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Source: *International Journal of Plant Sciences*, Vol. 172, No. 6 (July/August 2011), pp. 836-846
Published by: The University of Chicago Press
Stable URL: http://www.jstor.org/stable/10.1086/660195
Accessed: 21/02/2014 08:48

Int. J. Plant Sci. 172(6):836–846. 2011.

1058-5893/2011/17206-0007$15.00 DOI: 10.1086/660195

A NEW SPECIES OF *LECLERCQIA* BANKS, BONAMO ET GRIERSON (LYCOPSIDA) FROM THE MIDDLE DEVONIAN OF NORTH XINJIANG, CHINA, WITH A POSSIBLE CLIMBING HABIT

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A new herbaceous lycopsid species, *Leclercqia uncinata* Xu, Berry, Wang et Marshall, is established on the basis of compression fossils from the Middle Devonian of Xinjiang, NW China. The new species has slender axes and three-dimensional, seven-tipped leaves with a distally hooked central segment conforming to the original diagnosis of the genus, and it is relatively smaller than the type species, *L. complexa* from New York State. The sporangium contains the spore, which can be assigned to morphotaxon *Acinoporites lindlariensis*. In our preparation of compressions, iridopteridalean fertile appendages are found trapped between the distally hooked leaves of *L. uncinata*. A possible climbing habit of the new plant is discussed.

Keywords: Leclercqia, lycopsid, climbing habit, Xinjiang, Devonian, leaf.

Introduction

The herbaceous lycopsid *Leclercqia complexa* Banks, Bonamo and Grierson (1972) from Blenheim-Gilboa, New York State, is often quoted to be one of the most completely known Middle Devonian plants. As well as a detailed description of compression fossils, including three-dimensional leaves released from the matrix by maceration, significant advances were made in the understanding of pyritized cell casts and overall anatomical configuration (Grierson 1976), together with the variety of in situ spores (Richardson et al. 1993) now assigned to *Acinosporites lindlarensis* Riegel. The main distinguishing characteristic of the genus *Leclercqia*, on the basis of the type *L. complexa*, is the leaf morphology. The leaf is divided into five segments, with a long, central abaxially reflexed segment. On both sides, set approximately at right angles, are two straighter and shorter segments. On the basis of this distinctive leaf morphology, confident identification of the genus was subsequently made from the Middle Devonian of Belgium (Fairon-Demaret 1981); Germany (Fairon-Demaret 1980); Australia (Fairon-Demaret 1974; Meyer-Berthaud et al. 2003); Venezuela (Berry 1994); and Xinjiang, China (Xu and Wang 2008). *Leclercqia complexa* has also been identified from the Lower Devonian (Emsian) of Wyoming (Tanner 1984) and New Brunswick, Canada (Gensel and Albright 2006).

A second species of *Leclercqia*, *L. andrewsii* Gensel et Kasper, was reported from the Emsian of New Brunswick and Maine (Gensel and Kasper 2005). This species is especially distinctive because it has flattened, forklike five-tipped leaves.

Xu and Wang (2008) investigated some axes on a single small block previously attributed to *Protolepidodendron scharyanum* by Sze (1960), from the Hoxtolgay area of Xinjiang. In this very limited material, they were able, on the basis of the five-divided leaves, to transfer the specimens to *L.* cf. *complexa*.

Our excavations at the locality in North Xinjiang, China, have yielded an exceptional diversity of Middle Devonian plants, which have been the subject of two PhD theses (Fu 2006; Xu 2006) and promise to reveal much about the Devonian flora of this understudied region. One of the most abundant plants at this locality is *Leclercqia*, and therefore, we were able to examine the new collections in a more detailed and destructive way than was possible with Sze's specimen. The new fossils demonstrate leaf morphology significantly different from that of *L. complexa*, which may hint at the plant's habit and also warrants the creation of a new species.

Material and Methods

Hundreds of specimens were collected from a locality informally known as 251 Hill, ~500 m west of State Highway G217, ~10 km north of Hoxtolgay Town, Hoboksar Mongol Autonomous County, Xinjiang, China (lat. 46°36′55″N, long. 86°1′5″E). The geographic location is shown in figure 1 of Xu et al. (2008).

Specimens are preserved as compressions in green-yellow mudstone from the Hujiersite Formation. Other plant fossils previously described from this formation include *Lepidodendropsis theodori* Jongmans (Sze 1960; Dou 1983; Cai and Wang 1995), *Tsaia conica* Wang et al. (Wang et al. 2004), *Leclercqia* cf. *complexa* Banks, Bonamo et Grierson (Xu and Wang 2008), *Haskinsia hastata* Berry et Edwards (Xu et al. 2008), *Haskinsia sagittata* Edwards et Benedetto (Cai and Wang 1995; Xu et al. 2008), and *Compsocradus* sp. (Fu et al. 2011). The geological age of the Hujiersite Formation

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Manuscript received January 2011; revised manuscript received March 2011.

