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A new genus and species of the family Dirivultidae (Copepoda: Siphonostomatoida) from a deep-sea hydrothermal vent at the Juan de Fuca Ridge (the northeastern Pacific) withcomments of dirivultid distribution

Новый вид нового рода семейства Dirivultidae (Copepoda: Siphonostomatoida) с глубоководного гидротермального поля хребта Хуан-де-Фука (северо-восточная Пацифика), с замечаниями по распределению диривултид

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KEY WORDS: Copepoda, Siphonostomatoida, Dirivultidae, *Humesipontius* gen.n, deep-sea, hydrothermal vent, northeastern Pacific, distribution.

КЛЮЧЕВЫЕ СЛОВА: Copepoda, Siphonostomatoida, Dirivultidae, *Humesipontius* gen.n, глубоководное гидротермальное поле, северо-восточная Пацифика, распространение.

ABSTRACT. The female of *Humesipontius arthuri*, a new genus and species of the family Dirivultidae Humes et Dojiri, 1980, is described from Juan de Fuca Ridge. The absence of an endopod on swimming leg 4 separates the new genus from other 12 genera of dirivultids. The new genus shares with *Exrima* Humes, 1987 the following derived states: one terminal seta on the endopod of antenna elongate; inner margin of basis expanded ventrally and distally in swimming legs 1–3, and ventrally in swimming leg 4; both dorsal setae of the caudal ramus in disto-lateral positions. The close families Dirivultidae and Ecbathyriontidae differ from other siphonostomatoids by double segment in the middle part of antennule. Two-segmented endopod of leg 4 is the derived state of Dirivultidae. *Fissuricola* Humes, 1987, of uncertain family position, with reduced to vestige maxilla is included in Dirivultidae. Four main geographic regions illustrate general pattern of dirivultid distribution: Mid-Atlantic, East Pacific (East Pacific Rise 10–21°N + Guaymas Basin + Galapagos Rift), Northeast Pacific, West Pacific. Each region has at least one endemic genus and species of the primitive genera *Aphotopontius* Humes, 1987 and *Stygiopontius* Humes, 1987. Long history of dirivultids and potential polyphyly of *Aphotopontius* and *Stygiopontius* are suggested. Possession of 6 endemic genera and 33 species of dirivultids, as well as endemic family Ecbathyriontidae Humes, 1987, distinguish East Pacific as center of dirivultid diversity.

РЕЗЮМЕ. Самка *Humesipontius arthuri*, новый вид нового рода семейства Dirivultidae Humes et Dojiri, 1980, описан с хребта Хуан-де-Фука. Новый род отличается от других 12 родов семейства отсутствием эндоподита 4-й пары плавательных ног. Новый род и близкий к нему род *Exrima* Humes, 1987 характеризуются: наличием длинной терминальной щетинкой эндоподита антенн; увеличением внутреннего края базиса 1–4-й пар плавательных ног; дисто-латеральным положением двух дорзальных щетинок каудальных ветвей. Близкие семейства Dirivultidae и Ecbathyriontidae отличаются от других семейств отряда наличием двойного членика в средней части антеннул. Отличие семейства Dirivultidae от Ecbathyriontidae проявляется в наличии двухчленистого эндоподита 4-й пары плавательных ног. Род *Fissuricola* Humes, 1987, имеющий неопределенное таксономическое положение и характеризующийся редукцией максилл, введен в семейство Dirivultidae. Четыре основных географических области передают общую закономерность распределения диривултид: Срединно-Атлантический хребет, восточная Пацифика (Восточно-Тихоокеанское поднятие 10–21° с.ш. + Бассейн Гуаймас + Галапагосский рифт), северо-восточная Пацифика, западная Пацифика. Каждая область включает не менее одного эндемичного рода, а также виды примитивных родов *Aphotopontius* Humes, 1987 и *Stygiopontius* Humes, 1987. Предполагается длительная эволюция семейства и возможная полифилия *Aphotopontius* и *Stygiopontius*.

Наличие 6 эндемичных родов и 33 видов диривултид, а также эндемичного семейства Ecbathyriontidae Humes, 1987, характеризует восточную Пацифику как центр разнообразия диривултид.

Dirivultidae Humes & Dojiri, 1980 is a family of primitive siphonostomatoid copepods and the most numerous and abundant family of deep-sea hydrothermal vent copepods found in Atlantic and Pacific oceans [Heptner & Ivanenko, 2002, 2003; Ivanenko & Defaye, submitted]. Despite ongoing taxonomic studies of copepod diversity from the relatively well-investigated and modeled hydrothermal vents at the Juan de Fuca Ridge (JFR), new expeditions and methods of sampling have led to the discovery of copepods new to science or previously unknown from hydrothermal vent habitats [Humes, 1999a,b]. Discussion of zoogeography of dirivultids is restricted by analysis of the Eastern Pacific [Humes, 1991] and comments of species lists from different sites and regions. This paper describes a new genus and species of dirivultid copepod from JFR and discusses geographical distribution of dirivultids.

