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***Mooreonuphis vespa*, a new brooding species of Onuphidae (Annelida) from northern Spain (Bay of Biscay)**

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Abstract

A new species of the genus *Mooreonuphis* Fauchald, 1982 collected from the Cantabrian shelf (Bay of Biscay) is described. *Mooreonuphis vespa* sp. nov. constitutes the first record of this genus in European waters and is characterised by: conspicuous dark brown transverse segmental pigment bands; antennae and palps with 3–5 basal ceratophoral rings and a very long distal ring; unusually long and slender peristomial and dorsal cirri; simple branchiae from chaetiger 17–19. We present observations on its reproductive biology (including brooding behaviour) and remark on the biogeography of the genus.

Key words: Polychaetes, taxonomy, Cantabrian Sea, shelf, biodiversity, Tethyan seaway

Introduction

Members of the family Onuphidae are mostly tubicolous polychaetes that extend worldwide from the intertidal to abyssal depths. Knowledge of European onuphids has expanded over the last years with the description of several new species (Aguirrezabalaga *et al.* 2002; Pires *et al.* 2010; Budaeva 2012; Fauchald *et al.* 2012) and new species records (Rodríguez *et al.* 2009; Arias *et al.* 2010; Arias & Paxton 2013).

Onuphidae comprises two subfamilies, Hyalinoeciinae and Onuphinae (Paxton 1986), of which the latter is the more speciose in European waters. Within Onuphinae the most diverse European genera are *Diopatra* Audouin & Milne Edwards and *Paradiopatra* Ehlers with seven reported species each (Budaeva & Fauchald 2011; Arias & Paxton, in preparation.). The other European representatives of this subfamily are *Aponuphis* Kucheruk with five, *Onuphis* Audouin & Milne Edwards with four and *Rhamphobrachium* Ehlers and *Longibrachium* Paxton with one species each.

Recently, new reproductive strategies have been discovered, such as simultaneous hermaphroditism in *Diopatra marocensis* Paxton *et al.* (Arias *et al.* 2013) and a brooding *Rhamphobrachium brevibrachiatum* (Ehlers) with a sperm capsule attached to its tube that could represent a novel sperm transfer method in onuphids (Paxton & Arias 2013).

In the framework of a project aimed to investigate the benthic fauna of the Cantabrian Shelf and the Avilés Canyon (northern Spain, Bay of Biscay), undertaken during 1987/88, material was collected throughout different depths and substrates, and was deposited in the collection of the Department of Biology of Organisms and Systems (BOS), University of Oviedo, Spain. Re-examination of the polychaetes among this material, revealed the presence of a new species of the genus *Mooreonuphis* Fauchald, 1982. This new species represents the first record of *Mooreonuphis* from European waters, bringing the number of European Onuphinae genera to seven.

The main diagnostic feature of *Mooreonuphis* is the presence of compound lower limbate chaetae (=spinigers) on some anterior chaetigers. The genus has recently been reviewed, including the provision of a key to the 19 described species (Rupit-Arteaga *et al.* 2013). *Mooreonuphis* has been traditionally considered endemic to the

tropical and temperate waters of the Americas. However, the genus was also recorded from Africa (Núñez *et al.* 1999) and Paxton (2000) reported two new species from eastern Australia that are in the process of being described (Paxton, in preparation). Here we report the presence of a new species in Atlantic European waters (Bay of Biscay), showing that the presumed endemicity of this genus is actually a taxonomic artefact caused by the absence of detailed taxonomic studies on *Onuphis*/*Kinbergonuphis*/*Mooreonuphis* species in Europe and other regions.

The aim of the present paper is to describe and illustrate the new species, to compare it to the other morphologically similar species, to point out some of its reproductive and ecological features and to remark on the biogeography of the genus *Mooreonuphis*.

Material and methods

We have re-examined the polychaete material collected during the COCACE (Oceanographic Cruise of the Central Cantabrian Sea) project, conducted during 1987/88 to investigate the fauna of the Cantabrian Shelf and the Avilés canyon (Fig. 1), in a variety of substrates in the southern Bay of Biscay, north of the Iberian Peninsula (Louzao *et al.* 2010). Detailed station data is given in the 'Material examined' section of the description of the new species. The specimens were anaesthetised in 7% MgCl₂, fixed in 10% neutral buffered formalin, and later transferred to 70% ethanol. Specimens were examined under a dissecting stereomicroscope. Glycerol slides of parapodia were prepared to examine chaetal morphology and distribution and examined under a compound light microscope. Terminology follows Paxton (1986). The type specimens are deposited in the Museo Nacional de Ciencias Naturales de Madrid, Spain (MNCN) and the Australian Museum, Sydney, Australia (AM).

