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Source: Mammal Study, 49(2) : 145-149

Published By: Mammal Society of Japan

URL: <https://doi.org/10.3106/ms2023-0070>

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Rediscovery of type specimens of *Nesorhinus hayasakai* (Mammalia, Rhinocerotidae) from the Pleistocene of Taiwan

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Published online 18 December, 2023; Print publication 30 April, 2024

Abstract. Historically, the excavation in the 1970s and publication in the 80s of *Rhinoceros sinensis hayasakai* (now known as *Nesorhinus hayasakai*) represents a milestone in vertebrate paleontology in Taiwan. However, the type materials (including 22 syntypes) are missing after the 1984 publication due to the lack of proper curation and management and reflect the undervalued vertebrate paleontology in Taiwan. Here we found five original specimens out of 22 in two collections (National Taiwan University and Tainan City ZuoJhen Fossil Park). The original 22 specimens were recovered from two geographical localities and geological horizons: northern (Taoyuan, Tunghsiao Formation: Early Pleistocene) and southern (Tainan, Chiting Formation: Middle Pleistocene) Taiwan. Our rediscovery of long-forgotten type materials emphasizes the importance of proper specimen curation. Similarly, by clarifying the historical issues and collecting more fossils, vertebrate paleontology from Taiwan promises to offer novel perspectives to understand the origin of modern biodiversity and large-scale extinctions along the eastern margin of Eurasia.

Key words: island extinction, megafauna extinction, rhinoceros, type materials.

Historically, the discovery of *Rhinoceros sinensis hayasakai* Otsuka and Lin 1984 represents a milestone in vertebrate paleontology in Taiwan. The excavation along the Tsailiao River in Tainan in 1971 and 1972 led by Taiwan Provincial Museum (now known as National Taiwan Museum), National Taiwan University, and paleontologists from Japan (including one of our coauthors, H. Otsuka) is the first formal, large-scale international paleontological endeavor in Taiwan, which resulted in the establishment of a new subspecies of rhinoceros, *R. s. hayasakai* (Otsuka and Lin 1984), based on historic materials from the Early Pleistocene of Taoyuan (Hayasaka 1942) and the newly-collected specimens from the Middle Pleistocene of Tainan by the international collaboration in the 1970s, totaling at least five individuals. Otsuka and Lin (1984) did not designate a holotype for *R. s. hayasakai*; all described materials were then syntypes. Recently, Antoine et al. (2022) designated “Specimens 1 and 2” (originally also labelled as DGNTU-FV11a and DGNTU-FV11b; see Table 1) of

Otsuka and Lin (1984) as lectotype based on figures from the publications instead of examining the specimens first-hand (the remaining twenty specimens listed by Otsuka and Lin [1984] then became paralectotypes) and recognized the taxon as *Nesorhinus hayasakai* (Antoine et al. 2022).

In the original publication, Otsuka and Lin (1984) listed 22 specimens in total stored in three institutions (Table 1): National Taiwan University, Taiwan Provincial Museum (now known as National Taiwan Museum), and Tainan Prefectural Fossil Museum (now known as Tainan City ZuoJhen Fossil Park), and one private collection (Mr. M. S. Su). However, the ownership of newly excavated materials along the Tsailiao River in Taiwan in the early 1970s remains uncertain (likely due to the initial discovery by the local private collectors) even after the 1984 publication. The uncertain whereabouts of the type materials from Tainan resulted in multiple requests from Tainan City Government to National Taiwan Museum to return the type materials (links to two

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Table 1. List of all 22 original specimens (syntypes) of *Nesorhinus hayasakai* from the Pleistocene of Taiwan and their present status

