

## The first Mesozoic turtle from South Korea

Yuong-Nam Lee<sup>a,\*</sup>, J. Howard Hutchison<sup>b</sup>, Ki-Hong Chang<sup>c</sup>

<sup>a</sup> Geological Research Division, Korea Institute of Geoscience and Mineral Resources, Daejeon 305-350, Republic of Korea

<sup>b</sup> Museum of Paleontology, University of California, Berkeley, California 94720, USA

<sup>c</sup> Department of Geology, Kyungpook National University, Daegu 702-701, Republic of Korea

### ARTICLE INFO

#### Article history:

Received 17 April 2009

Accepted in revised form 9 July 2009

Available online 21 July 2009

#### Keywords:

*Kirgizemys*

“Macrobaenid” turtle

Geoncheonri Formation

Lower Cretaceous

Korea

### ABSTRACT

The partial carapace of a “macrobaenid” turtle from the Geoncheonri Formation (Lower Cretaceous) in Gyeongsan City near Daegu Metropolitan City, South Korea, is referred to *Kirgizemys* Nessov and Khozatzky, 1973. The specimen most closely resembles *K. exaratus* Nessov and Khozatzky, 1973 from the Albian of Kyrgyzstan. It is the first turtle fossil described from the Mesozoic sediments on the Korean peninsula.

© 2009 Elsevier Ltd. All rights reserved.

### 1. Introduction

Cretaceous vertebrate ichnocoenosis in South Korea is well known for its diversity and abundance. It includes various dinosaur footprints (Lee et al., 2001; Lee and Huh, 2002; Huh et al., 2003), avian ichnotaxa (Lockley et al., 1992; Yang et al., 1995; Kim et al., 2006), and pterosaur tracks (Hwang et al., 2002; Kim et al., 2006; Lee et al., 2008). Vertebrate body fossils are rare but they represent fishes (Lee, 1999), turtles, crocodylians (Yun et al., 2004; Lee and Lee, 2005), pterosaurs (Yun and Yang, 2001; Lim et al., 2002a) and dinosaurs (Lee et al., 1997; Park et al., 2000; Dong et al., 2001; Lim et al., 2001, 2002b; Kim et al., 2005; Lee, 2007; Lee and Lee, 2007; Lee, 2008) as well as dinosaur eggs in nests (Yun and Yang, 1997; Lee et al., 2000; Huh and Zelenitsky, 2002; Lee et al., 2007).

Among these vertebrate faunas, turtles remain as yet unstudied. Although some isolated turtle remains have been recently found in the Hasandong Formation, South Gyeongsang Province, they are not excavated and studied (see Lee et al., 2001 for a review). Before the discovery of Hasandong turtles, a turtle specimen was collected from the Geoncheonri Formation in Gyeongsan City, North Gyeongsang Province. The presence of this turtle was shortly mentioned in the literature (Lee et al., 2001, p. 365, table 1) and was also included in the map of *Kirgizemys* (Danilov et al., 2006, fig. 6). However, this Korean turtle has never been formally described in

detail. It consists of parts of the carapace including much of the lateral peripheral series, four costals including the first, and one neural. Therefore, the object of this paper is to describe the most complete of these materials from the Geoncheonri Formation and to investigate their affinity with Central and Eastern Asian turtle faunas.

### 2. Geological setting

The specimen was found on the north slope of the local road 919 in 1971 by one of authors (K.-H. Chang) in Gyeongsan City close to Daegu Metropolitan City (Fig. 1). It was in the dark gray mudstone of the lower part of the Geoncheonri Formation.

The Geoncheonri Formation (ca. 800 m thick) is the uppermost formation of the Hayang Group, belonging to the Gyeongsang Supergroup. The Gyeongsang Supergroup is widely distributed in the south-eastern part of the Korean Peninsula, mainly within the Gyeongsang Basin, which is the largest sedimentary basin of the Korea. It is divided into the Shindong and Hayang Groups, mainly comprised of thick siliciclastic sequences of alluvial, fluvial and lacustrine sediments, and the Yuchon Group characterized by the dominance of volcanic rocks (Chang, 1975).

The Hayang Group consists of Chilgok, Silla, Hakbong, Haman, Banyawol, Songnaedong, Chaeyaksan, and Geoncheonri formations in ascending order. The Geoncheonri Formation is conformably underlain by the Chaeyaksan Formation and overlain by the Jusasan Formation, the lowermost of the Yuchon Group. The Geoncheonri

\* Corresponding author.

E-mail address: [ylee@kigam.re.kr](mailto:ylee@kigam.re.kr) (Y.-N. Lee).

**Table 1**  
Measurements of carapace bones. Asterisks indicates as preserved

COSTALS			LC1	LC3	LC6	RC4		
Length along neural suture			NA	25.1	21.4	25.5		
Maximum width (minus rib end)			72.2	95.0	85.3	100.8		
NEURAL								
Midline length			27.4*					
Maximum width			23.1*					
PERIPHERALS	RP3	RP4	RP5	RP6	LP4	LP5	LP7	LP/10
Length along carina	31.4	31.8	32.5	35.6	34.3	34.5	34.6	38.4
Maximum height	24.8*	27.7	25.8	23.4*	25.4	25.3	NA	31.8*
Maximum width	14.2	11.9	14.4	14.3	14.2	14.1	16.4	6.3

Formation consists predominantly of dark gray interlaminated to thinly interbedded fine sandstone to siltstone and thinly laminated mudstone associated with calcareous silty mudstone, indicating shallow lacustrine deposits (Paik et al., 2000).

