A new lycopsid megaspore cone from the Upper Devonian of Chaohu, China

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Received April 2000; accepted for publication January 2001

A new small lycopsid cone, *Minostrobus chaohuensis* gen. et sp. nov., is described from the upper part of Wutung Formation (Famennian) of Chaohu, Anhui, China. Six sporophylls in each whorl are tightly arranged on the cone axis. Each sporophyll consists of a short pedicel and a narrow lamina with smooth margins. One spherical to spherical-ellipsoidal sporangium is attached directly to the adaxial surface of each sporophyll. Each sporangium contains four megaspores. A solid exarch protostele occurs at the centre of the cone axis, and a mesarch protostele in the base of the sporophyll. *M. chaohuensis* is interpreted as a small, herbaceous, heterosporous lycopsid.

ADDITIONAL KEY WORDS: fossil – Wutung formation.

INTRODUCTION

To date, few lycopsid cones have been described or reported from the Late Devonian (Chaloner, 1968; Fairon-Demaret, 1977, 1991; Chitaley & McGregor, 1988; Chitaley, 1996; Sze, 1936; Zhi, 1974; Arnold, 1933, 1935; Li, Dou & Sun, 1986). However, the late Middle and Late Devonian is a transitional period between the first appearance of lycopsids (Late Silurian and Early Devonian) and the acme of their diversity and evolution (Carboniferous), and so new information about Late Devonian lycopsids is both necessary and important.

In this paper, a new fossil cone from the Upper Devonian of Chaohu, Anhui, China, is described from many specimens that allow a good understanding of both morphology and anatomy.

LOCALITY, GEOLOGICAL AGE, MATERIAL AND METHODS

The specimens were collected from Shizikou, 3 km north of Chaohu City, Anhui Province, east China (Fig. 1). The locality is in a small quarry, on the south side of Beishan hill, c. 400 m west of a special railway track from the machine factory to the railway station. The GPS location of the locality is 31°38′08″N and 117°51′08″E (WSG84 datum). It is situated in the middle of 2-m thick lens of black shale (plant-bearing bed) below a prominent 1-m thick sheet sandstone and above a heavily mined out 1-m thick white soapy claystone.

The horizon is in the upper part of the Wutung Formation. According to Liao & Qi (1989) and Cai & Wu (1994), the age of the Wutung Formation is from Late Devonian to Early Carboniferous. The present specimens were collected from black shales which have also yielded (Fig. 2). *Leptophloeum rhombicum* Dawson, *Sublepidodendron mirabile* (Nathorst) Hirmer, *Sublep.*
wusihense (Sze) Sze, Cyclostigma kiltorkense Houghton, Lepidodendropsis hirneri Lutz, Lepidostrobus grabavi Sze, Hamatophyton verticillatum (Gu et Zhi) Li, Cai & Wang, Sphenophyllum lungtanense Gothan & Sze, and Archaeopteris macilenta Lesq. Cai & Wu (1994) have reported Retispora lepidophyta (Kedo) Playford, from the same bed. On the basis of the flora itself, the plant-bearing bed is Late Devonian (Famennian) (Cai & Wu, 1994).

The plant fossils are clearly exposed on the blackish matrix, and are coloured white (calcium), brown (iron oxide) and black (coal). Figure 8 shows a compression specimen, partly permineralized. The white areas are the sporangia and cone axis, the black parts are the sporophylls, the brown parts are the remains of permineralizations. Some megaspores are found in the white sporangia, and are black.

Several techniques have been used to extract maximum information from the specimens. The dégagement (Leclercq, 1960; Fairon-Demaret, Hilton & Berry, 1999) was very useful for compression specimens and revealing detailed data of cone morphology. Some megaspores were transferred from the sporangia to scanning electron microscopy (SEM) stubs by a small paintbrush. The permineralized specimen was extracted from the cone, and transferred to a SEM stub. After observation of general morphological features, it was broken in order to observe details of anatomical structure.

Photographs were taken using a large format camera and a Nikon SMZ-U Microscope with a Nikon C-FPS 230 fluorescent lamp. A JSM 6300 Scanning Electron Microscope was also used.

