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RESEARCH ARTICLE

First Asian fossil record of *Platydictya* (Amblystegiaceae) from the lower Miocene and its paleoenvironmental significance

Liyan GUO[1,2,4], Liang XIAO (✉)[1,2,4], Ya LI[2], Xiangchuan LI[1,2,4], Qin LENG[3], Nan SUN[1], Junfeng GUO[1], Chaofeng FU[1], Jianan WANG[1], Deshuang JI[1]

1 College of Earth Sciences and Resources & Key Laboratory of Western Mineral Resources and Geological Engineering (the Ministry of Education), Chang'an University, Xi'an 710054, China
2 State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China
3 Laboratory for Terrestrial Environments, Bryant University, Smithfield, RI 02917, USA
4 Shaanxi Key Laboratory of Early Life and Environments & State Key Laboratoty of Continental Dynamics, Northwest University, Xi'an 710069, China

Abstract Mosses form a diverse land plant group in modern vegetation but have rarely showed up in the fossil record compared with vascular plants. Here, we report an extraordinarily-preserved early Miocene moss fossil from the lower Laoliangdi Formation in the Pingzhuang Coal Mine in Chifeng, Inner Mongolia Autonomous Region, northern China. Although lacking rhizoids and most reproductive organs, the well-preserved fossil allows us to assign it to *Platydictya* cf. *jungermannioides* (Amblystegiaceae) based upon its detailed gross and micromorphology. The diagnostic characteristics include a small-sized body with slender stems bearing spirally arranged ovate-lanceolate leaves that lack costae. Leaf margins are mostly partly entire and partly dentate, a few dentate, and rarely completely entire. It represents the first fossil record of *Platydictya* in Asia. The specific living microenvironment of the extant *P. jungermannioides* enriched our understanding of the early Miocene environment that was previously based upon vascular plant fossils and sedimentary lithofacies in the area. Our early Miocene *Platydictya* cf. *jungermannioides* fossil lived in a warm and humid lush forest with a dense understory that received adequate water supplies.

Keywords moss, the Pingzhuang Coal Mine, Inner Mongolia, *Platydictya*, paleoenvironment

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E-mail: youmu4@sina.com

1 Introduction

Bryophytes compose the second most diverse phylum of land plants (Goffinet and Shaw, 2009). However, as non-vascular plants, they are extremely underrepresented in the fossil record. As the largest group of bryophytes, Musci (mosses) have their fossils rarely reported, particularly in pre-Cenozoic strata (Guo et al., 2016; Ignatov and Maslova, 2021). The oldest fossil record related to moss is *Parafunaria sinensis* discovered in the Cambrian Kaili Formation of Guizhou Province in China. It was proposed to be comparable to the living moss *Funaria hygrometrica* due to its 4–5 whorled leaves, obvious costae, shapes of capsule and seta, and complex rhizoid (or foot) (Yang et al., 2004). However, its unusually large size and antiquity make its affinity with mosses questionable (Ignatov and Maslova, 2021). Other pre-Cenozoic moss fossils are either incomplete for a definitive identification or to represent extinct lineages (Miller, 1980a, 1980b; Bomfleur et al., 2014; Ignatov and Maslova, 2021). Moss fossil records became much more abundant in the Cenozoic, and most of them can be compared to modern taxa (Frahm and Newton, 2005; Shelton et al., 2015).

Amblystegiaceae, comprising 39 genera, is a family of pleurocarpous mosses with ovate-lanceolate leaves that superficially resemble willow leaves (Harris, 2008). They are widely distributed in global temperate climate regions. However, their fossil records are apparently scarce, mainly from the upper Paleogene onward in the Northern Hemisphere (Table 1). In northern Europe, except for *Drepanocladus* from Eocene Cookson amber (Frahm, 2004), most of Amblystegiaceae fossils were found in the late Pleistocene–Holocene peat bogs in Sweden and Norway (Övestedal and Aarseth, 1975; Kuder and Kruge, 1998; Zazula et al., 2006; Elverland and Vorren, 2008; Van der Linden et al., 2008; Delgadillo, 2009; Kokfelt et al., 2010). In East Asia, there are only a few fossil records in the early Miocene Hannuoba Formation of Weichang area, Hebei Province of north-eastern China and from the late Pleistocene silicified deposits on the northern shore of Lake Usoriko in Japan (Satake et al., 1995; Guo et al., 2013). Particularly, Guo et al. (2013) reported a rich flora of mosses, including *Amblystegium varium*, *Drepanocladus subtrichophyllus*, and *Leptodictyum riparium* from the early Miocene (22.1 Ma) deposit at Weichang. In North America, Amblystegiaceae fossils are widely distributed in the Pliocene and the newer strata, such as *Cenococcum geophilum* in the Pliocene shallow ocean deposits (2.60–3.58 Ma) of north-eastern Greenland in the Arctic, *Leptodontium flexifolium* in the late Pleistocene peat deposits (12 ka) in the Yukon Territory of north-western Canada, and *Calliergon giganteum* and *Drepanocladus aduncus* in the late Pleistocene Late Glacial strata (12–11.5 ka) of Portland, Maine on the east coast of the United States (Janssens and Zander, 1980; Miller, 1980a, 1980b; Janssens, 1983; Janssens and Glaser, 1986; Matthews and Ovenden, 1990; Ovenden, 1993; Goetcheus and Birks, 2001; Bennike et al., 2002; Reyes et al., 2010; Thompson et al., 2011).

