



New insights in the biogeographical distributions of two Spionidae (Annelida) from the NE Atlantic and Mediterranean French coasts

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Abstract

We report the first occurrences of *Spiophanes afer* Meißner, 2005 and *Prionospio cristaventralis* Delgado-Blas, Díaz-Díaz & Viéitez, 2018 from French marine waters (from the southern part of the Bay of Biscay in NE Atlantic, and the Gulf of Lion in the Mediterranean Sea). Morphological characters of *S. afer* include the presence of an occipital antenna, dorsal ciliated organs extending to chaetigers 13–15, neuropodial hooks from chaetiger 15, ventrolateral intersegmental pouches from chaetigers 14–15, chaetal spreaders of “2+3 type”, and conspicuous dark brown pigmentation on parapodia of chaetigers 9–13. *Prionospio cristaventralis* has four pairs of branchiae (1st and 4th pinnate, 2nd and 3rd apinnate), ventral crests from chaetigers 11–12, high dorsal crests on chaetigers 10–11, and very large notopodial prechaetal lamellae on anterior chaetigers. Both records represent northern extensions of their known distributions. However, the presence of *S. afer* on French coasts may have been overlooked for several decades. The validity of the recently proposed *Spiophanes adriaticus* is questioned.

Key words: polychaetes, *Spiophanes adriaticus*, *Spiophanes afer*, *Prionospio cristaventralis*, Bay of Biscay, Gulf of Lion

Introduction

Spionidae (Annelida: Polychaeta) is a large taxon currently including 38 genera and 590 valid species worldwide (Read & Fauchald 2019). They inhabit both fresh and marine waters with silty, sandy and rocky bottoms, from shallow to deep waters, and from clean to polluted environments (Blake *et al.* 2017, Martinez & Adarraga 2019). In the Bay of Biscay and Mediterranean waters, new species are regularly recorded as progress is made in the systematics and biogeography of Spionidae (Aguirrezabalaga & Ceberio 2005; Meißner 2005; Çinar *et al.* 2015; Lavesque *et al.* 2015; Radashevsky *et al.* 2016; Surugiu 2016; Bogantes *et al.* 2018; Delgado-Blas *et al.* 2018; Delgado-Blas *et al.* 2019; Radashevsky *et al.* 2019).

Among spionids, species of *Spiophanes* and *Prionospio* are regularly found in samples from French coastal

marine waters. The genera *Prionospio* Malmgren, 1867 and *Spiophanes* Grube, 1860 comprise 104 and 31 species, respectively, of which nine and five have been reported from French waters (RESOMAR 2019; OBIS 2019): *P. caspersi* Laubier, 1962, *P. cirrifera* Wirén, 1883, *P. dubia* Day, 1961, *P. elhersi* Fauvel, 1928, *P. fallax* Söderström, 1920, *P. multibranchiata* Berkeley, 1927, *P. saldanha* Day, 1961, *P. sexoculata* Augener, 1918, *P. steenstrupi* Malmgren, 1867, and *S. bombyx* (Claparède, 1870), *S. kroyeri* Grube, 1860, *S. duplex* (Chamberlin, 1919), *S. reyssi* Laubier, 1964 and *S. viriosus* Meißner & Hutchings, 2003. However, in recent surveys along the French coast of the Bay of Biscay two additional spionid species hitherto not reported from the French Atlantic were collected: *Prionospio cristaventralis* Delgado-Blas, Díaz-Díaz & Viéitez, 2018 and *Spiophanes afer* Meißner, 2005. *Prionospio cristaventralis* was originally described from the Spanish Atlantic coast of the Bay of Biscay (Delgado-Blas *et al.* 2018), while *S. afer* was described from waters adjacent to the African continent (Mediterranean Sea and South Atlantic Ocean) with the type locality in the Spanish Mediterranean Sea between Cape San Antonio and the Port of Valencia (Meißner, 2005) (Fig. 1). The latter had never been recorded in Atlantic waters further north than on the continental shelf off Aveiro, Portugal (Gil 2011; Ravara & Moreira 2013, Delgado-Blas *et al.* 2019). Furthermore, NE Atlantic reports of *S. afer* are very rare, with records in the 1st and 2nd part of the SEPLAT 7 campaigns in 1981 and 1983 (Gil 2011), and in 1995 and 1996 (Ravara & Moreira 2013). Prior to our study, *S. afer* had also not been reported from the French Mediterranean coast.

In this study we analyse the geographical distributions of both species, and provide complementary morphological information.