All figured specimens (prefix PB) are housed at the Nanjing Institute of Geology and Palaeontology, The Chinese Academy of Sciences.

### DESCRIPTION OF SPECIMENS

#### MORPHOLOGY

This is based on 50 fragmentary cone specimens. The largest is 120 mm long (Fig. 3), and 6 mm wide, excluding the distal part of the sporophylls. In all cases, both ends of the cone are missing. The diameter of the preserved fragments does not appreciably change along their entire length. The holotype (Fig. 8) is 65 mm long, and 6 mm wide.

Most specimens show the cone axis (Figs 4, 10, 12, 14, 15), which is c. 1.2 mm wide. The sporophyll cushions are circular in profile, c. 0.4–0.7 mm in diameter (Figs 5, 12, 17). The morphology of the sporophyll bases are shown in Figures 14 and 15. The sporophyll bases are inserted at an angle of 20–30° from the upright, then curve distally at an angle of 80–90°. The sporophyll bases are arranged at an angle of about 30–40° clockwise (Fig. 15). The distance between whorls is about 1.5 mm. Three to four sporophyll bases are observed on one side of the compression (Fig. 12a). Each whole comprises six sporophyll bases.

At the base of the sporophyll is a short stalk,
Figures 3–10. Minostrobus chaohuensis gen. et sp. nov. Fig. 3. The longest preserved specimen. PB 18749. Scale bar = 8 mm. Fig. 4. Detail of cone axis and sporangia from Fig. 3, arrow. Scale bar = 1 mm. Fig. 5. Detail of the sporophyll cushions and bases. Scale bar = 2 mm. Fig. 6. One sporangium with two megaspores. Scale bar = 0.4 mm. Fig. 7. One cone. PB 18750. Scale bar = 8 mm. Fig. 8. One cone, with petrified part (arrow a), PB 18751, holotype specimen. Scale bar = 8 mm. Fig. 9. Detail of the sporophylls and sporangia from Fig. 8 (arrow b). Scale bar = 2 mm. Fig. 10. One sporangium at the adaxial surface of the sporophyll. PB 18752. Scale bar = 2 mm.
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Figure 11. A, one sporangium at the adaxial surface of sporophyll (based on the specimen of Fig. 3, arrow). Scale bar = 1.5 mm. B, sporangium with megaspores, arrow showing the sporophyll base (based on the specimen of Fig. 10, arrow). Scale bar = 2 mm.

Figure 12. A, sporophyll bases on the cone axis (based on the specimen of Fig. 14, arrow). Scale bar = 1 mm. B, sporophylls and cushions (based on the specimen of Fig. 17). Scale bar = 2 mm.

c. 0.5–0.7 mm wide and less than 0.5 mm long, inserted perpendicular to the axis (Figs 9, 10). Distal to the stalk, the leaf turns sharply to make an angle of 45° or less to the axis.

The distal part of the sporophyll is visible in most specimens (Figs 3, 5, 7–10, 13, 17, 18), and 6–8 mm long. It is flattened with smooth margins and forms a lamina, c. 1.5–2.2 mm wide (Figs 9, 17, 18). The lamina progressively tapers towards the apex of sporophyll, which is pointed and curved (Fig. 12b). A single vein is present in the specimen (Fig. 18), and extends to the sporophyll apex.

Every sporophyll is associated with one sporangium on its adaxial surface (Fig. 11a). Usually, the sporangia are white (Figs 3, 4, 6, 8–10, 16). A sporangium is spherical to spherical-elliptical in profile (3-D), about 2–3 mm in diameter. There is no pedicel. The sporangium is allied to the adaxial surface of the lamina (Figs 4, 9, 10). The surface of the sporangium is smooth, and about 0.2–0.4 mm thick (Figs 4, 6, 10). No dehiscence line nor mechanism have been observed.

The specimen, figured in Figures 6 and 10, shows that the megaspores are observed in side view. Two megaspores are very clearly visible (Fig. 6); the remaining ones overlap (Fig. 11b). In general, there are four megaspores on one sporangium. There are no empty sporangia and no microsporangia.

