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First island colonization by *Hystrix subcristata* (Mammalia, Rodentia): fossil evidence from Pleistocene southern Taiwan

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First island colonization by *Hystrix subcristata* (Mammalia, Rodentia): fossil evidence from Pleistocene southern Taiwan

Running Title: First porcupine record from Pleistocene Taiwan

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Abstract

Fossil records of porcupines (*Hystrix*) from island environments in East Asia have never been reported, leaving their Pleistocene dispersal and biogeographic history poorly understood. This study describes fossil remains of *Hystrix subcristata* from the Chochen–Tsailiao locality, southwestern Taiwan. The locality, part of the Chiting Formation in Tainan, is dated to the Middle Pleistocene. The collection includes a well-preserved upper molar (M1/2), a lower last premolar (p4), a fragmentary lower molar (m1/2), and three fragmentary incisors. Biometric analysis indicates that the Chochen–Tsailiao specimens are smaller than *H. refossa* but larger than *H. lagrelii* and *H. vinogradovi*, and closely comparable in size to *H. subcristata*. Morphological features further corroborate this identification. This discovery is the first record of *H. subcristata* from Taiwan, representing both its easternmost known occurrence and the first island evidence for the genus, contrasting with all prior records which consisted only of mainland forms.

Keywords: Eurasia, porcupine, Quaternary, Chochen–Tsailiao, biogeography

Introduction

The genus *Hystrix*, commonly known as Old World porcupines, is widely distributed across Eurasia from the Late Neogene through the Quaternary. The oldest known records include *H. kayae* Halaçlar et al., 2024 and *H. parvae* Kretzoi, 1951 found from the early Late Miocene of Anatolia and Europe, respectively. During the Late Miocene, *H. primigenia* Wagner, 1848 dominated western Eurasia, while *H. gansuensis* Wang and Qiu, 2002 was prevalent in the east. By the end of the Miocene and throughout the Pliocene, these lineages were largely replaced by *H. depereti* Sen, 2001b and *H. brevirostra* Wang and Qiu, 2020 (Wang and Qiu 2002; Lopatin et al. 2003; Sen 2001a; Van Weers 2004; Wang and Qi 2005; Halaçlar et al. 2025a; 2025b). During the Pleistocene, six *Hystrix* species have been reported across East and Southeast Asia, (see below). Among these, *H. subcristata* Swinhoe, 1870 is the most abundant (Tong 2005; 2008; The NOW Community 2025). The systematic position of *Hystrix subcristata* remains a subject of debate. Van Weers (1994) classified it as a subspecies within the subgenus *Acanthion*, specifically under *H. brachyura*, whereas Tong (2008), regarded it as a dinstinct species of *Hystrix*, based on morphological differences in skull compared with *H. cristata* and *H. brachyura*. Adding another layer of complexity, Lopatin (2020) later proposed

uniting all large Pleistocene porcupines from East and Southeast Asia under the single species, *H. kiangsenensis* Wang, 1931. Recent molecular studies have added further controversy: Rovie-Ryan et al. (2017) revealed genetic differentiation among *H. brachyura* populations from Peninsular Malaysia, Borneo, and Indochina, indicating a need for further investigation. An ancient DNA study by Sheng et al. (2020) demonstrated clear distinctions between *H. subcristata* from Tianyuan Cave and extant *H. cristata* and *H. africaustralis*, while simultaneously emphasizing similarities between the Tianyuan Cave porcupine and *H. brachyura*. Until more extensive systematic and molecular studies are conducted on *H. subcristata*, we follow Tong's (2008) classification of *H. subcristata* as a distinct species in this article, as it is based on extensive comparative analyses of both fossil and extant skulls. For the Late Pleistocene porcupine from Vietnam discussed herein, we adopt the nomenclature "*H. kiangsenensis*" following Lopatin (2020).