Since plant fossils were first reported in the Geoncheonri Formation in 1925, a series of paleontological study has been made with molluscs, spores and pollen, charophytes, and dinosaur footprints. Plant fossils from the Geoncheonri Formation were correlated with the Monobegawa Group and the Gyliak Series (Lower to “middle” Cretaceous) in Japan (Tateiwa, 1925, 1929). Yang (1978) noted that the co-occurrence of a pelecypod *Trigonioides* (s. s.) *paucisulcatus* in the Geoncheonri Formation and in the Gyliakian Goshonoura Group (Cenomanian to Turonian) of Japan (Ota, 1959). However, primitive angiosperm pollen (*Retimonocolpites peroreticulatus*, *R. sp. A*, *R. sp. B*, and *Tricolpites sp.*) and other palynological features suggest that the age of the Geoncheonri Formation is Aptian to Albian (Choi, 1985, 1989). The charophytes from the Geoncheonri Formation also indicate Aptian to Albian age (Choi, 1987).

### 3. Systematic palaeontology

Testudines Batsch, 1788

Cryptodiramorpha Lee, 1995

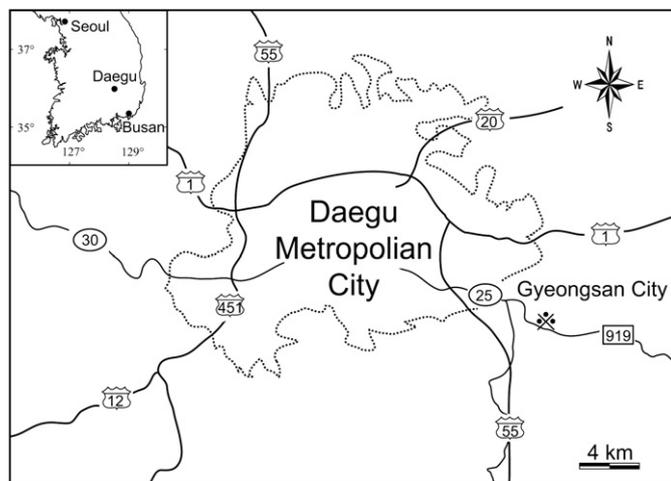
Eucryptodira Gaffney, 1975 (sensu Gaffney, 1984)

“Macrobaenidae” Sukhanov, 1964 (sensu Parham and Hutchison, 2003)

Genus *Kirgizemys* Nessov and Khosatzky, 1973

*Kirgizemys* cf. *K. exaratus* Nessov and Khosatzky, 1973

2001 Macrobaenidae indet., Lee, Yu and Wood, p.365, table 1.



**Fig. 1.** Sketch map in the vicinity of Daegu Metropolitan City showing the locality at which the specimen was discovered.

#### 3.1. Material

KIGAM VP 200506 (Korea Institute of Geoscience and Mineral Resources, Vertebrate Paleontology Catalogue Number), Carapace fragments including a neural, left costals 1, 3, 6, right costal 4, posterior part of right peripheral 2, right peripherals 3–6, left peripheral 4–5, 7, left peripheral 10 (Fig. 2).

#### 3.2. Locality and stratigraphy

From the Albian, Lower Cretaceous, of the Geoncheonri Formation in Gyeongsan City near Daegu Metropolitan City, South Korea.

#### 3.3. Abbreviations and terminology

Anatomical abbreviations of serial elements used in this paper - Carapacial bones (upper case) are denoted by a letter and position number (e.g., C2), with the lower numbers being more anterior: C = costal; P = peripheral; N = neural.

