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Thoridae (Crustacea: Decapoda) can penetrate the Abyss: a new species of *Lebbeus* from the Sea of Okhotsk, representing the deepest record of the family

Ivan MARIN

A.N. Severtzov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia.

Email: coralliodecapoda@mail.ru, vanomarin@yahoo.com

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Abstract. *Lebbeus sokhobio* sp. nov. is described from abyssal depths (3303−3366 m) in the Kuril Basin of the Sea of Okhotsk. The related congeners are deep-water dwellers with a very distant distribution and very similar morphology. The new species is separated by minor morphological features, such as the armature of the rostrum and telson, meral spinulation of ambulatory pereiopods and the shape of the pleonal pleurae. This species is the deepest dwelling representative of the genus *Lebbeus* and the family Thoridae. A list of records of caridean shrimps recorded from abyssal depths below 3000 m is given.

Keywords. Diversity, Caridea, barcoding, SokhoBio 2015, NW Pacific.

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Introduction

The fauna of benthic caridean shrimps (Crustacea: Decapoda: Caridea) living at depths of more than 3000 m is poorly known due to the technical difficulties of sampling. There are many records of caridean shrimps from the abyssal depths, but it is still expected that deeper sampling in different regions of the world oceans will provide new records and interesting scientific data. The deepest known records of caridean shrimps are *Parapontophilus abyssi* (Smith, 1884) (Crangonidae), collected from a depth of 5852 m (Chace 1984), *Glyphocrangon atlantica* Chace, 1939 (Glyphocrangonidae) from 6364–6373 m (Holthuis 1971; Gore 1985), and the bathypelagic *Heterogenys microphthalma* (Smith, 1885) and *Acanthephyra sica* Spence Bate, 1888 (Acanthephyridae) from 5060 m (Wicksten *et al.* 2017; Crosnier 1987) and 6890 m (Lörz *et al.* 2012), respectively. Such depths exceed the maximum available depths, for example, for cartilaginous fishes (Chondrichthyes) (4156 m; Priede & Froese 2013), but at the same time far from the depths available to abyssal fishes such as *Pseudoliparis swirei* Gerringer & Linley, 2017 (Actinopterygii: Liparidae) (6898–7966 m; Gerringer *et al.* 2017) and *Abyssobrotula galatheae* Nielsen, 1977 (Actinopterygii: Ophidiidae) (8370 m; Priede & Froese 2013) or the polychaete *Poecilochaetus vityazi* Levenstein, 1962 (Annelida: Poecilochaetidae), collected at a depth of 10 687 m from the Tonga Trench (Paterson *et al.* 2009). The deepest records of crustaceans are *Macrostylis* *mariana* Mezhov, 1993 (Isopoda: Macrodactylidae) and *Hirondellea gigas* (Birštein & Vinogradov, 1955) (Amphipoda: Hirondelleidae), recorded from hadal depths of 10 730 m (Mezhov 1993) and 10 897–10 994 m (e.g., Hessler *et al.* 1978; Kobayashi *et al.* 2012), respectively. The limiting factors for the deep-sea distribution of decapod crustaceans are still unknown due to the small number of collected samples and insufficient knowledge of the biology and ecology of such species. Wolff (1970) proposed the physiological limitation of hydrostatic pressure as a factor limiting the deeper distribution of species in Decapoda.

The deep-sea decapod fauna of the northwestern Pacific is relatively well studied (e.g., Bražhnikov 1907; Derjugin & Kobjakova 1935; Kobjakova 1936, 1937, 1955, 1958, 1962, 1967; Makarov 1938, 1962, 1966; Vinogradov 1947, 1950; Birštein & Vinogradov 1951, 1953; Uschakov 1953; Zarenkov 1960, 1965; Savilov 1961; Kurata 1964a, 1964b; Komai & Amaoka 1991; Komai 1991, 1994, 1997, 2015; Komai & Yakovlev 2000; Sedova 2004; Komai & Komatsu 2009; Spiridonov *et al.* 2013; Sedova & Andronov 2013; Sedova & Grigoriev 2013; Marin 2013, 2018; Marin *et al.* 2015; Matsuzaki *et al.* 2015; Komai & Matsuzaki 2016; Komai *et al.* 2016, 2017; Anosov *et al.* 2018; Komai & Hibino 2019), while abyssal records of decapods are still rare. Only seven benthic caridean species are known from the abyssal zone (depths of 3000−6000 m) in the northwestern Pacific: *Nematocarcinus longirostris* Spence Bate, 1888 (Nematocarcinidae); *Bathystylodactylus inflatus* Hanamura & Takeda, 1996, *Bathystylodactylus* cf. *bathyalis* (Cleva, 1994) (Stylodactylidae); *Glyphocrangon caecescens* Wood-Mason, 1891 (Glyphocrangonidae); *Neocrangon abyssorum* (Rathbun, 1902), *Sclerocrangon zenkevitchii* Birštein & Vinogradov, 1953 and *Placopsicrangon formosa* Komai & Chan, 2009 (Crangonidae) (Kobjakova 1937; Birštein & Vinogradov 1953; Hanamura & Takeda 1996; Kim *et al.* 2000; Burukovsky 2003; Komai 2004; Komai & Chan 2009; Komai & Komatsu 2016; Wicksten *et al.* 2017; Marin 2018). Several biological surveys were accomplished in the Kuril Basin – a relatively isolated and the deepest area of the Sea of Okhotsk (Vinogradov 1950; Birštein & Vinogradov 1953; Ushakov 1953; Savilov 1961; review in Marin 2018). Four species of benthic decapod crustaceans have been recorded in the Sea of Okhotsk deeper than 3000 m: *Neocrangon abyssorum* from a depth of 887–2975 m and possibly below 3000 m (Birštein & Vinogradov 1951; Zarenkov 1965; Kim *et al.* 2000; Marin 2018); *Sclerocrangon zenkevitchi* from 2995–3950 m (Birštein & Vinogradov 1953; Kim *et al.* 2000; Marin 2018); an undescribed species of the genus *Lebbeus* White, 1847 (Thoridae) from 3303–3366 m (Marin 2018); and *Munidopsis kurilensis* Marin, 2020 (Munidopsidae) from 3307–3350 m (Kobjakova 1937; Marin 2018, 2020). In addition, two bathypelagic species, *Hymenodora glacialis* (Buchholz, 1874) and *H. frontalis* Rathbun, 1902 (Acanthephyridae), were recorded at depths of 3300 and 4432 m, respectively (Kobjakova 1937; Marin 2018). Here the deep-sea species of the genus *Lebbeus*, previously recorded from the Kuril Basin of the Sea of Okhotsk (see Marin 2018), is described in detail as new to science.

The cosmopolitan thorid genus *Lebbeus* currently includes 68 valid species, representing the most species-rich genus within the family. Species of this genus are distributed from littoral to bathyal depths of both the northern and southern hemispheres (Fransen 1997; De Grave & Fransen 2011; Komai *et al.* 2012, 2019; Nye *et al.* 2013a; Komai 2013, 2015; Schiaparelli *et al.* 2015; Chan & Komai 2017). Most of the species are known as free-living, but some of them have symbiotic habits in shallow waters (e.g., Hayashi & Okuno 1997; Jonsson *et al.* 2001; Schiaparelli *et al.* 2015) or are associated with specific deep-sea biotopes such as hydrothermal vents (Nye *et al.* 2013a), cold seeps (Chan & Komai 2017) and in association with dead whale carcasses (Nye 2013). On the other hand, the geographical range of each species is rather limited, especially in deep-sea species, which leads to a high degree of endemism (e.g., Hayashi 1992; Komai *et al.* 2004, 2012; Komai 2015; Anosov *et al.* 2018); such endemic species are found in the Sea of Okhotsk (Hayashi 1992; Komai *et al.* 2004, 2012; see below). About half of all species of *Lebbeus* have been described from the northwestern Pacific, suggesting a possible radiation center of the genus in this region (Nye *et al.* 2013a). The Sea of Okhotsk is one of the "hot spots" of biodiversity in the genus *Lebbeus* with 16 described species (Bražhnikov 1907; Kobjakova 1936, 1937;

Urita 1942; Vinogradov 1950; Zarenkov 1960; Hayashi 1992; Komai 2015; Matsuzaki *et al.* 2015). At least seven species, namely *L. fujimotoi* Matsuzaki *et al.*, 2015, *L. heterochaelus* (Kobyakova, 1936), *L. longidactylus* (Kobyakova, 1936), *L. magnificus* Komai, 2015, *L. spinirostris* (Kobyakova, 1936), *L. ushakovi* (Kobyakova, 1936) and *L. vinogradovi* Zarenkov, 1960, have not been recorded from outside of the Sea of Okhotsk; some species are only known from their original descriptions (e.g., Anosov *et al.* 2018; Matsuzaki *et al.* 2015). Most species of *Lebbeus* are known from depths of less than 1500 m (e.g., Squires 1990; Hayashi 1992; Fransen 1997; De Grave & Fransen 2011; Komai 2013; Nye *et al.* 2013a, 2013b), with the deepest dwelling being *L. virentova* Nye *et al.*, 2013, recorded from a depth of 2294–2375 m in the Caribbean Sea, and *L. laurentae* Wicksten, 2010, recorded from a depth of 2618–2640 m at the East Pacific Rise in the northeastern Pacific (Wicksten 2010; Komai *et al.* 2012; Nye *et al.* 2013a, 2013b). The new species described here represents the deepest dwelling species within the genus and family, significantly increasing the bathymetric range of the genus to the abyssal depth of 3366 m. Moreover, the family Thoridae is now included in the list of deepest dwelling caridean shrimp families (see Table 1).

