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Revision of Ampharetidae (Polychaeta) with modified thoracic notopodia

I.A. Jirkov

Department of Hydrobiology, Biological Faculty, Moscow Lomonosov State University, 119899, Moscow, Russia.
e-mail: ampharete@yandex.ru

ABSTRACT: Ampharetidae comprises about 300 species and 100 genera, more than 50 are monotipic. As a first step towards a revision of the family, all 30 species with modified thoracic notopodia are reviewed. These 27 species had previously been organized into 11 genera, but several more genera need to be established if we follow a traditional approach to taxonomy of family. Based on a critical re-evaluation of 12 characters commonly used in ampharetid taxonomy and traditional weighting of these characters, it is proposed to combine these 30 species into 3 genera: *Anobothrus, Zatsepinia* and *Sosane*. *A posteriori* the following characters are of high value in ampharetid taxonomy: type of prostomium, modification of notopodia, presence/absence of a pair of well developed nephridial papillae behind the branchiae, presence/absence of a circular band on anterior thorax, number of uncinigers with modified notopodia, amount of uncinigers with neuropodia of thoracic type. The following characters are considered of low value for generic distinction among Ampharetidae: type of buccal tentacles, presence/absence of paleae, number of thoracic and abdominal uncinigers, pairs of branchiae, type of branchostyles. The taxonomic part of the paper includes redescriptions of 7 species based on type material and new records. *Anobothrus patersoni* sp.n., *A. mironovi* sp.n., and *A. nataliae* sp.n. are described as new to science. The species descriptions are accompanied by remarks on geographic and bathymetric distribution. The replacement of different species in different geographic areas is shown.

KEY WORDS: Polychaeta, Ampharetidae, new species.

Ревизия Ampharetidae (Polychaeta) с модифицированными торакальными нотоподиями

И.А. Жирков

Кафедра гидробиологии, Биологический факультет, Московский государственный университет им. М.В. Ломоносова, 119899, Москва, Россия.
e-mail ampharete@yandex.ru

Ampharetidae включают около 300 видов и всего около 100 родов, из которых половина — монотипичные. Как первый шаг ревизии семейства проведена ревизия всех 30 видов с модифицированными торакальными нотоподиями. Эти 30 видов ранее относили к 11 родам, но, если следовать традиционному подходу к таксономии семейства, следует выделить ещё несколько новых родов. Критический анализ 12 признаков, обычно используемых в таксономии семейства позволил сгруппировать

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эти 30 видов в три рода: *Anobothrus, Zatsepinia* и *Sosane*. *A posteriori* следующие признаки имеют высокий вес: тип простомиума, тип модификаций нотоподий, наличие/отсутствие пары хорошо развитых нефридиальных папилл позади жабр, наличие/отсутствие кольцевого пояска в передней части торакса, номер сегмента с модифицированными нотоподиями, число сегментов с невроподиями торакального типа. Следующие признаки имеют низкое значение и могут быть использованы только для видовой диагностики: тип ротовых щупалец, наличие/отсутствие опахал, число торакальных и абдоминальных сегментов и пар жабр, тип бранхостилей. Таксономическая часть статьи включает переописание 7 видов на основе типового материала и новых находок. Описаны новые для науки виды *Anobothrus patersoni* sp.n., *A. mironovi* sp.n., and *A. nataliae* sp.n. Описания видов дополнены данными по географическому распространению. Показано, что отдельные виды замещают друг друга в разных широтных и вертикальных зонах.

КЛЮЧЕВЫЕ СЛОВА: Polychaeta, Ampharetidae, новые виды.

Introduction

The objective of this study was to select reliable characters that can serve as a basis of the taxonomy of Ampharetinae. Traditionally used characters led to the erection of more than fifty monotypic genera for a total of about 300 species only! As Holthe (1986b) stated: «when all genera become monotypic, the generic category has become void of information». It looks like polychaetologists exactly follow the known rule that «If you can distinguish two animals, they belong to different genera; if you cannot, to different species». To accomplish a revision I selected a well-defined group of species with modified thoracic notopodia. These notopodia always present in the posterior thorax, differ by their location, shape, and chaetation pattern. The species studied constitute the entire tribe Sosanini Holthe, 1986b plus *Mugga* and *Muggoides* that are considered as genera «with uncertain tribal affinities» (Holthe, 1986b).

Below I use for generic and specific definitions number of segments (S), number of thoracic segments (TS), number of thoracic uncinigers (TU), number of abdominal uncinigers (AU), and number of uncinigers (U). For Ampharetidae TU–1 (1st TU) = S–7. Since TS depends on the position of the first segment with notopodia (it can be S–4, S–5 or even S–6 because notopodia on S–4 or even S–5 segments may be absent), the term TU is more preferable than TS.

Remarks to taxonomical value of characters

1. Prostomium. In most genera the prostomium is subdivided by a U-shaped groove, however, several genera lack such furrow at all (*Samythella*-type). The middle lobe is usually more or less rounded (*Ampharete*-type). In *Amage* and related genera it forms more or less developed lateral horns (*Amage*-type). In *Amphicteis* and *Hypania* there are two longitudinal ridges (they are never glandular contrary to some authors) on the middle lobe (*Amphicteis*-type). The U-shaped part is usually partly covered by branchial bases, therefore such a prostomium appears trilobed and is usually called so, although it has only two parts. The U-shaped part can bear a pair of transversal nuchal(?) organs of various shapes (*Amphicteis*, *Phyllocomus* and related genera, *Jugamphicteis*). I suppose it is plesiomorphic state, while (1) furrow, (2) lateral horns, (3) two longitudinal ridges and transversal nuchal organs, (4) undulating nuchal organs of *Jugamphicteis* are synapomorphies. The main types of prostomia along with possible ways of their evolution are shown in Fig. 1.

2. Nephridial papillae. All Terebellomorpha have specilized nephridia in the anterior part of the body. Their taxonomic importance has been shown by Fauvel (1897) and Hessle (1917). These nephridia open as nephridial papillae, however usually papillae are not seen or

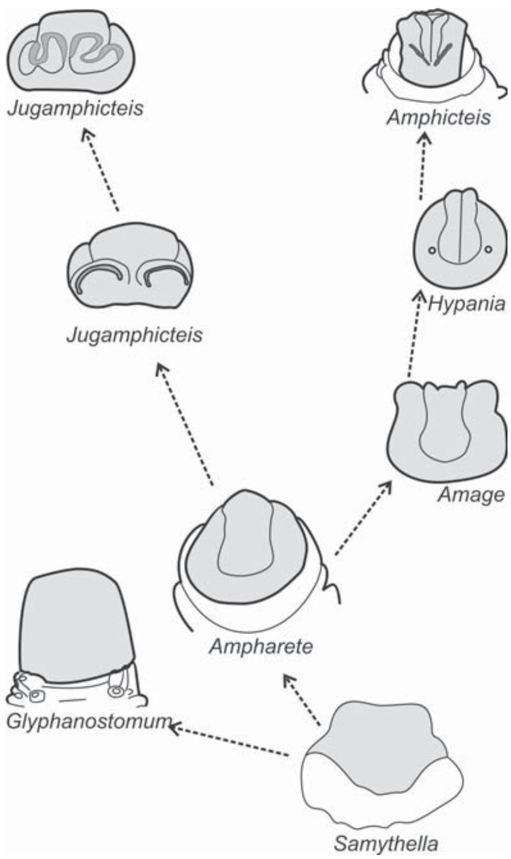

Fig. 1. Main types of prostomia and possible ways of their evolution.
Рис. 1. Основные типы простомиумов и возможные пути их эволюции.

hardly visible. They always open between notopodia and neuropodia. Ususally papillae are not visible, but several species of Ampharetinae also have prominent well visible nephridial papillae situated behind the branchia. These species belong to genera *Neosabellides*, *Gnathampharete* sensu lato, *Ampharete* sensu lato (Jirkov, 1997, 2001), and *Anobothrus* as it defined herin. I suppose such nephridial papillae as synapomorphic state developed independently several times.

3. Circular band in anterior thorax. In *Anobothrus* this band is completely circular, without a gap. It is not convex and resembles similar bands of some Sabellidae, as it does not stain (our observations). Usually this character is not mentioned in the descriptions, may be because it is uncommon in Ampharetidae and also because it is often poorly visible. Desbruyères (1976) and Holthe (1986b) compare this band with those of *Melinnampharete*, *Eusamythella*, and *Neosamytha*. However, the band in *Anobothrus* is *circular*, while in *Melinnampharete*, *Eusamythella*, and *Neosamytha* it can only be seen as a *dorsal* ridge. On the other hand, all species included here in the genus *Anobothrus* have absolutely identical bands (only their positions differ). I have found it in all examined species, so I assume that other species in this genus have it as well. The bands are visible to different degrees in different specimens of the same species, and staining does not help, contrary to the case of the band connecting modified notopodia. Circular band is synapomorphia.

4. Types of modification of notopodia and notopodial chaetae. The simplest is the modified notopodia similar in shape to others, but slightly shifted dorsally and connected by a low glandular band; their chaetae are more or less modified. SEM examination shows that chaetae of modified notopodia are covered with larger scales than other chaetae. This type of modification is known for *Anobothrus* Levinsen, 1884; *Anobothrella* Hartman, 1967; *Melythasides* Desbruyeres, 1986; *Sosanides* Hartmann-Schröder, 1965; *Zatsepinia* Jirkov, 1986. In taxa with the second type of modification (*Sosane* Malmgren, 1866; *Mugga* Eliason, 1955; *Muggoides* Hartman, 1965; *Sosanella* Hartman, 1965; *Sosanopsis* Hessle, 1917; ? *Melinnata* Hartman, 1965; Genus A sensu Uebelacker, 1984) both modified notopodia and their chaetae differ from others; modified notopodia are distinctly flattened across the body. The modified notopodia of this type gives us impressions how pectinariids anal hooks appear. A review of species with the second type of modification can be found in Jirkov (1994).

Type of modification of thoracic notopodia in *Anobothrus* and *Sosane* for my opinion does not seem to be homologous in the sense that it appears in these genera independently and are good synapomorphies.

Table 1. Taxonomic characters of Ampharetidae with modified notopodia.
(generic names after Jirkov (1994, 2001), for original names see generic definitions).

