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迄今世界最早被子植物花序化石的首次发现*

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提 要 首次报道迄今已知世界最早的被子植物花序化石——*Xingxueina heilongjiangensis* gen.et sp.nov.。该花序化石产于我国黑龙江鸡西早白垩世城子河组。花序由数十枚小花组成,其花粉具典型的被子植物特征,无明确的萌发口器。根据其所在层位下伏海相层化石佐证,以及与以色列等地早期被子植物花粉化石的对比等,该花序的地质时代可能为早白垩世 Hauterivian 晚期,或 Hauterivian 晚期至 Barremian 早期。文中还讨论了此花序及其花粉化石的发现在研究全球被子植物起源及早期演化等方面的重要意义。

关键词 花序 被子植物 最早期 鸡西 早白垩世

1 前言

1990—1991 年,笔者之一(孙革)与课题组郑少林、孙学坤、朴太元等,于黑龙江鸡西早白垩世城子河组首次发现了一批迄今已知世界最早的被子植物化石(孙革等,1992)。这些早期被子植物主要有:*Asiatifolium elegans* Sun, Guo et Zheng, emend. Sun et Dilcher, *Jixia pinnatipartita* Guo et Sun, emend. Sun et Dilcher, *Jixia chengzihensis* Sun et Dilcher (MS), *Jixia* sp., *Shenkuoa caloneura* Sun et Guo, emend. Sun et Dilcher, *Zhengia chinensis* Sun et Dilcher (MS)等。上述化石均为网状脉系的双子叶被子

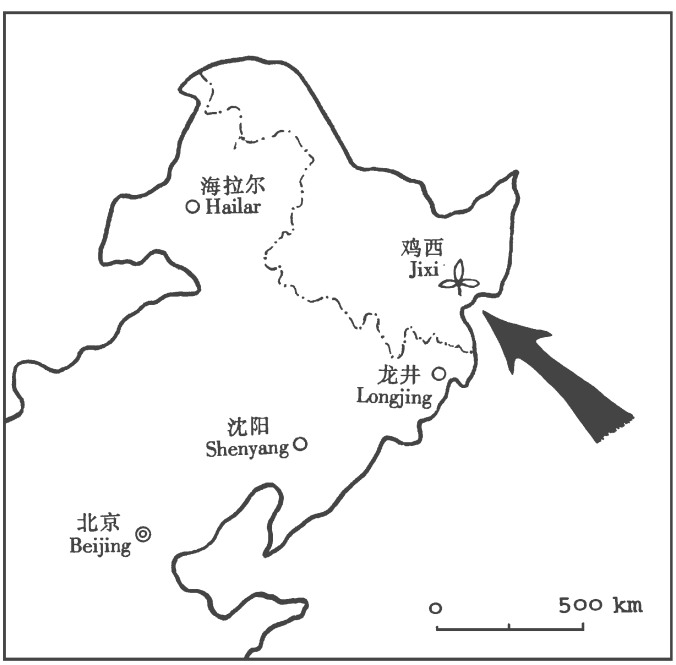

插图 1 黑龙江星学花序化石产地位置图
Geographic position of the locality of *Xingxueina heilongjiangensis* gen.et sp.nov.

* 国家自然科学基金(39370055)、中国科学院古生物与古人类学科特别支持经费(90020202)资助。

植物叶，形体小，具不规则羽状网状脉序，显示了较为原始的被子植物特征(孙革，1995；Sun and Dilcher，1996*)。此后不久，孙革在对上述化石材料的深入研究中，又首次发现了当前的花序及其花粉化石。1994 年起，经笔者共同研究，确认当前的花序化石是迄今已知世界最早的被子植物花序，当前的花粉是迄今已知中国最早的被子植物花粉(孙革，1995)。

当前的花序化石产于黑龙江省鸡西市城子河至滴道的公路北侧路堑、城子河组绿灰色粉砂岩之中(插图 1)。花序很小，长约 1.4cm，宽约 4mm，由数十枚螺旋状紧密排列的小花组成，每枚小花直径约 1mm，其上见大量被子植物花粉。花粉近圆形，直径仅 15—20μm，外壁呈细网状，具覆盖层及柱状层，无明确的萌发口器。花序基部具较长的花梗，其末端似与一双子叶被子植物叶片相连(插图 2)。