Results

Family Onuphidae Kinberg, 1865

Subfamily Onuphinae Kinberg, 1865

Genus *Mooreonuphis* Fauchald, 1982

Mooreonuphis Fauchald, 1982: 55. Paxton 1986: 56.

Type species: *Onuphis nebulosa* Moore, 1911 by original designation.

Diagnosis. Prostomium with oval frontal lips, short palps and short to long antennae, ceratophores with usually 3–5 rings; peristomial cirri present. Anterior 3–8 pairs of parapodia modified but not enlarged. Hooks of modified parapodia usually tridentate (rarely bi- and tridentate), pseudocompound with short hoods; median hook sometimes becoming simple and changing to “large median hook”. Ventral cirri subulate on anterior 3–6 (rarely more) chaetigers. Dorsal limbate chaetae from chaetiger 1, ventral limbate chaetae compound (= spinigers) from chaetiger 4 or later until replaced by bidentate hooded subacicular hooks from chaetiger 13–29. Branchiae usually as single filaments, rarely pectinate. Tubes round in section, ranging from thin mucous to tough parchment-like inner layer covered with sand or mud.

Mooreonuphis vespa sp. nov.

Figures 1–4; Table 1

Type material. Holotype: (MNCN 16.01/11013) COCACE station: D1 (43.80° N, 5.67 °W) 152 m, 84.46 % sand, 5.78 % silt, 9.76 % clay, 29 June 1987. Paratype: 1(AM W45287) COCACE station: B3 (43.70° N, 5.90° W) 117 m, 69.86 % sand, 12.77 % silt, 17.37 % clay, 5 July 1987

Type locality. North Western Atlantic, Bay of Biscay, Cantabrian Shelf, 43.80° N, 5.67 °W, 152 m.

Diagnosis. Colour pattern of dark brown transverse segmental pigment bands on yellowish background. Antennae moderately long to chaetigers 6–8; ceratophores weakly ringed with 3–4 basal rings and a very long

TABLE 1. Major distinguishing features of *Mooreonuphis stigmatis*, *M. bajacalifornica* and *M. vespa* **sp. nov.**

Features	<i>M. stigmatis</i> (Treadwell, 1922) holotype	<i>M. bajacalifornica</i> de León-González, 1982 holotype	<i>M. vespa</i> sp. nov. holotype
Dorsal colour pattern - peristomium	completely covered by dark brown pigment	posterior dark brown pigment band only	anterior and posterior brown pigment bands
Colour pattern - following chaetigers	two dark brown pigment bands	one posterior brown band only	two brown pigment bands
Length (mm) / number of chaetigers	61.8 / 114 (incomplete)	46 / 139 (incomplete)	68 / 179 (almost complete)
Width (mm)	1.6 (with parapodia)	1.5 (?with parapodia)	1.9 (without parapodia)
Palps reaching chaetiger	1	13+	2
Lateral antennae reaching chaetiger	5	18+	7-8
Median antenna reaching chaetiger	3	21	6-7
No. of ceratophoral rings	5	4	5-6
Length of ceratophoral rings	distal ring as long as all basals together	distal ring as long as all basals together	distal ring much longer than all basals together
Peristomial cirri to	anterior part of prostomium	anterior part of prostomium	far exceeding anterior margin of prostomium
Chaetigers with tridentate PCHs	1-3	1-5	1-5
Chaetigers with simple "large median hooks"	4-5	1-5	1-5
Chaetigers with cirriform ventral cirri	1-4	1-6	1-6
Chaetigers with spinigers	4-16	6-19	6-17
Number of teeth on pectinate chaetae	12-15	13	13-15
Subacicular hooks from chaetiger	16	20	18
Distal end of aciculae	tapered	expanded	tapered
Branchiae fom chaetiger	19	19	17
Ecology	in sand, shell fragments, dead corals; intertidal to 54 m depth	epizootic upon thorny oysters <i>Spondylus princeps</i> ; shallow water to 30 m depth	living in round tubes buried in sediment; continental shelf, 117-152 m depth
Reference	Treadwell 1922; Fauchald 1982	de León-González 1982	Present study

distal ring, longer than all basal rings together. Peristomial cirri unusually long and slender, far exceeding anterior margin of prostomium. First five pairs of parapodia modified, directed slightly anterolaterally with tridentate pseudocompound hooks and simple “large median hook”. Dorsal cirri very long from chaetiger 3 to 18–21. Spinigers from chaetiger 6 to 17–18, subacicular hooks from chaetiger 18–19. Branchiae as single filament, from chaetiger 17–19.

