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Revision of *Ampharete* (superspecies *finmarchica*) (Annelida: Ampharetidae)

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ABSTRACT. Illustrated descriptions of eight taxa of species rank of *Ampharete* similar to *Ampharete finmarchica*, five based on type materials, including *Ampharete britayevi* sp.n., others based on topotypes. A key for their identification is provided. Based on morphological data, it is proposed to erected these species as *Ampharete* (superspecies *finmarchica*). Of the 8 species in the superspecies, seven inhabit the Northern Pacific and one (*A. kerguelensis*) the Southern Hemisphere, therefore, it is likely that this group is of North Pacific origin, different species of which arose in different biomes.
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KEY WORDS: North Pacific, identification key, re-description, new species.

Ревизия *Ampharete* (superspecies *finmarchica*) (Annelida: Ampharetidae)

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РЕЗЮМЕ. Даны иллюстрированные описания восьми таксонов видового ранга *Ampharete* сходных с *Ampharete finmarchica*, пяти на основе типовых материалов, в том числе *Ampharete britayevi* sp.n. и трёх на основе топотиповых материалов и ключ для их определения. Основываясь на морфологии, предлагается классифицировать эти виды как *Ampharete* (superspecies *finmarchica*). Из восьми видов группы семь обитают в северной части Тихого океана, а один (*A. kerguelensis*) — в Южном полушарии, поэтому вполне вероятно, что эта группа имеет северотихоокеанское происхождение, разные виды которого возникли в разных биомах.
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KEY WORDS: север Тихого океана, ключ для определения, переописание, новый вид.

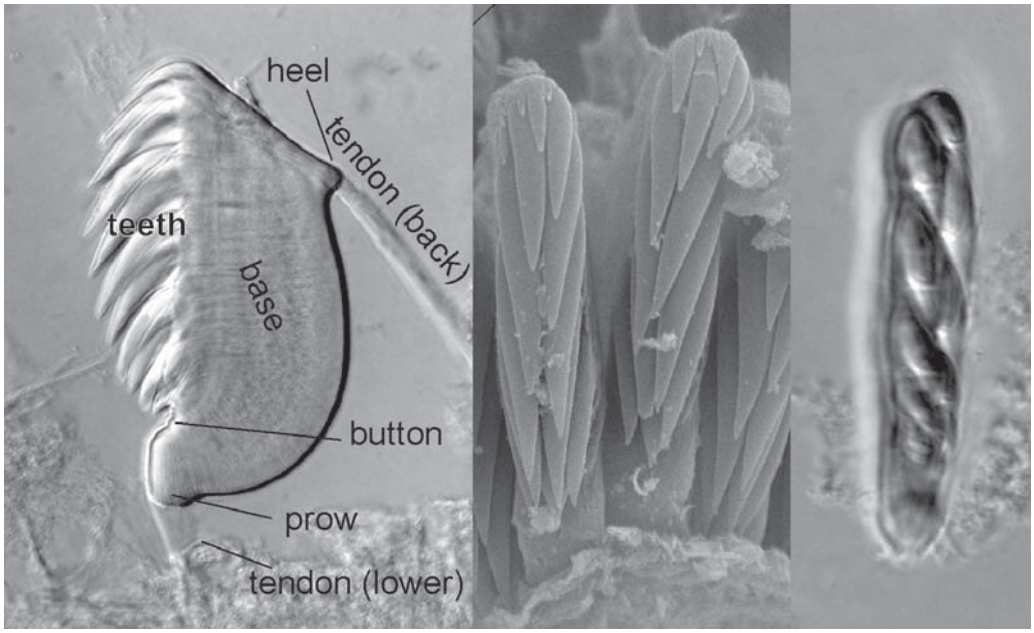

Fig. 1. Uncini and terminology of uncinal parts used in this paper.
Рис. 1. Неврохеты и термины, используемые для их описания в этой статье.

Introduction

Ampharetids have a worldwide marine distribution from the intertidal to abyssal depth and even a few (two or three) species are restricted to freshwater. *Ampharete* is the biggest genus within the family Ampharetidae. A total 55 nominal (43 accepted) taxa (Read, Fauchald, 2022a), from the about 300 known in the family, but this list includes some obvious mistakes, already rejected synonyms as valid species and vice versa so the number of valid species is uncertain even if we do not take into account the still undescribed species.

Moreover, as it is shown below there are conflicting data in the literature even regarding the volume of valid species. As a result, some records, especially of the most widespread *Ampharete finmarchica*, refer to undoubtedly other species. Therefore, as a part of an ongoing revision of the family, an audit of species similar to *A. finmarchica* was conducted and re-described, the key to their identification is provided and species ranges and biogeography of them are discussed.

Materials and methods

The study has been based mainly on the collections of Zoological Institute RAN, P.P. Shirshov Institute of Oceanology, Department of General Ecology and Hydrobiology of M.V. Lomonosov Moscow State University and Zoological Museum of M.V. Lomonosov Moscow State University; studied specimens are listed in species descriptions (the number of specimens is given in brackets) and in Supplement, ranges of most numerous species also mapped.

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, M.V. Lomonosov 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 neuropodium. For scanning electron microscopy (SEM), specimens stored in 70–75% ethanol

were placed in 100% ethanol, transferred to100% acetone then critical point dried, using CO_2 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.

Abbreviations and terminology

ORGANISATIONS.

DGEH — Department of General Ecology and Hydrobiology M.V. Lomonosov Moscow Lomonosov State University, Russia; IO RAN — P.P. Sirshov Oceanological Institute of the Russian Academy of Science, Moscow, Russia; NHM — National History Museum, London; ZIN — Zoological Institute of the Russian Academy of Science, St-Petersburg, Russia; ZMHU — Zoological Museum Hamburg University; ZMUM — Zoological Museum of M.V. Lomonosov Moscow State University.

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 is shown in Fig. 1.

Base — plate to which other parts are attached; Button — short projection of the upper part of the base below the main fang; Heel — the posterior part of the base at the footing of the neck, forming angle to which back tendon is attached; Prow — anterior part of the uncinal base; Paleae — notochaetae of S2. Many authors accept only enlarged chaetae as paleae. However, there is a cline in development of S2 notochaetae (illustration see Jirkov, 2001: 440) and "enlarged" is rather subjective and the source of confusion. See also Jirkov (2011).

Results

Ampharetidae Malmgren, 1866
Ampharete Malmgren, 1866

Type species: *Ampharete grubei* Malmgren, 1866.

synonyms:

Asabellides Annenkova, 1929; type *Sabellides sibirica* Wiren, 1883 by monotypy.

*Paramphar*ete Hartman, 1967; type *Paramphar*ete *weddellia* Hartman, 1967 by original designation.

Pseudosabellides Berkeley et Berkeley, 1943; type *Pseudosabellides littoralis* Berkeley et Berkeley, 1943 by original designation.

*Pteramphar*ete Augener, 1918; type *Pteramphar*ete *luederitzi* Augener, 1918 by monotypy.

Sabellides Milne Edwards in Lamarck, 1838; type *Sabella octocirrata* Sars, 1835 by monotypy.

? *Amythasides* Eliason, 1955; type *Amythasides macroglossus* Eliason, 1955 by monotypy.

DIAGNOSIS. Prostomium trilobed, middle lobe anteriorly rounded. A pair of nephridial papillae mid-dorsally posterior to branchiae, usually easily visible. Neuropodia of two types, all thoracic and AU1 and AU2 tori, remaining abdominal neuropodia pinnuli. Uncini pectinate, i.e. with series of equal teeth arranged like a comb (Fig. 1), in general, uncini are similar throughout the body, without a sharp change when changing the type of neuropodial type. Modified noto- and neuropodia absent.

REMARKS. 1. Proposed by me synonymy of *Ampharete* presently is discussed earlier (Jirkov, 1989, 1994, 2001, 2011) and mainly already widely accepted.

2. Following characters usually are included in generic diagnosis, but due variation within genera can't be part of the diagnosis. Buccal tentacles pectinate. Four (seldom 3) pairs of branchiae. Paleae from huge to absent. Number of AU usually constant for species (usually 12 or 13), but if it exceeds 14, then individual variation appears, the more variation the more AU number.

3. Within *Ampharete* the number of AU with tori is constant (always AU1 and AU2), despite the number of thoracic segments varies (can be 11 or 12). In other words, the total number of segments with tori (thoracic + abdominal segments) varies. Contrary within some other ampharetid genera, for example *Lysippe* Malmgren, 1866, the total number of segments with tori is constant, so the number of AU with tori varies follows the number of thoracic segments varies.

Within the genus, several groups of species are outlined. Species of such group are characterized by perfectly developed paleal chaetae sharply narrowed into slim filiform tip. Tips of paleal chaetae appear to be stout and curved under normal magnification. If not broken of, a filiform tip can be observed only under high magnification (Figs 4A–C, 8D, E, 12B–D, 15E–G, 21B, 24D). It is important to underline that only shape of paleal tips not the size and width of paleal chaetae is important. Paleal chaetae of other species of the genus, if present, even they are much thicker the most developed notochaetae, slowly tapering (Fig. 2). Within paleal bundle smallest (youngest?) chaetae can slightly differ. Especially this difference sharp in species with paleal chaetae slowly tapering, because only tips are visible outside a body (see photo Jirkov, 2018, Fig. 9A). It can confuse, especially when fully developed chaetae are broken,

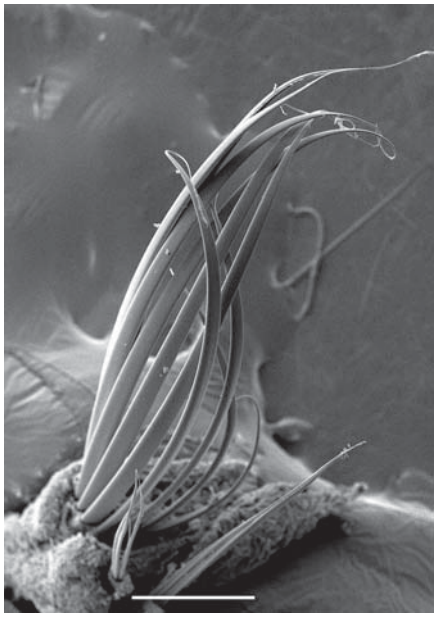

Fig. 2. Paleae *Ampharete* aff. *lindstroemi* Malmgren in Hessle, 1917.
Scale 0.3 mm.
Рис. 2. Опахала *Ampharete* aff. *lindstroemi* Malmgren in Hessle, 1917.
Масштаб 0,3 мм.

that is why Krüger *et al*. (2022) mentioned two types of paleal chaetae of *Ampharete acutifrons.*

Also, all species of *Ampharete* (superspecies *finmarchica*), except *A. goesi* have 13 AU — the number, no longer found within the genus (most *Ampharete* have 12 AU) and all species with known pygidium have two cirri of variable length (probably depending of fixation), while many other *Ampharete* lack such cirri. All of these characters are independent and rigidly connected. It is noteworthy in this respect the history of clarifying the taxonomic position of *A. seribranchia* described below. For establishing of subgenera it is necessary to made revision of the whole genus. At the same time, the considered aggregate of species is clearly isolated and therefore can be distinguished as a superspecies *Ampharete* (superspecies *finmarchica*). The superspecies rank is not often used in taxonomy of Polychaeta and never used in *Ampharete*. The usage of names of aggregates of species is regulated by Article 6.2 of ICZN.

Data on genetics are currently completely insufficient for use in taxonomy of the genus. In Genbank on 05/07/2022 there are 57 data on *Ampharete*. Of these, only 34 are identified to the species level. They belong to seven species, and only one species of the them (*A. finmarchica* itself) belong to considered *Ampharete* (superspecies *finmarchica*).

The superspecies includes eight taxa of species group. Whenever possible types have been investigated (species with investigated types are marked by *).

1. **Ampharete britayevi* sp.n.
2. *Ampharete eupalea* Chamberlin, 1920
3. *Ampharete finmarchica* (Sars, 1865) as *Amphicteis*
4. *Ampharete goesi* Malmgren, 1866
5. **Ampharete goesi brazhnikovi* Annenkova, 1929
6. **Ampharete kerguelensis* McIntosh, 1885
7. **Ampharete kudenovi* Jirkov, 1994
8. **Ampharete longipaleolata* Uschakov, 1950

About two thousand investigated specimens, including those collected close to the type localities of *A. finmarchica*, and its synonym *A. arctica* agree well with description of types by Holthe (1986a). Topotypes of *A. goesi* agree well with original description (types lost). Unfortunately, in the present circumstances investigation of type *A. eupalea* deposed in Canada is not possible.

4. *Ampharete labrops* Hartman, 1961 according to Banse (1979) and Hilbig (2000) has 13 AU. Unfortunately both did not described tips of paleae, so is this species the member of *Ampharete* (superspecies *finmarchica*) or not is not clear. Also the number of abdominal uncinigers is not mentioned in the original description and later redescription. Investigation of materials from Pacific North America is necessary.

Ampharete britayevi **sp.n.**
Fig. 3, 4.

MATERIAL. Holotype 1 ex. (DGEH), Vitjaz 10.1539 74 m 18.6.1952 62°13′ N 179°30′ E.

ADDITIONAL MATERIAL: *Ampharete seribranchiata* Treadwell, 1926: 7–8, fig. 15–17; type Cat. No. 1634, American Museum Natural History; type locality (according to the type's label): the Bering Straits Bet., King Id. and the two Diomedes.

