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ORIGINAL PAPER

A new species of *Drynaria* (Polypodiaceae) from the late Miocene of Yunnan, Southwest China and implications on the genus evolution

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Abstract

Drynarioid ferns comprise a large group in the Polypodiaceae family and are characterised by anastomosing venation and line of abscission between the pinna and the costa. In this paper, after morphological comparison with other ferns, we report and describe a new species, *Drynaria diplosticha* Y. Yu and S. P. Xie, sp. nov. from the upper Miocene sediments of the Bangmai Formation in Lincang City, Yunnan, China. This species is characterised by sori lining the midrib in two rows. The acute curvature of the midrib and the areolae at the base, as well as the slight decurrency, indicate that the fossil was connected to a costa. The occurrence of this fossil suggests that the climate in southwestern Yunnan during the late Miocene was humid and warm with clear seasonality influenced by monsoons which, based on other studies, were weaker than those experienced at present. Given that other Neogene drynarioid fossils (i.e. *Drynaria* cf. *propinqua* from the late Miocene and *Drynaria callispora*, *Drynaria dimorpha*, *Drynaria lanpingensis* from the late Pliocene) were reported exclusively from western Yunnan, that region might be a radiation centre of *Drynaria* in the Neogene where its extant species rapidly diversified and the distribution expanded. This may have been driven by the formerly proposed rapid topographic and climatic changes there. These *Drynaria* fossils may indicate that western Yunnan was one of the cradles of Drynarioid ferns during their early evolution.

Keywords *Drynaria* · Sori arrangement · Western Yunnan · Diversification · Seasonality

Introduction

Drynaria is a genus in the Polypodiaceae family which includes around 1000 species in more than 60 genera. Nearly all drynarioid ferns are epiphytic or epilithic in forested ecosystems. There are 16 living species in *Drynaria*, mainly distributed in Southeastern Asia and Oceania, except for two to three African species (Roos 1985). In China, drynarioids inhabit mainly the southern region and eight out of the nine domestic living species can be found in Yunnan Province.

Yunnan Province has long been recognised as a hotspot for plant diversity covered mainly by East Asia Flora (EAF) and has attracted the attention of many botanists and biogeographers (Chen et al. 2017). It is home to approximately 16,000 vascular plant species, representing 6% of higher plant species in the world. Today's highly diverse flora can be related in parts to the region's geological and biogeographic history. Plants that comprise the modern EAF, documented from the fossil records, were rapidly getting closer to modern taxa during the late Miocene and most of the clades in EAF originate from that time (Chen et al. 2017). Accordingly, angiosperms in western Yunnan showed more recent divergence than those in southeastern China, and the mean divergence time was just after the beginning of the Neogene (Lu et al. 2018). Due to this rapidly modernized and diversified floristic composition, fossil records of plants in many different clades were published in recent years (Wen et al. 2013; Jacques et al. 2014; Xie et al. 2016, 2018; Zhang et al. 2018). Until 2016, there were 384 fossil species of ferns, angiosperms and gymnosperms

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reported from the Cenozoic of Yunnan, particularly from the Neogene (Huang et al. 2016b).

We now know that many of today's filicalean ferns survive in the low-light regimes under niches created by angiosperm canopies. These niches may have played an important role in the evolutionary history of polypod ferns. They are understood to start their diversification in the Cretaceous, perhaps as an opportunistic ecological response to the diversification of angiosperms (Schneider et al. 2004). Schuettpelz and Pryer (2009) held the view that epiphytic ferns (e.g. Polypodiaceae), concurrent with angiosperm-dominated canopy development, began their rapid speciation in the Eocene. However, the first appearance of drynarioid ferns can only be traced back to the late Miocene, with the discovery of *Aglaomorpha heraclea* from Sumatra and *Drynaria* cf. *propinqua* from Lincang, (Roos 1985; Yuan et al. 2017). The lack of fossil records before that time has left the origin of *Drynaria* debatable to a large extent. Fossil records of *Drynaria* are rarely reported and all of them fall in Yunnan Province, including *Drynaria* cf. *propinqua* from the late Miocene and *Drynaria callispora*, *Drynaria dimorpha*, and *Drynaria lanpingensis* from the late Pliocene (Su et al. 2011; Wu et al. 2012; Huang et al. 2016a; Yuan et al. 2017).

In this paper, a new species of *Drynaria* collected from the upper Miocene Bangmai Formation of Lincang is described. Large parts of the pinna are preserved except for the missing apex. Sori are visible as well as the veins in the frond. Being the second *Drynaria* species to be found there after *Drynaria* cf. *propinqua*, its discovery improves the richness of the known *Drynaria* species in the Lincang basin. Combined with other *Drynaria* fossils, it provides further evidence on the diversification process and distributional changes of *Drynaria*, as well as palaeoclimatic inference.