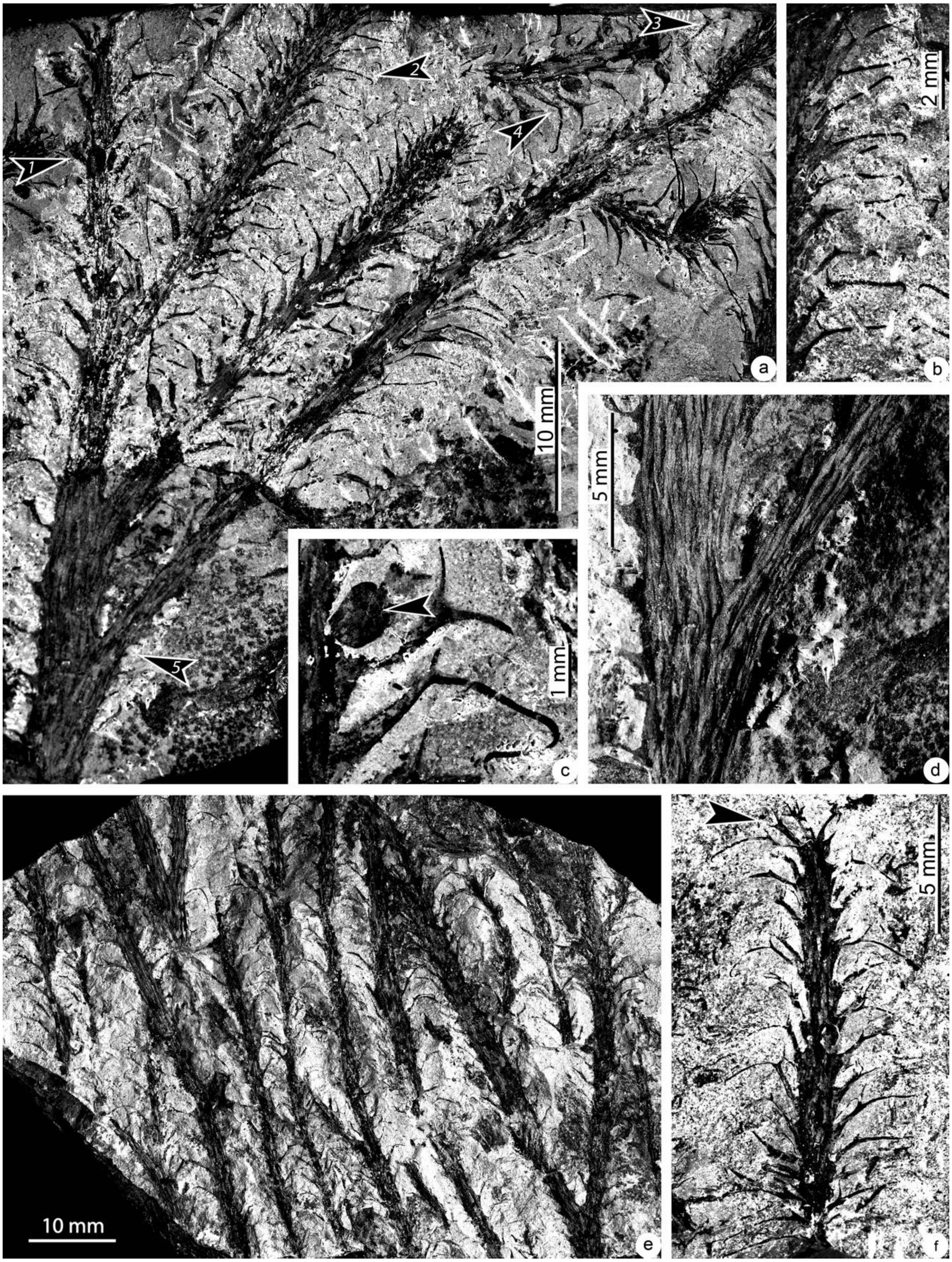

Fig. 1 *Leclercqia uncinata* sp. nov. from the Middle Devonian of Xinjiang, China. *a*, Paratype. Axis with three bifurcations. Note the asymmetrical, anisodichotomous lateral branching pattern. Attached and isolated axes have apex preserved. PB20930. *b*, Enlargement of

was regarded as late Mid-Devonian (Givetian) from the study of spores and plant megafossils (Cai and Wang 1995; Cai 2000; Xu et al. 2008).

Compressions were prepared with tungsten needles (Fairon-Demaret et al. 1999) to reveal morphological features. Photography was carried out with a Nikon D300 digital camera and 60-mm macro lens, with cross-polarized illumination. Some attached sporangia, although apparently open and infilled with sediment, were detached with as little attached sediment as possible and macerated (in hydrofluoric acid [HF]) to observe the in situ spores directly using SEM without oxidation. Although very few other spore types were detected, the majority of the spores and the few spore masses obtained clearly belong to morphon *Acinosporites lindlarensis* and are therefore inferred to have come from the plant under investigation. HF maceration of larger blocks containing leafy-stem specimens failed to yield the whole structure of either the leaf or the sporangium. All specimens are deposited at Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (reference numbers and prefix PB).

Systematic Paleobotany

Class—Lycopsida

Order—Protolepidodendrales

Family—Protolepidodendraceae

*Genus—*Leclercqia *Banks, Bonamo et Grierson (1972) emend. Bonamo, Banks et Grierson (1988) emend. Gensel et Kasper (2005)*

*Type Species—*Leclercqia complexa *Banks, Bonamo et Grierson (1972) emend. Bonamo, Banks et Grierson (1988)*

*Species—*Leclercqia uncinata *sp. nov. Xu, Berry, Wang et Marshall*

Diagnosis. As for the genus. Axes branching isodichotomously or anisodichotomously at angles of 15°–45°; 1.6–2.6 mm wide, at least 70 mm long. Leaf bases elongate-fusiform, 2.1 mm long and 0.4 mm wide, tightly arranged in helices or pseudowhorls; eight to 10 leaves inserted on the axis per gyre. Leaf consists of a basal segment, dividing just below the midpoint into three major segments, a long narrow central segment, and two further divided opposite lateral segments arranged three dimensionally; overall length up to 5.1 mm (basal segment plus central segment); basal segment 1.6–3.3 mm (2.4, $n = 31$) long, 0.4–0.5 mm (0.5, $n = 15$) wide in the middle; central segment 2.4–3.4 mm (2.9, $n = 26$) long, 0.3–0.4 mm wide at base, deflected abaxially, tapering distally and terminating in an abaxially tightly recurved hook; pairs of lateral major segments are divided near the base into two or very often three more or less equal minor segments; minor segments 1.2–1.7 mm (1.3, $n = 13$) long and 0.1–0.2 mm wide at the base, fused proximally into a unit up to 0.5 mm wide. Sporophyll similar in morphology to sterile leaf; no strobilus formed. Sporangium ovate to fusiform in lateral view, ovate in adaxial view, attached by an oval pad proximal to the division of the leaf, is 1.2–1.5 mm (1.3, $n = 13$) long and 0.6–0.9 mm (0.8, $n = 13$) wide/thick. Plant homosporous. In situ spores trilete, subtriangular-circular in amb, 40–50 μm in diameter (fig. 4); laesurae with labra that extend to prominent curvaturae perfectae close to equatorial margin; distal sculpture elements biform and closely packed into muronate ridges with lacunae; individual elements consist of basal verrucae surmounted by coni; there are longer composite spines on the equatorial margin, 3–4 μm in height.

