

New Fossil Liverworts from the Lower Cretaceous of Western Liaoning, China

GUO Caiqing^{1,2}, YAO Jianxin¹, ZHANG Jianwei³, WU Pengcheng² and LI Chengsen^{2,*}

1 Key Laboratory of Stratigraphy and Paleontology, Institute of Geology, Chinese Academy of Geological Science, Beijing 100037, China

2 Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China

3 Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Xinjiang 830011, China

Abstract: Sixteen liverwort specimens collected from the Lower Cretaceous Yixian Formation of Huangbanjigou Village, Liaoning Province, China are studied in this work. The plants are thalloid and preserved in brown arenaceous mudstone as impressions. Based on examinations, the liverworts are assigned to two new genera and five new species: *RiccardiOTHALLUS palmata* sp. nov., *Pallaviciniites stricta* sp. nov., *Pellites latithallus* gen. et sp. nov., *Conocephalumites hexagonites* gen. et sp. nov. and *Metzgerites multifidus* sp. nov., belonging to five families and five genera. The fossil research indicates that the divergence of families, Aneuraceae and Metzgeriaceae, Pallaviciniaceae and Hymenophytaceae, Pelliaceae and Fossombronaceae, was in the Lower Cretaceous (125 Ma). The research provides significant additions to the fossil liverwort records in Western Liaoning and offers fossil evidence for studying the classification and evolution of extant liverworts.

Key words: Liverworts, Early Cretaceous, classification, differentiation, Western Liaoning, China

1 Introduction

The Jehol Group, derived from the Jehol Series and first named by the American geologist Grabau in 1923 (Grabau, 1923), was investigated near “Lingyuan Province”, Western Liaoning. In 1962, Gu Zhiwei identified a fossil group represented by *Eosestheria* Chen, *Ephemeropsis trisetalis* Eichwald and *Lycopera* Muller in the Jehol group, which was regarded as the representation of the Jehol Biota (Gu Zhiwei, 1962). The Jehol Biota formed in the Early Cretaceous of the Mesozoic (Shen Yanbin et al., 1999; Zhang, 2001; Peng Yandong et al., 2003; Zhou et al., 2003; Sun et al., 2011; Shen Caizhi et al., 2016), and its range contained north China, Mongolia, Siberia, Kazakhstan, North Korea and a part of Japan. Liaoning is the distribution centre of the Jehol Biota (Xing, 2005), and its strata are primarily composed of intermediate-basic volcanic rocks and volcanoclastic rock with mixed lacustrine sedimentary rock interlayers, which formed during volcanic eruption events (Sun Yongshan, 2009). The strata of the Jehol Biota included three formations: the Dabeigou Formation, the Yixian

Formation and the Jiufotang Formation, which respectively represent three stages of the biota evolution. Our specimens were collected from the Jianshangou Bed of the Yixian Formation.

The Jianshangou Bed is one of the beds bearing richest fossil plant in west Liaoning (Ji Qiang, 2002; Jiang Zikun et al., 2013; Wang Sien et al., 2015). As early as 1999, Wu Shunqing described five bryophyte species collected from this bed: *Thallites riccoites* Wu, *Thallites dasyphyllus* Wu, *Thallites* sp. Wu, *Muscites tenellus* Wu, and *Muscites drapanophyllus* Wu (Wu Shunqing, 1999). Sun et al. reported three liverwort species and one moss species from the same bed in 2001: *Conocephalumites riccoites* Wu, *Thallites jianshangouensis* Sun et Zheng, *Metzgerites multiramea* Sun et Zheng, and *Muscites meteoroides* Sun et Zheng (Sun Ge et al., 2001). To date, three genera and eight species of bryophytes have been observed at this site. However, only the external morphology features were described in these studies; the systematic information has rarely been considered, and the phylogenies of seven species remain unclear. In this work, we continue to study several new fossil liverworts of the Early Cretaceous in Western Liaoning with regards to morphology and

* Corresponding author. E-mail: lics@ibcas.ac.cn

systematic paleontology, and attempt to identify important diagnostic features, as well as systematic and evolutionary characteristics.