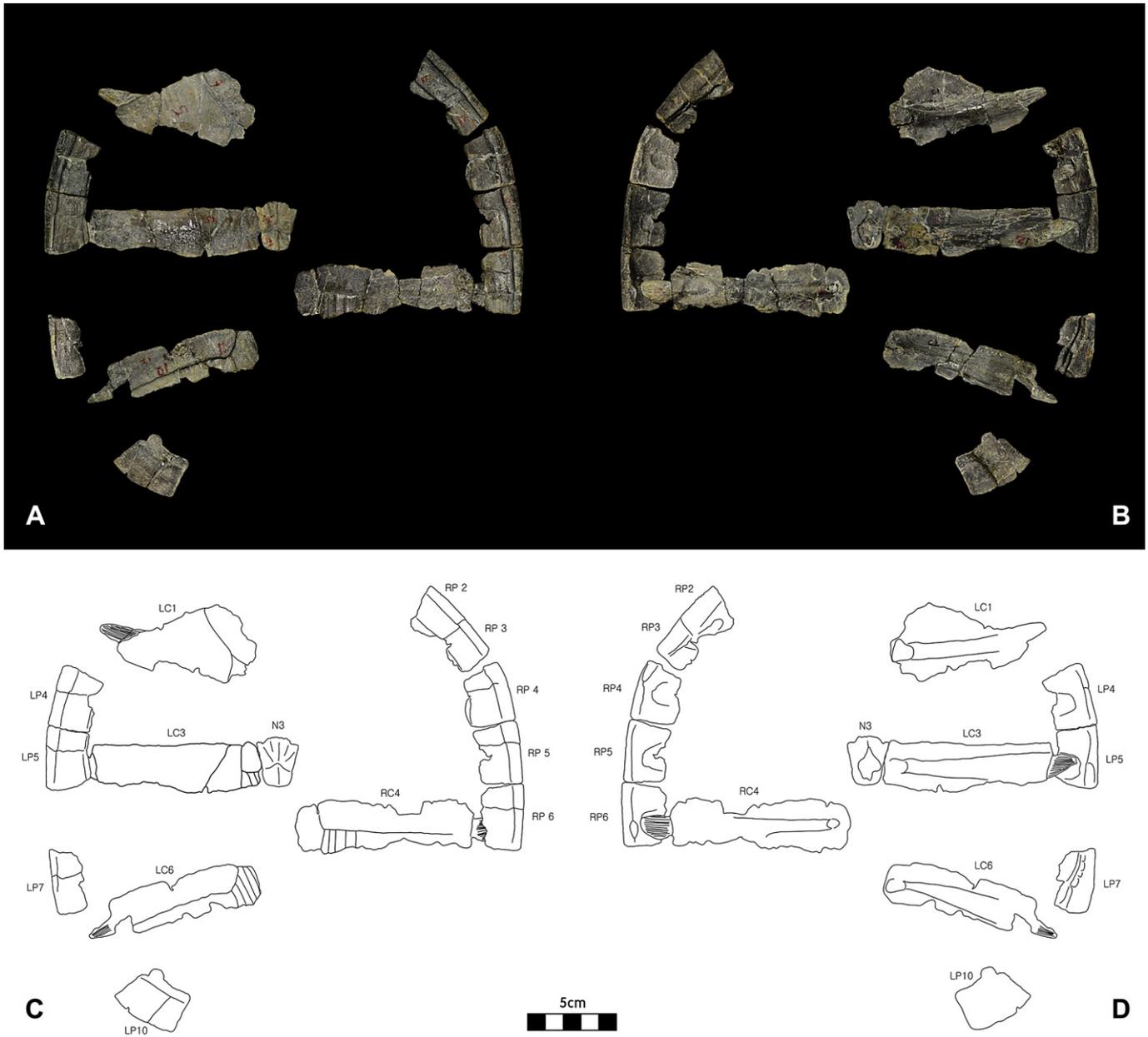
#### 3.4. Description

The intermarginal sulci of peripherals are well defined and step-down posteriorly but are not deeply impressed and lie at about the juncture of the anterior and medial one-third portions of the peripherals. The dorsal extent of the marginals is nearly coincident with the peripheral-costal suture except for P2-3.

The posterior one-third of the right P2 is preserved in articulation with the P3. The dorsal sutures are broken or chipped so that their full extent is uncertain. The free margins of P2-3 are rolled upward to form a trough with T-shaped lateral margin. The marginals extend only about one-half way up the visceral side but occupy three-quarters or more of the external surface. The dorsal surface of the marginals is sigmoidal in cross-section and roll down to a well-defined sulcus with the pleural surface. The pleural surface is relatively flat with only a broad sculpture of shallow troughs and ridges that lie normal to the pleural-marginal sulcus. The visceral surface of the posterior margin of P2 is notched by the pit for the termination of the hyoplastral buttress.

The P3 is the first full bridge peripheral and has two anterolateral elongated pits on the visceral side for the ultimate and penultimate articular processes of the hyoplastral buttress. These climb gently and anterolaterally. A broad medially open pit for the rib end of C1 enters the anterior half of the visceral side and terminates in the medial part of the peripheral lateral to the hyoplastral suture.

The P4 to P7 have upturned lateral carina. The plastral suture on P4-6 lies along the ventral margin viscerally. They have broad, U-shaped and medially exposed troughs on the dorsal portion that are for reception of the costal rib ends. The anterior and posterior depths of P4 are about equal high. The plastral suture of P4 tapers to



**Fig. 2.** A reconstruction of *Kirgizemys* cf. *K. exaratus* Nessov and Khosatzky, 1973. A, external view (photo); B, visceral view (photo); C, external view (line drawing); D, visceral view (line drawing).

a relatively sharp edge indicating the presence of peripheral-plastral fontanel in the area. The rib trough lies posterior to the center of P4.

The P5 is similar to P4 in size and shape. The anterior and posterior depths of P4 and P5 are about equally high when well preserved. However, the rib trough of P5 lies clearly posterior to the midlength point. The P6 is only represented by the right side. The plastral suture is at least one large shallow pit on the posterior half and the rib trough is posteriorly located. The P7 is only represented by the left side and the dorsal margin is not preserved. The plastral suture is thickened and marked by five shallow pits for the articular processes of the hypoplastron; the posterior most pit is trough-like and apparently continued onto P8 where it probably terminated. The plastral suture climbs posterodorsally. A broad shallow pit lies laterally to the suture on the posterior half of the peripheral for reception of the C5 rib end.

An isolated posterior left peripheral lacks the dorsal margin and is relatively thin throughout. It lacks a pit for the termination of the hypoplastral buttress and is thus not P8. The depth of the posterior end suture and the slight dorsal convergence of the interperipheral sutures suggest that this is a probably P10. The dorsal extent of the marginal surface on the visceral side is only about three-quarters that of the external surface. The free margin is not upturned and tapers to a sharp edge. There is no surface sculpture other than shallow irregular undulations.

