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Bone chip-filled burrows associated with bored dinosaur bone in floodplain paleosols of the Cretaceous Hasandong Formation, Korea

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Abstract

Borings in dinosaur bone, which are intimately associated with subjacent burrows filled with bone chips, are recognized from a Lower Cretaceous floodplain vertic-calcic paleosol, Dapveongri, Korea. The bored bone is an in situ weathered scapula of herbivore. The borings are ubiquitous within and on scapula, and have diverse orientations. They are mostly solitary with diameters from a few millimeters to 1 cm. The bone chip-filled burrows have similar diameters to those of borings and occur sporadically just below (within 10 cm downwards) the scapula. Some burrows are isolated and some are clustered. Burrow direction is also variable, and some burrows are intertwined, forming networks. The bone borings and related bone chip-filled burrows post-dated bone weathering processes such as cracking, fracturing, brecciation, and disintegration, which indicates that Dapyeongri bone borers preferred to feed upon dried skeleton. Dermestid beetles are the most likely organism for Dapyeongri bone borers and burrowers, considering that it is the most common carrion insect inhabiting vertebrate carcasses in dry decay stage. These bone borings and bone chip-filled burrows provide evidence that dermestid beetles played an important role as the last scavengers of dinosaur carcasses during the Early Cretaceous. Such scavenging by carrion insects under dry climate may have impacted negatively the dinosaur fossil preservation in Cretaceous deposits. The behavior of Dapyeongri bone borers/burrowers is compared with that of dung beetles documented from the Upper Cretaceous Two Medicine Formation [Chin and Gill, Palaios 11 (1996) 280-287], which cache subterranean burrows with organic matter transported from the surface. These unique trace fossils thus provide additional evidence for understanding Cretaceous trophic interaction between dinosaurs and insects. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Hasandong Formation; dinosaur; borings; burrows; carrion beetles; trophic interaction

1. Introduction

Taphonomy and paleoenvironments of dinosaur deposits have been studied in many aspects including lithology, bone occurrence, bone modification, paleosols, sedimentary structures, ichnofossils, and

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geochemistry (e.g. Dodson et al., 1980; Koster, 1987; Rogers, 1990; Avanzini et al., 1997; Fastovsky et al., 1997; Graham et al., 1997; Retallack, 1997; Tedesco, 1997; White et al., 1998). There are, however, few studies documenting ichnofossils generated by interaction of other organisms with dinosaurs. Rogers (1992) described macroborings by carrion beetles in dinosaur bones and addressed their paleoenvironmental

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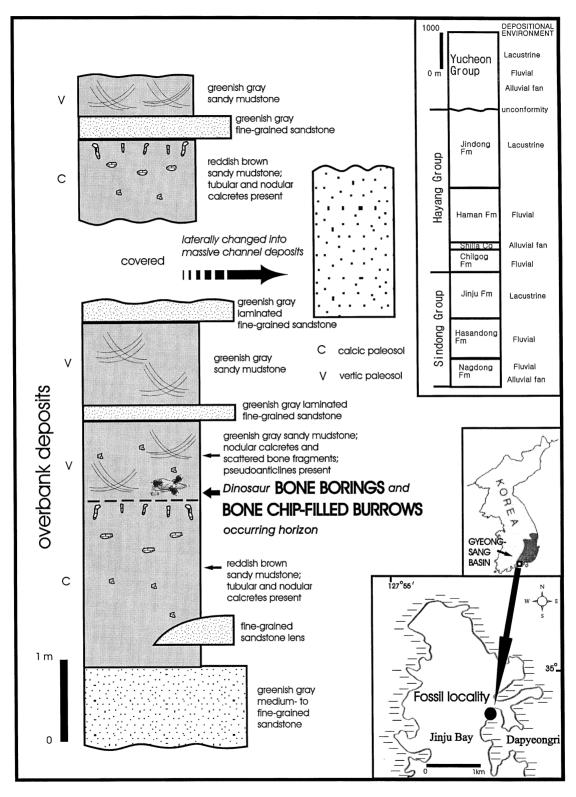


Fig. 1. Location map of study area and stratigraphic section of deposits containing bone borings and bone chip-filled burrows.

implications from the Upper Cretaceous Two Medicine Formation of Montana. Chin and Gill (1996) described dung beetle burrows preserved within dinosaur coprolites from the same formation and interpreted the nature of dung beetle/dinosaur interactions. These two studies provided significant insights into the interactions between dinosaurs and insects. The nature of interaction of other organisms with dinosaurs, however, is still largely unknown.

