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Adocus Kohaku, A New Species of Aquatic Turtle (Testudines: Cryptodira: Adocidae) from the Late Cretaceous of Kuji, Iwate Prefecture, Northeast Japan, with Special References to the Geological Age of the Tamagawa Formation (Kuji Group)

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Research Article

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Abstract

A nearly complete shell of the genus *Adocus* (Adocidae; Pan-Trionychia; Cryptodira; Testudines) was collected from the late Cretaceous (Turonian) Tamagawa Formation of Kuji Group at Kuji City, Iwate Prefecture, northeast Japan. This turtle shows unique features such as the loss of cervical scute, extreme expansion of marginal scutes overlying costal plates, and exclusion of the humeral- pectoral sulcus from entoplastron. Thus, *A. kohaku* is erected as a new species. As *A. kohaku* shows most derived position of *A. kohaku* within this genus, morphological diversity of the genus *Adocus* seems to have occurred rather early in its evolution in Eastern Asia.

Keywords: *Adocus Kohaku* sp. nov.; Cretaceous; Kuji Group; Reptilia; Testudines; U-Pb Dating

Institutional Abbreviation: KAM: Kuji Amber Museum; NIPR: National Institute of Polar Research; NMNS: National Museum Nature and Science; RH: Ren Hirayama.

Introduction

Kuji City of Iwate Prefecture, northeastern Japan has been well known as a rich source of ambers since the Neolithic era [1]. Recently, highly diverse vertebrate fauna, including more than 2000 isolated bones and teeth of turtles, crocodylomorphs and some dinosaurs, has been excavated from the upper part of the Tamagawa Formation of the Kuji Group of Kuji City [2-12].

Palynological analysis from this bone bed of the Tamagawa Formation suggests a fluvial depositional environment under a warm climate with humid conditions [13].

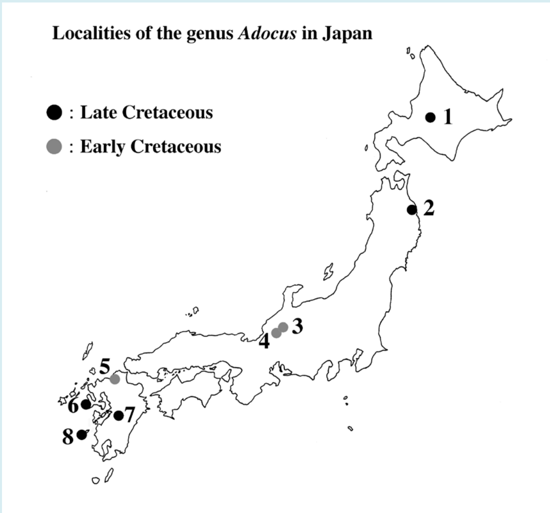

Figure 1: Localities of the genus *Adocus* in Japan. 1, *Adocus* sp. from Cenomanian of Mikasa, Hokkaido Prefecture [21]; 2, *Adocus kohaku* sp. nov. from Turonian of Kuji, Iwate Prefecture; 3, *Adocus* sp. from Aptian of Hakusan, Ishikawa Prefecture [22]; 4, *Adocus* sp. from Aptian of Katsuyama, Fukui Prefecture [18,19,23]; 5, *Adocus sengokuensis* from Barremian of Miyawaka, Fukuoka Prefecture [19]; 6, *Adocus* sp. from Santonian or Campanian of Nagasaki, Nagasaki Prefecture [24]; 7, *Adocus* sp. from Santonian? of Mifune, Kumamoto Prefecture [25]; 8, *Adocus* sp. from Campanian of Koshikijima, Kagoshima Prefecture [26].

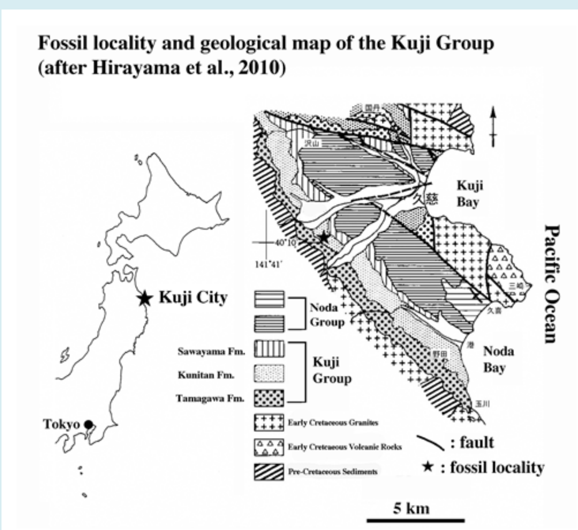

Figure 2: Fossil locality of *Adocus kohaku* sp. nov., and geological map of the Kuji Group [2,3].

