



Diopatra (Onuphidae: Polychaeta) from intertidal sediments in southwestern Europe

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Abstract

Intertidal populations of *Diopatra* from Spanish, Portuguese and French Atlantic beaches have traditionally been identified as *D. neapolitana*. This species is present, mainly in Spain and Portugal. However, at least some French beaches are occupied by a distinct species, *D. biscayensis*, here described as new. In addition, in Portugal and Spain, a third species, here described as new, *D. cryptornata*, will also key out as *D. neapolitana* using standard keys, but is morphologically distinct. The three species can be separated not only on traditional characters, but also on obvious differences in anterior morphology not usually considered in descriptions. The French habitats now occupied by *D. biscayensis*, previously had populations of *D. neapolitana* alone as documented by collections in the Paris Museum made by Quatrefages and Saint-Joseph in the mid-late 1800s. *Diopatra marocensis* has recently been reported from Atlantic waters, from both intertidal and subtidal areas. Since this species can be confused with the three species named above, a partial re-description based on paratype material is included here. Finally, a fifth species, *D. micrura*, has recently been described from the area and is here briefly characterized based on the original description. A key to all five species has been constructed.

Key words: Annelida; SW Europe; Atlantic Ocean; Intertidal

Tube-building polychaetes in the genus *Diopatra* are important ecosystem engineers of marine intertidal sediments worldwide. In Western Europe, the only *Diopatra* species consistently reported in over 150 years of intense sampling has been *D. neapolitana* delle Chiaje 1841 (and synonyms). Originally described from the Gulf of Naples, Mediterranean Sea, *D. neapolitana* has been widely reported from the Atlantic and Indian Oceans (e.g., Fauvel 1953; Day 1967). However, recent collections indicate that three *Diopatra* species are also present on the Atlantic coast of Europe: *D. neapolitana* and two previously undescribed species. Here we present a detailed morphological study confirming the morphological distinctness of the three species, and describing the two new species: *D. cryptornata* and *D. biscayensis*. *D. biscayensis* was referred to as *Diopatra* species A in a recent genetic study confirming its genetic distinctness from *D. neapolitana* (Berke et al. 2010). All three species reported here agree with *D. neapolitana* as traditionally accepted with the exception of the number of teeth on the pectinate chaetae (e.g., Fauvel 1923), but are morphologically distinct on the basis of obvious features not usually included in *Diopatra* descriptions.

In addition to the two new species described here, another new species of *Diopatra*, *D. micrura*, was described from the same area (Pires et al. 2010) and a species originally described from the Atlantic coast of Morocco, *D. marocensis* Paxton et al. 1995 has also been reported from the European coasts, in both subtidal and intertidal collections. We present an updated key based on morphological features not previously considered or not described for all *Diopatra* species reported from Western Europe to date.

Notes on some morphological features

Thanks to the intensive studies of Hannelore Paxton (Paxton 1986, 1993), 1998; Paxton et al. 1995) and Natalya

Budaeva (Budaeva & Fauchald, 2008) we have recently gained a good understanding of the morphology of onuphid polychaetes in general including *Diopatra*. The following notes build on their findings and expand our understanding of features rarely, if ever, detailed in species descriptions. Several of these features however are important for separation of the new species described here.

Anterior edge of prostomium and frontal lips.

Most commonly the front of the prostomium is rounded, but at least in one species it is triangular and sharply pointed with the lips attached by triangular bases along the sides of the triangular portion of the prostomium; the lips are obliquely conical, tapering to a blunt tip. Usually these lips are attached at the front of the rounded prostomium and are digitiform or subulate. The lips may be touching at the base, or they may be separated by a distinct gap. If a gap is present, the front edge of the prostomium may continue on the ventral side of the prostomium as a low ridge, separating the paired upper lips; this ridge fades out inside the outer mouth.

The upper lips.

These lips may be separated medially by the ventral ridge of the prostomium, or they may be touching along the midline. A gap between the lips may contain a distinct papilla of varying size. Each lower buccal lip is triangular or rectangular and somewhat sac-like. The ventral surface of this lip carries a very large papilla, more or less distinctly marked from the rest of the lip; this papilla is usually located in the middle of the ventral surface or it is located near or at the lateral tips of the lips. The papilla usually tapers to a blunt tip or may be nearly hemispherical.

The lower lips.

This lip is located at the posterior edge of the external mouth-opening, it is a curved flattened ridge, separated by distinct furrows into three parts; the medial part is quadrangular or obliquely rectangular; and may be rounded frontally. The two outer parts of the lower lips form a flattened ridge attached to the underlying lateral lips. In one species the lateral ends of the ridge project as free, distally rounded lappets *Diopatra biscayensis* (Plate 1b), new species.

Paired dorsal papillae on anterior segments.

One of the new species described below, *D. cryptornata*, has paired small papillae on each of several anterior segments, starting at segments 7 and 8 and ending at segments 33–38. Each papilla is digitiform, and usually white, standing out against the much darker integument of the same segments. It is visible from the dorsal side only by folding back the branchiae. The first few papillae are located distant from the midline, but from about the fifth papillated segment, the papillae are located roughly halfway between the midline of the segment and the base of the parapodia in the remaining papillated segments, forming a straight line. *Diopatra marocensis* has white pigmented patches in roughly the same position; these patches are much larger than the papillae and are not raised above the surface; they are bordered by a distinct dark pigment ring (Paxton et al. 1995: Fig. 1A).

The prechaetal lobes of the modified chaetigers

These lobes are usually distally rounded and become reduced to a low ridge covering the bases of the chaetae in the first several unmodified parapodia. However, at least in two species, a ventral lobe appears in one of the first unmodified parapodia in front of the prechaetal lobe. This lobe moves slightly dorsally in the next several anterior chaetigers and eventually takes the place of the prechaetal lobes proper. This lobe is usually flattened with a rounded free edge, but at least in one species it becomes elongated dorsally with a flattened conical free tip.