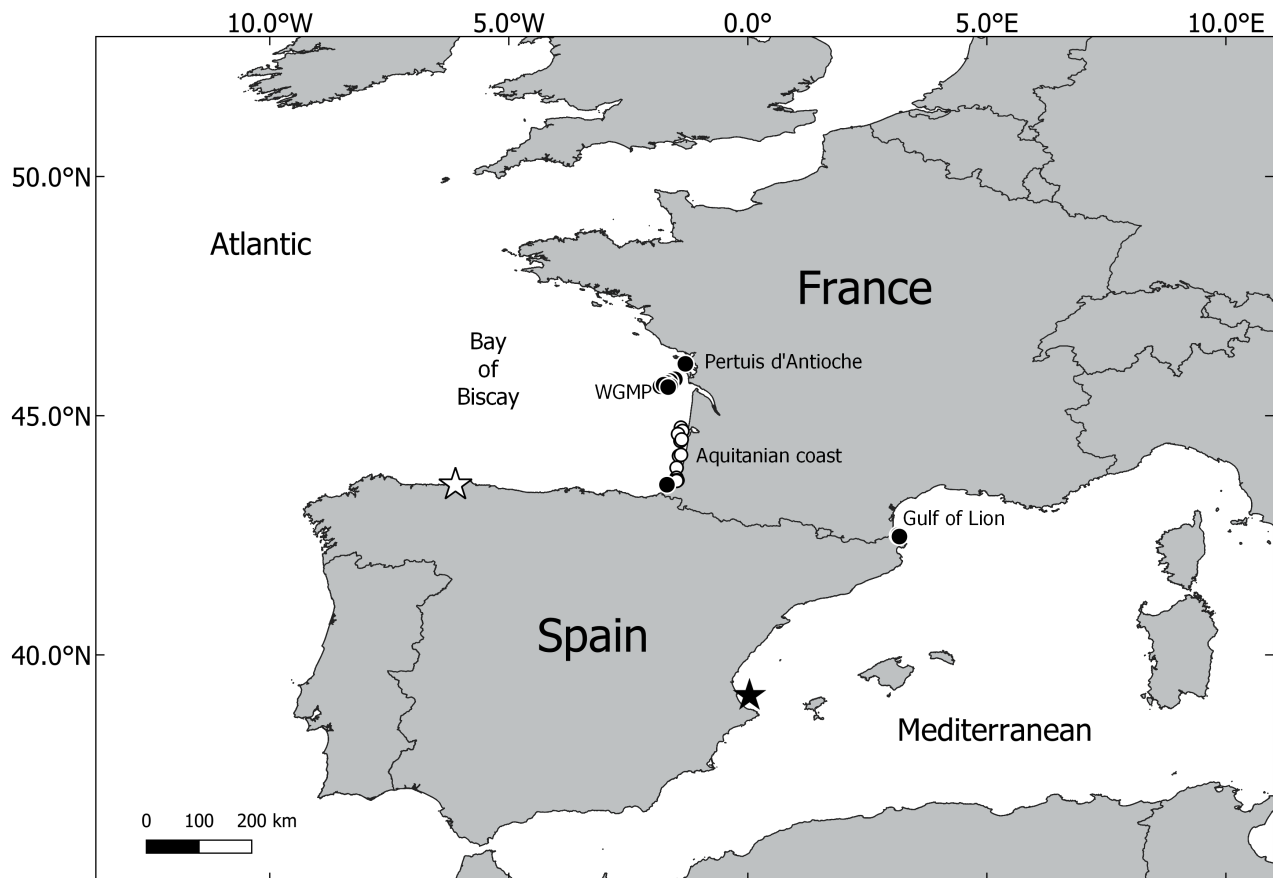


FIGURE 1. *Spiophanes afer* (black dots) and *Prionospio cristaventralis* (white dots) distributions along French coasts (WGMP: West Gironde Mud Patch). Black and white stars indicate the respective type localities.

Material and methods

Samples examined in the course of the present study were collected during several benthic ecology projects. OBIONE is an annual monitoring project implemented since 2011 on a subtidal SOMLIT (*i.e.*, French Coastal

Monitoring Network, Liénart *et al.* 2018) station located between Ré and Oléron islands (Pertuis d'Antioche) at 40 m water depth on muddy sands (Fig. 1, Table 1). The JERICO project was implemented from 2016 to 2018 at the West Gironde Mud Patch (WGMP), a 420 km² clay-silt sedimentary area, 25 km off the mouth of the Gironde Estuary in the Bay of Biscay (Deflandre 2016, Massé *et al.* 2016) (Fig. 1). The RTE (French transmission system operator: <https://www.rte-france.com/en>) is a biosedimentary study carried out in May 2018 on sandy sediments, from 20 to 120 m water depth, along the Aquitanian coast (southern Bay of Biscay). The REDIT, RNMCB and IBIS projects were implemented between 2009 and 2018 in the Gulf of Lion (French Catalan coast, NW Mediterranean).

TABLE 1. Sampling stations from where *Spiophanes afer* (*S.a.*) and *Prionospio cristaventralis* (*P.c.*) were collected. Coordinates are in WGS84. (HMS: Heterogeneous muddy sand).

| | Station | Y (N) | X (E) | Species | Years | Abundances | Depth (m) | Sediment |
|---------------------------|---------|----------|----------|-------------|---------|------------|-----------|-------------|
| Gulf of Lion | 26 | 42.4987° | 3.1465° | <i>S.a.</i> | 2017 | 2 | 31 | Sandy Mud |
| | 183 | 42.5083° | 3.1518° | <i>S.a.</i> | 2018 | 2 | 40 | Sandy Mud |
| | Em_30 | 42.4839° | 3.1467° | <i>S.a.</i> | 2017 | 1 | 31 | HMS |
| | Y30 | 42.5053° | 3.1452° | <i>S.a.</i> | 2010 | 1 | 30 | HMS |
| | Z40 | 42.4738° | 3.1699° | <i>S.a.</i> | 2010 | 3 | 40 | Sandy Mud |
| Pertuis d'Antioche | SOMLIT | 46.0842° | -1.3083° | <i>S.a.</i> | 2011-18 | 5 | 40 | Muddy Sand |
| WGMP | 1 | 45.7617° | -1.5278° | <i>S.a.</i> | 2016-18 | 1 | 40 | Mud |
| | 2 | 45.7244° | -1.6292° | <i>S.a.</i> | 2016-18 | 1 | 47 | Mud |
| | 3 | 45.6825° | -1.6917° | <i>S.a.</i> | 2016-18 | 1 | 56 | Mud |
| | 4 | 45.6139° | -1.8297° | <i>S.a.</i> | 2016-18 | 1 | 69 | Mud |
| | 7 | 45.6208° | -1.6253° | <i>S.a.</i> | 2016 | 1 | 53 | Mud |
| | 8 | 45.6483° | -1.7633° | <i>S.a.</i> | 2016-18 | 1 | 61 | Mud |
| | 9 | 45.5981° | -1.6689° | <i>S.a.</i> | 2016 | 1 | 55 | Mud |
| | P40 | 43.5572° | -1.6936° | <i>S.a.</i> | 2018 | 1 | 112 | Fine Sand |
| | P07 | 44.7500° | -1.4014° | <i>P.c.</i> | 2018 | 1 | 35 | Medium Sand |
| Aquitanian coast | P09 | 44.6433° | -1.4192° | <i>P.c.</i> | 2018 | 5 | 47 | Medium Sand |
| | P10 | 44.5981° | -1.4272° | <i>P.c.</i> | 2018 | 1 | 55 | Fine Sand |
| | P12 | 44.4736° | -1.4103° | <i>P.c.</i> | 2018 | 1 | 51 | Coarse Sand |
| | P13 | 44.6806° | -1.3708° | <i>P.c.</i> | 2018 | 1 | 35 | Medium Sand |
| | P14 | 44.6156° | -1.4608° | <i>P.c.</i> | 2018 | 3 | 59 | Medium Sand |
| | P15 | 44.5033° | -1.3856° | <i>P.c.</i> | 2018 | 1 | 46 | Coarse Sand |
| | P19 | 44.1597° | -1.4414° | <i>P.c.</i> | 2018 | 1 | 47 | Fine Sand |
| | P21 | 44.1808° | -1.3994° | <i>P.c.</i> | 2018 | 3 | 39 | Fine Sand |
| | P23 | 43.9119° | -1.4911° | <i>P.c.</i> | 2018 | 1 | 48 | Fine Sand |
| | P25 | 43.7014° | -1.4942° | <i>P.c.</i> | 2018 | 1 | 40 | Fine Sand |
| | P29 | 43.6494° | -1.4733° | <i>P.c.</i> | 2018 | 1 | 19 | Fine Sand |
| | P30 | 43.6458° | -1.5183° | <i>P.c.</i> | 2018 | 1 | 46 | Fine Sand |
| | P33 | 43.6369° | -1.4914° | <i>P.c.</i> | 2018 | 1 | 29 | Fine Sand |