The left C1 lacks the medial part of the posterior border and the anterior medial border. The medial border is chipped so that its suture is not preserved. The first dorsal rib head is well separated from the first costal rib (second dorsal) and its shaft extends about halfway along the length of the first costal rib on its anterior surface. The head of the first costal rib is dorsoventrally compressed and expanded medially. The distal end of the

first costal rib is straight and subovoid in cross-section. Its shaft forms a raised ridge on the visceral surface of the costal and terminates in a prominent point extending laterally from the main body of the costal. The costal in dorsal view is subtriangular and relatively thin throughout except for the rib tract but is otherwise thickest under the area of the first vertebral. The sulcus for the second vertebral is near to and approximately parallel to the neural margin but the sulcus for the first vertebral diverges anterolaterally at about a 45 degree angle and lies well lateral to the nuchal. There is no dentation of the costal margin overlying the lateral surface of the rib end suggesting the presence of a small carapacial fontanelle.

The left C6 appears to have parallel anterior and posterior borders and is broadly arched posteriorly. The sulci are well defined with the posterior part of the third pleural elevated above that of pleural 4 and the vertebral surface. The lateral anterior and posterior vertebral sulci form an angle of 140 degrees. The vertebral covered area occupies only about one-fifth the breadth of the costal. The surface of pleural 4 has longitudinal corrugations that fade out before reaching the next sulcus. The costal is thin except along the rib tracts. Viscerally, the head is distinct and sub circular in cross section and well elevated above the visceral surface. The rib tract forms a broad elevated ridge on the visceral surface and terminates in a strong pointed free end.

An isolated left costal lacks the distal part of the posterior suture and lacks an interpleural sulcus but has a stout, and slightly posteroventrally canted rib end that is less compressed than that of the C6 indicating that the costal is probably C5 and not C3. As for the other costals the part of the costal lateral to the rib end does not appear to have had a sutural contact with the peripheral and may have been exposed laterally. The vertebral covered surface occupies only about one seventh of the breadth of the costal. The vertebral-pleural sulcus is virtually parallel to the neural suture and lies in an impressed valley as does the intervertebral sulcus. The longitudinal corrugations that extend posteriorly from the preceding interpleural sulcus fade posteriorly.

Another isolated right costal is broader than C6 but lacks much of the posterior suture. It has an interpleural sulcus and the rib end is laterally compressed. The features are consistent with a right C3. The vertebral covered surface occupies only about one sixth of the costal width and had little angulation at the pleural juncture indicating a nearly rectangular vertebral. The sculpture, thickness and rib tract and head resemble that of the C4.

The only neural is distinctly longer than wide (midline length = 27.4 mm, maximum width = 23.1 mm), broader anteriorly (23.1 mm) than posteriorly (14.7 mm) and crossed by an intervertebral sulcus indicating either neural 3 or 5, but matches well with the assigned C3. The sulcus lies about two-thirds of the distance from the anterior margin and is deflected anteriorly on the midline. Although damaged on the anterior corners, it appears to have had short contacts with the preceding costals and is thus technically hexagonal. A low but distinct midline carina is present. The areas anterior to the intervertebral sulcus on either side of the midline carina are raised and have three anteriorly spreading ridges. There is a distinct step-down posterior to the sulcus. The areas on either side of the carina posterior to the sulcus are flat. The neural is relatively thin, 2.4 mm at the anterior margin and 4.2 mm at the thickest part of the lateral margin.

#### 4. Discussion

The absence of any plastral elements limits detailed comparisons but a lack of elevated plastral buttresses differs from the Pleurosternidae, Pleurosternidae, and Lindhomemydidae. The lack of dentation of the central plastral-carapacial contact indicates

a ligamental to weakly gomphotic attachment of the plastron and differs from Sinchelyidae Chkhikvadze, 1970 in this and other details.

The carapace generally resembles Upper Jurassic-Lower Cretaceous turtles Xinjiangchelyidae Nessov, in Kaznyshkin et al., 1990 (Sukhanov, 2000), "Sinemydidae" Yeh, 1963 (Sukhanov, 2000), and "Macrobaenidae" Sukhanov, 1964 (Sukhanov, 2000). It differs from the "Sinemydidae" and Xinjiangchelyidae in having the central vertebrals longer than wide and rectangular to only weakly hexagonal.

Seven genera are ascribed to the "Macrobaenidae" by Sukhanov (2000); Parham and Hutchison (2003) added a new genus and the shell of *Osteopygis* Cope, 1868. Of these, *Dracochelys* Gaffney and Ye, 1992 (Lower Cretaceous of China) is only known from the skull. The Korean material differs in having distinctly narrower vertebrals, lack or differences in sculpture, and usually also in size from *Asiachelys* Sukhanov, 2000 (Lower Cretaceous of Mongolia), *Ordosemys* Brinkman and Peng, 1993 (Lower Cretaceous of Inner Mongolia), *Judithemys* Parham and Hutchison, 2003 (Campanian of Canada), *Anatolemys* Khosatzky and Nessov, 1979 (Late Turonian-Santonian of Tadjikistan), *Parathalassemys* Nessov and Kravoskaya, 1984 (Cenomanian of Uzbekistan), *Osteopygis* Cope, 1868 (Late Cretaceous of eastern USA), *Aurorachelys* Vandermark et al., 2009 (Late Cretaceous of Canada), and *Macrobaena* Tatarinov, 1959 (Paleocene of Mongolia).

