ORIGINAL PAPERS

The Morphology of the Mandibles in Zoea I Larvae of the Burrowing Shrimp Genera *Upogebia* (Gebiidea) and *Nihonotrypaea* (Axiidea)

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Abstract—The mandibles in the first zoeal stage of five species of the burrowing shrimp genera *Upogebia* (infraorder Gebiidea) and *Nihonotrypaea* (infraorder Axiidea) have been examined by scanning electron microscopy. The general shape of the mandibles in *Upogebia* zoeae is similar to that in Anomura larvae; in *Nihonotrypaea*, it is intermediate between the mandibles of anomuran and caridean shrimp larvae. The asymmetry of the mandibles, which is more pronounced in *Nihonotrypaea*, is confirmed. Species-specific features of the structure of the incisor process are found in three *Upogebia* species, while two *Nihonotrypaea* species almost do not differ in the mandible structure in their zoea I larvae. The morphological features of the mandibles indicate differences in the diet of *Upogebia* and *Nihonotrypaea* larvae. Under natural conditions, zoea I of the studied *Nihonotrypaea* species may feed on diatoms, which should be taken into account when rearing these decapod larvae in the laboratory.

Keywords: Decapoda, Gebiidea, Axiidea, mandibles, zoea I, SEM

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INTRODUCTION

The morphology of mouth appendages in arthropods, particularly crustaceans, is of great interest not only for diagnosing species, but also for comparative studies and phylogenetic reconstructions [5, 7, 9, 11, 30, 32, 37, 41, 44]. However, the mandibles, which are the main masticating organs in decapod larvae, have long been neglected. Currently, there are generally accepted standards to describe larval decapod crustaceans, with some of them concerning the text description of appendages [10]. This standardization facilitates comparative analysis of the larval morphology of various species. The mandible in decapod larvae consists of two lobes: lateral, determining the general shape of the mandible, and gnathal, represented by the incisor and molar processes [14, 35]; the palp is absent in the initial stages of development. In light microscopy studies, the small size and complicated three-dimensional configuration of the mandibles impede the observation of certain details. Studies involving scanning electron microscopy (SEM) make it possible to examine the structure of the gnathal lobe in detail and determine the location of small structures on the surface of its processes [6, 17, 18, 34, 35, 47]. A comparison between the mandibles of nine decapod crustacean species from three infraorders (Anomura, Brachyura, and Caridea), based on the SEM data, made it possible to identify some taxon-specific sets of

characters and showed that the main shape, the structure, and the location of the armament of the zoeal mandibles can provide information for phylogenetic reconstructions [17]. Burrowing shrimps of the infraorders Axiidea and Gebiidea were not included in that study.

The systematic position of the group of burrowing shrimps, long considered together under the common name Thalassinidea, has been a subject of discussions among carcinologists for more than 70 years [2]. Gurney (1938, cited by [20]), using larval characteristics, placed Thalassinidea into Macrura Reptantia and differentiated two groups: the first included Axiidae and Callianassidae; the second included Laomediidae and Upogebiidae. Based on the morphology of adult animals, de Saint Laurent [12, 13] first identified the taxa Axiidea and Gebiidea, to which she assigned the rank of sections within the group Thalassinacea of the infraorder Reptantia. In the late 20th century, Thalassinidea were singled out into a separate infraorder [31, 39]. Molecular-genetic studies [8, 42, etc.] showed that Thalassinidea is not a monophyletic taxon; it has been divided into two infraorders, Axiidea and Gebiidea. Currently, most carcinologists adhere to this classification [40].

The history of the study of burrowing shrimps has shown that larval morphology is an important aspect of phylogenetic reconstructions. Earlier, we described
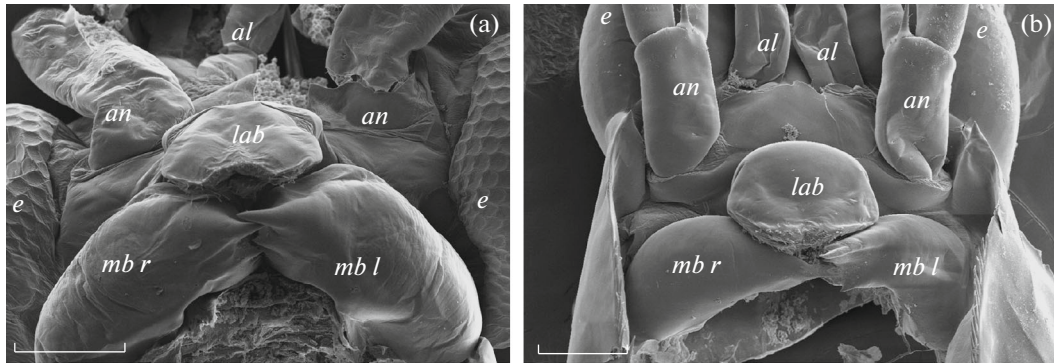
Fig. 1. Dissected zoea I of *Upogebia major* (a) and *Nihonotrypaea japonica* (b), ventral view: *al*, antennula; *an*, antenna; *e*, eye; *lab*, labrum; *mb l*, left mandible; *mb r*, right mandible. Scale bar: 100 μm.

the larval development of several members of axiideans and gebiideans [23−28]. The morphology of their larvae was studied using a light microscope; thus, the description of the zoeal mandibles was reduced to establishing the fact of the presence or absence of the palp bud. To fill this gap, we decided to investigate the structure of the larval mandibles in burrowing shrimps of the genera *Upogebia* and *Nihonotrypaea* using SEM. We believe that the data we obtained will not only extend the list of species-specific traits, but also become additional arguments in discussions on the phylogeny of Gebiidea and Axiidea. Understanding the morphology of the mandibles in larvae can also be useful for identifying the mode of their feeding, as well as for selecting a diet for different species of axiideans and gebiideans that are reared in culture.

