# New fossils of Late Pleistocene Sus scrofa from Yangjiawan Cave 2, Jiangxi, China (Postprint)

**Authors:** SUN Ji-Jia, ZHANG Bei, CHEN Xi, DENG Li, WEN Jun, TONG Hao-Wen

**Date:** 2020-09-15T00:00:00+00:00

## Abstract

The YJW (Yangjiawan) Cave 2 of Pingxiang in Jiangxi Province is a karst cave that developed in the Permian limestone of the Changxing Formation, which is filled with clay and grit of Late Pleistocene age. Six excavations have been conducted at the site since 2015. More than ten thousand mammalian fossils have been unearthed, and the wild boar fossils account for approximately 49%, which represents the richest wild boar fossil tooth collection of Pleistocene age in southern China. This study focuses on the studies of the canine teeth and the third molars, and mainly compares fossils of Sus peii and S. xiaozhu in South China and the data of extant S. scrofa respectively in dental morphology and odontometric data analyses which includes scatter plot analysis, regression analysis, coefficient of variation analysis and linear discriminant analysis. The typical scrofic type of the male' s lower canine teeth confirmed the identification of the suid fossils from YJW Cave 2 as S. scrofa. Although the male' s lower canines, the M2s and m3s, are among the most variable teeth in sizes, they stay in the ranges of S. scrofa; furthermore, the scatterplots of both the upper and lower third molars form two distinct clusters respectively, which can probably be attributed to sexual dimorphism rather than resulting from a mixture of different suid species. The post-Early Pleistocene suid fauna in southern China is almost only composed of S. scrofa, which is quite different from the adjacent Southeast Asia where the suid fauna is quite taxonomically diversified and dominated by the verrucosic type.

## Full Text

### New Fossils of Late Pleistocene *Sus scrofa* from Yangjiawan Cave 2, Jiangxi, China

**Ji-Jia Sun**[1,2,3], **Bei Zhang**[1,2,3], **Xi Chen**[4], **Li Deng**[5], **Jun Wen**[5], **Hao-Wen Tong**[1,2,3]* [1]Key Laboratory of Vertebrate Evolution and Human Origins,

Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China
[2]CAS Center for Excellence in Life and Paleoenvironment, Beijing 100044, China
[3]University of Chinese Academy of Sciences, Beijing 100049, China
[4]Nanjing Normal University, Nanjing 210023, China
[5]Pingxiang Museum, Pingxiang, Jiangxi 337000, China
*Corresponding author: tonghaowen@ivpp.ac.cn

**Abstract:** Yangjiawan (YJW) Cave 2 in Pingxiang, Jiangxi Province, is a karst cave developed in Permian limestone of the Changxing Formation, filled with Late Pleistocene clay and grit deposits. Six excavations have been conducted at the site since 2015, yielding over ten thousand mammalian fossils, of which wild boar teeth account for approximately 49%—representing the richest collection of Pleistocene wild boar dental fossils discovered in southern China to date. This study focuses on the canines and third molars, comparing the fossils with *Sus peii* and *S. xiaozhu* from South China and extant *S. scrofa* through dental morphology and odontometric analyses including scatter plot analysis, regression analysis, coefficient of variation analysis, and linear discriminant analysis.

The typical scrofic type of male lower canines confirms identification of the suid fossils from YJW Cave 2 as *S. scrofa*. Although male lower canines, M2s, and m3s exhibit high size variability, all measurements fall within the range of *S. scrofa*. Furthermore, scatter plots of both upper and lower third molars form two distinct clusters, likely attributable to sexual dimorphism rather than mixing of different suid species. Post-Early Pleistocene suid fauna in southern China is composed almost exclusively of *S. scrofa*, contrasting sharply with adjacent Southeast Asia where suid fauna is taxonomically diverse and dominated by the verrucosic type.

**Keywords:** Yangjiawan Cave 2, Pingxiang, Jiangxi; Late Pleistocene; *Sus scrofa*; teeth; intraspecific variation; sexual dimorphism

**Citation:** Sun J J, Zhang B, Chen X et al., in press. New fossils of Late Pleistocene *Sus scrofa* from Yangjiawan Cave 2, Jiangxi, China. *Vertebrata PalAsiatica*. DOI: 10.19615/j.cnki.1000-3118.200819

---

## 1. Introduction

Since 2014, a team from the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences has been excavating YJW Cave 1, and since 2015, YJW Cave 2, which lies only 50 meters away (Zou et al., 2016). The Yangjiawan caves are located in Shangli County, Pingxiang, Jiangxi Province, with Cave 2 precisely positioned at 27°46 25 N, 113°50 25 E. These karst caves are filled with Late Pleistocene clay and silt deposits. The mammalian fauna from YJW Cave 2 comprises 6 orders, 20 families, and approximately 40 species, all characteristic elements of the *Ailuropoda-Stegodon* fauna (Zhang et al., 2017, 2018; Jiangzuo et al., 2018; Tong et al., 2018). The site has yielded the most abundant and diverse fossil assemblage discovered in Jiangxi Province to date, with over 10,000 mammalian tooth fossils excavated, the majority belonging to wild pigs.

