

Morphological features of larvae of the genus *Argis* (Decapoda, Crangonidae) from coastal Kamchatka and adjacent waters

Морфология личинок креветок рода *Argis* (Decapoda, Crangonidae) из прикамчатских вод

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Larvae of five species of the family Crangonidae (*Argis crassa*, *A. dentata*, *A. lar*, *A. ochotensis* and *A. ovifer*) from plankton of east part of Okhotsk Sea and from Avacha Gulf are described. Morphological features of the larvae are compared for purpose of their identification in planktonic samples. The main morphological features of larvae at corresponding stages are revealed. Larvae of these species are similar in most features. Distinctions concern only several details of their structure. Figures of early and late stages of zoea are presented. It is shown that larvae of the genus *Argis* can have two or three zoeal stages. Generalized morphological characteristic for the larvae of shrimps from the genus *Argis* is given.

Описаны личинки пяти видов семейства Crangonidae (*Argis crassa*, *A. dentata*, *A. lar*, *A. ochotensis* и *A. ovifer*) из планктона восточной части Охотского моря и Авачинского залива. Сравниваются морфологические признаки личинок с целью их разделения в планктонных пробах. Выявлены основные морфологические различия личинок соответствующих стадий. По большинству признаков личинки этих видов сходны. Различия касаются лишь отдельных деталей строения. Приведены рисунки младших и старших зоеа. Показано, что личинки из рода *Argis* имеют две или три стадии зоеа. Дана обобщенная морфологическая характеристика для личинок креветок из рода *Argis*.

Key words: shrimps, larval morphology, shortened development, zoeal stages, decapodid, Crustacea, Decapoda, Crangonidae, *Argis*

Ключевые слова: креветки, морфология личинок, укороченное развитие, стадии зоеа, декаподит, Crustacea, Decapoda, Crangonidae, *Argis*

INTRODUCTION

Currently, genus *Argis* Krøyer, 1842 includes ten species (De Grave et al., 2009). Many of them are commercially important (Marin, 2013). Five species of this genus occur in marine waters near Kamchatka Peninsula: *Argis crassa* (Rathbun, 1999), *A. dentata* (Rathbun, 1902), *A. lar* (Owen, 1839),

A. ovifer (Rathbun, 1902) and *A. ochotensis* Komai, 1997 (Slizkin, 2006).

In northern part of Russian Far East marine waters, eastern and northern parts of Okhotsk Sea and deep-sea waters of Bering Sea have been most actively studied. Concerning decapods, the main attention was paid to Kamchatka crab and shrimps from the family Pandalidae. Biology and distribution of other commercial decapods from this area are less studied. Species without com-

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mercial value remained practically unexplored. Biology of shrimps from the genus *Argis* is studied insufficiently. Only fractional information on bottom depths of dwelling and heating environments in Okhotsk and Japan seas exist about species *A. ochotensis* and *A. ovifer*, and some more data exist about *A. dentata* and *A. lar* (Komai, 1997; Sokolov, 2001; Slizkin, 2006).

Larvae of shrimps from the genus *Argis* occur in plankton rarely and during short time due to shortened development of this group. Larvae were described only for three species from mentioned above. Zoea I of *A. crassa* and *A. dentata* were described in detail (Ivanov, 1968). There is also a description of two zoeal stages and one decapodid stage of larvae from Atlantic waters considered as *A. dentata* (Squires, 1965). Besides, Makarov (1966, 1967) gave poor description of larvae *A. lar* from plankton samples collected in eastern part of Okhotsk Sea.

During processing of planktonic samples from Avacha Gulf and eastern part of Okhotsk Sea we found a number of larvae, which obviously belonged to the genus *Argis*. All of them had features of larvae with shortened development. Some larvae were identified according to available descriptions of corresponding stages by Makarov (1966) and Ivanov (1968). More developed larvae correspond to description of larvae from waters of western Kamchatka, identified as *A. lar* by Makarov (1966). Description of morphology of separate zoeal stages that we found is presented below.

MATERIAL AND METHODS

Samples collection

Plankton samples were collected during research surveys, performed in eastern part

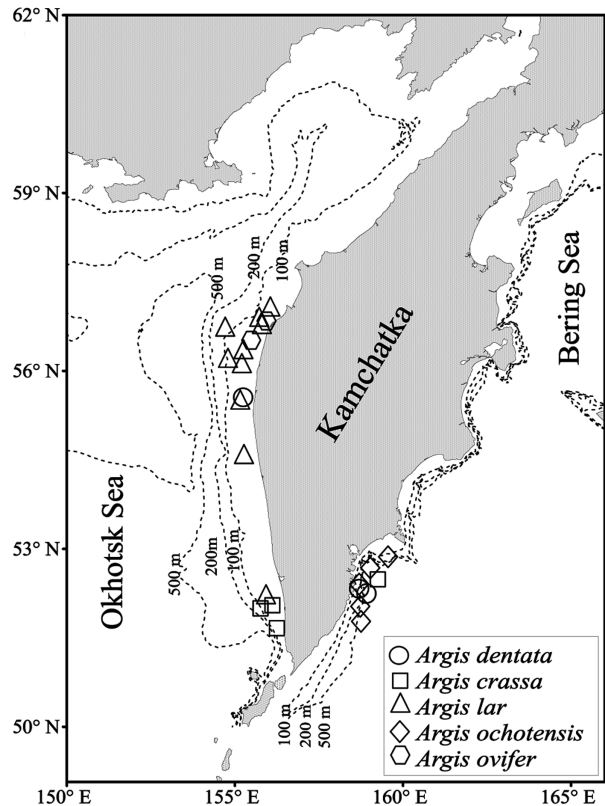


Fig. 1. Distribution of larvae samples, belonging to the genus *Argis*, in coastal Kamchatka and adjacent waters.

of Okhotsk Sea (above western Kamchatka shelf) in summer 2013, 2015, and 2016, and in the Pacific waters along southeastern coast of Kamchatka Peninsula (Avacha Gulf) in spring-summer 2009, 2014, 2016, and 2017 (Fig. 1; Table 1), according to fisheries research program of the Pacific Institute of Fisheries and Oceanography.

Ichthyoplanktonic gear with mouth diameter 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 in smaller bottom depths. Minimal bottom depth of larvae sampling was 9 m and maximal bottom depth was 1800 m. Planktonic samples were fixed in 4% formaldehyde. Larvae were examined with binocular microscope at 32-fold and 56-fold magnification.

Table 1. Data on collection of *Argis* larvae studied in present work, including locality, species, time period, and developmental stage

Regions	Period of collection		Larval stages					
			<i>A. dentata</i>	<i>A. lar</i>	<i>A. crassa</i>	<i>A. ovifer</i>	<i>A. ochotensis</i>	
							Form 1	Form 2
Western Kamchatka shelf	August	2013	–	II	–	–	–	–
	June–July	2015	–	II	II	II	–	–
	June–July	2016	I, II	II, III	I	II	–	–
Avacha Gulf	May	2009	–	I	–	–	I	–
	May–June	2014	I	–	–	–	I, II	I
	May	2016	–	–	I	–	–	I
	May	2017	–	–	–	–	–	I

Classification and morphology of larval stages

Classification was made following Zarenkov (1965) and Komai (1997). Larval description followed method proposed by Clark et al. (1998) and Garm (2004). Setal terminology is in accordance with Garm (2004). Long plumose setae on distal end of exopods were drawn truncated.

Abbreviations used in text and figures: *A1*, antennules (first pair of antennae); *A2*, antenna (second pair of antennae); *P1–P5*, first to fifth pereopods; *Mp 1–3*, first to third maxilliped, respectively; *Mx1*, maxillule; *Mx2*, maxilla; *GV*, general view; *T*, telson; *pl*, pleopods; *Sg*, scaphognathite; *Cp*, anterior ventral margin of carapace; *Sc*, scaphocerite; *TL*, total length; *CL*, carapace length; *RL*, rostrum length.

Available descriptions used in presenting certain stages (Ivanov, 1968; Makarov, 1966, 1967; Squires, 1965).

Measurements of larvae

Measurements of larvae were made with an ocular micrometer with precision of 0.1 mm as follows: carapace length (CL) from anterior tip of rostrum to posterior carapace margin; total length (TL) from anterior tip of rostrum to posterior margin of telson, excluding telson processes; rostrum

length (RL) from anterior tip of rostrum to eye socket.

RESULTS

Almost all zoea found in eastern part of Okhotsk Sea and identified as the genus *Argis* were very close in morphology to late zoeal stages of *A. lar* described by Makarov (1967). Also one larva caught in Avacha Gulf we identified as zoea I of the same species, since they obviously correspond by all features to the described zoea II and zoea III. In particular, these larvae were of close sizes and had smooth posterior margin of pleomeres and short spine of scaphocerite, which is characteristic to this species. Zoea III, almost indistinguishable from zoea II of *A. lar* by its morphology, was also found.

Two larvae of zoea II from northern part of western Kamchatka shelf strongly resemble in their morphology to the previous species, though having certain differences. These larvae had longer rostrum, with denticles on carapace in other position, larger quantity of setae on scaphognathite, endopod of antenna better developed. It is known that *A. ovifer* is the most closely related species to *A. lar* (Sokolov, 2001; Komai, 1997). Makarov (1941) even assumed that *A. ovifer* is a subspecies of *A. lar* (Slizkin, 2006). Therefore we identified these

larvae as *A. ovifer*. Similar larvae of zoea I were not caught.

Two larvae of zoea I, collected in Avacha Gulf, completely corresponded to description of *A. dentata*, given by Ivanov (1968). We found zoea II, morphologically corresponding to this species, in eastern part of Okhotsk Sea. This larva had rather long spine on scaphocerite, serrate pleon and anterior ventral margin of carapace, large number of setae in scaphognathite, and similar body length. Therefore, we believed that they were also *A. dentata*.

A few larvae of zoea I, identical to descriptions of Ivanov (1968) and Makarov (1967) for zoea I of *A. crassa*, were found in Avacha Gulf. One larva, corresponding to morphology of zoea II, was found in the eastern part of Okhotsk Sea. This larva had very long spine on scaphocerite, serrate pleon, and anterior ventral margin of carapace, a large number of setae on scaphognathite, characteristic shape of telson, and corresponding dimensions.

