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Late Cambrian missing link in macroborer evolution preserved in intraclasts

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ABSTRACT

Macroborings 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 macroborings 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 macroborings (*Trypanites* and cf. *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 macroborings, as well as the occurrence of macroborings penetrating the coating of iron- and/or manganese oxide-coated micritic clasts, indicate that these macroborings formed after the cementation of micritic substrates. The Hwajeol macroborings 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. *Gastrochaenolites* is the earliest of its kind, implying that there could be more kinds of macroborings hidden within Cambrian flat-pebble conglomerates.

1. Introduction

Macroborings, 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 physicochemical processes (Kobluk et al., 1978; Flügel, 2004). As metazoans diversified during the Cambrian Explosion, macroborers began to bore into solid substrates and form macroborings 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 macroborings from hardgrounds of middle to late Cambrian age (e.g., Brett et al., 1983; Chow and James, 1992), no detailed studies on these macroborings have been performed. Therefore, the reason for the rarity of macroborings 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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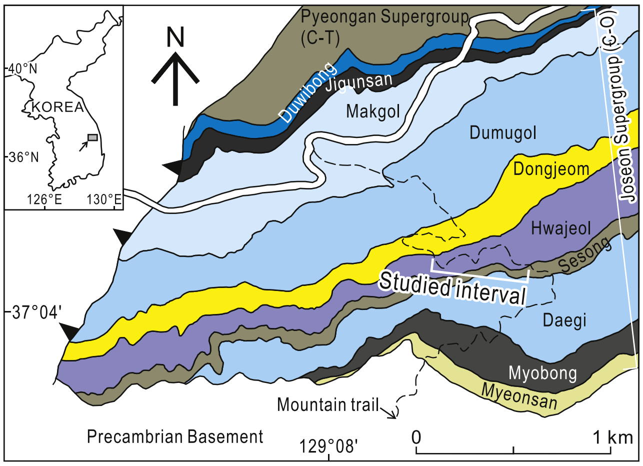

Fig. 1. Geological map of the study area (Seokgaejae section). Modified after Choi et al. (2004).

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–Semiacontiodus 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*.

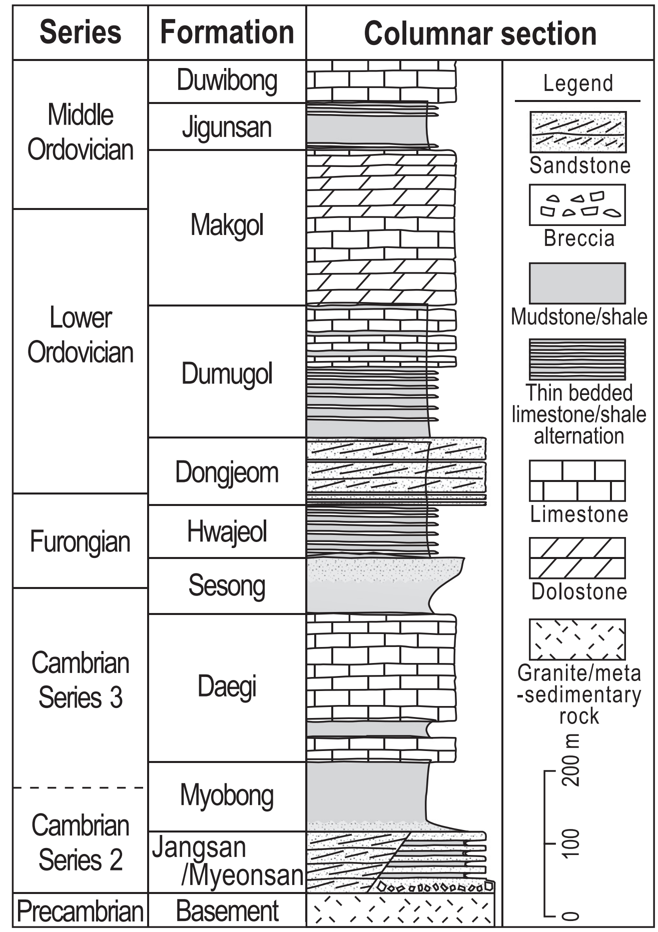

Fig. 2. Summary of the Cambro–Ordovician succession in the Taebaeksan Basin.