Material and methods

Fossil site

The fossil material was collected from the Bangmai Basin, one of the intermontane basins in Lincang. It is situated about 10 km northwest of Lincang City (23°54'N, 100°0′E), Yunnan Province, southwest China (Fig. 1). Due to the Cenozoic uplift, there are some north-south trending mountains in the region and valleys in between. The fossil plant was found in the Bangmai Formation which can be subdivided into three lithologic units. The lower basal conglomerate unit is dominated by grey glutenite and light-yellow fine to coarse sandstone. The unit in the middle comprises more variable lithology including dark grey-mudstone, dark-brown carbonaceous mudstone, grey-white sandstone, glutenite, siltstone and a thin coal seam. Plant fossils have also been discovered in this layer. The fossil-bearing upper unit is represented by grey mudstone and silty mudstone, intercalated with fine to coarse sandstone, and our fossil specimen was unearthed from this unit. This formation is overlaid by Quaternary sand and gravel and underlaid by middle Triassic granite with greyish coarse biotite, both in unconformable contact (Ge and Li 1999; Hu et al. 2009; Huang et al. 2015; Tao and Chen 1983; Wen et al. 2013). The Bangmai Formation is dominated by some evergreen genera, e.g. *Cyclobalanopsis*, *Castanopsis*, *Cinnamomus* (Jacques et al. 2011). This fossil association of Bangmai Formation is comparable with that of the Xiaolongtan Formation (Zhang 1996; Guo 2011; Jacques et al. 2011). Recent palaeomagnetic dating through the fluviolacustrine sequence of the Xiaolongtan Formation has limited its age to be within ca. 14.1–10 Ma (Li et al. 2015b; Zhang et al. 2019). Therefore, we use this dating as the age of the Bangmai Formation and inferring it as late Miocene.

Methods

In this study, one fern specimen was photographed with a Sony T70 digital camera. To obtain more details about the veins, sori and margin, a Leica MZ12.5 stereomicroscope with QWin image analysis software was used. Chemical treatment was conducted to the fossil specimen, but no in situ spores were obtained. The descriptive terminology follows Roos (1985). The fossil specimen is kept in the Institute of Palaeontology and Stratigraphy, Lanzhou University, Gansu Province, China. The extant material for morphological comparison is obtained from Herbarium Institute of Botany, CAS.

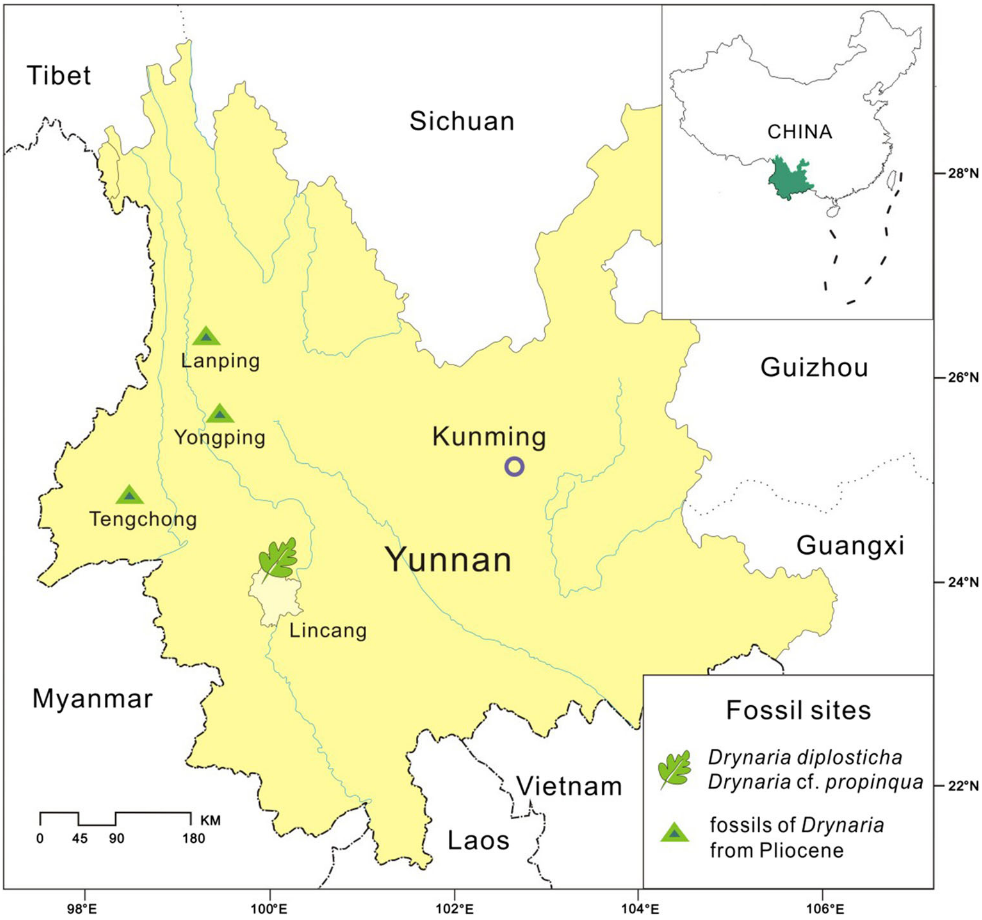
Systematics

Division Pteridophyta
Class Polypodiopsida Cronquist, Takhtajan. and Zimmermann, 1966
Order Polypodiales Link, 1833
Family Polypodiaceae von Berchtold and Presl, 1822
Genus *Drynaria* (Bory) Smith, 1841