Таблица 1. Таксономические признаки Ampharetidae с модифицированными нотоподиями.
(родовые названия по Жиркову (1994, 2001), для оригинальных названий см. диагноз рода.

species	1	2	3	4	5	6	7	8	9	10	11	12	13
characters	of generic level							of species level					
Anobothrus bimaculatus	1	?	?	1	6	?	?	?	?	11	4	0	?
A. mancus	1	1	?	1	7	?	?	?	?	11	4	0	?
**A. laubieri*	1	1	1	1	8	2	14	0	2	12	3	0	12
***A. patersoni*	1	1	1	1	8	2	14	0	2	12	4	0&1	12
***A. antarctica*	1	1	1	1	8	?	?	1	2	12	4	1	12
***A. glandularis*	1	1	1	1	8	?	?	0	2	12	4	0	12
***A. mironovi*	1	1	1	1	8	2	14	0	2	12	4	0	12
**A. gracilis*	1	1	1	1	8	2	14	0	2	12	4	0	13
**A. patagonicus*	1	1	1	1	8	?	?	0	1	12	4	0	15 18
A. paleatus	1	?	1	1	9	2	?	?	2	12	4	0	12 13
A. pseudoampharete	1	?	?	1	8	?	?	?	2	12	4	0	15
A. apaleatus	1	?	1	1	8	?	?	1	0	12	4	0	12
***A. nataliae*	1	1	1	1	9	2	14	0	2	12	4	0	12
S. bathyalis	?	0	0	2	9	?	?	0	1	9	3	0	12
**S. wahrbergi*	1	0	0	2	9	?	?	0	1	9	3	0	8
S. americana	?	?	0	2	10	?	?	?	1	10	3	0	?
S. cinctus	?	?	0	2	10	?	?	0	0	10	3	0	13
S. occidentalis Hartman	1	?	0	2	9	?	?	0	1	11	4	0	>7
***S.* sp.	1	0	0	2	10	?	?	0	0	12	4	0	11
**S. wireni*	1	0	0	2	10	2	14	0	0	12	4	0	11
***S. wireni* sensu Gibbs	1	0	0	2	10	?	?	0	0	12	4	0	12
S. hesslei	1	?	0	2	10	?	?	0	0	12	4	0	13
***S. kerguelensis*	1	0	0	2	10	2	14	0	0	12	4	0	13
***S. holthei*	1	0	0	2	10	2	14	0	0	12	4	0	14 17
S. occidentalis sensu Williams	1	?	0	2	10	?	?	0	1	12	4	0	12
**S. sulcata* s. str.	1	0	0	2	10	2	14	0	1	12	4	0	12
**S.* aff. sulcata	1	0	0	2	10	2	14	0	1	12	4	0	13
S. sp. Uebelacker	1	?	0	2	11	?	?	0	0	12	3	0	11
S. apalea	?	?	0	2	11	?	?	?	0	13	3	0	9 11
***Z. rittichae*	0	0	0	1	7	?	?	0	0	10	2	0	17
**Jugamphicteis* spp.	3	?	?	3	15	0	14	0	2	14	4	0	15
**Ampharete falcata*	1	1	0	4	13,14	2	14	1	2	12	4	0	12
**Ampharete vega*	1	1	0	4	13,14	2	14	1	2	12	4	0	24 28
Amphicteis vestis	1	?	0	3	15	0?	14?	0	2	14?	4	0	10 11
Ymerana pteropoda	2?	?	?	3	11	?	?	?	0	10	3	?	>7

Characters of generic level:
1 — prostomium 0 — *Samythella*-type, 1– *Ampharete*-type, 2 — *Amage*-type, 3 — *Jugamphicteis*-type
2 — pair of nephridial papillae behind branchiae: 0 — absent, 1 — present.
3 — circular band of anterior thorax: 0 — absent, 1 — present.
4 — type of modification: 1 — *Anobothrus*, 2 — *Sosane*, 3 — foliaceous rudimental notopodia of AU–1, 4 — enlarged rudimental notopodia of AU-1&2.
5 — number of U with modified notopodia.
6 — number of AU with neuropodia of thoracic type.
7 — number of last U with neuropodia of thoracic type.
Characters of specific level:
8 — buccal tentacles: 0 — smooth; 1 — pinnate.
9 — paleae: 0 — absent, 1 — smaller the most developed notochaetae, 2 — bigger the most developed notochaetae.
10 — number of TU.
11 — number of pairs of branchiae.
12 — type of branchostyles: 0 — smooth, 1 — papillate.
13 — number of AU.
? means absence of data
** — type(s) have been investigated; * — species have been investigated, characters of others are given according to their original descriptions, the data on number of AU with neuropodia of thoracic type of *A. paleatus* kindly provide me N. Budaeva, investigated type for my request. Rows with different shadow include different valid genera (totally 6 in the table). Lines within *Anobothrus* and *Sosane* separate genera following traditional generic characters (12 within *Anobothrus* and *Sosane* only).

Some genera have modified abdominal notopodia (I consider abdomen as part of the body without chaetigerous notopodia). In the simpler case (*Ampharete vega, A. falcata*) AU–1 and AU–2 have enlarged notopodia. These two segments have neuropodia of the thoracic type (see below).

Some other groups possess modified abdominal notopodia. One is the genus *Jugamphicteis*. This genus sharply differs from other Ampharetidae by its prostomium and it is the only genus where modified notopodia are situated on a segment with notopodia of the abdominal type.

Ymerana pteropoda also possesses modified abdominal notopodia on AU–1. Unfortunately, I have not been able to examine this species and the corresponding row in the Table 1 contains no data.

«*Amphicteis*» *vestis* also also possesses modified abdominal notopodia on AU–1. Sure it is not *Amphicteis* because of quite different prostomial shape, but certain position remains unclear awating studying types.

5. Number of uncinigers (U) with modified notopodia. Within Ampharetidae neuropodia always start from S–6, so this character is the same as the number of segments, but the number of U is much easier to count. Remarkably, notopodia of different kind of modification are situated on different U, supporting their independent origin and value as synapomorphies.

6, 7. Type of neuropodia (Fig. 7). Neuropodia of Ampharetidae are fin-shaped. In the most plesiomorphic genera (*Samythella*, *Phyllocomus* and others) they are the same throughout the body. But in most species thoracic and abdominal type of neuropodia are distinguished by Jirkov (2001). Mackie (1994) was first to note the difference between thoracic and abdominal neuropodia. Thoracic ones have uncini into more or less deep grooves while abdominal ones have uncini right on the edge of neuropodia. In some genera (e.g. *Amphicteis*, *Amage*) thoracic neuropodia are limited to the thorax, and abdominal neuropodia are limited to the abdomen. However, in other genera the change in type of neuropodia does not coincide with the transition between thorax and abdomen. For example, in *Melinna* spp. the last two TU have neuropodia of the abdominal type. All species of *Grubianella* have neuropodia of AU–1 of the thoracic type. All examined by me species of *Ampharete* and *Gnathampharete* (sensu Jirkov, 1997) have neuropodia of AU–1 and AU–2 of thoracic type, despite some variation in the number of TU. On the other hand, within *Lysippe* sensu Jirkov, 2001 the total number of neuropodia of thoracal type is constant, while the number of TU varies. The pattern of distribution and variation of thoracal type neuropodia are synapomorphies.

8. Buccal tentacles are smooth or pinnate (covered with cilia), arising from the buccal cavity and capable of being drawn into it. The presence of cilia is usually considered a generic character, but in my opinion the value of the character needs to be reconsidered because buccal tentacles of the juveniles are ciliated in *Alkmarija romijni* (Cazaux, 1982) and *Amphysamytha galapagensis* (Zottoli, 1983), whereas the adults have smooth buccal tentacles. Holthe (1986) also does not accept ornamentation (smooth/pinnate surface) of the buccal tentacles as a generic character and includes in *Melinnampharete* species with both smooth and pinnate tentacles. Only three genera (*Ampharete*, *Gnathampharete*, *Melinnampharete*) have ciliated (papillose) tentacles. Most of the *Anobothrus* species of *Anobothrus* have smooth tentacles except for *A. antarctica* that has papillose ones, also this species has papillose branchiae, while most others have smooth ones (see below). Neither smooth nor pinnate are apomorphic of plesiomorphic as this states seem easily transfer back and forth.

9. Paleae. Chaetae of notopodia of S–3 are called paleae. Paleae can be similar or even smaller or much larger than normal notochaetae. Usually the more pronounced the difference between palea and notochaetae is, the more important is the shape of paleae taxonomically. But within a genus the form of paleae can vary significantly. An *Ampharete* species studied by me shows the largest amplitude and the complete extent of variation (Fig. 2). *A. longipale-*

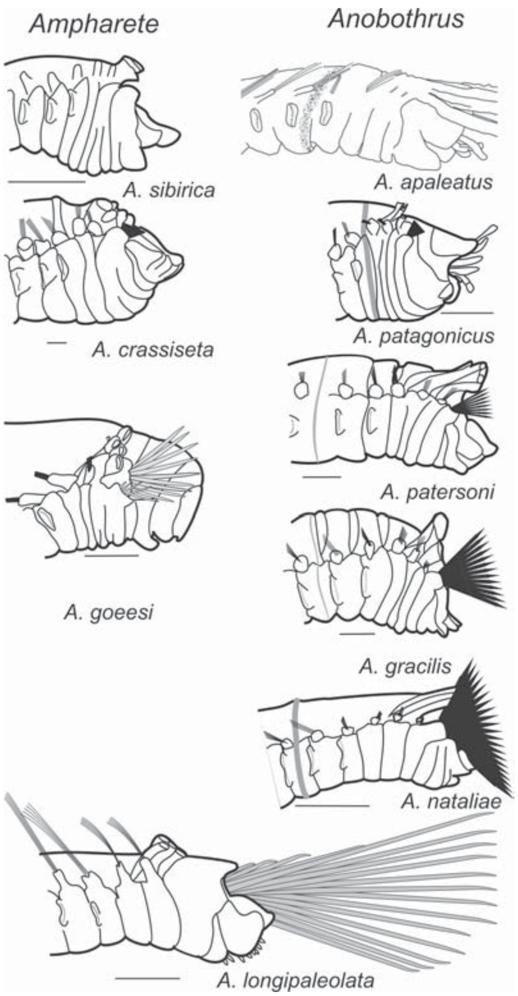

Fig. 2. Clines of paleal developing (modified after Jirkov, 2001: 440, *A. apaleatus* after Reuscher et al., in press).

Рис. 2. Клины развития опахал. По Жиркову (2001, изменено, *A. apaleatus* по Reuscher et al. (in press).

olata Uschakov, 1950 possesses very strong, huge paleal chaetae that are several times longer than the body width. Some species (*A. finmarchica* (Sars, 1865) and similar species) have paleal chaetae distinctly smaller than those in *A. longipaleolata*, but they are still much bigger than the most developed notochaetae. Paleal chaetae of *A. crassiseta* Annenkova, 1929 and *A. safronovae* Jirkov, 1996 are almost of the same size or even less than notochaetae. Paleal setae of *A. borealis* (Sars, 1856), *A. octocirrata* (Sars, 1835) are hardly visible. In *A. sibirica* (Wiren, 1883) and *A. petersenae* Jirkov, 1997 the paleae are absent. Paleae can also be absent in some specimens of *A. safronovae*. In reality the clinal variability of paleae chaetae size is even more gradually. *Anobothrus* gives another example of such a cline: the size of paleal setae decreases in the row *A. nataliae–A. patersoni–A. gracilis–A. patagonicus–A. apaleatus*. In 2001 I wrote that *Anobothrus* whithout paleae has not been found yet, now (Reuscher et al., in press) *A. apaleatus* has been described. Neither size of palea nor even presence/absence can be described in terms of apo- and plesiomorphic states due their extremely high variation.

