

Chelonian eggshells from the Lower Cretaceous Kuwajima Formation of the Tetori Group, Central Japan

SHINJI ISAJI¹, AI MATSUSHITA² AND REN HIRAYAMA³

¹Natural History Museum and Institute, Chiba, 955-2 Aoba-cho, Chuo-ku, Chiba 260-8682, Japan (e-mail: isaji@chiba-muse.or.jp)

²Faculty of Science, Toho University, 2-2-1 Miyama, Funabashi-shi, Chiba 274-8510, Japan

³School of International Liberal Studies, Waseda University, 1-17-14 Nishiwaseda, Shinjuku-ku, Tokyo 169-0051, Japan

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Abstract. Chelonian eggshell fossils from the Lower Cretaceous Kuwajima Formation of the Tetori Group are described. The eggs were originally spherical or ellipsoidal in shape. The eggshells consist of a single layer of spherulitic shell units composed of needle-like crystallites originating from a nucleation center. This corresponds to modern rigid-shelled chelonian eggs. The eggshell fragments are commonly found buried together and are known from deposits of subaerial environments, such as vegetated swamps. In contrast, the vast majority of turtle remains are known primarily from nearby shallow lake deposits, indicating that they are aquatic; no terrestrial turtles are known from this formation. These taphonomic settings suggest that the eggs were laid on land by lacustrine turtles in a process still apparent today.

Key words: chelonian eggshell, Kuwajima Formation, Tetori Group, Early Cretaceous

Introduction

Fossil eggshells of amniotic vertebrates have been found in deposits of various ages since the Late Triassic (Hirsch, 1989, 1994; Mikhailov *et al.*, 1996; Carpenter, 1999). The majority of fossil eggs found lack embryonic remains and therefore cannot be definitively correlated with a specific taxon (Mikhailov *et al.*, 1996). It is for this reason that the binomial nomenclature developed for ichnotaxa, as governed by the International Code of Zoological Nomenclature, was applied to fossil eggs by pioneering workers (e.g., Young, 1954, 1959, 1965; Zhao and Jaing, 1974; Zhao, 1975). This parataxonomic classification of fossil eggs has been enhanced by using ultrastructural observations of the crystallites composing eggshells. Erben (1970) was the first to provide an ultrastructural analysis of amniotic eggshells. Later, Mikhailov (1991) and Mikhailov *et al.* (1996) proposed a uniform method for description, and summarized the principles and application to fossil egg parataxonomy.

Studies of recent eggshells have revealed distinct taxonomic stability of structural types within large systematic groups of amniotes (e.g., Erben, 1970; Erben and Newesely, 1972; Ferguson, 1981, 1982; Hirsch, 1983; Hirsch and Packard, 1987; Hirsch and Bray, 1988; Mikhailov, 1987, 1991, 1995, 1997; Schleich and

Kästle, 1988). All members of each higher-level systematic taxon (e.g., Testudinata, Crocodylia, Squamata, and Aves) exhibit a unique basic type of eggshell structure (Hirsch, 1996; Mikhailov *et al.*, 1996). This stability enables us to make higher-level taxonomic assignments of fossil eggs based on shell structure to a certain degree.

Eggshell fossils are now known from the Lower Cretaceous Kuwajima Formation of the Tetori Group in Shiramine, Hakusan City, Ishikawa Prefecture. The horizon that contains eggshell fossils also yields a diverse vertebrate fauna, including fishes, anurans, turtles, choristoderes, lizards, pterosaurs, sauropods, nonavian theropods, hypsilophodontian-grade ornithopods, iguanodontids, birds, tritylodontid synapsids and mammals (for a taxonomical review, see Isaji *et al.*, 2005). Matsushita (2001) concluded that the eggshells can be classified into several types based on surface ornamentation and shell structure, one of which is identifiable as the Testudoid Basic Type established in the parataxonomic study of Hirsch (1996). Worldwide, a number of chelonian egg fossils have hitherto been reported from various deposits (e.g., Hirsch, 1983, 1996; Hirsch and Lopez-Jurado, 1987; Hirsch and Bray, 1988; Kohring, 1990; Fukuda and Obata, 1991; Joyce and Zelenitsky, 2002). However, their taphonomic settings are typically less well documented.