Among fossil vertebrates from the Tamagawa Formation, shell materials of fresh water turtles such as trionychids (Trionychidae) and the genus *Adocus* (Adocidae) are most abundant [8,9]. Species of *Adocus* were common non-marine turtles of Asia and North America from the early Cretaceous to Paleogene [14-17]. In Japan, this genus is also an abundant non-marine turtle in Early to Late Cretaceous sediments (Figure 1) [18,19], although most of materials are disarticulated shell elements. We here report on a new species of the genus *Adocus* based on a nearly complete shell and additional specimens from the Tamagawa Formation. All fossil materials are housed in the Kuji Amber Museum. Type specimen (KAM 01) was collected by Hirayama R, Sasaki K, Sonoda T and Shikama K, August 2008.

In addition, we revise the age of the bone bed based on zircons retrieved from the tuff bed overlaying the bone bed by using U-Pb dating method [20].

Geological Setting

The Kuji Group is distributed from the downtown area of Kuji City and neighboring Noda Village in the northeastern part of Iwate Prefecture, Japan. The central part of the Upper Cretaceous Kuji Group in the Kuji district appears as a band extending in a north-south direction, which is around 15 km in length and around 2 km in width, stretching from the northwest to the southeast (Figure 2) [2,3]. The Kuji Group tilts to the east towards the Pacific Ocean at 10-20 degrees and creates a half-basin structure [27]. This group is subdivided into three formations, Tamagawa, Kunitan, and Sawayama formations, in ascending order. [9,28].

The Tamagawa Formation was deposited from a terrestrial to shallow marine environment, and the faces are mostly made from conglomerate and siltstone. This formation is about 200 m thick and divided into three lithological parts. The lowest part is composed mainly of conglomerate, with beds of tuff, siltstone, and sandstone. The basal part is characterized by mudstone in reddish color. This reddish bed was exposed along the coastline of Noda-mura by the tsunami of 2011 [9]. The middle part of the bed is made of greenish sandstones and alternating layers of conglomerate and sandstone where amber and oyster bearing beds are found [29]. The highest part is comprised of conglomerate and sandstone as well as amber- rich and tuff intercalated siltstone.

The bone bed from which the specimen in this study was excavated, is located at the highest part of the Tamagawa Formation. A U-Pb dating of the volcanic ash overlying the bone bed comes to 90.51±0.54 Ma, which indicates that the upper part of the Tamagawa Formation is Turonian [20]. The lenticular tuff bed overlays the bone bed without significant hiatus.

The tuff bed forms a lenticular shape with approximately 10 m length along the river stream and 70 cm at maximum thickness (Figure 3). The tuff bed does not have allochthonous sand and eroded plant litter, meaning that although the tuff is a lenticular deposit, it is not secondarily deposited by stream migration but part of an autochthonous tuff bed from volcanic ash fall (Mitsuzuka, Master thesis).

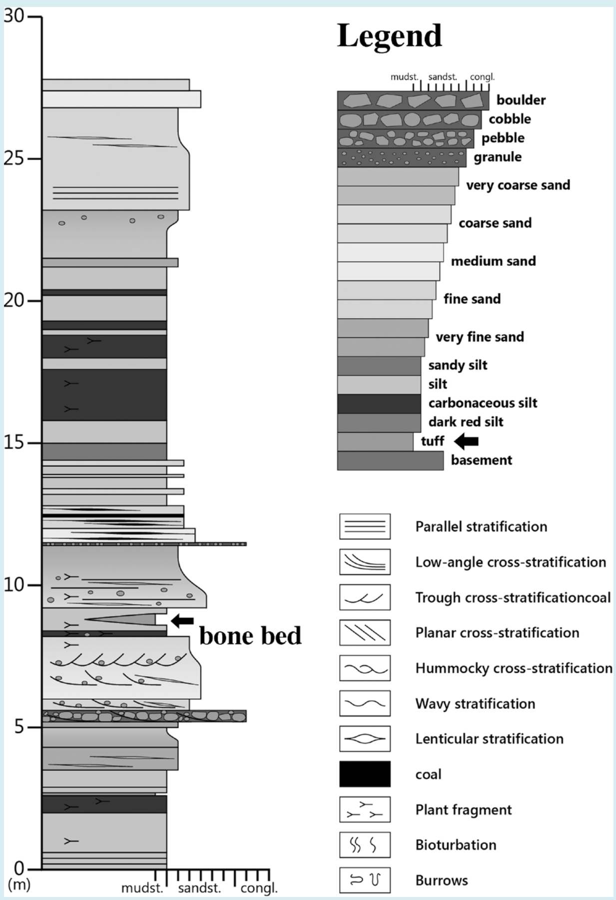

Figure 3: Geological column of the upper part of the Tamagawa Formation in the fossil locality at Kuji, Iwate Prefecture. Note that the bone bed is just overlaid by the volcanic tuff layer, showing the U/Pb dating after Hirayama, et al. [6].