Species *Drynaria diplosticha* Y. Yu and S. P. Xie, sp. nov. (Fig. 2)

Holotype: YNLC-LDGSW 2018–711(A, B) (Fig. 2a, b)
Repository: The fossil specimen is kept in the Institute of Palaeontology and Stratigraphy, Lanzhou University.
Type locality: Bangmai Village (N 23°54′, E 100°0′), Lincang, Yunnan, China.
Stratigraphy: Bangmai Formation, late Miocene.
Etymology: The specific epithet refers to the trait of the fossil specimen that sori line the midrib in two rows on each side.
Specific diagnosis: Fertile frond pinnatifid; sinus between two pinnae very close to costa or reaching it. Pinna oblong; base not

Fig. 1 Map showing the *Drynaria* fossil locations



constricted; margin generally entire, partially slightly undulate; midrib strong and a bit flexuous; lateral veins obvious and zigzag, not reaching margin; tertiary veins obvious and reticulate; areolae basically quadrangular; simple or forked small veinlets occasionally exist inside areolae. Sori orbicular or elliptic, exindusiate, each in one areola, arranged in two regular rows on each side of the midrib, closer to midrib than to margin.

Description: The fertile frond is oblong, glabrous and the main part of it measures 2.5-cm wide (Fig. 2a,b,f). The base is a bit excurrent on one side while the other wing is unobservable (Fig. 2g). The margin of the pinna is entire with partially slight undulation (Fig. 2a,b,f). The midrib is strong and a little flexuous. The lateral veins are obvious and zigzagging, alternate at the base but opposite at the top. There are 14 pairs of lateral veins preserved, each at an angle of 45–55° to the midrib (Fig. 2a,b,f). Tertiary veins connect the adjacent two lateral veins, thus forming similar-sized quadrangular areolae. The areolae line the midrib in at least two rows on either side. In each costal areola, there is a forked veinlet branching from the midrib (Fig. 2c–e). Other than that, short veins, either single or reticulate, can also be observed near the leaf margin or inside some areolae (Fig. 2d). Sori are exindusiate, orbicular or elliptic and are also in two regular lines, each in one areola except the tip part where there is a single sorus between every two adjacent lateral veins at each side of the midrib (Fig. 2). At one side of the midrib, the two rows of areolae and sori see a diversion from the midrib near the base (Fig. 2d). The midrib breaks along the costa, but the end curves to one side at the joining place.

Discussion

Systematic consideration

If we speculate from the obvious articulation of the midrib at the edge as well as the swerving and the irregularity of the areolae at the basal part, the fossil leaf grew from a costa to which the midrib forms an angle of about 120°. The fossil specimen, instead of being an entire frond, is a single pinna. These traits indicate that the fossil plant has a pinnately lobed or pinnatifid lamina and adjacent lateral lobes were at least very weakly connected in between if not separated.

The fossil we describe has visible characters including pinnatisect fronds, entire pinna with partial undulation, reticulate veins with occasional free veinlets, orbicular or longitudinally slightly oblong exindusiate sori. However, there remains a slight chance that the specimen is a pinna in a pinnatifid part of an inner dimorphic frond which is mainly pinnate.

