

Three new fossil records of *Equisetum* (Equisetaceae) from the Neogene of south-western China and northern Vietnam

Aye Thida Aung^{1,2,3}, Jian Huang¹, Truong Van Do^{4,5}, Ai Song^{1,6},
Jia Liu¹, Zhe-Kun Zhou^{1,7}, Tao Su^{1,2,3}

1 CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, China **2** University of Chinese Academy of Sciences, Beijing 100049, China **3** Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences, Yezin, Nay Pyi Taw 05282, Myanmar **4** Vietnam National Museum of Nature, Vietnam Academy of Science and Technology, Hanoi, 100803, Vietnam **5** Graduate University of Science and Technology, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet, Hanoi, Vietnam **6** Research Center for Earth System Science, Yunnan University, Kunming 650500, China **7** CAS Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650204, China

Corresponding author: Tao Su (sutao@xtbg.org.cn)

Academic editor: Nianhe Xia | Received 31 July 2019 | Accepted 11 October 2019 | Published 10 January 2020

Citation: Aung AT, Huang J, Do TV, Song A, Liu J, Zhou Z-K, Su T (2020) Three new fossil records of *Equisetum* (Equisetaceae) from the Neogene of south-western China and northern Vietnam. In: Jin X-H, Xia N-H, Tan Y-H (Eds) Plant diversity of Southeast Asia-II. *PhytoKeys* 138: 3–15. <https://doi.org/10.3897/phytokeys.138.38674>

Abstract

Three fossil species of *Equisetum* (Equisetaceae) were reported from the Neogene of south-western China and northern Vietnam, based on well-preserved rhizomes with tubers. *Equisetum* cf. *pratense* Ehrhart from the middle Miocene of Zhenyuan County, Yunnan Province, China is characterised by a bunch of three ovate tubers with longitudinal ridges on the surface. *Equisetum yenbaiense* A.T. Aung, T. Su, T.V. Do & Z.K. Zhou, **sp. nov.** from the late Miocene of Yenbai Province, Vietnam is characterised by four bunches of elongate tubers arranged in a whorl on a node. *Equisetum yongpingense* A.T. Aung, T. Su & Z.K. Zhou, **sp. nov.** from the late Pliocene of Yunnan is characterised by fibrous roots on most nodes and two to four bunches of large cylindrical tubers arranged in a whorl on a node. Floristic assemblages suggest that these species might have grown near a riverside or lakeshore. These new fossil records improve our understanding of species richness of *Equisetum* and their distribution range during the Neogene in Asia.

Keywords

Diversity, *Equisetum*, Miocene, Pliocene, rhizome tubers

Introduction

The order Equisetales, including Calamitaceae, Tchernoviaceae, Gonduanostachyaceae and Equisetaceae, has a very long evolutionary history that can be dated back to the Devonian (Gu and Shi 1974; Wang et al. 2005). Amongst the families, only Equisetaceae is extant. The earliest fossil record of Equisetaceae could be traced back to the Carboniferous, with *Equisetites hemingwayii* from the early Pennsylvanian of Yorkshire, UK (Kidston 1883). *Equisetum* (Horsetails) is the only living genus in the family Equisetaceae, with about 15 species distributed widely around the world, except for Antarctica (Kenrick and Crane 1997). It is characterised by hollow aerial stems with nodes and reduced leaves, which are similar to their arborescent ancestors. *Equisetum laterale* from the Middle Triassic of Australia is the oldest fossil species in *Equisetum* (Gould 1968). Even some *Equisetum*-like fossils from the Mesozoic have been identified as *Equisetum*, the divergence of *Equisetum* species occurred during the late Eocene (~40 Ma) according to molecular data, with the main radiation during the Neogene (Des Marais et al. 2003; Elgorriaga et al. 2018).

In *Equisetum* fossils, tuberous rhizomes are the most commonly preserved organ in the Cenozoic strata around the world, such as in North America (Lesquereux 1878; Bell 1949; Becker 1969; Skog and Dilcher 1994), Europe (Watson and Batten 1990; Denk et al. 2005) and Asia (Kon'no 1962; Wu 1999; Sun et al. 2001). In China, the fossil records are rich, but most fossils are limited in northern China, for examples, in the Lower Cretaceous Yixian Formation and Fuxin Formation in Liaoning (Chen et al. 1988; Sun et al. 2001), the Lower Cretaceous Muling Formation of Jixi Basin, Heilongjiang (Yang 2003) and the Middle Eocene Hunchun Formation in Jilin (Guo 2000). In south-western China, only four fossil records of *Equisetum* have been found, i.e. *Equisetum* cf. *oppositum* from the Paleocene-Eocene of the Niubao Formation in Nima Basin, northern Tibet (Yang et al. 2016), *Equisetum oppositum* from the Lower Oligocene Lawula Formation in eastern Tibet (Ma et al. 2012), *Equisetum* cf. *pratense* from the Lower Oligocene of Lühe coal-mine in south-central Yunnan (Zhang et al. 2007) and *Equisetum* sp. from the Middle Miocene Wulong Formation in southern Tibet (Geng and Tao 1982).

Although some species of *Equisetum* still survive in Asia nowadays, such as *Equisetum diffusum*, *Equisetum hyemale* and *Equisetum pratense*, its fossil records remain limited, especially during the Neogene. In this study, we describe three fossil species of *Equisetum* from the Neogene of south-western China and northern Vietnam. Further, we discuss the ecological and biogeographic implications, based on these new fossil records.

