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RESEARCH **Open Access**

The first fossil loggerhead sea turtle (Cheloniidae: *Caretta*) from the North Pacific and its nannofossil biostratigraphy

Yi-Lu Liaw[1†], Chih-Kai Chuang[2,3†] and Cheng-Hsiu Tsai[1,4*]

Abstract

The Taiwan waters (western North Pacific) include five sea turtle species without an associated fossil record. Here, we describe the first fossil sea turtle from Taiwan. This fossil material is a partial hypoplastron from the uppermost Yuching Shale in Tainan. The preserved morphology of this partial hypoplastron shows a slightly curved medial margin, a deep lateral notch, and a wide sutural anterior margin, indicating a taxonomic affinity to the genus *Caretta*. In comparison with extant *Caretta*, the preserved hypoplastral width at the sutural level (130.85 mm) suggests that this fossil belongs to an old subadult cf. *Caretta*. In addition, we also analyzed fossil foraminifera from the matrix of this hypoplastron, suggesting that the depositional environment was a continental shelf no more than 100 m deep. We further examined the nannofossils and found more than 200 calcareous nannofossils, including index fossils, such as *Pseudoemiliania lacunosa*, *Helicosphaera sellii*, and large *Gephyrocapsa* sp. (> 5.5 μm), corresponding to NN19a nannofossil biozone (Early Pleistocene in age). Given the first occurrence of the large *Gephyrocapsa* sp. and the last occurrence of *Helicosphaera sellii*, we narrowed down the age of this Pleistocene sea turtle from Taiwan to 1.57 to 1.28 million years ago. Our discovery of this Pleistocene sea turtle fossil represents not only the first cheloniid fossil in Taiwan but also the first well-dated fossil sea turtle from the global Pleistocene. The Taiwan waters during the Early Pleistocene may be a paleo-foraging ground for cf. *Caretta*, and future fieldwork and analysis should reveal a more detailed evolutionary history of sea turtles in the North Pacific. Our results also highlight the potential for more paleontological progress from Taiwan.

Keywords Calcareous nannofossil, Early Pleistocene, Foraminifera, Fossil record, Taiwan

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Introduction

Sea turtles (Chelonioidea), including six extant species of hard-shelled sea turtles (Cheloniidae) and the leatherback sea turtle (Dermochelyidae), are eye-catching creatures and occupy important ecological roles in marine ecosystems. Their evolutionary history can be traced back to the Early Cretaceous, and sea turtles survived the end-Cretaceous mass extinction (Hirayama, 1998; Motani & Vermeij, 2021). Sea turtles include some iconic features, such as paddle-like forelimbs and a lightweight shell. Cheloniid shells retain the large fontanelles in adulthood, and dermochelyid shells consist of slender plastral elements and thousands of carapacial ossicles (Wyneken, 2013). Numerous studies of the stem and crown sea turtles clearly show a much higher diversity prior to the Pleistocene (Cretaceous: Hirayama, 1998; Lehman & Tomlinson, 2004; Menon et al., 2024; Paleogene: Weems & Sander, 2014; Gard & Fordyce, 2017; Weems & Brown, 2017; Zvonok et al., 2019; and Neogene: Parham & Pyenson, 2010; Fitzgerald & Kool, 2015). By contrast, Quaternary or Pleistocene sea turtles are poorly known, hampering our understanding of the origin of extant sea turtles and the establishment of their modern ecological roles.

Located in the tropical and subtropical region of the western North Pacific with abundant deposits of the exposed Pleistocene sediments, the Taiwan waters likely included a high marine biodiversity during the Pleistocene, which is key to understanding the origin of modern biodiversity. Recent progress of marine fossils from the Pleistocene of Taiwan has shown the potential for a reconstruction of paleobiodiversity, such as marine invertebrates (Kiel et al., 2024), fishes (Lin et al., 2021), sea birds (Wu et al., 2023) and marine mammals (Tsai & Chang, 2019; Tsai et al., 2013). Yet, there remains no fossil sea turtle from Taiwan, despite the occurrence of five extant sea turtles in the Taiwan waters (TTWG, 2021). Here we describe the very first sea turtle fossil from Taiwan, which includes the anterior part of a hypoplastron and shows a close morphological similarity to the loggerhead sea turtle (*Caretta caretta*). Our detailed examination of calcareous nannofossils suggests the Early Pleistocene in age. This discovery of a Pleistocene cf. *Caretta* from Taiwan should encourage more finds to elucidate the evolutionary history of sea turtles and the turnover of marine ecosystems in the western North Pacific.

