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Dinosaur egg deposits in the Cretaceous Gyeongsang Supergroup, Korea: Diversity and paleobiological implications

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ABSTRACT

The taphonomy and depositional environments of dinosaur-egg-bearing deposits in the Cretaceous Gyeongsang Basin, Korea, are described and their paleobiological implications are discussed in the context of global geographic occurrences, geological ages, paleoenvironments, and lithology. The general depositional environment of dinosaur egg deposits in the Gyeongsang Supergroup is interpreted as dry floodplains with a semi-arid climate and intermittent volcanic activity. The diverse floodplain paleoenvironments include fluvial plains with meandering rivers to alluvial plains with episodic sheet-flooding. Both global and Korean dinosaur-egg-bearing deposits are generally restricted to the Late Cretaceous, a phenomenon for which two possible explanations are proposed. The first possible explanation for the temporal limitation of dinosaur egg preservation involves the appearance of angiosperms in the Late Jurassic, the Late Cretaceous ecological dispersion of angiosperm trees into swamps and floodplains, and the attendant change in herbivorous dinosaurs' diets. The second possible reason is related to nesting behavior in the Cretaceous. By contrast to the temporally limited occurrence of dinosaur eggs, paleoenvironments of nesting areas are diverse, ranging from inland areas to coastal areas. These hypotheses may provide new directions for the study and understanding of dinosaur egg distribution in the context of geologic time.

1. Introduction

Dinosaur eggs have been documented from many countries in the world including China, Mongolia, India, Korea, USA, Canada, Argentina, Spain, Portugal, France, Romania, and South Africa and have been predominantly found in Upper Cretaceous deposits (Carpenter and Alf, 1994; Weishampel et al., 2004). Although most studies of dinosaur eggs have focused primarily on taxonomy, recent work on taphonomy and paleoenvironments of dinosaur-egg-bearing deposits has addressed their sedimentology (Tandon et al., 1995; Mohabey, 2001; Cojan et al., 2003; Chiappe et al., 2004; Paik et al., 2004; Van Itterbeeck et al., 2004, 2005; Therrien, 2005; Díaz-Molina et al., 2007; Saneyoshi et al., 2008; Kim et al., 2009; Liang et al., 2009; Grigorescue et al., 2010). Such studies have provided useful information about the habitats and behavior of dinosaurs.

Cretaceous continental deposits in South Korea contain diverse dinosaur fossils, among which dinosaur tracks are the most abundant (Huh et al., 2003). Dinosaur clutches have been documented from the Boseong (Huh and Zelenitsky, 2002), Sihwa (Lee et al., 2000), and Gurye (Lee, 2008b) areas, from paleoenvironments interpreted as distal alluvial fans (Boseong; Paik et al., 2004) and distal alluvial fans, braided streams, and floodplains (Sihwa; Kim et al., 2009). In addition to these areas, dinosaur eggs of a variety of ages are known from a range of locations in the Cretaceous Gyeongsang Basin (Yun and Yang, 1997; Yun et al., 2004; Paik et al., 2006b; Fig. 1). Nesting environments of dinosaurs that inhabited the Korean Peninsula during the Cretaceous were clearly diverse, and therefore improving the understanding of the paleoenvironments and taphonomy of these egg-bearing deposits will contribute significantly to global understanding of Cretaceous dinosaur paleoecology.

The objectives of this study are (1) to describe the sedimentology of the dinosaur-egg-bearing deposits in the Gyeongsang Basin; (2) to interpret the paleoenvironments and preservation of these deposits; and (3) to discuss the paleobiological implications of global and Korean dinosaur-egg-bearing deposits in terms of paleogeography, geological ages, and paleoenvironments.

2. Geological setting

A change in the subduction direction of the Paleo-Pacific (Izanagi) Plate to an orientation that was oblique to the East Asian continental margin in the Late Jurassic and Early Cretaceous

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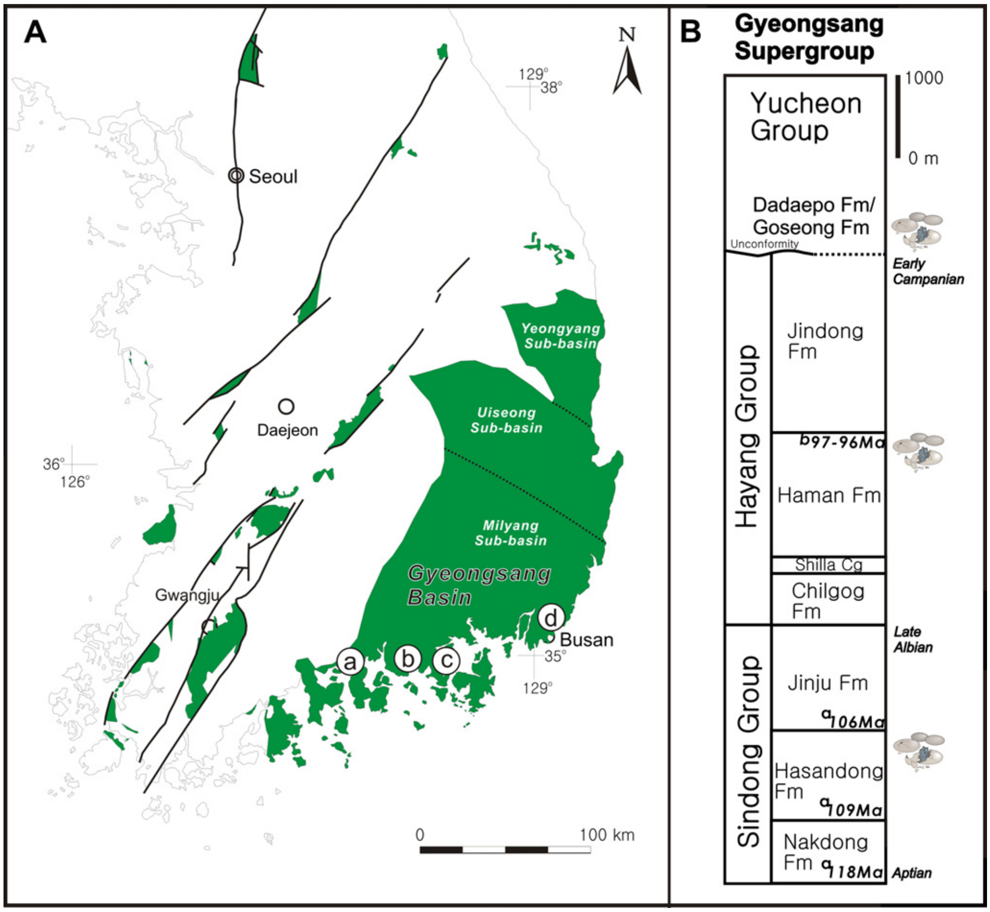

Fig. 1. (A) Cretaceous continental basins in southern Korea and location of dinosaur-egg-bearing deposits in the Gyeongsang Basin. (a) Hasandong egg deposits, Hadong County. (b) Haman egg deposits, Sacheon City. (c) Goseong egg deposits, Geoseong County. (d) Dadaepo egg deposits, Busan City. (B) Stratigraphy (Chang, 1975) and radiometric dates (a: Lee et al., 2010 and b: Jwa et al., 2009) for the Gyeongsang Supergroup.

(Maruyamat et al., 1997) created large-scale NE-trending left-lateral fault systems in the continental plate (Lee, 1999a; Okada, 1999, 2000), which resulted in the development of several continental pull-apart basins in what is now the Korean Peninsula (Lee, 1999b; Fig. 1). These epicontinental basins were filled with Early to Late Cretaceous alluvial to lacustrine deposits and material produced by local, intermittent volcanism.