A specimen may show one in situ megaspore (Figs 9, 10 arrow) or two (Fig. 21). The proximal pole of the megaspore is seen in Figure 22. The megaspore has a more or less circular amb and is nearly pear-shaped in equatorial view. Megaspores are 600–800 μm in equatorial width and 800–1300 μm in total height. The spore body is about 500–650 μm long. The gula is about 450–500 μm x 100–150 μm in height x basal width. Trilete ridges are elevated as a hologula. The trilete ridge is tongue-like in shape, with a round apex. There are three radial ridges, about half as long as the trilete ridge, which are attached to the base of the trilete ridge. The surface of gula is nearly smooth. The rest of the spore surface is covered with scattered biform ornamentation (Fig. 23). The bases of the biform ornamentation are tubercles bulbiferous in shape, about 10–18 μm in diameter and 10–25 μm long, with sharply pointed ends. Because of preparation problems, all megaspore surfaces are cracked.

ANATOMY

The centre of the cone axis is occupied by a xylem strand (0.2 mm diameter), also seen in compression (Fig. 4, black part). Two cross sections show the most striking structures of the central xylem strand (Figs 25, 31), which is about 250 μm in diameter. During preparation, the centre of the protostele broke and split (Figs 27, 31). The phloem and cortex cells are not preserved in these sections.

The xylem is all primary, exarch and forms a solid strand entirely composed of tracheids (Figs 26, 27, 31, 32). The protoxylem forms 12 ridges around the metaxylem core (Fig. 24). The protoxylem tracheids are circular in cross-section, c. 5–10 μm wide (Figs 26, 33). The metaxylem tracheids are polygonal in cross-section, 18–35 μm wide, and c. 1.5 μm in wall thickness (Fig. 28). The middle lamella is about 1.0 μm thick (Fig. 28).

The cylindrical xylem trace to the sporophyll (Figs 29, 30) is about 45–50 μm in diameter, and mesarch. The central annular protoxylem tracheids are circular, c. 4–5 μm wide. The peripheral metaxylem tracheids are circular to polygonal, c. 6–8 μm wide, and are scalariform and reticulate.

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A NEW UPPER DEVONIAN LYCOPSID CONE FROM CHINA

Figures 13-23. *Minostrobus chaohuensis* gen. et sp. nov. Figs 13, 14. Cones. PB 18753, 54a, 54b. Scale bar = 8 mm. Fig. 15. Detail of cone axis and the sporophyll bases from Fig. 14 (arrow). Scale bar = 0.5 mm. Fig. 16. One spherical sporangium at the adaxial surface of sporophylla. PB 18755. Scale bar = 3.2 mm. Fig. 17. Detail of the sporophyll cushions and sporophylls from Fig. 13 (arrow). Scale bar = 2 mm. Fig. 18. Detail of one sporophyll with one vein from Fig. 17 (arrow). Scale bar = 0.8 mm. Figures 19-23. SEM of megaspore. Fig. 19. One megaspore. Scale bar = 1 mm. Figs 20, 21. One megaspore. Scale bar = 200 μm. Fig. 22. The top view of one megaspore, with the trilete ridges. Scale bar = 200 μm. Fig. 23. The biform ornaments on the surface of megaspore (detail of Fig. 22 arrow). Scale bar = 20 μm.
Two longitudinal sections show the tracheids of the primary xylem (Figs 34, 39). The longitudinal sections of the whole strand are about 200–300 μm wide, and at least 450 μm long (Fig. 34). The annular protoxylem tracheids are on the outside, and c. 5 μm wide (Figs 35, 36). The thickenings are about 1 μm width. The distances between the secondary thickenings are 2–8 μm. The scalariform and reticulate metaxylem tracheids are 15–25 μm wide (Figs 37, 40, 41). The smaller scalariform tracheids (c. 15–18 μm wide) occur to the outside of the metaxylem. The secondary thickenings are c. 2 μm thick, and c. 3–4 μm apart. Reticulate tracheids occur at the centre of the xylem, and are of the greatest diameter (20–25 μm). The thickenings are c. 2 μm wide. The reticulate spaces are oval to elongate elliptical in shape, c. 8–20 μm wide along the long axis and 3–4 μm wide along the minor axis. Williamson’s striations are seen on some specimens (Figs 37, 40). There are at least six striations at one aperture. They are c. 0.3–0.4 μm wide, and about 1–2 μm apart. Two adjacent tracheid walls are seen in Figures 37 and 40.

