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Copepoda (Crustacea) of hydrothermal ecosystems of theWorld Ocean

Веслоногие ракообразные (Crustacea: Copepoda) гидротермальных экосистем Мирового Океана

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КЛЮЧЕВЫЕ СЛОВА: глубоководные гидротермы, холодные высачивания, копеподы, таксономия, биология, функциональная морфология, распространение.

ABSTRACT: Deep-sea hydrothermal ecosystems contain obligate taxa as well as species of oceanic ecosystem. Thus ecological attribution of any species discovered in a hydrothermal biotope is a key task of hydrothermal ecosystems investigation. 80 valid species of 20 families from 6 orders of the 10 that form the subclass Copepoda are discovered in deep-sea hydrothermal and seeping ecosystems. The most diverse order is Siphonostomatoida (4 families, 17 genera, 56 species), then Poecilostomatoida (4, 5, 9, respectively), Harpacticoida (8, 10, 11), Calanoida (2, 2, 2), Cyclopoida (1, 1, 1), and Misophrioida (1, 1, 1). Only Dirivultidae and Ecbathyriontidae (Siphonostomatoida) and some species of Poecilostomatoida are interpreted as obligate for the deep-sea hydrothermal ecosystems. Functional analysis of locomotory and mouth limb morphology allows us to formulate morphological criteria for understanding the specializations of hydrothermal copepods. Dirivultidae, the most abundant of these, are able to swim and crawl over the substrate, grazing on bacterial films and mats. Some species are symbionts of hydrothermal invertebrates. Their biomass exceeds 2.8–5.8 g/m^2 with quantities of more than 64,000 ind/m^2. As a whole, the fauna of hydrothermal copepods is studied insufficiently.

РЕЗЮМЕ: Глубоководные гидротермальные экосистемы содержат как облигатные таксоны, так и виды океанической экосистемы. Т.о. диагностика экологической принадлежности любых видов, обнаруженных в гидротермах, является первоочередной задачей при их исследовании. В глубоководных гидротермальных экосистемах обнаружено 80 видов 20 семейств 6 отрядов из 10, составляющих подкласс Copepoda. Наиболее разнообразны Siphonostomatoida (4 семейства, 17 родов, 56 видов), затем Poecilostomatoida (соответственно 4, 5, 9), Harpacticoida (8, 10, 11), Calanoida (2, 2, 2), Cyclopoida (1, 1, 1) и Misophrioida (1, 1, 1). Облигатно гидротермальными являются семейства Dirivultidae и Ecbathyriontidae (Siphonostomatoida) и некоторые виды Poecilostomatoida. Функционально-морфологический анализ локомоторных и ротовых конечностей позволил сформулировать морфологические критерии для понимания специализации гидротермальных копепод. Dirivultidae наиболее разнообразны и многочисленны, способны как плавать, так и ползать по субстрату, поглощая бактериальное обрастание. Часть видов — симбионты гидротермальных беспозвоночных. Их биомасса превосходит 2,8–5,8 г/м^2 при численности более 64 000 экз/м^2. В целом фауна гидротермальных копепод изучена недостаточно.

Introduction

This paper is an improved English version of “Copepoda”, a chapter of the monograph “Biology of Hydrothermal Systems” edited by A. Gebruk [2002].

Copepods (subclass Copepoda Milne-Edwards, 1840) are the most abundant animals living in diverse aquatic habitats, playing a significant role in marine life. In this paper we discuss the copepods of deep-sea hydrothermal fields and seeps, their taxonomic composition, distribution, morphological and biological traits, and the habitat specificity of obligate copepods [Heptner, Ivanenko, 2002].

We believe that deep-sea hydrothermal ecosystems and deep-sea cold seeps related to them are immersed means in the ocean ecosystem and are ecosystems of the enclave type. Two biological consequences follow from this: the influence of the hydrothermal systems on the oceanic ecosystem and vice versa. These influences are important generally and for estimation of the role of animals such as copepods that are not symbiotrophic, but consumers of the first order in hydrothermal ecosystems.

The first consequence is that some inhabitants of the hydrothermal zone and their developmental stages are carried away by currents. Vinogradov and Vinogradov [1998, 2002a,b] attempt to estimate the potential impact of the hydrothermal vent plume on the plankton above the Mid-Atlantic Ridge. They believe that the impact of the hydrothermal plume on productivity of the ambient oceanic water is negligible. However, planktonic hydrothermal animals are distributed by the plume and are recorded at a distance of up to 50–100 km from a vent. Dispersal distances of vent fauna may be much greater than Vinogradov and Vinogradov [1968; 2002a,b] suggest, as representatives of the obligate hydrothermal fauna are found in ephemeral habitats such as whale remains. At present, few such species are known, but their number is expected to increase [Tunnicliffe et al., 1998].

There is a probability that a species described from non-vent habitat may eventually be recognized as an obligate hydrothermal species. Until clear morphological or other criteria are available, its ecological affiliation would remain questionable. Some indications of possible reproductive and physiological criteria may be found in recent works [Vereshchaka et. al.,1998; Hourdez et al., 2000; Sell, 2000; Tsurumi et al., submitted].

On the other hand, some widely distributed oceanic species may find favorable or more favorable conditions in a hydrothermal ecosystem than in their original environment, and attain maximum abundance in the hydrothermal zone. Such a phenomenon is described for some oceanic species in the zone of an underwater mud volcano, Hokon Mosby, in the Norwegian Sea [Vinogradov, Vinogradov, 1998]. If an undescribed animal is found with such a distribution, the problems are similar as in the case of hydrothermal organisms found beyond the hydrothermal zone. For example, the family Erebonasteridae (Copepoda: Poecilostomatoida) was discovered by Humes [1987] in mantle cavity of a protobranch bivalve and termed "endemic" to the hydrothermal zone. Subsequently, new species and genera of this family were found in other deep-sea biotopes [Huys, Boxshall, 1990; Huys, 1991].

One reason for both problems is paradoxical: the recently discovered hydrothermal zone has been more thoroughly investigated than the adjacent non-vent oceanic benthic zone, although the non-vent benthic zone has been investigated for many decades. Moreover, the fauna of hydrothermal vents may be considered the best known of all deep-sea ecosystems; further exploration is constrained by insufficient knowledge of the adjacent benthic zone [McArthur, Tunnicliffe, 1998]. This makes comparison of the two systems difficult.

Species composition of copepods in both vent and non-vent ecosystems is inadequately known, and their biology and trophic interrelations need to be better studied. Thus, their occurrence within the hydrothermal biotope is not sufficient evidence for their belonging to the hydrothermal ecosystem. Scientists investigating hydrothermal copepods face the problem of diagnostics of ecological affiliation of the material collected from hydrothermal biotopes.

Characteristics of the material and collection methods

At present, copepod species considered endemic to hydrothermal ecosystems are known from 20 areas in the Pacific and Atlantic oceans (Tables 1, 2). Hydrothermal vents were discovered in over 40 localities and their number is still growing [Moskalev, 2002]. The source of the material is collections by expeditions of various countries. Most collections are from the Pacific Ocean, where initial investigations of the hydrothermal zone began.

Interpretation of the available materials of copepods should include consideration of the fact that hydrothermal ecosystems in the Pacific Ocean are entirely benthic ones. The Atlantic hydrothermal zone is generally the same, but some bresiliid shrimps, principal components of ecosystems of the Mid-Atlantic Ridge, can be described as nektobenthic organisms. These shrimp may be permanently in open water around a vent and/or at some distance from it, and can withstand current drift up to a rate of 17 cm/sec [Vinogradov, Vinogradov, 1998]. Among pelagic and benthic copepods, nektobenthic forms are unknown and unlikely, due to their small size (commonly 0.6–3.5 mm). Therefore, the whole list of species known from hydrothermal vents is represented by either benthic or near-bottom forms, or by symbiotic species including parasites.

We assume that all species of hydrothermal copepods must be attached in some way to a substratum (either living or non-living); otherwise they would be swept away from their habitat. This general ecological requirement permits evaluation of available specimens for their suitability to such a habitat and, in addition, of the occurrence of appropriate substrata for colonization by specialized hydrothermal copepods. Therefore, if new species that are typical planktonic forms are found in hydrothermal vents they can be inferred to have drifted into the hydrothermal zone from an adjacent ecosystem.

The vent copepod materials we consider here are collected by three main methods. Copepods living in the ground or on its surface are collected by a box corer. Species living among benthic animals are collected by a special sucking device — a slurp gun. Commensal species are washed off such principal substratum-forming species of the hydrothermal community as vestimentiferans, bivalves, and decapods. Vent copepods from plankton over hydrothermal vents are captured by a slurp gun deployed while a submersible is situated at a certain depth range [Vinogradov et al., 1997; Ivanenko, 1998a].

Numerous copepods collected by specially designed instruments such as "bushmasters" made for sampling of tube worms and associated fauna (C. Fisher, Pennsylvania State University, USA) and autonomous modules created for *in situ* experiments of colonization (Ifremer,

Table 1. Distribution of Copepoda in deep-sea hydrothermal vents; 1–16 — locations of the deep-sea hydrothermal sites from which the copepods were reported.
Таблица 1. Распределение копепод глубоководных гидротерм: 1–16 — места находок.