A few early larvae of zoea I, collected in Avacha Gulf in summer, were most of all morphologically close to *A. dentata*, but differed from it by smaller number of cuspidate setae in basal endite of maxillula and plumose setae in scaphognathite. These larvae were the largest that we found, and did not correspond to any of available descriptions. Only five species of genus *Argis* have been known in Kamchatka marine waters (Slizkin, 2006), and by process of elimination it could only be *A. ochotensis*. Besides, it is most similar to *A. dentata* (Sokolov, 2001). Larva of zoea II, morphologically similar to *A. dentata* but having some differences from this species and significant differences from other species of *Argis*, was found in Avacha Gulf. We also identified it as *A. ochotensis*, as only species which remained.

All studied larvae have number of common structural features. Below we present total characteristic of early and late larvae of the genus *Argis* from marine waters near Kamchatka Peninsula, and also descriptions of species by stages of development.

Larvae of various species of *Argis* in corresponding stages of development differ only in structure of carapace, telson, pleon, pleopods, maxillules and maxillas. Structure of antennules, maxillipeds, and pereopods in most cases is the same, therefore, we describe legs in detail only for the first species. Descriptions of individual species in stages of development are presented below.

Argis crassa

(Fig. 2)

Zoea I

Material examined. Avacha Gulf: 1 larva, 20 May 2016, over depth 157 m. Western Kamchatka shelf: 3 larvae, 6 June 2016, over depth 41–80 m. TL 6.7–7.8 mm. CL 1.6–2.0 mm. RL 0.63–0.95 mm.

Description. Carapace (Fig. 2, *Cp* (I), *GV* (I)): rostrum straight, not very long; eyes sessile; supraorbital spines absent; 3 or 4 small sharp spines located along anterior ventral margin; pterygostomial spine very small and short. Antennule (Fig. 2, *A1* (I)): peduncle unsegmented; outer flagellum with three aesthetascs and one strong seta terminally. Antenna (Fig. 2, *A2* (I)): protopod unsegmented, with one small distal spine; endopod of antenna slightly longer than scaphocerite; scaphocerite unsegmented, with 17 plumose setae on inner margin and one small seta on outer margin; spine of scaphocerite absent; base of endopod separated. Maxillule: coxal endite with seven papposerrate setae; basal endite with nine cuspidate setae; endopod 2-segmented, with proximal segment having one short simple and two strong papposerrate setae, and with distal segment having three strong terminal papposerrate setae. Maxilla (Fig. 2, *Sg* (I), *Sg* (I)*): coxal endite bilobed, with 11+4 papposerrate setae; basal endite trilobed, with 4+3+3 papposerrate setae; endopod unsegmented, trilobed, with 2+1+1+1 papposerrate setae; scaphognathite with 8–10 marginal plumose setae. First maxilliped: coxa with five papposer-

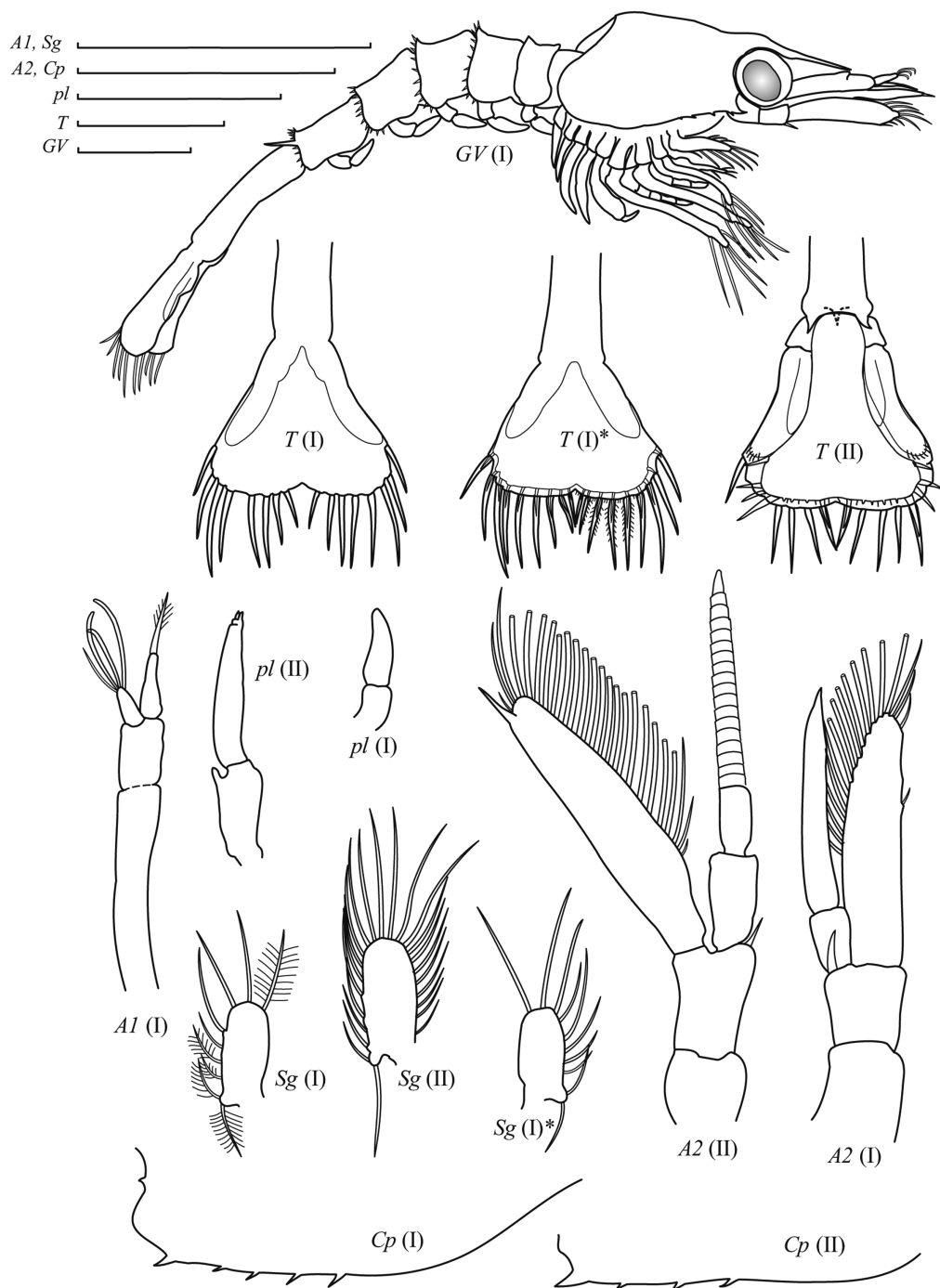


Fig. 2. Morphology of larvae of *Argis crassa*: (I) – zoea I; (II) – zoea II; GV – general view; T – telson; pl – pleopod; Sg – scaphognathite; A1 – antennule, A2 – antenna; Cp – anterior ventral margin of carapace. Same structure of another specimen marked with asterisk. Scale bars 1 mm.

rate setae; basis with 12 papposerrate setae; endopod 4-segmented, with 3, 1, 2, 3 papposerrate setae; exopod unsegmented, with one long plumose seta on lateral margin and three long terminal plumose setae. Second maxilliped: coxa with one papposerrate seta; basis with eight papposerrate setae arranged as 1, 1, 3, 3; endopod 5-segmented with 3+1, 1, 1+1, 2+1 and five papposerrate terminal setae; exopod unsegmented, with two subterminal and three long terminal plumose setae. Third maxilliped: coxa unarmed; basis with two papposerrate setae; endopod 5-segmented with 2, 1, 1+1; 2+2 and five papposerrate terminal setae; exopod unsegmented, with two subterminal and three terminal plumose setae. Pereiopods uniramous, well developed, segmented; first pereiopod with epipod in basis; subchela available; second pereiopod chelipedal; third, fourth and fifth pereiopods uniramous, 6-segmented, without setae. Pleon (Fig. 2, *GV* (I)) with five smooth pleomeres; posterior margin of 2nd–5th pleomeres with spicules; fifth pleomere with a pair of dorsolateral spines; anal spine absent. Pleopods uniramous, without setae (Fig. 2, *pl* (I)). Telson (Fig. 2, *T* (I), *T* (I)*) of peculiar shape, with rounded corners; small notch on posterior margin of telson of semicircular shape; telson not clearly separated from pleon; two larvae with 8+8 plumose setae, but one larva with 9+9 plumose setae, and one larva with 8+9 plumose setae; in larva with 9+9 plumose setae, next stage of zoea also with 9+9 setae visible through cuticle. Uropods absent.

Zoea II

Material examined. Western Kamchatka shelf: 1 larva, 9 June 2015, over depth 30 m. TL 8.4 mm. CL 2.02 mm. RL 0.82 mm.

Description. Carapace (Fig. 2, *Cp* (II)): eyes stalked; rostrum long, straight, facing forward, reaching front of ocular peduncle; pterigostomial spine present; three small spines along anterior ventral margin; pterygostomial spine present; supraorbital

spines absent. Antennule: peduncle 3-segmented, first segment with three small plumose setae on stylocerite, one strong spine located at half of segment length, and six or seven small plumose setae located terminally; second segment with six small plumose setae distally; third segment with one long and three or four short plumose setae terminally; outer flagellum 2-segmented, with four aesthetascs and one strong seta terminally. Antenna (Fig. 2, *A2* (II)): protopod 2-segmented, with one short spines; endopod 18–19-segmented; scaphocerite with 22 plumose setae along inner and posterior margin; outer setae on scaphocerite absent; spine of scaphocerite very long. Maxillule: endopod 2-segmented, with proximal segment having one short simple and two strong papposerrate setae, and with distal segment having three strong terminal papposerrate setae; basal endite with nine cuspidate setae; coxal endite with five distal and two lateral papposerrate setae; scaphognathite with 23 or 24 plumose setae. Maxilla: (Fig. 2, *Sg* (II)): coxal endite bilobed, with 10+4 papposerrate setae; basal endite trilobed, with 4+3+3 papposerrate setae; endopod unsegmented, trilobed, bearing 2+1+1+1 papposerrate setae; scaphognathite with 23 or 24 marginal plumose setae. First maxilliped: coxa with epipod and six papposerrate setae; basis with 12 papposerrate setae; endopod 4-segmented, with 4, 1, 2+1, 3 papposerrate setae; exopod unsegmented, with one long plumose seta on lateral margin and four long terminal plumose setae. Second maxilliped: coxa with one papposerrate seta; basis with eight papposerrate setae arranged as 2, 3, 3; endopod 5-segmented with 3+1, 1, 1+1, 2+1, 5 papposerrate terminal setae; exopod unsegmented, with two subterminal and four long terminal plumose setae. Third maxilliped: coxa unarmed; basis with two papposerrate setae; endopod 5-segmented with 2, 1, 1+1; 2+2, 5 papposerrate terminal setae; exopod unsegmented, with two subterminal and four terminal plumose setae. Pereiopods uniramous, well developed, segmented; first pereiopod with epipod on

basis, terminal segment having well developed subchela, and propodus and dactylus distinct; second pereopod with well developed chela; third, fourth and fifth pereopod uniramous, 7-segmented, without setae. Pleon with six pleomeres; posterior margin of 5th–6th pleomeres with spicules; fifth pleomere with a pair of long and sharp dorsolateral spines; small anal spine present. Pleopods (Fig. 2, *pl* (II)): protopod naked, bearing endopod in form of small tubercle and exopod without setae. Uropods absent. Telson (Fig. 2, *T* (II)) separated from pleon, with rounded corners, small semicircular notch as in zoea I, and 8+8 setae (inner six and outer two plumose only on proximal axis); small anal spine present; next decapodid stage seen through telson (five pairs of setae and well developed uropods visible through cuticle).

