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The plant *Leclercqia* (Lycopsida) in Gondwana: implications for reconstructing Middle Devonian palaeogeography

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Abstract – Abundant and well-preserved material of the ligulate lycopsid genus *Leclercqia* is reported from a new Middle Devonian locality in northeastern Queensland (Australia). The plants occur in a chert horizon in the Storm Hill Sandstone of the Dosey-Craigie Platform. Lithological data and conodont analyses combined with information from *in situ* spores provide an age for the plant levels ranging from Eifelian, possibly Middle Eifelian, to Early Givetian. Plant taxonomic identification is based on vegetative and fertile stems that display both external morphology and anatomy. This material represents the best documented occurrence of *Leclercqia* outside Laurussia and possibly the earliest in Gondwana; it provides evidence that colonization of Gondwana by the species *L. complexa* was contemporaneous to that of Siberia and Kazakhstan. Analysis of the distribution patterns of *L. complexa* suggests that it was adapted to a wide range of environments, but within certain limits which we hypothesize to be those of a climatic belt. Such considerations support previous studies using other biological data, such as faunas and palynomorphs, for reconstructing Devonian palaeogeography. They favour a close proximity of Laurussia and Gondwana rather than the occurrence of a wide ocean separating the two palaeocontinents in Middle Devonian times.

Keywords: Australia, Devonian, Gondwana, Lycopsida, palaeogeography.

1. Introduction

Devonian plate dynamics is an actively debated topic and different models are currently presented in the literature with regard to the drift history of Gondwana and to the time it collided with Laurussia. All models based on palaeomagnetic data assert that a large ocean separated Gondwana from Laurussia in Middle and Late Devonian times, an ocean which became closed by the Late Carboniferous (Tait *et al*. 2000; Van Der Voo, 1993). In contrast, models using biological, lithological or tectonic data suggest that the western border of this ocean was almost closed in the Devonian (Matte, 2001; McKerrow *et al*. 2000; Robardet *et al*. 1993). Supporting biological evidence is mainly represented by marine benthic faunas of invertebrates, by non-marine, marginal and terrestrial vertebrates, and by palynomorphs (Briggs, 1995; Feist, 2001; Janvier & Villaroel, 2000; Streel *et al*. 2000; Streel, Fairon-Demaret & Loboziak, 1990; Young, 1990; Young, Moody & Casas, 2000). Affinities of Middle and Late Devonian assemblages of plant macro-remains from northwestern Gondwana (especially Venezuela and Colombia) with contemporaneous assemblages from North America and Europe are also compatible with the latter models (Berry *et al*. 2000).

Fossil plant taxa based on macro-remains that provide information on ancient continental positions must fulfill three criteria: accurate systematic identification and monophyly for supra-generic taxa; reliable age determination, independent from macrofloral evidence; and extended geographic range. Few meet these requirements in the Middle Devonian, which explains the lack of large-scale biogeographic studies based on macro-plants for this period. *Leclercqia*, an early lycopsid genus of late Early to Middle Devonian age, is one of them. Unlike extant lycopsids, *Leclercqia* exhibits an unusual combination of characters, being ligulate and homosporous. As a member of the order Protolepidodendrales, it features forked microphylls (non-laminar leaves). The type species, *L. complexa*, is one of the best known Devonian plant taxa (Banks, Bonamo & Grierson, 1972; Bonamo, Banks & Grierson, 1988; Grierson, 1976; Grierson & Bonamo, 1979). This herbaceous plant of small stature consists of horizontal leafy stems that branch dichotomously and whose terminal parts are curved upwards, in an erect position. Microphylls are borne in low spirals. The most distinctive feature of the species relates to the three-dimensional morphology of its five, or

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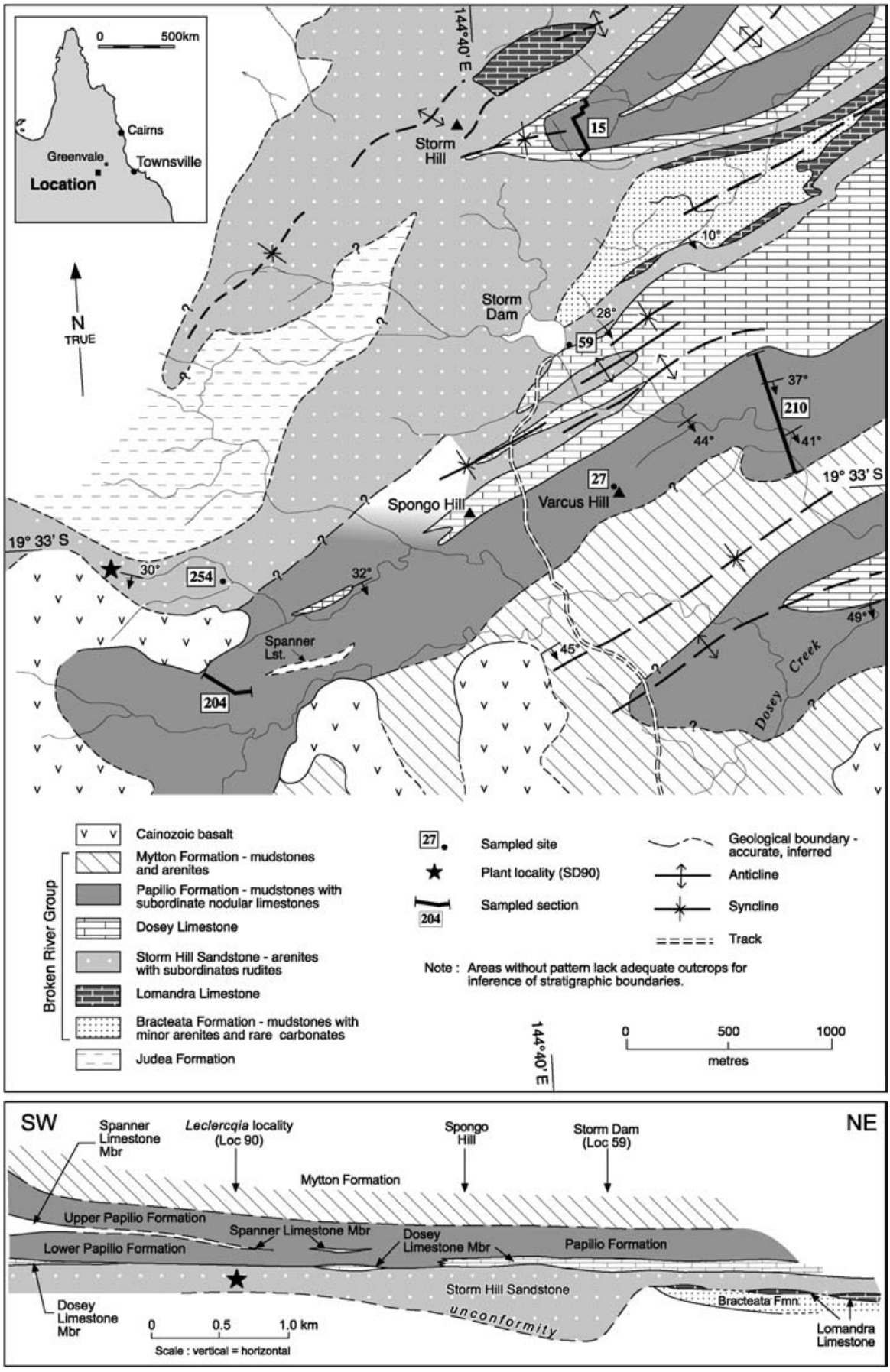


