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Two new species of *Oregodasys* (Gastrotricha: Macrodasyida: Thaumastodermatidae) from Carrie Bow Cay, Belize with ultrastructural observations of the epidermal glandular system

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Abstract

This study represents the first report of Gastrotricha from the coast of Belize. Two new species of *Oregodasys* (Macrodasyida: Thaumastodermatidae) are described from sublittoral sediments around the island of Carrie Bow Cay in the Belizean barrier reef complex. *Oregodasys norenburgi* **sp. nov.** is unique in the possession of paired red ocelli and in the quantity and distribution of lateral and posterior adhesive tubes. *Oregodasys katharinae* **sp. nov.** is allied with species that possess ventrolateral cirri in the posterior body region, but is distinguished based on the quantity of cirri and adhesive tubes and the bipartite structure of the caudal organ. Ultrastructural analysis of the bodywall of *O. katharinae* **sp. nov.** reveals a highly glandular epithelium covered by a bilayered cuticle consisting of a thin exocuticle and thicker endocuticle containing electron-dense elements. At least three types of papillae are present beneath the cuticle: blunt papillae, triangle-shaped papillae, and sensory papillae. The sensory papillae are two-part structures consisting of a porous epidermal cell and a monociliated epidermal cell. The ultrastructure of blunt papillae was not examined, but triangular papillae are formed from neck-like extensions of underlying glandulocytes and contain a pore to the external environment. Insunk glandulocytes are present between the various papillae and have an elongate neck that extends between epidermal cells. All glandulocytes contain a variety of membrane-bound secretory vesicles with a wide range of staining characteristics, from electron lucent to electron dense.

Key words: New species, gastrotrich, meiofauna, Central America, Caribbean

Introduction

Carrie Bow Cay is a small island off the coast of Belize built from Holocene carbonate sediments over 15m thick (Shinn *et al.* 1982). The cay is one of many islands located on the barrier reef complex of Belize – a complex approximately 250 km long and up to 32 km wide – that forms the largest continuous reef in the Caribbean Sea (Gischler & Hudson 2004). The biodiversity of both sedimentary and reef habitats around Carrie Bow Cay and adjacent islands has been extensively documented, especially regarding the invertebrate macrofauna (see Rützler & MacIntyre 1982 and references therein). Alternatively, the meiofauna of these Belizean islands remains poorly known. The first systematic surveys of "permanent" meiofauna—animals with maximum dimensions less than 1 mm throughout their ontogeny (Higgins & Thiel 1988)—began with Higgins (1983) survey of Kinorhyncha around Carrie Bow Cay. Higgins described one new genus and eighteen new species from sublittoral sediments, and attributed the high species richness of kinorhynchs to the ecological heterogeneity (e.g., patch reefs, mangroves, etc) that is characteristic of the region. Nine years later, Sterrer (1992) documented the first species of Gnathostomulida from Belize with the description of *Clausognathia* from the Southern Sandores. This was followed by reports of new species of gnathostomulids from a variety of islands around Belize (Sterrer 1998) and the wider Caribbean, including Carrie Bow Cay (Sterrer 2000). While kinorhynchs and gnathostomulids form a diverse part of the meiobenthic fauna, especially the fauna that is characteristic of organic-rich sediments, their species-richness is not necessarily

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indicative of meiofaunal biodiversity from other sediment types, namely coarse carbonate reef sands characteristic of reef flats around Carrie Bow Cay (Shinn *et al.* 1982).

The phylum Gastrotricha contains marine species that are exclusively meiobenthic, and in general, prefer clean fine to medium grain sediments (Todaro & Hummon 2008). Their microscopic size (0.1mm–3mm) and ciliated ventrum means that locomotion is generally restricted to the interstitial pore spaces, where they function as microphagous consumers and detritivores. At present, there are relatively few reports of marine gastrotrichs from the five ecoregions of the Tropical Northwestern Atlantic (aka wider Caribbean; Sullivan Sealey & Bustamente 1999). Hummon (2010) has recently described several new species from parts of the Caribbean and reviewed existing accounts of each region including reports from the South Florida ecoregion (Bush 1966; Thane-Fenchel 1970; Schoepfer-Sterrer 1974; Decho, Fleeger & Hummon 1985; Evans & Hummon 1991; Evans 1994), the Gulf of Mexico (Todaro 1994; Todaro *et al.* 1995; Hummon & Todaro 2007), the Bahamian ecoregion (Renaud-Debyser 1963), the Lesser Antilles ecoregion (Kisielewski 1984) and coastlines of the Central Caribbean ecoregion including Colombia (Hummon 1974) and Panama (Hochberg 2008). Additional unpublished records can be found in Hummon (2009); several species are also known from the adjacent Warm Temperate Southern Atlantic off the coast of Brazil (Todaro & Rocha 2004, 2005).

In January 2010, the Smithsonian Institution's field station at Carrie Bow Cay, which served as the site for past meiobenthic studies (Higgins 1983; Sterrer 1992, 1998, 2000), was used again as the location for new investigations of meiofaunal biodiversity and phylogeography. Over a 2-week period, sublittoral sites around Carrie Bow Cay including reef flats, patch reefs, troughs, and seagrass beds were sampled and analyzed for meiofauna. In this study, I document two new species of *Oregodasys* (Gastrotricha, Macrodasyida) from sublittoral sediments around the island. In addition, I provide an ultrastructural description of the epidermis of a single new species of *Oregodasys*, which is characterized by a dense distribution of epidermal glands and an important taxonomic character for the genus.

Material and methods

Gastrotrichs were collected from a variety of sublittoral sites around Carrie Bow Cay, Belize (Table 1) between January 13 and January 28, 2010. Sediments were collected by SCUBA in bags and buckets and brought back to the field station for subsampling. Extraction of gastrotrichs followed a standard protocol: 1) approximately 100 cm^3 of sediment was combined with ca. 900 cm^3 of 7% $MgCl_2$ in a 1 L erlenmeyer flask and allowed to rest for 15 mins; 2) the flask was gently shaken and the supernatant was decanted over a 48 µm mesh; and 3) the mesh was gently washed with seawater into a petri dish. Specimens were sorted with a Leica EZ4 stereomicroscope, transferred to a glass slide, and viewed with a Zeiss A1 compound microscope equipped with DIC (differential interference contrast). Light micrographs were captured with a Sony Handycam digital camera. Measurements of individual specimens were performed with an ocular micrometer. Lengths and positions of organ systems are described in terms of percentage body units, where total body length from anterior to posterior is 100 units.

Sediment that was left over after extraction was used for grain size analysis. All sediments were dried in an oven at 60º C for > 72 h and then sieved on a mechanical Gilson SS-15 Sieve Shaker with mesh sizes 2 mm, 1 mm, 500 µm, 250 µm, 125 µm and 63 µm. The different sieve fractions were weighed and entered into the program, GRANPLOTS with line segment (Balsille *et al.* 2002). Median grain size and skewness were calculated for Phi values and transformed to mm scale (Table 1).

For preparation for transmission electron microscopy and preparation of type specimens for museum archival, all gastrotrichs were fixed in 2.5% gultaraldehyde in 0.1M phosphate buffer saline (PBS; pH 7.4) for at least one week. Animals were then rinsed with PBS for 15 min, exposed to 1% OsO_4 for 1 hr (30 sec for the type specimens to increase contrast), rinsed again in PBS for 15 min, and dehydrated through an ethanol series. All animals were transferred to propylene oxide for 30 min and embedded in epon following a standard protocol (Electron Microscopy Sciences). For type material, resin with individual specimens was placed on

glass microscope slides and placed in an oven at 60º C for 24 hrs. All type specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC. For TEM, the singular specimen was embedded in an embedding mold, hardened in a 60º C oven for 24 hrs, and sectioned on a Reichert ultramicrotome with a glass knife. Sections were stained with lead citrate and uranyl acetate and viewed with a Phillips EM400 at the Materials Charactertization Laboratory at the University of Massachusetts Lowell.

Abbreviations: BL, total body length; PIJ, pharyngeointestinal junction; TbA, anterior adhesive tubes; TbL, lateral adhesive tubes; TbP, posterior adhesive tubes; TbVL, ventrolateral adhesive tubes.

