A Recent species of Frambocythere Colin, 1980 (Ostracoda, Crustacea) from a cave in South Korea; the first extant representative of a genus thought extinct since the Eocene

ROBIN J. SMITH*, JIMIN LEE2, YONG GEUN CHOI1, CHEON YOUNG CHANG2 & JEAN-PAUL COLIN4
1Lake Biwa Museum, 1091 Ootoshima, Kusatsu, Shiga 525-0001, Japan
2Daegu University, 15 Naeri-ri, Jillyang-up, Gyeongsan 712-714, South Korea
3Yeongwol Cave Eco-Museum, 1121-15 Yeongwol-dong-ro, Kimsakgat-myeon, Yeongwol-gun, Gangwon-do 230-821, South Korea
4Universidade de Lisboa, Faculdade de Ciências, Centro de Geologia, Campo Grande, C-6, 3° 1749-016 Lisboa, Portugal, and 3 Impasse des Biroulayres, 33610 Cestas, France
*Corresponding author (e-mail: smith@lbm.go.jp)

ABSTRACT – The non-marine ostracod genus Frambocythere Colin, 1980 (Limnocytheridae, Timiriaseviinae) had a previously known stratigraphical range from the Albian (Lower Cretaceous) through to the Lutetian (middle Eocene). However, during surveys of Seongryu Cave in Uljin-gun Province, South Korea, specimens of an extant species of Frambocythere were recovered. This extends the stratigraphical range of the genus by more than 40 million years to the present, and the species is, therefore, considered to be a relict ‘living fossil’. This newly described species is most similar in morphology to Frambocythere gr. tumiensis (Helmdach, 1978), reported from Thanetian (Paleocene) deposits of the Paris Basin. The living species was found in the hypogean realm, in contrast to the fossil species, which were all epigean. It is hypothesized that, like the genus Kovalevskiella Klein, 1963, which belongs to the same lineage, Frambocythere migrated from epigean to hypogean habitats. J. Micropalaeontol. 31(2): 131–138, July 2012.

KEYWORDS: Frambocythere, Eocene, Recent, hypogean, relict

INTRODUCTION
The genus Frambocythere Colin, 1980 (in Colin & Danielpol, 1980) consists of nine described species/subspecies and some species in open nomenclature, ranging from the Albian to the middle Eocene. It is widely distributed from Africa, SW Europe, India and China (Hou et al., 1978; Colin & Danielpol, 1980; Tambareau, 1984; Tambareau et al., 1991; Colin, 1993; 2011; Colin & Dépêche, 1997; Bhandari & Colin, 1999; Whatley & Bajpai, 2006). The genus belongs to the Kovalevskiella lineage (Limnocytheridae, Timiriaseviinae), which also includes the genera Kovalevskiella Klein, 1963, and Rosacythere Colin, 1980 (in Colin & Danielpol, 1980). Of this lineage, only five species, all belonging to the genus Kovalevskiella, are extant, found in central and southeastern Europe and Turkey (Danielpol, 1965; 1969; 1970; Colin & Danielpol, 1980; Karanovic, 2003; Özuluğ & Yaltaher, 2008). All five extant species are considered to be primarily hypogean, although Kovalevskiella bulgarica (Danielpol, 1970) has been recovered from a stream in Turkey (Özuluğ & Yaltaher, 2008). All other species of the lineage are extinct epigean species, typically found in lacustrine deposits.

During investigations of Seongryu Cave in Uljin-gun Province in South Korea, nine specimens of a living Frambocythere species were recovered and are the subject of this paper.

LOCALITY, MATERIAL AND METHODS
Seongryu Cave is a limestone cave in South Korea, and was designated as a Natural Monument (No. 155) of the Republic of Korea in 1963. The entrance of the cave is located at the riverside of the lower reaches of the Wangpicheon River (36° 57′ 21.87″N, 129° 22′ 44.34″E, about 20 m in elevation and about 3.5 km from the river mouth), which discharges into the East Sea (= Sea of Japan). The cave developed in the massive limestone of the Ordovician Geunnam Formation of the Joseon Supergroup (Kim et al., 2010). The cave is mostly horizontal, and its main passage and branches are about 330 m and 540 m long, respectively, making the total length of the cave about 870 m. The first 270 m section of the main passage from the entrance is open to tourists, and the remaining sections are closed to public access to protect the cavern environment. It contains numerous stalactites, stalagmites, columns and curtains around three large cavern lakes. The material of the present study was collected at the third cavern lake, in the protected area about 300 m from the cave entrance (Fig. 1).

