The palaeogeographical significance of specimens attributed to Protolepidodendron scharyanum Krejči (Lycopsida) from the Middle Devonian of North Xinjiang, China

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Abstract

Morphology of the leaves of stem compressions originally attributed to *Protolepidodendron scharyanum* from the Middle Devonian of North Xinjiang, China is reinvestigated. The leaf is three-dimensional, consisting of one central abaxial segment and four lateral adaxial segments, and does not conform to the once bifurcate leaf of *Protolepidodendron*. Specimens are therefore transferred to *Leclercqia* cf. *L. complexa*. This is the first unequivocal report of the genus *Leclercqia* in China based on complete leaf morphology. The distribution of *Leclercqia* is discussed, demonstrating a more or less cosmopolitan genus in the Middle Devonian. The Middle Devonian flora of North Xinjiang shows great similarity to that of Venezuela and North America, and almost no relationship with that of Yunnan, South China.

Keywords: Xinjiang, Leclercqia, Protolepidodendron, Devonian, palaeogeography

1. Introduction

Middle Devonian herbaceous lycopsids are widely accepted to have palaeobiogeographical significance if their leaf morphology has been correctly worked out and documented allowing accurate generic and specific determination (Bonamo, Banks & Grierson, 1988). There remain a few cases where historically important lycopsid discoveries have yet to be reinvestigated to determine their exact leaf morphology. One example is the report of Protolepidodendron scharyanum Krejči (the name should be P. scharianum Kräusel et Weyland, see Xu & Wang, in press) from Xinjiang, NE China. Specimens originally determined by Sze (1960, 1961) on the basis of once-divided leaves were later re-assigned to P. cf. cathaysiense Schweitzer et Cai by Cai & Wang (1995) who noticed one leaf that appeared to trifurcate. The question of the exact determination was left ambiguous as no spines were visible on the margin of leaves.

The identification of these specimens is important because of their palaeogeographical situation. *Protolepidodendron* Krejči ex Gothan (for authorship see Xu & Wang, in press) is generally held to refer to a herbaceous lycopsid

with once-bifurcate leaves (Gothan, 1921, pp. 225-6). Most specimens previously attributed to Protolepidodendron have been reassigned to Leclercqia Banks, Bonamo et Grierson (1972), which has a five-tipped leaf with a prominent central elongate segment and two pairs of shorter lateral segments (Banks, Bonamo & Grierson, 1972; Fairon-Demaret, 1974, 1980, 1981), and is found widely in Laurentia and Gondwana (Meyer-Berthaud et al. 2003). However Protolepidodendron from Yunnan, South China (Halle, 1936; Schweitzer & Cai, 1987) was transferred to Minarodendron Li (1990), characterized by trifurcate spiny leaves. Minarodendron (Protolepidodendron) cathaysiense Li (1990) is restricted to South China, the only plate yet to show a strongly endemic Middle Devonian macroflora (Wang et al. 2007). The palaeogeographical positions of the Kazakhstania plates, on one of which the locality was situated (Liao & Ruan, 1995), in the Middle Devonian is problematical (Scotese & McKerrow, 1990; Cocks & Torsvik, 2002; Torsvik & Cocks, 2004). This investigation is to demonstrate the true leaf morphology of Sze's (1960, 1961) specimens and therefore to determine if they show affinity to the more or less cosmopolitan herbaceous lycopsid flora or the endemic flora of Yunnan.

2. Material and methods

The detailed locality and horizon was not stated by Sze (1960, 1961), according to whom all materials were collected from the Hoxtolgay area, Hoboksar Mongol Autonomous County, North Xinjiang, NW China. The fossil-bearing horizon also yielded *Hostimella* sp., *Lepidodendropsis*? (*Colpodexylon*?) arborescens Sze, and Lepidodendropsis? dzungariensis Sze. The horizon is inferred to be the Hujiersite Formation (Givetian) from this fossil plant assemblage (Cai & Wang, 1995). A few localities (Fig. 1) are probably involved. More recently reported plants from the Hujiersite Formation of the Hoxtolgay area include: Sawdonia curstipa Wang & Hao (1996), Haskinsia sagittata (Cai & Wang, 1995; Xu et al. in press), H. hastata (Xu et al. in press), Colpodexylon gracilentum (H.-H. Xu, unpub. Ph.D. thesis, Nanjing Institute of Geology and Palaeontology, 2006), Tsaia conica (Wang et al. 2004), and Compsocradus sp. (H.-H. Xu, unpub. Ph.D. thesis, Nanjing Institute of Geology and Palaeontology,