Material and methods

The material was collected during the megafaunal sampling of the joint Russian–German SokhoBio (Sea of Okhotsk Biodiversity Study) 2015 Expedition by the R/V "*Akademik M.A. Lavrentyev*" in the Kuril Basin, the deepest part of the Sea of Okhotsk (see Fig. 1). Collection was made using an Agassiz Trawl (AGT) or an epibenthic sled (EBS) (see Malyutina *et al.* 2018). Station data for all AGT deployments are presented in Fig. 1 and also by Blagodatski *et al.* (2017) and Malyutina *et al.* (2018). Start and, sometimes, the end coordinates refer to the positions 'on ground' and 'off ground', respectively. The AGT used in the SokhoBio 2015 Expedition was of a standard design with frame dimensions (width × height) of 350 × 70 cm and a mesh size of 10 mm. In general, the AGT was deployed twice at each station; however, at some stations only one AGT was deployed. The AGT was pulled between 4 and

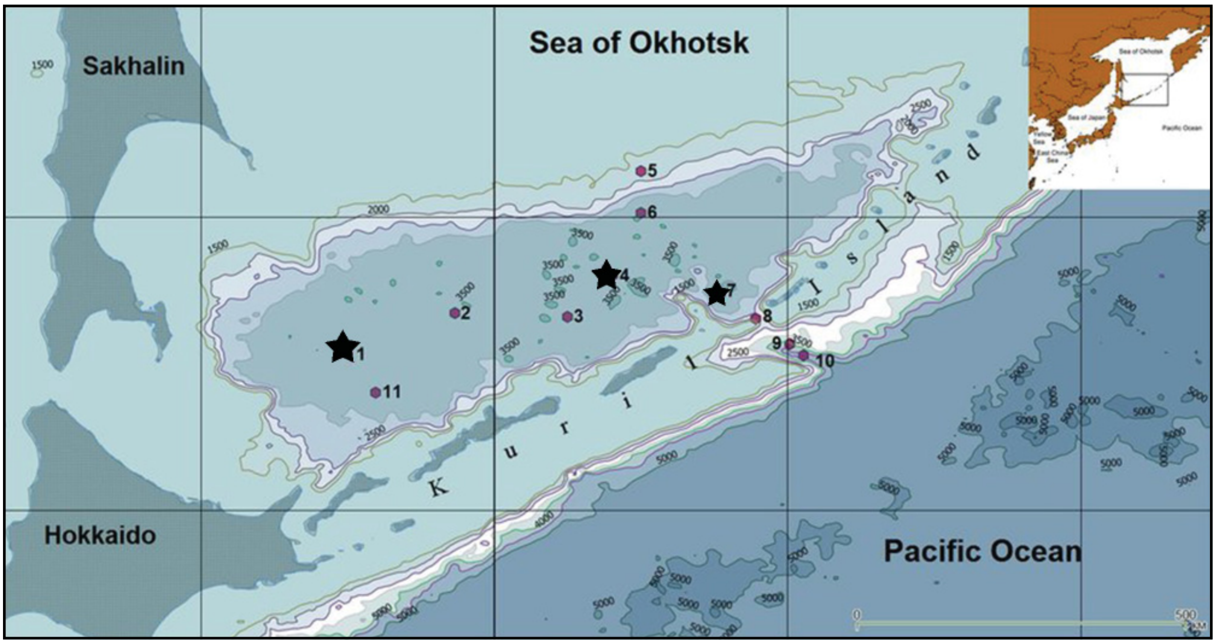

Fig. 1. Map of the stations of the SokhoBio 2015 Expedition on the R/V "*Akademik M.A. Lavrentyev*" in the Kuril Basin of the Sea of Okhotsk, northwestern Pacific. Insert in the upper right corner places the region of the sampling on the map of the northwestern Pacific area (after Blagodatski *et al.* 2017). Numbers 1–11 indicate the stations where benthic samples were collected; stars indicate the stations that yielded specimens of *Lebbeus sokhobio* sp. nov.

Table 1 (continued on next 3 pages). Caridean shrimp species hitherto recorded from depths below 3000 m.

Acanthephyridae Spence Bate, 1888			
Acanthephyra acutifrons Spence Bate, 1888	650–4926 m	Pacific	Kemp 1906; Chace 1940, 1986; Allen & Butler 1994
A. brevirostris Smith, 1885	1000–5394 m	N Atlantic	Smith 1885; Domansky 1986
A. curtirostris Wood-Mason, 1891	190–4970 m	Pacific, Indian and Atlantic Oceans	De Man 1920; Chace 1940, 1986; Crosnier & Forest 1973; Butler 1980; Krygier & Pearcy 1981; Allen & Butler 1994
A. eximia Smith, 1884	200–5111 m	Pacific and Atlantic; Mediterranean Sea	Pohle 1992; Poupin 1996; Linley *et al.* 2018
A. pelagica (Risso, 1816)	3635 m	South Ocean	Boschi *et al.* 1981; Wasmer 1986; Iwasaki & Nemoto 1987; Tiefenbacher 1994; Gorny 1999; Basher & Costello 2014
A. prionata Foxton, 1971	1900–4926 m	Atlantic, off East Africa; E Pacific	Foxton 1971; Allen & Butler 1994
A. quadrispinosa Kemp, 1939	5040–5060 m	Indian Ocean	Crosnier 1987
A. sica Spence Bate, 1888	400–6890 m	off New Zealand	Lörz *et al.* 2012
A. stylorostratis (Spence Bate, 1888)	3458 m	Atlantic and Pacific	Spence Bate 1888
Acanthephyra spp.	6007–6890 m	Pacific	Jamieson *et al.* 2009; Wicksten *et al.* 2017
Heterogenys microphthalma (Smith, 1885)	3197–5060 m	Indian Ocean; NE Atlantic	Alcock 1901; Domansky 1986; Crosnier 1987
H. monnioti Crosnier, 1987	2663–4035 m	Indian and Atlantic Oceans	Cardoso 2013
Hymenodora acanthitelsonis Wasmer, 1972	5041–5591 m	NW Pacific; NE Atlantic	Kikuchi & Omori 1985; Domansky 1986
H. frontalis Rathbun, 1902	586–4432 m	N Pacific	Rathbun 1902, 1910; Chace 1986; Marin 2018
H. glacialis Buchholz, 1874	from near the surface in polar seas to 5610 m	NE Atlantic, Pacific and South Oceans	Havens & Rork 1969; Butler 1980; Just 1980; Wasmer 1986; Domansky 1986; Iwasaki & Nemoto 1987; Hendrickx & Estrada Navarrete 1996; Wicksten 2002; Basher & Costello 2014
H. gracilis (Smith, 1886)	1000–3733 m	South Ocean	Spence Bate 1888; Wasmer 1986; Iwasaki & Nemoto 1987; Gorny 1999; Basher & Costello 2014
Meningodora mollis Smith, 1882	840–2985 m	Atlantic and Pacific	Chace 1940, 1986; Crosnier & Forest 1973; Kensley *et al.* 1987
M. vesca (Smith, 1886)	615—5367 m	Atlantic and Pacific	Chace 1940, 1986; Crosnier & Forest 1973; Kensley *et al.* 1987; Allen & Butler 1994
Notostomus elegans A. Milne-Edwards, 1881	0–3500 m	Atlantic and Pacific	Crosnier & Forest 1973; Chace 1986; Kensley *et al.* 1987
N. gibbosus A. Milne-Edwards, 1881	850–4000 m	Atlantic and Pacific	Crosnier & Forest 1973; Chace 1986; Kensley *et al.* 1987
Alvinocarididae Christoffersen, 1986			
Alvinocaris markensis Williams, 1988	1693–3650 m	Atlantic, Mid-Atlantic Ridge	Williams 1988; Wharton *et al.* 1997; Shank *et al.* 1999; Komai & Segonzac 2003; Martin & Haney 2005
A. methanophila Komai *et al.*, 2005	2155–3712 m	NW Atlantic	Komai *et al.* 2005
A. muricola Williams, 1988	1697–3277 m	Atlantic, Gulf of Mexico	Williams 1988; Komai & Segonzac 2005; Komai *et al.* 2005; Martin & Haney 2005

Table 1 (continued). Caridean shrimp species hitherto recorded from depths below 3000 m.

Chorocaris chacei Williams & Rona, 1986	1600–3650 m	Atlantic, Mid-Atlantic Ridge	Williams & Rona 1986; Williams 1987; Martin & Haney 2005; Komai & Segonzac 2008
C. vandoverae Martin & Hessler, 1990	3640 m	Pacific, Mariana Back Arc Basin	Martin & Hessler 1990; Martin & Haney 2005; Nye *et al.* 2012
Mirocaris fortunata (Martin & Christiansen, 1995)	850–3480 m	Atlantic, Mid-Atlantic Ridge	Martin & Christiansen 1995; Vereshchaka 1997; Shank *et al.* 1999; Komai & Segonzac 2003; Martin & Haney 2005; Komai *et al.* 2007; Fabri *et al.* 2011
M. indica Komai *et al.*, 2006	2422–3300 m	Indian Ocean, Central Indian Ridge	Komai *et al.* 2006
Opaepele susannae Komai *et al.*, 2007	1500–2986 m	Atlantic, Mid-Atlantic Ridge	Komai *et al.* 2007; Beltenev *et al.* 2009
Rimicaris exoculata Williams & Rona, 1986	1700–4088 m	Atlantic, Mid-Atlantic Ridge	Williams & Rona 1986; Martin & Haney 2005; Komai *et al.* 2007; Komai & Segonzac 2008; Nye *et al.* 2012
R. hybisae Nye *et al.*, 2012	2300–4960 m	Atlantic, Caribbean	Nye *et al.* 2012
R. kairei Watabe & Hashimoto, 2002	2415–3320 m	Indian Ocean, Central Ind. Ridge	Van Dover *et al.* 2001; Watabe & Hashimoto 2002; Martin & Haney 2005
Bythocarididae Christoffersen, 1987			
Bythocaris cryonesus Bowman & Manning, 1972	3803–3805 m	Arctic: Polar Sea; Iceland	Bowman & Manning 1972; Just 1980
B. curvirostris Kobjakova, 1957	2352–3965 m	Arctic: Polar Sea	Just 1980
Crangonidae Haworth, 1825			
Neocrangon abyssorum (Rathbun, 1902)	887–3200 m	N Pacific	Birštein & Vinogradov 1951; Zarenkov 1965; Hiller-Adams & Case 1985; Kim *et al.* 2000
Parapontophilus abyssi (Smith, 1884)	1400–5852 m	Pacific and Atlantic	Crosnier & Forest 1973; Chace 1984; Komai 2008
P. occidentalis (Faxon, 1893)	837–4082 m	E Pacific	Faxon 1893; Komai 2008; Hendrickx & Papiol 2015
P. profundus (Spence Bate, 1888) [*]	4755 m	Tasman Sea	Spence Bate 1888; Komai 2008
P. talismani Crosnier & Forest, 1973	3411–3517 m	NE Atlantic; Caribbean Sea	Crosnier & Forest 1973; Gore 1985; Komai 2008
Placopsicrangon formosa Komai & Chan, 2009	4807–4824 m	W Pacific: Taiwan	Komai & Chan 2009
Sclerocrangon zenkevitchii Birštein & Vinogradov, 1953	2995–3950 m	N Pacific	Birštein & Vinogradov 1953; Kim *et al.* 2000; Komai 2008
Disciadidae Rathbun, 1902			
Lucaya bigelowi Chace, 1939	4773 m	Atlantic: West Indies	Chace 1939
Eugonatonotidae Chace, 1937			
Eugonatonotus chacei Chan & Yu, 1991 (as *Galatheacaris abyssalis* Vereshchaka, 1997) [**]	2000–5000 m	W Pacific: Sulawesi	Vereshchaka 1997; Chow *et al.* 2000

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[*] Known from single holotype specimen.