Argis dentata

(Fig. 3)

Zoea I

Material examined. Avacha Gulf: 1 larva, 5 June 2014, over depth 115 m; 1 larva, May 2016. Western part of Okhotsk Sea: 1 larva, 6 June 2016, over depth 157 m. TL 7.4 and 8.1 mm. CL 1.8 and 2.1 mm. RL 0.9 mm.

Description. Carapace (Fig. 3, *GV* (I)): rostrum straight, slightly flattened, pointed, not so long; eyes sessile; supraorbital spines absent; three small spine available along anterior ventral margin, well noticeable; pterygostomial spine present. Antennule: peduncle unsegmented; outer flagellum with three aesthetascs and one strong seta terminally; distal part of terminal setae of antennule covered with short spicules. Antenna (Fig. 3, *Sc* (I)): protopod unsegmented, with one small distal spine; scaphocerite unsegmented, with 19–22 plumose setae on inner margin and one small seta on outer margin; apparent ugliness noticeable at one larvae (right A2 with two absolutely identical spines instead of one, and left A2 with only one similar spine); spine of scaphocer-

ite rather long; spine on right limb slightly shorter than on left one; base of endopodite separated. Maxillule: coxal endite with seven papposerrate setae; basal endite with nine cuspidate setae; endopod 2-segmented (proximal segment with one short simple and two strong papposerrate setae, distal segment with three strong terminal papposerrate setae). Maxilla (Fig. 3, *Mx* (I), *Sg* (I)): coxal endite bilobed, with 11+4 papposerrate setae; basal endite trilobed, with 4+3+3 papposerrate setae; endopod unsegmented, trilobed, with 2+1+1+1 papposerrate setae; in first specimen, one scaphognathite of maxilla armed with seven marginal plumose setae, but its other scaphognathite, with 8 setae. First maxilliped: coxa with five papposerrate setae; basis with 12 papposerrate setae; endopod 4-segmented, with 3, 1, 2, 3 papposerrate setae; exopod unsegmented, with one long plumose seta on lateral margin and three long terminal plumose setae. Second maxilliped: coxa with one papposerrate seta; basis with eight papposerrate setae arranged as 1, 1, 3, 3; endopod 5-segmented, with 3+1, 1, 1+1, 2+1 and five papposerrate terminal setae; exopod unsegmented, with two subterminal and three long terminal plumose setae. Third maxilliped: coxa unarmed; basis with two papposerrate setae; endopod 5-segmented, with 2, 1, 1+1; 2+2 and five papposerrate terminal setae; exopod unsegmented, with two subterminal and three terminal plumose setae. Pereiopods uniramous, well developed, segmented; first pereopod with epipod in basis and with terminal segment of subchela developed; second pereopod cheliped; third, fourth and fifth pereopod uniramous, 6-segmented, without setae; small gills available at base of pereiopods under carapace. Pleon (Fig. 3, *GV* (I)) with five smooth pleomeres; posterior margin of 1st–5th pleomeres with small spicules; fifth pleomere with one pair of long and sharp dorsolateral spines; sixth pleomere not clearly separated from telson; anal spine absent. Pleopods (Fig. 3, *pl* (I)) uniramous, without setae.

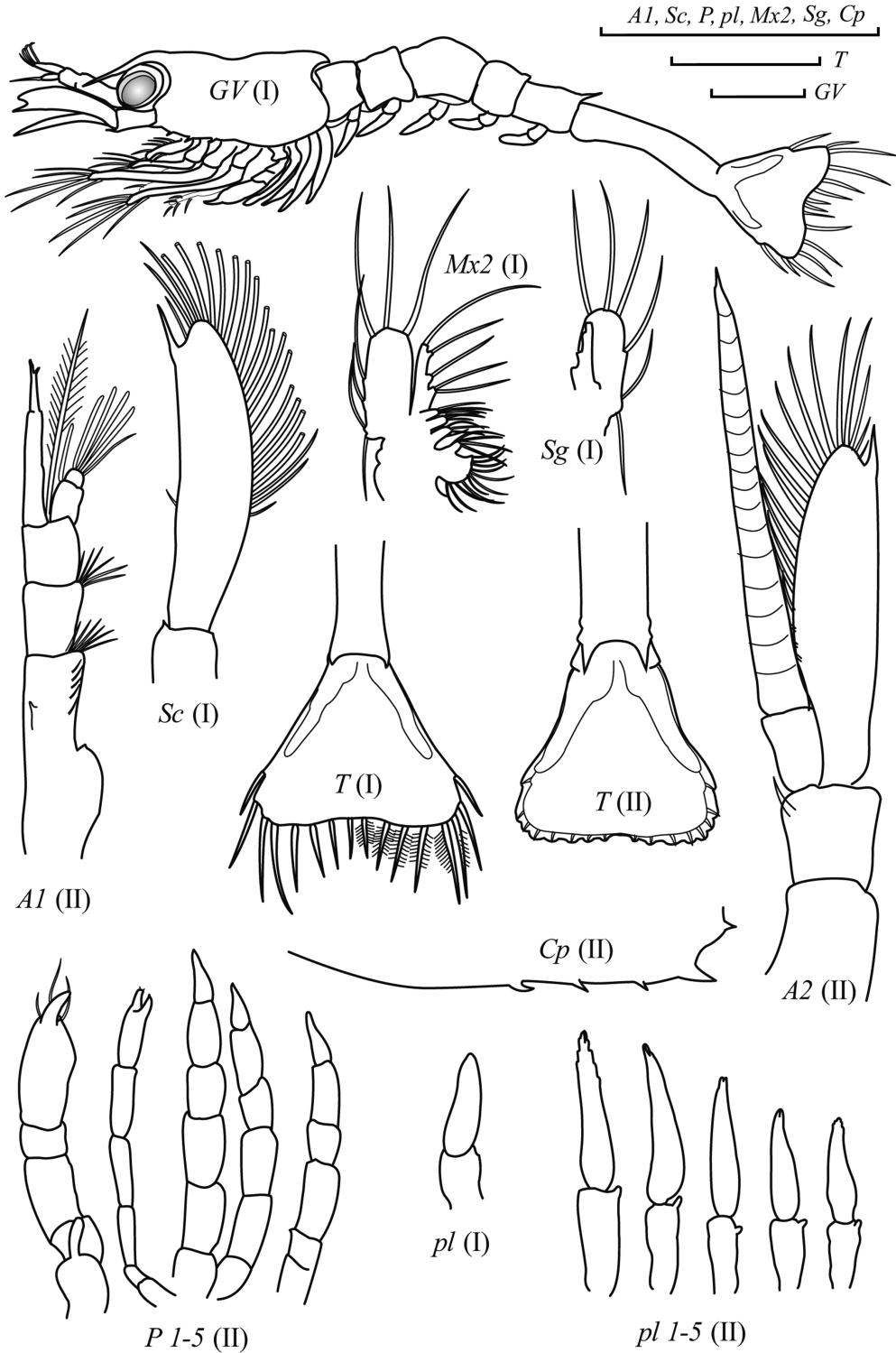


Fig. 3. Morphology of larvae of *Argis dentata*: (I) – zoea I; (II) – zoea II; GV, A1, A2, Cp, pl, Sg, T – as in Fig. 2; Sc – scaphocerite; Mx2 – maxilla; P1–5 – pereopods. Scale bars 1 mm.

Telson (Fig. 3, *T* (I)) not clearly separated from pleon, with small notch of triangular shape and with 8+8 setae. Uropods absent.

Zoea II

Material examined. Western part of Okhotsk Sea: 1 larva, 18 June 2016, over depth 25 m. TL 7.3 mm. CL 2.0 mm. RL 0.9 mm.

