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Authors: Takahashi, Akio, Kusaka, Akane, and Kamezaki, Naoki

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Skeletal Remains of *Mauremys reevesii* (Testudines: Geoemydidae) from a Late Medieval Archeological Site in Fukuyama City, Hiroshima Prefecture, Western Japan

Akio TAKAHASHI[1]*, Akane KUSAKA[1], and Naoki KAMEZAKI[2]

[1]*Department of Zoology, Faculty of Science, Okayama University of Science, Ridai-cho 1–1, Kita-ku, Okayama 700–0005, JAPAN*
[2]*Department of Biosphere-Geosphere Science, Faculty of Biosphere-Geosphere Science, Okayama University of Science, Ridai-cho 1–1, Kita-ku, Okayama 700–0005, JAPAN*

Abstract: Partial skeletal remains of *Mauremys reevesii*, consisting of the right second and third costals of an individual, were discovered from late medieval deposit of an archaeological site in Hiroshima Prefecture, Japan. Because the site was a local port town with relatively frequent commercial exchanges then, the turtle may have possibly been brought there through direct or indirect foreign trade in the 15th Century. Current Japanese populations of *M. reevesii* have generally been considered as descendants of artificially transported individuals from outside Japan in no earlier than the late Edo period (late 18th Century). However, the present finding suggests that the species was actually introduced to Japan in the late medieval period or even earlier.

Key words: Commercial exchange; Introduced species; *Mauremys japonica*; Turtle

Introduction

Mauremys reevesii (Gray, 1931) is a medium-sized geoemydid species widely distributed across China, the main islands of Japan (Honshu, Shikoku, Kyushu, and adjacent islands), the Korean peninsula, and Taiwan (Iverson, 1992; Lovich et al., 2011; TTWG, 2017). This species was previously assigned to the genus *Chinemys* (e.g., Smith, 1931; Nakamura and Uéno, 1963; Ernst and Barbour, 1989) and the subfamily "Batagurinae" (Hirayama, 1985; Gaffney and Meylan, 1988) based on its morphological characteristics. However, recent molecular analyses indicate that this species is nested within the genus *Mauremys* (Geoemydidae), forming a monophyletic clade along with *M. japonica* from Japan, *M. sinensis* from Taiwan, southeastern China and northern Indochina, and *M. nigricans* from southern China (Barth et al., 2004; Feldman and Parham, 2004; Spinks et al., 2004; TTWG, 2017).

The Japanese populations of *M. reevesii* were first described as *Emys vulgaris picta* Schlegel, 1844 and were believed to be indigenous for many years (e.g., Stejneger, 1907;

* Corresponding author. Tel and Fax: +81–86–256–9670;
E-mail address: akiotkh@gmail.com

Nakamura and Uéno, 1963; Sengoku, 1979; Hikida, 2002). However, unambiguous evidence of occurrence of this turtle in Japan has not been found at all in Quaternary fossils excavated (Hirayama, 2006; Hirayama et al., 2007; Goto, 2013; Takahashi, 2015), skeletal remains from archaeological sites (Takahashi, 2015, 2017), or in old literature or drawings produced earlier than the late Edo period (approximately 200 years ago: Hikida and Suzuki, 2010; Goto, 2015, 2016). In addition, a recent molecular study failed to detect any explicit differences between Japanese and non-Japanese samples of *M. reevesii*. These suggest that the current Japanese populations of the species are entirely of artificial origins (Suzuki et al., 2011).

Of these lines of evidence, however, the absence of *M. reevesii* from archeological sites need careful verification, because most skeletal remains of turtles documented in archeological excavation reports do not seem to have been convincingly identified, i.e., with appropriate comparative investigations of diagnostic characters in specimens examined. In addition, although approximately 2,000 archaeological excavation reports are published in Japan every year (Takada et al., 2015), most of these obviously lack review by zoological taxonomists in terms of accuracy in identification of non-domestic animal remains therein referred (Takahashi, 2015, 2017). Likewise, paleographical evidence as above may suffer overestimation, because absence of old (>200 yrPB) literature referring to a particular animal species can be purely fortuitous.

