ELSEVIER

Land plants in the Devonian Villavicencio Formation, Mendoza Province, Argentina

D. Edwards[a,*], E. Morel[b,c], D.G. Poiré[b], C.A. Cingolani[b]

[a]*Department of Earth Sciences, Cardiff University, P.O. Box 914, Cardiff, CF10 3YE, UK*
[b]*CIG (UNLP-CONICET), calle 1 n. 644, 1900-La Plata, Argentina*
[c]*Com. Invest. Científicas Prov. Bs. Aires and Departamento Científico de Paleobotánica, Museo de La Plata, Paseo del Bosque s/n, 1900-La Plata, Argentina*

Abstract

Plant assemblages are described from two localities, San Isidro Creek and Vaqueria, in the marine basal Devonian Villavicencio Formation in Mendoza Province, the Argentine Precordillera. Abundant smooth and more rarely axes with enations occur with rare fertile specimens and isolated swollen structures interpreted as sporangia. Sterile 'leafy' axes are placed in a new morphotaxon, *Bowerophylloides*, and a new genus, *Isidrophyton*, has been erected to accommodate sterile axes with vertically elongate, fusiform surface features and terminal sessile sporangia borne in pairs. The plants are at similar grades of organisation to those in coeval assemblages elsewhere, but cannot be assigned unequivocally to existing taxa. The locations of these Lochkovian assemblages are plotted on basal Devonian palaeocontinental reconstructions and it is concluded that the composition and the isolated position of the Argentina assemblages on the western margin of Gondwana at mid latitudes in a possibly cool temperate climate hint at a distinct phytogeographic unit. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Argentina; land-plants; Lochkovian; palaeogeography; Rhyniophytoids

1. Introduction

The dearth of plant megafossil localities at high latitudes in the southern hemisphere in Silurian and early Devonian times has been a major impediment to our detection of phytoprovincialism (e.g. Raymond, 1987; Edwards, 1990) in the early phases of the colonization of the land by plants. In addition, records from low latitude sites on Gondwana (e.g. the Australian *Baragwanathia* assemblages: Tims and Chambers, 1984; Rickards, 2000) have shaken complacency on conclusions relating to early radiations of vascular plants based on assemblages from the present circum-north Atlantic region. The

discovery, therefore, of a *Baragwanathia*-like plant in the Lower Devonian of the Precordillera of Argentina (Cuerda et al., 1987) stimulated the comprehensive search for further localities in the area. Some of the results of this project based on fieldwork in Mendoza Province are reported here (Fig. 1). Intensive searching and collecting was undertaken at two localities, San Isidro Creek and a roadside exposure at Vaqueria, where abundant plant remains occur in the Villavicencio Formation.

2. Localities, geology and age

2.1. San Isidro Creek (32°52′16″S/69°01′12″W; Fig. 1)

The exposure is in a gully on the north side of the

---

* Corresponding author. Fax: +44-2920-874326.
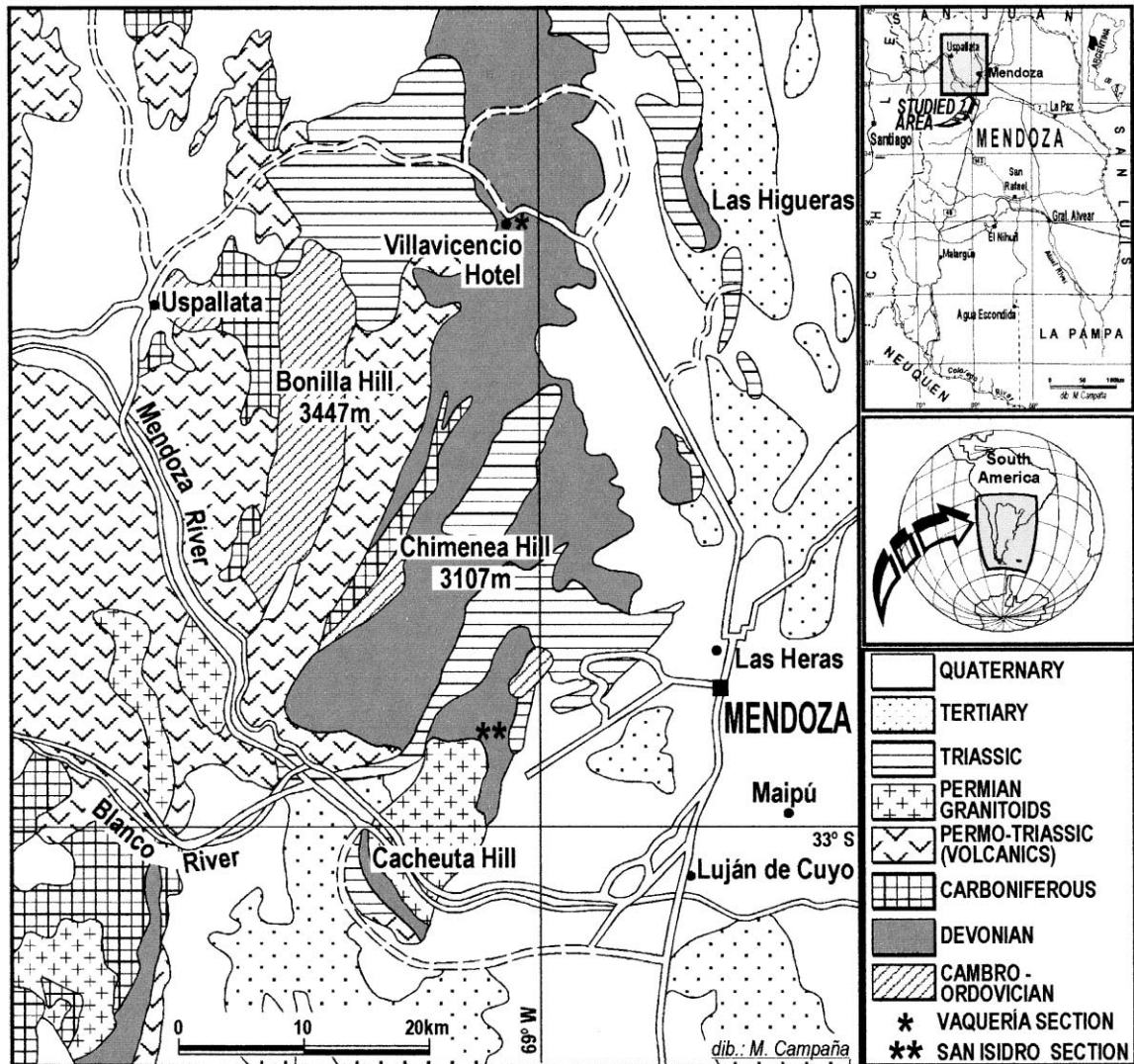 *E-mail address:* williamsc4@cardiff.ac.uk (D. Edwards).

Fig. 1. Geographical locations of plant-bearing localities 1–4 in Argentina.