Specimens were collected by one of us (Y.G. Choi) using a plankton net with a 110 μm mesh size, mostly at the edge of the lake at depths of 60–80 cm (the lake has a maximum depth of about 7 m). The substrate was muddy, containing calcium carbonate deposits. One female and two males were collected on 9 March 2002, and three females and three males were collected on 9 June 2002. The water temperature was 14.3°C (March) and 16.0°C (July), pH 8.1 (March) and 7.6 (July) and conductivity –54 mV (March) and –30 mV (July).

Co-occurring troglobionts included Pseudocrangonyx coreanus Ueno (Amphipoda), Orthomorpha sp. (Diplapoda), Kaoliniychus coreanus coreanus (Suzuki) (Opillionida), Gallosiana sp. (Grylloblattodea: Insecta) and Myotis daubentoni ussuriensis Ognev (Chiroptera: Mammalia).

Appendages were dissected and mounted in glycerol and drawn with the aid of a camera lucida. Carapaces are stored dry in micropalaeontological cavity slides. Carapaces used for SEM investigation were coated with gold before being photographed with a JEOL 5800 LV scanning electron microscope.

The holotype and allotype are deposited in the National Institute of Biological Resources (NIBR), Korea (Numbers: NIBRIV0000244931 and NIBRIV0000244932). The paratypes are deposited in the collections of the Department of Biological Science, Daegu University (Numbers: DB40029 to DB40032).
SYSTEMATIC DESCRIPTION

Superfamily Cytheroidea Baird, 1850
Family Limnocytheridae Klie, 1938
Subfamily Timiriaseviinae Mandelstam, 1960
(Emended by Colin & Danielopol, 1978)
Genus Frambocythere Colin, 1980
Frambocythere relicta n. sp.
(Figs 2–4)

Derivation of name. From the Latin, relictus, meaning left behind.

Diagnosis. Female: ventral and dorsal margins sub-parallel in lateral view, well-developed central sulcus, weakly developed anterior sulcus. Anterior margin rounded, posterior margin more truncate. Left valve with small caudal process and three stout, stubby spines on postero-ventral margin. ‘Raspberry-type’ micropustule ornamentation well developed. Male: slightly smaller than female, posterior less inflated than female. Hemipenis with large, straight, distal lobe with rounded tip, upper ramus hooked and small, lower ramus flattened with straight distal margin, rounded proximal margin. Copulatory process slender and simple.

Type material. Holotype: dissected male (NIBRIV0000244931). Allotype: dissected female (NIBRIV0000244932). Paratypes: dissected male (DB400029), dissected female (DB400030), whole female (DB40031), whole male (DB40032).

Type locality. The third cavern lake from the entrance of Seongryu Cave in Uljin-gun Province in South Korea, 36° 57′ 21.7″N, 129° 22′ 45.37″E.

Description. Carapace (Fig. 2) length and height – see Table 1. Female – lateral view sub-rectangular, dorsal and ventral margins more or less parallel. Ventral margin slightly sinuous. Dorsal margin straight in anterior half, slightly convex in posterior half. Anterior margin equally rounded. Postero-dorsal margin angular, postero-ventral margin rounded. Two sub-parallel sulci running from dorsal margin downwards and slightly towards anterior margin, one positioned at mid-length, one shorter sulcus in anterior quarter (indicated with arrows on Fig. 2B). Surface of valves strongly ornamented with ‘raspberry-type’ micropustules. Left valve with small caudal process and three short, stubby spines on postero-ventral margin. Right valve overlaps left. Hinge lophodont, with cardinal teeth on left valve; anterior tooth gently curved and about 1.4 times length of posterior tooth. Dorsal view rounded posteriorly, triangular anteriorly, with strong indentation at mid-sulcus. Maximum width at posterior third.

