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A new species of the genus *Manouria* (Testudines: Testudinidae) from the Upper Pleistocene of the Ryukyu Islands, Japan

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Abstract. An extinct tortoise known from the uppermost Pleistocene of the Ryukyu Islands is described as the new species, *Manouria oyamai* (Testudines: Testudinidae) based on the skull, lower jaw and some postcranial elements. The specimens of *M. oyamai* were newly collected from the latest Pleistocene fissure deposits on Okinawa and Tokunoshima Islands, Ryukyu Islands, Japan. This is the first fossil record of *Manouria* sensu stricto. Phylogenetic analysis shows that *Manouria* sensu stricto, comprising *M. emys*, *M. impressa* and *M. oyamai*, is monophyletic. *Manouria oyamai* flourished in the Central and South Ryukyus until the Late Pleistocene and became extinct there, along with other endemic terrestrial vertebrates, in the latest Pleistocene.

Key words: fossil tortoise, *Manouria oyamai* sp. nov., phylogeny, Pleistocene, Testudines, Testudinidae, Ryukyu Islands

Introduction

The Ryukyu Islands (Figure 1) extend approximately 1,100 km from Kyushu, Japan, south to Taiwan, and are an island-arc system bounded by the Ryukyu Trench to the east and the Okinawa Trough to the west (Kizaki et al., 1985). Their configuration has been influenced by tectonic and eustatic movements since the Late Miocene or Early Pleistocene (Kimura, 1996, 2000). The Islands can be divided into three regions, named North Ryukyus, Central Ryukyus and South Ryukyus, which are separated by two deep straits: Tokara Strait in the north, and Kerama Strait in the south. Tokara Strait has been considered a zoogeographical boundary, known as the “Watase Line,” between Oriental and Palearctic regions (Wallace, 1876; Brauns, 1884; Okada, 1927). The high variety and endemism of the modern terrestrial fauna in the Ryukyu Islands have been explained by immigration across ancient, temporary land bridges, vicariance and oceanic dispersal (Kizaki and Oshiro, 1977; Ujiié, 1990; Ota, 1998; Otsuka and Takahashi, 2000).

Latest Pleistocene deposits within fissures and caves,

which have been cut into rocks of the Middle Pleistocene Ryukyu Group and pre-Cenozoic basement rocks, have yielded abundant fossil terrestrial vertebrates (i.e., deer, rats, birds, frogs, turtles, etc.; see, e.g., Oshiro and Nohara, 2000), including extinct endemics. Among the endemics, a testudinid turtle occurs on Okinawa, Ie and Miyako Islands (Table 1). The fossil of this testudinid was first discovered on Okinawa Island by the late Seiho Oyama, in whose honor this species is named, and cited by Takai and Hasegawa (1971) as “a large turtle”. Hasegawa et al. (1973) subsequently reported an incomplete fossil humerus of “a large turtle” among fossil terrestrial vertebrates from Miyako Island, and identified it as “*Testudo* cf. *emys*”, that is to say, *Manouria* cf. *emys* (Schlegel and Müller, 1840). Since these reports, other occurrences of “*Testudo* cf. *emys*” have been reported as “*Testudo* sp. nov.” from Okinawa Island (Hasegawa, 1980; Oshiro, 1994) and Ie Island (Hasegawa et al., 1978). Unfortunately, these authors were unable to provide a diagnosis of the new testudinid species, because all reported specimens were incomplete humeral shafts and shells.

In August, 1999, we excavated a latest Pleistocene

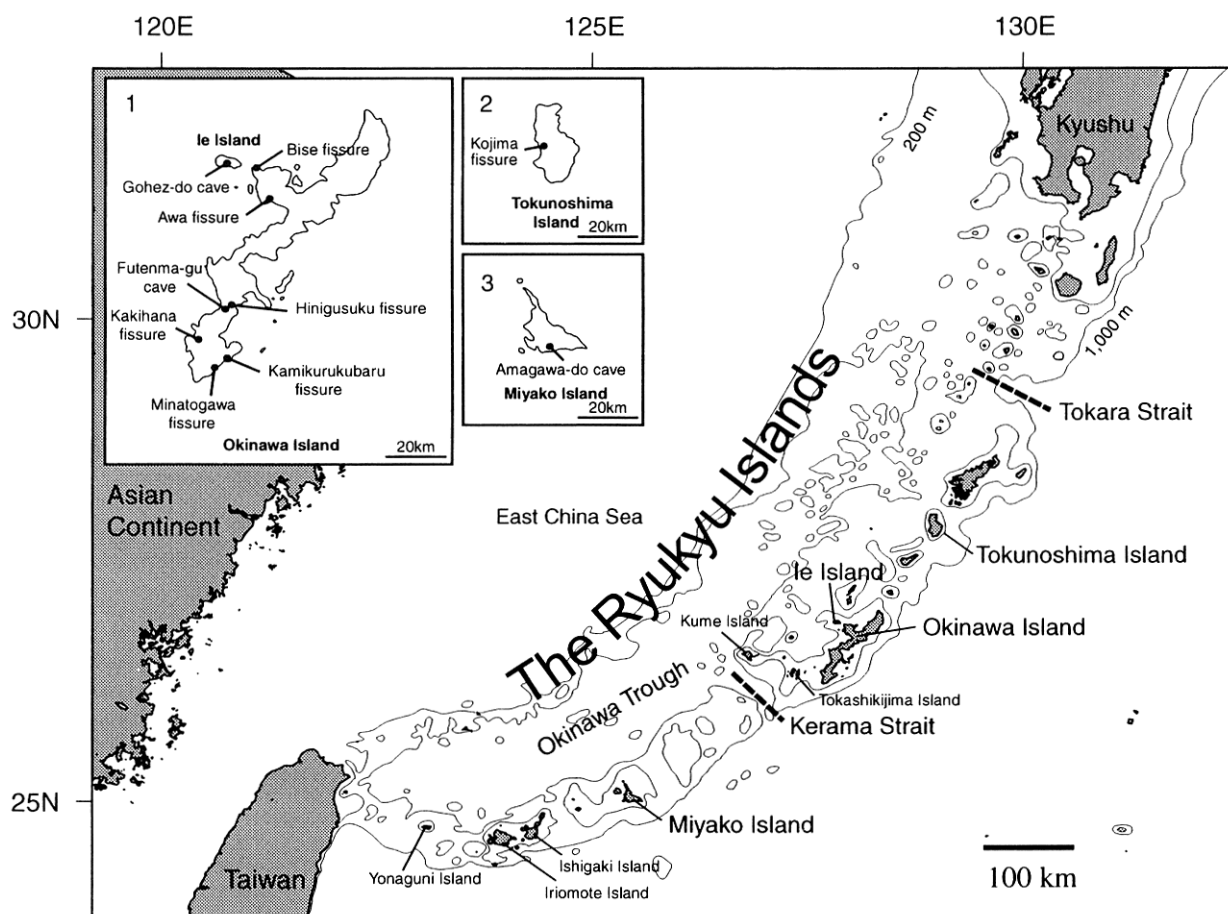


Figure 1. Geography of the Ryukyu Islands. The localities of fossil testudinids are shown in 1, 2 and 3.

Table 1. Previous reports of the fossil tortoises from the Ryukyu Islands.

Literature	Occurrences	Locality	Part	Identification
Takai and Hasegawa (1971)	Fissure deposits	Hinigusuku, Kitanakagusuku Village, Okinawa Is.	?	None. (as a large turtle)
Takai and Hasegawa (1971)	Fissure deposits	Kamikurukubaru, Chinen Village, Okinawa Is.	?	None. (as a large turtle)
Hasegawa <i>et al.</i> (1973)	Cave deposits	Amaga-do cave Miyako Is.	Right humerus (incomplete)	<i>Testudo cf. emys</i>
Hasegawa (1980)	Cave deposits	Gohez-do cave, Ie Is.	?	<i>Testudo sp. nov.</i>
Hasegawa (1980)	Fissure deposits	Minatogawa site, Okinawa Is.	?	<i>Testudo sp. nov.</i>
Oshiro (1987)	?	Kakihana, Naha city, Okinawa Is.	Right humerus (incomplete)	None. (Japanese local name only)
Oshiro (1987)	Cave deposits	Futenma gu (shrine) site, Ginowan City, Okinawa Is.	Right humerus (incomplete), and fragmented shell bones	None. (Japanese local name only)
Oshiro (1994)	Cave deposits	Futenma gu (shrine) site, Ginowan City, Okinawa Is.	Right humerus (incomplete), and fragmented shell bones (probably same specimens in Oshiro, 1987)	<i>Testudo sp. nov.</i>

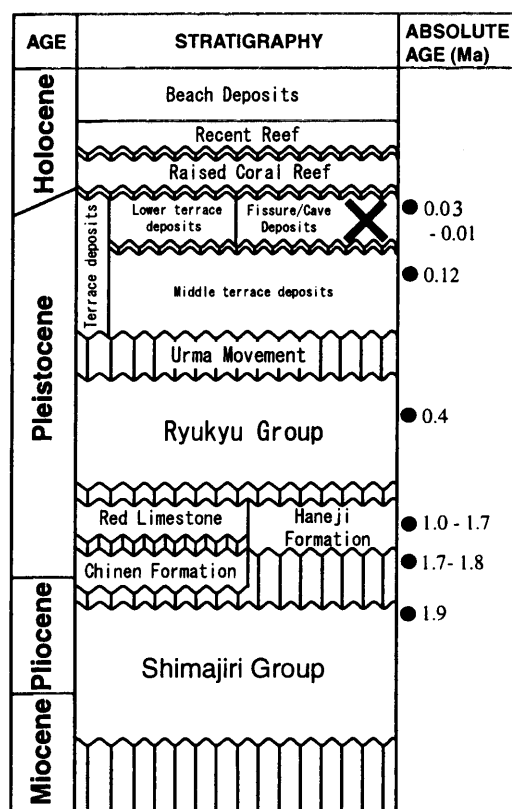


Figure 2. The Neogene Tertiary to Quaternary stratigraphy of the Ryukyu Islands (revised after Otsuka and Takahashi, 2000). X indicates the level of the fossil testudinid tortoises in the Ryukyu Island.

fissure deposit within the Naha Limestone of the Ryukyu Group at Kamikurukubaru, Chinen village, Okinawa Island, and discovered one partial shell of a testudinid filled with calcareous red soil. This specimen includes the skull, left posterior mandible and some postcranial elements which have not previously been recorded from the Ryukyu Islands except for the left humerus. In addition, we found an incomplete posterior left plastron at the same site in January, 2000.

In the present study, we describe this new species of testudinid, and clarify its phylogenetic position in the family Testudinidae. We have examined the latest Pleistocene testudinids from the Kamikurukubaru in Chinen village (specimens ESK-6150 and ESK-6151) along with reference specimens from localities on Okinawa and Tokunoshima Islands (Figure 1), which were all collected by the second author, Choukei Kishaba and Ki'ichi Maja.

Geological setting

Cenozoic strata on the Ryukyu Islands consist mainly of the Upper Miocene to Uppermost Pliocene Shimajiri Group, the Lowermost Pleistocene Chinen sandstone, an unnamed red limestone, the Haneji Formation, the Middle Pleistocene Ryukyu Group, Lower Pleistocene terrace deposits and Holocene beach deposits (Figure 2).

^{14}C ages of land snails which occurred with the testudinid fossils from the fissure deposits at Hinigusuku and Bise indicate ages of $28,160 \pm 770$ years BP and $23,050 \pm 70$ years BP, respectively. These ^{14}C ages are in accord with data presented by previous researchers from the fissure and cave deposits of Okinawa and Miyako Islands (Table 2), and imply that these deposits formed in the latest Pleistocene.

Materials and methods

The new specimen, ESK-6150, from fissure fill at Kamikurukubaru on Okinawa Island was collected in August, 1999, as a block of calcareous travertine enclosing an incomplete carapace. In the laboratory we used approximately 3% formic acid to remove the calcareous matrix (Figure 3), and discovered other skeletal elements including an incomplete skull, a posterior right mandible, a right scapula, coracoids and a left humerus. The other specimens were also collected from fissure fills at Hinigusuku in Kitanakagusuku village and Bise and Awa in Motobu town on Okinawa Island, and at Kojima in Isen town on Tokunoshima Island, and prepared in the same way.

Table 2. ^{14}C ages of fissure and cave deposits from the Ryukyu Islands.