DESCRIPTION. The single specimen 35 mm long, but not complete posteriorly. The middle lobe of the prostomium is rounded anteriorly, twice as long as the width. Buccal tentacles have not been preserved. Paleal chaetae much longer and thicker than the most developed notochaeta, directed forward, they go beyond the front edge of the prostomium. There are 42 paleal chaetae and they form 1,5 turns (Fig. 3B). The tip of the bristles pulled into a relatively long tip, much longer than in other species of the genus, this tip does not break off. Branchostyles missing. The attachment points of three pairs of branchostyles arranged in one transverse line, the

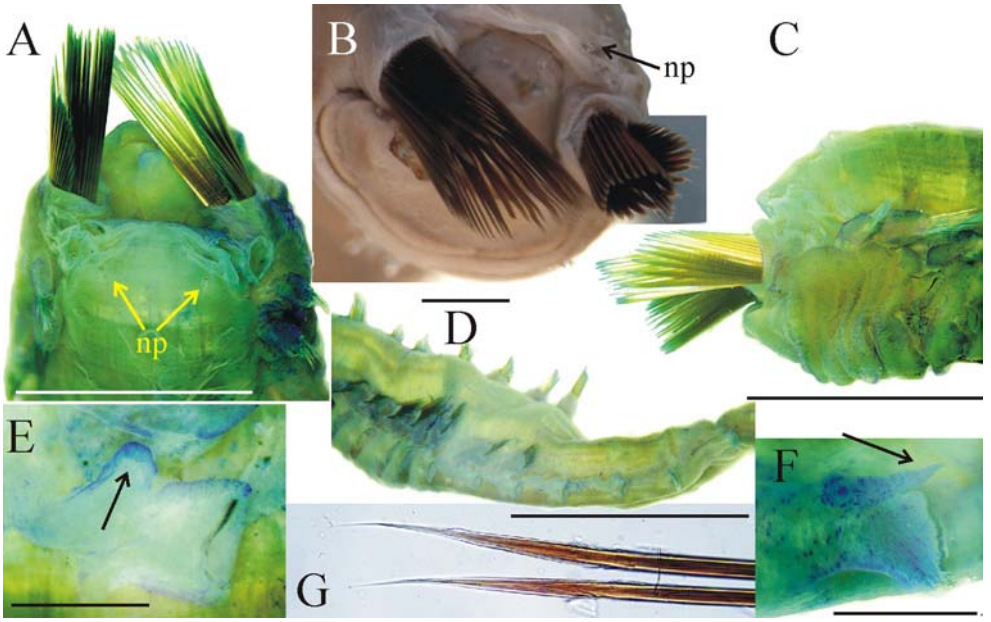

Fig. 3. *Ampharete britayevi* sp.n., external morphology.
A — dorsal view. np — nephridial papillae, B — antero-dorsal view, C — lateral view, D — thorax–abdomen junction, lateral view of posterior thorax and anterior abdomen, E — thoracic segment, pointed neuropodial lobe, F — abdominal segment pointed neuropodial cirrus, G — notochaetae TC10. Scales: A, C — 5 mm, other — 1 mm. Vitjaz 10.1539.
Рис. 3. *Ampharete britayevi* sp.n., внешняя морфология.
A — дорсальный вид. np — нефридиальные папиллы, B — антеро-дорсальный вид, C — вид сбоку, D — граница торакса и абдомена, вид сбоку последних торакальных и первых абдоминальных сегментов, E — торакальный сегмент, стрелка показывает лопасть невроподии, F — абдоминальный сегмент, стрелка показывает невроподиальный усик, G — нотохеты TC10. Масштаб: A, C — 5 мм, другие — 1 мм. Витязь 10.1539.

fourth behind the middle of the three, their branchophores clearly connected to the TC2 notopodia. A very wide gap between the groups of gills, its width greater than the diameter of the branchophore. Nephridial papillae caudal to the inner pair of gills, small (Fig. 3A). 14 TC, 12 TU. The only specimen at hand have incomplete abdomen with 7 AU, but highly likely that species have 13 AU as most species of *Ampharete* (*finmarchica*). Posterior thoracic neuropodia with additional lobe (Fig. 3E). Rudimentary notopodia small, abdominal neuropodia with short but distinct neuropodial cirri (Fig. 3F). Neuropodia of the thorax, AU1 and AU2 tori, the rest — pinnuli. The ventral surface up to and including TU9 transformed into ñontinuous glandular ventral shields extending from notopodia to notopodia. No ventral shield on TU10, in its place there is a thickening that occupies the entire ventral abdominal surface of the anterior half of the segment. Rudimentary notopodia of the abdomen practically absent. The notochaetae in two rows: the front ones are an order of magnitude thinner and several times shorter than the rear ones, the former narrow equally bilimbate. Uncini (Fig. 4) with two rows of teeth, usually up to eight in thorax and about six in abdomen. Thoracic and abdominal generally similar. The tube unknown.

REMARKS. Initially I thought that this species is *Ampharete seribranchiata* Treadwell, 1926 because the original description clearly states "The posterior region has 13 uncinigerous somites without capillary setae" and "On either side of the base of the peristomium is a band of 30 or more golden-yellow paleae arranged in a crescent" (Treadwell, 1926: 7) and the type locality is closed to our finding. As only species of *Ampharete* (*finmarchica*) have 13 AU *A. seribranchiata* as a member of this superspecies should have characteristic paleal chaetae. But when Senior Museum Specialist of AMNH Lily Berneker which I asked to investigate the type took photos and investigated paleal chaetae it turned out that the paleal chaetae taper into a threadlike vertex (Fig. 5), 33 paleal chaetae on one side and 29 or 30 on the other side. It cannot be at the same time 13 AU and slowly tapering paleal chaetae, because it cannot be never, I asked her to count the number of AU and it turned out that there are only 12 AU, not 13 AU.

Fig. 4. *Ampharete britayevi* sp.n. Uncini.
A — TU2, B — AU2, C — AU7. All scales are equal — 10 μm.
Рис. 4. *Ampharete britayevi* sp.n. Неврохеты.
A — TU2, B — AU2, C — AU7. Масштаб везде один — 10 μm.

Fig. 5. *Ampharete seribranchiata* Treadwell, 1926, paleae of holotype.
Рис. 5. *Ampharete seribranchiata* Treadwell, 1926, опахала голотипа.

Both these characters (shape of paleal chaetae and the number of AU) place *A. seribranchiata* outside *Ampharete* (*finmarchica*).

Berkeley, Berkeley (1942) considered this species as a junior synonym of *A. eupalea*. This synonymy was accepted by Hartman (1959) and Holthe (1986b), however, no one gave any argumentation and now it is obvious that it is not correct.

DIFFERENTIAL DIAGNOSIS. Two characters differ the new species from presently know and allow to describe the new species despite only one incomplete specimen is at hand.

1. *A. eupalea* has the largest number of paleal chaetae among known species of *Ampharete* (*finmarchica*), but it does not exceed 32 in 170 investigated specimens, while the new species has 42, it is far beyond individual variation of *A. eupalea* (see below). This number of paleal chaetae exceeds not only those of all other species of the group but probably even the family.

Fig. 6. Temir Alanovich Britaev.
Рис. 6. Темир Аланович Британев.

2. Presence of neuropodial cirri. Cirri are absent in other species of *Ampharete* (*finmarchica*), but it is not seldom character among other *Ampharete* outside the group.

RANGE. Known only from the type locality. Upper sublittoral. Probably similar to *A. eupalea.*

ETYMOLOGY. The species is named after my friend Temir Alanovich Britaev Dr. Sci., professor, Head of the Laboratory of Morphology and Ecology of Marine Invertebrates, A.N. Severtzov Institute of Ecology & Evolution RAS (Fig. 6).

Ampharete eupalea Chamberlin, 1920
Fig. 7, 8.

Ampharete eupalea Chamberlin, 1920: 25, Pl. V, fig 6, 7; type: №31, Victoria Memorial Museum, Ottawa; type locality: 70°24′N 161°25′W, 16–18 m; Berkeley, Berkeley, 1942: 201.

MATERIAL. 28 samples (173 specimens). Supplement Table.

DESCRIPTION. Up to 48 mm long. The middle lobe of the prostomium anteriorly rounded, about twice as long as the width. The buccal tentacles numerous (several dozen), with two rows of pinnules. The attachment points of the paleal chaetae form 270°–360° (Fig. 7D); they much thicker than the most developed notochaeta, but about the same length, reaching the anterior edge of the prostomium only when the prostomium drawn in; paleal chaetae themselves often straightened and pressed to the surface of the body; a similar position very rare in other species. In each group 16–32 chaetae (95% have more than 20) (Fig. 9), the number of chaetae not size-depended when the size of the worm exceeds 8 mm. Branchostyles cirriform, smooth, not longer than the width of the body. The attachment points of all 4 pairs of branchostyles are arranged in one almost straight transverse line, only the third pair is slightly caudal. Median gap between the branchiae absent. The connection of the gills with the notopodia typical: 3rd from the outside connected to the TC2 notopodia, the inner ones connected to the TC1 notopodia. One pair of nephridial papillae behind the branchiae clearly visible. 14 TC, 12 TU, 13 AU. Thoracic neuropodia and the two first AU tori, the rest — pinnuli. The ventral surface up to and including TU9 transformed into ñontinuous glandular ventral shields extending from notopodia to notopodia. No ventral shield on TU10, in its place there is a thickening that occupies the entire ventral abdominal surface of the anterior half of the segment.

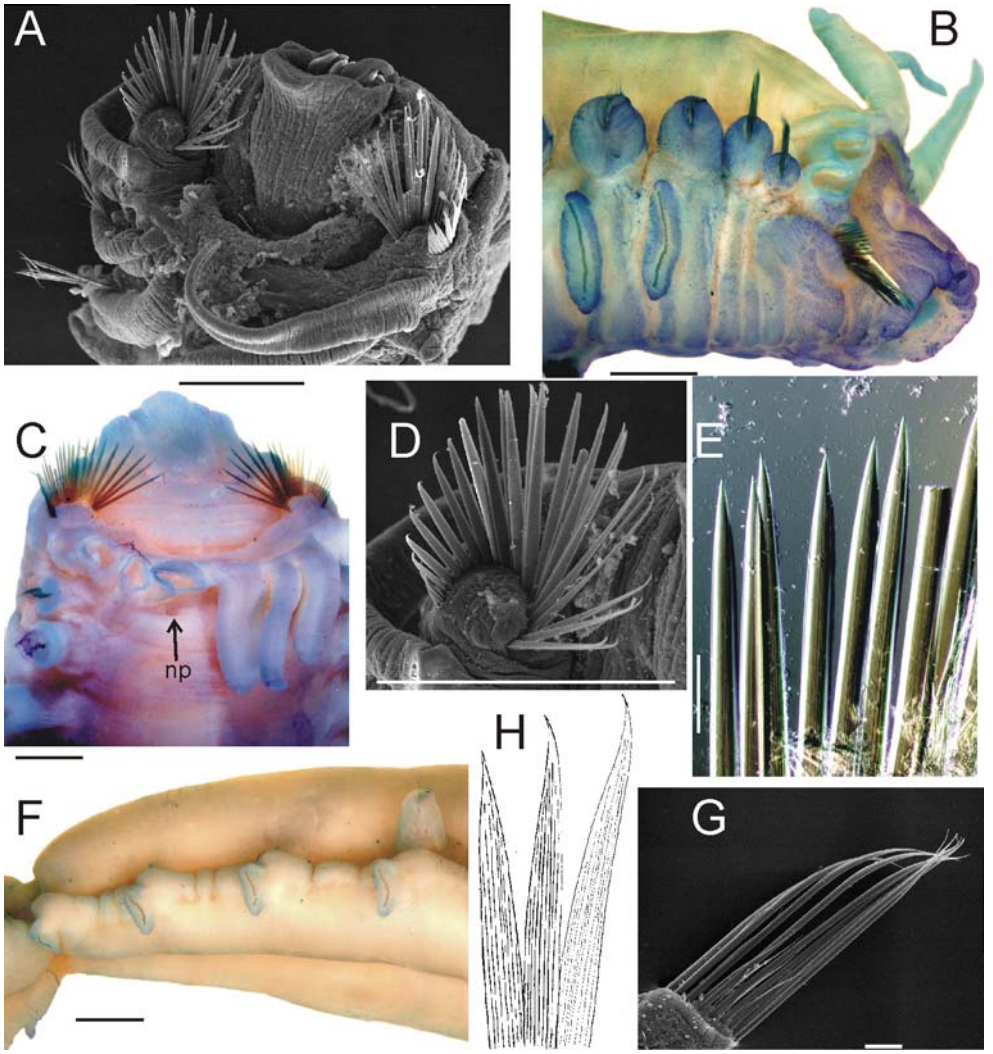

Fig. 7. *Ampharete eupalea* Chamberlin, 1920, external morphology.
A, C — dorsal view, B — lateral view; D — paleae total; E — tips of paleal chaetae; F — last TU and three first AU; G — notochaetae, H — paleal chaetae redrawn from the original description. Scales: A–D, F — 1 mm, E — 0.2 mm, G — 0.1 mm. A, D, G — Vitjaz 566; other — Vitjaz 570.

Рис. 7. *Ampharete eupalea* Chamberlin, 1920, внешняя морфология.
A, C — дорсальный вид, B — вид сбоку; D — общий вид опахал; E — вершины щетинок опахал; F — последний TU и три первых AU; G — нотохеты; H — щетинки опахал, перерисовано из оригинального описания. Масштаб: A–D, F — 1 мм, E — 0,2 мм, G — 0,1 мм. A, D, G — Витязь 566; прочие — Витязь 570.

Abdomen with small rudimentary notopodia, gradually disappearing caudally. Pygidium with 2 long lateral cirri and numerous short papillae. Thoracic and abdominal uncini with 5–6 teeth in two rows. The tube detritus, usually more or less densely encrusted with grains of sand with a diameter of about 0.25 mm.

