

Morphology of the larval stages of *Spirontocaris murdochi* Rathbun, 1902 (Decapoda: Thoridae) from adjacent waters of Kamchatka

Морфология личинок креветок *Spirontocaris murdochi* Rathbun, 1902 (Decapoda: Thoridae) из прикамчатских вод

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KEY WORDS: shrimp, larvae, morphology, stages of development, variability, Pacific Ocean, Sea of Okhotsk, Bering Sea.

КЛЮЧЕВЫЕ СЛОВА: креветки, личинки, морфология, стадии развития, изменчивость, Тихий океан, Охотское море, Берингово море.

ABSTRACT. Larval stages of shrimp *Spirontocaris murdochi* Rathbun, 1902 (Decapoda: Thoridae) from plankton in eastern part of Sea of Okhotsk, Pacific waters along southeastern coast of Kamchatka, and western part of Bering Sea are described. Main morphological differences from larvae of corresponding stages of other species of *Spirontocaris* were revealed. Individual variability in number of spines in anteroventral margin of carapace, segmentation of exopod of antenna and scaphocerite, level of development of pleopods, length of uropods, and shape of telson were found. Armament of maxillules in all stages, maxillae in early zoeae, relative length of rostrum, and morphology of pereopods can be considered the least variable and more reliable features for species identification. Asymmetry of morphology and arms of carapace, antennae, maxillules, maxillae, pereopods, and maxillipeds was revealed.

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РЕЗЮМЕ. Дано описание личиночных стадий креветки *Spirontocaris murdochi* Rathbun, 1902 (сем. Thoridae) из планктона восточной части Охотского моря, тихоокеанских вод вдоль юго-восточного побережья Камчатки и западной части Берингова моря. Выявлены основные морфологические отличия личинок *S. murdochi* от соответствующих стадий других видов *Spirontocaris*. Обнаружена инди-

видуальная изменчивость количества шипиков на антеровентральном крае карапакса, сегментации экзоподита антеннулы и скафоцерита, степени развития плеоподов, длины уроподов и формы тельсона. Вооружение максиллул на всех стадиях, максилл у младших зоэа, относительную длину роста, морфологию переоподов можно считать наименее вариабельными и более надежными признаками для видовой идентификации. Выявлена асимметрия морфологии и вооружения карапакса, антенн, максиллул, максилл, переоподов, максиллипедов.

Introduction

The genus *Spirontocaris* Bate, 1888 (Decapoda: Thoridae) currently includes 21 species [De Grave, Fransen, 2011], of which 10 species are known for the study area: *S. arcuata* Rathbun, 1902; *S. brashnikovi* Kobjakova, 1936; *S. brevidigitata* Kobjakova, 1936; *S. intermedia* Kobjakova, 1935; *S. lamellicornis* (Dana, 1852); *S. murdochi* Rathbun, 1902; *S. ochotensis* (Brandt, 1851); *S. phippisii* (Krøyer, 1841); *S. prionota* (Stimpson, 1864); *S. spinus* (Sowerby, 1805).

The biology of *Spirontocaris* in Russian waters is not well understood. Some information is available for the northern part [Vinogradov, 1947; Kobjakova, 1962; Bandurin, Karpinsky, 2015] and for the eastern part of the Sea of Okhotsk [Sokolov, 2001]. There is only fragmentary information on depths of habitat and temperature conditions for most species. There is very scarce information on the distribution of shrimp larvae of the genus *Spirontocaris* in the seas of Russian Far

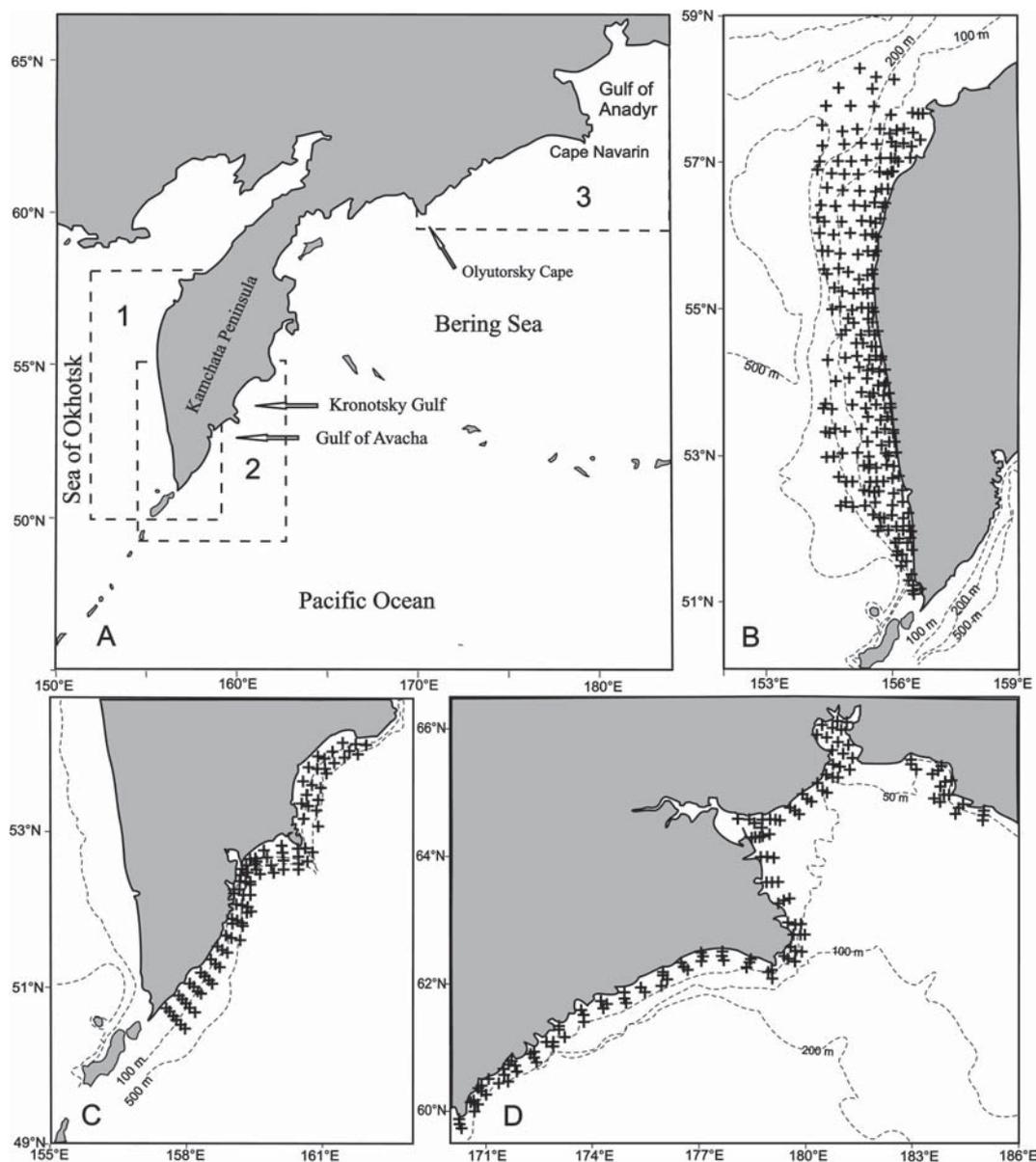


Fig. 1. Scheme of survey area: A — general scheme (1 — Western Kamchatka, 2 — Southeastern Kamchatka, 3 — Bering Sea). Station locations: B — Western Kamchatka, C — Southeastern Kamchatka, D — Bering Sea

Рис. 1. Карта-схема района исследований: А — общая схема (1 — Западная Камчатка, 2 — Юго-восточная Камчатка, 3 — Берингово море). Расположение станций: В — Западная Камчатка, С — Юго-Восточная Камчатка, D — Берингово море.

East, and especially in waters adjacent to Eastern Kamchatka and Chukotka. Only fragmentary data on the occurrence of larvae of this genus in the Kamchatka and Chukotka waters of the Bering Sea and in the northwestern Pacific along southeastern Kamchatka are available [Makarov, 1967, 1969; Sedova, Andronov, 2013; Sedova, Grigoriev, 2013; Sedova, Ptashkina, 2018; Sedova, Tepnin, 2019].