An intimate association of dinosaur bone chipfilled burrows with bored dinosaur bone has been discovered in a floodplain calcic paleosol of the Lower Cretaceous Hasandong Formation, Korea. From all indications, the bone chip-filled burrows described here have not yet been found in any other dinosaur-bearing deposit. In addition, it is a unique occurrence that these burrows are closely associated with bored bone. This paper describes the interrelationships among fossil dinosaur bone, bone borings, and burrows in immediately subjacent sediments. Observations indicate that borings and burrows were produced by the same organisms (presumably a type of beetle), which exploited isolated desiccated dinosaur bone in a floodplain setting. These relationships provide a rare glimpse of indirect trophic interactions between dinosaurs (albeit dead ones!) and insects. The objectives of this study are thus to: (1) describe the occurrence of dinosaur deposits in which bone borings and bone chip-filled burrows occur; (2) describe the preservational state of bone; (3) interpret the paleoenvironment and taphonomic pathway of the dinosaur deposit; (4) document the bone borings and bone chip-filled burrows; and (5) discuss their paleoenvironmental implications.

2. Geological setting

In southeastern Korea, a 9000 m thick sequence of non-marine deposits assigned to the Gyeongsang Supergroup (Cretaceous) is widely distributed (Fig. 1). They are divided into the Sindong, Hayang, and Yucheon groups, in ascending stratigraphical order, and their overall depositional environments are alluvial fan, fluvial, and lacustrine (Um et al., 1983; Choi, H.I., 1985). In the Gyeongsang Supergroup, body fossils are very rare, although invertebrate trace fossils and dinosaur tracks are abundant in places. During the Cretaceous, the Korean Peninsula was situated in mid-latitudes as it is today (Lee et al., 1987; Kim et al., 1993). Based on fossil records, paleosols, and lithology (Paik and Kim, 1997), the general paleoclimatic regime of the Gyeongsang Supergroup has been interpreted to have been warm and dry.

The Hasandong Formation, in which bone borings and bone chip-filled burrows occur, lies in the middle part of the Sindong Group. The Sindong Group generally has been assigned to the Hautervian using charophytes (Seo, 1985) and spores and pollen (Choi, D.K., 1985), although an early Aptian age was suggested from paleomagnetism (Doh et al., 1994). The Hasandong Formation is underlain by the Nagdong Formation, which consists of alluvial fan and fluvial deposits, and is overlain by the Jinju Formation, which consists of lacustrine and some fluvial deposits. The Hasandong Formation consists of alternating channel and interchannel deposits including some floodplain-lake deposits. The interchannel deposits are commonly reddish in color and typically contain pedogenic calcareous nodules (Um et al., 1983; Paik and Kim, 1995). Paleovertic features, such as deep desiccation cracks, slickensides, and pseudoanticlines, are also common in some Hasandong interchannel deposits (Paik, 1998; Paik and Lee, 1998). The paleoclimate of the Hasandong Formation has thus been interpreted to have been subarid and seasonal with wetting and drying cycles (Paik and Lee, 1995; Paik and Kim, 1995; Paik and Lee, 1999). Herbivorous and carnivorous dinosaur fossils occasionally occur in the Hasandong Formation (Lee et al., 1997; Paik et al., 1998a,b), but plant fossils are very rare. The same general taphonomic trend — abundant bone preservation and very rare plant preservation is found in the Jurassic Morrison Formation (Dodson et al., 1980). The paleoflora environment of the Hasandong Formation is interpreted as dry woodland on the basis of stable carbon-isotope analysis of pedogenic calcretes (Lee, 1999).

3. Dinosaur deposits

3.1. Hasandong Formation

In spite of the common occurrence of dinosaur tracks in the Cretaceous Gyeongsang Supergroup, dinosaur bone fossils are very rare, which may be attributed to limited exposure of outcrops compared with the exposures of non-marine Mesozoic deposits in China and North America. Only 15 dinosaur bone beds have been discovered in the Gyeongsang Supergroup, and all of these fossils occur as scattered fragments. Most occur in the Hasandong Formation. The dinosaur-bearing beds of the Hasandong Formation record three different taphonomic pathways (Paik et al., 1998a). The first type is represented by floodplain deposits preserved as calcic or vertic paleosols. These contain dinosaur bone fragments that were weathered, and partially disarticulated on floodplains and subsequently transported by floods to more distal floodbasins with further disarticulation, breakage and abrasion. The second type is represented by channel deposits with reworked bone fragments derived from channel migration and associated collapse of floodplain deposits. The third is reflected by marginal floodplain-lake deposits containing bone fragments transported from floodplains. Among them, the first type (floodplain paleosol deposits) is most common and exhibits the best preservation. Such preferred occurrence in floodplain calcic paleosols may be attributed to higher preservation potential in alkaline soils (Retallack, 1997). The dinosaur bone fragments in the Hasandong floodplain calcic paleosols are characteristically coated by micrite crusts (a few millimeters to a few centimeters thick), and hence preserved as irregular calcareous nodules (Paik et al., 1998a,b). These micritic nodules are pedogenic calcretes. Similar perimineralization features around vertebrate bone fragments in calcic paleosols were described in Late Permian floodplain deposits of Karoo Basin, South Africa (Smith, 1993).

