



이학석사 학위논문

The first adocid turtle in South Korea and the early evolutio n of the Adocidae

한국 최초의 아도쿠스科 거북과 아도쿠스科의 초기 진화

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지구환경과학부

김 도 현

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ABSTRACT

An adocid turtle was collected from the Lower Cretaceous Hasandong Formation, representing the first occurrence of the Adocidae in South Korea. The specimen consists of moderately preserved hard shells (carapace and plastron) with a limb bone (humerus). It turned out to be a new taxon named *Proadocus hadongensis*, n. gen. n. sp. *Proadocus* is characterized by combining synapomorphic characters of adocids and primitive characters ancestrally retained from basal pantrionychians. The pattern of marginal scales extension and pygal shape are shared with *Sinaspideretes wimani* and *Basilochelys macrobios*, the basal pantrionychian taxa of South East Asia in the Late Jurassic–Early Cretaceous. A cladistics analysis places it as the most basal taxon in Adocidae. Such phylogenetic position of *Proadocus* involves important implications about the origin and early evolution of the Adocidae. First, *Proadocus* supports the South East Asian origin of this family. Secondly, a new paleobiogeographic analysis, including *Proadocus* in Korea, requests a new interpretation of the adocid diversification and dispersion in East Asia during the Early Cretaceous.

Keywords: Turtle, Adocidae, Hasandong Formation, Early Cretaceous, Adocid evolution, South East Asia Student Number: 2021-28826

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I. INTRODUCTION

Adocids are freshwater cryptodiran turtles diagnosed with a unique shellsculpturing structure and were widely distributed in East and Central Asia and North America from the Early Cretaceous to the Paleogene (Sukhanov, 2000; Danilov et al., 2011; 2013). Adocids are considered an ingroup within Pan-Trionychia, and a sister clade to Nanhsiungchelyidae (Joyce et al., 2021). Adocidae is united with Nanhsiungchelyidae, forming the clade Adocusia (Danilov and Parham, 2006).

The early evolution and origin of the Adocidae are unclear due to the poor fossil record. *Yehguia tatsuensis* from the Late Jurassic of China, the basal-most adocid, is considered the oldest known record (Ye, 1963; Danilov and Syromyatnikova, 2009). However, Tong et al. (2014) regarded *Yehguia* as a junior synonym of *Sinaspideretes wimani*, an early pantrionychian from the Late Jurassic of China, and placed it as a basal-most taxon within Pan-Trionychia.

Previously, Cretaceous adocids have been well-reported in Japan, Mongolia, Laos, and Thailand, but not Korea (Danilov et al., 2011; Sonoda et al., 2015; Tong et al., 2019). This study reports the first adocid turtle in Korea based on two specimens. These specimens (NHCG 10102 and SNUVP 200209) are mainly shell materials from the Lower Cretaceous (upper Aptian) Hasandong Formation, Gyeongsang Supergroup. Both specimens were discovered from Janggu Island, Hadong County, South Gyeongsang Province (Fig. 1). The specimens show typical adocid synapomorphies: shell sculpturing with regular small pits, reduced rib heads, and thin rib shafts. Moreover, these specimens have a unique set of

primitive characters, suggesting that they are a new basal taxon within Adocidae. This study aims to describe this new taxon and discuss its cladistic position-related to the origin and early evolution of adocids.





I-1. Institutional abbreviations

Institutional abbreviations. **NHCG**, National Heritage Center Geology, Cultural Heritage Administration; **SNUVP**, Seoul National University, Vertebrate Paleontology.

II. MATERIALS AND METHODS

NHCG 10102 and SNUVP 200209 were collected in 2007 by National Heritage Center and in 2002 by Yuong-Nam Lee, respectively. The preparation of NHCG 10102 initially began at the National Heritage Center and finished at Seoul National University. Measurements of the specimens were taken using a measuring tape and a caliper. Comparisons to other adocid taxa were made based on published literature. Adobe Illustrator CC (version 24.0.1,

https://www.adobe.com/kr/products/illustrator.html) was employed to produce most of the figures. The anatomical terms were adapted from Kent and Carr (2000) and Danilov et al. (2011). The clade 'Pan-Trionychia' used in this study followed the establishment of nomenclature by Joyce et al. (2021).

The character list and data matrix used in the cladistic analysis were modified from Danilov and Syromyatnikova (2009) (see Appendix 1 and 2). Three additional taxa were added, *Basilochelys macrobios*, *Proadocus hadongensis*, and *Protoshachemys rubra*. However, six wildcard taxa were excluded *Apalone ferox*, *Basilemys praeclara*, *Basilemys sinuosa*, *Carettochelys insculpta*, *Xinjiangchelys levensis*, and *Zangerlia ukhaachely*, for improved resolution. *Yehguia tatsuensis* was changed into *Sinaspideretes wimani* along with its character scoring as the following redescription by Tong et al. (2014). The revised 74 characters and 20 taxa dataset was analyzed using TNT (Tree analysis using New Technology) Version 1.5 (Goloboff et al., 2008). All characters were treated as unordered and of equal weight. A traditional search (Wagner trees; swapping algorithm: tree bisection-reconnection; random seeds: 1; replicates: 1000; trees to save per replication: 10) was performed.

III. GEOLOGICAL SETTING

The Hasandong Formation is the middle unit of the Sindong Group, the lowest group within the Gyeongsang Supergroup. The formation conformably overlies the Nakdong Formation and underlies the Jinju Formation (Chang, 1975; Choi, 1985). It comprises fluvial deposits, including conglomerates, sandstones, and siltstones, with about 1,200 m thickness (Yang, 1982; Paik and Lee, 1994; Paik and Kim, 1995). The temporal climate was interpreted as semi-arid with alternating dry and wet seasons due to the presence of calcareous and vertisol paleosols found within the sediments (Choi, 1985; Paik and Lee, 1994; Paik and Kim, 1995; Paik, 1998; Paik and Lee, 1998; Paik et al., 1998; Paik et al., 2001). Fossils from the Hasandong Formation include mollusks, fishes, turtles, crocodiles, pterosaurs, and various dinosaurs (Table 1). The age of the Hasandong Formation was suggested as Aptian-Albian by molluscan fossils and early Aptian by ion microprobe U-Pb dating of a theropod tooth, respectively (Yang, 1982; Sano et al., 2006). Magnetostratigraphic analysis suggested a deposit age after Aptian for the Shindong Group, which includes the Hasandong Formation, and zircon age dating yielded a late Aptian age (Doh et al., 1994; Lee et al., 2010; Kang and Paik, 2013; Lee et al., 2018).