Locality and geological horizon

NTUM-VP 220325 was collected by LC Wang (a private collector) from Yuching Shale on the river bank (23° 07′ 30"N, 120° 27′ 12"E) of Zengwen River near Yufeng Bridge, Tainan City (Fig. 1A). Its geological horizon approximates the uppermost part of Yuching Shale, which is mainly composed of thick mudstone and sandy mudstone (Fig. 1B, C). The age of Yuching Shale (Fig. 1D) corresponds to the uppermost Liuchungchi Formation (also called Liuchungsi Formation) and the middle upper Gutingkeng Formation (also called Kutingkeng Formation) in southern Taiwan (Ho et al., 2005). Before the Central Geological Survey published the Geological Map of Taiwan in the 2000s, Yuching Shale had long been regarded as part of the Liuchungchi Formation (Hu & Tao, 2000, 2004). Microfossils and fragments of invertebrates are extremely abundant. Trace fossils, carbonized wood fragments, and cuttlebones are also present. In addition to our observations, fossil fishes and invertebrates (e.g., bivalves, crabs, colonial corals, gastropods, oysters, sea urchins) have also been reported from this area (e.g., Hsu et al., 2024; Hu & Tao, 2004; Lin et al., 2021). The geological age of the uppermost Yuching Shale has been debated; whether it belongs to the NN19a nannofossil biozone of the Early Pleistocene (Ho et al., 2005) or the NN19b nannofossil biozone (Chen, 2016) remains unresolved. We then carefully examined the calcareous nannofossils from the sediments associated with NTUM-VP 220325, which supports the Early Pleistocene in age (NN19a nannofossil biozone).

Materials and methods

We collected the sediments of the Yuching Shale from the field site and the matrix of NTUM-VP 220325 to analyze the depositional environment and to assess the geological age. The sediments larger than 63 μm were sieved and dried in the 50℃ oven. The dried samples were examined under a light microscope at 10× to 63× magnification. The sediments smaller than 63 μm from the matrix of NTUM-VP 220325 were sieved and prepared as smear slides. The slides were examined under a Zeiss Axioskop Polarizing Microscope at 1,600× magnification and photographed with a digital CCD of the microscope. Over 200 individuals of calcareous nannofossils were identified in this study. Taxonomy of nannofossils follows Perch-Nielsen (1985) and Hine and Weaver (1998). Identification of the index nannofossil *Gephyrocapsa* follows Raffi et al. (1993). The biostratigraphic age follows the Western Pacific core ODP Hole 1115B from Chuang et al. (2018).

For comparison with NTUM-VP 220325, we collected 14 sea turtle specimens in Taiwan, including seven *Chelonia mydas* (green turtle), three *Lepidochelys olivacea* (olive ridley sea turtle), two *Eretmochelys imbricata* (hawksbill sea turtle), one *Caretta caretta* (loggerhead sea turtle), and one *Dermochelys coriacea* (leatherback sea turtle). Eleven individuals were found dead on shore, and the other three died during the rescue. We then

