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A new species of the genus *Ocadia* (Testudines: Geoemydidae) from the middle Miocene of Tanegashima Island, southwestern Japan and its paleogeographic implications

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Abstract

A new geoemydid turtle, *Ocadia tanegashimensis* (Testudines: Geoemydidae) is described on the basis of a relatively well–preserved shell from the lower middle Miocene of Tanegashima Island, Kagoshima Prefecture, southwestern Japan. This species is clearly distinguished from two congeneric species (extant *O. sinensis* and *O. nipponica* from the middle Pleistocene of eastern Japan) due to the presence of the following character states: length of the entoplastron as long as the interhyoplastral suture, the costals dovetailed with one another in outline, the third pleural overlapping only the sixth and seventh peripherals. The present study suggests that the initial intrageneric diversification of *Ocadia* began not later than the early Miocene in eastern Asia.

Key words: Reptilia, *Ocadia tanegashimensis* **sp. nov.**, Miocene, Kawachi Formation, Kukinaga Group, paleogeography

Introduction

The genus *Ocadia* (Testudines: Geoemydidae) consists of the extant *O. sinensis* from northern Vietnam, southern China, and Taiwan (Iverson 1992) and *O. nipponica*, an extinct species from the middle Pleistocene of Chiba Prefecture, Honshu, Japan (Hirayama *et al*. 2007). In recent molecular phylogenetic studies, this genus has been frequently synonymized with *Mauremys* along with *Chinemys* (*e.g*., Fritz and Havaš 2007; Turtle Taxonomy Working Group 2007; Lovich *et al*. 2011) because *O. sinensis*, *M. japonica* and *Chinemys* spp. form a monophyletic clade and are included in a major, more inclusive clade with the other species of the genus *Mauremys* sensu stricto (Honda *et al*. 2002; Barth *et al*. 2004; Feldman and Parham 2004; Spinks *et al*. 2004; Sasaki *et al*. 2006; Jiang *et al*. 2011). However, to date, no diagnostic morphological features or synapomorphies are known for the clade embracing *O. sinensis*, *M. japonica*, and *Chinemys* spp. or the more inclusive clade including also all other species of *Mauremys* sensu stricto. To overcome this incongruence between phylogenetic relationships and taxonomic classification, two solutions have been proposed: placing all species into *Mauremys* or to recognize several distinct genera (Barth *et al*. 2004; Spinks *et al.* 2004). The oldest available name for the clade including *O. sinensis*, *M. japonica*, and *Chinemys* spp. is *Ocadia* (Barth *et al*. 2004). In the present study, *Ocadia* sensu stricto is tentatively retained, however.

From a paleontological perspective, lumping *Ocadia* with *Mauremys* and *Chinemys*, as suggested by Spinks *et al.* (2004), appears to eliminate the remarkable morphological differences between the three genera, as well as the long diversification history of the genus *Ocadia*. *Ocadia* is clearly distinct from the latter two genera in having several morphological traits, such as enlarged upper and lower triturating surfaces along with two lingual ridges,

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small foramen palatinum posterius, moderately developed plastral buttresses, and shortened gular scutes (Hirayama *et al.* 2007). Fossils referred to the genus *Ocadia* had been abundantly recorded from the Paleogene to the Quaternary of East Asia and Europe, but those from Europe (Lydekker 1889; Kuhn 1964) were recently re–examined and transferred to other genera such as *Palaeochelys*, *Palaeoemys*, and *Cuvierichelys* (de Broin 1977; Claude and Tong 2004; Hervet 2004). The East Asian fossils are represented by *O. sinensis* recorded from the Pliocene of China (Yeh 1963, 1994; Li *et al*. 2008) and Kyushu, Japan (Hirayama 2001), *O. nipponica*, and *Ocadia* sp. from the lower Miocene of Kyushu (Nagasaki Prefecture; Hirayama *et al*. 2012), the upper lower to lower middle Miocene of Honshu, Japan (Okayama and Fukushima Prefectures; Hirayama *et al*. 1982, 1983; Hasegawa *et al*. 2002), and the Pleistocene of Honshu (Hyogo and Kanagawa Prefectures; Hirayama 2006; Hasegawa *et al*. 2008). Most of these fossils need additional materials and further investigations, although it has been suggested that this genus had diversified and was widely distributed in eastern Asia during the Miocene (Hirayama *et al*. 2007).

We recently discovered a relatively well–preserved shell fossil belonging to the genus *Ocadia* from a Miocene shallow marine to brackish deposit on the southern part of Tanegashima Island, the Osumi Island Group, located south of Kyushu, Japan (Fig. 1A). This specimen is the oldest vertebrate fossil recorded from this island and is obviously different from the two known congeneric species (*O. sinensis* and *O. nipponica*). In this study, we describe the present fossil as a new species, and discuss its paleogeographic implications.

Material and methods

Tanegashima Island mainly consists of Paleogene basement rocks (Eocene to Oligocene Kumage Group), Miocene Kukinaga Group, Pleistocene marine and non–marine deposits (the Masuda, Hase, and Takenokawa Formations), and Holocene deposits (Hayasaka 1969; Kizaki 1985; Inoue 1992). Of these, the Kukinaga Group is composed of the Tashiro, Kawachi, and Osaki Formations in ascending order with conformity and their distributions are restricted to the southern part of the island (Fig. 1A and 1B). The present turtle fossil was collected from an outcrop of mudstone layers of the Kawachi Formation exposed by road construction along with a fragment of trionychid turtle shell and some molluscs (*Crassostrea* and *Vicarya*) in Kawachi, Minamitane–cho (the southern part of Tanegashima Island), Kagoshima Prefecture, Japan, in July 2003 (Fig. 1B and 2). The presence of marine invertebrate fossils such as bivalves and gastropods mentioned above, as well as pollen of mangrove plants indicate that this formation was formed in a tropical shallow marine coastal environment (Inoue 1992; Kojima and Otsuka 1995). The formation has never been dated, but Inoue (1992) estimated that it was formed in approximately 16 Ma on the basis of the molluscan fossils. Inoue (1992) also examined planktonic foraminiferans from the Hirota Mudstone and Sandstone Member (the second member from the top of the Osaki Formation) and correlated it with N13 to N15 (late middle to early late Miocene) of Blow (1969). Further, Ogasawara (1997) dated quartz–porphyry in the Tashiro Formation (underlying the Kawachi Formation) approximately to 15.6 Ma by using K–Ar dating and Yamaguchi *et al*. (2012) re–correlated the planktonic foraminiferal assemblage from the Osaki Formation in Inoue (1992) with M6 to PL2 (middle Miocene to early Pliocene) of Wade *et al.* (2011). In this study, we follow these previous works and consider the age of the Kawachi Formation as the early middle Miocene.

Morphological comparisons with the present specimen were made using skeletal adult specimens in the private collections of AT and of RH and also with the type specimen of *Ocadia nipponica* Hirayama *et al*. 2007 (CBM–PV686) preserved in vertebrate fossil collection of Natural History Museum & Institute, Chiba (CBM). Poorly defined or poorly preserved species were excluded from comparisons (e.g., *Clemmys schansiensis* and *Ocadia*? *perplexa*). Classification of the genus *Ocadia* followed Hirayama *et al*. (2007). Shell terminology followed Zangerl (1969). Measurements were taken to the nearest 0.1 mm using a digital slide caliper.

