

Late Pliocene diversity and distribution of *Drynaria* (Polypodiaceae) in western Yunnan explained by forest vegetation and humid climates



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ABSTRACT

The palaeodiversity of flowering plants in Yunnan has been extensively interpreted from both a molecular and fossil perspective. However, for cryptogamic plants such as ferns, the palaeodiversity remains poorly known. In this study, we describe a new ferny fossil taxon, *Drynaria lanpingensis* sp. nov. Huang, Su et Zhou (Polypodiaceae), from the late Pliocene of northwestern Yunnan based on fragmentary frond and pinna with *in situ* spores. The frond is pinnatifid and the pinnae are entirely margined. The sori are arranged in one row on each side of the primary vein. The spores have a semicircular to bean-shaped equatorial view and a tuberculate surface. Taken together with previously described fossils, there are now representatives of three known fossil taxa of *Drynaria* from the late Pliocene of western Yunnan. These finds suggest that *Drynaria* diversity was considerable in the region at that time. As *Drynaria* is a shade-tolerant plant, growing preferably in wet conditions in the understory of forests, its extensive existence may indicate forest vegetation and humid climates in western Yunnan during the late Pliocene. This is in line with results from floristic investigations and palaeoclimatic reconstructions based on fossil floras.

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1. Introduction

Yunnan, located in far southwestern China, has long been recognized as a hotspot for plant diversity (Wu, 1988; López-Pujol et al., 2006, 2011; Ruth et al., 2008; Turkington and Harrower, 2016). It is home to approximately 16,000 vascular plant species, which are grouped into more than 400 families (Wu, 1979) and represent 6% of the world's higher plant species. In addition, the region supports the highest species richness for many plant groups, e.g., *Rhododendron* (Fang and Min, 1995) and *Pedicularis* (Yu et al., 2015). Previous studies have traced the history of species diversification in Yunnan, using either molecular data (e.g., Chen et al., 2005; Wang et al., 2005; Yu et al., 2015) or fossil evidence (e.g., Xing et al., 2010, 2013; Xie et al., 2014; Meng et al., 2014, 2015; Anberree et al., 2015; Jia et al., 2015; Zhang et al., 2015; Liang et al., 2016). However, these studies focused chiefly on flowering

plants. Non-seed plants, such as ferns, have received much less attention.

Drynaria (Bory) J. Smith in Polypodiaceae is a fern genus that comprises sixteen living species, distributed mainly in tropical and subtropical areas of the Northern Hemisphere (Ching, 1978; Zhang et al., 2013). Yunnan is home to nine extant species of *Drynaria*, and is thought to be the diversity center of the genus (Zhang et al., 2013). Unlike many other fern groups (Jacques et al., 2013), the fossil record for *Drynaria* in Yunnan is relatively good. Three fossil species of the genus from Yunnan have been described previously, i.e., *Drynaria propinqua* (Wall. ex Mett.) J. Sm. ex Bedd. from the late Miocene Lincang, southwestern Yunnan (Wen et al., 2013); *Drynaria callispora* Su, Zhou et Liu from the late Pliocene Yongping, western Yunnan (Su et al., 2011); and *Drynaria dimorpha* J.Y. Wu et B.N. Sun from the late Pliocene Tengchong, southwestern Yunnan (Wu et al., 2012). To build a model that reflects the origin and evolution of *Drynaria* diversity and biogeography through the geological time in Yunnan, additional fossil discoveries are needed. Moreover, the relationship between habitat, climate and diversity for *Drynaria* in the past has yet to be examined. The elucidation of this relationship may lead to a better understanding of the origin for species richness of the genus in Yunnan.

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In this study, we describe a new fossil taxon of *Drynaria* based on two fertile fronds with *in situ* spores recovered from the late Pliocene Lanping, northwestern Yunnan, southwestern China. The fossilized fronds and spores are examined morphologically, and compared with formerly described fossil species of the genus. The late Pliocene diversity and distribution of *Drynaria* in western Yunnan is interpreted by integrating both the new and previous fossil taxa, and its correlation with palaeoenvironmental conditions is discussed briefly.