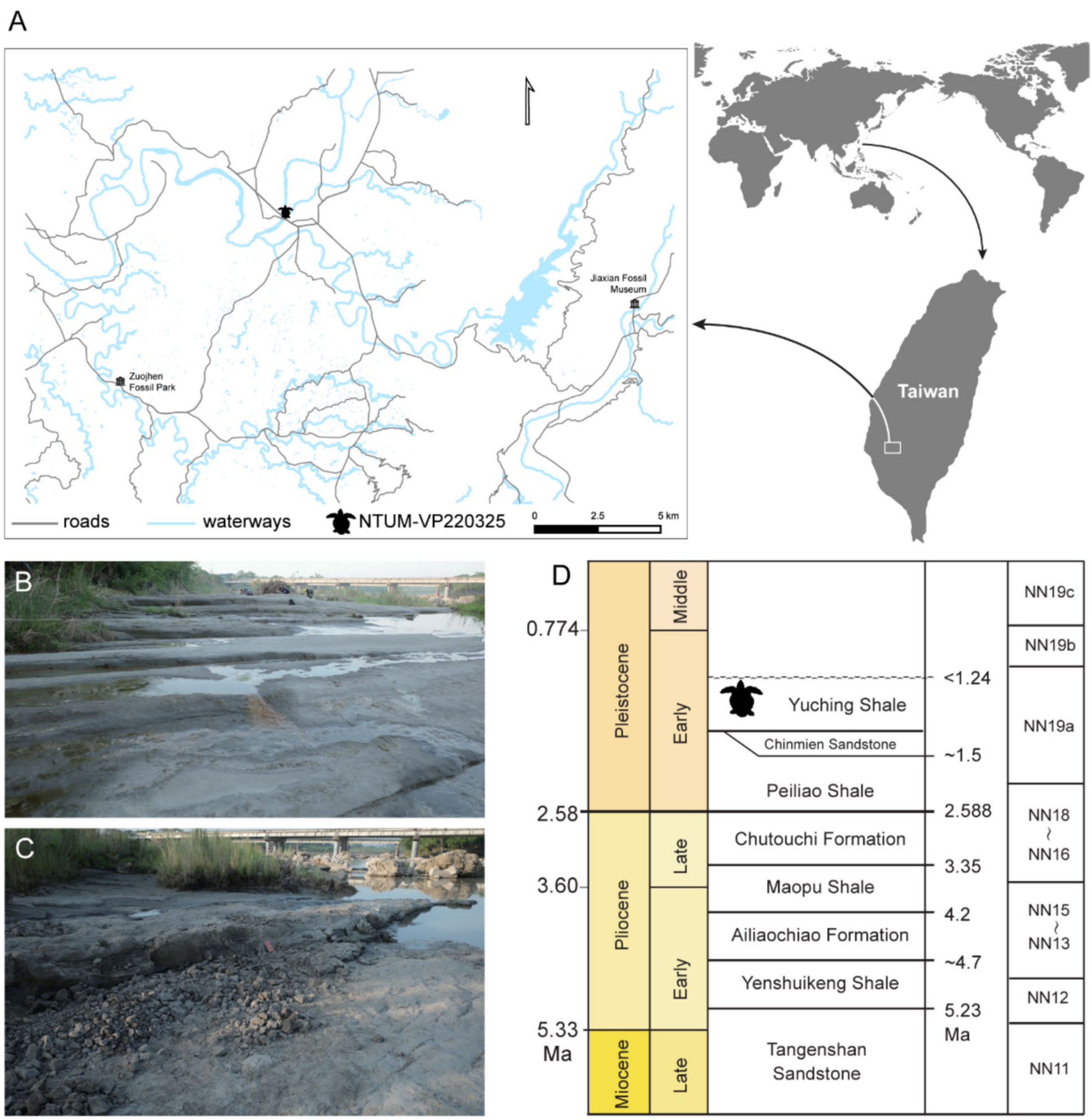

Fig. 1 The occurrence of the fossil cheloniid NTUM-VP 220325 from the Early Pleistocene of Taiwan. **A** Locality of the cheloniid hypoplastron, NTUM-VP 220325; **B**, **C** Photographs of the Yuching Shale outcrop, where NTUM-VP 220325 was collected from; **D** Generalized stratigraphic column. Vector data of rivers and roads were obtained from OpenStreetMap via the BBBike extract service (BBBike.org, 2024; OpenStreetMap contributors, 2024). Mapping and spatial analysis were conducted using QGIS (QGIS Development Team, 2024)

prepared the osteological specimens for morphological comparison.

Systematic paleontology

Testudines Batsch, 1788
Cryptodira Cope, 1868
Chelonioidea Baur, 1893
Cheloniidae Cope, 1867
Carettini Zangerl & Turnbull, 1955
Caretta Rafinesque, 1814
cf. *Caretta* sp.

Type species. *Caretta caretta* Linnaeus, 1758.

Referred specimen. NTUM-VP 220325, a partial right hypoplastron (Fig. 2A). The high-resolution 3D model of NTUM-VP 220325 is associated with this article online and freely available. The specimen was found by