Description. Carapace (Fig. 3, *Cp* (II)): eyes stalked; rostrum rather long, straight, facing forward, reaching far beyond front of ocular peduncle basis; pterigostomial spine present; three or four very thin spines located along anterior ventral margin; supra-orbital spines absent. Antennule (Fig. 3, *A1* (II)): peduncle 3-segmented; first segment with three small plumose setae on stylocerite, one strong spine at half of segment length, and six or seven small plumose setae terminally; second segment bearing six small plumose setae distally; third segment with one long plus three or four short plumose setae terminally; outer flagellum 2.5 times shorter than inner flagellum; 2-segmented, with four aesthetascs and one strong setae terminally, and with one aesthetasc on proximal segment. Antenna (Fig. 3, *A2* (II)): protopod 2-segmented, with one short spine; endopod two times as long as antennal scale, 17-segmented; scaphocerite with 22 plumose setae along inner and posterior margin; outer setae on scaphocerite absent; spine of scaphocerite longer than carapace. Maxillule: endopod 2-segmented, with proximal segment having one short simple and two strong papposerrate setae, and with distal segment having three strong terminal papposerrate setae; basal endite with ten cuspidate setae; coxal endite with five distal and two lateral papposerrate setae. Maxilla: scaphognathite with 18 plumose setae. First maxilliped: coxa with epipod and six papposerrate setae; basis with 12 papposerrate setae; endopod 4-segmented, with 4, 1, 2+1, 3 papposerrate setae; exopod unsegmented, with one long plumose seta on lateral margin and four long termi-

nal plumose setae. Second maxilliped: coxa with one papposerrate seta; basis with eight papposerrate setae arranged as 2, 3, 3; endopod 5-segmented, with 3+1, 1, 1+1, 2+1 and 5 papposerrate terminal setae; exopod unsegmented, with two subterminal and four long terminal plumose setae. Third maxilliped: coxa unarmed; basis with two papposerrate setae; endopod 5-segmented, with 2, 1, 1+1; 2+2 and 5 papposerrate terminal setae; exopod unsegmented, with two subterminal and four terminal plumose setae. Pereiopods (Fig. 3, *P 1–5* (II)) uniramous, well developed, segmented; first pereiopod with epipod on basis, terminal segment of subchela well developed, and propodus and dactylus distinct; second pereiopod with well developed chela; third, fourth and fifth pereiopods uniramous, 7-segmented, without setae. Pleon with six pleomeres; several very fine spicules available at posterior margin of 2nd–4th pleomeres; fifth pleomere with a pair of long and sharp dorsolateral spines; anal spine small. Pleopods (Fig. 3, *pl 1–5* (II)): protopod naked, bearing endopod in form of small tubercle and exopod without setae. Pleopods of various length, gradually decreased from first to fifth (fifth pair shortest). Uropods absent. Telson (Fig. 3, *T* (II)) relatively narrow and separated from pleon; its corners rounded; its posterior margin slightly convex, almost without notch; all setae broken. Next stage of zoea with 8+8 setae visible through cuticle.

Argis lar (Figs 4, 5)

Zoea I

Material examined. Avacha Gulf: 1 larva, early May 2009, over depth 53 m. TL 6.7 mm. CL 2.01 mm. RL 0.80 mm.

Description. Carapace: rostrum thin, not so long; eyes sessile; anterior margin smooth in front of one of its side; rather thin spine along anterior ventral margin visible on other side if carefully inspected; pterygostomial spine present. Antennule: peduncle unsegmented; outer flagellum with

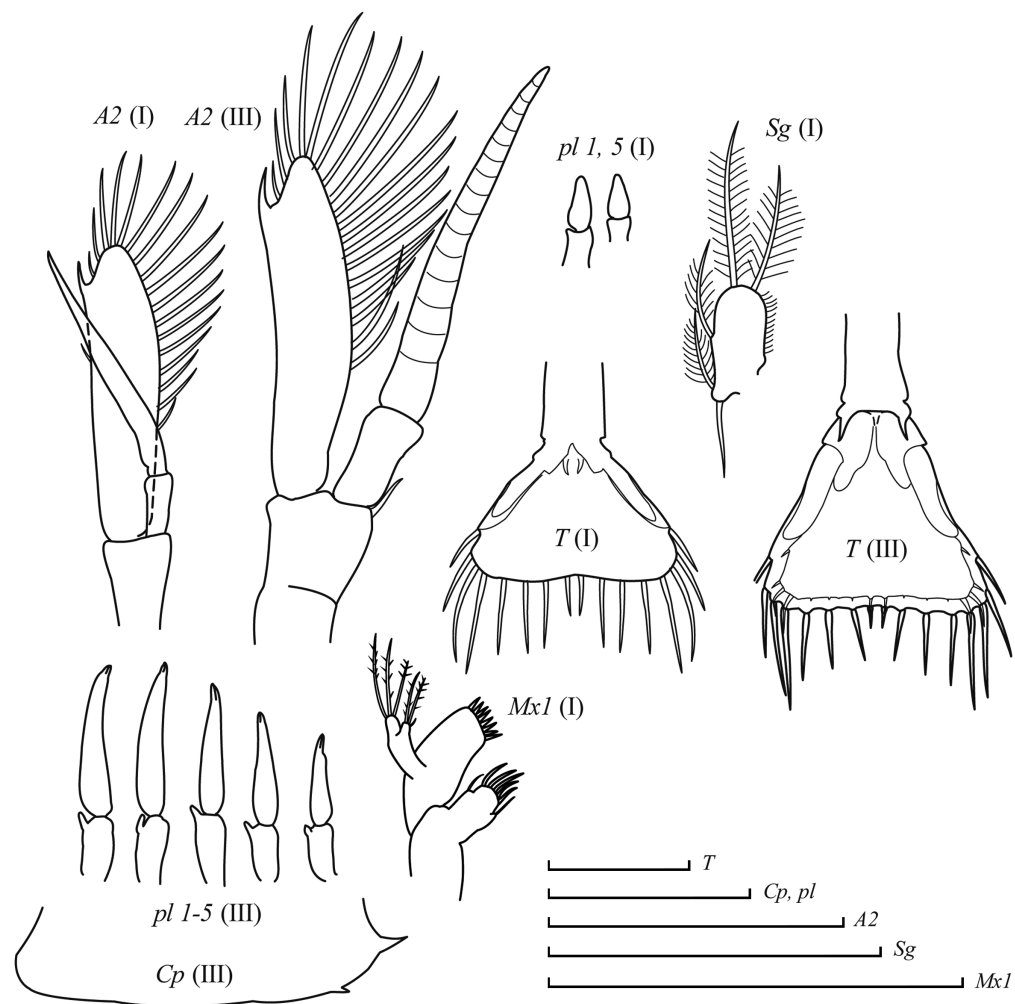


Fig. 4. Morphology of larvae of *Argis lar* at I and III zoal stages: (I) – zoea I; (III) – zoea III; *T*, *pl*, *Sg*, *A2*, *Cp* – as in Figs. 2–3; *Mx1* – maxillule. Scale bars 1 mm.

three aesthetascs and one strong seta terminally. Antenna (Fig. 4, *A2* (I)): protopod unsegmented, with one small distal spine; endopod slightly longer than scaphocerite; scaphocerite unsegmented, with 18 plumose setae on inner margin and one small seta on outer margin; spine of scaphocerite short. Maxillule (Fig. 4, *Mx1* (I)): coxal endite with seven papposerrate setae; basal endite with eight cuspidate setae; endopod 2-segmented (proximal segment with one short simple and two strong papposerrate setae, distal segment with three strong terminal papposerrate setae); scaphognathite

with five plumose setae. Maxilla (Fig. 4, *Sg* (I)): coxal endite bilobed, with 11+4 papposerrate setae; basal endite trilobed, with 4+3+3 papposerrate setae; endopod unsegmented, trilobed, bearing 2+1+1+1 papposerrate setae; scaphognathite with five marginal plumose setae. First maxilliped: coxa with five papposerrate setae; basis with twelve papposerrate setae; endopod 4-segmented, with 3, 1, 2, 3 papposerrate setae; exopod unsegmented, with one long plumose seta on lateral margin and three long terminal plumose setae. Second maxilliped: coxa with one papposerrate seta; basis

with eight papposerrate setae arranged as 1, 1, 3, 3; endopod 5-segmented, with 3+1, 1, 1+1, 2+1, 5 papposerrate terminal setae; exopod unsegmented, with two subterminal and three long terminal plumose setae. Third maxilliped: coxa unarmed; basis with two papposerrate setae; endopod 5-segmented, with 2, 1, 1+1; 2+2, 5 papposerrate terminal setae; exopod unsegmented, with two subterminal and three terminal plumose setae. Pereiopods uniramous, well developed, segmented; first pereiopod with epipod on basis and with terminal segment having subchela; second pereiopod cheliped; third, fourth and fifth pereiopod uniramous, 6-segmented, without setae. Small gills available at base of pereiopods under carapace. Pleon with five smooth pleomeres; posterior margin of 1st–5th pleomeres with spicules and slightly raised; fifth pleomere with a pair of dorsolateral spines. Pleopods (Fig. 4, *pl 1, 5* (I)) uniramous, short, tucked under pleon. Uropods absent. Telson (Fig. 4, *T* (I)) triangular, indented medially, with 8+8 setae (inner six plumose and outer two plumose only on proximal axis).

Zoea II

Material examined. Western Kamchatka shelf: 2 larvae, 4 and 6 Aug. 2013, over depth 28–53 m; 6 larvae, from 27 July to 6 Aug. 2015, over depth 15–80 m; 3 larvae, 24 June 2016, over depth 48 m. TL 6.5–7.7 mm. CL 1.5–2.0 mm. RL 0.57–0.8 mm.

Description. Carapace (Fig. 5, *GV*): eyes stalked, with ocular peduncle shorter than antennal peduncle; rostrum straight, facing forward, reaching front edge of ocular peduncle; pterigostomial spine present; one small spine located along anterior ventral margin in most larvae at least on one side; supraorbital spines absent. Antennule (Fig. 5, *A1*): peduncle 3-segmented; first segment with three small plumose setae on stylocerite, one strong spine at half segment length, and six or seven small plumose setae terminally; second segment bearing six small plumose setae distally; third segment with one long and three or four short plumose setae

terminally; outer flagellum with three or four aesthetascs and one or two strong setae terminally. Antenna (Fig. 5, *A2*): protopod unsegmented, with one short spine; endopod longer than antennal scale, 10–12-segmented; scaphocerite with 15–19 plumose setae along inner and posterior margin; outer setae on scaphocerite absent; spines of different lengths situated on right and left scaphocerite in some specimens; as a rule, spine of one scaphocerite reaching edge of plate, and spine of other scaphocerite not reaching (in five specimens, both spines short). Maxillule: basal endite with nine cuspidate setae; coxal endite with five distal and one or two lateral papposerrate setae. Maxilla: (Fig. 5, *Sg*): coxal endite bilobed, with 9–11+4 papposerrate setae; basal endite trilobed, with 4+3+3 papposerrate setae; endopod unsegmented, trilobed, bearing 2+1+1+1 papposerrate setae; scaphognathite with 13–18 marginal plumose setae. First maxilliped (Fig. 5, *Mp1*): coxa with epipod and six papposerrate setae; basis with twelve papposerrate setae; endopod 4-segmented, with 4, 1, 2+1, 3 papposerrate setae; exopod unsegmented, with one long plumose seta on lateral margin and four long terminal plumose setae. Second maxilliped (Fig. 5, *Mp2*): coxa with one papposerrate seta; basis with eight papposerrate setae arranged as 2, 3, 3; endopod 5-segmented, with 3+1, 1, 1+1, 2+1, 5 papposerrate terminal setae; exopod unsegmented, with two subterminal and four long terminal plumose setae. Third maxilliped (Fig. 5, *Mp3*): coxa unarmed; basis with two papposerrate setae; endopod 5-segmented, with 2, 1, 1+1; 2+2, 5 papposerrate terminal setae; exopod unsegmented, with two subterminal and four terminal plumose setae. Pereiopods (Fig. 5, *P 1–5*) uniramous, well developed, segmented; first pereiopod with epipod on basis, terminal segment having well developed subchela, and propodus and dactylus distinct; second pereiopod with well developed chela; third, fourth, and fifth pereiopods uniramous, 7-segmented, without setae; small gills situated at base of pereiopods under carapace. Pleon (Fig. 5, *GV*)