Male smaller than female with much less inflated posterior region. Left valve with one or two short, stubby spines. Dorsal view with maximum width just posterior of central sulcus.

Antennule (Fig. 3A) six segmented. First segment elongate, without setae. Second segment elongate with one long seta on ventral edge, and setules along dorsal edge. Third segment small, slightly elongate with one short, stout apical-dorsal seta. Fourth segment...
Recent *Frambocythere* from a cave in South Korea

![Image of Frambocythere relicta n. sp.](image)

**Fig. 2.** *Frambocythere relicta* n. sp.: A, external view of female left valve (DB40030); B, internal view of female left valve (arrows indicate sulci) (DB40030); C, external view of female right valve (DB40030); D, internal view of female right valve (DB40030); E, dorsal view of whole female carapace, anterior to right (DB40031); F, external view of male left valve (DB40029); G, dorsal view of whole male carapace, anterior to right (DB40032); H, external view of male right valve (DB40029).
longer, but thinner than third segment, with two apical-dorsal setae of differing lengths. Fifth segment longer than fourth, with three long and one shorter apical setae. Sixth segment small and elongate, with three long setae of differing lengths and long aesthetasc ya.

Antenna (Fig. 3B) with four segments. First segment elongate, tapering slightly distally. Spinneret seta long and thin, reaching to end of apical claws. Second segment quadrate, with one, stout, long apical-ventral seta. Third segment very elongate, with

**Table 1. Measurements of type specimens.**

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Length (μm)</th>
<th>Height (μm)</th>
<th>Width (μm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>NIBRIV0000244931, male (holotype)</td>
<td>385 (RV)</td>
<td>225 (RV)</td>
<td>—</td>
</tr>
<tr>
<td>NIBRIV0000244932, female (allotype)</td>
<td>410 (RV)</td>
<td>229 (RV)</td>
<td>—</td>
</tr>
<tr>
<td>DB40029, male (paratype)</td>
<td>370 (RV)</td>
<td>209 (RV)</td>
<td>—</td>
</tr>
<tr>
<td>DB40030, female (paratype)</td>
<td>415 (RV)</td>
<td>241 (RV)</td>
<td>—</td>
</tr>
<tr>
<td>DB40031, female (paratype)</td>
<td>402 (RV)</td>
<td>—</td>
<td>287 (Cp)</td>
</tr>
<tr>
<td>DB40032, male (paratype)</td>
<td>379 (RV)</td>
<td>—</td>
<td>244 (Cp)</td>
</tr>
</tbody>
</table>

RV, right valve; Cp, whole carapace.
aesthetasc and seta on ventral edge, two setae on dorsal edge, and one short, stout apical-ventral seta. Fourth segment quadrate with three curved apical claws.

Mandibular palp (Fig. 3C) with four indistinct segments. First segment elongate, with branchial plate on outer edge and one stout, long seta on inner edge. Second segment quadrate, with one stout, long seta on inner edge. Third segment indistinctly divided from second segment, with two apical setae on outer edge and one apical seta on inner edge. Fourth segment short and small, indistinctly separated from third segment, with four apical setae.

Mandibular coxa (Fig. 3D) with seven teeth, and large, distally rounded setulous seta between two largest teeth. Small subapical seta on outer edge of coxa.

Maxillula (Fig. 3E) with elongate palp and three slender and longer endites, which gently curve towards inner edge. Palp with two curved, long, stout apical setae. Second and third endites both with four apical setae. First endite with two apical setae.

Fifth limb (Fig. 3F) with four segments. First segment elongate with one long sub-proximal posterior seta, two setae on anterior edge and two apical-anterior setae. Second segment slender and elongate, with one short apical-anterior seta. Third and fourth segments approximately equal in length, fourth segment with short curved claw, with wide basal section, tapering gradually distally. Claw longer than claw of fifth limb.

Seventh limb (Fig. 3H) with four segments, all of which are more robust and wider than those of fifth and sixth limbs. First segment elongate with one long sub-proximal posterior seta, two setae on anterior edge and one apical-anterior seta. Second segment elongate, with one short apical-anterior seta. Third and fourth segments approximately equal in length. Claw of fourth segment long, mostly straight along length, with exception of distal tip; claw with sub-triangular base, narrow middle section and thinner final section.