Material and Methods

Two females were collected at Juan de Fuca Ridge, eastern Pacific (45°56.19' N, 129°58.9' W) with a tubeworm grab (R478-6613) by ROPOS (Remotely Operated Platform for Ocean Science) during cruise of NeMO (monitoring and sampling program on Axial Volcano) on September 15, 1998 at depth of 1520 m.

The specimens were cleared in steps through 50% lactic acid / 50% freshwater to 100% lactic acid, stained by adding a solution of chlorazol black E dissolved in 70% ethanol / 30% freshwater, and examined with bright-field or with differential interference optics. All measurements and dissections were made in lactic acid. Drawings were made with a camera lucida. The dissected specimen is preserved in glycerin.

Dirivultidae Humes et Dojiri, 1980

Humes & Dojiri, 1980: 149–151; Humes, 1987: 668–669, 1999c: 1058 (key of 11 genera).

REMARKS. The family Dirivultidae and the monotypic family Ecbathyriontidae Humes, 1987 have been reported from deep-sea hydrothermal vents and represent a monophyletic group of the order Siphonostomatoida. The derived state of the group is a double segment in the middle part of the antennule with 2 pairs of setae (the third article in antennule of *Humesipontius*) in females and males. The state is not shown for females of the modified genus *Dirivultus* Humes et Dojiri, 1980. Inner sinuous seta near in distal part of first segment (near its joining with sinuous second segments) of maxilla is a plesiomorphy of Siphonostomatoida found only in Dirivultidae and Ecbathyriontidae. A two-segmented abdomen, an elongate caudal rami and a pointed projection on exopod of antenna are the derived states of Ecbathyriontidae Humes, 1987, a sister family of Dirivultidae. The two-segmented endopod of leg 4 is the derived state of the family Dirivultidae. However the two-segmented abdomen of *Chasmatopontius* Humes, 1990 and the elongate caudal rami in *Aphotopontius baculigerus* Humes, 1987 and *A. limatulus* Humes, 1987 are supposed to be the result of convergent evolution in two families. The monotypic genus *Fissuricola* Humes, 1987 from East Pacific Rise with uncertain family position is interpreted here as a member of Dirivultidae. The assumed derived state of *Fissuricola* is the maxilla reduced to small vestige. The genus has the distal segment of the endopod of leg 4 armed with 4 setae in contrast with other dirivultid genera having at most 3 setae.

Humesipontius **gen. n.**

DIAGNOSIS. Lacking of endopod on swimming leg 4 and elongate seta of the first segment of endopod of maxilliped are the derived character state separating *Humesipontius* from 12 genera of dirivultids.

REMARKS. *Exrima* Humes, 1987 appears to be the sister group of *Humesipontius*. The two genera share three derived states: one terminal seta of the endopod of antenna is elongate; two dorsal setae of the caudal ramus are disto-lateral; the inner edge of basis is expanded distally on swimming legs 1–3 and ventrally in swimming leg 4.

TYPE SPECIES. *Humesipontius arthuri* is the type species designated here, and the only species in the genus.

ETYMOLOGY. The name *Humesipontius* is a combination of *Humesi* derived from family name of Arthur G. Humes (1916–1999) who contributed extensively to our knowledge of symbiotic and deep-sea hydrothermal vent copepods and the Greek word *pontios* (= of the sea) commonly using to form names of deep-sea copepods.

Humesipontius arthuri **sp.n.**
Figs 1–3.

The holotype (USNM 1006838) deposited at the National Museum of Natural History (Washington D.C., USA). Dissected paratype in the collection of the first author.

DESCRIPTION. Adult female. Body somewhat elongate (Fig. 1A). Total length, excluding caudal setae, 1.8 mm greatest width 0.64 mm. Prosome of 4 articulating parts: cephalothorax and 3 somites bearing legs 2–4, respectively. Tergites of these 3 somites point posteriorly. Urosome (Fig. 1B-D) of 5 articulating parts. Somite bearing leg 5 with dorsolateral projections, genital double-somite with spine-like caudo-lateral projections (Fig. 1C), 2 abdominal somites and anal somite. Gonopores dorso-lateral in the anterior half of the somite, copulatory pores ventral to the genital areas. Anal opening dorsal near the middle of the somite. Caudal ramus (Figs. 1D) with 6 setae and small flattened setules; two dorsal setae in the disto-lateral position. Rostrum weakly developed; oral cone short and robust (Fig. 1G).