creek. Some specimens were collected from the rock face, but most were on a small scree. At this locality, the Villavicencio Formation is composed of massive dark grey sandstones alternating with laminated pelite beds, heterolithic facies and laminated sandy heterolithic facies. The plants occur at four levels (see Logs SIF 1 and SIF 2, Fig. 2), each comprising laminated pelite facies (L) of thin to medium bedded, mid-grey, finely micaceous coarse siltstones/fine sandstones. On some bedding surfaces there is marked current alignment of debris. The bases of the units are generally ripple laminated, sitting directly on storm-generated, thick-bedded sandstones. Rip-up clasts of fine dark grey mudrock at the base of a bed, reflect the relatively high energy environment. All facies are typical of marine shallow shelf sands. The plants are preserved as coalified compressions or impressions. Treatment with Schultze's solution failed to reveal any anatomical detail. Some of the larger axes, including branching examples are preserved as casts, with a superficial coating of coaly material, or as concave moulds.
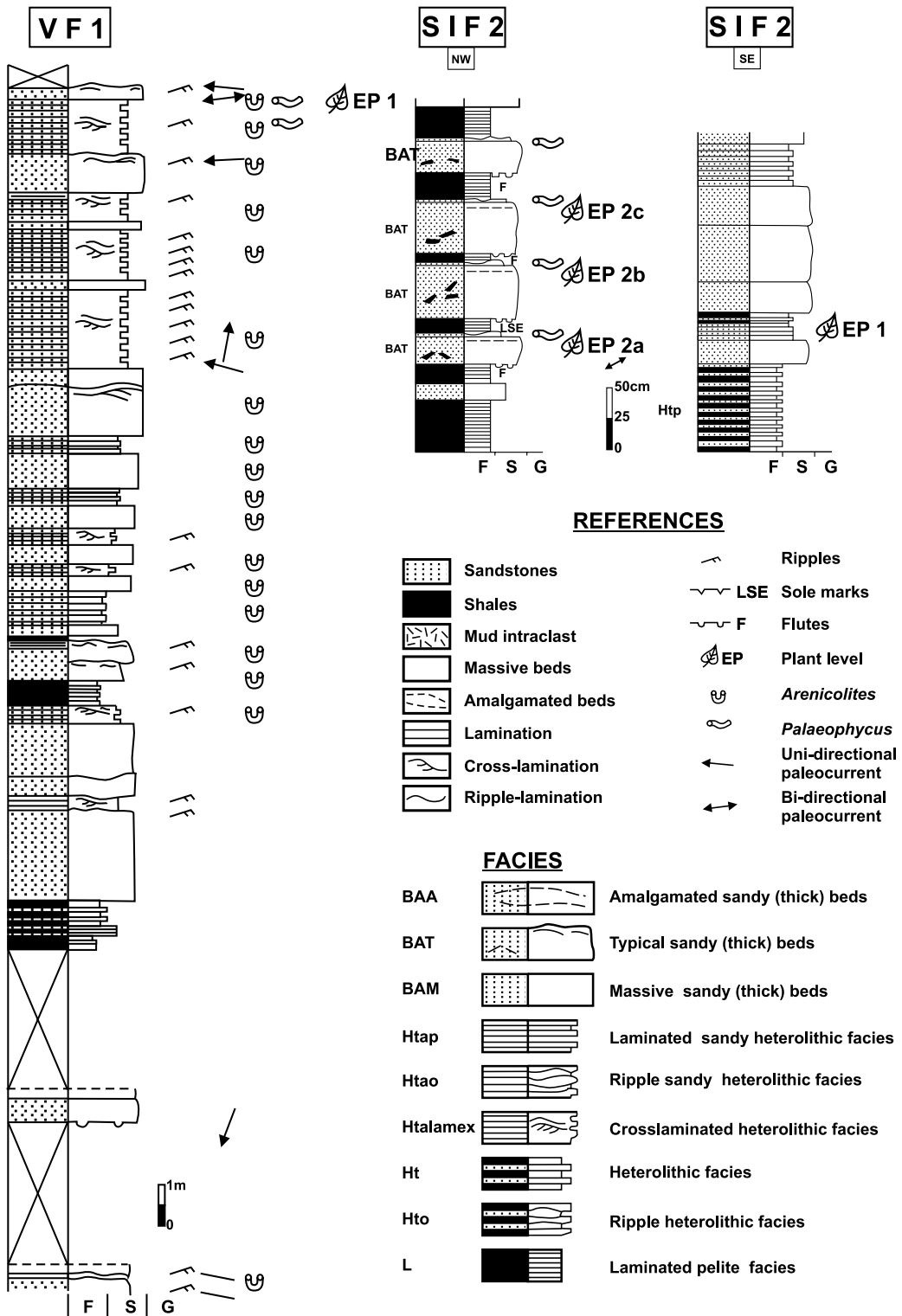
Fig. 2. Stratigraphic logs of the two plant-bearing localities (San Isidro SIF and Vaqueria VF1).

Below the Villavicencio Formation is the Empozada Formation dated as Ordovician from Llandeilo–Caradoc graptolites (Cuerda et al., 1988). The contact is faulted. The upper contact is also unconformable. The overlying formation is the volcanic Choiyoi Group of Permian–Triassic age. Palynological data (spores) provide an early Devonian age for the Villavicencio Formation, but the spores are poorly preserved and most range from mid-Lochkovian to possibly latest Pragian
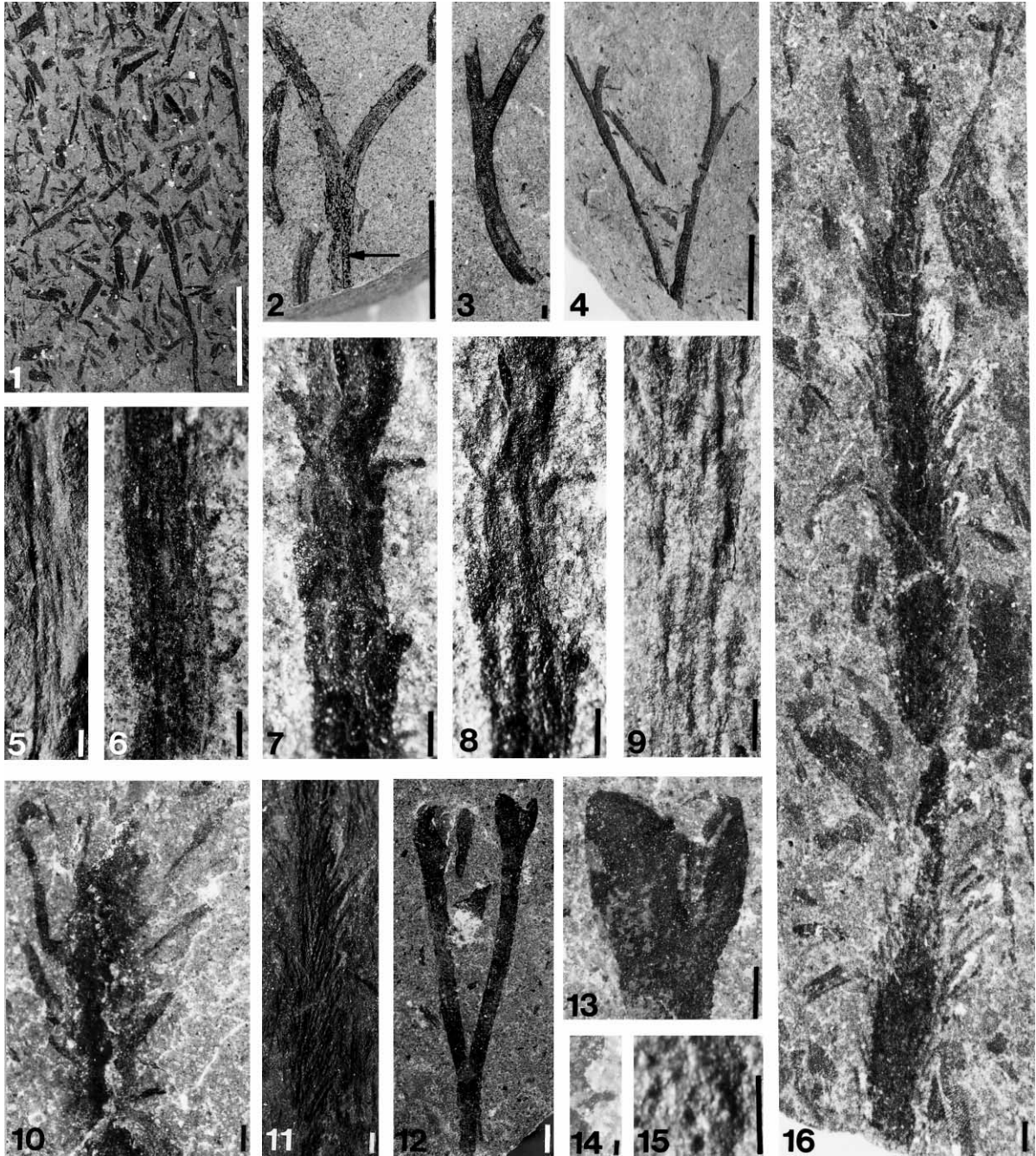
(Rubinstein, 1993a,b). Rubinstein considers a Lochkovian age as most appropriate.

2.2. Vaqueria, Mendoza (32°31′25″S/69°00′23″W)

This is a roadside exposure in which plants are very abundant at just one horizon, but occur sporadically throughout the mainly dark grey sandstones and pelites in rippled sandy heterolithic facies. The plant-rich horizon is in weakly rippled, finely laminated siltstones. Compared with San Isidro they are finer grained and laminated and lack micaceous grains. Some beds have a distinctive yellow/buff weathering. Debris is strongly current aligned and shows medium fragmentation suggestive of relatively little transport with deposition in a delta front in a lower energy environment than is indicated at San Isidro (See Log VF1, Fig. 2). Fossils are far more fragmentary than at San Isidro and with less coalified material. Many are stained yellow or orange, their margins delimited by residual coaly dust. Some show cavities traversed by acicular crystals. Rock fracture is very irregular, frequently following the uneven topography of the fossils themselves. No anatomical detail was resolved. The lowest parts of the formation are not exposed. The upper are unconformably overlain by the middle and upper Triassic Uspallata Group. There is no direct evidence for the age of the formation. Field relationships suggest it is the same as at San Isidro.

3. Plant descriptions

3.1. Sterile axes

3.1.1. Smooth (Plate I, 1–4)

At both localities, the vast majority of the fossils comprise short lengths of smooth unbranched axes. Branching examples, commoner at San Isidro, show isotomous branching usually with little change in diameter of the daughter axes and with only one branch point. In rare examples, daughter axes are considerably narrower than the main or may even appear lateral. Isotomously branching axes (<3 mm in diameter) are referred to *Hostinella*, although only one shows evidence of a central strand. Some of the coalified surfaces are minutely and longitudinally striate.

3.1.2. Unnamed axes with enations
(Plate I, 5–9; Table 1)

A small number of unbranched specimens are not smooth, but are united by superficial strong, broad longitudinal ribbing and by the bases of enations seen in profile on their sides. In unilateral light, their surfaces present a somewhat irregular appearance, with distinct 'summits' to the longitudinal ridges representing the bases of enations, but the latter also occur in oblique rows of two or three in some places (Plate I, 5, 6, 9). In surface view, the broad ridges may be lenticular with central prominence (Plate I, 7–9).

