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The first megafossil record of *Goniophlebium* (Polypodiaceae) from the Middle Miocene of Asia and its paleoecological implications

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Abstract

The first megafossil record of *Goniophlebium macrosorum* Xu et Zhou n. sp., is described from the Middle Miocene Climate Optimum (MMCO) (15.2–16.5 Ma) sediments in Wenshan, southeastern Yunnan, China. The fossils are with well-preserved leaf pinnae and *in situ* spores, and are represented by pinnatifid fronds and crenate pinna margins, with oval sori almost covering 3/5 area of areolae on each side of the main costa. *In situ* spores have verrucate outer ornamentation, and are elliptical in polar view and bean-shaped in equatorial view. The venation is characterized by anastomosing veins with simple included veinlets forming 2–3 order pentagonal areolae. All these morphological characters confirm the assignment of this species to the genus *Goniophlebium* (Polypodiaceae), now is distributed in southeastern Asia to Australia. Among living species, *G. macrosorum* shows the closest morphological affinity to the extant *Goniophlebium subamoenum*. The discovery of *G. macrosorum* suggests that *Goniophlebium* occurred in this region no later than the Middle Miocene. Moreover, the result of this study is consistent with the paleoenvironment of Wenshan flora as reconstructed in previous research, which concluded that modern evergreen broadleaved forests with complex ecological structure have been possibly established in southwestern China since at least 15 Ma.
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Keywords: *Goniophlebium*; Polypodiaceae; Miocene; Fern; Fossil; Yunnan

1. Introduction

Modern ferns started to diversify in the Late Cretaceous at the same time as the diversification of the angiosperms. The Polypodiaceae is the largest family of ferns with about 1200 living species today (Hennipman et al., 1990; Smith et al., 2006). The family has rich fossil records from the Paleozoic to Mesozoic (Schneider et al., 2004a) but declined in Cenozoic. However, the evolutionary history of Polypodiaceae is unclear due to scant investigations of Cenozoic fossil records in this family (Collinson, 2001). Among the modern species, the classification of Polypodiaceae is an updating one because of the high diversity within this family and the increase of new data. Prior to the application of molecular techniques, Ching (1978) undertook pioneering works on fern classification, clarifying the systematic position of the Polypodiaceae. After a series of revisions, *Goniophlebium* becomes better defined while many genera in Polypodiaceae remain to be clarified (Kramer and Green, 1990; Schneider et al., 2004b; Kreier et al., 2008).

The genus *Goniophlebium* is used now in a broad sense in general agreement, *Goniophlebium* was defined by Rödl-Linder (1990), but the genus was incorrectly replaced by other smaller genera such as *Polypodides* and *Polypodiastrum* (Hennipman et al., 1990). Besides, this genus was suggested different classifications judging from morphological evidence (Ching, 1978; Hennipman et al., 1990; Bosman, 1991). Lu and Li (2005) proposed that *Goniophlebium* represents a sister lineage to all other

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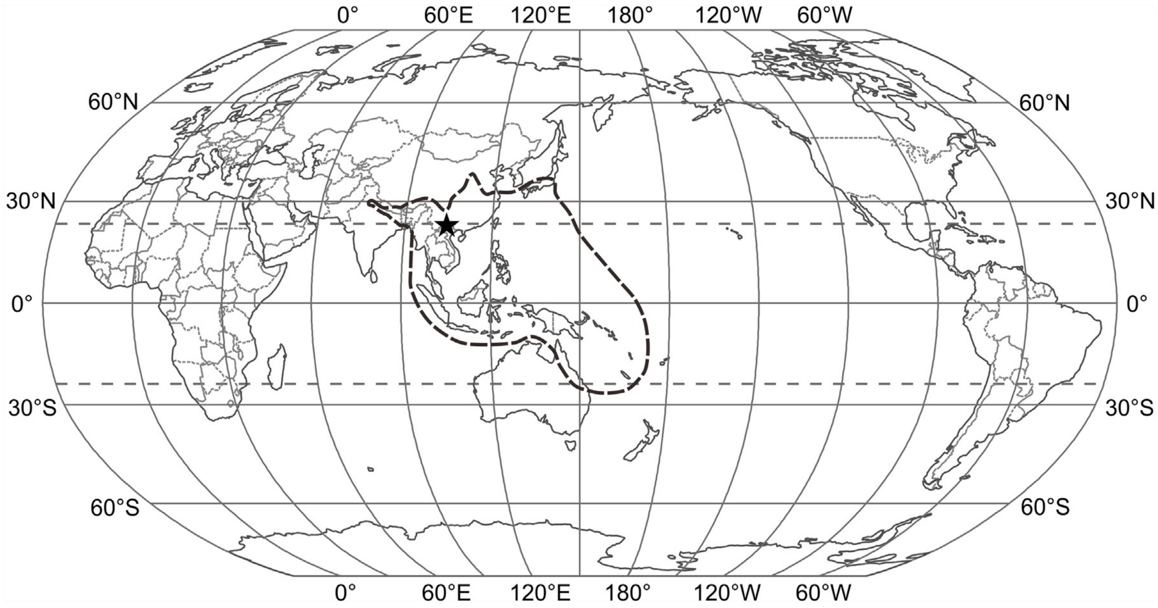