2 Materials and Methods

The specimens studied in this work were collected from Huangbanjigou Villiage, Shangyuan Town, Liaoning Province, China (Fig. 1). The specimens as impression fossils preserved in the seventh unit of the Jianshangou Bed; several fossils were also preserved as compression fragments and cellular structures of gametophytes. The seventh unit is 2.8 m thick and is primarily composed of arenaceous mudstones.

Sixteen fossil liverworts were studied in the laboratory, observed under a Zeiss Stereo Discovery V20 and photographed with a Japanese Cannon EOS 20D camera. Among the specimens numbered PEPB00001–00019, 8 samples are positive and negative, respectively, and all are in the collections of the Museum of Plant History, Institute of Botany, Chinese Academy of Sciences.

3 Systematics and Descriptions

3.1 Genus *Riccardiothallus*

Phylum Marchantiophyta

Class Jungermanniopsida

Order Metzgeriales

Family Aneuraceae

Genus *Riccardiothallus* Wu et Guo, 2012

Species type: *Riccardiothallus palmata* Wu et Guo sp. nov. (Fig. 2a–h and Fig. 3a–b).

Holotype: Specimen PEPB00007A (Fig. 2a).

Paratypes: PEPB00007 (A, B)–9(A, B); PEPB00010–

11; PEPB00017–18.

Repository: Museum of Plant History, Institute of Botany, Chinese Academy of Sciences.

Type locality: Huangbanjigou Villiage, Shangyuan Town, Liaoning, China.

Stratum and age: Yixian Formation, Early Cretaceous (125 Ma).

Etymology: The species name, *palmata*, is derived from the extant species *Riccardia palmata* (Hedw.) Carruth., which indicates the thallus is palmate-shaped.

Species diagnosis: Thalli palmate; irregular dichotomous branched three to four times, with branching angles less than 40°; branches are long, ribbon-like, and meanderingly extending, with rounded ends; ecostate and entire margins.

Description: Plants are prostrate thalloid, palmate, 0.7–2 cm long and 0.7–1.2 cm wide, and irregularly dichotomous (three to four times). The branches are long, ribbon-like, dense, and meanderingly extending, with lengths of 0.2 to 0.9 cm, widths of 0.05 to 0.1 cm, and branching angles less than 40°. The apical portions of branches are rounded; individual branch tops have two lobes, and the distance between lobes is 0.1–0.2 cm. The middle regions of the thallus are thicker than the wings, but there is no costa. Margins are complete. Air chambers, rhizoids and sporophytes are not observed.

Discussion and comparison: The new specimens possess irregularly dichotomous branched ecostate thalli with entire margins, which is typical of the fossil genus *Riccardiothallus* (Jungermanniopsida) (Guo et al., 2012). Based on these features, it is reasonable to designate the new fossil liverworts in this genus. New plants appear palmate in shape. The branches are long, ribbon-like, dense, and meanderingly extending, with rounded apical