The postchaetal lobes

These lobes are usually low rounded structures with a distinct elongated, subulate to triangular freely projecting elongated postchaetal lobe. At least one species has double elongated postchaetal lobes in anterior segments; one of the two new species described here, *D. biscayensis* (Plate 1f). The more dorsal of the two lobes corresponds to the single postchaetal lobe in other species and continues to the end of the fragmentary specimens. The ventral lobe is distinct in all modified segments, but becomes increasingly shorter and increasingly conical in the first ten unmodified chaetigers and is absent in more posterior chaetigers.

Description of species

The diagnoses and the key separate only the species included in this paper;

Diopatra biscayensis, new species

Plate 1

Diopatra sp. A. Berke et al. 2010

Material examined: USNM 1128516, Chatelaillon Plage, France, 25 June 2006 (9); USNM 1128517, Chatelaillon Plage, France, 25 June 2006 (1); USNM 1128523 Tharon Plage, France, 16 June 2006 (holotype, position, ca 47°17'N, 2°16'E). USNM 1128522 Chatelaillon Plage, France, 25 June 2006, (paratype); USNM 1128521, Tharon Plage, France, 16 June 2006 (9 paratypes) USNM 1149420, Mont Saint-Michel Bay, France, 25 June 2010; USNM 1149421, Mont Saint-Michel Bay, France, 25 June 2010; USNM 1149422, Mont Saint-Michel Bay, France, 25 June 2010.

Diagnosis: Upper lip without median papilla and ridge. Dorsum without ornamentation. First four to five chaetigers with bidentate pseudocompound hooks; hoods moderately long and pointed. *Two elongated postchaetal lobes in modified parapodia.* Paired dorsal papillae absent. Subacicular hooks present from chaetiger 7–12 (chaetiger 9 in holotype). *Pectinate chaetae with 18–20 or more teeth throughout body.*

Description: All specimens anterior fragments with numbers of segments varying between 21 and 61 and length from 24 to 70mm; all with same width at chaetiger 10, 10 mm. Length proportionate to segments present. Total number of segments and structure of posterior end of the body unknown. Anterior end including first five chaetigers slightly narrower than next following segments dorsally strongly convex; ventrum less convex and tilted dorsally with mouth region and first pair of parapodia pointed anteriorly. Mid-body segments transversely narrowly rectangular with both dorsal and ventral side slightly convex. Longitudinal mid-ventral groove present in all chaetigers, but especially distinct in anterior segments. Prostomium and prostomial appendages brown; body color (as preserved) light ochre without distinct color patterns.

Fold between prostomium and peristomium semicircular in dorsal view. Antennae and palps enormous, covering most of dorsum of prostomium; attached along posterior edge of prostomium (Plate 1a). Frontal edge of prostomium with paired frontal lips varying in shape from ovoid to basally narrowed, distally conical and tapering. Upper lips medially distinctly separated (Plate 1b); each cushion-shaped with large distal papilla separated from rest of cushion by groove. Laterally mouth bordered by low ridges. Lower lip divided by shallow grooves into two narrowly triangular, flattened parts connected by frontally truncate low medial section. Two triangular sections projecting laterally as free, triangular flaps. Palps of holotype reach chaetiger 3, in other specimens reach from chaetigers 1–3. All antennae similar in length, reaching chaetiger 5–6 in holotype; in other specimens reaching chaetigers 4–13 depending on size of specimen. Palpophores with 12 rings in holotype; other specimens with up to 15 rings. Antennophores with 12 rings in holotype, in other specimens with 11–15 rings. Palpophores and antennophores without lateral projections.

Peristomium slightly longer than first chaetiger in dorsal view; ventrally as a narrow ridge. Peristomial cirri present; about as long as peristomium. First five parapodia project mainly laterally, slightly anteriorly and ventrally; from chaetiger 6 parapodia projecting increasingly dorsally. First five parapodia with distinct, thick shafts slightly expanded distally (*i.e.*, slightly clavate); more posteriorly parapodia conical; decreasing in length, but distinct as short cones in last chaetigers present. First several parapodia with wide prechaetal lobes; each with a bluntly triangular median distal end (Plate 1e); further posteriorly prechaetal lobes becoming low oblique ridges continuous around superior side with postchaetal lobes. Anterior postchaetal lobes low ridges covering chaetal bases, but with two elongated digitiform, tapering or subulate lobes (Plate 1f). Ventralmost lobe decreasing in size through modified parapodia and absent from an early unmodified parapodium. Dorsalmost lobe gradually decreasing in size but still distinct at posterior end of fragments; becoming increasingly flattened triangular in posterior-most segments. First four chaetigers with cirriform ventral cirri (Plate 1e–f); fifth ventral cirrus triangular and flattened; from chaetiger 6 ventral cirri replaced by thick glandular flattened pads. Pads reaching greatest size at about chaetiger 20; more posteriorly glandular areas decreasing in size and becoming rounded.

The first four or five parapodia with 1–2 upper simple chaetae and 4–5 bidentate pseudocompound hooks. Hooks with short pointed hoods and smooth shafts (Plate 1c). Remaining parapodia mainly with strongly serrated limbate chaetae. Pectinate chaetae flat with straight distal margins, each with 18–20 teeth. Pectinate chaetae first present from chaetiger 6 in holotype, and from chaetigers 5–6 in other specimens. Starting from chaetiger 9 in holotype, and from chaetigers 7–12 in other specimens lower limbate chaetae replaced by thick bidentate subacicular hooks with very thin translucent guards (Plate 1d). Start of subacicular hooks weakly positively linked to increasing size of specimens.

