

贵州凤冈早志留世孢子组合的发现 及其古植物学意义^{*}

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提 要 系统描述贵州凤冈早志留世的孢子 5 属 12 种(类型), 其中包括 1 新种。根据其组合特征, 确认其时代为 Llandoveryan 晚期。通过对三缝孢的性状分析, 认为在早志留世 Llandoveryan 晚期已确有维管植物的存在。

关键词 孢子组合 维管植物起源 Llandoveryan 晚期 贵州凤冈

1 前言

维管植物的起源和早期演化长期以来是古生物学界最感兴趣的焦点问题之一。解决这个问题当然首先有赖于有关植物大化石的发现, 但作为植物重要器官的分散孢子在这方面也有着不可忽视的潜在的重要意义。30 多年来, 国外陆续在志留系发现的孢子组合已引起古植物学家的重视。我国志留纪的孢子过去发现甚少, 仅高联达(Gao, 1981)报道了贵州独山翁项组所产的孢子 *Leiotriletes*, *Retusotriletes*, *Apiculiretusispora* 和 *Ambitisporites*, 其时代为早志留世, 可惜未予描述和展示图版; 方宗杰等(1994)报道了云南曲靖晚志留世玉龙寺组的孢子, 称为 *Apiculiretusispora spicula*-*Emphanisporites negetus* 组合; 高联达(Gao, 1981), 蔡重阳等(Cai *et al.*, 1993)先后报道了新疆准噶尔盆地晚志留世乌吐布拉克组的孢子, 包括 *Ambitisporites avitus*, *A. dilutus*, *Archaeozonotriletes chulus* var. *nanus*, *Synorisporites libycus*, *Retusotriletes warringtonii*。

贵州凤冈硐卡拉(插图 1)的早志留世韩家店组以产 *Pinnatiramosus qianensis* Geng 植物化石而闻名于世。由于 *P. qianensis* 具有复杂的内部结构, 它的产出地层的时代被一些古植物学者(Edwards, 1990)所怀疑。1991 年 12 月, 我们对产有 *P. qianensis* 的地层进行了生物地层工作, 系统地采集了动物化石和微体植物样品, 在 *P. qianensis* 的产出层位之下的地层中分析出了孢子。经研究, 共计 5 属 12 种。根据其组合特征, 时代为 Llandoveryan 晚期, 为 *P. qianensis* 的时代确定提供了依据, 同时为我国早志留世孢子组合的研究和全球性对比提供了材料。

本文涉及的几丁虫、腕足类、双壳类分别由耿良玉、戎嘉余、方宗杰鉴定。笔者在野外工作中得到蔡重阳、方宗杰和贵州地质调查所张吉惠等的帮助, 在此一并表示感谢。

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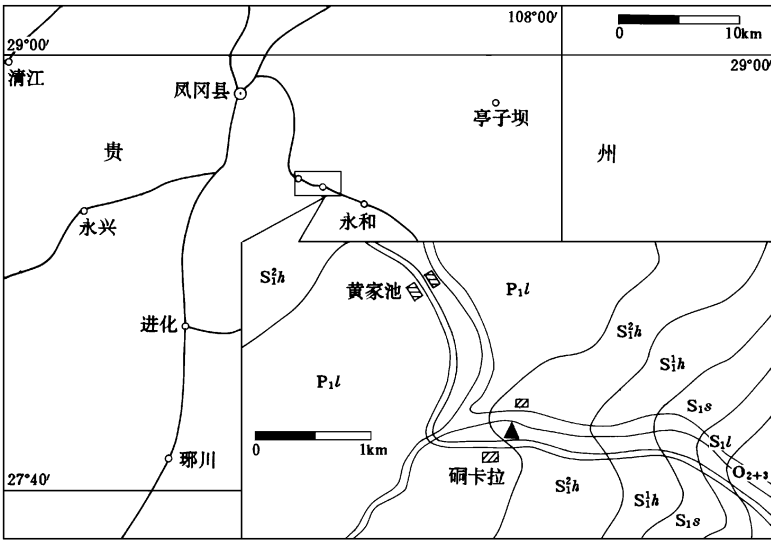


插图 1 贵州凤冈洞卡拉地理及地质略图
Geographical locality and geological map of the Dongkala Village,
Fenggang County, Guizhou

2 地层剖面

贵州凤冈洞卡拉早志留世地层自下而上分为龙马溪组、石牛栏组和韩家店组，现仅就与本文相关的韩家店组上部的地层剖面自上而下简述如下(插图 2)：

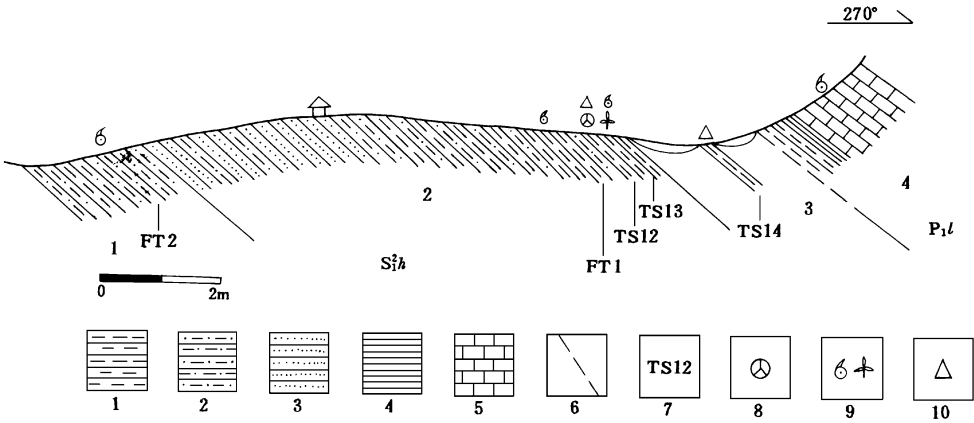


插图 2 贵州凤冈洞卡拉韩家店组上部地层剖面图

Stratigraphical section of the upper member of Hanjiadian Formation at Dongkala Village,
Fenggang County, Guizhou

- 1. 泥岩 (mudstone); 2. 泥质粉砂岩 (argillaceous siltstone); 3. 粉砂岩 (siltstone); 4. 页岩 (shale); 5. 灰岩 (lime-stone); 6. 假整合 (disconformity); 7. 采集号 (the number of samples); 8. 孢子 (spores); 9. 动、植物化石 (fossils of animal and plant); 10. 几丁虫 (Chintinzoa)。

下二叠统 梁山组(P₁l)

4. 下部灰白色薄层粘土岩和黑色碳质页岩, 含植物碎片; 上部灰、深灰色的微粒灰岩夹黑色泥质灰岩, 产 *Nakinella* sp., *Schubertella* sp., *Ozawainella* sp. 等。

——假整合——

下志留统 韩家店组上部(S₁^h)