We have been searching for historical records of freshwater turtles from paleontological and archeological sites, dating back to the late Edo period or earlier, on the main islands of Japan. During this effort, we detected new skeletal remains of *M. reevesii* from the Kusado Sengen-chō site of Fukuyama City in the southeastern part of Hiroshima Prefecture, western Japan (Fig. 1). The site accommodates the ruins of a medieval port town.

In this paper, we describe these skeletal remains and discuss their implications on the origin of *M. reevesii* on the main islands of Japan, as well as the use of this turtle by inhabitants of the Kusado Sengen-chō area in the corresponding date.

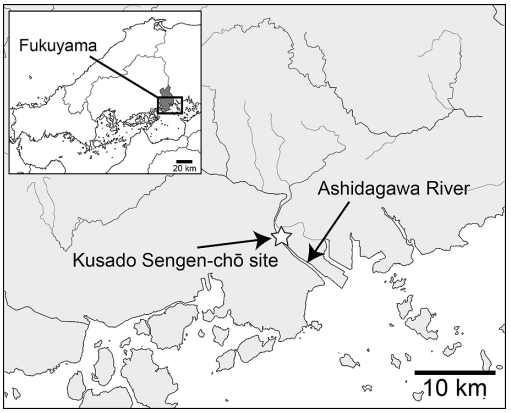

FIG. 1. Map of the Chugoku region, showing the location of the Kusado Sengen-chō site, Fukuyama City, Hiroshima Prefecture, western Japan.

MATERIALS AND METHODS

The skeletal remains of *M. reevesii* reported here were collected *in situ* along with those of five saltwater fishes, a domestic dog, and a Japanese marten (*Martes melampus*) from a blackish gray sand deposit, which filled a rectangular pit (SK2422) during the 30th excavation at the Kusado Sengen-chō site on November 19, 1981 (HPIK, 1994; Ishimaru and Matsui, 2008). However, this turtle had never been reported. These remains, consisting of two perfectly preserved costal bony plates with mutual sutural connections, are attributed to a single individual. The presence of the sulcus between the two pleural scutes on the dorsal surface of a costal plate, having a slight anterior midpoint projection and a shallow concavity of the posterior border of a vertebral scute, as well as absence of the sutural facet for the plastral buttress on the ventral surfaces, indicate that this specimen represents the right second and third costals (see below). The size and incomplete ossifica-

tions of the distal margins and growth rings no fewer than four on the area covered by the second vertebral scute indicate that the individual was subadult (i.e., an age before attaining sexual maturity) or young adult in ontogenetic stage (Lovich et al., 2011), even though the ring count does not accurately represent the age (Wilson et al., 2003). The specimen has no cut marks and no impact pits on both dorsal and ventral surfaces. The age of this archeological site has generally been divided into phases I, II, III, and IV (HPIK, 1994), and the deposit, in which the present specimen was found, has been correlated with the early phase IV, corresponding to the period from the late medieval (mid- to late 15th Century) to the late Muromachi in Japanese history on the basis of pottery chronology (HPIK, 1994). The specimen is currently deposited in the Hiroshima Prefectural Museum of History (HPMH; Fukuyama, Japan) as HPMH-30A00392.