Fig. 1. The distribution of extant *Goniophlebium* (the dotted lines) and the position of fossil site (the star in black).

microcoroids. After that, Kreier et al. (2008) revised the classification of *Goniophlebium*, they found the goniophleboid clade includes five well-supported subclades, i.e., *Goniophlebium* s.s., *Metapolypodium*, *Polypodiastrum*, *Polypodioides*, and *Schellolepis*. Considering *Goniophlebium* in a broad sense, 14 extant species originally belonging to Polypodioideae were assigned to the genus *Goniophlebium* in the subfamily Microsoroideae Nayar (Rödl-Linder, 1990; Schneider et al., 2004b; Kreier et al., 2008; Zhang et al., 2012). In this study, we follow this latest classification system, which was adopted by PPG I (2016). Ecologically, the majority of this genus grow as epiphytes in tropical to subtropical climates only in the Old World (Schneider et al., 2004b). *Goniophlebium* is now distributed from southeastern Asia to Australia (Fig. 1).

Despite several studies have addressed the classification of the genus (Schneider et al., 2004b; Kreier et al., 2008), we still need megafossils to provide solid proof for understanding the evolutionary history of Polypodiaceae. For ferns, megafossil records could offer more morphological information than spores, especially at the genus level. To the best of our knowledge, compared to the rich modern diversity, until now there is no confirmed Cenozoic megafossil record of genus *Goniophlebium* reported anywhere in the world. In the present study, we describe the first confirmed megafossil record of *Goniophlebium* on the basis of frond fossils collected from Wenshan, southeastern Yunnan. We further discuss its ecological implication.

2. Materials and methods

2.1. Fossil site

Frond fossils were collected from Dashidong village, the Wenshan Basin, southeastern Yunnan, China (23°24′N, 104°12′E, 1270 m a.s.l.; Fig. 2).The fossil site is located in the southeastern margin of the Tibetan Plateau, where is a world biodiversity hotspot and numerous fern species, including many endemic species, occur in this region (Yang et al., 2004).

This outcrop was previously assigned to the Xiaolongtan Formation, and considered to be the late Miocene based on biostratigraphy using palynology and plant megafossils (Wang, 1996; Xia et al., 2009). According to a recent magnetostratigraphic study (Lebreton-Anberrée et al., 2016), the sedimentary succession was assigned to Middle Miocene (15.2–16.5 Ma). The site is surrounded by mountains mainly composed of limestone and mudstone with ages ranging from Cambrian to Triassic. Frond fossils were found in creamy yellow calcareous mudstone from the upper layer of the strata, and the depositional environment is interpreted as a deep lake (Lebreton-Anberrée et al., 2015).

2.2. Morphological studies

Morphological studies were conducted on both frond fossils and *in situ* spores to determine the systematic position of these fossils. Specimens were photographed using a Nikon D700 digital camera (Nikon Corporation, Tokyo, Japan). Pictures of detailed morphology were taken using a Leica S8APO stereomicroscope (Leica Corporation, Wetzlar, Germany) connected to a Nikon D700 digital camera. The measurements of morphological characters were taken using a vernier caliper and the software Image J (version 1.44p, National Institutes of Health, USA). A small piece of matrix with sporangia was isolated from a fossil specimen (No. KUN PC2016 DMS0368a) and moved onto a glass slide with a needle. Spores were cleaned with a drop of 50% HNO_3 to remove organic matter following the method introduced by Traverse (2007). A drop of pure alcohol was added to clear the surface of spores before moving a single spore to a scanning electron microscope (SEM) stub. The stub was sputter-coated with gold palladium for 5 min. The spores

Fig. 2. Locality map showing the fossil site of Wenshan Basin (the leaf symbol) in Yunnan Province, southwestern China.

were examined under an SEM (Zeiss KYKY-1000, Germany). We selected twelve spores to measure the equatorial diameter and polar axis.

We examined the morphology of several genera that share similar morphology with *Goniophlebium* in Polypodiaceae, i.e., *Drynaria* (Bory) Smith, *Phymatopteris* Pichi Sermolli, *Phymatosorus* Pichi Sermolli, and *Polypodium* Linnaeus to compare with our fern fossils. All specimens being compared are collected from Herbarium of Xishuangbanna Tropical Botanical Garden (HITBC), and two databases, i.e., Global Plants on JSTOR (http://plants.jstor.org/), and the Chinese Virtual Herbarium (CVH; http://www.cvh.org.cn/).

We compared our fossils to all extant species of *Goniophlebium* using two quantitative features (length and width of pinna) and five qualitative features (shape of the apex, shape of the areolae, angle between costa and pinna, lateral pinna margin, and the basal shape of the pinna, known as decurrency) (Table 2). We follow the terminology for fronds and spores given in Roos (1983), Tryon and Lugardon (1991) and Zhang (2012). The spatial distribution data were derived from the Chinese Virtual Herbarium (www.cvh.org.cn) and the Global Biodiversity Information Facility (www.gbif.org) based on 14 extant species of *Goniophlebium*.