Sampling gear included a Smith-McIntyre grab (Pertuis d'Antioche), a Hamon grab (WGMP and Aquitanian coast), and a van Veen grab (Gulf of Lion), sampling 0.1 m² (Pertuis d'Antioche, Gulf of Lion) or 0.25 m² (WGMP and Aquitanian coast). All samples were washed through a 1 mm-mesh sieve and preserved with a 10% formalin/marine water solution on board. They were subsequently washed again through a 0.5 mm-mesh sieve. Extracted macrofauna was preserved in 70% ethanol. For identification a Leica M205C stereomicroscope equipped with a Leica MC190 HD camera and an Olympus BH2 light microscope were

used. Following Meißner (2005) we define body width in *Spiophanes* as the distance between the distalmost points of both parapodial rami from chaetiger 4 (chaetae and postchaetal lobes disregarded) seen from above. Some specimens were stained with a dark solution of methyl green in ethanol. Specimens were dipped into the solution for five minutes, allowed to destain in ethanol for a few seconds, then observed in water. Specimens of *P. cristaventralis* used for scanning electron microscopy (SEM) were critical point dried, gold coated, then examined and photographed with a Hitachi TM3030. Part of the studied material is deposited at the Muséum National d'Histoire Naturelle, Paris (MNHN) and the Senckenberg Museum, Frankfurt (SMF).

Results

This study focused on the examination of twenty-two specimens of both *S. afer* and *P. cristaventralis* (Table 1). While, *S. afer* was collected from all localities, *P. cristaventralis* was sampled only in the Aquitanian coast. Further descriptions of both species are provided in the systematic account section. In addition, among the nine *Spiophanes* specimens from the French Mediterranean coast off Banyuls-sur-Mer, four sampled in 2010 and previously identified as *Spiophanes viriosus* Meißner & Hutchings, 2003 were re-examined and eventually attributed to *S. afer*.

Systematic account

Spionidae Grube, 1850

Spiophanes Grube, 1860

Spiophanes afer Meißner, 2005 (Fig. 2)

Type locality. Between Cape San Antonio and Port of Valencia, Mediterranean Spanish coast (Fig.1).

Material examined. Non-type material: NE Atlantic Ocean, Bay of Biscay, Pertuis d'Antioche, 40 m, 3 specimens (September 2011, MNHN-IA- PNT 100; 2016, MNHN-IA- PNT 101 and 2018, SMF 28059), West Gironde (WGMP) and Aquitanian coast, 40–69 m, 3 specimens (2016, MNHN-IA- PNT 110; March, MNHN-IA- PNT 111; and August 2017, MNHN-IA- PNT 112); Mediterranean Sea, off Banyuls-sur-Mer, 30–40 m, 9 specimens (2010, MNHN-IA- PNT 106, MNHN-IA- PNT 107, MNHN-IA- PNT 108, MNHN-IA- PNT 109; 2017, MNHN-IA- PNT 102, MNHN-IA- PNT 103, MNHN-IA- PNT 105; and 2018 SMF 28060, MNHN-IA- PNT 104).

Description of material collected in the course of the present study. All specimens incomplete, 6.4–30 mm long for 22–60 chaetigers, 0.7–1.2 mm wide. Colour in alcohol pale white (West Gironde and Pertuis d'Antioche) to grey/brown (Banyuls sur Mer), except for dark pigmentation on parapodia of chaetigers 9–13 (Fig. 2A). Prostomium broad anteriorly, bell-shaped, with blunt, short anterolateral projections (Fig. 2A). Palps lost. Occipital antenna present. Up to four eye spots, rarely absent (see remarks). Dorsal ciliated organs as two straight ciliated bands along dorsum, extending usually to chaetigers 13–15 (Fig. 2A; see remarks).

