Palaeontology
The Palaeontological Association
www.palass.org

[Palaeontology, Vol. 55, Part 5, 2012, pp. 957–966]

# A NEW HOMOSPOROUS, ARBORESCENT LYCOPSID FROM THE MIDDLE DEVONIAN OF XINJIANG, NORTHWEST CHINA

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Typescript received 4 October 2010; accepted in revised form 10 January 2012

**Abstract:** A new arborescent lycopsid, *Hoxtolgaya robusta* gen. et sp. nov., is described from the Middle Devonian of Xinjiang, Northwest China. It has stems up to 90 mm wide with fusiform leaf bases and long linear microphylls. Sporophylls are not aggregated into strobili and are isomorphic, with sporangia homosporous and bearing *Acinosporites*-type microspores. A syndrome of characters in *Hoxtolgaya*, including the arborescence and the homospory, implies that the arborescent habit is not necessarily correlated with the heterospory in the early evolution of arborescent lycopsids. Homosporous, arborescent lycopsids probably represent one of the transient forms between the Devonian herbaceous protolepidodendrids and the Devonian–Carboniferous heterosporous arborescent lycopsids.

**Key words:** Homospory, *Hoxtolgaya*, Middle Devonian, arborescent lycopsids.

ARBORESCENT lycopsids (or rhizomorphic lycopsids), probably originating from the herbaceous, homosporous protolepidodendralean lycopsids flourishing in the Middle Devonian (Stewart and Rothwell 1993; Kenrick and Crane 1997; Wang *et al.* 2003*b*), are thought to be evolutionary innovations in accelerating full colonization of land by plants and are most conspicuous pioneers in the Mid–Late Devonian to develop the arborescent habit and the heterospory (Algeo *et al.* 1995, 2001; DiMichele and Bateman 1996; Wang *et al.* 2002, 2005; Klavins 2004). However, relatively little is known about the early evolution and acquisition sequence of the tree habit and heterospory characteristically transformed from the Devonian herbaceous lycopsid ancestors to their tree-like descendants.

The small arborescent lycopsids with bipolar growth habit in the Middle Devonian are pivotal to elucidate the origin, early evolution and diversification of tree-like lycopsids (Gensel and Berry 2001; Wang *et al.* 2005). They possess an intermediate height between the small herbaceous lycopsids and the giant counterparts, growing only a few metres high (Cai and Chen 1996; Bek *et al.* 2008, 2009). Such a median growth height appears not to satisfy a basic forestry definition for a tree with a single stem with a height of over 4 m (Dilcher *et al.* 2004). So far, Middle Devonian arborescent lycopsids have only been reported from China and Kazakhstan, including *Longostachys latisporophyllus* Cai et Chen (1996) and *Atasudendron mirum* Senkevitsch et Jurina (Senkevich *et al.* 1993), both of which are heterosporous and have an estimated height of 1.5–2 m.

This article presents a new homosporous arborescent lycopsid, *Hoxtolgaya robusta* gen. et sp. nov., from the Middle Devonian of Xinjiang, Northwest China. The new plant shares some key characters of protolepidodendrids and tree-like lycopsids, providing new insights into the early evolution and diversification of arborescent lycopsids.

## MATERIALS AND METHODS

About ninety pieces of specimens of the present plant were collected from the south slope of a small hill, *c.* 500 m west of State Highway G217, about 20 km north of Hoxtolgay Town, Hoboksar Mongol Autonomous County, Xinjiang, Northwest China (46°36′55″N, 86°1′5″E; Fig. 1). All specimens are green–yellow muddy sandstone compressions of the Hujiersite Formation. Other fossils found in the neighbouring beds include *Colpodexylon gracilentum* Dou (1983; Xu and Wang, 2011), *Leclercqia*