10. Number of TU. This meristic character is traditionally considered as one of the basic generic characters. It shows slightly *variability within a species.* In all species investigated by me at least about 1% of the specimens shows a different number from normal for certain species. As this number is low, it is necessary to check at least 300–400 specimens, which is evidently rarely done. Number of TU has no any value as apo- or plesiomorphic state.

11. Number of pairs of branchiae. The number of pairs of branchiae is mainly used as a generic character in the Ampharetinae. The plesiomorphic condition is probably the presence of four pairs. However, in some species the last pair of branchiae develops only in adult worms, e.g., *Alkmarija romijni* (Cazaux, 1982), *Ampharete acutifrons* (Clavier, 1984), *A. vega* (Jirkov, 2001), *Hobsonia florida* (Zottoli, 1974), *Hypania invalida* (Oustroumoff, 1899), *Paedampharete acutiseris* (Russell, 1987), *Phyllocomus* sp. (Harris, 1987), and *Samythella elongata* (Jirkov, 1986b). The characteristics of the adult branchial set develop gradually (position of branchostyles and and the shape of the branchophores) also develope only in adult worms. The shape of branchophores reflects movement of place of attachment of branchostyles during ontogenesis. Given such a variation, it can be assumed that one (or even two) pairs of branchiae do not develop in adults (juvenile condition); as an abnormality I have seen specimens of

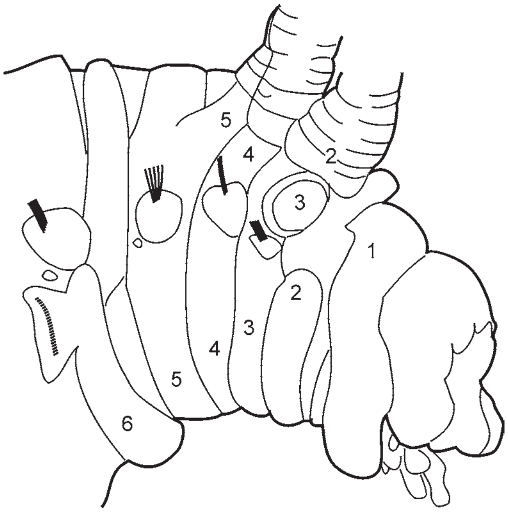

Fig. 3. Location of branchia, neuropodia and notopodia (after Jirkov, 2001: 441, *Amage anops*).
Рис. 3. Положение жабр, невро- и нотоподий. По Жиркову (2001: 441, *Amage anops*).

Samythella elongata with 5 branchiae instead of 6 (Jirkov, 1986b). Moreover, Fauvel (1927) for *Amage adpersa* and Annenkova (1930) for *Hypaniola kowalewskii* described individual variation in the number of branchiae. Species with a lower number of branchiae arose independently in different evolutionary branches: in each group that is large enough, one can find species identical in other generic characters but with different numbers of branchiae. Thus, it is incorrect to establish genera based on a difference in number of branchiae. Fauvel (1927) and Holthe (1986b) also included in one genus species with a different number of branchiae. Branchiae belong to S–2, S–3, S–4, and S–5 (Fig. 3), but in different genera they move in somewhat different position (Fig. 4). Number of branchiae has no any value as apo- and plesiomorphic state, but branchial arrangement seems can be used for this purpose. Remarkably species with *Anobothrus* and *Sosane*-type modified notopodia has different branchial arrangement.

12. Type of branchostyles. Branchiae (branchostyles) are usually described as smooth, pinnate, or foliose. In reality, however, this difference is not so clear. Smooth branchia are very rarely truly smooth but rather they are annulated or with more or less distinct transversal ridges. Species with pinnate branchiae can have one, two, or three pairs of branchiae, while others are smooth. This variability can be observed both intra- and interspecifically. Ontogenetically pinnate branchiae develop from smooth ones Harris (1987). Type of branchostyles has no any value as apo- and plesiomorphic state.

13. Number of AU. This meristic character is traditionally used as a basic species character. Usually it shows very small individual variation (< 1%) in species with a number of AU<14, but in species with more AU the more the number of AU the more its variation and so the taxonomic

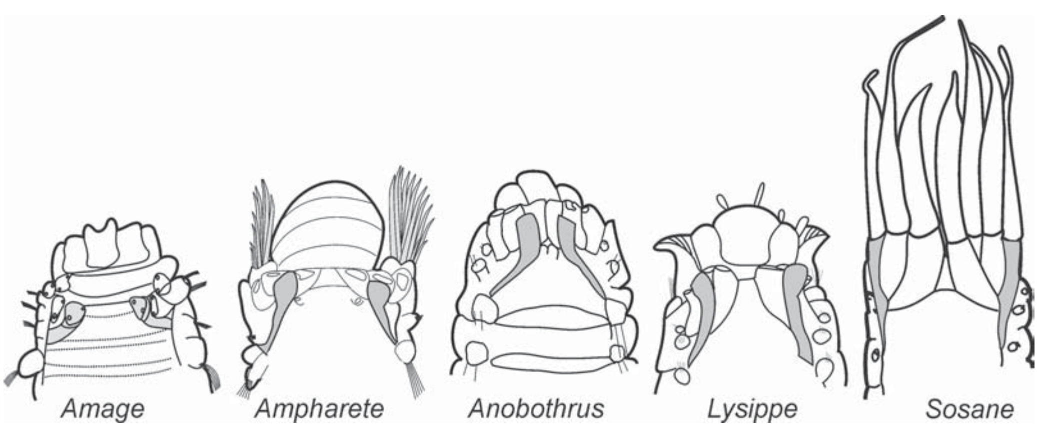

Fig. 4. Origin of branchia in different genera. Shaded branchiae of S-5 (after Jirkov, 2001: 441).
Рис. 4 Происхождение жабр в разных родах. Залиты серым жабры пятого сегмента. По Жиркову (2001: 441).

value of this character decreases. Exact number of AU has no any value as apo- and plesiomorphic state, but degree of variation has some. In all species with simple prostomia the number of AU is high and variable.

I agree with Holthe (1986b: 11) that «the purpose of evolutionary and phylogenetic systematics is not in the first hand to define taxa, but to discover monophyletic groups of species and classify accordingly». And all we can do is to use characters to judge which species are related. There is not much sense to state *a priori* whether certain characters are of generic or specific level, certain remarks on character variability can be done a priori indeed. I base my taxonomic system on the following major assumptions.

1. If a character shows interspecific variation it can not be used for generic classification.

2. Some characters are of lower, others of higher value. For example, a purely meristic character has a low taxonomic value. Taxa merely based on meristic characters can easily be artificial, as convergence originates easier in such characters. On the other hand, characters related to complex structures (like the structure of prostomium) have a higher value.

3. Genera should be erected on the basis of several functionally independent characters (=synapomorphic characters) showing distinct gaps. The more characters are involved, the higher is the probability that this similarity is due to common origin rather than due to homoplasy.

Among species listed in the Table 1 on the basis of the first 7 characters can be mark out 2 groups, which are evaluated here as *Anobothus* and *Sosane*. Besides, species of each group have the same branchial structure regardless the number of branchiae. The fact that these 8 characters are most likely independent and not functionally connected allows us suggets that these two genera are monophyletic taxa. It is very doubtful that homoplasy can create such a picture. These characters and their combination allow to separate genera, so they can be counted as «characters of generic importance, or level».

For the practical use of certain characters not only their presence in a certain taxon is important, but the fact that a set of these characters is constant. That is, characters typical for a natural group (in this case a genus) have prognostic properties. For example, all species possessing modified notopodia of *Anobothrus*-type and a prostomium of *Ampharete*-type should have a glandular ridge in the anterior thorax, a pair of nephridial papillae behind the medial branchiae, and neuropodia of thoracic type on the two anteriormost AU. This statement could easily be checked by studying the types of *A. bimaculatus* and *A. mancus*, which unfortunately are not available for me.

Thus, we observe «excessiveness» of diagnostic characters. For a purely utilitarian classification a smaller number of characters would be sufficient. But exactly this «excessiveness» makes us believe that the taxa are the natural groups.

If characters are not functionally connected, we can suppose that they evolve independently. As it follows from the theory of probability, a joint probability of independent events equals to multiplication of their probabilities. So we can count probability of accidental (i. e. convergent) origin of these independent characters as infinitely small. Therefore, it is not accidental, but is a result of their common origin. These characters are rarely important for generic diagnostics only but they can be used to recognize monophyletic groups of species. I am starting the analysis with characters only because the estimate of genotype similarity can easier be done by analysing morphological similarity.

The remaining six characters more or less vary within the genera and give us examples of mosaic evolution, convergence or clinal variation within each genus. Both in the case of meristic characters (9, 10, 12, 13) and in the case of continuous (degree of paleal development) we have clines that quite correspond to homological variability rows described by Vavilov (1922). Both the range of variation in these clines and frequency of distribution within a cline are specific for groups of related species. Four of these characters (9, 10, 12, 13) are meristic. However, the degree of variation in these characters is also characteristic for the genera and can be counted as an additional character of generic level. For example, *Anobothrus* has lower variation than *Sosane* in number of TU, number of AU and number of TU with modified notopodia, i.e. smaller degree of variation in meristic characters is characteristic for *Anobothrus*. Character 13 is dependent on characters 7 and 9. Paleae (character 8) demonstrate a distinct cline within several natural genera and provide an example of convergence, so I agree with Day (1964) who claims that this character is not suitable for separating natural groups of species. The type of branchostyles (character 11) is not considered suitable here for generic distinction as discussed above, and in agreement with earlier authors (Monro, 1939; Day, 1964; Kucheruk, 1976; Fauchald, 1977).

Material Studied

The present research is based on the following collections: Department of Hydrobiology of Moscow State University (DHMSU), National History Museum, former British Museum (Natural History) (NHM), Institute of Oceanology of the Russian Academy of Science (OIRAN), Zoological Institute of the Russian Academy of Science, St.-Petersburg (ZIN), Zoologisches Institut und Zoologisches Museum, Universität Hamburg (ZMH). More detailed locality information is given in species descriptions.

Parapodia were dissected and mounted on slides in glycerin jelly. For examination the worms were stained with methylene blue to reveal external morphology (structure of parapodia, prostomium, peristomium and pharynx). Stained worms were examined in water because ethanol immediately dissolves any staining. Even in water some structures can be seen for several minutes only, then staining penetrates into the tissues and contrast decreases. Worms slowly lose colour after they are put into ethanol and become completely colourless after a day, so the process can be repeated as many times as necessary. Drawings were made with the help of a camera lucida under a dissecting microscope.

Taxonomic section

Anobothrus Levinsen, 1884 emend.

(= *Anobothrella* Hartman, 1967; *Melythasides* Desbruyeres, 1976; *Sosanides* Hartmann-Schröder, 1965)

Type species: *Ampharete gracilis* Malmgren, 1866.

