



Two new xylophile cytheroid ostracods (Crustacea) from Kuril-Kamchatka Trench, with remarks on the systematics and phylogeny of the family Keysercytheridae, Limnocytheridae, and Paradoxostomatidae

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Abstract

Keysercythere reticulata **sp. nov.** and *Redekea abyssalis* **sp. nov.**, collected from the wood fall submerged in the Kuril-Kamchatka Trench (Northwestern Pacific), are only the second records of the naturally occurring, wood-associated ostracod fauna from a depth of over 5000 m. At the same time, *K. reticulata* is the second and *R. abyssalis* is the third representative of their respective genera. While *Keysercythere* Karanovic and Brandão, 2015 species are free-living, deep-sea taxa, all *Redekea* de Vos, 1953 live symbiotically on the body surface of wood-boring isopods, *Limnoria* spp. Since *R. abyssalis* is the only genus representative found in the deep sea, we hypothesize that its ancestor colonized this ecosystem as a result of the symbiotic relationship. Newly collected material enabled us to update molecular phylogeny of Cythreioidea based on 18S rRNA gene sequences, especially to clarify the current systematics of the families Keysercytheridae, Limnocytheridae, and Paradoxostomatidae. The resulting phylogenetic tree supports a close relationship between *Keysercythere* and *Redekea* and a distant relationship between two Limnocytheridae lineages, Timiria-seviinae and Limnocytherinae. Consequently, we propose a transfer of *Redekea* from Paradoxostomatidae to Keysercytheridae, and erecting of the two limnocytherid subfamilies onto the family level. The phylogenetic analysis also implies a close relationship between the nominal Limnocytherinae genus and *Keysercythere*+*Redekea* clade, albeit with a low posterior probability, requiring further studies to clarify this.

Key words

Cytheroidea, deep sea, molecular phylogeny, symbiosis, wood-fall fauna, 18S rRNA gene

Introduction

Wood debris is significant natural resource that provides food and habitat for various marine invertebrates whether it is washed ashore or sunk into shallow or deep seafloor (see review by Schwabe et al. 2015). Some invertebrates are highly dependent on these ephemeral habitats for their survival, e.g. the wood-boring bivalves such as genus *Xylophaga* Turton, 1822 (Turner 2002, Voight 2007, Bienhold et al. 2013). In addition, some animals utilize wood resources indirectly by parasitizing or living commensally on wood dwelling animals (e.g. Svavarsson 1982).

The class Ostracoda is ecologically diverse crustacean group inhabiting various aquatic environments, including wood fall. Wood-fall ostracods were first reported by de Vos (1953) who described three cytheroid ostracod species associated with the wood-boring isopod *Limnoria lignorum* (Rathke, 1799): *Aspidoconcha limnoriae* de Vos, 1953 and *Redekea perpusilla* de Vos, 1953 were described from the Netherlands part of the North Sea, while *Laocoonella commensalis* (de Vos, 1953) was described from the Caribbean Sea (Curaçao). The genus *Laocoonella* was proposed as the replacement name for *Laocoon* (see de Vos and Stock 1956), preoccupied by a parasitic mollusk genus. The three genera, *Aspidoconcha* de Vos, 1953, *Redekea* de Vos, 1953, and *Laocoonella* de Vos and Stock, 1956 are members to the families Keysercytheridae (Karanovic and Brandão 2015), Paradoxostomatidae (de Vos and Stock 1956, Wouters and de Grave 1992), and Cytheruridae (McKenzie 1972, Maddocks and Steineck 1987), respectively. They are rare examples of symbiotic lineages in their respective families, because most of their relatives are free-living ostracods. On the other hand, another ostracod family, Entocytheridae, consists of exclusively symbiotic species, and also contains two species, *Microsyssitria nhlabane* Hart and Clark, 1984 and *M. indica* Hart, Nair and Hart, 1967, living commensally on the wood-boring isopod *Sphaeroma terebrans* Bate, 1866 (Hart et al. 1967; Hart and Clark 1984).

Since their first discovery, xylophile ostracods have been reported from wood fall collected from both deep and shallow seas. Maddocks and Steineck (1987) found 14 species from experimental wood panels deployed on the deep-sea floor of Atlantic, Caribbean, and Panama Basins. Among those, two genera, *Thomontocypris* Maddocks, 1991 and *Xylocythere* Maddocks and Steineck, 1987, have been reported from distant hydrothermal vent fields. Their distribution suggests faunal similarity between different types of chemosynthetic ecosystems (Van Harten 1992, 1993, Maddocks 2005, Tanaka and Yasuhara 2016, Tanaka et al. 2019). Steineck et al. (1991) review of living and fossil deep-sea, wood-associated ostracods suggested an ancient origin of xylophile ostracod fauna.

Karanovic and Brandão (2015) were the first to discover a free living, deep-sea, wood-associated ostracod species from naturally sunken wood pieces. Their samples were collected from abyssal plain of the Northwestern Pacific Ocean, during the German-Russian deep-sea

expedition KuramBio (Kurile Kamchatka Biodiversity Studies) (Brandt and Malyutina 2015) on board of the RV *Sonne* in 2012 following the footsteps of the legendary expeditions with RV *Vityaz*. For this new taxon (species and genus), *Keysercythere enricoï* Karanovic and Brandão, 2015, they erected a cytheroid family, Keysercytheridae, and also included *Aspidoconcha* into it. Based on a comprehensive review of the wood-fall fauna, they suggested that Keysercytheridae originated in shallow waters, and that their putative ancestor may have populated deep sea via wood fall. Karanovic and Brandão (2015) also provide for the first time a key to all living cytheroid families based on the soft parts morphology.

The superfamily Cytheroidea is by far the most diverse extant ostracod lineage found in both marine and freshwater environments, from littoral to deep-sea regions, and comprises 44 families, with majority of representatives known from the fossil record and, therefore, only after their shells (see references in Yoo et al. 2019a). Since the shell alone has a limited number of characters that tend to be homoplastic (see Karanovic et al. 2020 and references therein) there are a number of cytheroids lineages with unresolved phylogenetic position. The first insight into the phylogenetic relationship between cytheroid families based on 18S rDNA (see Yamaguchi 2003) supported homoplasticity of major taxonomic characters of the shell, such as the structure of the hinge. Karanovic and Brandão (2015) also stressed that many families need to be revised from the point of the well-established, important taxonomic characters of the soft body parts, because many lineages seem to be polyphyletic. Among others, the authors question the position of *Redekea* in Paradoxostomatidae, due to the morphology of its mouth parts. They also failed to include a large, mostly freshwater family, Limnocytheridae in the key, arguing that its two, currently recognized, lineages have very different morphology of important soft body parts such as maxillula and the antennula. Beside, one (Timiriaseviinae) carries eggs in the posterior extension of the shell (brood pouch) and the other (Limnocytherinae) not.

During the KuramBio II expedition (RV *Sonne*, 250th Expedition) (Brandt et al. 2016, 2020), we retrieved several natural wood fragments from trawled bottom sediments and found a number of ostracods, including two undescribed species – one belonging to *Keysercythere* and the other to *Redekea*. This is the second record of wood-associated ostracod fauna from abyssal plains of the world. The aim of this study is to describe the two species and update current molecular phylogeny of Cytheroidea based on 18S rRNA gene, especially to clarify the position and systematics of Keysercytheridae, Limnocytheridae, and Paradoxostomatidae. For this purpose, we sequenced the 18S rRNA region of one Keysercytheridae representative (*Keysercythere enricoï*), two representatives of Paradoxostomatidae (the new *Redekea* and *R. californica* de Vos and Stock, 1956), and one representative of Limnocytheridae (*Gomphodella hirsuta* Karanovic, 2006). Our dataset also includes 18S rRNA gene sequences of other cytheroids taxa available on GenBank.

Materials and methods

Sampling

Wood fragments were collected from the sampling station SO250_9 at the Kuril-Kamchatka Trench region during the KuramBio II expedition (RV *Sonne*, 250th Expedition) on 19 August, 2016 by Agassiz-Trawl (AGT), trawled from 43° 48.43'N, 151° 44.35'E, 5134 m to 43° 47.64'N 151° 44.51'E, 5101 m. Details of the AGT deployments can be found in the KuramBio II Cruise Report (Brandt et al., 2016, 2020). The collected material was transferred to a bucket with seawater and fractionated with 500 µm and 300 µm sieves. A total of 203 ostracod specimens were picked from the remnants in the 300 µm sieve. In addition, three ostracod specimens were obtained by washing a body of *Limnoria* sp. The collected ostracod specimens were fixed in 96% ethanol and preserved at –20°C for taxonomic description and DNA extraction.

Morphological study

The soft body parts were separated from the valves and dissected using fine needles under a stereo-binocular microscope (SZX 12, OLYMPUS). The valves were preserved on a cardboard cell slide and the soft parts mounted in CMC-10 mounting media (Masters Company, USA), on glass slides. The specimens were then observed and sketched using a transmitted light binocular microscope (BX 51, OLYMPUS) with a differential interference contrast system and a camera lucida. The valves were platinum coated and photographed with the Hitachi S-4700 scanning electron microscope (SEM) at Eulji University (Seoul). All specimens studied herein were deposited in the Crustacea collection of the Senckenberg Research Institute and Natural History Museum Frankfurt (SMF).

Abbreviation used in taxonomic descriptions and figures

L, Length; **H**, Height; **RV**, Right valve; **LV**, Left valve; **A1**, Antennula; **A2**, Antenna; **Md**, Mandibula; **Mxl**, Maxillula; **L5-7**, 5th-7th limb; **Hp**, Hemipenis.

DNA extraction, amplification, and sequencing

DNA was extracted from all studied specimens with lysis buffer that was prepared according to Williams et al. (1992). All polymerase chain reactions (PCR) achieved total volume of 27 µl containing: 5 µl of diluted DNA template, 1 µl of each forward and reverse primer, 15 µl ultra distilled water and 5 µl AccuPower PCR Premix (Bioneer Inc.). Fragments of nuclear 18S rDNA were amplified using the primer pairs F1/R9 and F2/R8 from Yamaguchi and Endo (2003). However, these primers

were not successful for all specimens and resulted in relatively short sequences. Consequently, additional primers, described in Yu et al. (2006), were used in order to get longer sequences. The primer pair P1 and P2 was used for the initial amplification of all sequences. The PCR products from this reaction were than used as DNA templates with primer pairs P1-P1W1 and P2W1-P2 under the same PCR settings as the initial amplifications, with the exception that template was 1 µl or 1.5 µl and the water 17.5 µl to 18 µl. The PCR setting consisted of the initial denaturation for 5 min at 95°C. PCR setting followed by 35 cycles of 30 s denaturation at 94°C, 1 min annealing at 50°C, 1 min extension at 72°C. For all PCR amplification, a final extension was at 72°C for 10 min before decreasing to 4°C at the end. PCR products were electrophoresed with agarose 1%, 0.5X TAE buffer, and marker 100bp for 20 min at 100V to determine the presence the band size of DNA. PCR products were purified by ethanol precipitation method neutralizing by Sodium acetate pH 5.5 and sequenced in both strands to confirm sequence reliability by the Sanger method for dideoxy sequencing (Macrogen Inc., Korea).

Molecular phylogenetic analysis

All obtained sequences were visualized using Finch TV version 1.4.0 (<http://www.geospiza.com/Products/finchtv.shtml>) to check for the quality of signal and sites with possible low resolution, and corrected by comparing forward and reverse strands. BLAST algorithm (Altschul et al. 1990, 1997) was used to check the identity of obtained sequences. Sequences were aligned in MEGA X (Kumar et al. 2018) with ClustalW (Thompson et al. 1994) with default parameters. Beside newly obtained sequences, we also used 45 published sequences belonging to various cytheroid taxa (for the full list of GenBank numbers of the new and downloaded sequences, see Table 1). We have chosen *Terrestricythere pratensis* Schornikov, 1980, a member Terrestricytheroidea, the sister superfamily of Cytheroidea as the outgroup to root the tree. The ambiguous sites were removed from the alignment with the aid of GBLOCKS 0.91b (Castresana 2000). Final alignment was 1163 base pairs long and contained 207 parsimony informative sites. For the best fit evolutionary model, program jModelTest 2.1.6 (Darriba et al. 2010, Guindon and Gascuel 2003) was used with the Akaike information criterion (Hurvich and Tsai 1989), which proposed GTR+I+G model of molecular evolution (Tavaré 1986). Bayesian Inference, implemented in BEAST v2.5 (Bouckaert et al. 2014), was used to estimate phylogenetic relationships. Settings included the best fit evolutionary model with four gamma categories and a strict molecular clock. Yule process (Gernhard 2008) was used as a tree prior, with BEAST default log normal distribution of the species birth rate. The analysis run for 10,000,000 generations, sampling every 1,000 generations. Software Tracer (Rambaut et al. 2018) was used to visualize results of the BEAST analyses and FigTree v1.4.3 for tree visualization.