Holotype. PB20932 (the bifurcated branch indicated by arrowheads *1* and *B* in fig. 2*a*). Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Paratype. PB20930 (fig. 1*a*), PB20931 (fig. 1*d*), PB20933 (fig. 2*b*), Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Locality. 251 Hill, 10 km north of Hoxtolgay Town, Hoboksar County, Xinjiang, China.

Horizon. Hujiersite Formation (late Mid-Devonian).

Derivation. From the Latin *uncinatus* ("hooked"), referring to the distal hook on the central leaf segment.

Descriptions

Axes

Many leafy axes are arranged on the blocks either in a regularly subparallel fashion (figs. 1*e*, 2*b*) or disordered and frequently overlapping (fig. 2*a*). Axes are narrow, generally ranging from 1.6 to 2.6 mm wide. The broadest stem is up to 3.5 mm wide. Many examples have isotomous or near-isotomous bifurcations at angles of 15°–45°. The largest axis observed has a different branching pattern (fig. 1*a*); the main axis appears to give off three successive smaller branches on the right-hand side of the compression at an angle of ~35°–40°. These remain subparallel to each other over the extent of the specimen (fig. 1*a*).

The maximum length of the axes we measured is ~70 mm (fig. 2*a*). The axes are generally untapered, and the apex is hemispherical (fig. 1*a*), suggesting no secondary growth. Leaf bases, which are not prominent on the stem compressions, are tightly arranged on the surface of the stems in low helices to pseudowhorls and are elongate fusiform in shape, ~2.1 mm long and 0.4 mm wide (fig. 1*d*). Four to five neighboring leaf bases are seen on the stem surface, suggesting a total of eight to 10 leaves per gyre.

a portion of the axis indicated by arrowhead 2 in *a*, showing the distal hook of the central leaf segment. *c*, Close-up of the axis indicated by arrowhead *4* in *a*, showing an attached sporangium in a basal view with the oval attachment pad structure (arrowhead) and a leaf in lateral view; note that the central segment has a distal hook. *d*, Enlargement of the lower portion of the axis in *a* (arrowhead *5*), showing the tightly arranged, long fusiform leaf bases, illuminated from the left. Note that the shape of the leaf bases is enhanced visually when the photograph is rotated 90° clockwise. *e*, Paratype. Up to 12 nearly parallel axes, including isodichotomous divisions, in one block. PB20931. *f*, Ordinary leafy axis; note that the leaf has several tips (arrowhead) or a bifurcation into a short tip and longer deflected, distally hooked segments. PB20934.

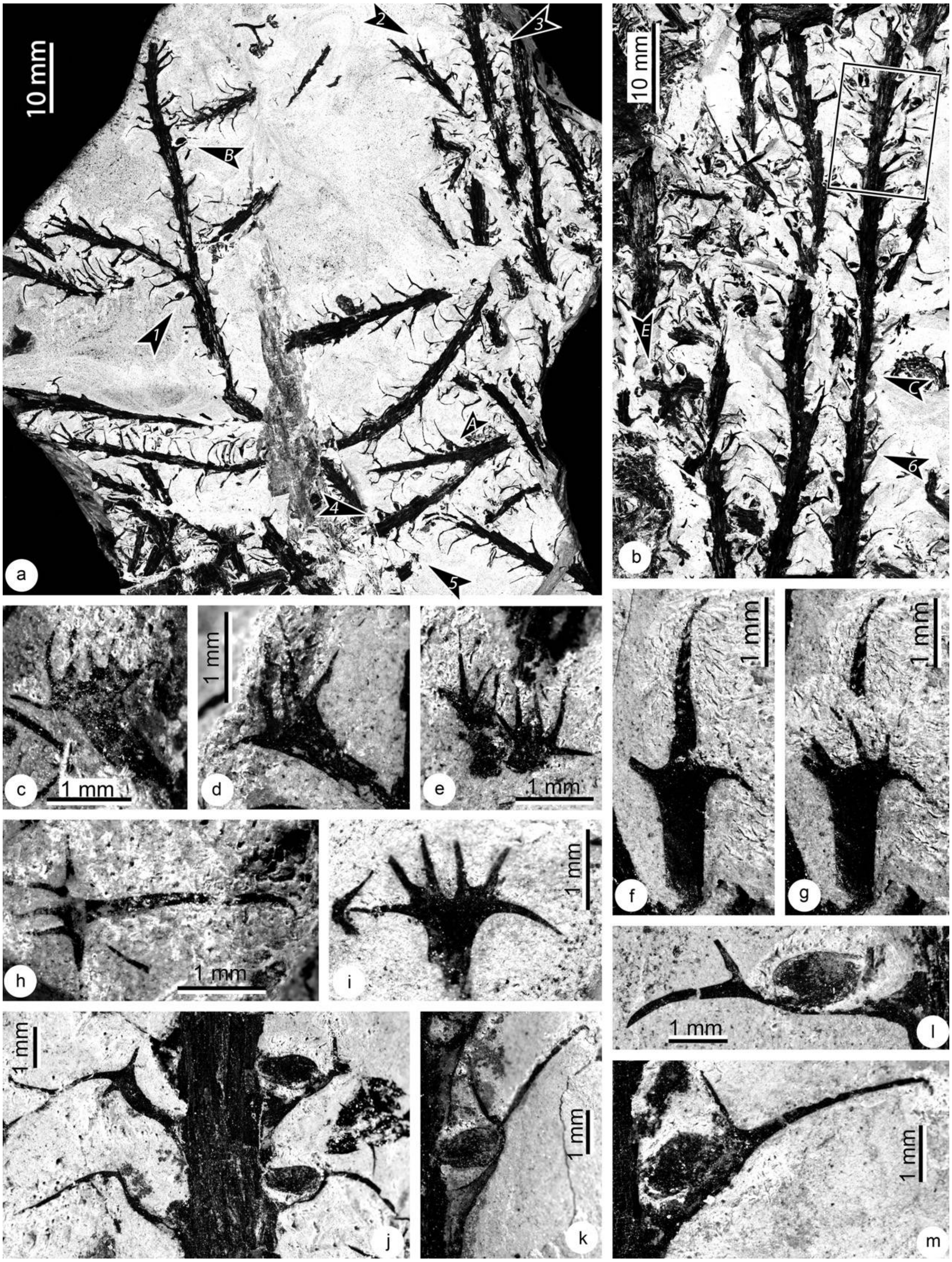

Fig. 2 *Leclercqia uncinata* sp. nov. from the Middle Devonian of Xinjiang, China. *a*, Abundance of leafy axes and the holotype axis (arrowheads *1* and *B*), with attached sporangia. PB20932. *b*, Paratype. Parallel fertile axes. PB20933. Sporangia *A–E* in *a* and *b* were detached to obtain in situ spores. The leafy axis in the box was serial dégaged to show the spatial relationship to *Compsocradus* appendages (see fig. 5). *c*,