According to the IUCN (2025), six *Hystrix* species are extant in East and Southeast Asia: *H. brachyura* (Malayan Porcupine), *H. pumila* (Philippine Porcupine), *H. sumatrae* (Sumatran Porcupine), *H. javanica* (Sunda Porcupine), and *H. crassispinis* (Thick-spined Porcupine). Of these, only *H. brachyura* inhibits the continental mainland, whereas the others are island endemics. Another genus within Hystricidae, *Atherurus*, is also represented in East Asia by a single species, *Atherurus macrourus*. This species is readily distinguished from *Hystrix* due to its significant smaller size (Lopatin and Serdyuk, 2021).

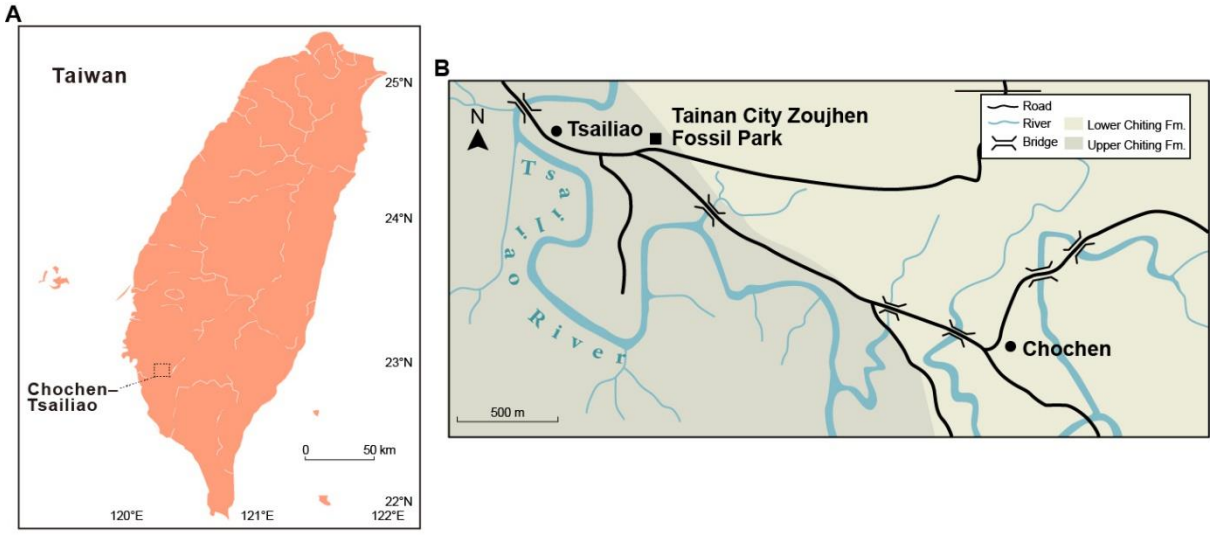

Figure 1. Locality of Chochen–Tsailiao in Tainan, Southern Taiwan. **A.** Site location of Taiwan (black rectangle); **B.** Detailed map of the Chochen–Tsailiao area (modified after Qi et al. 1999; Lin et al. 2025). Fossils were collected from reworked deposits within the riverbed along the Tsailiao River.

In this study, fossil porcupine specimens were collected from reworked deposits along the riverbed of Tsailiao River, in the Chochen–Tsailiao area of Tainan, southwestern Taiwan (Fig. 1). The associated vertebrate assemblage consists of primates, proboscideans, suids, cervids, rhinoceroses, crocodiles, snakes, a toad, a bird, and fishes (Shikama 1937, 1972; Shikama et al. 1975a, 1975b, 1976; Otsuka and Lin 1984; Qi et al. 1999; Tao and Hu 2001; Shieh and Chang 2007; Chang et al. 2012; Kawamura et al. 2016; Lin et al. 2021, 2025; Tsai and Mayr 2021). These fossils are widely attributed to the Middle Pleistocene Chiting Formation, which has yielded numerous mammal fossils (Qi et al. 1999; Ho et al. 2005; Shieh and Chang 2007;

Kawamura et al. 2016). Because many fossils were reworked from mixed marine and terrestrial deposits (Chen et al. 2011; Chen 2016; Lin et al. 2021), a conservative age range of the Chiting Formation, approximately 0.8–0.4 Ma (Middle Pleistocene; Chen 2016) is adopted for the Tsailiao porcupine remains.