Site	Island	Age	Literature
Minatogawa fissure	Okinawa Island	$18,250 \pm 650$ BP	Suzuki and Tanabe (1982)
Minatogawa fissure	Okinawa Island	$16,600 \pm 300$ BP	Suzuki and Tanabe (1982)
Minatogawa fissure	Okinawa Island	$9,865 \pm 35$ BP	Present study
Shimajiri cave	Okinawa Island	$15,200 \pm 100$ BP	Oshiro and Nohara (2000)
Hinigusuku fissure	Okinawa Island	$20,890 \pm 770$ BP	Otsuka and Takahashi (2000)
Hinigusuku fissure	Okinawa Island	$28,160 \pm 90$ BP	Present study
Bise	Okinawa Island	$23,050 \pm 70$ BP	Present study
Pinza-abu cave	Miyako Island	$25,800 \pm 900$ BP	Hamada (1985)
Pinza-abu cave	Miyako Island	$26,800 \pm 1,300$ BP	Hamada (1985)

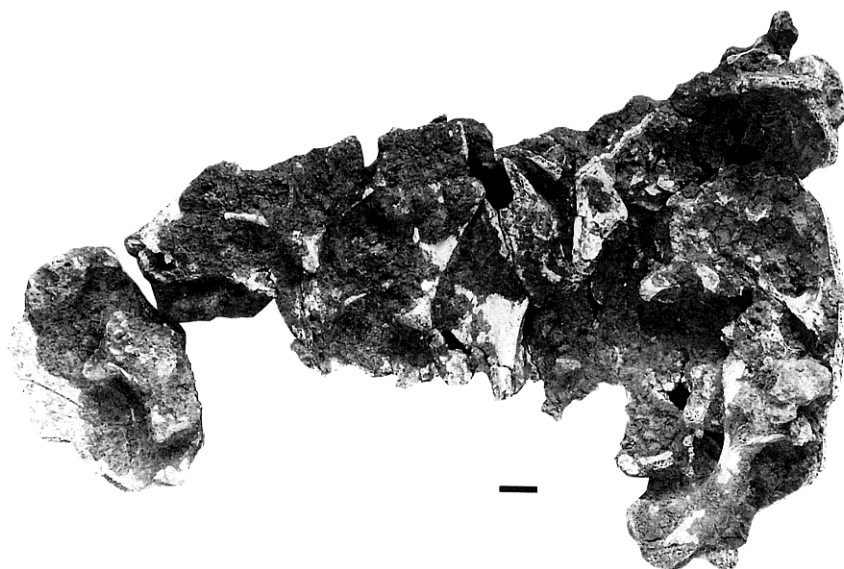


Figure 3. Picture showing the mode of preservation of fossil testudinid excavated from Kamikurukubaru, Chinen Village, Okinawa Island, in August 1999 (under preparation). Scale bar equals 1 cm.

This fossil testudinid was described by comparing it with 16 genera (including two extinct genera) of Testudinidae, with a geoemydine geoemydid, *Mauremys*, as the outgroup to determine the character states, polarities and distribution during phylogenetic analysis. The Geoemydidae has been considered as the closest sister group to Testudinidae, and *Mauremys* is a typical basal genus within Geoemydinae on the basis of morphological phylogenetic analyses (Hirayama, 1984; Gaffney and Meylan, 1988; Yasukawa *et al.*, 2001), although recent molecular phylogenetic analyses do not support the subfamilial relationship between Batagurinae and Geoemydinae in the family Geoemydidae (McCord *et al.*, 2000; Honda *et al.*, 2002a; Honda *et al.*, 2002b). Most characters used in our phylogenetic analysis were based on the data in Crumly (1982, 1984a), Meylan and Sterrer (2000), and on our observations of specimens in the RH collection (i.e., the private collection of the third author) and the ESK collections in our care (the acronym ESK refers to the Department of Earth Sciences, Faculty of Science, Kagoshima University). Some character states and polarities were modified on the basis of data in the published literature shown in appendix III. Skull terminology follows Gaffney (1972), and postcranial terminology follows Walker (1973) and Zangerl (1969).

Systematic paleontology

Order Testudines Linnaeus, 1758
Suborder Cryptodira Cope, 1868

Superfamily Testudinoidea Batsch, 1788

Family Testudinidae Batsch, 1788

Genus *Manouria* Gray, 1852

Type species.—*Manouria emys* (Schlegel and Müller, 1840).

Revised diagnosis.—Testudinid with enlarged foramen caroticum laterale at the juncture of the pterygoid or epipterygoid, palatine and parietal that pierces the anterolateral parietal flange, this being the only known autapomorphic character (Crumly, 1984a). The other diagnostic characters include: dorsal exposure of prootic wide, usually triangular with a posterior apex (Crumly, 1984a); surangular process absent (Crumly, 1982, 1984a); cervical scute present (Smith, 1931); inguinal scute large, often divided into two; latissimus dorsi and teres major scar located on the lateral side of distal shaft of humerus; Class II mental glands (Winokur and Legler, 1975).

Manouria oyamai sp. nov.

Figures 4–9a

Diagnosis.—Carapace extremely thin; scute sulci on carapace and plastron extremely wide and shallow; cervical scute long and narrow dorsally, reduced or absent ventrally.

Holotype.—ESK-6150 comprising incomplete skull, posterior right mandible, incomplete carapace with right inguinal buttress, right scapula, coracoids and left humerus.

Type locality.—Kamikurukubaru, Chinen village, Shima-

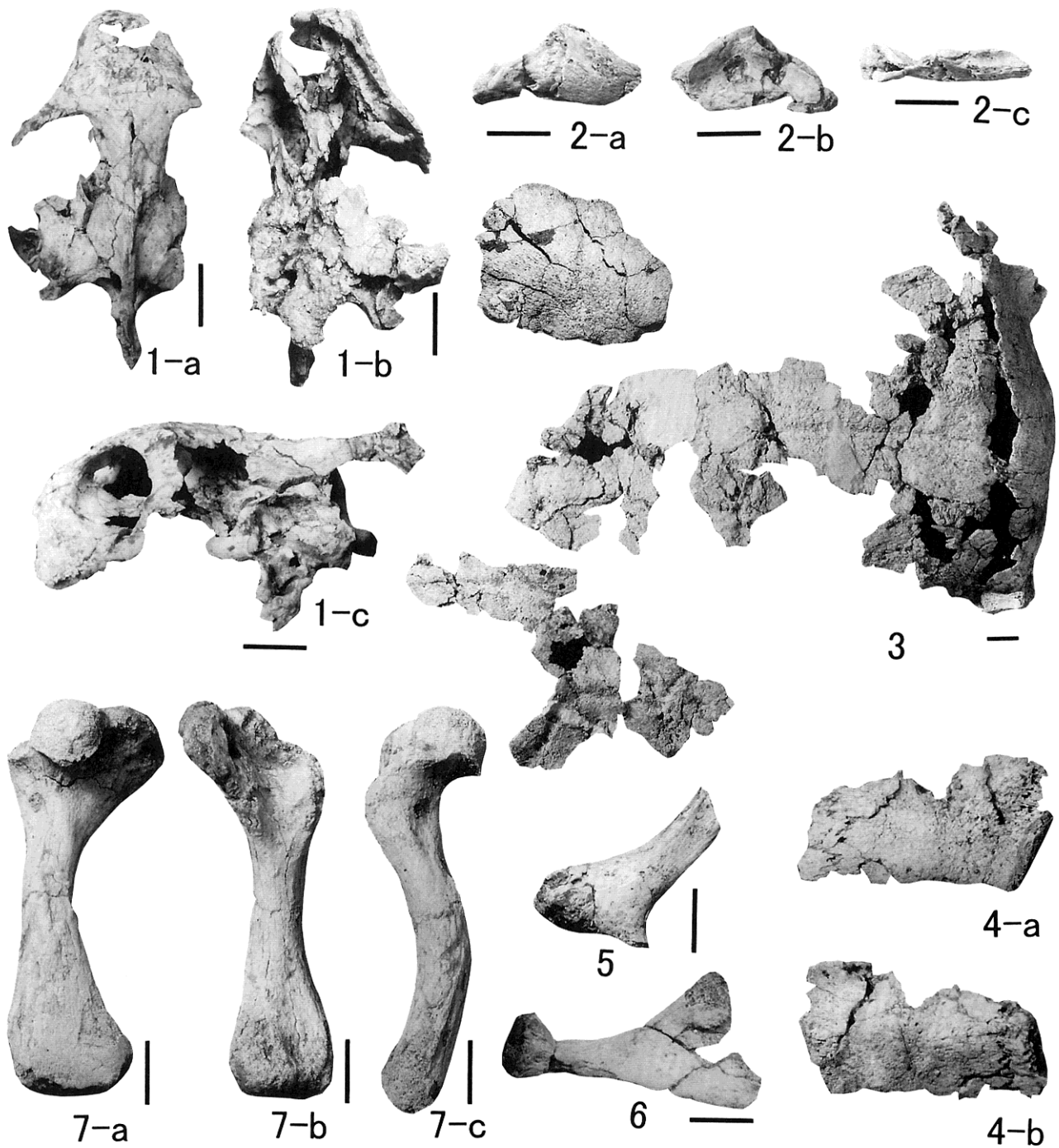


Figure 4. *Manouria oyamai* sp. nov., holotype, ESK-6150. 1. Skull in dorsal (a), ventral (b) and left lateral (c) views. 2. Lower jaw (right side) in lateral (a), medial (b) and dorsal (c) views. 3. Carapace (arranged) in dorsal view. 4. Peripheral bone in dorsal (a) and ventral (b) views. 5. Left coracoid. 6. Right scapula (posterior view). 7. Humerus (left) in dorsal (a), ventral (b) and lateral (c) views. Scale bars equal 1cm.

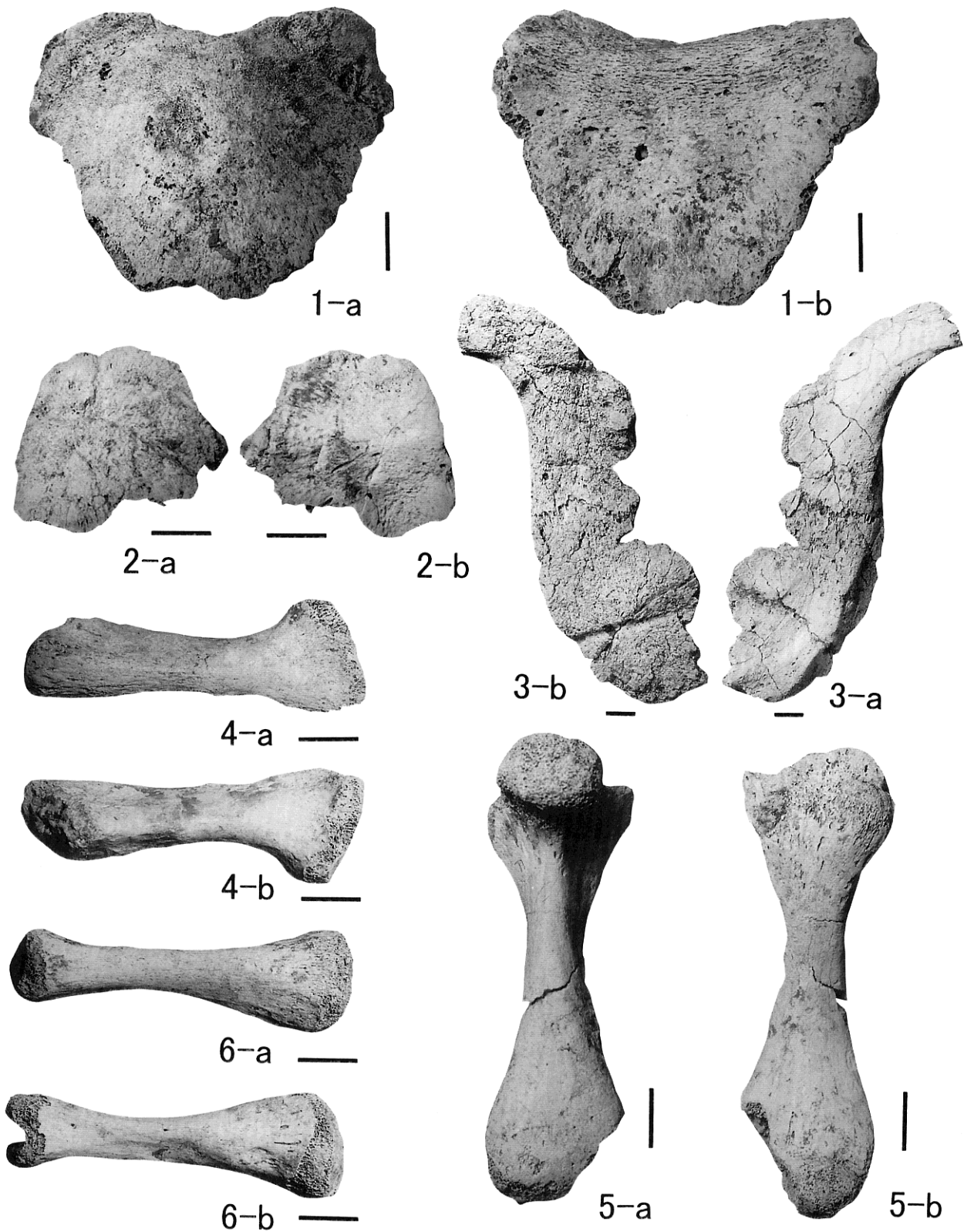


Figure 5. *Manouria oyamai* sp. nov., referred specimens. 1. Nuchal (ESK-6121). 2. Nuchal (ESK-6151). 3. Plastron (ESK-6151). 4. Right ulna (ESK-6129). 5. Right tibia (ESK-6131). 6. Right femur (ESK-6130) in dorsal, (a) and ventral, (b) views. Scale bars equal 1cm.