	Taxa	Location															
		Pacific ocean											Atlantic ocean				
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Order SIPHONOSTOMATOIDA Burmeister, 1834																	
Asterocheridae Giesbrecht, 1899																	
1.	*Cheramomyzon abyssale* Humes, 1989			*													
2.	*Collocherides brychius* Humes, 1999							*									
Dirivultidae Humes & Dojiri, 1981																	
3.	*Aphotopontius acanthinus* Humes et Luts, 1994		*														
4.	*Aphotopontius arcuatus* Humes, 1987	*		*	*												
5.	*Aphotopontius atlanteus* Humes, 1996												*				
6.	*Aphotopontius baculigerus* Humes, 1987	*			*												
7.	*Aphotopontius flexispina* Humes, 1987				*												
8.	*Aphotopontius forcipatus* Humes, 1987						*	*	*							*	
9.	*Aphotopontius hydronauticus* Humes, 1989			*													
10.	*Aphotopontius limatulus* Humes, 1987	*	*		*												
11.	*Aphotopontius mammillatus* Humes, 1987	*		*	*	*											
12.	*Aphotopontius probolus* Humes, 1990	*															
13.	*Aphotopontius rapunculus* Humes et Segonzac, 1998		*														
14.	*Aphotopontius temperatus* Humes, 1997												*				
15.	*Benthoxynus spiculifer* Humes, 1984						*	*	*								
16.	*Benthoxynus tumidiseta* Humes, 1989			*													
17.	*Ceuthoecetes acanthothrix* Humes, 1987	*	*	*	*												
18.	*Ceuthoecetes aliger* Humes et Dojiri, 1980	*	*	*	*												
19.	*Ceuthoecetes cristatus* Humes, 1987		*	*	*												
20.	*Ceuthoecetes introversus* Humes, 1987	*			*												
21.	*Chasmatopontius thescalus* Humes, 1990									*		*					
22.	*Dirivultus dentaneus* Humes et Dojiri, 1980[1]																
23.	*Dirivultus spinigulatus* Humes, 1999										*						
24.	*Exrima dolichopus* Humes, 1987			*													
25.	*Exrima singula* Humes, 1987				*												
26.	*Fissuricola caritus* Humes, 1987[2]				*												
	Gen. et sp. nov. Ivanenko et Ferrari, 2003 [3]							*									
27.	*Nilva torifera* Humes, 1987	*		*	*												
28.	*Rhogobius contractus* Humes, 1987	*		*	*												
29.	*Rhogobius pressulus* Humes, 1989	*															
30.	*Rimipontius mediospinifer* Humes, 1996													*		*	*
31.	*Scotoecetes introrsus* Humes, 1987		*	*													

1 — Galapagos Rift at 0°; 2 — East Pacific Rise at 10°N; 3 — East Pacific Rise at 13°N; 4 — East Pacific Rise at 17°N & 21°N; 5 — Guaymas Basin, 27°N; 6 — Gorda Ridge, 41°N; 7 — Juan de Fuca Ridge, 46°N; 8 — Explorer Ridge, 49°N; 9 — Mariana Back-Arc Basin, 18°N; 10 — New Ireland Basin, 3°S; 11 — Fiji Basin (17°S) and Lau Back-Arc Basin (23°S); 12 — Mid-Atlantic Ridge at 37°N (Lucky Strike, Menez Gwen); 13 — Mid-Atlantic Ridge at 29°N (Broken Spur); 14 — Mid-Atlantic Ridge at 26°N (TAG); 15 — Mid-Atlantic Ridge at 23°N (Snake Pit); 16 — Mid-Atlantic Ridge at 15°N (Logatchev).

Table 2 (continuing).
Таблица 2 (продолжение).

	Taxa	Location															
		Pacific ocean											Atlantic ocean				
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
32.	*Stygiopontius appositus* Humes, 1989			*	*												
33.	*Stygiopontius brevispina* Humes, 1991											*					
34.	*Stygiopontius bulbisetiger* Humes, 1996															*	
35.	*Stygiopontius cinctiger* Humes, 1987		*	*	*												
36.	*Stygiopontius cladarus* Humes, 1996													*		*	
37.	*Stygiopontius flexus* Humes, 1987		*			*											
38.	*Stygiopontius hispidulus* Humes, 1987		*	*	*												
39.	*Stygiopontius latulus* Humes, 1996															*	
40.	*Stygiopontius lauensis* Humes, 1991											*					
41.	*Stygiopontius lumiger* Humes, 1989				*												
42.	*Stygiopontius mirus* Humes, 1996		*													*	
43.	*Stygiopontius mucroniferus* Humes, 1987		*			*											
44.	*Stygiopontius paxillifer* Humes, 1989		*		*												
45.	*Stygiopontius pectinatus* Humes, 1987									*				*	*	*	
46.	*Stygiopontius quadrispinosus* Humes, 1987						*	*	*								
47.	*Stygiopontius regius* Humes, 1996															*	
48.	*Stygiopontius rimivagus* Humes, 1997												*				
49.	*Stygiopontius sentifer* Humes, 1987		*	*	*												
	Stygiopontius sp. Humes et Shank[4]				*												
50.	*Stygiopontius serratus* Humes, 1996															*	
51.	*Stygiopontius stabilitus* Humes, 1990			*						*							
52.	*Stygiopontius teres* Humes, 1996															*	
53.	*Stygiopontius verruculatus* Humes 1987		*		*												
Ecbathyriontidae Humes, 1987																	
54.	*Ecbathyrion prolixicauda* Humes, 1987	*	*	*	*												
Megapontiidae Heptner, 1968																	
55.	*Hyalopontius boxshalli* Humes, 1988	*															
Order POECILOSTOMATOIDA Thorell, 1859																	
Clausidiidae Giesbrecht, 1895																	
56.	*Hyphalion captans* Humes, 1987					*											
Erebonasteridae Humes, 1987																	
57.	*Amphicrossus altalis* Humes et Huys, 1992[5]							*									
58.	*Amphicrossus tuerkayi* Martinez-Arbizu, 1999										*						
59.	*Erebonaster protentipes* Humes, 1987					*											
Lubbockiidae Huys & Boettger-Schnack, 1997																	
60.	*Laitmatobius crinitus* Humes, 1987					*											
Oncaeidae Giesbrecht, 1893																	
61.	*Oncaea praeclara* Humes, 1988	*	*	*	*	*											
	Oncaea sp. [Ivanenko, 1998]													*			

Table 2 (continuing).
Таблица 2 (продолжение).

	Taxa	Location															
		Pacific ocean											Atlantic ocean				
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Order HARPACTICOIDA Sars, 1903[6]																	
Aegisthidae Giesbrecht, 1893																	
62.	*Andromastax muricatus* Huys et Conroy-Dalton, 1999	*															
Ancoroboridae Sars, 1909																	
63.	*Uptionyx verenae* Huys et Conroy-Dalton, 2000							*									
Argestidae Por, 1986																	
64.	*Argestoides prehensilis* Huys et Conroy-Dalton, 1997	*															
Ectinosomatidae Sars, 1903																	
65.	*Microsetella norvegica* Brady et Robertson, 1873													*			
Laophontidae Scott, 1905																	
66.	*Bathylaophonte azorica* Lee et Huys, 1999												*				
67.	*Bathylaophonte pacifica* Lee et Huys, 1999				*												
Tisbidae Stebbing, 1910																	
68.	*Cholidia polipi* Humes et Voight, 1997[7]							*									
69.	*Genesis vulcanoctopodi* Lopez-Gonzalez et al, 2000[7]			*													
Order CALANOIDA Sars, 1903[8]																	
Scolecitrichidae Giesbrecht, 1893																	
70.	*Grievella shanki* Ferrari et Markhaseva, 2000				*												
Spinocalanidae Vervoort, 1951																	
71.	*Isaacsicalanus paucisetus* Fleminger, 1983				*												
Order CYCLOPOIDA Burmeister, 1834																	
Cyclopinidae Sars, 1913																	
72.	*Barathricola rimensis* Humes, 1999								*								
Order MISOPHRIOIDA Gurney, 1933																	
Misophriidae Brady, 1878																	
73.	*Misophriopsis longicauda* Humes, 1999								*								

[1] *Dirivultus dentaneus* Humes & Dojiri, 1980 was found in 1966, off southern California (32°19.6'N, 117°19.08'W) associated with *Lamellibrachia,* depth 1225 m;

[2] in Dirivultidae after Ivanenko and Ferrari, 2003, in press;

[3] Ivanenko and Ferrari, 2003, in press;

[4] description was submitted for publication;

[5] The genus name *Amphicrossus* is preoccupied for Coleoptera (Nitidulidae) by Erichson in 1843 and not valid.

[6] see also the family names listed by Tsurumi and Tunnicliffe [2001];

[7] parasite of deep-sea octopus;

[8] see also Toda et al. [1994], Ivanenko [1998] and Tsurumi & Tunnicliffe [2001]. Ivanenko [1998] indicated adult subadult calanoids and different types of copepod's larvae.

France) are not considering by us and are awaiting study and description.

