

# Revision of the *Semicytherura henryhowei* group (Crustacea, Ostracoda) with the new records from Korea

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## Abstract

The genus *Semicytherura* Wagner, 1957 has nearly 300 species, is common in shallow and marginal marine habitats, and has a worldwide distribution. It is divided into several species groups, of which the *Semicytherura henryhowei* Hanai & Ikeya, 1977 group is one of the most frequently recorded in temperate Asia. A previous study indicated that many of its members are actually species complexes, and that several morphotypes could be distinguished by carapace shape and ornamentation. We review these complexes and conclude that the *henryhowei* group currently contains 29 species, nine of which are undescribed. We also provide an illustrated guide and a key to species, based on newly standardized carapace ridge terminology. This enabled us to describe one new species from the extant (i.e., present-day) sediments in Jeju Island, Korea, *S. kiosti* sp. nov. We also found one juvenile valve of *S. kazahana* Yamada, Tsukagoshi & Ikeya, 2005, the first official illustrated record of this species from Korean waters. Our revised spatial and temporal distributions of fossil and extant records from this group provide new insights into trans-Arctic interchange of ostracod fauna from the Late Miocene onwards.

## Key Words

Benthic Ostracoda, identification key, MarineGEO ARMS, new species, taxonomy, trans-Arctic interchange

## Introduction

*Semicytherura* Wagner, 1957 is a podocopid ostracod genus, belonging to the family Cytheruridae. It comprises at least 291 species, 126 of which are known only from the fossil record. A total of 283 of these species are listed in the World Register of Marine Species (Brandão et al. 2022), whereas at least the following eight are missing: *Semicytherura leptosubundata* (Ozawa & Kamiya, 2008), *S. obitsuensis* (Nakao & Tsukagoshi, 2020), *S. pseudoundata* Irizuki & Yamada in Irizuki et al. (2004), *S. robustundata* (Ozawa & Kamiya, 2008), *S. skipa* (Hanai, 1957), *S. subslipperi* Ozawa & Kamiya, 2008, *S. tanimurai* (Ozawa & Kamiya, 2008), and *S. tetragona* (Hanai, 1957). The last species was described as

*Cytherura tetragona* Hanai, 1957 and is still listed as such in the World Register of Marine Species (Brandão et al. 2022). However, *Cytherura* Sars, 1866 and *Semicytherura* show distinctive differences in carapace features, like hingement and calcified inner lamella (Wagner 1957; Athersuch et al. 1989; Whatley and Cusminsky 2010). Based on these, *Cytherura tetragona* should be re-assigned to *Semicytherura*, as already adopted by some ostracodologists [e.g., Yamada et al. (2005)].

There are more than 40 species of *Semicytherura* (including records in open nomenclature) reported from Japan and adjacent areas (Yamada et al. 2005). However, reports specifically from Korean waters are uncertain. The only officially published and illustrated species reported from Korea is a specimen assigned to *S. minaminipponica*

(Ishizaki, 1981) from the Plio-Pleistocene deposits of Jeju Island (Paik and Lee 1988). The study also mentions *S. henryhowei* Hanai & Ikeya in Hanai et al. 1977, as well as seven undescribed species left in the open nomenclature, but no images or illustrations are provided. Several other papers have been published that mention various *Semicytherura* species from Korea, but none of them offer taxonomic proof. For example, Ikeya and Cronin (1993) report *S. miurensis* (Hanai, 1957) in their factor 6 assemblage from the Korean Peninsula, in addition to another 15 *Semicytherura* species from both Japan and Korea but they do not specify which species occur where (Ikeya and Cronin 1993). Lee et al. (2000) list the following fossil species from the Korea's East coast: *S. elongata* (Edwards, 1944), *S. cf. elongata*, *S. cf. subundata* (Hanai, 1957), *S. wakamurasaki* Yajima, 1982, *S. cf. wakamurasaki*, and *S. daishakaensis* (Tabuki, 1986) (typographical error in Lee et al. 2000: *S. daishakensis*). They also list these extant (i.e., present-day) species: *S. hanaii* Ishizaki, 1981, *S. cf. henryhowei*, *S. cf. hiberna* Okubo, 1980, *S. miurensis*, *S. cf. miurensis*, *S. polygonoreticulata*, and *S. cf. sabula* (Frydl, 1982) (Lee et al. 2000). Schornikov and Zenina (2008) mention *S. kazahana* Yamada, Tsukagoshi & Ikeya, 2005, *S. mukaishimensis* Okubo, 1980, and *S. polygonoreticulata* (Ishizaki & Kato, 1976) occurring along the coastal zone of Jeju Island. Additionally, Yamada et al. (2005) refer to an unpublished Korean record of *S. kazahana* by Lee (1990; unpublished) as *Semicytherura* sp. B. Here, we provide the first published record including illustrations of *S. kazahana* from Korean waters.

*Semicytherura* species can be grouped based on their general shape and dominant carapace features. Yamada et al. (2005) report five species groups from Japan and adjacent areas: the *henryhowei*, *miurensis*, *skipa*, *hanaii*, *tetragona*, and *sabula* group. Here, we focus on species from the *henryhowei* group, which comprises animals of sub-rectangular to sub-trapezoid shape (right valves tend to be more sub-trapezoid and left valves more sub-rectangular), with thick carapace and a system of broad ridges (carinae) and a horizontal caudal process with varying degree of conspicuousness.

Prior to the study of Yamada et al. (2005), several *S. henryhowei* morphotypes have been recognized (see e.g., Okubo 1980). Phenotypic plasticity is rather common in shallow marginal marine genera [for detailed discussion on morphological variation in marginal marine ostracods, see Jöst et al. (2021)], and *Semicytherura* species primarily inhabit inner bays, tolerating brackish environments, and are often associated with plants (Boomer and Eisenhauer 2002; Szczechura and Aiello 2003; Yamada et al. 2005; Schellenberg 2007). Yamada et al. (2005) studied more than 200 specimens of different *S. henryhowei* morphotypes from Japan and found that they are, in fact, four separate species: *S. henryhowei*, *S. kazahana*, *S. slipperi* Yamada, Tsukagoshi & Ikeya, 2005, and *S. sasameyuki* Yamada, Tsukagoshi & Ikeya, 2005. Besides differences in the soft-body morphology, the species can be distinguished by differences in the carapace pore system, and ridge pattern (Yamada et al. 2005). Prior to this, Irizuki et al. (2004)

described *Semicytherura pseudoundata* Irizuki & Yamada, 2004 from the Early Miocene deposit of Japan. They noted its close morphological similarity to *S. henryhowei* and *S. undata* (Sars, 1866), but described it as new, based on the distinct differences in the ventral ridge (Irizuki et al. 2004). Additionally, Ozawa and Kamiya (2008) added four new Pleistocene species, following the application of the distinct ridge patterns as a species-specific taxonomic character introduced by Yamada et al. (2005). They described *S. robustundata* Ozawa & Kamiya, 2008, *S. subslipperi* Ozawa & Kamiya, 2008, *S. leptosubundata* Ozawa & Kamiya, 2008, and *S. tanimurai* Ozawa & Kamiya, 2008 as new members of the *henryhowei* group. Yamada and Tsukagoshi (2010) added two more extant species, *S. maxima* Yamada & Tsukagoshi, 2010 and *S. ikeyai* Yamada & Tsukagoshi, 2010. They also conducted a comparative morphological study to determine which of the species belongs to the *henryhowei* group. As a result, besides the above mentioned 12 species, the following 20 are also considered members (see Appendix 1): *S. balrogi* Brouwers, 1994; *S. subundata* (Hanai, 1957); *S. aff. S. henryhowei* sensu Cronin and Ikeya (1987); *S. aff. henryhowei* sensu Irizuki (1994); *S. cf. henryhowei* sensu Cronin (1989); *S. neosubundata* (Ishizaki, 1966); *S. simplex* (Brady & Norman, 1889); *Semicytherura* sp. 1–5 sensu Irizuki (1994); *Semicytherura* sp. sensu Irizuki et al. (2005); *Semicytherura* sp. 1 sensu Yasuhara and Irizuki (2001); *Semicytherura* sp. 2 sensu Yamada et al. (2002); *Semicytherura* sp. 1–2 sensu Ozawa et al. (2008); *Semicytherura* sp. A sensu Cronin and Ikeya (1987); *Semicytherura* sp. B sensu Whatley and Boomer (1995); and *Kangarina* sp. B sensu Valentine (1976) (Yamada and Tsukagoshi 2010).

The first treatise list reporting members of the *S. henryhowei* group included 30 species, whereas 20 of these were left in the open nomenclature (Yamada et al. 2005) (Appendix 1). This list was later revised and eight of these 20 open-nomenclature-records were identified to the species level (Yamada and Tsukagoshi 2010). However, four records previously left in the open nomenclature were added, six species records were re-assigned to other species, and several new species were added. Finally, the updated list contains 32 species in total, of which 16 were left in the open nomenclature and another 16 were identified (Yamada and Tsukagoshi 2010) (Appendix 1).

Here, following the scheme of the species-specific ridge pattern, we conducted a revision of the updated treatise list by Yamada and Tsukagoshi (2010) and found that, amongst the records of *S. henryhowei*, there are two occurrences where the specimens belong to a different species (see Table 1). We also found that seven of the sixteen species left in the open nomenclature belong to already described species of the *henryhowei* group, whereas nine species are new to science (Table 1). Additionally, we recognized six more species records that also belong to the *henryhowei* group, that were not included in the list of members by Yamada and Tsukagoshi (2010) [*S. quadraplana* Allison & Holden, 1971; *S. kaburagawensis* Tanaka, 2013; *S. usuigawensis* Tanaka, 2013;

*Semicytherura* sp. A and B sensu Yamada et al. (2004); and *Hemicytherura* sp. 3 sensu Ikeya and Itoh (1991)] (Appendix 1).

Our taxonomic revision changes the known geological age of *S. tanimurai*, *S. kazahana/sasameyuki*, and *S. undata*, as well as the geological age and spatial distribution of *S. balrogi* and *S. ikeyai*. Revised distribution and remarks on the geological age are discussed with updated (paleo-)distribution maps. Additionally, we describe one new species belonging to the *henryhowei* group, *S. kiosti* sp. nov. Jöst and Karanovic, and show the first official record of *S. kazahana* from Korean waters. Finally, we generated an identification key to the species of this group, including illustrations of all known members to aid future taxonomic research.

## Methods

### Project

The material provided here was collected as a part of an ongoing project that collaborates with the Marine Global Earth Observatory (MarineGEO) program and in partnership with the Korea Institute of Ocean Science and Technology (KIOST) on Jeju Island, Republic of Korea (ROK). The MarineGEO is under the umbrella of the Smithsonian's global Tennenbaum Marine Observatories Network (TMON) with its headquarters in Washington, D.C., USA (<https://marinegeo.si.edu/>). It is the first long-term research program with partners from all over the world, applying a standardized method of sampling (ARMS, Fig. 1) to study coastal marine biodiversity. Its main aim is to understand the role of biodiversity in sustaining resilient marine ecosystems. As such, a thorough taxonomic knowledge of the current species is indispensable.

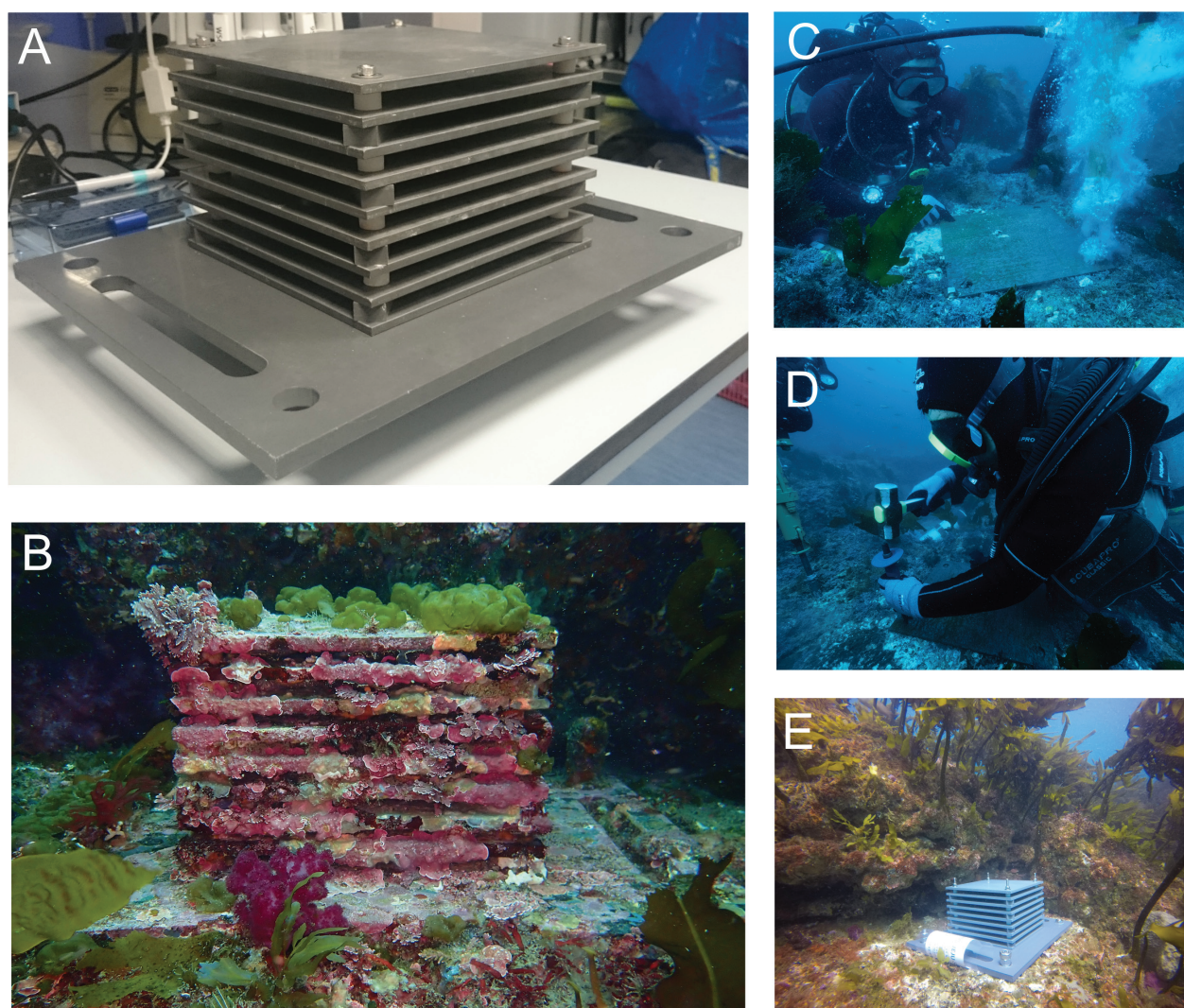
### Samples

Specimens were collected either from an Autonomous Reef Monitoring Structure (ARMS) (Fig. 1A, B, E), or from the sediment scoop samples (i.e., surface sediments) near the ARMS in August, 2019. The ARMS are standardized, three-dimensional samplers of marine biodiversity that are non-destructive to the environment. They are shelf-like units made of stacks of plates with different sized spacers in between the plates. Plate by plate, the units are assembled under water and left there, passively collecting the sample (i.e., surface and sedimentation-derived sediments) (Fig. 1C–E). For this study, ARMS were deployed by scuba at 19 m at Seongsan, Jeju Island, South Korea (Fig. 2) on the 3<sup>rd</sup> of October, 2018 and left under the water until retrieval on August 20<sup>th</sup>, 2019. On board the boat, the ARMS unit was immediately transferred to a recovery bin and submerged in the filtered seawater. Upon arrival on shore, the unit was disassembled inside the recovery bin and anything on and in between the plates was fixed with 99% ethanol. Living and dead ostracods were wet-picked in 99% ethanol from the 100–500 µm size fractions of the material collected by the ARMS unit and the scoop sample, respectively. Five of the 7 specimens presented here were recovered from the ARMS sample. Two specimens were recovered from a sediment scoop sample. The scoop sample was collected by SCUBA from the sea floor next to the ARMS structure during retrieval. A 50 mL conical tube was used to scoop up the sediment. Picking and sorting were done using a stereomicroscope (Olympus SZX12) in the Laboratory of Animal Systematics and Phylogeny at Hanyang University, ROK. Each disarticulated valve is counted as one specimen. One articulated male adult carapace was found and opened for the scanning electron microscope (SEM) imaging (LV: # 109\_1 (lost during imaging); RV: 109\_2).