Platydictya is a genus of small-sized mosses in the family Amblystegiaceae that are distributed widely in temperate and subtropical climatic zones of the Northern Hemisphere. The classification of this genus is still debatable. For example, Crum and Anderson (1981) and Vitt (1984) as well as Huttunen et al. (2013) assigned it to Hypnaceae and Plagiotheciaceae, respectively. While other researchers such as Kanda (1976), Noguchi (1991a,

Table 1 Global fossil records of Amblystegiaceae

Age	Genus/Species	Region	Location	References
Eocene 37–57 Ma	*Drepanocladus*	Europe	Baltic Saxon amber	Frahm, 2004
Early Miocene 22 Ma	*Amblystegium varium*, *Leptodictyum riparium*, *Drepanocladus trichophyllus*	Asia	Weichang mud shale, Hebei, China	Guo et al., 2013
Pliocene 3.58–2.60 Ma	*Cenococcum geophilum*	North America	Shallow water marine deposits of North-east Greenland	Bennike et al., 2002
Late Pliocene 3 Ma	*Calliergon giganteum*, *Campylium stellatum*, *C. arcticum*, *Drepanocladus aduncus*, *D. exannulatus*, *D.revolvens*, *D.uncinatus*, *Hygrohypnum polare*	North America	Alaska and northern Canada	Matthews and Ovenden, 1990
Early Pleistocene 2.0–2.5 Ma	*Calliergon giganteum*, *Drepanocladus crassicostatus*, *Scorpidium scorpioides, Platydictya* cf. *jungermannioides*	North America	Clastic rocks on Ellesmere Island	Ovenden, 1993
Middle Pleistocene 131 ± 11 ka	*Pseudocalliergon brevifolium*, *P. turgescens*, *Campylium stellatum*, *C. giganteum*	North America	Peat deposits in the east of the Beringian Land Bridge	Reyes et al., 2010
Late Pleistocene 18 ka	*Campylium hispidulum*, *C. stellatum*, *Drepanocladus brevifolius*, *Amblystegium serpens*, *A. varium*	North America	Bering Land Bridge Glacier Highlands on the northern Seward Peninsula	Goetcheus and Birks, 2001
Late Pleistocene 17.78 ± 0.6 ka	*Drepanocladus fluitans*	Asia	Paleosilicified sediments from the northern shore of Lake Usoriko, Japan	Satake et al., 1995
Late Pleistocene 12 ka	*Drepanocladus exannulatus*, *D. trichophyllus*	Europe	Marine clay of western Norway	Övestedal and Aarseth, 1975
Late Pleistocene 12 ka	*Leptodontium flexifolium*	North America	Peat deposits of the Yukon Territory, Canada	Miller, 1980b
Late Pleistocene 12–11.5 ka	*Calliergon giganteum*, *Drepanocladus aduncus*	North America	Late Glacial Strata, Portland, Maine, US	Geotcheus and Birks, 2001
Late Pleistocene 11.5–12.1 ka	*Calliergon richardsonii*, *C. stellatum*, *Drepanocladus revolensvar*, *Scorpidium scorpioides*	North America	North American glacial woodland marshes	Janssens and Zander, 1980
Pleistocene and Holocene	*Drepanocladus crassicostatus*	North America	Western of North America	Janssens, 1983
Holocene	*Drepanocladus fluitans*	Europe	Peat layer of Rownia pod Sniezka swamp, Poland	Kuder and Kruge, 1998
Holocene	*Drepanocladus fluitans*	Europe	Peat deposits of northern Sweden	Elverland and Vorren, 2008
Holocene 5 ka	*Warnstorfia fluitans*, *W. exannulata* *Straminergon stramineum*	Europe	Sedimentary sequence of coastal marshes in northern Norway	Van der Linden et al., 2008
Late Holocene 5 ka	*Drepanocladus exannulatus*, *D. purpurascens*, *D. procerus*, *D. schulzei*	Europe	Swedish subarctic peat bogs	Kokfelt et al., 2010

1991b) and Richard (2017) placed it in Amblystegiaceae. In this paper, we adopt the second taxonomy, which is widely used, such as by the "Flora Bryophytorum Sinicorum" ("Flora of Bryophytes of China") (Wu et al., 2005). Due to the lack of support tissues such as the costae of the leaf, *Platydictya* may be more susceptible to mechanical fragmentation during taphonomic processes, resulting in scarce fossil records. Up to the present, only one species, *Platydictya* cf. *jungermannioides*, was reported from the early Pleistocene Kobenhavn Formation (2–2.5 Ma) in the Ellesmere Island, North America by Ovenden (1993).

A large number of vascular plant fossils composed mainly of angiosperms and gymnosperms have been reported in the early Miocene Laoliangdi Formation of the Pingzhuang Coal Mine in the Yuanbaoshan District, Chifeng City, Inner Mongolia Autonomous Region, China (Shang et al., 2001). In this research, we report a *Platydictya* fossil with stems, leaves, and capsules found in the formation. This fossil preserves distinct micro-morphological features which allow us to make comparisons with both fossil and living mosses for an unambiguous identification. In common, the living *Platydictya* can only grow in moist environments such as the underside or the surrounding soil of wet tree trunks in dense forests. Based on the method of the nearest living relative's species (NLRs), the microhabitat which *Platydictya* fossil lived in is reconstructed. In addition, combining with vascular plant fossils and sedimentary lithofacies previously studied based upon Pingzhuang materials, we further infer paleoenvironmental and paleoclimatic signal for this early Miocene site.

