

Ocadia nipponica, a new species of aquatic turtle (Testudines: Testudinoidea: Geoemydidae) from the Middle Pleistocene of Chiba Prefecture, central Japan

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Abstract. A new species of the genus *Ocadia* (Testudines; Testudinoidea; Geoemydidae), *O. nipponica*, is described on the basis of a nearly complete skeleton from the Middle Pleistocene Kiyokawa Formation of the Shimosa Group at Sodegaura City, Chiba Prefecture, central Japan. *O. nipponica* is distinguished from *O. sinensis* (Gray) by its more extensive secondary palate, smoother shell surface, narrower second and third vertebral scutes, and larger size (carapace up to 33 cm long). Considering that the living species *O. sinensis* is distributed in the coastal area of eastern to southeastern Asia in subtropical to tropical climates, the new fossil species may have been thrived in warmer paleoclimatic conditions for the Japanese Islands in the Pleistocene age than hitherto have been estimated on the basis of floral evidences.

Key words: *Ocadia nipponica* sp. nov., Reptilia, paleoclimate, Pleistocene, Kiyokawa Formation, Chiba Prefecture

Introduction

In March 1999, the second author of this contribution discovered a molar tooth and femur of *Palaeoloxodon naumanni* (Makiyama, 1924), an extinct elephant, in an outcrop of the Middle Pleistocene Kiyokawa Formation, Shimosa Group, at Yoshinoda, Sodegaura City, Chiba Prefecture (Fig. 1; Kaneko *et al.*, 2000). During subsequent excavations that extended for 65 days, more than 500 specimens of terrestrial vertebrate fossils were collected from this locality (Okazaki *et al.*, 2004a; Kaneko and Okazaki, in press). Among fossils, chelonian materials such as *Mauremys yabei* (Shikama, 1949), an extinct species of geoemydid, as well as the remains of *Cervus nippon* (Cervidae; Artiodactyla; Hirayama *et al.*, 2002, 2004a, b, in press; Kaneko and Okazaki, in press; Takakuwa, in press), are the most abundant. In this article, we will describe a new species of herbivorous aquatic turtle, based on a nearly complete skeleton, and discuss its phylogenetic and paleoclimatic significance.

Geological setting

The Kiyokawa Formation represents the middle part of the Shimosa Group (Middle to Late Pleistocene)

and is distributed in the northern part of the Boso Peninsula, central Japan (Fig. 1; Okazaki *et al.*, 2004a, b). A tephra marker bed from the lowermost part of the Kiyokawa Formation, Ky2, is correlated with TB-7, another tephra bed from the Oiso district of Kanagawa Prefecture, which is estimated as 225 ± 24 Ka by the fission track dating method (Nakazato *et al.*, 2004; Okazaki *et al.*, 2004a). The Kiyokawa Formation rests unconformably upon the Kamiizumi Formation at Yoshinoda, being composed of fluvial and shoreface deposits in ascending order at the fossil-vertebrates-bearing locality. The fluvial deposits were formed during an early transgressive stage of relative sea level during an interglacial period.

The flood plain deposit of the Kiyokawa Formation yielding fossil vertebrates is divided into three depositional units by lithology and fossil assemblages; units A, B and C (Fig. 2; Okazaki *et al.*, 2004a, b). The lowermost unit A consists of massive muds with plant remains that are interpreted as wash load by flooding. Unit B is composed of ill-sorted muddy sands or sandy muds and contains numerous wood debris and isolated vertebrate remains, including isolated shells of *Mauremys yabei*, freshwater molluscan remains (e.g., *Anodonta* sp.), and mudstone gravels.

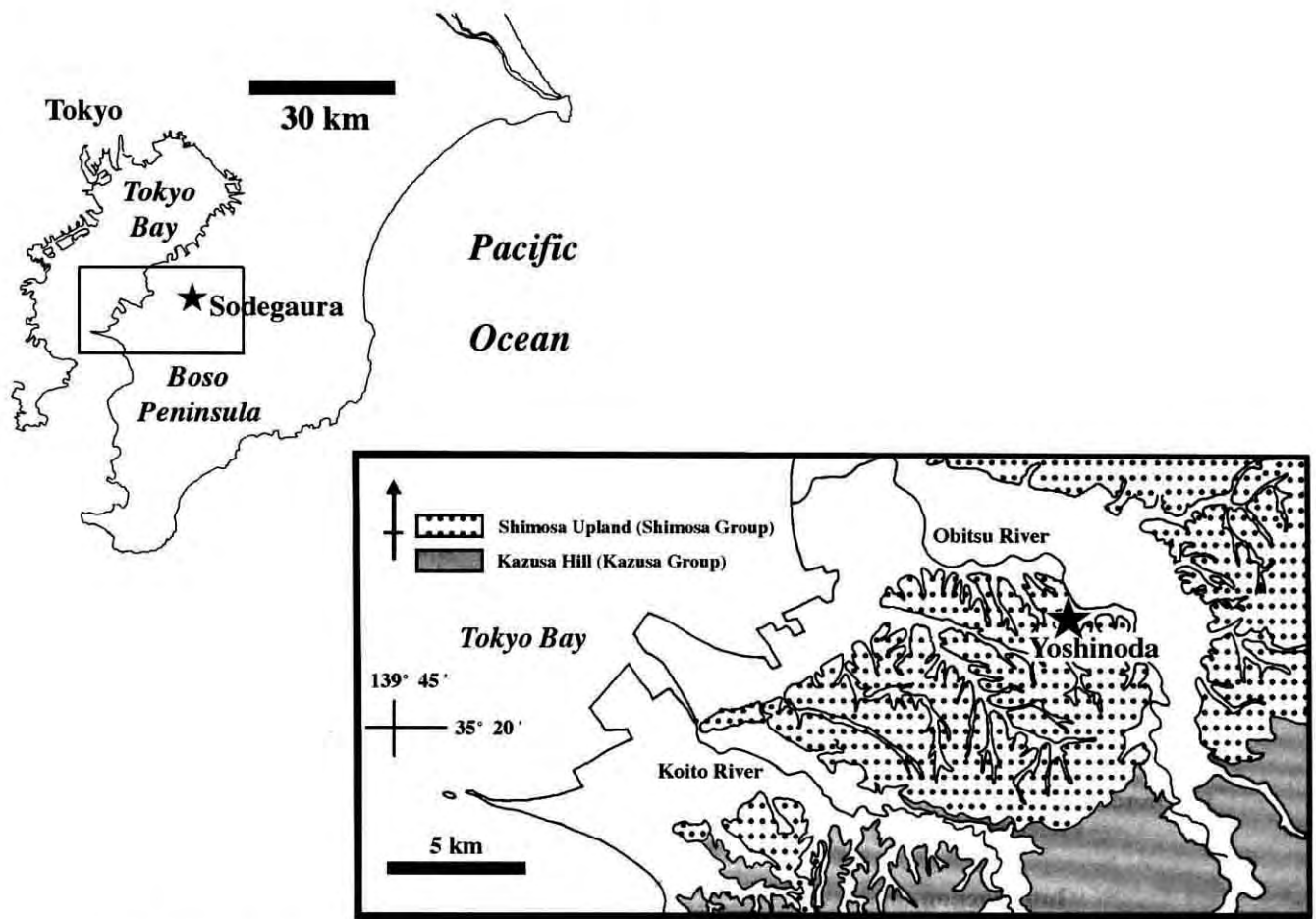


Figure 1. Locality map of *Ocadia nipponica* sp. nov. (Holotype; CBM-PV 686), and geology of the study site at Yoshinoda, Sodegaura, Chiba Prefecture (modified from Okazaki *et al.*, 2004).

It may have accumulated during a mudflow accompanied with flooding. These fossil assemblages indicate that these sediments come from a larger area than the stream channel. The uppermost unit C consists of massive muds and alternating layers of silts and fine-grained sands. Unit C contains in-situ freshwater bivalves and a nearly perfect skeleton of a turtle, the holotype of *Ocadia nipponica*, sp. nov. These fossils indicate that unit C was deposited in still water, such as a pond or shallow lake.

Material and methods

Comparative materials of living turtles, including 51 species of Geoemydidae among which are 75 specimens of *Ocadia sinensis* from China, are deposited in the private collection of Ren Hirayama.

The fossil specimen, a nearly complete skeleton of one individual, including associated skull and shell, was prepared using mechanical methods and often reinforced with super glue, because the bones were sometimes extremely damaged and fragile. Only its mold remained in some places. The skull and lower jaw was found isolated about 15 cm from the main part of the postcranial materials (Hirayama *et al.*, in press). The posterior portion of the carapace was disarticulated and scattered around the main part of the shell as well (Hirayama *et al.*, in press).

Institutional abbreviations for fossil materials. BMNH) Natural History Museum, London, UK; CBM-PV) Natural History Museum & Institute, Chiba, Japan; MNHN) Muséum National d'Histoire Naturelle, Paris, France; NSM) National Science Museum, Tokyo, Japan.