Suiformes, including Suidae and Tayassuidae, can be traced back to the Middle Eocene (Gentry and Hooker, 1988; Ducrocq, 1994; Ducrocq et al., 1998; Liu, 2001). The subfamily Suinae represents one of the most common components of Quaternary faunas in southern China, with three genera (*Potamochoerus*, *Dicoryphochoerus*, and *Sus*) and approximately 13 species reported, though the generic validity of Chinese *Dicoryphochoerus* requires further analysis as more material becomes available (Hou et al., 2018). Despite their abundance, Quaternary Suinae fossils in southern China are typically poorly preserved, often lacking crucial anatomical parts, leaving many taxonomic issues unresolved. While comparative skull studies are among the most effective vertebrate research methods, few skull specimens of Quaternary Suinae exist in China. Consequently, isolated tooth remains are abundant, and dental measurements and related analyses become important for species determination (Zeuner, 1963; Bökönyi, 1974; Mayer et al., 1998).

Researchers studying wild boars and domestic pigs typically measure the second and third molars, though the crown length of the second molar may be reduced by abrasion from adjacent molars (Higham, 1968; Flannery, 1983; Stampfli, 1983; Payne and Bull, 1988; Mayer et al., 1998). Adult individuals exhibit clear sexual dimorphism, with the most significant differences in the shape and size of the lower canine (Harrison and Bates, 1968; Payne and Bull, 1988; Mayer and Brisbin, 1991, 1993). Like other cave sites in southern China, YJW Cave 2 lacks skull material but has yielded numerous tooth fossils. This study aims to identify the pig fossils from YJW Cave 2 through morphological observation and measurement, comparing results with *S. xiaozhu* and *S. peii* from Liucheng Gigantopithecus Cave (LGC), Guangxi, and *S. scrofa* from Yanjinggou, Sichuan. The rich specimen collection also facilitates intraspecific variation studies, examining morphological characteristics and size variations between individuals and genders.

## 2. Materials and Methods

This study focuses on morphological identification and measurement analysis of canines, fourth premolars, and second and third molars excavated from YJW Cave 2 in 2018. The observed specimens include 10 male upper canines, 4 female upper canines, 27 male lower canines, 43 female lower canines, 50 left P4s, 37 right P4s, 14 left p4s, 14 right p4s, 46 left M2s, 60 right M2s, 62 left m2s, 55 right m2s, 41 left M3s, 25 right M3s, 73 left m3s, and 60 right m3s. Primary reference materials consist of third molar measurement data for *S. xiaozhu* and *S. peii* from LGC, Guangxi (Han, 1987). Higher-level classification follows McKenna and Bell (1997) and Frantz et al. (2016), while species-level classification follows Groves (1981).

Methods employed include morphological observation and comparison, with anatomical terminology and tooth crown measurement methods derived from Hardjasasmita (1987), Van der Made (1996), and Fujita et al. (2000) [Figure 1: see original paper]. Upper and lower teeth are denoted by uppercase and lowercase letters, respectively. Primary analytical methods include scatter plot analysis, regression analysis, coefficient of variation analysis, and linear discriminant analysis.

---

## 3. Systematic Paleontology

**Order Artiodactyla** Owen, 1848
**Suborder Suiformes** Jaeckel, 1911
**Superfamily Suoidea** Gray, 1821
**Family Suidae** Gray, 1821
**Subfamily Suinae** Zittel, 1893
**Genus *Sus*** Linnaeus, 1758
***Sus scrofa*** Linnaeus, 1758

### 3.1 Descriptions and Analysis of Morphology

Among all bones and teeth, the anatomical features of the male lower canine are among the most crucial for suid classification (Wilkinson, 1976) and may even be considered the most important character for distinguishing *Sus* species (Groves, 1981, 2007). Three main types of lower canine cross-sections exist: scrofic, verrucosic, and intermediate (Fujita, 2000) [FIGURE:1 A-C]. In all three types, the lingual (=anterior: Groves, 1981) face is always the broadest (Groves, 1981: P.11). In the scrofic type [Figure 1A: see original paper], the labial (inferior: Groves, 1981) face is the narrowest (Groves, 1981:p. 11). In the verrucosic type, the posterior face is the narrowest (Hardjasamita, 1987) [Figure 1C: see original paper]. In the intermediate type, the posterior face becomes as broad as the labial one (Fujita, 2000) [Figure 1B: see original paper]. Notably, Groves (1981:p. 11) stated that the inferior surface of the verrucosic type is as broad as the posterior surface, which corresponds to the "intermediate type" of Fujita et al. (2000).