3. 黄绿色泥岩, 大部被掩盖, 中部产几丁虫(TS₁₄, 样品号): *Eisenackitina daozenensis*; *Ancyrochitina brevicollis*; *Conochitina* sp. 1.5 m
2. 下部黄绿色含云母粉砂岩, 上部蓝灰色泥岩夹黄绿色泥岩。上部产腕足类(FT₁, 样品号): *Nalivkinia* sp., *Nucleospira pulchra*, *Protomegastrophia*? sp., *Lingula*? sp.; 双壳类(FT₁): *Cleionychia quadratus*; 几丁虫(TS₁₂): *Eisenackitina daozenensis*, *Ancyrochitina brevicollis*, *Conochitina* sp.; 植物(TS₁₃): *Pinnatiramosus qianensis*; 孢子(TS₁₂): *Ambitisporites avitus* Hoffmeister, *A. dilutus* (Hoffmeister) Richardson et Lister, *A. cf. dilutus* (Hoffmeister) Richardson et Lister, *Retusotriletes warringtonii* Richardson et Lister, *R. cf. warringtonii* Richardson et Lister, *R. cf. trianglatus* (Streel) Streel, *R. minor* Kedo, *R. cf. abundo* Rodriguez, *Apiculiretusispora spicula* Richardson et Lister, *Ap. sparsa* sp. nov., *Leiotriletes* sp., *Punctatisporites* sp. 此外还有四分体、疑源类和管胞碎片。5.2 m
1. 黄绿色含云母粉砂质泥岩夹蓝灰色泥岩。产腕足类(FT₂): *Nalivkinia* sp., *Nucleospira pulchra*, *Protomegastrophia*? sp., *Lingula*? sp.; 双壳类(FT₂): *Parallelodon cf. cybele*, *Parallelodon* sp., *Leptodesma* (*Leptodesma*) sp., *Cleionychia quadratus*。

蔡重阳等(Cai *et al.*, 1996) 根据这段地层所产的几丁虫、腕足类和双壳类, 确定其时代为 Llandoveryan 晚期, 相当于 Telychian。

3 组合特征及时代讨论

贵州凤冈早志留世的孢子组合共计 5 属 12 种(类型), 它们是: *Ambitisporites avitus*, *A. dilutus*, *A. cf. dilutus*, *Retusotriletes warringtonii*, *R. cf. warringtonii*, *R. cf. trianglatus*, *R. minor*, *R. cf. abundo*, *Apiculiretusispora spicula*, *Ap. sparsa* sp. nov., *Leiotriletes* sp., *Punctatisporites* sp.。本组合具有如下特征:

1). 具有类弓形脊的 *Ambitisporites* 是组合的主要属, 约占组合的 50%, 以具唇的 *A. cf. dilutus* 为主, *A. avitus* 和 *A. dilutus* 含量相对稍低。

2). 具有弓形脊的三缝孢十分发育, 其中以 *Retusotriletes* 最为丰富, 占组合的 40% 左右, 重要的是出现了 *Apiculiretusispora*, 此属已知最早出现于 Ludlowian 阶下部(Richardson and Lister, 1969)。Richardson 和 Edwards(1989)所列孢子演化形态事件中(表 I), 具刺弓形脊孢出现在第Ⅳ带的底部, 根据本文孢子组合产出地层的时代结论, 应改在第Ⅲ带的底部。

3). 与国外同期孢子组合相比, 分异度相对较高(表 II)。在利比亚、西南威尔士和美国的 Llandoveryan 晚期的孢子组合中多以 *Ambitisporites* 为主, 属种单一, 个体数量较少, 出现较少的 *Retusotriletes*, 而贵州凤冈的孢子组合属种较丰富(5 属 12 种)。

Hoffmeister(1959)首次从利比亚早志留世早期(Llandoveryan 期中期)地层中发现两种孢子 *Ambitisporites avitus* 和 *A. dilutus*, 引起了古植物学界的广泛注意。嗣后, 早志留世早期(Llandoveryan)的三缝孢先后在世界许多地区陆续发现。北美弗吉尼亚(Virginia)的下 Massamivtten 砂岩(Pratt *et al.*, 1978), 宾夕法尼亚(Pennsylvania)的 Tuscarora 组(Strother

and Traverse, 1978; Johnson, 1985), 纽约的 Medina 群 (Miller and Eames, 1982), 时代均为早志留世早期 (Llandoveryan 期早期), 产丰富的疑源类、四分体和二分体以及少许三缝孢, 以 *Ambitisporites* sp. 为主。Burgess (1991) 研究的西南威尔士早志留世早期 (Aeronian 晚期—Telychian) 微体植物, 大都以四分体为主, 只有 *Ambitisporites dilutus*, ? *A. vavrdovii* 等少许三缝孢。

Richardson 和 Lister (1969) 最早研究了英格兰和南威尔士早—晚志留世 (Wenlockian—Ludlowian) 的孢子组合, 包括 *Ambitisporites dilutus*, *A. cf. dilutus*, *A. cf. avitus*, *Retusotrilletes warringtonii*, *Archaeozonotrilletes chulus* var. *chulus*, *Ar. chulus* var. *nanus*, *Ar. chulus* var. *inframurinus*, *Ar. cf. diwellomedian*, cf. *Synorisporites verrucatus*, cf. *S. downtonensis*, cf. *Streelispota granulata*, *Apiculiretusispora synorea*, *Apiculiretusispora* sp. C—D。Richardson 和 Ioannides (1973) 研究了利比亚早—晚志留世 (Wenlockian 晚期—Ludlowian 晚期) 的孢子组合, 其分异度较 Hoffmeister (1959) 报道的早志留世早期 (Llandoveryan 中期) 孢子组合高得多, 包括 *Ambitisporites dilutus*, *A. avitus*, *Retusotrilletes warringtonii*, *R. cf. warringtonii*, *R. minor*, *Archaeozonotrilletes chulus* var. *chulus*, *Ar. chulus* var. *nanus*, *Emphanisporites cf. protophanus*, cf. *Synorisporites verrucatus*, *S. cf. verrucatus*。Smith (1975) 报道的爱尔兰早志留世晚期 (Wenlockian 早期) 地层中的孢子, 仅见 *Ambitisporites* sp.。Burgess 和 Richardson (1991) 报道的英格兰早志留世晚期 (Wenlockian) 的微体植物, 据对疑源类、四分体和三缝孢的研究, 可分早、晚期, 早期三缝孢有 *Ambitisporites avitus*, *A. dilutus*, *Archaeozonotrilletes chulus* var. *chulus*, *Ar. chulus* var. *nanus*; 晚期的孢子除早期的分子外, 还出现了 *Synorisporites cf. libycus*, *Emphanisporites cf. protophanus*。Wellman (1993) 报道的苏格兰早—晚志留世 (Wenlockian 晚期—Ludlowian 早期) 的微体植物, 以四分体为主, 含有较丰富的三缝孢, 包括 *Ambitisporites avitus*, *A. dilutus*, *Archaeozonotrilletes chulus*, *Chelinospora*? sp., *Cymbosporites* sp. A。

根据多年来积累的孢子化石资料, Richardson 和 McGregor (1986), Richardson 和 Edwards (1989) 将晚奥陶世至志留纪的孢子组合划分为若干组合带, 其中早志留世包括 4 个组合带: III. *murmsattennuata-murusdensa*, IV. *avitus-dilutus*, V. *chulus-nanus*, VI. cf. *protophanus*-cf. *verrucatus*。其中第 III 组合带几乎均由四分体和二分体组成, 三缝孢很少, 时限分布从 Ashgillian 至 Rhuddanian (Llandoveryan 早期), IV、V、VI 组合带是以三缝孢为主的组合带, 时限分布从 Aeronian 至 Gorstian 早期 (表 I)。