MATERIALS AND METHODS

The larvae of the burrowing shrimps were obtained from plankton samples collected in the waters off the Vostok Marine Biological Station, National Scientific Center of Marine Biology, Far Eastern Branch, Russian Academy of Sciences (Vostok Bay, Sea of Japan), shortly before sunrise, in June and August 2016 and 2017. To attract larvae, a torch with metal-halide lamps of 150 W was used. For SEM, larvae were fixed in a series of alcohol solutions (30, 50, and 70% ethanol) according to the previously proposed protocol [33] and stored in 70% ethanol. Zoeae I of the burrowing shrimps *Upogebia major* (De Haan, 1841), *U. issaeffi* (Balls, 1913), *U. yokoyai* Makarov, 1938 (family Upogebiidae), and *Nihonotrypaea japonica* (Ortmann, 1891) and *N. makarovi* Marin, 2013 (family Callianassidae) were identified to the species level based on their morphological characters using a key [1]. The left and right mandibles were dissected separately in 20−25 larvae of each species.

The dissected mandibles were dehydrated in series of ethanol (70, 90%, and two changes of 95% for 10 min each) and ethanol/acetone solutions (3 : 1, 1 : 1, 1 : 3, and two changes of acetone for 10 min each)

and dried in carbon dioxide to the critical point. The dried specimens were mounted on SEM stubs with self-adhesive carbon stickers and sputtered with chromium. Photographs were taken with a Zeiss Sigma 300VP scanning electron microscope at a voltage of 5 kV.

The description of the mandibles is given in accordance with the previously published works [6, 17]. The anterior (external) surface of the gnathal lobe of the mandible is the side facing the labrum; the posterior (inner) surface is the side opposite to the anterior surface. To denote the small cuticular structures on the surface of the mandibles that resemble setae but lack the basal ring at the base, we used the term "denticles" after Garm [16].

RESULTS

The main shape of the mandibles in zoea I of the genus *Upogebia* is a thick curved oval tube (Fig. 1a). The molar and incisor processes are medially oriented. In the distal part, the cross section of the mandible is inversely drop-shaped. The slender incisor process is directed ventrally and armed with a sharp spine; the wide molar process is located dorsally to the incisor. On the anterior, posterior, and upper surfaces of the molar process are solitary, rare, flat denticles with a length of 1−2 μm (Fig. 2g).
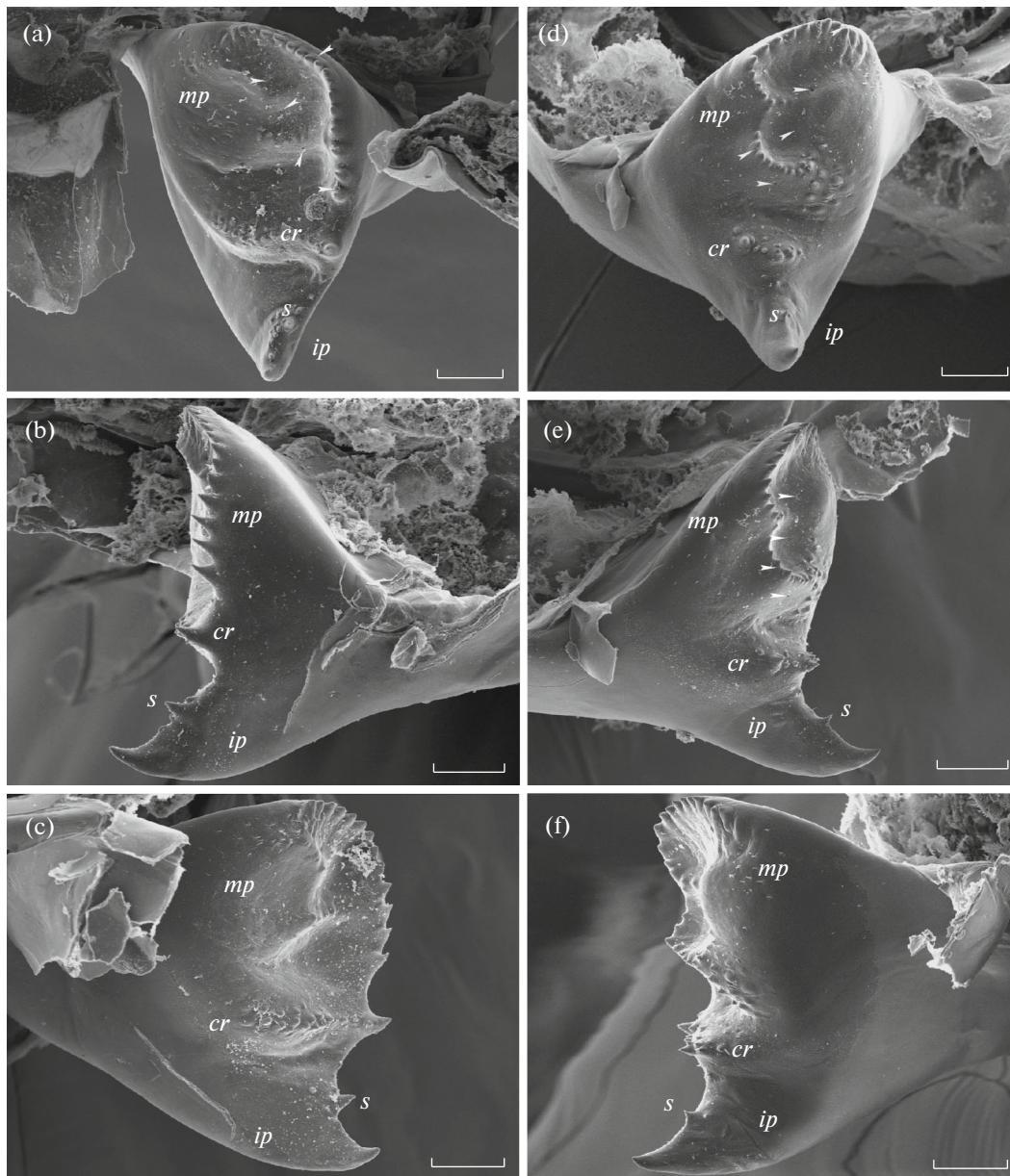
Upogebia major (De Haan, 1841) (Fig. 2)