The suid canine fossils from this deposit clearly exhibit the scrofic type, with the lingual surface being the broadest, the labial face the narrowest, and the posterior face lacking enamel. The lower canines of *S. xiaozhu* and *S. peii* from LGC are of the intermediate type (Chen, 2004), but closer to the verrucosic type based on figures by Han (1987:fig. 3 [Figure 3: see original paper]). Regarding lower canine teeth, fossils from YJW Cave 2 are more similar to *S. scrofa*

(Figs. 1G; 2: 8c, 9c). Male lower canine size from YJW Cave 2 varies considerably, likely representing different age classes according to Endo et al. (1994). Although female *S. scrofa* have the largest canine teeth among *Sus* species, overlapping with the male range (Groves, 1981), male lower canines remain easily distinguishable from females because female lower canines are not only obviously smaller but also possess a developed enamel-less root (Mayer and Brisbin, 1988). Furthermore, we observed that female lower canines have a relatively narrower posterior surface [FIGURE:2: 17-24].

Male lower canines of *S. scrofa* from YJW Cave 2 are fairly variable in size, closely related to their age stages (Fig. 2: 1-9); none possess roots, indicating that male lower canines continue growing throughout life. In contrast, female lower canines are much smaller with developed roots, but show far less size variability than males (Fig. 2: 10-24).

Male upper canines are much more robust, with a trapezoidal cross-section, grooved enamel, and enamel-free bands extending along the entire length of the rootless tooth, though size variation is limited (Fig. 3: 1-9). Female upper canines are much more reduced and compressed, with an atypical triangular cross-section, a developed root, and enamel covering only the crown portion (Fig. 3: 10).

Upper incisors are few and poorly preserved, while lower incisors are well represented. The most important characters of i2 are the bent tooth body and developed distal groove (Fig. 3: 12-13), whereas these characters are absent in i1 (Fig. 3: 11).

In form, P2 [FIGURE:4: 4] is similar to P3 but prominently smaller. P3 has a developed paracone, metacone, and protocone, as well as a prominent primocone (Fig. 4: 17). Both P2 and P3 have two roots. P4 has three main cusps: a paracone and metacone at the buccal side, and a protocone at the lingual side. The protocone varies greatly in both shape and size, primarily lying at the contact point between the protocone precrista and the postcrista of the protopreconule; furthermore, the general shape and size of the tooth are also very variable (Fig. 4: 5-17). P4 has four roots, though the two lingual roots commonly merge into one.

M1 [FIGURE:4: 19] is very similar to M2 in shape but much smaller. M2 has four equally developed cusps: a paracone and metacone at the buccal side, protocone and hypocone (=tetracone: Fujita et al., 2000) at the lingual side, with a moderately developed tetrapreconule occurring at the central area surrounded by the four major cusps, and the posterior cingulum (=pentapreconule: Fujita et al., 2000) being much more developed than the anterior one (Fig. 4: 20-34).

The p2 [FIGURE:4: 1] and p3 [FIGURE:4: 2] are similar in form, but the former is prominently smaller; both have developed protoconid and hypoconid. Both p2 and p3 have two roots. The p4 crown consists of four major cuspids: paraconid, protoconid, metaconid, and hypoconid, with a hypoendocristid developed at the lingual side of the hypoconid; at the buccal side, two vertical ridges occur at the anterior and posterior corners respectively [FIGURE:4: 3]. Normally p4 has two roots, though the posterior one is occasionally forked distally; anatomical study shows p4 has three root canals (Ide et al., 2013).

m1 [FIGURE:4: 18] is very similar to m2 in shape but relatively smaller. m2 has four main cuspids: protoconid and hypoconid at the buccal side, metaconid and entoconid at the lingual side. Furthermore, the pentaconid at the distal end and the hypopreconulid at the central part surrounded by the four main cuspids are also quite prominent (Fig. 4: 35–43). Both m1 and m2 have four roots. m2s are less variable in dimensions than M2s.