Description. Description based on holotype, with variation of paratype included. Holotype incomplete, consisting of 179 chaetigers, 68 mm long and 1.9 mm wide (at chaetiger 10, excluding parapodia). Paratype incomplete with 80 chaetigers, 30 mm in length, 1.1 mm in width.

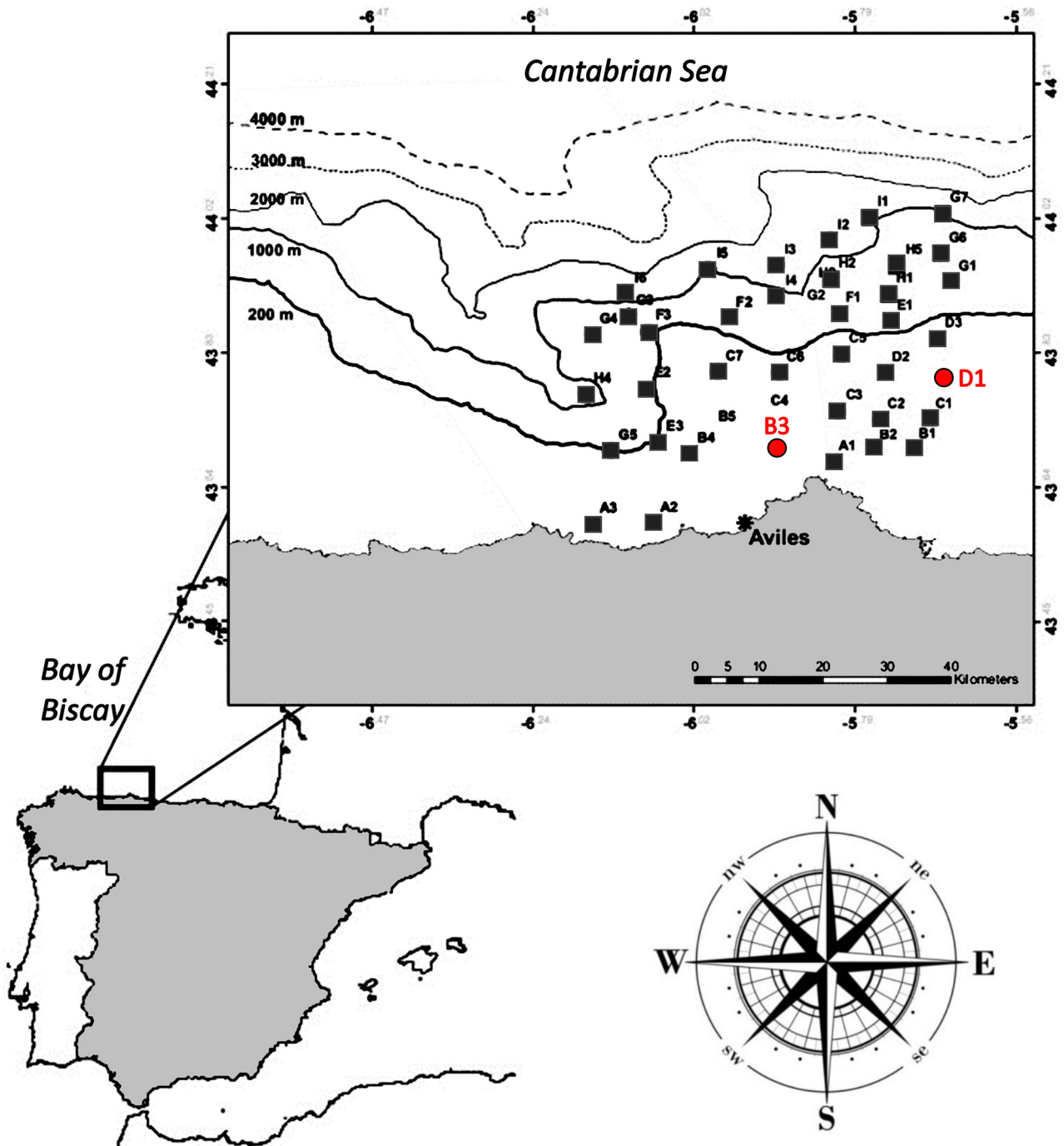


FIGURE 1. Distribution map of the sampling stations of the COCACE project. Stations with presence of *Mooreonuphis vespa* sp. nov. highlighted in red.

