

Review of the European *Amphitrite* (Polychaeta: Terebellidae) with description of two new species

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ABSTRACT: Taxonomy of six terebellids genera is discussed. It is shown that *Amphitritides*, *Neoamphitrite* and *Paramphitrite* only *Amphitrite* are junior synonyms of *Amphitrite*; the difference between *Amphitrite*, *Terebella* and *Eupolymnia* is illustrated. The review of a substantial number of specimens of 10 species of *Amphitrite* known from European waters has allowed for amendments of species descriptions and updates of species distributions. Two new species are described: *A. rzhavskiyi* sp.n. from the Mediterranean Sea and Scotland, UK and *A. buzhinskaje* sp.n. from the Sea of Japan and the Yellow Sea. *A. rzhavskiyi* sp.n. has three pairs of branchiae with cirriform filaments, 17 thoracic chaetigers, four pairs of nephridia and no eyespots. *A. buzhinskaje* sp.n. has three pairs of arborescent branchiae, 22–23 thoracic chaetigers and all abdominal neuropodia with a single row of uncini. It is proposed to accept *A. antarctica* Monro, 1936 as species rather than subspecies of *A. affinis*. One more species from the Arctic and North Pacific is found but not named due the lack of type materials of *A. cirrata*, the most similar species. The taxonomic weight of characters used for species definitions within *Amphitrite* is discussed. It is shown that species range is a good taxonomic character. A comprehensive identification key to all 14 European species of *Amphitrite* is provided.

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KEY WORDS: *Amphitritides*, *Neoamphitrite*, *Paramphitrite*, *Terebella*, *Eupolymnia*, generic characteristics, identification key, taxonomic revision, Mediterranean, North Atlantic, Sea of Japan, Yellow Sea.

Ревизия европейских *Amphitrite* (Polychaeta: Terebellidae) с описанием двух новых видов

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РЕЗЮМЕ: Обсуждена таксономия шести родов теребеллид. Показано, что *Amphitritides*, *Neoamphitrite* и *Paramphitrite* only *Amphitrite* — младшие синонимы *Amphitrite*; проиллюстрированы различия между *Amphitrite*, *Terebella* и *Eupolymnia*. Изучение обширного материала 10 видов *Amphitrite*, известных из европейских вод, позволило составить их переописания и уточнить видовые ареалы. Описано два новых вида: *A.*

rzhavskiy sp.n. из Средиземного моря и Великобритании и *A. buzhinskaje* sp.n. из Японского и Желтого морей. *A. rzhavskiy* sp.n. имеет три пары жабр в виде пучков коротких нитей, отходящих от общего основания, 17 торакальных щетинконосных сегментов, 4 пары нефридиев и не имеет глаз. *A. buzhinskaje* sp.n. имеет три пары древовидных жабр, 22–23 торакальных щетинконосных сегмента и все абдоминальные невроподии с неврохетами в один ряд. Предложено рассматривать *A. antarctica* Monge, 1936 как вид, а не как подвид *A. affinis*. Обсужден вес таксономических признаков, используемых для разделения видов *Amphitrite*. Показано, что ареалы видов являются хорошим таксономическим признаком. Дан ключ для определения всех 13 видов, известных из европейских вод.

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КЛЮЧЕВЫЕ СЛОВА: *Amphitritides*, *Neoamphitrite*, *Paramphitrite*, *Terebella*, *Eupolymnia*, родовые признаки, определительный ключ, таксономическая ревизия, Средиземное, Японское и Желтое моря, Северная Атлантика.

Introduction

Amongst the numerous terebellid genera, some (*Amphitrite* Müller, 1771, *Amphitritides* Augener, 1922, *Neoamphitrite* Hesse, 1917, *Paramphitrite* Holthe, 1976) are so similar that there is much confusion in applying generic names to certain species. Some authors have accepted *Amphitrite* and *Neoamphitrite* as valid (Uschakov, 1955; Fauchald, 1977; Hartman, 1969; Holthe, 1986; Hartmann-Schröder, 1996), but some have not (Fauvel, 1927; Pettibone, 1954; Imajima, Hartman, 1964; Day, 1967; Hartmann-Schröder, 1971; Hutchings, Glasby 1988; Jirkov, 2001; Hutchings *et al.*, 2017). If the genera are accepted as valid, the main difference between them is the shape of branchiae: formed as numerous simple filaments in *Amphitrite* and arborescent in *Neoamphitrite*. According to WoRMS (Read, Fauchald, 2020a, b), both genera are valid. To date, in WoRMS, 22 species of *Amphitrite* (Read, Fauchald, 2020a) and 12 species of *Neoamphitrite* (Read, Fauchald, 2020b) are listed as valid. However, of the 22 *Amphitrite* species listed as valid by Read, Fauchald (2020a), only three have cirri-form branchiae; the other 19 have arborescent branchiae and thus should have been moved to *Neoamphitrite*, but this has not been done.

Amphitritides Augener, 1922 was separated from *Amphitrite* because it has two pairs of branchiae and neuropodia with uncini in double rows along most of the abdomen; however, as will be shown below, many *Amphitrite* species have the same characters. Other characters of both genera are similar.

Paramphitrite Holthe, 1976 was described as a genus similar to *Amphitrite*, but differing in having 13 thoracic segments, instead of 17 or more, and two, instead of three, pairs of branchiae. However, as will be shown below, there are *Paramphitrite* species with 13–14 thoracic segments, *Amphitrite* species with 15 or more, and some *Amphitrite* species previously included in both *Amphitritides* and *Amphitrite* have two pairs of branchiae. Other characters of both genera are the same.

Nine species of *Amphitrite*, two species of *Amphitritides* and two species of *Paramphitrite* have been reported from European waters as valid (Arvanitidis, Koukouras, 1995; Hartmann-Schröder, 1996; Jirkov, 2001; Castelli *et al.*, 2008; Jirkov, Leontovich, 2013; Jirkov *et al.*, 2018), and one more species is described below as new. Additionally, a species from the Far Eastern seas previously identified as the European *Amphitrite grayi*, is described as new.

The purpose of the present study is to clarify the taxonomic status and ranges of European

species included in these genera basing on the review of a substantial number of specimens of all species of these genera known from European waters from the High Arctic to Mediterranean and the Black Sea. Generally, I follow Holthe's (1986) sense of species, as he has studied types, and Fauvel (1927) for species absent in Holthe (1986). Some remarks are given where applicable.

Methods

The study has been based mainly on the Department of General Ecology and Hydrobiology collection; studied specimens are listed in species descriptions and Table 2. All material, if not stated otherwise, is deposited at KGB and data are entered in the polychaetous database of the Department of General Ecology and Hydrobiology. The number of specimens from each locality is given in brackets.

Photographs were produced at the P.P. Shirshov Institute of Oceanology, at the Russian Academy of Science, Moscow, using a Leica DFC490 camera mounted on either a Leica M165C stereomicroscope, or a Leica DMI 4000B compound microscope; at the Department of Invertebrate Zoology, Biological Faculty, Moscow State University, using a Leica DFC425C camera mounted on a Leica DMI 5000B compound microscope; at the MNCN, through a Leica DFC550 camera mounted on a Leica MZ16A stereomicroscope. In order to increase contrast, specimens were stained with methylene blue (water solution); in some cases, for the same reason, histogram equalization in Corel Photopaint was applied. All uncini in each block are from single neuropodia. For scanning electron microscopy (SEM), specimens stored in 70–75% ethanol were placed in 100% ethanol, 100% acetone then critical point dried, using CO₂ as a transition fluid. Once dry, the specimens were sputter coated with gold. SEM micrographs were taken with a Camscan S-2 Cambridge instrument Scanning Electron Microscope. The SEM photographs were taken at the M.V. Lomonosov User Facilities Center, Moscow State University.

Types of four species (*A. affinis* Malmgren, 1866, *A. gracilis* (Grube, 1860), *A. gray* Malmgren, 1866*i*, *A. groenlandica* Malmgren, 1866) have been investigated by Holthe (1976a), investigated specimens fit his descriptions, so to my mind, there was no needs to their re-investigation. Types of *A. cirrata* (Müller, 1776), *A. figulus* (Dalyell, 1853), *A. rubra* (Risso, 1826) and *A. variabilis* (Risso, 1826) cannot be traced. Types of *A. birulai* Ssolowiew, 1899 have been investigated.

Abbreviations and terminology

ORGANISATIONS. APEM — APEM Ltd., UK; BDU — Biology Department of the University of Aveiro, Portugal; DGEH — Department of General Ecology and Hydrobiology Moscow Lomonosov State University, Russia; IO RAN — P.P. Shirshov Oceanological Institute of the Russian Academy of Science, Moscow, Russia; MNCN — National Museum of Natural Sciences, Madrid, Spain; ZIN — Zoological Institute of the Russian Academy of Science, St-Petersburg, Russia.

TAXONOMIC. AU — abdominal unciniger; C — chaetiger; S — segment; TC — thoracic chaetiger; TU — thoracic unciniger. The number following the abbreviation refers to the number of the segment (e.g. AU1 means the 1st abdominal unciniger).

The nomenclature of uncinal parts used in this paper mainly follows to Noguera *et al.* (2010) and is shown in Fig. 1A, B.

Base — plate to which other parts are attached;

Button — short projection of the upper part of the base below the main fang;

Crest — a series of usually transverse rows of teeth above the main fang.

Heel — the posterior part of the base at the footing of the neck, froming angle to which back tendon is attached;

Main Fang — biggest tooth;

Neck — part, connecting teeth (Main Fang+ Crest) and the base;

Prow — anterior part of the uncinal base;

Tendon — sinew, attached uncinus to muscles, there are two tendons: back tendon, attached to heel, and lower tendon, attached to prow.

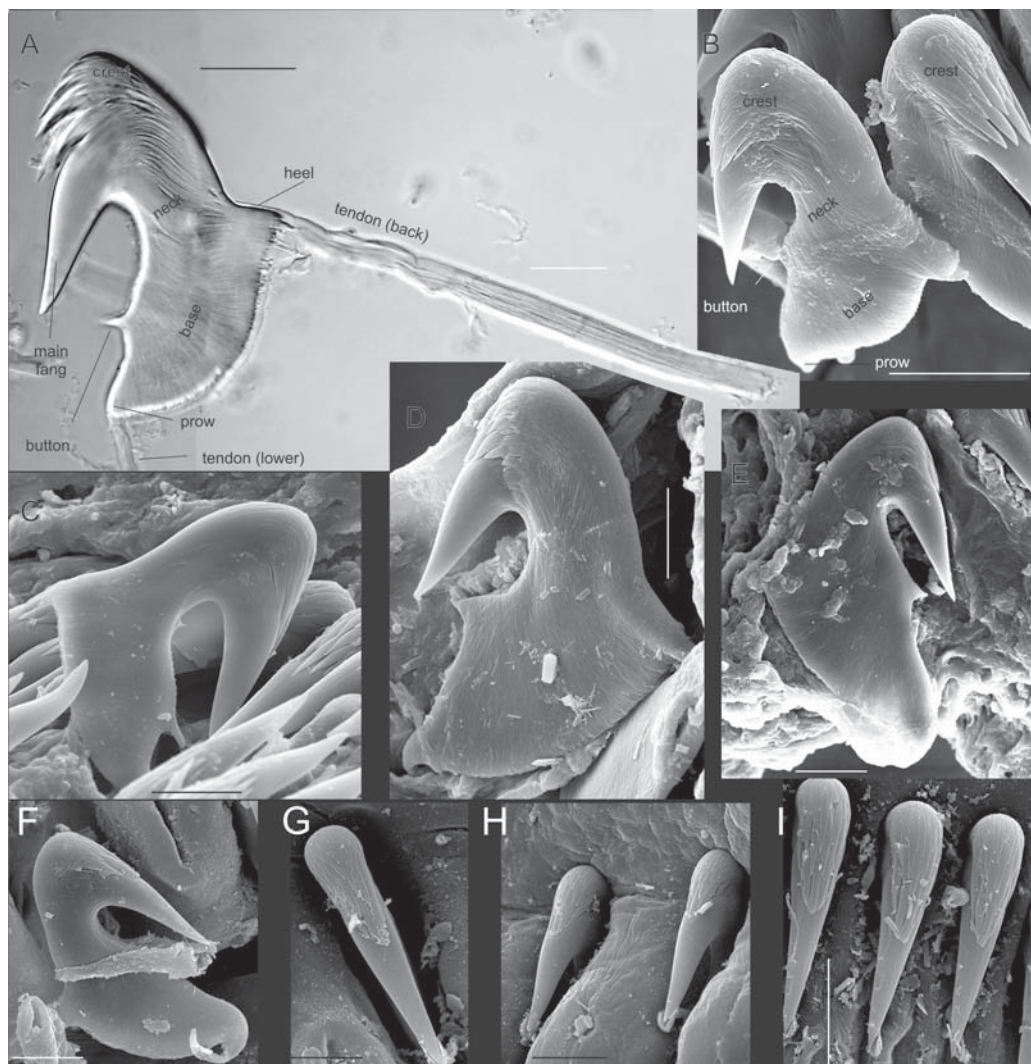


Fig. 1. Uncini and terminology of uncinal parts used in this paper (after Nogueira et al. 2010 with additions). A — *Amphitrite cirrata* (Müller, 1776), Alaid 8; B — *A. affinis* Malmgren, 1866, Alaid 8; C — *A. figulus* (Dalyell, 1853), Nilma 1977; D — *A. groenlandica* Malmgren, 1866, RT-61 26.95; E — *A. cirrata* (Müller, 1776), White Sea; F–H — *A. rzhavskiyi* sp.n. TC9, APEM 487849; I — *A. buzhinskaje* sp.n. TC17 Vostok 838. Scale bars: 20 µm.

Рис. 1. Неврохеты и термины, используемые для их описания в этой статье (по Nogueira et al. 2010 с добавлениями). А — *A. cirrata* (Müller, 1776), Алайд 8; В — *A. affinis* Malmgren, 1866 Алайд 8; С — *A. figulus* (Dalyell, 1853), Нильма 1977; D — *A. groenlandica* Malmgren, 1866, РТ-61 26.95; E — *A. cirrata* (Müller, 1776), Белое море; F–H — *A. rzhavskiyi* sp.n. TC9, АРЕМ 487849; I — *A. buzhinskaje* sp.n. TC17, Восток 838. Масштаб: 20 мкм.

Taxonomic characters used in *Amphitrite* species identification

The main diagnostic characters used to distinguish *Amphitrite* species are:

– Number of branchiae (two or three).

– Shape of branchiae: cirriform, pectinate or arborescent.

– Number of TC. If the number of TC exceeds 20, there is variation in the number of TC between individuals.

– Presence/absence of AU with uncini in double rows; if present, how many, particularly whether they are present only on some abdominal segments, or until end of the body.

– Number and position of nephridial papillae. An important character is the presence/absence of papillae on S4 and S5. Arvanitidis & Koukouras (1995) reported variation in the presence of nephridial papillae in S5–S7 in their *Amphitritides kuehlmanni* (Arvanitidis, Koukouras, 1995). If the total number of segments with papillae exceeds 10, there is variation in the number of papillae between individuals; also, it is necessary to remember that nephridial papillae, especially posterior ones, are barely visible to invisible in small (sexually immature?) worms. At the other extreme, sexually mature females may have nephridial papillae (except anterior) replaced by inflated shields (Jirkov *et al.*, 2018).

– Shape of uncini has some diagnostic value; however, as intraspecific variation may exceed interspecific differences, differences should only be considered where considerable and after review of intraspecific variation. Even the size of uncini may vary considerably within a single neuropodium. The shape of uncini hardly varies along the body; for example, in *A. birulai*, TU1, TU6 and AU16 have almost the same shape. However, as in many other genera (for example *Axionice* Malmgren, 1866, and *Terebella*), the shape of uncini often varies along the body; it is best to compare uncini from a certain segment; if differences occur (in other genera), the uncini of TU1 always differ from the others, so it is better to compare uncini from TU1 with those from other segments.

– Some authors (for example, Hutchings, Murray A., 1984; Hutchings, Glasby, 1988) use for terebellids “dental formulas”, which indicate the number of rows and teeth per row in the uncinal crest. However, in each row in the center there are large teeth, which become smaller and smaller towards the periphery, until they become indistinguishable from individual fibers. The same is true for the rows: the teeth of the lower rows are distinct, and towards the top they become smaller and smaller. The line between the tooth and the fiber is subjective, also the

rows are not regular. This is all visible on the scans in Fig. 1. In addition, both the number of rows and the number of teeth vary within a single neuropodium and the size of this variability is never estimated, giving at best ranges of values obtained when counting teeth in an unknown number of uncini. Therefore, I estimate the significance of the taxonomic feature “dental formulas” low and they are not given in the descriptions.

– Some other characters may be valuable in some instances. For example, comparative sizes of the last TU and the first AU neuropodia (as in the cases of *A. affinis* / *A. variabilis* and *A. grayi* / *A. buzhinskaje*).

– Shape of notochaetae seems to be of a low taxonomic value at species level, at least for characters visible under a compound microscope.

Results

Family Terebellidae Johnston, 1846 Genus *Amphitrite* Müller, 1771

Type species: *Amphitrite cirrata* Müller, 1771 by subsequent designation.

Synonyms:

Amphitritides Augener, 1922 (type species *Terebella gracilis* Grube, 1860 by subsequent designation);

Neoamphitrite Hesse, 1917 (type species *Amphitrite affinis* Malmgren, 1866 by subsequent designation);

Paramphitrite Holthe, 1976 (type species *Paramphitrite tetrabanchia* Holthe, 1976 by original designation).

Two (on S2, S3) to three (on S2–S4) pairs of branchiae. Branchiae formed of numerous simple filaments (hereafter called cirriform branchiae), pectinate (filaments attached to stem in a row) or arborescent. Lateral lobes of S1–S3 small. Nephridial papillae start from S3. Ventral pads well separated from tori, widest pad narrower than or equal to longest thoracic uncinal row. Notopodia from S4, extending for variable number of segments, usually terminating well before pygidium. Number of TC important to species diagnoses, but not number of abdominal segments. Notochaetae straight with more or less developed keels, keels appear as wings (=limbaton) under compound microscope (Fig. 2); with serrated tips. Notochaetae usually

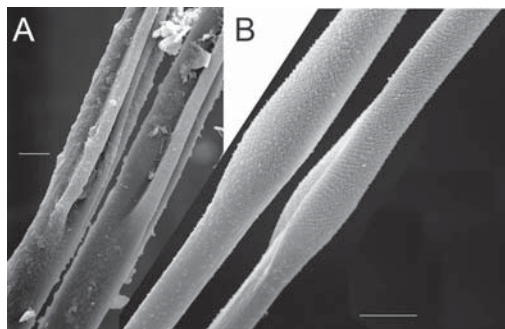


Fig. 2. Details of bilimbate notochaetae showing start of keels. A — *A. cirrata* (Müller, 1776), White Sea; B — *A. gracilis* (Grube, 1860), Gudauta. Scale bars: 10 μ m.

Рис. 2. Детали двусторонне окаймленных нотохеты, показывающие начало килей. А — *A. cirrata* (Müller, 1776), Белое море; В — *A. gracilis* (Grube, 1860), Гудаута. Масштаб: 10 мкм.

of two lengths, long and short, but otherwise similar. Neuropodia from S5 tori, abdominal may gradually or sharply become pinnuli-like; size of tori of S5<S6<S7: their dorsal margins are at almost the same level, their extension ventrally becomes gradually longer along body; from S7, for ca. 10 segments, neuropodia of same size, thereafter slowly shortening. Uncini avicular, from S11 (=C8) in double rows at least to end of thorax, sometimes also on some or numerous AU; uncini usually without manubrium, with two tendons or attachment point of posterior tendon slightly elongated forming short manubrium.

IDENTIFICATION KEY TO THE EUROPEAN SPECIES OF *AMPHITRITE*

1. 13–14 TC *A. birulai* Ssolowiew, 1899
– 17–19 TC 2
– >20 TC 10
2. Branchiae comprising numerous simple unbrached filaments 3

- Branchiae arborescent 6
- 3. Nephridial papillae on four segments (S3 and S6–S8) 4
- Nephridial papillae on seven segments (S3 and S6–S11, S11 = first segment with uncini in double rows) *A. gr. cirrata* Müller, 1776... 4
- 4. AU1 neuropodia less than half size of last TU neuropodia *A. aff. cirrata* Müller, 1776
- AU1 neuropodia slightly smaller than last TU neuropodia *A. cirrata* Müller, 1776
- 5. Branchial filaments arise from a short, wartlike symmetrical stem or directly from the body wall (Fig. 23A)
..... *A. fauveli* Jirkov, Ravara et Cunha, 2018
- Branchial filaments arise from a large, stout asymmetrical stem (Fig. 20D) *A. rzhavskiy* sp.n.
- 6 Two pairs of branchiae; uncini in double rows almost to pygidium .. *A. gracilis* (Grube, 1860)
- Three pairs of branchiae; uncini in single rows on all abdominal segments 7
- 7 17 TC 8
- 19 TC *A. groenlandica* Malmgren, 1866
- 8. Six pairs of nephridial papillae (on S3–S8) ... 9
- Nine pairs of nephridial papillae (on S3–S11) .
..... *A. edwardsii* (de Quatrefages, 1865)
- 9. AU1 neuropodia less than half size of last TU neuropodia (Fig. 3C); TU1 uncini with massive base and short neck to main fang (Fig. 3E) ...
..... *A. affinis* Malmgren, 1866
- AU1 neuropodia slightly smaller than last TU neuropodia (Fig. 24C); TU1 uncini with comparatively slim base and long neck to main tooth (Fig. 24D) *A. variabilis* (Risso, 1826)
- 10. No abdominal segments with uncini in double rows *A. grayi* Malmgren, 1866
- Uncini in double rows on fewer than five abdominal segments *A. figulus* (Dalyell, 1853)
- Uncini in double rows almost to end of abdomen 11
- 11. Two pairs of branchiae; 25–29 TC
A. kuehlmanni (Arvanitidis et Koukouras, 1995)
- Three pairs of branchiae; 22–24 TC
..... *A. rubra* (Risso, 1826)

Amphitrite affinis Malmgren, 1866 Figs 1B, 3.

Amphitrite affinis Malmgren, 1866: 377, tabl. XXII, fig. 56; Fauvel, 1927: 246–247, fig. 84 k, l; Hartmann-

Рис. 3. *Amphitrite affinis* Malmgren, 1866. А — вид сбоку MI-0015 2.22, здесь и далее цифры — номера сегментов, нефридияльные папиллы указаны стрелками; однако некоторые папиллы на фото не видны (но имеются у червей), то же относится и к другим рисункам; обычно это относится к папиллам на S3, скрытыми под жабрами, поэтому отсутствие стрелок не означает отсутствие папилл на соответствующем сегменте, для полной информации необходимо обращаться к описаниям; В — вид с брюшной стороны MI-0015 2.22; С — граница торакса и живота MI-0015 2.22, здесь и далее последняя нотоподия показана стрелкой; D — нотохеты TC 13, Persey 859; E — uncini TU1, Persey 859; F — uncini AU10, Persey 859. Масштаб: А — 5 мм, В — 2 мм, С — 1 мм, D — 0,2 мм, E — 50 мкм, F — 20 мкм.