TABLE 1. List of SCUBA sample locations around Carrie Bow Cay and abiotic characteristics of each location.

Station #	Coordinates	Depth (m)	Median Grain Size ϕ units (mm)	Size Class (Wentworth Scale)	Skewness
CBC10.01	16º 48.09N 88º 04.74W	10	0.3459 (1.1085)	Coarse sand	0.4935 (0.3562)
CBC10.04	16º 48.224N 88º 04.615W	15	-0.2474 (1.915)	Very coarse sand	0.5784 (0.3629)
CBC10.10	16º 48.127N 88º 04.607W	30	-0.1752 (1.1320)	Coarse sand	0.4935 (0.3562)
CBC10.11	16º 48.127N 88º 04.607W	42	0.6345 (0.6445)	Medium sand	0.3209 (0.7269)
CBC10.24	16º 47.466N 88º 04.568W	9	-0.1409 (1.1037)	Coarse sand	0.0337 (1.0584)

Skewness has no units; numbers in parentheses indicate transformed data. Wentworth scale based on Giere *et al.* (1988).

Taxonomic account

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

Family Thaumastodermatidae Remane, 1926

Subfamily Thaumastodermatinae Remane, 1927

Genus *Oregodasys* Hummon, 2008

Oregodasys norenburgi new species

(Figs. 1,2)

Diagnosis. Specimens with body lengths of 400 µm–500 µm long (mean 448 µm, n = 8). Maximum body width at mouth, PIJ and midpoint of body is 85/78/95 µm. Pharynx to 138 µm long (measured from the tip of the oral hood); oral hood to 50 µm long; mouth to 80 µm wide. Red ocelli present on either side of mouth. Cuticle is translucent and covered with ciliated papillae on dorsal and lateral surfaces. Numerous glandular cells fill the dorsal and lateral epidermis. Up to 16 TbA per side, somewhat staggered in position, inserting directly on body surface and leading imperceptibly to the adhesive tubes of the TbVL series. TbVL elongate, 68–82 per side, evenly spaced and sparse in the pharyngeal region, ca. 6–7 per side, becoming clustered in the trunk. TbL shorter than TbVL, to 19 per side, distinctly set off from TbVL and beginning at U80; extending to caudum. TbP 7 per side, fused at their base forming pedicles, with 6 TbP between the pedicles. Locomotory cilia form transverse rows on ventral surface from mouth margin to caudum. Hermaphroditic, with singular testes on right side as seen from below; egg dorsal at mid-body length; caudal organ is muscular; frontal organ not observed.

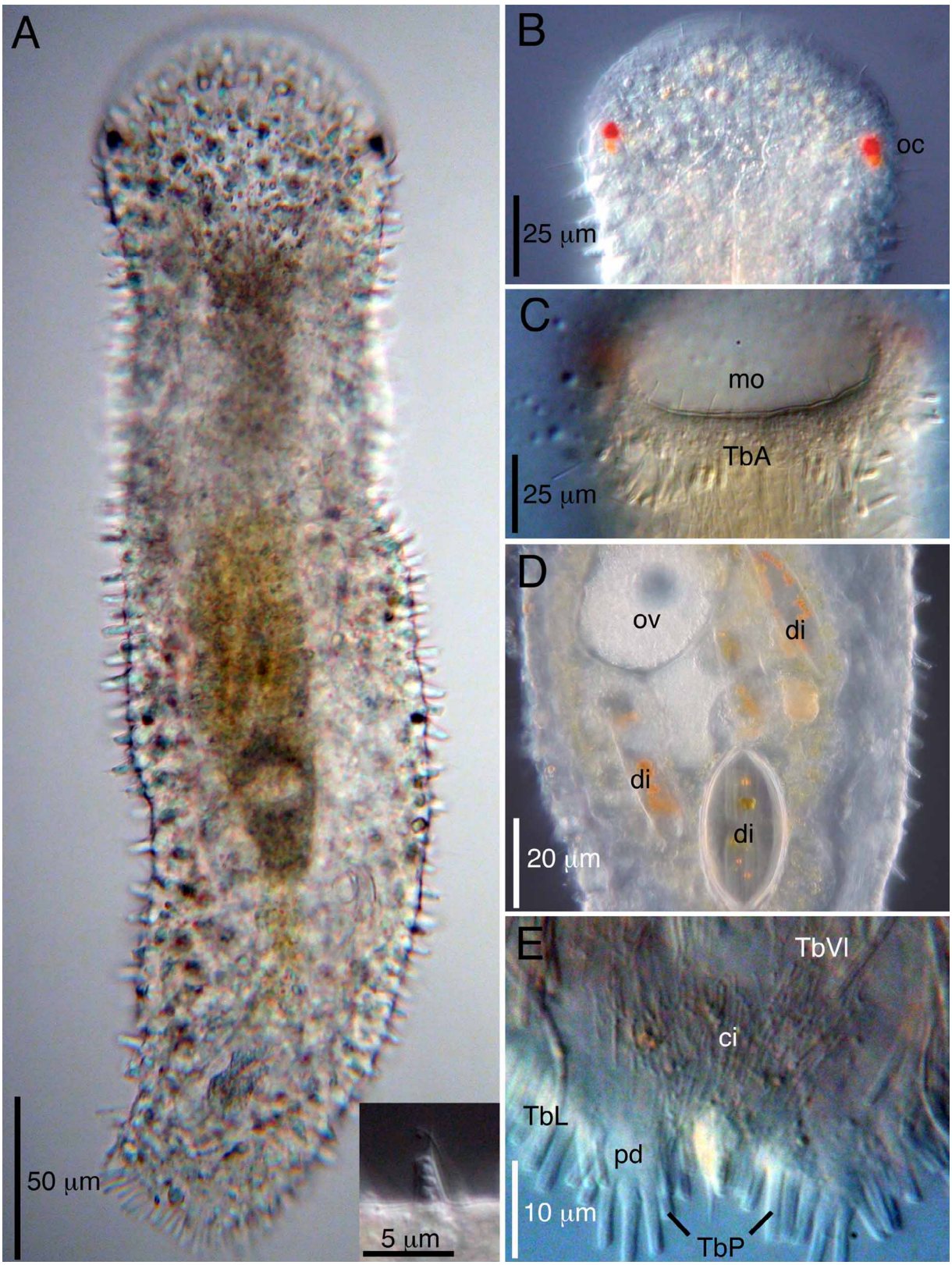

FIGURE 1. Habitus of *Oregodasys norenburgi* **sp. nov.**, multiple specimens. **A** Dorsal view. Inset: closeup of a papilla containing secretory vesicles. **B** Dorsal view of head region showing ocelli (*oc*). **C** DIC image of the ventral mouth (*mo*) margin showing the anterior adhesive tubes (*TbA*). **D** Dark-field image of the midgut region showing several ova (*ov*) and numerous diatom frustules (*di*). **E** DIC image of the posterior pedicles (*pd*), ventral view. Lateral adhesive tubes (*TbL*) are present on either side of the pedicles that bear the posterior adhesive tubes (*TbP*); locomotory cilia (ci) and ventrolateral adhesive tubes (*TbVL*) are also shown.

