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ORIGINAL ARTICLE

Brooding deep-water onuphid polychaetes (Annelida) from the Bay of Biscay

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Abstract

We report on three species of deep-water onuphid polychaetes (*Nothria maremontana*, *Paradiopatra hispanica* and *Rhamphobranchium brevibrachiatum*) from the Bay of Biscay from depths of 468 to 1186 m. The three species contained eggs and/or juveniles inside the parental tubes and *R. brevibrachiatum* had a cocoon-like capsule attached on the outside of its tube containing fibres and sperm. We present brief taxonomic descriptions of the three species, including some observations on ontogenetic chaetal changes in *N. maremontana*. The brooded eggs ranged from 300 to 340 µm in diameter in *N. maremontana*, while *R. brevibrachiatum* eggs ranged from 390 to 450 µm; juveniles consisted of 6 chaetigers for *N. maremontana* and 6–45 chaetigers for *P. hispanica*. We describe and illustrate the eggs, juveniles and sperm capsule. Although the origin of the sperm capsule is questionable, we reject the possibility of an unrelated passenger and speculate that the structures contained inside the capsule are long, thin spermatophores of a type not previously known for onuphids.

Key words: Avilés Canyon, benthic fauna, Cantabrian Sea, direct development, Spain, sperm

Introduction

Members of the polychaete family Onuphidae are mostly tubicolous and occur in all oceans from intertidal to the greatest depths. Knowledge of their reproductive biology is scant, particularly that of deep-water species, as its discovery depends on the fortuitous occasions when reproductively active animals are sampled. Onuphid oocytes are relatively large and develop by lecithotrophy, often inside the parental tube. The tube-brooded young have generally been referred to as ‘larvae’, before leaving the tube as juveniles of more than 20 segments to settle on their own (Paxton 1986a; Pires et al. 2012). Here we propose the terms ‘embryo’ and ‘juvenile’ for the directly developing young while they are in the parental tube, a concept that will be explored in the discussion below. Most reports of onuphid tube-brooders are from shallow-water habitats; only four brooding and two viviparous species are known from

depths below 200 m (Paxton 1986a; Budaeva & Fauchald 2010).

We have re-examined material collected during the COCACE (Oceanographic Cruise of the Central Cantabrian Sea) project undertaken during 1987/88 to investigate the fauna of the Cantabrian Shelf and the Avilés Canyon, Spain, in the Bay of Biscay (Louzao et al. 2010). Among the polychaetes collected in depths of 468–1186 m we discovered three species of brooding onuphids: *Nothria maremontana* André & Pleijel, 1989, *Paradiopatra hispanica* (Amoureux, 1972) and *Rhamphobranchium* (*Spinigerium*) *brevibrachiatum* (Ehlers, 1875) with eggs and/or developing juveniles inside their tubes. This is only the second report of brooding *Nothria* and *Paradiopatra*, the first being from the Antarctic by Hartman (1967a). *Rhamphobranchium* species have been reported with coelomic eggs or sperm (Paxton 1986b) and the closely related shallow-water *Brevibranchium maculatum* (Estcourt, 1966) as brooding

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eggs and juveniles within their tubes (Smith & Jensz 1968). However, the discovery of one specimen of *R. brevibrachiatum* with eggs inside its tube and a cocoon-like capsule containing sperm attached near the end of its tube was surprising.

Paradiopatra hispanica and *R. brevibrachiatum* have previously been reported from the Bay of Biscay (Amoureux 1972, 1974a; Campoy 1982; Glémarec 1991; Aguirrezabalaga et al. 2002), while this is the first report of *N. maremontana* since its original description from the Seine and Josephine sea mounts, situated between Madeira and the Iberian coast (André & Pleijel 1989). The aims of the present paper are to provide brief descriptions of the three species, to present some observations on ontogenetic chaetal changes in *N. maremontana*, and to describe and illustrate the developing juveniles of *N. maremontana* and *P. hispanica* and possible sperm of *R. brevibrachiatum*. In the discussion we review the lifestyle and reproductive strategies of the three species in an attempt to explore whether the sperm capsule is a novel strategy for the genus or whether we are dealing with an unrelated passenger.

Material and methods

The material was obtained from the benthic samples of the COCACE (Oceanographic Cruise of the Central Cantabrian Sea) project, conducted from April 1987 to February 1988 in a variety of substrates in the southern Bay of Biscay, north of the Iberian Peninsula. Benthic fauna were sampled using an anchor dredge and/or a Hessler and Sanders model epibenthic sledge (Louzao et al. 2010). Detailed station data are given in the 'Material examined' sections of the respective species. The specimens were anaesthetized in 7% MgCl₂, fixed in 10% neutral buffered formalin and later transferred to 70% ethanol. Specimens were stained with lithic carmine solution and examined under a dissecting stereo microscope. Lithic carmine staining increased the contrast of some morphological structures, such as ceratophore rings, branchiae, parapodial lobes and cirri. Glycerol slides of parapodia were prepared to examine chaetal morphology and distribution and examined under a compound light microscope. For a detailed ultrastructural analysis, specimens were dehydrated in an ascending series of graded ethanol, critical point-dried using acetone as intermediate liquid, mounted on aluminium stubs, sputter-coated with gold and imaged with a JEOL 6610 LV scanning electron microscope (SEM). The treatment of eggs, sperm and larvae for SEM examination was modified and they were rinsed in Millipore ultra-filtered seawater, fixed in buffered 2.5% glutaraldehyde in seawater (pH = 7.2) and submersed in acetone followed by critical point drying.

The specimens are deposited in the Collection of the Department of Biology of Organisms and Systems (Zoology) of the University of Oviedo (BOS) and the Australian Museum, Sydney (AM).

Taxonomy

Family Onuphidae Kinberg, 1865

Subfamily Hyalinoeciinae Paxton, 1986a

Genus *Nothria* Malmgren, 1866

Diagnosis

Prostomium with short palps, moderately long antennae, ceratophores with 2–5 rings. Anterior 2–3 pairs of parapodia enlarged, directed anteroventrally, with large auricular prechaetal lobes and uni- or bidentate simple or pseudocompound falcigers. Limbate chaetae and pectinate chaetae with rolled margins, so-called 'scoop-shaped' or flat, generally from chaetigers 2–3. Subacicular hooks in median position, generally from chaetigers 7–15. Branchiae present or absent, with single or pectinate filaments. Tubes dorsoventrally flattened with thin inner parchment-like layer covered with flat shells or shell fragments and other foreign particles.

Nothria maremontana André & Pleijel, 1989

(**Figures 1A–C, 2–4**)

Nothria maremontana André & Pleijel, 1989: 11, figures 1–3.

Material examined

COCACE stations: GI (43.93°N, 5.66°W) 468 m, 67% sand, 17% silt, 16% clay, 28 April 1987, 2 specimens (BOS), 2 specimens (AM W.45284); I4 (43.91°N, 5.90°W) 720 m, 42% sand, 29% silt, 29% clay, 26 February 1987, 2 specimens (BOS), 1 specimen (AM W.45283); I6 (43.92°N, 6.11°W) 1186 m, 38% sand, 30% silt, 32% clay, 4 July 1987, 1 specimen (BOS).