Morphological comparisons of the newly found remains were confined to the geoemydid turtles recorded from the Neogene to the Quaternary within the main islands of Japan as follows (see Hirayama, 2006; TEWG, 2015; TTWG, 2017, for review): *Cuora miyatai* from the Middle Pleistocene of Honshu and Kyushu (Shikama, 1949); *M. japonica* living in Honshu, Shikoku, and Kyushu, as well as known from the prehistoric to historic deposits of Honshu and Kyushu (Takahashi, 2015); *M. nigricans* and *M. sinensis* from the East Asian continental area (TTWG, 2017) and recorded from the Pliocene of Kyushu (as *Chinemys* cf. *nigricans* and *Ocadia sinensis*, Hirayama, 2001); *M. nipponica* from the Middle Pleistocene of Honshu (Hirayama et al., 2007); *M. reevesii* from Honshu, Shikoku, and Kyushu (Lovich et al., 2011; TTWG, 2017) and known from the early modern deposits of Honshu (Takahashi, 2015); *M. tanegashimensis* from the middle Miocene of Tanegashima Island (Takahashi et al., 2013); and *M. yabei* from the Middle to Late Pleistocene of Honshu (Shikama, 1949; Hirayama and Isaji, 2010). These comparisons were made mainly because the terrestrial vertebrate fauna within this island assemblage is generally considered to date back to the late early or early middle Miocene epoch, when this area was first isolated from the eastern part of the Eurasian continent (Takahashi et al., 2013; Okamoto, 2017). In addition, *M. mutica* from China, Vietnam, Taiwan, and the Southern Ryukyus (TTWG, 2017) was also included in the comparative taxa, because this species also has some local populations in the Kansai region of Honshu (Yasukawa et al., 1996). Based on literature information and absence of fossil records from Japan, the Kansai population of *M. mutica* is generally considered to have derived from individuals introduced from Taiwan during the period between the late 19th to the first half of the 20th centuries (Yasukawa et al., 1996; TTWG, 2017). However, there is no concrete evidence to verify this assumption. Morphological data were taken from the fossils and extant skeletal specimens in the collections of Okayama University of Science (OUS-AT); the Institute of Geology and Paleontology, Tohoku University (IGPS; stored in the Tohoku University Museum); the Natural History Museum and Institute, Chiba (CBM-PV); the Minamitane-cho Board of Education, Kumage (MTE); and Yuichirou Yasukawa (YY). Information was also taken from previously published literature. Taxonomy of the family Geoemydidae in this study follows TTWG (2017). Shell terminology follows Zangerl (1969) and measurements were taken to the nearest 0.1 mm using a digital slide caliper.

Species Account

Family Geoemydidae Theobald, 1868
Genus *Mauremys* Gray, 1869
Mauremys reevesii (Gray, 1931)
Figs. 2, 3A

Material

The right second and third costals with

FIG. 2. Right second and third costals of *Mauremys reevesii* (HPMH-30A00392) from a late medieval (mid- to late 15th Century) pit-filling deposit at the Kusado Sengen-chō site. Scale bar represents 1 cm.

mutual sutural connections attributed to a single individual (HPMH-30A00392).

Locality

The Kusado Sengen-chō site located in a delta within the downstream area of the Ashidagawa River, Fukuyama City, Hiroshima Prefecture, Japan.

Age

Late medieval (mid- to late 15th Century).

Description

The right second (26.5 mm long, 8.2 mm wide proximally, and 6.8 mm wide distally) and third (28.3 mm long, 8.2 mm wide proximally, and 6.7 mm wide distally) costals in complete preservation have sutural connections with each other. In each costal, the anteromedial border is much longer than the postelomedial border, indicating that the anterior neurals show hexagonal and short-sided anteriorly. The right second and third costals are covered medially by the second and third vertebrals and laterally by the right first and second pleurals and show growth rings. The dorsal view shows a distinct right lateral keel on these costals. The second vertebral is hexagonal in shape and concave