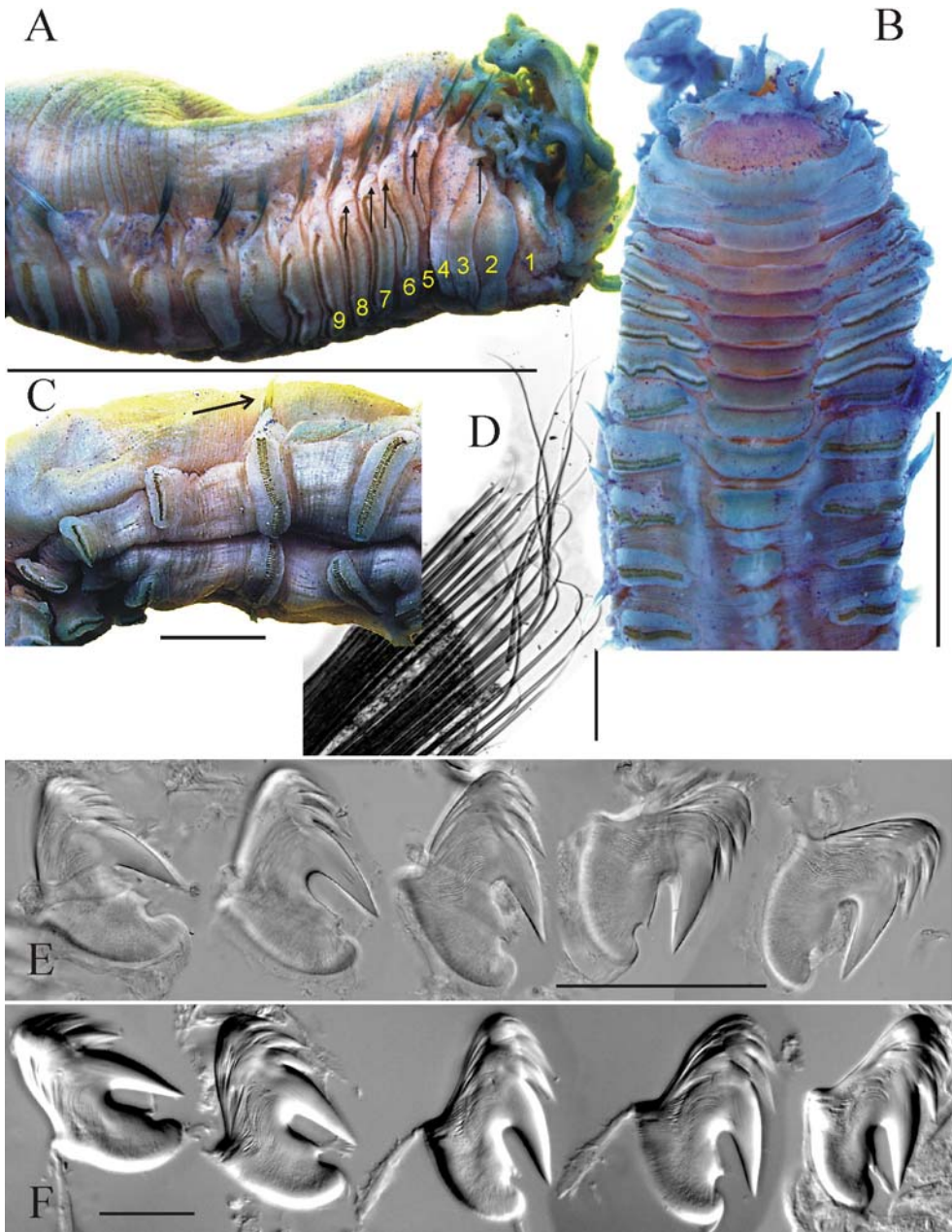


Fig. 3. *Amphitrite affinis* Malmgren, 1866. A — lateral view MI-0015 2.22, here and below numbers refer to number of segments, arrows point to nephridial papillae; however some papillae here and below are not visible on photos (but present in worms), usually this relates to papillae on S3 hidden by branchiae, so the absence of an arrow does not mean an absence of papillae on a certain segment, for complete information refer to descriptions; the same applies to other figures; B — ventral view MI-0015 2.22; C — thorax–abdomen border MI-0015 2.22 here and below last notopodia arrowed; D — notochaetae TC 13, Persey 859; E — uncini TU1, Persey 859; F — uncini AU10, Persey 859. Scale bars: A — 5 mm, B — 2 mm, C — 1 mm, D — 0.2 mm, E — 50 μm, F — 20 μm.

Schröder, 1971: 473; Jirkov, 1989: 126, Fig. 25.5; Jirkov, 2001: 509 — non Grainger, 1954: 521 (= *Amphitrite birulai*).

Neoamphitrite affinis — Zatsepin, 1948: 156, table XXXVIII, 13; Holthe, 1986: 98–100, fig. 41, map 40; Hartmann-Schröder, 1996: 514.

MATERIAL EXAMINED. 25 samples (36 specimens), from DGEH and ZIN collections (Appendix), 14–970 m.

DESCRIPTION. Up to 45 mm in length. Eyespots absent. Branchiae arborescent, decreasing in size posteriorly, last pair in small worms may be reduced to simple filament or even knob, or all branchiae of same size. Lateral lobes on S2–S4: small on S2, slightly developed on S3–S4, upper margin of lobes progressively more dorsal. Ventral pads smooth, well separated from neuropodia; last pad on S13. Six pairs of nephridial papillae; on S3, lateral to branchiae, large (equal in size to notopodial lobes, not visible on photo); on S4, lateral to notopodia; on S5–S8 between noto- and neuropodia, slightly posterior to row of uncini. Papillae of S4 and S5 clearly visible, less than half size of S3 papillae. Papillae of S6–S8 distinctly smaller than those of S4 and S5, inconspicuous on small worms (those with branchiae as simple filaments, at least third pair). Large females with these segments stained more or less reddish or purplish (depending on amount of methylene blue) around notopodia and papillae, while other segments do not stain (except, sometimes, lobes and lower lip); body surface around papillae inflated. Such difference in glandular contents of segments and their nephridia seems to be connected to reproduction and other functions of nephridia.

Notopodia from S4, present on 17 segments (rarely 18). Notochaetae narrow, bilimbate with serrated tips.

Neuropodia from S5; uncini facing forward; TU7–TU16 (last thoracic) with uncini in double rows (uncini face-to-face), rows well separated in all tori. Thoracic neuropodia large, almost reaching pads ventrally. Uncinal rows and neuropodia of AU1 two to three times shorter than those of last T). Uncini avicular, thoracic and abdominal similar. Tube muddy, wall thickness less than half that of inner diameter.

REMARKS. 1. The specimens examined include some collected close to the type locality (Kings Bay, Svalbard) and agree well with Holthe's (1986) description, based on the examined type.

2. *Amphitrite affinis antarctica* Monro, 1936 has been described and then accepted as a subspecies (Read, Fauchald, 2020g) or as a synonym (Hartman, 1959) of the nominal subspecies. According to the original description and confirmed by my examination, *A. affinis antarctica* differs in the number of nephridia: ten in *A. affinis antarctica* and only six in the nominal subspecies. This difference is more than the difference in the number of nephridia between *A. affinis* and *A. edwardsii*. The examined specimen of *A. affinis antarctica* (47°39'8 S 60°31'0 W, swimming, laminarian algae ZIN 1/43555) has the neuropodia of AU1 equal to those of the last TC. So, taking into consideration the huge gap in species range, I think these two differences justify the elevation of *A. affinis antarctica* to a species level.

DISTRIBUTION. Below tidal front (lower sublittoral) widespread in the North Polar Basin. Southermost European reports from Trondelag, Skagerrak, Oslofjorden, Swedish west coast (Holthe, 1986).

Unlikely reports. It is reported from the Mediterranean (Alós, 1984; Papazacharias, 1991; Mikac, 2015; Faulwetter *et al.*, 2017), but I failed to find it in collections from the Mediterranean; in the collection of MNCN, specimens identified as *A. affinis* in reality belong to *A. variabilis*, which is common in collections from the Mediterranean, so I suppose that all other reports are also based on misidentifications.

Amphitrite birulai Ssolowiew, 1899
Figs 4, 5.

Amphitrite birulai Ssolowiew, 1899: 198; Zatsepin, 1948: 156.

Paramphitrite birulai — Tzetlin *et al.*, 1983: 182 (synonymy); Jirkov, 2001: 519.

Paramphitrite tetrabranchia Holthe, 1976: 59; 1986: 107–108, fig. 46, map 45; Parapar *et al.*, 1991: 63–68, Fig. 2; Hartmann-Schröder, 1996: 519.

Amphitrite affinis — Grainger, 1954: 521 — non Malmgren, 1866.

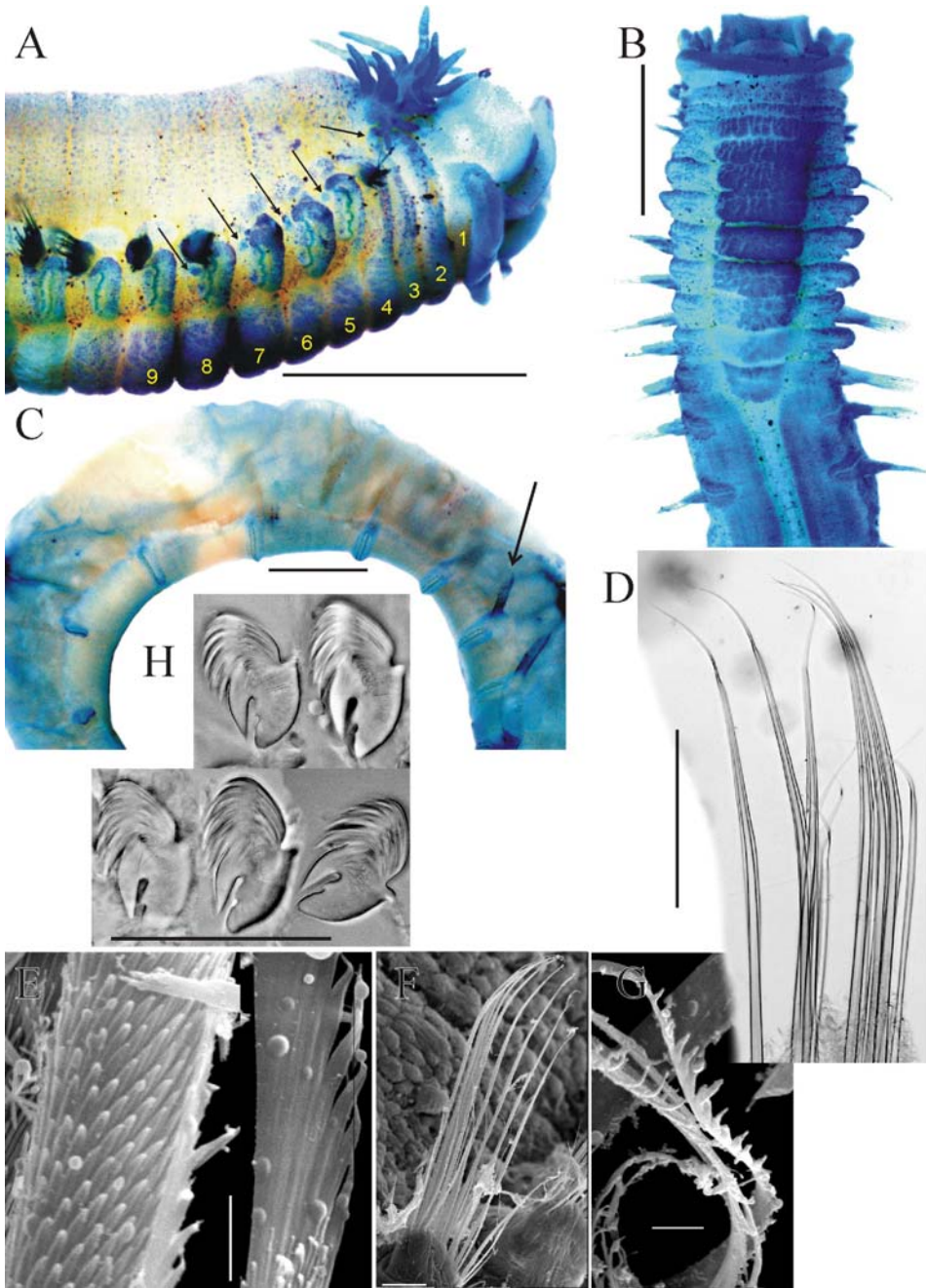


Fig. 4. *Amphitrite birulai* Ssolowiew, 1899. A — lateral view, White Sea; B — ventral view Black river; C — thorax–abdomen border; D — notochaetae TC9, BDUА 1372.02; E–G — SEM photos of notochaetae and details of their structure, White Sea; H — uncini AU16, BDUА 149.07 06. Scale bars: A–C — 1 mm, D — 0.2 mm, E, G — 3 μ m, F — 0.1 mm, H — 20 μ m.

Рис. 4. *Amphitrite birulai* Ssolowiew, 1899. А — вид сбоку, Белое море; В — вид с брюшной стороны Чёрная речка; С — граница торакса и живота; D — нотохеты TC9, BDUА 1372.02; E–G — СЭМ фото нотохет и детали их структуры, Белое море; H — uncini AU16, BDUА 149.07 06. Масштаб: А–С — 1 мм, D — 0,2 мм, E, G — 3 мкм, F — 0,1 мм, H — 20 мкм.

MATERIAL EXAMINED. *Amphitrite birulai*: Zoological Institute of Russian Academy of Science, 12 syntypes: ZIN 1/32181 (1 syntype), ZIN 2/32182 (6 syntypes), ZIN 3/32183 (3 syntypes), ZIN 4/32184 (1 syntype), ZIN 5/32185 (1 syntype); type locality, White Sea, additionally 39 samples (64 specimens) from APEM, DGEH, ZIN and BDUA collections (Appendix), 0–382 m.

DESCRIPTION. Rather small *Amphitrite*, up to 25 mm in length. Two pairs of branchiae, anterior ones distinctly larger. Branchiae pectinate with stem and several simple filaments attached to the stem on one side; filaments arranged in pairs, if more than about ten. Upper lip large, wide, slightly folded. Lower lip small. Eyespots absent or sparse in specimens studied. Lateral lobes small, slightly developed or absent; usually, lobes of S2 more developed than those of other segments. Ventral pads smooth, well separated, last pad on C9–C10. Five pairs of nephridial papillae: first pair lateral to second branchiae (on S3); and four pairs less than half size of first pair of papillae, between noto- and neuropodia of S5–S8; S4 without papillae.

Notopodia from S4, present on 13 segments (rarely 14, ZIN 2/32182). Notochaetae with narrow brims and serrated tips.

Neuropodia from C2; tori. Uncini in double rows (face-to-face, rows well separated), from C8 to C16–C18, more often C17. Neuropodia with uncini in double rows all of same size; first neuropodium with uncini in single row (whether on C16 or C18) half size of preceding one. Uncini avicular, crest teeth with several rows of teeth, more numerous than in other species studied here; thoracic and abdominal uncini all similar. Tube with thick wall, muddy, or covered with shell fragments.

REMARKS. 1. All 12 syntypes of *A. birulai*, including that pictured by Ssoloviev (1899) with characteristic fragment of tube, have pectinate branchiae, instead of the originally described cirriform morphology.

2. The number of segments with neuropodia with double rows of uncini is constant within species, if they end before C24. *A. birulai* however shows variation; occasionally, some spec-

imens from the same sample have different numbers of segments with uncini in double rows. For example, there are specimens with uncini in double rows to C16: APEM 40460 (1 sp.), APEM 40591 (1 sp.), APEM 41850 (1 sp.), as well as uncini in double rows to C18: APEM 41807 (1 sp.), APEM 41850 (3 sp.), BDUA0001371.03 (1 sp.)

3. Initially, I considered the distribution of *A. birulai* too wide for a single species. However, I have found only one difference between specimens from widely separated locations: the syntypes of *A. birulai* have muddy, thick-walled tubes, while specimens from BDUA (Portugal) have tubes without mud, covered by shell fragments. However, a specimen collected near Norway (Sygna 10-2) has its tube covered with sand and mud. Unfortunately, other specimens have no tubes. The morphology of all specimens is very similar. The shape of the uncini varies, but the difference between specimens from the White Sea and Iberian waters do not exceed variation within the White Sea or even within single neuropodia. However, most of the material examined was collected in the White Sea and only single or a few specimens are available from other localities, often in poor condition.

4. Studied here specimens collected near the type locality of *Paramphitrite tetrabanchia* (60°23' N, 05°03' E, depth 92–100 m; 60° 33' N, 05°01' E, depth 55 m, and NW of Bergen, 138 m) do not differ from the original description and later re-description. Although I have not examined types of *P. tetrabanchia*, I believe that, for the present time, it is reasonable to accept *P. tetrabanchia* as junior synonym of *A. birulai*. Otherwise, animals assigned to each name would have no morphological differences between them.

5. Holthe (1976) wrote in his description of *Paramphitrite tetrabanchia* Holthe (1976: 59) “Prostomium-peristomium without eyes” but later (Holthe, 1986), based on more extensive material from the same species, he wrote (Holthe, 1986: 107), “eyespot present”. Parapar et al (1991) also stated that eyespots were present. The specimens studied were fixed and stored in different ways; it is not yet possible to determine

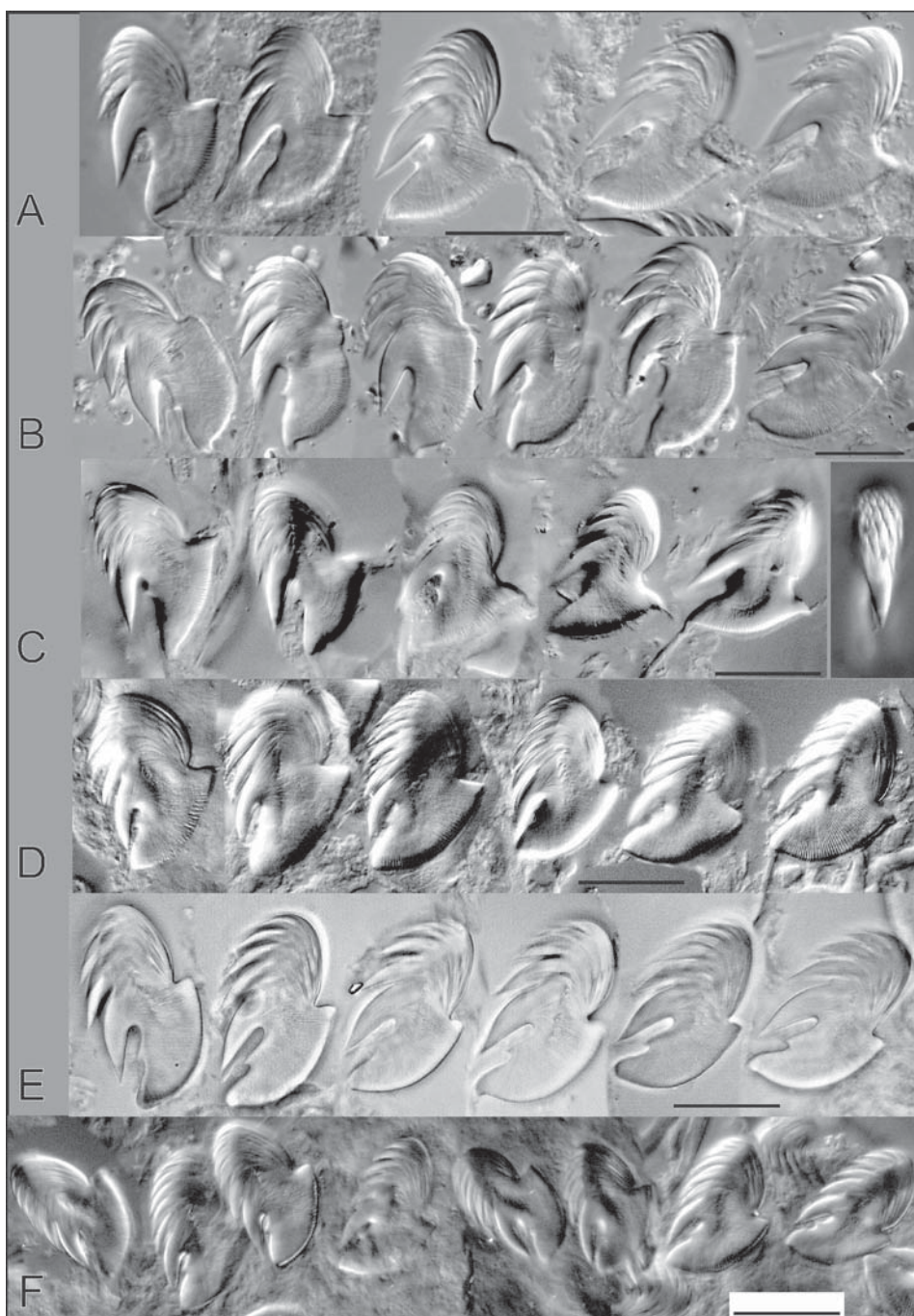


Fig. 5. Thoracic uncini of *Amphitrite birulai* Ssolowiew, 1899. TU1: A — ZIN6; B — ZIN3; C — Black river; D — APEM9533; E — BDUА 1372.02; TU7: F — APEM9533. Scale bars: 20 μ m. Uncini of each row are combined from the single slide from specified neuropodium.

Рис. 5. Неврохеты *Amphitrite birulai* Ssolowiew, 1899. TU1: A — ZIN6; B — ZIN3; C — Чёрная река; D — АРЕМ9533; E — БДУА 1372.02; TU7: F — АРЕМ9533. Масштаб: 20 мкм. Фотографии неврохет каждого вида сделаны с одного препарата с указанной невроподии.

whether the presence or absence of eyespots depends upon fixation, preservation or geographic variation.

6. Grainger (1954) reported *A. affinis* from 63°33' N 67°59' W, intertidal. All characters mentioned agree with *A. birulai*.

DISTRIBUTION. From high Arctic to Iberian Atlantic, shelf depth, common in estuaries.

Amphitrite buzhinskaje Jirkov, sp.n.

Figs 1I, 6, 7.

Neoamphitrite grayi — Annenkova, 1937: 192; 1938: 206; Uschakov, 1955: 392; Buzhinskaja, 1967: 114 — non Malmgren, 1866.

HOLOTYPE 42°36'N 131°09'E, 2 m, 09.1981, deposited at DGEH KGB MGU-Pol-32

PARATYPES **Sea of Japan**: DGEH collection, **Vostok Bay**, 42°54'34.7" N 132°44'23.1" E, 2,5 m 29.07.2009, st.768 KGB MGU-Pol-33 (1 specimen); 42°52'06.5" N 132°41'05.0" E, 8 m, 8.09.2009, st.831 KGB MGU-Pol-34 (1 specimen); 42°52'06.5" N 132°41'05.0" E, 7 m,

8.09.2009, st. 838 KGB MGU-Pol-35 (2 specimens); **Ussurijsky Bay**, 43°01'15.6" N 131°55'40.7" E, 8.10.2014 KGB MGU-Pol-36 (1 specimen); ZIN collection **Olga Bay** ZIN 1/32207, 8 m, 43°44'40" N 135°17'10" E, 22.07.1932 (1 sp.); **Expedition Bay** ZIN 7 42°39'10" N 130°44'44" E 3–4 m 23.10.1965 (5); ZIN 8, 5–6 m 21.10.1965; ZIN 10/36948 (2 sp.) (8); ZIN 11/36949 (1 specimen); ZIN 12–16 2 m 27–28.05.65 (7 specimens), **Vostok Bay** ZIN 27/46992 (1 specimen); **Yellow Sea**: ZIN 2/10973 42 m 6.7.1958 (1 specimen); ZIN 3/10974 51 m 14.9.1957 (1); ZIN 4/10975 55 m 25.10.57 (2); ZIN 5/10976 54 m 27.7.1957 (1 specimen); ZIN 6/10977 55 m 25.10.1957 (1 specimen)

ETYMOLOGY. The species is named after Russian polychaetologist Dr. G.N. Buzhinskaja (Fig. 8).