PLATE I

San Isidro, Mendoza Province, Argentina; Lochkovian
1. Typical debris showing some alignment. S.I.1. LPPB 12750. Scale bar = 10 mm.
2. *Hostinella* sp., arrow indicates central strand. S.I.2. LPPB 12751. Scale bar = 10 mm.
3. *Hostinella* sp. preserved as a cast with coalified coating. S.I.2. LPPB 12752. Scale bar = 1 mm.
4. *Hostinella* sp. with regular branching. S.I.2. LPPB 12753. Scale bar = 10 mm.
5. Axis with sporadic longitudinal depressions viewed by unilateral illumination. New sterile taxon. S.I.2. LPPB 12214. Scale bar = 1 mm.
6. Same axis as in 5 with lateral projections. Scale bar = 1 mm.
7, 8. Axis with surface ridging and lateral projections. New taxon. S.I.2. LPPB 12213: Scale bar = 1 mm.
9. Axis with longitudinal ridges. New taxon. S.I.1. LPPB 12212. Scale bar = 1 mm.
10. *Bowerophylloides mendozaensis* gen. et sp. nov. S.I.1. LPPB 12745. Scale bar = 1 mm.
11 and 16. *Bowerophylloides mendozaensis* gen. et sp. nov. (Holotype). S.I.1. LPPB 12211.
11. Unilateral illumination. Scale bar = 0.1 mm.
12–15. New fertile taxon. S.I.2. LPPB 12746.
12. Complete specimen. Scale bar = 2 mm.
13. Possible pair of terminal sporangia. Scale bar = 1 mm.
14. Projection from surface of subtending axis. Scale bar = 0.1 mm.
15. Magnified surface showing presumed bases of projections. Scale bar = 1 mm.
16. Whole specimen from 11. Scale bar = 1 mm.

Table 1
Dimensions of axes and enations from a new sterile taxon

Specimen no.	Axis (mm)		Enation (mm)	
	Width	Length	Width	Length
LPPB 12212 (Plate I, 9)	1.35–1.6	28	0.22	0.27
			0.19	0.27
			0.22	–
LPPB 12213 (Plate I, 7, 8)	1.9	16.5	0.3 (0.81 at base)	0.54
			0.22	–
			0.22 (0.6 at base)	0.95
			0.32	0.78
			0.32	0.46
LPPB 12214 (Plate I, 5, 6)	1.62	17.2	0.24	1.08
			0.19	–
			0.24	–

The latter are particularly evident as depressions, where a semi-compressed cast has become dislodged (Plate I, 5). In profile, the enations vary in length (maximum 1.1 mm) and shape. Most show expanded bases, either symmetric or ? proximally decurrent, these corresponding to the surface ridging. The majority become parallel sided, when ca 0.19–0.32 mm wide, and are perpendicular to the surface or curve distally. Apices are usually truncated, and despite repeated attempts at uncovering, it has been impossible to determine whether or not they were longer, and possibly tapering. A well defined 'phyllotaxis' could not be detected; neither could any vascular traces. Dimensions and shape are remarkably constant in the three largest specimens and they are clearly conspecific. However, there are more regularly striated axes, with no evidence for enations that might belong to the same taxon. Lenticular ridging has also been demonstrated in the new fertile taxon, *Isidrophyton*.

Comparisons: The morphological characters of the enations, particularly in profile are reminiscent of the leaf bases of certain microphyllous lycophytes (e.g. *Haskinsia* Grierson and Banks), but absence of anatomy prevents confident assignment to the tracheophytes. The spiny zosterophyllophytes and trimerophytes possessed far greater numbers of enations. Some are truncated (e.g. *Psilophyton princeps*) but all are far more frequent and pronounced than the Argentine examples, and few produce such modification of the topography of the axes.

Identification: In view of the uncertainty of the affinity of such axes (psilophyte v. lycophyte, or indeed even if tracheophyte), it would be unwise to assign them to an existing taxon (e.g. *Psilophytites* or *Lycopodites*) with major inherent implications for their distribution and evolutionary biology. Thus while it would seem appropriate to erect a new taxon for such plants, primarily to highlight this absence of knowledge in assessment of affinity, we are reluctant to do so here, because there remains the possibility that they are the proximal axes of *Isidrophyton*.

(ii) Longer enations, covering surface of axis: *Bowerophylloides mendozaensis* gen. et sp. nov. (Plate I, 10, 11, 16)

The specimen named *Baragwanathia* by Cuerda et al. (1987) lacks surface striations and the enations are much larger than those previously described. It is illustrated in detail here (Plate I, 11, 16), together with a more recently discovered specimen (Plate I, 10). Both are unbranched, and 38 and 28 mm long respectively. In the original specimen, closely inserted emergences cover the axis in Plate I, 16 such that its width is conjectural but is estimated at ca 1.7 mm from the band of more concentrated coalified material. The majority of the enations are remarkably regular in orientation, being directed forward at ca 50° near the base of the specimen and 20–35° more distally where angles are more variable. Spacing in profile is more or less regular, but there is no obvious phyllotaxy. In unilateral illumination, the axis appears longitudinally corrugated in places, but in others is traversed by oblique striations marking the superimposed basal regions of enations (Plate I, 11). Most of the enations are straight and parallel sided; some show slight basal curvature and expansion. Where parallel sided, they are 0.14–0.30 mm wide (mean = 0.23 mm), this variation possibly reflecting their planar nature. Maximum length is ca 2.00 mm, but most specimens have truncated tips and hence are possibly incomplete. The new specimen (Plate I, 10) has fewer, but larger (0.19–0.35 mm wide; mean = 0.27 mm) enations, more haphazardly organised but all uniformly and probably distally directed. They dip into the matrix, suggestive of stiff spatulate structures. Superficial attachment sites are marked by protuberances. None of the enations show any evidence of a central strand.

Comparisons: Although the original specimen was

assigned to *Baragwanathia* (Cuerda et al., 1987), such identification is not tenable, because: (1) there is little direct morphological similarity with Australian *Baragwanathia* with its elongate flexuous leaves (e.g. Lang and Cookson, 1935), (2) no anatomical evidence for microphylls. It provides a further good example of the problems of naming 'leafy' or spiny fragments. Even use of the taxon *Lycopodites* has connotations which are not warranted by the material (and see Seward, 1910). Considering the spiny 'psilophytes', the enations are far more substantial than in the most spinous examples such as '*Psilophyton*' *burnotense* (Schweitzer, 1980) where the orientation of spines with respect to the subtending axis is also different.

Regardless of the assignation, these fragments do superficially resemble material described as *Lycopodolica* (Ishchenko, 1975) and a single axis from Xinjiang (Cai et al., 1993). They demonstrate the widespread occurrence in the late Silurian/earliest Devonian of plants with such gross morphology, but, until anatomy or other morphological characters are obtained, are of but small significance to understanding the evolution and nature of early land vegetation. It is however considered important that they are recorded using a name that lacks any connotation of affinity. We therefore propose a new (morphotaxon) *Bowerophylloides* for leafy or 'spiny' axes where there is no anatomical information to allow further assignment.

Finally, the possibility that these axes with enations belong not to the plant but to the animal kingdom should be addressed, especially as Kenrick et al. (1999) recently reclassified some coalified Middle Ordovician fossils, *Boiophyton pragense* Obrhel, as dendroid graptolites. Certainly we have no direct anatomical evidence that the fossils derive from plants — a deficiency also holding for all other fossils, including fertile taxa at the Argentine locality and, furthermore, the truncated parallel-sided enations superficially resemble thecae. However, the original Argentine specimen has been examined by a number of graptolite researchers, A. Cuerda, R.B. Rickards (original collectors), D. Loydell and K. Saunders, who found no direct evidence for dendroid affinity. In addition, the orientation of the spatulate enations in the matrix suggests originally flattened structures. There is a superficial resemblance to dendroid taxa

such as *Inocaulis* (Kate Saunders, personnel communication, 2000). Indeed, a number of dendroid taxa have recently been transferred to noncalcified dasyclad algae (see LoDuca, 1997 and references therein). Hence, while mindful of the fact that the Argentine fossils share gross morphological features with certain groups of graptolites, balance of evidence and expert advice reassure us of their plant affinities.

INCERTAE SEDIS
Bowerophylloides gen. nov.
　　Sterile axes covered by crowded narrow, elongate projections, directed towards the apex.

Type species: Bowerophylloides mendozaensis gen. et sp. nov.
Diagnosis: Projections spatulate, at least 3.5 mm long and 0.14–0.35 mm wide, ?truncated tips.
Holotype: S.I.1. LPPB 12211
Illustrations: Plate I, 11, 16
Type locality: San Isidro Creek, Mendoza Province, the Argentine Precordillera
Horizon: Villavicencio Formation
*Age:* Lower Devonian (probably Lochkovian)

3.2. Fertile material

In situ spores have not been recovered in any of the mostly terminal 'expansions' that are here interpreted as sporangia.