Material and Methods

All specimens examined in this study are permanently housed at the Biodiversity Research Museum, Academia Sinica, and the National Museum of Nature and Science in Taiwan, under inventory numbers prefixed ASIZF and NMNS F, respectively. Dental terminology follows the conventions established by Van Weers (1990), Şen (2001a), Lopatin et al. (2003), Van Weers and Rook (2003), Azzara et al. (2022), and Halaçlar et al. (2025a; 2025b). Specifically, tooth wear stages are categorized using the "system of wear classes" defined by Van Weers (1990) and Van Weers and Rook (2003). For illustration purposes, all teeth are shown as left-sided, with underlined figure numbers denote mirrored specimens. All measurements were taken with an electronic caliper to an accuracy of 0.01 mm. The diagrams were generated using PAST version 5.00 (Hammer et al. 2001).

Terminology: I/i, upper/lower incisor; **P/p,** upper/lower premolar; **M/m,** upper/lower molar; **EH,** enamel height measured on the lingual side for upper teeth and on the labial side for lower teeth; **EH/L,** enamel height/length; **L,** maximum length along the longitudinal tooth axis situated in the middle crown height; **W,** maximum width along the transverse tooth axis in the middle crown height.

Systematic Paleontology

Order Rodentia Bowdich, 1821

Family Hystricidae Fischer De Waldheim, 1817

Genus *Hystrix* Linnaeus, 1758

Type species: *Hystrix cristata* Linnaeus, 1758.

Hystrix subcristata Swinhoe, 1870

Figure 2

Geographical Occurrence: East and Southeast Asia.

Chronological Occurrence: Early Pleistocene to Holocene.

Referred Material: ASIZF0101080, right upper incisor (I1); NMNS007351-F055793, right upper incisor (I1); NMNS007351-F055792, left upper first/second molar (M1/2); ASIZF0101081, lower incisor (i1); ASIZF0101082, right lower last premolars (p4); ASIZF0101083, left lower first/second molar (m1/2).

Locality: Chochen–Tsailiao, Tainan, Taiwan.

Age: Middle Pleistocene.

Measurements: See Table 1.

Description: I1 (Upper incisor): Two fragmentary upper incisors (ASIZF0101080 and NMNS007351-F055793) are measurable, with dimensions of L = 6.08 mm, W = 8.18 mm and L = 7.9 mm, W = 9.5 mm, respectively. The anterior portion of both I1s exhibits a medial curvature. In cross-section, the medial walls are gently curved, while the lateral walls display a wavy morphology. The enamel is notably thicker on the distal walls.

M1/2 (Upper molar): The occlusal view of specimen NMNS007351-F055792 presents an anteriorly oval and posteriorly square outline, with the anterior portion being larger than the posterior portion. Seven enamel islands are visible, and the absence of enamel folds indicates wear class G1, corresponding to an adult individual. Due to advanced wear, the hypostria and labial synclines are no longer discernible.

Table 1. Comparison of tooth measurements for the genus Hystrix from Chochen–Tsailiao (Taiwan), Zhongshan Cave and Tianyuan (China), Lang Trang Cave and Ma U`Oi (Vietnam), and living species. Measurements are in mm.