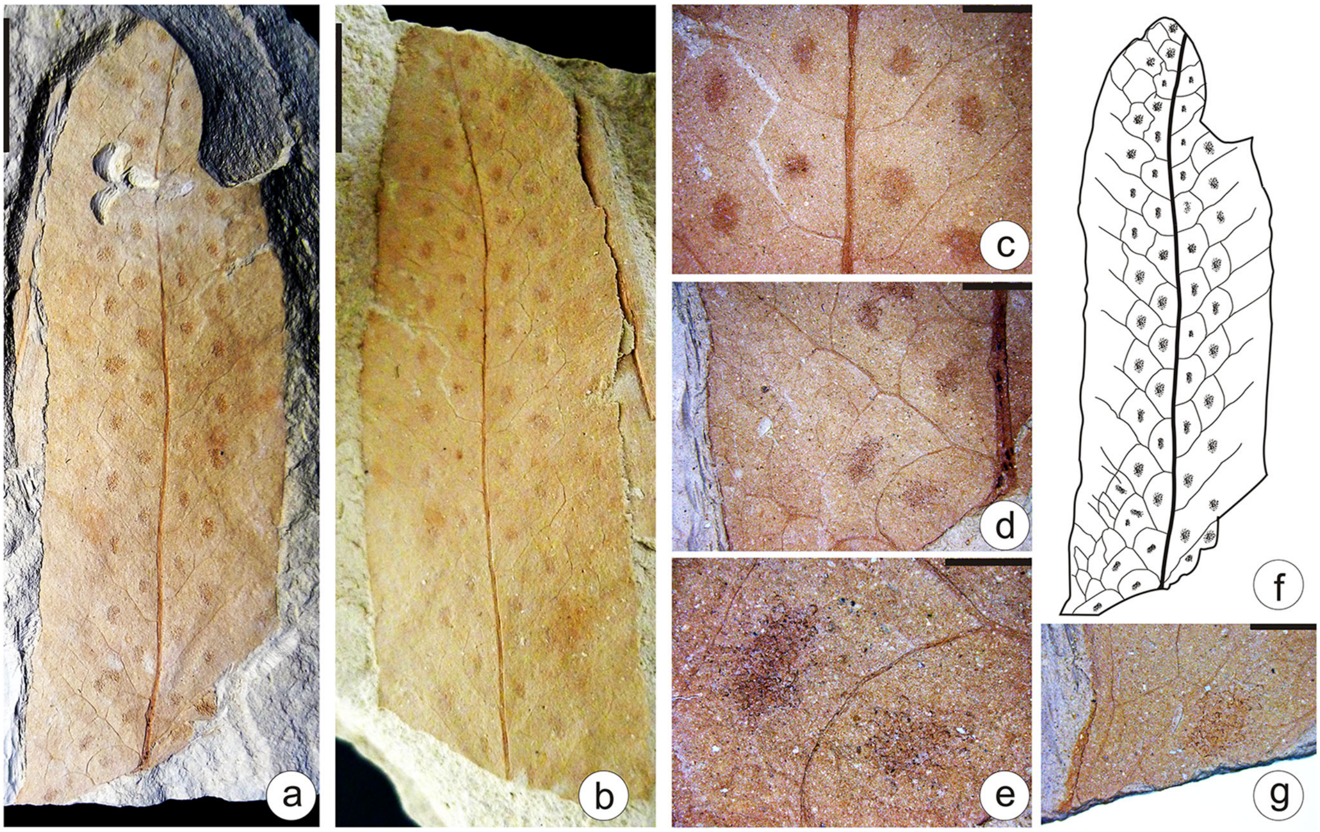


Fig. 2 *Drynaria diplosticha* sp. nov. **a**, **b** Holotype, pinna; specimen no. YNLC-LDGSW 2018-711 (A, B), scale bar 1 cm. **c** Close-up of **a** showing lateral veins, veinlets in costal areolae and sori arrangement, scale bar 2 mm. **d** Close-up of **a** showing veins, sori near base and the end of midrib, scale bar 2 mm. **e** Close-up of **a** showing the sori near the base, scale bar 1 mm. **f** Sketch of **a**. **g** Close-up of **a** showing the decurrency, scale bar 1 mm

From these traits, we find some families our fossil specimen can possibly belong to. Within the Dipteridaceae, species of *Dipteris* have reticulate veins with veinlets inside, but the lamina is fan-shaped or palm-shaped with several main veins parallel-arranged on each pinna and the sori are discrete or acrostichoid. In contrast, in the family Dryopteridaceae, *Cyrtomium* share similar traits with our fossil, but the pinna is pinnately lobed and bases of pinna are acroscopic or, less common, basiscopic to the stalk, which differ from the equilateral pinna in our fossil plant. Furthermore, between the forked parallel lateral veins, the areolae are slenderer and more oblique than those found in our fossil. In a third family, Thelypteridaceae, laminae are usually pinnate-pinnatifid. *Pronephrium* has all its veinlets forming oblique square areolae between long and densely arranged lateral veins, and sori tend to be confluent unless on juvenile frond. *Cyclosorus* can be distinguished by its pinnatifid pinna and *Ampelopteris*, *Stegnogramma* by their pinnatilobate pinna. They also have a unique vein pattern (i.e. goniopteroid). In a fourth family, Athyriaceae, *Anisocampium* have a pinnately-lobed lamina with anostomosing veins. But the areolae are rhomboidal, and the indusiate sori and serrate or pinnatifid margin are also distinguishable traits from our fossil.

Lastly, within a fifth family, Polypodiaceae, some genera (Table 1) share morphological similarity with our specimen (i.e. pinnately divided or pinnatifid glabrous lamina with distinct main veins and zigzagging lateral veins; orbicular or slightly elliptic sori arranged in lines, each located inside one quadrangular areola; no hydathodes observed; margin untoothed). *Polypodiodes* has similar morphological traits, except for several unique patterns. Its veins usually anastomose to form a row of very narrow areoles on each side of the costa, and sori are always in a single row along the costule. These characteristics are not observed in our fossil. *Polypodiastrum* has a similar vein pattern, but the laminae are all pinnate with rounded or adnate bases of pinnae overlapping rachis. Also different from our specimen, its sori distribute in one row on each side of the costa. In *Selliguea*, most plants have simple, palmately lobed or hastately lobed fronds, each with a limited number of lateral lobes. Sori form one row on either side of the midrib and its lateral veins are straighter than what we observe in our specimen. Its areolae are more or less obscure with free veinlets included. On the margin, there are always regular notches or teeth. These traits exclude our specimen from *Selliguea*. *Neolepisorus* differs by the simple fronds and its lateral veins much more obvious than the