Chaetal spreader of “2+3 type” with undulate glandular opening well developed in chaetigers 5–7 (Fig. 2B); opening of glandular organ absent on chaetiger 8, as lateral vertical slits on chaetigers 9–14. Ventrolateral intersegmental pouches present from chaetigers 14–15, fully developed from chaetigers 15–16. Dorsal ciliated crests distinct from chaetigers 17–19, moderately to well developed.

Neuropodium of chaetiger 1 usually with one stout, crook-like chaeta (see remarks) and numerous simple capillaries; notochaetae much longer than neurochaetae, almost twice as long as those of chaetiger 2 (Fig. 2C). Capillaries on chaetiger 2 twice as long as on chaetigers 3–4. From chaetiger 15, with quadridentate non-hooded neuropodial hooks, initially numbering 6–8 (4–7 in Mediterranean specimens). Bacillary chaetae as thin hirsute bristles with brush-like tip, sometimes exposed on chaetigers 5–7. Ventral sabre chaetae from chaetiger 4.

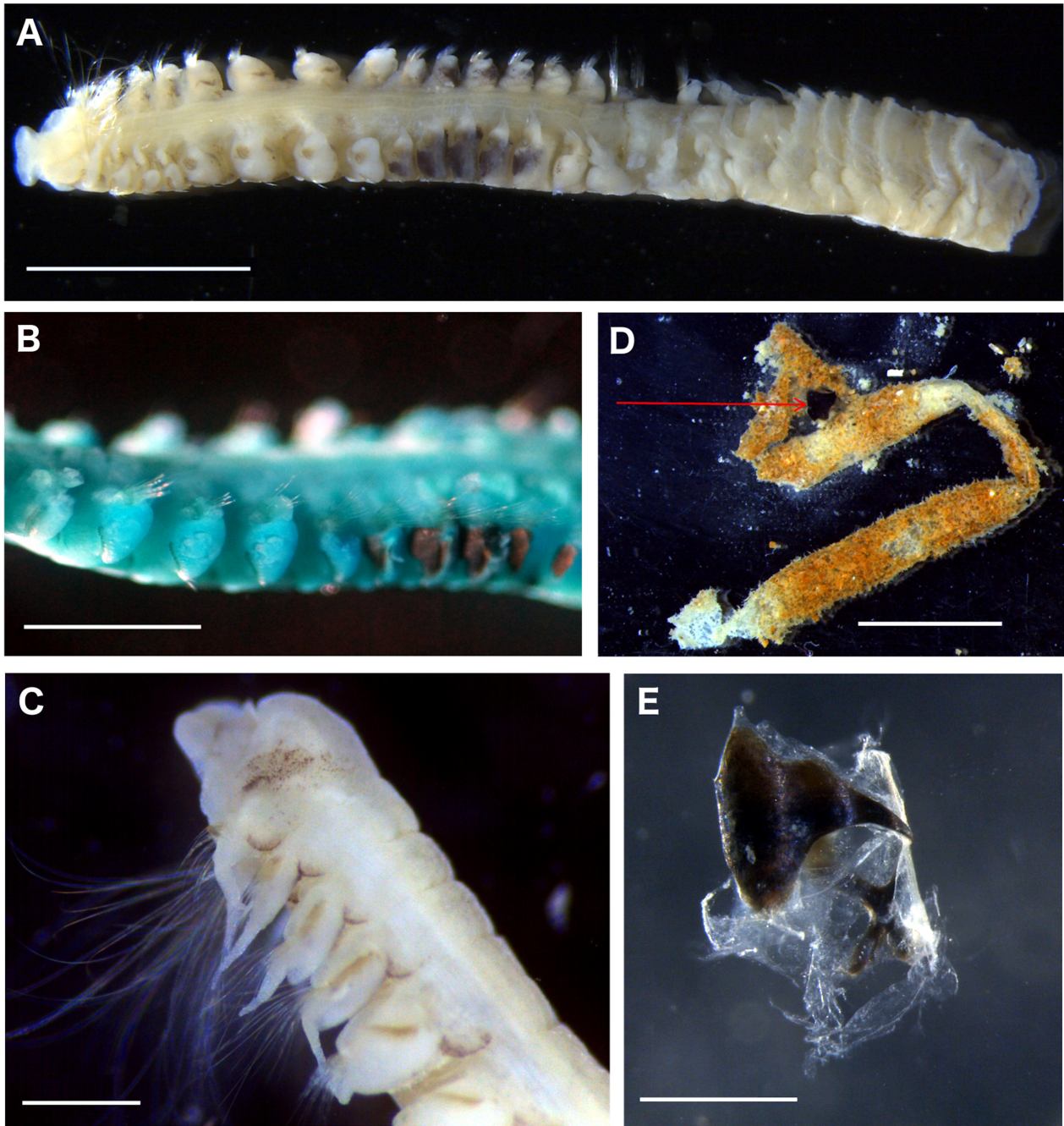


FIGURE 2. *Spiophanes afer*, MNHN-IA-PNT 101 (A, C, D, E), MNHN-IA-PNT 100 (B). A. Anterior fragment, dorsal view, B. Segments 4–13, lateral view, note chaetal spreader of “2+3 type” in chaetigers 5, 6 & 7 and dark brown pigment in chaetigers 9–13; blue colour due to staining with methyl green. C. Anterior region, ventro-lateral view, D. Tube, chitinous ring arrowed, E. Detail of chitinous ring. Scales: A=2 mm, B, E=1 mm, C=500 μ m, D=5 mm.

Pygidium unknown.

Tube. Tube coated with sand (Fig. 2D), sometimes with up to two dark, complex chitinous ring-like structures inside, divided into two parts linked by a transparent membrane, the bigger part nail-shaped with two lateral wings, the second x-shaped (Fig. 2D, E).