M3s of suid fossils from YJW Cave 2 generally have three lobes (Fig. 4: 44–52). The crown shape is triangular with a rounded right angle near the protocone. Some specimens bend toward the lingual side in the zone between the second and third lobes. Taking the left M3 as an example, the paracone is the highest among the cusps. The protocone and metacone are similar in height, while the hypocone is the smallest among the four main cusps in both size and height. A hypoectoconule usually develops between the protocone and hypocone. The hypopreconule that develops between the first and second lobe is somewhat large and may sometimes be as large as the protocone and metacone. The pentacone is large. A pentaectoconule may develop between the hypocone and pentacone, although it is sometimes missing. The pentapreconule is generally slightly smaller than the hypopreconule with the surrounding tip fully developed. Pentacone variability is relatively large, with some specimens splitting at the top and several small cusps attached around it. Each M3 cusp is relatively complicated with many deep grooves and small cristae developed, as well as some cusplets. In terms of shape, the M3 of pig fossils from YJW Cave 2 is relatively close to *S. peii* and *S. scrofa*. However, the third lobe of *S. peii* M3 is generally composed of a large cusp, with fewer small cusps and cristae developing in the first and second lobes. Variability is mainly manifested in total size and third lobe development. Therefore, the M3 of suid fossils from YJW Cave 2 should not be referred to *S. peii* but are likely closer to *S. scrofa* instead. M3 normally has five roots corresponding to each main cusp and the talon, though extra rootlets occasionally occur.

More than half of the m3s have four lobes with complex variability in the fourth lobe (Fig. 4: 53–62). Taking the left m3 as an example, the protoconid is generally lower than the metaconid and almost the same height as the hypoconid. The entoconid is generally lower than the hypopreconulid but higher than the protoconid. The hypopreconulid is similar in size to the pentapreconulid but higher than the latter. Hypoectoconulid variability is great in size and division at the top. Several deep grooves occur around the pentapreconulid when the crown is not yet abraded, separating it from surrounding cusps. The pentaectoconulid varies greatly in size and is not consistently present. The pentaconid is usually lower than the hypoconid but higher than the hexaconid, with a deep groove separating them. Variability of the fourth lobe mainly lies in the expanding of the heptaconid. Other variability occurs in heptaconid size and the presence of small cusps and cristid. In some specimens, a tendency to bend to the lingual side from the third lobe is also observed (Fig. 4). The m3 has five roots corresponding to each main cuspid and the talonid.

Variability of pig fossils from YJW Cave 2 is mainly manifested in total size and the condition of the third and fourth lobes. *S. peii* is characterized by a rectangular crown shape, a talonid with a pair of unseparated conids, fewer small cuspids, and only a small number of individuals developing a fourth lobe (Chen, 2004). Therefore, m3s from YJW Cave 2 should not belong to *S. peii* but are closer to those of *S. scrofa*.

Previous studies show that only *S. lydekkeri*, *S. scrofa*, and *S. australis* have four lobes in m3s (Han, 1987), meaning atypical verrucosic type suids in southern China shared some characters with boreal suid species during the Early Pleistocene. Concerning m3 significance in taxonomy, debate continues; study of pig remains from the Dadiwan Neolithic site shows m3 is the most variable tooth among cheek teeth, varying greatly in both size and talonid development (Qi et al., 2006). The present study also demonstrates that m3 has quite high coefficient of variation values (Figs. 5, 6; Table 1 ).

### 3.2 Data Analysis

This study uses data for *Sus peii* and *S. xiaozhu* from the Gigantopithecus Cave by Han (1987) for comparison. Scatter plots were drawn [Figure 5: see original paper], and regression analysis with 95% confidence was performed to obtain $R^2$ and P values. Length and width data were analyzed for coefficients of variation.

*Sus xiaozhu* was named by Han et al. (1975) based on small pig fossils from Bijiashan, Liuzhou, Guangxi. It is very small, with short upper and lower dentitions, a small M3 talon, and an m3 talonid with one cuspid. The M3 of *S. xiaozhu* is extremely small, allowing clear distinction from pig fossils of YJW Cave 2 and *S. peii* based solely on measurement data. The M3 distributions of *S. peii* and YJW Cave 2 suid specimens slightly overlap; the latter is generally narrower than *S. peii*, with greater length variation range than *S. peii* [Figure 5B: see original paper]. Notably, M3 length-width regression analysis for *S. peii* failed the P value test, indicating its regression equation is invalid and variation is great. P values for the other two are less than 0.05.

The $R^2$ value of *S. xiaozhu* is the largest, indicating small variability, while the other two show relatively large variability (Table 1). The m3 of *S. xiaozhu* is also extremely small, distinguishing it from *S. peii* and YJW Cave 2 pig fossils in size. Overlap between *S. peii* and YJW Cave 2 m3 fossils is larger, but generally, *S. peii* data distribution is still slightly wider with a smaller length variation range than YJW Cave 2 specimens [Figure 5B: see original paper]. P values for regression equations of m3 for all three species are less than 0.05, while the $R^2$ value of *S. xiaozhu* remains greater than the other two, indicating smaller variability (Table 1).