2. Materials and method

2.1. Fossil site, geological setting and fossil materials

The fossil site is located at the Fudong Village in Lanping County, northwestern Yunnan Province, southwestern China (26°28'N, 99°26'E; 2740 m a.s.l.; Fig. 1). This fossil site was first known for leaf impressions dominated by evergreen sclerophyllous oaks (*Quercus* sect. *Heterobalanus*; Tao, 1986). Sedimentary deposits at the fossil site belong to the Sanying Formation, which has been dated to be late Pliocene based on lithostratigraphical and biostratigraphical correlations (Writing Group of Yunnan Regional Geological Stratigraphy, 1978; Tao, 1986; Yunnan Bureau of Geology and Mineral Resources, 1990; Ge and Li, 1999) along with a mammal fossil find (Su et al., 2011). Recent magnetostratigraphical evidence has confirmed this age assignment (Li et al., 2013). Geological descriptions of the fossil site have been published previously (Tao, 1986; Huang et al., 2012; Ma, 2013). According to the stratigraphical reconstruction by Ma (2013), the Sanying Formation sediments at the fossil site measure about 900 m thick, consisting of 20 units (Fig. 2). The black-grey layers embedded in the purple-red argillaceous siltstone at the upper part have produced abundant fruit and seed entities, with fossil taxa representing *Sambucus* (Huang et al., 2012), *Cucubalus* (Huang et al., 2013), *Aralia* (Zhu

et al., 2015), and *Zanthoxylum* (Zhu et al., 2016). The yellow-grey claystone at the middle part of the sediments bears leaf impressions, with fossil taxa including *Acer*, *Berberis*, *Hippophae*, *Populus*, *Quercus* and *Salix* (Huang et al., 2015). It is from this yellow-grey claystone that two sporogenous fronds of *Drynaria* were unearthed. One specimen is comparatively complete, while the other is preserved only as a pinna.

2.2. Fossil examination and photography

The present *Drynaria* fossil frond and pinna were photographed in natural light using a digital camera (Leica, V-Lux40). Veins and areoles of the frond were imaged by a digital camera (Leica, DFC295) mounted on a stereoscopic microscope (Leica, S8APO). The *in situ* spores were examined by a scanning electron microscope (SEM, Zeiss, EVO LS10) using the following procedure. Firstly, a cluster of sporangia was sampled from a well-preserved sorus on the frond and placed on a concave glass slide under a stereomicroscope with a dissecting needle. To facilitate observation, the sporangia were treated as described in Liu and Basinger (2000) and Su et al. (2011). To separate single spores from the sporangia, the sporangia were tapped gently by an eyelash mounted on a dissecting needle. Both sporangia and single spores were then moved onto an SEM stub by the eyelash. The spores were first sputter-coated with gold palladium, and then were observed under the SEM before images were taken. The fossil specimens under investigation are currently housed in the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN).

3. Systematic result, description and remark

Family: Polypodiaceae Berchtold et J.S. Presl.

