



## A new *Drynaria* (Polypodiaceae) from the Upper Pliocene of Southwest China

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### ABSTRACT

A polypodiaceous fern, *Drynaria callispora* sp. nov., is described from the upper Pliocene Sanying Formation in western Yunnan Province, southwestern China. This species with well-preserved pinnae and *in situ* spores is the first convincing *Drynaria* fossil record. Detailed morphological investigation reveals that *D. callispora* is characterized by 1) pinnatifid fronds with entire-margined pinnae having straight or zigzag secondary veins; 2) finer venation showing void quadrangular areoles, but occasionally with one unbranched veinlet; 3) one row of circular sori on each side of the strong primary vein; and 4) *in situ* spores with verrucate exospores elliptical in polar view and bean-shaped in equatorial view. A morphological comparison shows that *D. callispora* is significantly different from all the fossil species previously identified as drynarioids. A phylogenetic analysis of *D. callispora* supports that the fossil is closely related to *D. sinica* Diels and *D. mollis* Bedd., two extant species distributing in the Himalayas. The discovery of the new fern indicates that the genus *Drynaria* became diversified in its modern distribution region no later than the late Pliocene and had retained a similar ecology to that of many modern drynarioid ferns ever since.

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### 1. Introduction

Drynarioid ferns are epiphytic and generally have humus-collecting structures (Janssen and Schneider, 2005). This group consists of two living genera, i.e., *Aglaomorpha* Schott and *Drynaria* (Bory) J. Smith, with 14 and 16 species, respectively (Roos, 1985). Drynarioids mainly distribute in southeastern Asia and Oceania; additionally, two species of *Drynaria* occur in central Africa, and one in Madagascar and adjacent islands (Roos, 1985). The modern diversity center of *Drynaria* is in southeastern Asia (Ching, 1978). Nine species of *Drynaria* occur in southern China (Lin et al., 2000). A recent phylogenetic analysis shows that *Aglaomorpha* is monophyletic, while *Drynaria* is paraphyletic with the species living in the Himalayas and southern China sister to *Aglaomorpha* (Janssen and Schneider, 2005).

It is now clear that the modern ferns started to diversify while the early angiosperms became flourished in the late Cretaceous (Schneider et al., 2004). However, the origins and phylogenetic patterns of ferns are still far from being clear largely due to their poor fossil record (Stockey and Rothwell, 2006; Axsmith, 2009). For example, although the fossil record of drynarioids shows that the early possible members of this group, e.g. *Astralopteris coloradica* (Brown) Reveal et Tidwell ex Rushforth, might emerge in the Cretaceous (Tidwell et al., 1967; Tidwell and Ash, 1994), the phylogenetic history of drynarioids is still highly debated, because of their poor preservation and insufficient diagnostic characters in fossils (Roos, 1985; Taylor et al., 2008). In his comprehensive treatment on the phylogenetic systematics of the subfamily Drynarioideae, Roos (1985) only accepted one fossil record, *Aglaomorpha heraclea* (Kunze) Copeland, from the upper Miocene of Palembang Province in Sumatra (Kräusel, 1929), as a confirmed drynarioid fern. In addition, another related drynarioid fossil, *Protodrynaria takhtajanii* Vikulin et Bobrov was later described from the Eocene–Oligocene boundary in Russia (Vikulin and Bobrov, 1987).

In the present study, we describe a new species of *Drynaria* with well preserved pinnae and *in situ* spores. The fossil specimens were collected from the upper Pliocene Sanying Formation in Yongping of Yunnan, southwestern China. Both morphological and phylogenetic approaches are used to evaluate the affinities of the new species with the modern

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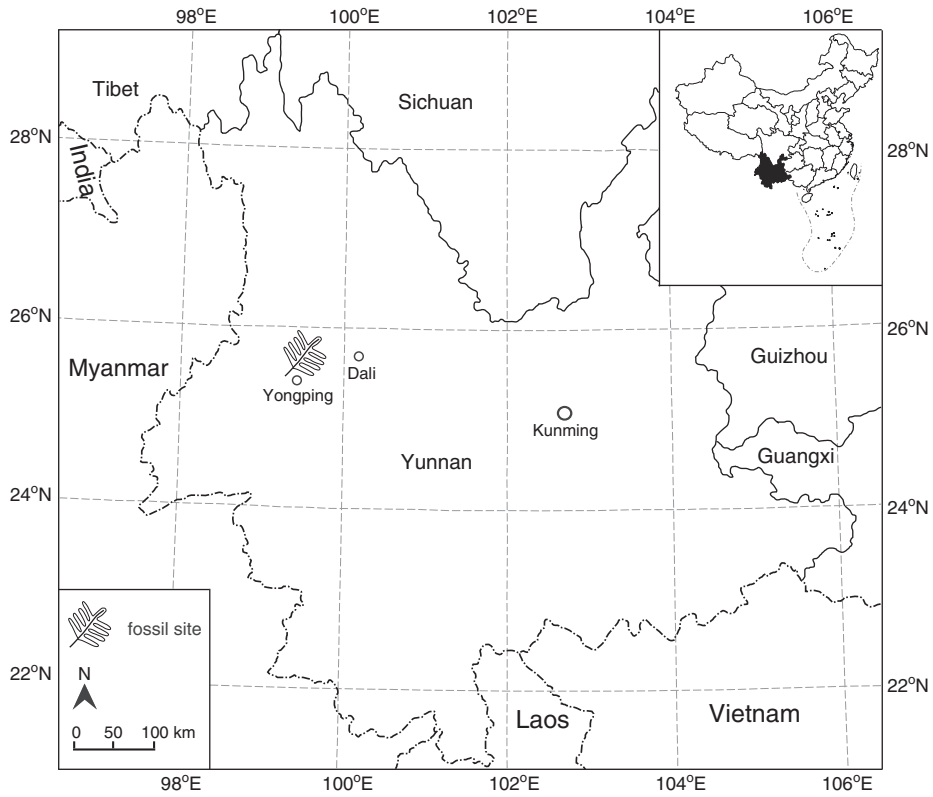


Fig. 1. Map of Yunnan Province, showing the location of fossil site.