Table 1. List of 18S rDNA sequences used for phylogenetic analysis.

Species	GenBank no.
<i>Actinocythereis costata</i> (Hartmann, 1978)	AB076652
<i>Albileberis sheyangensis</i> Chen, 1982	AY863436
<i>Aurila disparata</i> Okubo, 1980	AB076643
<i>Bicornucythere bisanensis</i> (Okubo, 1975)	AB076649
<i>Bradleya nuda</i> Benson, 1972	AB076647
<i>Bythoceratina hanejiensis</i> Nohara, 1987	AB076619
<i>Caudites asiaticus</i> Zhao and Whatley, 1989	AB076646
<i>Chelonocythereis omutai</i> Tanaka and Hayashi, 2019	LC380021
<i>Coquimba ishizakii</i> Yajima, 1978	AB076645
<i>Cythere lutea</i> O. F. Müller, 1785	AB076636
<i>Cytheromorpha acupunctata</i> (Brady, 1880)	AB076630
<i>Cytheropteron subuchioi</i> Zhao, 1988	AB076628
<i>Gomphodella hirsuta</i> Karanovic, 2006	MW338930
<i>Hemicytherura kajiyamai</i> Hanai, 1957	AB076627
<i>Hirsutocythere hanaii</i> Ishizaki, 1981	AB076653
<i>Howeina</i> sp.	AB076626
<i>Ishizakiella miurensis</i> (Hanai, 1957)	AB076632
<i>Keijia demissa</i> (Brady, 1868)	AB076622
<i>Keysercythere enricoi</i> Karanovic and Brandão, 2015	MW338924
<i>Kotoracythere inconspicua</i> (Brady, 1880)	AB076621
<i>Leptocythere lacertosa</i> (Hirschmann, 1912)	AB076631
<i>Leptocythere polymorpha</i> Schornikov, 1974	AB674963
<i>Leptocythere ventriculivosa</i> Chen, 1982	AY863435
<i>Limnocythere</i> sp.	AB076635
<i>Loxocorniculum mutsuense</i> Ishizaki, 1971	AB076629
<i>Metacypris digitiformis</i> Smith and Hiruta, 2004	AB674964
<i>Neomonoceratina crispata</i> Hu, 1976	DQ531763
<i>Neomonoceratina microreticulata</i> Kingma, 1948	AB076637
<i>Paradoxostoma setoense</i> Schornikov, 1975	AB076623
<i>Parakrithella pseudadonta</i> Hanai, 1959	AB076639
<i>Perissocytheridea japonica</i> Ishizaki, 1968	AB076642
<i>Pistocythereis bradyformis</i> (Ishizaki, 1968)	AB076650
<i>Pontocythere</i> sp.	AB076641
<i>Pontocythere subjaponica</i> (Hanai, 1959)	AB076640
<i>Psammocythere oviformis</i> Hiruta, 1991	AB674961
<i>Redekea abyssalis</i> sp. nov.	MW338927
<i>Redekea californica</i> de Vos and Stock, 1956	MW338929
<i>Robustaurila salebrosa</i> (Brady, 1869)	AB076644
<i>Semicytherura striata</i> (Sars, 1866)	AB076625
<i>Spinileberis quadriaculeata</i> (Brady, 1880)	AB076638
<i>Tanella opima</i> Chen, 1982	AY86343
<i>Tenedocythere transoceanica</i> (Teeter, 1975)	AB076648
<i>Trachyleberis</i> sp.	AB076651
<i>Uncinocythere occidentalis</i> (Kozloff and Whitman, 1954)	AB674962
<i>Xestoleberis hanaii</i> Ishizaki, 1968	AB076633
<i>Xestoleberis</i> sp.	AY191450
<i>Xiphichilus</i> sp.	AB076624
<i>Xylocythere sarrazinae</i> Tanaka, Lelièvre and Yasuhara, 2019	LC380020
<i>Terrestricythere pratensis</i> Schornikov, 1980	AB674959

Results

Molecular phylogeny

Tracer analysis of the BEAST results showed that the effective sample size for all measured parameters (posterior, likelihood, priors, tree likelihood, tree height, Yule model, birth rate, etc.) was far above the recommended 200, suggesting a sound estimation of the posterior distribution. The BEAST analyses produced the phylogram presented on the Fig. 1. The monophyly of Cytheroidea has not received a high posterior probability, with low support for the *Bythoceratina hanejiensis* Nohara, 1987, *Psammocythere oviformis* Hiruta, 1991, and *Uncinocythere occidentalis* (Kozloff and Whitman, 1954) branches. The monophyly of the rest of the cytheroids was, on the other hand, supported with the posterior probability of 0.99. While most terminal branches received a high support (from 0.98 to 1), the deeper phylogeny was not well-resolved leading to the uncertain phylogenetic relationships between cytheroids families. Nevertheless, the most important results of this analysis are the position of the genera *Gomphodella* De Deckker, 1981, *Limnocythere* Brady, 1868, *Keysercythere*, and *Redekea*. The first two genera although members of the same family, Limnocytheridae, are far apart on the tree, and belong to different lineages. While *Gomphodella* clusters (posterior probability 1) with another Timiriaseviinae genus (*Metacypris* Brady and Robertson, 1870), *Limnocythere* forms a clade with *Keysercythere* and *Redekea*. This clade received a very low support (0.67). The clade *Keysercythere-Redekea* received the highest posterior probability, and, at the same time, *Redekea* is on the tree far from other representatives of the family Paradoxostomatidae (*Chelonocythereis* Tanaka and Hayashi, 2019; *Paradoxostoma* Fischer, 1855, and *Xiphichilus* Brady, 1870) to which it belongs at the moment.

Taxonomy

Order Podocopida Sars, 1866

Superfamily Cytheroidea Baird, 1850

Family Keysercytheridae Karanovic and Brandão, 2015

Genus *Keysercythere* Karanovic and Brandão, 2015

***Keysercythere enricoi* Karanovic and Brandão, 2015**

Fig. 2

Material examined. Four specimens dissected, valves preserved in one cardboard cell slide (SMF 57049–57052). Seventy-five specimens undissected, stored in one vial filled with 80% ethanol. All specimens

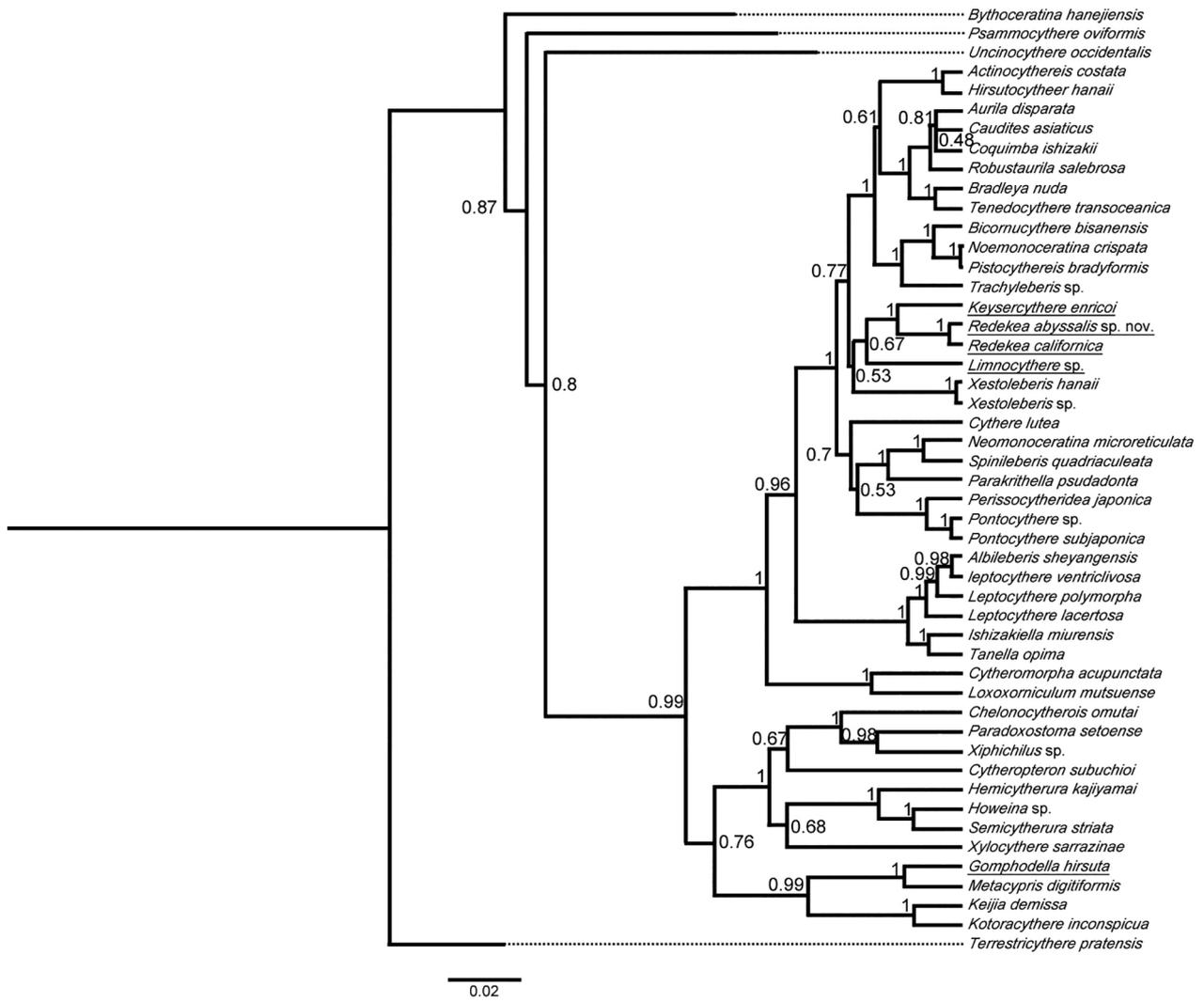


Figure 1. Bayesian inference cladogram of the cytheroidean families based on 18S rDNA sequences. Numbers above branches represent posterior probability. The discussed genera are underlined.

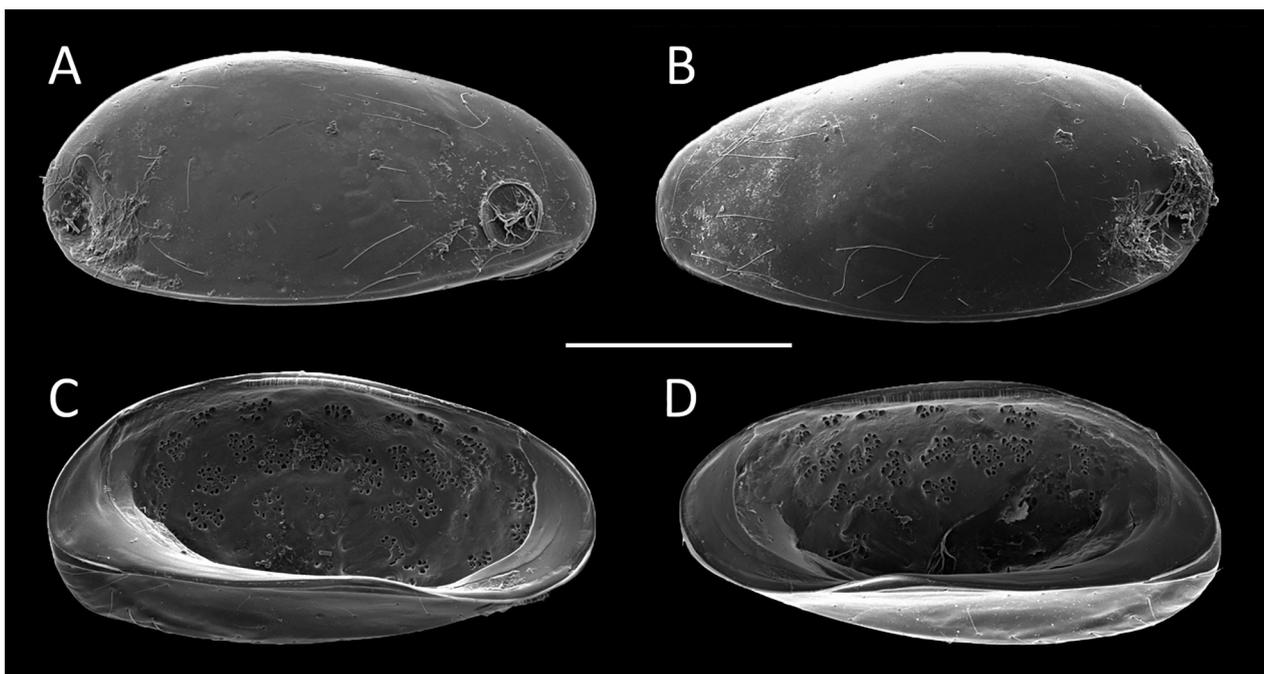


Figure 2. Scanning electron microscope images of valves of *Keysercythere enricoi*. A RV, external lateral view B LV, external lateral view C LV, internal lateral view D RV, internal lateral view. Scale bar: 200 μ m.

were collected from the sampling station SO250_9 of KuramBio II expedition (RV *Sonne*, 250th Expedition), trawled from 43°48.43'N, 151°44.35'E, 5134 m to 43°47.64'N 151°44.51'E, 5101 m by AGT on 19th August, 2016.