DESCRIPTION (based on holotype and paratypes). Up to 100 mm in length, for about 60 segments. Eyespots absent. Branchiae arbores-

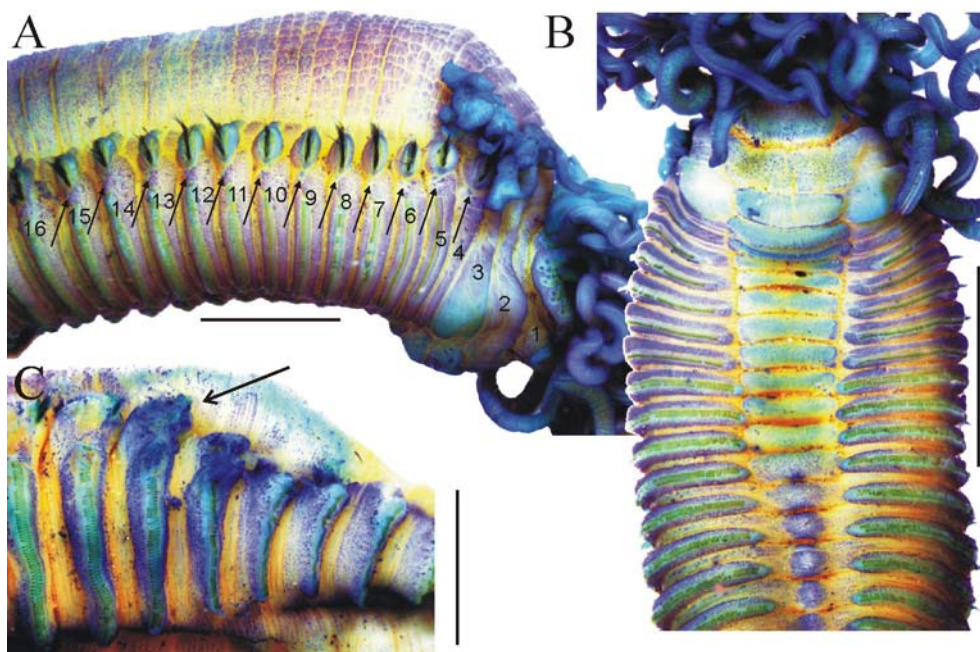


Fig. 6. *Amphitrite buzhinskaje* Jirkov, sp.n., external morphology. Holotype. A — lateral view; B — ventral view; C — thorax–abdomen border. Scale bars: A — 5 mm, B — 2 mm, C — 1 mm.

Рис. 6. *Amphitrite buzhinskaje* Jirkov, sp.n., внешняя морфология. Голотип. А — вид сбоку; В — вид с брюшной стороны; С — граница торакса и живота. Масштаб: А — 5 мм, В — 2 мм, С — 1 мм.

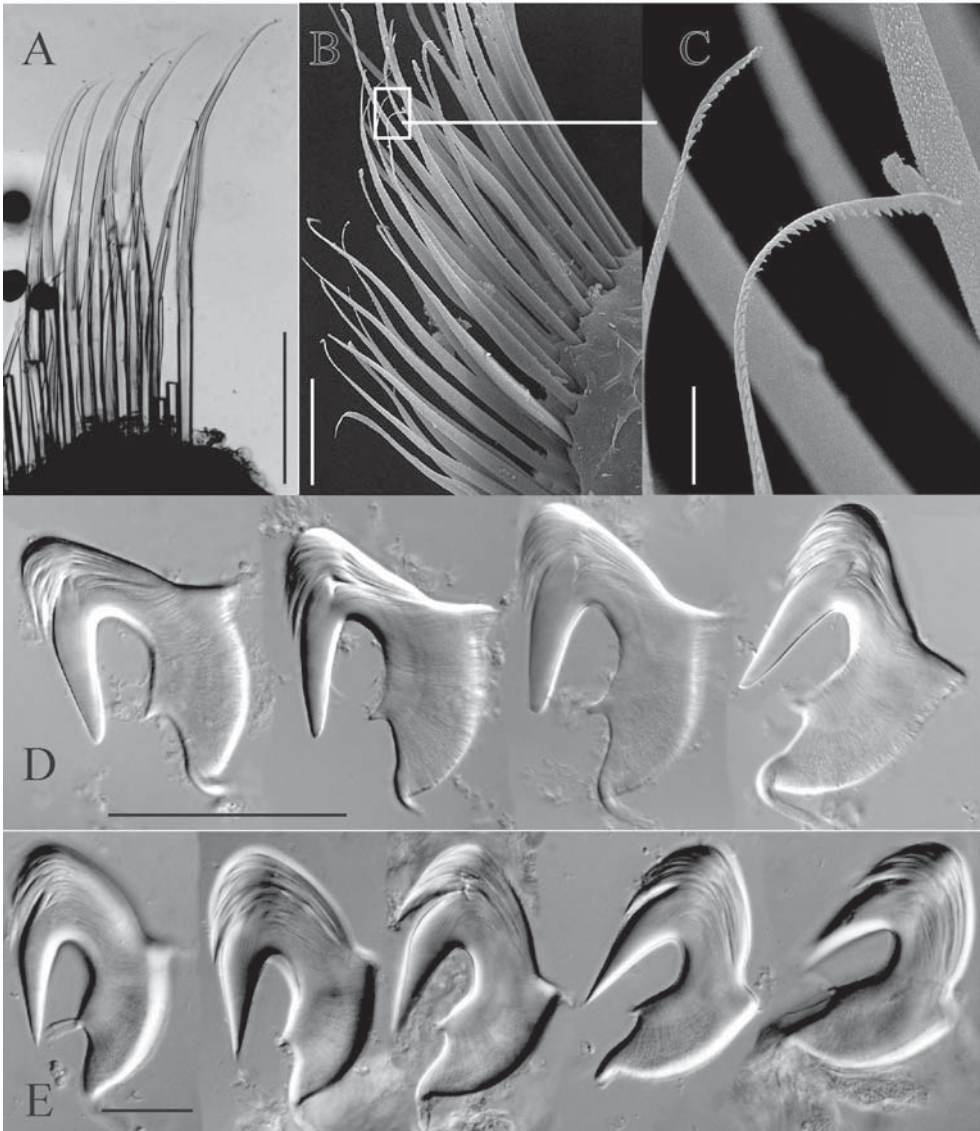


Fig. 7. *Amphitrite buzhinskaje* Jirkov, sp.n., chaetae. A–C — notochaetae TC5, holotype; B — notochaetae TC17, Vostok 838; C — details of B; D — uncini TU1, ZIN 12–16; E — uncini AU22, holotype. Scale bars: A — 0.2 mm, B — 0.1 mm, C — 10 μ m, D — 50 μ m, E — 20 μ m.

Рис. 7. *Amphitrite buzhinskaje* Jirkov, sp.n., щетинки. А–С — нотохеты TC5, голотип, В — нотохеты TC17, Восток 838; С — детали В; D — uncini TU1, ZIN 12–16; E — uncini AU22, голотип. Масштаб: А — 0,2 мм, В — 0,1 мм, С — 10 мкм, D — 50 мкм, E — 20 мкм.

cent with long branches, all of same size. Lateral lobes: S2 as thickening of anterior margin, S3 small, upper margin at level of upper margin of uncinal row of TU1, reaching pad ventrally, slightly lower at mid-length than at ventral and

dorsal margins; S4 small to inconspicuous below and in front of notopodia. Ventral pads smooth, well separated from neuropodia laterally, to TU10–TU11, narrower than longest thoracic uncinal row. Thirteen pairs of nephrid-



Fig. 8. Dr. Galina Nikolaevna Buzhinskaja.
Рис. 8. Галина Николаевна Бужинская.

ial papillae (visible in 8 specimen): large, lateral to branchiae on S3, lateral to notopodia on S4, others between noto- and neuropodia, just posterior to uncinal row; all papillae of same size.

Notopodia from S4, present on 21 segments, seldom (two specimen from ZIN 7 and ZIN 8) on 22 segments, and in one case (st. 838) on 23 segments. Notochaetae of two types, both: long, narrow, symmetrically narrow bilimbate with serrated tips.

Neuropodia from S5, uncini facing forward, TU7–TU20 (last thoracic) with uncini in double rows (uncini face-to-face); if 22 TC, present, last thoracic neuropodia with single (ZIN 8) or double (ZIN 7) rows of uncini; rows not separated, uncini intercalar. All abdominal neuropodia with single rows of uncini. Thoracic and abdominal neuropodia of same shape, all tori. Thoracic neuropodia large, ventrally almost reaching pads, uncinal row of TU1 ventrally shorter than on TU2, of TU2 than on TU3. Uncinal rows and neuropodia of AU1 almost same size as those of last TC (19 ex., other poorly preserved). Avicular crest of uncini with numerous teeth in several rows; thoracic and abdominal uncini all similar.

REMARKS. 1. Five species of *Amphitrite* have 20–23 TC and three pairs of branchiae. Three of them: *A. rubra* (Risso, 1826), *A. vigin-tipes* Grube, 1870 (according to Marenzeller, 1884) and *A. chloraema* (Schmarda, 1861) (according to Ehlers, 1901) have uncini in double rows almost to the pygidium. *Amphitrite pachyderma* Hutchings et Glasby, 1988 has uncini in double rows to C39–C43. Of these, only *A. grayi* Malmgren, 1866, as *A. buzhinskaje* sp.n., has 21 TC and all abdominal neuropodia with a single row of uncini. *Amphitrite buzhinskaje* sp.n. differs from *A. grayi* in that the neuropodia of AU1 are almost of the same size as those of the last TU (usually TU20), instead of two to three times shorter; *A. buzhinskaje* sp.n. has 12–13 segments with nephridial papillae, while *A. grayi* has 10–11. Also, *A. buzhinskaje* sp.n. inhabits shallow waters (in the Sea of Japan less than 10 m, in the Yellow Sea deeper, but still shallow), while *A. grayi* inhabits outer shelf depths, 20–500 m deep (Holthe, 1986, our data).

2. Paratypes from the ZIN collection, had been previously identified as *Neoamphitrite grayi* by Annenkova (1937, 1938), Buzhinskaja (1967) and Wu Bao-Ling (unpublished).

DISTRIBUTION. Probably low boreal and subtropical west Pacific species. I expect it to be found at shallow depths further south, above the tidal front (upper sublittoral).

Amphitrite cirrata Müller, 1776

Figs 1A, E, 2A, 9, 10.

Amphitrite cirrata Müller, 1776: 216; Malmgren, 1866: 375, tab. XXI, fig. 53; Fauvel, 1927: 251–252, fig. 86 i–o (partim); Zatsepin, 1948: 156, table XXXVIII, 12 (partim); Hartmann-Schröder, 1971: 471–472, Abb. 163; 1996: 506–507; Abb. 245; Holthe, 1986: 96–98, fig. 40, map 39; Jirkov, 1989: 126–127, Fig. 25.3 (partim); 2001: 509–510 (partim) — non Uschakov, 1955: 392, Fig. 147.3.

? *Nereis cirrosa* Linnaeus, 1767: 1085 — *nomen dubium*.

MATERIAL EXAMINED. 42 samples (125 specimens) from DGEH collection (Appendix), 6–24 m.

DESCRIPTION. Up to 200 mm in length. Eyespots absent. Branchiae usually as numerous simple filaments, arising from a very short stem, sometimes stem absent and filaments aris-

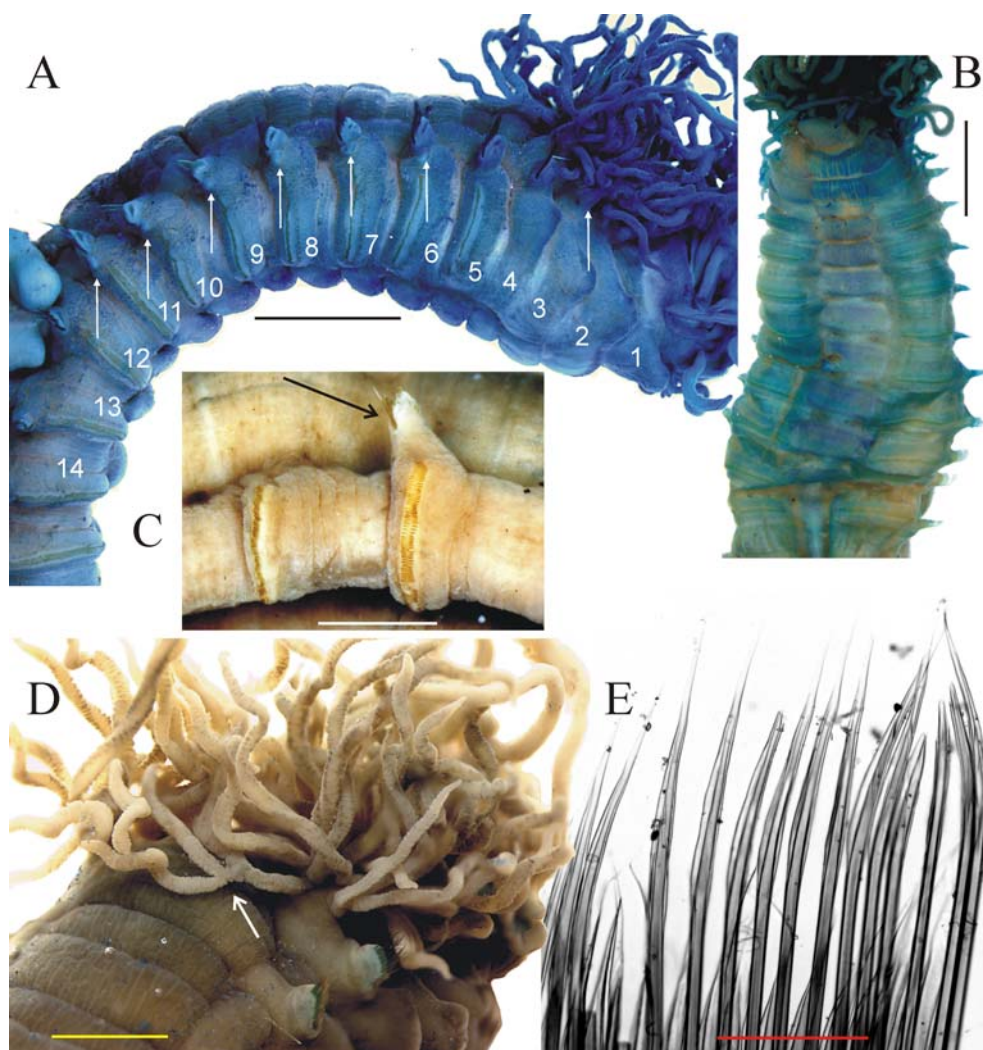


Fig. 9. *Amphitrite cirrata* Müller, 1776, external morphology. A — lateral view, WSBS; B — ventral view, WSBS; C — thorax–abdomen border, last notopodia arrowed, WSBS; D — branchia, branching arrowed, WSBS; E — notochaetae, WSBS. Scale bars: A, B — 2 mm, C, D — 1 mm, E — 0.2 mm.

Рис. 9. *Amphitrite cirrata* Müller, 1776, внешняя морфология. А — вид сбоку, ББС; В — вид с брюшной стороны, ББС; С — граница торакса и живота, ББС; D — жабра, место ветвления показано стрелкой, Persey 1271; E — нотохеты, ББС. Масштаб: А, В — 2 мм, С, D — 1 мм, E — 0,2 мм.

ing directly from body wall (12 of 97 examined worms); very rarely, some filaments branched (7 of 97 examined worms). S1 forms collar ventrally. Lobes of S2–S4 distinct, lateral: dorsally with semicircular lobes, gradually placed dorsally from S2 to S4, S2 additionally with lobe ventrally. Ventral pads up to TU8–TU12, some anteriorly wrinkled. Seven pairs of nephridial

papillae: one pair lateral to second branchiae (on S3) very large, almost half size of notopodia of TC1; six much smaller pairs between noto- and neuropodia of S6–S11 (first segment with double row of uncini), S4 and S5 without papillae.

Notopodia from S4, present on 17 segments. Notochaetae with serrated tips, of two types

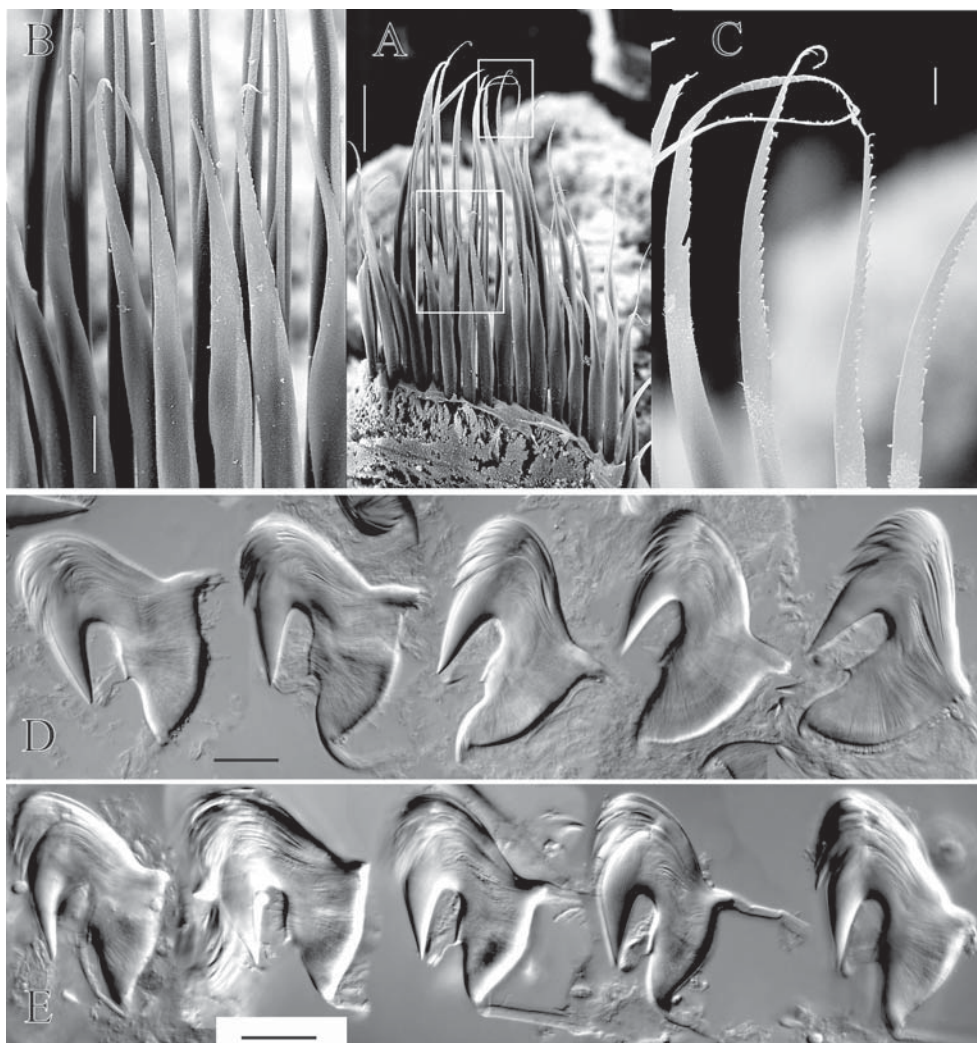


Fig. 10. *Amphitrite cirrata* Müller, 1776, chaetae. A–C — notochaetae Black river; B, C — details of A; D, E — uncini TU1; D — Ermolinskaja 77; E — uncini AU30 WSBS. Scale bars: A — 0.1 mm, B — 30 μ m, C — 10 μ m, D–E — 20 μ m.

Рис. 10. *Amphitrite cirrata* Müller, 1776, щетинки. A–C — нотохеты, Чёрная речка; B, C — детали A; D, E — uncini TU1; D — Ермолинская 77; E — uncini AU30, ББС. Масштаб: A — 0,1 мм, B — 30 мкм, C — 10 мкм, D–F — 20 мкм.

(longer and shorter), both slightly unequally bilimbate (keeled), with serrated tips.

Neuropodia (uncini face forwards) from C2. Uncini in double rows (uncini face-to-face, rows adjacent to each other) on TU7–TU16 (end of thorax), all abdominal uncini in single rows (uncini facing forwards). All neuropodia large; first nine neuropodia reaching ventral pads;

pads progressively less conspicuous posteriorly, with gap to neuropodia. All neuropodia tori; no abrupt change in size of neuropodia from thorax to abdomen. Uncini avicular; thoracic and abdominal uncini all similar. Tube muddy, thickness of tube wall several times less than inner diameter.

REMARKS. 1. The first pair of nephridial

paillae (near second pair of branchiae) is visible on worms 1 cm long and less than 1 mm wide, but the last six papillae are not visible in worms of that size, even after staining, and sometimes they are hardly visible without staining in larger worms. Probably, these papillae are present in sexually mature worms only. One specimen (SChS-2032 st. 381) has additional papillae on S12 (eight pairs of papillae in total); other specimens from the same sample have the typical seven pairs of papillae.

2. Müller's (1776) description is very short: "cincinnis utrinque tribus", meaning "curls three sides", i.e. three pairs of branchiae, which fits most European *Amphitrite*, all *Eupolymnia* and *Terebella*. The species is understood here as described later by Malmgren (1866) and Fauvel (1927). Müller (1771) discussed usage of the name *Spio cirrata* by König but gave no citation or even date for the König publication); however, as there was no description, *Amphitrite cirrata* Müller, 1771 is *nomen nudum*, and 1771 cannot be the year of publication. The concept of *Spio cirrata* König is unclear and, besides, as it was published before *Systema Naturae*, should not be accepted (ICZN, Art. 3.2). *Nereis cirrosa* L., is mentioned as a senior synonym by Read & Fauchald (2020h), as Müller (1771, 1776) refers to *Nereis cirrosa* L., probably as its synonym, but it is not clear; also, Linnaeus (1771) did not provide a reasonable description, so this name should be treated as *nomen dubium*.

3. Description given above based on shallow water (upper sublittoral) specimens of boreal regions. Preparing these paper to be published I found that more Arctic and deeper worms (94 specimens from 32 stations from DGEH and IO RAN collections, 23–295 m) belong to quite different species (Fig. 11). This species differs from upper sublittoral by the comparative size of AU1 and TU last neuropodia. Upper sublittoral species has AU1 neuropodia equal to neuropodia of last TU (Fig. 9D), while low sublittoral species has AU1 neuropodia about half size of last TU neuropodia (Fig. 11D). All other character of these species are similar. One specimen (Maslov st.226) has 19 notopodia and corresponding number of

double rows neuropodia, while on the other had 17 notopodia and corresponding number of double rows neuropodia. Unfortunately COVID-19 does not allows me to investigate ZIN collection and other collections outside Moscow, so distribution of these two species based on DGEH and IO RAN collections only. I do not described the new species and named it here as *Amphitrite* aff. *cirrata* because I have no specimens from the type locality. Guðmundur Guðmundsson in his letter to me wrote that "a couple of years ago the late Gudmundur Vidir Helgason, searched the collection of IINH and he did not find any ethanol nor formalin fixed specimens of *Amphitrite cirrata*". Original description is too brief to choose between these two species, so I cannot be absolutely sure that I am right thinking that upper sublittoral boreal species is *A. cirrata* s.str., but it is highly likely.

DISTRIBUTION. The type locality of *Amphitrite cirrata* was not stated in the original description at all but, judging by its title ("Animalium Daniae et Norvegiae indigenarum" = native animals of Norway and Denmark), it should be one of these countries. According to Hartman (1959), the type locality is Iceland. This seems strange today, as Iceland is neither Denmark nor Norway but, in 1776, Denmark, Norway and Iceland were a single country, so it does not contradict Müller's title. Norwegian polychaetologist Holthe (1986) also cited the type locality as Iceland. However, later Read, Fauchald (2020i) changed the type locality to "United Kingdom Exclusive Economic Zone", which cannot be accepted. Holthe (1986) investigated material from Scandinavian waters and Iceland. It is highly probable that the species does occur in Greenland and temperate North American waters.