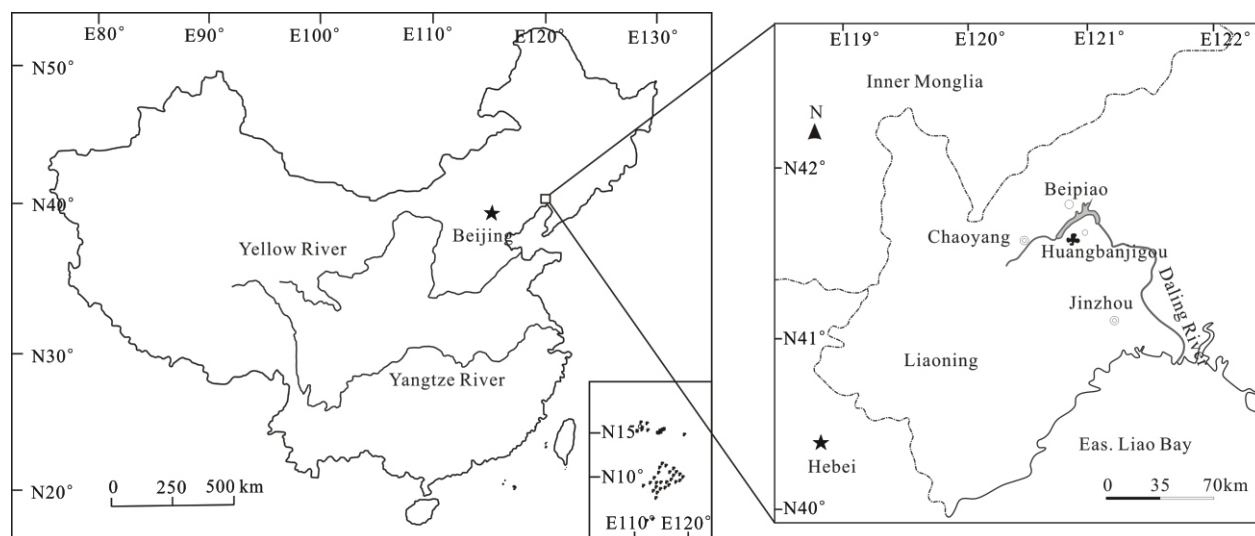


Fig. 1. Location of the fossil in Western Liaoning Province.



Fig. 2. Gametophyte morphology of fossil liverwort *Riccardiothallus palmate* (Scale bar=5 mm).

portions, unlike the flat thalli with short ribbon-like branches and straight apical portions in *Riccardiothallus devonicus* Wu et Guo (Guo et al., 2012) (Table 1). Hence, a valid name for the new species in this genus: *Riccardiothallus palmata* is established.

3.2 Genus *Pallaviciniites*

Phylum Marchantiophyta

Class Jungermanniopsida

Order Fossombroniales

Family Pallaviciniaceae

Genus *Pallaviciniites* R. M. Schust., 1966

Species type: *Pallaviciniites stricta* Wu et Guo sp. nov. (Fig. 3c–d)

Holotype: Specimen PEPB00019 (Fig. 3d).

Paratypes: PEPB00016, PEPB00019.

Repository: Museum of Plant History, Institute of Botany, Chinese Academy of Sciences.

Type locality: Huangbanjigou Villiage, Shangyuan Town, Liaoning, China.

Stratum and age: Yixian Formation, Early Cretaceous (125 Ma).

Etymology: The species name, *stricta*, indicates the branches extend straight.

Species diagnosis: Plant thalloid; irregular dichotomous branching (up to three times); branching angles less than 20°; nearly parallel neighbouring branches; branches are long and ribbon-like, with tapered apical portions; single costa and entire margins.

Description: The plant is thalloid, prostrate, 1.1–1.8 cm long and 0.4–1.7 cm wide, with irregular dichotomous branching (two to three times). Its branches are ribbon-shaped, long and thin, dense, and extend straight, with lengths of 1.3 cm, widths of 0.1 cm, and branching angles up to 20°. The apical portions are tapered. Two neighbouring branches are nearly parallel, and the distance between branches is very narrow. There is a single costa, which is thin and slender, and the thallus margins are complete. Reproductive organs are unknown.

Discussion and comparison: Following the morphological study of the specimens PEPB00016 and PEPB00019, and comparisons with related extant and other fossil liverworts, our specimens appear to be most closely related to the fossil genus *Pallaviciniites* (Pallaviciniaceae) (Table 2), e.g., the plants are thalloid, show irregular dichotomous branching, with long, ribbon-like branches, single costa and entire margins. Because of the age of the stratum in which the new liverworts found is Early Cretaceous, we therefore established the new fossil species of *Pallaviciniites stricta* in the genus *Pallaviciniites*.