Distribution. This species has been found from the abyssal plain of Northwestern Pacific, ranging from 39°43.47'N, 147°10.11'E, 5229 m to 39°42.54'N, 147°9.51'E, 5217 m (Karanovic and Brandão 2015). This study is the second record of *Keysercythere enricoi*, and it is collected from sunken natural wood pieces on deep-sea in the same way as previous report (Karanovic and Brandão 2015). Because we found this species approximately 600 km to the southwest from the type locality, it must be widely distributed in this area, and its distribution can be associated with natural wood falls scattered on the deep-sea floor.

DNA sequence. The 18S rDNA sequence of two specimens were obtained. GenBank accession numbers are MW338924 (1704 bp) and MW338925 (1256 bp).

Keysercythere reticulata sp. nov.

Figs 3–7

<http://zoobank.org/D8A5E8AE-C17D-4A2F-B762-F51E3C-BFCA70>

Material examined. Holotype: adult male (SMF 57053), RV L 0.38 mm, H 0.18 mm; LV L 0.38 mm, H 0.16 mm; dissected, soft parts mounted on two glass slide and valves on cardboard cell slide. **Paratypes:** 1 adult female (SMF 57054); dissected, soft parts mounted on a glass slide and valves on a cardboard cell slide: 1 juvenile (SMF 57055) in 80% ethanol.

Type locality. Kuril–Kamchatka Trench region, the sampling station SO250_9 of KuramBio II expedition (RV *Sonne*, 250th Expedition), trawled from 43°48.43'N, 151°44.35'E, 5134 m to 43°47.64'N 151°44.51'E, 5101 m by AGT on 19th August, 2016.

Diagnosis. Shell trapezoidal in lateral view, with inflated medial portion of the shell. L around 0.38 mm. External surface of carapace reticulated characterized by polygonal muri and pitted secondary reticulation within the fossae. Sensilla long existing non-collar pores surrounded with distorted shaped sieve pores (Type C pore; see review by Danielopol et al. 2018). Hp: ejaculatory duct coiled many times; hook-like process rectangular shape with round corners and a concave along distal margin; distal lobe broad sub-triangular shape.

Description of adult male (based on holotype SMF 57053). **Carapace** (Figs 3, 4A–D, G) trapezoidal in lateral view, with inflated medial portion of the shell (Fig. 3). L around 0.38 mm. Greatest H situated behind middle L, equaling 35% of total L. Dorsal margin somewhat roughly rounded, dorso-anterior margin converge rapidly anteriorly to a pointed tip located near the ventral margin, ventro-anterior margin relatively gently converge comparing with dorso-anterior margin, ventral margin concave immediately situated in front of middle L. Posterior margin slightly broader than anterior margin. Both valves bearing one protrusion on posterior end. External surface reticulated characterized by polygonal muri and pitted secondary reticulation within the fossae (Fig. 4A, D, G). Sensilla long existing non-collar pores surrounded with distorted shaped sieve pores (Fig. 4G); sieve pores clearly arranged in clusters, visible as pockmarks on the inside of the shell; approximate length major axis 6–30 µm and mi-

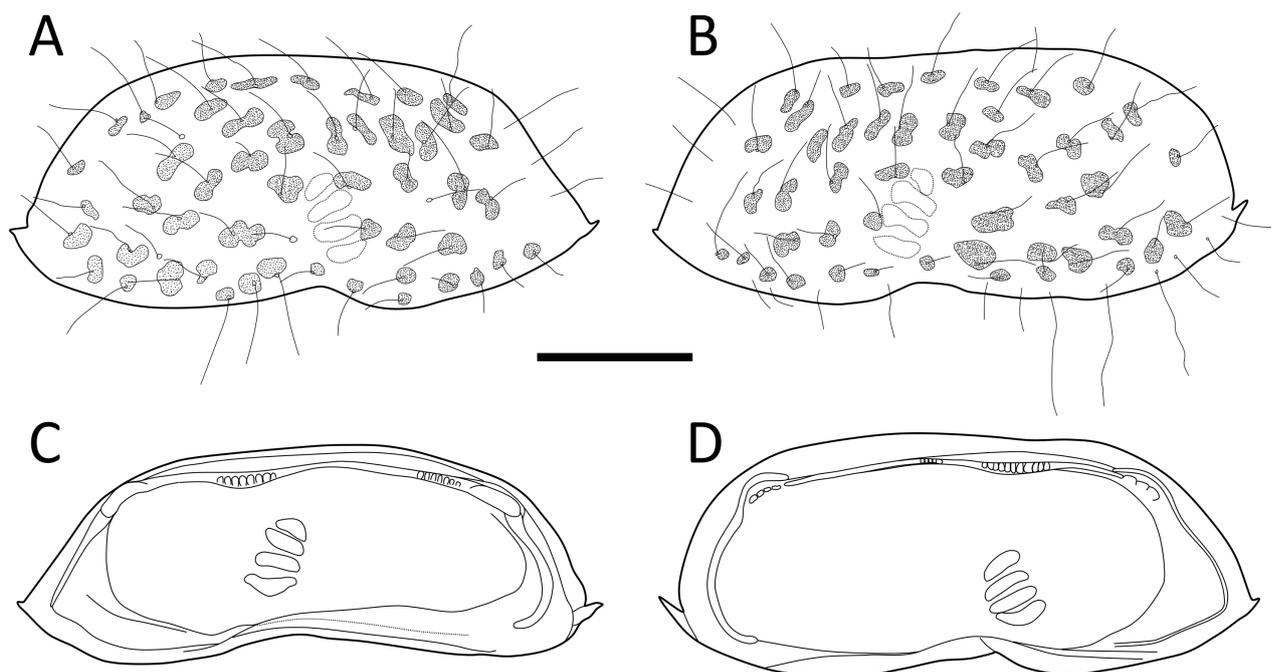


Figure 3. *Keysercythere reticulata* sp. nov., male, holotype (SMF 57053). **A** RV, external lateral view **B** LV, external lateral view **C** RV, internal lateral view **D** LV, internal lateral view. Scale bar: 100 µm.

nor axis 6–12 μm (Fig. 4B, D). Some simple pores (Type A sensu Puri and Dickau, 1969) existing on rim (Fig. 4H). Inner calcified lamella broadly developed anteriorly and posteriorly in both valves (Fig. 3). Four adductor muscle scars form a vertical row (Fig. 3). Hingement merodont: LV carrying dents in medial element, posterior element with several sockets, anterior element with several shallow sockets (Fig. 4D); RV with corresponding grooves in medial element, anterior and posterior elements elon-

gated knob with shallow dents (Fig. 4B). *AI* (Fig. 5A) six podomeres [four and five podomeres divided by suture, same as defined 4a and 4b by Smith and Tsukagoshi (2005) and Boxshall et al. (2010)]. First podomere bare. Second podomere 1.5 times as long as first podomere, with one lateral distal seta. Third podomere one-third as long as first podomere, with one long antero-distal seta. Fourth to sixth podomeres same length as third podomere. Fourth podomere with one long antero-distal seta and one

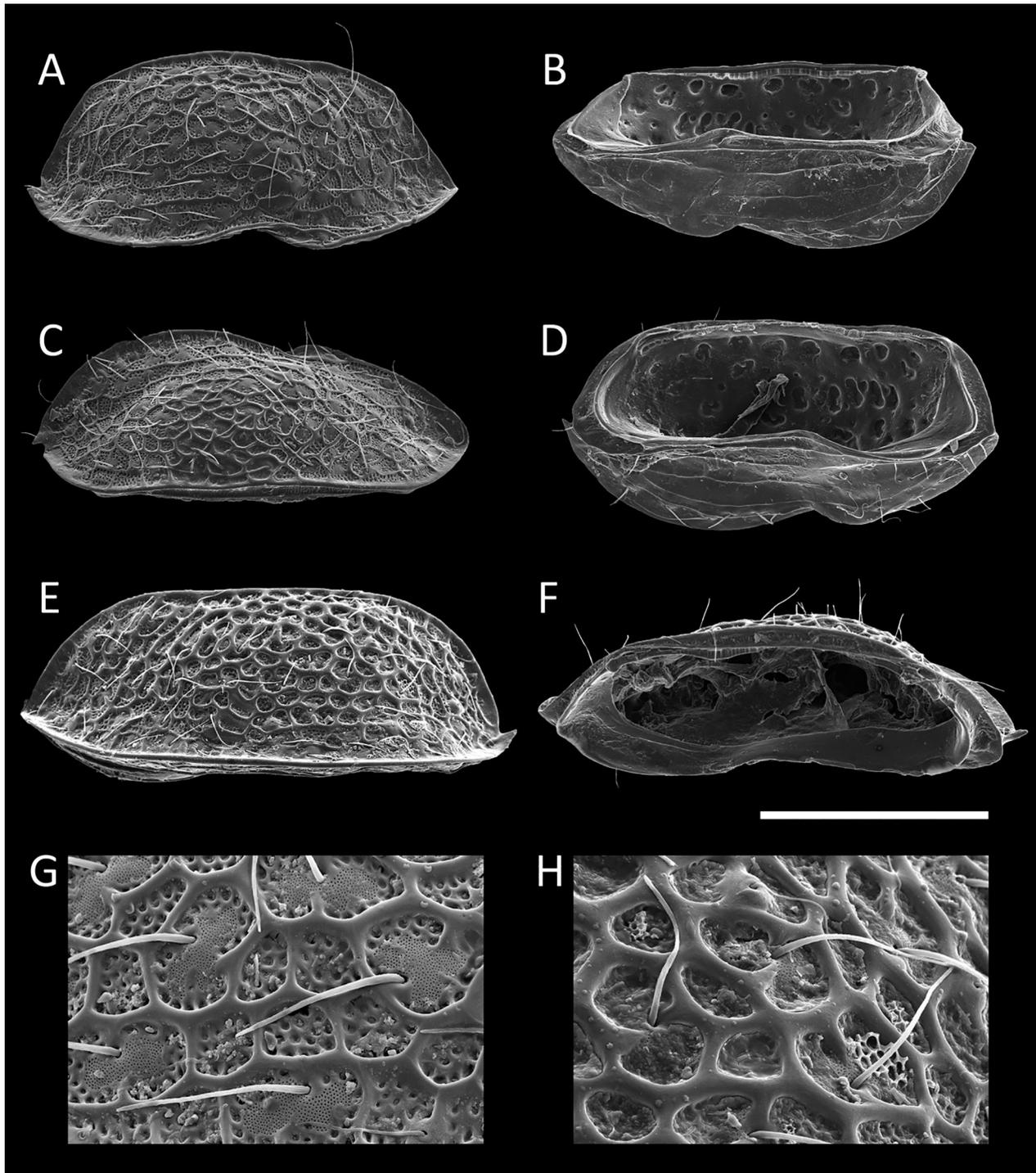


Figure 4. Scanning electron microscope images of valves of *Keysercythere reticulata* sp. nov. **A–D, G** male, holotype (SMF 57053) **E, F, H** female, paratype (SMF 57054). **A** RV, external lateral view **B** RV, internal ventro-lateral view **C** LV, external dorsal view **D** LV, internal ventro-lateral view **E** LV, external lateral view **F** LV, internal lateral view **G** RV, reticulation and pore system, external lateral view **H** LV, reticulation and pore system, external lateral view. Scale bar: 200 μm (**A–F**); 30 μm (**G, H**).