[**] *G. abyssalis* is a mesopelagic larva of *E. chacei*. The benthic species itself has not been recorded deeper than 1000 m, but *G. abyssalis* can be collected in mid-water when trawls are hauled up from abyssal depths. Nevertheless, the records of *G. abyssalis* and *E. chacei*, respectively, are presented here as they were published in the literature.

Table 1 (continued). Caridean shrimp species hitherto recorded from depths below 3000 m.

Glyphocrangonidae Smith, 1884			
Glyphocrangon atlantica Chace, 1939	3400–6373 m	Atlantic	Holthuis 1971; Gore 1985
G. caecescens Wood-Mason in Wood-Mason & Alcock, 1891	2698–3431 m	Pacific and Indian	Komai 2004; Komai & Komatsu 2016
G. longirostris (Smith, 1882)	680–3219 m		Hiller-Adams & Case 1985
Nematocarcinidae Smith, 1884			
Nematocarcinus acanthitelsonis Pequegnat, 1970	3138–3742 m	Atlantic	Crosnier & Forest 1973; Gore 1985
N. batei Burukovsky, 2000		N Pacific	Burukovsky 2003
N. challenger Burukovsky, 2006	5477 m		Burukovsky 2006
N. ensifer (Smith, 1882)	1000–3600 m	Atlantic	Crosnier & Forest 1973; Gore 1985
N. exilis (Spence Bate, 1888)	3300–4000 m	Atlantic: Mediterranean Sea	Company *et al.* 2004
N. lanceopes (Spence Bate, 1888)	3432 m	South Ocean	Spence Bate 1888; Hale 1941; Zarenkov 1968; Gutt *et al.* 1991, 1994; Gorny 1992, 1999; Arntz *et al.* 1999; Arntz 2003; Lovrich *et al.* 2005; Basher & Costello 2014
N. longirostris (Spence Bate, 1888)	2500–5340 m	Atlantic, Pacific, Indian and South Oceans	Spence Bate 1888; Zarenkov 1968; Iwasaki & Nemoto 1987; Gorny 1999; Burukovsky 2003; Yaldwyn & Webber 2011; Komai & Komatsu 2016
N. productus Spence Bate, 1888	631–3429 m	W Pacific	Chace 1986
Oplophoridae Dana, 1852			
Oplophorus sp.	944–5050 m	Pacific: off New Zealand	Lörz *et al.* 2012
Systellaspsis braueri (Ba1ss, 1914)	200–4000 m	N Atlantic and Pacific	Chace 1940, 1986; Crosnier & Forest 1973; Martin & Haney 2005
S. cristata (Faxon, 1893)	200–3200 m	Indian, Pacific and Atlantic Oceans	Holthuis 1951; Crosnier & Forest 1968; Foxton 1970
S. debilis (A. Milne Edwards, 1881)	150–5025 m	Indian Ocean	Crosnier 1987; De Man 1920; Chace 1940, 1986; Crosnier & Forest 1973; Baba *et al.* 1986; Kensley *et al.* 1987
S. pellucida (Filhol, 1884)	291–3292 m	Pacific and Atlantic	Crosnier & Forest 1973; Chace 1986; Chan & Yu 1986; Crosnier 1987; Cardoso & Young 2005; Komai *et al.* 2018
Pandalidae Haworth, 1825			
Stylopandalus richardi (Coutière, 1905)	0–3600 m	Indian, Pacific and Atlantic Oceans	Chace 1940, 1986; Hayashi & Miyake 1969; Crosnier & Forest 1973; Kensley *et al.* 1987
Pasiphaeidae Dana, 1852			
Parapasiphae compta Smith, 1884	4990 m	Atlantic	Crosnier 1988
Pasiphaea scotiae (Stebbing, 1914)	3660 m	South Ocean	Wasmer 1986; Iwasaki & Nemoto 1987; Tiefenbacher 1991, 1994; Gorny 1999; Basher & Costello 2014
Sergestidae Dana, 1852			
Eusergestes arcticus (Krøyer, 1855)	3935 m	South Ocean	Doflein & Balss 1912; Iwasaki & Nemoto 1987; Tiefenbacher 1994; Gorny 1999

Table 1 (continued). Caridean shrimp species hitherto recorded from depths below 3000 m.

Petalidium foliaceum (Spence Bate, 1888)	3935 m	South Ocean	Spence Bate 1888; Hale 1941; Iwasaki & Nemoto 1987; Tiefenbacher 1991, 1994; Gorny 1999
Sergestes arachnipodus (Cocco, 1832)	3300–4000 m	Atlantic: Mediterranean Sea	Company *et al.* 2004
Sergia robusta (Smith, 1882)	3300–4000 m	Atlantic: W Ionian Sea	Company *et al.* 2004
Stylodactylidae Spence Bate, 1888			
Bathylodactylus sp.	3922 m	Pacific: Clarion-Clipperton Zone	Amon *et al.* 2017
Bathystylodactylus bathyalis (Cleva, 1994)	3502–3515 m	W Pacific: Coral Sea	Cleva 1994
B. cf. *bathyalis* (Cleva, 1994)	4826 m	Pacific: Marianas Trench Marine Natl Monument	Wicksten *et al.* 2017
B. inflatus Hanamura & Takeda, 1996	3436–3452 m	W Pacific: Taiwan	Hanamura & Takeda 1996
Thoridae Kingsley, 1879			
Lebbeus sokhobio sp. nov.	3301–3366 m	NW Pacific: Sea of Okhotsk	Marin 2018; present study

1.5 nautical miles (depending on the depth) at a vessel speed of 1 knot, and trawling lasted for 10–20 minutes at a speed of 1.0 knot. As soon as the AGT arrived on deck, all animals were removed from the catch during sieving of the sediment. Large organisms removed from the AGT were stored in cooled seawater until further treatment, then preserved in a 96% solution of ethanol and stored at 0°C. Some specimens were photographed in parallel with the preservation process.

Drawings of preserved specimens were made with the help of a camera lucida attached to an Olympus binocular microscope. Postorbital carapace length (pcl., in mm), i.e., the length from the orbits to the posterodorsal margin of the carapace, and total body length (tl., in mm), i.e., the dorsal length from the tip of the rostrum to the distal margin of the telson, are used as standard measurements. The material is deposited in the Zoological Museum of Moscow State University, Moscow (ZMMU, holotype), the Zoological Museum of the National Scientific Center of Marine Biology FEB RAS, Vladivostok (MIMB) and Naturmuseum Senckenberg, Frankfurt am Main, Germany (SMF).

To study molecular genetic barcodes, fragments of the mitochondrial gene coding cytochrome c oxidase subunit I (COI mtDNA), mitochondrial 16S ribosomal RNA (16S rRNA) and nuclear 28S ribosomal RNA (28S rRNA) gene markers were amplified and sequenced. Total genomic DNA was extracted from muscle tissue using the innuPREP DNA Micro Kit (AnalitikJena, Germany) following the manufacturer's protocol. The COI mtDNA gene marker was amplified with the help of the universal primers LCO1490 (5'–ggtcaacaaatcataaagatattgg–3'), HC02198 (5'–taaacttcagggtgaccaaaaaatca–3') (Folmer *et al.* 1994), for 16S rRNA (16SAR–cgcctgtttatcaaaaacat, 16SBR–ccggtctgaactcagatcacgt) after Palumbi *et al.* (2002), for 28S rRNA (28SA–gacccgtcttgaaacacgga, 28SB–tcggaaggaaccagctacta) primers after Whiting *et al.* (1997). PCR was performed with the T100 amplificator (Bio–Rad, USA) under the following conditions: initial denaturation at 96°C for 1.5 minutes followed by 42 cycles of 95°C for 2 minutes, 49°C for 35 seconds, and 72°C for 1.5 minutes, followed by chain extension at 72°C for 7 minutes. A volume of 10µl of the reaction mixture contained 1µl of total DNA, 2µl of 5×PCR mix (Dialat, Russia) and 1µl of each primer. The amplification products were separated by using gel electrophoresis of nucleic acids on a 1.5% agarose gel in 1×TBE, and then stained and visualized with 0.003% EtBr using imaging UV software. DNA nucleotide sequences were determined using Genetic

Analyzer ABI 3500 (Applied Biosystems Inc.) and BigDye ver. 3.1 (Applied Biosystems Inc.) with direct and reverse primers.

The aligned sequences of the COI mtDNA gene markers, 635 base pairs in length, were analyzed for pairwise sequence divergence (*p*-distances) and used to construct the phylogenetic relationships, whereas data on 16S and 28S are only presented in the 'GenBank accession numbers' section, as there are no sequences to compare them to in GenBank (NCBI) or any other genetic database. The dataset of COI mtDNA gene marker alignments used in this study is presented in Appendix 1. The best evolutionary substitution model was determined using MEGA ver. 7.0. and jModeltest ver. 2.1.141 via the CIPRES Science Gateway ver. 3.3 (http://www.phylo.org/). Phylogenetic analysis was performed using MrBayes ver. 32.6 for the Bayesian analysis (BA) with an NKY+I+G evolutionary model and using RA×ML ver. 8.0.0 with a GTR+I+G evolutionary model for the Maximum-Likelihood analysis (ML). Bayesian analysis was carried out by sampling one tree every 1000 generations over 1 000 000 generations. Values of confidence (bootstrap support) >50% are presented for BA/ML analyses; the divergences of *p*-distances are calculated using the Kimura-2-parameter (K2P) model in MEGA. The phylogenetic tree obtained based on COI mtDNA is presented in Fig. 7; there are no data on other species of *Lebbeus* based on the other gene markers (16S rRNA and 28S r RNA) for any valuable analysis, so they are just presented in this paper for future research.

