
Early angiosperms from Lower Cretaceous of Jixi, China and their significance for study of the earliest occurrence of angiosperms in the world

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This paper reports the recent study of the earliest known angiosperms in the world found from the Lower Cretaceous of Jixi, China, and first demonstrates the general information on the oldest known inflorescences *Xingxuetina heilongjiangensis* Sun et Dilcher (MS) contained in the Jixi early angiosperms. The inflorescences possess numerous pollen *in situ*, very small, inaperturate and tectate-columellate in exine, and can be compared to those from Valanginian-Hauterivian of Israel studied by Brenner (1995). Based on the comparison and on the marine beds, yielding Valanginian-Hauterivian dinoflagellates, underlying conformably the angiosperm-bearing beds the Jixi angiosperms are considered Hauterivian or Hauterivian-Early Barremian in age. The paper has also discussed the findings of the angiosperm-like or questionable angiosperm material newly from China and previously from Mongolia, proposed there might exist an original centre of angiosperms in East Asia. However, it would not be excluded that there were two original centres (East Asia and Eastern Gondwanaland) where the earliest angiosperms evolved and developed in parallel during the early time of Early Cretaceous.

Key-words—Early angiosperms, Original centre, East Asia, Early Cretaceous, Jixi, China.

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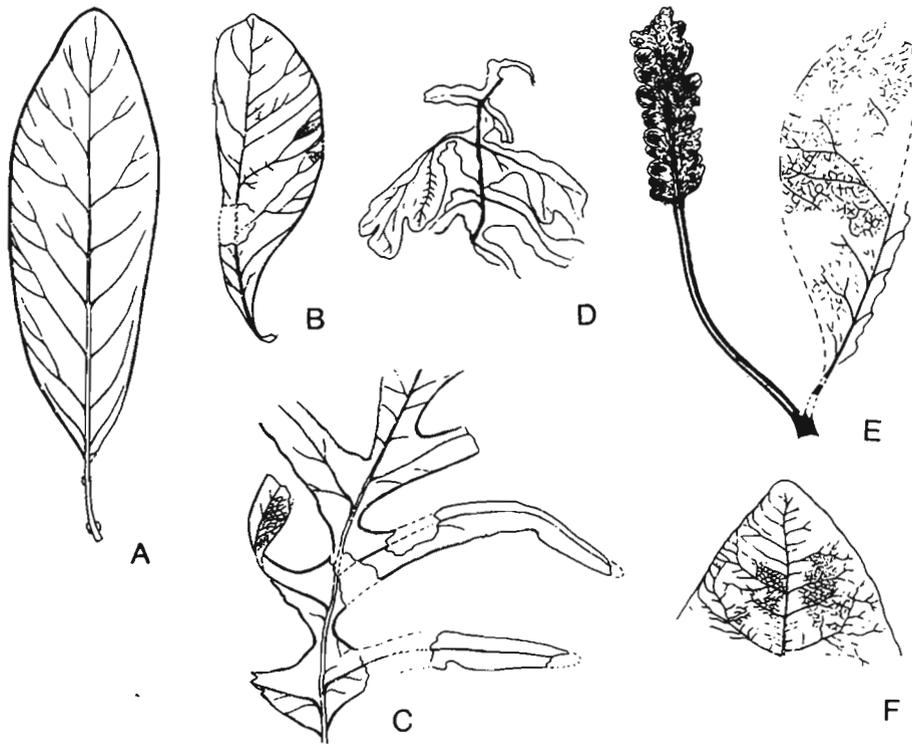
चीन में जिक्सि के अधरि क्रीटेशियस से प्रारम्भिक आवृतबीजी पौधे तथा विश्व में आवृतबीजीयों की प्रारम्भिकतम उपस्थिति के अध्ययन में इनका महत्व