Materials and methods

Fossil localities

Zhenyuan, south-western China (the middle Miocene). A fossil was found in the Dajie Formation, Sanzhangtian Village, Zhenyuan County, central Yunnan Province, south-western China (Fig. 1). The Dajie Formation, which is mainly distributed in

central Yunnan, is assigned to the middle Miocene in age, based on lithological and palynological comparisons (Bureau of Geology and Mineral Resources of Yunnan Province (BGMRYP) 1990). Fossil in this study is from light yellow mudstone of the upper layer in the stratum. Many plant fossil species have been previously reported from the same site, including *Palaeosorum ellipticum* (Jacques et al. 2013), *Bambusium angustifolia*, *B. latifolia*, *Bambusiculmus angustus*, *B. latus* (Wang et al. 2013), *Celastrus caducidentatus* (Liang et al. 2016a), *Populus zhenyuanensis* (Liang et al. 2016b), *Cladium zhenyuanensis* (Liang et al. 2017), *Zygogynum poratus* (Liang et al. 2018), and *Metasequoia* cf. *glyptostroboides* (Wang et al. 2019).

Yen Bai, northern Vietnam (the late Miocene). Fossils were found in the Co Phuc Formation, Hop Thanh Village, Tuy Loc Commune, Yen Bai Province, northern Vietnam (Fig. 1). The fossil site is situated in the Yen Bai Basin along the Red River Fault Zone, which is a main Cenozoic strike-slip zone in Southeast Asia. The Co Phuc Formation belongs to the late Miocene in age which mainly consists of siltstone and fine sandstone (Wysocka and Świerczewska 2010). The fossils included in this study were collected from the yellow siltstone of the upper layer. Plant fossils such as Polypodiaceae, Palmae and Lauraceae have been previously reported from the fossil site (Zeiller 1903; Colani 1920).

Yongping, south-western China (the late Pliocene). The fossils were found in the Sanying Formation, Longmen Village, Yongping County, Yunnan Province, south-western China (Fig. 1). According to a recent paleomagnetic study, the Sanying Formation was dated from the late Miocene to the early Pleistocene (Li et al. 2013). This formation is widely distributed in western and north-western Yunnan Province (BGMRYP 1990). Fossils here are from siltstone in the middle part of the stratum, which is dominated by *Quercus* section *Heterobalanus* (evergreen sclerophyllous oak) (Su 2010). Some other species, including *Drynaria callispora* (Su et al. 2011) and *Cedrus angusta* (Su et al. 2013b) have been reported from the same site. According to paleoclimate reconstruction using leaf assemblage of the flora, a warmer and more humid climate than nowadays existed in western Yunnan during the late Pliocene (Su et al. 2013a).

Morphological observation

Equisetum fossils were imaged to view gross morphology by using a digital camera (Nikon D700) with a Kaiser 5510 stand and oblique light. To observe morphological characters in detail, fossils were photographed by stereoscope microscopes (Leica A8APO and ZEISS Smart Zoom 5). The contrast of images was slightly adjusted using the software Adobe Photoshop (version CC 2018). Morphological characters were measured by ImageJ (version 1.52). For comparison with previously published fossil taxa, we checked fossil records from online databases, for examples, Web of Science and Google Scholar. All fossil specimens in this study are deposited in the Paleoecology Collections, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences and Vietnam National Museum of Nature, Vietnam Academy of Science and Technology.