Right mandible (Figs. 2a−2c). The surface of the incisor facing the molar process is covered with small tubercles and spines, with one of the spines being markedly larger than the others. The lower boundary of the molar process is the cross ridge with numerous small spines and tubercles at the apex and on the dorsal and ventral slopes. The length of the ridge is comparable with the length of the upper edge of the molar process; the height of the ridge increases from the anterior edge to the posterior one. On the posterior edge of the molar process, the ridge ends with a noticeable spine. The upper and posterior edges of the
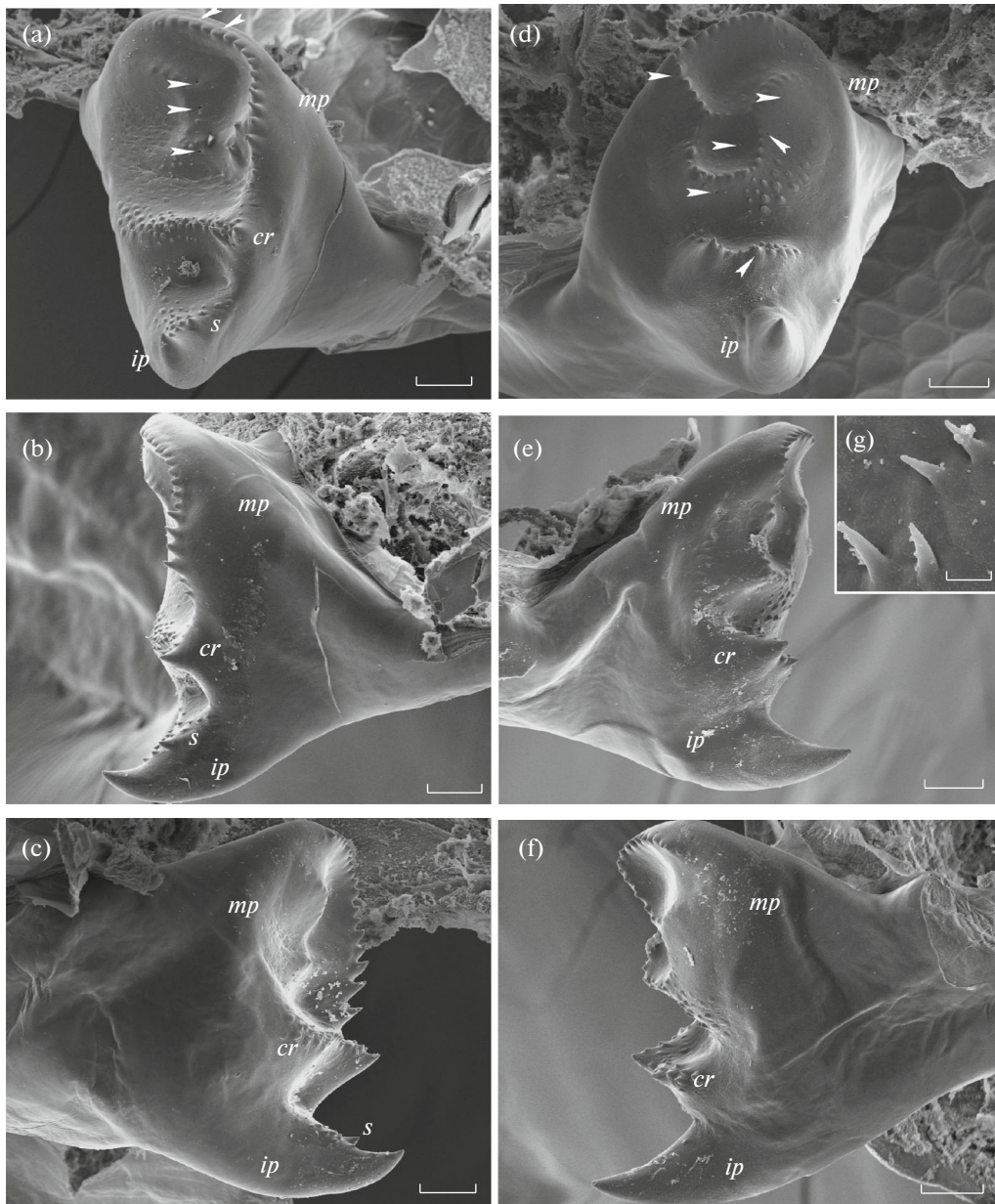
Fig. 2. The morphology of the right (a−c) and left (d−f) mandibles in zoea I of *Upogebia major* and the cuticle outgrowths on the mandible surface (g): (a, d) masticatory surface view; (b, e) posterior view; (c, f) anterior view. Letter designations are as follows: *cr*, cross ridge; *ip*, incisor process; *mp*, molar process; *s*, spine on the incisor process. Pores are indicated by arrows. Scale bars: (a−f) 20 μm and (g) 1 μm.

molar part of the mandible are elevated, armed with 15−19 spines of different sizes, reach the cross ridge, and, forming a continuous barrier with it, bound the masticatory surface on three sides. The relief on the masticatory surface of molar process is formed by gentle folds with small spines and/or tubercles at the apices and by cavities. Small spines and/or tubercles and small folds of the cuticle cover some areas of the masticatory surface. On the masticatory surface, three large pores at the base of the folds and a few small pores are visible. Small pores are found on the outer side of some spines of the upper edge of the mandible.

Left mandible (Figs. 2d−2f). The surface of the incisor is smooth, rarely with one or two small tubercles at the base. The cross ridge is separated from the masticatory surface by a deep cavity; small spines and tubercles are located at its apex and on the dorsal slope. The ridge is much shorter than the length of the upper edge of the molar process; the largest spine of the ridge is located at the posterior edge. The upper and posterior edges of the molar part of the mandible are slightly elevated, armed with 15−17 spines, but do not reach the cross ridge. The relief on the masticatory surface is formed by a low S-shaped fold of the cuticle

Fig. 3. The morphology of the right (a−c) and left (d−f) mandibles in zoea I of *Upogebia yokoyai*: (a, d) masticatory surface view; (b, e) posterior view; (c, f) anterior view. For letter designations, see Fig. 2. Scale bar: 20 μm.

with small spines at the apex and by cavities, as well as by small spines, tubercles, and cuticle folds. Three large pores are located at the base of the S-shaped fold. Small pores are found on the outer side of some spines of the upper edge of the mandible and on the cross ridge.