DIAGNOSIS. Prostomium *Ampharete*-type. One pair of notopodia in posterior thorax (usually TU–8 or TS–5 of the latter) slightly elevated, connected by a low glandular band (sometimes visible only after staining), modified notopodial chaetae sometimes only slightly differ from notopodial chaetae. Connecting band ciliated at least in the type species (Holthe, 1986a). Three or four pairs of branchiae, three pairs form transversal rows without any median gap, the forth (branchiae of S–6), if present, located behind the innermost and connected to them; the inner four branchiae more or less distinctly shorter than outer ones. Circular band in anterior thorax, anterior to notopodia of TU–3 or more rarely TU–2 or TU–1 (?). A pair of large nephridial papillae situated behind branchiae. Neuropodiae of first two AU of thoracic type, followed by normal abdominal ones.

Genus includes at least 13 species:

Anobothrus antarctica Monro, 1939;

Anobothrus apaleatus Reuscher, Fiege, Wehe, in press

Anobothrus bimaculatus Fauchald, 1972;

Anobothrus glandularis (Hartmann-Schröder, 1965) **comb.n**. as *Sosanides*;

Anobothrus gracilis (Malmgren, 1866) as *Ampharete*;

Anobothrus laubieri (Desbruyeres, 1978) as *Melythasides*;

Anobothrus mancus Fauchald, 1972;

Anobothrus mironovi **sp.n**.;

Anobothrus nataliae **sp.n**.;

Anobothrus paleatus Hilbig, 2000;

Anobothrus patagonicus (Kinberg, 1867) as *Ampharete*;

Anobothrus patersoni **sp.n**.;

A. pseudoampharete Schüller, 2008.

Not *Anobothrus trilobatus* Hartman, 1969. The species belong to the group of genera which I am revising now.

Not *Anobothrus nasuta* (Ehlers, 1887) as *Amphicteis*; nothing is known about the presence of modified notopodia in this species. Moreover, the species has a distinctly different branchial set (branchiae are widely apart) so I suppose it belongs to another genus.

REMARKS. Original descriptions of the type species of *Sosane* (*S. sulcata* Malmgren, 1866) and *Anobothrus* were not detailed enough and without illustration of modified notopodia. So Hartmann-Schröder (1971) synonymized these genera. Jirkov (1989) followed her opinion. After Holthe (1986a) redescribed the type material and illustrated the modified notopodia of *S. sulcata,* became obvious that these two genera are different. Hartmann-Schröder (1996) also followed his opinion.

Zatsepinia rittichae Jirkov, 1986 is similar to *Anobothrus* in the type of notopodial modification. However, it distinctly differs from other species of *Anobothrus* by the shape of prostomium and absence of a transversal band in the anterior thorax. These differences are believed sufficient to establish *Zatsepinia* as the third valid genus with modified thoracal notopodia.

Following genera are considered here as junior synonyms.

Sosanides Hartmann-Schröder, 1965 with the type species *S. glandularis* Hartmann-Schröder, 1965, see re-description below does not differ from *Anobothrus* s.str. and is considered here to be its junior synonym.

Melythasides Desbruyères, 1978 with the type species *M. laubieri* Desbruyères, 1978, differs from *Anobothrus* s.str. only in the number of pairs of branchiae: 3, instead of 4. However, branchial arrangement of different *Anobothrus* species presents an excellent example of a clinal variation: *A. glandularis* has all branchiae of equal size and shape, inner pair of branchiae of *A. antarctica* is slightly slimmer and can be much shorter than the others; the two inner pairs of branchiae of *A. gracilis* and *A. mironovi* are normally half as long and slimmer than the rest, and the posterior pair of branchiae of *A. patersoni* is only slightly bigger than the nephridial papillae. This sequence is quite similar to ontogenetic development of branchiae of *A. gracilis* and other ampharetids as mentioned above. *Melythasides laubieri* represents the next point of the cline as a species with completely reduced forth pair of branchiae. So it seems unreasonable to separate *M. laubieri* into its own monotypic genus based solely on this character. Holthe (1986b) proposed to make *Melythasides* a junior synonym of *Melinnampharete* Annenkova, 1937, but we cannot accepted it because *Melinnampharete* lacks modified notopodia and a different structure of anterior thoracic bands.

Anobothrella Hartman, 1967 with the type species *A. antarctica* Monro, 1939 differs from most *Anobothrus* species by presence of papillate branchiae and buccal tentacles. However, the same structure of branchostyles is also characteristic for some branchostyles of *Anobothrus patersoni* (for detalils see description below), and the degree of the development of papillae varies in *Anobothrus antarctica* and *A. patersoni*. Since the similarity of the remaining characters specific to *Anobothrus* is high, it seems more logical to put *A. antarctica* back in genus *Anobothrus*.

A couple of species described by Fauchald (1972): *A. bimaculatus* and *A. mancus* according to traditional approach should be moved into another genera. However K. Fauchald has not do it, probably because of the high similarity of them to *Anobothrus*. I agree with him.

Chaetae of modified notopodia of *Anobothrus* are smooth as is characteristic for most ampharetids, or covered with scales; however within this genus the difference between setae of modified and normal notopodia can be absent. For example, judging from our SEM micrograph, in *A. gracilis*, there is no difference (contrary to Hessle, 1917); but in *A. antarctica* and *A. glandularis* setae of normal notopodia are smooth, while modified are covered with scales.

Despite the number of branchiae not being considered here as a reliable generic character, the branchial arrangement is characteristic for *Anobothrus*: in all investigated species three pairs of branchiae are in straight transversal row without a medial gap; if a fourth pair of branchia (of S-5) is present, it is always placed behind and slightly lateral to the inner one.

A key to the known species of *Anobothrus* and a re-description of investigated species is given below. Species which I have not examined are given in the key and table only, as I have nothing to add to published descriptions.

KEY TO SPECIES

1. 11 TU 2
– 12 TU 3
2. Modified notopodia on TU–6 ... *A. bimaculatus*
– Modified notopodia on TU–7 .... *A. mancus*
3. Modified notopodia on TU–7 4
– Modified notopodia on TU–8 .. *A. nataliae* sp.n.
4. Paleae completely absent ....
– Paleae smaller than the most developed notochaetae, circular band anterior to notopodia of TU–1; 15–18 AU .... *A. patagonicus*
– Paleae bigger than the most developed notochaetae, circular band anterior to notopodia of TU–2 or TU–3, 12–13 AU 5
5. Circular band anterior to notopodia of TU–2; 3 pairs of branchiae .... *A. laubieri*
– Circular band anterior to notopodia of TU–3; 4 pairs of branchiae 6
6. Posterior branchophores at least two times slimmer and shorter than others, their branchostyles at least ten times shorter than others .... *A. patersoni* sp.n.
– Posterior branchophores of the same length as others, their branchostyles shorter than others no more than in 2–3 times 7
7. Branchostyles and buccal tentacles papillate, high of outer branchophores equal to 3–5 thier diameters ....*A. antarctica*
– Branchostyles and buccal tentacles smooth, high of outer branchophores less than 2 their diameters 8
8. 12 AU 9

– 13 AU .... *A. gracilis*
9. Both pairs of inner branchophores approximately 1.5 times slimmer than outer .... *A. mironovi* sp.n.
– All branchophores and branchostyles of equal size or inner pair slightly smaller ... *A. glandularis*

A. pseudoampharete Schüller, 2008 not included in the key.

Anobothrus antarctica Monro, 1939

Fig. 5

Anobothrus antarctica Monro, 1939: 139–140, fig. 22. Type: NHM 1941.3.3.1. Type locality: Sta. 103 67°03′ S 74°29′E 437 m.
Anobothrella antarctica — Hartman, 1967: 155–156, Pl. 45; Hartmann-Schröder, Rosenfeldt, 1989: 83; 1991: 82.
Neosamytha gracilis — Hartmann-Schröder, 1986: 89 (partim) — non Hartman, 1967.
Material examined. 23 specimens (19 samples) from collections of NHM (type), ZMH (identified by Dr. G. Hartmann-Schröder and Dr. P. Rosenfeldt as *Anobothrella antarctica* and *Neosamytha gracilis*) and ZIN (identified by Dr. V.G. Averintsev as *Anobothrus antarctica* and *Anobothrus patagonica*). Depth 175–2060 m.

DESCRIPTION. Up to 15 mm long (up to 45 mm according to Hartman, 1967). Prostomium *Ampharete*-type. Buccal tentacles numerous (more than 10), papillose. Paleae ca. 17–18 chaetae much bigger than the most developed notochaetae, long gradually tapering capillaries. Four pairs of branchiae. Branchophores very long, length of outer ones equal to 3–5 their diameters, connecting by lateral sides forming a high fold. No gap between inner branchiae. Position of branchostyle attachment form a broken line, the most caudal 3rd from lateral branchophore connected with notopodia of TS–3 (= S–5), medial one with notopodia of TS–2, both lateral pairs not associated with any segment. Diameter of inner branchophores slightly smaller than others, their branchostyles two times thinner than outer ones, length varying from almost equal to outer branchiophores to 2–3 times shorter (in holotype 3 times thinner and two times shorter). Anterior medial branchostyle of same diameter as outer ones, but usually half as long. Branchostyles densely papillate, size of papillae varying from hardly visible to quite distinct, making branchostyles appear shaggy (holotype with well developed papillae). Papillae appear to form transverse ridges. Branchophores also papillate, but more sparsely. A pair of large nephridial papillae between bases of branchophores of TS–3. Transverse band anterior to neuropodia of TU–3, characteristic for genus. 15 TS, 12 TU. Notopodia of TS–5 from last (TU–8) modified *Anobothrus*-type, connected dorsally with low glandular band. 12 AU, no rudimental notopodia and neuropodial cirri. Pygidium with numerous anal papillae, lateral ones not different. Notochaetae of modified notopodia covered with scales, others smooth. 35 uncini in TU–1 (holotype). Thoracic uncini with 2 rows of teeth, apical single or paired, some very small additional teeth present around apical; 4–5 teeth in profile. Tube thin-walled, muddy, covered with long foraminiferans oriented across.