REMARKS. I identify my specimens as this species despite the number of AU of holotype on which the original description is based is unknown as it is uncomplete posteriorly by: (1) the shape of the tips of the paleal chaetae (compare Fig. 7 D, E and H), (2) number of paleal chaetae (22–23 according original description), which is significantly greater

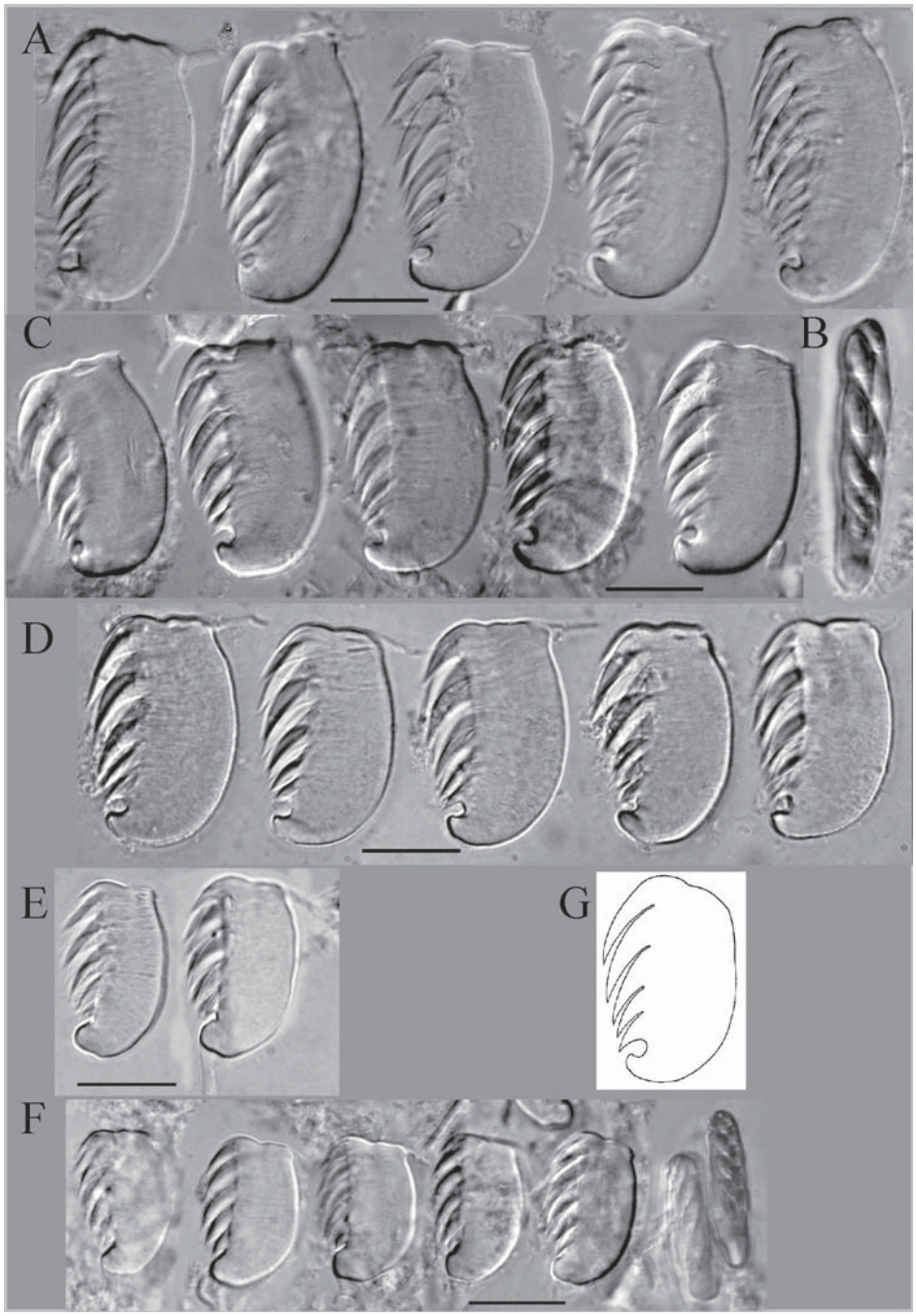

Fig. 8. *Ampharete eupalea* Chamberlin, 1920, uncini.
A, B — TU1; C — TU12; D — AU2; E — AU3; F — AU13; G — redrawn from the original description. All scales are equal — 20 μm. ZIN59.
Рис. 8. *Ampharete eupalea* Chamberlin, 1920, неврохеты.
A, B — TU1; C — TU12; D — AU2; E — AU3; F — AU13; G — из оригинального описания *A. eupalea*; H — из оригинального описания *A. seribranchiata* Treadwell, 1926. Масштаб везде один — 20 μm. ZIN59.

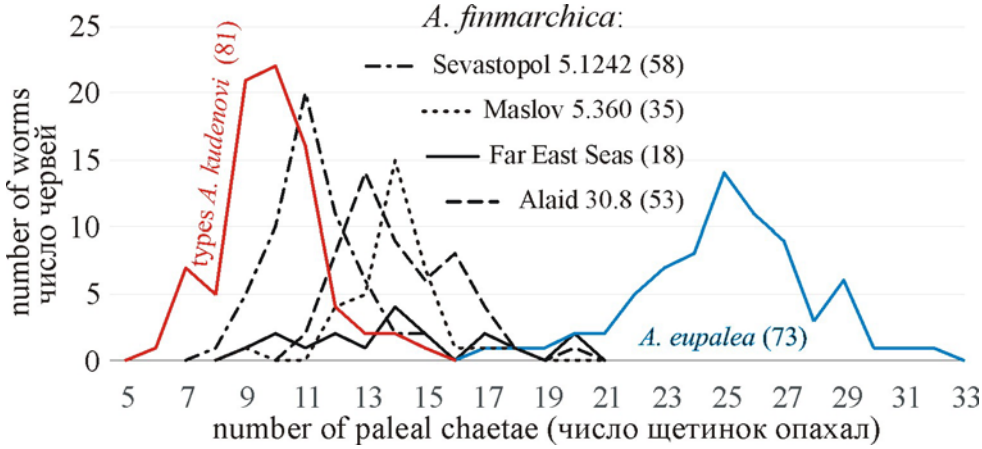

Fig. 9. *Ampharete eupalea* Chamberlin, 1920, *A. finmarchica* (Sars, 1865), and *A. kudenovi* Jirkov, 1994, variation of the number of paleal chaetae.
In parentheses number of specimens.
Рис. 9. *Ampharete eupalea* Chamberlin, 1920, *A. finmarchica* (Sars, 1865) и *A. kudenovi* Jirkov, 1994, изменчивость числа щетинок опахал.
В скобках число экземпляров.

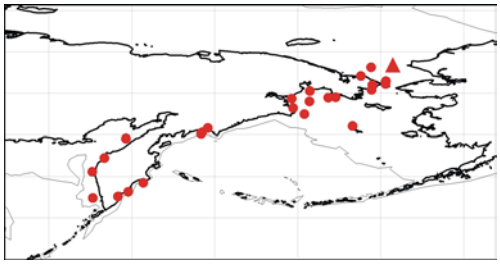

Fig. 10. Map showing sampling stations with specimens of *Ampharete eupalea* Chamberlin, 1920. 500 m isobath is shown, triangle — the type locality.
Рис. 10. Карта находок *Ampharete eupalea* Chamberlin, 1920.
Показана 500 м изобата, треугольник — типовая местность.

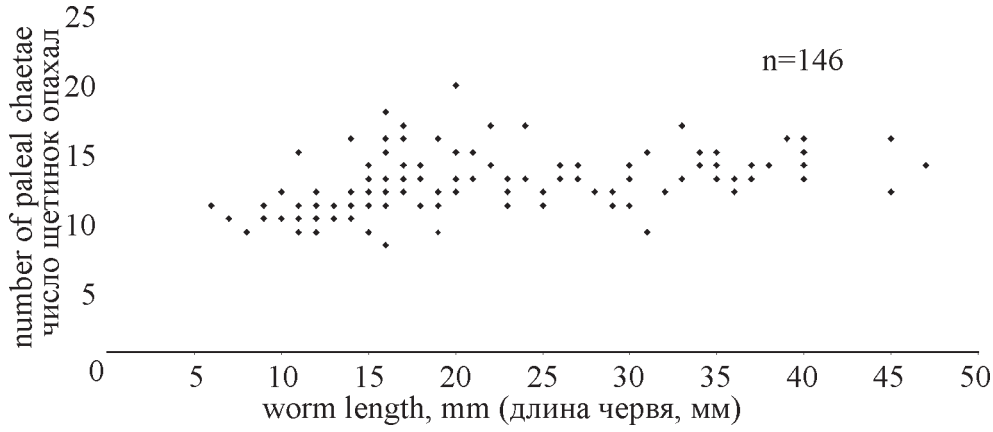

Fig. 11. *Ampharete finmarchica* (Sars, 1865), the relationship of the number of paleal chaetae with the size of the worm.
Рис. 11. *Ampharete finmarchica* (Sars, 1865), связь числа щетинок опахал с размером червя.

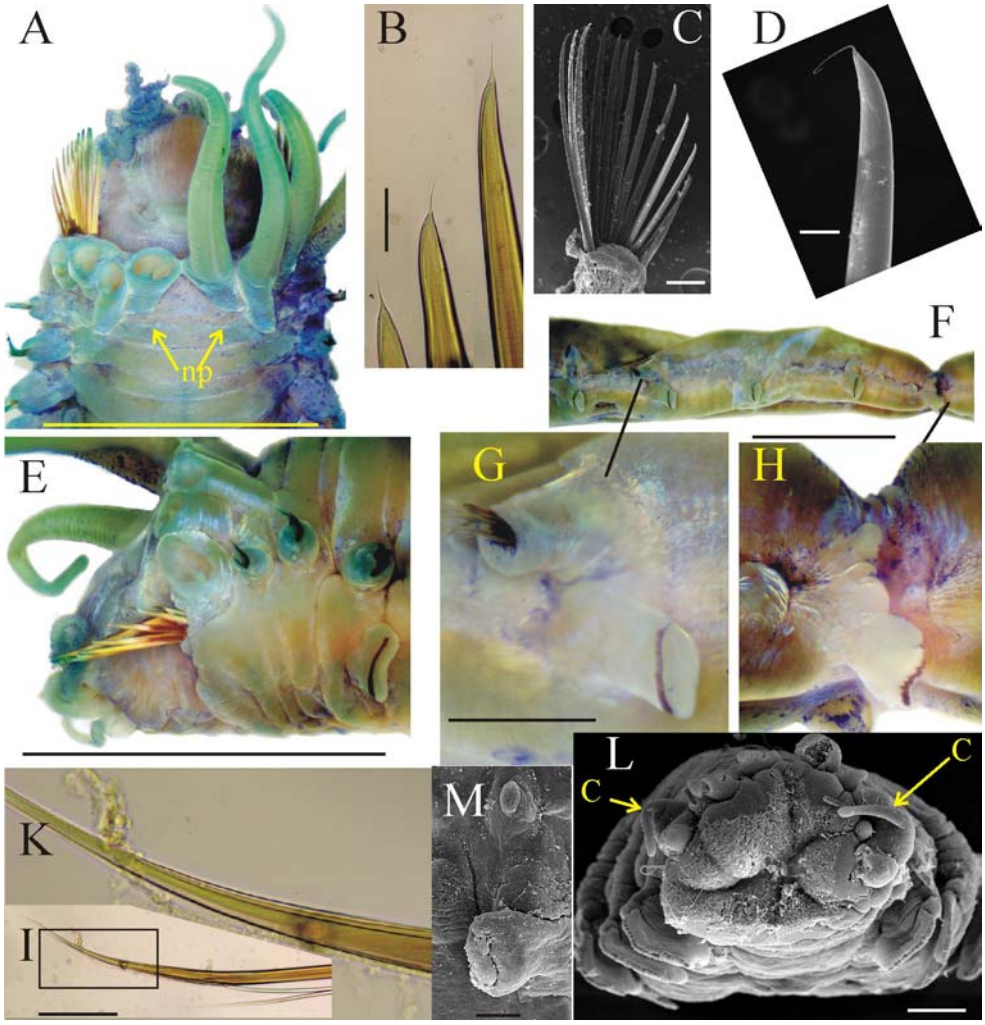

Fig. 12. *Ampharete finmarchica* (Sars, 1865), external morphology.
A — dorsal view, np — nephridial papillae; B–D — paleae and tips of its chaetae under stereomicroscope and SEM; E — lateral view; F — thorax–abdomen junction, lateral view of last two thoracic and three first abdominal segments; G — last thoracic parapodium; H — 3rd abdominal parapodium; I, K — notochaeta and its detail; L — pygidium, c — cirri. Scales: A, D, F — 5 mm, C, L — 0.3 mm, B — 0.1 mm, G, H — 1 mm, I —0.2 mm, D — 30 μm. A, E–H — Persey 652, B–D, I–L — Persey 133.

Рис. 12. *Ampharete finmarchica* (Sars, 1865), внешняя морфология.
A — дорсальный вид, np — нефридиальные папиллы; B–D — опахала и вершины их щетинок под световым и сканирующим микроскопом; E — вид сбоку; F — граница торакса и абдомена,, вид сбоку двух последних торакальных и трёх первых абдоминальных сегментов; G — последняя торакальная параподия; H — третья абдоминальная параподия; I, K — нотохета и её деталь; L — пигидиум, c — усики. Масштаб: A, D, F — 5 мм, C, L — 0,3 мм, B — 0,1 мм, G, H — 1 мм, I —0,2 мм, D — 30 μm. A, E–H — Персей 652, B–D, I–L — Персей 133.

than that of the other species of the superspecies (with exception of *A. britayevi*), (3) they were found near the type locality (4) no other species matches the original description has been found in extensive investigated materials from the Chukchi and Bering Seas.