Table 1 Comparison of pinna characters between *Drynaria* and other similar genera in Polypodiaceae (based on Wu et al. 2013)

Genus	Shape of lamina	Sinus in pinnatifid lamina	Margin	Lateral veins	veinlets	Areolae	Sori arrangement
Drynaria	Pinnatifid; rarely pinnate	Close to costa	Undulate or entire	Evident; zigzag or straight	Evident; inside areolae or at margin; simple or forked	Quadrangular; obvious	1 row; rarely several rows
Aglaomorpha	Most frond pinnatifid;	Close to costa	Esntire	Distinct; slightly zigzag	Obvious	Main areolae filled with small areolae and free veinlet	In rows with connecting veins
Selliguea	Simple or pinnatifid; lobes normally limited in number	Not close to costa	Notched or toothed; rarely entire	Distinct	Obscure	Obscure	1 row along midrib; less often many rows or linear
Phymatosorus	Deeply pinnatipartite or pinnate; rarely simple	Not close to costa	Entire or undulate	Indistinct	Obscure; single or forked	Obscure	1 row along midrib or irregularly scattered
Microsorum	Single, pinnatifid or trilobate	Not close to costa	Entire	Obvious	Forked	n/a	Scattered irregularly; sometimes in rows
Polypodiodes	Deeply pinnatisect	Not close to costa	Toothed or serrulate	Distinct; zigzag	Free	Narrow areolae along costa;1–2 rows along midrib, broad	1 row along midrib
Polypodiastrum	Pinnate	n/a	Toothed or serrulate	Distinct	Free; one in each costal areolae; many at margin	1–3 rows along midrib, costal areolae broad	1 row along midrib
Neolepisorus	Single	n/a	Entire or denticulate	Distinct	Obscure; simple or forked	Present or obscure	1 or 2 rows on either side of midrib, or in rows between lateral veins

connecting ones. Sori can be, in some cases, in several lines but highly irregular. In *Microsorum*, sori are more likely to scatter on the lamina than to form several irregular rows. Some fronds can be pinnatifid but most are simple or trifid. The pinnatifid lamina has its sinus much more distant to the costa than observed in our fossil. The elliptic primary areolae normally take up more than half of the width of a pinna, which is also distinct from our fossil. Though *Phymatosorus* shares similar traits to our fossil, *Phymatosorus scolopendria* in particular, there are still some differences. *Phymatosorus* has indistinct lateral veins and veinlets but on the contrary, the veins on our fossil are preserved rather distinctly. Another difference lies in the sinus between lateral lobes. In *Phymatosorus*, the margin of a pinna does not reach the costa but connect with the margin of the next pinna far from it. *Aglaomorpha* shares morphological similarities with our fossil, e.g. the shape of lamina (*Aglaomorpha coronans*) and the abscission line between the costa and the sinus. In contrast to our fossil, there are many hydathodes, each at the end of a free veinlet in small areoles. Also unique is the arrangement that sori are parallel to connecting veins. In *Drynaria*, each pinna has a line of abscission between the costa and the sinus, which is hardly articulate to the costa. The sinus can be very close to the costa, if not reaching it. The venation of our specimen is similar to *Drynaria roosii*. The absence of visible hydathodes on our specimen is congruent with this genus as well (Fig. 3).

Based on the aforementioned discussion, we categorize the fossil plant as *Drynaria*. The morphological comparison between this fossil pinna and the other species of *Drynaria* is listed in Table 2. There is no species in *Drynaria* that has two regularly arranged rows of sori, each in one areole, so we choose to place the fossil in a new species. It also holds a unique combination of traits like the entire margin with partial undulation, the evident quadrangular areolae, which are arranged in two rows on each side of the midrib and probably without secondary ones inside (Fig. 2). As it is the only pinna that survives, glandular patches or nectaries are not observed.

Drynaria roosii is considered the nearest living relative species (NLRs) to *Drynaria diplosticha* (Fig. 3). The lamina is pinnatifid up to 2–5 mm from costa, and the areolae are obvious and of very similar shape with our fossil (Fig. 3c). The arrangement of sori in the living species *Drynaria roosii* is described as "one row parallel to secondary veins" by Roos (1985). Though this could possibly be the same as our fossil if

Fig. 3 Extant *Drynaria roosii* (from Herbarium Institute of Botany, CAS). **a** Single foliage frond, scale bar 1 cm. **b** An individual pinna of foliage frond with sori, scale bar 1 cm. **c** An individual pinna of foliage frond without sori, scale bar 1 cm

Table 2 Comparison of pinna characters between *Drynaria diplosticha* and other fossil and extant species of *Drynaria* (revised from Wen et al. 2013)

