The oldest angiosperm——a tricarpous female reproductive fossil from western Liaoning Province, NE China*

DUAN Shuying (段淑英)

(Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China)

Received September 9, 1997

Abstract The fossil plant female reproductive organs each with a tricarpous were collected from the Yixian Formation, Chaoyang district, western Liaoning Province. The geological age of the Yixian Formation here is believed to be Late Jurassic, which places this fossil as the oldest angiosperm currently known. Its morphological characters are distinct from other known angiosperm reproductive organs as it has 3 ovaries, each with a terminal style and an apical stigma. 9 such organs compose a cyme. As this morphological arrangement is unique to this plant, a new genus and species has been established, named *Chaoyangia liangii* gen. et sp. nov.

Keywords: angiosperm female reproductive organ, cyme, Late Jurassic, Yixian Formation, Liaoning Province, China.

Fossil angiosperm flowers have been studied for more than 100 years and especially during recent 1—2 decades many new developments and scientific break-throughs have appeared, in particular, relating to the study of carbolic angiosperm flowers. This has led to an overall increase in the knowledge of the evolution of the earliest angiosperms. However, papers describing and interpreting primitive angiosperm inflorescences and infructescences are very few. This paper has studied a fossil plant cyme, which is composed of several female reproductive organs each with a tricarpous. The geological age of the cyme is Late Jurassic, placing it as the oldest currently recognised cyme in the world. The exquisite structure of the fossil and its oldest age have won the admiration of many botanists and palaeobotanists, and has considerably furthered our knowledge and understanding of the earliest angiosperms.

1 Description

Genus *Chaoyangia* nov.

Type species: *C. liangii* sp. nov.

Chaoyangia liangii Duan gen. sp. nov. (figures 1—4)

Diagnosis: Cyme composed of several female reproductive organs each with a tricarpous. Each organ with 3 distinct terminal styles and an apical stigma, each style linked to an ovary. Rachis with several parallel striations, branches opposite from a scape on an expanded node, and continuing to fork 2—3 times and becoming thinner distally. Reproductive organs terminate each rachis. Many thinner and forked linear appendages crowd on the outside of each organ.

Holotype: 9341 comprising fossil part (fig. 1) and counterpart (figure 2).

Locality and horizon: Chaoyang district, Liaoning Province, China. Yixian Formation of the

* Project supported by the Special Finances of Biological Sciences and Technology, Chinese Academy of Sciences (the special item of the Ministry of Finance of the People's Republic of China).

