

A transitional Ediacaran–Cambrian biota in the Abenójar anticline (Iberian Massif, Spain)

Una biota transicional Ediacárica–Cámbrica en el anticlinal de Abenójar (Macizo Ibérico, España)

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ABSTRACT

A sequence with a transitional Ediacaran–Cambrian biota is described from the Navezuelas stream valley, in the Abenójar anticline (Ibor Group, Central Iberian Zone, Spain). The sequence starts with fine-grained siliciclastics containing *Vendotaenia antiqua* and moulds of the early skeletal fossil *Cloudina* cf. *hartmannae*. These beds are followed by carbonates with *Cloudina* co-occurring at hand sample level with *Vendotaenia antiqua* together with protoconodonts similar to *Protohertzina unguiformis*, suggesting a terminal Ediacaran or lowermost Cambrian age. The detrital beds above this level have simple trace fossils of deposit feeders. Above an upper carbonate bed with tiny vendotaenids there is a trace fossil assemblage of Cambrian aspect, including *Treptichnus pedum* and ornamented burrows resembling the ventral surface of *Psammichnites*. The occurrence of protoconodonts is new to the Ediacaran–Cambrian transition in Europe, and this is the third time worldwide that these typically Cambrian fossils are found co-occurring unambiguously with the typically Ediacaran cloudinids, which suggests that the Ediacaran–Cambrian transition was biologically more gradual than previously thought.

Keywords: Cambrian explosion; *Cloudina*, Ibor Group; Precambrian; protoconodonts.

RESUMEN

Se describe una secuencia conteniendo una biota transicional ediacárica–cámbrica, en el valle del arroyo de las Navezuelas, anticlinal de Abenójar (Grupo Ibor, Zona Centroibérica, España). La secuencia empieza con capas siliciclásticas de grano fino conteniendo *Vendotaenia antiqua* y moldes de *Cloudina* cf. *hartmannae*, uno de los primeros animales con esqueleto mineralizado. Continúa con carbonatos con *Cloudina* fosfatizadas, coincidiendo en muestra de mano con *Vendotaenia antiqua* y con protoconodontos semejantes a *Protohertzina unguiformis*, lo cual sugiere una edad ediacárica terminal o cámbrica basal. Las capas detríticas sobre este nivel contienen pistas fósiles simples de organismos sedimentívoros. Sobre un estrato superior de carbonatos con pequeños vendoténidos se ha hallado un conjunto de pistas fósiles de aspecto cámbrico, incluyendo *Treptichnus pedum* y madrigueras ornamentadas semejantes a la superficie ventral de *Psammichnites*. El hallazgo de protoconodontos es nuevo para la transición Ediacárico–Cámbrico en Europa, y esta es la tercera vez a escala mundial que este tipo de fósiles típicamente cámbricos son hallados junto con cloudínidos, típicamente ediacáricos, lo cual sugiere que la transición Ediacárico–Cámbrico fue biológicamente más gradual de lo que se pensaba anteriormente.

Palabras clave: *Cloudina*; explosión cámbrica; Grupo Ibor; Precámbrico; protoconodontos.

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Introduction

In the time of Darwin, one of the biggest challenges for his theory of evolution was the apparently sudden occurrence of the first fossils in the stratigraphic column, at the point currently recognized as the Lower Cambrian (Chapter X in Darwin, 1859). Nowadays, this seeming jump in the fossil record has been tempered by a huge amount of data showing that the early animal evolution was a much more gradual process than previously thought, with simple multicellular organisms preceding the first skeletal animals, and these appearing before the Cambrian rise of shelly fossils (McMenamin, 1987; Knoll, 2003; Fedonkin *et al.*, 2007). However, a drastic evolutionary discontinuity is still widely thought to have occurred exactly at the Ediacaran–Cambrian boundary, where many Ediacaran organisms seem to disappear from the fossil record (Amthor *et al.*, 2003; Fedonkin *et al.*, 2007; Buatois *et al.*, 2014). In this usual view, that crisis preceded the rapid unfolding of the diversity of bilateral animals that characterizes the beginning of the Cambrian (the “Cambrian explosion”, Gould, 1989). According to this scheme, the Ediacaran to Cambrian transition signals a mass extinction followed by an evolutionary jump. This would explain why Ediacara-type fossils are absent from the Cambrian onwards, with a few exceptions (for example, Jensen *et al.*, 1998; Hagadorn *et al.*, 2000), although they could have been declining before the Ediacaran–Cambrian boundary (Darroch *et al.*, 2015).