Egg sacs not observed.

Antennule (Figs. 1E, E_1) 10-segmented. First segment the longest with 13 setae of which 4 setae are very short. Segment 2 subdivided, with 6 unequal setae, 1 seta is small. Segment 3 with 2 pairs of setae. Segments 4–7 with 2 setae, 1 seta near the middle, another seta near the distal edge. Segment 8 with 2 setae and an aesthetasc near the distal edge. Segment 9 and 10 with 2 and 11 setae, respectively. All setae smooth.

Antenna (Fig. 1F). Small coxa and elongate basis without setules. Exopod 1-segmented armed with 1 smooth terminal seta. Endopod 2-segmented: First segment unarmed and with setules, second segment with 3 setae and setules, 1 terminal seta very elongate.

Mandible (Fig. 2B) a stylet-like gnathobase flattened distally and with small terminal teeth.

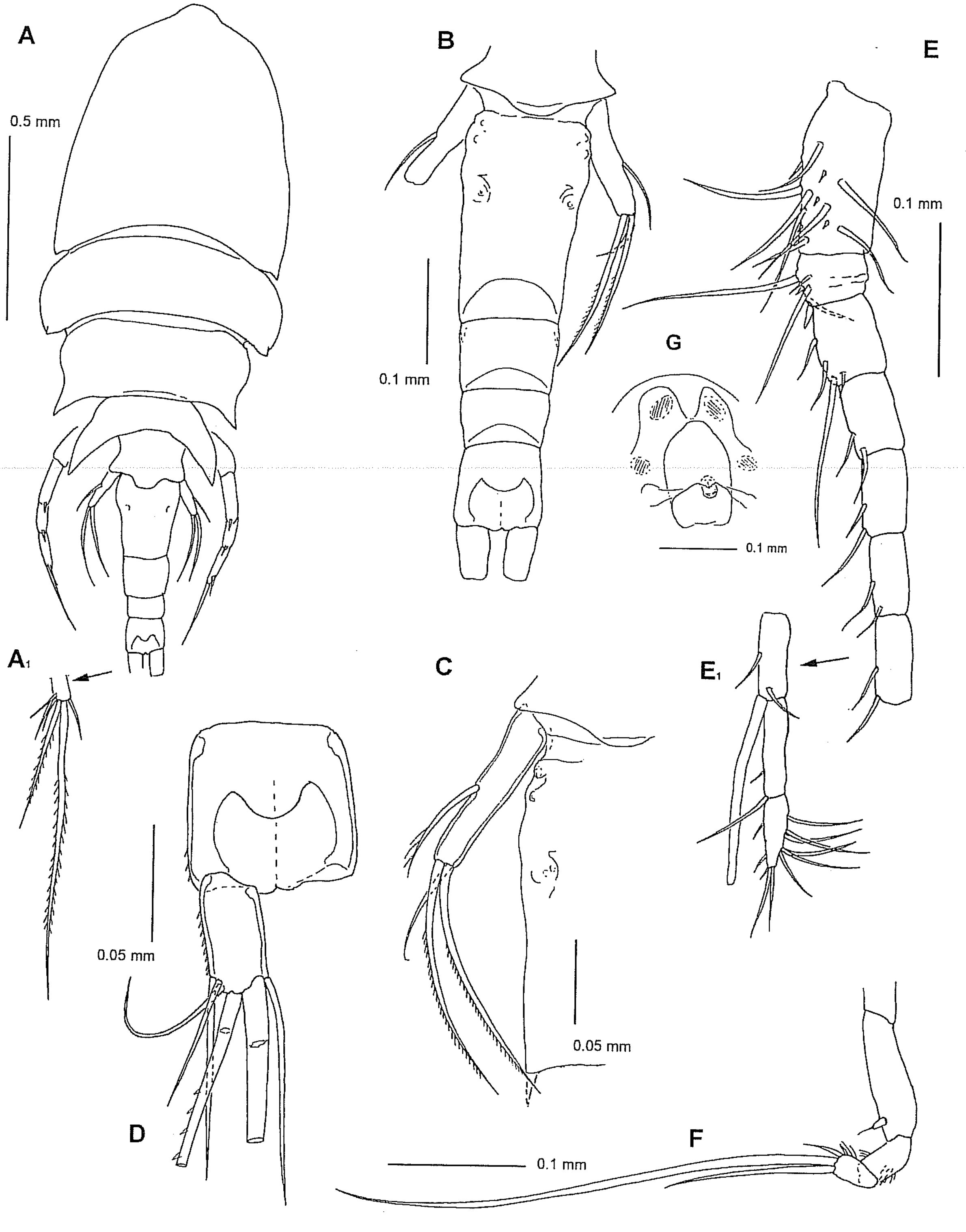

Fig. 1. Female of *Humesipontius arthuri* gen.n., sp.n. A — habitus, dorsal; A_1 — caudal ramus; B — urosome, dorsal; C — leg 5 and left side of genital double-somite, dorsal; D — anal somite and caudal ramus, dorsal; E—E_1 — antennule; F — antenna; G — oral cone, ventrolateral.

Рис. 1. Самка *Humesipontius arthuri* gen.n., sp.n. A — общий вид сверху; A_1 — каудальная ветвь; B — уросома, вид сверху; C — 5-я нога и левая сторона двойного генитального сегмента, вид сверху; D — анальный сегмент и каудальная ветвь, вид сверху; E—E_1 — антеннула; F — антенна; G — ротовой конус.