Upogebia yokoyai Makarov, 1938 (Fig. 3)

<u>Right mandible (Figs. 3a−3c).</u> The surface of the incisor facing the molar process is covered with small tubercles and spines; one of the spines is much larger than the others. The lower boundary of the molar pro-

cess is a cross ridge with small spines and tubercles located mainly on its apex, as well as on the dorsal and ventral slopes. The height of the ridge increases from the anterior edge to the posterior one. On the posterior edge of the molar process, the ridge ends with a noticeable spine. The upper and posterior edges of the molar part of the mandible are elevated, armed with 14−17 spines of various sizes, and reach the cross ridge. The relief on the masticatory surface of the molar process is formed by two short cuticle folds, not connected with each other, bearing rare small tubercles on the surface; two large pores are located at the base of the folds. Separate areas of the masticatory sur-

face are covered with small spines, tubercles, and cuticle folds. Small pores are found on the outer side of some spines of the upper edge of the mandible.

Left mandible (Figs. 3d–3f). Almost in the middle of the incisor, a conspicuous spine is located on the surface facing the molar process; solitary tubercles are visible at the base of the incisor. The upper and posterior edges of the molar part of the mandible are slightly elevated, armed with 12–15 spines, but do not reach the cross ridge. The cross ridge is approximately two times shorter than the dorsal edge of the masticatory surface and is separated from it by a deep cavity. Small spines and tubercles on the surface of the ridge are scarce and located at its apex and on the dorsal slope. The largest spine of the ridge is located at the posterior edge. The relief on the masticatory surface is formed by two low transverse folds of the cuticle, at the base of which two large pores and several small ones are visible. In some areas of the surface, there are small spines, tubercles, and cuticle folds. Pores are found on the outer side of some spines of the dorsal edge of the mandible.

Upogebia issaeffi (Balls, 1913) (Fig. 4)

Right mandible (Figs. 4a–4c). The incisor surface facing the molar process is covered with tubercles and small spines; two spines (at the apex and at the incisor base) are much larger than the others. The upper and posterior edges of the molar part of the mandible are elevated and armed with 17–20 spines of various sizes. Together with the cross ridge, which serves as the lower boundary, they bound the masticatory surface on three sides. At the apex and on the dorsal and ventral slopes of the cross ridge are numerous tubercles and small spines. The height of the ridge increases from the anterior edge to the posterior one. On the posterior edge of the molar process the ridge ends with a noticeable spine. The relief on the masticatory surface of the molar process is formed by two cross folds. Tubercles and small spines on the top of these folds are solitary; three large pores are located at the base. The masticatory surface is covered with small spines, tubercles, and cuticle folds. Small pores are found on the outer side of some spines of the dorsal edge of the masticatory surface.

Left mandible (Figs. 4d–4f). The surface of the incisor is smooth, sometimes with three or five small tubercles or spines at the base. The upper and posterior edges of the molar part of the mandible are slightly elevated, armed with 14–17 spines, but do not reach the cross ridge. The cross ridge of the molar process is short, two times shorter than the dorsal edge of the masticatory surface, and is separated from it by a deep cavity. Tubercles and small spines on its surface are located at the apex and on the dorsal slope. The largest spine of the ridge is located at the posterior edge. The relief on the masticatory surface is formed by an S-shaped cuticle fold with small spines and tubercles on

its top; three large pores are found at the base of the fold. In some areas of the masticatory surface are small spines, tubercles, and cuticle folds. Small pores are located on the outer side of some spines of the dorsal edge of the mandible.

Nihonotrypaea spp.

The main shape of the mandibles in zoea I of the genus *Nihonotrypaea* (Fig. 1b) is a thick curved oval tube. The molar and incisor processes are well separated from each other. In the distal part, the cross section of the mandible is comma shaped. The incisor process is located ventrally, markedly flattened in the antero-dorsal direction. The molar process is wide, located dorsally to the incisor, and oriented medially. On the lateral surfaces of the molar and incisor processes, as well as on the dorsal surface of the molar process, rows of flat denticles 2–6 µm in length are clearly visible (Fig. 5i). We could not find any noticeable differences between early larvae of the examined *Nihonotrypaea* species in the mandible structure. Therefore, we provide photographs of the mandibles of *N. japonica* (Fig. 5) and *N. makarovi* (Fig. 6) and a description common to both species.

Right mandible (Figs. 5a–5c; Figs. 6a–6c). The flattened incisor process is shifted towards the posterior lateral surface of the mandible. The incisor bears two terminal spines. On the outer side, a flat fold of cuticle, usually with one to three denticles on the top, closely adjoins the base of one of the spines. Between the terminal spines of the incisor and the molar process is a single spine and a group of several spines similar in size (Fig. 5g). The bases of the group of spines merge, forming a structure resembling a basal ring. In the lower part of the molar process, the relief on the masticatory surface is formed by small tubercles, as well as by several large and numerous small spines (Figs. 5a, 6a). In the upper part are several ridges with small spines on the surface. On the inner edge, each ridge ends with a spine bearing from two to seven denticles at the distal end (Fig. 5h). The dorsal edge of the molar process is slightly elevated and armed with small pointed spines. On the surface of both processes are pores, the largest of which are located between the ridges of the molar process and on the spines located between the terminal spines of the incisor and the molar.