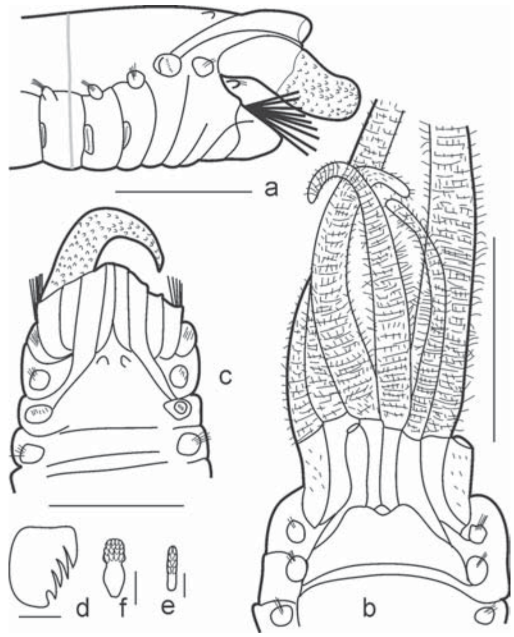

Fig. 5. *Anobothrus antarctica*.
a — anterior end, lateral view (ZHM P–19829), b, c — anterior end dorsal view (b — holotype, ZHM P–19829), d — TU–1 uncinus (holotype), e — thoracic uncinus, f — abdominal uncinus; a–d — original, e, f — from Monro, 1939. Scale a–c — 1 mm, d–f — 0.01 mm.
Рис. 5. *Anobothrus antarctica*.
a — передний конец сбоку (ZHM P–19829), b, c — передний конец со спины (b — голотип, ZHM P–19829), d — TU–1 uncinus (голотип), e — торакальная uncinus, f — абдоминальная uncinus; a–d — оригинал, e, f — по Monro (1939). Масштаб: a–c — 1 мм, d–f — 0,01 мм.

DISTRIBUTION. Circumantarctic, slope.

Anobothrus glandularis (Hartmann-Schröder, 1965) comb. n.

Fig. 6

Sosanides glandularis Hartmann-Schröder, 1965: 243–246, Abb. 242–244. type: ZMH P–15029 (HOLOTYPE), ZMH P–15305 (91 PARATYPES). Type locality: Isla Mocha, Chili, st. 76, 66 m.
Ampharete patagonica — Ehlers, 1913: 551 (non 1897: 129; 1901: 206) — non Kinberg, 1867.

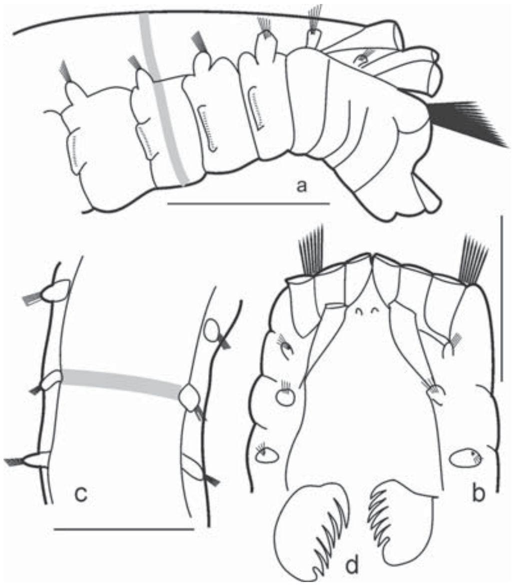

Fig. 6. *Anobothrus glandularis* (syntype).
a — anterior end, lateral view, b — anterior end dorsal view, c — dorsal view TU–7...TU–9, d — thoracic uncini. Scale 1 mm.

Fig. 6. *Anobothrus glandularis* (syntype).
а — передний конец сбоку, b — передний конец со спины, с — TU–7...TU–9, вид со спины, d — торакальные uncini. Масштаб 1 мм.

Material examined. Holotype and 91 paratypes, and one non-type specimen from 3 station.

DESCRIPTION. Up to 15 mm long. Prostomium *Ampharete*-type. Buccal tentacles numerous (more than 10), smooth. Paleae (8–16) much bigger than most developed notochaetae, gradually tapering long capillaries. Four pairs of branchiae. Branchophores relatively short (2 times shorter than in *A. antarctica*) connecting by lateral sides forming a fold. Positions of three branchostyles attachment on each side forming a broken line, the forth situated behind and between innermost and middle. No gap between anterior inner branchiae. Position of 4th branchophores varying, most commonly attached to inner and middle, but sometimes only slightly positioned anteriorly and remaining unattached. Forth branchophore connected to notopodia of S–5 (= TS–2), medial — with notopodia of S–4, both lateral pairs obviously not connected to segments. Diameter of all branchophores and branchostyles equal or inner pair slightly smaller than others. All branchostyles smooth. A pair of small, sometimes hardly visible nephridial papillae between bases of branchophores of S–2. Transversal band anterior to notopodia of TU–3, characteristic for the genus. 14 TS, 12 TU. Notopodia of TS–5 from last (TU–8) of modified *Anobothrus*-type and connected with low glandular band. 12 AU, no rudimental notopodia and neuropodial cirri. Pygidium with or without two small lateral lobes. Notochaetae of modified notopodia covered with scales, others smooth. Thoracic uncini with 6 teeth in profile.

REMARKS. Variation of meristic characters has been investigated in 26 complete worms, and one non-type specimen, all from collection of ZMH. Some variation was observed in the number of paleal setae only. See Remark to *A. patagonicus*.

DISTRIBUTION. Chile from Punta Tortuga to Galera 50–160 m (Hartmann-Schröder, 1965), Kaiser Wilhelm-II-Land depth 385 m (Ehlers, 1913: 551).

Anobothrus gracilis (Malmgren, 1866)

Fig. 7

Ampharete gracilis Malmgren, 1866: 365, fig. 75; type: Naturhistoriska Riksmuseet, Stockholm, has at least two samples of *Ampharete gracilis* (numbers 6562 and 6583) identified by Malmgren, these are not labeled as types, but may be syntypes of the species (Holthe, 1986 a). Type locality: Bohuslan, Sweden.

Anobothrus gracilis — Hessle 1917: 106–107, text fig. 12; Fauvel, 1927: 229–230, fig. 80 l-p; Annenkova, 1929: 496 (partim); Gorbunov, 1946: 39; Zatsepin, 1948: 150, tabl. XXXVII, 12; Holthe, 1977: 44; Banse, 1979: 1546 (synonymy); Holthe, 1986 a: 50–51, fig. 18, map 17; Hartmann-Schroder, 1996: 497–498, Abb. 242; Jirkov, 2001: 475–476 — non Uschakov, 1955: 372, fig. 138; Hartman, 1965b: 216, Hartman, Fauchald, 1971: 156; Hilbig, 2000: 192–194, fig. 8.9.

Sosane gracilis — Hartmann-Schröder, 1971: 463–464, Abb. 160, 161a; Jirkov, 1989: 114, fig. 22.1,2 (synonymy).

Ampharete arctica var. *gagarae* Uschakov, 1950: 248, fig. 32, table II, 7; 1955: 369, fig. 136.

Ampharete arctica — Tzetlin et al., 1983: 180 (partim) — non Malmgren, 1866.

Sosane sulcata nidrosiensis Bidenkap, 1907 — fide Hessle, 1917.

Material examined. 179 samples (612 specimens) from collections DHMSU, ZIN, OIRAN, ZMH, including topotype and types of *Ampharete arctica* var. *gagarae*; 9–1960 m, bottom temperature –1,66 – 9,22°C (Fig. 8).

DESCRIPTION. Up to 50 mm long. Tube long, muddy, smooth, thick-walled (thickness is several times less than inner diameter), anteriorly usually covered by flattened stones and shell fragments (similar to tubes of *Melinna elisabethae* and *Euchone analis*), in bigger worms these particles being more sparse. Prostomium *Ampharete*-type. Buccal tentacles numerous (tens), smooth. Paleae much longer than the most developed notochaetae, but of same width, gradually tapering long capillaries. The number of paleal setae 12 to 19, not related to length in worms longer than 20 mm. Four pairs of branchiae. First three branchostyles attach on each side of

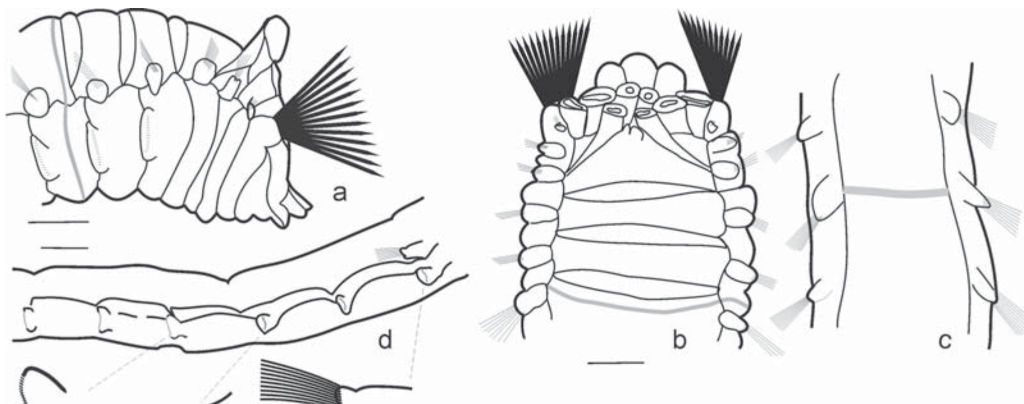
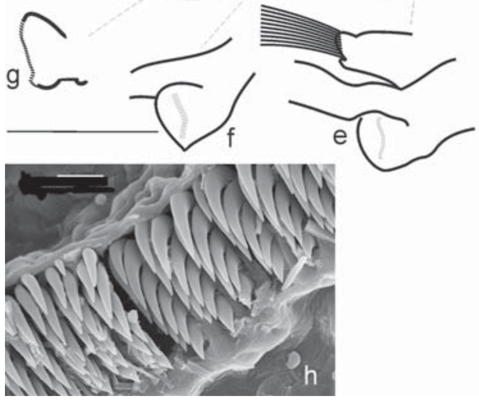

Fig. 7. *Anobothrus gracilis*.
a — anterior end lateral view, b — anterior end dorsal view, c — dorsal view TU–7...TU–9, d–g — lateral view TU–12...AU–5 and their parapodia: e — thoracal parapodium, f — thoracal type abdominal neuropodium; g — abdominal type abdominal neuropodium, h — thoracic uncini. Original, collection DHMSU: a, b — 69°30′N 45°00′E; c — 74°30′N 32°30′E; d–g — 68°54′N 46°16′ E; h — 68°50′N 45°00′E. Scales a–g — 1 mm, h — 10 μm.

