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A new species of *Chaetozone* (Polychaeta, Cirratulidae) from the Bay of Biscay offshore France, together with a review of *Chaetozone* species from the North Atlantic and adjacent waters

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Abstract

A new cirratulid species of the genus *Chaetozone* has been discovered offshore in fine muddy sediments in the Bay of Biscay, France. This species is unusual in having an expanded fusiform anterior body region and numerous subdermal glands along the entire body that produce an elaborate and distinctive pattern when stained with Methyl Green. The new species is compared with closely related congeners and a review of *Chaetozone* species from the North Atlantic Ocean is presented.

Key words: Annelida, *Chaetozone*, Bay of Biscay

Introduction

Chaetozone is the largest genus in the Cirratulidae with more than 50 species currently reported worldwide (Blake & Magalhães 2017). At least eight species of *Chaetozone* are known for the NE Atlantic Ocean including European and adjacent Arctic and subarctic locations, including the type species *C. setosa* Malmgren, 1867. Le Garrec *et al.* (2017) recently presented a summary of *Chaetozone* species from these waters as part of the discovery of an alien species, *C. corona* Berkeley & Berkeley, 1941, along the Brittany coast of France.

As part of a recent offshore survey in the Bay of Biscay, 22 specimens of an unknown species of *Chaetozone* were encountered. Study of these specimens suggested a close relationship with *C. larae* Elias, Rivero & Orensanz, 2016, a species recently described from offshore Argentina in the SW Atlantic Ocean. Following a careful morphological analysis, significant differences between *C. larae* and the Bay of Biscay specimens were identified and the species was confirmed as new to science.

The new species is here described and compared with its closest congeners. In addition, a brief review of known species of *Chaetozone* from the North Atlantic Ocean is presented.

Materials and methods

The first cruise of the JERICOBENT1 project (JERICOBENT1) took place on board the R/V *Côtes de la Manche* from 22 October to 2 November 2016 in the West Gironde Mud Patch (WGMP). The WGMP is a 420 km² clay-silt sedimentary area, located on the French Atlantic coast, 25 km off the mouth of the Gironde Estuary in the Bay of Biscay (Massé *et al.* 2016). Specimens of the *Chaetozone* species described in this paper were collected at Station JERICOBENT1 (62 m depth) using a Hamon grab (three replicates of 0.25 m²). Samples were sieved through a 1-mm mesh and immediately fixed in 5% buffered formalin. *Chaetozone* specimens were examined (by NL) under a Nikon SMZ 1500 stereomicroscope and a Nikon Eclipse E400 microscope, and photographed with a Nikon DS-Fi 2 camera. Length and width were measured with the NIS Elements Analysis software. JAB used a Wild M-5 Stereo

microscope and a Zeiss RA research microscope; the latter was equipped with Phase contrast and Nomarksii differential interference optics. A Nikon D-7100 camera was used with both microscopes; digital images were edited with Photoshop CS3. Some specimens were initially stained with a solution of Shirlastain A in water to highlight difficult-to-see surficial morphology; other specimens were further stained with a saturated solution of Methyl Green (MG) in ethyl alcohol in order to elucidate distinct staining patterns. Specimens used for examination with scanning electron microscopy (SEM) were prepared by critical point drying, coated with gold and examined and photographed with a Hitachi H2000.

The holotype and a set of paratypes are deposited at the Muséum National d'Histoire Naturelle, Paris (MNHN); additional paratypes are deposited at the Museum of Comparative Zoology, Harvard, Massachusetts, USA (MCZ). Additional specimens are lodged in the collection of the Arcachon Marine Station.

Abbreviations used on figures: br, branchia; dCr, dorsal crest; dGr, dorsal groove; nuO, nuchal organ; per, peristomium; pr, prostomium; pyg, pygidium; seg, segment; set, setiger; tn, tentacle.

Results

Taxonomic Account

Genus *Chaetozone* Malmgren, 1867

Type species: *Chaetozone setosa* Malmgren, by monotypy.

Diagnosis. (Modified after Blake 2015). Prostomium blunt to conical, usually lacking eyespots, with a pair of small nuchal slits or depressions at posterior edge; with a single pair of grooved dorsal tentacles arising from posterior edge of peristomium, or sometimes more posterior on an achaetous anterior segment, or rarely an anterior setiger. First pair of branchiae arising from an achaetous segment or first setiger; sometimes with first two pairs of branchiae on a single anterior segment. Body thick in anterior segments, sometimes distinctly swollen or fusiform, rarely with middle or posterior body segments beaded or moniliform. Chaetae include capillaries on most setigers and acicular spines in neuropodia and notopodia, spines typically concentrated in posterior segments, forming distinct cinctures with spines emerging from elevated membranes; cinctures with few to many spines alternating with capillaries; some species with posterior noto- and neuropodial sigmoid acicular spines numerous, encircling entire posterior parapodia; bidentate spines sometimes present in juveniles or occasionally in ventral-most position of far posterior setigers of adults accompanying unidentate spines in cinctures; some species with long, natatory-like capillaries, these sometimes limited to gravid individuals. Pygidium a simple lobe, disk like, or with long terminal cirrus.

Remarks. *Chaetozone*, with more than 50 species is the largest genus in the Cirratulidae (Blake & Magalhães 2017). This modified generic definition includes additional characters identified in recently described species as being important in species differentiation. These include details of where the dorsal tentacles and branchiae begin, the presence or absence of an achaetous segment between the peristomium and setiger 1, and details of the arrangement and morphology of the posterior acicular spines.

Historically, the name of the type-species, *Chaetozone setosa*, originally described by Malmgren (1867) from Spitzbergen in the Norwegian Arctic, was applied globally to cirratulid species having posterior cinctures of spines. New investigations have demonstrated that the majority of these records are actually distinct species (see Blake 1996; 2006, 2015; Chambers 2000; Doner & Blake 2006), with *C. setosa* itself limited to arctic and subarctic sites in the eastern North Atlantic (Chambers 2000; Blake 2015).

Species of *Chaetozone* are characterized by having posterior acicular spines arranged in spreading fascicles that either partially or completely encircle the posterior end of the body, producing distinctive cinctures with the numerous protruding spines forming a conspicuous armature. The parapodia are often enlarged with high membranes and a group of these segments may be shaped like an accordion. The number of spines in the cinctures has proven to be important in distinguishing one species from another. The acicular spines are typically unidentate and either blunt-tipped or pointed and accompanied by alternating capillaries. One group of *Chaetozone* species has spines with a fine tip that curves and attaches to the concave side of the shaft. In a few species, one or two bidentate spines occur with the acicular spines.