Left mandible (Figs. 5d–5f; 6d–6f). The flattened incisor process is shifted towards the anterior lateral surface of the mandible. The incisor bears two terminal spines. On the outer side, a flat fold of the cuticle, frequently without denticles, closely adjoins the base of one of the spines. As on the right mandible, between the terminal spines of incisor and the molar spine is a single spine and a group consisting of a large spine and 10–20 small spines lying to one side of it. A large spine located outside the masticatory surface is clearly visible on the inner side, in the molar part of the mandible
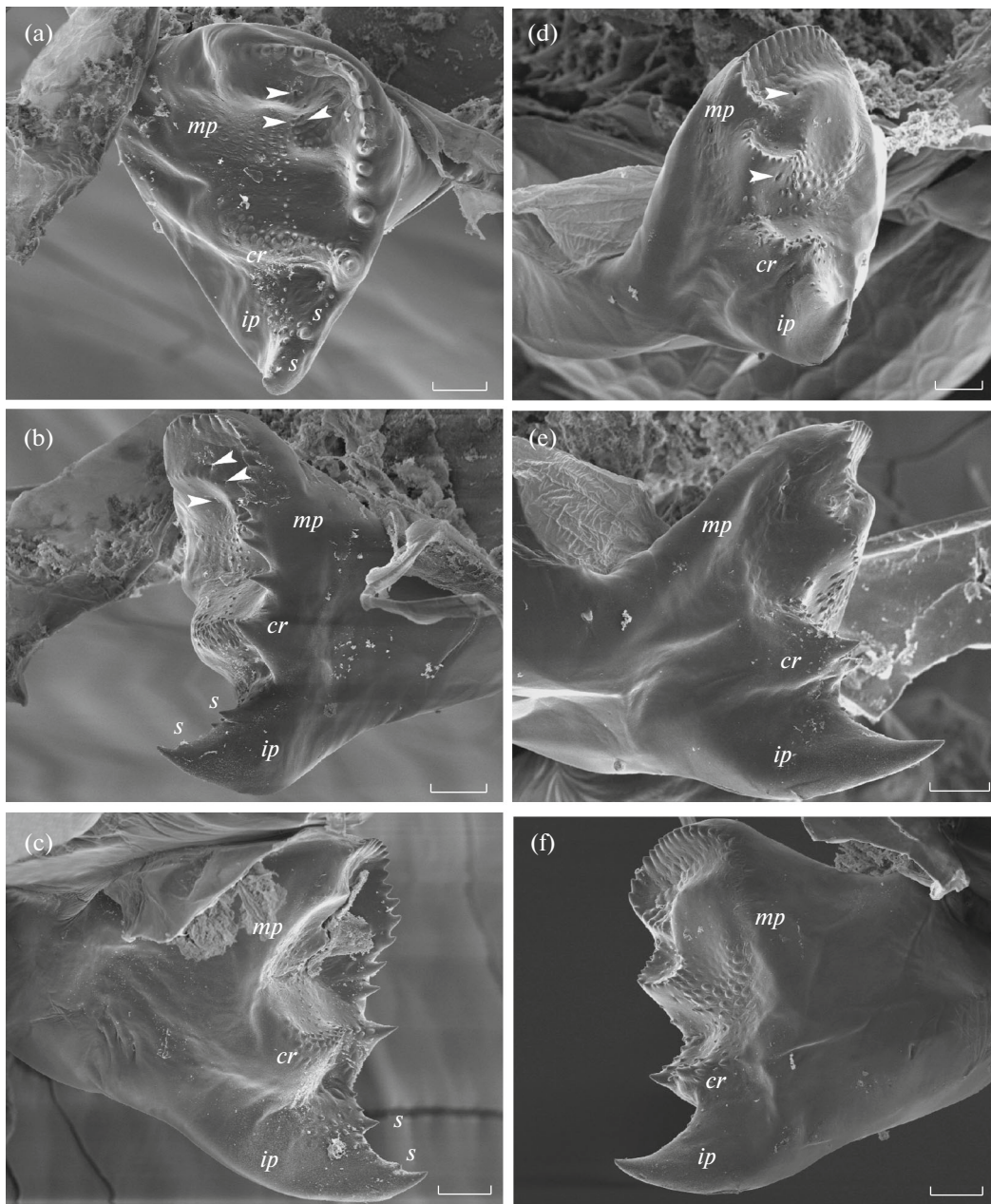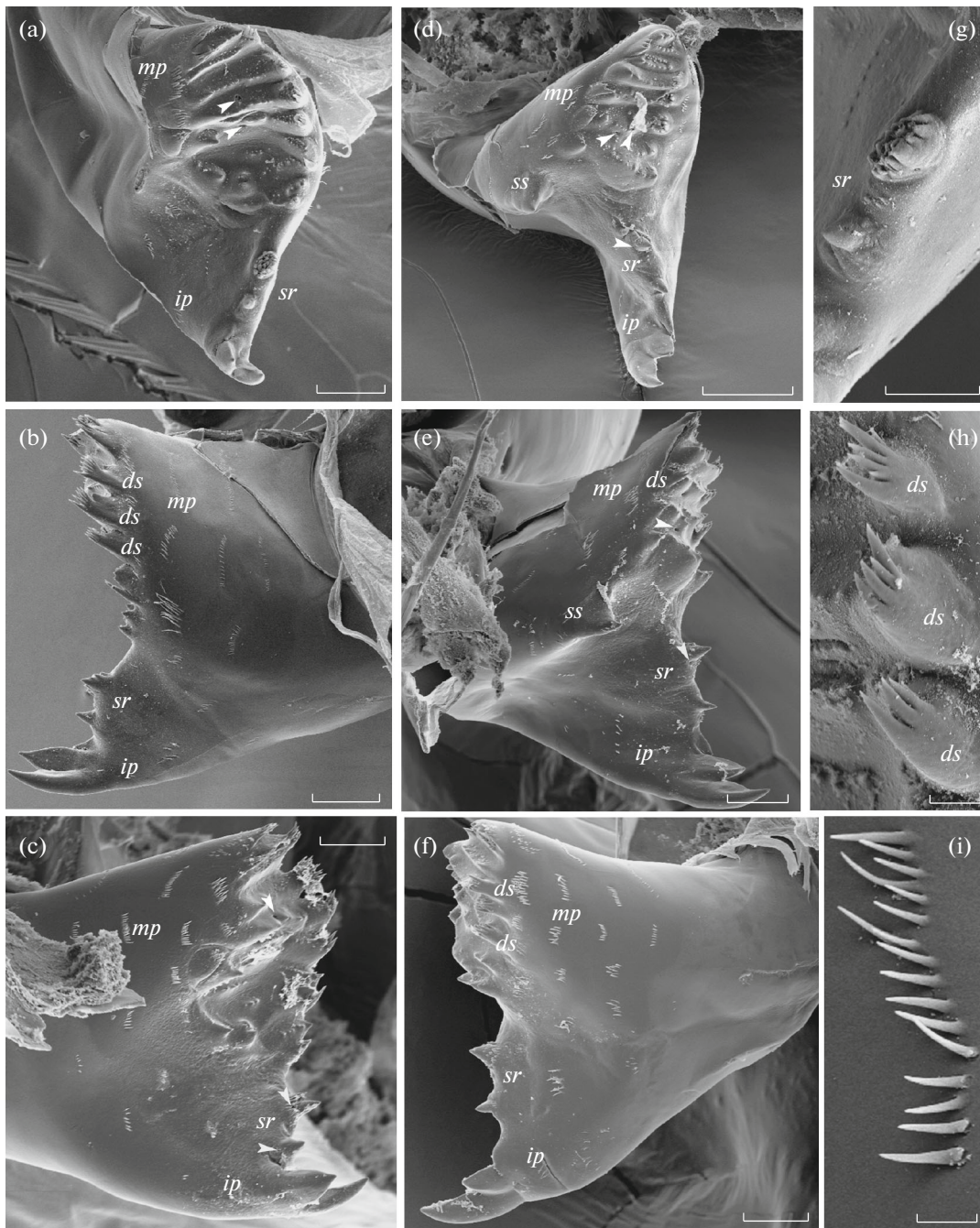
Fig. 4. The morphology of the right (a–c) and left (d–f) mandibles in zoea I of *Upogebia issaeffi*: (a, d) masticatory surface view; (b, e) posterior view; (c, f) anterior view. For letter designations, see Fig. 2. Scale bar: 20 μm.

