

A living fossil: modern and paleontological records of spiny sand crab *Lophomastix japonica* (Duruflé, 1889) (Anomura: Blepharipodidae) from the Russian coasts of the Sea of Japan and fossil *Lophomastix* sp. from the western coast of Kamchatka (Sea of Okhotsk)

Живое ископаемое: современные и палеонтологические данные о песчаном крабе *Lophomastix japonica* (Duruflé, 1889) (Аномура: Влефариподидеае) с российского побережья Японского моря и ископаемый *Lophomastix* sp. с западного побережья Камчатки (Охотское море)

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КЛЮЧЕВЫЕ СЛОВА: Разнообразие, Decapoda, Anomura, Blepharipodidae, Японское море, ископаемые, миоцен, Охотское море, Россия.

ABSTRACT. New records of the spiny sand crab *Lophomastix japonica* (Duruflé, 1889) (Decapoda: Blepharipodidae) from the Russian coasts of the Sea of Japan are reported, based on collected exuvii and a living specimen. Additionally, the fossil remains of a carapace of *Lophomastix* sp., morphologically similar to modern *L. japonica*, was found in Upper Miocene formations of the western coast of Kamchatka (Sea of Okhotsk), which confirms that the genus was previously distributed much further north. The article presents barcoding data (fragment of COI mtDNA) for *L. japonica* for the first time, which will allow for a more detailed study of the phylogeography of this species in the future.

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РЕЗЮМЕ. В статье представлены новые современные данные о песчаном крабе *Lophomastix japonica* (Duruflé, 1889) (Decapoda: Blepharipodidae) с российского побережья Японского моря, осно-

ванные на собранных экзuviaх и одном живом экземпляре. Более того, ископаемые остатки панциря *Lophomastix* sp., морфологически сходного с современным *L. japonica*, были найдены в верхнемiocеновых отложениях западного побережья Камчатки (Охотское море), что подтверждает, что род был распространен гораздо севернее, в Охотском море. В статье также впервые для *L. japonica* представлены данные штрихкодирования (фрагмент COI мтДНК), что позволит более подробно изучить филогеографию этого вида в будущем.

Introduction

Many groups of marine organisms that lead a cryptic lifestyle, for example, burrowing into a soft substratum or living among rocks/boulders, quite often fall out of hydrobiological studies, as well as biodiversity reviews, due to the difficulty of their collection. Such animals are usually called cryptobenthic. Usually these are small animals due to their lifestyle, but some cryptobenthic animals can reach a large biomass. The estimated biomass of the burrowing ghost shrimp *Nihonotrupaea japonica* (Ortmann, 1891) (Axiidea: Callinassidae) at the mouth of the Volchanka River in the Vostok Bay (Sea of Japan) reaches almost 200 ind/m², and a dry biomass of 120 g/m², which corresponds to



Fig. 1. Map of the modern distribution of the *Lophomastix japonica* (Duruflé, 1889) and the fossil record of carapace *Lophomastix* sp.
 Рис. 1. Карта современного распространения *Lophomastix japonica* (Duruflé, 1889) и палеонтологическая находка карапакса *Lophomastix* sp.

the maximum values of biomass for any other group of benthic animals in this area [Selin, 2015a], or approximately 33% of the average total biomass of the entire macrozoobenthos in some biotopes [Selin, 2013]. At the same time, mature individuals of burrowing mud shrimp *Upogebia major* (De Haan, 1841) (Gebiidea: Upogebiidae) can reach a body length of 118 mm in Peter the Great Bay [Selin, 2017]. Quite often these large and numerous organisms obviously affecting the ecosystem and nearby communities [Hong, 2013]. Accordingly, the search for and study of such animals is extremely important for ecological research of any level of complexity. In the Russian seas, one such cryptobenthic group, which has been well described only recently, are burrowing ghost shrimp (*Nihonotrypaea* spp., *Gilvossius* spp. and *Necallianassa truncata* (Giard et Bonnier, 1890)) and mud shrimps (*Upogebia* spp.), which are numerous in warm regions, such as the Black Sea [Marin, 2021] and the Sea of Japan [Marin, 2010, 2013b; Marin *et al.*, 2013; Selin, 2013, 2014, 2015a–c, 2017; Marin, Kornienko, 2014; Marin, Antokhina, 2020]. However, other burrowing crustaceans have not been well studied.

