

***Aponuphis* Kucheruk, 1978 (Annelida: Onuphidae) from western African waters**

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ABSTRACT: Ninety-one specimens of *Aponuphis* from 27 stations off the western African coast from Morocco to Angola as well as from two localities in the North Sea and from a single locality off Mallorca in the Mediterranean Sea were examined using light and scanning electron microscopy. A fragment of 16 rDNA was obtained for 29 specimens of *Aponuphis*. A Neighbor Joining analysis revealed the presence of two species complexes (*A. bilineata* species complex and *A. brementi* species complex), *A. ornata* and a potentially new species *Aponuphis* sp. Besides three typical color morphs characteristic to *A. bilineata*, *A. brementi*, and *A. ornata*, the large number of specimens displayed indistinct color patterns of transversal pigmented bands or dots on anterior chaetigers. Specimens with such coloration were found in *A. bilineata*, *A. brementi* and the new species *Aponuphis* sp. Only *A. ornata* showed constant “horse-shoe” color pattern.

How to cite this article: Borisova P.B., Schepetov D.M., Budaeva N.E. 2018. *Aponuphis* Kucheruk, 1978 (Annelida: Onuphidae) from western African waters // Invert. Zool. Vol.15. No.1. P.19–41. doi: 10.15298/invertzool.15.1.02

KEY WORDS: Onuphinae, fauna, East Atlantic, morphology, molecular analysis, 16S rDNA, color polymorphism.

Многощетинковые черви рода *Aponuphis* Kucheruk, 1978 (Annelida: Onuphidae) из вод Западной Африки

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РЕЗЮМЕ: Девяносто один экземпляр из рода *Aponuphis*, собранный на 27 станциях из восточной Атлантики, преимущественно с шельфа Западной Африки от Марокко

до Анголы, а также из Северного и Средиземного морей, был исследован методами световой и сканирующей электронной микроскопии. Получены последовательности участка гена 16S рДНК для 29 экземпляров из рода *Aponuphis*. На основе анализа последовательностей методом ближайшего соседа в исследованном материале обнаружены два видовых комплекса (комплекс видов *A. bilineata* и комплекс видов *A. brementi*), а также вид *A. ornata* и потенциально новый для науки вид *Aponuphis* sp. Анализ соответствия цветовых морф генетическим видам показал, что, наряду с тремя типовыми морфами, характерными для трех вышеперечисленных видов, имеется большое число экземпляров с неявной окраской в виде тонких поперечных дорзальных полосок или точек. Данные экземпляры встречаются как у нового, ранее неизвестного вида *Aponuphis* sp., так и в рамках видовых комплексов *A. bilineata* и *A. brementi*. Исключение составил *A. ornata* с характерным подковообразным рисунком на передних сегментах, все исследованные экземпляры которого обладали схожим паттерном.

Как цитировать эту статью: Borisova P.B., Schepetov D.M., Budaeva N.E. 2018. *Aponuphis* Kucheruk, 1978 (Annelida: Onuphidae) from western African waters // *Invert. Zool.* Vol.15. No.1. P.19–41. doi: 10.15298/invertzool.15.1.02

КЛЮЧЕВЫЕ СЛОВА: Onuphinae, фауна, восточная Атлантика, морфология, молекулярно-генетический анализ, 16S рДНК, цветовой полиморфизм.

Introduction

Aponuphis Kucheruk, 1978 has been described for *Onuphis*-like worms lacking peristomial cirri (Kucheruk, 1978). *Aponuphis* and *Onuphis* Audouin et Milne Edwards, 1833 are morphologically very similar genera sharing the presence of long multiringed palpophores exceeding in length the palpostyles. In both genera, the anterior three to seven pairs of parapodia are modified but not enlarged and bear bi- to tridentate (rarely quadridentate) pseudocompound falcigers with short pointed hoods. Simple strap-like branchiae, if present, start in the anterior part of the body and continue throughout the whole length of a worm.

In her generic revision of Onuphidae, Paxton (1986) assigned six species previously described as *Hyalinoecia* Malmgren, 1867 or *Onuphis* to *Aponuphis*. *Hyalinoecia* also lacks peristomial cirri and this character was considered to have high diagnostic value in early onuphid studies. Paxton (1986) has demonstrated that *Hyalinoecia* and *Aponuphis* belong to two different subfamilies: Hyalinoeciinae Paxton, 1986 and Onuphinae Kinberg, 1865 respectively. After Paxton's revision, two abran-

chiate species, *Aponuphis chistikovi* Detinova, 1985 from the Reykjanes Ridge in the northern Mid-Atlantic and *A. willsiei* Cantone et Bellan, 1996 from the Gulf of Marseille, Mediterranean were described. Recently, three new species have been described from eastern Australia (Paxton, 2017), bringing the total number of species in the genus to ten and expanding the geographical range of the genus to southern Pacific (Table 1).

Aponuphis has been previously reported from African waters (Fauvel, 1936; Rullier, 1965). Intes and Le Loeuff (1975) reported *A. bilineata* (Baird, 1870) from Senegal and Ivory Coast at depths around 100 m and *A. fauveli* (Rioja, 1918) from Senegal and Togo at depths between 25 and 200 m. Kirkegaard (1988) reported *Aponuphis* along the western African coast from Morocco to Gabon. He followed Bellan (1964) in combining all described species of *Aponuphis* into a single species, *A. bilineata*, with high intraspecific variation. However, he made an exception for *A. fauveli* based on the appearance of the branchiae on the first chaetiger and considered it as a valid species. Kirkegaard (1988) also reported a subspecies of *A. fauveli*, *A. fauveli africana* (Rullier, 1965), with the

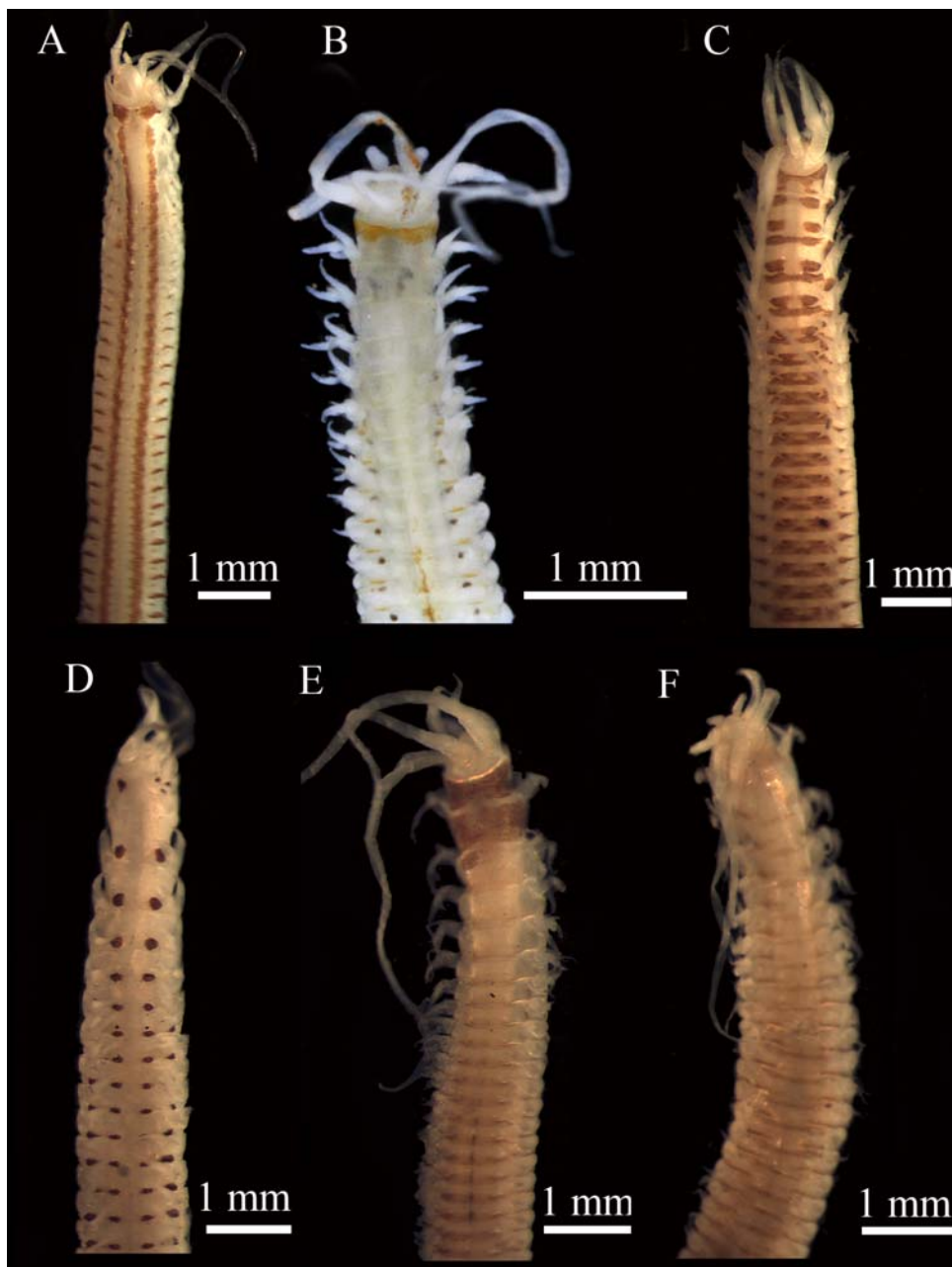


Fig. 1. Various color morphs in *Aponuphis*. A, B — *A. bilineata*; C — *A. ornata*; D–F — *A. brementi*.
 Рис. 1. Цветовые морфы в роде *Aponuphis*. A, B — *A. bilineata*; C — *A. ornata*; D–F — *A. brementi*.

distinct color pattern of two pigmented anterior segments with following 8–10 chaetigers bearing lunular rusty spots.

Recently Arias and Paxton (2015) have revised the fauna of *Onuphis* and *Aponuphis* from

southwestern Europe based on type and large non-type material of all valid species. They suggested synonymization of *Aponuphis rubra* (Langerhans, 1880) with *A. bilineata* and *A. fauveli* with *A. brementi* (Fauvel, 1916). Sever-

al color morphs were reported in species with branchiae. *A. bilineata* displayed two color morphs with typical pattern of two longitudinal dorsal stripes along the whole body (Figs 1A, 2A) and an additional much darker morph with the anterior part of the body almost completely pigmented. *A. brementi* bore a pair of dark dorsal round spots on each segment (Figs 1D, 2D), while *A. ornata* (Fauvel, 1928) had a typical “horse-shoe” pattern formed by a band and two large square spots on adjacent chaetigers (Figs 1C, 2C). The abranchiate *A. willsiei* lacked a color pattern. Arias and Paxton (2015) suggest that color morphs can be used in species identification in *Aponuphis*, however this character should be used with caution since some specimens may lose coloration in preserved condition.