This perspective about the Ediacaran to Cambrian transition must be questioned on the basis of recent data about the early skeletal organism *Cloudina*. Its fossils are widespread in late Ediacaran carbonates worldwide (Cortijo *et al.*, 2010), and its disappearance from the fossil record was taken as a major proof of an Ediacaran–Cambrian mass extinction (Amthor *et al.*, 2003; Knoll, 2003). However, new findings from China and Siberia demonstrate that the cloudinids coexisted with shelly animals previously considered to be typical of the lowermost Cambrian, such as anabaritids and protoconodonts (Yang *et al.*, 2016; Zhu *et al.*, 2017). If these transitional faunas represented the general trend, and not isolated cases, then they would bring a second turn of the screw for gradualism in our view of the

early animal evolution, implying the Ediacaran–Cambrian extinction event was not as dramatic as previously thought. This is suggested by the present work, where another one of these transitional faunas, consisting of *Cloudina* and protoconodonts, is reported for the valley of the Navezuelas stream in the Abenójar anticline (Iberian Massif, Spain), together with other fossils that depicts a possible Ediacaran–Cambrian transition and will help to disentangle the regional geology.

Material and methods

Fossil prospection was focused mainly on relatively fresh pieces found loose on exposures. The specimens were photographed using a Canon 7D MkII camera with the macro lenses Canon 100mm f2.8 and Canon 60mm f2.8. Microfossils were extracted from their carbonate matrix using 7–10% acetic acid buffered with calcium acetate during two to five days (Jeppson *et al.*, 1999). They were observed with a stereomicroscope Seben Incognita III and photographed by mounting on it a Canon S95 camera with a digiscoping adapter. The resulting images were digitally stacked to increase depth of field and focus. The photographs for the stackings of Fig. 5G to J were taken using an optical microscope Optika B-120 and a digital camera Bresser MikrOkular Full HD. All the specimens here described and illustrated are deposited in the Museo de Paleontología de Castilla-La Mancha (Cuenca, Spain) under the accession code MPCM-AB.

Since the most detailed geological map available for the northern part of the Abenójar anticline is rather incomplete in the Navezuelas stream area (MAGNA 1:50,000, sheet 783, Abenójar), some basic geological mapping was carried on, in order to clarify or confirm the stratigraphic succession of the fossils. This was a traverse, exposure-based mapping and consisted on location of the individual exposures using GPS and aerial photography (Apple maps), measurement of strike and dip of representative beds with a Brunton-type compass-clinometer, and rock sampling (Barnes and Lisle, 2004; Coe, 2010). The results were mapped on a portion of the corresponding national topographic map (sheet 783-I, Hojalora, 1:25,000) and complemented with information from the geological map 1:50,000.

Geological setting

Geology and paleontology of the Abenójar anticline

Ediacaran and Cambrian rocks are exposed in the core of a series of broadly northwest to southeast trending anticlines in the southeastern part of the Central Iberian Zone (Figure 1). These rocks are overlain by the Armorican Quartzite Formation and other Ordovician strata that dominate the landscape of the Toledo Mountains and Sierra Morena. These sediments record a back-arc basin behind the arc that originated the Ossa Morena Zone, at the northwestern margin of Gondwana, in temperate to subtropical

southern paleolatitude. The sediments were tectonically deformed during the Hercinian orogeny, together with those deposited from the Ordovician to the Devonian in the area (Eguíluz *et al.*, 2015).