**Table 1.** Revised species assignments of the members of the *Semicytherura henryhowei* group. Bold font indicates specimens of the treatise list by Yamada and Tsukagoshi (2010).

Author name	Species name	Revised species name
Cronin and Ikeya (1987)	<i>Semicytherura</i> aff. <i>S. henryhowei</i>	<i>S. balrogi</i>
Cronin and Ikeya (1987)	<i>Semicytherura</i> sp. A	<i>Semicytherura</i> sp. nov.
Cronin (1989)	<i>Semicytherura</i> cf. <i>S. henryhowei</i>	<i>Semicytherura</i> sp. nov.
Ikeya and Itoh (1991)	<i>Hemicytherura</i> sp. 3	<i>S. kiosti</i> sp. nov. Jöst & Karanovic
Irizuki (1994)	<i>Semicytherura henryhowei</i>	<i>S. balrogi</i>
Irizuki (1994)	<i>Semicytherura</i> aff. <i>S. henryhowei</i>	<i>Semicytherura</i> sp. nov.
Irizuki (1994)	<i>Semicytherura</i> sp. 1	<i>Semicytherura</i> sp. nov.
Irizuki (1994)	<i>Semicytherura</i> sp. 2	<i>Semicytherura</i> sp. nov.
Irizuki (1994)	<i>Semicytherura</i> sp. 3	<i>S. undata</i>
Irizuki (1994)	<i>Semicytherura</i> sp. 4	<i>Semicytherura</i> sp. nov.
Irizuki (1994)	<i>Semicytherura</i> sp. 5	<i>Semicytherura</i> sp. nov.
Irizuki et al. (2005)	<i>Semicytherura</i> sp.	<i>S. kazahana</i>
Ozawa et al. (2008)	<i>Semicytherura</i> sp. 1	<i>Semicytherura</i> sp. nov.
Ozawa et al. (2008)	<i>Semicytherura</i> sp. 2	<i>Semicytherura</i> sp. nov.
Whatley and Boomer (1995)	<i>Semicytherura</i> sp. B	<i>S. ikeyai</i>
Yajima (1988)	<i>Semicytherura henryhowei</i>	<i>S. sasameyuki</i> / <i>S. kazahana</i>
Yamada and Tsukagoshi (2010)	<i>Kangarina</i> sp. B sensu Valentine (1976)	<i>S. balrogi</i>
Yamada et al. (2002)	<i>Semicytherura</i> sp. 2	<i>S. tanimurai</i>
Yamada et al. (2004)	<i>Semicytherura</i> sp. A	<i>S. sasameyuki</i> / <i>S. kazahana</i>
Yamada et al. (2004)	<i>Semicytherura</i> sp. B	<i>S. slipperi</i>
Yasuhara and Irizuki (2001)	<i>Semicytherura</i> sp. 1	<i>S. kazahana</i>





**Figure 1.** Autonomous Reef Monitoring Structure (ARMS). **A.** Assembled ARMS; **B.** ARMS after one year of deployment at Seongsan (representative photo); **C–E.** ARMS installation by SCUBA (representative photos).

The SEM images were taken at Eulji University, ROK, with a Hitachi S-4700 scanning electron microscope after platinum coating.

The type material of *Semicytherura kiosti* sp. nov. (holotype: one male ARV, # 109\_2; paratypes: five RVs (# 68 female A, # 108 male A, # 177 female A-1, # 239 female A-2, # 240 female A) and our specimen of *S. kazahana*, are deposited in the National Institute of Biological Resources (NIBR) in Incheon, ROK (deposition number *S. kiosti*: DSEVIV0000003716; *S. kazahana*: DSEVIV0000003720). The new species is registered with ZooBank (*LSID*. urn:lsid:zoobank.org:act:DAA1DAD2-32A5-4F02-8143-D0D158F8568B).

## Maps and plot

Sampling location and geographic distribution of selected species were mapped with the software QGIS (version 3.16.8 Hannover; 1989, 1991, Free Software Foundation, Inc.). Continent shapefiles were acquired through open sources at <https://www.igismap.com>, country specific shape-

files through [https://gadm.org/download\\_country\\_v3.html](https://gadm.org/download_country_v3.html). Map depicting trans-Arctic interchange through time were generated with MapCreator (version 2.0; personal edition) and edited with vector graphics software Inkscape (0.92.1 version 3; 2007, Free Software Foundation, Inc.). Length/height plot was generated with SigmaPlot (version 10.0; 2006, Systat Software, Inc.) and edited with Inkscape 0.92.

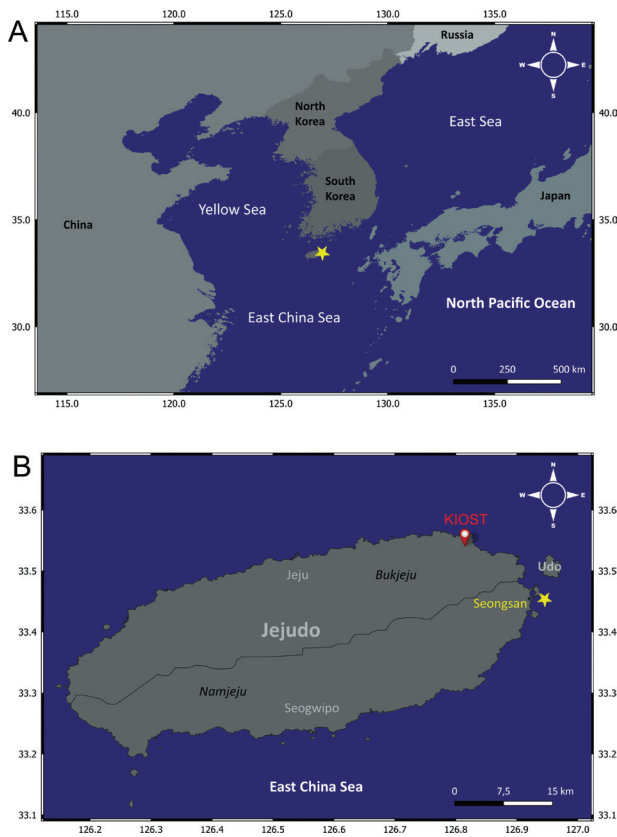
## Abbreviations

**ALV** Adult left valve;  
**ARV** Adult right valve;  
**A-1** A-1 instar (last juvenile molt before adult);  
**A-2** A-2 instar (second-last molt before adult).

## Data availability

Specimens are deposited at the National Institute of Biological Studies (NIBR, Incheon, South Korea) under the deposition numbers DSEVIV0000003716 (*S. kiosti*





**Figure 2.** Map of sampling location. **A.** Overview of Korea including adjacent countries and seas; **B.** Overview of Jeju Island with sampling location in yellow. Yellow star denotes the deployment site of the ARMS; red location pin icon points at the location of the Korea Institute of Ocean Science and Technology (KIOST) on Jeju Island; grey shades denote land masses, blue denotes seas. Coordinates given in decimal degrees.

sp. nov.) and DSEVIV0000003720 (*S. kazahana*). This published work and the nomenclatural acts it contains, have been registered in ZooBank (LSID: urn:lsid:zoobank.org:act:DAA1DAD2-32A5-4F02-8143-D0D158F8568B).

## Results

Yamada and Tsukagoshi (2010) provided a treatise list of all published members of the *henryhowei* group, and included a total of 32 species: 16 named and 16 left in the open nomenclature. We studied all species and identified all unnamed species based on distinctive ridge pattern and prominent carapace characteristics. A schematic explanation of the ridge terminology is given in Fig. 3. Additionally, we added seven more species, previously not included in the treatise list, namely *Semicytherura* sp. 1 sensu Yamada et al. (2002), *Semicytherura quadraplana* Allison & Holden, 1971, *Hemicytherura* sp. 3 sensu Ikeya and Itoh 1991, *Semicytherura kaburagawensis* Tanaka, 2013, *Semicytherura usuigawensis* Tanaka, 2013, and *Semicytherura* sp. A and B sensu Yamada et al. (2004) (Appendix 1). The following species assignments were concluded (see also Table 1):

*S. henryhowei* sensu Irizuki (1994) (pg. 13, pl. 3, figs 1, 2) is most likely *S. balrogi* Brouwers, 1994

The two valves pictured clearly show the anterior longitudinal ridge extending past the anterior third and connecting with the dorsal margin at the posterodorsal corner, which is characteristic for specimens of *S. balrogi* (Fig. 4P). True, *S. henryhowei* does not have such a long, smooth anterior longitudinal ridge (Fig. 4F). Additionally, *S. henryhowei* has a thin ridge branching off the dorsal margin at two-thirds of the valve length, in front of the posterodorsal corner, connecting with the anterior subvertical ridge within the dorsal half (Fig. 4F). The imaged left valve (fig. 1; Irizuki, 1994) shows no posterior subvertical ridge, whereas the right valve shows an inconspicuous, short posterior subvertical ridge, not merging with the ventral ridge. Both, *S. henryhowei* and *S. balrogi* lack the posterior subvertical ridge.

*Semicytherura* aff. *S. henryhowei* sensu Cronin and Ikeya (1987) (pg. 83, pl. 3, fig. 13) is most likely *S. balrogi*

The pictured left valve shows a conspicuous, long, arching anterior longitudinal ridge, running from the mid-height at the anterior margin to the posterodorsal corner without prominent ridges connecting it with the ventral ridge, which is typical of *S. balrogi* (Fig. 4P).

*Kangarina* sp. B sensu Valentine (1976) (pl. 5, fig. 15) is probably *S. balrogi*

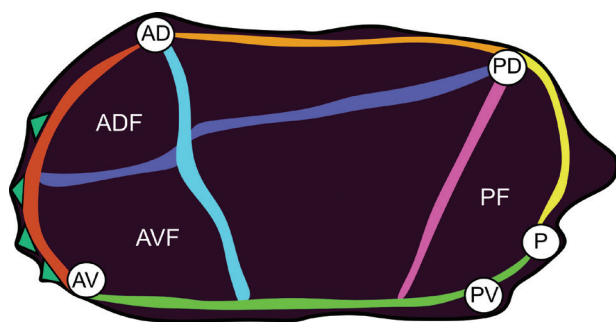
The pictured right valve has four anteroventral marginal denticles, a long anterior longitudinal ridge, and a ventral ridge that starts off anteriorly at the height of the third anteroventral marginal denticle, slightly arching toward the ventral margin, then both merging within the posterior third of the valve, before ascending toward the posterior ridge. All these characteristics are distinct patterns found in *S. balrogi* (Fig. 4P).

*S. henryhowei* sensu Ikeya and Itoh (1991) (pg. 143, fig. 22C) is most likely *S. ikeyai* Yamada & Tsukagoshi (2010)

The pictured left valve is characterized by a continuous anterior longitudinal ridge that connects with the dorsal margin at the posterior half, in front of the posterodorsal corner, which is typical for *S. ikeyai* (Fig. 4N).

*Semicytherura* sp. B sensu Whatley and Boomer (1995) (pg. 255, pl. 1, figs 6, 7) is most likely *S. ikeyai*

The pictured right and left valves show an anterior longitudinal ridge ascending in a nearly straight manner from the



**Figure 3.** Schematic drawing for terminology of major ridges (carinae) of the *Semicytherura henryhowei* group. Red: anterior ridge; orange: dorsal ridge; yellow: posterior ridge; green: ventral ridge; pink: posterior subvertical ridge; blue: anterior sublongitudinal ridge; turquoise: posterior subvertical ridge; Green triangles: anteroventral marginal denticles (crenulations); white dots: corners; AD: Anterodorsal; PD: posterodorsal; P: posterior; PV: posteroventral; AV: anteroventral; ADF: anterodorsal fossa; AVF: anteroventral fossa; PF: posterior fossa.

anterior margin at mid-height of the valve to the end of the anterior third above mid-height, where the anterior subvertical ridge crosses in the posteroventral direction and a thin ridge splits from the anterior half of the anterior subvertical ridge, and merging, as dorsal continuation of the anterior longitudinal ridge, with the dorsal margin in front of the posterodorsal corner. The ventral ridge is comparably thin. These are typical morphological traits of *S. ikeyai* (Fig. 4N). In case of the specimens of Whatley and Boomer (1995), the ridge connecting the anterior subvertical ridge with the dorsal margin is rather inconspicuous.

*Semicytherura* sp. sensu Irizuki et al. (2005) (pg. 42, pl. 4, fig. 7) is most likely *S. kazahana* Yamada, Tsukagoshi & Ikeya, 2005

The pictured right valve has a short anterior longitudinal ridge, which, with the anterior subvertical ridge, splits the anterior half of the valve into two fossae. The posterior ridge connecting the ventral ridge with the dorsal ridge is distinct. The ventral half of the anterior subvertical ridge is wider than the dorsal half. There appears to be five marginal anteroventral denticles, although the anterior edge of the specimen is not clear. All these characteristics resemble *S. kazahana* (Fig. 4H).

*Semicytherura* sp. 3 sensu Irizuki (1994) (pg. 13, pl. 3, figs 8–11) is most likely *S. undata* (Sars, 1866)

The imaged right and left valves have the ventral ridge typical for *S. undata* (Fig. 4L). It starts from, or close to, the anteroventral margin and runs in a slightly convex curve above the ventral margin until the anterior third to half of the valve length. From there, it descends in a straight, diagonal line toward the ventral margin until

merging with it and terminating at or behind the posterior third of the valve length. The subvertical dorsal ridge, however, is lacking in some specimens [pl. 3, figs 9–11 (Irizuki 1994)], which is uncharacteristic for *S. undata*. One pictured left valve [pl. 3, fig. 8 (Irizuki 1994)] has a short subvertical dorsal ridge, as typical for specimens of *S. undata* (Fig. 4L). The dorsal ridge of *S. undata* is characterized by a prominent, very short, “comma-shaped” ridge in the posteroventral area, which all specimens here show, although to a varying extent (Irizuki 1994).

