

云南曲靖早泥盆世龙华山工蕨(*Zosterophyllum longhuashanense* Li and Cai, 1977)标本的新观察*

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摘要 文中对云南曲靖下泥盆统徐家冲组 *Zosterophyllum longhuashanense* Li and Cai 模式标本进行了重新观察。该模式标本仅保存一段孢子囊穗, 由中央穗轴和疏松螺旋排列的孢子囊构成。穗轴中部可见一条宽约 0.3 mm 纵向延伸的维管束痕迹, 且较细的条带从中央维管束处分出, 延伸向孢子囊。孢子囊侧面观呈三角形或椭圆形, 高 2.2—3.1 mm, 侧面宽 1.3—2.8 mm。孢子囊沿近轴侧开裂为相等的两瓣。该化石植物的形态学特征以及度量数据均与工蕨属的模式种 *Zosterophyllum myretonianum* 极相似, 据此, 将 *Zosterophyllum longhuashanense* 修订为 *Zosterophyllum* cf. *myretonianum*。

关键词 工蕨属 泥盆纪 云南

1 简介

李星学、蔡重阳(1977)根据云南曲靖早泥盆世的化石标本建立了龙华山工蕨(*Zosterophyllum longhuashanense* Li and Cai, 1977)。龙华山工蕨的标本只有一块, 在最初发表的文献资料中, 图示较小, 也不清晰, 以至对于龙华山工蕨的形态特征, 诸多学者均有误解和质疑。Gerrienne(1988)认为 *Z. longhuashanense* 应归于孢子囊呈两行状排列的扁工蕨亚属(*Platyzosterophyllum*); Hao 等(2007)和 Edwards 等(2015)都认为 *Z. longhuashanense* 的孢子囊呈两行状排列。但是, 李星学、蔡重阳(1977)在建立 *Z. longhuashanense* 时, 对其特征描述中明确说明其孢子囊为明显的螺旋状排列, 但由于没有孢子囊直接覆盖于轴面上, 或缺乏被穗轴完全掩盖的孢子囊, 因此形成了一种孢子囊接近两列式的假象。为了更清楚认识 *Z. longhuashanense* 的形态学特征, 本文对 *Z. longhuashanense* 的模式标本(唯一一块标本)进行了重新观察。根据该标本所呈现的

植物形态学特征, 认为该标本应被修订为 *Zosterophyllum* cf. *myretonianum* Penhallow, 1892。

2 材料与方法

重新观察的化石材料仅包含一块化石标本, 即 *Zosterophyllum longhuashanense* 的模式标本, 为压型保存的植物化石, 采自云南沾益县龙华山剖面下泥盆统龙华山组(李星学、蔡重阳, 1977, 1978; 产地与地质图参见 Hao and Xue, 2013, fig. 2. 2)。该剖面龙华山组共分为五层, 岩性主要为泥岩及细砂岩, 标本采自第三层下部的褐黄色细砂岩中, 同层中还发现有 *Z. yunnanicum* Hsü(李星学、蔡重阳, 1978), *Hsüa robusta* Li(李星学、蔡重阳, 1978; 李承森, 1982)等。地质时代为早泥盆世布拉格期(Pragian)—埃姆斯期(Emsian)。

关于岩石地层单位“龙华山组”和“徐家冲组”的命名问题, 一直存在争议。根据对相关资料的分析总结, “龙华山组”与“徐家冲组”岩性相似, 层位相当, 所含化石组合面貌非常相似、对比良好、时代相

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近且地理位置很近,故两个地层单位应该合并(卢礼昌、欧阳舒,1976,1978;李星学、蔡重阳,1978;田家杰、朱怀诚,2005)。且“徐家冲组”是符合出版优先律的有效合法的岩石地层单位,应继续使用,而“龙华山组”应予废除,可用“徐家冲组”一名来代表沾益龙华山地区和翠峰山徐家冲附近出露的早泥盆世中晚期的沉积地层(彭辉平等,2016)。龙华山组的时代原定为早泥盆世埃姆斯期(卢礼昌、欧阳舒,1976;李星学、蔡重阳,1977),随着对徐家冲组生物地层学研究的深入,其时代限定为早泥盆世布拉格期—埃姆斯期(朱敏等,1994;朱敏、王俊卿,1996;田家杰、朱怀诚,2005;Wellman *et al.*, 2012)。