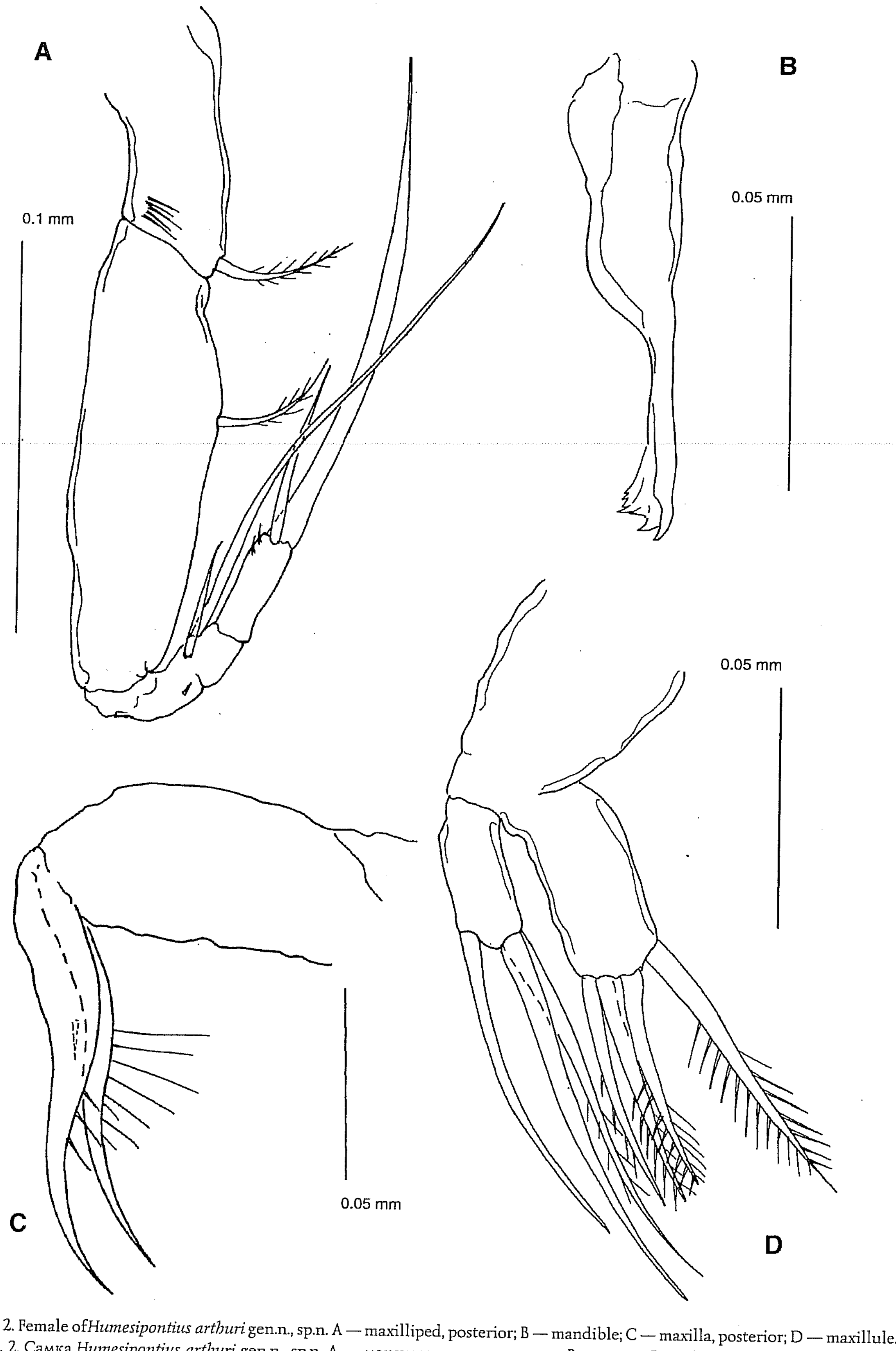

Fig. 2. Female of *Humesipontius arthuri* gen.n., sp.n. A — maxilliped, posterior; B — mandible; C — maxilla, posterior; D — maxillule.
Рис. 2. Самка *Humesipontius arthuri* gen.n., sp.n. A — максиллипед, вид с хвоста; B — мандибула; C — максилла, вид с хвоста; D — максиллула.

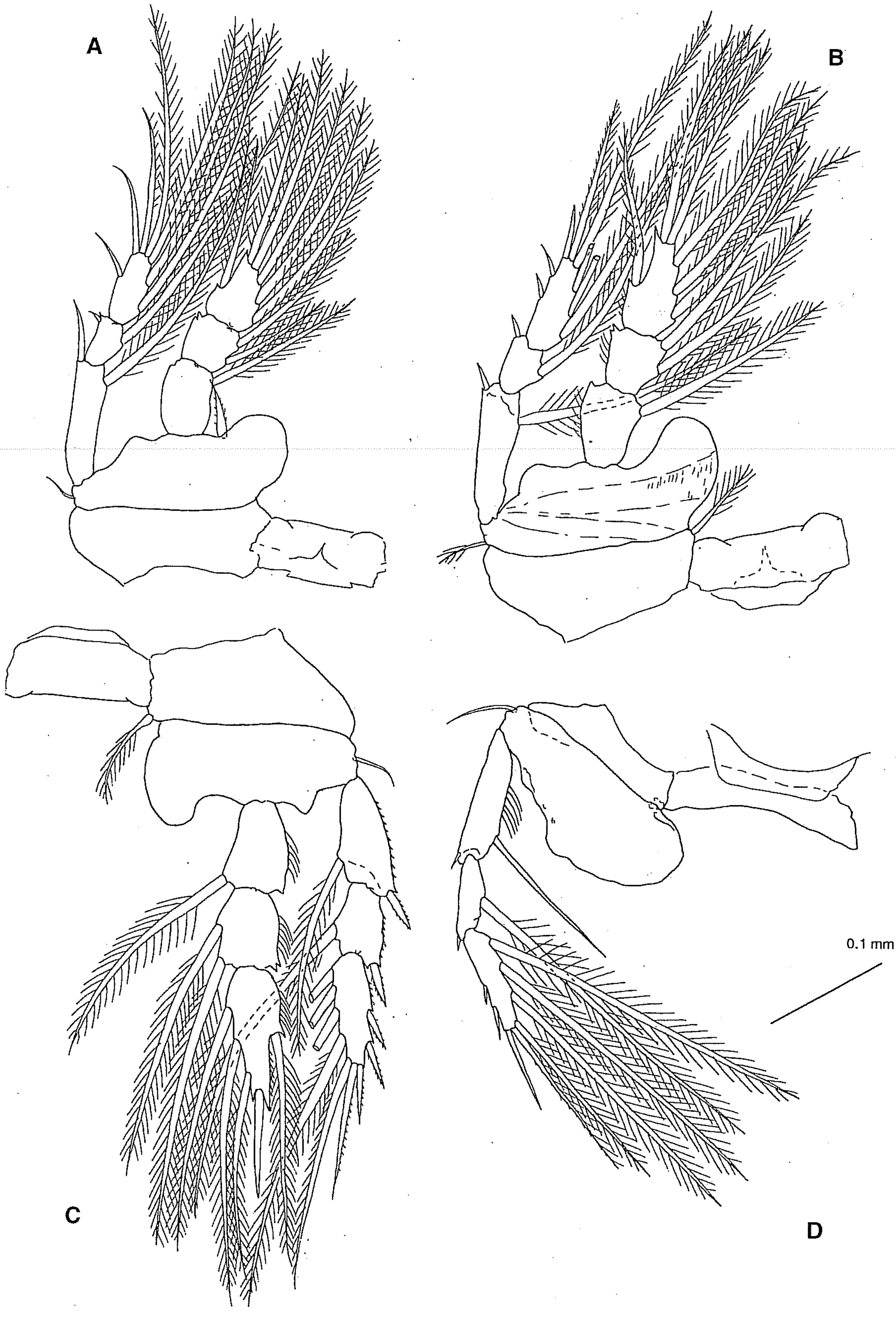

Fig. 3. Female of *Humesipontius arthuri* gen.n., sp.n. A–D — leg 1–4, anterior.
Рис. 3. Самка *Humesipontius arthuri* gen.n., sp.n. A–D — 1–4-я плавательные ноги, вид с головы.