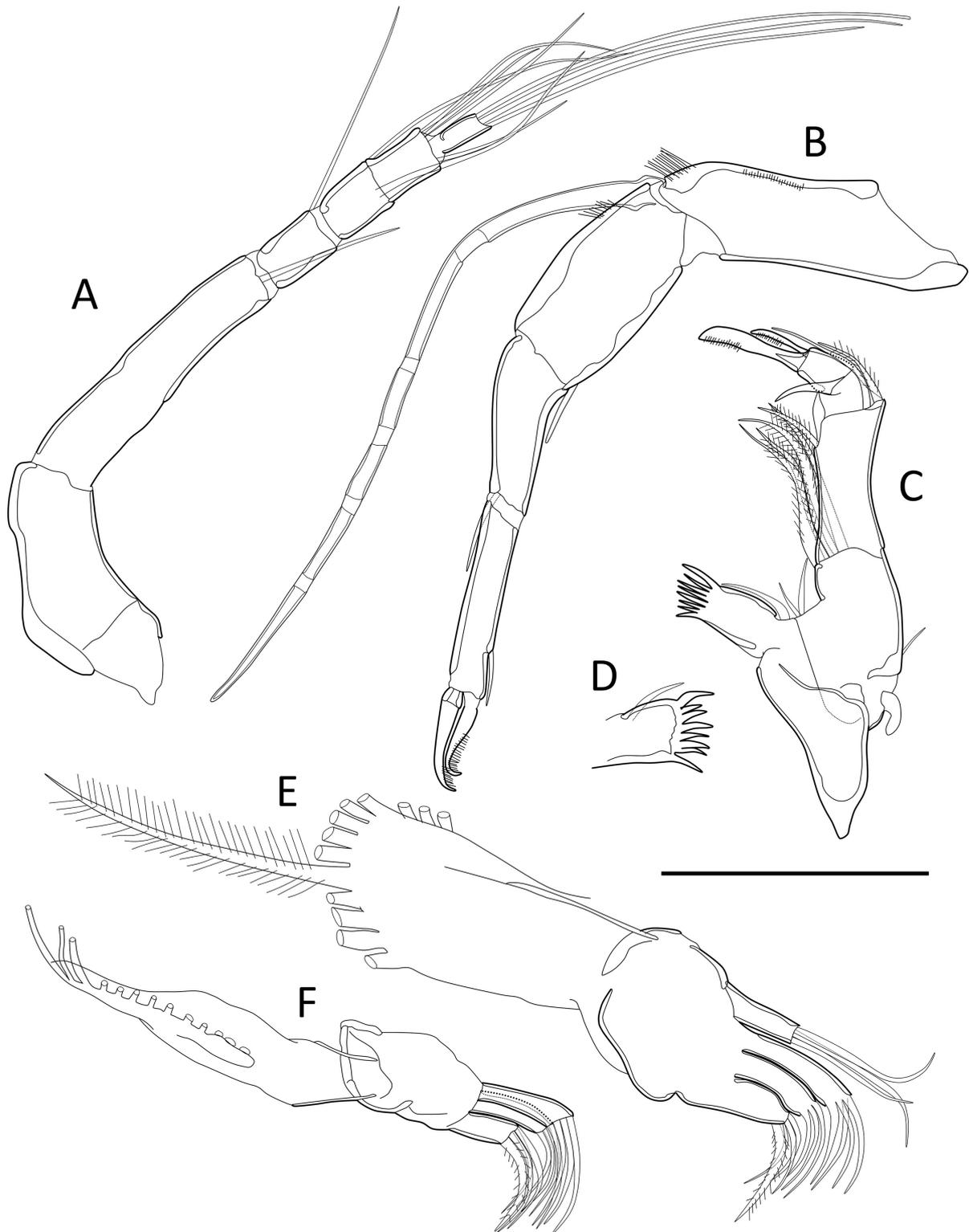


Figure 5. *Keysercythere reticulata* sp. nov. A–D, F male, holotype (SMF 57053) E female, paratype (SMF 57054). A A1 B A2 C Md D coxal endite of Md E Mx1 F Mx1, palp lost. Scale bar: 50 μ m.

long lateral distal seta. Fifth podomere with three long antero-distal setae and one long postero-distal seta. Sixth podomere with two long distal setae and one long blunt tipped distal seta. *A2* (Fig. 5B) five articulated podomeres. First podomere (basis) parallelogram-shaped, with setulae on antero-distal margin and one long six-annulated exopodite (spinneret seta) on antero-distal end. Second (first endopodal) podomere four-fifths as long as first podomere,

with one short postero-distal spine. Third (second endopodal) podomere two-thirds as long as first podomere, with one short antero-distal seta. Fourth (third endopodal) podomere four-fifths as long as first podomere, with one stout postero-distal claw with curved tip and a row of setulae on posterior margin. Fifth (fourth endopodal) podomere small, with one stout distal claw with a row of setulae on postero-distal margin. *Md* (Fig. 5C, D) coxa

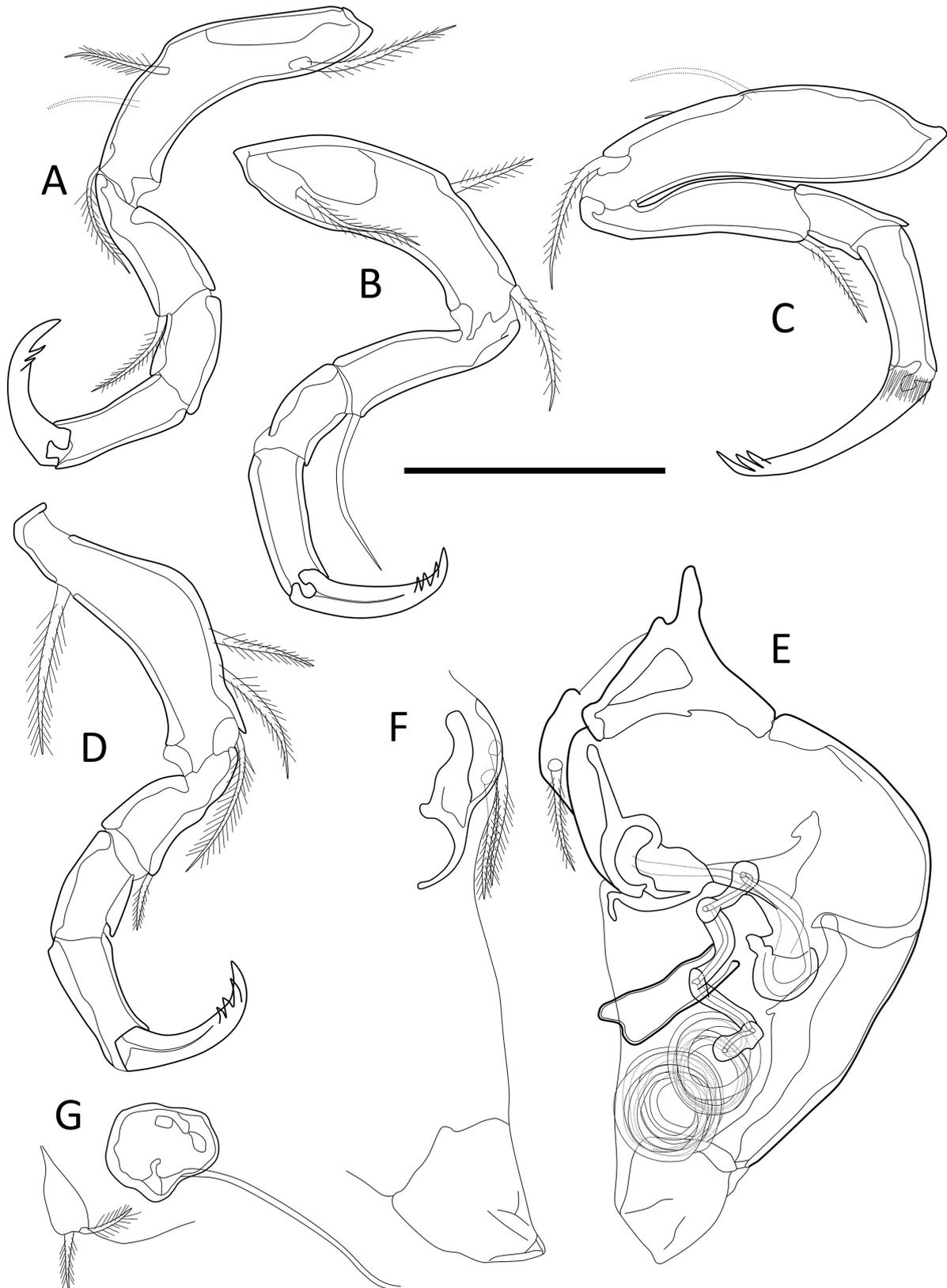


Figure 6. *Keysercythere reticulata* sp. nov. A–C, E, F male, holotype (SMF 57053) D, G female, paratype (SMF 57054). A L5 B L6 C L7 D L5 E left Hp F part of right Hp G female copulatory organ. Scale bar: 50 μ m.

with one dorsal seta. Coxal endite consisting of eight teeth. Palp consisting of four podomeres. First podomere (basis) with one finger-like shaped sheet (exopodite) near proximal end, one short seta on dorsal margin, two short setae on ventral margin, and four long setulous setae on

ventral side of distal margin. Second podomere with one setulous ventro-distal seta, one simple and setulous dorso-distal setae. Third podomere with one stout lateral distal claw. Fourth podomere with one broad and one slender distal claws each curved distally and with a row of setae

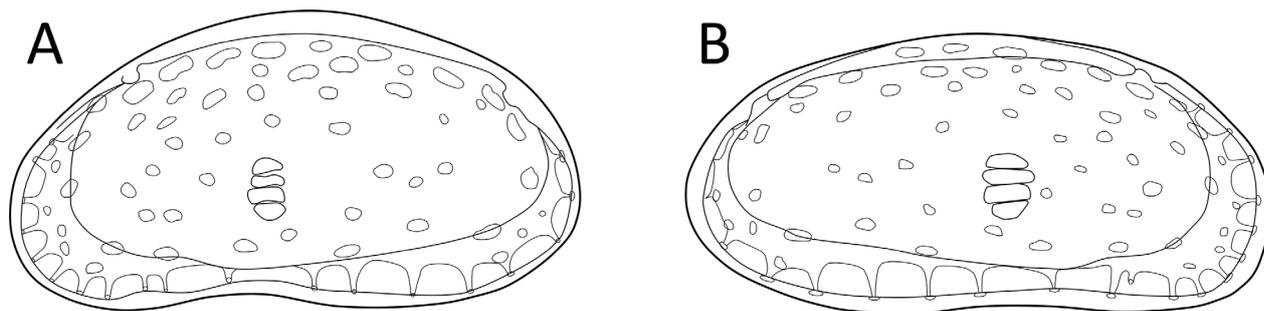


Figure 7. *Redekia abyssalis* sp. nov., male, holotype (SMF 57056). **A** RV, internal lateral view **B** LV, internal lateral view. Scale bar: 100 μ m.

on ventral margin. **Mxl** (Fig. 5F) branchial plate (exopodite) with 11 plumose setae. Basal podomere with one palp (lost) and three endites. Endites: dorsal one with four simple distal setae; middle one with three simple distal setae; ventral one with three simple distal setae and one setulous distal seta. **L5** (Fig. 6A) four articulated podomeres. First podomere with two plumose antero-lateral setae, one plumose antero-distal seta, and one plumose dorso-proximal seta. Second podomere half as long as first podomere, with one plumose antero-distal seta. Third podomere one-third as long as first podomere, bare. Fourth podomere half as long as first podomere, with one stout sclerotized distal claw with a few sharp spines on antero-distal margin. **L6** (Fig. 6B) four articulated podomeres. First podomere with one plumose antero-lateral seta, one plumose antero-distal seta, and one plumose dorso-proximal seta. Second podomere half as long as first podomere, with one long simple antero-distal seta. Third podomere one-fourth as long as first podomere, bare. Fourth podomere three-eighths as long as first podomere, with one stout sclerotized distal claw with a few sharp spines on antero-distal margin. **L7** (Fig. 6C) four articulated podomeres. First podomere with two simple antero-lateral setae and one plumose antero-distal seta. Second podomere three-fourths as long as first podomere, with one plumose antero-distal seta. Third podomere one-fourth as long as first podomere with a row of setulae on distal margin. Fourth podomere half as long as first podomere, with one stout sclerotized distal claw with a few sharp spines on antero-distal margin. **Brush-shaped organ** absent. **Hp and posterior body** (Fig. 6E, F) symmetrical. Ejaculatory duct coiled many times. Hook-like process rectangular shape with round corners and a concave along distal margin. Distal lobe broad sub-triangular shape. Posterior body left and right sides bearing two setulous furcal setae.