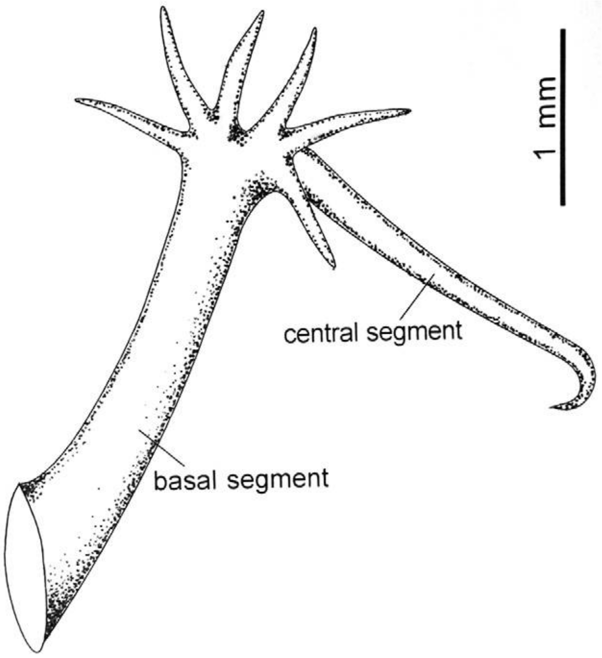

Fig. 3 *Leclercqia uncinata* sp. nov. from the Middle Devonian of Xinjiang, China. A reconstruction showing the gross morphology of a typical sterile leaf.

Leaves and Sporophylls

The leaf bases are decurrent, as seen in lateral view (fig. 2*j*, 2*k*), and leaves and leaf bases do not show any sign of abscission. Leaves have a long petiole and divide distally into three major parts, namely, a long, narrow undivided central segment and two lateral units each divided into two or three segments.

The basal segment is generally straight and is inserted on the axis at almost any angle above perpendicular, but 35°–40° is typical. It is narrow when observed in lateral view and much broader when compressed flat on the matrix (in adaxial view); therefore, it appears to have been a relatively flat near-lamina structure. It widens slightly at the point of division (fig. 2*f*, 2*g*, 2*i*). The central segment is, on average, significantly longer than the basal segment. It is inserted at an angle that is sometimes a straight extension of the basal segment but is otherwise abaxially recurved or bent by up to as much as 90° (fig. 1*f*), this observation being affected by the angle of compression. Most often, the central segment is orientated 10°–25° abaxially with respect to the orientation of the basal segment. Characteristically, and when well preserved and carefully uncovered, the central segment terminates in a tight abaxially recurved hook (figs. 1*b*, 1*c*, 2*h*, 2*m*). The tip of the hook may be recurved as much as 180° with respect to the subtending segment.

The majority of unprepared leaves show a division, with at least one shorter segment separating from the end of the basal segment (fig. 1*f*). In very few of the unprepared leaves, units of up to three lateral tips may be seen on either side of the division (fig. 2*i*), and in others up to six short lateral tips could be revealed by dégagement (fig. 2*c*, 2*d*, 2*e*). Where the central segment is present and a view of the top or bottom surface of the petiole lamina is visible in low-angle illumination, a transverse groove or ridge can be observed, marking the departure of the lateral units at an angle to the plane of the rest of the leaf (fig. 2*f*, 2*g*). Starting at this groove, tips of each lateral segment can be revealed by serial dégagement (fig. 2*f*, 2*g*). The lateral tips radiate outward from the base of the segment, where they are united in a broad base. The division of the lateral segment appears as a genuine trifurcation rather than two dichotomies. The lateral segments are much shorter than the central segment and in adaxial view can point parallel to the central segment, backward toward the axis, or in between these extremes, and they are rarely in the same plane as that defined by the basal segment. In the example illustrated (fig. 2*f*, 2*g*), only two lateral tips are initially exposed on the matrix surface (fig. 2*f*). Removing the base of the central segment exposes three other slender lateral tips on a coaly layer that slopes away from the stem and downward into the matrix (fig. 2*g*), suggesting that the bases of the opposing sets of lateral segments are joined by a transverse ridge of tissue rather than being completely separate. One of the lateral tips on the left is preserved, curved back underneath the position of the central segment. In one specimen, although the basal segment is not present, the central segment and five lateral tips are exposed almost flat (fig. 2*h*), contrasting with those examples where the basal segment and lateral segments are visible but not the central segment (fig. 2*c*–2*e*, 2*i*). Therefore, the total leaf morphology is highly three dimensional. It is very likely that segments out of the plane of the rest of the leaf would be overlooked or, where the leaf is exposed on the surface of the slab, left in the counterpart. A reconstruction of the gross morphology of a single typical sterile leaf is given (fig. 3).

We have observed the surfaces of many leaves with binocular microscopes and not seen a ligule. Attempts to macerate whole leaves for inspection by SEM have proved unsuccessful because the coalified compressions have too many fractures.

Sporophylls appear very similar to the sterile leaves, with at least five lateral tips and a central distally hooked segment (fig. 2*b*; leaf *D* in figs. 5*d*, 5*e*, 6*b*), with the exception that the basal segment is sometimes but not always curved around the sporangium up to the point of division (fig. 2*j*, 2*k*).