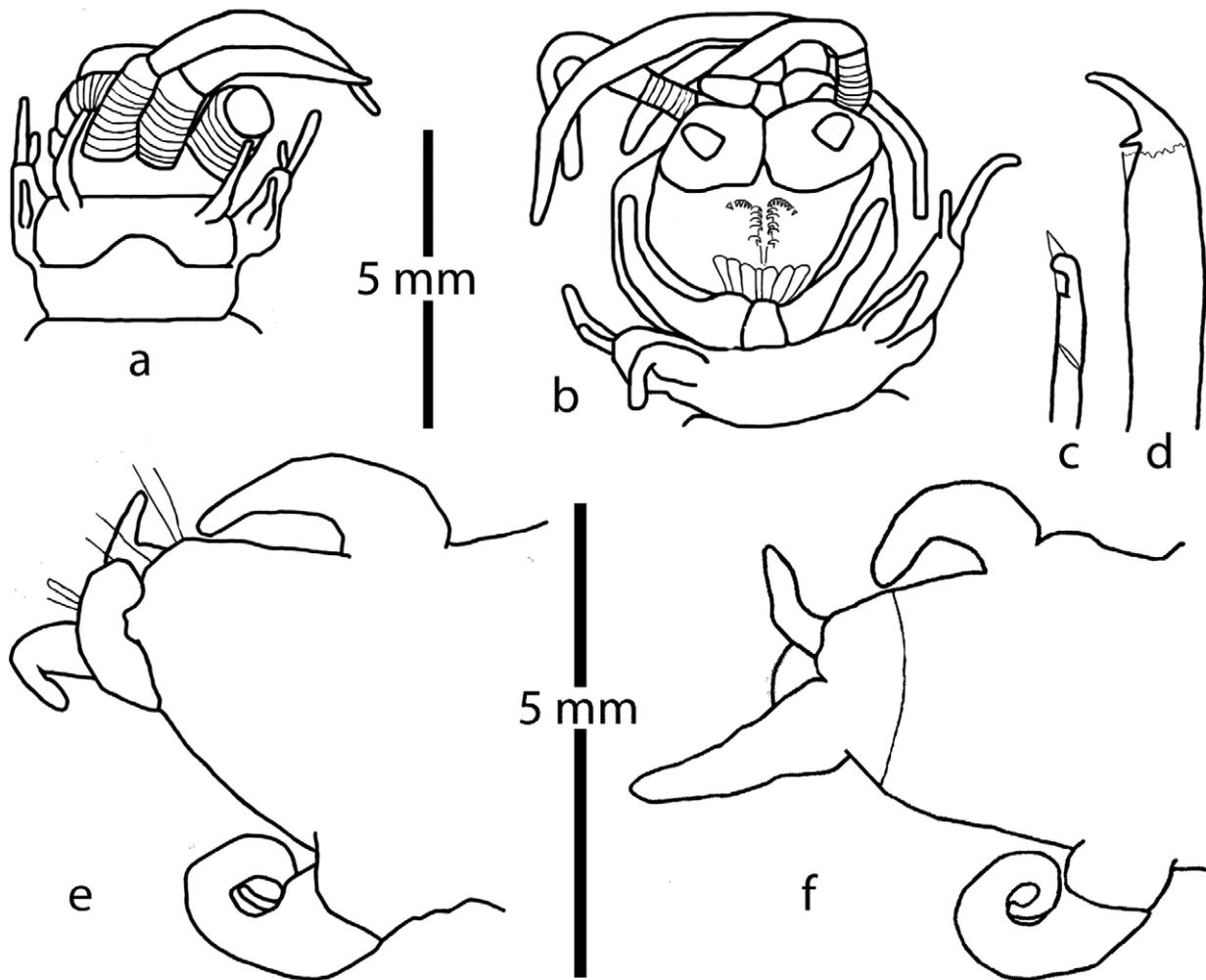


PLATE 1. *Diopatra biscayensis*. USNM 118523, holotype.

- a. dorsal view of anterior showing prostomium with palpophores and antennophores with proximal rings plus peristomium with peristomial cirri.
 b. ventral view of anterior showing upper and upper lips and lower external lips with free lappets at the lateral ends.
 c. and d. bidentate pseudocompound hooks from anterior modified parapodium.
 e. anterior view of modified parapodium 1 with dorsal and ventral cirri and single, wide prechaetal lobe; the acicular lobe is represented by the rounded middle lappet.
 f. posterior view of modified parapodium 2 with dorsal and ventral cirri and the double extended lobes of the postchaetal lobe of the parapodium.

Branchiae with up to six spiraled whorls of relatively short filaments present from chaetiger 4 and present through all segments in fragments.

Mandibles strongly sclerotized with calcareous distal cutting plates. Distal indentations along edge of cutting plates distinct. Maxillae strongly sclerotized with little evidence of calcifications. Maxillary formula: Mx I = 1 + 1; Mx II = 12 + 10; Mx III = 11 + 0; Mx IV = 6 + 8; Mx V = 1 + 1.

Tube basically cylindrical, upper end distally hooded and covered with debris consisting mostly of sea grass fragments and pieces of shells attached on all sides; permanently buried part of tube thin-walled and covered by fine sand.

Etymology. The name refers to the famously stormy bay along the coasts of France and Spain, the Bay of Biscay.

Discussion. Among the species reported in this paper, *Diopatra biscayensis* is uniquely characterized by the presence of double finger-shaped extensions of the postchaetal lobes in the modified anterior segments (Plate 1f). The free lappets at the lateral ends of the upper lips have not been mentioned in any other species (Plate 1b).

Geographical distribution. *Diopatra biscayensis* is known from the French west coast as far north as Mont Saint Michel Bay south to Arcachon.

***Diopatra marocensis* Paxton, Fadlaoui and Lechapt, 1995**

Plate 2a–b

Diopatra marocensis Paxton, Fadlaoui and Lechapt 1995: 950–954, figs. 1 and 2.

Material examined. USNM 170584, Sidi Boulbra, Moroccan Atlantic coast (4 paratypes); USNM 170585, Sidi Boulbra, Moroccan Atlantic coast, St. F, November 1990 (5 paratypes), (location given as 31°58' to 31°52'N, 9°26' to 9°36'W for all material treated in Paxton et al. 1995, including the paratypes listed above).

Diagnosis. . Upper lip with anterior median papilla and narrow ridge between halves. Anterior dorsum without ornamentation. First five chaetigers with bidentate pseudocompound hooks; hoods moderately long and pointed. Subacicular hooks present from chaetiger 15. Pectinate chaetae with 11–12 teeth in anterior chaetigers; in median chaetigers pectinate chaetae have 15–18 teeth.