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

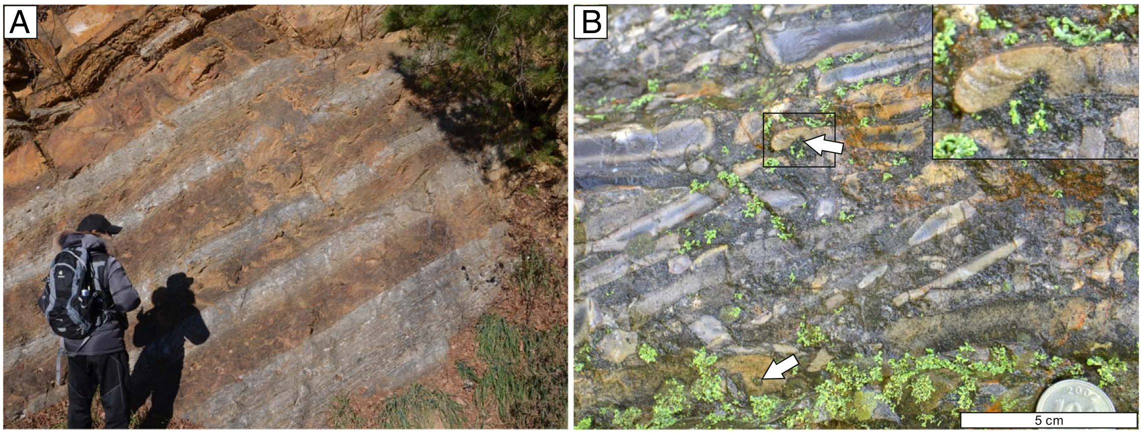

Fig. 3. Outcrop photographs of the Hwajeol Formation. (A) Meter-scale cyclic successions that are composed mainly of thinly bedded alternations of limestone and shale. (B) Flat-pebble conglomerate in the Hwajeol Formation. Note the occurrence of bored intraclasts (arrows).