贵州凤冈孢子组合与上述早志留世的孢子组合带很难进行准确的对比, 主要是因为这些组合是根据少量已知组合建立的, 带有经验性, 即未必能反映当时孢子分异度的全部客观实际, 故同一时期地层在不同地区中分析出的孢子的分异度不一致, 目前全球范围内早志留 8 世孢子组合的对比还有困难是可以理解的。

本孢子组合具有 12 种, 其中有几种三缝孢显示了强烈的早志留世的色彩, 在世界早志留世孢子组合中均有分布, 如 *Ambitisporites avitus*, *A. dilutus*, *A. cf. dilutus*, *Retusotrilletes warringtonii*, *R. cf. warringtonii*。组合中另有几种特殊的三缝孢, 其中 *Retusotrilletes cf. triangulatus* 的三射线顶部具三角形的外壁增厚区, 以往已知最低层位是在 Gedinian 的底部, 但类似特征的三缝孢 (e.g. *Retusotrilletes cf. goensis* Lele et Streel) 出现在 Ludlowian 上部

(Richardson and Ioannides, 1973)。 *Apiculiretusispora* 在本组合中的出现, 使人感到诧异, 因为此属的已知最低层位是 Ludlowian 下部。如果仅根据此两种孢子的机械对比, 本组合的时代似乎应该为晚志留世早期, 但是一些晚志留世早期形态和纹饰更复杂的种在本组中均未见, 如 VI 组合带的具辐射脊和瘤纹饰的 “*Emphanisporites*” cf. *protophanus*, cf. *Synorisporites verrucatus* 和上覆组合带中纹饰更明显、更复杂的 *Synorisporites lybicus*, *Zonotrilletes*? *poicilomorphus*, “*Emphanisporites*” *protophanus*, *E. neglectus* 和 *Brochotrilletes*? sp. 等在本组合中都未见, 故其时代很可能早于 Wenlockian 晚期。

本组合肯定要比 IV 组合带下部年轻, 除出现一些更年轻分子外, 其分异度也比 Hoffmeister (1959) 报道的孢子组合要高得多 (12 种对 3 种); 另一方面, 由于缺乏 *Synorisporites* 和 “*Emphanisporites*” 之类形态、纹饰更复杂的分子, 显然要比第 VI 带老。所以根据孢子的特征, 本组合的时代定为 Llandoveryan 晚期至 Wenlockian 早期是可取的。

如前所述, Richardson 和 Edwards (1989) 划分的早志留世 Llandoveryan 至 Wenlockian 的孢子 IV、V 组合带, 其定义是不充分的。V 组合带不仅延伸时代长, 从晚 Llandoveryan 至晚 Wenlockian, 而且带中的典型属种也很少, 总共只列了 6 种 (或变种), 其中有 4 种见于 IV 组合带, 包括同一种的两个变种 *Ar. chulus* var. *chulus* 和 *Ar. chulus* var. *nanus*, 这两个变种的最低层位见于 Wenlockian 期, 也就是说 V 带没有 Llandoveryan 晚期的特征种, 表明在 Llandoveryan 晚期发现的三缝孢还很少。

本组合的同层、上覆和下伏层位中的几丁虫、腕足类和双壳类化石的研究结果表明, 其时代为 Llandoveryan 晚期 (Telychianian)。因此, 本组合应相当于 Richardson 和 Edwards (1989) 的第 IV 带上部或第 V 带的下部。

4 孢子对探讨维管植物起源的意义

孢子作为植物的生殖器官, 对探讨早期维管植物的起源可以提供重要的证据, 数十年来的研究已取得了不少重大进展。

三缝孢的最初出现是植物演化的重要生物学事件, 但它们对探讨维管植物起源的意义却有争议, 因为从三缝孢性状讲, 部分苔藓类产生三缝孢子, 原始的蕨类都是三缝孢产生者 (有些蕨类植物产单缝孢子, 部分种子蕨亦产三缝或单缝孢-前花粉, 但它们在地史上出现较晚)。正如 Banks (1975) 指出的: “我们没有简单的标准来区分苔藓类或维管植物的孢子”。所以对早志留世发现的三缝孢亦应持谨慎态度。

Gray (1985) 认为: 现代苔藓类中的三缝构形不像在现代维管隐花植物即蕨类中那样典型, 古今对比的现实主义模式的可行性表明, 三缝孢子代表维管植物的结论较少推测。这里要详细论证的一点是, 如果说不是所有志留纪的三缝孢子都是维管植物所产出, 则至少前泥盆纪的具弓形脊的三缝孢 (*Retusotrilletes*, *Apiculiretusispora* 和 *Ambitisporites*) 均产自于维管植物, 这可以从四个方面去证实。

1). 在现代苔藓类 900—1 000 属中, 三缝孢主要见于藓类的 Anthocerotales, Sphagnales 和某些 Andreaeales; 在苔类中, 仅 Marchantiales (Hepaticae), Pottiales, Funariales 和 Iso-bryales 产生少量三缝孢, 但未发现可靠的弓形脊或类似对应物 (参见 Boros *et al.*, 1975)。

2). 化石非维管植物的原位孢子中至今未见可靠的具弓形脊三缝孢的报道。这里必须

指出的是泥盆纪很奇特的植物 *Protosalvania*, 此属植物究竟属于裸藻或红藻、苔藓、真蕨, 还是具陆生植物特征的一种藻类, 至今争议很多(Talyor, 1988), 尚无定论, 而且它的原位孢子的形态特征, 亦不太清楚。Niklas 和 Phillips(1976)称 *Protosalvania* 的原位孢子直径大于 $200\mu\text{m}$ (通常为四孢体 *Tetraspores* 或 *Tetrahedral tetrads*), 形态上与 *Retusotriletes* 相似。Gray(1985)认为它是一个与 *Retusotriletes* 并不能真正对比的例外, Talyor(1988)认为它不具有三缝, 在形态上与某些裸藻或红藻的孢子十分相似。

3). 具弓形脊三缝孢广泛见于晚志留世一早泥盆世的早期维管植物的原位孢子中, 例如 *Cooksonia* 被认为是早期维管植物的代表, *Cooksonia pertonia* Lang 的原位孢子有 *Ambitisporites*, *Retusotriletes* 和 *Aneurospora*(Fanning *et al.*, 1988; Rogerson *et al.*, 1993); Lang(1937)认为 *Cooksonia* 的原位孢子为 *Retusotriletes* 型, 形态特征上十分相似于散生的 *R. warringtonii*。

Rhynia major 的原位孢子为具弓形脊的三缝孢(Kidston and Lang, 1917), *Renalia huebei* 的原位孢子为 *Apiculiretusispora*(Gensel, 1976), *Psilophyton dawsoni* 的原位孢子为 *Retusotriletes*(Banks *et al.*, 1975), *Psilophyton crenulatus* 的原位孢子为 *Apiculiretusispora*(Gensel, 1979)。

早泥盆世全世界广泛发育的工蕨类的原位孢子几乎均具有弓形脊, 如 *Zosterophyllum cf. fertile*, *Z. llanoveranum*, *Z. yunnanense*, *Discalis longistipa*, *Sawdonia ornata*, *Rebuchia ovata* 等的原位孢子均为 *Retusotriletes*(Edwards, 1969; 郝守刚, 1985; Fanning *et al.*, 1990)。 *Sawdonia acanthotheca* 的原位孢子的三射线顶区具增厚, 与 *Retusotriletes cf. triangulatus* 可以对比(Gensel, 1982)。