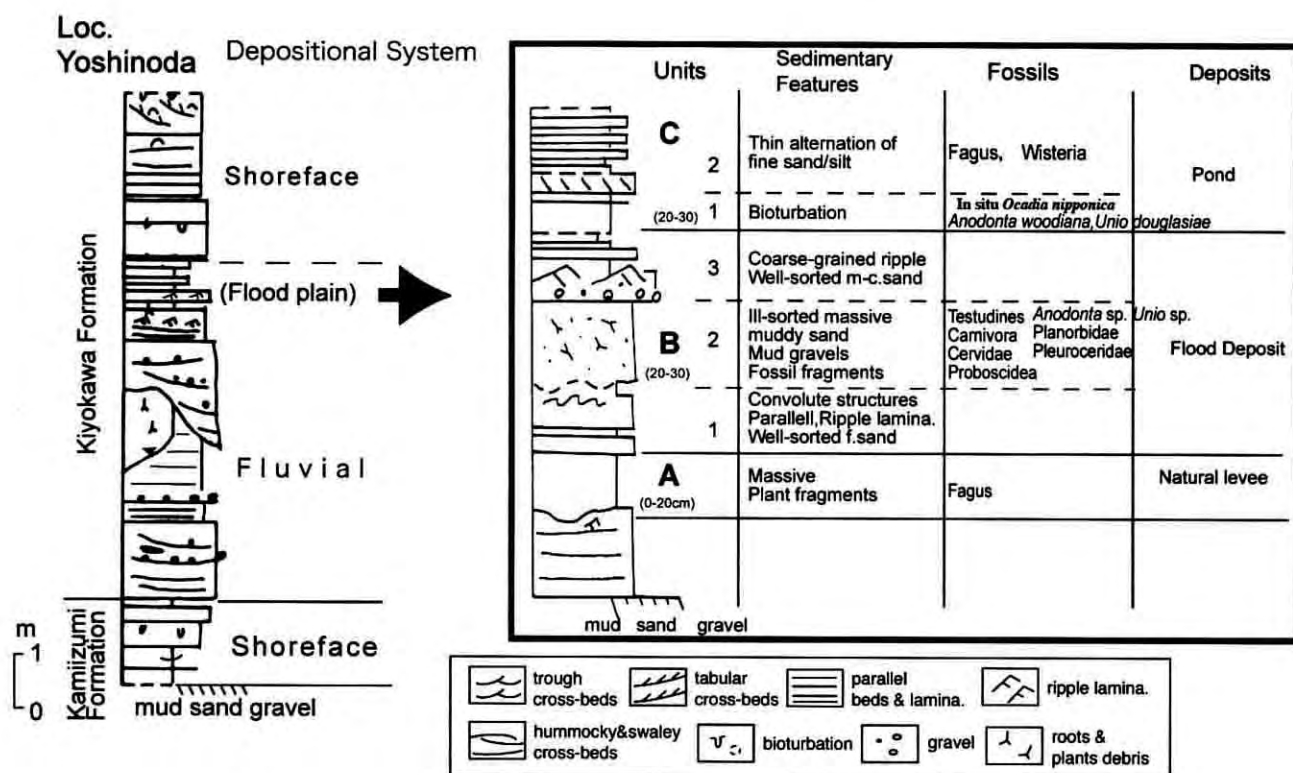


Figure 2. Columnar section and depositional facies of the locality of *Ocadia nipponica* sp. nov. (Holotype; CBM-PV 686) from the Kiyokawa Formation at Yoshinoda, Sodegaura, Chiba Prefecture. Modified from Okazaki *et al.* (2004).

Systematic paleontology

Order Testudines Batsch, 1788
 Suborder Cryptodira Cope, 1868
 Superfamily Testudinoidea Batsch, 1788
 Family Geoemydidae Theobald, 1868
 Genus *Ocadia* Gray, 1870

Type Species.—*Ocadia sinensis* (Gray, 1834)

Known Distribution.—Early Miocene? to Recent of Eastern Asia.

Emended Diagnosis.—Medium to large geoemydid with enlarged upper and lower triturating surfaces, decorated by lingual ridges; foramen orbito-nasale small; plastral buttresses moderately strong, developed along half way of the costal plates; gular scute shortened, often excluded from entoplastron; humero-pectoral sulcus intersecting anterior half of entoplastron.

Ocadia nipponica sp. nov.

Holotype.—CBM-PV 686; a nearly complete skeleton, including skull, lower jaw, much of the appendic-

ular skeletons and shell (Figs. 3–4, 5A, 6A and C, 7–9, and 10A).

Type Locality.—Yoshinoda (about 1.5 km south-east from the Kisarazu-kita exit of the Tateyama Highway), Takinokuchi, Sodegaura City, Chiba Prefecture, Japan.

Type Horizon.—lower part of the Kiyokawa Formation, Shimosa Group (Middle Pleistocene, about 0.22 m.y.a.).

Known Distribution.—Known only from the type locality and horizon.

Collector.—Naoki Kohno, Naotomo Kaneko, Hajime Taru, Yuji Takakuwa, Shinji Isaji, and Ren Hirayama, 29 October, 2001 to 3 July, 2002.

Etymology.—From Nippon, Japanese name of the Japanese nation,

Diagnosis.—Triturating surfaces of skull and lower jaw much broader than *O. sinensis*, as extensive as *Batagur baska*; shell length up to 33 cm long, about 20% larger than the largest individual of *O. sinensis*; external surface of carapace and plastron smooth except for scute sulci, without distinct ridges and annual growth sulci; second and third vertebrae nearly rectangular, as long as broad, much narrower than first vertebral.

Hypodigm.—holotype only.

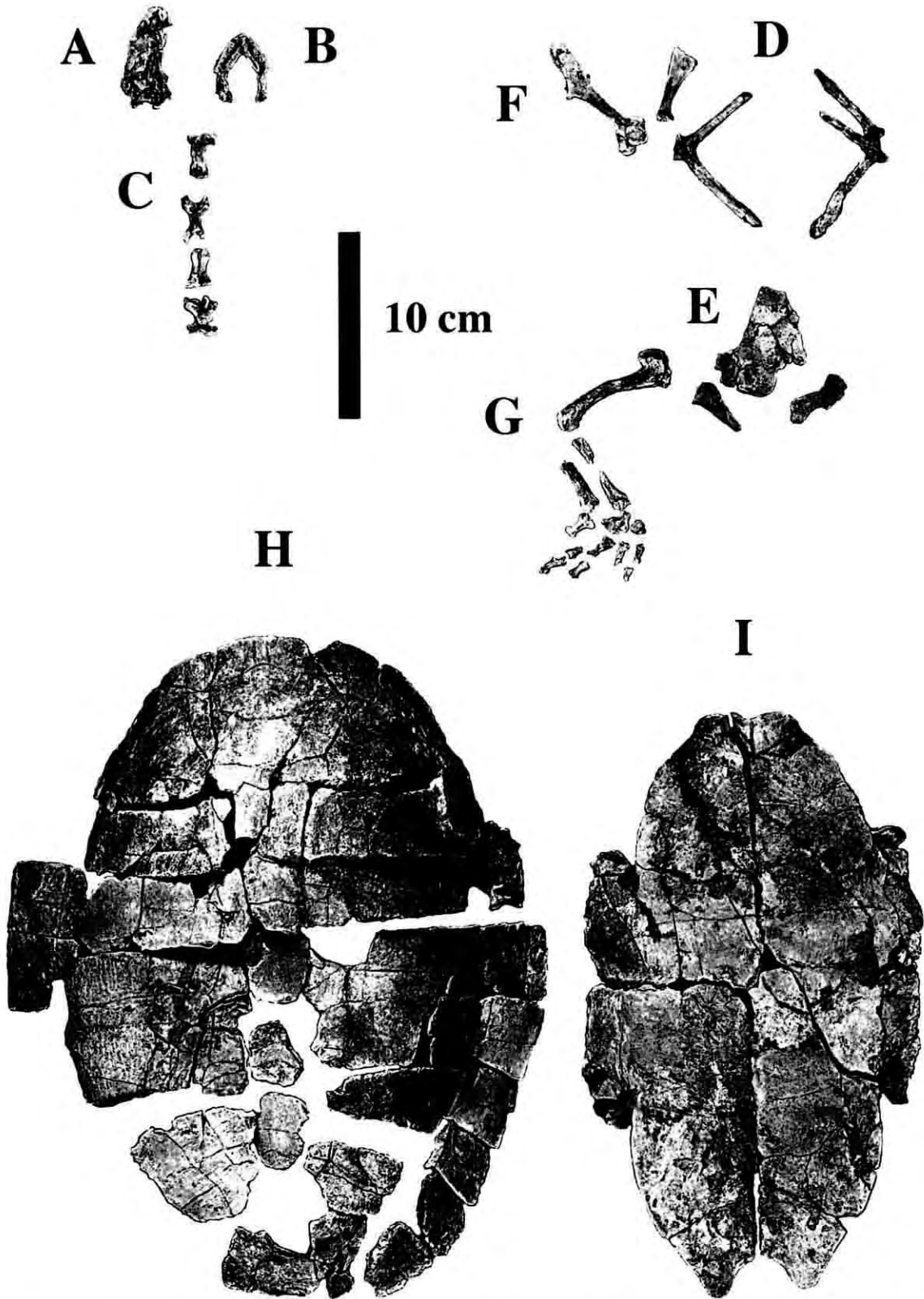


Figure 3. Skeleton of *Ocadia nipponica* sp. nov. (Holotype; CBM-PV 686). A: skull, B: lower jaw, C: cervical vertebrae, D: pectoral girdle, E: pelvic girdle, F: left humerus, G: left hind limb, H: carapace, I: plastron.

Description

Skull (Figs. 4A to F, 5A, 6A)

The skull is 54 mm long as preserved from the premaxilla to the occipital condyle. Most of dorsal elements and right half portion was broken and lost during the excavation, although it is quite possible that the skull was originally preserved almost completely (Figs. 4A to D).