Other characters now known to be important in distinguishing species or groups of species of *Chaetozone* include the nature of segment 1 and whether it is achaetous or represents the first setiger. The first segment may be partially or completely fused with setiger 1; in some species the dorsal tentacles and/or branchiae arise from segment 1. These characters and others in Table 1 help differentiate the twelve species now known to occur in the North Atlantic.

Due to the increasing number of species of *Chaetozone* being described, Blake (2015) listed a series of characters important for their identification and suggested that these could also be used to separate certain species into groups. The new species from the Bay of Biscay has several identifying characters including the presence of a distinct dorsal crest on the peristomium, a separate achaetous segment with branchiae anterior to the first setiger, a swollen fusiform-shaped anterior body region, and numerous subdermal glands that produce an elaborate and complex Methyl Green staining pattern.

***Chaetozone elakata* new species**

Figures 1–3

Material examined. Northeast Atlantic Ocean, offshore France, Bay of Biscay. R/V *Côtes de la Manche* Sta. JERICO-8, 45°38'55"N, 01°45'47"W, coll. 28 October 2016, 0.25m² Hamon grab, 62 m, holotype (MNHN-IA-TYPE 1800), 3 paratypes (MNHN-IA-TYPE 1801), 2 Paratypes, SEM (MNHN-IA-TYPE 1802) and 7 paratypes (MCZ 143234).

Description. A moderate-sized species with elongate body and conspicuous bulge in middle of thoracic region imparting distinct fusiform shape to anterior end (Figs. 1A, 3A, D). Anterior segments crowded, about four times as wide as long (Fig. 1A), then becoming longer, but still about twice as wide as long in middle body segments (Fig. 3A, D). Posterior segments narrowing, with parapodia becoming modified, with deep grooves between individual segments (Figs. 1C, 2F) and parapodia elevated with thin membranes bearing spreading fascicles of spines and alternating capillaries producing a prominent armature (Fig. 2B–C).

Holotype (MNHN-IA-TYPE 1800) complete, 45.4 mm long, 0.64 mm wide anterior to bulge, 1.01 mm across bulge, 0.65 mm posterior to bulge, with 111 setigerous segments; complete paratype an ovigerous female (MCZ 143234) 33 mm long, 0.4 mm wide anterior to bulge, 0.65 across bulge, 0.52 mm posterior to bulge, with 117 setigerous segments. Other complete paratypes with 92–104 setigerous segments. Most specimens with distinct dorsal groove, in expanded segments (Figs. 1A, 3B), absent in some specimens (Fig. 3A); weak depression present on individual segments along most of venter; absent in posterior segments. Color in alcohol light tan with no apparent pigment on body; numerous segmental subdermal glands visible under a coverslip at about 63x magnification; these stain with Methyl Green imparting distinct patterns (see below).

Prostomium triangular, narrowing to rounded tip (Fig. 1A–B); nuchal organs reduced to thin slits at posterior margin of prostomium, best seen with SEM (Fig. 2A); eyespots absent. Peristomium relatively narrow, divided into two distinct annular rings (Fig. 1A–B); first long, relatively smooth but with 2–3 weak lateral grooves best seen in SEM (Fig. 2A), second ring narrow, similar in size and appearance to following achaetous segment. Entire peristomium surmounted by a relatively smooth, elongate dorsal crest extending posteriorly to anterior border of achaetous segment 1 (Figs. 1A–B, 2A); dorsal tentacles arising from posterior margin of second peristomial ring (Fig. 1A–B). First segment achaetous with first pair of branchiae arising from posterior margin; second segment setigerous, with second pair of branchiae also on posterior margin, dorsal to notosetae (Fig. 1A–B); by about setiger 20, branchiae shifting to a more medial location and continuing to near posterior end (Fig. 1A).

Parapodia of anterior and middle segments reduced to low ridges or mounds from which setae arise; posterior setigers modified with swollen podia bearing raised membrane from which acicular spines arise forming prominent cinctures. Anterior setae all heavy broad capillaries numbering 8–10 in noto- and neuropodia with notosetae longer than neurosetae; capillaries of middle segments, 40–48 in neuropodia and 49–55 in notopodia, similar in number but 1–2 becoming thicker, narrowing abruptly to thin pointed capillary tip; transitioning in posterior segments to blunt-tipped acicular spines; long, thin, natatory-like capillaries absent, including in mature specimens. Neuropodial blunt-tipped acicular spines first appear in posterior body segments from setigers 74 in the holotype and 68–84 in paratypes; notopodial spines from setigers 82–98. Noto- and neuropodial spines initially numbering 2–3 in a fascicle with 5–6 capillaries, then increasing to 3–4 spines; posterior full cinctures from last 6–8 setigers

with up to 7–8 spines in noto- and neuropodia, with 15–16 spines on a side (Fig. 2C), each spine alternating with a thin capillary seta (Fig. 2D). High membranes of cinctured segments extending over dorsal midline forming shallow channel (Fig. 2C); ventral surface flattened. Individual spines weakly curved, with narrow bluntly pointed tip; each with narrow internal core clearly visible in light microscopy (Figs. 1D, 2D); spines appearing smooth externally in SEM (Fig. 2E). Body terminating in simple pygidium bearing short triangular lobe ventral to anal opening (Figs. 1C, 2F).

Methyl Green staining pattern. Numerous subdermal glands are concentrated on the prostomium, peristomium and in groups or bands along most of the body. These glands stain intensely with Methyl Green, creating a spectacular and distinctive staining pattern for this species (Fig. 3B–E). Except for the anterior tip, the prostomium stains intensely on all sides (Fig. 3B, E); the peristomium is intensely stained on the dorsal and lateral sides, with the dorsal stain extending along dorsal crest onto the anterior margin of segment 1 (Fig. 3B, E). The less intense stain on Fig. 3B compared with Fig. 3C is due to a longer period of differentiation and destaining to show areas where the stain is most intense and retained for the longest period of time. Along the body, the segments anterior to the swollen area have dorsal and lateral bands of stain; the lateral bands are located in the middle of each segment, anterior to the setal fascicle (Fig. 3E); dorsal to the notosetae, the stain expands into a prominent patch (Fig. 3B–C) which gives way to transverse intersegmental bands that cross the dorsum (Fig. 3B–C); between each of the dorsal bands are groups of stained glands producing a speckled pattern; ventrally, the banding is less prominent (Fig. 3E). The swollen area includes all of the features of the preceding segments except that entire area is more darkly stained, producing the most intense and obviously stained part of the body (Fig. 3B–D). Posterior to the swollen area, the staining pattern is similar to that of the anterior segmental area, but less intense. In the abdominal region, the stain is concentrated in thin transverse intersegmental bands and lateral longitudinal lines (Fig. 3D).

