

原始隐羊齿(*Cryptonoclea primitiva*) 花粉形态和气囊个体发育的观察

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内 容 提 要

详细描述了原始隐羊齿(*Cryptonoclea primitiva*)花粉的形态结构和气囊的个体发育过程。发现花粉在个体发育过程中形态变异是相当大的,在分散保存时,要避免人为分类。

关键词 原始隐羊齿 单气囊花粉 个体发育

一、前 言

原始隐羊齿(*Cryptonoclea primitiva*)是一种整体化石植物(whole fossil plant)(Taylor, 1981)。这种植物发现于中国贵州省水城地区汪家寨煤矿的煤核(coal balls)中,其地质时代是晚二叠世(P_2^3)(Li, 1986)。整个植物包括保存结构的种子,叶和花粉器官,并被认为大羽羊齿目(Gigantopteridales)的一个重要分子。虽然作为整体化石植物已对其各个部分(包括花粉)作了报道(Li, 1992),但其后对花粉的形态结构的进一步研究,才使我们对它有了更深的认识。因此有必要另作详细的补充描述。

另一方面,最近十几年发展起来的化石植物的生殖生物学(reproductive biology)研究已引起了广大植物学工作者的极大兴趣。现今,这个领域的研究不仅报道了化石种子的颈卵器、大配子体和胚(Taylor and Millay, 1979),而且还报道了与古花粉研究有关的花粉管(Rothwell, 1989)胚原细胞,叶原细胞(Taylor, 1981; Millay and Eggert, 1974)及花粉中的精子状内容物(Stewart, 1951)等。这些与化石植物生殖有关的形态结构极大地深化了人们对化石植物生殖器官的了解。通过生殖生物学的研究还建立了某些化石种子(胚珠)和孢子的个体发育系列,例如:靛籽属(*Callospermation*)的种子和宾纳芦孢穗(*Calamostachys binneyana*)的孢子弹丝的个体发育序列(Good, 1975; Rothwell, 1971, 1980)的建立,为进一步扫除某些种子和孢子的人为分类作出了贡献。然而,迄今很少有关于化石花粉气囊个体发育序列的报道。笔者最近的研究借助于对不同成熟程度的花粉囊中的原位花粉的详细观察,揭示了原始隐羊齿花粉的气囊个体发育序列。这个个体发育序列的建立不仅有助于我们对

• 国家自然科学基金和科学院基础学科特别支持费资助项目。

古花粉个体发育的进一步了解,而且对避免古花粉研究方面的人为分类也有很大作用,因此本文将详细描述这个序列。

二、术 语

由于本文所报道的花粉为一两侧对称结构,为了便于描述,除赤道面(即图版 I,图 7 的 A-A 切面)外,我们还定义了主切面(即图版 I,图 5 的 B-B)和次切面(即图版 I,图 6 的 C-C),赤道面定义是考虑到这类花粉在形态上同常见的单气囊花粉一致(Dibner, 1973),但因赤道上有一小凹面而又不同,所以必须定义另两个切面(见图版 I,图 5,7)。此外近极面有一个很大的“气囊—本体连接区”,所以,尽管两个极之间的轴是 3 个轴中最短的一个,但仍把图版 I 图 7 中的 A-A 平面看作赤道面。

三、聚合花粉囊的一般形态

尽管原始隐羊齿的聚合花粉囊的形态已在过去的文章中作了较详细的描述(Li, 1992),但为了便于读者理解,在这里仍需作一简单介绍。

原始隐羊齿的花粉器官与常见的聚合囊类似,但根据其器官连接及内含的孢粉的性质,可确认这是一种花粉器官,并且在形态上有点类似于靛羊齿目(Callistophytales)的 *Idanothekion* 属(Rothwell, 1982)。

此类花粉器官由一柄连接到复叶的小羽片的背面。聚合花粉囊辐射对称,由一圈细长的相互融合的(一般为 4—6 个)花粉囊围一中心柱构成(图版 I,图 1),远端无中空区。花粉囊为长指状,长 1 000—1 300 μm ,整个横切面为圆到椭圆形,直径 300—400 μm (图版 I,图 1;图版 II,图 7)。维管束由小羽片的二级侧脉经柄进入中心柱直达聚合花粉囊远端(图版 I,图 1)。横切面上此维管束通常由 8—10 个具梯形纹孔的管胞组成(图版 II,图 7)。围绕维管束的中心柱的其余部分为薄壁组织细胞。组成聚合花粉囊的每一个花粉囊十分细长,远端弓形,长 1 000—1 300 μm 。横切面为圆形,直径 150 μm 。向内的整壁略扁平。整壁细胞一般为薄壁的,向内的壁上的细胞有较厚的壁,但是向外壁的开裂附近有些细胞的壁较厚,它们可能与花粉器官的开裂机制有关(图版 I,图 2)。