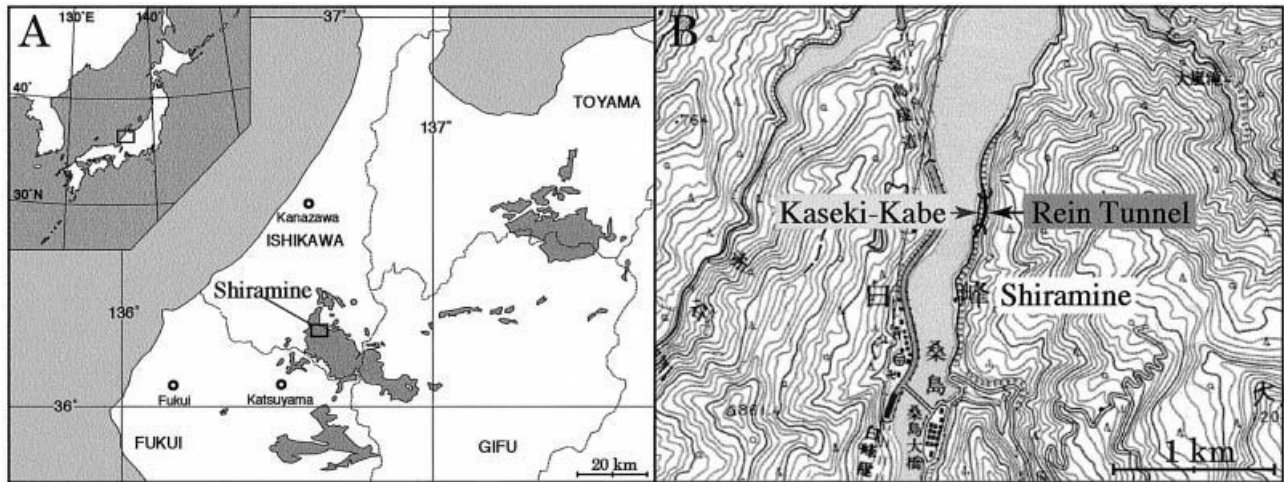


Figure 1. A. Map of north-central Honshu, Japan, showing the distribution of the Tetori Group (after Maeda, 1961). B. The Kaseki-Kabe and Rein Tunnel localities on 1:50,000-scale topographic map Quadrangle “Shiramine”.

We describe chelonian eggshell fossils from the Lower Cretaceous Kuwajima Formation of the Tetori Group, and also focus on the paleoautoecology of fossil turtles in relation to their mode of egg laying based on taphonomic settings.

Geological settings

The Tetori Group is widely distributed in central Honshu (Figure 1A). In the Shiramine area, the Tetori Group is divided into four formations: the Gomi-jima, Kuwajima, Akaiwa, and Kitadani formations in ascending order (Maeda, 1961). The Gomijima Formation consists mostly of conglomerates containing gravels derived from the basement Hida metamorphic rocks. The Kuwajima Formation is composed of a lower member of brackish muddy sandstones and an upper member of alternating beds of freshwater sandstones and mudstones. The Akaiwa Formation consists mostly of coarse-grained sandstones and contains interbedded conglomerates composed of orthoquartzites. The Kitadani Formation consists of alternating beds of mudstones and sandstones. The latter two formations also represent a variety of freshwater depositional environments.