Cortical cells are few and poorly preserved (Fig. 38). They are parenchyma cells, rectangular in outline, c. 70–90 μm in the long axis and 25–30 μm wide at the short axis. The walls are less than 1.0 μm wide.

SYSTEMATIC PALAEOBOTANY

The new fossil cones unquestionably belong to the Lycopsida. They have single veined sporophylls borne helically on the cone axis. Each sporophyll is associated with a single adaxial sporangium. The cone axis has an exarch primary xylem strand.

On the basis of small cone size, the shape and orientation of the sporangia, the four megaspores in each sporangium, and the small primary xylem strand in the cone axis, it is very difficult to place this cone fossil in an existing lycopsid strobilus taxon.

Division Lycopsida
Order Incertae Sedis
Genus *Minostrobus* gen. nov.

*Minostrobus chaohuensis* gen. et. sp. nov.

**Derivation.** Latin: *minor* = small; *strobus* = cone.

**Type species.** *Minostrobus chaohuensis* Wang gen. et. sp. nov.

**Diagnosis.** Cone with six sporophylls per gyre regularly arranged in a tight helix. Sporophyll with single vein, consisting of a lamina with a pointed apex and smooth margins, associated with a single adaxial sporangium. Sporangia spherical to spherical-elliptical in outline. Each sporangium with four megaspores, spore body with biform ornamentations. Xylem exarch in maturation. Plant probably heterosporous.

*Minostrobus chaohuensis* sp. nov.

**Derivation.** Chaohu. The locality of the fossils.

**Diagnosis.** Cone at least 12 cm long. Cone axis, c. 1.2 mm wide. Sporophyll cushion, circular in outline, c. 0.3–0.4 mm in diameter. Sporophylls inserted on the cone axis at an angle of 20–30°, and recurved distally to an angle of 80–90°. Six sporophylls of each gyre arranged on tight spiral whorls at the angle of 30–40° clockwise, vertical distance, c. 1.5 mm. Stalk of sporophyll 0.5–0.7 mm wide and less than 0.5 mm long. Distal part of sporophyll, 6–8 mm long. Lamina flattened and circular in profile c. 1.5–2.2 mm wide, with a pointed apex and smooth margins. One vein reaching the apex of sporophyll. Sporangium spherical or spherical-elliptical in profile, about 2–3 mm in diameter, without pedicel. Wall of sporangium smooth, about 0.2–0.4 mm thick. Megaspore more or less circular amb, nearly pear-shaped in equatorial view, about 600–800 μm in equatorial width and 800–1300 μm in total height. Spore body about 500–650 μm high. Gula about 450–500 μm × 100–150 μm height × basal width. Trilete ridges, tongue shaped, with a round apex, with three radial ridges at the lower part. Surface of gula smooth, rest of spore surface with scattered biform ornamentation. Base of biform ornamentation, tubercles bulbiferous in shape, about 10–18 μm in diameter and 10–20 μm in height. Apical spines, about 6–8 μm in basal diameter, and 18–25 μm long, with sharply pointed ends.