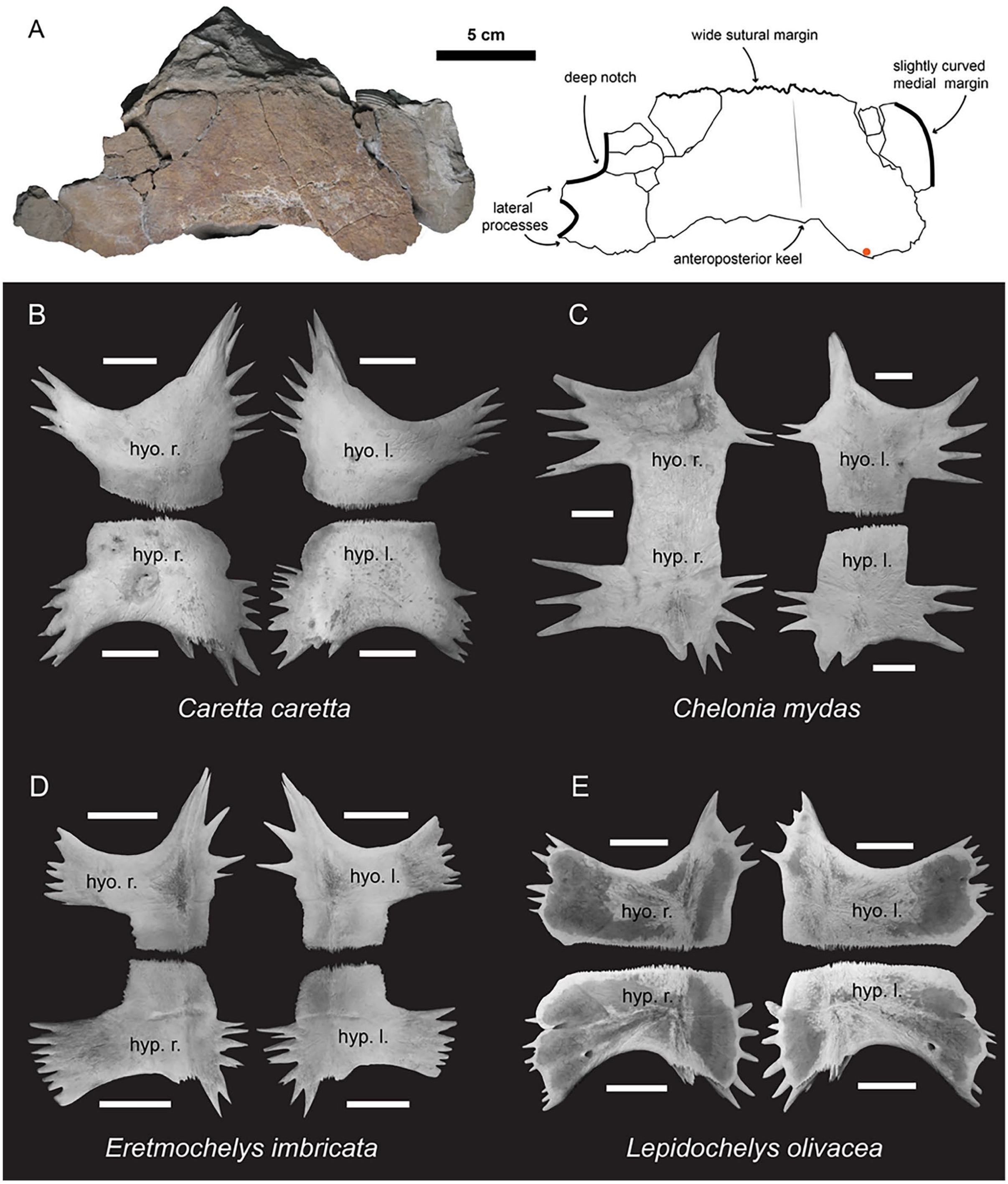

Fig. 2 Ventral views of the fossil and extant hyoplastra and hypoplastra of cheloniids. **A** Photograph and anatomical interpretations of the Pleistocene cf. *Caretta* (NTUM-VP 220325) with an orange point indicating where we measured the thickness; **B** *Caretta caretta* (NTUM-VP 2211081); **C** *Chelonia mydas* (NTUM-VP 2503251); **D** *Eretmochelys imbricata* (NTUM-VP 2503252); **E** *Lepidochelys olivacea* (NTUM-VP 2205281). *hyo.* Hyoplastron, *hyp.* Hypoplastron, *l.* left sided, *r.* right sided. Scale bar = 5 cm.

the private collector LC Wang and then donated to the author (Cheng-Hsiu Tsai, CHT) for permanent curation and research.

Description and comparison. NTUM-VP 220325 is a partial, flat (6.50 mm thickness, see Fig. 2 for the specific measured point) hypoplastron with a rough and textured ventral surface. The posterior margin of NTUM-VP 220325 is missing. A longitudinal keel runs along hypoplastron anteroposteriorly (Fig. 2A), as commonly seen in the Cheloniidae members. The wide hyo-hypoplastral suture indicates a relatively small lateral fontanelle (Fig. 2A), precluding the possibility that NTUM-VP 220325 belongs to *Chelonia mydas* (Fig. 2C) or *Eretmochelys imbricata* (Fig. 2D). A notch on the lateral side of NTUM-VP 220325 is much more prominent and deeper than that of *Lepidochelys olivacea* (Fig. 2E), but similar to that of a subadult *Caretta caretta*, NTUM-VP 2211081 (Fig. 2B). Posterior to the notch, two lateral processes are preserved; the tip of the anterior one is missing and the posterior one remains covered by the matrix. The slightly curved margin of the medial side is also comparable to the subadult *Caretta caretta*, NTUM-VP 2211081 (Fig. 2B). A notable difference between NTUM-VP 220325 and extant *Caretta caretta* is the thickness of the hypoplastron: 6.5 mm in the fossil specimen, NTUM-VP 220325, much thinner than extant subadult *Caretta caretta* (NTUM-VP 2211081, more than 10 mm), which likely represents an variation of this lineage. Publications and several specimens (i.e. USNM HERP 214140 and NHMUP B 32) indicate that adult *Caretta caretta* have a hypoplastron with a shallow lateral notch (Dodd, 1988), which differs from the subadult individuals (Fig. 6 of Valente et al., 2006 and Fig. 2B).

Overall, NTUM-VP 220325 is similar to a subadult *Caretta caretta*. We preclude the possibility of NTUM-VP 220325 belonging to the lineages of extant *Natator* (Australia), which is characterized with a large central fontanelle and closed lateral fontanelles (Fig. 16 of Zangerl et al., 1988). Similarly, given the limited materials and geological disparity, NTUM-VP 220325 unlikely belongs to the Miocene occurrence of extinct *Syllomus* (Fig. 20 of Hasegawa et al., 2005) and *Procolpochelys* (Fig. 3 of Hirayama & Nakagawa, 2012). Combining all the available morphological evidence (a wide hyo-hypoplastral suture and a deep notch on the anterolateral margin) and its geological age (Early Pleistocene), we identified NTUM-VP 220325 as cf. *Caretta* sp.

Remark.

The width at the sutural level of NTUM-VP 220325 is at least 130.85 mm, which is wider than that of NTUM-VP 2211081 (extant *Caretta caretta* specimen, 100.7 mm; Fig. 2B). According to previous studies of extant *Caretta caretta* (Dodd, 1988; Ishihara & Kamezaki, 2011; Witherington & Witherington, 2024), NTUM-VP 2211081 with a straight carapace length (SCL) 64.3 cm long, a curved carapace length 67 cm long, and a body mass 38.4 kg, likely belongs to a young subadult (between 10 to 30 years old). The Pleistocene cf. *Caretta* sp. NTUM-VP 220325 from Taiwan is at least 30 mm longer than that of NTUM-VP 2211081 at the hyo-hypoplastral suture, and its morphology is similar to subadult instead of adult specimens (see Description and comparison section), indicating that NTUM-VP 220325 was likely an old subadult cf. *Caretta* with a SCL no longer than 90 cm.

