**Diopatra tuberculantennata**, a new species of Onuphidae (Polychaeta) from Belize with a key to onuphids from the Caribbean Sea

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**Abstract**

A new species of the genus *Diopatra* Audouin & Milne-Edwards, 1833 from the intertidal zone in the vicinity of the Smithsonian field station (Carrie Bow Cay, Belize) is described. *Diopatra tuberculantennata* sp. nov. is identifiable by a combination of characters such as the presence of large lateral projections on both palpophores and antennophores, bidentate pseudocompound hooks with moderately long pointed hoods in the first five chaetigers, eyespots on the prostomium, mouch organs forming almost a circle and very large sensory papillae on antennostyles and frontal and upper lips. Five 28-chaetiger juveniles were found inside the parental tube of one specimen. A pattern of anterior segment regeneration is described based on 12 specimens. A key for 20 species of onuphids known from the Caribbean Sea with the notes on their distribution is provided.

**Key words:** diversity; taxonomy; juveniles; regeneration; distribution

**Introduction**

*Diopatra cuprea* (Bosc, 1802) was the only species of *Diopatra* reported by Fauchald (1980) from Belize. The species was found in the vicinity of Carrie Bow Cay (Smithsonian Institution’s Caribbean Coral Reef Ecosystems (CCRE) program) and near Colson’s Point, both in Dangriga district (Fig. 1). Fauchald’s and Meredith L. Jones’ material from Belize demonstrated some differences from the original description of *D. cuprea* mostly in size and color pattern. Specimens that were obtained near the shoreline comply with the descriptions of *D. cuprea*. However, specimens collected in coral reefs and fresh material collected at Carrie Bow Cay and three neighboring islands in November 2006 are obviously different from *D. cuprea* and are here described as a new species.

*Diopatra* contains approximately 50 species, widely distributed around the world, but typically inhabiting warm shallow waters. Although *Diopatra* has been historically clearly recognized by the presence of the spiraled branchiae and the peristomial cirri, the species of *Diopatra* demonstrate a wide range of intraspecific variability, and often lack distinct diagnostic characters (Paxton 1993; 2002). *Diopatra* species from Australia, Thailand, and complex of species frequently identified as *D. chilensis* were recently revised by Paxton (1993; 1998; 2002).

The new species differs from *D. cuprea* by the presence of large lateral projections on both palpophores and ceratophores. Three other species of *Diopatra* have similar projections on prostomial appendages and are compared to the new species below.

Twenty species of onuphids are presently recorded from the intertidal zone to bathyal depths of the Carib-
bean Sea. The most complete lists of Caribbean onuphids were published by Kiseleva (1968) and Fauchald (1980); a complete key has never been provided for the region. Here we present a key with notes on the geographical distribution of all onuphids currently known from the Caribbean basin based on literature and on material collected from Carrie Bow Cay and vicinity present in the collections of the National Museum of Natural History, Smithsonian Institution.

Material and methods

The specimens were shovel-sampled at 0.3–1.5 m depths. The obtained sediment was sieved through the 0.5 mm mesh size screen, and tubes with worms were handpicked and fixed in filtered 4% formalin in sea water and after 2–3 days transferred into 70% ethanol. The holotype and 15 paratypes of the new species are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Comparative material examined was borrowed from the Zoological Museum, University of Copenhagen (ZMUC) and the Natural History Museum, London (BMNH). Line drawings were made for the holotype (dorsal and ventral views) and paratypes (parapodia, jaws and chaetae).

For scanning electron microscopy (SEM), specimens stored in 70% ethanol were run through 75%, 95%, 100%, 100% ethanol, 10 minutes in each step, and critical point dried in a Balzers CPD-030 critical point dryer using ethanol as the transition fluid. After drying, specimens were sputter coated with 20–30 nm of gold:palladium alloy 60:40 wt % in a Cressington Scientific 108 sputter coater. SEM micrographs were taken in a Leica Stereoscan 440 SEM with a lanthanum hexaboride electron source. Terminology for prostomial appendages follows Paxton (1998).

Diopatra tuberculatennata, new species

Figs. 1–7


Type material: USNM 1112433, St. CBC-2006-34 (holotype); USNM 1112434, St. CBC-2006-31 (6 paratypes); USNM 1112435, St. CBC-2006-32 (1 paratype); USNM 1112436, St. CBC-2006-34 (1 paratype); USNM 1112437, St. CBC-2006-39 (1 paratype); USNM 1112438, St. CBC-2006-41 (3 paratypes); USNM 1112439, St. CBC-2006-43 (3 paratypes).

Non type material examined: USNM 61213, St. CB-01 (2); USNM 61214, St. CB-02 (1); USNM 61215, St. CB-06 (1); USNM 61216, St. CB-11 (1); USNM 61217, CB-16 (1); USNM 61218, St. CB-28 (2); USNM 61219, St. CB-34 (2); USNM 61223, St. CBC-F-28 (1); USNM 61222, St. CBC-F-09 (1); USNM 1112440, St. CBC-2006-01 (1); USNM 1112441, St. CBC-2006-03 (1); USNM 1112442, St. CBC-2006-05 (1); USNM 1112443, St. CBC-2006-07 (1); USNM 1112444, St. CBC-2006-10 (1);USNM 1112445, St. CBC-2006-11 (1); USNM 1112446, St. CBC-2006-12 (1); USNM 1112447, St. CBC-2006-13 (1); USNM 1112448, St. CBC-2006-16 (1); USNM 1112449, St. CBC-2006-17 (1); USNM 1112450, St. CBC-2006-21 (2); USNM 1112451, St. CBC-2006-23 (3); USNM 1112452, St. CBC-2006-26 (1); USNM 1112453, St. CBC-2006-28 (1); USNM 1112454, St. CBC-2006-29 (1); USNM 1112455, St. CBC-2006-31 (23); USNM 1112456, St. CBC-2006-32 (2); USNM 1112457, St. CBC-2006-37 (1); USNM 1112458, St. CBC-2006-39 (1); USNM 1112459, St. CBC-2006-41 (4); USNM 1112460, St. CBC-2006-43 (3); USNM 1112461, St. CBC-2006-51 (1); USNM 1112462, St. CBC-2006-52 (3).


