

## 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

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**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 stratigraphic 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 & Danielopol, 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 & Danielopol, 1980; Tambareau, 1984; Tambareau et al., 1991; Colin, 1993; 2011; Colin & Dépêche, 1997; Bhandari & Colin, 1999; Whatley & Bajpaj, 2006). The genus belongs to the *Kovalevskiella* lineage (Limnocytheridae, Timiriaseviinae), which also includes the genera *Kovalevskiella* Klein, 1963, and *Rosacythere* Colin, 1980 (in Colin & Danielopol, 1980). Of this lineage, only five species, all belonging to the genus *Kovalevskiella*, are extant, found in central and southeastern Europe and Turkey (Danielopol, 1965; 1969; 1970; Colin & Danielopol, 1980; Karanovic, 2003; Özüluğ & Yaltalier, 2008). All five extant species are considered to be primarily hypogean, although *Kovalevskiella bulgarica* (Danielopol, 1970) has been recovered from a stream in Turkey (Özüluğ & Yaltalier, 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), *Orthomorphella* sp. (Diplopoda), *Kaolinonychus 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).

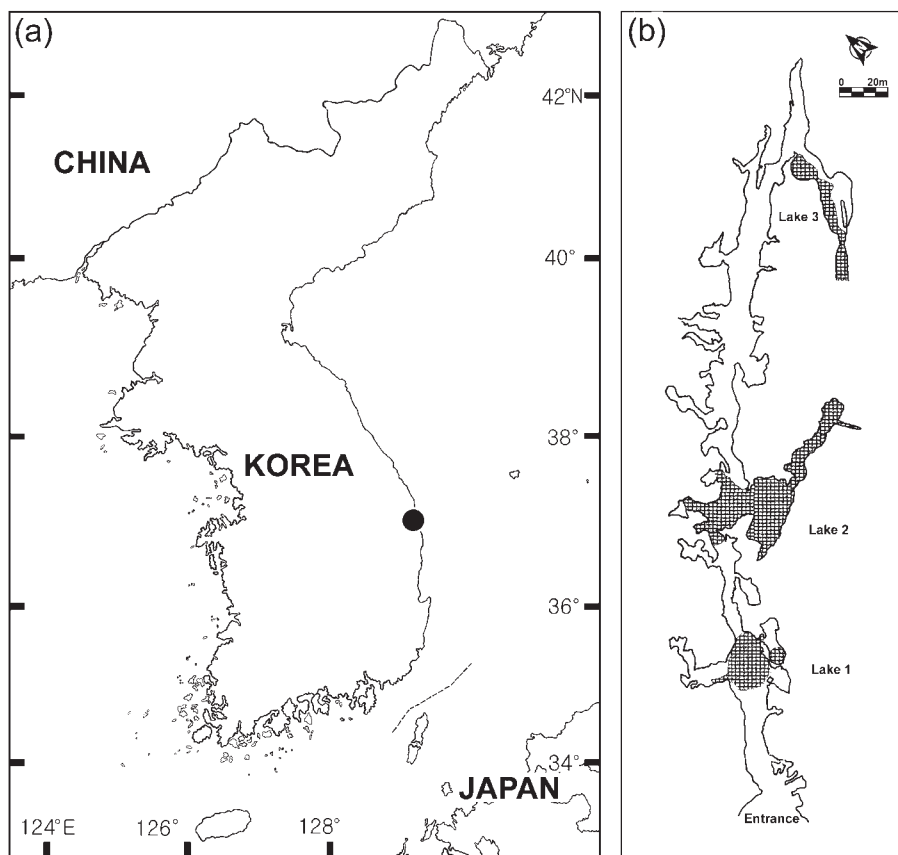


Fig. 1. (a) Location and (b) map of Seongryu Cave, showing main cavern and three cavern lakes.

#### 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 truncated. 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 hook-shaped and small, lower ramus flattened with straight distal margin, rounded proximal margin. Copulatory process slender and simple.

