

A new skull of the side-necked turtle  
(Order Testudines: Infraorder Pleurodira;  
Family Podocnemididae)  
from the Neogene of Myanmar

Ren HIRAYAMA\*, Teppei SONODA\*\*,  
Masanaru TAKAI\*\*\*, Thaung-HTIKE\*\*\*\*  
and Zin-Maung-Maung-THEIN\*\*\*\*\*

Abstract

A new turtle skull (NMMP-KU-IR-5300) was collected from the lowermost Irrawaddy Formation, or the upper parts of the Obogon- Irrawaddy transition zone, dated as early Late Miocene, in the Tebingan area, Magway Region, central Myanmar. This fossil is identified as the third skull of *Shweboemys pilgrimi*, an extinct side-necked turtle of Asia, based on its extreme development of the secondary palate. This specimen shows hitherto unknown unique characters such as extremely thick parietal bones and a rod-like elongate rostrum basisphenoidale.

---

\* School of International Liberal Studies, Waseda University, Tokyo, Japan

\*\* Fukui Prefectural Dinosaur Museum, Katsuyama, Japan

\*\*\* The Kyoto University Museum, Kyoto University, Kyoto, Japan

\*\*\*\* University of Banmaw, Banmaw, Myanmar

\*\*\*\*\* Department of Geology, University of Mandalay, Mandalay, Myanmar

## Introduction

Neogene non-marine sediments of Myanmar such as the Irrawaddy Bed are known as bearing rich terrestrial vertebrate fauna, including mammals and reptiles (Hirayama et al., 2015; Iijima et al., 2021; Takai et al., 2021; Longuet et al., 2023). *Shweboemys pilgrimi* is a rather rare fossil example of the side-necked turtles in Asia (Swinton, 1939; Wood, 1970; Gaffney et al., 2011). Hitherto, only two skulls of *S. pilgrim* (GSI 17255, holotype, and BMNH R.8432) have been reported possibly from the Khabo Formation (latest Middle Miocene), underlying the Irrawaddy Formation of Shwebo District of Myanmar (Swinton, 1939; Wood, 1970; Gaffney et al., 2011; Hirayama et al., 2020).

Here we report a well-preserved turtle skull (NMMP-KU-IR-5300) collected from the lowermost part of the Irrawaddy Formation or the upper parts of the Obogon–Irrawaddy transition zone of the Tebingan area by the Myanmar–Japan joint investigation in November 2017 (Fig. 1; Hirayama et al., 2020). This specimen shows some hitherto unknown characters of this species, shedding light on its phylogenetic relationships and unique occurrences.

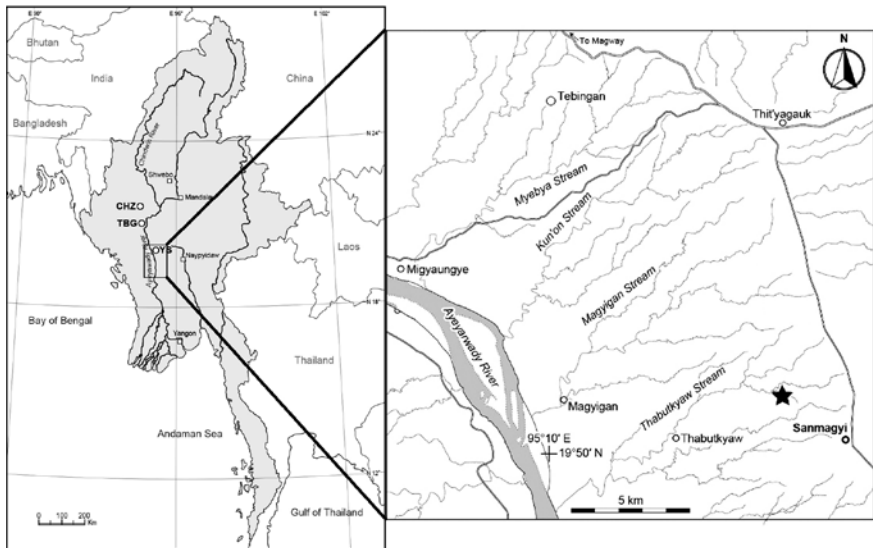


Figure 1. Map of *Shweboemys*

**Institutional Abbreviations**— **BMNH**, Natural History Museum, London; **GSI**, Geological Survey of India, Delhi; **NMMP-KU-IR**, Kyoto University Irrawaddy collection, National Museum of Myanmar, Palaeontology, Yangon.