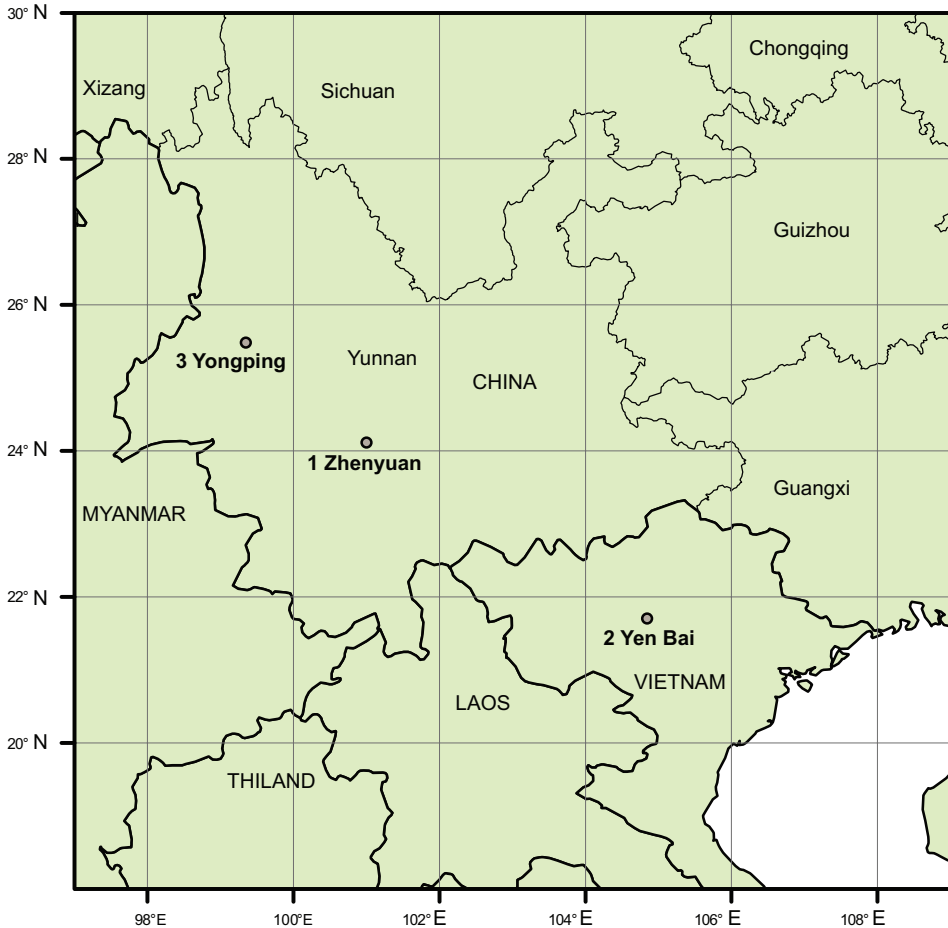


Figure 1. Map showing the locations of the fossils collected in this study. 1. Sanzhangtian, Zhenyuan County, Yunnan, south-western China (the middle Miocene); 2. Hop Thanh Village, Tuy Loc Commune, Yen Bai Province, northern Vietnam (the late Miocene); 3. Longmen, Yongping County, Yunnan Province, south-western China (the late Pliocene).

Results

Order Equisetales Dumortier

Family Equisetaceae A. Michaux ex Alph. De Candolle

Genus *Equisetum* Linnaeus

Equisetum fossils from Zhenyuan, south-western China

Equisetum cf. *pratense* Ehrhart

Specimens checked. XTBGSTZF0001 (Fig. 2A–B)

Locality. Dajie Formation, Sanzhangtian Village, Zhenyuan County, central Yunnan Province, South-western China (24.100N, 101.216E).

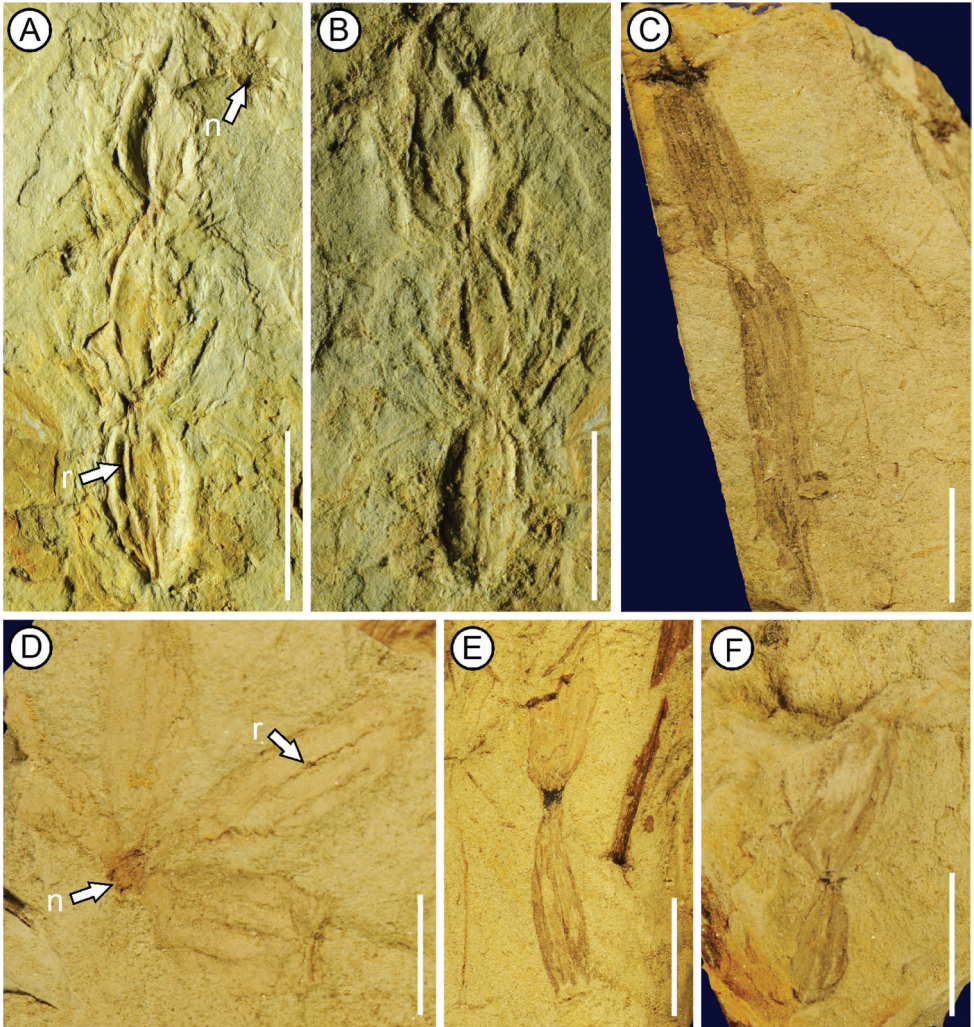


Figure 2. **A–B** *Equisetum* cf. *pratense* Ehrhart **C–F** *Equisetum* *yenbaiense* A.T.Aung, T.Su, T.V.Do & Z.K.Zhou, sp. nov. Specimen numbers: **A–B** XTBG SZTF0001 (counterparts) **C** XTBGVNMN4002 **D** XTBGVNMN4001 **E** XTBGVNMN4003 **F** XTBGVNMN4004. **n** = node; **r** = ridge. Scale bars: 1 cm.

Age. The middle Miocene.

Repository. Paleoecology Collections, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences.