In the plants of fossil genus *Thallites*, our new

Table 1 Comparison of fossil species of *Riccardiothallus*

Taxon	Thallus dimensions	Branching	Branching dimensions	Branching times	Branch shape	Branch angles	Costa	Margin	Location	Age	References
<i>R. devonicus</i>	2.1 cm long, 1.9 cm wide	Irregularly dichotomous	0.7–0.9 cm long, 0.1–0.2 cm wide	three to four times	Strap-like, flat	35–45°		Entire, the apical portions straight	Yunnan Province, China	Early Devonian	Guo et al., 2012
<i>R. palmata</i>	0.7–2 cm long, 0.7–1.2 cm wide	Irregularly dichotomous	0.2–0.9 cm long, 0.05–0.1 cm wide	three to four times	Ribbon-like, palmate-shaped	Up to 40°		Entire, the apical portions rounded	Liaoning Province, China	Early Cretaceous	This paper

Table 2 Comparison of fossil species of *Pallaviciniites*

Taxon	Thallus dimensions	Branching	Branching dimensions	Branching times	Branch shape	Branch angles	Costa	Margin	Location	Age	References
<i>P. devonicus</i>	–	Regularly dichotomous	0.19–0.23 cm wide	Two to three times	Strap-like	–	Single, two to several cells thick	With finely serrate	New York	Late Devonian	Schuster, 1966
<i>P. riccioites</i>	1.1 cm long, Up to 2.0 cm wide	Irregularly dichotomous	–	Three to five times	Strap-like, linear, forked	–	Single, strong	–	Liaoning Province, China	Early Cretaceous	Sun Ge et al., 2001
<i>P. sandaolingensis</i>	Up to 5 cm long, 0.3–0.6 cm wide	Irregularly dichotomous	–	Up to five times	Strap-like	30°–75°	Single, strong	Entire	Sandaoling Coal Field, China	Middle Jurassic	Li et al., 2016
<i>P. stricta</i>	1.1–1.8 cm long, 0.4–1.7 cm wide	Irregularly dichotomous	1.3 cm long, 0.1 cm wide	Two to three times	Long ribbon, nearly parallel	Less than 20°	Single, thin and slender	Entire	Liaoning Province, China	Early Cretaceous	This paper



Fig. 3. Gametophyte morphology of fossil liverworts (Scale bar=5 mm).

(a)–(b), *Riccardothallus palmate*; (c)–(d), *Pallaviciniites stricta*; (e), (h), *Pellites latithallus*; (f'), *Conocephalumites hexagonites*; (f''), Showing air chambers (Scale bar=1 mm); (g), *Metzgerites multifidus*.

specimens are very similar to the species *Thallites riccioites* (Wu Shunqing, 1999; Sun Ge et al., 2001) collected from the Jianshangou bed. They possess typical features of *Pallaviciniites*, so we designate these two species in the genus. However, the branches of the new plants generally extend straight, with taped apical portions. The neighbouring branches are almost parallel and the costa is single, thin and slender, differing from the fork-shaped branching with rounded ends and strong and protruding costa in *Thallites riccioites* (Wu Shunqing, 1999; Sun Ge et al., 2001). We therefore assigned the species *Thallites riccioites* to the new fossil genus *Pallaviciniites* with a new combination: *Pallaviciniites riccioites* (Wu) Wu et Guo comb. nov., and established the name *Pallaviciniites stricta* for our new specimen. The classification and systematic positions of other species in the genus *Thallites* need to be further studied in future work.

3.3 Genus *Pellites*

Phylum Marchantiophyta

Class Jungermanniopsida

Order Pelliales

Family Pelliaceae

Genus *Pellites* Wu et Guo gen. nov.

Type species: *Pellites latithallus* Wu et Guo sp. nov.

Etymology: The generic name, *Pellites*, is derived from the extant genus *Pellia* Raddi, indicating their affinity.

Generic diagnosis: Flat thalloid; regular dichotomous, sparse and broad branches; no costa; wavy margins.

Species: *Pellites latithallus* sp. nov. (Fig. 3e, h)

Holotype: Specimen PEPB00001B (Fig. 3e)

Paratypes: PEPB00001 (A, B)

Repository: Museum of Plant History, Institute of Botany, Chinese Academy of Sciences.

Type locality: Huangbanjigou Villiage, Shangyuan Town, Liaoning, China.

Stratum and age: Yixian Formation, Early Cretaceous (125 Ma).