All eggshell fossils were found from a locality known locally as Kaseki-Kabe (Figure 1B). The Kaseki-Kabe is placed stratigraphically in the uppermost part of the Kuwajima Formation. The Kaseki-Kabe locality is composed of alternating beds of fine-grained sandstones, mudstones, and thick coarse-grained sandstones. These beds represent a variety of depositional

environments on a floodplain. Three facies of bone-bearing beds (Facies I: Carbonaceous sandstones; Facies II: Dark grey fine-grained silty sandstones; Facies III: Dark greenish-grey mudstones) are present in the interchannel deposits of floodplain origin (Isaji *et al.*, 2005). Bone-bearing rocks were collected from the construction of a road tunnel (“Rein Tunnel” in Figure 1B) through the Kaseki-Kabe during 1997–2000. The detailed stratigraphical arrangement of the three facies is currently unknown, as they have not been studied *in situ* in the tunnel boring.

Numerous remains of aquatic life including charophytan zygotes, unionid bivalves, viviparid gastropods, ostracods, aquatic vertebrates such as fishes and chirostoderes, indicate that the Facies I and II were deposited in shallow lake environments. On the other hand, numerous *in situ* rootlets, terrestrial gastropods and vertebrates including lizards, tritylodontid synapsids and mammals indicate that the Facies III represents subaerial environments, probably vegetated swamps. As well preserved small bones occur in each facies, it is unlikely that selective dissolution of vertebrate skeletal remains took place, so this factor cannot account for the faunal differences observed. For detailed information about the fossil assemblages of each facies, see Figure 2 in Isaji *et al.* (2005).

At present, the Kuwajima Formation is assigned to the Neocomian on the basis of biostratigraphical correlations to the other nonmarine formations, most of which cannot be dated directly by reliable index fossils or radiometric analyses. Therefore, its precise age must be determined by future work. Speculations