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

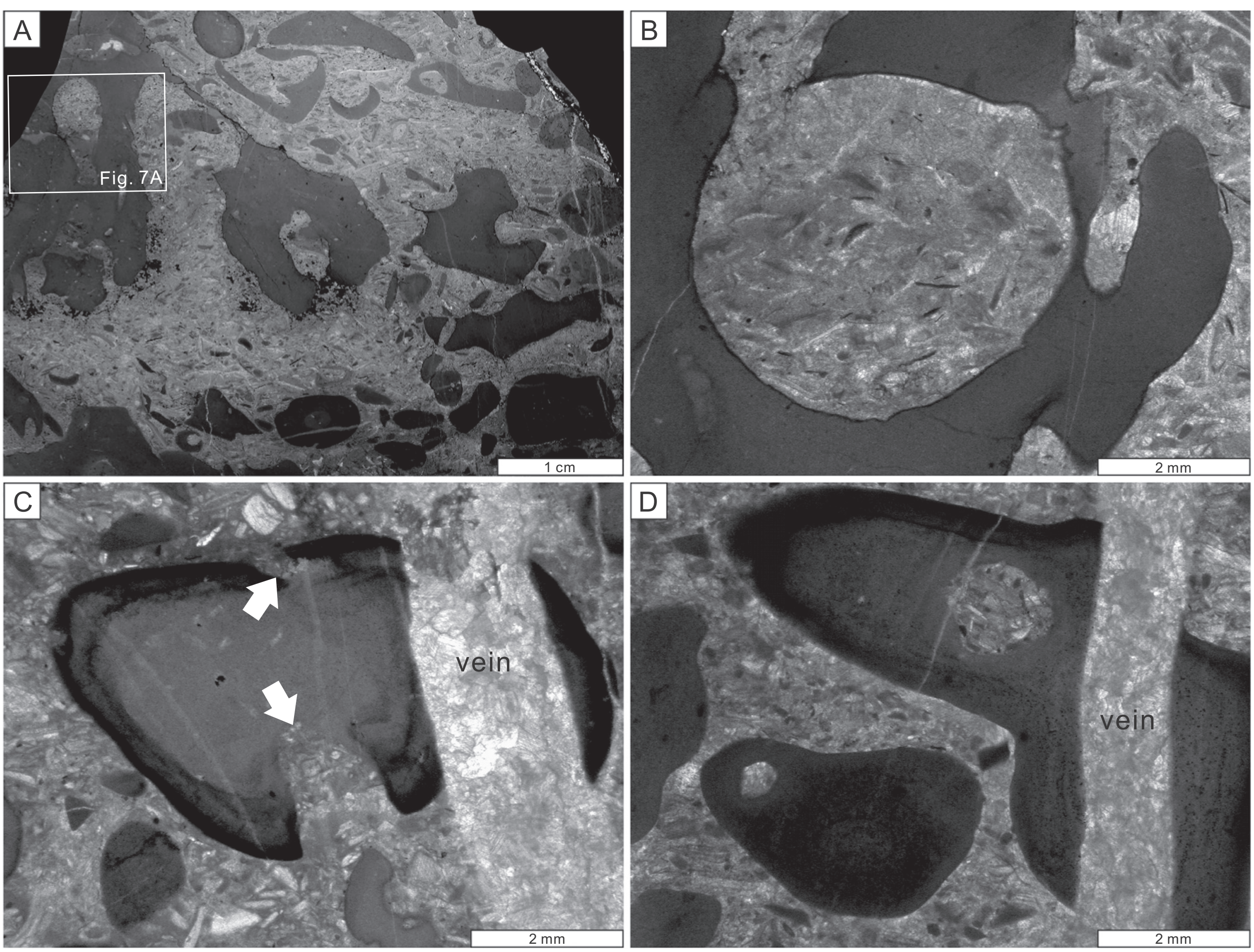

Fig. 4. Borings identified from clasts of the Hwajeol flat-pebble conglomerates. (A) Photomicrograph showing many bored intraclasts. (B) Two macroborings within a single clast. Note that these two borings differ in shape and size. (C) Two macroborings (white arrows) penetrating an iron-stained clast. (D) Transverse cut of a macroboring within a clast.