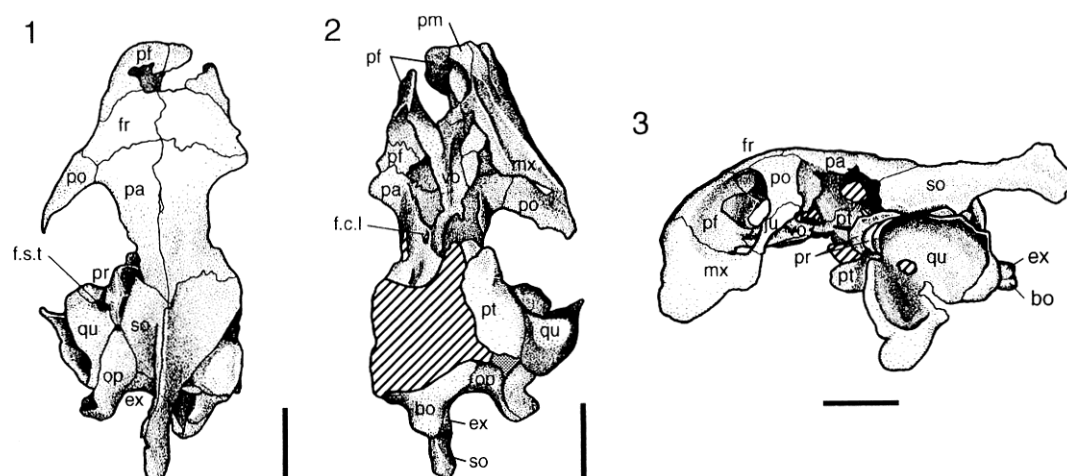


Figure 6. Skull of *Manouria oyamai* sp. nov., ESK-6150 in (1) dorsal (2) ventral and (3) left lateral views. Hatched areas indicate broken surfaces. Shaded areas denote unremovable matrix. Scale bar equals 1 cm. Abbreviations: bo, basioccipital; ex, exoccipital; f.c.l, foramen caroticum laterale; fr, frontal; f.s.t, foramen stapedio-temporale; ju, jugal; op, opisthotic; pa, parietal; pf, prefrontal; pl, palatine; pm, premaxilla; po, postorbital; pr, prootic; pt, pterygoid; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer.

jiri District, Okinawa Island, Ryukyu Islands, Japan.

Age.—Latest Pleistocene.

Referred specimens.—Awa specimen: ESK-6139 (left humeral shaft collected by Choukei Kishaba at Awa, Motobu town, Okinawa Island). Bise specimen: ESK-6152 (a peripheral collected by Ki'ichi Maja at Bise, Motobu town, Okinawa Island). Kamikurukubaru specimens: ESK-6151 (a right hypoplastron and xiphiplastron), ESK-6153 and 6154 (plastron fragments), ESK-6155 (left humeral shaft), ESK-6156 (right humeral shaft), ESK-6157 (right humeral shaft) and ESK-6158 (right humeral shaft). These specimens were collected by the second author at Kamikurukubaru, Chinen village, Okinawa Island. Hinigusuku specimens: ESK-6121 (incomplete nuchal), ESK-6122 and 6123 (costal fragments), ESK-6124 (incomplete 8th costal), ESK-6125 (a peripheral), ESK-6126 (left coracoid), ESK-6127 (incomplete left humerus), ESK-6128 (distal part of right humerus), ESK-6129 (right ulna), ESK-6130 (left femur), ESK-6131 (left tibia) and ESK-6138 (distal part of left femur). ESK-6138 was collected by C. Kishaba. The others were collected by the second author at Hinigusuku, Kitanakagusuku village, Okinawa Island. Tokunoshima specimen: ESK-6132 (incomplete nuchal). The specimen was collected by the second author at Isen town, Tokunoshima Island.

Etymology.—The species name honors the late Seiho Oyama, who was the first to discover a fossil of this species.

Description

Skull

The slightly deformed skull (ESK-6150; Figure 6) is incompletely preserved. It lacks the right premaxilla, maxilla, postorbital, pterygoid, jugal, palatine, quadrate and prootic, and both sides of the epipterygoids, squamosals, quadratojugals, and basisphenoid. It is long, narrow and arched, and about 63.1 mm long, 21.7 mm wide and 25.9 mm high. Preserved skull elements are damaged to varying degrees. On the dorsal surface, there are no visible sulci of scales on the head, as seen in most testudinids mentioned by Crumly (1984a).

Skull roof elements

Premaxilla.—The left premaxilla is incompletely preserved. It contacts the left maxilla laterally and the vomer posteriorly. On the triturating surface, the labial ridge and the posterior region abutting the vomer are extremely eroded.

The premaxillary ridge, which is well developed and reaches the junction of the premaxillae in *Gopherus* and *Stylomys*, is absent (Crumly, 1984a,b; Gaffney and Meylan, 1988; Meylan and Sterrer, 2000), and the premaxillary pit is deep and surrounded by labial and transverse ridges. The ridge is also absent in *Mauremys* and most testudinids, whereas it is incipiently developed in some *Manouria emys* and most *M. impressa* (Crumly, 1984a). The absence of the premaxillary ridge is a plesiomorphic condition (Crumly, 1984a; Meylan and Sterrer, 2000).

The foramen praepalatium pierces the posterior region of the premaxilla on the triturating surface. It is distinct from the nutritive foramina seen in *Mauremys* and most testudinids. Meylan and Sterrer (2000) inferred the presence of the distinct foramen praepalatium as a plesiomorphic character state.

Maxilla.—The left maxilla is missing the lingual part of the triturating surface. It contacts the left premaxilla anteriorly, the left prefrontal dorsally and the left jugal posteriorly. On the triturating surface, the transverse ridge (Meylan and Sterrer, 2000) extends onto the premaxillo-maxillary suture as seen in *Astrochelys*, some *Chelonoidis*, some *Dipsochelys*, *Geochelone* and *Manouria emys*. The presence of the transverse ridge in accordance with the premaxillo-maxillary suture is an intermediately derived condition (Meylan and Sterrer, 2000).

The median maxillary ridge extends between the labial and lingual ridges, and is interrupted by the transverse ridge at the anterior end of the maxilla. This condition of the median maxillary ridge is also seen in *Astrochelys*, *Chelonoidis*, some *Dipsochelys*, *Geochelone*, *Indotestudo*, *Mala-cochersus*, *Manouria*, *Stylemys* and some *Testudo*. The configuration of this ridge in the holotype is intermediately derived (Meylan and Sterrer, 2000), and is somewhat denticulate. A denticulated median maxillary ridge was reported in *Chelonoidis denticulata* and *Manouria emys* (Crumly, 1984a).

The lingual ridge is developed on the maxilla in most testudinids except for *Chersina*, *Homopus*, *Kinixys*, *Psammobates* and *Pyxis*, and extends from the maxilla to the premaxilla in some *Geochelone*, *Gopherus*, *Hesperotestudo* and *Manouria* (Meylan and Sterrer, 2000). However, it is not possible to confirm the presence or absence of the lingual ridge on the holotype of *Manouria oyamai* sp. nov. Meylan and Sterrer (2000) observed that most testudinids, other than diminutive African forms (i.e., *Chersina*, *Homopus*, *Kinixys*, *Psammobates* and *Pyxis*) have the labial, median maxillary and lingual ridges, and the holotype of *M. oyamai* probably possessed these too.

The posterior maxillary process is absent from the holotype of *Manouria oyamai* sp. nov., although it is present in most testudinids. This process is also absent in *Mauremys*, some *Astrochelys*, some *Chelonoidis*, some *Kinixys*, *Manouria* and *Stylemys*. The absence of the posterior maxillary process is plesiomorphic (Meylan and Sterrer, 2000).

Prefrontal.—The prefrontals are incompletely preserved with most of the right prefrontal, and the posterior dorsal roof of the left prefrontal is missing. The left prefrontal contacts the left maxilla laterally, the left frontals posteriorly, and the vomer and palatine ventrally. The descending posterior walls of fossa nasalis are partly broken. However, they are well developed ventrally and a relatively

wide ethmoid fissure is recognizable. The wide ethmoid fissure has been treated as a synapomorphy of Testudinidae (“ventral processes of the prefrontals” of Loveridge and Williams, 1957; Crumly, 1982; Crumly, 1984a,b; Gaffney and Meylan, 1988, mean processus frontalis circumolfactorius of Bour, 1981). Crumly (1982, 1984a) noted that the ethmoid fissure in *Manouria* and *Psammobates* is relatively narrower and less heart-shaped compared with other testudinids. However we observed that *Manouria impressa* (RH268) and *Testudo graeca* (ESK-6183 and 6224) have wide ethmoid fissures with undeveloped descending posterolateral wall of the prefrontal. The width of the ethmoid fissure is likely to relate the development of the descending posterolateral wall of fossa nasalis. The character state of the ethmoid fissure in the holotype is similar to that of *Manouria emys* and *Psammobates*.

Frontal.—The frontals are well preserved and contact the prefrontals anteriorly and the parietals posteriorly. The left frontal also contacts the left postorbital posterolaterally. Each frontal is trapezoidal dorsally, and is slightly wider than long.

Parietal.—The parietals are preserved, although the descending flange of the left one has been broken away. The parietals contact the frontals anteriorly and the supraoccipital posteriorly. The left parietal contacts the left postorbital laterally, and the right parietal contacts the vomer ventrally. Dorsally, no posterolateral processes extend from the postorbital to the supraoccipital spine.

On the lowest part of the left inferior parietal process, there is a comparatively large opening that runs from within the braincase to the anterolateral parietal flange (see f.c.l. in Figure 6). Bour (1981) identified and described this opening as the foramen caroticum laterale (anterior epipterygoid foramen of Crumly, 1982). The foramen caroticum laterale, in which the canalis caroticus lateralis from the canalis caroticus internus exits through the pterygoid to the sulcus cavernosus, is known in some emydids, geoemydids and testudinids (Albrecht, 1967, 1976). Furthermore, Crumly (1984a) determined that the canalis caroticus lateralis first runs to the sulcus cavernosus, and then pierces the braincase wall anteriorly, in *Chelonoidis carbonaria*, *Homopus areolatus*, *Manouria* and some *Psammobates* (e.g., *P. oculiferus*). He also clarified that the foramen caroticum laterale appears on the lowest anteromedial part of the parietal flange in *G. carbonaria*, and on its lowest anterolateral part in *H. areolatus*, *Manouria* and some *Psammobates*. Bour (1984) also observed this condition in *Chelonoidis carbonaria*, *Cylindraspis vosmaeri*, *Cylindraspis peltastes*, *Manouria emys*, *Pyxis arachnoides*, *P. planicauda* and *Homopus areolatus*. The foramen caroticum laterale in *H. areolatus* is located very posteriorly to the parietal flange (Crumly, 1984a). In living *Manouria*, the foramen is pre-

sent in the juncture of the pterygoid or epipterygoid, palatine and parietal. In some *Psammobates*, however, the foramen is present above the epipterygoid, and the pterygoid and epipterygoid do not contribute to the formation of the foramen caroticum laterale (Crumly, 1984a). The character condition in the holotype is similar to living *Manouria*, and evidently is an intermediately derived condition.

Jugal.—The dorsal portion of the left jugal contacts the left postorbital dorsally and the left maxilla ventrally.

Palatal complex

Vomer.—The vomer is poorly preserved with its posterior part having crumbled away. It contacts the left premaxilla and the maxillae anteriorly, the right anterior palatine laterally, and the basal descending process of the right parietal posteriorly. On the ventral midline, there is a medial vomerine ridge (Crumly, 1982) and the vomer is bent sharply downward in the anterior region. The incomplete vomer in the holotype likely divided the palatine into two parts, as seen in some *Mauremys* and most testudinids. Meylan and Sterrer (2000) pointed out that the development of the posterior extension of the vomer is quite variable, both among the testudinids and their close relatives.

Pterygoid.—The left posterolateral part of the pterygoid is poorly preserved with its medial and posterior regions crushed and distorted. It contacts the quadrate laterally, but has been dislocated from the basioccipital posteriorly and the prootic dorsally. Ventrally, the left processus interferenstralis is covered by the left pterygoid as seen in *Mauremys* and most testudinids. The character condition in the holotype is plesiomorphic (Meylan and Sterrer, 2000).