Description of adult female (based on paratype SMF 57054). **Carapace** (Fig. 4E, F, H) trapezoidal in lateral view, with inflated medial portion of the shell. LV, L 0.43 mm, H 0.17 mm. Dorsal and ventral margins almost flat. Both valves bearing one protrusion on posterior end. Muri of surface reticulation thicker than that of male. **Mxl** (Fig. 5E) branchial plate (exopodite) with 13 plumose setae. Basal podomere with one palp (endopodite) and three endites. Palp consisting of one podomere, with three simple

distal setae. Endites: dorsal one with four simple distal setae; middle one with four simple distal setae; ventral one with three simple distal setae and one setulous distal seta. **L5** (Fig. 6D) small difference against male's L5: one plumose antero-distal seta shorter rather than that of male. **Copulatory organ and posterior body** (Fig. 6G) female genital opening paired. Sclerotized framework of genital opening roughly circular. Spermathecal duct long connecting with genital opening. Genital lobe paired with each two setulous furcal setae.

Etymology. Named after reticulated surface ornamentation of the carapace.

Distribution. Only recorded from the type locality.

Remarks. *Keysercythere reticulata* can be easily distinguished from the only other species of the genus, *Keysercythere enricoi*, by the carapace surface ornamentation: the former has a strongly reticulated, while the latter has smooth surface. Ventral margin of valves is concave in the new species versus convex in *K. enricoi*. The morphology of Hp is also different: the hook-like process is rectangular and the distal lobe is broad sub-triangular in the new species, while the hook-like process is semi-circular and the distal lobe is acute sub-triangular with sharply bended tip in *K. enricoi*.

Genus *Redekia* de Vos, 1953

Redekia abyssalis sp. nov.

Figs 8–10

<http://zoobank.org/D30A4580-7909-4541-A076-F41B02BD-1B2B>

Material examined. **Holotype:** adult male (SMF 57056), LV; L 0.32 mm, H 0.16 mm; RV; L 0.31 mm, H 0.17 mm. Dissected, soft parts mounted on two glass slides and valves on a cardboard cell slide. **Paratypes:** 1 adult male (SMF 57057); dissected, soft parts mounted on a glass slide and valves on a cardboard cell slide; 2 female (SMF 57058, 57059); dissected, soft parts mounted on a glass slide and valves on a cardboard cell slide.

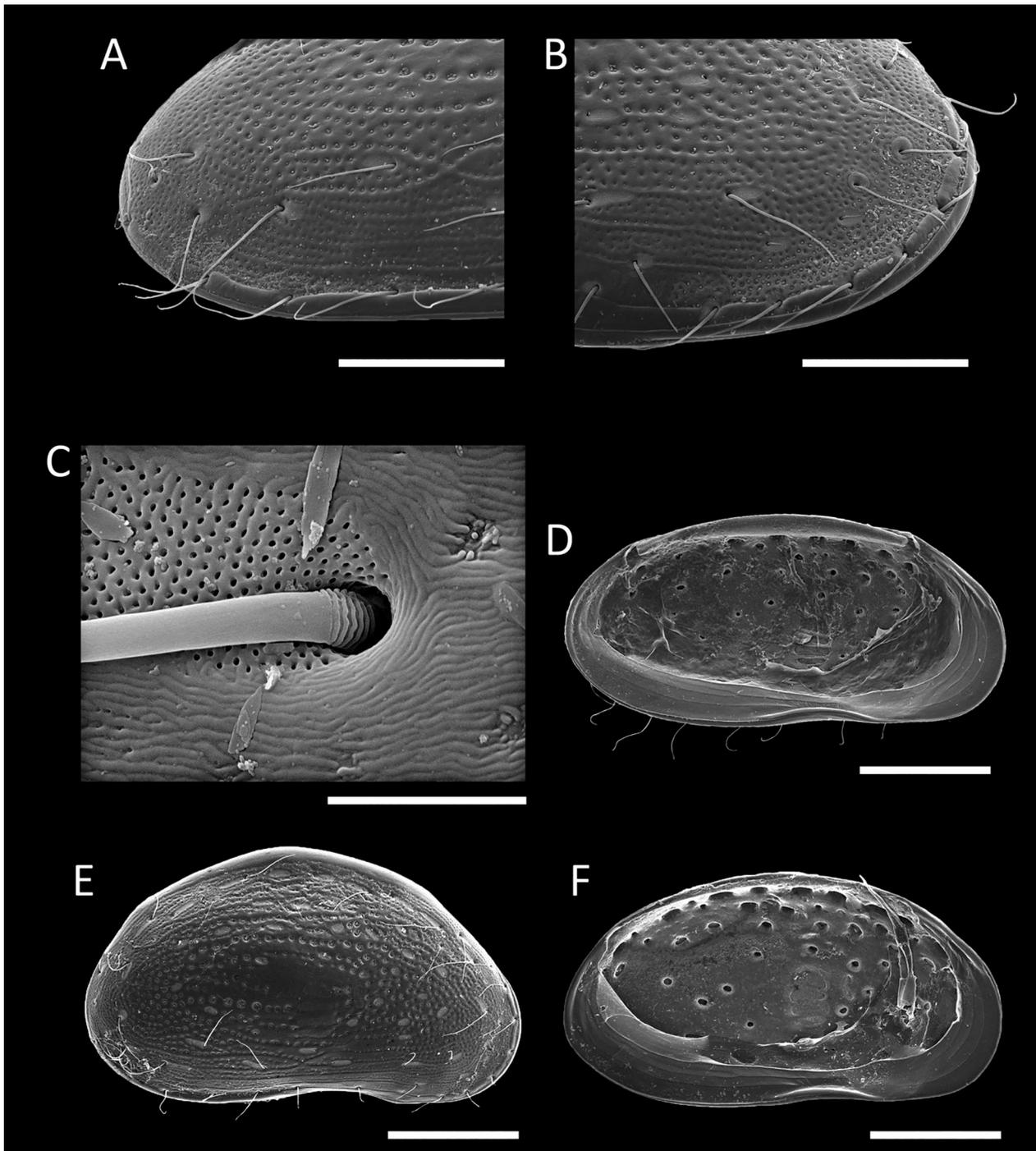


Figure 8. Scanning electron microscope images of valves of *Redekea abyssalis* sp. nov. **A–D** male, holotype (SMF 57056) **E, F** female, paratype (SMF 57058). **A** RV, posetro-ventral area, external lateral view **B** RV, antero-ventral area, external lateral view **C** RV, pore system, external view **D** LV, internal lateral view **E** RV, external lateral view **F** LV, internal lateral view. Scale bars: 50 µm (A–C); 100 µm (D–F).

Type locality. Kuril–Kamchatka Trench region, the sampling station SO 250_9 of KuramBio II expedition (RV *Sonne*, 250th Expedition), trawled from 43°48.43'N, 151°44.35'E, 5134 m to 43°47.64'N 151°44.51'E, 5101 m by AGT on 19th August, 2016. Holotype (SMF 57056) and 2 paratypes (SMF 57058, 57059) were obtained by washing a body of *Limnoria* sp.

Diagnosis. Shell sub-triangular in lateral view. LV; L 0.32 mm, H 0.16 mm: RV; L 0.31 mm, H 0.17 mm. Great-

est H situated just behind middle L. External surface of carapace covered with shallow pits except central and mid-ventral areas of valves; pits size increasing from marginal to near central area of valves. Sensilla long existing non-collar pores surrounded with sieve pores. Hp: ejaculatory duct short and curved; hook-like process elongated conical shape; distal lobe sub-triangular.

Description of adult male (based on holotype SMF 57056). **Carapace** (Figs 7, 8A–D) sub-triangular in lat-

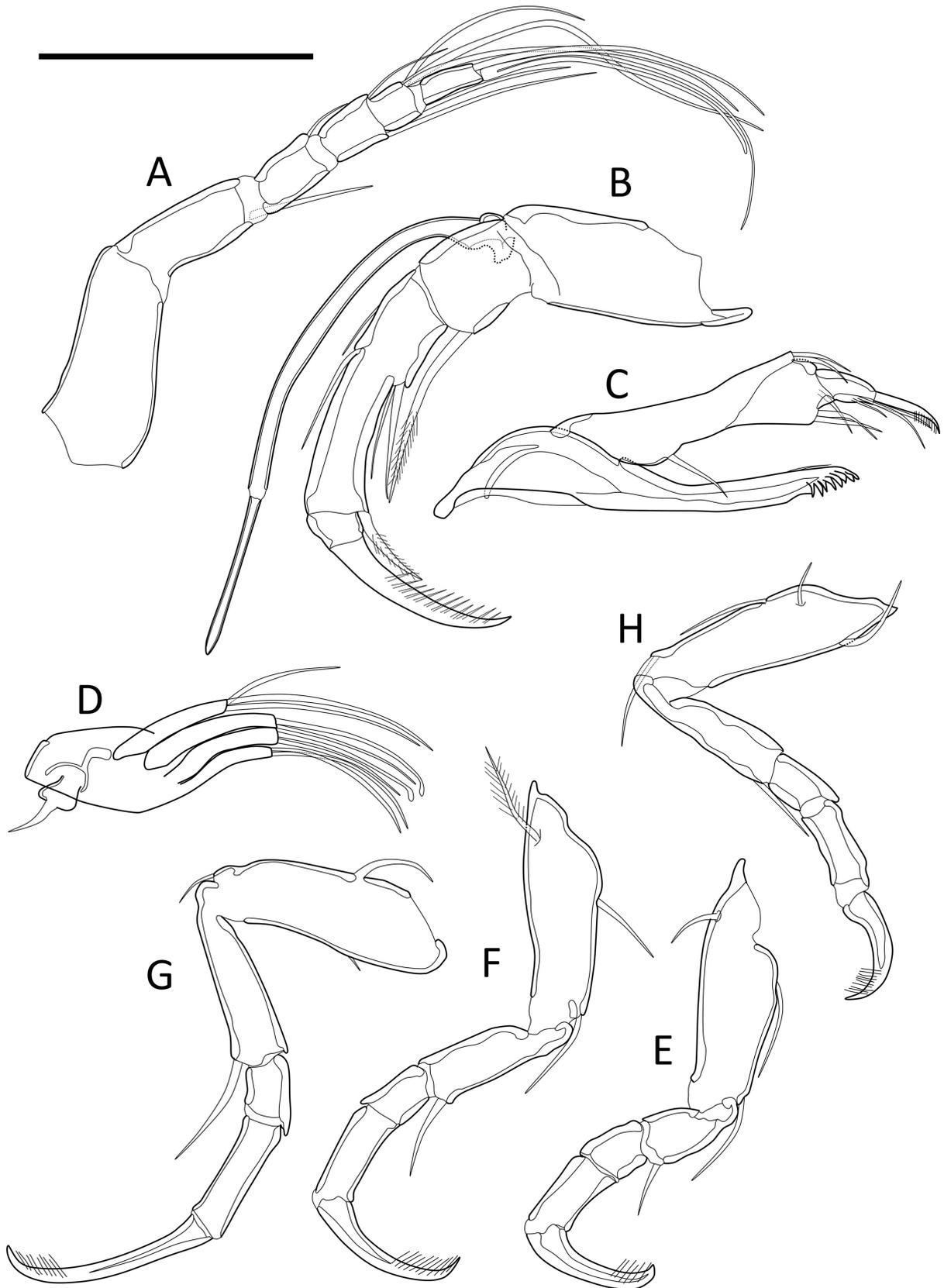


Figure 9. *Redekea abyssalis* sp. nov. **A–G** male, holotype (SMF 57056) **H** female, paratype (SMF 57058). **A** A1 **B** A2 **C** Md **D** Mx1 **E** L5 **F** L6 **G** L7 **H** L5. Scale bar: 50 μ m.

eral view. LV; L 0.32 mm, H 0.16 mm; RV; L 0.31 mm, H 0.17 mm. Greatest H situated just behind middle L. Dorsal margin arched; RV more steeply arched than LV. Anterior margin rounded; RV narrower than LV. Ventral

margin of both valve weakly concave situated in front of middle L. Posterior margin rounded. External surface covered with shallow pits except central and mid-ventral areas of valves; pits size increasing from marginal to near

