephalodasys interinsularis* sp. nov.**
Figs. 2–5A, 6

Habitat/type locality. The new species was collected from rather fine calcareous biogenous sand from a sublittoral shoal between Lee Stocking Island and Norman's Pond Cay at a water depth of approximately 2 m (N 23°45.972´;

W 76°06.897′). The area between both islands (Fig. 1) has the properties of a tidal channel and hence a strong tidal current was present at the time of sampling. Apart from *Cephalodasys*, the sample also contained specimens from the gastrotrich taxa *Macrodasys*, *Paraturbanella*, *Tetranchyroderma* (Macrodasyida) and *Draculiciteria* (Paucitubulatina).

Material examined. Two specimens were studied alive and a third specimen was studied after fixation. Among the two live specimens, one individual was fully mature and the second was a subadult. The third specimen was fixed and studied with light and electron microscopy. Since only a single mature specimen was studied alive, this specimen is designated as the holotype even though it is no longer extant (International Code of Zoological Nomenclature/ICZN, Articles 73.1.1 and 73.1.4, International Commission on Zoological Nomenclature 1999, 2008, 2012). The specimen prepared for SEM (see Fig. 6A-F) is designated as a paratype specimen (ICZN, Recommendation 73D) and is stored in the collection of the National Museum of Natural History/Smithsonian Institution (USNM 1274540). Digital light microscopic and SEM images of this paratype are also kept in the collection. Digital files (images and videos) of the holotype and the other live specimen (see Figs. 3, 4, 5A) are also deposited at the National Museum of Natural History. The latter individual is designated as a further paratype specimen (ICZN, Recommendation 73D), which is no longer extant. A fourth specimen of *Cephalodasys* that was studied alive (see Fig. 5B) probably does not belong to the new species (see discussion for details).

Diagnosis. *Cephalodasys* with a body length of 471 µm. Body divided into pyriform head, neck, and trunk regions, the latter two inconspicuously separated from each other at the level of the pharyngeal pores that are positioned close to the posterior end of the pharynx. Caudal trunk end rounded. The rather long buccal cavity is hourglass-shaped and has a strengthened cuticular lining. Intestine/midgut linear and without obvious differentiation. Arrangement of TbA/TbVL/TbP is 2x3/2x5/11–12, respectively. TbA arise directly from the body surface, a fleshy base is not present. TbVL present in the trunk region only, TbD and ventral adhesive tubes (TbV) are absent. Unpaired ovary in a dorsolateral position in the posterior half of the trunk, pair of short and stout testes posterior to the pharyngeal pores, with short and caudally directed sperm ducts that fuse ventral to the midgut. An unpaired male gonopore is present at the site of sperm duct fusion. A frontal organ as putative sperm storing device is situated just posterior to the mature oocyte, a caudal organ is absent. Arrangement of cilia does not deviate from other *Cephalodasys* (see diagnosis above).

Etymology. The species name is compound from the Latin words *inter* (= between) and *insularis* (= belonging to an island) and denotes the type locality, a sublittoral sandbar between two islands. The name shall not indicate that the new species is limited to that special habitat. However, during our stay on Lee Stocking Island in 2010, we did not find the species at any other sampling station.

Description. The following description is based on the adult specimen that was studied alive and digitally documented, viz. the holotype (Figs. 2–4). A full overview of morphometric variability across all three studied specimens, including one subadult individual, is provided in Table 1. It has to be stressed, however, that in particular length measurements of the fixed specimen may be erroneous due to contractions and/or shrinkage artefacts.

Habitus. The new *Cephalodasys* is a medium-sized macrodasyid gastrotrich with a total body length of 431–471 µm (n=2). Like most other species of *Cephalodasys*, it has a distinct, pear-shaped head that is delineated from the neck region at U11 by a constriction (Figs. 2, 3, 4A–C, 5A, 6A, C). The trunk region (approximately U35–U100) is slightly wider than the neck region (approximately U11–U35) and ends with a rounded caudum (Figs. 2, 3, 5A). Body widths are 47/37/42/48/51/25 µm at U5/11/25/50/75/94.5, respectively (see Table 1). The outline of the animal appears irregularly undulated, which is likely the result of the soft and folded integument (Figs. 2, 3A–B). The body is ventrally flat but dorsally convex. In the testicular region, the trunk cross section appears to be trilobate. The cuticle is smooth and shows no ornamentations; epidermal glands per se are absent but the epidermis appears finely granular under the light microscope (e.g. Fig. 4A, C, E).

Adhesive tubes. The new species of *Cephalodasys* has adhesive tubes in an anterior (TbA), ventrolateral (TbVL), and posterior (TbP) series; ventral tubes and dorsal tubes are absent (Fig. 2). There are three TbA per side (n=3) present at the transition from head to neck regions (U10.5–U12, n=3). The tubes are of equal size (length: 7–11.5 µm, width: 1.5–2.5 µm, n=3) and are arranged in parallel (Figs. 2, 3A, 4C, 6C–D). Their longitudinal axis is slightly tilted toward the midline of the animal (approximately 7°, see Fig. 6C). If a living, anaesthetized specimen gets slight pressure from the cover slip, TbA may appear aligned parallel to the longitudinal axis of the animal (see Fig. 4C). TbA arise directly from the ventral body surface but there is a shallow pit anterior to them (Fig. 6B).