Close-up of the leaf indicated by arrowhead *1* in fig. 1*a*. *d*, Close-up of the leaf indicated by arrowhead *3* in *a*. *e*, Two overlapping distal leaves indicated by arrowhead *5* in *a*, showing two lateral major segments, each divided into two to three minor segments. *f*, *g*, Two stages of serial dégagement of the leaf indicated by arrowhead 2 in *a*. *f*, Leaf appears hastate, with two lateral segments. *g*, After removal of proximal part of central segment, revealing three additional tips going down into the matrix. *h*, Enlargement of the leaf indicated by arrowhead *3* in fig. 1*a*. Central segment on right, five lateral minor segments on left; the basal segment is not visible. *i*, Enlargement of an isolated leaf from the block illustrated in *a*, showing two lateral major segments, each divided into three minor segments. *j*, Portion of fertile axis indicated by arrowhead *4* of *a*, showing the basal segment curving around the margin of the sporangium. *k*, Sporophyll with sporangium, enlarged from portion of arrowhead *6* of *b*. *l*, Sporophyll with adaxial sporangium, enlarged from arrowhead *1* of *a*. *m*, Sporangium *A* in *a* and the distally hooked sporophyll.

Sporangia

Sporangia in lateral view are ovate to fusiform and broader ovate in adaxial or abaxial view, 1.2–1.5 mm (1.3, $n = 13$) long and 0.6–0.9 mm (0.8, $n = 13$) wide/thick (figs. 1*c*, 2*j*–2*m*). Sporangia are attached on the adaxial surface of the sporophyll by a pad (fig. 1*c*). The attachment point is ~2 mm from the base of the sporophyll, more than two-thirds of the leaf length before its division (fig. 2*j*–2*m*). The attachment pad, visible on the abaxial surface of some isolated sporangia, is circular and ~0.2 mm in diameter (fig. 1*c*). The dehiscence of the sporangium is not clear.

Spores

A number of spores macerated from sporangia were studied by SEM, including spores masses (fig. 4*a*, 4*f*, 4*g*) and separated spores (fig. 4*c*, 4*i*). The spores are trilete and subtriangular-circular in equatorial view (fig. 4*a*, 4*c*). Laesurae are accompanied by labra and extend almost to the equatorial margin, where they link into curvaturae perfectae (fig. 4*c*). Proximal to these curvaturae, the spore surface appears unsculptured (fig. 4*b*, 4*g*). The curvaturae delimit a ring of more prominent equatorial spines that are composite in character. There is a basal element that either can be bulbous or tapers from a basal maximum (fig. 4*e*). Each spine shows a constriction or ridge at approximately halfway along its length. These basal elements are topped with microconi that are <1 μm in height (fig. 4*d*, 4*e*, 4*j*). The total spine dimensions are 1–2 μm in diameter and 3–4 μm in height. In contrast, the distal surface is sculptured with biform elements. The basal part is verrucate (fig. 4*i*, 4*j*). These coalesce to form a variety of murornate patterns; the muri are broad, enclosing lacunae that are 2–10 μm in diameter (fig. 4*d*, 4*h*, 4*j*). The verrucae are surmounted by spines that are similar to the equatorial sculpture in being composite (fig. 4*j*), with a prominent midlength constriction. The maximum diameter of the spores is 40–50 μm (mean, 43 μm), on the basis of 10 specimens.

Spatial Relationship to Compsocradus *Fossils*

The fossil flora from the 251 Hill locality is diverse. Among the most common fossils is the iridopteridalean *Compsocradus* (see Fu et al. 2011), the smaller axes and appendages of which have also recently been described as *Ramophyton givetianum* Wang (2008). The plant has three orders of branching, and the largest axes are ~6 mm wide. The axes of all orders have attached appendages that dichotomize equally three or four times and terminate in paired ellipsoidal sporangia.

We noticed that fertile appendages of *Compsocradus* are found both rarely isolated on the surface of the slabs (fig. 2*a*, top) and commonly very close to the surface of the axes (fig. 2*b*, box; fig. 5*a*, arrowheads).

In order to establish exactly how closely positioned the *Compsocradus* appendages were to the lycopsid axes and leaves, we performed a 12-stage serial dégagement of one area, summarized in figures 5 and 6. Two leaves, *A* and *B*, were shown to overlie the axis surface and the *Compsocradus* appendage (figs. 5*a*, 5*b*, 6*a*). Two further leaves, *C* and *D*, were shown to be at a lower level in the matrix than the ap-

