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First record of Early Devonian (Lochkovian) flora from the Santa Rosa Formation - Alarache, Southern Bolivia

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ABSTRACT

New information on plants and palynomorphs from Angosto de Alarache, South Bolivia, is presented. The plant remains appear at the base of the section. Dichotomizing sterile forms are assigned to *Hostinella* sp. and scarce stems terminated in spherical structures are interpreted as indetermined sporangia. The palynological association 1 recovered from this level contains abundant phytodebris, trilete spores, few cryptospores, algae, very poorly preserved chitinozoans, and other elements (fungi, ?lichens). Trilete spores assignable to *Apiculiretusispora* sp., *Punctatisporites* sp. and *Retusotriletes* sp., are obtained from the maceration of some isolated sporangia. The dichotomous branching of the stems and the trilete spores recovered from the isolated sporangia support its tracheophyte affinity. The palynological assemblage 2, obtained three metres above, contains abundant phytodebris and more diverse palynomorphs. Two new species (*Retusotriletes albarinii* n. sp., *Acinosporites macgregorii* n. sp.) are described. Based on the presence of the trilete spores *Dictyotriletes emsiensis* (ALLEN) MCGREGOR, *Retusotriletes maculatus* MCGREGOR and CAMFIELD, *Apiculiretusispora plicata* (ALLEN) STREEL and the absence, mainly of *Verrucosisporites polygonalis* LANNINGER and *Urochitina loboi* VOLKHEIMER et al., we propose a Lochkovian age but restricted up to the Late not latest Lochkovian, and the correlation with the lower part of the *Emsiensis* Zone of the Amazon Basin and the MN Zone of Western Europe. The abundance of fragmented stems of varied size and parallel to bedding planes, along with the isolated sporangia in the plant assemblage suggests a short distance transportation under low energy conditions, probably from marginal palaeoenvironments to low energy marine settings.

KEYWORDS **Primitive plants. Miospores. Lochkovian. Tarija Basin. Southern Bolivia.**

INTRODUCTION

The origin and early evolution of land plants in the mid-Palaeozoic era, between 480 and 360 million years ago, was an important event in the history of life, with far-reaching consequences for the evolution of terrestrial organisms and global environments. Land plant records from the Lower Devonian rocks of southern South America are still scarce. They are known especially from the Tarija Basin at the central and southern parts of Bolivia and Precordillera range from Western Argentina (e.g., Edwards et al., 2001a, b; Morel et al., 2006, and references therein), Paraná Basin from Brazil (Gerrienne et al., 2001, and references therein), and Uruguay (Sprechmann et al. in Grahn, 2003; Fig. 1). Morel et al. (1995) illustrates *Cooksonia* cf. *caledonica* from the Kirusillas Formation (Fm), near Tarija city (southern Bolivia), an assemblage attributed to the Ludlow (late Silurian) on the basis of other palaeontological records of the related stratigraphical units such as the Cancañiri, Tarabuco and Kirusillas formations from other localities (Fig. 2A). Later, Edwards et al. (2001a) describe in detail the above mentioned plant assemblage composed of sterile coalified compressions and impressions of parallel-sided stems, some of them with branching typical of *Hostinella.* In rare specimens, globular or elliptical structures with marginal features are interpreted as sporangia, although neither spores nor tracheids are found. Limachi et al. (1996) defined a *Cooksonia* sp. Zone spanning the Ludlow and Pridoli (Fig. 3). Edwards and Wellman (2001) summarise the records of land plants and palynofloras during the Late Silurian to Early Devonian around the world, and

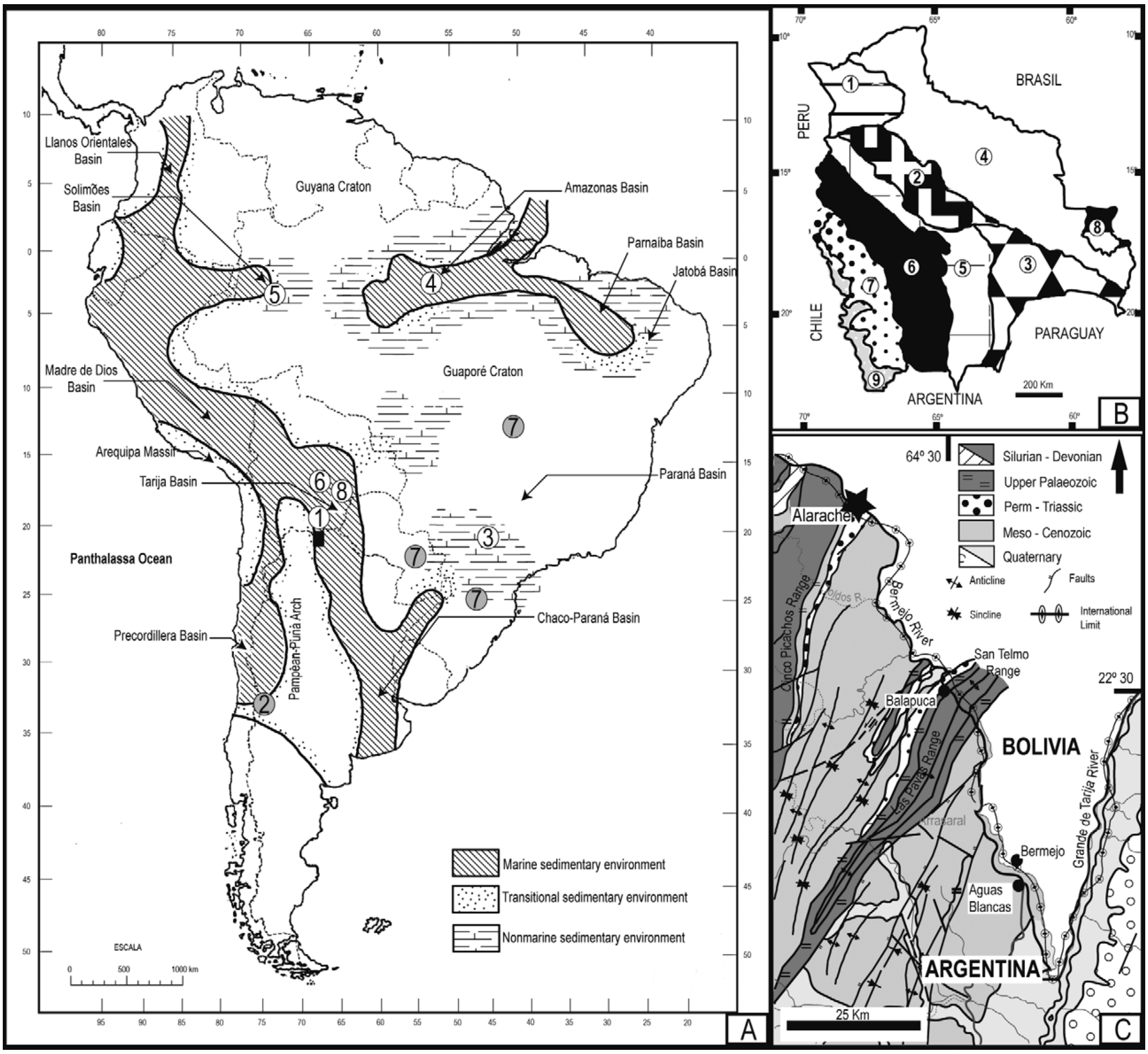

FIGURE 1 **A) Map showing the basins and palaeogeography of South America during the Lochkovian (based on Melo, 1988; Grahn, 2003, 2005). The black rectangle indicates the study area and the numbers, the location of the assemblages compared to the association here presented: 1- Edwards et al. (2001a), 2- Edwards et al. (2001b), LéHerissé et al. (1996), 3- Gerrienne et al. (2001), 4- Melo and Loboziak (2003), 5- Rubinstein et al. (2005), 6- McGregor (1984), 7- Grahn et al. (2000), 8- Grahn (2002). B) Geological Provinces from Bolivia: 1: Madre de Dios, 2: Beni, 3: Chaco, 4: Guaporé Craton, 5: Subandean (north and south), 6: Eastern Cordillera, 7: Altiplano, 8: Pantanal, 9: Western Cordillera (after Suárez Soruco, 2000). C) Geological map (modified from Salfity et al., 1998) of the studied area at southernmost Bolivia to northern Argentina.**

notice that palynological records in South America are still scarce (see also Melo and Loboziak, 2003; Rubinstein et al., 2005) with reference to the ones from North America and Europe (e.g., Richardson and McGregor, 1986; Streel et al., 1987; Steemans, 1989; Wellman, 2004).

The aim of this contribution is to present the first record of a primitive plant assemblage containing indetermined sporangia and its spores, and two palynological associations, one from the plant level and the other a few meters above, both from the Santa Rosa Fm at the southernmost Bolivian Alarache locality. A comparison and correlation with coeval and other similar floras from South America and other regions beyond Gondwana is proposed. Taphonomic features are analysed and related to previous palaeoenvironmental interpretations.