Ampharete crassiseta Annenkova, 1929, also described from the Far Eastern Seas, has the same number of paleal chaetae (17–24), but they gradually taper into a long thread-like top.

RANGE (Fig. 10). Along Asia from the south of the Chukchi Sea to the south of Kamchatka and the

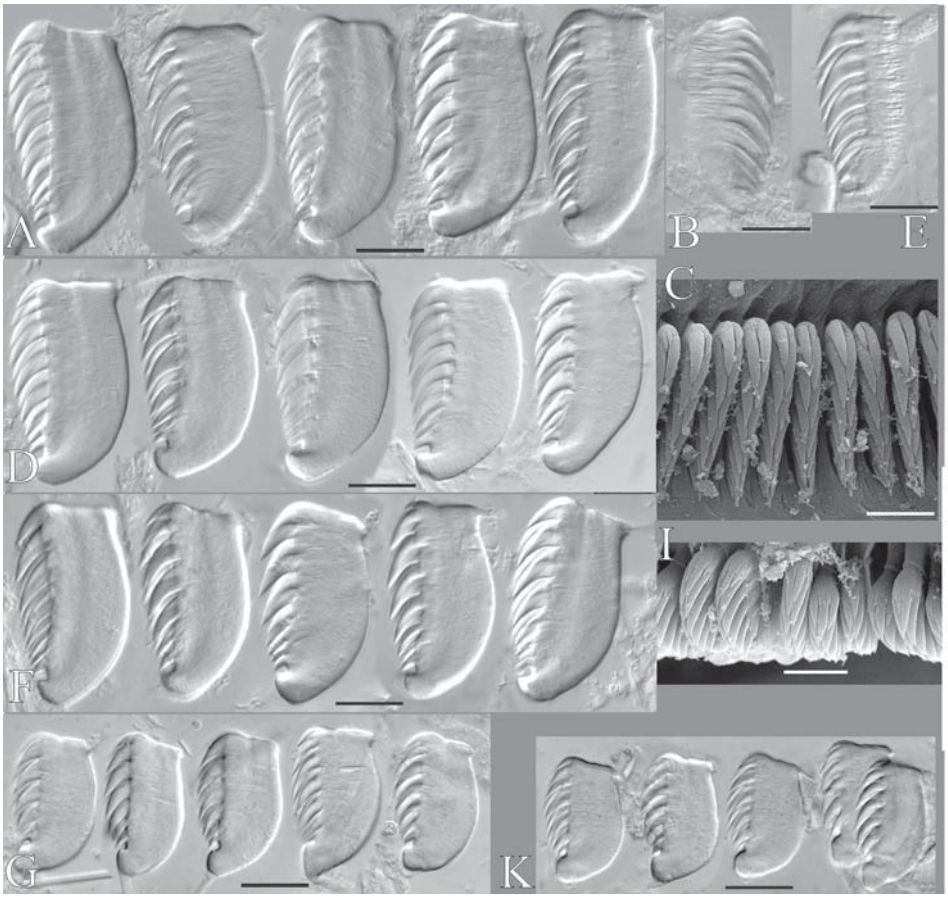

Fig. 13. *Ampharete finmarchica* (Sars, 1865), uncini.
A, B — TU1; C — middle TU; D, E — TU12; F — AU2; G — AU3; I, K — AU13. All scales are equal — 20 μm. All worms Persey 133.
Рис. 13. *Ampharete finmarchica* (Sars, 1865), неврохеты.
A, B — TU1; C — среднего TU; D, E — TU12; F — AU2; G — AU3; I, K — AU13. Все масштабы одинаковы — 20 μm. Все Персей 133.

Sea of Okhotsk along Kamchatka. Upper sublittoral, 17–89 m. Abundant in places, up to 64 specimens per square m.

Ampharete finmarchica (Sars, 1865)
Figs 12–14.

Ampharete finmarchica (type: Zoologisk Museum, Oslo, two syntypes (Holthe, 1986a); type locality: Ramfjorden, Troms, Norway); Hartmann-Schröder, 1971: 458–459, Abb. 158; 1996: 493–494, Abb. 240; Holthe, 1986a: 38–39, fig. 11, map 10; Jirkov, 1989: 109, fig. 22. 4, 5; 2001: 465–466; Hilbig, 2000: 182–184, fig. 8.4; Parapar *et al*., 2011, Fig.2, 3.

Ampharete arctica Malmgren, 1866: 364–365, fig. 77 (type locality: Spitsbergen, Finmarken, Bahusia (Bohuslen), Sweden); Augener, 1928: 777–778; Annenkova, 1929: 490–491, fig. 36; Zatsepin, 1948: 150, table XXXVII, 11; Uschakov, 1955: 369, fig. 136 3; Chlebovitch, 1964: 175; Tzetlin *et al*., 1983: 180 (partim) — non Imajima, Hartman, 1964: 331.

non *Ampharete arctica* var. *gagarae* Uschakov, 1950: 248, fig. 32, table. II, 7; 1955: 369, fig. 136 И–Л = *Anobothrus gracilis* fide Jirkov, 2001.

non *Ampharete brevibranchiata* Treadwell, 1926: 6–7, fig. 11–14.

MATERIAL. 361 samples (ca. 2000 specimens). Supplement.

DESCRIPTION. Up to 60 mm long (up to 70 by Augener (1928). The middle lobe of the prostomium anteriorly rounded, about twice as long as the width. Buccal tentacles pinnate. Paleal chaetae (Fig. 12A–E) much longer and thicker than the most developed

Fig. 14. Map showing sampling stations with specimens of *Ampharete finmarchica* (Sars, 1865).
Red — this study, blue triangles — type localitites of *A. finmarchica* and *A. arctica*.
Рис. 14. Карта находок *Ampharete finmarchica* (Sars, 1865).
Красный — эта работа, синие треугольники — типовые местности *A. finmarchica* и *A. arctica*.

notochaeta, directed forward they usually reach the level of the front edge of the prostomial middle lobe, if the front part of the body is protruding, then they reach at least the front edge of the prostomial lateral lobes. Each palea with 7–21 paleal chaetae, usually dark cupper colors. Its tops short pointed (the tip often breaks off). The attachment places of the branchostyles (Fig. 13A) located almost in a straight line, the groups of gills close, the gap between them no wider than the diameter of the branchophore or absent. The third branchophore from the edge clearly associated with the notopodia TC2 (= CT6). At the base of the internal branchophores a pair of small nephridial papillae, in few worms, after staining TC3 papillae become visible. Branchostyles cirriform smooth. 14 TC, 12 TU. The notopodia almost hemispherical, the notochaeta slightly protrude from them. 13 AU (as an exception — 14 AU). Rudimentary notopodia small, no neuropodial cirri (Fig. 13H, M). Neuropodia of thorax, TU1 and TU2 tori (Fig. 13G), the rest — pinnuli (Fig. 13H). Pygidium with a pair of lateral cirri and several short papillae (Fig. 13L). Notochaetae (Fig. 13I, K). narrow equally bilimbate. Uncini TU1 (Fig. 13A) in profile are 6–7-toothed, the teeth located in the uncini in two rows (Fig. 13C) from the rostrum itself, the size of the teeth increases apically, the total number of teeth about 12–14; in addition, usually small ones present at the very top. Several uncini in the process of being formed, only their teeth have fully formed, but not the base (Fig. 13B, E). Abdominal uncini (Fig. 13F–K) with fewer teeth in profile, but at the top some teeth arranged in three rows, the number of apical teeth also increases. The tube cylindrical, thick, dense, finely sandy-silty, with a large admixture of detritus, can be encrusted with grains of sand, pebbles, etc., the thickness of the walls several times smaller than the inner diameter, 3–4 times longer than the worm.

VARIABILITY. The number of paleal chaetae of different population slightly varies, but the difference in not valuable (Fig. 9).

The number of paleal chaetae does not depend on the worm size in diapason 5–50 mm (Fig. 11). The shape of the bristles also does not change. In the ZIN collection (67/30177) there is one specimen from the Kara Sea with a normally developed right side of the body, whereas there were no fangs on the left, additionally it had 14 AU.

REMARK. Parapar *et al*. (2011) wrote that presence of "ciliated formation in the dorsal part of abdominal segments after disappearance of notopodial ramus could lead to the erroneous observation of the presence of rudimental notopodia". However present observation shows that rudimental notopodia really present (Fig. 13M), while ciliated formations are absent. The explanation is probably following: Parapar *et al.* (2011) have dealt with fresh material, whereas the age of the studied material is about a century, during this time the cilia were lost, exposing rudimental notopodia, which masked the ciliated formation in the Parapar *et al.* (2011) material.

Hartman (1956, 1959) and, following her, Holthe (1986b) and Read, Fauchald (2022b) accepted *Ampharete brevibranchiata* Treadwell, 1926 as junior synonym of *A. arctica*. However, in a very incomplete description of *A. brevibranchiata*, it is indicated that it has 12 AU not 13 AU as Hartman (1956) wrote with reference to Berkeley, Berkeley (1952). It does not allow to agree with Hartman synonymy. Among species occurring in the type locality *A. brevibranchiata* (Bering Strait), *A. crassiseta* is the most similar species, but for a final conclusion, a study of the holotype is necessary.

RANGE (Fig. 14). The species is widely distributed in the Northern Pacific: south to the Sea of Japan along Asia, (but absent in the Japan waters) and California along North America. On all the shelves of the Arctic Ocean, but it penetrates into the Atlantic along the American coast only as far as Newfoundland. Along Europe, the species goes as far as the North Sea, including Skagerrak, Kattegat and Öresund (Holthe, 1986a), but probably not further to the south. Despite Holthe (1986a, only data from literature) and Zettler *et al*. (2018) reported it as widely distributed in the North Sea. The specimens I studied from UK territorial waters, identified previously as *A. finmarchica* in reality were either

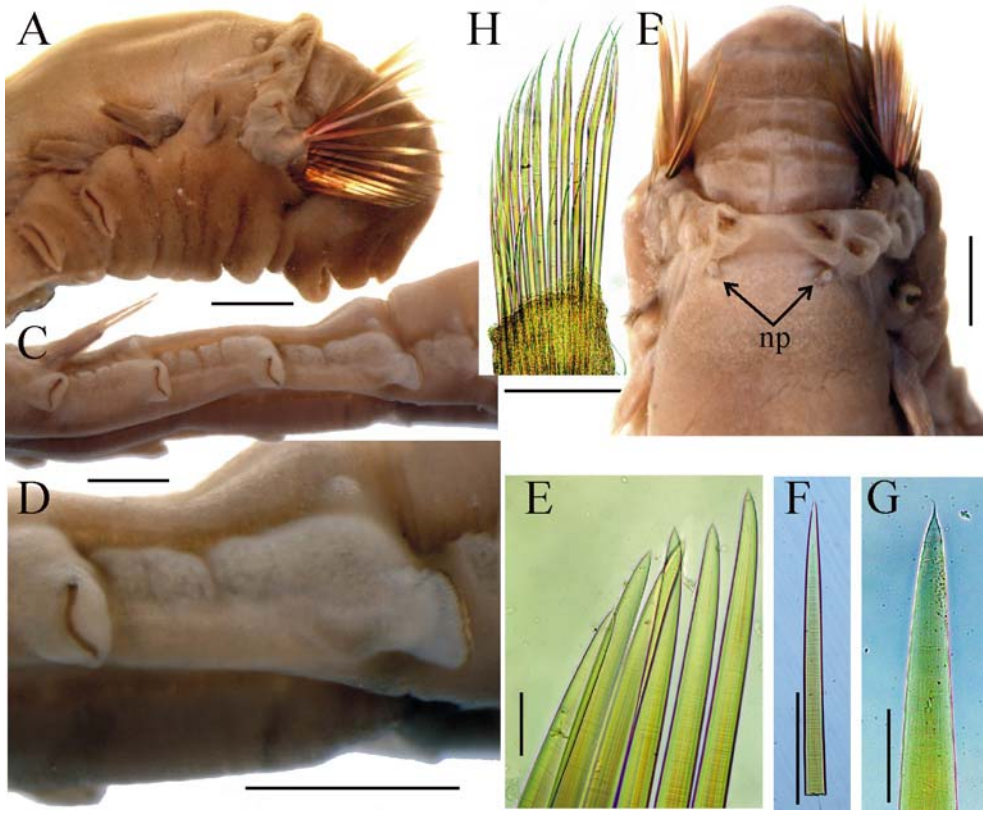

Fig. 15. *Ampharete goesi* Malmgren, 1866, external morphology.
A — lateral view; B — dorsal view, np — nephridial papillae; C — last thoracic and three first abdominal segments; D — the same enlarged AU2 and AU3, showing change of neuropodial shape; E–G — paleal chaetae; H — notochaetae TC6. Scales: A–D, F, H — 0.5 mm, E, G — 0.1 mm, A–E — Molchanov 14.1201, F, G — syntype of *Ampharete goesi brazhnikovi*, H — Vitjaz 1529.
Рис. 15. *Ampharete goesi* Malmgren, 1866, внешняя морфология.
A — вид сбоку; B — дорсальный вид, np — нефридиальные папиллы; C — последний торакальный и три первых абдоминальных сегмента; D — то же, увеличено AU2 и AU3, показано изменение формы невроподий; E–G — щетинки опахал; H — нотохеты TC6. Масштаб: A–D, F, H — 0,5 мм, E, G — 0,1 мм, A–E — Молчанов 14.1201, F, G — синтип *Ampharete goesi brazhnikovi*, H — Витязь 1529.

Ampharete aff. *lindstroemi*, or *Anobothrus gracilis*. Dr. Worsfold (APEM, letter 23/12/2021) wrote me that *A. finmarchica* is absent in huge collections from this region. Within the North Polar Basin species inhabits exclusively shelf. South to Iceland it can be found as deep as 2708 m. Within Pacific is probably inhabits lower sublittoral.