与当前花序及上述其它被子植物化石共生的蕨类及裸子植物主要有 *Equisetites burejensis* Vachr.，*Coniopteris burejensis* (Zal.) Seward，*Onychiopsis elongata* (Geyl.) Yok.，*Cladophlebis* sp.，*Acanthopteris gothanii* Sze，*Arctopteris* sp.，*Nilssonia sinensis* Yabe et Oishi，*Pseudocycas*? sp.，*Ginkgo* sp.，*Sphenobaiera* sp.，*Sphenolepis kurriana* Harris，*Elatocladus submanchurica* Yabe et Oishi，*Schizolepis* sp.，*Sagenopteris* sp.等。

当前花序所在的早期被子植物化石层之下为海相层，两者为连续沉积。经孙学坤、何承全研究，该海相层所含沟鞭藻化石主要有 *Canningia pistica* Hably，*Kiokansium polypes* (Cooks. et Eis.) Below，*Muderongia testudinaria* Burger，*M. tetracantha* (Gocht) Alberti，*Oligosphaeridium complex* (White) Davey et Williams，*Palaeoperidinium cretaceous* Pocock 等，时代为早白垩世 Valanginian—Hauterivian 期(孙革、郑少林等，1992)。当前花序所含花粉与以色列 Valanginian 晚期—Hauterivian 期被子植物花粉相近(Brenner，1994 函告；参见 Brenner，1996)，结合上述共生被子植物大化石的时代特征，笔者认为当前花序化石的时代很可能为早白垩世 Hauterivian 晚期，或 Hauterivian 晚期—Barremian 早期。

当前花序化石及其花粉的发现，为研究全球最早期被子植物的花及其演化、以及被子植物起源及起源中心等，提供了宝贵的材料及研究线索。与此同时，也为深入研究北半球早白垩世含煤地层对比及恢复东亚滨太平洋地区的古地理古气候等，提供了新的依据。

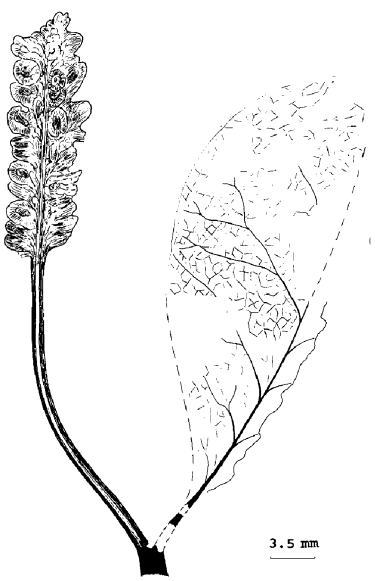

插图 2 *Xingxueina heilongjiangensis* gen. et sp. nov. 及其似连生的双子叶被子植物叶片形态

Xingxueina heilongjiangensis gen. et sp. nov. and its seemingly connected dicot leaf. 黑龙江鸡西，早白垩世城子河组

From Lower Cretaceous Chengzihe Formation of Jixi，Heilongjiang，China

* Sun G. and Dilcher D. L.，1996；Early angiospems from Lower Cretaceous of Jixi，China and their significance of study of the earliest occurrence of angiosperms in the world. Paleobotanist (in press).

2　属种描述

被子植物门　Angiospermae

双子叶植物纲　Dicotyledonae

星学花序属(新属)　*Xingxueina* gen·nov·

模式种　*Xingxueina heilongjiangensis* gen·et sp·nov·

词源　属名赠于国际著名古植物学家李星学院士，以表示对他在研究我国东北白垩纪被子植物作出重要贡献的敬意。

属征　见种的特征。

时代分布　早白垩世，中国黑龙江省。

黑龙江星学花序(新属、新种)　*Xingxueina heilongjiangensis* gen·et sp·nov·

(图版Ⅰ，图 1—7；图版Ⅱ，图 1—6；插图 2)

特征　花序似穗状，形体小，长约 1.4cm，顶端未保存，宽约 4.2—4.6mm，由数十枚小花组成，螺旋状紧密排列于花序轴上。花序轴粗壮，较直，宽约 1.3—1.5mm。小花近圆形，直径约 0.8—1.5mm，其细部构造尚不明。苞片角质层的内表面具发育的细条纹，略弯曲，多彼此平行，其上见大量被子植物花粉；苞片外表面不平坦，具不规则凹坑。花粉小，近圆形，直径约 15—20μm，外壁呈细网状纹饰，网眼小(直径约 0.2—1.0μm)，网脊宽约 0.3μm，略平滑，具明显的覆盖层及柱状层。未见明确的萌发口器。