Diagnosis

Based on specimens wider than 1.9 mm at chaetiger 10 excluding parapodia. First pair of parapodia extending beyond frontal margin of prostomium, with simple bidentate falcigers. Second pair of parapodia with bidentate, weakly pseudocompound falcigers. Third pair of parapodia with bidentate compound falcigers, limbate and pectinate chaetae. Pectinate chaetae with rolled lateral margins, with 16–20 teeth. Simple branchiae from chaetigers 9–10. Subacicular hooks from chaetigers 10–12. Eyes present or absent.

Description

All specimens incomplete, lacking posterior ends (Figure 1A–C); smallest specimen (Figure 2C) measuring 8 mm for 22 chaetigers, width 0.6 mm (at chaetiger 10, excluding parapodia); largest specimen (Figure 2A) measuring 25 mm in length for 35 chaetigers, width 2.7 mm. Alcohol-stored specimens overall cream-coloured, no pigment pattern. Following description based on specimens wider than 1.9 mm.

Prostomium (Figure 2A,B) anteriorly rounded; paired ovoid frontal lips almost twice as long as wide. Palps reaching chaetiger 1, lateral antennae reaching chaetigers 4–8, median antenna reaching chaetigers 7–10; ceratophores of antennae with three

rings. Two eyespots present only on largest specimen, situated near bases of lateral antennae; lacking in all other specimens. Peristomium half as long as first chaetigers, peristomial cirri as long as peristomium.

Anterior three pairs of parapodia modified; first pair greatly enlarged, extending beyond anterior margin of prostomium (Figure 2A,B), with large auricular prechaetal lobes, subulate postchaetal lobes, digitiform dorsal cirri, and subulate ventral cirri (Figure 2D,E). Second pair of parapodia (Figure 2F) similar but smaller and with smaller prechaetal lobes. Third pair of parapodia (Figure 2G) only slightly larger than subsequent parapodia, with further reduced prechaetal lobes; ventral cirri cone-

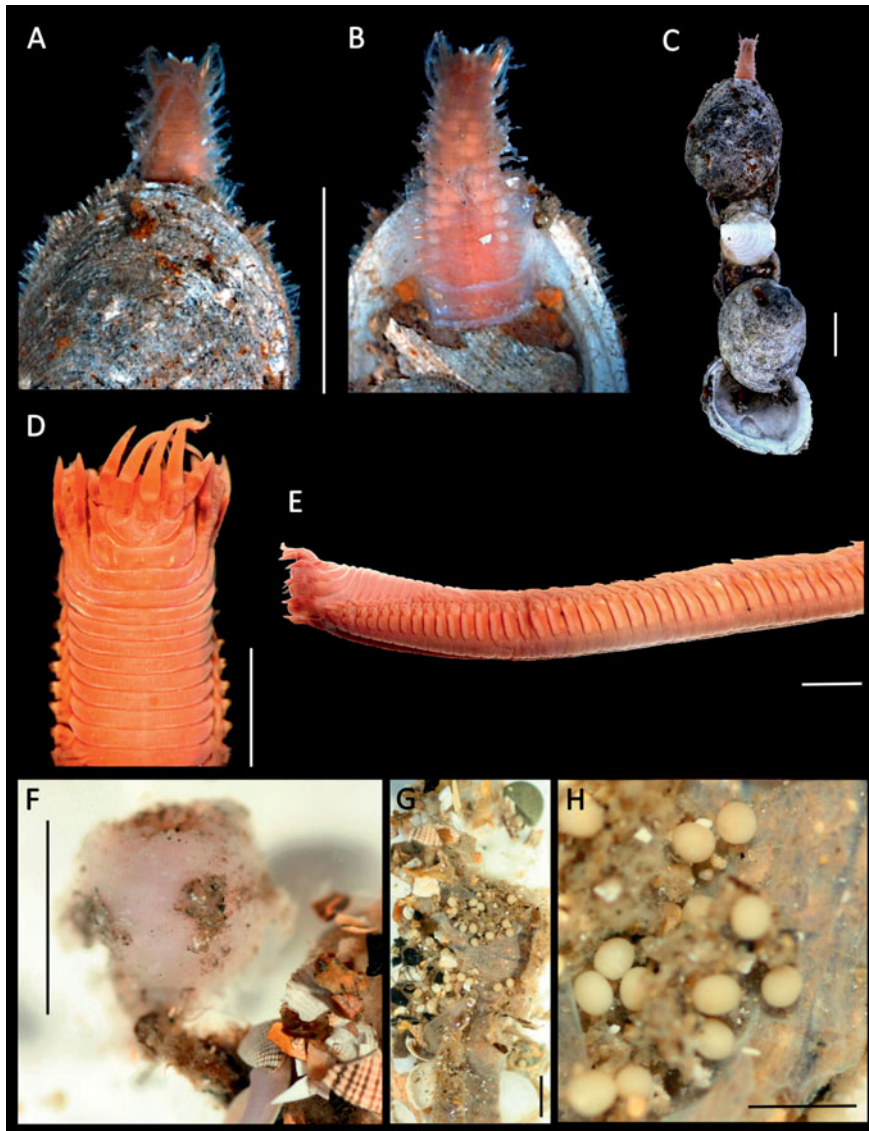


Figure 1. Photographs of *Nothria marentana* and *Rhamphobranchium brevibrachiatum*. (A) *Nothria marentana*, in tube, dorsal view; (B) same, ventral view; (C) same, dorsal view; (D) *Rhamphobranchium brevibrachiatum*, anterior region, dorsal view; (E) same, lateral view; (F) sperm capsule attached to *R. brevibrachiatum* tube; (G) opened *R. brevibrachiatum* tube showing inside with eggs; (H) same, enlarged. Scale bars: (A–E) 1 cm; (F,G) 3 mm; (H) 1 mm.