Studies of shrimp meroplankton are largely hampered by poor knowledge of the morphological features of species at different stages of their larval development, as well as the lack of identification keys. Early

larvae have been described for only six of the above species. Early zoeae of *S. intermedia* [Ivanov, 1971], *S. arcuata*, *S. ochotensis* [Haynes, 1981] and *S. murdochii* [Haynes, 1984] have been reared in the laboratory from ovigerous females. Larvae of *S. phippisii* and *S. spinus* have been described from plankton [Squires, 1993]. There is description of a few zoeal stages of larvae from western Kamchatka waters, which were improperly identified as *S. intermedia* and incomplete description of unidentified larvae of genus *Spirontocaris* from plankton in eastern part of the Sea of Okhotsk [Makarov, 1967].

Table. Data of the collection of larvae studied in the present study, including times, locality, and available stages of *Spirontocaris murdochi* larvae collected.
Таблица. Характеристика использованного материала для изучения морфологии личинок *Spirontocaris murdochi*

Stage	Region	Date of surveys	Bottom depth, m	Larvae analyzed
I	WK	7–9.06.2016	21–87	6
	SEK	4–19.04.2017	560–655	2
II	SEK	19.04–16.05.2017	49–787	8
III	WK	13–24.06.2015	22–123	12
	SEK	19.04–16.05.2017	49–2000	4
	BS	15–19.07.2010	64	2
IV	WK	13.06–07.07.2015	69–80	3
	SEK	26.04.2017	86	1
	BS	19.07.2010	27	6
V	BS	17–19.07.2010	27	4
VI	BS	17.08–13.09.2010	51–52	3

Designations: WK — Western Kamchatka (eastern part of the Sea of Okhotsk); SEK — Southeastern Kamchatka (Pacific Ocean); BS — Bering Sea; I–VI — zoeal stages.

Shrimp larvae of this genus are regularly found in plankton throughout the growing season in small amount (usually no more than 30 larvae per m²) over bottom depths of 5 to 2000 m (usually 30 to 150 m). Analyzing samples from adjacent Kamchatka waters of 2015–2017, we found many larvae in different stages of development, clearly belonging to genus *Spirontocaris*. Series of successive developmental stages for each available species were selected based on common morphology and size. Since first three zoeal stages of *S. murdochi* were obtained in laboratory and partly described by Haynes [1984], we were able to distinguish these forms from plankton samples. Missing stages were selected for them based on similarity of structure and size.

Objective of this work is to describe features of larval development of *S. murdochi* from adjacent Kamchatka waters and to identify reliable characters for species identification.

Materials and methods

SAMPLES COLLECTION. Material for this work was collections of plankton samples from Olyutorsko-Navarin-sky region and Gulf of Anadyr in July–September 2010, eastern part of the Sea of Okhotsk in June–July 2015 and 2016, as well as Pacific waters off southeastern coast of Kamchatka in April–May 2017 (Fig. 1, Table). Ichthyoplanktonic conical gear with a mouth diameter of 80 cm and mesh size 0.56 mm was used. Vertical total haul from bottom to surface was carried out with bottom depth 500 m and less, and from 500 m to surface above higher bottom depths. In the waters of the Pacific Ocean, sampling was carried out over bottom depth of 9–3000 m, and in the Okhotsk and Bering Seas at bottom depth of 5–560 m. Carrying out the sampling in the Okhotsk and Bering Seas (except the coastal part of Western Kamchatka), research vessels began stations from the south and moved northward. Off the southeastern

coast of Kamchatka and in the coastal part of West Kamchatka stations was carried out from north to southward. Morphology of 51 larvae was studied in detail (Table).

IDENTIFICATION OF DEVELOPMENTAL STAGES. When determining the larval stage, we proceeded from the fact that, in zoea I antennules have an unsegmented peduncle, scaphocerite does not have a formed spine, and the number of terminal setae on telson is less by one pair in comparison to subsequent stages. Zoea II, in our opinion, should not have free uropods, the antennae peduncle is two-segmented, and the antennae flagellums are not segmented, telson bearing 8 pairs of terminal setae, scaphocerite with a spine. In zoea III uropods are present; their endopod is much shorter than the exopod and bearing usually 2 small apical setae. Lateral spines in telson appear at subsequent stages, telson gradually narrows, branches in uropods lengthen, and number of setae increases. Not later than in zoea IV, the peduncle of the antennule consists of three segments, the outer flagellum of the antennule is segmented. In the following stages, the number of segments of the outer flagellum and inner flagellum of the antennule increases. The number of setae in scaphognathite and basal endite of maxillule increases after each molt. The pleopods are gradually becoming more complicated (from complete absence in zoea I to biramous with apical spines in late zoea). The decapodid stage differs from the zoea by reduced exopod of the pereopods, a smaller number of terminal setae on telson, a very long endopod of antenna, and a characteristic maxillary structure.

SPECIES IDENTIFICATION. A series of larvae was selected based on similarity of morphology and size. Identification of early larvae was carried out on description of zoea I–III of *S. murdochi* [Haynes, 1984]. There are features by which early larvae can be identified as *S. murdochi*:

- rostrum very thin and long;
- long thin dorsolateral spines in fourth and fifth pleonal somites;
- 2-segment peduncle and non-segmented branches of antennule in zoea II;
- 2 setae in tip of antennal flagellum;
- 4–5 separated segments in tip of scaphocerite;

– spine of scaphocerite is absent in zoea I, and in zoea II and zoea III it reaches approximately to anterior margin of scaphocerite;

– anal spine in zoea I;

– wide and deep semicircular notch in telson in zoea I–III;

– presence of 7 pairs of terminal setae in telson in zoea I and 8 pairs — in zoea II and zoea III;

– basal endite with 10 cuspidate setae of maxillule in zoea I; 9 setae in basal endite in zoea II–III, 11 setae in zoea II and 12–13 setae in zoea III;

– 5 plumose setae in scaphognathite of zoea I;

– pereopods in zoea I–III unsegmented, there are rudiments of all five pairs of pereopods already in zoea I;

Subsequent stages were selected from plankton. In late larvae distal segments of third–fifth pairs of pereopods were strongly elongated and pointed. This feature distinguishes this series of larvae from all others and corresponds to morphology of distal segments of juveniles and adults of *S. murdochi* [Hayashi, 1977]. In most other species of genus *Spirontocaris* these segments are much shorter and less pointed.

Larvae described in this study differ from zoea of *S. ochotensis* described by Haynes [1981] by presence of rostrum, larger body size, absence of supraorbital spines in zoea I, large number of anteroventral small spines, and smaller number of setae in both basal endite of maxillule and scaphognathites.

Our larvae differ from zoea of *S. spinus* described by Squires [1993] by smaller body size, absence of supraorbital spines, fewer setae in scaphognathite and basal endite of maxillule, absence of pleopods in stage I, and less developed appendages in late stages.

Our larvae differ from zoea of *S. phippsii* described by Squires [1993] by smaller size, the presence of spines in anteroventral margin, fewer setae in telson, absence of supraorbital spines, fewer setae in scaphognathite and basal endite of maxillule, absence of pleopods in zoea I, less developed pereopods in later stages.

Our larvae differ from zoea of *S. intermedia*, described by Ivanov [1971], by longer rostrum, telson shape, fewer setae in basal endite of maxillule and in scaphognathite, and absence of external proximal seta in scaphocerite.

Our larvae differ from zoea of *S. arcuata* described by Haynes [1981], by very long rostrum, larger body size, larger number of anteroventral small spines, absence of external proximal setae in scaphocerite, shape of telson, and a wider notch in the telson.

DESCRIPTION AND MEASUREMENTS OF LARVAE. The carapace, pleon, telson, and separate appendages are described and illustrated in detail. Only the appendages featuring morphological differences are presented in Figures 2–7. The general appearance and specific appendages are demonstrated. Only those setae and spines that are preserved on existing specimens were drawn in the figures. Some of the long setae were cropped. Pubescence and armature of setae were not depicted in figure in most cases, so as not to obstruct image.

Measurements of the larva with the ocular micrometer were carried out as follows: total length from the anterior tip of rostrum to the median margin of telson, excluding telson processes (TL); carapace length from the anterior tip of rostrum to the posterior median margin of carapace (CL); rostrum length from its anterior tip to the base of eyes (RL). The data were rounded to the nearest 0.1 mm. Larval description followed method proposed by Clark *et al.* [1998].

ABBREVIATIONS. A1 — antennule; A2 — antenna; Ca — carapace; GV — general view of larva; TL — total length of larva; CL — carapace length; RL — rostrum length; Mx1 — maxillule; Mx2 — maxilla; Sg — scaphognathite; Sc — scaphocerite; Mp1–3 — first–third maxillipeds, respectively; P1–P5 — first–fifth pereopods; pl1–pl5 — first–fifth pleopods; T — telson; *a.i.* — *appendix interna*; WK — Western Kamchatka (eastern part of the Sea of Okhotsk); SEK — southeastern Kamchatka; BM — Bering Sea. Asterisk (*, ** or ***) in appendages numbers means various variants.