Age of the Bone Bed in Previous Works

The bone bed from which the specimen in this study was excavated is conformably overlaid by a tuff bed in the outcrop of the tributary of the Osawada River (Figure 2). To date, different ages have been suggested for this bed [9,30,31] (Table 1). We emended the age of the bone bed based on the zircon of the tuff bed by using U-Pb dating method. The U-Pb dating is a widespread age-determination method for geological materials that depends on the accumulation of stable isotopes of Pb (^{206}Pb and ^{207}Pb) by radioactive decay of U (^{235}U and ^{238}U). The method has been often applied the zircon, $ZrSiO_4$ in chemical formula. Zircon is very resistant to physical and chemical weathering within a closed system and very common in volcanic ash. In addition, zircon crystals concentrate U but discriminate against Pb during their formation, resulting in high ratio of U/Pb. The two distinct decay chains (^{235}U-^{207}Pb and ^{238}U-^{206}Pb) are useful for obtaining an accurate age because of the coexistence of their own decay rates. Each decay chain individually expresses the age, as the two U-Pb decay chains independently results in a continuous change with time. Based on the features, the "concordia diagram" was introduced in order to verify whether the dual decay chains evolve within a closed system. The data of U-Pb dating are on the concordia line, meaning that the 235U-207Pb age equals the 238U-206Pb age. indicating no effect of the loss and gain of Pb or U.

Materials and Methods

A nearly complete shell (KAM 01; Figure 3) was collected by Sasaki, Hirayama, Sonoda, and Shikama from the amber collecting site nearby the Kuji Amber Museum in August of 2008. The occurrence of KAM 01 was briefly reported in an assemblage of semi-articulated shell elements in Hirayama, et al. [2,3]. KAM 01 was prepared by mechanic method. Additional materials were found from 2012 to 2019 from same locality, including KAM 16, another partially articulated specimen (Figure 4A).

Zircon Extraction

We sampled several hundred grams of tuff from the field. Zircon grains were extracted from the tuff sample by the following standard method; 1) crushing the tuff sample into the fine powder (<2.0 micrometer), separating zircons by panning in water, 3) removing heavy minerals other than zircon by heavy-liquid method, 4) removing magnetic mineral by using neodymium magnet, 5) sorting out zircon grains by hand-picking under microscope, 6) molding hand-picked zircon in epoxy resin and polishing to a middle cross-section of the height, 7) determining the analysis point based on the Cathodoluminescence imaging of zircon crystals. These procedures were conducted on NIPR and NMNS.

Sensitive High-Resolution Ion Microprobe (SHRIMP)

SHRIMP is an important tool for geologic materials. It is a high precision secondary ion mass spectrometer (SIMS) and makes in situ isotopic and chemical surface analysis of solid targets by bombarding the sample with an ion beam with 10-30 µm in diameter. SHRIMP is used for U-Pb geochronology, stable isotope analysis, trace element analysis.

Several Standard Reference were used; TEMORA2 (U-Pb value; 416.8±0.3Ma), OT4 (U-Pb value; 191.1±0.3Ma):

191.4±1.5 Ma, SoriZ93 (U-Pb value; 93.9±0.6Ma).

These ratios of U-Pb were known were used for correction U-Pb data.

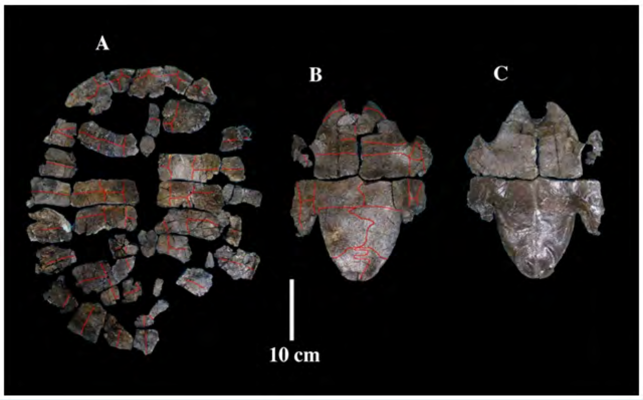

Figure 4: Turtle shell of *Adocus kohaku* sp. nov., holotype, KAM 01. **A**, carapace in dorsal view; **B**, plastron in ventral view; **C**, plastron in dorsal view. Red lines show scute sulci on shell surface.

Comparative Materials

Taxa of the genus *Adocus* from the Early Cretaceous of Japan such as *A. sengokuensis* Sonoda, et al. [19], and from the Late Cretaceous such as *A. amtgai* were examined for comparison.

Systematic Paleontology

Testudines Batsch, 1788
Cryptodira Cope, 1868
Pan-Trionychia Hummel, 1929
Adocidae Cope, 1870
Type Genus. - *Adocus* Cope, 1868
Known Distribution. - Early Cretaceous to Eocene of Asia and Late Cretaceous to Paleocene of North America.
Emended Diagnosis. - Thoracic rib heads of costals highly reduced; attachment area of xiphiplastron for pelvic girdle enlarged, forming semicircular concavity and rim; midline plastral scute sulcus sinuous.

Genus *Adocus* Cope, 1868

Type Species. -*Adocus beatus* (Leidy, 1865)
Known Distribution. - Early Cretaceous to Eocene of Asia and Late Cretaceous to Paleocene of North America.
Emended Diagnosis. - Fifth to eleventh marginal scutes medially enlarged, overlying distal portion of costal plates.