Very little genetic data are known for *Aponuphis*. A single specimen of *Aponuphis bilineata* was used in a phylogenetic analysis of Eunicida (Struck *et al.*, 2006). Two more species were included in the analysis of phylogenetic relationships within Onuphidae, where *Aponuphis* was shown to be monophyletic and sister to *Onuphis* (Budaeva *et al.*, 2016). However, the analysis included only few representatives of both genera and larger taxon sampling is required to confirm their phylogenetic status.

Both *Onuphis* and *Aponuphis* are tubicolous sediment dwellers constructing cylindrical tubes with inner mucous or parchment-like layer covered with mud or sand particles, rarely tough and smooth, lacking any foreign particles (Paxton, 2017). Unlike species-rich *Onuphis* with world-wide distribution, *Aponuphis* is a relatively small genus comprising ten species reported only from the North Atlantic and eastern Australia (Paxton, 1986, 2017; Arias, Paxton, 2015) (Table 1).

The goal of the present study is to examine material of *Aponuphis* from the western African waters combining morphological and molecular methods. We aim to assess the correspondence of the color morphs with the morphological and genetic species in *Aponuphis* and to clarify their distribution in the eastern Atlantic.

Materials and Methods

Study area

Material used in the present study was borrowed from the collection of the University Museum of Bergen. The samples were collected during two projects: Canary Current Large Marine Ecosystem (CCLME) project and Guinea Current Large Marine Ecosystem (GCLME) project. Ninety-one specimens from 27 stations were collected between 2005 and 2012 along the western African coast from Morocco to Angola using a grab or a sledge (Appendix 1). The sampled depth range was from 7 to 518 m however most of the samples were obtained at depths around 60–100 m. In addition, the specimens from two stations from the North Sea and from a single locality off Mallorca in the Mediterranean Sea were examined. Panmap (Diepenbroek *et al.*, 2000) was used to build the distribution maps of the studied species.

Morphology

Part of the material was fixed in 4% formalin and later transferred into 75% ethanol. Specimens used for DNA analysis were fixed in 96% ethanol. Morphology of the specimens was studied using light and scanning electron microscopy. Identification of different morphotypes was done using a Leica MZ16 dissecting microscope. Slides of parapodia and chaetae were photographed using a Leica DM6000 B light microscope. For scanning electron microscopy, specimens were dehydrated in a graded ethanol series, critical-point dried, sputter coated with gold and examined with a ZEISS Supra 55VP scanning electron microscope and a Camscan S-2 scanning electron microscope. All materials are deposited in the University museum of Bergen (ZMBN).

Molecular methods

We have sampled 29 specimens of *Aponuphis* representing six different color morphs. In

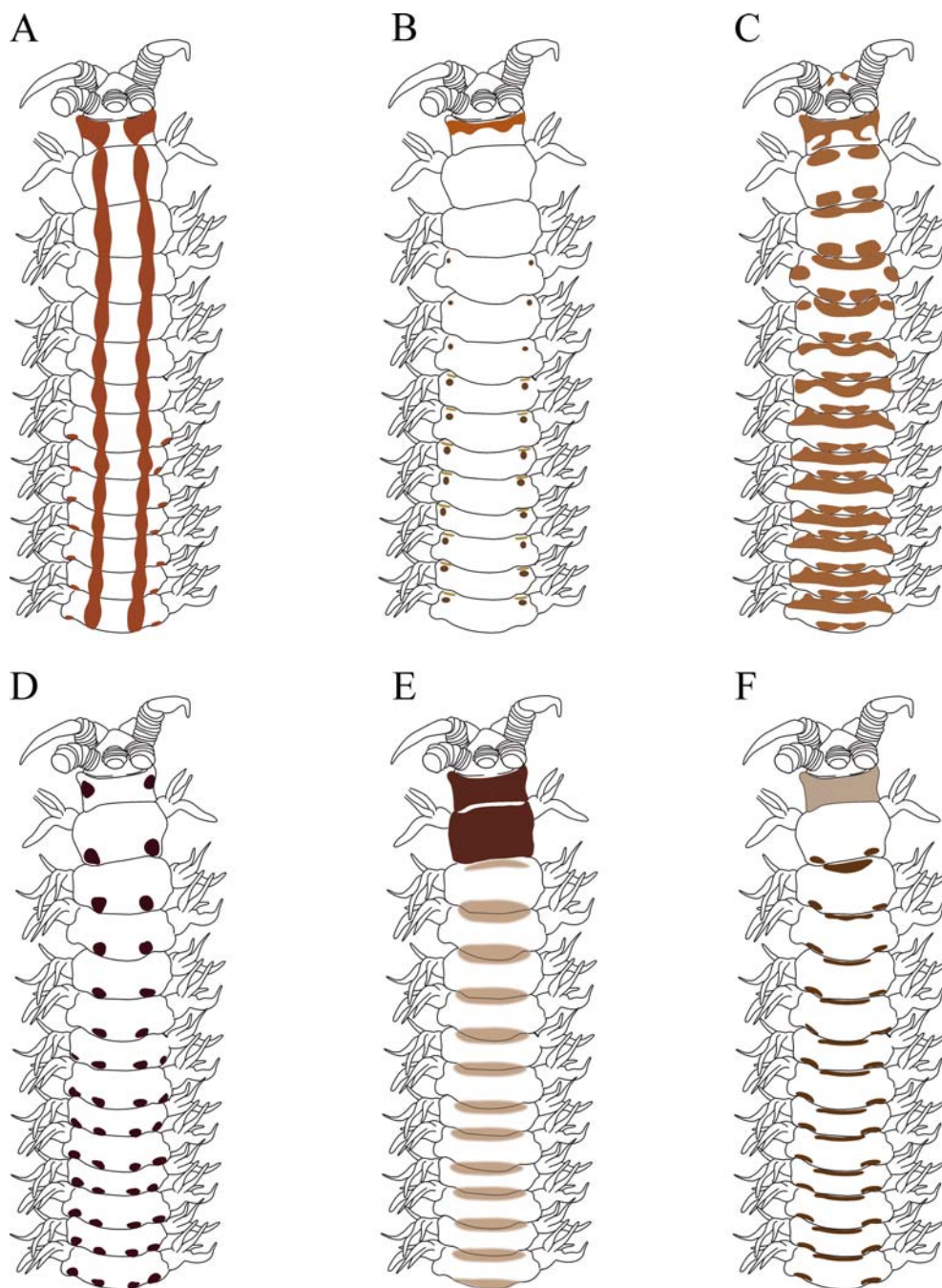


Fig. 2. Schematic interpretation of various color morphs in *Aponuphis*. A, B — *A. bilineata*; C — *A. ornata*; D–F — *A. brementi*.

Рис. 2. Схематическое изображение цветовых морф в роде *Aponuphis*. A, B — *A. bilineata*; C — *A. ornata*; D–F — *A. brementi*.

Table 1. Valid species of *Aponuphis* and their synonyms.
Таблица 1. Валидные виды рода *Aponuphis* и их синонимы.

Species	Synonymised names
<i>Aponuphis annae</i> Paxton, 2017	
<i>Aponuphis bellani</i> Paxton, 2017	
<i>Aponuphis bilineata</i> (Baird, 1870)	<i>Aponuphis rubra</i> (Langerhans, 1880)
<i>Aponuphis brementi</i> (Fauvel, 1916)	<i>Aponuphis fauveli</i> (Rioja, 1918)
<i>Aponuphis chistikovi</i> Detinova, 1985	
<i>Aponuphis danicae</i> Paxton, 2017	
<i>Aponuphis grubii</i> (Marenzeller, 1886)	<i>Aponuphis bilineata grubii</i> (Marenzeller, 1886)
<i>Aponuphis ornata</i> (Fauvel, 1928)	
<i>Aponuphis rigida</i> (Claparède, 1868)	
<i>Aponuphis willsiei</i> Cantone et Bellan, 1996	<i>Aponuphis willsii</i> [auct.]

addition, three sequences of 16S rDNA of *A. fauveli*, *A. bilineata* and *Aponuphis* sp. were retrieved from GenBank. Seven sequences representing four *Onuphis* species were included in the analysis to check the monophyletic status of both genera. *Hyalinoecia tubicola* (O.F. Müller, 1776) and *Nothria conchylega* (Sars, 1835) belonging to the sister subfamily Hyalinoeciinae were used as outgroups. Collection data and Genbank accession numbers of all specimens included in the molecular analysis are shown in Table 2.

Genomic DNA was extracted from 96% ethanol fixed samples using silica gel (glass milk). A fragment of mitochondrial gene 16S rDNA (~400 bp) was amplified using the following primers: forward 16Sar1 CGCCTGTT-TAACAAAAACAT (Palumbi *et al.*, 1991) and reverse 16SR CCGRTYTGAAGCTCAGCT-CACG (Puslednik, Serb, 2008). The total volume of PCR was 20 µl. PCR were performed using two commercial Evrogen™ kits following the instructions provided by the producer: Encyclo Plus PCR kit (0.1 µl 50X Encyclo DNA Polymerase; ddH₂O; 4 µl 5X Encyclo Red buff-

er; 0.4 µl 50X dNTP; 0.2–0.5 µl (10 Pmol/µl) of each primer) and Screen Mix 5X (4 µl Screen Mix 5X; ddH₂O; 0.2–0.5 µl (10 Pmol/µl) of each primer) with 1–2 µl of DNA template. PCR thermal conditions were: 1 cycle: 95°C/5 min; 35–40 cycles: 95°C /15 s, 50–52°C/40 s, 72°C/45 s; 1 cycle: 72°C/2 min. The results of PCR were verified using 1% agarose gel electrophoresis with ethidium bromide. Purification of the PCR products was done using Ethanol/EDTA/Sodium Acetate Precipitation. Sequencing reactions for both strands of the amplified genes were performed using BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) using the same primers as for PCR. Products were sequenced using Applied Biosystems automated sequencer ABI 3500.

Sequence contigs were assembled in Codon-Code Aligner v. 6.0. Alignment was conducted using the MUSCLE (Edgar, 2004) algorithm implemented in MEGA v. 7.0 (Kumar *et al.*, 2016) with the following settings: -400 gap opening penalty, -50 gap extension penalty. We used Neighbor Joining algorithm implemented in MEGA v.5.1 to provide graphical interpreta-

Table 2. List of species used in the phylogenetic analyses with description of color morphs, geographical localities and GenBank accession numbers.

Таблица 2. Список видов, использованных в молекулярном анализе, с указанием цветовой морфы, географического местонахождения и регистрационного номера ГенБанка для каждого экземпляра.