Biology and ecology. Several paratypes are females with oocytes packed together in various stages of maturation; the largest eggs observed were 134–140 µm in the widest dimension. Specimens live in a muddy habitat (median grain size = 25 µm; 1.08% of organic carbon) offshore of the Gironde estuary (60 km) (Masse *et al.* 2016). This species is important (13% of total abundance) in the local benthic community, which is dominated by polychaetes (16 species belonging to 14 families).

Remarks. *Chaetozone elakata n. sp.*, with its fusiform shape due to expanded anterior body segments, is most similar to *C. gibber* Woodham & Chambers, 1994 from the NE Atlantic and Mediterranean Sea, *C. hartmanae* Blake, 1996 from off California in shelf and slope depths, *C. larae* from the SE Atlantic off Argentina in shelf depths, and to some extent *C. bathyala* Blake, 2015 from eastern Canada.

Chaetozone gibber differs from *C. elakata n. sp.* in having the expanded segments only dorsally enlarged providing a humped shape to the body instead of a more complete fusiform shape. In addition, the posterior cinctures of *C. gibber* are only partially developed with eight spines on a side instead of up to 16. The first segment of *C. gibber* is the first setigerous, whereas in *C. elakata n. sp.* the first segment is an achaetous segment anterior to setiger 1. Methyl Green stain has not been tested on *C. gibber*.

Chaetozone hartmanae has a similar fusiform shape as *C. elakata n. sp.*, but the posterior cinctures have fewer than 10 spines on a side and, more importantly, the noto- and neuropodial spines differ in morphology with the notopodial spines being straight rather than curved and the neuropodial spines having a curved apex with serrations on the convex side (Blake 1996). Additionally, the first segment of *C. hartmanae* is the first setigerous and also bears the first branchiae. The Methyl Green staining pattern in *C. hartmanae* is reduced to a band of speckles on the anterior and posterior margins of each segment.

Chaetozone larae is similar to *C. elakata n. sp.* in having a similarly expanded fusiform shape to the anterior body segments, a peristomium divided into two annular rings, one long and one narrow, and with both surmounted by a low dorsal crest. *Chaetozone larae* and *C. elakata n. sp.* also have a separate achaetous segment following the peristomium from which the dorsal tentacles arise. However, *C. larae* is reported to also have the first pair of branchiae on the achaetous segment instead of setiger 1 as in *C. elakata n. sp.* In addition, *C. larae* has posterior cinctures with 11–13 spines on a side whereas *C. elakata n. sp.* has posterior cinctures with 15–16 spines on side. In addition, the neuropodial spines generally begin more anteriorly in *C. larae*, from setigers 43–74 versus setigers 68–84 in *C. elakata n. sp.*; however, the segment where the spines begin is typically size related. The illustrations of the spines of *C. larae* in Elias *et al.* (2016) suggest that they are shorter and with more of a curvature than those