UNLIKELY REPORTS. *Ampharete arctica* sensu Imajima and Hartman, 1964 has 7 AU so without any doubt belong to different species.

Ampharete goesi Malmgren, 1866
Figs 15, 16.

Ampharete goesi Malmgren, 1866: 364 (type: not in any Swedish museum, probably lost (Holthe, 1986a); type locality: Spitsbergen; Augener, 1928: 778; Annenkova, 1929: 492, fig. 37; Zatsepin, 1948:150, table. XXXVII, 10; Pettibone, 1954: 317; Uschakov, 1955: 369, fig. 137E; Hartmann-Schröder, 1971: 457; 1996: 494; Holthe, 1986 a: 40–41, fig. 12, map 11; Jirkov, 1989: 109, fig. 22. 6, 2001: 466–467.

MATERIAL: 53 samples (95 specimens). Supplement Table.

DESCRIPTION. Up to 50 mm long. Middle lobe of prostomium about three times longer than the width. The buccal tentacles almost smooth, covered with very small (no more than 1/5 of the tentacle diameter) poorly visible cilia. Paleal chaetae 13–21 on each side (10–23 according to Holthe, 1986a), much longer and thicker than the most developed notochaeta, directed forward they reach the level of

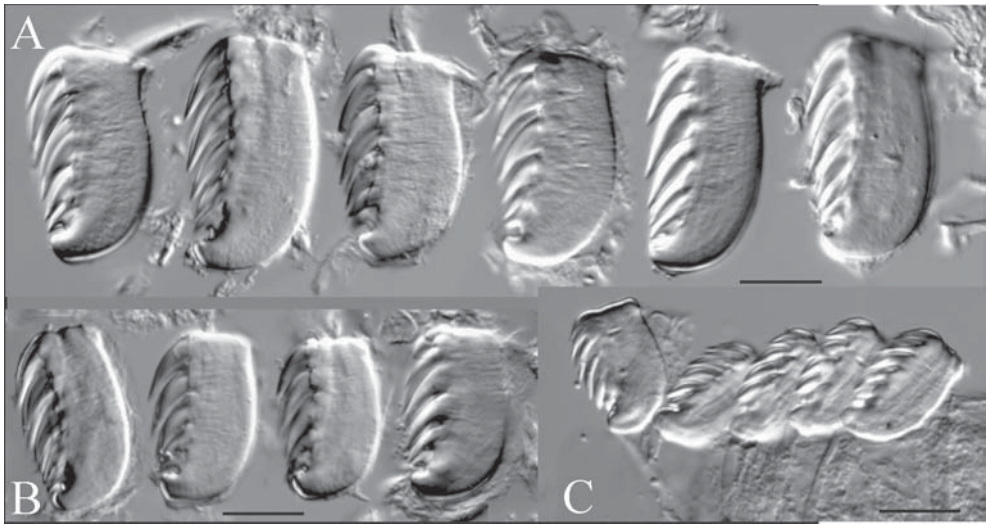

Fig. 16. *Ampharete goesi* Malmgren, 1866, uncini.
A — TU1; B — TU12; C — AU18. All scales are equal — 20 μm. Schmidt 2401.
Рис. 16. *Ampharete goesi* Malmgren, 1866, неврохеты.
A — TU1; B — TU12; C — AU18. Масштаб везде один — 20 μm. Шмидт 2401.

Fig. 17. Map showing sampling stations with specimens of *Ampharete goesi* Malmgren, 1866.
500 m isobath is shown, triangle — the type locality.
Рис. 17. Карта находок *Ampharete goesi* Malmgren, 1866.
Показана 500 м изобата, треугольник — типовая местность.

the anterior margin of the middle lobe. Their tips (Fig. 15E–G) short-pointed (the tip often breaks off). The place of branchostyles attachment of the three branchostyles are located almost in a straight line, without a gap between in the middle, the fourth (3rd outside) behind the middle of the three; this branchophore clearly related to the notopodia TC2 (= CT6). A pair of small nephridial papillae caudal to the bases of the medial branchophores (Fig. 15B). Branchostyles cirriform smooth. 14 TC, 12 TU. 16–18 AU. Neuropodia of the thorax, AU1 and AU2 tori, the rest — pinnuli (Fig. 15C, D). Abdomen with very small rudimentary notopodia, neuropodia with a short cirrus. Pygidium with two moderate-length lateral cirri and numerous low papillae. Notochaeta (Fig. 15H) widely equally bilimbate border, Thoracic uncini (Fig. 16A, B) with 2 vertical rows of teeth with 5 teeth in each, abdominal (Fig. 16C) similar, but the caudally number of rows in the upper part of the uncini increases to 3. The tube very similar to the *A. finmarchica* tube: thick, silty, often encrusted with foraminifera, fragments of shells or sea urchin needles, the wall thickness is several times smaller than the diameter of the inner hole.

RANGE (Fig. 17). From the Barents to Japan Sea, probably circumpolar.

Ampharete goesi brazhnikovi Annenkova, 1929
Fig. 15F, G.

Ampharete goesi brazhnikovi Annenkova, 1929 (type: ZIN 1/30254 and 2/30255); type locality: Sea of Okhotsk southern Sakhalin, 10–12 fms); Uschakov, 1955: 369, fig. 137Ж.

MATERIAL: two syntypes.

DESCRIPTION. The subspecies has been described by two syntypes. Description of the syntype

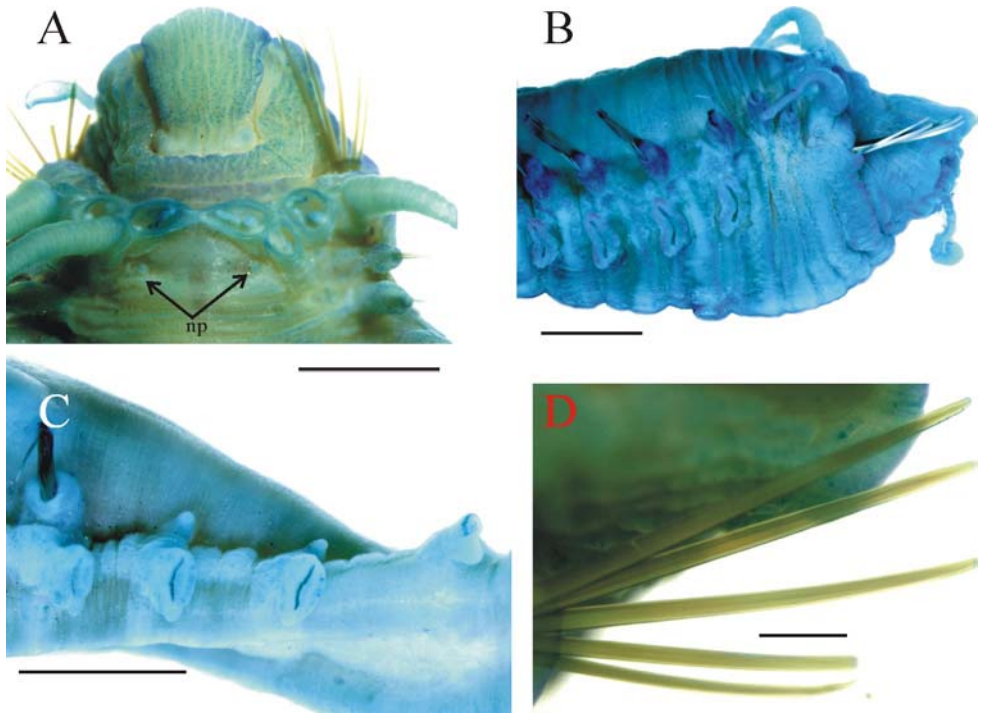

Fig. 18. *Ampharete kerguelensis* McIntosh, 1885 s.str., external morphology.
A — dorsal view, np — nephridial papillae; B — lateral view; C — last thoracic and three first abdominal segments; D — paleae. Scales: A–C — 1 mm, D — 0.2 mm. ZIN 2/16252.
Рис. 18. *Ampharete kerguelensis* McIntosh, 1885 s.str., внешняя морфология.
A — дорсальный вид, np — нефридиальные папиллы; B — вид сбоку; C — последний торакальные и три первых абдоминальных сегмента; D — опахала. Масштаб: A–C — 1 мм, D — 0,2 мм. ZIN 2/16252.

1/30254. 29 mm long. The thorax dissected on the entire length of the dorsum. Oral tentacles losted. Paleal chaetae: on the left, all are cut off at the root, on the right side 15 chaetae, most of them broken off, they much longer and thicker than the most developed notochaeta, they go forward beyond the anterior margin of the prostomium; several preserved chaetae have tips (Fig. 15F, G) as in other species of the superspecies, including *A. goesi* s.str. The branchial groups without medial gap. The places of branchostyles attachment of the three branchophores form almost in a straight line, the 4th (3rd outside) between the 2nd and 4th distinctly behind them; this branchophore is clearly associated with the notopodia TC2 (= CT6). Caudal to the bases of the medial branchophores a pair of small nephridial papillae. Branchostyles missing. 14 TC, 12 TU. 16 AU. Abdomen with very small rudimentary notopodia, neuropodia without cirri. Pygidium with two moderate-length lateral cirri and numerous low papillae. The tube missing. All the parapodia intact, so the drawings of the chaetae illustrating the original description are not made from this syntype, but from a lost fragment of the 2/30255 syntype, which, judging by the shape and number of the paleal chaetae slowly tapering in filiform tips, does not fit original description, it belongs to other species, probably *A. crassiseta*, but it is not in a good condition, so cannot be identified with certainty.

REMARK. There is no reason to accept this subspecies as valid.

Ampharete kerguelensis McIntosh, 1885 s.str.
Figs 18, 19.

Ampharete kerguelensis McIntosh, 1885: 426, Pl. XLVII, 10; XXVIA, 22–24; Monro, 1939:138.

non *Ampharete kerguelensis* Monro, 1936: 173; Day, 1967: 700; Hartman, 1966: 77; 1967:154 (=*Ampharete* sp.)

non *Ampharete kerguelensis* Augener, 1926: 223 (=?*Anobothrus glandularis*).

TYPE MATERIAL. 2 syntypes: NHM 85.12.1. 314; type locality: 48°45′S 69°14′E 127 fms.

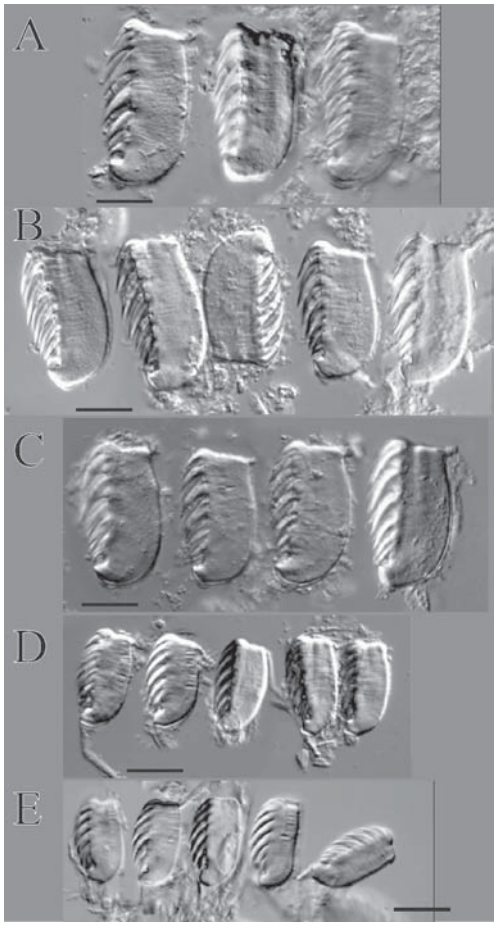

Fig. 19. *Ampharete kerguelensis* McIntosh, 1885 s.str., uncini.
A — TU1; B — TU12; C — TU2; D — AU3; E — AU13. All scales are equal — 20 μm. ZIN 2/16252.
Рис. 19. *Ampharete kerguelensis* McIntosh, 1885 s.str., неврохеты.
A — TU1; B — TU12; C — TU2; D — AU3; E — AU13. Масштаб везде один — 20 μm. ZIN 2/16252.

NON TYPE MATERIAL. ZMHU-19821, 49°50′ S, 69°33′ E., 150 m, previously identified by Monro (1939) as *A. kerguelensis* (25); ZIN 2/16252, 49° 38.7′S 70°43.7′ E 141 m, Ob 121 (1), previously identified by V.G. Averintsev as *A. kerguelensis* — non NHM 1936.2.8.2661–2663, South Georgia (4).

DESCRIPTION. Up to 33 mm long. The middle lobe of the prostomium obtusely rounded. Eye spots on the prostomium absent. Buccal tentacles pinnate. Paleal chaetae (Fig. 18D) about 5–12 on each side light yellow about the same length, but much thicker than the most developed notochaeta, directed forward reach the level of the anterior edge of the middle lobe of the prostomium or, at least, extend beyond its posterior edge. The places of attachment of the three branchophores in each group form an almost straight row, the fourth is located at the back between the inner and middle, this branchophore is clearly associated with the TC2 notopodia. The gap between groups of branchophores varies from almost absent to approximately equal to the diameter of the branchophore. Branchostyles of the usual structure for the family: smooth, irregularly transversely wrinkled; bent back, they reach 7–8 TC. At the inner corners of the bases of the inner pair of branchophores there are small nephridial papillae (Fig. 18A), the same papillae present behind the notopodia TC3. 14 TC, 12 TU. 13 AU. Rudimentary notopodia small, neuropodial cirri absent. Neuropodia of the thorax, AU1 and AU2 tori, the rest — pinnuli. Pygidium with two long lateral cirri and more or less pronounced numerous low papillae. Uncini (Fig. 19) generally similar: TU1 uncini with 5 teeth in two rows, AU13 uncini with two rows near the prow and three at the top, 5–6 teeth in profile. The tube unknown.