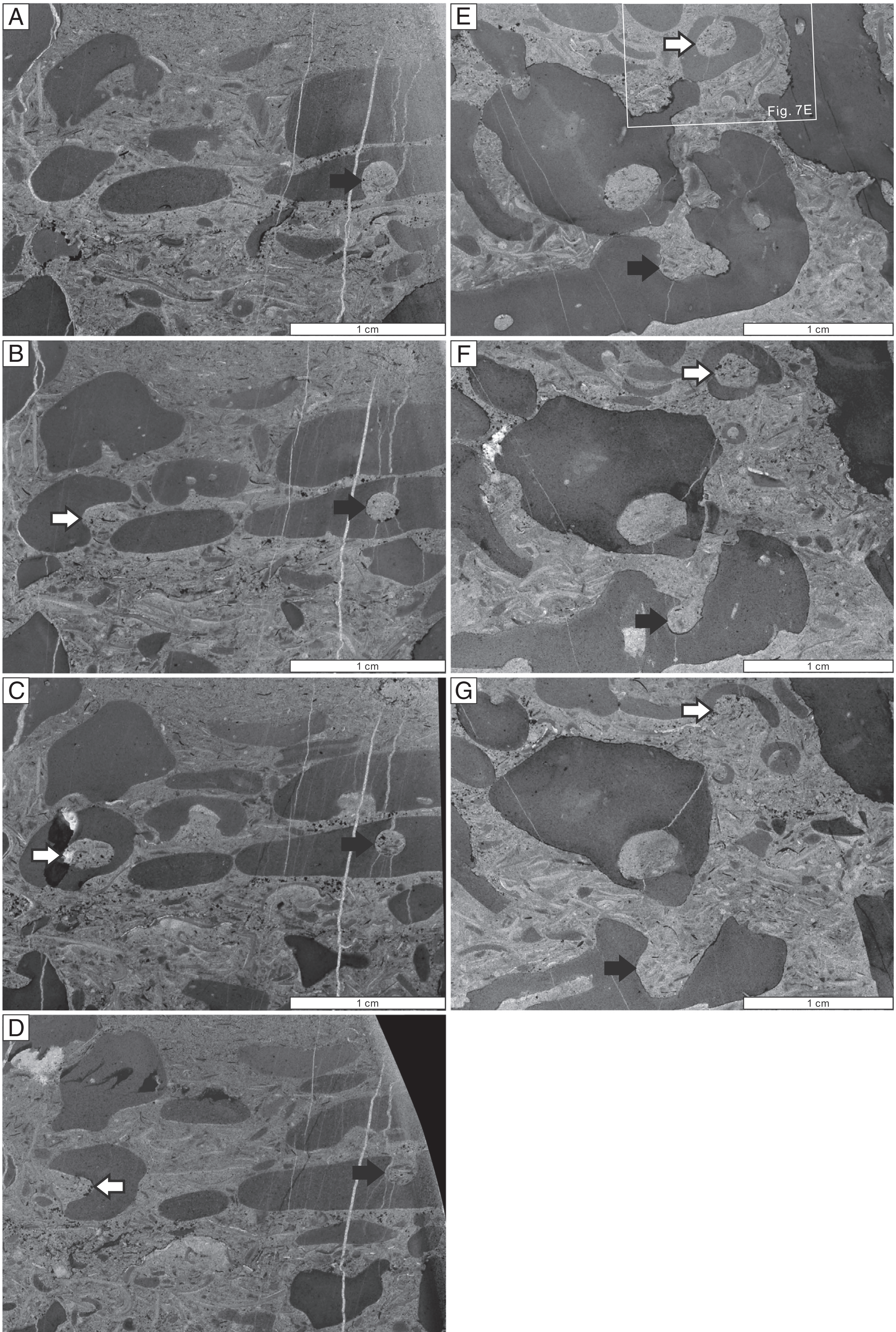

Fig. 5. Serial thin sections showing the three-dimensional structures of macroborings. (A–D) *Trypanites* (arrows). (E–G) cf. *Gastrochaenolites* (arrows).

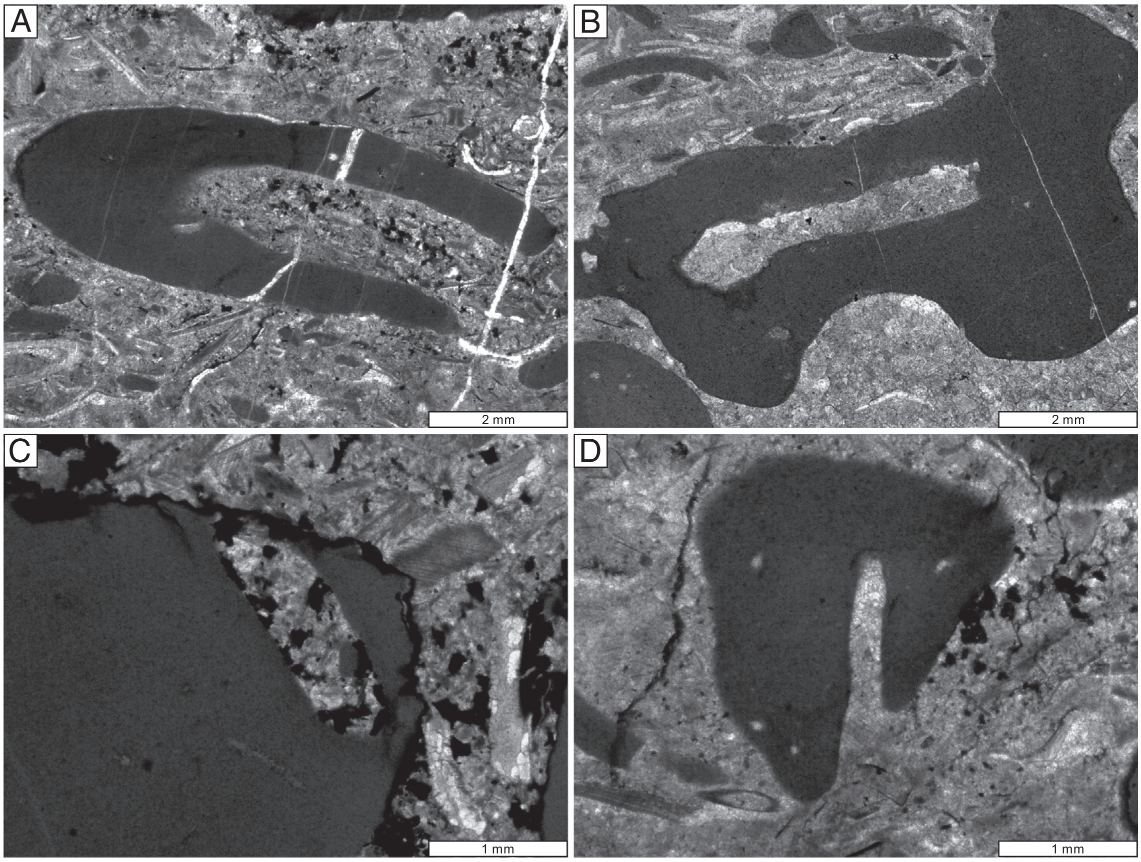

Fig. 6. Photomicrographs of *Trypanites*.