The Gyeongsang Basin, the largest of these sedimentary basins, is located in the southeastern Korean Peninsula (Fig. 1). It formed in response to wrench-faulting associated with regional, north-trending, left-lateral simple shear due to the highly oblique subduction of the Izanagi Plate (Hwang et al., 2008). The Gyeongsang Basin covers about one quarter of South Korea and contains a 9000-m-thick succession of deposits assigned to the Gyeongsang Supergroup.

The Gyeonsang Basin is composed of three sub-basins that developed through syndepositional fault movement during deposition of the Hayang Group: from north to south, these are the Yeongyang, Euiseong, and Milyang sub-basins. The dinosaur-egg-bearing deposits examined in this study are from the Milyang sub-basin (Chang, 1975) which unconformably overlies pre-Cretaceous granitic rocks and Precambrian gneiss (Choi, 1985). The basin fill in the Milyang sub-basin is divided into four rock units: in chronological order, these are the Sindong, Hayang, and Yucheon groups, and the Bulguksa granites (Chang, 1975).

Dinosaur fossils are common in the Gyeongsang Supergroup. Dinosaur bones are most abundant in the Sindong Group (Paik et al., 1998, 2001), whereas most of the dinosaur eggs and trackways are in the Hayang and Yucheon groups (Huh et al., 2003; Paik et al., 2006a,b). Dinosaur eggs are most common in the fluvial Goseong Formation (Yucheon Group), but are also known from the Hasandong (Sindong Group), Haman (Hayang Group), and Dadaepo (Yucheon Group) formations, all of which are also of fluvial origin.

Depositional ages of the dinosaur-egg-bearing formations (Fig. 1) were determined by several means. The youngest detrital zircon age of the Hasandong Formation is 109 Ma (LA–ICP–MS U–Pb; Lee et al., 2008). Tuff deposits (Gusandong Tuff) intercalated with the uppermost part of the Haman Formation yielded an age of 96–97 Ma (LA–ICP–MS U–Pb zircon; Jwa et al., 2009). The Goseong Formation is Campanian to Maastrichtian on the basis of paleomagnetic data (Paik et al., 2006b). The minimum age of the underlying Hayang Group is Early Campanian (Lee et al., 2010), and the Dadaepo Formation is correlated with the Goseong Formation.

3. Dinosaur-egg-bearing deposits

3.1. Hasandong Formation

The Hasandong Formation consists of fluvial deposits with interlayered lacustrine deposits and is characterized by abundant intercalations of red to purple layers and common calcic and vertic paleosols (Paik, 1998; Paik and Lee, 1998). The formation contains sauropod dinosaur bones (Dong et al., 2001; Paik et al., 2001) and teeth of sauropods (Lee et al., 1997; Yun et al., 2007), ornithopods, and theropods (Paik et al., 1998; Lee, 2008a). Dinosaur bones are generally preserved in paleosols with calcic and vertic features, and some are preserved in calcrete nodules (Paik et al., 2001). Sparse sauropod tracks are also present (Yun and Yang, 1997). A unique example of dermestid borings in sauropod bone associated with bone-chip-filled burrows has been documented in floodplain deposits of the Hasandong Formation (Paik, 2000). Other fossils in this formation include crocodile (Yun et al., 2007), turtle, fish, pelecypod, and gastropod remains (Yun and Yang, 2001; Yun et al., 2005).

Although dinosaur bones are present throughout the Hasandong Formation (Paik et al., 1998, 2001), dinosaur eggs are known from only two levels in the formation (Yun and Yang, 1997). The occurrences of eggshell-bearing deposits could be observed only in the second level which is about 17.5 m above the first level (Yun and Yang, 1997), since the record of the first level was excavated. A partially preserved clutch of six or seven fragmented ornithopod eggs, in which two or three eggs have the egg morphology, was discovered in distal floodplain deposits of the upper part of the Hasandong Formation at Sumunri, Hadong County (Yun and Yang, 1997). The upper part of the Hasandong Formation consists predominantly of meandering channel and interchannel deposits (Paik and Kim, 1995; Paik and Lee, 1998). The eggs are of the angustispherulitic morphotype, are classified as ovaloolithidae (Mikhailov, 1991) and would have been 69–89 mm in diameter (Yun and Yang, 1997). The eggs are from a greenish-gray sandy mudstone representing a calcic paleosol at stage 3 of development (Machette, 1985; Fig. 2). It is inferred that the eggs were hatched and that the fragmented shells were then preserved *in situ* by calcareous pedogenesis. The eggs are 50 cm below the interface between a calcic paleosol and an overlying vertic paleosol (Fig. 2). Bivalve fragments are associated with the egg deposit, and dinosaur bone fragments are present in channel and floodplain deposits a few tens of meters above the egg deposit (Paik et al., 1998). Composite calcic paleosols and thin layers of calcrete-intraclast conglomerate are interlayered with strata below the egg deposits.

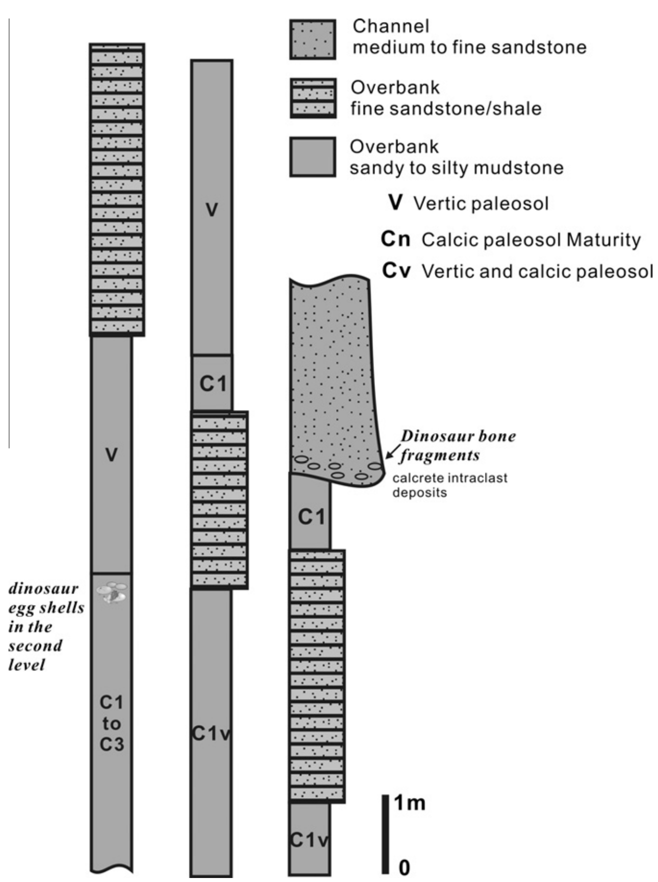

Fig. 2. Stratigraphic sections of dinosaur-egg-bearing deposits (second level) in the Hasandong Formation at Sumunri, Hadong County.

The overall paleoenvironmental setting of the Hasandong nesting site can be envisaged as a distal floodplain with meandering rivers and floodplain lakes considering the common development of calcic paleosols (Fig. 2). The association of vertic paleosols (Fig. 2) also suggests that the climate was semi-arid, with seasonal alternation of wetting and drying. A dry woodland associated with the Hasandong floodplain (Lee, 1999b) was inhabited by sauropods, ornithopods, and theropods, and crocodiles, turtles, fish, and mollusks lived in the aquatic environments.