Etymology: The species name, *latithallus*, indicates the branches are very broad.

Species diagnosis: General features are typical for the genus: Regular dichotomous branching (one to two times), fork-shaped, with branching angles ranging from 20° to 35°; the branches are short, strap-like, sparse and broad, with heart-shaped apical portions, and wavy margins.

Description: Flat thalli, 1.3 cm in length and 2 cm in width; regular dichotomous branching (one to two times). The branches are sparse, short, strap-like and very broad, 0.3–1.3 cm in length and 0.1–0.3 cm in width, with branching angles measuring 20°–35°. The apical portions

are heart-shaped. The gametophyte margins are wavy. The middle of the thallus is thicker than the wings, and no costa or reproductive organs are observed.

Discussion and comparison: The plants of specimen PEPB00001B possess flat thalli, regular dichotomous branching, with broad branches, no costa, and wavy margins. These features most closely resemble the extant genus *Pellia* (Pelliaceae) (Wu Pengcheng et al., 2012). As a fossil liverwort collected from the Early Cretaceous, it is appropriate to assign it to a new genus, *Pellites*, in the family Pelliaceae (Table 3). The thallus of *Pellites latithallus* is similar as that of *Thallites jianshangouensis* (Sun Ge et al., 2001), which is also found in the Jianshangou bed, but the thallus of the former is regularly dichotomous (one to two times), the branches are sparse, strap-shaped, short and very broad, with heart-shaped tapered apical portions, wavy margins, and no costa; in contrast, the latter is four to five times irregularly dichotomous, the branches are dense and thin, with fork-shaped tops, and the apical portions are rounded and widening with a distinctive costa and smooth margins. Moreover, the species *Hepaticites yaoi* from the Jurassic of the Junggar Basin and Barkol District in Xinjiang, China, closely resembles our specimens. However, the thalli of *Hepaticites yaoi* bifurcate irregularly several times with branching angles ranging between 50° and 60°. In addition, *Hepaticites yaoi* has a single, strong costa (up to 0.5 mm in width) and lateral ribs (Wu Xiangwu, 1996), which are not present on the thalli of the present specimens *Pellites latithallus*.

3.4 Genus *Conocephalum*

Phylum Marchantiophyta

Class Marchantiopsida

Order Marchantiales

Family Conocephalaceae

Genus *Conocephalum* Wu et Guo gen. nov.

Type species: *Conocephalum hexagonites* Wu et Guo sp. nov.

Etymology: The genus name is after the extant genus *Conocephalum* Hill, indicating its affinity to this genus.

Generic diagnosis: Regular dichotomous ecostate thallus; branches are long and ribbon-like; cells on the upper surface of the thallus are hexagonal; complete margins.

Species: *Conocephalum hexagonites* sp. nov. (Fig. 3f^l)

Holotype: Specimen PEPB00002 (Fig. 3f^l).

Paratypes: PEPB00002.

Repository: Museum of Plant History, Institute of Botany, Chinese Academy of Sciences.

Type locality: Huangbanjigou Villiage, Shangyuan Town, Liaoning, China.

Stratum and age: Yixian Formation, Early Cretaceous (125 Ma).

Etymology: The species name, *hexagonites*, indicates the cells on the upper surface of the thallus are hexagonal.

Species diagnosis: The general features are typical of the genus. Plants are thalloid, prostrate, and show regular dichotomous branching (three to four times), with long, ribbon-like branches, meanderingly extending, and branching angles of less than 20°. Cells on the upper surface of the thallus are irregular polygonal or hexagonal.

Description: Plants are thalliod, prostrate, 2 cm long, and 0.9 cm wide, and show regular dichotomous branching (three to four times). The branches are long, ribbon-like, meanderingly extending, 0.5–1.2 cm long and 0.03–0.1 cm wide, with branching angles up to 20°. The upper surface cells of the thallus are irregular polygonal or hexagonal, arranged along the long axis of the thallus close to the midrib, becoming smaller at the wings and near the branch tops. The polygonal or hexagonal cell structures are probably residual air chambers and can be seen by the naked eye (Fig. 3f²). There is no costa and thallus margins are complete.

