Late Cambrian missing link in macroborer evolution preserved in intraclasts

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\textbf{A B S T R A C T}

Macroboring s are known to be rare to absent in middle to late Cambrian successions, the time interval between the end-early Cambrian archaeocyath extinction and the advent of new boring organisms during the mid-late Ordovician (the Ordovician Bioerosion Revolution). The occurrence of macroboring s was controlled mainly by hard-substrate availability; archaeocyath reefs and hardgrounds provided synsedimentarily lithified substrates during the early Cambrian and Ordovician, respectively. In this study, we report bioerosion structures from micritic intraclasts of flat-pebble conglomerates in the Hwajeol Formation (Furongian), Taebaeksan Basin, Korea. Two types of macroboring s (\textit{Trypanites} and cf. \textit{Gastrochaenolites}) are recognized, both of which penetrate micritic clasts and are filled with bioclastic grainstone matrix. Several lines of evidence, including the sharp boundaries and unaltered shapes of macroboring s, as well as the occurrence of macroboring s penetrating the coating of iron- and/or manganese oxide-coated micritic clasts, indicate that these macroboring s formed after the cementation of micritic clasts. The Hwajeol macroboring s would have formed on micritic clasts and/or hardgrounds that were eroded and formed flat pebbles. The presence of bioerosion structures within clasts of the Hwajeol flat-pebble conglomerates supports a previous hypothesis that macroborers survived in hardgrounds during the middle to late Cambrian, after the extinction of archaeocyath reefs. In addition, the Hwajeol cf. \textit{Gastrochaenolites} is the earliest of its kind, implying that there could be more kinds of macroboring s hidden within Cambrian flat-pebble conglomerates.

\textbf{1. Introduction}

Macroboring s, borings that are sufficiently large to be seen by the naked eye, are formed by organisms that bore into hard substrates by means of physical and/or physiochemical processes (Kobluk et al., 1978; Flügel, 2004). As metazoans diversified during the Cambrian Explosion, macroborers began to bore into solid substrates and form macroboring s in early Cambrian archaeocyath reefs (James et al., 1977), and began to diversify in the mid-late Ordovician, the event known as the Ordovician Bioerosion Revolution (Wilson and Palmer, 2006), a part of the Great Ordovician Biodiversification Event. Many new ichnogenera are added during the Ordovician Bioerosion Revolution, with diverse categories of architectural design, which might have been induced by several causes including increase in hard substrate availability induced by calcite sea geochemistry as well as increased predation (Palmer and Wilson, 2004; Buatois et al., 2016; Mángano et al., 2016). Understanding early diversification pattern of macroborings would certainly enhance our knowledge on the paleoecology during the Great Ordovician Biodiversification Event.

There is a distinct gap in the known temporal range of macroborings; they are apparently absent from middle to upper Cambrian successions (Wilson et al., 1992; Taylor and Wilson, 2003; Wilson and Palmer, 2006; Buatois et al., 2016). It has been suggested that macroborers survived within hardgrounds during the middle to late Cambrian after the decline of archaeocyath reefs at the end of the early Cambrian (James et al., 1977). Although there are a few reports of rare undescribed macroboring s from hardgrounds of middle to late Cambrian age (e.g., Brett et al., 1983; Chow and James, 1992), no detailed studies on these macroboring s have been performed. Therefore, the reason for the rarity of macroboring s from the geological record during this time interval is still unknown. In this study, we report abundant bioerosion structures in micritic clasts within flat-pebble conglomerates deposited during the late Cambrian (Furongian) in the Taebaeksan Basin, Korea (Hwajeol Formation). The presence of bioerosion features within flat-pebble conglomerates may help to elucidate the previously unknown evolutionary history of macroborers and their interactions with the surrounding environment.