2 Materials and methods

The moss fossil was collected from the argillaceous shale of the Laoliangdi Formation in the Pingzhuang Coal Mine (Fig. 1). The coal mine is located in the south-eastern part of the Chifeng City, which has large coal reserves with more than ten coal seams (Yu et al., 2009). The strata containing coal seams are mainly composed of dark gray sandstones and siltstones and are mainly in the middle and upper members of the Xingyuan Formation and the lower member of the Yuanbaoshan Formation, both of which are lower Cretaceous in age (Fig. 1). Abundant fossils have been discovered from these Cretaceous layers as well as the overlying Cenozoic shale strata (Yu et al., 2009). The 25−51 m thick Laoliangdi Formation overlies the Yuanbaoshan Formation with an angular unconformity (Fig. 1). It comprises sedimentary rock assemblages including dark gray shale, yellowish gray and dark gray sandstones, siltstones intercalated with glutenite (Yan et al., 2008). Abundant plant macro- and micro-fossils (spore and pollen grains) have been discovered from the shale at the bottom of this formation, where our moss fossil was collected. The thickness of this shale is more than 10 m (Tao et al., 1994) and was dated biostratigraphically as early Miocene based upon the assemblage of plant macro- and micro-fossils (Zhang, 1986; Tao et al., 1994).

The fossil specimen was observed and photographed using a Leica M165FC fluorescent stereo microscope and a VHX-1000 ultra-depth-of-field three-dimensional microscope. In addition, stem and leaf fragments were taken by a scalpel and a dissecting needle and soaked in distilled water for several hours for softening. They were then treated with hydrochloric acid (HCl) for 2 h and hydrofluoric acid (HF) for 10–12 h to remove the calcareous and siliceous sediments. Without any further chemical treatment, the water-neutralized specimens were then observed and photographed by a Leica DM1000 optical microscope. A small piece of the specimen was observed directly under the FEI Quanta 650 FEG scanning electron microscopy (SEM).

For systematics and nomenclature, we follow those of Hu and Wang (1994).

3 Systematic paleobotany

3.1 Fossil description

Order: Hypnales (M. Fleisch.) W. R. Buck & Vitt

Family: Amblystegiaceae G. Roth

Genus: *Platydictya* Berk.

Species: *Platydictya* cf. *jungermannioides* H. Crum, 1964

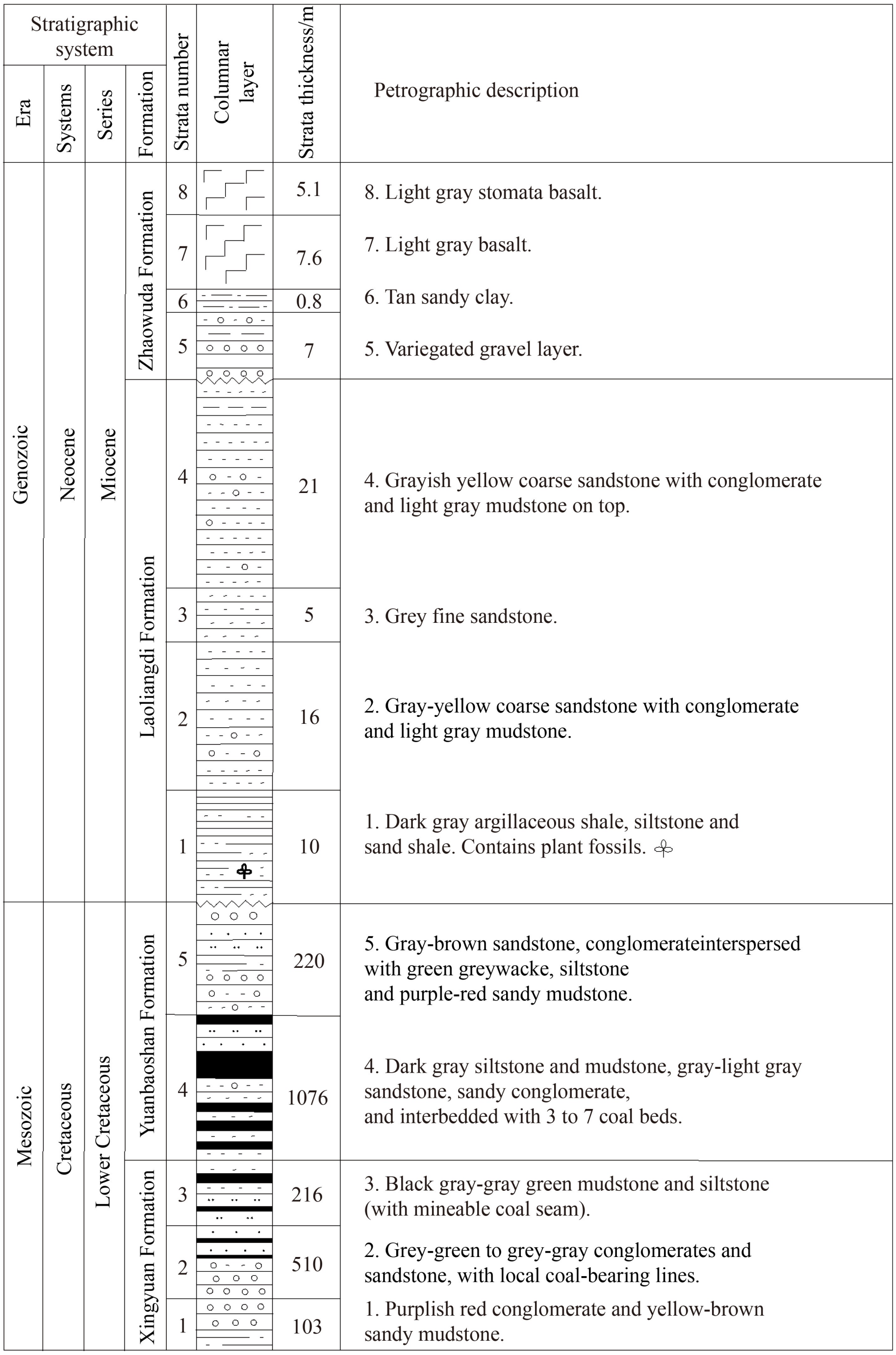
Studied specimen: PZX-17-013.