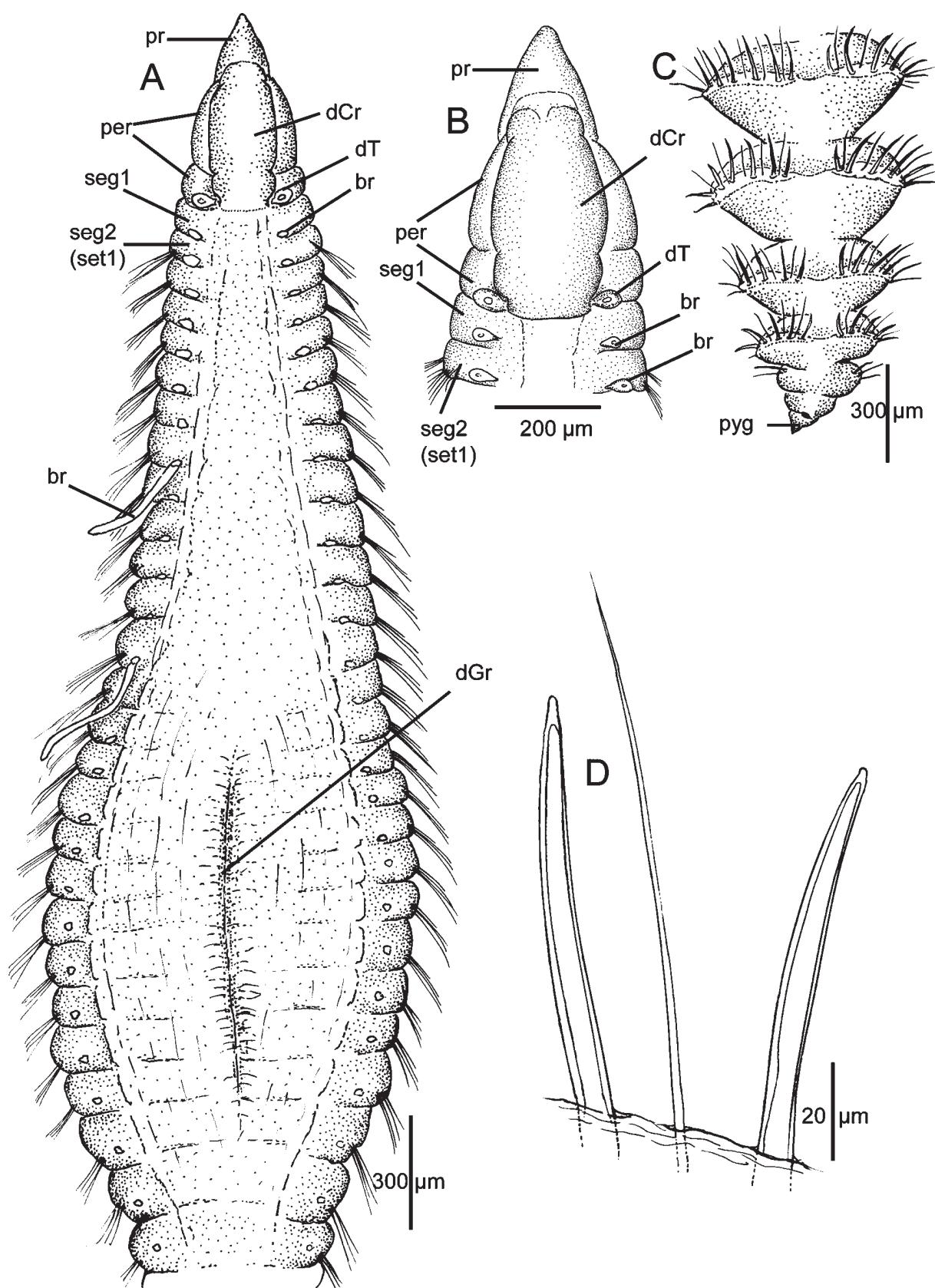


FIGURE 1. *Chaetozone elakata* n. sp. A, anterior end of body, dorsal view; B, detail of pre-setigerous region and setigers 1–3, dorsal view; C, far posterior segments and pygidium, dorsal view; D, posterior notopodial spines and capillary. Paratypes (MCZ 143234).

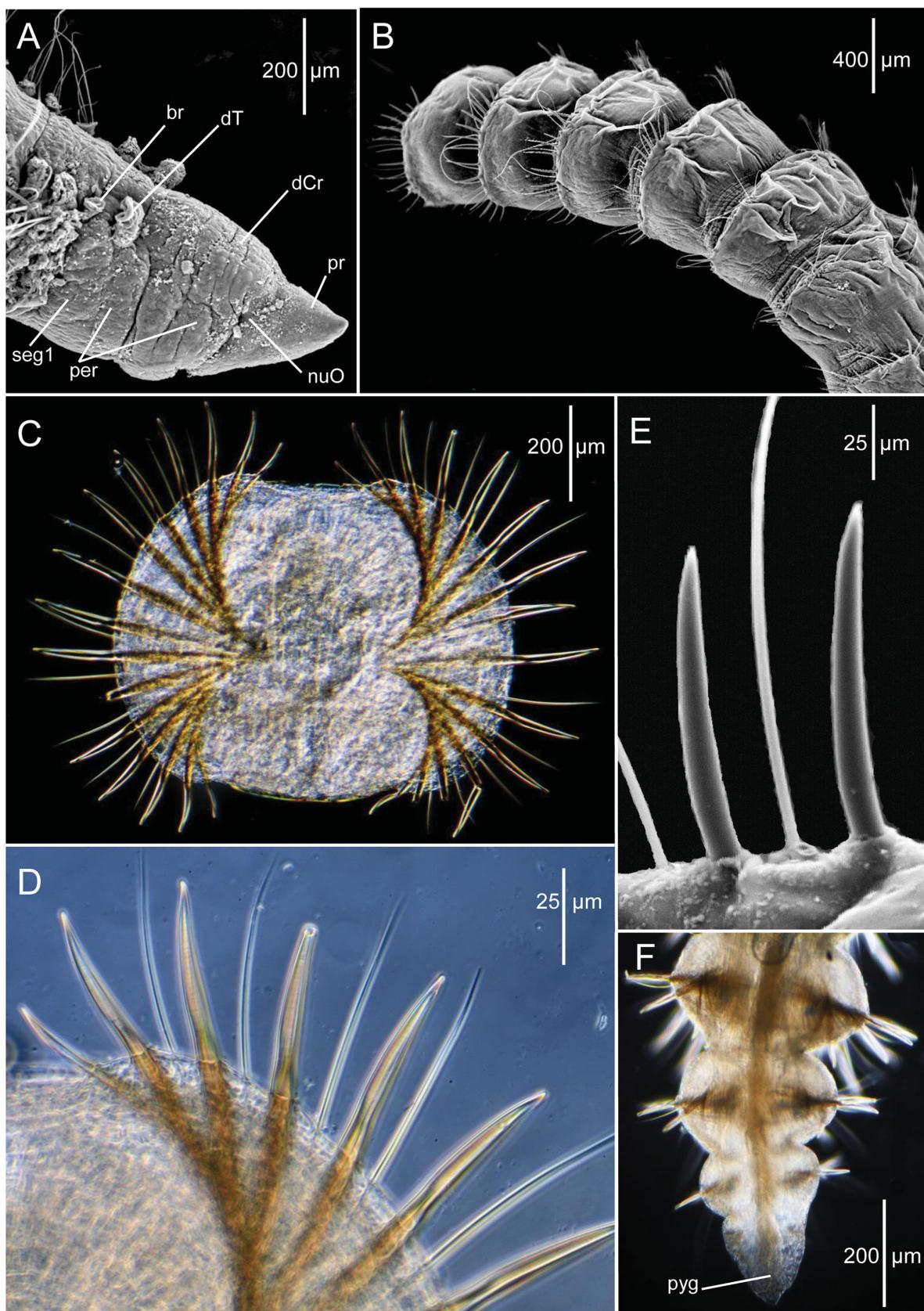


FIGURE 2. *Chaetozone elakata* n. sp. A, SEM of pre-setigerous region and anteriormost segment, right lateral view; B, SEM of posterior segments, right lateral view; C, Photomicrograph of far posterior parapodium, cross section, anterior view; D, detail of notopodial spines and capillaries from same; E, SEM of notopodial spines; F, Photomicrograph of posterior end and pygidium, dorsal view. A–B, E, paratype (NMHN-1A-TYPE 1802); C–D, F, paratypes MCZ (143234).