Genus: *Drynaria* (Bory) J. Smith

Species: *Drynaria lanpingensis* sp. nov. Huang, Su et Zhou

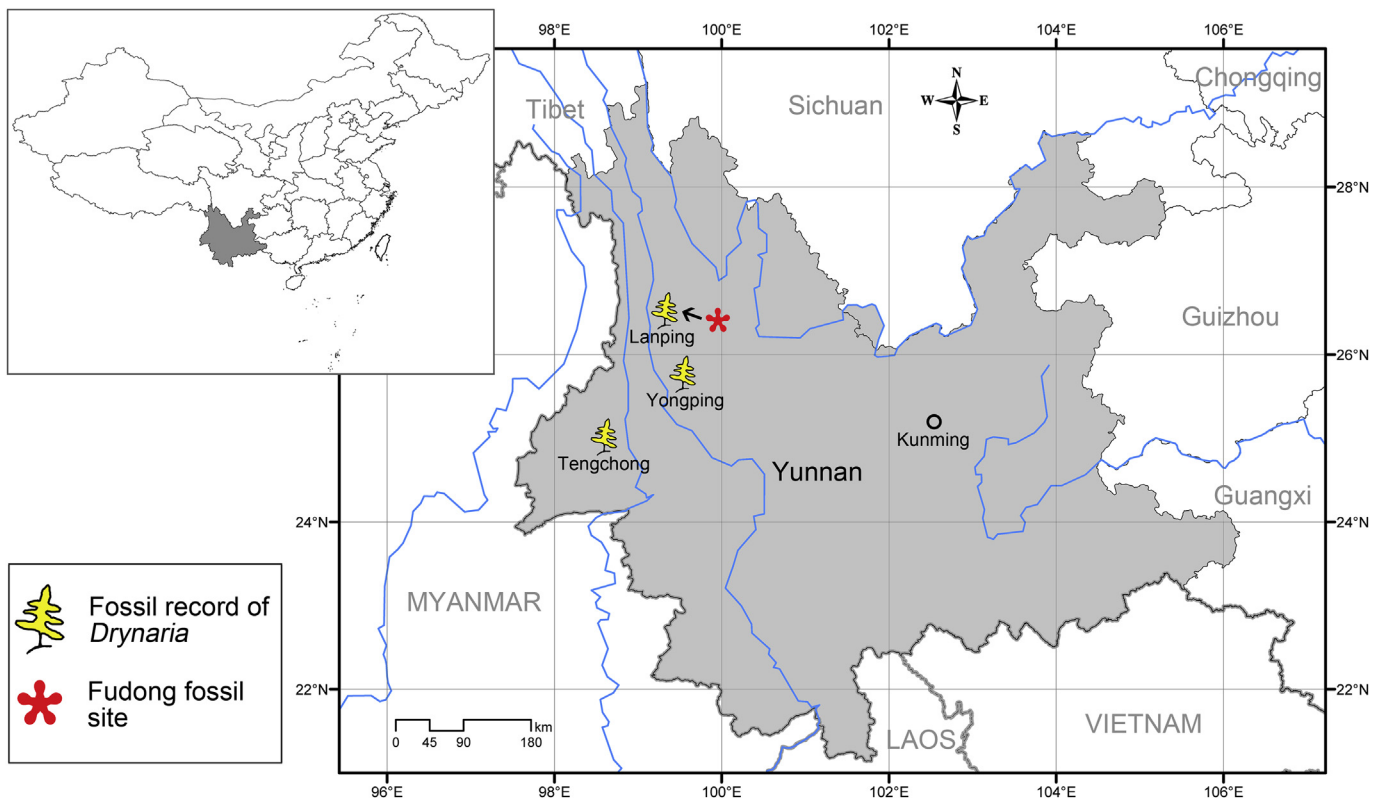


Fig. 1. Map showing the geographical location of the fossil site and the other two sites that have produced fossils of *Drynaria*.