Adocus kohaku, New Species

Holotype. - KAM 01, a nearly complete shell (Figure 3).
Type Locality. - Kokuji, Kuji, Iwate Prefecture, Japan.
Type Horizon. - Tamagawa Formation, Kuji Group (Turonian, Late Cretaceous).
Etymology. - Named after Japanese name of amber as this fossil was associated with numerous ambers.
Diagnosis. - *Adocus* with cervical scute completely lost; fifth to tenth marginal scutes medially enlarged, overlying at least distal half of second to seventh costal plates; three pairs of inframarginals.
Referred Materials. - KAM 16, anterior portion of carapace (Figure 4A); OSD 249, right ninth peripheral (Figure 4C); OSD 520, entoplastron (Figure 4D); OSD 1901, partial carapace and plastron; OSD 1929, right third costal (Figure 4B); OSD 2278, right costal; OSD 2332, nuchal.

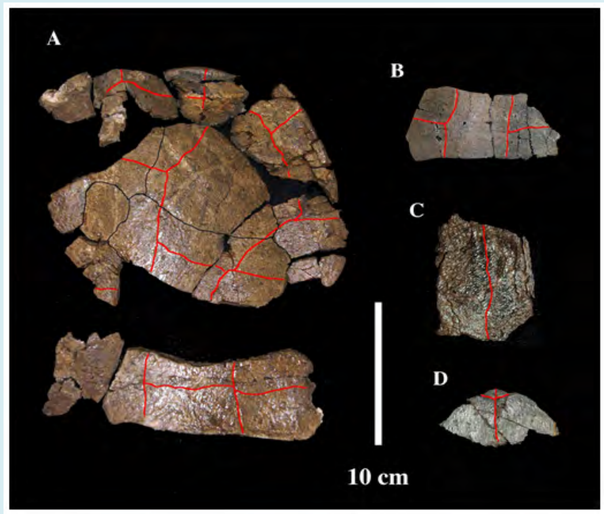

Figure 5: Referred materials of *Adocus kohaku* sp. nov. **A**, KAM 16, partial carapace, including nuchal, first to fourth neurals, right first, second and third costals, right first to fourth peripherals; **B**, OSD 1929, right third costal; **C**, OSD 249, right ninth peripheral; **D**, OSD 520, entoplastron. Red lines show scute sulci on shell surface.

Description

Shell (Figures 3 to 5)

In KAM 01 (holotype of *A. kohaku*), both carapace and plastron are well preserved, but some neurals, costals, and peripherals are lost. The carapace is estimated to be about 45 cm long, whereas the plastron is 30 cm long as preserved in KAM 01. An isolated right ninth peripheral suggests a much larger individual with at least 60 cm long carapace are present (Figure 4C). The shell surface is covered by typical adocid sculpturing, consisting of relatively small and regular grooves and pits.

Most of scute sulci are well preserved and clearly visible in KAM 01 and additional specimens. They, however, are extremely shallow as well as in the other *Adocus* species, only about 0.1 to 0.2 mm in depth, whereas living aquatic turtles with similarly sized shell, such as geoemydids, have the scute sulcus of at least 0.5 mm in depth (Hirayama, personal observation). Terrestrial turtles such as Testudinidae have the deepest scute sulcus. For instance, extant *Manouria emys* (RH 940; carapace 38 cm long) has the scute sulcus of 1.7 mm in depth. As the depth of scute sulcus is correlated with the thickness of the scale in extant turtles (Hirayama, personal observation), living *Adocus* should have had very thin scutes.

Carapace

The carapace is oval-shaped, widened slightly posteriorly, with a very shallow anterior emargination formed by the nuchal and anterior part of the first peripherals. The carapace seems low-domed, as in other *Adocus*, although it is difficult to see its exact nature due to the postmortem distortion.

The nuchal is a relatively wide hexagonal and slightly emarginated anteriorly in both KAM 01 and 16. Its free edge is rounded and upturned in the cross-section as well as in the first peripherals. The anterior border of the nuchal is relatively wide; the ratio of the anterior width of the nuchal to its maximal width is about seven-tenths, which is nearly identical with other *Adocus*. The anterolateral and posterolateral borders of the nuchal are nearly straight or slightly convex and about of the same length. As in other *Adocus*, the posterior border of the nuchal is concave and contacts with the first neural.

The neurals are represented by six elements; the third to fifth neurals are missing in KAM 01, whereas the first to fourth neurals are preserved in KAM 16. All neurals are longer than they are wide, and relatively thin and flat. The neural formula is typical of adocids: the first neural is hexagonal short-sided posteriorly, the second neural is rectangular, third to fifth neurals are hexagonal and short-sided anteriorly and the sixth neural is heptagonal in shape. The second neural of KAM 01 is very small, only about one half of the first neural in length. The seventh and eighth neurals seem absent, as in other *Adocus*.

There are two suprapygals in most species of *Adocus*, although only the second suprapygal is partially preserved in KAM 01.

The pygal is a slightly longer than wide, trapezoidal, and has straight lateral borders. The pygal morphology in KAM 01 is similar with that in other members of the Adocidae.

The costals are preserved, except for the left first and right second ones in KAM 01, whereas the right first, second and fourth costals are preserved in KAM 16. Ribheads of the costals are highly reduced and the ventral sides of costals are nearly flat as in other adocids. The seventh and eighth costals contact each other along the midline as in other *Adocus*.