All these methods seem to be adequate to answer a wide range of problems occurring in the investigation of hydrothermal copepods. Still, it should be pointed out that no purposeful, systematic, integral, and coordinated investigations of hydrothermal copepods have been made in spite of more than 20 years of exploration of the hydrothermal zone. Available collections are mostly occasional and are a by-product of general investigations [Humes, 1999a, b, c]. A review of the distribution of copepods of hydrothermal biotopes [Humes, Segonzac, 1998] concludes that few localities have been surveyed, different methods have been applied, and no quantitative samples have been taken. The number of specimens collected in the same locality varies widely

Table 2. Copepoda from deep-sea cold seeps.
Таблица 2. Копеподы из глубоководных холодных высачиваний.

I. West Florida Escarpment
Order SIPHONOSTOMATOIDA
Family *incertae sedis* (close to Asterocheridae)
  1. *Bythocheres prominulus* Humes, 1988
Order POECILOSTOMATOIDA
Family Erebonasteridae
  2. *Amphicrossus spinulosus* (Humes, 1988) [The genus name is preoccupied and not valid]
II. Sagami Bay, Japan
Order HARPACTICOIDA
Family Cerviniidae Sars, 1903
  3. *Neocervinia itoi* Lee & Yoo, 1998
Family Normanellidae Lang, 1944
  4. *Normanella bifida* Lee & Huys, 1999
  5. *Sagamiella latirostrata* Lee & Huys, 1999
Order POECILOSTOMATOIDA
Family Clausidiidae Embleton, 1901
  6. *Hyphalion sagamiense* Toda et al., 1982
III. Mid-Okinawa Trough, Japan
Order POECILOSTOMATOIDA
Family Clausidiidae Embleton, 1901
Hyphalion sp. (Hashimoto et al., 1995)
IV. Paita zone, off Peru, 6°S
Order POECILOSTOMATOIDA
Family Clausidiidae Embleton, 1901
  7. *Hyphalion tertium* Defaye & Toda, 1994

(from one to over 8,000), indicative of irregular collecting. Therefore, conclusions based on such materials are rough and preliminary. This limitation becomes evident when attempts are made to analyze the distribution of this group or of a particular species [Humes, Segonzac, 1998].

Taxonomic composition

Over the last decade, taxonomic lists of copepods of hydrothermal vents and cold seeps were published repeatedly [Humes, 1991; Tunnicliffe, 1991; Tunnicliffe et al., 1998; Humes, Segonzac, 1998]. Nevertheless, the late professor Arthur Humes (1916–1999), the premier authority on taxonomy of deep-sea hydrothermal and symbiotic copepods, estimated the level of knowledge of this fauna, especially in the western Pacific Ocean, as extremely incomplete. Conclusions from species check lists, especially regional lists, should be accepted with caution; according to Humes [1988], the lists of copepods of particular hydrothermal fields and cold seeps reflect the number and completeness of collections rather than reality.

Currently, in hydrothermal ecosystems, 80 valid species belonging to six of the ten orders in the subclass Copepoda (Table 1, 2) have been found. To those species listed in the latest summary [Humes, Segonzac, 1998] we add 13 species. Like Humes and Segonzac [1998], we do not include in the list some benthopelagic copepods from cold seep areas in Sagami Bay, Japan [Toda et al., 1994] and three species of poecilostomatoid copepods of the family Erebonasteridae [Humes, 1973; Huys, Boxshall, 1990; Huys, 1991], one of which seems to be connected with vestimentiferans from a region off Guyana.

Reviewing Tables 1 & 2, attention should be paid to the taxonomic diversity of hydrothermal and seep representatives of all six orders at the level of families, genera, and species. The best-represented order in the hydrothermal zone is the Siphonostomatoida: of 40 families in the order, 4 families, 17 genera, and 56 species are found in the hydrothermal zone (70% of all hydrothermal copepod species). The Poecilostomatoida (61 families in the order), are represented by 4 families, 5 genera, and 9 species in the hydrothermal zone; Harpacticoida (54 families) are represented by 8 families, 10 genera, and 11 species. Taxonomic diversity of Calanoida (43 families), Cyclopoida (15 families), and Misophrioida (3 families) is low (2, 2, 2; 1, 1, 1; and 1, 1, 1 families, genera, and species respectively), totaling about 4% of hydrothermal species reported to the present [Gebruk, 2002]. Indicating total number of families we follow the list of recent crustacean families updated by Martin and Davis [2001].

At the family level, the order of diversity in the hydrothermal zone is somewhat different. The most diverse are the harpacticoids, with 14.8% of all families represented in the hydrothermal zone. Siphonostomatoids follow with 10%, the cyclopoids have 6.7% and the poecilostomatoids have 6.6%.

The aforementioned data, on the one hand, reflect an actual diversity of taxa and indicate that Siphonostomatoida is the most successful in colonization of hydrothermal vents. On the other hand, the harpacticoids, which mostly live on the ground or in interstitial habitats, are definitely underrepresented. This is confirmed by similar values of diversity for taxa in families, genera, and species (8, 10, and 11). Such values are usually characteristic of an initial stage of investigation of any fauna. A different explanation may be assumed for Poecilostomatoida (4, 5, and 9). In this case (if collecting methods are adequate) competitive suppression by siphonostomatoids, which are biologically very similar to poecilostomatoids, may have taken place.

As to Misophrioida, Cyclopoida, and Calanoida, the reasons for their taxonomic scarcity in collections must be different. The order Misophrioida is poor in species, though it is widely distributed near benthic biotopes. Although cyclopoids are found in deep-sea benthic communities [Martínez Arbizu, 1997, 2000], most of them are shallow water, specialized parasites or purely planktonic animals. The calanoids are all planktonic or epibentic. Thus, the presence in the hydrothermal zone of one or two species from each order should be understood as an occasional drift from the adjacent oceanic ecosystem. The same seems to be true of the occurrence in the hydrothermal zone of a genus and species from the subclass Tantulocarida [Huys, Conroy-Dalton, 1997]. Attributed, together with Copepods, to class Maxillopoda, this group comprises ectoparasites of copepods and of other crustaceans and is widely distributed.

Similar conclusions may be obtained by considering the deep-sea hydrothermal biotope as a refuge for primitive or relic forms [McArthur, Tunnicliffe, 1998].

Order Siphonostomatoida

Of four identified families, two endemic families — Dirivultidae and the monotypic Ecbathyriontidae — are sister groups (see Ivanenko & Ferrari, 2003). The third family, Megapontiidae, cannot be combined with the former two. It possesses some primitive traits, its few species are planktonic [Heptner, 1968], and a sole species may be found in the hydrothermal environment occasionally. The same may be true of occurrences in hydrothermal communities of two genera of the primitive family Asterocheridae, which has numerous representatives recorded as symbionts of various invertebrates, mainly littoral ones [Ivanenko, 1997, 1998b; Ivanenko, Smurov, 1997].

Order Poecilostomatoida

Of four families of the order Poecilostomatoida, only three species of the families Clausidiidae and Erebonasteridae can be considered as endemics of deep-sea hydrothermal vents. The latter family shows number of primitive characters of the order. The Lubbockiidae and Oncaeidae are represented mainly by widely distributed, planktonic forms.

Order Harpacticoida

The order Harpacticoida, with ten species discovered in biotopes of hot vents and cold seeps, does not manifest primitive traits. The Harpacticoida is a cosmopolitan order; that a few taxa from specious families are found in the hydrothermal zone is obviously because collecting methods have not adequately sampled copepods of this group. The discovery of many undescribed harpacticoids collected during Canadian [Tsurumi & Tunnicliffe, 2001], French and Russian cruises on Atlantic and Pacific Oceans supports this conclusion.

Orders Misophrioida, Cyclopoida, and Calanoida

In contrast to the previous order, the order Misophrioida with only one species being found in the hydrothermal vent. Species of this order are living in the benthic zone and in anchialine caves [Boxshall, Jaume, 2000]. All species are cosmopolitan and there are no reasons to consider the hydrothermal zone as a specific refuge of primitive forms of this order.

The order Cyclopoida is represented presently in the hydrothermal zone by only one species belonging to the family Cyclopinidae, the most primitive in this order [Jaume, Boxshall, 1997; Martínez Arbizu,1997, 2000]. This family is cosmopolitan, like the Misophriidae, and cannot belong to groups that found refuge in the hydrothermal zone.

Finally, from the order Calanoida, which has become specialised to a planktonic mode of life, two species are found in the hydrothermal zone at present. These species belong to widely distributed families [Schulz,1996; Ferrari, Markhaseva, 2000].

In summary, it may be concluded that although primitive taxa are present in many orders recorded from the hydrothermal vents, the actual association of primitive forms with the hydrothermal vents can be assumed only for siphonostomatoids and perhaps for poecilostomatoid copepods. These two groups, especially the family Dirivultidae (Siphonostomatoida), tend to prefer the hydrothermal biotope**.** This preference seems to depend on their biology and morphology.

Biological and morphological traits

The available publications on hydrothermal copepods mainly describe new taxa and deal less with their distribution. Morphological traits are mentioned as far as they are necessary for systematics. There are no papers dealing specifically with the biology (locomotion, feeding) of hydrothermal copepods. Taxonomic studies contain scarce data on feeding [Humes, Dojiri, 1980a; Humes, 1987, 1996, 1999a, b, c; Humes, Lutz, 1994]. An attempt at understanding the life cycle with consideration of ontogenesis of dirivultids and the spatial distribution of developmental stages has been made only by Ivanenko [1998a]. Therefore, we have begun a functional-morphological analysis of structures used in locomotion and feeding of hydrothermal copepods. Available collections and published data were analyzed.