3.2. Study area

The Hasandong Formation in study area (Dapyeongri) (Fig. 1) consists of channel deposits

and thick floodplain deposits, including crevasse channel/splay deposits exposed along the coastal cliff faces; the calcic–vertic paleosols commonly occur in the floodplain deposits. Dinosaur deposits were discovered in two horizons. One occurs in floodplain deposits, while the other occurs in calcrete intraclastic channel deposits. The dinosaur bone deposit associated with bone boring and bone chip-filled burrows occurs in the floodplain deposits (Fig. 1).

The floodplain bone deposit is a type of cumulate-truncated paleosol profile (Mariott and Wright, 1993) consisting of a reddish-brown calcic paleosol (lower part) and a greenish-gray verticcalcic paleosol (upper part) (Fig. 1). Planar to cross-laminated fine sandstone (crevasse splay deposits) overlies the bone deposit with an erosive contact, and grades into mudstone in which calcrete nodules are scattered. The contact between the calcic and vertic-calcic paleosols is irregular (a few centimeters to decimeters of relief) and generally gradational. In places, however, truncation of the lower calcic paleosol is distinct. The lower calcic paleosol is composed of sandy mudstone and is bioturbated in upper part. Tubular and nodular calcretes are scattered (especially in the upper part), and ornithoid egg-shell fragments are included. Some well-rounded pebbles consisting of crystalline rock, variegated sandstone, and mudstone with pedogenic calcite rims are, in places, present just below the upper vertic-calcic paleosol in which dinosaur bone fragments occur.

The vertic–calcic paleosol generally consists of sandy mudstone in which pseudoanticlines and calcrete nodules occur. The calcrete nodules in the vertic–calcic paleosol are generally concentrated in the lower part. In places, calcrete intraclastic deposits, including calcrete ooids, occur in patches in the lower part of vertic–calcic paleosol and show reverse grading.

In the basal part of the vertic–calcic paleosol, a sauropd scapula fragment (~1.5 m long, 25 to over 40 cm wide, and a few to 10 cm thick), a rib fragment (40 cm long and 2 to 2.5 cm wide), and theropod tooth fragments occur. The Scapula fragment occurs 10 to 20 cm above the lower surface of the calcic paleosol, and the rib fragment occurs 7 m away from the scapula and just above the higher surface of the lower calcic paleosol (50 cm above scapula horizon). Theropod tooth fragments occur between these two bone fragments. Above the scapula, smaller bone fragments (less than a few centimeters) and tiny bone and teeth chips are scattered throughout the lower part of the verticcalcic paleosol. In the upper part bone chips are rarely observed. Bone fragments are generally encrusted with micrites and thus preserved as nodules. Irregular micrite patches formed around aggregated bone chips. Curved to circumgranular cracks are present in these micrite nodules and patches (Fig. 3B), and calcite aureoles formed around bone chips, which indicates their pedogenic origin. It is characteristic that bone chips are mostly concentrated around the scapula and some chips occur around the rib fragment. Bone chips are rare away from scapula and rib bone. In places, Scovenia type invertebrate traces occur in calcic and vertic-calcic paleosols around the scapula.

4. Paleoweathering of dinosaur bones

The scapula is preserved in a severely weathered state. Its surface is generally cracked, fractured, and partially brecciated (Figs. 2 and 3). Bone tissue structures are preserved only in the compact surface bone (a few millimeters to 2 cm thick), and the central cancellous bone tissues are mostly disintegrated and filled with sandy mudstone, calcite, and bone chips. The external bone shape is thus partially destroyed due to disintegration of bone. Dislocation of bone is also observed in places. Thin cracks normal to bone surface are common, and generally filled by iron-oxides. Some cracks are tapering outerward and innerward. Sheet cracks along bone layers occasionally occur in surface compact bone. Spalled-off tiny bone chips are scattered around these weathered surfaces (Fig. 2A). Bone mineral is mainly francolite and partially chloritized. Internal openings of compact and cancellous bone are mostly filled with micrite and microspar, and are surrounded by partially silicified rinds consisting of blocky quartz. Irregular calcrete rinds formed around the weathered scapula surface, and small pedogenic calcrete nodules are present in the disintegrated internal

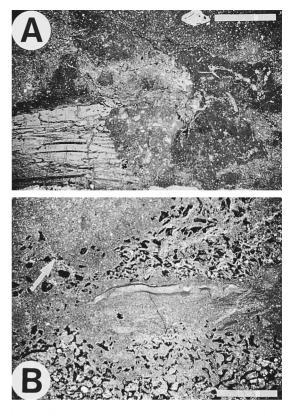


Fig. 2. Thin section photomicrographs of in situ weathering of Dapyeongri bored bone. Scale bars are 2.5 mm. (A) Cracking and spalling-off of surficial compact bone. (B) Disintegration of central cancellous bone. Bone boring (arrow) post-dated disintegration.

part. Bone borings and burrows are common within and around the scapula. Detailed features of borings and burrows are described in the following section.