doi: 10.1111/j.1475-4983.2012.01177.x

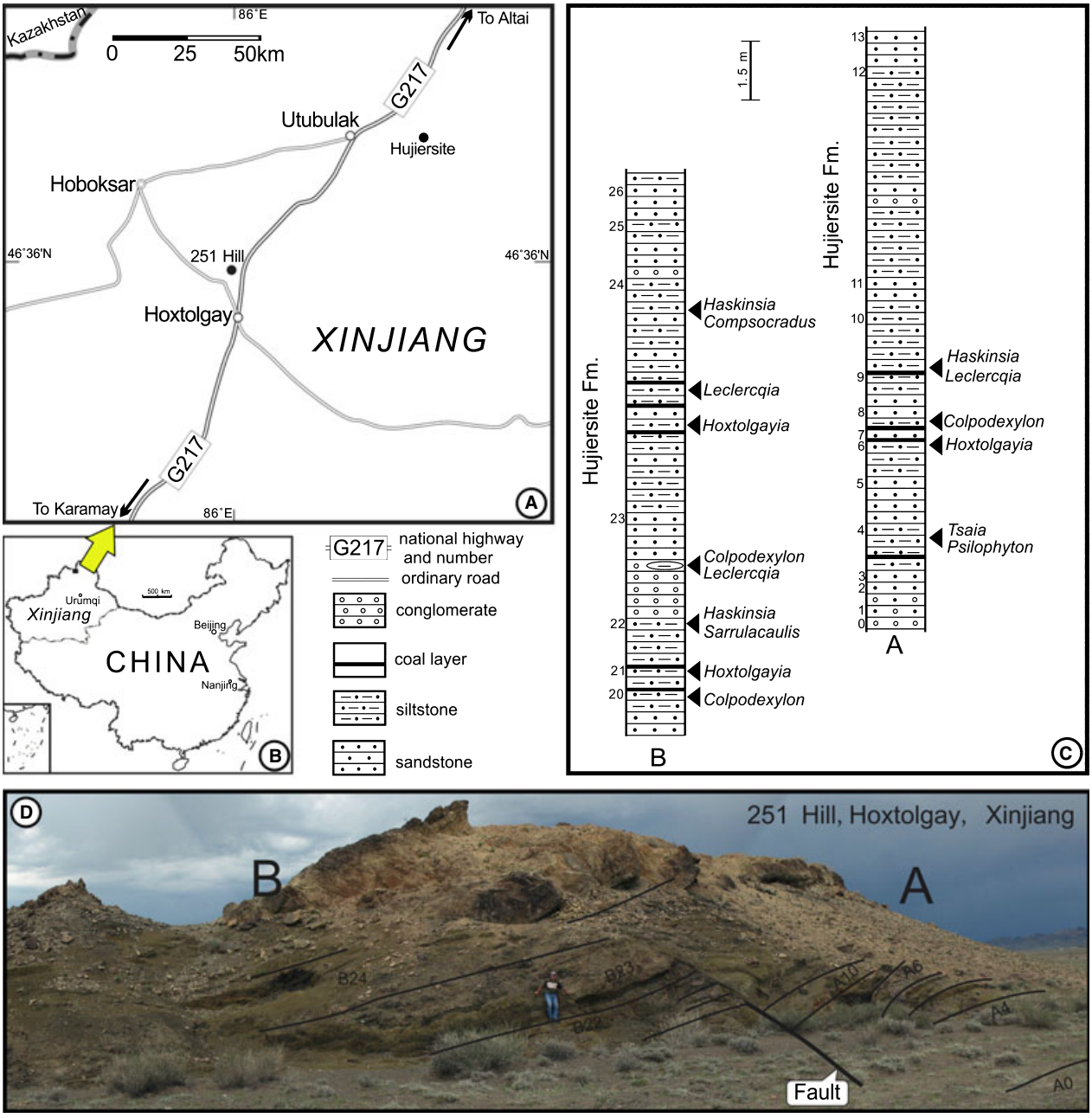



**FIG. 1.** Composite figure with locality maps (A, B), simplified geological columns (C) and field photography of the section with *Hoxtolgaya robusta* gen. et sp. nov. fossil material (D). A, Location of the 251 Hill section is marked by a solid disc, showing the close-up of the area in Figure 1B. C, Geological columns of the 251 Hill section; plant megafossil samples are marked as solid triangles; the numbers beside the column indicate the upper boundary of each bed. D, Field photography of the 251 Hill section; the 251 Hill section is divided into two parts, A and B, by a fault. Beds are marked from A0 to A 13 and B20 to B26.

cf. *complexa* Banks *et al.* (Sze, 1961; Xu and Wang, 2008), *L. uncinata* Xu *et al.* (2011*a*), *Compsocradus givetianus* Fu *et al.* (2011), *Serrulacaulis spineus* Xu *et al.* (2011*b*), *Tsaia conica* Wang *et al.* (2004), *Haskinsia sagittata* Edwards et Benedetto (Cai and Wang, 1995) and *H. hastata* Berry et Edwards (Xu *et al.*, 2008; Fig. 1). The geological age of the fossil-bearing horizon was regarded as late Mid Devonian (Givetian) based on biostratigraphical and lithological studies (Cai and Wang 1995; Cai 2000; Wang *et al.* 2004; Xu *et al.* 2008). However, ongoing palynological study of the plant fossil–bearing beds of our fossil localities, which was never carried out before, suggests an Eifelian age (J. Marshall, pers. comm. 2010). Currently, we assign our plant-bearing beds a Mid Devonian age.

Morphological features were revealed by removing the matrix using sharp needles (dégagement, Fairon-Demaret

*et al.* 1999). Sporangia were detached from the slabs and macerated separately with hydrofluoric acid followed by neutralizing by repeated rinsing in distilled water. The macerated spores were analysed using SEM and LM. Macro- and microphotography were carried out with a Nikon D300 digital camera and crossed polarized illumination and Leica MZ 16A microscope.

*Repository.* All figured materials are housed at Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, with reference numbers and prefix PB.