Results and discussion

First fossil cheloniid from Taiwan

The fossil hypoplastron NTUM-VP 220325 from the uppermost Yuching Shale shows *Caretta* affinities in the wide hyo-hypoplastral sutural margin, the deep notch on the lateral side, and the slightly curved margin of the medial side (Fig. 2A, B), and most likely belongs to a subadult cf. *Caretta*, given the preserved size. The thickness of NTUM-VP 220325 is much thinner than that of extant *Caretta caretta*. The thickness of the plastron in sea turtles is related to protection against potential predators, resistance to high pressure, and muscle attachments for locomotion and respiration (Pritchard, 2007). Interestingly, extant *Caretta caretta* are durophagous and primarily consume hard-shelled prey (Molter et al., 2022). A sturdy plastron with associated strong jaw and musculature (Jones et al., 2012) provides powerful bites to crush the hard-shelled prey. Due to the limited evidence, it remains uncertain whether NTUM-VP 220325 with a thinner hypoplastron represents a distinct species from extant *Caretta caretta* or occupies a disparate niche. Future fieldwork and discoveries of more complete sea turtle fossils from the Pleistocene will likely reveal the Pleistocene ecosystem in the marine realm.

NTUM-VP 220325 represents the very first fossil cheloniid from Taiwan. Interestingly, *Caretta caretta* have been documented with foraging behaviors in the Taiwan waters (TTWG, 2021), but the sea turtle sighting project in Taiwan with more than three thousand data points only recorded one dead *Caretta caretta* (Hoh et al., 2022). Further, *Caretta caretta* included only 7% of stranding/bycatch, which was significantly lower than *Chelonia mydas* at 83%, based on the stranding/bycatch reports in Taiwan (Cheng et al., 2019). This disparity likely results from the fact that the Taiwan waters nowadays are the nesting and foraging grounds of *Chelonia mydas* (Cheng et al., 2018; Fong et al., 2025). Given the abundant hard-shelled invertebrates in the Yuching Shale associated with NTUM-VP 220325, we hypothesize that the Taiwan waters during the Early Pleistocene might also be the foraging ground of cf. *Caretta*. The discovery of more fossil sea turtles would help test this hypothesis and further elucidate the faunal turnover in the western North Pacific.

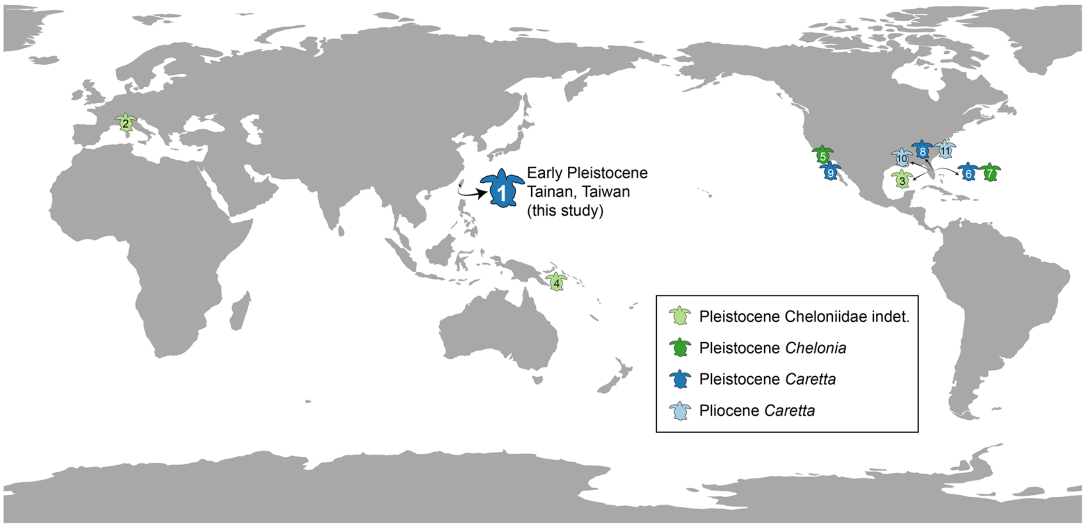

Fig. 3 Global distribution of the genus *Caretta* from Pliocene and fossil sea turtles from Pleistocene; see Table 1 for the data sources. The vector data were downloaded from Natural Earth (2024). Mapping was conducted using QGIS (QGIS Development Team, 2024)

A Pleistocene sea turtle dated with calcareous nannofossils

The extant cheloniids occur in tropical to temperate waters worldwide (TTWG, 2021), but the evolutionary history of this lineage remains poorly known due to the extremely rare Pleistocene sea turtle fossils (Fig. 3; Table 1). The Pleistocene sea turtle record includes *Chelonia* and *Caretta* from North America, but no detailed description was provided. Prior to Pleistocene, the confirmed fossils of the genus *Caretta* were from the Pliocene of southeastern North America (Fig. 3). From the Early Pliocene (4.5 to 5 Ma) of Florida, Dodd and Morgan (1992) reported several *Caretta* materials, including at least seven individuals. Zug (2001) described a nearly complete skull from the Early Pliocene of North Carolina and established a new species, *Caretta patriciae*. Additional fossil taxa from the Eocene and Miocene of Europe and northern Africa are regarded as *Caretta* or *Caretta caretta*, but their taxonomic assignments remain problematic and require detailed re-examination (see Dodd, 1992a, b). Interestingly, Lockley et al. (2019) found the possible hatchlings trackways of *Caretta caretta* from the Late Pleistocene of South Africa. Clusa et al. (2013) estimated a Pleistocene colonization of the Mediterranean population of *Caretta caretta* according to the genetic approach, but there remains no fossil evidence to support this hypothesis. Our review here shows the limited