## Geological settings

Geology of the Tebingan area, central Myanmar is well summarized by Takai et al. (2021) and Longuet et al. (2023). In the Tebingan area, the fluvial Irrawaddy Formation conformably overlies the shallow marine Obogon Formation (Middle Miocene) of the Pegu Group (Takai et al. 2021; Longuet et al., 2023). Most vertebrate fossils from the Tebingan area are collected from the lowermost part of the Irrawaddy Formation or the upper parts of the Obogon- Irrawaddy transition zone (Figure 2; Takai et al., 2018a, b, 2021). The geological age of the Irrawaddy Formation in Tebingan area is estimated from the combination of several mammals' genera with a well-established

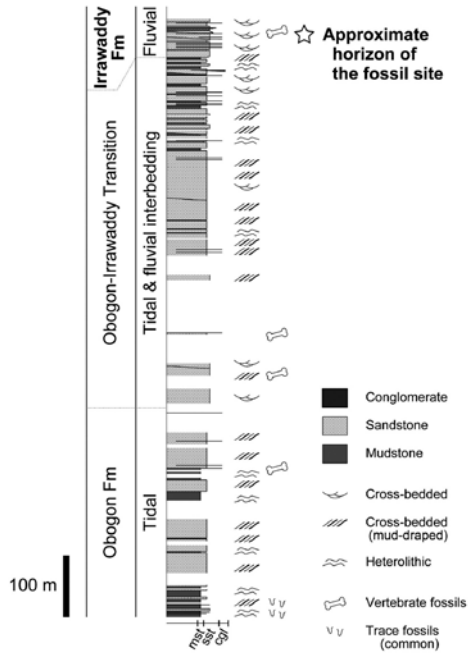


Figure 2. Colmunar section of the Tebingan area

chronological distribution in the Siwalik deposits (Northern Pakistan), suggesting an early Late Miocene age (9–8Ma) (Takai et al. 2021; Longuet et al., 2023).

## SYSTEMATIC PALEONTOLOGY

Order Testudines Batsch, 1788

Infra-order Pleurodira Cope, 1865

Family Podocnemididae Cope, 1868

Genus *Shweboemys* Swinton, 1939

**Type Species:** *Shweboemys pilgrimi* Swinton, 1939

**Revised Diagnosis:** Extreme development of the secondary palate with a long medial trough; medial contact of palatines long, almost half of cranial length; palatines has very little basisphenoid contact and very narrowly separates the pterygoids; dermal roof elements of palatines extremely thick.

Type Specimen: Geological Survey of India number 17255, a partial skull (Swinton, 1939; Wood, 1970; Gaffney et al., 2011).

**Type Locality:** “One mile NNE of Mauktet, Shwebo District, Burma” (Swinton, 1939; Wood, 1970; Gaffney et al., 2011).

**Type Horizon:** possibly Khabo Formation (latest Middle Miocene), underlying the Irrawaddy Formation, of Shwebo District of Myanmar (Hirayama et al., 2020), although speculated as 'Irrawaddy Beds, Pliocene or Pleistocene' in Wood (1970) and 'Miocene age cannot now be excluded' in Gaffney et al. (2011).

**Referred specimen:** NMMP-KU-IR-5300, a partial skull (Figs. 3 to 5).

**Locality:** about 3 km northwest to Sanmagyi, Tebingan area, central Myanmar (Fig. 1).

**Horizon:** the lowermost part of the Irrawaddy Formation, or the upper parts of the Obogon- Irrawaddy transition zone (early Late Miocene; Fig. 2).

## Description

This skull is 112 mm long, and 110 mm wide as preserved (Fig. 3). Most of bone sutures are visible. Squamosal., premaxilla, vomer, quadrate, exoccipital, supraoccipital, basioccipital, prootic, and opisthotic are not