5. Bone borings and bone chip-filled burrows

Borings are ubiquitous within and on the scapula (Fig. 3). They are mostly solitary and generally occur at intervals of a few tens of centimeters to a few millimeters. They show both non-tapering and tapering shafts, and adjacent borings are in places coalesced. Boring direction varies from normal to oblique to parallel to bone surface. Borings extend from compact surface bone into internal disintegrated bone, and cut across bone

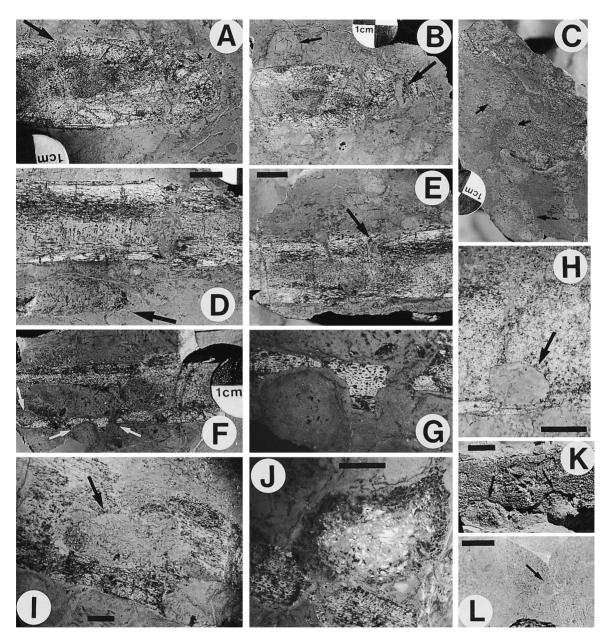


Fig. 3. Borings in Dapyeongri dinosaur bone. A to J and L are polished slabs. Scale bars in D, E, I, K, and L are 1 cm and scale bars in H and J are 5 mm. (A, B) Subvertical borings (arrows) post-dating bone weathering. Pedogenic curved to circumgranular cracks (smaller arrow) occur in surrounding calcrete. (C) Subhorizontal borings (upper arrows) in disintegrated bone associated with bone chip-filled burrow (lower arrow) just below. (D) Association of subhorizontal bone chip-filled burrow (arrow) with bored bone just above. (E) Curved oblique boring (arrow). (F) Subhorizontal borings (arrows). (G) Close view of F. (H) Subhorizontal boring (arrow) post-dating bone cracking. (I) Curved oblique boring (arrow) partially filled with bone chips. (J) Bone chip aggregate (arrow) occurring just above bored bone. (K) Subhorizontal borings (arrows). (L) Boring (arrow) with calcite rind in disintegrated bone.

cracks. The absence of cracks on the boring walls and the tapering of cracks into the boring walls suggest that the borings post-dated cracks. Apertures of some borings are present out of the bone surface. In the transverse section, borings are circular, and in the longitudinal section are generally straight to curved. The diameters of borings vary from a few millimeters to 1 cm. One boring shows a diameter increase from 5 mm within the compact surface bone to 7 mm within the internal disintegrated bone. The total length of boring is unknown because most borings are observed in section. Borings were filled with silty mudstone, micrite, and bone chips. Bone chips are generally scattered within borings, but in some borings bone chips are concentrated in terminal parts (Fig. 3I). A tear-shaped pore (0.6 mm in diameter) with a micrite wall occurs in internal disintegrated bone, and is filled with microspar. It seems to be a cast of larval case. Irregular aggregates of bone chips are present just above the bone surface (Fig. 3J).

It is unique that burrows, which are selectively filled with bone chips, occur sporadically just below (within 10 cm) the scapula (Fig. 4). Such bone chip-filled burrows also occur just above the scapula in places. Bone chips decrease away from the scapula, and are rarely present in host silty mudstone (Fig. 5). Accordingly, burrows occurring in lower reddish-brown silty mudstone are rarely filled with bone chips and non-calcified, whereas burrows just below the scapula are commonly filled with bone chips and generally calcified. Some burrows are isolated (Fig. 5), and some are clustered (Fig. 6). As in bone boring, burrow direction

Fig. 4. (A) Bone chip-filled burrows (arrows) occurring just below Dapyeongri bored bone. (B, C) Close views of the burrows seen in A.