Occurrence: Pingzhuang Coal Mine, Yuanbaoshan District, Chifeng City, Inner Mongolia Autonomous Region, China.

Stratum and age: Lower member of the Laoliangdi Formation, early Miocene.

Repository: Geological Museum of Chang'an University, Xi'an, China.

Description: The specimen contains about 10 branches; 8 are attached while 2 are separated. Their similar structure and texture suggest that they very likely belong to the same plant (Fig. 2(a)). The plant is slender and small, occupying an area of only about 1.25 cm × 1 cm. No rhizoids have been observed. Branches are 0.6–1.2 cm in length. Their stems are more or less erect and branched irregularly (Figs. 2(a)–2(c)). Leaves are sparsely and spirally arranged on the stems. They are ovate-lanceolate to lanceolate and very small, only 0.15–0.3 mm in length and 0.04–0.06 mm in width. They seem to be chartaceous in texture and are very thin, almost semitransparent (Figs. 2(b)–2(f)). No costae have been observed on them (Figs. 2(b)–2(f)). Leaf base is thickened and embraces the stem. No stipules were found (Fig. 2(d)). Capsule-like structures are seen on the tip of a branch (Fig. 2(g)) but



Stratigraphic system				Strata number	Columnar layer	Strata thickness/m	Petrographic description
Era	Systems	Series	Formation				
Genozoic	Neocene	Miocene	Zhaowuda Formation	8		5.1	8. Light gray stomata basalt.
				7		7.6	7. Light gray basalt.
				6		0.8	6. Tan sandy clay.
				5		7	5. Variegated gravel layer.
			Laoliangdi Formation	4		21	4. Grayish yellow coarse sandstone with conglomerate and light gray mudstone on top.
				3		5	3. Grey fine sandstone.
				2		16	2. Gray-yellow coarse sandstone with conglomerate and light gray mudstone.
				1	♣	10	1. Dark gray argillaceous shale, siltstone and sand shale. Contains plant fossils. ♣
Mesozoic	Cretaceous	Lower Cretaceous	Yuanbaoshan Formation	5		220	5. Gray-brown sandstone, conglomerateinterspersed with green greywacke, siltstone and purple-red sandy mudstone.
				4		1076	4. Dark gray siltstone and mudstone, gray-light gray sandstone, sandy conglomerate, and interbedded with 3 to 7 coal beds.
			Xingyuan Formation	3		216	3. Black gray-gray green mudstone and siltstone (with mineable coal seam).
				2		510	2. Grey-green to grey-gray conglomerates and sandstone, with local coal-bearing lines.
				1		103	1. Purplish red conglomerate and yellow-brown sandy mudstone.

Fig. 1 Stratigraphic column of the Pingzhuang Coal Mine, showing the plant fossiliferous layer (indicated by ♣).

their fine structures are not preserved.

Leaf margins are mostly partly entire and partly dentate, a few dentate, and rarely completely entire (Figs. 3(a)–3(d)). The leaf margins are also thickened, likely with more than one layers of cells while most of the other part of the leaf has only a single cell layer. The cells at leaf margins are rhomboid, irregularly quadrilateral, or polygonal (Figs. 3(d)–3(f)). The cells at leaf apex are rectangular or rhomboid, with a length-to-width ratio of 3:1–4:1. The marginal cells in the middle and base of the leaf are rhomboid or square, with a length of 20–40 μm and a width of 6–7 μm.

Line drawings are made to clearly show leaf morphology and microstructure of current fossil (Figs. 4(a)–4(c)).