类似的例子可以举出很多, 正如 Fanning 等(1990)所言, 具弓形脊三缝孢与早期维管植物关系密切。

4). 从散生的孢子组合看, 具弓形脊的孢子在早志留世开始出现, 真正的高度分异和发展从 Siegenian 开始(Fanning *et al.*, 1990)。从早期维管植物的发展看, 最早的植物大化石在早志留世晚期(Wenlockian)已经发现, 如发现于爱尔兰的 *Cooksonia* 状孢子囊(Edwards, 1979), 在 Siegenian 维管植物的组成分子渐趋复杂, 其中不少类型演化趋势各不相同, 进入了一个分异辐射和大发育时期(李星学等, 1981)。由此可见, 具弓形脊三缝孢的发生、发展和分异与维管植物的发生、发展和分异基本上是平行的。

上述四个方面的证据表明了具弓形脊三缝孢子与早期维管植物的密切关系。即使对分散三缝孢子的植物亲缘关系持最谨慎态度的 Banks(1975)也认为: 虽然一般不能确定分散三缝孢从什么植物来的, 但其中有些是可以与有机连接的孢子囊内发现的原位孢子相比较的, ……且其相似程度如此之高, 不能归之于偶然的原因。对于贵州凤冈早志留世的 *Ambitisporites*, *Retusotriletes* 和 *Apiculiretusispora* 来说, Banks 之言也是完全适用的, 换句话说, 本组合中的具弓形脊的三缝孢极可能均产自维管植物, 如果其时代(Telychian)鉴定可靠, 那就意味着早志留世 Llandoveryan 晚期已确有维管植物的存在。这一观点的确立有助于将 *Pinnatiramosus qianensis* Geng 这一植物解释为维管植物。

此外, 要说明的是贵州凤冈早志留世孢子组合的分异度已经比较高, 近 10 余种具弓形脊三缝孢似乎不可能出自同一种植物, 也就是说, 在我国西南地区早志留世可能存有多种维

管植物。

5 属种描述^{*}

厚环环形弓脊孢 *Ambitisporites avitus* Hoffmeister

(图版 I, 图 5, 8)

- 1959 *Ambitisporites avitus* Hoffmeister, p. 332, pl. 1, figs. 1—8.
 1973 *Ambitisporites avitus*, Richardson and Ioannides, p. 277, pl. 5, figs. 1—8.
 1975 *Ambitisporites avitus*, Smith, pl. 1, figs. a—f.
 1986 *Ambitisporites avitus*, Richardson and McGregor, pl. 1, fig. 1.
 1993 *Ambitisporites avitus*, Wellman, p. 56, pl. 4, figs. 9—11.

赤道轮廓圆形—亚圆形, 大小 $43-67\mu\text{m}$ (测 4 粒), 三射线清楚, 简单, 直或稍弯曲, 伸达赤道环内缘。赤道部位加厚形成环, 在射线末端部位较厚, 一般为 $3.8-7.8\mu\text{m}$, 辐间区赤道环较窄, 一般为 $2.5-3.0\mu\text{m}$ 。外壁表面光滑, 未见褶皱。棕色。

比较 当前标本与产自利比亚早志留世的 *A. avitus* Hoffmeister (pl. 1, figs. 1—8) 在大小、形态、射线和赤道环的特征上基本一致。

薄环环形弓脊孢 *Ambitisporites dilutus* (Hoffmeister) Richardson et Lister

(图版 I, 图 4)

- 1959 *Punctatisporites?* *dilutus* Hoffmeister, p. 334, pl. 1, figs. 9—13.
 1969 *Ambitisporites dilutus* (Hoffmeister) Richardson et Lister, p. 229.
 1975 *Ambitisporites dilutus*, Richardson and Ioannides, p. 277, pl. 6, figs. 1—5.
 1986 *Ambitisporites dilutus*, Richardson and McGregor, pl. 1, fig. 2.
 1993 *Ambitisporites dilutus*, Wellman, p. 56, pl. 5, figs. 1, 2, 4.

赤道轮廓亚三角形, 三边凸出, 角部尖圆, 大小 $30-38\mu\text{m}$ (测 3 粒)。射线明显, 开裂, 未见唇, 伸达赤道环内沿。赤道部位加厚呈环, 间辐区宽 $1.0-2.0\mu\text{m}$, 射线末端宽 $2.0-2.5\mu\text{m}$ 。表面光滑或具细小颗粒, 直径 $\leq 0.5\mu\text{m}$ 。棕黄色。

比较 当前标本与产自利比亚早志留世的 *Punctatisporites?* *dilutus* Hoffmeister (p. 334, pl. 1, figs. 9—13) 在形态、射线、赤道环等特征上十分相似。Richardson 和 Lister (1969, p. 229) 以其具有赤道环而归于 *Ambitisporites*。当前标本与 *A. dilutus* 的特征一致, 当属同种。与 *A. avitus* Hoffmeister (p. 332, pl. 1, figs. 1—8) 相比, 它们的特征十分相近, 唯后者的赤道环明显, 且厚。

薄环环形弓脊孢 (比较种) *Ambitisporites cf. dilutus* (Hoffmeister) Richardson et Lister

(图版 I, 图 1—3)

- 1969 *Ambitisporites cf. dilutus* (Hoffmeister) Richardson et Lister, p. 229, pl. 40, figs. 3.

赤道轮廓圆形, 大小 $32-45\mu\text{m}$ (测 6 粒)。射线清楚, 直或微弯曲, 具唇, 宽 $1.0-2.0\mu\text{m}$, 伸达赤道环内沿。外壁在近极区较薄, 厚度小于 $1.0\mu\text{m}$, 赤道部位加厚呈环, 宽一般为 $3.0-6.0\mu\text{m}$, 射线末端赤道环略宽于辐间区。外壁表面光滑或具细小颗粒, 直径小于 $0.5\mu\text{m}$ 。

^{*} 因篇幅关系, 本文仅对组合中的主要孢子属种进行描述, 其他疑源类、管胞碎片等将另文发表。

μm 。棕色。

比较 当前标本,尤其是图版 I 图 2 的标本与 Richardson 和 Lister(1969)所定的 *Am-bitisporites cf. dilutus*(Hoffmeister)(p. 229, pl. 40, fig. 3)在形态、大小、射线和赤道环的特征上基本一致。与 *A. dilutus*(Hoffmeister)Richardson et Lister(1969)相比,后者的射线未见唇。与 *Archaeozonotriletes chulus*(Cramer)(Richardson and Lister, 1969, p. 234)相比,后者的近极区十分薄,而远极-赤道区的加厚十分明显。

瓦氏弓脊孢 *Retusotriletes warringtonii* Richardson et Lister

(图版 I, 图 12)

1969 *Retusotriletes warringtonii* Richardson et Lister, p. 216, pl. 37, figs. 7, 8.

1986 *Retusotriletes warringtonii*, Richardson and McGregor, pl. 1, figs. 3.