Description. Only one bunch of tubers are preserved on the specimen, tubers are ovate in shape, three tubers of equal size are arranged in one row (Fig. 2A–B). The length and width of the tubers are ~ 0.9 to 1.2 cm and 0.6 to 0.8 cm, respectively. Two to three longitudinal ridges are present on the surface of each tuber (Fig. 2A–B). The tip of the tuber is mucronate (Fig. 2A–B). These characters fit well within the morphology of *E. cf. pratense*, a fossil species reported from the early Oligocene in the Lühe coal-mine, south-central Yunnan (Zhang et al. 2007; Linnemann et al. 2018).

Equisetum fossils from Yen Bai, northern Vietnam*Equisetum yenbaiense* A.T.Aung, T.Su, T.V.Do & Z.K.Zhou, sp. nov.

Holotype. XTBGVNMN4001 (Fig. 2D).

Paratypes. XTBGVNMN4002–4004 (Fig. 2C, E–F).

Locality. Hop Thanh Village, Tuy Loc Commune, Yen Bai Province, northern Vietnam (21.725N, 104.849E).

Age. The late Miocene.

Repository. Paleoecology Collections, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences and Vietnam National Museum of Nature, Vietnam Academy of Science and Technology.

Etymology. The species name ‘*yenbaiense*’ means that fossils are from Yen Bai Province, northern Vietnam.

Diagnosis. Rhizomes with internodes and nodes, node round; Four bunches of tubers arranged in a whorl on a node (Fig. 2D); most tubers elongate in shape, with one to two tubers in each bunch (Fig. 2C–D); longitudinal ridges on the surface of tuber; the tip of tuber mucronate (Fig. 2F).

Description. Rhizomes have both internodes and nodes (Fig. 2D). The internode is ~0.2–0.3 cm in width, the length could not be observed, three longitudinal ridges are on the surface of the internode (Fig. 2D). The node is round and ~0.2 cm in diameter (Fig. 2D). Four bunches of tubers attach to one node and arrange in a whorl (Fig. 2D). Only one tuber is preserved on each bunch, but it is likely that there are more than one tuber on each bunch (Fig. 2E–F). Most tubers are elongate (Fig. 2D); few are elliptical (Fig. 2F), being ~0.8 to 3.0 cm long and 0.4 to 1.0 cm wide. Two to four ridges are on the surface of each tuber (Fig. 2D). The tip of tuber is mucronate (Fig. 2F).

Equisetum fossils from Yongping, South-western China*Equisetum yongpingense* A.T.Aung, T.Su & Z.K. Zhou, sp. nov.

Holotype. XTBGYP0748 (Fig. 3A).

Paratypes. XTBGYP0747 (Fig. 3B), XTBGYP1014 (Fig. 3C), XTBGYP1015 (Fig. 3D), XTBGYP0750 (Fig. 3E), XTBGYP0749 (Fig. 3F).

Locality. Sanying Formation, Longmen Village, Yongping County, western Yunnan Province, south-western China (25.518N, 99.519E).

Age. The late Pliocene.

Repository. Paleoecology Collections, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences.

Etymology. The species name ‘*yongpingense*’ means that fossils are from Yongping County, south-western China.

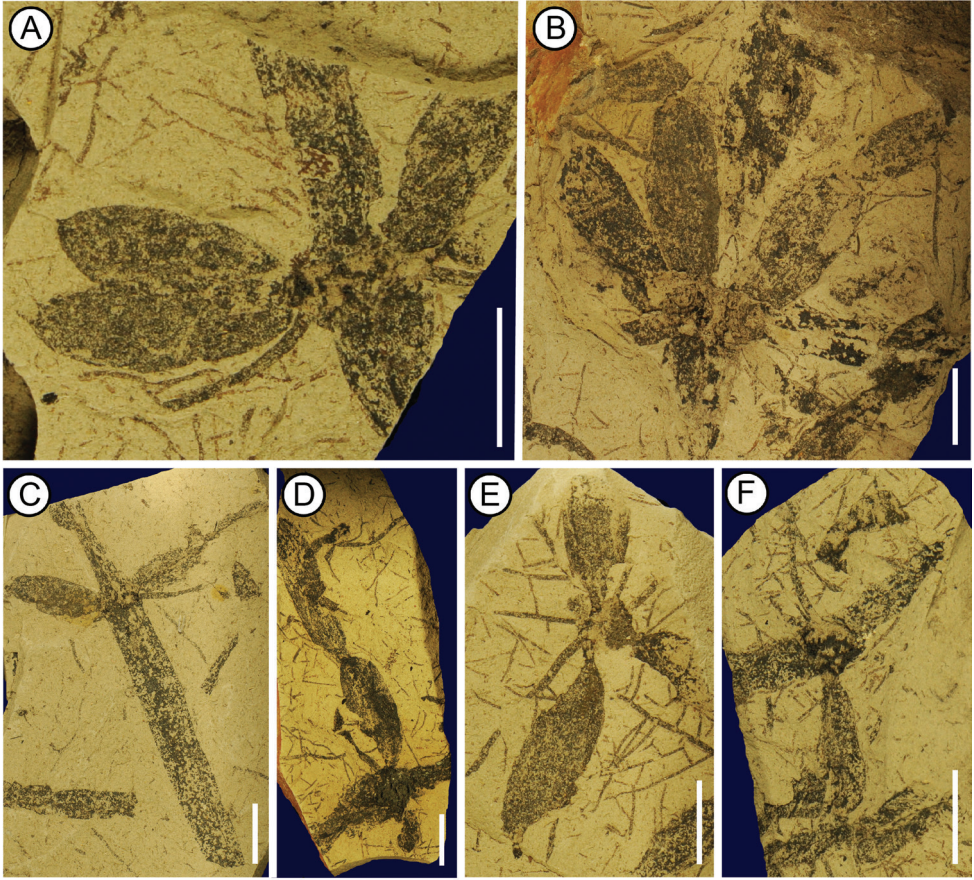


Figure 3. *Equisetum yongpingense* A.T.Aung, T.Su & Z.K.Zhou, sp. nov. Specimen numbers: **A** XTBYGP0748 **B** XTBYGP0747 **C** XTBYGP1014 **D** XTBYGP1015 **E** XTBYGP0750 **F** XTBYGP0749. Scale bars: 1cm.