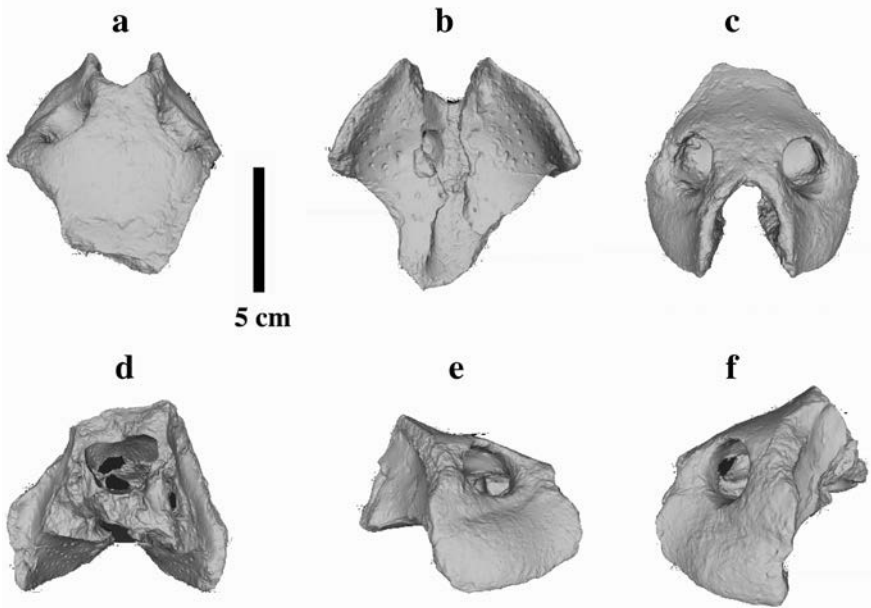


Figure 3. 3D images of Tebingan *Shweboemys*

preserved in NMMP-KU-IR-5300. The parietal contacts the palatine anteroventrally, as in BMNH R.8432, a unique feature shared by *Stereogenys* (Gaffney et al., 2011). Posterior border of the parietal is extremely thick, at least 17 mm in thickness (Fig. 4). The maxilla has rather deep labial ridges which are not well preserved in former two specimens. Both maxilla and palatine developed extensive secondary palate with a narrow median trough only shared by *Stereogenys* (Fig. 3b).

The palatines have a very slight midline contact with the basisphenoid as in BMNH R.8432, separating the pterygoids on the midline (Gaffney et al., 2011). The rostrum basisphenoidale is a rod-like elongate structure as in living Podocnemididae (Gaffney, 1979; Fig. 5).

## Discussion

Turtles except for stem and basal taxa are subdivided into two major groups, cryptodires (Cryptodira) and pleurodires (Pleurodira) (Joyce, 2007;



Figure 4. *Shweboemys* occipital bones



Figure 5. *Shweboemys* braincase@

Schoch and Sues, 2015). Pleurodires, or side-necked turtles, are distinguished from cryptodires by its unique movement of the neck in horizontal plane (Williams, 1950). They first appeared in the Middle Jurassic and mainly flourished at the former Gondwana continent, including Africa, South America, and Australia. Pleurodires have been also reported from India and Myanmar, as this area was a part of Gondwana continent during the Mesozoic age, although they disappeared in Asia during the Neogene (Gaffney et al., 2006, 2011).

Distinctive characters, such as an extreme development of the secondary palate with a long medial trough, the parietal contact with the palatine anteroventrally, and very slight midline contact of palatine with the basisphenoid, show NMMP-KU-IR-5300 is identified as *Shweboemys pilgrimi* Swinton, 1939 (Gaffney et al., 2011). Thus, this is the third skull of *S. pilgrimi*, although no shell materials of the side-necked turtles are hitherto reported from the Neogene deposits of Myanmar.

Its parietal bone is enormously thick, at least 17 mm thick, hitherto unknown character in any pleurodires (Fig. 4). Thickness of the parietal of turtles of this size should be less than 5 mm (Gaffney, 1979). This unique feature might be the reason why only skulls were hitherto discovered for this taxon. Most of fossil materials of turtles are shell remains because of its tough structures, whereas cranial parts are seldom preserved as they are normally very fragile bones (Scheyer et al., 2017). Fossil turtle shells are rather abundant in the Tebingan area and are identified as cryptodires, including the Trionychidae, Carettochelyidae, Goemydidae, and large Testudinidae (Chavasseau et al., 2013; Sonoda et al., in preparation), but no shell remains of pleurodires have been reported to date. Some taxa such as *Meiolania* and *Platysternon*, however, have their fossil records largely biased by cranial bones, as they have very stout skulls, whereas their shells are very thin and fragile in structures (Gaffney, 1983, 1996; Hirayama, 2001). Thus, *Shweboemys* might be another rare case among turtle evolution with unique combination of sturdy skull and fragile shell.