赤道轮廓三角形,三边凸出,角部浑圆或尖圆。大小 $38-42\mu\text{m}$ 。三射线清楚,直或微弯曲,具唇,宽 $1.2-2.8\mu\text{m}$,长约等于 $4/5-1R$ 。弓形脊明显,完全,多沿赤道延伸,宽小于 $1.0\mu\text{m}$ 。外壁厚 $1.0-2.0\mu\text{m}$,表面光滑。棕色。

比较 当前标本与产自大不列颠 Welsh Borderland 早志留世的 *Retusotriletes warringtonii*(Richardson and Lister, 1969, p. 216, pl. 37, figs. 7, 8)在形态、射线、弓形脊和外壁等特征上基本一致,唯后者的个体偏小($18-36\mu\text{m}$)。Richardson Ioannides(1973)描述此种时,认为个体大小在 $17-45\mu\text{m}$ 之间。

瓦氏弓脊孢(比较种) *Retusotriletes cf. warringtonii* Richardson et Lister

(图版 I, 图 13)

赤道轮廓三角形,三边凸出,角部浑圆。大小 $40-48\mu\text{m}$ (测 3 粒)。三射线清楚,微弯曲,具唇,宽 $1.0-1.4\mu\text{m}$,长近等于 $1R$ 。弓形脊明显,完全,沿赤道延伸,宽小于 $1.0\mu\text{m}$ 。外壁厚小于 $1.0\mu\text{m}$,有时可有微弱褶皱,表面光滑。深棕色。

比较 当前标本与产自大不列颠 Welsh Borderland 早志留世的 *Retusotriletes warringtonii*(Richardson and Lister, 1969, p. 216, pl. 3, figs. 7, 8)在大小、射线、弓形脊和外壁等特征方面较相似,但后者的个体较小($17-45\mu\text{m}$),射线的唇较厚($1-2\mu\text{m}$),外壁稍厚($1.5-2.0\mu\text{m}$),表面不具有褶皱,因此当前标本种的鉴定作了保留。

三角弓脊孢(比较种) *Retusotriletes cf. triangulatus*(Streel)Streel

(图版 I, 图 6, 7)

赤道轮廓亚圆形。大小 $46-61\mu\text{m}$ (测 6 粒)。三射线清楚,直,少许开裂,长约等于 $4/5-5/6R$,末端与弓形脊相连,弓形脊弱,不甚明显。接触区中心具有一个三角形的加厚区,分布于射线长 $1/3$ 的区域内。外壁厚 $1.0\mu\text{m}$ 左右,或具少许褶皱,表面光滑,有的表面具有不明显的颗粒,直径小于 $1.0\mu\text{m}$ 。棕色。

比较 当前标本与 Streel(1966)描述的 *Retusotriletes triangulatus* 在形态、射线和接触区的三角形加厚区等特征上相似,但后者的弓形脊发育,表面的外壁未见褶皱。与 *Retusotriletes cf. goensis* Lele et Streel(Richardson and Ioannides, 1973, p. 271, pl. 1, figs. 1-6)相比,后者的个体相对较小(描述为 $27-50\mu\text{m}$),射线弯曲,接触区的加厚呈三角形或不规则

形态。

R. cf. triangulatus 的相似标本最早见于 Geddinnian, 而本文的标本产于 Llandoveryan 晚期。

细小弓脊孢 *Retusotriletes minor* Kedo

(图版 I, 图 11)

1963 *Retusotriletes minor* Kedo, p. 35, pl. I, fig. 27.

1973 *Retusotriletes minor* Kedo, Richardson and Ioannides, p. 270, pl. 1, figs. 17–19.

赤道轮廓圆形。大小 $35-38\mu\text{m}$ (测 2 粒)。三射线清楚, 简单, 直, 近极区的中间射线常开裂, 长约 $4/5R$, 末端与弓形脊相连。弓形脊完全, 宽小于 $1.0\mu\text{m}$ 。外壁厚 $1.0-1.5\mu\text{m}$, 表面光滑。棕色。

比较 当前标本与 Richardson 和 Ioannides (1973) 描述的产自利比亚志留纪的 *Retusotriletes minor* Kedo 在形态、大小、射线、弓形脊和外壁特征上基本一致, 唯后者的个体偏小 ($17-36\mu\text{m}$)。与 *R. warringtonii* (Richardson and Lister, 1969, p. 271, pl. 39, figs. 7, 8) 相比, 后者的赤道轮廓呈三角形, 射线具有发达的唇。

宽弓脊孢(比较种) *Retusotriletes cf. abundo* Rodriguez

(图版 I, 图 14)

赤道轮廓三角形, 角部浑圆, 三边凸出。大小 $42-46\mu\text{m}$ (测 2 粒)。三射线清楚, 开裂, 直, 长约等于 $2/3-4/5R$, 末端与弓形脊相连。弓形脊清楚, 多沿近赤道延伸, 在射线末端略内凹, 宽 $1.0-2.0\mu\text{m}$ 。外壁厚 $1.0-1.4\mu\text{m}$, 表面光滑。棕色。

比较 当前标本与 Rodriguez (1978) 所定的 *Retusotriletes abundo* (Pl. I, fig. 6) 相比, 主要的差异在于后者的赤道轮廓呈圆形, 射线的唇宽 (宽 $6-8\mu\text{m}$), 两边平行, 但是它们在大小、射线的长短, 弓形脊, 外壁等特征上具有一定的相似性, 本文暂时将其定为比较种。

锥刺具饰弓脊孢 *Apiculiretusispora spicula* Richardson et Lister

(图版 I, 图 10)

1969 *Apiculiretusispora spicula* Richardson et Lister, p. 220, pl. 38, figs. 3, 4.

1986 *Apiculiretusispora spicula*, Richardson and McGregor, pl. 2, fig. 14.

赤道轮廓三角形, 三边凸出, 角部浑圆。大小 $45-48\mu\text{m}$ (测 2 粒)。三射线清楚, 直, 具窄唇, 宽 $1.0-2.0\mu\text{m}$, 长约 $3/4-4/5R$, 末端与弓形脊相连。弓形脊较完全, 在射线末端内凹。外壁厚 $1.0-2.0\mu\text{m}$, 近极区的外壁略薄, 表面纹饰减弱或近光滑, 远极和赤道部位具有锥刺纹饰, 基部呈圆形, 直径 $0.5-1.0\mu\text{m}$, 高相当于基部直径的 2 倍, 约为 $1.0-2.0\mu\text{m}$ 。纹饰分布较密, 间距 $1.0-3.0\mu\text{m}$ 。棕黄色。

比较 当前标本与产自大不列颠的 Welsh Borderland 和南威尔士的 *Apiculiretusispora spicula* (Richardson and Lister, p. 220, pl. 38, figs. 3, 4) 在形态、射线、弓形脊和纹饰等特征上基本一致, 仅后者的个体稍小 (原描述为 $30-46\mu\text{m}$)。与 *Apiculiretusispora brandtii* Streel (1964, pl. 1, figs. 6–10) 相比, 后者的个体较大 (原描述为 $60-101\mu\text{m}$)。

据目前的资料, 本种最早出现于北非的 Ludlowian, 而 *Apiculiretusispora* 属的已知最早记录是 Ludlowian 下部。此属种在本组合中的出现, 表明 *Apiculiretusispora* 属的时限可以

下延至 *Llandoveryan* 晚期。

稀刺具饰弓脊孢(新种) *Apiculiretusispora sparsa* sp. nov.