Diagnosis. Rhizomes with internodes and round nodes; fibrous roots on most nodes; two to four bunches of tubers arranged in a whorl on a node (Fig. 3A); tubers cylindrical in shape, one to two tubers on each bunch (Fig. 3A–B); longitudinal ridges not observed on the surface of tuber; the tip of tuber mucronate (Fig. 3A).

Description. Rhizomes have both internodes and nodes (Fig. 3A). The internode is ~0.5 to 0.8 cm wide, the length is up to 5.1 cm (Fig. 3A). The node is round and ~0.7 to 1.0 cm in diameter (Fig. 3A–B). Most nodes have fibrous roots ~0.1 to 0.2 cm wide. Two to six bunches of tubers attach on one node and are arranged in a whorl (Fig. 3A–B). One to two tubers are preserved on each bunch (Fig. 3A–B). Tubers are cylindrical, ~1.5 to 3.4 cm long and 0.6 to 1.2 cm wide (Fig. 3A–F). Ridges were not observed on the surface of each tuber (Fig. 3A–B, E). The tip of tuber is mucronate (Fig. 3A).

Discussion

In this study, we reported three new fossil records of *Equisetum* from south-western China and northern Vietnam, based on well-preserved rhizomes with tubers. In *Equisetum*, tubers are the most commonly preserved organ in the fossil records. They are mainly characterised by either a single tuber or one bunch of tubers with longitudinal ridges on the surface, present on fossils we collected (Figs 2–4). These three new fossil records vary in morphological characters, such as the shape and size of tubers (Table 1). They are also different from living species of *Equisetum*, for example, *Equisetum pratense*, as they have larger tuber sizes, based on available information (Zhang et al. 2007; Sun et al. 2013).

Equisetum cf. *pratense* from the middle Miocene of Zhenyuan, south-western China have an ovate tuber shape, which is similar to most fossil records of *Equisetum*, but different from some fossil species, for example, the tubers of *Equisetites longevaginatus* are elliptical or round in shape (Table 1). The size of tubers in *E.* cf. *pratense* is smaller than other fossil species, such as *Equisetum oppositum*, *Equisetum* cf. *oppositum* and *Equisetum hunchunense* (Table 1). Generally, all observed morphological characters of the fossil, such as the size and shape of tubers, as well as the mucronate tip of tubers, were in accordance with *E.* cf. *pratense*, a fossil species previously reported from the early Oligocene of the Lühe coal-mine, south-central Yunnan (Zhang et al. 2007). However, we only found one bunch of tubers at the fossil site, whereas the fossils from the Lühe coal-mine have one to four bunches of tubers with an acervate arrangement on rhizome nodes. More fossils are needed to further determine the arrangement of tubers to better understand the systematic relationship between these two fossil records. Judging by the high morphological similarity, we assign the fossil from Zhenyuan as *E.* cf. *pratense*.

For *Equisetum yenbaiense* from the late Miocene of northern Vietnam, the tuber arrangement is a whorl on a rhizome node, which also occurs in *E. hunchunense* and *E.* cf. *arcticum*. However, both *E. hunchunense* and *E.* cf. *arcticum* have two to three tubers per bunch, whereas *E. yenbaiense* only has one or two tubers per bunch, which might be partly due to the preservation of the fossil. In addition, there are more than three tubers per bunch in *E. oppositum* and *E.* cf. *oppositum* (Table 1). The shape of tubers in *E. yenbaiense* is elongate, the ratio between length and width is higher than most other fossil species, except for *E.* cf. *arcticum*. We noted that the tuber size in *E. yenbaiense* is larger than that in *E.* cf. *arcticum* (Table 1). Therefore, we designate the new fossil specimens from northern Vietnam as a new species, namely, *E. yenbaiense* A.T. Aung, T. Su, T.V. Do & Z.K. Zhou, sp. nov.

In *Equisetum yongpingense*, there are two to four bunches of tubers arranged in a whorl on a node, which has the same pattern as *E. hunchunense* and *E.* cf. *arcticum*. The tip of the tubers is mucronate in *E. yongpingense*, which is also present on other previously reported fossil species (Table 1). However, the tuber shape of *E. yongpingense* is cylindrical, which is different from other fossil records. Ridges on the surface of tubers are not prominent in *E. yongpingense*, whereas ridges are present in other fossil species.