Two genera of "Macrobaenidae", *Hangaiemys* and *Kirgizemys*, come closest to resembling the Korean species. Two species of *Hangaiemys* had been recognized, but Danilov et al. (2006) recently concluded that *Kirgizemys* Nessov and Khosatzky, 1973 is a subjective senior synonym of *Hangaiemys* Sukhanov and Narmandakh, 1974. Therefore, five species of *Kirgizemys* are currently recognized.

The Korean specimen differs from *Kirgizemys hoburensis* (Sukhanov and Narmandakh, 1974) by the rib end of C1 ending in the central part of P3 and not continuing onto P4, sharp free margin of the peripherals rather than rounded, rib ends broader and with shallower insertion into the bridge peripherals, more marked sculpture, probably single rather than double pit for the hypoplastral buttress in P8, less hexagonal and less extensive overlap of the vertebrals onto the costals, less overlap of the pleurals onto the peripherals, and presence of fontanelles over the costal rib ends.

The more poorly known *K. leptis* (Sukhanov and Narmandakh, 2006), Albian, Mongolia resembles the Korean specimen in the greater curling of the marginal free margins but otherwise differs from it as in *K. hoburensis* where comparisons were available. *K. dmitrievi* Nessov and Khosatzky, 1981 from the Neocomian of the Gusinoje Ozero Group, Baikal Lake region, Burjatia is very fragmentary but differs from the Korean specimen in the lack of prominent sculpture. Recently, a new specimen of *K. dmitrievi*, including parts of the shell, first known skull, and some non-shell postcrania have been reported from the type area of the species (Danilov et al., 2006).

*Kirgizemys kansuensis* (Bohlin, 1953) from the Minhe Formation (Campanian-Maastrichtian), western Gansu Province, China resembles the Korean specimen in the sharp angulation of the dorsal and ventral arms of the bridge peripherals but lack the strong sculpture, the pleurals appear to overlap the peripherals more and the visceral and external extent of the posterior marginals appear to be more equal.

Of the five nominal species of *Kirgizemys*, the genotypic species, *K. exaratus* is the best known. The Korean specimen exhibits a strong similarity of *K. exaratus* from the upper Albian of Kyzylodzhun, southeastern Fergana, Kyrgyzstan (Nessov, 1987, figs. 2, 3b). They share the anterior placement of the intermarginal sulci, wide vertebral one but relatively narrow and subrectangular vertebrals 2-3, presence of corrugated sculpture beginning the vertebral and

pleural sulci but fading out posteriorly, sigmoid cross section of the anterior marginal surfaces, termination and placement of the anterior buttress on the P2, strong lateral carinae of the bridge peripherals, insertion of the hypoplastral buttress in P8, presence of a plastral fontanel in the area of P5–P6, placement and shallow insertion of the C4 rib on P6, shallow insertion of the articular processes of the plastron into the peripherals, alignment of the marginal–pleural sulcus with the peripheral–costal suture, and exposure of the lateral face of the distal rib ends. The Korean specimen differs from *K. exaratus* in the more angular conjunction of the dorsal and ventral arms of the bridge peripherals and relatively shorter ventral arms. These differences may only represent individual variation or diagenetic distortions considering especially the variation noted in *Nessov and Khosatzky (1977)* for *K. exaratus*.

The enigmatic *Tienfucheloides undatus* *Nessov, 1978* from the lower Upper Cretaceous of Uzbekistan is only known from shell fragments that show similarity in the sculpture of the carapace, however, it differs in having a much coarser sculpture, greater depth of the rib insertion into the peripherals, more deeply gomphotic plastral articulation, and greater overlap of the pleurals on the peripherals. *Jastmechyi jastmelchyi* (*Chkhikvadze, 1981*) from the Lower Cretaceous of Mongolia differs in having greater vertebral overlap on the costals and peripherals (*Chkhikvadze, 1987*).

*Kirgizemys* is reported elsewhere in Central and Eastern Asia (*Nessov, 1981, 1984, 1995; Sukhanov, 2000*) and reportedly ranges in age from Early Cretaceous (Neocomian, Aptian–Albian) to Late Cretaceous (Campanian–Maastrichtian). The generic attribution of the later species is in need of review, but the Korean material clearly resembles the older species, specifically *K. exaratus*, from the Albian of Kyrgyzstan. The Korean record of the genus constitutes the most easterly record of the genus, indicating that *Kirgizemys* was more widely distributed in Asia than we thought before (see *Danilov et al., 2006, fig. 6*).

## Acknowledgements

We thank V.B. Sukhanov for access to unpublished material of *Hangaiemys* and J.F. Parham and Bit Na Ra Kim for photographs and illustrations of this material. The initiation of our cooperation by C.B. Wood is gratefully acknowledged. This research was supported by the National Research Project (No. 09-9106) of the Korea Institute of Geoscience and Mineral Resources (KIGAM) funded by the Ministry of Land, Transport and Marine Affairs of Korea. The authors sincerely thank two anonymous reviewers for their helpful discussions and suggestions to improve the manuscript.