REMARK. The AU number is not specified in the original description. Monro (1936) and Hartmann (1966) consider it to be characterized by the presence of 12 AU. The studied synthypes are two fragments. McIntosh cut off the front part of the larger specimen for the drawing, which was subsequently lost and only the last 5 TC and the abdomen consisting of 13 AU were preserved. The smaller specimen lacks the end of the abdomen. Specimens Monro (1939) and ZIN 2/16252 were also collected near Kerguelen Island and can be considered topotypes. Their paleal chaetae are identical to the syntype. The abdomen was preserved only in 4 specimen of Monro and 1 specimen of ZIN. All of them had 13 AU.

UNLIKELY REPORTS. *Ampharete kerguelensis* sensu Monro (1936), Hartman (1966) and Day (1967) have 12 AU and thus refer to a different species. Hartman (1967) did not give description, but as Hartman (1966) is present in synonymy and due great depth (2119–2727 m) highly likely refer to a different species. Specimens NHM 1936.2.8.2661–2663 are *Ampharete* sp. as they have 12AU.

RANGE. Because the species has been identified incorrectly too often, for sure it is known from lower sublittoral of Kerguelen Isl. only.

Ampharete kudenovi Jirkov, 1994
Figs 20–23.

Ampharete kudenovi Jirkov, 1994: 28–30, fig. 1.

MATERIAL: 13 samples (107 specimens): types: 98 specimens Odissey 33.21, 48°16′N 154°44′E, 140–150 m, 3/8/1984 (holotype and 66 paratypes),

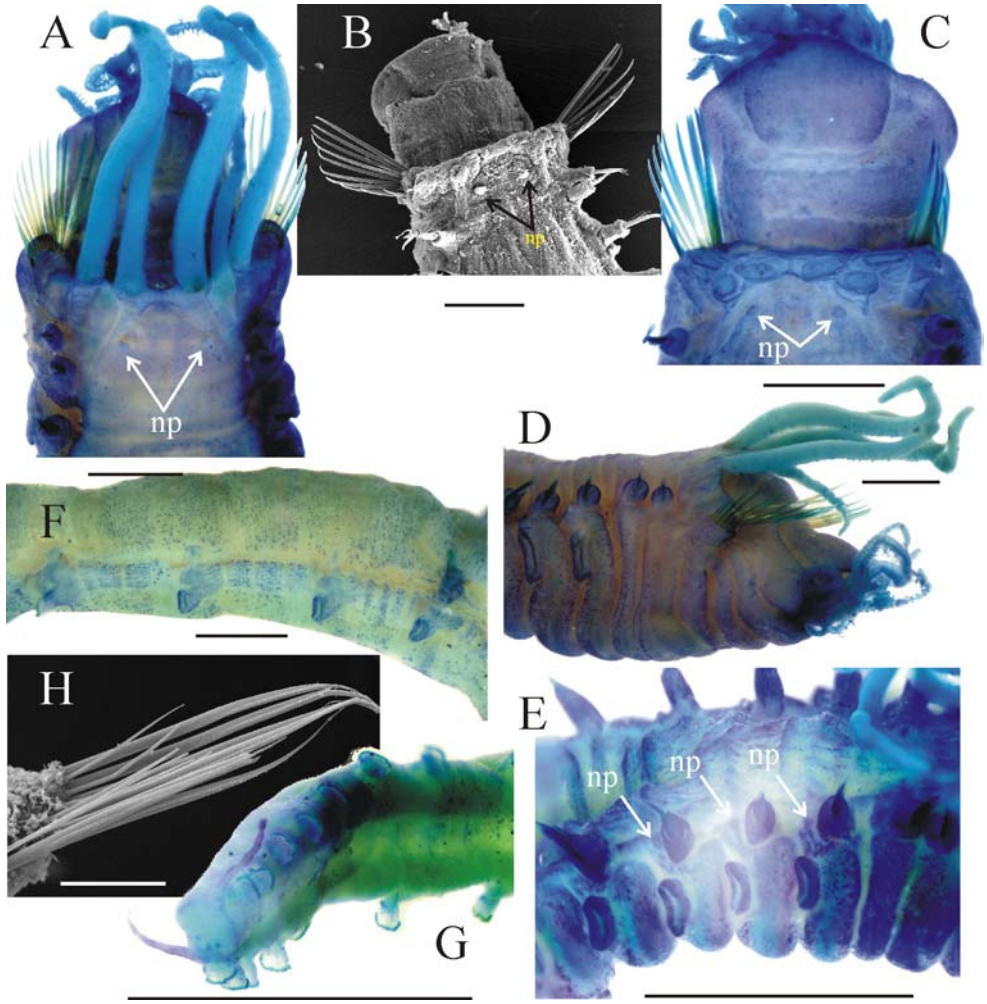

Fig. 20. *Ampharete kudenovi* Jirkov, 1994, external morphology.
A–C — dorsal view, np — nephridial papillae; D — lateral view; E — TU1–TU4 showing nephridial papillae; F — last TU and three first AU; G — posterior part, showing pygidial cirri; H — notochaetae TC11. Scales: A–D, F — 0.5 mm, E, G — 2 mm, H — 0.1 mm. A, D — holotype, other paratypes Odissey 1.81.21.
Рис. 20. *Ampharete kudenovi* Jirkov, 1994, внешняя морфология.
A–C — дорсальный вид, np — нефридиальные папиллы; D — вид сбоку; E — TU1–TU4 показаны нефридиальные папиллы; F — последний TU и три первых AU; G — конце абдомена, показаны усики пигидияwing pygidial cirri; H — нотохеты TC11. Масштаб: A–D, F — 0,5 мм, E, G — 2 мм, H — 0,1 мм. A, D — голотип, прочие паратипы Одиссей 1.81.21.

Odissey 33.22, 50°40′N 154°33′E, 1000 m, 6/8/1984 (1); Odissey 34.12, 46°58′N 152°17 E, 450–480 m, 30/12/1984 (29); Vitjaz 3569, 39°44′ N 142°18′ E, 423 m (1); Odissey 34.1, 1320 m, 10/12/1984 (2); Odissey 1, 1320 m (1); Odissey 16, 880 m 26/7/1987 (1); Korolev 37.20, 58°35.56′ N 170°28.1′ W, 630 m, 20/7/1984 (1). Deposed at DGEH. Vitjaz 2 135 48°56′ N 145°25′E, 140 m, 24/9/1948 (1); Vitjaz 10.1576, 60°30′N 168°46′E, 227 m, 25/6/1952 (1); Vitjaz 12.1739, 52°12′N 154°28′E, 359 m, 28/9/1952 (1); Vitjaz 12.1857, 56°30′N 143°10′E, 234 m, 19/10/1952 (1); Vitjaz 12.1916, 48°36′N 144°52′E, 111 m, 31/10/1952 (1) Deposed at IO RAN.

DESCRIPTION. Up to 26 mm long. The middle lobe of the prostomium obtusely rounded, along its posterior edge a more or less pronounced glandular field. No eye spots on the prostomium. Buccal ten-

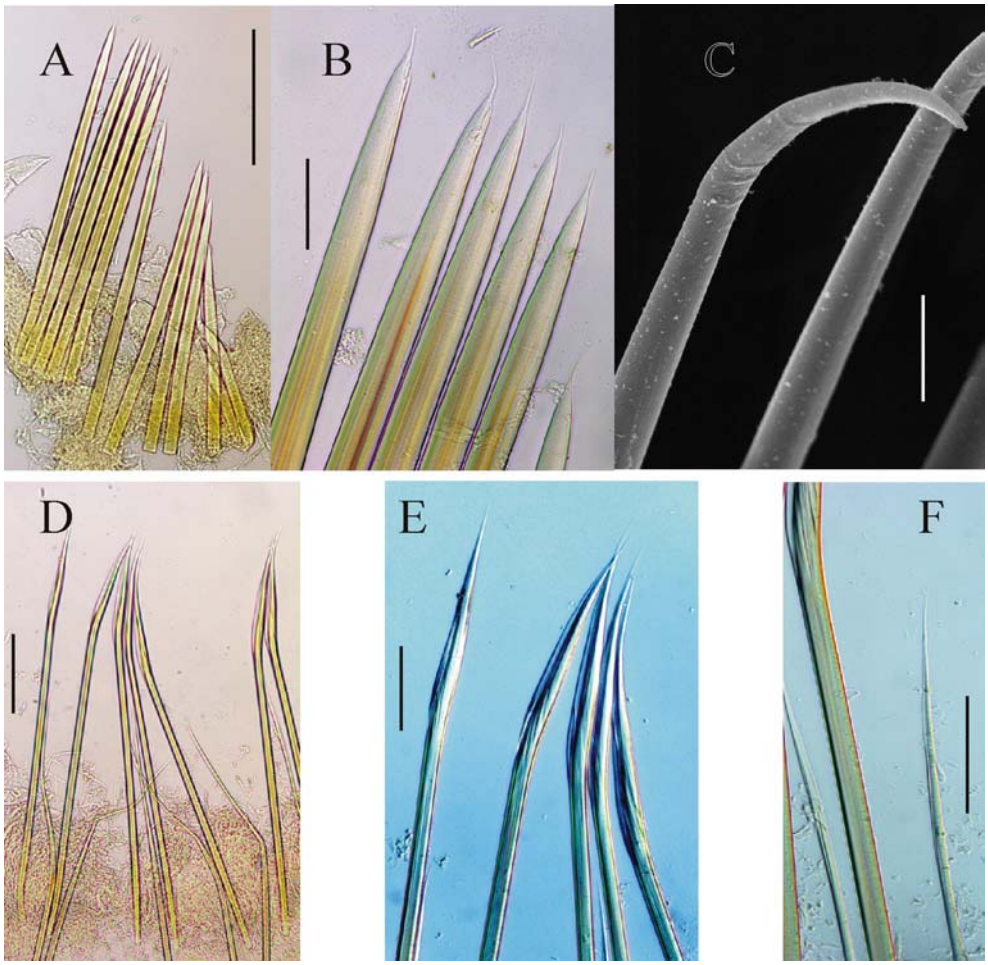

Fig. 21. *Ampharete kudenovi* Jirkov, 1994, notochaetae.
A–C — paleae; D–F — notochaetae. Scales: A — 0.5 mm, B, E, F — 0.1 mm, C — 30 μm, D — 0.2 mm. All paratypes Odissey 1.81,21.
Рис. 21. *Ampharete kudenovi* Jirkov, 1994, нотохеты.
A–C — щетинки опахал; D–F — нотохеты. Маштаб: A — 0,5 мм, B, E, F — 0,1 мм, C — 30 μm, D — 0,2 мм. Все — паратипы Одиссей 1.81,21.

tacles pinnate. Paleal chaetae (Fig. 21A–C) much longer and thicker than the most developed notochaeta, directed forward reach the level of the anterior margin of the middle lobe of the prostomium or at least erased beyond its posterior margin. 6–15 light yellow paleal chaetae on each side (70% have 9–11). 4 pairs of branchiae. Groups of branchophores close, the gap between them varies from almost absent to approximately equal to the diameter of the branchophore. The attachment points of the three branchophores in each group form an almost straight row (Fig. 20C). The fourth located at the back between the inner and middle, it is clearly associated with the TC2 notopodia. Branchostyles of the usual structure for the family: smooth, irregularly transversely wrinkled; bent back, they reach TC7–8. At the inner corners of the bases of the inner pair of branchophores there are small nephridial papillae (Fig. 20A, C), the same papillae present behind the TC3–TC5 notopodia (Fig. 20E), in half of the examined specimens they very clearly visible after staining, in the rest, for the most part, not so good condition are noticeable only on TC3. 14 TC, 12 TU. 13 AU (about 5% — 14AU). Rudimentary notopodia small, no neuropodial cirri. Neuropodia of the thorax, AU1 and AU2 tori, the rest — pinnuli (Fig. 20F). The ventral