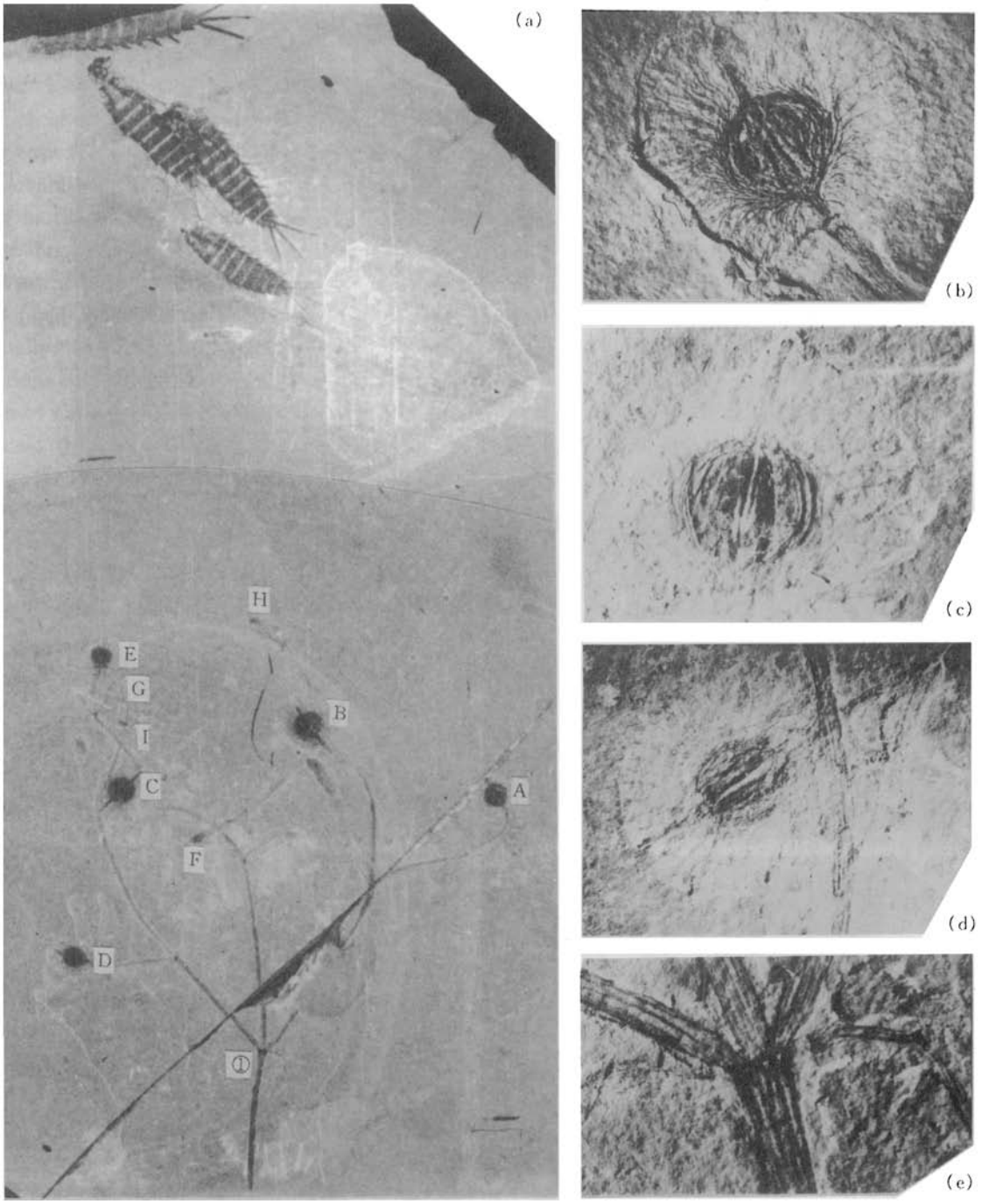

Fig. 1. *Chaoyangia liangii* comprising part. (a) *Chaoyangia liangii* and *Ephemeropsis trisetalis* on the same plane, ×0.7; (b) B, ×3; (c) E, ×4; (d) F, ×6; (e) ① ×6.

Late Jurassic.

Derivatio nominis: The genus name after the location of the fossil, the species name is in honour of the fossil collector Liang Shikuan.