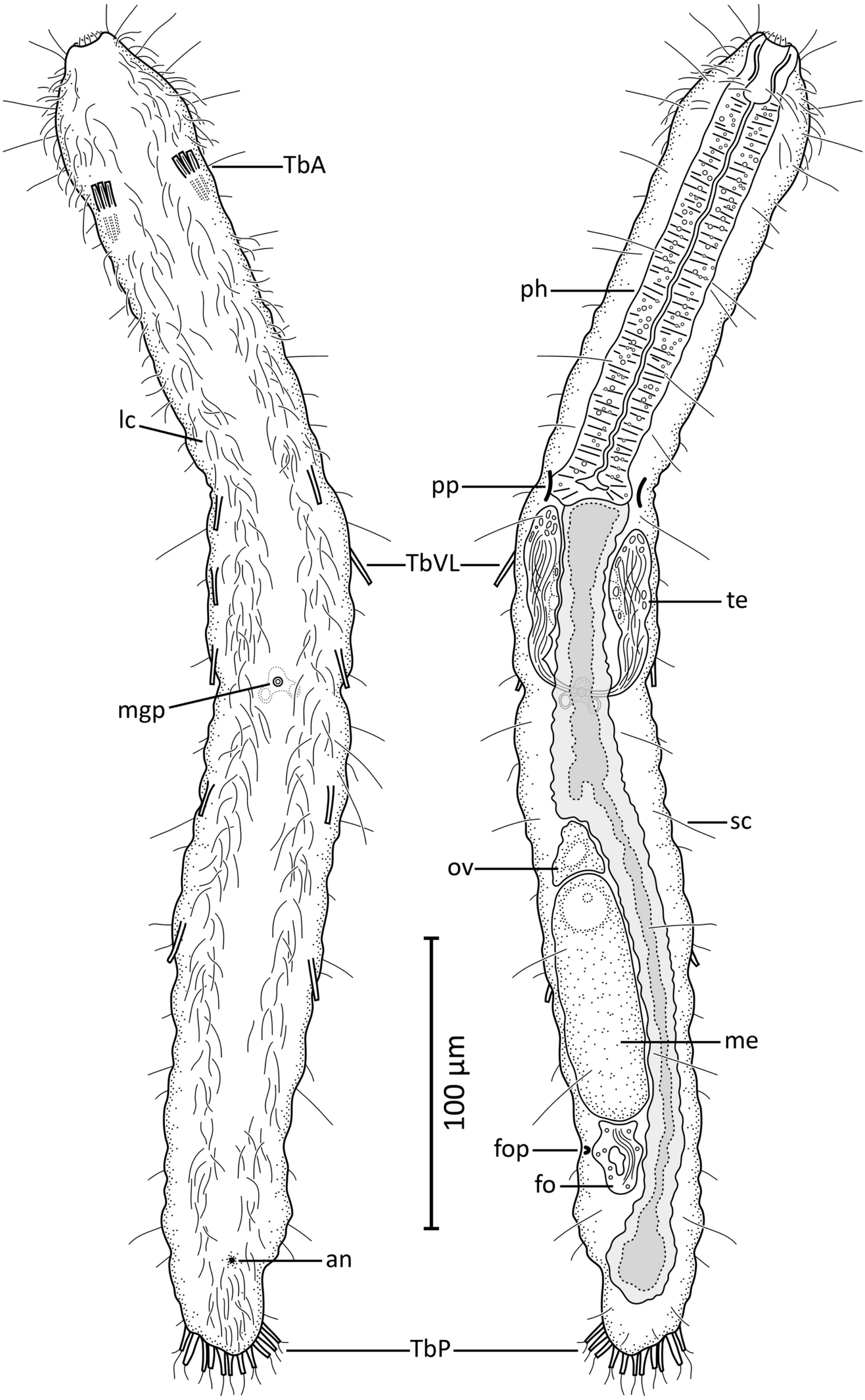

FIGURE 2. *Cephalodasys interinsularis* **n. sp.** Schematic drawings of the holotype specimen. Left: Ventral view. Right: Combined dorsal and internal view. an, anus; fo, frontal organ; fop, frontal organ pore; lc, locomotory cilia; me, mature egg; mgp, male genital pore; ov, ovary; ph, pharynx; pp, pharyngeal pores; sc, sensory cilia; TbA, anterior adhesive tubes; TbP, posterior adhesive tubes; TbVL, ventrolateral adhesive tubes; te, testis.

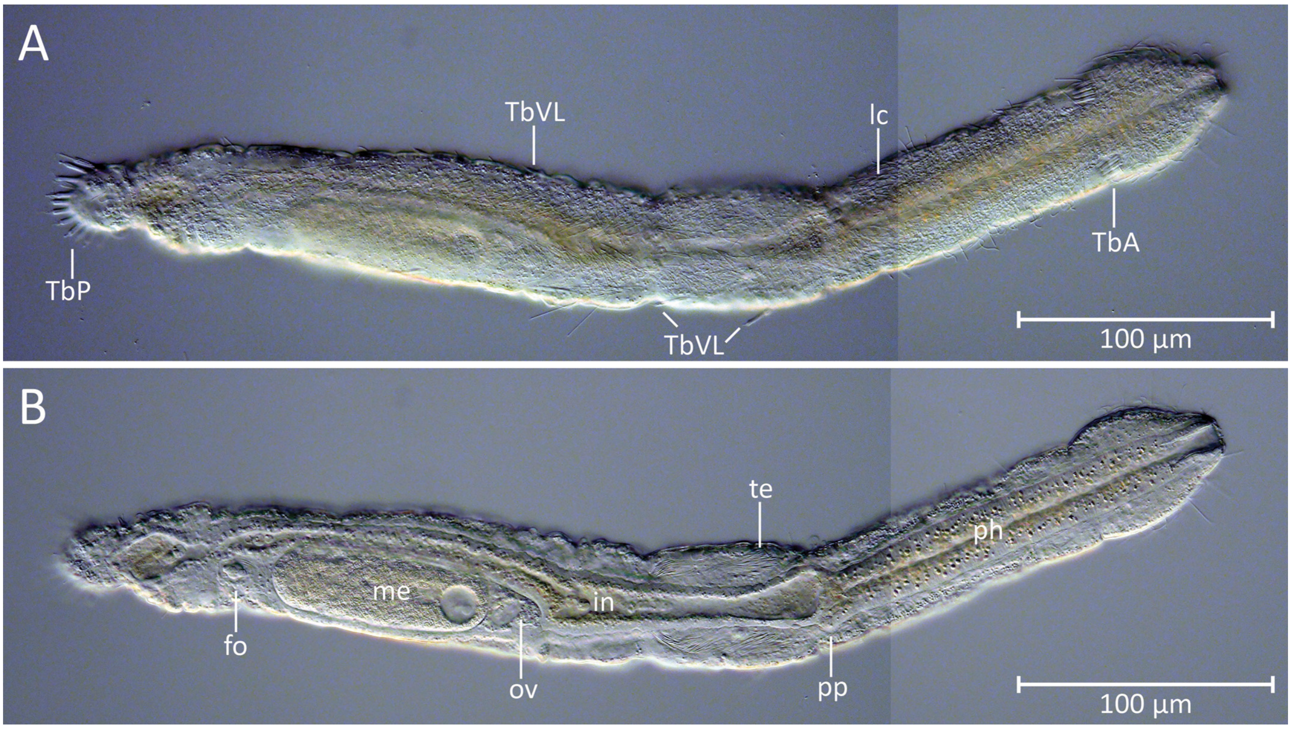

FIGURE 3. *Cephalodasys interinsularis* **n. sp.** Light microscopic images (differential interference contrast, DIC) of the holotype specimen, assembled from two images, respectively. A) Ventral view showing the adhesive tubes and locomotory cilia. B) Horizontal focal plane showing internal organs. fo, frontal organ; in, intestine; lc, locomotory cilia; me, mature egg; ov, ovary; ph, pharynx; pp, pharyngeal pores; TbA, anterior adhesive tubes; TbP, posterior adhesive tubes; TbVL, ventrolateral adhesive tubes; te, testis.