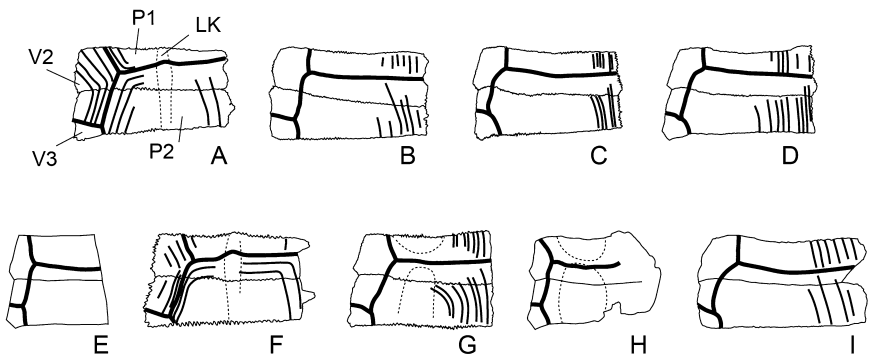

FIG. 3. Line drawings of the right second and third costals of the Kusado Sengen-chō material (A, HPMH-30A00392), *Mauremys japonica* (B, OUS-AT510), *M. mutica* (C, OUS-AT314), *M. nigricans* (D, YY uncatalogued specimen), *M. nipponica* (E, CBM-PV 686; modified from Hirayama et al. [2007: Figure 9]), *M. reevesii* (F, OUS-AT309), *M. sinensis* (G, OUS-AT420), *M. tanegashimensis* (H, MTE1; modified from Takahashi et al. [2013: FIGURE 4]), and *M. yabei* (I, IGPS 65678) in dorsal view. Abbreviations: LK, lateral keel; P, pleural scute; V, vertebral scute. Not scaled.

posteriorly. The intersection point of the sulcus between the second and third pleurals and the right lateral keel is slightly projected anteriorly.

Comparisons

Within the present comparative taxa, the present material (HPMH-30A00392) is similar to *M. japonica*, *M. mutica*, *M. nigricans*, *M. nipponica*, *M. reevesii*, *M. sinensis*, *M. tanegashimensis*, and *M. yabei*, but is clearly different from *C. miyatai* in having the hexagonal anterior neurals short-sided anteriorly (Stejneger, 1907; Smith, 1931; Fang, 1934; Shikama, 1949). This feature has long been used as one of the diagnostics to identify genus rank within the family Geoemydidae (e.g., Boulenger, 1889; Smith, 1931; Hirayama, 1985; Gaffney and Meylan, 1988; Yasukawa et al., 2001). Thus, we have excluded *C. miyatai* from the following comparisons.

The growth rings on the carapace (Fig. 3, Table 1: character 1) are found in HPMH-30A00392, *M. japonica*, *M. mutica*, *M. nigricans*, *M. reevesii*, *M. sinensis*, and *M. yabei* (Stejneger, 1907; Fang, 1934; Yasukawa et al., 1996; Hirayama et al., 2007; Hirayama and Isaji, 2010); however, they are absent from *M. nipponica*, and *M. tanegashimensis* (Hirayama et al., 2007; Takahashi et al., 2013). In addition, the posterolateral side of the second vertebral is nearly straight (Fig. 3, Table 1: character 2) in HPMH-30A00392, *M. japonica*, *M. nipponica*, *M. reevesii*, *M. sinensis*, and *M. tanegashimensis* (Boulenger, 1889; Stejneger, 1907; Hirayama et al., 2007; Hirayama and Isaji, 2010; Takahashi et al., 2013) but is distinctly concave medially in *M. mutica*, *M. nigricans*, and *M. yabei* (Fang, 1934; Yasukawa et al., 1996; Shikama, 1949). Moreover, the posterior side of the second vertebral is concave widely in HPMH-30A00392 (Fig. 3, Table 1: character 3), which is shared by a few *M. japonica* (4/14 individuals examined), *M. nigricans*, *M. nipponica*, *M. reevesii*, some *M. sinensis* (4/7 individuals examined), and *M. yabei* (Boulenger, 1889; Stejneger, 1907; Shikama, 1949; Hirayama et al., 2007; Hirayama and Isaji, 2010). On the other hand, most of *M. japonica* (10/14 individuals examined), *M. mutica*, some *M. sinensis* (3/7 individuals examined), and *M. tanegashimensis* lack this character (Fang, 1934; Yasukawa et al., 1996; Hirayama et al., 2007; Takahashi et al., 2013). Furthermore, the distinct continuous longitudinal keel on the second and third costals (Table 1: character 4) in HPMH-30A00392 is shared exclusively with *M. reevesii* (Boulenger, 1889; Lovich et al., 2011) among the eight taxa that were compared. *M. sinensis* and *M. tanegashimensis* also have a longitudinal keel on the costals, but it is obtuse and discontinuous (Ernst and Barbour, 1989; Takahashi et al., 2013), which is different from that of the present material and *M. reevesii*. On the other hand, *M. japonica*, *M. mutica*, *M. nigricans*, *M. nipponica*, and *M. yabei* obviously lack this feature (Stejneger, 1907; Fang, 1934; Shikama, 1949; Yasukawa