(图版 I, 图 9)

赤道轮廓三角形, 三边凸出或平直, 角部浑圆。大小 $42-(48)-52\mu\text{m}$ (测 5 粒), 全模标本 $50.2\mu\text{m}$ 。三射线清楚, 具唇, 宽 $1.0-4.0\mu\text{m}$, 向末端唇渐细, 长约等于 $3/4-4/5R$, 末端与弓形脊相连。弓形脊可见, 沿赤道延伸, 在射线末端内凹, 宽 $1.2-2.2\mu\text{m}$ 。外壁厚 $0.8-1.2\mu\text{m}$, 近极区的外壁略薄, 表面光滑, 远极区和赤道部位具有粒或刺, 分布稀疏, 纹饰细弱, 基部呈圆形, 长和宽均小于 $0.5\mu\text{m}$, 末端尖或钝, 间距 $2.0-6.0\mu\text{m}$, 一般为 $3.5-5.0\mu\text{m}$ 。棕黄色。

比较 本新种以个体大小, 发育的唇, 尤其是稀疏分布的细弱纹饰为特征。 *Apiculiretusispora spicula* (Richardson and Lister, 1969, p. 220, pl. 38, figs. 3, 4) 的纹饰以刺和瘤为主, 相对较粗大 (宽 $0.5-1.0\mu\text{m}$, 高 $1.0-2.0\mu\text{m}$), 分布较密 (间距 $1.0-3.0\mu\text{m}$)。本新种与 *Apiculiretusispora microconus* Richardson et Lister (1969, p. 219, pl. 37, figs. 15, 16) 颇相近, 两者纹饰均较细弱, 主要区别在于后者的个体较小 ($13-24\mu\text{m}$), 纹饰分布较密 (间距 $1.0-2.0\mu\text{m}$)。当前新种与 *Apiculiretusispora* 中其它已知种的区别就在于发育的唇和稀疏分布的细弱纹饰。

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DISCOVERY OF EARLY SILURIAN SPORES FROM FENGANG, NORTHERN GUIZHOU, AND ITS PALAEOBOTANICAL SIGNIFICANCE

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Key words spores, origin of vascular plants, late Llandoveryan, Fenggang County of Guizhou

Summary

The origin and early evolution of vascular plants has long been one of the most interesting topics among botanists. To be sure, to solve this kind of problem depends obviously first of all on the discovery of relevant megafossil plants. Nevertheless, dispersed spores have unnegligible meaning and potential value in this regard. The record of Silurian spores has been successively accumulated and attracted much attention from the palaeobotanical circle since the end of the fifties. However, little has been known about the Silurian spores in China. Gao (1981) reported, without illustration, several forms including *Leiotriletes*, *Retusotriletes*, *Ambitisporites* and *Apiculiretusispora* from the “Wenlock” Wenxiang Formation in Dushan, S. Guizhou. Recently, Fang Zongjie *et al.* (1994) mentioned that they discovered some spores from the Late Silurian Yulongsi Formation in Qujing, E. Yunnan and named them the *Apiculiretusispora spicula*-*Emphanisporites neglectus* assemblage. Rather diverse spores have also been reported from the Late Silurian Wutublak Formation in the Junggar Basin, N. Xinjiang, including *Ambitisporites avitus*, *A. dilutus*, *Archaeozonotriletes chulus* var. *nanus*, *Synorisporites libycus* and *Retusotriletes warringtonii* (Gao, 1981; Cai *et al.*, 1993).

The well-known Hanjiadian Formation which outcrops at Dongkala, Fenggang County, N. Guizhou (Text-fig. 1) is famous because it contains the possible vascular plant *Pinnatiramosus qianensis* Geng (1986). The “Wenlock” age of this formation was doubted by some palaeobotanists (e. g. Edwards, 1990) for the complexity of internal structure in this peculiar plant. In December 1991, one of the authors (Wang, Y.) and several colleagues from the Nanjing Institute visited the locality to make more detailed biostratigraphic investigation and systematical collection of fossils and rock samples for palynological study. The samples immediately beneath the chitinozoan-bearing bed have proven to be palyniferous. Based on the characteristics of the spore assemblage (with 12 species or forms of 5 genera) and especially the chitinozoans, brachiopods and bivalves, the Hanjiadian Formation is most possibly of the Early Silurian (late Llandoveryan—Telychian) age.

The chitinozoans, brachiopods and bivalves mentioned below were identified by Geng Liang-yu, Rong Jia-yu and Fang Zong-jie of NIGP respectively, while the field work was done with the help of Cai Chong-yang, Fang Zong-jie of Nanjing Institute, and Zhang Ji-hui of Guizhou Institute of Geological Survey. To all these colleagues the authors wish to express their sincere thanks. The authors are also grateful to Gordon, D. Wood (Houston, USA) for his suggestions and technical comments.

I STRATIGRAPHIC NOTES

The Early Silurian strata at Dongkala, Fenggang, Guizhou are divided in ascending order into the Longmaqi, Shiniulang and Hanjiadian Formations. The outcrop section in the upper part of the Hanjiadian Formation, which is directly involved in the present paper, is briefly described as follows (Text-fig. 2):

Overlying strata:

Lower Permian; Lianshan Formation (P_{1L})

4. Lower part consisting of greyish white thin-bedded clays and black carbonaceous shales, containing fragments of plants; the upper part composed of grey, dark grey fine-grained limestones intercalated with muddy limestone, yielding the fusulinids *Nankinella* sp., *Schubertella* sp., *Ozawainella* sp., etc.

————— Disconformity —————

Lower Silurian Hanjiadian Formation (S_{1h})

3. Yellowish green mudstones (partly covered by Quaternary deposits). Middle part yielding chitinozoans (Sample number TS¹⁴): *Eisenackitina daozenensis*, *Ancyrochitina brevicollis* and *Conochitina* sp. 1.5m
2. Lower part consisting of micaceous siltstones, while upper part composed of bluish grey mudstone intercalated with yellowish green mudstone, yielding the brachiopods (Sample number FT⁻¹) *Nalivkina* sp., *Nucleospira pulchra*, *Protomegastrophia*? sp. and *Lingula*? sp.; the bivalves (FT⁻¹) *Cleionychia quadratus*; the chitinozoans (TS⁻¹²) *Eisenackitina daozenensis*, *Ancyrochitina brevicollis* and *Conochitina* sp.; the plant remains of *Pinnatiramosus qianensis*; the spores

(TS-12) *Ambitisporites awitus* Hoffmeister, *A. dilutus* (Hoffmeister) Richardson et Lister, *Retusotriletes warringtonii* Richardson et Lister, *R. cf. warringtonii*, *R. cf. triangulatus* (Streel) Streel, *R. minor* Kedo, *R. cf. abundo* Rodriguez, *Apiculiretusispora spicula* Richardson et Lister, *Ap. sparsa* sp. nov., *Leiotriletes* sp. and *Punctatisporites* sp., in addition to richer tetrads, a few acritarchs and fragments of tracheids. 5.2m

1. Yellowish micaceous sandy mudstone intercalated with bluish grey mudstone, yielding the brachiopods (FT-2) *Nalivkina* sp., *Nucleospira pulchra*, *Protomegastrophia*? sp., *Lingula*? sp. and the bivalves (FT-2) *Parallelodon cf. cybela*, *P. arallelodon* sp., *Leptodesma* (*Leptodesma*) sp., *Cleionychia quadratus*. >5.0m

After a discussion in some detail, Cai *et al.* (1996) suggested that the upper part of the Hanjiadian Formation should be of the late Llandovery (Telychian) age.