Figure 1. For legend see facing page.

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sometimes more, forked leaves. These comprise a long central, abaxially recurved segment and at least two pairs of shorter lateral ones arising at about two-thirds the leaf length. The lateral segments are variously orientated, often in a plane at right angles to the median segment. The ligule is borne on the upper surface of the central segment, distal to microphyll insertion on the supporting axis (Grierson & Bonamo, 1979). Spores yielded by this plant belong to the *Acinosporites lindlarensis* Riegel (1968) type of dispersed palynomorphs (Richardson, Bonamo & McGregor, 1993).

Leclercqia has been reported from several localities in North America and Europe. Its published occurrence in Gondwana is scanty. It presently consists of one leafy vegetative stem compression of probable Givetian age from the Campo Chico Formation of western Venezuela (Berry, 1994; Berry, Casas & Moody, 1993), and several axes from the Late Givetian of the Burdekin Basin in Queensland, Australia (Fairon-Demaret, 1974). The latter include anatomically preserved and fertile specimens still to be illustrated, and belong to *L. complexa* (M. Fairon-Demaret, pers. comm.). *Leclercqia* includes at least one other morphotype which likely represents a new species (Berry, 1994; Richardson, Bonamo & McGregor, 1993). Proper description and taxonomic treatment of this material from the Emsian of Maine and New Brunswick (Kasper, 1977; Kasper & Forbes, 1979) are in preparation (P. Gensel, pers. comm.).

The plant record of Middle Devonian age is notably poor in Australia (Talent *et al*. 2000). This paper reports the occurrence of abundant and well-preserved material of *Leclercqia complexa* from a new Middle Devonian locality in the Broken River region of Queensland (northeastern Australia). Plant taxonomic identification is based on a large number of anatomically preserved vegetative and fertile stems. A survey of the stratigraphic and geographic occurrences of the genus *Leclercqia* is provided. Biological and evolutionary patterns assessed from this distribution are used to test the conflicting geodynamic scenarios provided so far for the Middle Devonian.

2. Plant material and methods

The fossiliferous outcrop is located close to Storm Dam, 227 km on a bearing of 260° W from Townsville (Fig. 1). Plants are permineralized in a chert horizon intercalated within the Storm Hill Sandstone Formation. The rock matrix contains a monospecific assemblage consisting of abundant leafy axes of small size. Most have undergone compression during burial and appear somewhat flattened in transverse section. The description is based on about 30 specimens lying in various planes within the sediment. Maceration of pieces of chert in hydrofluoric acid (HF) to isolate plant remains was unsatisfactory partly due to the resulting brittleness of the material and to the production of insoluble salts that crystallized around surviving organic material. Peel-sections were made from anatomically preserved specimens using 40 % HF (Galtier & Phillips, 1999). Observation of the best sections using light microscopy provided cellular details from various tissues in axes and in their attached microphylls. Few axes display sporophylls (=fertile leaves). All exhibit open sporangia, and a few spores lying against sporangial walls were observed in light microscopy. Dispersed spores were obtained from a single block containing abundant axes. The matrix was partly embedded then macerated in HF for several days. The process released abundant miospores in the vicinity of some axes. A number were collected and observed with the scanning electron microscope.

3. Stratigraphic context and age

Leclerquia complexa occurs (Fig. 1) in the Storm Hill Sandstone in an interval of 40–65 cm of greenish-grey cherts underlain by siltstones and overlain by arkosic arenites and arkosic siltstones, dipping south at 26–48°, at the junction of two small unnamed gullies on Australian 1:100 000 Topographic Survey sheet 7858 Wando Vale at grid reference [0253438, 7836555]. The locality, SD 90 of Mawson & Talent (1989; see also Talent *et al*. 2002), is 2.6 km west–southwest of Storm Dam, 70 km southwest of Greenvale in the Townsville hinterland of northeast Queensland. The horizon appears to be about 70 or 80 m above the base of the Storm Hill Sandstone and to underlie (and thus be slightly older than) developments of Dosey Limestone that wedge out towards the *Leclercqia* locality from east and west (cf. Fig. 1).

The Storm Hill Sandstone is one of six units making up the Broken River Group of the Dosey-Craigie Platform of the Townsville hinterland of northeastern Australia. The Broken River Group tends to pass laterally southwestwards from the vicinity of Storm Dam (Fig. 1) from an exclusively marine platform sequence of highly fossiliferous carbonate and clastic units into a decreasingly marine sequence with increase in thickness of the Storm Hill Sandstone. The latter has been interpreted as a deltaic complex (Mawson &

Figure 1. Geology in the vicinity of Storm Dam, northeast Australia, in relation to the *Leclercqia complexa* locality (SD 90), with diagrammatic section aligned through Storm Dam and the *L. complexa* locality to show its relationship to the stratigraphy of the area. Because of generally poor exposures, thicknesses of stratigraphic units are approximate. Area near Spongo Hill without pattern lacks adequate outcrop for inference of stratigraphic boundaries.