Species	Clade code	Color pattern	Catalogue number	Country	GenBank Accession Number
<i>A. bilineata</i>	Clade A	two longitudinal stripes	ZMBN 91345	Morocco, 29.0031°N 11.2162°W, 106 m	KX874564
	Clade A	two longitudinal stripes	ZMBN 91346	Morocco, 29.6089°N 10.2905°W, 102 m	KX874565
	Clade A	two longitudinal stripes	ZMBN 91348	Morocco, 32.5418°N 9.6138°W, 101 m	KX874566
	Clade A	two longitudinal stripes	ZMBN 111713	W. Sahara, 27.1015°N 13.672°W, 125 m	KX874568
	Clade A	two longitudinal stripes	ZMBN 111714	Morocco, 29.0031°N 11.2162°W, 106 m	KX874562
	Clade A	two longitudinal stripes	ZMBN 91344	Morocco, 29.0031°N 11.2162°W, 106 m	KX874563
	Clade A	two longitudinal stripes	ZMBN 91718	Norway, 61.213°N 1.816°E, 148 m	KX874572
	Clade A	two longitudinal stripes	ZMBN 91720	Norway, 61.432°N 1.927°E, 266 m	KX874573
	Clade B	two longitudinal stripes	ZMBN 91347	Morocco, 29.6089°N 10.2905°W, 102 m	KX874567
	Clade B	two longitudinal stripes	ZMBN 111719	Morocco, 29.6089°N 10.2905°W, 102 m	KX874561
	Clade C	paired lateral dots	ZMBN 111716	Spain, Mallorca, 39.72125°N 3.46395°E, 10-18 m	KX874569
	Clade C	paired lateral dots	ZMBN 111717	Spain, Mallorca, 39.72125°N 3.46395°E, 10-18 m	KX874570
<i>A. brementi</i>	Clade D	light-brown peristomium, thin transversal stripes	ZMBN 91341	Benin, 6.0358°N 1.3557°E, 44 m	KX874580
	Clade D	light-brown peristomium, thin transversal stripes	ZMBN 91352	Gabon, 2.453°S 9.045°E, 109 m	KX874574
	Clade E	dark peristomium and chaetiger 1, transversal bands	ZMBN 91342	São Tomé and Príncipe, 1.6193°N 7.3364°E, 47 m	KX874578
	Clade E	dark peristomium and chaetiger 1, transversal bands	ZMBN 91343	São Tomé and Príncipe, 1.6193°N 7.3364°E, 47 m	KX874579
<i>A. fauveli</i>	Clade E	dark peristomium and chaetiger 1, transversal bands	ZMBN 91312	Cameroon, 3.291°N 9.5695°E, 37 m	KJ027318 ^a
<i>A. brementi</i>	Clade F	2-4 brown dorsal spots on anterior segments	ZMBN 91415	W. Sahara, 27.0158°N 13.5021°W, 32 m	KX874576
	Clade F	2-4 brown dorsal spots on anterior segments	ZMBN 91414	W. Sahara, 27.0158°N 13.5021°W, 32 m	KX874577

Table 2 (continued).
Таблица 2 (продолжение).

<i>A. brementii</i>	Clade F	?	ZMBN 91340	Gabon, 2.8702°S 9.4242°E, 105 m	KX874581
	Clade F	light-brown peristomium, thin transversal stripes	ZMBN 111724	Cape Verde, 15.444°N 23.1366°W, 82 m	KX874582
	Clade F	light-brown peristomium, thin transversal stripes	ZMBN 111725	Nigeria, 4.0718°N 6.6437°E, 40 m	KX874583
	Clade F	2-4 brown dorsal spots on anterior segments	ZMBN 91412	Morocco, 33.6879°N 7.6144°W, 55 m	KX874575
<i>Aponuphis</i> sp.	Clade F	?	USNM 1207008	Banyuls, France, 42.4892°N 3.1873°E, 70 m	KJ027319 ^a
<i>A. ornata</i>	Clade I	“horse-shoe” pattern	ZMBN 111727	Morocco, 32.4725°N 9.2744°W, 40 m	KX874586
	Clade I	“horse-shoe” pattern	ZMBN 111728	Morocco, 33.6879°N 7.6144°W, 55 m	KX874585
	Clade I	“horse-shoe” pattern	ZMBN 91354	Morocco, 32.4725°N 9.2744°W, 40 m	KX874587
	Clade I	“horse-shoe” pattern	ZMBN 91357	Morocco, 33.6879°N 7.6144°W, 55 m	KX874588
	Clade I	“horse-shoe” pattern	ZMBN 91355	Morocco, 32.4725°N 9.2744°W, 40 m	KX874589
<i>Aponuphis</i> sp.	Clade G	colorless peristomium, thin transversal stripes	ZMBN 111729	Senegal, 14.4596°N 17.6104°W, 498 m	KX874590
<i>Aponuphis</i> sp.	Clade G	colorless peristomium, thin transversal stripes	ZMBN 111730	Mauritania, 17.3388°N 16.7587°W, 518 m	KX874591
<i>A. bilineata</i>	Clade H	?		Qawra, Malta	AY838824 ^b
<i>Onuphis elegans</i> (Johnson, 1901)				not reported	AY838839 ^b
			USNM 1121747	Washington, USA	GQ478128 ^c
<i>Onuphis iridescens</i> (Johnson, 1901)				Bamfield, Canada	HM746715 ^d
<i>O. cf. iridescens</i>			USNM 1121744	California, USA	GQ478127 ^c
<i>Onuphis opalina</i> (Verrill, 1873)			USNM 1207006	Massachusetts, USA	KJ027343 ^a
			ZMBN 91332	Newfoundland Great Bank, Canada	KJ027344 ^a
<i>Onuphis shirikishinaen sis</i> (Imajima, 1960)			ZMBN 91333	Primorsky Krai, Russia	KJ027345 ^a

Table 2 (continued).
Таблица 2 (продолжение).

Species	Clade code	Color pattern	Catalogue number	Country	GenBank Accession Number
<i>Hyalinoecia tubicola</i> (O.F. Müller, 1776)			ZMBN 91320	Bergen, Norway	KJ027333 ^a
<i>Nothria conchylega</i> (Sars, 1835)			ZMBN 91331	Kuril Islands, Sea of Okhotsk, Russia, 46.9712°N 152.2017°E, 245 m	KJ027342 ^a

a — sequences from Budaeva *et al.* (2016), b — sequences from Struck *et al.* (2006), c — sequences from Zanol *et al.* (2010), d — sequences from Paul *et al.* (2010).

a — последовательности из Budaeva *et al.* (2016), b — последовательности из Struck *et al.* (2006), c — последовательности из Zanol *et al.* (2010), d — последовательности из Paul *et al.* (2010).

tion of the species tree based on p-distance. Bootstrap was performed in 100,000 iterations to provide the node support. Automatic Barcode Gap Discovery (ABGD) (Puillandre *et al.*, 2012) based on pairwise differences available at <http://www.abi.snv.jussieu.fr/public/abgd/> was used to define species boundaries.

Molecular analysis

The dataset had 397 aligned positions with 129 parsimony informative positions and 161 variable sites. *Aponuphis* appeared monophyletic with 100 bootstrap support. *Onuphis* appeared monophyletic and sister to *Aponuphis* with high bootstrap support (BS 96).

The ABGD analysis of the 16S rDNA dataset recovered nine potential species of *Aponuphis* (Fig. 3A–I). We were not able to find morphological differences between the clades identified as *A. bilineata* and *A. brementi* and therefore treat them as species complexes which require further investigation and formal description of potentially new species. Pairwise genetic distances between the putative species are shown in Table 3.

The *Aponuphis bilineata* species complex formed a monophyletic clade with 100 bootstrap support. This clade was subdivided into three subclades (Fig. 3A–C) with 3.9–5.4% genetic distances between them. Specimens with the typical two longitudinal stripes along the

body were separated into two clades: clade A (BS 100) found in the North Sea and in the northwestern African waters and clade B (BS 100) reported from Morocco. Two specimens from Mediterranean (Spain) with previously unknown color pattern of paired lateral dots formed clade C (BS 100).

The *Aponuphis brementi* species complex (BS 96) also consisted of three monophyletic subclades (Fig. 3D–F) with 5.2–9.3% genetic distances between them. Clade D (BS 100) comprised two specimens from Gabon and Benin with indistinct coloration of slightly brownish peristomium and thin transversal stripes on the anterior body segments. Clade E (BS 100) combined specimens from São Tomé and Príncipe and *A. fauveli* previously reported from Cameroon by Budaeva *et al.* (2016). All specimens had a distinct color pattern of a darkly pigmented peristomium and chaetiger 1 with subsequent brownish dorsal stripes located at the segment borders. Clade F (BS 99) was of wide distribution from the French coast to Gabon and combined specimens with two color morphs: previously described very distinct color pattern of paired dorsal dark brown spots and the pattern similar to the specimens from the clade D with indistinct dorsal transversal bands.

Clade G (BS 100) comprised two specimens from the deep (about 500 m) localities off Mauritania and Senegal. The specimens shared the presence of branchiae starting from chaetiger 5