There is no consensus on the naming of these Ediacaran-Cambrian beds, with different stratigraphic names depending on the region and author (see a detailed discussion in Pieren Pidal, 2000). Here I will follow the lithostratigraphic terminology proposed by Nozal Martín *et al.* (1988), which seems to fit well the Abenójar anticline. Nozal Martín *et al.* (1988) defined the Domo Extremeño Group (~ Lower Alcludian) and the overlying Ibor Group (~ Upper Alcludian) from the cores of the Ibor

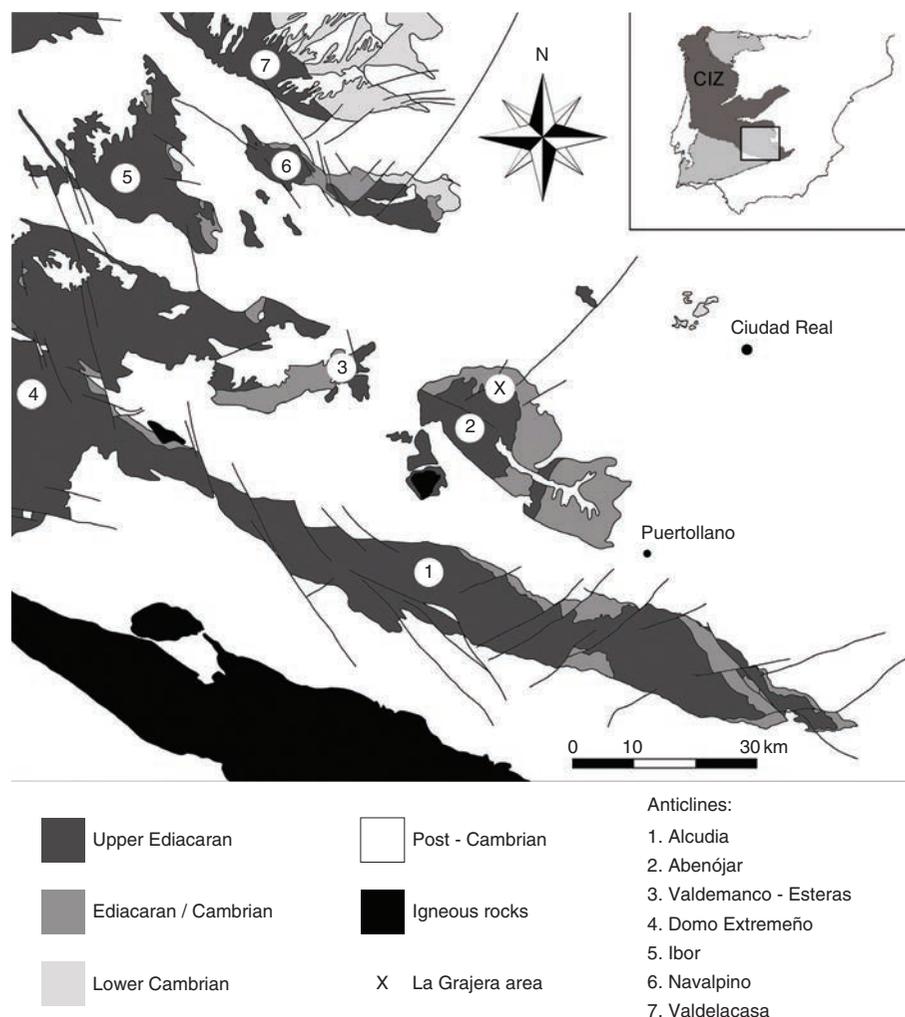


Figure 1.—Geological map of the region, showing the Abenójar anticline and the other anticlinal structures with Ediacaran to Cambrian rocks in the Central Iberian Zone (CIZ).

and Navalpino anticlines, northwest of Abenójar (Fig. 1). The Upper Alcludian, which was defined in the Alcudia anticline, seems quite different in lithology and fossils (see Pieren Pidal, 2000, 2009; Simón, 2017) compared to the Ibor Group from Abenójar.