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इस शोध-पत्र में चीन में जिक्सि के अधरि क्रीटेशियस से प्राप्त आवृतबीजी पौधों के आधार पर विश्व में प्रारम्भिकतम आवृतबीजी पौधों का अध्ययन किया गया है तथा सबसे पुराने पुष्पविन्यास *जिंक्सुवेना हीलोंगजियंगैन्सिस* सन व दिलचर (पाण्डुलिपि) पर सामान्य जानकारी प्रस्तुत की गई है। पुष्पविन्यासों में स्वस्थाने बहुत परागकण हैं जो बहुत छोटे, बिना छिद्र वाले, टेक्टेट-कॉल्यूमेलेट प्रकार के हैं तथा ब्रेनर (1995) द्वारा इस्राइल के वालन्जिनियन-हॉटीरीवियन से तुलनीय हैं। ये आवृतबीजी पौधे हॉटीरीवियन अथवा हॉटीरीवियन-प्रारम्भिक बैरेमियन आयु के प्रस्तावित किये गये हैं। इसी शोध-पत्र में चीन से आवृतबीजी-सदृश अथवा संदेहात्मक आवृतबीजी सामग्री, जो पहले मंगोलिया से ज्ञात थी, के बारे में भी विवेचना की गई है तथा प्रस्तावित किया गया है कि पूर्व एशिया में ही आवृतबीजी पौधों के उद्भव का केन्द्र था। तथापि, यह भी नकारा नहीं जा सकता कि इनके दो मूल उत्पत्ति केन्द्र (पूर्व एशिया एवं पूर्वी गोंडवानाभूमि) थे जहाँ पर कि प्रारम्भिकतम आवृतबीजी पौधों की प्रारम्भिक क्रीटेशियस काल में उत्पत्ति हुई तथा विकास हुआ।

THE origin of the angiosperms continues as one of the major unsolved mysteries in paleobotany today. However, the recent discoveries of the extremely early dicotyledonous angiosperms from Lower Cretaceous Chengzihe Formation of Jixi, eastern Heilongjiang, China provide valuable new data con-

cerning the nature of early angiosperms (Sun *et al.*, 1992; Sun, 1995). These early angiosperms consist of *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, *Zhengia*



Text-figure 1—Some early angiosperms from Lower Cretaceous Chengzihe Formation of Jixi, China. **A, B.** *Astatiifolium elegans* Sun, Guo et Zheng, emend. Sun et Dilcher, X 1.7, X 1.5; **C.** *Jixia pinnatipartita* Guo et Sun, emend. Sun et Dilcher, x 2; **D.** *J. chengzihensis* Sun et Dilcher (MS), X 2; **E.** *Xingxueina hellongjiangensis* Sun et Dilcher (MS), x 2.2; **F.** *Shenkuoa caloneura* Sun et Guo, x 2.

chinensis Sun et Dilcher (MS), etc. All these angiosperms possess simple and microphyllous leaves (max. 4.8 cm long), pinnate and irregular venations with reticulations. Some of them are recognized in cuticular characters in which stomata are anomocytic and anisocytic in type. Some angiosperm inflorescences were also found which are small (ca. 1.4 cm long and 0.4 cm wide), catkin-like, with very small pollen (ca. 15-20 μm in diameter), inaperturate, fine reticulate and tectate-columellate in exine (Text-figure 1).

Besides these angiosperms, there are abundant ferns, Bennettitales, Cycadales, Ginkgoales, conifers and Catoniales, associated with the angiosperms, including *Equisetites burejensis* Vachr., *Coniopteris burejensis* (Zal.) Seward, *Onychiopsis elongata* (Geyl.) Yok., *Arctopteris* sp., *Cladophlebis* sp., *Acan-*

thopteris gothanii Sze, *Nilssonia sinensis* Yabe et Oishi, *Pseudocycas* sp., *Ginkgo* spp., *Sphenobaiera* cf. *ikorfatensis* (Sew.) Florin, *Elatocladus submanchurica* Yabe et Oishi, *Sphenolepis kurruana* (Dunk.) Schenk, *Schizolepis* sp., *Sagenopteris* sp., etc.