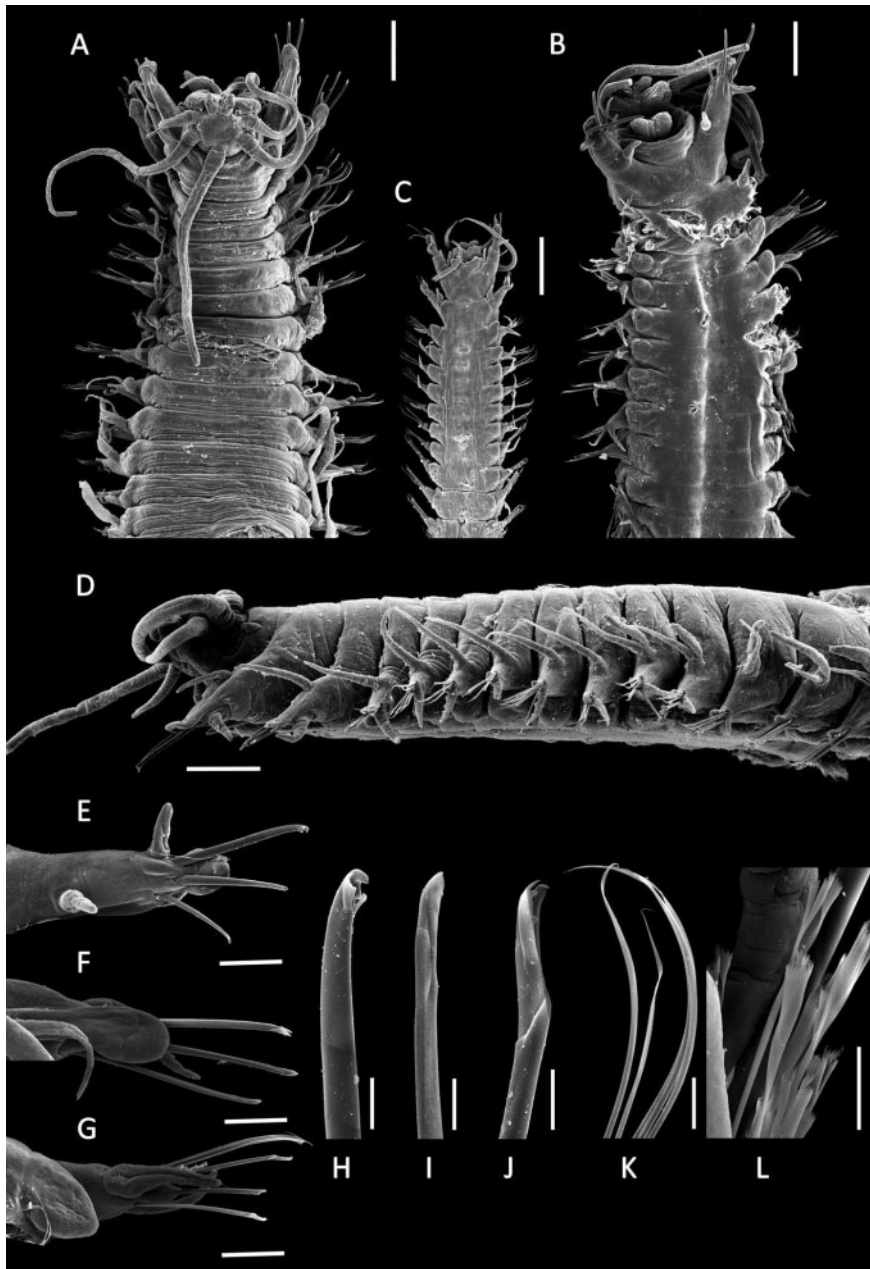


Figure 2. SEM images of *Nothria marentana*. (A) Anterior region of specimen of 2.7 mm width, dorsal view; (B) same of specimen of 2.4 mm width, ventral view; (C) same of specimen of 0.6 mm width, ventral view; (D) same of specimen of 1.4 mm width, lateral view; (E) parapodium 1 of specimen of 2.4 mm width, ventral view; (F) parapodium 2 of specimen of 2.7 mm width, dorsal view; (G) parapodium 3 of specimen of 2.4 mm width, ventral view; (H) simple bidentate falciger from chaetiger 1; (I) pseudocompound bidentate falciger from chaetiger 2; (J) compound bidentate falciger from chaetiger 3; (K) limbate chaetae from chaetiger 4; (L), pectinate chaetae from chaetiger 3. Scale bars: (A,B) 1 mm; (C,D) 500 μm ; (E-G) 100 μm ; (H-L) 30 μm .

like. From chaetiger 4 onwards parapodial structures becoming more uniform; dorsal cirri gradually becoming thinner and shorter, prechaetal lobes becoming short and rounded, postchaetal lobes gradually decreasing, absent from chaetigers 13–14, ventral cirri replaced by round glandular pads from chaetiger 4. Simple branchiae present as a short filament from chaetiger 9, strap-like from chaetiger 10 (Figure 2A,D).

First pair of parapodia with 1–2 thick and 1–2 thinner simple bidentate hooded falcigers (Figure 2H). Second pair of parapodia with 1–2 thick and 1–2 thinner, weakly pseudocompound bidentate hooded falcigers (Figure 2I). Third pair of parapodia with 3–4 thinner, compound bidentate hooded falcigers (Figure 2J), 3–4 limbate chaetae (Figure 2K) and numerous (up to 20) pectinate chaetae with 18–20 teeth and rolled lateral margins (Figure 2L).

Falcigers absent from chaetiger 4, limbate and pectinate chaetae present up to end of body. Sub-acicular hooks present singly from chaetigers 10–11, as pairs from chaetiger 11–12.

Tubes (Figure 1A–C) flattened, covered with shells of *Limopsis aurita* (Brocchi, 1814).

Remarks

This is the first report of *Nothria maremontana* since its original description from the sea mounts Seine and Josephine, situated between Madeira and the Iberian coast in 250–450 m from similar substrates, where the bivalve *Limopsis* was extremely common and also used in tube construction.

André & Pleijel (1989) reported the absence of eyes in their three type specimens and considered this feature to be an important character. In our specimens eyes were present in the largest specimen (larger than the type specimens) and absent in all others. The presence/absence of eyes is a characteristic that has also been observed in other species of *Nothria*, e.g. *N. abyssia* Kucheruk, 1978 and *N. otsuchiensis* Imajima, 1986 (Budaeva & Paxton 2013).

In general, our specimens agree very well with the original description except for some chaetal details. The pectinate chaetae were reported to have 16–17 teeth while in our specimens they ranged from 18 to 20. The falcigers of chaetiger 1 were described as ‘pseudocompound (articulation hardly visible)’, although the two longest falcigers (André & Pleijel

1989: figure 3a) appear to be simple. The chaetal distribution on the first three chaetigers is size-dependent and ontogenetic variation will be discussed below. While this is a general problem with Onuphidae, a recent detailed study of such changes in two species of *Nothria* has shown that stabilization of certain features is reached relatively late in this genus and renders some species descriptions doubtful (Budaeva & Paxton 2013).

Ontogenetic chaetal variation. Eight specimens ranging in width from 0.6 to 2.7 mm were examined. Based on their chaetal distribution, the specimens at hand were divided into three stages (Figure 3). Stage 1: width 0.6–1.0 mm; stage 2: width 1.0–1.9 mm; stage 3: width 1.9–2.7 mm, with a stabilized adult chaetal complement.

Chaetal composition of the first pair of parapodia. The smallest specimen, measuring 0.6 mm wide, had 2 compound and 1 pseudocompound falcigers. Specimens ranging from 1.0 to 1.9 mm had 1–2 weakly pseudocompound falcigers and 2 simple falcigers, while the largest specimens measuring 2.4 and 2.7 mm had only 3 simple falcigers each.

Chaetal composition of the second pair of parapodia. The smallest specimen (0.6 mm) had only 3 compound falcigers. All larger specimens had pseudocompound falcigers; in the largest specimens (2.4 and 2.7 mm), the pseudocompound fracture was very weak, appearing almost simple.