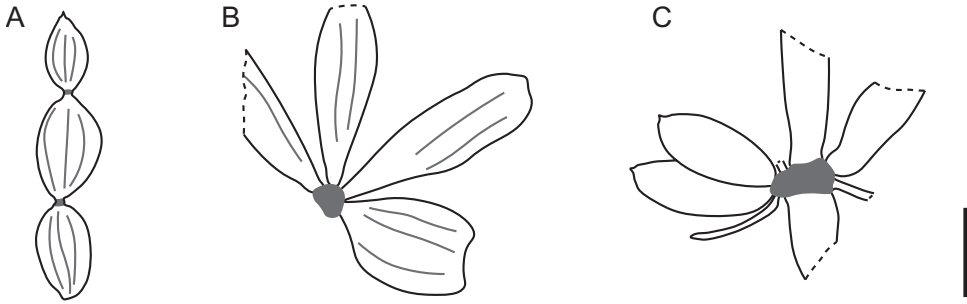


Figure 4. Reconstruction of *Equisetum* from **A** Zhenyuan, south-western China, specimen number XTBGSTZF0001 **B** Yanbei, northern Vietnam, specimen number XTBGVNMN4001; and **C** Yongping, south-western China, specimen number XTBGYP0748. Scale bar: 1.5 cm.

Table 1. Morphological comparisons between new fossil records in this study and previously reported *Equisetum* and *Equisetites* fossil species.

Species	Tuber arrangement	Number of tubers per bunch	Shape of tuber	Tuber length (cm)	Tuber width (cm)	Age	Locality	References
<i>Equisetum</i> sp.	?	3	Elliptical	1.0–1.2	0.6–0.8	Miocene	Iceland	Denk et al. 2005
<i>Equisetum</i> cf. <i>arcticum</i>	Whorl	2–3	Elongate, ovate, round	1.5–2.5	0.5–0.7	Oligocene to Miocene	America	Becker 1969
<i>Equisetum hunchunense</i>	Whorl	2–3	Elliptical, ovate	1.5	0.4–0.9	Eocene	China	Guo 2000
<i>Equisetum jiuquanense</i>	Single to acervate	2–3	Elliptical, ovate, round	0.3–0.8	0.4–0.7	Early Cretaceous	China	Sun et al. 2013
<i>Equisetites longevaginatus</i>	Single or opposite	2–3	Elliptical, round	0.5–0.8	0.3–0.5	Cretaceous	China	Sun et al. 2001
<i>Equisetum oppositum</i>	Opposite	6	Round, elliptical, ovate	1.0–1.6	0.8–1.2	Early Oligocene	China	Ma et al. 2012
<i>Equisetum</i> cf. <i>oppositum</i>	Single	5–6	Elliptical, ovate, and nearly round	1.0–1.6	0.8–1.2	Paleocene–Eocene	China	Yang et al. 2016
<i>Equisetum</i> cf. <i>pratense</i>	?	3	Ovate	0.9–1.2	0.6–0.8	Middle Miocene	China	This study
<i>Equisetites vittatus</i>	Whorl	1–2	Elliptical, elongate	0.8–3.0	0.4–1.0	Late Miocene	Vietnam	This study
<i>Equisetum yongpingense</i>	Whorl	1–2	Cylindrical	1.5–3.4	0.6–1.2	Late Pliocene	China	This study

In *E. yongpingense*, fibrous roots were also observed on the rhizome node, which is not observed on other fossil species. Therefore, we name these fossil specimens from Yongping as *E. yongpingense* A.T.Aung, T.Su & Z.K.Zhou, sp. nov.

The three new fossil records described in this study expand the distribution of *Equisetum* during the Neogene in Asia. These findings and previous fossil records indicate that *Equisetum* has been widely distributed in Asia since the Paleocene and become diverse in Asia since the Oligocene. According to fossil assemblages, *Equisetum* mainly grew under wet conditions. Other taxa that were reported from the same stratum in Zhenyuan, such as *Palaeosorum ellipticum* (Jacques et al. 2013), *Bambusium angustifolia*, *B. latifolia*, *Bambusiculmus angustus*, *B. latus* (Wang et al. 2013) and *Metasequoia* cf. *glyptostroboides* (Wang et al. 2019), tend to grow near the riverside or lakeshore. Therefore, we considered that *E. cf. pratense* might favour a similar habitat. In addition,

E. yongpingense was found in the Upper Pliocene of western Yunnan, where numerous fruits from *Trapa*, an aquatic plant, had also been found in the same layer (Su 2010). Therefore, this habit might have persisted throughout the Cenozoic. Tubers indicate a perennial living form and should contribute to the adaptation of *Equisetum* under seasonally unfavourable conditions by storing starch (Taiz and Zeiger 2010). Eventually, tubers became important elements in local vegetation, which was evidenced by the abundance of specimens in many fossil sites (Becker 1969; Guo 2000; Ma et al. 2012; Yang et al. 2016).

Acknowledgements

We thank members from Paleocology Research Group in Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences (CAS) for fossil collection; the Public Technology Service Center, XTBG for imaging; Dr. X-Y Liu and Dr. J-Y Wu for reviewing this manuscript and many constructive suggestions. This work is supported by the NSFC (National Natural Science Foundation of China)–NERC (Natural Environment Research Council of the United Kingdom) joint research programme (41661134049 and NE/P013805/1), the National Natural Science Foundation of China (41922010, U1502231, 31800183), Strategic Priority Research Programme of CAS (XDA20070301 and XDB26000000), Natural Science Foundation of Yunnan Province (2019FB026), and Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences (CAS-SEABRI) (No. Y4ZK111B01).