The earliest record of *S. scrofa* in southern China is from the Yanjinggou area. Colbert and Hooijer (1953) provided some tooth length measurement data in their article. The M3 range is 33.5–41.5 mm. The M3 length range of *S. peii* given by Han is 34.6–42.0 mm. The M3 length from YJW Cave 2 is 29.1–41.0 mm. The Yanjinggou m3 variation range is 39.0–41.0 mm. The m3 length of *S. peii* is 35.0–44.3 mm, and the m3 length from YJW Cave 2 is 32.1–49.1 mm. Data for *S. scrofa* from Yanjinggou is closer to that of YJW Cave 2. Albarella et al. (2015), when studying Eurasian *S. scrofa*, calculated average m3 length and first lobe width for South and Southeast Asian *S. scrofa* as 37.1 mm and 17.1 mm, respectively. Average length and width of *S. peii* from Gigantopithecus Cave were 38.5 mm and 19 mm. Average m3 length and first lobe width of YJW Cave 2 suid fossils were 38.7 mm and 17.1 mm. On average, YJW Cave 2 suid fossils are closer to *S. scrofa*.

This study calculated coefficient of variation using length and width data for the three species. The coefficient of variation for M3 of *S. xiaozhu* and YJW Cave 2 suids is similar, both larger than *S. peii* data in terms of length or width. *S. peii* shows smaller variability, different from the length-width combination variability. The m3 of *S. xiaozhu* shows large variability, indicating volatile length or width. Overall variability of YJW Cave 2 suid fossils is larger than that of *S. peii*.

Among molars of *S. scrofa* from YJW Cave 2, M2s [Figure 6D: see original paper] and m3s [Figure 6B: see original paper] are among the most variable teeth in dimensions (Table 1). Regarding the relatively smaller fossil species *S. liuchengensis*, it has simpler and smaller teeth, with M3 having a reduced talon and m3 having no more than three lobes (Han, 1987). Concerning *S. australis*, it was regarded as a synonym of *S. peii* by Chen (2004). Moreover, *S. scrofa* from YJW Cave 2 has the typical scrofic type male lower canine, different from Early Pleistocene *Sus* species of southern China.

The fossil species *S. lydekkeri* is a boreal taxon that mainly appeared in northern China during the Early to Middle Pleistocene, distinguishable from *S. scrofa* primarily by its relatively larger size and atypical scrofic male lower canine (Young, 1932), i.e., intermediate between scrofic and verrucosic conditions (Fujita et al., 2000; Chen, 2004; Dong, 2008). Therefore, recent authors treated it as a subspecies of *S. scrofa* (van der Made, personal communication; Fujita et al., 2000). Notably, the skull material of *S. lydekkeri* from the Nihewan Basin is likely a young adult male rather than a female as originally identified by Liu et al. (2017), but its relatively narrower posterior face is an exception, falling within the intermediate type range and agreeing well with its species features.

Through morphological and data comparison, this study concludes that suid tooth fossils from YJW Cave 2 should belong to *S. scrofa*. Although suid fossils are very common in Pleistocene mammalian faunas of southern China, they are far less diversified compared with their Southeast Asian counterparts at the species level (Hardjasasmita, 1987; Frantz et al., 2016), and most Southeast Asian *Sus* species show a verrucosic type cross-section in the male lower canine (Hardjasasmita, 1987)—a crucial feature separating them from southern Chinese species. The verrucosic type male lower canine has never been reported for Chinese Pleistocene *Sus* species. Furthermore, compared with Early Pleistocene suid faunas of southern China, Middle-Late Pleistocene ones are much less diversified.

Cherin et al. (2018) proposed that *S. scrofa* and Early-Middle Pleistocene *S. lydekkeri* are the *Sus* species with the most numerous plesiomorphic characters, followed by the monophyletic group of suines with verrucosic lower canines, including Pliocene *S. arvernensis*, *S. strozzii*, and verrucosic pigs from insular Southeast Asia. They considered the verrucosic canine a plesiomorphic character, agreeing with Groves (1981) that the scrofic canine is derived. Furthermore, some authors (Groves, 1981; Groves and Grubb, 1993) divided living *Sus* species into two groups based on lower canine morphology: the "scrofic group" includes only *S. scrofa*, while the "verrucosic group" consists of other species. Cherin et al. (2018) even proposed that the position of *S. strozzii* in their phylogenetic tree provides the first cladistic evidence of affinity between European fossil species and far-separated insular Southeast Asian verrucosic pigs. We suggest that the phylogenetic significance of the lower canine should be urgently re-evaluated, and other teeth should receive equal consideration, as some authors have proposed that molar shape in Eurasian wild boar populations is biogeographically structured into clearly defined Western and Eastern clusters (Evin et al., 2015).