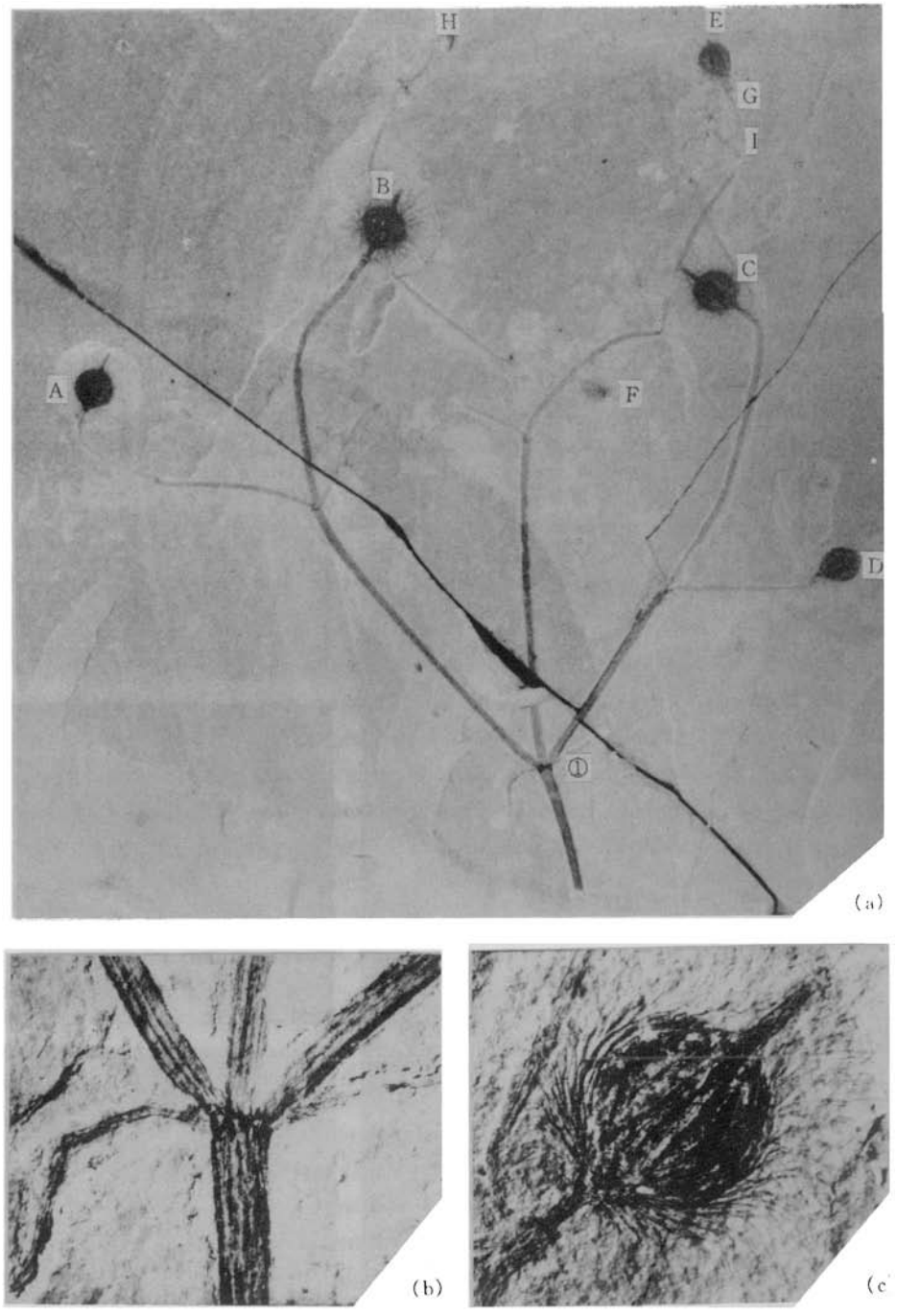

Fig. 2. *Chaoyangia liangii* counterpart. (a) *Chaoyangia liangii*, ×1; (b) ① ×6; (c) C ×5.

Remarks: This fossil plant is a part of a cyme, which is composed of 9 round or elliptic female reproductive organs of different sizes each with a tricarpous (A—I). Of these, 6 organs are visible to the naked eye (A—F) and 3 very small organs (G—I) are nearly invisible to the naked eye, but visible under the binocular microscope. All of them have the same structure: 3 stigmas, 3

styles and 3 ovaries. The diameter of the ovaries ranges from 4 to 6 mm, with 3 very clear styles positioned at the top of each. Styles are more than 3 mm long and some show stigmas at their apex, a clear carpophore at the base of the ovary, about 1.5 mm long and 0.6—0.8 mm wide which is distinctly separated from the rachis. Around the organs crowd very thin and delicate linear appendages. Outside of the larger organs (for example B, C) the appendages are thicker and fork more, some are folded on top of each other, but are never reticulated; outside of the smaller organs the appendages are thinner and less forked. The rachis has several parallel-striations, and branching is opposite from a scape which is about 1.2—1.5 mm wide at its lower part. On the lowest node two thinner rachises (1 and 0.9 mm wide respectively) and two small leaves (?) are arranged opposite from the scape. Each rachis continues to fork 2—3 times and becomes thinner distally. On the rachis about 7—10 mm below the smaller organs (F-I) very small tooth-like projections occur (fig.3(c), (d), fig.4), but these do not occur below the larger organs. The function of these projections is not known. The small leaves (?) are only visible on the branching nodes, they are very fine and possess parallel veins as shown clearly on the first forked node (fig.1(e), figure 2(b)).