四、花粉的形态结构

在花粉囊内可见大量原位花粉(图版 I,图 1,9,10)。这些花粉相当小,形态十分罕见,以至最初被认为是形态上未成熟的花粉。以后的检验表明,无论在开裂的花粉囊和基质中均未发现形态上更成熟的花粉。因此它们代表一组不同发育阶段的花粉,其中有一些实际上是成熟的花粉。

花粉由本体和气囊组成,通常花粉为一扁椭圆体。最长的轴在赤道面内,一端有一凹面。孢粉的大小不等,在赤道面内测得花粉的最大长度为 15—19.5 μm (平均 18 μm)(等于本体的长度),整个宽为 12—17.5 μm (平均 15 μm)(图版 I,图 10,11;插图 1,2)。

极面观,花粉在赤道平面内为长椭圆形。本体细长,为 9.5 \times 18 μm 。在赤道上有两个半月形气囊瓣位于中心体两侧;长轴与主切面平行。据位置这两个气囊瓣叫作“赤道气囊瓣”。

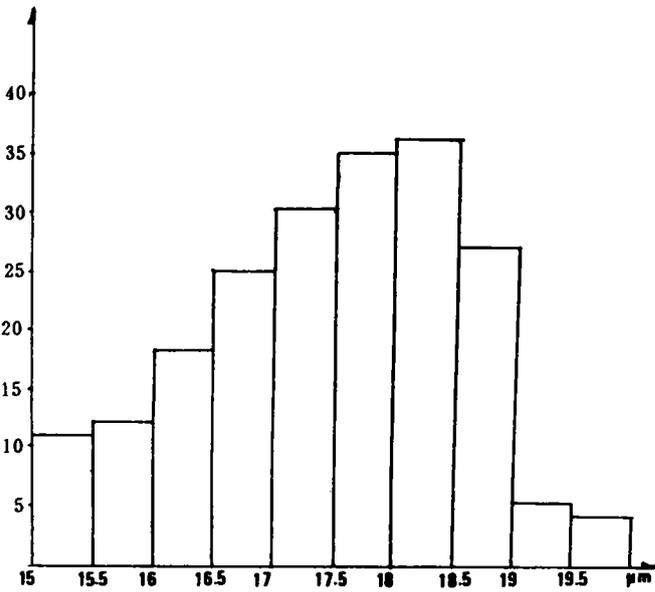


插图 1 原始隐羊齿 (*Cryptonoclea primitiva*)
示本体的长度纵轴为花粉数, 横轴为花粉大小。

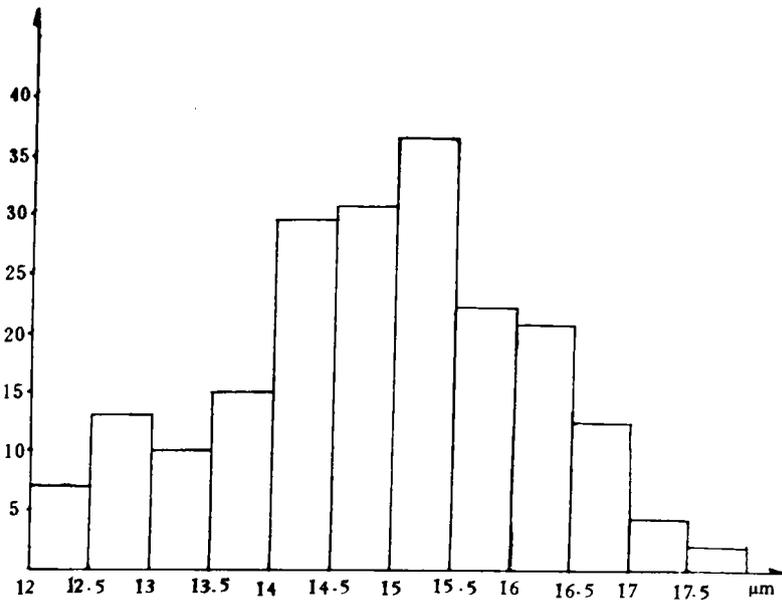


插图 2 原始隐羊齿 (*Cryptonoclea primitiva*)
大小示花粉(包括赤道气囊瓣)纵轴为花粉数, 横轴为花粉。

它们长 $18\mu\text{m}$, 宽 $3\mu\text{m}$ (图版 I, 图 5; 图版 II, 图 6; 插图 3)。

从侧面观, 次切面内, 花粉粒在赤道上有两个倒铃状椭圆体。在次切面内, 测得赤道气囊

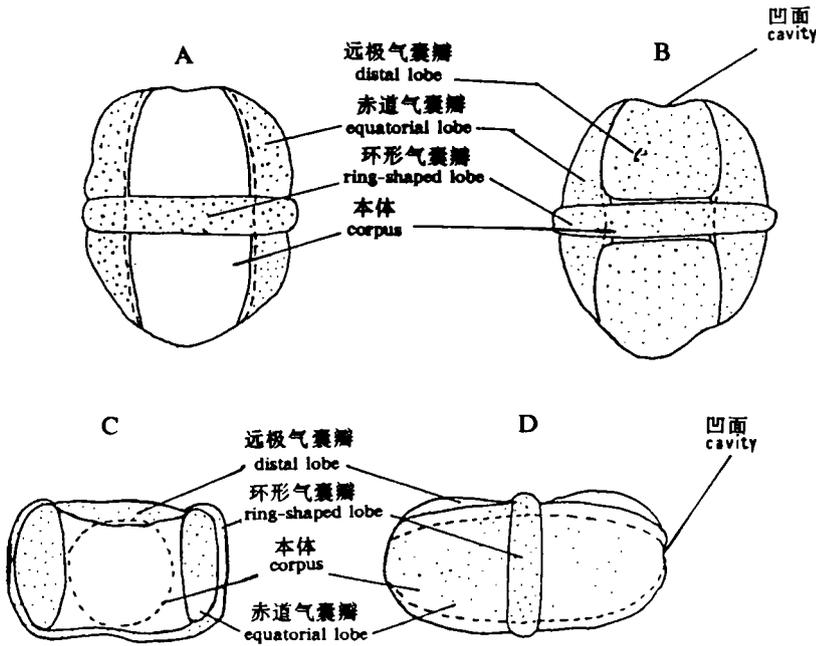


插图3 原始隐羊齿(*Cryptonoclea primitiva*)

示气囊瓣。A. 远极面观, 据图版 I, 图 5; 图版 II, 图 1.5.6 复原。B. 远极面观, 据图版 I, 图 5.11; 图版 II, 图 3.5.6 复原。C. 聚焦于次切面侧面观, 据图版 I, 图 7; 图版 II, 图 4.5 复原。D. 聚焦于主切面侧面观, 据图版 I, 图 6; 图版 II, 图 3.4.5 复原。