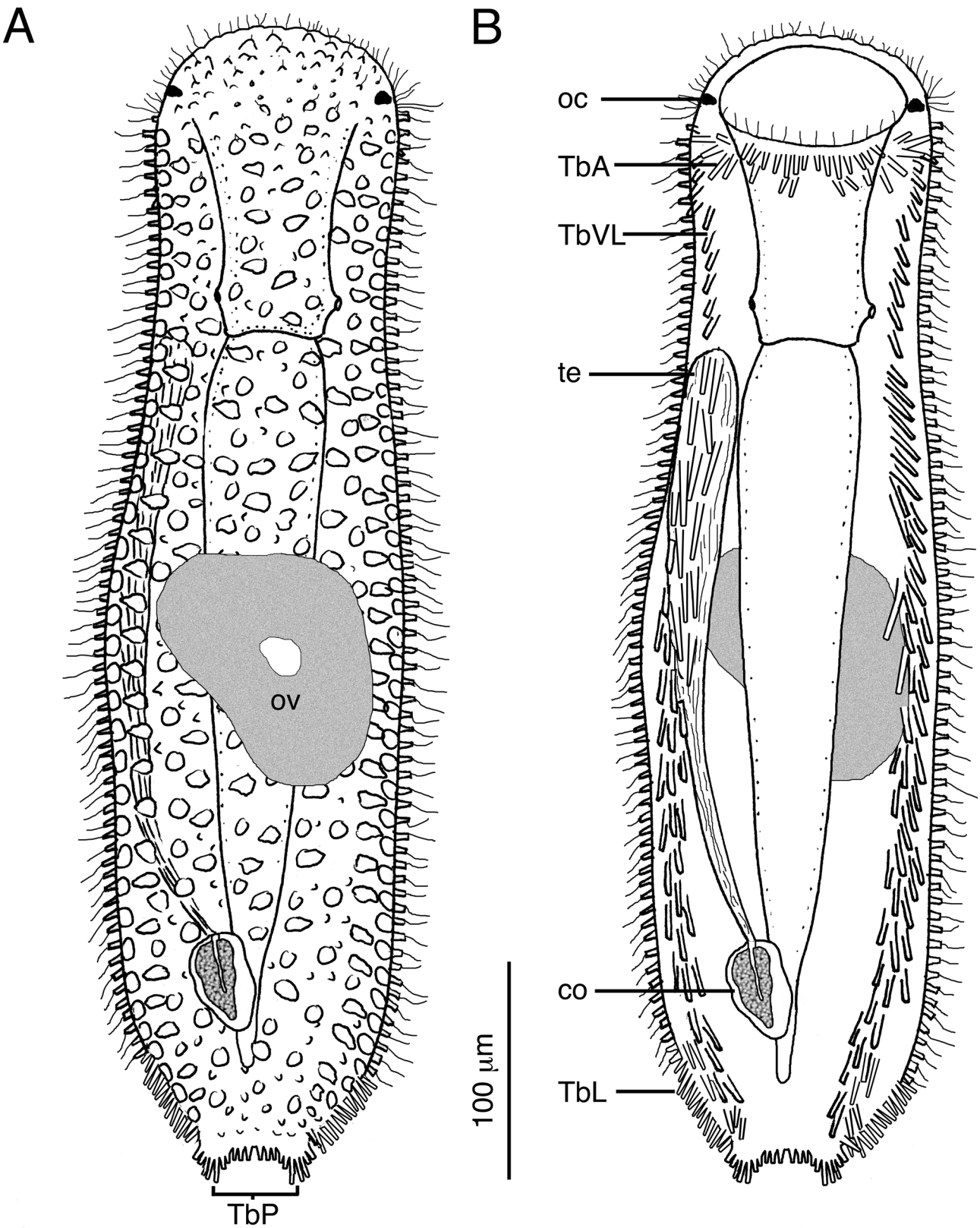

FIGURE 2. *Oregodasys norenburgi* **sp. nov. A** Dorsal view of an adult as seen from below: mature ova (*ov*); posterior adhesive tubes (*TbP*). **B** Ventral view of an adult as seen from below: caudal organ (*co*); ocelli (*oc*); anterior adhesive tubes (*TbA*); lateral adhesive tubes (*TbL*); ventrolateral adhesive tubes (*TbVL*); testis (*te*).

Type material. The description of *Oregodasys norenburgi* **sp. nov.** is taken from twelve specimens from stations CBC10.01, CBC10.04, CBC10.11 and CBC10.24. All specimens were measured in vivo. One

specimen from station CBC10.01 was prepared as a permanent wholemount (Holotype: USNM # 1146555, BL = 350 μm). Red ocelli no longer evident in the type specimen.

Type locality. Holotype station CBC10.01 is an open plain at 10 m depth. Other localities include: CBC10.04, Carrie Bow Cay Reef, sand patches between corals on top of ridge; CBC10.11, Carrie Bow Cay Reef, deep outer slope; CBC10.24, small sand patches on ridge.

Etymology. The species is named after the organizer of the Smithsonian field research workshop, Dr. Jon Norenburg.

Ecology. The new species was present at three stations in moderate abundance. Most specimens with numerous diatoms in gut. Grain size analysis (Table 1) from stations CBC10.04 and CBC10.11 shows a positive skewness, indicating that grain sizes larger than the median predominate; a negative skewness for CBC10.24 indicates a prevalence of grain sizes smaller than the median. All sediment with low amounts of organic detritus.

Description. Specimen length ranged from 350 μm to 500 long (n=8). The type description is based mostly on an adult specimen of approximately 500 μm total body length. All animals appear shiny under reflected light (dissection microscope) and opaque under transmitted light due to the highly glandular bodywall epithelium. Ocelli red, approximately 3–4 μm in diameter, present on either side of the ventral mouth margin and easily observed with a dissection microscope. Red pigments are never present as circular "eyepsots," but instead are scattered across several cells. Head with papillated oral hood to 50 μm long. Tip of hood with slightly scalloped margin but void of papillae. Numerous scattered sensory cilia to 7 μm long across hood margin. Pharynx reaches 138 μm in length (range: 125 μm–138 μm) to tip of oral hood. Body width at mouth/neck/PIJ/trunk are 82/70/74/84 μm, respectively.

Body covering of papillae to 12 μm long. Most papillae with a blunt end and a single lateral extension. Several papillae are closely associated with an apparent sensory cilium to 15 μm long. Papillae completely cover the dorsal body surface except for the tip of the oral hood. The lateral and ventrolateral body surfaces are completely covered with papillae. Most papillae appear to be associated with an underlying epidermal gland of 8– 12 μm diameter that is highly refractile with transmitted light. Some papillae contained ovoid secretions from the underlying glands (Fig. 1A). Some epidermal glands contained ovoid secretions that were colored brown, green or orange. Most epidermal glands were colorless.

Adhesive tubes present in four series. Anterior adhesive tubes (TbA) form a transverse row beneath the ventral mouth margin and arc slightly toward the lateral body margin. Up to 16 TbA per side, inserting directly on body surface, and somewhat staggered in placement. The most medial tubes are approximately 6––8 μm long; tubes toward the lateral margins up to 13 μm long. The ventrolateral adhesive tubes (TbVL) are positioned on either side of the ventral locomotory cilia and extend from approximately U12 to the caudal end. Anteriorly, the TbVL grade imperceptibly with the TbA, but are easily distinguished from them due to their arrangement in a singular column. The TbVL in the pharyngeal region (U12–U28) are shorter (ca. 15 μm) and less numerous (< 15/side) than those in the trunk region. In the trunk, the TbVL are highly elongate (up to 25 μm) and clustered; numerous tubes insert in proximity to one another along the length of the column. There are up to 70 tubes per side in the trunk region. A distinct set of lateral adhesive tubes (TbL), up to 15 μm long and 19/side, are set off from the TbVL at ca. U80, where they form a lateral column that leads to the caudum. The caudum is formed of two pedicles, each bearing 7 posterior adhesive tubes (TbP). The two most lateral and medial tubes are shorter (ca. 6–7 μm) than the three median tubes (ca. 12–15 μm). Six adhesive tubes, to 12 μm long, are positioned between the two pedicles.

The ventral ciliature forms a continuous series of transverse rows from the ventral mouth margin to the caudal pedicles. A singular region around the anus, ca. U90, is devoid of cilia. Cilia extend up to 15 μm long.

The digestive tract begins with a wide mouth, to 82 μm, covered by an oral hood that extends to U10. The pharynx narrows to ca. 50 μm at the PIJ. The pharyngeal pores, which were observed in only one specimen due to the opacity of the body wall, were at ca. U26. The intestine is narrow to broad depending on its contents. Several specimens possessed numerous diatom frustules in their guts. The anus opens ventrally around U89.

Animals are simultaneous hermaphrodites. A single testis is present on the animal's right side (as observed from above) and extends from the PIJ to the caudal organ. Vas deferens opens into a muscular, pear-

shaped caudal organ on the right side of the body; up to 47 µm long and 25 µm wide. Frontal organ not observed. Mature ovum (63 µm long x 40 µm wide) dorsal above gut in mid-trunk region.