References

- Becker HF (1969) Fossil plants of the Tertiary Beaverhead basins in southwestern Montana. *Palaeontographica Abteilung B* 127: 1–142.
- Bell WA (1949) Uppermost Cretaceous and Paleocene floras of western Alberta. *Geological Survey of Canada. Bulletin* 13: 1–231. <https://doi.org/10.4095/101514>
- Bureau of Geology and Mineral Resources of Yunnan Province (BGMRYP) (1990) *Regional Geology of Yunnan Province*. Geological Publishing House, Beijing.
- Chen F, Meng XY, Ren SQ, Wu CL (1988) The Early Cretaceous flora of Fuxin and Tiefa Basin, Liaoning Province. Geological Publishing, Beijing.
- Colani M (1920) Étude sur les flores Tertiaires de quelquesgisements de lignite del' Indochineet Yunnan. *Bulletin Survey Geologique Indochine* 8(1): 1–58. <https://doi.org/10.5962/bhl.title.113040>
- Denk T, Grimsson F, Kvaček Z (2005) The Miocene floras of Iceland and their significance for late Cainozoic North Atlantic biogeography. *Botanical Journal of the Linnean Society* 149(4): 369–417. <https://doi.org/10.1111/j.1095-8339.2005.00441.x>
- Des Marais DL, Smith AR, Donald MB, Kathleen MP (2003) Phylogenetic relationships and evolution of extant horsetails, *Equisetum*, based on chloroplast DNA sequence data

- (*rbcL* and *trnL-F*). International Journal of Plant Sciences 164(5): 737–751. <https://doi.org/10.1086/376817>
- Elgorriaga A, Escapa IH, Rothwell GW, Tomescu AMF, Ruben Cuneo N (2018) Origin of *Equisetum*: Evolution of horsetails (Equisetales) within the major euphyllophyte Glade Sphenopsida. American Journal of Botany 105(8): 1286–1303. <https://doi.org/10.1002/ajb2.1125>
- Geng GC, Tao JR (1982) Tertiary plants from Xizang. Nanjing Institute of Geology and Palaeontology and Institute of Botany. Paleontology of Xizang. Science Press, Beijing, 110–125.
- Gould RE (1968) Morphology of *Equisetum laterale* Phillips, 1829, and *E. bryanii* sp. nov. from the Mesozoic of south-eastern Queensland. Australian Journal of Botany 16(1): 153–176. <https://doi.org/10.1071/BT9680153>
- Gu Z, Shi L (1974) Fossil plants of China (volume I), Palaeozoic plants from China. Science Press, Beijing.
- Guo SX (2000) New material of the Late Cretaceous flora from Hunchun of Jilin, Northeast China. Acta Palaeontologica Sinica 39(suppl.): 226–250.
- Jacques FMB, Su T, Zhou ZK (2013) The first fossil Microsoroid fern (*Palaeosorum ellipticum* gen. et sp. nov.) from the middle Miocene of Yunnan, SW China. Journal of Systematics and Evolution 51(6): 758–764. <https://doi.org/10.1111/jse.12030>
- Kenrick P, Crane PR (1997) The origin and early diversification of land plants: A cladistic study. Smithsonian Institution Press, Washington DC.
- Kidston R (1883) On the affinities of the genus *Pothocites*, Paterson; with the description of a specimen from Glencartholm, Eskdale. Annals & Magazine of Natural History 65(65): 297–314. <https://doi.org/10.1080/00222938309459157>
- Kon’No E (1962) Some species of *Neocalamites* and *Equisetites* in Japan and Korea. Science Reports of the Tohoku University 5: 24–47.
- Lesquereux L (1878) Contributions to the fossil flora of the western territories. II. The Tertiary flora. In: Hayden FV (Ed.) Report of the US Geological Survey. Government Printing Office, Washington DC, 67–69.
- Li SH, Deng CL, Yao HT, Huang S, Liu CY, He HY, Pan YX, Zhu RX (2013) Magnetostratigraphy of the Dali Basin in Yunnan and implications for late Neogene rotation of the south-east margin of the Tibetan Plateau. Journal of Geophysical Research. Solid Earth 118(3): 791–807. <https://doi.org/10.1002/jgrb.50129>
- Liang XQ, Ferguson DK, Su T, Zhou ZK (2016a) Fossil leaves of *Populus* from the Middle Miocene of Yunnan, SW China. Journal of Systematics and Evolution 54(3): 264–271. <https://doi.org/10.1111/jse.12193>
- Liang XQ, Ferguson DK, Jacques FMB, Su T, Wang L, Zhou ZK (2016b) A new *Celastrus* species from the middle Miocene of Yunnan, China and its palaeoclimatic and palaeobiogeographic implications. Review of Palaeobotany and Palynology 225: 43–52. <https://doi.org/10.1016/j.revpalbo.2015.11.005>
- Liang XQ, Lu P, Tiwari A, Su T, Zhou ZK (2017) New fossil record of *Cladium* (Cyperaceae) from the Middle Miocene of Zhenyuan, SW China, and the palaeobiogeographical history of the genus. Review of Palaeobotany and Palynology 237: 1–9. <https://doi.org/10.1016/j.revpalbo.2016.10.006>