Results

ZOEA I

Material examined: larvae were caught on July 6–9, 2016 at three stations in southern part of Western Kamchatka shelf over bottom depths of 21–87 m and off the southeastern coast of Kamchatka in April 2017 in two stations over bottom depth of 560 and 655 m.

Dimensions: TL 4.51 ± 0.06 (4.3–4.9) mm, CL 0.86 ± 0.03 (0.7–0.9) mm, RL 0.54 ± 0.02 (0.5–0.7) mm.

Carapace (Fig. 2, GV, Cp, Cp*, Cp**, Cp***): rostrum long, directed forward (in 1/3 of studied specimens it reaches front margin of eyes, in the majority — not much longer); eyes cylindrical, anterior and posterior dorsomedian papillae present; pterygostomial spine present; anteroventral margin with 3–4 small spines (in 1/3 of specimens in one side of carapace only 2 spines); supraorbital spines absent.

Antennule (Fig. 2, A1): peduncle unsegmented, with 1 long plumose seta terminally; short outer flagellum with 3 aesthetascs and 1 spinous process.

Antenna (Fig. 2, A2, A2*): protopod unsegmented, with 1 distal spine; endopod shorter than scaphocerite or approximately equal in length; with 1 terminal spine and 1 long terminal plumose setae, base of flagellum is not separated; scaphocerite 5–6-segmented, 4–5 short segments distally, with 7–9 plumose setae in inner margin, 1–2 plumose setae in outer margin, and 1 small simple seta in apex.

Maxillule (Fig. 2, Mx1): coxal endite with 5 papposerrate setae and 2 lateral plumose setae, basal endite with 10 cuspidate setae; endopod with 1 short simple and 5 strong papposerrate setae.

Maxilla (Fig. 2, Mx2): coxal endite bilobed with 8–9+3 and 2+1 papposerrate setae; basal endite bilobed with 4+1 papposerrate setae in each lobe; endopod unsegmented, trilobed, bearing 3+2+3 papposerrate setae; scaphognathite with 5 marginal plumose setae.

First maxilliped (Fig. 2, Mp1): coxa with 3+1+2 setae, very small epipod present; basis with 6+3+4 setae; endopod 4-segmented, with 3, 1, 2, 1+3 papposerrate setae; exopod unsegmented, with 1 or 2 subterminal setae on lateral margin and 3 long terminal plumose setae. Number of setae in right and left appendages differed in half of specimens.

Second maxilliped (Fig. 2, Mp2): coxa with 1 papposerrate setae; basis with 2+3+3 papposerrate setae; endopod 4-segmented with 3, 1, 2, 5+1 papposerrate setae; exopod 2-segmented, with 2 subterminal and 3 terminal long plumose setae.

Third maxilliped (Fig. 2, Mp3): coxa unarmed; basis with 1+1+2 papposerrate setae; endopod 5-segmented with 2, 0, 1, 2, 1, 4+1 papposerrate setae; exopod unsegmented, with 2 subterminal and 3 terminal plumose setae.

Pereopods (Fig. 2, P1–P5): unsegmented, unarmed; pereopods 1–2 biramous, pereopods 3–5 uniramous.

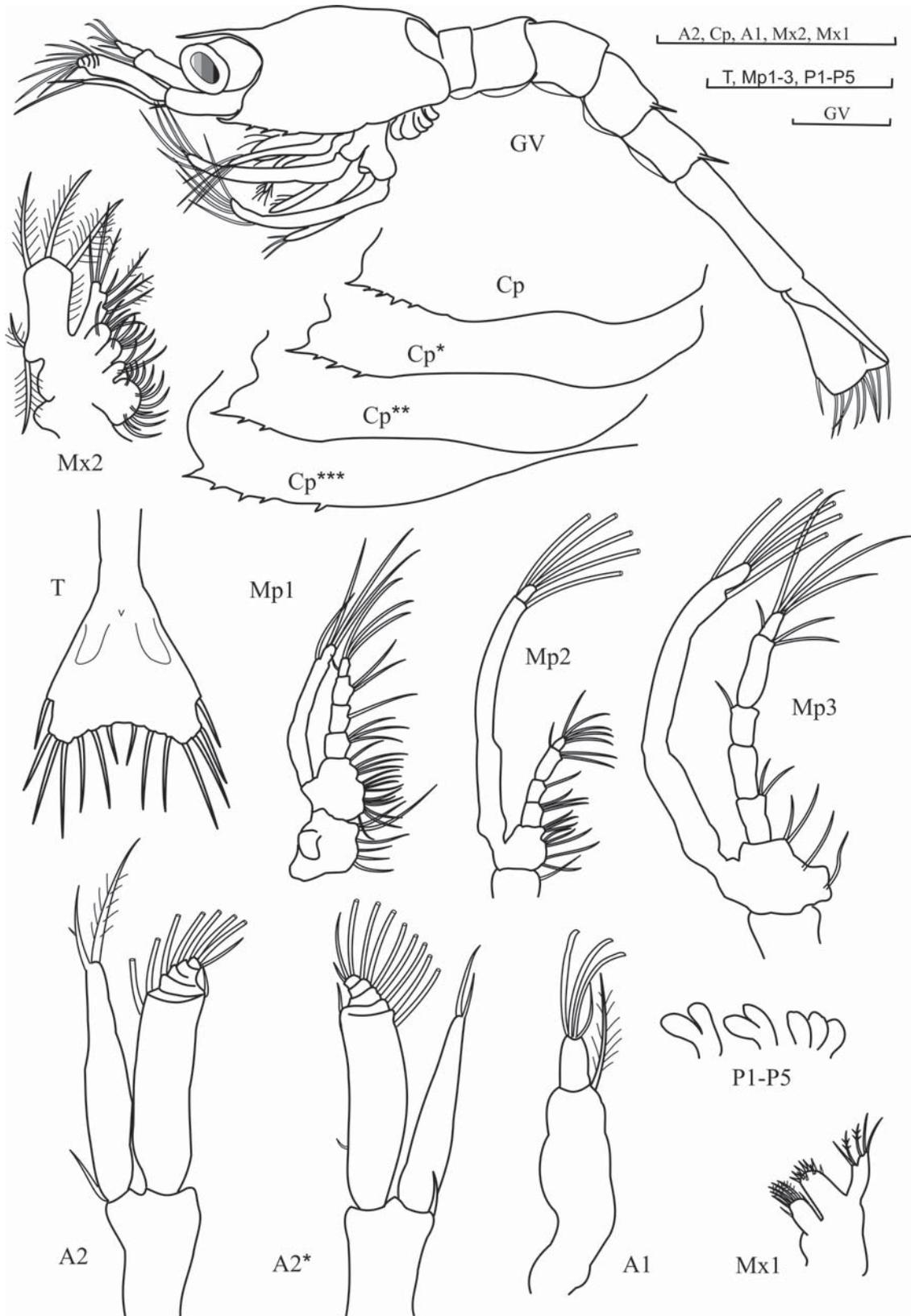


Fig. 2. Zoea I *Spirontocaris murdochi* Rathbun, 1902. Scale 0.5 mm.

Рис. 2. Зоэа I *Spirontocaris murdochi* Rathbun, 1902. Масштаб 0,5 мм.