***Oregodasys katharinae* sp. nov.**
(Figs. 3–5)

Diagnosis. Specimens with body lengths to 370 µm long. Maximum body width at mouth/PIJ/midpoint of body is 65/87/95 µm, respectively. Pharynx to 115 µm long (measured from the tip of the oral hood); oral hood to 50 µm long; mouth to 65 µm wide. Ocelli absent. Cuticle is translucent and covered with blunt and triangular papillae on dorsal, lateral and ventrolateral surfaces. Numerous glandular cells fill the dorsal and lateral epidermis. Up to 16 TbA per side form two rows that cluster toward the lateral body margin, inserting directly on body surface. TbVL form a column of ca. 40 tubes down to pedicles, evenly spaced and sparse in the phayrngeal region, becoming more clustered in the trunk. TbL present just anterior to the caudal pedicles, to 10 per side, distinctly set off from TbVL and beginning at ca. U83, extending to caudum. TbP 2 per side, fused at their base forming pedicles, with 14 TbP between the pedicles. Ventral cirri present, 9 per side to 50 µm long, in caudal region. Locomotor cilia form transverse rows on ventral surface from mouth margin to caudum. Hermaphroditic, with singular testes on right side as seen from above; egg dorsal at mid-body length; caudal organ is clearly bipartite with distinct muscular and non-muscular regions; frontal organ is sac-like.

Type material. The description of *Oregodasys katharinae* **sp. nov.** is taken from 12 specimens from station CBC10.11. All specimens were measured in vivo. Holotype (USNM # 1146556) is ca. 312 µm long, dorsoventrally oriented, with visible caudal organ.

Type locality. CBC10.11 is a deep outer slope at 42 m depth. CBC10.10 is a sand trough next to a ridge along the Carrie Bow Cay Reef at 30 m depth.

Etymology. The species is dedicated to friend and colleague, Dr. Katharina Jörger, who collected and helped to sort the new species.

Ecology. Few specimens present at CBC10.10, but moderately abundant at CBC10.11. Grain size analysis (Table 1) reveals a positive skewness, indicating that grain sizes larger than the median are predominant. Sediment with low amounts of organic detritus.

Description. Specimen length varied from 215 µm (n=1, juvenile) to 370 long (adult range: 300 µm–370 µm, n=11). The type description is based mostly on one adult specimen of approximately 370 µm total body length. All animals possess a highly glandular bodywall epithelium that is shiny under reflected light. Head has a glandular oral hood to 50 µm long. Tip of hood with smooth margin and void of papillae. Numerous short, scattered cilia to 8 µm long occur along the hood margin. Pharynx reaches 115 µm in length (range: 82 µm–115 µm) to tip of oral hood. PIJ at U31. Pharyngeal pores not observed. Body width at mouth/neck/PIJ/trunk are 72/70/74/90 µm, respectively.

Body covering of two shapes of papillae, blunt and triangular, each ca. 7–13 µm long; each triangular papilla is closely associated with a sensory cilium to 10 µm long. Approximately 40 sensory cilia/side. Papillae scattered on dorsal surface but abundant on lateral and ventrolateral body surfaces. Triangular papillae are associated with an underlying epidermal gland to 8 µm diameter; glands often brown in color and refractile with transmitted light. Blunt papillae may be associated with an underlying epidermal gland, but this was not always evident.

Adhesive tubes present in four series. Up to 16 anterior adhesive tubes (TbA) per side form two transverse rows beneath the ventral mouth margin. The more anterior row is formed of 8–10 tubes (ca. 8–10 µm long), with the two medial tubes the shortest (ca. 6 µm). A second transverse row is positioned posterior of the first row and contains 5–6 tubes (ca. 8–10 µm long) that become clustered toward the lateral body margin. The ventrolateral adhesive tubes (TbVL) are positioned on either side of the ventral locomotory cilia and extend from approximately U17 to the caudal end. In the pharyngeal region, the TbVL form a singular column of six evenly spaced tubes, each ca. 12–15 µm long. In the trunk, the TbVL are slightly more elongate (up to 20 µm)

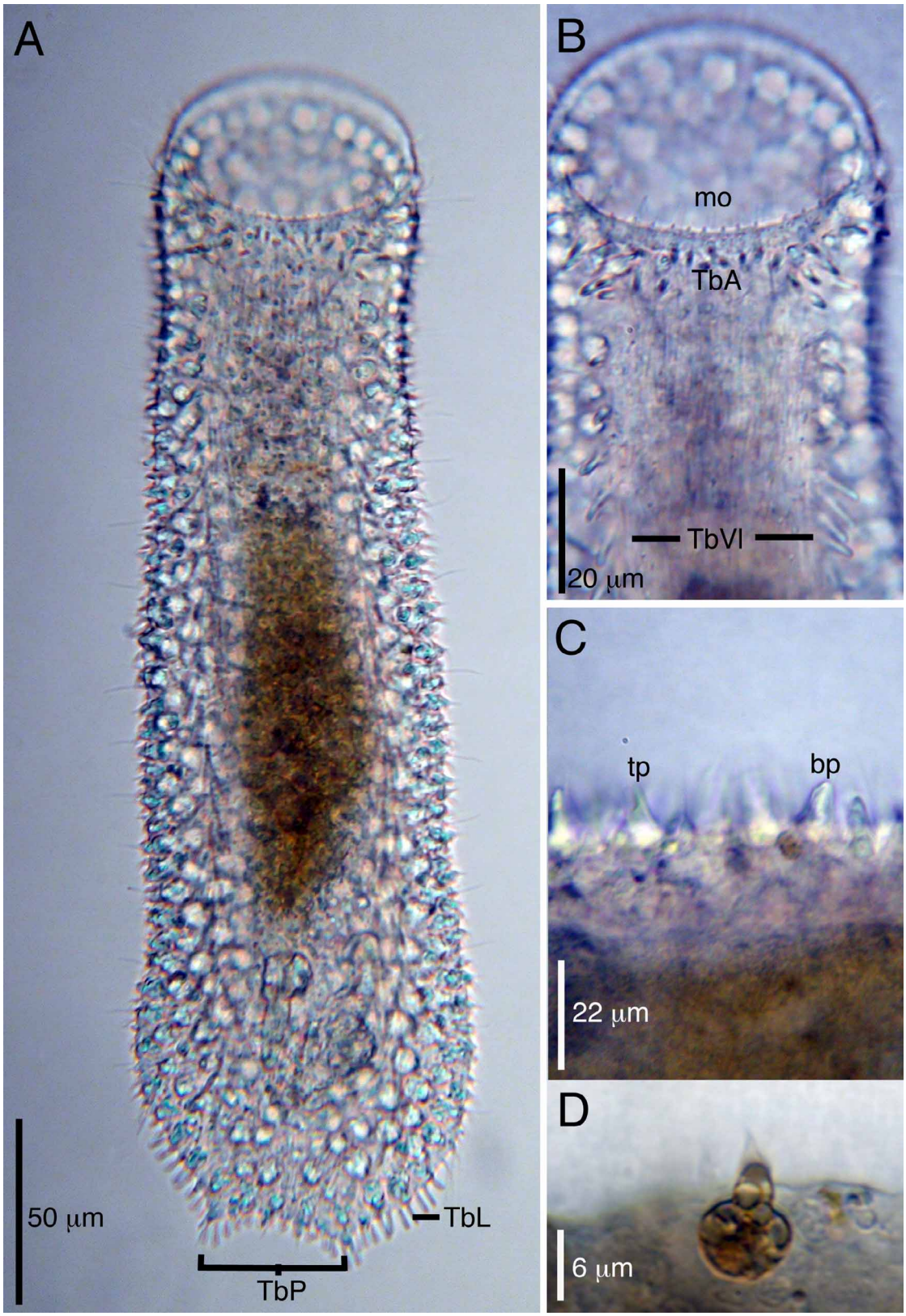

FIGURE 3. Habitus of *Oregodasys katharinae* **sp. nov. A** Ventral view showing lateral adhesive tubes (*TbL*) on the posterior body margin, and posterior adhesive tubes (TbP). **B** Closeup of the anterior end, ventral view, showing the mouth (*mo*), anterior adhesive tubes (*TbA*) and ventrolateral adhesive tubes (*TbVL*). **C** Closeup of the lateral body wall showing the triangle-shaped papillae (*tp*) and blunt papillae (*bp*). **D** Closeup of a triangular papilla from a specimen that was made into a permanent wholemount. The vesicles of the underlying glandulocyte stained darkly after osmium tetroxide fixation.