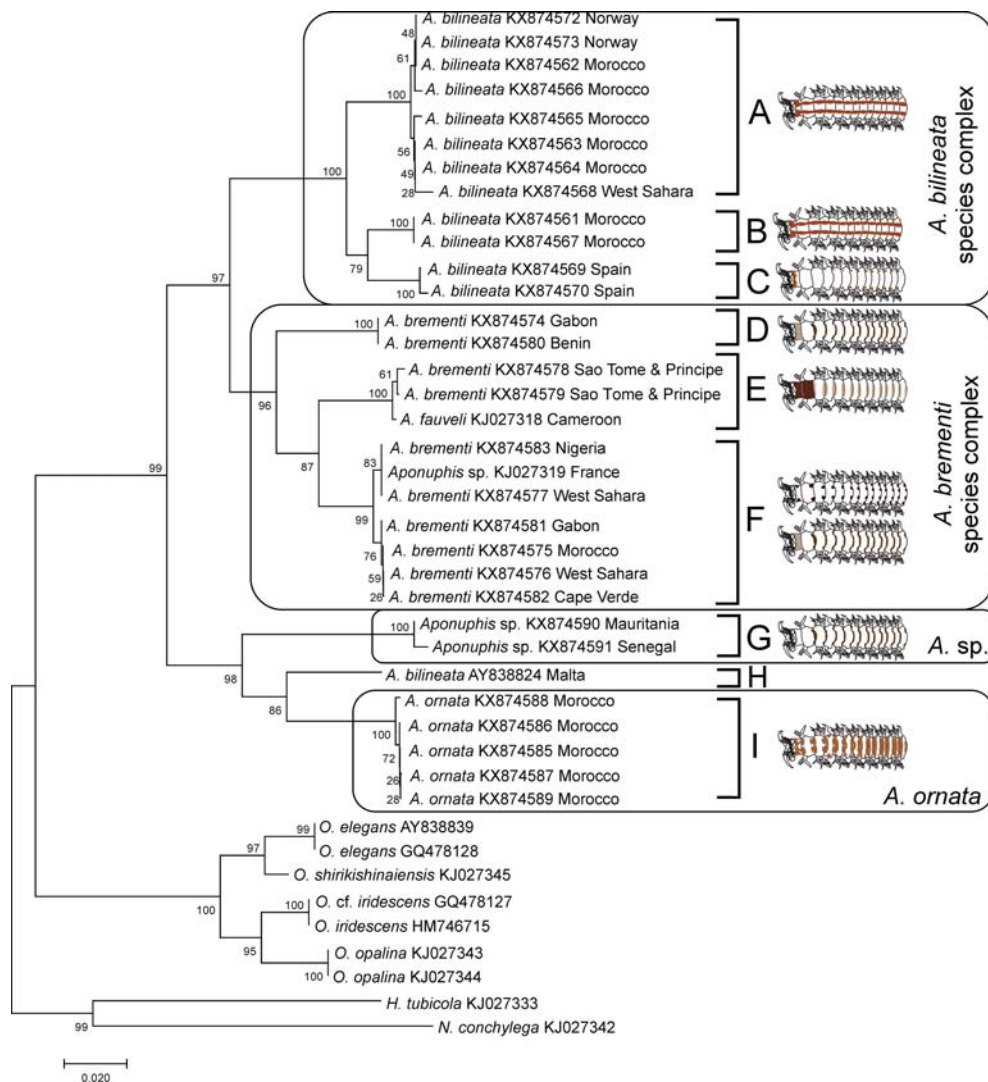


Fig. 3. Phylogenetic tree resulting from the Neighbor Joining analysis of 16S rDNA sequences of *Aponuphis* species. Numbers on nodes indicate bootstrap support. Capital letters correspond with the clades discussed in the text.

Рис. 3. Филогенетическое дерево, построенное методом ближайшего соседа на основе последовательностей гена 16S рДНК для видов *Aponuphis*. Значения в узлах дерева отображают поддержку бутстреп. Заглавные буквы соответствуют кладам, обсуждаемым в тексте.

and possibly represent a new species. The color pattern of the two studied specimens was indistinct with the peristomium lacking pigmentation and transversal stripes present on anterior chaetigers. Clade H was represented by a single specimen reported from Malta by Struck *et al.*

(2006) under the name *A. bilineata*. The color pattern of this specimen is unknown, and its taxonomic position is unresolved. Clade I (BS 100) combined all specimens from Morocco with typical “horse-shoe” color pattern on anterior segments identified as *Aponuphis ornata*.

Table 3. Estimates of evolutionary divergence over 16S rDNA sequence pairs between the *Aponuphis* clades revealed in the analysis. Clade codes correspond with those on Fig. 3.
Таблица 3. Оценка эволюционных дистанций между последовательностями гена 16S рДНК у видов *Aponuphis*. Обозначения клад соответствуют таковым на рис. 3.

Clade code	<i>A. bilineata</i> species complex			<i>A. brementi</i> species complex			<i>Aponuphis</i> sp.	<i>A. bilineata</i> (Struck <i>et al.</i> , 2006)	<i>A. ornata</i>
	A	B	C	D	E	F	G	H	I
A									
B	4.9%								
C	5.4%	3.9%							
D	11.7%	11.8%	12.3%						
E	12.3%	13.0%	11.0%	9.3%					
F	12.0%	12.1%	11.0%	6.3%	5.2%				
G	16.7%	17.7%	16.9%	15.2%	15.8%	15.9%			
H	15.7%	16.5%	16.9%	14.0%	17.4%	15.0%	11.2%		
I	15.7%	16.4%	16.9%	15.3%	17.4%	17.8%	10.6%	7.5%	

Taxonomic account

Aponuphis bilineata (Baird, 1870)
species complex
Figs. 1, 2, 4, 5.

Hyalinoecia bilineata Baird, 1870: 358–359; Rioja, 1918: 44; Fauvel, 1936: 51; Bellan, 1960: 18; Intes, Le Loeuff, 1975: 309.

Hyalinoecia rubra Langerhans, 1880: 292.

Aponuphis bilineata. — Kucheruk, 1978: 91; Aguirrezabalaga *et al.*, 2002: 27; Arias, Paxton, 2015: 358–360.

MATERIAL EXAMINED:

Western Africa, RV *Fridtjof Nansen*: ZMBN 91344, Morocco, St. GR37 (1 DNA voucher); ZMBN 91345, Morocco, St. GR37 (1 DNA voucher); ZMBN 91346, Morocco, St. GR40 (1 DNA voucher); ZMBN 91348, Morocco, St. GR49 (1 DNA voucher); ZMBN 111713, West Sahara, St. GR28 (1 DNA voucher); ZMBN 111714, Morocco, St. GR37 (1 DNA voucher); ZMBN 111719, Morocco, St. GR40 (1 DNA voucher); ZMBN 91413, Morocco, St. GR37 (1 DNA voucher); ZMBN 91348, Morocco, St. GR-49 (1); ZMBN 91344, West Sahara, St. GR-28 (8); ZMBN 91347, Morocco, St. GR40 (6); ZMBN 91341, Morocco, St. SL38 (5, 1 on SEM stub); ZMBN 91342, Guinea, St. 7GU-3C (1); ZMBN 91415, Morocco, St. GR37 (1 on SEM

stub); ZMBN 91340, São Tomé and Príncipe, St. E5-7-5B (10).

Mediterranean: ZMBN 111716, Spain, off Mallorca, 39.72125°N 3.46395°E, 10–18 m (1 DNA voucher); ZMBN 111717, Spain, off Mallorca, 39.72125°N 3.46395°E, 10–18 m (1 DNA voucher).

North Sea: ZMBN 91718, Norway, St. SFB-11_11, 61.213°N 1.816°E, 148 m (1 DNA voucher); ZMBN 91720, Norway, St. SFNE-01_11, 61.432°N 1.927°E, 266 m (1 DNA voucher).

TYPE LOCALITY: off Cornwall, Great Britain, 73 m.

REMARKS: Antennae reach chaetiger 10–15 (Fig. 4A). First 6–7 chaetigers with tridentate falcigers (Fig. 4E, F), bidentate falcigers were reported in previous descriptions (Arias, Paxton, 2015) but were absent in the studied material. Subulate ventral cirri present on the first five chaetigers (Fig. 4B, C). Branchiae simple strap-like, starting from chaetiger 5. Subacicular hooks from chaetiger 10 (Fig. 4D). Three clades are recovered within *A. bilineata* (Fig. 3A–C). Two clades (A and C) have the typical color pattern of two large spots on the peristomium continuing into two longitudinal orange stripes on the dorsal side. Additional lateral

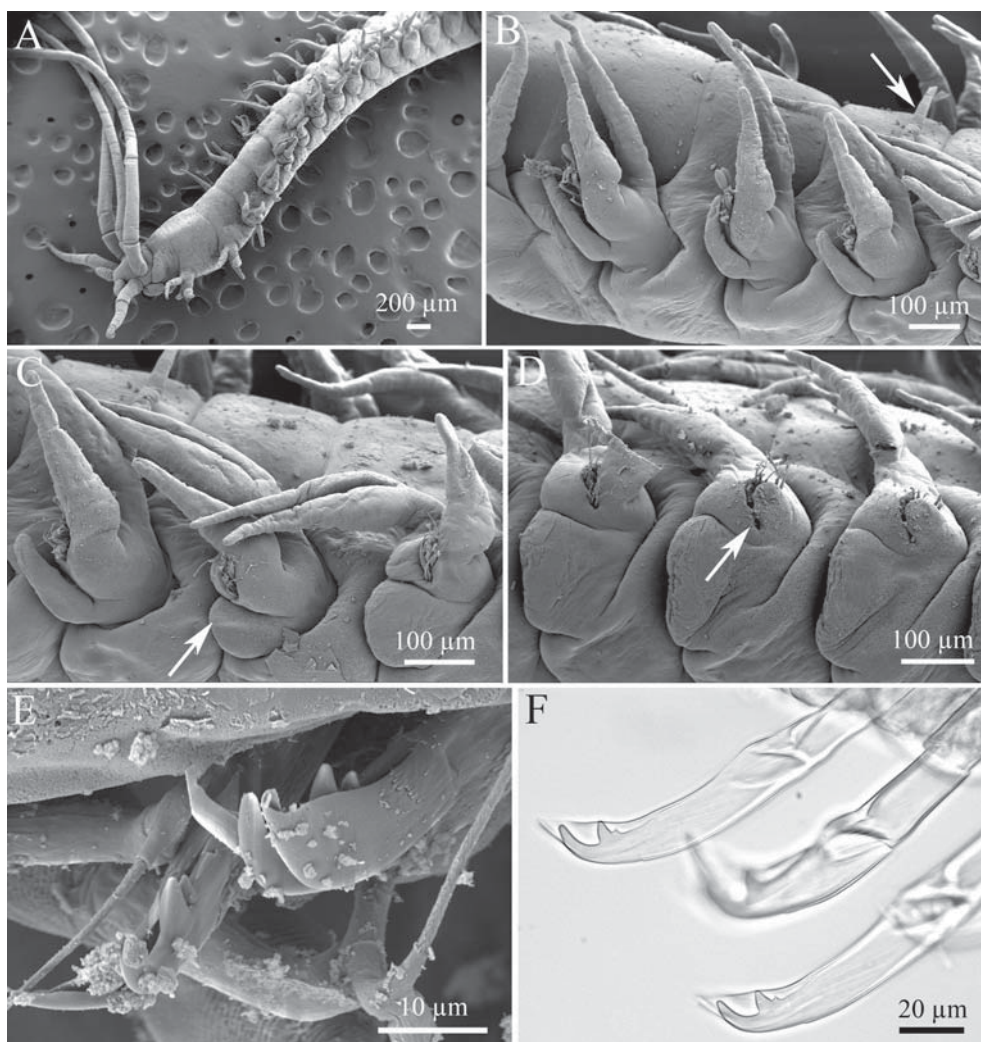


Fig. 4. Morphology of *Aponuphis bilineata*. A — anterior part of the body, lateral view; B — parapodia of chaetigers 3–5, arrow indicates the first branchia on parapodium 5; C — parapodia of chaetigers 5–7, arrow indicates ventral glandular pad on parapodium 6; D — parapodia of chaetigers 9–11, arrow indicates subacicular hooks on parapodium 10; E, F — pseudocompound falcigers from anterior parapodia. A–E — scanning electron micrographs; F — light micrograph.