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 macroboring 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

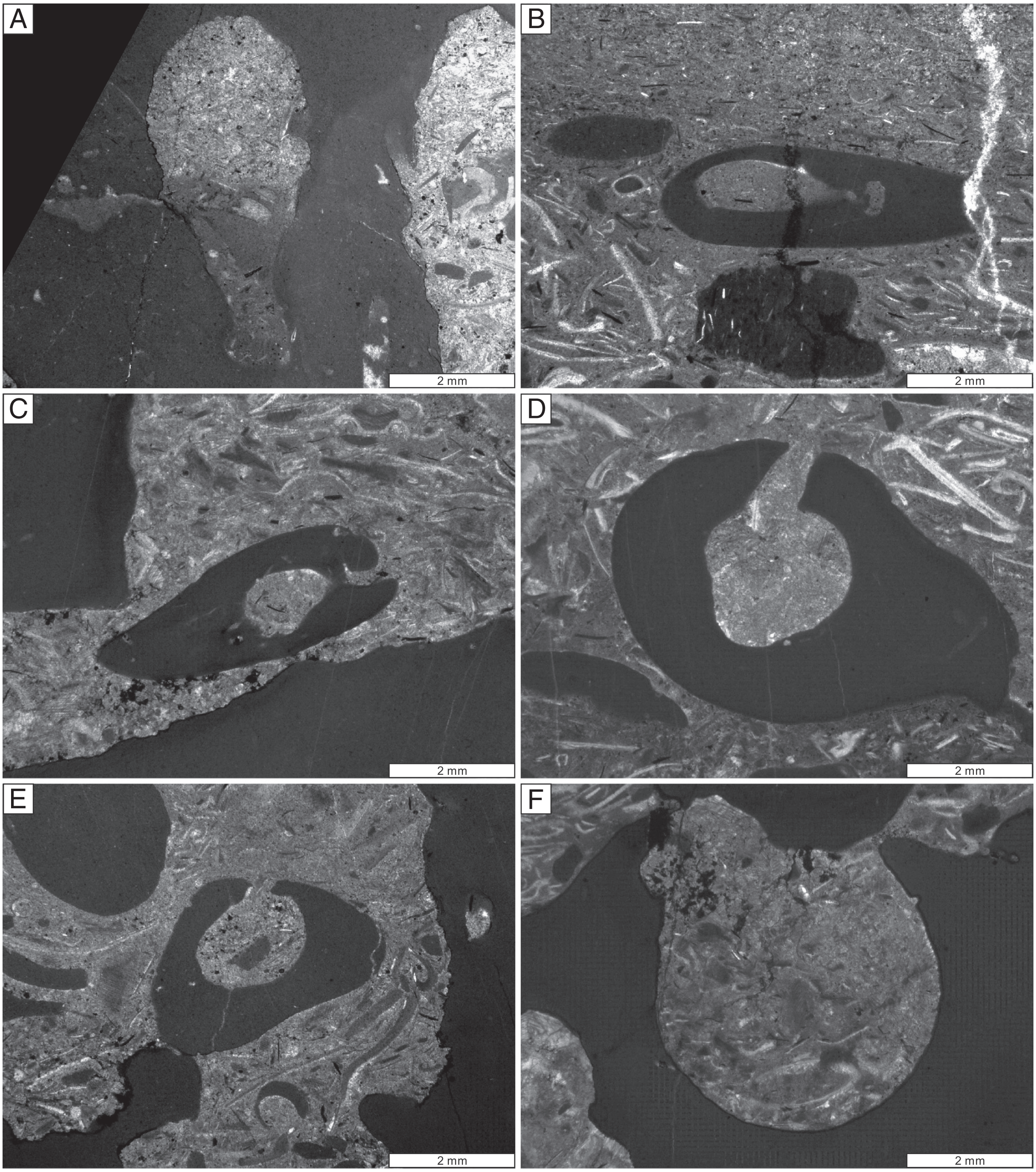

Fig. 7. Photomicrographs of cf. *Gastrochaenolites*. (A–C) Vase-shaped structure. (D–E) Round-bottomed flask shape. (F) Spherical or oval-shaped without necks.

(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 domichnia.