*Semicytherura* sp. B sensu Yamada et al. (2004) is most likely *S. slipperi* Yamada et al., 2005

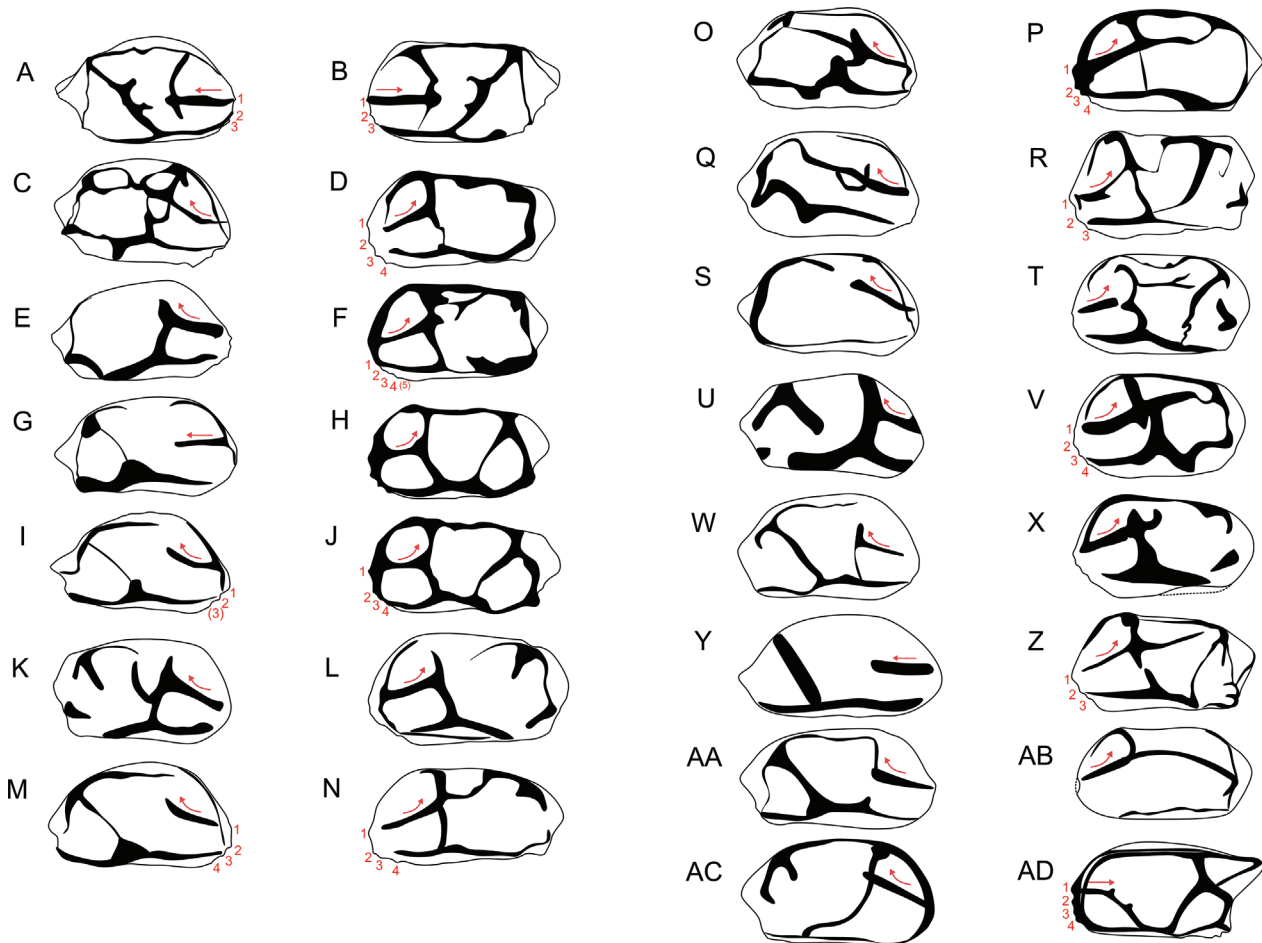
The pictured left valves (pg. 383, text-figs 2C, E) are characterized by a short anterior longitudinal ridge, steeply running upward in a straight fashion, thickening toward its posterior end at the anterior third of the valve-length (Fig. 4D). The posterior subvertical ridge is lacking. The ventral part of the anterior subvertical ridge is not a smooth continuation of the slightly curved, prominent dorsal part, but connecting to the ventral ridge in a rather inconspicuous zig-zag manner. Four anteroventral marginal denticles are present (Yamada et al. 2004).

*Semicytherura* sp. A sensu Yamada et al. (2004) is either *S. sasameyuki*, or *S. kazahana* Yamada, Tsukagoshi & Ikeya, 2005

The pictured left valve (pg. 383, text-fig. 2A) shows the typical ridge pattern of *S. kazahana* [pg. 247, fig. 2C, pg. 253, fig. 6; (Yamada et al. 2005)] and *S. sasameyuki* [pg. 247, fig. 2D; pg. 255, fig. 8; (Yamada et al. 2005)]. The anterior subvertical ridge smoothly connects to the anterior longitudinal ridge with its dorsal part, and to the ventral ridge with its ventral part. The posterior subvertical ridge is smooth, tapering toward ventral and connecting with the ventral ridge. The four comparably large, acuminate, anterior marginal denticles can indicate the specimen’s association to both, *S. sasameyuki* (Fig. 4J), which always shows four marginal denticles, as well as to *S. kazahana* (Fig. 4H), which may either show four or five marginal denticles, or none at all (see pg. 243, fig. 6A–D, four denticles; E, zero denticles; F, five denticles; Yamada et al. 2005). For a definite distinction between the two species, soft-body analysis is necessary.

*Semicytherura* sp. 1 sensu Yasuhara and Irizuki (2001) is most likely *S. kazahana*

The pictured adult left and juvenile right valves (pg. 93, pl. 11 figs 7, 8) show the typical ridge pattern of *S. kazahana* and *S. sasameyuki* (Yamada et al. 2005). However, the adult valve shows the presence of four anteroventral marginal denticles (pg. 93, pl. 11, fig. 7), whereas they are absent



**Figure 4.** Illustrated guide of major ridge systems of the *Semicytherura henryhowei* species complex. **A.** *Semicytherura kiosti* sp. nov. Jöst and Karanovic male ARV; based on # 109\_2 herein; **B.** *Semicytherura kiosti* sp. nov. Jöst and Karanovic male ALV; based on # 109\_1 herein; **C.** *Semicytherura robustundata* Ozawa & Kamiya, 2008 ARV; based on Ozawa and Kamiya 2008; **D.** *Semicytherura slipperi* Yamada, Tsukagoshi & Ikeya, 2005 ALV; based on Yamada et al. 2005; **E.** *Semicytherura subslipperi* Ozawa & Kamiya, 2008 ARV; based on Ozawa and Kamiya 2008; **F.** *Semicytherura henryhowei* Hanai, 1977 ALV; based on Yamada et al. 2005; **G.** *Semicytherura leptosubundata* Ozawa & Kamiya ARV; based on Ozawa and Kamiya 2008; **H.** *Semicytherura kazahana* Yamada, Tsukagoshi & Ikeya, 2005 ALV; based on Yamada et al. 2005; **I.** *Semicytherura subundata* (Hanai, 1957) ARV; based on Ozawa and Kamiya 2008; **J.** *Semicytherura sasameyuki* Yamada, Tsukagoshi & Ikeya, 2005 ALV; based on Yamada et al. 2005; **K.** *Semicytherura tanimurai* Ozawa & Kamiya, 2008 ALV; based on Ozawa and Kamiya 2008; **L.** *Semicytherura undata* (Sars, 1865) ARV; based on Cronin and Ikeya 1987; **M.** *Semicytherura maxima* Yamada & Tsukagoshi, 2010 ARV; based on Yamada and Tsukagoshi 2010; **N.** *Semicytherura ikeyai* Yamada & Tsukagoshi, 2010 ARV; based on Yamada and Tsukagoshi 2010; **O.** *Semicytherura* sp. nov. sensu Irizuki 1994 (S. sp. 4) ALV; based on Irizuki 1994; **P.** *Semicytherura balrogi* Brouwers, 1994 ARV; based on Brouwers 1994; **Q.** *Semicytherura* sp. nov. sensu Irizuki 1994 (S. sp. 5) ALV; based on Irizuki, 1994; **R.** *Semicytherura* sp. nov. sensu Cronin and Ikeya 1987 (S. sp. A) ARV; based on Cronin and Ikeya 1987; **S.** *Semicytherura* sp. nov. sensu Cronin 1989 (S. sp. cf. *henryhowei*) ALV; based on Cronin 1989; **T.** *Semicytherura* sp. nov. sensu Irizuki 1994 (S. sp. 2) ARV; based on Irizuki 1994; **U.** *Semicytherura simplex* (Brady & Norman, 1889) ALV; based on Hu 1978; **V.** *Semicytherura* sp. nov. sensu Ozawa et al. 2008 (S. sp. 1) ARV; based on Ozawa et al. 2008; **W.** *Semicytherura pseudoundata* Irizuki & Yamada, 2004 ALV; based on Irizuki et al. 2004; **X.** *Semicytherura* sp. nov. sensu Ozawa et al. 2008 (S. sp. 2) ARV; based on Ozawa et al. 2008; **Y.** *Semicytherura neosubundata* (Ishizaki, 1966) ALV; based on Ishizaki 1966; **Z.** *Semicytherura* sp. nov. sensu Irizuki 1994 (S. sp. aff. *henryhowei*) ARV; based on Irizuki 1994; **AA.** *Semicytherura kaburagawensis* Tanaka, 2013 RV; based on Tanaka and Hasegawa 2013; **AB.** *Semicytherura* sp. nov. sensu Irizuki 1994 (S. sp. 1) ALV; based on Irizuki 1994; **AC.** *Semicytherura usuigawensis* Tanaka, 2013 RV; based on Tanaka and Hasegawa 2013; **AD.** *Semicytherura quadraplana* Allison & Holden, 1971 ALV; based on the original drawing in Allison and Holden 1971. Red arrows indicate whether anterior sublongitudinal ridge is horizontal or sloped; red numbers indicate the anteroventral marginal denticles.

in the juvenile valve (pg. 93, pl. 11, fig. 8 in Yasuhara and Irizuki 2001). This variation in number of anteroventral denticles indicates that the specimens of Yasuhara and Irizuki (2001) belong to *S. kazahana* (Fig. 4H), unless they

present juvenile and adult of separate species. However, although the geographical distribution of *S. kazahana* and *S. sasameyuki* overlaps, their microhabitats differ with the former being a phytal species typical of rocky shore



environments, and the latter living on the silty sands of inner bays (Yamada et al. 2005). This speaks for the presence of just one of the two species, here *S. kazahana*, due to the varying number of anteroventral marginal denticles.

*S. henryhowei* sensu Yajima (1988) is either *S. sasameyuki*, or *S. kazahana*

The pictured right valve (pg. 1076, pl. 1, fig. 12) shows a prominent posterior subvertical ridge, which is absent in *S. henryhowei* (Fig. 4F). Additionally, *S. henryhowei* has small, rounded, anterior marginal denticles, whereas this specimen shows four distinct and pointy anterior denticles. The ridge pattern, and number and shape of anteroventral denticles, marks this specimen as, either *S. sasameyuki* or *S. kazahana*. Whereas *S. sasameyuki*, so far, has only been reported from extant sediments of Japan, *S. kazahana* has a Pleistocene record from Korea (Lee 1990, unpublished), an extant Japanese distribution (Yamada et al. 2005; living specimens collected 1977–2000), as well as an extant Korean distribution (this study; valves collected 2019). Our species re-assignment indicates a Japanese Miocene existence of either of the species.

*Semicytherura* sp. 2 sensu Yamada et al. (2002) is most likely *S. tanimurai* Ozawa & Kamiya, 2008

The pictured right valve exhibits a prominent anterior subvertical ridge with a posterior branch at its dorsal half (pg. 122, pl. 1, fig. 16; Ozawa and Kamiya 2008), typical of *S. tanimurai* (Fig. 4K). Although this upward-curved branch is sharper, more like a V-shape in *S. tanimurai* (Fig. 5A), whereas this specimen shows a rounder U-shape (Fig. 5B). Additionally, the ventral ridge is slightly different at its posterior half, as it continues to the posterior tip of the ventral margin (anteroventral corner) (Fig. 5B), whereas in *S. tanimurai* it discontinues after merging with the ventral margin ahead of the anteroventral corner (Fig. 5A). Hence, our species re-assignment to *S. tanimurai* is tentative.

*Hemicytherura* sp. 3 sensu Ikeya and Itoh 1991 is most likely *S. kiosti* Jöst & Karanovic, sp. nov.

The pictured right valve (pg. 138, fig. 17A) shows all distinct carapace characteristics of *S. kiosti* sp. nov.: three small anteroventral marginal denticles, a prominent posterior subvertical ridge starting at the posterodorsal corner and merging with the ventral ridge at around mid-length, a posterior ridge connecting posterodorsal and posteroventral corners in a straight line, and a horizontal, straight, and short sublongitudinal anterior ridge (Fig. 4B, AA).

The following three species were not included in the list of members of the *S. henryhowei* complex by Yamada

and Tsukagoshi (2010), however, based on their prominent ridge systems, they also belong to this species group (Fig. 4AA, AC, AD).

*Semicytherura kaburagawensis* Tanaka, 2013

The species is characterized by a broad, sigmoid ventral ridge that starts as a thin ridge at anteroventral margin, running parallel to ventral margin toward posterior, growing broader and forming a sigmoid curve at posterior third of carapace length at merging point with subvertical dorsal ridge (pg. 144, fig. 4.2 in Tanaka and Hasegawa 2013). Subvertical dorsal ridge prominent, starting from posterodorsal corner in a bifurcated manner (Fig. 4AA). Posterior ridge branch thin, merging with ventral ridge at posteroventral corner; subvertical dorsal ridge branch thick, merging with ventral ridge at posterior third of carapace length. Posterior ridge, subvertical dorsal ridge, and ventral ridge form a rectangular posterodorsal fossa. Anterior sublongitudinal ridge short, mildly arched, slightly ascending, terminating at anterior third of carapace length. Posterior half of subvertical dorsal ridge running from anterodorsal corner (eye tubercle according to type description) ventrally, in a straight, horizontal line, merging with dorsal end of anterior sublongitudinal ridge. Anterior half of subvertical dorsal ridge not observed.

*Semicytherura usuigawensis* Tanaka, 2013

The species is characterized by a long, sigmoid subvertical dorsal ridge, running from posterodorsal corner ventrally through anterior sublongitudinal ridge, and merging with ventral ridge at posterior third of carapace length (pg. 144, fig. 4.3 in Tanaka and Hasegawa 2013). Posterior subvertical ridge very short. Posterior ridge broad, terminalizing at mid-height. Elliptical anterodorsal fossa (Fig. 4AC).

*Semicytherura quadraplana* Allison & Holden, 1971

The species is characterized by four anteroventral marginal denticles, a downward arching anterior sublongitudinal ridge that fuses with the ventral half of its anterior subvertical ridge, which, in turn, connects to the ventral ridge within the anterior half of the carapace length (pg. 194, fig. 20b in Allison and Holden 1971). The dorsal half of the anterior subvertical ridge is very short, the posterior subvertical ridge bifurcate, forming an elliptical posterodorsal fossa (Fig. 4AD).

The following nine species did not fit the ridge pattern of any of the known species of the group, hence are undescribed species of the *henryhowei* group:

*Semicytherura* sp. 1 (pg. 13, pl. 3, fig. 6),  
*Semicytherura* sp. 2 (pg. 13, pl. 3, fig. 7),  
*Semicytherura* sp. 4 (pg. 13, pl. 3, figs 12–15),  
 and *Semicytherura* sp. 5 (pg. 13, pl. 3, figs 16, 17) sensu Irizuki (1994)

*Semicytherura* sp. 1 is too poorly preserved to make any definite statements. However, it appears to exhibit a long anterior longitudinal ridge, arching over the entire length of the valve exterior and terminating when merging with the dorsal ridge below the caudal process (Fig. 4AB). This is a unique feature, not observed in any of the other species of the *S. henryhowei* complex. *Semicytherura* sp. 2 has a conspicuous anterior subvertical ridge shaped like a large “3” (Fig. 4T). Additionally, it sports two, horizontal dorsal ridges, the one closer to the dorsal margin is curved, and the one below is straight and forking at its dorsal end. *Semicytherura* sp. 4 (Fig. 4O) sports a long anterior longitudinal ridge, as do *S. balrogi*, *S. robustundata*, and *S. ikeyai* among the described species of the *S. henryhowei* group. Unlike the three described species, however, its dorsal branch at the anterior third of the anterior longitudinal ridge is short and does not merge with the dorsal margin. Additionally, its anterior subvertical ridge that connects the anterior longitudinal ridge with the ventral ridge is not straight as in *S. balrogi* (Fig. 4P) and *S. ikeyai* (Fig. 4N), but more of a zig-zag line, similar to *S. robustundata* (Fig. 4C). However, whereas in *S. robustundata* this connection is described as a “U-shape” and a “T-shape” (upside-down T) (Fig. 6B), here, it is a hook-shape and upside-down T or Y (Fig. 6A). *Semicytherura* sp. 5 (Fig. 4Q) is characterized by a long anterior longitudinal ridge ascending from mid-height at the anterior margin to the posterodorsal corner, parallel to the likewise ascending ventral ridge, which is situated above the ventral margin (Fig. 4Q). This main pattern of two long, parallel ridges running across the valve is very conspicuous and characteristic of this undescribed species.