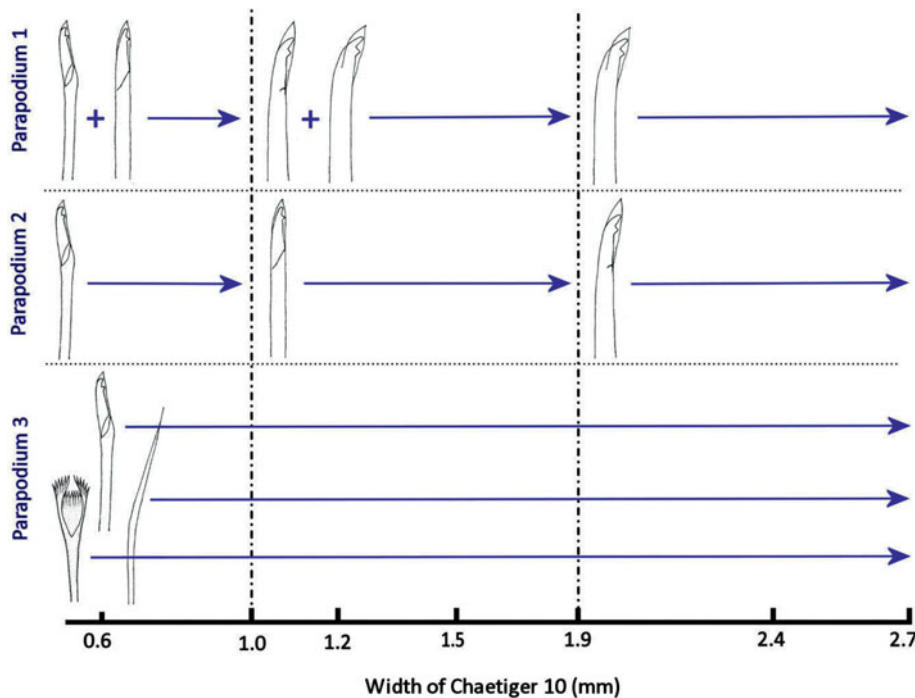


Figure 3. *Nothria maremontana*. Diagram of chaetal replacement in parapodia 1–3 in relation to body width of specimens (in mm).

Chaetal composition of the third pair of parapodia. All specimens irrespective of size had 3–4 compound falcigers, accompanied by 1–4 limbate and 6–20 pectinate chaetae.

Biology

Of the eight specimens examined, four were still in their tubes when collected, although none were complete specimens. Four specimens, ranging in width from 1.0 to 2.7 mm, contained eggs in their body cavity from chaetigers 17–18 to the end of the fragments. It is interesting to note here that although specimens of 1.0 and 1.2 mm width were ovigerous, they had not yet reached the stabilized chaetal distribution, as their parapodia 2 still had pseudocompound and none of the almost simple falcigers, placing them still in stage 2. One of the tubicolous specimens had 8 early juveniles and 27 eggs in its tube; the number of eggs in a tube varied from 27 to 30. The eggs measure about 300–340 μm in diameter and their surface is pitted, as is typical for the subfamily Hyalinoeciinae (Figure 4A,B). The early juveniles (Figure 4C) are oblong and full of yolk and have 6 chaetigers.

An early juvenile measures 650 μm in length and 250 μm in height at about the midpoint, which is the thickest part of the body. The anterior part has a clearly delineated prostomium with 2 tiny palps and 3 antennae. The anterior two pairs of parapodia have started to develop and are directed anteriorly, while the next three are directed laterally and are less distinct. The chaetae of the anterior parapodia were not well enough preserved to describe. The clearest chaetae were from chaetiger 6 and represent presumably 2 larval limbate chaetae and a provisional subacicular hook (Figure 4D). Although the pygidium is not yet delineated, the dorsal pygidial cirri are present.

Distribution

Nothria maremontana occurs in the northeastern Atlantic on the Seine and Josephine seamounts and in the southern Bay of Biscay, in 250–1186 m depth. However, specimens previously reported as *Nothria lepta* (Chamberlin, 1919) from northwestern Spain and the Cachucho Canyon (Bay of Biscay) (Amoureux 1972, 1974a,b) may also represent *N. maremontana*.

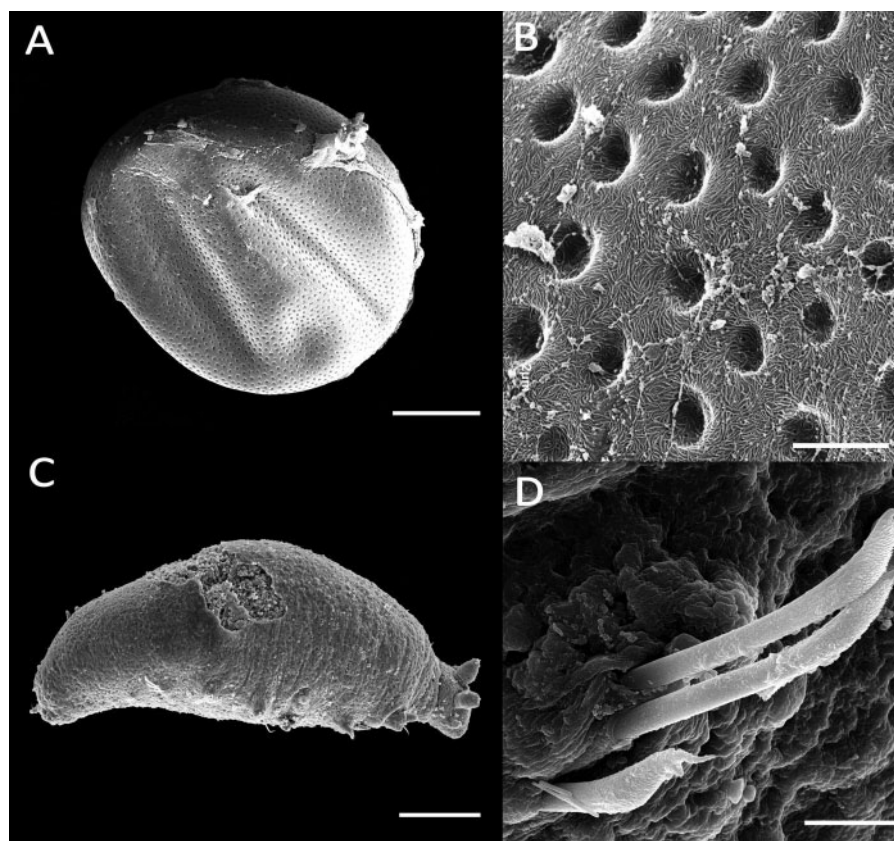


Figure 4. SEM images of *Nothria maremontana* egg and early juvenile. (A) Egg removed from tube; (B) enlargement of egg surface; (C) 6 chaetiger juvenile, lateral view; (D) larval chaetae from chaetiger 6. Scale bars: (A) 100 μm ; (B) 10 μm ; (C) 100 μm ; (D) 10 μm .

Subfamily Onuphinae Kinberg, 1865

Genus *Paradiopatra* Ehlers, 1887

Diagnosis

Prostomium with short palps and short to moderately long antennae, median antenna shorter than lateral antennae, ceratophores usually with 3–5 rings. Anterior 2–4 pairs of parapodia modified but not enlarged, directed anterolaterally, with pseudocompound falcigers with moderately long to long pointed hoods. Limbate chaetae from chaetigers 3–5, flat pectinate chaetae starting later; subacicular hooks in ventral position usually from chaetigers 9–12.

Branchiae with single or pectinate filaments or absent. Tubes round in transverse section, with inner parchment-like layer covered with foreign particles.

Paradiopatra hispanica (Amoureux, 1972)

(Figure 5)

Nothria hispanica Amoureux, 1972: 76–77, figures 2, 3; 1982: 49; Campoy 1982: 554–555.

Sarsonuphis hispanica – Fauchald 1982: 74; Glémarec 1991: 549.