Pigmentation. These observations are based on specimens fixed in formalin solution then preserved in 70% ethanol. Dark pigment on chaetigers 9–13 (Fig. 2A, B), most intense anterior to the parapodia and around the opening of the glandular organ, entirely encompassing parapodium on chaetigers 10–11; pigmented area smaller on chaetiger 9 compared to 10–13. Among our specimens, slight variations were observed: in specimens from

the Pertuis Charentais, dark pigmentation of chaetigers 9–13 was more intense than in other localities; West Gironde and Aquitanian specimens were almost completely unpigmented (apart from chaetigers 9–13), while those of Pertuis d’Antioche showed variable patterns of blots of light brown pigment on anterior segments including the peristomium (Fig. 2C).

Methyl green staining pattern. No particular pattern.

Remarks. To date, three valid species of *Spiophanes* are known, presenting the following combination of morphological characters: presence of an occipital antenna, glandular organs in chaetigers 5–7 with “2+3” chaetal spreader type, and obvious dark pigment on chaetigers 9–13. These species are *S. afer* from seas around Africa, *S. kimballi* Meißner, 2005 from off California, USA, and *S. viriosus* Meißner & Hutchings, 2003 from Eastern Australia. The species are easily distinguished by the extension of the dorsal ciliated organs which reach chaetigers 13–15 in *S. afer*, chaetigers 17–18 in *S. viriosus*, and chaetigers 11–13 in *S. kimballi* (Meißner, 2005), this latter exhibiting a distinctive shape. Also, in *S. afer*, ventrolateral intersegmental pouches begin from chaetiger 14 and are first fully developed between chaetigers 15–16. In contrast, they are fully developed from between chaetigers 14–15 in *S. viriosus*, whereas in *S. kimballi* pouches were only observed in reproductive specimens (Meißner, 2005). In addition, to our knowledge, both *S. kimballi* and *S. viriosus* have never been recorded far from their original distribution areas.

Recently a fourth species presenting the same above-mentioned character combination has been described from the Adriatic Sea: *Spiophanes adriaticus* D’Alessandro, Castriota, Maggio, Nasi, Carletti, Auriemma & Romeo 2019 (D’Alessandro *et al.* 2019). However, we are not entirely convinced that *S. adriaticus* is a new species. Based on the type of chaetal spreader (“2+3” with undulate opening in chaetigers 5–7), D’Alessandro *et al.* (2019) acknowledged morphological similarities between *S. adriaticus* and *S. afer* and discussed characters in disagreement between the two species. Accordingly, the first morphological difference is the presence of eyes in adult specimens in *S. adriaticus* whereas they were reported to be only rarely present in juvenile *S. afer* and absent in adult specimens. It has to be considered that the description of *S. adriaticus* is based exclusively on recently collected material preserved in 96% ethanol whereas the description of *S. afer* was undertaken based on material from museum collections collected decades ago and fixed in formalin. Formalin and ethanol preserve pigmentation in a different way, and pigment is well maintained in freshly preserved ethanol material (see *e.g.* figure 13 page 229 in Meißner *et al.* 2014 and page 396 in Meißner & Götting 2015). A second distinctive morphological feature is the length of the dorsal ciliated organs running to about chaetigers 13–15 in *S. afer* and to about chaetigers 11–12 in *S. adriaticus*. However, the illustrations supposedly documenting this in *S. adriaticus* are difficult to interpret and suggest that dorsal ciliated organs could reach chaetiger 13. The third differential character listed by the authors is the shape of parapodia, without detailing the differences. Based on the illustrations provided, such differences are not obvious to us. A fourth distinction is that dorsal ciliated crests are described as usually distinct from chaetigers 18–19 in *S. afer*, and from chaetigers 14–17 in *S. adriaticus*. The crests are usually not well preserved in every specimen and the differentiation between the first presence and their appearance as distinct crest is not clear-cut and might be biased. We do not think that this character is the most reliable but it could of course be an indication of species-level differences. We think the examination of a greater number of specimens from different locations, differently preserved, collected in different seasons, and belonging to different age classes is required before defining stable differential characters. D’Alessandro *et al.* (2019) presented results of morphological examination of 20 specimens collected at two different locations in the Adriatic Sea, but did not conclusively assess ontogenetic variability of various morphological characters. In any case, we are missing comparative studies of morphologically similar species from the publication by D’Alessandro *et al.* (2019). Also, the deposition of type material in museum collections is compulsory but official registration numbers were not provided by the authors. D’Alessandro *et al.* (2019) also retrieved molecular information from their Adriatic specimens but the publication is missing sequence information (*e.g.* GenBank accession numbers). More importantly, the presented phylogenetic analysis of *Spiophanes* species undertaken by D’Alessandro *et al.* (2019) includes only species distantly related to *S. adriaticus*/*S. afer* (based on our judgement of their morphology), and hence neither supports nor rejects the hypothesis of *S. adriaticus* being a formerly unknown *Spiophanes* species. Thus, the separation of *S. afer* and *S. adriaticus* is not well resolved yet, and we reject a formal acceptance of this species and urge the authors to provide registration numbers for type material.

All our specimens are in good agreement with the original description of *S. afer* and only the presence of eye spots was observed to vary.

The main variation observed between our specimens consists in differences in the extension of the dorsal ciliary band: Mediterranean individuals have dorsal ciliary bands mainly extending to chaetiger 13 (instead of chaetiger 15 for Pertuis d'Antioche individuals, or intermediate for West Gironde and Aquitania individuals). However, within localities the dorsal ciliary band extension also varied (to chaetigers 9–14 in Banyuls-sur-Mer, to chaetigers 11–14 in West Gironde). Intraindividual variation was also observed on a specimen showing asymmetric bands: one extending to chaetiger 13 and the other to chaetiger 14 (MNHN-IA-PNT 105). Other observed variations were: no eye spot on one specimen (MNHN-IA-PNT 101), three eye spots on two specimens (MNHN-IA-PNT 100 and MNHN-IA-PNT-105), and two crook-like chaetae on chaetiger 1 neuropodium of one specimen (MNHN-IA-PNT 111). Mediterranean individuals are generally darker and initially have 4–7 neuropodial hooks (6–8 in the Atlantic).