**Type locality:** Belize, Carrie Bow Cay, 16.8027° N, 88.0819° W, 0.5 m. Coordinates of all stations are given in Table 1, map of stations is shown in Figure 1.

**FIGURE 1.** Distribution of *Diopatra tuberculatennata* sp. nov.
### TABLE 1. Station list.

<table>
<thead>
<tr>
<th>Station</th>
<th>Locality</th>
<th>Biotope</th>
<th>Latitude °N</th>
<th>Longitude °W</th>
<th>Dept h, m</th>
<th>Date</th>
<th>Collector</th>
</tr>
</thead>
<tbody>
<tr>
<td>CB-01</td>
<td>Carrie Bow Cay</td>
<td>sparse Thalassia, just west of island</td>
<td>16.8027</td>
<td>88.0819</td>
<td>1</td>
<td>04.04.1976</td>
<td>Jones, M.L.</td>
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<tr>
<td>CB-02</td>
<td>Carrie Bow Cay</td>
<td>north-west of island, general transect from bare sand area to coral rubble</td>
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<td>88.0819</td>
<td>1.5</td>
<td>05.04.1976</td>
<td>Jones, M.L.</td>
</tr>
<tr>
<td>CB-06</td>
<td>Carrie Bow Cay</td>
<td>sandy areas at top of intertidal around island</td>
<td>16.8027</td>
<td>88.0819</td>
<td>0.3</td>
<td>06.04.1976</td>
<td>Jones, M.L.</td>
</tr>
<tr>
<td>CB-11</td>
<td>Carrie Bow Cay</td>
<td>100 m NNE of island, associated with Acropora curvicornis rubble</td>
<td>16.8027</td>
<td>88.0819</td>
<td>0.7</td>
<td>07.04.1976</td>
<td>Jones, M.L.</td>
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<tr>
<td>CB-16</td>
<td>Carrie Bow Cay</td>
<td>sparse Thalassia, just west of island</td>
<td>16.8027</td>
<td>88.0819</td>
<td>1.5</td>
<td>11.05.1977</td>
<td>Jones, M.L.</td>
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<tr>
<td>CB-28</td>
<td>Carrie Bow Cay</td>
<td>north-west of island, Thalassia and coarse sand</td>
<td>16.8027</td>
<td>88.0819</td>
<td>1.5</td>
<td>13.05.1977</td>
<td>Jones, M.L.</td>
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<td>CB-34</td>
<td>Carrie Bow Cay</td>
<td>100 m north of island</td>
<td>16.8027</td>
<td>88.0819</td>
<td>1.5</td>
<td>14.05.1977</td>
<td>Jones, M.L.</td>
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<td>CBC-F-28</td>
<td>Carrie Bow Cay</td>
<td>east of island, about 60 feet from shore, Thalassia and sand</td>
<td>16.8027</td>
<td>88.0819</td>
<td>0.5</td>
<td>04.11.1977</td>
<td>Fauchald, K.</td>
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<tr>
<td>CBC-F-09</td>
<td>Carrie Bow Cay</td>
<td>north of island, sand and small rubble</td>
<td>16.8027</td>
<td>88.0819</td>
<td>0.6</td>
<td>12.04.1979</td>
<td>Fauchald, K.</td>
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<td>Budaeva, N.</td>
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<td>88.0819</td>
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<td>Budaeva, N.</td>
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<td>88.0819</td>
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<td>Budaeva, N.</td>
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<td>88.0819</td>
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<td>4.11.2006</td>
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<td>north-east of island, Thalassia and sand</td>
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<td>88.0819</td>
<td>1</td>
<td>4.11.2006</td>
<td>Budaeva, N.</td>
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<td>north-east of island, Thalassia and sand</td>
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<td>88.0819</td>
<td>0.5</td>
<td>5.11.2006</td>
<td>Budaeva, N.</td>
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<td>CBC-2006-13</td>
<td>Carrie Bow Cay</td>
<td>north-east of island, Thalassia and sand</td>
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<td>88.0819</td>
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<td>5.11.2006</td>
<td>Budaeva, N.</td>
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<tr>
<td>CBC-2006-16</td>
<td>Carrie Bow Cay</td>
<td>north-west of island, near berth, Thalassia and sand</td>
<td>16.8027</td>
<td>88.0819</td>
<td>1</td>
<td>6.11.2006</td>
<td>Budaeva, N.</td>
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<td>CBC-2006-17</td>
<td>Carrie Bow Cay</td>
<td>north-west of island, near berth, Thalassia and sand</td>
<td>16.8027</td>
<td>88.0819</td>
<td>1</td>
<td>6.11.2006</td>
<td>Budaeva, N.</td>
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<td>CBC-2006-21</td>
<td>Carrie Bow Cay</td>
<td>west of island, Thalassia and sand</td>
<td>16.8027</td>
<td>88.0819</td>
<td>1</td>
<td>6.11.2006</td>
<td>Budaeva, N.</td>
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<tr>
<td>CBC-2006-23</td>
<td>Carrie Bow Cay</td>
<td>east of island, Thalassia and sand</td>
<td>16.8027</td>
<td>88.0819</td>
<td>0.3</td>
<td>6.11.2006</td>
<td>Budaeva, N.</td>
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<tr>
<td>CBC-2006-26</td>
<td>Cat Cay</td>
<td>border between sand and Thalassia</td>
<td>16.6714</td>
<td>88.1990</td>
<td>0.5</td>
<td>7.11.2006</td>
<td>Budaeva, N.</td>
</tr>
<tr>
<td>CBC-2006-28</td>
<td>Cat Cay</td>
<td>border between sand and Thalassia</td>
<td>16.6714</td>
<td>88.1990</td>
<td>0.5</td>
<td>7.11.2006</td>
<td>Budaeva, N.</td>
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<td>CBC-2006-29</td>
<td>Cat Cay</td>
<td>border between sand and Thalassia</td>
<td>16.6714</td>
<td>88.1990</td>
<td>0.5</td>
<td>7.11.2006</td>
<td>Budaeva, N.</td>
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<td>CBC-2006-31</td>
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<td>border between sand and Thalassia</td>
<td>16.6714</td>
<td>88.1990</td>
<td>0.5</td>
<td>7.11.2006</td>
<td>Budaeva, N.</td>
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<td>CBC-2006-32</td>
<td>Carrie Bow Cay</td>
<td>west of island, Thalassia and sand</td>
<td>16.8027</td>
<td>88.0819</td>
<td>0.7</td>
<td>8.11.2006</td>
<td>Budaeva, N.</td>
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<td>CBC-2006-34</td>
<td>Carrie Bow Cay</td>
<td>east of island, Thalassia and sand</td>
<td>16.8027</td>
<td>88.0819</td>
<td>0.5</td>
<td>8.11.2006</td>
<td>Budaeva, N.</td>
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<tr>
<td>CBC-2006-37</td>
<td>South Water Cay</td>
<td>south of island, coarse sand, Thalassia and sand</td>
<td>16.8133</td>
<td>88.0834</td>
<td>0.3</td>
<td>9.11.2006</td>
<td>Budaeva, N.</td>
</tr>
<tr>
<td>CBC-2006-41</td>
<td>Twin Cays</td>
<td>North point, inside Thalassia bed, sand and peat</td>
<td>16.8346</td>
<td>88.1044</td>
<td>0.7</td>
<td>9.11.2006</td>
<td>Budaeva, N.</td>
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<tr>
<td>CBC-2006-43</td>
<td>South Water Cay</td>
<td>north of island, coarse sand and mud, Thalassia</td>
<td>16.8189</td>
<td>88.0814</td>
<td>0.7</td>
<td>11.11.2006</td>
<td>Budaeva, N.</td>
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<tr>
<td>CBC-2006-51</td>
<td>Ragged Cay</td>
<td>north-west side of nothern island, Thalassia, sand, mud</td>
<td>16.8535</td>
<td>88.1289</td>
<td>0.5</td>
<td>12.11.2006</td>
<td>Budaeva, N.</td>
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<tr>
<td>CBC-2006-52</td>
<td>Sand Bores between Carrie Bow Cay and Wee Wee Cay</td>
<td>&quot;open sea&quot;, coarse sand</td>
<td>16.7719</td>
<td>88.1114</td>
<td>1.5</td>
<td>13.11.2006</td>
<td>Budaeva, N.</td>
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</table>
Diagnosis: Palpophores and antennophores with large lateral projections on median rings; first five chaetigers with bidentate pseudocompound hooks; hoods moderately long and pointed; nuchal organs forming almost closed circles; very large sensory papillae irregularly distributed on antennostyles and on frontal, upper and lower lips.