3.2 Comparison and discussion

The presence or absence of costae is an important feature to classify mosses (Newton et al., 2007). Most extant mosses possess costae. However, our moss fossil does not

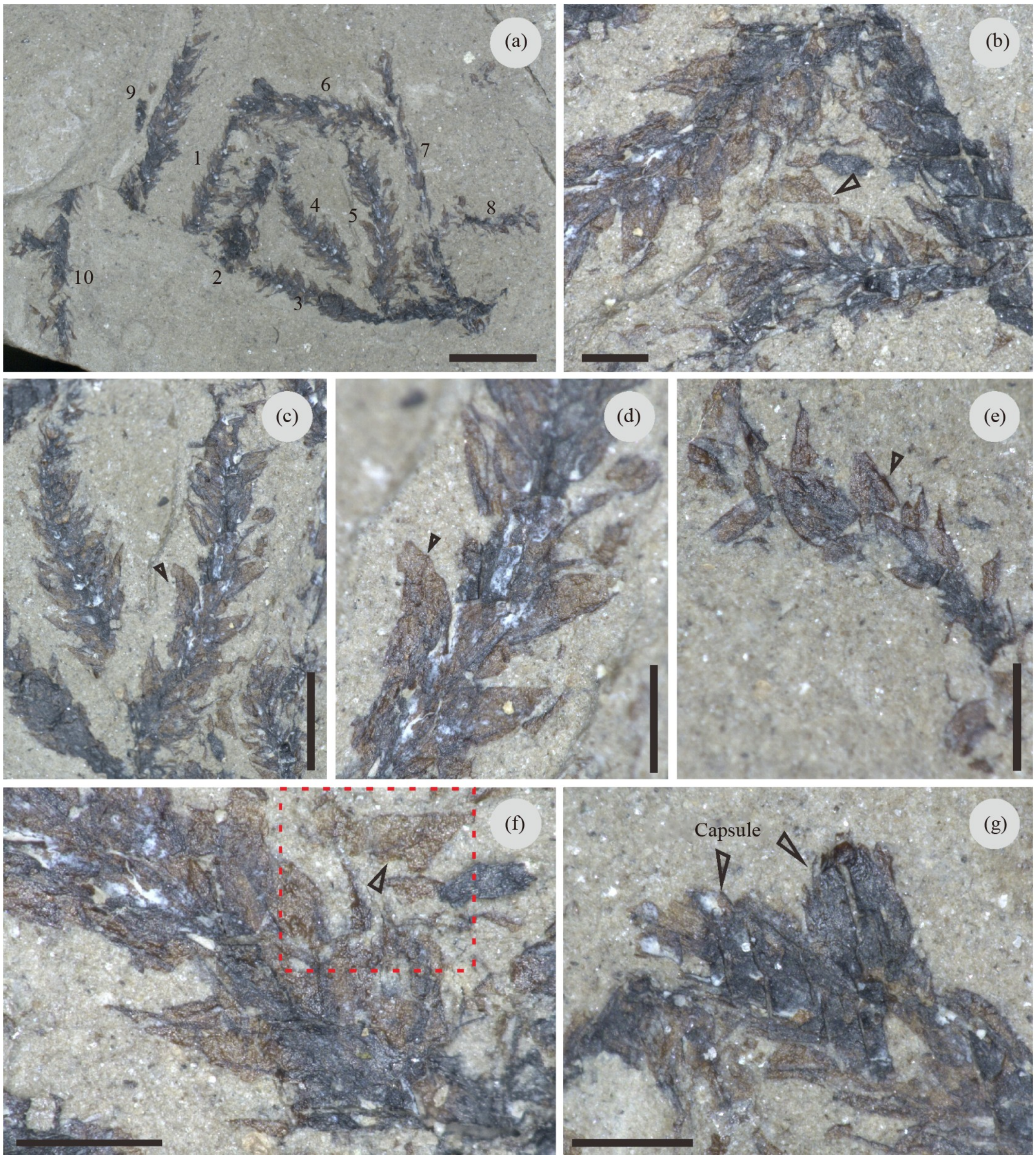


Fig. 2 Photographs showing gross morphology of the fossil (specimen # PZX-17-013). (a) The complete specimen, showing eight (1–8) connected and two (9–10) isolated branches. The stems are more or less erect and irregularly branched. Scale bar = 2 mm. (b–f) Closer up images of some branches, showing the size, shape, and texture of leaves. The arrows indicate that the leaves are homogeneous without a costa. (b) Branch 5. Scale bar = 0.4 mm. (c) Branches 4–5. Scale bar = 0.5 mm. (d) Closer up of (c), showing a fine tooth (arrow) at the leaf margin. Scale bar = 0.2 mm. (e) Branch 8. Scale bar = 0.5 mm. (f) Branch 5. A leaf within the red box (also indicated by an arrow) is obviously homogeneous. Scale bar = 0.5 mm. (g) The apical part of Branch 6. The arrows indicate the capsules. Scale bar = 0.5 mm.

have costae. In addition, it is a small-sized moss with ovate-lanceolate leaf shapes. We thus compare our fossil with the 14 living moss species possessing ovate-lanceolate leaves without costae. The comparison of the gross morphological characteristics is shown in Table 2.

Our fossil has its leaf margins mostly partly entire and partly dentate, with teeth mainly distributed at the basal part of the leaf. A few leaves are completely dentate while completely entire leaves can also be rarely observed. Our fossil has its leaf margins partially dentated or completely dentated, with teeth mainly distributed at the basal part of the leaf. Among the 14 living moss species listed in Table 2, *Aulacopilum abbrevium*, *Braunia alopecura*, *Hedwigia ciliata*, *Leucodon pendulus*, and *Leptopterigynandrum incuryatum* are excluded because their leaf margins are completely entire. The irregular branching of stems of our specimen further exclude the four species with feathery branching: *Campylophyllum halleri*, *Palisadula chrysophylla*, *Schwetschkeopsis fabronia*, and *Entodon dolichocucullatus*. The gross morphology of our fossil in general falls within the range of those of the remaining five species,