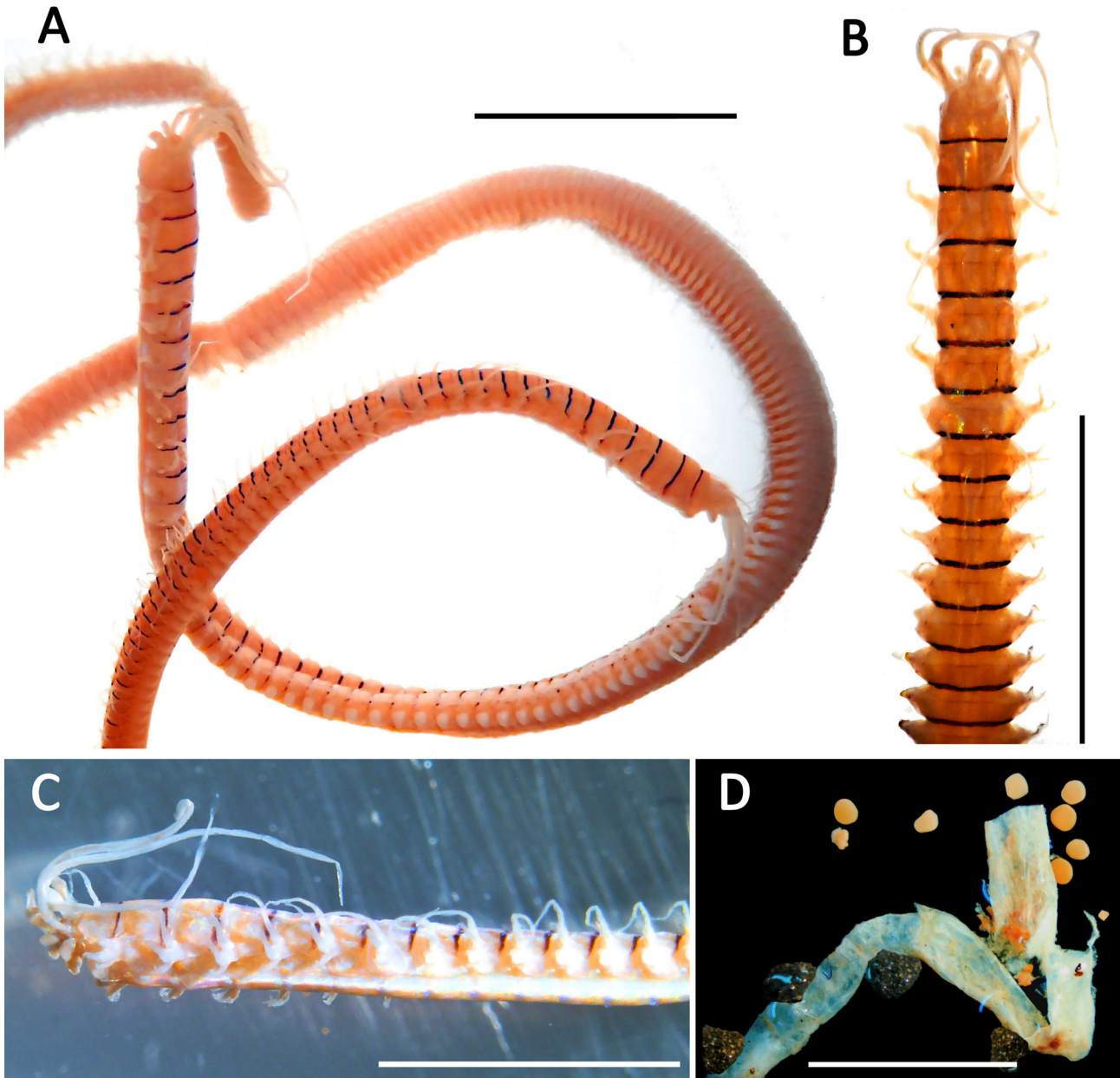


FIGURE 2. Photos of *Mooreonuphis vespa* sp. nov. (holotype MNCN 16.01/11013, A–D; paratype AM W45287, A right). A, Whole specimens; B, anterior end, dorsal view; C, anterior end, lateral view; D, general view of tube and eggs. All scale bars = 1 cm.