(Figs. 5d, 5e; 6d, 6e). In the lower part of the molar process, the relief on the masticatory surface is formed by small tubercles, several large spines, and groups of small spines. In the upper part are several ridges with small spines on the surface. Spines with denticles at the distal end may be located both on the inner and outer edges of the ridge (Figs. 5b, 5e; 6b, 6e). The dorsal edge of the molar process is slightly elevated; it may bear several small spines. On the surface of both processes are pores, the largest of which are located between the ridges of the molar process and on the spines located between the terminal spines of incisor and the molar.

Among the examined mandibles of larval *Nihonotrypaea*, we noted some specimens with spines and ridges on the masticatory surface that were heavily worn (Fig. 7). On the masticatory surface of the mandibles in larval *Nihonotrypaea*, there were often food remains, in which fragments of pennate diatoms were found (Fig. 8). On the surface of the mandibles in zoea of *Upogebia*, the traces of wear were almost invisible; food remains were rare and consisted of small loose lumps.
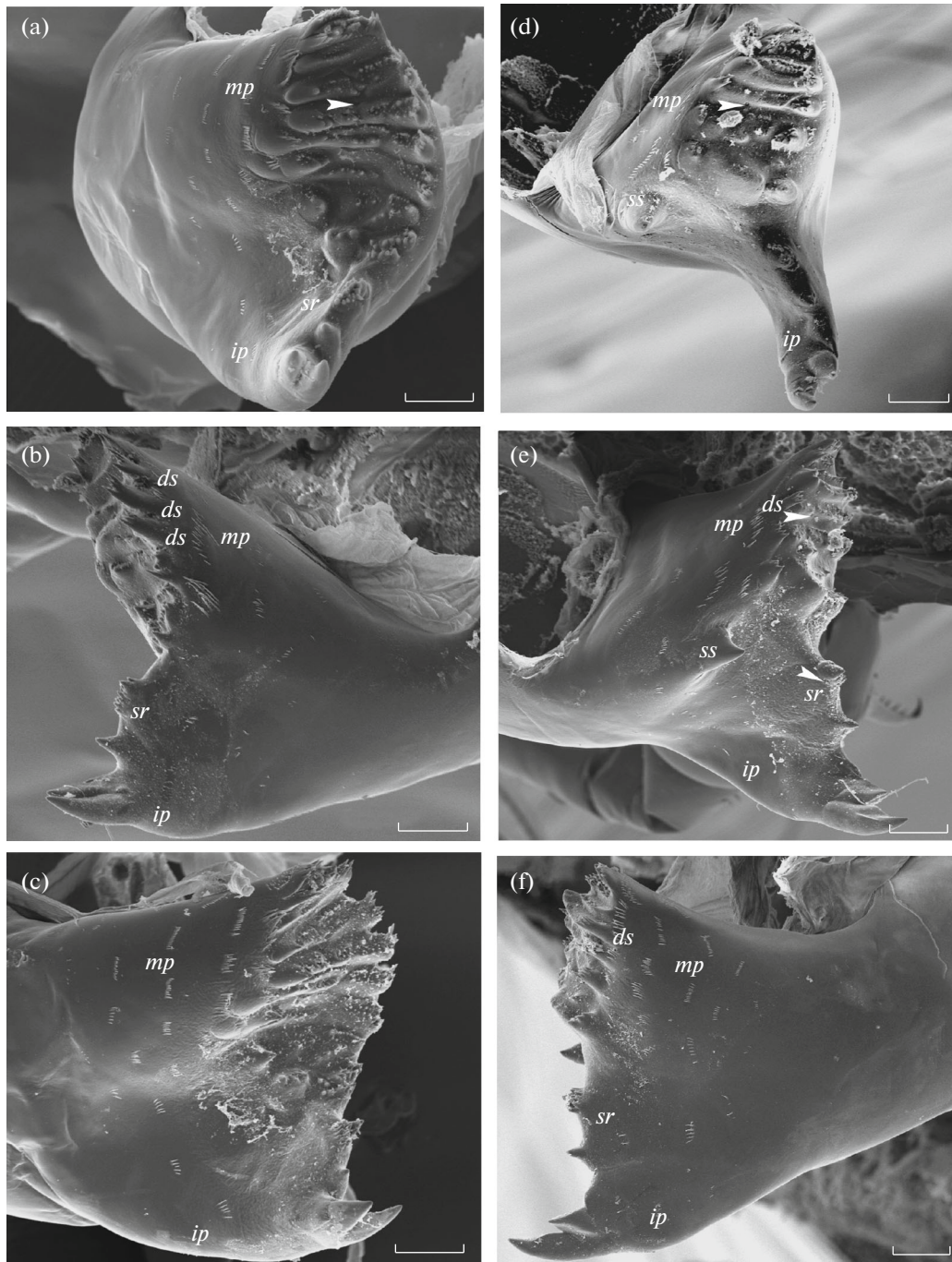
Fig. 5. The morphology of the right (a−c) and left (d−f) mandibles in zoea I of *Nihonotrypaea japonica* and the cuticle outgrowths on the mandible surface (g−i): (a, d) masticatory surface view; (b, e) posterior view; (c, f) anterior view; (g) spines (*sr*) between the incisor and molar processes of the right mandible; (h) spines with denticles at the distal end (*ds*); (i) row of denticles on the mandible surface. Letter designations are as follows: *ss*, separately located spine in the molar part of the left mandible; for other designations, see Fig. 2. Scale bars: (a–f) 20, (g) 10, (h) 4, and (i) 2 μm.