Posterior to the TbA and inside the body, one can observe two parallel filaments per TbA that seem to anchor each adhesive tube. Each adhesive tube has a slight furrow extending down its longitudinal axis, which probably indicates the presence of a duo-gland adhesive system (Fig. 6D). Terminally, each TbA has two tiny pores (Fig. 6D). Between U35 and U75, there are five pairs of bilateral-symmetrically arranged TbVL (n=3). The tubes appear long and slender and measure 10–16.5 µm in length and 1–1.8 µm in width (n=3). Their insertion points are somewhat ventral in position but mainly lateral to the bands of locomotory cilia (Figs. 2, 4E, 5A). Hence, the TbVL are hardly visible from the dorsal side. In both adults and subadults, there is a consistent pattern concerning the arrangement of TbVL: the spaces between the 1st, 2nd and 3rd tubes is about half the distance (25.5–34.5 µm) of that between tubes 3, 4, and 5 (47–60.5 µm). Caudally, there are 11–12 TbP (n=3) arranged along the posterior margin (Figs. 2, 3A, 5A). Lengths of individual TbP vary within and between specimens, generally from 6.5–13 µm (n=3), while the width is more consistent (2–2.25 µm, n=3). One or two short cilia may arise from the distal tip of each TbP (Fig. 4F).

Cilia. Locomotory cilia on the ventral side are arranged in two longitudinal columns beginning at the anterior end and extending to the ventral anus at U94.5. Posterior to the anus, there is a short uniform field of ventral locomotory cilia, i.e. both longitudinal columns fuse (Figs. 2, 4E, 6A–C). In the neck region, the space between the two columns is closer than on the rest of the body, giving the false impression that they fuse (Figs. 4C, 6C). The lateral flanks of the pear-shaped head bear additional cilia (Fig. 6B) that extend around the lateral and dorsal portion of the head to create a closed ciliary ring (Fig. 4A). The length of the locomotory cilia is ca. 10 µm. Dorsolaterally on the head region and along the whole trunk there are long (25–30 µm) and stiff sensory cilia (e.g. Fig. 6B). These cilia are present along the length of the body: five pairs of cilia are present on the head and 11–12 pairs are bilaterally distributed along the neck and trunk. Shorter sensory cilia (5–7 mm) are present on the flanks of the neck, trunk, and the dorsal side of the caudum. Approximately 25 short cilia surround the mouth opening (Fig. 6B–C).

Sensory organs. Apart from the sensory cilia, there are no other obvious sensory organs (e.g., tentacles, pigmented eye spots) on the head region. However, dorsal to the pharynx there is a bilateral pattern of small vesicles (Fig. 4B). These may belong to a pair of photoreceptive head sensory organs that are, for instance, also known from *Cephalodasys maximus* (see, e.g., Wiedermann 1995).

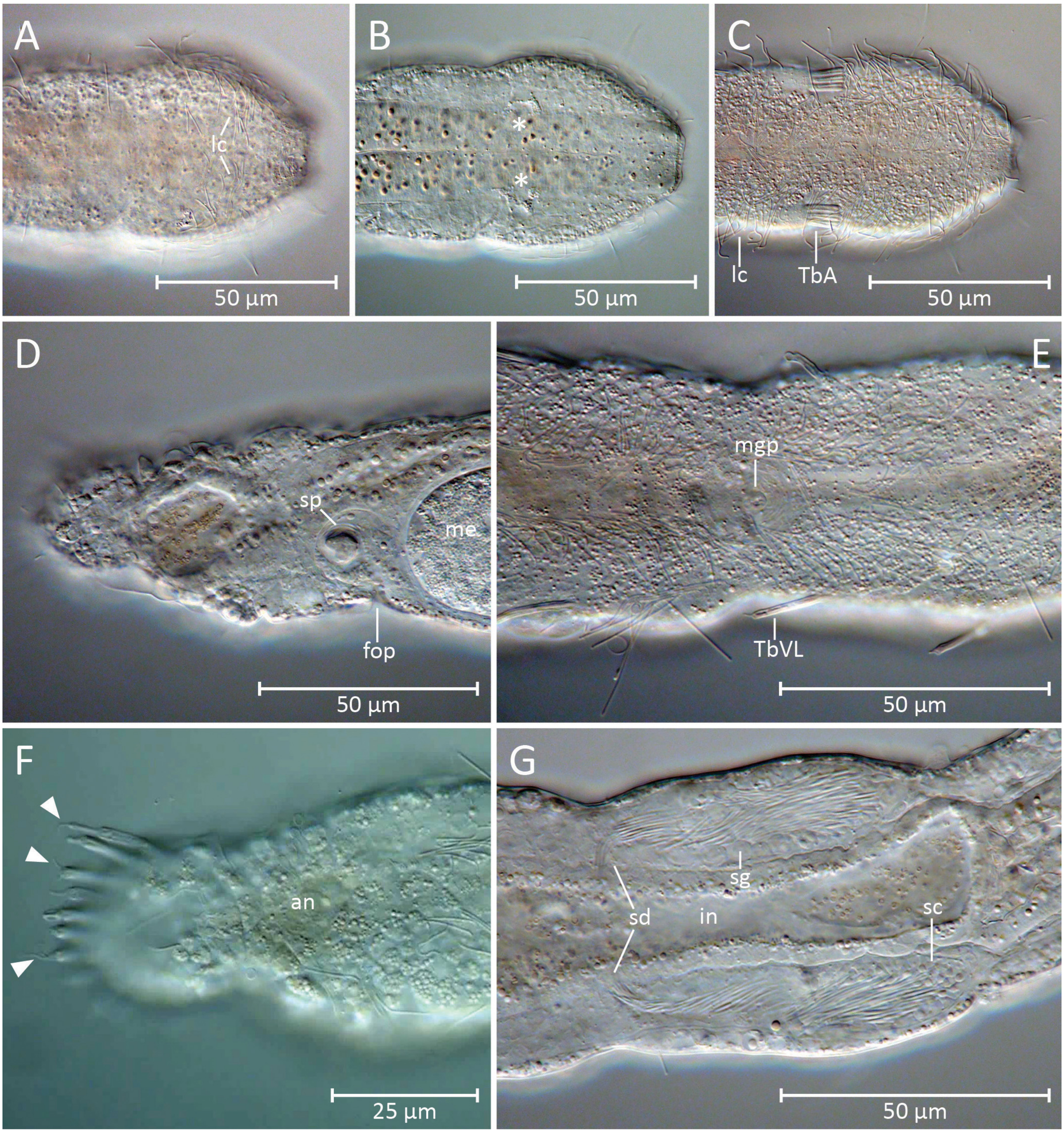

FIGURE 4. *Cephalodasys interinsularis* **n. sp.** Light microscopic images (DIC) of the holotype specimen. A) **-** C) Head region at different focal planes (dorsal to ventral). Note the paired array of vesicles dorsal to the pharynx (asterisks in B). D) Detail of the posterior trunk region showing the frontal organ. The roundish structure to the left of the frontal organ is the terminal section of the intestine. E) Ventral view of the mid trunk with adhesive tubes and the male gonopore. Note also the finely granular epidermis. F) Posterior adhesive tubes. Note the short associated sensory cilia (arrowheads). G) Mid trunk with paired testes. an, anus; fop, pore of frontal organ; in, intestine; lc, locomotory cilia; me, mature egg; mgp, male genital pore; sc, spermatocytes; sd, sperm ducts; sg, spermatogonia; sp, foreign spermatozoa (allosperm) within the frontal organ; TbA, anterior adhesive tubes; TbVL, ventrolateral adhesive tubes.