Description: Holotype complete specimen with 93 chaetigers, 43 mm long, 1.3 mm wide (at chaetiger 10, without parapodia) (Fig. 2A–C). Complete specimens range from 0.6 mm width (41 chaetiger) to 1.3 mm width (93 chaetigers). The greatest width of incomplete specimen is 2 mm. Anterior end of body including first five chaetigers cylindrical, median and posterior parts of body dorsally flattened. Living specimens white dorsally, light rose-colored laterally and ventrally with scattered small brown spots, similar spots also on antennae and palps. Brown band across chaetiger 5 (retained in most of preserved specimens). Some ethanol-stored specimens with brown pigmentation dorsally in branchial region and brown antennae, in most cases of the same color as body pigmentation. Staining with Methylene Blue yielding following, distinct patterns: Each chaetiger in posterior 1/3 of body with wide, dark blue dorsal and ventral glandular cross-bands. Dorsal cirri, frontal, upper and lower lips and palpostyles also staining dark blue; remaining body pale blue.

Prostomium with subulate frontal lips (Figs. 2A, 3A, K). Upper lips elongate; lower lip with median incision. Palps of holotype reaching chaetiger 2, varying in other specimens from chaetigers 1–3. All antennae about equal in length, reaching chaetiger 7 in holotype; in other specimens reaching chaetigers 4–13. Length of antennae quite variable, slightly depending on size of specimen (Fig. 4). Palpophores of holotype with five rings; other specimens with up to six rings. Antennophores of holotype with eight rings, other specimens with 4–8 rings. Both palpophores and antennophores with large lateral projections on median rings (Figs. 2A, B, 3A). Palpophore projections usually on second ring, rarely on third. Second and third ring of holotype lateral antennophores with projections, in other specimens on second to fourth ring. Projections of median antennophore on second to fourth rings in holotype; in other specimens projections present from first to fifth rings. Palps, antennae, frontal, upper lips and anterior margin of lower lip covered by randomly distributed large sensory papillae (Fig. 3B–D, K). Nuchal grooves curved, forming nearly circle in adults (Fig. 2B). One pair of small brown eyespots present near base of lateral antennae. Peristomium as long as first chaetiger. Peristomial cirri about as long as peristomium.