Of the dermal roofing elements, only the left prefrontal, postorbital, jugal, and quadratojugal are preserved (Figs. 4A, B, E and F). The prefrontal consists of a dorsal plate and a vertical plate. In lateral view, the vertical plate of the prefrontal meets the maxilla and palatine. The postorbital is a large element that forms most of the relatively long postorbital bar, as in *O. sinensis* and species of *Mauremys*. In lateral view, the postorbital contacts the jugal, quadratojugal, and squamosal. Only a tiny portion of the quadratojugal and squamosal is preserved.

Palatal elements are well preserved on the left side (Figs. 4C, D). The premaxilla is a small element that meets the maxilla laterally, and its counterpart medially. It forms the anterior portion of the broad secondary palate. The maxilla forms the majority of the upper triturating surface which has a single coarsely denticulated lingual ridge. The medial contacts of the maxillae are much longer than in *O. sinensis* (Figs. 5A, 6A, B). This results in *O. nipponica* having a much broader upper triturating surface than *O. sinensis*. The upper triturating surface of the fossil taxon is posteromedially about 30% broader than that of *O. sinensis*, being almost comparable with that of *Batagur baska* in its extent (Gaffney, 1979). The palatine has no contribution to the upper triturating surface as in the living species. Only the posterior portion of the vomer that is located between the palatines is well preserved in ventral view. The foramen praepalatium is situated between the maxilla and vomer, concealed from ventral view by the shelf of the upper triturating surface of the maxilla. The foramen orbito-nasale located between the prefrontal, maxilla, and palatine is minute as in living *O. sinensis* (Figs. 4A, B, E, F).

Except for the missing supraoccipital, the basicranial and braincase elements of *O. nipponica* are well preserved (Figs. 4A–F). The pterygoid contacts anteriorly the vomer, palatine, maxilla, medially the other pterygoid and basisphenoid, and basioccipital, posterodorsally the prootic, and posterolaterally the quadrate. The processus pterygoideus externus is partly developed as in living *O. sinensis*. The small foramen palatinum posterius is bordered by the palatine and pterygoid as in *O. sinensis* (Figs. 4C, D, 4A). The fora-

men posterius canalis carotici interni is located at the posterior end of the pterygoid. The dorsal portion of the basisphenoid and basioccipital is partially exposed, showing a shallow sella turcica and low dorsum sellae (Figs. 4A, B). The foramen stapedio-temporale is located between the prootic and quadrate in dorsal view. The processus trochlearis oticum is formed by the prootic and quadrate as a relatively insignificant shelf as in *O. sinensis*.

Lower jaw (Figs. 4G to J, 6C)

The lower jaw is perfectly preserved in CBM-PV 686. The dentary has an enlarged lower triturating surface with a coarsely denticulated lingual ridge as in *O. sinensis*. The lower triturating surface of *O. nipponica* is much broader than in living species such as the upper triturating surface (Figs. 4I–L, 6C, D). This broader triturating surface results in a distinct lateral shelf anterior to the processus coronoideus in *O. nipponica*. The other elements, the prearticular, angular, articular, coronoid, and surangular, are comparable with *O. nipponica*. The processus coronoideus is moderately developed as in most geoemydids.

Shell (Figs. 7–9, 10A)

Most of the carapacial elements are preserved in CBM-PV 686 (Figs. 7A, 9A). The total length of the carapace is estimated as 33 cm long when reconstructed. The shell surface is very smooth, except for the scute sulci, and lacks any distinct longitudinal ridge. In contrast, *O. sinensis* has three rows of interrupted knobs on the neurals and costals and well developed annual growth rings on each scute area (Fig. 7A).

The carapace bones consist of one nuchal, eight neurals, two suprapyrgals, eight pairs of costals, eleven pairs of peripherals, and one pygal as a plesiomorphic condition of geoemydids. Only a few posterior parts, including the sixth neural and first suprapygal, were missing. The nuchal and second suprapygal are irregularly hexagonal. The first neural is barrel-shaped, the second to eighth neurals are hexagonal and short sided anteriorly, and the first suprapygal is trapezoidal, as in many geoemydids, including *O. sinensis* (Fig. 10). The first costal has a sutural facet for the axillary buttress of the hyoplastron, which runs about halfway along the first costal (Fig. 6B). A sutural facet for the inguinal buttress of the hyoplastron is developed between the fifth and sixth costals, running about halfway along the costals as well (Fig. 7B). Axillary and inguinal musk duct foramina are found in the third and seventh peripherals as a synapomorphic character of geoemydids (except for *Morenia*; Hira-

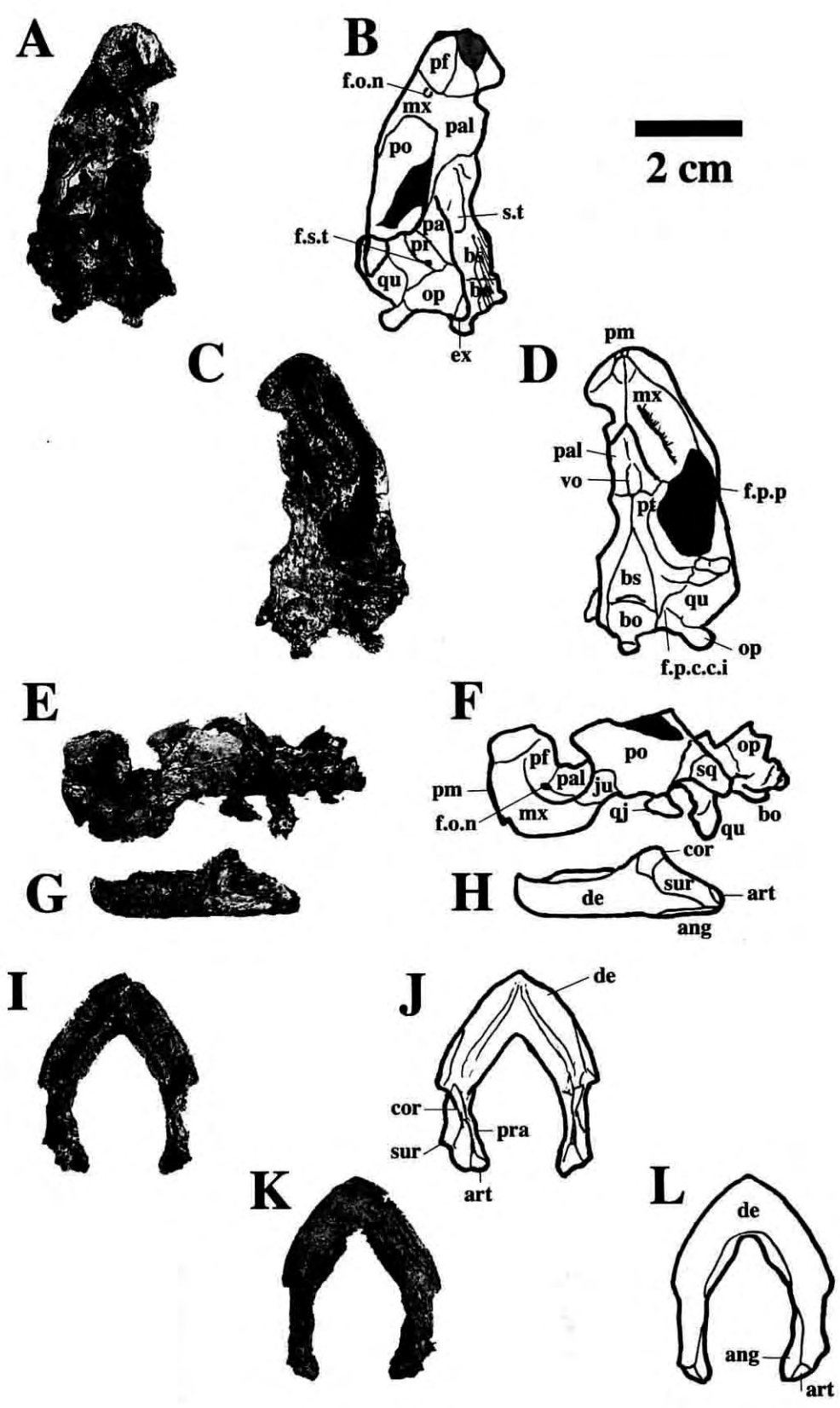


Figure 4.