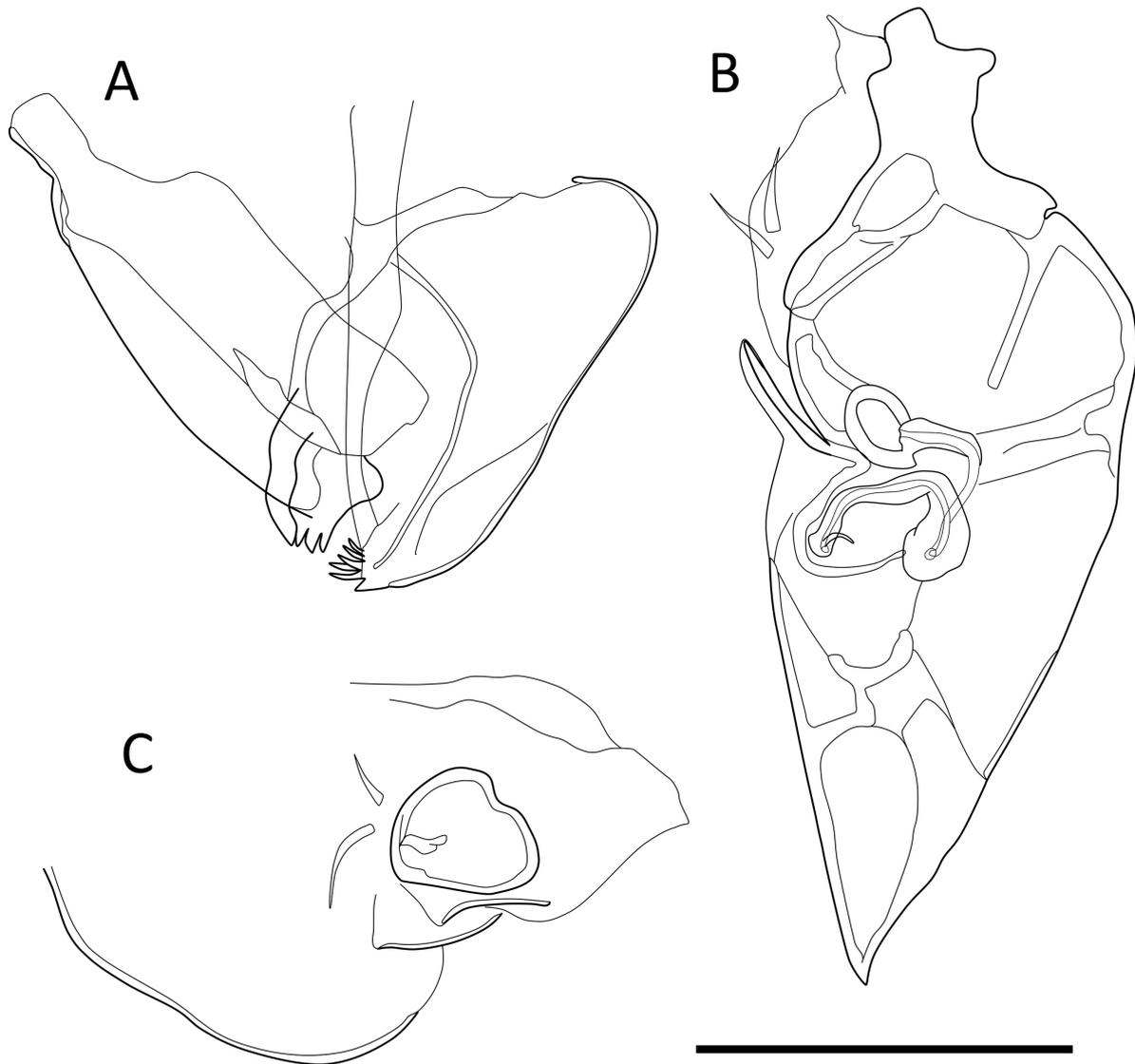


Figure 10. *Redekkea abyssalis* sp. nov. **A, B** male, holotype (SMF 57056) **C** female, paratype (SMF 57058). **A** Oral cone **B** left Hp **C** female copulatory organ. Scale bar: 50 μ m.

central area of valves (Fig. 8A, B). Sensilla long existing non-collar pores surrounded with sieve pores (Fig. 8C): circular shaped sieve pores in anterior and posterior areas, approximate diameter 4 μ m; elliptical shaped sieve pores in other areas, approximate length major axis 10–20 μ m and minor axis 4–9 μ m. Inner calcified lamella broadly developed in both valves (Figs 7, 8D). Four adductor muscle scars form a vertical row (Fig. 7). Hinge-ment lophodont (Figs 7, 8D). *A1* (Fig. 9A) six podomeres [four and five podomeres divided by suture, same as defined 4a and 4b by Smith and Tsukagoshi (2005) and Boxshall et al. (2010)]. First podomere bare. Second podomere three-fifths as long as first podomere with one postero-distal seta. Third podomere two-fifths as long as first podomere with one short antero-distal seta. Fourth to sixth podomeres same length as third podomere. Fourth podomere with one short antero-distal seta and one long postero-distal seta. Fifth podomere with three long antero-distal setae and one long postero-distal seta. Sixth podomere with two long distal setae and one long blunt tipped distal seta. *A2* (Fig. 9B) five podomeres. First

podomere (basis) parallelogram-shaped, with one long two-annulated exopodite (spinneret seta) on antero-distal end. Second (first endopodal) podomere half lengths as first podomere, with one long setulose postero-distal seta. Third and fourth podomeres fused. Third (second endopodal) podomere half lengths as first podomere, with one short antero-middle seta, one short antero-distal seta, and two short postero-distal setae. Fourth (third endopodal) podomere same length as first podomere, with one stout setulose postero-distal seta. Fifth (fourth endopodal) podomere one-fourth as long as first podomere, with one stout distal claw with a row of spines on posterior margin. *Md* (Fig. 9C) coxa with one slender dorsal seta. Coxal endite consisting of eight teeth. Palp consisting of three podomeres. First podomere (basis), with one short seta on ventral margin and two short dorso-distal setae. Second podomere with two short ventro-distal setae and one lateral distal seta. Third podomere, with two slender setae on ventral margin, one slender distal seta, and one stout distal claw curved distally with a row of setae on ventral margin. *Mxl* (Fig. 9D) branchial plate (exopodite) strong-

ly reduced, consisting with 1 seta. Basal podomere with one palp (endopodite) and three endites. Palp consisting of one podomere, with three simple distal setae. Endites: dorsal one with one simple and one spatula-like distal setae; middle one with one simple and one spatula-like distal setae; ventral one with two simple distal setae. **L5** (Fig. 9E) four articulated podomeres. First podomere with one antero-lateral seta, one antero-distal seta, and one dorso-lateral seta. Second podomere one-fourth as long as first podomere, with one antero-distal seta. Third podomere one-eighth as long as first podomere, bare. Fourth podomere one-fourth as long as first podomere, with one stout sclerotized distal claw with a few spines on antero-distal margin. **L6** (Fig. 9F) four articulated podomeres. First podomere with one antero-lateral seta, one antero-distal seta, and one plumose dorso-lateral seta. Second podomere half as long as first podomere, with one thick antero-distal seta. Third podomere one-sixth as long as first podomere, bare. Fourth podomere one-third as long as first podomere, with one stout sclerotized distal claw with a few spines on antero-distal margin. **L7** (Fig. 9G) four articulated podomeres. First podomere with one antero-lateral spine, one antero-distal seta, and one dorso-lateral seta. Second podomere four-fifths as long as first podomere, with one thick antero-distal seta. Third podomere one-fifth as long as first podomere, bare. Fourth podomere three-fifths as long as first podomere, with one long stout sclerotized distal claw with a few spines on antero-distal margin. **Brush-shaped organ** absent. **Oral cone** (Fig. 10A) subtriangular in lateral view, with six teeth on apex and one rake-like organ with three teeth. **Hp and posterior body** (Fig. 10B) symmetrical. Ejaculatory duct short and curved. Hook-like process elongated conical shape. Distal lobe subtriangular. Posterior body left and right sides bearing two furcal setae.

Description of adult female (based on paratype SMF 57058). **Carapace** (Fig. 8E, F) sub-triangular in lateral view. LV; L 0.33 mm, H 0.20 mm; RV; L 0.33 mm, H 0.18 mm. **L5** (Fig. 9H) longer than that of male in appearance. Four articulated podomeres. First podomere with two antero-lateral seta, one antero-distal seta, and one dorso-lateral seta. Second podomere four-fifths as long as first podomere, with one antero-distal seta. Third podomere two-fifths as long as first podomere, bare. Fourth podomere three-fifths as long as first podomere, with one stout sclerotized distal claw with a few spines on antero-distal margin. **Copulatory organ and posterior body** (Fig. 10C) female genital opening paired. Sclerotized framework of genital opening roughly circular. Genital lobe paired with each two furcal setae.

Etymology. The species epithet ‘*abyssalis*’ refers to the abyssal zone of the Pacific Ocean where the species was discovered.

Distribution. Only recorded from the type locality.

DNA sequence. The 18S rDNA sequences of two paratypes (SMF 57057, SMF 57058) were obtained. Gen-

Bank accession numbers are MW338926 (1177 bp) for SMF 57058 and MW338927 (1685 bp) for SMF 57057.

Remarks. To date, the genus *Redekea* comprised two species: the type species, *R. perpusilla* de Vos, 1953 and *R. californica* de Vos and Stock, 1956. *Redekea abyssalis* resembles these two species in the general carapace and appendage morphology. However, there are small, but consistent differences between the new and the other two species. First of all, *R. abyssalis* is larger, with valve size approximately 0.3 mm, while the other two species measure approximately 0.2 mm. Secondly, *R. abyssalis* **sp. nov.** has a slender valve outline than *R. perpusilla*, and broader than *R. californica*. Thirdly, the distal claw of the male L5 in *R. abyssalis* has a sharply bended tip, the bending in *R. perpusilla* occurs at about mid-length, while in *R. californica* the claw is evenly curved from the proximal end all the way to its tip. Finally, distal lobe and hook-like process of Hp in *R. abyssalis* is shorter and narrower than that of the other two species.

Discussion

This study is only the second example of ostracods collected from the natural sunken wood in deep sea. As such, it is an important contribution to our knowledge of the natural distribution of organisms that are confined to unstable environments, such as wood pieces submerged in the deep-sea floor. According to our study, *Keysercythere enricoi* has a relatively wide distribution, being found 600 km from its type locality. Cytheroids do not have a planktonic larval stage and swimming ability (e.g. Rodriguez-Lazaro et al. 2012). In addition, the three species, *K. enricoi*, *K. reticulata*, and *R. abyssalis* have not been reported from other than wood-fall habitats in the Northwest Pacific during previous studies (Karanovic and Brandão 2015, Yoo et al. 2019b, Brandão et al. 2020). These facts indicate that the three ostracod species strongly rely on the scattered wood falls as their habitat. A wide geographical distribution of some deep-sea wood-fall fauna was explained by stepping-stone hypothesis (e.g. Romano et al. 2020). Maddocks and Steineck (1987) also noticed that ostracods used experimentally deployed wood fall as their transit points, therefore we can postulate that the three species we recorded use naturally occurring wood fall as their (only) passageways, additionally stressing out the importance of this ephemeral habitats for the life in the deep sea. Two previously known *Redekea* species were found on the body surface of *Limnoria* sp. living on the wood submerged in the shallow water, or washed up in the intertidal zone. In this study, *R. abyssalis* was found at more than 5,000 m, and some individuals were obtained by washing the bodies of *Limnoria* sp. It is likely that *R. abyssalis* colonized deep sea though its symbiotic relationship. A high morphological and molecular (based on the 18S rRNA) similarity between previously known and the new species suggests their close relation-

ship and a common ancestor that might have lived not so long time ago in the shallow waters. Some morphological characters of *Redekea abyssalis*, such as a larger carapace and a reduced exopodite of the Mx1 in comparison to the two shallow water species, may additionally support the hypothesis that it originated from shallow water ancestors. A similar scenario has been suggested for unrelated ostracod lineage, Bairdioidea (see Danielopol 1976).

With deeper branches having a very low support in terms of the posterior probability, results of our phylogenetic analyses do not offer meaningful solution for the interfamily relationships in the superfamily Cythreioidea. This may also be the consequence of using only one genetic marker, as it has been shown that multi-gene phylogenies provide a better signal than single-gene ones (see, for example, Gontcharov et al. 2004, Castresana 2007). The 18S rRNA marker we use has been extensively applied to infer phylogenetic relationships on different taxonomic levels, including the large-scale studies of the animal kingdom (Field et al. 1988). However, this marker cannot resolve nodes at all taxonomic levels and its efficacy varies considerably among clades, which is interpreted as an effect of rapid ancient radiation within short periods (Meyer et al. 2010). In ostracods this marker alone or in combination with other markers is also commonly used for inferring phylogenetic relationships between ostracod subclasses (Yamaguchi and Endo 2003; Tinn and Oakley 2008), families (Hiruta et al. 2016), or some of the lower systematic units (Tanaka et al. 2014; Karanovic and Sitenikova 2017). Pham et al. (2020) provided an overview of intrageneric and intrafamily distance of several genetic markers, including 18S rRNA for the entire ostracod subclass Myodocopa. They confirm that this gene varies greatly, depending on the taxon in question, but in some genera of the family Polycopidae between species distances are unusually high (see also Tanaka et al. 2014). Despite some cavities that one-gene phylogeny or incongruence between lineages in 18S phylogenetic signals may cause, our results offer a degree of clarification of the problematic systematics of some cytheroids families. This supports Karanovic and Brandão (2015) suggestions that many of those families need to be revised because several well-established and commonly used taxonomic characters display high level of interfamily variability. One example is *Redekea*. This genus was initially considered to be similar to the genus *Cytherois* Müller, 1884 (see de Vos 1953; McKenzie 1969). However, the phylogenetic position of *Redekea* has not been resolved, with some authors (Wouters and de Grave 1992, Tanaka and Hayashi 2019, Yoo et al. 2020) suggesting that it belongs to Paradoxostomatidae, while others doubt this but provide no clear solution (McKenzie 1972, Karanovic and Brandão 2015). Karanovic and Brandão (2015) noted that *Redekea* does not have reduced mandibular palp and styliform coxa, key taxonomic characters of the Paradoxostomatidae members. The results of our analysis confirm that *Redekea* should be excluded from Paradoxostomatidae and placed within Keysercytheridae as this branch received the highest posterior probability support. The synapomorphies of *Redekea* and *Keysercythere* are as

follows: large sieve pores or pore-clusters on carapace; sixth-segmented, slender A1; broad distal claw of mandibular palp.