Original specimen number in 1984	Preserved material	Locality	Geological horizon	Possible original institution	Status
Specimen 1 or DGNTU-FV11a (now known as NTUGeo-10901)	Right maxilla with P3–M3	Taoyuan (northern Taiwan)	Tunghsiao Fm. (Early Pleistocene)	NTUGeo	Lectotype*, rediscovered by this study
Specimen 2 or DGNTU-FV11b	Left maxilla with P1–M2	Taoyuan (northern Taiwan)	Tunghsiao Fm. (Early Pleistocene)	NTUGeo	lectotype, missing
Specimen 3	Left mandible with m1–m3	Taoyuan (northern Taiwan)	Tunghsiao Fm. (Early Pleistocene)	NTUGeo	paralectotype, missing
Specimen 4	Right maxilla with P1–M3	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	NTM	paralectotype, missing
Specimen 5	Left mandible with incisor–m3	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	NTM	paralectotype, missing
Specimen 6	Left humerus	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	NTM	paralectotype, missing
Specimen 7	Right humerus	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	NTM	paralectotype, missing
Specimen 8	Left ulna	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	NTM	paralectotype, missing
Specimen 9	Right ulna	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	NTM	paralectotype, missing
Specimen 10	Left radius	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	NTM	paralectotype, missing
Specimen 11	Left femur	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	NTM	paralectotype, missing
Specimen 12	Right femur	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	NTM	paralectotype, missing
Specimen 13	Left tibia	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	NTM	paralectotype, missing
Specimen 14	Right tibia	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	NTM	paralectotype, missing
Specimen 15, or PC-116	Left mandible with m1–m3	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	ZFP	paralectotype, missing
Specimen 16, or PC-117 (now known as ZFP-R0002)	Left mandible with p4–m2	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	ZFP	paralectotype, rediscovered by this study
Specimen 17, or PC-119	Left M1	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	ZFP	paralectotype, missing
Specimen 18, or PC-121	Right m2	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	ZFP	paralectotype, missing
Specimen 19, or CM-001 (now known as ZFP-R0001)	Left mandible with p4–m2	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	ZFP	paralectotype, rediscovered by this study
Specimen 20, or CM-002	Right m1	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	ZFP	paralectotype, missing
Specimen 21, or YB-001 (now known as ZFP-R0003)	Right mandible with m1–m2	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	ZFP	paralectotype, rediscovered by this study
Specimen 22 (now known as ZFP-R0114)	Left M1	Tainan (southern Taiwan)	Chiting Fm. (Middle Pleistocene)	private collection	paralectotype, rediscovered by this study

*Antoine et al. (2022) designated the lectotype and other specimens became paralectotypes. Fm: formation.

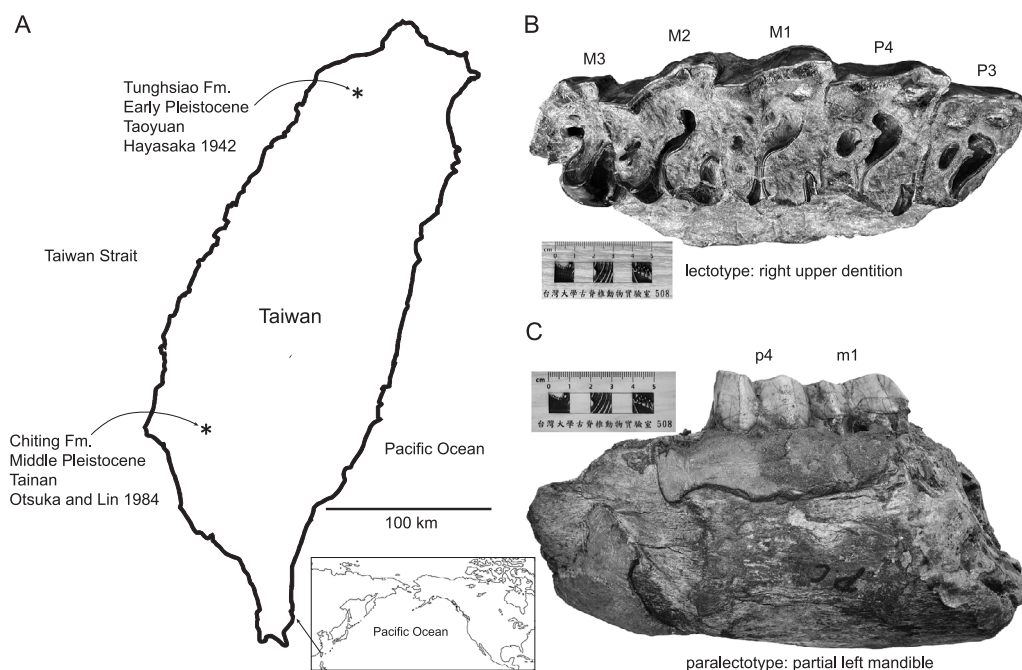


Fig. 1. Map and relocated type materials of *Nesorhinus hayasakai*. A, two localities for the type materials of *Nesorhinus hayasakai*; B, occlusal view of NTUGeo-10901 (previously known as specimen 1 or DGNTU-FV11a) from the Pleistocene of Taoyuan, the lectotype in the NTU collection; C, lateral view of ZFP R0002 (previously known as “specimen 16”) from the Pleistocene of Tainan, a paralectotype in the ZFP collection.