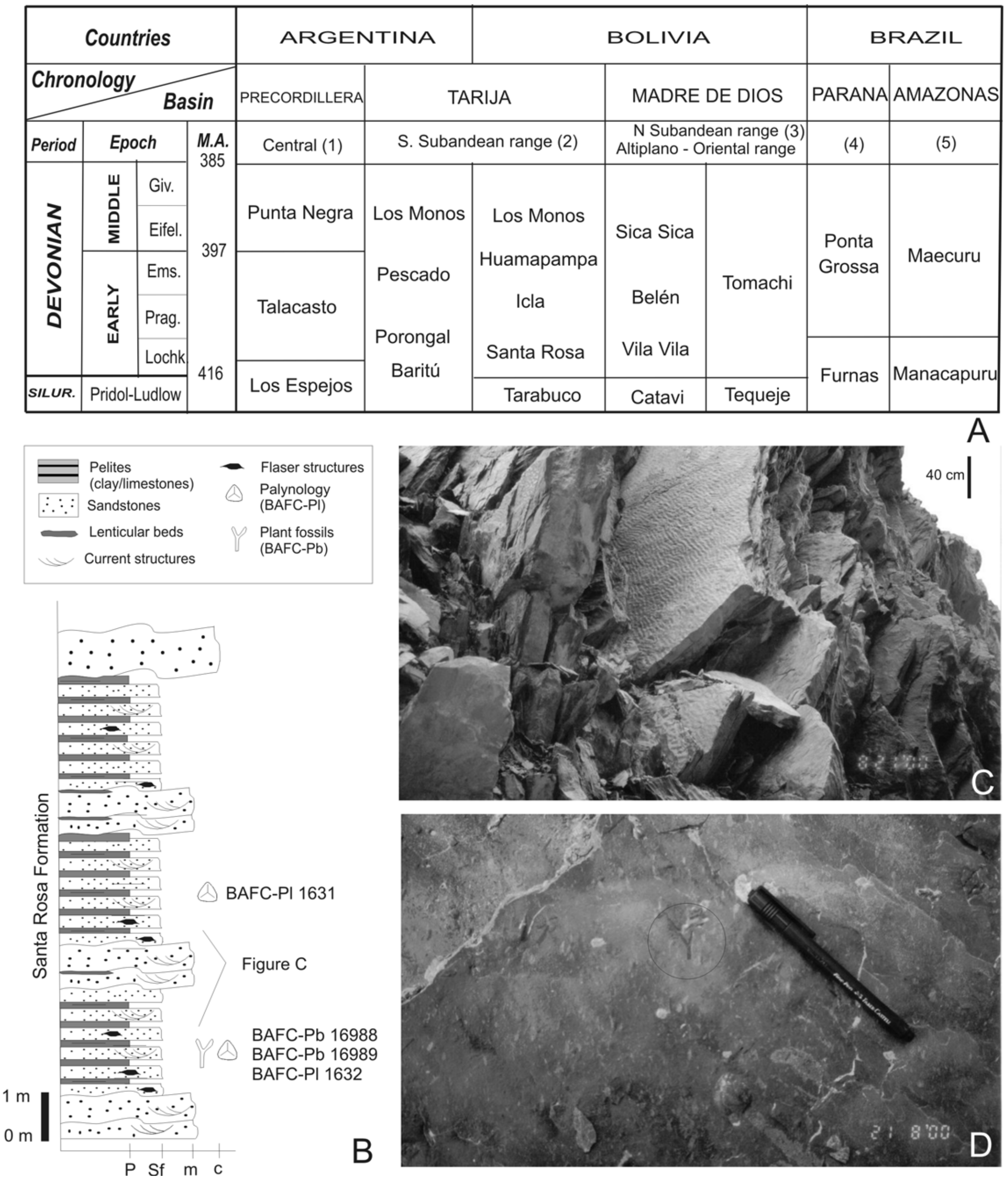

FIGURE 2 **A) Correlation of Late Silurian to Lower Devonian units of Argentina, Bolivia and Brazil. References: (1) Rubinstein (1999, 2000); (2) Starck (1996, 1999), Suárez Soruco (2000); (3) Díaz Martínez (1999), Suárez Soruco (2000); (4) Melo and Loboziak (2003), Grahn (2003). Absolute time dates (Gradstein et al., 2004). B) Schematical lithological section of Santa Rosa Formation. C) Section of the outcrop showing tabular banks of medium- grained sandstone with current structures interbedded with pelitic levels bearing plants and palynomorphs. Scale: 40 cm. D) Stems on bedding plane corresponding to BAFC-Pb 16988. Scale (pen): 15 cm.**

MATERIAL AND METHODS

The plant specimens were studied with a stereo microscope under magnifications between 8x and 50x. The illustrations were taken with a *Sony Cyber-shot DSC-P200* 7.2 megapixel camera. Three different techniques were performed to extract the palynological material from the pelitic rocks and from the sporangia and coalified plant remains. A standard palynological method was carried out on pelitic samples corresponding to BAFC-Pl 1631 and 1632 to obtain organic residues. They were extracted from crushed samples, treated first with hydrochloric acid and later with hydrofluoric acid to remove carbonate, silica and silicates, respectively, and finally mounted on slides with glycerine jelly. A second technique followed conventional treatments into HCl/HF of isolated thin laminae (of aproximately 2 cm x 2 cm wide and long x 1-2 mm high) from both plant bedding surfaces of BAFC-Pb 16988 and 16989 samples bearing sporangia and abundant stem fragments. The residues obtained contained many spores and plant debris and several slides with jelly-glycerine were mounted. The last attempt to extract spores from sporangia consisted in the separation of three sporangia from the rock mechanically. They were observed and photographed under the stereo microscope and then treated with nitric acid (40%) and sodium carbonate to release and oxidise the organic material including spores. The resulted splinters were mounted on a slide with jelly-glycerine.

Identification of palynomorphs was undertaken using both *Leitz Orthoplan* and *Nikon Eclipse* 80*i* binocular transmitted light microscopes, with x1000 maximum magnification. The photomicrographs were obtained with *Motic* (2.0 megapixels) and *Pax-it* (3.1 megapixels) videocamera and the illustrations were quoted with the BAFC-Pl acronym followed by the England Finder reference. The studied samples, mega and microfossils, are deposited at the Department of Geology of Natural and Exact Sciences Faculty (University of Buenos Aires) under the quotation BAFC-Pb 16988, 16989 (plants and palynology) and BAFC-Pl 1631 and 1632 (palynology). Sample processing was undertaken at the Palynostratigraphy and Paleobotany Laboratory belonging to the same institution. Detailed surface studies on both plant remains and spores were illustrated under SEM photographed with a Phillips serie XL model 30 at the Natural Science Argentine Museum "Bernardino Rivadavia" (MACN) of Buenos Aires (Argentina). The specimens were coated with a fine film of 200-300 Å Gold-Palladium, using a sputter-coater "Termo VG Scientific SC 7620". After this study, coverslips bearing the isolated spores were removed and mounted on slides with jelly-glycerine to be re-illustrated under the light microscope.

STRATIGRAPHY OF THE AREA

The stratigraphy of Late Silurian to Devonian rocks from North Argentina and South Bolivia (Fig. 2A) is

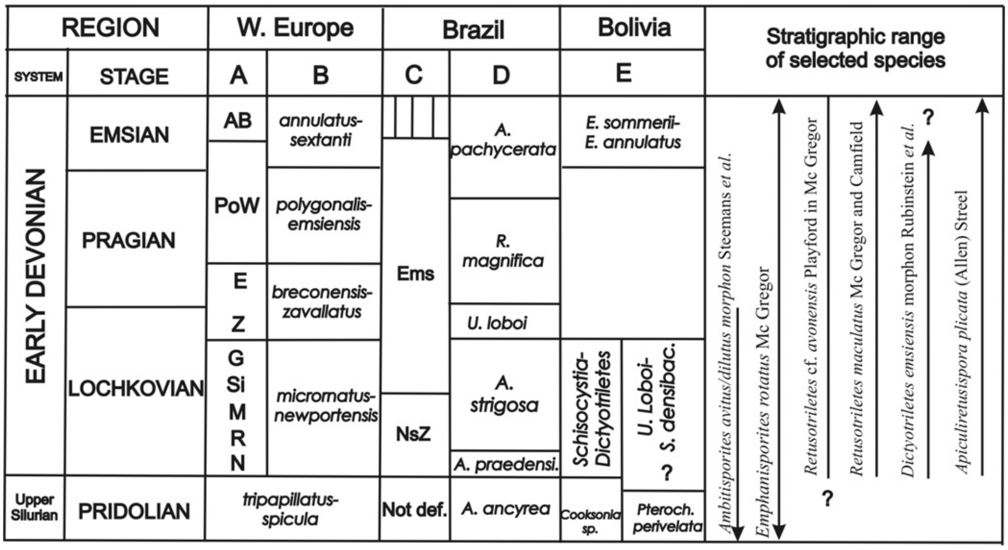

FIGURE 3 **Correlation chart of Late Silurian to Lower Devonian Argentina, Bolivia and Brazil biostratigraphical units and stratigraphical range of selected species present in assemblage 2. Arrows indicate the extension of their ranges and interrogation symbol, doubtful records. Ranges of taxa are based on selected literature: McGregor and Camfield (1976), McGregor (1979, 1984), Richardson and McGregor (1986), Turnau (1986), Steemans (1989), Steemans et al. (1996), Vavrdová et al. (1996), Edwards and Richardson (1996), Melo and Loboziak (2003), Rubinstein et al. (2005). Biostratigraphy. A: Streel et al. (1987), Steemans (1989); B: Richardson and McGregor (1986), C: Melo and Loboziak (2003), Rubinstein et al. (2005); D: Grahn et al. (2003), Grahn (2005); E: Limachi et al. (1996).**

included on Starck's (1995) tectonic-stratigraphical framework, where the Silurian-Jurassic interval is divided into two units separated by an unconformity of regional character at the end of the Devonian. In the first Silurian-Devonian interval, the Cinco Picachos, Las Pavas and Aguaragüe Supersequences are characterized by stacked, kilometer scale, coarsening-upward shale and sandstone facies. Under this scheme, the Santa Rosa (or Porongal after Starck, 1996) Fm is included in the Cinco Picachos Supersequence. The Santa Rosa Fm conformably overlies the Tarabuco Fm and is transitional to the overlying Icla Fm (Fig. 2A). The lithologies of the two former units are very similar and consist of micaceous sandstones with minor amount of silty mudstones beds, while the latter is dominated by fine sediments (lime/claystones). The best sections of these units crop out at the Tarabuco and Angosto de Alarache regions, but are also recognized in other Subandean regions and the Eastern Cordillera (e.g., Starck, 1996; Suárez Soruco, 2000; Fig. 1B). The Santa Rosa Fm thickness varies between 100 and 700 m (Suárez Soruco and Díaz Martínez, 1996; Limachi et al., 1996). A correlation of the Devonian units with others in southern South America is also presented in the Fig. 2A.