Body Fossils	References		
Bivalves	Yang (1982)		
	Yun and Yang (2001)		
Fishes	Lee et al., (2001)		
	Yabumoto et al. (2006)		
Turtles	Lee and Tomida (2004)		
Crocodylians	Lee and Lee (2005)		
·	Yun et al. (2007)		
Pterosaurs	Yun and Yang (2001)		
	Lim et al. (2002)		
	Yun et al. (2007)		
	Park et al. (2020)		
Dinosaurs	Paik et al. (1998)		
Sauropoda	Park et al. (2000)		
	Dong et al. (2001)		
	Yun et al. (2007)		
	Park (2016)		
Theropoda	Park et al. (2000)		
L	Lim et al. (2002)		
	Lee (2007)		
	Yun et al. (2007)		
	Lee (2008)		
Ornithopoda	Lee and Lee (2007)		
Egg Fossils	References		
Eggs	Yun and Yang (1997)		
	Lee et al. (2001)		
	Huh et al. (2003)		
	Lee et al. (2008)		
	Paik et al. (2015)		
	Lee et al. (2018)		

TABLE 1. Various body and egg fossils reported from the Hasandong Formation.

IV. SYSTEMATIC PALEONTOLOGY

Testudines Batsch, 1788 Cryptodira Cope, 1868 Pan-Trionychia Hummel, 1929 Adocusia Danilov and Parham, 2006 Adocidae Cope, 1870 *Proadocus hadongensis* gen. et sp. nov.

Holotype. NHCG 10102 (Figs. 2–7), four separated shell pieces, including neurals, costals, peripherals, pygal, suprapygals, entoplastrons, epiplastrons, hyoplastrons, hypoplastrons, and a right humerus.

Type locality. Janggu Island, Hadong County, South Gyeongsang Province, South Korea.

Type horizon. Lower Cretaceous Hasandong Formation (upper Aptian), Gyeongsang Supergroup.

Referred specimen. SNUVP 200209 (Fig. 8), a right 3rd peripheral.

Etymology. *Pro*: Latin, ancestor; *Adocus*: the type genus of Adocidae; hadong: named after the type locality of holotype, Hadong County; *ensis*: Latin, from a place.

Diagnosis. *Proadocus hadongensis* is characterized by the following combination of characters: large marginal scales 11th and 12th (shared with *Ferganemys itemirensis, Ferganemys verzilini,* and *Protoshachemys rubra*); wider than long 3rd vertebral (shared with *Adocus aksary*); wedge-shaped anterior margin of

entoplastron between epiplastron (shared with *Adocus* spp.). Differs from *Adocus* spp. by restriction of 8th-10th marginal scales in the peripherals. Differs from *Ferganemys* spp. by extension of marginal scales 4th-7th onto the costals. Differs from *Protoshachemys rubra* by shell sculpturing structure with regular pits and grooves, widened postneural part of the carapace, and absence of the serrations in posterior peripherals. Differs from *Shachemys* spp. by extension of marginal scales 4th-7th onto the costals, having neural series, presence of 1st suprapygal, shell sculpturing structure with regular pits and grooves, with regular pits and grooves, no epi-entohyoplastral hinge, and peripherals with upturned free edge.



FIGURE 2. Photograph of carapace of *Proadocus hadongensis* gen. et sp. nov. (NHCG 10102, holotype) in dorsal view.



FIGURE 3. Line drawing of carapace of *Proadocus hadongensis* gen. et sp. nov. (NHCG 10102, holotype) in dorsal view. Sutures are drawn in solid lines, whereas the scute sulci are drawn in dotted lines. The dark grey area indicates a matrix, and the light grey indicates damaged portions.



FIGURE 4. Photograph of plastron of *Proadocus hadongensis* gen. et sp. nov. (NHCG 10102, holotype) in ventral view.



FIGURE 5. Line drawing of plastron of *Proadocus hadongensis* gen. et sp. nov. (NHCG 10102, holotype) in ventral view. Sutures are drawn in solid lines, whereas the scute sulci are drawn in dotted lines. The dark grey area indicates a matrix.



FIGURE 6. Photographs and line drawings of disarticulated shell materials in NHCG 10102. (A) 1st costal and (B) 2nd costal in dorsal views. The dark grey area indicates a matrix. Light grey indicates damaged portions.



FIGURE 7. Photographs and line drawings of disarticulated humerus material of *Proadocus hadongensis* gen. et sp. nov. (NHCG 10102, holotype). (A) Lateral, (B) dorsal, (C) ventral, and (D) medial views.



Dorsal and (B) posterior views.

V. DESCRIPTION

NHCG 10102 contains the shells (Figs. 2–6) and a right humerus (Fig. 7). The shells comprise the main body (Figs. 2–5) and disarticulated materials (Fig. 6). The main body is separated into two pieces and is dorsoventrally compressed, distorted from its original shape (see Table 2 for measurements). The length of the preserved shell, including disarticulated parts, is about 26 cm, and its estimated total length is about 28 cm. Since no fontenelle is visible, it is considered to be a mature individual. The referred material, SNUVP 200209, is an isolated 3rd peripheral element (Fig. 8), of which the overall shape is similar to the corresponding part in NHCG 10102.

TABLE 2. Measurements of materials in NHCG 10102 and SNUVP 200209 (in mm). The tilde symbol (~) indicates that the measurement is given in terms of the specimen as preserved.