瓣比本体厚, 其厚度为 $9-11\mu\text{m}$, 而本体厚度为 $6-9\mu\text{m}$ (图版 I, 图 7; 图版 II, 图 2.5; 插图 3)。在远极面上有 2 个气囊瓣, 它们对称于次切面, 2 个赤道气囊瓣由它们相连接。按位置, 这 2 个气囊瓣叫作“远极气囊瓣”。在主切面内, 远极气囊瓣高度为 $2\mu\text{m}$ (图版 I, 图 3.7, 11; 图版 II, 图 3.5; 插图 3)。次切面内有一环形气囊瓣, 它同赤道气囊瓣相连。在次切面内, 这气囊瓣的周围为 $15\times 10\mu\text{m}$ (图版 II, 图 3.4; 插图 3)。按形状, 这个瓣叫作“环形气囊瓣”。

简言之, 常见的花粉在形态上有一个凹面和 5 个气囊瓣: 两个赤道气囊瓣, 两个远极气囊瓣, 和一个环形气囊瓣, 但因为这些瓣相互连接形成一个完整的气囊, 所以在本质上, 这类花粉是单气囊的。

因为在远极面上有 2 个位于远极气囊瓣和环形气囊瓣间的小的“非气囊区”或“气囊—本体连接区”, 所以很易区分成熟花粉的远极面和近极面(近极面只有环形气囊瓣), 所以“非气囊区”相当大(图版 I, 图 11; 图版 II, 图 1.5)。未发现明显的萌发区, 但在少数标本内, 在远极面上可见一平行于次切面的裂口, 它可能代表萌发缝。

上述花粉的形态不仅在光学镜下观察到, 而且为扫描电镜所证实。图版 II 的图 1—3 清楚地显出所有气囊瓣的外形和长轴端的凹面。同时还表明花粉外表纹饰是网带小颗粒的。

花粉的内部结构亦为扫描电镜所证实。图版 II, 图 4—6 表明, 在气囊区, 花粉壁的外层同外壁内层是分离的, 但在气囊的向内的侧有明显的蜂窝状结构联系这两层。因为花粉有明显的气囊—本体连接区, 所以此气囊在本质上不同于假气囊, 这样虽然同其他具气囊花粉,