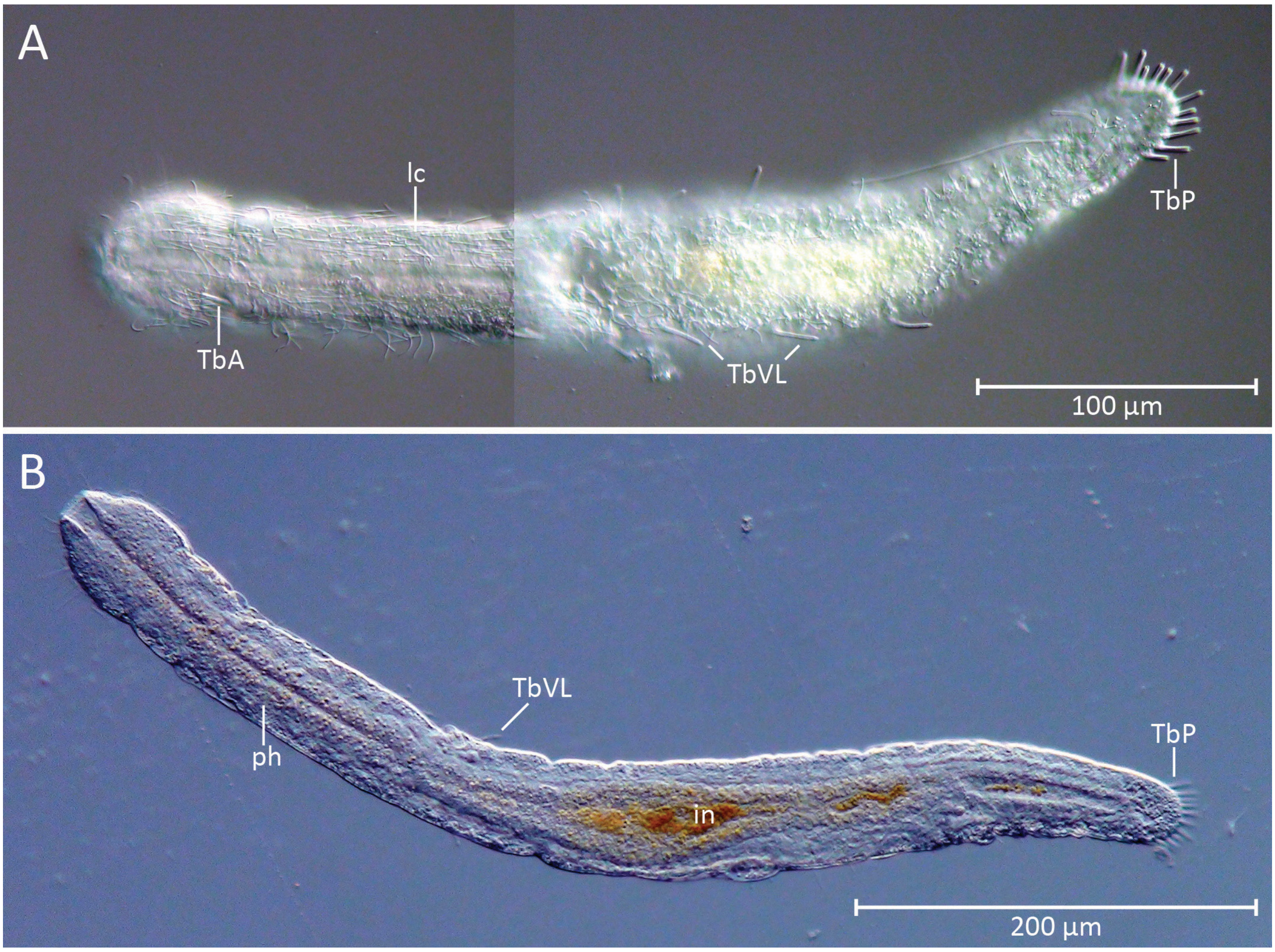

FIGURE 5. A) *Cephalodasys interinsularis* **n. sp.** Light microscopic image (DIC, ventral view) of a subadult specimen, assembled from two images. The depicted animal is a paratype specimen that is no longer existent. B) An undetermined specimen of *Cephalodasys*. It represents a very large subadult or post-reproductive animal that had only four instead of five pairs of ventrolateral adhesive tubes. in, intestine; lc, locomotory cilia; ph, pharynx; TbA, anterior adhesive tubes; TbP, posterior adhesive tubes; TbVL, ventrolateral adhesive tubes.

Digestive tract. The gut tube is divided into an anterior glandulo-muscular pharynx and a posterior intestine (Figs. 2, 3B). The pharynx makes up 38–40% (adult specimens, n=2) of the total length of the whole gut tube (Tables 1 and 2). The circular mouth opening is terminal (only inconspicuously tilted, see Fig. 6B) and has a diameter of ca. 10 µm. Apart from the short cilia mentioned above, there are no other structures such as longitudinal ridges or hooks that line the mouth. However, the cuticular wall of the cylindrical to slightly hourglass-shaped buccal cavity (25–30 µm long) is thickened (Fig. 3B). The width of the pharynx (22 µm) is nearly equal along its whole length; it is only slightly narrower around the buccal cavity (U0–U05), and increases in width at the level of the pharyngeal pores. The position of the pores is at U31–U35 in adult specimens (n=2). The actual pores are inconspicuous slits that lie dorso-laterally in the body wall (Fig. 6B); the pharyngeo-intestinal junction is at U36–U38 in adult specimens (n=2). The shape of the intestine is quite irregular and the diameter varies considerably along its course. In the region where a large ovum is situated in adult specimens, the intestine forms a drawn-out curve to the right side of the trunk and its diameter is slightly reduced (Figs. 2, 3B). The intestine ends in a ventral anus at U94.5 (n=2). In this area, the terminal part of the intestine may be widened (see, e.g., Fig. 4D). Although no distinct regionalization of the intestine is visible, the abundance of small refractive spheres in its wall cells increases from anterior to posterior, possibly due to increased resorption processes in the midgut.