Specimen No.	Materials	Length	Width
NHCG 10102	Carapace	260~	203
	Plastron	159~	136~
	Right humerus	39	13
SNUVP 200209	Right 3 rd peripheral	30~	26~

V-1. Carapace

The preserved carapace of NHCG 10102 is nearly complete, and the outline is oval and posteriorly widened in dorsal view (Fig. 4). Costals 3rd–6th are subsided underneath the medioventral part of the peripheral, resulting in a slight distortion of the structure. The scute sulci are narrow and shallow, about 0.3 mm depth, as in typical adocids (Hirayama et al., 2020). The external surface of the shell is sculptured in small pits scattered regularly, as in *Adocus* and *Ferganemys* (Danilov et al., 2013) (Fig. 9A).

Four middle and posterior neurals are preserved in NHCG 10102, which are longer than wide. The 3rd-5th neurals are hexagonal and nearly the same size, whereas the 6th neural is heptagonal and much smaller than the anterior ones. The neural series does not reach the anterior border of the 2nd suprapygal as in typical adocids (Tong et al., 2016).

The 3rd-11th peripherals are preserved on the right, while the 7th-11th peripherals are on the left side in NHCG 10102. Most peripherals are rectangular and wider than long, whereas the 8th and 10th are pentagonal, and the 11th is longer than wide. The free edge of the anterior peripherals is upturned in both NHCG 10102 and SNUVP 200209, forming a lateral projection as in *Adocus* and *Ferganemys* (Syromyatnikova, 2011) (Fig. 8B). The degree of the peripheral upturn posteriorly decreases.

A nearly complete costal series is preserved in NHCG 10102, except for the left 1st and 2nd costals. The right 1st costal is fragmentary, while all other costals are preserved in nearly complete condition. The overall shape of the costals is flat and dorsally convex on the medial surface. The ventral side of the right 2nd costal has a

reduced rib head attachment with a thin rib shaft as in typical adocids (Danilov et al., 2013) (Fig. 10). A triangular-shaped free rib remains at the ventrolateral side of the costal (Fig. 10). A thin rib shaft is also present on the ventral side of the left 6th-7th costals. Both 6th-8th costals from each side meet at the midline of the shell as in typical adocids. Due to the subsidence of the costals 3rd-6th, it is hard to identify the position of the sutures between these plates.

The pygal is well preserved in NHCG 10102, and it is trapezoidal and wider than long as in typical nanhsiungchelyids (Danilov and Syromyatnikova, 2008). The pentagonal 1st suprapygal is smaller than the 2nd suprapygal, a typical feature among adocids (except *Shachemys*) and nanhsiungchelyids (Syromyatnikova, 2011; Tong et al., 2014).

The 3rd-12th marginal scales are preserved on the right, and the 8th-12th on the left side in NHCG 10102. Their shapes are highly variable, from rectangular to heptagonal. Most of the marginals are almost similar in size, whereas the 11th and 12th ones are much larger than others, as in *Ferganemys itemirensis* and *Ferganemys verzilini* and *Protoshachemys rubra* (Syromyatnikova, 2011; Tong et al., 2019) (Fig. 4). The 4th-7th marginals extend onto the costals, and 8th-10th marginals are restricted in the peripherals, while 11th-12th marginals extend onto the costals and suprapygal as in *Protoshachemys rubra* (Tong et al., 2019) (Fig. 4). Partial 1st and 2nd vertebrals and complete 3rd-5th vertebrals are preserved in NHCG 10102. The 3rd and 4th vertebrals are hexagonal, whereas the 5th is oval. The 3rd and 5th vertebrals are wider than long, while the 4th is slightly longer than wide. Their size decreases posteriorly. The 5th vertebral is the smallest in the series, about 90% length of the 4th one. The medial margin of the 3rd and 4th vertebrals are wedged between two pleurals. Both 4th pleurals are nearly complete in NHCG 10102. They are pentagonal and wider than long. Other elements are hard to describe due to damage or subsidence of costals.



FIGURE 9. Shell sculpturing in (A) carapace and (B) plastron of *Proadocus hadongensis* gen. et sp. nov. (NHCG 10102).



FIGURE 10. 2nd costal of *Proadocus hadongensis* gen. et sp. nov. (NHCG 10102, holotype) in ventral view. Abbreviations are as follows: f.r, free rib; r.a, ribhead attachment; r.s-rib shaft. The light grey area indicates damaged portions.

V-2. Plastron

The plastron is nearly complete in NHCG 10102 (Fig. 4). Overall, it is flat and thin. The scute sulci are narrow and shallow, as in the carapace. The scute sulci are absent on the internal surface as in typical adocids (Danilov and Syromyatnikova, 2008). The shell is sculptured with small pits scattered regularly, as in the carapace (Fig. 9B).

The entoplastron is nearly complete, whereas the epiplastrons are poorly preserved in NHCG 10102. The entoplastron is hexagonal to slightly oval and wider than long as in adocids and nanhsiungchelyids (Tong et al., 2014). Its anterior margin is wedged as in *Adocus* (Syromyatnikova, 2011).

Both hyoplastron and hypoplastrion are relatively well preserved in NHCG 10102. The right axillary/inguinal buttress is completely preserved, whereas only the partial posterior portion of the inguinal buttress remains on the left. The pointed axillary notch is narrower than the inguinal notch, while the shape of the inguinal notch is unclear due to its slight damage. The suture of the left and right hypoplastron is long, as in *Adocus* and *Ferganemys verzilini* (Syromyatnikova, 2011; Hirayama et al., 2020).

The plastral lobes are partially preserved in NHCG1010. The scute sulci are located on both lobes. The lateral border of the anterior lobe is rounded, whereas that of the posterior lobe is nearly straight.

The posterior gular is partially preserved, whereas the right extragular is complete in NHCG 10102. The sulcus of the extragular with the humeral and gular are nearly straight, and its lateroposterior margin does not extend onto the hyoplastron. The posterior border of the gular is pointed and extended onto the entoplastron.