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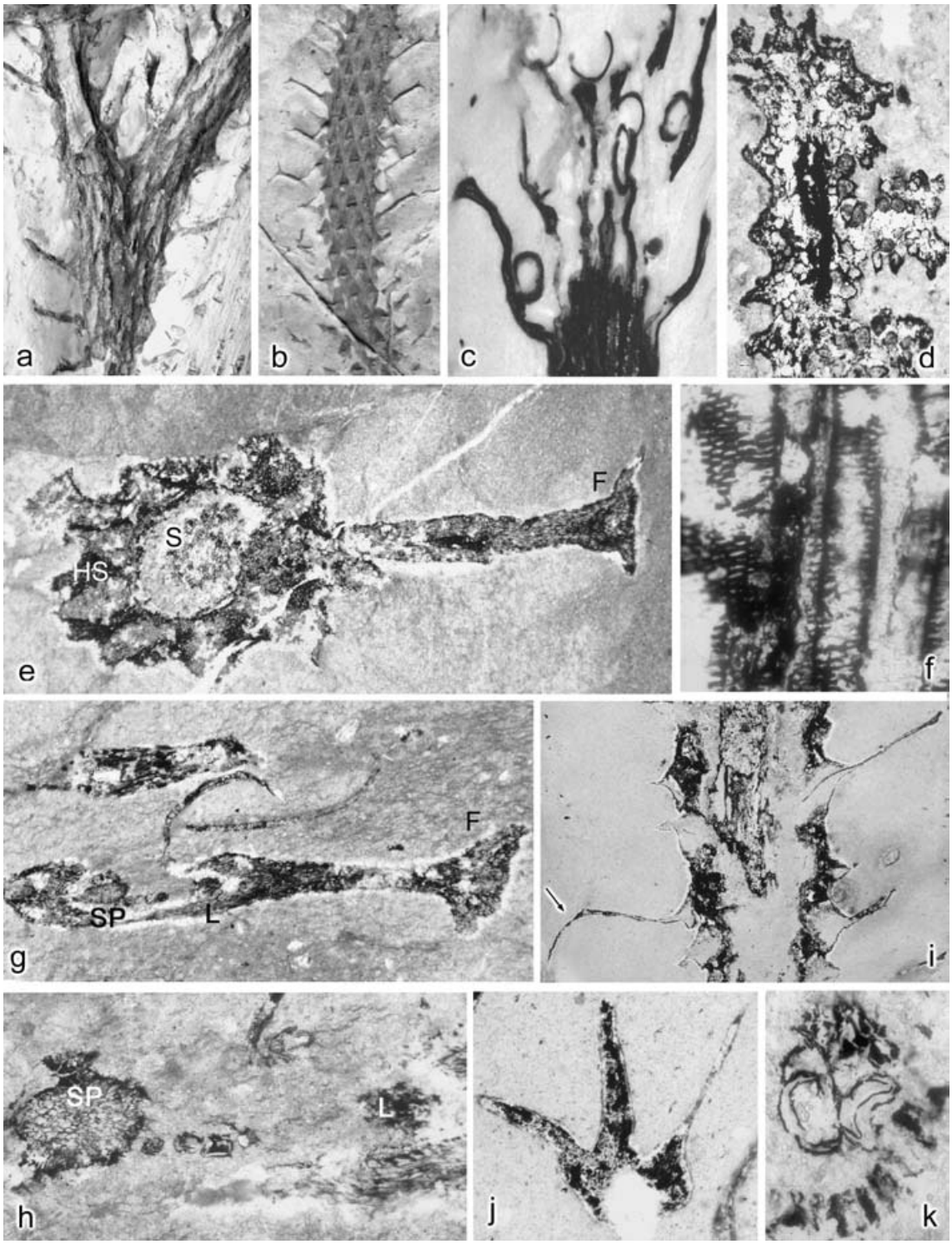


Figure 2. *Leclercqia complexa*, Storm Dam (Queensland). (a) Dichotomizing stem showing protolepidodendroid pattern in external view. Ulg 14001-1.×3.5. (b) Stem adpression showing low-angled arrangement of microphylls. Ulg 14001-2. × 3.3. (c) Portion of stem bearing sporophylls in longitudinal section. Ulg 14004-1. × 12. (d) Transverse section of flattened protostele with prominent ridges of protoxylem. Ulg 14002-17. × 60. (e) Transverse section of stem with attached microphyll. S: stele; HS: hypodermal sclerenchyma; F: fork. Ulg 14001-20 (3). × 24. (f) Metaxylem tracheids in longitudinal section. Ulg 14001-21 (10). × 600. (g) Part of sporophyll before forking (F) showing sporangial pad (SP) and ligule (L) within depression. Ulg 14004-5 (13). × 34. (h) Section distal to preceeding view, with similar orientation and in same specimen. Detail of sporangial pad (SP) and ligule (L). Ulg 14004-5 (14). × 100. (i) Longitudinal section of stem showing downturned long median segment of a microphyll at arrow. Ulg 14001-21 (13). × 8.3. (j) Section through three of the four lateral segments of a microphyll. Ulg 14001-23 (15). × 38. (k) Portion of sporangial wall with two spores attached. Ulg 14001-5 (2). × 254.

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Talent, 1989; Sloan *et al*. 1995; Withnall *et al*. 1993). Over much of the Dosey-Craigie Platform, the Storm Hill Sandstone consists of 50–100 m or so of arenites (often coarse) and pebble conglomerates, but may be 600 m or so in thickness in the southwest part of the Dosey-Craigie Platform where it crops out poorly. Its sedimentology has been examined only cursorily.