Age	Locality	Species	I1		M1/2		p4		m1/2		References
			L	W	L	W	L	W	L	W	
			(n) mean (range)		(n) mean (range)		(n) mean (range)		(n) mean (range)		
Middle Pleistocene	Tsialiao	*H. subcristata*	(2) 7 (6.08-7.9)	(2) 8.8 (8.19-9.5)	8.4	7.61	9.2	7.24	8.34	8.4	This study
Middle Pleistocene	Zhongshan cave	*H. subcristata*	(12) 6.63 (5.45-7.7)	(12) 8.46 (6.93-9.61)	8.2 (6.12-10.3)	7.72 (6.21-9.52)	(19) 9.54 (7.8-10.8)	(18) 7.63 (5.89-8.86)	(55) 8.7 (6.63-10.48)	(55) 7.62 (6.39-9)	Fan et al. 2024
Late Pleistocene	Tianyuan	*H. subcristata*	(5) 6.8 (6-8)	(5) 5.8 (5-7)	(5) 7.4 (6-8)	(5) 7.1 (6.5-7.5)	(3) 10.5 (8.5-12)	(3) 8 (7-9)	(13) 8 (7-9.5)	(13) 7.5 (6.5-9)	Tong 2005
Late Pleistocene	Lang Trang Cave	*"H. kiangsenensi"*	6.5	8,5			10.1	6			Lopatin 2020
Middle-Late Pleistocene	Ma U'Oi	*Hystrix brachyura*					8.25	5.15	8.07-8.1	5.86-5.96	Bacon et al. 2006
Recent	(modern)	*Hystrix brachyura*					6.2-7.5	5.2-6.8	5.9-7.7	5-7.3	Bacon et al. 2006

i1 (Lower incisor): The lower incisor (ASIZF0101081) is fragmentary and unmeasurable, although the preserved portion exceeds 5 mm in length.

p4 (Lower fourth premolar): In occlusal view, the p4 (ASIZF0101082) has an anteroposteriorly pyriform shape, with the anterior part elongated and the posterior wider. The occlusal surface shows that eruption has just begun, corresponding to wear class B2. This places the specimen in age class VI according to Van Weers's (1990) classification, indicating a subadult individual. All cusps of the p4 have recently erupted, and there are four lingual synclines. The protoconid is robust and clearly connected to the metaconid via the anterolophulid. The labial mesofossettid and anterofossettid remain connected to all flexids and posterofossettid. The entoconid is weakly developed, whereas the mesolophid is strong, with both positioned posteriorly. On posterior wall, there is a contact area with m1.

Figure 2. The porcupine material from Chochen–Tsailiao locality. **A**, right upper incisor (NMNS007351-F055793); **B**, right upper incisor (ASIZF0101080); **C**, left upper first/second molar (NMNS007351-F055792); **D**, lower incisor (ASIZF0101081); **E**, right lower last premolar (ASIZF0101082); **F**, left lower first/second molar (ASIZF0101083). Occlusal view: A1, B1, C1, E1, F1; Lingual view: C2, D2, F3; Labial view: C3, E2, F2; lateral view: A2, B2, D1 and posterior view: E3.

m1/2 (Lower molar): Although the anterolingual part of specimen ASIZF0101083 is missing, its occlusal outline remains discernible. The anterior part of the m1/2 is shifted labially and the posterior lingually, forming a more robust structure in the posterolingual corner. The tooth is significantly worn, with the wear extending near the hypostriid, which appears to have moved anteriorly on the labial wall. All lophids are connected, and there are six distinct enamel islands. The broken part of the specimen indicates the presence of two enamel roots corresponding to two of these islands. The tooth is assigned to wear class T2, representing an old individual.

Comparison and Discussion

Most studies have emphasized four key dental characters for distinguishing *Hystrix* species: overall size, occlusal outline, occlusal pattern, and degree of hypsodonty (enamel height) (Van Weers 1990; Şen 2001a, b; Lopatin et al. 2003; Van Weers and Rook 2003; Şen and

Purabrishemi 2010; Flynn and Wu 2017; Fejfar and Sabol 2022; Azzarà et al. 2022; Halaçlar et al. 2023). As shown in Figure 3, cheek teeth from Chochen–Tsailiao locality consistently fall within the morphological range of *Hystrix subcristata*. Table 1 indicates that the specimens are relatively smaller than *H. magna*, *H. kiangsenensis*, and *H. refossa* Gervais, 1852, yet relatively larger than *H. lagrelii*, *H. vinogradovi*, and the extant *H. brachyura*.