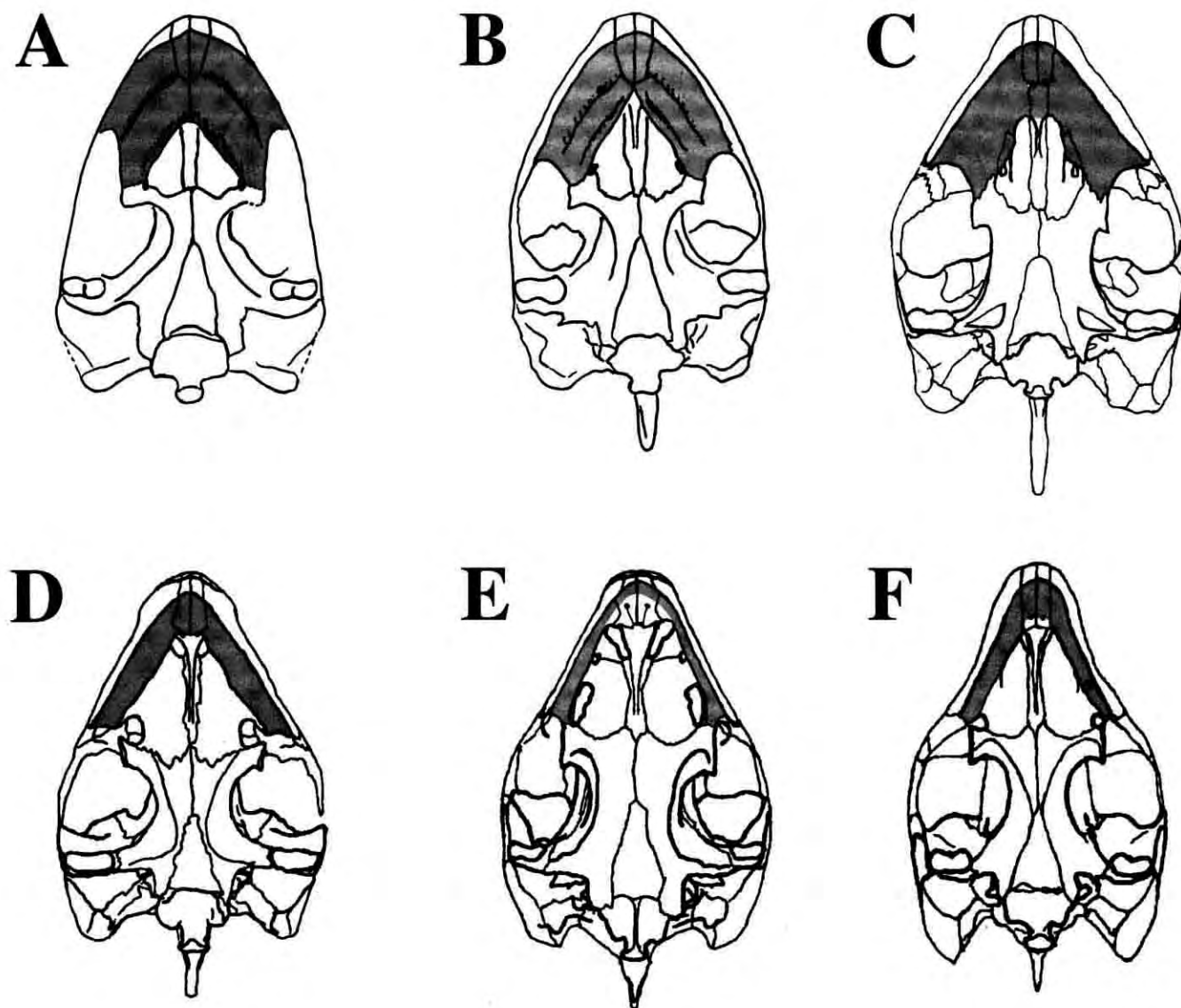


Figure 5. Skulls of East Asian Geoemydidae (ventral views). Shaded areas show the upper triturating surfaces. Not to scale. A: *Ocadia nipponica* sp. nov., reconstruction based on the holotype (CBM-PV 686; CBL 54 mm), B: *O. sinensis* (RH 401; condylobasal length (= CBL) 45 mm), C: *Chinemys reevesii* (RH 100; CBL 52 mm), D: *Cuora flavomarginata* (RH 65; CBL 42 mm), E: *Mauremys japonica* (RH 67; CBL 33 mm), F: *Geoemyda japonica* (collection of National Science Museum, Tokyo; CBL 30 mm).

yama, 1985).

Scutes overlying the carapace consist of one cervical, five vertebrals, four costals, and twelve pairs of

marginals as in generalized testudinoids. The cervical scute is narrow and much longer than broad. The first vertebral is rather broad, but contacts the second mar-

◀ **Figure 4.** Skull and lower jaw of *Ocadia nipponica* sp. nov. (Holotype; CBM-PV 686). A, B: dorsal view of skull; C, D: ventral view of skull; E, F: left lateral view of skull; G, H: left lateral view of lower jaw; I, J: dorsal view of lower jaw; K, L: ventral view of lower jaw. Gray shaded areas denote matrix that could not be removed. Abbreviations: ang, angular; art, articular; bo, basioccipital; bs, basisphenoid; cor, coronoid; de, dentary; ex, exoccipital; f. o. n, foramen orbito-nasale; f.p.c.c.i, foramen posterius canalis carotici interni; f.p.p, foramen palatinum posterius; fr, frontal; f.s.t, foramen stapedio-temporale; ju, jugal; mx, maxilla; op, opisthotic; pa, parietal; pal, palatine; pf, prefrontal; pm, premaxilla; po, postorbital; pr, prootic; pra, prearticular; pt, pterygoid; qj, quadratojugal; qu, quadrate; sq, squamosal; s.t, sella turcica; sur, surangular; vo, vomer.

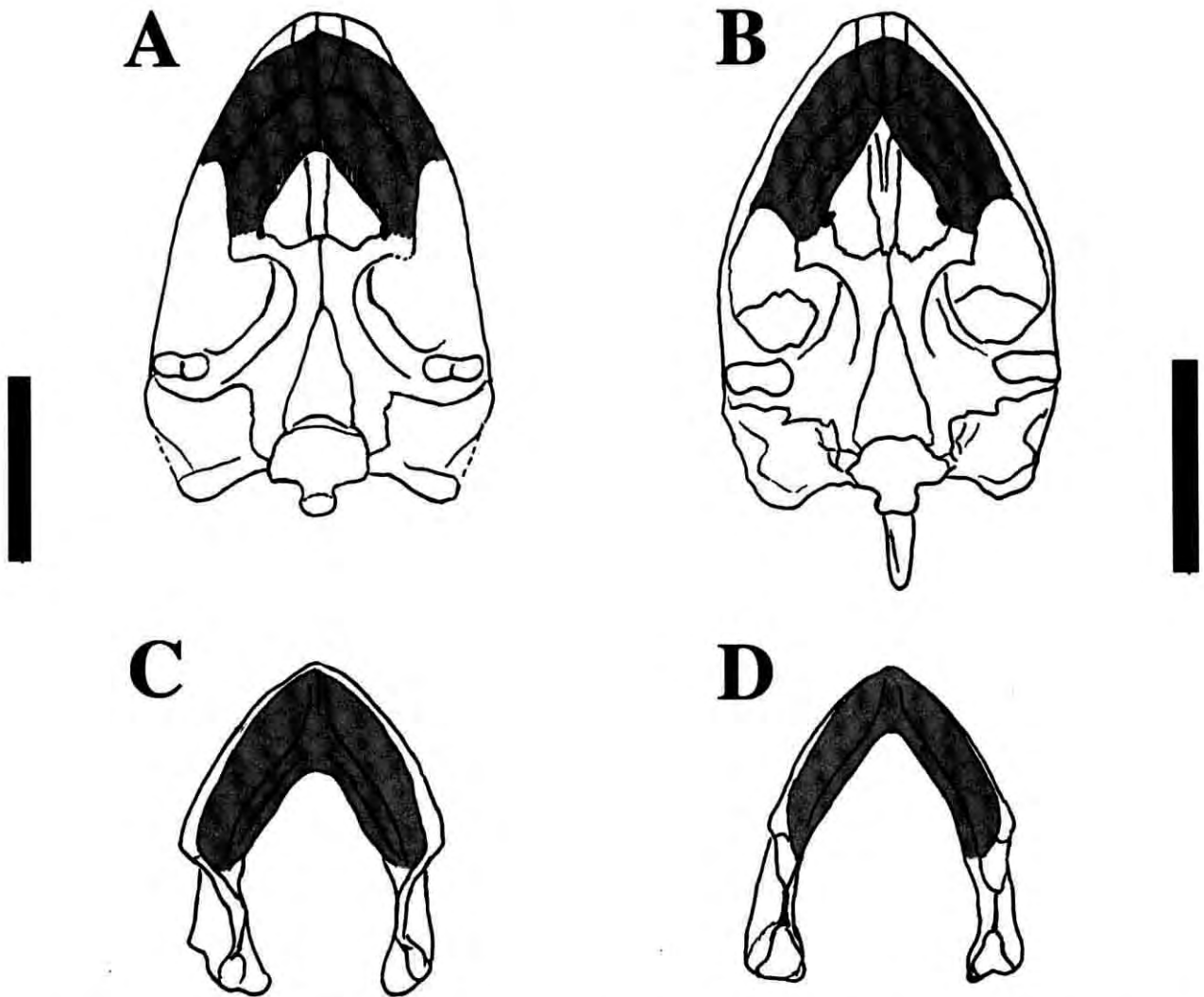


Figure 6. Comparison of upper and lower triturating surfaces of *Ocadia nipponica* sp. nov. and *O. sinensis*. Shaded areas show the triturating surfaces. Scale bar is 2 cm. A, C: reconstruction of *O. nipponica* sp. nov., based on the holotype (CBM-PV 686). B, D: *O. sinensis*; RH 401. A, B: ventral views of skull. C, D: dorsal views of lower jaw.

ginal along a corner only. Measurements of the first to third vertebrals are the following (in mm):

First vertebral: maximum width 82, maximum length 61.

Second vertebral: maximum width 71, maximum length 66.

Third vertebral: maximum width 69, maximum length 72.

Thus, in *O. nipponica* the second and third vertebrals are nearly rectangular, nearly as long as broad, much narrower than the first, whereas in *O. sinensis*

the second and third vertebrals are a more rectangular shape, broader than long, much broader than the first (Fig. 10). There are no unusual scute contacts in CBM-PV 686 as in some *Geoemydidae* and *Testudiniidae* (e.g., the sixth marginal—third costal contact in *Mauremys japonica*).