Quadrate.—The left quadrate is incompletely preserved. Laterally, the greater part of the dorsal roof, the lateral wall and the stapedia notch are missing. The processus articularis is partially broken and the condylus mandibularis is damaged. In most testudinids, except for some *Chersina*, some *Dipsochelys*, *Pyxis arachnoides*, and *Testudo kleinmanni*, the incisura columellae auris, which traverses the stapes, is usually enclosed by the quadrate (Crumly, 1982, 1984a; Gaffney, 1979). Bour (1980) described this condition as “commisura quadrati”. The quadrate contacts the left prootic, opisthotic and pterygoid medially. The anterior region of the quadrate, along with the lateral part of the prootic, combines to form a relatively large trochlear process. An enlarged trochlear process is seen in some *Astrochelys radiata*, most *Chelonoidis*, some *Geochelone pardalis*, some *G. sulcata* and *Manouria* (Crumly, 1982, 1984a).

Braincase element

Prootic.—The left prootic is well preserved and contacts

the left quadrate laterally and the left opisthotic posteriorly but is separated from the supraoccipital medially. The dorsal exposure of the prootic is triangular in outline, and wider anteriorly than long. A wide, anteriorly expanded prootic is present as seen in some *Chelonoidis denticulata*, some *Indotestudo forstenii* and *Manouria*, and was inferred to be a primitive condition by Crumly (1982; 1984a), although he also observed that the degree of dorsal exposure of the prootic varies considerably. Meylan and Sterrer (2000) did not use the “prootic shape” character state of Crumly (1984a), and redefined this state based on its overall width. Following Meylan and Sterrer (2000), the dorsal exposure of the prootic in the holotype is about equal to, or slightly wider than, its length. It is considered to be a plesiomorphic condition.

Dorsally, the foramen stapedio-temporale is situated in the middle of the lateral margin, contacting the left quadrate that contributes to form the lateral wall of the foramen stapedio-temporale.

Opisthotic.—The left opisthotic is completely preserved. It is separated from the left prootic anteriorly, the supraoccipital medially and the left quadrate laterally, whereas it contacts the left exoccipital medially. The right opisthotic is incompletely preserved, lacking its lateral portion, and is separated from the supraoccipital medially and the right exoccipital posteriorly.

Exoccipitals.—The left exoccipital is completely preserved, but the lateral part of the left one is missing. They contact the supraoccipital dorsally, the opisthotics laterally and the basioccipital ventrally, and form the longitudinally elongated foramen magnum and the relatively slender condylus occipitalis. On the posterolateral surface of the left exoccipital, there are two foramina nervi hypoglossi, a medial larger one and a lateral smaller one.

Basioccipital.—The basioccipital is incompletely preserved, with the majority of it having crumbled away. It contacts the exoccipitals dorsally, and also forms the condylus occipitalis posteriorly.

Supraoccipital.—The supraoccipital is relatively well preserved. It is separated from the left prootic and opisthotics laterally, and the exoccipitals ventrally. The supraoccipital spine is long, extending posteriorly beyond both quadrates. Ventrally, the flattened area of the supraoccipital spine rapidly reduces at a point that is one-fourth the distance from the entrance of the foramen magnum to the posterior end of the supraoccipital spine. As a result, approximately three-quarters of the posterior portion of supraoccipital spine forms a blade-like edge. This condition is also seen in *Astrochelys yniphora*, most *Geochelone pardalis* and *G. sulcata*, and some *Manouria emys* (Crumly, 1982).

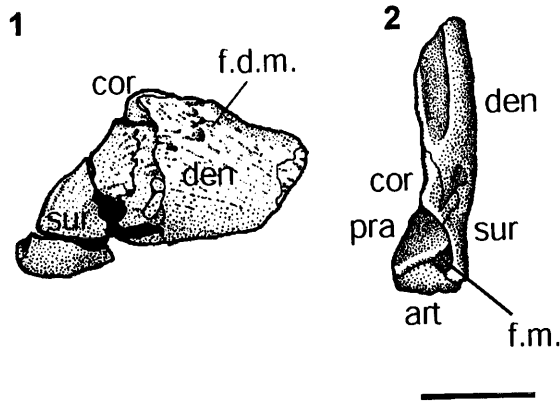


Figure 7. Lower jaw of *Manouria oyamai* sp. nov. (ESK-6150). 1. Right lateral view. 2. Dorsal view. Scale bar = 1 cm. Abbreviations: art, articular; cor, coronoid; den, dentary; f.d.m., foramen dentofaciale majus; f.m., fossa meckelii; sur, surangular; pra, prearticular.

Lower jaw

The lower jaw (Figure 7) is represented by the posterior half of the right side. The preserved lower jaw elements comprise the dentary, the coronoid, the surangular, the articular and the prearticular.

Dentary.—The right side of the dentary is missing its anterior half and the labial and lingual ridges on the triturating surface are slightly eroded. It contacts the coronoid dorsally, the surangular and the prearticular posteriorly, and the prearticular medially. Laterally, the foramen dentofaciale majus is located along with a few nutritive foramina. Medially, the sulcus cartilaginis meckelii is relatively well developed.

Coronoid.—The right coronoid is completely preserved. It is overlapped laterally by the dentary, and contacts the surangular ventrally and the prearticular medially.

Surangular.—The right surangular is preserved, except for the area around the foramen nervi auriculotemporalis, which is partially broken. It contacts the dentary anteriorly, the coronoid dorsally, and the articular posteriorly. The surangular does not interdigitate with the dentary, as seen in *Gopherus*, *Hesperotestudo*, *Manouria*, *Psammobates*, *Pyxis* and *Stylemys* (Crumly, 1982, 1984a; Meylan and Sterrer, 2000). The condition seen in the holotype is plesiomorphic. Moreover, the postdentary elements in the holotype show up as quite massive, as seen in *Gopherus*, *Hesperotestudo* and *Manouria* (Crumly, 1982; 1984a). The massive postdentaries may also be apomorphic.

Articular.—The right articular is preserved. It contacts the surangular and the angular laterally, and prearticular medially.

Prearticular.—The right prearticular is incompletely preserved. It contacts the coronoid dorsally and the dentary anteriorly and the articular posteriorly.

Shell

The shell of the holotype, ESK-6150, is incompletely preserved (Figure 8). It is made up of four neurals (the fourth, fifth, seventh and eighth), twelve costals (the left first, the right second and third, the fourth and fifth pairs, the left sixth, the seventh and eighth pairs) and four peripherals (the right fourth to seventh). The shell is flattened and is covered by the first, third, fourth and fifth vertebral scutes, the left first, right second, paired third and fourth pleural scutes, and the fifth to eighth marginal scutes. Two nuchals (ESK-6121, 6132), three costals (ESK-6122–6124) and two peripherals (ESK-6125, 6152) are present in reference specimens. ESK-6121 is covered by the first vertebral and a pair of the first marginal scutes. ESK-6132 is covered by a cervical, the first vertebral and a pair of the first marginal scutes.

The specimens of the plastron are also incompletely preserved. ESK-6151 is the posterior half of the right side of the plastron, composed of the left hypoplastron and the xiphiplastron. The right posterior half of the plastron is covered by the right abdominal, femoral, inguinal, and anal scutes. The other plastral materials, ESK-6153 and 6154, are fragments in which the original arrangement is unclear.

As in living *Manouria* (*Manouria emys*, ESK-6170, RH68; *M. impressa*, RH268), no concentric growth lines of the scutes sculpture the exterior surface of the shell in the holotype. The scute sulci on the shell are also extremely wide (about 3.1–3.8 mm on the carapace and 3.9–6.0 mm on the plastron) and shallow without distinct edges along the sulci in comparison with other testudinids in which the scute sulci are usually well impressed with distinct edges except for *Dipsochelys*. By contrast, *M. emys* (ESK-6170, carapacial length; 500 mm) and *M. impressa* (RH268, carapacial length; 240 mm) have narrow scute sulci (about 1.0–2.6 mm and about 1.0 mm wide on the carapace, respectively) with distinct edges. All shell elements are extremely thin.

Carapace.—The nuchal, ESK-6121, from Hinigusuku, Kitanakagusuku village, Okinawa Island, is missing its anterior part, where the single cervical and a pair of the first marginal scutes covered dorsally. The preserved part of nuchal is flattened and covered by the first vertebral and a pair of the first pleural scutes. It is 66.9 mm in maximum length, 46.0 mm in maximum width, 9.9 mm thick in the anterior thickened zone and 1.6 mm thick in the posterior region.

Another nuchal, ESK-6132, from Kojima, Isen Town, Tokunoshima Island, is missing the left-lateral side and the posterior region. It is 33.6 mm in maximum length and

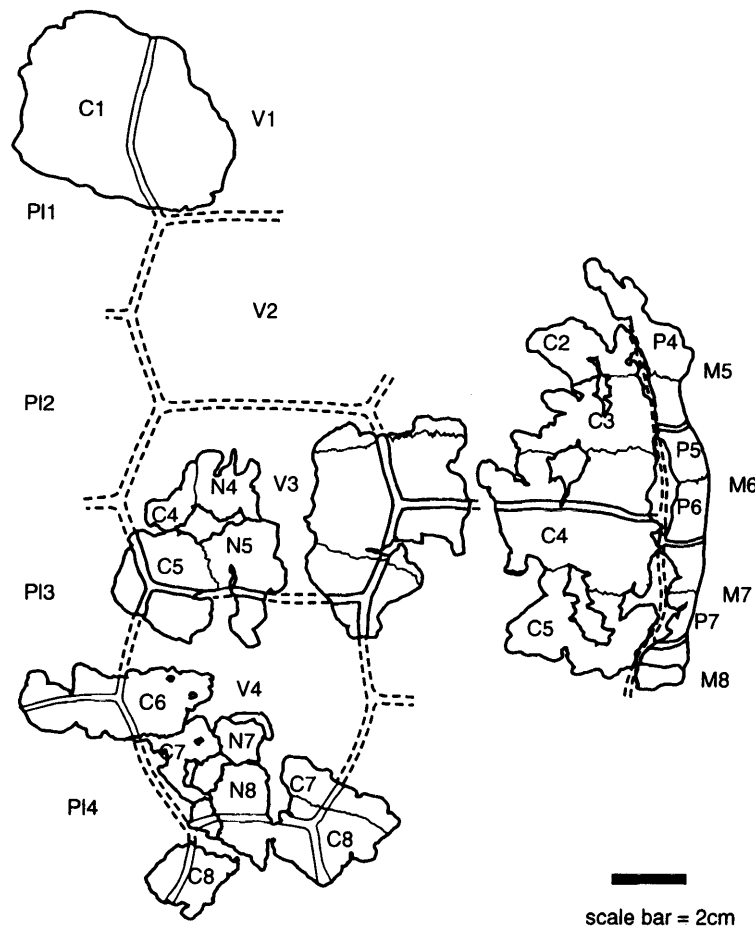


Figure 8. Carapace of *Manouria oyamai* sp. nov., of the holotype, ESK-6150 (dorsal view). Abbreviations: C, costal bone; M, marginal scute, N, neural bone; P, peripheral bone; PI, pleural scute, V, vertebral scute.

36.3 mm in maximum width, 5.7 mm thick in the anterior thickened zone and 1.0 mm thick in the posterior edge, and is emarginated anteriorly. Dorsally, it is overlapped by a cervical, the first vertebral and a pair of the first marginals. The cervical is long and narrow dorsally, and invisible ventrally. In primitive fashion, the dorsal cervical scute is wider than long, as also seen in *Mauremys japonica*, *Astrochelys*, *Dipsochelys*, *Gopherus*, some *Homopus*, some *Kinixys*, some *Malacochersus*, *Manouria*, and some *Psammobates*. Although this character is slightly variable, the elongated cervical scute seen in ESK-6132 is an intermediately derived condition (Crumly, 1984a; Meylan and Sterrer, 2000).

In all the specimens, the nuchal is extremely thin, even on the ventral thickened zone, compared with the other testudinids. The inferred (restored) shape of the nuchal, based on ESK-6121 and ESK-6132, is hexagonal in outline, with short lateral articulations directed anteriorly.

The neurals in the holotype, ESK-6150, are poorly pre-

served, and are very thin, about 0.7–2.4 mm thick. The fourth neural, which contacts the left fourth costal laterally and the fifth neural posteriorly, is lacking most of the anterior and right lateral regions. The fifth neural, which contacts the fourth neural and the left fifth costal, lacks most of its periphery. The dorsal vertebrae of the fourth and fifth neurals are missing. The seventh neural, which contacts the left seventh costal laterally, the eighth neural posteriorly and the eighth dorsal vertebra ventrally, is missing most of the anterior and right lateral areas. The eighth neural, which contacts the seventh neural anteriorly, and the left seventh and a pair of the eighth costals laterally, is missing the right lateral and posterior fringes and the sacral vertebrae. It is elongate-hexagonal, with short articulations directed anteriorly.