Description. All specimens incomplete; largest (in USNM 17585) consisting of 77 chaetigers, 25mm long and 4 mm wide at chaetiger 10, forming base for description.

Prostomium rounded (Plate 1a); frontal lips nearly as long as length of prostomium, distinctly separated medially and subulate or digitiform. Bases of palps and antennae large, filling out whole margin of prostomium. Palpophores with 8 rings of which distalmost one about one-third longer than others. Antennophores with 8 or 9 short rings plus a distal ring about twice as long as other rings. Lateral projections absent on palpophores and antennophores. Palps reaching posterior margin of peristomium; lateral antennae reaching chaetiger 3 and median antenna reaching chaetiger 4 or margin between chaetigers 4 and 5. Antennal styles only slightly longer than antennophores; slender and digitiform.

Upper lips (Plate 2b) deeply separated medially with a distinct, rounded papilla between lips, roughly midway along length of gap between lips. Shape of each lip roughly triangular, with an indistinctly marked, truncate distal papilla at far lateral ends. Paired lateral lips cushion-shaped. Lower lips tripartite, with a rectangular median section and paired high wings laterally; lateral end of each wing attached directly to outer edge of lateral lips.

Five first parapodia modified; relatively long and tapering. Preacicular lobe rounded and supplemented by a transverse fold near parapodial bases. Postacicular lobe a low fold covering posterior chaetal bases, apart from a long, tapering median lobe. Both dorsal and ventral cirri long, tapering and cirriform in first four parapodia; ventral cirrus rounded and truncate by chaetiger 5. Unmodified parapodia triangular and directed obliquely dorsally; preacicular and postacicular lobes low, transverse folds; postacicular lobe retaining elongated median lobe in all chaetigers present, median lobe becoming increasingly shorter, and conical in outline in more posterior chaetigers.

Modified anterior parapodia with 4–5 bidentate pseudocompound chaetae with moderately long, pointed hoods. Unmodified parapodia with slender, limbate chaetae with lower part of limbation distinctly serrated. Lowermost limbate chaetae replaced from about chaetiger 15 by single, rarely double, bidentate subacicular hook. Pectinate chaetae present from about chaetiger 6; anterior pectinate chaetae with about 12 teeth; median pectinate chaetae with about 15–20 teeth. Shafts of limbate chaetae and subacicular hooks increasingly copper-colored posteriorly.

Branchiae present from chaetiger 4 through chaetiger 35, each with a relatively short, thick stem and 5 to 6 whirls of short, digitiform filaments.

Jaws distinctly sclerotized along cutting edges; supporting structures barely sclerotized except along distal margin. Mandibles distinctly calcified distally in a rounded structure; distal end with a distinct notch near median edge. Maxillary formula is 1+1, 8+8, 6+0, 7+10, 1+1.

Remarks. A very noticeable feature of *D. marocensis* is the anterior dorsal color pattern. Each of the immediate post-modified segments have paired dorsolateral eyespots with a central white (or light-colored) area bordered by a distinct dark (or black) ring. This pattern was illustrated by Paxton et al. (1995) and is still visible in the nine specimens examined here.

Geographical distribution. *Diopatra marocensis* is known from the Atlantic Ocean off Morocco and along the west coast of the Iberian Peninsula.

***Diopatra micrura* Pires, Paxton, Quintino and Rodrigues. 2010**

Diopatra micrura Pires, Paxton, Quintino and Rodrigues, 2010: 17–33, figs. 1–8.

Diagnosis. Presence of median papilla of upper lip unknown. Anterior dorsum without ornamentation. First four to five chaetigers with bidentate pseudocompound hooks; hoods moderately long and pointed. Subacicular hooks present from chaetigers 8–13. *Pectinate chaetae with 5–10 teeth throughout body.*

Remarks. *Diopatra micrura* lacks the double elongated postchaetal lobes in the anterior modified chaetigers present in *D. biscayensis*. It also lacks the dorsal papillae present in *D. cryptornata* and the characteristic ring-shaped color patches on anterior segment characteristic of *D. marocensis*. The anterior edge of the prostomium is rounded, in contrast to the pointed triangular edge present in *D. neapolitana*. This species appears to be best characterized by not having any of the unique features characterizing the other species treated here.

Geographical distribution. *Diopatra micrura* is known from intertidal and shallow subtidal areas south and west of Portugal in the Atlantic Ocean.

***Diopatra cryptornata*, new species**

Plate 2c–e

Material examined: USNM 112825, Obidos, Portugal, Spring 2008, coll. F. Lima (holotype; (position, ca 39°41'N, 9°21'E), USNM 1180239, Huelva, Spain, 1 July 2006 (1); USNM 112814, Obidos, Portugal, 15 May 2006 (1 paratype); USNM 112824, Obidos, Portugal, Spring 2008, coll. F. Lima (1 paratype); ; USNM 112826, Obidos, Portugal, Spring 2008, coll. F. Lima (1 paratype); USNM 112827, Obidos, Portugal, Spring 2008, coll. F. Lima (1 paratype) USNM 112836, Obidos, Portugal, Spring 2008, coll. F. Lima (1 paratype); USNM 118237, Obidos, Portugal, Spring 2008, coll. F. Lima (1 paratype); USNM 118238, Obidos, Portugal, Spring 2008, coll. F. Lima (1 paratype); USNM 112839, Obidos, Portugal, Spring 2008 (1 paratype).

Diagnosis: Upper lips without median papilla and ridge. *Paired dorsal papillae from chaetigers 7 or 8 through chaetigers 33–38.* Postchaetal lobes of anterior modified chaetigers with a single elongated papilla. *First four chaetigers with falcate pseudocompound hooks;* hoods short and bluntly pointed. Subacicular hooks present from chaetigers 16–19 (chaetiger 16 in holotype). Pectinate chaetae with 5–7 teeth throughout body (as far as known).