Anterior end of body slender and nearly cylindrical, becoming broader and slightly depressed between chaetigers 8–10. Colour pattern in ethanol stored specimens, consisting of two dark brown transverse dorsal pigment bands on peristomium and each segment. One very thin band initially at anterior end of segments, shifting to middle by chaetiger 7, second thick band always near posterior end of each segment, representing intersegmental dark bar (Figs 2A–C, 3A). Prostomium anteriorly weakly incised with frontal and upper lips stout and oval, latter without median section (Fig. 3A, B). Palps reaching chaetiger 2, lateral antennae reaching chaetiger 7–8, median antenna reaching chaetigers 6–7; antennae with gradually tapering styles and weakly ringed ceratophores with 3–4 basal rings and very long distal ring being slightly longer than all basal rings together (Fig. 3A). Small eyespot between bases of palp and lateral antenna. Nuchal grooves straight with small middorsal separation laterally curving towards eyespots (Fig. 3A). Peristomium half as long as first chaetiger. Peristomial cirri unusually long and slender, far exceeding anterior margin of prostomium (Figs 2C, 3A), inserted distally on peristomium slightly lateral to lateral antennae (Fig. 3A). Lower lip with median section.

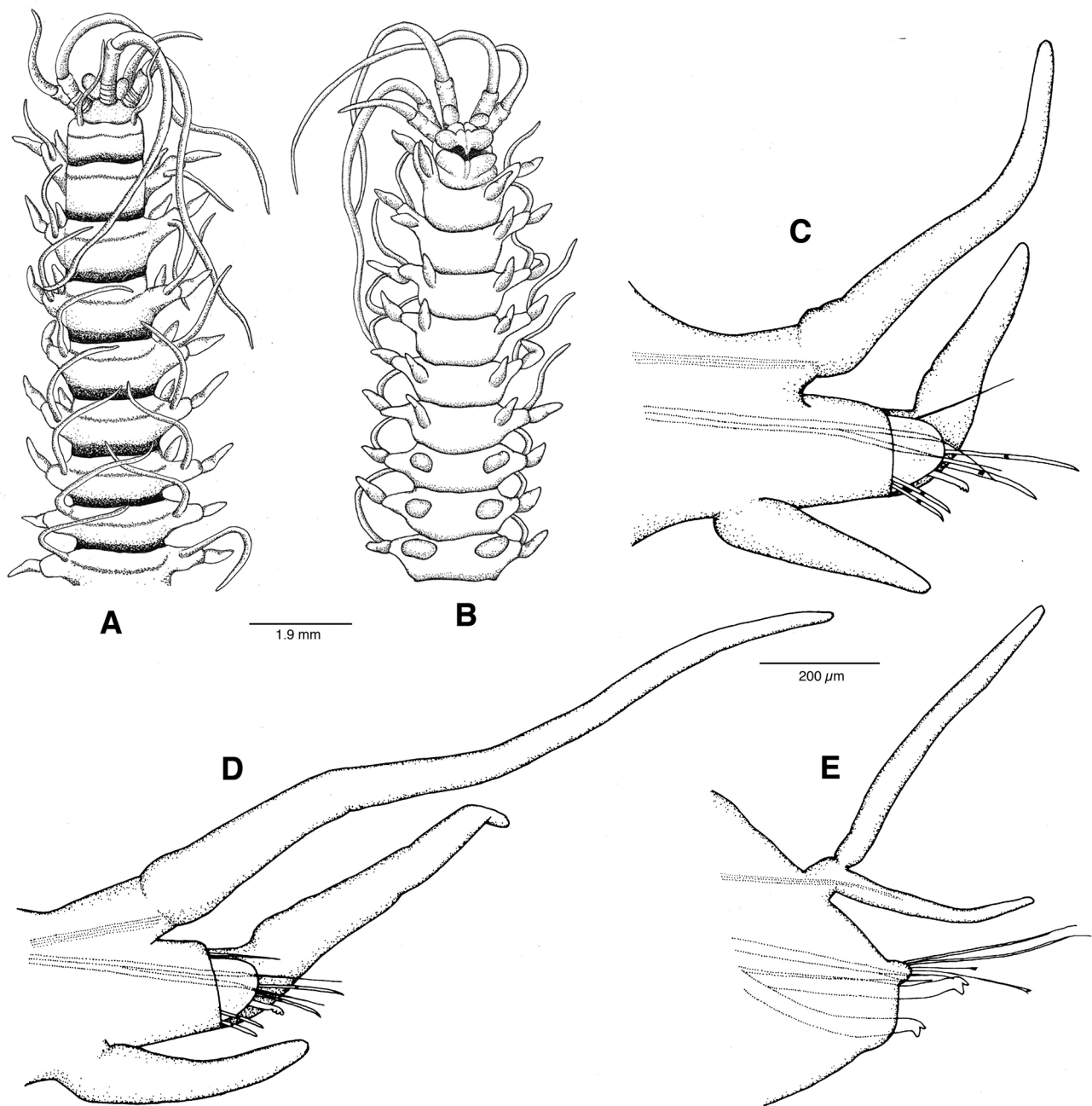


FIGURE 3. Line drawings of *Mooreonuphis vespa* sp. nov. (holotype MNCN 16.01/11013, A, B); paratype AM W45287, C–E). A, Anterior end, dorsal view; B, same, ventral view; C, parapodium 1, anterior view; D, parapodium 3, anterior view; E, parapodium 76, posterior view.