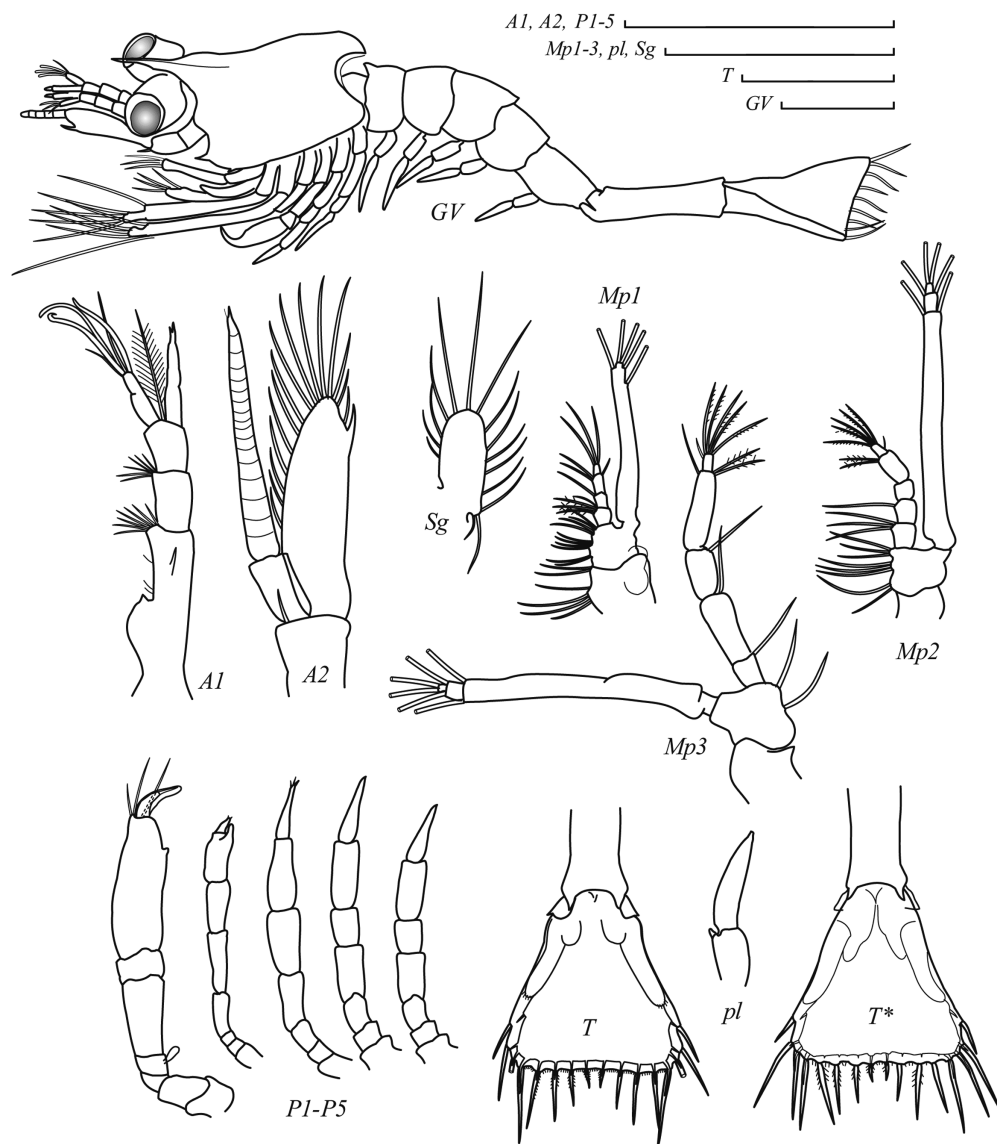


Fig. 5. Morphology of larvae of *Argis lar* at II zoal stage: *GV*, *T*, *A1*, *A2*, *pl*, *Sg*, *P1-5* – as in Figs. 2–3; *Mp1* – first maxilliped; *Mp2* – second maxilliped *Mp3* – third maxilliped. Same structure of another specimen marked with asterisk. Scale bars 1 mm.

with six pleomeres; posterior margin of pleomeres without spicules; fifth pleomere with a pair of dorsolateral spines. Pleopods (Fig. 5, *pl*): protopod naked, bearing endopod in form of small tubercle and exopod without setae; length of pleopods decrease from first to last. Uropods absent. Telson (Fig. 5, *T*, *T**) separated from pleon, triangular, without notch, with 8+8 setae (inner six plumose and

outer two plumose only on proximal axis); small anal spine present. Next stage visible through telson cuticle; in some specimens, this stage possibly decapodid since only five pairs of spines present at terminal edge of telson (one pair central, four pairs at the edges); in other specimens, this stage obviously with eight pairs of terminal setae, therefore, it representing not decapodid but zoea.

Zoea III

Material examined. Western Kamchatka shelf: 1 larva, 24 June 2016, over depth 27 m. TL 6.8 mm. CL 1.5 mm. RL 0.7 mm.

Description. Carapace (Fig. 4, *Cp* (III)): eyes stalked; rostrum very long, straight, reaching front of ocular peduncle; pterigostomial spine present; anterior ventral margin smooth, without spines; pterygostomial spine present; supraorbital spines absent. Antennule as in zoea II. Antenna (Fig. 4, *A2* (III)): protopod 2-segmented, with one short spine; endopod much longer than antennal scale, 15-segmented; scaphocerite with 19 plumose setae along inner and posterior margin; outer setae on scaphocerite absent; spine of scaphocerite in one antenna reaching edge of plate, in other antenna, it much shorter. Maxillule: endopod with five papposerrate setae; basal endite with ten cuspidate setae on one maxillule, and eleven setae on other maxillule; coxal endite with nine papposerrate setae. Maxilla: coxal endite bilobed, with 9–11+4 papposerrate setae; basal endite trilobed, with 4+3+3 papposerrate setae; endopod unsegmented, trilobed, bearing 2+1+1+1 papposerrate setae; scaphognathite in one maxilla with 17, and in other one, with 20 marginal plumose setae. First to third maxillipeds as in zoea II. Pereiopods as in zoea II. Pleon with six pleomeres; spicules at posterior margin absent; fifth pleomere with a pair dorsolateral spines; anal spine present. Pleopods (Fig. 4, *pl 1–5* (III)) as in zoea II. Uropods absent. Telson (Fig. 4, *T* (III)) as in zoea II. Next larval stage, visible through telson cuticle, with five pairs of setae (i.e. as in decapodid); consequently, zoea III evidently latest stage of zoea.

Argis ochotensis (Figs 6, 7)

Zoea I

We describe here two forms of zoea I of *A. ochotensis*, which have slight differences, but clearly belong to the same species. Spe-

cies *A. ochotensis* is currently divided into two subspecies: *A. o. ochotensis* Komai, 1998 and *A. o. kamtshatica* Sokolov, 2001. We assume that “form 1” refers to *A. o. kamtshatica*, because it is caught over the bottom depth less than 100 m, which is typical for this subspecies. “Form 2” is caught in deep part of Avacha Gulf. It is known that adult representatives of *A. o. ochotensis* inhabit greater bottom depths (Slizkin, 2006).

Form 1

Material examined. Avacha Gulf: 1 larva, early May 2009, over depth 94 m. TL 7.6 mm. CL 1.8 mm. RL 1.0 mm.

Description. Carapace: rostrum long, pointed; eyes sessile; supraorbital spines absent; four very thin spines set along anterior ventral margin; pterygostomial spine present. Antennule (Fig. 6, *A1*): peduncle unsegmented; outer flagellum with three aesthetascs and one strong seta terminally; terminal setae of antennule shortly pubescent only in its distal part. Antenna (Fig. 6, *A2*): protopod unsegmented, with one small distal spine; endopod slightly longer than scaphocerite; scaphocerite unsegmented, with 17–18 plumose setae on inner margin and one small seta on outer margin; spine of scaphocerite extending beyond edge of plate; base of endopod separated, 6-segmented. Maxillule (Fig. 6, *Mx1*): coxal endite with seven papposerrate setae; basal endite with eight cuspidate setae; endopod 2-segmented (proximal segment with one short simple and two strong papposerrate setae; distal segment with three strong terminal papposerrate setae). Maxilla (Fig. 6, *Mx2*): coxal endite bilobed, with 11+4 papposerrate setae; basal endite trilobed, with 4+3+3 papposerrate setae; endopod unsegmented, trilobed, with 2+1+1+1 papposerrate setae; scaphognathite with five marginal plumose setae; microtriches as in Fig. 6. First maxilliped (Fig. 6, *Mp1*): coxa with five papposerrate setae; basis with twelve papposerrate setae; endopod 4-segmented, with 3, 1, 2, 3 papposerrate setae; exopod