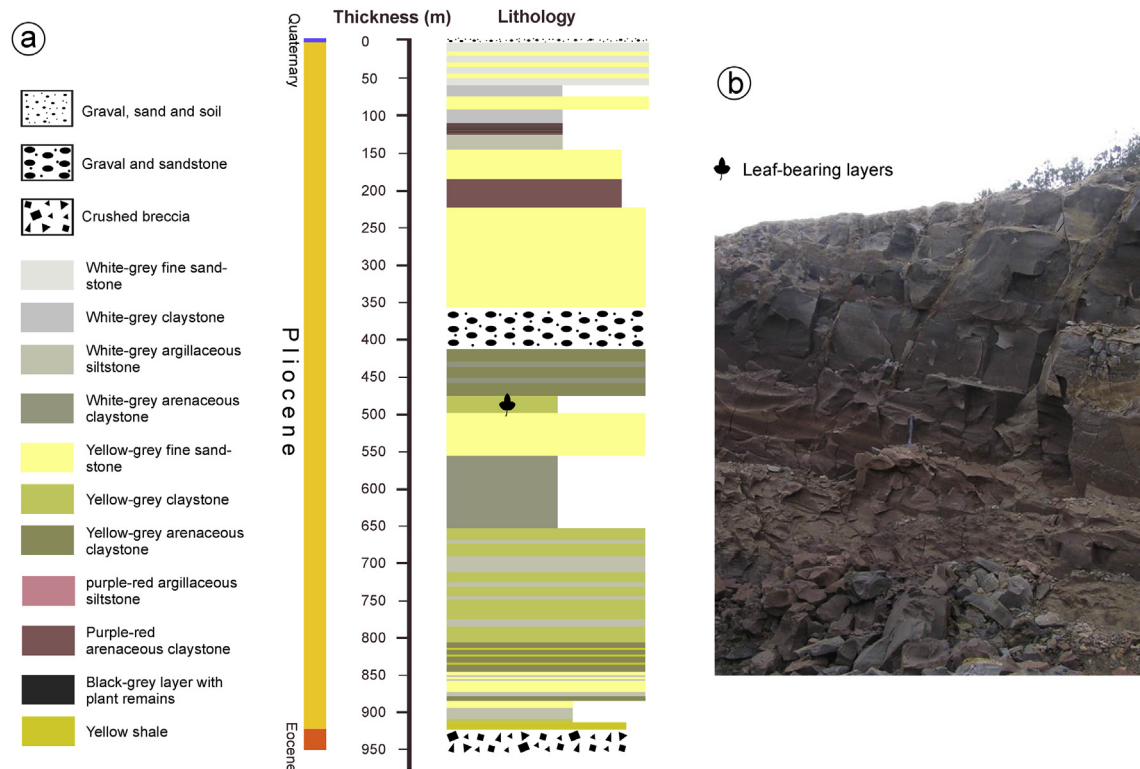


Fig. 2. Geological settings of the Sanying Formation sediments at the fossil site after Ma (2013) (a), and outcrops that bear the fossils of *Drynaria lanpingensis* sp. nov. (b).

Holotype: LP 001.

Paratype: LP 002.

Type locality: Fudong Village, Lanping County, northwestern Yunnan Province, southwestern China (26°28'N, 99°26'E).

Geological horizon: Sanying Formation of the late Pliocene.

Etymology: The specific epithet *lanpingensis* refers to the Lanping County where the fossil site is located.

Diagnosis: Frond pinnatifid; pinnae entirely margined; sori round, arranged along and close to the primary vein of the pinnae; areoles quadrangular, pentagonal to irregular, occasionally bearing an unbranched veinlet; spores monolete, semicircular to bean-shaped in equatorial view, and tuberculate and verrucate on surface.

Description: The description of *D. lanpingensis* sp. nov. is based on two specimens: a frond and a pinna, both fertile (Fig. 3). The frond is pinnatifid, with a stalk of only 3 cm long appearing (Fig. 3). Five fragmentary pinnae are preserved on one side of the stalk. The pinnae are entire at margin, at least 4 cm long observable and around 1 cm wide. Space between adjacent pinnae is almost equal to the breadth of the pinnae. The primary vein of the pinnae is soundly developed, while the secondary veins are difficult to see (Fig. 3). Areoles are quadrangular, pentagonal to irregular, and one unbranched veinlet occasionally occurs in the areole (Fig. 4). The sori are round in shape and 1–2 mm in diameter, with the indusial missing (Fig. 3). The sori are closely located to the primary vein of the pinnae and are arranged in one row on each side of the primary vein. The *in situ* spores are monolete, and semicircular to bean-shaped from an equatorial view. The exospores are intensively tuberculate and verrucate (Fig. 5).

Remark: *Drynaria* in the Polypodiaceae is a morphologically distinctive genus by having some diagnostic characters, e.g., pinnatifid frond, sori arranged along the primary vein of the pinnae, an unbranched veinlet occasionally occurring in the areole, and monolete spores that are semicircular to bean-shaped with a

verrucate surface. Our fossil frond and pinna share these key characteristics and therefore can be clearly placed in this genus. The newly described *Drynaria*, *D. lanpingensis*, differs from *D. propinqua* from the late Miocene Lincang by having wider pinnae, and differs from *D. dimorpha* from the late Pliocene Tengchong by having larger space between adjacent pinnae and tuberculate spores. It appears similar to *D. callispora* from the late Pliocene Yongping, but slight differences still exist. Fronds of *D. lanpingensis* have pentagonal areoles and their spores have sparse verrucae as compared to *D. callispora*. It is worth mentioning that these two fossil taxa are both recovered from the Sanying Formation.

4. Discussion

With the newly described fossil occurrence considered, there are now three fossil records of *Drynaria* from the late Pliocene of Yunnan (Table 1). They represent three different taxa, i.e., *D. lanpingensis*, *D. callispora*, and *D. dimorpha*, coming from Lanping, Yongping and Tengchong, respectively. This suggests that *Drynaria* diversity was already considerable in western Yunnan during the late Pliocene. Today, nine living species of *Drynaria* can be found in Yunnan, with the majority of species growing near the Hengduan Mountains in western part of the province (Zhang et al., 2013). The inferred late Pliocene diversity may help explain modern *Drynaria* species richness in Yunnan. Moreover, as these three fossil species are discovered from different areas, i.e., western, southwestern and northwestern Yunnan, the genus probably had a wide biogeographic range in western Yunnan during the late Pliocene. Therefore, we hypothesize that the modern patterns of *Drynaria* diversity and distribution in Yunnan were largely established by the late Pliocene. This is the first study in which fossils have been used to infer the origin of modern fern richness and distribution in Yunnan.