如 *Vesicaspora* 相比, 它的气囊的发育是不充分的, 但仍不失为一种单气囊花粉。有时在花粉的本体内有一深色内容物(图版 I, 图 5—8), 它们可能代表细胞核。

五、花粉气囊的个体发育

上述花粉的形态和大小有时似乎变化很大(图版 I, 图 10, 11; 图版 II, 图 8; 插图 1, 2), 但这种变化只反映花粉不同的发育阶段。

我们观察了一组大小不同的花粉, 所见的最小的花粉, 直径 $8\mu\text{m}$, 长 $10\mu\text{m}$, 为一短椭圆形, 在次切面上为圆形。此时只有环形气囊瓣, 并且长轴一端的凹面非常明显(图版 I, 图 4, 8; 图版 II, 图 8, 9; 插图 4, B)。接着, 花粉的发育显然与赤道气囊瓣的形成有关, 因此花粉的长大主要在赤道面及主切面内, 结果花粉变成扁椭圆体, 大小为 $18\times 15\times 10\mu\text{m}$ 。同时长轴端的凹面相应的变得模糊(图版 II, 图 1, 6; 插图 4, C)。最后, 花粉开始分化出两个远极气囊瓣(图版 II, 图 3; 插图 4, D)。直到远极面因远极气囊的发育而使环形瓣变得十分模糊(图版 I, 图 11; 插图 4, E), 甚至变得象一条长槽(图版 I, 图 3; 插图 4, F)。为了显示原始隐羊齿花粉气囊的不同发育阶段, 我们在插图 4 中复原了其全过程, 其中 A 为假设的第一阶段。

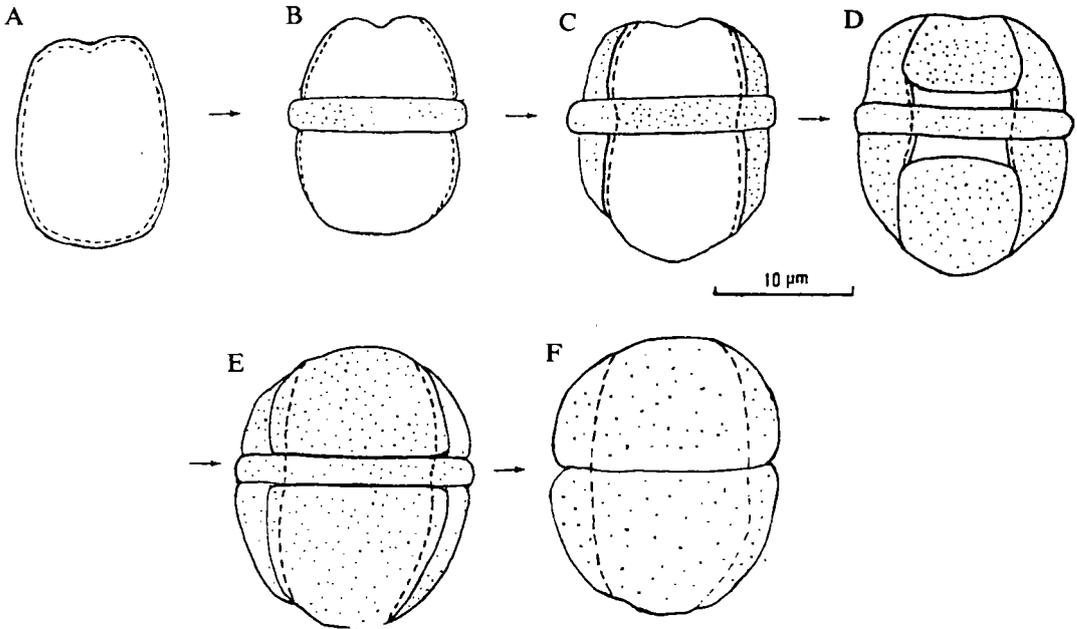


插图 4 原始隐羊齿(*Cryptonoclea primitiva*)花粉气囊的个体发育系列复原

图中花粉的极面观—远极面。虚线所围为自体, 有点的区为气囊瓣, 无点的区为气囊—自体连接区。A. 极不成熟的花粉, 无气囊瓣(假设阶段)。B. 不成熟花粉, 示环形气囊瓣, 此花粉源于未成熟的花粉囊(据图版 I, 图 4, 8; 图版 II, 图 8, 9)。C. 未成熟花粉, 未环形气囊瓣和 2 个赤道气囊瓣(据图版 II, 图 1, 6)。D. 接近成熟的花粉, 示环形气囊瓣, 2 个赤道气囊瓣和 2 个不全的远极气囊瓣。此类花粉常在快成熟的花粉囊中见到(据图版 II, 图 3)。E. 快成熟的花粉, 示环背气囊瓣, 2 个赤道气囊瓣和 2 个远极气囊瓣(据图版 I, 图 11)。F. 完全成熟的花粉, 示环形气囊瓣变得模糊不清, 2 个赤道气囊瓣和 2 个充分发育的远极气囊瓣。此花粉见于基质, 偶尔可在花粉囊中见到(据图版 I, 图 3)。