Unlikely reports. Fauvel (1927) reported the species from the Azores, Morocco, and Mediterranean, as well as the Arctic and temperate Atlantic. Although he described 7 pairs of nephridial papillae in true segments, I doubt that this relates to worms from these regions. I did not find *A. cirrata* amongst worms investigated from the Mediterranean, Azores, Atlantic coast of the Iberian Peninsula or even the UK but, instead, found two other *Amphitrite* species

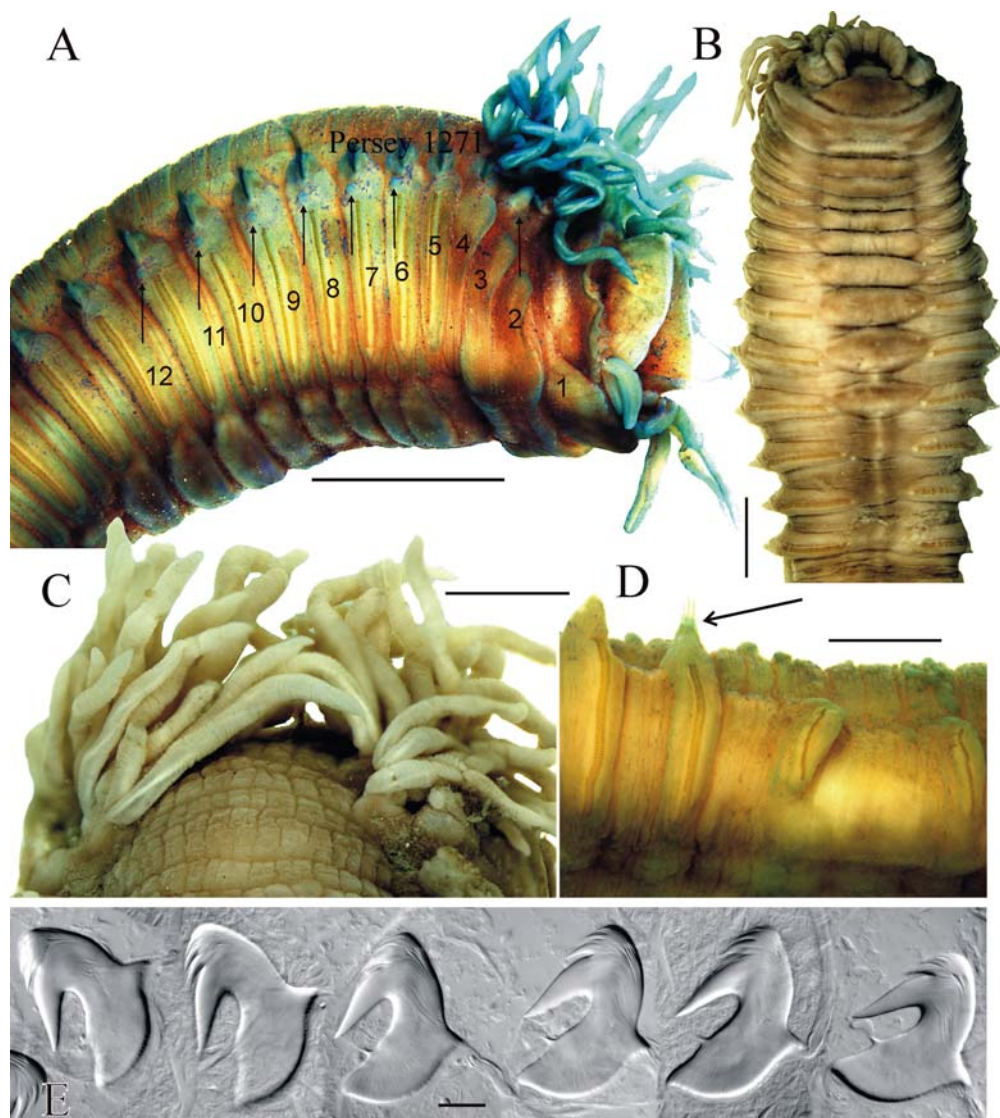


Fig. 11. *Amphitrite* aff. *cirrata*. A — lateral view, Persey 1271; B — ventral view, Persey 1270; C — branchiae, Persey 1270; D — thorax–abdomen border, last notopodia arrowed, Persey 1271; E — uncini TU1, Persey 1271. Scale bars: A, B — 2 mm, C, D — 1 mm, E — 20 mm.

Fig. 11. *Amphitrite* aff. *cirrata*. A — вид сбоку, Персей 1271; B — вид с брюшной стороны, Персей 1270; C — жабры, Персей 1270; D — граница торакса и живота, последняя нотоподия показана стрелкой, Персей 1271; E — неврохеты TU1, Персей 1271. Масштаб: A, B — 2 мм, C, D — 1 мм, E — 20 мкм.

with cirriform branchiae, both with four pairs of nephridial papillae: *A. rzhavskiyi* sp.n. in shallow water, *A. fauveli* in deep water. Reports from Arctic probably belong to *A. aff. cirrata*, at least *A. cirrata* s.str. strictly limited to boreal upper sublittoral.

All investigated specimens from Pacific belong to *Amphitrite* aff. *cirrata*, so I suppose that other Pacific data (Uschakov, 1955; Imajima & Hartman, 1964, Hobson, Banse, 1981) belong to this species instead of *Amphitrite cirrata* s.str.

Worms reported as *A. cirrata* from California have “nephridia in setigers 3 to 5” (Hartman, 1969: 583), while *A. cirrata* s.str. has no papillae on S4 or S5. Also, Hartman (1969: 583) wrote: “Thoracic uncini... in double rows from setiger 7”; this is most probably a *lapsus calami* (should be from C8). Although the segment at which uncini in double rows begin is very stable in Terebellini and Artacamini (Jirkov, 2001), some variation may occur. For *Axionice elongata*, an even earlier beginning was reported (Jirkov, Leontovich, 2017), so Hartman’s report could also describe a variation in the character of worms from California. Hartman’s material obviously needs to be re-examined and perhaps belongs to a new, undescribed species.

Day (1967) reported the species from the Cape of Good Hope and Senegal; this seems very doubtful, judging from the verified distribution (perhaps he had at hand *A. rzhavskyi* sp.n., described below); Holthe (1986) excluded Senegal and the Cape of Good Hope from its range. Day, like Hartman (1969), reported “thoracic uncini from segment 5 and arranged in two rows from setiger 7 to 16” (Day, 1967: 747). As with Californian worms, it is either *lapsus calami* or variation, or the character of worms from South Africa.

A. cirrata profunda Fauvel, 1909 is a *nomen nudum*, probably the same as *A. fauveli* (Jirkov *et al.*, 2018).

Amphitrite edwardsii (Quatrefages, 1866)
Figs 12, 13.

Terebella edwardsii Quatrefages, 1866: 354.

Amphitrite edwardsi — Fauvel, 1927: 245–246, Fig. 84 a–i.

MATERIAL EXAMINED. APEM 39607 (1 sp.) (Belfast Lough), APEM 36707 (1 sp.) (Orkney); BDUA DBVA0000591 38°38′–38°42′ N 09°25′–09°30′ W 30–60 m (1 specimen).

DESCRIPTION. Up to 50 mm in length. Eyespots absent. Branchiae arborescent, stem more or less flattened, little or no difference in size between first and third branchiae. Lateral lobes on S2–S4 distinct, S2 ventro-lateral, S3 almost not extending onto ventrum, distinctly

dorsal to S2 lobes, S4 at level of notopodia; all lobes of similar size. Ventral pads smooth, well-separated from neuropodia, last pad on TU9. Nine pairs of almost equal-sized nephridial papillae, on S3–S11; lateral to branchiae on S3; lateral and slightly posterior to notopodia on S4; between notopodia and neuropodia on S5–S11, at posterior margin of neuropodia.

Notopodia from S4, present on 17 segments. Notochaetae of two types (longer and shorter), both narrow, symmetrically bilimbate with serrated tips.

Neuropodia (uncini facing forward) from S5, uncini in double rows (face-to-face) on TU7–TU16, rows well separated; all abdominal neuropodia with uncini in single rows. Rows of uncini distinctly shorter on TU1 than on TU3. Rows of uncini on AU1 half size of last TU. Thoracic and abdominal neuropodia tori, becoming more pinnuli-like posteriorly, but uncini still far from margin (real pinnuli have uncini on the edge). Uncini avicular, thoracic and abdominal uncini all similar.

REMARKS. 1. The original description is not informative. The species concept accepted here follows Fauvel (1927).

2. Fauvel (1927) reported length up to 150 mm.

DISTRIBUTION. Western Europe (type locality St. Vaast, Channel, France) from Scotland to southern Portugal.

Unlikely reports. Also, reported from the Falkland Islands (Monro, 1930), Japan (Imajima & Hartman, 1964), British Columbia and Washington (Banse, Hobson, 1968; Hobson, Banse, 1981). All these reports need confirmation. The true range of *A. edwardsii* s.str. is probably limited to southern boreal European waters, as with *A. grayi* (Atlantic species) and *A. buzhinskaje* (Pacific species), clarified here. Specimens from the Falkland Islands [judging from Monro’s (1930) description] have 10 instead 9 nephridial papillae and uncini with distinctly shorter main teeth. Reports from the Mediterranean are probably due to the misidentification of *A. variabilis*, as I have not found *A. edwardsii* in my examined material, while *A. variabilis* is abundant (see below).

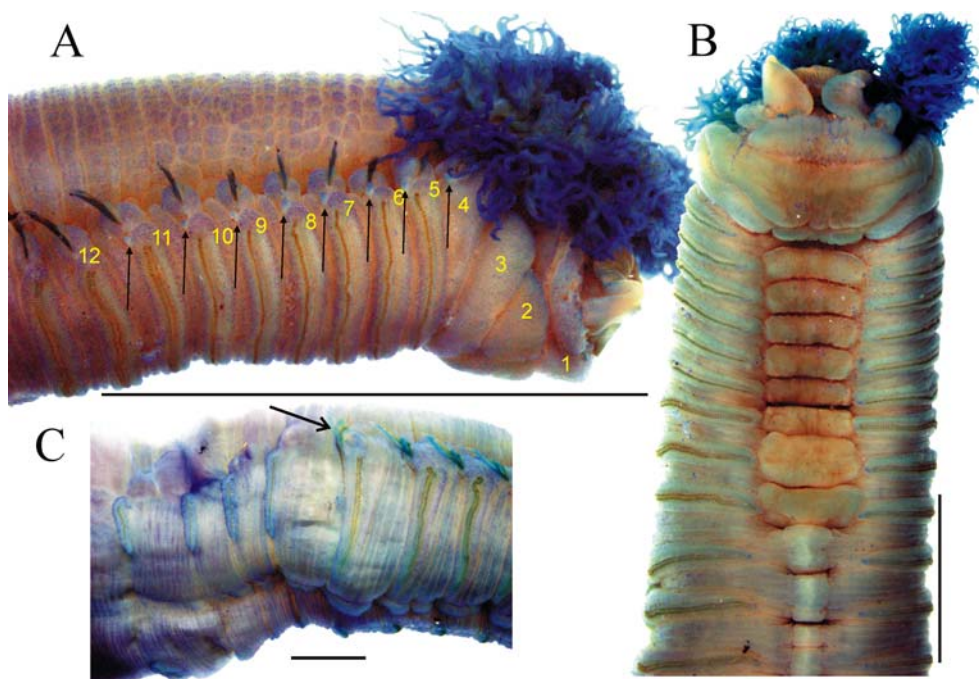


Fig. 12. *Amphitrite edwardsii* (Quatrefages, 1866), external morphology. A — lateral view APEM 7172; B — ventral view, APEM 004088; C — thorax—abdomen border, APEM 004088. Scale bars: A — 5 mm, B — 2 mm, C — 1 mm.

Рис. 12. *Amphitrite edwardsii* (Quatrefages, 1866), внешняя морфология. А — вид сбоку, АРЕМ 7172; В — вид с брюшной стороны АРЕМ 004088; С — граница торакса и живота, АРЕМ 004088. Масштаб: А — 5 мм, В — 2 мм, С — 1 мм.

Amphitrite figulus (Dalyell, 1853)

Figs 1C, 14, 15.

Terebella figulus Dalyell, 1853: 191–197 Pl. XXVII 1, 2, Pl. XXVIII 1, 2.

Amphitrite figulus — Hartmann-Schröder, 1971: 473–475, Abb. 164; Jirkov, 2001: 511.

Neoamphitrite figulus — Zatsëpin, 1948: 157, table XXXVIII, 15; Uschakov, 1955: 392; Holthe, 1986: 100–101, fig. 42, map 41; Hartmann-Schröder, 1996: 515–516, Abb. 251.

Amphitrite johnstoni — Malmgren, 1866: 377, tab. XXI, fig. 56; Fauvel, 1927: 248–249, fig. 85a–e.

MATERIAL EXAMINED. 40 samples, 58 specimens, 1–48 m (Appendix).

DESCRIPTION. Up to 250 mm length. Eyespots absent. Branchiae arborescent, with thick stem and long branches, first branchiae twice size of branchiae of third ones. Lateral lobes of S2 and S3 distinct; higher on S3 than S2; small or inconspicuous on S4. About 14 ventral pads.

Nephridial papillae very small and difficult to count, even after staining, especially in small worms, present at least on segments 3–18, progressively shorter.

Notopodia from S4, present on 23–27 segments. Notochaetae of two types (longer and shorter), both narrow, symmetrically bilimbate with serrated tips.

Neuropodia from S5, facing forwards, uncini in double rows from C8 to C23–S29 (uncini face-to-face), i.e. at least one abdominal neuropodium with uncini in double row; rows well separated; all neuropodia tori, no abrupt change in size or shape of neuropodia, either from thorax to abdomen, or at transition from neuropodia with double rows of uncini to those with a single row. Uncini avicular, crest with numerous teeth in several rows; thoracic and abdominal uncini all similar.

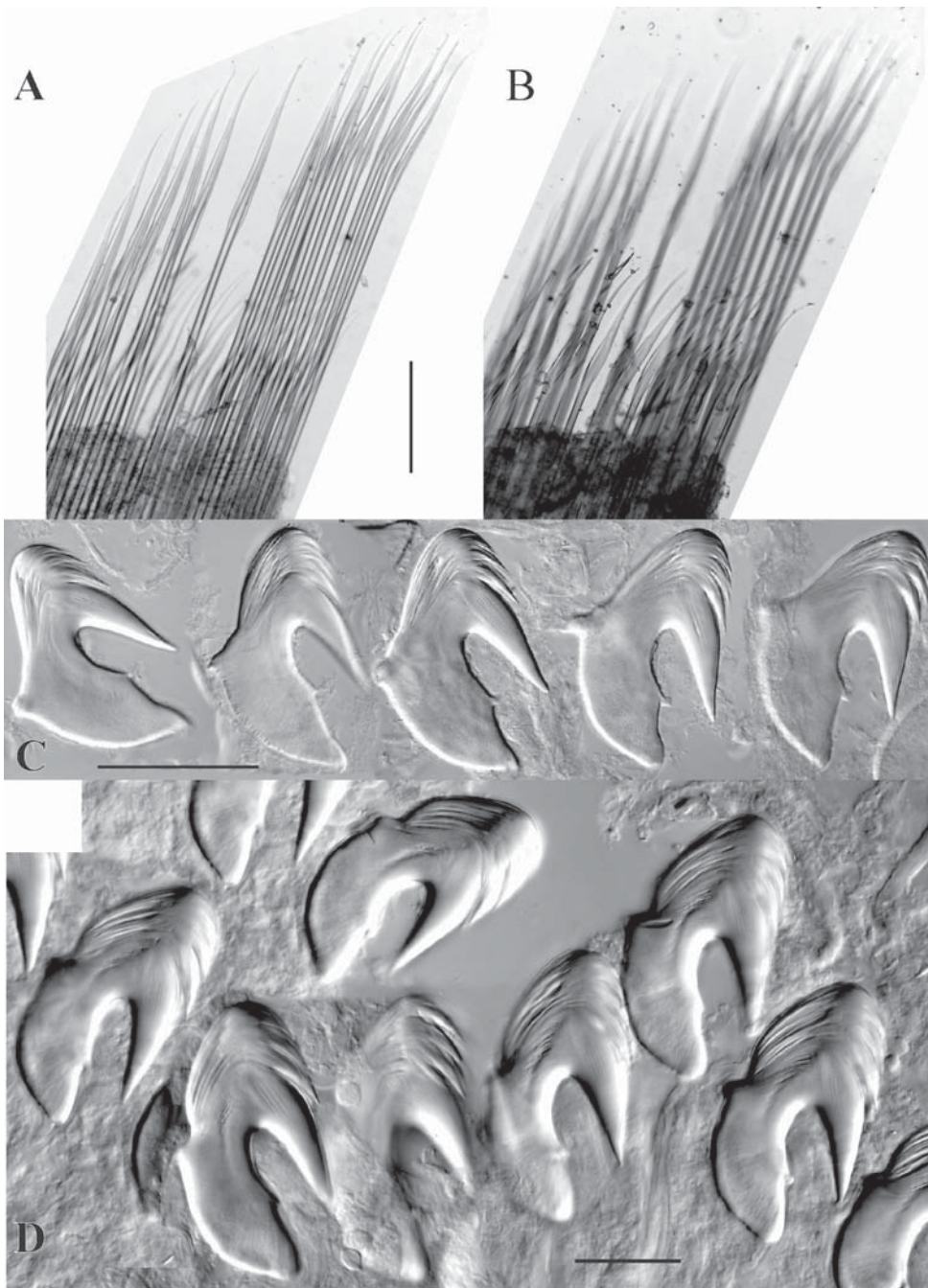


Fig. 13. *Amphitrite edwardsii* (Quatrefages, 1866), chaetae. A, B — notochaetae TC14, APEM 004088, different optical slices; C — uncini TU1, APEM 004088; D — uncini AU11, APEM 004088. Scale bars: A — 0.2 mm, C — 50 μ m, D — 20 μ m.

Рис. 13. *Amphitrite edwardsii* (Quatrefages, 1866), щетинки. А, В — нотохеты TC14, АРЕМ 004088, различные оптические срезы; С — uncini TU1, АРЕМ 004088; D — uncini AU11, АРЕМ 004088. Масштаб: А — 0,2 мм, С — 50 мкм, D — 20 мкм.



Fig. 14. *Amphitrite figulus* (Dalyell, 1853), external morphology. A — lateral view, WSBS; B — ventral view, Nilma 77; C — thorax–abdomen border Black river scale bar: 1 mm. A, C — 1 mm, B — 2 mm.
 Рис. 14. *Amphitrite figulus* (Dalyell, 1853), внешняя морфология. А — вид сбоку, БС; В — вид с брюшной стороны, Нильма 77; С — граница торакса и живота, Чёрная речка. Масштаб: А, С — 1 мм, В — 2 мм.

REMARKS. *Amphitrite johnstoni* has been accepted as a junior synonym of *A. figulus* since McIntosh (1875). Although McIntosh did not explain the reasons for the synonymy, comparison of both original descriptions and consideration of the proximity in the type localities (Great Britain for *Terebella figulus*; Sweden — Bohuslän and Koster, 5–9 m deep, southern Norway and Britain for *Amphitrite johnstoni*), the synonymy seems adequate.

DISTRIBUTION. Boreal Atlantic from the White Sea to the UK. Western Pacific from Shantar Isl. (Sea of Okhotsk) to Peter the Great Bay (Sea of Japan). Above tidal front (upper sublittoral).

Unlikely reports. Often reported from the Mediterranean, but *A. figulus* was absent in the material I examined from the Mediterranean, while the very similar *A. rubra* was abundant. So, perhaps Mediterranean reports are based on misidentifications.

Amphitrite gracilis (Grube, 1860)
 Figs 2B, 16, 17.

Amphitritides gracilis — Hartmann-Schröder, 1971: 476; 1996: 507–508, Abb. 246; Holthe, 1986: 104–106, fig. 45, map. 44; Jirkov, 2001: 512.

MATERIAL EXAMINED. 4 samples (> 125 specimens) from DGEH collection: 43°06' N 40°37' E (23), 26.4.2011; 45°48' N 32°37' E, 08.1982 (>100 specimens); UK (Lundy, Bristol Channel): APEM 1224 (1 specimen) and APEM 1178 (1 specimen).

DESCRIPTION. Rather small *Amphitrite*, up to 20 mm in length. Eyespots absent. Two pairs of arborescent branchiae, branched two or three times, first branchiae larger than second ones. Lateral lobes indistinct. About ten smooth, well-separated ventral pads, pad width not exceeding length of tori. Nephridial papillae: large pair lateral to second branchiae (on S3); S4 and S5 without papillae; variable number from S6:

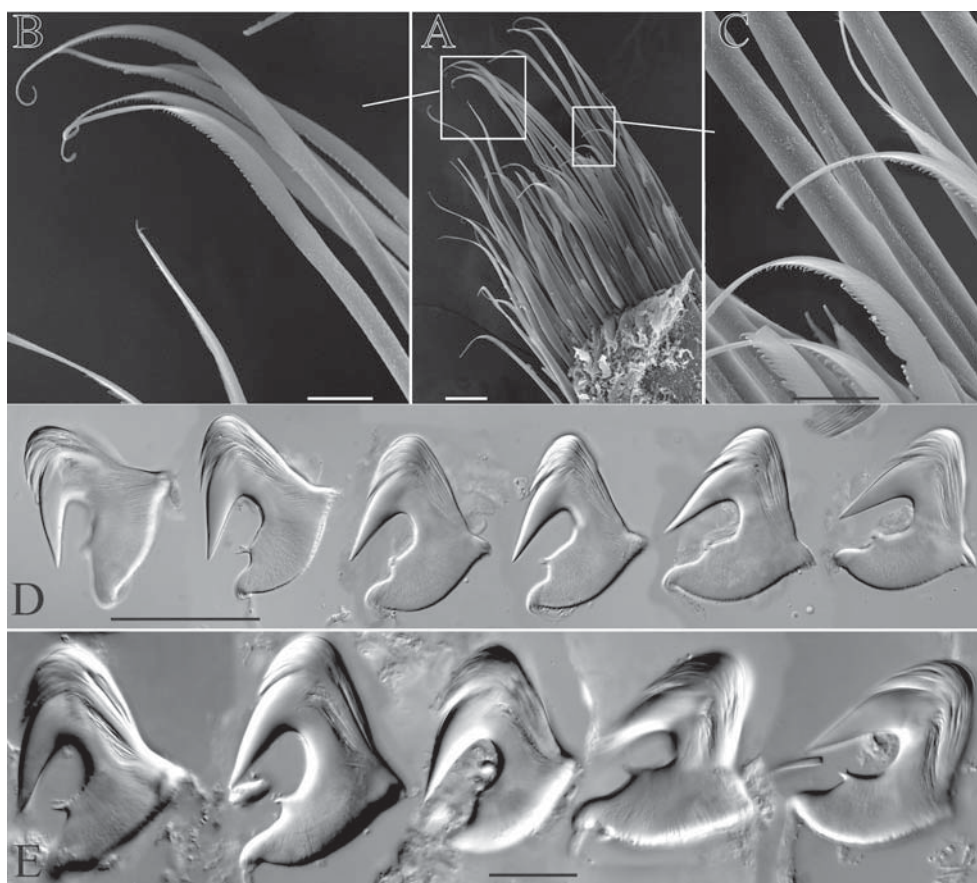


Fig. 15. *Amphitrite figulus* (Dalyell, 1853), chaetae. A–C — notochaetae, Ermolinskaja Bay, 1984; B, C — details of A; D — uncini TU1, Nilma, 1977; E — uncini AU4, Nilma, 1977. Scale bars: A — 0.1 mm, B, C — 30 μ m, D — 50 μ m, E — 20 μ m.

Рис. 15. *Amphitrite figulus* (Dalyell, 1853), щетинки. А–С — нотохеты, Ермолинская губа, 1984; В, С — детали А; D — uncini TU1, Нильма, 1977; E — uncini AU4, Нильма, 1977. Масштаб: А — 0,1 мм, В, С — 30 мкм, D — 50 мкм, E — 20 мкм.

six in topotypes, seven in material from the Black Sea.

Notopodia from S4, present on 17–19 segments. Notochaetae of two types: long and short, symmetrically wide, bilimbate, with base of blade sharper and wider than in other species investigated here with serrated tips.

Neuropodia from S5, all neuropodia tori; no abrupt change in size or shape of neuropodia from thorax to abdomen. Uncini facing forward, in double rows (uncini face-to-face), from TU7 almost to pygidium, rows well separated. Uncini avicular, crest with numerous teeth in several rows; thoracic and abdominal uncini all similar.

REMARKS. 1. The variation in the distribution of nephridial papillae is also known from the literature: eight segments in the type (Holthe, 1986), or nine, according to Fauvel (1927). It is not yet possible to decide whether this variation reflects geographic variation only or if there are different species, due to the lack of the material between the type locality (Scilly Is.) and the Black Sea, and the absence of DNA data.