3.2. Haman Formation

The Haman Formation is characterized by abundant red to purple layers and consists of tabular sandstone layers with thin mudstone interlayers deposited by sheet-floods on an alluvial plain. Lake-margin deposits are present in the uppermost part of the Haman Formation, and minor tuffaceous deposits are locally present. Desiccation cracks and ripple marks are common in these sheet-flood deposits. The Haman Formation contains tracks of sauropods and ornithopods, bird tracks (including the oldest known webbed tracks), and pterosaur tracks (Kim, 1969; Baek and Yang, 1998; Kim et al., 2006; Kim et al., 2012a,b). Impressions of dinosaur skin have also been documented from the Haman Formation (Kim et al., 2010; Paik et al., 2010).

The upper part of the Haman Formation along the coast of Sinsudo Island in Samcheonpo contains dinosaur eggs (Fig. 3A). The 10 dinosaur eggs are spherical to subspherical, and 80–150 mm long. They are filispherulitic in morphotype and classified as faveoloolithid (Yun et al., 2004). The eggs are fragmented and preserved as a partial clutch (Fig. 3B and C). The egg-bearing deposit is in alluvial plain deposits consisting of thin- to thick-bedded tabular tuffaceous sandstone and mudstone deposited by episodic flooding (Fig. 3). *In situ* calcified gymnosperm wood and reworked wood fragments are locally present in the fine-grained layers. The mudstones contain ornithopod footprints (Fig. 3D), and pedogenic calcrete nodules at stages 2–3 of development (Machette, 1985) are present in some of the mudstone layers. The egg deposit is in a thick bed of tuffaceous, medium- to fine-grained sandstone (Fig. 3E). The eggs are in the middle of the bed, and calcified gymnosperm wood fragments are present in the upper part of the bed (Fig. 3F). Massive tuff deposits (Fig. 3G) and shaly lacustrine deposits overlie the egg-bearing unit (So et al., 2007).

The presence of the Haman eggs as a partial clutch indicates that they were preserved *in situ*. The general paleoenvironmental setting of the Haman nesting site is interpreted as a dry alluvial plain with intermittent sheet-flooding under a semi-arid climate affected by volcanic activity and the local growth of gymnosperm trees (Chough and Sohn, 2010; Kim et al., 2011).

3.3. Goseong Formation

The Goseong Formation is characterized by common tuffaceous deposits and red beds, and is divided into lower, middle, and upper parts. The lower part consists mainly of greenish-gray to variegated, tuffaceous, pebble-bearing sandstone, greenish-gray to purple mudstone, and tuff. The middle part consists predominantly of redbeds containing rare dinosaur and turtle eggs, and an upper part composed of purple to greenish-gray sandstone and mudstone with tuff intercalations. The paleoenvironmental change from the underlying Jindong Formation, in which dinosaur tracks are abundant, to the Goseong Formation records the transition from

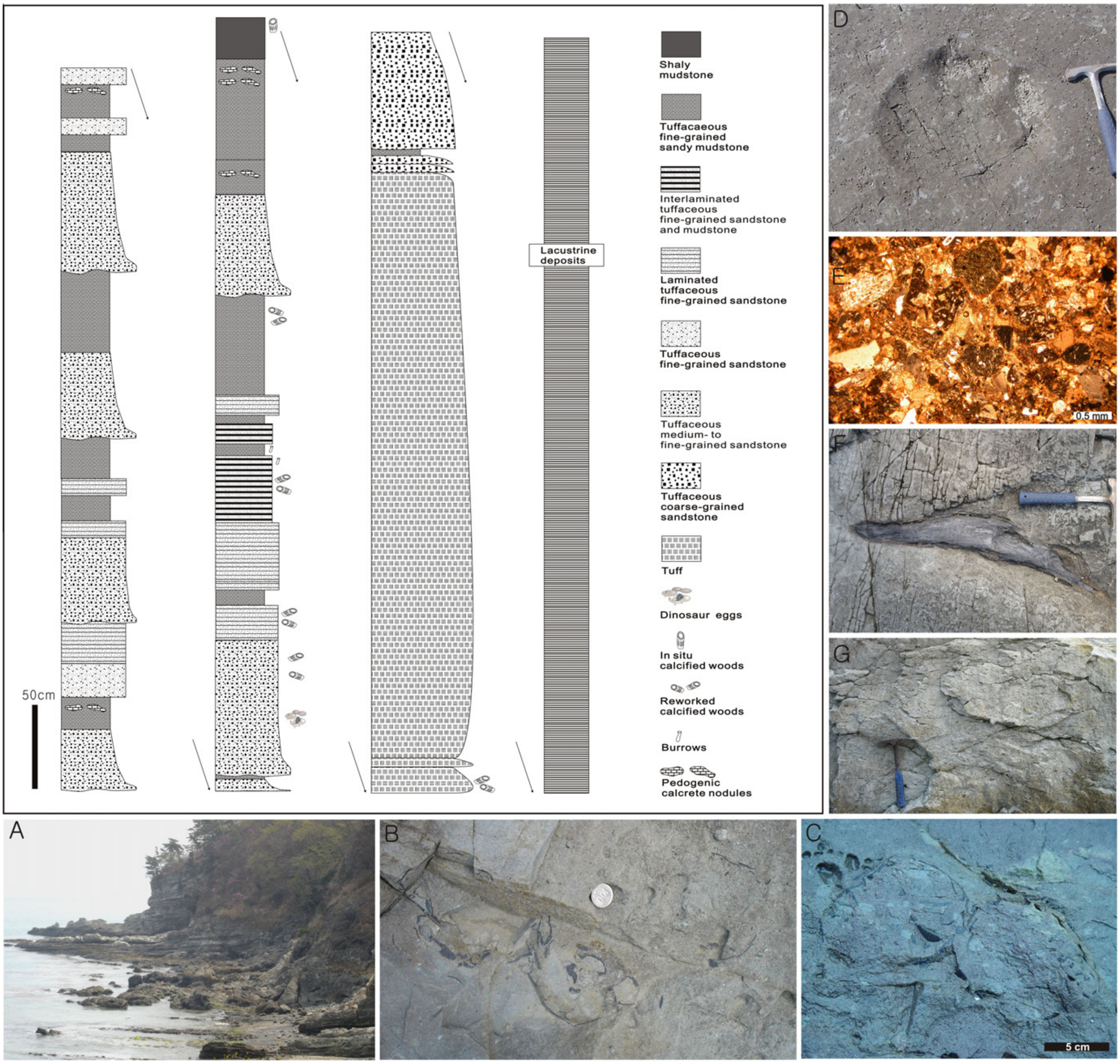

Fig. 3. Stratigraphic sections and occurrences of dinosaur-egg-bearing deposits in the Haman Formation at Sinsudo Island, Sacheon City. (A) Overall view of the outcrops exposed along rocky coast. (B and C) Partial clutches of dinosaur eggs in tuffaceous sandstone. (D) Ornithopod footprint preserved in mudstone. (E) Thin section photomicrograph of the tuffaceous sandstone. (F) Calcified wood fragment associated with a dinosaur egg bed. (G) Acidic tuff bed.

an under-filled lake basin to an over-filled lake basin associated with fluvial environments (Paik et al., 2006b).

Dinosaur eggs are known from five locations in the Goseong Formation, and turtle eggs from one location (Yang et al., 2006). The dinosaur eggs are prolatospherulitic in morphotype, are classified as spheroolithidae (Huh et al., 2006), and are considered to be affiliated with ornithopods. Jaw fragments containing partial ornithopod teeth have been recovered from this formation (Paik et al., 2009).