本研究宏观照相采用的仪器设备为 Nikon D800 数码相机和 Nikkor 105 mm 微距镜头,以完整展示整块标本的形态特征。微观照相则是采用 Leica M125 立体显微镜和 Digital Camera 6.0 数码成像系统,针对需要局部放大以展示细节的区域,如孢子囊的开裂线,维管束等进行拍照。但是照片难以完全展示标本的一些细节及高低关系,为此,采用显微镜绘图臂手工绘图,并将手绘图扫描至电脑,运用 CorelDRAW 软件清绘,实现图片电子化。最后,基于标本和拍摄的照片,本文使用 Image J 软件对植物化石的各种形态学特征进行度量,如孢子囊的高宽,囊柄的长宽,孢子囊开裂线的宽度等。

3 系统古生物学

工蕨纲 Class Zosterophyllopsida Banks, 1975

工蕨目 Order Zosterophyllales Banks, 1968

工蕨科 Family Zosterophyllaceae Banks, 1968

工蕨属 Genus *Zosterophyllum* Penhallow, 1892

模式种 *Zosterophyllum myretonianum* Penhallow, 1892

米尔顿工蕨(比较种) *Zosterophyllum cf. myretonianum* Penhallow, 1892

(插图 1-A—F, 2)

1977 *Zosterophyllum longhuashanense* Li and Cai, 李星学、蔡重阳, 17 页,图版 II, 图 21, 21a;插图 1。

标本 PB6463(模式标本),保存在中国科学院南京地质古生物研究所。

描述 标本为一段孢子囊穗,无顶端和基部,保存长度 35 mm,最宽处达 7 mm。孢子囊穗由中央

穗轴和疏松螺旋排列的孢子囊构成。中央穗轴宽约 1.8 mm,穗轴中部可见一条宽约 0.3 mm 纵向延伸的深色条带,可能是穗轴内部维管束的痕迹。可见较细的条带从中央条带处分出,延伸向孢子囊(插图 1-F, 2)。

孢子囊穗上可识别出至少 12 个孢子囊。标本中未见正面观的孢子囊,但是不同孢子囊着生的位置并不相同(插图 1-A, 2)。现将一些具有代表性的孢子囊着生情况描述如下。本文描述中,上下关系指的是孢子囊着生位置的上下(参见插图 1),而高和低则是指在显微镜下所看到的孢子囊相对于观察者的近和远,孢子囊高,意味着在显微镜下观察时,孢子囊可能位于穗轴上接近观察者的一侧。

孢子囊 3、5、9 都是侧面着生的,但着生的角度及囊柄的角度都不同。孢子囊 12 的囊柄位于穗轴的中间(插图 1-E),低处的穗轴发生断裂,与孢子囊 12 所在平面存在高度差。孢子囊 11 与穗轴连接处断开,其比穗轴所在平面更低。尽管我们观察的是压型化石标本,但是依然可以识别出高低不同的孢子囊,这表明孢子囊在穗轴上呈螺旋排列。

孢子囊侧面观呈近三角形或椭圆形,高 2.2—3.1 mm(均值 2.7, $n=8$),侧面宽 1.3—2.8 mm(均值 1.9, $n=7$)。靠近囊穗上部的孢子囊顶端比较圆润(插图 2,孢子囊 11 和 12),接近囊穗下部的孢子囊顶端具尖角(插图 1-C, D, F)。从现有标本看,孢子囊间隔由囊穗基部向顶端似有变小的趋势。孢子囊基部迅速狭缩成一宽约 0.3—0.8 mm(均值 0.6, $n=7$),长约 1.3—2.7 mm(均值 1.9, $n=7$)的囊柄。囊柄先以较小角度(30° — 60°)自穗轴伸出,稍向外延伸后急弯向上,呈 C 型,使孢子囊几乎平行于穗轴生长。囊柄与孢子囊接合处不清楚。