In the Abenójar anticline, the Domo Extremeño Group is exposed as a thick sequence of turbidites and gravitational breccias representing a relatively deep depositional environment. This unit starts

with 500-600 m of turbidites and follows with about 1,000 m of breccias. Near the Abenójar village, the breccias contain organized carbonates that may have fallen from a relatively shallow platform (Ortega Girones & Sánchez Vizcaino, 1987). There is an unconformity between the Domo Extremeño and Ibor Groups, being this feature apparent in the Tirteafuera river northwest of the Cerro de Cañuelo (Ortega & González-Lodeiro, 1986).

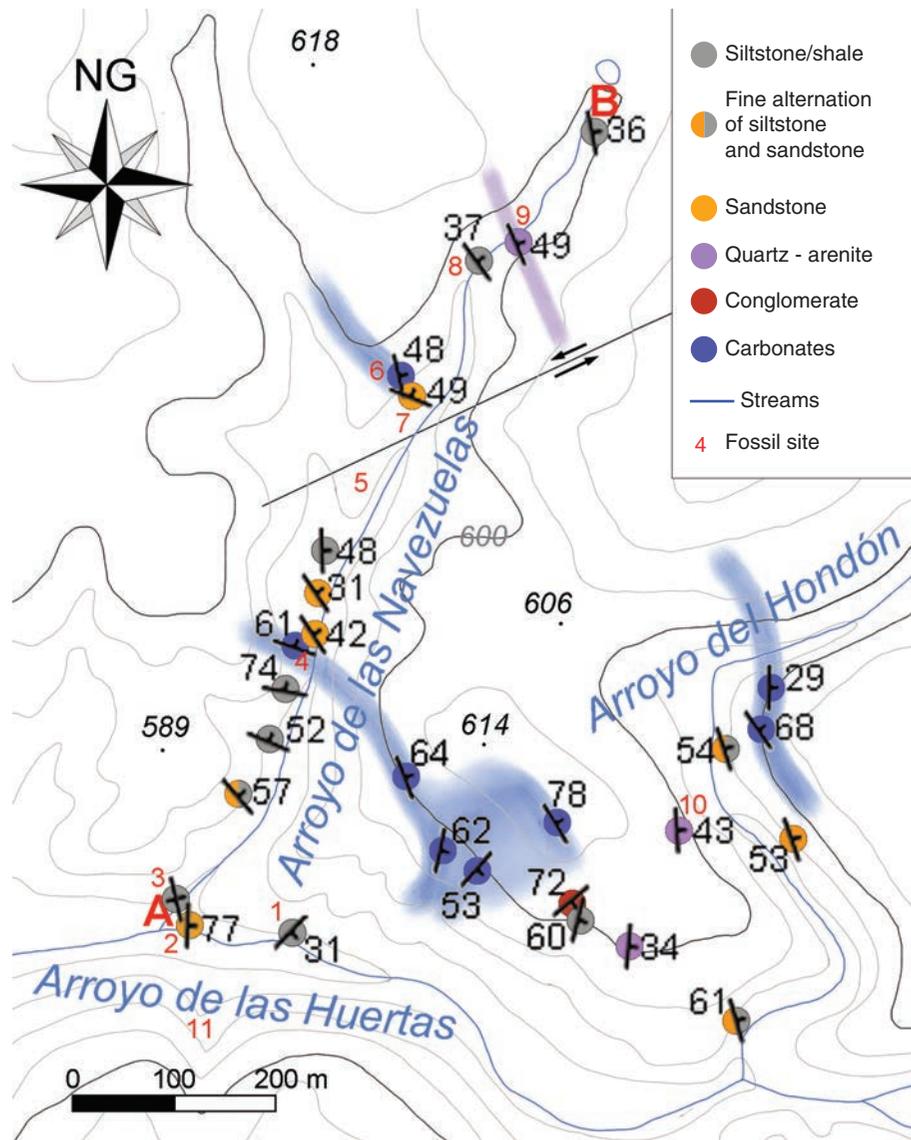


Figure 2.—Large scale geological map of the Navezuelas stream area. Due to the high tectonic complexity and limited exposures of the zone, no cartographic extrapolation has been done, and only the obvious extension of carbonates (blue) and quartz-arenites (purple) observed in the field is shown. Each sampling point is at the intersection of the symbol of the corresponding strike and dip. NG = geographic north. A and B mark the approximate base and top of the stratigraphic column of Fig. 3. Interval between topographic curves = 10 m.