Biostratigraphically, the Jixi early angiosperm-bearing beds mentioned above, overlay conformably Valanginian-Hauterivian marine beds yielding dinoflagellates, e.g., *Canningia pistica* Helby, *Kiokansium polypes* (Cooks. et Eis.), below, *Muderongia australia* Helby, *M. testudinaria* Burger, *M. tetracantha* (Gocht) Alberti, *Oligosphaeridium complex* (White) Davey et Williams, *Paleoperidium cretaceum* Pocock, etc. (Sun, Zhang et al., 1992). With considerations that the Jixi early angiosperms are more primitive in floristic charac-

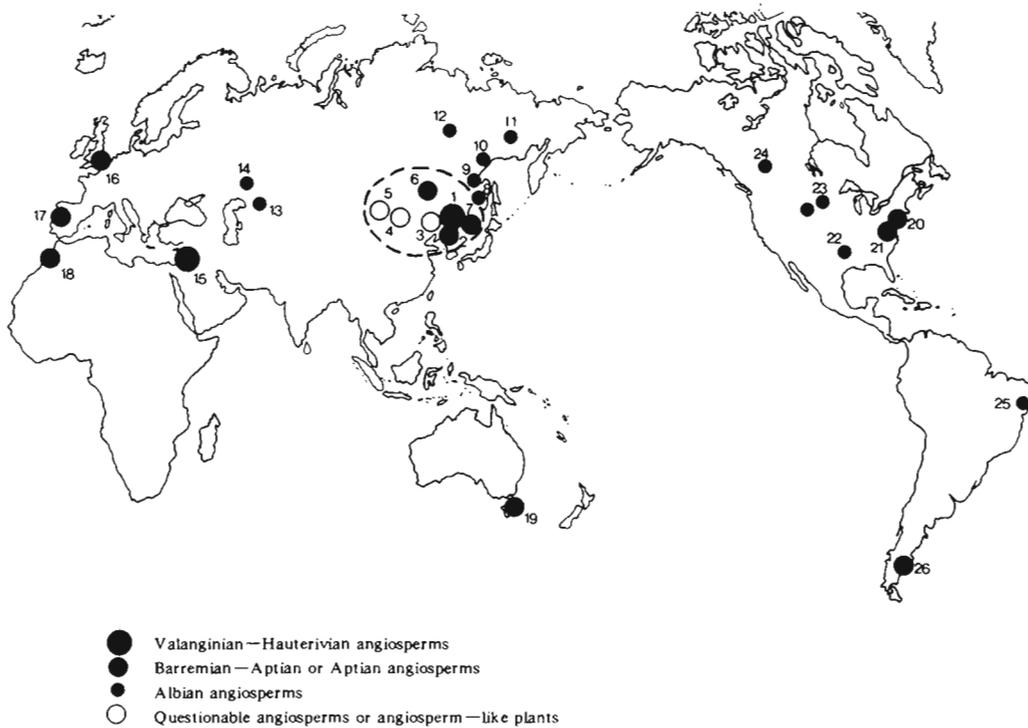
PLATE 1

All the specimens were collected from the Lower Cretaceous Chengzihe Formation of Jixi, Heilongjiang, China; and are housed in Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China. Unless otherwise stated, all the photographs are x natural size.

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| <p>1-9. <i>Astatiifolium elegans</i> Sun, Guo et Zheng, emend. Sun et Dilcher; fig. 9 is enlargement of fig. 1, X 2, PB16766; fig. 2 is counterpart of fig. 1, PB16767; fig. 7 is enlargement of fig. 3, X 2, PB16768; fig. 8 is enlargement of fig. 5, X 2, PB16772; 4, 6: PB16771, JS10003.</p> <p>10. <i>Jixia pinnatipartita</i> Guo et Sun, emend. Sun et Dilcher PB16773.</p> | <p>11. <i>Jixia chengzihensis</i> Sun et Dilcher (MS) X 2, PB16774.</p> <p>12-14. <i>Shenkuoa calooneura</i> Sun et Guo fig. 13, X 2; fig. 14 showing irregular venation in detail, X 5; PB16775.</p> <p>15. <i>Zhengia chinensis</i> Sun et Dilcher (MS) JS10004.</p> |
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PLATE 1