II SPORE ASSEMBLAGE CHARACTERISTICS AND AGE IMPLICATIONS

The spore assemblage obtained from the upper Hanjiadian Formation is composed of some 12 species (forms) referred to 5 genera, which are: *Ambitisporites awitus*, *A. dilutus*, *A. cf. dilutus*, *Retusotriletes warringtonii*, *R. cf. warringtonii*, *R. cf. triangulatus*, *R. minor*, *R. cf. abundo*, *Apiculiretusispora spicula*, *Ap. sparsa* sp. nov., *Leiotriletes* sp. and *Punctatisporites* sp. This assemblage shares the following features:

1. As the main component, *Ambitisporites* with quasi-curvature occupies about 50% of the assemblage in quantity, mainly represented by *A. cf. dilutus*, while *A. awitus* and *A. dilutus* are relatively lower in proportion.

2. Retusoid spores are abundant, with *Retusotriletes* up to 40% in content. Note worthy and somewhat surprising is the occurrence of *Apiculiretusispora*, for the known earliest record of this genus was from the lower Ludlowian (Richardson and Lister, 1969). The following Table I is thus adapted after Richardson and Edwards (1989). In the evolutionary events of spore morphology, the first occurrence of retusoid spores was originally placed at the base of Zone IV, now it has been descended down the base of Zone III.

3. As compared with the roughly contemporaneous assemblages presently known, the Hanjiadian spore suite exhibits a comparatively higher diversity (Table II). For instance, the Llandovery assemblages recorded from Libya (Hoffmeister, 1959), SW Wales (late Aeronian—Telychian; Burgess, 1991) and the United States (Pratt *et al.*, 1978; Strother and Traverse, 1978; Johnson, 1985; Miller and Eames, 1982) are all depauperate in trilete spores, mainly represented by 2 or 1 species of *Ambitisporites*.

The palynomorph assemblage of Wenlock to Ludlow strata in England and South Wales first recorded by Richardson and Lister (1969) comprises *Ambitisporites dilutus*, *A. cf. dilutus*, *A. cf. awitus*, *Retusotriletes warringtonii*, *Archaeozonotriletes chulus* var. *chulus*, *Ar. chulus* var. *nanus*, *Ar. chulus* var. *inframurinus*, *Ar. cf. divellomedian*, cf. *Synorisporites verrucatus*, cf. *S. downtonensis*, cf. *Streelispora granulatus*, *Apiculiretusispora synorea* and *Apiculiretusispora* spp. The assemblage of late Wenlock to late Ludlow

from Libya studied by Richardson and Ioannides (1973) shows, as one can expect, much higher diversity than that of middle Llandovery of Libya by Hoffmeister (1959) and contains *Ambitisporites dilutus*, *A. awitus*, *Retusotriletes warringtonii*, *R. cf. warringtonii*, *R. minor*, *Archaeozonotriletes chulus* var. *chulus*, *Ar. chulus* var. *nanus*, *Emphanisporites cf. protophanus*, cf. *Synorisporites verrucatus* and *S. cf. verrucatus*. Smith (1975) reported the presence of *Ambitisporites* in the early Wenlockian of Ireland. Based on plant microfossils (acritarchs, tetrads and trilete spores), Bugess and Richardson (1991) have recognized two assemblages in the Wenlock strata of England. The early Wenlock is characterized by the presences of *Ambitisporites awitus*, *A. dilutus*, *Archaeozonotriletes chulus* var. *chulus* and *Ar. chulus* var. *nanus*, and the late Wenlock by the appearances of *Synorisporites cf. S. libycus* and *Emphanisporites cf. protophanus*, in addition to the persisting forms. The assemblages known from the late Wenlock to early Ludlow in Scotland (Wellman, 1993) contain abundant coherent tetrads in associated with some trilete spores, such as *Ambitisporites awitus*, *A. dilutus*, *Archaeozonotriletes chulus*, *Chelinospora* sp. and *Cymbosporites* sp. *A.*

According to palynological data accumulated since 1959, Richardson and McGregor (1986), and Richardson and Edwards (1989) have established some assemblage zones for Late Ordovician to Silurian, including 4 zones for the Early Silurian, which are, in ascending order: III. *murusattenuata*-*murusdensa*; IV. *awitus*-*dilutus*; V. *chulus*-*nanus*; VI. cf. *protophanus*-cf. *verrucatus*. Among them, Zone III (Rhuddanian-lowest Aeronian) is largely represented by tetrads and dyads with few trilete spores, whereas Zones IV, V and VI are mainly composed of trilete spores, ranging from Aeronian to early Gorstian.

It is difficult to correlate the present assemblage with the zones discussed above. One of the reasons seems to come from the empirical character of generalization and zonation which was made on the basis of a few known assemblages, implying that the very low diversity in the Early Silurian is possibly more apparent than real. On the other hand, of course one must be very cautious about the relatively higher diversity which may result from a "splitter" standpoint in classification as adopted here following other palynologists, or from contamination during the sample-maceration process. However, the latter possibility can be excluded because the processing was done twice very carefully with the same result. Judging from the assemblage itself, some of the species have already been known in the Early Silurian, and all the spores are basically in the same colour—brown or dark brown; i. e., TAI Index = 4 + -5, and thus it is believed that these components are indigeneous.

Several species in the assemblage reveal an Early Silurian aspect, for instance, the species *Ambitisporites awitus*, *A. dilutus*, *A. cf. dilutus*, *Retusotriletes warringtonii* and *R. cf. warringtonii* have been known to occur down to Early Silurian; in Llandovery (Hoffmeister, 1959) and late Wenlock—late Ludlow (Richardson and Ioannides, 1971) in Libya; and in Wenlock of England (Burgess and Richardson, 1991). On the other hand, several peculiar and characteristic forms have never been recorded below Ludlow. The earliest known occurrence of

Retusotriletes cf. *triangulatus* with thickened apical area was from the base of Geddinnian, although similar spores (e. g., *R.* cf. *goensis* Lele et Streel) have been reported in the upper Ludlow (Richardson and Ioannides, 1971), and *Apiculiretusispora* was from the lower Ludlow. If special emphasis is just laid upon these two forms, one would assume that the present assemblage should not be older than Late Silurian (Ludlow) in age. However, some forms with more complex morphology and sculptures from late Wenlock to Ludlow have not been observed in our assemblage for instance, “*Emphanisporites*” cf. *E. protophanus* and cf. *Synorisporites verrucatus* of Zone VI (late Wenlock), and *Synorisporites lybicus*, *Lophozonotriletes*? *poicilomorphus*, “*Emphanisporites*” *protophanus*, *E. neglectus* and *Brochotriletes*? sp. of Zone VII (Ludlow). Consequently, the absence of these forms suggests that the Fenggang assemblage is most likely older than late Wenlock-Ludlow.

The present assemblage is definitely younger than the lower part of Zone IV (*avitus-dilutus*) for its higher diversity than that of Libya (Hoffmeister, 1959), and some forms display a younger aspect; on the other hand, it should be older than the late Wenlock (upper part of Zone V, and Zone VI) because of the absences of *Synorisporites*, “*Emphanisporites*”, etc. Therefore, if one considers the age solely based on palynological evidence, it seems appropriate to date the Fenggang assemblage late Llandovery (Telychian) to early Wenlock. However, as stated above, the definition of Early Silurian (especially Llandovery to early Wenlock) seems far from complete because Zones IV and V of Richardson and Edwards (1989) are based on rare known records. Zone V not only has a very long range (from late Llandovery to late Wenlock), but also contains a few typical forms, only comprising 6 species, including two varieties (*Ar. chulus* var. *chulus* and *Ar. chulus* var. *nanus*) with the earliest record in upper part of Telychian, and the other 4 species which have been known in Zone IV. In other words, there is not any typical forms of the late Llandovery.