The rostrum basisphenoidale in NMMP-KU-IR-5300 is a rod-like elongate structure as in living Podocnemididae (Gaffney, 1979; Fig. 5). The rostrum basisphenoidale is short and subdivided in most turtles. A rod-like elongate rostrum basisphenoidale has been only known in the Chelonioida (marine turtles) and extant Podocnemididae (Gaffney, 1979; Hirayama, 1998). Thus, this feature could be another synapomorphy of this family, although its functional meaning is unknown.

NMMP-KU-IR-5300 should be the youngest fossil record of the side-necked turtles in Asia, as the former materials of *Shweboemys* were possibly derived from the latest Middle Miocene Khabo Formation. Thus, Asian pleurodires distributed from India to Myanmar are considered to have become extinct by the Late Miocene mainly because of biological competition with

advanced cryptodiran turtles such as the geoemydids and trionychids. NMMP-KU-IR-5300 should be important for understanding the faunal succession of non-marine turtles of Southeastern Asia.

## Conclusion

A new turtle skull (NMMP-KU-IR-5300) from the lowermost Irrawaddy Formation, or the upper parts of the Obogon- Irrawaddy transition zone (early Late Miocene) in the Tebingan area, central Myanmar is identified as the third skull of *Shweboemys pilgrimi*, an extinct pleurodires of Asia, based on its extreme development of the secondary palate. This should be the youngest fossil record of the side-necked turtles in Asia, as the former materials were possibly derived from the latest Middle Miocene Khabo Formation. This specimen shows hitherto unknown unique characters such as extremely thick parietal bones and a rod-like elongate rostrum basisphenoidale. Its thick parietal bones suggest the reason why only skulls have been collected for this taxon. A rod-like elongate rostrum basisphenoidale could be an another synapomorphy of the Podocnemididae.

## Acknowledgements

We would like to especially thank to the Ministry of Culture for the permission of paleontological research in Myanmar. Staff of the Department of Archaeology and National Museum (Yangon), E. S. Gaffney (American Museum of Natural History), and S. Chapman (Natural History Museum at London) helped our research of materials of *Shweboemys*. This research was partially supported by JSPS with Grants-in-Aid for Scientific Research to MT (Nos. 16405018, 20405015 and 26304019).

## References

Chavasseau O., Aung Aung Kyaw, Chaimanee Y., Coster P., Emonet E.-G., Aung Naing Soe, Rugumbrung M., Soe Thura Tun, and Jaeger J.-J. (2013) Advances in the biochronology and biostratigraphy of the continental Neogene of Myanmar. In: Wang X., Flynn L.J., and Fortelius M. (eds.), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*. Columbia University Press, New York, pp. 461–474.



