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A new highly diverse palynoflora from the Lower Devonian Nogueras Formation of the Iberian Peninsula

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ABSTRACT
A new well-preserved spore assemblage has been discovered from the Lower Devonian Nogueras Formation of Mezquita de Loscos (Teruel Province, north-eastern Spain). The palynoflora includes 34 spore species belonging to 20 genera, among which 14 are new for the locality, e.g. *Apiculretisispora*, *Brochotrites*, *Cirratiradites*, *Iberoespora*, *Knoxisporites* and *Verrucosisporites*. The assemblage is mainly composed of trilete spores, while triapillate and monolete forms are also observed. An early Pragian age is suggested for the fossil site. Specimens of *Latosporites ovalis*, a species previously well-documented only from the late Pragian–Emsian of Saudi Arabia and Brazil, are found in this assemblage and represent to date the earliest known occurrence of this species. Besides the description of the palynoflora, we also provide here a synthesis of the plant-bearing localities of the study area.

1. Introduction
The Early Devonian flora of Mezquita de Loscos (Teruel Province, eastern Iberian Chains, Figure 1) probably represents the most diverse plant megafossil and dispersed spore assemblages of Iberian Peninsula of that age. During the last years, several fossil sites have been discovered in this area (Figure 2(a)). A wide variety of plant morphologies have been recently reported including, among others, a branching system interpreted as belonging to a basal euphyllophyte, diverse dichotomous branching remains, a set of globular structures and flattened stems, various remains of *Taeniocrada*-like stems, a dichotomous branching assigned to the genus *Hostinella*, as well as a genus-level diversity of spores as follows: *Ambitisporites*, *Amicosporites*, *Aneurospora*, *Brochotrites*, *Chelinospora*, *Cymbosporites*, *Dibolisporites*, *Emphanisporites*, *Gneudnaspora*, *Retusotriletes* and *Scylaspora* (see Cascales-Miñana et al. 2011, 2015).

To date, all plant-bearing sites discovered from the Mezquita de Loscos locality belong to the Nogueras Formation (Figure 2(b)). Overall, the Nogueras Formation consists of a series of shallow-water marine deposits with bioclastic limestones, marls and shales; it has been attributed a Lochkovian–Pragian age (Figure 2(b), see also Carls and Valenzuela-Ríos 1999). During more than 30 years, a wide range of palaeontological studies have focused on the Nogueras Formation (e.g. Liñán et al. 1983), from which various fossil animal groups have been discovered, such as fish microremains (e.g. Botella and Valenzuela-Ríos 2002; Carls and Valenzuela-Ríos 2002; Botella et al. 2006, 2012), brachiopods (e.g. Carls et al. 1993; Schemm-Gregory 2011), conodonts (e.g. Carls 1999; Carls and Valenzuela-Ríos 2002) and ostracods (e.g. Dojen 2005).

Because the Nogueras Formation represents mainly a deltaic-marine environment, the plant macroremains collected so far are poorly preserved and fragmentary. The shale beds of Nogueras Formation have nevertheless yielded a diverse and well-preserved palynoflora, as shown in a previous study (i.e. Cascales-Miñana et al. 2015). Intensive search in nearby strata have yielded new records of plant remains. In this contribution, new insights into the spore diversity of the Lower Devonian Nogueras Formation at Mezquita de Loscos are presented. The palaeogeographic implications of spore diversity as well as its morphological affinities are discussed.

2. Stratigraphical setting
The Nogueras Formation is exposed in the area known as the Axial Depression of the Càmaras River (ADCR, see Carls 1983; Carls and Valenzuela-Ríos 1999, 2002; Gámez Vintaned et al. 2005, and references therein) located between the Zaragoza and Teruel provinces (north-eastern Iberian Peninsula, Figure 1). The new fossil
site, referred herein as Loscos 4 (LC4, lat. 41° 4’ 00.69” N, long. 1° 4’ 52.36” W), is located within this formation at the section known as South of Barranco Santo Domingo, which exposes Lochkovian and Pragian strata (see Dojen 2005, and references therein). A short part of the section is shown in Figure 3. This short section (i.e. Figure 3(b)) starts with a 47-cm-thick bed of sandstone (Bed 50), which overlies a cliff on the right bank of the creek composed of an alternation of sandstone and shale. Upwardly, the lithology is composed of an alternation of clay and thinly bedded sandstone. Most rocks in these beds contain mica except for the uppermost 25 cm of clay (Bed 57), which lay directly below an interval covered by vegetation. Sediments are predominantly grey in colour. The succession ends with a thick packet of limestone (110 cm) composed of four major beds (Bed 58). The fossils come from clay beds, within a 40 cm interval, 180–183 cm above the top of Bed 50, the thick basal sandstone (Figure 3(b)).
Assigning this short section to the units described by Dojen (2005) for the Nogueras Formation is not easy. In Dojen’s synthetic stratigraphic column (Figure 3(a)), relatively thick successions of comparable alternation of sandstone and clay are assigned to units $d_2b^{\beta}_1$ and $d_2b^{\beta}_2$, in the earliest Pragian and just above the guide Bed A with the brachiopod *Vandercammenina sollei*. The guide Bed A is topped by a 1-m-thick limestone packet (lower parts of unit $d_2c^{\alpha}_1$), which could be correlated with the thick limestone packet (Bed 58) of Loscos 4. Below this limestone, there are marl and thin limestone beds that could be equivalents of the covered interval (Bed 57) at Loscos 4. Downwardly, the clay and sandy intercalation containing the present fossils at Loscos 4 is also comparable to the sequence of Dojen (2005), although their respective thicknesses are different: 3.02 m at Loscos 4 and 1.6 m in Dojen’s synthetic column. We therefore think that Loscos 4 belongs to the $d_2b^{\beta}_2$ unit of Dojen (2005) and the covered part plus the limestone packet to its $d_2c^{\alpha}_1$ unit (Figure 3(a)).