*Semicytherura* sp. A of Cronin and Ikeya (1987) (pg. 83, pl. 3, fig. 10)

The pictured left valve has a very prominent, thick posterior subvertical ridge, tapering toward its ventral tip (Fig. 4R). The ventral ridge is straight, horizontal, and tapering toward posterior. The anterior longitudinal ridge starts below the mid-height of the valve at the ventral margin, and ascends as a curve toward the anterior third of the valve length, where it connects with the anterior subvertical ridge above the mid-height of the valve. Behind the anterior subvertical ridge, it continues in a thin, zig-zag fashion, merging with the dorsal margin/ridge at the mid-length of the valve. The caudal process is broadly triangular, inconspicuous, above the mid-height. The carapace surface is covered in fine pits and thin reticulation.

*Semicytherura* cf. *S. henryhowei* of Cronin (1989) (pg. 135, pl. 3, figs 3, 4)

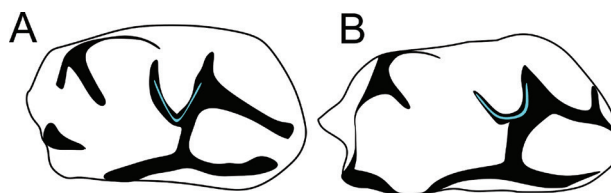
The pictured right and left valves are characterized by the absence of the anterior and posterior subvertical ridges (Fig. 4T). The valves are less ornamented by thick ridges, but rather show near-circular inflations in their posterior and anterior halves. The anterior longitudinal ridge starts from the anterior margin at the mid-height of the valve, and ascends toward the end of the anterior third of the valve length, on top of the anterior inflation. A deep, median sulcus separates the anterior longitudinal ridge from its continuation, which merges with the dorsal ridge slightly in front of the posterodorsal corner. The carapace is ornamented by fine pits and thin reticulation.

*Semicytherura* sp. 1 of Ozawa et al. (2008) (pg. 167, pl. 2, figs 14, 15)

The pictured right and left valves are characterized by comparably thick ridges (Fig. 4V). The ventral ridge is distinct, rising from the anterior to the end of the anterior third of the valve length, where the anterior subvertical ridge connects with it at its peak. It then drops in a straight line to the ventral margin, from where it rises again in a curved fashion to the dorsal corner. The anterior sublongitudinal ridge is long, thick, but its posterior end is either thinner and lower where it connects with the posterodorsal corner (pg. 167, pl. 2, fig. 14; Ozawa et al. 2008), or it terminates as a thick ridge without connecting to the posterodorsal corner (pg. 167, pl. 2, fig. 15; Ozawa et al. 2008). Both valves have four anteroventral marginal denticles.

*Semicytherura* sp. 2 of Ozawa et al. (2008) (pg. 167, pl. 2, fig. 16)

The pictured left valve lacks a prominent posterior subvertical ridge, and the anterior sublongitudinal ridge continues after the anterior subvertical ridge as a short, upward-curved extension (Fig. 4X). The carapace is ornamented by fine pits and reticulation.



**Figure 5.** Shape details of posterodorsal branch of anterior subvertical ridge in *Semicytherura* sp. 2 sensu Yamada et al. 2002 proposed *S. tanimurai* Ozawa & Kamiya, 2008 and *S. tanimurai* original type. A. *Semicytherura tanimurai* Ozawa & Kamiya, 2008. B. *Semicytherura* sp. 2 sensu Yamada et al. 2002 proposed *S. tanimurai* Ozawa & Kamiya, 2008. Turquoise highlights the specific shape caused by the different angles, the dorsal branch forks off the anterior subvertical ridge in both specimens.

*Semicytherura* aff. *henryhowei* of Irizuki  
(1994) (pg. 13, pl. 3, fig. 3)

The pictured left valve shows an anterior sublongitudinal ridge that continues as a thinner ridge after the crossing of the anterior subvertical ridge. The posterior sublongitudinal ridge is present, but inconspicuous (Fig. 4Z). True,

*S. henryhowei* has a short anterior sublongitudinal ridge, terminating when crossing with the anterior subvertical ridge at the end of the anterior third of the valve length, and the posterior subvertical ridge is absent (Fig. 4F). Additionally, *S. henryhowei* has either four or five anteroventral marginal denticles, whereas this species has three (Fig. 4Z).

Key to the species of the *henryhowei* group based on the most prominent carapace characteristics

- 1 Anterior sublongitudinal ridge horizontal, straight ..... 2
  - Anterior sublongitudinal ridge ascending or descending, either in straight line or curved ..... 5
- 2 Anterior subvertical ridge absent ..... 3
  - Anterior sublongitudinal ridge connected to anterior subvertical ridge ..... 4
- 3 Posterior subvertical ridge prominent, straight; ventral ridge of moderate width (Fig. 4Y) ..... *Semicytherura neosubundata* (Ishizaki, 1966)
  - Posterior subvertical ridge thin or inconspicuous; ventral ridge alate (Fig. 4G) ..... *Semicytherura leptosubundata* (Ozawa & Kamiya, 2008)
- 4 Ventral half of anterior subvertical ridge connected to dorsal ridge; 3 anteroventral marginal denticles (Fig. 4A, B) ..... *Semicytherura kiosti* sp. nov. Jöst & Karanovic
  - Ventral half of anterior subvertical ridge short or absent; 4 anteroventral marginal denticles (Fig. 4AD) ..... *Semicytherura quadraplana* Allison & Holden, 1971
- 5 Anterior sublongitudinal ridge short, terminating at anterior third of valve length; anterior subvertical ridge absent ..... 6
  - Anterior sublongitudinal ridge posteriorly connected to other ridge/ridges going in posterior direction and/or anterior subvertical ridge present ..... 8
- 6 Posterior subvertical ridge present ..... 7
  - Posterior subvertical ridge absent (Fig. 4S) ..... *Semicytherura* sp. nov. sensu Cronin 1989 (*Semicytherura* sp. cf. *henryhowei*)
- 7 Four anteroventral marginal denticles (Fig. 4M) ..... *Semicytherura maxima* Yamada & Tsukagoshi, 2010
  - Less than four anteroventral marginal denticles (Fig. 4I) ..... *Semicytherura subundata* (Hanai, 1957)
- 8 Posterior subvertical ridge absent or short (not connected to ventral ridge) ..... 15
  - Posterior subvertical ridge long, connecting posterodorsal corner to ventral ridge ..... 9
- 9 Posterior fossa present ..... 10
  - Posterior fossa absent ..... 13
- 10 Anterior sublongitudinal ridge long; three anteroventral marginal denticles (Fig. 4Z) ..... *Semicytherura* sp. nov. sensu Irizuki, 1994 (*Semicytherura* sp. aff. *henryhowei*)
  - Anterior sublongitudinal ridge short, terminating at anterior third of valve length ..... 11
- 11 Anterior subvertical ridge connected to ventral ridge ..... 12
  - Anterior subvertical ridge not connected to ventral ridge; dorsal half of anterior subvertical ridge straight, vertical, connected to anterodorsal corner (Fig. 4AA) ..... *Semicytherura kaburagawensis* Tanaka, 2013
- 12 Zero, four, or five anteroventral marginal denticles; in dorsal view, three pores along exterior margin and two pores anterior along interior margin (Fig. 4H) ..... *Semicytherura kazahana* Yamada, Tsukagoshi & Ikeya, 2005
  - Four anteroventral marginal denticles; in dorsal view, four pores along exterior margin and one pore anterior along interior margin (Fig. 4J) ..... *Semicytherura sasameyuki* Yamada, Tsukagoshi & Ikeya, 2005
- 13 Anterior subvertical ridge with prominent, short posterior half not connected to anterodorsal corner, and thin ventral half connecting with ventral ridge (Fig. 4W) ..... *Semicytherura pseudoundata* Irizuki & Yamada, 2004
  - Anterior subvertical ridge connecting anterodorsal corner with ventral ridge ..... 14
- 14 Ventral ridge prominent, thick (Fig. 4T) ..... *Semicytherura* sp. nov. sensu Irizuki 1994 (*Semicytherura* sp. 2)
  - Ventral ridge with thick anterior half, thin posteriorly from merging point with anterior subvertical ridge (Fig. 4R) ..... *Semicytherura* sp. nov. sensu Cronin and Ikeya 1987 (*Semicytherura* sp. A)
- 15 Posterior ridge long, connecting posterodorsal corner with posteroventral corner (Fig. 4L) ..... *Semicytherura undata* (Sars, 1866)
  - Posterior ridge short, not reaching posteroventral corner ..... 16
- 16 Bifurcated ridge from posterodorsal corner; posterior ridge branch longer than posterior subvertical ridge branch (Fig. 4AC) ..... *Semicytherura usuigawensis* Tanaka, 2013
  - Bifurcated ridge from posterodorsal corner; posterior ridge branch shorter than posterior subvertical ridge branch ..... 17
- 17 Anterior subvertical ridge with posterodorsal branch at ventral half; dorsal half short (Fig. 4K) ..... *Semicytherura tanimurai* (Ozawa & Kamiya, 2008)
  - Anterior subvertical ridge without posterodorsal branch at ventral half; dorsal half long, connecting with dorsal margin/ anterodorsal corner (Fig. 4U) ..... *Semicytherura simplex* (Brady & Norman, 1889)



- 18 Anterior subvertical ridge connecting with dorsal margin/ridge ..... 22  
 – Anterior subvertical ridge short, not connecting with dorsal margin/ridge ..... 19  
 19 Anterior sublongitudinal ridge long, connecting anterior margin/ridge with posterodorsal corner ..... 20  
 – Anterior sublongitudinal ridge short, terminalizing at least within anterior half of carapace length ..... 21  
 20 Anterior subvertical ridge connecting to ventral ridge (Fig. 4O) .....  
 ..... *Semicytherura* sp. nov. sensu Irizuki 1994 (*Semicytherura* sp. 4)  
 – Anterior subvertical ridge not connecting to ventral ridge (Fig. 4Q) .....  
 ..... *Semicytherura* sp. nov. sensu Irizuki 1994 (*Semicytherura* sp. 5)  
 21 Anterior longitudinal ridge terminating at mid-length of valve; distinct dorsal ridge; short posterior ridge not connected with posteroventral corner (Fig. 4X) ..... *Semicytherura* sp. nov. sensu Ozawa et al. 2008 (*Semicytherura* sp. 2)  
 – Anterior longitudinal ridge terminating at anterior third of valve length; no obvious dorsal ridge; thin posterior ridge connected with posteroventral corner (Fig. 4E) ..... *Semicytherura subslipperi* Ozawa & Kamiya, 2008  
 22 Anterior sublongitudinal ridge short, terminating within anterior half of valve length ..... 23  
 – Anterior sublongitudinal ridge long, either connecting to other ridges/margins or terminating at posterior third of valve length ..... 24  
 23 Short, thin, bifurced ridge branching off dorsal ridge in anteroventral direction at posterior third of valve length; four or five anteroventral marginal denticles (Fig. 4F) ..... *Semicytherura henryhowei* Hanai & Ikeya in Hanai et al. 1977  
 – Dorsal ridge without branches at posterior third of valve length; four anteroventral marginal denticles (Fig. 4D) .....  
 ..... *Semicytherura slipperi* Yamada, Tsukagoshi & Ikeya, 2005  
 24 Anterior subvertical ridge connecting with ventral ridge ..... 25  
 – Ventral half of anterior subvertical ridge absent; posterior part of long anterior longitudinal ridge connecting with posterior ridge (Fig. 4AB) ..... *Semicytherura* sp. nov. sensu Irizuki 1994 (*Semicytherura* sp. 1)  
 25 Posterior part of long anterior sublongitudinal ridge either connecting with posterodorsal corner or terminating within posterior third of valve length ..... 26  
 – Posterior part of long anterior sublongitudinal ridge connecting with dorsal margin/ ridge at posterior third of valve length; four anteroventral marginal denticles (Fig. 4N) ..... *Semicytherura ikeyai* Yamada & Tsukagoshi, 2010  
 26 Ventral half of anterior subvertical ridge simple, thin, straight line, connecting to ventral ridge; four anteroventral marginal denticles (Fig. 4P) ..... *Semicytherura balrogi* Brouwers, 1994  
 – Ventral half of anterior subvertical ridge no simple, thin, straight line ..... 27  
 27 Ventral half of anterior subvertical ridge connecting to ventral ridge as U-shape on top of upside-down T-shape (Figs 4C, 6b) ..... *Semicytherura robustundata* (Ozawa & Kamiya, 2008)  
 – Ventral half of anterior subvertical ridge thick, short; thick ridge connecting posterior part of long anterior sublongitudinal ridge to ventral ridge as upside-down Y-shape (Figs 4V, 6a) .....  
 ..... *Semicytherura* sp. nov. sensu Ozawa et al. 2008 (*Semicytherura* sp. 1)

## Systematics

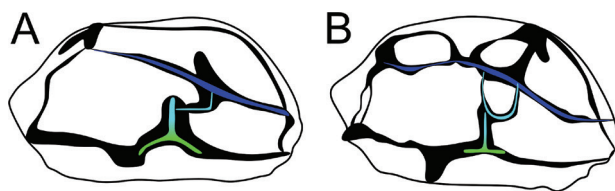
### Description of the group's characteristics

Superfamily CYTHERACEA Baird, 1850  
 Family CYTHERURIDAE Müller, 1894  
 Subfamily CYTHERURINAE Müller, 1894  
 Genus *SEMICYTHERURA* Wagner, 1957

The *Semicytherura henryhowei* Hanai & Ikeya, 1997 species group

**Revised diagnosis of the species group.** External view. Thick carapace, sub-rectangular to sub-trapezoid in lateral view (right valves more sub-trapezoid, left valves more sub-rectangular). External ornamentation of prominent ridges including anterior ridge from anteroventral to anterodorsal corner (Fig. 3, red), anterior longitudinal ridge (short or long, horizontal or arched; Fig. 3, blue), ventral ridge from anteroventral to posteroventral or posterior corner, depending on species-specific length of ridge (Fig. 3, green),

posterior ridge from posterior to posterodorsal corner (Fig. 3, yellow), dorsal ridge from posterodorsal to anterodorsal corner (Fig. 3, orange), anterior subvertical ridge from anterodorsal corner to ventral ridge (depending on species-specific length of ridge) at anterior half of valve (Fig. 3, turquoise), and posterior subvertical ridge from posterodorsal corner to ventral ridge (depending on species-specific length of ridge) at posterior half of valve (Fig. 3, purple). Ridges vary in length and degree of conspicuousness. Not all ridges are present in all species. In species where anterior subvertical ridge is connected with dorsal and/or ventral ridge(s), anterior fossa(e) form (Fig. 3). Anterior fossa(e) elliptic/rectangular (*S. subslipperi*, Fig. 4E, ventral only; *S. usuigawensis*, Fig. 4AC, dorsal only; *S. kazahana*, Fig. 4H; *S. sasameyuki*, Fig. 4J; *S. simplex*, Fig. 4U) to triangular/trapezoid (*S. kiosti* sp. nov., Fig. 4A, B, dorsal only; *S. henryhowei*, Fig. 4D) in shape. Likewise, prominent posterior ridge, as well as distinct posterior subvertical ridge connecting with ventral ridge, form a posterior fossa (e.g., *S. kiosti* sp. nov., Fig. 4A, B; *S. kazahana*, Fig. 4H; *S. sasameyuki*,



**Figure 6.** Connection details between anterior sublongitudinal ridge and ventral ridge in *Semicytherura robustundata* Ozawa & Kamiya, 2008 and *Semicytherura* sp. nov. sensu Irizuki 1994 (*S.* sp. 4). **A.** *Semicytherura* sp. nov. sensu Irizuki 1994 (*S.* sp. 4); **B.** *Semicytherura robustundata* Ozawa & Kamiya, 2008. Blue denotes the anterior sublongitudinal ridge; green denotes the ventral ridge; turquoise denotes the connecting ridge system.

Fig. 4J; *S. kaburagawensis*, Fig. 4AA; *S. quadraplana*, Fig. 4AD). Anterior margin with zero up to five denticles ventrally (Fig. 3, green triangles). Horizontal caudal process with varying degree of conspicuousness; generally, at or above mid-height.