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2. Geological setting and methods

The Sino-Korean Block, a microcontinent comprising northern China and a major part of Korea, was located at the eastern margin of Gondwana during the early Paleozoic (McKenzie et al., 2011). At the eastern margin of the Sino-Korean Block, the thick Cambro–Ordovician succession of the Joseon Supergroup was deposited in the Taebaeksan Basin, Korea (Fig. 1) (Chough, 2013). The supergroup contains mixed siliciclastic–carbonate successions unconformably overlying Precambrian basement rocks and overlain by siliciclastic sedimentary rocks of the Carboniferous–Triassic Pyeongan Supergroup (Fig. 2). The Taebaek Group is a subunit of the Joseon Supergroup, and contains the Jangsan/Myeonsan, Myobong, Daegi, Sesong, Hwajeol, Dongjeom, Dumugol, Makgol, Jigunsan, and Duwibong formations in ascending stratigraphic order (Choi et al., 2004; Kwon et al., 2006).

The Hwajeol Formation, the uppermost unit of the Cambrian succession in the study area, is represented by thinly bedded alternations of limestone and shale constituting meter-scale shallowing-upward cyclic successions, with several centimeter- to decimeter-thick flat-pebble conglomerate beds generally composed of micritic intraclasts and a bioclastic grainstone matrix (Fig. 3). The depositional environment of the Hwajeol Formation was interpreted to be inner to outer ramp (Kwon et al., 2006). Identification of the Asioptychaspis, Quadraticephalus, and Eosaukia trilobite biozones (Sohn and Choi, 2005, 2007), together with the Proconodontus tenuiserratus, P. posterocostatus, P. muelleri, Eoconodontus notchpeakensis, Cambrooistodus minutus, Cordylodus proavus, and Fryellodontus inornatus–Monocostodus sevierensis–Semicontiodus lavadamensis conodont biozones (Jeong and Lee, 2000; Lee and Seo, 2008; Lee, 2014), within the formation indicate an age of late Jiangshanian to informal Stage 10.

All macroborings reported in this study were found in clasts within flat-pebble conglomerates of the Hwajeol Formation exposed along the mountain trail (Seokgaejae section; Fig. 1). Macroborings can be recognized in outcrop, but are generally too small to be clearly observed (Fig. 3B). To ascertain the nature of the borings, thin sections were made in the laboratory (Fig. 4). Several sets of serial thin sections were made to assess the three-dimensional structures of the borings (Fig. 5).

3. Bioerosion structures

The clasts in the flat-pebble conglomerates are composed mainly of micrite with a small amount of bioclastic material, and are imbedded within a bioclastic grainstone matrix composed mainly of trilobites and some echinoderm fragments. These intraclasts are a few millimeters to 1 cm thick, a few to 10 cm wide, and generally well-rounded with sharp erosional boundaries. Macroborings within clasts exhibit sharp margins, and the host and infilled sediments have different compositions; i.e., the clasts are micritic and the surrounding grainstone is bioclastic (Fig. 4). The directions of bioerosion structures commonly vary within a single clast. Some macroborings penetrate reddish iron and/or manganese oxide-rich coatings on the clasts (Fig. 4C). Many identified macroborings are circular to ellipsoidal in shape, possibly representing transverse to subtransverse cuts of the borings (Figs. 4D and 5). However, it is not possible to identify the boring shape based solely on the transverse cuts. We classified macroborings based on some longitudinal and sublongitudinal cuts, augmented by several sets of serial thin sections (Fig. 5). Two types of macroborings are identified in this study: Trypanites and cf. Gastrochaenolites.

3.1. Trypanites

Trypanites in the Hwajeol conglomerates are characteristically unbranched, straight tubular structures that generally have a relatively constant diameter from the entrance to the end (Fig. 6). They are 0.25–1.2 mm in diameter and 1.1–4.6 mm long. Their length-to-width ratios range between 4 and 10, though their true dimensions are uncertain. This structure may be assigned to Trypanites or Skolithos depending on the substrate: Trypanites penetrate hard substrates, whereas Skolithos form in soft substrates. The nature of this structure is discussed below (Section 3.3).