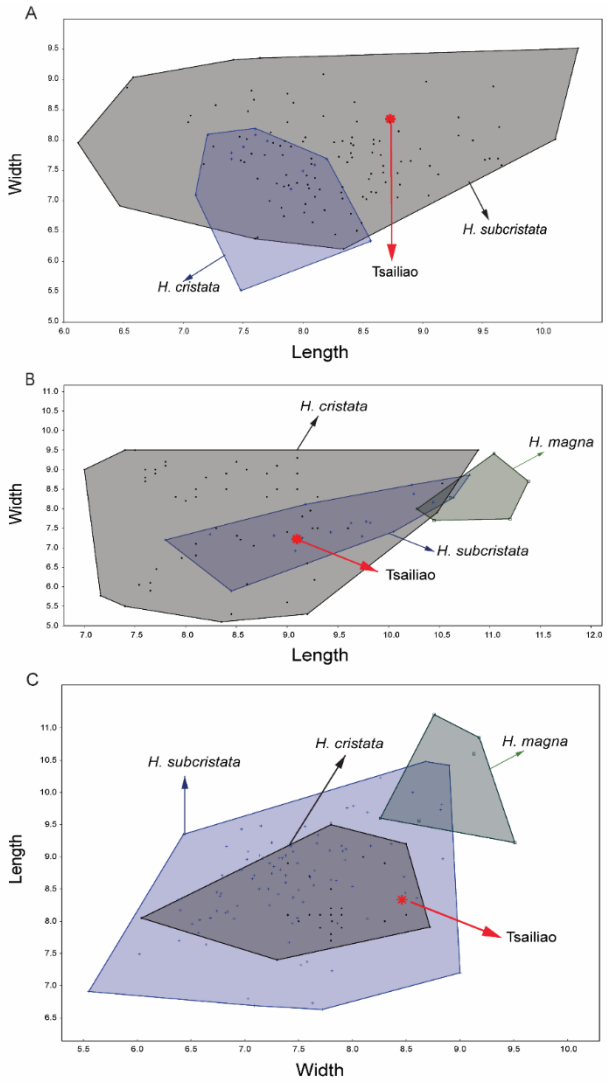

Figure 3. Biometrical comparison of some East and Southeast Middle Pleistocene and modern porcupines. **A.** upper first/second molar; **B.** lower last premolar; **C.** lower first/second molar. Data source: Fan et al. (2024), Tong (2005) and Azzara et al. (2022)

H. refossa is a very large, hypsodont porcupine distributed widely across Eurasia during the Plio–Pleistocene. The size of its cheek teeth far exceeds those of the Chochen–Tsailiao specimens, as illustrated by Van Weers (1994, fig. 1). For example, the p4 of *H. refossa* ranges from 10–13 mm in length and 8–10.5 mm in width; our specimens are considerably smaller than this range. This size discrepancy is consistent across all other teeth examined. *H. vinogradovi* is a small Pleistocene porcupine with a paleobiogeographical distribution across Europe and West-Central Asia (Baryshnikov 2003; Kuzmin et al. 2017; Lopatin 2019). This species is considerably smaller than *H. subcristata*, and given its distinct paleobiogeography,

which is geographically distant from Taiwan, this species is therefore excluded from consideration. Likewise, *H. lagrelii*, the smallest known Pleistocene *Hystrix* has p4–m3 series measuring only 21–22 mm, significantly smaller than the >35 mm series typical of *H. subcristata* specimens from Zhoukoudian (Tong 2008, tables 2 and 3). The Chochen–Tsailiao specimens are consequently too large to belong to *H. lagrelii*.

Size comparison thus narrows the possible affinities of the Taiwanese fossils to *H. kiangsenensis* and *H. subcristata*. The p4 specimen from Lang Trang Cave (Vietnam) assigned to *H. kiangsenensis* is comparable in size to the Chochen–Tsailiao p4; however, the Taiwanese specimen exhibits greater hypsodonty, and in lateral view, *H. kiangsenensis* displays a distinctly squarer morphology (Figure 4).