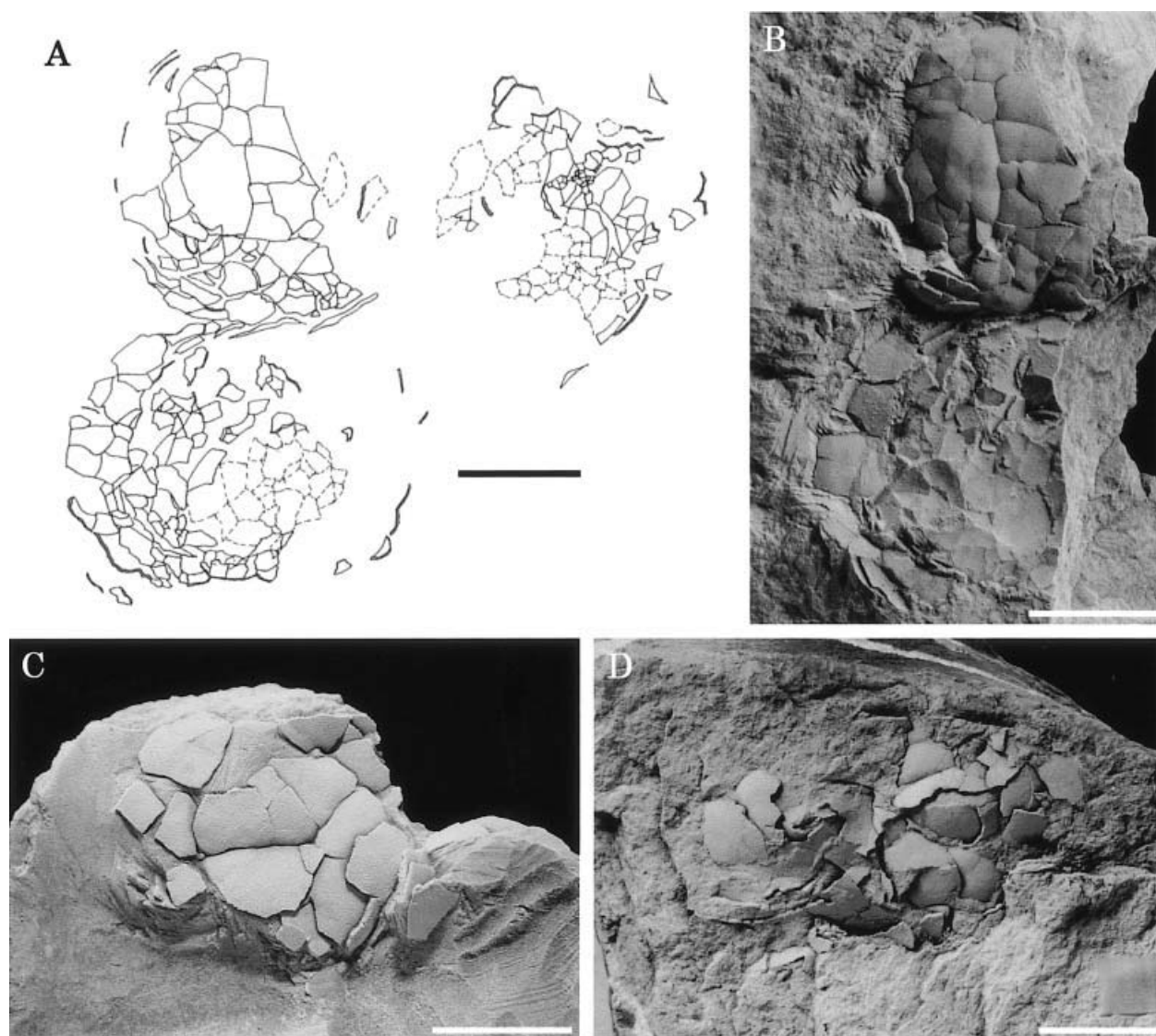


Figure 2. Modes of occurrence of eggshell fossils. **A.** Sketch of SBEI-288. Note three eggs buried together on the bedding plane. **B.** Two eggs left side as in A, another one is on the opposite side of the counterpart. **C.** A single egg (SBEI-2027). **D.** Concentrations of eggshell fragments of a single structural type (SBEI-885). Scale bars = 10 mm.

concerning the geologic age of the Kuwajima Formation and Tetori Group are given in Barrett *et al.* (2002), Tsubamoto *et al.* (2004), and Isaji *et al.* (2005).

Materials and methods

Eighteen specimens are known, 17 of which were found in the dark greenish-grey mudstones of Facies III. Only one fragment was found within the dark grey fine-grained silty sandstones of Facies II.

Observations were done within the general morphology: egg shape and size, surface ornamentation,

shell thickness, and histostructural features exposed in radial thin sections and on fractured surfaces. These are criteria for higher-level taxonomic assignments of eggshells (Mikhailov, 1991). Small pieces of eggshell fragments were embedded in epoxy resin and thin-sectioned for light and polarizing microscopy. To confirm the presence of aragonite, some thin sections were stained with manganese sulfate and silver sulfate by using the method of Friedman (1959). Fractured shell pieces were coated with platinum without any preparation, and the outer shell surface and internal shell structure were examined by scanning electron