Text-figure 2—Geographical distributions of Early Cretaceous angiosperms and the presumed original centre of the angiosperms in the world. 1. Jixi (China); 2. Longjing (China); 3. Jianshangou (China); 4. Manlaj (Mongolia); 5. Gurvan-Eren (Mongolia); 6. Vitim River (Russian); 7. S. Primorye (Russian); 8-12. Eastern Siberia (Russian); 13, 14. W. Kazakhstan; 15. Isreal; 16. S. England; 17. Portugal; 18. Morocco; 19. Victoria (Australia); 20. Maryland (USA); 21. N. Virginia (USA); 22. Oklahoma (USA); 23. S. Dakota (USA); 24. Wyoming (USA); 25. Alberta (Canada); 26. Pernambuco (Brasil); 27. Patagonia (Argentina).

teristics than those from the Potomac Group of North America (Late Barremian-Albian, mainly), South Primorye of Russia (Aptian-Albian) and Dalazi of Jilin, China (Aptian-Albian), etc. and the Jixi angiosperms pollen can be compared to those from Valanginian-Hauterivian of Isreal (Brenner, 1995; Sun, 1995), the authors considered that the Jixi early angiosperms probably as Hauterivian or Hauterivian-Early Barremian in age (Sun *et al.*, 1992; Sun, 1995).

COMPARISON OF JIXI ANGIOSPERMS TO RELEVANT EARLY CRETACEOUS ANGIOSPERMS THROUGH THE WORLD

The well-known Early Cretaceous angiosperms in the world have been recorded from the Potomac

Group of North America (Fontaine, 1889; Berry, 1911; Brenner, 1963; Doyle & Hickey, 1972; Hickey & Doyle, 1977; Upchurch, 1984; Retallack & Dilcher, 1986; Crane *et al.*, 1993) and Portugal (Saporta, 1894; Teixeira, 1948; Crane *et al.*, 1995). These early angiosperms generally possess larger leaves palmate or palmately divided in shape, more or less regular in venations and monocolpate or triaperturate angiosperm pollen belonging to Late Barremian-Albian (Brenner, 1963; Doyle & Hickey, 1976; Retallack & Dilcher, 1986).

In former Soviet Union, more than 80 species of Early Cretaceous angiosperms were reported from South Primorye, eastern Siberia and Kazakhstan (Vachrameev, 1952; Samylyna, 1961; Krassilov, 1967;

PLATE 2

- 1-6. *Xingxuetina heilongjiangensis* Sun et Dilcher gen. et sp. nov. (MS).
- 1, 2. Inflorescence connected seemingly with a dicotyledonous angiosperm leaf. 2, X 2. No.: SC10025.
- 3-6. Pollen *in situ* from the inflorescence.
5. Showing the tectate-columellate exine of the pollen in detail from

fig. 6. 3: SEM0759, X 667. 4. SEM0761, X 2667; 5: SEM0779, X 13.3k; 6: SEM0782, X 4.4k.

- 7-9. *Zhengia chinensis* Sun et Dilcher gen. et sp. nov. (MS).
7. Showing a leaf, No.: SC01996.
8. A stoma from fig. 9, SEM0690, X 3.0k.
9. Stomatal zone in lower cuticle, SEM0689, X 650.