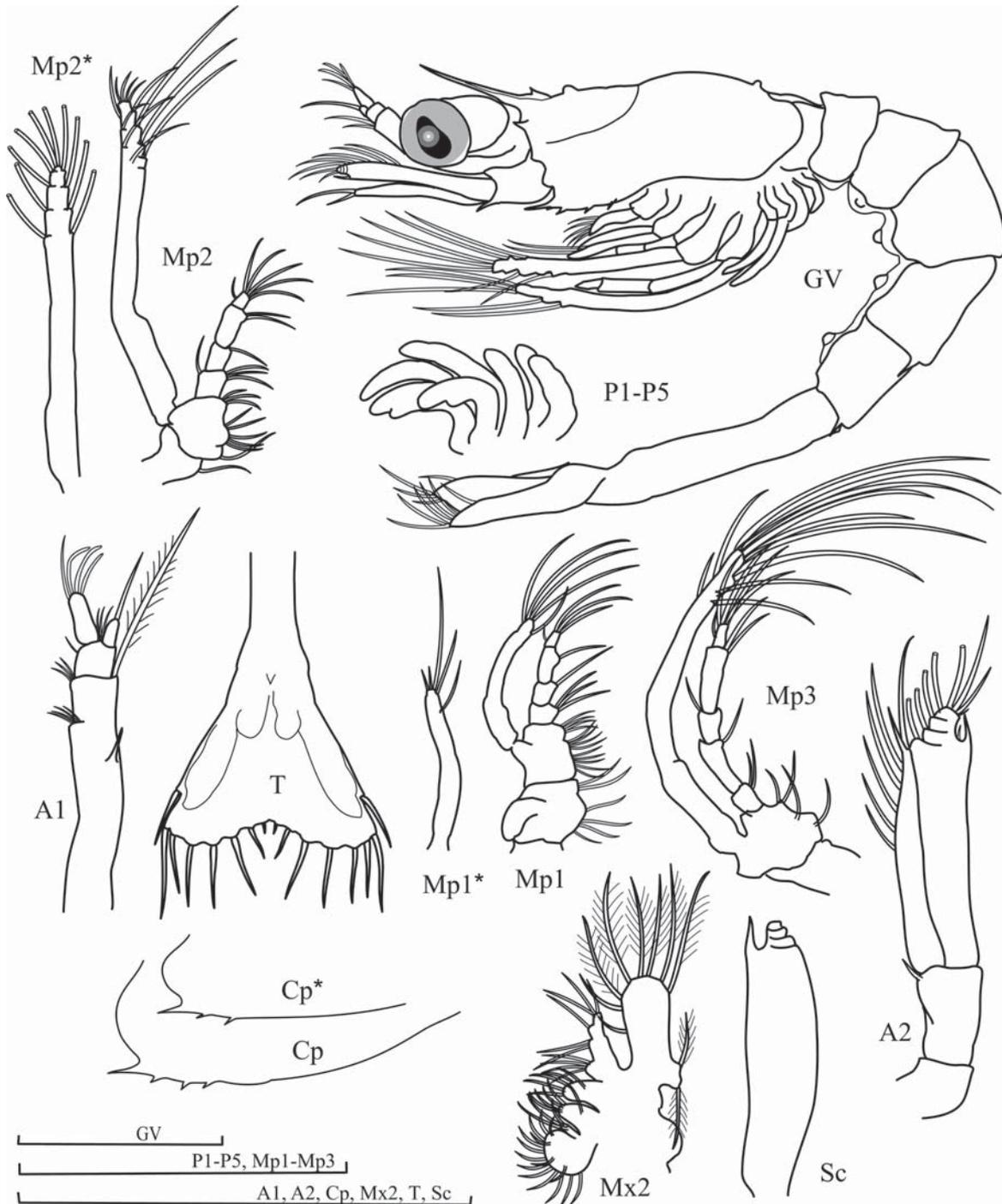


Fig. 3. Zoea II *Spirontocaris murdochi* Rathbun, 1902. Scale 1.0 mm.

Рис. 3. Зоэа II *Spirontocaris murdochi* Rathbun, 1902. Масштаб 1,0 мм.

Pleon (Fig. 2, GV): five pleomeres; fourth and fifth pleomeres with a pair of dorsolateral spines, anal spine small.

Pleopods: absent.

Uropods: absent.

Telson (Fig. 2, T): triangular, indented medially, with 7+7 setae (inner 5 plumose and the outer 2 plumose only on

proximal axis). In terminal margin a deep and wide semicircular notch.

ZOEA II

Material examined: larvae were caught in 6 stations from April 19 to May 16, 2017 in the Gulf of Avacha (southeastern Kamchatka) over bottom depth of 49 to 655 m.

Dimensions: TL 5.71 ± 0.18 (5.0–6.7) mm, CL 1.36 ± 0.02 (1.2–1.4) mm, RL 0.6 ± 0.05 (0.5–0.7) mm.

Carapace (Fig. 3, GV, Cp, Cp*): eyes stalked, with ocular peduncle shorter than antennal peduncle; rostrum slightly raised up, usually not much short than front margin of eye; supraorbital spines small; pterygostomian spine long, thin; in anteroventral margin 2–4 small spines (in most specimens the number of spines varies in the left and right).

Antennule (Fig. 3, A1): peduncle 2-segmented, with large spine ventrally and 4 small plumose setae in the outer margin positioned at about two third the length of the first segment and with 1 long plumose seta terminally, distal segment with 4 short plumose setae terminally; outer flagellum with 3–4 aesthetascs and 1 spinous process terminally; small inner flagellum unsegmented, with 1 long plumose seta.

Antenna (Fig. 3, A2, Sc): peduncle 2-segmented; scaphocerite 4–5-segmented, 3–4 short segments distally, with 11–13 plumose setae on inner margin and 2 small simple setae on apex; spine in scaphocerite not long (usually reaches front margin of scale); endopod with 1 terminal spine and 1 long terminal plumose seta (in some specimens shorter than scaphocerite, in the rest it is approximately equal in length).

Maxillule: coxal endite with 8–9 papposerrate setae, basal endite with 11 cuspidate setae in both limbs; endopod unchanged.

Maxilla (Fig. 3, Mx2): scaphognathite with 9–10 marginal plumose setae; coxal endite, basal endite and endopod unchanged.

First maxilliped (Fig. 3, Mp1): coxa, epipod and basis unchanged; exopod unsegmented, with 1 or 2 setae subterminal and 3 long terminal plumose setae. Number of setae in many specimens differed in right and left appendages.

Second maxilliped (Fig. 3, Mp2): coxa and basis unchanged; endopod 4-segmented with 3+1, 1, 2, 5+1 papposerrate setae; exopod 2-segmented, with 11–12 long plumose setae.

Third maxilliped (Fig. 3, Mp3): coxa, basis and endopod unchanged; exopod unsegmented, with 12 plumose setae. In many specimens 2–4 apical setae in exopod were thin and short (Fig. 3, Mp1*, Mp2*).

First and second pereopods (Fig. 3, P1–P2): long, biramous, unsegmented; without swimming setae; there are rudiments of chela.

Third to fifth pereopods (Fig. 3, P3–P5): long, uniramous, unsegmented.

Pleon (Fig. 3, GV): 6 pleomeres; fourth and fifth pleomeres with a pair of dorsolateral spines, anal spine small.

First pleopods: absent.

Second to fifth pleopods: small buds.

Uropods: absent.

Telson (Fig. 3, T): triangular; not separated from sixth pleomere; 8+8 plumose setae, outer plumose seta in proximal axis only. The telson shape is shown in the figure.

ZOEA III

Material examined: larvae were caught in three stations in the Gulf of Avacha (southeastern Kamchatka) from April 19 to May 16, 2017 over bottom depth of 49 to 2000 m, as well as at 6 stations in the western Kamchatka shelf from June 13 to 24, 2015 over bottom depths of 23–123 m, and in the Bering Sea in August 2010 over bottom depth of 64 m.

Dimensions: TL 6.47 ± 0.1 (5.3–7.4) mm, CL 1.46 ± 0.04 (1.2–1.7) mm, RL 0.58 ± 0.02 (0.4–0.7) mm.

Carapace (Fig. 4, GV Cp, Cp*): rostrum thin, slightly raised up; usually not longer than the front margin of eye;

pterygostomian spine long; anteroventral margin by 1–2 small spines at least in one side; supraorbital spines large and thin.

Antennule (Fig. 4, A1, A1*): peduncle unchanged; inner flagellum unsegmented, with 1 long plumose seta; in half of larvae outer flagellum unsegmented, with 4–5 terminal and 2 subterminal aesthetascs, in the rest two-segment ones.

Antenna (Fig. 4, A2, A2*): peduncle unchanged; endopodite in most larvae is two-segmented, in some it is unsegmented, nearly equal scaphocerite, with 1 short spine and 1 small reduced seta terminally; scaphocerite 3–4-segmented, 2–3 short segments distally, with 19–20 plumose setae in inner margin; spine on scaphocerite extends beyond edge of plate by at least 1/3 of its length of spine.

Maxillule: coxal endite with 9–10 papposerrate setae, basal endite in 1/3 larvae with 12 cuspidate setae in both appendages, in 2/3 of larvae basal endite with 12 setae in one appendage, and with 13 ones in other; endopod unchanged.

Maxilla (Fig. 4, Mx2, Sg): coxal endite bilobed with 9–10+5 and 2+1 papposerrate setae; basal endite bilobed with 5+1 papposerrate setae in each lobe; endopod unchanged; scaphognathite with 12–16 marginal plumose setae.

First to third maxilliped (Fig. 4, Mp1–3): the first pair of maxillipeds with larger epipod, the rest unchanged; endopod, coxa and basis of second and third pairs unchanged; exopod of second and third pairs of maxillipeds bear 10–12 and 12–13 setae respectively; distal segments separated.