The Alarache Devonian section was recently analysed and correlated with other numerous sections of northern Argentina and south central Bolivia by Álvarez et al. (2003). They establish a model of facies distribution in a sequence stratigraphic framework between the Ludlow to Frasnian for this region, integrating mostly unpublished palaeontological studies. "Psilophyta" remains are mentioned as part of the genetic sequences III and V attributed to the Lochkovian and earliest Pragian Santa Rosa Fm (around 300 m thick). The section analysed herein corresponds to the former (L. Albariño, pers. comm.). It is located at the Angosto de Alarache (64º 34' 01'', 22º 14' 48''), near Tarija city (Tarija Department), southern Bolivia (Figs. 1A-1C). The section containing the fossils is not thicker than 10 m and comprises, from base to top, a tabular bank of medium- grained sandstones with current structures (planar cross- bedded stratification and straight or sinuous ripples, Figs. 2B, C) overlain by laminated and massive siltstone layers and heterolithic facies. The latter are composed of an alternation of thin fine sandstone layers with flaser to rippled structures, and 15 to 20 cm thick laminated and massive siltstones that bear plant remains (BAFC-Pb 16988 and 169989, and BAFC-Pl 1632, palynological association 1). Abundant to scarce, coalified stem compressions and impressions are preserved in several levels parallel to the bedding (Fig. 2D). Above this, there is another section around 4 m thick, composed of a sandstone bed bearing current structures followed by a dark grey claystone bed that yielded the palynological assemblage 2 (BAFC-Pl 1631, Fig. 2B).

PLANT FOSSILS

Mega and mesofossils

GENUS ***Hostinella*** BARRANDE *ex* STUR, 1882

Type species: *Hostinella hostinensis* (BARRANDE) BARRANDE *ex* STUR, 1882

Remarks: The generic status was clarified by Bonamo (1983)

Hostinella sp.
Figures 5B, D, E, G, L, M, O

Description: Sterile stems occur in both samples BACF-Pb 16988 and 16989 (Figs. 4A, 5A, C), but are only abundant in the latter, where they form mats, parallel to bedding, covering bedding planes in a layer less than a cm thick. Most stems are preserved as fragmentary coalified films. They are narrow (1.5 to 4 mm), and average 4 to 10 cm in length. Their surface is generally smooth although some samples show fine longitudinal striations on the surface (Figs. 5G, K) and evidence of a central strand (Figs. 5G, L) approximately 0.2 mm wide. Branching, when preserved is more or less dichotomous at angles from 20º to 55º and usually with little decrease or no change in diameter of the daughter branches (Figs. 5B, D, M).

Remarks: The smooth, dichotomous branching, sterile stems with evidence for vascularization are usually assigned to the genus *Hostinella* (Edwards, 1979). Differences in size range of stems could reflect different ontogenic stages or fragmentation. The morphology of these stems is similar to the scarce specimens attained to sporangia recovered from the same plant levels (Fig. 6M).

Comparisons: Similar stems of erect plants are described and illustrated from the middle Silurian deposits in Ireland (Edwards and Feehan, 1980), the Ludlow Kirusillas Fm in Bolivia (Morel et al., 1995; Edwards et al., 2001a), the Early Lochkovian of the Paraná Basin in Brazil (Gerrienne et al., 2001) and the Lochkovian of the Argentinian Precordillera (Edwards et al., 2001b). All these *Hostinella* sp. records are similar in branching system, striations on the surface of stems to the specimens found at Alarache but the latter are somewhat larger in diameter especially with respect to the other Bolivian and Brazilian material.

Indeterminate stems
Figures 5H, I, J, N

Description: Some stem compressions present in sample BACF-Pb 16989, are about 1.2 mm wide and 3.5 cm

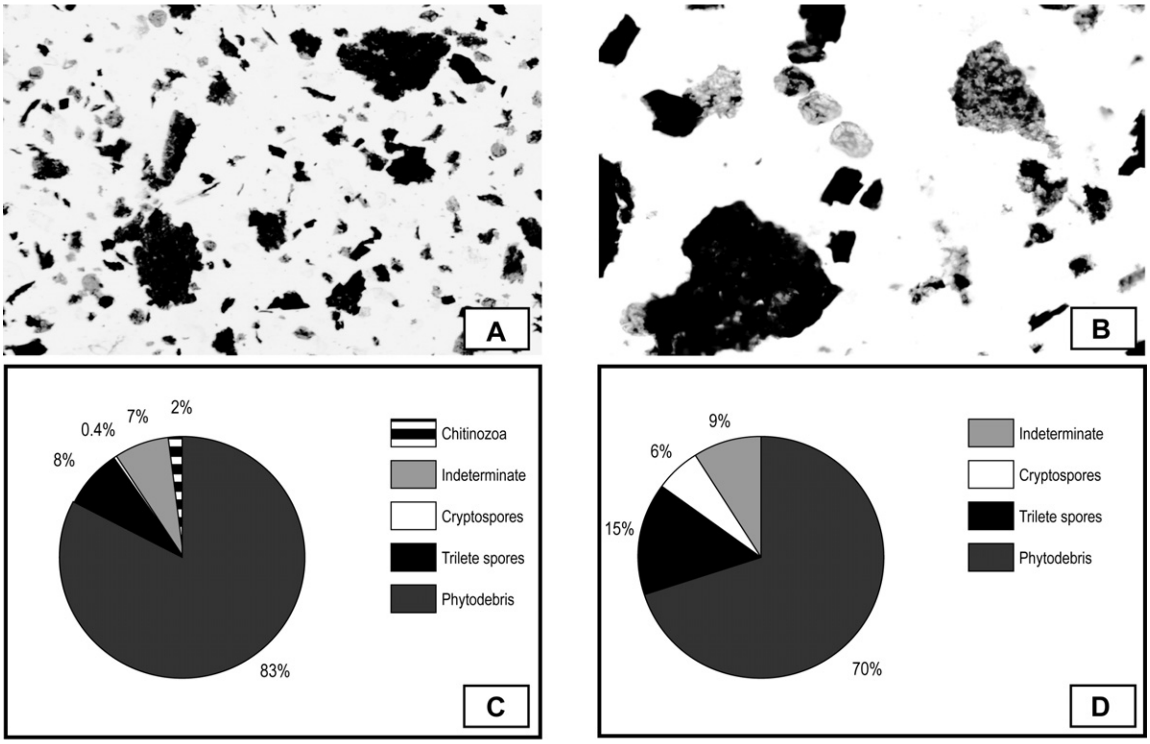

FIGURE 4 **A) BAFC-Pl 16988 Palynofacies (Scale x4). B) BAFC-Pl Palynofacies 16988 (Scale x10). C) Relative abundance of major groups of palynomorphs and phytodebris (assemblage 1). D) Relative abundance of major groups of palynomorphs and phytodebris (assemblage 2).**

long and are covered with projections more or less domed shaped that have wide bases around 0.5-0.6 mm and taper averaging 0.7- 0.8 mm high with truncated tips (Fig. 5H). The arrangement of these protuberances appears to be helical (Fig. 5J), although random distribution cannot be discarded.

Remarks and comparisons: Protuberances in the stems studied may resemble bases of enations, and on this basis they could be assigned to the form genus *Psilophytites* HØEG 1952. Its original definition is similar to the usage of *Hostinella*, based on Early Devonian fragmentary sterile stems with spreading undivided spines. Nevertheless, as stated by Edwards (1979), there are several plants covered with appendages which are claimed to be trimerophytes, zosterophylls and lycopods from the Silurian to Devonian floras, and due to the uncertainty of the origin of these protuberances, we leave this species as indeterminate.

Fertile species
Indetermined sporangia
Figures 6A-M, Figures 7G, J, N, Figures 8A-F, H, Q, R

Description: Short stems bear terminal sporangia that in compression are more or less discoidal structures, isodiametric, 2-4 mm in diameter (see Figs. 6A-M). A narrow marginal band, c. 0.15-0.20 mm wide, extends around the margin, and is probably not present at the junction with the subtending stem. Poorly preserved subtending stems are observed in few specimens (Figs. 6A, D) comprising a short axis of around 0.6 mm in width that expands to c. 1.33 mm towards the junction with the sporangium. This junction seems to be a straight line. The sporangium is about three times as wide as the top of the stalk. Due to the poor preservation, dehiscence features are not discernible. *In situ* spores: the three isolated sporangia yielded many trilete spores with a quite distinctive trilete mark to a slightly marked laesurae, subcircular amb, acavate exine, curvaturae indistinct and exine finely granular to laevigate, diameter 35-50 μm (Figs. 7G, J, N, 8E, F, Q, R). They occurred mostly single and some tetrads were observed but all were so fragile that they could not be picked to be prepared for SEM illustration.

Remarks: Considering that all the isolated sporangia in the assemblage show the same morphological features as the ones at the tip of short stems, we consider them part of the same taxon. Whilst frequently observed in pairs, some are more irregularly shaped due to fragmentation or poor preservation (Figs. 6 K, L). It is of interest that sporangia born on short stalks are smaller than isolated ones.