3. Systematic results

Order Filicales Link

Family Polypodiaceae Berchtold et Presl

Subfamily Microsoroideae Nayar

Genus *Goniophlebium* (Blume) Presl

Goniophlebium macrosorum Xu et Zhou n. sp.

(Fig. 3)

Etymology: The specific epithet, *macrosorum*, refers to one of specific characters of this species, i.e., large-sized sori located in the first order areola.

Holotype: KUN PC2016DMS0368 (Fig. 3A).

Paratypes: KUN PC2016DMS2690 (Fig. 3C); KUN PC2016DMS2696 (Fig. 3D).

Table 1
Morphological comparisons of selected modern ferns in Polypodiaceae similar to fossils in this study. The detailed morphology of modern ferns are from Zhang (2012) and Zhang et al. (2013).

Genus	Apex of pinna	Veins pattern	Costa areola	Pattern of sori
Goniophlebium macrosorum Xu et Zhou n. sp.	Obtuse	Veins anastomose with simple included veinlet, 2–3 order areolae	Regular pentagonal	One row wider oval parallel near costa
Goniophleboium (Blume) Presl.	Obtuse/acuminate	Veins anastomose with simple included veinlet, ≥one order areola/unobserved	Regular pentagonal	One row middle or wider oval parallel near costa
Drynaria (Bory) Smith	Obtuse/acuminate	Anastomosing with branched included veinlet, third order veins forming irregular areolae occur between parallel secondary veins	Irregular	One row oval parallel near costa
Phymatopteris Pichi Sermolli	Obtuse/acuminate	Obvious second parallel vein	Irregular	One row oval parallel near costa
Phymatosorus Pichi Sermolli	Acuminate	Obvious second parallel vein/no obvious veins	Irregular/no areola	One or two row smaller oval parallel near costa
Polypodium Linnaeus	Obtuse	Free vein forked	No areola	One row oval parallel in middle of pinnae

Repository: Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN).

Type locality: Dashidong Village, Wenshan County, Yunnan Province, China (Fig. 2).

Diagnosis: Frond with at least 8 pairs of elliptic pinnae; pinnae apex obtuse; first order areolae regularly pentagonal, anastomosing areolae with included veins; medium sori oval, ~2.4 mm in diameter, covering 3/5 area of areola; exospores verrucate.

Description: Sterile frond with preserved part is pinnatifid, 15–20 cm long, comprising at least 8 pairs of pinnae (Fig. 3A). Lateral pinnae are alternate. Terminal pinna is longer than lateral pinna (Fig. 3B). Pinnae are 1.5–4.5 cm long and 1–1.5 cm wide (Fig. 3A and B). Pinnae are elliptic with crenate margin (Figs. 3 and 4A and B). Apex of pinna is obtuse; basal part of pinna (or decurrency) is adnate-conform or coadunate near the costa (Figs. 3A, 4A and B). The angle between costa and pinna is 60°–90°. The venation of pinna is reticulate with strong costa, second vein is anastomosing with simple veinlets forming pentagonal shaped areolae with sori locating along the costa (Fig. 3E). Second and third order areolae are pentagonal but irregular. No forked and short veins present from last order irregularly empty areolae near the margin of pinna (Fig. 3B).

Two lines of oval sori are located along two sides of the costa in the first order pentagonal shaped areolae, oval sori are 1.5–2.0 mm in diameter (Fig. 3E). There is no indusia preserved in our fossils. *In situ* spores are monolete (bilateral), elliptical in polar view, and bean shaped in equatorial view (Fig. 5A). The surface ornamentation is verrucate (Fig. 5B). Spores are medium-sized, equatorial diameter is 26.9–70.6 μm (50.8 μm in average), and polar axis is 12.3–49.3 μm (29.9 μm in average).

4. Discussion

4.1. Systematic assignment

The fossils of this study have pinnatifid fronds, anastomosing veins, and one row of oval or oblong sori. These traits are characteristic of the family Polypodiaceae (Zhang et al., 2013). Under the gross morphological characters such as size, apex of lamina, shape of lamina, division of the lamina (adnate-conform decurrency), there are five modern genera of ferns in Polypodiaceae that share morphological similarities with our fossils, i.e., *Drynaria* (Bory) Smith., *Phymatopteris* Pichi Sermolli, *Phymatosorus* Pichi Sermolli, *Polypodium* Linnaeus, and *Goniophlebium* (Blume) Presl. However, modern species of *Drynaria* have anastomosing with occasionally branched included veinlets and irregular costa areolae, whereas our fossils have anastomosing with included veinlets and regular pentagonal areolae. Besides, the genus *Drynaria* has prominulous veins, secondary veins run straight near not joined the margin or sometimes more or less irregularly zigzag, third order veins forming irregular areolae with some branched veins occur between these parallel secondary veins (Su et al., 2011). However, our fossils have secondary veins from primary vein, every two secondary veins forked and met forming regular pentagonal areolae. The genus *Phymatopteris* has narrow irregular areolae with second order parallel veins, whereas our fossils have regular pentagonal-shape first order areolae. The genus *Phymatosorus* has obvious secondary parallel veins; irregular or no areolae, and one or two rows of smaller sori, but our fossils have pentagonal areolae with one row of medium size sori along the costa. The modern species *Polypodium vulgare* Linnaeus has free branching veins without areola, but regular pentagonal areolae present in