3.3.1. Site 1

Site 1 is composed of alternating coarse- and fine-grained beds (Figs. 4 and 5A). The coarse-grained beds are generally less than 1 m thick and include tuffaceous sandstone and calclithitic sandstone. The fine-grained beds range from a few decimeters thick to over 1 m thick, and consist of sandy mudstone, sandy shale, and cherty mudstone. The sandstone beds commonly have erosive lower contacts and gradational upper contacts. U-shaped channel structures are present in the tuffaceous, pebble-bearing, coarse-grained sandstone, and concave and convex bedforms are present in some sandstone beds. The calclithitic mudstone beds are generally reddish and contain pedogenic calcrete nodules (Fig. 5B), lenses, or beds. These deposits are interpreted as floodplain deposits with crevasse channel/splay deposits.

Dinosaur eggs are present at two horizons. The eggs in the lower horizon are preserved as isolated clusters of fragments in mudstone, with the fragments distributed subparallel to the bedding (Fig. 5C). Calcite films are present between the egg clusters and surrounding mudstone, and are associated with pedogenic calcrete nodules at stages 2–3 of development (Machette, 1985). The eggs

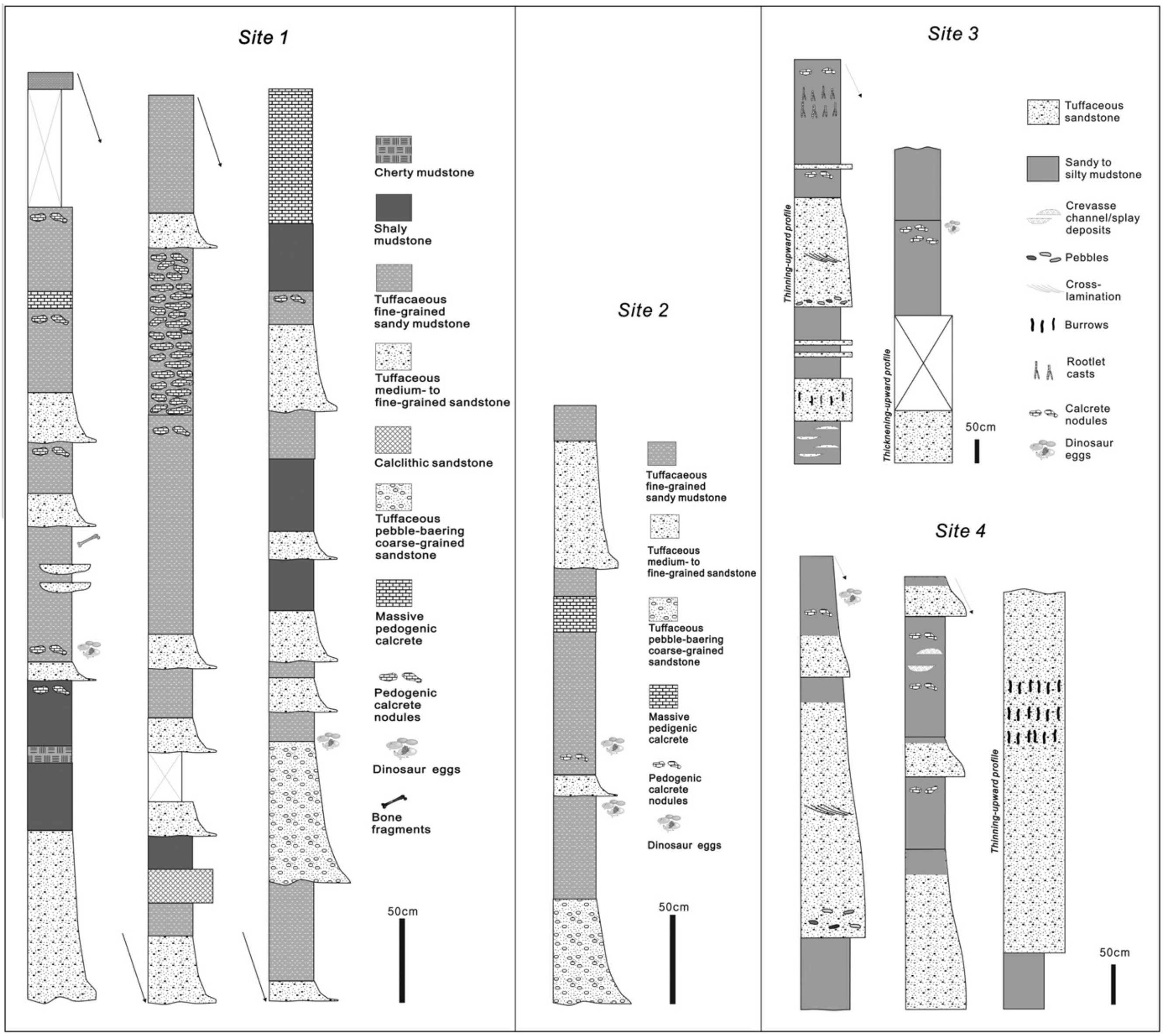

Fig. 4. Stratigraphic sections of dinosaur-egg-bearing deposits in the Goseong Formation, Goseong County.

in the upper horizon are between the sandstone and overlying mudstone. They are also fragmented and oriented subparallel to the bedding. Some fragments exhibit a circular to elliptical distribution in plan view (Fig. 5D).

3.3.2. Site 2

Site 2 deposits are a few decimeters above site 1 deposits based on measured sections, and consist of pebble-bearing tuffaceous channel sandstone and tuffaceous floodplain mudstone with scattered and coalesced pedogenic calcrete at stages 2–3 of development (Machette, 1985). Dinosaur eggs are at two levels in a mudstone layer (Figs. 4 and 5E). In the lower level, two topless eggs, which may represent hatched eggs, are exposed and form a partial clutch (Fig. 5F). In the upper layer, one egg is exposed.

3.3.3. Site 3

At site 3, strata consist of interlayered tuffaceous sandstone and sandy to silty mudstone (Fig. 4). The sandstone consists of meandering channel deposits with thinning-upward patterns and crevasse channel/splay deposits. The channel deposits are over 2 m thick and fine upward (Fig. 6A). Some of the crevasse channel/splay deposits have a thickening-upward pattern, and some form lenses. The red and green mudstone layers are floodplain deposits with pedogenic calcrete nodules and pedotubules at stages 2–3 of development (Machette, 1985; Fig. 6B). Dinosaur eggs are present in greenish-gray calcareous mudstone as a partially arranged clutch (Fig. 6C). The eggs are topless, and calcite films 1–2 mm thick are present along the eggshells.