This unconformity and the usually intense tectonic deformation of the Domo Extremeño are probably consequences of the Cadomian orogeny that affected the margin of Gondwana at the end of the Proterozoic (Vidal *et al.*, 1994).

The Ibor Group in Abenójar comprise a highly heterolithic sequence of carbonates and terrigenous beds, with frequent lateral changes and irregular thicknesses. Ortega Girones & Sánchez Vizcaíno (1987) named the northern part of this unit in the anticline “sucesión detrítico-carbonatada de La Grajera-Cañuelo”; for simplicity, here I will call it La Grajera-Cañuelo unit. They divided it into a lower part (120-350 m), dominated by lutites and carbonates (with limestones, dolostones, arkoses, greywackes, quartz-arenites and conglomerates), and an upper part (120-450 m), more terrigenous and flysch-like (with lutites, arkoses, greywackes and conglomerates) but with a conspicuous dolostone level near the top. The entire unit corresponds to a sedimentary environment of proximal shallow platform (Roiz & Vegas, 1980; Ortega Girones & Sánchez Vizcaíno, 1987).

The published fossil record from the Domo Extremeño and Ibor Groups in the Abenójar anticline is rather scarce and few of the findings are accompanied by supporting images or descriptions. It can be summarized as follows:

a) Domo Extremeño Group: carbonaceous microfossils are present in the limestones near the Abenójar cemetery (Ortega Girones & Sánchez Vizcaíno, 1987). The early skeletal fossil *Cloudina* ex. gr. *hartmannae* was cited by Zhuravlev *et al.* (2012) from carbonates within the breccias in a locality that seems to be the same whose coordinates provided Vidal *et al.* (1994) for a *Cloudina* site in the Tirteafuera river, south of the Abenójar village.

b) Lower part of the La Grajera-Cañuelo unit: from the Tirteafuera river locality cited above, Vidal *et al.* (1994) illustrated a thin section showing *Cloudina* remains with polygonal shape that resemble *Cloudina carinata* (Cortijo *et al.*, 2010). Another *Cloudina* species, reported as *C.* ex. gr. *hartmannae*, was found by Zhuravlev *et al.* (2012, their figs. 3-5) as sections and *steinkerns* from limestones of what appears to be the same locality. They also describe and illustrate a possible fragment of *Sinotubulites* sp. that may be from the same site, but this is not clearly

specified. According to these authors, the trace fossils *Cochlichnus* and *Planolites*, and abundant carbonaceous filaments identified as vendotaenids, appear in the locality, but this material is neither shown nor described and its stratigraphic position is not detailed. Vendotaenids were also cited by Fernández Remolar *et al.* (2005), from a terrigenous series associated to the “lower limestones”, probably corresponding to the lower La Grajera-Cañuelo unit. Ortega Girones & Sánchez Vizcaíno (1987) reported carbonaceous microfossils from the limestones of this part of the sequence.

c) Upper part of the La Grajera-Cañuelo unit: the trace fossils found by García-Hidalgo (1993) at the top of the “Capas del Arroyo Hondón” correspond to this upper part. He described them as *Palaeophycus*-type burrows, with possible *Belorhaphé?* and *Phycodes?* but bioturbation was so intense in some levels that identification of individual traces was difficult. Fernández Remolar *et al.* (2005) illustrated possible Cambrian skeletal fossils from the “upper limestones” (the higher dolostone level of the La Grajera-Cañuelo unit, García-Hidalgo, personal communication), but the remains are so poorly preserved that identification seems impossible.

These data suggest that the most probable age for the Domo Extremeño Group in the Abenójar anticline is late Ediacaran, whereas the Ibor Group could record the transition between the terminal Ediacaran and the lowermost Cambrian (Jensen & Palacios, 2016). These ages are coherent with detrital zircon radiometric geochronology of the Lower and Upper Alcuadian from other anticlines such as the Alcuadia valley (Talavera *et al.*, 2012, 2015).