No conodont data are available for the Storm Hill Sandstone, but its age may be viewed as bracketed by the ages of the top of the Lomandra Limestone, and the age of the base of the Dosey Limestone. At its type section in Lomandra Creek, 6.5 km northeast of Storm Dam, the Lomandra Limestone is known to span an interval from high in the late Emsian *serotinus* Conodont Zone to early in the *costatus* Conodont Zone (early Eifelian: Mawson & Talent, 1989). Sparse conodont data from various localities in the Dosey Limestone, including locality SD 15, SD 59 on the eastern abutment of Storm Dam (Fig. 1), the stratotype section for the Dosey Limestone at SD 170 in Lomandra Creek, and various other occurrences in tributaries of Page and Bracteata creeks northwest and north respectively of Figure 1 (Mawson & Talent, 1989), are consistent with the base of the Dosey Limestone falling within the former *ensensis* Conodont Zone, that is, the interval spanning the Eifelian–Givetian boundary. The best estimate of the age of the *Leclerqia complexa* occurrence in the Storm Dam area therefore is within the intervening interval, that is, somewhere in the *australis* and *kockelianus* Conodont zones (Middle Eifelian), but presumably pre-dating the Eifelian–Givetian boundary.

4. Description

4.a. Axis morphology and anatomy

Axes range from 1.5 to 4 mm in diameter (Fig. 2a, b). They are parallel-sided and show no conspicuous tapering. A few specimens display isotomous dichotomies; the resulting branches diverge at about 50° (Fig. 2a). The proximal and terminal parts of the plants are not preserved. The most complete segment is 9 cm long. Axes lying at the surface of the rocks generally exhibit a typical 'protolepidodendroid' pattern (Fig. 2a). This configuration is obtained when the fracture plane which exposes the axis passes through the cortex at subsurface level. It reveals a network of dark hypodermal sclerenchymatous elements alternating with light fusiform areas of parenchyma connected to the microphyll bases (compare with Fig. 2e); meshes of parenchyma range from 1.3–2.5 mm high and 0.4–0.6 mm wide. More rarely, the stem surface exhibits a pattern of contiguous diamond-shaped structures like that illustrated in Figure 2b. In this case, the specimen is fractured along the angular boundary that separates the soft parenchyma tissue from the more rigid schlerenchyma (Fig. 2e). Sites where microphylls go down into the matrix are represented by a transversely elongated zone in the middle of each diamond-shaped structure.

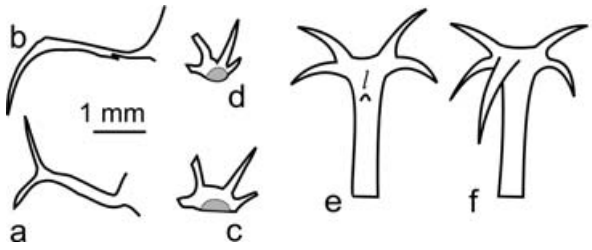


Figure 3. Microphylls of *Leclercqia complexa*, Storm Dam (Queensland). (a–d) Camera lucida drawings of adpressions. Ulg 14001. (a) Two lateral segments in profile view. (b) Long median segment in profile view. (c, d) Two pairs of lateral segments in adaxial view. In grey, depression corresponding to insertion of long median segment. (e) Reconstructed microphyll in adaxial view showing ligule (l) on upper surface. (f) Reconstructed microphyll in abaxial view.

All axes display a massive cylinder of primary xylem at the centre (S, Fig. 2e). In transverse section, the largest protosteles are about 1.3 mm in their widest dimension; 18–21 prominent protoxylem ridges occur at the periphery (Fig. 2d). Metaxylem tracheids in undeformed specimens range from 30–51 μm in diameter. In longitudinal section, wall ornamentation in these elements consists of scalariform to oval pits in multiseriate rows (Fig. 2f). Tissues immediately bordering the stele are not preserved (Fig. 2e).

4.b. Microphyll morphology and anatomy

There are nine to eleven microphylls per gyre, borne in a low spiral and inserted at 45–55° (Fig. 2b); they are three-dimensional, non-laminate, and forked at 1.7–3.6 mm from insertion point (Fig. 2b, e, g). The proximal part of the microphylls, before division, is approximately 100 μm deep and 300 μm wide in its middle part. The combination of lateral and face views indicates that microphylls divide into five segments (Fig. 3e, f), an abaxially recurved central one (Figs 2i; 3b) flanked on each side by a pair of segments extending in the opposite direction (Figs 2j; 3a, c, d). The four lateral ones often occur in the same plane adaxially (Fig. 3c, d); they have comparable lengths and range 0.6–1 mm long. The central abaxial segment is the longest and exceeds 1.3 mm in length.

Sporophylls which are morphologically similar to the vegetative leaves are concentrated in some areas of the stems but not arranged in strobili (Fig. 2c). Each bears one sporangium ranging from 400 to 500 μm in diameter and up to 700 μm long on its upper surface. The sporangium wall is one cell thick (Fig. 2k) and each sporangium is attached by a circular pad in a shallow depression (SP, Fig. 2g, h). Cells of the pad are almost isodiametric and average 12 μm in diameter. They clearly differ from those of the adaxial surface of