DISCUSSION

The study of mandible morphology in zoea I of five species of burrowing shrimp showed that the asymmetry of the mandibles in *Upogebia* is less pronounced than in *Nihonotrypaea*. In *Upogebia*, the incisor process of the right mandible is usually covered with tubercles and bears one or two spines; the incisor process of the left mandible is smooth or with a single spine, as that in *U. yokoyai*. Due to the asymmetry of the molar processes, the cuticle folds and the cavities between them on the masticatory surfaces of the opposite mandibles fit one into another, providing maximum contact. In zoeae of *Nihonotrypaea makarovi*

Fig. 6. The morphology of the right (a–c) and left (d–f) mandibles in zoea I of *Nihonotrypaea makarovi*: (a, d) masticatory surface view; (b, e) posterior view; (c, f) anterior view. For letter designations, see Fig. 5. Scale bar: 20 μm.

and *N. japonica*, the differences between the right and left mandibles are more pronounced. The flattened incisor process of the right mandible is shifted towards its posterior edge; the incisor process of the left mandible is shifted towards the anterior edge. On the right mandible, spines with denticles at the distal end are present only on the inner edge of the masticatory surface of the molar process; on the left mandible, they are present on the outer and inner edges. *Nihonotrypaea* have a large separately located spine that obviously does not participate in food processing on the inner side of the molar process of the left mandible, outside the masticatory surface. Its role in the functional morphology of the mandibles in early zoea remains to be determined. Despite the fact that the right and left mandibles in *Nihonotrypaea* zoeae differ
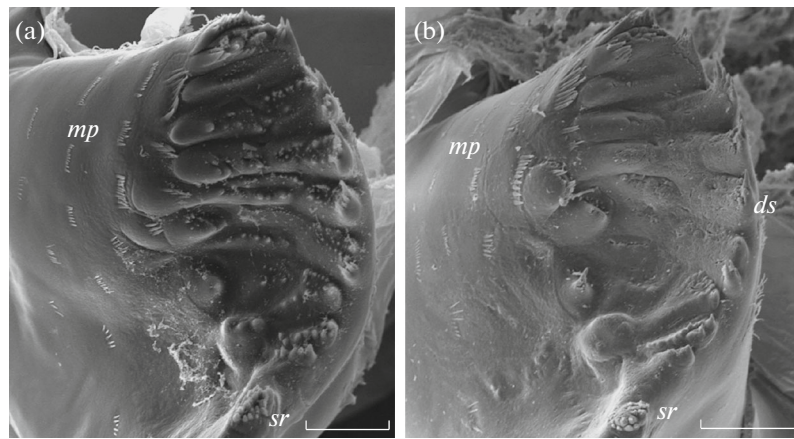
Fig. 7. The molar process of the right mandible in zoea I of *Nihonotrypaea makarovi* with different degrees of wear: (a) ridges and small spines are clearly visible on the masticatory surface of the molar process (*mp*); (b) ridges are worn, and small spines on the masticatory surface are absent. For letter designations, see Fig. 5. Scale bar: 20 μm.
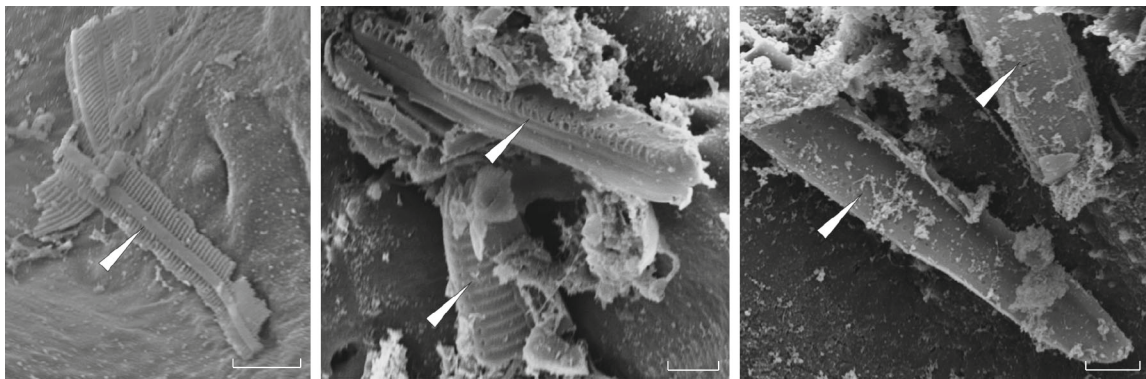
Fig. 8. The remains of pinnate diatoms (indicated by arrows) from the mandible surface in zoea I of *Nihonotrypaea makarovi*. Scale bar: 2 μm.

markedly, their asymmetry does not reach the extreme degree characteristic of larval burrowing shrimps from the families Axianassidae and Laomediidae (infraorder Gebiidea) [19, 43, 46].