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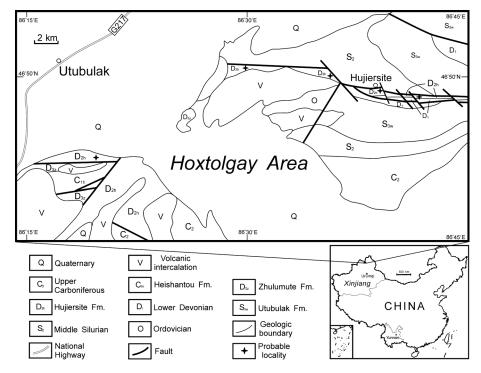


Figure 1. Generalized geological and geographical map showing probable localities of Sze's (1960, 1961) collection in Xinjiang, NW China, and the relative generalized position of the Yunnan Middle Devonian flora.

A total of six specimens (PB3246–PB3251) attributed to *Protolepidodendron scharyanum* by Sze are preserved as compressions and deposited at Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. A short leafy stem on the reverse side of Sze's specimen PB3246 was uncovered using serial dégagement (Fairon-Demaret, Hilton & Berry, 1999). Leaves on the counterpart to Sze's specimen PB3246 (PB3247) are also illustrated. Macrophotography was carried out using a Nikon D100 digital camera with cross-polarized illumination.

3. Description

The new fragmentary unbranched axis with persistent leaves described here is 22 mm long and 3.8–4.2 mm wide (Fig. 2a). The surface of the stem was highly compressed, so that it is hard to recognize patterns of leaf bases. Leaves in profile are linear with a swollen base, showing an abaxially recurved tip (Fig. 2a, leaves 1, 3 and 4) distal to a division, or a division to form two or more segments (Fig. 3). The angle between leaf and stem ranges from 40° (Fig. 2a) to 50° (Fig. 2b).

Serial dégagement was performed on leaf 2 (Fig. 2a). Like most partly prepared leaves, this leaf shows three segments (b, c) and d in Fig. 3e) before dégagement. In addition, an obvious wider segment was buried in the matrix under the segment d (Fig. 3e). After removing segment d, the long central segment E was finally exposed (Fig. 2c; Fig. 3f). Segment E was also revealed after segment E was removed (Fig. 2d; Fig. 3g).

The unforked part of the leaf is 0.33-0.41 mm wide. The leaf divides 3.4-3.8 (mean 3.61, n=4) mm from the base, forming a long central segment (up to 3.1 mm long, Fig. 2a, leaf 3; Fig. 3d) recurved abaxially and a pair of lateral laminae that each bifurcates proximally into two slender segments 0.77-1.54 mm in length. The arrangement of all five segments is always three-dimensional. It is impossible

to discern the proximal ends of all segments. In some leaves, four distal segments could be seen at the same time, e.g. Sze's (1960, 1961) specimen PB3247 (Fig. 2b, arrow; Fig. 3a); leaf 5 on the new stem (Fig. 2a; Fig. 3b).

4. Discussion

Bifurcate leaves were for a long time accepted as a distinctive character of the genus *Protolepidodendron*. Schweitzer & Cai (1987), for the first time, noted the trifurcate and spiny microphylls in specimens previously attributed to *P. scharyanum* by Halle (1936) from the Middle Devonian of Yunnan, South China, and placed the specimens in a new species, *P. cathaysiense*, effectively enlarging the generic concept. Additional specimens of *P. cathaysiense* were studied by Li (1990). Multiperforate bordered pits in the tracheids, as well as the trifurcate leaves, supported transfer to the new genus *Minarodendron* Li. *Minarodendron* is widely accepted as an endemic lycopsid that is probably related to *Leclercqia* (Kenrick & Crane, 1997). Therefore *Protolepidodendron* is no longer recognized in South China.