The Navezuelas stream area

The Navezuelas stream is located in the La Grajera area (X in Figure 1), north of the Abenójar village. Here the Ibor Group is exposed mainly along the stream valleys and ridges of an Appalachian-type landscape. Exposures are usually of about 10-100 m²; they are scattered and often separated by tenths of meters. Fig. 2 shows the data collected during the geological mapping of the area, along the Navezuelas valley and eastwards to the Hondón stream. At this large scale, the frequent folds, fractures and small faults make risky any cartographic extrapolation, so

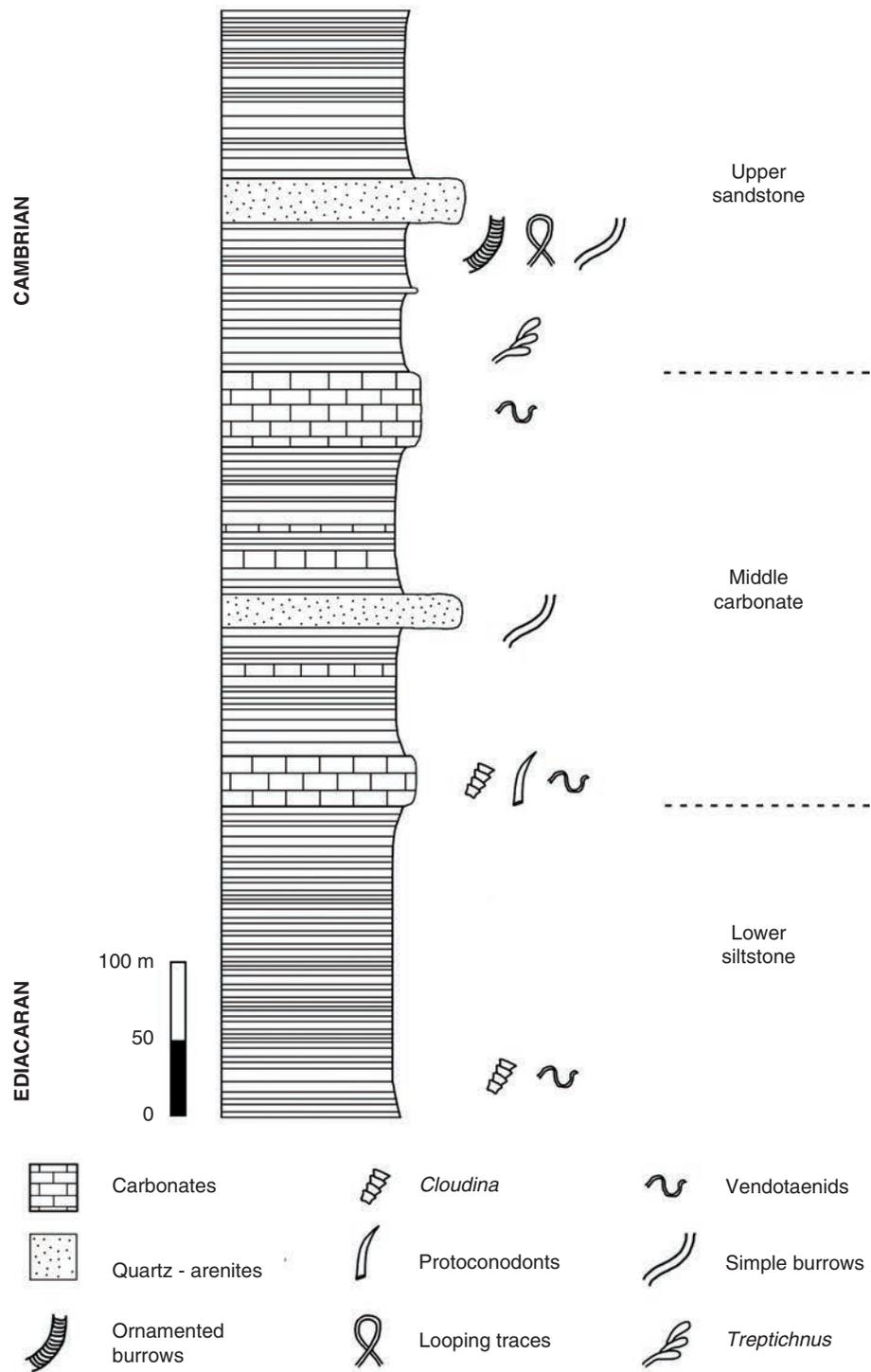


Figure 3.—Simplified stratigraphic column of the Navezuelas stream, approximately from A to B of Fig. 2 but including fossils found more eastwards. Thickness of individual beds is exaggerated for clarity, and no faults are represented.