Table 2

Morphological comparison between *Goniophlebium macrosorum* Xu et Zhou n. sp. and extant species of *Goniophlebium.* The detailed morphology of living species in *Goniophlebium* follows Rödl-Linder (1990) and Zhang et al. (2013). Data are from the Flora of China (Zhang et al., 2013) and herbarium specimens. AC, basal pinnae shape is adnate-conform or coadunate; GA1, veins anastomose with simple included veinlet forming regular pentagonal costal areolae with wider sori and other 2–3 order areolae; GA2, primary first order areolae presents marginal free vein, without second empty areolae or irregular second order areolae; GA3, veins and areolae are absent; GA4, veins anastomose into one series of regular primary pentagonal costal areolae with medium size sori and irregular second empty areolae; PC, basal pinnae shape is petiolate-conform; PCC, basal pinnae shape is near petiolate-conform with cordate, subcordate or cuneate near the costa.

Species	Length of pinna (cm)	Width of pinna (cm)	Apex shape	Areolae shape type	Angle between costa and pinna	Lateral pinna margin	Decurrency
Goniophlebium macrosorum Xu et Zhou n. sp.	1.5–4.5	1.0–1.5	Obtuse	GA1	>60°, no basal pinnae preserved	Crenate	AC
G. subamoenum.	0.6–3.6	0.8–1.0	Obtuse	GA1	>60°, basal pair of pinna <60°	Crenate	AC
G. argutum	10–15	1.5–2.5	Acute	GA2	<60°	Near entire and undulate	PC
G. dielseanum	10–15	0.8–1.2	Acuminate	GA2	>60°	Serrate or undulate	AC
G. lachnopus	2.0–3.0	0.5–0.7	Obtuse	GA2 with especially clear vein and oval sori	>60°	Involute with crenate	PCC
G. wattii	4.0–5.0	1.2–1.4	Obtuse	GA2 with especially thin vein and big size sori	~90°	Entire	AC
G. niponicum	3.0–5.0	0.5–1.0	Obtuse	GA2 with especially thin vein and oval sori	>60°, basal pair of pinna <60°	Entire	AC
G. bourretii	4.0–7.0	0.6–0.8	Obtuse	GA3	~90°, basal pair of pinna <60°	Serrate	AC
G. amoenum	10–13	1.5–2.0	Acuminate	GA4	>60°, basal pair of pinna <60°	Serrate	AC
G. chinense	3.0–5.0	0.5–0.7	Obtuse	GA4	~60°, basal pair of pinna <60°	Sinus	AC
G. mengtzeense	10–15	1.5–2.0	Acute	GA4	~60°	Crenate	PCC
G. persicifolium	10–20	1.0–2.5	Acute	GA4	<60°	Crenate	PCC
G. subauriculatum	14–20	~2.0	Acuminate	GA4 with narrow areolae, thin vein	>60°	Serrate	PCC
G. formosanum	5.0–8.0	0.8–1.0	Obtuse	Unobserved	>60°, basal pair of pinna <60°	Entire	AC
G. manmeiense	20–30	5.0–7.0	Obtuse	Unobserved	>60°	Crenate	AC