Paradiopatra hispanica – Paxton 1986a: 38; Aguirrezabalaga et al. 2002: 20–23, figure 2a–h.

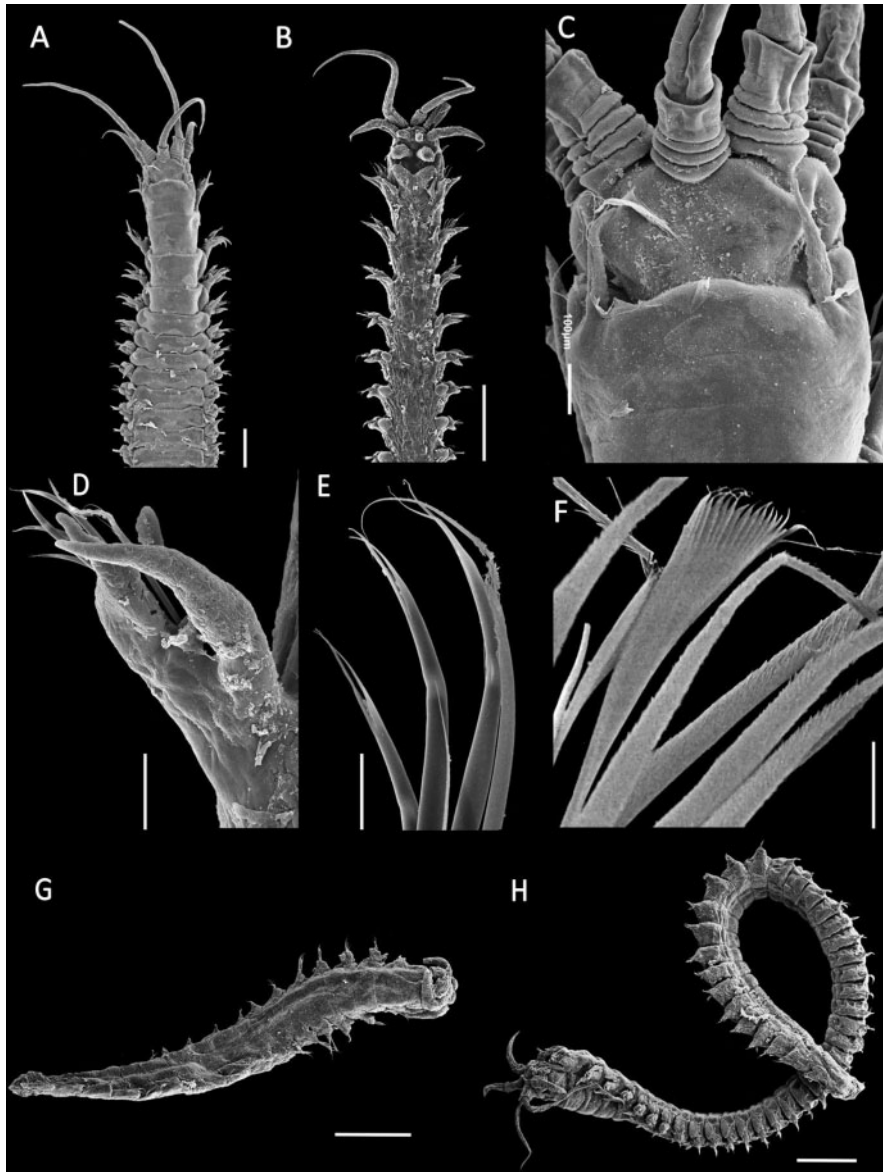


Figure 5. SEM images of *Paradiopatra hispanica*. (A) Anterior region, dorsal view; (B) same, ventral view; (C) same, enlarged dorsal view; (D) parapodium 2, dorsal view; (E) pseudocompound falcigers from chaetiger 2; (F) limbate and pectinate chaetae from median parapodium; (G) 16 chaetiger juvenile, dorsal view; (H) 45 chaetiger juvenile, lateral view. Scale bars: (A,B) 1 mm; (C,D) 100 μ m; (E) 50 μ m; (F) 10 μ m; (G,H) 500 μ m.

Material examined

COCACE station: G3 (43.88°N, 6.11°W) 571 m, 41% sand, 30% silt, 29% clay, 3 July 1987, 8 specimens (AM W.45285); 5 specimens (BOS).

Diagnosis

Anterior 3 pairs of parapodia with pseudocompound bi- and tridentate falcigers with long pointed hoods; ventral cirri subulate on first 3 chaetigers; subacicular hooks starting from chaetigers 11–15; branchiae absent; peristomial cirri present.

Description

All specimens incomplete, lacking posterior ends; smallest specimen measuring 12 mm for 53 chaetigers, width 0.6 mm (at chaetiger 10, excluding parapodia); largest specimen measuring 52 mm in length for 110 chaetigers, width 0.8 mm. Alcohol-stored specimens overall cream-coloured, no pigment pattern.

Prostomium (Figure 5A–C) anteriorly rounded, wider than long, with paired ovoid frontal lips. Antennae on anterior part of prostomium, ceratophores of palps and antennae with 2–4 proximal rings and long distal ring, lacking lateral projections; palpal styles reaching chaetiger 1, styles of lateral antennae reaching chaetigers 3–5, median antennae 2–3. Eyes absent. Peristomium about as long as chaetiger 1, peristomial cirri subulate, about half as long as peristomium.

Anterior three pairs of parapodia (Figure 5D) modified and directed anterolaterally. Prechaetal lobes rounded on all parapodia; postchaetal lobes subulate in first chaetigers, decreasing rapidly in size, absent from chaetiger 9. Dorsal cirri subulate in anterior parapodia, becoming smaller and digitiform in median region. Ventral cirri subulate on first three chaetigers, fourth and fifth transitional, replaced by ventral pads from chaetiger 6. Branchiae absent.

Modified parapodia with dorsal fascicle of 1–2 limbate chaetae and ventral fascicle of 3–5 bi- to tridentate pseudocompound falcigers with long pointed hooks (Figure 5E). Two fascicles of simple limbate chaetae starting from chaetiger 4. Ventral fascicle of limbate chaetae replaced by paired bidentate subacicular hooks from chaetigers 11–14. Pectinate chaetae with 13–15 teeth (Figure 5F), very sparse, present or absent in median and posterior parapodia; when present, never more than one per parapodium.

Tube with inner parchment-like layer, covered by thin, smooth muddy layer on distal part only, lower part only transparent secreted layer.

Remarks

This is a common species in the Bay of Biscay. Our specimens agree well with the original description and the specimens reported by Aguirrezabalaga et al. (2002). Amoureux (1972) described *Paradiopatra hispanica* as having subacicular hooks from chaetiger 15. However, in a later publication, based on the examination of large numbers of specimens he remarked on the large range of appearance of subacicular hooks from chaetigers 11–15 and correctly attributed it to size-dependency (Amoureux 1982).

Biology

Some of the specimens were still in their tubes when collected, and four had juveniles within the tubes. One tube had 10 poorly preserved 6 chaetiger early juveniles and 2 tubes had 12 chaetiger juveniles of 2.6 mm length and 16 chaetiger juveniles of 3.6 mm length (Figure 5G); one tube contained two 45 chaetiger juveniles of 9.0 mm length (Figure 5H).