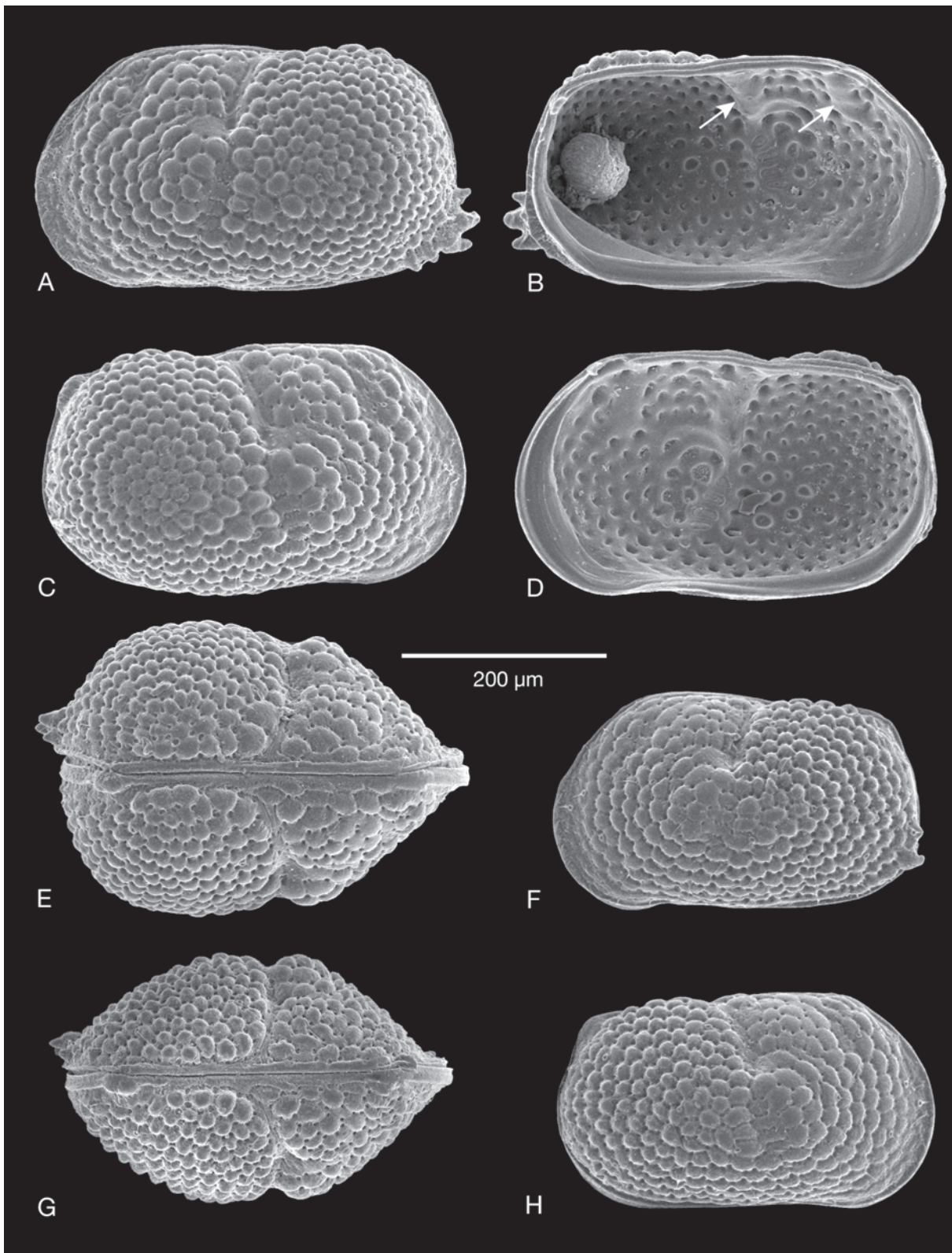
**Type material.** Holotype: dissected male (NIBRIV0000244931). Allotype: dissected female (NIBRIV0000244932). Paratypes: dissected male (DB40029), dissected female (DB40030), whole female (DB40031), whole male (DB40032).

**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



**Fig. 2.** *Frambocythere relictata* 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).



**Fig. 3.** *Frambocythere relicta* n. sp.: **A**, antennule (NIBRIV0000244931); **B**, antenna (NIBRIV0000244931); **C**, mandibular palp (NIBRIV0000244932); **D**, mandibular coxa (NIBRIV0000244931); **E**, palp and endites of maxillula (NIBRIV0000244932); **F**, fifth limb (NIBRIV0000244932); **G**, sixth limb (NIBRIV0000244932); **H**, seventh limb (NIBRIV0000244932).