Table 1. Comparisons of the geoemydid turtle found from the Kusado Sengen-chō site with eight species of the genus *Mauremys* sharing the frontally short sided anterior neurals. Character 1: growth rings on the carapace present; character 2: posterolateral side of the second vertebral nearly straight; character 3: posterior side of the second vertebral distinctly concave widely; and character 4: longitudinal continuous lateral keel on the second and third costals. Symbols + and – indicate presence and absence, respectively.

species	characters			
	1	2	3	4
Kusado Sengen-chō turtle	+	+	+	+
M. japonica	+	+	+/–	–
M. mutica	+	–	–	–
M. nigricans	+	–	+	–
M. nipponica	–	+	+	–
M. reevesii	+	+	+	+
M. sinensis	+	+	+/–	–
M. tanegashimensis	–	+	–	–
M. yabei	+	–	+	–

et al., 1996; Hirayama et al., 2007). Based on these morphological characteristics, HPMH-30A00392 was assigned to *M. reevesii*.

Discussion

In the present study, partial carapacial material of a geoemydid turtle from a late medieval deposit (mid- to late 15th Century) in the Kusado Sengen-chō site was identified as *M. reevesii* with certainty. This finding, remarkably predating the previous archeological and paleographic records of this species from Japan (Hikida and Suzuki, 2010; Goto, 2015, 2016; Takahashi, 2015), brings into question the generally prevailing notion that the current populations of this species in the main islands of Japan are descendants of individuals artificially introduced from East Asian continental areas, such as China, Korea, and Taiwan, approximately 200 years ago (Suzuki et al., 2011).

Based on a large number of archeological remains obtained from 49 archeological excavations for 36 years, the Kusado Sengen-chō site is considered to have been a flourishing local port town from the late 13th to the early 16th centuries (late medieval period or the Muromachi period in Japanese history: Iwamoto, 2000). For example, a lot of medieval potteries that are contemporaneous with the present turtle remains have been excavated from this site, including those obviously transported from other parts of Japan, as well as from China, the Korean peninsula, and Vietnam (Suzuki, 1994). These artifacts indicate that the Kusado Sengen-chō site had a relatively high volume of commercial transactions. Thus, the *M. reevesii* individual found at this site might have been brought to Fukuyama from abroad or from another domestic port town through commercial exchange. The present finding also implies that the ancestors of the current feral populations of this species on the main islands of Japan include those introduced during the late 15th Century or even earlier.

A large number of *M. japonica* shells with distinct butchering marks have also been recovered from a later pit (ca. late 15th Century to early 16th Century: late phase IV) (Fukushima, 1995; Goto, 2013; Takahashi and Kusaka, unpublished data). This suggests that the people who lived within this site in the 15th to 16th centuries preferred this freshwater turtle as diets (Goto, 2013). In comparison, the present skeletal material of *M. reevesii* is estimated to be slightly older (the mid- to late 15th Century deposit in a pit). This may reflect that *M. reevesii* was less popular as diet of the Kusado Sengen-chō people or rarer in the Fukuyama area than *M. japonica* during the late medieval period.

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Literature Cited

Barth, D., Bernhard, D., Fritzsch, G., and Fritz, U. 2004. The freshwater turtle genus *Mauremys* (Testudines, Geoemydidae)—a textbook example of an east–west disjunction or a taxonomic misconcept? *Zoologica Scripta* 33: 213–221.