Distribution

Portugal, Bay of Biscay, English Channel, SW of British Isles; at depths of 505–1113 m.

Genus *Rhamphobrachium* Ehlers, 1887*Diagnosis*

Prostomium with short palps and antennae, ceratophores with 2–5 rings. Anterior 3 pairs of parapodia enlarged, directed anterolaterally, with 3 distally recurved hooks each, hooks with 2 rows of moveable spines, chaetal sacs extending to chaetigers 30–60. Limbate and flat pectinate chaetae from chaetiger 4; subacicular hooks in ventral position from chaetigers 10–16. Branchiae with single or pectinate filaments. Tubes round in transverse section, with inner parchment-like layer covered with foreign particles.

Subgenus *Spinigerium* Paxton, 1986*Diagnosis*

Lower limbate chaetae pseudocompound to compound (= spinigers).

***Rhamphobrachium (Spinigerium) brevibrachiatum* (Ehlers, 1875) (Figures 1D–H, 6)**

Diopatra brevibrachiata Ehlers, 1875: 49, plate 3, figures 11–21.

Rhamphobrachium brevibrachiatum – Ehlers 1887: 72; Fauvel 1923: 417, figure 165a–e; Bellan 1964: 89,

figures 5–7; Amoureux 1972: 75; 1974: 136; Cam-poy 1982: 552–553; George & Hartmann-Schröder 1985: 90–91, figures 23a–d.

Rhynchobranchium (Spinigerium) brevibrachiatum
Paxton 1986b: 89, figure 9a–g; Imajima 1999: 108, figures 56a–f, 57a–s.

Material examined

COCACE stations: I2 (43.99°N, 5.83°W) 1025 m, 58% sand, 18% silt, 24% clay, 2 July 1987, 1 specimen (BOS); I6 (43.92°N, 6.11°W) 1186 m, 38% sand, 30% silt, 32% clay, 4 July 1987, 1 specimen (AM W.45286).

Diagnosis

Antennae on median part of prostomium; falcigers present on chaetiger 4 in juveniles, rarely in adults. Branchiae from chaetigers 11–13, maximum of 4–7 filaments by chaetiger 30; subacicular hook present singly from chaetigers 10–17, as pairs from 12–20.

Description

Specimens incomplete, lacking posterior ends; one specimen in two parts measuring together 23 mm for 60 chaetigers (3 mm for prostomium and anterior 9 chaetigers, 20 mm for subsequent 51 chaetigers), width 1.6 mm (at chaetiger 10, excluding parapodia); one specimen 51 mm for 80 chaetigers, width 4.1 mm. Alcohol-stored specimen overall cream-coloured to pinkish, with brown pigment on antennae, peristomial cirri and first three pairs of parapodia.

Prostomium (Figure 1D,E) anteriorly rounded; paired globular frontal lips. Antennae on median part of prostomium; ceratophores of palps and antennae with 2–4 proximal rings and long distal ring, styles subulate with thin ends, palpal styles reaching peristomium to chaetiger 1, styles of antennae reaching chaetigers 2–3. No eyespots visible. Nuchal grooves with large middorsal separation. Peristomium about as long as chaetiger 1, peristomial cirri subulate, inserted subdistally on peristomium, longer than ceratophores, inserted far apart.

Anterior 3 pairs of parapodia modified and prolonged, each with 3 short papilliform lobes and 1 longer postchaetal lobe, and with subulate dorsal and ventral cirri. From chaetiger 4 low prechaetal and short, rounded postchaetal lobes, latter absent from about chaetiger 10. Dorsal cirri subulate, becoming gradually thin and threadlike. Single branchial filaments from chaetigers 11–13, bifid from 15–16, reaching a maximum of 4–7 filaments at chaetigers 26–30 before decreasing again from chaetigers 40–50 to eventually 1 filament.

Modified parapodia with long, recurved hooks with moveable spines and long chaetal sacs. On chaetiger 4, upper fascicle of simple limbate chaetae and lower fascicle of compound limbate chaetae (spinigers); smaller specimen with one compound falciger, larger specimen without. Thereafter, upper fascicle with pectinate chaetae with 12–14 teeth and simple limbate chaetae, only compound limbate chaetae in lower fascicle; bidentate subacicular hook present singly from chaetigers 10–17, as pairs from 12–20.

Tube with inner parchment-like layer, covered with foreign particles on outside. Lower external part of tube smooth, covered by sand and small particles, distal part covered by sand and shell fragments (Figure 1F,G).

Remarks

The specimens agree well with the definition of *Rhynchobranchium brevibrachiatum* as given by Paxton (1986b). The smaller specimen had one compound falciger in the lower fascicle of chaetiger 4, while they were lacking in the larger specimen. It is a characteristic of the species that smaller specimens have 1–7 compound falcigers, but that these falcigers are rarely present in the larger specimens. This suggests ontogenetic variation and that the presence of falcigers is a juvenile character. Imajima (1999) examined a large number of specimens and remarked that all juveniles had compound falcigers while most adults lacked them. Based on a previous study (Paxton 1986b), we can support this statement and must caution that while adults generally lack composite falcigers on chaetiger 4, they may be present in a minority of large, even ovigerous specimens.

Biology

The smaller of the two specimens was collected inside its tube, with its prostomium protruding from the tube. Attached to the distal part of the tube was a white, cocoon-like capsule (Figure 1F) that we assumed to be an egg case. It was damaged on one side, with a deep fissure. Upon opening it completely we found that it did not contain any eggs. It appeared to be a fibrous hollow ball (Figure 6A, insert) filled with a gelatinous liquid. When inspected by light microscopy we saw that the inner walls were covered with large fibres and very small sperm-like structures. Upon staining these small structures, we observed that they were indeed sperm with an elongated head of the ect- or ent-aquasperm type. We bisected the capsule and investigated its content with SEM imaging, revealing large numbers of fibres lined up lengthwise (Figure 6A). With higher magnification, the individual fibres appeared as 'pipes',