## References

- Batsch, A.J.G.C., 1788. Versuch einer Anleitung, Zur Kenntniß und Geschichte der Thiere und Mineralien. I. Akademische Buchhandlung, Jena, p. 528.
- Böhlh, B., 1953. Fossil reptiles from Mongolia and Kansu. Report from the scientific expedition to the north-western provinces of China under the leadership of Dr. Sven Hedin. The Sino-Swedish expedition, VI. Vertebrate Palaeontology 6, 1–113.
- Brinkman, D.B., Peng, J.-H., 1993. *Ordosemys leios*, n. gen., n. sp., a new turtle from the Early Cretaceous of the Ordos Basin, Inner Mongolia. Canadian Journal of Earth Sciences 30, 2128–2138.
- Chang, K.H., 1975. Cretaceous stratigraphy of southeast Korea. Journal of Geological Society of Korea 11, 1–23 (in Korean, English abstract).
- Chkhikvadze, V.M., 1970. New late Eocene turtles from Zaisan and the oligomerization of the horny scutes of plastron of some Testudinata. In: Materialy Po Evoliutsii Nazemnykh Pozvonochnykh. Academy of Sciences of the USSR, pp. 58–62 (in Russian).
- Chkhikvadze, V.M., 1981. On the question of the origin of bigheaded turtles. In: General Questions of Palaeobiology. Izdatel'stvo 'Metsniereba', Tbilisi, pp. 131–146 (in Russian).
- Chkhikvadze, V.M., 1987. Sur la classification et les caractères de certaines tortues fossiles d'Asie, rares et peu étudiées. Studia Geologie Salamanticensia, Volume Especial 2. Studia Palaecheloniologica 2, 55–86.
- Choi, D.K., 1985. Spores and pollen from the Gyeongsang supergroup, southeastern Korea and their chronologic and paleoecologic implications. Journal of Paleontological Society of Korea 1, 33–50.
- Choi, D.K., 1989. Palynology of the Geoncheonri Formation (Lower Cretaceous), Geoncheon–Ahwa area, Korea. Journal of Paleontological Society of Korea 5, 1–27.
- Choi, S.J., 1987. Study on the Lower Cretaceous charophytes from the Upper Gyeongsang Supergroup. Journal of Paleontological Society of Korea 3, 79–92.
- Cope, E.D., 1868. Description of a new genus and species of Cheloniidae, *Osteopygis emarginatus*. Proceedings of the Academy of Natural Sciences, Philadelphia 1868, 147.
- Danilov, I.G., Averianov, A.O., Skutchas, P.P., Rezvyi, A.S., 2006. *Kirgizemys* (Testudines, 'Macrobaenidae'): new material from the Lower Cretaceous of Buryatia (Russia) and taxonomic revision. Fossil Turtle Research 1, 46–62.
- Dong, Z.M., Paik, I.S., Kim, H.J., 2001. A preliminary report on a sauropod from the Hasandong Formation (Lower Cretaceous), Korea. In: Deng, T., Wang, Y. (Eds.), Proceedings of the 8th Annual Meeting of the Chinese Society of Vertebrate Paleontology. China Ocean Press, Beijing, pp. 41–53.
- Gaffney, E.S., 1975. A phylogeny and classification of the higher categories of turtles. Bulletin of the American Museum of Natural History 155, 387–436.
- Gaffney, E.S., 1984. Historical analysis of theories of chelonian relationship. Systematic Zoology 33, 283–301.
- Gaffney, E.S., Ye, X., 1992. *Dracocheilus*, a new cryptodiran turtle from the Early Cretaceous of China. American Museum Novitates 3048, 1–13.
- Huh, M., Zelenitsky, D.K., 2002. Rich dinosaur nesting site from the Cretaceous of Bosung County, Chullanam-do Province, South Korea. Journal of Vertebrate Paleontology 22, 716–718.
- Huh, M., Hwang, K.G., Paik, I.S., Chung, C.H., Kim, B.S., 2003. Dinosaur tracks from the Cretaceous of South Korea: distribution, occurrences and paleobiological significance. The Island Arc 12, 132–144.
- Hwang, G.K., Huh, M., Lockley, M.G., Unwin, D.M., Wright, J.L., 2002. New pterosaur tracks (Pterarchnidae) from the Late Cretaceous Uhangri Formation, south-western Korea. Geological Magazine 139, 421–435.