Rear of female body (Fig. 4A) with finger-like caudal seta and numerous long, stout setules protruding below. Caudal ramus with two posterior, and one anterior stout, hirsute setae.

Hemipenis (Fig. 4B) with large basal capsule, with rounded outer edge, and straighter inner edge. Distal lobe large and elongate, not significantly curved, with evenly rounded tip. Upper ramus small, consisting of a rounded base tapering and curving distally to form a hook-shape. Lower ramus elongate with straight upper edge and curved lower edge, and with well-defined tip. Copulatory process slender, tapering gradually along length with blunt tip.

Remarks. The carapace shape of Frambocythere relicta n. sp. is most similar to that of Frambocythere gr. tumiensis (Helmdach, 1978) reported from the Thanetian (upper Paleocene) of the Paris Basin (Ducasse et al., 1985). Both species have a weakly developed anterior sulcus, and the general lateral outline and ornamentation

Fig. 4. Frambocythere relicta n. sp.: A, posterior of female body (NIBRIV0000244932) (cs, caudal seta); B, hemipenis (NIBRIV0000244931) (dl, distal lobe; ur, upper ramus; lr, lower ramus; cp, copulatory process).
are very similar. *Frambocythere relicta* n. sp. is slightly less elongate than *Frambocythere* gr. *tumiensis*, and the latter has only very small spines on the postero-ventral margin of the left valve.

_Frambocythere valeroni_ Tambareau, 1991 (in Tambareau et al., 1991) from the Ypresian (early Eocene) of SW France is also similar to *Frambocythere relicta* n. sp.; both _F. valeroni_ and _Frambocythere relicta_ n. sp. have a weakly developed anterior sulcus. However, _F. valeroni_ is more elongate than _Frambocythere relicta_ n. sp. with a maximum height in lateral view anterior of mid-length.

**DISCUSSION**

**Hypogean Ostracod Fauna of South Korea**

Previous surveys of seven limestone caves during the 1960s in the northeastern part of South Korea revealed three hypogean species/subspecies of ostracods: *Pseudocandona morimotoi* (McKenzie, 1972), *Cavernocypris coreana coreana* (McKenzie, 1972) and *Cavernocypris coreana elongata* (McKenzie, 1972). All three taxa are potentially endemic to the Korean Peninsula, although at least one, *C. coreana elongata*, is not restricted to cave environments as it was later found in spring runoffs at the surface (Chang et al., 2012). _Frambocythere relicta_ n. sp. increases the known cave ostracod fauna of South Korea to four species, and is the first representative of the superfamily Cytheroidea in the hypogean realm of South Korea.

**The Kovalevskiella-lineage**

The genera _Frambocythere_, _Kovalevskiella_ and _Rosacythere_ Colin, 1980 (in Colin & Danielpol, 1980) form the _Kovalevskiella_-lineage, characterized by a small-sized carapace (0.5 mm or less), ornamentation in ‘rosettes’ or ‘raspberry-type’ micropustules, an inverse hingement with positive elements on the left valve, the right valve overlapping the left, no, one or two near-vertical sulci, and marked sexual dimorphism with the females having a well-developed brood pouch (Colin & Danielpol, 1980). The lineage has a history stretching back to the latest Bajocian (Middle Jurassic), approximately 168 Ma ago, represented by a _Rosacythere_ species from the Paris Basin (Oertli, 1957; Colin & Carbonel, 1996). Living representatives consist of five species of _Kovalevskiella_, found in the hypogean realm of central and southeastern Europe and Turkey (Danielpol, 1965; 1969; 1970; Colin & Danielpol, 1980; Karanovic, 2003; Özuluğ & Yaltalıer, 2008). Later, the _Kovalevskiella_-lineage was included in the _Kovalevskiella–Abrotocythere_ Group, which includes the genera _Kovalevskiella_, _Rosacythere_, _Frambocythere_, _Abrotocythere_ Zhao, 1987, and _Dolekhiella_ Gidó et al., 2007 (Gidó et al., 2007).