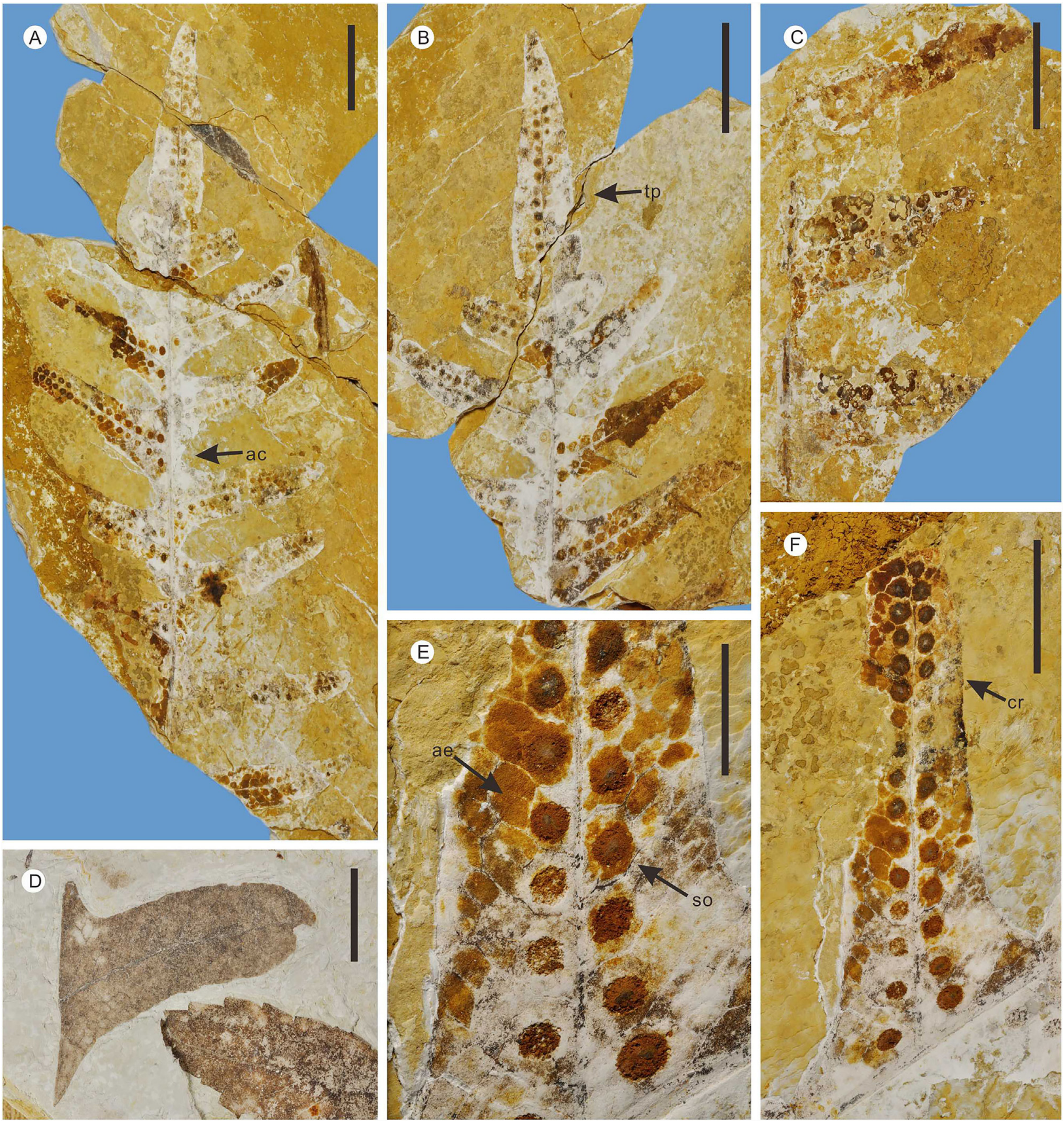

Fig. 3. *Goniophlebium macrosorum* Xu et Zhou n. sp. from Wenshan, Yunnan, China. (A) KUN PC2016DMS0368a, scale bar = 2 cm; (B) KUN PC2016DMS0368b (counterpart), scale bar = 2 cm; (C) KUN PC2016DMS2690, scale bar = 2 cm; (D) KUN PC2016DMS2696, scale bar = 1 cm; (E and F) the detailed morphology of pinna and areolae from KUN PC2016DMS0368, scale bars = 0.5 cm (E), 1 cm (F). ac: adnate-conform decurrency; ae: areola; cr: crenate; so: sorus; tp: terminal pinna.

fossils in this study. Finally, the detailed morphology of our fossils is most similar to the genus *Goniophlebium*, i.e., elliptic pinnae with crenate margin, obtuse apex and veins anastomosing with simple included veinlets and pentagonal areolae, and adnate-conform decurrency (Figs. 3 and 4A and B; Table 1).

Our identification is corroborated by the morphology of *in situ* spores. They are monolete (bilateral), elliptical in polar view, and bean shaped in equatorial view (Fig. 5A). The surface ornamentation is verrucate (Fig. 5B). These gross morphological characters provide limited information on the taxonomic determination of polypodiaceous ferns because they are also present in other genera of Polypodiaceae, such as *Drynaria* and *Polypodium* (Tryon and Lugardon, 1991), but they are consistent with our fossil identification based on the fronds.

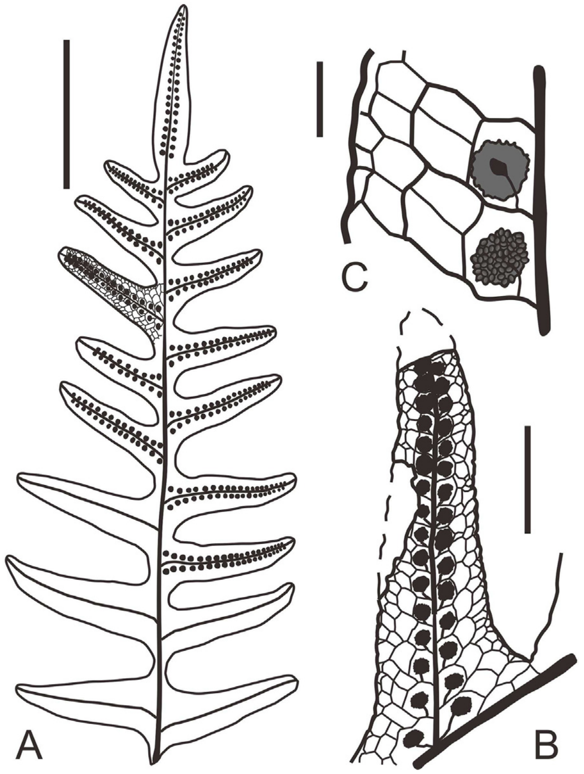

Fig. 4. Drawings of *Goniophlebium macrosorum* Xu et Zhou n. sp. (A) Reconstruction of frond, scale bar = 5 cm; (B) pinna with the arrangement of sori, scale bar = 1 cm; (C) patterns of venation and the arrangement of sori, scale bar = 3 mm.