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; Whisonant, 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,

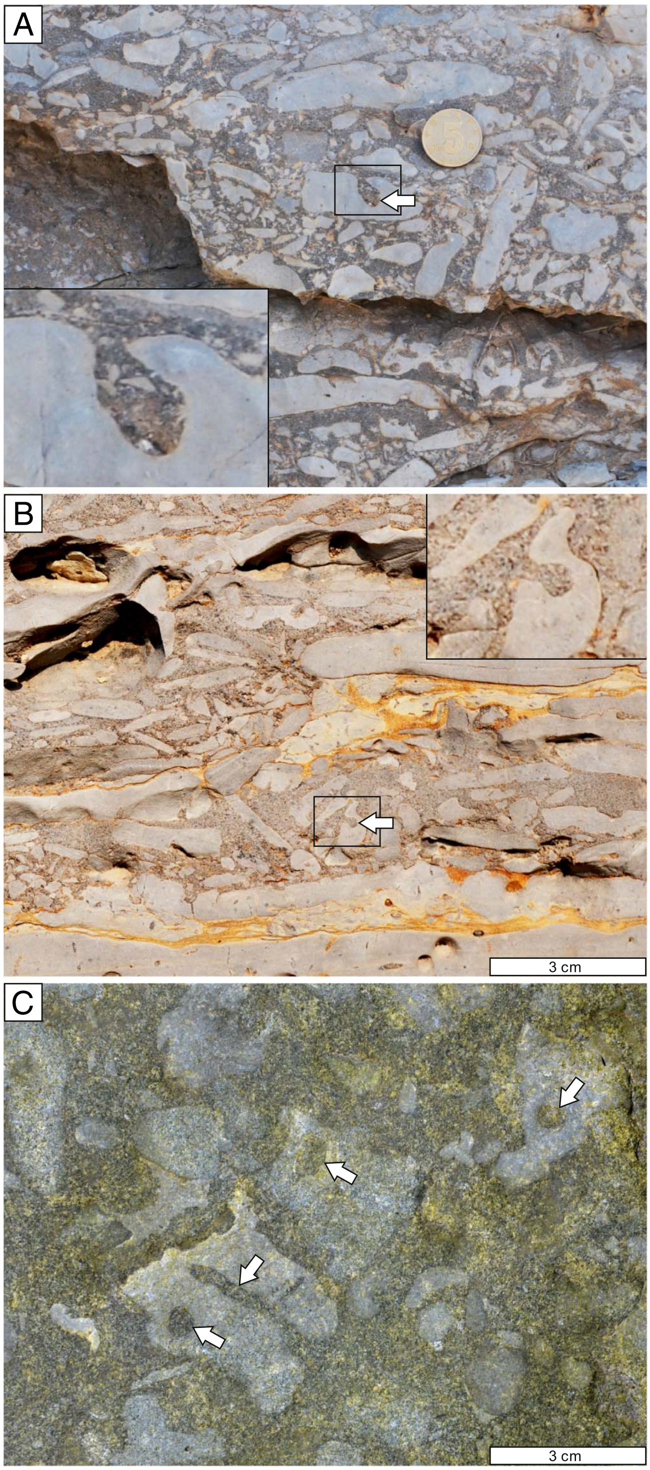

Fig. 8. Photographs of macroborings with flat-pebble conglomerates from other localities. (A) cf. *Gastrochaenolites* from Wuhai, Inner Mongolia, China (Cambrian Series 3, Abuqiehai Formation). (B) cf. *Gastrochaenolites* from Jinan, Shandong, China (Furongian, Chaomidian Formation). (C) *Trypanites* from Port au Port Peninsula, Newfoundland, Canada (Cambrian Series 3, March Point Formation).

1993; Srinivasan and Walker, 1993; Lee et al., 2015) in middle–upper Cambrian deposits worldwide (Table 1; Fig. 8). We interpreted these structures as borings on the basis of their sharp boundaries and the different composition of the host- and infilling sediments, similar to the borings in the Hwajeol Formation. Macroborings have also been reported within middle to late Cambrian reefs such as thrombolites or stromatolites (Kennard et al., 1989; Koerschner and Read, 1989; Waters, 1989; Glumac, 2001), as well as lithistid sponge–microbial reefs (Kruse and Reitner, 2014; Lee et al., 2016). None of these borings (or boring-like structures) have been studied in detail except for recently reported *Trypanites* from siltstone pebbles of the lower and upper Cambrian successions of Baltica (Vinn and Toom, 2016).