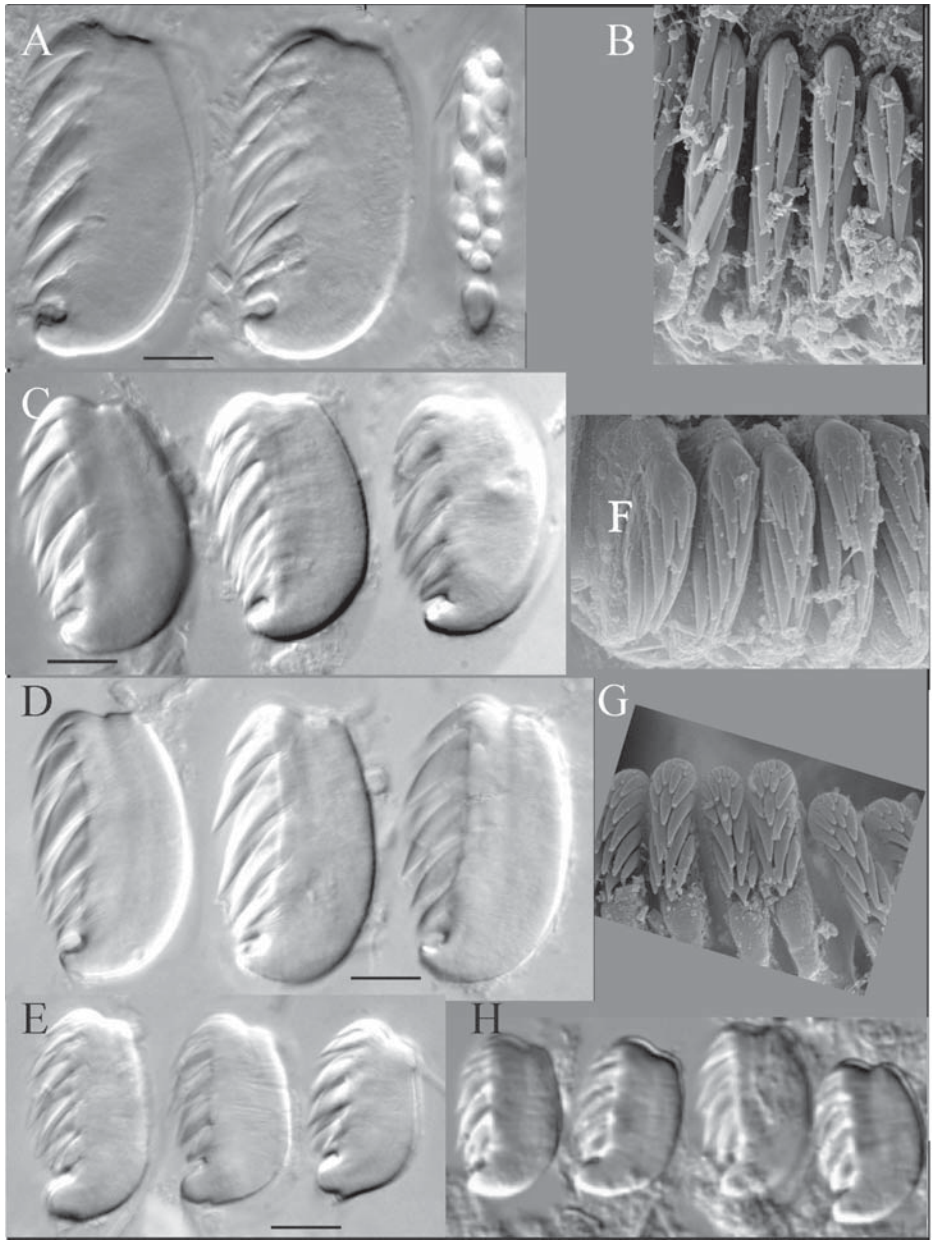

Fig. 22. *Ampharete kudenovi* Jirkov, 1994, uncini.
A — TU1; B — TU9; C — TU12; D — AU2; E — AU3; F — AU4, G, H — AU13. All scales are equal — 10 μm. All paratype Odissey 1.81.21.
Рис. 22. *Ampharete kudenovi* Jirkov, 1994, неврохеты.
A — TU1; B — TU9; C — TU12; D — AU2; E — AU3; F — AU4, G, H — AU13. Масштаб везде один — 10 μm. Все паратипы Одиссей 1.81.21.

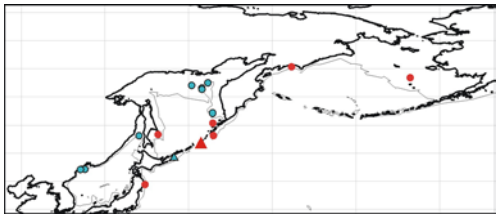

Fig. 23. Map showing sampling stations with specimens of *Ampharete kudenovi* Jirkov, 1994 and *A. longipaleolata* Uschakov, 1950.
Red — *A. kudenovi*, blue — *A. longipaleolata* 500 m isobath is shown, triangles — the type localities.
Рис. 23. Карта находок *Ampharete kudenovi* Jirkov, 1994 и *A. longipaleolata* Uschakov, 1950.
Красные — *A. kudenovi*, синие — *A. longipaleolata.* Показано 500 м изобата, треугольники — типовые местности.

surface up to and including TU9 is transformed into ñontinuous glandular ventral shields extending from notopodia to notopodia. No ventral shield on TU10, in its place a thickening may be present that occupies the entire ventral abdominal surface of the anterior half of the segment. Notochaetae (Fig. 20H), long and short; probably short ones forming ones. Long notochaetae in a light microscope bilimbate (keels in SEM), very unequal (Fig. 21D, E). Uncini (Fig. 22) generally similar: thoracic uncini in profile 5–6 teeth, teeth arranged in two rows in a checkerboard pattern, the size of the teeth gradually increases apically. Abdominal uncini AU1 similar to thoracic ones; caudally, the number of rows of teeth increases and AU13 uncini in 3–4 rows of teeth. Pygidium with two long lateral cirri and more or less numerous low papillae (Fig. 20G). Tube: transparent organic base covered with fragments of bryozoans, shells, sea urchin spines, mica, etc., without the slightest admixture of the usual for family silt or detritus.

REMARK. The species is very similar to *A. finmarchica*, and the only reason why I described this species is sharp difference in tube structure. The use of tubes structure for identification may seem doubtful, however, reviewed tubes of *A. finmarchica* from the extensive materials collected from Newfoundland to the Sea of Japan, including samples in which *A. finmarchica* has been found together with *A. kudenovi*, showed that the structure were found to be very monomorphic and tubes of *A. finmarchica* composed of silt-detrital particles, completely absent in tubes of *A. kudenovi*, usually more or less densely encrusted in the anterior part of the tube, are found as grains of sand. However, tubes are not always preserved. The number of paleal chaetae of *A. kudenovi* does not differ from that of *A. finmarchica* (Fig. 9). The paleal chaetae of *A. kudenovi* are lighter than those of *A. finmarchica* and relatively shorter, the tips break off extremely rarely. Tips of paleal chaetae of *A. kudenovi* are pointed a little gradually than of *A. finmarchica*. Also, nephridial papillae behind notopodia are extremely seldom visible in *A. finmarchica*, while often can be seen in *A. kudenovi*. But these differences cannot be used for identification. I found the only other difference between these species in structure of notochaetae: limbation of *A. kudenovi* is much wider and shorter than of *A. finmarchica* (compare Fig. 7k, i and Fig. 16d, e). Unfortunately, this character is not convenient for identification of these common species and even is not visible on each slide. The situation is similar to Oweniidae, some species are very easily differed by their tubes, but if tubes are absent, preparation of slides is necessary.

RANGE (Fig. 23). North-west Pacific, including Sea of Okhotsk and the Bering Sea, lower sublittoral and slope.

Ampharete longipaleolata Uschakov, 1950
Figs 24–26.

Ampharete longipaleolata Uschakov, 1950: 218–219, fig. 33 (type locality, restricted: pacific coast of the southern Kuril Islands, 414 m 14/9/1949); 1955: 367–368.

MATERIAL. 16 samples (45 specimens): 3 syntypes ZIN 1/15243; DGEH: Hydrobiolog 25, 500 m, 5/6/1984 (2); Hydrobiolog 129, 48°15′ N 141°11′ E 650 m, 7/8/1984 (1); Hydrobiolog 193, 46°00′ N 138°20′ E, 700 m, 4/9/1984 (1); Odissey 1.84.16, 880 m (2); Odissey 33.13, 44°52′ N 149°27,7′ E, 920 m, 25/7/1987 (1); Odissey 34.1A, 42°12.76′ N 130° 59.22′ E 640 m, 7/12/1984 (6); IO RAN: Zhemchug 105, 2083 m (1); Zhemchug 111, 375 m (1); Vitjaz 2.31, 57°45.3′ N 153°45′ E, 440 m, 18/8/1948 (19); Vitjaz 2.34, 58°43′ N 155°56′ E, 296 m, 19/8/1948; Vitjaz 2.59, 57°00′ N 150°53,5′ E, 355 m, 29/8/1948 (2); Vitjaz 12.1739, 52°12′ N 154°28′ E, 359 m, 28/9/1952 (1); Vitjaz 12.1745, 53°3′ N 154°30′ E, 299 m, 29/9/1952; Vitjaz 12.1770, 56°30′ N 152°38′ E, 524 m, 4/10/1952 (4); Vitjaz 12.1781, 56°53′ N 152°36′ E, 551 m, 4/10/1952 (6); Vitjaz 39.5640, 44º41′N, 148º57′E, 10/09/1966, 780 m (1); Vitjaz 59.7458 42°15′N 131°40′ E, 630–750 m, 27/5/1976 (1).

DESCRIPTION. Up to 40 mm in length. The middle lobe of the prostomium blunt-rounded in front, at the base with a whitish glandular field, black eye spots outside the corners of the furrow. Palae unusually well developed. Their bases sharply enlarged, forming cylindrical outgrowths, from which the paleal chaetae come out, forming a complete spiral and even more. Chaetae light yellow, several times thicker and 4 times longer than the most developed notochaeta, extending far beyond the

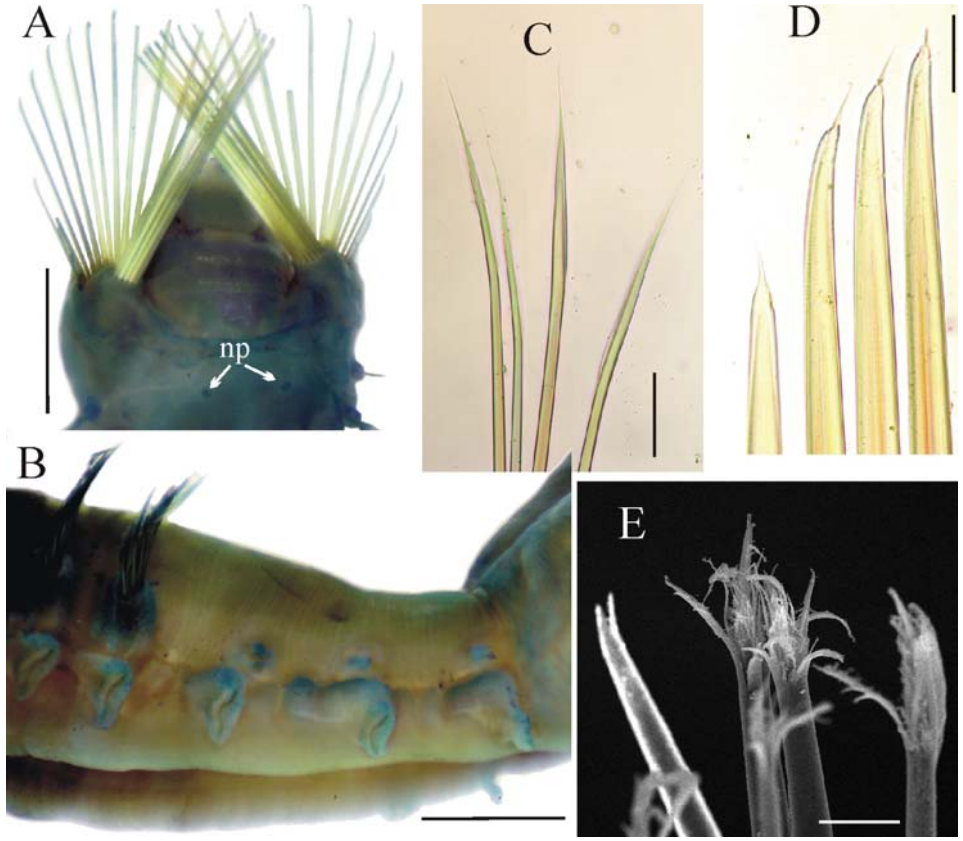

Fig. 24. *Ampharete longipaleolata* Uschakov, 1950, external morphology.
A — dorsal view. np — nephridial papillae, B — thorax-abdomen junction, lateral view of last two thoracic and three first abdominal segments, C — notochaetae, D, E — paleal chaetae, E — disheveled at the end. Scales: A — 2 mm, B — 1 mm, C–E — 0.1 mm. A, B — syntype, C–E — Odissei 1.84,16.
Рис. 24. *Ampharete longipaleolata* Uschakov, 1950, внешняя морфология.
A — дорсальный вид. np — нефридиальные папиллы, B — граница торакса и абдомента, вид сбоку двух последних и трёх первых абдоминальных сегментов, C — нотохеты, D, E — щетинки опахал, E — с разлохмаченной вершиной. Масштаб: A — 2 мм, B — 1 мм, C–E — 0,1 мм. A, B — синтип, C–E — Одиссей 1.84,16.

level of the anterior edge of the prostomium, by 2–5 of its length (Fig. 24A). In each group 10–26 of them (in the syntypes 15–20), the number of paleal chaetae increases with the increase in the size of the worm (Fig. 25). The tips of paleal chaetae sharply narrow into a short thread-like tip in worms large 20 mm, in smaller worms tips slowly tapering to filament. Many of the paleal chaetae disheveled at the end, which does not happen in other species of the superspecies. Branchophores form an almost straight line, the second pair of branchiae from the middle is slightly behind the others. Branchostyles smooth, bent back, they reach about C6. At the base of the internal branchophores a pair of small nephridial papillae. 14 TC, 12 TU. 13 AU. Rudimentary notopodia small, no neuropodial cirri. Neuropodia of the

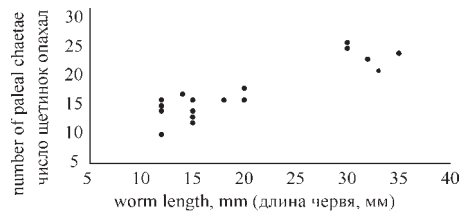

Fig. 25. *Ampharete longipaleolata* Uschakov, 1950, the relationship of the number of paleal chaetae with the size of the worm, Vitjaz 2.31.
Рис. 25. *Ampharete longipaleolata* Uschakov, 1950, связь числа щетинок опахал с размером червя, Витязь 2.31.