Reproductive organs. The new species is hermaphroditic with paired testes and an unpaired ovary. The paired testes are present between U36.5–U38 and U49–U50 (n=2) and are broad and club-shaped (12–13 µm wide) with short, caudally projecting vasa deferentia (Figs. 2, 4G). The sperm ducts immediately curve medio-ventrally and

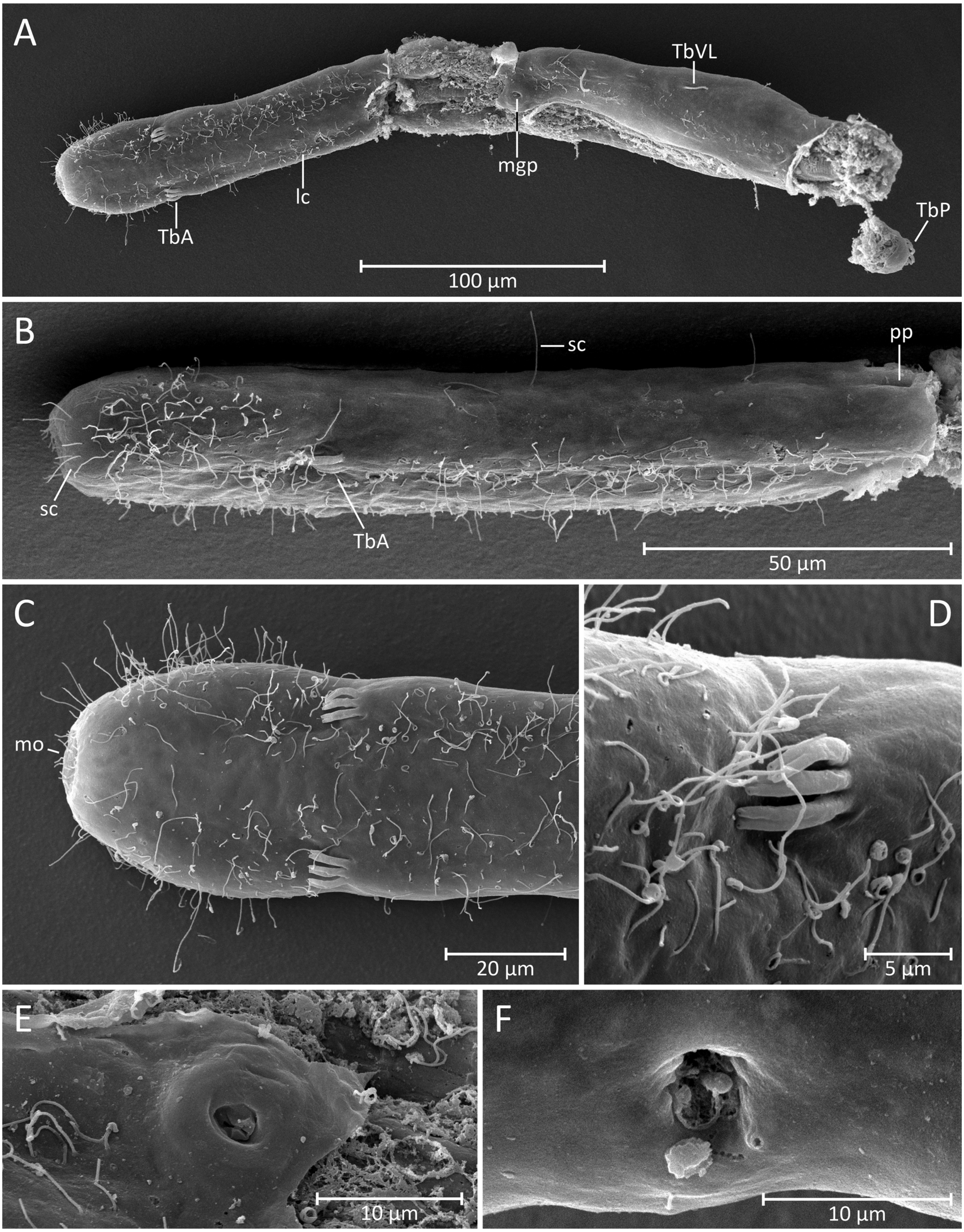

FIGURE 6. *Cephalodasys interinsularis* **n. sp.** Scanning electron microscopic images of the second paratype specimen (USNM 1274540). A) Habitus, seen from ventral to ventrolateral (animal twisted and damaged). B) Pharyngeal region, lateral view. C) Head region, ventral view. D) Close-up of the anterior adhesive tubes. Note the longitudinal furrow and two apical pores on each tube. E) Close-up of the ventral male genital pore. F) External pore of the frontal organ on the left side. lc, locomotory cilia; mgp, male genital pore; mo, mouth; pp, pharyngeal pores; sc, sensory cilia; TbA, anterior adhesive tubes; TbP, posterior adhesive tubes; TbVL, ventrolateral adhesive tubes.

TABLE 1. Meristic and morphometric characters of the four investigated specimens of the new and one undescribed species of *Cephalodasys* from the Bahamas. Abbreviations: L, length; LPh, length of pharynx; Lt, total body length; n.a., not applicable; pos., position; PP, pharyngeal pores; PhJIn, pharyngeo-intestinal junction; TbA, anterior adhesive tubes; TbP, posterior adhesive tubes; TbVL, ventrolateral adhesive tubes; W, width; Wt, trunk width.

specimen ID (name of folder with digital material, i.e. images and videos)	notes		Lt [µm]	LPh [µm]	PhJIn [U]	pos. PP [µm]	pos. PP [U]	pos. anus [µm]
C_interinsularis_n_sp_adult	mature	holotype	471	171	U36	164	U35	445
C_interinsularis_n_sp_adult_F-100414-2A	mature (SEM and LM)	paratype	431	165	U38	135	U31	408
C_interinsularis_n_sp_subadult	developing testes visible, no ovary	paratype	378	163	U43	153	U40.5	355
Cephalodasys_sp_subadult	no testes, no ovary	different species	603	215	U35.5	199	U33	586

specimen ID (name of folder with digital material, i.e. images and videos)	notes		pos. anus [U]	Wt at U5 [µm]	Wt at TbA [µm]	Wt at U25 [µm]	Wt at U50 [µm]	Wt at U75 [µm]
C_interinsularis_n_sp_adult	mature	holotype	U94.5	47	37	42	48	51
C_interinsularis_n_sp_adult_F-100414-2A	mature (SEM and LM)	paratype	U94.5	45	36	39	47	44
C_interinsularis_n_sp_subadult	developing testes visible, no ovary	paratype	U94	43	35	40	48	41
Cephalodasys_sp_subadult	no testes, no ovary	different species	U97	54	46	47	57	54

specimen ID (name of folder with digital material, i.e. images and videos)	notes		Wt at anus [µm]	pos. testes plus vasa deferentia [µm]	TbA per side	pos. TbA [µm]	pos. TbA [U]	L TbA [µm]
C_interinsularis_n_sp_adult	mature	holotype	25	172–237	3	53	U11	10
C_interinsularis_n_sp_adult_F-100414-2A	mature (SEM and LM)	paratype	27	165–212	3	49	U11	7
C_interinsularis_n_sp_subadult	developing testes visible, no ovary	paratype	27	164–209	3	44.5	U12	11.5
Cephalodasys_sp_subadult	no testes, no ovary	different species	32	n.a.	3	63	U10.5	10.5