Drynaria is a shade-tolerant plant, usually epiphytic or occasionally epilithic, and grows in the understory of forests or on rocks

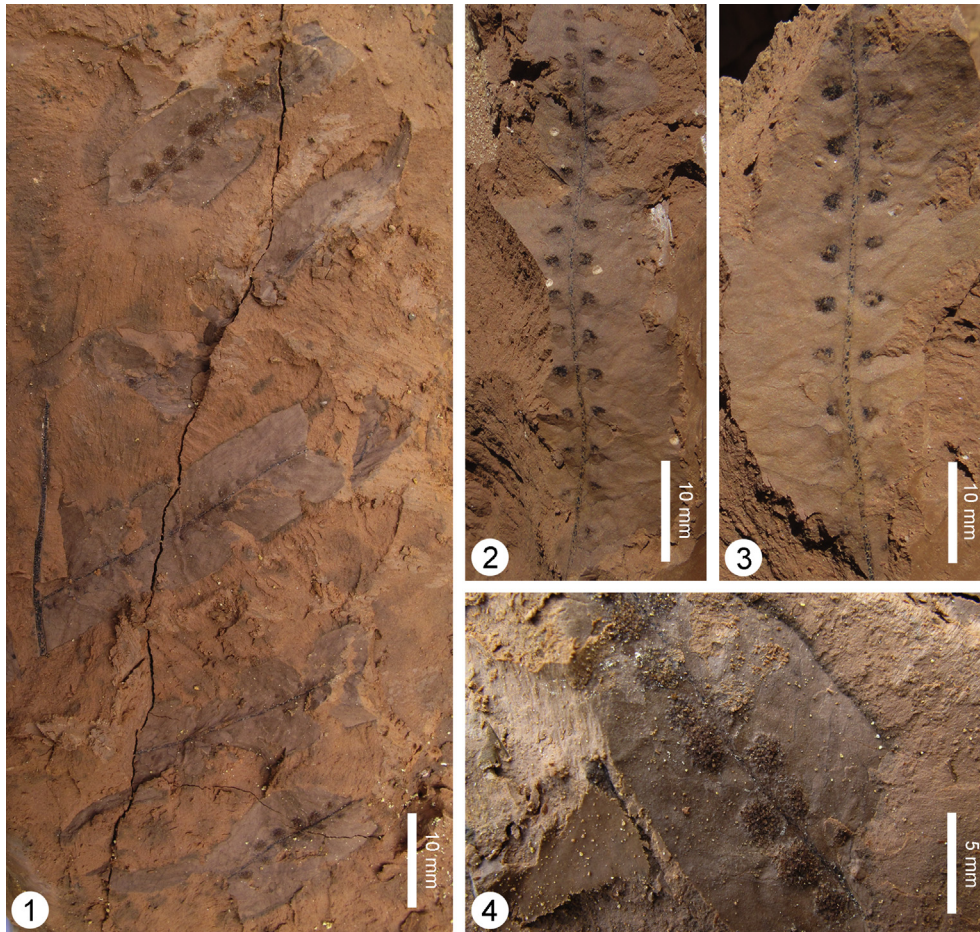


Fig. 3. Fragmentary fossil frond and pinna of *Drynaria lanpingensis* sp. nov. with *in situ* spores from the late Pliocene Lanping, northwestern Yunnan. 1. Fragmentary frond, LP 001; 2. Fragmentary pinna, LP 002; 3. Counterpart of LP 002; 4. An amplified pinna of the fragmentary frond.

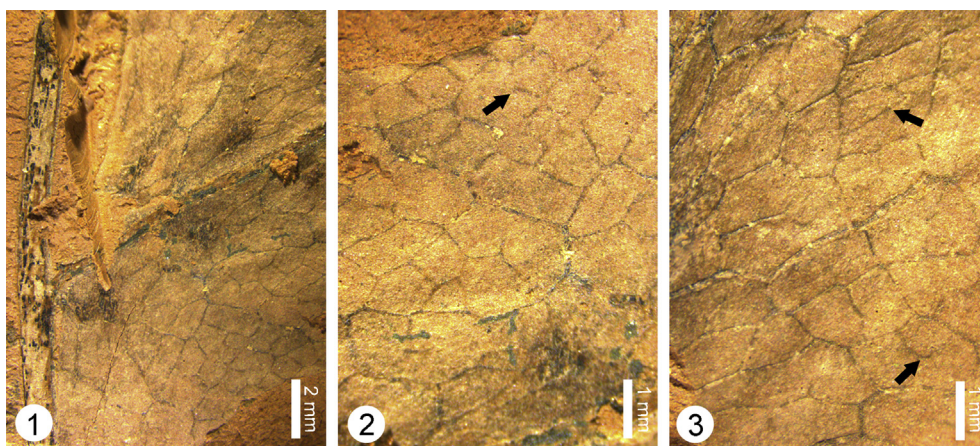


Fig. 4. Details of the veins and areoles with arrows showing the unbranched veinlets in the areoles (LP 001).