First to second pereopods (Fig. 4, P1–P2): biramous, with protopod; exopod without setae, endopod with 2–3 small setae.

Third to fifth pereopods (Fig. 4, P3–P5): uniramous, unsegmented.

Pleon unchanged.

First pleopod (Fig. 4, pl1): absent in 2/3 studied larvae; rest in form of very small tubercle or absent.

Second pleopod (Fig. 4, pl2, pl2*): small buds in 2/3 studied larvae; rest in form of round bilobed tubercles.

Third to fifth pleopods (Fig. 4, pl3–5, pl3*): bilobed buds in 2/3 studied larvae; rest have long bifurcated tubercles. Uropods (Fig. 4 T, T*, T**): biramous; endopod small with 1–2 short plumose setae apically; exopod well developed, reach terminal margin of telson, with 10–12 marginal plumose setae and very small spine in outer margin. One specimen had 3 apical setae in e left endopod, and 2 apical setae in the right.

Telson (Fig. 4, T, T*, T**): separated from sixth pleomere, with a pair of lateral short simple setae followed by 7+7 plumose setae; a wide deep notch in terminal margin.

ZOEA IV

Material examined: larvae were caught it two stations over the Western Kamchatka shelf from June 13 to July 7, 2015 above bottom depth of 69–80 m; two specimens from the Olutoro-Navarinsky region were also studied, which were caught in late August over bottom depth of 27 m and off the coast of southeastern Kamchatka on April 26, 2017 over bottom depth of 86 m.

Dimensions: TL 7.43 ± 0.13 (6.8–7.8) mm, CL 1.74 ± 0.02 (1.5–1.8) mm, RL 0.77 ± 0.04 (0.6–0.9) mm.

Carapace (Fig. 5, GV): unchanged.

Antennule (Fig. 5, A1): peduncle 3-segmented, first segment with 5–6 small plumose setae distally; second segment with 6 small and 1 long plumose setae distally; third segment with 3 long plumose setae distally; inner flagellum 3-

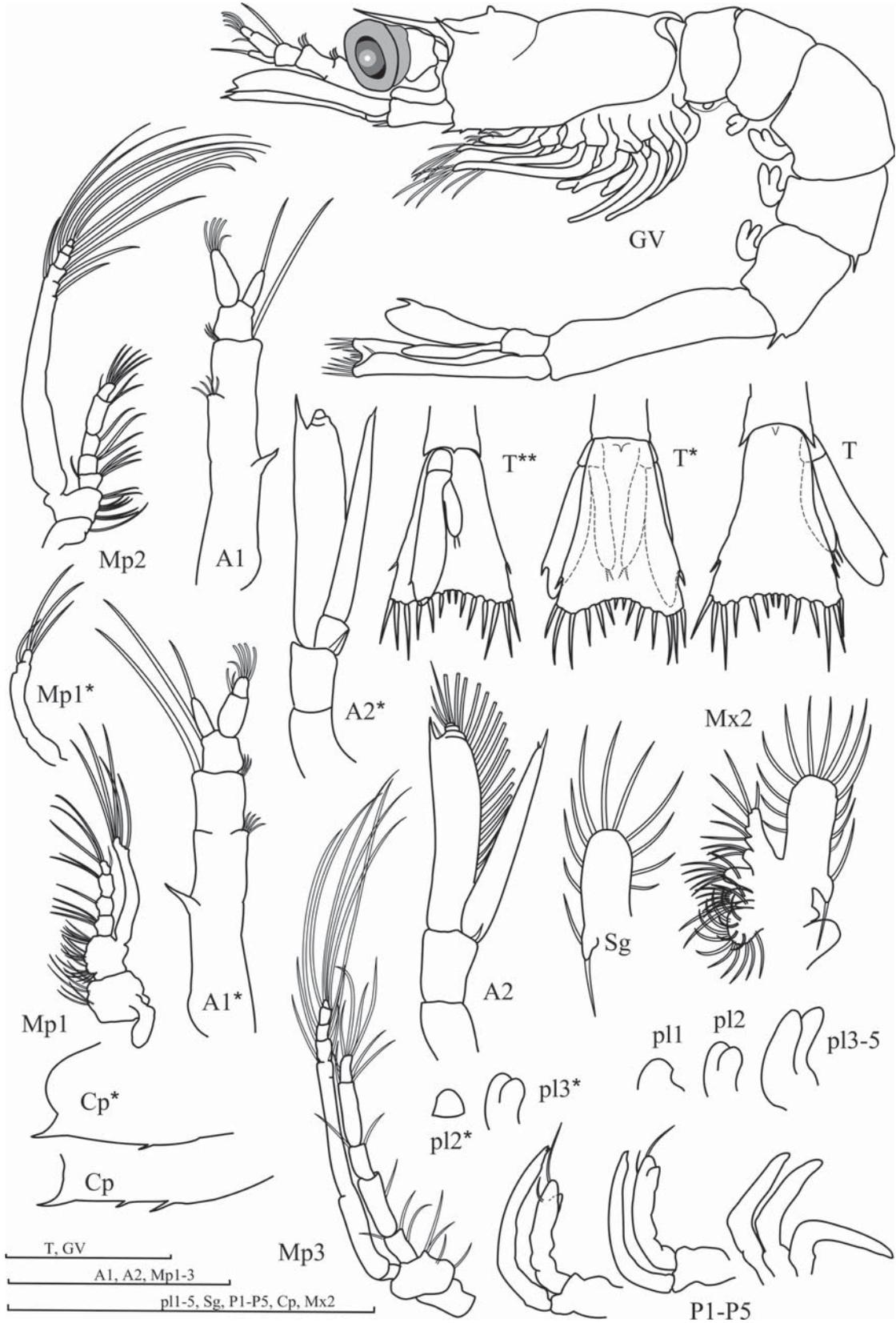


Fig. 4. Zoea III *Spirontocaris murdochi* Rathbun, 1902. Scale 1.0 mm.

Рис. 4. Зоэа III *Spirontocaris murdochi* Rathbun, 1902. Масштаб 1,0 мм.