Table 1 Compilation of the Pleistocene sea turtles and Pliocene *Caretta* across the globe

	Identification	Material	Region/Country	Geological age	References
1	cf. *Caretta* sp.	Shell element (hypoplastron)	Taiwan	Early Pleistocene	This study
2	Cheloniidae indet	Shell element	Bergeggi, Italy	Quaternary	Chesi & Delfino (2006:107)
3	Cheloniidae indet	Shell element (hypoplastron)	Florida, USA	Early Pleistocene	Hulbert and Morgan (1989, Table 1)
4	"*Chelone*" *murua* (*nomen dubium*)	Post-cranial and shell elements	Papua New Guinea	Pleistocene?	Turtle Extinctions Working Group (2015)
5	*Chelonia mydas*	Post-cranial element (carapace)	California, USA	Late Pleistocene	Hudson and Brattstrom (1977:19)
6	*Caretta caretta*	Skull (squamosal)	Florida, USA	Pleistocene	Hay (1917:43)
7	*Chelonia mydas*	Post-cranial element (humerus)	Florida, USA	Pleistocene	Hay (1917:44)
8	*Caretta caretta*	Shell element (costal)	Florida, USA	Early to Middle Pleistocene	Morgan and Portell (1996, Table 1)
9	*Caretta caretta*	Shell element (hypoplastron, parts of carapace or plastron)	Cedros Island, Mexico	Terminal Pleistocene	Des Lauriers (2006)
10	*Caretta* sp.	Skull, mandibles, and shell elements	Florida, USA	Early Pliocene	Dodd and Morgan (1992)
11	*Caretta patriciae*	Skull	North Carolina, USA	Early Pliocene	Zug (2001)