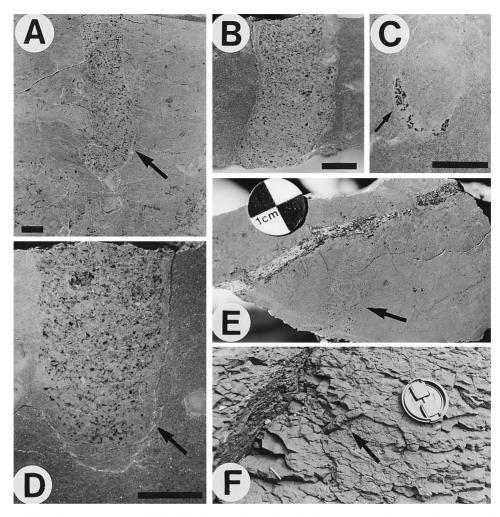


Fig. 5. (A-E) Solitary burrows (arrows) filled with dinosaur bone chips (dark spots) occurring around Dapyeongri bored bone (polished slabs). Scale bars are 5 mm. Bone chips are rare in surrounding sandy mudstone. Meniscate structures are slightly visible in B and D and in some burrows (C), bone chips are concentrated in the terminal part (arrow). In E, bone chip-filled burrow occurs just below weathered bone. (F) Burrow containing no bone chips. This burrow occurs away from the bored bone.

is also diverse from normal to oblique to horizontal to the bedding. Most burrows are non-tapering and cylindrical, except some smaller irregular burrows, and some burrows are curved. Branched burrows are not observed, but some burrows are intertwined to form networks (Fig. 6C–E). The diameters of most burrows are about 1 cm, although some are no more than a few millimeters. The burrow length is generally a few centimeters. In places, composite burrows are present; that is, smaller burrows penetrate the fills of larger burrows. The bone chips are common in larger burrows, whereas bone chips are rare or absent in secondary, smaller burrows. Meniscate filling formed in some of the horizontal and vertical burrows. The meniscate structure in vertical burrows shows concave downward lamination.

The bone chips in the burrow fills are fine- to coarse-grained sand (mostly medium) (Fig. 7). They are partially chloritized and microcracked as in above, in situ weathered scapula bone. The finer-grained components of the fills are composed of micrite and scattered quartz silts and fine sands. Circumgranular to curved cracks and fitted struc-

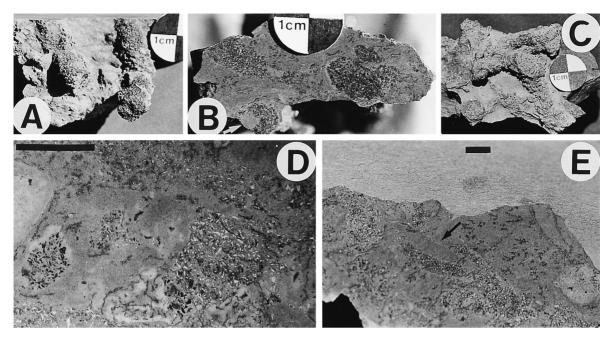


Fig. 6. Clusters of bone chip-filled burrows. Scale bars in D and E are 5 mm. (A) Closely spaced subvertical burrows. (B) Horizontal section of A, showing association of subhorizontal and subhorizontal burrows. Smaller burrow (arrow) containing no bone chips is visible in one burrow. (C–E) Intertwined burrows. Smaller burrow (arrow) cutting earlier formed bone chip-filled burrow can be seen in E (polished slab).

ture of adjacent peloids are present in burrowinfilling micrite, indicating pedogenic origin. Such preferred calcretization in bone chip-filled burrows seems to have been attributed to their permeable textures during pedogenesis. Some burrows are distinctly lined and, in some cases, the lining consists of bone chips. Pedogenic calcite rinds (less than 1 mm to a few millimeters thick) occur around some burrows.

6. Discussion

The isolated occurrence of disarticulated and fragmented bones and teeth in Dapyeongri floodplain dinosaur deposits suggests that they were preserved after transportation from the site of death. The truncation of lower calcic paleosol, the association of pebbles with large bone (scapula) fragment, and partially graded occurrence of bone fragments suggest that the Dapyeongri bone fragments were deposited by floods. However, the lack of sorting of bone fragments and the position of large scapula in hydraulically incompatible muddy deposits are unusual for transported bone fragments. These features are possible if flooding occurred as mass flow and if the transported sediments consisted mainly of muds. But the lower stage of calcrete development, general upward decrease in paleosol development, and the occurrence of channel deposits just 2 m above the dinosaur deposits suggest that Dapyeongri bone deposits are proximal floodplain deposits. It is thus implausible that transported sediments were chiefly composed of muds. Moreover, the in situ weathering of bone prior to boring indicates that the bone fragments were not buried simultaneously by transported sediments. Rather, they were exposed after deposition for some period. Pebbles only occur near the scapula, and bone chips are not scattered throughout the deposits but are concentrated around only larger bone fragments (scapula and rib). In these respects, Dapyeongri bone fragments are not considered to have been hydraulically transported. They are deemed rather to be in situ remains.