……*continued on the next page*

TABLE 1. (Continued)

specimen ID (name of folder with digital material, i.e. images and videos)	notes		W TbA [µm]	TbVL per side	L TbVL [µm]	W TbVL [µm]	TbP	L TbP [µm)
C_interinsularis_n_sp_adult	mature	holotype	2–2.5	5	13.5–16.5	1.8	11	6.5–10.5
C_interinsularis_n_sp_adult_F-100414-2A	mature (SEM and LM)	paratype	1.5	5	10–11.5	1	11	n.a.
C_interinsularis_n_sp_subadult	developing testes visible, no ovary	paratype	2	5	12–14	1.7	12	7–13
Cephalodasys_sp_subadult	no testes, no ovary	different species	2.5	4	10–12	1.7	11	7–10

specimen ID (name of folder with digital material, i.e. images and videos)	notes		W TbP [µm]	ratio of LPh to total digestive tract	pos. testes plus vasa deferentia [U]
C_interinsularis_n_sp_adult	mature	holotype	2.25	38%	U36.5–U50
C_interinsularis_n_sp_adult_F-100414-2A	mature (SEM and LM)	paratype	1.5–2	40%	U38–U49
C_interinsularis_n_sp_subadult	developing testes visible, no ovary	paratype	2	46%	U43–U55
Cephalodasys_sp_subadult	no testes, no ovary	different species	2.25	37%	n.a.

TABLE 2. Meristic and morphometric characters with diagnostic value of all known species of *Cephalodasys*. Abbreviations: a, absent; IT, intertidal; n.a., not applicable; p, present; ?, unknown character; the question mark in brackets (?) denotes an unsure character state. Further abbreviations: See Table 1.

species	Lt [µm]	LPh [µm]	position of PhJIn	ratio of LPh to total digestive tract[a]	shape of anterior end ("head")	shape of caudum
Cephalodasys cambriensis	990	290	U30	32%	pyriform	rounded disc
Cephalodasys caudatus	700–800	220	U33	39%	rhombic, *Dactylopodola*-like	elongate lobe
Cephalodasys dolichosomus	615–772	205–215	U28–U33	29%	pyriform	rounded, slightly flared
Cephalodasys hadrosomus	322	152	U47	53%	rounded	rounded
Cephalodasys littoralis	600–650	200	U35.5	39%	pyriform	tapering
Cephalodasys maximus	700	235	U33.5	36%	pyriform	rounded disc
Cephalodasys miniceraus	464[g]	138	U32	36%	with hornlike lobes, *Turbanella*-like	tapering
Cephalodasys pacificus	294–368	105–125	U34–U37	37%	pyriform	rounded, slightly flared
Cephalodasys palavensis	400–500	ca. 140	U38	44%	rhombic, *Dactylopodola*-like	tapering with blunt apex
Cephalodasys saegailus	492–517	191–196	U38–U39	37%	pyriform	rounded, slightly flared
Cephalodasys swedmarki	500	238	U47	51,5%	pyriform to ovoid	rounded
Cephalodasys turbanelloides	1000	367	U36.5	38%	pyriform	rounded to parable-shaped
Cephalodasys sp. nov.	431–471	171–215	U35.5–U36	38–40%	pyriform	rounded

……continued on the next page

TABLE 2. (Continued)

species	position of testes plus vasa deferentia	TbA per side	L TbA [µm]	W TbA[b]	TbVL per side	L TbVL [µm]	TbVL in the pharyngeal region[c]	TbV
Cephalodasys cambriensis	U30.5–U68.5	5-6	8	common	15-20	8-12	p	a
Cephalodasys caudatus	U37–U64.5	3	12	common	12–15	12	p	a
Cephalodasys dolichosomus	U28/33–U50+[d]	4	8–9	common	6	15–18	a	a
Cephalodasys hadrosomus	?[e]	6	8	common	a	n.a.	n.a.	a
Cephalodasys littoralis	U36–U67.5[f]	4 -5	?	common	13–14	?	p	a
Cephalodasys maximus	U33.5–U92	5	?	common	14	?	a	a
Cephalodasys miniceraus	?[g]	2	8–9	common	9–12	5–6	p	a
Cephalodasys pacificus	U32–U75+[d]	5–6	6.5–9	very thin	3 -7 (often 5)	9–13	a	a
Cephalodasys palavensis	U38–U73+[d]	4	5	very thin	10	5	p	a
Cephalodasys saegailus	U38–U51+[d]	4	6–8	common	10	10–16	p	p (2 pairs)
Cephalodasys swedmarki	?[e]	4	4–8	common	5	16–21	a	a
Cephalodasys turbanelloides	U35.5–U77+[d]	6–7	10	common	15–20	9–12	p	a
Cephalodasys sp. nov.	U36.5–U50	3	10–11.5	common	5 (4)	10–16.5	a	a

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TABLE 2. (Continued)

species	TbDL	TbP	L TbP [µm]	TbP arranged in two arcs	frontal organ	caudal organ	epidermal glands	finely granular epidermis
Cephalodasys cambriensis	a	17	8-12	a	p	p	a	p
Cephalodasys caudatus	a	10–12	12	a	p	p	a	p
Cephalodasys dolichosomus	a	16	7–10	a	?	?	a	p
Cephalodasys hadrosomus	a	20	9 -13	p	?	?	p	a
Cephalodasys littoralis	a	14–16	5 and 8–10	a	p	p	a	?
Cephalodasys maximus	p (11 pairs)	20	&	a	p	p	p	?
Cephalodasys miniceraus	a	6–8	10–13	a	?	?	a	p
Cephalodasys pacificus	a	13–17	7.5–8.5	a	p	a	a	p
Cephalodasys palavensis	a	10	5	a	p	a	a	?
Cephalodasys saegailus	a	18	5–7 and 8–10	p (?)	?	?	a	p
Cephalodasys swedmarki	a	10–12	9–10	a	?	?	a	p
Cephalodasys turbanelloides	a	10–15	ca. 10	a	?	?	a	p
Cephalodasys sp. nov.	a	11–12	6.5–13	a	p	a	a	p