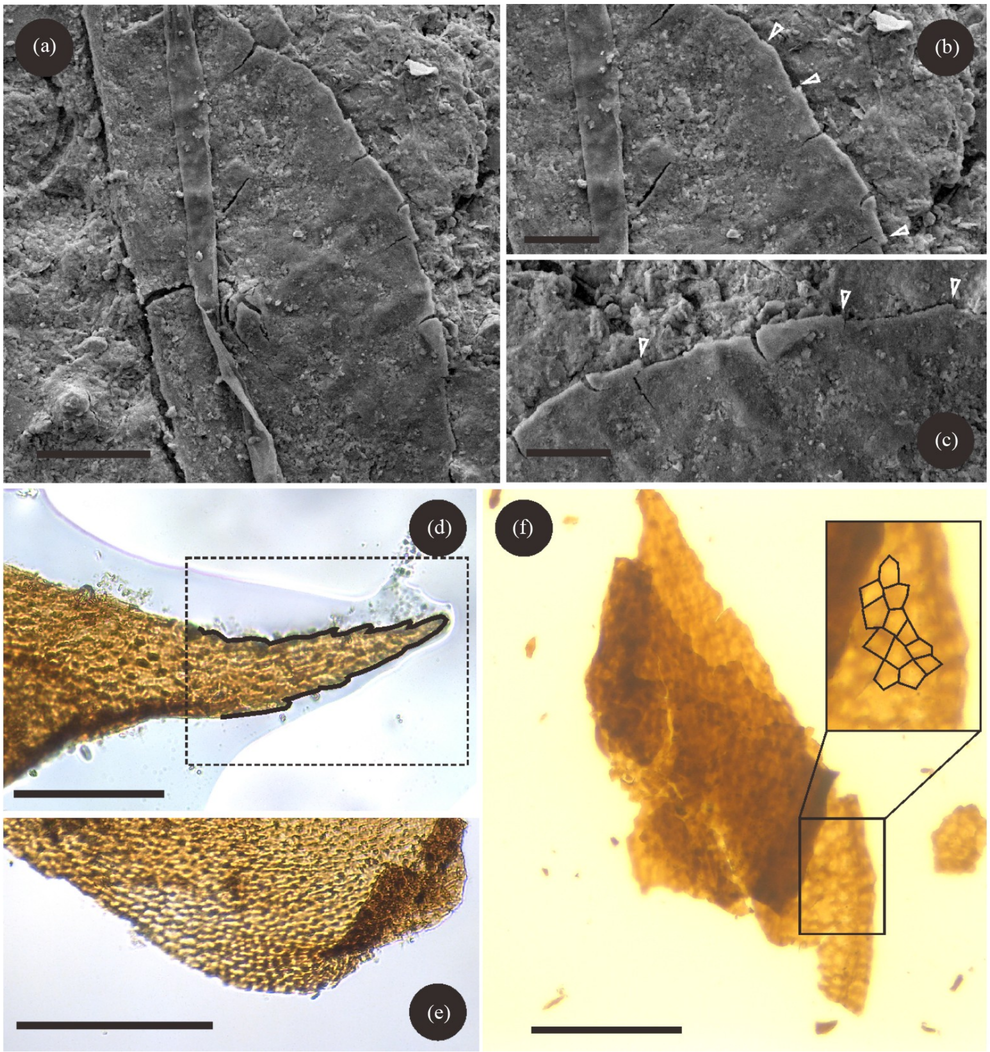


Fig. 3 SEM (a–c) and light microscope (d–f) photographs showing micro-morphology of leaves. (a–c) A leaf fragment observed under SEM. Scale bar = 0.1 mm. (a) A folded leaf, showing that the middle part of it is flat thus with no costa. (b–c) Closer up images of (a), with the fine teeth at leaf margins indicated by arrows. (d–f) Leaf fragments observed under LM. (d) The apical part of a leaf. The dentate margins are highlighted. Scale bar = 0.1 mm. (e) Fragments of a leaf base and part of the stem. Leaf base is thickened, no stipules. Cells at leaf margin are polygonal in shape while those in the middle are columnar or long quadrilateral. Scale bar = 0.2 mm. (f) Two leaf fragments, showing their thin and almost semitransparent texture. Leaf margin is thickened, with about two layers of cells while there is only one cell layer of the most part of the leaf. Cells are rhombus or irregularly quadrilateral in shape. Scale bar = 0.2 mm.

Platydictya jungermannioides, *Campylium porphyriticum*, *Venturiella sinensis*, *Pinnatella anacamptolepis*, and *Leucomium strumosun*, except that the size of our specimen is visibly smaller. The presence of capsules on Branch 6 indicates that our fossil is at its mature stage. It is known that as a moss has a high content of water, it would generally shrink due to dehydration when it was preserved in sediments. However, our fossil has leaves stretching naturally, showing little sign of shrinkage, likely due to very quick burial during early stage of the taphonomic process, such as being suddenly embedded by large amount of sediments. To understand the degree of shrinkage for a moss fossil preserved during such an early fossilization process, we subjected fully watered fresh mosses under 10 kg weight for 24 h. The compacted mosses still show their stretching status but have been dehydrated, similar to the condition of our fossil. The compacting resulted in a reduction of stem length by about 0.25–0.4 times and of leaf size by 0.3–0.5 times. Applying these ratios, we were able to estimate the possible actual sizes of our fossil. The stem length would be about 1–2 cm and the leaves are about 0.5 mm long with the largest width about 0.1 mm, most comparable to *Platydictya jungermannioides* among the above-mentioned five moss species. In addition, the leaf cell arrangement of our fossil also resembles that of *Platydictya jungermannioides*.