Species-specific traits associated with armament of the incisor process of the mandibles were noted in *Upogebia* zoea. In *U. major*, there is one noticeable spine on the incisor surface of the right mandible, while in *U. issaeffi* there are two spines; on the incisor of the left mandible, these spines are absent in both these species. In *U. yokoyai*, the spines are visible on the incisor processes of both mandibles. In zoeae of *N. makarovi* and *N. japonica*, no interspecies differences in the structure of mandibles were found. The SEM study showed that the mandibles in *Upogebia* zoeae are similar in their general shape to the previously described mandibles of Anomura larvae [17]. A certain similarity is also observed in the structure of the molar process: in *Upogebia*, the same as in anomuran larvae, its posterior edge is armed with a row of spines. However, the masticatory surface of the molar

process in *Upogebia* is relatively smooth; spines on the incisor process are small, if present. The general shape of the mandibles in larval *Nihonotrypaea* has a form that is intermediate between those in anomuran and caridean shrimp larvae: the molar process, like that in anomuran larvae, is quite broad, with several ridges on its surface, while the incisor is strongly flattened in the antero-dorsal direction, like that of the mandibles in Caridea larvae [17]. Thus, our data on the morphology of the mandibles in larvae of members of Axiidea and Gebiidea generally correspond to the position of these groups in a phylogenetic tree reconstructed based on the nucleotide sequences of mitochondrial genomes [29], in which Gebiidea is a sister group to Meiura (i.e., Brachyura and Anomura), while Axiidea does not cluster with Gebiidea.

Larval *Nihonotrypaea* have spines that bear two to seven denticles at the distal end on the posterior edge of the molar process of the right mandible, as well as on the anterior and posterior edges of the left mandible (Fig. 5h). An analysis of the data published in the lit-

erature showed that similar cuticular structures ("finger-like projections") are present on the molar process of the adult shrimp *Desmocaris bislineata* Powell, 1977 (Palaemonoidea: Desmocarididae) [5, pp. 10/28, Fig. 6c]. Spines of a similar type ("stout spines with small denticles on the distal end") cover the entire molar process surface of the mandibles in *Tethysbaena argentarii* (Stella, 1951) [41, p. 345, Fig. 29], which is a member of the order Thermosbaenacea within the group Pancarida, a sister group to Peracarida that contains approximately 35 species that inhabit hot vents, caves, ground waters, and, rarely, the marine interstitial zone [3].

Analyzing the homology of *lacinia mobilis* of the mandibles in Peracarida and other crustaceans, Richter et al. [41] noted the presence of a number of spines (a "spine row") between the incisor and molar processes of the mandible in adult members of Peracarida and Syncarida, as well as in Euphausiacea and some larval Decapoda. In various members of crustaceans, this row of spines can be represented by a group of small spines or several denticles on a small outgrowth. Some elements of this row in different taxa seem to be mobile; thus, the assumption was made that they may be *laciniae mobiles* [41]. At the common base of the group of spines, located between the molar process and the terminal spines of the incisor of mandibles in larval *Nihonotrypaea* (Fig. 5g) is a structure that resembles a basal ring, which indicates the possible articulated connection of this formation with the cuticle. The presence of a pore at the base of one of the spines of this group suggests the sensory function of this formation [18].

It was long believed that decapod zoeae are carnivorous, but, as has been shown, their diet consists of diatoms, autotrophic dinoflagellates, and heterotrophic prey, including zooplankton [15]. A study of the functional morphology of the mouthparts and the composition of undigested remains from the guts of zoeae of the burrowing shrimp *Nihonotrypaea harmandi* (Bouvier, 1901) showed that these larvae regularly feed on phytoplankton, in particular diatoms, which causes the surface of their mandibles to wear [45]. During our study, in some mandible specimens from zoeae of *N. makarovi* and *N. japonica* we also noted marked wear of the masticatory surface (Fig. 7) and found fragments of pennate diatoms (Fig. 8). The lifespan of zoea I of *N. japonica* and *N. makarovi* from hatching from an egg to molting into the zoea II stage is 3–4 days [36, our unpublished data]. The wear of the masticatory surface within such a short period of time suggests that the proportion of diatoms in the diet of early zoea of *Nihonotrypaea* is quite large.

A study of the feeding spectrum of planktonic decapod larvae and their selection of food objects, carried out using the methods of flow cytometry and molecular analysis, confirmed that pico- and nano-plankton is an important supplement to the diverse and variable diet of these larvae [15]. As was noted for zoeae of *Upogebia* spp., which were also used in the experiments, a substantial part of their diet is comprised of unarmoured dinoflagellates, ciliates, and nano- and pico-plankton. In zoeae of *U. major*, *U. issaeffi*, and *U. yokoyai* that we studied, food residues on the masticatory surface of mandibles were rare and were small, loose lumps; traces of wear on the mandible surface were barely noticeable. This indirectly confirms that the diet of larvae of these species, as a rule, consists of small food objects that do not have a rigid shell.

A sufficient quantity and quality of food in the early stages is one of the major factors that control the survival and successful development of decapod larvae. A shortage of food at this time can affect their development, survival [4], and settlement [38]. When rearing decapod larvae under laboratory conditions, we, like many other researchers, successfully used nauplii of *Artemia* sp. for the cultivation of *U. issaeffi* and *U. yokoyai*. However, we failed to grow *N. makarovi* to the megalopa stage and the mortality of larvae was already very high at the initial stages of development. Other researchers who study the larval development of callianassids have also encountered this problem [21, 22]. Previously, the suggestion was made that *Artemia* sp. nauplii are not the optimum diet for larvae of the burrowing shrimp *N. harmandi* [45]. Based on the data on the mandible morphology in zoeae of *Upogebia* and *Nihonotrypaea* that we obtained, it can be assumed that *Upogebia* zoeae in a laboratory culture can compensate for a shortage of food by consuming bacteria and other pico-plankton that are available in the water, but for *Nihonotrypaea* larvae, a lack of diatoms, which apparently constitute the basic part of their diet, can be a cause of their mortality.

Thus, the SEM study of early larvae of five burrowing shrimp species has shown that the degree of asymmetry of the mandibles in *Nihonotrypaea* zoea is greater than that in *Upogebia* zoea; the species-specific traits of the mandible structure in *Upogebia* zoea have been revealed. A similarity in the general shape of the mandibles between zoeae of *Upogebia* and Anomura is observed. The shape of the mandibles in *Nihonotrypaea* zoea is intermediate between those in Anomura and Caridea. In *Nihonotrypaea* zoea, spines with denticles at the distal end are found on the molar process of the mandibles. Similar spines occur in adult caridean shrimps of the family Desmocarididae and members of Pancarida. The differences in the mandible morphology between *Upogebia* and *Nihonotrypaea* indicate their different diets, which should be taken into account when cultivating larvae.

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