The plastron is almost completely preserved in CBM-PV 686 (Figs. 8, 9B). It consists of one pair of epiplastra, one entoplastron, one pair of hyoplastra, hypoplastra, and xiphiplastra. The dorsal portion of the epiplastra, which are underlain by the gulars, is moderately large and thickened as in *O. sinensis* (Fig. 7B). The lateral margin of the posterior lobe, consist-

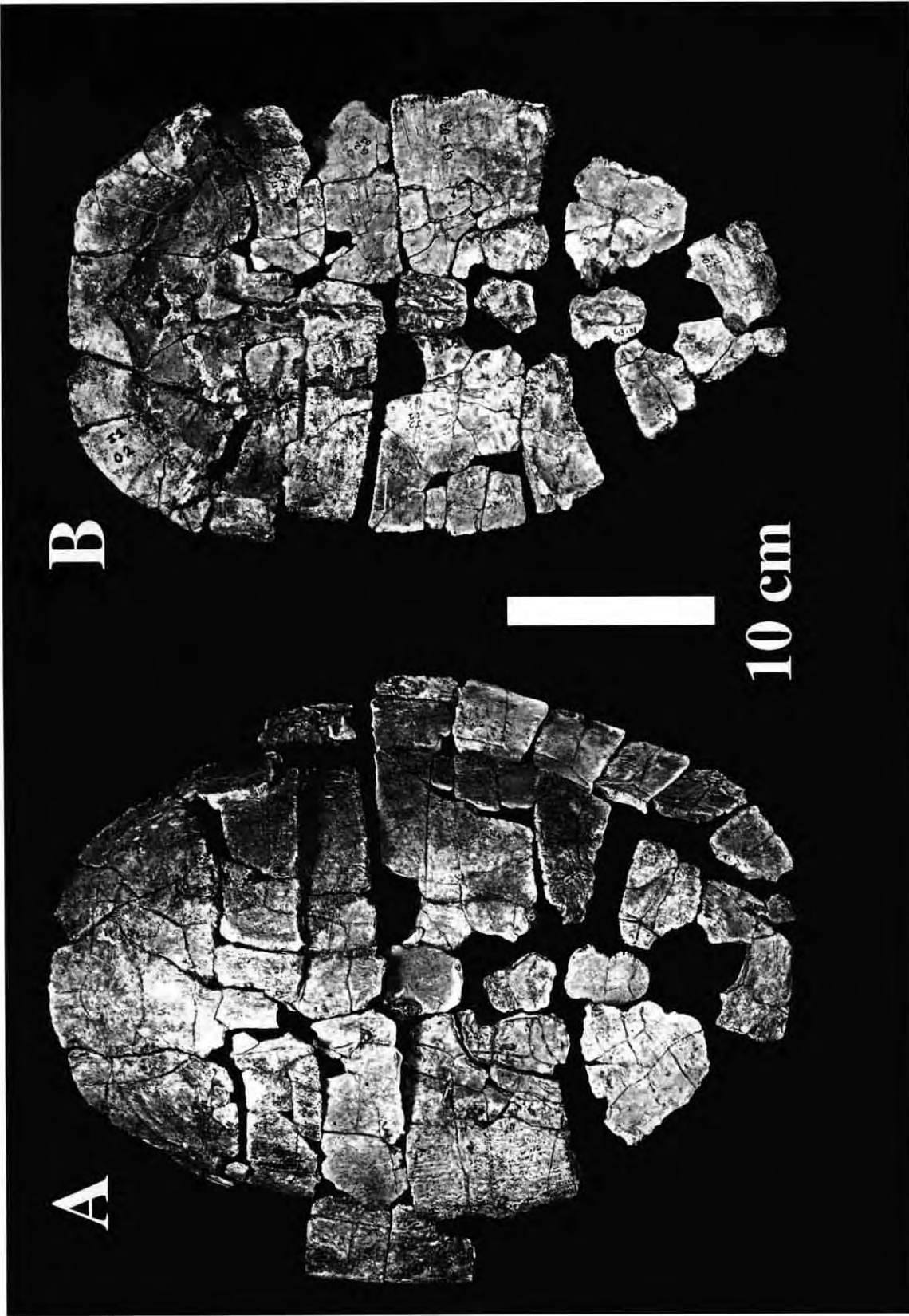


Figure 7. Carapace of *Ocadia nipponica* sp. nov. (Holotype; CBM-PV 686). A: dorsal view, B: ventral view (posterior part of peripherals removed).

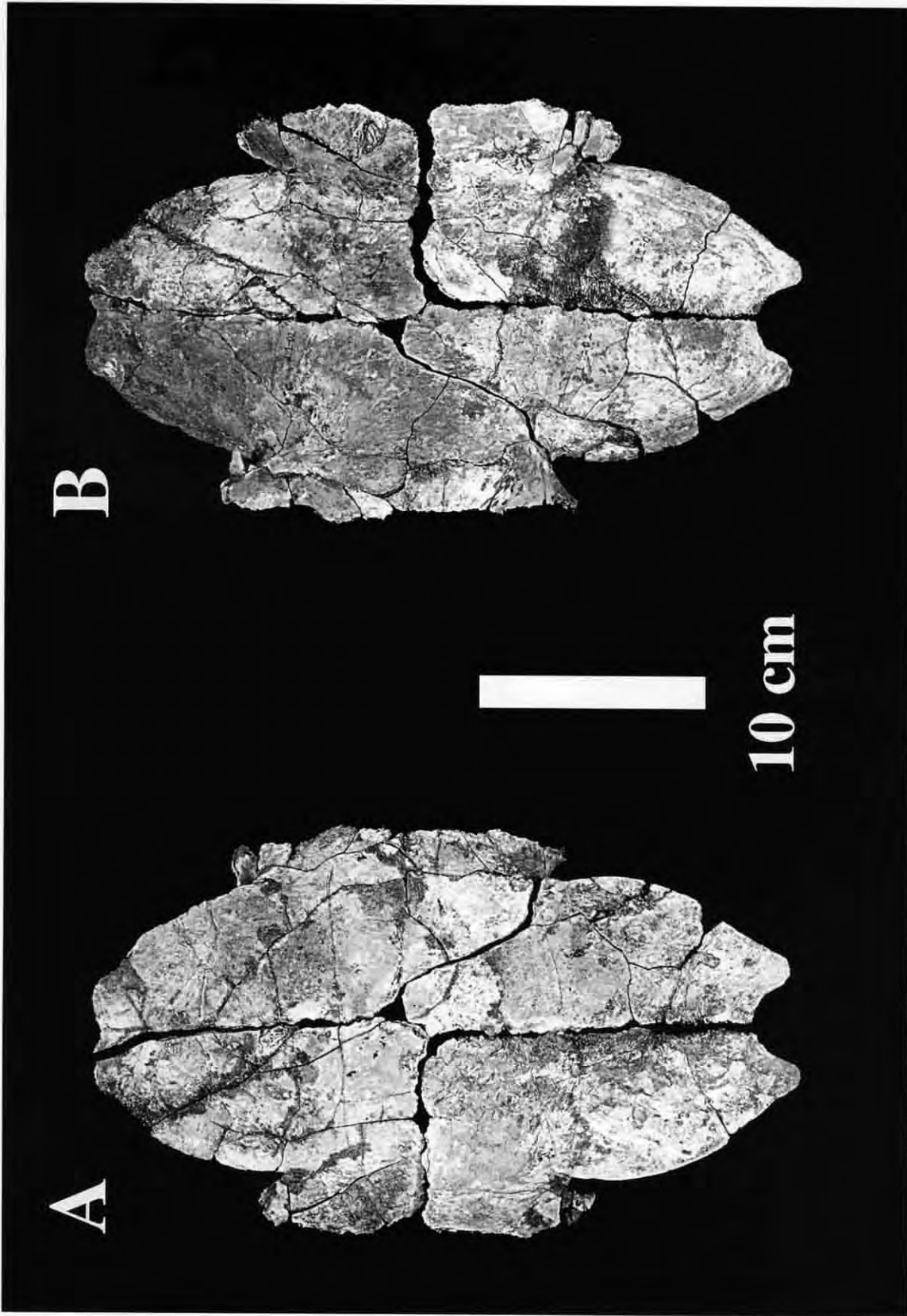


Figure 8. Plastron of *Ocadia nipponitca* sp. nov. (Holotype; CBM-PV 686). A: ventral view, B: dorsal view.