Regarding the living form of wild boar in China, its classification remains debated. The traditional scenario places all living wild pigs in the species *S. scrofa*, designating different subspecies for different regions. In Central China, wild pigs were previously named *S. scrofa chirodonta* (Heude, 1888) or *S. scrofa moupinensis* (Milne-Edwards, 1871) (Allen, 1940; Groves, 1981), both of which recent authors have elevated to species level: *S. chirodontus* Heude, 1888 and *S. moupinensis* Milne-Edwards, 1871 (Keuling et al., 2017).

---

## 4. Study on Intraspecific Variation of *Sus scrofa*

Suid fossils from YJW Cave 2 have been identified as *S. scrofa* primarily based on canine characters, excluding the possibility of co-existing suid species. However, significant attention must be paid to the great variation of third molars in both size and form [Figure 6: see original paper].

In this study, length (L) and widths of the first lobe (Wa), second lobe (Wb), and third lobe (Wc) of third upper and lower molars of *S. scrofa* from YJW Cave 2 were analyzed by scatter diagram. M3 length ranges between 29.1–41.0 mm, while widths are fairly variable. As shown in Fig. 6, data points show a trend of dividing into two groups, especially in the second lobe of M3 [Figure 6A: see original paper]. We interpret this as representing sexual dimorphism. Provisional groups were obtained based on this separation [FIGURE:6A, B], and further verification was conducted using PAST 3.26 (Hammer et al., 2001) to perform linear discriminant analysis (LDA) on length versus widths of the first, second, and third lobes of third molars. LDA is an effective feature extraction method that brings objects of the same category together while separating different categories as much as possible. By projecting data into different classifications, four groups were obtained. M3 data points [FIGURE:6C: a, b] and m3 data points [FIGURE:6C: c, d] each divided into two groups, indicating that the same anatomical object can indeed be separated into two groups. It is reasonable to attribute this to gender difference. Therefore, it may be possible to analyze sexual dimorphism in *S. scrofa* using only length versus widths of the first, second, and third lobes of third molars [Figure 6C: see original paper].

---

## 5. Conclusion

Late Pleistocene suid fossils from YJW Cave 2 are significantly larger than *S. xiaozhu*, overlap with *S. peii* to a certain extent, and are closest to *S. scrofa*. Morphologically, cheek tooth crown folds are more complicated than in *S. peii*. In crown measurements, they are narrower than *S. peii* and close to *S. scrofa*. Moreover, male lower canines of the fossil suid from YJW Cave 2 demonstrate a typical scrofic type. Therefore, suid fossils from YJW Cave 2 should be classified as *S. scrofa*. The large number of *S. scrofa* teeth from YJW Cave 2 provides material for studying intraspecific variation. After studying canine teeth and 209 upper and lower third molars, results display obvious sexual dimorphism.

---

## Acknowledgements

We thank the following institutions and individuals for their assistance: The Cultural Relics Bureau of Jiangxi; Bureau of Culture, Radio, Television and Press and Publication of Pingxiang; Bureau of Culture, Radio, Television and Press and Publication of Shangli County for strong support of field surveys and excavations; Mr. Yang Zhangqian and his family for providing fossil clues and various conveniences; Mr. Yang Jingbo and his family for providing convenient living conditions; Dr. Wang Qiang for preliminary contact work; Dr. Zhao Keliang, Dr. Ge Junyi, and Mr. Yang Qingjiang for participating in partial field work and sampling; Liu Yuchun, Li Yan, Xiang Fei, Peng Wei, Li Wentao, Zhou Yunsong, Liu Guijun, Luo Na, and others from Pingxiang Museum for excavation work; Cui Xindong for assistance with data analysis; Cai Jiachen for photo processing; Prof. J. Van der Made for sharing bibliography and fruitful discussions; and Prof. Dong W and Dr. Hou S K for critical manuscript reviews. This work was supported by the Strategic Priority Research Program of Chinese Academy of Sciences (XDB26000000), the National Natural Science Foundation of China (41572003), and the Special Fund for Fossil Excavation and Preparation, CAS.