六、讨 论

从上面复原的原始隐羊齿的花粉的不同阶段可以看出,花粉在个体发育过程中其形态的变异是相当大的。它们分散保存时很可能被认为是不同的种,不同的属,甚至连极面的确定都有可能不同。因此对原位孢粉个体发育序列的观察和复原,不仅有助于我们对古代植物的生殖机制的了解和丰富人们的化石植物生物学知识,而且有助于避免古孢粉学研究中的人为分类。另外,从上述花粉的个体发育序列中可以看出,此类花粉虽为单气囊的,但气囊的发育不是一次成就的,而是分区(按气囊瓣)逐步形成的。这在其他单气囊甚至多气囊花粉中是否有类似的发育过程是一个值得进一步探讨的问题。

联系对花粉个体发育和对气囊区超微结构的观察,可以清楚地看到,在原始隐羊齿中,花粉壁的外层同外壁内层最初是合一的,而气囊的形成是同这两层之间的蜂窝状结构的形成和径向管的不断扩张有关。有人曾对现代苏铁的花粉壁进行超微结构的观察,发现其外壁外层同外壁内层之间有蜂窝状结构的形成和径向管扩张,不过由于在现代苏铁的花粉中径向管的扩张尺度非常有限,以致只能由电镜来观察,所以尽管它的结构可能有助于花粉的传播,但并不认为它已形成明显的气囊(Audran, 1981; Taylor, 1982)。在原始隐羊齿中,径向管的扩张非常明显,已达到了形成气囊的阶段。然而看来这些径向管最终并未同外壁内层完全脱离,所以气囊的发育是不完全的。此外由于在花粉的有些部分(即气囊—本体连接区)并不形成蜂窝状结构,因此,这种气囊显然不是假气囊。看来,原始隐羊齿花粉所具的气囊在系统发育上很可能为一过渡类型,而进一步发育则导致多气囊花粉的形成。

参 考 文 献

- Audran, J. C., 1981: Pollen and tapetum development in *Cretozamia mexicana* (Cycadaceae): sporal origin of the exinic sporopollen in cycads. *Rev. Palaeobot. Palynol.* **133**: 315—346.
- Dibner, A. F., 1973: Morphology and classification of Late Paleozoic monosaccate miospores. *Rev. Palaeobot. and Palynol.* **116**: 263—270.
- Good, C. W., 1975: Pennsylvanian-age calamitean cones, elater-bearing spores, and associated vegetative organs. *Palaeontographica. B.* **153**: 28—99.
- Li Zhong-ming, 1992: Reconstruction of a new member of Gigantopteridales. *Cathaya*, **4**: 161—178.
- Millay, M. A. and Eggert, D. A., 1974: Microgametophyte development in the Paleozoic seed fern family Callistophytaceae. *Amer. J. Bot.* **61**: 1067—1075.
- Millay, M. A. and Taylor, T. N., 1974: Morphological studies of Paleozoic saccate pollen. *Palaeontographica B.* **147**: 75—99.
- Rothwell, G. W., 1971: Ontogeny of the Paleozoic ovule. *Gallosperrmarion pusillum*. *Amer. J. Bot.* **58**: 707—715.
- Rothwell, G. W., 1972: Evidence of pollen tubes in Paleozoic pteridosperms. *Science*, **175**: 772—774.
- Rothwell, G. W., 1981: The Callistophytaceae (Pteridospermopsida), Part I: Reproductive features. *Palaeontographica B.* **173**: 86—106.
- Rothwell, G. W., 1982: Callistophytales (Pteridospermopsida): reproductive sophisticated Paleozoic gymnosperms. *Rev. Palaeobot. Palynol.* **32**: 103—120.
- Stewart, W. N., 1951: A new *Pachytesta* from the Berryville locality of southeastern Illinois. *Amer. Midl. Natur.* **46**: 717—742.