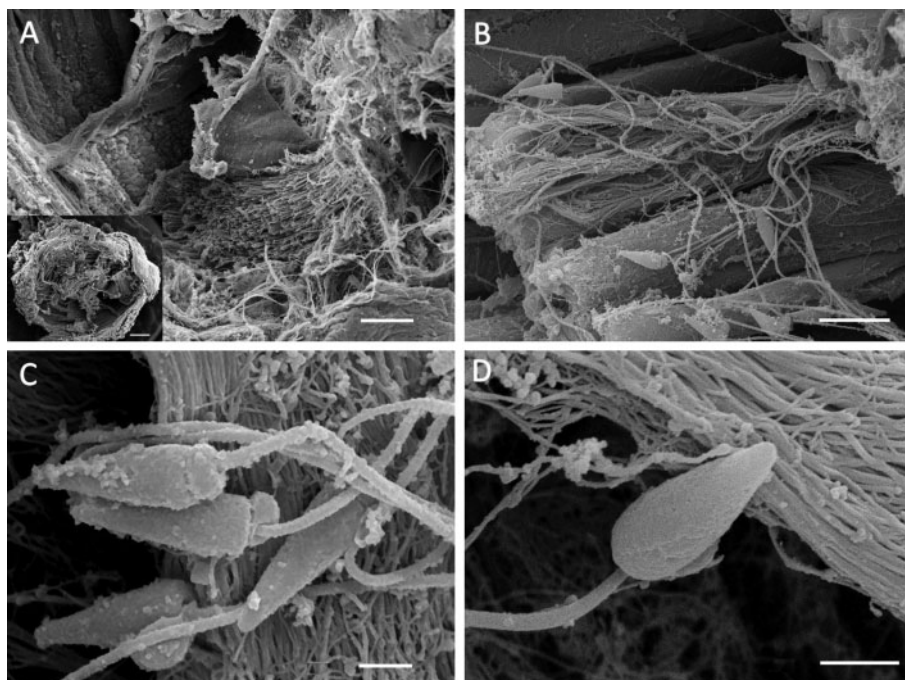


Figure 6. SEM images of sperm capsule attached to tube of *Rhamphobranchium brevibrachiatum*. (A) Part of sperm capsule wall with cut spermatophores; inset, basal part of capsule at lower magnification; (B) enlarged? spermatophores, thin fibres and spermatozoa; (C) several spermatozoa; (D) enlarged spermatozoon with displaced mid-piece. Scale bars: (A) 200 μm ; (B) 5 μm ; (C,D) 1 μm .

associated with thinner fibres and a number of sperm with long tails trailing over the 'pipes' (Figure 6B). We speculate that the 'pipes' are possible spermatophores and presume that the associated free sperm have escaped from some of the damaged spermatophores. The bundles of thinner fibres aligned in the same direction with some of the spermatophores (Figure 6B) may represent the remains of the matrix of some damaged spermatophores. The sperm heads are spindle-shaped with a spherical mid-piece (Figure 6C), that became dislodged in some preparations (Figure 6D). The sperm head is about 3.1 μm long, with a diameter of 1.1 μm at its thickest point near the mid-piece, which is about 0.5 μm long. The tails measure 30 μm in length.

When the worm's tube was opened it was found to contain 24 eggs in its anterior to median part, enclosed in a clear, soft envelope (Figure 1G). The eggs (Figure 1H) were circular, with a diameter varying from 390 to 450 μm and appeared to have been recently laid, as there was no sign of cleavage.

Distribution

The species was originally described from the English Channel and has been reported in the eastern North Atlantic from the Channel to the Mediterranean, as well as from the western North Atlantic (USA) and Pacific (Japan) at 120–1470 m.

Discussion

The Onuphidae is one of the most successful deep-water polychaete families, inhabiting tubes that have been constructed by the inhabitants. Species of the genus *Nothria* build characteristic flattened tubes where the outer layer of foreign particles is attached with the flat or concave side to the inner secreted lining. The first parapodia are prolonged and have thick chaetae, allowing the animal to protrude from the tube (Figure 1A,B) and move in a caterpillar-like fashion known as epibenthic crawling. Species of *Paradiopatra* and *Rhamphobranchium*, on the other hand, construct a variety of round tubes. The inner parchment-like layer may be covered on the outside by sand or mud (*P. hispanica*), or attached foreign particles like broken shells, foraminiferans and sand as in the case of *R. brevibrachiatum* (Figure 1F,G). The upper part of the tube with the foreign materials is above the substrate, similar to *Diopatra* tubes, and the lower smooth part is embedded in the sediment, making the animal sedentary. While the anterior-most parapodia of *Paradiopatra* are not prolonged and the chaetae are short and delicate, the *Rhamphobranchium* species have prolonged anterior parapodia with very long, extensile chaetae with a distal hook and two rows of spines along the length, presumably a catching device.

Reproductive strategies of onuphids range from free-spawning to various forms of brooding, including brooding inside the body (viviparity) as defined

by Wilson (1991). Eggs range from 175 to 1400 μm in diameter, and while some species exist as free trochophores for a short period, none are planktotrophic; they soon settle and build their tubes. Brooding species undergo direct development in the parental tube, in attached egg cases, or in jelly masses (Paxton 1986a; Budaeva & Fauchald 2010).

Both indirectly and directly developing polychaetes of various families have generally been referred to as 'larvae', although in a strict sense the latter (such as brooded onuphids) are not really larvae because they are not pelagic and their larval characteristics are greatly suppressed or lost. Schroeder & Hermans (1975) caution to distinguish between 'embryo' and 'larva', where in the former the developmental stage is enclosed by a structure that limits its dispersal, and in the latter the eggs are shed directly into the sea and fertilized externally; accordingly, the onuphid tube young qualify as embryos. This terminology, however, appears inappropriate for the total time spent in the parental tube, as they remain until they consist of at least 20 chaetigers. We propose to refer to the young onuphids during early development as 'embryos' and thereafter (when segments and jaws develop) as 'juveniles', as externally brooded young of the family Syllidae are referred to (Franke 1999). After the young leave the tube to enter the adult environment on their own they are still referred to as juveniles until they qualify for the term 'adults'.

Table I is a list of brooding and viviparous deep-water onuphids. We have included the two viviparous species, as they may be born before their yolk resources have been exhausted and spend some time in the parental tube before they settle. With the addition of the three species of the present study, this list consists of nine species in seven genera. We know of only one previous report of a brooding *Nothria*. Hartman (1967a) remarked that eggs were deposited in the tube of an Antarctic worm from the South Shetland Islands collected at a depth of 3678–3816 m that she identified as *Nothria* near *conchylega*. Four of our *N. maremontana* specimens contained eggs in their body cavities, one specimen had eggs and juveniles in its tube and others had eggs (Figure 4A) only. The pitted eggs (Figure 4B) measured 300 μm in diameter and the early juveniles consisted of 6–7 chaetigers (Figure 4C), all being of the same stage. No information is available on the morphology of spermatozoa and sperm transfer methods in *Nothria*.

Hartman (1967a) reported several tubes of *Paradiopatra antarctica* (Monro, 1930) with eggs (diameter 1170 μm) and juveniles with the largest having 24 chaetigers. One small individual, measuring 4

mm long, was interpreted as a reduced male. Our *P. hispanica* specimens had no eggs, only developing juveniles in their tubes and the 6 chaetiger, 12 chaetiger and 16 chaetiger (Figure 5G) juveniles within three tubes also developed synchronously, as reported by Hartman. One tube with two 45 chaetiger individuals (Figure 5H) could possibly be considered as pygmy males, as developing juveniles in tubes usually do not exceed 30 chaetigers. The largest onuphid juveniles found in a parental tube were *Fauchaldonuphis paradoxa* (Quatrefages, 1866), measuring 15 mm and consisting of 90 chaetigers (Paxton 2005). However, these individuals were still yolk-laden from chaetiger 15 onwards, while our *P. hispanica* specimens appeared like miniature adults and were yolk-free.

Several ovigerous *Rhamphobranchium* species have been reported previously, while this is the first report of eggs in the parental tube. The eggs were large, ranging from 390 to 450 μm in diameter, recently laid as they had not yet started to cleave. Because of their large size we expect that they would have undergone direct development and remained in the parental tube until capable of building their own tubes. In a study of ontogenetic changes of *Rhamphobranchium ehlersi* Monro, 1930, based on juvenile specimens that were collected in the same sample as the adults, the smallest specimens consisted of 31 chaetigers, suggesting that they were recently released (Paxton 1986a). Brooding has been reported for the closely related genus *Brevibranchium*, with *B. maculatum* (Estcourt, 1966) hatching eggs of 300–500 μm diameter and having 7 to 28 chaetiger juveniles in brood chambers partitioned off from the main tube (Smith & Jenz 1968).