**Internal view.** Recurved inner lamella not present in all species of the group; lacking in at least the following species: *S. balrogi*, *S. simplex*. Recurved inner lamella subject to sexual dimorphism in at least the following species: *S. kiosti* sp. nov., *S. slipperi*, *S. maxima*, *S. ikeyai*.

### Description of species

#### *Semicytherura kazahana* Yamada, Tsukagoshi & Ikeya, 2005

Fig. 7

**Note.** First published record of the species from Korean waters. NIBR deposition number: DSEVIV0000003720.

**Synonymy.** (*Semicytherura henryhowei* sensu Yajima 1988: pg. 1076, pl. 1, fig. 12); (This specimen is either *S. kazahana* or *S. sasameyuki*, see Discussion). *Semicytherura quadrata* sensu Ishizaki 1968: pg. 20, pl. 4, figs 11, 12. *Semicytherura* sp. B sensu Lee 1990 (unpublished): pl. 27, figs 12, 13. *Semicytherura* sp. 1 sensu Yasuhara and Irizuki 2001: pg. 93, pl. 11, fig. 8. *Semicytherura kazahana* Yamada, Tsukagoshi & Ikeya, 2005: pgs 247, 253, 254, figs 2C, 6, 7.

**Diagnosis.** Juvenile. Sub-rectangular to sub-trapezoid lateral outline, as typical for species of the *S. henryhowei* group. Anteroventral margin here without crenulations [there are records of specimens showing four or five anteroventral marginal denticles; see Yamada et al. (2005)]. Carapace surface finely pitted. Dorsal margin weakly descending toward posterior. Acute caudal process at mid-height. Ventral margin weakly descending toward anterior. Thick, prominent ridges on carapace, as typical for the *S. henryhowei* group.

Anterior longitudinal ridge short, slightly ascending in straight line until posterior end of anterior one-third of valve length. Prominent, continuous ventral ridge running horizontally in antero-posterior direction, curving at posterior third of valve length. Two elliptical fossae in anterior half; sub-trapezoid fossa in posterior half.

**Material.** Juvenile, right valve # 70, from ARMS sediment (i.e., surface and sedimentation-derived sediments).

**Locality and age.** Seongsan (성산), Jeju Island, ROK (33°27'13"N, 126°56'45"E) (Fig. 2), 19 m water depth. Extant (collection date 2019; surface and sedimentation-derived sediments, valve only, no soft body).

**Description.** Heavily calcified, thick valve, sub-rectangular in lateral view. Maximum height at anterior third. Dorsal margin is weakly ascending towards posterior. Ventral margin is weakly descending towards posterior. Anterodorsal margin is smooth, obliquely rounded; anteroventral margin without visible marginal denticles, but partially broken; posterior margin is slightly curved above the caudal process. Acute posterior caudal process at mid-carapace.

The carapace surface is covered in fine pits and pores with sensory hairs. Valve with thick ridges; ventral ridge prominent; slightly ascending toward posterior third; then describing a steep drop toward the edge of the ventral margin and ascending again in a straight line toward the posterior margin, resembling the lower loop of a large S-shape; the upper loop of the S-shape is the thick posterior end of the dorsal ridge at the postero-dorsal corner; interconnection between posterodorsal and posteroventral loops by a thin descending posterior subvertical ridge, completing the S-shape; anterior longitudinal ridge short; starting at mid-height from anterior margin, slightly ascending until terminating at posterior end of anterior third of valve length; dorsal half of anterior subvertical ridge steeply running upward and bending backward to anterodorsal corner, forming elliptical, anterodorsal fossa; ventral half of anterior subvertical ridge less prominent, zig-zag course, connecting to ventral ridge at mid-length of carapace, forming elliptical, anteroventral fossa.

**Reticulation.** Surface finely pitted (Fig. 7D, E) with prominent, species-specific ridge system.

**Pores.** Some simple pores with sensory hairs (Fig. 7D).

**Hingement.** Merodont hinge with a socket at each end of a ridge structure in the right valve (Fig. 7C) [not collected, but complementary negative structures in the left valve (tooth at each end of a groove)]. Typical for genus. Hingeline arched.

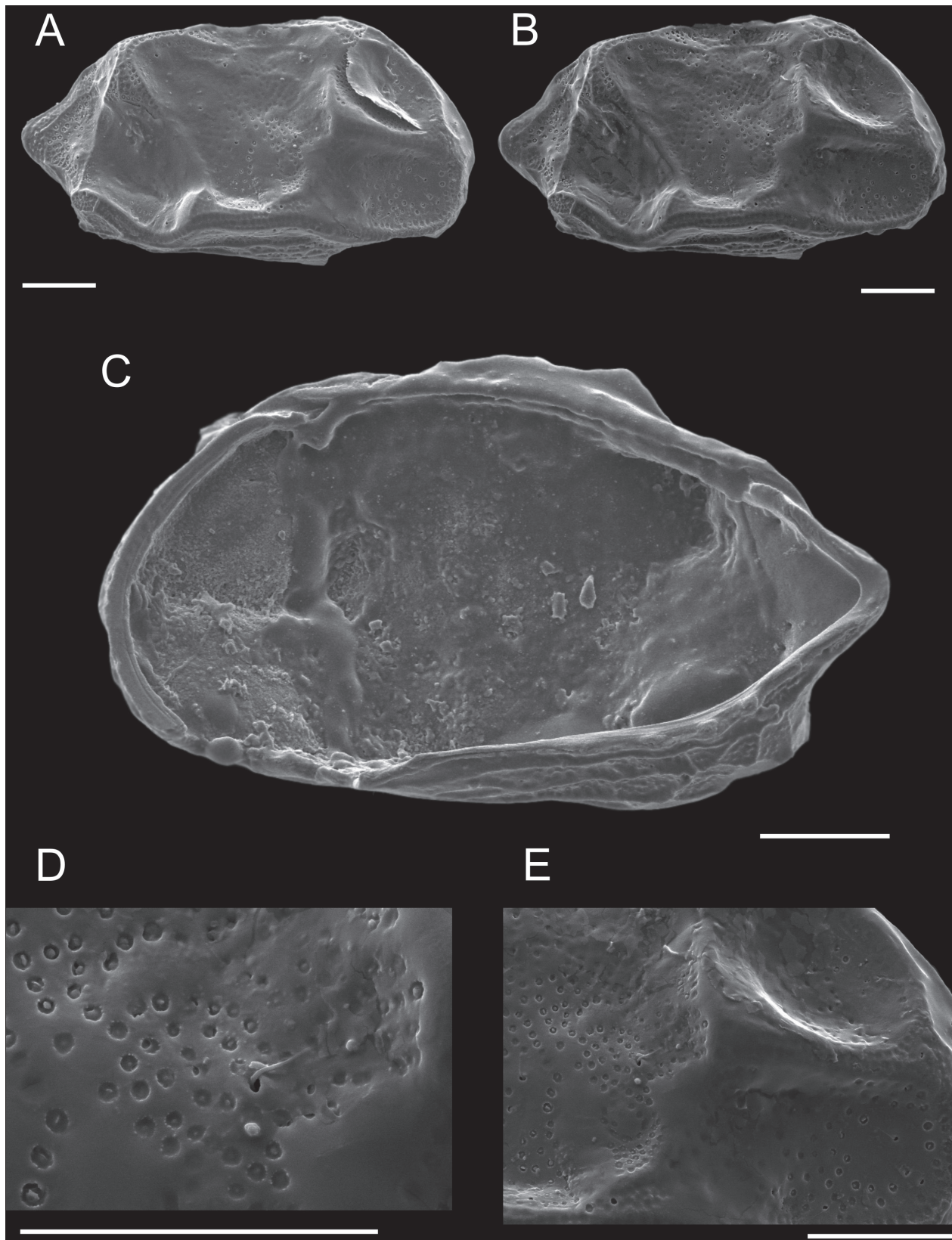
**Adductor muscle scars.** Not observed.

**Recurved inner lamella.** Absent in juveniles [see e.g., *S. subundata* in Ozawa and Kamiya (2008), pg. 143, fig. 4; *S. kiosti* Jöst & Karanovic sp. nov., Fig. 12 herein].

**Dimensions.** Carapace dimensions: length: 0.3064 mm, height: 0.166 mm.

**Occurrence.** Extant sediments, Korea (this study; surface and sedimentation-derived sediments collected 2019), and Japan (Yamada et al. 2005; living specimens, surface sediment collection: 1977–2000); Pleistocene sediments, Korea (Lee, 1990; unpublished); (potentially) Miocene sediments, Japan (Yajima 1988) (after species re-assignment, this study; uncertain whether *S. kazahana* or *S. sasameyuki*, see Discussion).

**Remarks.** Our specimen greatly resembles the juvenile specimen of *Semicytherura* sp. 1 sensu Yasuhara and



**Figure 7.** *Semicytherura kazahana* external and internal lateral views. A–E. Specimen # 70 A-1RV; A–B, D–E. Lateral external view; D. Details of pore with sensory hair and pitted carapace surface; E. Details of anterior subvertical ridge; C. Lateral internal view. Scale bars: 50 µm.

Irizuki 2001 (pg. 93, pl. 11, fig. 8), which was assigned to *S. kazahana* herein. The specimen of Yasuhara and Irizuki displays small, rounded anterior marginal denticles,

which are absent in our specimen. However, *S. kazahana* has shown to display differing numbers of crenulations along its anterior margin (Yamada et al. 2005).



***Semicytherura kiosti* Jöst & Karanovic, sp. nov.**

<https://zoobank.org/DAA1DAD2-32A5-4F02-8143-D0D158F8568B>

Figs 8–12

**Note.** NIBR deposition number: DSEVIV0000003716.

**Synonymy.** *Hemicytherura* sp. 3 sensu Ikeya and Itoh 1991: pg. 138, fig. 17A.

**Etymology.** After the collaborating institution, Korea Institute of Ocean Science and Technology (KIOST), who provided the samples and funding for the Marine-GEO project in Korea.

**Diagnosis.** Sub-rectangular lateral outline (especially LV), as typical for species of the *S. henryhowei* group. Anteroventral margin with three crenulations (denticles). Carapace surface roughly pitted with finer, smaller pits at marginal areas. Dorsal margin straight, horizontal. Broadly acute caudal process above mid-height. Ventral margin straight, horizontal, but posterior half obscured by ventral ridge. Thick, prominent ridges on carapace, as typical for the *henryhowei* group. Prominent posterior subvertical ridge forming large, subtriangular fossa in posterior half of valve. Prominent, horizontal, straight anterior longitudinal ridge forming large, subtrapezoid fossa with dorsal half of anterior subvertical ridge.

**Holotypes.** Two valves: adult male left valve, # 109\_1 (lost, only SEM) and right valve, # 109\_2 from ARMS sediment (i.e., surface and sedimentation-derived sediments).

**Paratypes.** Five valves: # 68 (female ARV) and # 108 (male ARV) from ARMS sediment (i.e., surface and sedimentation-derived sediments), and # 177 (female A-1RV), # 239 (female A-2RV), # 240 (female ARV) from scoop sediment (i.e., surface sediment).

**Type deposition.** Specimens are deposited at the National Institute of Biological Studies (NIBR, Incheon, South Korea) under the deposition number DSEVIV0000003716.

**Type locality and age.** Seongsan (성산), Jeju Island, ROK (33°27'13"N, 126°56'45"E) (Fig. 2), 19 m water depth. Extant (collection date 2019; surface and sedimentation-derived sediments; valves only, no soft bodies).

**Description.** Heavily calcified, thick valve, sub-rectangular (LV) to ovoid (RV) in lateral view. Right valve larger than left valve (see Fig. 8, length/height plot, # 109\_1 and # 109\_2). Maximum height at anterodorsal corner. Dorsal margin is horizontal, straight, parallel to ventral margin. Ventral margin is obscured by overhanging ventral ridge at posterior half. Anterodorsal margin is smooth, obliquely rounded; antero-ventral margin with three small, acute marginal denticles; posterior margin is ascending in a straight line above the caudal process. Broadly acute posterior caudal process above mid-carapace.

The carapace surface is covered in rough pits, and pores with sensory hairs. Finer, smaller pits at marginal areas. Valve with thick ridges; anterior sublongitudinal ridge short, horizontal, straight line, terminating at anterior third of valve length; prominent posterior subvertical ridge connecting posterodorsal corner with ventral ridge at mid-length of valve; posterior ridge branching off posterodorsal corner and running in a straight, vertical manner to posterior corner; posterior subvertical ridge,

posterior ridge and posterior half of ventral ridge form large, subtriangular fossa; anterior longitudinal ridge, dorsal half of anterior subvertical ridge, and anterodorsal margin form large, subtrapezoid fossa. Right valves slightly higher and longer than left valves. Females longer and slightly higher than males (see length/height plot, Fig. 8).

**Reticulation.** Surface covered in large pits with prominent, species-specific ridge system.

**Pores.** Some simple pores with sensory hairs.

**Hingement.** Merodont hinge with a socket at each end of a ridge structure in the right valve (Figs 9A, C, 10B, F, I). Complementary negative structures in the left valve (tooth at each end of a groove) (no SEM). Typical for genus. Hingeline arched.

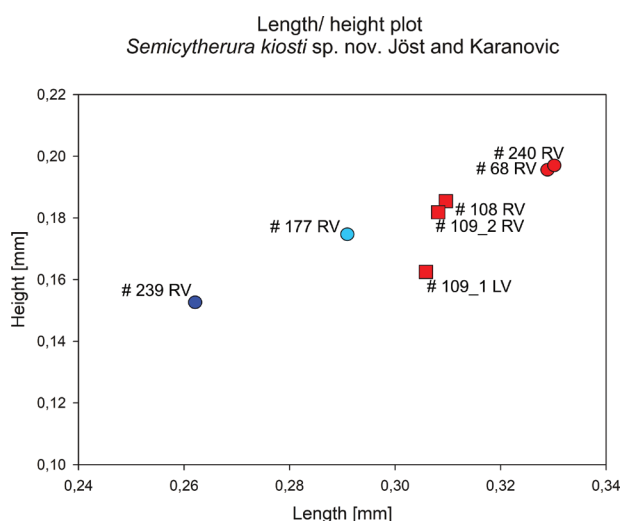
**Adductor muscle scars.** Vertical row of 4 adductor scars in ventro-median area (Fig. 9). Uppermost and lowermost scar less elongate in comparison with the middle two scars. At least 8 dorsal scars in upper half of valve (Fig. 11B). 2 mandibular scars slightly below, in front of adductor scars (Fig. 11F, blue arrows). 2 frontal scars in front of two uppermost adductor scars (Fig. 11F, white arrows).

**Recurved inner lamella.** Strongly recurved in male adult (#109\_2); absent in female adult (#240); not developed at juvenile stages (# 239) yet (Fig. 12).

**Dimensions.** Carapace dimensions of holotype: female ARV (# 240): length: 0.330 mm, height: 0.197 mm. Carapace dimensions of paratypes: female ARV: (# 68): length: 0.329 mm, height: posterior margin obscured by glue, ~ 0.196? mm; male ALV (# 109\_1): length: 0.306 mm, height: 0.162 mm; male ARV (# 109\_2): length: 0.308 mm, height: 0.182 mm; male ARV (# 108): length: 0.310 mm, height: 0.185 mm; female A-2RV (# 239): length: 0.262 mm, height: 0.153 mm; female A-1RV (#177): length: 0.291 mm, height: 0.175 mm (Fig. 8).

**Occurrence.** Extant sediments, Korea (Jeju Island; surface and sedimentation-derived sediments collected 2019) and Japan (Sendai Bay, Matsushima Bay, Pacific Ocean; surface sediments collected 1985, 1986, 1988).