- Taylor, F. N., 1982: Ultrastructure studies of Paleozoic seed fern pollen: sporoderm development. *Rev. Palaeobot. Palynol.* **37**: 29—53.
- Taylor, F. N. and Millay, M. A., 1979: Pollination biology and reproduction in early seed plants. *Rev. Palaeobot. Palynol.* **27**: 329—355

[1992年6月28日收到]

OBSERVATION ON POLLEN MORPHOLOGY AND SACCUS ONTOGENESIS IN *CRYPTONOCLEA PRIMITIVA*

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Key words: *Cryptonoclea primitiva*, monosaccate pollen, ontogenesis

Summary

INTRODUCTION

As a whole fossil plant, including structurally preserved seed, leaf and pollen-bearing organ, *Cryptonoclea primitiva* was known from coal balls of the Wangjiazhai Mine in Shuicheng Area, Guizhou, China. The specimens belong to the upper Upper Permian (P_2^2) in stratigraphic position, and the taxon has been assigned to the order Gigantoteridales.

All parts of the whole fossil plant, including pollen, have already been described in the last paper, but the present investigation further enriches our knowledge of this kind of pollen, and therefore it is necessary to give an additional explanation here.

On the other hand, the studies on reproductive biology of fossil plants, which are rapidly developing for the last ten years, have captured the fascination of many palaeobotanists. Previous reports in this field involved not only archegonium, cellularized megagametophyte and embryo of seeds but also embryonal cell, prothallial cell, pollen tube and even spermlike content, with the establishment of some ontogenetic sequences of ovules (seeds) and spores, such as ovules of *Callospermarian* and elaters of the spores of *Calamostachys binneyana*. These led to the removal of some artificial taxa in taxonomy of the ovules and spores. However, up to now the ontogenesis of pollen saccus has rarely been reported. Through detailed observation on *in-situ* pollen of *Cryptonoclea primitiva*, the ontogenetic sequence of the pollen saccus has been demonstrated and will be described in detail here. This will enrich our knowledge of ontogenesis of fossil pollen and avoid emergence of artificial classification in palaeopalynology.

TERMINOLOGY

The determination of the equatorial face takes into consideration the identity with common monosaccate pollen (Dibner, 1973). But there is a little difference between them in the small concavity on the equatorial face (P1. I, figs. 5, 7). Therefore, except for the equatorial face (A-A of P1. I, fig. 7), the primary plane (B-B of P1. I, fig. 5) and the secondary plane (C-C of P1. I, fig. 6) are defined in order to describe them conveniently. Moreover, there is a large "saccus-corporis attachment region" on the polar surface. Hence A-A of P1. I, fig. 7 is considered as the equatorial face although the axis between both proximal and distal surfaces is the shortest one of the three axes.

GENERAL FEATURES OF SYNGANGIUM

In morphology the synangium of *Cryptonoclea primitiva* was described in the last paper but it is necessary to give a simple explanation in order to understand their *in-situ* pollen.

The pollen-bearing organ of *Cryptonoclea primitiva* is similar to a common synangium, but it is doubtless that these synangia are a kind of pollen-bearing organs based on organic attachment and the nature of grains, which are morphologically somewhat similar to those in the genus *Idanothekion* of the order Callistophytales.

The pollen-bearing organs of this type are represented by synangia, each of which is borne on the abaxial surface of the pinnules by a stalk. The synangium is radially symmetrical, consisting of a longitudinally elongate and fused ring, commonly 4—6 sporangia (P1. I, fig. 1) surrounding a central column, without distal hollow.

The synangia are digital, ranging between 1 000 and 1 300 μm in length, roughly circular to elliptical in cross-section, and measuring 300—400 μm in maximum diameter (P1. I, fig. 1; P1. II, fig. 7).

A vascular strand from secondary lateral veins of pinnules traverses the stalk and enters the central column of synangium, extending up the central column for the length of the column (P1. I, figs. 1, 2).

The vascular strand makes up about 10 tracheids with scalariform pitting (P1. II, fig. 7). The strand in the central column is surrounded by parenchyma.

The sporangia are slender, elongate in shape, with arching distal end and are circular in transverse section, measuring 150 μm in maximum diameter and 1 000—1 300 μm in length, but their inwardly directed walls are slightly flattened.

Generally it seems that the cells on the sporangial wall near the central column of synangium have thicker wall than others, but some of the cells near the dehiscence on the outwardly directed sporangial wall exhibit thickened walls which may be related to dehiscence function (P1. I, fig. 2).

MORPHOLOGY OF POLLEN

A lot of *in-situ* grains were observed in sporangia (P1. I, figs. 1, 9, 10). These grains are rather small and so unusual in morphology that all of them were initially thought to be immature grains morphologically. Subsequently, examination indicates that they represent a series of grains in different development stages and some of them are actually mature grains since whatsoever may represent morphologically more mature grains has not been found in the dehiscent sporangia, even in matrix with synangia.