Рис. 4. Морфологические признаки *Aponuphis bilineata*. А — передний отдел тела, вид сбоку; В — параподии 3–5-го сегментов, стрелка указывает на первую жабру на 5-м сегменте; С — параподии 5–7-го сегментов, стрелка указывает на вентральную железистую подушечку на 6-м сегменте; D — параподии 9–11-го сегментов, стрелка указывает на субацикулярные крючья на 10-м сегменте; E, F — псевдосочлененные крючковидные щетинки на передних параподиях. А–Е — сканирующие электронные микрофотографии; F — световая микрофотография.

pigmented spots are visible on each segment at the bases of the parapodia (Figs 1A, 2A). This pattern was named by Arias & Paxton (2015) as morph (1). Morph (2) was described as “peri-

stomium and first 3–4 chaetigers with two large brownish spots almost filling dorsal surface of segment, sometimes coalescing medially; from chaetiger 4–5 to median region two longitudinal

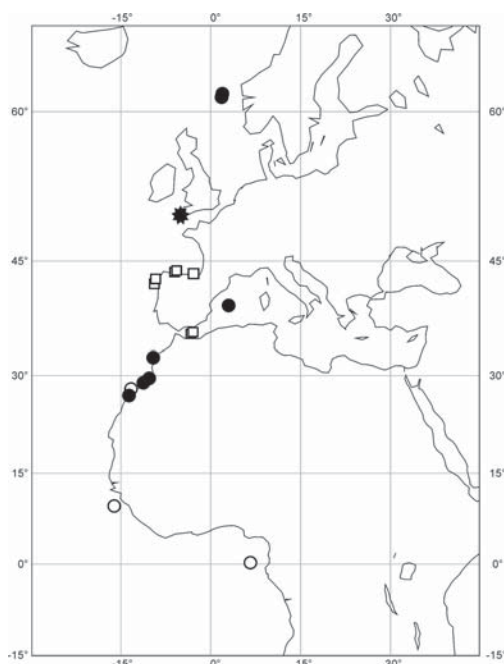


Fig. 5. Distribution of *Aponuphis bilineata*. Black star indicates the type locality; black circles indicate localities from which genetic data were available; white circles indicate localities without genetic data; white squares indicate data from literature (Arias, Paxton, 2015).

Рис. 5. Распространение *Aponuphis bilineata*. Черной звездой отмечено типовое местонахождение; черными кругами отмечены станции, для которых получены молекулярно-генетические данные; белыми кругами отмечены станции, для которых молекулярно-генетических данных нет; белыми квадратами отмечены данные из литературы (Arias, Paxton, 2015).

dorsal pigmented stripes discourging laterally close to parapodia” (Arias, Paxton, 2015). This morph was not present in the studied material. Clade C comprised specimens collected off Mallorca, Spain with slightly pigmented peristomium and a pair of lateral pigmented dots on each segment (Figs 1B, 2B) representing the third previously unknown color morph in this species complex.

DISTRIBUTION: East Atlantic, North Sea, Mediterranean, in western Africa from Morocco to São Tomé and Príncipe. Clade A — North Sea, off Morocco and Western Sahara, 101–266

m; clade B — off Morocco, 102 m; clade C — off Mallorca, Spain, 10–18 m (Fig. 5).

Aponuphis brementi (Fauvel, 1916) species complex
Figs. 1, 2, 6, 7.

Hyalinoecia brementi Fauvel, 1916: 5, Figs. 2–3.

Aponuphis brementi. — Paxton, 1986: 54; Arias, Paxton, 2015: 360–361, Fig. 7C.

Hyalinoecia fauveli Rioja, 1918: 45; Fauvel, 1923: 424, Fig. 167a–h; 1936: 52; Bellan, 1960: 18; Intes, Le Loeuff, 1975: 309; Amoureux, 1977: 55; Kirkegaard, 1988: 33.

Hyalinoecia fauveli africana Rullier, 1965: 37; Kirkegaard, 1988: 33.

Aponuphis fauveli. — Paxton, 1986: 54; Aguirrezabalaga *et al.*, 2002: 27.

MATERIAL EXAMINED: RV *Fridtjof Nansen*: ZMBN 91340, Gabon, St. 5G-12 (1 DNA voucher on SEM stub); ZMBN 91341, Benin, St. 7BN-1E (1 DNA voucher); ZMBN 91342, São Tomé and Príncipe, St. 7SP-03 (1 DNA voucher); ZMBN 91343, São Tomé and Príncipe, St. 7SP03 (1 DNA voucher); ZMBN 91352, Gabon, St. 5G-10 (1 DNA voucher on SEM stub); ZMBN 91412, Morocco, St. GR56 (1 DNA voucher on SEM stub); ZMBN 91414, Western Sahara, St. GR27 (1 DNA voucher); ZMBN 91415, Western Sahara, St. GR27 (1 DNA voucher); ZMBN 111724, Cape Verde, St. SL02 (1 DNA voucher); ZMBN 111725, Nigeria, St. 6N-15 (1 DNA voucher); ZMBN 91312, Cameroon, St. 5C-11 (1); ZMBN 91349, São Tomé and Príncipe, St. 5SP-03 (1); ZMBN 111731, Angola, St. 7AN-01 (8, 2 on SEM stub); ZMBN 111732, Angola, St. 7AN-02 (1); ZMBN 116036, Angola, St. 7AN-04 (6); ZMBN 116037, Cape Verde, St. SL02 (1); ZMBN 116039, Ghana, St. 7GH-1E (1); ZMBN 116040, Ghana, St. 7GH-04 (2); ZMBN 116041, Ghana, St. 7GH-7D (1); ZMBN 116043, Morocco, St. GR56 (2); ZMBN 116044, Nigeria, St. 5N-17 (1); ZMBN 116045, Nigeria, St. 6N-15 (2); ZMBN 116046, Nigeria, St. 6N-23 (1).

TYPE LOCALITY: Monaco, Mediterranean.

REMARKS: Antennae reach chaetiger 15–20 (Fig. 6A). First six chaetigers with tridentate pseudocompound falcigers (Fig. 6D). Bidentate falcigers reported by Arias and Paxton

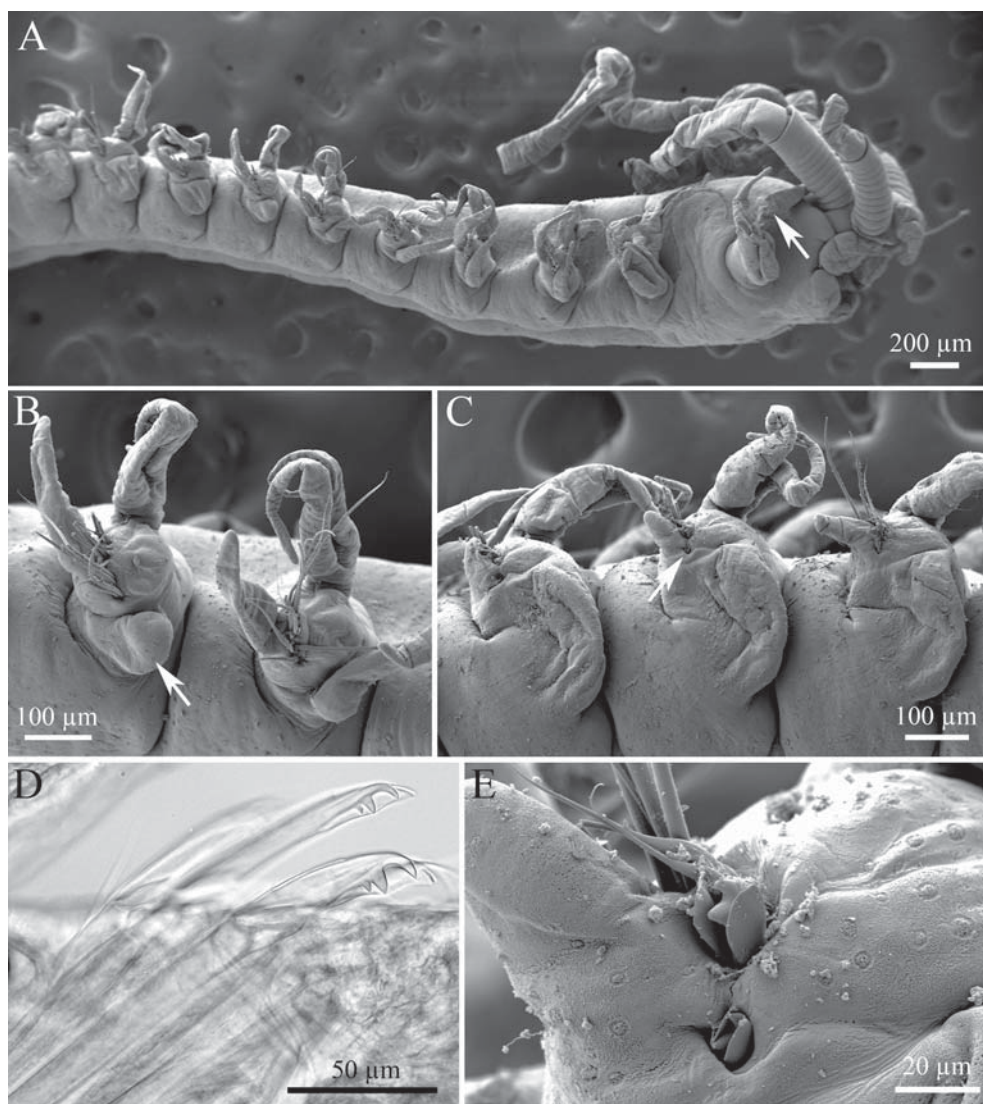


Fig. 6. Morphology of *Aponuphis brementi*. A — anterior part of the body, lateral view, arrow indicates the first branchia on chaetiger 1; B — parapodia of chaetigers 7–6, arrow indicates ventral glandular pad on parapodium 7; C — parapodia of chaetigers 12–14, arrow indicates subacicular hooks on parapodium 13; D — tridentate pseudocompound falcigers; E — subacicular hooks. A–C, E — scanning electron micrographs; D — light micrograph.

Рис. 6. Морфологические признаки *Aponuphis brementi*. А — передний отдел тела, вид сбоку, стрелка указывает на первую жабру на 1-м сегменте; В — параподии 6–7-го сегментов, стрелка указывает на вентральную железистую подушечку на 7-м сегменте; С — параподии 12–14-го сегментов, стрелка указывает на субакикулярные крючья на 13-м сегменте; Е — трехзубые псевдосочлененные щетинки; Е — субакикулярные крючья. А–С, Е — сканирующие электронные микрофотографии, D — световая микрофотография.