The left first, the right second and third, the pairs of fourth and fifth, the left sixth, and the pairs of seventh and eighth costals are preserved in ESK-6150. Most of them are about 0.7–3.2 mm thick, but the medial edge of the first

costal is 5.9 mm thick. The width of the fourth costal decreases from the proximal to the distal end. Conversely, the width of the fifth costal increases from the distal to the proximal end. This costal wedging pattern is seen in almost all testudinids (Auffenberg, 1974). Dorsally, the sulci between the pleurals are inscribed on the left side of the first, fifth, sixth, eighth, and the right side of the fourth and eighth costals. These even-numbered costals are slightly concave or flattened, whereas all odd-numbered costals are flattened. In *Manouria emys* (ESK-6170; RH68) and *M. impressa* (RH268), the even-numbered costals are convex, while the odd-numbered costals are flattened.

The left first costal has lost its fringe area, and its exterior surface is covered by the first vertebral and first pleural scutes. The sulcus on the first vertebral scute curves medially from the posterior to anterior.

The right second costal contacts the third costal posteriorly. The third costal contacts the second costal anteriorly and the fourth costal posteriorly. The left fourth costal contacts the fourth neural medially and the left fifth costal posteriorly. The right fourth costal contacts the third costal anteriorly and the fifth costal posteriorly. The width of the third costal decreases from the distal to the proximal end. The right fifth costal contacts the fourth costal anteriorly and the ascending process of the right inguinal buttress ventrally.

The rib ends of these costals disappear at the border of the fifth, sixth and seventh peripherals. On the other hand, the proximal processes of the fifth, sixth and seventh peripherals extend medially at the distal ends of the respective costals in dorsal view. The relationship between costals and peripherals is known for most testudinids (Auffenberg, 1974). The left seventh costal contacts the seventh and the eighth neurals medially, the sixth costal anteriorly and the eighth costal posteriorly. The right seventh costal contacts the eighth costal posteriorly. The eighth costals contact the seventh costals anteriorly and the eighth neural medially. Ventrally, the ilium-attachment scars are located on the medial part of the internal surface of the proximal eighth costals. In *Hesperotestudo bermudae*, and some *Homopus areolatus*, this scar is located on the proximal part of the seventh and the eighth costals (Meylan and Sterrer, 2000).

The right fourth, fifth, sixth and seventh peripherals forming the “bridge” are relatively well preserved, except for the distal parts. They are about 1.9–2.1 mm thick. These peripherals are extremely thin and are sutured in order. The right fifth and sixth peripherals contact the right third and the fourth costals, respectively, by the dorsally extended distal peripheral processes. These peripherals do not coalesce with the costals. The overlapping of the fifth, sixth, seventh and eighth marginal scutes on the

peripherals do not reach the costals. The sulci between the pleural and marginal scutes coincide with the border of the costals and the peripherals. It is thin besides the thickened part and is not reverted.

Moreover, two peripherals, ESK-6125, from Hinigusuku, and ESK-6152 from Bise, Okinawa Island are preserved except for their proximal parts, so it is not possible to determine their original locations. They are uniformly thin (7.7 mm in ESK-6125 and 7.9 mm in ESK-6152 even on the thickened zone), and slightly reverted. Each peripheral is overlapped dorsally by two marginal scutes. The shallow and wide vertical scute sulci are also visible. The overlapping areas covered by the marginal scutes ventrally are quite narrow, and do not reach the thickened zone.

Plastron.—The plastral materials are sparse. The holotype, ESK-6150, includes the ascending process of the right inguinal buttress. ESK-6151, one of the referred specimens, consists of the right posterior half of a plastron.

The ventral part of the right inguinal buttress is missing on the holotype, ESK-6150. This buttress is very thin, slender and embedded in the ventral surface of the right fifth costal. The inguinal buttress is embedded in the distal part of the right posterior fifth costal, as also seen in *Mauremys japonica*, some *Indotestudo*, *Kinixys*, *Psammobates* and some *Stylemys*. Meylan and Sterrer (2000) suggested that the condition in which the inguinal buttress contacts the fifth costal is a primarily derived one.

ESK-6151, from Kamikurukubaru, is relatively well preserved, consisting of the incomplete right hypoplastron and the xiphiplastron (lacking their medial parts), which contact each other. These are very thin (about 10.4 mm in maximum thickness in the inguinal notch, and 2.3 mm in minimum thickness in the medial part of the right xiphiplastron), including the dorsolateral margins covered by the scutes. The right hypoplastron is covered by the right abdominal, femoral and inguinal scutes. The right xiphiplastron that is covered by the femoral and anal scutes is notched posteriorly, also covered by the femoral and anal scutes.

The abdominal scute contacts the femoral and inguinal scutes posteriorly. The right femoral scute is large, being about three times as long as the anal scute, and broadly contacts the inguinal scute anterolaterally on the plastral surface. In primitive fashion, the abdominal scute intervenes between the inguinal and femoral scutes, as also seen in *Mauremys*, *Homopus*, some *Psammobates* and *Stylemys* (Bramble, 1971; Meylan and Sterrer, 2000). The character condition seen in the holotype is apomorphic (Meylan and Sterrer, 2000).

The inguinal scute is vertically divided into two portions, a large anterior one and a small posterior one. The anterior one contacts the abdominal, and does not contact the femoral, whereas the posterior one contacts the abdominal

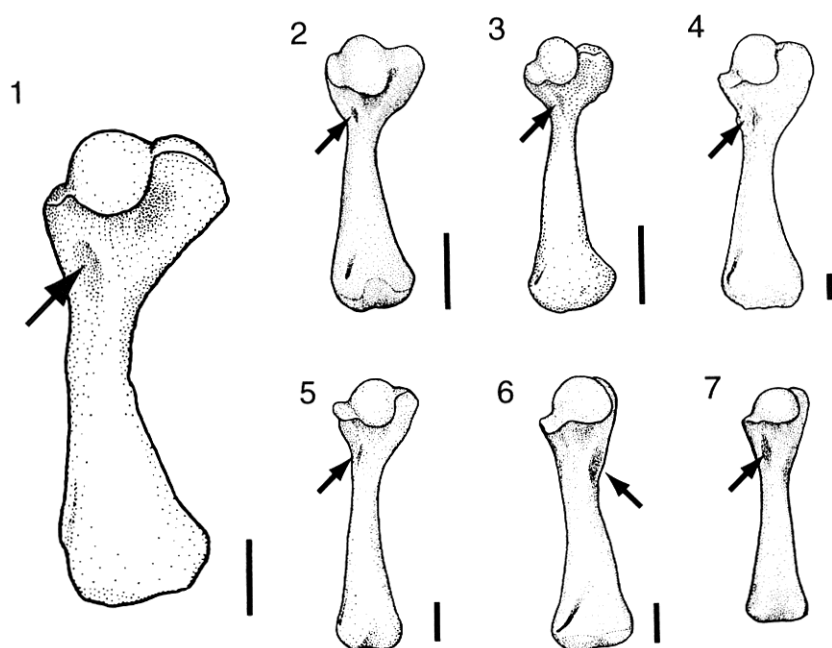


Figure 9. The left humeri of the Emydidae, Geoemydidae and Testudinidae. The arrows indicate the scar of the insertion of the latissimus dorsi muscle (dorsal view). The latissimus dorsi scar is located on the lateral process in *Manouria oyamai* (1: holotype, ESK-6150), *Emys orbicularis* (Emydidae; 2: ESK-6198), *Mauremys mutica* (Geoemydidae; 3: ESK-6176), *Manouria emys* (4: RH68), *Manouria impressa* (5: RH268) and *Testudo graeca* (7: ESK-6224), on the medial process in *Geochelone pardalis* (6: ESK-6224).

and femoral. In emydids and geoemydids, the inguinal scute is single (Hirayama, 1984). In *Manouria*, the inguinal scute is obviously divided into two or three parts (Crumly, 1984a), and divided inguinal scutes are also seen in some *Geochelone pardalis*, *G. sulcata*, *Gopherus agassizii*, *Homopus areolatus*, *H. femoralis*, *Malacochersus*, some *Psammobates tentorius*, *Testudo graeca*, *T. kleinmanni* (Loveridge and Williams, 1957; Bramble, 1971). Divided inguinal scutes are considered to be an apomorphic condition (Crumly, 1984a).

Pectoral girdle

Scapula.—The entire scapular prong and dorsal half of the acromion process are missing from the right scapula of the holotype, ESK-6150. The glenoid fossa of the scapula is shallow and narrow. The angle between the acromion process and the body of the scapula is estimated at approximately 110°–120° as seen in *Astrochelys*, *Dipsochelys* spp., *Geochelone*, some *Gopherus*, some *Hesperotestudo*, and *Psammobates* (Bour, 1994; Meylan and Sterrer, 2000). Bour (1984) also observed this condition in *Cylindraspis vosmaeri*, *Cylindraspis peltastes*, *Chelonoidis carbonaria*, *Manouria emys*, *Pyxis arachnoides*, *Pyxis planicauda*, and *Homopus areolatus*. Gerlach and Canning (1998) recorded that the angle in *Dipsochelys* spp. also measures 100°–130° variably in lateral views, however the measurements

used in Bour (1984) and Gerlach and Canning (1998) are incomparable to those of Meylan and Sterrer (2000) because they did not show the measuring criterion of the angle for the samples. Therefore, we follow the data shown by Meylan and Sterrer (2000) tentatively in the present study. The angle of the acromion process in the holotype is considered to be a primarily derived condition.

Coracoid.—Both coracoids are preserved in the holotype, ESK-6150. The right coracoid is about 42.9 mm long, but the coracoid blade is crushed and fragmented. The left coracoid is about 42.6 mm long and 23.0 mm wide, but lacks its central part of the blade. The preserved length of the left coracoid, ESK-6126, from Hinigusuku, is about 52.8 mm, but it is missing the proximal anterior blade.

The blades of these coracoids are fan-shaped as seen in all testudinids (Auffenberg, 1974). This character has also been considered as a synapomorphy in the Testudinidae (Auffenberg, 1974; Crumly, 1984a, b; Gaffney and Meylan, 1988).

Humerus

The left humerus of the holotype, ESK-6150, is about 64.9 mm in preserved length, but is missing the proximal part of the lateral process and the distal articular surface.

The humeral shaft is cylindrical, relatively slender, and

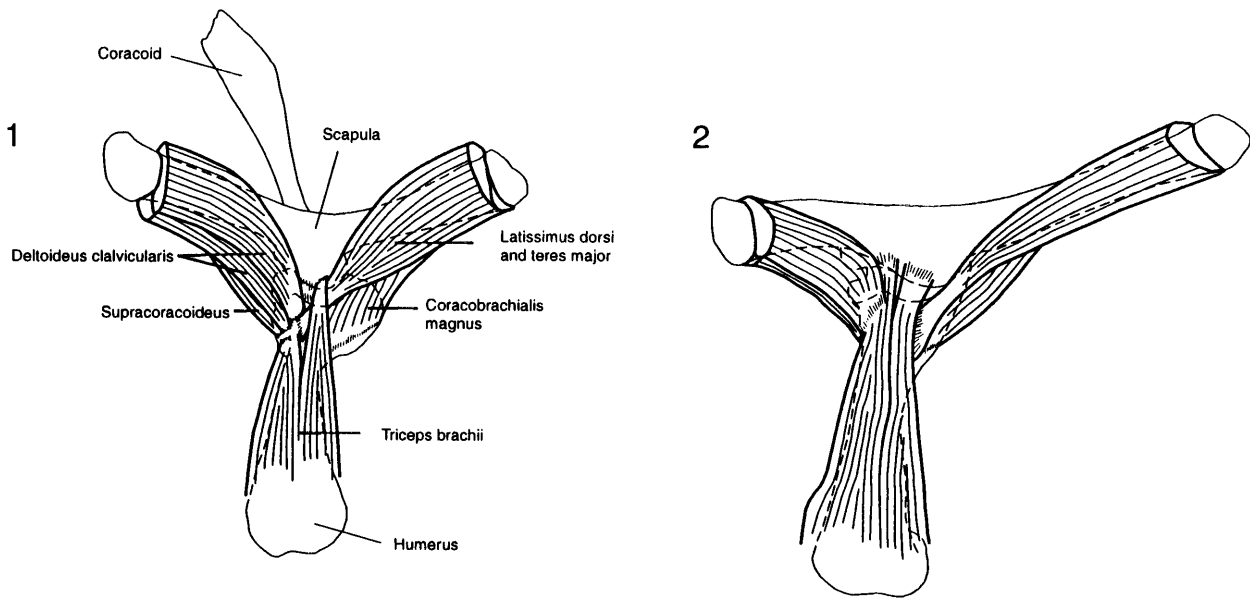


Figure 10. Left pectoral muscles of *Emys orbicularis* (Emydidae: 1) and *Geochelone pardalis* (Testudinidae: 2). The latissimus dorsi and teres major insert on the lateral process in *E. orbicularis*, and on the medial process in *G. pardalis*.

somewhat curved ventrally from the proximal to the distal end. The caput humerus is long and narrow, and is oval in outline, as seen in *Manouria*. The medial process (i.e. the greater trochanter of Meylan and Sterrer, 2000) does not extend beyond the caput humerus, as seen in *Mauremys*, some *Gopherus*, *Hesperotestudo bermudae*, *Malacochersus* and *Manouria*. This character, as seen in the holotype, is plesiomorphic (Meylan and Sterrer, 2000). In ventral view, the intertubercular fossa between the medial and lateral processes is relatively narrow and long, as it is in *Manouria*.