The right pectoral and humeral are well preserved, while the left is partially preserved in NHCG 10102. The sulcus between two scutes on the right side laterally contributes to the axillary notch as in typical adocids (Danilov and Syromyatnikova, 2008). The pectoral is medially widened, and its anterior margin is excluded from the entoplastron.

Both sides of the abdominal and the right femoral are well preserved, but the left femoral is partially preserved in NHCG 10102. The abdominal is longer than the femoral as in typical adocids (except *Adocus planus*) (Syromyatnikova et al., 2012).

Four inframarginals are located on the plastral bridge, as in typical *Shachemys* (France, 2004). These are entirely preserved on the right side in NHCG 10102. The inframarginals are longer than wide as in *Adocus* (except *Adocus amtgai* and *Adocus planus*) and *Ferganemys* (Syromyatnikova et al., 2012). The anteroposterior length of the inframarginals becomes longer through the 1st-4th. The longest 4th inframarginal is about 25% longer than the 3rd one. The 3rd inframarginal is mediolaterally the most slender among these.

The plastral midline sulcus coincides with the plastral symphysis only in the partial anterior portion of the abdominal, and it is highly sinuous as in typical adocids (Danilov et al., 2011) (Fig. 5).

V-3. Limb bone

The right humerus is well preserved without slight damage in the shaft, lateral process, and distal part. The overall shape of the humerus is curved, the proximal part runs dorsally from the shaft at an almost vertical angle, and the distal part runs ventrally from the shaft at an angle of about 10° (Fig. 7A, D). The caput humerus is oval in dorsal view (Fig. 7B). The medial process is located in a more proximal position than the caput humerus and forms an angle slightly closer to the horizontal from the shaft. The lateral process is estimated to be much smaller than the medial process, even considering there is slight damage in it (Fig. 7B, C). In ventral view, the wide and deep intertubercular fossa is well developed between the medial process and the remained part of the lateral process (Fig. 7C). Despite damage in the medial side of the distal part, the capitellum and trochlea are preserved well, and they are in approximately equal size (Fig. 7B, C). The overall morphology of humerus is similar to those of other adocids (Meylan and Gaffney, 1989; Syromyatnikova et al., 2013).

VI. CLADISTIC ANALYSIS

The cladistic analysis produced the 11 most parsimonious trees with 123 steps; the consistency index is 0.634, and the retention index is 0.750. The 50% majority-rule consensus tree puts Proadocus in the most basal position within Adocidae, sister to all other adocids, including Adocus, Ferganemys, Protoshachemys, and Shachemys (Fig. 11). Proadocus and other adocids share three unambiguous synapomorphies: weakly developed rib heads (character 38: state 1); absence of rib thickenings (39:1); the presence of sculpturing of the shell surface with relatively small and regular pits or dots (71:1). Adocus, Ferganemys, Protoshachemys, and Shachemys share only one unambiguous synapomorphy: more prolonged than the wide shape of pygal (character 36: state 0). Protoschachemys is located within Shachemydinae, as suggested by the comparative analysis of Tong et al. (2019); however, it forms a polytomy with Ferganemys and Shachemys. These three taxa share two unambiguous synapomorphies: anteriorly shortened and truncated entoplastron (58:1); extragular-humeral sulcus close or coincides with the epi-entohyoplatsral suture (65:1). Basilochelys and Sinaspideretes are located in a more basal position than Adocidae and Nanhsiungchelyidae, similar to the results of Tong et al. (2009; 2014) (Fig. 11).



FIGURE 11. Majority 50% consensus of the 11 most parsimonious trees.

VII. DISCUSSION

VII-1. Comparisons to related taxa

Proadocus exhibits a set of primitive characters; marginal scales 4th-7th and 11th-12th extending onto the costals and suprapygal, and wider than long pygal, which are differentiated from most of other adocid genera and species (Fig. 12). These characters are inferred to be retained ancestrally from basal pantrionychians in Late Jurassic–Early Cretaceous; *Sinaspideretes wimani* from the Sichuan Basin of China and *Basilochelys macrobios* from the Phu Kradung Formation of Thailand. *Sinaspideretes* has 4th-7th and 11th-12th marginal scales extending onto the costals and suprapygal (Tong et al., 2014) (Fig. 13), and *Basilochelys macrobios*, also has a similar pattern of marginal scale extension even if it is not matched precisely with *Proadocus* as in *Sinaspideretes*. Its marginals, 6th-7th and 11th-12th, extend onto the costals and suprapygal (Tong et al., 2009) (Fig. 13). In addition, they have wider than long pygal bone (Tong et al., 2009; 2014).

Compared to nanhisiungchelyids, they have wider than long pygal as in *Proadocus* and basal *pantrionychians*; however, their marginal scale extension pattern is far different, restricted in only posterior parts, as in two adocid genera, *Shachemys* and *Ferganemys* (Tong et al., 2009; Syromyatnikova, 2011). Since our cladistics analysis puts two basal pantrionychians and *Proadocus* in a polyphyletic relationship and supports the monophyly of the clade Adocusia (Fig. 11), it would be more reasonable to interpret that this set of primitive characters may exist at the common ancestors of Adocidae and Nanhsiungchelyidae and separately retained or lost in either family after their divergence than they were independently evolved in

each clade. *Sinaspideretes* and *Basilochelys* are probably taxa close to the origin of these families, as suggested by the comparative analysis of Tong et al. (2009; 2014).

It seems that the primitive characters in basal pantrionychian taxa and *Proadocus* evolved independently within adocids into various directions; *Adocus* expanded marginal extension to the whole middle and posterior parts of costals and suprapygal (Sonoda et al., 2015; Hirayama et al., 2020), whereas *Ferganemys*, and *Shachemys* lessened it to the end of the posterior part (France, 2004; Syromyatnikova, 2011) (Fig. 12). And all these three genera evolved the pygal longer than wide. *Protoshachemys rubra*, the early shachemydine taxon in the Early Cretaceous from Thailand, has 4th-7th and 11th-12th marginal scales extending onto the costal and suprapygal. It is inferred that this marginal extension pattern character evolved independently in *Protoshachemys* since it forms a polytomy with other shachemydine genera (Fig. 11).