The grains are commonly flattened-ellipsoid in shape, consisting of a central body (or corpus) and saccus, with a small concavity at only end of the major axis situated on the equatorial plane. They are varying in size, measuring 15—19.5 μm in maximum length (18 μm on the average) which is equal to the length of a corpus, and 12—17.5 μm in total width (15 μm on the average) on equatorial face (P1. I, figs. 10, 11; Text-figs. 1, 2). In polar view, the grains are commonly elongate-ellipsoid in equatorial plane; the corpus appears slender-elongate, measuring $9.5 \times 18 \mu\text{m}$ in equatorial plane and 6—9 μm thick in the secondary plane. Two semilunate saccus lobes are situated on either side of the corpus on the equator, with two major axes of the lobes parallel to the primary plane. The lobes are called "equatorial saccus lobes" based on position, measuring 18 μm in length and 3 μm in width in equatorial face (P1. I, fig. 5; P1. II, fig. 6; Text-fig. 3).

In lateral view toward the secondary plane the grains display two dumbbell-like ellipses on the equator. The equatorial saccus lobes are thicker (9—11 μm) than the corpus in the secondary plane (P1. I, fig. 7; P1. II, figs. 2, 5; Text-fig. 3). Two saccus lobes, through which the equatorial lobes connected to each other, occur on the distal surface and are symmetrical to the secondary plane. Based on their position, the lobes are named "distal saccus lobes", measuring 2 μm in maximum height (P1. I, figs. 3, 7, 11; P1. II, figs. 3, 5; Text-fig. 3). A circular saccus lobe, which surrounds the corpus and is connected to equatorial lobes, is situated in the secondary plane, measuring $15 \times 10 \mu\text{m}$ in periphery (P1. I, figs. 3, 4; Text-fig. 3). According to the shape this lobe is called the "circular saccus lobe".

In short, the common grains morphologically contain a small concavity and five saccus lobes, including two equatorial lobes, two distal lobes and one circular lobe; however, since these lobes are connected with each other to form an entire saccus, the grains of this type are monosaccate in nature.

It is easy to distinguish the distal area from the proximal in mature grains as except in distal lobes there are two smaller "bladder free areas" which are rather large due to the presence of only a circular lobe proximally (P1. I, fig. 11; P1. II, figs. 1, 5), or "saccus-corpus attachment regions" distally, which sit between distal lobes and the circular lobe. No definite germination aperture has been found but a slit parallel to the secondary plane is observed on the distal surface of a few grains.

The above-described morphology of grains has been shown by light microscope and

proved by SEM. P1. II, figs. 1—3 reveal clearly the outline of all saccus lobes and small concavity at the end of the major axis, while the SEM micrographs show the external ornamentation of grains, which is reticular with small granula.

The internal pollen structure is demonstrated by observation under SEM. P1. I, figs. 4—6 indicate the sexine separated from the nexine in the saccus region. The prominent alveolate organization which is directed inwards and by which the sexine and nexine are connected in the saccus region, occurs in the saccus which is distinct from the pseudosaccus in feature in the presence of an obvious saccus corpus attachment region. Therefore, the grains represent one type of monosaccate pollen, although the saccus of these grains was not fully developed, as compared with other monosaccate pollen grains, such as *Vesicaspora*.

In the corpus of the pollen, sometimes the content (P1. I, figs. 5—8) may represent the nucleus.

ONTOGENESIS OF POLLEN SACCUS

The above-described morphology and size of the pollen sometimes seem to be variable (P1. I, figs. 10, 11; P1. II, fig. 8; Text-figs. 1, 2), but the variability reflects only different development stages of the pollen. During observation on a series of pollen variable in size, at first it will be found that the smallest pollen, measuring $8\ \mu\text{m}$ in diameter and $10\ \mu\text{m}$ in length, is short-ellipsoid in shape, with a round cross-section in the secondary plane and has only the obvious circular lobe; however, the concavity at the end of the major axis is very prominent (P1. I, figs. 7, 8; P1. II, figs. 8, 9; Text-fig. 4B). Next pollen increases in size on equatorial face and primary plane due to the development of equatorial lobes and becomes flattened-elliptical, measuring $18 \times 15 \times 10\ \mu\text{m}$, while the concavity begins to become obscure (P1. II, figs. 1, 6; Text-fig. 4C). Finally the pollen differentiates two distal lobes (P1. I, fig. 3; Text-fig. 4D). The more strongly the distal lobes are developed, the more obscure has become the distal part of the circular lobe (P1. I, fig. 3; Text-fig. 4E), which even looks like a furrow in the mature pollen (P1. I, fig. 3; Text-fig. 4F). This ontogenetic sequence of the pollen is shown in text-fig. 4, in which A represents the hypothetical first stage.