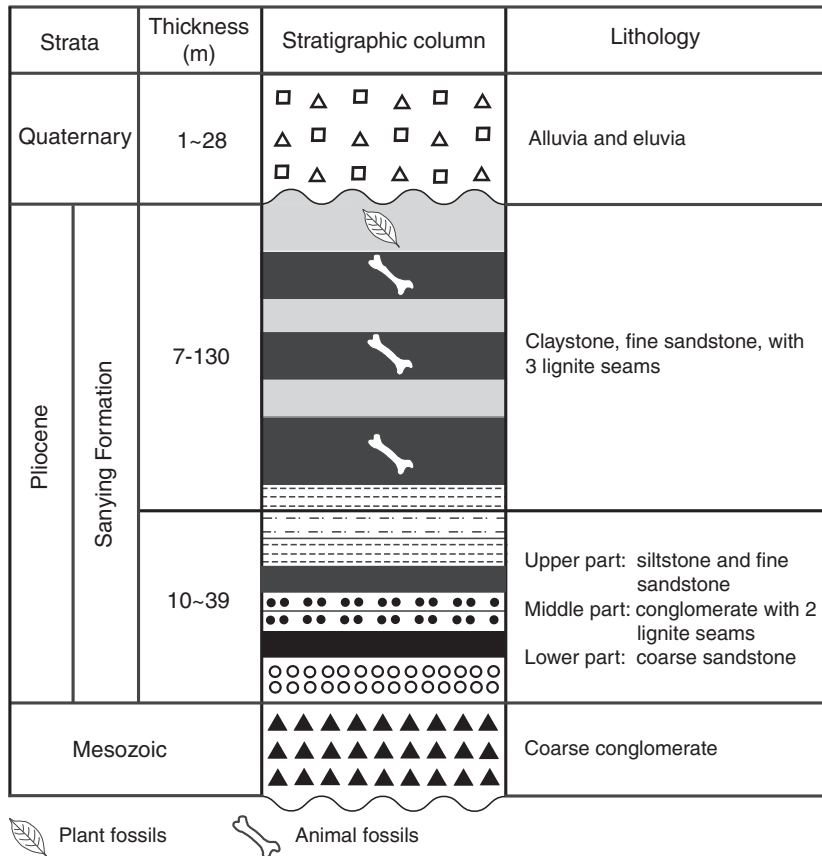


Fig. 2. Stratigraphy of the Sanying Formation in the Yangjie coalmine (after Bureau of Geology of Yunnan Province (BGYP), 1979).

drynarioids. The discovery of this fern not only provides a rare opportunity to recognize the diversity of drynarioids in the Cenozoic, but also improves our understanding of the phylogeny of this group.

## 2. Materials and methods

### 2.1. Fossil site

The fossil fronds studied here were collected from the Yangjie coalmine, about 10 km north of Yongping County, western Yunnan Province (25°30'48" N, 99°31'11" E; 1715 m a.s.l.; Fig. 1). The strata in the coalmine, known as the Sanying Formation, (Fig. 2) consist of two units (Bureau of Geology of Yunnan Province, BGY, 1979). The basal unit is 10–39 m thick and is further subdivided into three parts. The gray fine sandstone and siltstone is on the top, the brown-yellow conglomerate with two lignite seams is in the middle, while the coarse sandstone occurs on the base. The overlying unit is 7–130 m thick, which, in descending order, is composed of the plant fossil-bearing gray clay, followed by three animal fossil-bearing lignite seams, and the fine sandstone in the bottom (Fig. 2). Based on the information of the local geological structure, stratigraphy, and fossil evidence, Ge and Li (1999) confirmed the age assignment of the Sanying Formation as late Pliocene, previously proposed by other researchers (e.g. Tao and Kong, 1973; Writing Group of Cenozoic Plants of China (WGCP), 1978; Yunnan Bureau of Geology and Mineral Resources (YBGMR), 1978; Hu, 1980; Resources of Yunnan Bureau of Geology and Mineral (RYBGM), 1990; Tang and Hu, 1993; Zong et al., 1996). Mammal fossils such as *Cervavitus* sp., recently found in the Sanying Formation, further support the age assignment of the formation (T. Deng, personal communications). The fossil fern fronds and pinnae studied here were uncovered from the plant fossil-bearing clay (Fig. 2), in which the most abundant fossil leaves unearthed are evergreen sclerophyllous oaks (*Quercus* section *Heterobalanus* Menitsky).

### 2.2. Morphological study

Morphological studies on both the fossil fronds and *in situ* spores were conducted to determine the taxonomy of the fossils. Digital images of the fossil fronds were first captured with Canon SX 100.

After the sori in the middle part of a pinna were located in a well-preserved specimen (Plate I, 6; YP 01), a group of sporangia from one sorus was sampled (Plate II, 4) with an aid of a dissecting needle under a dissecting microscope (Nikon SMZ 1500). The sporangia were placed on a concave glass slide. The preparation for SEM examination follows the procedures described by Liu and Basinger (2000) and Liu et al. (2001) and briefly stated in the following. A drop of 65% nitric acid was added to the sporangia on the slide for one-minute maceration till the material became transparent. A specially prepared dissection needle with a human hair mounted atop was applied to remove the transparent material to another clean glass slide with one drop of glycerol. *In situ* spores were checked and pictured under a compound microscope (Nikon Eclipse E200). Finally, either a single spore or a clump of spores was removed by the needle onto an SEM stub while a drop of pure alcohol was applied to remove the glycerol from the surface of spores. The stub was sputter-coated with gold palladium for 5 min. The spores were examined under SEM (KYKY-1000). The terminology of frond and spore used in the present study follows Roos (1985), Tryon and Lugardon (1990); Harris and Harris (1994); and Xiang and Wu (2007).

### 2.3. Phylogenetic analysis

To integrate a fossil into a phylogeny of extant species, we need to focus on the morphological characters present on fossils, as they are the only characters available in the fossils. Several methods can be used for such a task. One approach focuses only on morphological characters to reconstruct the phylogeny, but not all available information, such as molecular data of the modern species, is used (Hermsen and Hendricks, 2008). The second approach, known as the Total Evidence, the Supermatrix Approach, or the Simultaneous Analysis, is based on a single matrix including both molecular data and morphological characters (Kluge, 1989; Nixon and Carpenter, 1996; de Queiroz and Gatesy, 2007). As no molecular data are available from the fossils, it includes a large amount of missing molecular data in the matrix, which may result into a poor resolution of the phylogeny. Lastly, the third approach, the Molecular Scaffold, is an alternative to overcome the phylogenetic resolution problem (Springer et al., 2001). This approach starts with a molecular phylogeny reconstructed for the modern species.