One such cryptobenthic species, and in many ways a somewhat mysterious one, because only a few people have seen it alive, is the spiny sand crab *Lophomastix japonica* (Duruflé, 1889) (Decapoda: Anomura: Ble-

pharipodidae), which is not a true crab, but actually an anomuran that lives in the sandy biotopes of the Sea of Japan, the Pacific coasts of the Japanese Islands, the coast of South and North Korea and even the northern part of the Yellow Sea. Records of this species in the Russian part of the Sea of Japan as well as the specimens in the museum collections are quite rare, so any information on *L. japonica* is extremely valuable. Representatives of the genus *Lophomastix*, as well as the related genus *Blepharipoda* Randall, 1840, are the sister taxa to all other known Anomura [Bracken-Grissom *et al.*, 2013]. Their remains, very similar to modern species, were found in the deposits of the Eocene and Miocene of the east coast of the USA (Washington) [Schweitzer, Boyko, 2000; Nyborg, Vega, 2008]. According to such records, it is possible to mark speciation during phylogenetic reconstruction of the family and the related taxa. In Russia, the fossil finds of these crabs have not yet been described.

In the course of intensive study of biodiversity of decapod crustaceans of Peter the Great Bay of the Sea of Japan since 2015, numerous exuvii of *L. japonica* were found in different localities of the mainland coastline. Finally, a live specimen was caught in the Gornostai (Shitovaya) Bay of the Ussuri Bay (43°06'45.1"N 132°00'53.7"E) (part of Peter the Great Bay) of the Sea of Japan and is described in detail here. Moreover, in the

Zoological Museum of Moscow State University (ZMMU) collection we found a fossil anterior part of the carapace of a *Lophomastix* sp. from Miocene deposits of the western coast of Kamchatka (Sea of Okhotsk).

Material and methods

The single live specimen of *L. japonica* and the exuvii were collected using SCUBA diving equipment in the sublittoral zone at a depth of 5–10 meters as well as being found in the littoral zone along the Russian coasts of the Sea of Japan from 2016 to 2021.

Total genomic DNA was extracted from muscle tissue using the innuPREP DNA Micro Kit (AnalytikJena, Germany). The COI mtDNA gene marker was amplified using the universal primers LCO1490 (5'-GGTCAACAAATCAT-AAAGATATTGG-3') and HC02198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer *et al.*, 1994). Polymerase chain reaction (PCR) were performed on an amplifier T100 (Bio-Rad, USA) under the following conditions: initial denaturation at 96 °C for 1.5 min followed by 42 cycles of 95 °C for 2 min, 49 °C for 35 sec., and 72 °C for 1.5 min. Each chain reaction was concluded by an extension step, set at 72 °C for 7 min. The volume of 10 µL of reaction mixture contained 1 µL of total DNA, 2 µL of 5xPCR mix (Dialat, Russia), 1 µL of each primer and 5 µL of H₂O. The amplification products were separated using gel electrophoresis of nucleic acids on a 1.5% agarose gel in 1xTBE, and then stained and visualized with 0.003% EtBr using imaging UV software. PCR products were then sequenced using Genetic Analyzer ABI 3500 (Applied Biosystems, USA) and BigDye 3.1 (Applied Biosystems, USA) with forward and reverse primers. The obtained sequences are deposited in the GenBank (NCBI) database for further molecular genetic studies.

The collected specimens are deposited in Zoological Museum of Moscow State University, (ZMMU) and the Orlov Paleontological Museum of the Paleontological Institute of Russian Academy of Sciences, Moscow, Russia (PIN). Carapace length (CL), as measured from the midpoint of the anterior margin (including rostrum) to the midpoint of the posterior concavity, is used as standard measurement. Only primary synonyms are given.