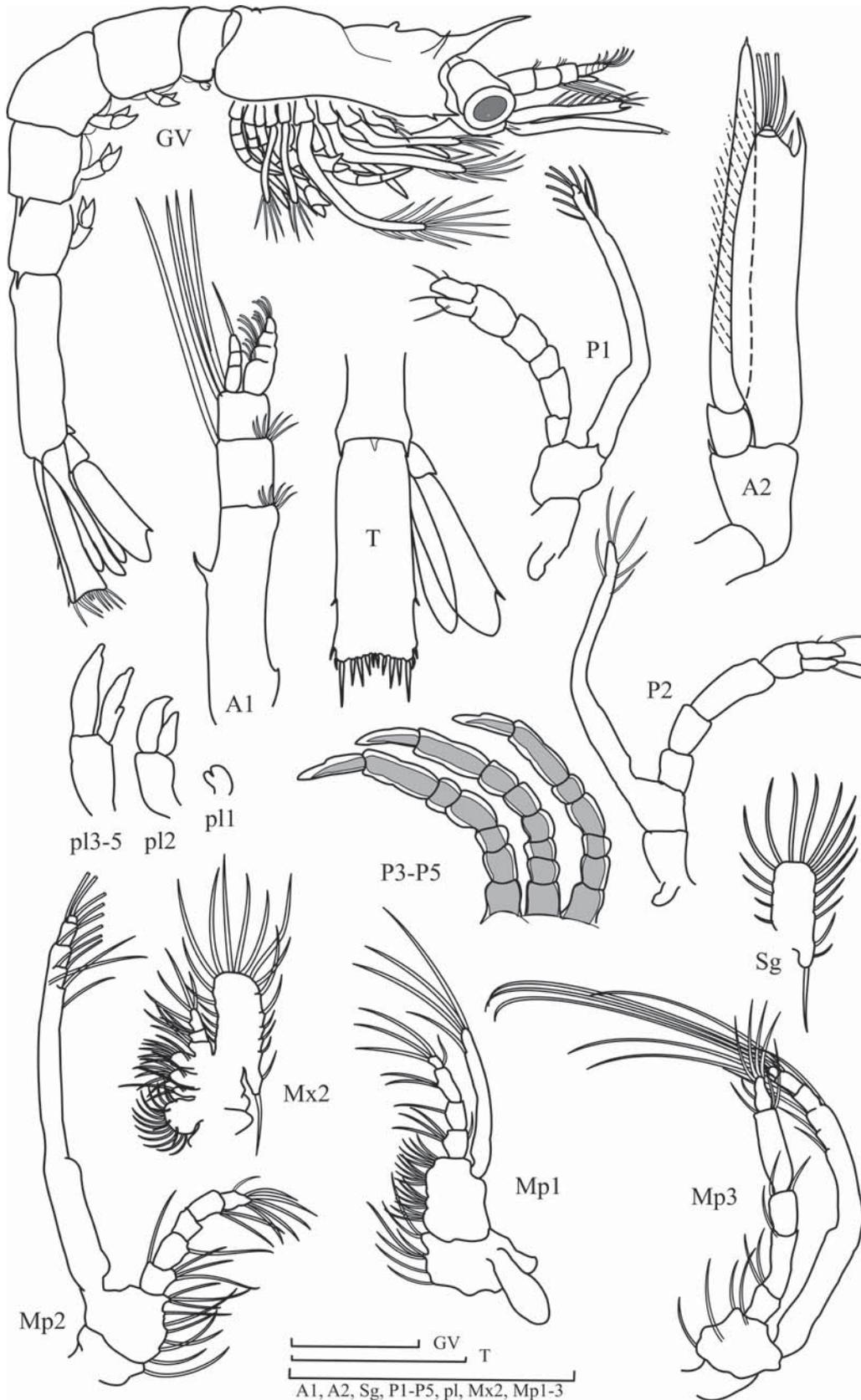


Fig. 5. Zoea IV *Spirontocaris murdochi* Rathbun, 1902. Scale 1.0 mm.

Рис. 5. Зоэа IV *Spirontocaris murdochi* Rathbun, 1902. Масштаб 1,0 мм.

segmented, distal segment with 1 long plumose seta; outer flagellum 4-segmented with 3+3+3+(2–3) aesthetascs.

Antenna (Fig. 5, A2): endopod longer than scaphocerite; spine at the end of the endopod small; the protopod of the endopod separated; scaphocerite 2–3-segmented, with 20–30 plumose setae along inner and posterior margin; spine on scaphocerite extends beyond anterior margin of scale (in some specimens in half of its length of spine).

Maxillule: coxal endite unchanged, basal endite with 13–14 cuspidate setae (most of studied larvae bear 13 spines in one maxillule, and 14 in the other), endopod unchanged.

Maxilla (Fig. 5, Mx2, Sg): coxal endite, basal endite and endopod unchanged; scaphognathite with 16–20 marginal plumose setae.

First–third maxilliped (Fig. 5, Mp1–3): coxa, basis and endopod unchanged; exopods of the first–third pairs of maxillipeds bear 5–14–16 setae respectively; in base of all maxillipeds there are underdeveloped gills.

First to second pereopods (Fig. 5, P1–P2): biramous, with 2-segmented protopod; exopod of the first pair with 8–10 long plumose setae, chela forming, with 6–8 plumose setae available. Chela in the first pair of pereopods is not much larger in size than in P2. In base there are underdeveloped gills.

Third to fifth pereopods (Fig. 5, P3–P5): uniramous, 7-segmented, with elongated distal segments. In base there are underdeveloped gills. Next stage is visible through cuticle in six larvae. It is clear that in stage V these segments will be pointed and long.

Pleon unchanged.

First pleopods (Fig. 5, pl1): rounded buds bilobed in the apex.

Second to fifth pleopods (Fig. 5, pl2–5): biramous, protopod naked, endopod of the fourth and fifth pleopods can be with rudiment of appendix interna.

Uropods (Fig. 5, T): biramous; endopod slightly shorter than exopod; exopod reach posterior margin of telson, with 12–15 plumose setae and very small spine in outer margin.

Telson (Fig. 5, T): expands slightly towards the end, with 2 pair of lateral spines and 6 pairs of terminal posterior processes, with notch in terminal margin.

ZOEA V

Material examined: 4 specimens from the western part of the Bering Sea, caught over bottom depth of 27 m.

Dimensions: TL 8.64±0.08 (8.6–8.7) mm; CL 1.9±0.11 (1.8–2.0) mm; RL 0.78±0.07 (0.7–0.8) mm.

Carapace unchanged.

Antennule (Fig. 6, A1): peduncle unchanged; inner flagellum 4-segmented, distal segment of inner flagellum much longer than others; outer flagellum 5-segmented.

Antenna (Fig. 6, A2): peduncle 2-segmented, scaphocerite 3–4-segmented, spine on scaphocerite long; endopod longer than scaphocerite.

Maxillule: coxal endite with 9–11 papposerrate setae, basal endite with 15 cuspidate setae, endopod unchanged.

Maxilla (Fig. 6, Mx2): coxal endite bilobed with 11+5 and 2+1 papposerrate setae; basal endite bilobed with 6+1 papposerrate setae in each lobe; endopod unchanged; scaphognathite with 18–24 marginal plumose setae.

First maxilliped (Fig. 6, Mp1): with large epipod, coxa and basis unchanged; exopod 2-segmented, with 1 or 2 setae subterminally on lateral margin and 3 long terminal plumose setae.

Second and third maxilliped (Fig. 6, Mp2–3) unchanged. At the base there are gills.

Pereopods (Fig. 6, P1–3): exopod of the first pair with 12–14 long plumose setae; the second pair with 10–11 plumose setae available; third to fifth pair uniramous, distal segments long, pointed. At the base there are gills.

Pleon unchanged.

First pleopods (Fig. 6, pl1): long bilobed buds.

Second to fifth pleopods (Fig. 6, pl2–5): biramous, protopod naked, without spines; endopod with small *appendix interna* (*a.i.*).

Telson (Fig. 6, T): long margins expand slightly towards the end, with 2 pair of lateral spines and 6 pairs of terminal posterior processes and wide semicircular notch in terminal margin. Next stage of zoea is visible through cuticle.

ZOEA VI

Material examined: 3 larvae of this stage were caught in Olyutoro-Navarinsky region on September 10–13, 2010 over bottom depth of 51–52 m.

Dimensions: TL 9.47±0.42 (8.9–10.5) mm. CL 2.07±0.08 (1.9–2.2) mm. RL 1.1–1.15 mm.

Carapace (Fig. 7, GV): rostrum slightly longer than the front margin of eye; supraorbital spines large; pterygostomi-an spine present; anteroventral margin without spines.

Antennule (Fig. 7, A1): peduncle unchanged; inner flagellum 5-segmented, with long distal segment; outer flagellum 6-segmented.

Antenna (Fig. 7, A2, Sc): peduncle unchanged; endopod 20–30-segmented, 1.5–2 time longer than scaphocerite; base with 2–3 short terminal setae. End of scaphocerite in left leg is not segmented, in the right one with separated 1–2 short segments; spine on scaphocerite reach anterior margin of scale. Scaphocerite bearing about 30 setae.

Maxillule: coxal endite with 11 papposerrate setae; basal endite with 16 cuspidate setae in one appendage and 17 in the other; endopod unchanged.

Maxilla (Fig. 7, Mx2): coxal endite unchanged; basal endite bilobed with 7+1 papposerrate setae in each lobe; endopod unchanged; scaphognathite with 25–28 marginal plumose setae.

Maxillipeds (Fig. 7, Mp1–3): $\dot{\text{I}}\dot{\text{d}}1$ with large bilobed epipod and 5 terminal plumose setae in exopod; $\dot{\text{I}}\dot{\text{d}}2$ with small epipod and 10–11 plumose setae in exopod; $\dot{\text{I}}\dot{\text{d}}3$ unchanged.

Pereopods (Fig. 7, P1–P3): exopod of the first pair with 3 distal separated segments and 10–11 long plumose setae, chela in the first pair is much larger than in the second one; the second pair with 9–10 plumose setae; third to fifth pair uniramous; distal segments thin and long, pointed. At the base of pereopods and maxillipeds there are gills.

Pleon unchanged.

Pleopods (Fig. 7, pl1–5): protopod naked; first pleopod small, biramous; second to fifth pleopods bearing endopods with *a.i.* and 5–6 small spines, and exopods also with 8–10 small spines terminally.

Telson (Fig. 7, T): margins laterally parallel, with 2 pair of lateral spines and 6 pairs of terminal posterior processes; terminal margin of telson with small wide notch. The next stage is visible through the cuticle — decapodite with prominent terminal margin, a pair of central setae, 3 pairs of angular setae, and 3 pairs of lateral spines.