Discussion: The species PEPB00002 bears the common features of the extant genus *Conocephalum* (Conocephalaceae): The plant has a thallus and shows forked branching; polygonal or hexagonal air chambers are present on the upper surface of the thallus; there is no costa and thallus margins are complete. In particular, the obvious polygonal or hexagonal air chambers on the surface of the thallus are typical features of this genus (Wu Pengcheng et al., 2012). As a new fossil plant collected from the Jianshangou bed, we prefer to establish the new genus of *Conocephalumites* in the family Conocephalaceae (Table 4), and we recognize a new species *Conocephalumites hexagonites* in this genus.

3.5 Genus *Metzgerites*

Phylum Marchantiophyta

Class Jungermanniopsida

Order Metzgeriales

Family Metzgeriaceae

Genus *Metzgerites* Wu et Li, 1992

Type species: *Metzgerites multifidus* Wu sp. nov. (Fig. 3g).

Holotype: Specimen PEPB00003 (Fig. 3g)

Paratypes: PEPB00003.

Repository: Museum of Plant History, Institute of Botany, Chinese Academy of Sciences. **Type locality:** Huangbanjigou Villiage, Shangyuan Town, Liaoning, China.

Table 3 Comparison of the genus *Pellites* gen. nov. with other genera in the family Pelliaceae

Taxon	Thallus dimensions	Branching	Branching times	Branch shape	Branch angles	Costa	Margin	Sporogonium	Capstule	Location	Age	References
<i>Pellia</i>	2–4 cm long, 0.5–0.7 cm wide	Forked or irregular	Sparse	Ribbon	–	Single, not distinctive	Wavy, tops with scales	–	Spherical	Japan, India, Liaoning, etc.	Present	Wu Pengcheng et al., 2012
<i>Pelliates</i>	–	–	–	–	–	–	–	Erect, with a broad, squarish foot	Spherical	India	Early Cretaceous	Narkhede and Bhowal, 2009
<i>Pellites</i>	1.3 cm long, 2 cm wide	Forked, regularly dichotomous	One or two times	Strap-like, broad	20°–35°	Ecosta	Wavy	–	–	Liaoning, Province, China	Early Cretaceous	This paper

Table 4 Comparison of the genus *Conocephalumites* gen. nov. with other genus in the family Conocephalaceae

Taxon	Thallus dimensions	Branching	Branching dimensions	Branching times	Branch shape	Branch angles	Costa	Margin	Location	Age	References
<i>Conocephalum</i>	1–10 cm long, 0.2–1.5 cm wide	Forked	–	Several times	Ribbon-like	–	Not distinctive	Lobed	Japan, Russia, Liaoning, China, etc.	Present	Wu Pengcheng et al., 2012
<i>Conocephalumites</i>	2 cm long, 0.9 cm wide	Regularly dichotomous	0.5–1.2 cm long, 0.03–0.1 cm wide	three to four times	Ribbon-like, meandering	up to 20°	Ecosta	Entire	Liaoning, China	Early Cretaceous	This paper

Stratum and age: Yixian Formation, Early Cretaceous (125 Ma).

Etymology: The species name, *multifidus*, indicates the thallus is multiply branched.

Species diagnosis: General features are typical of the genus. The plant is thalloid and shows irregular dichotomous branching (five to six times). Branches are forked-shape, dense, and strap-like, with rounded apical portions and branching angles less than 30°. The costa is strong and the margins are complete.

Description: The plant is thalloid, fan-shaped, 1.7 cm long and 3 cm wide. The branches are irregularly dichotomous (five to six times), forked-shape, dense and short, 0.3–1.4 cm long and 0.01–0.1 cm wide, with branching angles less than 30°. The apical portions of the branches are rounded, and the ends of the branches generally show two forked lobes. The costa is single, strong, up to 0.3 mm wide. The margins are complete and smooth. Air chambers and sporophytes are not observed.