3.2.1. PLANTAE: INCERTAE SEDIS
Isidrophyton iñiguezii gen. et sp. nov. (Plate II, 1–6)

Description: Overall height of the more completely preserved specimen is ca 30 mm with at least 4 dichotomies (Plate II, 1); axis diameter is 1.3 mm at base decreasing to ca 0.75 mm below the best preserved, terminal presumed sporangia. However diameter of the axes is difficult to measure accurately because their sides are not strictly parallel. This results from longitudinal ridging (<4 per diameter), where the ridges are not continuous over a long length, but form irregular elongate lenticular structures (Plate II, 3). The latter become somewhat less pronounced distally, but individual axes are very variable. Branching is more or less isotomous, with a marked decrease in diameter above
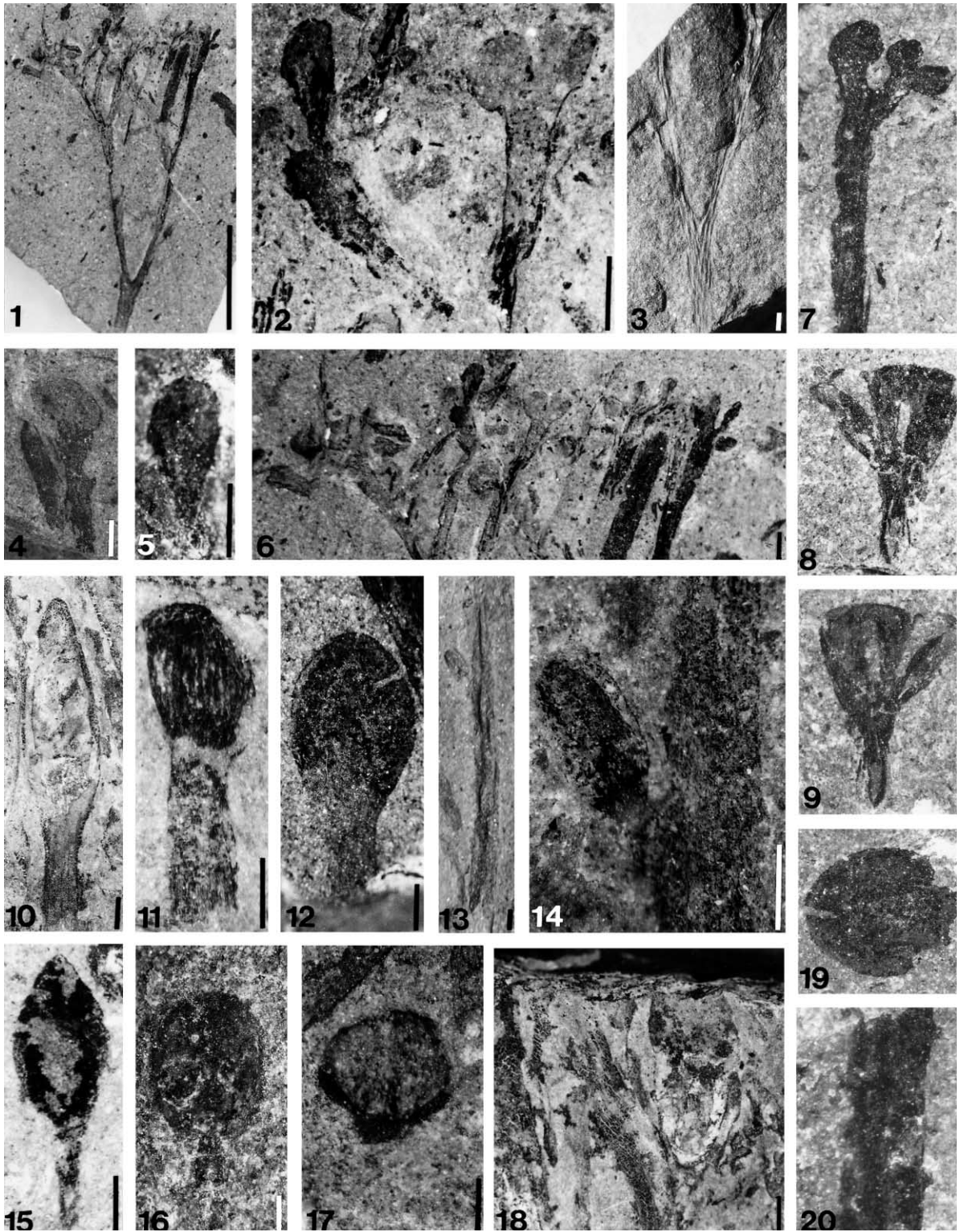
the basal dichotomy. Thereafter extent and nature of branching is more difficult to determine, as the axes (now all approximately the same diameter) occur at different levels in the sediment. Branching angles vary between ca 20 and 35°, the smaller occurring distally.

Ultimate branching occurs immediately below the sporangia, which are all at more or less the same horizontal level (Plate II, 6). At least nine are preserved on the holotype. The subtending axes show ill-defined ridging. There are no obvious sporangial stalks. The terminal expansions may be ±isodiametric to slightly horizontally extended (Plate II, 2, 4–6) or the sectional shape of biconvex lenses. If the former they tend to be flatter. Such combined evidence suggests that the sporangia were ellipsoidal in life. Members of the pair tend to show the two major orientations. In side view, the sporangia are <1.2 mm wide and in full face view, <2.8 mm wide. Height is more difficult to measure ranging between 0.54–1.3 mm. Some sporangia bear a broad vertical or slightly oblique groove or ridge, but there is no direct evidence for any dehiscence features. A second specimen (ca 12 mm high) shows three sporangia terminating an axis with undulating edges and grooves that become less marked below the sporangia. The pair of sessile sporangia are more or less isodiametric (ca 0.8 mm), but the single example, is horizontally elongate (1.58 × 1.08 mm) and presumably compressed at right angles to the others. Whether or not there is an additional sporangium in the matrix below or in the counterpart could not be elucidated. The sporangia show a strong curvature when compared with the subtending axes.

Comparisons: The distinctive features of the more complete specimen are the irregularly ridged, isotomously branching axes and terminal sporangia borne in pairs just above the ultimate branch point on axes a little narrower than the sporangia themselves. The sporangia are laterally flattened but not hemispherical. Short and wide terminal sporangia characterise the genus *Cooksonia* Lang, 1937, and the shape in face view of the Argentine material resembles that in *C. hemisphaerica*, where there is however often a more distinct marginal border. Further differences include the consistently paired arrangement of the sporangia and furrowed axes. Paired sporangia of broadly similar appearance occur in two lower Emsian taxa from Belgium. In *Foozia minuta* (Gerrienne, 1992), a single pair terminates a usually unbranched slender, smooth lateral 'appendage', borne laterally on a broad axis with striated appearance, the latter thought due to the presence of numerous vascular strands. The plant was thus thought to have cladoxylalean affinities. The second taxon from the same locality (Gerrienne, 1998) was not so well preserved, and the paired

PLATE II

San Isidro (1–9, 12–17, 19, 20) and Vaqueria, Villavicencio (10, 11, 18), Mendoza, Argentina: Lochkovian

1–6. *Isidrophyton iñiguezii* gen. et sp. nov. S.I.2. 12608.
1.   Complete specimen. Scale bar = 10 mm.
2.   Close up of tips. Scale bar = 1 mm.
3.   Counterpart (b) photographed in unilateral illumination. Scale bar = 1 mm.
4.   Uncovered sporangium on counterpart (3). Scale bar = 1 mm.
5.   Single sporangium showing symmetry. Scale bar = 1 mm.
6.   Distal regions with sporangia all at one level. Scale bar = 1 mm.
7.   Fragment of *Isidrophyton*. S.I. LPPB 12758. Scale bar = 1 mm.
8, 9. Part and counterpart. S.I. LPPB 12757. Scale bar = 1 mm.
10.   Isolated fusiform ?sporangium. V. LPPB 12748. Scale bar = 1 mm.
11.   Indeterminate striated structure. V. LPPB 12749. Scale bar = 0.5 mm.
12.   Isolated sporangium. S.I.2 LPPB 12746. Scale bar = 1 mm.
13, 14. Striated axis with ?lateral sporangium: new taxon E. S.I.2. LPPB 12747. 13. Scale bar = 1 mm. 14. Scale bar = 1 mm.
15.   cf. *Tortilicaulis* sp. S.I.1. LPPB 12745. Scale bar = 1 mm.
16.   Oval structure associated with axis. S.I.2. LPPB 12754. Scale bar = 1 mm.
17.   ?Sporangium, S.I.1. LPPB 12755. Scale bar = 1 mm.
18.   Typical appearance of fragmentary fossils at Vaqueria. V.LPPB 12756. Scale bar = 1 mm.
19.   Coalified body with central slightly raised circular area. S.I. LPPB 12760. Scale bar = 1 mm.
20.   Fragment with similar projections to those in Plate I, 5–9. S.I. LPPB 12759. Scale bar = 1 mm.

sporangia are on less frequent lateral 'branches' borne on smooth axes of similar diameter to the axis. This plant was grouped with those such as *Renalia* where sporangia terminate lateral axes, a branching pattern quite distinct from that seen in *Isidrophyton*. With the exception of *Cooksonella/Junggaria* from Kazakhstan (Senkevitch, 1975, 1986) and China (Cai et al., 1993) with its highly distinctive bordered sporangia and the recently discovered new species of *Pertonella* from Brazil (Gerrienne, 1999; Gerrienne et al., 2001), axes of plants with terminal sporangia are quite smooth. However numerous elongate protuberances producing a very irregular outline occur in the Rhynie Chert taxon, *Nothia aphylla*, whose affinities remain obscure but whose sporangia, unlike those in the Mendoza specimens, are arranged in lax, irregular strobili (El-Saadawy and Lacey, 1979). Thus, the combination of characters described here is not seen in any early land plants and merits the erection of a new genus. Absence of any evidence for conducting tissue precludes unequivocal assignment to the tracheophytes and it is better left as incertae sedis, although it could be described as rhyniophytoid.