3.2. Clavate borings (cf. Gastrochaenolites)

Gastrochaenolites are unbranched, clavate (club-shaped) borings
within lithic substrates (Fig. 7) (Kelly and Bromley, 1984). Three major types of clavate borings are recognized from the clasts in the Hwajeol flat-pebble conglomerates. The first type is vase-shaped with an elongate neck (Fig. 7A–C). The chambers are elongate and oval-shaped (1.4–3.8 mm in diameter), with the length of the neck usually being half of the chamber length. The second type is characterized by a round-bottomed flask shape (Fig. 7D–E). This type possesses a circular to irregular chamber (1–3.5 mm in diameter), with the neck clearly distinguished from the chamber. The neck of the flask-shaped type is relatively short (half to one-fifth of chamber length), and the neck diameter is generally consistent along its length. The third type is spherical or oval-shaped without a neck, and is usually larger in size (6–8 mm in diameter) than the other two types (Fig. 7F).

Although it was not possible to conduct a full ichnotaxonomical analysis on the Hwajeol clavate borings because they may have been altered during erosional processes, many of them can be compared with
Fig. 5. Serial thin sections showing the three-dimensional structures of macroborings. (A–D) *Trypanites* (arrows). (E–G) *cf. Gastrochaenolites* (arrows).
previously reported macroborings except for their small size. The first two types of clavate structures (the vase- and flask-shaped structures) are similar to *G. lapidicus* Kelly and Bromley, 1984 and *G. orbicularis* Kelly and Bromley, 1984, respectively. Although size of the macroborings is not a criterion for diagnosing trace fossil, the Hwajeol macroborings are much smaller than previously reported *Gastrochaenolites* (cf. Kelly and Bromley, 1984), suggesting that they may reflect a different sort of process. We tentatively classified the first two types of Hwajeol clavate borings as cf. *Gastrochaenolites*. The spherical structures most likely indicate modification of the vase- and flask-shaped structures by erosion processes: the spherical structures are larger and have much wider openings than the other structures. It is possible that the spherical structures are similar to the semi-circular borings of Johnson et al. (2010); however, due to the rarity of these spherical structures, it is not currently possible to confirm their origin.

3.3. Borings vs. burrows: formation mechanisms of the bioerosion structures

Many of the flat-pebble conglomerates in the Hwajeol Formation consist of micritic clasts, which makes it difficult to determine whether the trace fossils are true borings formed in a hardground or burrows excavated in a firmground that subsequently lithified to form a hardground. Therefore, it is necessary to consider the origin of these trace fossils. The sharp boundaries of the bioerosion structures suggest that the structures were formed either in a firmground or a hardground. All the bioerosion structures analyzed in this study lack evidence of compaction, consistent with their formation after cementation of the micritic substrate. The strongest evidence for the structures being borings is that they penetrate the iron-oxide coatings on micritic clasts (Fig. 4C), indicating that the structures were formed after formation of the clasts and coatings. As the iron-rich coatings formed along the outer boundaries of well-rounded clasts, and formation of the coating during exposure on the seafloor would have required a certain length of time, it is possible to assume that the clast would have been well-cemented, rounded by erosion, and then coated with iron and/or manganese oxide minerals (cf. Myrow et al., 2004).

The various directions of entry of borings into micritic intraclasts indicate that they formed during clast transportation, although it is not possible to fully discard the possibility that at least some of them formed in the hardground prior to the formation of intraclasts. Some of the borings experienced abrasion after their formation, as evinced by the occurrence of some clavate borings without necks and spherical structures that are notably larger than the other clavate borings.

4. Discussion

4.1. Evolution of the clavate macroboring *Gastrochaenolites*

The Hwajeol clavate borings are the earliest known of its kind. The oldest previously reported *Gastrochaenolites* are from the Lower Ordovician (Floian) strata of Utah, USA (Benner et al., 2004) and from the Lower–Middle Ordovician boundary beds of Sweden (Ekdale and Bromley, 2001) and Estonia (Vinn and Wilson, 2010). Except for these occurrences, *Gastrochaenolites* has only rarely been reported from Paleozoic strata: the only other known occurrence is from the lower Carboniferous (Mississippian) of Arkansas, USA (Wilson and Palmer, 1998). *Gastrochaenolites* became abundant during the Mesozoic, formed by gastrochaenid and lithophagid bivalves that appeared in the Late Triassic (Carter and Stanley, 2004). The current study extends the record of these clavate borings to the late Cambrian. Similar *Gastrochaenolites*-like structures also occur in the middle and upper Cambrian flat-pebble conglomerates of the western and central Sino-Korean Block, respectively, thereby supporting the hypothesis (Fig. 8A, B).