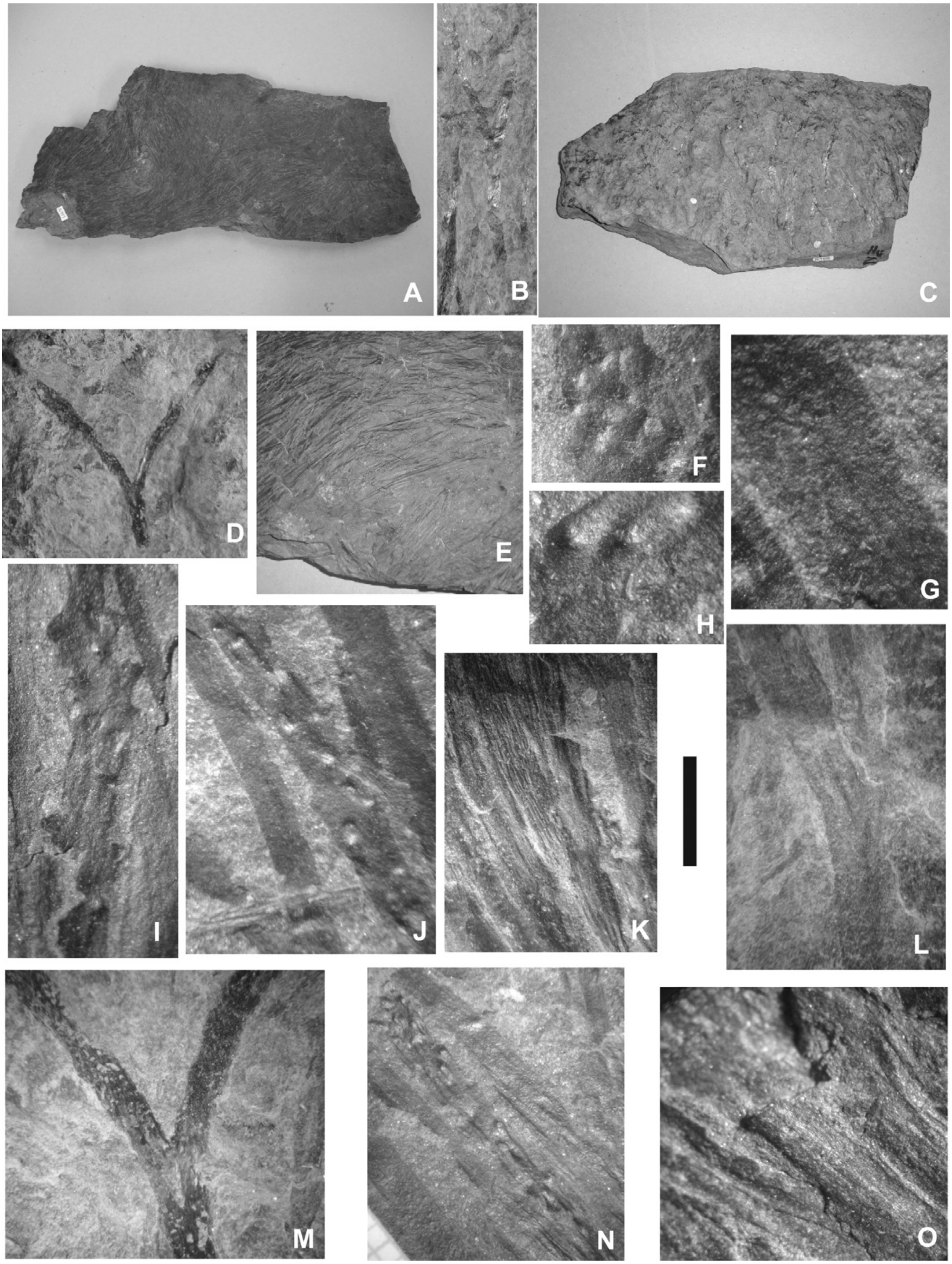

FIGURE 5 **A and C) Large blocks BAFC-Pb 16989 and 16988 bearing plant remains. B, D, G, K, L, M, O) Sterile stems attributed to *Hostinella* sp. (Scales: B: 30 mm; D: 20 mm; G: 5.8 mm; K: 3.6 mm; L: 5.8 mm; M: 8.2 mm; O: 2 mm). E) Abundant concentrations of stems on bedding plane. F) Indeterminate specimen. (Scale: 2.4 mm). H, I, J, N) Indeterminate stems with protuberances. (Scales: H: 1 mm; I: 2.5 mm; J: 3.3 mm; N: 5mm).**

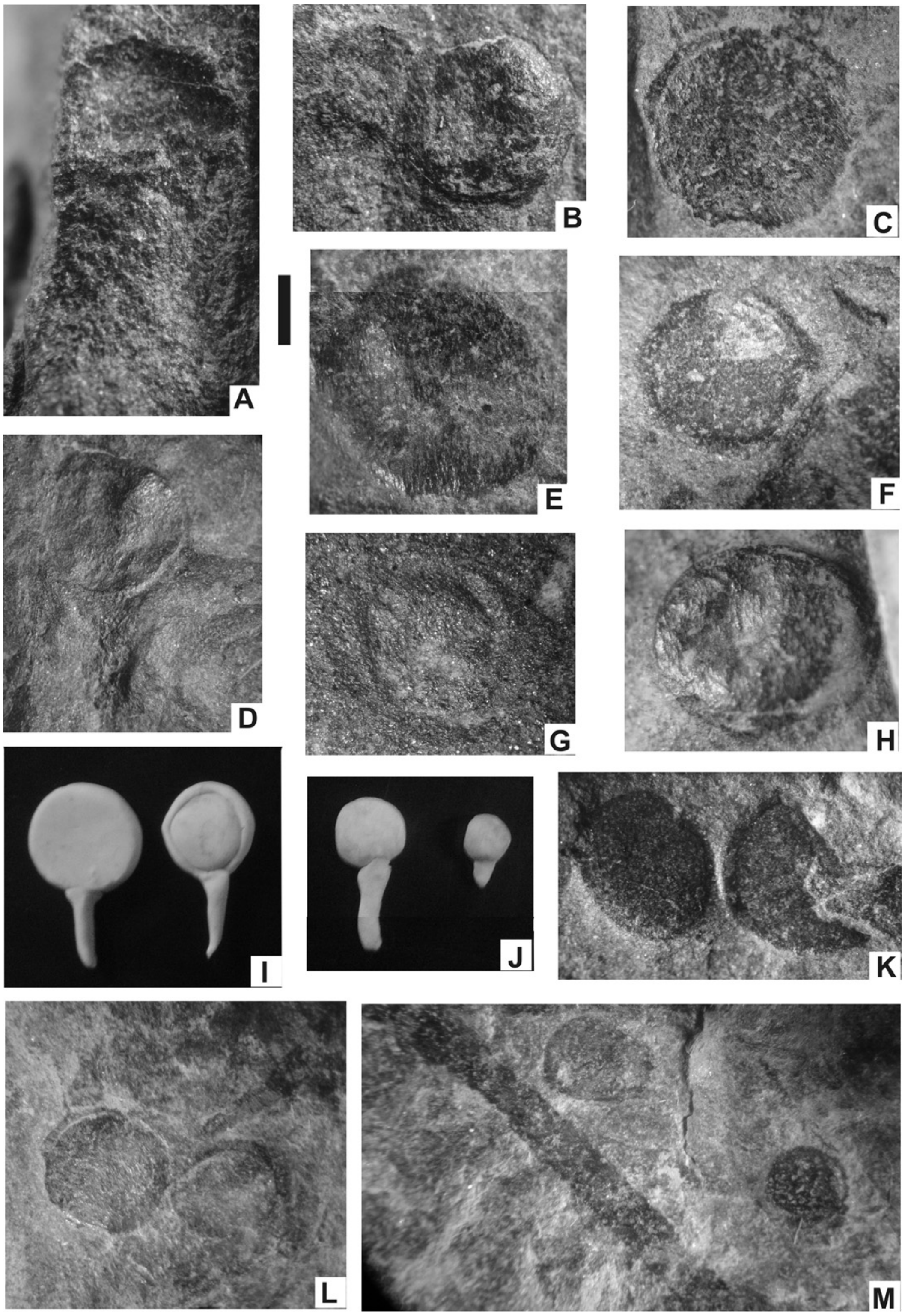

FIGURE 6 **A, D) Indetermined sporangia attached to stalks. (Scales: A: 0.8 mm; D: 1.6 mm). B, K, L) Isolated sporangia in pairs. (Scales: B: 1.1 mm; K: 1.5 mm; L: 2.0 mm). C, E-H) Isolated sporangia with marginal band. (Scales: C: 1.3 mm; E: 0.6 mm; F: 1.0 mm; G: 1.2 mm; H: 1.2 mm). I-J) Reconstruction of sporangia modelled in clay. I: Transverse section of the sporangia showing the thickened wall. J: Sporangia compressed and uncompressed in external view. M) Simple sterile stems and sporangia interspersed variably abundant. (Scale: 2.5 mm).**

Comparisons and interpretations: One of the most similar genus of sporangia to the specimens from Alarache is *Cooksonia* LANG (1937). This genus embraces originally short and wide sporangia terminating isotomously branching stems. The morphology of stems includes anatomical features such as annular tracheids and epidermal cell (see Edwards, 1970). Unfortunately, a central strand is observed only on some of the sterile stems studied whilst *bona fide* tracheids and stomata were not recovered. Our specimens of sporangia were probably originally spherical structures, and are generally preserved in lateral view (see Figs. 6D, I, J). They do not show any mark of a subtending stem on its centre like in *Cooksonia pertoni* LANG as illustrated by Rogerson et al. (1993) and *Cooksonia paranensis* GERRIENNE et al. 2001. *Cooksonia caledonica* EDWARDS 1970 and *C. hemisphaerica* LANG emend. EDWARDS 1979 are similar in its shape (semiglobose, globose or discoidal in proximal-distal arrangement). The former species differs from our material in its reniform outline and smaller size (around 1.2-2.0 mm high and 1.3-3.0 mm wide) although both develop a marginal band. We interpret that this marginal band, in our material, could represent the impression/compression of a thick wall of the sporangia as shown in the Figs. 6I-J. The globose structures attributed to *Cooksonia* cf. *caledonica* and *Cooksonia hemispherica* by Edwards et al. (2001a) in the Tarija region are quite different from our specimen, mainly by their unusual shape, the angle of branching of the stems bearing sporangia, and the smaller diameter of the latter. *Cooksonia paranensis* is distinguished from our species in having plate-shaped or bowl-shaped sporangia that is sunken in its stem rendering a triangular amb.

Several *in situ* spores were found in different species of *Cooksonia* that have been summarized and/or discussed by several authors such as Allen (1980, 1981), Gensel (1980), Rogerson et al. (1993), Edwards et al. (1994), Balme (1995), Edwards and Richardson (1996), Wellman and Gray (2000), Edwards and Wellman (2001),Wellman (2004) among others. From these spore records, "*Cooksonia" crassiparietillis* YURINA 1964 (see Edwards and Richardson, 1996), from the Early Devonian of Russia, yielded spores similar to *Apiculiretusispora* sp. but with slightly larger sculptural elements (see McGregor, 1973). Allen (1981) refers to *Cooksonia hemisphaerica* EDWARDS 1979 from the late Silurian of Wales, as producing azonate-laevigate trilete spores later assigned to *Apiculiretusispora* sp., and considered inmature (cf. Balme, 1995, p. 93). Fanning et al. (1992) describe cf. *Cooksonia caledonica*/*Renalia* from the Early Devonian of England, which yielded small (15-20 μm) spores assigned to *Apiculiretusispora* sp. Gensel (1980) mentions that the majority of the *in situ* spores from *Horneophyton lignieri* by Bhutta (1972), are trilete, apiculate and with curvaturate comparable to *Apiculiretusispora plicata* (ALLEN) STREEL (see additional comments on Edwards and Richardson, 1996). Wellman (2004) found *Emphanisporites decoratus* related to *Horneophyton lignieri* from the Rhynie chert plants of the Early Devonian. He also found *Apiculiretusispora plicata* from *Rhynia gwynne-vaughanii* while *Retusotriletes* species were recovered from *Aglaophyton*, *Asteroxylon*, *Nothia*, *Trichopherophyton* and *Ventarura* plants species. It is interesting to point out that trimerophytes have similar homosporous spores to those of rhynialeans but more consistently curvaturate assignable to *Retusotriletes* and *Apiculiretusispora* genera (see Gensel, 1980; Balme, 1995; Edwards and Richardson, 1996). This is the main reason why it is difficult to attribute a fructification to a major plant group on the basis of its spore content.