Description: All specimens posteriorly incomplete. Anterior end including first five chaetigers tilted slightly dorsally, dorsum convex, ventrum flattened, narrowing from anterior end to segment 6. Body abruptly wider at segment 6. Cross-section of rest of body basically rectangular with dorsum slightly convex. Central ventrum flattened with enormously expanded glandular bases of ventral cirri forming curved outer surfaces. Anteriormost parapodia directed anteriorly and ventrally, other modified parapodia gradually shifting to fully lateral positions and directions. Anterior dorsum dark brownish purple, fading from about chaetiger 10 posteriorly to narrow bands on either side of the intersegmental grooves. Prostomium dark brown, including antennophores and bases of frontal lips; ceratostyles and palpostyles and tips of frontal lips light, brownish yellow. Peristomial cirri and dorsal cirri light colored. Ventrum of five first chaetigers irregularly dark brown with light colored ventral cirri. Modified parapodia irregularly pigmented with brown.

Prostomium (Plate 2c) rounded in dorsal view with antennae and palps forming a posterior curved line. Palps reaching chaetiger 2 in holotype, in other specimens reaching chaetigers 2–4. Lateral antennae reaching chaetiger 10 in holotype; truncated in some specimens, when intact reaching chaetigers 8 to 15. Median antenna reaching chaetiger 12 in holotype; in other specimens reaching chaetigers 8–19. Palpophores of holotype with 12 rings; other specimens with 8 to 12 rings. Antennophores of holotype with 12 rings, other specimens with between 8 and 12 rings. Rings smooth in all anterior appendages. Nuchal grooves and eyes not seen. Peristomium dorsally slightly narrower than first chaetiger; laterally expanding so at junction with first chaetiger peristomium distinctly wider than first chaetiger. Peristomial cirri about twice as long as peristomial length. Frontal lips subulate; upper lips (Plate 2d) separated medially, each lip a transverse cushion with a thick medial papilla. Lateral lips low folds, anteriorly tucked under paired upper lips and ventrally fused to distalmost end of upper lips. Lower lips a thick curved structure divided into three parts; two lateral parts thick, increasingly flattened towards lateral side and directly attached to lateral lips; median section quadrangular or rectangular.

A pair of white papillae present dorsally on each segment from chaetiger 7 through end of fragments. Papillae located somewhat lateral to midline of each segment in first three to five papillated segments. More posterior papillae located roughly mid-way between midline and parapodial bases forming distinct longitudinal lines; most papillae digitiform, but especially from about chaetiger 20 may be spherical or clavate suggesting partial retractability. Last pair of papillae present on chaetiger 33 in holotype. In other specimens papillae present from chaetiger 7–9 to end of fragments (roughly segments 33–35), except in specimen from Huelva in which very small papillae are present to chaetiger 38.

First parapodia (Plate 2e) located ventrally and projecting laterally and slightly anteriorly. Second to fifth parapodia increasingly lateral in position projecting more directly laterally. Main prechaetal lobes distally rounded covering only dorsalmost fascicle of chaetae; three smaller fascicles of chaetae each bordered by low, oblique prechaetal lobes. Main postchaetal lobe triangular in first parapodia, covering upper chaetae. Postchaetal lobes becoming relatively low ridges with projecting subulate, median papilla. In other modified parapodia. Parapodia shifting dorsally from chaetiger 6 becoming increasingly short conical structures directed dorsally. Prechaetal lobes obliquely rounded with high end dorsally; covering increasingly three lower fascicles as these fuse into single major fascicle. From chaetiger 6 to about chaetiger 20 postchaetal lobes with a basal, low ridge, with a distinct median lobe projecting beyond chaetae; dorsal chaetae shifting gradually in position to emerging along dorsal edge

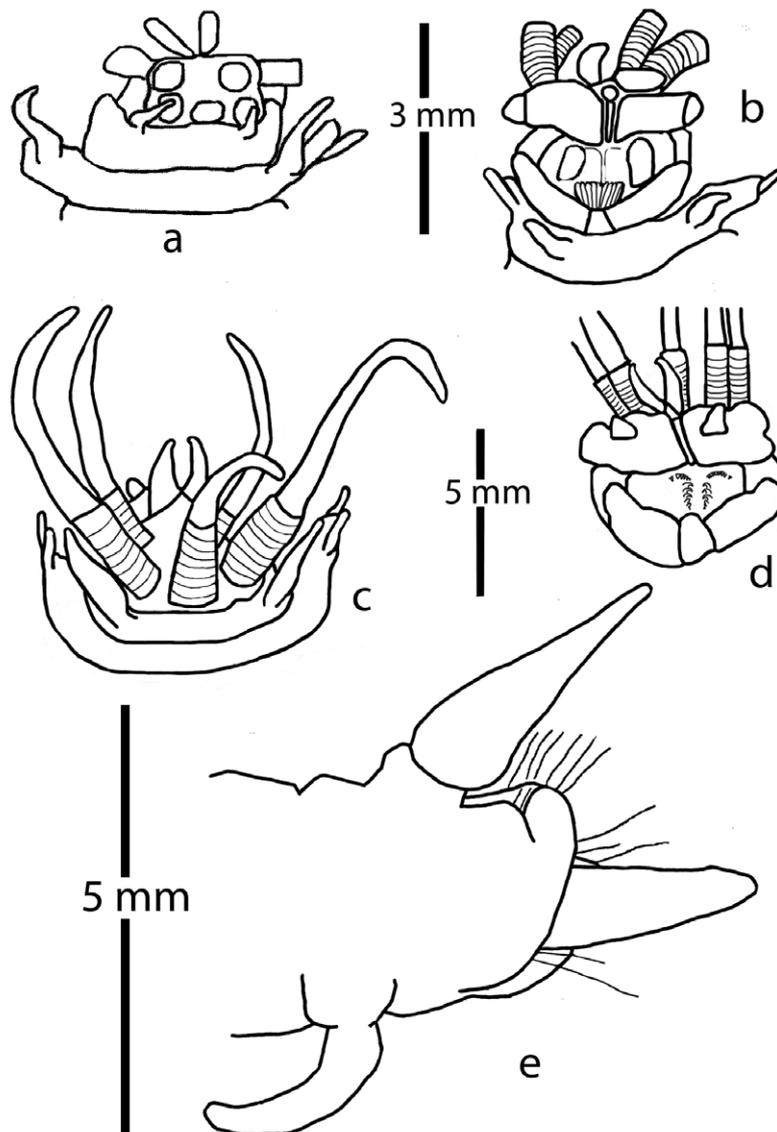


PLATE 2. *Diopatra marocensis* Paxton et al 1995; USNM 17584, paratype

- a. dorsal view of anterior of small specimen showing prostomium with palpophores and antennophores removed to show horse-shoe pattern of placement plus peristomium with peristomial cirri.
 b. ventral view of anterior of small specimen showing upper and upper lips and lower external lips