Table 1. Formula for the armature of legs 1–4. Roman numerals indicate spines, Arabic numerals, setae.
Таблица 1. Формула вооружения 1–4-й пары плавательных ног. Римские цифры соответствуют шипам, арабские — щетинкам.

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-I	I-1; I-1; II ,1,4	0-1; 0-2; 1,2,3
Leg 2	0-1	1-0	I-1; I-1; II,II,4	0-1; 0-2; 1,2,3
Leg 3	0-1	1-0	I-1; I-1; II,II,5	0-1; 0-2; 1,I,3
Leg 4	0-0	1-0	I-1; I-1; II,I,5	absent

Maxillule (Fig. 2D) with inner lobe bearing 4 long setae ornamented with stout setules, and smaller outer lobe articulating and with 2 terminal and 1 subterminal setae.

Maxilla (Fig. 2C) with flattened 1st segment and sinuous 2nd segment carrying median setules. First segment with long seta located near joining of the segments and repeating form of the 2nd segment with median setules.

Maxilliped (Fig. 2A) 4-segmented. Short syncoxa with row of setules and inner seta bearing slender setules. Long basis with inner seta carrying short setules. First segment of endopod subdivided and with one short proximal seta and 2 distal setae, one of which is very elongate. Second segment with 2 setae, one of which is claw-like and elongate. All setae of endopod smooth.

Legs 1–4 (Fig. 3A–D) biramous, with 3-segmented rami except for leg 4 which lacks endopod. Inner margin of basis is expanded ventrally and distally in swimming legs 1–3, and ventrally in swimming leg 4. Outer spines are slender. Inner seta of proximal segment of endopod of leg 4 is smooth. Formulae for the armature of legs in the Table 1.

Leg 5 (Fig. 1C) consisting of an elongate, articulating segment with 4 setae: 3 distal and 1 medial. All setae with setules.

Color of living specimens unknown.

Male. Unknown.

ETYMOLOGY. The species name is derived from the given name of Arthur G. Humes.

Discussion

Little is known about the biology and functional morphology of dirivultids [Ivanenko, 1998; Vereshchaka et al., 1998; Heptner & Ivanenko, 2002, 2003; Tsurumi et al., submitted], and a phylogenetic analysis will be the subject of a later publication. Numerous data suggest that Dirivultidae is one of the largest family of invertebrates found in the deep-sea hydrothermal vents. There are 53 species belonging to 13 genera of dirivultids (Table 2). This is about 71% of all copepods of 6 orders reported from the deep-sea hydrothermal vents [Heptner & Ivanenko, 2003]. Fourteen species of dirivultids belong to 10 genera with 1 or 2 species (6 genera are monotypic); *Ceuthoecetes* Humes & Dojiri, 1980 contains 4 species. Thirty-five species or 66% of all dirivultids belong to the primitive genera *Aphotopon-*

Table 2. Distribution of Dirivultidae and Ecbathyriontidae in deep-sea hydrothermal vents; 1–16 — number of the deep-sea hydrothermal sites from which the copepods were reported (see below).
Таблица 2. Распределение копепод семейства Dirivultidae and Ecbathyriontidae в глубоководных гидротермах. 1–16 — места находок.

	Location															
	Pacific ocean											Atlantic ocean				
	EP					NEP			WP			MAR				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Dirivultidae Humes et Dojiri, 1980																
1. *Aphotopontius acanthinus* Humes et Luts, 1994		+														
2. *Aphotopontius arcuatus* Humes, 1987	+		+	+												
3. *Aphotopontius atlanteus* Humes, 1996												+				
4. *Aphotopontius baculigerus* Humes, 1987	+			+												
5. *Aphotopontius flexispina* Humes, 1987				+												
6. *Aphotopontius forcipatus* Humes, 1987						+	+	+							+	
7. *Aphotopontius hydronauticus* Humes, 1989			+													
8. *Aphotopontius limatulus* Humes, 1987	+	+		+												
9. *Aphotopontius mammillatus* Humes, 1987	+		+	+	+											
10. *Aphotopontius probolus* Humes, 1990	+															

1–16 — number of the deep-sea hydrothermal sites from which the copepods were reported (modified after Humes & Segonzac, 1998; Heptner & Ivanenko, 2003). EP — (East Pacific Rise + Guaymas Basin + Galapagos Rift): 1 — Galapagos Rift, 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. NEP — Northeast Pacific: 6 — Gorda Ridge, 41°N; 7 — Juan de Fuca Ridge, 46°N; 8 — Explorer Ridge, 49°N. WP — West Pacific: 9 — Mariana Back-Arc Basin, 18°N; 10 — New Ireland Basin, 3°S; 11 — Lau Back-Arc Basin, 23°S. MAR — Mid-Atlantic Ridge: 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).

