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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. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia.
Email: coralliodecapoda@mail.ru, vanomarin@yahoo.com
urn:lsid:zoobank.org:author:B26ADAA5-5DBE-42B3-9784-3BC362540034

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 microphthalmus (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 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 10687 m from the Tonga Trench (Paterson et al. 2009). The deepest records of crustaceans are Macrostylis
*mariana* Mezhov, 1993 (Isopoda: Macroductylidae) 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 & Amoaka 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 (Glyphocragonidae); *Neocrangon abyssorum* (Rathbun, 1902), *Sclerocrangon zenkevitchii* Birštein & Vinogradov, 1953 and *Placopsis crangon 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; Komai 2004, 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. frontalisi* 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;
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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. heterochaetus (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 & Peary 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; Bashier & 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. stylostratis* (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 microphthalmalma* (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 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; Bashier & Costello 2014 |
| *H. gracilis* (Smith, 1886) | 1000–3733 m | South Ocean | Spence Bate 1888; Wasmer 1986; Iwasaki & Nemoto 1987; Gorny 1999; Bashier & Costello 2014 |
| *Meningodora mollis* Smith, 1882 | 840–2985 m | Atlantic and Pacific | Chace 1940, 1986; Crosnier & Forest 1973; Kelsney *et al.* 1987 |
| *M. vesca* (Smith, 1886) | 615–5367 m | Atlantic and Pacific | Chace 1940, 1986; Crosnier & Forest 1973; Kelsney *et al.* 1987; Allen & Butler 1994 |
| *Notostomus elegans* A. Milne-Edwards, 1881 | 0–3500 m | Atlantic and Pacific | Crosnier & Forest 1973; Chace 1986; Kelsney *et al.* 1987 |
| *N. gibbosus* A. Milne-Edwards, 1881 | 850–4000 m | Atlantic and Pacific | Crosnier & Forest 1973; Chace 1986; Kelsney *et al.* 1987 |
| Alvinocarididae Christoffersen, 1986 |
| *Alvinocaris markensis* Williams, 1988 | 1693–3650 m | Atlantic, Mid-Pacific 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 2003; Komai *et al.* 2005; Martin & Haney 2005 |
Table 1 (continued). Caridean shrimp species hitherto recorded from depths below 3000 m.

| Species                        | Depth Range (m) | Locations                                    | References                                                                 |
|-------------------------------|-----------------|----------------------------------------------|-----------------------------------------------------------------------------|
| Chorocaris chacei             | 1600–3650       | Atlantic, Mid-Atlantic Ridge                 | Williams & Rona 1986; Williams 1987; Martin & Haney 2005; Komai & Segonzac 2008 |
| C. vandoverae Martin & Hessler, 1990 | 3640           | Pacific, Mariana Back Arc Basin              | Martin & Hessler 1990; Martin & Haney 2005; Nye et al. 2012                 |
| Mirocaris fortunata (Martin & Christiansen, 1995) | 850–3480        | 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       | Indian Ocean, Central Indian Ridge            | Komai et al. 2006                                                          |
| Opeaepele susannae Komai et al., 2007 | 1500–2986      | Atlantic, Mid-Atlantic Ridge                 | Komai et al. 2007; Beltenev et al. 2009                                      |
| Binocaridexexculata Williams & Rona, 1986 | 1700–4088      | 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       | Atlantic, Caribbean                          | Nye et al. 2012                                                             |
| R. kairei Watabe & Hashimoto, 2002 | 2415–3320      | 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      | Arctic: Polar Sea; Iceland                   | Bowman & Manning 1972; Just 1980                                           |
| B. curvirostris Kobjakova, 1957 | 2352–3965      | Arctic: Polar Sea                            | Just 1980                                                                  |
| Crangonidae Haworth, 1825      |                 |                                              |                                                                            |
| Neocarangon abyssorum (Rathbun, 1902) | 887–3200       | N Pacific                                     | Birštein & Vinogradov 1951; Zarenkov 1965; Hiller-Adams & Case 1985; Kim et al. 2000 |
| Parapontophilus abyssi Smith, 1884 | 1400–5852      | Pacific and Atlantic                          | Crosnier & Forest 1973; Chace 1984; Komai 2008                             |
| P. occidentalis (Faxon, 1893)  | 837–4082        | E Pacific                                     | Faxon 1893; Komai 2008; Hendrickx & Papiol 2015                           |
| P. profundus (Spence Bate, 1888) * | 4755           | Tasman Sea                                    | Spence Bate 1888; Komai 2008                                               |
| P. talismani Crosnier & Forest, 1973 | 3411–3517      | NE Atlantic; Caribbean Sea                    | Crosnier & Forest 1973; Gore 1985; Komai 2008                             |
| Placopiscragon formosus Komai & Chan, 2009 | 4807–4824      | W Pacific: Taiwan                            | Komai & Chan 2009                                                          |
| Sclerocrangon zenkevitchii Birštein & Vinogradov, 1953 | 2955–3950      | N Pacific                                     | Birštein & Vinogradov 1953; Kim et al. 2000; Komai 2008                     |
| Disciadidae Rathbun, 1902      |                 |                                              |                                                                            |
| Lucaya bigelowi Chace, 1959    | 4773            | Atlantic: West Indies                         | Chace 1939                                                                 |
| Eugonatonotidae Chace, 1937    |                 |                                              |                                                                            |
| Eugonatonotus chacei Chan & Yu, 1991 (as Galatheacaris abyssalis Vereshchaka, 1997) ** | 2000–5000       | W Pacific: Sulawesi                           | Vereshchaka 1997; Chow et al. 2000                                          |