Cone axis with primary xylem strand about 250 μm.
Figures 25–33. *Minostrobus chaohuensis* gen. et sp. nov. SEMs. Fig. 25. One cross view of the cone axis, a primary xylem strand at the centre. Scale bar = 300 μm. Fig. 26. Tracheids. Scale bar = 20 μm. Fig. 27. Mesarch primary protostele from Fig. 25 (arrow a). Scale bar = 50 μm. Fig. 28. Polygonal metaxylem tracheid. Scale bar = 5 μm. Fig. 29. Mesarch primary protostele from one sporophyll base from Fig. 25 (arrow b). Scale bar = 30 μm. Fig. 30. Mesarch primary protostele from the sporophyll base from Fig. 32 (arrow). Scale bar = 10 μm. Fig. 31. The centre primary xylem strand. Scale bar = 100 μm. Fig. 32. Other section view of cone axis. Scale bar = 100 μm. Fig. 33. Tracheids. Scale bar = 20 μm.
Figures 34-41. *Minostrobus chaohuensis* gen. et sp. nov. Fig. 34. One longitudinal section. Scale bar = 50 μm. Fig. 35. Detail of the tracheids from Fig. 34 (arrow). Scale bar = 20 μm. Fig. 36. Annular tracheids. Scale bar = 5 μm. Fig. 37. Reticulate tracheid with Williamson's striations. Scale bar = 10 μm. Fig. 38. Cortical cells. Scale bar = 50 μm. Fig. 39. Longitudinal section. Scale bar = 50 μm. Fig. 40. Williamson's striations. Scale bar = 5 μm. Fig. 41. Scalariform and reticulate tracheids. Scale bar = 20 μm.
in diameter, exarch. 12 ridges of protoxylem around the metaxylem core. Annular protoxylem tracheids circular in profile in cross section, c. 5–10 μm wide. Scalariform and reticulate metaxylem tracheids polygonal in cross section, c. 15–35 μm wide, Williamson’s striations in the aperture. A vascular strand at sporophyll base, about 45–50 μm in diameter, mesarch. Cortical cells, rectangular in outline, c. 70–90 μm long and 25–30 μm wide, cell wall less than 1.0 μm thick.

Holotype. Specimen PB 18751, Figure 8.

Locality. A small quarry, south side of Beisham hill, Sizikou, 3 km north of Chaohu City, Anhui Province, China.

Horizon. The upper part of Wutung Formation (Upper Devonian-Famennian).

COMPARISON

Minostrobus chaohuensis is a distinctive lycopsid cone, characterized by the tight helically arranged sporophylls, each sporophyll associated with an adaxial sporangium, which contains with four megaspores. Vascular tissue is an exarch protostele.

Barostrobus famennensis Fairom-Demare is a lycopsid cone from the Upper Devonian of Belgium (Fairom-Demare, 1977, 1991). The cone is up to 14 cm long, 0.6 cm wide, excluding the distal part of sporophylls, and bears helically arranged sporophylls. The sporophylls consist of a thickened pedicel and a narrowly triangular lamina with the margins slightly enveloping the sporangium, and toothed margins. One slightly reniform sporangium is disposed on the adaxial surface of each sporophyll pedicel and attached by a slender stalk. Spores are regarded as megaspores. A solid space terete exarch protostele occupies the centre of the cone axis. The size of cone and the exarch protostele are very similar to M. chaohuensis. However, B. famennensis is clearly distinct from M. chaohuensis by its sporophylls (length, number, shape, enveloping the sporangium and margins), the sporangium with pedicel, number of megaspores on each sporangium and the features of megaspore.

Brack-Hanes & Thomas (1983) have suggested that the name Lepidostrobus be used only for microscope cones and that Flemingites be used for biosporangiate cones. Lepidostrobus grabaui Sze (Sze, 1936; Gu, 1974) was found in the same bed as the present cone. The cone of L. grabaui is 8–10 cm long and about 1.0 mm wide. Sporophylls are linear, about 8–10 mm long and 1 mm wide. Each sporangium is c. 4 mm long and 1 mm wide. Because of the limited description, comparison with M. chaohuensis is very difficult, but it differs in the cone size and sporophyll shape. Flemingites gallowayi (Arnold) Brack-Hanes & Thomas, if confirmed to be Upper Devonian, was found from the ‘Pocono’ Formation of Pennsylvania, USA (Arnold, 1933, 1935; Brack-Hanes & Thomas, 1983). The cone is 10 cm long and 3.5 cm wide. Sporophylls, about 10–15 mm long, are borne at right angles to the cone axis in whorls, 12–20 in number. The sporangium is elongate, with either microspores and megaspores. There is pith in the cone axis. The distinct differences between L. gallowayi and M. chaohuensis are in size of cone, shape and number of sporophylls, and presence of microscopes. The other species of Lepidostrobus and Flemingites do not resemble M. chaohuensis in dimensions, structures of sporophylls and sporangia or anatomical structure.