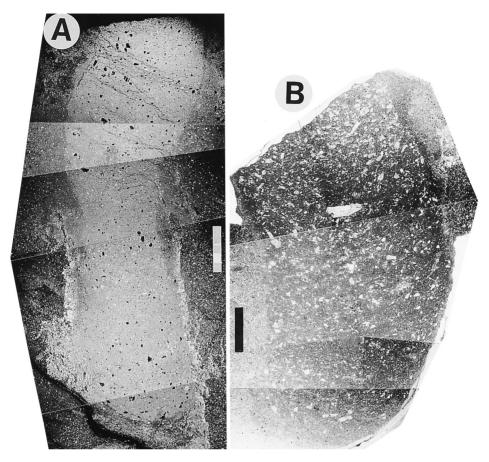


Fig. 7. Thin section photomicrographs of two bone chip-filled burrows under plane-polarized light (A) and plane light (B), showing variation in density of bone chip filling. Scale bars = 2.5 mm.

The occurrence of Dapyeongri bone deposits in vertic-calcic paleosol indicates that the paleoclimate of Dapyeongri floodplain was arid and seasonal (alternating wet and dry periods). Such conditions are similar to those of the dinosaur deposits of Upper Cretaceous Two Medicine Formation (Rogers, 1990), in which borings in dinosaur bones were documented (Rogers, 1992). Rogers (1992) suggested that the presence of bored bones reflects the activity of carrion beetles and a subaerial depositional setting wherein dinosaur carcasses were susceptible to desiccation. The borings cut across bone cracks, and disintegrated bones produced by in situ weathering indicate that Dapyeongri bone borers preferred to feed upon dried skeletons. Considering that dermestid beetles are the most common carrion insects inhabiting vertebrate carcasses in dry decay stage (Bornemissza, 1957; Goff, 1993; Moon and Moon, 1997), it is suggested that they are the most likely organism for Dapyeongri bone borers. The oldest fossil record of dermestid beetles has been reported from the Lower Cretaceous (Crowson, 1981). Thus, the traces of Dapyeongri bone borers support the existence of dermestid beetles during the Cretaceous, along with the similar bone borings documented from the Upper Cretaceous Two Medicine Formation (Rogers, 1992). The selective and ubiquitous occurrences of bone borings in scapula, not in small bone fragments, suggest that Dapyeongri bone borers also preferred large skeletons for feeding, as those of the Two Medicine Formation.

The intimate association of bone chip-filled

burrows with bored scapula, and similarities between burrows and borings with respect to diameter and bone chips, suggest that the producing organisms are the same and that bone chips within burrows originated from comminution by the bone borers. The limited occurrence of bone chips in burrows near bored scapula only, and the rare presence of bone chips in enclosing sediments, indicate that bone chips were transported by burrowers and not by flooding. It appears that nests were developed beneath bored bone, considering the presence of intricate networks and the localized occurrence of bone chip-filled burrows. The occurrence of smaller burrows within larger burrows indicates that smaller burrowers exploited the tunnels excavated by larger burrowers. Such behavior of Dapyeongri burrowers, in general, is similar to that of dung beetles from the Two Medicine Formation (Chin and Gill, 1996), except that they are associated with bored bone instead of dung pats and that infilling materials consist of bone chips instead of comminuted plant fragments. Thus, it seems that Dapyeongri beetles fed upon and gnawed dried bone and provisioned subterranean burrows with bone chips produced by boring, in the same way that dung beetles cache burrows with fecal materials transported from dung pats (Chin and Gill, 1996). However, it is uncertain whether the bone chips in burrows were utilized

for food, because extant carrion beetles usually do not eat bone chips.

Conclusively, these bone borings and bone chipfilled burrows indicate that the Dapyeongri dinosaur carcasses were exploited by carrion insects and provide evidence that dermestid beetles played an important role as the last scavenger of dinosaur carcasses during the Early Cretaceous. Such scavenging of carrion insects under dry climates may have a negative impact on the dinosaur fossil preservation. Dermestid beetles may have utilized desiccated dinosaur carcasses during dry seasons under arid and seasonal climate (this study and that of Rogers, 1992), whereas dung beetles utilized herbivorous dinosaur dung in rainy seasons under semi-arid/monsoonal climate (e.g. Upper Cretaceous Two Medicine Formation; Chin and Gill, 1996) (Fig. 8).