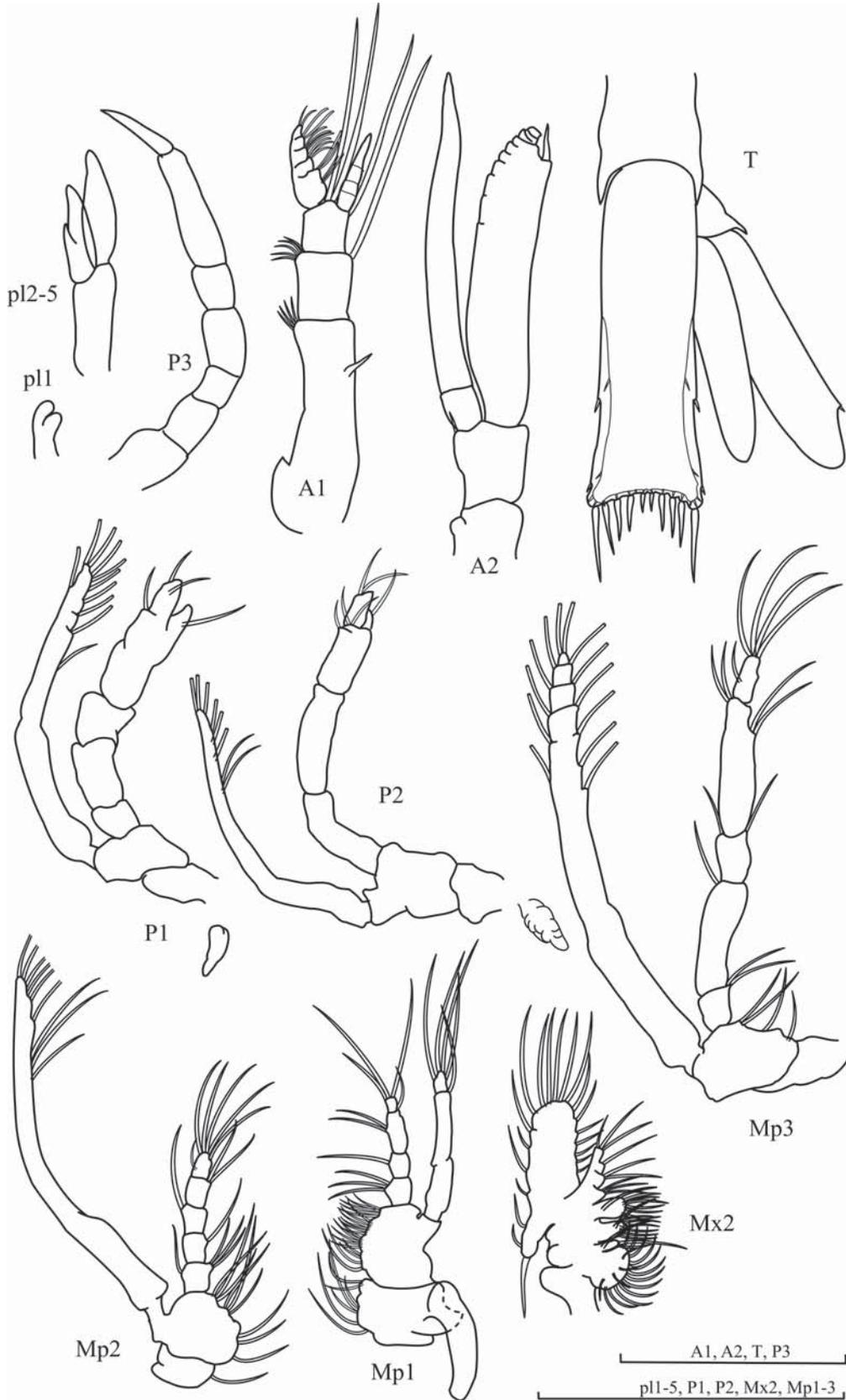


Fig. 6. Zoea V *Spirontocaris murdochi* Rathbun, 1902. Scale 1.0 mm.
 Рис. 6. Зоэа V *Spirontocaris murdochi* Rathbun, 1902. Масштаб 1,0 мм.

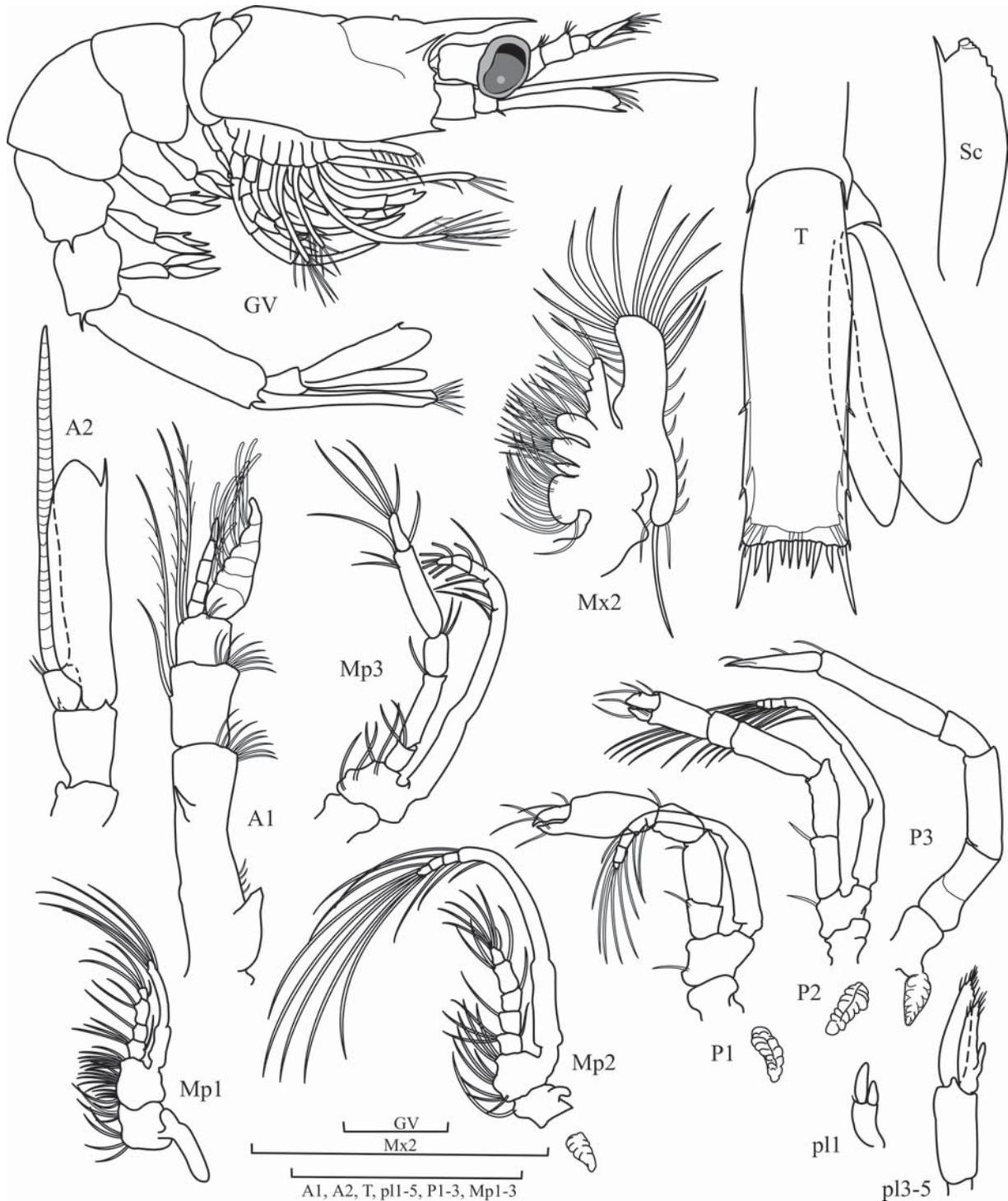


Fig. 7. Zoea VI *Spirontocaris murdochi* Rathbun. Scale 1.0 mm.

Рис. 7. Зоэа VI *Spirontocaris murdochi* Rathbun, 1902. Масштаб 1,0 мм.

Discussion

Morphological characters of the larvae of the family Thoridae have been described in sufficient detail [Lebour, 1921; Gurney, 1942; Pike, Williamson, 1961;

Makarov, 1967; Haynes, 1985]. Main morphological features that distinguish zoeal stages of *Spirontocaris* from other genera of this family are presence additional seta in end of antennal flagellum in early larvae, presence of exopods in first two pairs of pereopods in

all stages of zoea, dorsolateral spines in 4th–5th or only in 5th pleonal somites, presence of five pairs of pereopods in first stage. Additional distinguishing features that have been identified as a result of our research are as follows:

- presence of spine in scaphocerite already in zoea II;
- obligatory presence of supraorbital spines, appearing from zoea I or zoea;
- presence of pterygostomial spine in all larval stages;
- segmentation of scaphocerite;
- asymmetry in armament of appendages.