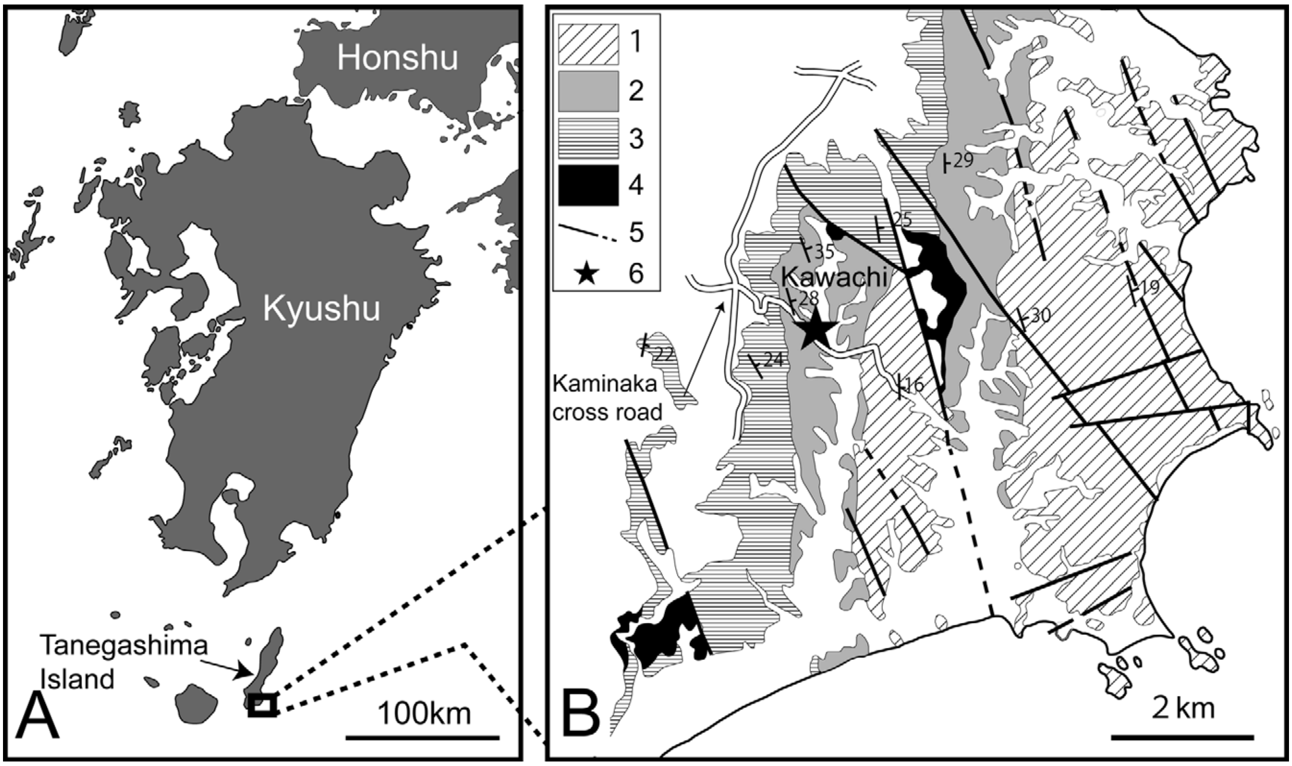

FIGURE 1. Location of Tanegashima Island, southwestern Japan (A) and locality of the present turtle fossil (MTE1, B) with adjacent geological map. 1, Osaki Formation; 2, Kawachi Formation; 3, Tashiro Formation; 4, Kumage Group; 5, fault; 6, fossil locality. The geological map used was a modified version of the map presented by Inoue (1992).

Systematics

Testudines Batsch, 1788

Cryptodira Cope, 1868

Testudinoidea Batsch, 1788

Geoemydidae Theobald, 1868

Ocadia Gray, 1870

Type species. *Ocadia sinensis* (Gray, 1834).

Included species. *Ocadia sinensis* (Gray, 1834); *O. nipponica* Hirayama *et al*., 2007.

Revised diagnosis. Modified on the basis of Smith (1931), Bourret (1941), Ernst and Barbour (1989), Hirayama *et al*. (2007), and this study: medium to large–sized hingeless geoemydids with following combination of character states: hexagonal neural plates short–sided in front; posterior margin of the carapace unserrated; second and third vertebral scutes frequently showing nearly rectangular in shape, as long as wide; the entoplastron intersected by the humero–pectoral sulcus; the plastral buttresses moderately developed, extending to half way of the costal plates; median length of the gular shorter than the interhumeral sulcus and the gular often isolated from the entoplastron; enlarged upper and lower triturating surface decorated by the lingual ridges; the upper triturating surface with a denticulate median ridge; and the foramen palatinum posterius small.

Remarks. Recent molecular phylogenetic analyses have shown that the genus *Ocadia* is included in a clade with *Chinemys* spp. and *Mauremys japonica* and that these taxa form another more inclusive clade with the remaining living species of *Mauremys* (*Mauremys* sensu lato, Honda *et al.* 2002; Barth *et al.* 2004; Feldman and Parham 2004; Spinks *et al.* 2004; Sasaki *et al.* 2006; Jiang *et al.* 2011). However, no synapomorphic morphological character states are known for the two clades (e.g., Honda *et al.* 2002; Hirayama *et al.* 2007). Actually, because *Ocadia* differs much from *Chinemys* and *Mauremys* in several skull and shell characters (e.g., McDowell 1964; Hirayama 1985; Gaffney and Meylan 1988; Yasukawa *et al.* 2001), we retain the genus *Ocadia* for disclosing its past species diversity from paleontological view in the present study.

Ocadia tanegashimensis sp. nov.

(Suggested Japanese name: Tanegashima hanagame)
(Figs. 2–4; Table 1)

Holotype. A shell, deposited in the collection of the Minamitane–cho Board of Education (MTE1).

Type locality. South slope located approximately 1.5 km southwest from the Kaminaka crossroad on Prefectural Road 588, Kawachi, Minamitane–cho, Kagoshima Prefecture, Japan.

Horizon. Middle part of Kawachi Formation (early middle Miocene), Kukinaga Group.

Etymology. The specific epithet refers to the name of the island (Tanegashima Island) from which the fossil was discovered.

Diagnosis. A medium–sized geoemydid species larger than *O. sinensis*, characterized by a combination of the following character states: the first vertebral expanded anterolaterally, reaching the second marginal; the second and third vertebral scutes much narrower than the first vertebral anteroposteriorly; a medial and two lateral obtuse discontinuous keels on carapace; length of the entoplastron as long as the interhyoplastral suture; the costals dovetailed with one another in outline; the third pleural overlapping only the sixth and seventh peripherals.

Description. Shell. The shell is incompletely preserved and strongly depressed dorsoventrally. It lacks the eighth neural; the first and second suprapygals; the right fifth, eighth and eleventh peripherals; the left sixth and eleventh peripherals; and the pygal. The shell margin is not emarginated anterolaterally and posterolaterally. The shell surface is smooth, lacks growth annuli, and has an obtuse medial and two lateral discontinuous knob–like longitudinal keels. The carapace and plastron are moderately thick (carapace: 10.3 mm thick in the middle of the thickened part of the nuchal, 9.4 mm in the posterior part of the fifth neural, and 8.5 mm in the second peripheral; plastron: 11.5 mm thick in the left lateral part of the gular lip, 8.0 mm in the posterior corner of the entoplastron, 4.9 mm in the posterolateral corner of the right hyoplastron, and 12.8 mm in the posteriormost part of the left femoral lip).

The nuchal is hexagonal and slightly short–sided posteriorly. The first neural is barrel–shaped and the second to seventh neurals are hexagonal and short–sided anteriorly. Widths of the costals are variable; the second, fourth, sixth, and eighth costals are distally expanded, whereas the third and fifth costals are distally contracted. The first costal contacts the first to third peripherals and the second costal connects the third and fourth peripherals laterally. The remaining costals articulate with the adjacent two peripherals distally.

The cervical scute is rectangular and longer than wide in dorsal view and trapezoidal and much wider than long in ventral view. The first vertebral is slightly longer than wide (83.7 mm long and 81.2 mm wide) and laterally notched, reaching the posteromedial corner of the second marginal. The second and third vertebrals are nearly rectangular in shape and narrower than the first vertebral (the second, 67.4 mm long and 67.6 mm wide; the third, 70.3 mm long and 73.2 mm wide). The fourth is obviously wider than the second and third vertebrals. The first pleural contacts the posterolateral corner of the first marginal anteromedially and the second to fifth marginals anterolaterally. The second pleural appears to contact the fifth and sixth marginals laterally, and the third pleural contacts the sixth to eighth marginals. The fourth pleural contacts the eighth to tenth marginals. Of the four pleural scutes, the first covers four and the second and fourth cover three peripherals, whereas the third covers only two peripherals (the sixth and seventh).

Plastron. The plastron preserves all components: the epiplastra, the entoplastron, the hyoplastra, the hypoplastra and the xiphiplastra. The maximum plastron length is estimated to be approximately 325 mm. The presence of a shallow but distinct ventral concavity on the plastron in ventral view and the absence of the laterally rounded posterior lobe suggest that this individual is male (Ernst and Barbour 1989; Zhang *et al*. 1998).