Anterior chaetigers (1 to 6) subequal in length, slightly longer than those following. First five pairs of parapodia modified, not enlarged, directed slightly anterolaterally, with prechaetal fold, round prechaetal lobe and long subulate postchaetal lobe (Fig. 3C, D). Prechaetal lobe becoming low by chaetiger 10, postchaetal lobe becoming successively shorter, reduced to small knob by chaetiger 20. Ventral cirri subulate on anterior six chaetigers, replaced by round glandular pads from chaetiger 7 (Fig. 3B). Dorsal cirri of first two parapodia about twice as long as postchaetal lobe (Fig. 3C), longer from chaetiger 3 to 18–21, about twice as long as postchaetal lobe (Fig. 3D). Branchiae as single filaments, strap-like, from chaetiger 17 in holotype (19 in paratype); first branchiae shorter than dorsal cirri, successively becoming longer, reaching beyond dorsal mid-line, still twice as long as dorsal cirrus at chaetiger 76 (Fig. 3E), reduced to small papilla by chaetiger 130 in holotype, absent shortly thereafter.

Aciculae yellowish with tapering distal ends, generally two per parapodium. First five chaetigers (Figs 2C, 3A,

B) with following chaetal complement going from superior to inferior part of chaetal fan: one slender limbate chaeta, two long-appendaged tridentate pseudocompound hooks (Fig. 4A), one simple tridentate “large median hook” (Fig. 4B) and two short-appendaged tridentate pseudocompound hooks (Fig. 4C). Appendages of both types of hooks gradually becoming shorter (Fig. 4D), appearance of short-appendaged pseudocompound hooks progressively resembling distal end of simple large median hook (Fig. 4E). From chaetiger 6 to chaetigers 17 in holotype (18 in paratype) simple limbate chaetae and compound spinigers (Fig. 3F) replacing pseudocompound hooks. Bidentate subacicular hooded hooks replacing ventral spinigers from chaetiger 18 in holotype (left 21, right 19 in paratype) to end of the fragments (Fig. 3E); pectinate chaetae flat, with 12–15 teeth (Fig. 4G).