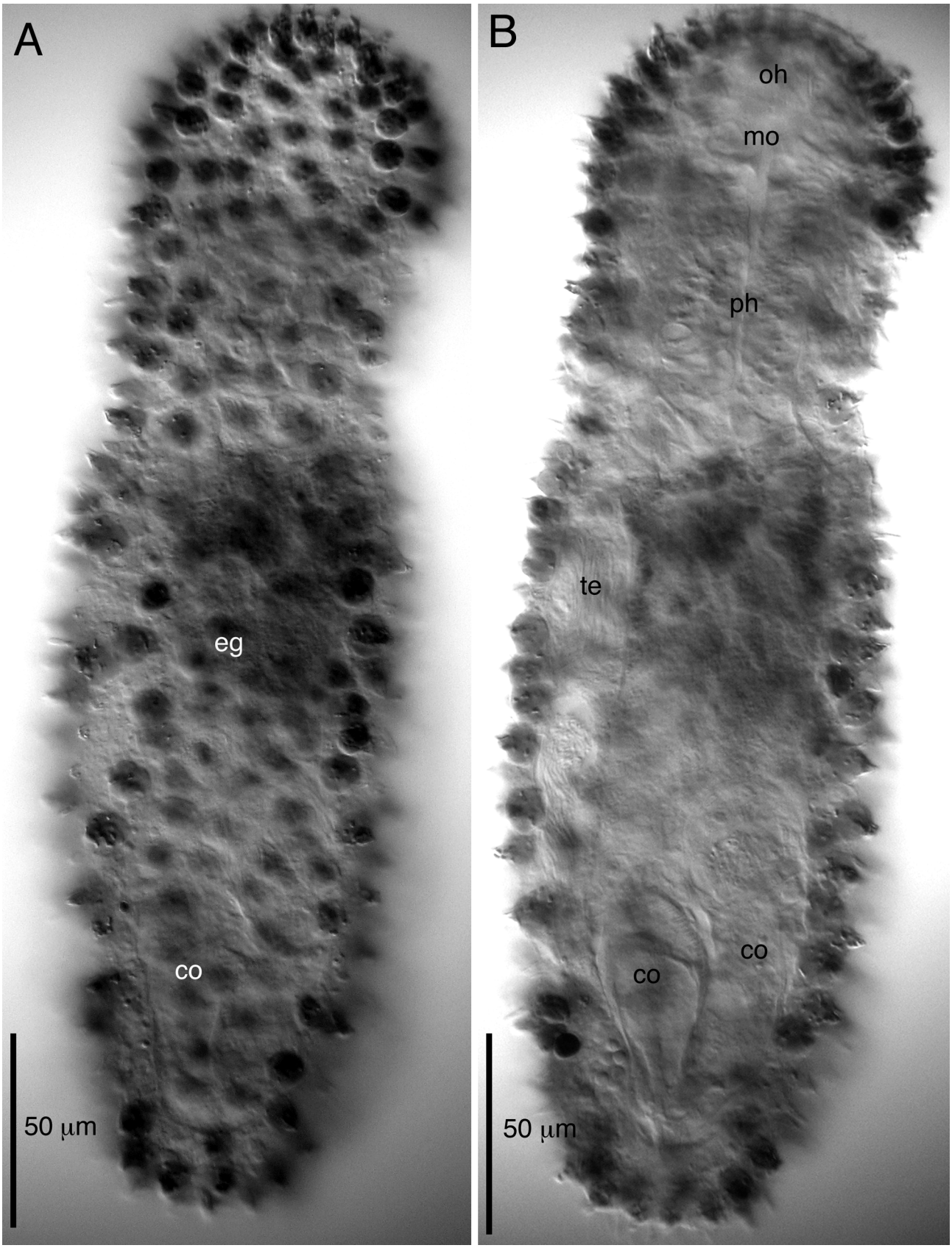

FIGURE 4. *Oregodasys katharinae* **sp. nov.**, transmitted light images of the holotype after resin impregnation. **A** Dorsal view showing numerous epidermal glandulocytes (*eg*) and one-half of the caudal organ (*co*). **B** Ventral view showing the oral hood (*oh*), mouth region (mo), pharynx (*ph*), singular testis (*te*) and bipartite caudal organ.

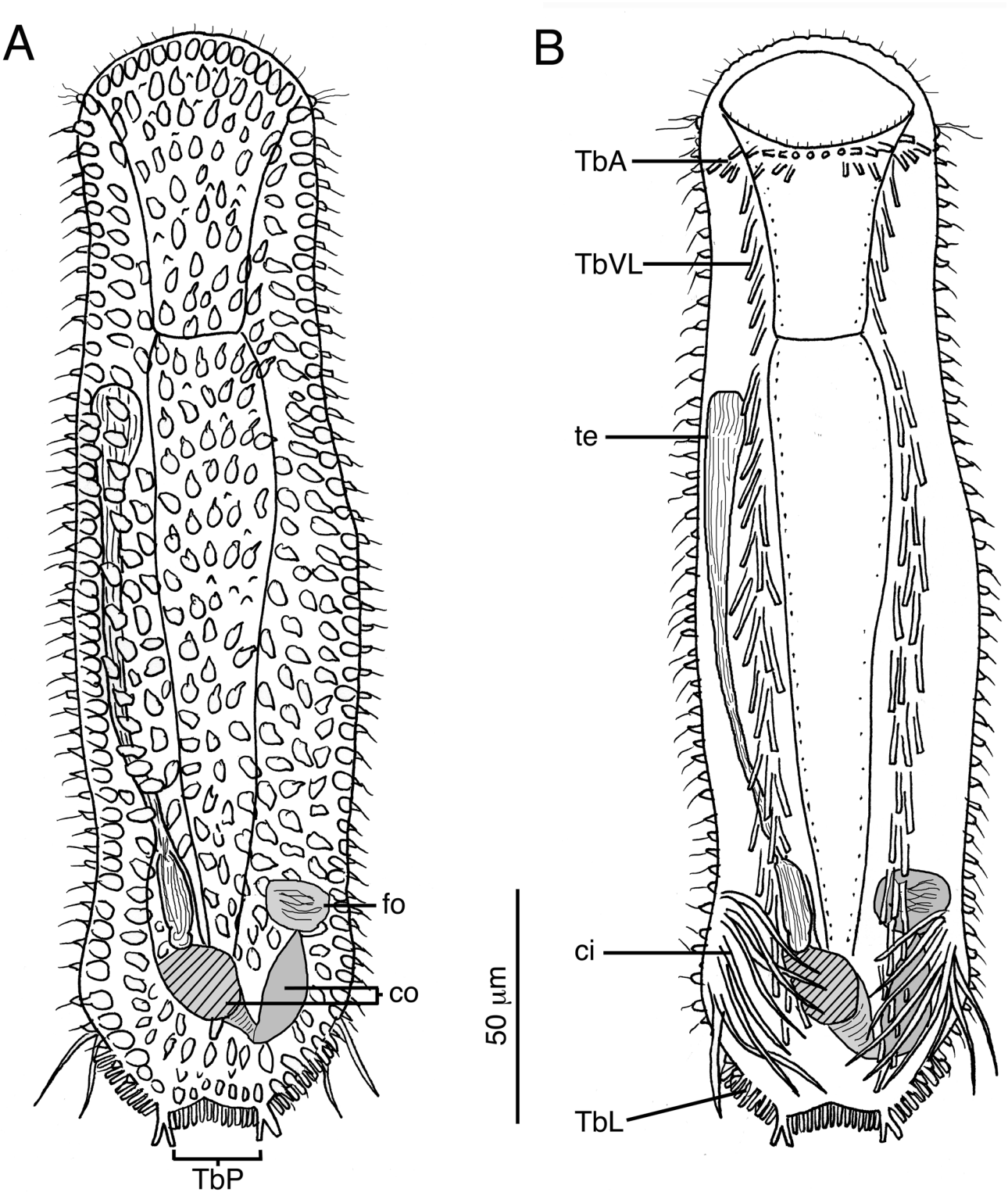

FIGURE 5. *Oregodasys katharinae* **sp. nov. A** Dorsal view of an adult as seen from below: bipartite caudal organ (*co*); frontal organ (*fo*); posterior adhesive tubes (*TbP*). **B** Ventral view of an adult as seen from below: cirri (*ci*); anterior adhesive tubes (*TbA*); lateral adhesive tubes (*TbL*); ventrolateral adhesive tubes (*TbVL*); testis (te).