**Plate I.** *Drynaria callispora* sp. nov. Scale bar = 1 cm.

1. Pinnatifid sterile frond showing the stalk and the opposite arrangement of the two basal pinnae. Paratype YP754.
- 3, 4, 7, 8, 12. Sterile pinnae showing the form of apex and base.
3. Paratype YP15.
4. Paratype YP12.
7. Paratype YP06.
8. Paratype YP11.
12. Paratype YP14.
- 2, 5, 6, 9–11. Fertile pinnae showing the arrangement of sori along the primary vein.
2. Paratype YP04.
5. Paratype YP07.
6. Holotype YP01.
9. Paratype YP08.
10. Paratype YP05.
11. Paratype YP03.

**Plate II.** *Drynaria callispora* sp. nov. (see on page 136)

- 1, 2. Close-up of a sterile pinna. Paratype YP11.
1. Details of the strong primary vein and zigzag to straight secondary veins. Scale bar = 5 mm.
2. Detail of areoles, showing one unbranched veinlet occasionally occurred in some areoles (arrows). Scale bar = 2 mm.
3. Close-up of a fertile pinna, showing the position of sori close to the primary vein. Paratype YP04. Scale bar = 5 mm.
4. Detail of a sorus, showing numerous sporangia (arrow) where samplings for *in situ* spores were made. Holotype YP01. Scale bar = 0.5 mm.
- 5–8. *In situ* spores extracted from Holotype YP01. Light (5) and scanning (6–8) micrographs.
5. Light micrograph of a single *in situ* spore, separated after maceration. Note the monolet and planoconvex form. Scale bar = 10  $\mu$ m.
6. A clump of *in situ* spores under SEM, showing the bean-shaped form and verrucate exospores. Scale bar = 50  $\mu$ m.
7. Scanning electron micrograph of a single *in situ* spore, separated after maceration, showing the verrucate exospores. Scale bar = 10  $\mu$ m.
8. Details of the verrucate exospores of Fig. 7, showing different verrucae in size and shape. Scale bar = 10  $\mu$ m.

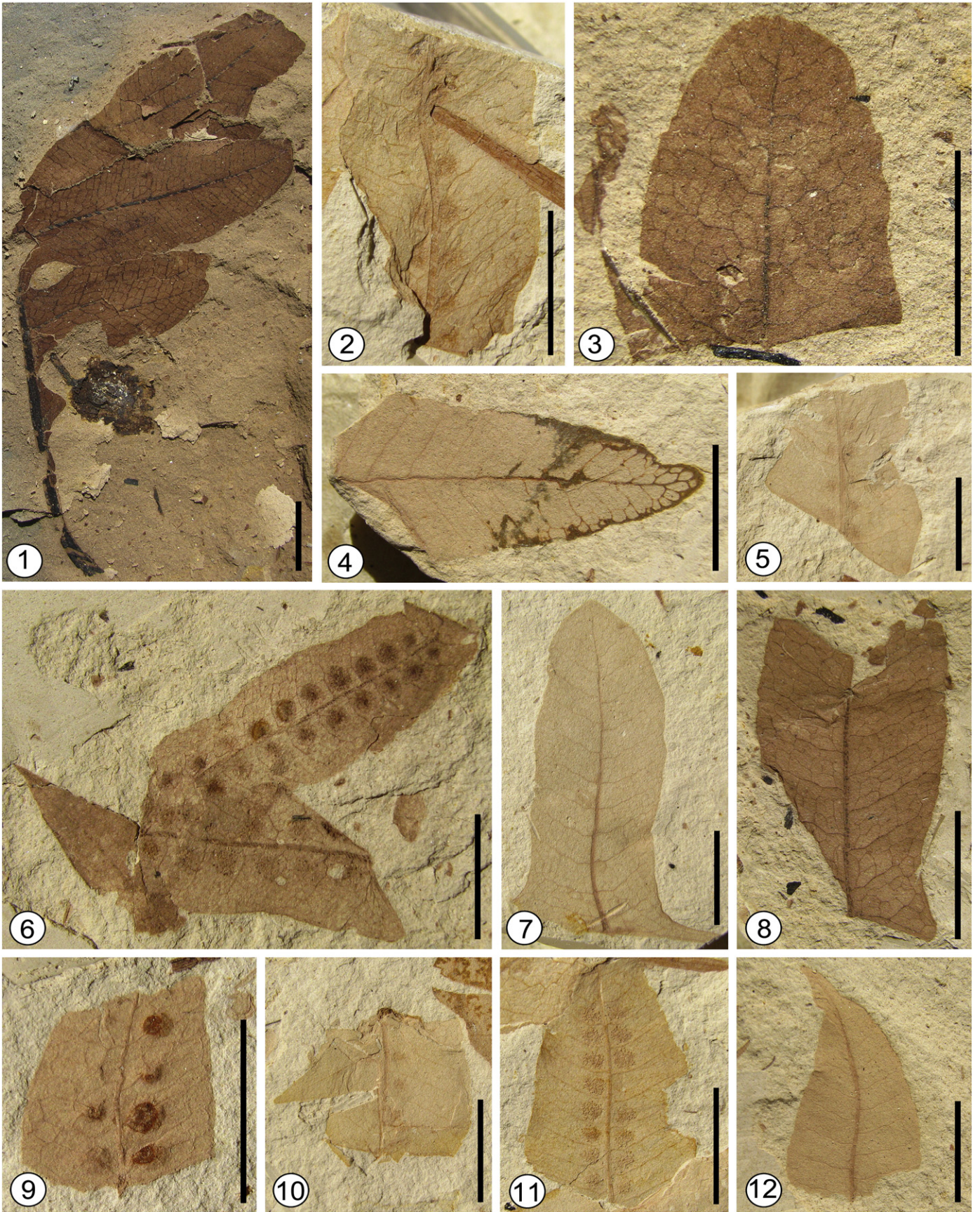


Plate I.