### 3. Material and methods

Four samples (LC4-a, LC4-b, LC4-c, LC4-d) were recently collected for palynological studies from an outcrop exposing the Nogueras Formation close to the Mezquita de Loscos locality (Figures 1 and 3(b)). The samples were processed in the laboratory of Palaeobiogeology–Palaeobotany–Palaeopalynology of the University of Liège using standard palynological HCl-HF-HCl acid maceration techniques (see e.g. Steemans et al. 2009, and references therein for details). Each sample was crushed, and around 30 g was demineralised in HCl-HF: The residue was briefly oxidised in HNO$_3$ and KCIO$_3$ and sieved through a 12-μm mesh. A hot bath in 25% HCl eliminated the remaining fine mineral particles. All samples were rinsed through a 12-μm mesh. After processing, first results showed the presence of palynomorphs in all samples. However, only two of them (i.e. LC4-a and LC4-b) contain a truly rich assemblage of miospores and very rare acritarchs (Figure 3(b)). Overall, specimens are moderately preserved, brown to dark brown in colour. Acritarchs have not been studied and it could not be determined if they are *in situ*. Despite that incertitude, the assemblage is clearly strongly influenced by continental input.

Complementarily, a sample for a conodont study was also collected (LC4-e, Figure 3(b)). This sample was processed using also standard techniques (see e.g. Valenzuela-Rios 1994, and references therein for details) in the laboratory of the Department of Geology of the University of Valencia. No conodonts on the sampled level were found.

### 4. Results and discussion

Within the examined samples, the most abundant taxa are as follows (in alphabetical order): *Acinosporites* spp. (Figure 4(a)),
Ambitisporites avitus/dilutus Morphon in Steemans et al. (1996),
Ambitisporites eslae Richardson et al. 2001, Amicosporites sp.,
Aneurospora cf. A. bollandensis in Breuer and Steemans (2013),
Aneurospora spp. (Figure 4(b)), Apiculiretusispora plicata Steeel 1967 (Figure 4(c)),
Archaeozonotritetes chilus/lanus Morphon in Steemans et al. (1996),
Brochotriletes foveolatus Naumova 1953 (Figure 4(d)),
Brochotriletes sp., Chelinospora favosa Steemans 1989, Chelinospora cf. C. baculoreticulata Steemans 1989,
Cirratriradites diaphanus Steemans 1989 (Figure 4(e)),
Coronaspora cf. C. inornata in Breuer and Steemans (2013),
Coronaspora sp. (Figure 4(f)), Cymbohilates baqaensis Breuer et al. 2007 (Figure 4(g)),
Cymbosporites cf. C. proteus McGregor...
The spore assemblage demonstrated here is dominated by taxa of the late Pridoli, Lochkovian and early Pragian age, such as the triplariform forms *Ambitisporites eslæ*, *Retusotriletes maculatus*, *Cirratriradites diaphanus* and *Ibereospora guzmæni* (see e.g. Richardson and McGregor 1986; Rodriguez 1978, 1983; Steemans 1989; Richardson et al. 2001). The earliest record of *Cirratriradites diaphanus* is from the lower part of the Lochkovian (not the lowest part, see Steemans 1989). *Emphanisporites zavallatus* var. *gedinniensis* is only known from the late Lochkovian and early Pragian (Steemans and Gerrienne 1984; Streel et al. 1987; Steemans 1989). *Verrucosisporites polygonalis* is known to appear just above the Lochkovian–Pragian boundary in many places on Baltica and Gondwana, such as northern Saudi Arabia (Richardson and McGregor 1986; Streel et al., 1987; Steemans 1989; Breuer et al. 2005). Other taxa, namely *Aneurospora* cf. *A. bollandensis*, *Coronaspora inornata*, *Latosporites ovalis* and *Zonotriletes brevivelatus*, are known to appear in the mid-late Pragian or in the Emsian from Saudi Arabia (Breuer and Steemans 2013). The first appearance of the latter three is unclear. However, in Saudi Arabia where they were described, their age does not reach the middle Pragian (Breuer et al. 2007; Breuer and Steemans 2013). Evidence as a whole suggests an early Pragian age for this new fossil site mainly because the concurrent stratigraphic distribution of *Emphanisporites zavallatus* var. *gedinniensis* (index species of Oppel zone BZ, Steemans 1989, p. 178) and *Verrucosisporites polygonalis* (index species of Oppel zone PoW, Steemans 1989, p. 182) (see Figure 4). An early Pragian age is, in addition, consistent with the stratigraphic position of the sampled levels (Figure 3(a)) and with the evidence supplied by the presence of some marine invertebrates as e.g. *Vandercammenina sollei* which marks the beginning of the Pragian in Rhenish facies (Dojen 2005, see also Carls 1987 and Carls and Valenzuela–Ríos 1999 for further discussion), below sampled levels. Furthermore, the first known *Plicostropheodonta* is found at unit d2c3 (Figure 3), which is early Pragian in age, and is located above the levels studied here. So, the lowest occurrences of these two taxa bracket the age of our findings and limit it to early Pragian, which is consistent with the spore association (Figure 5).