(2015) were not observed. Subulate ventral cirri present on anterior six chaetigers (Fig. 6B). Branchiae starting from chaetiger 1–2. One small

specimen (width 0.8 mm) had branchiae from chaetiger 4. Later appearance of branchiae was reported in juveniles of *A. ornata* and *A. bre-*

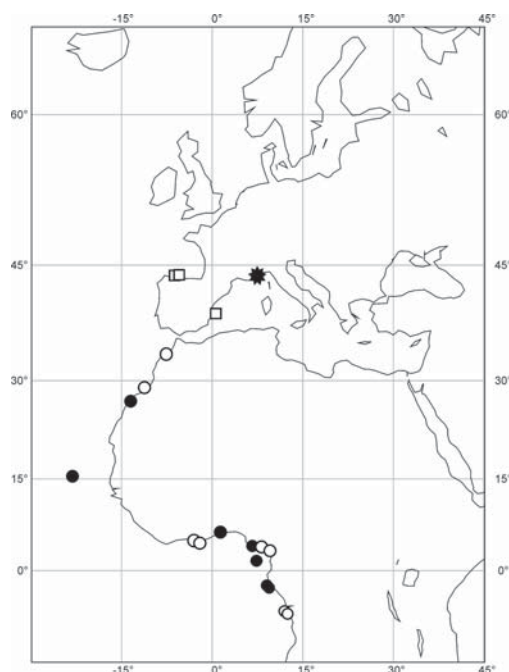


Fig. 7. Distribution of *Aponuphis brementi*. Black star indicates the type locality; black circles indicate localities from which genetic data were available; white circles indicate localities without genetic data; white squares indicate data from literature (Arias, Paxton, 2015).

Рис. 7. Распространение *Aponuphis brementi*. Черной звездой отмечено типовое местонахождение; черными кругами отмечены станции, для которых получены молекулярно-генетические данные; белыми кругами отмечены станции, для которых молекулярно-генетических данных нет; белыми квадратами отмечены данные из литературы (Arias, Paxton, 2015).

menti by Arias & Paxton (2015). Subacicular hooks from chaetiger 12–13 (Fig. 6C, E). Three color morphs were found in *A. brementi*. Seven specimens from Morocco (GR27, GR37, GR56) had the typical pattern with two large dorsolateral dark brown spots on the peristomium and all subsequent chaetigers (Figs 1D, 2D). In specimens from Ghana (7GH-1E), Cameroon (5C-11), São Tomé and Príncipe (7SP-03) and Angola (7AN-01, 7AN-04), the peristomium and the first chaetiger were completely dark in color with subsequent chaetigers bearing thin

transversal bands (Figs 1E, 2E). A similar color morph has been reported by Kirkegaard (1988) for *Hyalinoecia fauveli africana*, a subspecies subsequently synonymized with *A. brementi* by Arias & Paxton (2015). Seventeen specimens from Cape Verde (SL02), Ghana (7GH-7D), Benin (7BN-1E), Nigeria (6N-15, 5N-17, 6N-23), Gabon (5G-12) and Angola (7AN-2, 7AN-04) were with slightly pigmented peristomium and thin dark transversal stripes on anterior segments (Figs 1F, 2F). Clade E comprised specimens with a dark peristomium and first segment (Fig. 3E). Clade F combined specimens with two color morphs: the typical morph with dorsal brown spots and the morph with thin transversal stripes (Fig. 3F). The latter morph was also found in clade D (Fig. 3D).

DISTRIBUTION: Clade D — off Benin and Gabon, 44–109 m; clade E — off Cameroon and São Tomé and Príncipe, 37–47 m; clade F — widely distributed in Eastern Atlantic from France to Gabon, depth range in studied material 32–156 m (Fig. 7).

Aponuphis ornata (Fauvel, 1928)

Figs. 1, 2, 8, 9.

Hyalinoecia bilineata ornata Fauvel, 1928:12; 1936: 52, Fig. 3.

Aponuphis ornata. — Paxton, 1986: 54; Arias, Paxton, 2015: 361–363, Figs 7D–E, 8, 9.

MATERIAL EXAMINED: RV *Fridtjof Nansen*: ZMBN 91354, Morocco, St. GR50 (1 DNA voucher); ZMBN 91355, Morocco, St. GR50 (1 DNA voucher); ZMBN 91357, Morocco, St. GR56 (1 DNA voucher); ZMBN 111727, Morocco, St. GR50 (1 DNA voucher, on SEM stub); ZMBN 111728, Morocco, St. GR56 (1 DNA voucher, on SEM stub); ZMBN 91353, Morocco, St. GR50 (1); ZMBN 91356, Morocco, St. GR56 (1).

TYPE LOCALITY: off Morocco, north-western Africa.

REMARKS: Antennae reaching chaetigers 10–15 (Fig. 8A). First 5–6 pairs of parapodia with bi- and tridentate pseudocompound falcigers (Fig. 8D, E). First five chaetigers with subulate ventral cirri (Fig. 8B). Branchiae from chaetiger 4–5, simple, strap-like. Subacicular

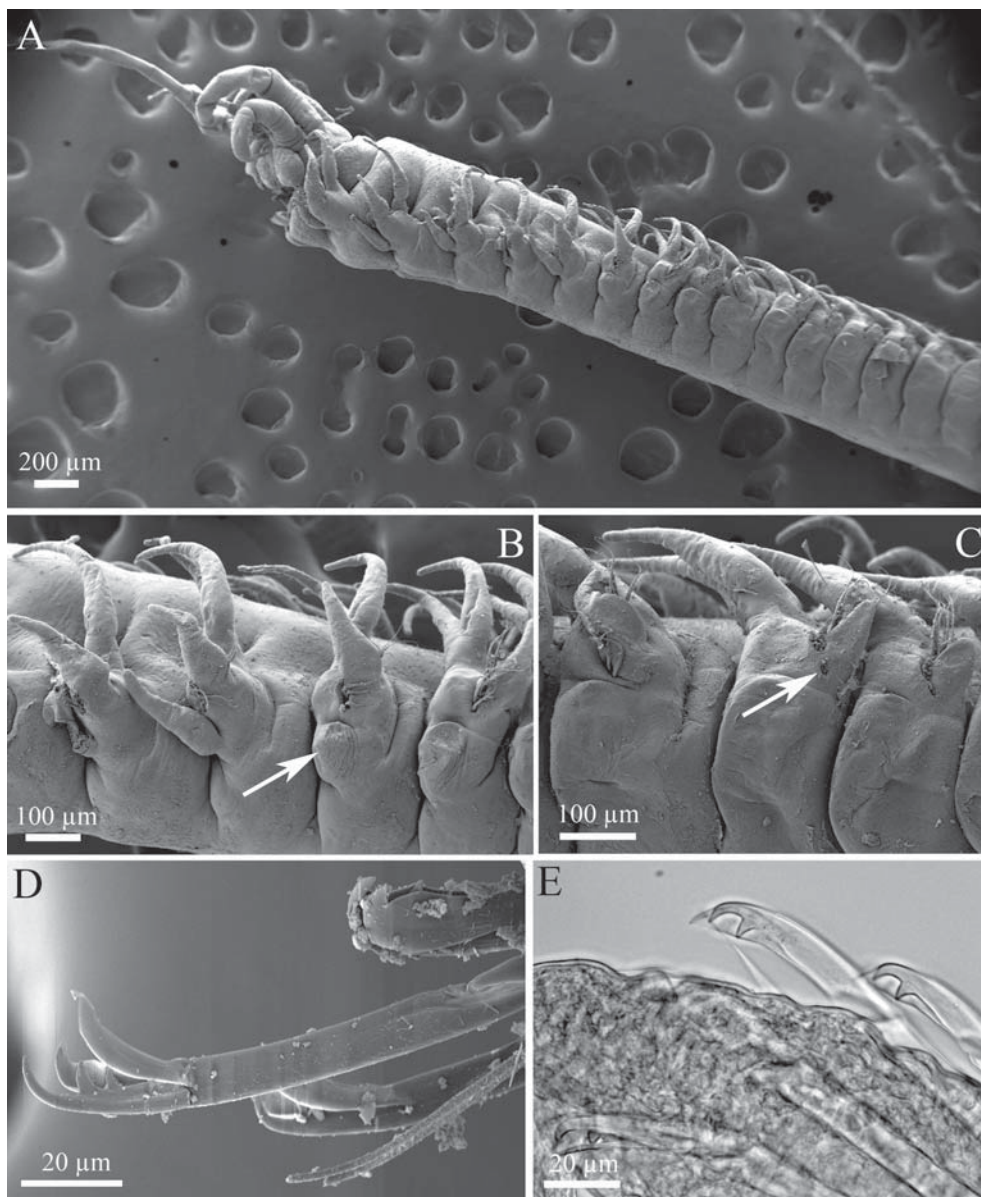


Fig. 8. Morphology of *Aponuphis ornata*. A — anterior part of the body, lateral view; B — parapodia of chaetigers 3–6, arrow indicates ventral glandular pad on parapodium 6; C — parapodia of chaetigers 9–11, arrow indicates subacicular hooks on parapodium 10; D — tridentate pseudocompound falciger; E — bidentate pseudocompound falciger. A–D — scanning electron micrographs; E — light micrograph.

Рис. 8. Морфологические признаки *Aponuphis ornata*. А — передний отдел тела, вид сбоку; В — параподии 3–6-го сегментов, стрелка указывает на вентральную железистую подушечку на 6-м сегменте; С — параподии 9–11-го сегментов, стрелка указывает на субакикулярные крючки на 10-м сегменте; D — трехзубая псевдосочлененная крючковидная щетинка; E — двузубые псевдосочлененные крючковидные щетинки. А–D — сканирующие электронные микрофотографии; E — световая микрофотография.



Fig. 9. Distribution of *Aponuphis ornata*. Black star indicates the type locality; black circles indicate localities from which genetic data were available; white square indicates data from literature (Arias, Paxton, 2015).

Рис. 9. Распространение *Aponuphis ornata*. Черной звездой отмечено типовое местонахождение; черными кругами отмечены станции, для которых получены молекулярно-генетические данные; белым квадратом отмечены данные из литературы (Arias, Paxton, 2015).

hooks from chaetiger 10 (Fig. 8C). All studied specimens were collected close to the type locality and had the typical color pattern. Peristomium with two large dorsal spots fusing medially; anterior chaetigers with “horse-shoe” pattern. Each “horse-shoe” spot is formed by pigmentation on adjacent chaetigers: two lateral square spots at the posterior margin of an anterior chaetiger and a transversal band on the anterior margin of a posterior chaetiger. Posterior chaetigers with wide pigmented transversal bands (Figs 1C, 2C).

DISTRIBUTION: East Atlantic, off Morocco, Bay of Biscay and Atlantic Iberia, Western and Central Mediterranean Sea (Arias, Pax-

ton, 2015). Depth range in studied material 40–55 m (Fig. 9).

Aponuphis sp.
Figs. 10, 11.