3.3.4. Site 4

Site 4 strata consist of tuffaceous meandering channel and crevasse/splay sandstones and sandy to silty floodplain mudstones (Fig. 4). The channel sandstone beds are up to 5 m thick, exhibit thinning- and fining-upward patterns (Fig. 6D), are planar- to cross-laminated in their centers, and locally contain trace fossils. The mudstone is calcareous and has pedogenic calcrete nodules at stage 2 of development (Machette, 1985). Dinosaur eggs are present in greenish-gray mudstone. The eggs occur as a clutch, but are not arranged (Fig. 6E). Turtle eggs are also present in floodplain mudstone of the Goseong Formation and are associated with

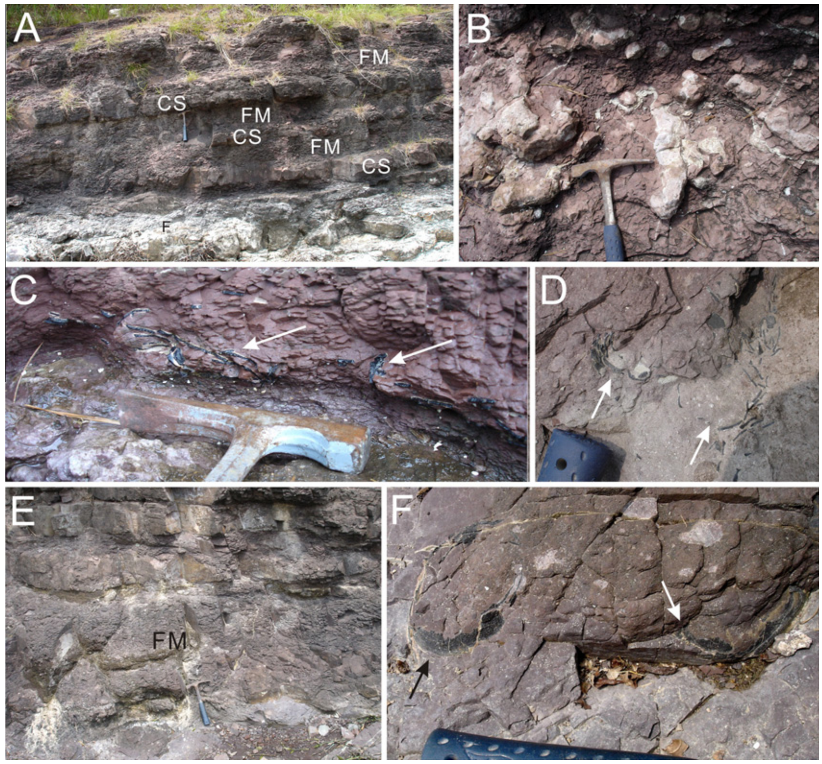

Fig. 5. Dinosaur-egg-bearing deposits at sites 1 (A–C) and 2 (D–F) in the Goseong Formation. (A) Dinosaur-egg-bearing overbank deposits consisting of floodplain sandy mudstone (FM) and crevasse splay fine-grained sandstone (CS). (B) Pedogenic nodular calcretes in floodplain mudstone. (C) Dinosaur eggshell fragments (arrows) in floodplain mudstone. (D) Partial clutch of dinosaur eggs (arrows) in floodplain mudstone. (E) Dinosaur-egg-bearing floodplain mudstone (FM). (F) Partial clutch of dinosaur eggs (arrows) in floodplain mudstone.

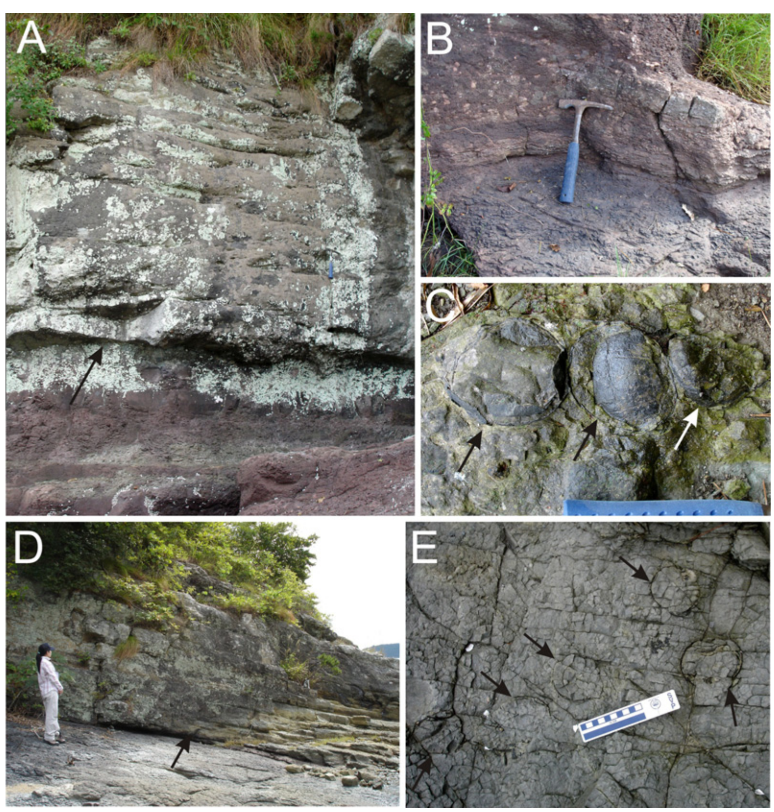

Fig. 6. Dinosaur-egg-bearing deposits at sites 3 (A–C) and 4 (D–E) in the Goseong Formation. (A) Thinning-upward point-bar deposits (upper part) (arrow) associated with dinosaur-egg-bearing deposits. (B) Floodplain mudstone associated with pedogenic nodular calcretes. (C) Partial clutch of dinosaur eggs (arrows) in floodplain mudstone. (D) Channel sandstone beds (upper part) (arrow) overlie floodplain mudstone (lower part). (E) Partial clutch of dinosaur eggs in floodplain mudstone.