Fig. 7. *Anobothrus gracilis*.
a — передний конец сбоку, b — передний конец со спины, c — TU–7...TU–9, вид со спины, d–g — TU–12...AU–5 вид сбоку и их параподии: e — торакальная параподия, f — абдоминальная невроподия торакального типа; g — абдоминальная невроподия абдоминального типа, h — торакальные uncini. Оригинал, коллекция кафедры гидробиологии МГУ: a, b — 69°30′ N 45°00′E; c — 74°30′N 32°30′E; d–g — 68°54′N 46°16′ E; h — 68°50′N 45°00′E. Масштаб: a–g — 1 мм, h — 10 мкм.

adult worms forming straight transversal line, the forth is situated more posteriorly and between innermost and middle. No gap between anterior inner branchiae. Small gap between posterior inner branchiae, in smaller worms less and can even be absent. Branchophores joined by their sides forming a high fold. Posterior (forth) branchophore connecting to notopodia of S–5 (= TS–2), median one with notopodia of S–4, both lateral pairs not showing any distinct connection with segments. Diameter of inner branchophores and branchostyles 1.5–2 times less than in the bigger outer ones, inner branchostyles distinctly shorter. All branchostyles smooth. A pair of nephridial papillae between bases of branchophores of S–5, as distance between these bases can be small, sometimes papillae hardly visible. Nephridial papillae present behind notopodia of TU–1 and TU–2, but usually hardly visible. Transversal band before notopodia of TU–3, characteristic for genus. 14–15 TS, 12 TU, notopodia of S–4 small, tufts only or even absent. Dorsum of anterior thorax often segmented. Notopodia of TS–5 from last (TU–8) *Anobothrus*-type modified and connected with low glandular ciliated (Holthe, 1986a). band. Normally 13 AU, as exception (<1% of population) up to 16 AU. Neuropodia of first two AU of thoracic type. No rudimentary notopodia and neuropodial cirri. Pygidium with or without small rounded papillae, without lateral cirri. All notochaetae both modified and normal notopodia are covered with scales. Uncini of TU–1: number ca. 80 per neuropodium; in profile 6 teeth, teeth in two rows, apical sometimes single, totally 11–12 teeth, no additional small apical teeth. Uncini of last AU: number ca. 50 per neuropodium; in profile 6 teeth, teeth in three rows. Tube thin-walled, detritus.

SIZE-DEPENDED VARIATION. Small worms (ca. 5 mm long) already have definitive number of TS and AU. But the number of paleal setae is lower (7–8). The most important difference can be seen in branchial structure: specimens of 4 mm length have 3 pairs of branchiae only, specimens of 6 mm length have 4 pairs of branchiae, but the 4th (posterior inner) pair is 3 times shorter and narrower than the others, and situated distinctly caudally to its definitive position. Branchial structure of small worms is very similar to one of adult *A. patersoni*.

REMARKS. Like any widespread species *A. gracilis* has a long list of synonymy. As usual, there is no possibility to decide which species authors deal with. Some examples below show that a complete list of synonymy cannot be given without re-investigation of the material.

Zatsepin (1948) mistakenly wrote that the 13th pair of notopodia was modified, in reality it is the 11th pair situated on S–13. Nevertheless, his data on biology and distribution of the species does relate to *A. gracilis* s. str., as there is no similar species within the Arctic basin.

«Hartman (1965) and Hartman and Fauchald (1971) described specimens from the deep Atlantic Ocean with 13 rather than 12 thoracic uncinigers; these specimens are no longer considered as belonging to this species. Hartman (1969) described specimens from California with 13 uncinigers; this is a lapsus calami. California specimens have 12 uncinigers, as originally described for this species» (Fauchald, Hancock, 1981: 40).

However in *A. gracilis* sensu Hartman (1965b), Hartman and Fauchald (1971) and Fauchald and Hancock (1981) modified notopodia are the third from the last or last so it does not agree with species diagnosis. Moreover I doubt that it is *Anobothrus*, because known species of *Anobothrus* never has modified the third from the last notopodia. At the same time it is usual for *Sosane* so mentioned specimen probably belong to *Sosane*.

Specimens of Annenkova (1929) deposed in ZIN are mainly (7 specimens) true *A. gracilis* s. str., and one *Lysippe labiata* and one *Sosane wireni*.

Syntypes of *Ampharete arctica* var. *gagarae* Uschakov, 1950 are deposed in ZIN. Most of them are quite typical *Anobothrus gracilis*. There are some worms of other genera, obviously placed there erroneously. Misidentification of *Anobothrus gracilis* as *Ampharete finmarchica* is quite common. I have found such a misidentification while checking collections of ZIN and OIRAN; it is reflected in the given synonymy. More examples can be found in Banse (1979). The reason is probably that modified notopodia only slightly differ from others, the connecting glandular band is often hardy visible without staining, and the circular band is also poorly visible.

Anobothrus gracilis sensu Uschakov 1955: fig. 138 has a different branchial structure and cannot be *Anobothrus gracilis* s. str. However, as there are no longer any specimens identified by P.V. Uschakov in the ZIN collection, it is not possible to check his identification. In any case, the specimen figured was not *Anobothrus* because of the form of the branchial arrangement, which does not occur within this genus.

Hessle (1917) investigated the «Originalexemplar» *Sosane sulcata nidrosiensis* Bidenkap, 1907 and concluded that this subspecies is *A. gracilis*.

Hilbig (2000) described 14 AS for specimens examined by her. Despite *A. gracilis* does can have other than 13 AS number, such specimens are ugly, and species with normal 14 AS should be different species.

DISTRIBUTION. *A. gracilis* is the most common species of the genus. The map (Fig. 8) reflects the samples checked by me. The actual distribution is likely to be wider, but I doubt that all records belong to the same species, this is supported by the long list of erroneous identifications, partly discussed above. The species appears to be widely distributed in the Arctic and the North Pacific, usually at shelf and slope depths; in the Arctic it is usually found distinctly shallower than in the North Pacific (it is usual type of distribution) and judging from investigated material it is replaced at deeper sites by *A. mironovi* in the North Pacific and by *A. laubieri* in the Arctic. It is not clear whether it occurs in the North Atlantic.

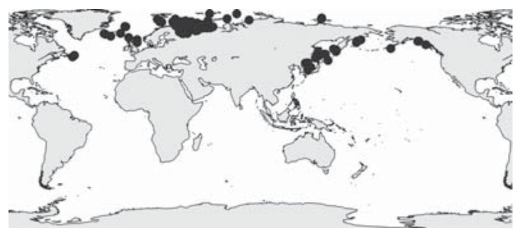

Fig. 8. *Anobothrus gracilis* species range.
Рис. 8. Ареал *Anobothrus gracilis*.

***Anobothrus laubieri* (Desbruyeeres, 1978)**

Anobothrus laubieri — Jirkov, 2001: 476–477.
Melythasides laubieri Desbruyères, 1978: 232–235, fig. 1. Type: Muséum National d'Histoire naturelle, Paris, no. AK 134 (holotype); United States National Museum of Natural History, Washington, D.C. and Allan Hancock Foundation, Los Angeles, California (paratypes) (Holthe, 1986 a). Type locality: 76°54′N, 1°49′E, 3193 m. Jirkov, 1982: 131; Holthe, 1986 a: 78–81, fig. 33, map 32; 1986c: 228.
Melinnampharete laubieri — Holthe 1986b: 98.
Eclysippe vanelli — Kirkergaard, 1982: 257 — non Eliason, 1955.
Eclysippe sp. A — Biljard&Carey,1980.
Owenia fusiformis — Hlebovich 1964: 174 (partim) — non delle Chiaje,

Material examined. 57 samples (568 specimens), collections of DHMSU, ZIN, OIRAN, the Arctic ocean from the Norwegian Sea to the Chuckchee Sea, 155–3965 m, bottom temperature –1.04 – 2.52°C (Fig. 9).

DESCRIPTION. Up to 11 mm long. Tube usually densely covered with shell fragments of *Globigerina* or other sand particles. Prostomium *Ampharete*-type. Buccal tentacles smooth. Paleae (ca. 15) much longer than the most developed notochaetae, but of the same width, long, gradually tapering capillaries. Three pairs of branchiae. Position of

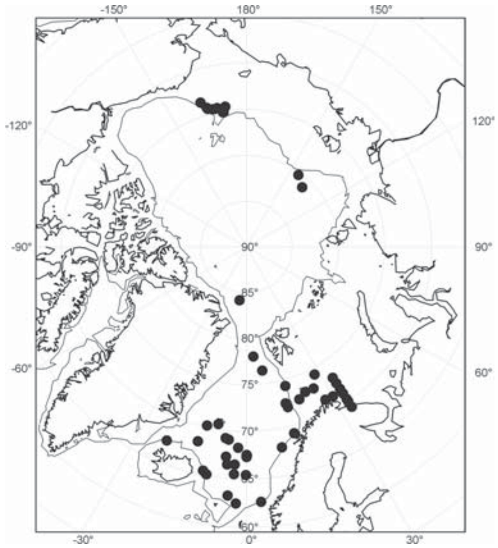

Fig. 9. *Anobothrus laubieri* species range. Isobath 500 m is shown.

Fig. 9. Ареал *Anobothrus laubieri,* показана изобата 500 м.

branchostyle attachments forms straight transversal line. No gap between anterior inner branchiae. Branchophores joined by their sides forming a high fold. Medial branchophore seems to be connected with notopodia of S–3, both lateral pairs not showing any distinct connection with segments. All branchophores and branchostyles smooth, medial one of each group usually two times wider and distinctly longer than other two. A pair of nephridial papillae behind branchophores, papillae situated very close to each other thus appearing like a single one. Similar situation sometimes observed in *Ampharete* spp. (for example is characteristic for *Ampharete littoralis* Annenkova, 1934) and probably is a specific character. Transversal band anterior to notopodia of TU–2 (instead usual TU–3) characteristic for genus. 15 TS, 12 TU. Notopodia of TS–5 from last (TU–8) modified *Anobothrus*-type. 12 AU; no rudimental notopodia and neuropodial cirri. Neuropodiae of first two AU of thoracic type. All uncini avicular. Tube thin-walled, detritus; in the Norwegian Sea densely covered with *Globigerina* shells, tubes from other regions (slope of the North Polar Basin near New Siberian Isl. and the Chuckchee Sea) without *Globigerina* shells possibly because *Globigerina* absent there).

REMARKS. 1. Within the North Polar Basin *A. laubieri* can be found in sympatry with *A. gracilis*. Despite the presence of many differences between these species, most of the differences are hardly visible (number of branchiae, AU). The easiest way to separate them is to use the position of the circular band.

2. *Eclysippe vanelli* sensu Kirkergaard 1982, judging from our data on ampharetid distribution within the North Polar Basin should be *A. laubieri*. The brief description given by Kirkergaard agrees with both species. The same probably concern to Biljard and Carey (1980) data.

3. *Owenia fusiformis* sensu Hlebovich 1964 (deposed in ZIN) partly is *A. laubieri*.

DISTRIBUTION. Deep-water Arctic species, mainly deeper than 2000 m (Fig. 9).

Anobothrus mironovi sp.n.

Fig. 10

Material examined. 14 samples (169 specimens) from collection of OIRAN; HOLOTYPE and most of PARATYPES deposed in OIRAN; 2 PARATYPES in NHM 1994.849–850. R/V Kurchatov cruise 4, stat. 235 19°51′S, 80°35′W, 3160 m (2), R/V Vitjaz cruise 24, stat. 3577 38°4′ N, 143°29′E, 3042 m (37), stat. 3594 40°55’N, 144°48′E, 3880 m (112), stat. 3594 40°54’ N, 144°53’ E, 3860 m (3), cruise 29, stat. 4181 42°38′N, 125°1′W, 1698 m (1), cruise 45, stat. 6095 57°36′N, 148°36′W, 3240 m (2), stat. 6106 58°15′N, 142°36′W, 3610 m (1), stat. 6106 58°15′N, 142°34′W, 3620 m (1), stat. 6111 56°17′N, 137°51′W, 2880 m (2), stat. 6118 56°28′N, 136°46′W, 2245 m (1), stat. 6121 56°45′N, 136°1′W, 1600 m (1), stat. 6127 55°2′ N, 134°49′W, 1100 m (3), stat. 6132 53°48′N, 163°29′W, 1360 m (2), R/V Zhemchug stat. 44 1250 m (1). Type locality: 40°55′N 144°48′E, 3880–3890 m, (st. 3594 cruise 24 R/V Vitjaz, 23.05.1957) (Fig. 11).