侧面观孢子囊近轴一侧可见开裂线(插图 1-B, F),开裂线沿凸起的边缘延伸,宽约 0.1 mm,可能延伸至孢子囊的基部。沿开裂线,孢子囊被分为几乎相等的两瓣。有的孢子囊侧面观可保存为开裂的两瓣,两瓣尽管被压在一起,但是通过显微观察,仍可识别出高低不同层面的两瓣(孢子囊 4,插图 1-C, D)。这也表明孢子囊开裂成两个相等的瓣。

产地层位 云南沾益县龙华山,下泥盆统布拉格阶—埃姆斯阶徐家冲组。

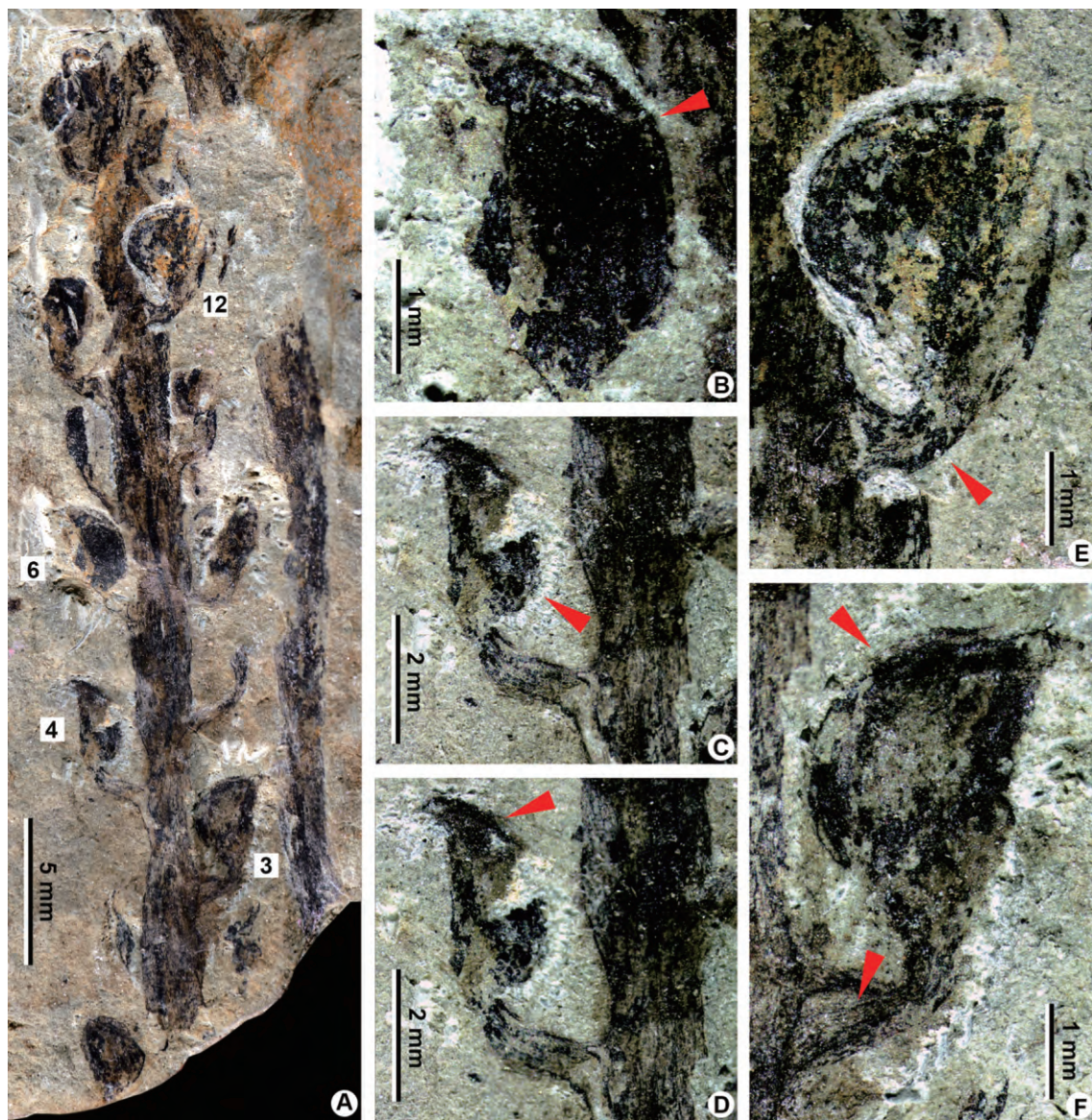


插图 1 云南沾益下泥盆统徐家冲组的米尔顿工蕨(比较种)

Zosterophyllum cf. *myretonianum* from the Lower Devonian Xujiachong Formation of Zhanyi, Yunnan Province.

A. *Zosterophyllum longhuashanense* 的模式标本(见李星学、蔡重阳, 1977, 图版 2, 图 21, 21a, 插图 1), 框中数字为孢子囊编号, PB6463。B. 图 A 中孢子囊 6 的放大图, 箭头所示部分为孢子囊的开裂线。C, D. 图 A 中孢子囊 4 针对不同对焦区域的放大图, 图 C 箭头指示孢子囊较低瓣(远离观察者)清晰, 图 D 箭头指示孢子囊较高瓣(靠近观察者)清晰, 示孢子囊 4 尽管为侧面保存, 两瓣被压在一起, 但是依然可以识别出来。E. 孢子囊 12 的放大图, 箭头所示为弯曲的囊柄, 着生于穗轴中间层。F. 孢子囊 3 的放大图, 上部箭头所示为孢子囊的开裂线, 下部箭头所示为连接孢子囊与穗轴的维管束。

A. The type specimen of *Zosterophyllum longhuashanense*, PB6463 (see Plate 2, Figure 21, 21a; Text-figure 1; Li and Cai, 1977). Numbers indicate individual sporangia. B. Enlargement of the sporangium 6 in fig. 1-A, note the dehiscence line (arrow). C, D. Enlargement of the sporangium 4 in fig. 1-A. The lower valve (farther to the observer) is focused in fig. 1-C, while the upper valve (closer to the observer) is focused in fig. 1-D. E. Enlargement of the sporangium 12 in fig. 1-A, note the sporangium stalk is curving and born at the central position of the spike axis (arrow). F. Enlargement of the sporangium 3, note the dehiscence line is distinct (the upper arrow) and the vascular strand is shown connecting sporangium with the spike axis (the lower arrow).