Fig. 26. *Ampharete longipaleolata* Uschakov, 1950, uncini.
A — TU1; B, C — TU12; D — AU2; E — AU3; F — AU11. All scales are equal — 10 μm. Odissei 1.84.16.
Рис. 26. *Ampharete longipaleolata* Uschakov, 1950, неврохеты.
A — TU1; B, C — TU12; D — AU2; E — AU3; F — AU11. Масштаб везде один — 10 μm. Одиссей 1.84.16.

thorax, AU1 and AU2 tori, the rest — pinnuli. Pygidium with two long lateral cirri and more or less numerous low papillae. Notochaeta also very large, approximately equal in length to the width of the body narrow bilimbate. Uncini with two rows of teeth, usually 6 in each. Thoracic and abdominal similar. The tube loose, detritus-like, sometimes densely plastered with large grains of sand, the

thickness of its walls much smaller than the diameter of the inner hole.

REMARK. In the ZIN collection of 14 specimens, mentioned in the original description, only 3 have been preserved (one without the end of the thorax) from st. 101 R/V Toporok from a depth of 414 m. The original description also includes a find near Northern Sakhalin at a depth of 65 m, this material in ZIN collection is absent. Judging by the fact that all other known findings I have reviewed, located exclusively on slope, worms from 65 m should belong to a different species. Such species really exist and inhabits shallow depth near Sakhalin. It also have numerous very long paleae, but paleal chaetae slowly tapering to slim tips and it has 12 AU. Therefore, I consider it necessary to limit the type locality only to the area where the preserved syntypes were collected

RANGE (Fig. 23). North-west Pacific, including Sea of Okhotsk and the Japan Sea, slope 375–2083 m.

KEY TO IDENTIFICATION SPECIES OF *AMPHARETE* (SUPERSPECIES *FINMARCHICA*)

It is strongly recommended to identify several specimens together rather than single individual.

1. Paleal chaetae several times thicker than the most developed notochaetae, sharply pointed into a short filiform tip (may break off) (Figs 3A–C, 7D, E, 12B–D, 15E–G, 18D, 20A–C, 24D–E). *Ampharete* (*finmarchica*) 2
– Paleal chaetae, if present and thicker than the most developed notochaetae, gradually taper into a long filiform tip (Fig. 2) ..... other *Ampharete*
2. More than 40 paleal chaetae .... *Ampharete britayevi* sp.n.
– Less than 30 paleal chaetae 3
3. Paleal chaetae significantly exceed body width, protrude far beyond anterior margin of prostomium (Fig. 24A) .. *Ampharete longipaleolata*
– Paleal chaetae are less than or equal to the body width, if they protrude beyond the anterior edge of the prostomium, then not significantly (Figs 7A–C, 12A, E, 18A, B, 20A–D) 4
4. Less than 20 paleal chaetae 5
– 20–30 paleal chaetae (Figs 7, 9) .... *Ampharete eupalea*
5. 13 AU 6
– 16–18 AU ..... *Ampharete goesi*
6. North hemisphere 7
– South hemisphere ..... *Ampharete kerguelensis*
7. Tube inlay is covered by muddy-detritus, limbation of notochaetae narrow and equal (Fig. 12K) ..... *Ampharete finmarchica*
– Tube inlay is covered by exclusively fragments of bryozoans, shells, sea urchin spines, mica, etc., without trace of mud and detritus, limbation of at least some notochaetae wide and unequal (Fig. 21E) ..... *Ampharete kudenovi*

Biogeography

Of the seven species, six species inhabit temperate waters of the Northern Pacific and only one (*A. kerguelensis*) the Southern Hemisphere. None enter subtropical areas. Two Pacific species (*A. finmarchica* and *A. goesi*) enter the Arctic Ocean. The range of penetration of them into the Atlantic sector depends on the preferred habitat depths. *A. finmarchica* inhabiting greater depths penetrate further, up to the North Sea. *A. goesi* living at depths does not go beyond the Barents Sea. It is significant that out of 1,371 specimens of the genus *Ampharete* collected from 224 samples in Icelandic waters, 822 specimens were *A. finmarchica* (60%) and none of *A. goesi* were found (Parapar *et al*., 2011). Holthe (1986a) cites numerous finds of *A. finmarchica* in the North Sea according to literature data, but his own data are limited to the southern coast of Scandinavia and the Skagerrak. All worms from UK waters investigated by me and previously identified as *A. finmarchica* actually belonged to either *Ampharete* aff. *lindstroemi* or *Anobotrus gracilis*. Highly likely, the southern range border of *A. finmarchica* within the North Sea coincides with the southern range border of such a species as *Nothria hyperborean* (Hansen, 1878) (Onuphudae), which is also widely distributed in the lower temperate sublittoral of the Northern Pacific and the Arctic Ocean, see range map Jirkov (2001: 257). The biogeographic boundary that runs along the border between the Northern and Norwegian Seas is not associated with abrupt changes in hydrology, it is probably the boundary between the biome of the lower sublittoral of Norway, formed after the disappearance of the glacier, and the biome of the lower sublittoral of the temperate zone of Europe, which existed during periods of glaciation south to the glacier. The situation along the American coast is probably similar, but the published data is insufficient.

The high diversity of species of subspecies b makes the origin of the entire group in the temperate waters of the Northern Pacific probable, and their actual absence in the Atlantic makes the origin of the entire group in the

temperate waters of the Northern Pacific probable. Within the Northern Pacific different species live in different biomes: the upper (*A. britayevi* sp.n., *A. eupalea*, *A. goesi*) and lower (*A. finmarchica*) sublittorals and bathyal (*A. kudenovi* and *A. longipaleolata*).

Supplementary data. The following Table is available online.

Table. Finds of the most common species of *Ampharete* (superspecies *finmarchica*).

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References

Annenkova N.P. 1929. Beiträge zur Kenntnis der Polychaeten-Fauna der USSR. I. Fam. Pectinariidae Quatrefages (Amphictenidae Malmgren) und Ampharetidae Malmgren // Annuaire du Musee Zoologique de l'Academie des Sciences de l'URSS. Vol.30. No.3. P.477–502.

Augener H. 1926. Polychaeta. III. Polychaeten von Neuseeland II. Sedentaria // Videns. Medd. Nat. For. Copenhagen. Bd.81. S.157–294.

Augener H. 1928. Beitrag zur Polychaetenfauna der Ostsee // Zeitschrift fur Morphologie und Okologie der Tiere. Bd.11. H.1/2. S.102–104.

Banse K. 1979. Ampharetidae (Polychaeta) from British Columbia and Washington // Canadian Journal of Zoology. Vol.57. No.8. P.1543–1552.

Berkeley E.B., Berkeley C. 1942. North Pacific Polychaeta, chiefly from the west coast of Vancouver Island, Alaska and Bering Sea // Canadian Journal of Science, Ottawa. Vol.20. P.183–208.

Berkeley E., Berkeley C. 1952. Canadian Pacific Fauna. 9. Annelida // Fisheries Research Board of Canada. Vol.9b. No.2. P.1–139.

Chamberlin R.V. 1920. Annelids, parasitic worms, protozoans, etc. Part B: Polychaeta // Report of the Canadian Arctic Expedition 1913–18, Thomas Mulvey, Ottawa. Vol.9. P.1–41.

Chlebovitch V.V. 1964. [Bristleworms (Polychaeta) from the northern part of the Greenland Sea, Spitzbergen and Franz-Joseph Land] // Trudy Arkticheskogo i Antarcticheskogo nauchno-issledovatelskogo instituta. Vol.259. P.167–180 [in Russian].

Day J.H. 1967. A monograph on the Polychaeta of Southern Africa. London. British Museum (Natural History). Vol.2. Sedentaria. 416 p.

Hartman O. 1956. Polychaetous annelids erected by Treadwell, 1891 to 1948, together with a brief chronology // Bulletin of the American Museum of Natural History. Vol.109. No.2. P.239–310.

Hartman O. 1959. Catalogue of the polychaetous annelids of the world. Part I and II // Allan Hancock Foundation Publications. Occasional Paper. Vol.23. P.1–628.

Hartman O. 1961. Polychaetous annelids from California // Allan Hancock Pacific Expeditions. Vol.25. 226 p.

Hartman O. 1966. Polychaeta Myzostomidae and Sedentaria of Antarctica. Antarctic Research Series. 158 p.

Hartmann-Schröder G. 1971. Annelida, Borstenwürmer, Polychaeta // Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Maermalen und nach ihrer Lebensweise. Jena: Gustav Fischer Verlag. 594 S.

Hartmann-Schröder G. 1996. Annelida, Borstenwürmer, Polychaeta // Die Tierwelt Deutschlands un der angernzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise. Jena, Germany: Gustav Fischer. 648 S.

Hilbig B. 2000. 8. Family Ampharetidae Malmgren, 1867 // J.A. Blake, B. Hilbig, P.V. Scott (eds.). Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel, Vol.7 – The Annelida. Part 4. Polychaeta: Fabelligeridae to Sternaspidae: Santa Barbara: Santa Barbara Museum of Natural History. P.169–230.

Holthe T. 1986. Evolution, systematics, and distribution of the Polychaeta Terebellomorpha, with a catalogue of the taxa and a bibliography // Gunneria. Vol.55. P.1–236.

Holthe T. 1986. Polychaeta Terebellomorpha // Marine Invertibrates of Scandinavia, Vol.7. 192 p.

Imajima M., Hartman O. 1964. The polychaetous annelids of Japan. Part II. Los Angeles, California. The University of Southern California Press. Allan Hancock Foundation publications occasional paper. 452 p.

Jirkov I.A. 1989. [Bottom fauna of the USSR seas. Polychaeta]. Moscow. Moscow State University Press. 141 p. [In Russian]

Jirkov I.A. 1994. [Two new species of the genus *Ampharete* (Polychaeta, Ampharetidae) from the North-Western Pacific with discussion on the taxonomic significance of paleae in Ampharetinae] // Zoologicheskii zhurnal. Vol.73. No.4. P.28–32 [in Russian].

Jirkov I.A. 2001. [Polychaeta of the Arctic Ocean]. Moscow. Yanus-K. 632 p. [In Russian]

Jirkov I.A. 2011. Discussion of taxonomic characters and classification of Ampharetidae (Polychaeta) // Italian Journal of Zoology. Vol.78. P.78–94.

Krüger L., Dietrich A., Bastrop R., Bick A. 2022. From synonym to valid species: Redescriptions of *Ampharete acutifrons* (Grube, 1860) and *A. cirrata* Webster & Benedict, 1887, and brief descriptions of *A. baltica* Eliason, 1955 and *A. grubei* Malmgren, 1865 (Annelida: Terebellida: Ampharetidae) // Zootaxa. Vol.5174. No.4. P.357–380.

Malmgren A.J. 1866. Nordiska Hafs-Annulater // Öfversigt af Königlich Vetenskapsakademiens förhandlingar, Stockholm. Bd.22. H.5. S.355–410.

McIntosh W.C. 1885. Report on the Annelida Polychaeta collected by H.M.S. Challenger during the years 1873–1876 // Report on the Scientific Results of the Voyage of H.M.S.Challenger during the years 1872–76. Vol.12. P.1–554, plates 551–539a, 551 maps.

Monro C.C.A. 1936. Polychaete worms II // Discovery Reports, Cambridge. Vol.12. P.59–197.

Monro C.C.A. 1939. Polychaeta. B.A.N.Z. // Antarctic Research Expedition Reports. Vol.4. No.4. P.87–156, 128 figures.

Parapar J., Helgason G.V., Jirkov I., Moreira J. 2011. Polychaetes of the genus *Ampharete* (Polychaeta: Ampharetidae) collected in Icelandic waters during the BIOICE project // Helgoland Marine Research. Vol.66. P.331–344.

Pettibone M.H. 1954. Marine polychaete worms from Point Barrow, Alaska, with aditional records from the North Atlantic and North Pacific // Proceedings of the United States National Museum. Vol.103. No.3324. P.203–356.

Read G., Fauchald K. (eds.). 2022a. World Polychaeta Database. *Ampharete* Malmgren, 1866. Accessed through: World Register of Marine Species at: https://www.marinespecies.org/aphia.php?p=taxdetails&id=129155 on 2022-07-23

Read G., Fauchald K. (eds.). 2022b. World Polychaeta Database. *Ampharete brevibranchiata* Treadwell, 1926. Accessed through: World Register of Marine Species at: https://www.marinespecies.org/aphia.php?p=taxdetails&id=338621 on 2022-05-07

Sars M. 1865. Fortsatte Bidrag til Kundskaben om Norges Annelider // Forhandlinger fra Videnskabs-Selskabet i Christiania. S.5–20.

Treadwell A.L. 1926. Polychaetous annelids collected by Captain R.A. Bartlett in Alaska in 1924, with descriptions of new species // American Museum Novitates. No.223. P.1–8.

Tzetlin A.B., Jirkov I.A., Markelova N.P. 1983. [Polychaeta of the White Sea (Spiomorpha, Drilomorpha, Terebellomorpha)] // Sbornik trudov Zoologicheskogo Muzeya MGU. Vol.20. P.166–186 [in Russian].

Uschakov P.V. 1950. [Polychaetes from the Sea of Okothsk] // Issledovaniya dal'nevostochnykh morei USSR. Vol.2. P.140–236, plates 141–142 [in Russian].

Uschakov P.V. 1955. [Polychaeta of the Far Eastern Seas of the USSR] // Opredeliteli po faune SSSR, izdavaemye Zoologicheskim Institutom AN SSSR. No.56. 445 p. [In Russian]

Zatsepin V.I. 1948. [Class Polychaeta] // N.S. Gaevskaya (ed.). Opredelitel' fauny i flory severnykh morei SSSR. Moscow: Sovetskaya Nauka. P.94–167 [in Russian].

Zettler M.L., Beermann J., Dannheim J., Ebbe B., Grotjahn M., Günther C.P., Gusky M., Kind B., Kröncke I., Kuhlenkamp R., Orendt C., Rachor E., Schanz A., Schröder A., Schüler L., Witt J. 2018. An annotated checklist of macrozoobenthic species in German waters of the North and Baltic Seas // Helgoland Marine Research. Vol.72. No.5. P.1–10.

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