*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.

| Family                      | Species                                | Depths (m)                  | Locality                               | References                                      |
|-----------------------------|----------------------------------------|-----------------------------|----------------------------------------|------------------------------------------------|
| Glyphocrangonidae           | Glyphocrangon atlantica               | 3400–6373 m Atlantic        | Holthuis 1971; Gore 1985               |
|                             | G. caecescens                          | 2698–3431 m Pacific and Indian | Komai 2004; Komai & Komatsu 2016       |
|                             | G. longirostris                        | 680–3219 m                 | Hiller-Adams & Case 1985               |
| Nematocarcinidae            | Nematocarcinus acanthitelsonis         | 3138–3742 m Atlantic        | Crosnier & Forest 1973; Gore 1985      |
|                             | N. batei                                | 5477 m                     | Burukovsky 2003                       |
|                             | N. challenger                          | 1000–3600 m Atlantic        | Crosnier & Forest 1973; Gore 1985      |
|                             | N. longirostris                        | 3300–4000 m Atlantic: Mediterranean Sea | Company et al. 2004 |
|                             | N. lanceopes                           | 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; Bashier & Costello 2014 |
|                             | N. productus                           | 631–3429 m W Pacific        | Chace 1986                             |
| Oplophoridae                | Oplophorus sp.                          | 944–5050 m Pacific: off New Zealand | Lörz et al. 2012 |
|                             | Systellaspsis braueri                  | 200–4000 m N Atlantic and Pacific | Chace 1940, 1986; Crosnier & Forest 1973; Martin & Haney 2005 |
|                             | S. cristata                            | 200–3200 m Indian, Pacific and Atlantic Oceans | Holthuis 1951; Crosnier & Forest 1968; Foxton 1970 |
|                             | S. debilis                             | 150–5025 m Indian Ocean     | Crosnier 1987; De Man 1920; Chace 1940, 1986; Crosnier & Forest 1973; Baba et al. 1986; Kelsley et al. 1987 |
|                             | S. pellucida                           | 291–3292 m Pacific and Atlantic | Crosnier & Forest 1973; Chace 1986; Chan & Yu 1986; Crosnier 1987; Cardoso & Young 2005; Komai et al. 2018 |
| Pandalidae                  | Styloplanus richardi                   | 0–3600 m Indian, Pacific and Atlantic Oceans | Chace 1940, 1986; Hayashi & Miyake 1969; Crosnier & Forest 1973; Kelsley et al. 1987 |
| Pasiphaeidae                | Parapasiphale scottae                   | 4990 m Atlantic             | Crosnier 1988                          |
|                             | Pasiphaeida scottae                    | 3660 m South Ocean          | Wasmer 1986; Iwasaki & Nemoto 1987; Tiefenbacher 1991, 1994; Gorny 1999; Bashier & Costello 2014 |
| Sergestidae                 | Eusergestes arcticus                   | 3935 m South Ocean          | Doflein & Balss 1912; Iwasaki & Nemoto 1987; Tiefenbacher 1994; Gorny 1999 |
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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

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

| Species | Depth | Location | References |
|---------|-------|----------|------------|
| *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 |
| **Styloactylidae** Spence Bate, 1888 | | | |
| *Bathylocastus* 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 |
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. 3.2.6 for the Bayesian analysis (BA) with an NKY + I + G evolutionary model and using RAxML 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 rRNA) 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;
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 aesthetase-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 sokkobi* 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 2/5; 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 spines, 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) 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* (Kroyer, 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 dactyl of the ambulatory pereiopods, armed with numerous small accessory spinules, the new species may be close to...
Lebbeus sokhobio sp. nov. 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 sokkobio* 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. sokkobio* 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; Lefèbure 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 (Vesicomidae); 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* are 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 |
MARIN I., Thoridae (Crustacea: Decapoda) can penetrate the Abyss

| Species                  | Accession Numbers                                      |
|--------------------------|--------------------------------------------------------|
| 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                                     |