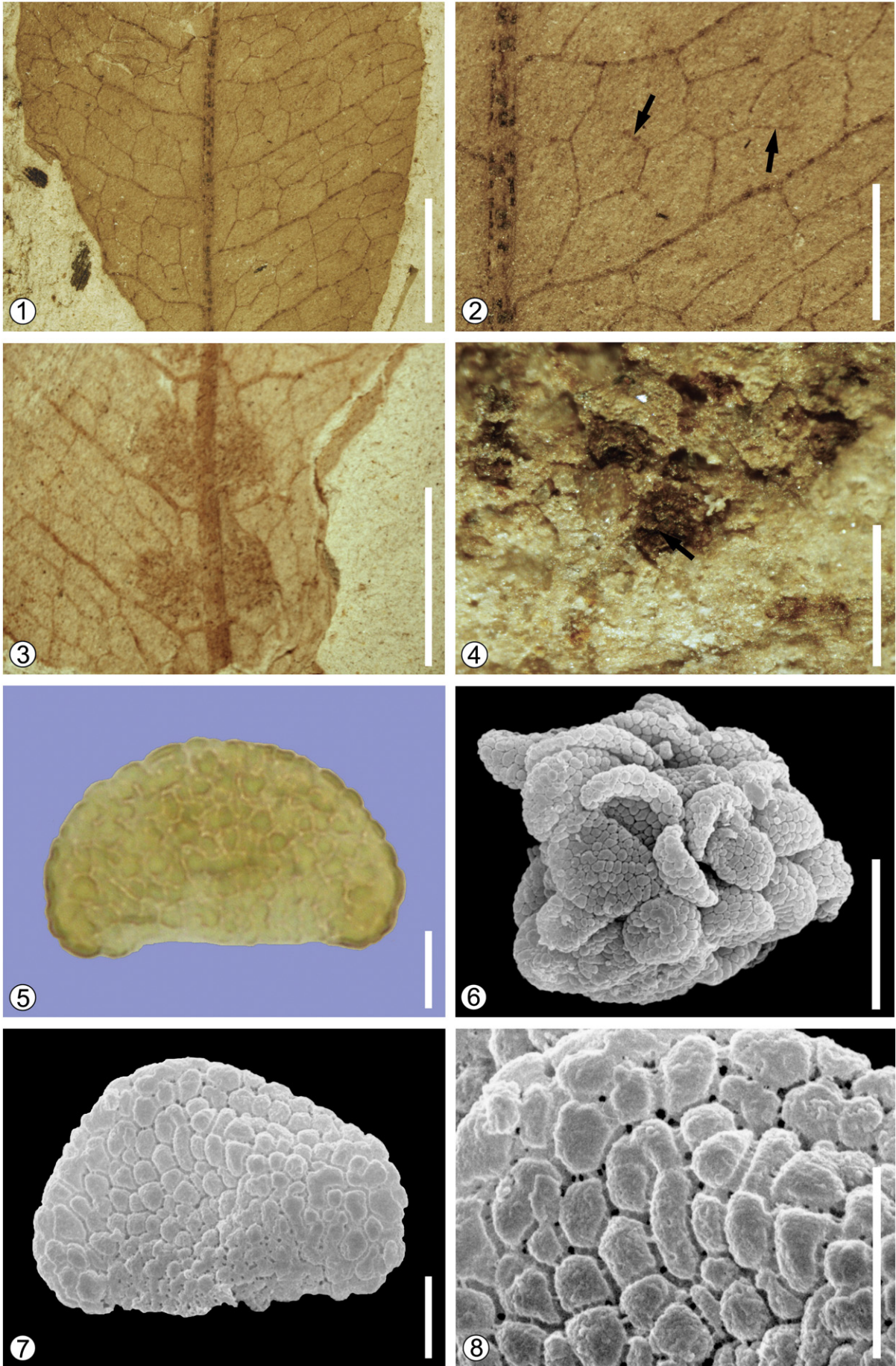
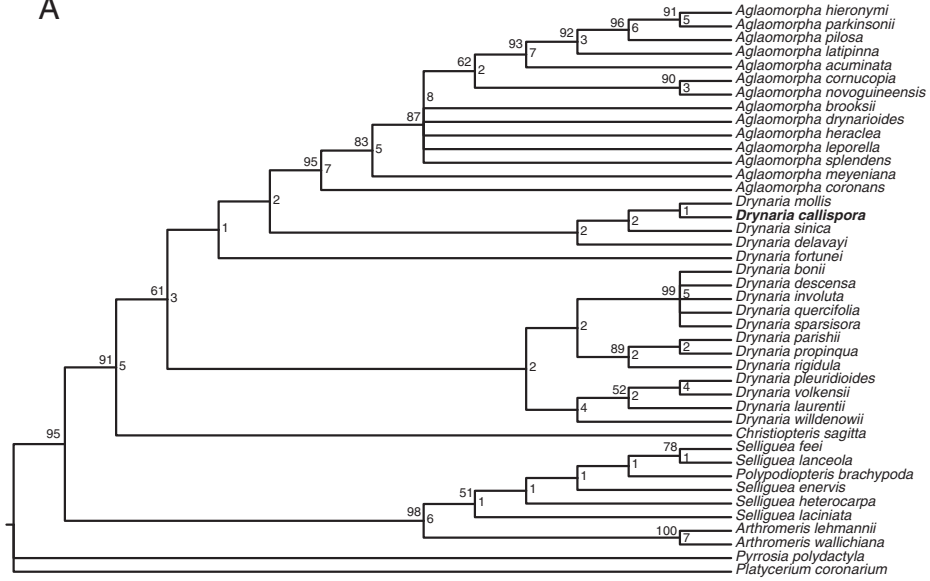
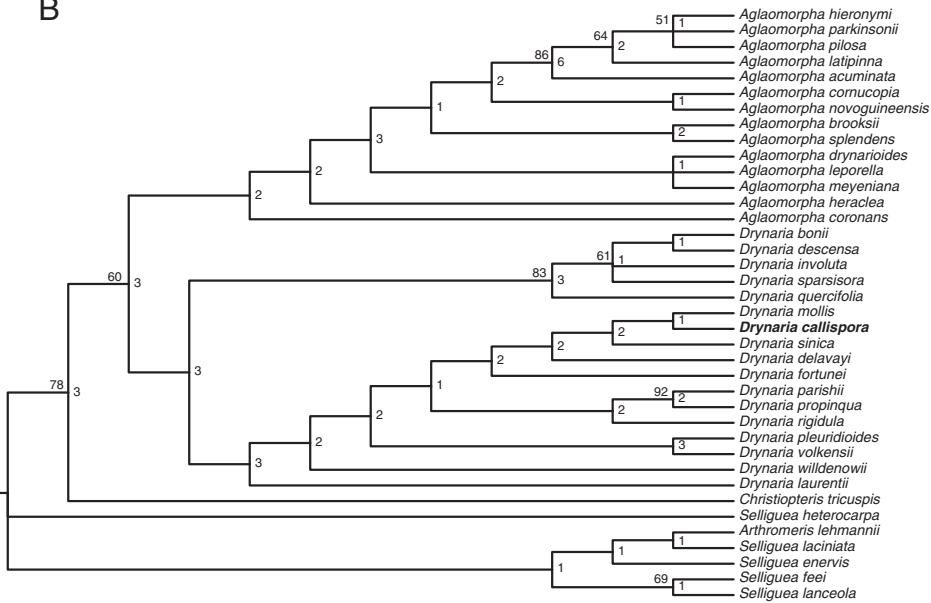