The peripheral series is represented by the almost complete first to eleventh peripherals on the left side and the first to second, and fourth to eighth peripherals on the right side in KAM 01, whereas the first to third peripherals on the tight side are preserved in KAM 16. The free edges of the anterior peripherals (first to third) are upturned. The second and third peripherals on the left side seem fused together in KAM 01 as in the first and second peripherals in the second specimen of *A. amtgai*. The bridge peripherals (fourth to eighth) are mostly rectangular and seriously crushed in dorsal-ventral planes. The posterior peripherals (ninth to eleventh) are wider than the anterior ones with upturned free edges.

The cervical scute is completely absent on all nuchals (KAM 01, 16, and OSD 2332) of *A. kohaku*, whereas this scute is retained in other *Adocus*.

The first vertebral is trapezoidal, widened anteriorly and in contact with the second marginals, as in all other *Adocus*. The second to fourth vertebrals are longer than they are wide. The third vertebral seems longer than others. The fourth vertebral is constricted posteriorly, as in other *Adocus*. The fifth vertebral is possibly as small and ovate as in *A. amtgai*, although its exact outline is uncertain.

The pleurals are much longer than wide because of extreme expansion of the marginals onto the costals (Figure 5). The second to fourth pleurals are especially elongated proportionally, much narrower than the marginals on costals. In other *Adocus*, the pleurals are much wider than the marginals on the costals, or as wide as the marginals, as in *A. amtgai* (Figures 6 and 7).

The marginals are represented by a nearly complete set of scutes (12 pairs) on the left side in KAM 01. The first to third marginals are restricted to the peripherals and cover approximately half of their dorsal side. The fourth marginal overlaps onto the costals in KAM 16. The right fourth marginal overlaps the first costal only by its anteromedial part, whereas this scute overlaps the second costal by its posteromedial part in KAM 16. Thus, the overlapping of the marginals onto the costals begins with the fourth marginal as in *A. aksary*, *A. amtgai*, and *A. inexpectatus*. The fifth to tenth marginals overlap the corresponding costals (second to eighth), covering at least one- third of their width as in *A. amtgai*. The seventh to tenth marginals cover the distal half of costals, much broader than pleurals on costals.

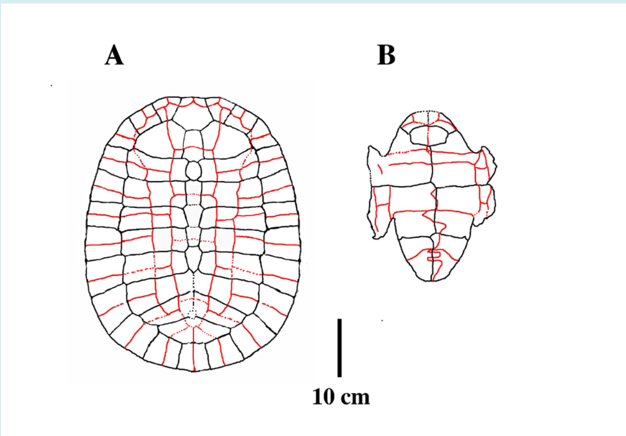

Figure 6: Shell restoration of *Adocus kohaku* sp. nov., largely based on KAM 01, with additions from KAM 16. Red lines show scute sulci on shell surface.

Plastron

The plastron is almost completely preserved in KAM 01 (Figures 4B and C). The anterior lobe of the plastron is wider than it is long (the length of the anterior lobe is about one half of its width), truncated anteriorly and does not reach the anterior carapace rim as in A. aksary and A. amtgai. The length of the anterior lobe makes up 30% of the plastron length as in *A. amtgai*. The posterior lobe narrows posteriorly and is more acute than in other *Adocus* except for *A. amtgai*. The length of the plastral bridge is 40% of the plastron length. The gular and anal notches are absent as in other *Adocus*.

The epiplastron has a relatively wide and straight (truncated) anterior border, although the anteromedial area of epiplastra was broken during excavation. The dorsal surface of the epiplastron is concave.

The entoplastron is a large hexagonal element, much wider than it is long and with short lateral borders. The entoplastron of *A. kohaku* (KAM 01 and OSD 520) is shorter and wider than other species of *Adocus*.

The hyoplastra and hypoplastra have no peculiarities and make equal contributions to the bridge length. The left hyoplastron and the right hypoplastron have a long contact that separates the right hyoplastron from the left hypoplastron as in other *Adocus*.

The xiphiplastron is longer than it is wide, narrowed posteriorly and with a nearly straight lateral border as in *A. amtgai*. The length of the xiphiplastron is ~75% of the posterior lobe length along the midline. Internally, it bears a large semicircular depression and rim for the pelvic girdle. This unique structure was figured for *Adocus* from North America by Hay [32], and appears to be present in all adocids (Hirayama, pers. obs.)

The plastral scutes are represented by a complete set in KAM 01, including two pairs of gulars, extragulars, humerals, pectorals, abdominals, femorals, anals and three inframarginals.