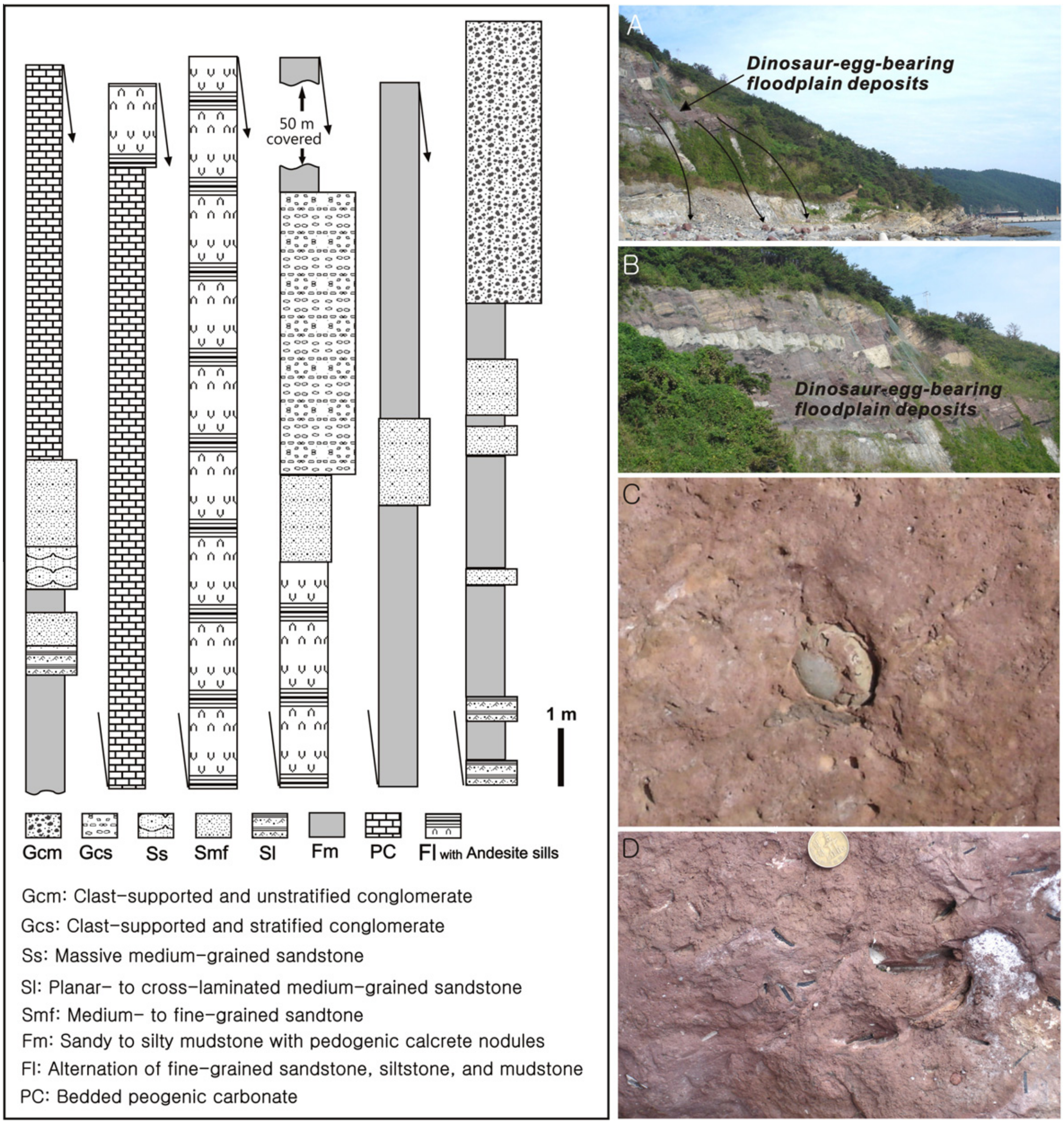

Fig. 7. Stratigraphic sections and occurrences of dinosaur-egg-bearing deposits in the Dadaepo Formation at Busan City. (A) Overall view of the outcrops exposed along the rocky coast. Dinosaur eggs and shell fragments in rocks that have fallen from the floodplain deposits (arrows) in a coastal cliff. (B) Dinosaur-egg-bearing floodplain deposits. (C) Oval dinosaur egg preserved in floodplain mudstone with calcic paleosol. (D) Reworked eggshell fragments in floodplain mudstone with calcic paleosol.

pedogenic calcrete. The arrangement of dinosaur eggs in clutches indicates that they were preserved *in situ*. The overall paleoenvironmental setting of the Goseong Formation nesting sites is interpreted as a dry floodplain with meandering channels that accumulated under semi-arid conditions with intermittent volcanic activity.

3.4. Dadaepo Formation

The Dadaepo Formation consists of alluvial fan, fluvial, and floodplain lake deposits, composed of channel conglomerate and sandstone, floodplain mudstone, and lacustrine shale and mudstone (Fig. 7). The sandstone and mudstone are locally tuffaceous or cherty. Pedogenic calcrete is common in the floodplain mudstone, and palustrine compound calcrete beds are present in the floodplain lake deposits. Dinosaur bone fragments have been reported from the conglomerates, and petrified wood from lake-margin deposits.

Dinosaur eggs were found in a block of reddish mudstone that had fallen from a coastal cliff consisting of fluvial deposits of conglomerate, sandstone, and mudstone (Fig. 7A and B). The conglomerate units are very thick-bedded to massive (amalgamated) and are clast-supported. They are unstratified or stratified, and the gravels are mostly epiclastic and well-rounded. The sandstone units are medium- to thick-bedded and fine- to medium-grained, with local bioturbation. The egg-bearing mudstone units generally contain pedogenic calcrete nodules at stages 2–3 of development (Machette, 1985), and pedogenic slickensides and trace fossils are locally present. Most of the eggs are preserved as fragments in clusters, although some isolated, elliptical eggs are present (Fig. 7C and D). Some of the egg fragments are encrusted by thin calcite layers. The eggs are ratite in morphotype and classified as elongatoolithidae. Alluvial plain and lake margin deposits underlie the egg-bearing fluvial deposits.

The preservation of eggs as fragments and isolated eggs indicates that they were transported, but the presence of eggshell

Locality	Formation	Age	Egg type	Lithology	Depositional environment	Paleoclimatic condition
Busan	Dadaepo	Upper Cretaceous	Elongatoolithid	Tuffaceous sandy mudstone (calcic paleosols) Tuffaceous fine-grained sandstone	Floodplain on alluvial plain	Semi-arid
Goseong	Goseong	Upper Cretaceous	Spheroolithid	Tuffaceous sandy mudstone (calcic paleosols) Tuffaceous medium- to fine-grained sandstone	Floodplain associated with meandering river	Semi-arid
Sacheon	Haman	Upper Cretaceous	Faveoloolithid	Tuffaceous sandy mudstone (calcic paleosols) Tuffaceous medium- to fine-grained sandstone	Floodplain on alluvial plain	Semi-arid
Hadong	Hasandong	Lower Cretaceous		Sandy mudstone (calcic paleosols)	Floodplain associated with meandering river	Semi-arid
Boseong (Paik et al., 2004)	Seonso Conglomerate	Upper Cretaceous	Faveoloothid Spheroolithid	Tuffaceous sandy mudstone (calcic paleosols)	Floodplain on alluvial fan	Semi-arid
Gurye (Lee, 2008b)	Geumnaeri	Upper Cretaceous		Tuffaceous sandy mudstone (calcic paleosols)	Floodplain on alluvial fan	Semi-arid
Shiwha (Kim et al., 2009)	Shiwha	Lower (?) Cretaceous	Faveoloothid Dendroolithid	Gravelly siltstone/sandstone Conglomerate	Channel Floodplain on alluvial fan	Semi-arid

Fig. 8. Summary of dinosaur-egg-bearing deposits in the Cretaceous continental basins in Korea.

fragments in the mudstone as clusters and the absence of any other size-equivalent clastic fragments with the egg fragments indicate that they were reworked near the nests. The eggs were probably preserved by calcareous pedogenesis. The presence of the egg deposits in floodplain mudstone with interlayered sheet sandstone units, and the absence of lenticular-bedded fining-upward sandstone patterns associated with the egg deposits suggest that the floodplain was not associated with meandering rivers but was instead dominated by episodic flooding. The tuffaceous sediment composition suggests that volcanic activity took place intermittently around the basin. The presence of vertic paleosol features in the Dadaepo egg deposits indicates that conditions alternated between dry and wet during deposition. The general paleoenvironmental setting of the Dadaepo nesting site is interpreted as a dry floodplain with episodic flooding under a semi-arid climate with intermittent volcanic activity and gymnosperm trees growing sparsely near small ponds.

Morphological features of the dinosaur eggs and the occurrences and paleoenvironmental setting of the dinosaur egg deposits in the Gyeongsang Basin (this study) and other Cretaceous continental basins in Korea are summarized in Fig. 8.

4. Variation and restricted occurrences of dinosaur-egg-bearing deposits and their paleobiological implications

Although diverse kinds of dinosaur eggs have been reported from many countries around the world (Carpenter and Alf, 1994; Weishampel et al., 2004) since the first discovery of dinosaur eggs in the Gobi Desert by Roy Chapman Andrews in 1923, the paleoenvironmental setting of dinosaur nesting areas was not well understood until the initiation of sedimentological and stratigraphic studies in the last two decades (Tandon et al., 1995; Varricchio et al., 1999; Lopez-Martinez et al., 2000; Mohabey, 2001; Cojan et al., 2003; Chiappe et al., 2004; Paik et al., 2004; Van Itterbeeck et al., 2004, 2005; Therrien, 2005; Sankey, 2005a,b; Díaz-Molina et al., 2007; Salgado et al., 2007; Saneyoshi et al., 2008; Fanti and Miyashita, 2009; Kim et al., 2009; Liang et al., 2009; Grigorescue et al., 2010). The geographic occurrences, depositional ages, paleoenvironments, and lithology of dinosaur-egg-bearing deposits documented from both previous studies and the present work (Fig. 9) are here summarized and analyzed from a paleobiological perspective.