Plate II (caption on page 134).

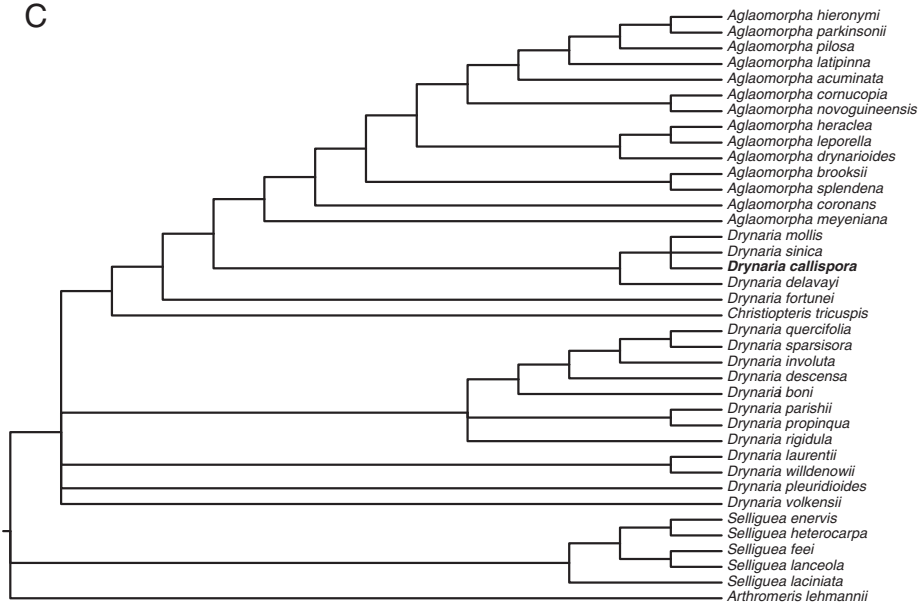
A



B



C



Then this phylogeny is used as a backbone constraint in a morphological phylogenetic reconstruction including the fossils and all the extant species. Under the Molecular Scaffold, information of fossil species cannot change phylogenetic relationships among the modern taxa. As these three approaches are different, they sometimes give different results (Manos et al., 2007). It is believed that the Molecular Scaffold appears often a better approach to be employed when dealing with fossil taxa in phylogenetic reconstructions as it prevents from including a large amount of missing data (Manos et al., 2007). In this study, we only have one fossil species that should be included in the phylogeny; therefore, all three methods can be easily used.

The morphological character states for the extant drynarioids were after Janssen and Schneider (2005). The choice of the outgroup, *Christiopteris tricuspis*, for drynarioids follows Schneider et al. (2008). The coding for the outgroup and the Chinese fossil follows the character definitions by Roos (1985) (Appendix A). Four chloroplast loci, viz. *rbcl*, *rps4*, *rps4-trnS* and *trnL*, make the molecular dataset (from Genbank). Molecular sequences of the extant drynarioids are from Schneider et al. (2008), except for *Drynaria sinica*, whose sequences are from Janssen and Schneider (2005).

All cladistic analyses were carried out with PAUP\* version (Swofford, 1998), with the following options: TBR branch swapping, random addition sequence, 1000 replications, multrees on. Bootstraps were calculated with the same software and 1000 bootstrap replicates, using the same search options but only 10 addition replicates. Decay indices were calculated using TreeRot.v3 (Sorenson and Franzosa, 2007). No support value was calculated for the Molecular Scaffold Analysis as most of nodes were constrained by the scaffold.

Mesquite version 2.71 (Maddison and Maddison, 2009) is used to reconstruct morphological character evolution by parsimony optimization. Character evolution was reconstructed based on the three consensus trees derived from these three different analyses.

### 3. Systematics

Order—Filicales Link

Family—Polypodiaceae Berchtold et J.S. Presl

Genus—*Drynaria* (Bory) J. Smith

Species—*Drynaria callispora* Su, Zhou et Liu sp. nov. (Plates I and II)

Holotype: YP01 (Plate I, 6).

Paratypes: YP754 (Plate I, 1), YP04 (Plate I, 2), YP15 (Plate I, 3), YP12 (Plate I, 4), YP07 (Plate I, 5), YP06 (Plate I, 7), YP11 (Plate I, 8), YP08 (Plate I, 9), YP05 (Plate I, 10), YP03 (Plate I, 11), and YP14 (Plate I, 12).

Repository: Specimens are kept in the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN).

Type locality: Top clay layer of the Sanying Formation, Upper Pliocene, Yangjie coalmine, Yongping County, Yunnan Province, southwestern China (Fig. 1).

Etymology: The specific epithet *callispora* is proposed to represent the beautiful and well-preserved *in situ* spores. In Old Greek, *kallos* means “beauty”, while *spora* denotes “spore”.

Diagnosis: Fronds pinnatifid with winged stalk; margin of pinnae entire, base excurrent; apex of sterile pinnae acute or obtuse, base more or less constricted; fertile pinnae with acute apex, base not constricted. Veins prominulous; primary vein strong and straight; secondary veins straight or sometimes zigzag; areoles irregular or quadrangular, occasionally with one unbranched veinlet. Sori round, apparently lacking indusia, close to the primary vein and arranged in one row on each side of the primary vein; one sorus per areole along

**Table 1**

Statistical results of the three cladistic analyses carried out in the present study.