The epiplastra are mostly preserved, lacking only the lateral margin of the left epiplastron. Of these, the right is 56.7 mm long and 57.2 mm wide. They have a relatively wide epiplastral lip represented by dorsal overlapping of the gular scute (15.7 mm in the right) and lack the epiplastral excavation. The interepiplastral suture is short (24.3

mm) and approximately two–fifths of the median length of the entoplastron (57.4 mm) in ventral view. It is also short (25.3 mm) dorsally and approximately half of the median length of the entoplastron (43.7 mm). The hyoplastra lack most of the axillary buttresses, the anterolateral fringes corresponding to a portion of the bridge to the carapace, and the posterolateral part of the left forelobe. The left hyoplastron (109.6 mm long and 108.7 mm wide) preserves the upper part of the axillary buttress, suturing with the middle parts of the left first costal in ventral view. The interhyoplastral suture is 62.6 mm, slightly longer than the median length of the entoplastron in ventral view. The hypoplastra are also preserved but their anterolateral and anteromedial corners and the ascending processes of the inguinal buttresses are missing. However, the left fifth costal preserves the sutural facet in ventral view, indicating that the inguinal buttresses extend to the middle part of the fifth costals. The xiphiplastra are nearly completely preserved, missing just small portions in their anteromedial parts and the posteromedial part of the left xiphiplastron. The left xiphiplastron is 77.9 mm long and 68.63 mm wide. Length of the interhypoplstral suture is 58.1 mm.

FIGURE 2. Picture showing occurrence of *Ocadia tanegashimensis* (MTE1) from the Kawachi Formation in Kawachi, Minamitane–cho, southern part of Tanegashima Island.

The gular scutes reach the anterior tip of the entoplastron. Length of the intergular sulcus (35.6 mm) is slightly shorter than that of the interhumeral sulcus (36.2 mm). The humero–pectoral sulcus intersects the posterior part of the entoplastron. It slightly bends backward on the hyoplastra. The pectoro–abdominal sulcus arches over the lateral part of the hyoplastra. The axillary and right inguinal scutes are invisible, although the left inguinal is present and is isolated from the femoral scute as in *O. sinensis*.

Comparisons. The musk duct foramen in the right third peripheral of the present material (MTE1) indicates that this taxon belongs to the family Geoemydidae (Hirayama 1985; Joyce and Bell 2004). MTE1 is similar to *Chinemys*, *Cuvierichelys*, *Mauremys*, *Ocadia*, *Palaeochelys*, *Sacalia*, and *Siebenrockiella* in lacking the plastral hinge and in having the entoplastron intersected by the humero–pectoral sulcus and the neurals short–sided anteriorly. In addition, MTE1 has four informative character states for genus level taxonomy (Table 1): (1) second and third vertebrals nearly rectangular, as long as wide (modified from Hirayama *et al*. 2007), (2) absence of serration on the posterior margin of the carapace (e.g., Ernst and Barbour 1989; Yasukawa *et al*. 2001), (3) medial length of the gular shorter than the interhumeral sulcus (Hirayama *et al*. 2007), and (4) the plastral buttresses moderately developed, extending to half way of the costals (Hirayama *et al*. 2007). Of these, the character (3) and (4) are known as diagnostic characters for the genus *Ocadia* (Hirayama *et al*. 2007), but variably seen in several comparative taxa (Table 1). Character (1) is shared exclusively with *O. nipponica*, some *O. sinensis*, and some *Palaeochelys* (*P. crocheti* and *P. laurenti*). A similar state is seen in *M. gaudryi*, some *M. japonica*, *M. massiliensis*, and *M. sarmatica*, in which the second and third vertebrals are much wider than long (de Broin 1977; Hervet 2004; Takahashi per. obs. on *M. japonica*). Character state (2) is informative for discriminating *Ocadia* from several species of *Mauremys* as well as a few *Palaeochelys* (*P. laurenti*), and *Siebenrockiella* (Sacco 1889; Ernst and Barbour 1989; Hervet 2004; Claude *et al.* 2007; Chesi *et al.* 2009). Among the comparative genera, all of these four character states seen in MTE1 are exclusively shared with the genus *Ocadia* (Table 1). The other character states (5–10) are not informative for genus level identification. Thus, in the following, we compare MTE1 within *Ocadia*.

TABLE 1. Comparisons of the Tanegashima geoemydid (MTE1) with hingeless geoemydids (see Appendix) having the entoplastron intersected by the humero–pectoral sulcus and the neurals short–sided anteriorly. Symbols, +, –, and ?, indicate presence, absence, and undetermined status of a given character state. Character state (1): second and third vertebrals rectangular and as long as wide, character state (2): posterior margin of the carapace unserrated, character state (3): medial length of the gular shorter than interhumeral sulcus, character state (4): plastral buttresses developed, extending halfway of the costals, character state (5): medial and two lateral obtuse discoutinuous keels on the carapace present, character state (6): first vertebral scute expanded anterolaterally, reaching the second marginal, character state (7): second and third vertebral scutes much narrower than the first anteroposteriorly, character state (8): length of entoplastron nearly as long as interhyoplastral suture, character state (9): costals dovetailed with one another in outline, and character state (10): third pleural overlapping only sixth and seventh peripherals.

Genus	Species	Character state									
		1	2	3	4	5	6	7	8	9	10
MTE1		+	+	+	+	+	+	+	+	+	+
Chinemys	*Ch. fenhoense*	–	+	?	?	–	–	–	–	–	–
	Ch. nigricans	–	+	–	–	–	–	–	–	–	–
	Ch. reevesii	–	+	+/–	–	+	+/–	+/–	–	–	–
Cuvierichelys	*Cu. parisiensis*	?	+	+	?	–	?	?	–	–	?
Mauremys	*M. annamensis*	–	+	+/–	+	–	+/–	+	–	–	–
	M. campanii	–	–	–	?	?	+	+	+	–	–
	M. gaudryi	–	?	–	?	–	+	+	–	–	–
	M. japonica	–	–	+/–	–	–	+/–	+	–	–	–
	M. leprosa	–	+	–	–	+	+	–	–	–	–
	M. massiliensis	–	+	–	?	+	+	–	–	?	–
	M. mutica	–	–	+/–	–	–	+/–	+	+	–	–
	M. portisi	–	–	–	?	–	+	–	–	–	–
	M. pygolopha	–	–	–	–	–	–	–	+	–	–
	M. rivulata	–	+	–	–	+	–	–	–	–	–
	M. sarmatica	–	+	–	–	–	+	+	+	–	–
	M. thanhinensis	–	+/–	+/–	–	–	+/–	+	+	–	–
	M. yabei	–	?	–	–	–	+	+	+	–	–
Ocadia	*O. nipponica*	+	+	+	+	–	+	+	–	–	–
	O. sinensis	+/–	+	+/–	+	+	–	–	–	–	–
Palaeochelys	*P. crocheti*	+	+	+	–	–	–	+	+	–	–
	P. laurenti	+	–	+	–	–	+/–	+	–	–	–
	P. vallisnerii	–	+	+	–	–	+	+	–	–	–
Sacalia	*Sacalia* spp.	–	+	+/–	–	–	–	+/–	–	–	–
Siebenrockiella	*S. crassicollis*	–	–	–	+	–	–	+/–	–	–	–
	S. leytensis	–	–	–	+	–	–	–	–	–	–