Fossil and molecular evidence suggests that bryophytes evolve very slowly (Blöcher and Frahm, 2002), which leads to limited differences between many ancient and

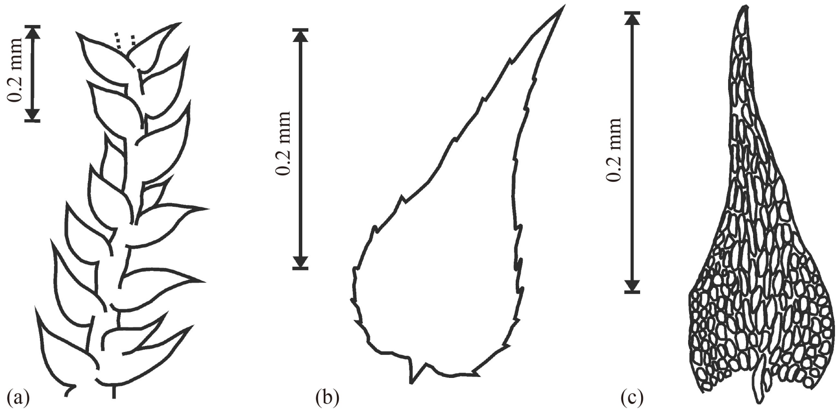


Fig. 4 Line drawings showing part of Branch 4 (a) and two leaves (b–c). Scale bar = 0.2 mm. (a) Branch 5 in Fig. 2(a) showing the arrangement of leaves on the stem. Fine teeth on leaf margins are not shown. (b) A leaf with dentate margins. Teeth are denser at the lower part. (c) A leaf showing its cell outlines.

Table 2 Feature comparison of the studied fossil with extant species containing ovate-lanceolate leaves lacking costae

Family	Species	Stem branching	Stem form	Stem length/cm	Leaf shape	Leaf margin	Leaf length/mm	Leaf width/mm	Costae	Stipule
	Platydictya cf. *jungermannioides*	Irregular branching	More or less erect	0.6–1.2	Ovate-lanceolate acuminate	Partly entire and partly dentate (particularly at base)	0.14–0.25	0.04–0.06	Absent	Invisible, likely absent
Amblystegiaceae	*Platydictya jungermannioides* (Brid.) Crum	Irregular branching	Erect	1–1.5	Ovate-lanceolate or lanceolate	Dentate or partly (at base) dentate	0.2–0.35	0.06–0.09	Absent or inconspicuous	Absent
Amblystegiaceae	*Campylium porphyriticum* C. Muell.	Irregular branching	Erect or decumbent	1–2	Ovate heart-shaped	Dentate	0.6–0.9	0.5	Two short middle costae, one long middle costa or none	Present
Amblystegiaceae	*Campylophyllum halleri* (Hedw.) Fleisch.	Subpinnate branching	Decumbent	2–5	Base ovate, distally lanceolate and everted	Dentate at upper part	0.6–0.8	0.5	Short or absent	Absent
Erpodiaceae	*Aulacopilum abbreviatum* Mitt.	Irregular branching	Decumbent amphitropous	0.5–1	Ovate-lanceolate	Entire	0.5–0.7	<0.2	Absent	Absent
Erpodiaceae	*Venturiella sinensis* (Vent.) C. Müll.	Irregular branching	Decumbent and serried	1–2.5	Ovate-shaped or ovate-lanceolate	Dentate at upper part	1–2.5	0.5	Absent	Absent
Hedwigiaceae	*Braunia alopecura* (Brid.) Limpr.	Irregular branching	Strong	2	Broad ellipse or ovate curving	Entire	1.5–2	0.7–1.1	Absent	Absent
Hedwigiaceae	*Hedwigia ciliata* (Hedw.) Ehrh.	Irregular branching	Thick andstrong	3–5	Ovate-lanceolate, concave	Entire	1.3–3.3	0.6–0.9	Absent	Absent
Leucodontaceae	*Leucodon pendulus* Lindb.	Branches serried	Branches short and overhanging	2–3	Long oval and adnate	Entire	2–2.5	1–1.5	Absent	Absent
Myuriaceae	*Palisadula chrysophylla* (Card.) Toy.	Branches serried	Erect and outstretched	2	Ovate	Dentate nucleus	2–5	1–1.5	Short	Absent
Thamnobryaceae	*Pinnatella anacamptolepis* (C. Mull.) Broth.	Irregular branching	Decumbent	Up to 5	Base oblate semicircular and short leaf apex lanceolate	Dentate at upper part	1.8–2	1	Two short middle costae, one long middle costae or none	Absent
Eucomiaceae	*Leucomium strumosun* (Hornsch.) Mitt.	Irregular branching	Decumbent	2	Acuminate lanceolate	Invisible	1.5–2	0.5	Absent	Absent
Fabroniaceae	*Schwetschkeopsis fabronia* (Schwaegr.) Broth.	Pinnate branching	Decumbent extension	1.5–3	Ovate-lanceolate, mucronate	Entire, occasionally dentate	0.5–0.7	<0.2	Absent	Absent
Thuidiaceae	*Leptopterigynandrum incuryatum* Broth.	Branches serried	Decumbent tilting stand	>5	Ovate or broadly ovate	Entire	1.4	<0.5	Two middle costae, short	Present
Entodontaceae	*Entodon dolichocucullatus* S.Okam.	Irregularly pinnate branching	Decumbent	5–8	Linear lanceolate	Dentate at upper part	0.8–1.1	<0.5	Absent	Present