Locomotion

The natural distribution of hydrothermal copepods on a substratum confirmed by photographs has been published only in the description of the siphonostomatoid dirivultid *Aphotopontius acanthinus* (Siphonostomatoida) from recently extinguished hydrothermal vents of the East Pacific Rise [Humes, Lutz, 1994]. The photographs clearly show dark-pigmented crustaceans distributed in great quantities on bacterial films, colonies of the barnacle *Lepetodrilus elevatus* McLean*,* and shells and limbs of hydrothermal crabs *Bythograea thermydron* Williams. Abundance of these copepods of size 0.7–1.2 mm is 5–12 specimens per cm^2 of the light surfaces of crab shells, where they are clearly seen. Their distribution also suggests that the copepods are free-living and may swim and move over the substratum.

Reconstruction of a possible mechanism of movement over substrata for *A. acanthinus* and its ecological analogs is made with consideration of the published data on morphology of siphonostomatoids and representatives of other orders present in the hydrothermal zone. Additionally, consideration was given to the morphology of *A. mammillatus* from the Guaymas Basin, a species closely related to *A. acanthinus,* whose morphology was studied previously [Ivanenko, Heptner, 1998].

Any movement over a surface consists at last of two phases: attachment to a substratum in the initial or final point of the track and movement. The cycle is then

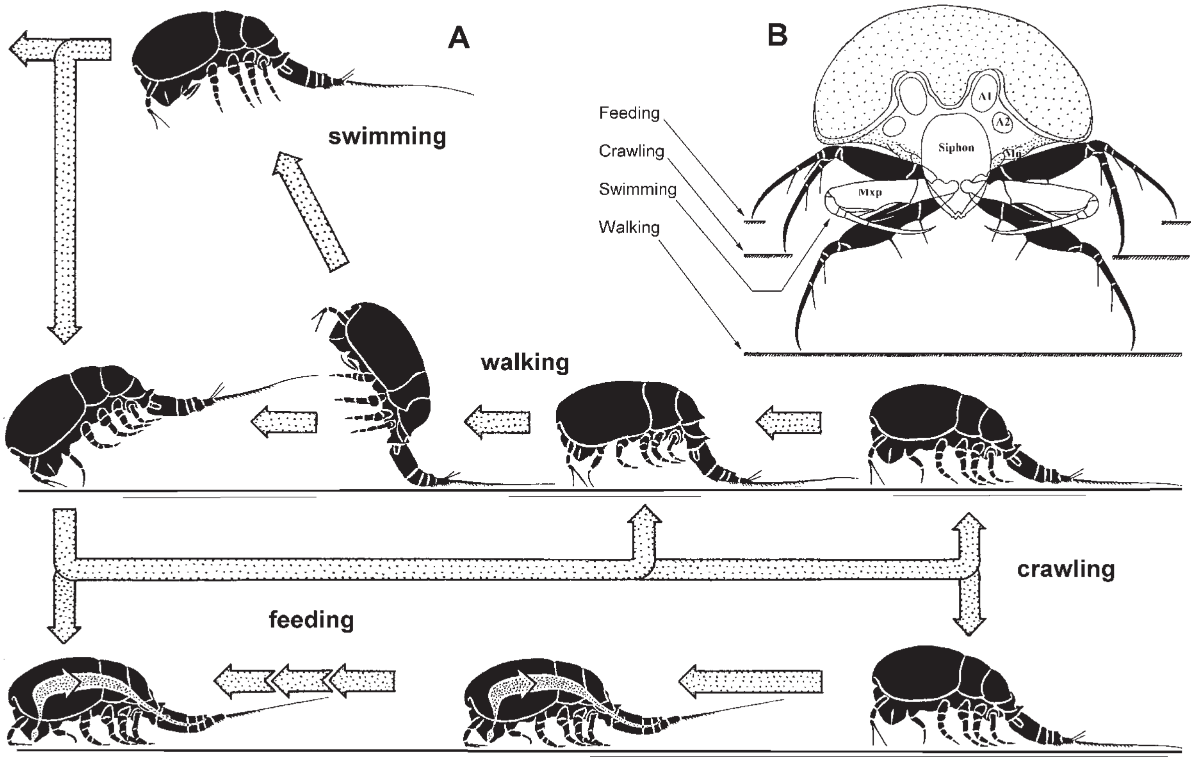

Fig. 1. Position of the body, limbs (A), and maxillipeds (B) of *Aphotopontius mammillatus* at different kinds of locomotion.

Рис. 1. Положение тела, конечностей (А) и максиллипед (В) *Aphotopontius mammillatus* при различных способах передвижения.

repeated. The body may be fixed on a substratum by siphonostomatoid and poecilostomatoid copepods by means of maxillipeds. Their morphology indicates the possibility of a wide grasping of the substratum and then a leaning on it; the grasping however, is not reliable. Thus, the maxilliped mainly performs the function of securing the body in position (Fig. 1B).

Movement should be performed, as in most copepods, by four pairs of biramous limbs that appear initially like swimming limbs. Closer examination shows characteristic anatomical traits that enable the copepods to use their limbs both for support and for movement over substrata.

The functional meaning of these traits may be interpreted in the framework of a general evolutionary trend of limbs in Copepoda that accompanied a transition via a benthic stage from a planktonic to a parasitic mode of life or, more generally, to life on substrata. The limbs of *A. mammillatus* are considered to be the middle of an evolutionary series (Fig. 2) that begins with the swimming limbs in a typically planktonic species, *Paraeuchaeta elongata* (Esterly) (Calanoida) (Fig. 2, *1*) and ends at a large (15–20 mm) crawling parasitic copepod, *Rhodinicola gibbosa* Bresciani (Poecilostomatoida) (Fig, 2, *5*). The latter species is very similar to a caterpillar or a millipede with a low number of segments. Each component of this series is shown as a body segment with the third pair of limbs, as this pair is less modified in most orders. Drawings of the two first components of the series are made from preparations; the third is taken from the literature [Bresciani, 1964]. Conclusions about potential positions of the limb branches and of particular segments are based on analysis of the possibilities of their movement in relation to articular surfaces.

The ***swimming type*** in the evolutionary series mentioned above is characterized by a body with a round cross-section and by an elongated (length >1.5X segment depth) classic limb unit widening distally with a long apical spine on the exopod. In reality, "the paddle" may be even wider, as the drawing is made from the limb arrested in a position where the exopod is not abducted to the outside. Protopods are combined into a general functional unit by a narrow coxal plate twice as long as the basis. The width of coxa and basis is approximately equal to the maximum width of the exopod. The endopods are short and seem to be immovable.

The ***crawling type*** is characterized by a flattened body with a flat ventral surface. Limbs are short (length < 0.5X segment depth), are not combined into an entire functional unit (there is no coxal plate), and seem capable of independent movement. The coxa and basis are fused and form a very wide protopod, the width of which is more than twice the sum width of the branches. Both branches of each limb are equal in size and are situated horizontally and in parallel to each other, with apices