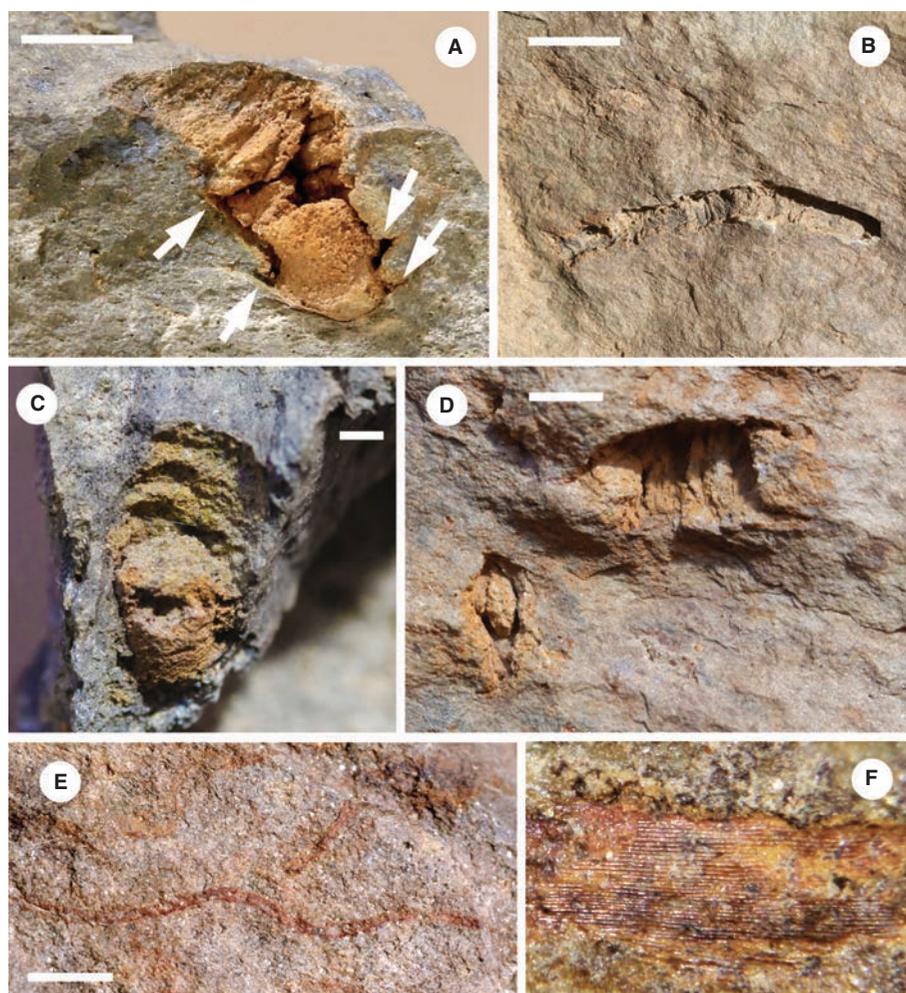


Figure 4.—Fossils from the lower siltstone of the sequence. A–D. Moulds of *Cloudina* cf. *hartmannae* in siliciclastics from point 3. A. Specimen MPCM-AB-0022, obtained from a freshly broken siltstone, showing flanges (arrowed) interpreted as a funnel-in-funnel structure. Scale bar = 3 mm. B. External mould with transversal wrinkles and annulations. MPCM-AB-0021. Scale bar = 5 mm. C. Internal and external mould. MPCM-AB-0024. Scale bar = 1 mm. D. Two specimens showing differently oriented sections. MPCM-AB-0021. Scale bar = 2 mm. E. *Vendotaenia antiqua* preserved as a reddish sinuous ribbon. MPCM-AB-0023. Point 2. Scale bar = 5 mm. F. Detail of the specimen showing very fine longitudinal striation.