Dinosaur eggs have been found worldwide except in Oceania and Antarctica. Their ages, however, are largely restricted to the Late Cretaceous, with the exception of occurrences in the Late Triassic in South America and the Jurassic in the USA, Europe, India, and South Africa (Hirsch et al., 1989; Weishampel et al., 2004; Reisz et al., 2005; Fig. 9). In Korea, dinosaur eggs have been found only in Cretaceous deposits (Fig. 9), even though both Jurassic (Daedong Group) and Cretaceous continental deposits are present.

Although dinosaur bones and tracks have been found globally in deposits of the entire Mesozoic Era, dinosaur eggs and clutches in Triassic, Jurassic, and even Early Cretaceous rocks are rare. It is not reasonable to presume that dinosaurs did not lay eggs in the Triassic and Jurassic periods, and it is improbable that the temporal restriction of dinosaur egg occurrences is a function of biased discoveries or reports. Instead, the temporally limited distribution of known dinosaur eggs is probably a function of preservational conditions.

The preservational conditions of dinosaur eggs can be considered in terms of physical, chemical, and biological aspects. The physical requirements for egg preservation can be dominated by depositional environments and the grain size of the sediment in which eggs are laid. Depositional environments of Cretaceous dinosaur nesting areas are diverse and include alluvial fan, fluvial plain, wetland margin, lake margin, eolian interdune, and littoral environments (Fig. 9). Sediment grain sizes of Cretaceous egg deposits vary from conglomerate and sandstone to mudstones (Fig. 9). The diversity of depositional conditions and sediment grain sizes associated with egg deposits is so broad that they cannot be the reason for temporal restriction of dinosaur egg preservation: similar alluvial and lacustrine deposits consisting of conglomerate, sandstone, and mudstone are also common in egg-poor Triassic and Jurassic stratigraphic successions.

The chemical conditions for egg preservation are related to mineral composition, pedogenesis, and diagenesis of egg deposits.

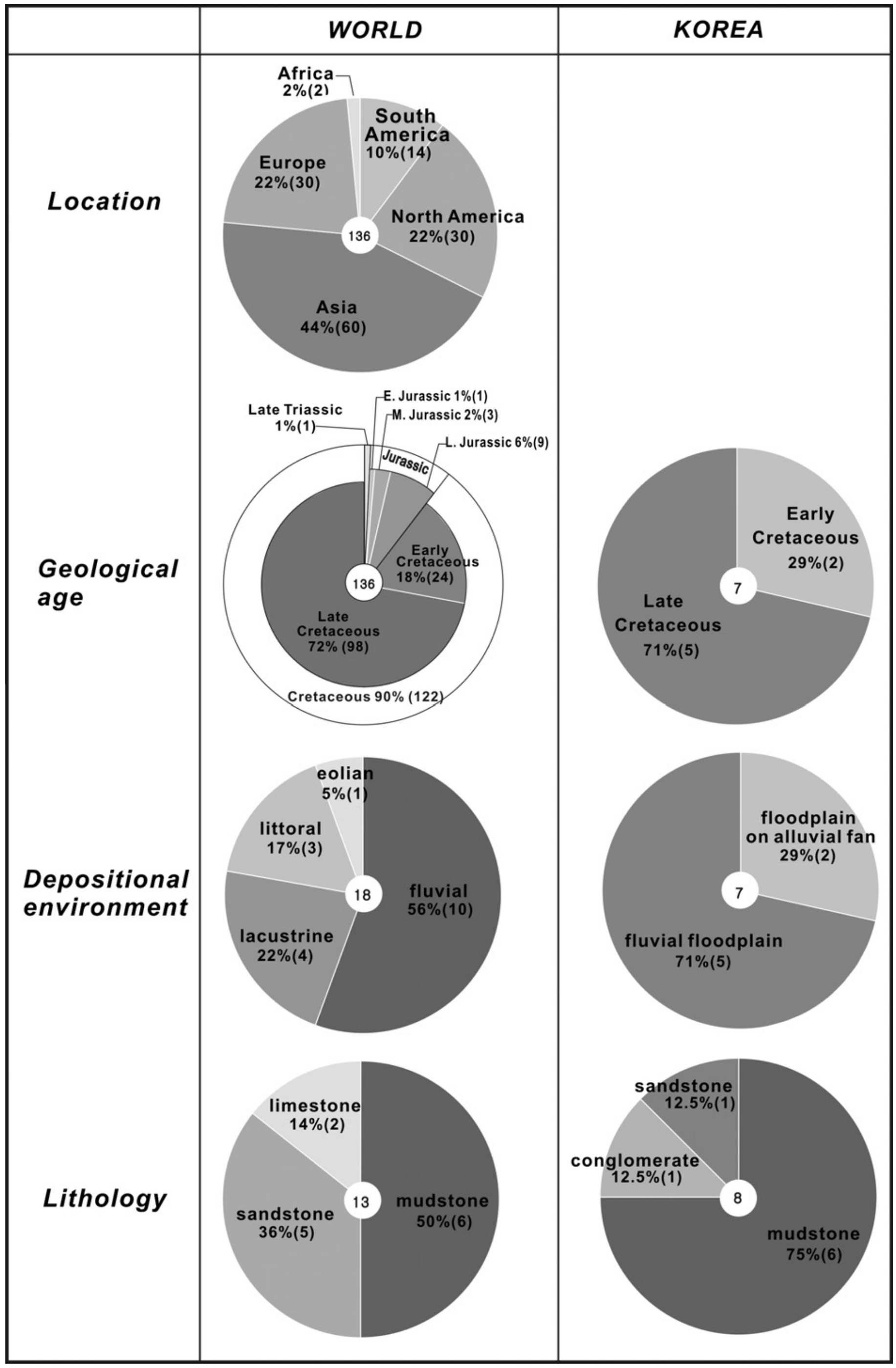

Fig. 9. Pie diagrams showing occurrences of dinosaur eggs in terms of location, geological age, depositional environment, and lithology. The data for location and geological age of global occurrences are from Weishampel et al. (2004). The data for depositional environment and lithology of global occurrences are from a limited literature of taphonomic and paleoenvironmental studies on dinosaur-egg-bearing deposits.

There is no one specific mineral composition or diagenetic feature that seems to be critical to the preservation of Cretaceous dinosaur eggs, although they are commonly associated with pedogenic calcrete that facilitated egg preservation (Varricchio et al., 1999; Paik et al., 2004; Therrien, 2005; Van Itterbeeck et al., 2004, 2005). The development of calcic paleosols is not restricted to the Cretaceous. Therefore, a specific chemical condition can be excluded as a probable cause for the temporally restricted occurrence of dinosaur eggs.