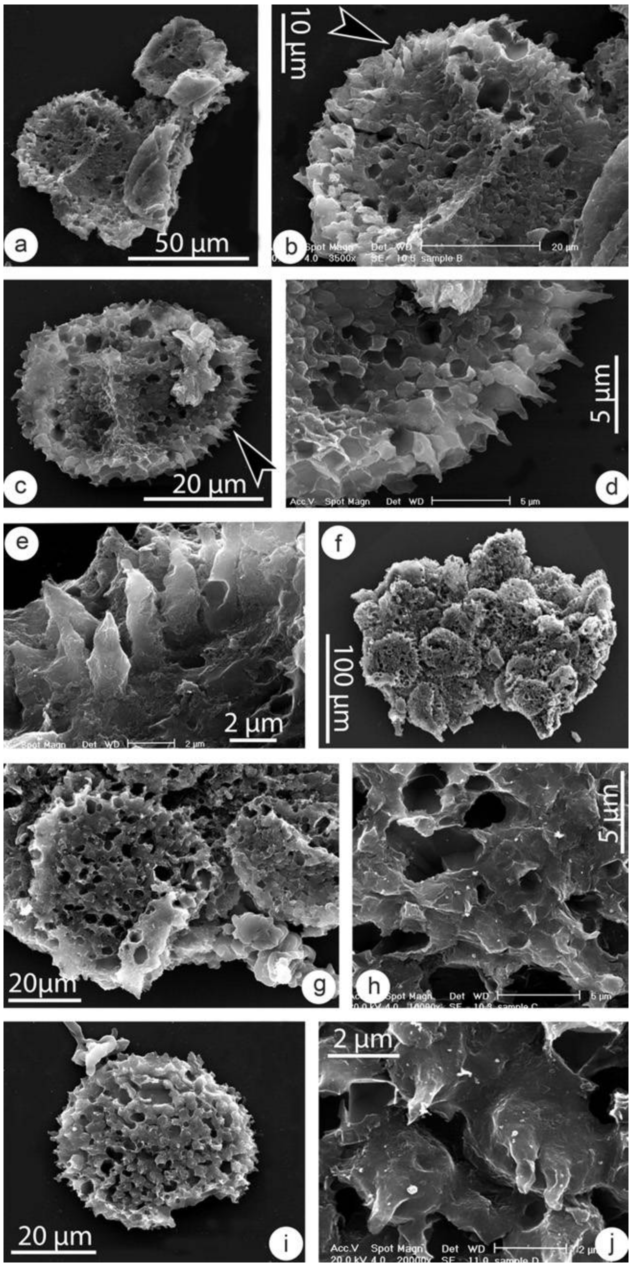

Fig. 4 Scanning electron photomicrographs of in situ spores of *Leclercqia uncinata* sp. nov. Note that the spores show considerable pyrite damage that might be affecting the shape of the spines both at the equator and on the distal surface. *a*–*e*, In situ spores detached from sporangium *B* (fig. 2*a*). *a*, Part of spore mass. *b*, Enlargement of a spore from the mass in *a*, showing the trilete rays with labra, curvaturae, and equatorial distal sculpture. *c*, Trilete spore with equatorial spines. *d*, Enlargement of the sculpture (arrowhead) in *c*. *e*, Close-up of the sculpture (arrowhead) in *b*. *f*–*h*, In situ spores detached from sporangium C (fig. 2*b*). *f*, Part of sporangial mass of spores. *g*, Spores from the mass in *f*. *h*, Enlargement of a portion of the spore in *g*, showing distal degraded spinelike sculpture. *i*, *j*, In situ spores detached from sporangium *E* (fig. 2*b*). *i*, Distal view of a single spore, showing the muronate ridges made up of coalescing biform sculpture. *j*, Enlargement of the distal sculpture of the spore in *i*. This shows the lacunae between the muri and the presence of basal verrucae surmounted by composite spines ~4 μm in length.

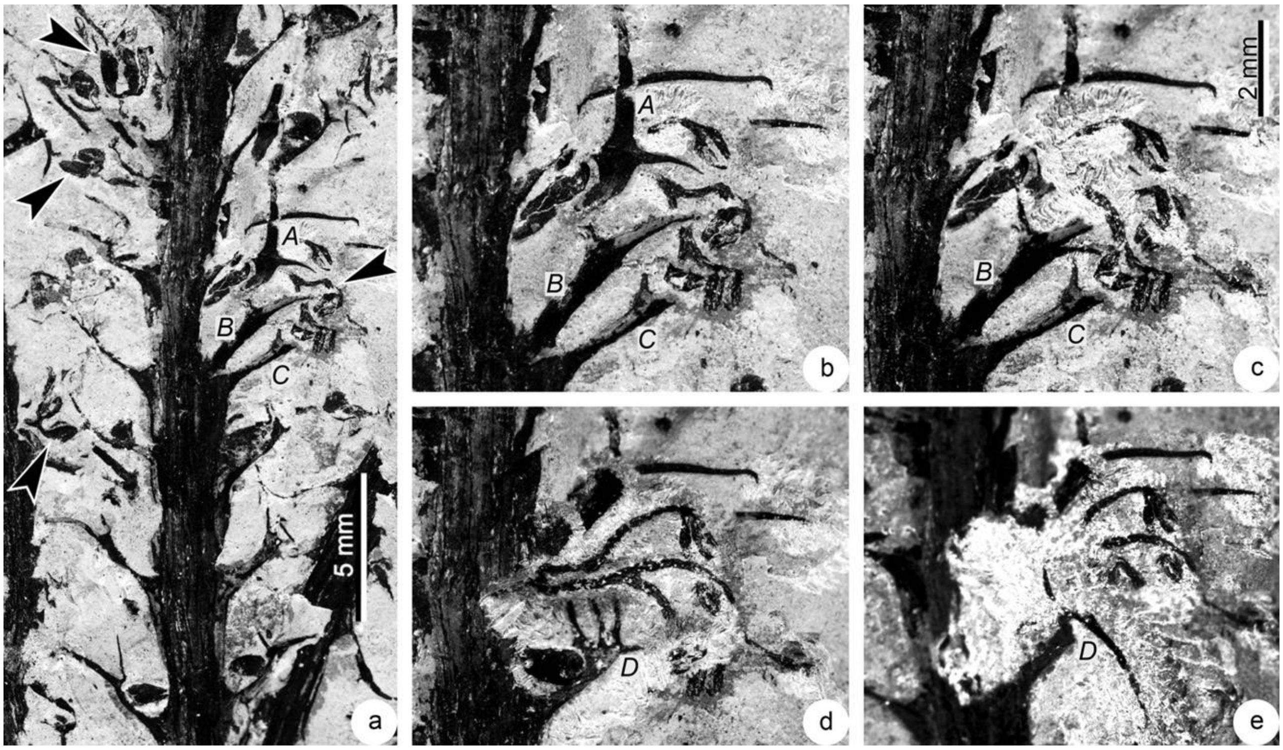

Fig. 5 Selected stages of serial dégagement of *Leclercqia* leaves and *Compsocradus* appendages. *a*, Close-up of the area in the box in fig. 2*b*, showing *Compsocradus* appendages (arrowheads) and *Leclercqia* axes. Leaves uncovered are labeled *A*–*D*. Before preparations. *b*–*e*, Selective successive stages of dégagement. Note that leaves *A* and *B* are higher to the observer than leaves *C* and *D*. Summarized in fig. 6.

pendage (figs. 5*c*, 5*d*, 5*e*, 6*b*). Therefore, the appendage, no longer attached to the parent plant but in good condition with attached sporangia, is preserved within the zone of spikey, space-filling leaves around the outside of the *Leclercqia* stem. This is also likely to be the case with many other examples of the detached fertile trusses of *Compsocradus* we observed.

Comparisons

The new plant obviously belongs to the protolepidodendracean lycopsids in having helically inserted forked leaves and adaxial sporangia, and it is most similar to the genus *Leclercqia*. In regard to the leaf morphology, it conforms to the original diagnosis of the genus, which states that leaves divide “near their midpoint into one elongate, central and two divided lateral segments” (Banks et al. 1972, p. 35). It is not necessary here to repeat the comparisons between *Leclercqia* and other genera such as *Protolepidodendron*, *Colpodexylon*, *Haskinsia*, and so on, which have been discussed at length by other authors (Banks et al. 1972; Fairon-Demaret 1974; Grierson 1976; Grierson and Banks 1983; Edwards and Benedetto 1985; Bonamo et al. 1988; Berry 1994; Xu and Wang 2008). We here focus on comparisons among the species and occurrences of *Leclercqia* (table 1).