Systematic account

Order Decapoda Latreille, 1802
 Infraorder Anomura MacLeay, 1838
 Superfamily Hippoidea Latreille, 1825
 Family Blepharipodidae Boyko, 2002
 Genus *Lophomastix* Benedict, 1904

Lophomastix japonica (Duruflé, 1889)
 Figs 2, 3a.

Blepharopoda japonica Duruflé, 1889: 93–95 [type locality — Hakodate, Japan].

Blepharopoda fauriana Bouvier, 1898a: 566–567 [type locality — Hakodate, Japan].

Lophomastix brevirostris Urita, 1934: 149–154, figs. 1, 2 [type locality — West Sakhalin, Russia].

Lophomastix tchangsii Yü, 1935: 51 [type locality — Chefoo, China].

Lophomastix japonica: Shen, 1949: 162–165, pls. 16, 17.

MATERIAL EXAMINED. Northern Pacific, Russia, Sea of Japan, Peter the Great Bay: 1 male (CL 27 mm), ZMMU Ma-3574, Vladivostok, Ussuri Bay, Gornostay (Shitovaya) Bay, 43°06'45.1"N 132°00'53.7"E, burrowing in fine sand bottom, depth 7 m, coll. K. Dudka, Sept. 2021; 1 exuvium (LEMMI), Srednaya Bay, 42°38'56.1"N 131°12'41.6"E, on fine sand bottom, depth 5–7 m, coll. I. Marin, June 2016; 1 exuvium (CL 24 mm) (LEMMI), Gorshkova Bay, 42°40'24.5"N 131°13'30.8"E, on fine sand bottom, depth 8 m, coll. I. Marin, June 2016; 2 exuvia (CL 22, 24 mm) (LEMMI), Bojsman Bay, 42°47'03.1"N 131°18'18.6"E, on littoral, coll. E.A. Dunaev, July 2015; 1 dead damaged specimen (CL 21 mm) (LEMMI) — Bojsman Bay, 42°47'03.1"N 131°18'18.6"E, on littoral, coll. E.A. Dunaev, September 2018.

DIAGNOSIS (after Boyko, 2002): Outer-ocular spines triangular; rostrum not produced anteriorly as far as anterolateral spines; branchiostegite weakly spinose. Dorsal flagellum of antennule with 39–54 articles, ventral flagellum with 10–13 articles. Antennal flagellum with 8–12 articles. Pereopod II dactylus with tapered rounded heel. Pereopod III dactylus with bifurcated heel. Pereopod IV dactylus with produced acute heel.

The collected specimens completely correspond to the re-description of the species presented by Boyko [2002]. To compare individual populations and perform phylogeographic analyses, it is important to use barcoding (analysis of COI mtDNA gene marker variability).

COLORATION. From uniformly creamy to brown with light brown highlights along the edges and grooves of the carapace and appendages. The setae and bristles are dark (Fig. 2; [Marin, 2013a]).

BODY SIZE. The largest studied specimen is CL. 27 mm.

GENBANK ACCESSION NUMBERS. OM305089, OM305090.

DISTRIBUTION. The species is known from the Russia of the Sea of Japan (Posyeta Bay; Patrocl Bay; Peter the Great Bay; Sakhalin: Aniva Bay (Korsakov)) [Makarov, 1938; Marin, 2013a; Petryashev, 2005; Urita, 1934], Japan (Hokkaido: off Oshoro; Hokodate; Honsu: Aomori) [Duruflé, 1889; Bouvier, 1898a, b; Miyake, 1957; Konishi, 1987], Korea (Hamgyong-bukto: Kankyo-hokudo; Hamgyong-namdo: Kankyo-nandô; Kangwon-do: Kôgen-dô; Jeju island) [Kamita 1957; Oh, 1996, 1999] and China (Yellow Sea; Chefoo; Rizhao) [Yü, 1935; Qiang *et al.*, 2016; Ding *et al.*, 2016].

Lophomastix sp. Fig. 3b.

MATERIAL EXAMINED. Fossil record: 1 extant (fossil) anterior part of carapace (approximate CL. 35 mm), PIN 5856 — Upper Miocene, western coast of Kamchatka (Sea of Okhotsk), Kovran village, 57°12'12.1"N 156°53'08.8"E, Voy Cape, exact locality unknown, November 1987, coll. N.N. Kalandadze (PI RAS).