## References

Allen G M, 1940. Mammals of China and Mongolia. New York: American Museum of Natural History. Part 2: 1114-

Albarella U, Dobney K, Rowley-Conwy P, 2015. Size and shape of the Eurasian wild boar (*Sus scrofa*), with a view to the reconstruction of its Holocene history. *Environ Archaeol*, 14: 103-136

Bökönyi S, 1974. History of domestic mammals in Central and Eastern Europe. *Technol Cult*, 17: 108

Chen G F, 2004. Artiodactyla. In: Zheng S H ed. *Jianshi Hominid Site*. Beijing: Science Press. 1-412

Cherin M, Sorbelli L, Crotti M et al., 2018. New material of *Sus strozzii* (Suidae, Mammalia) from the Early Pleistocene of Italy and a phylogenetic analysis of suines. *Quat Sci Rev*, 194: 94-115

Colbert E H, Hooijer D A, 1953. Pleistocene mammals from the limestone fissures of Szechwan, China. *Bull Am Mus Nat Hist*, 102: 1-134

Dong W, 2008. Early Pleistocene suid (mammal) from the Dajushan, Huainan, Anhui Province (China). *Vert PalAsiat*, 46:

Ducrocq S, 1994. An Eocene peccary from Thailand and the biogeographical origins of the artiodactyl family Tayassuidae. *Palaeontology*, 37: 765-779

Ducrocq S, Chaimanee Y, Suteethorn V et al., 1998. The earliest known pig from the Upper Eocene of Thailand. *Palaeontology*, 41: 147-156

Endo H, Kurohmaru M, Hayashi Y, 1994. An osteometrical study of the cranium and the mandible of the Ryuku wild pig in Iriomote Island. *J Vet Med Sci*, 56(5): 855-860

Evin A, Dobney K, Schafberg R et al., 2015. Phenotype and animal domestication: a study of dental variation between domestic, wild, captive, hybrid and insular *Sus scrofa*. *BMC Evol Biol*, 15: 1-16

Flannery K V, 1983. Early pig domestication in the Fertile Crescent: a retrospective Look. In: Young T C et al. ed. *The Hilly Flanks. Essays on the Prehistory of Southwestern Asia Presented to Robert J. Braidwood*, November L5, 1982. 163-

Frantz L, Meijaard E, Gongora J et al., 2016. The evolution of Suidae. *Annu Rev Anim Biosci*, 4: 61-85

Fujita M, Kawamura Y, Murase N, 2000. Middle Pleistocene wild boar remains from NT Cave, Niimi, Okayama Prefecture, West Japan. *J Geosci Osaka City Univ*, 43: 57-95

Gentry A W, Hooker J J, 1988. The phylogeny of the Artiodactyla. In: Benton M J ed. *The Phylogeny of the Tetrapods*. Oxford: Clarendon. 235-272

Groves C, 1981. Ancestors for the pigs: taxonomy and phylogeny of the genus *Sus*. *Tech Bull*, 3: 1-96

Groves C, 2007. Current views on taxonomy and zoogeography of the genus *Sus*. In: Albarella U et al. eds. *Pigs and Humans: 10,000 years of Interaction*. Oxford: Oxford University Press. 15-29

Groves C, Grubb P, 1993. The suborder Suiformes. In: Oliver W ed. *Pigs, Peccaries, and Hippos: Status Survey and Conservation Action Plan*. Gland, Switzerland: International Union for Conservation of Nature and Natural Resources (IUCN). 1-4

Hammer Ø, Harper D A T, Paul D R, 2001. Past: paleontological statistics software package for education and data analysis. *Palaeontol Electron*, 4: 1-9; http://palaeo-electronica.org/2001_1/past/issue1_{01}.htm

Han D F, Xu C H, Yi G Y, 1975. Quaternary mammalian fossils from Bijiashan, Liuzhou, Guangxi. *Vert PalAsiat*, 13: 250-

Han D F, 1987. Artiodactyla fossils from Liucheng Gigantopithecus cave in Guangxi. In: *Memoirs of Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica*, No. 18. Beijing: Science Press. 135-208

Hardjasasmita H S, 1987. Taxonomy and phylogeny of the Suidae (Mammalia) in Indonesia. *Scrip Geol*, 85: 1-68

Harrison D L, Bates P J J, 1968. *The Mammals of Arabia*. London: Ernest Benn Limited. 308-313

Heude P M, 1888. Etude sur les Suilliens. Chapter I. *Mém Hist Nat Emp Chinois*, 2(3): 52-64

Higham C, 1968. Size trends in prehistoric European domestic fauna, and the problem of local domestication. Helsinki: *Acta Zool Fenn*, 120: 1-21

Hou S K, Su D F, Kelley J et al., 2018. New fossil suid specimens from the terminal Miocene hominoid locality of Shuitangba, Zhaotong, Yunnan Province, China. *J Mammal Evol*, 26: 557-571

Ide Y, Nakahara T, Nasu M et al., 2013. Postnatal mandibular cheek tooth development in the miniature pig based on two-dimensional and three-dimensional X-ray analyses. *Anat Rec*, 296(8): 1247-1254