Existing records of caridean shrimps below depths of 3000 m are presented in Table 1. It is based on the available literature found on the Internet using keywords as well as on a special search for scientific information in libraries using reference journals and electronic catalogs to search in publications not found on the Internet. It is possible that some pelagic species (e.g., members of Oplophoridae, Pasiphaeidae and Sergestidae) can be caught by trawls when they were hauled up from abyssal depths. The table includes all published records of caridean shrimps when the sampling depth was indicated as being deeper than 3000 m, without any assessment. Moreover, pelagic shrimps are often eurybathic and recorded by video vehicles from abyssal depths (e.g., Lörz *et al.* 2012; Jamieson *et al.* 2009; Wicksten *et al.* 2017; pers. obs.). Some remarks, for example for *Galatheacaris abyssalis* Vereshchaka, 1997, are presented in the text (see Table 1).

Results

Class Malacostraca Latreille, 1802
Order Decapoda Latreille, 1802
Family Thoridae Kingsley, 1879
Genus *Lebbeus* White, 1847

Lebbeus sokhobio sp. nov.

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Figs 1–6

Lebbeus sp. – Marin 2018: 331.

Type material

Holotype

SEA OF OKHOTSK • ♀; NE slope of Kuril Basin, st. 1-10; 46°08.9′ N, 145°59.4′ E–46°09.0′ N, 145°59.5′ E; depth 3303–3308 m; 10 Jul. 2015; ZMMU Ma5836.

Paratypes

SEA OF OKHOTSK • 1 ♂; same collection data as for holotype; ZMMU Ma6096 • 1 ♀; NE slope of Kuril Basin, st. 4-3; 47°14.0′ N, 149°34.8′ E; AGT; depth 3366 m; 16 Jul. 2015; ZMMU Ma6097 • 1 ♀, 1 ♂; NE slope of Kuril Basin, st. 4-9; 47°13.6′ N, 149°39.2′ E; EBS; depth 3365 m; 16 Jul. 2015;

SMF 51579 • 2 ♂♂, 1 juv.; NE slope of Kuril Basin, st. 4-10; 47°12.2′ N, 149°36.7′ E; EBS; depth 3366 m; 17 Jul. 2015; MIMB 39426 • 1 ♀; NE slope of Kuril Basin, st. 7-12; 46°54.6′ N, 151°03.7′ E; AGT; depth 3301 m; 22 Jul. 2015; MIMB 39427.

Etymology

This new species is named after the SokhoBio (Sea of Okhotsk Biodiversity Study) Expedition 2015, which allowed the collection of numerous deep-sea species such as this one.

Description

Carapace (Figs 2, 3A–B). Smooth, without setae; dorsal surface slightly convex in males and gibbous in females, with well-marked postrostral median ridge armed with 2 postrostral teeth located at about anterior 0.2 of carapace length (Fig. 5); antennal tooth situated slightly below suborbital angle (Figs 3A–B, 5); supraorbital tooth large, directed forward, with deep notch below base, situated anterior rostral base; suborbital lobe prominent, triangular; anterolateral margin between antennal and pterygostomial teeth strongly sinuous, with deep concavity below antennal tooth; pterygostomial tooth acute, smaller and more slender than antennal and supraorbital teeth, overreaching anterior margin of carapace (Fig. 3A–B).

Orbits. Well developed, orbital margin with slight convexity posteriorly, base of eyestalk located between this convexity and suborbital lobe.

Rostrum. Relatively long, compressed, reaching distal margin of basal segment of antennular peduncle (Fig. 3A–B), about 0.3 times as long as carapace; rostral formula 1–2+2/1–3 (Fig. 5), with well-developed dorsal and ventral lamina; lateral rostral carina obsolescent, situated above level of proximal orbital margin (Fig. 2A).

Pleon (Figs. 2, 3C). Smooth and unarmed dorsally; pleomere II with distinct anterior transverse groove on tergum; pleurae of pleomeres I–IV rounded, pleurae of pleomere IV pointed posteroventrally in some specimens (Fig. 3C); pleurae of pleomere V (Fig. 3C) with small posteroventral tooth; pleomere VI (Fig. 3G) with small posteroventral teeth and posterolateral process terminating acutely. Telson (Fig. 3G) slender, about 4 times as long as proximal width, narrowing posteriorly, with 3–5 (usually 4) pairs of small submarginal dorsal spines at 0.4, 0.75, 0.8 and 0.9 of telson length; posterior margin armed with 3 or 4 pairs (usually 4, but 3 pairs in possibly damaged specimens) of unequal spines or spiniform setae (Fig. 3H).

Eyes (Fig. 3A–B). Normal, well developed, subpyriform, with subcylindrical eyestalk and large dilated cornea; eyestalk about as long as wide; cornea subglobose, without papilla; ocellus absent.

Antennula. Antennular peduncle (Fig. 3A, D–E) well developed; basal segment about twice as long as wide, with dorsodistal margin armed with 3 slender spines; stylocerite well developed, acute, nearly reaching distal margin of basal segment, mesial margin sinuous; intermediate segment (article 2) stout, about 1.5–2.0 times as long as wide, with slightly convex mesial margin bearing long plumose setae and slender distolateral tooth; distal segment (article 3) short, about as long as wide, about half the length of intermediate segment, with acute dorsolateral subdistal tooth, with long plumose setae along mesial margin; upper antennular flagellum with aesthetasc-bearing portion consisting of 10–12 articles. No sexual dimorphism detected.

Antenna (Fig. 3F). Normal, well developed; basicerite armed with small tooth ventrolaterally; carpocerite overreaching midlength of scaphocerite; flagellum well developed; scaphocerite wide, greatly overreaching antennular peduncle, about 3 times as long as maximal width, with well-developed distolateral tooth reaching distal margin of blade.

Mouthparts. Typical for genus, without distinctive features. Mandible with 2-segmented palp; incisor process well-marked, terminating in sharp tip, bearing 4 distinct teeth and several additional denticles; molar process terminating distally. Maxilla I consisting of well-developed and partly fused endites, armed with spiniform setae and unsegmented bilobed palp. Maxilla II with simple, slender blunt palp; upper endite bilobed, fringed with setae; lower endite reduced; scaphognathite well developed, with rounded posterior lobe. Maxilliped I with partly fused endites, bearing short stout setae along distal margin as well as some elongated setose setae along distodorsal angle; exopod well developed, with

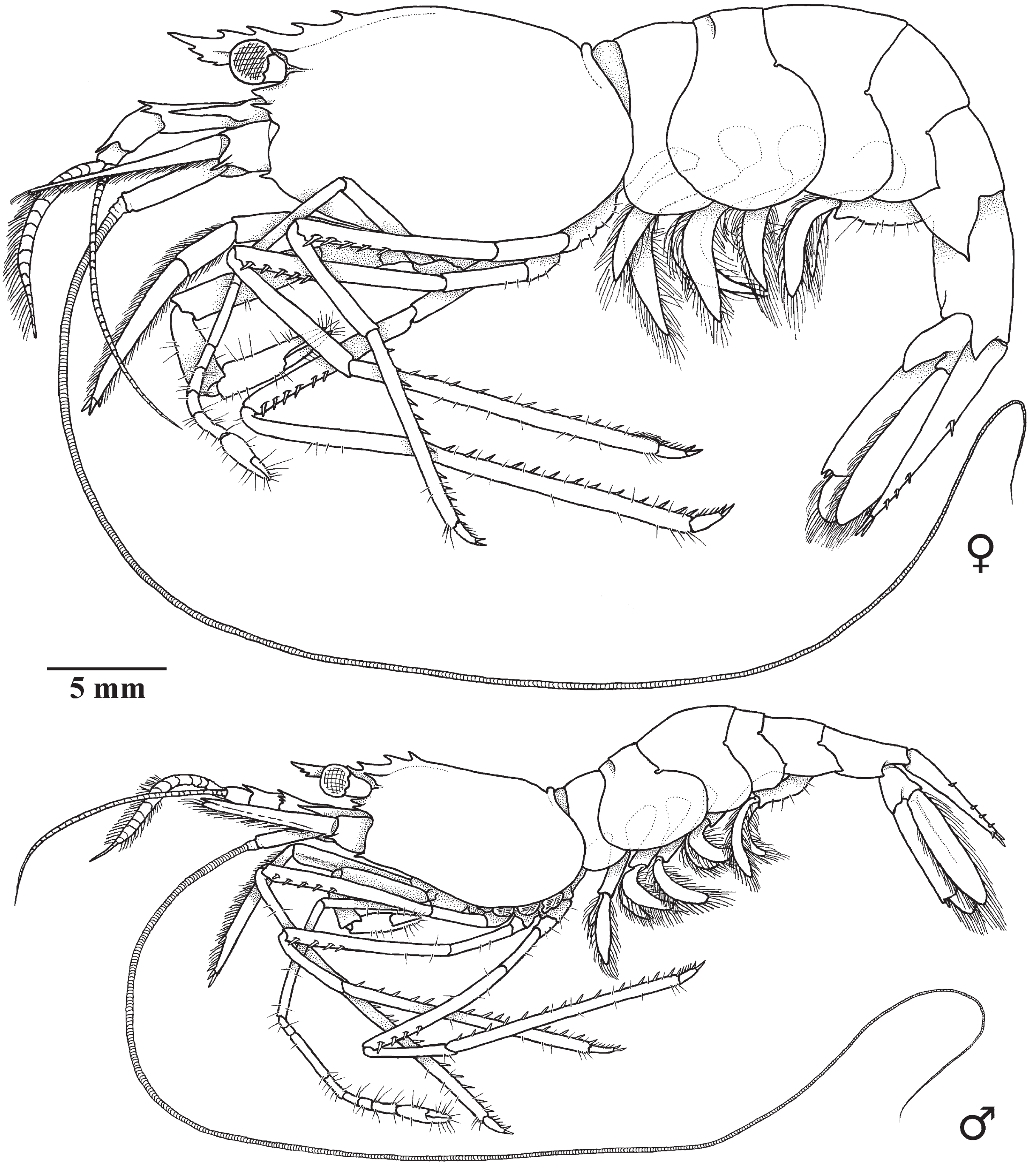

Fig. 2. *Lebbeus sokhobio* sp. nov., general view, ♀ from st. 4-3 (paratype, ZMMU Ma6097) and ♂ from st. 4-9 (paratype, SMF 51579).