4.2. *Morphological comparison with extant* Goniophlebium

Our fossil specimens share two morphological characters with 14 extant species of *Goniophlebium*, namely the base of the pinna and the shape of areolae. The basal shape of the pinna (or decurrency) of our fossils is adnate-conform or coadunate (AC) (Fig. 3A). This character appears in 10 species in the genus *Goniophlebium* (e.g., *Goniophlebium subamoenum*, *Goniophlebium wattii*, *Goniophlebium amoenum*). There are two other types of decurrency in *Goniophlebium*, namely petiolate-conform (PC) (e.g., *Goniophlebium argutum*) and near petiolate-conform with cordate, subcordate, or cuneate basal segment near the costa (PCC) (e.g., *Goniophlebium lachnopus*, *Goniophlebium mengtzeense*, *Goniophlebium persicifolium*). Our fossils belong to the AC type (Fig. 3; Table 2).

The second important morphological character is the shape of areolae in *Goniophlebium*, which we classified into four categories (Table 2). In the first type, veins anastomose with simple included veinlet forming regular pentagonal costal areolae with wider sori and other 2–3 order areolae (GA1) (*G. subamoenum*) (Fig. 6C and D); in the second type, primary first order areolae presents marginal free vein, without second empty areolae or irregular second order areolae (GA2) (*G. argutum*); in the third type, veins and areolae are absent (GA3) (*Goniophlebium bourretii*); and in the fourth type, veins anastomose into one series of regular primary pentagonal costal areolae with medium-sized sori and irregular second empty areolae (GA4) (*G. amoenum*, *G. amoenum* var. *pilosum*, *Goniophlebium chinense*, *G. mengtzeense*, *G. persicifolium*). Our fossils match the GA1 type.

Our fossils have pinnae with obtuse apex, crenate lateral margin, and the angle between costa and pinna is 60°–90°. These characteristics show a high morphological similarity to *G. subamoenum*. Therefore, we consider *G. subamoenum* as its nearest living relative. However, the pinnae of our fossils are 1.5–4.5 cm long and 1.0–1.5 cm wide, whereas they are much smaller in *G. subamoenum* (0.6–3.6 cm long, 0.7–1.0 cm wide); besides, the vein pattern of modern *G. subamoenum* is thinner than our fossils (Table 2). Furthermore, outer layer of spores is a key character in the extant species, but there is no outer layer preserved in our fossils possibly because of sedimentary and taphonomic biases.

4.3. *Fossil records of Polypodiaceae*

There are many fossil records possibly related to Polypodiaceae that were mostly preserved by spores or shoots. Recently, Su et al. (2011) reported fossil record of genus *Drynaria* from the Upper Pliocene of Yongping County in western Yunnan. Schneider et al. (2015) published amber fossil of genus *Pleopeltis* (Polypodiaceae) from the Middle Miocene of West Indies. Xie et al. (2016) reported first megafossil of genus *Neolepisorus* (Polypodiaceae) from the Upper Miocene of Lincang city in southwestern Yunnan. Huang et al. (2016) described the megafossil of genus *Drynaria* (Polypodiaceae) from the Upper Pliocene of Lanping in northwestern Yunnan. However, compared with abundant modern fern species, well-preserved megafossils during the Cenozoic are still rare, and the systematic positions of some of these fossils remain unclear (Fryns and Van, 1973; Soeder, 1985; Baranova, 1987; Groff and Kaplan, 1988; Harington, 2003; Gladenkov, 2010). Therefore, some fossil records initially described as Polypodiaceae were later assigned to other families after more detailed morphological observation (Collinson, 2001; Kvacek, 2001; Kvaček et al., 2004). Polypodiaceae fossils have been reviewed several times, Jacques et al. (2013) listed unconfirmed fossil records with polypodiaceous affinities subject to revision as belonging to other fern groups, and no fossil record of *Goniophlebium* has been confirmed yet. With further investigation on previous paleobotanical studies, we conclude that our fossils represent the first confirmed megafossil record of the genus *Goniophlebium* (Blume) Presl in Polypodiaceae in the world, and we assigned it as a new species, namely *Goniophlebium macrosorum* Xu et Zhou n. sp.