and clustered; generally two tubes insert in proximity to one another along the length of the column. There are up to 30 tubes/side in the trunk region. A clustered set of lateral adhesive tubes (TbL), up to 7 µm long and 10/side, are set off from the TbVL at ca. U87, where they form a column that leads to the caudum. The caudum is formed of two pedicles, each bearing 2 posterior adhesive tubes (TbP). Each pedicle measures to 12 µm in

total length (including the tubes). Up to 14 adhesive tubes, to 8 μm long, are positioned between the two pedicles.

Nine ventral, elongate cirri per side are present in the posterior trunk region, beginning at U77, and positioned lateral to the TbVL and anterior to the TbL. Each cirrus is curled medially and extends up to 50 μm long.

The ventral ciliature forms a cotinuous series of transverse rows from the ventral mouth margin to the caudal pedicles. Cilia are 12–15 μm long.

The digestive tract begins with a wide mouth, to 70 μm, covered by an oral hood that extends to U14. The hood is covered with epidermal glands but appears free of papillae. The anterior margin of the hood, ca. 5 μm, is free of glands. Numerous short cilia extend along the margin of the hood. The pharynx extends up to 115 μm long and narrows to ca. 50 μm at the PIJ around U41. The intestine is narrow and tapers toward the posterior end where it terminates in an anal pore at U89. A single juvenile specimen measuring 215 μm long had the following set of measurements: mouth, 38 μm wide; oral hood, 25 μm long; and pharynx, 83 m long.

Animals are simultaneous hermaphrodites. A single testis is present on the animal's right side (as observed from above) and extends from the PIJ to the caudal organ. Vas deferens opens into a muscular, upside-down, pear-shaped caudal organ on the right side of the body at ca. U72. The organ is clearly bipartite. The right half of the organ is 52 μm long and 25 μm wide. Distally, where the vas deferens enters into the caudal organ, the organ is bulbous (to 25 μm wide) and wrapped in strong circular muscles. Caudally, the organ narrows to ca. 10 μm but retains a circular muscle sheath. The other half of the organ is somewhat spindle-shaped (ca. 50 μm long x 18 μm wide) and devoid of musculature. Distally, the organ widens into a sac-shaped frontal organ (ca. 35 μm diameter), devoid of musculature and containing spermatozoa (allosperm), which is in proximity to maturing ova. A single mature ovum was measured as 55 μm long x 40 μm wide in one adult specimen.

Ultrastructural Observations of *O. katharinae* sp. nov. The ultrastructure of the body wall of a single specimen was observed to document characteristics of the cuticle, epithelium and epidermal glandular system (Fig. 6). Externally, the monolayered epithelium (Fig. 6A) is bound by two cuticular layers, a thin exocuticle (Fig. 6D, F; also called the lamellar layer of Rieger & Rieger 1977) and thicker endocuticle (Fig. D, F; also called the basal layer of Rieger & Rieger 1977). The exocuticle appears to consist mostly of 1–2 electron-dense sheaths, each ca. 10 nm in thickness, though fixation was relatively poor and it is difficult to distinguish whether the sheets are constructed as monolayers or bilayers (see Rieger & Rieger 1977 for explanation). The exocuticle lines the dorsal, lateral and ventral epidermis including the anterior adhesive tubes (TbA), ventral locomotory cilia, and sensory cilia. Cross sections through individual cilia revealed only 1–2 exocuticular sheaths on most locomotory cilia, and more than one sheath on some sensory cilia. Poor fixation made it difficult to determine the maximum number of exocuticular sheaths on sensory cilia or along the general body wall; however, in some regions of the body, the exocuticle was up to 53 nm thick, indicating multiple exocuticular sheaths.

The underlying endocuticle is 100–510 nm thick and homogeneous in appearance, displaying only a granular texture (Fig. 6). The endocuticle varies in thickness across a cross section of the body: endocuticle lining the ventral epidermis is ca. 100–240 nm thick; endocuticle lining lateral body wall is 100–250 nm thick; and endocuticle lining the dorsal epidermis is 140–510 nm thick. In general, most of the body is covered by a thin endocuticle from 100–200 nm thick, but the endocuticle thickens in regions around the dorsal and lateral papillae and where electron-dense elements are located. Endocuticle at the base of an individual triangular papilla may reach 460 nm in thickness, but it quickly thins out toward the apical end of the papilla and appears more similar to the endocuticle that lines the general body wall. Dorsally, there are several electron-dense elements up 326 nm thick and 950 nm long that are embedded within the endocuticle, making the total endocuticule up to 510 nm thick. These elements have a homogeneuos, electron-dense apperance and are distinguishable from the rest of the endocuticle by their unique bicorn hat shape (Fig. 6B, D, E). The elements are not obviously associated with any papillae or sensory structures; however, serial sections were not examined.