Distal segments of the third–fifth pereopods in zoea IV–VI described in this work are thin, elongated, and pointed (Fig. 7, P3). By this feature this species can be easily distinguished from others congeneric species. Distal segments of pereopods of adults of *S. murdochi* were of the same shape [Hayashi, 1977].

During entire period of development from first to last zoeal stage, larvae of *S. murdochi* grows by 110% (TL) and 14.07% (CL). Body length of individual larvae of corresponding stages differs insignificantly. The coefficient of variation of TL does not exceed 9.3%, and on average is 5.8%. There were no significant differences in size of larvae of this species in different years. Average increase of TL for one stage is over 16.1%, average increase of CL is 27.7%. Increment in one stage is from 5 to 34% of total length. Over entire period from zoea I to decapodid larvae increase by 66.7–109.8%. Comparative length of rostrum of caridean shrimps of many species in zoeal stages can vary [Sedova, Grigoriev, 2014, 2017; Sedova, 2019]. This is typical for larvae of *S. murdochi*. In different larvae of the same species and stage, ratio of carapace length to rostrum length somewhat may vary. Ratio CL/RL of *S. murdochi* varied in zoea I from 1.2 to 1.9, in zoea II from 2.0 to 2.3, in zoea III from 1.9 to 2.9.

Many researchers use number of spines in anteroventral margin of carapace to separate early larvae of family Thoridae, especially for genus *Eualus* Thallwitz, 1892 [Ivanov, 1971; Haynes, 1985; Terossi *et al.*, 2010]. Anteroventral margin of carapace of zoea I of *S. murdochi* usually bear 3–4 spines. 1/3 of larvae bear only 2 spines in one side of carapace. Anteroventral margin of carapace of the same species in zoea II bearing 2–4 spines in norm, in zoea III bearing 1–2 spines, in zoea IV — 1 spine only in one side. Position of these spines in anteroventral margin may also some differ. In late zoeae number of spines gradually decreases to complete disappearance by the end of planktonic period.

Previously we observed variability in number of anteroventral spines for some species of family Crangonidae. For example, larvae of *Crangon dalli* Rathbun, 1902 normally bear 2 spines in anteroventral margin of carapace, but in some larvae we found additional spine behind pterygostomial spine [Sedova, Grigoriev, 2014]. Thus, this feature cannot be considered

reliable for species identification. It is better to use it as additional one.

There is variability in segmentation of antennule outer flagellum in zoea II and zoea III. Some individual variability was also observed for antennae. Number of separated segments at tip of scaphocerite may vary. For example, in first stage, there may be four or five detached segments in the end of appendage, in the third stage — two segments may be detached in one appendage and one in the other. Segmentation of scaphocerite in larvae of *S. murdochi*, in contrast to other species, last until stage V–VI. Length of spine in scaphocerite in left and right antennae is usually slightly different. This asymmetry is characteristic for larvae of genera *Pandalus* Leach, 1814 and *Argis* Krøyer, 1842 [Sedova, Grigoriev, 2017, 2018]. Length of flagellum in antenna and length of apical setae in flagellum may somewhat vary in various larvae.

Some asymmetry in number of setae in scaphognathite of *S. murdochi* was observed in late larvae. In early larvae number of setae in right and left maxilla was always the same. This pattern is typical for most caridean shrimps. In most of studied specimens of *S. murdochi* in zoea II–V number of spines and setae in basal endite of right and left maxillule differs by one. As a rule, larger larvae have more setae in this structure.

Exopods of first pair of maxillipeds in approximately 1/3 of studied larvae in stage I were armed with 4 setae in one limb and 5 setae in the other. Very often in early larvae, and sometimes in late larvae, from 1 to 4 terminal setae were shortened and thinner. In several larvae of *S. murdochi* exopods were absent in one or two maxillipeds, which is a clear deformity. Individual variability of pereopods is expressed in number of swimming setae in exopods and in relative fatness of chelae.

Structure of pleopod is often used to determine developmental stage of larvae of caridean shrimps [Haynes, 1985]. However, this structure may vary in various specimens. Most significant individual differences in larvae of *S. murdochi* in degree of pleopod development were revealed for zoea III. Differences are expressed in length and size of pleopods, as well as in presence of apical spines and underdeveloped of *appendix interna*. Depth of terminal notch in telson is also variable feature, especially in zoea II–III. Relative length of uropods can also vary, especially in zoea III.

Asymmetry of some body structures of larvae of caridean shrimp is known for many species. For example, in larvae of genus *Pandalus* number of swimming setae in right and left maxillipeds, and pereopods often differ [Sedova, Grigoriev, 2017]. In representatives of family Crangonidae number of sensory setae and length of spine in scaphocerite can be different in paired appendages [Sedova, Grigoriev, 2015, 2018]. For larvae of *Spirontocaris* asymmetry of structure of carapace and some appendages (especially arms of maxillules, maxillae, pereopods, maxillipeds, structure of anten-

nae) is the norm. Larvae of this genus with the same number and length of setae and spines in right and left appendages are less common.

Above shelf of Western Kamchatka larvae of *S. murdochi* were caught only in southern area. In June–July 2015 larvae were found above bottom depths from 15 to 123 m. In June 2016 larvae in zoeal stage I were caught only in three stations above bottom depths of 50–70 m. Near southeastern coast of Kamchatka in March–May 2017 larvae of this species were more abundant. They were caught from southern part of Gulf of Avacha to northern part of Kronotsky Gulf over bottom depths from 49 to 787 m. Maximum density was 40 larvae/m². In Bering Sea in July–August 2010 zoeae of this species were caught in Olyutoro-Navarin-sky region above bottom depths of 27–94 m. In Gulf of Anadyr only 3 larvae of zoea VI were caught in northern part in August 17, 2010 in 2 stations over bottom depth 20 and 38 m.

Main patterns of development of larvae of genus *Spirontocaris* generally coincide with the data obtained for other caridean shrimps. Unlike many other shrimps, early zoea of genus *Spirontocaris* develop mainly over inner shelf. This is obviously caused by biology of adult forms, among which only *S. arcuata* and *S. spinus* are found beyond 250 m of bottom depth [Slizkin, 2006].

Larvae of *S. murdochi* were relatively abundant compared to larvae of other species of *Spirontocaris*. Most of larvae of this genus were caught above bottom depths of 30–70 m. The first three stages of *S. murdochi* were found in deep-water stations. Zoeal stages of *S. murdochi* were caught over wider range of bottom depths than larvae of other species of the genus. Earliest zoeae of *S. murdochi* appear very early off southeastern coast of Kamchatka, presumably in March, since larvae in stage III were already caught in mid-April. According to Sokolov [2001], *S. murdochi* is relatively cold-water species, therefore release of larvae occurs early. Along western coast of Kamchatka first larvae of this species appeared in April, since ice cover in inner shelf lasts longer here, than near eastern coast of Kamchatka, where influence of Pacific waters affects.

Conclusions

As a result of this study, we were able to make descriptions of missing zoea IV–VI for *S. murdochi*. Larvae of *S. murdochi* in zoea I were found to be closest in morphology and size to zoeal stages of *S. arcuata*. Separating larvae of these species in samples is the most difficult. Zoea of *S. murdochi* differ from zoea of *S. arcuata* in some larger size, fewer small spines in anteroventral margin, telson shape, longer rostrum, and long thin dorsolateral spines in 4 and 5 somites [Haynes, 1981, 1984].

Larvae of *S. murdochi* hatch from smaller eggs and with less developed pereopods than larvae of *S. spinus* and *S. phippisii*, therefore their development includes

more larval stages. Through cuticle of telson in zoea VI of *S. murdochi* next stage with characteristic features of decapodite is clearly visible, therefore, it can be argued that this species develops through six zoeal stages.

For larvae of *S. murdochi* significant individual variability was found in number of spines in anteroventral margin of carapace, level of development of pleopods, length of endopod of uropods, and depth of terminal notch, especially in zoea III. We assume that late larvae have no less variability. Armament of maxillules in all stages, maxillae in early larvae, relative length of rostrum, and morphology of pereopods can be considered the least variable and more reliable features for species identification of larvae. Asymmetry was revealed in morphology of carapace, antennule and antennae, armament of maxillules, maxillae, maxillipeds and pereopods, significant differences in size of zoeal stages in different years were not revealed.

In Avacha Bay duration of development of early hatching larvae is maximum (about 3 months). In the region of along Western Kamchatka and in the western part of Bering Sea early hatching larvae develop in 2.5 months, because hatch in higher water temperatures.

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