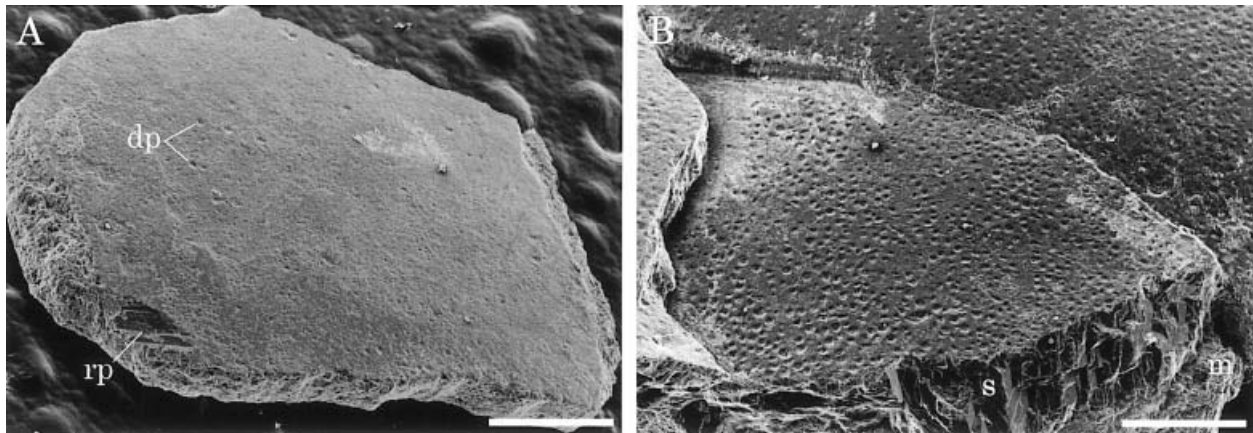


Figure 3. Outer shell surface of eggshell fossils. **A.** An isolated eggshell fragment (SBEI-290). **B.** Concentrated fragments covered by numerous secondary dissolution pits (SBEI-885). Scale bars = 500 μm . Abbreviations: dp, dissolution pit; m, matrix; rp, recrystallized part; s, shell

microscopy (HITACHI S-800). Secondary deposits could not be completely removed in all cases. Terminology used in this description is that of Hirsch (1996).

The specimens numbered with prefix SBEI are stored in the Shiramine Institute of Paleontology.

Description

Eggshells occur at Kaseki-Kabe in different taphonomical settings (Figure 2): some eggs buried together (Figures 2A, B), single egg (Figure 2C), concentrations of eggshell fragments of a single structural type (Figure 2D), and isolated eggshell fragments. Eggshell fragments are commonly found buried together, and isolated fragments are rare. Concentrations of fragments of mixed structural types are not found. No embryonic remains were found within any of the specimens.

All eggshells are black or dark brown in color, indicating that the original minerals have been diagenetically converted into other minerals. In fact, aragonite, which would be expected for chelonian eggshells (Hirsch, 1983), was not found in thin section by staining.

Although the eggshells have been compressed, their original shape and size can be established based on some specimens. One specimen (SBEI-288) contains three eggs buried together on the bedding plane (Figure 2A). The shapes of the compressed eggs are round or slightly elliptical, indicating that they were originally spherical or ellipsoidal in shape. The diameter of these egg fossils is about 25.0 to 27.5 mm.

The outer surface of the shell is smooth (Figure

3A). Occasional small depressions (diameter 28.5 to 38.0 μm) are found on the shell surface. They sometimes cover the whole shell surface of some specimens (Figure 3B). They are similar to the dissolution pits observed in the experimental study of avian eggshells buried in volcanic ash by Hayward *et al.* (1991). It seems that these depressions may have been formed secondarily as a result of the acidity of the encasing sediments. Differential preservation of eggshell surfaces may be attributable to local differences in pH through the taphonomic processes.

Shell thicknesses vary among the different fragments examined (Figure 4). Thinner ones (SBEI-274, 290) and thicker ones (SBEI-285, 288, 885) range in thickness from 200 to 250 μm and from 400 to 430 μm , respectively.

The eggshell microstructure is usually well preserved, although eggshells are subject to some diagenesis. Eggshell consists of a single layer of spherulitic shell units composed of needlelike crystallites originating from a nucleation center (Figures 4, 5). The shell units are about 165–185 μm wide and 220–250 μm high in SBEI-290, and about 195–215 μm wide and 400–430 μm high in SBEI-885. In thin sections, viewed under ordinary light, the radiating striations originating from the nucleation center of the shell unit are observable (Figures 4A, D). Under polarized light, the shell unit exhibits an incomplete extinction cross (Figures 4B, E). Different extinction patterns between SBEI-274 and SBEI-285 seem to be due to diagenetic alteration since the latter shows distinct cleavage in its inner and outer portions.