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TABLE 2. (Continued)

species	type locality and position (if provided in original description)	habitat / ecology	depth	reference
Cephalodasys cambriensis	Llandwyn and Rhosneigr, Anglesey, Wales (Irish Sea)	beach slope around low water line, fine to fairly fine sand (200–350 µm)	IT	Boaden 1963
Cephalodasys caudatus	Puri Beach, Orissa, India (N 19°48'06"; E 85°51'14") (Bay of Bengal)	beach slope between low and half tide levels, coarse and medium sand	IT	Rao 1981
Cephalodasys dolichosomus	different coastal sites of Egypt and Israel (Red Sea)	low water line to sublittoral, very fine to very coarse sand (silicious or coralline)	IT, 0.5–8 m	Hummon 2011
Cephalodasys hadrosomus	Santa Maria di Leuca, Apulia, Italy (N 39°47'; E 18°18') (Ionian Sea)	medium to coarse sand, mixed with shell and coral gravel	4 m	Hummon et al. 1993
Cephalodasys littoralis	Camp Américain, Bassin d'Arcachon, France (Atlantic)	moist sand at the low water line, varying salinity between 29–33 ppm	IT	Renaud-Debyser 1964
Cephalodasys maximus	Stoller Grund, outer Kiel fjord, Germany (Baltic Sea)	mid-coarse sand	7–8 m	Remane 1926
Cephalodasys miniceraus	El Rodadero Beach, Santa Marta, Colombia (Caribbean Sea)	intertidal sand, mean grain size 189–203 µm	IT	Hummon 1974b
Cephalodasys pacificus	Santa Cruz, Galapagos Archipelago, Ecuador (Pacific)	beach sand (coralline?), close to the high water line	IT	Schmidt 1974
Cephalodasys palavensis	Golfe d'Aigues-Mortes, France (Mediterranean)	coarse calcareous sand	IT	Fize 1963
Cephalodasys saegailus	Marsa Matruh, Sidi Abd al-Rahman, Egypt (Mediterranean)	very fine to fine, well to medium-well sorted sands, feeds on a diversity of diatoms	3 m	Hummon 2011
Cephalodasys swedmarki	Firemore Beach, Scotland (N 57°49'; W 05°41'); Glen Brittle, Isle of Skye; Ile de Jarre, France	fine to medium fine sand, medium-well or poorly sorted	IT / 8 m	Hummon 2008
Cephalodasys turbanelloides	Hallö / Väderöarna, Sweden (Skagerrak)	medium to fine grained sand	22 m	Boaden 1960
Cephalodasys sp. nov.	shoal close to Lee Stocking Island, Bahamas (N 23°45.972´; W 76°06.897´) (Caribbean Sea)	fine calcareous sand	2 m	this study

a: this ratio has been re-measured from the drawings of the original descriptions
b: 'common' means that TbA are comparably wide as other tubes of the animal
c: considered are TbVL anterior to the pharyngeal pores
d: termination of vasa deferentia was not observed
e: description based on protogynous specimens
f: posterior termination of testes in *C. littoralis* is unsure
g: description based on subadult specimens

join in an unpaired ventral male gonopore (Figs. 4E, 6E). Based on light microscopic observations, the male gonopore appears as a simple circular opening (Fig. 4E). However, scanning electron microscopy of that region indicates a slightly more complex, valve-like structure (Fig. 6E). Furthermore, light microscopy reveals a trefoil-shaped structure directly underneath the male gonopore, possibly a glandular organ that aids sperm transfer in that species (indicated in the schematic drawing, see Fig. 2). At the anterior pole and along the median wall of each testis, cell-like compartments with granular content can be observed in some optical layers (Fig. 4G). We interpret this as early germ cell stages. According to this interpretation, spermatogenesis proceeds from posterior to anterior and spermiogenesis medio-laterally. A single mature egg is present dorso-lateral to the intestine and on the left side of the trunk between U65 and U85. The egg contains numerous small spheres, probably yolk material, and has a large globular nucleus, ca. 15 µm in diameter (Fig. 3B). Smaller oocytes with ovoid nuclei (6 x 12.5 µm) are present anterior the single large egg. Hence, oogenesis proceeds antero-posteriorly. Posterior to the mature egg on the left side of the posterior trunk (between about U82.5 and U88.5) there is an accessory reproductive organ, viz. the frontal organ. The shape of this structure is somewhat ovoid but irregular and lacks any obvious musculature. In its center, the putative organ lumen, there is a grain-like inclusion and few filiform structures coiled around it (Figs. 3B, 4D). We interpret these structures as foreign spermatozoa of a mating partner. The putative wall epithelium of the frontal organ is probably secretory since some small vesicles can be observed. Light and SEM observations indicate a lateral external pore to the frontal organ (Figs. 4D, 6F); an internal pore was not observed. Apart from the structure associated with the male gonopore, no further accessory reproductive organ (i.e. a caudal organ) is present.

Discussion

Cephalodasys Remane, 1926 is currently classified within the taxon Cephalodasyidae Hummon & Todaro, 2010 that originally comprised the six genera *Cephalodasys*, *Dolichodasys*, *Megadasys*, *Mesodasys*, *Paradasys*, and *Pleurodasys* (Hummon & Todaro 2010). Recently, *Megadasys* was transferred to the taxon Planodasyidae Rao & Clausen, 1970 due to similarities with species of *Crasiella* concerning reproductive anatomy and sperm ultrastructure (Guidi *et al.* 2014). The taxon *Cephalodasys* Remane, 1926 so far comprises twelve species (Hummon & Todaro 2010, Hummon 2011, Kieneke & Schmidt-Rhaesa 2015, Todaro 2015). Two species were initially described as members of *Paradasys* (see Boaden 1960, 1963) but were later relocated to *Cephalodasys* (Hummon 1974a). Furthermore, the taxon *Psammodasys* that was introduced by d'Hondt (1974) is now identified and accepted as a junior synonym of *Cephalodasys* (Hummon 2008: p. 121, Hummon & Todaro 2010). A characteristic feature of the majority of species of *Cephalodasys* is a distinct head region that is wider than the neck; a furrow directly anterior to the TbA is often present and further demarcates the two regions (Remane 1926). The head region is pear-shaped in most species, including the new one, but several variants do exist. For example, both *C. caudatus* Rao, 1981 and *C. palavensis* Fize, 1963 have oval- to rhombic-shaped heads that superficially resemble those of *Dactylopodola*. However, the head of species of *Dactylopodola* contains almost the entire length of the pharynx, which is never the case in any species of *Cephalodasys*. Other deviations are noted for *C. hadrosomus* Hummon, Todaro & Tongiorgi, 1993 and *C. miniceraus* Hummon, 1974, which have a rounded head and a head bearing inconspicuous lateral, ciliated hornlike lobes, respectively. It is questionable if *C. hadrosomus* and *C. miniceraus* belong to the genus at all, as Hummon (1974b) states in his original description of *C. miniceraus* that this species only barely fits the generic diagnosis. Nevertheless, we include both species in our emended taxonomic key (see below).