Boulenger, G. A. 1889. *Catalogue of the Chelonians, Rhynchocephalians, and Crocodiles in the British Museum (Natural History)*. Taylor and Francis, London.

Ernst, C. H. and Barbour, R. W. 1989. *Turtles of the World*. Smithsonian Institution Press, Washington, D. C.

Fang, P. W. 1934. Notes on some chelonians of China. *Sinensia* 4: 145–199.

Feldman, C. R. and Parham, J. F. 2004. Molecular systematic of Old World stripe–necked turtles (Testudines: *Mauremys*). *Asiatic Herpetological Research* 10: 28–37.

Fukushima, M. 1995. Chapter IV-7. Faunal and plant remains. p. 135–139. *In*: Hiroshima Prefectural Institute for the Kusado Sengen-chō Site Investigations (ed.), *Kusado Sengen-chō Site, a Medieval Port Town in Hiroshima*. Report of Archaeological Investigations, volume IV—Excavations in the southern half of the south area. Hiroshima Prefectural Board of Education. Yamawaki Printing Co., Ltd., Hiroshima, Japan.

Gaffney, E. S. and Meylan, P. A. 1988. A phylogeny of turtles. p. 157–219. *In*: M. J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds*. Oxford University Press, New York.

Goto, Y. 2013. *Mauremys japonica* excavated from the medieval ruins called "Kusado Sengen-cho" was used as food. *Bulletin of the Herpetological Society of Japan* 2013: 128–130.

Goto, Y. 2015. A record of *Mauremys japonica* captured in Edo City (present Tokyo Prefecture) in 1824. *Bulletin of the Herpetological Society of Japan* 2015: 18–20.

Goto, Y. 2016. Two sketches of *Mauremys japonica* imported from China, which were drawn by Kurimoto Tanshu in the latter half of the Edo era. *Bulletin of the Herpetological Society of Japan* 2016: 119–122.

Hikida, T. 2002. *Hachurui no shinka* [*Natural History of the Reptiles*]. University of Tokyo Press.

Hikida, T. and Suzuki, D. 2010. The introduction of the Japanese populations of *Chinemys reevesii* deduced from descriptions in the pharmacopias of the Edo Era. *Bulletin of the Herpetological Society of Japan* 2010: 41–46.

Hirayama, R. 1985. Cladistic analysis of batagurine turtles (Batagurinae: Emydidae: Testudinoidea); a preliminary result. *Stvdia Geologica Salmanticensia, volumen especial 1, Stvdia Palaeocheloniologica* I: 141–157.

Hirayama, R. 2001. Fossil turtles from the Tsubusgawa Formation (Pliocene) of Ajimu-cho, Oita Prefecture, northern Kyushu, Japan. *Research Report of the Lake Biwa Museum* 18: 79–96.

Hirayama, R. 2006. Review of fossil turtles of Japan. *Fossils* 80: 47–59.

Hirayama, R. and Isaji, S. 2010. Additional turtle fossils from the Kiyokawa Formation of the Shimosa Group (Middle Pleistocene) at Sodegaura City, Chiba Prefecture, Japan. *Journal of the Natural History Museum and Institute, Chiba* 11: 29–35.

Hirayama, R., Kaneko, N., and Okazaki, H. 2007. *Ocadia nipponica*, a new species of aquatic turtle (Testudines: Testudinoidea: Geoemydidae) from the Middle Pleistocene of Chiba Prefecture, central Japan. *Paleontological Research* 11: 1–19.

HPIK (Hiroshima Prefectural Institute for the Kusado Sengen-chō Site Investigations). 1994. *Kusado Sengen-chō Site, a Medieval Port Town in Hiroshima*. Report of Archaeological Investigations, volume II—Excavations in the southern half of the north area. Hiroshima Prefectural Board of Education. Yamawaki Printing Co., Ltd., Hiroshima, Japan.