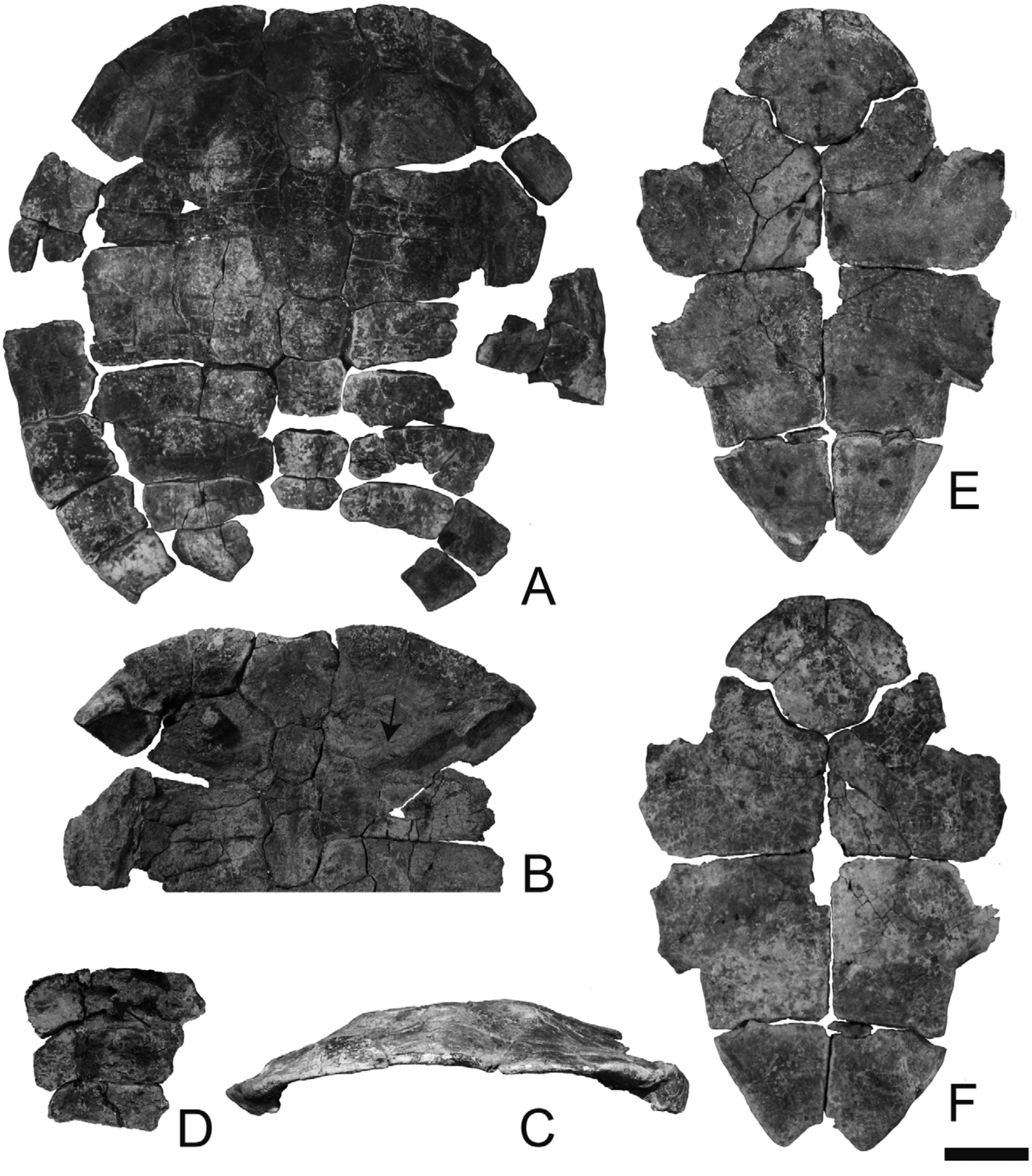

FIGURE 3. *Ocadia tanegashimensis* (MTE1) from Tanegashima Island. A–C, the carapace in dorsal (A), ventral (B) and anterior (C) views. D, left fifth to seventh costals in ventral view. E–F, the plastron in dorsal (E) and ventral (F) views. Arrows indicate locations of upper ends of the plastral buttresses. Scale bar: 5 cm.

Within the genus *Ocadia*, MTE1 exclusively shares the first vertebral expanded anterolaterally and reaching to the second marginal (character 6) with *O*. *nipponica* (Hirayama *et al.* 2007). On the other hand, it shares the tricarinate discontinuous knob–like keels (character state 5) only with *O*. *sinensis* (Table 1, Smith 1931; Ernst and Barbour 1989; Hirayama *et al*. 2007). Ernst and Barbour (1989) also described that the dorsal keels on the carapace disappear in aged individuals of *O*. *sinensis*. This suggests that absence of the keels in *O*. *nipponica* could be attributed to loss resulting from aging. Moreover, the second and third vertebrals in MTE1 are much narrower than the first (character state 7), which is one of the diagnostic characters for *O*. *nipponica* (Hirayama *et al*. 2007).

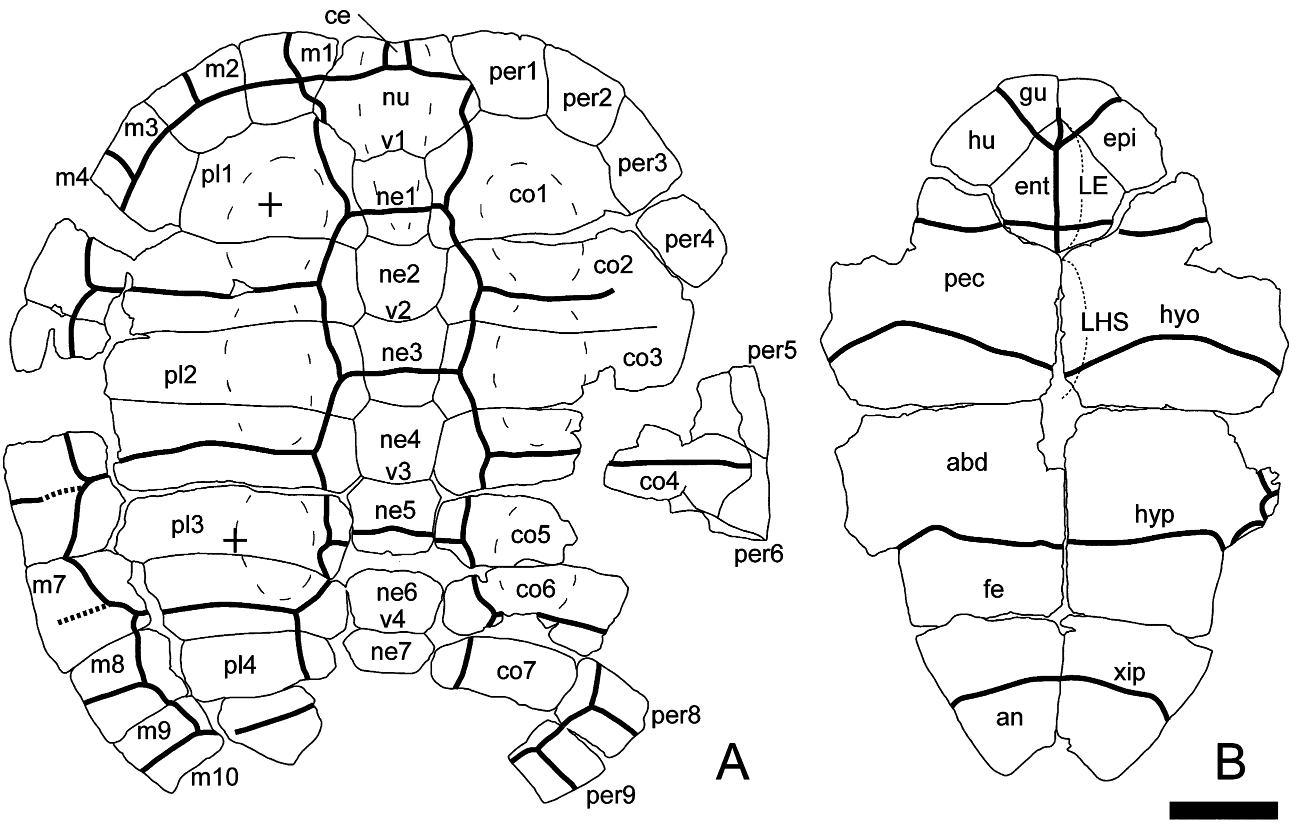

FIGURE 4. Illustration of *Ocadia tanegashimensis* (MTE1) from Tanegashima Island. A, the carapace in dorsal and B, the plastron in ventral views. Abbreviations: abd, abdominal; an, anal; ce, cervical; co, costal; ent, entoplastron; epi, epiplastron; fe, femoral; gu, gular; hu, humeral; hyo, hyoplastron; hyp, hypoplastron; LE, length of the epiplastron; LHS, length of the hyoplastral suture; m, marginal; ne, neural; nu, nuchal; pec, pectoral; pl, pleural; v, vertebral; xip, xiphiplastron. Symbol +: locations of upper ends of the plastral buttresses in ventral view. Scale bar: 5 cm.