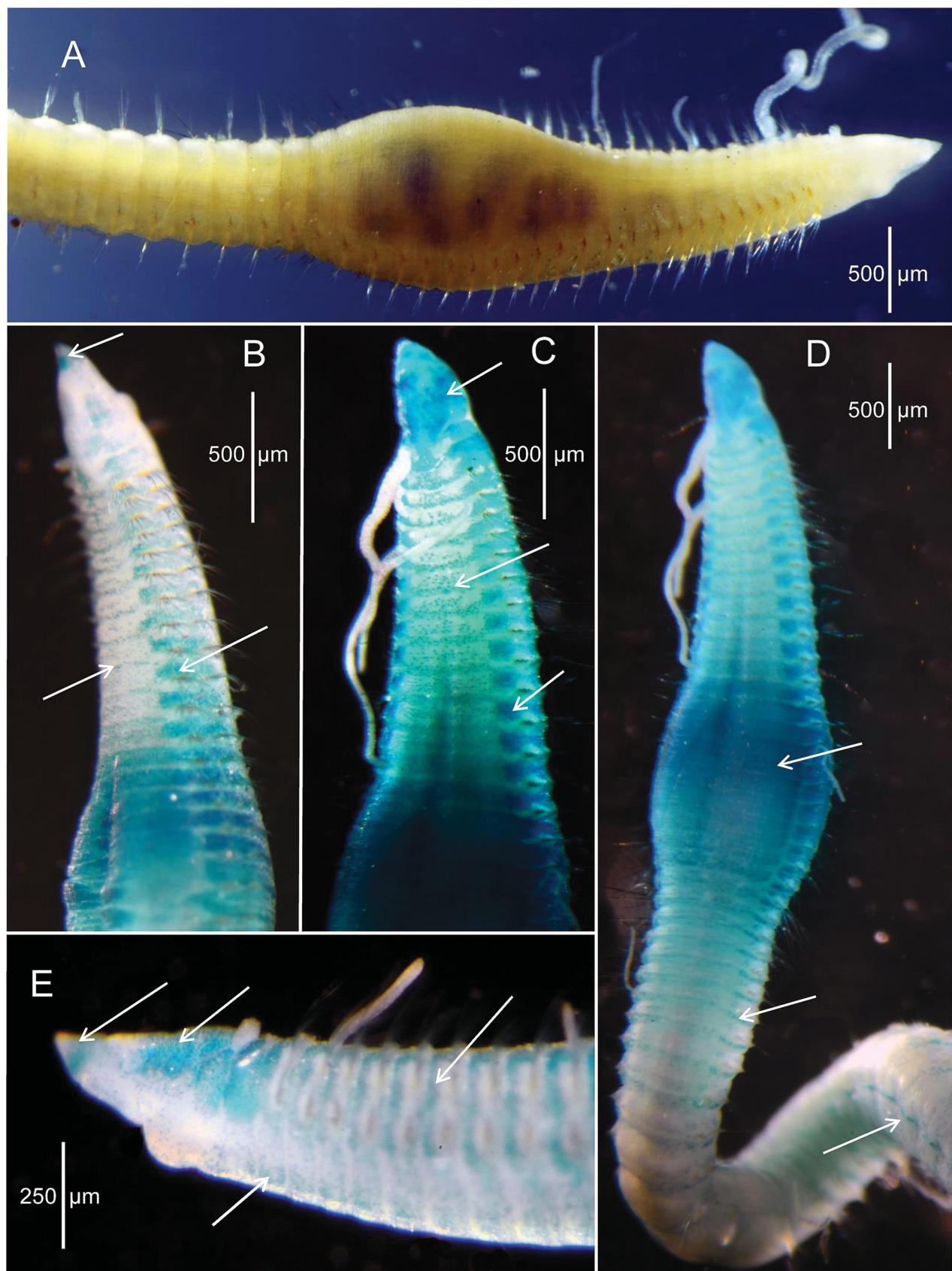


FIGURE 3. *Chaetozone elakata* n. sp. Photomicrographs. A, anterior end of unstained paratype, right lateral view; B–E, paratypes stained with Methyl Green: B, anterior end, dorso-lateral view; C, another specimen, dorsal view; D, same specimen with anterior and middle segments; E, third specimen, anterior end, left lateral view. Arrows denote stained areas described in text. A, paratype (NMHN-1A-TYPE 1802); B–E, paratypes MCZ (143234).

of *C. elakata n. sp.* The most distinctive difference between these species, however, is with the Methyl Green staining pattern: *C. larae* has no defined pattern, whereas *C. elakata n. sp.* has numerous subdermal glands that stain with Methyl Green and produce distinctive staining patterns along the entire body. *Chaetozone bathyala* has weakly expanded anterior segments, but this area is not prominent and does not resemble the swollen segments of *C. elakata n. sp.* The presence of a complete post-peristomial achaetous segment preceding the first setigerous segment has been reported for several North American species:

Chaetozone bathyala, *C. careyi* Blake, 2015, *C. malmgreni* Blake, 2015, *C. palaea* Blake, 2006, *C. pigmentata* Blake, 2015, and *C. pugettensis* Blake, 2015. Blake (2015) provided comparative details of these species; none of these species has a large swollen anterior region similar to that of *C. elakata n. sp.*

Etymology. The epithet is derived from *elakate*, Greek for spindle, referring to the distinctive spindle or fusiform shape of the anterior segments of these worms.

Distribution. Bay of Biscay, 60 m in muddy sediments.

Discussion

As part of a recent review of European species of *Chaetozone*, Le Garrec *et al.* (2017) recorded eight species of the genus in European waters. Of these *C. zetlandica* McIntosh, 1911 and *C. caputesocis* (de Saint-Joseph, 1894) are poorly known, and do not fully agree with the current definition of *Chaetozone*: *C. zetlandica* has spines limited to the neuropodia and also has been recorded with bidentate hooks; *C. caputesocis* has spines in both noto- and neuropodia but these are not arranged in cinctures. Both species have been referred to the genus *Caulieriella* in recent papers (Gillandt 1979; Woodham & Chambers 1994; Hartmann-Schröder 1996). Another species, *Tharyx vivipara* Christie, 1984, described from the UK, was referred to *Chaetozone* by Petersen (1999), but has not been redescribed as such. Therefore, pending a review of these three poorly known species, only six species of *Chaetozone* have been well described and documented from European waters: *C. setosa* Malmgren, 1867, the type species; *C. carpenteri* McIntosh, 1911; *C. christiei* Chambers, 2000; *C. corona*; *C. gibber*, and *C. jubata* Chambers & Woodham, 2003. *Chaetozone elakata n. sp.* joins this group as the seventh well-documented species in European waters. Except for *C. jubata*, which is a deep-water species from depths of 350–1800 m, the other six European species of *Chaetozone* all occur in subtidal sediments to depths of no more than 100 m.

Elsewhere in the North Atlantic, five species of *Chaetozone*, all previously identified as *C. setosa*, have recently been described from eastern North America. These are *C. anasima* Doner & Blake, 2006, *C. diodonta* Doner & Blake, 2006, and *C. hystricosa* Doner & Blake, 2006, all from nearshore and shelf depths off New England; and *C. bathyala* Blake, 2015 and *C. pigmentata* Blake, 2015, from off Eastern Canada in Arctic and subarctic waters from shelf and slope depths.