Cai & Wang (1995) re-examined Xinjiang specimens attributed to *P. scharyanum*, from which three leaf distal segments were recognized (Cai & Wang, 1995, pl. 16, figs 1, 2). Specimens were transferred to *Protolepidodendron* cf. *P. cathaysiense*. However we recognize three-dimensional, five-tipped leaves from the newly studied leafy stem, and the specimens should therefore be reassigned to *Leclercqia*.

The type species, *L. complexa*, at the type locality in New York State, was measured as: stem 3.5–7.0 mm wide, leaf 4.0–6.5 mm long as a whole and bearing one-half to two-thirds of its length a pair of lateral divisions. The central and the lateral segments of the leaf are 2.5–3.0 mm and 1.0–2.0 mm long respectively (Banks, Bonamo & Grierson, 1972). These measurements are well matched

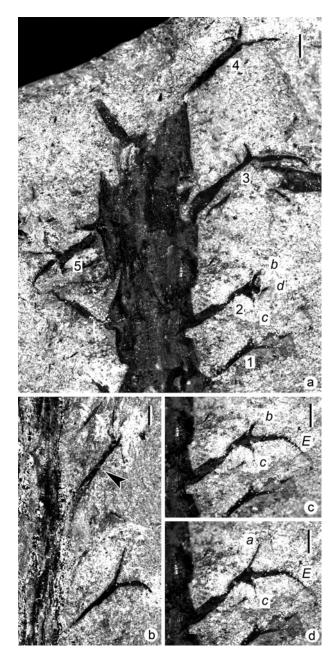


Figure 2. Leclercqia cf. L. complexa from the Middle Devonian of North Xinjiang, China. (a) New discovered short leafy stem on the reverse side of PB3246 (Sze, 1960, 1961). (b) Enlargement of leaves in Sze's unprepared specimen PB3247, upper leaf partially prepared, four segments visible distally (arrow); lower unprepared leaf shows typical bifurcation as observed in Protolepidodendron scharyanum Kräusel et Weyland. (c, d) Stages of serial dégagement to the leaf 2 in (a). Lettering of segments follows Fairon-Demaret (1980). All scale bars = 1 mm.

with dimensions of the present plant. No information about the ligule, sporophylls, sporangia, spores or anatomy was available, so, it is proper to attribute the present plant to *Leclercqia* cf. *L. complexa* (cf. Berry, 1994). *L. complexa* differs from a second species, *L. andrewsii* Gensel et Kasper, from the Lower Devonian of New Brunswick, Canada (Gensel & Kasper, 2005), in that the median and lateral

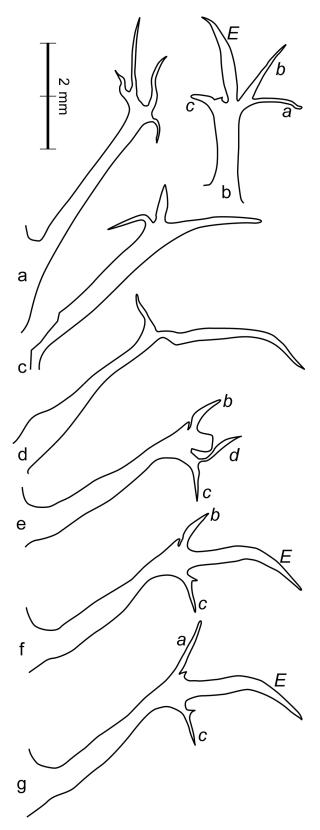


Figure 3. *Leclercqia* cf. *L. complexa* from the Middle Devonian of North Xinjiang, China. Line drawings of leaves in Figure 2. (a) Arrowed leaf in Figure 2b; (b,c,d) correspond to leaves 5, 4 and 3 in Figure 2a; (e,f,g) three stages of serial dégagement to the leaf 2 in Figure 2a (f and g correspond to Fig. 2c and d). Lettering of segments follows Fairon-Demaret (1980). Scale bar = 2 mm.

segments of the leaf in the latter are all in one plane and adaxially recurved.