nationwide online news requesting the original specimens back to Tainan: a 2011 report (<https://www.chinatimes.com/amp/newspapers/20110427000585-260107>, Accessed 17 October 2023) and a 2019 account (<https://news.ltn.com.tw/news/life/breakingnews/2896302>, Accessed 17 October 2023). This taxonomic note aims to correct the initial misunderstanding of specimen curation from the excavation in the 1970s and to document our rediscovery of five type materials (out of 22 specimens) of *N. hayasakai*.

Materials and methods

No holotype was designated in the original publication (Otsuka and Lin 1984), making all the described materials syntypes. Recently, Antoine et al. (2022) designated DGNTU-FV11a and DGNTU-FV11b (right and left upper dental series from the same individual, according to Hayasaka 1942) as lectotype. However, the lectotype designation by Antoine et al. (2022) was based on published figures in the literature instead of examining the actual specimens. Our intense search for the original materials shows that DGNTU-FV11b is likely lost, and we found DGNTU-FV11a is now catalogued as NTU-Geo 10901. In addition, four paralectotypes are relocated in the collection of Tainan City

Zuojhen Fossil Park; see Table 1 for the details and status of the 1984 specimens. To avoid problematic specimen curation and facilitate future research, we 3D-scanned the rediscovered type materials and uploaded all the files for free access on the Zenodo data repository: <http://zenodo.org/record/8419681> (DOI: 10.5281/zenodo.8419681).

Institutional Abbreviations: NTM, National Taiwan Museum, Taipei, Taiwan (previously known as Taiwan Provincial Museum); NTUGeo, Geo-specimen Cottage, Department of Geosciences, National Taiwan University, Taipei, Taiwan; ZFP, Tainan City Zuojhen Fossil Park, Tainan, Taiwan (previously known as Tainan Prefectural Fossil Museum).

Results

We extensively searched for the long-missing type materials of *N. hayasakai* (= *R. s. hayasakai*, including 22 specimens) in various museum/university collections and confirmed the existence of five original specimens in two collections (Fig. 1; Table 1): National Taiwan University and Tainan City Zuojhen Fossil Park (see Table 1 for detailed information). Both collections have been indicated in the Otsuka and Lin (1984) publication as the original repositories, but only one for NTU

(should have included three) and four for ZFP (should have included seven), strongly indicating the lack of proper curation of fossil materials. Of note, we also found ‘Specimen 22’, which was the only specimen in the private collection in 1984, but this specimen was accidentally purchased by Tainan City ZuoJhen Fossil Park (without knowing the identity of being a syntype) in 2018. By stark contrast, the NTM collection should have included 11 specimens of the type materials from the Pleistocene of Tainan as listed by Otsuka and Lin (1984), but none of them could have been found in the collection. This unexpected result supports our initial hypothesis that the ownership of those fossil materials remains problematic because the fossil was found and partially collected by private collectors. The National Taiwan Museum (including National Taiwan University), during the excavation in the early 1970s, was more likely to help local collectors and had no role in claiming the ownership of fossil specimens, resulting in the unaltered ownership of fossils by private collectors. This interpretation also explains the unusual accession number for each specimen in the 1984 publication (numerating the specimens from 1 to 22) instead of official museum cataloging numbers.

Similarly, three historic specimens from the NTU collection were included by Otsuka and Lin (1984) without a consistent cataloging system; the first two specimens were referred to as specimens 1 and 2, or DGNTU-FV11a and DGNTU-FV11b, but the third specimen was only specimen 3. This inconsistency indicates the problematic curation system and results in the loss of some historic specimens because specimens 2 (or DGNTU-FV11b) and 3 were not found and likely lost. During our specimen search, the cataloging system for the only relocated specimen in the NTU collection also changed from DGNTU-FV11a to NTUGeo-10901, indicating the instability of the curation system for the vertebrate paleontology collection.