DESCRIPTION. Up to 40 mm long (holotype — 30 mm). Tube long, muddy, smooth, thin-walled (thickness much less than inner diameter). Prostomium *Ampharete*-type. Usually a pair of black subepidermal spots near the base of prostomial middle lobe. Buccal tentacles numerous (tens), smooth. Paleae much longer than the most developed notochaetae, but of the same width, gradually tapering long capillaries. Number of paleal setae 12–20 (17 in holotype), not related to length in worms longer 25 mm Four pairs of branchiae. Three branchostyles attached on each side of adult worms forming a straight transversal line, the forth situated more posteriorly and between innermost and middle ones. No gap between anterior inner branchiae pairs. Branchophores joined by their sides forming high fold. Posterior (forth) branchophore connects with notopodia of S–5. Diameter of outer branchophores 1.5 times bigger than inner ones. Almost all branchostyles lost, but judging by those present, inner branchostyles distinctly shorter and slimmer than outer ones. All branchostyles smooth. A pair of nephridial papillae behind inner anterior branchiae lying in the narrow gap between posterior inner pair. Nephridial papillae present behind notopodia of TU–1 and TU–2, but usually hardly visible. Transversal band in

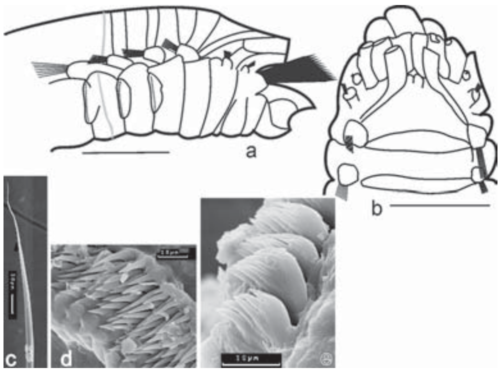

Fig. 10. *Anobothrus mironovi* sp.n.
a — anterior end, lateral view, b — anterior end dorsal view (palea not shown), c — notochaeta, d — thoracic uncini, e — abdominal uncini. Scales a, b — 1 mm. A, b — holotype, c–e — paratype.

Fig. 10. *Anobothrus mironovi* sp.n.
a — передний конец сбоку, b — передний конец со спины (опахала не показаны), c — нотохета, d — торакальные uncini, e — абдоминальные uncini. Шкала: a, b — 1 mm. A, b — голотип, c–e — паратип.

front of notopodia of TU–3, characteristic for the genus. 14–15 TS, 12 TU, notopodia of S–4 small tufts only or even absent. Dorsum of anterior thorax often segmented. Notopodia of TS–5 from last *Anobothrus*-type modified and connected with low glandular band. 12 AU (exceptionally 11 AU), without rudimental notopodia and neuropodial cirri. Pygidium with small rounded papillae. Neuropodiae of first two AU of thoracic type. All notochaetae both modified and normal notopodia are smooth. Uncini of TU–1: number — ca. 80 per neuropodium; 5 teeth in profile, teeth in two rows, basal tooth single, apical usually paired, totally 8–9 (the fine structure of uncini is difficult to observe within the resolution of available light microscopy so this may need to be revised) teeth, there is no additional small apical teeth.

REMARKS. The species is very similar to *A. gracilis*, particularly in the branchial arrangement, but the difference in size between inner and outer branchiae is slightly less, and the distance between posterior inner branchiae is slightly bigger than in *A. gracilis*. More fundamentally they differ by the number of AU. Worms with damaged abdomen can be identified by uncini, which have in profile 5 teeth instead 6 in *A. gracilis*. As this difference is small and difficult to see, it is necessary to count accurately, since the teeth rows are easily confused.

ETYMOLOGY. The species is named after Dr. Sc. A. Mironov, curator of OIRAN collection and my friend.

Fig. 11. *Anobothrus mironovi* sp.n. species range.
Рис. 11. Ареал *Anobothrus mironovi* sp.n.

DISTRIBUTION. Bathyal widely distributed Pacific species: 880–3890 m (Fig. 11).

Anobothrus nataliae sp.n.

Fig. 12

Material examined. 12 samples (20 specimens) from collection of OIRAN and ZIN; HOLOTYPE and 3 PARATYPES deposed in OIRAN, the rest — in ZIN. Type locality: R/V Dmitriy Mendeleev st. 544 Sigsbee trawl 891 m (HOLOTYPE & 3 PARATYPES) 9°56,0′S 79°26,6′W, 14 paratypes have been collected in the Yellow Sea, 7–45 m (there is no coordinates).

DESCRIPTION. Holotype is longest fragment of 20 mm long, the whole length of worms seems to be about 30 mm. Tube long, muddy smooth, thick-walled (thickness same as inner diameter). Prostomium *Ampharete*-type. Buccal tentacles numerous (tens), smooth. Paleae much longer and wider than the most developed notochaetae, near the middle sharply tapering to a long capillary tip. The number of paleal setae distinctly bigger than in other species: 22–27 (25 in holotype). Four pairs of branchiae. Places of three branchostyles attachment on each side of worm form straight transversal line, forth behind and between innermost and middle. No gap between anterior inner branchiae pairs. Branchophores joined by their sides forming high fold. Posterior (forth) branchophore connects with notopodia of S–5. Two pairs of inner branchophores half as long and narrower than outer ones. All branchostyles smooth, cirriform. Generally branchial arrangement very similar to *A. gracilis*. A pair of very long nephridial papillae opening between inner anterior branchiae. Nephridial papillae present behind notopodia of TU–1 and TU–2, but usually hardly visible. Transversal band in front of notopodia of TU–3 characteristic for the genus. 14 TS, 12 TU. Dorsum of anterior thorax often segmented. Notopodia of 4th from last TS (TU–9) *Anobothrus*-type modified and connected with very high folder (high several times more than width), grandular band found at its highest part. 12 AU. Abdominal segments without rudimental notopodia and neuropodial cirri. Neuropodia of first two AU of thoracic type. All notochaetae both modified and normal notopo-

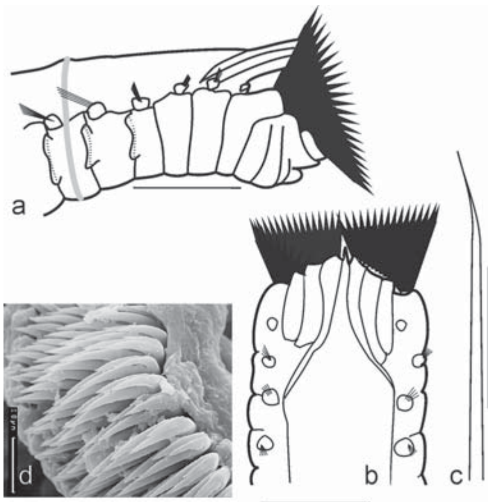

Fig. 12. *Anobothrus nataliae* sp.n.

a — anterior end, lateral view, b — anterior end dorsal view, c — palea, d — thoracic uncinus (paratypes). Scales: a, b — 1 mm, c — 0.5 mm.

Fig. 12. *Anobothrus nataliae* sp.n.

a — передний конец сбоку, b — передний конец со спины, c — щетинка опахала, d — торакальные uncinus (паратип). Масштаб: a, b — 1 мм, c — 0,5 мм.

dia are smooth. Setae of normal notopodia slightly geniculate, limbate proximally to knee, width of limb equal to 1/3 of total seta width; limbate part of seta covered with scales. Uncini of TU–1: number — ca. 100 per neuropodium; in profile 7 teeth, teeth in two rows. No additional small apical teeth.

REMARKS. 1. Species differs from others by its distinctly higher number of paleal setae and the number of modified thoracic segments: TU–9, instead TU–8 or before as usual.

2. The species has been found, but not described by Dr. B.L.Wu (part of specimens, deposited in ZIN).

ETYMOLOGY. The species is named after my colleague Dr. Natalia Yu. Dnestrovkaja.

DISTRIBUTION. Known only from the type localitie. Should be expected to be widely distributed in tropic-subtopic Pacific.

Anobothrus patagonicus (Kinberg, 1867)

Fig. 13

Ampharete patagonica Kinberg, 1867: 343. Type locality. Patagonia.

? *Ampharete patagonica* — Ehlers 1897: 129;1901: 206 — non *Ampharete patagonica* Ehlers 1913: 551 (= *Anobothrus glandularis*).

Anobothrus patagonicus — Hessle 1917: 107; Benham 1927: 119–120, Pl. III, fig. 87–93; Monro 1939: 138; Hartman 1966: 79–81, pl. 25, fig.14; Averintsev 1982: 34–35.

Material examined. 5 samples (21 specimens) from collection of NHM, previously ident. by Benham (1927) and Monro (1939) and ZIN, previously ident. by Averintsev (1982) 7–223 m (Рис. 15).

DESCRIPTION. Up to 19 mm long. Prostomium *Ampharete-type*. Usually a pair of black subepidermal spots near base of prostomial middle lobe. Buccal tentacles smooth. Paleae (ca. 15) smaller than the most developed notochaetae, long fine gradually tapering capillaries. Four pairs of branchiae. Three pairs of branchostyles attach on each side of adult worms to form a straight transversal line, the forth behind and between innermost and middle. No gap between anterior inner branchiae pairs. Branchophores joined by their sides forming high fold. Posterior (forth) branchophore connecting to notopodia of S–5 (= TS–2), median one with notopodia of S–4, both lateral pairs not showing any distinct connection with segments. Diameter of inner branchophores and branchostyles 1.5–2 times smaller (not less as in other species) than outer ones, outer branchostyles can be distinctly shorter. All branchophores and branchostyles approximately equal in size. A pair of nephridial papillae situated just behind inner anterior branchiae in narrow gap between posterior and inner branchophores. Transversal band before notopodia of TU–1 (instead usual TU–3) characteristic for the genus. 15 TS, 12 TU, notopodia

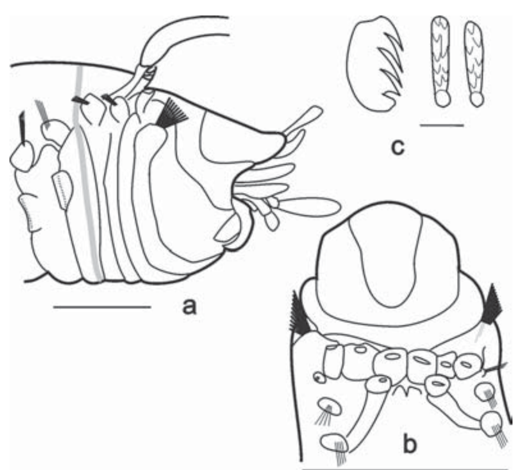

Fig. 13. *Anobothrus patagonicus.*

a — anterior end, lateral view (ZIN 15/4266), b— anterior end dorsal view (Benham material), c — TU–1 uncini. Scales a, b — 1 mm, c — 0.01 mm.