DISCUSSION

From the development stages of the pollen in *Cryptonoclea primitiva* it is found that the pollen grains are so variable in morphology that they could be assigned to different species and genera, and the polar surface may be differently defined when the pollen grains are dispersed. Hence the observation and establishment of the ontogenetic sequence will be helpful not only in understanding the reproductive function of fossil plants and enriching our knowledge of their reproductive biology but also in removing artificial taxa in palaeopalynology. In addition, the ontogenetic sequence demonstrates that the pollen grains

first differentiate the saccate lobes and then the lobes form the saccus. It is necessary to make a further discussion of the problem on the presence or absence of such an ontogenetic sequence in other pollen.

Observations on the ontogeny of pollen grains and ultrastructure of their saccus region indicate that the sexine is not initially separated from the nexine; then the alveolate organization is formed between both of them, and the radial tubes are expanded. These lead to the forming of the saccus. This process has been found in living cycads (Audran, 1981; Taylor, 1982), and may be helpful in dispersing the pollen grains but it is believed that no saccus is formed in living cycads since the expansion is so limited that it can be observed only under E. M. In the present pollen the expansion is so obvious that it could form the saccus. But the radial tubes are not separated from the nexine, and so the saccus is not fully developed. On the other hand, the saccus is apparently not pseudosaccate in nature due to the presence of the saccus-corporis region, in which there are no alveolate organizations. It seems that the pollen grains of *Cryptonoclea primitiva* are an intermediate between polysaccate and monosaccate pollen in phylogeny.

图 版 说 明

所有化石切片保存在中国科学院植物研究所。

图 版 I

1. 2. *Cryptonoclea primitiva* 花粉器官

1. 聚合花粉囊接近正中的纵切面。示聚合花粉囊壁、维管束(箭头所示)和花粉。切片号:GP2 309-4-3B/2。
2. 图1放大。注意维管束(下面的箭头)和花粉囊壁细胞的加厚的细胞壁(上面的箭头)。花粉囊的外面向着照片的上部。切片号:GP2 309-4-3B/26。

3—8. *Cryptonoclea primitiva* 的花粉

3. 花粉极面观, 聚焦位于远极面, 示远极气囊瓣和表面纹饰。切片号:SP3。
4. 未成熟花粉侧面一极面观, 示表面纹饰和明显的凹面(对着照片的左上方)。切片号:SP3。
5. 花粉极面观, 聚焦于赤道面, 示赤道气囊瓣侧面连接到本体上。B-B代表主切面。切片号:SP3。
6. 花粉侧面观, 聚焦于主切面, 示赤道气囊瓣比本体厚。C-C代表次切面。切片号:SP3。
7. 花粉侧面观, 聚焦于次切面, 亦赤道气囊瓣同本体的连接。A-A代表赤道面。切片号:SP3。
8. 未成熟花粉极面观, 聚焦于赤道面, 示环形气囊瓣及无明显的赤道气囊瓣。切片号:SP3。

9—11. *Cryptonoclea primitiva* 花粉

所有的图源于标本 GP2 309-4-3A。

9. 聚合花粉囊横切面, 示4个花粉囊和所含花粉。
10. 图1放大, 示原位花粉。
11. 花粉极面观, 图2箭头所示花粉的放大, 示花粉远极面纹饰和远极气囊瓣。注意2条远极气囊-花粉连接区。

图 版 I

1—9. *Cryptonoclea primitiva* 花粉

- 1—6. 源于标本 GP2 309-4-3A; 7. 源于标本 GP2 309-3-3B; 8. 9. 源于标本 GP2 713-2A。
1. 花粉侧面-极面观, 示近极面, 环形气囊瓣(箭头所示)垂直于赤道。注意对着照片右边是长轴端的凹面。
 2. 花粉极面观, 示赤道气囊瓣(箭头所示)。
 3. 花粉侧面-极面观, 示 2 个远极气囊瓣和 1 个环形气囊瓣(箭头所示)。注意 2 条气囊—本体连接区。
 4. 花粉侧面观, 通过次切面的正中切面, 示环形气囊瓣。
 5. 两粒花粉侧面观, 左边的花粉通过主切面的正中切面, 示环形气囊瓣、远极气囊瓣及近极面的花粉气囊连接区; 右下边花粉平行于次切面的切面, 示赤道气囊瓣。注意花粉的近极面不同于远极面(箭头所示)。
 6. 花粉侧面观, 通过赤道面的正中切面, 示两个赤道气囊瓣。
 7. 聚合花粉囊的横切面, 示维管束, 管胞为梯纹纹孔。下图为上面方框中图的 10 倍。
 8. 原位未成熟花粉, 示长轴远端的一明显凹面。
 9. 未成熟花粉的侧面观, 通过赤道面的正中切面, 示环形瓣和一凹面(箭头所示), 无赤道气囊瓣。