Danziella artesiana (DANZÉ-CORSIN) EDWARDS 2006 is another comparable plant bearing sporangia recorded from the Lower Devonian (Pragian–Emsian) of northern France. This genus and species, probably related to the zosterophylls, differ in having dichotomously branching with bivalved sporangia inserted on axis at c. 90° and arranged at irregular intervals on all sides of the fertile axis, which are subtended by long straight stalks. On the contrary, stems here described are more or less isotomous at angles from 20º to 55º and sporangia are distally inserted. The morphology of isolated sporangia is similar to the ones here presented in being spheroidal to reniform, 2 to 3 mm, somewhat laterally compressed and show a more or less continuous dark line around the distal margin (dehiscence zone). They differ in being composed by two equal valves and the border generally tapers towards the stalk. This feature is not clearly seen in our specimens (Fig. 6D). None vascular anatomy nor *in situ* spores are known from this species to make a more accurate comparison but their morphological differences support they are not co- specific taxa.

The Alarache's sporangia yielded trilete spore specimens assignable to the dispersed spore *Apiculiretusispora* sp. and some others, with exines chagrinate to laevigate and indistinct to distinct curvatures, are related to *Punctatisporites* or *Retusotriletes* genera, respectively. Nevertheless, the rarity of sporangia recorded in vegetative connection with stems and the lack evidence of anatomical features prevent a more specific designation.

PALYNOLOGY

Anteturma: Proximegerminantes POTONIÉ, 1970
Turma: Triletes REINSCH emend. DETTMANN, 1963
Suprasubturma: Acavatitriletes DETTMANN, 1963
Subturma: Azonotriletes LÜBER emend. DETTMANN, 1963
Infraturma: Retusotrileti STREEL, 1964

GENUS ***Retusotriletes*** NAUMOVA 1953 *emend.* STREEL, 1964

Type species: *Retusotriletes simplex* NAUMOVA, 1953

Retusotriletes albarinii n. sp.
Figures 7E, F, N; Figures 8S, T; Figures 9L, Q

2002 *Retusotriletes* sp. STEPHENSON and MITCHELL, p. 48, fig. 3(14).
1984 *Retusotriletes* cf. *avonensis* PLAYFORD in MCGREGOR, p. 34, pl. 1, fig. 16; pl. 5, fig. 4.
1984 *Retusotriletes warringtonii* RICHARDSON and LISTER 1969 in MCGREGOR 1984, p. 35, pl.1, fig. 28; pl. 5, fig. 24.

Holotype: Figure 8T, Figure 9Q, BAFC-Pl 1631 (SEM) P35.
Paratypes: Figures. 7E, F, N, Figure 8S, Figure 9L.

Diagnosis: Spores radial, trilete; amb subtriangular to quadrangular. Laesurae extended between three fifths and three quarters of the equatorial margin and are bounded by elevated straight to somewhat sinuous lips that vary from 2 to 5 μm in overall width. The equatorial region is variably thickened along the curvature somewhat resembling a cingulum, up to 7 μm in maximun width. Exoexine laevigate to chagrinate.

Dimensions (7 specimens): Equatorial diameter 35-80 μm.

Derivatio nominis: Dedicated to the geologist Luis Albariño.

Remarks: The thickened portion of the curvature is not a constant feature. It is frequently observed on one or two of the edges of the contact areas, so it is not a true equatorial crassitude.

Comparisons: *Ambitisporites warringtonii* (RICHARDSON and LISTER 1969) RICHARDSON et al. 2001 from the Late Silurian-Early Devonian of United Kingdom, differs from this species in having a more triangular amb, longer laesurae and minor diameter (22-32 μm). *Retusotriletes avonensis* PLAYFORD 1964, from the Early Carboniferous of Canada, is similar to this species but it is distinguished by the presence of a dettached intexine (“mesosporoid”), by its larger width, the more regular equatorial thickening and the infragranulate ornamentation. The distinction of both species from this new taxon supports the re-assignment of the specimens in the synonymy list.

Infraturma: Murornati POTONIÉ and KREMP, 1954

GENUS ***Acinosporites*** RICHARDSON, 1965

Type species: *Acinosporites acanthomammillatus* RICHARDSON, 1965

Acinosporites macgregorii n. sp.
Figure 7H; Figures 9H, M, N

Holotype: Figure 9M, BAFC-Pl 1631(2) O21/1.
Paratypes: Figure 7H; Figures. 9H, N.

Diagnosis: Spores, trilete; amb subtriangular to triangular, interradial margins straight, slightly convex, rounded vertices. Laesurae extended two quarters of the distance to the equatorial margin and it can be drawn by the ornamentation.The equatorial region can appear thicker along the margin due to the density of the ornaments. Exine’s thickness indistinct. Extended contact areas, which are well delimited at each vertex. The ornamentation on the distal face consists of fused elements forming rugulae of 1 μm in width to 4 μm in length maximum, which can be surmounted by spines or gemmae and some discrete elements, interspersed, as grana, spines and cones, 2-4 μm basal width to 2 μm of height.

Dimensions (13 specimens): Equatorial diameter 39(45)50 μm.

Derivatio nominis: Dedicated to the paleontologist Duncan McGregor.

Comparisons: *Acinosporites ledundae* OTTONE 1996 has rugulae composed by biform verrucae but along with other elements such as baculae, coni and capilli. *Dibolisporites* sp. in MCGREGOR 1984 (Upper Santa Rosa and Icla formations from Bolivia) has more discrete ornaments and the size range is larger than this species. *Verruciretusispora lobozi-akii* HIGGS, FINUCANE and TUNBRIDGE 2002 (pp. 145-148, pl. 1, figs. 1-5, 9, 11) from the Famennian of Turkey, differs from this species in having a smaller size range and the ornamentation consists mainly of discrete verrucae.

Infraturma: Apiculati (BENNIE and KIDSTON, 1886) POTONIÉ 1956

GENUS ***Dibolisporites*** RICHARDSON 1965 emend. PLAYFORD 1976

Type species: *Dibolisporites echinaceus* (EISENACK) RICHARDSON, 1965.