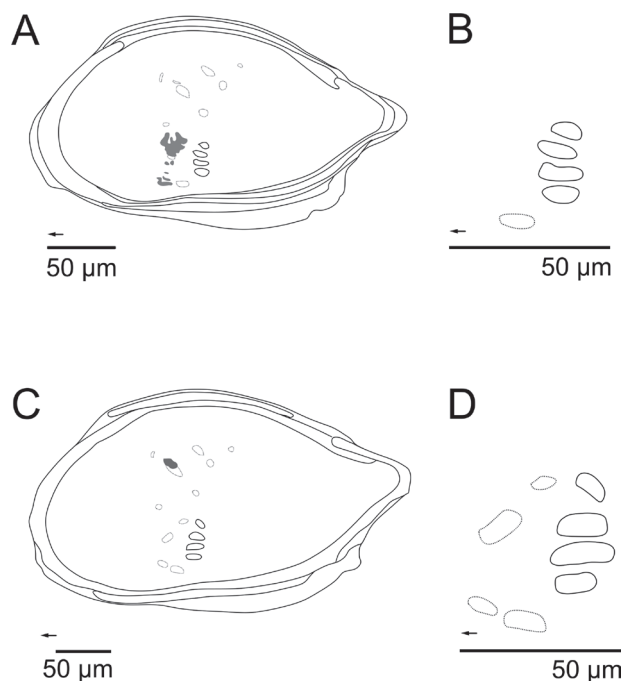
**Remarks.** The present species is characterized by a short, straight, horizontal anterior longitudinal ridge (Fig. 4B, AA). Of all known members of the *henryhowei* group, *Semicytherura kiosti* shares this trait only with *S. leptosubundata* (Fig. 4G) and *S. neosubundata* (Fig. 4Y). Morphological distinction between the three species based on prominent ridge patterns is straightforward. *Semicytherura kiosti* has an obvious anterior subvertical ridge, which is lacking in the other two species. *Hemicytherura* sp. 3 sensu Ikeya and Itoh 1991 is identical to our specimens of *S. kiosti* (fig. 17A in Ikeya and Itoh 1991). *Hemicytherura* Elofson, 1941 can easily be differentiated from the other members of the *Semicytherura henryhowei* group by the carapace surface features. Species of *Hemicytherura*, do exhibit something like ridges, but these do not resemble the characteristic ridge system of thick carinae of the *S. henryhowei* group. Rather, *Hemicytherura* is categorized by the characteristic fossa reticulation units that form around pores (Tanaka et al. 2011). Species of the *S. henryhowei* complex also show a less coarsely pitted surface ornamentation when compared to the *Hemicytherura* species.



**Figure 8.** Length/height plot of *Semicytherura kiosti* sp. nov. Jöst & Karanovic. Circles indicate female, squares indicate males. Adult valves depicted in red, juveniles in blue: light blue: A-1 stage, dark blue: A-2 stage; LV indicates left valve, RV indicates right valve.

## Discussion

According to the key to Cytheruridae genera (see Athersuch et al. 1989), *Semicytherura* can be easily distinguished from all other genera by its conspicuously recurved posterior inner lamella, which is sometimes referred to as “marginal infoldment” (Ozawa and Kamiya 2008). A detailed study on its ultrastructure showed that it is a prismatic structure, different from the epidermis in other podocopid ostracods (Yamada et al. 2004), hence the term “prismatic layer” (Yamada et al. 2005). More recently, it was recognized that this layer may be sexually dimorphic in some species (Yamada et al. 2005; Whatley and Cusminsky 2010). While Whatley and Cusminsky (2010) mention three species in which males lack the recurved inner lamella, we checked the literature and found that at least 11 species express sexual dimorphism in this characteristic trait. In *Semicytherura slipperi* Yamada, Tsukagoshi & Ikeya, 2005 (see pg. 252, fig. 5A–D in Yamada et al. 2005), *S. maxima* Yamada & Tsukagoshi, 2010 (see pg. 293, figs 2G, H, 3C, D), *S. clavata* (Brady, 1880) (see Whatley and Cusminsky 2010; no internal view provided in original description), and *S. contraria* (Zhao & Whatley, 1989) (see pg. 175, pl. 1, fig. 14), males show a more pronounced expression than females. In *S. obitsuensis* (Nakao & Tsukagoshi, 2020) (see pg. 5, fig. 4B), *S. ikeyai* Yamada & Tsukagoshi, 2010 (see pg. 297, figs 11G, H, 12C, D), and *S. kiosti* sp. nov. Jöst & Karanovic (Fig. 12), females completely lack the recurved inner lamella. Also, adult females of *S. balrogi* Brouwers, 1994 lack the recurved inner lamella, although no information was given for males (pl. 6, figs 1, 2). Furthermore, *S. tauronae* Brouwers, 1994 (pl. 1, fig. 4), *S. henryi* (Brouwers, 1994) (pl. 6, figs 3, 4), *S. simplex* (Hu, 1978) (pg. 134, text-fig. 5B), and *S. skagwayensis* Brouwers, 1994 (pl. 6, fig. 5) also do not exhibit this character in adult valves of, at least, in one sex (Brouwers

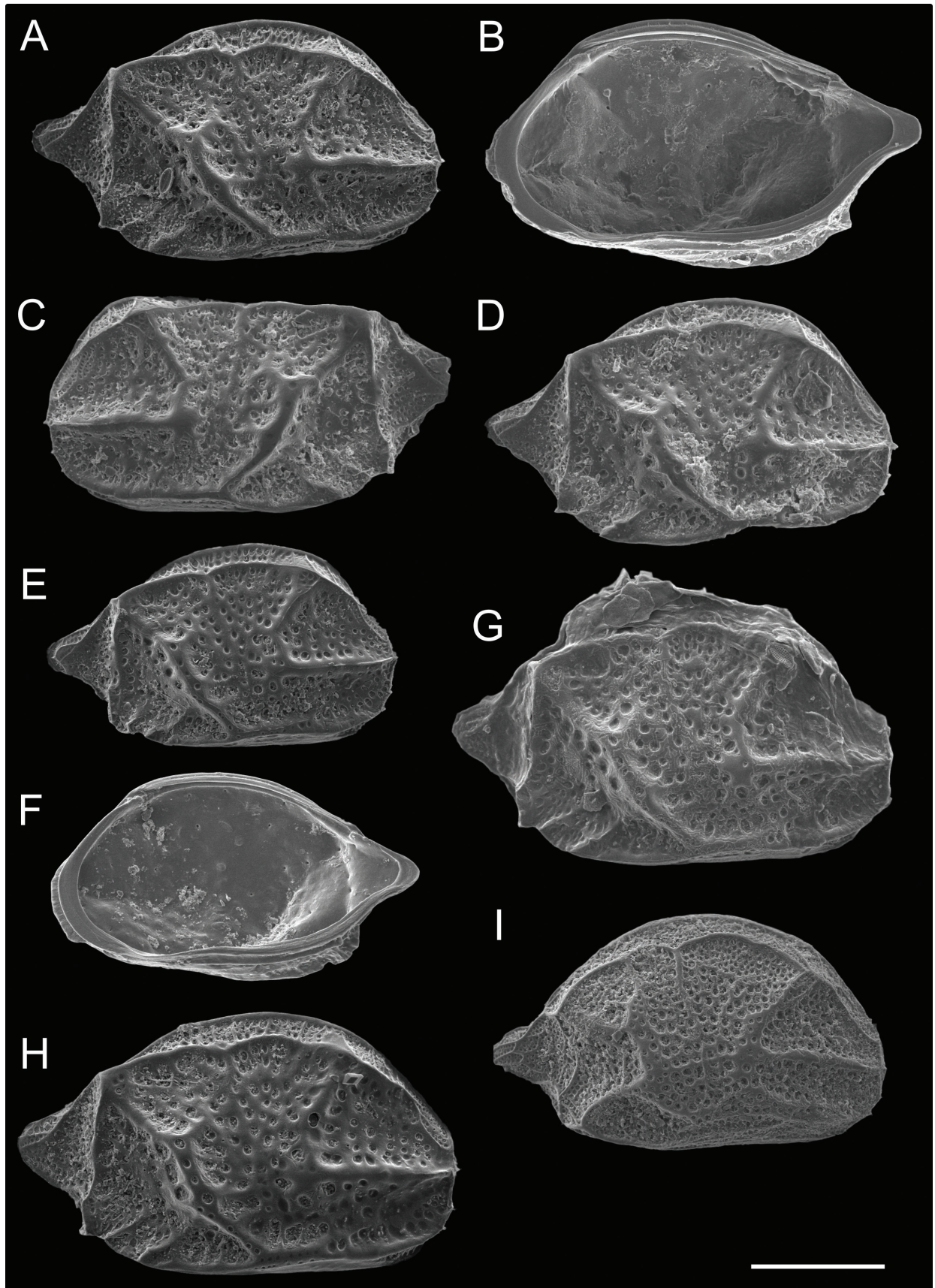


**Figure 9.** Line drawings of *Semicytherura kiosti* sp. nov. Jöst & Karanovic internal view with details on muscle imprints. **A, B.** Specimen #239 juvenile (A-2, female) RV lateral internal view; **C, D.** Specimen #240 female ARV lateral internal view. **A.** Lateral internal view of RV; **B.** Adductor muscle scar cluster in bold, one of two mandibular muscle scars depicted as dotted line; **C.** Lateral internal view of RV; **D.** Adductor muscle scar cluster in bold, two mandibular muscle scars depicted as dotted line. Dotted line indicates frontal, mandibular, and dorsal muscle scars; bold line indicates adductor muscle scars; females lacking strongly recurved inner lamella as observed in adult male. Arrow indicates anterior direction. Grey shaded shapes indicate dirt covering muscle scars. Scale bars: 50 µm.

1994). These observations call for a revision of the identification key by Athersuch et al. (1989). However, this is beyond the scope of our paper.

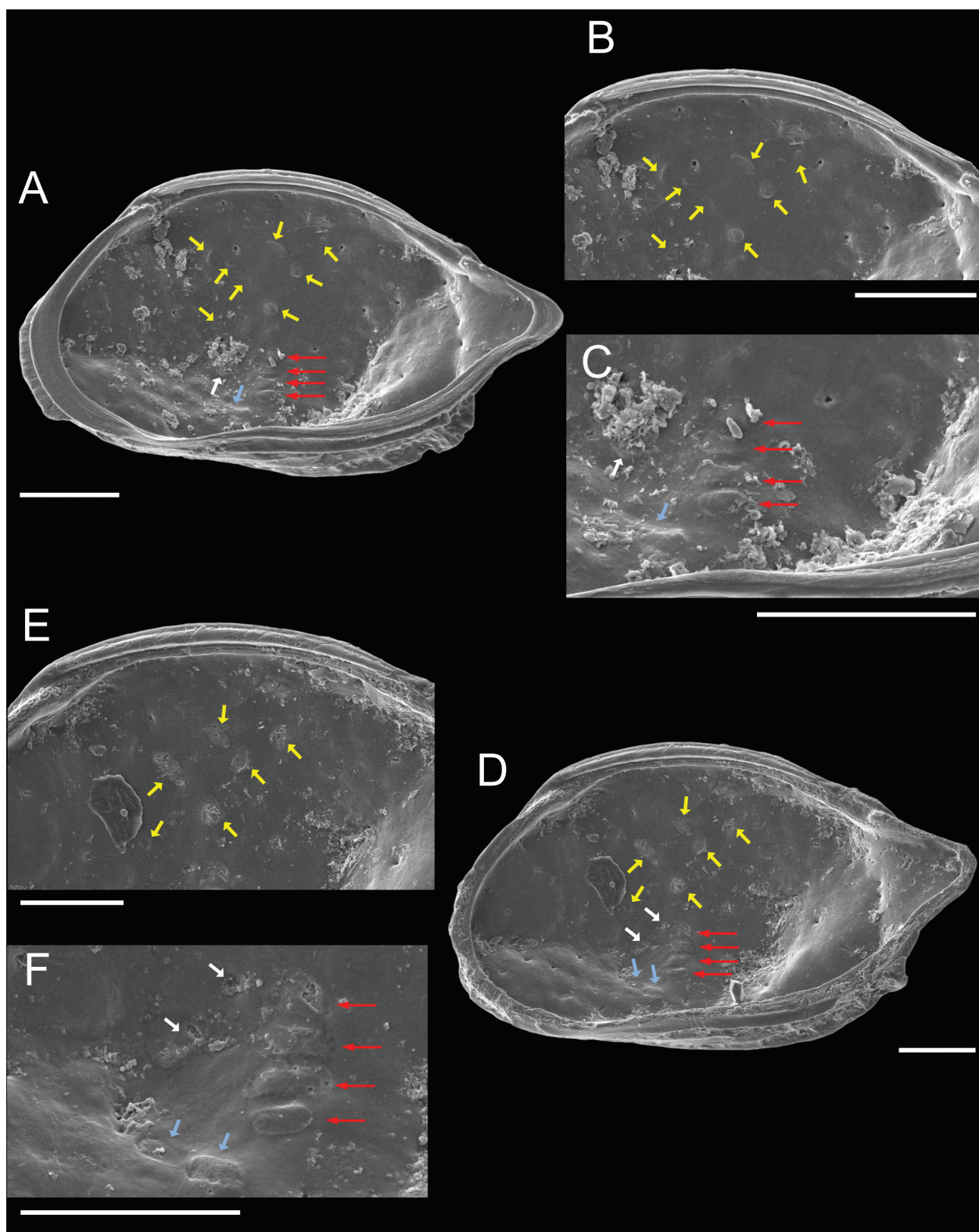
Detailed discussions on the speciation process of the *S. henryhowei* group, including geological and geographical distribution maps, as well as implications for the group’s species diversity, are provided by Yamada et al. (2005; figs 11, 12), and Yamada and Tsukagoshi (2010; fig. 19). The authors also introduced subgroups based on differences in the carapace surface ornamentation, and further found that, although sharing a common ancestor in the North West Pacific, up until the Early Miocene, the species of each subgroup show distinct ecological differences (Yamada and Tsukagoshi 2010). Yamada et al. (2005) also discussed the phenomenon of trans-Arctic migration of ostracod fauna from the North West Pacific through the Bering Sea to the North Atlantic Ocean using the *S. henryhowei* group as a higher taxon. However, a distinction on species level within the group was not conducted. As a full review of the geographical and geological distribution of all 29 species of the *henryhowei* group is beyond the scope of this paper, here we focus on the species that, following the species-reassignments herein, underwent interesting changes in respect to the geological ages and/or (paleo-)distributions. We dis-





**Figure 10.** *Semicytherura kiosti* sp. nov. Jöst & Karanovic external and internal lateral views. **A–C.** Specimen # 109 adult male; **A, B.** # 109\_2 RV; **A.** lateral external view; **B.** lateral internal view; **C.** # 109\_1 LV, lateral external view; **D.** Specimen # 108 male ARV, lateral external view; **E, F.** Specimen # 239 female A-2RV; **E.** lateral external view; **F.** lateral internal view; **G.** Specimen # 68 female ARV, lateral external view; **H.** Specimen # 240 female ARV, lateral external view; **I.** Specimen # 177 female A-1RV, lateral external view. Scale bar: 100 µm.