Isidrophyton gen. nov.

Distal parts of plants comprise isotomously branching axes with terminal sporangia. Axes covered by irregular longitudinally elongate fusiform structures. Sporangia in pairs borne immediately above branch points; sporangia ellipsoidal and strongly patterned or rarely discoidal.

Type species: Isidrophyton iñiguezii gen. et sp. nov.

Etymology: Genus after the locality; species is in honour of the late Bolivian-Argentine clay mineralogist A.M. Iñiguez Rodrigues, who made major contributions to Argentine geology

Diagnosis: As for genus. Axes 0.75–1.3 mm wide. Sporangia 0.54–1.3 mm high, <2.8 mm maximum width

Holotype: S.I.2. LPPB 12608a, b, c.

Illustrations: Plate II, 1–6

Type locality: San Isidro Creek, Mendoza Province, the Argentine Precordillera

Horizon: Villaviecencio Formation

Age: Lower Devonian (probably Lochkovian)

3.2.2. New taxon (of Salopella type) (Plate I, 12–15): San Isidro

The specimen is ca 25 mm long showing single isotomous branching with a small angle (20°), 15 mm below the elongate terminal expansions interpreted as sporangia (Plate I, 12). The axes are parallel-sided with little change in diameter after branching (1.3–1.0 mm). They are preserved as a sometimes powdery coalified film, whose surface is punctuated by depressions and elevations (ca 200 µm wide) suggestive of the bases of some kinds of enations or hairs (Plate I, 15), but the axial margins are quite smooth. However, Plate I, 14 shows the base of a possible outgrowth preserved on a sliver of matrix below the dichotomy. It shows a widening symmetrical base, ca 140 µm at the estimated junction with the axis, is 40 µm wide when parallel sided and ca 200 µm long. The tip is truncated, but this may be a taphonomic effect. The axes themselves, comprising at least two layers of coaly material widen distally into the terminal sporangia (Plate I, 13) whose bases are distinguished by a marked change in the thickness of the coal. The left hand example is incomplete distally, but from staining and traces of coal on the matrix was rounded but slightly asymmetric at the tip. It is 3.4 mm high and 2.3 mm at maximum width. The surface has a pronounced longitudinal groove to the left of the centre. The right hand expansion is forked distally, the crotch extending proximally as a broad groove. The left hand segment (as seen in Plate I, 13) is marginally bevelled and rounded at its apex; the right hand one is mucronate. It is possible that the latter is incomplete. Whether or not the bifurcating structure represents two fused sporangia, a bifurcating one or a single sporangium that has split open cannot be decided. The latter seems unlikely from the relative levels in the fossil. Removal of the carbon and examination by SEM does not reveal spores or cellular tissue. Tracheids have not been isolated from the axes.

Comparisons: Erect, solitary fusiform sporangia occur in *Salopella*, *Aglaophyton* and *Tortilicaulis*. The latter has distinctive spiralling in the sporangium wall, while *Aglaophyton*'s preservation in silica makes direct comparisons unrewarding. *Salopella* was erected by Edwards and Richardson (1974) as a form genus for compression fossils of fusiform sporangia and in *S. marcencsis* the concept was extended to include bifurcating examples (Edwards et al.,

1994). However, the outline described here, particularly in the slight asymmetry of the tip and the low length to width ratio, does not exactly match any existing species of *Salopella*. Further, to date all axes attached to *Salopella* sporangia are smooth, although protuberances/enations of the type described here could easily be overlooked or destroyed during fossilisation. Thus, two options are available: to create a new species of *Salopella* or a new genus to emphasise the differences in shape and surface characteristics. While mindful of the pitfalls of diagnosing new taxa on a small number of specimens, the latter might be considered useful here (as was the case for *Isidrophyton*) to emphasise the diversity in the South American assemblage. For the same reason we hesitate to use *Salopella*. Data accumulated since it was erected, mainly relating to in situ spores (e.g. Edwards et al., 1994), confirm that convergence in sporangium shape masks major differences in affinity. Hence, the use of such a paraphyletic genus as *Salopella* in, for example detection of palaeogeographic patterns, is limited. We therefore conclude that the Argentine specimen should be placed in a new genus to emphasise its distinctiveness, but are reluctant to name and characterise it until further specimens become available.

More fragmentary fertile specimens

These range from well-defined shapes attached to short lengths of axes to isolated circular and elliptical discs, the latter usually 0.5–0.8 mm maximum diameter and occassionally with more heavily coalified rims.

3.2.3. cf. Tortilicaulis sp. (Plate II, 15): San Isidro

Occurring among numerous smooth unbranched axes is a single fusiform sporangium attached to an unbranched axis 1.58 mm long that tapers from 0.5 mm below the sporangium to 0.3 mm wide proximally. The sporangium, 2.5 mm high and 1.48 mm at its widest point (that coincides with mid-height), has an extremely glossy appearance but with some oblique striations.

Comparisons: In shape and surface features the sporangium resembles the northern hemisphere late Silurian/early Devonian genus *Tortilicaulis* (Edwards, 1979; Edwards et al., 1994), but more information is needed to permit detailed comparison. The single specimen is thus named cf. *Tortilicaulis* sp.

3.2.4. Isolated sporangium. (Plate II, 12): San Isidro

Plate II, 12 shows an elliptical swelling terminating a short length of unbranched axis ca 1.67 mm wide. The overall length of the specimen is 6 mm, but the height of the presumed sporangium (?3.6 mm) is difficult to define, because it tapers into the axis with gradual decrease in density of coaly material. Its maximum width is 3 mm and its surface is strongly convex. The indentation, top right, suggests cracking on compaction, but unlike many of the axes on the same block that are preserved as coaly coverings to sediment casts, this specimen consists of a single layer of carbon.

Comparisons: The specimen has the overall shape of a *Sporogonites* sporangium (Halle, 1916, 1936) but we hesitate to so name it because of the lack of further detail and its very fragmentary nature.

3.2.5. Specimen S.I.2. LPPB 12747 (Plate II, 13, 14): San Isidro

This comprises an unbranched axis, ca 18 mm long, and 1.53 mm maximum diameter with a very irregular longitudinally furrowed surface (Plate II, 13) and a vertically elongate, elliptical structure probably attached to its left hand edge. Attachment is equivocal because the curved structure (0.5 mm wide) extending between the axis and the lateral structure is not coalified, but occurs as a darker stain on the rock. The lateral structure is 1.9 mm long and 1.0 mm wide with a flat surface except for a marginal band on the adaxial side that slopes into the matrix (Plate II, 14). Longitudinally elongate depressions (ca 0.95×0.49 mm) noted on other areas of the axis may represent the attachment sites of further lateral structures.

Comparisons: The specimen is so fragmentary and uninformative that comparisons, e.g. with taxa with lateral sporangia such as *Zosterophyllum*, are not productive and so we merely record its presence in the assemblage.

3.3. Further Incertae Sedis: San Isidro (Plate II, 8, 9, 11, 17, 19)

These include circular or oval structures, which may or may not be attached to axes. An example is the association in Plate II, 11 of an oval structure (3.9×3.2 mm), at least three layers thick with

Table 2
Lochkovian localities with plant megafossils (see also Fig. 3a and 3b)

	Age	Authors	Geographic area	Composition	Facies
1.	*Uniformis* zone (graptolites (g))	Obrhel (1968)	Bohemia, Czechoslovakia	*Cooksonia downtonensis* (≡ *C. hemisphaerica*)	Marine (deep)
2.	*Micrornatus-newportensis* (lower-middle) (spores (s), fish (f))	Lang (1927) Edwards (1975)	Forfar, Scotland	*Zosterophyllum myretonianum* *Cooksonia caledonica*	ORS (internal facies)
2.	*Micrornatus-newportensis* (lower-middle) (s, f)	Edwards (1972)	Arbilot, Scotland	*Z. fertile*	ORS (internal facies)
3.	*Micrornatus-newportensis* (lower) (s, f)	Edwards and Fanning (1985)	Targrove, Shropshire, England	*Tortilicaulis transwalliensis*, *Resilitheca*, *Uskiella reticulata*, *Tarrantia salopensis*, *C. hemisphaerica*, *C. pertoni*, *C. cambrensis*, *C. caledonica*, *Salopella marcensis*	ORS fluviatile (distal)
3.	*Micrornatus-newportensis* (lower)	Edwards et al. (1994)	Brown Clee Hill, Shropshire, England	*Salopella* cf *marcensis*, *Tortilicaulis offaeus*, *Resilitheca salopensis*, *C. pertoni*, *Grisellatheca salopensis*, *C. hemisphaerica*, cf. *Sporogonites*, *Pertonella* sp., *Fusitheca fanningiae*, *Culullitheca richardsonii*, Spherical sporangia × 5, oval sporangia × 5, *Tarrantia salopensis*, reniform sporangia × 2, Various other unnamed rhyniophytoids	ORS fluviatile (distal)
3.	?	Edwards and Kenrick unpublished	Cwm Mill, Gwent, Wales	*Z. fertile*, *Cooksonia* sp.	ORS fluviatile (distal)
4.	*Micrornatus-newportensis* (upper) (s,f)	Leclercq (1942) Gerrienne (1993)	Nonceveux, Belgium	*Z. fertile*, *Hostinella* sp., *Pachytheca* sp., *Taeniocrada decheniana*	Marine (Rhenish)
3.	Upper Gedinnian (s)	Edwards and Richardson (1974) and unpublished	Newton Dingle + environs, Shropshire, England	*Z.? fertile*, *Salopella allenii*	ORS fluviatile (medial)
3.	*Breconensis-zavallatus* (s)	Edwards and Kenrick (unpublished)	Allt Ddu, Brecon Beacons, Powys, Wales	*Salopella allenii*, *C.* cf. *caledonica*, *Deheubarthia splendens*, *Gosslingia breconensis*, *Z. fertile*. *Z.* sp., *Uskiella* sp.	ORS fluviatile (medial)
4.	*Breconensis-zavallatus* (s)	Steemans and Gerrienne (1984) Gerrienne (1993)	Gileppe, la Vesdre, Belgium	*Gosslingia breconensis*, *Pachytheca* sp., *Prototoxites* sp., *Psilophytites gileppensis*	Marine (Rhenish)