Ishimaru, E. and Matsui, A. 2008. Uses of animal resources at the Kusado Sengen-chō Site. *Bulletin of Hiroshima Prefectural Museum of History* 10: 11–34.

Iverson, J. B. 1992. *A revised checklist with distribution maps of the turtles of the World*. Privately published, Richmond, Indiana.

Iwamoto, S. 2000. *Kusado Sengen* [*The Kusado*

Sengen-chō Site]. Kibito Kouko Library 6. Kibito Publishing, Okayama, Japan.

Lovich, J. E., Yasukawa, Y., and Ota, H. 2011. *Mauremys reevesii* (Gray 1831)—Reeves' turtle, Chinese three-keeled pond turtle. *In*: A. G. J. Rhodin, P. C. H. Pritchard, P. P. van Dijk, R. A. Saumure, K. A. Buhlmann, J. B. Iverson, and R. A. Mittermeier (eds.), *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group*. *Chelonian Research Monographs* 5: 050.1–050.10, doi:10.3854/crm.5.050.reevesii.v1.2011, http://www.iucn-tftsg.org/cbftt/

Nakamura, K. and Uéno, S.-I. 1963. *Japanese Reptiles and Amphibians in Colour*. Hoikusha, Osaka.

Okamoto, T. 2017. Historical biogeography of the terrestrial reptiles of Japan: a comparative analysis of geographic ranges and molecular phylogenies. *In*: M. Motokawa and H. Kajihara (eds.), *Species Diversity of Animals in Japan. Diversity and Commonality in Animals*. Springer, Tokyo.

Sengoku, S. 1979. *Amphibians and Reptiles in Color*. Ieno-hikari Kyo-kai, Tokyo.

Shikama, T. 1949. The Kuzuü ossuaries, geological and palaeontological studies of the limestone fissure deposits, in Kuzuü, Totigi Prefecture. *Scientific Reports of Tohoku University, second series (Geology)* 23: 1–201 (with 32 plates).

Smith, M. A. 1931 reprinted 1973. *The Fauna of British India, Including Ceylon and Burma. Reptilia and Amphibia. Vol. 1.-Loricata, Testudines.* First published in 1931 by Taylor and Francis Ltd., London and reprinted 1973 by Ralph Curtis Books, Florida.

Spinks, P. Q., Shaffer, H. B., Iverson, J. B., and McCord, W. P. 2004. Phylogenetic hypotheses for the turtle family Geoemydidae. *Molecular Phylogenetics and Evolution* 32: 164–182.

Stejneger, L. 1907. Herpetology of Japan and adjacent territories. *Bulletin of the United States National Museum* 58: 1–557.

Suzuki, D., Ota, H., Oh, H-S., and Hikida, T. 2011. Origin of Japanese populations of Reeve's pond turtle, *Mauremys reevesii* (Reptilia: Geoemydidae), as inferred by a molecular approach. *Chelonian Conservation and Biology* 10: 237–249.

Suzuki, Y. 1994. Chapter IV-1. Pottery and clay objects. p. 55–88. *In*: Hiroshima prefectural Institute for the Kusado Sengen-chō Site Investigations (ed.), *Kusado Sengen-chō Site, a Medieval Port Town in Hiroshima*. Report of Archaeological Investigations, volume II—Excavations in the southern half of the north area. Hiroshima Prefectural Board of Education. Yamawaki Printing Co., Ltd., Hiroshima, Japan.

Takada, Y., Morimoto, S., Tanaka, S., Shoji, Y. Fukuyama, E., Yada, T., and Nagasima, Y. 2015. Construction of the comprehensive database of archaeological site reports in Japan. *Special issue of Computer and Humanities Symposium* December 2015: 139–144.

Takahashi, A. 2015. History of extant freshwater turtles of Japan based on fossil and skeletal remains. *Bulletin of the Herpetological Society of Japan* 2015: 133–143.

Takahashi, A. 2017. Quaternary terrestrial and freshwater turtle fauna of the Ryukyu Archipelago, Japan, and its paleozoogeographic implications. *Kaseki Kenkyukai Kaishi* [*Journal of Fossil Research*] 50: 10–21.