First five parapodia projecting laterally, directing slightly anteriorly but not enlarged. More posterior parapodia similar; ridge-shaped and located laterally. Prechaetal lobes rounded, postchaetal lobes a low ridge covering bases of chaetae, but with distinct median subulate projection, gradually decreasing in size towards posterior region but still distinct at posterior end of the body (Fig. 3L, M). First five chaetigers with small ventral protrusions at base of postchaetal lobes (Fig. 2F). Ventral cirri cirriform on first five chaetigers in holotype (Fig. 2A), in other specimens varying between four and five chaetigers (Fig. 3F), apparently almost independently of size of specimen (Fig. 5).

Anterior projecting parapodia (Figs. 2F, 3M) with 1–2 upper simple chaetae and 4–5 bidentate pseudocompound hooks (Figs. 2N, 3H). Hooks with moderately long pointed hoods and two rows of blunt small spines along their shafts. Remaining parapodia with mainly strongly serrated limbate chaetae (Figs. 2O, 3E). Pectinate chaetae are flat with straight distal margins, each has 18–20 teeth. Pectinate chaetae from chaetiger 6 in holotype, from chaetigers 5–6 in other specimens (Figs. 2L, 3I), one unusual specimen had pectinate chaeta with very long teeth in second parapodia (Figs. 2M, 3J). Starting from chaetiger 9 in holotype, and from chaetigers 7–12 in other specimens, lower limbate chaetae replaced by thick bidentate subacular hooks (Fig. 2G, H, J, K) with very thin translucent guards. Start of subacular hooks slightly positively linked to increasing size of specimens (Fig. 5).

Branchiae with up to five spiraled whorls of relatively short filaments (Fig. 2H, I) starting from chaetiger 5 (Figs. 2B, 3G) and continuing to chaetiger 34 in holotype, varying from chaetigers 14–37 in other specimens. Position of the last branchia strongly correlated with width of specimen (Fig. 5). Best developed branchiae present on chaetigers 6–7; branchiae becoming gradually reduced towards posterior chaetigers, but almost all branchiae with several filaments; only last 1–2 pairs single.
FIGURE 2. *Diopatra tubercul antennata* sp. nov: A, anterior end, ventral view; B, anterior end, dorsal view; C, pygidium, ventral view; D, maxillae; E, mandibles; F, parapodium of chaetiger 1, anterior view; G, parapodium of chaetiger 40, anterior view; H, parapodium of chaetiger 25, anterior view; I, parapodium of chaetiger 5, anterior view; J, subacicular hook from chaetiger 25; K, subacicular hook from chaetiger 40; L, pectinate chaeta from chaetiger 12; M, pectinate chaeta from chaetiger 2; N, pseudocompound hooded hook from chaetiger 2; O, serrated limbate seta from chaetiger 12.
Mandibles weakly sclerotized with calcareous distal cutting plates (Fig. 2E). Distal indistinct indentations along edge of cutting plates present. Sclerotization of maxillae invisible, appearing white, thick and calcareous (Fig. 2D). Maxillary formula (based on five specimens): Mx I = 1 + 1; Mx II = 8–9 + 9–10; Mx III = 7–8 + 0; Mx IV = 6–7 + 7–9; Mx V = 1 + 1.

Pygidium with four anal cirri, ventral longer than dorsal ones (Fig. 2C). Tube, as characteristic for Diopatra, cylindrical and covered with debris, mostly parts of sea grass and pieces of shells attached on all sides of tube; permanently buried part of tube thin-walled and covered by fine sand.

Intraspecific variability of the main morphological characters shown in Table 2.
TABLE 2. Intraspecific variability of the main morphological characters of *Diopatra tuberculantennata* sp. nov.

<table>
<thead>
<tr>
<th>Character</th>
<th>Range</th>
<th>Mean</th>
<th>SD</th>
<th>N</th>
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<tr>
<td>Lateral antennae reach chaetiger</td>
<td>4–13</td>
<td>8.06</td>
<td>2.01</td>
<td>54</td>
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<tr>
<td>Median antenna reaches chaetiger</td>
<td>1–11</td>
<td>7.57</td>
<td>2.09</td>
<td>51</td>
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<tr>
<td>Maximal number of rings on ceratophores</td>
<td>4–8</td>
<td>5.71</td>
<td>0.74</td>
<td>55</td>
</tr>
<tr>
<td>Branchiae start from chaetiger</td>
<td>5</td>
<td>invariant</td>
<td></td>
<td>57</td>
</tr>
<tr>
<td>Branchiae end on chaetiger</td>
<td>14–37</td>
<td>28.31</td>
<td>5.60</td>
<td>45</td>
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<tr>
<td>Number of chaetigers with pseudocompound hooks</td>
<td>5</td>
<td>invariant</td>
<td></td>
<td>57</td>
</tr>
<tr>
<td>Number of chaetigers with cirriform ventral cirri</td>
<td>4–5</td>
<td>4.38</td>
<td>0.49</td>
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<tr>
<td>Subacicular hooks start from chaetiger</td>
<td>7–12</td>
<td>9.33</td>
<td>0.78</td>
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<tr>
<td>Number of chaetigers (complete specimens)</td>
<td>41–93</td>
<td>66.00</td>
<td>0.28</td>
<td>17</td>
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<tr>
<td>Width (at chaetiger 10), mm</td>
<td>0.6–2</td>
<td>1.18</td>
<td>0.33</td>
<td>49</td>
</tr>
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</table>

**FIGURE 4.** *Diopatra tuberculantennata* sp. nov.: relationship between body width (chaetiger 10, without parapodia) and length of antennae.