Table 2 (*continued*)

	Age	Authors	Geographic area	Composition	Facies
5.	Upper Gedinnian (field relations)	Schweitzer (1983)	Rhineland, Germany	*Drepanophycus spinaeformis*, *Taeniocrada* sp.?, *Zosterophyllum rhenanum*	Marine littoral
6.	?basal Gedinnian (Ainasu) (faunas, g)	Senkevitch (1975)	Balkhash, Kazakhstan	*Cooksonella sphaerica*, *Taeniocrada pilosa*, *Jugumella burubaensis*	Marine
	?Upper Gedinnian (Kokbaital)	Senkevitch (1986)	Balkhash, Kazakhstan	*Tastaephyton bulakus*, *Taeniocrada pilosa*, *Mointina quadripartita*, *Jujumella jugata*, *J. burubaensis*, *Balchaschella tenera*	
7.	Gedinnian indet. ?	Stepanov (1975)	Kuzbass, Siberia	*Zosterophyllum*, *C. pertoni*, *Stolophyton acyclicus*, *Juliphyton glazkini*, *Uksunaiphyton ananievi*, *Pseudosajania pimula*, *Salairia bicostata*	Marine
8.	Gedinnian ?	Li and Cai (1978)	E. Yunnan, south-west China	*Zosterophyllum* sp.	?
9.	?Lochkovian undet. (corals)	J. Tims (pers. Commun.)	Tyers, Victoria, Australia	*Baragwanathia longifolia*, *Zosterophyllum* n. sp., *Baragwanathia* n. sp.	Marine
10.	Gedinnian indet. (s)	Høeg (1942)	Spitsbergen	Sterile remains only: *Hostinella*, *Taeniocrada*, *Zosterophyllum*	ORS (internal)
11.	?Lochkovian (s)	Edwards et al. (work in progress), this paper	Precordillera, Argentina	*Isidrophyton iñiguezii*, cf. *Salopella*, cf *Tortilicaulis*, *Bowerophylloides mendozaensis*	Marine
12.	Uppermost Lochkovian (inverts, g)	Basinger et al. (1996)	Bathurst Island, Arctic Canada	not specified	Marine
13.	?uppermost Silurian Lochkovian (s)	Mussa et al. (1996) Gerrienne (1999) Gerrienne et al. (2001)	Paraná Basin, Brazil	*Cooksonia* cf. *pertoni* *Sporogonites* sp. nov. cf. *C. cambrensis* *Pertonella* sp. *Salopella* sp. ?leafy and spinous axes	?Marine

bevelled edge, with a short 'rod' (a three dimensional cast of an axis 0.6 mm in diameter), while Plate II, 17 shows an elliptical structure (2.0 × 1.7 mm) with marked convex curvature producing a pouched effect in the vicinity of a flattened tongue-like extension (0.9 mm wide) of an encircling narrow flat border. Such structures are probably not sporangia, but their nature remains obscure. The oval body in Plate II, 19 has a centrally placed slightly raised ±circular area ca half the total diameter. Such zonation is characteristic of *Pachytheca* Hooker, but is insufficiently well preserved to permit unequivocal argument to that genus. Similar bodies have also been identified as *Cooksonia* sporangia (Gerrienne et al., 2001) or may represent isolated masses of spores from that genus.

Plate II, 8 and 9 shows part and counterpart of a small basically triangular shaped fragment ca 5.5 mm long with one tapering and apparently frayed end. The expansion is divided into two segments: one has a flat truncated tip with bevelled edge and tapers to the point where attached to a second segment, with indistinct outline and is extended into the matrix. The

clearer fragment has a vertical ridge extending almost to the apex. Although apparently terminal structures, the subtending axis does dip into the matrix below the terminal expansion.

3.3.1. cf. Salopella sp. (Plate II, 10); Vaqueria

This fusiform structure terminating a short unbranched axis (2.13 mm diameter) showed the preservation described above and is the most convincing sporangium at the locality. It is 3–3.5 mm wide at its maximum point, and about 8 mm long; its base not clearly delimited. While it is possible that it possessed a border, the undulating surface complicates interpretation. Further, the narrow marginal coalified band runs down the edges of the axis, which also has a central longitudinal ridge.

Comparisons and identification. In gross morphology, the specimen has similarities with *Sporogonites*, *Salopella* and inferred compressed *Aglaophyton*. Absence of any distinctive characters favours assignation to *Salopella* sp. In size, it is closest to the type species *S. allenii* from the Lochkovian of the Welsh Borderland (Edwards and Richardson, 1974).

3.3.2. Specimen V. LPPB 12749 (Plate II, 11); Vaqueria

The fragment, ca 2.3 mm long, has two parts separated by a constriction. The presumed apex (0.7 mm wide and ca 1.00 mm long) has a rounded but asymmetric outline marked by a narrow rim and conspicuous longitudinal ridges ca 0.04 mm wide. The coalified material is thicker and more glossy than in the remaining part that is 0.5 mm wide and featureless. A number of analytical techniques have failed to reveal any anatomical detail.

Comparisons. This specimen has no morphological counterpart elsewhere, but further specimens preferably with anatomical information, are required to allow circumscription and naming.

4. Discussion

The quality of the utility of any fossil assemblage to wider issues, be they evolutionary or phytogeographic, depends on (1) confidence of identification of its members, (2) independent evidence for its age, and (3) an assessment of the extent to which taphonomic processes have affected its composition. Such quality controls are particularly important when only one or two assemblages are available from a remote geographic area, as is the case here.

4.1. Composition of assemblages

The Mendozan assemblage contains some endemics, but also plants particularly those represented by isolated sporangia that are superficially similar to common taxa in the present northern hemisphere, and thus might infer cosmopolitan distribution of those plants. In the absence of any anatomy, and in particular in-situ spores it would be unwise to conclude that sporangia, for example, assigned to *Salopella* on sporangial shape were closely related to Australian or British examples. At best, the common occurrence indicates similarities in grade of organisation.

The Mendozan assemblages are thought to occur in Lochkovian, i.e. basal Devonian, rocks, but their position in the Lochkovian, a time interval of ca seven million years, cannot be determined. This is unfortunate because in the one localised geographic area (Wellman et al., 2000) where assemblages occur throughout the Lochkovian (southern Britain, Edwards, 1990), a major diversification of tracheophytes, particularly of zosterophylls, occurred towards the end of the interval, whereas rhyniophytes and rhyniophytoids dominated at its beginning. The grades of organisation of the Argentine plants are more closely comparable to the older examples from the northern hemisphere, and also to the numerous assemblages recorded in the Furnas Formation, Paraná Basin, Brazil and dated as Lochkovian on spores (Gerrienne et al., 2001).