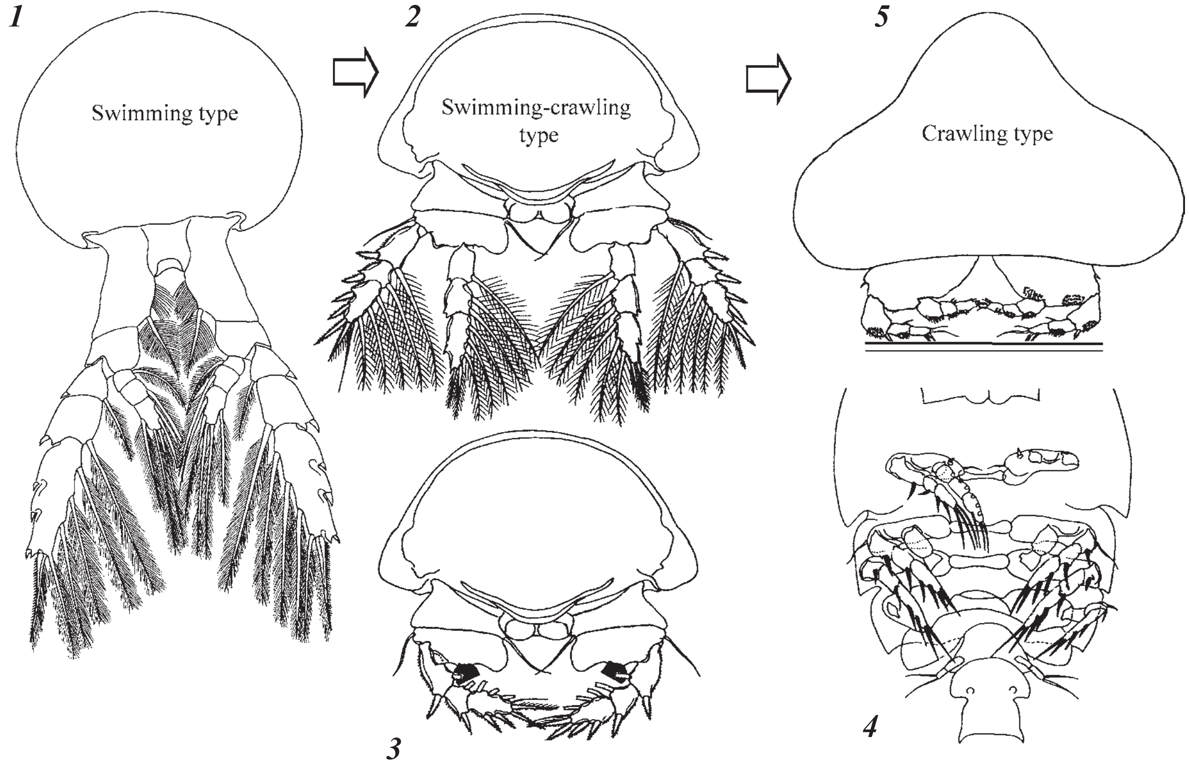

Fig. 2. Main trends of specialization of locomotory appendages in Copepoda. *1* — *Pareuchaeta elongata* (Calanoida), *2* — *Aphotopontius mammillatus* (Siphonostomatoida), position of limbs (legs 1–4) in swimming, *3* — same, in crawling over the substratum, *4* — same, ventral view, the rami may be pressed to the body still farther, *5* — *Rhodinicola gibbosa* (Poecilostomatoida), after Bresciani, 1964.

Рис. 2. Основные направления специализации локомоторных конечностей у Copepoda. *1* — *Pareuchaeta elongata* (Calanoida), *2* — *Aphotopontius mammillatus* (Siphonostomatoida), положение (ног 1–4) при плавании; *3* — то же при передвижении по субстрату. *4* — то же, вентрально: ветви могут пригибаться к телу еще сильнее, *5* — *Rhodinicola gibbosa* (Poecilostomatoida), по Bresciani, 1964.

towards the horizontal body axis, i.e., they are turned medially by 90° to their position in the swimming type. They lean on outer spines and serrulated callous swellings on the outer side of branches. There are no swimming setae.

Thus, transition from swimming type to crawling type is characterized by: (1) flattening and widening of the ventral body side; (2) shortening, widening, and enlargement of the protopodal part of the limbs; (3) thinning down, shortening, and equaling of length of branches; and (4) formation of ability to bend ventromedially. These traits seem to be general. Available data suggest forms exhibiting these patterns of change are present in all 8 orders of podopleic copepods. These patterns are clearly seen in species capable both of swimming and crawling and in flattened, differently specialized ectoparasitic forms [Kabata, 1979].

The intermediate ***swimming-crawling type*** must possess all the aforementioned traits, but the traits are probably not all expressed clearly. Intermediate types probably retain some traits of the initial swimming type. Indeed, *A. mammillatus* (Fig. 2, *2*) possesses the sturdy coxa and basis, (widened laterally in accordance with the flattened and widened ventral side of the flattened body), connected, as in swimming forms, by a coxal plate but widened and thinned into an entire functional unit. Both rami with swimming setae are short and of equal size. Thus the limb length generally does not exceed the segment depth. The apical spine of the exopod is short and is comparable in length with the lateral spines, which are elongated in comparison with the swimming type.

Articular surfaces of all segments of the exopod enable the branch to bend and move medioventrally and its outer spines, elongated in comparison with the swimming type, and serrulated edges form a supporting rib. The functional unit of both limbs leans on this rib in the course of movement (Fig. 2, *3–4*). The endopods when bent are placed under the exopods and do not participate in support and in crawling over substrata. In this way, the swimming limb is transformed into a stiff plate grasping the ground by its outer spines and serrulated edges and pushing the body forward by rearward movement of the limb unit. Proportions of all four limbs are such that at a difference in the absolute size of limbs all their supporting surfaces are at the same level. This ensures a reliable cohesion with substrata in the course of movement and feeding.

If the limbs transformed from the swimming type into the crawling type (rather than into the walking type) as described above are extended anteriorly, to make the next "step", there is a danger that the body could slip posteriorly, if the limbs only occasionally touch the substratum. This danger may be avoided by a suitable elevation of the body on the maxillipeds leaning on the substratum (Fig. 1A; crawling, B).

The species *A. mammillatus* may move using one more movement type, similar to the movement of a geometrid caterpillar (*Geometra*). This may be inferred from the forward-arching abdomen and its ability to bend the body in the thoracic region (Fig. 1, walking). Because of these traits, a copepod, leaning on the substratum with its maxillipeds, having maximally bent the body in the thoracic region, and having maximally pulled the bent abdomen underneath, is ready to take a "step" or jump forward make by relaxation of the maxillipeds and straightening the body. Attachment by the maxillipeds to the substratum at a new point subsequently occurs. Unbending, it leans on the substratum with its ventral, spiny fields of the anal segment and caudal rami and with the ventral sides of its elongated inner caudal setae with flat spinules (Fig. 3, *4–6*). The same assortment of spiny surfaces may be used in crawling.

Thus, *A. mammillatus* probably can move by swimming, crawling, walking in short geometrid-like darts or jumps, or by an alternation of these kinds of movements depending on the circumstances (Fig. 1A–B). This species and morphologically, taxonomically, and ecologically related copepods must be well adapted for movement in the hydrothermal biotope.

Morphological traits of limbs of the swimming-crawling type found in the taxonomic literature are characteristic of all representatives of orders of copepods discovered in the hydrothermal zone, including the most specious genera *Aphotopontius* and *Stygiopontius* (Siphonostomatoida). These genera also possess a proper armament with spinules of the distal part of the abdomen. Unfortunately, in drawings in taxonomic papers, this armament is not shown for all species possessing it [Ivanenko, Heptner, 1998]. The latter is not surprising, as taxonomists have not been engaged in functional analysis of movement and these structures have no special taxonomic significance.

The criteria for locomotion of copepods on a substratum, formulated above, indicate that not all copepods captured in the hydrothermal zone are actually specific for such ecosystems. For example, *Hyalopontius boxshalli* (Siphonostomatoida) and *Isaacsicalanus paucisetus* (Calanoida) have limbs of the typical swimming planktonic type. On the other hand, *Oncaea* (Poecilostomatoida), recorded in the hydrothermal zone and common in ocean plankton, possesses limbs of the typical swimming-crawling type. According to recent data, they feed on integuments of various planktonic animals [Go et al., 1998]. Frequently, they attach to soft-bodied animals: chaetognaths, appendicularians, salpae, siphonophores, and pteropods, causing serious damage. According to observations in nature, these copepods can move over the body of a temporary host-prey, in full agreement with the structure of their limbs [Go et al., 1998]. In the hydrothermal zone suitable prey are numerous and it may be assumed that *O. praeclara* is an endemic hydrothermal species.

The limbs of "hydrothermal" Cyclopoida and Misophrioida belong to the swimming-crawling type, characteristic of most podoplean copepods. However, it has not yet been possible to find any other arguments supporting hydrothermal specificity of representatives of these taxa.

Feeding

Data on feeding of copepods of the order **Siphonostomatoida** are scarce and are mostly speculative. Humes and Dojiri [1980a] indicate that *Dirivultus dentaneus* living on vestimentiferans feed on the tissue of lamellar plates or on slime covering them. The description of *D. dentaneus* contains photographs of the crustacean on the body of a vestimentiferan during feeding showing round, perforated wounds remaining on the latter's integument. This is the sole evidence on feeding by this group and by hydrothermal copepods generally. Thus, feeding by Siphonostomatoida may be estimated only by general notions of specialization of this group and of its functional-morphological traits.

At present, the Siphonostomatoida comprise over 1840 species [Ho, 2001]. The order consists entirely of the species variously specialized as parasites or commensals of a wide range of invertebrates and vertebrates. They are characterized as such by the common structural plan of the mouth complex. In the simplest case it forms a conus of the labrum and labium, abundantly supplied with muscles, narrowing distally, with lateral surfaces in dense contact. The lips (labrum and labium), especially the labium, are armed with apodemes, externally similar to jaws of mammals. The stylet-form, usually piercing, and distally serrated mandibles are extended to the oral cavity from its sides through special directing canals of the labium. In most species, the mouth conus is elongated into a proboscis, so-called oral siphon, a sucking organ, whose length in the extreme case approaches the body length [McKinnon, 1988]. In a typical case, the Siphonostomatoida feed by piercing (or tearing) of host integuments with stylet-like mandibles and sucking through the siphon either body juices or tissues finely crushed by the serrated ends of the mandibles.

A short siphon is a general trait of all Siphonostomatoida recorded in the hydrothermal zone. For elucidation of potential adaptations to life in the hydrothermal zone the short siphon is categorised into four types by differences in feeding and mode of life.

Rarest in the hydrothermal zone is the Type 1 siphon of *Hyalopontius* (Megapontiidae), which is clearly planktonic. This siphon ends in a small sucking or, more likely, a contact sensory disk. The anatomy and functional morphology of the siphon of this type are well studied [Heptner, 1968; Boxshall, 1990].