Fig. 13. *Anobothrus patagonicus.*

a — передний конец сбоку (ZIN 15/4266), b — передний конец со спины (материал Benham), c — TU–1 uncini. Масштаб: a, b — 1 мм, c — 0,01 мм.

of S–5 small tufts only. Notopodia of TS–5 from last (TU–8) *Anobothrus*-type modified and connected with low glandular band, 15–18 AU, without rudimental notopodia and neuropodial cirri. Pygidium with small rounded papillae only. Notochaetae narrow limbate, smooth or covered with fine scales (not clear for me). Uncini of TU–1: number — ca. 30 per neuropodium; in profile 4–5 teeth, teeth in two rows, apical pair distinctly smaller or absent, totally 7–9 teeth. Tube muddy-detritus, densely covered by small stones, shells, spines of sea urchin etc.

REMARKS. 1. Some specimens of Ehlers (1897, 1901, 1913) are deposited in ZMH. One tube (V–4927, corresponding to Ehlers (1897, 1901), contains part of tube with small particles of body wall of some Polychaeta; other (V–8596, corresponding to Ehlers (1913), depth 385m) contains well preserved *A. glandularis*.

2. Materials of Benham (1927) and Monro (1939) are deposed in NHM (1928.2.29.185 and 1941.3.3.1356, accordingly). Benham (1927: 119) described his specimen as having «about 15» AU, however his worm had 17. Monro (1939) wrote that the specimen from st. 53 had 18 AU, however there are only 15. The glandular band across the TU–8 was not observed by Benham (1929) nevertheless after staining of his worm the modification is obvious.

DISTRIBUTION. Shelf species (10–400 m): Magellan Strait and East Antarctica: Cape Virginia, Patagonia (Kinberg), South Georgia (Hessle), the Ross Sea 76°56′S 164°12′E, 160 fms. (Benham), Kerguelen 20–30 m, King George Land (Monro), the Davis Sea 66°32′S 93°00′E 15–49 m (Averintsev, 1982).

Anobothrus patersoni sp.n.

Fig. 14

Material examined. 13 samples (34 specimens) from collection of OIRAN; HOLOTYPE and most of PARATYPES deposed in OIRAN; 2 PARATYPES in NHM 1994.847–848. R/V Vitjaz cruise 14, stat. 2144 48°25′N, 156°34′E, 6860 m (3), cruise 19, stat. 3102 41°16′N, 147°27,7′E, 5210 m (1), stat. 3166 44°42,9′N, 153°49′E, 5027 m (1), stat. 3214 38°10,9′N, 143°56,2′E, 6156 m (10), cruise 20, stat. 3225 37°51,2′N, 144°13′E, 5290 m (7), cruise 29, stat. 4213 34°54′N, 123°55′W, 4231 m (1), stat. 4265 24°57′N, 113°24′W, 3260 m (1), cruise 39, stat. 5612, 8292 m (1), stat. 5617 6692 m (1), stat. 5625 6210 m (1), stat. 5633 6136 m (1), cruise 45, stat. 6109 56°12′N, 139°43′W, 3460 m (1), cruise 65, stat. 7943 45°34′N, 12°34′W, 4880 m (5). Type locality: 37°51′ N 144°13′E, depth 5290–5390 m, (st. 3225 cruise 20 R/V Vitjaz) (Fig. 15).

DESCRIPTION. Up to 36 mm long (holotype — 28 mm). Tube of detritus, soft, smooth, thin-walled (thickness of wall several times less than inner diameter), sporadically covered with sand grains, protruding above its surface. Prostomium *Ampharete*-type. Buccal tentacles few and smooth. Paleae (9–16) longer than the most developed notochaetae, but of the same width, gradually tapering long capillaries. Four pairs of branchiae. Anterior branchophores forming a straight transversal line, and joined by their sides forming high fold. No gap between anterior inner branchophores. Inner branchophores distinctly connected with notopodia of S–4. Forth branchophores several times thinner than others, arising from notopodia of S–5, running anteriorly and medially and join anterior ones between inner and medial ones; reaching only half the height of anterior branchophores. Branchostyles of 4th branchiae not well separated from branchophore, so they are usually present, even if other branchostyles lost. This character of 4th branchiae resembling juvenile condition of other species. Degree of development of 4th branchostyles varying from almost absent (do not

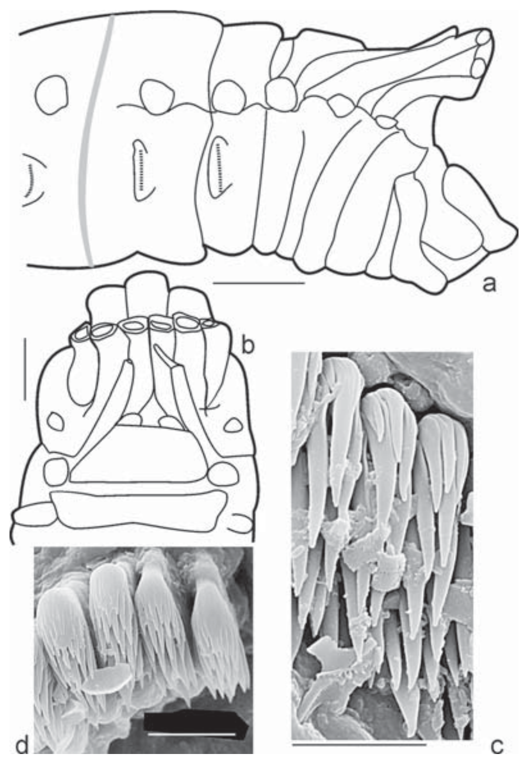

Fig. 14. *Anobothrus patersoni* sp.n.

a — anterior end lateral view, b — anterior end dorsal view, c — thoracal uncini, d — abdominal uncini (a, b — holotype). Scales a, b — 1 mm, c, d — 10 mkm.

Fig. 14. *Anobothrus patersoni* sp.n.

a — передний конец сбоку, b — то же, со спины, c — торакальные uncini, d — абдоминальные uncini (a, b — голотип). Масштаб: a, b — 1 мм, c, d — 10 мкм.

extend even above anterior branchophores) to weakly developed (an order of magnitude smaller than others). Most specimens without their anterior branchostyles, those present cirriform. Outer branchostyle (preserved in specimen from st. 3225 R/V Vitjaz) smooth, irregularly wrinkled. Inner one (preserved in two specimens from st. 3214 & 3225 R/V Vitjaz) densely covered with small cirriform papillae, similar to *A. antarctica*. Middle branchostyle (preserved in two specimens from st. 3225 & 6109 R/V Vitjaz) smooth in first and covered with small cirriform papillae, being shorter than inner ones. Species probably characterised by smooth outer, smooth or seldom papillate middle and densely papillate inner anterior branchostyles. Forth branchostyle covered with small papillae. There is a pair of large nephridial papillae just behind inner anterior branchophores and between posterior inner ones. Transversal band in front of notopodia of TU–3 characteristic for the genus. 15 TS, 12 TU, notopodia of S–4 small tufts only. Anterior thorax often distinctly segmented dorsally. Notopodia of TS–5 from last (TU–8) *Anobothrus*-type modified and connected with low glandular band. 12 AU, without rudimental notopodia and neuropodial cirri. Neuropodia of first two AU of thoracic type. Pygidium with small rounded papillae only. All notochaetae both modified and normal notopodia are smooth. Uncini of TU–1: number — ca. 50 per neuropodium; in profile 5 teeth, teeth in two rows, apical can be single or paired, totally 9–10 teeth.

REMARKS. The species differs by unusual branchial structure: there is no other ampharetins with normally reduced forth pair of branchia as it is characteristic for *A. patersoni*.

It is interesting that both abyssal species (*A. patersoni* and *A. laubieri*) have reduced branchiae.

ETYMOLOGY. Species is named after Dr. G.L.J. Paterson (The Natural History Museum).

DISTRIBUTION. Exclusively abyssal species (3260–8292 m). North Pacific and North Atlantic, possibly widely distributed (Fig. 15).

Fig. 15. *Anobothrus patersoni* sp.n. species range.
Рис. 15. Ареал *Anobothrus patersoni* sp.n.

Some zoogeographic remarks

Within the well sampled areas of the Arctic and North Pacific there is a bathymetric replacement of species. Within the Arctic, the shelf species *A. gracilis* does not occur deeper than 512 m. In greater depth it is replaced by the mainly abyssal (Jirkov, Mironov, 1985; Jirkov, 2001) *A. laubieri*. In the North Pacific, the same shelf species *A. gracilis* is replaced by the slope species *A. mironovi*, which in turn is replaced by *A. patersoni* in abyssal depths. Less samples from the antiboreal and antarctic waters were available for study, but the same situation seems to take place here. In Antarctic waters: *A. patagonicus* — antarctic shelf, *A. antarctica* — antarctic slope species and *A. pseudoampharete* — abyssal one. In antiboreal waters *A. glandularis* seems to be a shelf species, deeper it replaced by *A. mironovi*. In the abyssal depth, judging from species with similar distribution, *A. patersoni* could be expected to occur. *A. nataliae* seems to be pacific tropic shelf species. Unfortunately there is no data available from the North Atlantic. «*Anobothrus gracilis*» has been reported from this region a lot of times, but which species is really occurring here is unknown till now. All know species inhabit Pacific and Antarctic, only *A. laubieri* is exclusively Arctic. *A. apaleatus* found in Pacific hot vents in slope depth (524–2219 m).

Insertae sedis

Ampharete kerguelensis sensu Augener, 1926.
Ampharete kerguelensis — Augener 1926: 223 — non McIntosh, 1885.
Material examined. Both SYNTYPES of *Ampharete kerguelensis* (deposed in NHM reg. no. 85.12.1.314) and one specimen from ZMH (reg. no. V–5913), identified by Augener (1926) as *Ampharete kerguelensis*.

Types of *Ampharete kerguelensis* s.str. McIntosh, 1885 are quite typical *Ampharete*. The single syntype of this species with preserved abdomen has 13 AU, contrary to all previous published accounts. Specimen of *Ampharete kerguelensis* sensu Augener (1926) in reality is not *Ampharete kerguelensis* s.str., but is quite typical *Anobothrus*, belonging to unknown species. It is not well preserved, and has 12 TU, 14 TS and 12 AU and crenulated ventral collar on S–3.

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