The type species, *Leclercqia complexa*, from the Middle Devonian of Blenheim-Gilboa, New York State, has been studied morphologically both from compressions and from leaves and cuticles isolated from the matrix by HF maceration. We can offer comparisons based only on the study of compressions. However, our specimens have the advantage of having a very clear contrast to the matrix and are therefore far easier to study on the rock than the New York specimens. We were also able to make direct comparisons to specimens from New York (Blenheim-Gilboa) held in the Cardiff University paleobotany collections.

The principal difference between the Xinjiang specimens and the type species is in the detail of leaf morphology. In the Xinjiang plant, the central segment of the leaf is most often longer than the basal segment, and the distal tip of the central segment is curled into a tight hook. In the New York species, the central segment is shorter than the basal segment, and the tip is straight or curved. In New York State, the most common leaf morphology is with a total of five segments. Very occasionally (Bonamo et al. 1988), one of the lateral major segments might be divided into three, probably unequal, minor segments, leading to a total of six tips. However, such leaves were extremely rare and not observed on the rock (P. M. Bonamo, personal communication). In the Xinjiang species, it is very common to have three segments making up the lateral units each side of the main tip; the three minor segments appear to arise from a basal trifurcation near the base of the lateral major segment, and we strongly suspect this to be the most common form of the leaf.

Despite these minor differences, the three-dimensional structure of the two species *L. complexa* and *L. uncinata* is very

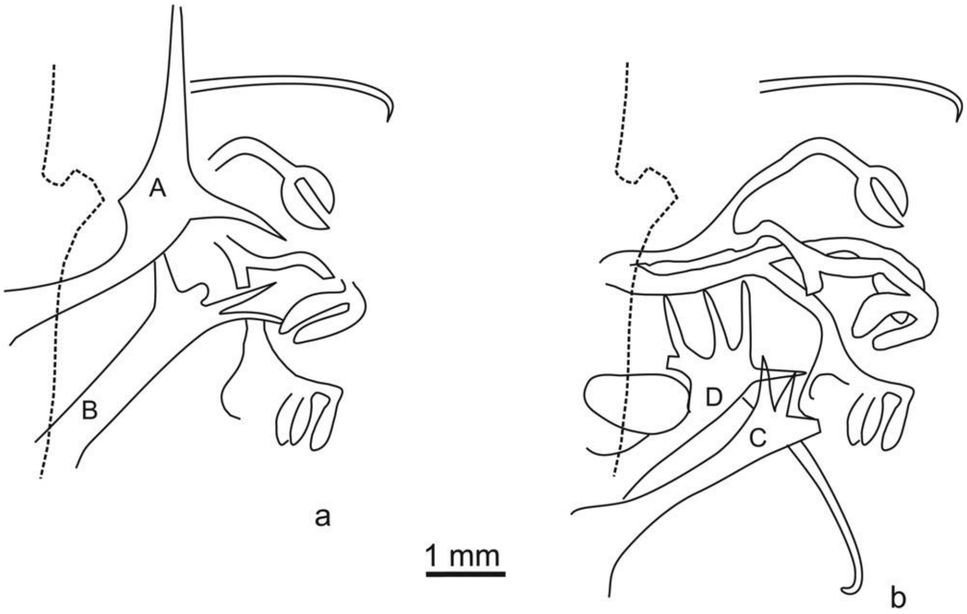

Fig. 6 Line drawings of serial dégagement of *Leclercqia* leaves and *Compsocradus* appendages by the *Leclercqia* axis (from the box in fig. 2*b*; for close-up, see fig. 5). *a*, Initial stages, showing two leaves (*A* highest, *B* lowest) overlying partially exposed dichotomous fertile appendage of *Compsocradus*. Dashed line shows the widest outline of the axis margin, which here underlies the leaves. *b*, Final stages, showing two further leaves (*C* higher, *D* lower) that lie underneath the level of the *Compsocradus* appendage. The dashed line shows the widest outline of the axis margin, at this stage above the sporangium of leaf *D* and above the proximal part of the *Compsocradus* appendage.

similar because of the fundamental division into a central segment and two opposite lateral major divided segments. We emphasize the apparently three-dimensional nature of the division of the leaf into three major segments in both *L. uncinata* and *L. complexa* (see fig. 1 of Bonamo et al. 1988). *Leclercqia complexa* has the leaf morphology most similar to that of the Xinjiang plant among known types.

The second species of *Leclercqia*, *L. andrewsii*, from the Early Devonian of New Brunswick, Canada (Gensel and Kasper 2005), is characterized by a relatively flat, essentially two-dimensional organization of leaf segments at the point of division, although all segments curve upward after the point of forking. Although a prominent central segment is also seen in leaves of *L. andrewsii*, it is relatively smaller than that in the present species. Two distinctive, opposite, three-dimensional lateral major segments are not observed. Therefore, there is a far greater difference between the leaves of *L. andrewsii* on the one hand and *L. complexa* and *L. uncinata* on the other than between the latter two species.

The occurrence of our new species from Xinjiang, clearly distinct from but very similar to *L. complexa*, makes specific identification more challenging than in those specimens where it is impossible to demonstrate the complete morphology of individual leaves. One example is the occurrence of *Leclercqia* in Australia, where the leaf morphology was reconstructed to have five segments on the basis of several views of partially visible permineralized divided leaves (Meyer-Berthaud et al. 2003) rather than leaves that could be completely revealed by uncovering. This is additionally highlighted by the small diameters of the axes of both Xinjiang and Australian *Leclercqia* compared with those from the *L. complexa* type locality (table 1). Additionally, *L. complexa* has wider occurrences and a larger range of dimensions of axes, leaves, and sporangia than do the other two species (table 1).