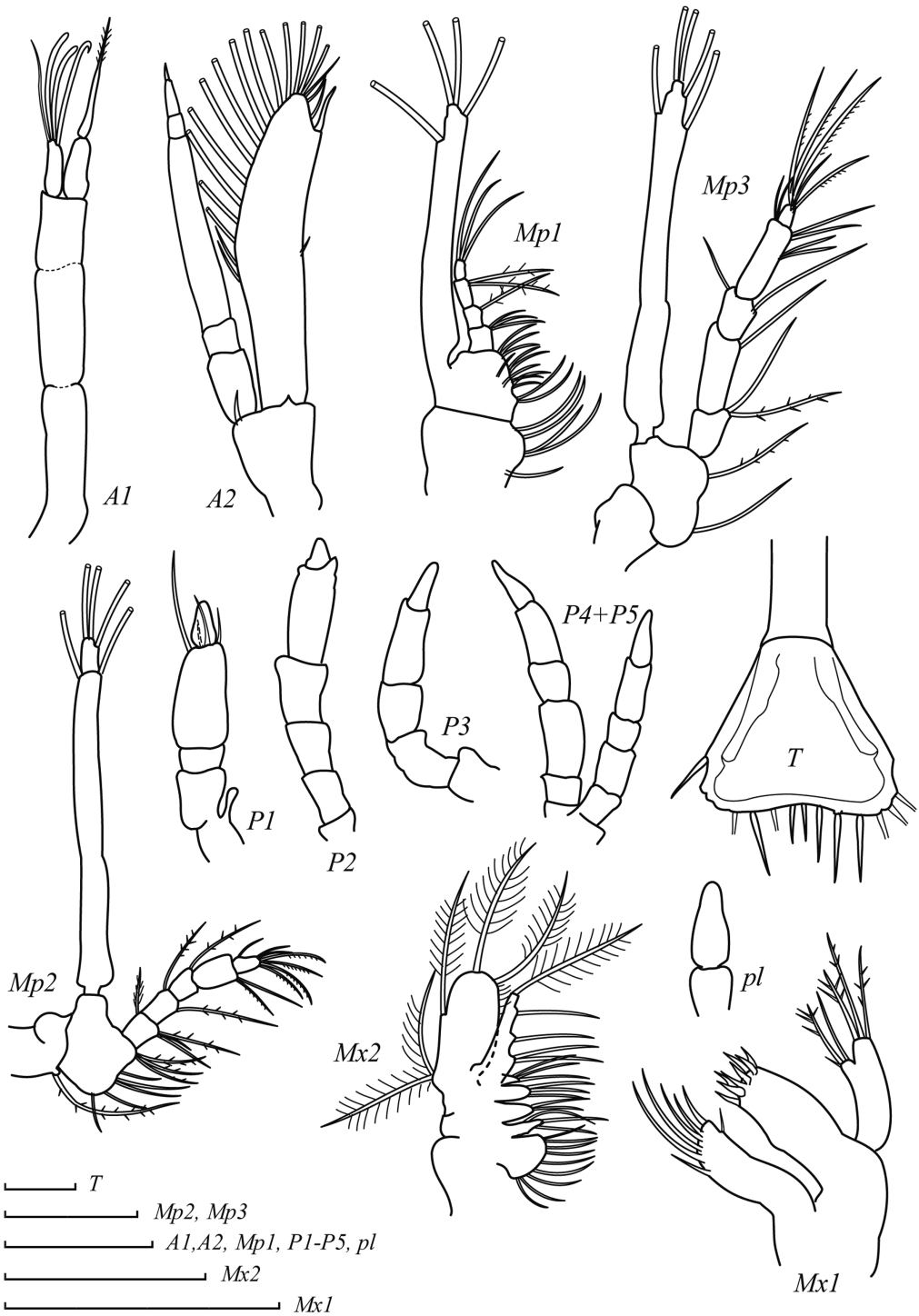


Fig. 6. Morphology of larvae of *Argis ochotensis* at I zoal stage (form 1): *T*, *A1*, *pl*, *A2*, *P1-5*, *Mx1*, *Mx2*, *Mp1*, *Mp2*, *Mp3* – as in Figs. 2–5. Scale bars 1 mm.

unsegmented, with one long plumose seta on lateral margin and three long terminal plumose setae. Second maxilliped (Fig. 6, *Mp2*): coxa with one papposerrate seta; basis with eight papposerrate setae arranged as 1, 1, 3, 3; endopod 5-segmented, with 3+1, 1, 1+1, 2+1, 5 papposerrate terminal setae; exopod unsegmented, with two subterminal and three long terminal plumose setae. Third maxilliped (Fig. 6, *Mp3*): coxa unarmed; basis with two papposerrate setae; endopod 5-segmented, with 2, 1, 1+1; 2+2, 5 papposerrate terminal setae; exopod unsegmented, with two subterminal and three terminal plumose setae. Pereiopods (Fig. 6, *P1*, *P2*, *P3*, *P4+P5*) uniramous, well developed, segmented; first pereiopod with epipod on basis and with terminal segment having subchela; second pereiopod cheliped; third, fourth and fifth pereiopods uniramous, 6-segmented, without setae; small gills located at base of pereiopods under carapace. Pleon with five smooth pleomeres; posterior margin of 2nd–5th pleomeres with spicules; fifth pleomere with a pair of dorsolateral spines; anal spine absent. Pleopods uniramous, without setae (Fig. 6, *pl*). Telson (Fig. 6, *T*) separated from pleon, with small notch of triangular shape and with 8+8 setae. Uropods absent.

Form 2

Material examined. Avacha Gulf: 1 larva, 5 May 2014, over depth 500 m; 1 larva, 24 May 2016, over depth 100 m; 1 larva, 17 May 2017, over depth 72 m. TL 7.7–8.3 mm. CL 1.8–2.05 mm. RL 0.6–0.8 mm.

Description. These larvae are similar to the form 1 (Fig. 7, *GV* (I), *Cp* (I)) by most features, but differ by few insignificant features. Rostrum shorter. Telson indistinctly separated from pleon, wider (Fig. 7, *T* (I)). Seta on end of distal segment of antennules pubescent along whole its length (Fig. 7, *A1* (I)). Basal endite of maxillule with nine cuspidate setae; extreme seta on one maxillulae sometimes greatly shortened. Scaphocerite relatively narrow, with longer spine and more number of setae on inner margin (Fig.

7, *A2* (I)). Endopod of antenna consisting of four segments, but much longer than in larvae of form 1. Chela of *P2* significantly underdeveloped (Fig. 7, *P1*, *P2* (I)). Pleopods better developed: small tubercle developed at place of endopod (Fig. 7, *pl* (I)).

Zoea II

Material examined. Avacha Gulf: 1 larva, 16 June 2014, over depth 49 m. TL 10.6 mm. CL 2.5 mm. RL 0.95.

Description. Carapace (Figs. 7 *Cp* (II)): eyes stalked; rostrum long, straight, facing forward, reaching front of ocular peduncle; pterigostomial spine present; three or four very thin spines located along anterior ventral margin; pterygostomial spine present; supraorbital spines absent. Antennule (Fig. 7, *A1* (II)): peduncle 3-segmented; first segment with three small plumose setae on stylocerite, one strong spine at half of segment length, and six or seven small plumose setae terminally; second segment with six small plumose setae distally; third segment with one long and three or four short plumose setae terminally; outer flagellum 2-segmented, with four aesthetascs and one strong seta terminally. Antenna (Fig. 7, *A2* (II)): propod 2-segmented, with one short spine; endopod longer than scaphocerite, 5-segmented; scaphocerite with 23 or 24 plumose setae along inner and posterior margins; outer setae on scaphocerite absent; spine of scaphocerite by half its length extending beyond edge of plate. Maxillule: basal endite with nine cuspidate setae; coxal endite with five distal and one or two lateral papposerrate setae. Maxilla: scaphognathite with 17 or 18 plumose setae. First maxilliped: coxa with epipod and 6 papposerrate setae; basis with 12 papposerrate setae; endopod 4-segmented, with 4, 1, 2+1, 3 papposerrate setae; exopod unsegmented, with one long plumose seta on lateral margin and four long terminal plumose setae. Second maxilliped: coxa with one papposerrate seta; basis with eight papposerrate setae arranged as 2, 3, 3; endopod 5-segmented, with 3+1, 1, 1+1, 2+1, 5 papposerrate terminal setae;

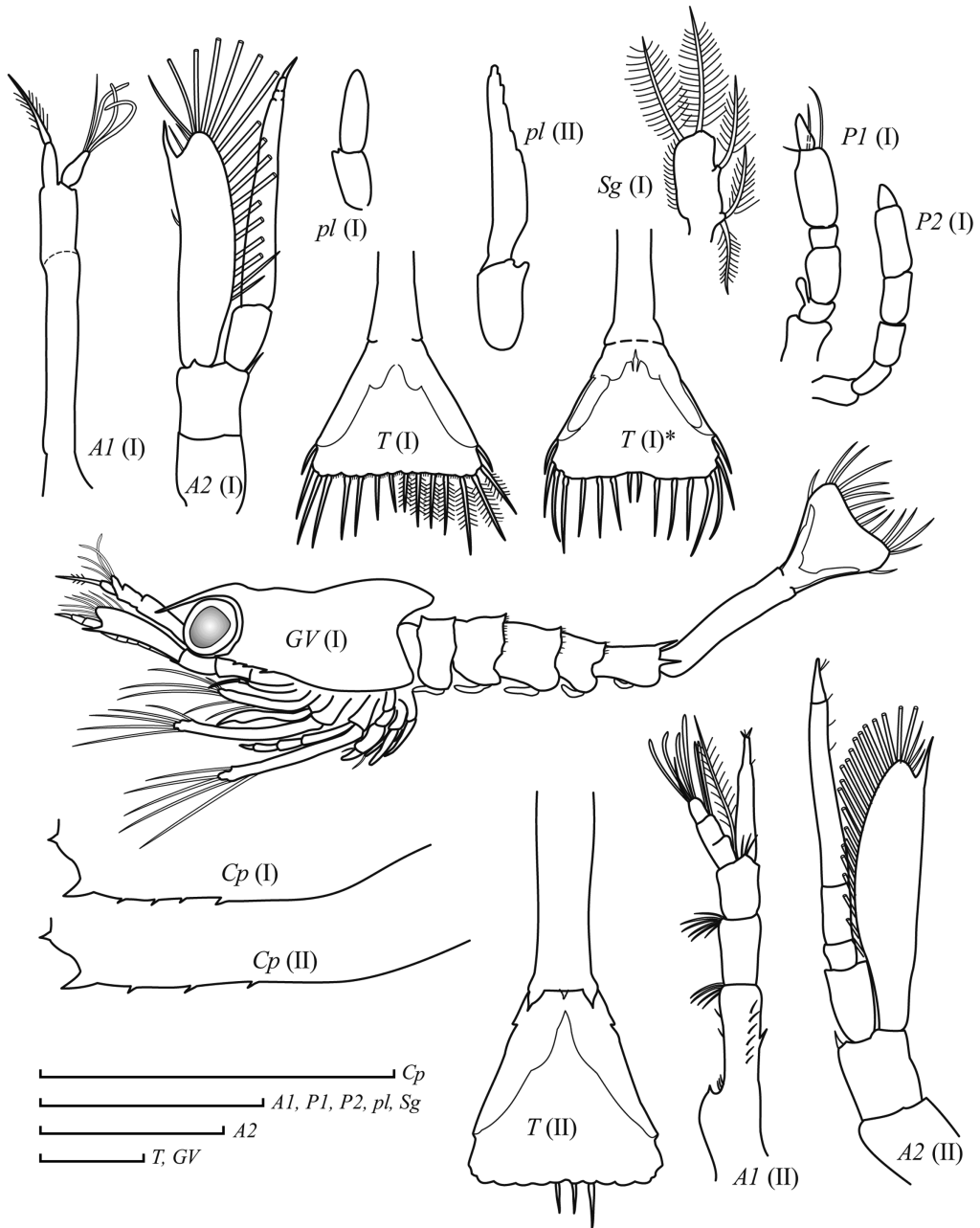


Fig. 7. Morphology of larvae of *Argis ochotensis* at I and II zoeal stages: (form 2): (I) – zoea I; (II) – zoea II; *T*, *A1*, *pl*, *Sg*, *A2*, *P1*–*2*, *Cp* – as in Figs. 2–3. Same structure of another specimen marked with asterisk. Scale bars 1 mm.