Trypanites and *Trypanites*-like borings have been reported from Furongian siltstone pebbles and hardgrounds, respectively, and are the only known types of macroboring in middle–upper Cambrian strata (Brett et al., 1983; Chow and James, 1992; Vinn and Toom, 2016). Johnson et al. (2010) reported shallow semi-spherical borings from Furongian quartzite boulders that cannot be assigned to any known ichnogenus. Cf. *Gastrochaenolites* from the Hwajeol Formation is the third known type of Cambrian macroboring developed in hard substrates after *Trypanites* and the semi-spherical borings of Johnson et al. (2010); this finding suggests that there may be more kinds of borings hidden within middle–upper Cambrian successions, possibly within flat-pebble conglomerates (Fig. 8). The existence of these various Cambrian borings as well as their architectural designs suggest that diversification of domichnial macroborers could have initiated prior to the Ordovician Bioerosion Revolution, though ichnodiversity and ichnodisparity of macroborings throughout the Cambrian is still much less than those of the mid–late Ordovician (cf. Wilson and Palmer, 2006; Buatois et al., 2016) (Table 2; Fig. 9). Evolution of macroborers would have been closely related with substrate availabilities, which changed according to environmental conditions throughout the early Paleozoic (detailed in next section).

4.3. Sedimentological and paleoecological implications of the Hwajeol macroborings

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 by 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).

The mobilized clasts were probably the only hard substrates available during the deposition of Hwajeol Formation, which would have forced macroborers to inhabit the clasts, as evinced 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 flat-pebble conglomerates, although fragments of echinoderms, which are common encrusters of the latest Cambrian Series 3 and Furongian firmgrounds and hardgrounds, were found within the grainstone matrix of the flat-pebble conglomerates (Brett et al., 1983; Sumrall et al., 1997; Kruse and Zhuravlev, 2008). It is possible that Cambrian encrusters were not yet adapted to mobilized hard substrates such as intraclasts (Vinn and

Table 1
Summary of the reported (or photographed) middle-late Cambrian domichnial macroborings.

Location	Age	Formation	Substrate	Description	Reference
Estonia	Furongian (late?)	Ülgase Formation	Rounded quartzose siltstone cobbles; dark-colored phosphatized exterior; no encruster	*Trypanites*; simple cylindrical shape with single openings; ~2 mm deep, 0.2–0.4 mm in diameter; perpendicular to the surface	Vinn and Toom (2016)
Utah, USA	Jiangshanian	Orr Formation (Johns Wash Limestone Member)	Fenestral facies consist of mudstones and pelletoidal wacke-packstone	No description	Rees et al. (1976)
Minnesota/Wisconsin, USA	Jiangshanian	Tunnel City Group	Slightly glauconitic mud/lime mudstone clast within flat-pebble conglomerate	No description (ca. 1–2 mm diameter, semi-spherical?, sharp margin)	Eoff (2014)
Tennessee, USA	Paibian–Stage 10	Maynardville Formation and Copper Ridge Dolomite	Thrombolite (*Renalcis-Epiphyton-Girvanella* boundstone; bioherms with clotted fabric), digitate stromatolite	Boring filled with geopetal sediment and calcite cement (~1.5 mm diameter)	Glumac (2001)
Virginia, USA	Paibian–Jangshanian	Conococheague Formation	Micritized clasts with iron-stained borders; Thrombolites containing mud-rich fingers	Borings (0.3–3 mm diameter)	Whisonant (1987), Koerschner and Read (1989)
Montana/Wyoming, USA	Paibian–Jiangshanian	Snowy Range Formation	Micritic clasts within flat-pebble conglomerates; clasts iron-coated	Sharp-walled, vertical, cylindrical holes (2–3 mm diameter) filled with calcite spar and light colored border (oxidation?)	Brett et al. (1983), Myrow et al. (2004)
Alberta, Canada	Paibian	Waterfowl Formation	*Renalcis-Girvanella* framestone; pelmatozoan columns	Borings perpendicular to surfaces; filled with peloids and calcite spar	Waters (1989)
Virginia, USA	Guzhangian–Paibian	Nolichucky Formation	Clasts within flat-pebble conglomerates; clast composition vary (peloidal grainstone, lime mudstone, wackestone, reworked clasts); red-stained borders	No description	Markello and Read (1982)
South Dakoda, USA	Guzhangian	Deadwood Formation	Quartzite boulder	Semi-spherical structure with 0.6–4.3 mm diameter (mean diameter = 2.2 mm)	Johnson et al. (2010)
Australia	Late Drumian	Ranken Limestone	Metazoan-microbial reef, microbially bound mud, stromatolite, skeletal bioclast	Boring filled with geopetal-peloidal infill (~1 mm diameter)	Kruse and Reitner (2014)
Newfoundland, Canada	Drumian–Stage 10	March Point, Petit Jardin and Berry Head formations	Locally stained truncated surfaces developed within carbonates (oolites, ribbon rock, mudstone, and stromatolite)	*Trypanites*? sp.; borings cut ooids and cements (ca. 0.3–1 mm diameter); some with pyritic coating	Kennard et al. (1989); Chow and James (1992), Cowan and James (1992, 1993)
Tennessee, USA	Drumian–Guzhangian	Maryville Limestone	Burrowed mudstone	Sharp wall, filled with cement and sediment (~1 mm diameter, ~5 mm length)	Srinivasan and Walker (1993)
Argentine Precordillera	Stage 5–Guzhangian?	La Laja Formation	Micritic clasts of flat-pebble conglomerate	No description (ca. 2–4 mm diameter, partly exhumed?)	Pratt and Bordonaro (2007), Gomez and Astini (2015)
Shandong, China	Late Stage 5	Zhangxia Formation	Lithistid sponge–microbial reef	Perpendicularly penetrate sponge, partly curved (~0.2 mm diameter, ~1 mm length)	Lee et al. (2016)
Shandong, China	Late Stage 5	Zhangxia Formation	Oncolitic wackestone	Curved; sharp wall with scalloped upper surface	Lee et al. (2015)
Arizona, USA	Stage 5	Muav Limestone	Pelmicrite clasts within flat-pebble conglomerate	No description	Rose (2006)