Overall, the Chochen–Tsailiao porcupine teeth are fully consistent with *H. subcristata* in both biometric and morphological characteristics. Taken together, this strong agreement supports their assignment to *H. subcristata*, a species previously also reported from East and Southeast Asia.

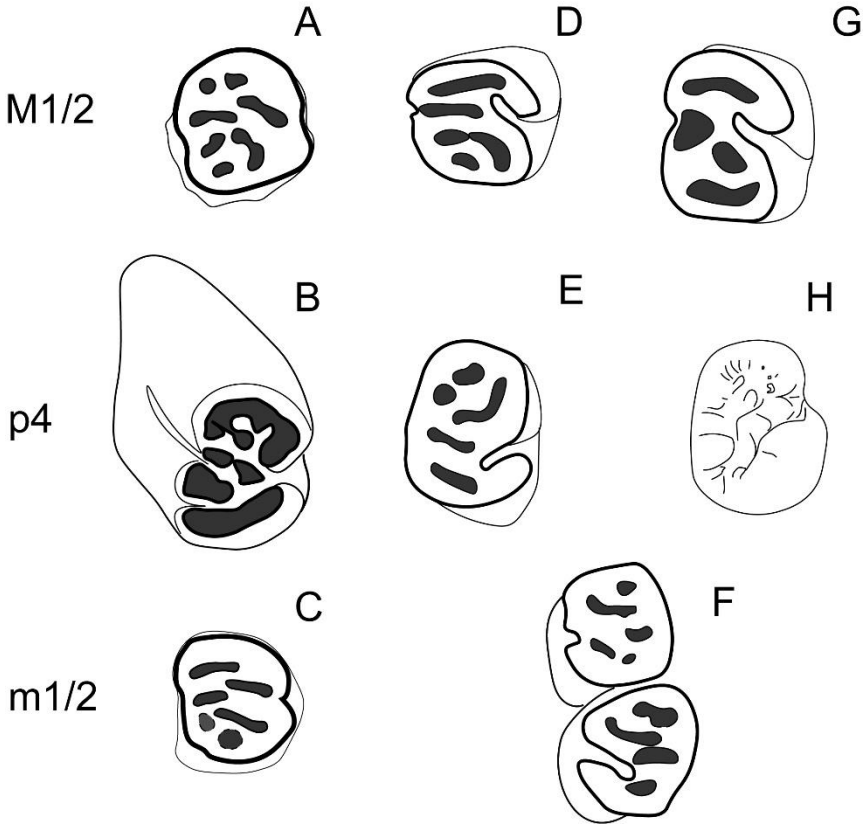

Figure 4. Morphological comparison of Middle Pleistocene porcupine specimens from East and Southeast Asia. **A**, **B**, **C**: *Hystrix subcristata* specimens from the Chochen–Tsailiao locality in Taiwan (This study). **D**: *H. subcristata* specimen from Tianyuan Cave (Tong 2005). **E**, **F**: *H. subcristata* specimens from Tangzigou (Jin et al. 2012). **G**: "*H. kiangsenensis*" specimen from Lang Trang Cave (Lopatin et al. 2022). **H**: "*H. kiangsenensis*" specimen from Lang Trang Cave (Lopatin 2020).

Conclusions

The Middle Pleistocene *Hystrix subcristata* fossils from the Chochen–Tsailiao locality in southwestern Taiwan represent an important paleontological discovery. Biometric and

morphological analyses confirm their taxonomic identification as *H. subcristata*. The specimens closely match *H. subcristata* from East and Southeast Asia in both size and morphology, while distinctly differing from larger Pleistocene porcupines like *H. refossa* and smaller species such as *H. lagrelii* and *H. vinogradovi*. This discovery marks the first record of *H. subcristata* in Taiwan, extending its known distribution eastward. Crucially, this finding represents the first island record of the species. This finding significantly broadens the paleobiogeographical range of *Hystrix* and offers new evidence for Quaternary mammal dispersal between continental East Asia and adjacent islands.

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