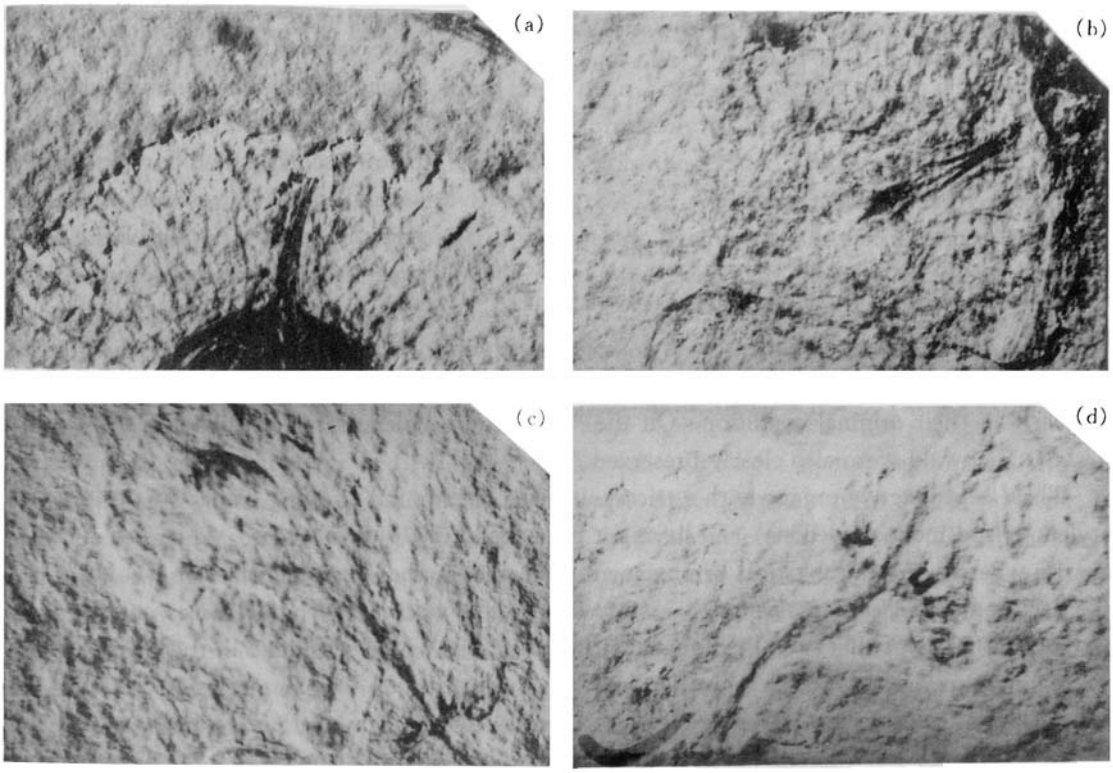

Fig. 3. (a) Style and stigma, ×10; (b) G in fig. 1 showing 3 styles and linear appendages, ×10; (c) H in fig. 1 showing styles and tooth-like projection, ×6; (d) tooth-like projection under G in fig. 1, ×10.