Discussion and comparison: The new fossil liverwort bears the general morphological features of the genus *Metzgerites* (Metzgeriaceae): Flat thallus, forked branching, strong costa, several cell layers, and no air chambers (Wu Xiangwu and Li Baoxian, 1992; Sun Ge et al., 2001). Therefore, this species is assigned to this fossil genus. Based on the detailed differences in gametophyte morphology of this species with other species in the same genus (*Metzgerites*) (Table 5), we establish a new species *Metzgerites multifidus* here. The new species somewhat resembles the species *Metzgerites multiramea* from the Jianshangou Bed. However, the gametophyte of *Metzgerites multifidus* bears five to six irregularly dichotomous branches; the branches are dense, strap-like and have round ends; the ventral costa shows no setae. In contrast, *Metzgerites multiramea* shows dichotomous branching, with sparse, ribbon-like branches, tapered apical portions, and ventral costa with setae (Sun Ge et al., 2001).

4 Discussion

Based on the analysis of chloroplast DNA sequences of approximately 6,000 modern liverworts species of approximately 350 genera and observations of the fossil liverworts found, Heinrichs et al. established a phylogenetic hypothesis of the diversification of liverworts (Forrest et al., 2006; He-Nygrén et al., 2006; Heinrichs et al., 2007; Hernick et al., 2008; Chang and Graham, 2011; Shaw et al., 2011; Feldberg et al., 2014; Villarreal et al., 2015). In these study, they estimated the divergence time of some leafy liverworts, and suggested that the separation of the families of Aneuraceae and

Metzgeriaceae probably was in the Late Oligocene (25.2–23.8 Ma), whereas the divergences of Pallaviciniaceae and Hymenophytaceae, and Pelliaceae and Fossombroniaceae were, respectively, in the Late Cretaceous (78.8–74.7 Ma) and Early-Middle Triassic (252–237 Ma).

The liverworts from Western Liaoning were deposited in the Lower Cretaceous Yixian Formation. The stratigraphic age of these liverworts suggests that they existed or were already diverse in the Early Cretaceous at least. Based on their systematic positions, we assumed that the separation of families of Aneuraceae and Metzgeriaceae, and Pallaviciniaceae and Hymenophytaceae occurred in the Early Cretaceous (125 Ma), which is earlier than suggested by the former research. The early Cretaceous species *Pellites latithaillus* in this work and *Pelliaites deccanii* Narkhede et Bhowal from the Late Cretaceous (Narkhede and Bhowal, 2009) also indicate that the divergence of Pelliaceae and Fossombroniaceae occurred in the Early Cretaceous, later than the time derived from DNA sequences analysis. Therefore, our research provides significant additions to the fossil liverwort records in this district, and offers fossil evidence for studying the classification as well as systematic and evolutionary relationship of extant liverworts.

Table 5 Comparison of the species of *Metzgerites*

Taxon	Thallus dimensions	Branching	Branching dimensions	Branching times	Branch shape	Branch angles	Costa	Margin	Location	Age	References
<i>M. exiliformis</i>	0.5 cm long, 0.16–0.2 cm wide	–	–	Single or sparse	Ribbon-like	–	Single, strong, 15–20 columns of cells, with ventral cillum	Erect, flat	Hebei, China.	Middle Jurassic	Wu and Li, 1992
<i>M. yixianensis</i>	1.4 cm long, 0.1–0.2 cm wide	Forked	–	Single or sparse	Ribbon, edges parallel	–	Sing. strong, 0.03 cm wide, with ventral cillum	Erect or curved downward	Hebei, China.	Middle Jurassic	Wu and Li, 1992
<i>M. multiramea</i>	1.5–2.5 cm long, 1–2 cm wide	Forked	–	Two to three times	Ribbon-like, tapered ends	–	Strong, with ventral cillum	Erect or curved downward	Liaoning, China	Early Cretaceous	Sun Ge et al., 2001
<i>M. multifidus</i>	1.7 cm long, 3 cm wide	Irregularly dichotomous	0.3–1.4 cm long, 0.01–0.1 cm wide	Five to Six times, dense	Ribbon-like, round ends	less than 30°	Single, strong, up to 0.03 cm wide	Entire	Liaoning, China	Early Cretaceous	This paper