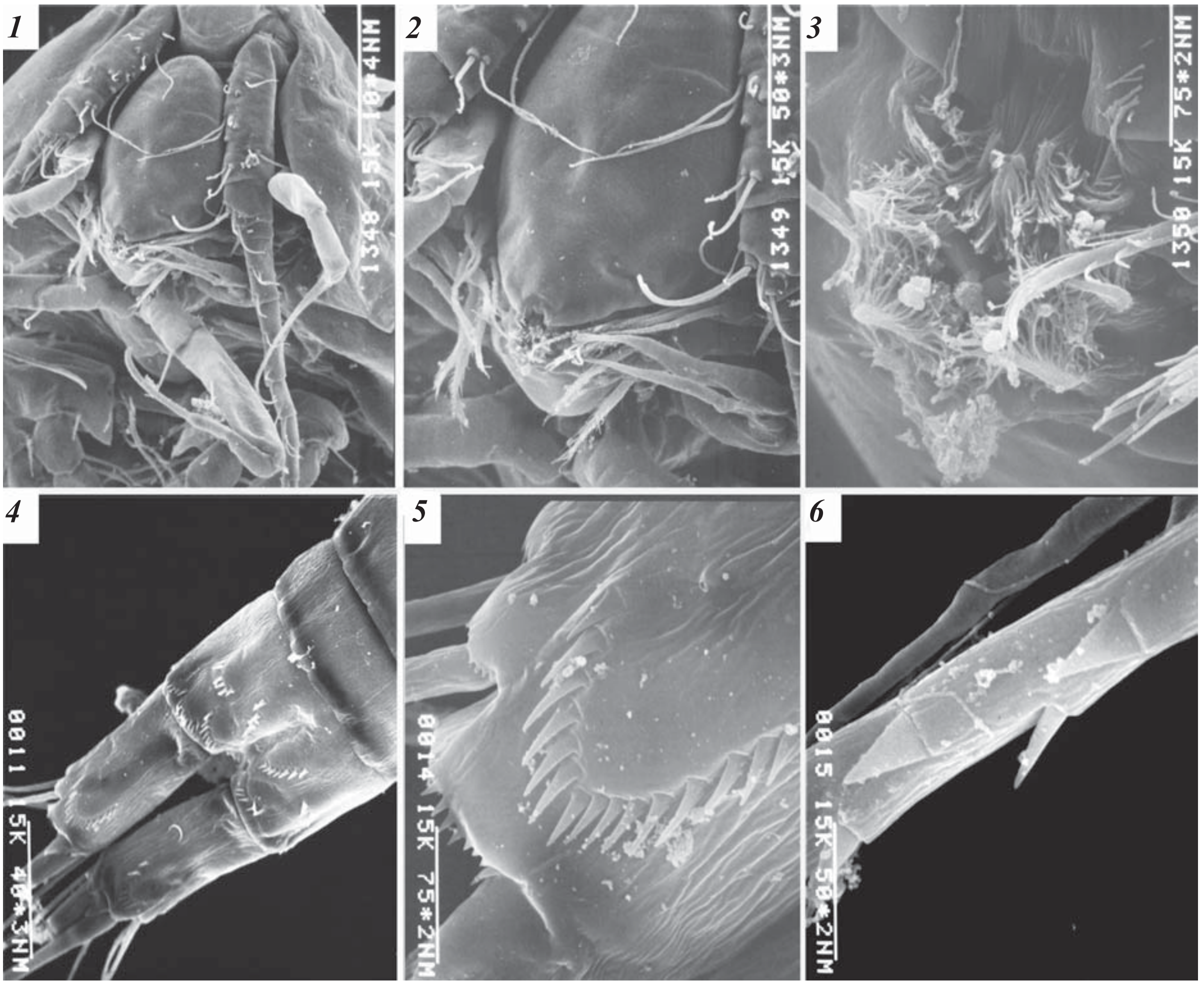

Fig. 3. *1* — general view of siphon and adjacent appendages of *Aphotopontius mammillatus*, *2* —oral complex with pressed setae of maxillule and somewhat removed left maxilla, *3* — plumose setules of the end of labium surrounding the opening of oral cone from below, *4* — epicuticular spiny fields of ventral side of anal segment and caudal rami, *5* — epicuticular spiny arch of right caudal ramus, *6* — supporting flat spinules of ventral side of elongated caudal setae. Scale line is: 100 microns for *1*; 40 microns for *2* and *4*; 7.5 microns for *3* and *5*; 5 microns for *6*.

Рис. 3. *1* — общий вид сифона и прилегающих конечностей *Aphotopontius mammillatus*; *2* — ротовой комплекс с прижатыми щетинками максиллулы и несколько отведенной в сторону левой максиллой; *3* — оперенные щетинки торцевого края нижней губы, обрамляющие отверстие ротового конуса снизу; *4* — опорные шиповатые поля вентральной стороны анального сегмента и каудальных ветвей, *5* — шиповатая опорная дуга правой каудальной ветви; *6* — опорные плоские шипы вентральной стороны удлиненных щетинок каудальных ветвей. Масштабная линейка: 100 микрон для *1*; 40 микрон для *2* и *4*; 7.5 микрон для *3* и *5*; 5 микрон для *6*.

A typical piercing siphon (Type 2), indicating a parasitic mode of life, is present in monotypic *Cheramomyzon* (Asterocheridae) and *Bythocheres* (fam. *incertae sedis*). The former genus belongs to the family comprising specialized ectoparasites and cavity parasites of echinoderms, bryozoans, cnidarians, and sponges. Hosts of the second genus are not yet known.

Type 3, found in a few peculiar species, comprises siphons of five species from the genera *Dirivultus, Ceuthoeces*, and*Nilva* (Dirivultidae). The siphon of this type is elongated into a cylindrical (*Dirivultus*) or almost cylindrical, relatively wide and rather long tube, directed ventrally or anterio-ventrally up to the anterior body margin (*Dirivultus*). Its end, armed along its edge with circular serrated swellings of the labium or of both lips, is transformed into a peculiar cutting borer. The animal lowers the siphon into soft tissues of gill lamellae of vestimentiferans and, as seen in photographs of *D. dentaneus*, tightly presses its body to a host's integument by means of antennae transformed into strong hooks. Similar hook-like maxillipeds at the cephalic end of the copepod also seem to be depressed into tissues and its body is situated on the surface of tissues at an angle corresponding to the slope of the siphon axis. No such adaptations for attachment to the host were observed in other genera of this family. By alternating strain of an antenna on one side and relaxation of another antenna on the other, a copepod may rotate to the right or left around the tubular siphon by a certain angle. As a result, the cutting edge of the siphon penetrates tissues and cuts a

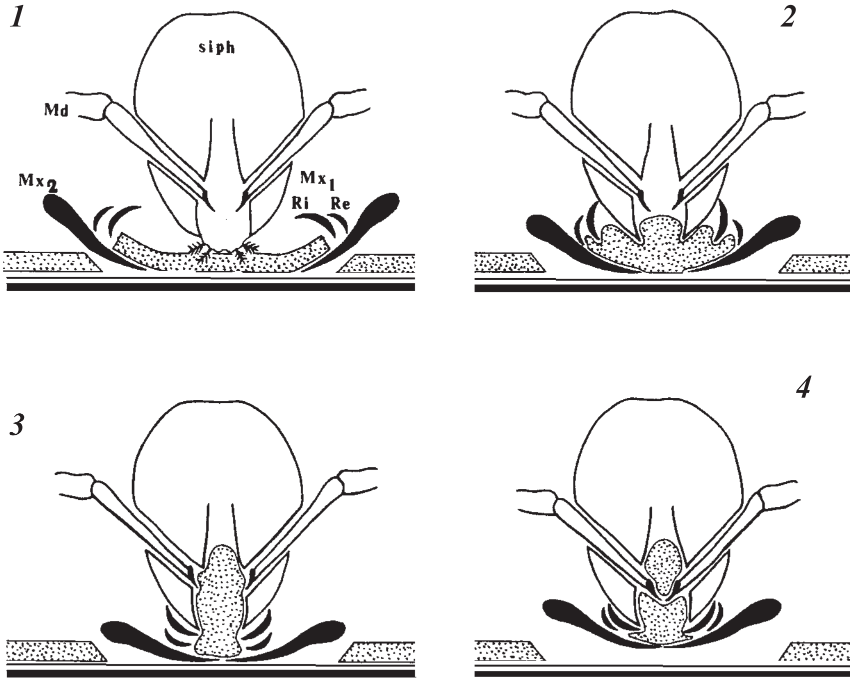

Fig. 4. Hypothetical phases of *Aphotopontius mammillatus* feeding. *1* — cutting and beginning of raking of a food substratum by maxillae with its simultaneous grasping by labrum and labium; *2* — beginning of formation of food parcel with participation of maxillules; *3* — finishing of formation of food parcel and its drawing into the oral cavity; *4* — cutting off a first portion from food parcel and its swallowing.

Рис. 4. Гипотетические фазы питания *Aphotopontius mammillatus*. *1* — подрезание и начало подгребания пищевого субстрата максиллами с одновременным его захватом верхней и нижней губами; *2* — начало формирования пищевого комка при участии максиллул; *3* — окончание формирования пищевого комка и его втягивание в ротовую полость; *4* — отрезание от комка первой порции и ее заглатывание.

round hole. The copepod obtains its food through this hole. Thus copepods of *Dirivultus, Ceuthoeces*, and *Nilva* may be considered as a group specialized in feeding on specific hydrothermal animals.