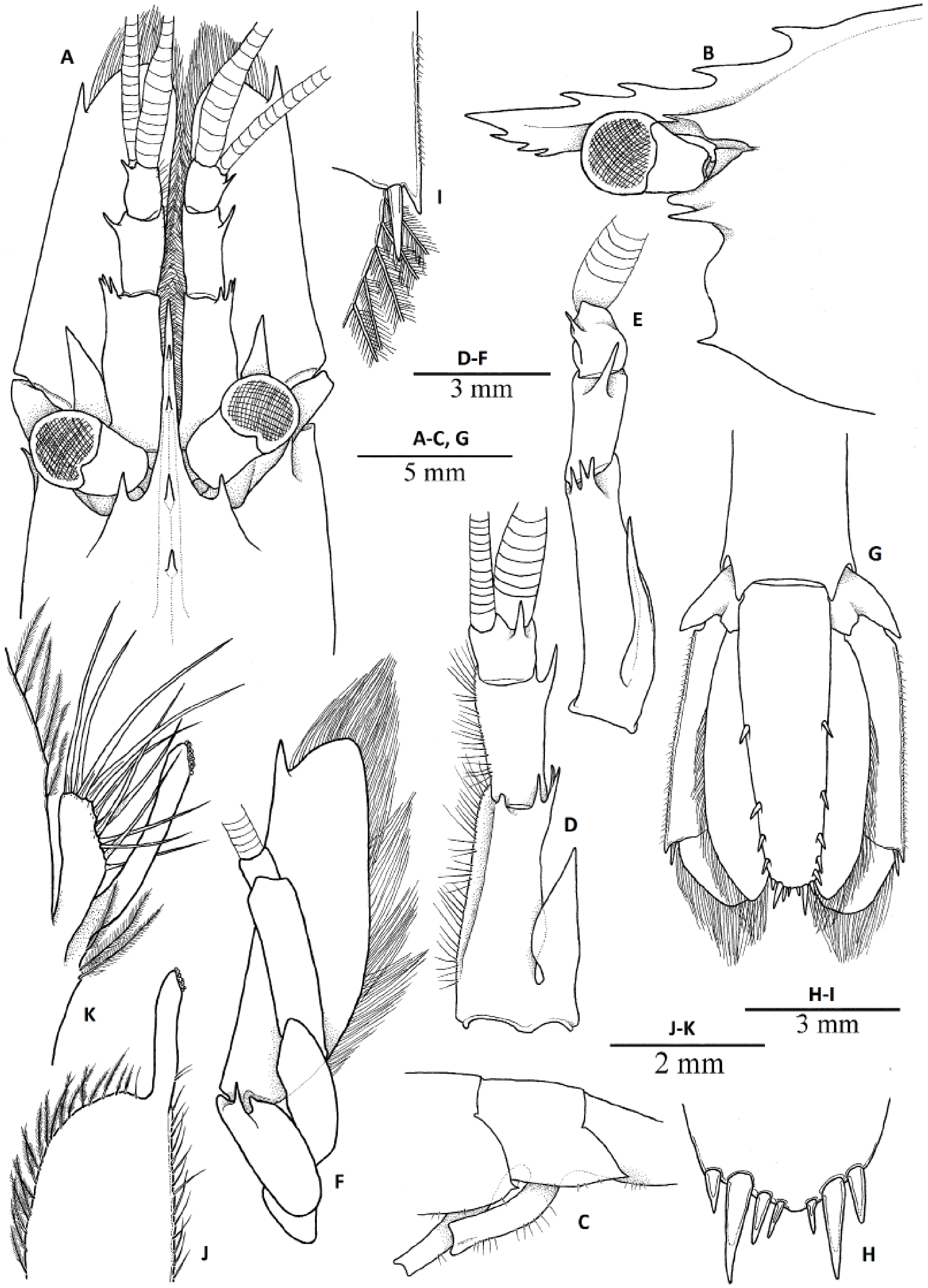

Fig. 3. *Lebbeus sokhobio* sp. nov., ♀ from st. 4-3 (paratype, ZMMU Ma6097) (A–I) and ♂ from st. 4-10 (paratype, MIMB 39426) (J–K). **A–B**. Anterior part of carapace. **C**. Abdominal pleonites IV–V, lateral view. **D–E**. Antennula. **F**. Antenna. **G**. Telson and uropods. **H**. Distal margin of telson. **I**. Distolateral margin of exopod. **J**. Endopod of pleopod I. **K**. Endopod of pleopod II.

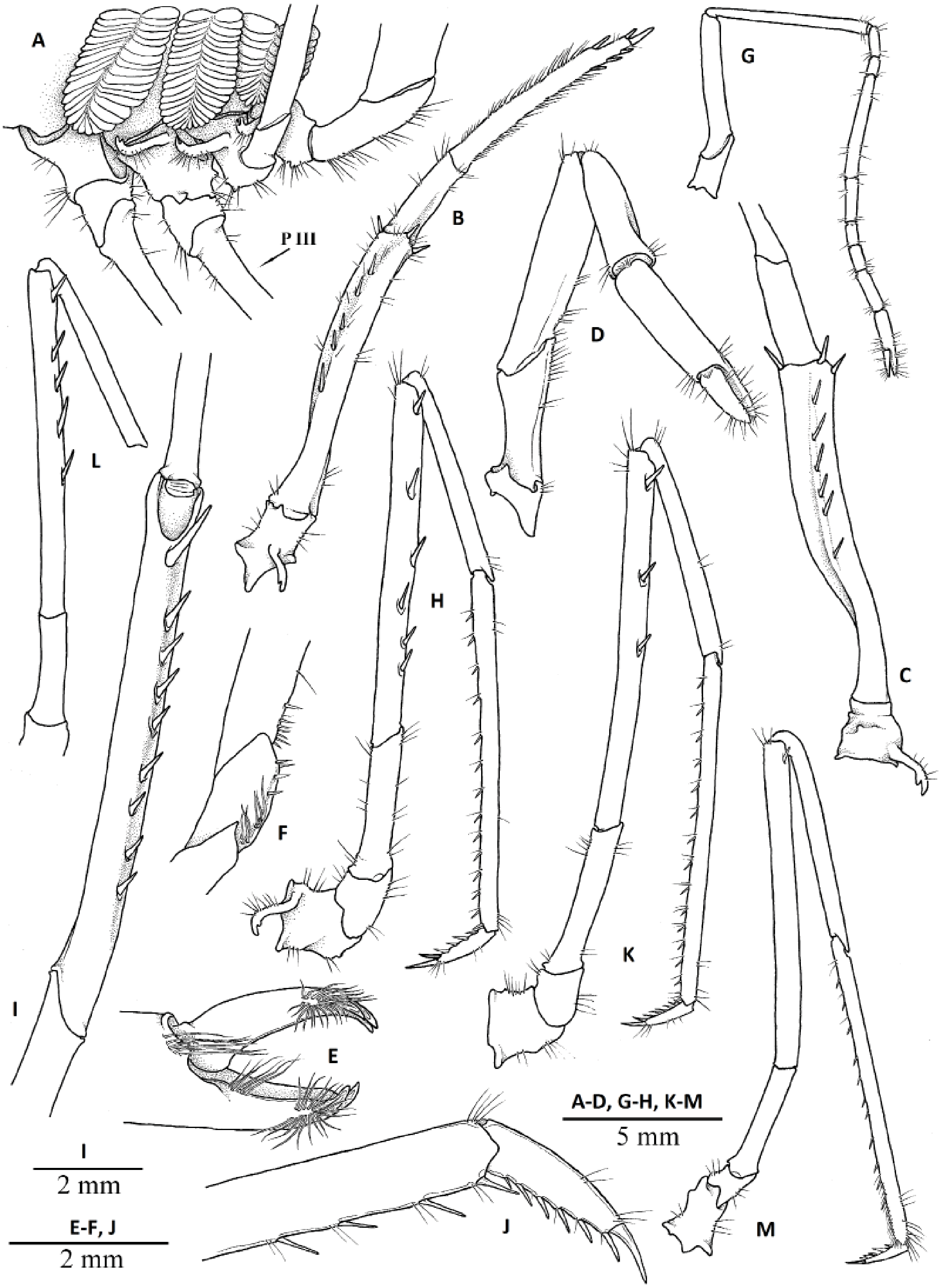

Fig. 4. *Lebbeus sokhobio* sp. nov., ♀ from st. 4-3 (paratype, ZMMU Ma6097) (A–H, J–K, M) and ♂ from st. 4-9 (paratype, SMF 51579) (I, L). **A**. Basal segments of pereiopods I–III. **B**. Maxilliped III. **C**. Antepenultimate segment of maxilliped III. **D**. Pereiopod I. **E**. Chela of pereiopod I. **F**. Proximal segments of pereiopod I. **G**. Pereiopod II. **H**. Pereiopod III. **I**. Merus of pereiopod III. **J**. Dactylus of pereiopod III. **K**. Pereiopod IV. **L**. Merus of pereiopod IV. **M**. Pereiopod V.

well-marked caridean lobe with many setae; palp 2-segmented; epipod ear-shaped, bilobed distally. Maxilliped II with well-developed exopod, fringed with setae distally; ischium stout, with long setae along lateral margin; propodus short, length equal to that of dactylus, with convex dorsal margin furnished with long simple setae, ventral margin unarmed; dactylus convex, armed with numerous stout, long, simple setae along distal margin; exopod flagellate; epipod well-marked, distally bilobed, with podobranch. Maxilliped III (Fig. 4B–C) moderately long and stout, slightly overreaching scaphocerite and antennular peduncle; epipod well developed; exopod absent; antepenultimate article about 6 times as long as wide, slightly tapering distally, with longitudinal row of long spiniform setae along lateral surface and 3 long spiniform setae on distal margin; penultimate article about twice as long as wide, smooth; terminal segment about 7 times as long as wide, with distal margin oblique, armed with row of spines along distomesial margin.