Furthermore, MTE1 has three peculiar character states: length of the entoplastron nearly as long as the interhyoplastral suture (character 8), the second to sixth costal bones showing dovetailed shapes (character 9), and the third pleural overlapping only the sixth and seventh peripherals (character 10). Character 8 is also shared with several species of *Mauremys* (*M. campanii*, *M. mutica*, *M. pygolopha*, *M. sarmatica*, *M. thanhinensi*s, *M. yabei*, and *P. crocheti*; Shikama 1949; de Broin 1977; Hervet 2004; Claude *et al.* 2007; Takahashi pers. obs. on *M. mutica*). In MTE1, the even–numbered costal plates are expanded whereas the odd–numbered plates exclusive of the first one are narrower distally (character 9). In contrast, the costals in the other comparative taxa are nearly rectangular. The third pleural covers only two peripherals, the seventh and eighth (character 10) in MTE1, but overlaps three peripherals in the two congeneric species as well as the other comparative species (the sixth to eighth, generally, but very rarely the fifth to seventh in *O. sinensis*). Based on these features, MTE1 is clearly distinguished from *O. sinensis* and *O. nipponica*.

Discussion

The present results reveal that the genus *Ocadia* consists of the extant *O. sinensis*, *O. nipponica* from the middle Pleistocene of eastern Japan, and *O. tanegashimensis* from the lower middle Miocene of Tanegashima Island, southwestern Japan at present. *Ocadia*? *perplexa* from the Pliocene of Mongolia (Gilmore 1931) needs verification of its generic status because it is represented only by three partial shell fragments lacking diagnostic features for the genus. Fossils referred to the genus have also been recorded from the upper lower Miocene (ca. 18 Ma ago: Komatsubara *et al.* 2005) of Nagasaki Prefecture (Hirayama *et al.* 2012, Fig. 5A), the uppermost lower to lower middle Miocene of Fukushima (Blow's [1969] N.8–N.9 zones, Hasegawa *et al.* 2002; see Sudo *et al.* 2005 for its biostratigraphic correlation) and Okayama (Blow's [1969] N.8 zone: Hirayama *et al*. 1982, 1983; see Taguchi *et al.* 1979 and Nomura 1992 for its biostratigraphic correlation and Takemura *et al.* 2003 for its radiometric age) Prefectures (Fig. 5B), and the Pleistocene of Hyogo (Hirayama 2006) and Kanagawa Prefectures (Hasegawa *et al*. 2007), Japan. Of these, the specimen from Fukushima has been considered to be conspecific with those from Okayama by Hasegawa *et al*. (2002), because they share the following character states: absence of longitudinal keels, no growth annuli on the carapace, and a larger carapace than *O. sinensis*. In addition, the fossil from Nagasaki is similar to those from Fukushima and Okayama in sharing these three morphological features (Hirayama unpublished data). However, *O. tanegashimensis* clearly differs from these late early to early middle Miocene fossils in having three discontinuous keels on the carapace and the dovetailed costals with one another in outline. Thus, the occurrences of *O. tanegashimensis* and relevant congeners from the upper lower to lower middle Miocene of Japan suggest that at least two species of *Ocadia* were distributed in the area around Tanegashima Island and from Fukushima to Nagasaki around late early Miocene (Fig. 5A).

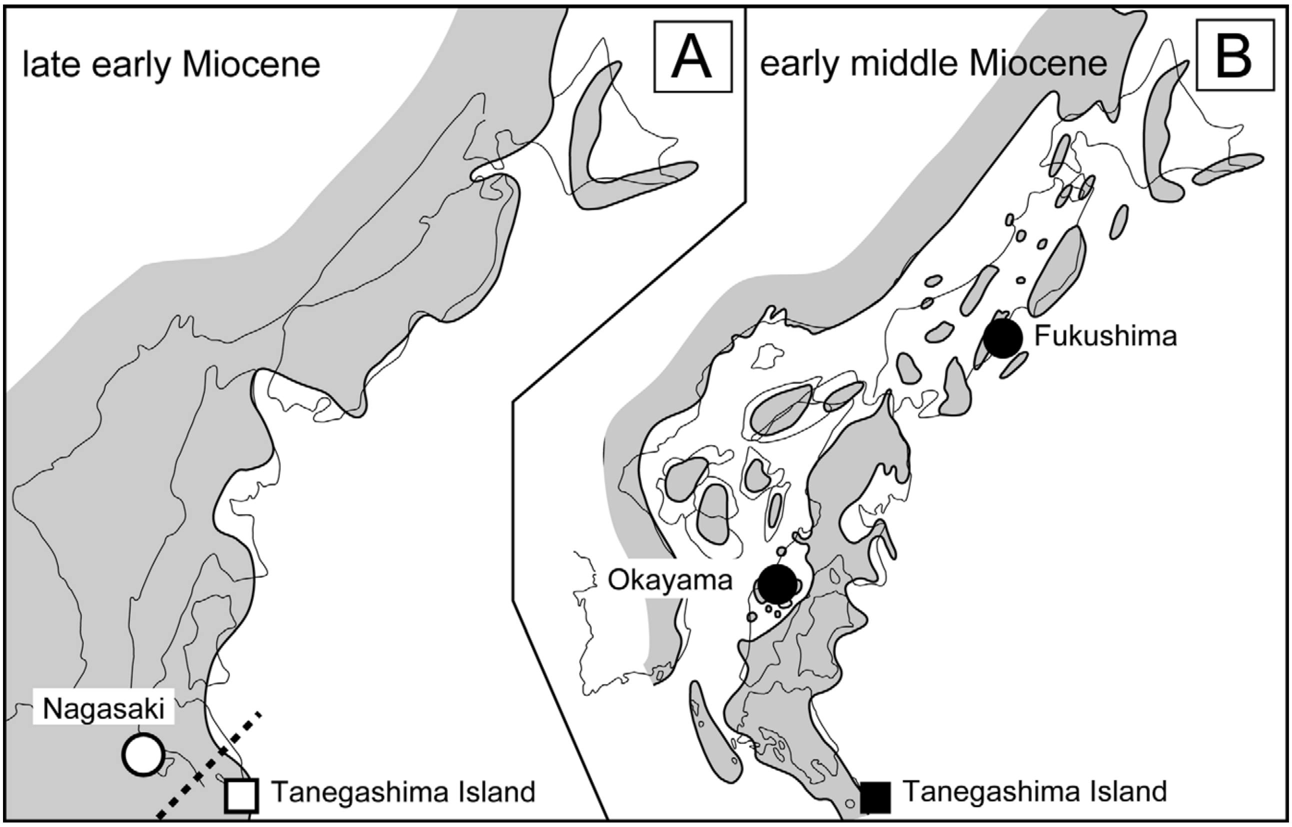

FIGURE 5. Occurrences of *Ocadia* fossils in late early (A) and early middle (B) Miocene of Japan. Paleogeographic maps of mainland Japan and adjacent regions in these ages follows Ogasawara (1994) with slight modification on the basis of Yamamoto *et al*. (2000). Filled circle: localities of the latest early to early middle Miocene specimens from Okayama and Fukushima Prefectures, open circle: locality of the late early Miocene specimens from Nagasaki Prefecture, filled square: locality of *O. tanegashimensis*, open square: putative occurrence of ancestral stock of *O. tanegashimensis*. Gray areas denote land.

According to generally prevailing Miocene paleogeographic hypotheses (Iijima and Tada 1990; Ogasawara 1994), Japan had mostly been a part of the eastern margin of the Eurasian continent until the late early Miocene and subsequently divided into several islands by tectonic subsidence caused by the opening of the Japan Sea (counter–clockwise rotation of northeastern Japan from approximately 25 to 14 Ma and clockwise rotation in southwestern Japan from approximately 16 to 15 Ma; Otofuji *et al*. 1985; Baba *et al*. 2007) in the late early to early middle Miocene (Fig. 5). Occurrences of two distinct lineages of the genus *Ocadia* from the lower middle Miocene of Tanegashima and from the upper lower to lower middle Miocene of Fukushima, Nagasaki, and Okayama suggest that each was differentiated from different ancestors not on the proto–Japanese Islands but on the eastern margin of the Eurasian continent in the late early Miocene. It is interesting that this view is concordant with the recent molecular clock estimation which states that the separation of *Ocadia* from its close relatives (i.e., an ancestral lineage shared with *Ocadia*, *Chinemys*, and *M*. *japonica*) occurred in 18–23 Ma ago (the early Miocene; Barth *et al*. 2004). In contrast, the geographic patterns of the early to middle Miocene *Ocadia* from Japan challenge the paleogeographic hypothesis deduced from the Early to Middle Miocene *Stegolophodon* (*S. pseudolatidens*) from Japan (Saegusa 2008). In terms of the latter inference, further discoveries of Miocene *Stegolophodon* are strongly desired for verification due to the paucity of specimens from southwestern Japan.