	Species	Shape of pinna	Margin	Midrib	Lateral veins	Areolae	Sori arrangement	Hair	Reference
Fossil	*D. diplosticha*	Oblong	Slightly undulate	Obvious	Obvious, zigzag, not reaching margin	Present	Along midrib, two rows at each side	Absent	This study
	D. callispora	Ovate-oblong	Entire	Obvious	Straight or sometimes zigzag	Present	Two rows along midrib	n/a	Su et al. (2011)
	D. dimorpha	Shell-shaped	Teeth	Obvious	Zigzag	Present	Two rows along midrib	n/a	Wu et al. (2012)
	D. lanpingensis	Oblong	Entire	Obvious	Not obvious	Present	Two rows along midrib	n/a	Huang et al. (2016a)
Extant	*D. bonii*	Broadly lanceolate	Entire or faintly sinuolate	Visible	Obvious, zigzag, reaching margin	Present	Multirows along midrib	Absent	Wu et al. (2013)
	D. delavayi	Ovate-oblong	Dense shallow notch	Gibbous	Gibbous, zigzag	Prominent	Two rows along midrib	Present	Wu et al. (2013)
	D. mollis	Oblong	Entire	Gibbous	Gibbous	Prominent	Two rows along midrib	Present	Wu et al. (2013)
	D. parishii	Oblanceolate	Entire or slightly folded	Gibbous below	Visible, straight	Present	Two rows along midrib	Absent	Wu et al. (2013)
	D. propinqua	Oblong	Teeth	Obvious	Obvious, straight, not reaching margin	Present	Two rows along midrib, one sorus between lateral veins	Absent	Wu et al. (2013)
	D. quercifolia	Broadly lanceolate	Teeth	Visible	Visible, straight	Present	Two rows between lateral veins	Absent	Wu et al. (2013)
	D. rigidula	Narrowly linear	Teeth	Gibbous	Gibbous, straight	Prominent	Two rows along midrib	Absent	Wu et al. (2013)
	D. roosii	Lanceolate	Inconspicuous teeth	Visible	Visible, zigzag	Present	Multirows along midrib	Present	Wu et al. (2013)
	D. sinica	Oblong	Teeth	Gibbous	Gibbous	Prominent	Two rows along midrib	Present	Wu et al. (2013)
	D. sparsisora	Quadrangular-ovate	Entire	n/a	Straight	n/a	Two rows between lateral veins	n/a	Roos (1985)
	D. involuta	Quadrangular	Entire	Gibbous	Gibbous, straight	Prominent	Two rows between lateral veins	n/a	Roos (1985)
	D. descensa	Quadrangular-ovate	Entire	n/a	Obvious, zigzag	n/a	Two rows between lateral veins	n/a	Roos (1985)
	D. laurentii	Quadrangular-ovate	Teeth	n/a	Straight	n/a	Two rows along midrib	n/a	Roos (1985)
	D. volkensii	Quadrangular-ovate	Teeth	Gibbous	Zigzag	Present	Two rows along midrib	n/a	Roos (1985)
	D. willdenowi	Quadrangular-ovate	Teeth	Gibbous	Straight	Prominent	Two rows along midrib	n/a	Roos (1985)
	D.pleuridioides	Quadrangular-ovate	Entire	Visible	Zigzag	Present	Two rows along midrib	n/a	Roos (1985)

each row bears two sori, this is very rare and is always more or less irregular (Fig. 3b).

Our fossil holds distinctive characters differing from former-reported *Drynaria* fossils mainly in terms of the array of sori besides tiny differences in vein type. This character also distinguishes our fossil species from the other 15 extant species whose sori form either one row parallel to the midrib or two rows parallel to the secondary veins (Table 2).

Biogeography and diversification

Our fossil, together with *Drynaria propinqua* and *Drynaria* cf. *propinqua* in the same sedimentary layer, marks the oldest discovery of *Drynaria* and later *Drynaria dimorpha*, *Drynaria lanpingensis* and *Drynaria callispora* were reported from the northeast of Lincang. At present, eight of the nine living species of *Drynaria* in China can be found in Yunnan (*Drynaria quercifolia* excluded), which indicates that this genus has thrived continuously there until the present day.

The native range of the nine Chinese living species extends from tropical South and East Asia, Southeast Asia to Australia and Oceania (Wu et al. 2013). However, all the *Drynaria* fossils reported have been from western Yunnan—this may indicate that region is a distributional center where *Drynaria* developed and spread out to the rest of its extant eastern Asia habitats nearby. Yunnan being the geographical center of the extant *Drynaria* habitats also supports this hypothesis. The distribution of *Drynaria delavayi* and *Drynaria baronii* expanded to the north (e.g. Gansu, Qinghai, Shanxi) while *Drynaria propinqua*, *Drynaria parishii*, *Drynaria quercifolia*, *Drynaria bonii*, and *Drynaria rigidula* mainly to the south (southeastern Asia, southern China etc.). *Drynaria mollis* spread to the west (Nepal, northern India, Tibet) and *Drynaria roosii* to eastern China and southeastern Asia.