Pereiopod I (Fig. 4D). Moderately robust; coxa with epipod and setobranch; basis stout, unarmed; ischium stout, about twice as long as wide, with long, simple setae along ventral margin; merus slender, about 4 times as long as wide, with row of spiniform setae proximally (Fig. 4F); carpus robust, about half the length of merus and slightly shorter than propodus, about twice as long as wide, slightly flaring distally; distal margin slightly overlapping carpo-propodal articulation; mesial surface with grooming apparatus consisting of shallow concavity and complex of short, stiff setae; propodus (palm) about 3 times as long as wide, subcylindrical, smooth; fingers (Fig. 4E) stout, about half the length of palm, subspatulate, about as long as wide; cutting edges straight, with strong distal teeth.

Pereiopod II (Fig. 4G). Relatively slender, unarmed; coxa with setobranch and epipod; basis small, about as long as wide; ischium about 4 times as long as wide, smooth; merus about 7 times as long as wide; carpus subdivided into 7 sub-articles with ratio of about 1:1:4:2:1:1:2; propodus (palm) subcylindrical, slightly shorter than distal carpal segment, about twice as long as wide and twice as long as fingers, with straight smooth margins; fingers slender, about 1.5 times as long as wide, with straight cutting edges.

Pereiopods III–V. Similar, relatively slender. Pereiopod III (Fig. 4H) coxa with setobranch and terminally hooked epipod; basis with small lobe distoventrally, about as long as wide; ischium about 3.5–4.0 times as long as wide; merus about 9 times as long as wide, armed with 5–8 movable spines on lateral surface adjacent to ventral margin on distal ⅘; carpus about 6 times as long as maximal width, slightly widened distally; propodus about 10–11 times as long as wide, with straight margins, ventral margin armed with tooth-like setae; dactylus (Fig. 4J) slender, terminating in elongate curved unguis, with 6–7 small accessory spinules, increasing in length distally. Pereiopods IV (Fig. 4K) and V (Fig. 4M) without epipod; merus of pereiopod V (Fig. 4L) with a single spine subterminally; propodus of pereiopod V with brush-like cluster of setae (Fig. 4M) (grooming apparatus) on flexor margin distally.

Pleopods. Endopod of pleopod I with terminally located appendix interna and row of curved spinule-like setae along mesial margin in males (Fig. 3K). Pleopod II in males with appendix masculina shorter than appendix interna (Fig. 3J), truncate terminally, bearing 10–12 long simple setae on distal and mesial surfaces. Uropods moderately slender, exceeding telson (Fig. 3G); distolateral margin of exopod with fixed posterolateral tooth and slender mobile spine (spiniform seta).

Coloration. Body and appendages entirely vermilion, antennular and antennal flagella white; corneas of eyes with golden reflection (Fig. 6).

Size. Largest female (holotype) has pcl. 19.0 mm and tl. 62 mm. Largest male has pcl. 17.0 mm and tl. 56 mm.

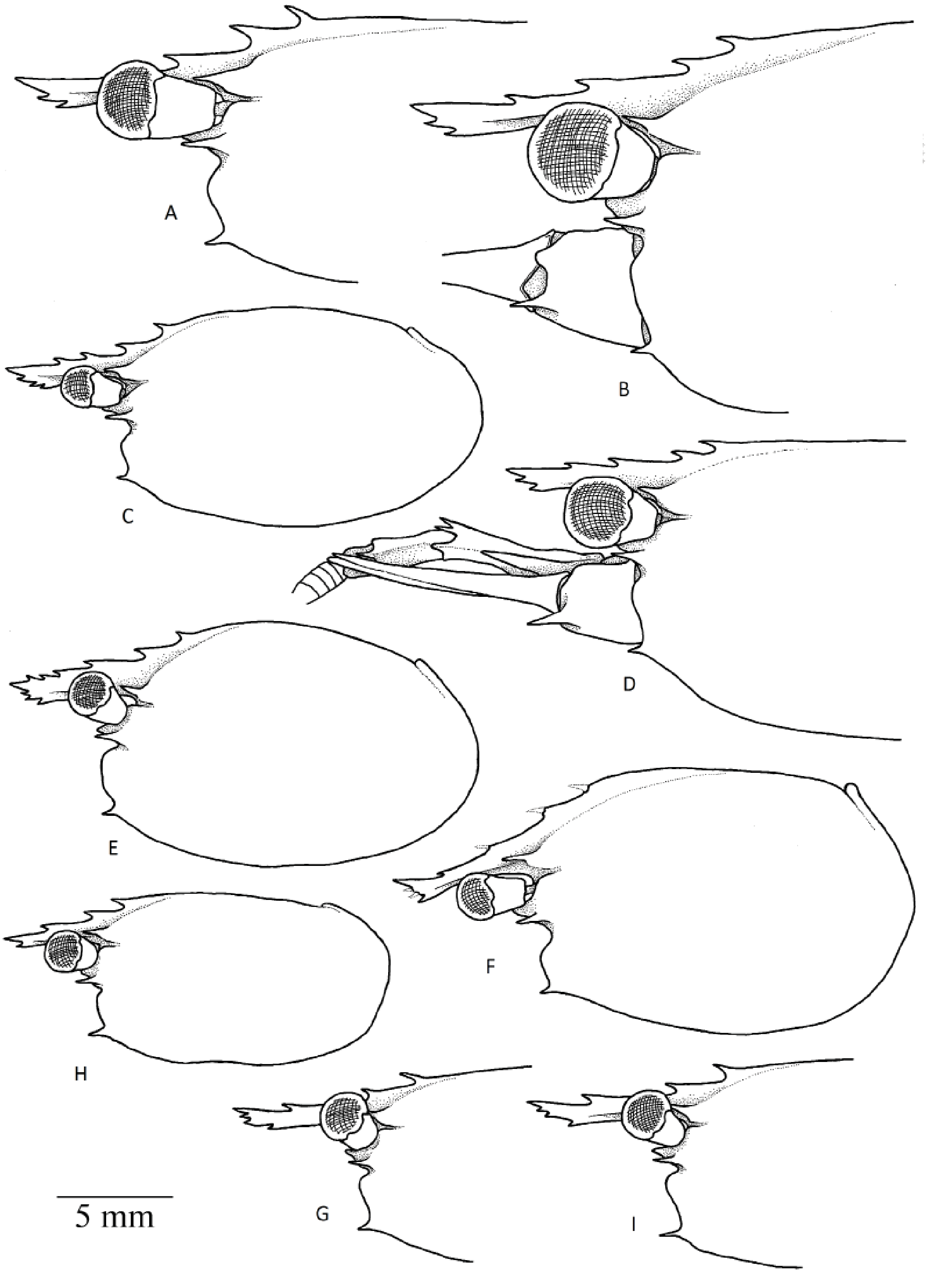

Fig. 5. *Lebbeus sokhobio* sp. nov., carapaces. **A**. ♂ from st. 4-9 (paratype, SMF 51579). **B**. ♀ from st. 1-10 (holotype, ZMMU Ma5836). **C**. ♀ from st. 7-12 (paratype, MIMB 39427). **D**. ♀ from st. 4-9 (paratype, SMF 51579). **E**. ♂ from st. 1-10 (paratype, ZMMU Ma6096). **F**. ♀ from st. 4-3 (paratype, ZMMU Ma6097). **G**. ♂ from st. 4-10 (paratype, MIMB 39426). **H**. Juvenile from st. 4-10 (paratype, MIMB 39426). **I**. ♂ from st. 4-10 (paratype, MIMB 39426).

Remarks

The new species described here belongs to the species group of the genus *Lebbeus* characterized by the presence of strap-like epipods on maxilliped III and pereiopod III. This species group includes *L. africanus* Fransen, 1997, *L. antarcticus* (Hale, 1941), *L. bidentatus* Zarenkov, 1976, *L. brevirostris* Chang *et al.*, 2010 (described based on a possibly juvenile specimen), *L. carinatus* Zarenkov, 1976, *L. cristatus* Ahyong, 2010, *L. formosus* Chang *et al.*, 2010, *L. indicus* Holthuis, 1947 (questionable), *L. java* Komai *et al.*, 2019, *L. kuboi* Hayashi, 1992, *L. lamina* Komai, 2013, *L. laurentae* Wicksten, 2010, *L. microceros* (Krøyer, 1841), *L. pacmanus* Komai *et al.*, 2012, *L. polyacanthus* Komai et al., 2004, *L. profundus* (Rathbun, 1906), *L. saldanhae* (Barnard, 1947), *L. shinkaiae* Komai *et al.*, 2012, *L. similior* Komai & Komatsu, 2009, *L. thermophilus* Komai *et al.*, 2012, *L. tosaensis* Hanamura & Abe, 2003, *L. unguiculatus* Chang *et al.*, 2010, *L. vicinus* (Rathbun, 1902), *L. virentova* Nye *et al.*, 2013, *L. washingtonianus* (Rathbun, 1902) and *L. wera* Ahyong, 2009. The wide geographical distribution and isolation of some deep regions (e.g., Antarctica vs the Sea of Okhotsk, etc.) suggests the hypothesis that numerous endemic deep water species are present within this group (e.g., Hayashi 1992; Komai *et al.* 2004, 2012, 2019; Komai 2013, 2015; Anosov *et al.* 2018). *Lebbeus sokhobio* sp. nov. is the only species of this group found in the northern part of the NW Pacific, the Sea of Okhotsk. The geographically closest species is *L. lamina* described from deep waters off the Izu Islands, Japan.