Although *O*. *tanegashimensis* was discovered from shallow marine sediment (the Kawachi Formation), this species appears to have had a freshwater habitat because *O*. *sinensis* occurs in subtropical rivers, ponds, and lakes in lowland areas of Taiwan, southern China, and northern Vietnam (Iverson 1992; Ernst and Barbour 1989). *Ocadia nipponica* has also been discovered from fluvial deposit, and is considered to be a freshwater species. Co–occurrence of *O*. *tanegashimensis* and a shell fragment of a trionychid turtle supports this ecological inference. In contrast, Hirayama *et al*. (1982, 1983) presumed that the late early to early middle Miocene *Ocadia* from shallow marine sediments in Okayama occurred in habitats like the extant estuarine *Batagur* species (*Batagur* sensu lato, see Praschag *et al.* 2007, 2009). This presumption appears to be very unlikely because it was deduced from the hypothesis that the genus *Ocadia* is allied to the "*Batagur* complex" (McDowell 1964) consisting of *Batagur baska* sensu lato, *B. borneoensis*, *Chinemys*, *Heosemys annandalii*, *Malayemys*, and *Ocadia*. However, recent molecular phylogenetic analyses showed that the "*Batagur* complex" is not monophyletic (*e.g.*, Barth *et al.* 2004; Spinks *et al*. 2004; Sasaki *et al.* 2006). This suggests that *O*. *tanegashimensis* from the Kawachi Formation may have been transported from a nearby lowland area via a river.

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References

Baba, A.K., Mastuda, T., Itaya, T., Wada, Y., Hori, N., Yokoyama, M., Eto, N., Kamei, R., Zaman, H., Kidane, T. & Otofuji, Y. (2007) New age constraints on counter–clockwise rotation of NE Japan. *Geophysical Journal International,* 171, 1325–1341.
http://dx.doi.org/10.1111/j.1365-246x.2007.03513.x

Barth, D., Bernhard, D., Fritzsch, G. & 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.
http://dx.doi.org/10.1111/j.0300-3256.2004.00150.x

Batsch, A.J.G.K. (1788) *Versuch einer Anleitung, zur Kenntniss und Geschichte der Thiere und Mineralien*. Jena, Akademische Buchhandlung, 528 pp.

Blow, W.H. (1969) Late Middle Eocene to Recent planktonic foraminiferal biostratigraphy. *In*: Bronnimann, P. & Renz, H.H. (Eds), *Proceedings of the First International Conference on Planktonic Microfossils, Geneva 1967, Vol1.*, pp. 199–422.

Boulenger, G.A. (1889) *Catalogue of the Chelonians, Rhynchocephalians, and Crocodiles in the British Museum (Natural History)*. Taylor and Francis, London, 311 pp.

Bourret, R. (1941) *Les Tortues de L'Indochine.* Station Maritime de Cauda, Province de Nhatrang, 235 pp.

de Broin, F. (1977) Contribution à l'étude des Chéloniens. Chéloniens continentaux du Crétacé et du Tertiaire de France. *Mémoire du Muséum national d'Histoire naturelle de Paris, Série C,* 38, 1–366.

Chesi, F., Delfino, M. & Rook, L. (2009) Late Miocene *Mauremys* (Testudines, Geoemydidae) from Tuscany (Italy): evidence of terrapin persistence after a mammal turnover. *Journal of Paleontology*, 83, 379–388. http://dx.doi.org/10.1666/08-134.1

Chow, M.C. (1961) A new Pleistocene turtle from Hsiangfen, Shansi. *Acta Paleontologica Sinica*, 9, 426–430.

Claude, J. & Tong, H. (2004) Early Eocene testudinoid turtles from Saint–Papoul, France, with comments on the early evolution of modern Testudinoidea. *Oryctos*, 5, 3–45.

Claude, J., Suteethorn, V. & Tong, H. (2007) Turtles from the late Eocene–early Oligocene of the Krabi Basin (Thailand). *Bulletin de la Société Géologique de France*, 178, 305–316. http://dx.doi.org/10.2113/gssgfbull.178.4.305

Cope, E.D. (1868) On the origin of genera. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1868, 242–300.

Diesmos, A.C., Parham, J.F., Stuart, B.L. & Brown, R.M. (2005) The phylogenetic position of the recently rediscovered Philippine forest turtle (Bataguridae: *Heosemys leytensis*). *Proceedings of the California Academy of Science*s, 56, 31–41.

Ernst, C.H. & Barbour, R.W. (1989) *Turtles of the World*. Smithsonian Institution Press, Washington, D.C., 313 pp.

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

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

Fritz, U. & Havaš, P. (2007) Checklist of chelonians of the world. *Vertebrate Zoology*, 57, 149–368.

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

Gilmore, C.W. (1931) Fossil turtles of Mongolia. *Bulletin of the American Museum of Natural History*, 59, 213–257.

Glaessner, M.F. (1926) Neue Emydenfunde aus dem Wiener Becken und die fossilen *Clemmys*–Arten des Mittelmeergebietes. *Sitzungsberichte der Akademie der Wissenschaften in Wien, mathematisch–naturwissenschaftliche Klasse, Abteilung 1*, 135, 51–71.

Gray, J.E. (1834) Characters of several new species of freshwater tortoises (*Emys*) from India and China. *Proceedings of the Zoological Society of London*, 1834, 53–54.

Gray, J.E. (1870) *Supplement* to the *Catalogue* of *Shield Reptile*s *in the Collection of the British Museum*. *Part I. Testudinata. (Tortoises)*. British Museum, London, 120 pp.

Hasegawa, Y., Hirayama, R. & Hashimoto, K. (2002) Miocene turtle (*Ocadia* sp.: Family Bataguridae; Superfamily Testudinoidea) from the Takaku Group, Ushio, Iwaki city, Fukushima Prefecture, Japan. *Bulletin of Gunma Museum of Natural History*, 6, 53–58. [in Japanese with English abstract]

Hasegawa, Y., Taru, H. & Matsushima, Y. (2007) Naumann's elephant and associated with *Ocadia* assemblage. *In*: *Jubilee Publication in Commemoration of Prof. Kamei Tadao's 80th Birthday*, pp. 141–144. [in Japanese with English abstract]

Hayasaka, S. (1969) Molluscan fauna of the Kukinaga Group in Tané–ga–shima, south Kyûshû, Japan. *Reports of the Faculty of Science, Kagoshima University (Earth Science and Biology)*, 2, 33–52.

Hervet, S. (2004) Systématique du groupe « *Palaeochelys* sensu lato – *Mauremys* » (Chelonii, Testudinoidea) du Tertiaire d'Europe occidentale: principaux résultats. *Annales Paléontologie*, 90, 13–78. http://dx.doi.org/10.1016/j.annpal.2003.12.002

Hirayama, R. (1985) Cladistic analysis of batagurine turtles (Batagurinae: Emydidae: Testudinoidea); A Preliminary Result. *Studia Geologica Salmanticensia, volumen especial, 1* (*Studia Palaeocheloniologica I)*, 141–157.