FIGURE 12. Comparison of marginal scales patterns between Proadocus and two basal pantrionychians. Marginal scales are drawn in dotted line with red color. Sinaspideretes after Tong et al. (2014); Basilochelys after Tong et al. (2009).

(2011).

VII-2. Origin and diversification of adocids

The report of basal adocid taxon in the Lower Cretaceous Formation of Gyeongsang Basin in Korea implies critical paleobiogeographic interpretations about the origin and diversification of Adocidae. Its relationship to the basal pantrionychians in the Upper Jurassic-Lower Cretaceous Formation in Thailand and South China supports the South East Asian origin of Adocidae, which is supplemented by the oldest record of adocid in Thailand (Tong et al., 2016; Danilov et al., 2011). Analyzing the temporal and geographic distribution of adocids during the Early Cretaceous period (Fig. 14), the minimum divergence dates of Adocidae were suggested to the pre-Valanginian. According to a paleobiogeographic study by Fernandez et al. (2009), South East Asian regions seemed to be isolated from the Asian mainland by possible geographic barriers during the Valanginian-Barremian, which is supported by uncorrelated temporal faunal assemblages between two regions while the high correlation was shown in pre-Valanginian. Howerver, records of adocid have been reported in strata of that period in both South East Asia (Thailand) and Mainland (Japan) (Hirayama et al., 2000; Danilov et al., 2011; Tong et al., 2016); thereby, it can be interpreted that the earliest adocid group dispersed to Northern Asian region from South East Asia before the beginning of isolation. And one 'hypothetical lineage' in Adocidae retaining primitive characters of basal pantrionychians, to which the ancestor of *Proadocus* belongs, also may have stepped on the path to North East Asia at that age.

Entering the Aptian, the biogeographic situation seemed to have changed, and the faunal assemblage of the two regions began to show a correlation

again (Fernandez et al., 2009). The distributional aspect of temporal adocids also corresponds to this biogeographic scenario, supported by the first occurrence of *Shachemys* outside South East Asia (Japan and middle Asia) in the post–Aptian age (Danilov et al., 2011) (Fig. 14).

The pathway from South East Asia to North East Asia would have been an important dispersing route for the early Cretaceous adocids. Adocids would have spread along the periphery of the continents, viewing that the inland zone connecting South East Asia and North East Asia (China) is excluded from the geographic distribution of adocids during the Cretaceous (Fig. 14) with a dominance of other turtle groups (Tong et al., 2016). These significant dispersing events were likely to happen twice during the early Cretaceous, first in pre-Valangian for the earliest adocid group, and second in the post-Aptian for *Shachemys*.

Vicariance caused by possible geographic barriers may have promoted allopatric speciation, evolving different adocids in two regions during the Early Cretaceous. The representative South East Asian adocid taxon, *Shachemys*, shows more derived morphologies than Northern Asian adocids, including *Adocus* and *Proadocus* (Hirayama, 2002; France, 2004; Tong et al.,2019); the absence of neural series and small dotted shell sculpturing which inferred to be the result of the high endemism (Fernandez et al., 2009).

The Gyeongsang Basin in southeastern Korea was geographically adjacent to the Lower Cretaceous Kanmon Group in southwestern Japan. And the previous lithostratigraphic and geochronologic studies suggested their correlation and depositional origin from the same basin (Katsube and Hayasaka, 2009; Lee et al., 2018). In addition, the similarity of the non-marine mollusk taxa yielded from

the Hasandong Formation of the Gyeongsang Basin and the Sengoku Formation in the Kanmon Group proves a biostratigraphic correlation of two regions in the Early Cretaceous, especially in freshwater fauna (Kozai et al., 2005). The well-known adocid taxon in the Kanmon Group is *Adocus sengokuensis* from the Sengoku Formation (Sonoda et al., 2015). Despite relatively insufficient materials, it shows clear morphological differences with *Proadocus*; narrow lateral projection of the first pleural scale bordered by the 4th and 5th marginals, and restriction of the 4th marginal scale to the peripheral (Sonoda et al., 2015). Thus, it is reasonably concluded that at least two or more diversified adocid taxa existed in the Gyeongsang Basin in the Early Cretaceous.

	Age	Middle Asia &Kazakhstan	Mongolia	China	Laos & Thailand	Japan	Noth America	Korea
	Maa.							
	Cam.	Adocus	Adocus				Adocus	
	San. Con. Tur.	Shachemys	<i>Adocus</i> Shachemydine			Adocus Shachemys		
	Cen.	Adocus Ferganemys	Adocus					
	Alb.	Ferganemys						
					Shachemys			
	Apt.					Adocus		Proadocus
	eocomian				lsanemys, Protoshachemys	Adocidae		
0	Ž v				Basilochelys			
Jurassi	L.Jurassi			Sinaspideretes				

FIGURE 14. Temporal and geographic distribution of basal pantrionychians and adocids during the Late Jurassic–Cretaceous (modified from Danilov et al., 2011). The basal pantrionychian taxa are written in red color.

VIII. CONCLUSIONS

A new turtle collected from the Lower Cretaceous Hasandong Formation in Korea is classified into the new genus and new species of Adocidae, Proadocus hadongensis. This taxon shows typical adocid synapomorphic characters and is also characterized by retaining primitive characters of basal pantrionychian taxa in the Late Jurassic-Early Cretaceous of South China and South-East Asia. Along with these morphological features, a cladistics analysis suggests Proadocus is one of the most basal taxa in Adocidae. The report of the basalmost adocid taxon, which is close to the early pantrionychian group in South East Asia, offers a new outlook on the early evolution of Adocidae with critical paleobiogeographic interpretations. It supports that Adocidae may have originated in South East Asia from early pantrionychian groups or their close relatives. And the possible geographic barrier believed to have been located on the border of South East Asia and the Asian mainland would have affected the dispersion and diversification of Adocidae during the Early Cretaceous. The correlation of the Gyeongsang Basin to the Kanmon Group with comparisons of two adocid taxa yielded from either region implies the potential presence of more adocid taxa in the Gyeongsang Basin during the Early Cretaceous. For more concretization of our hypotheses about the early evolution of the Adocidae, more specimens and research of Early Cretaceous adocids would be required, along with uncovering the true identity of potential 'Korean adocids' in the Gyeongsang Basin.