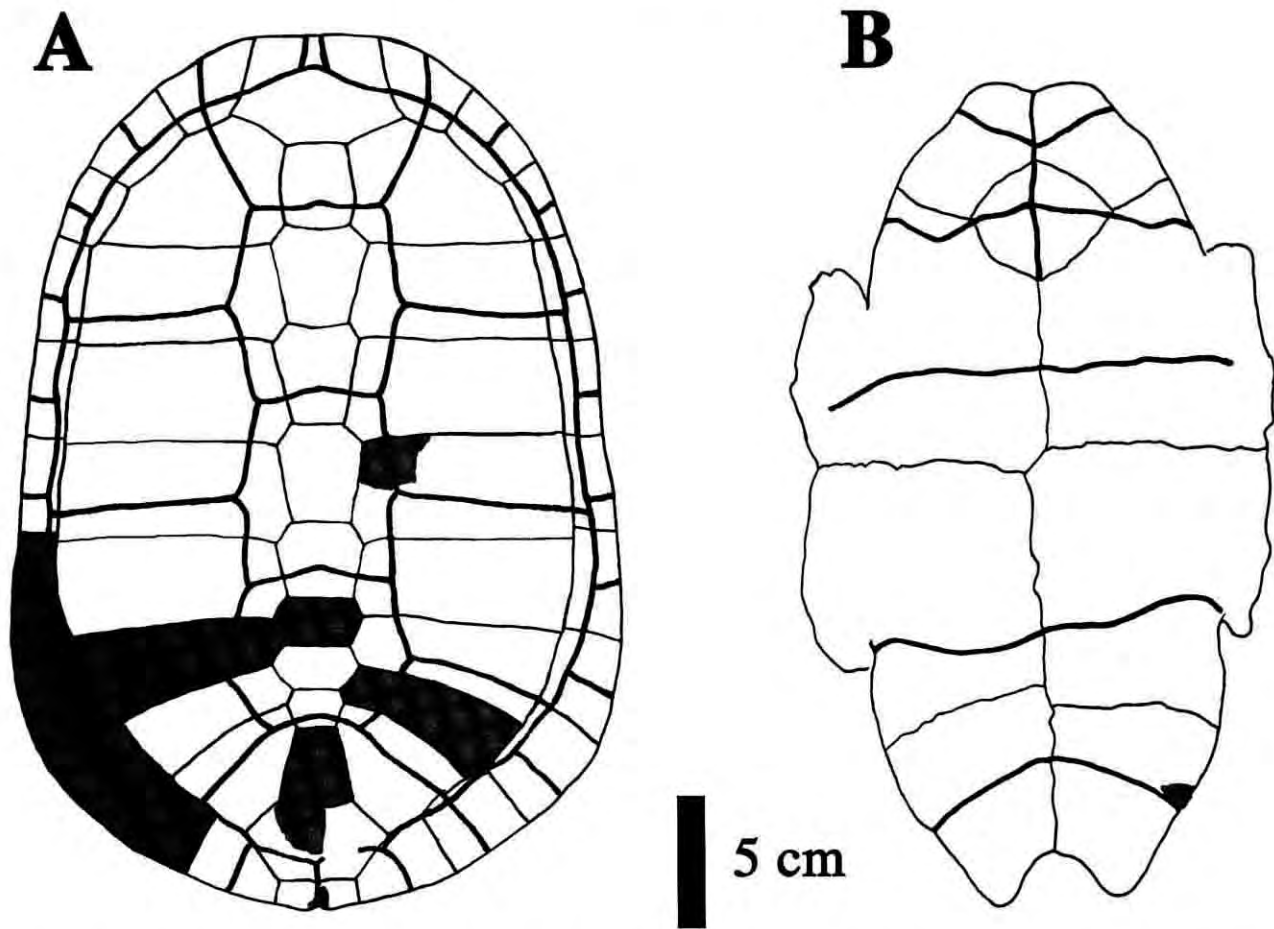


Figure 9. Shell reconstruction of *Ocadia nipponica* sp. nov., based on the holotype (CBM-PV 686). A: carapace, dorsal view. B: plastron, ventral view. Bold line shows scute sulci on shell surface. Shaded area shows missing portion.

ing of hypoplastron and xiphiplastron, expands convexly toward lateral. This suggests that this individual was a female with a relatively broader plastral lobe as seen in the population of *O. sinensis* (Ernst and Barbour, 1989; Zhang *et al.*, 1998; Hirayama, pers. obs.).

The scutes overlying the plastron consist of one pair of gulars, humerals, pectorals, abdominals, femorals, and anals as in most testudinoid turtles. It is likely that the axillary and inguinal scutes were originally present, but it is hard to discern their sulci on the plastron.

In living *O. sinensis*, the position of the gular scutes is rather highly variable relative to the entoplastron. Among 32 prepared specimens of this species in the RH collection, which were collected in Taiwan, five individuals show gulars that are completely excluded from the entoplastron, and in a further eight individuals the gular barely overlaps the anterior portion of the entoplastron. In the remaining individuals, the gu-

lar scutes are “normally” overlying on the entoplastron as is the case in most turtles with shell scutes retained. Thus, about 40% (thirteen individuals) of this population has distinctly short gular scutes such as were figured by Bourrett (1941). In CBM-PV 686, the gular is distinctly short, completely restricted to the epiplastron (Fig. 9B). The gular of most turtles is usually much longer, partially overlapping the entoplastron, with the exception of a few geoemydids (two species of *Geoemyda* and *O. sinensis*) and testudinids (e.g., *Geochelone* and *Kinixys*) as shown in the Appendix. Thus, short gulars that are excluded from the entoplastron are considered synapomorphic for *O. nipponica* and *O. sinensis*.

The humero-pectoral sulcus intersects the anterior half of the entoplastron in *O. nipponica* and *O. sinensis*, but intersects the posterior portion of the entoplastron, or is located posterior to the entoplastron in other geoemydids.

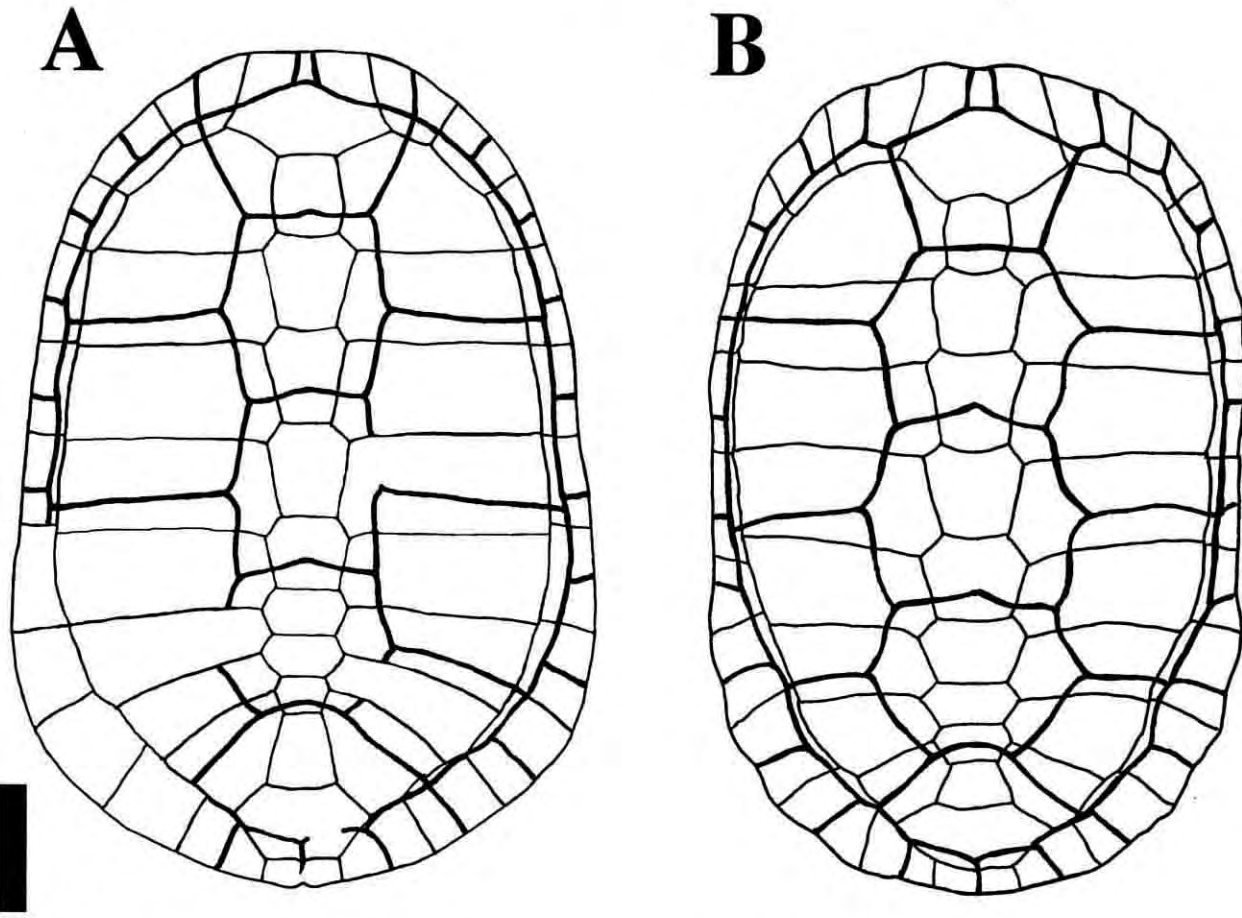


Figure 10. Shell comparison of *Ocadia nipponica* sp. nov. and *O. sinensis* in dorsal view. A: *O. nipponica* sp. nov. based on the holotype (CBM-PV 686), B: *O. sinensis*; RH 401. Bold line shows scute sulci on shell surface. Scale bar is 5 cm.

Axial skeletons (Figs. 3C, 7B).

The fifth to eighth cervical vertebrae were found disarticulated from the anterior portion of the shell. The fifth to seventh cervical vertebrae are procoelous as in all testudinoids (Williams, 1950). The eighth cervical vertebra, 22 mm long, is well preserved, showing its biconvex central articulation with anterior double joint structure, a synapomorphy of testudinoids (Williams, 1950; Hirayama *et al.*, 2000).

The first thoracic vertebra is preserved in situ beneath the nuchal and first neural plates in situ (Fig. 7B). Its anterior central articular facet is inclined anteroventrally, an apomorphic feature for the Testudinoidea and Trionychoidea, or Chelomacryptodira (Gaffney and Meylan, 1988). Among thoracic centra, only the first two are preserved.

An isolated caudal vertebra with procoelous centrum was also collected.

Appendicular skeleton (Figs. 3D–G)

Both pectoral and pelvic girdles were recovered from inside the shell. It is likely that they were originally preserved completely, but damaged during the excavation and preparation. The coracoid is narrowly fan-shaped, typical for aquatic turtles such as geoemydids. The pubes are tightly united together along their medial border, suggesting that CMB-PV 686 was an old individual (Fig. 3E).