Hirayama, R. (2001) Fossil turtles from the Tsubusagawa Formation (Pliocene) of Ajimu–cho, Oita Prefecture, northern Kyushu, Japan. *Research Report of the Lake Biwa Museum*, 18, 79–96. [in Japanese with English abstract]

Hirayama, R. (2006) Review of fossil turtles of Japan. *Fossils*, 80, 47–59. [in Japanese]

Hirayama, R., Kaneko, N. & 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. http://dx.doi.org/10.2517/1342-8144(2007)11[1:ONANSO]2.0.CO;2

Hirayama, R., Taguchi, E. & Okazaki, Y. (1982) Discovery of the second specimen of brackish–water turtle from the Miocene Bihoku Group at Niimi City, Okayama Prefecture, west Japan. *Bulletin of the Mizunami Fossil Museum*, 9, 111–116. [in Japanese]

Hirayama, R., Shibata, A., Akagi, S. & Kamei, T. (1983) Miocene turtle from the Bihoku Group, Okayama Prefecture, Japan. *Journal of Geological Society of Japan*, 89, 239–241. [in Japanese] http://dx.doi.org/10.5575/geosoc.89.239

Hirayama, R., Nakajima, Y., Takahashi, A., Sonoda, T., Kato, K. & Kawano, S. (2012) Cranial morphology of *Ocadia* sp. (Geoemydidae: Testudines) from the Lower Miocene of Nagasaki Prefecture, and its systematic position. *Abstracts with Programs, the 2012 Annual Meeting, the Palaeontological Society of Japan*. pp. 19. [in Japanese]

Honda, M., Yasukawa, Y. & Ota, H. (2002) Phylogeny of the Eurasian freshwater turtles of the genus *Mauremys* Gray 1869 (Testudines), with special reference to a close affinity of *Mauremys japonica* with *Chinemys reevesii*. *Journal of Zoological Systematics and Evolutionary Research*, 40, 195–200. http://dx.doi.org/10.1046/j.1439-0469.2002.00176.x

Iijima, A. & Tada, R. (1990) Evolution of tertiary sedimentary basins of Japan in reference to opening of the Japan Sea. *Journal of the Faculty of Science, University of Tokyo, section 2, Geology, Mineralogy, Geography, Geophysics*, 22, 121–171. http://dx.doi.org/10.3720/japt.57.171

Inoue, K. (1992) Stratigraphy and geologic age of the Miocene Kukinaga Group in Tanegashima Island, Kagoshima Prefecture, Japan. *Bulletin of the Mizunami Fossil Museum*, 19, 347–362. [in Japanese with English abstract]

Iverson, J.B. (1992) *A revised checklist with distribution maps of the turtles of the World*. Privately published, Richmond, Indiana, 363 pp.

Iverson, J.B. & McCord, W.P. (1989) The proper taxonomic allocations of *Emys nigricans* Gray, *Emys muticus* Cantor, and *Geoclemys kwangtungensis* Pope. *Amphibia–Reptilia*, 10, 23–33.
http://dx.doi.org/10.1163/156853889X00278

Jiang, Y., Nie, L.W., Huang, Z.F., Jing, W.X., Wang, L., Liu, L. & Dai, X.T. (2011) Comparison of complete mitochondrial DNA control regions among five Asian freshwater turtle species and their phylogenetic relationships. *Genetics and Molecular Research*, 10, 1545–1557.
http://dx.doi.org/10.4238/vol10-3gmr1205

Joyce, W.G. & Bell, C.J. (2004) A review of the comparative morphology of extant testudinid turtles (Reptilia: Testudines). *Asiatic Herpetological Research*, 10, 53–109.

Kizaki, K. (1985) *Geology of the Ryukyu Arc*. Okinawa Times, Naha, 278 pp. [in Japanese]

Kojima, K. & Otsuka, H. (1995) Pollen assemblages of the Miocene Kukinaga Group in Tanegashima, south Kyushu, Japan. *Reports of the Faculty of Science, Kagoshima University*, 28, 243–268. [in Japanese with English abstract]

Komatsubara, J., Ugai, H., Danhara, T., Iwano, H., Yoshioka, T., Nakajima, T., Kano, K. & Ogasawara, K. (2005) Fission–track age and inferred subsidence rate of the Lower to Middle Miocene Nojima Group in NW Kyushu. *Journal of the Geological Society of Japan*, 111, 350–360 (in Japanese with English abstract).
http://dx.doi.org/10.5575/geosoc.111.350

Kuhn, O. (1964) *Fossilium Catalogus. 1. Animalia, Pars 107, Testudines*. W. Junk, The Hague, Netherlands, 299 pp.

Li, J., Wu, X. & Zhang, F. (2008) *The Chinese Fossil Reptiles and Their Kin. Second Edition*. Science Press, Beijing, 473 pp.

Loveridge, A. & Williams, E.E. (1957) Revision of the African tortoises and turtles of the suborder Cryptodira. *Bulletin of the Museum of Comparative Zoology*, 115, 163–557.

Lovich, J.E. & Ernst, C.H. (1989) Variation in the plastral formulae of selected turtles with comments on taxonomic utility. *Copeia*, 1989, 304–318.
http://dx.doi.org/10.2307/1445426

Lovich, J.E., Yasukawa, Y. & Ota, H. (2011) *Mauremys reevesii* (Gray 1931) – Reeves' turtle, Chinese three–keeled pond turtle. *In*: Rhodin, A.G.J., Pritchard, P.C.H., van Dijk, P.P., Saumure, R.A., Buhlmann, K.A., Iverson, J.B. & Mittermeier, R.A. (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.

Lydekker, R. (1889) *Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History), Part III. The Order Chelonia*. British Museum, London, 239 pp.

McDowell, S.B. (1964) Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. *Proceedings of the Zoological Study of London*, 143, 239–279.
http://dx.doi.org/10.1111/j.1469-7998.1964.tb03860.x

Nakamura, K. (1934) On *Clemmys mutica* (Cantor) with special reference to its variation and distribution. *Annotationes Zoologicae Japonenses*, 14, 425–435.

Nomura, R. (1992) Miocene benthic foraminifera from the Bihoku Group: The geologic age of the Foram. Sharp Line in southwest Honshu and the relation to the opening of the Sea of Japan. *Journal of the Geological Society of Japan*, 98, 587–610.
http://dx.doi.org/10.5575/geosoc.98.587

Ogasawara, K. (1994) Neogene paleogeography and marine climate of the Japanese Islands based on shallow–marine molluscs. *Palaeogeography, Palaeoclimatology, Palaeogeography*, 108, 335–351.
http://dx.doi.org/10.1016/0031-0182(94)90241-0

Ogasawara, M. (1997) K–Ar age and geochemical characteristics of the quartz–porphyry at Shimama, southern Tanegashima, and K–Ar age of a lamprophyre from northern Tanegashima: implications for Miocene igneous activities in the Outer Zone of Southwest Japan. *Journal of Mineralogy, Petrology and Economic Geology*, 92, 454–464.
http://dx.doi.org/10.2465/ganko.92.454

Otofuji, Y., Matsuda, T. & Nohda, S. (1985) Opening mode of the Japan Sea inferred from the paleomagnetism of the Japan Arc. *Nature*, 317, 603–604.
http://dx.doi.org/10.1038/317603a0

Praschag, P., Hundsdörfer, A.K. & Fritz, U. (2007) Phylogeny and taxonomy of endangered South and South–east Asian freshwater turtles elucidated by mtDNA sequence variation (Testudines: Geoemydidae: *Batagur*, *Callagur*, *Hardella*, *Kachuga*, *Pangshura*). *Zoologica Scripta*, 36, 429–442.
http://dx.doi.org/10.1111/j.1463-6409.2007.00293.x

Praschag, P., Holloway, R., Georges, A., Päckert, M., Hundsdörfer, A.K. & Fritz, U. (2009) A new subspecies of *Batagur affinis* (Cantor, 1847), one of the world's most critically endangered chelonians (Testudines: Geoemydidae). *Zootaxa*, 2233, 57–68.

Sacco, F. (1889) I cheloni astiani del Piemonte. *Memorie della Reale Accademia delle Scienze di Torino*, 39, 427–461.

Saegusa, H. (2008) Dwarf *Stegodon* from the Miocene of Japan: Passengers on sinking boats. *Quaternary International*, 182,

49–62.
http://dx.doi.org/10.1016/j.quaint.2007.08.001

Sasaki, T., Yasukawa, Y., Takahashi, K., Miura, S., Shedlock, A.M. & Okada, N. (2006) Extensive morphological convergence and rapid radiation in the evolutionary history of the family Geoemydidae (Old world pond turtles) revealed by SINE insertion analysis. *Systematic Biology*, 55, 912–927.
http://dx.doi.org/10.1080/10635150601058014

Shikama, T. (1946) The Kuzuü ossuaries, geological and palaeontological studies of the limestone fissure deposits, in Kuzuü, Totigi Prefecture. *Scientific Reports of Tohoku Imperial University, second series (Geology)*, 23, 1–201. [with 32 pls., published in 1949]

Smith, M.A. (1931). *The Fauna of British India, Including Ceylon and Burma. Reptilia and Amphibia. Vol. 1.– Loricata, Testudines*. Taylor and Francis Ltd., London, 185 pp., 3 pls.