Under the SEM, the nucleation centers are clearly

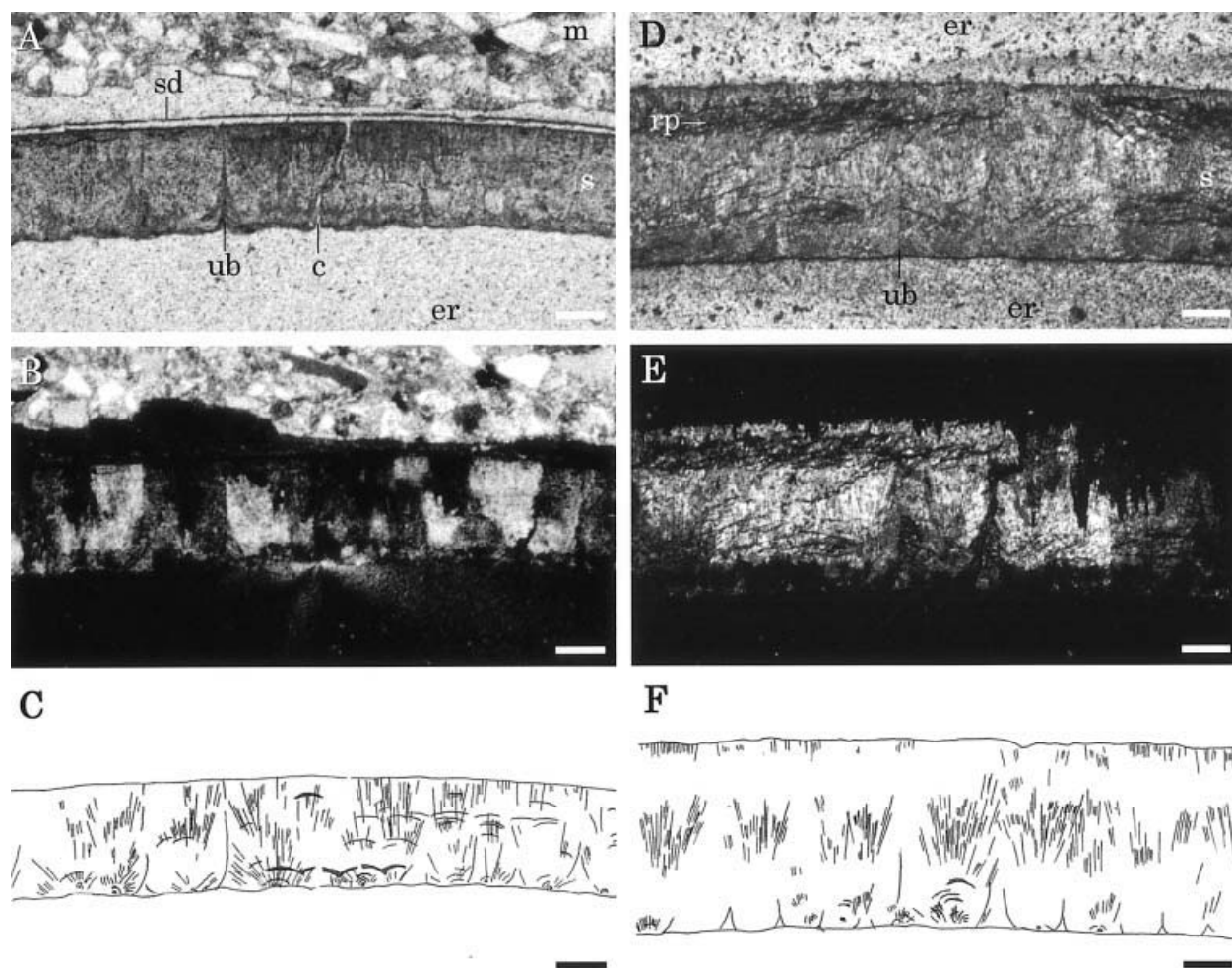


Figure 4. Radial thin sections of eggshell fossils. **A.** SBEI-274 viewed under ordinary light. **B.** Same as A, viewed under polarized light. **C.** Sketch of radiating striations of the shell unit based on A and B. **D.** SBEI-285 viewed under ordinary light. **E.** Same as D, viewed under polarized light. **F.** Sketch of radiating striations of the shell unit based on D and E. Outside of eggshell is up. Scale bars = 100 μm . Abbreviations: c, crack; er, epoxy resin; m, matrix; rp, recrystallized part; s, shell; sd, secondary deposit; ub, unit boundary