exopod unsegmented, with two subterminal and four long terminal plumose setae. Third maxilliped: coxa unarmed; basis with two papposerrate setae; endopod 5-segmented, with 2, 1, 1+1; 2+2, 5 papposerrate termi-

nal setae; exopod unsegmented, with two subterminal and four terminal plumose setae. Pereiopods uniramous, well developed, segmented; first pereiopod with epipod on basis, with terminal segment having well

developed subchela, and with propodus and dactylus distinct; second pereiopod with well developed chela; third, fourth and fifth pereiopods uniramous, 7-segmented, without setae. Pleon with six pleomeres; several very fine spicules available in posterior margin of third and fourth pleomeres; fifth pleomere with a pair of long and sharp dorsolateral spines; anal spine small. Pleopods (Fig. 7, *pl* (II)): protopod naked, bearing endopod in form of small tubercle and exopod without setae. Uropods absent. Telson (Fig. 7, *T* (II)) relatively narrow, separated from pleon, triangular, without notch, with 8+8 setae (six inner setae and two outer

ones plumose only on proximal axis); small anal spine present.

Argis ovifer
(Fig. 8)

Zoea II

Material examined. Western Kamchatka shelf: 1 larva, 28 June 2015, over depth 20 m; 1 larva, 24 June 2016, over depth 27 m. TL 6.5–6.6 mm. CL 1.5–1.67 mm. RL 0.7–0.75 mm.

Description. Carapace (Figs. 8, *Cp*): eyes stalked; rostrum rather long; pterigostomial spine present; one small spine available in middle of anterior ventral margin; pterygo-

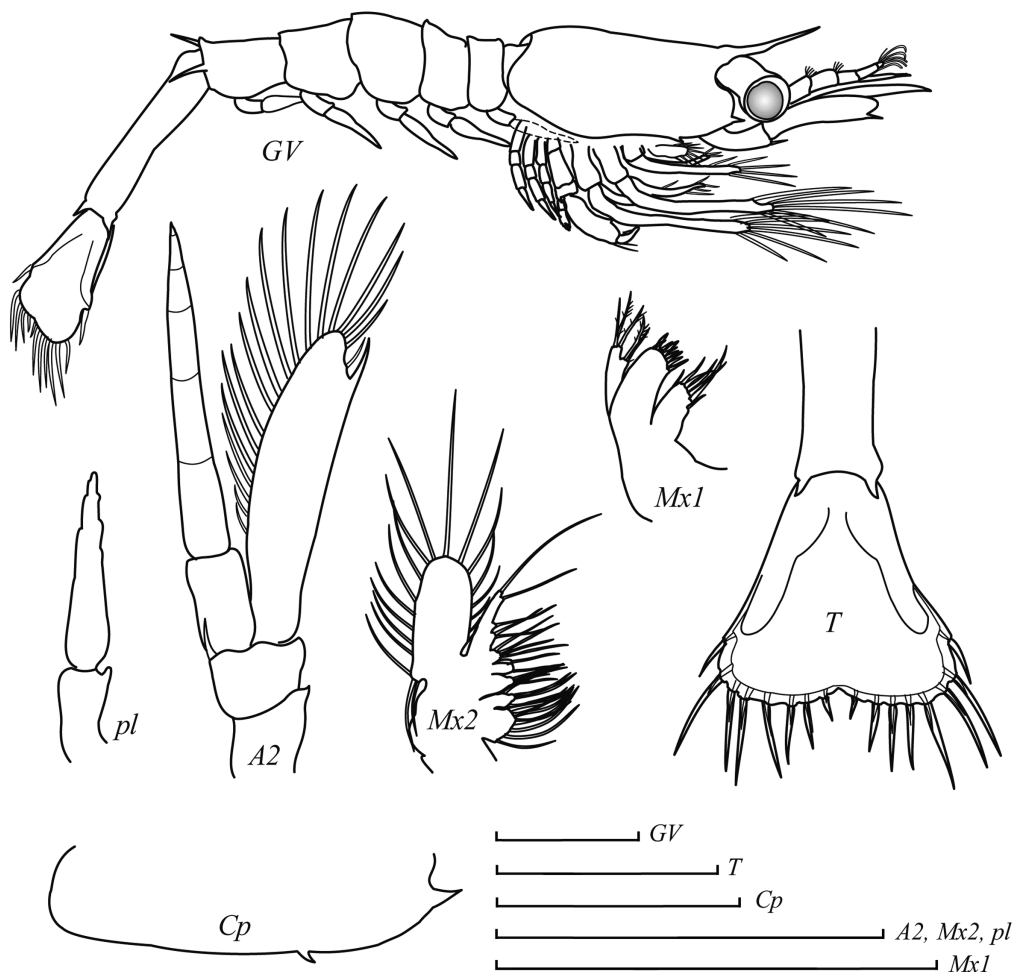


Fig. 8. Morphology of larvae of *Argis ovifer* at II zoeal stage: *GV*, *T*, *pl*, *A2*, *Cp*, *Mx1*, *Mx2* – as in Figs. 2–4. Scale bars 1 mm.

stomian spine present; supraorbital spines absent. Antennule: peduncle 3-segmented; first segment with three small plumose setae on stylocerite, one strong spine at half of segment length, and six small plumose setae terminally; second segment with six small plumose setae distally; third segment with one long and four short plumose setae terminally; outer flagellum with four aesthetascs and one strong setae terminally. Antenna (Fig. 8, *A2*): protopod 2-segmented, with one short spine; endopod longer than antennal scale, 6-segmented; scaphocerite with 18 or 19 plumose setae along inner and posterior margin; outer setae on scaphocerite absent; scaphocerite with outer spine in both antennae. Maxillule (Fig. 8, *Mx1*): endopod with five strong papposerrate setae; basal endite with nine cuspidate setae; coxal endite with seven papposerrate setae. Maxilla: (Fig. 8, *Mx2*): coxal endite bilobed, with 9+4 papposerrate setae; basal endite trilobed, with 4+3+3 papposerrate setae; endopod unsegmented, trilobed, bearing 2+1+1+1 papposerrate setae; scaphognathite with 16 marginal plumose setae. First maxilliped: coxa with epipod and six papposerrate setae; basis with 12 papposerrate setae; endopod 4-segmented, with 4, 1, 2+1, 3 papposerrate setae; exopod unsegmented, with one long plumose seta on lateral margin and four long terminal plumose setae. Second maxilliped: coxa with one papposerrate seta; basis with eight papposerrate setae arranged as 2, 3, 3; endopod 5-segmented, with 3+1, 1, 1+1, 2+1, 5 papposerrate terminal setae; exopod unsegmented, with two subterminal and four long terminal plumose setae. Third maxilliped: coxa unarmed; basis with two papposerrate setae; endopod 5-segmented, with 2, 1, 1+1; 2+2, 5 papposerrate terminal setae; exopod unsegmented, with two subterminal and four terminal plumose setae. Pereiopods uniramous, well developed, segmented; first pereopod with epipod on basis, with terminal segment having well developed subchela, and with propodus and dactylus distinct; second pereopod with well developed che-

la; third, fourth and fifth pereopods uniramous, 7-segmented, without setae. Pleon (Fig. 8, *GV*) with six pleomeres; spicules at posterior margin of pleomeres absent; fifth pleomere with a pair of dorsolateral spines; anal spine small. Pleopods (Fig. 8, *pl*): protopod naked, bearing endopod in form of small tubercle and exopod without setae. Uropods absent. Telson (Fig. 8, *T*) separated from pleon, with rounded corners, small semicircular notch and 8+8 setae (six inner and two outer setae plumose). Next stage (zoea III) with eight pairs of setae, visible through cuticle, on telson.

DISCUSSION

Zoea of individual species of the genus *Argis* differ mainly by the morphology of antennae, abdomen, anteroventral margin of carapace and scaphognathite (Table 2).

Lengths of spine on the scaphocerite of left and right antennae may slightly vary. For example, in *A. lar*, spine of scaphocerite short on left antenna, and almost reaching edge of plate on right one. Some asymmetry is also observed in the number of setae on scaphocerite and scaphognathite.

Zoea I of *A. lar* and *A. ovifer*, as well as *A. dentata* and *A. ochotensis*, were the most similar in morphology. Zoea II of *A. lar* and *A. ovifer* differ from other species by smooth pleomeres, small spine of scaphocerite and only one spine on carapace. They differ among themselves mainly by shape of telson, length of rostrum and spine on scaphocerite.

Zoea I of *A. dentata* and *A. ochotensis* differ from the first two species by serrated margin of pleomeres in abdomen and carapace, and also by the long spine on scaphocerite. Zoea I of *A. crassa* differs from all other species by absence of spine on scaphocerite and characteristic shape of telson. Zoea II of *A. dentata*, *A. ochotensis*, and *A. crassa* are similar to each other by spicules on pleon and carapace, and very long spine on scaphocerite. Zoea II of *A. dentata* differ among them mainly by shape of telson and number of spines on basal endite of maxillule.