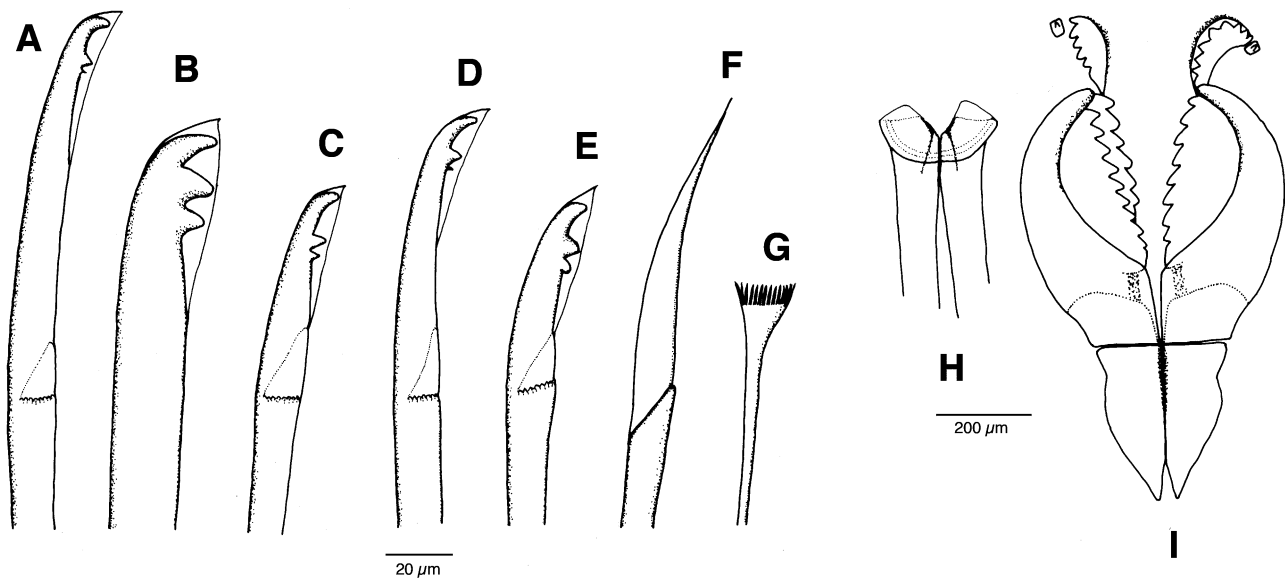


FIGURE 4. Line drawings of *Mooreonuphis vespa* sp. nov. (paratype AM W45287). A, Long-appendaged tridentate pseudocompound hook from chaetiger 1; B, tridentate simple “large median hook” from chaetiger 3; C, short-appendaged tridentate pseudocompound hook from chaetiger 1; D, tridentate long-appendaged pseudocompound hook from chaetiger 4; E, tridentate short-appendaged pseudocompound hook from chaetiger 4; F, spiniger from chaetiger 6; G, pectinate chaeta from chaetiger 76; H, mandibles, ventral view; I, maxillae, dorsal view.

Mandibles (Fig. 3H) small in relation to maxillae, with white calcified cutting plates and slender shafts. Maxillae (Fig. 3I) weakly sclerotised; maxillary formula (based on paratype): Mx I = 1 + 1; Mx II = 9 + 8; Mx III = 7 + 0; Mx IV = 6 + 8; Mx V = 1 + 1. Mx VI absent. Tube cylindrical in shape, parchment-like and externally covered with sand-grains (Fig. 2D).

Etymology. The specific name ‘*vespa*’ is originally from the Latin and refers to the dorsal striped colour pattern of transverse dark bands on yellowish background (Fig 2A–C), which is reminiscent of the striped abdomen of the hornets (*Vespa* spp.).

Distribution and ecology. *Mooreonuphis vespa* sp. nov. is known from the southern part of the Bay of Biscay (Western Atlantic) from the Cantabrian Sea shelf, depth range 117–152 m in sandy substrate. This species was only collected singly at two stations, indicating a very low population density and suggesting that it is apparently a very rare species with a restricted distribution along the Bay of Biscay.

Biology. The holotype was collected inside its tube, with its anterior end protruding from the tube. When the tube was dissected it was found to contain 14 eggs in its median part, enclosed in a clear and thin envelope (Fig. 2D). The eggs were spherical, ranging from 510 to 680 µm in diameter and all appeared to have signs of cleavage, thus indicating a synchronous development of embryos. Because of their large egg-size, *M. vespa* sp. nov. larvae are expected to undergo direct development and presumably remain in the parental tube until they are able to settle and build their own tubes.

Remarks. Some *Mooreonuphis* spp. have distinctive patterns of dark pigment on the anterior dorsal end (Fauchald 1982a). *Mooreonuphis vespa* sp. nov. is characterised by having segmental dark brown pigment bands, resembling the colour pattern of *M. intermedia* (Kinberg), *M. stigmatis* (Treadwell) and *M. bajacalifornica* de León-González. The new species has one narrow anterior and one wide posterior band on each segment, starting

with the peristomium and continuing for many following chaetigers. The pattern is similar in *M. bajacalifornica* but here the anterior narrow band is lacking and only one posterior segmental band is present. *Mooreonuphis intermedia* and *stigmatis* have two segmental bands and the peristomium is solidly dark.

Mooreonuphis intermedia differs from the other three species by lacking simple “large median hooks” in the anterior chaetigers. *Mooreonuphis vespa* **sp. nov.** closely resembles *M. bajacalifornica* and *M. stigmatis* also in other respects. These three species have “large median hooks”, single strap-like branchiae starting from chaetiger 17–19 and other similar morphometrics that are detailed in Table 1. The unique features of *M. vespa*, **sp. nov.** are its colour pattern, its ceratophores with their very long distal ring, long dorsal cirri and postchaetal lobes, and extremely long peristomial cirri.