MATERIAL EXAMINED: RV *Fridtjof Nansen*: ZMBN 111729, Senegal, St. GR08 (1 DNA voucher on SEM stub); ZMBN 111730, Mauritania, St. GR11 (1 DNA voucher).

DESCRIPTION: Two incomplete studied specimens 1.0 and 0.8 mm wide consisting of 37 and 44 chaetigers respectively. Prostomium rounded with ovoid frontal lips. Antennae relatively short, reaching chaetiger 7–10 (Fig. 10A). Palps reaching chaetiger 8–10. Ceratophores of lateral antennae with seven rings. First six pairs of parapodia modified, directed laterally. Branchiae simple, strap-like from chaetiger 5 (Fig. 10B). Exclusively tridentate pseudocompound falcigers with short pointed hoods present on first four pairs of parapodia (Fig. 10C). Fourth pair of parapodia with only one falciger. Pectinate chaetae with 9–11 distal denticles, from chaetiger 10. Subacicular hooks from chaetiger 10. Color pattern of dorsal transversal thin stripes on anterior chaetigers.

DISTRIBUTION: Northeastern African waters from Mauritania to Senegal. Depth range 498–518 m (Fig. 11).

Discussion

The polychaete fauna of western African waters, including the onuphid fauna, is largely understudied. Many of the African onuphids have been described in the early XX century (Augener, 1918; Fauvel, 1928). The names of species described from European waters were traditionally used in identification of the local African fauna. Application of scanning electron microscopy and molecular tools most probably should lead to the discovery of a high diversity of annelids in western African waters. One example of such hidden diversity has been uncovered in the recent study of another onuphid genus, *Diopatra*, revealing at least six new species in

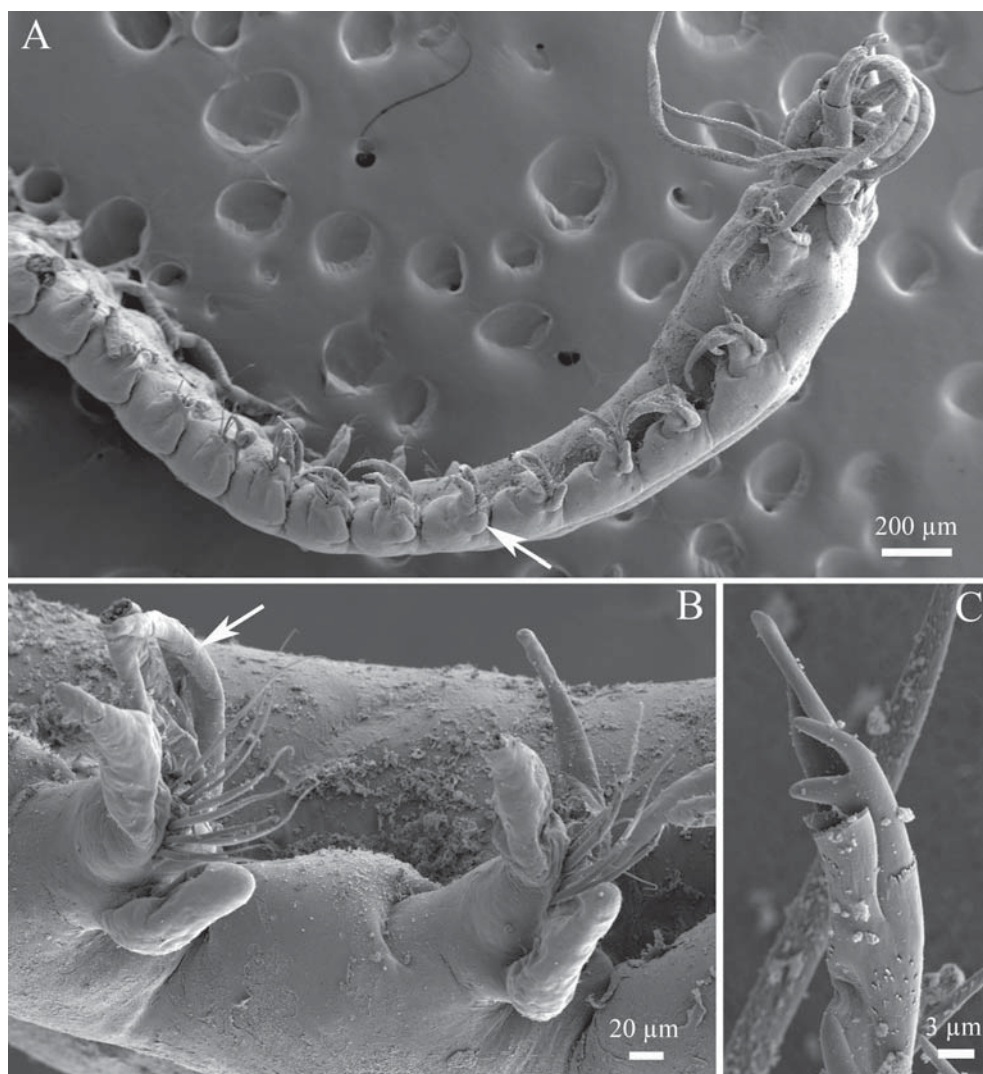


Fig. 10. Morphology of *Aponuphis* sp. — anterior part of the body, lateral view, arrow indicates ventral glandular pad on chaetiger 6; B — parapodia of chaetigers 4–5, arrow indicates the first branchia on parapodium 5; C — tridentate pseudocompound falciger. A–C — scanning electron micrographs.

Рис. 10. Морфологические признаки *Aponuphis* sp. А — передний отдел тела, вид сбоку, стрелка указывает на вентральную железистую подушечку на 6-м сегменте; В — параподии 4–5-го сегментов, стрелка указывает на первую жабру на 5-м сегменте; С — трехзубая псевдосочлененная крючковидная щетинка. А–С — сканирующие электронные микрофотографии.

western Africa based on morphological and molecular data (Hektoen, Budaeva, 2016).

Aponuphis has a relatively simple external morphology with slightly modified anterior parapodia, only four types of chaetae, and simple branchiae. All diagnostic characters are high-

ly variable even at intraspecific level which makes species difficult to define. As a result, several authors suggested synonymization of all *Aponuphis* species into one or two species (Bellan, 1964; Kirkegaard, 1988) which, however, has not been corroborated by the most recent



Fig. 11. Distribution of *Aponuphis* sp. Black circles indicate localities from which genetic data were available.

Рис. 11. Распространение *Aponuphis* sp. Черными кругами отмечены станции, для которых получены молекулярно-генетические данные.

studies (Arias, Paxton, 2015). On the other hand, *Aponuphis* is the only genus within onuphids with reported distinct color morphs characteristic for a certain species. Although it has been suggested that color morphs can be used in species identification (Arias, Paxton, 2015), it remained unclear how these morphs correspond with genetic species in *Aponuphis*.

We have considerably increased the amount of genetic data known for *Aponuphis*. Until now, the GenBank database contained data on three species. Our results show that the GenBank record for *A. bilineata* (AY838824) is most probably a misidentification, since this sequence was very divergent from all *A. bilineata* sequences obtained in the present study. This single record was recognized as a provisional species by the ABGD analysis and its taxonomical status remains unresolved. The GenBank record for *A. fauveli* (KJ027318) clustered within

the *A. brementi* species complex confirming the synonymization of these two species proposed by Arias & Paxton (2015). This specimen fell into clade E with the peristomium and first chaetiger being darkly pigmented. *Aponuphis* sp. (KJ027319) from off the Mediterranean French coast also clustered within the *A. brementi* species complex within clade F with a wide geographical distribution. The color pattern of this specimen is unknown.

Genetic distances between the subclades within the two proposed species complexes (*A. bilineata* species complex and *A. brementi* species complex) were considerably smaller (3.9–5.4% and 5.2–9.3% respectively) than those between the *Diopatra* species reported by Pires *et al.* (2010) but were similar or even higher than the genetic distances between the *Onuphis* species included in the present study (2.1–26.9%). The ABGD analysis suggested that each of the subclades within the *A. bilineata* and *A. brementi* species complexes should be treated as a separate species. We did not find clear morphological differences between the specimens from different subclades and thus do not formally describe them as species in the present study. Nevertheless, our results indicate the presence of genetic diversity within *A. bilineata* and *A. brementi* that should be investigated further based on examination of additional material and genetic markers.

Aponuphis sp. (clade G) was recognized by the ABGD analysis as a separate species. We only had two specimens of this presumably new species and thus do not describe it as a new species. *Aponuphis* sp. does not have a distinct color pattern but resembles one of the color morphs of *A. brementi*. However, it occurs much deeper than other species (about 500 m deep) and has branchiae starting from chaetiger 5 unlike *A. brementi* with branchiae appearing on chaetiger 1–2.

In general, we suggest that color pattern cannot be used as a single diagnostic character in *Aponuphis* species identification. The presence of typical coloration such as two longitudinal stripes in *A. bilineata*, paired large dorsal spots in *A. brementi* and the “horse-shoe” pat-

tern in *A. ornata* allows identification of a species with confidence. However, specimens with less prominent coloration, usually seen as somewhat darker pigmented peristomium and transversal brownish bands on anterior chaetigers, may belong to a range of different species.

Geographical ranges of several *Aponuphis* species have been extended in the present study. Arias and Paxton (2015) reported *A. bilineata* from the eastern Atlantic and Mediterranean. We have found this species complex much further to the north in the North Sea and also down to the south off, Morocco, Western Sahara and Guinea. In addition, ten specimens with typical bilineate pattern were reported from São Tomé and Príncipe. The geographical range of *A. brementi* in the eastern Atlantic and Mediterranean (Arias, Paxton, 2015) is here extended to the African coast down to Gabon confirming the synonymization of *A. fauveli* with its subspecies *A. fauveli africana* reported from Morocco to Gabon with *A. brementi*. In fact, the color pattern of *A. fauveli africana* resembles the color pattern of *A. brementi* from clade E in the present study and examination of more material may lead to the resurrection of the subspecies *A. fauveli africana* and elevation to the status of full species with darkly pigmented peristomium and chaetiger 1. The geographical range of *A. ornata* originally described from Morocco (Fauvel, 1928) and later reported from the Bay of Biscay, Atlantic Iberia and Mediterranean (Arias, Paxton, 2015) remained unchanged.

Currently *Aponuphis* comprises ten valid species known from the Northern and Eastern Atlantic and eastern Australia. Our findings suggest that the genetic diversity within the genus may be considerably higher than it was accepted before. Each of the three provisional species within *A. bilineata* and *A. brementi* species complexes may represent a new species. In addition, the deep-water *Aponuphis* sp. form Senegal and Mauritania as well as erroneously identified *A. bilineata* from Malta (Struck *et al.*, 2006) may also represent new species. Undoubtedly further investigations involving testing of nuclear genetic markers and morphological variation in *Aponuphis* species is required.