The gulars are relatively wide, like in *A. beatus* and *A. amtgai*. The gulars are excluded the entoplastron in KAM 01, whereas they slightly cover the latter in OSD 520 as in most other species of *Adocus*. The extragulars are relatively small, covering about one-fourth of the external surface of the epiplastra, with short medial borders that comprise about three-fifths of length of the epiplastral symphysis as in *A. beatus* and *A. amtgai*, whereas in other species they are usually longer. The lateral borders of the extragulars are strongly elongated, reaching the epi-hyoplastral suture posteriorly as in
A. amtgai.

The pectorals are extremely shortened, slightly longer medially than laterally and excluded from the entoplastron. The pectorals of other species of *Adocus* are variable: overlapping (*A. beatus*, *A. amtgai*, "*A.*" *orientalis* and *A. inexpectatus*) or not overlapping the entoplastron as in other species such as *A. bossi* from North America (Figure 8).

The abdominals are long and contribute to the rim of the inguinal notch. The femoral-anal sulcus is strongly sinuous.

The inframarginals are relatively narrow and restricted to hyo-hypoplastra as in other *Adocus* except for *A. amtgai*. There are only three inframarginals in KAM 01, whereas four inframarginals are usually found in most species of *Adocus*. The second inframarginal is much longer than others, spanning the hyo-hypoplastral suture. In other *Adocus*, the inframarginals are usually represented by four pairs, except for *A. bossi* which has three. The midline sulcus is strongly sinuous. The skin-scute sulcus lies close to the free edge of the plastral lobes.

Discussion

Age of the Bone Bed

Cathodoluminescence images of the zircon grains showed a rhythmic oscillatory pattern that showed the zircons were from igneous origin. As a result of U-Pb dating, the ratio of $^{206}Pb/^{238}U$ to $^{207}Pb/^{235}U$ almost fit the concordant curve. It showed preservation of closed system. The dating of each zircon grain mostly concentrated on a single cluster. The U-Pb dating of lenticular tuff was 90.51 ± 0.54 Ma (MSWD=0.91).

Ages of the Bone Bed of Previous Studies

Age	Material	Author
Boundary of Coniacian- Santonian	palynostratigraphy U-Pb dating carbon isotope excursion	Arimoto, et al. [30]
From boundary between Coniacian-Santonian to lower Campanian	Palynostratigraphy	Umetsu and Kurita [31]
Lower Coniacian	palynostratigraphy U-Pb dating carbon isotope excursion	Nishi, et al. [33]
Lower to middle Santonian	palynostratigraphy U-Pb dating carbon isotope excursion	Arimoto, et al. [33]
Upper Turonian	U-Pb dating	This study

Table 1: Comparison of the geological ages proposed for the bone bed of the Tamagawa Formation in previous research and this study.

Most previous studies considered the age of the bone bed ca. 86 Ma [31,34] (Table 2). These age inferences were commonly based on the palynostratigraphy. In the upper Tamagawa Formation of the Tamagawa Coast that might correlate to the bone bed, primitive and low-diverse Triprojectate pollens such as *Aquilapollenites* were found [9,31]. Triprojectates were index fossils expressing the border between Santonian and Coniacian (*ca*. 86 Ma). Arimoto, et al. [34] also depended on this argument.

We, however, question the validity of the previous dating by palynostratigraphy. 1), Umetsu and Kurita [31] offered references of Nichols, et al. [35] and Takahashi [36], in which the emergence of Triprojectates was around the border between Santonian and Coniacian. However, some other studies reported the emergence age of triprojectates in the Turonian [37]. In addition, Tanaka and Hirano [38] also pointed out a possibility that the triprojectate pollen was firstly appeared in the East Asia and subsequently spread across the North Hemisphere. Thus, the emergence would have been much earlier. Furthermore, recently Legrand, et al. [13] investigated pollen composition of the outcrop of the bone bed. They did not find triprojectates, but found other pollens and spores that were not inconsistent with Turonian flora [13].

Some researchers inferred the age based on carbon isotope oscillation [30,33,34]. Although the oscillation fits the Coniasian to Santonian, it also fits the Late Turonian. Thus, it is not valid evidence indicating an accurate age. The U-Pb age of the tuff overlaying the bone bed without hiatus nearly shows the single clustered peak, strongly indicating the accurate age of the bone bed.

Adocus kohaku is identified as a member of Adocidae based on the following characters [17]: (1) adocid-type of sculpturing, (2) narrow and shallow scute sulci, (3) weak ribheads, (4) weak rib thickenings of the costals, and (5) relatively long posterior plastral lobe (>30% of plastron length). *Adocus kohaku* is assigned to the genus *Adocus* based on the marginals that overlap onto the costals in the middle and posterior parts of the carapace.