The new species most closely resembles a group of four species (*C. dolichosomus* Hummon, 2011, *C. maximus* Remane, 1926, *C. pacificus* Schmidt, 1974, and *C. swedmarki* Hummon, 2008) that share two characters: a pear-shape head and TbVL beginning in the region of the pharyngeal pores (Table 2). Among these four species, both *C. dolichosomus* and *C. swedmarki* are most similar to the new species, however, *C. dolichosomus* has a longer adult body (615–772 µm compared to 431–471 µm) and a different number of adhesive tubes in each group (2 x 4 TbA, 2 x 6 TbVL, 16 TbP). In constrast, *C. swedmarki* coincides with the new species in many characters (500 µm total body length, 2 x 5 TbVL, 10–12 TbP, see Table 2). The main and consistent difference between the two species is observed with the TbA, which are present as 3/side in the new species and 4/side in *C. swedmarki*. The only other species to possess 3 TbA/side is *C. caudatus* Rao, 1981, but this species differs in several other characters: a rhombic head, an elongate lobe on the caudal end, and more abundant TbVL (12–15 per side), two pairs of which are present in the pharyngeal region (Table 2). Further differences between *C. swedmarki* and the new species are present in the size of the pharynx relative to the total gut tube length (51.5% in *C. swedmarki*, 38–40% in the new species, see Table 2) and the arrangement of the TbVL. In *C. swedmarki*, the first two pairs of TbVL (1 and 2) and last two pairs (4 and 5) of TbVL are closely set, but tube 3 is equidistant between them (see Hummon 2008). In the new species, the first three pairs follow in a more or less equal distance from each other (about 30–35 µm), while pairs 3 & 4 and pairs 4 & 5 are separated up to 70 µm from each other. The encountered differences between *C. swedmarki* and the Caribbean individuals are possibly the result of a separate lineage evolution. Therefore, the specimens found around Lee Stocking Island are hypothesized as a separate species under the unifying species concept (de Queiroz 2009). *Cephalodasys swedmarki* and *C. interinsularis* **n. sp.** may represent sister species. In the wider Caribbean or Tropical Northwestern Atlantic marine realm (*sensu* Spalding *et al.* 2007), *C. interinsularis* **n. sp.** is the third recorded species of *Cephalodasys* in addition to *C. miniceraus* and *C. pacificus* (see Hummon 2010).

As already mentioned in the materials section, a fourth individual of *Cephalodasys* was extracted from the same sample (Fig. 5B). This specimen was 603 µm long and lacked any obvious reproductive features, suggesting it was either a very large subadult or perhaps post-reproductive. In addition to the large size, the specimen had fewer TbVL than the new species (see Table 1). While it is possible that this individual is a variant of *C. interinsularis* **n. sp.** because of the identical number of just three TbA per side, we hesitate to include it in the description of the new species until such time that additional (and adult) specimens of similar size and morphology can be observed. At this stage, we consider this individual a member of another undescribed species.

Key to species of *Cephalodasys*

The shape of the head, the outline of the caudal end, and the number and distribution of adhesive tubes are the main characters for delimiting morphological species of *Cephalodasys*. Other characters such as the ratio of pharynx to intestine length, the length of the testes, and the presence of accessory reproductive organs may also provide useful information (see Table 2).

1a Anterior body end forms a distinct pyriform or oval head region that is well separated from the remaining body 3

1b A head region is only inconspicuously delimited from a subsequent neck and trunk and does not show a pyriform or oval shape 2

2a Anterior end is simply rounded; an inconspicuous lateral indentation may be present at the level of TbA; posterior trunk end blunt to slightly rounded; small animals (Lt: 322 µm); so far only females or protogynous specimens known; numerous small epidermal glands arranged in a paired lateral column along the whole body; tube arrangement: TbA 2x6, TbVL absent, TbP 20 . . . . *C. hadrosomus* Hummon, Todaro & Tongiorgi, 1993

2b Anterior end is trapezoid and forms a pair of short lateral "hornlike lobes"; posterior trunk end triangular and drawn-out to a median tip; medium-sized animals (Lt: 464) though as yet only subadult specimens have been found; tube arrangement: TbA 2x2, TbVL 2x9-12, TbP 2x3–4 . . . . *C. miniceraus* Hummon, 1974

3a TbVL present in the pharyngeal and intestinal region of the body 4

3b TbVL absent from pharyngeal region, present only in the intestinal region; the most anterior pair close to the pharyngeal pores 8

4a Two pairs of TbV present around U50 and insert slightly more ventral than TbVL, medium-sized animals (Lt: 492–517 µm); rounded and slightly flared caudal end; tube arrangement: TbA 2x4, TbVL 2x10, TbV 2x2, TbP 18 . . . . *C. saegailus* Hummon, 2011

4b TbV absent 5

5a TbA 3 per side; cadum as elongate lobe; rather large animals (Lt: 700-800 µm); tube arrangement: TbA 2x3, TbVL 2x12–15, TbP 2x5–6 . . . . *C. caudatus* Rao, 1981

5b TbA at least 4 per side 6

6a Caudum as rounded disk; very large animals (Lt: 990 µm); tube arrangement: TbA 2x5–6, TbVL 2x15–20, TbP 17 . . . . *C. cambriensis* (Boaden, 1963)

6b Caudum rounded; very large animals (Lt: 1 mm); tube arrangement: TbA 2x6–7, TbVL 2x15–20, TbP 10–15 . . . . *C. turbanelloides* (Boaden, 1960)

6c Caudum tapers and terminates with a blunt apex; 4 or 5 TbA per side 7

7a TbVL 10 per side; medium-sized animals (Lt: 400–500 µm); tube arrangement: TbA 2x4 (TbA are very thin), TbVL 2x10, TbP 2x5 . . . . *C. palavensis* Fize, 1963

7b TbVL 13–14 per side; rather large animals (Lt: 600–650 µm) with a distinctly narrowed neck region; tube arrangement: TbA 2x4–5, TbVL 2x13–14, TbP 2x7–8 . . . . *C. littoralis* Renaud–Debyser, 1964

8a TbVL 14 per side; TbD present, rather large animals (Lt: 700 µm); caudum ends as rounded disk; tube arrangement: TbA 2x5, TbVL 2x14, TbD 2x11, TbP 2x10 . . . . *C. maximus* Remane, 1926

8b Fewer TbVL (maximum 7) per side; TbD absent 9

9a TbA 4 per side 10
9b Number of TbA other than 4 per side 11
10a TbVL 5 per side; medium-sized animals (Lt: 500 µm) with a rounded caudum; tube arrangement: TbA 2x4, TbVL 2x5, TbP 10–12. . . . .*C. swedmarki* Hummon, 2008.
10b TbVL 6 per side; long and slender animals (Lt: 615–772 µm) with a rounded but slightly flared caudum; tube arrangement: TbA 2x4, TbVL 2x6 (terminal pair of TbVL is more isolated from the remaining TbVL), TbP 16 . . . .*C. dolichosomus* Hummon, 2011
11a TbA 5–6 per side; rather small animals (Lt: 294–368 µm) with rounded, slightly flared caudum; tube arrangement: TbA 2x5–6 2x4 (TbA are very thin), TbVL 2x3–7 (commonly 5), TbP 13–17 . . . . *C. pacificus* Schmidt, 1974
11b TbA 3 per side; medium-sized animals (Lt: 431–471 µm) with a simply rounded caudum; tube arrangement: TbA 2x3, TbVL 2x5, TbP 11–12 . . . . *C. interinsularis* (this study)

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