Dibolisporites sp.
Figure 8U; Figure 9Y

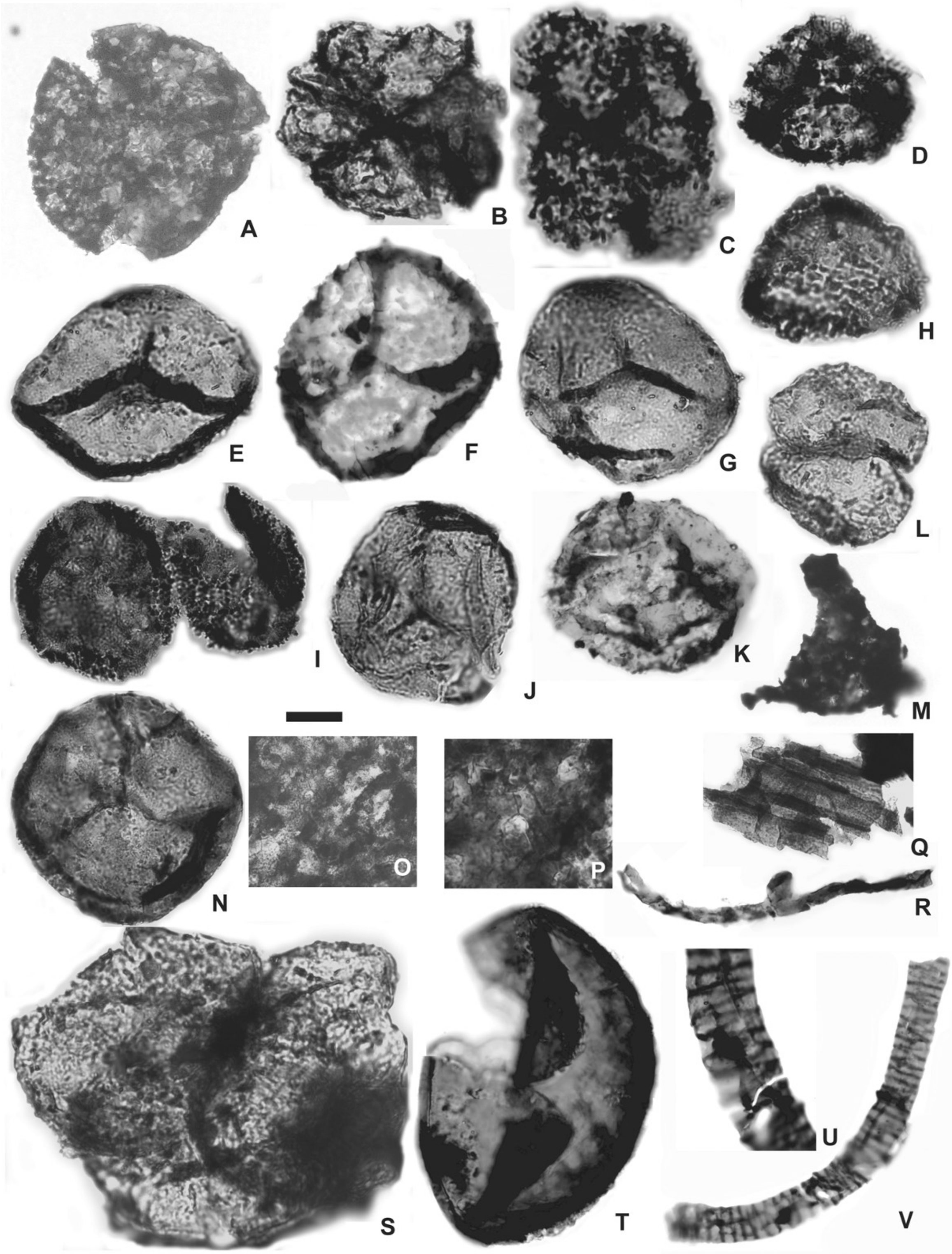

FIGURE 7 **A) Algae. BAFC-Pl: 1632(1) L41. B) *Quadrisporites variabilis* (Cramer) Ottone in Ottone and Rossello. BAFC-Pl: 16988(3) H47.C) *Quadrisporites granulatus* (Cramer) Ströther. BAFC-Pl: 16988(4) D24/2.D. *Dibolisporites* sp. cf. D) *wetteldorfensis* Lanninger. BAFC-Pl: 16989(4) F46. E) *Retusotriletes albarinii* n. sp. BAFC-Pl:16988(4) A50/3. F) *Retusotriletes albarinii* n. sp. Corroded specimen. BAFC-Pl: 16988(3) C57/4. G) *Punctatisporites* sp. BAFC-Pl: 16988(4) D37/1. H) *Acinosporites mcgregorii* n. sp. BAFC-Pl: 16988(3) F44. I) *Acinosporites* sp. BAFC-Pl: 16988(3) J54. J) *Apiculiretusispora* sp. BAFC-Pl: 16989(4) M55. K) ?*Chelinohilates* sp. BAFC-Pl: 16989(3) E35/1. L) *Dyadospora* sp. BAFC-Pl: 16988(3) E45/2. M) *Acyrochitina ancyrea* Eisenack. BAFC-Pl: 1632(1) W56/2. N) *Retusotriletes albarinii* n. sp. BAFC-Pl: 16989(3) V32/2. O) Dispersed cuticle. BAFC-Pl: 16988(1) X45. P) Detail of pore. BAFC-Pl:16988(1) X 45. Q) Possible outer cortical tissue or collenchyma. BAFC-Pl: 16989(4) W 50. R) Fungal hyphae. BAFC-Pl: 16989(3) U25/2. S) Tetrad BAFC-Pl: 16988(3) K46/1. T) *Hemiruptia legaultii* Ottone. BAFC-Pl: 16988(4) C25/1. U) Detail of V. BAFC Pl: 16989(3) C32. V) Helical to annular tube. BAFC-Pl: 16989(3) C32. Scale bar: B-L, N-P, R: 15 µm; A, M, Q, S, U: 20 µm; T: 40 µm.**

Description: Trilete spores, amb subtriangular, apices rounded. Trilete mark indistinct. Distal face ornamented with stout baculae and spinae with rounded endings (3-8 μm in height and 1-2 μm in width), supported by a broad base (3-6 μm). Appendages closely set so the bases are frequently connected.

Dimensions (4 specimens): Equatorial diameter 70-85 μm.

Comparisons: This species is very similar to *Dibolisporites*? *nodosus* TURNAU 1986 but differs in bearing stout baculae and spinae surmounted on a wider base than the latter.

COMPOSITION OF THE ASSEMBLAGES AND TAPHONOMIC FEATURES

Mega and mesofossils

Two large blocks (BAFC-Pb 16988 and 16989, Figs. 4A, 5 and 6), composed of gray pelite to very fine-grained sandstone, contain abundant concentrations of plant debris on successive bedding planes levels with a micaceous matrix. The assemblage shows low diversity (three species) and comprises mainly simple sterile stems variably abundant (Figs. 5A, E) and of varied length (*Hostinella* sp. and indeterminate species). Some smooth specimens are dichotomously branched (*Hostinella* sp.). Another specimen illustrated in Fig. 5F, resembling *Protosalvinia ravena*? WHITE and STADNICHENKO (see Taylor and Taylor, 1993), is indeterminate. Few small (around 1 mm) spheroidal black and perforated specimens were recovered when sporangia material was prepared for SEM study under the stereoscope. The celular reticulum of one specimen is illustrated (Figs. 8I, J, L). Many phytodebris were recovered from maceration of some rock samples with abundant stems and sporangia (see Figs. 7 and 8). Neither pyrite nor iron oxides are present on the fossils or dispersed on the rocks.

Palynology

Assemblage 1

The maceration of samples bearing plant remains and isolated sporangia (BAFC-Pb 16988, 16989, BAFC-Pl 1632) yielded around 80% of phytodebris and low diversity palynomorphs (Figs. 4C, E). Trilete spores are dominant (85%) and the rest are mostly cryptospores (dyads or simple spores with indistinct mark, 14%) and poorly preserved chitinozoans. The spores are assigned to *Punctatisporites* spp., *Retusotriletes albarinii*, *Retusotriletes* spp., *Apiculiretusispora* sp., *Acinosporites* sp., *A. mcgregorii*, *Dibolisporites* sp. Other elements are the cryptospores ?*Chelinohilates* sp., *Dyadospora* sp., the prasynophytes *Hemiruptia legaultii* OTTONE, *Quadrisporites variabilis* (CRAMER) OTTONE in OTTONE and ROSSELLO, *Quadrisporites granulatus* (CRAMER) STRÖTHER, together with fungal hyphae and other phytodebris (see Figs. 7, 8 and 9). Of particular importance is the recovering of *in situ* trilete spores (Figs. 8E, F) from the three sporangia isolated from the rocks.

Assemblage 2

The upper pelitic layer bearing fragmentary plant debris yielded a more diverse spore assemblage (BAFC-Pl 1631) and comprises abundant phytodebris (70%) and palynomorphs (Figs. 4D, F). Among the trilete spores, which are dominant, most of the species are assignable to *Punctatisporites* and *Retusotriletes* genera, *Ambitisporites avitus/dilutus* morphon STEEMANS ET AL. and *Apiculiretusispora plicata* (ALLEN) STREEL. The rest are less frequent and include *Dictyotriletes emsiensis* (ALLEN) MCGREGOR, *retusotriletes maculatus* MCGREGOR and CAMFIELD, *emphanisporites rotatus* MCGREGOR, ?*retusotriletes paraguayensis* MENÉNDEZ and PÖTHE DE BALDIS, *Retusotriletes albarinii*, *Acinosporites mcgregorii*, *Dibolisporites* sp. cf. *D. wetteldorfensis* LANNINGER, and *Dibolisporites* sp. (see Figs. 8P, S-U and 9). The cryptospore group is composed of tetrads and dyads. Some scattered single forms without visible trilete mark can be attributed to sphaeromorphs like ?*Leiosphaeridia* (Figs. 8V, 9E, I, T). There are also abundant cuticular debris displaying perforations resembling simple stomata (Figs. 9V, W), fungal hyphae (Fig. 9U) and some tracheid-like sheets.

DISCUSSION AND CONCLUDING REMARKS

Botanical affinities

Many morphological, anatomical and geochemical studies have improved the knowledge on the differences between vascular and non-vascular plants in primitive or earlier records. Kenrick (in Edwards, 2000) highlighted the absence of branching in the development of modern liverworts, hornworts and moss sporophytes and that the same evidence can be applied to earlier records. Stomata on cuticles of stems and sporangia (Edwards et al., 1986), and tracheids related to the lignification of the walls (Niklas and Smocovitis, 1983) are two important anatomical features that are used to distinguish among early vascular plant and non-vascular groups. The latter feature is exclusive from tracheophytes while the former is not exclusive of this group. In bryophytes there are quite simple structures like pores (see Edwards et al., 1986).