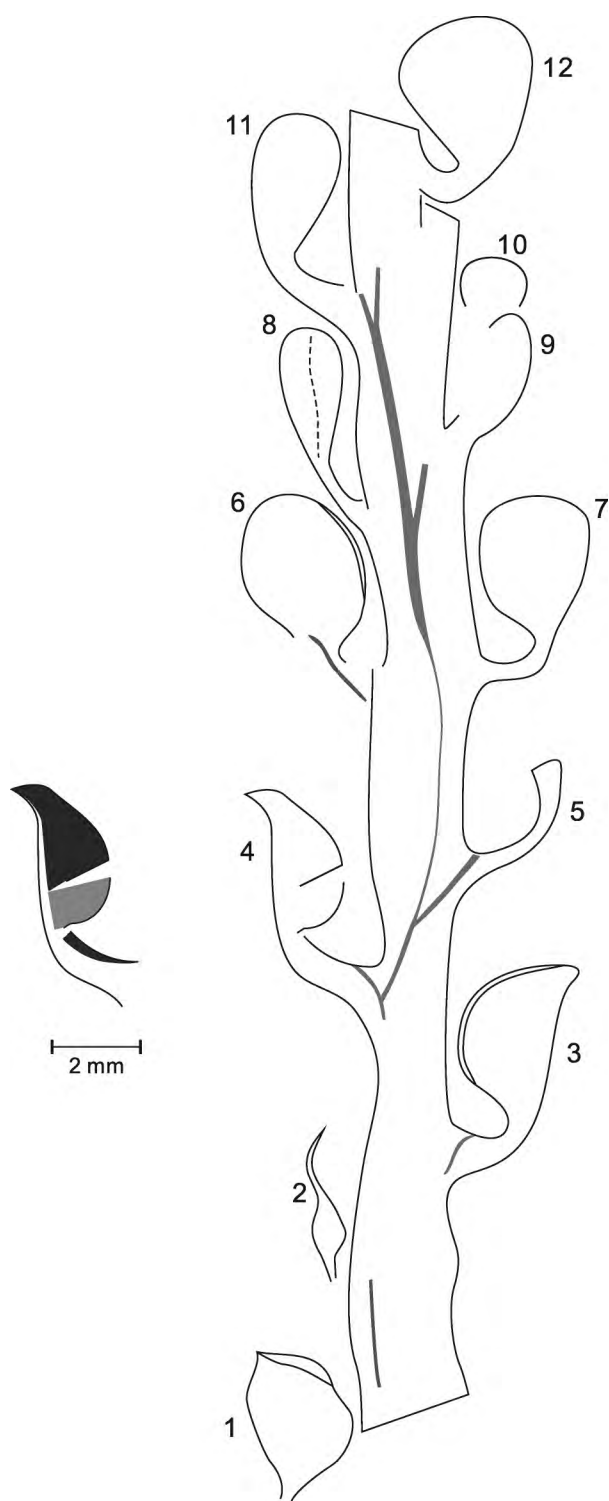


插图2 米尔顿工蕨(比较种)孢子囊穗线条图,根据插图1-A标本绘制。标本中的维管束以灰色区域表示。左侧为孢子囊4,相对于观察者而言,深色区域高于浅色区域。

Line-drawing of the spike of *Zosterophyllum* cf. *myretonianum*, based on the specimen illustrated in Text-figure 1-A. Vascular strand of the spike is drawn in dark. The sporangium 4 is also shown in the left figure, and the black valve is higher than the grey one to the observer.

4 讨论

本文所观察的标本具有茎轴侧面螺旋着生的孢子囊,未见有孢子叶,该孢子囊穗完全属于工蕨类植物,应归为工蕨属(*Zosterophyllum*) (Edwards, 1975; Gensel and Andrews, 1984; Hao *et al.*, 2007)。工蕨属各种之间的对比主要从以下四个方面进行:1)孢子囊及孢子囊穗的大小;2)孢子囊在囊穗上的着生方式;3)孢子囊嵌入主轴的类型;4)孢子囊的形状(Edwards, 1969a, 1975)。

根据孢子囊在孢子囊穗上的着生方式,通常将工蕨属分为两个亚属,即工蕨亚属(*Zosterophyllum*)与扁工蕨亚属(*Platyzosterophyllum*),前者孢子囊在穗轴上呈螺旋排列,后者呈两行状排列(Lang, 1927; Croft and Lang, 1942; Hueber, 1972)。目前只有 *Z. llanoveranum* (Croft and Lang, 1942; Edwards, 1969b), *Z. fertile* (Edwards, 1969a), *Z. divaricatum* (Gensel, 1982) 和 *Z. spectabile* (Schweitzer, 1979) 这四种归为扁工蕨亚属。而 Gerrienne (1988)、Hao 等 (2007)、Edwards 等 (2015) 均认为 *Z. longhuashanense* 孢子囊呈两行状排列,应归为扁工蕨亚属。然而,本文对 *Z. longhuashanense* 模式标本的重新观察表明,其孢子囊的着生方式为螺旋着生,其仍应归为工蕨亚属。