At the same time, the phylogenetic significance of grouping based on marked morphological features is rather doubtful (Komai *et al.* 2019) and has not yet been proven due to the lack of sufficient genetic data (see below). However, based on the presence of epipods on the basis of pereiopods I–III, the shape and armament of telson, with 4 pairs of dorsal spines, and the relatively slender dactyli of the ambulatory pereiopods, armed with numerous small accessory spinules, the new species may be close to

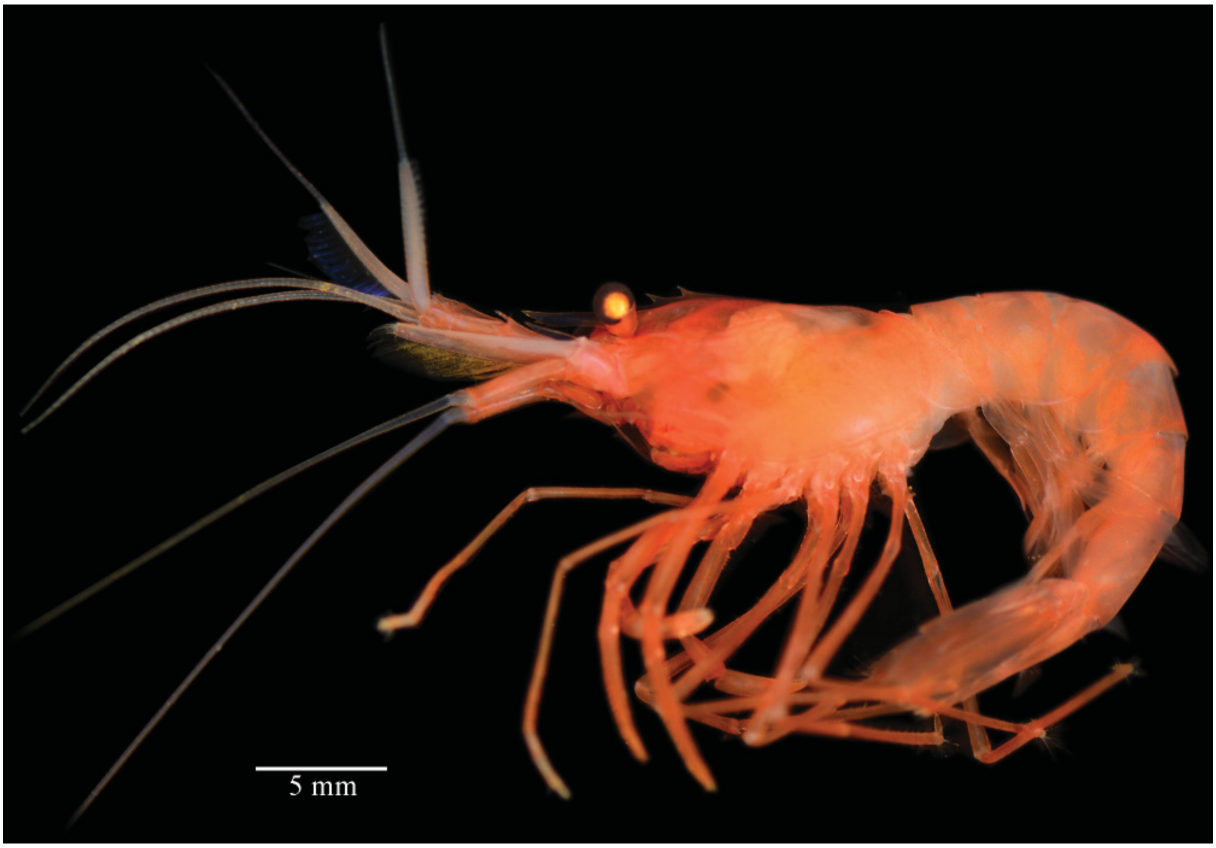

Fig. 6. *Lebbeus sokhobio* sp. nov., ♂ from st. 4-9 (paratype, SMF 51579), live coloration.

L. africanus from Mauritania, at a depth of 1500 m (Fransen 1997), *L. antarcticus* from the South Ocean, at depths of 450–1775 m (Nye *et al.* 2013b), *L. bidentatus* known from off Chile, at a depth of 1680 m (Zarenkov 1976; Fransen 1997), *L. carinatus* collected off Peru, at depths of 1680–1860 m (Zarenkov 1976; Fransen 1997), *L. cristatus* from New Zealand, at depths of 1231–1226 m (Ahyong 2010), *L. formosus* from Taiwan, at depths of 635–1982 m (Chang *et al.* 2010), *L. java* from south of Java, at depths of 637–689 m (Komai *et al.* 2019), *L. saldanhae* collected along the coasts of South Africa (Saldanha Bay), at a depth of about 265 m (145 fms) (Fransen 1997), *L. similior* from Japan, at a depth of 1196 m (Komai & Komatsu 2009), *L. unguiculatus* from Taiwan and Japan, at depths of 742–1262 m (Chang *et al.* 2010; Komai 2011), *L. vicinus* known from along the Pacific coasts of North America from Alaska to Mexico, at depths of 954–2824 m (Rathbun 1902, 1904; Wicksten & Mendez 1982) and *L. virentova* from the Mid-Cayman Spreading Center, Caribbean Sea, at a depth of 2294–2375 m (Nye *et al.* 2013a). The morphological features shared among these species include: short styliform rostrum, not reaching distal margin of second antennular segment, armed with 4 or more dorsal teeth, including postrostral teeth and with more than 1 ventral tooth; distinct U- or V-shaped notch inferior to base of supraorbital tooth; sinuous anterolateral margin of carapace between antennal and pterygostomial teeth with deep excavation below antennal tooth; pleomere II with distinct anterior transverse groove on tergum; basal antennular segment with 2 or 3 dorsodistal teeth; dactyli of ambulatory pereiopods armed with accessory spiniform spinules over entire length of flexor margin (after Nye *et al.* 2012, with some modifications).

Some morphological features allow the separation of *L. sokhobio* sp. nov. from some of the other species in this group mentioned above. The new species is distinguishable from *L. java* by the different rostral formula and the presence of 4 (2+2) dorsal rostral teeth (vs 3 (2+1) in *L. java*); the presence of 4 or 5 pairs of dorsal spines on the telson (vs 3 in *L. java*); inner distal spines on the telson much shorter than those in *L. java* (Komai *et al.* 2019: fig. 2e); shorter stylocerite of the basal antennular segment not reaching the distal margin of the segment (vs reaching the distal margin in *L. java*; Komai *et al.* 2019: fig. 2b); distal part of penultimate article of maxilliped III (Fig. 4A) with fewer but more slender spines than in *L. java* (Komai *et al.* 2019: figs 2g, 3a); merus of pereiopod III armed with 6–9 movable teeth at the distal angle (vs a maximum of 5 in *L. java*); and the different number of lateral spines on the meri of pereiopods III–V (see Fig. 4F–G, I–K vs Komai *et al.* 2019: figs 3e–f).

Lebbeus virentova can be separated from the new species by its shorter rostrum, with 3 postrostral teeth (Nye *et al.* 2013a: fig. 2a–b) (vs rostrum significantly overreaching cornea, with only 2 postrostral teeth in *L. sokhobio* sp. nov.; Figs 3B, 5), the presence of 3 well marked dorsal rostral teeth (Nye *et al.* 2012: fig. 2b) (vs only 2 teeth in the new species; Figs 3B, 5), and its white coloration (Nye *et al.* 2013a: fig. 5) (vs vermillion coloration in the new species; Fig. 6). Moreover, *L. virentova* is known only from the Caribbean Sea.

Another very geographically distant species, *L. laurentae*, although rather poorly described, can be separated from *L. sokhobio* sp. nov. by the more slender distal part of the rostrum and its feebly marked dorsal and ventral armature (Wicksten 2010; Komai *et al.* 2012) in contrast to the rostrum of the new species, which has well-marked dorsal teeth and some extension in the distal part, with well-developed ventral teeth (Figs 3B, 5).

Lebbeus sokhobio sp. nov. can be separated from *L. antarcticus* by the more slender distal part of the rostrum (Nye *et al.* 2013b: fig. 8b) (vs rostrum with some extension in the distal part, with well-developed ventral teeth in the new species; Figs 3B, 5) and the presence of 3 postrostral teeth (see Nye *et al.* 2013b: fig. 8b) (vs 2 in the new species).

Lebbeus cristatus and *L. formosus* differ from the new species in having a more slender and short rostrum (Ahyong 2010: fig. 1a–c; Chang *et al.* 2010: fig. 4a–b), a different armature of the distal margin of the basal antennular segment (Ahyong 2010: fig. 1d; Chang *et al.* 2010: fig. 4a–b) and of the posterior margin of the telson (Ahyong 2010: fig. 1g; Chang *et al.* 2010: fig. 4e), and a smaller number of lateral spines on the meri of pereiopods III–V (Ahyong 2010: fig. 1d–g; Chang *et al.* 2010: fig. 5e, g–h).

Lebbeus lamina and *L. unguiculatus* can also be clearly separated from the new species. *Lebbeus lamina* can be separated by its shorter rostrum and 3 postrostral dorsal teeth (vs only 2 in the new species), 7 pairs of small dorsal sublateral spines (vs only 4 pairs of relatively long spines in the new species), a different armature of the posterior margin of the telson (5–6 pairs of distal spines in *L. lamina* vs 4 in the new species), a smaller number of meral spines (4 in *L. lamina* vs 5–9 in *L. sokhobio* sp. nov.) and stouter dactyli of pereiopods III–V (after Komai 2013). *Lebbeus unguiculatus* differs in having a shorter rostrum and longer stylocerite, rounded pleura of pleonite IV (vs pointed in the new species), a different armature of the posterior margin of the telson (5 pairs of distal spines in *L. unguiculatus* vs 4 in the new species) and fewer lateral spines on the meri of pereiopods III–V (after Chang *et al.* 2010).

Genbank accession numbers

COI: MN590012 (holotype), MN590013–MN590015, MN608153–MN608155.

Genetic differences

The intraspecific pairwise genetic distances (*p*-distances) within the studied population of *Lebbeus sokhobio* sp. nov. (n = 7) is 0.004±0.002 (d±ES), which is rather low. Also, the genetic differences between specimens from different stations and the intraspecific differences among specimens from one station are very similar. Genetic *p*-distances between known species of the genus vary from 0.014 to 0.16 substitutions per 100 nucleotide positions (see Table 2), showing that the interspecific genetic differences of closely related species from different, sometimes very distant, regions of the World Ocean (e.g., *L. antarcticus*, *L. virentova* and *L. sokhobio* sp. nov.; see Fig. 7) are only slightly different from the intraspecific differences within the Kuril Basin of the Sea of Okhotsk. Unfortunately, much genetic data from genetic markers other than COI mtDNA are not currently available. However, it is very interesting that the genetically closest (= phylogenetically related) species among representatives of the genus *Lebbeus* are distributed most distantly – *L. antarcticus* from the Southern Ocean and *L. virentova* from the Caribbean (see Fig. 7). The genetic *p*-distances (Table 2) between these species are lower than previously documented for caridean shrimps (Knowlton *et al.* 1993; Knowlton & Weigt 1998; Hebert *et al.* 2003; Sites & Marshall 2004; Zakšek *et al.* 2007; Lefébure *et al.* 2006a, 2006b; Marin 2017).