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APPENDIX 1. Character statements

Below are the characters modified in this study from Danilov and Syromyatnikova (2009).

Character 34. Suprapygals:

- (0) two suprapygals equally divided into two
- (1) first suprapygal much smaller than second
- (2) only one suprapygal remains
- (3) both suprapygals are absent

Character 49 (original characters 49 and 50 united). Overlapping of marginal

scales onto the costals in the middle and posterior part of the carapace:

- (0) absent or only in posterior part
- (1) Present in whole middle and posterior part
- (2) Present in partial middle and posterior part

Character 50 (original character 51). Sulcus between pleural III and marginals

VII–IX:

- (0) clearly situated on costals or situated near suture of peripherals and costals
- (1) clearly situated on peripherals
- (2) Only VII is situated on costals, and others are on peripherals (new state)

Below is the new character that is added in this study (modified from Hirayama et al. 2000: character 72).

Character 57. Entoplastron:

- (0) narrow (W<L like Ordosemys)
- (1) broad (like testudinoids)
- (2) very broad (like nanhsiungchelyids and Adocus)

APPENDIX 2. Data matrix

Xinjiangchelys tianshanensis

Adocus aksary

Adocus beatus

Anomalochelys angulate

Basilemys nobilis

Basilemys variolosa

Basilochelys macrobios

?1?0?0??????101?????00??0?0001??01000??010?0?02200000110?0????1????00101

Ferganemys itemirensis

Ferganemys verzilini

Hanbogdemys orientalis

Kharakhutulia kalandadzei

Nanhsiungchelys wuchingensis

1111111????11?1?1?????011?011?11???0???0021???10001??01201110101?2??1?100

Proadocus hadongensis

Protoshachemys rubra

Shachemys ancestralis

Shachemys baibolatica

Shachemys laosian

0011?0?0????1?0100??????200000-22000?1111311101000000?1120000011000001011

Sinaspideretes wimani

Zangerlia neimongolensis

0?1?00001100?00111111?001111????10010???0??1001?000111012001011011001?0100

Zangerlia testudinimorpha

국문초록

아도쿠스科(Adocidae)는 백악기 전기부터 신생대 제 3 기까지 아시아와 북미의 일부 지역에 걸쳐 분포했던 민물 거북 분류군으로, 잠경아목(Crvptodira) 범자라上科(Pan-Trionychia)에 속한다. 그 화석은 일본과 태국, 몽골 등의 동아시아에서 많은 수가 발견되어 왔으나 본 논문이 발표되기 이전까지 한반도에서는 그 기록이 보고된 바가 없다. 2002 년과 2007 년, 경상남도 하동군 장구섬의 하부 백악기 압트절(Aptian)에 해당하는 하산동층에서 배갑(背甲)과 복갑(腹甲)의 여러 부위, 그리고 오른쪽 상완골(上腕骨)에 해당하는 거북의 골격 화석들이 발견되었다. 이 거북에서는 아도쿠스科를 정의하는 대표적인 공유파생형질인 갑 표면의 규칙적인 구멍과 홈(pits and grooves) 형태의 장식 구조, 측갑판의 복면부에 나타나는 얇은 늑골간(肋骨幹)과 축소된 형태의 늑골두(肋骨頭)가 확인되며 이에 따라 이 거북은 한반도 최초의 아도쿠스科로 분류되었다. 그리고 이 거북이 지닌 또다른 특징인 연갑판(marginal scute)이 측판(peripheral)을 넘어 늑골판(costal)까지 확장되는 현상이 4-7 번, 11-12 번의 연갑판에서 나타나는 것과 가로길이가 세로길이보다 더 긴 넓적한 형태의 둔부판(pygal)은 후기 쥐라기 후기-전기 백악기에 동남아시아 지역에 분포했던, 초기의 범자라上科 분류군들에서 나타나는 원시적인 형질이다. 이것은 이 거북이 아도쿠스科 에서 가장 원시적인 분기적 위치에 해당함을

나타낸다. 이에 따라 이 거북은 '하동에서 발견된 원시적인 아도쿠스' 라는 뜻을 지닌 ·프로아도쿠스 하동엔시스(*Proadocus* hadongensis)라는 이름의 아도쿠스科의 신속 신종으로 명명하였다. 한반도 하부 백악기 퇴적층에서 원시적인 아도쿠스科 신속 신종의 발견은 고생물지리학적인 분석과 더불어 아도쿠스科의 초기 진화에 대해 많은 새로운 가설들을 제시한다. 프로아도쿠스와 동남아시아의 초기 범자라上科들과의 형태적 연관성은 아도쿠스科가 동남아 지역에서 초기 범자라上科 조상들로부터 기원하여 아시아의 다른 지역으로 퍼져 나갔음을 암시한다. 그리고 전기 백악기 아도쿠스科의 분포와 당시 동아시아의 고지리학적 환경을 종합해 볼 때, 아도쿠스科는 동남아시아와 동아시아내륙 사이에 지리적 장벽이 존재하지 않았던 발랑절(Valanginian) 이전에 분기하여 북쪽의 아시아로 퍼져 나갔을 것으로 추론된다. 또한 이후 발랑절-바렘절(Barremian) 기간에 존재했던 지리적 장벽은 동남아시아와 동북아시아 지역에서 서로 다른 아도쿠스科 분류군들의 이소적 종분화를 촉진시켰을 것으로 보이며 이는 동남아시아를 대표하는 샤키미스(Shachemvs)속과 동북아시아의 다른 아도쿠스科들과의 뚜렷한 형태적 차이에서 드러난다. 일본의 하부 백악기에 해당하는 칸몬그룹(Kanmon Group)은 한반도의 경상분지와 같은 분지에서 기원하였으며 유사한 민물환경에 놓여있었음이 여러 층서학 및 생층서학 연구를 통해 제시되고 있다. 그리고 칸몬그룹의 센고쿠층(Sengoku Formation)에서 발견된 또 다른 아도쿠스科 종인 아도쿠스 센고쿠엔시스(Adocus sengokuensis)는 프로아도쿠스와

뚜렷한 형태적인 차이를 보인다. 이는 전기 백악기동안 한반도와 일본의 분지에서 아도쿠스科의 종분화가 상당히 진행되었음을 의미하며 더 많은 아도쿠스科의 종들이 경상분지에 생존했을 가능성을 제시하고 있다.