The specimens of *Coronaspora* and of *Zonotriletes* reported from this study have been left in open nomenclature because they are poorly preserved, but some are quite similar to *Coronaspora inornata* and *Zonotriletes brevivelatus* and are tentatively referred to the latter species. If confirmed, the presence of *Coronaspora inornata* and *Zonotriletes brevivelatus* in the early Pragian assemblage of Loscos 4 would represent the earliest occurrence of both species. Of special interest in this study is the presence of several specimens of *Latosporites ovalis*. This monolette species has previously been reported only from the Gondwana plate, in Saudi Arabia (Breuer and Steemans 2013) and in Brazil (Grahn et al. 2013), where its age ranges from the late Pragian to the Emsian. There is also a possible report of this species from Euramerica (Wellman 2006). The Loscos specimens of *Latosporites ovalis* are hence to date the earliest representatives of the species. It should be noted that older occurrences of monolette spores exist as specimens of the monolette genus *Devonomonoletes* have recently been found in the Pridoli of Saudi Arabia (Pierre Breuer pers. comm.). The joint presence at the locality of the late Silurian/early Pragian and the late Pragian/Emsian species could be interpreted as indicating that the late Silurian/early
The palaeogeographic affinities of those Silurian and Early Devonian spores seem to be north-western Gondwanan. However, we have found a single specimen of *Emphasisporites zavallatus var. gedinniensis* which belongs to the *S-Z* (*sinuosus-zavallatus*) Province (Steemans and Lakova 2004) situated on the eastern margin of the Old Red Sandstone Continent (ORSC). Despite the rarity of specimens, the presence of that species is surprising in a region showing Gondwanan affinities. This finding provides an interesting feature to the spore assemblage and encourages further prospections in the area. The position of the Iberian Peninsula within the Armorican microcontinent between Gondwana and the Avalonia–Baltica region in Laurussia (Cocks and Torsvik 2002, 2006, 2011) is actually consistent with the observation of a spore assemblage with mixed origins. Actually, this is not the first time that typical miospore taxa from Baltica are observed on the Iberian area (Richardson et al., 2001). For example, *Streelispora newportensis* Richardson and Lister 1969 is absent on the Gondwana Plate, except one specimen in the MG-1 well in Tunisia (Loboziak et al. 1992), but abundant in the Lochkovian from the Western part of the ORSC (Richardson and Lister 1969; Steemans 1989; Richardson et al., 2001; Steemans and Lakova 2004).

The Spanish assemblages described are very different from coeval assemblages from Euramerica from the terrestrial floodplain deposits of the Anglo-Welsh Basin described by Wellman et al. (1998) and the nearshore marine deposits of the Ardennent-Rhenish region described by Steemans (1989). They have much more in common with Northern Gondwana, but as this study shows are somewhat of a mix and do contain some Euramerican elements. Previous studies have emphasised that the Palaeozoic miospores from Spain were not well known except in the late Silurian and the earliest Lochkovian (see e.g. Richardson et al., 2001, and references therein). So far, despite that Rodriguez (1983) also studied late Silurian–Lochkovian assemblages from the Cantabrian zone of the Iberian Peninsula, the only palynological study covering the Lochkovian of the studied area has been published by Cascales-Miñana et al. (2015) who documented a Lochkovian association of plant megafossils and dispersed spores from the Nogueras Formation. Now, the new spore assemblage described herein, also collected from the Nogueras Formation at Mezquita de Loscos (Teruel Province, north-eastern Spain), includes 20 genera, among which 14 are new for the plant-bearing locality, representing a highly diverse palynoflora documented in this area. The early Pragian age assigned to the assemblage indicates that the Nogueras Formation, despite representing a predominantly marine environment, bears plant remains over its whole extension dated from the Lochkovian to the Pragian. In addition, our study shows that the stratigraphic distribution of some important Gondwanan spore taxa such as the monolete form *Latosporites ovalis*, which was previously documented only in the late Pragian–Emsian time interval, can be downwardly extended into, at least, the early Pragian. The spore assemblage shows north-western Gondwanan affinities, which supports a position of the Iberian Peninsula between Gondwana and Laurussia region during Early Devonian times.

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**Disclosure statement**

No potential conflict of interest was reported by the authors.

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