Adults of several *Rhamphobranchium* species have been reported with sperm morulae and free sperm in their body cavity, and small specimens of *R. ehlersi* with coelomic sperm morulae and free sperm were interpreted as a case of protandry (Paxton 1986a,b), although nothing is known about sperm transfer.

When we first observed the white capsule attached to the tube of our *R. brevibranchiatum* specimen, we expected it to contain eggs, as occurs in some *Diopatra* species. However, as described above, it was more or less hollow with fibres and sperm around the inner walls of the capsule (Figure 6A,B). Brooding in polychaetes is usually coincident with sperm transfer between individuals in the form of spermatophores or spermatozeugmata that are transferred during copulation/pseudocopulation or float through water to be collected by the females (Rouse 1999). Aggregate sperm transfer by means of spermatophores in polychaetes has been reported for a number of families, among which Spionidae and

Table I. Summary of brooding records for deep-water onuphid species.

Species	Egg diameter (µm)	Brood size	Type of development	Location	Depth (m)	Observation	Reference
<i>Hyalinoecia araucana</i> Carrasco, 1983	?	45–69	I	Central Chile	600	3 to 13 chaetiger juveniles in parental tube	Carrasco 1983
<i>Hyalinoecia bermudensis</i> (Hartman, 1965)	?	3	II	Off Bermuda	700–2500	Anterior half of body with large eggs, posterior half with two embryos	Hartman 1965
<i>Kinbergonuphis notialis</i> (Monro, 1930)	?	12–28	I	Antarctic	210–2900	2–3 eggs and up to 29 chaetiger juveniles in each of numerous lateral capsules of parental tube	Hartman 1967a,b (as <i>Nothria notialis</i>)
<i>Leptoecia vivipara</i> (Averincev, 1972)	?	7	II	Off Enderby Land and Christensen Coast, Antarctic	437–1180	7 to 13 chaetiger juveniles in body cavity	Averincev 1972 (as <i>Paronuphis abyssorum</i>); Orensanz 1990
<i>Nothria</i> nr. <i>conchylega</i> (Sars, 1835)	?	?	I	South Shetland Islands	3678–3816	Eggs in parental tube	Hartman 1967a
<i>Nothria maremontana</i> André & Pleijel, 1989	300–340	27–30	I	Bay of Biscay	720–1186	Eggs and 6 chaetiger juveniles in parental tube	Present study
<i>Paradiopatra antarctica</i> (Monro, 1930)	1170	24	I	Antarctic	220–1153	Eggs, up to 24 chaetiger juveniles inside parental tube – pygmy male firmly appressed to female	Hartman 1967a,b; Averincev 1972 (as <i>Paronuphis antarctica</i>)
<i>Paradiopatra hispanica</i> (Amoureux, 1972)	?	10	I	Bay of Biscay	556	6 to 45 chaetiger juveniles in parental tube	Present study
<i>Rhamphobranchium brevibrachiatum</i> (Ehlers, 1875)	390–450	24	I	Bay of Biscay	1025–1186	Eggs inside parental tube	Present study

Note: Type of development: I, brooding in parental tube, direct development; II, brooding inside body, viviparity.

Siboglinidae are the best documented. Many spionids have buoyant spermatophores and all known siboglinids release their sperm through bundles or spermatophores (Blake & Arnofsky 1999; Young 2003). Hsieh & Simon (1990) reported demersal spermatophores for *Kinbergonuphis simoni* (Santos et al., 1981), the only known sperm transfer mode in the family Onuphidae. In laboratory experiments male worms were observed to release mushroom-shaped spermatophores as clumps from the tube openings. When spermatophores were placed near the tube openings of females, within a minute the females extended part of their body from the tube and picked up the spermatophores with their anterior parapodia and palps, pulling them into their tubes.

The capsule attached to the *R. brevibrachiatum* tube raises some vexing questions.

- (1) Could it be a *Rhamphobranchium* sperm capsule? The morphology of the sperm with its elongated nucleus approaches that of an ent-aquasperm. However, it is its confinement to the capsule that marks it as such a contrast to the ect-aquasperm. While the ent-aquasperm is also shed into the ambient water like the ect-aquasperm, it differs in that it reaches the female and may be stored in spermathecae, or, in the case of sedentary polychaetes, in the tube (Jamieson & Rouse 1989). Sperm of the same kind as that found inside the capsule (Figure 6C,D) occur in two other onuphids, the brooding

- K. simoni* (Hsieh & Simon 1990) and *Diopatra marocensis* Paxton, Fadlaoui & Lechapt, 1995 (Arias et al. 2013).
- (2) Do the large fibres represent spermatophores from which the free sperm have escaped? The large fibres inside the capsule (Figure 6A,B) do not appear to be part of the capsule structure and we cannot think of another explanation than that they are spermatophores and thus the source of the free sperm in the capsule. Long thin spermatophores are also found in spionids, e.g. *Polydora websteri* Hartman, 1943, although they are not contained in a capsule, but are ejected singly from the worm tube and are buoyant, floating in the water (Rice 1978).
 - (3) What could the possible sperm transfer method be? It would be easier to explain if the sperm capsule were attached to the motile *Nothria* than to the sedentary *Rhamphobrachium*. How would a male tubeworm be able to attach a sperm capsule to the distal end of a female's tube? One possibility is that the aggregation of tubes could be dense enough to allow nearby neighbours extending from their own tubes to reach a number of other tubes. *Diopatra* tubes can occur in great densities, but *Rhamphobrachium* specimens are less numerous. In benthic samples they are generally found in densities of up to four to five specimens per grab sample (0.25 cm²) (N. Budaeva, personal communication March 2013), and may be close enough for some success.

One could imagine that a male might extend from its tube, project the long anterior parapodia, extend their protrusible chaetae and attach the capsule to the tube of a nearby female. The female might dig into the capsule and extract spermatophores. One capsule could even serve several females if nearby females were also able to reach it, remove some spermatophores and place them into their own tubes to fertilize their eggs. Or, as a much simpler solution, perhaps the capsule might disintegrate and the released spermatophores would be drawn into the tube of the female and her neighbours. A similar process occurs in many siboglinids like *Riftia pachyptila* Jones, 1981, where the sperm bundles separate into individual sperm shortly after they are released in seawater (Young et al. 1996; Young 2003).

- (4) Has the sperm capsule been placed there by another animal? We think this is very unlikely in view of the fact that the sperm found inside the capsule closely resemble those of two other tube-brooding onuphid species. Furthermore, it is quite likely that if this cocoon-like structure had attached accidentally to the *R. brevibrachiatum* tube, it might have been considered as food and engulfed.

In conclusion, we report here the discovery of *Nothria marentana* and *Paradiopatra hispanica* tubes with eggs and/or juveniles, and a *Rhamphobrachium brevibrachiatum* tube containing eggs, demonstrating that the three species are tube-brooders. Furthermore, we speculate that the structures contained inside the capsule attached to the *R. brevibrachiatum* tube are long, thin spermatophores of a type not previously known for onuphids.

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