주요어: 거북, 아도쿠스科, 하산동층, 전기 백악기, 아도쿠스科 진화, 동남아시아

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감사의 글

고생물 연구실에 입학했던 2021 년 3 월, 선배들께서 작성하신 졸업논문을 읽으며 '정말 멋있다. 나도 이렇게 훌륭한 연구성과와 함께 무사히 학위를 마치는 순간이 올까?' 생각을 했던 적이 있습니다. 그리고 2 년이라는 시간이 흘러 저에게도 학위과정을 마치고 졸업을 맞이하는 시간이 찾아왔습니다.

졸업논문의 마지막 란에 자판을 얹으며 도움을 주신 분들을 한분 한분 떠올려 보았습니다. 그리고 2 년전, 제가 '멋있다'는 생각했던 선배들 뒤에는 그 '멋있음'을 만들어준 수많은 감사한 이들이 존재했구나 하는 것을 깨닫게 되었습니다. 저 역시, 혼자의 힘이었으면 학위를 무사히 마치는 것이 절 때 쉽지 않았을 것 입니다. 이에 '석사 김도현'을 만들어 주신 분들께 깊은 마음을 담아 감사의 인사를 전하고자 합니다.

가장 먼저 감사를 표하고 싶은 분은 저의 지도 교수님이신 이용남 교수님 입니다. 어릴 적 교수님께서 집필하신 책을 읽으며 고생물학자라는 꿈을 키워온 저에게 교수님의 제자로 있으며 가르침을 받았던 시간은 더할 나위 없는 행복이었습니다. 교수님께서는 부족한 저에게 세심한 지도와 함께 많은 조언을 아끼지 않으셨고 가치가 높은 표본을 연구할 수 있는 기회를 주시며 단지 공룡을 좋아하는 소년에서 고생물학을 연구하는 학자로 나아가는 길을 열어주셨습니다. 앞으로

진학할 박사과정, 그리고 그 이후 수행해 나갈 연구자로서의 모든 여정에서도 교수님께서 주신 은혜와 가르침을 잊지 않고 더욱 훌륭한 고생물학자로 거듭나겠습니다.

귀중한 시간 내어 저의 논문 심사에 참여해주신 정해명 교수님과 우주선 교수님께도 감사드립니다. 두분께서는 다른 분야의 어렵고 생소한 내용이었을 저의 발표를 귀 기울여 들어 주셨고 많은 관심과 흥미를 보여주시며 제가 보람을 느낄 수 있도록 해주셨습니다. 그리고 여러 조언을 통해 논문과 연구결과의 완성도를 더욱 높이는데 도움을 주셨습니다. 국내에서 손꼽히는 척추동물 박제 표본 제작 전문가이신 이태원 선생님은 저의 연구결과의 숨은 은인 중 한 분이십니다. 선생님께서는 제가 연구하는 거북이란 분류군의 해부학적인 특징에 대해 많은 가르침을 주셨고 어렵게 모아오신 표본들을 제공 해주시며 제 표본과 비교할 수 있게 도와 주셨습니다. 선생님 덕분에 저는 더욱 질 높은 연구를 수행 하며 연구결과에 대한 더 큰 확신을 얻을 수 있었습니다. 표본을 처음 발굴하고 제가 편리하게 연구를 수행할 수 있게끔 미리 화석처리작업을 수행 해주신 공담용 연구워님 및 정승호 연구원님께도 감사의 인사를 전하고 싶습니다.

이어서 저와 대학원에서 가장 많은 시간을 보내며 도움을 주신 연구실 동료 분들께 감사를 드리고 싶습니다. 연구실의 선배들은 막내이자 많이 부족한 저를 항상 챙겨주며 많은 가르침을 주셨고 연구 외에도 저의 일상에서 좋은 일 슬픈 일이 있을 때 마다 함께 해

주셨습니다. 저의 집안에 부고가 있었을 때, 마다하지 않고 먼 길을 달려와 슬퍼하던 저를 위로해 주시던 순간은 평생 잊지 못할 것입니다.

저와는 알게 된지 10년이 넘어가는 연구실의 큰형 박진영 형은 저에게 있어 또 다른 스승이자 편한 친구 같은 존재 입니다. 형은 오랜 시간 동안 쌓아 오신 경험과 지식으로 저의 연구에 많은 도움을 주셨고 아낌없는 조언을 통해 제가 나아갈 방향을 제시해 주셨습니다. 또한 특유의 유머와 입담으로 항상 연구실 분위기를 밝게 만들어 주신 형 덕분에 더 많이 웃으며 즐거운 대학원 생활을 보낼 수 있었습니다.