4.4. *Ecological implications*

According to previous studies based on megafossils and pollen grains, Wenshan flora is diverse in the floristic composition. Many well-preserved fossils have been reported in the strata, for examples, *Bauhinia wenshanensis* (Meng et al., 2014), *Pinus premassoniana* (Zhang et al., 2015a), *Sequoia maguanensis* (Zhang et al., 2015b), *Calocedrus shengxianensis* (Zhang et al., 2015c), *Rosa fortuita* (Su et al., 2016), *Burretiodendron miocenicum* (Lebreton-Anberrée et al., 2015), and *Mahonia*

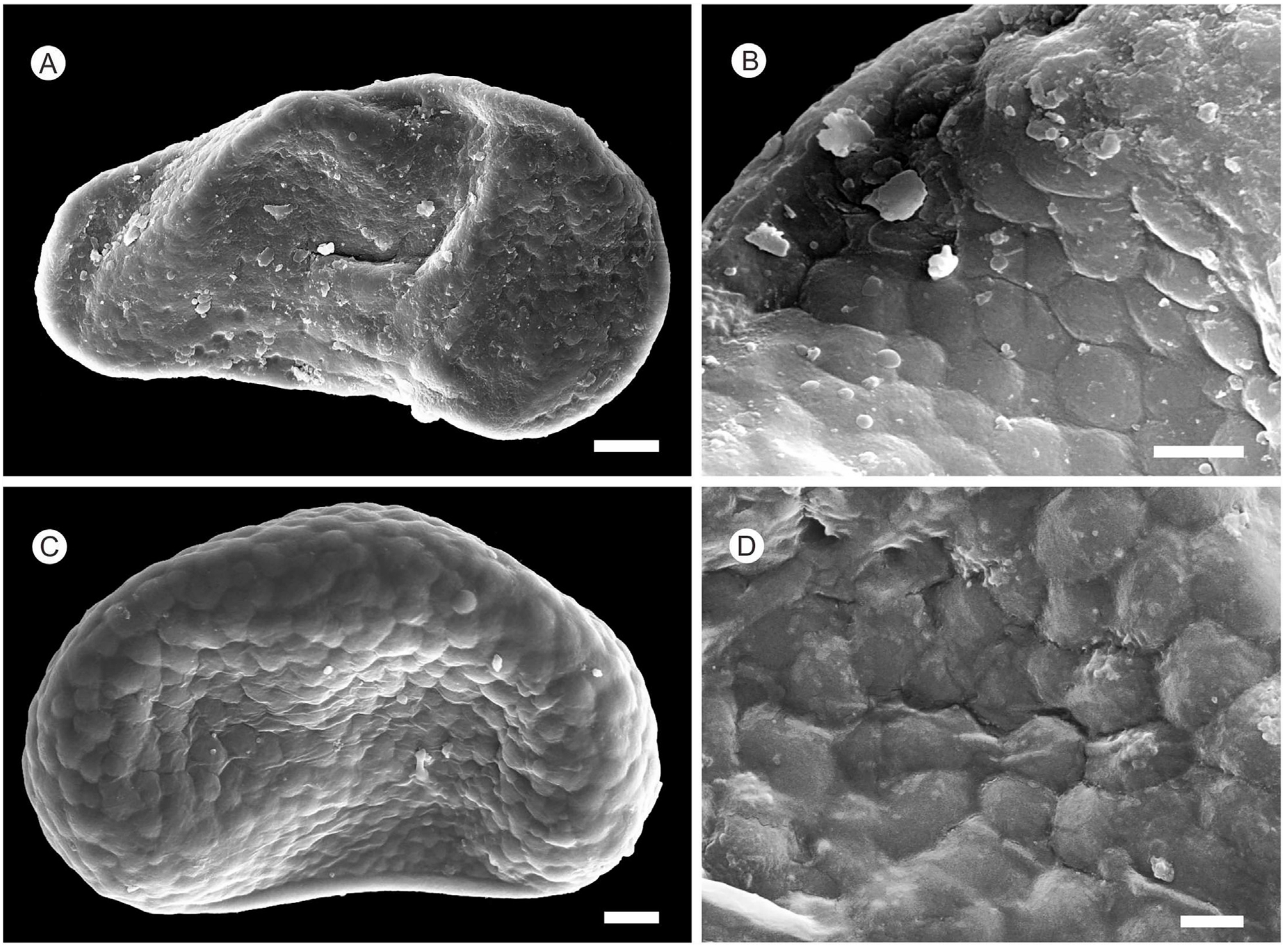

Fig. 5. *In situ* spores of *Goniophlebium macrosorum* Xu et Zhou n. sp. (A and B) and *G. subamoenum* (C and D). (A) Spores from fossil, elliptical in polar view, and bean shaped in equatorial view, scale bar = 5 μm; (B) the surface ornamentation is verrucate, scale bar = 2 μm. (C) *G. subamoenum* has bean-shaped similar with fossil spores, scale bar = 5 μm; (D) *G. subamoenum* has similar surface with fossil, verrucate ornamentation, scale bars = 2 μm.

mioasiatica (Huang et al., 2015). This vegetation type and paleoclimatic conditions were suitable for the survival of many living ferns, including *Goniophlebium* (Hennipman et al., 1990; Rödl-Linder, 1990; Bosman, 1991; Kreier et al., 2008). In addition, a detailed palynological study of the strata has been recently reported (Li et al., 2015), indicating warm and humid climate condition in Wenshan during that time, which further supports the interpretation of the climate condition in this study.