## SYSTEMATIC PALAEONTOLOGY

*Remarks.* On the basis of microphylls and adaxial sporangia attached to the sporophylls, the present plant is classified into the class Lycopsida. The characteristic leaf base, large-sized stem and oval sporangium indicate that this plant has a closer affinity to arborescent lycopsids, which constitute a monophyletic group Isoëtales *sensu lato* (DiMichele and Bateman 1996; Kenrick and Crane 1997; Wang *et al.* 2003*a*). However, the present plant is homosporous. A new taxon under the class Lycopsida has to be instituted for the present plant, but the suprageneric classification remains uncertain.

Class LYCOPSIDA
Order INCERTAE SEDIS
Family INCERTAE SEDIS

### Genus HOXTOLGAYA gen. nov.

*Type species. Hoxtolgaya robusta* sp. nov. from the Middle Devonian of Xinjiang, China.

*Derivation of name. Hoxtolgaya* is from the type locality of the present plant, Hoxtolgay Town, Xinjiang, China.

*Diagnosis.* Homosporous, arborescent lycopsid. Leaf bases fusiform, tightly arranged in a pseudowhorled fashion. Leaf persistent, long linear with a middle vein from the basal and minute teeth in the basal margins. Fertile zone without specialized strobili. Isomorphic sporophyll curving downwardly from the basal. Sporangium oval in shape, attaching to the sporophyll by a pad.

### *Hoxtolgaya robusta* sp. nov.
Figures 2, 3

*Derivation of name.* The species epithet, *robusta*, refers to the robust stem of the plant.

*Holotype.* PB20913A (Fig. 2D).

*Paratypes.* PB20910 (Fig. 2A); PB20911 (Fig. 2B); PB20912 (Fig. 2C).

*Type locality and horizon.* Hoxtolgay Town, Hoboksar, Xinjiang, China. The Hujiersite Formation (Mid Devonian).

*Diagnosis.* Stems up to 90 mm wide. Leaf bases up to 5.9 mm long and 2.4 mm wide, with a furrow in the middle portion. Leaf 22–35 mm long and 0.8–2.1 mm wide, the basal marginal tooth on the leaf 0.15–0.2 mm long. Sporangium 2.5–3.2 mm in diameter, probably dehiscences longitudinally. *In situ* spore 34–52 $\mu$m in diameter, the amb subtriangular with convex sides and rounded apices; triradiate ridges membranous, 1.2–3.4 $\mu$m in height; distal exine is thick and ornamented with contorted anastomosing ridges that are 1–3 $\mu$m in width; proximal surface is laevigate.

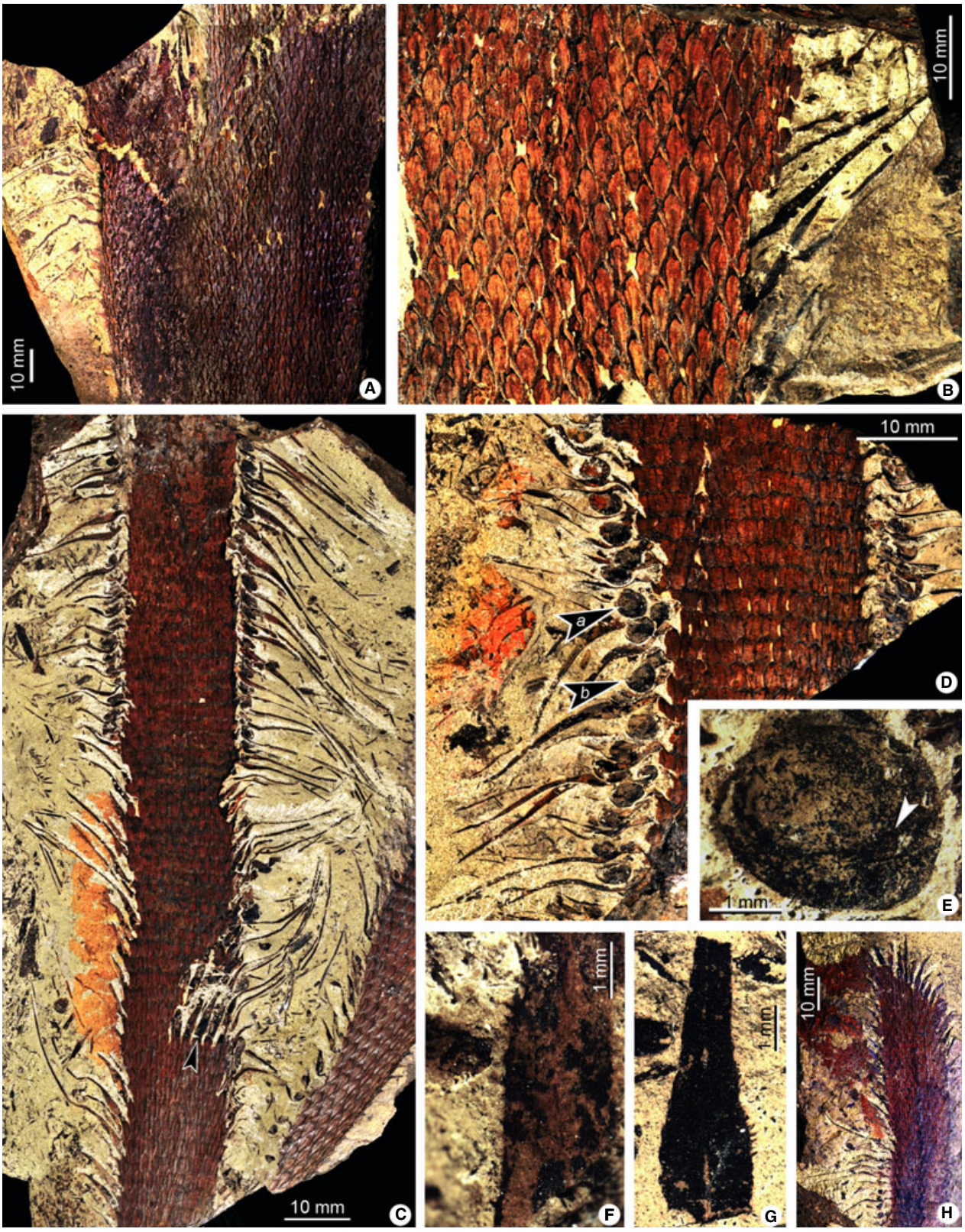
*Description.* Specimens present here consist of vegetative and fertile leafy stems. All stems have the same general appearance of leaf base and leaf shape, and only the width and the preserved length of stems vary. The width of the measurable portion of the stems, excluding leaves, ranges from the largest, 90 mm (Fig. 2A), to the smallest, about 17 mm (Fig. 2C). Both sides of the widest stem are parallel to each other, which is presumably the upright trunk and has no obvious tapering. However, the lack of stem-base specimens limits the potential for estimating the height of the plant in the living state.