花梗(pedicle)较粗壮，略弓曲，长约 2.0cm，宽约 1.2—1.5mm，其基部末端似与一双子叶被子植物叶片相连。该叶片近椭圆形，全缘，长约 3.5cm，宽约 2.0cm；叶柄长约 4.5mm。中脉明显，宽约 0.4—0.5mm，侧脉互生或亚对生，以宽角自中脉伸出，在中脉至叶缘距离约 1/2或 2/3 处分叉 1—2 次，之后交于边缘脉(intermarginal vein)；三级脉较细，与其次级脉结成多边形细脉网。

讨论　当前花序以其形体小、具较粗壮花序轴及较长的花梗、并产大量无萌发口器的被子植物花粉等为特征，区别于以往报道的任何早期被子植物花序。

以往报道的全球“最早”的被子植物花序化石是产于北美东部波托马克群(Albian 期)的双性花花序 *Virginianthus* (Friis *et al*.，1994)，其小花也很小，直径仅 2.2mm，具花梗；但其花粉具单沟，且时代较当前花序偏新。陶君蓉等(1992)曾报道产于中国吉林龙井大拉子组(Aptian—Albian 期)的雌性花托 *Archimagnolia*，该化石为印痕保存，特征欠完整，尚缺乏解剖研究，其时代也较当前花序偏新。

当前花粉的外部形态及无萌发口器(inaperturate)等特征，与 Brenner(1996)及 Brenner 等(1992)报道的、产于以色列 Valanginian—Hauterivian 海相夹层的被子植物无沟花粉十分相似；Brenner 认为两者可能属于同一种花粉(1994，函告)。但从细部结构特征看，当前花粉外壁的网脊(muri)相对较平滑，网眼略小，与以色列上述花粉似存在一定差别。常见于北半球早白垩世的被子植物花粉 *Clavatipollenites* 在外形上与当前花粉也有些相似，但前者具单沟。

在系统分类及演化方面，长期以来不少学者认为被子植物单沟花粉的沟状萌发口器(sulcus)源于具单沟花粉的裸子植物。Crane 等(1995)结合分支系统学研究，提出最早的被子植物源于兼具买麻藤目(Gnetales)及本内苏铁目特征的祖先类群。最近，Brenner(1996)提出了被子植物单沟花粉起源及演化的新模式，他认为早期被子植物具单沟花粉的沟(sulcus)是源于被子植物本身的早期演化，即由无沟(inaperturate)演化到具单沟(monosulcate)，并非起源于非被子植物的祖先类群。当前我国的花序及花粉新材料在一定程度上为 Brenner 的上述假说提供了证据。因为 Brenner 依托的以色列化石材料尽管时代也比较早，但为取自钻孔岩芯的分散花粉，无花粉母体生殖器官及整个植物体的其它证据。而我国的无沟被子植物花粉直接产于花序本身。尽管限于目前化石材料的保存状况尚难以确定当前花序是双性花抑或单性花，但从萤光显微镜下观察及角质层分析所显示的当前花粉的诸多原位特征看，似可以肯定当前我国无沟花粉的花药(anther)来自于当前花序的小花本身。此外，与当前花序似连生的双子叶被子植物叶片也可作为辅证。

当然，从我国鸡西早期被子植物化石材料看，与当前花序共生的还有其它 6 个双子叶被子植物分类群，它们的花序及花粉等特征还有待于进一步发现和研究，较之上述早期被子植物更早些的原始被子植物还有待于探寻。

Friis 和 Endress(1990)曾提出木兰亚纲的现生类群显示了有花植物最原始的特征。Crepet 和 Nixon(1994)提出被子植物的祖先类群可能具小而简单的花，这些花由轮状部分组成，形似现代金粟兰科、悬铃木科、黄杨科及樟科的花，并提出金粟兰(*Chloranthus*)和金鱼藻属(*Ceratophyllun*)是被子植物“最初的分枝”。当前我国的花序似着生于枝叶顶端的轴上，其似连生的叶子与木兰亚纲的叶子较为相似。当前的花粉也与木兰亚纲的一些分类群，如金粟兰科的草珊瑚属(*Sarcandra*)及胡椒科的豆瓣绿属(*Piperomia*)等的花粉有些接近。据此，笔者推测，当前花序很可能属于原始的木兰亚纲(Magnoliidae)。当然，其详细的系统分类位置还有待于今后新材料的进一步发掘和研究再作确定。