As previously noted, the occurrence of eye spots is likely linked to preservation method. The dorsal ciliary band extension and initial number of neuropodial hooks are likely to be linked to the development stage and, consequently, to body size (Meißner 2005). Accordingly, our Mediterranean specimens were smaller, measuring 0.8–1 mm wide vs. 1–1.2 mm wide for the Atlantic specimens. However, these characters vary within and among our populations.

The dark chitinous rings found in the tubes of Atlantic specimens have also been reported by D'Alessandro *et al.* (2019). Following these authors, they could have a support function.

Habitat. From intertidal to depths up to 60 m (Meißner, 2005). Between 40 and 112 m, usually in muddy sediments, sometimes on fine sand (*e.g.*, on the Aquitanian coast, this study).

Distribution. Mediterranean Sea: off Spain, off Israel, off France (this study); South Atlantic Ocean: off Namibia; North Atlantic Ocean: Bay of Biscay (this study); Indian Ocean: off South Africa;

Prionospio Malmgren, 1867 *sensu stricto*

Prionospio cristaventralis Delgado-Blas, Díaz-Díaz & Viéitez, 2018 (Fig. 3, 4)

Type locality. Between Cabo Vidio and Cabo de Peñas, Asturias, Spain (Fig. 1).

Material examined. Non-type material: Atlantic, Bay of Biscay, station P21, 39 m, 3 specimens (May 2018, MNHN-IA- PNT 113); Atlantic, Bay of Biscay, station P14, 59 m, 3 specimens (May 2018, MNHN-IA- PNT 114), mounted for SEM; SMF 25 327, Atlantic, Bay of Biscay, station P09, 47 m, 5 specimens (May 2018).

Description. Complete specimen, 22.6 mm long (about 65 chaetigers), 0.9 mm wide. Pale white in alcohol (Fig. 3A). Prostomium bottle-shaped, broadly rounded (Fig. 3A, D), dorsoventrally flattened on anterior margin (Fig. 4A, C); long, narrow caruncle extending to end of chaetiger 2, sinusoidal at posterior end (Fig. 3D); nuchal organs U-shaped. Two pairs of black subdermal eyes in trapezoidal arrangement; those of anterior pair small round, those on posterior pair large crescent-shaped (Fig. 3A).

Four pairs of long branchiae on chaetigers 2–5 (Figs 3A, C, D; 4A, B), first pair slightly longer than fourth, both with long, slender, dense digitiform pinnules on posterior stem faces and very long, naked, smooth distally pointed tips. Pairs 2 and 3 apinnate, shorter than pinnate pairs, but slightly longer than notopodial lamellae.

Notopodial postchaetal lamellae joining dorsally forming dorsal crests (Fig. 4B) from chaetigers 9 to 19, highest on chaetigers 10–11.

Anterior neuropodial prechaetal lamellae connected through poor-developed ventral crests from chaetigers 9 to 14, forming central U-shaped short depressions (Fig. 4D); subsequent chaetigers without ventral crests.

Neuropodial sabre chaetae from chaetiger 10, one per fascicle, stout, distinctly curved, basally smooth, heavily granulated medially and distally, with sheaths. Neuropodial hooded hooks from chaetiger 15, up to 10 per fascicle. Hooks with five pairs of small teeth above large main tooth, and short, small secondary hoods (Fig. 4E).

Pygidium with two short bulbous cirri (Figs. 3B, 4F).

Methyl green staining pattern. Peristomium and posterior dorsal part of prostomium deeply stained, as notopodial lamellae of chaetigers 1–5 and neuropodial lamellae of chaetiger 1, anterior part of caruncle and posterior part of prostomium pigmented (Fig. 3C, D).