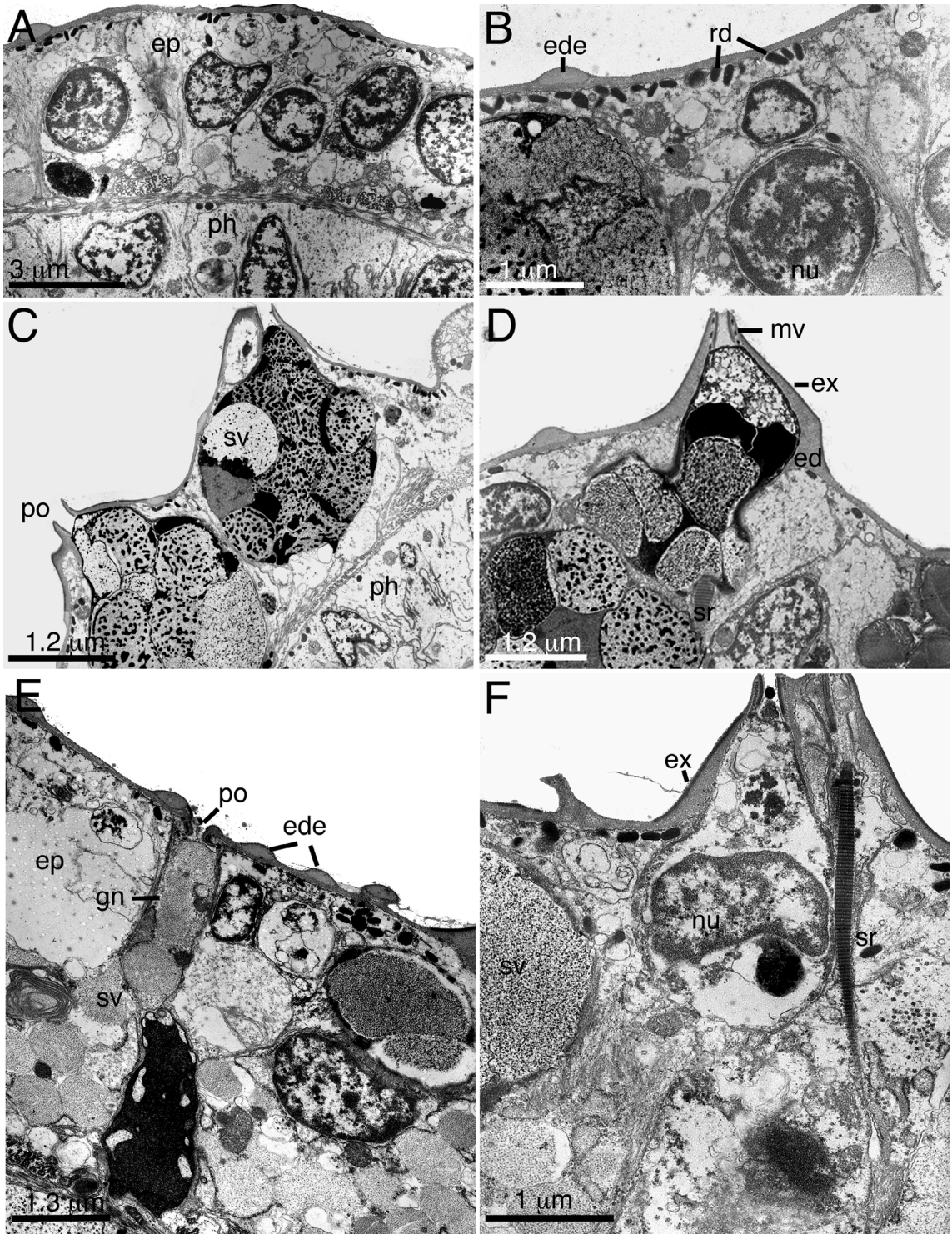

FIGURE 6. Ultrastructure of the bodywall of *Oregodasys katharinae* **sp. nov. A** Section through the dorsal epidermis (*ep*) at the level of the pharynx (*ph*). **B** Closeup of the apical region of the dorsal epidermis showing rod-like secretory inclusions (*rd*) below the plasma membrane. A single electron-dense element (*ede*) is present within the endocuticle. **C** Longitudinal section through two adjacent epidermal glands showing the apical pore (*po*) and numerous secretory vesicles (*sv*) with different staining characterstics. **D** Apical end of an epidermal gland showing the microvillar collar (*mv*) that forms the apical pore. The overlying exocuticle (*ex*) and endocuticle (ed) are generally thickest around the papillary glands. Note the presence of a portion of a striated rootlet (*sr*) at the base of the photograph. **E** Section through an insunk epidermal gland. Note the elongate gland neck (*gn*) between epidermal cells that leads to a small pore (*po*). Electron-dense elements are abundant in the endocuticle around insunk epidermal glands. **F** Longitudinal section through a portion of a papilla that contains two cell types: a porous cell with an apical opening and large nucleus (nu) on the left, and a sensory cell with a striated rootlet (sr) and apical cilium (out of the field of view) on the right.

The epidermis is cellular and monolayered. All cells are irregular in shape and contain a large nucleus, various-sized electron-lucent vesicles, few mitochondria, ER and Golgi (Fig. 6A). Adhearens junctions anchored most cells to each another; septate junctions were more common in the dorsal epidermis than the ventral epidermis. The dorsal epidermis contained abundant electron dense, rod-shaped secretions to 170 nm x 240 nm, present just below the plasma membrane (Fig. 6A, B). These secretions were present in all examined epidermal cells, but were less abundant in the lateral and ventral epidermis. Several dorsal epidermal cells contained dense tonofilaments that appeared to anchor the cells to the underlying basal lamina (not shown). These filaments were similar to filaments present in the anterior adhesive tubes, which are located on the ventral mouth margin (not shown). The adhesive tubes are duogland and contained at least one adhesive gland with large vesicles to 280 nm diameter (see Tyler & Rieger 1980 for detailed descriptions of the duogland system) and one releasing gland with small vesicles to 65 nm in diameter. The precise number of glands in each adhesive tube was not quantified because no cross sections were analyzed.

Scattered throughout the dorsal and dorsolateral epidermis were abundant epidermal gland cells (glandulocytes). Glandulocytes were associated with triangular papillae (Fig. 6C, D) or insunk into the epidermis (Fig. 6E). No sections were taken through the blunt-ended papillae. All gland cell perikarya are monocellular and flask shaped with a basal nucleus and voluminous secretory portion. Most glandulocytes were associated with a triangular papilla that extends above the epithelium and appears volcano-like in longitudinal section. The papilla itself is not formed of epidermal cells but instead is formed from an individual glandulocyte that is generally sandwiched between epidermal cells. The apical portion of the glandulocyte opens via a singular pore that is formed by microvillar extensions of the apical side of the glandulocyte (Fig. 6D). The opening of the pore is lined by both exo- and endocuticle (Fig. 6D). Membrane-bound secretion vesicles are present just below the pore (Fig. 6C, D). The bulk of the glandulocyte perikaryon is taken up by numerous membrane-bound secretion vesicles, all of which show irregular staining. Secretory vesicles range from ca. 300 nm–2 µm in diameter. Individual vesicles within a single glandulocyte may display a range of staining characteristics, including contents that appear as either electron dense, finely-granular, flocculent, or a range of all three within a single vesicle. Some vesicles are electron lucent but may contain wisps of flocculent material. There was no obvious difference between staining characteristics of vesicles in papillary versus insunk glandulocytes. The perikaryon of insunk glandulocytes was often positioned between and below the general epithelium, with the nucleus and other organelles pressed up against the basal lamina (Fig. 6E). Each glandulocyte presented an apical neck that extended up to 5 µm long between epidermal cells. The necks open to apical pores to 300 nm wide. No microvilli were observed at the apical end. The lip of the pore is formed from the bilayered cuticle, with both layers turning inward to line the pore. Electron-dense elements within the endocuticle were often, but not always, present in proximity to the apical pore of the insunk glandulocyte. In nearly all glandulocytes, most of the cellular organelles including the nucleus, mitochondria, ER and Golgi were compressed in the basal region of the glandulocyte. Several of the triangle-shaped papillae were in proximity to sensory cilia, and striated rootlets were regularly observed in cells adjacent to, but not necessarily part of, the papillae. One glandulocyte appeared to contain portions of a striated rootlet within the cell itself (Fig. 6D); unfortunately, serial sections of the glandulocyte were not analyzed. Longitudinal muscles and neurons were present beneath some, but not all of the glandulocytes.

Discussion

The first species of *Oregodasys* (formerly known as *Platydasys*, see Hummon 2008) described was *O. maximus* (Remane, 1927) from the North Sea. Since then, eleven species of *Oregodasys* have been described globally, of which ten species are known from the northern hemisphere: *O. ruber* (Swedmark, 1956), *O. tentaculatus* (Swedmark, 1956), *O. rarus* (Forneris, 1961), *O. mastigurus* (Clausen, 1965), *O. ocellatus* (Clausen, 1965), *O. phacellatus* (Clausen, 1965), *O. styliferus* (Boaden, 1965), *O. itoi* (Chang, Kubota & Shirayama, 2002), *O. kurnowensis* Hummon, 2008 and *O. cirratus* Rothe and Schmidt-Rhaesa, 2010. Only a single species is documented from the southern hemisphere, *O. pacificus* (Schmidt, 1974), which was

described from Santa Cruz in the Galapagos Islands. Species of *Oregodasys* are infrequent in littoral and sublittoral sediments and rarely abundant when present, but easily distinguished from other species of Thaumastodermatidae by the structure of their cuticle, which lacks scales or spines and is instead ornamented with papillae that overly a highly glandular epidermis. This study documents two new species of *Oregodasys* from the Caribbean, including an ultrastructural description of the bodywall of one new species, and is the first report of gastrotrichs from the barrier reef complex in Belize.

Two species of *Oregodasys* were found at various sublittoral sites off Carrie Bow Cay: *O. norenburgi* **sp. nov.** and *O. katharinae* **sp. nov.** Each species differs from its congeners with some respect to the quantity and distribution of adhesive tubes, presence or absence of sensory organs, and presence or absence of elongate cirri. Specifically, *O. norenburgi* **sp. nov.** differs from most species of *Oregodasys* by possessing paired red ocelli, which allies it with *O. ocellatus* and *O. ruber*, two species currently only known from more northern latitudes. However, *O. norenburgi* **sp. nov.** differs from *O. ocellatus* by lacking dorsolateral adhesive tubes and possessing a different quantity and distribution of lateral (TbL) and posterior (TbP) adhesive tubes. *O. norenburgi* **sp. nov.** differs from *O. ruber* by lacking paired head appendages and in the structure of the posterior end, which bears paired pedicles and several TbP that are absent in *O. ruber*.