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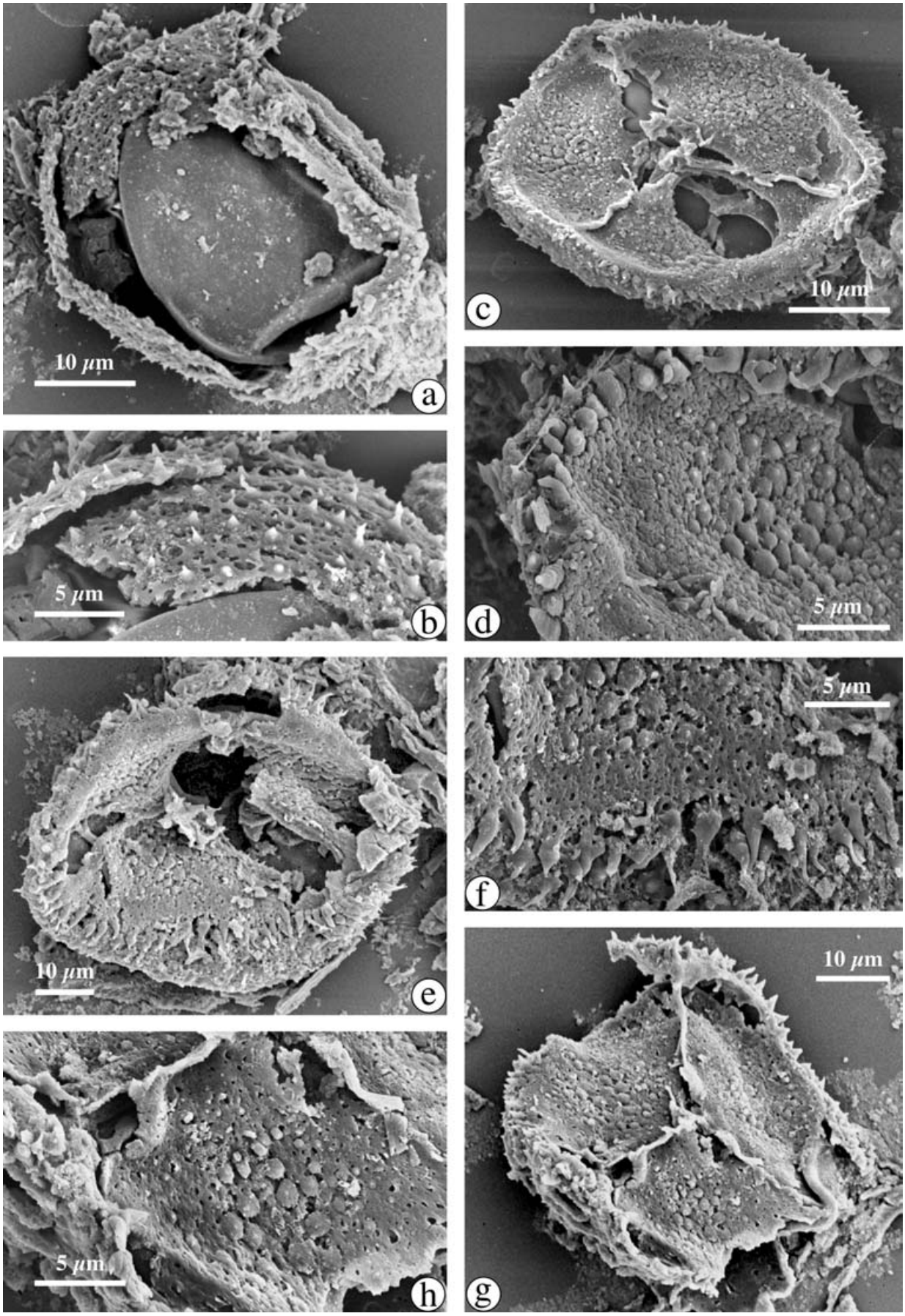


Figure 4. For legend see facing page.

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the sporophyll which are elongate and average 11 μm wide and 48 μm long. In the best preserved sporophylls a fragment of tissue raised within the same depression and distal to the sporangial pad is interpreted as a ligule (L, Fig. 2g, h). A ligule is also observed on the adaxial surface of well-preserved sterile microphylls.

4.c. Spores

Dispersed miospores released from the matrix in the vicinity of axes are highly coalified, poorly preserved and often damaged. They range from 50–65 μm in equatorial diameter, are circular in polar view and show a trilete suture (Fig. 4c, g). The exine exhibits a bilayered structure, the endexine being separated from the ectexine and forming a laevigate inner body as illustrated in some broken specimens (Fig. 4a, b). Sculpture on the distal surface shows lacunae and comprises spinae and biform elements (tuberculae surmounted by spinae) on muri (Fig. 4a, b). A row of curvatural biform elements is often present (Fig. 4c, d–f). The largest ornamentations on the proximal surface consist of grana concentrated in a small rounded area more or less centred in each interadial area (Fig. 4d, h). Sections of spores observed in light microscopy show the separate layers of the exine (Fig. 2k).

5. Systematic identification

The new Australian specimens display a suite of characters including a herbaceous habit, low-angled phyllotaxis, 'protolepidodendroid' pattern of axis surface, protostelic anatomy, and scalariform to pitted metaxylem tracheid ornamentation typical of the Protolepidodendrales (Bonamo, Banks & Grierson, 1988; Kenrick & Crane, 1997). The five-forked morphology of their ligulate leaves is a distinctive character of the genus *Leclercqia*. Assignment to the species *L. complexa* is based on the three-dimensional arrangement of the leaf segments and pattern of sporangial attachment. Dimensions of axes and leaves, and of stelar diameter, are consistent with those reported in the literature. The preserved sporangia appear smaller than those described from New York State and Germany (Banks, Bonamo & Grierson, 1972; Fairon-Demaret, 1980). This difference cannot be tested statistically due to the small number of sporangia available. Given the close similarity between all other characters of the new Australian specimens and those of *L. complexa* reported to date, we do not feel justified in assigning the former to a different species based on this single feature.

Leclercqia includes a second morphotype which many view as a second species of *Leclercqia* rather than a variant of *L. complexa* although both produce *Acinosporites lindlarensis* type of spores (Berry, 1994; Richardson, Bonamo & McGregor, 1993; Gensel, pers. comm.). It is currently represented by axes from Maine and New Brunswick no younger than early Middle Devonian. They differ from *L. complexa* by their leaves in which the median segment is not directed downwards (Kasper, 1977; Kasper & Forbes, 1979; W. R. Tanner, unpub. Ph.D. thesis, Southern Illinois Univ., 1983). This second species is designated '*Leclercqia* sp.' in the present paper. The Australian specimens do not share its leaf morphology.