The straight and wide stems (Fig. 2B–D), rather than dichotomous ones, are common in our collection. The leaf bases on the stems are contiguous to each other and tightly arranged in a pseudowhorled fashion (Fig. 2A–D), fusiform or shield-like in shape, up to 5.9 mm long and 2.4 mm wide (Fig. 2A, B). A vertical furrow can be seen in the middle of well-preserved leaf bases (Fig. 2D), and no vascular bundle, ligular pits or parichnos are found.

Leaves are always found connected to stems with a various range of width, implying that leaves are probably persistent. The leaf is inserted densely to the axis approximately 60 degrees against the stem, 22–35 mm long (Fig. 2A–D). Vegetative leaves orient upwardly at an acute angle (Fig. 2B, C, H), while in some cases, they curves abaxially at the periphery of stems (Fig. 2A, C). The leaf is linear and probably has a single central vein throughout its length (Fig. 2B, G). The whole leaf consists of the wider, shorter basal portion and the narrower, longer upper portion. The basal portion is up to 2.1 mm wide, with tiny teeth on the margins (Fig. 2F, G). The individual tooth is 0.15–0.2 mm long (Fig. 2F, G). The leaf in the upper is narrower, 0.8 mm wide (Fig. 2B–D), tapering to the apex (Fig. 2D, H).

Sporophylls associated with a single sporangium attached adaxially aggregate into the fertile zone rather than strobili as in most arborescent lycopsids. The fertile zone occurs upper (Fig. 2C) or lower (Fig. 2H) than the vegetative zone in the stem. Sporophylls curve downwardly or are horizontal (Fig. 2C, D, H). The fertile zone is 12 mm to up to 26 mm wide (Fig. 2C,

D, H) and at least 80 mm long (Fig. 2C), without obvious tapering. Sporophylls are isomorphic to vegetative leaves. The sporangium is attached on the adaxial surface of the sporophyll, *c.* 2 mm high from the base, by a pad (Fig. 2D, E). The sporangium is oval in shape, but sometimes appears fusiform in contour (Fig. 2C, D) probably caused by compression,