Table 1 was developed to bring together the morphology and distributional records of 12 confirmed species of *Chaetozone* in North Atlantic waters in order to assist future workers with the identification of specimens encountered. It is noteworthy, that except for *C. corona*, which appears to have been introduced to European waters and elsewhere from California (Le Garrec *et al.* 2017), the other 11 species have only local or regional distributions. We anticipate that many additional species await discovery, especially in the deeper shelf and slope depths throughout the North Atlantic Ocean. A key for species of *Chaetozone* from North Atlantic waters is provided.

Key to 12 *Chaetozone* species from the North Atlantic Ocean

(Note: Recent published descriptions of *Chaetozone caputesocis* and *C. zetlandica* do not fully agree with the definition of *Chaetozone* and are not included in the following key; MG = Methyl Green).

- | | | |
|---|---|------------------|
| 1 | Anterior body with distinctly enlarged fusiform segments anterior to abdominal segments | 2 |
| - | Anterior body segments only slightly enlarged, gradually tapering posteriorly | 3 |
| 2 | Anterior body segments enlarged dorsally into hump-backed configuration; peristomium not divided into rings, dorsal tentacles arising from posterior margin of peristomium; posterior parapodia with partial cinctures, up to 8 spines on a side; MG pattern not tested | <i>C. gibber</i> |

-	Anterior segments enlarged forming distinct fusiform shape; peristomium with two distinct rings, dorsal tentacles arising from smaller second peristomial ring; posterior parapodia with complete cinctures, up to 16 spines on a side; elaborate MG staining pattern throughout body	<i>C. elakata n. sp.</i>
3	First complete body segment asetigerous; first branchiae on asetigerous segment; eyes absent; long natatory-like capillaries present or absent	4
-	First complete body segment setigerous; first branchiae either on posterior margin of peristomium or setiger 1; eyes present or absent; long natatory-like capillaries absent	7
4	Peristomium with dorsal crest; dorsal tentacles in notch between peristomium and setiger 1; long natatory-like setae on all segments from setigers 18–21; deep groove present along venter; MG stains peristomial area, stripes on anterior thoracic segments, and posterior cinctured segment	<i>C. setosa</i>
-	Peristomium without dorsal crest; dorsal tentacles arising from posterior margin of peristomium; long natatory setae present or absent; ventral groove present or absent; MG pattern present or absent	5
5	Body pigmented; neuropodial spines first present from anterior one-third of body (setigers 5–25 in 80-setiger specimens); long natatory-like capillaries present on sexually matures specimens or absent; MG pattern present or absent	6
-	Body not pigmented; neuropodial spines from mid-body, setiger 25 in 50-setiger specimen; long natatory setae from setiger 2 to about setiger 25; MG pattern not tested	<i>C. jubata</i>
6	Body heavily pigmented with numerous brown to black pigment speckles over entire body; with a prominent mid-ventral ridge along entire length of body formed of ventromedial bulges on each segment; with weak mid-dorsal groove in middle body segments; neuropodial spines from setigers 5–26; posterior cinctures reduced, with 13–19 spines on a side; no MG pattern	<i>C. pigmentata</i>
-	Body with anterior segments with diffuse black pigment, not discrete speckles, limited to certain areas of the body, not all over; mid-ventral ridge low, not conspicuous; posterior cinctures well developed, with elevated membranes with 20–22 spines on a side; with distinct MG staining pattern, with all of prostomium staining except tip and most of peristomium staining, forming “mask” over the head region	<i>C. bathyala</i>
7	First pair of branchiae on setiger 1; eyespots present	8
-	First pair of branchiae on posterior margin of peristomium; eyespots present or absent	9
8	Peristomium with dorsal crest; neuropodial spines from setiger 6–9; anterior neuro- and notopodial spines short, curved, pointed; posterior spines long, straight, pointed	<i>C. carpenteri</i>
-	Peristomium without dorsal crest; neuropodial spines from setiger 30; neuro- and notopodial spines, short, curved with blunt tip	<i>C. christiei</i>
9	Peristomium with prominent dorsal crest; prostomial eyespots present; neuropodial acicular spines from setiger 1; notopodial acicular spines from setiger 1–8; prominent MG stain on prostomium and peristomium	<i>C. corona</i>
-	Peristomial crest absent; prostomial eyespots absent; neuropodial and notopodial spines from middle and posterior segments	10
10	Bidentate hooks and acicular spines in posterior cinctures	<i>C. diodonta</i>
-	Bidentate hooks absent	11
11	Acicular spines with sharp tips curving back and fusing with shaft, from posterior one-third (setigers 50–55 in neuropodia and 45–50 in notopodia); cinctures with 16–24 spines on a side; MG stains prostomium	<i>C. anasima</i>
-	Acicular spines short, straight, thick with blunt tips, from mid-body (setigers 40–45 in neuropodia and 45–50 in notopodia); cinctures with 12–14 spines on a side; no MG pattern	<i>C. hystricosa</i>

Notes on the coordinates and depths of the type specimens of *Chaetozone anasima* and *C. hystricosa*.

While preparing the Discussion for this paper the published descriptions of the various North Atlantic species of *Chaetozone* were examined. During the course of this review, it became apparent that some errors were present in the field collection data presented by Doner & Blake (2006) for *C. anasima* and *C. hystricosa*. In order to document the correct data, the following corrected latitudes, longitudes, and depths are presented together with the actual dates the specimens were collected.

Chaetozone anasima Doner & Blake, 2006, collected Massachusetts Bay, August 2002, R/V *Aquamonitor*: Sta. FF11-1, 42.658550°N, 70.499931°W, 88 m, coll. 12 Aug 2002, Holotype (MCZ 65293); Sta. FF11-2, 42.658318°N, 70.500053°W, 88 m, coll. 12 Aug 2002, 10 paratypes (MCZ 65295); Sta. FF14-2, 42.416752°N, 70.654884°W, 73 m, coll. 12 Aug 2002, 6 paratypes (MCZ 65294); Sta. FF04-2, 42.288132°N, 70.424881°W, 90 m, coll. 14 Aug 2002, 6 paratypes (MCZ 65296).