Acknowledgements

The authors thank Canary Current Large Marine Ecosystem (CCLME), Guinea Current Large Marine Ecosystem (GCLME) and the Norad funded EAF-Nansen program www.eaf-nansen.org for access to material. We are grateful to the University Museum of Bergen for supporting the visit of PB to the Museum with funding granted by the JRS Biodiversity Foundation to the project «Marine Invertebrates of West Africa» Life program. We would like to thank Irina Ekimova for help with molecular lab work. We are also grateful to Egil Severin Erichsen, Irene Heggstad and Katrine Kongshavn for assistance with SEM. Participation of NB in this study was supported by a Marie Curie International Incoming Fellowship (Project PRODEEP) and the Research Council of Norway (top-up financing of Marie Curie Fellows).

References

- Aguirrezabalaga F., Ceberio A., Paxton H. 2002. Onuphidae (Polychaeta) from the Capbreton Canyon (Bay of Biscay, NE Atlantic) with the description of *Paradiopatra capbretonensis* sp. nov. // *Steenstrupia*. Vol.27. No.1. P.19–28.
- Amoureux L. 1977. Annélides polychètes errantes recueillies sur les pentes du talus continental à l'entrée de la Manche, avec la description de deux espèces nouvelles. Campagne 1973 de la "Thalassa" // *Cahiers de Biologie Marine*. Vol.18. No.4. P.391–411.
- Arias A., Paxton H. 2015. *Onuphis* and *Aponuphis* (Annelida: Onuphidae) from southwestern Europe, with the description of a new species // *Zootaxa*. Vol.3949. No.3. P.345–369.
- Augener H. 1918. Polychaeta // *Beitrag zur Kenntnis der Meeresfauna Westafrikas*. Vol.2. No.2. P.67–625.
- Baird W. 1870. Remarks on several genera of annelids belonging to the group Eunicea with a notice of such species as are contained in the collection of the British Museum and a description of some others hitherto undescribed // *Journal of the Linnean Society of London*. Vol.10. P.341–361.
- Bellan G. 1960. Annélides polychètes. Résultats Scientifiques de la Campagne du N.R.P. "Faial" dans les eaux côtières du Portugal // *Lisboa*. Vol.2. P.1–31.
- Bellan G. 1964. Contribution à l'étude systématique, bionomique et écologique des annélides polychètes de la Méditerranée. Thèse, Faculté des Sciences de l'Université d'Aix-Marseille. 371 p.
- Budaeva N., Schepetov D., Zanol J., Neretina T., Willassen E. 2016. When molecules support morphology: Phylogenetic reconstruction of the family Onuphidae

- (Eunicida, Annelida) based on 16S rDNA and 18S rDNA // Molecular phylogenetics and evolution. Vol.94. P.791–801.
- Detinova N.N. 1985. [Polychaetous annelids of Rejkjanes Ridge (North Atlantic)] // Trudy Instituta Okeanologii PP Shirshova. T.120. P. 96–136 [in Russian].
- Diepenbroek M., Grobe H., Sieger R. 2000. PanMap. <http://www.pangaea.de/Software/PanMap>
- Edgar R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput // Nucleic acids research. Vol.32. No.5. P.1792–1797.
- Fauvel P. 1916. Deux polychètes nouvelles (*Disoma watsoni* n. sp., et *Hyalinoecia brementi* n. sp.) // Bulletin d'Institut Oceanographique (Monaco). Vol.316. P.1–10.
- Fauvel P. 1923. Faune de France: Polychètes errantes. Paris: Paul Lechevalier. 488 p.
- Fauvel P. 1928. Annélides Polychètes nouvelles du Maroc // Bulletin de la Société Zoologique de France. Vol.53. P.9–13.
- Fauvel P. 1936. Contribution à la faune des Annélides Polychètes du Maroc // Mémoires de la Société des Sciences Naturelles du Maroc. Vol.43. P.1–143.
- Hektoen M., Budaeva N. 2016. Diversity and phylogeny of *Diopatra* bristle worms (Onuphidae, Annelida) from West Africa // 12th International Polychaete Conference. National Museum Wales, Cardiff, 01–05 August 2016. Abstract. P.27.
- Intes A., Le Loeuff P. 1975. Les annelides polychetes de Cote d'Ivoire. I-Polychetes errantes-compte rendu systematique // Cahiers de la Office de la Recherche Scientifique et Technique des outre mer (Oceanographie). Vol.13. No.4. P.267–321.
- Kirkegaard J. B. 1988. The polychaeta of West Africa. Part II. Errant species. 2. Nephtyidae to Dorvilleidae // Atlantide Report. Vol.14. P.7–89.
- Kucheruk N.V. 1978. [Deep-water Onuphidae (Polychaeta) from the collections of the 16th cruise of the R/V Dmitry Mendeleev (to the generic classification of the family Onuphidae)] // Trudy Instituta Okeanologii AN SSSR. T113. P.88–106 [in Russian].
- Kumar S., Stecher G., Tamura K. 2016. MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets // Molecular Biology and Evolution Vol.33. P.1870–1874.
- Langerhans P. 1880. Wurmfauna von Madeira // Zeitschrift für wissenschaftliche Zoologie. Bd.33. S.267–316.
- Palumbi S.R., Martin A., Romano S., McMillan W.O., Stice L., Grabowski G. 1991. The Simple Fool's Guide to PCR, Version 2 edition. Department of Zoology, University of Hawaii — Honolulu. 46 p.
- Paul C., Halanych K.M., Tiedemann R., Bleidorn C. 2010. Molecules reject an opheliid affinity for *Travisia* (Annelida) // Systematics and Biodiversity. Vol.8. No.4. P.507–512.
- Paxton H. 1986. Generic revision and relationships of the family Onuphidae (Annelida: Polychaeta) // Records of the Australian Museum. Vol.38. No1. P.1–74.
- Paxton H. 2017. Three new species of *Aponuphis* (Annelida: Onuphidae) from eastern Australia // Zootaxa. Vol.4344. P.246–260.
- Pires A., Paxton H., Quintino V., Rodrigues A.M. 2010. *Diopatra* (Annelida: Onuphidae) diversity in European waters with the description of *Diopatra micrura*, new species // Zootaxa. Vol.2395. P.17–33.
- Puillandre N., Lambert A., Brouillet S., Achaz G. 2012. ABGD, Automatic Barcode Gap Discovery for primary species delimitation // Molecular Ecology. Vol.21. No.8. P.1864–1877.
- Puslednik L., Serb J.M. 2008. Molecular phylogenetics of the Pectinidae (Mollusca: Bivalvia) and effect of increased taxon sampling and outgroup selection on tree topology // Molecular Phylogenetics and Evolution. Vol.48. P.1178–1188.
- Rioja E. 1918. Datos para el conocimiento de la fauna de anélidos poliquetos del Cantábrico (2^a Parte) // Trabajos del Museo Nacional de Ciencias Naturales, Madrid, Serie Zoológica. Vol.37. P.1–99.
- Rullier F. 1965. Contribution à la faune des annélides polychètes du Dahomey et du Togo // Cahiers ORSTOM. Série Océanographie. Vol.3. No.3. P.5–66.
- Struck T.H., Purschke G., Halanych K. M. 2006. Phylogeny of Eunicida (Annelida) and exploring data congruence using a partition addition bootstrap alteration (PABA) approach // Systematic Biology. Vol.55. No.1. P.1–20.
- Zanol J., Halanych K.M., Struck T.H., Fauchald K. 2010. Phylogeny of the bristle worm family Eunicidae (Eunicida, Annelida) and the phylogenetic utility of non-congruent 16S, COI and 18S in combined analyses // Molecular Phylogenetics and Evolution. Vol.55. No.2. P.660–676.

Responsible editor I.A. Jirkov

Appendix 1. List of stations of RV *F. Nansen* with materials used in this study.

Приложение 1. Список станций НИС «Ф. Нансен», с которых были получены материалы для данной работы.

Station	Country	Coordinates	Depth, m	Date	Fixative
5G-12	Gabon	S 2,8702° E 9,4242°	105	08.07.2005	96% Ethanol
6N-15	Nigeria	N 4,0718° E 6,6437°	40	19.06.2006	4% Formalin
6N-23	Nigeria	N 3,9223° E 8,1641°	84	22.06.2006	96% Ethanol
7AN-02	Angola	S 6,7076° E 11,9659°	106	11.07.2007	96% Ethanol
7AN-01	Angola	S 7,1452° E 12,4721°	50	11.07.2007	96% Ethanol
7AN-04	Angola	S 7,1452° E 12,4721°	65	12.07.2007	96% Ethanol
7BN-1E	Benin	N 6,0358° E 1,3557°	44	11.06.2007	96% Ethanol
7GH-1E	Ghana	N 4,9613° W 3,0146°	52	6.06.2007	?
7GH-7D	Ghana	N 4,5382° W 2,0449°	76	7.06.2007	?
7GH-04	Ghana	N 4,6427° W 2,7353°	156	6.06.2007	?
7GU-3C	Guinea	N 9,6211° W 16,1102°	94	11.05.2007	4% Formalin
7SP-03	São Tomé and Príncipe	N 1,6193° E 7,3364°	47	18.06.2007	96% Ethanol
5SP-03	São Tomé and Príncipe	N 1,6361° E 7,2091°	79	26.06.2005	96% Ethanol
5C-11	Cameroon	N 3,2913° E 9,5675°	37	23.06.2005	96% Ethanol
E5-7-5B	São Tomé and Príncipe	?	?	2008	4% Formalin
GR08	Senegal	N 14,4596° W 17,6104°	498	05.11.2011	96% Ethanol

Station	Country	Coordinates	Depth, m	Date	Fixative
GR11	Mauritania	N 17,3388° W 16,7587°	518	10.11.2011	96% Ethanol
GR28	W. Sahara	N 27,1015° W 13,672°	125	03.12.2011	96% Ethanol
GR37	Morocco	N 29,0031° W 11,2162°	106	08.12.2011	96% Ethanol
GR40	Morocco	N 29,6089° W 10,2905°	102	09.12.2011	96% Ethanol
GR49	Morocco	N 32,5418° W 9,6138°	101	11.12.2011	96% Ethanol
GR50	Morocco	N 32,4725° W 9,2744°	40	13.12.2011	96% Ethanol
GR56	Morocco	N 33,6879° W 7,6144°	55	15.12.2011	96% Ethanol
5N-17	Nigeria	N 3,9435° E 8,1848°	78	20.06.2005	96% Ethanol
SL02	Cape Verde	N 15,444° W 23,1366°	82	9.06.2011	96% Ethanol
SL38	Morocco	N 28,0125° W 13,274°	103	29.06.2012	96% Ethanol
GR27	Morocco	N 29,0031° W 11,2162°	106	8.12.2011	96% Ethanol