Jiangzuo Q G, Zhang B, Deng L et al., 2018. Fossil Carnivora (Mammalia) from Yangjiawan Cave 2, Pingxiang, Jiangxi, with remarks about the tooth identification of Quaternary Carnivores. Paper presented at proceedings of the sixteenth annual meeting of the Chinese Society of Vertebrate Paleontology. Beijing: China Ocean Press. 119-146

Keuling O, Podgórski T, Monaco A et al., 2017. Chapter 21: Eurasian wild boar *Sus scrofa* (Linnaeus, 1758). In: Melletti M, Meijaard E eds. *Ecology, Conservation and Management of Wild Pigs and Peccaries*. Cambridge: Cambridge University Press. 202-233

Liu L P, 2001. Eocene suoids (Artiodactyla, Mammalia) from Bose and Yongle Basin, China, and the classification and evolution of the Paleogene suoids. *Vert PalAsiat*, 39: 115-128

Liu W H, Dong W, Zhang L M et al., 2017. New material of Early Pleistocene *Sus* (Artiodactyla, Mammalia) from Yangshuizhan in Nihewan Basin, North China. *Quat Int*, 434: 32-47

McKenna M C, Bell S K, 1997. *Classification of Mammals Above the Species Level*. New York: Columbia University Press.

Mayer J J, Brisbin I L Jr, 1988. Sex identification of *Sus scrofa* based on canine morphology. *J Mammal*, 69: 408-412

Mayer J J, Brisbin I L Jr, 1991. *Wild Pigs in the United States: Their History,* *Morphology, and Current Status*. Athens: University of Georgia Press. 1–313

Mayer J J, Brisbin I L Jr, 1993. Distinguishing Feral Hogs from introduced wild boar and their hybrids: a review of past and present efforts. In: Hanselka C W, Cadenhead J F eds. *Feral Swine: A Compendium for Resource Managers*. San Angelo: Texas Agricultural Extension Service. 28–49

Mayer J J, Novak J M, Brisbin I L Jr, 1998. Evaluation of molar size as a basis for distinguishing wild boar from domestic swine: employing the present to decipher the past. In: Nelson S M ed. *Ancestors for the Pigs: Pigs in Prehistory*. Philadelphia: University of Pennsylvania Press. 39–53

Milne-Edwards A, 1871. Descriptions of new species: in footnotes. In David A, *Journal d' un voyage en Mongolie et en Chine fait en 1866-68. Nouv Arch Mus d' Hist Nat Paris Bull*, 7: 91–93

Payne S, Bull G, 1988. Components of variation in measurements of pig bones and teeth and the use of measurements to distinguish wild from domestic pig remains. *Archaeozoology*, 2: 27–66

Qi G Q, Lin Z Y, An J Y, 2006. Animal remains from Dadiwan site. In: The Gansu Provincial Institute of Cultural Relics and Archaeology ed. *Dadiwan in Qin' an—Report on Excavations at a Neolithic Site* (Vol II). Beijing: Cultural Relics Publishing House. 861–910

Stampfli H R, 1983. The fauna of Jarmo with notes on animal bones from Matarrah, the Amuq, and Karim Shahir. In: Braidwood L S et al. eds. *Prehistoric Archaeology Along the Zagros Flanks*. Chicago: Verlag nicht ermittelbar. 431–

Tong H W, Deng L, Chen X et al., 2018. Late Pleistocene proboscideans from Yangjiawan caves in Pingxiang of Jiangxi, with discussions on the *Stegodon orientalis-Elephas maximus* assemblage. *Vert PalAsiat*, 56: 306–326

van der Made J, 1996. Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. *Contrib Tert Quat Geol*, 33: 3–254

Wilkinson A F, 1976. The Lower Miocene Suidae of Africa. In: Savage R J G, Coryndon S C eds. *Fossil Vertebrates of Africa*, vol 4. London/New York: Academic Press. 173–282

Young C C, 1932. On the Artiodactyla from the Sinanthropus site at Choukoutien. *Pal Sin*, Ser C, 8(2): 1–100

Zeuner F E, 1963. *A History of Domesticated Animals*. London: Hutchinson. 1–560

Zhang B, Zou S L, Chen X et al., 2017. Mammalian fossils from Yangjiawan Cave 2 of Pingxiang, Jiangxi Province and the indication of age. *Quat Sci*, 37: 155–165

Zhang B, Chen X, Tong H W, 2018. Tooth remains of Late Pleistocene moschid and cervid (Artiodactyla, Mammalia) from Yangjiawan and Fuyan Caves of southern China. *Quat Int*, 490: 21–32

Zou S L, Chen X, Zhang B et al., 2016. Preliminary report on the Late Pleistocene mammalian fauna from Shangli County, Pingxiang, Jiangxi Province. *Acta Anthropol Sin*, 35: 109–120