Longostachys latisporophyllum (Zhu, Hu & Fang) Cai & Chen is a lycopsid from the Middle Devonian of China (Cai & Chen, 1996). The cone of L. latisporophyllum is similar to M. chaohuensis in size, the position of the sporangium at the adaxial surface of sporophyll near base, and each sporangium having four megaspores. The distinctive difference is in the shape of sporophylls and megaspores, and anatomy of the xylem. In L. latisporophyllum, the sporophyll margin is spiny, the surface of the megaspores is smooth and secondary xylem is present.

Lycopodites oosensis Kräusel & Weyland is from the Upper Devonian of Germany (Kräusel & Weyland, 1937). The cone of this plant has sessile sporangia similar to M. chaohuensis. However, the distinct differences are its much smaller size, different shape and number of sporophylls, and the size of microspores (? isospores, about 90–120 μm).

Compared with some other lycopsid cones from the Carboniferous and Permian, the distinctive features to M. chaohuensis are the small size of cone, the sporangium without stalk, and each sporangium with four megaspores.

The megaspores of M. chaohuensis are very similar to the dispersed megaspores Lagenicula in shape and ornament. Lagenicula is an important megaspore of the Lower Middle Carboniferous (Tourmaisian–Westphalian) (Balme, 1995; Chen & Ouyang, 1987). However, there is a report that the age of this megaspore is Late Devonian (Famennian) Chi & Hills, 1976; Chen & Ouyang, 1987).

DISCUSSION

Minostrobus is a lycopsid fructification form genus from the Upper Devonian, but such an isolated cone sets more problems than it solves.

The parent plant of M. chaohuensis is unknown. In the same bed, lycopsids include leptophloeum rhombicum, Sublepidodendron mirabile, Sublepirodendron wushihense, Cyclostigma kiltorkense and Lepidodendropsis hirmeri. The reproductive cone of L. rhombicum and C. kiltorkense are known (Li et al., 1986; Chaloner, 1968), and differ from M. chaohuensis in cone size, sporophyll
number and megaspores. Although the cone of S. mirabile and S. wusihense are unknown, some newly collected specimens show that they are more closely related to Lepidostrobus grabaui Sze. Lepidodendropsis hirmi is a small lycopsid. The stem is 3–6 mm wide; 10–15 leaf cushions occur a pseudo-whorled arrangement. The single veined leaf is linear, about 15–16 mm long and 0.1–0.5 mm wide. It is possible that M. chaohuensis belonged to a small heterosporous lycopsid.

Lycopsids, described and reported from the Upper Devonian, include Cyclostigma kiltoerkense Haughton an arborescent, heterosporous cyclostigmaceous lycopsid (Chaloner, 1968). Bisporangiostrobus harristii Chitaley & McGregor is an arborescent, elagulate, heterosporous, cyclostigmaceous lycopsid (Chitaley & McGregor, 1988). Leptophloeum rhombicum Dawson is an arborescent form (Li et al., 1986). Flemingate gallowayi (Arnold) was viewed as an arborescent, heterosporous lycopsid (Arnold, 1933, 1935; Gensel & Andrews, 1986). Lepidostrobus grabaui Sze is probably an arborescent lycopsid. Barostrobus fagenensis Fairon-Demaret is a probably herbaceous, heterosporous lycopsid (Fairon-Demaret, 1977, 1991). Lycopodium oosensis Kräusel & Weyland is a very small herbaceous, homosporous, lycopodiaceous lycopsid (Kräusel & Weyland, 1937). Clevelandodendron ohienois is an unbranched slender monopodial, heterosporous isotetalean plant (Chitaley, 1996).

On the basis of this information on cones or cone form genera, herbaceous/arborescent and homosporous/heterosporous lycopsid had already evolved by the Upper Devonian, and the main lineages – lepidodendropsids, lycopodiaceans, isotaleans and cyclostigmaceans – are represented.

ACKNOWLEDGEMENTS

I thank Professors Zhou Zhiyan and Wu Xiangwu for providing valuable information; and Dr C. M. Berry for advice and correction of the English.

This paper was supported by Chuangxin Fund of NIGPAS, CAS, the National Natural Science Foundation of China (Grant nos 49972008), Laboratory of Palaeobiology and Stratigraphy, NIGPAS, and MSBRDP project (no. G2000077700).

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