Although, *Limnocythere* appears as a sister taxon to *Keysercythere+Redekea*, a low support for this branch indicates that further studies should be carried out in order to understand this relationship, if any. A potential phylogenetic signal might be a corresponding pattern of tubules associated with sieve pore canals in *Keysercythere* and *Limnocythere* (see Danielopol et al. 2018), but shell structures alone are difficult to use for resolving phylogenetic relationships since many of them seem to be homoplastic (see the Introduction). On the other hand, the tree provides an insight into the problematic systematics of Limnocytheridae, as *Gomphodella* and *Metacypris* stand far apart from *Limnocythere*. The first two genera are members of the well-established subfamily Timiriaseviinae (see Martens 1995, Karanovic and Humphreys 2014), and *Limnocythere* is the nominal genus of Limnocytherinae. The phylogenetic relationship between some Timiriaseviinae genera has been studied by several authors using cladistics methods based on morphological set of characters (Gidó et al. 2007, Savatentalinton et al. 2008, Karanovic and Humphreys 2014). Although, the resulting phylogenetic trees differ (depending on the genera included), they all basically support two living lineages: one containing genera distributed in Europe and Asia, and other having a Gondwana distribution. Recently, Danielopol et al. (2018) proposed further division of the subfamily Timiriaseviinae into three tribes: Timiriaseviini, Cytheridellini, and Gomphodellini, the last established in the same publication. Their decision was based on the presence/absence of sieve pore canals on the shell, types of other shell pores, and morphology of the A1. They failed to allocate several of the currently recognized Timiriaseviinae genera (mainly due to the lack of published information), but their results show that some of the Timiriaseviinae genera are more similar to Limnocytherinae in terms of sieve pores, than they are to each other. Sieve pores, like many other shell structures seem to be homoplastic within cytheroids lineages and often dependent on the environmental conditions (Frenzel et al. 2017, Boomer et al. 2017). Presence of a brood chamber in Timiriaseviinae was considered an important synapomorphic characters, but since this is often variable even within one genus (see Danielopol et al. 2018), this character may rather be considered a plesiomorphic one. The position of the seta on the segment of the A1 (apical in *Limnocythere*, lateral, or absent in Timiriaseviinae) may bear a stronger phylogenetic signal, as well as the fact that most Timiriaseviinae have a 6-segmented, while Limnocytherinae have a 5-segmented A1. However, two characters that strongly support monophyly of Timiriaseviinae and their distant relationship with Limnocytherinae are a strongly reduced maxillular palp and movable distal lobe of the hemipenis. Namely, in all Timiriaseviinae species described so far, second segment of the maxillular palp is strongly reduced while it is normally developed in Limnocytherinae. Distal lobe in Limnocytherinae is tightly fused with the main body. Limnocytherinae

species in addition have simple upper ramus and elaborately developed lower ramus of the hemipenis, while the situation is opposite in Timiriaseviinae (see Martens 2003). All these morphological characters and the result of molecular phylogeny together strongly support our decision to elevate the two subfamilies, Limnocytherinae and Timiriaseviinae, onto a higher taxonomic level.

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References

- Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ (1990) Basic local alignment search tool. *Journal of Molecular Biology* 215(3): 403–410. [https://doi.org/10.1016/S0022-2836\(05\)80360-2](https://doi.org/10.1016/S0022-2836(05)80360-2)
- Altschul SF, Madden TL, Schäffer AA, Zhang J, Zhang Z, Miller W, Lipman DJ (1997) Gapped BLAST and PSIBLAST a new generation of protein database search programs. *Nucleic Acids Research* 25 (17): 3389–3402. <https://doi.org/10.1093/nar/25.17.3389>
- Baird W (1850) The natural history of the British Entomostraca. Ray Society, London, 364 pp. <https://doi.org/10.5962/bhl.title.39641>
- Bienhold C, Pop Ristova P, Wenzhöfer F, Dittmar T, Boetius A (2013) How Deep-Sea Wood Falls Sustain Chemosynthetic Life. *PLoS ONE* 8(1): e53590. <https://doi.org/10.1371/journal.pone.0053590>
- Boomer I, Frenzel P, Feike M (2017) Salinity-driven size variability in *Cyprideis torosa* (Ostracoda, Crustacea). *Journal of Micropalaeontology* 36: 63–69. <https://doi.org/10.1144/jmpaleo2015-043>
- Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu C-H, Xie D, Suchard MA, Rambaut A, Drummond AJ (2014) BEAST 2: A Software Platform for Bayesian Evolutionary Analysis. *PLoS Computational Biology* 10(4): e1003537. <https://doi.org/10.1371/journal.pcbi.1003537>
- Boxshall GA, Danielopol DL, Horne DJ, Smith RJ, Tabacaru I (2010) A critique of biramous interpretations of the crustacean antennule. *Crustaceana* 83: 153–167. <https://doi.org/10.1163/001121609X12530988607434>
- Brady GS (1868) Ostracoda. In: De Folin L, Perier L (Eds) *Les Fonds de la Mer*, 1. Savy, Paris.
- Brady GS (1870) Notes on Entomostraca taken chiefly in the Northumberland and Durham District (1869). *Transactions of the Natural History Society of Northumberland and Durham* 3: 361–373.
- Brady GS, Norman AM (1889) A monograph of the marine and fresh-water Ostracoda of the North Atlantic and of Northwestern Europe. Section 1. Podocopa. *The Scientific Transactions of the Royal Dublin Society* 2 (4): 63–270.
- Brady GS, Robertson D (1870) The Ostracoda and Foraminifera of Tidal Rivers. *Annals and Magazine of Natural History*, series 4, 6: 1–33, 307–309.
- Brandão SN, Baumann E, Jöst AB, Karanovic I, Tanaka H, Yasuhara M, Yoo H, Saeedi H, Brandt A (2020) Ostracoda. Biodiversity and Biogeography of Ostracoda (Crustacea) from the deep NW Pacific. In: Saeedi H, Brandt A (Eds) *Biogeographic Atlas of the Deep NW Pacific Fauna*. Pensoft, Sofia, 287–338. <https://doi.org/10.3897/ab.e51315>
- Brandt A, Malyutina MV (2015) Introduction to KuramBio. *Deep-Sea Research Part II Topical Studies in Oceanography* 111: 1–9. <http://dx.doi.org/10.1016/j.dsr2.2014.11.001>
- Brandt A, Shipboard scientific party (2016) RV *Sonne* SO-250 Cruise Report / Fahrtbericht Tomakomai - Yokohama (Japan) 16.08-26.09.2016. KuramBio II (Kuril Kamchatka Biodiversity Studies), University of Hamburg, Hamburg, 174 pp.
- Brandt A, Brix S, Riehl T, Malyutina M (2020) Biodiversity and biogeography of the abyssal and hadal Kuril-Kamchatka trench and adjacent NW Pacific deep-sea regions. *Progress in Oceanography* 181: 102232. <https://doi.org/10.1016/j.pocean.2019.102232>
- Castresana J (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* 17: 540–552. <https://doi.org/10.1093/oxfordjournals.molbev.a026334>
- Castresana J (2007) Topological variation in single-gene phylogenetic trees. *Genome Biology* 8, 216. <https://doi.org/10.1186/gb-2007-8-6-216>
- Danielopol DL (1976) Supplementary data on *Pussella botosaneanui* Danielopol, 1973 (Ostracoda, Bairdiidae). *Vie Milieu* 26: 261–273.
- Danielopol DL, Cabral MC, Lord A, Carbonel P, Gross M, Stoica M, Humphreys WF, Namiotko T, Tóth E, Küllköylüoğlu O, Piller WE, Nunes T (2018) Sieve-type pore canals in the Timiriaseviinae—A contribution to the comparative morphology and the systematics of the Limnocytheridae (Ostracoda, Crustacea). *Zootaxa* 4495: 1–64. <https://doi.org/10.11646/zootaxa.4495.1.1>
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772. <https://doi.org/10.1038/nmeth.2109>
- De Vos APC (1953) Three new commensal ostracods from *Limnoria lignorum* (Rathke). *Beaufortia* 4: 21–31. <https://repository.naturalis.nl/pub/505113>
- De Vos APC, Stock JH (1956) On commensal Ostracoda from the wood-infesting isopod *Limnoria*. *Beaufortia* 5: 133–139. <https://repository.naturalis.nl/pub/505049>
- De Deckker P (1981) Taxonomy and ecological notes of some ostracods from Australian inland waters. *Transactions of the Royal Society of South Australia* 105(3): 91–138.
- Field KG, Olsen GJ, Lane DJ, Giovannoni SJ, Ghiselin MT, Raff EC, Pace NR, Raff RA (1988) Molecular phylogeny of the animal kingdom. *Science* 239: 748–753. <https://doi.org/10.1126/science.3277277>
- Fischer S (1855) Beitrag zur Kenntnis der Ostracoden. *Abhandlungen der Mathematisch-Physikalischen Classe der koeniglich-Beyerischen Akademie der Wissenschaften*. 7(3): 635–666.
- Frenzel P, Ewald J, Pint A (2017) Salinity-dependent sieve pore variability in *Cyprideis torosa*—an experiment. *Journal of Micropalaeontology* 36: 57–62. <https://doi.org/10.1144/jmpaleo2016-009>
- Gernhard T (2008) The conditioned reconstructed process. *Journal of Theoretical Biology* 253: 769–778. <https://doi.org/10.1016/j.jtbi.2008.04.005>