Approach	Morphological analysis	Combined analysis	Molecular scaffold analysis
Number of trees	8	4	4
L (steps)	504	1538	546
Ci	0.292	0.591	0.269
Ri	0.617	0.693	0.566

the primary vein, compital. *In situ* spores elliptical in polar view, bean-shaped in equatorial view, monolete, planoconvex, and exospores verrucate.

**Description:** The description of *Drynaria callispora* is based on 12 specimens at our disposal, among which one represents a basal part of a sterile frond (Plate I, 1), and the other 11 specimens are partially preserved either fertile or sterile pinnae (Plate I, 2–12).

A fragmentary portion of sterile frond is pinnatifid, with a stalk 2.5 cm long preserved (Plate I, 1). One wing with excurrent base is observed near the basal part of frond, and its length is 0.4 cm. Pinnae are lanceolate with entire margin (Plate I, 1, 3, 4, 6–8, 11 and 12). The basal pinnae are opposite in arrangement (Plate I, 1). Sterile pinnae are ~3.3–5.5 cm long and ~1.2–1.7 cm wide (Plate I, 1 and 7). The apex of sterile pinnae is acute or obtuse; the basal part is excurrent and slightly constricted (Plate I, 1, 7 and 8). The widest part is near the middle of the pinnae (Plate I, 1, 7 and 8). Fertile pinnae are ~5.5 cm long and 0.9–1.5 cm wide. The apex of the fertile pinnae is acute, and the base is excurrent without constriction (Plate I, 6). Veins are prominulous. Secondary veins run straight or sometimes more or less irregularly zigzag. They connect with the primary vein in an acute or vertical angle and are not joined near the margin (Plate II, 1 and 2). Irregular to quadrangular areoles occur between the adjacent secondary veins (Plate II, 1). One unbranched veinlet occasionally occurs in the areoles (Plate II, 2).

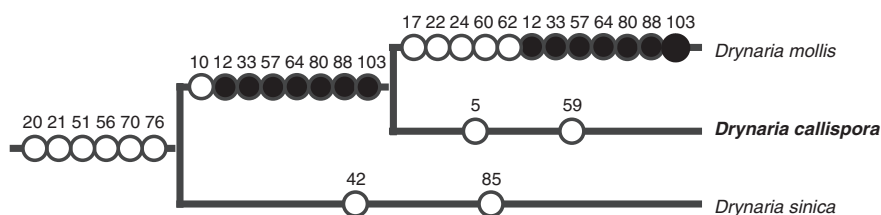
Sori are closely located to the primary vein and are equally arranged in one row on each side of the primary vein (Plate I, 2, 5, 6, 9–11). Sori are compital and round, 1.0–1.5 mm in diameter, each of which lacks indusia and covers about half of the areole (Plate II, 3). *In situ* spores are monolete and planoconvex, elliptical in polar view and bean-shaped in equatorial view (Plate II, 5–7). Polar axis ~30 μm long, and equatorial axis ~50 μm long. Exospores are intensively verrucate, and verrucae are of different sizes (Plate II, 8).

### 4. Phylogenetic results

In the morphological analysis, 110 characters are phylogenetically informative. Twenty-six morphological characters could be coded for *Drynaria callispora*. The cladistic analysis based exclusively on morphological characters yielded nine equi-parsimonious trees and their strict consensus tree is shown in Fig. 3A. The combined analysis using both morphological and molecular data resulted in four equi-parsimonious trees and the strict consensus tree can be found in Fig. 3B. The Molecular Scaffold Analysis produced four most parsimonious trees and their consensus tree is given in Fig. 3C. Statistical data of these analyses are presented in Table 1.

The results of the three analyses are partly incongruent (Fig. 3A–C). However, regarding the systematic position of *D. callispora*, the three

**Fig. 3.** Strict consensus trees corresponding to three different cladistic analyses. Numbers on branches represent bootstrap values based on 1000 replications, while numbers in the nodes represent Bremer indices. A, The strict consensus tree of four most parsimonious trees based on the combination of morphology and four genetic regions (*rbcl*, *rps4*, *rps4-trnS* and *trnL*). B, The strict consensus tree of eight most parsimonious trees based on morphological data only. C, The strict consensus of four most parsimonious trees based on the scaffold method.



**Fig. 4.** Character evolution of the clade with the fossil, performed by using Mesquite v.2.71 (Maddison and Maddison, 2009). Changes that are differently reconstructed by Acctran or Deltran options are represented by filled circles, whereas changes that are reconstructed the same way by Acctran and Deltran are represented by open circles. The character number and definition are after Janssen and Schneider (2005).

consensus trees appear consistent. In all cases, the fossil species shows close affinities with *D. mollis* and *D. sinica*. In the morphological and combined analyses, *D. callispora* is sister to *D. mollis*, and *D. sinica* to the clade composed of *D. mollis* and *D. callispora*, while the Molecular Scaffold Analysis suggests that the fossil and the two extant ferns are united in a monophyletic clade, though the relationships among them cannot be further resolved.

The evolution of characters is reconstructed for the clade *Drynaria callispora*, *D. mollis* and *D. sinica* (Fig. 4). As there is no difference in character reconstruction for the morphological and combined analyses for this clade, we represent it on the same figure. Reconstruction for the Molecular Scaffold Analysis only introduces lack of resolution compared to the former two. *D. callispora* shares two synapomorphies with *D. mollis* and *D. sinica*, i.e. irregular branching points of costular tertiary vein and secondary vein (character 20) and aeroles with 0–1 veinlet (character 21). The other four synapomorphies of this clade are not preserved on the fossil (characters 51, 56, 70, and 76). In addition, *D. callispora* and *D. mollis* have one synapomorphy, viz. entire margin of pinnae (character 10). Finally, *D. callispora* has two autapomorphies, viz. some pinnae with clear basal constriction (character 5) and no spine on spores (character 59).