本文研究的标本仅保存了一段孢子囊穗,无原位孢子保存,孢子囊属于中等大小(高 2.2—3.1 mm, 宽 1.3—2.8 mm),该宽度依据孢子囊侧面观度量所得,可能会比实际值偏小。孢子囊高度与本文标本近似的有 *Z. tenerum* (Hao and Xue, 2013) 与 *Z. australianum* (Lang and Cookson, 1931), 但 *Z. tenerum* 的孢子囊间隔大且与穗轴重合者甚多,本文标本未见孢子囊与穗轴重合的现象,故造成两行排列的假象。*Z. australianum* 的孢子囊排列成紧密的囊穗,不同于本文标本中呈现出的稀疏排列。

本文标本的孢子囊皆为侧视,为近三角形或椭圆形,这种形状的孢子囊也见于 *Z. fertile* (Edwards, 1969a, 插图 1-d; Edwards, 1972, 插图 1-c), *Z. myretonianum* (Edwards, 1975, 插图 1-c, 1-d) 与 *Z. sichuanense* (耿宝印, 1992)。但是 *Z. fertile* 的孢子囊排列紧密,呈两行状排列,侧视有明显的基瓣,这些与本文标本不同。*Z. sichuanense* 的孢子囊高(1.7—2.3 mm)远小于本文标本,且囊柄较长(2.7—3.9 mm),但是其囊柄的形态与本文标本近

似,都自穗轴向上斜出后弧形弯曲,与孢子囊近轴边构成“C”型。关于 *Z. sichuanense*, Edwards 等(2015)提及正在开展重新研究,可能会将它修订到别的属。

本文标本茎轴表面有宽约 0.3 mm 的中央维管束,可见较细的维管束从其中分出,延伸向孢子囊柄,在工蕨属中,这种情况也发现于 *Z. sichuanense* (耿宝印,1992)和 *Z. rhenanum*(Kräusel and Weyland,1935)中。另外,曲靖徐家冲组的早期石松类 *Drepanophycus qujingensis* 的繁殖部分茎轴上也可见呈条带状的维管束(Li and Edwards,1995)。这些类似的形态学特征可能暗示它们在内部结构上的相似性。

工蕨属的模式种 *Z. myretonianum* 由 Penhallow 在 1892 年根据苏格兰早泥盆世地层中的标本建立。最初的描述中,Penhallow 将工蕨属定义为:有匍匐茎的水生植物,呈现小角度的二歧分枝和线型叶。孢子囊椭圆形,短柄,无苞片,形成疏松排列的孢子囊穗。而关于模式种 *Z. myretonianum* 只是提及其茎轴宽 2 mm,叶线宽 1.5 mm,叶脉不明显。孢子囊宽 2.5—4 mm,圆形或椭圆形(Penhallow,1892)。此后,根据产自苏格兰模式标本产地附近的新标本,Lang(1927)、Lele 和 Walton(1961)及 Walton(1964)对 *Z. myretonianum* 的近地及地下部分,分枝模式等进行了详细研究,发现 *Z. myretonianum* 呈现簇状,H 型分枝常见,尤其常见于植物的基部区域,形成匍匐茎或根状茎。分枝多发生于基部区域,地上营养部分的茎轴没有发生分枝。Lang 和 Cookson(1931)及 Edwards(1975)对 *Z.*

myretonianum 繁殖部分的研究发现:*Z. myretonianum* 的孢子囊螺旋或两行状排列,形成紧密或疏松的孢子囊穗。孢子囊从囊穗的基部到顶部形状和大小都有变化,顶部的孢子囊小且为近圆形,基部的孢子囊较大且为卵形,正面观呈肾形。孢子囊沿凸起的边缘开裂为相等的两瓣。Allen(1980)对 *Z. myretonianum* 的孢子形态进行了简述,孢子外壁光滑,直径 25—35 μm 。关于 *Z. myretonianum* 茎轴的解剖结构,目前并没有研究。