- Liang XQ, Lu P, Zhang JW, Su T, Zhou ZK (2018) First fossils of *Zygogynum* from the Middle Miocene of Central Yunnan, Southwest China, and their palaeobiogeographic significance. *Palaeoworld* 27(3): 399–409. <https://doi.org/10.1016/j.palwor.2018.05.003>
- Linnemann U, Su T, Kunzmann L, Spicer RA, Ding WN, Spicer TEV, Zieger J, Hofmann M, Moraweck K, Gärtner A, Gerdes A, Marko L, Zhang ST, Li SF, Tang H, Huang J, Mulch A, Mosbrugger V, Zhou ZK (2018) New U-Pb dates show a Paleogene origin for the modern Asian biodiversity hot spots. *Geology* 46(1): 3–6. <https://doi.org/10.1130/G39693.1>
- Ma HJ, Zhang ST, Su T, Wang L, Sui SG (2012) New materials of *Equisetum* from the Upper Miocene of Mangkang, eastern Xizang and its ecological implications. *Journal of Jilin University* 42(suppl. 3): 189–195. [Earth Science Edition]
- Skog JE, Dilcher DL (1994) Lower vascular plants of the Dakota Formation in Kansas and Nebraska, USA. *Review of Palaeobotany and Palynology* 80(1–2): 1–18. [https://doi.org/10.1016/0034-6667\(94\)90089-2](https://doi.org/10.1016/0034-6667(94)90089-2)
- Su T (2010) On the establishment of the leaf physiognomy climate model and a study of the late Pliocene Yangjie flora, Southwest China (PhD thesis). Graduate University of the Chinese Academy of Sciences, Beijing.
- Su T, Jacques FMB, Liu YS, Xiang JY, Xing YW, Huang YJ, Zhou ZK (2011) A new *Drymaria* (Polypodiaceae) from the Upper Pliocene of Southwest China. *Review of Palaeobotany and Palynology* 164(1–2): 132–142. <https://doi.org/10.1016/j.revpalbo.2010.11.011>
- Su T, Jacques FMB, Spicer RA, Liu YS, Huang YJ, Xing YW, Zhou ZK (2013a) Post-Pliocene establishment of the present monsoonal climate in SW China: Evidence from the late Pliocene Longmen megafloora. *Climate of the Past* 9(4): 1911–1920. <https://doi.org/10.5194/cp-9-1911-2013>
- Su T, Liu YS, Jacques FMB, Huang YJ, Xing YW, Zhou ZK (2013b) The intensification of the East Asian winter monsoon contributed to the disappearance of *Cedrus* (Pinaceae) in southwestern China. *Quaternary Research* 80(2): 316–325. <https://doi.org/10.1016/j.yqres.2013.07.001>
- Sun G, Zheng SL, Dilcher DL, Wang YD, Mei SW (2001) Early angiosperms and their associated plants from western Liaoning, China. Shanghai Scientific and Technological Education Publishing House, Shanghai.
- Sun BN, Du BX, Ferguson DK, Chen JL, He YL, Wang YD (2013) Fossil *Equisetum* from the Lower Cretaceous in Jiuquan Basin, Gansu, Northwest China and its paleoclimatic significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* 385(1): 202–212. <https://doi.org/10.1016/j.palaeo.2013.06.005>
- Taiz L, Zeiger E (2010) *Plant Physiology*. 5th Edition. Sinauer Associates Inc., Sunderland.
- Wang DM, Hao SG, Wang Q (2005) *Rotafolia songziensis* gen. et comb. nov., a sphenopsisid from the Late Devonian of Hubei, China. *Botanical Journal of the Linnean Society* 148(1): 21–37. <https://doi.org/10.1111/j.1095-8339.2005.00387.x>
- Wang L, Jacques FMB, Su T, Xing YW, Zhang ST, Zhou ZK (2013) The earliest fossil bamboos of China (middle Miocene, Yunnan) and their biogeographical importance. *Review of Palaeobotany and Palynology* 197: 253–265. <https://doi.org/10.1016/j.revpalbo.2013.06.004>
- Wang L, Kunzmann L, Su T, Xing YW, Zhang ST, Wang YQ, Zhou ZK (2019) The disappearance of *Metasequoia* (Cupressaceae) after the middle Miocene in Yunnan, Southwest China:

- Evidences for evolutionary stasis and intensification of the Asian monsoon. Review of Palaeobotany and Palynology 264: 64–74. <https://doi.org/10.1016/j.revpalbo.2018.12.007>
- Watson J, Batten DJ (1990) A revision of the English Wealden flora. II. Equisetales. Bulletin of the British Museum (Natural History), Geology 46: 37–46.
- Wu SQ (1999) A preliminary study of the Rehe flora from western Liaoning. Palaeoworld 11(1): 7–37.
- Wysocka A, Świerczewska A (2010) Lithofacies and depositional environments of Miocene deposits from tectonically controlled basins (Red River Fault Zone, northern Vietnam). Journal of Asian Earth Sciences 39(3): 109–124. <https://doi.org/10.1016/j.jseas.2010.02.013>
- Yang XJ (2003) New material of fossil plants from the early Cretaceous Muling Formation of the Jixi Basin, eastern Heilongjiang Province, China. Acta Palaeontologica Sinica 42: 561–584.
- Yang GL, Wang ZX, Chen JW, Yan DF, Sun BN (2016) *Equisetum cf. oppositum* (Equisetaceae) from the Paleocene-Eocene of Tibet in southwestern China and its paleo environmental implications. Arabian Journal of Geosciences 9: 749. <https://doi.org/10.1007/s12517-016-2777-z>
- Zeiller R (1903) Flore fossile des gîtes de charbon du Tonkin: Texte. Imprimerie Nationale, Paris. <https://doi.org/10.5962/bhl.title.64389>
- Zhang YL, Ferguson DK, Ablaev AG, Wang YF, Li C-S, Xie L (2007) *Equisetum cf. pratense* (Equisetaceae) from the Miocene of Yunnan in Southwestern China and its paleoecological implications. International Journal of Plant Sciences 168(3): 351–359. <https://doi.org/10.1086/510411>