많은 지식과 함께 꼼꼼함과 세심함을 갖춘 연구실의 브레인 이성진 형은 제가 연구결과를 도출하고 이를 논문으로 작성하는데 많은 조언과 도움을 주었습니다. 또한 덜렁대는 성격으로 인해 실수가 잦은 저를 위해, 논문에서 빠뜨린 부분 및 잘못된 표현, 오타 등을 찾아내어 정정해 주었습니다. 연구실에서 저의 옆자리에 계신 김수환 형은 제가 연구과정 중 어려움에 직면 할 때면 귀찮은 내색하나 없이 발벗고 다가와 해결을 위해 노력해 주었습니다. 또한 제가 연구실의 생활에 지루함을 느끼지 않도록 함께 간식을 나눠먹고 수다를 떠는 시간을 자주 보내며 뛰어난 유머감각으로 저를 자주 웃게 해주었습니다. 컴퓨터 프로그램 작동부터 드론 조종까지 못하는 게 없는 연구실의 장인 윤한상 형은 처음 입학해 연구실에서의 업무가 서툰 저를 위해 장비 조작 및 출장 시의 행정업무 등에 관해 많은 것을 가르쳐 주었습니다. 저의 짓궂은 장난에도 항상 호탕하게 웃어주고 연구실에서 마주칠 때마다 반가운 농담과 함께 인사를 건네주던 형 덕분에 더욱 편하고 즐거운

연구실 생활을 할 수 있었습니다. 현재 미국에서 열심히 공부중인 손민영 형과 김뇌헌 형 또한 빠뜨릴 수 없는 연구실의 고마운 일원들 입니다. 고생물학에 대한 열정은 그 누구도 따라 올 수 없는 민영이형은 제가 연구 도중 필요한 논문이나 자료를 찾는데 많은 도움을 주었으며 고생물학 관련 궁금증이 생길 때마다 달려가면, 모르는 게 없는 박학다식함으로 저의 부족한 지식을 채워주었습니다. 특유의 샤프함과 함께 의자에서 엉덩이를 떼는 시간이 손에 꼽는 성실함을 갖춘 뇌헌이형은 저와 학년이 제일 가까운 선배로 대학원에서 처음 입학했을 때 아직 학부생의 티를 벗지 못한 저에게 대학원에서의 생활 및 학업에 대해 많은 도움과 조언을 주었습니다.

그 외 다른 연구실 및 기관에 계신 선배들께도 감사의 인사를 드리고 싶습니다. 국립과천과학관에 계신 이정모관장님께서는 학부생 때부터 뵐 때마다 제가 고생물학자로의 진로로 나아가는데 있어 많은 격려와 응원의 말씀을 주셨습니다. 수많은 지식, 경험과 함께 대중들을 사로잡는 입담에 유머까지 갖추신 관장님을 보며 많은 것을 느끼고 배우고 있습니다. 국립대구과학관에 계신 최병도 박사님은 비록 몸담고 있는 곳이 달라 자주 뵙지는 못했지만 만날 때마다 기분 좋게 술잔을 기울일 수 있는 편한 형이자 깊이 있는 조언을 아낌없이 주시는 학계의 든든한 선배입니다. 현재 연구자 뿐 아니라 박물관의 학예사로도 멋진 모습을 보여주고 계신 박사님을 통해 큰 동기부여를 얻고 있습니다. 현재 중국에서 공부중인 전주완 형은 제가 고등학생 때부터 진로에 대한

많은 상담을 해주시며 이 분야로 오는데 큰 도움을 주었습니다. 형이 보여주신 어른스러움과 제틀함은 제가 꼭 닮고 싶은 부분 중 하나입니다. 많이 부족한 저의 곁을 항상 지켜주며 응원을 아끼지 않았던 친구들에게도 감사의 인사를 전하고자 합니다. 어릴 때부터 항상 붙어다닌 동네 친구 김지훈은 저에게 좋은 일이 생기면 누구보다 크게 웃어주고 슬픈 일이 생기면 누구보다 든든하게 어깨를 두드려 주는 멋진 친구입니다. 이 친구의 존재 덕분에 고향 내려가는 일이 언제나 즐겁고 행복합니다. 대학교 친구들인 권혜진, 김민준, 김연성, 강지석, 신민구, 박장혁, 정유경, 백유경, 이혂아, 김미송은 함께 어울려 놀 때 그 누구보다 유쾌하지만 자기의 분야에 임할 땐 진중한 모습으로 최선을 다할 줄 아는 근사한 친구들입니다. 저와 비슷한 나이대에도 불구하고 더 어른스러운 모습을 보여주며 항상 많이 배우는 녀석 들이기도 합니다. 저와는 취미생활을 공유했던 학교 동아리의 동기 선후배들, 그리고 체육관의 동료 들에게도 꼭 감사의 뜻을 표하고 싶습니다. 제가 피곤에 찌든 얼굴로 매트 위에 들어서도 웃는 얼굴로 환영해 주고 아직 갈 길이 먼 제게 문무를 두루 갖추었다는 멋진 말로 칭찬을 아끼지 않던 여러분 덕분에 취미생활을 학업과 일상의 큰 원동력으로 삼은 채 나아갈

수 있었습니다.

이외에도 지면상 이름을 전부 담을 순 없지만, 그동안 저와 함께 해주시고 크고 작은 응원을 통해 제가 더 나아갈 수 있는 힘을 주신 모든 분들께 진심 어린 감사의 말씀을 전합니다.

어릴 적부터 가져온 고생물학자라는 꿈에 드디어 첫발을 내딛게 되었습니다. 가족의 응원과 사랑이 아니었더라면 그 용기 조차 낼 수 없었을 것입니다. 아들의 말 한마디면 언제나 시간 내어 머나먼 거리의 공룡박물관으로 운전대를 잡으시고 책장 가득 공룡 관련 책을 채워 주셨던 부모님, 우리 오빠 멋있는 공부한다며 주변 친구들에게 자랑하던 동생의 모습을 떠올리며 꿈을 향해 한걸음 한 걸음 더 나아가겠습니다. 힘겨운 시간이 찾아올 때면 가족들의 얼굴을 떠올리며 이겨내고 더 멋진 학자이자 든든한 아들, 오빠로 거듭나겠습니다.

마지막으로, 저에게 너무나 큰 사랑을 주셨고 누구보다 저의 꿈을 응원 해주셨던, 그리고 하늘나라에서 여전히 저를 지켜 봐주고 계실 두 분의 할아버지와 외할머니께도, 너무 감사드리고 사랑한다는 말을 전하고 싶습니다.