The single type of spores found in close association with the new specimens possesses the diagnostic characters of the dispersed spore taxon *Acinosporites lindlarensis*, that is, curvatural spinae and a distal sculpture of ridges surmounted by spinae and biform elements. They also exhibit a distinct endexine, like spores found *in situ* within the *Leclercqia complexa* type material (Richardson, Bonamo & McGregor, 1993). These spores conform to Type I (precisely Subtypes IA and IB; compare our Fig. 4a, b and c with Richardson, Bonamo & McGregor's figs 3A, 4B and 4C respectively) from a range of six types (I–VI) that forms a morphological continuum established for *A. lindlaren*sis (Richardson, Bonamo & McGregor, 1993). Type I spores are dominant within sporangia of *L. complexa*. By contrast, sporangia of *Leclercqia* sp. contain Type V spores which are morphologically similar to immature spores of *L. complexa*. Such considerations are additional arguments indicating that the new Australian specimens are best attributed to the species *L. complexa*.

6. *Leclercqia* distribution

Leclercqia and its type-species *L. complexa* have a long stratigraphic range which spans at least two phytozones, the Cladoxyl zone IV (ex-Banks' *Hyenia* zone IV) and the *Svalbardia* zone V (Banks, 1980; Edwards, Fairon-Demaret & Berry, 2000). The earliest occurrences of the genus consist of Late Emsian specimens referable to *L. complexa* and to '*Leclercqia* sp.' (Table 1). The latter does not extend beyond the late Early Devonian or the early Middle Devonian and its occurrence is restricted to what is now North America,

Figure 4. *Acinosporites lindlarensis*, dispersed miospores associated with *L. complexa* axes. Scanning electron microphotographs. (a) Broken spore illustrating the bilayered exine, the intexine forms a laevigate inner body. (b) Detail of distal surface of specimen illustrated in (a), showing lacunae and elements on muri. (c) Spore in equatorial view showing trilete suture, curvatural ornaments and grana in the centre of each interradial area on the proximal surface. (d) Detail of previous view. (e) Spore in equatorial view. (f) Detail of previous view showing curvatural spinae. (g) Spore in equatorial view. (h) Detail of previous view showing proximal ornamentation of grana.

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Table 1. Published occurrences of *Leclercqia*

Species	Authors	Locality	Age
L. complexa	Fairon-Demaret, 1974	Burdekin Basin, Queensland, Australia	Late Givetian
L. complexa	Fairon-Demaret, 1981	Ronquières, Belgium	Late Givetian
L. complexa	Fairon-Demaret, 1980	Elberfeld, Germany	Givetian
L. cf. complexa	Berry, Casas & Moody, 1993; Harvey, 1999	Sierra de Perijá, Venezuela	Mid- to Late Givetian (spores)
L. complexa	Banks, Bonamo & Grierson, 1972; Richardson, Bonamo & McGregor, 1993	Schoharie Co, NY, USA	Early Givetian
L. complexa	This paper	Broken River region, Queensland, Australia	Eifelian
L. cf. complexa	Fairon-Demaret, 1981	Oé, Belgium	Eifelian
Leclercqia sp.	Kasper & Forbes, 1979	Baxter State Pk, Maine, USA	Emsian (lithology), Emsian/ Eifelian (palynomorphs), **Eifelian** (flora), Eifelian-Famennian (radiometric data)
Leclercqia sp.	Kasper, 1977; Richardson, Bonamo & McGregor, 1993	New Brunswick, Canada	Late Emsian
L. complexa	W. Tanner, unpub. thesis, So. Illinois Univ., 1983	Beartooth Butte, Wyoming, USA	Mid-Siegenian (fishes); Mid- to **Late Emsian** (spores)

in the palaeocontinent Laurussia (Fig. 5). Specimens referred to as *Leclercqia* cf. *complexa* in Table 1 are poorly preserved or fragmentary and, for these reasons, do not provide the entire range of features displayed by the type material. However, their leaves are similar in size and shape to those of *L. complexa* and, although it remains to be proved, the probability is high that they belong to this species. Their record is included with that of *L. complexa* in Figure 5. The most numerous occurrences of *Leclercqia* reported in the literature are middle Middle Devonian. The exceptionally well-preserved type material from New York State is Early Givetian (Richardson, Bonamo & McGregor, 1993). The latest well-documented occurrences of the genus are Late Givetian, from European and Australian localities (Fairon-Demaret, 1974, 1981) (Table 1).

Occurrences of *L. complexa* outside Laurussia are few, but we suspect that this species had a much wider geographic extent than that known from the literature. To date, there have been two reports of fragmentary specimens with leaves identical to those of *L. complexa* in Gondwana (Table 1, Fig. 5). One corresponds to axis fragments from the Late Givetian of the Burdekin Basin in Queensland (Fairon-Demaret, 1974), the other to a specimen from the Lower Member of the Campo Chico Formation of the Sierra de Perijá in Venezuela (Berry, 1994). Localization of the latter area during the Middle Devonian has been a matter of debate but recent study of vertebrates from the Campo Chico Formation supports its Gondwanan character (Berry *et al*. 2000; Young, Moody & Casas, 2000). Another source of uncertainty concerning the Venezuelan material was its age (Berry, Casas & Moody, 1993), but recent study of a palynological assemblage from the Lower Member of the Campo Chico Formation gives a Middle to Late Givetian age to the outcrop that yielded *Leclercqia* (Harvey, 1999). The new material from Storm Dam is the third and best documented report of *L. complexa* in Gondwana. It may represent the earliest occurrence of *Leclercqia* based on macro-remains for the palaeocontinent.

A number of *Leclercqia* specimens with incomplete microphylls may represent broken or improperly degaged specimens, which may have been inappropriately designated as *Protolepidodendron scharianum*, a taxon which, if valid, differs from *Leclercqia* by its bifurcate leaves. Part of Kräusel and Weyland's original collection of *P. scharianum* from Germany was indeed reassigned to *L. complexa* after careful study (Fairon-Demaret, 1980). According to Iurina's (1988) synthesis of Devonian plant assemblages from the former USSR, many deposits ranging from Eifelian to Givetian in age have yielded specimens of *P. scharianum* in Kazakhstan and Siberia (Fig. 5). It is likely that some, if not all, of these records actually belong to *L. complexa* (Berry, 1996 and pers. comm.; Fairon-Demaret, 1980). Reports of *Protolepidodendron* in China require careful re-examination. Specimens from the Middle Devonian of the Xingxiang province, an area that belonged to the Kazakhstan palaeo-plate, are also suspected to belong to *Leclercqia* (Berry, 1996). Specimens from the Givetian of Yunnan previously referred to as *Protolepidodendron cathaysiense* (Schweitzer & Cai, 1987) are now assigned to the endemic genus *Minarodendron* (Li, 1990). This taxon may be related to *Leclercqia* (Kenrick & Crane, 1997); it differs essentially by its trifurcate and spiny eligulate microphylls. As the plant fossil record from the Middle Devonian of China is gradually becoming better known (Wang & Berry, 2001), it appears that *Leclercqia complexa* was absent from the northern and southern Chinese blocks.