REMARKS. The discovered remains of the carapace are severely damaged, the most anterior and all the posterior regions are lost (see Fig. 3b). The carapace is probably slightly longer than wide; mesogastric region smooth laterally with medial triangle of jagged, setose, corneous grooves; CG4 with two sinuous, crenulate lateral elements each approximately one-third carapace width; hepatic region with scattered, transverse, corneous lines; metagastric region strongly carinate, covered in short corneous grooves; CG5 absent; CG6 sinuous and crenulate, oblique lateral elements separate from posteromedial and deeply indented concave element; CG7 absent; cardiac region smooth laterally, with triangle of setose punctae medially; CG8 faint, paralleling medial portion of CG6 but extending more laterally.

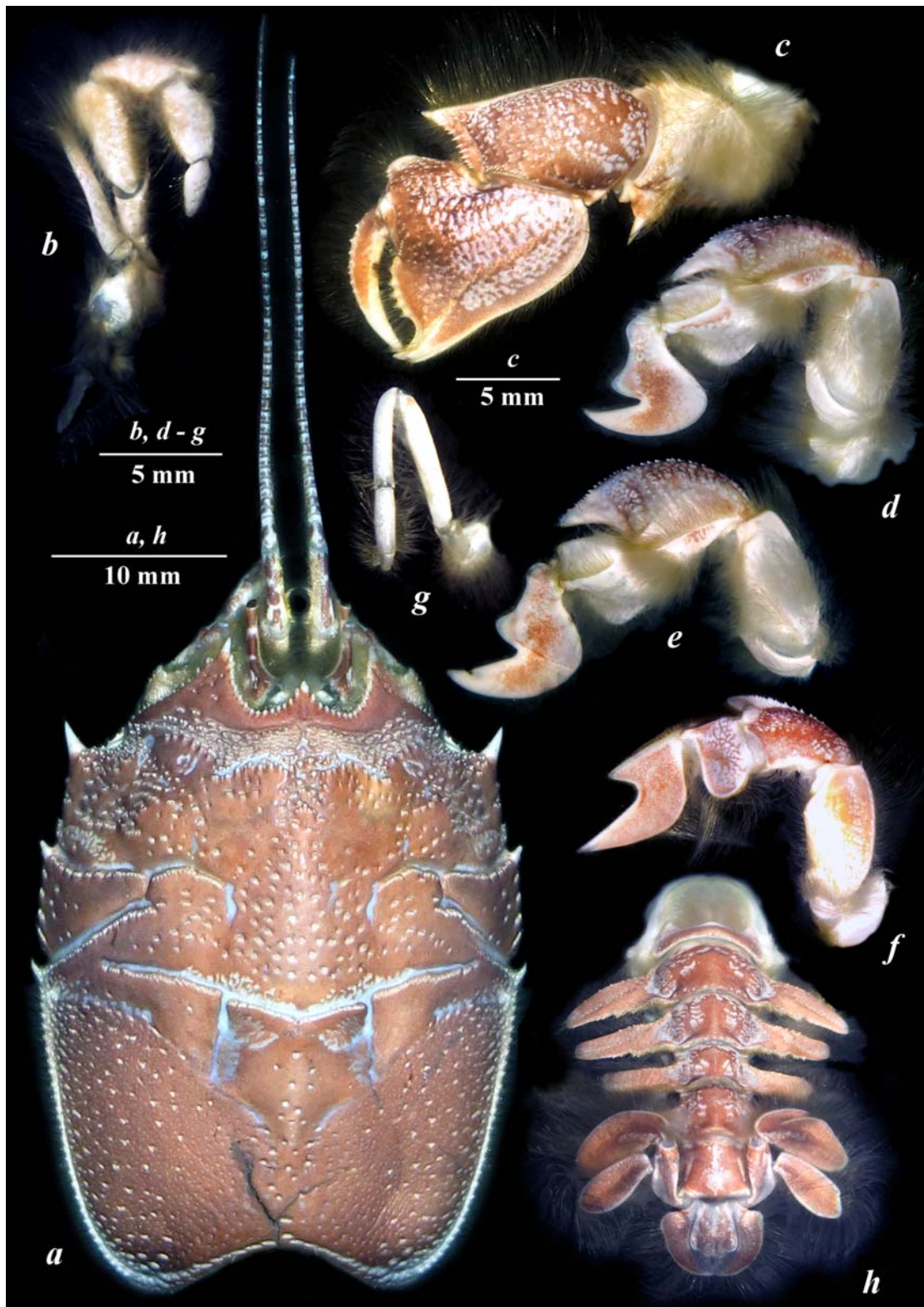