- Gaffney, E.S. (1979) Comparative cranial morphology of recent and fossil turtles. *Bulletin of the American Museum of Natural History*, 164:65-375.
- Gaffney, E.S. (1983) Cranial morphology of the extinct horned turtle, *Meiolania platyceps*, from the Pleistocene of Lord Howe Island. *Bulletin of the American Museum of Natural History*, 175:361-480.
- Gaffney, E.S. (1996) The postcranial morphology of *Meiolania platyceps* and a review of the Meiolaniidae. *Bulletin of the American Museum of Natural History*, 229:1-165.
- Gaffney, E. S., Meylan, P. A., Wood, R. C., Simons, E., and Campos, D. D. (2011) Evolution of the side-necked turtles: the family Podocnemididae. *Bulletin of the American Museum of Natural History*, 350:1-237.
- Gaffney, E. S., Tong, H. and Meylan, P.A. 2006. Evolution of the side-necked turtles: the families Bothremydidae, Euraemydidae, and Araripemydidae. *Bulletin of the American Museum of Natural History*, 300:1-698.
- Hirayama, R. (1998) Oldest known sea turtle. *Nature*, 392:705-708.
- Hirayama, R. (2001) Fossil turtles from the Tsubusagawa Formation (Pliocene) of Ajimucho, Oita Prefecture, northern Kyushu, Japan. *Research Report of the Lake Biwa Museum*, 18:79-96, 7 pls. (in Japanese with English abstract)
- Hirayama, R., Sonoda, T., Takai, M., Thaug-Htike, Zin-Maung-Maung-Thein, and Takahashi, A. (2015) *Megalochelys*: gigantic tortoise from the Neogene of Myanmar. *PeerJ*, Program and abstracts of the 5th Turtle Evolution Symposium, p. 50-51.
- Hirayama, R., Sonoda, T., Takai, M., Thaug-Htike and Zin-Maung-Maung-Thein, (2020) A new side-necked turtle (Order Testudines: Infraorder Pleurodira) from the Neogene of Myanmar. *Abstracts of the 169th Regular Meeting of the Palaeontological Society of Japan*, p. 26. (in Japanese)
- Iijima, M., Takai, M., Nishioka, Y., Thaug-Htike, Zin-Maung-Maung-Thein, Egi, N., Kusuhashi, N., Tsubamoto, T., Kono, R., and Hirayama, R. (2021) Taxonomic overview of Neogene crocodylians in Myanmar. *Journal of Vertebrate Paleontology*, 40 (6) DOI: 10.1080/02724634.2021.1879100, pp. 1-17.
- Joyce, W. G. 2007. Phylogenetic Relationships of Mesozoic Turtles. *Bulletin of the Peabody Museum of Natural History* 48, Issue 1, pp. 3–102.
- Longuet, M., Zin-Maung-Maung-Thein, Thaug-Htike, Man-Thit-Nyein and Takai, M. (2023) New fossil remains of Rhinocerotidae (Perissodactyla) from the early Late Miocene Tebingan area, central Myanmar. *Historical Biology*, DOI: 10.1080/08912963.2023.2218873, pp. 1-14.
- Scheyer, T. M., Syromyatnikova, E. V. and Danilov, I. G. (2017) Turtle shell bone and osteoderm histology of Mesozoic and Cenozoic stem-trionychian Adocidae and Nanhsiungchelyidae (Cryptodira: Adocusia) from Central Asia, Mongolia, and North America. *Fossil Record* 20: 69-85.
- Schoch R.R. and Sues, H.-D. (2015) A new stem-turtle from the Middle Triassic of Germany and the evolution of the turtle body plan. *Nature* 523: 584-587

- Swinton, W.E. (1939) A new fresh-water tortoise from Burma. Records of the Geological Survey of India 74 (4): 548–551.
- Takai, M., Kusuhashi, N., Nishioka, Y., Thaung-Htike, Zin-Maung-Maung-Thein (2018a) Geological setting and transition of the Neogene mammal fauna in central Myanmar. Fossil 103: 5–20. (in Japanese with English abstract)
- Takai, M., Kusuhashi, N., Nishioka, Y., Thaung-Htike, Zin-Maung-Maung-Thein (2018b) Errata of “Takai et al. (2018a) Geological setting and transition of the Neogene mammal fauna in central Myanmar. Fossil 103: 5–20.” Fossil 104: 51–54. (in Japanese)
- Takai, M., Khin Nyo, Kono, R., Thaung-Htike, Kusuhashi, N., Zin-Maung-Maung-Thein (2021) New hominoid mandible from the early late Miocene Irrawaddy Formation in Tebingan area, central Myanmar. Anthropological Science 120 (1): 87–98.
- Williams, E.S. (1950) Variation and selection in the cervical central articulations of living turtles. Bulletin of the American Museum of Natural History, 94:505–602.
- Wood, R.C. (1970) A review of the fossil Pelomedusidae (Testudines, Pleurodira) of Asia. Breviora 357: 1–24.

## Explanation of figures

- Figure 1. Index map of the study area indicating the villages of Tebingan and Sanmagyi. Modified from Longuet et al. (2023).
- Figure 2. Columnar section of the Tebingan area, indicating the vertebrate fossil-bearing horizons (After Takai et al., 2021).
- Figure 3. NMMP-KU-IR-5300, reconstructed 3D images of the skull of *Shweboemys pilgrimi* Swinton, 1939, from the early Late Miocene in the Tebingan area, central Myanmar. a: dorsal view, b: ventral view, c: anterior view, d: occipital view, e: right lateral view, f: left lateral view.
- Figure 4. Occipital view of NMMP-KU-IR-5300, showing its thick cross section of the parietal bones, roofing the braincase.
- Figure 5. Oblique-occipital view of NMMP-KU-IR-5300, showing the braincase, with a rod-like elongate rostrum basisphenoidale.