Diopatra cryptornata USNM 112825, holotype

- c. dorsal view of anterior of large specimen showing prostomium with palpophores and antennophores with proximal rings plus peristomium with peristomial cirri.
 d. ventral view of anterior of large specimen showing upper and upper lips and lower external lips.
 e. anterior view of parapodium of chaetiger 1 showing dorsal and ventral cirri, prechaetal lobes with distal ear-shaped extension; the upper edge of the acicular lobe and the extended tapering section of the postchaetal lobe.

of parapodia with median lobe shifting to a position between dorsal chaetal fascicle and remaining ventral chaetae. Median lobe increasingly tapering from a wide base; gradually decreasing in size towards posterior region but still distinct at end of all fragmentary specimens. Ventral cirri subulate on first four chaetigers, ear-shaped in chaetiger 5 becoming a large, flattened glandular structure curving around lower lateral side of body covering about 1/3 of total width of ventrum from chaetiger 6.

Anterior modified parapodia with 3–4 upper simple chaetae and 6–8 falcate pseudocompound hooks in lower fascicles. Hooks with short, bluntly pointed hoods and smooth shafts. Remaining parapodia mainly with strongly serrated limbate chaetae. Pectinate chaetae flat with straight distal margins, each with six coarse teeth in all chaetigers. Pectinate chaetae first present from chaetiger 6 in holotype, and from chaetigers 5–6 in other specimens. Starting from chaetiger 16 in holotype, and from chaetigers 17–19 in other specimens, lower limbate chaetae replaced by paired thick bidentate subacicular hooks with very thin translucent guards. One hook located at lower edge of chaetal fascicle and parallel to lower chaetae; second hook originating at about same location in parapodia, but directed distinctly ventrally; second hook located in front of inflated bases of ventral cirri; usually considerably larger than first hook.

Branchiae with more than 10 spiraled whorls of long filaments present from chaetiger 4 or 5 continued to end of all fragments. Best developed branchiae present on chaetigers 6–7; branchiae becoming gradually reduced but with several filaments at end of fragments.

Mandibles well sclerotized with partially calcareous distal cutting plates. Distal indentations along edge of cutting plates distinct. Maxillae heavily sclerotized; teeth flattened and triangular. Maxillary formula (based on one paratype): Mx I = 1 + 1; Mx II = 7 + 7; Mx III = 7 + 0; Mx IV = 7 + 9; Mx V = 1 + 1.

Tube cylindrical and covered with debris, mostly sea grass fragments and pieces of shells attached on all sides; permanently buried part of tube thin-walled and covered by fine sand.

Etymology. The species is named for the presence of the paired dorsal papillae, well hidden under the large and bushy branchiae (cryptos – hidden; ornata- ornamented).

Discussion. Two features appear to make *Diopatra cryptornata* unique. The dorsal papillae have not been mentioned for any species of *Diopatra* as far as we can determine. In addition, all species of *Diopatra* described so far have at least some bidentate or tridentate pseudocompound hooks. In this species all hooks are falcate. Paired subacicular hooks appear to be common among species of *Diopatra*; at least all three species treated in this paper have them.

Geographical distribution. *Diopatra cryptornata* is known from two localities, Huelvas, Spain, west of Gibraltar, and the type locality, Obidos, Portugal.

***Diopatra neapolitana* delle Chiaje 1841**

Plate 3

Diopatra gallica Quatrefages 1866 (<XREF>Quatrefages, 1866a): 338–340, pl. 6 bis, figs. 1–3. (<XREF>Quatrefages, 1866b).
Diopatra neapolitana. Saint-Joseph 1898 (<XREF>Saint-Joseph, 1898): 243–254, pl. 13, figs. 31–33, pl. 14, figs. 34–39 (<XREF>Saint-Joseph, 1898).

Material examined: USNM 1128511, Socoa, France., 27 June 2006, (10); USNM 1128509, Socoa, France, 27 June 2007 (1); USNM 1128510, Aveiro, Portugal, 16 May, 2006 (1); USNM 1128519, Aveiro, Portugal, 16 May, 2006 (9); USNM 1128520, Aveiro, Portugal, 18 May, 2006 (9); Aveiro, Portugal, (1); USNM 1128515, Castropol, Spain, 27 May 2006 (1); . USNM 1128513, Huelva Spain, 1 July 2006, coll. SAW et al. (2, marked specimens 1 and 2); USNM 1128516, Huelva, Spain, 1 July 2006 (8); USNM 1128508, Laredo, Spain, 28 June 2006 (2); USNM 1128512, Laredo, Spain, 28 June 2006 (9).