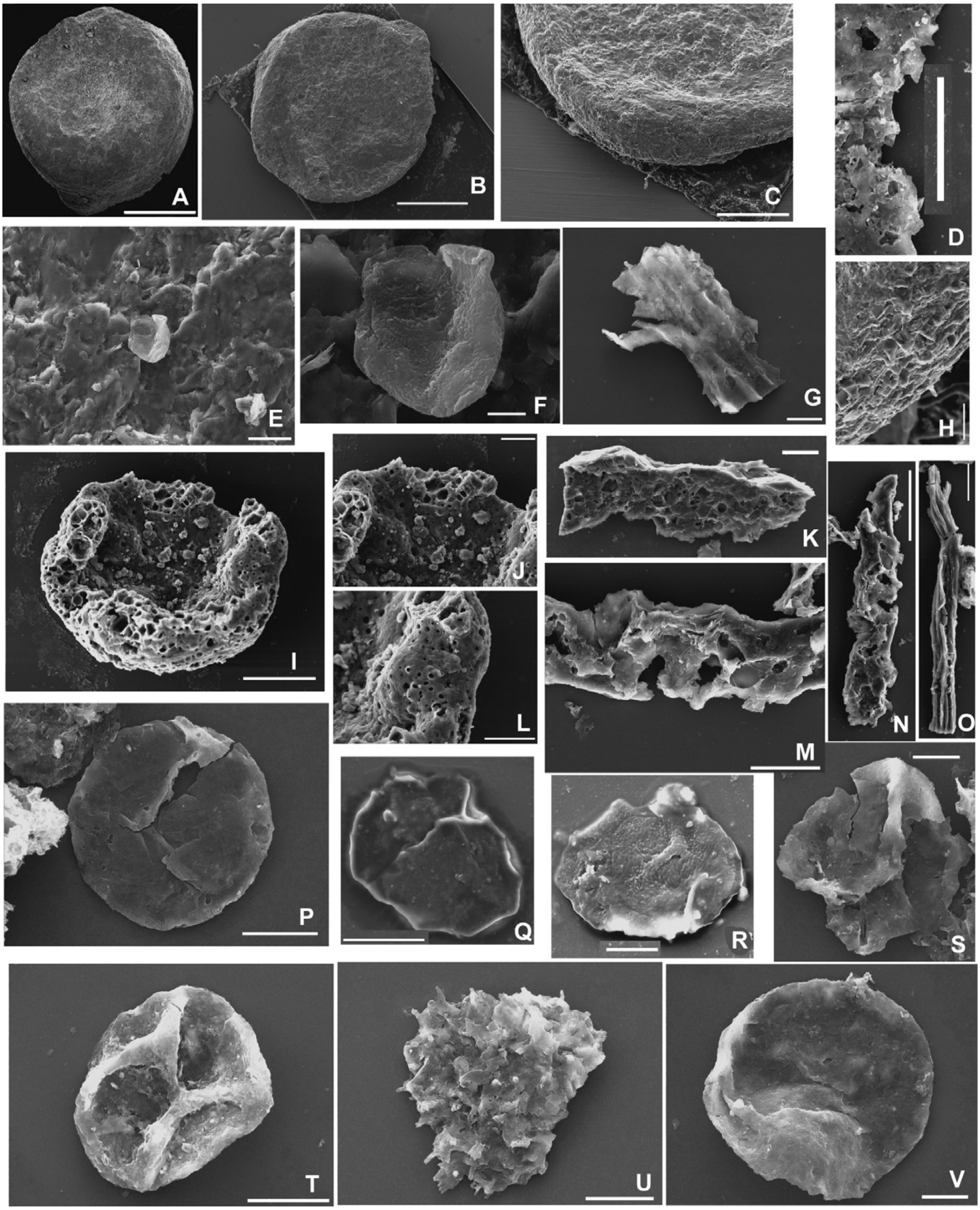

FIGURE 8 **A) External view of sporangium (scale: 1,000 μm). B) Internal view of sporangium (scale: 1000 μm). C) Sporangium margin (scale: 250 μm). D) Fragment of tissue from a sporangium with detail of pore (or holes?) (scale: 50 μm). E) Spore *in situ* (scale: 20 μm) on the inside part of the sporangium. F) Detail of distal face of *in situ* spore (scale: 5 μm) (?*Apiculiretusispora* sp.). G) Epidermal cells presumably from the stems (scale: 20 μm). H) Detail of the sporangium wall (scale: 50 μm). I) Curious phytodebris (scale: 50 μm). J) Detail of I (scale: 20 μm). K) Transverse section of phytodebris (scale: 20 μm). L) Idem J (scale: 2 μm). M) Detail of N (scale: 2 μm). N) Phytodebris (scale: 50 μm). O) Elongated cells probably from the sterome of stems. P) *Punctatisporites* sp. (scale: 20 μm). Q) ?*Punctatisporites* sp. (scale: 20 μm). R) ?*Apiculiretusispora* sp. (scale: 10 μm). S. *Retusotriletes albarinii* n. sp. (scale: 15 μm). T) *Retusotriletes albarinii* n. sp. (scale: 20 μm). U. *Dibolisporites* sp. (scale: 25 μm). V) Cryptospore (scale: 10 μm).**

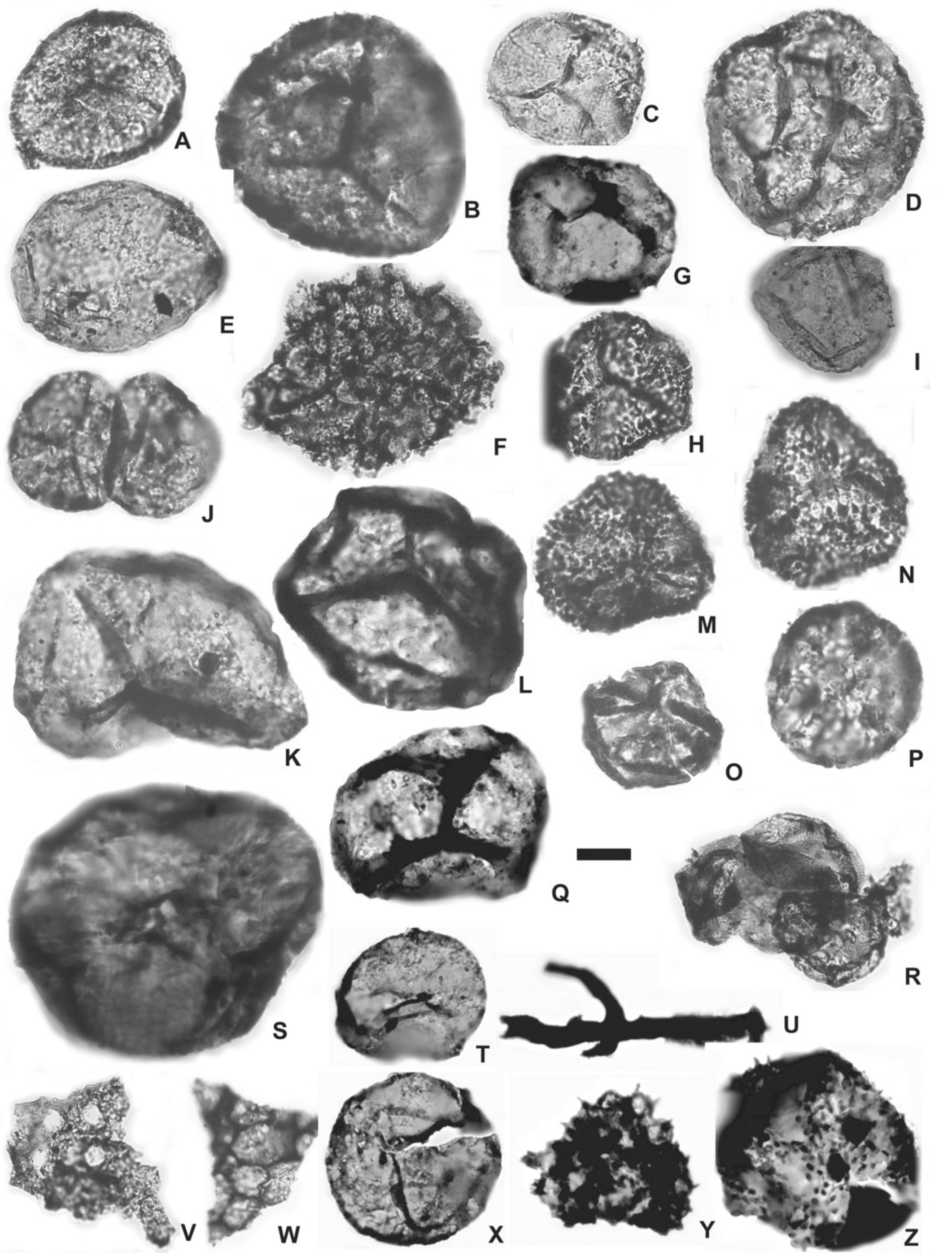

FIGURE 9 **A)** ***Ambitisporites avitus/dilutus*** **morphon** Steemans. **Corroded specimen. BAFC-Pl: 1631 (1) P42. B)** ***Ambitisporites avitus/dilutus*** **morphon** Steemans. **Corroded specimen. BAFC-Pl: 1631(2) P47/2. C)** ***Apiculiretusispora plicata*****. BAFC-Pl: 1631(1) M37. D)** ***Apiculiretusipora*** **sp. BAFC-Pl: 1631(1) O50/2. E) ?Cryptospore. BAFC-Pl: 1631(1) P46/4. F)** ***Dictyotriletes emsiensis*** **morphon** rubinstein **et al. BAFC-Pl: 1631(1) H34. G)** ***Apiculiretusispora*** **sp. BAFC-Pl: 1631(meb) N37/1. H)** ***Acinosporites mcgregorii*** **n. sp. BAFC-Pl: 1631(1) F25/3. I)** ***?Leiosphaeridia.*** **BAFC-Pl: 1631(1) F51/3. J) Dyad (the specimen on the left show a false trilete). BAFC-Pl: 1631(2) S44. K)** ***Retusotriletes*** **sp. BAFC-Pl: 1631(2) K39/1. L)** ***Retusotriletes albarinii*** **n. sp. BAFC-Pl: 1631(3) R21. M)** ***Acinosporites mcgregorii*** **n. sp. BAFC-Pl: 1631(2) O21/1. N)** ***Acinosporites mcgregorii*** **n. sp. BAFC-Pl: 1631(2) A22. O)** ***Emphanisporites rotatus*** McGregor**. BAFC-Pl: 1631(1) Y44/4. P)** ***Retusotriletes maculatus*** mcgregor **and** camfield**. BAFC-Pl:1631(2) P43/1. Q)** ***Retusotriletes albarinii*** **n. sp. Same specimen illustrated in Figure 8T. BAFC-Pl: 1631(meb) P35. R) Tetrad BAFC-Pl: 1631(1) A32/4. S)** ***?Retusotriletes paraguayensis*** menéndez **and** pöthe de baldis**. BAFC-Pl: 1631(3) B21. T) ?Cryptospore. Same specimen illustrated in Figure 8V. BAFC-Pl: 1631(meb) L37/3. U) Fungal hyphae. BAFC Pl: 1631(meb) M42/2. V) Cuticle debris. BAFC-Pl: 1631(1) X29. W) Cuticle debris. BAFC-Pl: 1631(1) X50/2. X)** ***Punctatisporites*** **sp. Same specimen illustrated in Figure 8P. BAFC-Pl: 1631(meb) M40/1. Y)** ***Dibolisporites*** **sp. Same specimen illustrated in Figure 8U. BAFC-Pl: 1631(meb) L40/3. Z)** ***Dibolisporites*** **sp. cf.** ***D. wetteldorfensis*** lanninger**. BAFC-Pl: 1631(meb) P38. Scale bar: A-I, K-Q, S, T, Z: 15 µm; J, R, U-Y: 20 µm.**

Edwards (1996) points out that even if low stomatal frequencies are found on the Late Silurian and Early Devonian examples, the number increased when next to the sporangia and on the sporangia themselves. Stomata were investigated on cuticles of two isolated sporangia but only poorly preserved and doubtful structures were observed (Fig. 8D). Several tracheid-like and other sterome structures (Figs. 8K, M, O) were recovered (BAFC-Pb 16988 and 16989) and resemble to the phytodebris illustrated from Silurian and Devonian rocks (e.g., Edwards, 1970; Banks, 1975; Niklas and Smocovitis, 1983; Kenrick et al., 1991; Wellman and Richardson, 1993; Taylor and Taylor, 1993; Wellman and Gray, 2000) with affinity to vascular and nonvascular plants. Wellman and Richardson (1993) have illustrated several cuticle sheets and tubular structures from the Silurian of Scotland that are comparable to the ones recovered here, such as cuticle sheets with simple pores (or holes?, Fig. 8D). Others, such as the specimen illustrated in Figs. 7Q and 8O, are comparable to the specimens of presumed conducting tissues illustrated by Edwards (2000, figs. 6, e, f) where epidermal cells with elongated and evenly spaced cells are preserved. They were related to bryophytes in both articles. Moreover, tubes with anular rings very similar to the ones in Figs. 7U, V were related to Nematophytes by Banks (1975) and Wellman and Richardson (1993). On the other hand. that large forms (more than 70 μm in diameter) assigned to ?*Leiosphaeridia* and *Retusotriletes* genera, are related to *Nematothallus* and *Protosalvinia* nonvascular plants (see Balme, 1995). Regarding the *in situ* spores, genera such as *Ambitisporites*, *Streelispora*, *Synorisporites*, *Aneurospora*, *Retusotriletes* and *Apiculiretusispora* are yielded from different species of Rhyniophytoids sporangia. All of them are homosporous with a spore diametre around 22 to 80 μm, and are more likely related to tracheophytes (see Edwards and Richardson, 1996).