In the absence of obvious physical or chemical controls that limited the temporal distribution of dinosaur egg preservation, it is possible that specific biological conditions were required. The Late Jurassic appearance of angiosperms may be related to the restriction of dinosaur egg preservation to Cretaceous deposits. In the Triassic and Jurassic periods, gymnosperm tree forests were probably a major dinosaur habitat, and dinosaurs probably made nests there. Clutches and hatched eggs in forest areas would have had low preservation potential because forests are not generally

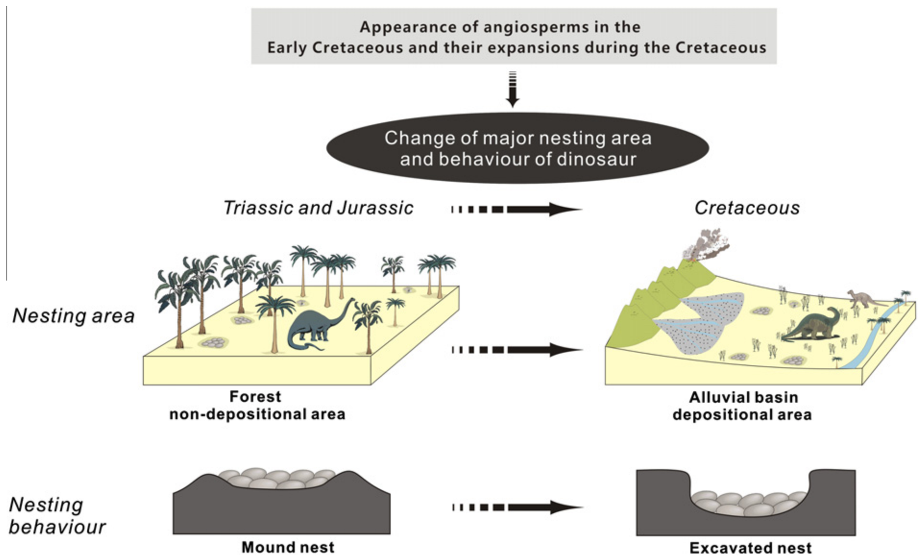

Fig. 10. Schematic diagram showing hypothetical causes of temporal restriction of dinosaur egg preservation in the (Late) Cretaceous.

associated with rapid burial due to flooding. In addition high organic content in forest areas resulting in low pH can be a negative condition for the preservation of eggs. The appearance of angiosperms in the Late Jurassic and their expansion throughout the Cretaceous may have changed dinosaur habitats. The Late Cretaceous spread of angiosperm trees through floodplains and swamps (Coiffard and Gomez, 2010) may have caused the expansion of dinosaur habitat from forest areas (non-depositional areas) to alluvial basins (depositional areas). The probable expansion of dinosaur habitat in the Cretaceous is supported by a demonstrated change in the diet of herbivorous dinosaurs during the Cretaceous, from gymnosperms to both gymnosperm and angiosperm vegetation (Ryan and Vickaryous, 1997).

The nesting behavior of dinosaurs may have contributed to the preservation of dinosaur eggs. In general, eggs laid in mound nests have little potential to be preserved *in situ* because the hatched eggs are exposed to scavenging and can be eroded and transported easily by flooding. In contrast, egg clutches or hatched eggs laid in excavated nests have higher potential to be preserved *in situ* by burial due to subsequent flooding. Little is known of the prevalence of mound nests in the Triassic and Jurassic periods. Excavated nests have been documented from some of the Late Cretaceous egg-bearing deposits (Cojan et al., 2003; Chiappe et al., 2004; Paik et al., 2004; Salgado et al., 2007), although mound nesting is also known from Late Cretaceous egg deposits of coastal plain settings (Lopez-Martinez et al., 2000).

Given that over 1000 dinosaur genera are known and that dinosaurs existed for about 170 million years, it is highly improbable that all of the Triassic and Jurassic dinosaurs had the same nesting behavior and that dinosaurs changed their nesting behavior from mound nesting to excavated nesting during the Cretaceous. Although excavated nesting is better than mound nesting from the perspective of egg taphonomy, dinosaur nest type cannot be the exclusive explanation for the temporally restricted distribution of dinosaur eggs in the Late Cretaceous. If biological conditions were in some way related to the temporal restriction of dinosaur egg distribution, the absence of dinosaur eggs in Australia could be attributed to the limited development of the Late Cretaceous continental deposits in Australia (Australia Department of National Development, 1966; Myers and Hocking, 1988).

Paleoenvironments of dinosaur nesting areas ranged from inland areas (alluvial fan, fluvial plain, desert, lake) to coastal areas (coastal plain, beach, lagoon; Fig. 9). The nesting environments of Korean Cretaceous dinosaurs also show variable settings, from alluvial fan areas to fluvial plain areas (Fig. 9). A diversity in dinosaur nesting environments may have mirrored the taxonomic diversity of dinosaurs, suggesting that dinosaurs avoided competition for nesting areas by exploiting a wide range of possible sites. The dominance of floodplains and lakes as dinosaur nesting areas in the Cretaceous (Fig. 9) suggests that the major habitat of dinosaurs in general was inland alluvial areas. The common development of paleosols with pedogenic calcrete in the dinosaur-egg-bearing deposits (Tandon et al., 1995; Varricchio et al., 1999; Paik et al., 2004; Van Itterbeeck et al., 2004, 2005; Therrien, 2005; Salgado et al., 2007) suggests that nesting areas were partially vegetated.

The variable host-rock lithology of Cretaceous dinosaur-egg-bearing deposits, from clastic mudstone, sandstone, and conglomerate to carbonate rocks (Fig. 9) suggests that Cretaceous dinosaurs exploited a range of sediment textures and compositions for their nesting, although fine-grained sediment is most common for egg-bearing deposits. The absence of marked lithologic change from nest-bearing deposits to overlying units indicates that dinosaurs preferred stable depositional environments for nesting.

5. Conclusions

1. Dinosaurs exploited the Gyeongsang Basin as nesting areas throughout the Cretaceous.
2. The general depositional environments of dinosaur egg deposits in the Gyeongsang Supergroup are interpreted as dry floodplains with episodic volcanic activity. The floodplains represent a variety of fluvial systems, from fluvial plains with meandering rivers (Hasandong and Goseong formations) to alluvial plains with episodic sheet-flooding (Haman and Dadaepo formations).
3. Dinosaur nesting areas in the Gyeongsang Basin were dominated by a semi-arid climate, which resulted in formation of calcic soils that facilitated preservation of dinosaur eggs.
4. Both global and Korean dinosaur-egg-bearing deposits are largely restricted to the Late Cretaceous. Based on the similar ranges of continental sedimentary depositional environments throughout the entire Mesozoic, biological conditions probably played a more important role in this temporal restriction than did physical or chemical conditions.

5. Two hypotheses are suggested for probable biological causes of the temporally restricted occurrence of dinosaur-egg-bearing deposits (Fig. 10). (A) The appearance of angiosperms in the Late Jurassic and their environmental dispersion through swamps and floodplains during the Late Cretaceous allowed a change in the diet of herbivorous dinosaurs. This phenomenon may have resulted in the expansion of dinosaurs' habitat from forests (non-depositional areas) to alluvial basins (depositional areas). Such an expansion of dinosaur habitat may have increased the preservational potential of clutches and hatched eggs because of the prevalence of rapid burial by flooding in alluvial environments. (2) A predominance of excavated nesting over mounded nesting in the Late Cretaceous may have enhanced the preservational potential of dinosaur eggs.
6. Although dinosaur egg distribution is temporally limited, the paleoenvironments in which they are preserved are diverse, ranging from inland areas (alluvial fan, fluvial plain, desert, lake) to coastal areas (coastal plain, beach, lagoon). This suggests the possibility that dinosaurs minimized competition for nesting areas by adopting more diverse nesting sites.
7. There is little change in lithology from nest-bearing deposits to overlying sediment, indicating that dinosaurs preferred stable sedimentary environments for their nesting sites.
8. Although these observations are not unequivocally tested in the present study, they should provide new ways to understand both the paleobiological significance of paleoenvironments and the temporal restriction in the occurrence of dinosaur eggs.

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