2. McIntosh (1922) considered this species to be a junior synonym of *A. scylla* (Savigny, 1822). However all that is known from the original description of that species is that its members have 19 TC. So, the lack of detailed

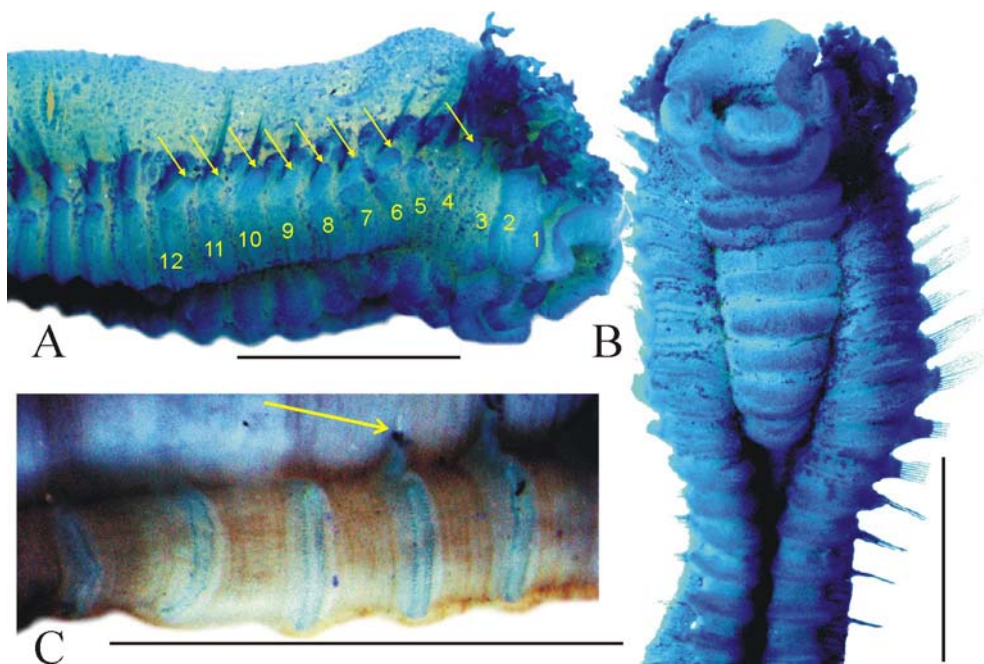


Fig. 16. *Amphitrite gracilis* (Grube, 1860), external morphology. A — lateral view, Gudauta; B — ventral view, Gudauta; C — thorax–abdomen border APEM. All scale bars: 1 mm.

Рис. 16. *Amphitrite gracilis* (Grube, 1860), внешняя морфология. А — вид сбоку, Гудаута; В — вид с брюшной стороны, Гудаута; С — граница торакса и живота АРЕМ. Масштаб: 1 мм.

information forces us to consider *A. scylla* as *nomen dubium*.

DISTRIBUTION. East boreal Atlantic, from the Black Sea and Mediterranean and to northern Scotland. Probably upper sublittoral.

Amphitrite grayi Malmgren, 1866
Fig. 18.

Amphitrite grayi Malmgren, 1866: 377, tab. XXII, fig. 56; Hartmann-Schröder, 1971: 473–474; Jirkov, 1989: 127, Fig. 25.2; 2001: 511.

Neoamphitrite grayi — Zatsepin, 1948: 157, table XXXVIII, 16; Holthe, 1986: 101–103, fig. 43, map 42; Hartmann-Schröder, 1996: 516 — non Annenkova, 1937: 192; 1938: 206; Uschakov, 1955: 392; Buzhinkaja, 1967: 114 (= *Amphitrite buzhinskajae* sp.n. see above).

MATERIAL EXAMINED. 5 samples (5 specimens) 245–445 m (Appendix).

DESCRIPTION. All investigated specimens are incomplete; estimated length of complete specimen at least 50 mm, judging from size of available fragments, proportions of thorax and abdomen, and widths and lengths of members of

other species of *Amphitrite*. Eyespots absent. Branchiae arborescent with long branches. Lateral lobes: thickening of anterior margin for S2; small, with upper margin at level of upper third of uncinal row of TU1 on S3, ventrally reaching pad, slightly lower at mid-length; small to inconspicuous below and in front of notopodia on S4. Ventral pads smooth, well separated from neuropodia laterally; after TU7 (first with uncini in double row), pads less conspicuous. Ten or eleven pairs of nephridial papillae: large, lateral to branchiae on S3; lateral to notopodia on S4; between noto- and neuropodia from S5 to S12–S13, on posterior margins of neuropodia.

Notopodia from S4, present on 21 segments. Notochaetae of two types: long and short, both bilimbate with serrated tips.

Neuropodia from S5, uncini facing forwards, TU7–TU20 (last thoracic) with uncini in double rows (face-to-face); rows well separated. Thoracic neuropodia large, ventrally almost reaching pads; on TU1 and TU2, ventrally shorter

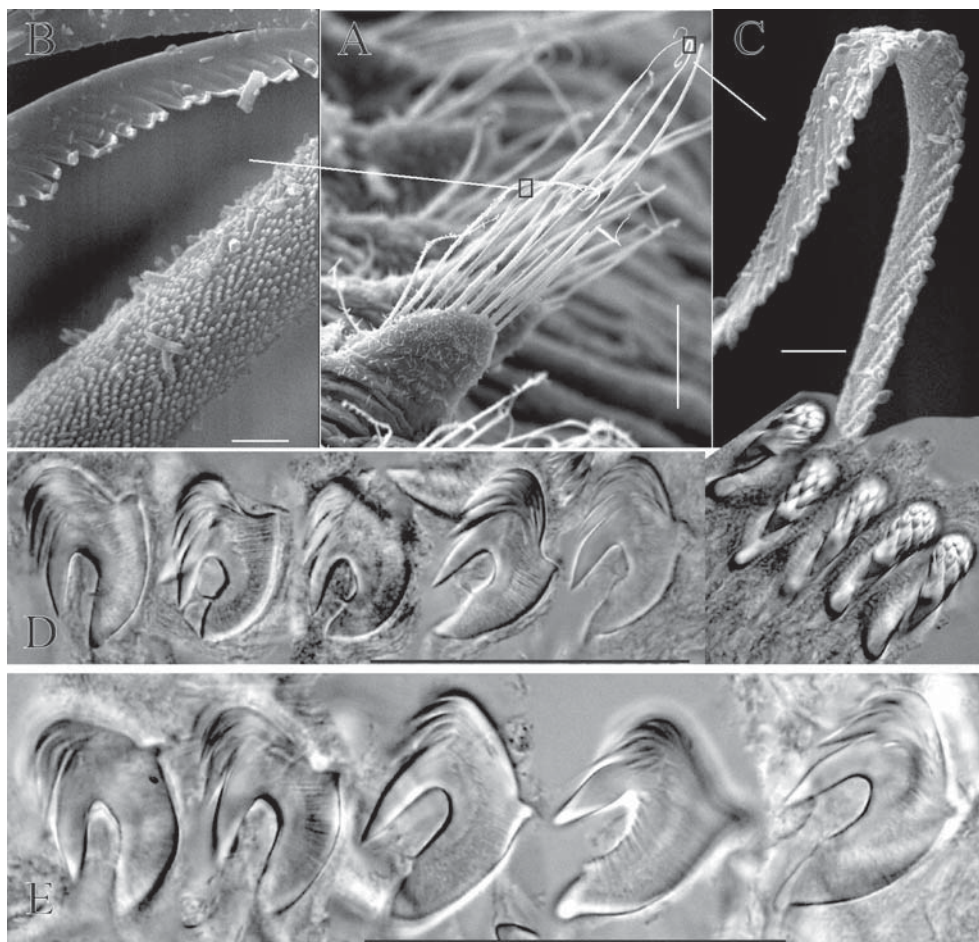


Fig. 17. *Amphitrite gracilis* (Grube, 1860), chaetae. A–C — notochaetae, Gudauta; B, C — details of A; D, E — uncini, Gudauta: D — TU1; E — AU4. Scale bars: A — 0.1 mm, B, C — 3 μ m, D, E — 50 μ m.

Рис. 17. *Amphitrite gracilis* (Grube, 1860), щетинки. А–С — нотохеты, Гудаута; В, С — детали; А; D, E — uncini, Гудаута: D — TU1; E — AU4. Масштаб: А — 0,1 мм, В, С — 3 мкм, D, E — 50 мкм.

than on TU3. Uncinal rows and neuropodia of AU1 two to three times shorter than those of last TC. Uncini avicular. Tube of muddy-detritus, thick walled.

REMARKS. 1. The papillae are clearly visible on S4–S6 but sometimes not visible on other segments, even in comparatively large worms; instead, a porous cushion is present. This difference in the distribution of nephridia seems related to reproduction and other functions of the nephridia.

2. Specimens examined include some collected close to the type locality (Bohuslan, Swe-

den) and agree well with Holthe's (1986) description, based on the type.

3. Holthe (1986) reported nephridial papillae on S3–S12 only, but investigated worms show slight variation.

DISTRIBUTION. Boreal Atlantic: European waters from the northern North Sea (type locality Bohuslan, Sweden) to the south-western Barents Sea, Newfoundland. Below tidal front (lower sublittoral).

Unlikely reports. Reports from the Sea of Japan (Annenkova, 1937, 1938; Uschakov, 1955; Buzhinkaja, 1967) refer to *Amphitrite*

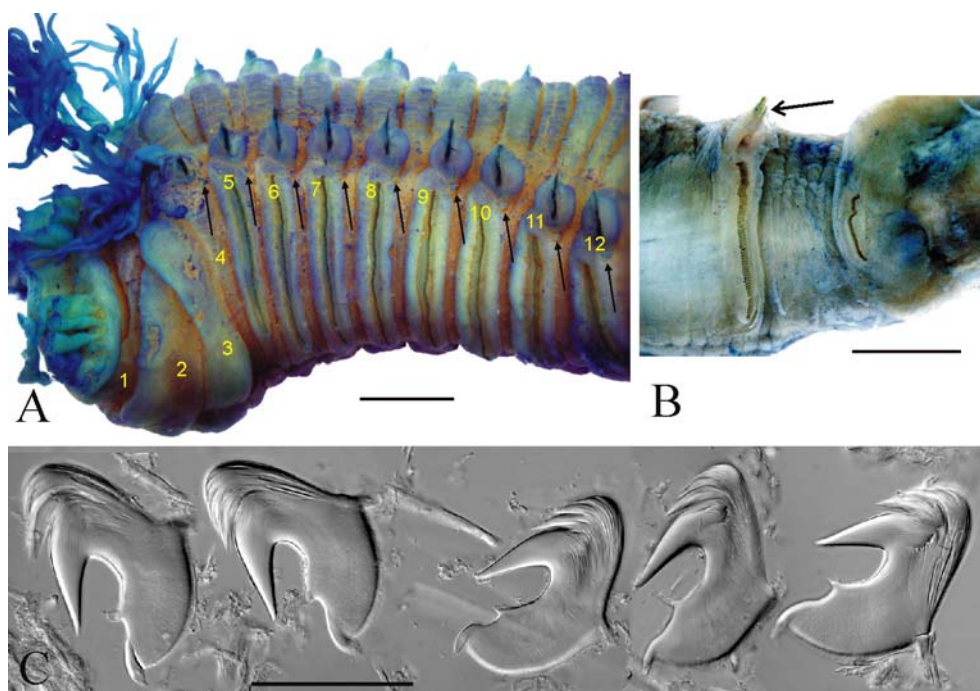


Fig. 18. *Amphitrite grayi* Malmgren, 1866. A — lateral view, Persey-3 3520; B — thorax–abdomen border, Persey-3 3520; C — uncini TU1, Sevastopol 1354. Scale bars: A, B — 1 mm, C — 50 μ m.

Рис. 18. *Amphitrite grayi* Malmgren, 1866. А — вид сбоку, Персей-3 3520; В — граница торакса и абдомена, Персей-3 3520; С — uncini TU1, Севастополь 1354. Масштаб: А, В — 1 мм, С — 50 мкм.

buzhinskaje (see above). Contrary to Holthe's (1986) statement, totally absent from the Arctic.

Amphitrite groenlandica Malmgren, 1866
Figs 1D, 19.

Amphitrite groenlandica Malmgren, 1866: 376, fig. 52; Fauvel, 1927: 250–251, fig. 86; Hartmann-Schröder, 1971: 473; Jirkov, 2001: 511–512.

Neoamphitrite groenlandica — Zatsëpin, 1948: 157, table XXXVIII, 14; Uschakov, 1955: 392, Fig. 147 G; Pettibone, 1956: 322; Holthe, 1986: 103–104, fig. 44, map 43; Hartmann-Schröder, 1996: 516.

MATERIAL EXAMINED. 27 samples, 43 specimens, from DGEH and ZIN collections (Appendix), 75–388 m.

DESCRIPTION. Up to 190 mm length. Eyespots absent. Branchiae arborescent with long branches. Lateral lobes of S2–S4: S2 appear as thickenings of anterior margins; small on S3, with upper margin level with middle of TU1 tori, reaching pad ventrally, slightly lower at mid-length; on S4, small to inconspicuous be-

low and in front of notopodia. Ventral pads smooth, well separated from neuropodia, completely absent from around TU10. Eleven to thirteen pairs of nephridial papillae: from S3 to S13–S15; sometimes varying within a single individual: e.g. to S13 on one side, to S15 on another. Papillae of S3 lateral to branchiae, lateral to notopodia on S4, others between noto- and neuropodia, posterior to tori; all papillae small.

Notopodia from S4, present on 19 segments. Notochaetae bilimbate, with serrated tips.

Neuropodia from S5, uncini facing forward, TU7–TU18 (last thoracic) uncini in double rows (face-to-face), rows well separated, all neuropodia tori. Thoracic neuropodia large, ventrally almost reaching pads; shorter on TU1 and TU2 than on TU3. Uncinal rows and neuropodia of AU1 about 3/4 to 1/2 length of those of last TC, varying among material from sample sample. Uncini avicular. Tube walls distinctly thick, as wide as inner diameter of tube, muddy.

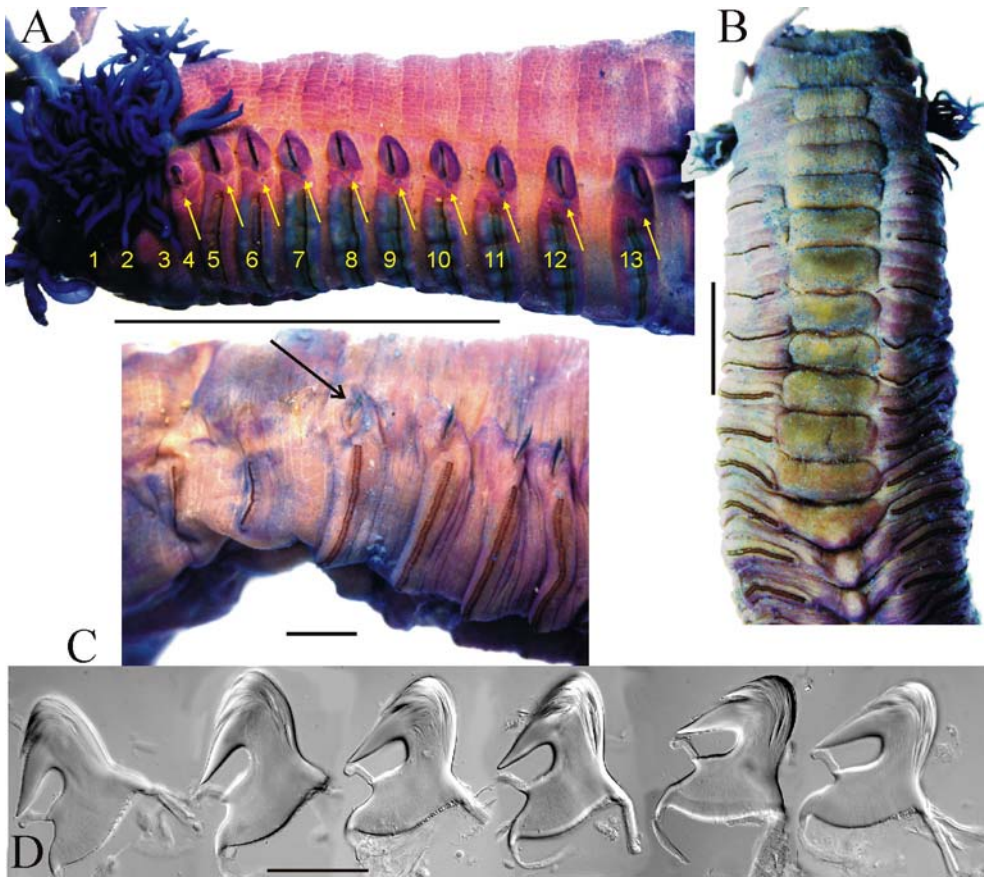


Fig. 19. *Amphitrite groenlandica* Malmgren, 1866. A — lateral view, Persey 3360; B — ventral view, RT-61 26.95; C — thorax–abdomen border, RT-61 26.95; D — uncini TU1, Alaid 7. Scale bars: A — 5 mm, B — 2 mm, C — 1 mm, D — 50 μ m.

Рис. 19. *Amphitrite groenlandica* Malmgren, 1866. А — вид сбоку, Persey 3360; В — вид с брюшной стороны, RT-61 26.95; С — граница торакса и живота, RT-61 26.95; D — uncini TU1, Алайд 7. Масштаб: А — 5 мм, В — 2 мм, С — 1 мм, D — 50 мкм.

REMARK. Specimens examined agree well with Holthe's (1986) description, based on the type.

Recently published description of new species *A. undevigintipes* (Choi, Kim et Yoon, 2020) did not provided with information, allows to differ new species from *A. groenlandica*. Authors wrote: "the new species is clearly differentiated from *N. groenlandica* by two characteristic features. The uncini in the first abdominal chaetiger are arranged in a single row in *N. undevigintipes* sp. nov., but in double rows in *N. groenlandica*, and the new species has 12

ventral shields, but *N. groenlandica* has 14". However both statements are not correct. Probably species differ by the comparative sizes of the last TU and the first AU neuropodia AU1 neuropodia of *A. groenlandica* twice smaller than of last TU while equal in *A. undevigintipes*.

DISTRIBUTION. Type locality Aukpadlartok (West Greenland, 457 m deep) and Sukkertoppen (Norway, 366 m deep). High boreal below tidal front (lower sublittoral). Absent in high Arctic. Southermost European reports from middle Norway (Holthe, 1986). Maine. Pettibone (1956) reported depth limits as 15–940 m.

Unlikely reports. Reports from the North Sea (Hartmann-Schröder, 1996) and western Ireland (Holthe, 1986, unverified records) need in confirmation. Reports from Pacific (Bering Sea to the Sea of Japan and southwestern Alaska) probably belong to *A. undevigintipes*.

Amphitrite rubra (Risso, 1826)

Fig. 20.

Amphitrite rubra Risso, 1826: 408–409; Fauvel, 1927: 249–250, Fig. 85 h–l — non Imajima, Hartman, 1964: 337. *Terebella multisetosa* Grube, 1838: 19–24. *Terebella spiralis* Grube, 1860: 97–98. *Terebella compacta* Grube, 1863: 55–56, plate V fig. 6. ?*Amphitrite incana* Claparède, 1870: 129–132, Pl. XIII, fig. 6.

MATERIAL EXAMINED. 20 samples (30 specimens) from Mediterranean coasts of Spain (Almería, Málaga, Balears, Valencia, Chafarinas Is.) and Naples, 3–9 m (MNHN).

ADDITIONAL MATERIAL EXAMINED. *A. vigintipes* (Grube, 1870) ZIN 1/32269 Nagasaki 26.0.1901.

DESCRIPTION. Fauvel (1927) reported up to 100 mm length, 8 mm in diameter and 100 segments. Examined specimens did not exceed 50 mm in length. Eyespots absent. Branchiae arborescent with thick stem and long branches, first branchiae only slightly larger than third ones. Lateral lobes on S1–S3, poorly developed; lobes of S4 very small. 13–15 pairs of nephridial papillae: first three on S3–S5, long, cylindrical, at least twice size of others; others small, wart-like, between noto- and neuropodia; number of papillae may vary within same worm, from one side of body to another. Ventral pads to ca. TU11.

Notopodia from S4, present on 22–24 segments. Notochaetae of two types, longer and shorter, both narrow, bilimbate, with serrated tips.

Neuropodia from S5, uncini facing forwards, in double rows (face-to-face) from TU7, almost to end of body, rows well separated; all neu-

ropodia tori, gradually reducing in size towards pygidium; no abrupt change in size of neuropodia, either from thorax to abdomen or at transition between neuropodia with double rows of uncini to those with single-rows. Length of anterior neuropodial tori at least as long as width of widest ventral pad. Uncini avicular with short tendon. Preserved specimens colourless. Fauvel (1927) reported body of variable colour: pinkish white to wine-coloured and reddish; gills red, tentacles white.

REMARKS. 1. Hutchings & Glasby (1988: 4) wrote: "A type of *A. rubra* has been examined (MNHN UB 392) and the specimen does not belong in the genus *Amphitrite*". The short re-description of the paratype (MNHN UB 392) was published later (Hutchings, Glasby, 1995), with the conclusion that the species probably belonged to *Longicarpus* Hutchings, Murray, 1984, as the paratype had "anterior uncini long-handled" (p. 152). However, close examination of their drawing (Fig. 2b, reproduced Fig. 19F) shows that the appendage they call long-handled is actually short and the figured uncini, as well as the uncini of the examined worm, do not much differ from TU1 uncini of other *Amphitrite*, especially from those of *A. vigintipes* (Fig. 19G). Also, they mentioned "Nephridial papillae on segments 3–5 and possibly 6", which corresponds with my observation: papillae on S3–S5 much more visible than on subsequent segments, which may not be visible at all, being replaced by pads in mature females, as in *A. fauveli* (Jirkov *et al.*, 2018). The only difference is the number of notopodia: "19 pairs on segments 5 to 23; posterior segments with few or no notosetae" (Hutchings, Glasby, 1995). The difference may be either individual variation or (more probably) notochaetae lost during preservation. In either case, I do not consider the difference significant enough even to change the species diagnosis. Unfortunately, I cannot investigate Hutchings & Glasby's (1988)

Рис. 20. *Amphitrite rubra* (Risso, 1826) and *A. vigintipes* (Grube, 1870). А — вид сбоку, MNCN 478; В — вид с брюшной стороны, MNCN 478; С — граница торакса и абдомена, MNCN 478; D — нотохеты TC22, MNCN 1756; E — uncini TU1, MNCN 1756; F — MNHN UB 392 перерисовано из Hutchings and Glasby (1995); G — *A. vigintipes* (Grube, 1870) ZIN 1/32269, uncini TU 1. Масштаб: А — 5 мм, В — 2 мм, С — 1 мм, D — 0,2 мм, E–G — 50 мкм.