There is a shallow scar lacking the distinct border on the dorsolateral surface of the proximal shaft of the humerus (Figure 9). This scar is regarded as the insertion of a tendon formed by the convergence of the latissimus dorsi and teres major muscles (Walker, 1973), and is usually invisible in emydids, geoemydids and most testudinids (Crumly, 1984a; Gaffney and Meylan, 1988; Meylan and Sterrer, 2000). Crumly (1984a) inferred this to be the latissimus dorsi scar, and described the latissimus dorsi muscle inserting onto the proximal shaft on the ulnar (medial) side of the humerus among testudinids, except for *Manouria* that usually lacks this scar. He also noted that emydids and geoemydids usually do not have a latissimus dorsi scar even in large-size groups, and that chelydrids have a visible scar on the lateral side of the humeral shaft. He concluded that the muscle scars seen in chelydrids and testudinids are not homologous. Meylan and Sterrer (2000) observed for Testudinidae that there is no obvious latissimus dorsi scar in *Gopherus*, *Hesperotestudo*, *Manouria*, and *Stylemys*. In

the present study, *Emys orbicularis*, *Mauremys* and most of the testudinids were dissected and the location and development of the “latissimus dorsi scar” was checked. Our observations show that the latissimus dorsi and teres major muscles insert on the dorsal surface of the distal part of the lateral process at least in *Emys*, *Mauremys*, *Dipsochelys*, *Manouria*, and *Testudo horsfieldii*. In contrast, the muscles insert on the distal part of the medial process in *Chelonoidis*, *Geochelone*, *Indotestudo*, *Kinixys*, *Malacochersus* and *Testudo* except for *T. horsfieldii* (Figure 10). With regard to extinct testudinid species, the latissimus dorsi and teres major scar is located on the lateral process in *Stylemys nebrascensis* (Hay, 1908, fig. 491) and on the medial process in *Testudo cubensis* (Williams, 1950, pl. 5). Therefore, the latissimus dorsi and teres major scar seen in chelydrids, emydids, geoemydids and testudinids is likely to be homologous, and the character condition seen in the holotype is considered to be plesiomorphic.

Our dissections and observations also reveal that this muscle scar is undeveloped in *Emys*, *Mauremys*, some *Chelonoidis*, some *Dipsochelys*, *Kinixys*, *Manouria* and *Testudo graeca*. The muscle scar is present in other examined testudinids. Therefore, the presence of the developed latissimus dorsi and teres major scar is considered to be apomorphic.

There is a distinct ectepicondylar groove on the anterior part of the dorsal right distal humerus. Unfortunately, the presence or absence of the ectepicondylar foramen is not confirmed, because the distal articular surface of the humerus has been considerably eroded. In *Mauremys*,

some *Astrochelys*, some *Chelonoidis*, some *Hesperotestudo*, some *Indotestudo*, some *Kinixys*, *Malacochersus*, some *Manouria*, *Stylemys* and *Testudo horsfieldii*, the ectepicondylar foramen opens with a groove. In *Chersina*, some *Hesperotestudo*, *Homopus*, some *Indotestudo*, some *Kinixys*, some *Manouria*, *Psammobates*, *Pyxis* and *Testudo graeca*, both ectepicondylar foramen and groove are absent (incorrectly described as an “entepicondylar foramen” by Crumly, 1984a and Meylan and Sterrer, 2000). Crumly (1984a) considered the presence of the ectepicondylar foramen to be primitive, whereas Meylan and Sterrer (2000) considered its absence to be primitive. The coding for the character in Meylan and Sterrer (2000) is probably incorrect, because the ectepicondylar foramen is usually present with a groove in emydids, geoemydids and other outgroup taxa such as trionychoids, chelonoids, chelidrids, etc. used for testudinids.

Ulna

The right ulna, ESK-6129, from Hinigusuku, is missing the proximal end. The biceps scar is poorly developed, and located about two-thirds of the distance from the distal to the proximal medial surface.

Femur

The right femur from Hinigusuku, ESK-6130, lacks the fibular condyle and the trochanter minor, while the caput femoris, trochanter major, and tibial condyle are considerably eroded. This femur is 80.7 mm in length, 26.5 mm in proximal width, 23.9 mm in maximum measurable distal width, and 9.9 mm in minimum shaft width. The trochanter major and minor are coalesced by a ridge, which has been considered as a synapomorphy for Testudinidae (Auffenberg, 1974). The intertrochanteric fossa is deep, and longer than wide.

The distal part of the right femur, ESK-6138, from Kamikurukubaru, has a ridge developed between the tibial and fibular condyles on the distal articulation surface, as seen in *Mauremys* and *Manouria*.

Tibia

The right tibia, ESK-6131, from Hinigusuku, is slightly eroded on both proximal and distal ends. It is nearly straight from the distal to proximal ends in outline, measuring 59.6 mm long, 13.6 mm wide proximally and 18.3 mm wide distally. The cnemial crest is not developed.

Phylogenetic analysis

Genus *Manouria* Gray (1852), which comprises two living species, *M. emys* and *M. impressa*, was proposed by Gray (1852) and assigned to the Emydidae by having divided supracaudal scutes based on *M. fusca* (Gray, 1852).

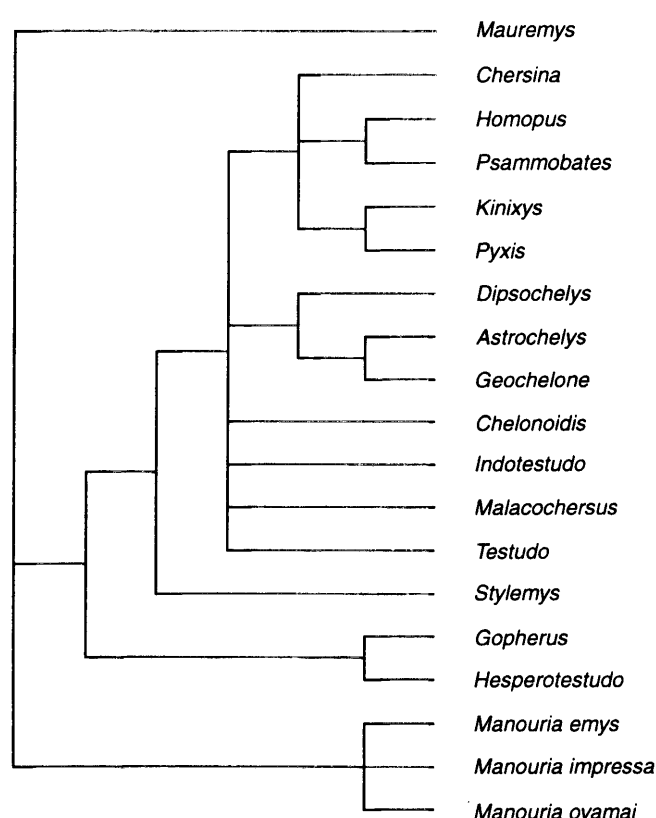


Figure 11. Strict consensus tree of 60 trees, 92 steps (CI = 0.467, RI = 0.592) for 32 characters showing the phylogenetic position of *Manouria oyamai* sp. nov. among the Testudinidae. The phylogenetic analysis was executed by PAUP* 4.0b1 for 16 genera of testudinids and an outgroup *Mauremys*. The taxa examined in the analysis are shown in Appendix III.

Later, Gray (1860) moved the genus from the Emydidae to the Testudinidae on the basis of a new specimen. Blyth (1853) described *Testudo phayrei* from Burma (Myanmar) and Anderson (1872) clarified that it resembles *M. fusca* but differs in the pectoral scutes contacting each other. Also, he synonymized *M. fusca* and *Testudo phayrei* with *T. emys* (Lidth de Jeude, 1895). *Manouria impressa* was also originally described as “*Geoemyda impressa*” by Günther (1882).

After that, “*Testudo*” *emys* and “*Geoemyda*” *impressa* were transferred to the genus *Testudo* (e.g., Smith, 1931) or *Geochelone* (e.g., Williams, 1952), or subgenus *Manouria* of genus *Geochelone* (e.g., Auffenberg, 1974). Bour (1980) suggested reelevating *Manouria* from subgeneric to generic status along with other subgenera of *Geochelone*. Recently, genus *Manouria* has come to be accepted by many researchers (e.g., Obst, 1983; Hoogmoed and Crumly, 1984; Crumly, 1984a,b; Crumly, 1988; Meylan and Sterrer, 2000) and *M. emys* has been divided into two subspecies, *M. e. emys* and *M. e. phayrei* (Wirot, 1979; Ernst and

Table 3. Osteological differences between *Manouria* including *Manouria oyamai* and fossil records of “*Manouria*” (Auffenberg, 1974).

Taxa	Relative age	Locality	Enlarged foramen caroticum laterale	Supracaudal scute divided	Latissimus dorsi insertion	Inguinal scute divided more than two
Extant two species of <i>Manouria</i>	Recent	Southeast Asia	+	+	lateral process	double
<i>Manouria oyamae</i> sp. nov.	Late Pleistocene	Ryukyu Islands, Japan	+	?	lateral process	double
? <i>Testudo margae</i> Hoojer, 1948	Pleistocene	Celebes, Indonesia	?	?	medial process	?
<i>Testudo punjabiensis</i> Lydekker 1889	Pliocene	Punjab, India	?	?	?	?
<i>Hadrianus corsoni</i> (Leidy, 1871)	Late Eocene	Wyoming, U.S.A.	?	+	?	?
<i>Hadrianus robustus</i> Gilmore, 1915	Late Eocene	Utah, U.S.A.	?	?	?	?
<i>Testudo insolitus</i> Matthew and Granger, 1923	Late Eocene	Promontory Bluff, Mongolia	?	?	?	?
<i>Hadrianus tumidus</i> Hay, 1908	Late Eocene	Utah, U.S.A.	?	?	?	single
<i>Hadrianus utahensis</i> Gilmore, 1915	Late Eocene	Utah, U.S.A.	?	?	?	?
<i>Testudo eocaenica</i> Hummel, 1935	Middle Eocene	Bavaria, Germany	?	+	?	?
<i>Hadrianus majusculus</i> Hay, 1904a	Early Eocene	New Mexico, U.S.A.	?	?	?	single
<i>Hadrianus obailiensis</i> Chkikvadze, 1970	Eocene	Georgian SSR, Kazakhstan	?	?	?	?

Barbour, 1989; Iverson, 1992; Liat and Das, 1999; Schaffer and Morgan, 2002).

Manouria Gray (1852) has been cited as the most basal member within the Testudinidae (Crumly, 1982, 1984a,b; Gaffney and Meylan, 1988; Meylan and Sterrer, 2000). The two living species of *Manouria* are peculiar in having an enlarged foramen caroticum laterale piercing the lateral wall of the cranial cavity (Bour, 1981; Crumly, 1984a,b). Hoogmoed and Crumly (1984) described *Manouria* as being mainly characterized by the following features: broad triangular cervical scute; split supracaudal scutes (split both dorsally and ventrally); primitive (class II) mental glands; absence of the surangular process; the presence of an enlarged foramen caroticum laterale. However, these features, other than the last one, are primitive characters.

The phylogenetic analysis with PAUP* 4.0b (Swofford, 1998) was executed using 32 characters for 17 genera (16 testudinids and a geoemydid turtle, *Mauremys*, as outgroup to root dendrograms) in morphological data. The polarities of some characters cited in Meylan and Sterrer (2000) were modified, and a new character, “insertion of the muscle latissimus dorsi,” is included in the present analysis. As a result, 60 equally parsimonious trees (92 steps with a CI of 0.467 and an RI of 0.592) were detected by the branch and bound search option (Figure 11; Appendices I, II). Recent DNA-based phylogenetic analyses frequently contradict hypotheses based on morphology (e.g., “Geoemydinae” of Honda *et al.*, 2002), although as yet there is no comprehensive systematics of testudinids at the generic level based on molecular data. Our results, based on morphological data, show that fossil testudinids from the Ryukyu Islands belong to *Manouria*. This result supports the idea that genus *Manouria* is monophyletic, composed of *M. emys*, *M. impressa* and *M. oyamai*, and is the most basal in the Testudinidae.