Due to the lack of other fossil evidence, it is hard to clarify the extent and time of this putative spreading out. However, since no other drynarioid fossils are found in South or East Asia, there is at least a probability that this territorial expansion happened mainly in the Quaternary, later than all known fossil species. Thus, there is a possibility that *Drynaria* was restricted to western Yunnan until the end of the Neogene, albeit this assertion may change with more fossil discoveries.

Similar to the earlier than late Miocene radiation of *Aglaomorpha* (Roos 1985), *Drynaria* had diversified no later than the late Miocene when *Drynaria diplosticha* and *Drynaria* cf. *Propinqua* survived together, followed by a higher level of diversification in the Pliocene with the discovery of *Drynaria callispora*, *Drynaria dimorpha* and *Drynaria lanpingensis*. The process of the enrichment of *Drynaria* may be roughly inferred by these fossil records. Potential relationships among different Drynarioids species analysed by morphological cladistic analysis (Su et al. 2011) showed that *Drynaria propinqua* and *Drynaria roosii* (the NLRs of *Drynaria diplosticha*) are in comparatively distant relationship, each representing one small clade. The discovery of our fossil indicates that diversification of *Drynaria diplosticha* and *Drynaria propinqua* may have taken place earlier than the appearance of other known fossil species. In other words, they may have been "old species" in each branch of *Drynaria*. Later than that, *Drynaria callispora* and *Drynaria roosii*, which have close morphological and molecular affinity with *Drynaria diplosticha*, evolved, representing a late diversification in this clade. Of course, the possibility remains that many fossils of species living at that time have not yet been discovered, this cannot be said with absolute certainty. With more fossils reported in the future, there can be changes in the cladistic order of drynarioids.

Yunnan is the only region in which almost every living species of *Drynaria* in China occurs. The diversity of *Drynaria* fossils discovered in western Yunnan may indicate a high speciation rate with a number of new species occurring not far from each other. Along with the fact that they are discovered in western Yunnan exclusively, these fossils may suggest that western Yunnan served as one of the cradles of Drynarioid ferns during their early evolution. It seems likely that diversification had already taken place in the Neogene before the huge expansion started.

The East Asian Flora has been subdivided into two parts—the Metasequoia flora in the eastern China and the Rhododendron flora in the west (Wu and Wu 1996). Western Yunnan is mainly within the Rhododendron flora. Unlike the Metasequoia flora where many ancient relict lineages survive today despite their wide distribution in geological past, the Rhododendron Flora comprises more newly-formed clades (three fourth of them originated no earlier than Neogene) (Chen et al. 2017). Lu et al. (2018) drew the similar conclusion using angiosperm species. *Drynaria* is likely to be one of these clades where quick speciation happened during or after the Neogene.

Assuming the same habitat inclination as extant *Drynaria roosii*, *Drynaria diplosticha* was likely to be shade-tolerant and occurred in the understory of forests, either epiphytic or occasionally epilithic. The discovery of *Drynaria diplosticha*, as well as the other ferns, may indicate the existence of a multi-layered forest system (Wen et al. 2013). This forest system could have triggered the quick diversification of polypod ferns by providing large amount of newly formed niches (Schuettpelz and Pryer 2009). Ferns and angiosperms took the opportunity offered by these niches to rapidly expand their habitat both on forest floors as well as within canopies. There was a pronounced increase of epiphytic fern diversity after the Eocene (Schuettpelz and Pryer 2009), which may be stimulated by these niches and environmental changes.

Palaeoclimatic implication

Ferns may respond to climate shift faster than most of the angiosperms due to their short generation time (Schneider et al. 2004). The putative climate shifts may influence the fern components to a large degree, resulting in the rapid speciation and the prosperity of some clades. The quick diversification of *Drynaria* showed by the constant discovery of fossil specimens may be a climatic response.

Drynaria roosii (the NLRs of *Drynaria diplosticha*) is distributed in southern China and some regions in South Asia and Southeast Asia. The majority of these regions have an annual temperature between 16 and 20 °C and an annual precipitation from 900 to 1800 mm (National Meteorological Information Center 2019). The discovery of *Drynaria diplosticha*, together with the other drynarioids, hints similar climatic condition in western Yunnan at that time. This is congruent with previous investigations (Jacques et al. 2011). During the late Miocene and the late Pliocene, the mean annual temperature in western Yunnan (Lanping, Tengchong, Eryuan, Longling etc.) was higher than today and saw a drop from less than 1 °C to over 5 °C (Xu 2002; Xu et al. 2004; Kou et al. 2006; Xu et al. 2008; Wu et al. 2009; Sun et al. 2011; Xie et al. 2012, 2016; Hoke et al. 2014). *Drynaria* living there may have become cold resistant with the continuously lowering temperature. Changes in precipitation differ from place to place and are hugely influenced by the methods applied in different investigations (Xie 2007; Hoke et al. 2014). In spite of that, there are limited records inferring a MAP lower than 800 mm during both late Miocene and late Pliocene in western Yunnan and with most results MAP is over 1000 mm (Xu 2002; Xu et al. 2008; Wu et al. 2009; Sun et al. 2011; Su et al. 2013; Xie et al. 2016). Indeed, as indicated from the fossils, western Yunnan continued to be wet during the Neogene. Despite the cooling trend and the slight difference in precipitation, the environment stayed warm and humid with continuous existence of many fern species (Huang et al. 2016b; Xie et al. 2018).