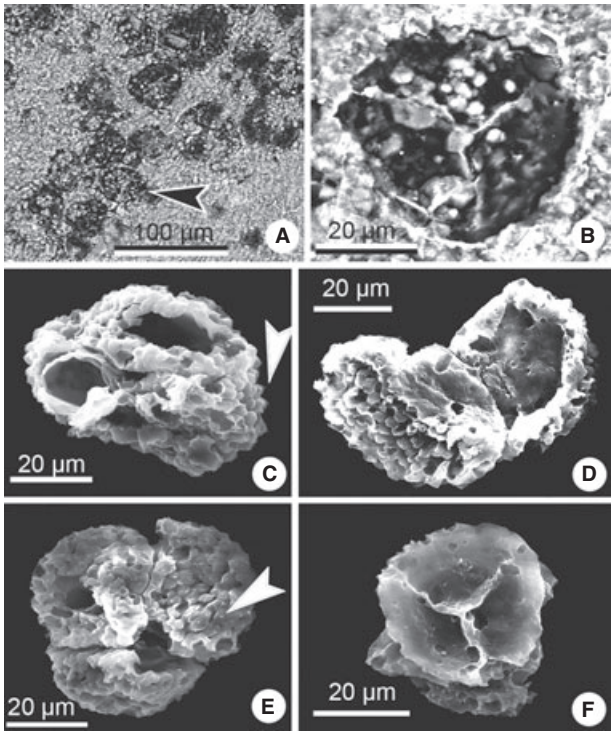



**FIG. 3.** *Acinosporites*-type in situ spores isolated from the sporangia of *Hoxtolgaya robusta* gen. et sp. nov., Middle Devonian of Xinjiang, China. A, SEM view of the sporangium indicated by arrow *b* in Figure 2D, showing the microspores mass inside the sporangium. B, Enlargement of the arrowed microspore in A. C, The distal surface of the microspore; note the biform sculptures (arrow). D, The fragment of a tetrad. E, A tetrad with distal biform sculptures. F, The proximal view of the spore.

2.5–3.2 mm in diameter (Fig. 2D, E). The attachment pad of the sporangium is round, 0.4 mm in diameter (Fig. 2E). The sporangium probably dehiscences longitudinally (Fig. 2E).

Trilete microspores extracted from sporangia are observed by SEM directly (Fig. 3A, B). The *in situ* spore is 34–52 $\mu$m (41, n = 30) in diameter (Fig. 3C–F). The amb is subtriangular with convex sides and rounded apices (Fig. 3C, D); triradiate ridges are membranous, 1.2–3.4 $\mu$m (2.3, n = 20) in height, almost reach the equatorial margin; distal exine is thick and ornamented with contorted anastomosing ridges that are measured 1–3 $\mu$m (2, n = 20) in width. The ridges are superimposed by slender cones or spines with pointed or occasionally blunt and expanded apices, 0.6–1.5 $\mu$m (1, n = 20) in height, 0.5–1.2 $\mu$m (0.7, n = 20) in width at basal (Arrow in Fig. 3C, E). The ornamentation is confined to the distal surface and equatorial margin; ridges are fused into tight concertina-like folds around the equator. Proximal surface is laevigate (Fig. 3F).

In the light of the apparent biform sculpture in the distal surface, these microspores are closely related to a Devonian dispersed spore genus *Acinosporites* Richardson and in turn to the species *A. acanthomammilatus* Richardson (1964) by the nature of distal ornaments except that the latter is considerably larger (100–106 $\mu$m in size). The difference in size, on the other hand, implies the immaturity of the present in situ spores. No megaspore is found from all the sporangia of the plant, by observation, maceration, or macerated contents of sporangia or the matrix of the fertile stems.

*Reconstruction.* *Hoxtolgaya robusta* consists of a spiral pattern of tightly arranged fusiform leaf bases, long linear leaves with basal, tiny, marginal teeth and adaxially attached sporangia. The fertile zone of *Hoxtolgaya* has not specialized into the strobilus borne at the apex of stems. Leaves curve upwardly; sporophylls are more or less isomorphic except its drooping shape as a whole. A portion of the stem, both vegetative and fertile, is reconstructed (Fig. 4). Having observed a large number of the fossil axes of the present plant, we believed that *Hoxtolgaya* is a homosporous plant rather than the male representative of a heterosporous plant.

## COMPARISONS

*Hoxtolgaya robusta*, with persistent leaves, unspecialized fertile zones and homosporous habit, shows similarities to the members of herbaceous protolepidodendrids, such as *Leclercqia complexa* Banks *et al.* and *L. uncinata* Xu *et al.* (Bonamo *et al.* 1988; Xu *et al.* 2011*b*), which morphologically are characterized by leaves with distinctive leaf shapes with complex lobing or toothed marginal outline. However, the salient differences are the large-sized stem and relatively simple leaf shape of the present plant.

*Hoxtolgaya* is highly comparable to the Silurian–Devonian lycopod *Baragwanathia*, which is placed by most authors in the Drepanophycales and is known as having long stems up to 6.5 cm in diameter, with narrow linear leaves up to 4 cm long and fertile zones on the stem where sporophylls indistinguishable from the leaves bear

**FIG. 2.** *Hoxtolgaya robusta* gen. et sp. nov. from the Middle Devonian of Xinjiang, China. A, The widest leafy stem/trunk. PB20910. B, A leafy stem showing fusiform leaf bases with lateral leaves curving adaxially. PB20911. C, A leafy stem with both the vegetative (lower) and the fertile (upper) portions. Leaves curving upwardly; sporophylls attached with oval sporangia curving downwardly from the basal. PB20912. D, Fertile stem with dozens of sporangia attached and sporophylls curved abaxially. The numerous spores were seen by SEM in the sporangium indicated by arrow *b* directly. The detached sporangium was macerated to obtain in situ spores. Holotype: PB20913A. E, A sporangium with attachment pad (arrowed), enlargement of the sporangium indicated by arrow *a* in D. F, Enlargement of a portion of the leaf indicated by the arrow in C, showing the toothed margin of the leaf. G, An isolated leaf with toothed margins and the middle vein. PB20914A. H, A stem with the fertile zone in the lower and with sporangia attached, and the vegetative portion in the upper. PB20929.