visible along fractured surfaces that traverse the center of the shell units (Figures 5A, D). Some nucleation centers are located as large holes (diameter about 50 μm) on the inner shell surface. This presumably resulted from diagenetic dissolution because the nucleation centers were originally filled with spherical organic cores (Hirsch, 1983; Schleich and Kästle, 1988). The lateral surface of the shell unit shows weak radiated striations or a granular appearance that appears to be the lateral terminations of needle-like crystallites (Figure 5B). Recrystallized parts are locally found and recognizable as large crystallites, which have a distinct cleavage surface (Figures 3A, 5). No pores were found in the fractured radial surface under the SEM. This indicates that the small depressions on the outer shell surface are not pore openings (Figure 3).

Discussion

Modern chelonian eggshells can be divided by physical properties into soft-, pliable-, and rigid-shelled eggs (Hirsch, 1983, 1996). Rigid-shelled eggs are composed of a well organized, thick, interlocking calcareous layer and a thin shell membrane; accordingly, they are well represented in the fossil record (Hirsch, 1983). Rigid-shelled chelonian eggs have been described as the Spherurigidis Morphotype of the Testudoid Basic Type by Hirsch (1996). The spherulitic shell units composed of radiating spicular crystallites observed in the eggshells of Kaseki-Kabe are typical for the Spherurigidis Morphotype.

Shell thickness varies among the different fragments examined in this study. It is well known that the thick-