Besides, the genus *Goniophlebium* is found in the tropical regions. *G. macrosorum* might be hemi-epiphytic living in humid forest with temperate to tropical climate during the Middle Miocene, when the habitat of the extant *Goniophlebium* (Fig. 6A and B; Table 1) (Rödl-Linder, 1990) and the components of Wenshan fossil assemblage are considered.

Generally, taking the results above and discovery of the fern fossils in this study into consideration, we conclude that *Goniophlebium* has existed in East Asia since at least the Middle Miocene (15.2–16.5 Ma), and it indicates that the hemi-epiphytic fern history of Yunnan could be dated back at least to the Middle Miocene. Furthermore, the hemi-epiphytic ferns with complex ecological structures have been established in humid subtropical evergreen broadleaved forests in Yunnan for at least 15 Ma.

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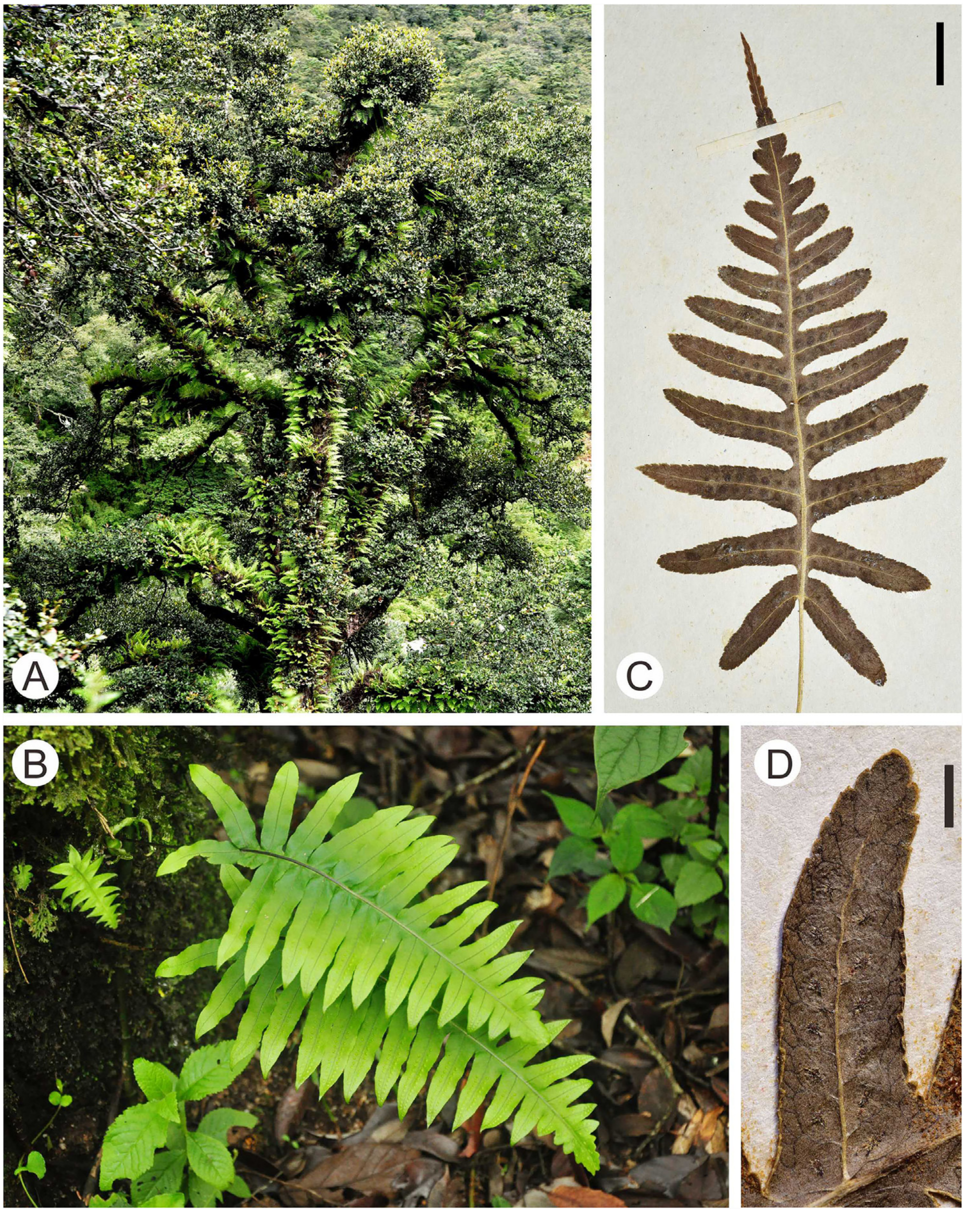

Fig. 6. Frond morphology and habitat of extant Goniophlebium. (A) The epiphytic habitat of *Goniophlebium hendersonii*, Jilong, Tibet; (B) the ground-grow habitat of *G. subamoenum*, Lancang, Yunnan; (C) frond morphology of extant species, *G. subamoenum*, scale bar = 1 cm; (D) pinnae of *G. subamoenum* with specific vein and areola pattern, scale bar = 2 mm.

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