Finally, Type 4 is characteristic of 47 species comprising 45 species belonging to 9 genera of the family Dirivultidae, one species of the family Ecbathyriontidae, and, presumably, one species of the genus *Collocherides* of the family Asterocheridae. This taxonomically diverse but ecologically uniform group has elaborated adaptations for consumption of bacteria, an enormous food resource characteristic of the hydrothermal ecosystem.

The possibility of bacterial consumption by copepods was initially assumed theoretically from the ecological significance of a wide distribution of copepods in various hydrothermal biotopes [Dinet et al., 1988]. Dinet et al. [1988] believe that the structure of mouthparts of hydrothermal siphonostomatoids is more suitable for feeding on finely grained food than for sucking of liquid, as is typical of this order generally. This was confirmed by the presence of numerous partly dissolved bacteria surrounded by mucous envelopes in the foregut of these copepods. It was concluded that bacteria might make a significant part of their food and may explain the affinity of siphonostomatoids to vestimentiferans. More positively but still tentatively, Hume and Luts (1994) hypothesized that bacterial mats might support a big population of the copepod *A. acanthinus* on the East Pacific Rise.

Further discussion is based on the structure of the siphon and mouth complex of *A. mammillatus* as a typical model object (Fig. 3, *1–3, 4*). All other species of the fourth group repeat the same structure, with minor variations.

In *A. mammillatus*, a short and robust siphon is present. There is an oral cone producing a functional complex with the mandibles, small adhering maxillules, and maxillae (Fig. 3, *1*). The oral cone proper consists of a bulky and slightly wider labrum and somewhat smaller labium supplied with strong muscles. The lips have an apodemal skeleton, externally similar to the skeleton of the upper and lower jaws of vertebrates. This convergence implies that analogous grasping movements, probably by the labium whose skeleton is stronger and more complex, are possible. The ventral margin of the labium is surrounded by plumose ornamentation, probably sensory organs (Fig. 3, *3*). Characteristic of the siphonostomatoids is a narrow gnathobase of the mandible differing from the classic piercing type only in a slightly wider spatulate serrated edge, penetrating the oral cone through directing canals of the labium (Fig. 4). Functionally, each maxilla is a lobe that can tightly adhere to lateral surfaces of the oral cone, overlapping the line of lip closure. Maxillae are somewhat larger, have greater freedom of movement, and are structured so they can act as a shovel or brush. They may adhere to the lateral surfaces of the oral cone over the maxillae (Fig. 3, *1–2*). In this group of copepods, neither antennules, nor antennae, nor the oral complex and maxillipeds have morphological modifications, characteristic of siphonostomatoid symbionts and parasites, that provide a strong grasping of host tissues for prolonged attachment of copepods to the host. It may be assumed that these copepods feed on loose and mucous bacterial films and mats, common in the bacterial hydrothermal biotope.

Considering the morphology of the mouth complex, we believe that feeding by species of this group occurs in the following way (Fig. 4, *1–4*). The animal, settled onto a substratum or moving over it as described in the previous section, estimates the quality of food material perhaps with plumose sensory ornamentation of the labium. Then, both pairs of maxillae open, the lips open like jaws, and the food material is grasped (Fig. 4, *1*). Simultaneously, the maxillae rake up the food material from the side and the maxillulae, moving in the same direction, aid in formation of a food parcel pushed towards the lips. This food parcel is prevented from moving upwards and to the side; thus the maxillulae and the maxillae together perform the delimiting function of cheeks (Fig. 4, *2–3*). The food parcel in the cone is cut by the mandibles and swallowed, following which both pairs of maxillae press from the outside and push another portion of the food into the cone (Fig. 4, *4*) until the food parcel is consumed. Then the copepod grabs a new parcel of food.

Thus it may be assumed that the species of this taxonomically diverse and ecologically the most numerous group of hydrothermal copepods are classic grazers and specifically consumers of the first order, exploiting the great resource of primary organic matter formed in the hydrothermal zone.

It is possible that one representative of the family Asterocheridae, *Collocherides brychius*, also specializes in feeding on bacteria. This species was found in samples with vestimentiferans from low-temperature vents on the Juan de Fuca Ridge [Humes, 1999a]. According to the description and figure, it possesses the Type 4 oral complex. It is interesting that other species of this genus are symbionts and live in the stomach of shallow-water ophiuroids. However, neither ophiuroids nor any other echinoderms are found in this well-explored locality.

Naturally, a more detailed analysis of copepod feeding and the background of adaptations to feeding on bacteria would discover special adaptations among diverse taxa belonging to this ecological group. In general, they vary in their mode of attachment. For example, *Stygiopontius sentifer*, living on tubes of polychaete *Alvinella pompejana* Desbruyères et Laubier, possesses thick grasping maxillipeds with an accessory spine. *S. pectinatus*, found in the gill cavity of the shrimps *Rimicaris exoculata* Williams et Rona and *Chorocaris chacei* (Williams et Rona), has claw-like setae on its antennae and somewhat thickened maxilliped claws. Similarly, *S. latulus* and *S. mirus* co-exist with shrimps and have thick strong spines on apical segments of the endopod of their second pair of limbs. These limbs are directed mediodorsally and the maxilliped is reinforced by an additional prominence. These adaptations may be for attachment to the body or limbs of shrimps. However, these are special adaptations within a general morphological type and do not change the conclusion that species in the entire group are grazers.

What is the origin of such an unusual feeding and life history adaptation for hydrothermal siphonostomatoids? Two assumptions are possible. The first assumption is that Dirivultidae initially were grazers. The second is that they later turned to symbiosis and its extreme form, parasitism. This may be disputed because the hydrothermal biotope is exotic and deep-sea habitats are relatively small in area; thus, their bacterial aggregations are fragmentary in comparison with the great diversity of oceanic, shallow-water biotopes inhabited by siphonostomatoids. Morphologically it is much easier to change to feeding on bacterial aggregations by utilizing a mouth apparatus of the gnawing type. Nevertheless the grazing siphonostomatoids possess the pairs of antennae, maxillipeds, and mandibles characteristic of sucking siphonostomatoids.

Therefore, we believe that Dirivultidae probably originated as copepods with a primitive feeding apparatus of the sucking type used to feed on mucus exuded by vestimentiferans or other invertebrates surrounded by a rich bacterial flora. They evolved to a free-living mode of life by specializing on consumption of bacteria that are more available than the original food for this family. Ecologically, it is a transition from second to first order consumers. The physical texture of the food might be important. Loose mucous bacterial colonies may have been more available for the earlier sucking mouth apparatus of siphonostomatoids, the mouthparts of which subsequently adapted to ingestion of bacterial colonies.

That copepods in this group are free-living is confirmed indirectly by their pigmentation (symbiotic or parasitic forms frequently are characterized by absence of pigmentation). Thus, *Aphotopontius acanthinus* is black, as seen from a photograph [Humes, Lutz, 1994]. Numerous specimens of *Stygiopontius flexus*, seen clearly in fresh samples taken with a slurp gun together with fragments of mats of the bacterium *Beggiatoa* Trevisan, are the bright red typical of deep-sea crustaceans [Humes, 1987].

A more detailed functional-morphological analysis supported by purposeful collecting should reveal transitional, undiscovered species and it should be possible to follow the main evolutionary stages from symbiotic feeding and facultative grazing via facultative symbiosis to obligate grazing.

At present, the role of this group of siphonostomatoids in hydrothermal trophic webs is not clear. It is not known if any animals consume them. They may perform a kind of grooming for hydrothermal animals abundantly fouled by bacteria. This large group must play a significant role in transformation of primary organic matter. The task for the future is quantitative estimation of this role. Proper quantitative samples are needed.

Nevertheless, the first attempt at assessment of abundance of copepods on the substratum may be made now. From photographs [Humes, Lutz, 1994: 343, Fig. 5A-B], it is possible to calculate the biomass of *Aphotopontius acanthinus* on a flat surface. This calculation is based on 96 specimens of copepods clearly visible on the carapace of *Bythograea thermydron* Williams (life-size photograph). The measured area of the carapace is 15/cm^2 and the total density of copepods is 64,000/m^2.

Using Chislenko nomograms [Chislenko, 1968], with consideration of the body form and the average size of a female (1.04 mm), the weight of one specimen is determined at 0.044-0.090 mg. Thus the biomass is 2.8-5.8 g m^{-2} of flat surface. The actual biomass must be significantly higher, probably several times higher, as (1) the irregular natural surface of the hydrothermal biotope recalculated per m^2 is much greater than the flat surface assumed in the calculation; and (2) abundance of copepods on the ground, where they in some places sit close to each other, much exceeds the density on the crab shell, as seen in the photograph [Humes, Lutz, 1994, Fig. 5A].