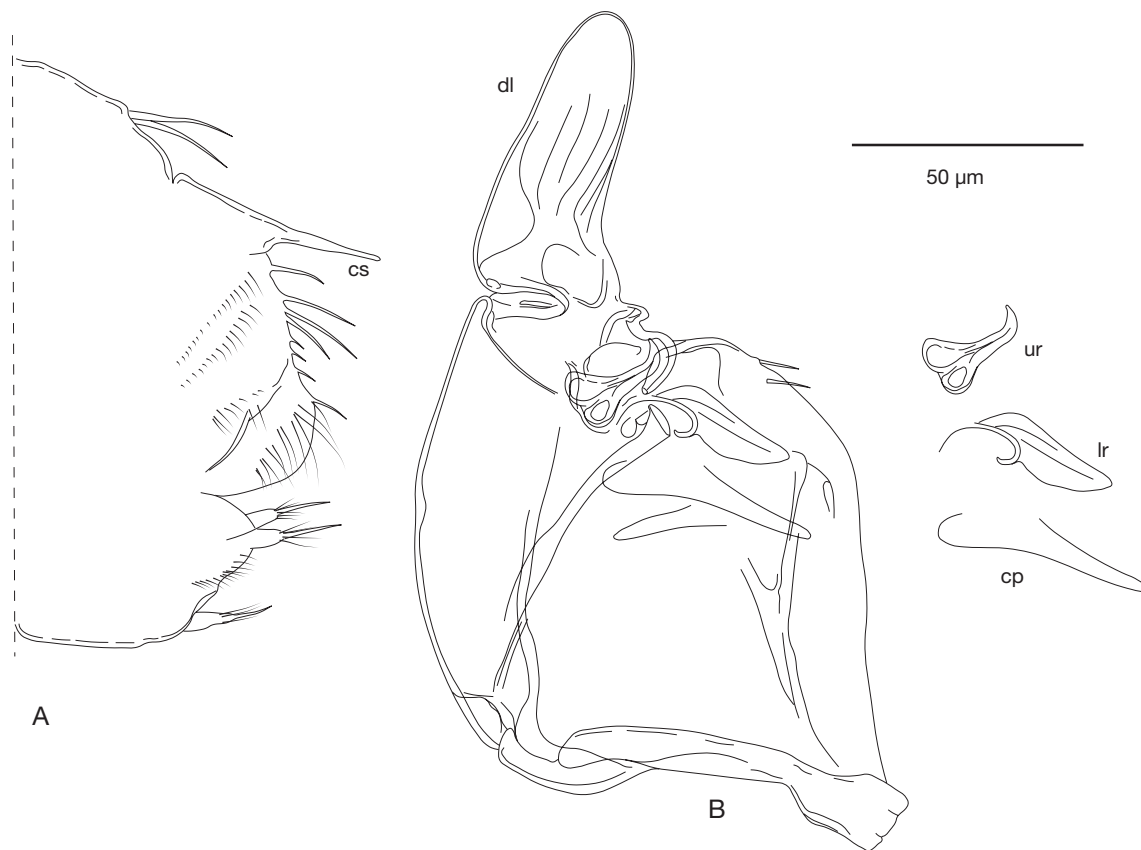
**Table 1.** Measurements of type specimens.

Specimen	Length ( $\mu\text{m}$ )	Height ( $\mu\text{m}$ )	Width ( $\mu\text{m}$ )
NIBRIV0000244931, male (holotype)	385 (RV)	225 (RV)	—
NIBRIV0000244932, female (allotype)	410 (RV)	229 (RV)	—
DB40029, male (paratype)	370 (RV)	209 (RV)	—
DB40030, female (paratype)	415 (RV)	241 (RV)	—
DB40031, female (paratype)	402 (RV)	—	287 (Cp)
DB40032, male (paratype)	379 (RV)	—	244 (Cp)

RV, right valve; Cp, whole carapace.

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



**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).

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, gradually tapering distally.

Sixth limb (Fig. 3G) with four segments, longer than fifth limb. First segment elongate with one long sub-proximal posterior seta, two setae on anterior edge and one apical-anterior seta. 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

are very similar. *Frambocythere relictata* 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 relictata* n. sp.; both *F. valeroni* and *Frambocythere relictata* n. sp. have a weakly developed anterior sulcus. However, *F. valeroni* is more elongate than *Frambocythere relictata* 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 relictata* 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 & Danielopol, 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 & Danielopol, 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 (Danielopol, 1965; 1969; 1970; Colin & Danielopol, 1980; Karanovic, 2003; Özüluğ & Yaltaher, 2008). Later, the *Kovalevskiella*-lineage was included in the *Kovalevskiella*-*Abrotocythere* Group, which includes the genera *Kovalevskiella*, *Rosacythere*, *Frambocythere*, *Abrotocythere* Zhao, 1987, and *Dolekiella* 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 & Danielopol, 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 palaeobiogeographical 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. relictata* 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* spp., 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 relictata* 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* (Danielopol, 1969) is most similar to that of *Frambocythere relictata* n. sp.; other species either have fewer antennule segments (*Kovalevskiella rudjakovi* (Danielopol, 1969)) or one fewer apical seta on the fourth antennule segment (*Kovalevskiella phreaticola* (Danielopol, 1965), *Kovalevskiella bulgarica* (Danielopol, 1970) and *Kovalevskiella dani* Karanovic, 2003). The antenna of *Frambocythere relictata* 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 relictata* 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. rudjakovi* 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 (Danielopol, 1965) (two setae in *Frambocythere relictata* 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 *Dolekiella* Gidó *et al.*, 2007.

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

#### 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 *Kovalevskiella*, is an atavistic feature that has resurfaced in the extant *Kovalevskiella*. This would require that *Frambocythere* is the ancestor of *Kovalevskiella*, which a detailed analysis of the appendages does not exclude (see above). It would also require the species to have reverted from asexual to sexual reproduction, as all *Kovalevskiella* 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 *Kovalevskiella* species with atavistic features. Molecular comparisons of *Frambocythere relicta* n. sp. with extant *Kovalevskiella* species could test this hypothesis.

#### From the epigean to hypogean realm

Danielopol (1970; 1980) hypothesized that the hypogean species of the *Kovalevskiella*-lineage living today in central and south-eastern 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; *Kovalevskiella* 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.

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