in deciduous forests (Zhang et al., 2013). Hence, the existence of *Drynaria* implies a forest vegetation type. As mentioned above, the fronds of *D. lanpingensis* are preserved together with leaf remains of various woody species, such as *Acer*, *Berberis*, *Hippophae*, *Populus*, *Quercus* and *Salix* (Huang et al., 2015). Among these leaf remains, *Quercus* sect. *Heterobalanus* is the dominant element (Tao, 1986). This floristic composition indicates an evergreen sclerophyllous forest mixed with a few deciduous trees or shrubs at Lanping

during the late Pliocene. The presence of *Drynaria* is in accordance with this interpretation. Similarly, the two *Drynaria* fossil species from the late Pliocene Yongping and Tengchong may also indicate forest vegetation at these two areas. Other known fossil taxa from the late Pliocene Yongping are dominated by *Heterobalanus*, also suggesting an evergreen sclerophyllous forest in which *Drynaria* once lived (Su et al., 2015). This is a situation similar to the late Pliocene Lanping. Fossil taxa from the late Pliocene Tengchong are

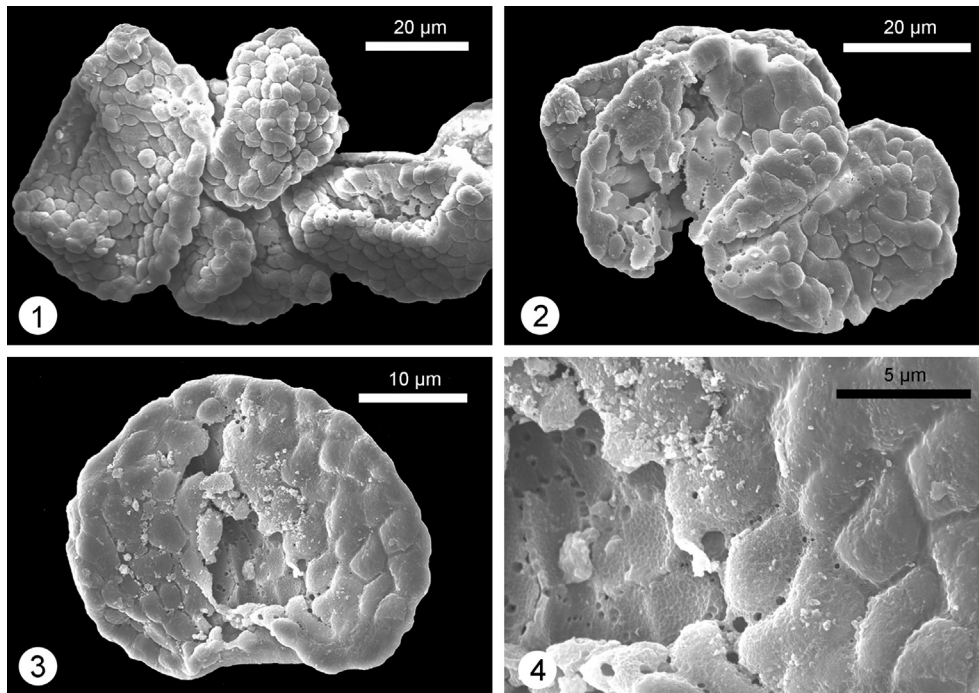


Fig. 5. Spores of *Drynaria lanpingensis* sp. nov. observed under the SEM (LP 001).

Table 1

Known fossil taxa of *Drynaria* from the late Pliocene of Yunnan, southwestern China.