产地层位 黑龙江鸡西城子河，早白垩世城子河组。

当前化石及相关化石材料的采集工作中，曾得到郑少林、朴太元、尚玉珂、孙学坤、虞子冶、李春田及赵衍华等的大力协助。在花粉化石的研究中，曾得到美国纽约大学 G·Brenner 博士和南京地质古生物所王鑫甫、欧阳舒、曹流等的指导帮助。标本照相及绘图等工作曾得到茅永强、宋之耀以及美国佛罗里达大学 F·Lott 和 M·Muller 等的热情帮助。文稿完成后，承刘裕生博士审阅并提出宝贵意见。笔者一并表示衷心的谢意。

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DISCOVERY OF THE OLDEST KNOWN ANGIOSPERM INFLORESCENCES IN THE WORLD FROM LOWER CRETACEOUS OF JIXI, CHINA

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Key words angiosperm, inflorescence, Early Cretaceous, Jixi, Heilongjiang

ABSTRACT

A new discovery of the oldest known angiosperm (dicotyledonous) inflorescences in the world, *Xingxueina heilongjiangensis* gen·et sp·nov·from Lower Cretaceous Chengzihe Formation of Jixi, eastern Heilongjiang, China, is reported for the first time·

The inflorescence is elongate, spike-like, small in size, about 14mm long by about 4mm wide, consisting of numerous small florets borne helically upon a stout axis·The pedicle below the attachment of the florets is slightly arching, about 20 mm long by 1.5 mm wide and appears to be borne on the axis of a leaf·Florets are crowded, rounded in form and small in size, about 1.1—1.5 mm in diameter·Structure of individual floret has not been understood but in situ pollen were found· Pollen are nearly circular, 15—20 μm in diameter, seemingly inaperturate, with exine reticulate and tectate-columellate·

Associated with the present inflorescence, there are other early angiosperms including *Asiatifolium elegans* Sun, Guo et Zheng, emend·Sun et Dilcher, *Jixia pinnatipartita* Guo et Sun, emend· Sun et Dilcher, *J· chengzihensis* Sun et Dilcher(MS), *J*·sp·, *Shenkuoa caloneura* Sun et Guo, emend·Sun et Dilcher, *Zhengia chinensis* Sun et Dilcher(MS), etc·(Sun and Dilcher, 1996, in press)·Moreover, there are also abundant ferns, cycadophytes, ginkgoales, conifers and catoniales, such as *Equisetites burejensis* Vachr·, *Coniopteris burejensis* (Zal·)Seward, *Onychiopsis elongata* (Geyl·)Yok·, *Cladophlebis* sp·, *Acanthopteris gothanii* Sze, *Arctopteris* sp·, *Nilssonia sinensis* Yabe et Oishi, *Pseudocycas*? sp·, *Ginkgo* sp·, *Sphenobaiera* sp·, *Sphenolepis kurriana* Harris, *Elatocladus submanchurica* Yabe et Oishi, *Schizolepis* sp·, *Sagenopteris* sp·, etc· Based on the Valanginian—Hauterivian dinoflagellates from the marine beds underlying conformably the angiosperm-bearing beds in the formation, and on the correlations of the present angiosperm pollen to those from late Valanginian—Hauterivian of Isreal, the present inflorescences are considered late Hauterivian or late Hauterivian—early Barremian in age (Sun, 1995)·

Angiospermae

Dicotyledonae

***Xingxueina* gen. nov.**

Type-species *Xingxueina heilongjiangensis*

Etymology The generic name is in honour of Professor Li Xingxue, the academician of the Academy of Sciences, China, for his contributions to the study of the early angiosperms in Northeast China.

Diagnosis See the descriptions of the type species below.

Age and Distribution Early Cretaceous; eastern Heilongjiang, China.

***Xingxueina heilongjiangensis* gen. et sp. nov.**

(Pl. Ⅰ, figs. 1—7; pl. Ⅱ, figs. 1—6; Text-fig. 2)

Diagnosis Inflorescence elongate, spike-like, about 14mm long by 4.2—4.6mm wide, consisting of numerous small florets borne helically upon a stout axis. The pedicle below the attachment of the florets slightly arching, about 1.5 mm wide by 20 mm long and appears to be borne on the axis of a leaf. Florest subtended by bracts, nearly rounded, small, 0.8—1.5 mm in diameter and crowded helically upon the axis. Structure of the individual floret not understood but pollen *in situ* have been found. Pollen are nearly circular, 15—20μm in diameter, seemingly inaperturate, exine reticulate and tectate-columellate, muri more or less smooth, 0.3μm wide, areole irregularly polygonal, about 0.2—1.0μm in diameter.