Fig. 3 for the global distribution of the fossil sea turtles

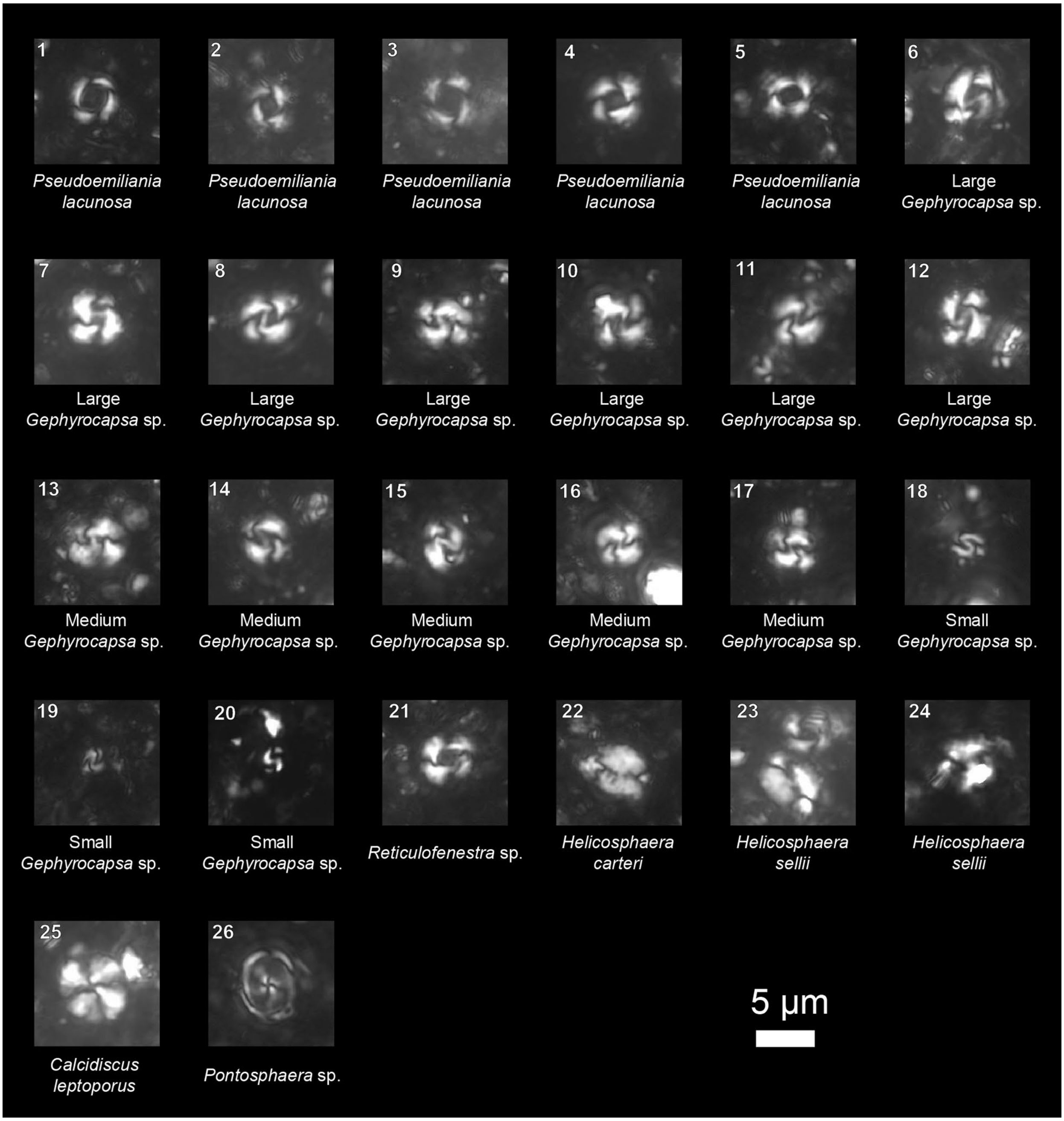

Fig. 4 Calcareous nannofossils identified under 1600 × polarizing microscopy in the matrix of NTUM-VP 220325 from Yuching Shale. 1–5, *Pseudoemiliania lacunosa*; 6–12, Large *Gephyrocapsa* sp.; 13–17, Medium *Gephyrocapsa* sp.; 18–20, Small *Gephyrocapsa* sp.; 21, *Reticulofenestra* sp.; 22, *Helicosphaera carteri*; 23–24, *Helicosphaera sellii*; 25, *Calcidiscus leptoporus*; 26, *Pontosphaera* sp. Scale bar = 5 μm.

fossil evidence for the *Caretta* lineage globally (Fig. 3). Our discovery of the Pleistocene cf. *Caretta* from southern Taiwan opens up a new potential area to reveal the evolutionary history of this sea turtle lineage and represents the first well-described Pleistocene sea turtle with a detailed survey of the planktonic foraminifera and calcareous nannofossils.

We collected and identified several shallow sea benthic foraminifera, such as *Operculina ammonoide*, *Pseudorotalia* sp., and the cupuladriids bryozoans, from the uppermost Yuching Shale. This composition suggests that the depositional environment was a continental shelf no more than 100 m deep (Gallagher et al., 2009). Also, the calcareous nannofossils from the matrix associated with the fossil hypoplastron NTUM-VP 220325 include *Pseudoemiliania lacunosa*, *Reticulofenestra* sp., *Helicosphaera carteri*, *Helicosphaera sellii*, *Calcidiscus leptoporus*, *Pontosphaera* sp., and three size groups of *Gephyrocapsa* sp. (Fig. 4). The presence of index fossils, such as *Pseudoemiliania lacunosa*, *Helicosphaera sellii*, and large *Gephyrocapsa* sp. (> 5.5 μm), corresponds to NN19a nannofossil biozone (Fig. 5), indicating the Early Pleistocene in age (Hine & Weaver, 1998). Our results, therefore, supported the conclusions of Ho et al. (2005), instead of Chen (2016), who claimed that the uppermost of Yuching Shale falls within the NN19b nannofossil biozone. According to the last local occurrence of *Helicosphaera sellii* at 1.28 Ma (million years ago) and the first local occurrence of large *Gephyrocapsa* sp. at 1.57 Ma (Chuang et al., 2018), We further narrowed down the geological age of NTUM-VP 220325 to 1.57 to 1.28 Ma (Fig. 5). The geological age immediately precedes the Middle Pleistocene Transition (1.25–0.75 Ma), a time when ice age cycles shifted from 41 thousand years (kyr) to 100 kyr (See ODP Hole 1115B *Trilobatus sacculifer* $\delta^{18}O$ in Fig. 5 for the changes of climate periodicity and long-term cooling). Studies show that this event is most likely triggered by the change in the atmosphere CO_2 levels and ocean carbon cycle (Herbert, 2023). Our finding on the composition of planktonic foraminifera from the uppermost Yuching Shale could shed light on the ecological changes in the marine plankton communities in the western North Pacific. Our study also highlights the potential of more paleontological discoveries in Taiwan and nearby areas to explore the evolution and turnover of the marine biodiversity and ecosystem in the western North Pacific.

Conclusions

Our study confirms that a fossil hypoplastron from the Early Pleistocene (1.57–1.28 Ma) belongs to a cf. *Caretta* subadult, and this fossil record represents not only the first fossil sea turtle from Taiwan but also the first well-dated sea turtle fossil from the Pleistocene.