Discussion and comparison: The fossil is composed of 9 (A—I) reproductive organs each with a tricarpous. The structure of each organ is the same and has been interpreted as a tricarpous flower with 3 styles (and apical stigmas) connecting 3 ovaries. According to the arrangement of the large and small organs, this flower belongs to a cyme; for example, F branched from B, G branched from C, F and G are much smaller than B and C (fig. 2(a)). This structure is unique

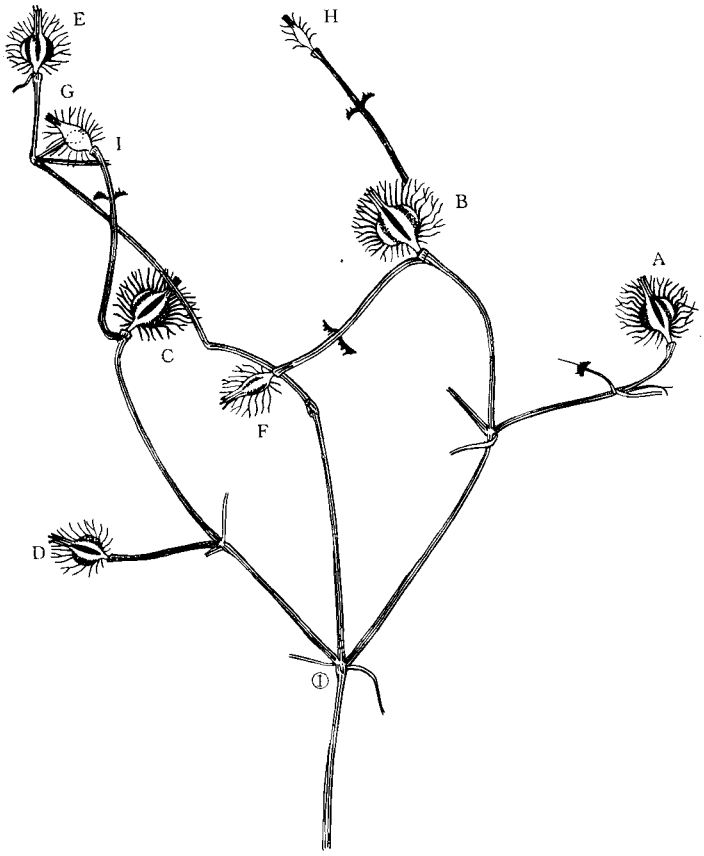

Fig. 4. Sketch of *Chaoyangia liangii* from figure 1(a).

to angiosperms, indicating that this plant with such reproductive organs could not belong to plants of other affinities such as algae, bryophytes, ferns or gymnosperms. Thus, this plant is an angiosperm without doubt. The crowded linear appendages may be kinds of strigose or spines, growing from the exocarp and may serve to protect the reproductive organs. Our investigations did not find any stamens (perianth, petal, filament or anther) and did not recover any pollen from the stigmas, as only the female reproductive organs were observed. From these observations they are inferred to be young fruits. The combination of the thin and delicate scape (without a main vascular strand but composed of several parallel vascular strands), and the delicate nature of the leaves make it clear that this plant may be a herb, which probably lived in the water or a marshland environment with seasonal variation in habitat. The fossil preservation retaining such fine details indicates that the fossil was not transported a great distance as the fossils are nearly in their original condition. On the same bedding plane insect fossils of *Ephemeropsis trisetalis* Eichwald were also clearly preserved.

These reproductive organs with a tricarpous have been found in living plants (the original dicotyledons and monocotyledons) and have not been found in the fossil record. It was to our great surprise when this morphological arrangement appeared in the Yixian Formation, because it is considered an advanced angiosperm character, rather than a primitive character as would be anticipated from fossils of this age. Primitive angiosperm fossils have been found in the Dalazi Formation of Jilin Province[1], which is not far from Chaoyan district. The characters of the leaves are very small, with very simple reticulative veins, the fruits were close to that of the living plants of the Magnoliaceae. Such fossils have never been found in western Liaoning. In recent years some scholars have suggested that some kind of herb may be the oldest angiosperm according to their studies of the plastid gene rbcL[2]. However, to date their reproductive organs are unknown. In our investigation we did not find the whole plant of the cyme because the fossils were fragmented prior to deposition, so that only this part of the plant has been identified. This creates a problem of how to compare the fossil with any living angiosperm plant. We think it is likely that this plant may be a short branch on the systematic evolution tree, and perhaps represents a failed experiment in plant diversification, an evolutionary dead-end playing no part in the subsequent plant

evolution. So it is here considered suitable not to assign this fossil plant to any living angiosperm family.