## 5. Discussion

### 5.1. Morphological comparisons with the extant *Drynaria* ferns

The Pliocene fern *Drynaria callispora* clearly displays some distinctive morphological characters of the genus *Drynaria* (Appendix B). *Drynaria* is characterized by the drynarioid venation pattern (Lin et al., 2000), meaning that the veins are prominulous and anastomosing, forming irregular quadrangular areoles; and for most living *Drynaria* species, except *D. involuta*, *D. fortunei*, and *D. pleuridioides*, veinlets are only occasionally present in the areoles. This venation pattern is clearly exhibited in *D. callispora*. Furthermore, the fronds are pinnatifid in *D. callispora* and most of the extant *Drynaria*, except for those of *D. rigidula*, which are once pinnate. Other characters, e.g., lack of contraction in fertile pinnae, the distribution of sori on the abaxial surface, and the roundness of sori, are present in *D. callispora* and shared with all the extant *Drynaria* ferns. *D. callispora* can be obviously distinguished from another genus of drynarioids, *Aglaomorpha*, by the shape of frond petiole because *Drynaria* usually has stalked fronds, whereas *Aglaomorpha* often has sessile fronds (Roos, 1985). The inclusion of *D. callispora* in *Drynaria* is confirmed by all the three phylogenetic analyses.

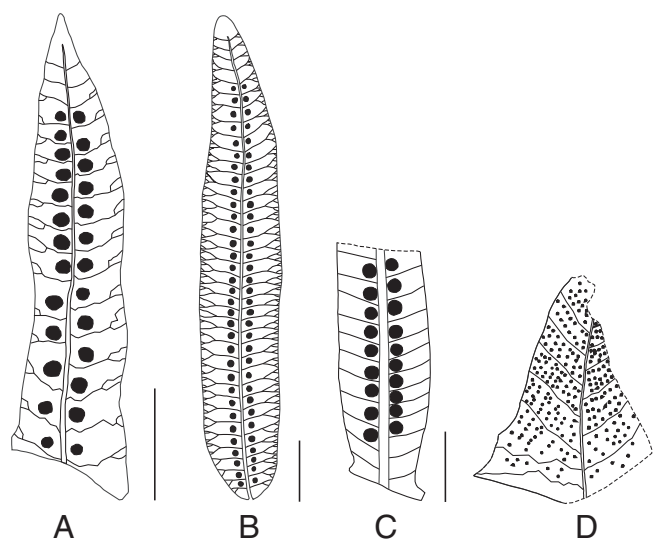
The phylogenetic analyses also reveal the affinities of the Chinese fossil *Drynaria* at the specific level. *D. callispora* is placed in a clade composed of *D. mollis* and *D. sinica* (Fig. 3A–C), now growing in the Himalayas. Therefore, *D. callispora* is a member of the northern *Drynaria*. The sister relationship between *D. callispora* and *D. mollis* is supported by the entire margin of pinnae (character 10, Fig. 4).

*In situ* spores were extracted from the specimen YP01 (Plate I, 6). These spores are elliptical in polar view and bean-shaped in equatorial view, and have verrucate exospores (Plate II, 5–8), all of which can be

seen in many species of *Drynaria* (Roos, 1985; Tryon and Lugardon, 1990). However, it is necessary to mention that these gross morphological characters of spores provide limited information on taxonomic determination of polypodiaceous ferns at the generic level (Tryon and Lugardon, 1990). Although exospore ornamentation is usually one of the most diagnostic characters for spore identification (Beijing Institute of Botany, 1976), it may not be critical for intrafamilial determinations. The exospore of *D. callispora* is verrucate, which is also present in many other genera of Polypodiaceae, e.g., *Goniophlebium* and *Polypodium* (Beijing Institute of Botany, 1976).

### 5.2. Fossil record of drynarioids

Fossil record of the drynarioids is poor (Van Uffelen, 1991) because only few fossils resembling the living *Drynaria* have been occasionally discovered from the Mesozoic and Cenozoic (Taylor et al., 2008). Although some *Drynaria*-like fossils have been documented, their morphology fails to show a close resemblance to the extant *Drynaria* (Tidwell et al., 1967; Taylor et al., 2008). For example, Bayer (1899) reported three new species of *Drynaria* from the Cenomanian of the Czech Republic, i.e. *D. astrostigma*, *D. dura*, and *D. tumulosa* and further transferred *Lambertiaphyllum durum* into this genus. The form of pinnae in these fossils is somewhat similar to that of *Drynaria*, but their taxonomy cannot be confirmed due to poor preservation and no *in situ* spores. Both the type and arrangement of sori have revealed that these fossils have to be transferred to the Matoniaceae instead



**Fig. 5.** Comparative drawings of fertile pinnae in *Drynaria callispora*, *Astralopteris coloradica* and *Aglaomorpha heraclea*. A, *Drynaria callispora* (no. YP 01, this study). B, *Astralopteris coloradica* (after Tidwell et al., 1967). C, *Protodrynaria takhtajanii* (after Vikulin and Bobrov, 1987). D, *Aglaomorpha heraclea* (after Roos, 1985). Scale bars = 1 cm.



**Table 2**  
Morphological comparisons of selected *Drynaria*-like fossil ferns, including *Drynaria callispora* (present study), *Astralopteris coloradica* (Tidwell et al., 1967), *Protodrynaria takhtajanii* (Vikulin and Bobrov, 1987) and *Aglaomorpha heraclea* (Kräusel, 1929; Roos, 1985).

Species	Lobation	Margin of pinna	Secondary veins	Costa areoles	Distribution of sori
<i>Drynaria callispora</i>	Pinnatifid	Entire	More or less zigzag	Quadrangular	One row parallel to primary veins
<i>Astralopteris coloradica</i>	Pinnate	Entire	Straight	Irregular	One row parallel to primary veins
<i>Protodrynaria takhtajanii</i>	Pinnatifid	Entire	Straight	–	One row parallel to primary veins
<i>Aglaomorpha heraclea</i>	Pinnatifid	Entire	More or less zigzag	Quadrangular	One row parallel to tertiary veins