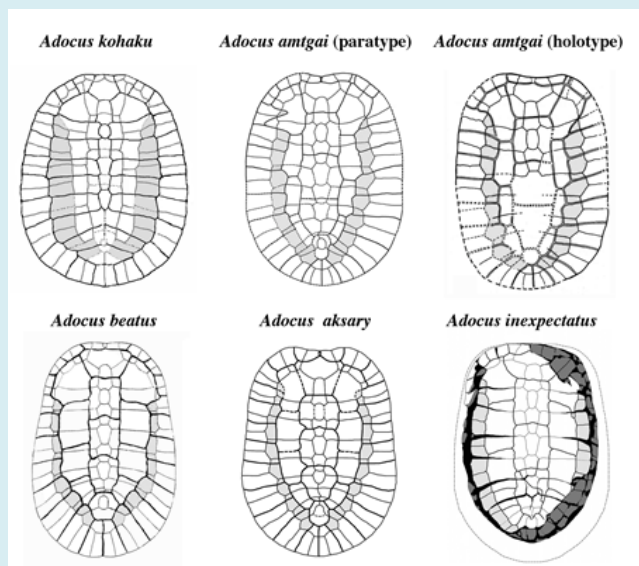

Figure 7: Carapaces of the species of *Adocus* (in dorsal views). Light gray areas show the marginal scutes covering costal plates. *A. amtgai* after Sukhanov [39] and Syromyatnikova, et al. [17], *A. beatus* after Hay [32], *A. aksary* after Syromyatnikova and Danilov [14], *A. inexpectatus* after Danilov, et al. [16]. Not to scale.

Adocus are generally considered to be a fresh water aquatic turtle based on limb and shell morphology [17,40]. Cranial morphology suggests herbivorous feeding habitat like living *Dermatemys mawii* [40].

A. *sengokuensis* is thought to be the most basal species of this genus because of the presence of a wide cervical scute and its small size (carapace less than 30 cm long as estimated). Its geological age (late Barremian of the Early Cretaceous) is also the oldest among species of *Adocus* [19]. Other species of *Adocus* share the reduced cervical scute and larger size with shell up to at least 35 cm long.

The extension of the marginals onto the costals begin with the fourth (or third) marginals in *A. aksary*, *A. amtgai*, *A. inexpectatus*, and *A. kohaku*, taxa from the Late Cretaceous and Paleogene of Asia, whereas in other species of *Adocus* from North America and the Early Cretaceous of Asia it begins with fifth marginals as more basal state of this genus (Figure 6, Table 1) [17,19]. Thus, those taxa of Asian *Adocus* from the Late Cretaceous to Paleogene are considered to be a monophyletic group sharing additional marginal extension on costals [16]. In addition to the members of this derived clade, there are other more conservative and poorly known taxa of *Adocus* in Asia from the Late Cretaceous characterized by the overlapping of the marginals onto the costals beginning with the fifth marginal such as *A. foveatus* from the Santonian of Tajikistan, and *A. kizylkumensis* from the Cenomanian of Uzbekistan [14,17].

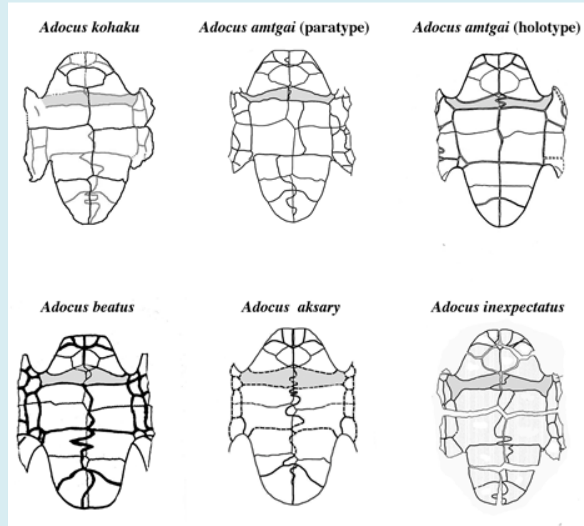

Figure 8: Plastra of the species of *Adocus* (in ventral views). Light gray areas show the pectoral scutes. *A. amtgai* after Sukhanov [39] and Syromyatnikova, et al. [17], *A. beatus* after Hay [32], *A. aksary* after Syromyatnikova and Danilov [14], *A. inexpectatus* after Danilov, et al. [16]. Not to scale.

	A. sengokuensis	*Adocus* sp.	*A. aksary*	*A. amtgai*	*A. kohaku*	*A. beatus*	*A. bossi*	*A. inexpectatus*
Locality	Japan	Japan	Uzbekistan	Mongolia	Japan	USA	USA	China
Geological age	Early Cretaceous (Barremian)	Early Cretaceous (Aptian)	Late Cretaceous (Turonian)	Early Late Cretaceous	Late Cretaceous (Turonian)	Late Cretaceous (Maastrichtian)	Late Cretaceous (Maastrichtian)	Paleogene (Late Eocene)
Carapace length	29	37	40	40	60	50	70	35
Cervical scale	Wide	Narrow	Narrow	Narrow	Absent	Narrow	Narrow	Narrow
Second to fourth pleurals	Wide (width makes up 60% of length)	Wide (width makes up 60% of length)	?	Narrow (width makes up 30% of length)	Narrow (width makes up 30% of length)	Wide (width makes up 60% of length)	Wide (width makes up 60% of length)	Wide (width makes up 60% of length)
Marginals overlapping on to the costals	Beginning with fifth marginal	Beginning with fifth marginal	Beginning with third or fourth marginal	Beginning with fourth marginal	Beginning with fourth marginal	Beginning with fifth marginal	Beginning with fifth marginal	Beginning with fourth marginal
Width of pleurals and marginals on costals	Pleurals much wider than marginals	Pleurals much wider than marginals	Pleurals much wider than marginals	Marginals as wide as pleurals	Marginals wider than pleurals	Pleurals much wider than marginal	Pleurals much wider than marginal	Pleurals much wider than marginal