extant bryophytes in morphology. Some previously-reported fossil bryophytes with the features more or less similar to our fossil have been found in strata with different ages, with the earliest dating back to the Paleozoic (Oostendorp, 1987; Amaral et al., 2004; Moisan et al., 2012). Most of the well-preserved moss fossils before Cenozoic were classified into the broad morphological genus *Muscites*. Among them, only the specimens from the Late Triassic Madygen Flora in the Canadian Arctic have their micro-morphological structures described, including the absence of costae (Moisan et al., 2012). However, there is a distinct difference in leaf shape between them and our fossil, nearly rounded versus ovate-lanceolate. Some fossils found in the Northern Hemisphere show similar growth pattern as well as leaf shape to our specimen (Baker et al., 1993; Satake et al., 1995; Kuder and Kruge, 1998; Geotcheus and Birks, 2001; Bittmann, 2007; Reyes et al., 2010; Guo et al., 2013). The most similar one is *Amblystegium varium* found in the adjacent early Miocene strata at Weichang which also has ovate-lanceolate leaves arranged spirally on stems of similar length (Guo et al., 2013). However, the Weicheng fossil bears costae, obviously different from our specimen. *Campylium* fossils of Amblystegiaceae found in the Pleistocene also have ovate-lanceolate leaves without costae and irregularly branched stems. However, its leaves are significantly larger than ours, and its stem length is more than 2 cm, much longer than that of our fossil (Matthews and Ovenden, 1990; Goetcheus and Birks, 2001).

In summary, after comparing our moss fossil with both fossil and living taxa, we conclude that our fossil bears the most similarity with the modern moss species *Platydictya jungermannioides*. All characteristics that can be observed from our specimen fall within the range of those in the living species. However, the lack of some key characteristics, such as those of rhizoids and reproductive organs prevents us from assigning our fossil to the living species directly. Tentatively, we name our specimen *Platydictya* cf. *jungermannioides*, with the abbreviation cf. (for “confer”) added before the species epithet to indicate the species level uncertainty due to its incomplete preservation.

Fossils of *Platydictya* are extremely rare. Ovenden (1993) reported *Platydictya* cf. *jungermannioides* fossils from the Ellesmere Island in the Canadian Arctic but no images or detailed descriptions were provided. Before our specimen, no fossil of *Platydictya* has been reported from Asia, although living *Platydictya* plants are currently growing in the studied area (Zhang, 2008). The studied *Platydictya* fossil found at the Pingzhuang Coal Mine is the first record of this genus in Asia, suggesting that this genus may have lived in the Chifeng area from the early Miocene to the present.

4 Paleoenvironmental significance

Paleobotanists reconstruct the ecology and environment of ancient forests almost exclusively from vascular plants, knowing little about their understory and even less concern forest floors due to the rarity of bryophyte fossils. Thus the exceptionally preserved moss fossil studied here, combined with the narrow ranges of ecological tolerances of mosses (Miller, 1984; Zazula et al., 2006), provides a unique opportunity to infer microhabitats of an ancient forest that rarely left any trace in the fossil record.

Mosses have a high requirement for humidity. Plants in the Amblystegiaceae are basically aquatic, demanding a high level of water supplies (Yang et al., 2004). Living species of *Platydictya* are widely distributed in the temperate to subtropical humid to semi-humid areas, especially in the temperate monsoon climate region in mountainous and hilly forests. *Platydictya jungermannioides* grows in moist environments such as the underside or surrounding soils of wet tree trunks in dense forests. In addition, the excellent preservation condition of our specimen as well as our compaction experiment confirmed that our fossil was highly likely buried *in situ*, fresh with adequate water before it was rapidly covered by sediments. We thus believe that the original living microhabitat of our fossil should be humid with sufficient water supplies.

Although both fossil and living species of *Platydictya* have been found in the Chifeng area mentioned above, it can only demonstrate that the microenvironment of the plants is humid. The early Miocene flora of the Pingzhuang site has been well established to be the transitional type between evergreen deciduous broad-leaved mixed forest and coniferous broad-leaved mixed forest (Shang et al., 2001) based from vascular plant fossils dominated by angiosperms of Fagaceae, Populaceae, Betulaceae, and Ulmaceae, as well as gymnosperms represented by the family Taxaceae (Zhang, 1986). This transitional type of forest now grows in the temperate to subtropical semi-humid climate (Tao et al., 1994). By contrast, vegetation in the current Pingzhuang area is dominated by grasses and shrubs belonging to the semi-arid temperate climate region. The climate of the basin during the early Miocene was thus much more humid and warmer than it is today. Moreover, the depositional environment of the lower Laoliangdi Formation is of lacustrine or swamp facies inferred from the composition of the sedimentary record (Shang et al., 2001), further confirmed that the Pingzhuang basin has a temperate or subtropical humid to semi-humid climate in the early Miocene. The existence of *Platydictya* cf. *jungermannioides* and its preservation condition confirms a very wet microenvironment under such as ecological background, likely a forest that is dense and humid enough to provide a lush understory layer for the growth of this moss species.

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