Fig. 2. Morphology of *Lophomastix japonica* (Durufle, 1889), ♂ (CL 27 mm), ZMMU Ma-3574: *a* — carapace; *b* — maxilliped III; *c* — pereiopod I (gnathopod); *d* — pereiopod II; *e* — pereiopod III; *f* — pereiopod IV; *g* — pereiopod V; *h* — abdominal somites, uropods and telson.

Рис. 2. Морфология *Lophomastix japonica* (Durufle, 1889), ♂ (CL 27 мм), ZMMU Ma-3574: *a* — карапакс; *b* — максиллипеда III; *c* — переопода I (гнатопода); *d* — переопода II; *e* — переопода III; *f* — переопода IV; *g* — переопода V; *h* — брюшные сомиты, уropоды и тельсон.

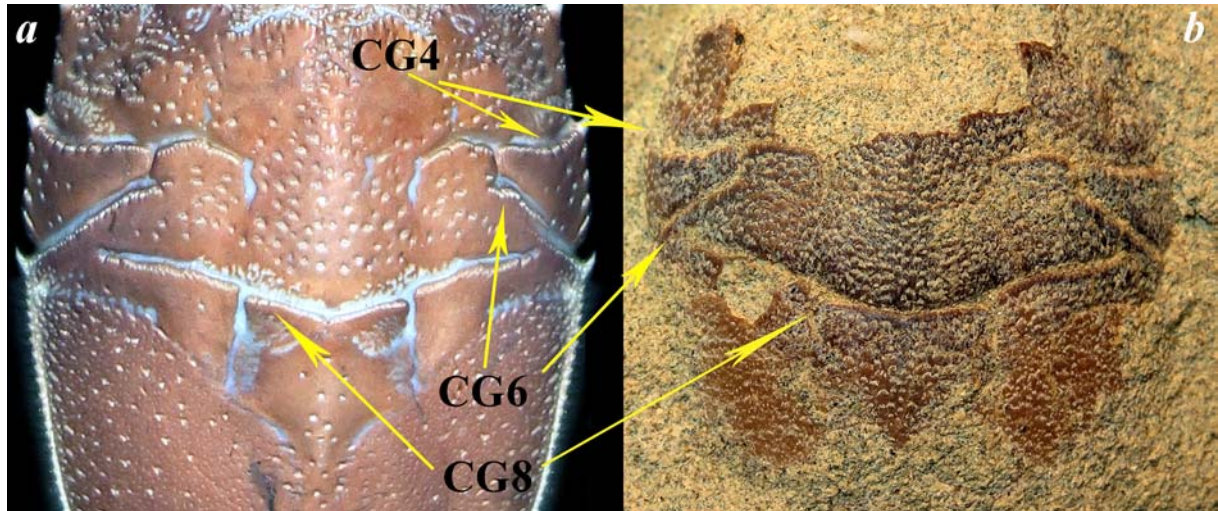


Fig. 3. The comparison of carapaces: *a* — modern *Lophomastix japonica* (Durufié, 1889), ♂ (CL 27 mm), ZMMU Ma-3574; *b* — fossil carapace of *Lophomastix* sp., sex unknown (CL 35 mm), PIN 5856, from the western coast of Kamchatka.

Рис. 3. Сравнение панцирей: *a* — современный *Lophomastix japonica* (Durufié, 1889), ♂ (CL 27 мм), ZMMU Ma-3574; *b* — ископаемый карапакс *Lophomastix* sp., пол неизвестен (CL 35 мм), PIN 5856, с западного побережья Камчатки.