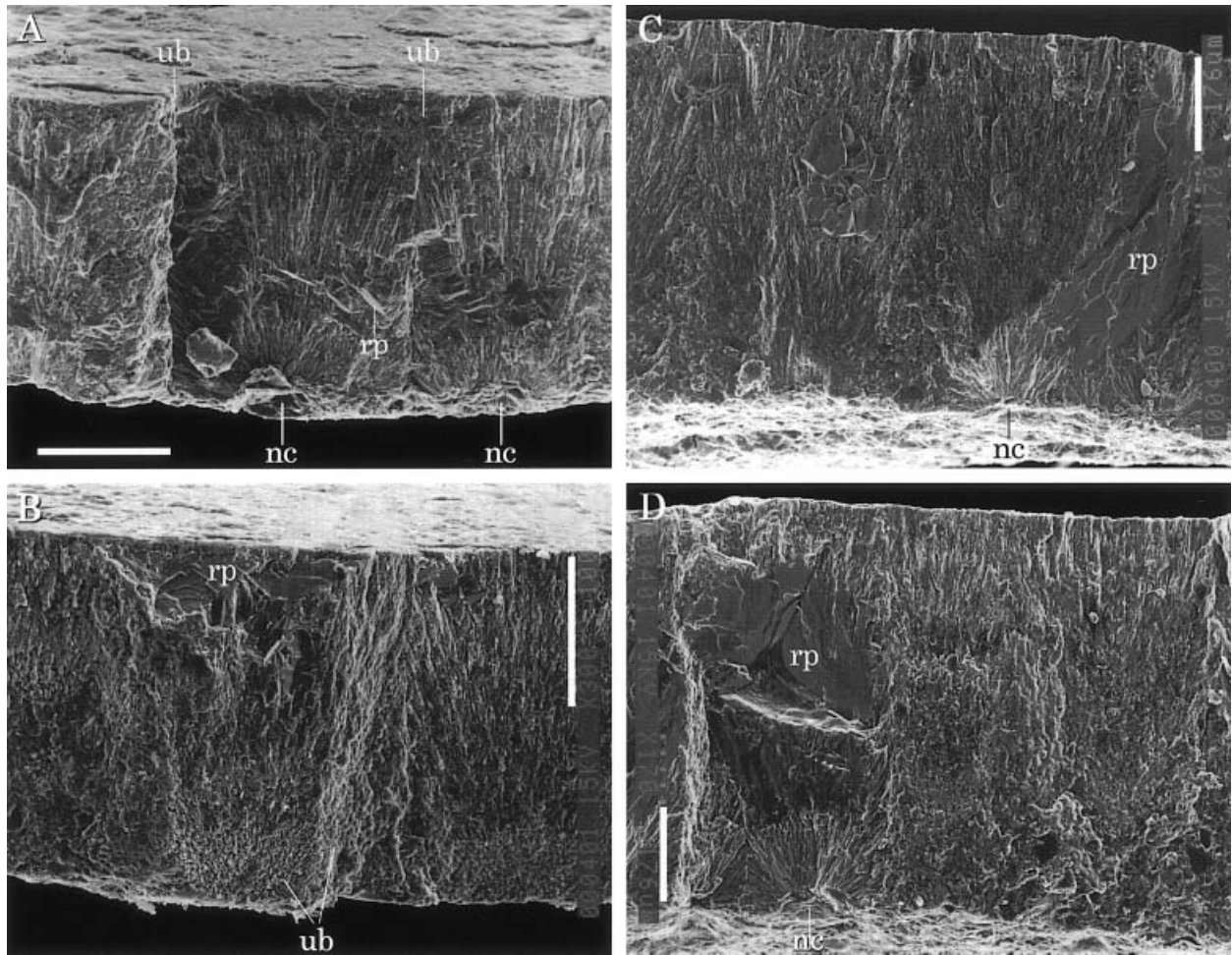


Figure 5. Fractured radial surface of eggshell fossils. **A, B.** SBEI-290. **C, D.** SBEI-885. Outside of eggshell is up. Scale bars = 100 μm . Abbreviations: nc, nucleation center; rp, recrystallized part; ub, unit boundary

ness of amniotic eggshells can vary in a single egg and may vary within a clutch or between various clutches of the same species (Mikhailov *et al.*, 1996). Therefore, it is unknown whether some differences recognized in chelonian eggshells examined are due to intraspecific or interspecific variations.

Depositional environments of the bone-bearing beds in the Kuwajima Formation are strongly correlated with the composition of their vertebrate fossil assemblages (Isaji *et al.*, 2005). For example, the lizards, tritylodonts and mammals, which appear to be reliable terrestrial animals, have been recovered from the vegetated swamp deposits, but they are extremely rare in the shallow lake deposits. On the contrary, the chelonian bones occur mainly in the shallow lake deposits, but they are rare in the vegetated swamp deposits, indicating that the turtles were lake inhabitants. The

fossil turtles are identifiable as three groups of cryptodiran turtles: Trionychoidea (in the sense of Trionychia by Meylan and Gaffney, 1989), Testudinoidea and Sinemydidae. Their limb morphology and their phylogenetic relationships also indicate that they appear to be aquatic (Hirayama, 2000).

In contrast, the chelonian eggshells are usually found in the vegetated swamp deposits of Kaseki-Kabe. Since the eggshell fragments are commonly found buried together and are composed of a single structural type, they appear not to have been transported for long distances from another depositional environment, and are regarded as parautochthonous remains. Egg clusters may be regarded as autochthonous remains, representing eggs buried in a nest (Figures 2A, B).

The maximum body sizes of the fossil turtles found

from Kaseki-Kabe are estimated to be less than 30 cm for Trionychoidea, 20 cm for Testudinoidea, 25 cm for Sinemydidae (Hirayama, 2000). Considering a relationship between the size of the extant turtles' body and their eggs (Ernst and Barbour, 1989), all three fossil turtles were capable of laying eggs of the size in question.

It appears reasonable to conclude that the eggs were laid in subaerial environments by aquatic turtles, although they cannot be linked to a specific taxon found from Kaseki-Kabe. This conclusion is consistent with observations of the nesting behavior of all recent freshwater cryptodiran turtles.

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