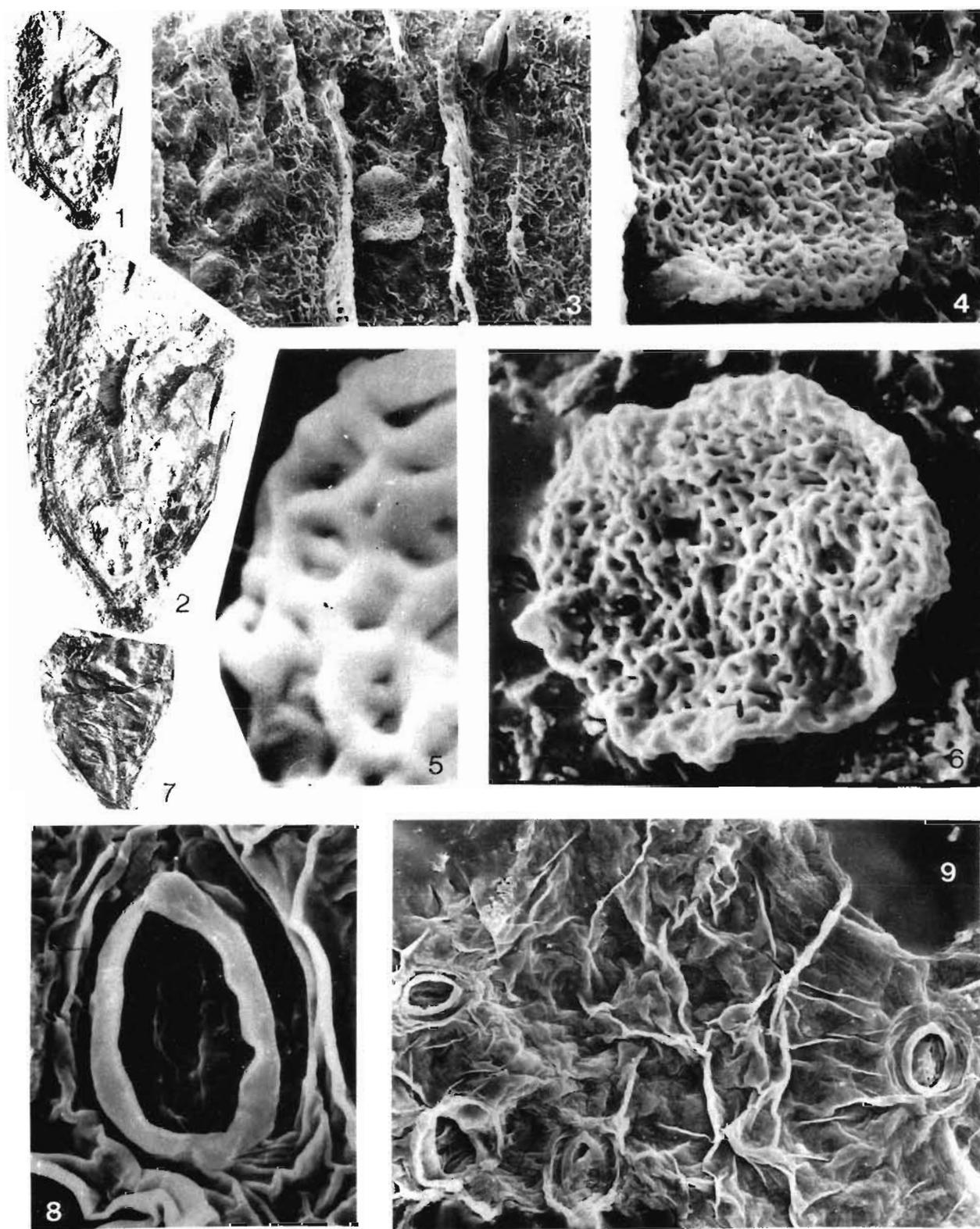


PLATE 2

Vachrameev & Kotova, 1977). Their foliar physiology can basically be comparable to those of the Potomac Group and Portugal mentioned above, and aged mainly in Aptian-Albian or Barremian-Albian (Vachrameev, 1988).

In South Hemisphere, an early angiosperm plant with flower and leaves was found from the Korumburra Group of Victoria, Australia (Taylor & Hickey, 1990); and some early angiosperms were reported from the Baquero Formation of Patagonia, Argentina (Romero & Archangelsky, 1986) and Santana Formation of northeastern Brasil. However, all the angiosperms are Aptian or Albian age.