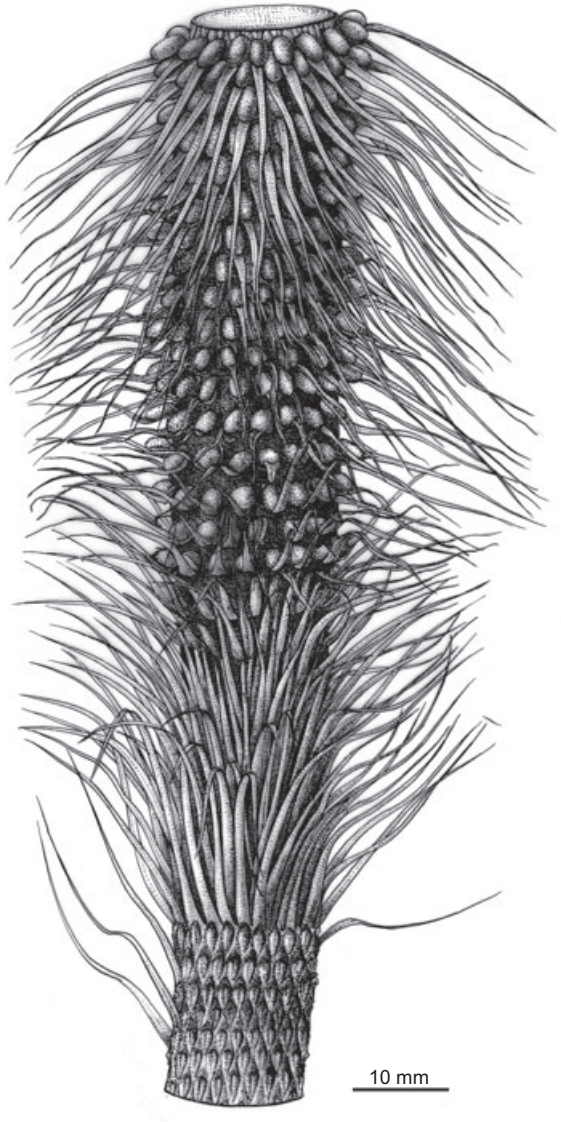



**FIG. 4.** Reconstruction of a portion of the leafy stem of Middle Devonian lycopsid *Hoxtolgaya robusta* gen. et sp. nov. from Xinjiang, China.

axillary sporangia with microspores only (Chaloner and Boureau 1967; Stewart and Rothwell 1993). Plants in Drepanophycales are regarded as large-sized herbaceous (without secondary thickening) lycopsid, whose leaves might not be persistent and make them different from the present plant. But their further relationship is needed to be confirmed.

*Hoxtolgaya robusta* lacks parichnos scars on leaf bases, the pattern of which is common among the Devonian herbaceous lycopsids. In contrast, compression–impression specimens of typical arborescent lycopsids bear prominent leaf cushions derived from the bases of linear, nonpersistent leaves with associated parichnos scars, such as *Lepidodendron* Sternberg (1820). The shape and arrangement of leaf bases of *H. robusta* are reminiscent of the leaf cushions of Carboniferous arborescent lycopsid, such as *Lepidodendron dicentricum* Felix and *Lepidodendron hickii* Watson (DiMichele 1979, 1981, 1983), whose rhomboidal leaf cushions are greater in their vertical than in transverse dimensions; a leaf scar with a vascular bundle scar and flanking parichnos scars, as well as a ligular pit, is usually situated just above the middle of the cushion.

*Hoxtolgaya robusta* shows larger size and form than any other Middle Devonian arborescent lycopsids (Table 1), such as *Longostachys latisporophyllus* (Zhu *et al.*) Cai et Chen, *Atasudendron mirum* Senkevitsch et Jurina and *Mixostrobilus givetensis* Senkevitsch, Jurina et Arkhangelskaya. *Longostachys latisporophyllus* is a well-known arborescent lycopsid from the Givetian of Hunan, South China, and shows potentially affinities with the Carboniferous Lepidodendrales (Cai and Chen 1996). The plant has bipolar growth, dichotomized rhizomes and trunks with dichotomous branches forming a crown of twigs. Isomorphic sporophylls aggregate into terminal strobilus with megasporangia. The maximum width of stem of *Longostachys*, 3.5 cm, is smaller than that of the present plant. On the other hand, leaf cushions of *Longostachys* are smaller and are not contiguous to each other as those of the present plant; sporophylls of *Longostachys* are spoon-like in form in the surface view, with longer spiny appendages on the margin, showing difference from the linear leaves with toothed, basal margins of the present plant.