Table 2. Main differences of zoeal larvae of *Argis* in Kamchatka and adjacent waters.

Features	<i>A. lar</i>	<i>A. ovifer</i>	<i>A. dentata</i>	<i>A. ochotensis</i>		<i>A. crassa</i>
				Form 1	Form 2	
Zoea I						
TL, mm	6.7	–	7.4–8.1	7.6	7.7–8.3	6.7–7.8
Spine of scaphocerite	short	–	long	moderate	long	absent
Number of setae on basal endite of Mx1	8	–	9	8	9	9
Notch on terminal margin of telson	present	–	present	present	absent	present
Number and position of spines in anterior ventral margin of carapace	1 ahead	–	3	3	4	3–4
Number of setae on scaphognathite	5	–	6–7	5	5	9–10
Zoea II						
TL, mm	6.1–7.7	6.5–6.6	7.3	–	10.6	8.4
Rostrum	reaching anterior edge of eye	slightly protruding in front of eyes	long	–	reaching anterior edge of eye	slightly protruding in front of eyes
Spine of scaphocerite	short	reaching apex of scaphocerite	long	–	slightly protruding beyond apex of scaphocerite	long
Spicules on pleomeres	absent	absent	present	–	present	present
Notch on terminal margin of telson	absent	present	present	–	absent	present

Table 2. Continued.

Features	<i>A. lar</i>	<i>A. ovifer</i>	<i>A. dentata</i>	<i>A. ochotensis</i>		<i>A. crassa</i>
				Form 1	Form 2	
Number and position of spines on anterior ventral margin of carapace	1 ahead	1 at middle	3	–	3–4 tiny	4
Number of spines on basal endite of Mx 1	9	9	10	–	9	9
Number of setae on scaphognathite	13–18	15–17	19	–	18	23–24
Next stage	Zoea or Decapodid	Zoea	Zoea	–	–	Decapodid

Most of larvae were caught above bottom depths no more than 80 m. The greatest depths were observed for *A. ochotensis*, and the smallest for *A. lar* and *A. ovifer*.

Sokolov (2001) found only four species of adult *Argis* in bottom haul above shelf of western Kamchatka (*A. dentata*, *A. ochotensis*, *A. lar* and *A. ovifer*), whereas *A. crassa* was not recorded. In our material, larvae of *A. crassa* were collected both in Avacha Gulf and in the eastern part of Okhotsk Sea. On the contrary, adults of *A. ochotensis* were abundant in eastern part of Okhotsk Sea, and larvae of this species were not found in this region. Perhaps this is due to the fact that adults were sampled off the shelf, but plankton samples were taken over the shelf.

Makarov (1967) described young and older larvae of *A. lar*. Unfortunately, descriptions were incomplete, with many important features missing. Zoea I, described by Makarov (1967) and referred to as *A. lar*, does not correspond to any known zoea I of *Argis*, including ours. In our opinion, that larva does not belong to the genus *Argis* and does not correspond to zoea II described by Makarov (1967). Zoea I, described by Makarov (1967), was too small in size compared to his next described stage. Spine on scaphocerite was not formed; instead, a thin seta was present. Endopod of antenna was already divided into several segments. Telson had only seven pairs of terminal plumose setae. Other features not described.

Early larvae, described by Makarov (1967) as *A. lar*, correspond to our larvae by most features. But in our zoea II, setae on pleopods are absent. Makarov (1967) did not describe the structure of maxillules and maxillae, so it is difficult to understand, which stage of zoea corresponds to described larva.

Above we showed that number of stages of zoea in *A. lar* can be different in individual specimens. This is because in some cases in the second stage, future stage of zoea with eighth pairs of setae can be visible through integument of telson, and sometimes the

decapodid with five pairs of setae on telson can also be visible. In the latter case, third stage was clearly the last in zoea.

Our late larvae were caught one month earlier than Makarov's larvae in the same area. In addition, late larvae of *A. lar* from Makarov's description (1967) correspond to the last zoea by number of characters. As shown in figure from Makarov (1967), it is clear that next stage must be the decapodid.

Therefore, we believe that these larvae are the third, that is the last, zoeal stages of this species. In addition to larvae of *A. lar*, Makarov (1967) described late larvae of the genus *Argis*, which he called *Nectocrangon* sp. (A). According to few features described by him, these larvae are most like to be our *A. dentata*, though spines on scaphocerite in our larvae are longer. Shape of the telson in our larvae is also slightly different. These larvae differ from our *A. ochotensis* in size and larger number of segments of endopod antenna. Thus, larvae described by Makarov (1967) have intermediate features between *A. dentata* and *A. ochotensis*.

Dobkin (1963) believed that in larvae with shortened development (such as Crangonidae), all stages of postembryonic development become obligatory, and there are no optional ones at all. Makarov (1967) noted that the number of late stages varies, and their development is not necessary for each individual. These stages are optional. We observed this phenomenon in *A. lar* in adjacent Kamchatka waters. One specimen of zoea II of *A. ovifer* showed next stage of zoea through cuticle, hence this species can also have three stages of zoea. The same was observed in zoea II of *A. dentata*. In this case, the last and penultimate stages of zoea practically do not differ in morphology.

In addition to larvae of *A. lar*, Makarov (1967) described older larvae of the genus *Argis*, which he named *Nectocrangon* sp. A. These larvae, according to features described, mostly correspond to our *A. ochotensis* I (form 1). Compared to the form 2, they had spicules on pleon, spines on carapace and shorter spine on scaphocerite.

The shape of telson in zoea II of *Nectocrangon* sp. A differs from the shape of telson in our zoea II of *A. ochotensis* (form 2).

Adult representatives of four species of the genus *Argis*, earlier found over the western Kamchatka shelf are: *A. dentata*, *A. ochotensis*, *A. lar* and *A. ovifer*. Mature *A. ochotensis* were first sampled in waters off Kamchatka in 2001 and identified as a new subspecies (Sokolov, 2001: *A. ochotensis kamtschatica*). This is probably due to the fact that this species was previously mixed with *A. ovifer*, because *A. ochotensis* was described as a separate species only in 1997 (Komai, 1997). In that period, researches of shrimps in the north-western part of Russian Pacific waters were not carried out, and data on distribution of species of crangonids in Avacha Gulf were absent. Perhaps that is why this species was previously known only from Okhotsk Sea.

Makarov (1967) also described larvae of another species from the family Crangonidae with short development. The author referred to them as *A. crassa*. These larvae do not correspond to reliable description of early larvae of this species given by Ivanov (1968). In many ways, these larvae belong to some other genera of the same family.

In our material, several zoea I were identified as *A. crassa* based on structure of the scaphocerite, maxilla and telson. We found significant individual variability of this species in the length of rostrum, number of setae on on telson, number of spines of carapace, depth of notch on telson, and number of setae on scaphognathite. Larva described by Makarov (1967) as *A. crassa* may be one of varieties of zoea II of this species, since in our material late larvae were with individual features, given by Makarov (1967). Probably it is rather variable species, though its zoea differs from other species. Variability of number of setae on telson is also known for species from the family Thoridae. For example, specimen of *Spirontocaris phippi* (Kroyer, 1841) can be with eight and nine pairs of setae on telson, whereas in *Lebbeus groenlandicus* (Fabricius, 1775) this number

varies between 19 and 21 (Squires, 1965; Haynes, 1978).

According to Zarenkov (1965), shrimps from the family Crangonidae with shortened development, living in the north-western Pacific, may be species belonging to the genera *Sclerocrangon* Sars, 1883, *Rhynocrangon* Zarenkov, 1965 and *Metacrangon* Zarenkov, 1965 having eggs of about the same size as in *Argis*. Unknown larvae, described by Makarov (1967), have seven pairs of setae on telson, which distinguish them from zoea of *Argis* and *Sclerocrangon*. Description by Makarov (1967) lacks many important features to safely refer larva to any genus.

Larvae described from plankton of Canada by Squires (1965) as *A. dentata* do not correspond to description of larvae reared in laboratory (Ivanov, 1968). Probably, Squires (1965) mistakenly described another species of the genus *Argis*. Two species of the genus *Argis* are found in the northern part of Atlantic Ocean off the coast of Canada: *A. dentata* and *A. levior* (Rathbun, 1902). We assume that Squires (1965) described larvae of *A. levior*, because they differ from all known larvae of the genus *Argis* by number of some features. These larvae are somewhat similar to *A. ovifer* and *A. lar*, but are distinguished from them by larger size, more advanced endopod of antenna, serrated margin of carapace, and number of spines on scaphognathite.

Shorter development is also known in the Antarctic shrimp *Notocrangon antarcticus* (Pfeffer, 1887), whose larvae were described by Makarov (1968a, 1973). Larvae from the genus *Sclerocrangon* were also described by Makarov (1968b). Some stage of larvae from the genera *Argis* and *Sabinea* from Atlantic were described by Squires (1965).

Larvae of several genera of Crangonidae with shortened larval development have different number of stages of zoea. Pelagic larvae are absent in many species of the genus *Sclerocrangon* (Zarenkov, 1965). Larvae of the genus *Sclerocrangon*, as a rule, have only one stage of zoea and develop

on pleopods of female (Makarov, 1973). Larvae of *Notocrangon* as well as of Arctic *Sabinea septemcarinata* (Sabine, 1820) develop with three larval stages (Gurney, 1942; Makarov, 1973).

CONCLUSION

Previously it was thought that larval development of the genus *Argis* may contain two zoeal and one decapodid stages (Squires, 1965; Makarov, 1967; Makarov, 1973).

Analysis of the studied material and comparison with the works of other authors helped to identify main structural features of larvae of the genus *Argis* and their differences from other genera of family Crangonidae, living in the north-western Pacific. Below are these main features:

- 1) pleopods developed in all stages;
- 2) all pereopods uniramous, epipod available on pereopod 1;
- 3) telson terminal margin with eight or nine pairs of setae in all stages of zoea;
- 4) basis of endopod of antenna 2 separated in all stages;
- 5) in stage zoea I, basal endite of maxilla 1 armed with eight or nine spines; in stage zoea II, it with nine or ten spines;
- 6) late larvae with anal spine;
- 7) uropods absent in all zoeal stages.

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