- Gidó Z, Artheau M, Colin JP, Danielopol D, Marmonier P (2007) Description of the stygobiotic crustacean *Dolekiella europaea* gen. nov. sp. nov. (Ostracoda, Limnocytheridae) from Southern France. *Vie et Milieu* 57: 109–116.
- Gontcharov AA, Marin B, Melkonian M (2004) Are combined analyses better than single gene phylogenies? A case study using SSU rDNA and *rbcL* sequence comparisons in the Zygnematophyceae (Streptophyta). *Molecular Biology and Evolution* 21: 612–624. <https://doi.org/10.1093/molbev/msh052>
- Guindon S, Gascuel O (2003) A simple, fast and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* 52: 696–704. <https://doi.org/10.1080/10635150390235520>
- Hart CW Jr., Clark J (1984) A new commensal ostracod of the genus *Microsyssitria* from South Africa (Ostracoda: Entocytheridae: Microsyssitriinae). *Proceedings of the Biological Society of Washington* 97 (1): 217–220.
- Hart CW Jr., Nair B, Hart DG (1967) A new ostracod (Ostracoda: Entocytheridae) commensal on a wood-boring marine isopod from India. *Notulae Naturae, Academy of Natural Sciences of Philadelphia* 409: 1–11.
- Hiruta S (1991) A new species of marine interstitial Ostracoda of the genus *Psammycythere* Klie from Hokkaido, Japan. *Zoological Science* 8: 113–120.
- Hurvich CM, Tsai C (1989) Regression and time series model selection in small samples. *Biometrika* 76: 297–307. <https://doi.org/10.1093/biomet/76.2.297>
- Hiruta SF, Kobayashi N, Katoh T, Kajihara H (2016) Molecular phylogeny of cypridoid freshwater ostracods (Crustacea: Ostracoda), inferred from 18S and 28S rDNA. *Zoological Science* 33: 179–185. <https://doi.org/10.2108/zs150103>
- Karanovic I (2006) On the genus *Gomphodella* (Crustacea: Ostracoda: Limnocytheridae) with descriptions of three new species from Australia and redescription of the type species. *Species Diversity* 11: 99–135. <https://doi.org/10.12782/specdiv.11.99>
- Karanovic I, Brandão SN (2015) Biogeography of deep-sea wood fall, cold seep and hydrothermal vent Ostracoda (Crustacea), with the description of a new family and a taxonomic key to living Cytheroidea. *Deep-Sea Research Part II Topical Studies in Oceanography* 111: 76–94. <https://doi.org/10.1016/j.dsr2.2014.09.008>
- Karanovic I, Humphreys WF (2014) Phylogeny and diversity of Timiriaseviinae ostracods (Podocopida, Cytheroidea) with description of a new species from arid Western Australia. *Systematics and Biodiversity* 12: 93–110. <https://doi.org/10.1080/14772000.2014.882870>
- Karanovic I, Pham TMH, Yoo H, Nakao Y, Tsukagoshi A (2020) Shell and appendages variability in two allopatric ostracod species seen through the light of molecular data. *Contributions to Zoology* 89: 247–269. <https://doi.org/10.1163/18759866-20191423>
- Karanovic I, Sitnikova TY (2017) Phylogenetic position and age of Lake Baikal candonids (Crustacea, Ostracoda) inferred from multi-gene sequence analyzes and molecular dating. *Ecology and Evolution* 7: 7091–7103. <https://doi.org/10.1002/ece3.3159>
- Kozloff EN, Whitman DC (1954) *Entocythere occidentalis* sp. nov., a cytherid ostracod commensal on western species of *Pacifastacus*. *American Midland Naturalist* 52: 159–163. <https://doi.org/10.2307/2422053>
- Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across Computing Platforms. *Molecular biology and evolution* 35: 1547–1549. <https://doi.org/10.1093/molbev/msy096>
- Maddocks RF (1991) Revision of the family Pontocyprididae (Ostracoda), with new anchialine species and genera from Galapagos Islands. *Zoological Journal of the Linnean Society* 103: 309–333. <https://doi.org/10.1111/j.1096-3642.1991.tb00907.x>
- Maddocks RF (2005) Three new species of podocopid ostracoda from hydrothermal vent fields at 9°50'N on the East Pacific Rise. *Micropaleontology* 51: 345–372. <https://doi.org/10.2113/gsmicro-pal.51.5.345>
- Maddocks RF, Steineck PL (1987) Ostracoda from experimental wood-island habitats in the deep sea. *Micropaleontology* 33: 318–355. <https://doi.org/10.2307/1485572>
- Martens K (1995) On the validity and the taxonomic position of the Cytheridellini (Crustacea, Ostracoda, Limnocytheridae). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 92: 273–280.
- Martens K (2003) On the evolution of *Gomphocythere* (Crustacea, Ostracoda) in Lake Nyassa/Malawi (East Africa), with the description of 5 new species. *Hydrobiologia* 497: 121–144. <https://doi.org/10.1023/A:1025417822555>
- McKenzie KG (1969) Notes on the paradoxostomatids. In Neale JW (Ed) *The Taxonomy, Morphology and Ecology of Recent Ostracoda*, Oliver and Boyd, Edinburgh, 48–66.
- McKenzie KG (1972) New data on the ostracode genera *Laocoonella* de Vos and Stock, *Redekia* de Vos, and *Aspidoconcha* de Vos; with a key to the family Xestoleberididae and a resume of symbiosis in Ostracoda. *Beaufortia* 19: 151–162. <https://repository.naturalis.nl/pub/504808>
- Meyer A, Todt C, Mikkelsen NT, Lieb B (2010) Fast evolving 18S rRNA sequences from *Solenogastres* (Mollusca) resist standard PCR amplification and give new insights into mollusk substitution rate heterogeneity. *BMC Evolutionary Biology* 10: 70. <https://doi.org/10.1186/1471-2148-10-70>
- Müller GW (1884). Zur näheren Kenntnis der Cytheriden. *Archiv für Naturgeschichte*. 50: 1–18.
- Nohara T (1987) Cenozoic ostracodes of Okinawa-jima. *Bulletin of College of Education, University of Ryukyus*, 105 pp.
- Pham TMH, Tanaka H, Karanovic I (2020) Molecular and morphological diversity of *Heterodesmus* Brady and its phylogenetic position within Cypridinidae (Ostracoda). *Zoological Science* 37: 240–254. <https://doi.org/10.2108/zs190118>
- Puri HS, Dickau BE (1969) Use of normal pores in taxonomy of Ostracoda. *Transactions Gulf Coast Association of Geological Societies* 19: 353–367.
- Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior Summarization in Bayesian Phylogenetics Using Tracer 1.7. *Systematic Biology* 67(5): 901–904. <https://doi.org/10.1093/sysbio/syy032>
- Rodriguez-Lazaro J, Ruiz-Muñoz F, Viehberg FA (2012) A general introduction to ostracods: morphology, distribution, fossil record and applications. In: Horne DJ, Holmes JA, Rodriguez-Lazaro J (Eds) *Ostracoda as proxies for Quaternary climate change*. Elsevier, Netherlands 1–14. <https://doi.org/10.1016/b978-0-444-53636-5.00001-9>
- Romano C, Nunes-Jorge A, Le Bris N, Rouse GW, Martin D, Borowski C (2020) Wooden stepping stones: diversity and biogeography of deep-sea wood boring Xylophagidae (Mollusca: Bivalvia) in the North-East Atlantic Ocean, with the description of a new genus. *Frontiers in Marine Science* 7: 579959. <https://doi.org/10.3389/fmars.2020.579959>
- Sars GO (1866) Oversigt af Norges marine Ostracoder. *Forth Vid Selsk Christiania* 8: 1–130.

- Savatnalinton S, Borgonie G, Martens K (2008) On *Thaicythere srisumona* n. gen., n. sp. (Ostracoda) from Thailand, with notes on the phylogeny of the subfamily Timiriaseviinae Mandelstam. 1960. *Crustaceana* 81: 411–432. <https://doi.org/10.1163/156854008783797543>
- Schornikov EI (1980) New ostracods species of the coral reefs of the Red Sea and Aden's Bay. In Preobrazhensky BV, Krasnov EV (Eds) *Biology of Coral Reefs. Morphology, Systematics, Ecology*, Nauka, Moscow, 131–158. (in Russian)
- Schornikov EI (1993) Systematical problems of the ostracods of family Paradoxostomatidae and reclassification of *Paradoxostoma s.l.* from Peter the Great Bay (Sea of Japan). In Kafanov AI (Ed) *Ecosystems Research: Coastal Communities of Peter the Great Bay, Far East Branch*, Academy Sciences USSR, Vladivostok, 153–166. (in Russian)
- Schwabe E, Bartsch I, Błażewicz-Paszkowycz M, Brenke N, Chernyshev AV, Elsner NO, Fischer V, Jażdżewska A, Malyutina MV, Miljutin D, Miljutina M, Anastassya A, Kamenev GM, Karanovic I, Würzberg L (2015) Wood-associated fauna collected during the KuramBio–expedition in the North West Pacific. *Deep-Sea Research Part II Topical Studies in Oceanography* 111: 376–388. <https://dx.doi.org/10.1016/j.dsr2.2014.08.001>
- Smith RJ, Tsukagoshi A (2005) The chaetotaxy, ontogeny and musculature of the antennule of podocopan ostracods (Crustacea). *Journal of Zoology* 265: 157–177. <https://doi.org/10.1017/S095283690400617X>
- Steineck PL, Maddocks RF, Coles G, Whatley RC (1990) Xylophile Ostracoda in the deep sea. In: Whatley R, Maybury C (Eds) *Ostracoda and global events*. British Micropaleontological Society Publication Series, Chapman and Hall, London, 307–319.
- Svavarsson J (1982) *Limnoria borealis* (Isopoda, Flabellifera) and its commensal, *Caecijaera borealis* (Isopoda, Asellota), found in Icelandic waters. *Sarsia* 67: 223–226. <https://doi.org/10.1080/00364827.1982.10421337>
- Tanaka H, Hayashi R (2019) *Chelonocytherois omutai* gen. et sp. nov. (Crustacea: Ostracoda) from the back of loggerhead sea turtles. *Zootaxa* 4626: 506–522. <https://doi.org/10.11646/zootaxa.4624.4.4>
- Tanaka H, Yasuhara M (2016) A new deep-sea hydrothermal vent species of Ostracoda (Crustacea) from the Western Pacific: implications for adaptation, endemism, and dispersal of ostracodes in chemosynthetic systems. *Zoological Science* 33: 555–565. <https://doi.org/10.2108/zs160079>
- Tanaka H, Lelièvre Y, Yasuhara M (2019) *Xylocythere sarrazinae*, a new cytherurid ostracod (Crustacea) from a hydrothermal vent field on the Juan de Fuca Ridge, northeast Pacific Ocean, and its phylogenetic position within Cytheroidea. *Marine Biodiversity* 49: 2571–2586. <https://doi.org/10.1007/s12526-019-00987-3>
- Tanaka H, Tsukagoshi A, Karanovic I (2014) Molecular phylogeny of interstitial Polycopidae ostracods (Crustacea) and descriptions of a new genus and four new species. *Zoological Journal of the Linnean Society* 172: 282–317. <https://doi.org/10.1111/zoj.12176>
- Tavaré S (1986) Some Probabilistic and Statistical Problems in the Analysis of DNA Sequences. *Lectures on Mathematics in the Life Sciences* 17: 57–86.
- Thompson JD, Higgins DG, Gibson TJ (1994) CLUSTAL W: Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research* 22: 4673–4680. <https://doi.org/10.1093/nar/22.22.4673>
- Tinn O, Oakley TH (2008) Erratic rates of molecular evolution and incongruence of fossil and molecular divergence time estimates in Ostracoda (Crustacea). *Molecular Phylogenetics and Evolution* 48: 157–167. <https://doi.org/10.1016/j.ympev.2008.03.001>
- Turner RD (2002) On the subfamily Xylophaginae (Family Pholadidae, Bivalvia, Mollusca). *Bulletin of the Museum of Comparative Zoology at Harvard College* 157: 223–307.
- Van Harten D (1992) Hydrothermal vent Ostracoda and faunal association in the deep sea. *Deep-Sea Research Part A: Oceanographic Research Papers* 39: 1067–1070. [https://doi.org/10.1016/0198-0149\(92\)90040-Z](https://doi.org/10.1016/0198-0149(92)90040-Z)
- Van Harten D (1993) Deep sea hydrothermal vent eucytherurine Ostracoda: the enigma of the pore clusters and the paradox of the hinge. In McKenzie KG, Jones PJ (Eds) *Ostracoda in the earth and life sciences*, A.A. Balkema, Rotterdam, 571–580.
- Voight JR (2007) Experimental deep-sea deployments reveal diverse northeast Pacific wood-boring bivalves of Xylophaginae (Myoida: Pholadidae). *Journal of Molluscan Studies* 73: 377–391. <https://doi.org/10.1093/mollus/eym034>
- Williams BD, Schrank B, Huynh C, Shownkeen R, Waterston RH (1992) A genetic mapping system in *Caenorhabditis elegans* based on polymorphic sequence-tagged sites. *Genetics Society of America* 131: 609–624.
- Wouters K, de Grave S (1992) *Redekea perpusilla* de Vos, 1953 (Crustacea: Ostracoda: Paradoxostomatidae), first record for the British Isles. *Irish Naturalists' Journal* 24 (1): 23–26. <https://www.jstor.org/stable/25539680>
- Yamaguchi S (2003) Morphological evolution of Cytherocopine ostracods inferred from 18S ribosomal DNA sequences. *Journal of Crustacean Biology* 23: 131–153. <https://doi.org/10.1163/20021975-99990322>
- Yamaguchi S, Endo K (2003) Molecular phylogeny of Ostracoda (Crustacea) inferred from 18S ribosomal DNA sequences: Implication for its origin and diversification. *Marine Biology* 143: 23–38. <https://doi.org/10.1007/s00227-003-1062-3>
- Yoo H, Tanaka H, Tsukagoshi A, Karanovic I (2019a) Cytheroid ostracods from South Korea, with description of a new species. *Zoosystema* 41: 419–441. <https://doi.org/10.5252/zoosystema2019v41a22>
- Yoo H, Tanaka H, Lee W, Brandão SN, Karanovic I (2019b) Six new *Krithe* from the Kuril-Kamchatka Trench, with the first insight into phylogeography of deep-sea ostracods. *Progress in Oceanography* 176: 102128. <https://doi.org/10.1016/j.pocean.2019.102128>
- Yoo H, Le TVA, Karanovic I (2020) Two Paradoxostomatidae (Ostracoda) species from South Korea with a key to genera of the family. *ZooKeys* 943: 21–39. <https://doi.org/10.3897/zookeys.943.52938>
- Yu N, Zhao M, Chen L, Yang P (2006) Phylogenetic relationship of Podocopida (Ostracoda: Podocopa) based on 18S ribosomal DNA sequences. *Acta Oceanologica Sinica* 25: 99–108.