The genus _Frambocythere_ was erected for fossil species with a ‘raspberry-type’ ornamentation, two near-vertical sulci on each valve, an inverse overlap and strong sexual dimorphism, originally for specimens from the Late Maastrichtian of northern Spain (Colin, 1980, in Colin & Danielpol, 1980). Subsequently, other fossil species have been included in the genus, ranging from the Albian (Colin, 1993; Colin & Dépêche, 1997) through to the Lutetian (middle Eocene) (Tambareau, 1984; Tambareau et al., 1991), with a very wide palearcticogeographical distribution from central Africa (Colin, 1993; Colin & Dépêche, 1997), SW Europe, China (Hou et al., 1978), Iran (Vaziri Moghaddam et al., 2010) and India (Bhandari & Colin, 1999; Whatley & Bajpaj, 2006). _Frambocythere_ species usually had a bisexual mode of reproduction, although asexual populations are known (Tambareau et al., 1991). The living Korean _Frambocythere_ species greatly extends the stratigraphical range by approximately 40 Ma to the present, and increases the known (palaeo-)biogeographical range by approximately 1400 km to the far east of Eurasia.

The genus _Kovalevskiella_ is similar to _Frambocythere_, but differs from it in that it has only one sulcus on each valve. It is known from lacustrine deposits in the late Oligocene and Miocene of Western Europe and the Pliocene of the Paratethys (Carbonel et al., 1986). Living representatives are now restricted to the hypogean realm of central and southeastern Europe, and Turkey. Males have not been reported for any of the species in the genus and it is considered to be entirely parthenogenetic. The genera _Kovalevskiella_ and _Frambocythere_ are considered to be more closely related to each other than to other genera in the group (Gidó et al., 2007; Colin, 2011).

The anterior sulcus of _Frambocythere_, the feature that separates the genus from _Kovalevskiella_, is rather weakly developed in _F. relicta_ n. sp. and two of the younger fossil forms, _F. gr. tumiensis_, and _F. valeroni_, compared with other fossil species. The anterior sulcus is probably a plesiomorphic character within the _Frambocythere–Kovalevskiella_ lineage, which became reduced and eventually lost in some taxa, giving rise to the genus _Kovalevskiella_. The difference between _Frambocythere_ species with a reduced anterior sulcus and _Kovalevskiella_ species is, therefore, rather small. However, the anterior sulcus is a persistent character in numerous species/subspecies of _Frambocythere_, and has a good fossil record dating back to the Cretaceous, long before species without it, i.e. _Kovalevskiella_ ssp., appeared. Its presence, even when weakly developed (and its absence in _Kovalevskiella_), can therefore be used to help identify phylogenetic lineages within the group, and so we consider it to be a useful generic character.

**Comparison of Frambocythere relicta n. sp. with living Kovalevskiella ssp**

The living Korean _Frambocythere_ species provides an opportunity to compare the appendages of these two genera for the first time. Of the five extant _Kovalevskiella_ species, the antennule of _Kovalevskiella cvetkovi_ (Danielpol, 1969) is most similar to that of _Frambocythere relicta_ n. sp.; other species either have fewer antennule segments (_Kovalevskiella radjakovi_ (Danielpol, 1969)) or one fewer apical seta on the fourth antennule segment (_Kovalevskiella phreaticola_ (Danielpol, 1965), _Kovalevskiella bulgarica_ (Danielpol, 1970) and _Kovalevskiella dani Karonovic, 2003). The antenna of _Frambocythere relicta_ n. sp. most closely resembles that of _K. bulgarica_, as other _Kovalevskiella_ species have one fewer seta on the anterior margin of the second endopodal segment, including _K. cvetkovi_. The mandibular palp of _Frambocythere relicta_ n. sp. is similar to those of three _Kovalevskiella_ species, _K. phreaticola_, _K. cvetkovi_ and _K. bulgarica_; the mandibular palps of _K. dani_ and _K. radjakovi_ have fewer setae on the second and third segments. The other appendages of _Frambocythere_ and _Kovalevskiella_ are very similar, although _K. phreaticola_ appears to have only one seta on the dorsal margin of the first segments of the sixth and seventh limbs (Danielpol, 1965) (two setae in _Frambocythere relicta_ n. sp. and other _Kovalevskiella_ species). As no males of _Kovalevskiella_ are known, a comparison of the male sexual organ of _Frambocythere_ cannot...
be made. However, the general structure of the male sexual organ does resemble those of the other two extant Timiriaseviinae genera, Metacypris Brady & Robertson, 1870 and Dolekilla Gidó et al., 2007.