**Remarks:** *Diopatra dubia* Day, 1960, *D. papillata* Fauchald, 1968 and *D. angolensis* Kirkegaard, 1988 are the three other species in the genus known to have lateral projections on the ceratophores (Tab. 3). The new species can be distinguished from the other species by having scattered large sensory papillae on all styles of the prostomial appendages, frontal and upper lips. *Diopatra tuberculantennata* differs from *D. dubia* in having subulate frontal lips instead of partly fused spade-shaped ones; the nuchal grooves form almost a circle instead of being crescentic; the antennae are relatively longer, reaching chaetiger 8 instead of chaetigers...
2–3; the pseudocompound hooks have moderately long, pointed hoods on the first five chaetigers instead of having hooks with very long hoods in the first four chaetigers, and in having, rather than lacking eyes. From *D. angolensis*, *D. tuberculantennata* can be distinguished by the size and distribution of the lateral projections on the ceratophores. *Diopatra angolensis* has very small lateral projections on the three basal rings of the antennophores, while *D. tuberculantennata* has large projections on the median rings on both antennophores and palpophores; the basal rings of the ceratophores are always smooth. In addition, *D. tuberculantennata* has fewer branchial chaetigers (not more than 32 instead of 55) and the subacicular hooks start from chaetiger 9 (7–12) rather than from chaetiger 13 (14). *Diopatra angolensis* has long hoods on the anterior pseudocompound hooks instead of the moderate ones present in *D. tuberculantennata*. From *D. papillata*, *D. tuberculantennata* differs in having five anterior chaetigers with pseudocompound hooded hooks instead of three such chaetigers.

**TABLE 3.** Comparison of *Diopatra tuberculantennata* sp. nov. with *D. dubia*, *D. papillata* and *D. angolensis*.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Frontal lips</td>
<td>spade-shaped, fused</td>
<td>subulate</td>
<td>subulate</td>
<td>subulate</td>
</tr>
<tr>
<td>Eyes</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>Shape of nuchal grooves</td>
<td>crestentic</td>
<td>no data</td>
<td>forming nearly circle</td>
<td>forming nearly circle</td>
</tr>
<tr>
<td>Size of sensory papillae</td>
<td>small</td>
<td>?</td>
<td>small</td>
<td>large</td>
</tr>
<tr>
<td>Number of rings on ceratophores</td>
<td>4–5</td>
<td>5–6 (rarely 7 on median antenna)</td>
<td>7–8</td>
<td>6 (4–8)</td>
</tr>
<tr>
<td>Lateral projections on antennophores</td>
<td>present</td>
<td>present</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Lateral projections on palpophores</td>
<td>present</td>
<td>absent</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>Size of lateral projections</td>
<td>large</td>
<td>large</td>
<td>small</td>
<td>large</td>
</tr>
<tr>
<td>Length of antennae</td>
<td>up to chaetigers 1–2</td>
<td>up to chaetiger 9</td>
<td>up to chaetigers 12–14</td>
<td>up to chaetiger 13</td>
</tr>
<tr>
<td>Start of branchiae</td>
<td>5 (4–6)</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>End of branchiae</td>
<td>28 (25–33)</td>
<td>35</td>
<td>60</td>
<td>28 (14–37)</td>
</tr>
<tr>
<td>Number of chaetigers with pseudocompound hooks</td>
<td>4 (invariant)</td>
<td>3 (invariant)</td>
<td>5 (invariant)</td>
<td>5 (invariant)</td>
</tr>
<tr>
<td>Hoods on pseudocompound hooks</td>
<td>long, pointed</td>
<td>moderately long, pointed</td>
<td>long, pointed</td>
<td>moderately long, pointed</td>
</tr>
<tr>
<td>Start of subacicular hooks</td>
<td>9 (10–11)</td>
<td>10</td>
<td>13</td>
<td>9 (7–12)</td>
</tr>
<tr>
<td>Number of chaetigers with cirriform ventral cirri</td>
<td>3–4</td>
<td>4</td>
<td>4</td>
<td>4–5</td>
</tr>
<tr>
<td>Number of examined specimens</td>
<td>2 paratypes + 9</td>
<td>literature data</td>
<td>holotype</td>
<td>50 (including holotype and 15 paratypes)</td>
</tr>
<tr>
<td>Locality</td>
<td>off South West Africa</td>
<td>upper end of the Gulf of California</td>
<td>off South West Africa, Angola</td>
<td>Belize, east of Dangriga</td>
</tr>
<tr>
<td>Depth, m</td>
<td>50–412</td>
<td>73–110</td>
<td>27–75</td>
<td>0–2</td>
</tr>
</tbody>
</table>

**Biological notes:** Five 28-chaetiger juveniles about 3 mm long and 0.3 mm wide were found inside the parental tube of one specimen (Fig. 6A, B). All juveniles have well developed prostomial appendages with sensory papillae (Fig. 6C, H). Antennophores have 3–4 rings with small lateral projections. Palpophores have 3 rings with tiny projections on the middle rings (Fig. 6D, E, G). Nuchal grooves are slightly crescentic (Fig. 6G, I). Distribution of chaetae is the same as in adults except that the pseudocompound hooded hooks are
present on first four rather than on five chaetigers as in the adults (Fig. 6F). Peristomial cirri are present. Pro-
visional larval chaetae are absent. Spiraled branchiae with up to four filaments start from chaetiger 5 and are 
present on six chaetigers.