Chaetozone hystricosa Doner & Blake, 2006, collected Massachusetts Bay, August 2003, R/V *Aquamonitor*: Sta. FF14-3, 42.41680°N, 70.65480°W, 73 m, coll. 06 Aug 2003, holotype (MCZ 65297); FF04-2, 42.28858°N, 70.42513°W, 90 m, coll. 07 Aug 2003, 10 paratypes (MCZ 65298); FF04-3, 42.28835°N, 70.42509°W, 90 m, coll. 07 Aug 2003, 10 paratypes (MCZ 65299).

TABLE 1. Taxonomic Characteristics of 12 Species of *Chaetozone* from the North Atlantic Ocean and *Chaetozone larae* from the Southwest Atlantic Ocean.

Species of <i>Chaetozone</i>	Nature of Segment 1	Position of first pair of branchiae	Position of the paired tentacles	Nature of posterior cinctures	Nature of posterior spines	Companion setae with spines	Long, natory- like notosetae
<i>setosa</i> Malmgren, 1867—Type species	Achaetous, incomplete, partially fused to setiger 1	Achaetous segment 1	In notch between posterior peristomium and segment 1	Complete, with 10–12 spines in notopodium and 10–12 in neuropodium; 20–24 spines on a side; high, thin parapodial membranes	Broad, curved, pointed, with internal striae	Alternating, long thin capillaries	Present
<i>larae</i> Elias, Rivero & Orensanz, 2016	Achaetous (complete)	Achaetous segment 1	On achaetous segment 1	Partial, 5 spines in notopodium and 6–7 in neuropodium; 11–13 spines on a side; parapodial membranes weakly developed	Short, curved, pointed	Alternating, thin capillaries	Absent
<i>elakata</i> Blake & Lavesque n. sp.	Achaetous (complete)	Posterior to tentacles on segment 1	Posterior margin of second peristomial ring	Complete, 7–8 spines per ramus; 14– 16 spines on a side; parapodia with well-developed, high membranes	Moderate, curved, pointed	Alternating, thin capillaries	Absent
<i>anasima</i> Doner & Blake, 2006	Setiger 1	Peristomium, lateral to dorsal tentacles	Posterior margin of peristomium	Complete, 10–14 spines in notopodia; 6–10 in neuropodia; 16–24 on a side; parapodia with low membranes	With sharply pointed tip, curving back and merging with shaft, forming rounded tip	Alternating, thin, smooth capillaries	Absent
<i>bathyala</i> Blake, 2015	Achaetous (complete)	Segment 1	Posterior margin of peristomium on last peristomial ring	Complete, 8–10 spines in notopodia; 10–12 spines in neuropodia; 20–22 spines on a side; with high parapodial membranes	Thick, bluntly pointed	Capillaries in upper part of notopodia & lower part of neuropodia	Present, sexually mature specimens
<i>carpenteri</i> McIntosh, 1911	Setiger 1	Setiger 1	Peristomium posterior to dorsal crest	Partial, 5–6 spines per ramus; 10–12 on a side; parapodia with moderately developed membranes	Anterior spines short, curved, pointed; posterior spines long, straight, pointed	Alternating, long, thin capillaries	Present
<i>christiei</i> Chambers, 2000	Setiger 1	Setiger 1; posterior and lateral to dorsal tentacles	Posterior margin of peristomium	Partial, 3–5 spines in notopodia; 4–5 spines in neuropodia; 7–10 spines on a side; parapodia weakly developed low ridges	Short, curved, with blunt tip	Alternating, thin capillaries	Absent

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TABLE 1. (Continued)

Species of <i>Chaetozone</i>	Approximate ¹ segmental origin of spines	Dorsal longitudinal groove or ridge	Ventral longitudinal groove or ridge	Pygidium	Methyl Green stain	Distinctive characteristics	Distribution/ References
<i>setosa</i> Malmgren, 1867—Type species	Mid-body; ~40 in neuropodia; ~50 in notopodia on specimens with up to 85 setigers	Weakly developed, limited to anterior segments	Deep mid-ventral groove	Small ventral lobe	Peristomium stains, ventral bands on anterior and far posterior segments	Peristomial crest; long capillaries; mid-ventral groove along body	E. North Atlantic, Arctic and subarctic, 30–110 m; (Petersen 1999; Chambers 2000; Blake 2015)
<i>larvae</i> Elias, Rivero & Orensanz, 2016	Mid-body; 43–74 in neuropodia; 40–75 in notopodia	Shallow groove on swollen anterior segments of some specimens	Absent	Rounded cushion ventral to anal opening	No pattern	Anterior body region with fusiform shape; achaetous segment with both dorsal tentacles and first branchiae.	SW Atlantic, off Argentina, 70 m. (Elias <i>et al.</i> 2016)
<i>elakata</i> Blake & Lavesque n. sp.	Posterior one-third of body; 75–90 in neuropodia; 85–98 in notopodia	Prominent mid- dorsal groove present on swollen anterior segments of some specimens	Weak mid-ventral depression on individual segments of some specimens	Triangular- shaped lobe	Distinctive pattern on head and parapodia; intersegmental bands on dorsum and venter along entire body	Anterior body region with fusiform shape; dorsal peristomial crest; achaetous segment with first branchiae; MG pattern.	E. North Atlantic, Bay of Biscay, France, 60 m (This study)
<i>anasina</i> Doner & Blake, 2006	Posterior one-third; 50–55 in neuropodia; 55–60 in notopodia	Absent	Shallow mid- ventral groove	Ventral cup- like lobe	Prostomium stains; rest of body unstained	Flip-tipped spines; peristomium entirely smooth	W. North Atlantic, New England, nearshore, low water to 75–84 m. (Doner & Blake 2006)
<i>bathyvala</i> Blake, 2015	Anterior one-third from 18–35 in neuropodia; 30–50 in notopodia	Absent	Weak ridge	Short protruding dorsal lobe	Pre-setiger area with distinct pattern: prostomium stains except tip; stain in grooves of peristomial rings.	Anterior segments darkly pigmented; capillaries of cinctures in upper and lower parts of fascicles	W. North Atlantic, Eastern Canada, off Baffin Island and Newfoundland, 300– 1770 m. (Blake 2015)
<i>carpenteri</i> McIntosh, 1911	Anterior setigers, 6–9 in neuropodia; not clear for notopodia	Absent	Longitudinal groove	Simple ventral lobe	Not tested	Spines from anterior setigers heavy, curved; spines of posterior setigers long, straight	E. North Atlantic, off Spain and Algeria, 45 m; Mediterranean and Tyrrhenian Sea, 42–98 m; Adriatic Sea, 31–37 m. (Chambers <i>et al.</i> 2011)
<i>christiei</i> Chambers, 2000	Setiger 30 in neuropodia; setiger 50 in notopodia	Absent	Longitudinal groove	Flattened, leaf- like lobe ventral to anal opening	Pygidium a flattened leaf-like lobe	Pygidium a flattened leaf-like lobe	E. North Atlantic; UK coasts, Ireland, France, German Bight, intertidal to 40 m in sand. (Chambers 2000; Chambers <i>et al.</i> 2007)