4.2. Taphonomic biases

Our studies of Lochkovian assemblages in Britain indicate that the type of rock, particularly in relation to grain size and environments of deposition, strongly affect the type of plant fragment preserved. Thus, the amazingly diverse mid-Lochkovian mesofossils from the Welsh Borderland (Edwards, 1996) were recovered from very fine grained, fluvial rocks that settled out in low energy environments and would not be
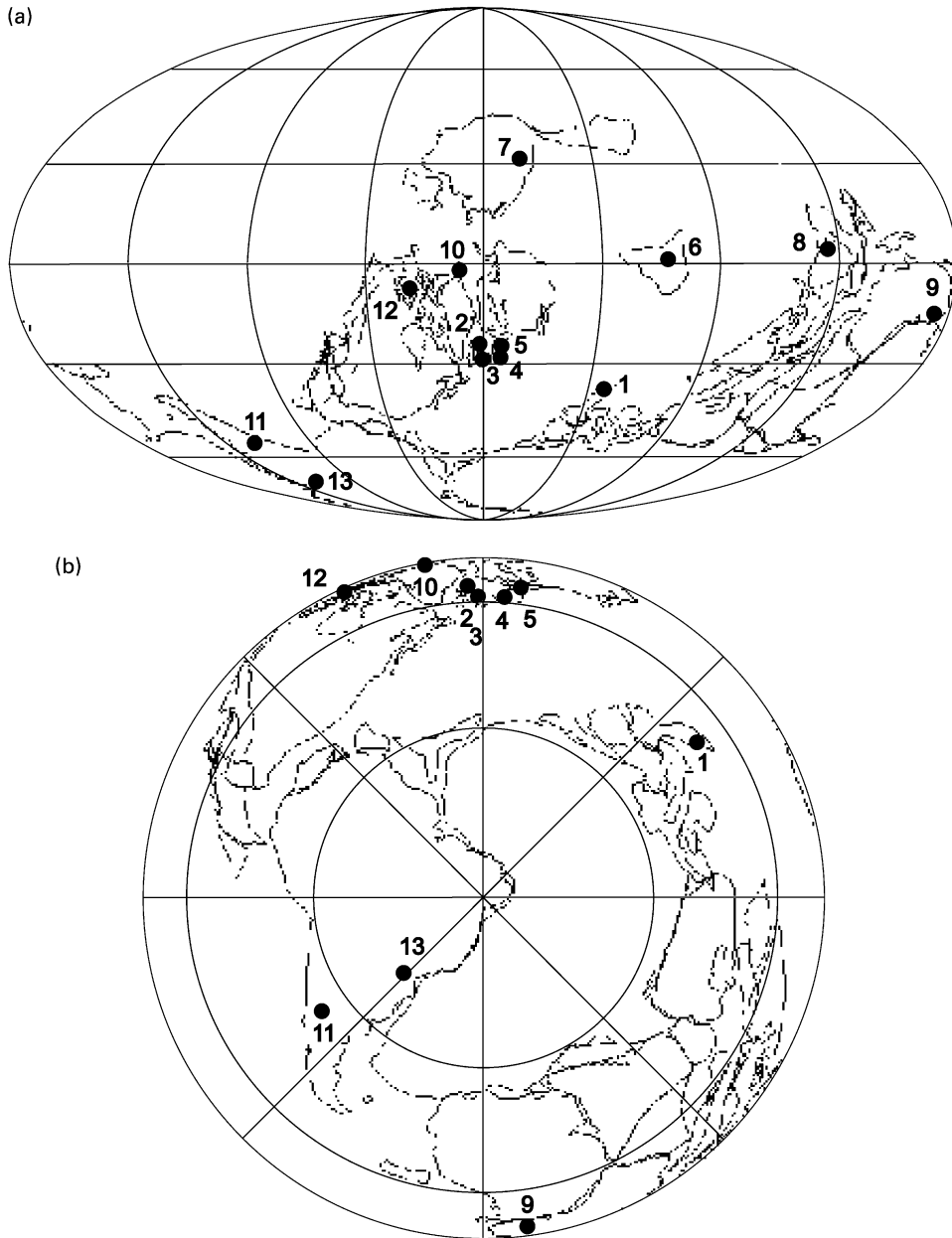
Fig. 3. Positions of Lochkovian plant-assemblages plotted on palaeocontinental reconstructions taken from Eldridge et al., 1996. (a) = equatorial view; (b) = S. polar projection.

expected to occur in the Mendozan rocks, where the matrix is coarser and fragments much larger. In the Welsh Borderland, fossils of similar dimensions including *Zosterophyllum* and *Salopella*, occur in micaceous sandstones (Edwards and Richardson, 1974). Thus the Mendozan assemblages, that were preserved in storm-dominated, shallow-marine, shelf sands (Poiré and Morel, 1996) and were presumably transported (and sorted) some distance from where the plants originally grew, may not be typical of

Lochkovian vegetation of the area. Well-preserved spore assemblages that might give a better picture of the diversity in land plants are not available for study (Rubinstein, 1993a).

4.3. Comparisons with Lochkovian assemblages and palaeogeographical consideration

Table 2 provides lists of taxa from globally distributed localities. Fig. 3(a) and (b) shows equatorial and polar views of the Eldridge et al. (1996) reconstruction of continents in Lochkovian times. The numbers refer to Table 2. Most of the occurrences are circumequatorial. The Brazilian locality is at the highest latitude and within ?30° of the Lochkovian south pole. Mendoza was ca 50°S, on the western margin of Gondwana. Apart from rhyniophytoid taxa resembling *Tortilicaulis* and *Salopella* and leafy axes, e.g. *Lycopodolica* and unnamed ones from Xinjiang China, whose affinities are highly conjectural, there are no common taxa. Perhaps the most significant absences in the Mendozan assemblages are the zosterophylls, particularly *Zosterophyllum*, and examples of *Cooksonia* s.s. The low diversity may be taphonomic or geographical. The geographically closest assemblage from Brazil comprises plants of similar grades of organisation, but has greater number of plants with terminal sporangia, including a new *Cooksonia* species, *Sporogonites*, *Pertonella* and *Tarrantia*, and is dated on spores as Lochkovian. There are no taxa in common.

The absence of *Cooksonia* in the Mendoza assemblage is puzzling. Its record (as *Cooksonia* cf. *caledonica*) in the Upper Silurian of Bolivia (Morel et al., 1995; Edwards et al., 2001) was cited as evidence for its cosmopolitan distribution; its tolerance of cold-stressed conditions at high latitude confirmed by the presence of a further species in the slightly younger rocks of Brazil (Gerrienne et al., 2001). It is also noteworthy that *Cooksonia* is also found in the Lochkovian of Bohemia then situated on the northeastern margin of Gondwana at mid latitudes. However, the low diversity of this latter assemblage might well be taphonomic; the fossils occur in marine rocks with graptolites. In the Devonian northern hemisphere, the Siberian records are the only ones outside equatorial regions and at a latitude comparable to the Argentine one. Scrutiny of the species has shown major diversity with a high proportion of endemism (Stepanov, 1975). Including more familiar taxa are *Zosterophyllum* and *C. pertoni*. However the assemblage was sufficiently distinct to prompt Edwards (1990) to suggest tentatively that it might demonstrate a northern floral province, alongside those of Laurussia, Kazakhstan (plus Xinjiang) and Australia in early Devonian times.

To suggest that the Argentine Precordillera plants also belong to a distinct phytogeographic unit is clearly premature on such limited evidence. However, their isolated palaeogeographic position on the western seaboard of Gondwana (ca 50°S) possibly in a different climate from the majority of coeval assemblages at low latitude (Fig. 3a) hints at this. Scotese et al. (1999) postulated a cool temperate climate while Parrish (1990) inferred abundant precipitation from westerlies and polar easterlies. The mixture of Eastern Americas and Malvinokaffric Realm marine faunas representative of an intermediate temperature mass are in contrast with the cool Malvinokaffric faunas reported at slightly higher palaeolatitudes in Salta and Jujuy Provinces, and in Bolivia and in Peru (Boucot, 1988). Cooler winter temperatures would also have been experienced by the plants recorded in Brazil located within 30° of the Lower Devonian South Pole. Here cool climate Malvinokaffric rocks and faunas occur in the overlying Ponta Grossa Formation, although the presence of kaolinite (if contemporaneous) in the underlying Furnas Formation itself is suggestive of warm climate conditions (Ramos and Formoso, 1976). Apart from a small number of axes with enations, the Argentine plants differ from those of Brazil in lacking the latter's postulated adaptations for cool hardiness (Gerrienne et al., 2001).

References

Basinger, J.F., Kotyk, M.E., Gensel, P.G., 1996. Early land plants from the Late Silurian–Early Devonian of Bathurst Island,

Canadian Arctic Archipelago. Current Research 1996-B. Geol. Surv. Can., 51–60.

Boucot, A.J., 1988. Devonian biogeography: an update. In: Mcmillan, N.J., Embry, A.F., Glass, D.J. (Eds.), Devonian of the World, vol. III. , pp. 211–227.

Cai, Chong-Yang, Dou, Ya-Wei, Edwards, D., 1993. New observations on a Pridoli plant assemblage from north Xinjiang, northwest China, with comments on its evolutionary and palaeogeographical significance. Geol. Mag. 130, 155–170.

Cuerda, A.J., Cingolani, C., Arrondo, O., Morel, E., Ganuza, D., 1987. Primer registro de plantas vasculares en la Formación Villavicencio, Precordillera de Mendoza, Argentina. IV Congreso Lantinoamericano de Paleontología. Actas 1, 179–183.

Cuerda, A.J., Lavandaio, E., Arrondo, O., Morel, E., 1988. Investigaciones estratigráficas en el Grupo Villavicencio, Canota, prov. De Mendoza. Asoc. Geol. Argentina, Rev. 43 (3), 356–365.

Edwards, D., 1972. A *Zosterophyllum* fructification from the Lower Old Red Sandstone of Scotland. Rev. Palaeobot. Palynol. 14, 77–83 (Jubilee Volume for Professor S. Leclercq).

Edwards, D., 1975. Some observations on the fertile parts of *Zosterophyllum myretonianum* Penhallow from the Lower Old Red Sandstone of Scotland. Trans. R. Soc. Edinb. 69, 251–265.

Edwards, D., 1979. A late Silurian flora from the Lower Old Red Sandstone of south-west Dyfed. Palaeontology 22, 23–52.

Edwards, D., 1990. Constraints on Silurian and Early Devonian phytogeographic analysis based on megafossils. Palaeozoic Palaeogeography and Biogeography, McKerrow, W.S., Scotese, C.R. (Eds.), Geol. Soc. Lond., Mem. 12, 233–242.