The complete development from egg to 40-chaetiger larva has been described for only one member of the 
genus Diopatra, D. marocensis Paxton et al., 1995 (Fadlaoui et al. 1995). As D. marocensis, D. tuberculante-
nata broods larvae and juveniles, with direct development inside the parental tube and thus belongs to 
group I designated by Paxton (1993). Although 28-chaetiger juveniles of D. marocensis are slightly larger 
(width: 0.49 mm, length: 4 mm), they represent an earlier stage of development than in the new species in that 
provisional chaetae are still present, peristomial cirri are absent and branchiae appear only on two chaetigers. 
This difference could be related to differences in a brood size. Size of adults is relatively similar in the two 
species but brood size of D. marocensis is 20–100 (Fadlaoui et al. 1995) whereas we found only 5 juveniles 
inside the tube of D. tuberculantennata.

Twelve specimens with regenerating anterior ends of the body were found in the examined material. 
Together they represent five consecutive stages of regeneration (Fig. 7). Different stages were recognized

FIGURE 5. Diopatra tuberculantennata sp. nov.: relationship between body width (chaetiger 10, without parapodia) 
and number of chaetigers, end of branchiae, start of subacicular hooks and number of cirriform ventral cirri.

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based on degree of development of regenerated part of the body, e.g. number of chaetigers and presence of chaetae.

Stage I: Short round prostomium with antennae represented by five tubercles and mouth aperture starting to form on the anterior end (where the worm was cut, Fig. 7A, B, I).

Stage II: Regenerating anterior end starting to differentiate ventrally into prostomium, peristomial ring and four chaetigers with parapodia visible as ventro-lateral bulges; prostomial appendages increasing in

**FIGURE 6.** *Diopatra tuberculatennata* sp. nov., juvenile: A, dorso-lateral view (scale 200 µm); B, ventral view (scale 200 µm); C, distal end of lateral antennostyle (scale 10 µm); D, anterior part of the body, dorsal view (scale 200 µm); E, prostomium, frontal view (scale 200 µm); F, parapodium of chaetiger 2, lateral view (scale 20 µm); G, prostomium, dorsal view (scale 100 µm); H, enlarged sensory papilla (scale 2 µm); I, nuchal groove (scale 20 µm); (br) branchia, (dc) dorsal cirrus, (fl) frontal lip, (la) lateral antenna, (lp) lateral projection of ceratophore, (ma) median antenna, (ng) nuchal groove, (p) palp, (pc) peristomial cirrus, (pg) pygidium, (ph) pseudocompound hook, (sp) sensory papilla, (ul) upper lip, (vc) ventral cirrus.
length to form five short cylindrical bosses; mouth aperture increasing in size, triangular in shape; frontal lips appear as two weakly developed, but distinct expansions (Fig. 7C, D, J).

**FIGURE 7.** Regeneration of *Diopatra tuberculatennata* sp. nov.: Stage I – A, anterior part of the body, frontal view (scale 200 µm); B, prostomium, lateral view (scale 100 µm); I, mouth aperture (scale 10 µm); Stage II – C, dorsal view (scale 100 µm); D, ventral view (scale 100 µm); J, mouth aperture (scale 20 µm); Stage III – G, ventral view (scale 100 µm); H, frontal view (scale 100 µm); Stage IV – K, ventral view (scale 100 µm); L, dorso-lateral view (scale 100 µm); M, parapodium of chaetiger 1 (scale 20 µm); E, provisional curved chaeta from chaetiger 1 (scale 10 µm); Stage V – N, lateral view (scale 200 µm); O, nuchal groove (scale 20 µm); F, pseudocompound hooded hooks from chaetiger 2 (scale 20 µm); (br) branchia, (cht) chaetiger, (cph) ceratophore, (dc) dorsal cirrus, (fl) frontal lip, (la) lateral antenna, (ll) lower lip, (lp) lateral projection of ceratophore, (ma) median antenna, (map) mouth aperture, (ng) nuchal groove, (p) palp, (pc) peristomial cirrus, (pcht) provisional chaeta, (per) peristomium, (pr) prostomium, (ul) upper lip, (vc) ventral cirrus.
Stage III: Prostomium, peristomium and five chaetigers distinctly separated from each other; prostomial appendages becoming conical with two-ringed ceratophores and sensory papillae present on palpostyles and antennostyles; frontal lips appear as hemispherical tubercles; upper lips forming two well separated spherical structures, lower lip present as a fold behind upper lips; nuchal grooves visible as thin almost straight lines widely separated middorsally; peristomial cirri absent; parapodia are trilobate without chaetae, gradually decreasing in size towards the posterior end of the regenerating part (Fig. 7G, H).

Stage IV: Segmentation more marked, but border between prostomium and peristomium on the dorsal side still absent. All prostomial styles longer and covered by well developed sensory papillae; ceratophores have three rings; frontal lips becoming more elongate; lower lip still not separated from peristomium; nuchal grooves becoming more curved and thicker; peristomial cirri visible as bulges on the dorsal side; first 1–3 curved chaetae, resembling provisional chaetae of *D. marocensis* (Fadlaoui *et al.* 1995), appear in anterior parapodia of regenerating part (Fig. 7E, K–M).