7. Conclusions

- 1. Borings in dried dinosaur bone, which are intimately associated with burrows filled with bone chips derived from the bored bone just above, are recognized in a Lower Cretaceous floodplain vertic-calcic paleosol, Dapyeongri, Korea.
- 2. The intimate association of bone chip-filled burrows and bored bone, along with similarities

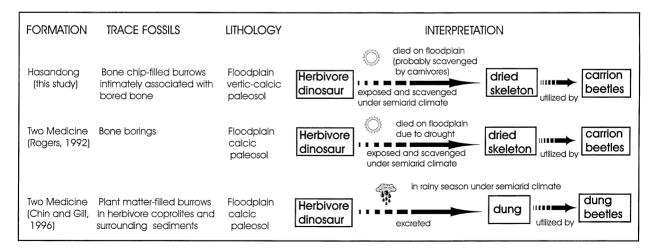


Fig. 8. Comparison of interpreted trophic interactions between dinosaurs and beetles in Cretaceous floodplain deposits.

in size and infills of in-borings and burrows, suggest that the burrowing and boring organisms were one and the same.

- Considering that they are the most common carrion insects inhabiting vertebrate carcasses in dry decay stage, dermestid beetles are the most likely producers of Dapyeongri bone borings and burrows.
- 4. The behavior of Dapyeongri bone borers/ burrowers is similar to that of dung beetles documented from the Upper Cretaceous Two Medicine Formation (Chin and Gill, 1996), which cache subterranean burrows with organic matter transported from the surface. These trace fossil associations provide additional evidence for Cretaceous trophic interaction between dinosaurs and insects.

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References

- Avanzini, M., Frisia, S., Van Den Driessche, K., Keppens, E., 1997. A dinosaur tracksite in an Early Liassic tidal flat in northern Italy: paleoenvironmental reconstruction from sedimentology and geochemistry. Palaios 12, 538–551.
- Bornemissza, G.F., 1957. An analysis of arthropod succession in carrion and the effect of its decomposition on the soil fauna. Austral. J. Zool. 5, 1–12.
- Chin, K., Gill, B.D., 1996. Dinosaurs, dung beetles, and conifers: participants in a Cretaceous food web. Palaios 11, 280–287.
- Choi, D.K., 1985. Spores and pollen from the Gyeongsang Supergroup, southeastern Korea and their chronologic and paleoecologic implications. J. Paleontol. Soc. Korea 1, 33–50.

- Choi, H.I., 1985. Sedimentology and its implication for stratigraphic classifications of the Cretaceous Gyeongsang Basin. J. Geol. Soc. Korea 21, 26–37.
- Crowson, R.A., 1981. The Biology of the Coleoptera. Academic Press, New York. 802 pp.
- Dodson, P., Behrensmeyer, A.K., Bakker, R.T., McIntosh, J.S., 1980. Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation. Paleobiology 6, 208–232.
- Doh, S.J., Hwang, C.S., Kim, K.H., 1994. A paleomagnetic study of sedimentary rocks from Kyeongsang Supergroup in Milyang Subbasin. J. Geol. Soc. Korea 30, 211–228.
- Fastovsky, D.E., Badamgarav, D., Ishimoto, H., Watabe, M., Weishampel, D.B., 1997. The paleoenvironments of Tugrikin–Shireh (Gobi Desert, Mongolia) and aspects of the taphonomy and paleoecology of Protoceraptos (Dinosauria: Ornithishichia). Palaios 12, 59–60.
- Goff, M.L., 1993. Estimation of postmortem interval using arthropod development and successional patterns. Forens. Sci. Rev. 5, 81–94.
- Graham, S.A., Hendrix, M.S., Barsbold, R., Badamgarav, D., Sjostrom, D., Kirschner, W., McIntosh, J., 1997. Stratigraphic occurrence, paleoenvironment, and description of the oldest known dinosaur (Late Jurassic) from Mongolia. Palaios 12, 292–297.
- Kim, I.S., Kang, H.C., Lee, H.K., 1993. Paleomagnetism of Early Cretaceous sedimentary rocks in Chingyo–Sachon area, southwestern Gyeongsang Basin. J. Kor. Inst. Min. Geol. 26, 519–539.
- Koster, E.H., 1987. Vertebrate taphonomy applied to the analysis of ancient fluvial systems. In: Ethridge, F.G., Flores, R.M., Harvey, M.D. (Eds.), Recent developments in fluvial sedimentology, SEPM Spec. Publ. 39, 159–168.
- Lee, Y.I., 1999. Stable isotopic composition of calcic paleosols of the Early Cretaceous Hasandong Formation, southeastern Korea. Palaeogeogr., Palaeoclimatol., Palaeoecol. 150, 123–133.
- Lee, G., Besse, J., Courtillot, V., 1987. Eastern Asia in the Cretaceous: new paleomagnetic data from south Korea and a new look at Chinese and Japanese data. J. Geophys. Res. 92, 3580–3596.
- Lee, Y.N., Yang, S.Y., Park, E.J., 1997. Sauropod dinosaur remains from the Gyeongsang Supergroup, Korea. In: Yang, S.Y., Huh, M., Lee, Y.N., Lockley, M. (Eds.), Uhangri Dinosaur Center and Theme Park in Korea, Paleontol. Soc. Korea, Spec. Publ. 2, 103–114.
- Mariott, S.B., Wright, V.P., 1993. Paleosols as indicators of geomorphic stability in two Old Red Sandstone alluvial suites, South Wales. J. Geol. Soc. London 150, 1109–1120.
- Moon, T.Y., Moon, G.J., 1997. Medicolegal entomology. Kosin J. Health Sci. 7, 33–52.
- Paik, I.S., 1998. Vertic paleosols from the Sindong Group: occurrences, paleoenvironments and stratigraphy. J. Geol. Soc. Korea 34, 58–72.
- Paik, I.S., Kim, J.Y., 1995. Calcareous paleosols from the upper Hasandong Formation in the vicinity of Jinju, Korea: implications in floodplain sedimentation and paleoclimate. J. Geol. Soc. Korea 31, 482–498.