The most common organisms that form clavate borings are bivalves.
(Kelly and Bromley, 1984; Wilson and Palmer, 1998; Carter and Stanley, 2004; Wilson et al., 2014). However, it is possible that the Paleozoic clavate borings were produced by somewhat different organisms. For example, Benner et al. (2008) reported an enigmatic soft-bodied organism from Ordovician *Gastrochaenolites* in Utah and proposed that this organism was responsible for the formation of the boring. At present, it is unclear whether this organism also made the Hwajeol clavate borings, given their differences in size (5–10 mm for the Utah vs. 1–4 mm for the Hwajeol material). Whatever organism made these clavate structures, it most likely formed these structures as domicnian.

4.2. Evolution of macroborers prior to the Ordovician Bioerosion Revolution

The presence of macroborings within the flat-pebble conglomerates of the Hwajeol Formation supports a previous hypothesis of the existence of borings within middle–late Cambrian hardgrounds (James et al., 1977; Kobluk et al., 1978; Wilson and Palmer, 2006). The Hwajeol macroborings consist of at least two different types, indicating the existence of at least two different kinds of macroborers. In addition to this study, many previous studies have reported (or illustrated) macroborings from flat-pebble conglomerates (Rees et al., 1976; Markello and Read, 1982; Whisnant, 1987; Osleger and Read, 1991; Myrow et al., 2004; Rose, 2006; Johnson et al., 2010; Eoff, 2014; Gomez and Astini, 2015; Vinn and Toom, 2016) as well as hardgrounds (Brett et al., 1983; Chow and James, 1992; Cowan and James, 1992,

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**Fig. 7.** Photomicrographs of cf. *Gastrochaenolites*. (A–C) Vase-shaped structure. (D–E) Round-bottomed flask shape. (F) Spherical or oval-shaped without necks.
...these mobilized clasts were probably the only hard substrates available during the deposition of the Hwajeol Formation, which would have forced macroborders to inhabit the clasts, as evidenced by the variable directions of macroborings in the Hwajeol intraclasts (Vinn and Toom, 2016). This was not likely an ideal condition for borers, as evinced by their rarity compared with Middle-Late Ordovician hardgrounds (e.g., Brett and Liddell, 1978; Wilson and Palmer, 2006). Of note, hard-substrate encrusters are absent from the Hwajeol Formation (Lee et al., 2015). It is possible that Cambrian encrusters were not yet adapted to mobilized hard substrates such as intraclasts (Vinn and Zhuravlev, 2008). Intraclasts of flat-pebble conglomerates might have been a common type of hard substrate in the late Cambrian (Wright and Cherns, 2016), in addition to thin limestone hardgrounds where these intraclasts would have originated. Their mobilized nature differentiates these clasts from other hard substrates such as reefs or hardgrounds. Formation of intraclasts is closely related to co-occurring characteristic lithofacies; i.e., thinly bedded limestone–shale (or marlstone) alternations. Thin limestone beds would have been lithified by the extensive early cementation of carbonate that began with the middle Cambrian (Zhuravlev and Wood, 2008; Lee et al., 2015). These thin limestone beds would have been reworked by storms or tsunamis in deep subtidal environments, forming thin intraclasts (e.g., Sepkoski, 1982; Sepkoski et al., 1991; Myrow et al., 2004). The flat-pebble conglomerates would have diminished as hardgrounds became thicker and more resistant to reworking by storms by the Middle Ordovician (Wright and Cherns, 2016). It has been suggested that as extent and depth of burrowing increased during the Great Ordovician Biodiversification Event (Droser and Bottjer, 1988, 1989; Bottjer et al., 2000), thin limestone beds diminished as early cementation of sediments were limited by biotic mixing of sediments (Sepkoski et al., 1991) or in-depth cementation of carbonate sedimentation due to oxidation induced by burrowing activities (Wright and Cherns, 2016).