Overall, all features of the female appendages of Frambocythere relicta n. sp. appear in at least one extant Kovalevskia species, confirming that these two genera are very closely related. Additionally, all features in Kovalevskia appear in Frambocythere relicta n. sp.; thus, Frambocythere is not excluded from being the ancestor of Kovalevskia.

Relict species or atavistic characters?
There are two scenarios that could potentially explain the presence of an extant Frambocythere species after the apparent extinction of all other species of the genus. The first is that it is a true survivor of the genus Frambocythere and, while other species of the genus succumbed to extinction tens of millions of years ago, a lineage survived to the present day. The other scenario is that its anterior sulcus of the carapace, the morphological feature that separates Frambocythere from the genus Kovalevskia, is an atavistic feature that has resurfaced in the extant Kovalevskia. This would require that Frambocythere is the ancestor of Kovalevskia, which a detailed analysis of the appendages does not exclude (see above). It would also require the species to have reverted from sexual to asexual reproduction, as all Kovalevskia species, both fossil and extant, are parthenogenetic. Such a reversion to sexual reproduction would also be an atavistic feature, and is something that has not been recorded in ostracods. Two atavistic features occurring in the same species (the re-emergence of the anterior sulcus and the reversion to sexual reproduction) is considered to be unlikely, and so we favour the first scenario, i.e. Frambocythere relicta n. sp. is a relict species of the genus, and not a Kovalevskia species with atavistic features. Molecular comparisons of Frambocythere relicta n. sp. with extant Kovalevskia species could test this hypothesis.

From the epigean to hypogean realm
Danielopol (1970; 1980) hypothesized that the hypogean species of the Kovalevskia-lineage living today in central and southeastern Europe, and Turkey are relicts of an ostracod fauna that lived in surface waters during the Tertiary. While some surface species became extinct, others migrated to the hypogean realm; Kovalevskia is postulated to have penetrated the subterranean realm between the Lower Oligocene and Lower Pleistocene (Danielopol, 1980). Carbonel et al. (1986) further suggested that this migration to the hypogean realm was facilitated by their morphology, broad ecological ranges and parthenogenetic mode of reproduction. We hypothesize that a similar scenario may have occurred in the genus Frambocythere; it too was originally widely distributed and long ranging, and was an epigean taxon, but today, it is apparently restricted to Korea in a hypogean habitat. However, Frambocythere relicta n. sp. is a sexual species, suggesting that at least in this case, parthenogenesis was not an important pre-adaptation for colonizing the hypogean realm.

The long gap (approximately 40 Ma) between the youngest fossil Frambocythere known (an epigean species) and the living hypogean specimens could indicate that Frambocythere entered the hypogean realm an extremely long time ago, and thus ‘disappeared’ from the epigean fossil record. However, data on fossil freshwater ostracod taxa in eastern Asia are scarce, and so we cannot rule out that younger epigean Frambocythere species existed in this region. We are, therefore, unable at present to estimate the timing of the colonization of the hypogean realm by the genus to any satisfactory degree.

ACKNOWLEDGEMENTS
We thank the Natural Heritage Division of the Cultural Heritage Administration and the Office of Seongryu Cave, Ulijin County, Republic of Korea for their help with this study. We also thank Dan Danielopol (University of Graz) and Dave Horne (University of London) for their useful reviews and comments. This work was partly supported by the project of Discovery of Indigenous Species from Korea sponsored by the National Institute of Biological Resources (NIBR) under the Ministry of Environment, Korea.

Manuscript received 1 December 2011
Manuscript accepted 13 January 2012

REFERENCES