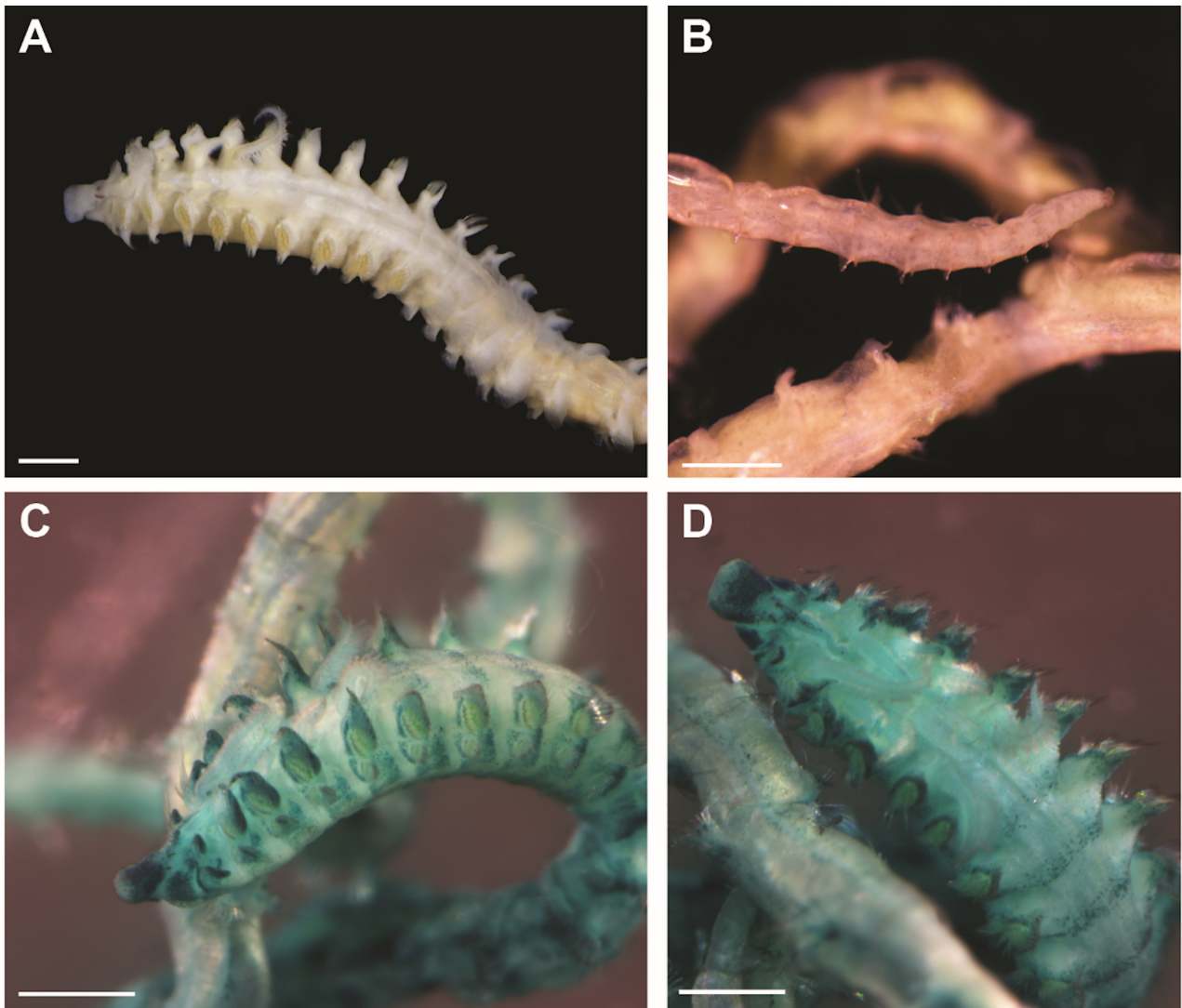


FIGURE 3. *Prionospio cristaventralis*, MNHN-IA-PNT-113. A. Anterior part; B. Pygidium; C. Anterior part, lateral view (Methyl green staining applied); D. Anterior part, dorsal view (Methyl green staining applied). Scales A–D=0.5 mm.

Remarks. The specimens of *P. cristaventralis* from French coast mostly fit in the type description but present a few variations: neuropodial postchaetal lamellae on chaetiger 1 slightly larger than notopodial one (much larger in Spanish specimens), notopodial postchaetal lamellae with pointed tips on chaetigers on chaetigers 2–5 (2–3 in Spanish specimens), dorsal crest begins on chaetiger 9 (10 in Spanish specimens), ventral crest poorly developed (well-developed in Spanish specimens), and sheath on sabre chaetae (absent in Spanish specimens).

Habitat. Shallow waters from 24 to 34 m (Delgado-Blas et al., 2018), in fine to coarse sand from 20 to 60 m (this study).

Distribution. Atlantic Ocean. Cantabrian Sea, Asturias, Spain (Delgado-Blas et al., 2018), Aquitanian coast, Bay of Biscay, France (this study, Fig. 1).

Discussion

Prionospio cristaventralis was recently described from museum specimens collected in the South Bay of Biscay in 1998 (Delgado-Blas et al. 2018) and there is no other information on its geographic distribution to date. These specimens were initially identified as *P. fallax* Söderström, 1920 or *P. caspersi* Laubier, 1962 (Delgado-Blas et al. 2018). Accordingly, specimens of these two species from South Western Europe, especially in the Bay of Biscay, should be re-examined and specimens collected *de novo* will require careful identifications. The

Spanish type locality and the Aquitanian coast are quite close to each other, but the benthic communities of the latter area are still poorly known. However, the seasonal fluctuations in water circulation south to the Bay of Biscay, with eastward drift in autumn/winter and westward drift in spring/summer (Charria *et al.* 2013) may lead to connectivity between northern Spanish and southwestern French coasts, suggesting that the species may be naturally present on the Aquitanian coast.