Table 2
Stratigraphic ranges of architectural designs of domichnial macroborings during the early Paleozoic. Red circles indicate those reported in this study. Categories of architectural designs and classification of ichnotaxa are adapted from Buatois et al. (2016, 2017). C1: Terreneuvian, C2: Cambrian Series 2, C3: Cambrian Series 3, C4: Furongian, EO: Early Ordovician, MO: Middle Ordovician, LO: Late Ordovician.

Architectural designs	C1	C2	C3	C4	EO	MO	LO
Cylindrical vertical to oblique borings		O	O	O	O	O	O
Elliptical vertical to oblique borings							O
Pouch borings							O
Clavate-shape borings				O	O	O	O
Branched tubular borings							O
Multiple attachment bioerosional traces					O		O

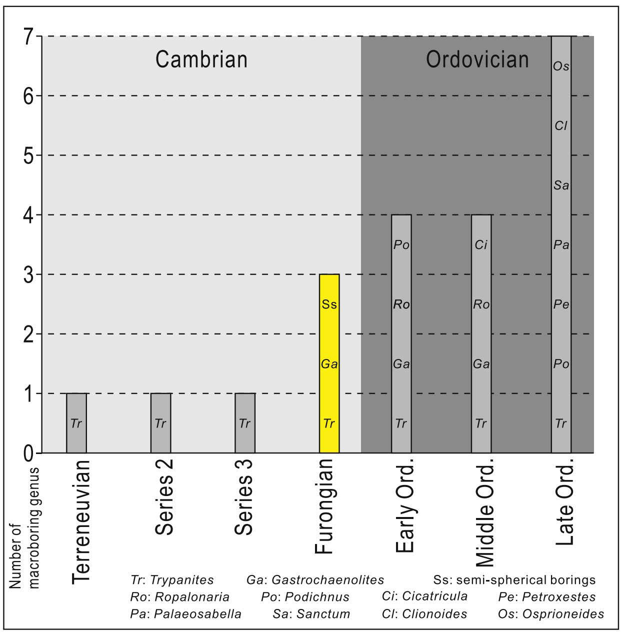

Fig. 9. Occurrences of domichnial macroboring ichnogenera in the early Paleozoic. Gray bars are drawn based on Wilson and Palmer (2006) and Buatois et al. (2016). Yellow bars are drawn based on the discussion herein. Hwajeol cf. *Gastrochaenolites* is regarded as *Gastrochaenolites* in this figure. (For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

Toom, 2016); they might not have tolerated the times of disturbance when clasts were rolling. However, this phenomenon may have been caused by regional variations in echinoderm fauna as the middle–late Cambrian hardgrounds of the same platform were only rarely encrusted by stromatolites and ?sponges (Lee et al., 2015), suggesting that echinoderms that thrived in eastern Gondwana were not able to encrust hard substrates during the Cambrian, because the echinoderms of the middle Cambrian of western Gondwana (Zamora et al., 2010) and the early to late Cambrian of Laurentia (Brett et al., 1983; Peel, 2017) were able to encrust firmgrounds and hardgrounds, respectively. The hard substrate community would have eventually migrated to non-mobilized substrates such as hardgrounds and reefs and thrived there (Wilson and Palmer, 2006), as such substrates widely developed by the Ordovician (Wilson et al., 1992).

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.

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