The **Poecilostomatoida** are much lower than siphonostomatoid copepods in the number of species and specimens in the hydrothermal environment. Poecilostomatoids are symbionts or predators, obligately connected with the host, and thus are consumers of the second and higher orders. Feeding type is thought to be a scraping type of feeding [Huys, Boxshall, 1991]. However, even a superficial examination of their mouth appendages contradicts this assumption. Their mouth apparatus is characterized by low lips that are not protruding, serrated, or spiny along their edges, and do not close. Between the lips, strong, flat, serrated, cutting mandibles are situated. The antennae and especially the maxillipeds are transformed into short, but strong, organs of grasping and attachment. On the whole, the mouth apparatus appears as a rather rough, cruel, and even ferocious construction. Considering the mouth appendages, the poecilostomatoids must gnaw or cut out pieces of host integument with their mandibles. To do this, they adhere tightly to the host by means of their antennae and maxillipeds. For instance, Go et al. [1998] recently reported that *Oncaea* feeds on the integuments of various planktonic animals and inflicts especially heavy injuries to chaetognaths.

Such a mouth apparatus is rather specialized and seems to be unsuitable for feeding on bacteria and on dispersed food generally. Discovery of specific hydrothermal forms among symbionts is unlikely as they have, as a rule, a rather wide range of hosts in comparison with trophically specialized groups.

The few species of **Harpacticoida** represented in the hydrothermal zone possess, as the whole order does, a rather uniform mouth apparatus with typically gnawing mandibles. Most of them live on or in the ground; some live in the pelagic zone. Most species are very small, so when they are found in samples of material washed off other animals, harpacticoids probably are using these animals as non-specific substrata and are not true symbionts. Meanwhile, the presence of siphon-like mouth apparatuses in some representatives of this group (for example Tisbidae) requires further functional-morphological investigation.

The species list contains representatives of families living in plankton (Aegisthidae, Normanellidae), on soft grounds (Ancoroboridae, Cerviniidae), and mining ground (Ectinosomatidae). On the whole, the Harpacticoida, because of their ecological universality, are clearly not characteristic of the hydrothermal zone and the authors of some descriptions of new species are not certain of the biological connection of these forms with that environment [Conroy-Dalton, Huys, 1999].

Concluding the section on feeding, it should be recognized that by the character of their trophic adaptations, only the siphonostomatoids (the family Dirivultidae and the closely related to it the monotypic family Ecbathyriontidae) might be considered as a group of copepods specific to hydrothermal ecosystems and maximally adapted to them. This idea is confirmed by their taxonomic diversity and high abundance. Formation of specific hydrothermal taxa in other groups of copepods is rather improbable. If such taxa are discovered, they will most probably be a few symbiotic species of poecilostomatoids, connected with obligate hydrothermal species, consumers of the first order.

The complete absence of reports of obligate filter-feeding copepods (order **Calanoida**) in the presence of abundant bacterial suspension in the water surrounding vents is remarkable. It may be because planktonic Calanoida possess a true filtering apparatus, but have no morphological adaptations allowing them to stay in the hydrothermal ecosystem which is flushed by bottom currents. In this order, only the maxilla and maxillipeds, and only in predatory and omnivorous forms, may perform grasping functions. In filter feeders they are an important component of the filtering apparatus itself.

Reproduction

The data on reproduction of hydrothermal copepods are scarce and are available only for the family Dirivultidae. The material for investigation of reproduction was not collected purposefully and the existing theories are based on taxonomic treatment of benthic samples and collections of plankton over the hydrothermal field “Broken Spur” on the Mid-Atlantic Ridge [Ivanenko, 1998a].

The females of all dirivultids deposit one, frequently two (rarely more) large eggs rich in yolk into each of two egg-sacks. The egg-sacks, clearly seen in a photograph [Humes, Dojiri, 1980a], are situated on the sides of the abdomen and do not interfere with movement over substrata. Humes [1987] believes that eggs are laid often, resulting in a high abundance of dirivultids. In the hydrothermal biotope, their populations are composed of numerous adult females and males. Abundance of the latter is several times lower than that of females. It seems that each male copulates with several females. Abundant collections have been examined, but there are no published records of nauplii and copepodids within the hydrothermal zone, except a copepodid of the fifth stage, identified as *Aphotopontius temperatus* Humes, 1997 [Humes, 1997]. Having analyzed the description of the 5th and 6th (mature) stages of this species and compared it with the description of development of another siphonostomatoid [Ivanenko et al., 2001], we believe that the 5th copepodid stage of the female of this species is interpreted erroneously and is the 4th stage, and a mature female of the 6th stage is only the 5th stage. We assume that *A. temperatus* Humes, 1997 can be a junior synonym of *A. atlanteus* Humes, 1996.

In samples from the pelagic zone, at 80-300 m over vents of the Mid-Atlantic Ridge, Ivanenko [1998a] found all stages of dirivultids, including junior developmental stages, lecithotrophic nauplii, single adult males, and females with egg-sacks. Based on this finding, he assumes that the adults ascend to the pelagic zone for copulation, egg laying, hatching and development of juveniles and settle on the substratum by the last copepodid stage.

In the scheme suggested by Ivanenko [1998a], migration of adults to the pelagic zone for reproduction have to be reconsidered. First, previous collections containing females with egg-sacks indicate that they reproduce in the same place where they feed, i.e., on the substratum. This is especially important and expedient in the case of multiple egg laying. Secondly, migration to the pelagic zone of adults of about 1 mm would cause loss of the productive part of the population, as they would not be able to return to the bottom. The adults recorded in the pelagic zone are, rather, a part of the population unavoidably lost from the hydrothermal biotope because of removal by currents. Moreover, all three dirivultid species discovered in the pelagic zone [Ivanenko, 1998a] were described from the material washed off shrimps, *Rimicaris* Williams et Rona, almost surely their symbionts. It means that adult copepods might get to the pelagic zone by their own migration, but by transport on actively swimming nektobenthic shrimps. Such problems may be elucidated by further collections in the Pacific Ocean, where the dominant species in the ecosystem are vestimentiferans and not swimming shrimps.

The presence of other dirivultid stages in the plankton seems to be regular and natural, considering their distribution [Humes, 1991a]. Lecithotrophic nauplii are a characteristic, well-known, and highly efficient adaptation to prolonged wandering in the pelagic zone.

At the same time the presence of earlier developmental stages in benthic biotopes is not excluded. Recently, earlier copepodid stages were also found by Ivanenko (unpublished data) among mature stages of dirivultids in benthic collections sampled in different localities on East Pacific Rise and are awaiting investigation.

Symbiosis

Symbionts of invertebrates make up over 35% of known species of the subclass Copepoda [Ho, 2001]. The siphonostomatoids and poecilostomatoids, as mentioned above, are known mainly as symbionts of aquatic invertebrates and vertebrates. Many species of hydrothermal copepods seem to be also symbiotic. Humes and Segonzac [1998] suggest a possible symbiosis of copepods with 5 species of crustaceans, 14 species of bivalves, 4 species of polychaetes, and 11 species of vestimentiferans. They believe that not all these cases of symbiosis are true commensalism. Parasitic interrelations are also possible (see our discussion of feeding apparatuses).

The occurrence of free-living (non-symbiotic) copepods in the families Dirivultidae and Ecbathyriontidae presents an untypical but definitely primitive mode of life in the order Siphonostomatoida. The discovery of such dirivultids is essential to consideration of preadaptations of the siphonostomatoids' feeding apparatus that allowed them to establish symbiotic relationships with various groups of aquatic animals.

Unfortunately, shortcomings in collecting interfere with reliable and unambiguous interpretation of data concerning symbiosis. The problem of symbiosis of copepods in the hydrothermal zone requires special collecting methods and is still unsolved.

Distribution

One of the most complicated, interesting, and significant problems concerning hydrothermal fauna is its distribution. Naturally, theories have been developed principally with reference to the macrobenthos [Tunnicliffe et al., 1998; Mironov et al, 2002; Van Dover et al., 2002]. Discussion of geographic distribution of copepods became possible when collections from four localities in the Pacific Ocean and two localities in the Atlantic Ocean were examined [Humes, 1988d; 1991b]. Initial analysis revealed that poecilostomatoid and siphonostomatoid copepods make up the bulk of the fauna, with some genera widely distributed.

With additional sampled locations, it has become obvious that the base of copepod diversity consists of 51 valid species of the endemic family Dirivultidae, the most numerous and most successful group of copepods known from deep-sea hydrothermal vents [Ivanenko, Ferrari, 2003]. The bulk of its diversity is represented by 33 species belonging to the genera *Aphotopontius* and *Stygiopontius.*

According to recent data, the center of copepod species diversity is the East Pacific Rise and the same is true of other groups of animals [Tunnicliffe et al., 1998]. This region is one of the best explored and so the observation that the East Pacific Rise is more species-rich than other localities may be an artifact. Generally, wide distribution of copepods depends on distribution by naupliar and copepodid stages. However, how they are distributed from a certain point, by means of which currents, and to what distance remains unknown.

Special attention should be paid to investigations of the fauna of ground seawater of the ocean floor in zones of hydrothermal activity. Physically, the rocky bottom probably contains a general system of ground water, similar to that on land. A specific phreatic fauna populates the latter. If such a system exists in the ocean, it may be populated with its own fauna and be a pathway of distribution of hydrothermal copepods. In this case, the connection of distinct hydrothermal communities may be stronger than it looks on the bottom surface.

In conclusion, its should be stressed that the relatively small number of localities where material has been collected and the fact that the material was obtained as a by-product of other biological projects makes all conclusions on distribution of hydrothermal copepods very general and preliminary.

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