- Kaznyshkin, M.N., Nalbandyan, L.A., Nessov, L.A., 1990. Turtles from the Middle and Late Jurassic of Fergana (Kirgiz SSR). Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva 33, 185–204 (in Russian).
- Khosatzky, L.I., Nessov, L.A., 1979. Kkrupnye Cherepakhi Pozdnego Mela Srednei Azii. Large Turtles of the Late Cretaceous of Middle Asia, 89. Akademiya Nauk SSSR, Trudy Zoologicheskogo Instituta, pp. 98–108 (in Russian).
- Kim, H.M., Gishlick, A.D., Tsuihiji, T., 2005. The first non-avian maniraptoran skeletal remains from the Lower Cretaceous of Korea. Cretaceous Research 26, 299–306.
- Kim, J.Y., Kim, S.H., Kim, K.S., Lockley, M.G., 2006. The oldest record of webbed bird and pterosaur tracks from South Korea (Cretaceous Haman Formation, Changseon and Sinsu islands): more evidence of high avian diversity in East Asia. Cretaceous Research 27, 56–69.
- Lee, E.S., 1999. Cretaceous Freshwater Fishes from Dongmyeong Formation. Unpublished MS Thesis, Kyungpook National University, Daegu, p. 63.
- Lee, M.S.Y., 1995. Historical burden in systematics and the interrelationships of 'parareptiles'. Biological Reviews 70, 459–547.
- Lee, H.J., Lee, Y.-N., 2005. A new protosuchian (Archosauria: Crocodyliformes) skull from the Hasandong Formation (Lower Cretaceous) of Hadong County, South Korea. Journal of Vertebrate Paleontology 3, 83A.
- Lee, Y.-N., 2007. New theropod teeth from the Juji Island (Hasandong Formation), Daedo-ri, Hadong County, South Gyeongsang Province. Journal of the Geological Society of Korea 43, 151–166.
- Lee, Y.-N., 2008. The first tyrannosauroid tooth from Korea. Geosciences Journal 12, 19–24.
- Lee, Y.-N., Huh, M., 2002. Manus-only sauropod tracks in the Uhangri Formation (Upper Cretaceous), Korea and their paleobiological implications. Journal of Paleontology 76, 558–564.
- Lee, Y.-N., Lee, H.-J., 2007. The first ornithopod tooth in Korea. Journal of Paleontological Society of Korea 23, 213–225 (in Korean, English abstract).
- 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.G. (Eds.), International Dinosaur Symposium for Uhangri Dinosaur Center and Theme Park in Korea. Journal of Paleontological Society of Korea, Special Publications 2, pp. 103–114.
- Lee, Y.-N., Yu, K.-M., Wood, C.B., 2001. A review of vertebrate faunas from the Gyeongsang Supergroup (Cretaceous) in South Korea. Palaeogeography, Palaeoclimatology, Palaeoecology 165, 357–373.
- Lee, Y.-N., Kim, B.C., Lee, Y.S., Kee, W.-S., 2007. New dinosaur egg site found in the Namyang Basin, Hwaseong City, Gyeonggi Province. Journal of Paleontological Society of Korea 23, 15–26 (in Korean, English abstract).
- Lee, Y.-N., Lee, H.-J., Lü, J., Kobayashi, Y., 2008. New pterosaur tracks from the Hasandong Formation (Lower Cretaceous) of Hadong County, South Korea. Cretaceous Research 29, 345–353.
- Lee, Y.-N., Jeong, K.S., Chang, S.K., Choi, M.Y., Choi, J.I., 2000. The preliminary research on the dinosaur eggs and nests found in the reclaimed area south to the Siwha Lake, Gyeonggi Province, Korea. Journal of Paleontological Society of Korea 16, 27–36 (in Korean, English abstract).
- Lim, J.D., Martin, L.D., Baek, K.S., 2001. The first discovery of a brachiosaurid from the Asian continent. Naturwissenschaften 88, 82–84.
- Lim, J.D., Baek, K.S., Yang, S.Y., 2002a. A new record of a pterosaur from the Early Cretaceous of Korea. Current Science 82, 1208–1210.
- Lim, J.D., Martin, L.D., Baek, K.S., 2002b. The first megalosaurid tooth from South Korea. Current Science 82, 326–328.