	Location															
	Pacific ocean											Atlantic ocean				
	EP					NEP			WP			MAR				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Dirivultidae Humes et Dojiri, 1980																
11. *Aphotopontius rapunculus* Humes et Segonzac, 1998		+														
12. *Aphotopontius temperatus* Humes, 1997												+				
13. *Benthoxynus spiculifer* Humes, 1984						+	+	+								
14. *Benthoxynus tumidiseta* Humes, 1989			+													
15. *Ceuthoecetes acanthothrix* Humes, 1987	+	+	+	+												
16. *Ceuthoecetes aliger* Humes et Dojiri, 1980	+	+	+	+												
17. *Ceuthoecetes cristatus* Humes, 1987		+	+	+												
18. *Ceuthoecetes introversus* Humes, 1987	+			+												
19. *Chasmatopontius thescalus* Humes, 1990									+		+					
20. *Dirivultus dentaneus* Humes et Dojiri, 1980 *																
21. *Diriviltus spinigulatus* Humes, 1999										+						
22. *Exrima dolichopus* Humes, 1987			+													
23. *Exrima singula* Humes, 1987				+												
24. *Fissuricola caritus* Humes, 1987				+												
25. *Humesipontius arthuri* gen.n., sp.n.							+									
26. *Nilva torifera* Humes, 1987	+		+	+												
27. *Rhogobius contractus* Humes, 1987	+		+	+												
28. *Rhogobius pressulus* Humes, 1989	+															
29. *Rimipontius mediospinifer* Humes, 1996													+		+	+
30. *Scotoecetes introrsus* Humes, 1987		+	+													
31. *Stygiopontius appositus* Humes, 1989			+	+												
32. *Stygiopontius brevispina* Humes, 1991											+					
33. *Stygiopontius bulbisetiger* Humes, 1996															+	
34. *Stygiopontius cinctiger* Humes, 1987		+	+	+												
35. *Stygiopontius cladarus* Humes, 1996													+		+	
36. *Stygiopontius flexus* Humes, 1987		+			+											
37. *Stygiopontius hispidulus* Humes, 1987		+	+	+												
38. *Stygiopontius latulus* Humes, 1996															+	
39. *Stygiopontius lauensis* Humes, 1991											+					
40. *Stygiopontius lumiger* Humes, 1989				+												
41. *Stygiopontius mirus* Humes, 1996		+													+	
42. *Stygiopontius mucroniferus* Humes, 1987		+			+											
43. *Stygiopontius paxillifer* Humes, 1989		+		+												
44. *Stygiopontius pectinatus* Humes, 1987									+				+	+	+	
45. *Stygiopontius quadrispinosus* Humes, 1987						+	+	+								
46. *Stygiopontius regius* Humes, 1996															+	
47. *Stygiopontius rimivagus* Humes, 1997												+				
48. *Stygiopontius sentifer* Humes, 1987		+	+	+												
49. *Stygiopontius sepacrius* Humes et Shank **				+												

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

	Location															
	Pacific ocean											Atlantic ocean				
	EP					NEP			WP			MAR				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
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	+	+	+	+												

* *Dirivultus dentaneus* Humes et Dojiri, 1980 was found in 1966, off southern California (32°19.6'N, 117°19.08'W) associated with *Lamellibrachia*, depth 1225 m.
** Description of a new species was submitted by Humes and Shank.

tius Humes, 1987 and *Stygiopontius* Humes, 1987 with 12 and 23 species respectively. *Aphotopontius* is distinguished by having one inner seta on the proximal segment of leg 4; the seta is absent in *Stygiopontius*. Both genera show numerous plesiomorphies [Ivanenko & Heptner, 1998] and do not have clear apomorphies.