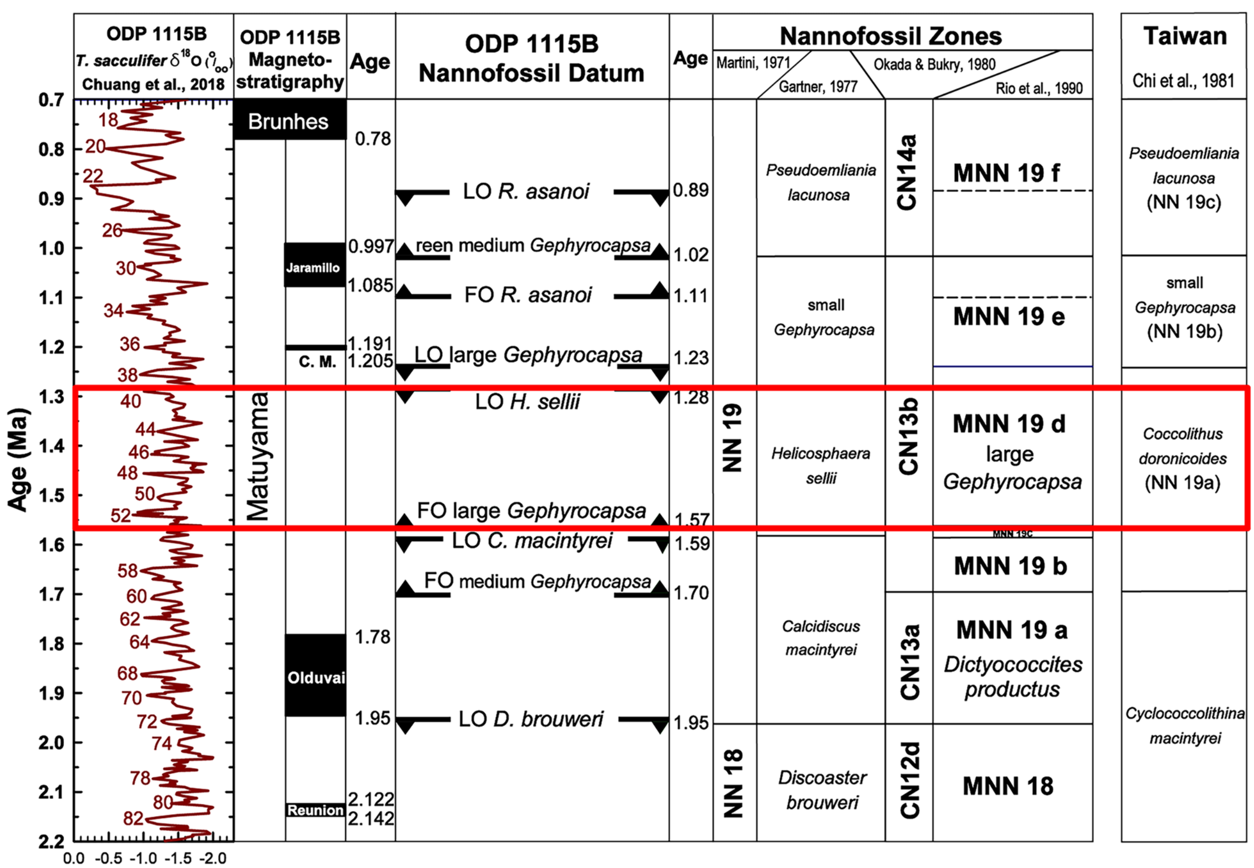

Fig. 5 Pleistocene calcareous nannofossils biozonation. The nannofossil zones follow Martini (1971), Gartner (1977), Okada and Bukry (1980), and Rio et al. (1990), and Taiwan nannofossil biozone (Chi et al., 1981). The marine oxygen isotope chronostratigraphic framework and magnetostratigraphy follow Chuang et al. (2018). *C. M.* Cobb Mountain, *CN.* Calcareous nannofossil, *FO.* first occurrence, *LO.* last occurrence, *MNN.* Mediterranean Neogene nannofossils, *NN.* Neogene nannofossils, reen., re-entrance

The thin hypoplastron of this new fossil differs from extant *Caretta caretta*, likely resulting from variation among this clade. We further propose that cf. *Caretta* likely foraged in the Taiwan waters during the Early Pleistocene, given the abundant fossil invertebrates from the same locality. Future fieldwork and more in-depth analyses promise to uncover the previously unknown evolutionary history of the marine ecosystem in the western North Pacific.

Abbreviations

GSMMA	Geological Survey and Mining Management Agency (previously Central Geological Survey), Taipei, Taiwan
NMB	Naturhistorisches Museum Basel, Basel, Switzerland
NHMUP	Natural History Museum University of Pisa, Pisa, Italy
NMMBA	National Museum of Marine Biology and Aquarium, Pingtung, Taiwan
NTOU	National Taiwan Ocean University, Keelung, Taiwan
NTUM-VP	Vertebrate Paleontology (Laboratory of Evolution and Diversity of Fossil Vertebrates), Museum of Zoology, National Taiwan University, Taipei, Taiwan
SDNHM	San Diego Natural History Museum, San Diego, United States
TCS	Taiwan Cetacean Society, New Taipei, Taiwan
USNM HERP	National Museum of Natural History, Smithsonian Institution, Division of Amphibians and Reptiles, Washington, D.C., United States

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13358-025-00392-3.

Supplementary material 1.

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Author contributions

CHT conceived and designed the research. YLL collected and analysed the sea turtle data. CKC collected and analysed the microfossil data. All authors discussed, wrote, and reviewed the drafts of the manuscript and approved the final submission.

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Data availability

No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate

All the procedures follow the Wild Conservation Act 2013 in Taiwan, with the consent of Ocean Affairs Council (applied 20 Apr. 2022, No. 1110040459 & 1110003950). No animals were harmed in this study.

Competing interests

The authors declare no competing interests.

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