The left humerus is the only fore limb material that is preserved. It is 70 mm long, including a large pathological swelling on the distal end. This element should have been 50 mm long in a healthy individual (Fig. 3F).

The left hind limb is rather well preserved, including the femur (67 mm long), tibia, fibula, astragalus, calcaneum, metacarpals, and digital bones (Fig. 3G). Its elongate and slender proportions show that *O. nip-*

ponica was a typical aquatic turtle like living *O. sinensis* (Joyce and Gauthier, 2004).

Discussion

The presence of anterior and posterior musk duct foramina that are enclosed in the third and seventh peripherals demonstrates that CBM-PV 686 is a member of the family Geoemydidae (Hirayama, 1985; Joyce and Bell, 2004).

Derived characters, such as enlarged upper and lower triturating surfaces decorated by lingual ridges, and short gular scutes excluded from the entoplastron, are shared by both CBM-PV 686 and *Ocadia sinensis*. Thus, it is reasonable to hypothesize that this specimen is a close relative of *O. sinensis*.

CBM-PV 686, however, has much broader triturating surfaces than *O. sinensis*. Its degree of development seems more similar to *Batagur baska* (Boulenger, 1889; Gaffney, 1979). The external shell surface is quite smooth, lacking distinct ridges, whereas *O. sinensis* has distinct annual growth sulci and three rows of knobs on the carapace. The carapace of CBM-PV 686 is 33 cm long, whereas the maximum carapace length of *O. sinensis* is only reported to be 27 cm (Chen and Lue, 1998; Zhang *et al.*, 1998; Hirayama, pers. obs.). Finally CBM-PV 686 has narrower second and third vertebral scutes than *O. sinensis*. All these differences are considered enough grounds to distinguish a fossil taxon from the living species. Thus, we propose a new species of the genus *Ocadia*, *O. nipponica*.

Phylogenetic hypotheses of geoemydids have been proposed based on both morphology (e.g., Hirayama, 1985; Yasukawa *et al.*, 2001) and, more recently, molecular data (e.g., Honda, 2002a, b; Spinks *et al.*, 2004), showing a large discrepancy among the results. Feldman and Parham (2004) provided a new view on phylogenetic relationships among nine species of Eurasian extant geoemydids such as *Mauremys*, *Chinemys*, and *O. sinensis* using sequence data of the mitochondrial DNA. Phylogenetic trees proposed by Feldman and Parham (2004) show that both *Chinemys* and *O. sinensis* are situated within the genus *Mauremys* and that species combined from a monophyletic clade within Geoemydidae. They placed both species of *Chinemys* (*C. reevesii* and *C. nigricans*) and *O. sinensis* within *Mauremys*, to avoid use of paraphyletic genus names and the proliferation of new names. Other molecular phylogenetic studies also support the close phylogenetic relationships of *Chinemys* and *O. sinensis* with *M. japonica* and/or other *Mauremys* species (e.g. Wu *et al.*, 1998; McCord *et al.*, 2000; Honda *et*

al., 2002b; Barth *et al.*, 2004; Sasaki *et al.*, 2004; Spinks *et al.*, 2004). Nonetheless, we have no good morphological characters that would corroborate this molecular hypothesis.

Even if the new phylogenetic tree was accepted, we suggest that generic names *Chinemys* and *Ocadia* should be preserved, because they exhibit extremely different morphology, especially in cranial characters, such as an extensive secondary palate (Figs. 4A–C, 5). On the other hand, species of *Mauremys* (sensu McDowell, 1964) retain a primitive primary palate (Fig. 4E). The presence of an extensive secondary palate with lingual ridges in *O. nipponica* and *O. sinensis* should be sufficient for the retention of their own generic name. As a consequence, members of the *M. mutica* group should have their own generic name such as *Cathaiemys* (Lindholm, 1931), and a new genus for *M. japonica* (and possibly *M. yabei*, an extinct species, as discussed later) should be proposed to ensure that all generic names refer to monophyletic groups. We suppose it should more properly reflect the morphological diversifications of this group such as large variation of the triturating surfaces.

A certain number of fossil geoemydids from Eurasia have been placed in *Ocadia* based on shell morphology alone (Lydekker, 1889; Kuhn, 1964). Unfortunately, all shell characters (e.g., moderately developed plastral buttresses) used in the literature for the definition of the genus *Ocadia* are plesiomorphic for Geoemydidae, and this is not useful for modern systematics (Hirayama, 1985). Nonetheless, at least one shell character, short gular excluded from the entoplastron, might be useful in defining this genus as a clade. Such a short gular can be found in some Paleogene geoemydids, such as *Ocadia crassa* (BMNH 32349) from the Late Eocene of the UK, and *Palaeochelys* (= *Cuvierichelys*) *parisiensis* from the Late Eocene of France (Lydekker, 1889; de Broin, 1977; Hervet, 2004; Hirayama, pers. obs.). Interestingly, the syntype of *P. parisiensis* (MNHN 8236 GY7), a newly prepared partial skull, includes a small part of the upper triturating surfaces of the maxilla with lingual ridge (Hirayama, pers. obs.). Short gulars are also present in large geoemydids (carapace is up to 36 cm long) from the early Miocene of Niimi, Okayama Prefecture of western Japan (Hirayama *et al.*, 1982, 1983). A large geoemydid was reported as *Ocadia* from the Early Miocene of Fukushima Prefecture, northeastern Japan, although it lacks most of the plastron (Hasegawa *et al.*, 2002). Thus, these geoemydids might be actual fossil taxa of the genus *Ocadia*, although the lack of good cranial material makes this inconclusive.

Fossil material referred to the living species, *O.*

sinensis, was reported from the Pliocene of China and Japan (Yeh, 1963, 1994; Hirayama, 2001). Some more fragmentary shell materials reported from the Early Pleistocene of western Japan by Otsuka (1969) and Hirayama and Inoue (1981) are possibly fossil *Ocadia* mainly because of its large size (shell length estimated as more than 30 cm) and smoother shell surface than *O. sinensis*.

Therefore, CMB-PV 686 is the first example of a good shell and skull association of a fossil *Ocadia*. *O. nipponica* demonstrates that this genus might have been well diversified in East Asia in the past, possibly as far back as the Miocene.

O. sinensis is an aquatic plant-eating turtle, well adapted to coastal environments in subtropical to warm temperate zones (Bourret, 1941; Iverson, 1992; Chen and Lue, 1998, 1999). Its northern limit appears to be controlled by a mean annual temperature of about 16°C. If *O. nipponica* required physiological conditions similar to those living species, then its presence could be a good paleontological index for the middle Pleistocene of Japan. However, a mean annual temperature of 16°C appears to be too warm and is contrary to estimations based on floral evidences (Momohara *et al.*, in press; Okuda *et al.*, in press).

O. nipponica cooccurs with some postcranial remains of *Mauremys yabei*, another extinct species of aquatic turtle, from the Kiyokawa Formation of Yoshinoda locality (Hirayama *et al.*, 2004b, in press). *M. yabei* was originally reported as *Clemmys yabei* on the basis of some shell material from Pleistocene cave fissure deposits of Kuzuu, Tochigi Prefecture, central Japan (Shikama, 1949). *M. yabei* is estimated to have had a maximum carapace length of only 20 cm long, much smaller than *O. nipponica*. Because *M. yabei* has both anterior and posterior musk duct foramina, this species appears to belong to the family Geoemydidae as well, although the genus *Clemmys* is a member of the family Emydidae in its more recent circumscription (McDowell, 1964; Gaffney and Meylan, 1988; Yasukawa and Hirayama, 2001). The extremely broad plastron suggests that this species is the sister taxon of *M. japonica*, a living endemic species of the Japanese main islands (Kyushu, Shikoku, and Honshu Islands; Hirayama *et al.*, in press). *M. yabei*, however, is easily distinguished from the living species in the possession of a narrower, almost triangular cervical, and posterior plastral buttress that reaches the sixth costal, and by lacking apomorphic features of *M. japonica*, such as serrated peripherals, and a very broad first vertebral that reaches the second marginals (Hirayama *et al.*, in press). *Cuora miyatai* is a third extinct Pleistocene geoemydid from the Japanese mainlands (Shi-

kama, 1949; Hasegawa, 1981). This geoemydid is known from several localities of the cave fissure deposits of Tochigi, Yamaguchi, and Oita Prefectures, and is extremely similar in both shell and skull morphology to living *Cuora flavomarginata*, although a few plastral features such as much narrower entoplastron suggest that *C. miyatai* should be considered an extinct species of this genus with hinged plastron (Yasukawa and Hirayama, 2001). Fossil material of *M. japonica* is restricted to a few remains from Neolithic sites of the Jomon period of western Japan (Yabe, T., pers. comm.). *M. yabei* seems too different and specialized to be considered the direct ancestor of the living species.

Thus, at least three fossil endemic species of geoemydids lived on the Japanese main islands during the Pleistocene. Together with the trionychid *Pelodiscus sinensis*, *M. japonica* is the sole remaining turtle to naturally inhabit the Japanese main islands (Hirayama *et al.*, 2004b). Based on the lack of any fossil record, *Chinemys reevesii*, a geoemydid widely distributed in Japan today, may be considered a recent immigrant, possibly from the Korean Peninsula (Yasukawa, Y., pers. comm.). The fossil record suggests that geoemydid turtles were diverse in Japan during the Pleistocene. Their endemic speciation seems deeply linked with the geographical isolation of Japan from the continental region since the beginning of the Pleistocene. The extinction of these endemic terrestrial turtles may have taken place during the Late Pleistocene, possibly caused by the extremely low temperatures during the latest glacial period, or by predatory pressure from humans who were immigrating from the continent as well as the Ryukyu Islands (Takahashi *et al.*, 2003, 2004).