In summary, the rarity of sporangia recorded in vegetative connection with stems and the lack or doubtful evidence of anatomical features prevent a more specific designation for sporangia. Nevertheless, the presence of trilete spores assigned to the genus *Apiculiretusispora*, in the organic residue recovered from its maceration and the presence of at least some dichotomously branched stems allow us to propose a tracheophyte affinity for them. More detailed studies or new discoveries are needed to establish a more accurate plant affinity. Besides, some other palynomorphs and phytoclasts recorded in both palynoassemblages suggest the presence of Bryophytes as part of the plant assemblages.

Age and comparison of the assemblages

Edwards et al. (2001a) describe a diverse plant assemblage from the Kirusillas Fm (late Siluran) in the Tarija region (see Fig. 1A), that appears to be partially similar to the Alarache's assemblage, at least in the common appearance of globose structures that they attributed to *Cooksonia* cf. *caledonica* and *Cooksonia hemispherica*. Nevertheless, the absence of *in situ* and dispersed spores in the quoted assemblages prevents us to give a more precise comparison. Limachi et al. (1996) proposed the *Cooksonia* sp. Zone spanning the Ludlow and Pridoli (see Fig. 3) mainly based on this record, and suggested a correlation with the *Sanjuanetes chaparensis* and *Clarkeia antisiensis* Zones, based on invertebrate fossils from the Kirusillas and Tarabuco formations from several localities of Bolivia including the Alarache section (see Figs. 1 and 2A). Instead, our assemblages come from the Santa Rosa Fm and their differences in composition confirm they are not correlable. Other plant assemblages attributed to the Lochkovian-Pragian are described from Mendoza, Argentina Precordillera range (Edwards et al., 2001b; Morel et al., 2006) and Paraná Basin, Brazil (Gerrienne et al., 2001) (see Fig. 1A), which only share stems attributed to *Hostinella*. So, it is not enough to support any correlation.

Melo and Loboziak (2003) has defined in the Amazon Basin (Brazil, see Fig. 1A) the *Dictyotriletes emsiensis* Interval Zone (Ems) based on the appearance of this taxon and attributed to the latest Lochkovian through Pragian, possibly attaining the early Emsian (Early Devonian). Therefore, *Dictyotriletes emsiensis* occurring in our association 2 supports the correlation at least with the lower part of the *Emsiensis* Zone (Melo and Loboziak, 2003; Melo, 2005a; see Fig. 3). Rubinstein et al. (2005) have documented an assemblage from a borehole of the Solimôes basin (Brazil, see Fig. 1A) where greatly diversified, poorly to regularly preserved miospores led to propose the *Dictyotriletes* morphon and its occurrence conforms a zonal range extending from the MN and BZ Zones (see Fig. 3). They propose a correlation with the Z Phylozone of the BZ Oppel Zone after Steemans (1989) due to the presence of *Urochitina loboi* VOLKHEIMER ET AL. Few species are common with Alarache's assemblages: *Dictyotriletes emsiensis*, *Retusotriletes maculatus*, *Emphanisporites rotatus*, *Ambitisporites avitus/dilutus*. Nevertheless, the absence of *Urochitina loboi* and *Verrucosisporites polygonalis* LANNINGER among other species in our assemblages prevents its correlation. In addition, dispersed and *in situ* spores from the Rhynie chert plants correlative to the *Verrucosisporites polygonalis-Dictyotriletes emsiensis* (PE) Zone (Wellman, 2004), is dated by radiometric techniques indicating a Pragian (Early Devonian) age (Rice et al. in Wellman, 2004). This assemblage shares *Apiculiretusispora plicata* and *Dictyotriletes subgranifer* (= *D. emsiensis* morphon RUBINSTEIN ET AL., 2005) with our assemblage 2. Instead, Rhynie chert assemblage contains *Verrucosisporites polygonalis* that appears later in the Z Phylozone from the BZ Oppel Zone of the latest Lochkovian in the Western Europe (see Steemans, 1989), *Emphanisporites decoratus* ALLEN and *Camptozonotriletes caperatus* MCGREGOR that are absent in ours supporting an older age for the latter (see Fig. 3). Other palynological assemblage from the Lochkovian Santa Rosa Fm is described by McGregor (1984) at Tarabuco (Bolivia, see Fig. 1A). Common species are *Apiculiretusispora plicata*, *Retusotriletes* cf. *avonensis* (= *R. albarinii* n. sp.), and *Retusotriletes maculatus* (see Fig. 3). Lobo Boneta (1989) characterizes the Santa Rosa Fm base by the *Leiofusa bernesgae* zone and the upper part is the *Dictyotriletes* sp. Zone. Following Limachi et al. (1996) Bolivian biostratigraphy, assemblage 2 could be correlated to *Dictyotriletes – Schizocystia saharica/pilosa* Biozone (see Fig. 3), based on common species such as *Dictyotriletes subgranifer*, *D. emsiensis*, *Apiculiretusispora plicata*, *Retusotriletes maculatus* but acritarchs and chitinozoans mentioned as well, are not present in our assemblages. This biozone is attributed to the Lochkovian *s.l.* and identified in Tequeje and Vila Vila formations in northern Bolivia (e.g., Vavrdová et al.,1996) and upper Santa Rosa and Icla formations in its southern part (see Fig. 2A). Melo (2005b) informs the occurrences of scarce and poorly preserved miospores from the Santa Rosa Fm at the same locality, and suggests a Late Lochkovian age based on the determination of *Dictyotriletes emsiensis*.

Concerning the chitinozoans, scarce and fragmentary specimens are found in assemblage 1 and are assigned to *Ancyrochitina ancyrea* Eisenack (Fig. 7M). It is a cosmopolitan species ranging from the Silurian to Givetian (e.g. Grahn, 1998), but characteristic of the late Ludlow from Brazil, Bolivia and Peru basins (see Figs. 1A and 3; Grahn et al., 2000; Grahn, 2002). Limachi et al. (1996) proposed the *Urochitina loboi/Sphaerochitina densibaculata* Zone of ?Late Silurian – Lochkovian age, that was recognized in the subsurface of northern Argentina and Tequeje, Tarabuco and Santa Rosa formations from Bolivia (see Grahn, 2002). This zone was recorded in the Talacasto Fm (Le Hérissé et al., 1996) from Precordillera Argentina (see Figs. 1A and 2A) akin to the upper Lochkovian based on the index species *Urochitina loboi* and *Schizocystia pilosa* JARDINÉ et al. (see Fig. 3), which are not present in the Alarache's assemblages. Instead, common species of both assemblages are *Dictyotriletes emsiensis*, *Emphanisporites rotatus*, and *Retusotriletes maculatus*. Finally, Grahn (2005) presents a new biozonation scheme for western Gondwana. He establishes a correlation between previous chitinozoan and miospores biozones mainly from Brazil (Melo and Loboziak, 2003; Rubinstein et al., 2005) and Western European miospore zonation (Streel et al., 1987; Steemans, 1989). He restricts the age of the *Urochitina loboi* Zone to the latest Lochkovian, and proposes its correlation to the Z Zone of the BZ Zone from the latter zonation and partially to the Ems Zone of Solimôes and Paraná basins (see Fig. 3).

In conclusion and, considering all the data gathered above, the age of the assemblage 2 here described is attributed to the Lochkovian on the basis of the appearance of *Dictyotriletes emsiensis* and the presence of *Apiculiretusispora plicata*, *Retusotriletes* cf. *avonensis* (= *R. albarinii* n. sp.) and *Retusotriletes maculatus*. Additionally, the absence in the Alarache's assemblages of other key species such as *Urochitina loboi* would restrict its age up to the Late not latest Lochkovian (see Fig. 3). Both evidences support its correlation with the lower part of the Ems Zone of the Amazon Basin and the MN Zone of the Western Europe. Thus, the plant and palynoassemblage 1 three meters below the palynoassemblage 2 are also akin to the same lapse.

Palaeoenvironmental inferences

Souza Cruz et al. (2001) interpret the whole Santa Rosa Fm cropping out from North of Argentina to South of Bolivia, as fluvial braided and braid delta systems with shallow marine incursions. Instead, Albariño et al. (2002) describe for the same region the beginning of an important marine transgression developed in a general siliciclastic wave-dominated ramp model since the Lochkovian. In this trangressive event, represented by shoreface facies that end with shallower platform, marginal or transitional facies, the Alarache section corresponds to a marginal palaeoenvironment close to the basin's border (see Fig. 1A). The abundance of fragmented stems of varied size parallel to bedding planes, especially on the BAFC-Pb 16988, along with the isolated sporangia, suggests that they were transported for a short distance but under low energy conditions, probably from marginal palaeoenvironments to low energy marine settings. Other components, likely terrestrial in origin were recorded in the assemblage 1, such as cryptospores, indeterminate forms and tubes of *Nemathothallus* and fungi hyphae, support the interpretation of a landscape where probably both bryophytes and early vascular land plants grew, as small shrubs constrained to wetter parts in plains along the rivers. These areas would have became flooded periodically by marine or mixed waters due to the presence, at least in the assemblage 1, of aquatic to marine *Quadrisporites* and *?Leiosphaeridia* species (acritarchs) and scarce chitinozoans. Low energy currents could have produced the dettachment of the sporangia from their stalks but prevented removing them from the same depocentre. The palynomorphs would have been present in the shallow column of water and they could have settled in the same sediments as well. The frequent mode of preservation of the sporangia in pairs, somewhat closely set, observed in our material (see Fig. 6K, L), could be related to their isotomous dichotomy arrangement of the fertile stems.

All these evidences added to the absence of rooting systems allow to interpret the plant deposits as para-autochtonous to allochthonous that were transported for a short distance but under low energy conditions mainly associated to decantation process under very low energy currents in shallow ponds (e.g., flooded alluvial plains or protected bays). These marginal to low energy marine palaeoenvironments are coherent with Starck (1996) and Álvarez et al. (2003)'s interpretation for the region embracing our outcrop (see Fig. 1).

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