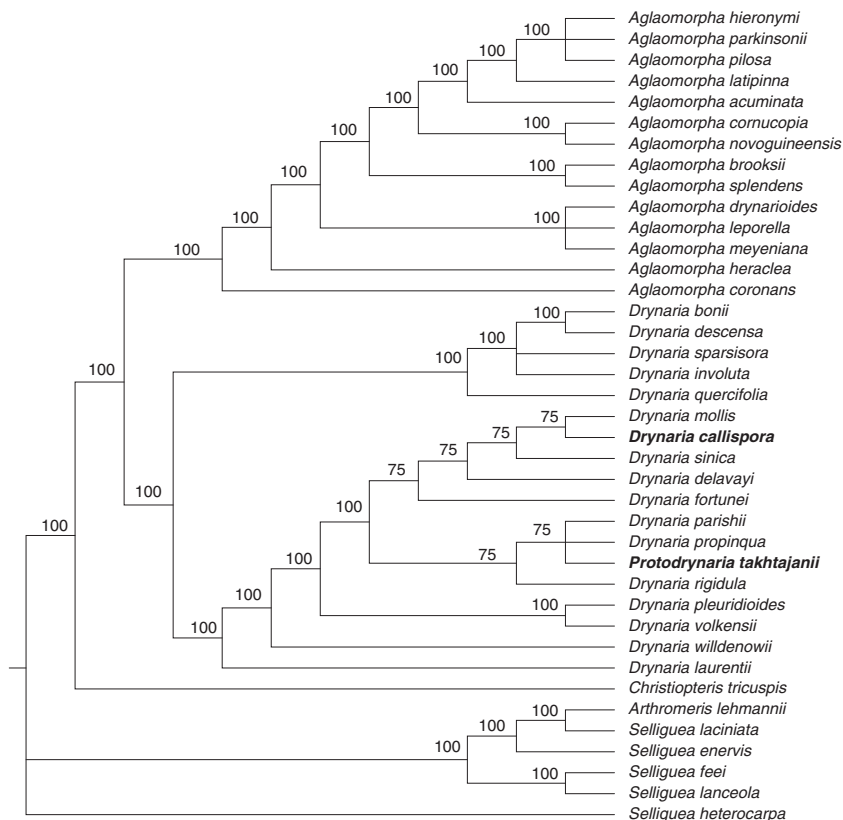
(Nathorst, 1908; Harris, 1961; Van Konijnenburg-van Cittert, 1993; Kvaček and Dašková, 2010).

Another *Drynaria*-like fossil, *Astralopteris coloradica* (Fig. 5B), was extensively described from the Cretaceous Dakota Sandstone of east-central Utah and southwestern Colorado (Tidwell et al., 1967). *D. callispora* is similar to *A. coloradica* in sorus arrangement in that both species have anastomosing veins with compital sori, which are round and arranged in one row on each side of the primary vein (Fig. 5A and B; Table 2). But the fronds of *D. callispora* are pinnatifid, whereas those of *A. coloradica* are pinnate (Table 2). Moreover, *A. coloradica* does not have quadrangular coastal areoles, an important character in the extant species of *Drynaria*. Tidwell et al. (1967) described this fern as a new extinct genus *Astralopteris* being related to *Drynaria*. More recently, Skog and Dilcher (1994) suggested that *A. coloradica* might have affinity with the Matoniaceae.

*Protodrynaria takhtajanii* from the Eocene–Oligocene boundary of Kursk Province in Russia (Vikulin and Bobrov, 1987) appears to share the same arrangement of sori and the form of frond with *D. callispora* (Fig. 5A and C, Table 2), but the venation pattern of *P. takhtajanii* is close to that of *Crypsinus*, i.e. *C. laciniatus* (Vikulin and Bobrov, 1987), as far as distinct primary veins are concerned. Only one specimen was reported; therefore, the dimorphy of the fronds, a character often

encountered in *Drynaria*, could not be studied. In addition, the venation pattern of the Russian fossil is not well preserved. Until now, studies of *P. takhtajanii* are not able to prove either drynarioid or selliguooid affinities (van Uffelen, 1991). To access the potential relationships between *P. takhtajanii* and *D. callispora*, we included *P. takhtajanii* in a morphological cladistic analysis. The strict consensus of 32 trees was not fully resolved; therefore, we constructed a majority rule consensus (Fig. 6). *P. takhtajanii* shows affinities with *D. parishii* and *D. propinqua*; in other trees, it is sister-group of *D. mollis*. Our results are in favor of drynarioid affinities for *P. takhtajanii*. However, there is no close relationship between *P. takhtajanii* and *D. callispora*.

So far, the only convincingly published fossil record of drynarioids is from the late Miocene of Palembang Province in Sumatra (Fig. 5D; Kräusel, 1929; Roos, 1985). The fossil was once named *Polypodium quercifolium* and later transferred to *Drynaria* (Kräusel, 1929). This fossil fern shares several characters with *D. callispora* such as more or less zigzag secondary veins, quadrangular costa areoles, and round and compital sori, but can be likely distinguished from *D. callispora* based on the distribution pattern of sori on pinnae (Fig. 5D). Roos (1985) agreed with Kräusel (1929) that the fossil species from Sumatra represents a basal pinna of a fertile frond and further



**Fig. 6.** Majority-rule consensus of the morphological analysis including *Protodrynaria takhtajanii*. Numbers over the nodes represent the occurrence percentage of the clades.

proposed that the fossil could be assigned to a living species, *Aglaoomorpha heraclea*, judging from the similar morphology of pinnae, quadrangular costa areoles, and sori arranged in two rows parallel to the tertiary veins. In this regard, *A. heraclea* might represent the earliest fossil record of the extant drynarioids (Roos, 1985).

### 5.3. Ecology of *Drynaria callispora*

Among the specimens of *Drynaria* studied here, all represent fragments or a portion of a frond, which may indicate the incompleteness of fossils, is derived from either fossilization or deciduousness of pinnae. In the extant *Drynaria*, individual pinnae may naturally fall off from rachises. There is an abscission layer between a pinna and rachis (Roos, 1985). During the winter or dry season, the pinnae can likely fall off from rachises along this layer (Lin et al., 2000). If this is the case in the Pliocene fossil, it may suggest that the seasonality of western Yunnan already occurred in the late Neogene (Sun and Wang, 2005; Jacques et al., in press).

The associated leaf assemblage with *Drynaria callispora* is mainly dominated by evergreen sclerophyllous oaks (*Quercus* section *heterobalanus*) (Zhou, 1992). The modern *Drynaria* ferns are mostly epiphytic, and *D. mollis* and *D. sinica*, the two most closely living relatives of the fossil (Fig 3A–C), can be found growing on evergreen sclerophyllous oaks (Lin et al., 2000; personal observations). Therefore, *D. callispora* may also represent an epiphyte and have lived in a similar ecological habitat as the modern *Drynaria* in the Himalayas. This type of vegetation, today present in western Yunnan, may have existed at least since the late Pliocene.

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