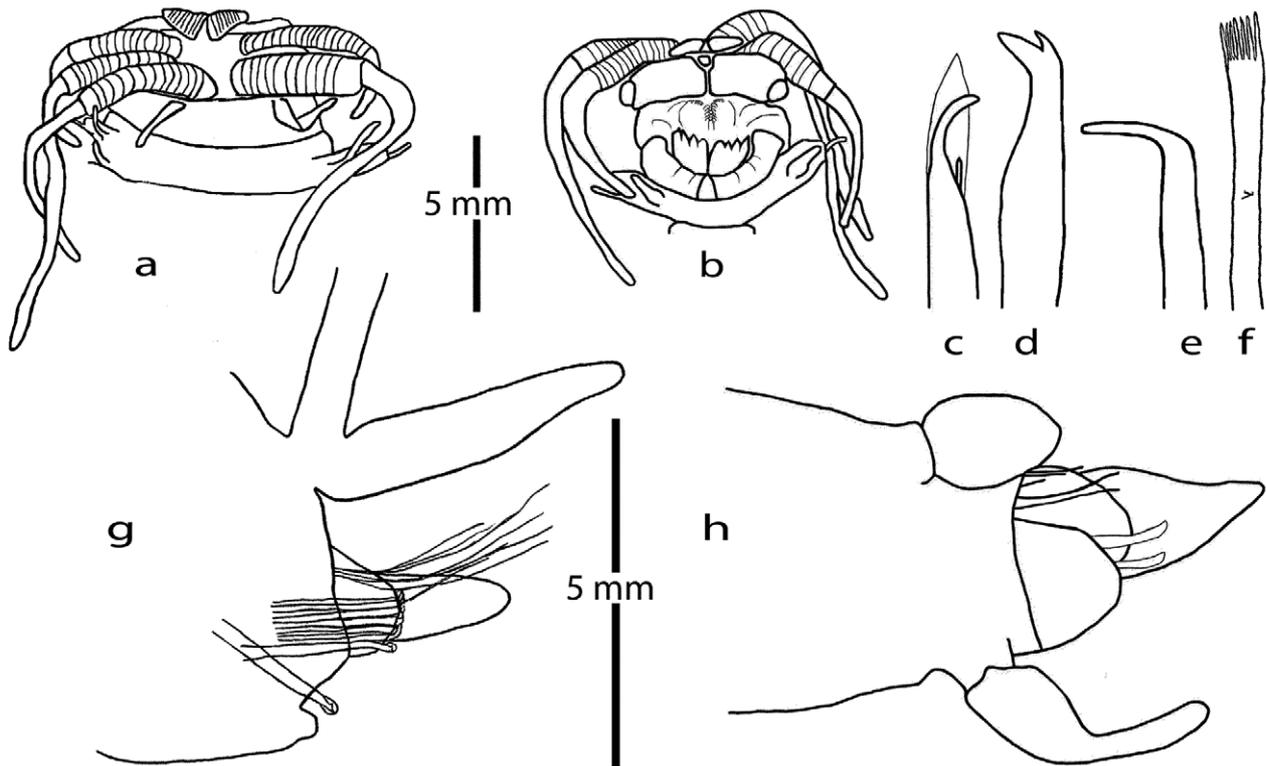


PLATE 3. *Diopatra neapolitana*. Delle Chiaje 1841, Aveiro, Portugal, USNM 1128510.

- a. dorsal view of anterior showing prostomium with palpophores and antennophores with proximal rings and triangular support for the frontal lips plus the peristomium with peristomial cirri.
- b. ventral view of anterior showing upper and upper lips and lower external lips with semicircular lateral ends. Note the rounded papilla at the junction of the four buccal lips
- c. distal end of pseudocompound chaeta from first modified chaetiger.
- d. subacicular hook from median chaetiger,
- e. distal end of median acicula from median chaetiger, showing distal strongly bent end.
- f. pectinate chaeta from median chaetiger.
- g. anterior view of parapodium 25 showing vertical row of distally bent acicula (see also fig. 3e) and showing positions and emergence of two thick bidentate subacicular hooks, one just below the ventral edge of the limbate chaetae and parallel to those chaetae and one at an angle to the other chaetae and emerging below the lower edge of the limbate chaetae.
- h. anterior view of parapodium in first modified chaetiger showing dorsal and ventral cirri, a transverse prechaetal fold, a distally rounded prechaetal lobe covering upper chaetae, the rounded postchaetal lobe and the posteriorly directed elongated postchaetal lobe.

Additional material examined: USNM 5105, Gulf of Naples, Italy, (transferred from Stazione Zoologica). Arcachon Beach, France, types of *Diopatra gallica* collected and identified by Armand de Quatrefages. Arcachon Beach collected and identified by Antoine de Saint-Joseph; these previously reported lots from Arcachon Beach are kept in the Muséum National d'Histoire Naturelle, Paris.

Diagnosis: Upper lip with anterior median papilla between halves, ridge absent. Anterior dorsum without ornamentation. First four to five chaetigers with bidentate pseudocompound hooks; hoods moderately long and pointed. Subacicular hooks present from chaetigers 14-18. Pectinate chaetae with 5-6 teeth throughout body.

Description: Specimen described from Aveiro (USNM 1128510); a complete specimen with approximately 130 segments, 55mm long and about 10mm wide at chaetiger 10. Anterior end dorsally strongly convex and ventrally flattened, median part wider than anterior end with both dorsal and ventral sides weakly convex. Body tapering from about chaetiger 100 to posterior end. Living specimens whitish dorsally and light rose-colored laterally and ventrally with scattered small brown spots, similar spots also present on antennae and palps. A brown band present across chaetiger 5 (retained in most preserved specimens). A few specimens stored in ethanol have brown pigmentation dorsally in the branchial region.

Prostomium rounded posteriorly in dorsal view (Plate 3a) with palps and antennae attached along hemispherical posterior edge. Both palps and antennae very large filling in nearly totally dorsal surface of prostomium (Plate 3a). Palps reaching chaetiger 2 in specimen described; in other specimens reaching chaetigers 1–3. All antennae similar in length, reaching chaetiger 7 in specimen described; in other specimens reaching chaetigers 4–13. Palpophores with five rings in specimen described; other specimens with up to six rings. Antennophores in specimen described with eight rings, other specimens with 4–8 rings. Antennophores and palpophores lack lateral papillae. Nuchal grooves are curved, forming nearly a circle in adults. One pair of small brown eyespots present near bases of lateral antennae. Peristomium as long as first chaetiger. Peristomial cirri about as long as peristomium. Frontal lips attached to sides of a triangular, pointed median prostomial tip. Lips short and blunt possibly contracted. Upper lips (Plate 3b) well separated transversely elongated cushions with a distinct papilla attached near midline. A thin flap of tissue linking frontal and upper lips near base. Tripartite lower lip fused to underlying structure except in far lateral edge, median portion quadratic lateral portions distally rounded with the outer edges forming semi-circular free edges. This lip with a semicircular cross-section, rather than being flattened.