Discussion

Our rediscovery of type materials allows some morphological examination. All fossil rhinoceroses from the Pleistocene of Taiwan have long been considered the same species without a second thought. For example, the recent study (Antoine et al. 2022) also lumped materials from Taoyuan (northern Taiwan, early Pleistocene) and Tainan (southern Taiwan, middle Pleistocene) as a single taxonomic unit for the phylogenetic analysis.

Interestingly, for example, we found the well-developed crista in the rediscovered ZFP-R0114 (the left upper M1 from the middle Pleistocene of Tainan), whereas NTUGeo-10901 from the early Pleistocene of Taoyuan (now the lectotype of *Nesorhinus hayasakai*) has no crista on the upper molars. However, the crista on the upper molar seems variable (e.g., Antoine et al. 2022); new fossil materials from the Pleistocene of Taiwan and functional analyses should help resolve this character distribution and functional implications. In addition, the geological age difference (early Pleistocene in Taoyuan while middle Pleistocene in Tainan) can be up to one million years, although the precise dating of each rhinoceros fossil-producing formation remains uncertain and requires further detailed geological investigation. For example, multiple elephant species roamed Taiwan during the Pleistocene, e.g., *Stegodon* (Hayasaka 1930) or *Palaeoloxodon* (Tan 1931), or the existence of large carnivores, e.g., *Homotherium* (Tsai and Tseng 2022) or *Toyotamaphimeia* (Cho and Tsai 2023), suggesting a diverse ecosystem that could have supported an additional rhinoceros species. Future excavation and further detailed study should test this taxonomic hypothesis and better reconstruct the Pleistocene ecosystem in Taiwan.

The field of vertebrate paleontology in Taiwan is still in its infancy and requires more attention. Our rediscovery of a publicly well-known (as shown by the request of the Tainan Government for the return of type materials from National Taiwan Museum) but scientifically poorly-known Pleistocene rhinoceros demonstrates the need of systematically curating the specimens and developing the paleontological research in Taiwan. For example, in terms of specimen curation, historic fossils in Taiwan are often without proper curation or management and lead to the missing status (e.g., Liaw and Tsai 2023 for the *Mauremys* fossil; Tsai and Tseng 2022 for the *Homotherium* fossil), whereas fossils originally found in Taiwan but curated in Japan (Taiwan was part of Japan from 1895 to 1945) can still be located and studied (Cho and Tsai 2023). Paleontological research in Taiwan has been ignored for decades. However, the geographic position and geological setting of Taiwan should bring new insights into island biogeography (Antoine et al. 2022; Rozzi et al. 2023) and the origin of modern biodiversity. Pleistocene extinctions have been discussed quite extensively (Fricke et al. 2022), but the global patterns and the cause of regional extinctions require data from rather underexplored areas, such as Taiwan. Understanding the megafaunal extinctions in

the Pleistocene not only provides insights into the origins of modern biodiversity but also the accumulated knowledge of the past, emerging as a new field – conservation paleobiology (Barnosky et al. 2017; Dietl et al. 2015), helps how best to respond to the sixth mass extinction. By clarifying the historical issues and collecting more new fossil materials for future research, not only fossil rhinoceroses, but also other fossil vertebrates from Taiwan promise to offer a novel perspective to understand and decipher the origin of modern biodiversity and large-scale evolution along the eastern margin of Eurasia.

Acknowledgments: We thank CM Kuo (Tainan City Zuoqhen Fossil Park), WS Chen and CY Lee (National Taiwan University), YY Sun and H Yeh (National Taiwan Museum) for allowing the access to collections; IL Lu and his 3DR INTERNATIONAL LTD for 3D scan; Tainan City Government for administrative support; the anonymous reviewers for constructive suggestions. CHT was supported by the Taiwan Ministry of Science and Technology (MOST 108-2621-B-002-006-MY3; 111-2621-B-002-006; 112-2621-B-002-005; now known as National Science and Technology Council), public donations to the Lab of Evolution and Diversity of Fossil Vertebrates (FD107028), National Taiwan University.

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Received 17 October 2023. Accepted 2 November 2023.
Editor was Naoki Kohno.