The second new species, *O. katharinae*, is distinguished from six of the eleven described species by the presence of cirri, which are elongate, tube-like structures that project off the ventrolateral bodywall in the posterior body region. Cirri are often difficult to observe and generally bend medially beneath an animal's body. *O. katharinae* **sp. nov.** is allied with the five remaining species that possess cirri: *O. itoi*, *O. mastigurus*, *O. cirratus*, *O. pacificus* and *O. phacellatus*. Among these species, *O. cirratus* possesses cirri along the length of the body, and so differs from the condition present in *O. katharinae* **sp. nov.** and the remaining four species, where cirri are restricted to the posterior end. *O. katharinae* **sp. nov.** is broadly similar to all four species in the relative body shape and distribution of adhesive tubes, but can be distinguished from *O. mastigurus* and *O. phacellatus* by its smaller body size and restricted distribution of TbL to the posterior trunk region. Relative to *O. itoi*, the new species possess fewer TbVL in the trunk (30 TbVL in *O. katharinae* **sp. nov.** vs. 90 TbVL in *O. itoi*) and does not appear to possess the fringe of spiny processes on its posterior margin; however, this latter characteristic may only be observable with SEM (see Chang *et al.* 2002). *O. katharinae* **sp. nov.** differs further from *O. itoi* and possibly *O. pacificus* by possessing a clearly bipartite caudal organ, which has very distinct muscular and non-muscular portions (easily observed in both living and preserved type specimens). *O. katharinae* **sp. nov.** further differs from *O. pacificus* in the structure of the caudal end and in the possession of more ventral cirri (8 cirri per side in *O. katharinae* vs. 4–5 cirri per side in O. *pacificus*).

Ultrastructure of *O. katharinae* sp. nov. The ultrastructure of the body wall of *O. katharinae* **sp. nov.** was examined with electron microscopy to determine how it differs from other gastrotrichs with sculptured cuticles (Fig. 6; see also Rieger & Rieger 1977), and to gain preliminary insights into the structure of the epidermal glandular system. To date, only two species of *Oregodasys* have been examined with electron microscopy: *O. cirratus* was examined with scanning electron microscopy (SEM, Rothe & Schmidt-Rhaesa 2010) and an unidentified species was examined with transmission electron microscopy (TEM, Ruppert 1991:Fig. 54). My analyses with TEM on *O. katharinae* reveal that the body wall is broadly similar to previous descriptions. The new species has a relatively thin cuticle consisting of few exocuticular sheaths – probably up to 5 sheaths based on the maximum thickness of the exocuticular region (53 nm) and the general thickness of most individual sheaths (10 nm). This thickness fits well within Rieger and Rieger's (1977) range measured for other species of Thaumastodermatidae including species of *Tetranchyroderma* (10–50 nm) and *Diplodasys* (40–50 nm), and also characteristic of species with smooth cuticles (see Rieger and Rieger 1977, Table 1). The maximum thickness of the cuticle, including both exo- and endocuticular layers, in *O. katharinae* **sp. nov.** was 510 nm around areas that contained electron-dense elements. These elements are hat-shaped endocuticular thickenings (Fig. 6B, E); unfortunately, the plane of section did not allow for determination of their three-dimensional structure, so describing such thickenings as scales is premature. By comparison, SEM of the surface of *O. cirratus* by Rothe and Schmidt-Rhaesa (2010) revealed small protuberances scattered among the papillae that might have a similar ultrastructure as the thickenings in *O. katharinae* **sp. nov.** (see Fig. 3B, E of Rothe and Schmidt-Rhaesa 2010), but without more data on their fine

structure, they cannot be homologized. In general, the electron-dense elements of *O. katharinae* sp. nov. were abundant around insunk epidermal glands; however, they were not restricted to regions around these glandulocytes, so a functional connection cannot be assumed.

The bodywall epithelium of *O. katharinae* **sp. nov.** is similar to that observed in a range of other macrodasyidan gastrotrichs (see Rieger 1976; Ruppert 1991). One of the defining characteristics of species of *Oregodasys* is, however, the presence of papilla-like structures scattered across the epidermis. Many of these papillae are associated with epidermal glandulocytes and others appear to be strictly sensory (Fig. 6F). The sensory papillae of *O. katharinae* **sp. nov.** have a two-part structure: a flask-shaped cell with an external opening and an adjacent sensory cell with a striated rootlet and apical cilium. Both cells are closely associated with each other and form a singular elevated unit. Curiously, the flask-shaped cell is reminiscent of an epidermal glandulocyte but without any secretory vesicles as present in typical glandulocytes (described below). The entire structure is similar to some papillae described in *O. cirratus* by Rothe and Schmidt-Rhaesa (2010). In the latter species, papillae termed sensory papillae type 3 (see Fig. 3J, K of Rothe & Schmidt-Rhaesa 2010) are characterized by an elevated surface with a pore and a cilium. Two other types of sensory papillae occur in *O. cirratus*, but neither have an external opening. One might hypothesize that the lack of secretory vesicles in the flask-shaped cell, combined with its proximity to a monociliated cell, indicates that the entire papilla is itself sensory and not exocrine as is the case with the glandulocytes. In this case, the porous cell might function as an inlet for dissolved chemicals in the interstital waters.

In *O. katharinae*, there are also two types of papillae that are closely associated with epidermal glandulocytes, the triangular papillae and the blunt papillae. Based on TEM sections, the triangular papillae are actually formed from epidermal glandulocytes (Fig. 6C, D); unfortunately, no sections through the blunt papillae were observed, so it remains unknown if they are also secretory. Rothe and Schmidt-Rhaesa (2010) examined a related species, *O. cirratus*, and also found two types of papillae based on studies with SEM. One type of papilla, termed scale-like papillae (see Fig. 3I of Rothe and Schmidt-Rhaesa 2010), has a similar morphology and association with epidermal glands as the triangular papillae of *O. katharinae* **sp. nov.** The second type of papilla, termed papillae-like porus, is a much smaller papilla, but was not observed in *O. katharinae* **sp. nov.**, at least based on the limited TEM sections. Still, the new species does possess at least one type of insunk epidermal gland that may correspond to the papillae-like porus, but without the obvious elevated appearance (Fig. 6E). A fine structural account of the papillae in *O. cirratus*, with additional observations of *O. katharinae* **sp. nov.** will be required before any statements of homology can be made.

In terms of fine structure, there are limited details on gastrotrich glandulocytes. To date, only Teuchert (1977) has provided an account of epidermal glands in a gastrotrich (*Turbanella cornuta* Remane, 1925), with Ruppert (1991; Fig. 54) providing supplementary information based on observations of species of *Oregodasys*. Both accounts agree with the observations of *O. katharinae* **sp. nov.**: all glands are monocellular and flask-shaped, with a basal nucleus and large volume containing membrane-bound secretion vesicles. The secretion vesicles in both the insunk and papilla-associated glands of *O. katharinae* **sp. nov.** are similar to those described for other macrodasyidan gastrotrichs: vesicles are membrane-bound and contain a variety of substances that stain irregularly. The vesicles may be electron lucent or electron dense; the latter vesicles may have an entirely homogeneous appearance – as finely granular or as electron dense "ink spots" – or may be heterogeneous in staining quality. And while a comparative study of glands in different parts of the body was not made, a preliminary assessment would suggest that the irregularity in vesicle staining is probably uniform across the body, and may be indicative of different chemical contents within individual vesicles. Ruppert (1991) hypothesized that the contents might have a repugnatorial function, which would explain why species of *Oregodasys* possess a higher abundance of glandulocytes relative to other thaumastodermatid gastrotrichs (and species of other clades) – they lack the "standard" form of armored cuticle that might be a deterrent to predators.

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