Two generic groups of Dirivultidae can be separated on the base of derived characteristics. A group of three genera found on vestimentiferans (*Ceuthoecetes, Dirivultus, Nilva* Humes, 1987) has derived (1) oral cone with round distal opening forming by labrum and labium and (2) maxillae lacking elongate sinuous seta on first segment. A close relationship of this group with the genera *Stygiopontius* and *Scotoecetes* Humes, 1987 is suggested by the armament of the endopod of leg 4: 0; 1,1. Another group of 3 genera (*Exrima*, *Benthoxynus* Humes, 1984, *Rimipontius* Humes, 1996) has a derived state of the 2-segmented endopod of leg 4 armed by one terminal seta. *Humesipontius,* lacking endopod of leg 4 and close to *Exrima,* belongs to this group.

Four main geographic regions (see table 2) are chosen here to illustrate a general pattern of dirivultid distribution: East Pacific Rise (10–21°N) + Guaymas Basin + Galapagos Rift — EP (1–5); Northeast Pacific — NEP (6–8); West Pacific — WP (9–11); Mid-Atlantic Ridge — MAR (12–16). Each region has at least one endemic genus. The endemic genera for the regions are *Rimipontius* — MAR; *Chasmatopontius* — WP; *Humesipontius* — NEP; *Ceuthoecetes, Exrima, Fissuricola, Nilva, Rhogobius* Humes, 1987, *Scotoecetes* — EP. The absence of endemic genera and species in Guaymas Basin and of endemic genera in Galapagos Rift, as well as the number of common species and genera endemic for the EP, indicate a close connection of both sites with East Pacific Rise (10–21°N). Humes [1991] noted the absence of *Stygiopontius* from the Galapagos Rift and estimated endemism of many copepods from the Guaymas Basin. The last conclusion is not supported by the latest data. The unity of WP is confirmed by the finding of *Chasmatopontius thescalus* Humes, 1990 in such distant localities as Mariana and Lau Back-Arc basins.

All regions have representatives of two primitive genera *Aphotopontius* and *Stygiopontius* except the poorly-investigated West Pacific where *Aphotopontius* has not been reported. There are only two other examples of similarities on the generic level. NEP and EP contain dirivultids of the genus *Benthoxynus,* and the monophyletic group of two endemic genera *Humesipontius* and *Exrima* from each region supports a link between regions. Discovery of the genus *Dirivultus* in EP and WP suggests a link between these regions. However, dirivultids associated with vestimentiferans are still studied insufficiently and new findings can change our understanding of their distribution restricted to EP and WP now.

Four species belonging to the genera *Aphotopontius* and *Stygiopontius* were found in different regions: *A. forcipatus* Humes, 1987 (MAR and NEP); *S. pectinatus* Humes, 1987 (MAR and WP); *S. mirus* Humes, 1996 (MAR and EP); *S. stabilitus* Humes, 1990 (EP and WP). Finding of 3 species from 13 species of dirivultids found in Atlantic ocean and 3 distinct regions of Pacific ocean is remarkable and can connect with youngness of the MAR comparing with Pacific ocean [Tunnicliffe et al., 1998].

Six endemic genera, 31 endemic species from 33 species from EP comprise 62% of known species and 77% of genera of dirivultids. All these distinguish EP as the center of dirivultid diversity with highest endemism on generic and species levels. The endemic family Ecbathyriontidae close to Dirivultidae confirms this state.

The presence of endemic genera and species in other 3 regions indicates significant diversity in these regions and a possible polyphyletic nature of specious genera *Aphotopontius* and *Stygiopontius*. The potential polyphyly is supported by the morphological analysis of dirivultids illustrating mosaic distribution of many characters [Ivanenko & Heptner, 1998].

Occurrence of 4 common species of *Aphotopontius* and *Stygiopontius* in different regions and oceans may result from a long history of dirivultids confirmed by (1) the remarkable diversity of the group and their exclusive occurrence in the deep-sea hydrothermal vents of Atlantic and Pacific oceans, (2) occurrence of endemic genera and common species of the primitive genera in different regions, (3) fewer genera of dirivultids of EP shared with dirivultids of MAR than shared between EP with NEP and WP, (4) primitive position of dirivultids in the order Siphonostomatoida, (5) description of Cretaceous siphonostomatoid on gills of an ancient fish, which is the oldest fossil of copepod [Cressey & Boxshall, 1989].

If the ancestor of dirivultids existed from the period of Tethys Sea, then the dispersal of dirivultids may have followed the main currents of the ancient sea westward [Tunnicliffe et al., 1998] and was not direct from Pacific to Atlantic. The puzzling finding of *A. forcipatus*, *S. mirus*, and *S. pectinatus* in distinct parts of the Pacific and Atlantic oceans supports this pattern even if further studies will discover some morphological distinctions for the copepods from different regions. More study of dirivultids from different regions is necessary to test this hypothesis.

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