Geographic distribution of the dispersed spore taxon *Acinosporites lindlarensis* is more extended than that

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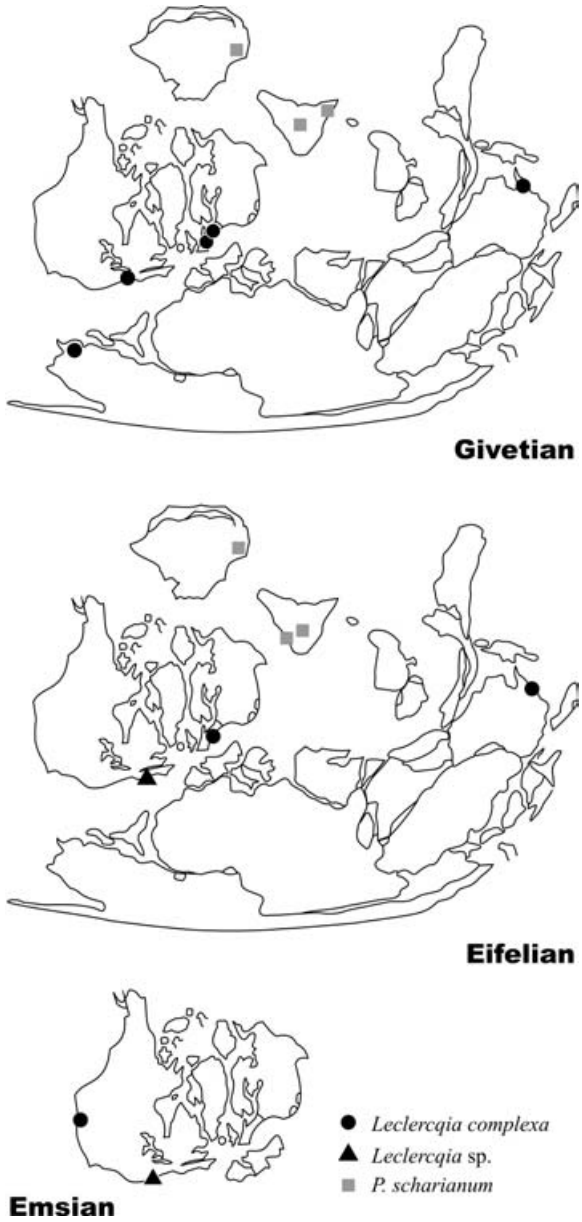


Figure 5. Distribution of *Leclercqia* in the Late Emsian and Middle Devonian. Palaeogeographic reconstructions according to Scotese's PALEOMAP project 2000 (http://www.scotese.com/earth.htm).

of *Leclercqia* and includes more records in western and northern Gondwana (Richardson, Bonamo & McGregor, 1993). Its stratigraphic range, however, casts doubt on its exclusive affinities with *Leclercqia*. Earliest occurrence of *A. lindlarensis* is a little older (mid-Emsian) than that of *Leclercqia*, according to Richardson, Bonamo & McGregor (1993), and much older (Mid-Siegenian or older) according to Le Hérissé (1983) and Steemans (1989). Last occurrence is older than that of *Leclercqia* according to Richardson, Bonamo & McGregor (1993), younger (Early Frasnian) according to other authors (Loboziak & Streel, 1989; McGregor & Playford, 1992). Such discrepancies in appreciating the stratigraphic range of this spore taxon underline the difficulties in identifying it accurately. Inconsistencies between the dispersed palynomorph and macro-remains may be due to their respective incompleteness, inaccurate identification of the micro-remains and to the possibility that *A. lindlarensis* spores were produced by other genera than *Leclercqia*. For these reasons, discussion and hypotheses put forward below concerning biogeographical patterns of *Leclercqia* are based exclusively on the record of macro-remains.

7. Discussion

The earliest evidence of *Leclercqia* occurs in late Early Devonian deposits from North America. It consists of leafy axes assigned to two species. Based on this evidence and until new findings eventually contradict the following, we hypothesize that the centre of origination of the genus occurred in the western part of Laurussia. Diversification was early and limited, with a single species surviving the early Middle Devonian and spreading over other continental plates. If, as suggested by one of us (JT), the new Australian remains of *L. complexa* are Eifelian, they largely pre-date the preceding records of the species in Gondwana. In that case, extension of the species to the southern continent occurred at the same time as extension to other palaeo-plates situated in the northern hemisphere (Kazakhstan, Siberia). The record of *L. complexa* in Gondwana is scanty and occurs in widely disjunct areas. It does not give any clue as to whether colonization proceeded gradually from the hypothesized centre of origination or via long distance dispersal. Other major points in the distribution patterns of *Leclercqia* are: (1) the extensive stratigraphic range of the species *L. complexa* that exceeded 10 million years in Laurussia (Late Emsian to Late Givetian) and at least 5 million years in Gondwana (Middle Eifelian? to Late Givetian); (2) the wide geographic distribution of this species in Laurussia, Kazakhstan, Siberia, and the northern edge, from east (Australia) to west (Venezuela), of Gondwana; (3) its absence from both North and South China but the occurrence of a related genus, *Minarodendron*, in South China. The high stability over time and absence of conspicuous geographic variation in the morphology and anatomy of *L. complexa* are noteworthy. The only reported difference is an evolution in spore ornamentation from a type V ('immature') stage mostly represented in specimens of Emsian age to a Type I ('mature') stage in those of the Middle Devonian (Richardson, Bonamo & McGregor, 1993).