- Paik, I.S., Kim, H.J., 1997. Paleoclimatic records of the Gyeongsang Supergroup. In: Woo, Y.K. (Ed.), Collected Monographs for Memory of Retirement of Professor Hee In Park, 111–118.
- Paik, I.S., Lee, Y.I., 1995. Short-term climatic changes recorded in Early Cretaceous floodbasin deposits, Korea. In: Chang, K.H. (Ed.), Environmental and Tectonic History of East and Southeast Asia with Emphasis on Cretaceous Correlation (IGCP 350), Proc. 15th Int. Symp. of Kyungpook National University, 395–417.
- Paik, I.S., Lee, Y.I., 1999. Desiccation cracks in vertic paleosols of the Cretaceous Hasandong Formation, Korea: genesis and paleoenvironmental implications. Sed. Geol. 119, 161–179.
- Paik, I.S., Lee, Y.I., Kim, H.J., 1998a. Dinosaur beds of the Gyeongsang Supergroup: taphonomy and paleoenvironments. J. Geol. Soc. Korea 34, 243–265.
- Paik, I.S., Lee, Y.I., Lee, Y.U., Cheong, D.K., Kimm, S.J., 1998b. Dinosaur beds in the Cretaceous Hasandong Formation in the vicinity of Jinju City, Gyeongnam, Korea. J. Paleont. Soc. Korea 14, 14–32.
- Retallack, G.J., 1997. Dinosaurs and dirt. In: Wolberg, D.L., Stump, E., Rosenberg, G.D. (Eds.), Dinofest Int., Proc. Symp., Arizona State University. The Academy of Natural Sciences, pp. 345–360.

Rogers, R.R., 1990. Taphonomy of three dinosaur bone beds

in the Upper Cretaceous Two Medicine Formation of northwestern Montana: evidence for drought-related mortality. Palaios 5, 394–413.

- Rogers, R.R., 1992. Non-marine borings in dinosaur bones from the Upper Cretaceous Two Medicine Formation, northwestern Montana. J. Vert. Paleontol. 12, 528–531.
- Seo, S.J., 1985. Lower Cretaceous geology and paleontology (Charophyta) of central Gyeongsang Basin, South Korea. Ph.D. Thesis, Kyungbuk National University, 177 pp. (unpublished).
- Smith, R.H.M., 1993. Vertebrate taphonomy of Late Permian floodplain deposits in the southwestern Karoo Basin of South Africa. Palaios 8, 45–67.
- Tedesco, L.P., 1997. Depositional sequences, paleoenvironmental setting and preservational potential: Lower Cretaceous Glen Rose Formation, central Texas. In: Wolberg, D.L., Stump, E., Rosenberg, G.D. (Eds.), Dinofest Int., Proc. Symp., Arizona State University. The Academy of Natural Sciences, pp. 361–376.
- Um, S.H., Choi, H.I., Son, J.D., Oh, J.H., Kwak, Y.H., Shin, S.C., Yun, H.S., 1983. Geological and geochemical studies on the Gyeongsang Supergroup in the Gyeongsang Basin. Korea Inst. Energ. Res. Bull. 36 124 pp.
- White, P.D., Fastovsky, D.E., Sheehan, P.M., 1998. Taphonomy and suggested structure of the dinosaurian assemblages of the Hell Creek Formation (Maastrichtian), eastern Montana and western North Dakota. Palaios 13, 41–50.