Further evidence for clear seasonality in the late Miocene (Xu et al. 2008; Xing et al. 2012; Li et al. 2015a; Huang et al. 2016a) may potentially be inferred by our fossil. Under the assumption that the leaf fell off naturally (which happens in most cases), the abscission layer can be recognised on our fossil, by which an individual pinna articulates with the costa. It goes along the costa at the basiscopic side while separate at the other. The pinna fell off entirely before the fossilization process and, if considered a common phenomenon, this may indicate the existence of clear seasonality during that time. The abscission occurred at the start of winter or dry season just like leaves in deciduous forest at present. The seasonality was thought to be weaker than now, given that Lincang had a more humid winter (Jacques et al. 2011, 2014).

The implication on palaeoclimate is also supported by the expansion of drynarioids. *Drynaria* thrives primarily in tropical areas like Southeast Asia. Habitats of most species of *Drynaria* are mainly to the south of Yunnan Province except *Drynaria delavayi* and *Drynaria baronii* who live chiefly to the north. This can be related to the climatic changes throughout time. Along with the cooling trend, most of the Drynarioid ferns gradually enlarged their habitats to the south faster than to the north.

Regional topographical changes may influence the local climate and subsequently lead to floral changes and rapid speciation. Situated at the southeastern margin of the Tibet Plateau, Yunnan experienced fast-altering altitude and topography which may lead to variation in precipitation, monsoon intensity, etc. (Xie et al. 2012, 2016; Zhang et al. 2012; Su et al. 2013). In the Neogene, Yunnan showed a pattern of high elevation in the north and lower in the south. Northwestern Yunnan might have been at a high elevation throughout the Neogene until now. The northeastern part was higher and colder than present in late Miocene (Jacques et al. 2011; Li et al. 2019). By contrast to the northern part of Yunnan, Lincang was at relatively lower altitude with a tropical palaeoflora where tropical or subtropical plant elements took up more than 60% (Jacques et al. 2014). There might have been an altitudinal difference of over 1700 m between Lincang (southwestern Yunnan) and Xianfeng (northeastern Yunnan) (Jacques et al. 2014). Until now, the only two specimens of *Drynaria* from the Miocene were discovered in the southwestern part of Yunnan. We may infer that *Drynaria* was restricted by regional difference of climate in Yunnan province during that time. Hoke et al. (2014) suggested that, in contrast to the northern area of Yunnan, the southern part saw a huge surface uplift for more or less 1 km after the late Miocene. The northeastern distributional expansion of some species may have happened as a result of the declining altitudinal difference and temperature difference.

Habitats across a wide range of altitude would have formed due to the rapid topographic shifts leading to more diversified and complicated lineages. In western Yunnan, there are some large parallel mountains that run north to south, e.g. Hengduan Mountain, Ailao Mountain, Gaoligong Mountain. West-east isolation caused by these mountains and the valleys in-between may have played a significant role in speciation (Chen et al. 2017). This isolation also may have blocked the longitudinal expansion of *Drynaria*, resulting in the deficiency of Neogene fossil records in some warm and humid places like southeastern Yunnan (e.g. Xiaolongtan flora, Xia et al. 2009; Wenshan flora, Li et al. 2015a). Another impact of this topographical setting is the existence of north-south corridors that enhanced the latitudinal species exchanges. These corridors may have facilitated the migration of the drynarioid ferns from southern Yunnan to the northwestern region (e.g. Lanping, Yongping, Tengchong).

Conclusion

Based on specific morphological comparison with other ferns, our fossil is recognised as a new species of *Drynaria*—*Drynaria* *diplosticha* sp. nov. Together with another fossil, *Drynaria* cf. *propinqua*, reported from the same geological age, we conclude that *Drynaria* diversified no later than the late Miocene. Previously, all reported *Drynaria* fossils have been from western Yunnan. Western Yunnan may have been a radiation center of *Drynaria* in the Neogene where its extant species rapidly diversified and the distribution expanded. Indeed, western Yunnan may have been at least one of the cradles of drynarioids during their early evolution. Our fossil further suggests that Lincang was a humid and warm region during the late Miocene and that there was clear seasonality at that time. The diversification of drynarioid ferns since the late Miocene may also be related to the fast topographical alteration of western Yunnan.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animal rights and informed consent statement This article does not contain any studies with human or animal subjects.

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