In China, before 1992, the Early Cretaceous angiosperms were mainly recorded from the Dalazi Formation of Longjing, Jilin, including *Celastrophyllum* sp., *Platanus* cf. *newberryana* Heer, *Ranunculophyllum pinnatisectum* Tao et Zhang, *Saliciphyllum longifolium* Font., *Sapindopsis magnifolia* Font., *Sassafras* sp., *Yanjiphyllum ellipticum* Zhang, etc. (Zhang, 1980; Tao & Zhang, 1990, 1992). Their foliar features can be compared to those of the Potomac Group of North America and aged in Aptian-Albian. Besides, some angiosperm monocolpate and triaperturate pollen were found from the Bayanhua Group of Eren, Nei Mongol, e.g., *Brenneripollis* sp., *Clavatipollenites hughesii* Couper, *Astropollis asteroides* Hedl. et Norris, *Tricolpites lembodes* Wang et Song; their age is middle-Late Albian (Wang & Song, 1992).

Thus, it seems that the Jixi early angiosperms of China are more primitive than those relevant Early Cretaceous angiosperms known in the world both in floristic characters and biostratigraphic evidence. Krassilov (1982) reported two new taxa of angiosperm fruits from Gurvan-Eren, Mongolia; however, their nature has been recognized in question (Friis, 1985), although the material and its paleophytogeographic position are very important. It would be mentioned that the Jixi angiosperm inflorescences (*Xingxueina heilongjiangensis*) contain numerous inaperturate pollen *in situ* which resemble those from the Valanginian-Hauterivian of Isreal, studied by Brenner (1995). Therefore, the above-mentioned Jixi early angiosperms would be regarded as the oldest known angiosperm megafossils, including the inflorescences so far known in the

world. The new material from Jixi, China provides a whole new set of characters important in understanding the nature of the world's early angiosperms during the earlier time of the Early Cretaceous.

SIGNIFICANCE FOR STUDYING THE EARLIEST OCCURRENCE OF ANGIOSPERMS IN THE WORLD

The problem concerning where is the original site (centre) of angiosperms, has been interested by paleobotanists for nearly a century. Axelrod (1959) proposed that the angiosperms arose in the tropics and spread poleward, which has widely been acceptable, so far. The hypothesis is mainly based on that most of primitive modern taxa of angiosperms are living in the tropics or nearby the region. Doyle (1984) considered that the Northern Gondwana province (Northern Africa and South America) represents the most probable site for the initial radiation of the angiosperms. However, Brenner (1995) has believed that the pollen sulcus was derived from within the angiosperm lineage, not from a non-angiospermous ancestor, and the inaperturate pollen from Valanginian-Hauterivian of Isreal were the oldest pollen of the angiosperms in the world; thus he proposed that the Eastern Gondwanaland was the original site of the angiosperms.

It is interesting that the Jixi angiosperm pollen, seemingly inaperturate too, are very similar to those from the Isreal mentioned above (communicated by Brenner, 1994). It is much possible that the angiosperm pollen from Isreal and Jixi, China are the same or very close in age. However, the Jixi angiosperm megafossils consist of more than seven taxa in composition, at least. The fact seems to imply that there might exist some more primitive angiosperms in Northeast China or its neighbouring areas at an earlier time. It is worthy to mention that we have found some questionable angiosperms and angiosperm-like plants from the Yixian Formation of Jianshangou, western Liaoning, China, very recently. These material are very close in affinity to those from the Lower Cretaceous of Mongolia studied by Krassilov (1982). Krassilov described two new taxa (i.e., *Gurvanella dictyoptera* Krass. and *Erena steniptera* Krass.) as angiosperm fruits belonging to Neocomian; and proposed the "Central Asian origin of the angiosperms" (Krassilov, 1977, 1982). While the similar

questionable angiosperms or angiosperm-like material from the Jianshangou in China mentioned above is considered as about Berriasian or just the time spanning Jurassic-Cretaceous boundary in age. Therefore, it seems logical to consider that the East Asia region, including northeastern China and central-eastern Mongolia, would have been the original centre of the angiosperms in the world, from where the earliest angiosperms had evolved and radiated to the Eastern Gondwanaland and other regions (Text-figure 2).

However, since the oldest known angiosperm pollen were also found from the Valanginian-Hauterivian of Israel, it can not be excluded that there might exist two original centres in the world, i.e., both the East Asia and Eastern Gondwanaland. The earliest angiosperms of the Eastern Gondwanaland were probably parallel to those of the East Asia to evolve and develop during the early Early Cretaceous.

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