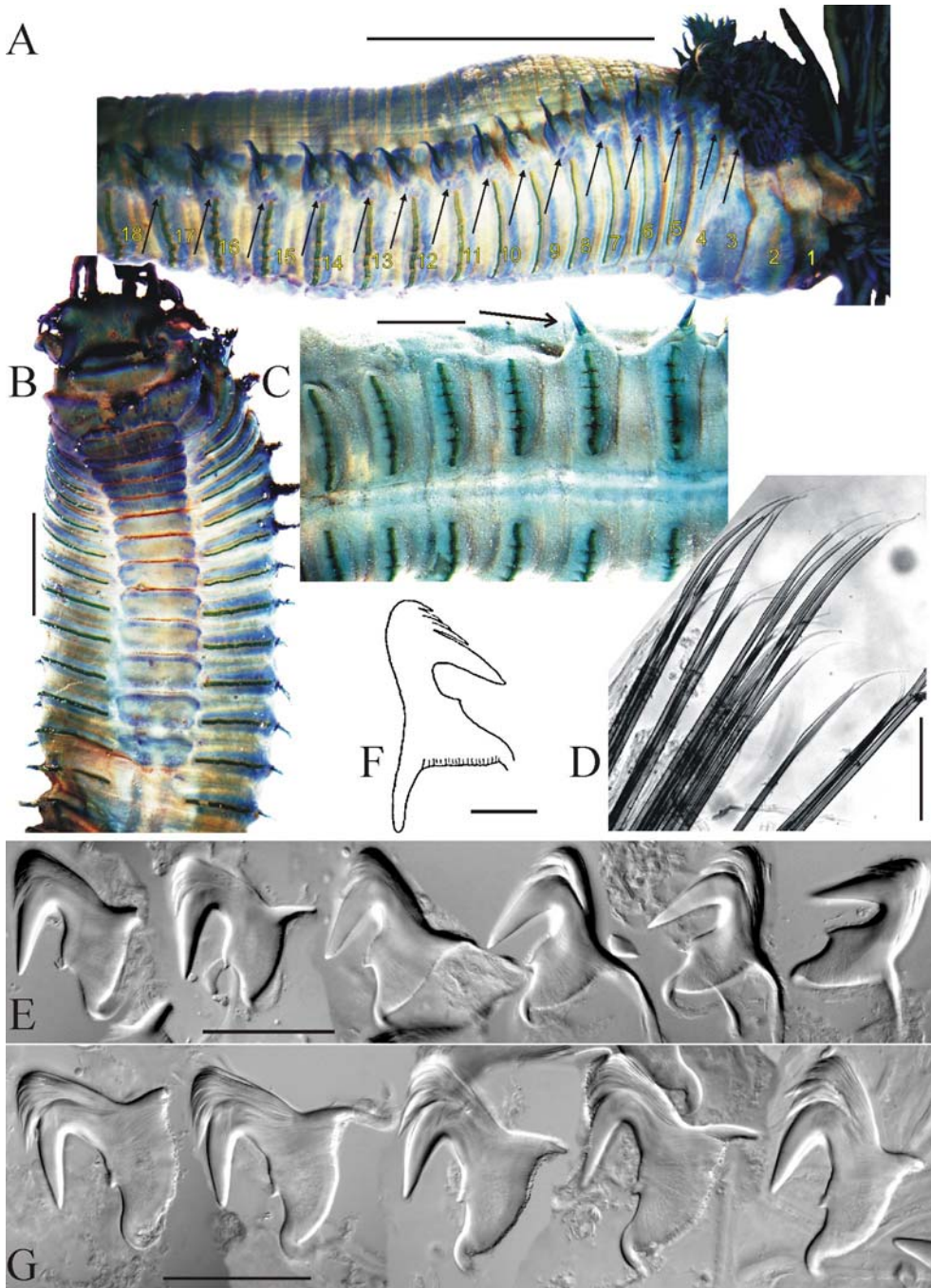


Fig. 20. *Amphitrite rubra* (Risso, 1826) and *A. vigintipes* (Grube, 1870). A — lateral view, MNCN 478; B — ventral view, MNCN 478; C — thorax–abdomen border, MNCN 478; D — notochaetae TC22, MNCN 1756; E — uncini TU1, MNCN 1756; F — MNHN UB 392 redrawn from Hutchings and Glasby (1995); G — *A. vigintipes* (Grube, 1870) ZIN 1/32269 uncini TU 1. Scale bars: A — 5 mm, B — 2 mm, C — 1 mm, D — 0.2 mm, E–G — 50 µm.

paratype as “there is no trace of this species in the database” (e-mail from Prof. Meziane, curator of the MNHN collection of Polychaeta 21/01/2017). In this paper, *A. rubra* is accepted in the sense of Fauvel (1927) as studied specimens agree well with the generic diagnosis above and Fauvel’s (1927) species description.

2. *Terebella multisetosa* Grube, 1838 (type locality Italy), according to the original description, has three pairs of branchiae and 22 TC. The only species which matches these characters in the investigated area is *A. rubra*, so I agree with Fauvel (1927) that these species are synonyms.

3. *Terebella spiralis* Grube, 1860 (type locality Cherso, Greece), according to the original description, has 22–25 TC and nephridial papillae up to (and including) S17. The only species which matches these characters in the investigated area is *A. rubra*. I do not consider small differences in number of TC and nephridial papillae to be important enough to separate species, so I agree with Fauvel (1927) that these species as synonyms.

4. *Terebella compacta* Grube, 1863 (type locality Croatia), according to the original description, has three pairs of branchiae, 22–23 TC, and ventral pads occupying a small part of the ventral surface. The only species which matches these characters in the investigated area is *Amphitrite rubra*, so I agree with Fauvel (1927) that these species as synonyms.

5. *Amphitrite incana* Claparède, 1870 (type locality Gulf of Naples), according to the original description, has three pairs of branchiae and 23 TC, as do members of *A. rubra*. However, as the figured notochaetae seem geniculated the species may belong to *Terebella*.

DISTRIBUTION. Type locality Nice, Southern France. Probably Mediterranean endemic, above the tidal front (upper sublittoral).

Unlikely reports. Widely reported; however, close examination shows that at least some records are based on misidentifications. For example, Australian waters are inhabited by *A. pachyderma* (Hutchings, Glasby, 1988), instead of *A. rubra*. Imajima & Hartman (1964) reported only 20 TC (distinctly less than for European specimens) for specimens from Japan (Imajima,

Hartman, 1964: 337): “uncini... in double rows from the seventh (TU? – IJ) to the first abdominal parapodia. Nephridial papillae occur on segments 3 to 15”. Obviously, this is a quite different species, as Mediterranean specimens have uncini in double rows almost to the end. I also investigated a specimen of *A. vigintipes* with 22 TC and uncini in double rows almost to the pygidium (ZIN 1/32269); it has only six pairs of nephridia (S3–S8), as previously mentioned by Marenzeller (1884); it is obviously a quite different species, although Imajima & Hartman (1964) regarded it as a junior synonym of *A. rubra*. So, considering the existence of two species that may be confused with *A. rubra*, the presence of this species in Japanese waters requires verification.

Amphitrite rzhavskyi Jirkov, **sp.n.**

Figs 1F–H, 21, 22.

Holotype Melilla 35°10'59" N 02°25'43" E; missing posterior end, but otherwise well-preserved (MNCN 16.01/17775).

Paratypes: Mediterranean, Melilla: MNCN 16.01/5479 (1 specimen), UK: APEM 487849, Loch Spelve KGB MGU-Pol-37 (2 sp.); APEM 41398 Loch Sunart KGB MGU-Pol-38 (1 specimen); APEM518609 Summer Isles KGB MGU-Pol-39 (2 specimens); APEM489074 Sound of Mull KGB MGU-Pol-40 (1 specimen).

ETYMOLOGY. Species is named after my late friend Dr. Alexandr Rzhavsky (Fig. 23).

ADDITIONAL MATERIAL EXAMINED.

A. oculata Hesse, 1917: 3 samples (5 specimens) from Japan ZIN 1/31909 Misaki, Okayama 10–15 m 23.07.1917 (1 spec.); ZIN 2/31910 Tsuruga, Fukui 15–20 m 1917 (2 specimens); ZIN 3/31911 3.3.1911 Misaki, Okayama (2 specimens). *A. kerguelensis* McIntosh, 1876: MNCN 3558 62°38' S 60°40' W 21.01.1995 (1 specimen); ZIN 3/16456 66°33'8" S 93°0'34" E 46 m 21.02.1966 (1 specimen).

DESCRIPTION (based on holotype and paratypes). Up to 100 mm in length, 6 mm width; paratypes with 17 TC and about 50 AU. Long buccal tentacles, about as long as body length or longer. Eyespots absent. Branchiae as

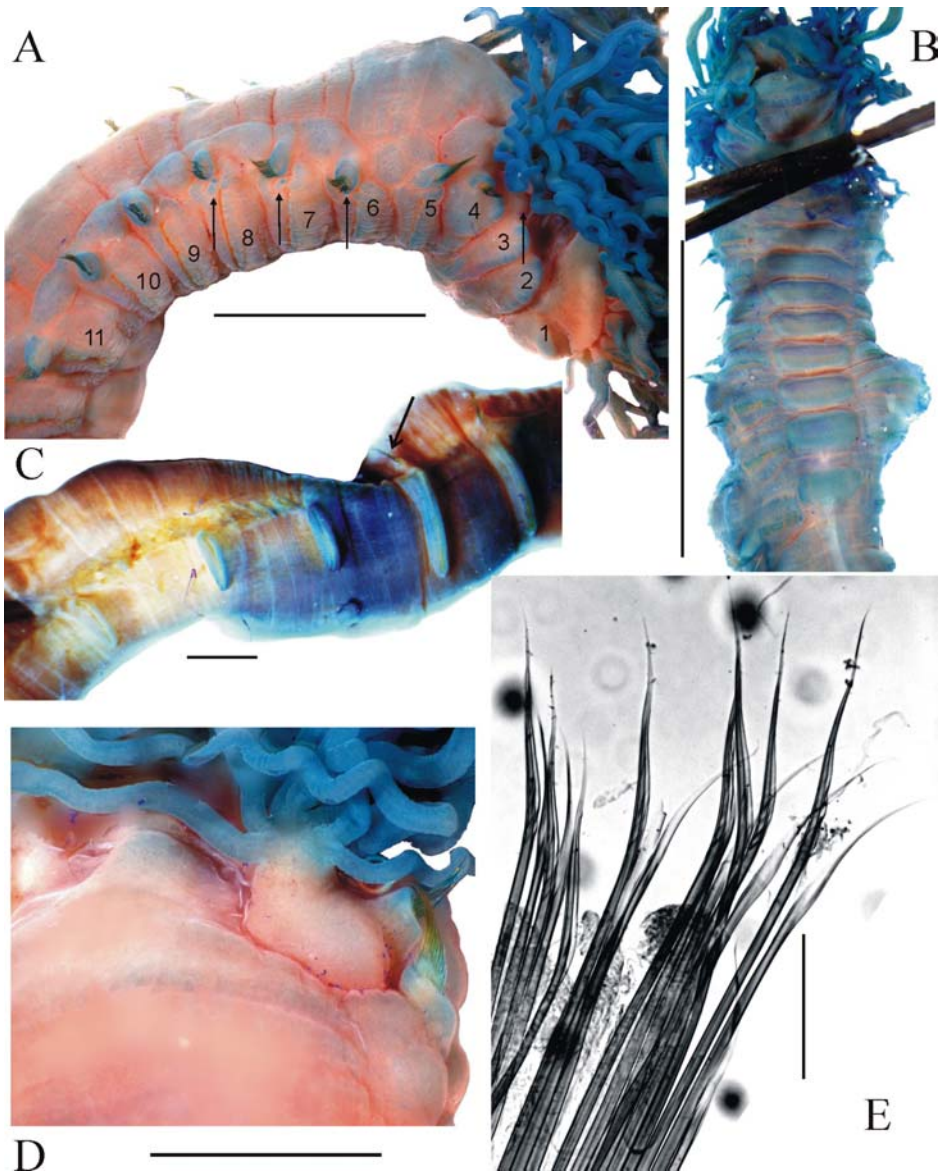


Fig. 21. *Amphitrite rzhavskiyi* Jirkov, sp.n., external morphology. A — lateral view, holotype; B — ventral view, holotype; C — thorax–abdomen border, holotype; D — branchia, holotype; E — notochaetae TC14, MNCN 5479. Scale bars: A — 2 mm, B — 5 mm, C, D — 1 mm, E — 0.2 mm.

Рис. 21. *Amphitrite rzhavskiyi* Jirkov, sp.n., внешняя морфология. А — вид сбоку, голотип; В — вид с брюшной стороны, голотип; С — граница торакса и абдомена, голотип; D — жабра, голотип; E — нотохеты TC14, MNCN 5479. Масштаб: А — 2 мм, В — 5 мм, С, D — 1 мм, E — 0,2 мм.

numerous simple filaments, arising from tip of stem. Stem with broad base, upper half abruptly narrowing on outer side, while inner side remains as basally. S1 forms ventral collar. Lobes

of S2–S4 small gradually reduced backwards. Ventral pads up to TU9, smooth. Four pairs of nephridial papillae: one pair laterally from second par of branchiae (S3), very large almost half

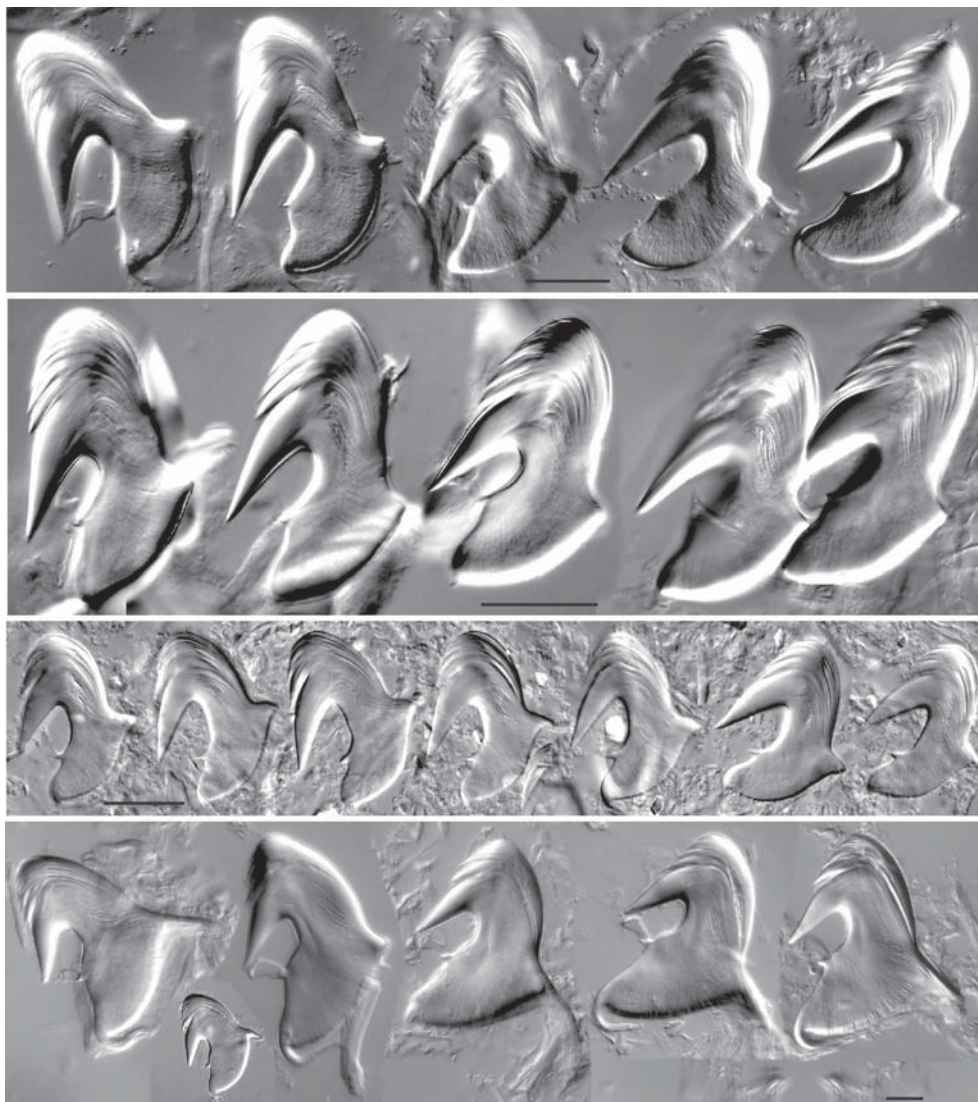


Fig. 22. *Amphitrite rzhavskiyi* Jirkov, sp.n., chaetae. A — uncini TU1, MNCN 5479; B — uncini A26, MNCN 5479; C — *A. oculata* Hesse, 1917, ZIN 3; D — *A. kerguelensis* McIntosh, 1876, MNCN 3558. Scale bars: 20 μ m.

Рис. 22. *Amphitrite rzhavskiyi* Jirkov, sp.n., щетинки. А — uncini TU1, MNCN 5479; В — uncini A26, MNCN 5479; С — *A. oculata* Hesse, 1917, ZIN 3; D — *A. kerguelensis* McIntosh, 1876, MNCN 3558. Масштаб: 20 мкм.

size of first notopodia; three much smaller pairs between noto- and neuropodia of S6–S8; S4 and S5 without papillae.

Notopodia from S4, present on 17 segments. Notochaetae assymmetrically bilimbate, with serrated tips.

Neuropodia (uncini facing forward) from C2. Uncini in double rows (uncini face-to-face) on TU7–TU16 (end of thorax), all abdominal neuropodia with uncini in single rows (uncini facing forwards). All neuropodia large, first nine pairs reaching ventral pads. Tori of anterior



Fig. 23. Dr. Alexandr Vladimirovich Rzhavskiy (25.08.1959–30.07.2018). Photo: T.A. Britaev.

Рис. 23. Александр Владимирович Ржавский (25.08.1959–30.07.2018). Фото Т.А. Бритаева.

neuropodia at least as long as width of widest ventral pad. Tori of AU1 less than half length of tori of last TU. Uncini avicular, thoracic and abdominal uncini all similar. Pygidium crenulate, without papillae. Tube unknown.

REMARKS. The new species differs from other *Amphitrite* species with cirriform branchiae in the shape of its branchiae. Branchial filaments of *A. rzhavskiy* sp.n. arise from asymmetrical stem, while *A. cirrata* (Fig. 9D), *A. oculata* and *A. fauveli* (Fig. 24A, also see Jirkov *et al.*, 2018, Fig. 2A–C) have branchial filaments arising from a very short, wartlike stem or directly from the body wall; *A. kerguelensis* has the filaments of third branchiae arising from the inner side of a large stout stem (Fig. 24B). The new species is similar to *A. fauveli* and *A. oculata*, in having 4 pairs of nephridial papillae, which differs them from *A. kerguelensis* having 7 pairs of papillae (Fig. 3B) and *A. cirrata* (Fig. 3A) having 8 pairs of papillae. *A. rzhavskiy* sp.n. similar to other *Amphitrite* with cirriform branchiae, but *A. kerguelensis*, by the absence of nephridial papillae on S4 and S5, and absence of a high dorsal collar. *A. kerguelensis* has this papillae (Fig. 24D), and branchiae on S4 attach to a high dorsal collar (Fig. 24B). The TU1 uncini

of the new species differ from other *Amphitrite* with cirriform branchiae (Figs 10D, E, 22C, D, also see Jirkov *et al.*, 2018, Fig.) in their distinctly narrower necks; they are most similar to those of *A. oculata* (Fig. 22C), but differ from the last by more numerous teeth in a crest and more rounded base margin between prow and heel.

I also consider the species' distinct range as evidence of its validity. All species with cirriform branchiae have different ranges. *A. rzhavskiy* sp.n. is found in the upper sublittoral Mediterranean and western European waters, north to the north-western UK. *A. cirrata* inhabits shelf waters of Arctic and boreal regions of the northern Atlantic and northern Pacific. *A. fauveli* inhabits slope waters of the north-eastern Atlantic. *A. oculata* is reported from Japan (Hessle, 1917; Imajima, Hartman, 1964, our data), Australia (Hutchings, Glasby 1988) and Italy (Castelli *et al.*, 2008). However, considering the similarity between individuals of *A. rzhavskiy* sp.n. and *A. oculata*, it is highly likely that the report from Italy actually belongs to *A. rzhavskiy* sp.n. The range of *A. kerguelensis* is limited to the Southern Ocean.

DISTRIBUTION. Currently known from the upper sublittoral from northern Scotland to the Mediterranean; judging by *Pista unibranchia* Day, 1963, which in the Mediterranean is limited to upper sublittoral depths, it is expected above the tidal front (upper sublittoral) further south, at least probably to the Gulf of Guinea and even as far as the Indian Ocean.

Amphitrite variabilis (Risso, 1826) sensu
Fauvel, 1927
Fig. 25.

Terebella variabilis Risso, 1826: 408–409.

Amphitrite variabilis Fauvel, 1927: 247–248, Fig. 85 f, g.

MATERIAL EXAMINED. 21 samples (26 specimens) from Mediterranean coasts of Spain (Valencia), North Africa (Melilla), and Naples (MNHN and ZIN: 1/3267, 2/32268).

DESCRIPTION. Fauvel (1927) reported up to 150 mm length. Examined specimens seen not to exceed 55 mm in length. Eyespots absent. Branchiae arborescent. Lobes poorly developed on S3 & S4, better developed on S2 but still

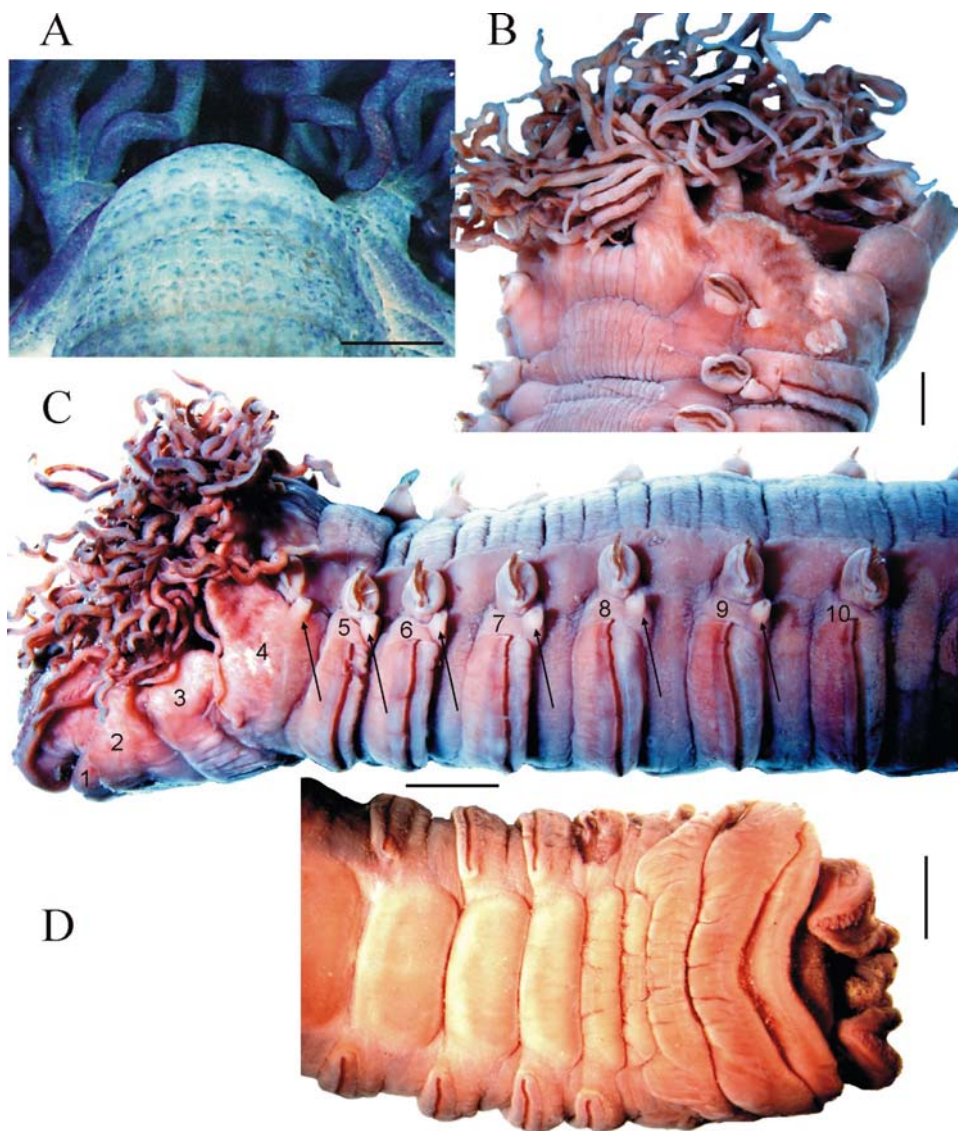


Fig. 24. *Amphitrite fauveli* Jirkov, Ravara et Cunha, 2018 and *A. kerguelensis* McIntosh, 1876. A — branchia *A. fauveli* (after Jirkov *et al.*, 2018); B–D — *A. kerguelensis*, MNCN 3558: B — branchia, C — lateral view, D — ventral view. Scale bars: A, B — 1 mm, C, D — 2 mm.