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<table>
<thead>
<tr>
<th>Location</th>
<th>Age</th>
<th>Substrate Description</th>
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</tr>
</thead>
<tbody>
<tr>
<td>Estonia</td>
<td>Furongian (late?)</td>
<td>Rounded quartzose siltstone cobbles; dark-colored phosphatized exterior; no encruster</td>
<td>Vinn and Toom (2016)</td>
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<tr>
<td>Utah, USA</td>
<td>Jiangshanian</td>
<td>Fenestral facies consist of mudstones and pelletoidal wacke-packstone</td>
<td>Rees et al. (1976)</td>
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<tr>
<td>Minnesota/Wisconsin, USA</td>
<td>Jiangshanian</td>
<td>Slightly glauconitic mud/lime mudstone clast within flate-pebble conglomerate</td>
<td>Eöff (2014)</td>
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<td>Tennessee, USA</td>
<td>Paibian–Jiangshanian</td>
<td>Thrombolites (Renalcis-Girvanella boundstone; bioherms with clotted fabric), digitate stromatolite</td>
<td>Glumac (2001)</td>
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<tr>
<td>Virginia, USA</td>
<td>Paibian–Jiangshanian</td>
<td>Micritized clasts with iron-stained borders; Thrombolites containing mud-rich fingers</td>
<td>Whisonant (1987), Koerschner and Read (1989)</td>
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<td>Montana/Wyoming, USA</td>
<td>Paibian–Jiangshanian</td>
<td>Micritic clasts within flate-pebble conglomerates; clasts iron-coated</td>
<td>Brett et al. (1983), Myrow et al. (2004)</td>
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<td>Alberta, Canada</td>
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<td>Renalcis-Girvanella framestone; pelmatozoan columns</td>
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<td>Virginia, USA</td>
<td>Guzhangian–Paibian</td>
<td>Clasts within flate-pebble conglomerates; clast composition varies, peloidal grains, line mottling, wackestones</td>
<td>Markello and Read (1982)</td>
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<td>South Dakota, USA</td>
<td>Drumian-Stage 10</td>
<td>Locally stained truncated surfaces developed within carbonates (oolites, ribbon rock, mudstone, and stromatolites)</td>
<td>Kennard et al. (1989); Chow and James (1992, 1993), Shinnava and Wilber (1992)</td>
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<td>Arizona, USA</td>
<td>Stage 5–Guzhangian</td>
<td>Metazoan-microbial reef, micritically bound mud, locally stained truncated surfaces developed within carbonates (oolites, ribbon rock, mudstone, and stromatolites)</td>
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<td>Shandong, China</td>
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<td>Micritic class of flat-pebble conglomerate</td>
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<td>New Zealand, Canada</td>
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<td>No description</td>
<td>Johnson et al. (2010)</td>
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Table 1: Summary of the reported (or photographed) middle-late Cambrian domichnial macroborings.
Table 2

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</table>

Multiple attachment bioerosional traces: O

**Fig. 9.** Occurrences of domichnial macroboring ichnogenera in the early Paleozoic. Gray bars are drawn based on Wilson and Palmer (2006) and Buatois et al. (2016). Yellow bars are drawn based on the discussion herein. Hwajeol cf. *Gastrochaenolites* is regarded as *Gastrochaenolites* in this figure. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Conclusions

Based on detailed microfacies analysis, we report the macroborings *Trypanites* and cf. *Gastrochaenolites* from micritic intraclasts in the flat-pebble conglomerates of the Furongian Hwajeol Formation, Korea. Abundant macroborings might have been responsible for the formation of flat-pebble conglomerates by promoting breakage of thin limestone beds to form intraclasts. The occurrence of macroborings in the middle to upper Cambrian succession fills the gap between the archaeocyath extinction by the end-early Cambrian and Early Ordovician hardgrounds, thus confirming a previous idea that the macroborers would have inhabited hardgrounds instead of reefs during the middle and late Cambrian. The current study therefore suggests how the early macroborers had adapted to such environmental changes. Further studies on Cambrian macroborings, especially those within flat pebbles, will help us to understand the early evolution of these enigmatic macroborers as well as their paleoecology.

Acknowledgments

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