Discussion

Brooding in the parental tube has been reported for two *Mooreonuphis* species: *M. jonesi* Fauchald and *M. stigmatis* (Fauchald 1982b; Budaeva & Fauchald 2010 respectively). The size of the ovate coelomic *M. jonesi* eggs was about 175–190 µm for the maximum diameter. A single distinct ovoid chamber inside the parental tube contained larvae in about ten layers of five to six each, separated by thin sheaths, in different stages of development. In the other brooding species, *M. stigmatis*, the eggs were 300–350 µm, the developing larvae numbered only 5–16 per brood, developed synchronously, and were found in the posterior end of the tube. The comparison between these three *Mooreonuphis* species is an example of the trade-off between egg size and egg number, *M. jonesi* producing a large number of small eggs compared to *M. vespa* **sp. nov.** with a small number of large eggs. The egg size of *M. stigmatis* is intermediate but the number of eggs is similar to that of *M. jonesi*. However, whilst the data of *M. jonesi* is based on large numbers of specimens, the data on both *M. stigmatis* and *M. vespa* **sp. nov.** is based on a very limited sample size that precludes any further interpretations.

The genus *Mooreonuphis* was reported to be currently represented by 19 species with all but four living in shallow waters (less than 200 m) and limited to the coasts of the Americas (Rupit-Arteaga *et al.* 2012). The species are small-sized, with limited geographic distributions, and were considered by Paxton (1986) the result of comparatively recent speciation, occupying a derived position in her cladogram. As part of their genetic phylogenetic study of Eunicidae Zanol *et al.* (2010) analysed eight species of onuphids in six genera and concluded, in contrast, that *Mooreonuphis* is basal in Onuphinae. However, in a molecular phylogeny study with an increased taxon sampling *Mooreonuphis* and its sister genus *Kinbergonuphis* are derived genera (Budaeva, pers. com. June 2013). *Mooreonuphis* was generally considered endemic to the New World and it seemed reasonable to assume that the centre of origin of the genus was somewhere in the Americas and that the present distribution was due to dispersal.

Nevertheless, the genus *Mooreonuphis* was also reported from Cape Verde archipelago, northwestern Africa (Núñez *et al.* 1999) and two new species of *Mooreonuphis* have been discovered in Australia (Paxton 2000) and are in the process of being described (Paxton, in preparation). These two species differ from all other known species in being abranchiate. This could be attributed to their small size (width about 0.5 mm). However, other *Mooreonuphis* species of this size from the Americas do have branchiae. Furthermore, the Australian species have pseudocompound hooks on only three chaetigers and lack any simple “large median hooks”, making them quite distinct from the remaining species.

The biogeography of the genus becomes more complicated with the discovery of *M. vespa* **sp. nov.** from the Bay of Biscay. One of the possible explanations is that it could be an introduced or alien species. But we do not think so because it differs from all previously described species and was collected at two different localities at 117–152 m in the Bay of Biscay, 10–30 km from the shoreline (Fig. 1).

Glasby (2005) discussed polychaete distribution patterns and one of his conclusions was that vicariance has been influential in the present day distributions of polychaetes. The order Eunicida has a good fossil record, dating back to the latest Cambrian, but it was not until Mid Ordovician that they diversified significantly (Hints & Eriksson 2007). Additional data from the Early Ordovician to Late Devonian suggests that eunicidans may have been abundant in the northern Gondwana regions (Eriksson *et al.* 2004). To account for the present day distribution of *Mooreonuphis* it is tempting to hypothesise that the origin of the genus occurred at a period before the supercontinent Gondwana started the slow break up process between the Jurassic and Cretaceous, isolating the ancestors of the present day Australian *Mooreonuphis* species. The formation of the Tethyan seaway in Early

Cretaceous is compatible with the continuous distribution around the margins of the Tethyan Sea that included the current Bay of Biscay and the North-West of Africa. The Tethyan seaway could have allowed *Mooreonuphis* to colonise the Atlantic and Pacific sides of the Americas and through time establish the present day distribution. However, at the present time *Mooreonuphis* is still an undersampled and incompletely documented genus. It is very likely that more species will be discovered and more detailed discussions of its biogeography should be deferred until a later time.

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