Рис. 24. *Amphitrite fauveli* Jirkov, Ravara et Cunha, 2018 и *A. kerguelensis* McIntosh, 1876. А — жабра *A. fauveli* (after Jirkov *et al.*, 2018); В–D — *A. kerguelensis*, MNCN 3558: В — жабра, С — вид сбоку, D — вид с брюшной стороны. Масштаб: А, В — 1 мм, С, D — 2 мм.

small. Ventral pads smooth, well separated from neuropodia; last pad on ca. TU10. Six pairs of almost equal-sized nephridial papillae on S3–S8: lateral to branchiae on S3; lateral and slightly posterior to notopodia on S4; between noto- and neuropodia on S5–S8, on posterior margin

of neuropodia. First three pairs cylindrical, others as small warts between noto- and neuropodia, slightly posterior to row of uncini.

Notopodia from S4, present on 17 segments. Notochaetae of two types, long and shorter, both bilimbate, with serrated tips.

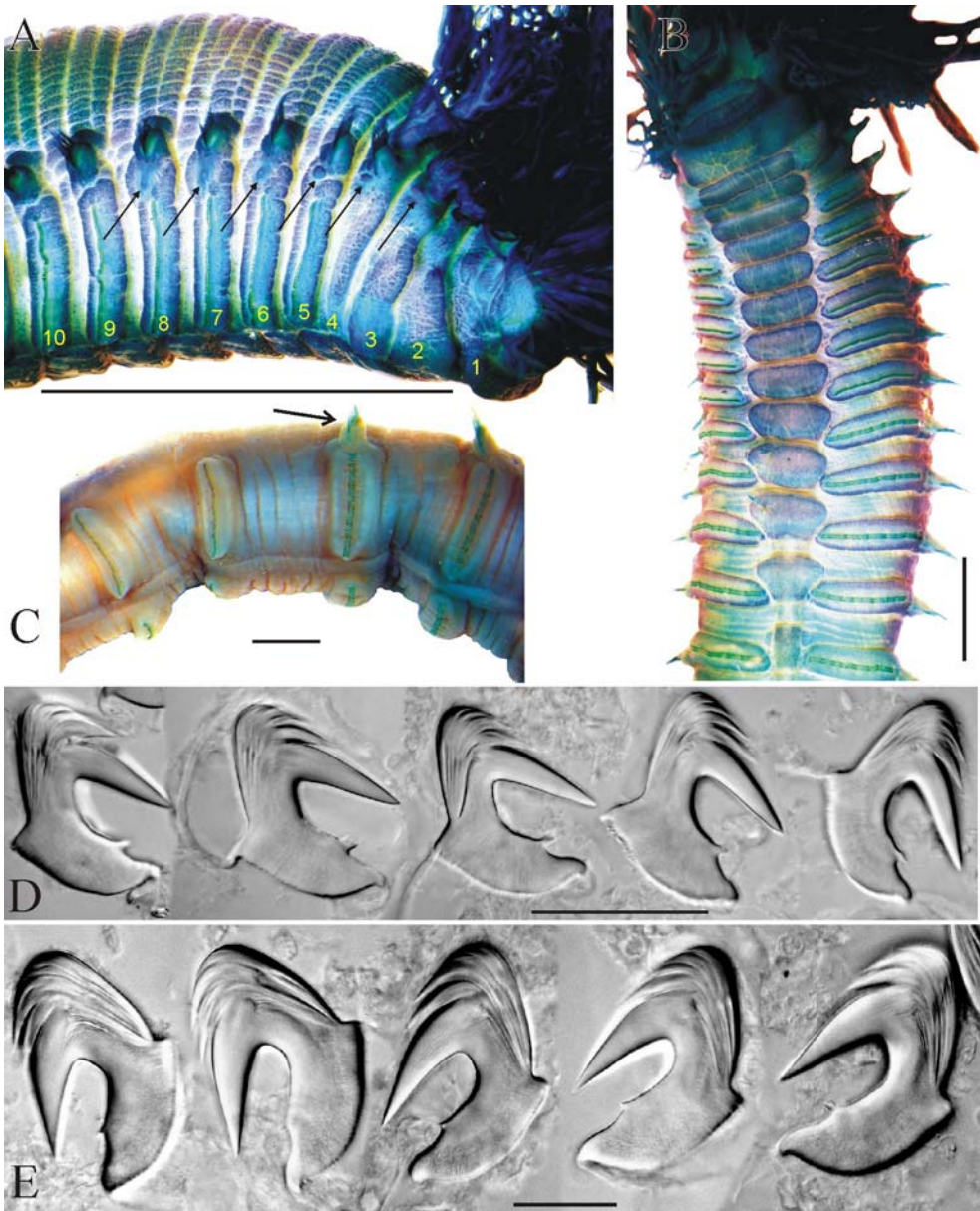


Fig. 25. *Amphitrite variabilis* (Risso, 1826) sensu Fauvel, 1927. A — lateral view, MNCN 653; B — ventral view, MNCN 653; C — thorax–abdomen border, MNCN 653; D — uncini TU1, MNCN 1773; E — uncini AU35, MNCN 1773. Scale bars: A — 5 mm, B — 2 mm, C — 1 mm, D — 50 μ m, E — 20 μ m.

Рис. 25. *Amphitrite variabilis* (Risso, 1826) sensu Fauvel, 1927. А — вид сбоку, MNCN 653; В — вид с брюшной стороны, MNCN 653; С — граница торакса и живота, MNCN 653; D — uncini TU1, MNCN 1773; E — uncini AU35, MNCN 1773. Масштаб: А — 5 мм, В — 2 мм, С — 1 мм, D — 50 мкм, E — 20 мкм.

Neuropodia (uncini facing forward); from S5: uncini in double rows (face-to-face) on TU7–TU16, rows well separated, thoracic and abdominal neuropodia tori, thoracic neuropodia reaching ventral pads. Uncinal rows of anterior neuropodia at least 1.5 times as long as width of widest ventral pad. All neuropodia tori; no abrupt change in size or shape of neuropodia between thorax and abdomen. Uncini avicular; thoracic and abdominal uncini all similar.

REMARKS. *Amphitrite variabilis* is similar to *A. affinis* in terms of the number of TC, nephridia, and branchiae. Probably for this reason, *A. affinis* has been recorded from as far from its true range as Iberian waters. These two species differ in the shape of their uncini: narrower and with longer necks in *A. variabilis* than in members of *A. affinis*.

The original description is not satisfactory and I am not sure that Risso (1826) had this species at hand. In this paper, the species is accepted in the sense of Fauvel (1927).

DISTRIBUTION. Type locality Nice, Southern France. The species seems to be endemic to the Mediterranean (upper sublittoral).

Discussion of generic synonymy

Status of *Neoamphitrite* Hessle, 1917

One of the reasons for establishing *Neoamphitrite* was the shape of the branchiae, which differs from *Amphitrite*. Those of *Amphitrite* s.str. are described as “short filaments” (Uschakov, 1955: 392), “sessile filaments” (Fauchald, 1977: 129) or “simple filaments” (Holthe, 1986: 93). The type species of *Amphitrite*, *A. cirrata*, has filaments attached to a reduced stem; the filaments are usually unbranched: among examined specimens of *A. cirrata*, 12 have unbranched filaments arising directly from one point on the body wall, 88 have unbranched filaments arising from a reduced stem and 7 have branchiae with at least some branched filaments. Hutchings & Glasby (1988) also mentioned that “some species such as *Amphitrite robusta* Johnson, 1901 have branchiae which are intermediate between those of *Amphitrite* sensu stricto and those of *Neoamphitrite*” (p. 3). Some other

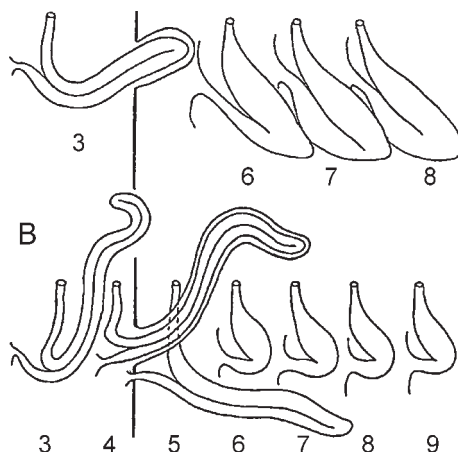


Fig. 26. Nephridial system of *Amphitrite* and *Neoamphitrite*. A — *Amphitrite* (species figured by Hessle is probably *A. oculata* Hessle, 1917 as this was the only species with four pairs of nephridia known at that time); B — *Neoamphitrite*. Modified from Hessle (1917). Numbers refer to segment number.

Рис. 26. Нефридиальная система *Amphitrite* и *Neoamphitrite*. А — *Amphitrite* (изображена вероятно *A. oculata* Hessle, 1917, поскольку в то время это был единственный известный вид с четырьмя парами нефридиев); В — *Neoamphitrite*. По Hessle (1917). Цифры — номера сегментов.

species of *Amphitrite* s.str. (*A. kerguelensis* and *A. rzhavskyi* sp.n.) have branchiae with a distinct stem.

Hessle (1917) also used the structure of the nephridial system for distinguishing *Neoamphitrite* from *Amphitrite* (Fig. 26). However, for most species this information is absent and so cannot be used at the present stage of our knowledge. It also requires dissection and cannot be applied to rare species or type material. Hessle (1917) did not use type species of *Amphitrite* and *Neoamphitrite* as examples of the nephridial system. He pictured *Amphitrite* with four pairs of nephridia (the only *Amphitrite* known at that time with this number was *A. oculata*) and *Neoamphitrite* with seven pairs of nephridia; the only *Amphitrite* known at that time with this number was *A. kerguelensis* (see above) and it does not belong to *Neoamphitrite* sensu Hessle, 1917. Also, according to Hessle (1917), *Amphitrite* differs from *Neoamphitrite* in the absence

of nephridia on segments S4 and S5. This is true for all species with cirriform branchiae from the Northern Hemisphere, but not for *A. kerguelensis*, so the absence of nephridial papillae on S4 and S5 and the structure of branchiae are independent characters that may combine in different ways.

Fauchald (1977) also distinguished *Amphitrite* from *Neoamphitrite* by their lateral lobes: absent in *Amphitrite*, present in *Neoamphitrite*. However, Hessle (1917) reported both genera as having lateral lobes. According to my data, there is no difference between European species (including types of both genera) in the development of lateral lobes; usually, the lobes are small, but *A. kerguelensis* has large lateral lobes on S4 (Fig. 24C) and small on S1–S3.

In conclusion, there is no valid reason to accept *Neoamphitrite* as a distinct genus. This is even reflected in WoRMS: *Amphitrite grayi* Malmgren, 1866 is listed in WoRMS as *Amphitrite grayi* (Read, Fauchald, 2020c) and also as *Neoamphitrite grayi* (Read, Fauchald, 2020d). The same is true for *Amphitrite edwardsii*, which is listed in WoRMS as *Amphitrite edwardsii* (Read, Fauchald, 2020e) and also as *Neoamphitrite edwardsi* (sic!) (Read, Fauchald, 2020f). So I agree with many authors (Fauvel, 1927; Pettibone, 1954; Imajima, Hartman, 1964; Day, 1967; Hutchings, Glasby, 1988; Hutchings *et al.*, 2017) that *Neoamphitrite* should be accepted as a junior synonym of *Amphitrite*.

Status of *Amphitritides* Augener, 1922

Amphitritides differs from *Amphitrite* by:

- Two pairs of branchiae and neuropodia with double rows of uncini through most of the abdomen (Augener's original diagnosis). However, some species currently assigned to *Amphitrite* have two pairs of branchiae and at least *A. rubra* and *A. vigintipes* have neuropodia with double rows of uncini throughout most of the abdomen; nevertheless, both are so similar to other species of *Amphitrite* that I have no doubt of their generic affiliation.

- The number of TC: 16–17 in *Amphitrite*; 18 or more in *Amphitritides* (Fauchald, 1977). This is obviously not correct, as no presently known species of *Amphitrite* has 16 TC, while *Amphitrite glasbyi* Londoño-Mesa, Carrera-Parra, 2005 has 39 TC.

- Absence of lateral lobes (Holthe, 1986; Hartmann-Schröder, 1996; Londoño-Mesa, 2009). The development of lateral lobes in *Amphitrite* varies to a great extent, from poorly developed or absent (*A. groenlandica*) to well-developed (*A. kerguelensis*); these lobes are less well-developed than in *Axionice* or *Scionella* (Jirkov, Leontovich, 2017). Small worms of all investigated species have lobes that are poorly-developed or absent. The situation is quite different from *Axionice* and *Pista*, in which small specimens have well-developed lateral lobes (see Jirkov, Leontovich, 2017). So, this character does not seem good enough to be used at the generic level in the *Amphitrite*–*Amphitritides* case.

In summary, I see no characters that allow differentiation between *Amphitritides* and *Amphitrite*. This is even reflected in the generic affinities of species. For example, *Amphitritides pectinobranchiata* Hartmann-Schröder, 1965 is obviously closer to species assigned to *Amphitrite* (*A. birulai* and *A. pauciseta*) at the time of its description than to *Amphitritides*, as Arvanitidis & Koukouras (1995) correctly stated. Parapar *et al.* (1991) also mentioned the similarity between *Amphitritides* and *Paramphitrite*. The notochaetae and uncini, development of nephridial papillae (absence on S4 and S5, as in many species of *Amphitrite*) and development of ventral pads (limited to ventral surface) are exactly the same in *Amphitritides gracilis* as in *Amphitrite*. So, to my mind, *Amphitritides* should be accepted as another junior synonym of *Amphitrite*.

Status of *Paramphitrite* Holthe, 1976

Both genera may have two pairs of branchiae: all species of *Paramphitrite*, and some of *Amphitrite*. *Paramphitrite* has fewer TC, only 13–14 but, taking into account that different

species of *Amphitrite* have 15–45 TC, this difference does not seem reasonable to separate genera. Nephridial papillae in *Paramphitrite* are present on S3, and S5–S8 or S6–S8, between parapodial lobes, exactly as in some species of *Amphitrite*. Uncini are in double rows on S11–S20, as with over half the species of *Amphitrite*. Both genera have more or less developed lateral lobes at S2–S4. According to Holthe (1976), *Paramphitrite* differs from *Amphitrite* in the presence of arborescent branchiae (first pair) and from *Neomphitrite* in the presence of almost cirriform branchiae (second pair); as I consider *Neomphitrite* to be a junior synonym of *Amphitrite*, this does not matter. According to Holthe (1976), *Amphitritides* differs from *Paramphitrite* in having branchiae with distinct stems and the absence of lateral lobes. However, *Amphitrite birulai*, a species previously included in *Paramphitrite* and, as shown below, the senior synonym of the type species of *Paramphitrite*, has both pairs of branchiae with distinct stems, if the worm and, accordingly, branchiae are large enough. In summary, I see no character that allows differentiation between *Paramphitrite* and *Amphitrite*. So, I consider *Paramphitrite* should be accepted as a junior synonym of *Amphitrite*.

Species included in *Amphitrite*

Amphitrite, in the sense accepted here (including *Amphitritides*, *Neoamphitrite* and *Paramphitrite* as junior synonyms), includes (Table 1) 42 distinct species: 39 described and valid and two described herein (plus *A. sp. A* sensu Kritzler, 1984). Many of the nominal species were poorly described and re-investigation of type material (which does not always exist) or topotypes is necessary.

Taxonomic position of species excluded from the genus *Amphitrite*

Amphitrite harpa Hutchings et Glasby, 1988 has different types of notochaetae, straight on anterior notopodia and geniculated on posterior ones, like many *Terebella*. So, Arvanitidis &

Koukouras (1995) supposed that this species should be transferred to *Terebella*. I agree with them.

Amphitrite lobocephala Hsieh, 1994. According to characters mentioned in the original description (shape of branchiae, arrangement of lateral lobes, uncini arranged back-to-back and others), this species agrees well with species formerly belonging to *Lanice*. Nogueira *et al.* (2013) came to the same conclusion, but did not make the necessary taxonomic amendments. I do not understand why it was described under *Amphitrite*. Our phylogenetic analysis (Jirkov, Leontovich, 2017) shows that it should be transferred to *Axionice*, as we consider that *Lanice* should be accepted as its junior synonym.

Amphitrite luna Dalyell, 1853 (type locality Scotland) and *A. ramosa* Risso, 1826 (type locality Mediterranean France) are indeterminate because their original descriptions did not provide sufficient details, so I consider it better to accept them as *nomina dubia* (glossary of ICZN: “a name of unknown or doubtful application”) and to disregard them.

Amphitrite meckelii Delle Chiaje, 1828 (as *Amphitrite* di Meckel, type locality Gulf of Naples) was synonymised by Fauvel (1909) with *Eupolymnia nebulosa* (Montagu, 1819), without any argumentation. The original description does not provide enough information even to be sure about generic affiliation.

Amphitrite olfersii Delle Chiaje, 1828 (as *Amphitrite* di Olfers, type locality Gulf of Naples) was synonymised by Fauvel (1909) with *Amphitrite rubra* without any argumentation. The original description does not provide enough information even to be sure in generic affiliation.

The notochaetae pictured in the original description of *Amphitritides kuehlmanni* Arvanitidis et Koukouras, 1995 are geniculated and the species probably belongs to *Terebella*; however until a re-examination of the types is performed, it is better to keep this species inside *Amphitrite*.

Terebella laevirostris Claparède, 1869 (type locality Gulf of Naples) was synonymised, with doubt, by Fauvel (1927) with *Amphitrite graci-*

Table 1. Synoptic table of valid *Amphitrite* species.
 Table 1. Сводная таблица валидных видов *Amphitrite*.

species	TC	branchiae		nephridia		on S5	uncini in double row to chaetiger	source
		pairs	shape	pairs	on S4			
<i>A. pauciseta</i> Day, 1963	13	2	cirriform	2?	?	?	16	Day, 1967
<i>A. birulai</i> Ssolowiew, 1899	13–14	2	pectinate	5	no	yes	16–19	syntypes, present study
<i>A. pectinobranchiata</i> Hartmann-Schröder, 1965	13	2	branched	>1	?	?	17	Hartmann-Schröder, 1965
<i>A. hydrothermalis</i> (Reuscher et al., 2012)	15	3	branched	1	no	no	19	Reuscher, Fiege, Wehe, 2012
<i>A. leptobranchia</i> Caullery, 1944	17	2	branched	?	?	?	?	Caullery, 1944
<i>A. affinis</i> Malmgren, 1866	17	3	branched	6	yes	yes	17	present study
<i>A. alcornis</i> Fauvel, 1909	17	3	branched	?	?	?	17	Fauvel, 1909
<i>A. antarctica</i> Monro, 1936	17	3	branched	10	yes	yes	17	Monro, 1936
<i>A. edwardsii</i> (de Quatrefages, 1865)	17	3	branched	9	yes	yes	17	Fauvel, 1927; present study
<i>A. jucunda</i> (Kinberg, 1866)	17	3	branched	?	?	?	?	Kinberg, 1866
<i>A. malayensis</i> Caullery, 1944	17	3	branched	?	?	?	?	Caullery, 1944
<i>A. marchilensis</i> Hartmann-Schröder, 1965	17	3	branched	9	yes	yes	?	Hartmann-Schröder, 1965
<i>A. ramosissima</i> Marenzeller, 1884	17	3	branched	6	yes	yes	17	Marenzeller, 1884;
<i>A. robusta</i> Johnson, 1901	17	3	branched	9	yes	yes	17	Imajima, Hartman, 1964
<i>A. sibogae</i> Caullery, 1944	17	3	branched	?	?	?	?	Hilbig, 2000
<i>A. variabilis</i> (Risso, 1826)	17	3	branched	6	yes	yes	17	Caullery, 1944
<i>A. cirrata</i> (Müller, 1776)	17	3	cirriform	7	no	no	17	Fauvel, 1927; present study
<i>A. aff. cirrata</i>	17	3	cirriform	7	no	no	17	present study
<i>A. "cirrata" sensu Hartman, 1969</i>	17	3	cirriform	>3	yes	yes	17	Hartman, 1969

Table 1 (continued).
Table 1 (продолжение).

species	TC	branchiae		nephridia		uncini in double row to chaetiger	source
		pairs	shape	pairs	on S4		
<i>A. fauveli</i> Jirkov et al., 2018	17	3	cirriform	4	no	no	Jirkov et al., 2018
<i>A. kerguelensis</i> McIntosh, 1876	17	3	cirriform	7	yes	yes	present study
<i>A. oculata</i> Hesse, 1917	17	3	cirriform	4	no	no	Imajima, Hartman, 1964; present study
<i>A. rzhavskiyi</i> sp.n.	17	3	cirriform	4	no	no	present study
<i>A. gracilis</i> (Grube, 1860)	17–19	2	branched	9	no	no	present study
<i>A. iihya</i> Hutchings et Glasby, 1988	18–20	2	branched	10	no	no	Nogueira, Hutchings, 2007
<i>A. haematina</i> (Grube, 1872)	18–19	2	branched	?	?	?	Grube, 1872
<i>A. scylla</i> (Savigny, 1822)	19–20	2	branched	9	no	no	Savigny, 1822; McIntosh, 1922
<i>A. carawa</i> Nogueira et Hutchings, 2007	19–22	2	branched	17	no	no	Nogueira, Hutchings, 2007
<i>A. groenlandica</i> Malmgren, 1866	19	3	branched	11–13	yes	yes	present study
<i>A. undevigintipes</i> (Choi, Kim, Yoon, 2020)	19			13	yes	yes	Choi, Kim, Yoon, 2020
<i>A. bruneocomata</i> (Ehlers, 1887)	22–30	2	branched	10–23	no	no	Londoño-Mesa, 2009
<i>A. kuehlmanni</i> Arvanitidis et Koukouras, 1995	25–29	2	branched	11–13	no	yes	Arvanitidis et Koukouras, 1995
<i>A. buzhinskajae</i> sp.n.	21–22	3	branched	12–13	yes	yes	present study
<i>A. chloraema</i> (Schmarda, 1861)	22	3	branched	?	?	?	Schmarda, 1861

Table 1 (continued).
Table 1 (продолжение).

species	TC	branchiae		nephridia		uncini in double row to chaetiger	source
		pairs	shape	pairs	on S4		
<i>A. figulus</i> (Dalyell, 1853)	23–27	3	branched	ca. 16	yes	24–31	present study
<i>A. grayi</i> Malmgren, 1866	21	3	branched	9–10	yes	21	present study
<i>A. pachyderma</i> Hutchings et Glasby, 1988	22–24	3	branched	7	yes	39–43	Hessle, 1917; Hutchings, Glasby, 1988
<i>A. rubra</i> (Risso, 1826)	22–24	3	branched	13–15	yes	almost last	present study
<i>A. vigintipes</i> (Grube, 1870)	20–22	3	branched	6	yes	almost last	Grube, 1870; Marenzeller, 1884; present study
<i>A. attenuata</i> Moore, 1907	25	3	branched	?	?	25	Moore, 1907
<i>A. sp. A</i> Kritzler, 1984	29–32	3	branched	?	?	end of thorax	Kritzler, 1984
<i>A. glasbyi</i> Londoño-Mesa et Carrera-Parra, 2005	39	3	branched	8	yes	39	Londoño-Mesa, Carrera-Parra, 2005
<i>A. ventricosa</i> Bosc, 1802	50?	3	branched	?	?	?	Bosc, 1802
<i>A. brunnea</i> (Stimpson, 1854)	?	3	branched	?	?	?	Stimpson, 1854

Species are sorted in ascending order of the number of TC, then by the number of pairs of branchia, then by the shape of branchia. Species having these three characters similar are sorted alphabetically.

lis without any argumentation. The original description has no data on the number of segments and branchiae. The taxonomic status of species is not clear.

I agree with Nogueira (2008) that *Terebella ornata* Leidy, 1855 (type locality USA Rhode Island) seems not to belong to *Amphitrite*, due to the presence of uncini with shafts and branchiae that distinctly differ from other species of *Amphitrite*, resembling those of some *Axionice* sensu Jirkov & Leontovich (2017). However, as I have not seen specimens of this species and existing descriptions are not complete, I cannot come to any conclusion; it does not seem reasonable to change the generic diagnosis to accommodate *T. ornata*.