Table 6 List of the Bryophytes of the Jianshangou Bed, Yixian Formation, Western Liaoning, China

Fossil species	Phylum	Class	Order	Family	The extant Genus	Affinity with extant species	The number of specimens	References
<i>Pallaviciniites riccioites</i>	Jungermanniopsida	Not clear	Fossombroniales	Pallaviciniaceae	<i>Pallavicinia</i>		PB18220–18223	Wu Shunqing, 1999; Sun Ge et al., 2001
<i>Thallites dasyphyllus</i>							PB18972–18973	
<i>Thallites</i> sp.							PB18224	
<i>Muscites tenellus</i>							PB18225	Wu Shunqing, 1999
<i>Muscites drepanophyllus</i>							PB18226	
<i>Muscites meteoroides</i>	Musci		Not clear	Not clear	Not clear		PB18231	
<i>Thallites jianshangouensis</i>	Marchantiophyta	Not clear					PB18978, PB18978A	Sun Ge et al., 2001
<i>Metzgerites multiramea</i>							PB18968–18971	
<i>Metzgerites multifidus</i>							PB18956, PB18974, PB18976–18977, ZY3032	
<i>Riccardiothallus palmata</i>							PEPB000003	
<i>Pallaviciniites stricta</i>							PEPB000007A, B–9A, B, PEPB00010–11, 17–18	
<i>Pellites latithallus</i>	Jungermanniopsida		Fossombroniales	Pallaviciniaceae	<i>Pallavicinia</i>		PEPB000016, 19	This paper
<i>Conocephalum</i>							PEPB000001A, B	
							PEPB000002	
	Marchantiopsida		Marchantiales	Conocephalaceae	<i>Conocephalum</i>			

5 Conclusion

Sixteen liverwort specimens collected from the Lower Cretaceous Yixian Formation in Western Liaoning, China were studied in the present study. Based on the investigation, five liverwort species were found to belong to five families, five genera, and two new genera, and five new species were established: *Riccardiothallus palmata* sp. nov., *Pallaviciniites stricta* sp. nov., *Pellites latithallus* gen. et sp. nov., *Conocephalumites hexagonites* gen. et sp. nov., and *Metzgerites multifidus* sp. nov.. In Tables 1–5, new fossil species (genera) of the Jianshangou Bed are compared in detail with other fossils and modern species (genera) of the same genus (family) in terms of morphological features of gametophytes (Tables 1–5), and the evidence to establish new fossil genera and species is demonstrated.

According to previous studies in the Jianshangou Bed of the Yixian Formation, eight bryophyte species have been reported in this district (Wu Shunqing, 1999; Sun Ge et al., 2001; Li Ruiyun et al., 2016), comprising one family, two genera and five species of liverworts: *Thallites riccioites*, *Thallites* sp., *Thallites dasyphyllus*, *Thallites jianshangouensis* and *Metzgerites jianshangouensis*; and one genus and three species of mosses: *Muscites tenellus*, *Muscites drepanophyllus* and *Muscites meteoroides*. Our study added bryophyte flora of the Yixian Formation, in Western Liaoning, to five families, seven genera and thirteen species, i.e., five families, six genera, and ten species of liverworts, and one genera and three species of mosses. In these bryophytes, only seven species of liverworts can be confirmed in regards to their systematic positions: *Riccardiothallus palmate* (Aneuraceae), *Pallaviciniites riccioites* and *Pallaviciniites stricta* (Pallaviciniaceae), *Pellites latithallus* (Pelliaceae), *Conocephalumites hexagonites* (Conocephalaceae), *Metzgerites multifidus* and *Metzgerites multiramea* (Metzgeriaceae), belonging to five families and five genera; the classifications of the other six species are still unclear (Table 6).

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About the first author

GUO Caiqing, female; born in 1975 in the province of

Heilongjiang; Ph.D, and research assistant of the Institute of Geology, Chinese Academy of Geological Science. Now she is mainly engaged in the researches of paleobotany, paleoclimate, paleoenvironment, and phytogeography.