Extension of gulars on to entoplastron	?	present	present	present	absent or present	absent or present	present	present
Pectorals extension on to the entoplastron	present	present	present	present	absent	present	absent	present
Number of inframarginals	?	4 pairs	?	3 or 5 pairs	3 pairs	4 pairs	3 pairs	4 pairs
Lateral border of Xiphiplastron	?	Rounded	Rounded	Nearly straight	Nearly straight	Rounded	Rounded	Rounded

Table 2: Comparison of some species of Adocus in shell characters (after Syromyatnikova, et al. [17]; Danilov, et al. [16]; Sonoda, et al. [19], with modifications).'?' denotes impossibility of measuring.

In all North American *Adocus*, the marginals primitively overlap onto the costals beginning with the fifth marginal as well. Nonetheless, *Adocus* from North America share relatively large size with at least a 50 cm long shell presumed as a synapomorphic character uniting them [32,41]. It seems apparent that the North American clade of *Adocus* originated from Asia during the early Late Cretaceous as suggested by both morphological analysis and the fossil record [19].

Adocus kohaku shares the additional more derived characters with *A. amtgai*; cervical scute highly reduced or lost; significantly wider fourth to twelfth marginals; very narrow second to fourth pleurals; the shorter of the pectorals. Therefore, *A. kohaku* and *A. amtgai* form an advanced clade within this genus (Figure 9). *Adocus kohaku*, however, has furthermore derived characters such as complete loss of cervical scute, wider marginal scutes on costal plates, and pectoral scute excluded from entoplastron (Figure 6). Additional remains of *A. kohaku* such as OSD 249 suggest this species had at least 60 cm long carapace, the largest among *Adocus* in Asia (Figure 5C). This large size is also considered as another derived state in *A. kohaku*. Thus, *A. kohaku* is the most advanced species of this genus, although its geological age (late Turonian) is rather early in the fossil record of *Adocus*. Such early occurrence of a derived taxon (*A. kohaku*) suggests early development of morphological diversifications within this genus. Similar, early diversification among Pan-Trionychia is also proposed in the family Nanhsiungchelyidae [42].

Occurrences of both most basal (*A. sengokuensis*) and most derived (*A. kohaku*) taxa of this genus from Japan implies Eastern Asia was the center of early diversification of this group during the Cretaceous since the Early Cretaceous [2-5,43-50].

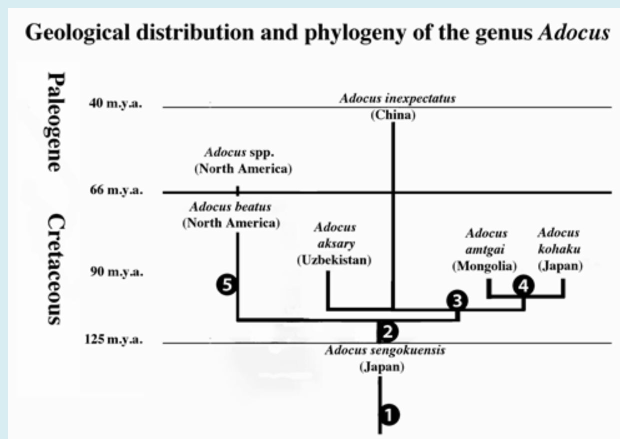

Figure 9: Geological distribution and phylogeny of the representative taxa of the genus *Adocus*. 1 ~ 5 show the following synapomorphic characters at each node. **1**, fifth to eleventh marginal scutes medially enlarged, overlying distal portion of costal plates; **2**, cervical scute reduced to much longer than wide; **3**, fourth marginal scute overlaps onto the costal plates; **4**, pleural scutes are much longer than wide because of extreme expansion of marginals on the costal plates; **5**, large size with carapace more than 50 cm long.

Conclusion

A nearly complete shell of the genus *Adocus* (Adocidae; Trionychia; Cryptodira; Testudines) was collected from the late Cretaceous (Turonian) Tamagawa Formation of Kuji Group at Kuji city, Iwate Prefecture, northeast Japan. This turtle shows unique features such as the loss of cervical scute, extreme expansion of marginal scutes overlying costal plates, exclusion of the humero-pectoral sulcus from entoplastron, and three pairs of inframarginals. Thus, *A. kohaku* is proposed as a new species. Additional remains of *A. kohaku* suggest this species had carapace length of at least a 60 cm long, the largest among *Adocus* in Asia. As *A. kohaku* is a derived taxon within this genus, its occurrence in the early Late Cretaceous suggests early development of morphological diversifications within this genus, as previously proposed for the Nanhsiungchelyidae. Occurrences of both most basal (*A. sengokuensis*) and most derived (*A. kohaku*) taxa from Japan implies eastern Asia was the center of diversification of this clade.

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