Fossil species	Locality	Latitude/longitude	Age	Preservation	Reference
<i>D. lanpingensis</i>	Fudong, Lanping	26°28′/99°26′	Late Pliocene	Fronds with <i>in situ</i> spores	This study
<i>D. callispora</i>	Yangjie, Yongping	25°30′/99°31′	Late Pliocene	Fronds with <i>in situ</i> spores	Su et al., 2011
<i>D. dimorpha</i>	Tuantian, Tengchong	24°41′/98°38′	Late Pliocene	Fronds with <i>in situ</i> spores	Wu et al., 2012

much more diverse; in addition to *Drynaria*, around 30 genera have been recognized, including *Cinnamomum*, *Cornus*, *Ilex*, *Lindera*, *Machilus*, *Myrica* and *Robia* (Sun et al., 2011). Therefore, we can deduce that *D. dimorpha* existed with an evergreen broad-leaved forest at Tengchong. Considered together, the floristic components of these three late Pliocene floras suggest that *Drynaria* coexisted with woody species in the understory of forests in western Yunnan during the late Pliocene. Notably, this is a commonly observed ecological characteristic of extant *Drynaria* species.

Drynaria is distributed in tropical to subtropical regions mainly in southeastern Asia which nowadays generally have humid climates (Ching, 1978; Zhang et al., 2013). Climatically, the genus may prefer moist habitats, also because it is a shade plant. In several palaeoclimatic investigations (Kou et al., 2006; Sun et al., 2011; Xie et al., 2012; Su et al., 2013; Huang et al., 2015), the late Pliocene precipitation in western Yunnan has been extensively reconstructed using two quantitative approaches: Coexistence Approach

(CA; Mosbrugger and Utescher, 1997) and Climate–Leaf Analysis Multivariate Program (CLAMP; Wolfe, 1993). Mean values of mean annual precipitations (MAPs) estimated from the late Pliocene for five localities in western Yunnan range from 850 mm to 1500 mm (Huang et al., 2015). Meanwhile, the calculated growing season precipitations (GSPs) for the late Pliocene Yongping and Tengchong are 1735.5 ± 217.7 mm (Su et al., 2013) and 1834.3–1901.2 mm (Xie et al., 2012), respectively (Table 2). To provide a better view of the precipitation distribution in the late Pliocene of western Yunnan, the MAP estimates for five sites are displayed using spatial analysis tools from the geographical information software ArcGIS 9.3 (Esri Company, Redlands). The illustration shows that western Yunnan generally had humid climates during the late Pliocene (Fig. 6). The overall humid conditions may further explain the diversity and distribution of *Drynaria* in western Yunnan at that time.

The climate of Yunnan is controlled by two summer monsoon systems, namely the Indian summer monsoon and East Asian summer monsoon. The Ailao Mountain in central Yunnan serves as

Table 2

Late Pliocene precipitations in western Yunnan, with climate data based on published sources as cited.

Locality	Longitude/latitude	Age	MAP/GSP (mm)	Approach	Reference
1. Lanping	99°26′/26°28′	Late Pliocene	552–1151/–	CA/–	Huang et al., 2015
2. Eryuan	99°49′/26°00′	Late Pliocene	619.9–1484.3/–	CA/–	Kou et al., 2006
3. Yongping	101°48′/25°51′	Late Pliocene	–/1735.5 ± 217.7	–/CLAMP	Su et al., 2013
4. Yangyi	99°15′/24°57′	Late Pliocene	797.5–1254.7/–	CA/–	Kou et al., 2006
5. Longling	98°50′/24°41′	Late Pliocene	815.8–1254.7/–	CA/–	Kou et al., 2006
6. Tengchong	98°38′/24°41′	Late Pliocene	1377–1695/1834.3–1901.2	CA/CLAMP	Sun et al., 2011; Xie et al., 2012