Stage V: Segmentation is well developed, prostomium, peristomium and seven following chaetigers are separated from each other; all prostomial structures are present and have shape closely similar to the normal condition, but width of regenerating part only about 1/2 the width of the normal segments of the non-regenerating body; each antennophore has four rings with small lateral projections on the second and third rings; lower lip is distinct, nuchal grooves are crescentic, wide straps; eyespots are present; spiraled branchiae with up to 4 filaments appear starting from chaetiger five; ventral cirri cirriform on first four chaetigers; pseudocompound bidentate hooded hooks present in first four chaetigers (Fig. 7F, N, O).

The consecutive stages of regeneration imitate the ontogenesis in the genus *Diopatra*, but with some interesting differences. In the development of *D. marocensis* palpostyles and antennostyles form first, followed by the frontal lips. Peristomial cirri appear at a very late (more than 38-chaetiger) stage when juveniles leave the parental tubes (Fadlaoui *et al.* 1995). A similar pattern of development of the prostomium and peristomium was shown in the present study. Provisional curved chaetae that are characteristic of all *Diopatra* larvae were found in the first and second chaetigers of a regenerating specimen (stage IV). At stage V the provisional chaetae were replaced by pseudocompound hooded hooks. The early appearance of segmentation and chaetae in ontogenesis, rather than early development of prostomial appendages is the main difference between ontogenesis and regeneration.

The ability to regenerate the anterior part of the body has been described in onuphids but only for three species from the genus *Diopatra*: *D. amboinensis* Audouin et Milne-Edwards, 1833 (Pflugfelder 1929 in Hyman 1940); *D. dextrignatha* Paxton & Bailey-Brock, 1986 (Bailey-Brock 1984 as *D. leuckarti* Kinberg, 1865; Paxton & Bailey-Brock 1986) and *D. neapolitana* (Delle Chiaje, 1841) (Conti, unpublished data in Bely 2006; see full review in Bely 2006).

The current species shows an ability to develop a new prostomium, peristomium and several chaetigers even in a case when more than 9-10 anterior chaetigers had been lost: We found regenerating specimens with subacicular hooks that normally start from chaetiger 9 in the first to the fourth chaetiger.

Although posterior segment regeneration is very common among polychaetes (Bely 2006) we did not find specimens showing this state in our material.

**Distribution:** Caribbean Sea, East off Dangriga, Belize. Depth 0.5–2 m. Usually on the border between free sand and areas covered with *Thalassia*.

**Etymology:** The specific name, *tuberculatennata*, refers to the unusual surface of antennae with its randomly dispersed large sensory papillae, each of which has a tubercular shape.

A key to Onuphidae from the Caribbean Sea

1 Subacicular hooks in median position in fascicle, pectinate chaetae scoop-shaped.................................2
- Subacicular hooks in ventral position in fascicle, pectinate chaetae flat..........................................................5

2 Peristomial cirri absent; tubes transparent, wholly secreted by inhabitants, round in transverse section ....
........................................................................................................................................................................... Hyalinoecia spp. (see below)
- Peristomial cirri present; tubes with a parchment-like inner lining and an outer layer of foreign particles
3 Anterior projecting parapodia with large auricular prechaetal lobes and a postchaetal lobe with a median
subulate projection; simple branchiae from chaetiger 11–12; tube flat and covered by small stones and
pieces of shells.................................................................................................................................................. Nothria conchylega Sars, 1835

**Distribution:** Arctic, North Atlantic, Mediterranean Sea, Eastern Russian seas, West Indies, Indian
Ocean, South Africa; shallow waters – 4000 m (Kiseleva 1968; Fauchald 1982).

- Anterior projecting parapodia with bi- to trilobate prechaetal and short, subconical postchaetal projection
.................................................................................................................................................................4

4 Branchiae start from chaetiger 12, with up to 4 filaments; tridentate pseudocompound hooks present on
first two chaetigers..................................................................................................................... Anchinothria pourtalesii (Ehlers, 1879)

**Distribution:** off Florida, off Cuba; 435–557 m (Ehlers 1879; Fauchald 1982).

- Branchiae absent; bidentate pseudocompound hooks present on first two chaetigers ..................
.................................................................................................................................................................. Anchinothria glutinatrix (Ehlers, 1887)

**Distribution:** Atlantic Ocean, Caribbean Sea, off the Sambos; 432 m (Ehlers 1887; Fauchald 1982).

5 Branchiae with filaments in spiraled arrangement ..................................................................................6

- Branchiae with filaments in pectinate arrangement or branchiae absent ........................................8

6 Pseudocompound hooks on anterior projecting parapodia tridentate. Diopatra tridentata Hartman, 1944

**Distribution:** North Carolina, Southern California, south to Octavia Bay, Colombia including the Gulf of
California north to Consag Rock; Caribbean Sea and West Indies; Brazil; 5–75 m (Hartman 1944; Gathof
1984; Leon-Gonzalez et al. 2004).

- Pseudocompound hooks on anterior projecting parapodia bidentate .....................................................7

7 Rings of ceratophores and palpophores smooth; relatively small sensory papillae on all ceratostyles orga-
nized in 16–18 longitudinal rows ................................................................................................................. Diopatra cuprea (Bosc, 1802)

**Distribution:** New England to Florida, Gulf of Mexico, Panama, Brazil, West and South Africa, Indian
Ocean; 0–90 m (Kiseleva 1968; Fauchald 1980; Gathof 1984).

- Rings of ceratophores and palpophores with large lateral projections; relatively large sensory papillae
scattered on both palpostyles and antennostyles .................................................................... Diopatra tubercul antennata sp. nov.