At the same time, available barcoding data show that all of the deepest dwelling species belong to the same phylogenetic clade (see Fig. 7; 'Deep-sea *Lebbeus*' clade) showing a low level of divergence among species, whereas their species are very widely distributed. Similar small interspecific distances of about 1–2% are also known from very distantly living species of other deep-sea caridean shrimps (e.g., *Mirocaris* Vereshchaka, 1997 (Alvinocarididae); Shank *et al.* 1999; Vereshchaka *et al.* 2015; data from GenBank), as well as other deep-sea invertebrate taxa such as bivalve mollusks (e.g., *Abyssogena* Krylova *et al.*, 2010 (Vesicomyidae); Liu & Zhang 2018) and octocorals (France & Hoover 2002). Low interspecific genetic differences in COI mtDNA were observed exclusively in deep-sea taxa, but, for example, not in all studied deep-sea caridean shrimps (e.g., Shank *et al.* 1999; Vereshchaka *et al.* 2015; Zhang *et al.* 2017). As suggested by France & Hoover (2002), possible explanations for such reduced rates of divergence include a lower rate of evolution for octocoral mitochondrial genomes (also supported by Shearer *et al.* 2002) and the presence of a gene, mtMSH, which may code for a mitochondrial DNA mismatch-repair system (Culligan *et al.* 2000). The purpose of this study is not to try to answer the question of why the interspecific distances of the deep-sea clade within the genus *Lebbeus* as so low, given the small amount of genetic data available, but it can be concluded that interactions (= gene flow) between populations from the Sea of Okhotsk, the Caribbean and Antarctica are more difficult to imagine than to assume the presence of some mechanism interfering with the standard rates of evolution in the COI mtDNA gene of deep-sea species. In addition, in closely related shallow-water taxa, such as the

Table 2. Pairwise interspecific genetic (COI mtDNA) distances (*p*-distance ± SE) between species of the genus *Lebbeus* White, 1847 with all available data (GenBank (NCBI) + personal data). Bold indicates the lowest rates (< 0.05 substitutions per 100 nucleotides (< 5%)) of interspecific divergence.

	L. sokhobio	***L. antarcticus***	***L. virentova***	***L. formosus***	***L. carinatus***	***L. java***	***L. kiae***	***L. polaris***
L. antarcticus	**0.014 ±0.005**							
L. virentova	**0.015 ±0.005**	**0.007 ±0.003**						
L. formosus	0.058 ±0.009	0.049 ±0.009	0.054 ±0.009					
L. carinatus	0.065 ±0.010	0.061 ±0.010	0.056 ±0.010	0.061 ±0.010				
L. java	0.087 ±0.011	0.080 ±0.011	0.080 ±0.011	0.088 ±0.011	0.080 ±0.011			
L. kiae	0.139 ±0.015	0.139 ±0.015	0.136 ±0.015	0.143 ±0.015	0.141 ±0.016	0.160 ±0.016		
L. polaris	0.145 ±0.013	0.144 ±0.013	0.142 ±0.013	0.146 ±0.013	0.148 ±0.013	0.159 ±0.013	0.115 ±0.011	
L. groenlandicus	0.160 ±0.016	0.164 ±0.016	0.160 ±0.016	0.166 ±0.016	0.154 ±0.015	0.172 ±0.016	0.141 ±0.015	0.149 ±0.013

Fig. 7. Phylogenetic relationships within Thoridae (*Hippolyte* Leach, 1814 as outgroup) based on COI mtDNA gene markers. Bootstrap support (> 50%) is shown by the numbers along the branches (BA/ML analysis). Line thickness is also correlated with support values.

widely distributed and abundant *Thor amboinensis* (De Man, 1888) (Thoridae), geographic variability is well reflected in genetic changes (Fig.7; Titus *et al.* 2018 for *T. amboinensis*). The Canadian clade of *Lebbeus polaris* (Sabine, 1824) (see Fig. 7) shows a higher degree of COI mtDNA variability than deep-sea *Lebbeus* species from different regions of the world. Perhaps the use of other gene markers will allow deep-sea species to be divided more clearly, using molecular genetic methods, but at the moment there is an insufficient amount of genetic information for comparison in international depositories (e.g., GenBank (NCBI) database).

Distribution

Lebbeus sokhobio sp. nov. is so far known only from the Kuril Basin of the Sea of Okhotsk and is probably endemic for this region in accordance with current knowledge of the limited geographical ranges of species in the genus *Lebbeus* (e.g., Hayashi 1992; Komai *et al.* 2004, 2012; Komai 2015; Anosov *et al.* 2018). In the same bathymetric range along the neighboring Kuril-Kamchatka Trench and the adjacent abyssal plain of the northwestern Pacific, no specimens of this genus were collected, neither during earlier expeditions to the area or as the result of the more recent deep-sea trawling of the KuramBio I–II (Kuril-Kamchatka Biodiversity Studies) Expeditions (Brandt & Malyutina 2012; Brandt *et al.* 2016; Malyutina *et al.* 2018; pers. obs.).

Discussion

Species of caridean families, including Thoridae, hitherto recorded from abyssal depths (below 3000 m) are presented in Table 1. Among them, Acanthephyridae covers the widest bathymetric range, having been collected from the surface in polar seas to depths of at least 6890 m (e.g., Kensley *et al.* 1987; Hendrickx & Estrada Navarrete 1996; Wicksten 2002; Basher & Costello 2014; Linley *et al.* 2018), with some species living within all of this large bathymetric range, e.g., *Hymenodora glacialis* (Havens & Rork 1969; Butler 1980; Just 1980; Wasmer 1986; Domansky 1986; Iwasaki & Nemoto 1987; Hendrickx & Estrada Navarrete 1996; Wicksten 2002; Basher & Costello 2014). Representatives of *Lebbeus* are similarly found in a very wide bathymetric range, from the intertidal zone to the deepest areas (3301–3366 m), in the Sea of Okhotsk.

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Appendix 1. List of additional nucleotide sequences (alignments) of COI mtDNA used for molecular-genetic analysis.

Taxon	GenBank (NCBI) reference
Lebbeus antarcticus	KC494749, KC494750, KC494751, KC494752
Lebbeus carinatus	AF125421, AF125422
Lebbeus formosus	MK409684
Lebbeus groenlandicus	DQ882084, FJ581737, MG312804, MG315672, MG321028, MH242822
Lebbeus java	MK409683
Lebbeus kiae	KT187241, KT187242, KT187243
Lebbeus polaris	FJ581738, FJ581739, HM425371, HQ966810, KP759419, KP759420, MG312952, MG315175, MG317301, MG317885, MG318898, MG319773, MG319844, MG319853, MG319864, MG320139, MG320699, MG321050, MG935131
Lebbeus virentova	JQ837265, KJ566966
Eualus amandae	KC494753, KC494755, KC494757
Eualus avinus	DQ882064, DQ882065
Eualus barbatus	DQ882067, DQ882068, DQ882069
Eualus biunguis	DQ882071, DQ882072, DQ882074
Eualus fabricii	FJ581627, FJ581628, MG313581, MG315523, MG319600
Eualus gaimardii	DQ882075, FJ581629, GU680599, JQ305958, KJ833719, MG311508, MG314000, MG316319, MG316770
Eualus macilentus	FJ581633, FJ581634, FJ58163
Eualus occultus	MG935395
Eualus pusiolus	KT209086, KT209346, KT209527, MG935120
Eualus subtilis	MH242750, MH242751
Eualus suckleyi	DQ882076, DQ882077, MH242752
Spirontocaris arcuata	KJ833723
Spirontocaris holmesi	DQ882153, KJ833721, MG314460
Spirontocaris lamellicornis	DQ882155, DQ882157, MG317259, MH242976, MH242977
Spirontocaris lilljeborgii	FJ581902, FJ581903, KT208836, KT209558, MG934951, MG935142
Spirontocaris ochotensis	KJ833722
Spirontocaris phippsi	DQ882159, MG312751, MG316040
Spirontocaris prionota	MH242978
Spirontocaris sica	DQ882160, DQ882162, KJ833724
Spirontocaris snyderi	KJ833720
Spirontocaris spinus	DQ882163, FJ581908, FJ581909, FJ581910, MG312738, MG313477, MG314259

Thor amboinensis	GQ260961, JQ180245, KU201280, KU201284, KU496552, KX926338, KX926345, KX926393, MF378785, MF378797, MF378800, MF378803, MF378804, MF378805, MF378806, MF378807, MF378808, MF378811, MF378815, MF378817, MF378819, MF378820, MF378821, MF378844, MF378866, MF378880, MF378919, MF378921, MF378964, MF378987, MF378991, MF379021, MF379022
Thor manningi	KX589004
Thoralus cranchii	KJ841675, KT209005, KT209433
Heptacarpus sitchensis	MH242790
Heptacarpus tenuissimus	MH242791
Heptacarpus tridens	MH242792
Heptacarpus sp.	MF745573, MG936583
Outgroup	
Alcyonohippolyte commensalis	KX589001
Alcyonohippolyte dossena	KX589002
Alcyonohippolyte tubiporae	KX589000
Hippolyte bifidirostris	KX588969
Hippolyte catagrapha	KX588970
Hippolyte clarki	KX588971, KX588972
Hippolyte edmondsoni	KX588973, KX588974
Hippolyte holthuisi	KX588978
Hippolyte inermis	KX588976, KX588977
Hippolyte leptocerus	KX588981, KX588982
Hippolyte niezabitowskii	KX588985
Hippolyte obliquimanus	JF794718, JF794734
Hippolyte pleuracanthus	KX588986, KX588987
Hippolyte prideauxiana	KX588989
Hippolyte sapphica	KX588990, KX588991
Hippolyte varians	KT208694, KX588996, MG935168
Hippolyte ventricosa	KX588997, KX588998
Hippolyte williamsi	JF794738, KX588999
Hippolyte zostericola	KU906017, KU906112

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