Terebella viminalis Grube, 1855 (type localities Trieste and Palermo, Italy) was synonymised by Fauvel (1909) with *Amphitrite variabilis* without any argumentation. According to the original description, *T. viminalis* has three pairs of branchiae and 16 TC, while *A. variabilis* has 17 TC; its taxonomic status is not clear.

Several other species assigned to *Amphitrite* (some were initially described as *Terebella* Linnaeus, 1767) have been described from European waters in the XIX century (Delle Chiaje, 1828; Grube, 1838, 1855, 1860, 1863; Claparède, 1870). However, their original descriptions usually lack sufficient detail even to be sure about generic affiliation; they may be species of *Amphitrite*, *Terebella* or even *Eupolyornia* Verrill, 1900. These three genera differ in the shape of their notochaetae: straight serrated in *Amphitrite* (Figs 4D–G, 7A–C, 9E, 10A–C, 14A–C, 16A–C, 19D, 20E), geniculated serrated in *Terebella* (Fig. 27) and smooth in *Eupolyornia* (Fig. 30D), *Amphitrite*, *Terebella* (Fig. 26) and *Eupolyornia* (Fig. 29) are similar in external morphology, the only difference: *Amphitrite* (Figs 3B, 4B, 6B, 9B, 11B, 13B, 15B, 18B, 19B, 20B, 23D) and *Terebella* (Fig. 28B) have distinct ventral pads, limited to ventral surface, while *Eupolyornia* has ventral pads extending laterally and with blurred borders (, but this difference is overlooked earlier. Also these three genera have avicular uncini, but *Eupolyornia*

differ by first row of thees above main fung: it consist from numerous much smaller teeth in *Amphitrite* (Figs 1, 3E, F, 4H, 5, 7D, E, 10D–E, 11E, 13C, D, 15D, E, 17D, E, 18C, 19D, 20E, G, 22, 25D, E) and *Terebella* (Fig. 30A–D) and only one or two comparatively big tooth in *Eupolyornia* (Fig. 31A–C, E). However, such details are totally absent in original descriptions published before the XX century, so the taxonomic status of these species cannot be solved without examination of types.

Discussion of species ranges

Species range is a good character to assist with identification. Taxonomically similar species may have different, usually complimentary, ranges. Usually, a species' range lies within a limited suite of ecological characters; for example, it is unlikely that the same species inhabits both intertidal and abyssal zones. *A. cirrata* provides a good example. Previously, the species range was believed to include shallow Arctic and Mediterranean and deep Atlantic waters but our investigation shows that, in reality, *A. cirrata* s.str. inhabits only shallow Arctic and boreal waters, while the deep Atlantic and shallow Mediterranean are inhabited by two other, previously overlooked, species. A similar species distributional pattern probably produced the *A. affinis* – *A. edwardsii* – *A. variabilis* and shallow *A. figulus* – *A. rubra* groups: Arctic-boreal-Mediterranean and boreal-Mediterranean species respectively. All species of these groups were reported from Mediterranean waters, but I failed to find more northern species in collections from the Mediterranean (specimens identified as *A. affinis* in reality are *A. variabilis*), while Mediterranean species were common, so I consider reports of *A. affinis*, *A. edwardsii* and *A. figulus* from the Mediterranean to be based on misidentifications.

A. birulai provides a quite different example. The range of this species is wider than that of any other species of the genus. It is common in waters with reduced salinity (estuaries, the White Sea), while it is uncommon in water with normal salinity. In low salinity waters, biomes

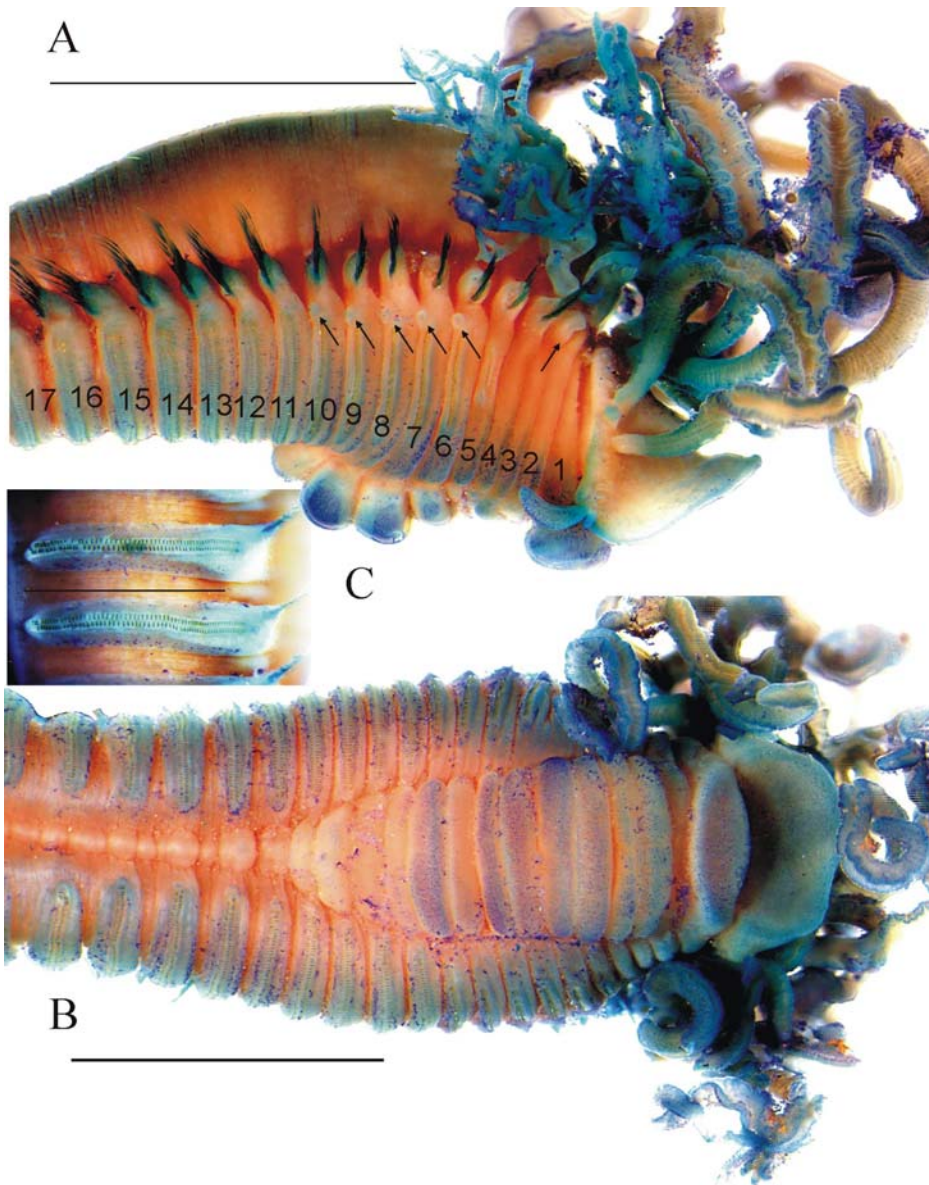


Fig. 27. *Terebella lapidaria* Linnaeus, 1767, external morphology. A — lateral view; B — ventral view; C — middle body segments. All MNCN 5684. Scale bars: A, B — 2 mm, C — 1 mm.

Рис. 27. *Terebella lapidaria* Linnaeus, 1767, external morphology. A — вид сбоку; B — вид с брюшной стороны; C — сегменты из середины тела. Все фото MNCN 5684. Масштаб: A, B — 2 мм, C — 1 мм.

are not in normal conditions, so *A. birulai* may be characterized as cenophobe species (Razumovskyi, 1999), which would explain the greater variation in some characters (the num-

bers of TU and segments with neuropodia with uncini in double rows, tube structure, presence/absence of eyespots) of this species compared to other *Amphitrite*.

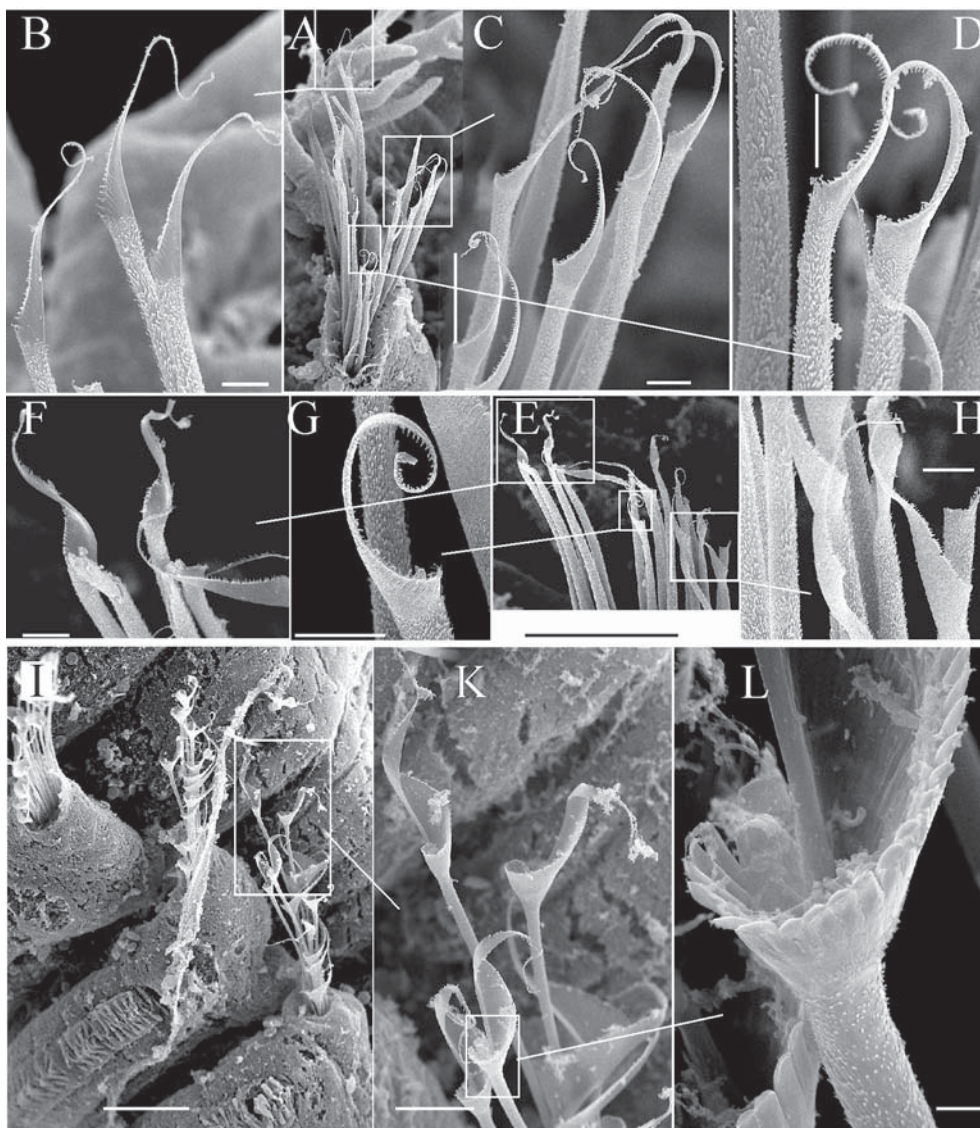


Fig. 28. *Terebella lapidaria* Linnaeus, 1767, notochaetae. A–D — TC1: C, D — details of A; E–H — TC15 F, H — details of E; I–L — TC near pygidium, K — details of I, L — details of I MNCN 5684. Scale bars: A, E, I — 0.1 mm, B–D, F–I — 10 μ m, K — 30 μ m, L — 3 μ m.

Рис. 28. *Terebella lapidaria* Linnaeus, 1767, нотохеты. A–D — TC1: C, D — детали A; E–H — TC15 F, H — детали E; I–L — TC вблизи пигидиума, K — детали I, L — детали I MNCN 5684. Масштаб: A, E, I — 0,1 мм, B–D, F–I — 10 мкм, K — 30 мкм, L — 3 мкм.

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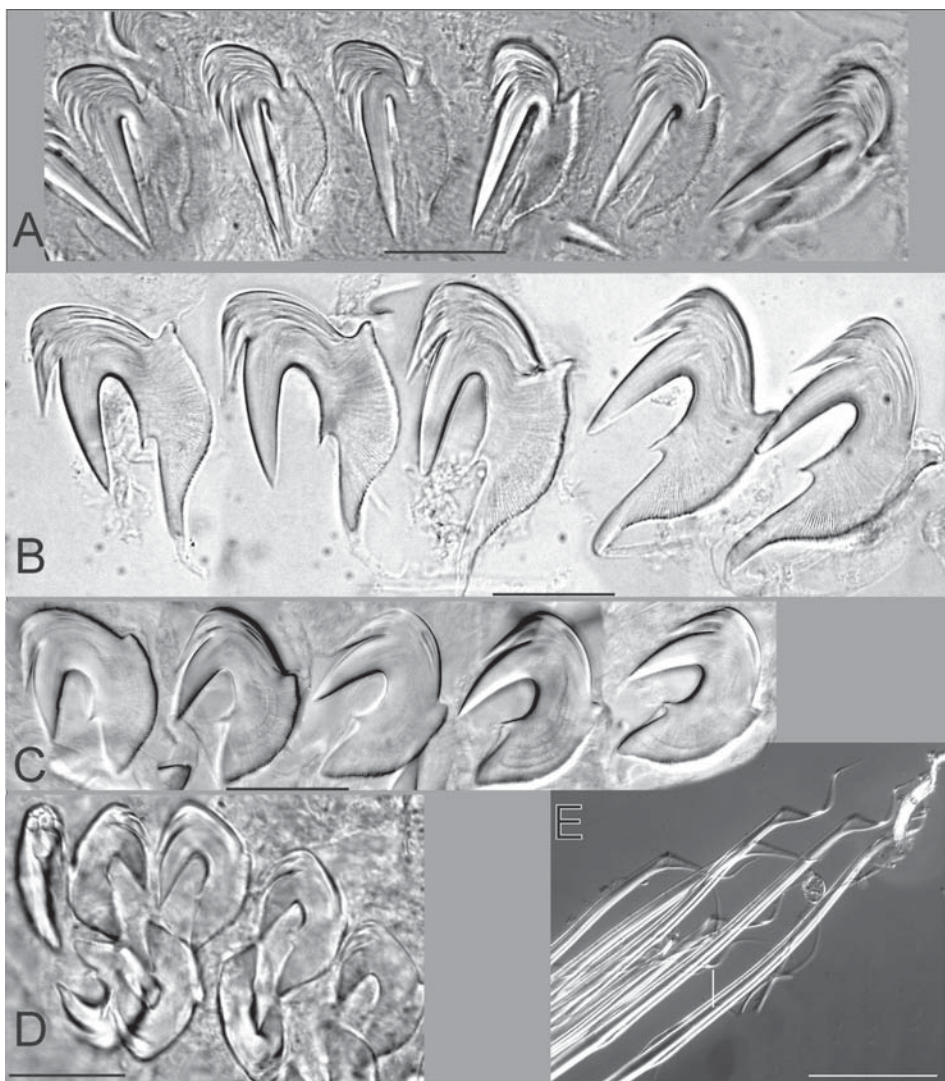


Fig. 29. *Terebella lapidaria* Linnaeus, 1767, uncini. A — TU1; B — TU2; C — TU13; D — TU50; E — TC2. All MNCN 5684. Scale bars: A–D — 25 μ m, E — 0.1 mm.

Рис. 29. *Terebella lapidaria* Linnaeus, 1767, uncini. A — TU1; B — TU2; C — TU13; D — TU50; E — TC2. Все MNCN 5684. Масштаб: A–D — 25 мкм, E — 0,1 мм.

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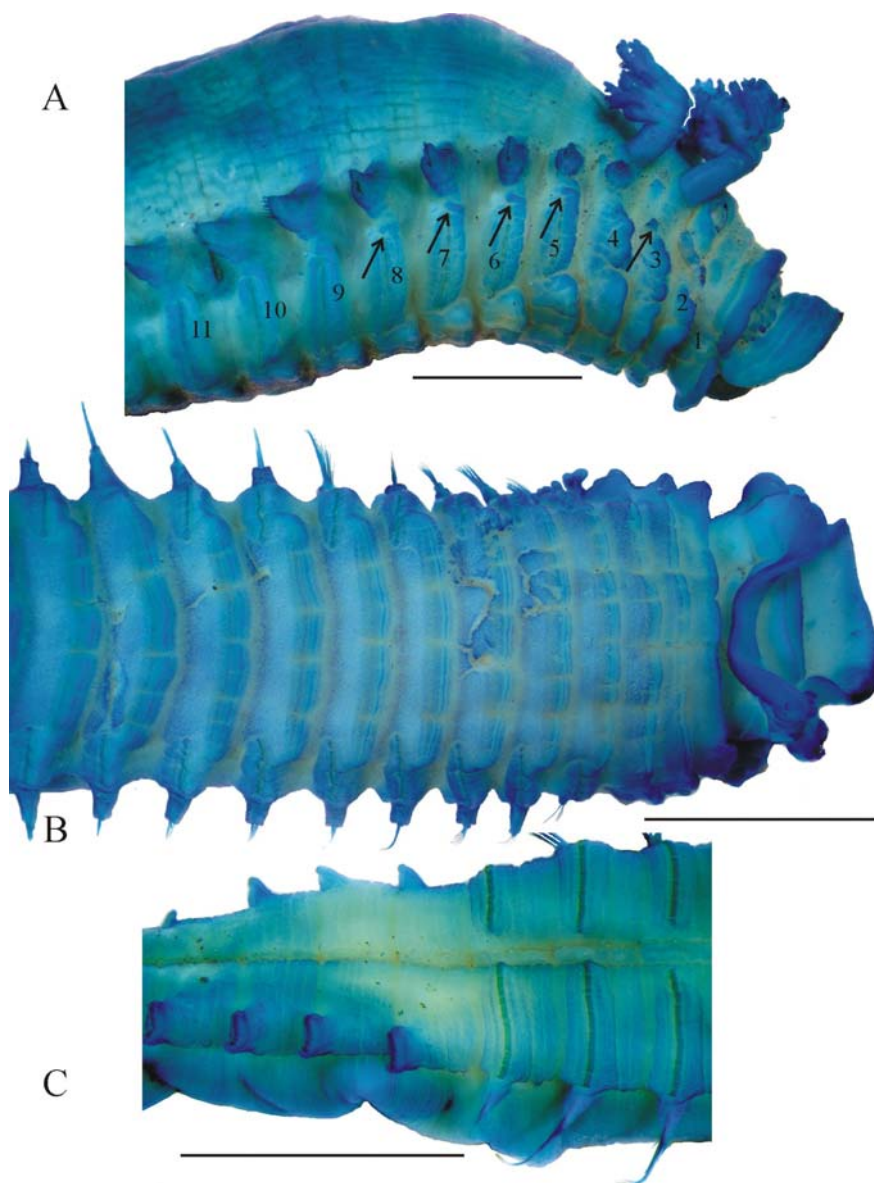


Fig. 30. *Eupolymnia nesidensis* (delle Chiaje, 1828), external morphology. A — lateral view, MNCN474; B — ventral view, MNCN476; C — thorax–abdomen border, MNCN476. Scale bars 2 mm.

Рис. 30. *Eupolymnia nesidensis* (delle Chiaje, 1828), внешняя морфология. А — вид сбоку, MNCN474; В — вид с брюшной стороны, MNCN476; С — граница торакса и живота, MNCN476. Масштаб 2 мм.

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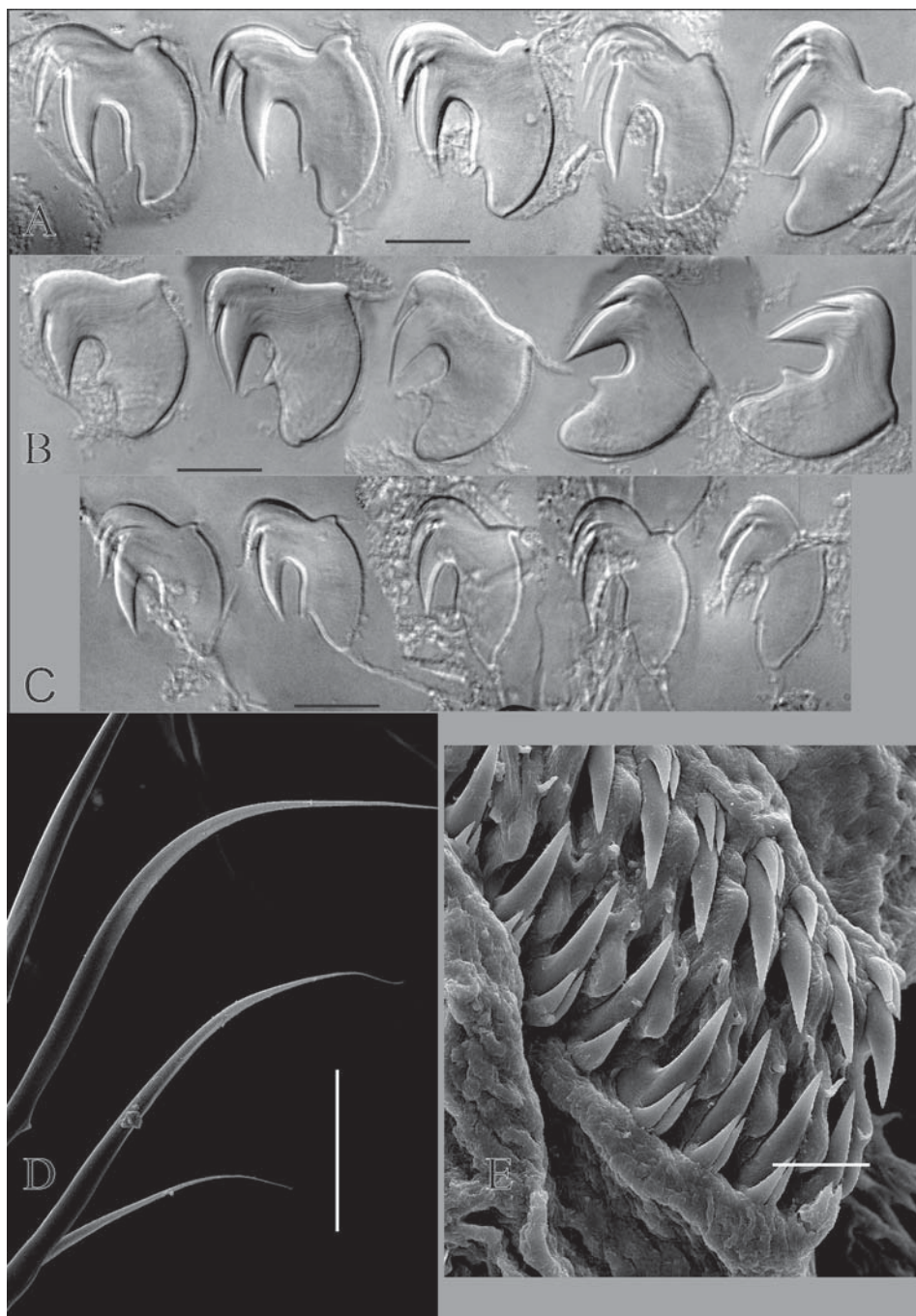


Fig. 31. *Eupolymnia* chaetae. A–D — *Eupolymnia nesidensis* (delle Chiaje, 1828), MNCN476: A — uncini TU1, B — uncini TU11, C — uncini AU15; D — tip of notochaeta; E — *Eupolymnia nebulosa* (Montagu, 1818), thoracal uncini. Scale bars: A–C — 20 μ m, D — 0.1 mm, E — 30 μ m.

Рис. 31. *Eupolymnia* щетинки. A–D — *Eupolymnia nesidensis* (delle Chiaje, 1828), MNCN476: A — uncini TU1, B — uncini TU11, C — uncini AU15; D — вершины нотохет; E — *Eupolymnia nebulosa* (Montagu, 1818), торакальные uncini. Масштаб: A–C — 20 мкм, D — 0,1 мм, E — 30 мкм.

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