**Distribution:** Caribbean Sea, Belize, east off Dangriga; 0–2 m.

8 Peristomial cirri inserted in the middle of peristomium ........... Americanonphis magna (Andrews, 1891)

**Distribution:** subtidal sand flats from North Carolina through the Caribbean Sea and the Gulf of Mexico
(Fauchald 1980); West Indies, South Florida (Kiseleva 1968).

- Peristomial cirri inserted along frontal edge of peristomium ..............................................................9

9 First three pairs of parapodia projecting and prolonged with three distally curved weakly pseudocom-
 pound hooks; branchiae start from chaetiger 16–17.............. Rhamphobrachium agassizii Ehlers, 1887

**Distribution:** Eastern North Atlantic: Florida and Puerto Rico; Western North Atlantic: Azores, Morocco
and Ivory Coast; 40–2165 m (Paxton 1986).

- Anterior parapodia projecting, may be slightly enlarged but never prolonged ..........................10

10 Pseudocompound hooks on first projecting parapodia with long pointed hoods; branchiae absent ........
........................................................................................................................................................................ Paradiopatra fragosa Ehlers, 1887

**Distribution:** Atlantic Ocean, Caribbean Sea off Sand Key, off Marquesas, off Bahia Honda; 557–792 m
(Ehlers 1887; Fauchald 1982).

- Pseudocompound hooks on first projecting parapodia with short blunt hoods ..........................11

11 Ceratophores of antennae with more than 10 rings; ringed palpophores longer than palpostyles .....12

- Ceratophores of antennae with less than 10 rings; ringed palpophores as long as or shorter than palpo-
styles ..........................................................................................................................................................13

12 Branchiae simple and strap-like; digitiform postchaetal projections present on first 10 chaetigers ........
...........................................................................................................................................................................

**Onuphis opalina** Verrill, 1873  
**Distribution:** Atlantic Ocean off New England (Verrill 1873; Fauchald 1982); from the Gulf of St.
Lawrence to off Chesapeake Bay, possibly also the West Indies; 26–2300 m (Kiseleva 1968; Hobson
1971).

- Branchiae pectinate with up to 6 filaments; digitiform postchaetal projections distinct on at least first 60
chaetigers ...................................................................................................................................................

**Onuphis eremita** Audouin & Milne-Edwards, 1833  
**Distribution:** Central California; Caribbean Sea, Mexico, Guatemala, Mediterranean Sea, Indian Ocean,
West and South Africa, China; 15–1600 m (Kiseleva 1968; Fauchald 1982).

13 Compound spinigers present.................................................... **Mooreonuphis dangrigae** (Fauchald, 1980)  
**Distribution:** Caribbean Sea, Belize, west off Dangriga; 0–1.5 m (Fauchald 1980; 1982); Gulf of Mexico,
offf Tabasco and Campeche (Granados-Barba & Solis-Weiss 1994).

- Compound spinigers absent.............................................................................................................................14

14 Anterior projecting parapodia without large median simple tridentate hooks; both bidentate and tridentate
pseudocompound hooks present on anterior parapodia........ **Kinbergonuphis geminata** (Fauchald, 1980)  
**Distribution:** Known from the single locality north of Dangriga, Belize (Fauchald 1980; 1982).

- Anterior projecting parapodia with large median simple tridentate hooks present; only tridentate
pseudocompound hooks present on anterior parapodia............................................................................. 15

15 Tridentate pseudocompound hooks present on 8 chaetigers... **Kinbergonuphis vermillionensis** (Fauchald,
1968)  
**Distribution:** Gulf of California (Fauchald 1968; 1982) West Atlantic, Panama, Galeta reef, *Thalassia
Zone* (Fauchald 1977; 1982).

- Tridentate pseudocompound hooks present on first 6–7 chaetigers.........................................................16

16 Tridentate pseudocompound hooks present on first 6 chaetigers; cirriform ventral cirri present on first 8–
11 chaetigers; subacicular hooks start from chaetiger 16–20 ... **Kinbergonuphis pulchra** (Fauchald, 1980)  
**Distribution:** Belize, west off Dangriga (Fauchald 1980; 1982); continental shelf of the Gulf of Califor-
nia, from the Pacific side of the Baja California Peninsula; 0–55 m (Leon-Gonzalez 1994).

- Tridentate pseudocompound hooks present on first 7 chaetigers; cirriform ventral cirri present on first 11–
13 chaetigers; subacicular hooks start from chaetiger 22–23 ... **Kinbergonuphis virgata** (Fauchald, 1980)  
**Distribution:** Known from the single locality north of Dangriga, Belize (Fauchald 1980; 1982).

The following species of *Hyalinoecia* have been reported from the Caribbean Sea. The taxonomy of this
genus is poorly resolved and needs to be revised before a key to the species of *Hyalinoecia* from the Carib-
bean Sea can be provided.

*H. branchiata* Treadwell,1934: Puerto Rico; 548 m (Treadwell 1934).  
*H. juvenalis* Moore, 1911: from Southern California, south of Panama, and into West Indian region
through Colombia, Venezuela, and the West Indies; 15–410 m. (Moore 1911; Hartman 1944).  
*H. tubicola* Malmgren, 1867: Greenland, Norway, North Sea, Mediterranean Sea, Red Sea, Florida, West
Indies, Gulf of Mexico, Japan, Indian ocean, West and South Africa; 13–4300 m (Kiseleva 1968).  
*H. varians* Baird, 1870: West Indies (Baird 1980).

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