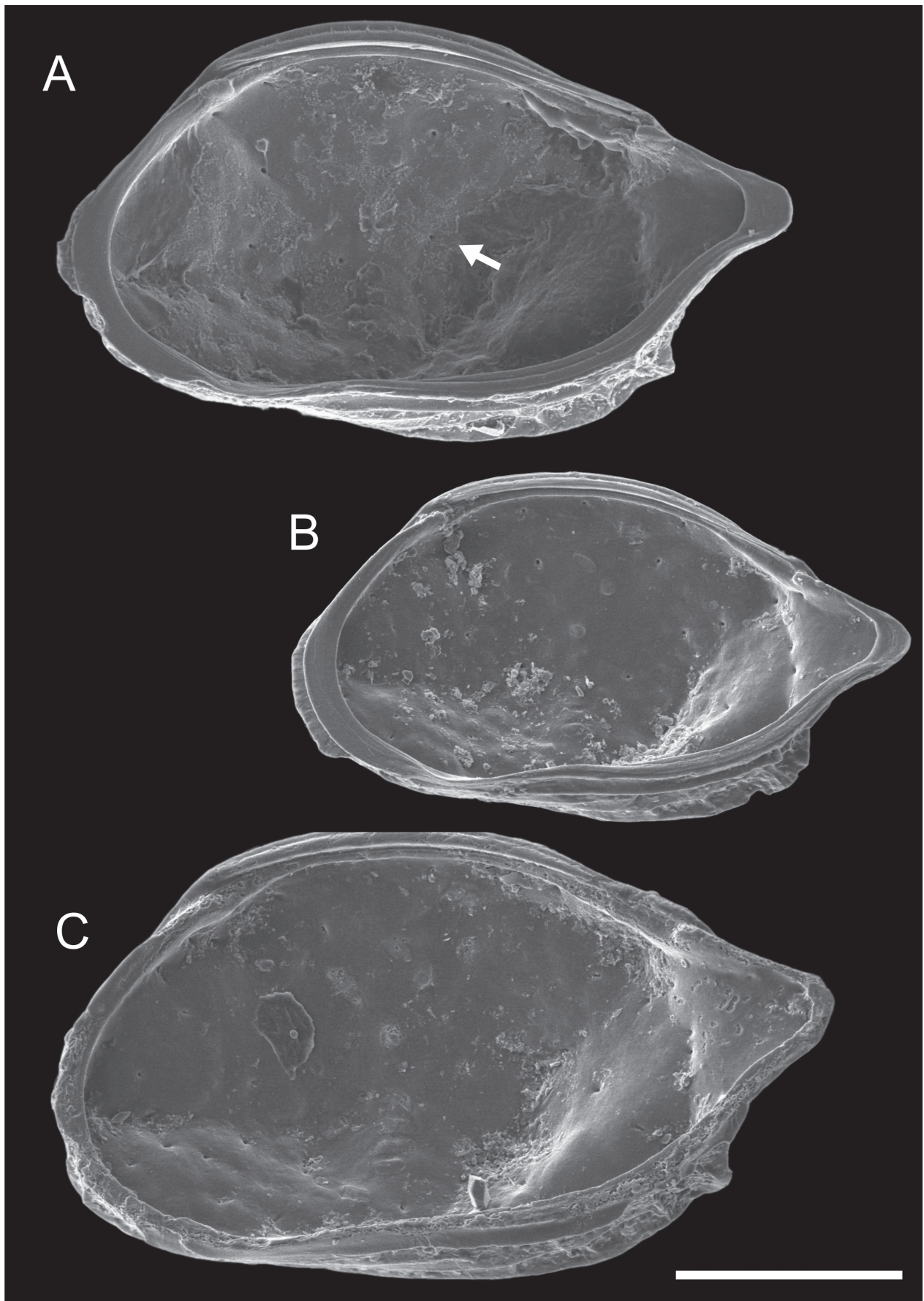




**Figure 11.** *Semicytherura kiosti* sp. nov. Jöst & Karanovic muscle scar details. **A–C.** Specimen # 239 female A-2RV lateral internal view; **D–F.** Specimen # 240 female ARV lateral internal view. Red arrows indicate adductor muscle scars; yellow arrows indicate dorsal muscle scars; blue arrows indicate mandibular muscle scars; white arrows indicate frontal muscle scars. Not all muscle scars simultaneously visible in both specimens. Scale bars: 50 µm.

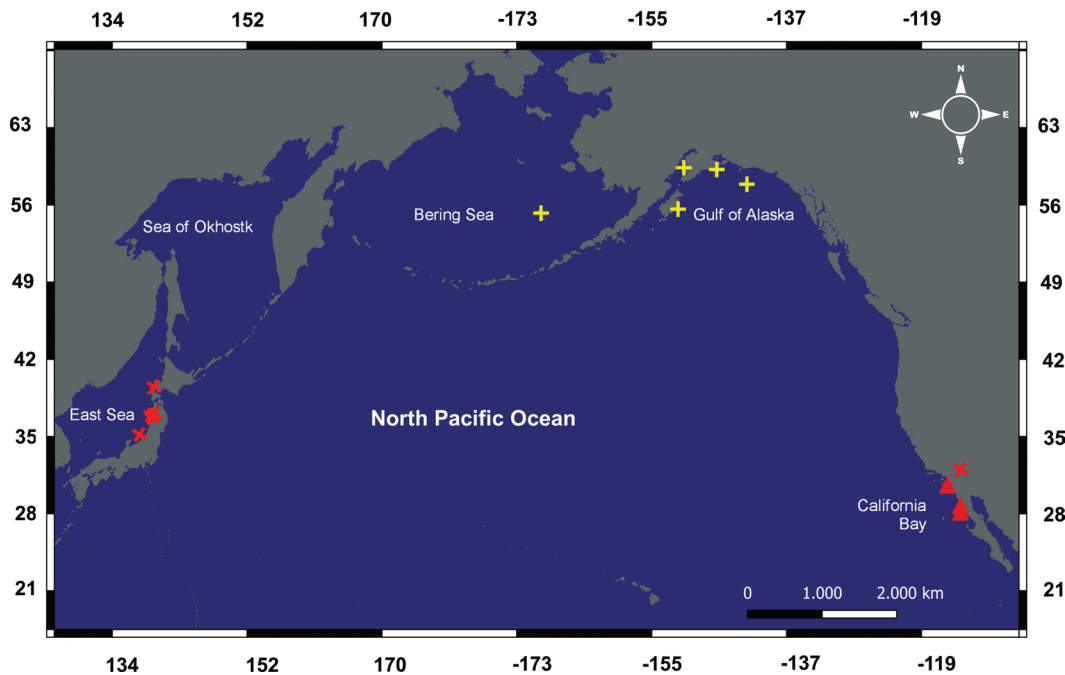
covered changes to the geological distribution in at least five members of the species complex (*S. balrogi*, *S. ikeyai*, *S. tanimurai*, *S. sasameyuki/kazahana*, *S. undata*). In at least three of them (*S. balrogi*, *S. ikeyai*, *S. undata*), these chang-

es also affected their geographical distribution. In respect to *S. balrogi* and *S. undata*, our findings give new insights into trans-Arctic interchange of ostracod fauna on species level. Details are discussed for each species separately.

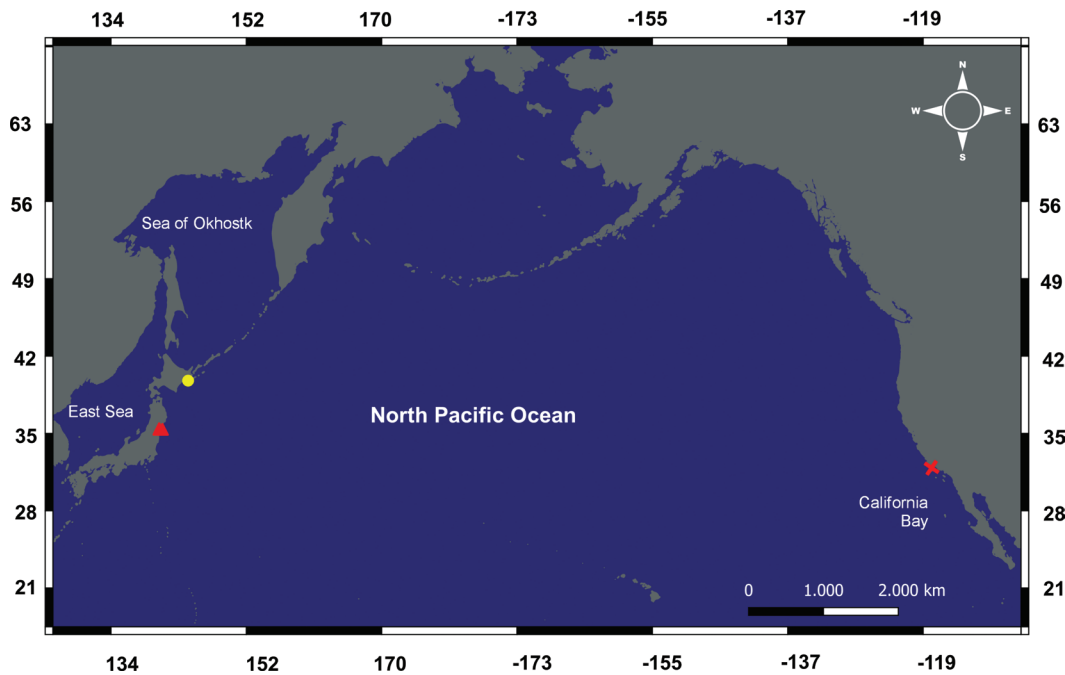


**Figure 12.** *Semicytherura kiosti* sp. nov. Jöst & Karanovic internal view details, recurved inner lamella. **A.** Male adult right valve (# 109\_2) depicting strongly recurved inner lamella (white arrow); **B.** Female juvenile right valve (# 239) lacking recurved inner lamella; **C.** Female adult right valve (# 240) lacking recurved inner lamella.





**Figure 13.** (Paleo-)distribution of *Semicytherura balrogi* Brouwers, 1994. Yellow denotes known records, red denotes new (re-assigned) records. Cross (red) and plus (yellow) denote new and known fossil records, respectively; triangle (red) denotes (new) extant records (for sample details, see Valentine 1976; Brouwers 1981, 1982a, b, 1983).



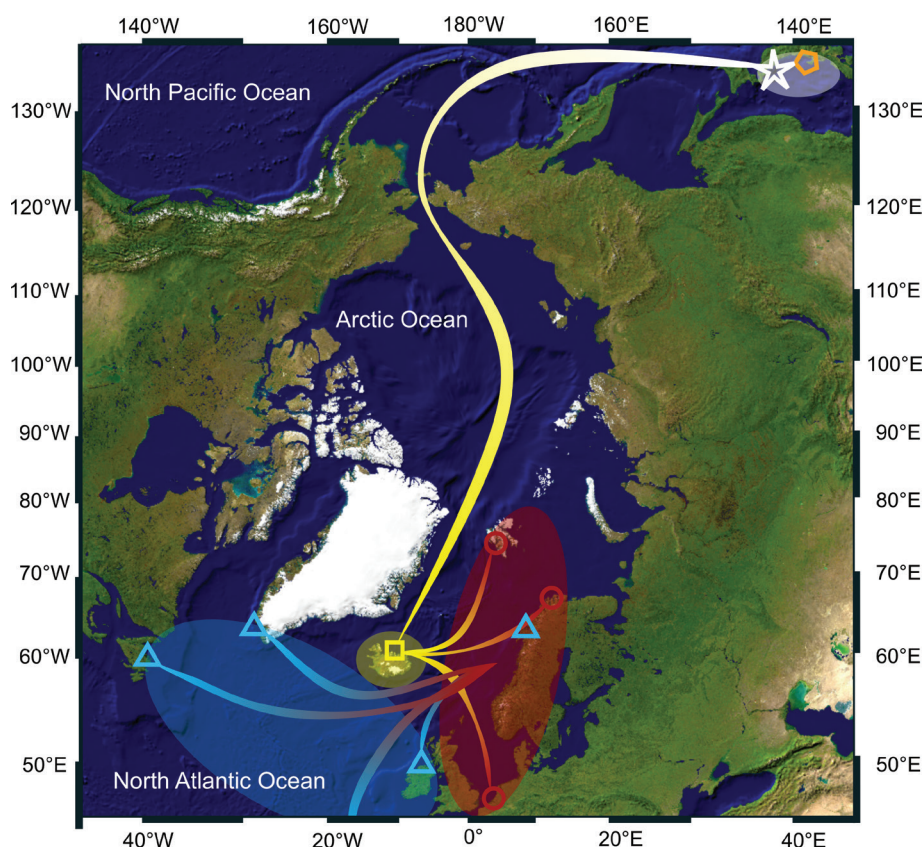
**Figure 14.** (Paleo-)distribution of *Semicytherura ikeyai* Yamada & Tsukagoshi, 2010. Yellow denotes known records, red denotes new (re-assigned) records. Cross (red) denotes (new) fossil records, triangle (red) and dot (yellow) denote extant (i.e., valves from 1985, 1986, 1988; living from 1992) new and known records, respectively.

*Semicytherura* aff. *undata* was reported from high latitudes in North America (Fig. 13, yellow) from the Pleistocene through the Holocene (Brouwers 1994). Our revision indicates that *S.* aff. *undata* is actually *S. balrogi*, and after the assessment of its records, we can conclude that *S. balrogi* also appears at lower latitudes of North America, from the Early Pleistocene and the Holocene, respectively (Valentine 1976) (Fig. 13, red). Additionally, we added the Miocene (Irizuki 1994) and the Pleistocene (Cronin

& Ikeya, 1987) records from Japan (Fig. 13, red crosses). According to these new insights, *S. balrogi* first occurred in the North Pacific around Japan during the Miocene, and from there, spread in a circumpolar fashion into the North Atlantic, where it occurs as far south as California Bay (Valentine 1976; Brouwers 1981, 1982a, b, 1983).

*Semicytherura ikeyai* was described from the extant sediments (i.e., living specimens collected 1992) of the Eastern North Pacific in Akkeshi Bay, Japan (Yamada





**Figure 15.** Trans-Arctic Interchange demonstrated on (paleo-)records of *Semicytherura undata* (Sars, 1866). White star denotes re-assigned Miocene record; yellow rectangle denotes Pliocene record; orange pentagon denotes Pleistocene records; red circles denote Holocene records; light-blue triangles denote modern records. Shaded areas indicate assumed area of occurrence based on records. Lines indicate possible migration routes, color-coded by temporal scheme.

and Tsukagoshi 2010) (Fig. 14, yellow). Our results added others extant (i.e., primarily valves collected 1985, 1986, 1988) Japanese records (Ikeya and Itoh 1991), and extended its distribution further south than previously reported, to the Sendai and Matsushima Bay area (Fig. 14, red triangle). Additionally, we report the first fossil record of the species from the Pleistocene core sediments of ODP site 893 in California Bay, which is also the first known occurrence from the Western North Pacific (Fig. 14, red cross) (Whatley and Boomer 1995).

*Semicytherura tanimurai* is an extinct species occurring in the Pleistocene formations of Japan (Ishizaki and Matoba 1985; Ozawa 1996; Ozawa and Kamiya 2008). Here, we add an older Japanese record from the Pliocene Sasaoka Formation (Yamada et al. 2002).

*Semicytherura sasameyuki* and *S. kazahana* are inner bay species commonly known from the extant silty-sand surface sediments of Japan (living specimens collected 1977–2000; Yamada et al. 2005). *Semicytherura kazahana* is also known from Pleistocene (Lee 1990; unpublished), as well as extant sediments (this study) of Korea. Here, we add an older Japanese record from the Miocene (Yajima, 1988). As *S. sasameyuki* and *S. kazahana* are difficult to clearly distinguish based on carapace features only, the latter record is not certain.

*Semicytherura undata* is a species with primarily circumpolar (paleo-)distribution, but also occurring as far

south as South-West France (Guillaume et al. 1985). This record should be revised in the future, since the species seems to be a predominantly cold water inhabitant. Its known geological age dates back to the Pliocene of Iceland (Cronin 1991) (Fig. 15, yellow square), with the Pleistocene records from Japan (Cronin and Ikeya 1987; Ozawa and Kamiya 2005) (Fig. 15, orange pentagon), the Holocene records from the Netherlands (Wagner 1957), Norway (Neale and Howe 1975), and Spitzbergen (Hartmann 1992) (Fig. 15, red circles), and an extant distribution including the waters around Great Britain (Brady 1868; Athersuch et al. 1989), North America (Cronin 1989), Norway (Sars 1926; Freiwald and Mostafawi 1998), France (Guillaume et al. 1985), and Greenland (Penney 1989) (Fig. 15, turquoise triangles). According to this, the species first occurred in the North Atlantic during the Pliocene, and from there, spread to the North Pacific via the Bering Strait before its closure during the Pleistocene glaciations. However, our taxonomic revision revealed a Miocene record from the North Pacific (Japan) (Irizuki 1994), significantly changing the current view on evolution and migration patterns of this species (Fig. 15, white star). Our new insights indicate that *S. undata* originated in the North Pacific (Fig. 15, white shaded ellipse) during the Miocene and spread to the North Atlantic through the Arctic during the Late Miocene opening of the Bering Strait (5.32 Myr ago) (Gladenkov et al. 2002) (Fig. 15, white to

yellow route). This major geological event led to a connection between the North Pacific and the North Atlantic waters, which, especially for Asian and North American biotas, is of a great paleogeographic and biogeographic significance (Marincovich and Gladenkov 1999). Our interpretation is supported by the Pliocene record from Iceland (Fig. 15, yellow rectangle), located within the North Atlantic gateway to the Arctic (Cronin 1991), as well as its Holocene distribution, which is primarily focused in the sub-polar North Atlantic (Fig. 15, red circles). *Semicytherura undata* is the 14<sup>th</sup> known cold water ostracod species involved with the trans-Arctic interchange, in addition to 13 such species reported by Irizuki (1994).