Takahashi, A., Ōki, K., Ishido, T., and Hirayama, R. 2013. A new species of the genus *Ocadia* (Testudines: Geoemydidae) from the middle Miocene of Tanegashima Island, southwestern Japan and its paleogeographic implications. *Zootaxa* 3647: 527–540.

TEWG (Turtle Extinctions Working Group: Rhodin, A. G. J., Thomson, S., Georgalis, G., Karl, H.-V., Danilov, I. G., Takahashi, A., de la Fuente, M. S., Bourque, J. R., Delfino, M., Bour, R., Iverson, J. B., Shaffer, H. B., and van Dijk, P. P.). 2015. Turtles and tortoises of the world during the rise and global spread of humanity: first checklist and review of extinct Pleistocene and Holocene chelonians. *In*: A. G. J. Rhodin, P. C. H. Pritchard, P. P. van Dijk, R. A. Saumure, K. A. Buhlmann, J. B. Iverson, and R. A. Mittermeier (eds.), *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle*

Specialist Group. Chelonian Research Monographs 5: 000e.1–66.

TTWG (Turtle Taxonomy Working Group: Rhodin, A. G. J., Iverson, J. B., Bour, R. Fritz, U., Georges, A., Shaffer, H. B., and van Dijk, P. P.). 2017. Turtles of the world: annotated checklist and atlas of taxonomy, synonymy, distribution, and conservation status (8th ed.). *In*: A. G. J. Rhodin, J. B. Iverson, P. P. van Dijk, R. A. Saumure, K. A. Buhlmann, P. C. H. Pritchard, and R. A. Mittermeier (eds.), *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs* 7: 1–292. doi: 10.3854/crm.7.checklist.atlas.v8.2017.

Yasukawa, Y., Hirayama, R., and Hikida, T. 2001. Phylogenetic relationships of geoemydine turtles (Reptilia: Bataguridae). *Current Herpetology* 20: 105–133.

Yasukawa, Y., Ota, H., and Iverson, J. B. 1996. Geographic variation and sexual size dimorphism in *Mauremys mutica* (Cantor, 1842) (Reptilia: Bataguridae), with description of a new subspecies from the Southern Ryukyus, Japan. *Zoological Science* 13: 303–317.

Wilson, D. S., Tracy, C. R., and Tracy, C. R. 2003. Estimating age of turtles from growth rings: a critical evaluation of the technique. *Herpetologica* 59: 178–194.

Zangerl, R. 1969. The turtle shell. p. 311–339. *In*: C. Gans and T. Parsons (eds.), *Biology of the Reptilia, Volume 1*. Academic Press, New York.

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Appendix 1

Specimens examined: *Cuora miyatai*, IGPS Reg. 65667; *Mauremys japonica*, OUS-AT1, 83, 139–142, 247, 330, 425, 467, 509–510, 550, 571; *M. mutica*, OUS-AT146, 248, 252, 257, 267, 311, 313–314, 316, 398, 505; *M. nigricans*, YY one uncatalogued specimen; *M. nipponica*, CBM-PV 686 (holotype); *M. reevesii*, OUS-AT137, 273–274, 291, 295, 301, 308–310, 530, 548, 564, 566–567, 568–570; *M. sinensis*, OUS-AT40, 86, 138, 174, 383–384, 420; *M. tanegashimensis*, MTE1 (holotype); *M. yabei*, IGPS 65678 (holotype). Abbreviations are as follows: CBM-PV, vertebrate collection of the Natural History Museum and Institute, Chiba; IGPS, collections of the Institute of Geology and Paleontology, Tohoku University, Sendai, stored in the Tohoku University Museum; MTE collections of the Minamitane-cho Board of Education, Kumage; OUS, turtle collection stored at the Department of Zoology, Faculty of Science, Okayama University of Science, Okayama; YY, Turtle collection of Yuichirou Yasukawa.