Discussion The present inflorescence is characterized by its small size, stout and long pedicle and the presence of inaperturate pollen *in situ* and differs from other early angiosperm reproductive material known in the world. The present pollen bear some resemblance to the angiosperm pollen from late Valanginian—Hauterivian of Isreal (Brenner, 1996) but differ in having smaller aerole and smoother muri on the exine. Morphologically, the present pollen are more or less similar to the *Clavatipollenites* from Lower Cretaceous, but differ mainly in being non-monosulcate.

Small bisexual florets, *Virginiathus*, described from the Albian of the Potomac Group of North America, have been known as "the earliest inflorescences" before (Friis *et al.*, 1994). But, they are quite younger than the present Chinese inflorescences. Tao et Zhang (1992) reported a receptacle fossil, *Archimagnolia*, from the Aptian—Albian Dalazi Formation of eastern Jilin, China. However, the impression fossil has not been studied anatomically and it is also younger than the present inflorescence in age. Brenner (1996) reported on the oldest known angiosperm pollen from a core sample taken from two wells with sediments of late Valanginian to Hauterivian age in Isreal (Brenner and Bickoff, 1992). He suggested that the earliest known angiosperm pollen "consist of very small, circular and inaperturate forms with tectate-columellate exine". It is significant to note that the pollen Brenner reports are known only from dispersed pollen grains while we have the same pollen type in *situ* from an inflorescence which is seem-

ingly attached to a dicotyledonous leaf. Previously, it was thought that the sulcus of monosulcate angiosperm pollen was derived from a gymnosperm ancestor which had monosulcate pollen. While Brenner(1996)proposes a new model for the evolution of the monosulcate aperture in angiosperms. He suggests that the sulcus was developed from within the angiosperm lineage and that its presence in the angiosperms is entirely an angiosperm feature and not derived from a non-angiospermous ancestor. The present Chinese new material with the same type angiosperm pollen from the inflorescence *in situ* seems to give a support to Brenner's hypothesis in a certain degree. The occurrence of very similar, small, circular, inaperturate, reticular, tectate-columellate pollen from Lower Cretaceous of both China and Isreal, provides a whole set of new characters useful in understanding the nature of the world's earliest angiosperms. Friis and Endress(1990) suggest that the extant members of the Magnoliidae exhibit the most primitive characters of all flowering plant groups. They review the early fossil record about the primitive nature of the extant Magnoliidae. However, Crane *et al*.(1995)present the basal angiosperms as being represented by a monosulcate pollen type and derived from an ancestral complex shared with the Gnetales and Bennettitales. Some revisions appear to be needed with the recent hypothesis by Brenner(1996)and the present fossil flower *Xingxueina* provides many new characters that should be considered in the overall evaluation of primitive or early angiosperm characters.

Locality and Horizon Lower Cretaceous Chengzihe Formation; Jixi of Heilongjiang, China.

图 版 说 明

本文描述的化石标本保存于中国科学院南京地质古生物研究所标本室;标本产于黑龙江鸡西城子河,早白垩世城子河组。

图 版 Ⅰ

1—7. *Xingxueina heilongjiangensis* gen. et sp. nov.

1—3.示花序;野外号:WR47—100,登记号:SC10025;1.×1;2.×2;3.局部放大,×3。1A、2A为与花序可能连生的双子叶被子植物叶片;登记号:SC10026;1A.×1; 2A.×2。

4—7.示花粉。4.示花粉壁构造,SEM 0779,×20K。5.示小花角质层构造(内表面)及花粉,SEM 0759,×1.0K。6,7.示花粉形态,SEM 0782、0784;×4.4K,1.5K。

图 版 Ⅱ

1—6. *Xingxueina heilongjiangensis* gen. et sp. nov.

1,2.示花粉,图2为图1的放大,SEM 0760、0761,×1.8K,4.0K。3.示花粉,SEM 0801,×3.6K。4.示小花角质层构造(内表面)及花粉,SEM 0793,×540。5.示花粉壁构造,SEM 0781,×12K。6.示花粉,SEM 0774,×4.4K。