The carapace of *Lophomastix* sp. is very similar to *L. japonica*, but due to severe damage, accurate species identification and comparison is not possible.

Discussion

According to molecular genetic studies, the family Blepharipodidae is basal to all sand crabs of the superfamily Hippoidea, including families Albuneidae and Hippidae [Ahyong *et al.*, 2009; Schnabel *et al.*, 2011; Bracken-Grissom *et al.*, 2013]. The present-day diversity of the family Blepharipodidae includes only 6 extant species: 4 species of the genus *Blepharipoda* Randall, 1840 and 2 species of *Lophomastix* (*L. japonica* from the northwestern Pacific Ocean and *L. diomedea* Benedict, 1904 from the northeastern Pacific Ocean (Californian coast)) [Boyko, 2000, 2020]. Several more fossil forms have been described: *L. antiqua* Schweitzer et Boyko, 2000 from late Eocene marine rocks [Schweitzer, Boyko, 2000], and *L. boykoi* Nyborg et Vega, 2008, *L. kellyi* Nyborg et Vega, 2008 and *L. altoonaensis* Nyborg et Vega, 2008 from the upper Eocene – upper Oligocene Lincoln Creek Formation and the lower to middle Miocene Astoria formation of Washington State, USA [Nyborg, Vega, 2008], which means that northeastern Pacific species were previously common in more northern latitudes. Our record from the Upper Miocene formations from western Kamchatka also confirms that northwestern species also occurred further north at approximately the same time.

The discovery of a sand crab of the genus *Lophomastix* in the Eocene-Miocene deposits of western Kamchatka, although this is the first record, is not surprising. The deposits of the Miocene climatic optimum of western Kamchatka are dominated by thermophilic species (bivalve mollusks of the genera *Glycymeris* da

Costa, 1778, *Ostrea* Linnaeus 1758, *Pecten* O.F. Müller, 1776, *Brachidontes* Swainson, 1840, *Pteria* Scopoli, 1777 (Mollusca: Bivalvia), gastropods of the genera *Cancellaria* Lamarck, 1799, *Miltha* Lamarcký, 1798y, *Gibbula* Risso, 1826, *Siphonalia* A. Adams, 1863, *Cornus* Linnaeus, 1758, *Ficopsis* Conrad, 1866†, *Parasyrinx* Finlay, 1924† (Mollusca: Gastropoda) as well as burrowing shrimp of the genus *Callinassa* Leach, 1814 (Crustacea: Decapoda) characteristic of modern areas of warm shallow waters [Sinelnikova, 1975; Devjatkin, 1991]. From this region, a fossil whale was described, which apparently fed on warm and rich shallow water cryptobenthic organisms, similar to the modern Gray Whale *Eschrichtius robustus* Lilljeborg, 1861 [Tarasenko *et al.*, 2018]. It is believed that in the Eocene, the North Asian shelf basins had stable connections with the North American ones, which provided a certain exchange of species complexes between these regions. Later, with the steady change of seasons and the onset of climate cooling, modern animal species began to form and animals less adapted to the changed conditions began to go extinct [Devjatkin, 1991].

Unfortunately, the ecology of representatives of Blepharipodidae, and especially crabs of the genus *Lophomastix*, remains practically unexplored. It is known, for example, that *L. diomedea* is a significant component of the diet of the shark *Heterodontus francisci* (Girard, 1855) in Baja California [Cortés-Fuentes *et al.*, 2020]. At some moments (apparently during molting), the bottom of many of the shallow sandy bays of southern Primorye (Posjeta Bay and southern part of Peter the Great Bay) is literally covered with the exuvia of these crabs (pers. observ.), which indicates their high concentration and very high biomass in certain biotopes. It is very likely that in the Sea of Japan, burrowing crabs *L. japonica*, as well as burrowing callianassid shrimp

[see Selin, 2013, 2015, 2015a–c, 2017], play an important and noticeable ecological role as a component of macrozoobenthos.

Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

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