Spinks, P.Q., Shaffer, H.B., Iverson, J.B. & McCord, W.P. (2004) Phylogenetic hypotheses for the turtle family Geoemydidae. *Molecular Phylogenetics and Evolution*, 32, 164–182.
http://dx.doi.org/10.1016/j.ympev.2003.12.015

Stejneger, L. (1907) *Herpetology of Japan and adjacent territory.* United States National Museum Bulletin 58, Smithsonian Institution, Washington, 577 pp.
http://dx.doi.org/10.5479/si.03629236.58.i

Sudo, I., Yanagisawa, Y. & Ogasawara, K. (2005) Tertiary geology and chronostratigraphy of the Joban areas and its environs, northeastern Japan. *Bulletin of the Geological Survey of Japan*, 56, 375–409.

Taguchi, E., Ono, N. & Okamoto, K. (1979) Fossil molluscan assemblages from the Miocene Bihoku Group in Niimi City and Ohsa–Chô, Okayama Prefecture, Japan. *Bulletin of the Mizunami Fossil Museum*, 6, 1–15. [in Japanese with English abstract]

Takemura, A., Miyake, M., Matsuda, T., Iwano, H. & Danbara, T. (2003) Fission–track ages of the Miocene Shiomachi Formation in the Miyoshi area, Hiroshima Prefecture, southwest Japan. *Journal of the Geological Society of Japan*, 109, 305–309.
http://dx.doi.org/10.5575/geosoc.109.305

Taylor, E.H. (1920) Philippine turtles. *Philippine Journal of Science*, 16, 111–144 + pls 1–7.

Theobald, W. (1868) Catalogue of the Reptiles of British Birma, embracing the provinces of Pegu, Martaban, and Tenasserium; with descriptions of new or little known species. *Journal of the Linnean Society*, 10, 4–67.
http://dx.doi.org/10.1111/j.1096-3642.1868.tb02007.x

Turtle Taxonomy Working Group (2007) An annotated list of modern turtle terminal taxa, with comments on areas of taxonomic instability and recent change. *In*: Shaffer, H.B., FitzSimmons, N.N., Georges, A. & Rhodin, A.G.J. (Eds.), *Defining Turtle Diversity: Proceedings of a Workshop on Genetics, Ethics, and Taxonomy of Freshwater Turtles and Tortoises*. *Chelonian Research Monographs*, 4, 173–199.

Wade, B.S, Pearson, P.N., Berggren, W.A. & Pälike, H. (2011) Review and revision of Cenozoic tropical planktonic foraminiferal biostratigraphy and calibration to the geomagnetic polarity and astronomical time scale. *Earth–Science Review*, 104, 111–142.
http://dx.doi.org/10.1016/j.earscirev.2010.09.003

Wermuth, H. & Mertens, R. (1961) *Schildkröten, Krokodile, Brückenechsen*. Gustav Fischer Verlag, Jena, 422 pp.

Yamaguchi, T., Mashiba, H. & Kamiya, T. (2012) Miocene ostracodes from the Osaki Formation, Kukinaga Group, Tanegashima, Southwest Japan, and their significance for the biogeography of the Indo–West Pacific. *Paleontological Research*, 16, 107–123.
http://dx.doi.org/10.2517/1342-8144-16.2.107

Yamamoto, Y., Kurita, H. & Matsubara, T. (2000) Eocene calcareous nannofossils and dinoflagellate systs from the Iwaya Formation in Awajishima Island, Hyogo Prefecture, southwest Japan, and their geologic implications. *Journal of the Geological Society of Japan*, 106, 379–382. [in Japanese with English abstract]
http://dx.doi.org/10.5575/geosoc.106.379

Yasukawa, Y., Hirayama, R. & Hikida, T. (2001) Phylogenetic relationships of Geoemydine turtles (Reptilia: Bataguridae). *Current Herpetology*, 20, 105–133.
http://dx.doi.org/10.5358/hsj.20.105

Yasukawa, Y., Ota, H. & 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.
http://dx.doi.org/10.2108/zsj.13.303

Yeh, H.K. (1963) Fossil turtles of China. *Palaeontologia Sinica, New Series C*, 150, 1–112 (in Chinese with English summary).

Yeh, H.K. (1994) *Fossil and Recent Turtle of China*. Science Press, Beijing, 112 pp.

Zangerl, R. (1969) The turtle shell. *In*: Gans, C. & Parsons, T. (Eds.), *Biology of the Reptilia, Vol.1*. Academic Press, New York, pp. 311–339.

Zhang, M., Zong, Y. & Ma, J. (1998) *Fauna Sinica, Reptilia, vol.1, General accounts of Reptilia, Testudoformes and Crocodiliforms*. Science Press, Beijing, 213 pp. [in Chinese]

APPENDIX.

Specimens examined and sources of morphological data used for detailed comparisons in Table 1. Abbreviations: AT, private turtle collection of Akio Takahashi; RH, private turtle collection of Ren Hirayama.

Chinemys fenhoense: Chow (1961). *Chinemys nigricans*: RH 855, RH b–11; Fang (1934); Wermuth and Mertens (1961); Ernst and Barbour (1989); Iverson and McCord (1989); Lovich and Ernst (1989). *Chinemys reevesii*: AT 4, 137, 145, 150–151, 272, 274, 276, 297, 299; Stejneger (1907); Wermuth and Mertens (1961); Ernst and Barbour (1989); Lovich and Ernst (1989). *Cuvierichelys parisiensis*: de Broin (1977); Hervet (2004); Hirayama, personal observation. *Mauremys annamensis*: AT 121, 136; Bourret (1941); Wermuth and Mertens (1961); Ernst and Barbour (1989); Yasukawa *et al*. (2001). *Mauremys rivulata*: AT 143; Hirayama (1985); Ernst and Barbour (1989); Lovich and Ernst (1989). *Mauremys campanii*: Chesi *et al*. (2009). *Mauremys gaudryi*: de Broin (1977). *Mauremys japonica*: AT 74, 83, 139–142, 247; Stejneger (1907); Wermuth and Mertens (1961); Hirayama (1985); Ernst and Barbour (1989); Yasukawa *et al*. (2001). *Mauremys leprosa*: RH 453–454, 929; Boulenger (1889); Loveridge and Williams (1957); Wermuth and Mertens (1961); Hirayama (1985); Ernst and Barbour (1989); Lovich and Ernst (1989); and Yasukawa *et al*. (2001). *Mauremys massiliensis*: de Broin (1977); and Hervet (2004). *Mauremys mutica*: AT 8, 146, 167, 185, 225, 227–228, 257, 260, 264, 267; Nakamura (1934); Wermuth and Mertens (1961); Ernst and Barbour (1989); Lovich and Ernst (1989); Yasukawa *et al*. (1996). *Mauremys portisi*: Sacco (1889). *Mauremys pygolopha*: de Broin (1977); Hervet (2004). *Mauremys sarmatica*: Glaessner (1926); Hervet (2004). *Mauremys thanhinensis*: Claude *et al*. (2007). *Mauremys yabei*: Shikama (1946). *Ocadia nipponica*: Hirayama *et al*. (2007). *Ocadia sinensis*: AT40, 86, 138, 174; RH201–204, 206–207, 274, 340–341, 348, 355–357, 363, 373–375, 377–383, 386, 390–391, 393–396; Boulenger (1889); Stejneger (1907); Bourret (1941); Ernst and Barbour (1889); Lovich and Ernst (1989). *Palaeochelys crocheti*: Hervet (2004). *Palaeochelys laurenti*: de Broin (1977); Hervet (2004). *Palaeochelys vallisnerii*: de Broin (1977); Hervet (2004). *Sacalia* spp.: AT 88 (*S. quadriocellata*); Smith (1931); Bourret (1941); Hirayama (1985); Ernst and Barbour (1989); Lovich and Ernst (1989); Yasukawa *et al*. (2001). *Siebenrockiella crassicollis*: AT 142, 147; Boulenger (1889); Bourret (1941); Wermuth and Mertens (1961); Ernst and Barbour (1989); Yasukawa *et al*. (2001). *Siebenrockiella leytensis*: personal specimen of Y. Yasukawa; Taylor (1920); Ernst and Barbour (1989); Diesmos *et al*. (2005).