- Lockley, M.G., Yang, S.Y., Matsukawa, A., Fleming, F., Lim, S.K., 1992. The track record of Mesozoic birds: evidence and implications. *Philosophical Transaction Royal Society London B* 336, 113–134.
- Nessov, L.A., 1978. An archaic Late Cretaceous turtle from western Uzbekistan. *Paleontologicheskii Zhurnal* 1978 (4), 101–105 (in Russian).
- Nessov, L.A., 1981. [On turtles of the family Dermatemydidae from the Cretaceous of the Amur River basin, and some other rare discoveries of the remains of ancient turtles of Asia]. In: [Herpetological research in Siberia and the Far East]. Leningrad, pp. 69–73 (in Russian).
- Nessov, L.A., 1984. Data on Late Mesozoic turtles from the USSR. *Studia Geologic Salamaticensia, Volume Especial 1: Studia Palaecheloniologica* 1, 215–223.
- Nessov, L.A., 1987. On some Mesozoic turtles of the Soviet Union, Mongolia and China, with comments on systematics. *Studia Geologica Salamaticensia. Studia Palaecheloniologica* 2, 87–102.
- Nessov, L.A., 1995. On some Mesozoic turtles of the Fergana depression (Kirgizstan) and Dzhungar Alatau ridge (Kazakhstan). *Russian Journal of Herpetology* 2, 134–141.
- Nessov, L.A., Khosatzky, L.I., 1973. Early Cretaceous turtles from south-eastern Fergana. In: [Questions of Herpetology] *Doklady III Vsesoyuznoi Gerpetologicheskoi Konferentsii. Izdatel'stvo 'Nauka', Leningrad*, pp. 132–133 (in Russian).
- Nessov, L.A., Khosatzky, L.I., 1977. Mesozoic turtles of the USSR. In: [Questions of Herpetology] *Doklady IV Vsesoyuznoi Gerpetologicheskoi Konferentsii. Izdatel'stvo 'Nauka', Leningrad*, pp. 157–159 (in Russian).
- Nessov, L.A., Khosatzky, L.I., 1981. Cherepakhi rannego mela Zabaykal'ya. (Turtles from the Early Cretaceous of the Trans-Baikal region.). In: Borkin, L.Y. (Ed.), *Gerpetologicheskoye Issledovaniya v Sibiri i na Dal'nem Vostoke. Zoologicheskii Institut AN SSSR, Leningrad*, pp. 74–78 (in Russian).
- Nessov, L.A., Krasovskaya, T.B., 1984. Preobrazovaniya v sostave kompleksov cherepakh mela Sredney Azii. (Transformations in the composition of turtle communities during the Cretaceous in Middle Asia.). *Vestnik Leningradskogo Universiteta, Seriya 3. Biologii* 1984, 15–25 (in Russian).
- Ota, Y., 1959. *Trigonioides* and its classification (studies on the molluscan fauna of the Cretaceous Inkstone series, part 2). *Transactions and Proceedings of Palaeontological Society of Japan, New Series* no. 34, 97–104.
- Paik, I.S., Kim, H.J., Lee, J.D., Kim, I.S., Kim, J.S., Moon, B.C., 2000. Comparative sedimentology for the lacustrine deposits of the Upper Gyeongsang supergroup in the southeastern Gyeongsang Basin, Korea. *Journal of Korean Earth Science Society* 21, 423–436 (in Korean, English abstract).
- Parham, J.F., Hutchison, J.H., 2003. A new eucryptodiran turtle from the Late Cretaceous of North America (Dinosaur Provincial Park, Alberta, Canada). *Journal of Vertebrate Paleontology* 23, 783–798.
- Park, E.J., Yang, S.Y., Currie, P.J., 2000. Early Cretaceous dinosaur teeth of Korea. In: Lee, Y.-N., (Ed.), 2000 International Dinosaur Symposium for Kosong County in Korea. *Journal of Paleontological Society of Korea, Special Publication* 4, pp. 85–98.
- Sukhanov, V.B., 1964. Subclass Testudinata. In: Orlov, Y.A. (Ed.), *Osnovy Paleontologii. Zemnovodnyye, Presmykayushchiesya i Ptitsy. Nauka, Moscow*, pp. 354–438 (in Russian).
- Sukhanov, V.B., 2000. Mesozoic turtles of Middle and Central Asia. In: Benton, J.M., Shishkin, M.A., Unwin, D.M., Kurochkin, E.N. (Eds.), *The age of dinosaurs in Russia and Mongolia. Cambridge University Press, Cambridge*, pp. 309–367.
- Sukhanov, V.B., Narmandakh, P., 1974. A new Early Cretaceous turtle from continental deposits of the Northern GobiFauna and Biostratigraphy of the Mesozoic and Cenozoic of Mongolia. *Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspedititsii* 1, 192 (in Russian).
- Sukhanov, V.B., Narmandakh, P., 2006. New taxa of Mesozoic turtles from Mongolia. In: Danilov, I.G., Parham, J.F. (Eds.), *Fossil Turtle Research, vol. 1. Russian Journal of Herpetology* 13 (Suppl.), 119–127.
- Tatarinov, L.P., 1959. New turtle of the family Baenidae from the Lower Eocene of Mongolia. *Paleontologicheskii Zhurnal* 1, 100–113 (in Russian).
- Tateiwa, I., 1925. Geologic age of the Nagdong flora. *Journal of Geological Society of Tokyo* 32, 493–512 (in Japanese).
- Tateiwa, I., 1929. Geologic atlas of Korea, no. 10, Keishu, Eisen, Taikyuu and Wakwan sheets. *Geological Survey of Chosen, Korea*, 12 (in Japanese, English abstract).
- Vandermark, D., Tarduno, J.A., Brinkman, D.B., Cottrell, R.D., Mason, S., 2009. New Late Cretaceous macrobaenid turtle with Asian affinities from the High Canadian Arctic: dispersal via ice-free polar routes. *Geology* 37, 183–186.
- Yang, S.Y., 1978. Ontogenetic variation of *Trigonioides* (s. s.) *paucisulcatus* (Cretaceous non-marine Bivalvia). *Transactions and Proceedings of Palaeontological Society of Japan, New Series* no. 111, 333–347.
- Yang, S.Y., Lockley, M.G., Greben, R., Erickson, B.R., Lim, S.K., 1995. Flamingo and duck-like bird tracks from the Late Cretaceous and Early Tertiary: evidence and implications. *Ichnos* 4, 21–34.
- Yeh, H.K., 1963. Fossil turtles of China. *Palaeontologica Sinica, New Series C* 18, 52–55.
- Yun, C.S., Yang, S.Y., 1997. Dinosaur eggshells from Hasandong Formation, Gyeongsang Supergroup, Korea. *Journal of Paleontological Society of Korea* 13, 21–36 (in Korean, English abstract).
- Yun, C.S., Yang, S.Y., 2001. First discovery of big pterosaur teeth in Korea. *Journal of Paleontological Society of Korea* 17, 69–76 (in Korean, English abstract).
- Yun, C.S., Lim, J.D., Yang, S.Y., 2004. The first crocodyliform (Archosauria: Crocodylomorpha) from the Early Cretaceous of Korea. *Current Science* 86, 1200–1201.