The *L. complexa* specimens described here possess type I *in situ* spores. The record of dispersed palynomorphs identical to those type I spores ranges from Early Eifelian to Givetian; on the other hand, the dispersed palynomorphs similar to type V *in situ* spores of *Leclercqia* sp. dominate the *A. lindlarensis*

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spore assemblages of Late Emsian age (Richardson, Bonamo & McGregor, 1993). This is indirect evidence indicating that the age of the new Australian specimens, which possess type I *in situ* spores, is likely younger than Late Emsian.

Distribution of taxa is related to the potential for dispersal, establishment and growth of the plant, a series of syndromes that interact with geography. Indeed, physical barriers may prevent dispersion, and position of continents, in terms of latitude as well as relative position to oceans, may affect climates and environmental conditions to which organisms are adapted (Hallam, 1994). Evaluating how organisms dispersed, settled and evolved on ancient continents may therefore provide clues to the geodynamics of the continents they colonized.

Homosporous pteridophytes which produce numerous spores and are potentially self-fertile have theoretically high dispersal capacities. How far spores can be transported and retain their germination capacities is a subject that has been well studied for ferns but not for other pteridophytes. Numerous studies on fern biogeography have demonstrated the potential for these plants to disperse viable spores over distances exceeding 500 miles (Kato, 1993; Tryon, 1970, 1986). Literature on lycopsid dispersal is rare, and one may legitimately question the dispersal capacities of these plants which have a spore wall lacking an outer perispore layer. A recent paper investigating the distribution of the extant tropical Lycopodiacean genus *Huperzia* suggests that, although rare, a few species show transoceanic spore dispersal (Wikström, Kenrick & Chase, 1999). We cannot rule out the possibility that *Leclercqia* spores had this capacity.

Ecological requirements for the settlement of *Leclercqia complexa* are difficult to assess on the sole basis of its morphological and anatomical features. *L. complexa* formed monotypic dense stands of small-statured, probably clonal, plants with rigid dissected leaves, a set of characters generally associated with xeromorphy. The cuticle, however, does not show any xeromorphic specialization such as sunken stomata (Banks, Bonamo & Grierson, 1972). Other characters may rather support opposite environmental preferences and one may argue that the elongated, downturned middle segment of the microphylls functioned as the drip tips of angiosperm leaves in the wet tropics. Spicer (1989) argued that most herbaceous Devonian plants exhibited constructions tolerating a high range of environments and, therefore, exhibited a wide geographical distribution. Current evidence from *Leclercqia* shows that the distribution patterns of Middle Devonian species may be more complex. From the two known species of *Leclercqia*, only one succeeded in colonizing extensive territories outside Laurussia. Because they produced similar spores, limitation in geographic and stratigraphic expansion of *Leclercqia* sp. was more likely related to requirements for settlement than for dispersal. We

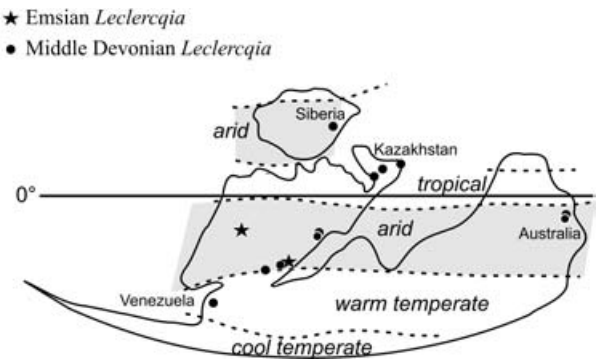


Figure 6. *Leclercqia* late Early and Middle Devonian occurrences plotted on reconstruction from Scotese, Boucot & Chen Xu in PALEOMAP project 2000 (http://www.scotese.com/climate.htm).

therefore suggest that, for reasons that we are presently unable to assess, *L. complexa* tolerated a greater range of environmental conditions to develop and grow than *Leclercqia* sp. Absence of the former in the Chinese blocks, however, indicates that although broad, it distribution was not cosmopolitan and showed constraints. From an evolutionary point of view, we hypothesize that the long and geographically extensive establishment of *Leclercqia complexa* is due to traits that ensured advantages to this species under environmental conditions that remained almost unchanged across the areas where it is reported and during the extensive time interval of its record. Based on these evolutionary and environmental considerations, the geographic reconstructions for the Middle Devonian that we favour are those in which *L. complexa* occurrences are distributed in the same climatic belts. The one that fits these requirements best is provided by Scotese, Boucot & Chen Xu in the 2001 paleomap project (http://www.scotese.com/climate.htm). Most of the *L. complexa* sites on this reconstruction occur in the so-called 'arid' belts on each side of the equator, the Siberian sites in the northern hemisphere, the Laurussian and Australian ones in the southern hemisphere (Fig. 6). Kazakhstan and Venezuela, which correspond to different climatic conditions, are either misplaced or the sites that *L. complexa* inhabited on these plates enjoyed local conditions comparable to those in the favourable belts. Palaeogeographic reconstructions such as that proposed by Tait *et al.* (2000) in which the distribution of *L. complexa* spans a large latitudinal range are expected to induce a more extensive diversification of the genus than that reported and are not likely to match these requirements.

8. Conclusion

The Gondwanan record of Middle Devonian plants is remarkably poor. This paper increases the database of such remains in order better to assess biogeographic patterns at a time when early land plants exhibited

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considerable diversity (Knoll *et al*. 1984; Raymond & Metz, 1995). It confirms the occurrence in eastern Gondwana of *Leclercqia*, a genus which may have originated in Laurussia and which includes one of the most successful Middle Devonian plants.

Before sufficient data can be accumulated for appropriate quantitative analyses, we have joined the debate concerning Devonian positions of Gondwana relative to Laurussia with biogeographic information on *Leclercqia* because it is easily identifiable, has a satisfying record of correctly dated deposits and shows a broad but not fully cosmopolitan distribution. Biological and evolutionary considerations suggest that scenarios assessing proximity of the two continents may be better resolved following the distribution patterns of *Leclercqia*.

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