In view of the above, Sze's (1960, 1961) specimens of *P. scharyanum*, assigned to *P. cf. cathaysiense* by Cai & Wang (1995), are hereby transferred to *L. cf. complexa*. This is the first confirmed record of *Leclercqia* on the basis of demonstration of leaf morphology in Chinese Middle Devonian strata.

Until now, the Middle Devonian lycopsid flora of North Xinjiang contains *Haskinsia sagittata* Edwards et Benedetto (Cai & Wang, 1995), H. hastata Berry et Edwards (Xu et al. in press), Colpodexylon Banks, Archaeosigillaria Kidston (Dou et al. 1983) and Leclercqia (this work). The floral assemblage shows much more similarity to that of North America (see Grierson & Banks, 1963, 1983) and Venezuela (see Berry, Casas & Moody, 1993; Berry & Edwards, 1995, 1996) than to that of the Xichong Formation, Yunnan (Wang et al. 2007). The only exception is an unusual form of Colpodexylon in Yunnan (Schweitzer & Cai, 1987), new specimens of which show no Colpodexylon ('embayed xylem' - Banks, 1944) structure and which therefore may be transferred to a new genus (Y. Wang et al. unpub. data). The transfer of P. cf. cathaysiense to Leclercqia therefore emphasizes the palaeophytogeographical separation of North Xinjiang from Yunnan.

Since its establishment, Leclercqia has been reported from the Early to Middle Devonian more or less worldwide, including the type locality in New York State, USA (Banks, Bonamo & Grierson, 1972), Australia (Fairon-Demaret, 1974; Meyer-Berthaud et al. 2003), Germany (Fairon-Demaret, 1980), Belgium (Fairon-Demaret, 1981), Venezuela (Berry, 1994), New Brunswick, Canada (Gensel & Kasper, 2005; Gensel & Albright, 2006) and Xinjiang, China (this work). The position and boundaries of the plates that later make up the Kazakhstania plate are uncertain in Middle Devonian time (Torsvik & Cocks, 2004). Middle Devonian plant localities in North Xinjiang and Kazakhstan were potentially close or even on the same microplate (Liao & Ruan, 1995) and have similar members of Middle Devonian flora (Ananiev, 1960; Jurina, 1988; Cai & Wang, 1995). It is likely that some Kazakhstan specimens currently attributed to Protolepidodendron may be transferred to Leclercqia after further investigation.

Evidence from spores supports the occurrence of *Leclercqia* in North China. As the dispersed spore *Dibolisporites heitaiensis* Ouyang (1984) from the Middle Devonian of Heilongjiang, NE China, shows great similarity to the *in situ* spore of *L. complexa* (Richardson, Bonamo & McGregor, 1993), Ouyang (1984) suggested that megafossils of *Leclercqia* would probably be discovered from the Middle Devonian of North China as well as Siberia. Geng (1992) reported *L. complexa* from the Lower Devonian (Pragian) of Sichuan, South China. But the assignment was rejected (Cai & Wang, 1995) because of the lack of typical features of *Leclercqia*.

When marked on the Middle Devonian paleogeographical and palaeoclimatic reconstruction, occurrences of *Leclercqia* are widely distributed, most of which are in the arid climatic belt (Meyer-Berthaud *et al.* 2003). *Leclercqia* in Xinjiang suggests a tropical distribution. Considering the occurrence also in the warm temperate climatic belt (Venezuela: Berry, 1994), we suggest that *Leclercqia* is more or less cosmopolitan in the Middle Devonian, with the only notable exception being South China, rather than distributed in the same so-called arid climatic belt as proposed by Meyer-Berthaud *et al.* (2003).

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