Z. myretonianum 在中国最早发现于云南曲靖翠峰山桂家屯组中(李星学、蔡重阳,1977,见图版 I,图 1—7,8,8a;插图 4),一共有八块标本,其中六块为 H 型分枝或二歧式分枝(图版 I,图 1—4,6,7,文献同上),枝轴宽度为 2.5—4 mm,个别可见清晰的中央维管束痕,还有两块为保存不完全的孢子囊穗(图版 I,图 5,8),孢子囊穗由孢子囊螺旋疏松排列而成,穗轴宽约 0.9 mm。孢子囊正视呈肾形或宽楔形,长 1.8 mm,最宽处约 1.6 mm,末端最厚,发育切向裂缝。囊柄长 1.5—2 mm,宽 0.2—0.3 mm,以约 60°伸出穗轴,然后外弯向上,使孢子囊与囊穗近于平行(表 I)。四川江油雁门坝地区平驿铺组中也发现有 *Z. myretonianum*(耿宝印,1992,图版 1,图 1—9),一共有两块标本,仅见植物的直立部分,茎轴长至少 77.3 mm,宽 0.9—1.8 mm。孢子囊螺旋疏松排列成囊穗,形状为圆至广椭圆形或肾形,宽 2—5 mm,高 2—3 mm,沿远端开裂成对等的两瓣,囊柄以 30°—40°自穗轴伸出,长 1.2—3.0 mm,宽 0.5—0.8 mm,孢子赤道轮廓圆至椭圆形,直径 15—42 μm ,三射线简单,外壁光滑。

表 I 不同产地的米尔顿工蕨度量对比表。单位均为 mm。

Measurements of *Zosterophyllum myretonianum* from different localities. All units in mm.

种名	产地	时期	茎轴	孢子囊						作者
			宽度	形状(正面观及侧面观)	高	宽	囊柄长度	囊柄宽度	着生角度	
<i>Zosterophyllum myretonianum</i>	苏格兰	Lochkovian—Pragian	0.9—3.0	肾形/近三角形	1.7—4.2	2.7—5.0	0.9—2.5	—	—	Edwards, 1975
	中国云南	Pragian	—	肾形或宽楔形/无	1.8	1.6	1.5—2.0	0.2—0.3	60°	李星学、蔡重阳, 1977
	中国四川	Pragian	0.9—1.8	圆至广椭圆形或肾形/无	2.0—3.0	2.0—5.0	1.2—3.0	0.5—0.8	30°—40°	耿宝印, 1992
<i>Zosterophyllum cf. myretonianum</i>	中国云南	Pragian—Emsian	1.8	无/近三角形或卵形	2.2—3.1	1.3—2.8	1.3—2.7	0.3—0.8	30°—60°	本文

本文标本与苏格兰、四川、云南等地的 *Z. myretonianum* 标本无论是形态特征还是度量数据方面(表 I)都较相似。本文标本的孢子囊侧面观与苏格

兰的标本孢子囊侧面观很相似,都呈现近三角形,且孢子囊皆沿边缘开裂为相等的两瓣(Edwards, 1975)。它们的时代均为早泥盆世。苏格兰 *Z. my-*

retonianum 地质时代从 Lochkovian 期至 Pragian 期,我国四川、云南等地 *Z. myretonianum* 地质时代是 Pragian 期,而本文标本的地质时代为 Pragian—Emsian 期。从测量数据来看,本文标本所具有的形态学度量数据均在 *Z. myretonianum* 的形态学范围内(表 I)。由于本文标本中孢子囊未见正面观,其宽度测量皆为侧面观的数据,应小于实际宽度,故不与其他地区标本的孢子囊宽度数据作比较。本文标本的孢子囊着生于穗轴的角度为 30° — 60° ,发现于四川的标本着生角度为 30° — 40° ,而云南的标本为 60° ,这一结果也基本相符。由于本文标本仅有一块,所体现的形态学特征不足以与 *Z. myretonianum* 的多种形态学特征进行对比,因此我们将本文的标本修订为 *Zosterophyllum* cf. *myretonianum*。

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NEW OBSERVATIONS ON THE SPECIMEN ATTRIBUTED TO *ZOSTEROPHYLLUM LONGHUASHANENSE* FROM THE LOWER DEVONIAN OF QUJING, YUNNAN, SOUTHWESTERN CHINA