## Conclusions

Thorough taxonomic and systematic revisions are essential for an accurate documentation of the past and present biodiversity, with the ultimate aim to assess the impact of environmental disruptions on the species extinction and distribution. In this paper, we use homologous ornamentation patterns found across the *Semicytherura henryhowei* species group, the most common and diverse representatives of this ostracod genus. The genus and the entire order where it belongs (Cytheroidea) are best known from the fossil record, and have been important tools and proxies in paleostudies. Therefore, understanding shell morphology is important for a proper assessment of biodiversity and paleoclimate across geological ages. Our revision resulted in 29 species belonging to the *henryhowei* group, from 32 reported before (Appendix 1). By providing a taxonomic key to this group, we facilitate future species identifications. In addition, we describe one new species, as well as one new species record from Jeju Island in Korea, collected as a part of the MarineGEO ARMS project. Our taxonomic revision concluded changes in current species assignments, which resulted in the new insights regarding oldest records of *S. tanimurai* and *S. sasameyuki/kazahana*. Additionally, both geological age and spatial (paleo)distribution of *S. balrogi*, *S. ikeyai*, and *S. undata* are revised. The temporal distribution was adjusted from the Pleistocene to the Miocene, highlighting the importance of opening and closing of the Bering Strait for the faunal exchange in the Northern Hemisphere.

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## Appendix 1

**Table A1.** Treatise list reporting *Semicytherura henryhowei* group.

Author name	Species name Yamada et al. 2005	Species name Yamada and Tsukagoshi 2010	Species name Jöst et al., this study	Locality	Geologic time
Allison and Holden (1971)	Not included	Not included	<i>S. quadraplana</i>	Tropical East Pacific	Extant
Athersuch et al. (1989)	<i>S. undata</i>	<i>S. undata</i>	<i>S. undata</i>	British	Extant
Brady (1868)	<i>C. undata</i>	<i>C. undata</i>	<i>C. undata</i>	British	Extant
Brouwers (1994)	<i>S. balrogi</i>	<i>S. balrogi</i>	<i>S. balrogi</i>	North America	Holocene
Cronin and Ikeya (1987)	<i>S. subundata</i>	<i>S. subundata</i>	<i>S. subundata</i>	Japan/ Omma-Manganji	Pleistocene
Cronin and Ikeya (1987)	<i>S. aff. henryhowei</i>	<i>S. aff. henryhowei</i>	<i>S. balrogi</i>	Japan/ Omma-Manganji	Pleistocene
Cronin and Ikeya (1987)	<i>S. sp. A</i>	<i>S. sp. A</i>	<i>S. sp. nov.</i>	Japan/ Omma-Manganji	Pleistocene
Cronin and Ikeya (1987)	Not included	<i>S. undata</i>	<i>S. undata</i>	Japan/ Omma-Manganji	Pleistocene
Cronin (1989)	<i>S. undata</i>	<i>S. undata</i>	<i>S. undata</i>	North America	Extant
Cronin (1989)	<i>S. cf. henryhowei</i>	<i>S. cf. henryhowei</i>	<i>S. sp. nov.</i>	North America	Extant
Cronin (1991)	<i>S. undata</i>	<i>S. undata</i>	<i>S. undata</i>	Iceland	Pliocene
Freiwald and Mostafawi (1998)	<i>S. undata</i>	<i>S. undata</i>	<i>S. undata</i>	North Norway	Extant
Guillaume et al. (1985)	<i>S. undata</i>	<i>S. undata</i>	<i>S. undata</i>	South-west France	Extant
Hanai (1957)	<i>C. quadrata</i>	<i>S. henryhowei</i>	<i>S. henryhowei</i>	Japan (Hayama)	Extant
Hanai (1957)	<i>C. subundata</i>	<i>C. subundata</i>	<i>C. subundata</i>	Japan/ Sawane	Pleistocene

Author name	Species name Yamada et al. 2005	Species name Yamada and Tsukagoshi 2010	Species name Jöst et al., this study	Locality	Geologic time
Hanai (1961)	<i>S. quadrata</i>	Not included	Not included	Japan (Hayama)	Extant
Hanai (1961)	<i>S. subundata</i>	Not included	Not included	Japan/ Sawane	Pleistocene
Hanai et al. (1977)	<i>S. henryhowei</i>	Not included	Not included	Japan (Hayama)	Extant
Hartmann (1992)	<i>S. undata</i>	<i>S. undata</i>	<i>S. undata</i>	Spitzbergen	Holocene
Hu (1978)	<i>S. simplex</i>	<i>S. simplex</i>	<i>S. simplex</i>	Southern Taiwan	Pleistocene
Hu (1981)	<i>S. simplex</i>	<i>S. simplex</i>	<i>S. simplex</i>	Southern Taiwan	Pleistocene
Hu (1984)	<i>S. simplex</i>	<i>S. simplex</i>	<i>S. simplex</i>	Southern Taiwan	Pleistocene
Ikeya et al. (1985)	<i>S. henryhowei</i>	<i>S. henryhowei</i>	<i>S. henryhowei</i>	Japan (Hamana-ko)	Extant
Ikeya et al. (1985)	<i>S. sp. D</i>	<i>S. sasameyuki</i>	<i>S. sasameyuki</i>	Japan (Hamana-ko)	Extant
Ikeya and Itoh (1991)	<i>S. henryhowei</i>	<i>S. henryhowei</i>	<i>S. henryhowei</i>	Japan (Sendai Bay)	Extant
Ikeya and Itoh (1991)	Not included	Not included	<i>S. kiosti</i> sp. nov. Jöst and Karanovic ( <i>Hemicytherura</i> sp. 3)	Japan (Sendai Bay)	Extant
Ikeya and Suzuki (1992)	<i>S. henryhowei</i>	<i>S. henryhowei</i>	<i>S. henryhowei</i>	South West Japan Sea	Extant
Irizuki (1994)	<i>S. henryhowei</i>	<i>S. henryhowei</i>	<i>S. balrogi</i>	Japan/ Fujikotogawa	Miocene
Irizuki (1994)	<i>S. aff. henryhowei</i>	<i>S. aff. henryhowei</i>	<i>S. sp. nov.</i>	Japan/ Fujikotogawa	Miocene
Irizuki (1994)	<i>S. subundata</i>	<i>S. subundata</i>	<i>S. subundata</i>	Japan/ Fujikotogawa	Miocene
Irizuki (1994)	<i>S. sp. 1</i>	<i>S. sp. 1</i>	<i>S. sp. nov.</i>	Japan/ Fujikotogawa	Miocene
Irizuki (1994)	<i>S. sp. 2</i>	<i>S. sp. 2</i>	<i>S. sp. nov.</i>	Japan/ Fujikotogawa	Miocene
Irizuki (1994)	<i>S. sp. 3</i>	<i>S. sp. 3</i>	<i>S. undata</i>	Japan/ Fujikotogawa	Miocene
Irizuki (1994)	<i>S. sp. 4</i>	<i>S. sp. 4</i>	<i>S. sp. nov.</i>	Japan/ Fujikotogawa	Miocene
Irizuki (1994)	<i>S. sp. 5</i>	<i>S. sp. 5</i>	<i>S. sp. nov.</i>	Japan/ Fujikotogawa	Miocene
Irizuki et al. (1994)	Not included	<i>S. pseudoundata</i>	<i>S. pseudoundata</i>	Japan/ Toyama	Miocene
Irizuki et al. (2005)	Not included	<i>S. sp.</i>	<i>S. kazahana</i>	Japan/ Meimi	Pleistocene
Irizuki (2007)	Not included	<i>S. subundata</i>	<i>S. subundata</i>	Japan/ Kuwae	Pliocene
Ibid.	Not included	<i>S. subslipperi</i>	<i>S. subslipperi</i>	Japan/ Kuwae	Pliocene
Ishizaki (1966)	<i>Cytherura neosubundata</i>	<i>Cytherura neosubundata</i>	<i>Cytherura neosubundata</i>	Japan/ Tatsunokuchi	Pliocene
Ishizaki (1966)	<i>S. quadrata</i>	<i>S. henryhowei</i>	<i>S. henryhowei</i>	Japan/ Hatatate	Miocene
Ishizaki (1968)	<i>S. quadrata</i>	<i>S. kazahana</i>	<i>S. kazahana</i>	Japan (Uranouchi Bay)	Extant
Ishizaki (1971)	<i>S. quadrata</i>	<i>S. sasameyuki</i>	<i>S. sasameyuki</i>	Japan (Aomori Bay)	Extant
Ishizaki and Matoba (1985)	<i>S. henryhowei</i>	<i>S. tanimurai</i>	<i>S. tanimurai</i>	Japan/ Sasaoka	Pleistocene
Ishizaki and Matoba (1985)	<i>S. subundata</i>	<i>S. subundata</i>	<i>S. subundata</i>	Japan/ Shibikawa	Pleistocene
Lee (1990)	<i>S. sp. B</i>	<i>S. kazahana</i>	<i>S. kazahana</i>	Korea (Jeju Island)	Pleistocene
Neale and Howe (1975)	<i>S. undata</i>	<i>S. undata</i>	<i>S. undata</i>	North Norway	Holocene
Okubo (1980)	<i>S. henryhowei</i>	<i>S. sasameyuki</i>	<i>S. sasameyuki</i>	Japan (Seto Inland Sea)	Extant
Ozawa (1996)	<i>S. subundata</i>	<i>S. subundata</i>	<i>S. subundata</i>	Japan/ Omma-Manganji	Pleistocene
Ozawa (1996)	<i>S. cf. undata</i>	<i>S. robustundata</i>	<i>S. robustundata</i>	Japan/ Omma-Manganji	Pleistocene
Ozawa (1996)	<i>S. sp. 4</i>	<i>S. subslipperi</i>	<i>S. subslipperi</i>	Japan/ Omma-Manganji	Pleistocene
Ozawa (1996)	<i>S. sp. 5</i>	<i>S. leptosubundata</i>	<i>S. leptosubundata</i>	Japan/ Omma-Manganji	Pleistocene
Ozawa (1996)	<i>S. sp. 6</i>	<i>S. tanimurai</i>	<i>S. tanimurai</i>	Japan/ Omma-Manganji	Pleistocene
Ozawa and Kamiya (2005)	Not included	<i>S. robustundata</i>	<i>S. robustundata</i>	Japan/ Omma-Manganji	Pleistocene
Ozawa and Kamiya (2005)	Not included	<i>S. leptosubundata</i>	<i>S. leptosubundata</i>	Japan/ Omma-Manganji	Pleistocene
Ozawa and Kamiya (2005)	Not included	<i>S. subslipperi</i>	<i>S. subslipperi</i>	Japan/ Omma-Manganji	Pleistocene
Ozawa and Kamiya (2005)	Not included	<i>S. undata</i>	<i>S. undata</i>	Japan/ Omma-Manganji	Pleistocene
Ozawa and Kamiya (2008)	Not included	<i>S. robustundata</i>	<i>S. robustundata</i>	Japan/ Omma-Manganji	Pleistocene
Ozawa and Kamiya (2008)	Not included	<i>S. subslipperi</i>	<i>S. subslipperi</i>	Japan/ Omma-Manganji	Pleistocene
Ozawa and Kamiya (2008)	Not included	<i>S. leptosubundata</i>	<i>S. leptosubundata</i>	Japan/ Omma-Manganji	Pleistocene
Ozawa and Kamiya (2008)	Not included	<i>S. tanimurai</i>	<i>S. tanimurai</i>	Japan/ Omma-Manganji	Pleistocene
Ozawa et al. (2008)	Not included	<i>S. subundata</i>	<i>S. subundata</i>	Japan/ Ogikubo	Pliocene
Ozawa et al. (2008)	Not included	<i>S. sp. 1</i>	<i>S. sp. nov.</i>	Japan/ Ogikubo	Pliocene
Ozawa et al. (2008)	Not included	<i>S. sp. 2</i>	<i>S. sp. nov.</i>	Japan/ Ogikubo	Pliocene
Penney (1989)	<i>S. undata</i>	<i>S. undata</i>	<i>S. undata</i>	Greenland	Extant
Sars (1926)	<i>C. undata</i>	<i>C. undata</i>	<i>S. undata</i>	Norway	Extant
Tanaka and Hasegawa (2013)	Not included	Not included	<i>S. kaburagawensis</i>	Japan/ Itahana	Miocene
Tanaka and Hasegawa (2013)	Not included	Not included	<i>S. usuigawensis</i>	Japan/ Itahana	Miocene
Tsukagoshi and Kamiya (1996)	<i>S. aff. henryhowei</i>	<i>S. sasameyuki</i>	<i>S. sasameyuki</i>	Japan (Maizuru Bay)	Extant
Valentine (1976)	<i>Kangarina</i> sp. B	<i>Kangarina</i> sp. B	<i>S. balrogi</i>	North America	Holocene
Wagner (1957)	<i>S. undata</i>	<i>S. undata</i>	<i>S. undata</i>	Netherlands	Holocene
Whatley and Boomer (1995)	<i>S. sp. B</i>	<i>S. sp. B</i>	<i>S. ikeyai</i>	ODP site 893	Pleistocene
Yajima (1988)	<i>S. henryhowei</i>	<i>S. henryhowei</i>	<i>S. sasameyuki/ kazahana</i>	Japan/ Mizunami	Miocene
Yamada and Tsukagoshi (2010)	Not included	<i>S. maxima</i>	<i>S. maxima</i>	Japan (Akkeshi Bay)	Extant
Yamada and Tsukagoshi (2010)	Not included	<i>S. ikeyai</i>	<i>S. ikeyai</i>	Japan (Akkeshi Bay)	Extant
Yamada et al. (2002)	<i>S. subundata</i>	<i>S. subundata</i>	<i>S. subundata</i>	Japan/ Sasaoka	Pliocene
Yamada et al. (2002)	<i>S. sp. 1</i>	<i>S. subslipperi</i>	<i>S. subslipperi</i>	Japan/ Sasaoka	Pliocene
Yamada et al. (2002)	<i>S. sp. 2</i>	<i>S. sp. 2</i>	<i>S. tanimurai</i>	Japan/ Sasaoka	Pliocene
Yamada et al. (2004)	Not included	Not included	<i>S. sasameyuki/ kazahana</i> (S. sp. A)	Japan/ fish tank University of Tsukuba	Extant
Yamada et al. (2004)	Not included	Not included	<i>S. slipperi</i> (S. sp. B)	Japan (Akkeshi Bay)	Extant
Yamada et al. (2005)	<i>S. henryhowei</i>	<i>S. henryhowei</i>	<i>S. henryhowei</i>	Japan (Hayama)	Extant
Yamada et al. (2005)	<i>S. slipperi</i>	<i>S. slipperi</i>	<i>S. slipperi</i>	Japan (Akkeshi Bay)	Extant
Yamada et al. (2005)	<i>S. kazahana</i>	<i>S. kazahana</i>	<i>S. kazahana</i>	Japan (Aburatsubo Bay)	Extant
Yamada et al. (2005)	<i>S. sasameyuki</i>	<i>S. sasameyuki</i>	<i>S. sasameyuki</i>	Japan (Maizuru Bay)	Extant
Yamane (1998)	<i>S. henryhowei</i>	<i>S. sasameyuki</i>	<i>S. sasameyuki</i>	Japan (Seto Inland Sea)	Extant
Yasuhara and Irizuki (2001)	Not included	<i>S. henryhowei</i>	<i>S. henryhowei</i>	Japan (Osaka Bay)	Extant
Yasuhara and Irizuki (2001)	Not included	<i>S. sp. 1</i>	<i>S. kazahana</i>	Japan (Osaka Bay)	Extant