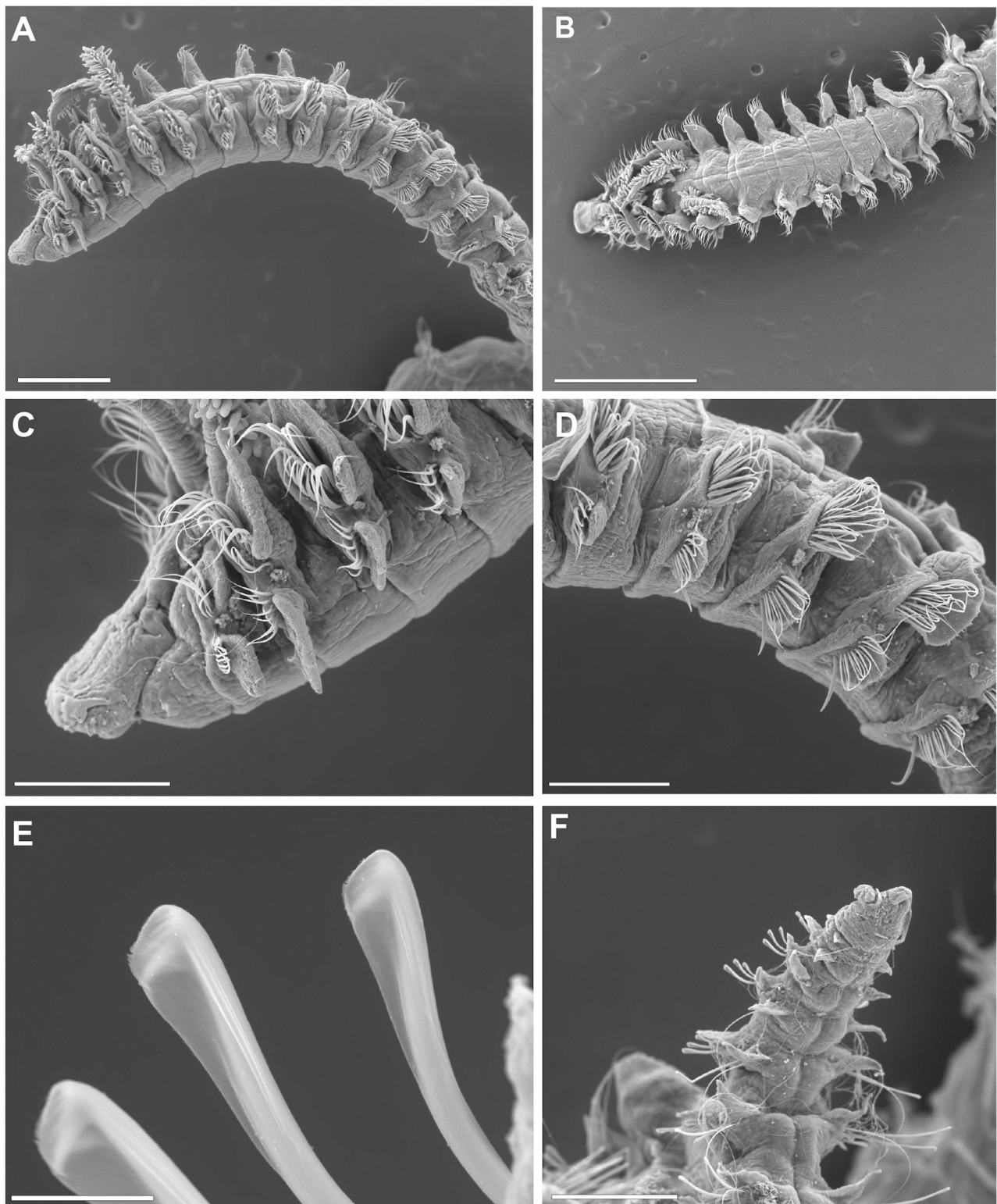


FIGURE 4. *Prionospio cristaventralis* SEM, MNHN-IA-PNT-114. A. Anterior region, lateral view B. Anterior region, dorsal view; C. Anterior region, lateral view; D. Chaetigers 9 to 13, lateral view; E. Neuropodial hooded hooks from far posterior; F. Pygidium, dorsal view. Scales: A, C, F=500 μ m, B=1 mm, C=125 μ m, D=250 μ m, E=15 μ m.

Spiophanes afer was described from its type locality in the Mediterranean Sea near Valencia, but additional records from various localities around the African continent outlined a rather large distribution range (e.g. off Israel, Mozambique, South Africa, Namibia, and Angola) (Meißner 2005; Gil 2011; Moritz 2012). In the Mediterranean the species was reported from the Spanish coast (Meißner 2005; same records confirmed by Delgado-Blas *et al.* 2019), the Adriatic Sea (Mikac 2015), the Aegean Sea off Turkey (Dagli *et al.* 2011; Çinar *et al.* 2014), and Israel (Meißner 2005). Some specimens in our local collection (initially misidentified as *S. viriosus*) were collected off Banyuls-sur-Mer in 2010, and thus represent the first confirmed occurrence of *S. afer* on the French Mediterranean coast. The northern-most records in the Atlantic came from Portugal, off Sines (1980s, Gil 2011) and from off Aveiro (1995–1996, Ravara & Moreira 2013). Considering this, our recent sample of *S. afer* from Pertuis d’Antioche makes it the northern-most record from the NE Atlantic. Moreover, its arrival in the area seems recent since the only *Spiophanes* species known from there to date was *S. bombyx* (de Montaudouin & Sauriau 2000). This latter species has a very different morphology and is unlikely to be confused with *S. afer*.

Also, it has been suggested that most records of *S. kroyeri* from the Western Mediterranean, including the Adriatic, and South European Atlantic refer to *S. afer* (Gil 2011; Mikac 2014). *Spiophanes kroyeri*, being an Arctic species, is unlikely to occur in Southern Europe (Meißner 2005). In French marine waters, *S. kroyeri* has been reported from the Bay of Biscay in the Atlantic (Glémarec 1969; Amoureux 1971; Lagardère 1972) and from Cerbère to Saint Raphael (RESOMAR 2019) in the Mediterranean. However, some specimens of *Spiophanes* from the Bay of Biscay (not *S. bombyx*) show “0+1 type” chaetal spreaders on chaetigers 5–7 and lack pigmentation on chaetigers 9–13. Despite resembling *S. kroyeri*, we suggest they more likely belong to a different, undescribed species (Jourde and Lavesque, unpublished data). *Spiophanes duplex*, described from Southern California, was also reported from the French Mediterranean during 1969–1972 and then in 2009, together with *S. viriosus* (OBIS, 2019; RESOMAR, 2019) and has not been recorded since then. In 2012, *S. afer* was reported between Italy and Spain, including Corsica (OBIS 2019), suggesting that the previous reports of *Spiophanes* in the Mediterranean Sea may also refer to this species. Therefore, despite the fact that we are reporting *S. afer* as present on the French Mediterranean coast at least since 2010, the literature and databases strongly suggest that it has been present in the area for a longer period of time.

In summary, the present state of knowledge on the spatio-temporal distribution of the species of *Spiophanes*, and particularly *S. afer*, does not allow an assessment of its real distribution in Europe. Further investigations will require that museum and private collections be checked, and new morphological and molecular analyses on fresh material (or preserved in a compatible way for DNA extraction) be carried out. In particular, acquisition of DNA sequences of *S. afer* from its type locality is needed to clarify the status of *S. adriaticus*.

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