The chitinozoans, brachiopods and bivalves from the same bed as the spores, or from the immediately overlying or underlying beds (Fig. 2) indicate the late Llandovery age of the upper Hanjiadian Formation. From the palynological standpoint as discussed above there are no ample grounds for us to object this dating. If the dating is reliable, it means that the present assemblage has made important supplementary content to the Llandovery, i. e., it is corresponding to the upper part of Zone IV or the lower part of Zone V, and throws light on the appearance of vascular plants during the Llandovery time.

III. SIGNIFICANCE ON THE ORIGIN OF EARLY VASCULAR PLANTS

The first appearance of trilete spores in strata is one of the important events in plant evolution, although their bearing on the origin of vascular plants is a matter of discussion. Because trilete spores have been known not only in pteridophytes but also in some bryophytes. Just as Banks (1975b, p. 734) pointed out: “To date there are no techniques that will demonstrate the division to which a given spore belongs (e. g., bryophytes vs. tracheophyte)”.

Gray (1985, p. 21) arrived at the following inference after surveying the relevant data: "There are dispersed spores obtained by maceration of the rock and oxidation of the organic microfossils found within. Thus the parent plants of these spores are unknown. No megafossil evidence accompanied the spores to give a clue as their affinities. The similarity of some of them to Devonian spores whose affinity is known, or suspected, could lead one to conclude that some Silurian spores come from vascular land plants". This subject can be further discussed and we have arrived at the conclusion that even if not all triletes were produced by vascular plants, at least those retusoid spores (*Retusotriletes*, *Apiculiretusispora* and to some extent *Ambitisporites*) of pre-Devonian were derived from vascular plants. The arguments are given as follows:

1. Among the 900—1 000 genera of living bryophytes, trilete spores are mainly seen in Musci, such as Anthocerotales, Sphagnales and some of Andreareales; while in liverworts, only a few trilete spores occur in Marchantiales (Hepaticae), Pottiales, Funariales and Isobryales. In both cases, there are no retusoid spores or their analogies (Boros *et al.*, 1975; Gray, 1985).

2. No reliable retusoid trilete spores have been known in the *in situ* spores of nonvascular plants. The only possible exception is the strange plant *Protosalvania* of Devonian age. However, much dispute and various assumptions have arisen about its botanical affinities, such as euglenid, red alga, bryophyte, fern or certain kind of algae with some features of vascular plant. None of these assumptions has been firmly demonstrated, even its spore morphology is still unclear. Niklas and Phillips (1976) mentioned that the *in situ* spores often in tetraspores or tetrads are larger than 200 μm across, and morphologically similar to *Retusotriletes*, but Taylor (1988) suggests that these spores have no trilete, and are very close to spores of some living plants of euglenid or red alga in morphology.

3. *In situ* retusoid trilete spores have been widely reported from Late Silurian to Early Devonian vascular plants, such as *Ambitisporites*, *Retusotriletes* and *Aneurospora*-type spores in *Cooksonia pertonia* Lang (Fanning *et al.*, 1988; Rogerson *et al.*, 1993); the *Retusotriletes*-type recorded by Lang (1937) in *Cooksonia* is very similar to *R. warringtonii*.

Retusoid spores are also documented from *Rhynia major* (Kidston and Lang, 1917). *Renalia huebei* produced *Apiculiretusispora*-type spores (Gensel, 1976); *Psilophyton dawsoni* contains *Retusotriletes* (Banks *et al.*, 1975) and *Psilophyton crenulatus* bears *Apiculiretusispora*.

Almost all *in situ* spores found in zosterophyllids are widely developed in Early Devonian of the globe and show a retusoid character. For instance, the species *Zosterophyllum* cf. *Z. fertile*, *Z. llanoveranum*, *Z. yunnanense*, *Discalis longistipa*, *Sawdonia ornata*, *Rebuchia ovata*, etc. produced *Retusotriletes*-type spores (Edwards, 1969; Hao Shou-gang, 1985; Fanning *et al.*, 1990). Spores comparable with *R.* cf. *R. triangulatus* have been isolated from *Sawdonia scanthotheca* (Gensel, 1982).

More examples can be listed. As Fanning *et al.* (1990) summarized: There is a close relationship between retusoid spores and vascular plants.

4. Judging from the known dispersed spores, retusoid forms had come into existence in the Early Silurian (Llandovery), such as *Ambitisporites*, *Retusotriletes* and *Apiculiretusispora*. However, their high development and differentiation started from Siegenian (Fanning *et al.*, 1990). The earliest record of megafossil vascular plants has been known in the late Early Silurian (Wenlock), such as the *Cooksonia*-type sporangia from Ireland (Edwards, 1979), and towards Siegenian the vascular plants became progressively diverse in composition and showed different evolutionary trends in morphology, indicating the onset of great radiation and development (Li *et al.*, 1981).

The evidence discussed here supports the assumption of a close connection in time and space between retusoid spores and vascular plants. Even Banks (1975a) who is most cautious with reasonable reservation about the botanical significance of dispersed spores also mentioned: "Although generally one can not determine the dispersed trilete spores derived from what kind of plants, however, some of them are comparable to the *in situ* spores found in organically connected sporangia,and the similarity is so high, can not be casual.....". This observation can be applied to the Fenggang spores. In other words, the retusoid spores in the present assemblage are highly probably produced by vascular plants. This implies that vascular plants had already appeared in the Llandovery (Telychian), provided the dating is correct. This conclusion lends support to explain *Pinnatiramosus qianensis* as a vascular plant. In addition, the rather high diversity seems to indicate more than one single species of vascular plants existing in SW China during that time although this inference needs more evidence to be substantiated.

IV DESCRIPTION OF NEW SPECIES

Apiculiretusispora sparsa sp. nov.

(Pl. I, fig. 9)

Characteristic features Miospores radial, trilete. Amb triangular, with rounded apices and convex or straight sides. Laesurae distinct, accompanied by lips, three-fourths to four-fifths of spore radius in length, merged into the curvaturae perfectae, which coincide with the equator, ca. $1.2-2.2\mu\text{m}$ wide. Exine $0.8-1.2\mu\text{m}$ thick. Contact area slightly thinner, and smooth. Exine equatorially and distally sculptured by minute and sparse spines or grana, circular at the base, $0.5\mu\text{m}$ wide and high, mostly sharp or acute at the top, $2.0-6.0\mu\text{m}$ (generally $3.5-5.0\mu\text{m}$) spaced apart. Equatorial diameter indicating ranges of $42-(48)-52\mu\text{m}$ (measured from 5 specimens), mode $50.2\mu\text{m}$. Brown in colour.

Comparison This new species is characterized by the size, well-developed lips, especially sparse and minute ornaments which distinguish it from the known species of *Apiculiretusispora*. It differs from *Ap. spicula* Richardson et Lister (1969, p. 220, pl. 38, figs. 3, 4) in having large and dense spines and con. ($0.5-1.0\mu\text{m}$ wide, $1.0-2.0\mu\text{m}$ high, $1.0-$

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