Discussion

Manouria oyamai differs from the two living species of *Manouria* by having an extremely thin and flattened carapace, slightly convex or flattened, even-numbered costals in dorsal view, and extremely wide scute sulci on the shell. Many fossil species reported in Tertiary and Quaternary deposits of East and Southeast Asia were placed in this genus by Auffenberg (1974) (Table 3; Auffenberg, 1974; Yeh, 1963, 1994).

Hummel (1935) and Rollius (1966) believed that the ancestor of *Manouria* was traceable to *Testudo eocaenica* from the Middle Eocene of Germany. Auffenberg (1971) agreed with Hummel (1935) and Rollius (1966), and synonymized *Hadrianus* and *T. eocaenica* with *Manouria*, although he did not cite distinctive osteological reasons for this. Subsequently, Auffenberg (1974) tentatively placed *Testudo insolitus*, *T. margae* and *T. punjabiensis* in *Manouria*.

Crumly (1983) evaluated fossil testudinids from China and Mongolia based on published descriptions, and recommended synonymizing *Kansuchelys*, *Sinohadrianus*, *Testudo sharanensis* and *Testudo yushensis* with *Manouria*. He also agreed with Auffenberg (1971) in synonymizing *Hadrianus* with *Manouria* in the basis of shared primitive characters. Later, Crumly (1984b) suggested that *Kansuchelys* differs from *Manouria* in its neural pattern, which is hexagonal and has the short articulation always directed anteriorly as seen in *Stylemys*, and he also suggested that *Sinohadrianus* may not be a testudinid.

Crumly (1984a) discovered that the inguinal scute is composed of two or three parts in the living species of *Manouria*. However, the divided inguinal scute is also seen in some *Geochelone pardalis*, *G. sulcata*, *Gopherus agassizii*, *Homopus areolatus*, *H. femoralis*, *Malacochersus*,

Psammobates tentorius, *Testudo graeca*, and *T. kleinmanni* (Loveridge and Williams, 1957; Bramble, 1971). These occurrences imply that the divided inguinal scutes are not a synapomorphic character of *Manouria*. However, it is evident that *H. majusculus* and *H. tumidus* differ from *Manouria* by having a single inguinal scute.

Testudo margae Hooijer (1948) is likely excluded from *Manouria*, because of its undeveloped latissimus dorsi scar on the medial process of the humerus, as seen in Middle Pleistocene specimens in the Celebes (Hooijer, 1954). In several testudinids, *Dipsochelys*, *Manouria*, *Stylomys* (*S. nebrascensis*), *Testudo graeca* and *T. horsfieldii*, the latissimus dorsi scar is located on the dorsal surface of the lateral process. Several specimens of *Hadrianus corsoni* have concentric growth lines on its shell (Hay, 1908; Parham, per. comm.) that are absent in *Manouria emys* and *M. impressa*.

Fossil species assigned to “*Manouria*” by Auffenberg (1974) are polyphyletic, because *Hadrianus corsoni*, *H. majusculus*, *H. tumidus* and *Testudo margae* are distinct from *Manouria* in several characters. All the fossil specimens assigned to “*Manouria*” consist of carapace fragments lacking cranial information. We agree that fossils previously assigned to “*Manouria*” are primitive testudinids, but some “*Manouria*” apparently differ from *Manouria sensu stricto* by having a single inguinal scute and the latissimus dorsi and teres major scar located on the medial process of the humerus (Table 3).

Nowadays, three genera and species of geoemydid turtles (*Cuora flavomarginata*, *Geoemyda japonica* and *Mauremys mutica*) are living in the Ryukyu Islands. *Pelodiscus sinensis* is widely distributed in eastern Asia including Taiwan and Japan (Iverson, 1992), but the distribution of this species in the Ryukyus has been formed by artificial transportation (Sato and Ota, 1999). The present natural distributions of *M. mutica* and *C. flavomarginata* in the Ryukyu Islands are restricted to Yonaguni, Iriomote and Ishigaki Islands and Iriomote and Ishigaki Islands in Yaeyama group of the South Ryukyus, respectively. However, they are also widely distributed in eastern Asia (Ernst and Lovich, 1990; Yasukawa *et al.*, 1996). The populations of both species in the Yaeyama group of the South Ryukyus have been classified as distinct subspecies, *C. f. evelynae* (Ernst and Lovich, 1990; demoted from full species to subspecies by McCord and Iverson, 1991) and *M. m. kami* (Yasukawa *et al.*, 1996) respectively. *Geoemyda japonica*, which is living in Okinawa, Kume and Tokashiki Islands, is an endemic species of the Central Ryukyus (Yasukawa *et al.*, 1992). The close relatives of these three species (i.e., *C. galbinifrons*, *M. annamensis* and *G. spengleri*) are distributed from southern China to northeastern Indochina (Iverson, 1992; Yasukawa and Ota, 1999; Yasukawa *et al.*, 2001).

Fossil *Geoemyda japonica* was reported from Okinawa and Ie Islands (Hasegawa *et al.*, 1978; Hasegawa, 1980) and Kume Island (Takahashi and Otsuka, unpublished data), and incomplete postcranial fossil specimens of *Cuora* sp. (*sensu stricto*) were yielded by latest Pleistocene fissure deposits of Kume and Okinawa Islands (Takahashi and Otsuka, unpublished data). The specimens of *Cuora* sp. include the incomplete ilia of which the anterodorsal portions are about as long as the posterodorsal portion and xiphiplastra without anal notch. Yasukawa *et al.* (2001) clarified that the anterodorsal portion of the iliac blade is about twice as long as the posterodorsal only seen in “*Cistoclemmys*” within metataxonomic “*Geoemydinae*”. The fossil localities of *Cuora* sp. are restricted to the Central Ryukyus. On the other hand, *Mauremys mutica* has never been reported as a fossil.

Manouria oyamai is found with many terrestrial fossil vertebrates (Paleolithic human known as Minatogawa Man, deer such as *Cervus astylodon* and *Dicruceros? sp.*, geoemydid turtles such as *Geoemyda japonica* and *Cuora* sp., a wild cat, a wild boar, rats, birds including raptorial, lizards, and frogs, among others) in latest Pleistocene fissure and cave deposits over a wide area, ranging from Miyako Island in the South Ryukyus, to Okinawa, Ie and Tokunoshima Islands in the Central Ryukyus (e.g., Hasegawa, 1980, Otsuka and Takahashi, 2000; Matsuoka, 2000). The latest Pleistocene fossil terrestrial vertebrate assemblage of Miyako Island is peculiar and characterized by *Diplothrux legata*, *Microtus* sp., and *Felis* sp. with extinct endemics such as *Capreolus miyakoensis*, *Sus* sp. and others. Oshiro and Nohara (2000) considered that they could have migrated from the continent to Miyako Island directly through a temporary narrow land bridge based on geological and geographic data. The fossil humerus of *M. oyamai* from Miyako Island (reported as “*Testudo cf. emys*” by Hasegawa *et al.*, 1973) which was not figured or fully described needs to be reexamined morphologically and additional specimens uncovered in Miyako Island. It is noteworthy that *Manouria oyamai* was found with Paleolithic human remains from the Minatogawa site on Okinawa Island (Minatogawa Man) and Gohezu-do Cave on Ie Island. Sonddar (2000) suggested that a dramatic faunal turnover occurred in the latest Pleistocene based on the replacement of fossil herbivores in the section of the Minatogawa site (fissure); the Ryukyu deer (*Cervus astylodon*) was yielded by the lower part, whereas *Sus scrofa* was found with Minatogawa Man abundantly in the upper part (Hasegawa, 1980).

We have recently examined the Imadomari - Akagimata vertebrate assemblage from the shallow-marine and lacustrine Haneji Formation (Figure 2) in the northern part of Okinawa Island. The stratigraphic interval with vertebrate fossils has an Early Pleistocene age of 1.5 ± 0.3 Ma,

based on fission-track dating (Otsuka and Takahashi, 2000). This fossil assemblage is composed of the Ryukyu deer (*Cervus astylodon*), *Muntiacus* sp., a large rodent, geoemydid turtles (including *Geoemyda japonica*; Takahashi and Otsuka, unpublished) and terrestrial snakes, but *M. oyamai* and hominid fossils are not present (Otsuka and Takahashi, 2000).

The 14 living genera of testudinids are widely distributed worldwide in most areas of temperate to tropical, subhumid to arid grassland, savanna and forest, except for the Australian region (Auffenberg, 1974; Iverson, 1992). The two living *Manouria*, *M. emys* and *M. impressa* are distributed in southern China, Indochina, the Malay Peninsula, Myanmar, eastern India, and the islands of Sumatra and Borneo, and southern China, Indochina, the Malay Peninsula and Myanmar, respectively (Iverson, 1992). They inhabit evergreen rain forest or bamboo forest of high-elevation areas up to 1,200m (Liat and Das, 1999). In the Ryukyu Islands, *M. oyamai* was found from nonmarine fissure and cave deposits cutting into raised Ryukyu limestone, which is distributed on lowland areas mainly up to about 150m above sea level. In this respect, the habitat of *M. oyamai* in the latest Pleistocene could have differed greatly from that of living *Manouria*.

The presence of *M. oyamai* in latest Pleistocene deposits of the Ryukyus means that *Manouria* ranged from Southeast Asia to the Ryukyu Islands during the latest Pleistocene, as well as geoemydids such as *Geoemyda* and *Cuora*. The present terrestrial vertebrate fauna (including varied amphibian species) in most islands of the Ryukyus follows the continental islands pattern, with most of the animals showing high variation and endemism while also having close relatives on the continental mainland and Taiwan (e.g., Ota, 1998). However, the Central and South Ryukyus are separated by the Kerama Strait, which exceeds 200 m in depth and was not exposed subaerially by sea-level regression during the last glacial period, so it was not possible for *M. oyamai* and other terrestrial vertebrates to migrate from the South to the Central Ryukyus. Based on biological, biostratigraphic and paleontological data, it could be supposed that the ancestral forms of *M. oyamai*, *Cuora* sp. and other terrestrial vertebrates migrated from mainland Asia to the Central Ryukyus over a temporary Middle Pleistocene land bridge. Later, the temporary peninsula-like land bridge was cut by the Kerama strait, which formed during the Late Pleistocene, but these immigrants survived in the Central Ryukyus until the Late Pleistocene (Otsuka and Takahashi, 2000).

The thin carapace with wide scute sulci of *M. oyamai* also implies insular adaptation, such as is known among the giant tortoises of the Mascarenes, Aldabra and Galapagos Islands (Pritchard, 1979; Bour, 1994; pers. obs. by Hirayama). However, the descendants of *M. oyamai* might

have become extinct along with other endemics such as *Cervus astylodon* and *Dicrocercus*? sp. at the hands of Paleolithic humans at the end of the latest Pleistocene. Abrupt extinctions of endemic terrestrial vertebrates (e.g., deer and tortoises) by human colonization of islands going back to the Middle Pleistocene are a phenomenon that is recognized worldwide (Sondar, 2000).

Conclusion

Manouria oyamai is the first fossil record of this genus worldwide. Taxa previously assigned to "*Manouria*" by Auffenberg (1974), including *Hadrianus* and some fossil "*Testudo*", are considered to be polyphyletic. *Manouria* comprises the extant *M. emys* and *M. impressa*, in addition to *M. oyamai* from the Pleistocene of the Ryukyus. The relatively thin shell of *M. oyamai* suggests that this tortoise was well adapted for an insular environment without large predators. Presumed abrupt extinction of *M. oyamai* as well as the other large terrestrial mammals in the Ryukyu Islands might very possibly have been caused by human colonization during the latest Pleistocene.

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Appendix I: Characters and character status used in the phylogenetic analysis.