Edwards, D., 1996. New insights into early land ecosystems: a glimpse of a Lilliputian world. Rev. Palaeobot. Palynol. 90, 159–174.

Edwards, D., Fanning, U., 1985. Evolution and environment in the late Silurian–early Devonian: the rise of the pteridophytes. Phil. Trans. R. Soc. Lond., Ser. B 309, 147–165.

Edwards, D., Richardson, J.B., 1974. Lower Devonian (Dittonian) plants from the Welsh Borderland. Palaeontology 17, 311–324.

Edwards, D., Fanning, U., Richardson, J.B., 1994. Lower Devonian coalified sporangia from Shropshire: *Salopella* Edwards and Richardson and *Tortilicaulis* Edwards. Bot. J. Linn. Soc. 116, 89–110.

Edwards, D., Morel, E.M., Paredes, F., Ganuza, D.G., Zúñiga, A., 2001. Plant assemblages from the Silurian of southern Bolivia and their palaeogeographic significance, Botanical Journal of the Linnean Society 135, 229–250.

Eldridge, J., Walsh, D., Scotese, C.R., 1996. Plate Tracker for Windows, v. 2.0. Paleomap Project, Arlington, Texas.

El-Saadawy, W.-S., Lacey, W.S., 1979. The sporangia of *Horneophyton lignieri* (Kidston and Lang) Barghoorn and Darrah. Rev. Palaeobot. Palynol. 28, 137–144.

Gerrienne, P., 1992. The Emsian plants from Fooz-Wépion (Belgium). III. *Foozia minuta* gen. et sp. nov., a new taxon with probable cladoxylalean affinities. Rev. Palaeobot. Palynol. 74, 139–157.

Gerrienne, P., 1993. Inventaire des végétaux éodévoniens de Belgique. Ann. Soc. Geol. Belg. 116, 105–117.

Gerrienne, P., 1998. *Deuterophyton stockmansii* gen. et sp. nov. du Dévonien inférieur de Belgique et identification d'un nouveau groupe de plantes vasculaires primitives. C. R. Acad. Sci. Paris 326, 369–375.

Gerrienne, P., 1999. Lower Devonian plant mesofossils from the Paraná Basin, Brazil: general introduction, description, age significance and correlation with floral succession from Laurussia and Gondwana. In: M.A.C. Rodrigues, E. Pereira (Editors), Ordovician–Devonian palynostratigraphy in Western Gondwana: update, problems and perspectives. Faculdade de Geologia, Rio de Janeiro, pp. 165–178.

Gerrienne, P., Bergamaschi, S., Pereira, E., Rodrigues, M-A.C., Steemans, P., 2001. An Early Devonian flora, including *Cooksonia*, from the Paraná Basin (Brazil). Rev. Palaeobot. Palynol. 116 (1–2).

Halle, T.G., 1916. A fossil sporogonium from the Lower Devonian of Röragen in Norway. Bot. Not., 79–81.

Halle, T.G., 1936. Notes on the Devonian genus *Sporogonites*. Svensk Bot. Tidsk. 30, 613–623.

Høeg, O.A., 1942. The Downtonian and Devonian Flora of Spitsbergen. Norg. Svalb.-Og Ishavs-Unders. Skrifter 83, 1–228.

Ishchenko, T.A., 1975. Pozdnesiluriiskaya flora Podolii: (the late Silurian flora of Podolila). Akad. Nauk Ukrainskoi CCR, Inst. Geol. Nauk, Izd. Naukova Dumka, Kiev, 1–80.

Kenrick, P., Kvacek, Z., Bengston, S., 1999. Semblant land plants from the middle Ordovician of the Prague Basin reinterpreted as animals. Palaeontology 42, 991–1002.

Lang, W.H., 1927. Contributions to the study of the Old Red Sandstone flora of Scotland. VI. On *Zosterophyllum myretonianum*, Penh., and some other plant-remains from the Carmyllie Beds of the Lower Old Red Sandstone. Trans. R. Soc. Edinb. 55, 443–455.

Lang, W.H., 1937. On the plant-remains from the Downtonian of England and Wales. Phil. Trans. R. Soc. Lond., B 227, 245–291.

Lang, W.H., Cookson, I.C., 1935. On a flora, including vascular land plants, associated with *Monograptus*, in rocks of Silurian age, from Victoria, Australia. Phil. Trans. R. Soc. Lond. B 224, 421–449.

Leclercq, S., 1942. Quelques plantes fossiles recueillies dans le Dévonien inférieur des environs de Nonceveux (Bordure orientale du bassin de Dinant). Bull. Soc. Géol. Belg. 65, 193–211.

Li, Xing-Xue, Cai, Chong-Yang, 1978. A type-section of Lower Devonian strata in southwest China with brief notes on the succession and correlation of its plant assemblages. Acta Geol. Sin. 52, 1–12 (in Chinese with English abstract).

LoDuca, S.T., 1997. The green alga *Chaetocladus* (Dasycladales). J. Paleontol. 71, 940–949.

Morel, E., Edwards, D., Iñigez Rodriguez, M., 1995. The first record of *Cooksonia* from South America in Silurian rocks of Bolivia. Geol. Mag. 132(4), 449–452.

Mussa, D., Borghi, L., Bergamaschi, S., Schubert, G., Pereira, E., Rodriguez, M.A.C., 1996. Estudo Preliminar da Tafolora de Formação Furnas, Bacia de Paraná, Brasil. Anal Acad. Braz. Ci. 68, 65–89.

Obrhel, J., 1968. Die Silur-und Devonflora des Barrandiums. Paläont. Abh. Berlin 2, 635–793.

Parrish, J.T., 1990. Gondwanan paleogeography and paleocli-matology. In: Taylor, T.N., Taylor, E.L. (Eds.), Antartic Paleobiology. Its Role in the Reconstruction of Gond-wana. Springer, New York.

Poiré, D., Morel, E., 1996. Procesos sedimentarios vinculados a la depositación de niveles con plantas en secuencias Siluro-Devó-nicas de la Precordillera, Argentina. Acta VI Reunión Argentina de Sedimentol., 205–210.

Ramos, A.N., Formoso, M.L.L., 1976. Clay mineralogy of the sedi-mentary rocks of the Paraná Basin, Brazil. Rev. Brasil. Geosci. 6, 15–42.

Raymond, A., 1987. Paleogeographic distribution of Early Devo-nian plant traits. Palaios 2, 113–132.

Rickards, R.B., 2000. The age of the earliest club mosses: the Silur-ian *Baragwanathia* flora in Victoria, Australia. Geol. Mag. 137, 207–209.

Rubinstein, C.V., 1993a. Primer registro de miosporas y acritarcos del Devonico Inferior, en el Grupo Villavicencio, Precordillera de Mendoza, Argentina. Ameghiniana 30, 219–220.

Rubinstein, C.V., 1993b. Investigaciones palinológicas en el Paleo-zoico Inferior de Argentina. Zentral. Fuer Geol. Palaeontol. 1, 217–230.

Schweitzer, H.-J., 1980. Die Gattungen *Renalia* Gensel und *Psilo-phyton* Dawson im Unterdevon des Rheinlandes. Bonner Paläo-bot. Mitt. 6, 1–34.

Schweitzer, H.-J., 1983. Die Unterdevonflora des Rheinlandes. Palaeontographica B 189, 1–138.

Scotese, C.R., Boucot, A.J., McKerrow, W.S., 1999. Gondwana paleogeography and paleoclimatology. J. Afr. Earth Sci. 28, 99–114.

Senkevitch, M.A., 1975. Novie Devonskie Psilofitovie Kazakhstana (New Devonian psilophytes from Kazachstan). Esheg. Vses. Paleontol. Obschestva 21, 288–298 (in Russian).

Senkevitch, M.A., 1986. Fossil plants in the Tokrau horizon of the upper Silurian. In: Nikitin, I.F., Bandaletov, S.M. (Eds.), The Tokrau horizon of the Upper Silurian Series: Balkhash Segment. Nauka, Alma-Ata, p. 236 (in Russian).

Seward, A.C., 1910. Fossil plants II. Cambridge University Press, Cambridge (624 pp.).

Steemans, P., Gerrienne, P., 1984. La micro-et macroflore du Gedinnien de la Gileppe, Synclinorium de la Vesdre, Belgique. Ann. Soc. Géol. Belg. 107, 51–71.

Stepanov, S.A., 1975. Fitostratigrafiya opornikh razrezov devona olrani Kuzbassa (Phytostratigraphical evidence from Devonian sections in the outer part of the Kuzbass): Trudy, Sibir. Nauchno-Issledovatel. Inst. Geol., Geofiz. i Mineral. Sirya (SNIIGGIMS), Vip. 211, Zapadno-Siber. Knizhnoe Izdatel., Novosibirsk, 150 pp. (in Russian).

Tims, J.D., Chambers, T.C., 1984. Rhyniophytina and Trimerophy-tina from the early land flora of Victoria, Australia. Palaeontol-ogy 27, 265–279.

Wellman, C.H., Habgood, K., Jenkins, G., Richardson, J.B., 2000. A new plant assemblage (microfossil and megafossil) from the lower Old Red Sandstone of the Anglo-Welsh Basin: its implications for the palaeoecology of early terrestrial eco-systems. Rev. Palaeobot. Palynol. 109, 161–196.