There are only a few primitive angiosperm fossil reproductive organs which can be compared with our fossil. One fossil, *Gurvanella dictyoptera* Krassilov, found in the Gurvan-Eren Formation of the Early Cretaceous of Mongolia[3] is of superficial similarity to our fossil. However, it was described as "fruits winged, stalked, bilocular, symmetrical, wing membraneous, reticulate" and Krassilov compared it with the living angiosperm *Ptelea trifoliata* L. (Rutaceae). The cyme found in China is very different from this, so the two fossils could not belong to the same genus. Furthermore, the fossils found in Mongolia are only two individual fruits, and are poorly preserved. Each has a very short style, the stigma is not visible and the wing membrane (?) is incomplete, so its nature as a winged fruit is dubious. It was found in the Early Cretaceous (more than 100 million years old). There were neither leaves nor stem or rachis on this fossil. It is suggested by the present author that when studying fossils of this age where whole plant information is so limited, comparing them with living plants and placing them in the same genus and species as living plants is inappropriate.

2 The geological age of the fossil

The fossil plant was excavated from the Yixian Formation of Chaoyang district, western Liaoning Province. The geological age of Yixian Formation has been discussed for a long time. It constitutes part of the famous Rehol (Rehe) biota from the 1920s. The Rehol biota contains very plentiful fossils called the *Eosestheria-Ephemeropsis-Lycoptera* assemblage. Its geological age ranges from the Late Jurassic to the Early Cretaceous. Some scholars consider it to be of Late Jurassic while others consider it to be of the Early Cretaceous. This stratigraphic dispute still continues. From the assemblage of fossil plants, it is the author's opinion that the Yixian Formation should belong to the Late Jurassic. The present author has studied many details concerning the Middle Jurassic floras and the Early Cretaceous floras in N and NE China[4—6]. The two periods contained very rich fossil plant assemblages with each having more than 100 species. For example, a lot of ferns, cycadales and bennetitales, as well as ginkgoales and coniferales, the large leaves of ginkgophytes (*Ginkgo*, *Ginkgoites*, *Baiera*, *Sphenobaiera*, etc.) developed luxuriantly. Of course, the species are very different in the assemblages of two periods. The abundance of plant materials is reflected in a large number of coal mines extracting coals from both of these periods. However, the Late Jurassic flora is seldomly encountered, as is also the case in Russia and Japan[7]. In N and NE China the localities of the Late Jurassic floras are less than 10 and the fossil plants are less than 60 species[8—10], mostly the fragments of gymnosperms, for example the genera *Elatocladus*, *Elatides Pityophyllum*, *Schizolepis*, *Phoenciopsis* and *Czekanowskia*. Large leaf genera of the ginkgophytes were found very rarely. There are few fragments of ferns and horsetails, for example, a few species of *Onychiopsis*, *Cladophlebis* and *Equisetum*. This situation indicates that during the Middle Jurassic and the Early Cretaceous the climate was very warm and humid, very suitable for plant growth. In contrast to this, the Late Jurassic climate was warm but very dry.

During the last decade according to concepts of biostratigraphy and event stratigraphy some scholars have considered the Rehol biota to be divided into two parts: the Late Jurassic part (*Eosestheria-Ephemeropsis-Lycoptera* assemblage in the restricted sense) and the Early

Cretaceous part. The Yixian Formation and Jiufotang Formation are assigned to the Late Jurassic[11]. This opinion has gained support from other scholars according to their studies of different fossils[12], but there is a different view from some who consider the Yixian Formation to be of Early Cretaceous age[13]. At the same time when the fossil plant described above was deposited, the famous oldest fossil bird: *Confuciusornis sanctus* Hou occurs in the same locality and horizon. After comparison *Confuciusornis* with *Archaeopteryx* found in marine strata in Germany, Hou et al. considered the Yixian Formation to be Late Jurassic[14] too.