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Key words *Zosterophyllum*, Devonian, Yunnan

Abstract

Zosterophyllum longhuashanense was established from the Lower Devonian of Qujing, Yunnan Province (Li and Cai, 1977). Its establishment was based on only one specimen that was not well illustrated. Some authors (Gerrienne, 1988; Hao *et al.*, 2007; Edwards *et al.*, 2015) thought that the sporangia of *Z. longhuashanense* were two-rowed arranged, rather than being spirally arranged as originally described by Li and Cai (1977). The present study re-

observes the type specimen of *Z. longhuashanense* and indicates a zosterophyll spike with spirally arranged sporangia. According to the morphological features, the specimen previously attributed to *Z. longhuashanense* is transferred to *Zosterophyllum* cf. *myretonianum*.

Class Zosterophyllopsida Banks, 1975

Order Zosterophyllales Banks, 1968

Family Zosterophyllaceae Banks, 1968

Genus *Zosterophyllum* Penhallow, 1892

Type species *Zosterophyllum myretonianum* Penhallow, 1892

***Zosterophyllum* cf. *myretonianum* Penhallow, 1892**

(Text-figs. 1-A—F, 2)

1977 *Zosterophyllum longhuashanense*, Li and Cai, pp 17, pl. II, fig. 21, 21a; Text-fig. 1.

Specimen PB6463 (original Type specimen), deposited at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Description A part of zosterophyll spike, without apical or basal part, is preserved up to 35 mm long and 7 mm in maximum width. The spike consists of an axis with sporangia loosely and spirally arranged. The spike axis is about 1.8 mm wide. A vertical ribbon-like band is seen on the surface of the axis, which might represent the vascular strand inside the axis. More slender bands are seen to depart from the central one, extending to individual sporangia (Text-figs. 1-F, 2).

At least twelve sporangia are recognized from the spike. Sporangia are arranged in lateral or sub-lateral positions relative to the central axis, none is seen in face view (Text-figs. 1-A, 2). In the description of the sporangium, the up or down refers to their positions shown in the text-figure. The high or low refers to the sporangial positions relative to the observer. The higher sporangium means that the sporangium is closer to the observer under microscope.

The sporangia 3, 5, 9 are directly attached on the surface of the axis, but the attached angles of stalks vary. The sporangium 12 attached to the middle part of the spike axis (Text-fig. 1-E) can be seen by the broken axis in the lower position. The sporangium 11 breaks from the axis in the basal

portion and can be seen lower than the axis. These sporangia, though being preserved as compression, can be recognized helically arranged on the spike axis.

The sporangium is roughly triangular or elliptical shaped in lateral view, 2.2—3.1 mm in height ($\bar{X}=2.7$, $n=8$), 1.3—2.8 mm in lateral width ($\bar{X}=1.9$, $n=7$). The upper sporangia, probably near the apex of spike, appear subcircular (11, 12 in text-fig. 2), whilst the lower ones have acuminate apices (text-fig. 1-C, D, F). The distance between neighboring sporangia becomes wider from the up spike to the down. Sporangium stalk is 0.3—0.8 mm in width ($\bar{X}=0.6$, $n=7$) and 1.3—2.7 mm in length ($\bar{X}=1.9$, $n=7$). The stalk departs from the axis in narrow angles (30° — 60°), with a slight extending then curve adaxially as C-shaped. The sporangium appears to grow paralleled with the spike axis. The junction between the stalk and the sporangium is not clear.

The sporangium dehiscence line is seen from the adaxial side of the sporangium, up to 0.1 mm wide along the distal margin (text-fig. 1-B, F). The sporangium dehisces into two equal valves. Two dehisced but still connected valves are seen from the sporangium 4 (text-fig. 1-C, D). The two valves are overlapped but are seen in different heights to the observer.

Locality and horizon Qujing, Yunnan. Xujiachong Formation (Pragian—Emsian).