Conclusion

A new species, *Ocadia nipponica*, is described on the basis of a nearly complete skeleton (CBM-PV 686) from the Middle Pleistocene nonmarine deposits of the Kiyokawa Formation at Yoshinoda, Sodegaura City, Chiba Prefecture, central Japan. *O. nipponica* is distinguished from the living species, *O. sinensis*, by the possession of a more extensive secondary palate, smoother shell surface, narrower second and third vertebral scutes, and its larger size. Two extinct species of turtles, *O. nipponica* and *Mauremys yabei*, from the Kiyokawa Formation are considered as endemic to the Japanese main islands as well, suggesting a much larger taxonomic diversity of geoemydid turtles in the Japanese Islands during the Pleistocene than hitherto considered. This also implies warmer pa-

leoclimatic conditions in the Japanese Islands during the Pleistocene than hitherto estimated on the basis of floral evidence alone.

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Appendix. Variation of gular scutes of extant Testudinoidea examined.

Institutional abbreviations are the followings:

AT: private collection of Akio Takahashi (Ryukyu University)
 ER: private collection of Erik (Kagoshima University)
 KU, KUZR: Kagoshima University (uncatalogued)

MCZ: Museum of Comparative Zoology, Harvard University
 NSM: National Science Museum, Tokyo, Japan
 RH: private collection of Ren Hirayama (Waseda University)
 RU: Ryukyu University (uncatalogued)
 YY: private collection of Yuichiro Yasukawa (Ryukyu University)
 Number shows the available catalogued number of the specimen in each collection.

Taxa	Gular completely excluded from the entoplastron	Gular just attached to the entoplastron	Gular overlying the entoplastron
Geoemydidae			
<i>Batagur baska</i>			RH 1014, ER
<i>Callagur borneoensis</i>			RH b-10, AT 120, MCZ 42198
<i>Chinemys nigricans</i>			RH b-11, RH 855, 921
<i>Chinemys reevesii</i>			RH 1, 3, 15, 16, 45, 46, 47, 48, 49, 51, 73, 74, 75, 78, 79, 80, 81, 82, 85, 86, 87, 88, 91, 92, 94, 95, 97, 160, 161, 216, 217, 232, 300, 303, 348, 426, 633, 722, 811, 931, 977, KU, NSM, AT 82, 137, 145, 150, 272, 274, 276, 291, 297, 299, 306
<i>Cuora amboinensis</i>			RH 34, 35, 36, 110, 111, 145, 148, 149, 150, 837, 838, 839, 840, 841, AT 9, 80, 300, 301
<i>Cuora aurocapitata</i>			RH 905, 915, RH b-13
<i>Cuora flavomarginata</i>			RH 53, 63, 64, 65, 104, 105, 106, 208, 209, 210, 429, 430, 431, 432, 433, 435, 436, 437, 438, 439, 440, 445, 627, 628, 629, 697, 787, 788, 793, 794, 795, 942, 943, 982, AT 49, 73, 204, 215, 217, 218, 219, NSM
<i>Cuora galbinifrons</i>			RH 736, 894, 895, 897, 900, 916, AT 24, KUZR 57209
<i>Cuora mccordi</i>			RH 934, 949, 950
<i>Cuora mouhotii</i>		RH 240, 269	RH 246, 247, 273, 687, 892, 896
<i>Cuora pani</i>			RH 902, 903, 952
<i>Cuora trifasciata</i>			RH 219, 250, RU
<i>Cuora zhoui</i>			RU
<i>Cyclemys dentata</i>			RH 134, 136, 137, 138, 139, AT 89, 90, 91, 92, 93
<i>Geoclemys hamiltonii</i>			RH 920, MCZ 120333
<i>Geoemyda japonica</i>	KU (:AT 15), KUZR 62043, 62044, 62046, 62049, 62051, 62053, 62054, 62055, 62056	RH 481, NSM, KUZR 62042, 62048, 62052	KUZR 62045, 62050
<i>Geoemyda spengleri</i>	RH b-29, RH 863, AT 278, KUZR 59219		
<i>Hardella thurjii</i>			RH b-35
<i>Heosemys depressa</i>			RH 1047
<i>Heosemys grandis</i>			RH 581, AT 110
<i>Heosemys leytensis</i>			YY
<i>Heosemys spinosa</i>			RH 185, 267, 330, AT 56, 97

Continued

Taxa	Gular completely excluded from the entoplastron	Gular just attached to the entoplastron	Gular overlying the entoplastron
<i>Hieremys annandalii</i>			RH 236, 872, 928, 1059, AT 166
<i>Kachuga dhongoka</i>			RH 1018
<i>Kachuga smithii</i>		RH 281	RH b-48, b-49, b-50, b-51, b-52
<i>Kachuga tecta</i>			RH 957, 1020, 1021, 1022
<i>Kachuga tentoria</i>			RH 234
<i>Malayemys subtrijuga</i>	RH 142		RH 33, 140, 141, 143
<i>Mauremys annamensis</i>			RH b-9, AT 121, 136
<i>Mauremys japonica</i>			RH 2, 9, 67, 71, 72, 76, 83, 156, 181, 184, 253, 270, 279, 297, 956, NSM a, b
<i>Mauremys leprosa</i>			RH 453, 454, 666, 929, 930
<i>Mauremys mutica</i>		RH 55	RH 54, 195, 196, 197, 198, NSM a, b, c, AT 4, 8, 134, 146, 225, 227, 228
<i>Mauremys rivulata</i>			RH b-24, RH 887, 888, 891, AT 143
<i>Melanochelys trijuga</i>			RH 238, AT 87
<i>Morenia petersi</i>		RH b-42, b-43, b-45	RH b-38, b-39, b-40, b-41, b-44, b-46, b-47
<i>Notochelys platynota</i>			RH 858, 962, AT 77
<i>Ocadia sinensis</i>	RH 347, 355, 382, 394, 396	RH 206, 275, 340, 376, 380, 383, 390, 394	RH 52, 202, 204, 205, 207, 274, 309, 341, 342, 348, 356, 357, 373, 375, 377, 378, 381, 393, 395, AT 40, 86, 138
<i>Orlitia borneensis</i>			RH 871, 1003, AT 144
<i>Rhinoclemys annulata</i>			RH 861, 862
<i>Rhinoclemys funerea</i>			RH 979
<i>Rhinoclemys pulcherrima</i>			RH b-17, b-18, b-19, RH 836, AT 133
<i>Rhinoclemys punctularia</i>		RH b-20	RH 239, 457, 510, AT 132
<i>Sacalia bealei</i>			RH 524
<i>Siebenrockiella crassicollis</i>			RH 37, 151, 320, AT 42, 147
Emydidae			
<i>Chrysemys picta</i>			RH 114
<i>Clemmys guttata</i>			RH 912
<i>Deirochelys reticularia</i>			RH 309, 456, 743, 744
<i>Emys blandingii</i>			RH 963
<i>Emys marmorata</i>			RH 1013, 1016
<i>Emys orbicularis</i>			RH 498, 1010
<i>Glyptemys insculpta</i>			RH 244, 909, 910, 911
<i>Graptemys barbouri</i>			RH 332
<i>Graptemys kohni</i>			RH 127
<i>Graptemys ouachitensis</i>			RH 955
<i>Graptemys pseudogeographica</i>			RH 518
<i>Malaclemys terrapin</i>			RH 119, 121, 276, 789
<i>Pseudemys rubriventris</i>			RH 288
<i>Terrapene carolina</i>			RH 69, 317, 859, 860
<i>Terrapene ornata</i>			RH 967, 969
<i>Trachemys scripta</i>			RH 14, 56, 98, 99, 102, 304, 305, 745, 802, 922, 1015

Continued

Taxa	Gular completely excluded from the entoplastron	Gular just attached to the entoplastron	Gular overlying the entoplastron
Testudinidae			
<i>Dipsoschelys</i> sp.	KU		
<i>Geochelone carbonaria</i>	RH 123, 286, 753		RH 243
<i>Geochelone chilensis</i>	RH 505, 643, 663, 882, 995		
<i>Geochelone denticulata</i>	RH 634, 686		
<i>Geochelone elegans</i>	RH 876, 877, 878, 879, 880, 932, 933, 993, 994, 1023		
<i>Geochelone pardalis</i>		RH 925	
<i>Geochelone radiata</i>	RH 875		
<i>Geochelone sulcata</i>	RH 913		
<i>Gopherus polyphemus</i>			RH 334, 335, 336, 337, 785
<i>Indotestudo elongata</i>	RH 1004		RH 745
<i>Indotestudo forsteni</i>			RH 919
<i>Kinixys belliana</i>	RH 997		RH 255, 998
<i>Kinixys homeana</i>	RH 509, 918, 923		
<i>Kinixys erosa</i>	RH 917, 975		
<i>Manouria emys</i>			RH 68, 940
<i>Psammobates tentorius</i>			RH 991, 992
<i>Testudo graeca</i>			RH 965, 1005, 1006, 1007, 1011
<i>Testudo hermanni</i>			RH 546, 1017
<i>Testudo horsfieldii</i>		RH 971a, 971b	RH 544, 545, 971
<i>Testudo kleinmanni</i>			RH 990