The in situ spores of the present plant can be assigned to the spore morphotaxon *Acinosporitis lindlarensis* Riegel 1968. Richardson et al. (1993) described 14 spore morphotypes of *A. lindlarensis* from *Leclerqia*, using both sporangia and dispersed spores. The specimens of *Leclerqia* ranged in age from Emsian to Givetian, including material from the type species *L. complexa*. This type material has also been described by Streel (1972), using spores isolated from the sedimentary matrix of *L. complexa* specimens. The in situ spores from Xinjiang are similar to type IA of Richardson et al. (1993) but differ in possessing much shorter equatorial spines (<4 compared to 6–10 μm) that are composite (biform) rather than simply tapering to a point. However, they share the characters of distal muri and polygonal lacunae. Type V of Richardson et al. (1993) also shows similarities with the specimens from Xinjiang in possessing densely packed distal verrucae; the curvatural spines are similarly short but again differ in being evenly tapered rather than composite. The spores also differ in size from those from *L. complexa*, being in the range of 53–92 μm in diameter (Streel 1972), whereas the Xinjiang specimens are all 50 μm or less in diameter (average, 43 μm). It is unclear whether these differences are because the Xinjiang specimens represent immature spores. Studies of dispersed spores from the same locality show a maximum size of 59 μm. This suggests that the in situ specimens are probably immature. However, the two populations show no real difference in the average size, with the dispersed population being 45 μm and the in situ specimens 43 μm.

Table 1

Comparison of Dimensions between the Species and Occurrences of *Leclercqia*

Species	Axis width	Leaf before division (length, width)	Central tip (length, width)	Lateral tip (no.; length, width)	Sporangium (length, width)	Locality	Authors
L. complexa	3.5–7.0	3.5–4.0,[a] .5	2.5–3.0	1.0–2.0 (4)	1–2	New York State	Banks et al. 1972
L. complexa	1.5–4	1.7–3.6	1.3	.6–1.0 (4?)	NA	Queensland, Australia	Meyer-Berthaud et al. 2003
Leclercqia sp.	2.5–4.5	2–3	1.6–3	.8–1.3, .2–.3 (4)	NA	Queensland, Australia	Fairon-Demaret 1974
L. complexa	<7	3.0–3.9[a]	2.1–3, .4–.6	1.0–1.8, .2–.3 (4)	1.2–1.5, .8–1.1	Elberfeld, Germany	Fairon-Demaret 1980
L. complexa	2.2–10	1.3–2.3, .7–.9	1.6–2.7, 0.3	.5–1 (4)	.8–1.6, .4–.7	New Brunswick, Canada	Gensel and Albright 2006
L. cf. *complexa*	3.3	5	2.7	1.8 (4)	NA	Sierra de Perija, Venezuela	Berry 1994
L. cf. *complexa*	3.8–4.2	3.4–3.8, .3–.4	3.1	.8–1.5 (4)	NA	Xinjiang, China	Xu and Wang 2008
L. andrewii	10–15	2.1–2.7, .5–.6	1.4–2.0, .3–.4	.6–.7 (2; inner), 1.0–1.5 (2; outer)	2.3–2.7, 1.2–1.6	New Brunswick, Canada	Gensel and Kasper 2005
L. uncinata	1.6–3.5	1.6–3.3, .4–.5	2.4–3.4, .3–.4	1.2–1.7, .1–.2 (6)	1.2–1.5, .6–.9	Xinjiang, China	This study

Note. All units are in millimeters. NA = not available; ? = probable.

[a] Data from calculation.

Discussion

The unusual branching pattern of one of our specimens of *Leclercqia uncinata*, which shows successive lateral branches (fig. 1*a*), if not caused by taphonomic probability may reflect the habit of the plant, suggesting that the plant had a creeping rhizome from which many aerial axes arose in parallel (fig. 1*e*), for example. However, no evidence of an actual rhizome is found from our specimens. For example, the largest axis has leaves even on what might be the lower surface. Therefore, we think that this specimen is probably part of the aerial system of the plant, most probably near the ground on account of the large diameter. Alternately, the densely branched axes are reminiscent of some stems, especially the distal portion of Middle to Late Devonian bipolar lycopsids, such as *Longostachys latisporophyllus* Cai and Chen (1996) and *Sublipidodendron grabaui* (Sze) Wang and Xu (2005).

The new species of *Leclercqia* from Xinjiang has morphological differences from *L. complexa* that may reflect its habit. In our specimens, the tips of the central segment are abaxially recurved into a tight hook. One obvious interpretation of this morphology is that the hooks on the upward-oriented leaves are climbing hooks—that is to say they were able to support or partially support the weight of the plant by attaching to other elements of the vegetation.

On the slab that contains many of our axes, we noticed the presence of small, fertile dichotomizing axes (appendages) of larger euphyllophyte plants (*Compsocradus*, the type species of which has axes 2–6 mm in width; see Berry and Stein 2000). Although there are a few such appendages isolated on the surface of the slab, most are found tangled within the leaves around *Leclercqia* axes. As noted, we examined one such area by serial dégagement and demonstrated that the dichotomizing fertile axes were found in the sediment between the top layer and the bottom layer of leaves inserted on the neighboring axis. Although none of the hooks was actually attached to the euphyllophyte material, the hooks are exactly the right size to attach to the appendages found. Our hypothesis is that the leaves were modified for attachment to shrubby euphyllophytes with small appendages. The events that caused transport and burial of this material in the floodplain/channel system may have pulled the two plants apart, ripping off the delicate appendages then buried in a telltale position.

Unfortunately, this attractive hypothesis cannot be tested using biomechanical properties of the axes, as they are not anatomically preserved. The hooks we observe are crude compared with, for example, the climber hooks and tendrils attributed to Pennsylvanian seed ferns (Kerp and Krings 1998). Examples of climbing strategies in Devonian plants are rare, with the only example known to us being the occurrence of *Cladoxylon tanaiticum* axes directly attached to a log from the Famennian of the Donetz Basin (Snigirevsky 1992).

Alternatively, we also note that there are always dense axes preserved in single *Leclercqia* slab, as in the case of both Xinjiang (fig. 1*e*) and New York State (Banks et al. 1972; Grierson 1976) specimens. These densely arranged axes, with multitipped leaves with or without distal hooks, might act as filters and capture plant appendages (this study) or animal fragments (see Shear et al. 1984).

Acknowledgments

We thank Dr. D. Edwards, Cardiff University, for instructive suggestions and L. Axe, Cardiff University, for laboratory help. This study is supported by the Chinese Academy of Sciences (grant KZCX2-EW-QN113), the NSFC (grant 40902005), and the Sino-British Fellowship Trust.

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