Mandibles weakly sclerotized with calcareous distal cutting plates. Distal indentations along edge of cutting plates present, but not very distinct. Maxillae white, thick and calcareous. 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.

First five parapodia not enlarged, located laterally, projecting laterally, ventrally and slightly anteriorly. Prechaetal lobes (Plate 3h) rounded covering dorsalmost chaetal fascicle. Postchaetal lobes low oblique folds covering chaetal bases distinct; median lobe subulate. Parapodia of chaetiger 6 to about chaetiger 20 increasingly conical and directed dorsally.

Postbranchial parapodia (Plate 3g) bluntly conical, and directed laterally. Prechaetal lobes low folds; postchaetal lobes a similar fold, with a distinct projecting lobe attached medially; medial lobe decreasing in size posteriorly but still recognizable at posterior end of body. First five chaetigers with small ventral protrusions at base of postchaetal lobes. Ventral cirri cirriform on first four chaetigers; rounded in chaetiger 5 and represented by rounded glandular pads in remaining chaetigers. Other specimens examined with cirriform ventral cirri in either four or five chaetigers, apparently independently of size of specimen.

Modified parapodia with 1–2 upper simple chaetae and 4–5 bidentate pseudocompound hooks. Hooks with moderately long pointed hoods (Plate 3c) and two rows of blunt small spines along the shafts. Remaining parapodia mainly with strongly serrated limbate chaetae. Pectinate chaetae flat with straight distal margins; each with 5–7 coarse teeth (Plate 3f). Pectinate setae present from chaetiger 6. First present from chaetigers 14–18 in specimens examined, lower limbate chaetae replaced by two thick bidentate subacicular hooks (Plate 3d) with thin translucent guards. Upper subacicular hook emerging just below ventral edge of limbate chaetae; running parallel to these chaetae; lower subacicular hooks distinctly at an angle to other chaetae emerging well below lower edge of limbate chaetae. Modified parapodia with one or two acicula, each acicula distally tapering to straight blunt tips; in unmodified segments about five acicula in a single row; each acicula distally sharply bent dorsally (Plate 3g).

Branchiae with up to five spiraled whorls of relatively short filaments first present at chaetiger 5 and continuing to chaetiger 34 in specimen examined; posterior extent of branchiae varying from chaetigers 14–37 in other specimens. Position of the last branchia strongly correlated with width of specimens. Best developed branchiae present on chaetigers 6–7; branchiae becoming gradually reduced posteriorly but almost all branchiae with several filaments; only last 1–2 pairs single.

Mandibles weakly sclerotized with calcareous distal cutting plates. Distal indentations along edge of cutting plates present, but not very distinct. Maxillae white, thick and calcareous. 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.

Modified parapodia with 1–2 upper simple chaetae and 4–5 bidentate pseudocompound hooks. Hooks with moderately long pointed hoods (Plate 3c) and two rows of blunt small spines along the shafts. Remaining parapodia mainly with strongly serrated limbate chaetae. Pectinate chaetae flat with straight distal margins; each with 5–7 coarse teeth (Plate 3f). Pectinate chaetae present from chaetiger 6. First present from chaetigers 14–18 in specimens examined lower limbate chaetae replaced by two thick bidentate subacicular hooks (Plate 3d) with thin translucent guards. Upper subacicular hook emerging just below ventral edge of limbate chaetae; running parallel to these chaetae; lower subacicular hooks distinctly at an angle to other chaetae emerging well below lower edge of limbate chaetae. Modified parapodia with one or two acicula, each acicula distally tapering to straight blunt tips; in unmodified segments about five acicula in a single row; each acicula distally sharply bent dorsally (Plate 3g).

Pygidium with four pygidial cirri of which two ventral cirri are longer than two dorsal ones.

Tube cylindrical; covered with debris, mostly sea grass fragments and pieces of shells attached on all sides of tube; permanently buried part of tube thin-walled and covered by fine sand.

Discussion. The specimen from the Gulf of Naples (USNM 4105) is rather poorly preserved; it is larger than the specimens from Aveiro, but resembles them in most features. The structure of the prostomium is essentially identical, including the triangular support for the frontal lips. The upper lips are inflated so the free distal semicircular end is indistinct in this specimen. An unusual feature in both specimens is the triangular support for the frontal lips, and, at least in well preserved material, the semicircular lateral ends to the lower lips.

Geographical distribution. *Diopatra neapolitana* has been widely reported from the Indian Ocean and the Atlantic Ocean. In addition to the type locality in the Gulf of Naples, we can confirm that the species is present along the Atlantic coasts of Spain, Portugal and France. The other localities must be verified by comparisons of specimens taking into the consideration that even the relatively limited area studied here contains four species with which it may be confused.

Key to species included in this paper

1. Anterior modified parapodia with two elongated postchaetal lobes, anterior pectinate chaetae with 18–20 or more teeth *D. biscayensis*, **new species**
2. Anterior modified parapodia with a single elongated postchaetal lobe, anterior pectinate chaetae with no more than 12 teeth 2
3. Anterior dorsum without paired papillae; anterior pseudocompound chaetae bidentate 3
4. Anterior dorsum with paired papillae from chaetigers 7–8 through chaetigers 33–39; anterior pseudocompound chaetae falcate *D. cryptornata*, **new species**
5. Anterior dorsum with paired large white, black-ringed patches. Anterior pectinate chaetae with 11–12 teeth and median pectinate chaetae with 15–18 teeth. *D. marocensis* Paxton et al. 1995
6. Anterior dorsum without large white patches. Pectinate chaetae with less than 10 teeth throughout 4
7. Frontal lips supported by sharply pointed triangular projection from the prostomium; pectinate chaetae with less than 10 teeth throughout *D. neapolitana* (delle Chiaje 1841)
8. Frontal lips supported by transverse frontal edge of the prostomium, pectinate chaetae with about 10 teeth in the posterior end *D. micrura* Pires et al. 2010

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