*Atasudendron mirum* and *Mixostrobilus givetensis* are based on the silicified materials from the late Middle Devonian of Kazakhstan (Jurina 1988; Senkevich *et al.* 1993), which share the same geological age and palaeoterrain with the present plant (Zhou and Lin 1995). *Atasudendron mirum* was once described as *Lepidodendropsis kazachstanica* Jurina, having elongate-rhomboid, pseudowhorled-arranged leaf cushions, and short and simple leaves with wide basal and acute apex. It differs from *Hoxtolgaya robusta* in the smaller sized and entire leaves. *Mixostrobilus givetensis* differs from the present plant in its simple, entire leaves and bearing both micro- and megasporangia distributed irregularly.

*Chamaedendron multisporangiatum* Schweitzer et Li is described from the early Late Devonian of Wuhan, South China, as a heterosporous, arborescent lycopsid with the maximum stem width of 7 mm only, isomorphic sporophylls with dentate margins are distributed over fertile regions, and no strobilus is formed (Schweitzer and Li 1996). The sporangia arrangement of *Chamaedendron* is described as 4–6 megasporangia on the adaxial surface of megasporophyll and 12 microsporangia on the microsporophyll. A more reasonable interpretation was argued that those

**TABLE 1.** Comparisons of *Hoxtolgaya robusta* and some Devonian tree-like lycopsids.

| Taxa | Stem width/ growth height | Sporophyll/strobilus | Sporangium/spore | Age/Locality | References |
|---|---|---|---|---|---|
| *Hoxtolgaya robusta* | Up to 90 mm/3–4 m | Linear, with marginal tooth/no strobilus | Sessile, oval/ *Acinosporites*-like microspores | Early Middle Devonian/ Xinjiang, China | Present paper |
| *Longostachys latisporophyllus* | Up to 35 mm/about 1.5 m | Spoon-like, with spiny appendages/ Megasporangiate stobilus | Sessile, ellipsoidal/ *Laevigatisporites*-type megaspores | Late Middle Devonian, Hunan, China | Cai and Chen (1996) |
| *Atasudendron mirum* /Mixostrobilus givetensis | Up to 100 mm/ 1–2 m | Simple, entire/ Bisporangiate strobilus | Stalked, elongate to ellipsoidal/microspores 40–76 $\mu$m in size; megaspores 480–650 $\mu$m in size | Late Middle Devonian, Kazakhstan | Senkevich et al. (1993) |
| *Chamaedendron multisporangiatum* | Up to 7 mm/*c.* 0. 5 m | Spindle-shaped, with dentate margins/no strobilus | ?/Megaspores about 750 $\mu$m in size | Early Late Devonian, Hubei, China | Schweitzer and Li (1996) and Wang and Berry (2003) |
| *Leptophloeum rhombicum* | 300–400 mm/ 10–25 m | Peltate in outline/strobilus | Elongate to ellipsoidal/? | Early Late Devonian, Hubei, China | Li *et al.* (1986) and Wang *et al.* (2005) |
| *Cyclostigma kiltorkense* | Up to 300 mm | Linear, up to 15 cm long/Megasporangiate strobilus | Ellipsoidal/megaspore 760–1520 $\mu$m in size | Late Late Devonian, Kilkenny, Ireland, and Bear Island, Norway | Chaloner (1968) and Schweitzer (1969) |
| *Sublepidodendron grabaui* (Sze) Wang et Xu | 32–100 mm/? | Linear, entire/ Megasporangiate strobilus | Sessile, elliptical/mega spore 1200 $\mu$m in size | Late Late Devonian, Anhui, China | Wang and Xu (2005) |
| *Sublepidodendron songziense* Chen ex Wang *et al.* | Up to 50 mm/ 4–8 m | Linear, entire/ possibly separate microsporangiate and megasporangiate strobili | Sessile, oval or elliptical/*Lycospora*-type microspore, 18–42 $\mu$m in size; *Triletes*-type megaspore, 250–550 $\mu$m in size | Late Late Devonian, Hubei and Anhui, China | Wang *et al.* (2003*a*, *b*) |
| *Minostrobus chaohuensis* Wang | Up to 42 mm/? | Linear, entire/ monoecious, separate microsporangiate and megasporangiate strobili | Sessile, spherical or spherical-elliptical in outline/*Lycospora*-type microspore, 20–30 $\mu$m in size; megaspore *c.* 600–800 $\mu$m in equatorial width and 800–1300 $\mu$m in total height | Late Late Devonian, Anhui, China | Wang *et al.* (2012) |

mega-/microsporangia are actually megaspores (see Wang and Berry 2003). *Chamaedendron* is similar to *Hoxtolgaya* in having unspecialized fertile zones. However, *Chamaedendron* is smaller than the present plant; the teeth on the leaf margins are larger than those of the present plant.