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TABLE 1. (Continued)

Species of <i>Chaetozone</i>	Nature of Segment 1	Position of first pair of branchiae	Position of the paired tentacles	Nature of posterior cinctures	Nature of posterior spines	Companion setae with spines	Long, natatory- like notosetae
<i>corona</i> Berkeley & Berkeley, 1941	Setiger 1	Last peristomial ring, lateral to dorsal tentacles	Posterior margin of peristomium	Partial, with 4–6 spines in notopodia and 6–8 in neuropodia; with up to 14 spines on a side; parapodia with moderately developed membranes	Weakly curved, tapering to narrow tip, notoacicular spines longer, thinner than neuroacicula	Long, thin capillaries	Absent
<i>diodonita</i> Doner & Blake, 2006	Setiger 1	Peristomium, lateral to dorsal tentacles	Posterior margin of peristomium	Partial, 6–7 spines per ramus; 12–14 on a side; parapodia with weakly developed parapodial membranes	Heavy, with blunt tip; bidentate hooks also present	Alternating capillaries	Absent
<i>gibber</i> Woodham & Chambers, 1994	Setiger 1	Setiger 1	Posterior margin of peristomium	Partial, 4 spines in noto- and neuropodia; up to 8 spines on side; parapodia with low, weakly developed membranes	Broad, with blunt tip	Alternating, slender capillaries	Absent
<i>hystericosa</i> Doner & Blake, 2006	Setiger 1	Peristomium, lateral to dorsal tentacles	Posterior margin of peristomium	Complete, 6–7 spines per ramus; 12–14 spines on a side; parapodia with well-developed, high membranes and deep cinctures	Short, thickened, straight, with blunt tip	Alternating thin, smooth capillaries	Absent
<i>jubata</i> Chambers & Woodham, 2003	Achaetous anterior to setiger 1; not clearly stated	Posterior to tentacles on achaetous segment	Posterior margin of peristomium	Complete, with 12–14 per ramus or 24–28 on a side; parapodia with well- developed, high membranes	Straight, with blunt tip (?)	Alternating, thin capillaries	Present
<i>pigmentata</i> Blake, 2015	Achaetous (complete)	Segment 1	Posterior margin of peristomium	Partial, with 2–5 spines in notopodia; 6–7 in neuropodia; 10–12 on a side; membranes?	Notopodial: long, narrow, pointed; neuropodial: short, curved, pointed	Alternating capillaries	Present, sexually mature specimens

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TABLE 1. (Continued)

Species of <i>Chaetozone</i>	Approximate ¹ segmental origin of spines	Dorsal longitudinal groove or ridge	Ventral longitudinal groove or ridge	Pygidium	Methyl Green stain	Distinctive characteristics	Distribution/ References
<i>corona</i> Berkeley & Berkeley, 1941	Setiger 1 in neuropodia, 1–8 in notopodia on specimens with 60 setigers	Absent	Shallow channel	Terminal anus with blunt, ventrally directed lobe	Pyrostomium, peristomium, and edges of setiger 1 stain intensely; tip of pyrostomium does not stain	Dorsal peristomial crest; neuropodial spines from chaetiger 1; prominent eyespots	E. North Pacific, Brazil; Bay of Biscay, Mediterranean Sea; low water to ca. 120 m (Blake 1996; Le Garrec et al. 2017)
<i>diodonta</i> Doner & Blake, 2006	Bidentate neuro-hooks from 11–15 and simple neuro-spines from 61; noto-spines from 67; noto-bidentate hooks from 90	Absent	Mid-ventral groove	Ventral saucer-shaped lobe or disk	No pattern	With both bidentate hooks and unidentate spines along body and in posterior cinctures	W. North Atlantic, off New England, George Bank, 100–160 m (Doner & Blake 2006)
<i>gibber</i> Woodham & Chambers, 1994	Mid-body; setigers 50–80 in neuropodia; 90–100 in notopodia	Absent	Longitudinal groove	Simple ventral lobe	Not tested	Anterior segments dorsally swollen “hump-backed”; reduced number of posterior spines	E. North Atlantic, UK; England & Wales; Mediterranean Sea, coast of France; subtidal to 45 m. (Woodham & Chambers 1994)
<i>hystericosa</i> Doner & Blake, 2006	Mid-body; 40–45 in neuropodia; 45–50 in notopodia	Absent	Mid-ventral groove	Simple rounded lobe	No pattern	Similar to <i>C. anasima</i> but spines with blunt tips	W. North Atlantic, New England, nearshore, low water to 70–100 m. (Doner & Blake 2006)
<i>jubata</i> Chambers & Woodham, 2003	Mid-body; from ca. setiger 25 in both rami	Absent	Longitudinal groove	With scoop-shaped lobe ventral to anus	Not stated	Body shape tapers from wide to narrow along body; long capillaries	E. North Atlantic, off Iceland, Faroe-Shetland Channel, Norway, 350–1800 m; off Norway. (Chambers & Woodham 2003); Chambers et al. 2007
<i>pigmentata</i> Blake, 2015	Anterior one-third from 5–25 in neuropodia: 30–50 in notopodia	Weak dorsal groove	Prominent ridge	Simple ventral lobe	No pattern	Body covered with brown pigment; noto- and neuro-acicular spines different shape; prominent mid-ventral ridge; weak mid-dorsal groove	W. North Atlantic, Eastern Canada, off Baffin Island to Labrador, 130–245 m. Also Alaskan Arctic in ca. 40 m. (Blake 2015)

1. Segments where noto- and neuropodial acicular spines begin must account for size variation; typically spines begin in anterior, middle, or posterior regions of the body and actual segment distribution is rarely exact, and related to age.

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