1. Premaxillary ridge ("Median premaxillary ridge" of Crumly, 1984a): (0) = absent, (1) = incipiently developed, (2) = developed.
2. Foramen praepalatium (Meylan and Sterrer, 2000): (0) = present, (1) = not distinguishable from the nutritive foramina.
3. Transverse ridge (Meylan and Sterrer, 2000): (0) = absent, (1) = on the maxilla-premaxilla suture, (2) = restricted to the premaxilla.
4. Median maxillary ridge (Meylan and Sterrer, 2000): (0) = absent, (1) = restricted to the maxilla, (2) = extends from the maxilla to the premaxilla.
5. Lingual ridge (Meylan and Sterrer, 2000): (0) = absent, (1) = restricted to the maxilla, (2) = extends from the maxilla to the premaxilla.
6. Number of triturating ridges on the maxilla (Meylan and Sterrer, 2000): (0) = one, labial only, (1) = three.
7. Posterior maxillary process (Crumly, 1982, 1984a; Meylan and Sterrer, 2000): (0) = absent, (1) = present.
8. Ethmoid fissure (revised after Crumly, 1984a): (0) = narrow, (1) = slightly broader, (2) = broad.
9. Enlarged foramen caroticum laterale piercing the anterolateral parietal flange (revised after Crumly, 1984a): (0) = absent, (1) = present and the medial roof of the foramen caroticum laterale opens, (2) = present and the lateral roof of the foramen caroticum laterale opens, (3) present, its lateral roof opens but the foramen caroticum laterale is located far posterior to the parietal flange.
10. Length of the vomer (Meylan and Sterrer, 2000): (0) = not dividing the palatines, (1) = dividing the palatines not pterygoids, (2) = dividing the palatines, pterygoids, not reaching the basisphenoid, (3) the vomer reaches the basisphenoid.
11. Posterior extension of the pterygoid (Meylan and Sterrer, 2000): (0) = covers the processus interfenestralis, (1) = not covering the processus interfenestralis.
12. Quadrate enclosing stapes (Meylan and Sterrer, 2000): (0) = no, (1) = yes.
13. Dorsal exposure of the prootic (Meylan and Sterrer, 2000): (0) = wide, (1) = narrow, (2) = absent.
14. Surangular process (Meylan and Sterrer, 2000): (0) = absent, (1) = present.
15. Cervical scute (Meylan and Sterrer, 2000): (0) = wider than long, (1) = longer than wide, (2) = absent.
16. Ilium attachment scar (Meylan and Sterrer, 2000): (0) = the costal 8 only, (1) = the costal 7 and 8.
17. Inguinal buttress contacts (Meylan and Sterrer, 2000): (0) = the costal 5 and 6, (1) = the costal 5 only, (2) = the costal 6 only, (3) = the peripherals only.
18. Femoral-inguinal scute contacts (Meylan and Sterrer, 2000): (0) = absent, (1) = small in the inguinal notch, (2) = broad on the plastral surface.
19. Number of inguinal scute (revised after Crumly, 1984a): (0) = single, (1) = more than two.
20. Angle of the acromion process to the body of the scapula (Meylan and Sterrer, 2000): (0) = 80–110°, (1) = 110–120°, (2) = >120°.
21. Coracoid blade shape (Meylan and Sterrer, 2000): (0) = long and narrow, (1) = wide, fan shaped.
22. Greater trochanter (Meylan and Sterrer, 2000): (0) = not extending beyond the humeral head, (1) = extending well beyond the humeral head.
23. Insertion of the latissimus dorsi and teres major muscles: (0) = insert on the distal to the lateral process, (1) = insert on the distal to the medial process.

24. Latissimus dorsi and teres major scar (revised after Crumly, 1984a and Meylan and Sterrer, 2000): (0) = absent or invisible, (1) = developed.
25. Ectepicondylar foramen (Crumly, 1984a): (0) = enclosed, (1) = a groove, (2) = absent.
26. Trochanters of femur (Meylan and Sterrer, 2000): (0) = separated, (1) = coalesced.
27. Suprapygial scute (Meylan and Sterrer, 2000): (0) = divided, (1) = single.
28. Posterior epiplastral excavation (Meylan and Sterrer, 2000): (0) = absent, (1) = present.
29. Gular scutes contact the entoplastron (Meylan and Sterrer, 2000): (0) = yes, (1) = no
30. Pectoral scute shape (Meylan and Sterrer, 2000): (0) = broad and trapezoidal, (1) = narrow and parallel-sided, (2) = not meeting medially.
31. Mental glands (Winokur and Legler, 1975): (0) = the class II mental glands, (1) = the class I mental gland, (2) absent.
32. Armor (Meylan and Sterrer, 2000): (0) weak or absent, (1) = strong.

Appendix II. Data matrix of phylogenetic analysis for family Testudinidae and an outgroup taxa, *Mauremys*. The missing data were represented by “?”. The polymorphic character states were shown as following symbols: a = (0, 1), b = (0, 2), c = (1, 2), d = (2, 3), e = (0, 1, 2), and f = (1, 2, 3).

CHARACTERS	1										2										3											
TAXA	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
Bataguridae																																
<i>Mauremys</i>	0	0	0	0	0	0	0	0	0	a	0	0	1	0	a	0	a	0	0	0	0	0	0	0	a	0	0	0	0	0	a	0
Testudinidae																																
<i>Chersina</i>	0	0	0	0	0	0	1	2	0	1	1	a	0	1	c	0	0	c	0	0	1	1	?	1	2	1	1	1	a	1	2	0
<i>Astrochelys</i>	0	0	1	1	1	1	a	2	0	c	0	1	0	1	0	0	2	c	0	1	1	1	1	1	a	1	1	1	a	1	2	1
<i>Chelonoidis</i>	0	0	a	1	1	1	a	2	a	c	0	1	a	1	c	0	b	c	0	b	1	1	1	a	a	1	1	1	a	1	2	0
<i>Dipsochelys</i>	0	0	a	c	1	1	1	2	0	f	0	a	a	1	0	0	0	2	0	1	1	1	0	a	0	1	1	1	1	1	2	0
<i>Geochelone</i>	0	0	1	1	c	1	1	2	0	e	0	1	a	1	2	0	2	1	a	1	1	1	1	1	0	1	1	1	a	1	2	1
<i>Gopherus</i>	2	a	0	2	2	1	1	2	0	d	a	1	a	0	0	0	2	1	a	c	1	a	?	0	0	1	1	1	0	0	1	0
<i>Hesperotestudo</i>	0	a	2	2	2	1	1	?	?	c	0	1	a	0	1	a	0	2	0	c	1	a	?	0	c	1	1	1	0	1	?	1
<i>Homopus</i>	0	0	0	0	0	0	1	2	3	1	1	1	1	1	a	a	3	0	1	0	1	1	?	1	2	1	1	0	1	1	2	1
<i>Indotestudo</i>	0	0	0	1	1	1	1	2	0	1	0	1	a	1	c	0	a	1	0	0	1	1	1	1	c	1	1	a	0	0	?	0
<i>Kinixys</i>	0	0	0	0	0	0	a	2	0	2	0	1	1	1	e	0	1	1	0	0	1	1	1	0	c	1	1	1	a	0	2	a
<i>Malacochersus</i>	0	0	0	1	1	1	1	2	0	d	1	1	2	1	a	0	3	1	1	0	1	0	1	1	1	1	0	0	1	1	2	0
<i>Manouria emys</i>	a	0	1	1	2	1	0	1	2	1	0	1	0	0	0	0	0	1	1	0	1	0	0	a	e	1	0	1	a	2	0	1
<i>Manouria impressa</i>	a	0	0	1	2	1	0	c	2	1	0	1	0	0	0	0	0	1	1	0	1	0	0	0	e	1	0	0	0	2	0	1
<i>Manouria oyamai</i> sp. nov.	0	0	1	1	?	1	0	1	2	?	0	?	0	0	1	0	1	2	1	1	1	0	0	1	a	1	?	?	?	?	?	?
<i>Psammobates</i>	0	0	0	0	0	0	1	1	?	1	1	1	1	0	e	0	1	a	1	1	1	1	?	0	2	1	1	1	0	1	?	1
<i>Pyxis</i>	0	0	0	0	0	0	1	2	0	c	1	0	a	0	1	0	3	2	0	0	1	1	?	0	2	1	1	1	1	0	2	0
<i>Stylemys</i>	2	0	0	1	1	1	0	?	?	1	0	1	a	0	1	0	e	0	0	0	1	1	0	1	1	1	1	1	0	a	?	0
<i>Testudo</i>	0	0	0	a	1	1	1	c	0	c	a	1	c	1	1	0	3	1	a	0	1	1	a	a	c	1	1	1	0	0	2	0

Appendix III. Skeletal materials examined in the present study and referred character states and descriptions used in the phylogenetic analysis.

Emyridae

Emys orbicularis: ESK-6198; Winokur and Legler (1975), Gaffney (1979), Loveridge and Williams (1957), Meylan and Sterrer (2000).

Geoemydidae

Mauremys japonica: ESK-6165, RH207; Meylan and Sterrer (2000).

Mauremys mutica: ESK-6163, 6164, 6165; Winokur and Legler (1975), Gaffney (1979), Meylan and Sterrer (2000).

Testudinidae

Astrochelys yniphora: Crumly (1982), Crumly (1984a), Meylan and Sterrer (2000).

Chelonoidis carbonaria: ESK-6230, RH286, 753; Boulenger (1889), Loveridge and Williams (1957), Winokur and Legler (1975), Crumly (1982), Bour (1984), Crumly (1984a).

Chelonoidis chilensis: RH505, 544, 643, 663; Boulenger (1889), Winokur and Legler (1975), Crumly (1982), Meylan and Sterrer (2000).

Chelonoidis denticulate: ESK-6198, RH680, 686; Winokur and Legler (1975), Crumly (1982), Crumly (1984a), Meylan and Sterrer (2000).

Chersina angulata: Loveridge and Williams (1957), Winokur and Legler (1975), Gaffney (1979), Crumly (1984a), Meylan and Sterrer (2000).

Dipsochelys spp.: *D. dussumieri*, an unregistered specimen of Izu Andyland; Winokur and Legler (1975), Crumly (1982), Crumly (1984a), Bour (1994), Gerlach and Canning (1998), Meylan and Sterrer (2000).

Geochelone elegans: ESK-6178, 6201; Boulenger (1889), Smith (1931), Winokur and Legler (1975), Crumly (1982), Crumly (1984a), Meylan and Sterrer (2000).

Geochelone pardalis: ESK-6179, 6195, RH925; Loveridge and Williams (1957), Winokur and Legler (1975), Crumly (1982), Crumly (1984a), Meylan and Sterrer (2000).

Geochelone sulcata: ESK-6192; Loveridge and Williams (1957), Winokur and Legler (1975), Crumly (1982), Crumly (1984a), Meylan and Sterrer (2000).

Gopherus agassizii: Auffenberg (1976), Bramble (1971), Winokur and Legler (1975), Crumly (1984a).

Gopherus berlandieri: Auffenberg (1976), Bramble (1971), Winokur and Legler (1975), Crumly (1984a), Meylan and Sterrer (2000).

Gopherus flavomarginatus: Winokur and Legler (1975), Auffenberg (1976), Bramble (1971), Crumly (1984a), Meylan and Sterrer (2000).

- Gopherus polyphemus*: Winokur and Legler (1975), Auffenberg (1976), Bramble (1971), Gaffney (1979), Crumly (1984a), Meylan and Sterrer (2000).
- [†]*Hesperotestudo Bermudae*: Meylan and Sterrer (2000).
- [†]*Hesperotestudo* spp.: Hay (1908), Meylan and Sterrer (2000).
- Homopus areolatus*: Winokur and Legler (1975), Loveridge and Williams (1957), Gaffney (1979), Bour (1984), Crumly (1984a), Meylan and Sterrer (2000).
- Indotestudo elongate*: ESK-6184, 6194, RH187; Smith (1931), Winokur and Legler (1975), Crumly (1982), Meylan and Sterrer (2000).
- Indotestudo forstenii*: RH752; Smith (1931), Crumly (1982), Meylan and Sterrer (2000).
- Kinixys belliana*: ESK-6181, RH255; Loveridge and Williams (1957), Winokur and Legler (1975), Crumly (1984a), Meylan and Sterrer (2000).
- Kinixys erosa*: Loveridge and Williams (1957), Winokur and Legler (1975), Crumly (1984a), Meylan and Sterrer (2000).
- Kinixys homeana*: ESK-6217, RH509; Loveridge and Williams (1957), Winokur and Legler (1975), Gaffney (1979), Crumly (1984a).
- Malacochersus tornieri*: ESK-6185; Loveridge and Williams (1957), Winokur and Legler (1975), Crumly (1984a), Meylan and Sterrer (2000).
- Manouria emys*: ESK-6170, RH68, Crumly (1982), Bour (1984), Crumly (1984a), Meylan and Sterrer (2000).
- Manouria impressa*: RH268; Crumly (1982), Crumly (1984a).
- Psammobates tentorius*: Loveridge and Williams (1957), Crumly (1984a), Meylan and Sterrer (2000).
- Pyxis arachnoids*: Boulenger (1889), Winokur and Legler (1975), Gaffney (1979), Bour (1981, 1982, 1984), Crumly (1984a), Meylan and Sterrer (2000).
- [†]*Stylemys nebrascensis*: Hay (1908).
- [†]*Stylemys* sp.: Meylan and Sterrer (2000).
- Testudo graeca*: ESK-6183, 6224; Loveridge and Williams (1957), Winokur and Legler (1975), Crumly (1984a), Meylan and Sterrer (2000).
- Testudo horsfieldii*: ESK-6182, 6232, RH544; Crumly (1984a).