*Cyclostigma kiltorkense* Haughton ex Heer is an arborescent lycopsid species of biostratigraphic importance in the late Late Devonian as an index fossil, showing some features of Carboniferous forms in leaf cushion and large stems up to 30 cm in width with dichotomized branches (Chaloner and Boureau 1967; Chaloner 1968; Cai and Wang 1995; Wang 2008). *Cyclostigma kiltorkense* differs from *Hoxtolgaya robusta* in its much longer linear leave up to 15 cm, distinctive parichnos scars upon the circular leaf scars and the strobilus with megasporangia.

*Barsostrobus famennensis* Fairon-Demaret is a heterosporous lycopsid from the late Late Devonian of Belgium, having a long slender strobilus (Fairon-Demaret 1977). The strobilus is 14.5 cm long and 0.6 cm wide, and the

sporophyll consists of a thickened pedicel and a narrow lamina in triangular shape with a toothed margin similar to that of the present plant, except for the pedicel. However, the axis of *Hoxtolgaya* is wider than that of *Barsostrobus*; the latter consists of stalked megasporangium near the base of its sporophyll, while the sporangium of *Hoxtolgaya* is attached by a pad.

*Sublepidodendron* (Nathorst) Hirmer is thought to be a heterosporous, arborescent lycopsid with a wide distribution from the Upper Devonian to the Lower Carboniferous (Chaloner and Boureau 1967; Wang *et al.* 2003*a*). The characters of the two well-known species, *S. songziense* Chen ex Wang *et al.* (2002, 2003*a*) and *S. grabaui* (Sze) Wang and Xu (2005), include elongated fusiform leaf cushions separated by the interareas, simple linear leaves with smooth margins, terminal megasporangiate strobilus and exarch stele with secondary xylem, the morphological characters of which differs from the present plant.

## DISCUSSION

The tree habit (or bipolar growth habit *sensu lato*) and heterospory are thought to be relevant in the evolution of arborescent lycopsids (DiMichele and Bateman 1992, 1996; Bateman *et al.* 1992; Kenrick and Crane 1997), but such a traditional viewpoint is being challenged by the discovery of the Middle Devonian homosporous, arborescent *Hoxtolgaya*. Our results demonstrate that the tree habit is not necessarily associated with heterospory in the early evolution of arborescent lycopsids.

Banks (1960) hypothesized that there might be a pool of similar herbaceous lycopsids in the Devonian, from which the arborescent lycopsids could have arisen as several evolutionary lines, one of which was the homosporous arborescent form (Thomas 1978). Here, *Hoxtolgaya robusta* provides the earliest macrofossil evidence for such homosporous arborescent forms. Its character combination is noticeably different from the Mid–Late Devonian and Carboniferous arborescent lycopsids. Considering the large amount of heterosporous lycopsids from the Late Devonian (see Stewart and Rothwell 1993; Wang *et al.* 2003*b*), homosporous arborescent habit probably underwent a transient evolutionary stage that was by far only known from the Middle Devonian. Furthermore, *Hoxtolgaya* may represent one of the missing links between the Early–Mid Devonian herbaceous protolepidodendrids and the Devonian–Carboniferous heterosporous arborescent lycopsids.

Arborescent lycopsids are one of the most conspicuous pioneers to develop the tree habit (Algeo *et al.* 2001). Along with the other independent evolutionary lineages (i.e. cladoxyleans and progymnosperms) from the late Middle Devonian, arborescent lycopsids might have developed into the earliest tree and forest on land (Mosbrugger 1990; Schweitzer 1990; Dilcher *et al.* 2004; Stein *et al.* 2007). However, Middle Devonian fossil plants are often fragmentarily preserved so that it is nearly impossible to obtain a whole fossil tree showing roots, trunk/stem and intact branches. Usually, tree height is estimated from the basal trunk/stem diameter and the nature of the trunk taper (Mosbrugger 1990). An example of the Middle Devonian tree-like forms is the early fern *Calamophyton* Kräusel and Weyland, which is estimated to be smaller than 4 m with a stem diameter slightly larger than 75 mm (Mosbrugger 1990; Schweitzer 1990). In this study, the arborescent lycopsid *Hoxtolgaya*, although no anatomical materials are found to verify the secondary growth, has a stem width up to 90 mm that is larger than that of any other coeval lycopsids, cladoxyleans and progymnosperms. *Hoxtolgaya robusta* probably represents one of the precursors of the earliest tree and forest in the Devonian land ecosystems, implying that the tree habit may have an earlier origin, not later than the Mid Devonian.

*Acknowledgements.* We thank Prof. J. E. A. Marshall, University of Southampton (UK), and Prof. J. B. Richardson, Natural History Museum (London, UK), for suggestions on the palynological study; Mrs. Lindsey Axe, Cardiff University (UK), for laboratory help; and Mr. Sun Ying-Bao, Institute of Botany, the Chinese Academy of Sciences, for line drawings. This work is supported by Chinese Academy of Sciences (KZCX2-EW-QN113), National Natural Science Foundation of China (Nos. 40902005 and 40972015).

*Editor.* Barry Lomax

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