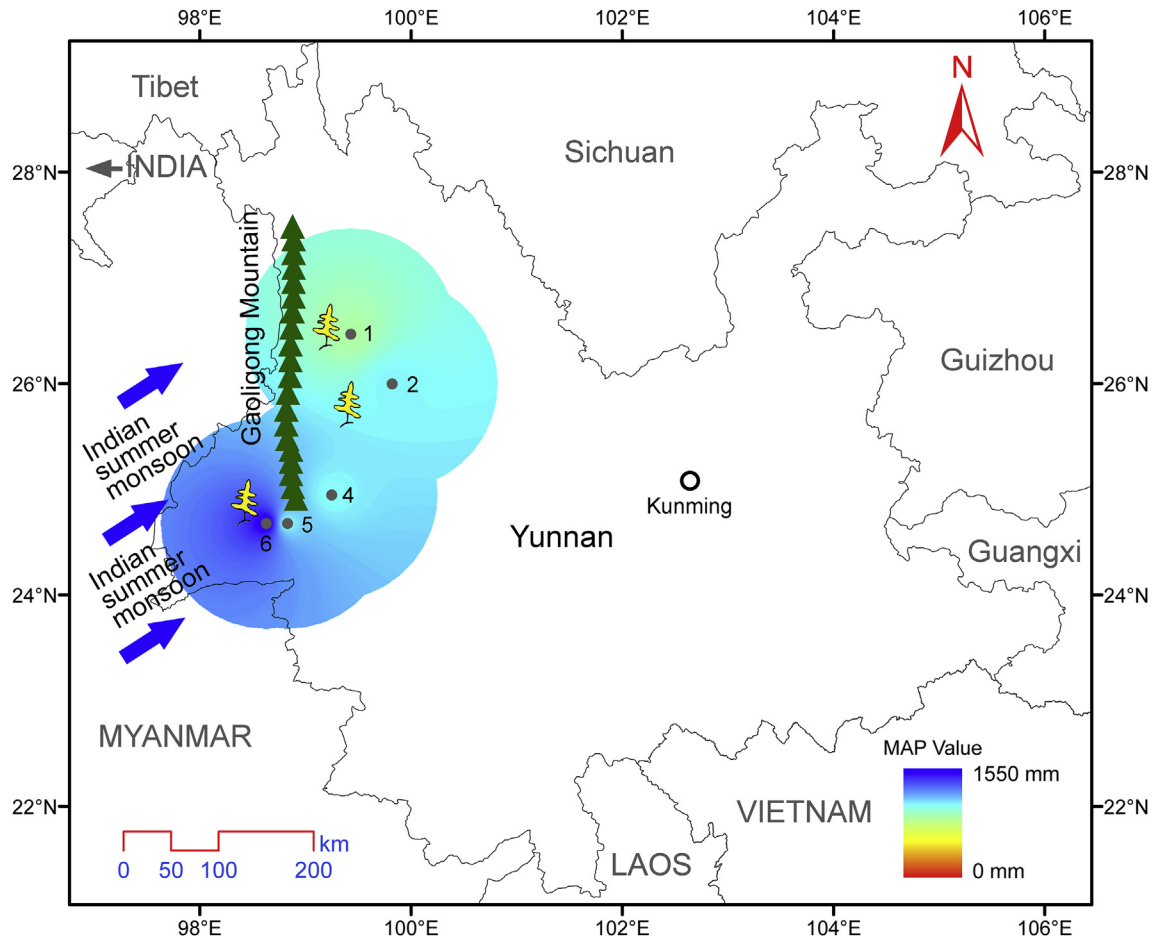


Fig. 6. Reconstructed precipitation distribution in western Yunnan during the late Pliocene. The sites are numbered after Table 2.

the boundary zone of the two monsoons: western Yunnan is mainly under the influence of the Indian summer monsoon, while eastern Yunnan is mainly under the impact of the East Asian summer monsoon (Li and Li, 1992). This pattern may have been largely established by the late Miocene (Jacques et al., 2011). In western Yunnan, the Gaoligong Mountain is considered to play a significant role in the monsoon climate, as it obstructs the moist air flow brought by the Indian summer monsoon from the southwest (Sun et al., 2011; Su et al., 2013). Among the above six places, Tengchong and Longling are located to the west of the Gaoligong Mountain while the other four are situated to the east of the mountain. One possible explanation for the inferred humid conditions in western Yunnan during the late Pliocene is that the Gaoligong Mountain had a lower altitude at that time; as a consequence, the mountain could not effectively block the eastward moist air stream associated with the Indian summer monsoon (Sun et al., 2011; Su et al., 2013).

Based on the above discussion, forest vegetation and humid conditions may have provided suitable habitats for the diversity and distribution of *Drynaria* in western Yunnan during the late Pliocene. This is the first interpretation linking the biodiversity of ferns to environmental conditions in Yunnan in the past.

5. Conclusion

Including the newly described fossil taxon, *D. lanpingensis*, there are three fossil taxa of *Drynaria* from the late Pliocene of western Yunnan. As *Drynaria* is an epiphytic plant that grows preferably in the understory of forests with relatively humid climates, the

inferred *Drynaria* diversity and distribution in western Yunnan during the late Pliocene can be explained by forest vegetation and humid climates reconstructed from fossil floras. This study provides an example of how looking at historical plant diversity from a fossil perspective can be used to make inferences regarding the palaeoenvironment.

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