Several years ago the oldest angiosperm flora in the world was found in the Chenzihe Formation of Heilongjiang Province, NE China by Sun Ge et al.[15]. However, this flora comprises chiefly the leaves of angiosperms and the geological age was believed to be Early Cretaceous. So the fossil cyme found in the Yixian Formation is the oldest angiosperm reproductive organ in the world known up to now.

Acknowledgement The author would like to express her warm thanks to many professors and experts in the Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, who helped to study the fossil, especially to Prof. Li Zhenyu, who gave valuable advice. Dr. Zhang Daming helped with photography under the binocular microscope. The author is very grateful to Dr. J. Hilton in the Laboratory of Palaeobotany, who helped make a linguistic revision of the manuscript.

References

1 Tao Junrong, Zhang Chuanbo, Two angiosperm reproductive organs from the Early Cretaceous of China, *Acta Phytotaxonomica Sinica* (in Chinese with English abstract), 1992, 30(5): 423.
2 Chase, M.W., Soltis, D. E., Olmstead, R. G. et al., Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene rbcL, *Ann. Missou. Bot Gard.*, 1993, 80(3): 528.
3 Krassilov, V. V., Early Cretaceous flora of Mongolia, *Palaeontographica*, Abt. B, 1982, 181:1.
4 Duan Shuying, *The Jurassic Flora of Zhaitang, Western Hills of Beijing*, Stockholm: Stockholm University Press, 1987, 1—95.
5 Deng Shenghui, *Early Cretaceous Flora of Huolinhe Basin, Inner Mongolia, Northeast China* (in Chinese with English abstract), Beijing: Geological Publishing House, 1995, 1—125.
6 Duan Shuying, Chen Ye, Study on the morphology of *Nilssoniopteris buolinbensis* Duan et Chen sp. nov., *Palaeobotanist*, 1996, 45:355.
7 Vachrameev, V.A., *Jurassic and Cretaceous Floras and Climates Throughout the World* (in Russian), Moscow: Nauka, M., 1988, 1—230.
8 Yang Xuelin, Sun Liwen, Fossil plants from the Shahezi and Yingchen Formations in southern part of the Songhuajiang-Liaohe basin, NE China, *Acta Palaeontologica Sinica* (in Chinese with English abstract), 1982, 21 (5):588.
9 Cao Zhengyao, Fossil plants from the Longzhaogou group in Eastern Heilongjiang Province (II), *Fossils From the Middle-Upper Jurassic and Lower Cretaceous in Eastern Heilongjiang Province, China* (in Chinese with English abstract), Harbin: Heilongjiang Science & Technology Publishing House, 1983, 22—50.
10 Duan Shuying, Jurassic floras and dinosaurs of China, *The Continental Jurassic, Flagstaff: Museum of Northern Arizona Bulletin*, 1996, (60): 319.
11 Liu Benpei, Chen Fen, Wang Wuli, On the non-marine Juro-Cretaceous boundary in eastern Asia in the light of event stratigraphy, *Earth Science* (in Chinese with English abstract), 1986, Sep., 11(5): 465.
12 Ren Dong, Lu Wuli, Guo Ziguang et al., *Faunae and Stratigraphy of Jurassic—— Cretaceous in Beijing and the Adjacent Areas*, Beijing: Seismic Press, 1995, 1—222.
13 Li Peixian, Su Deying, Li Yougui et al., The chronostratigraphic status of the Lycopteris-bearing bed, *Acta Geologica Sinica* (in Chinese with English abstract), 1994, 68(1): 87.
14 Hou Lianhai, Zhou Zhonghe, Gu Yucai et al., Introduction to Mesozoic birds from Liaoning, China, *Vertebrata Pal. Asiatica* (in Chinese with English abstract), 1995, 33(4): 261.
15 Sun Ge, Guo Shuangxing, Zheng Shaolin et al., First discovery of the earliest angiospermous megafossil flora in the world, *Science in China*, Ser. B, 1993, 36(2): 249.