only the raw data are shown here. In spite of tectonic deformation, these data depicts a stratigraphic sequence that seems to be relatively continuous. It can be broadly divided into three lithostratigraphic units (Fig. 3), here named after its stratigraphic position and characteristic lithology. Rock types are in general the same that were described in more detail by Ortega Girones & Sánchez Vizcaino (1987) for the La Grajera-Cañuelo unit.

(I) Lower siltstone: bluish grey and thinly bedded (1–2 cm thick) siltstone, accompanied by some similarly thin beds of shale and others of fine, ochraceous

sandstone. This unit outcrops along the final part of the Navezuelas stream, with the best exposures being near its mouth at the Huertas stream. A thickness of approximately 240 m can be estimated for the studied part along the Navezuelas valley. The restriction of lithologies to fine-grained siliciclastics suggests a low energy sedimentary environment, may be a distal platform not as shallow as in the following units.

(II) Middle carbonate: this unit is well defined by the presence of two conspicuous carbonate levels at its base and top. They are both approximately 10 m thick in the Navezuelas valley, but the top of

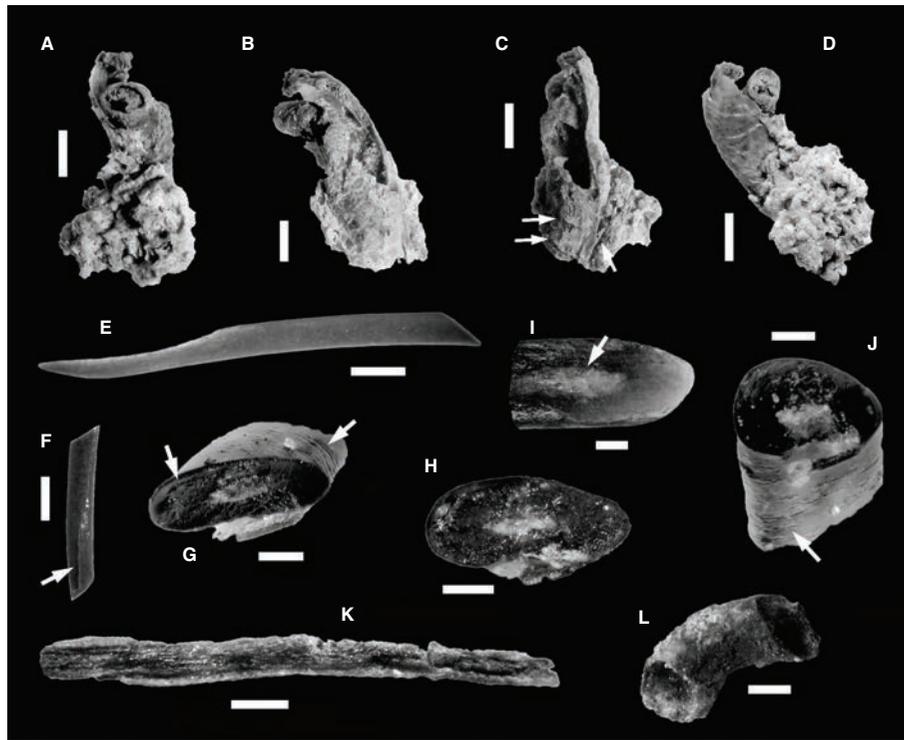


Figure 5.—Microfossils obtained from acid maceration of the lower carbonate level (point 4). Scale bars represent 50 μm in G to J, and 300 μm in the other images. A-D. *Cloudina* sp. (MPCM-AB-0013), different views of the same specimen. Transversal grooves defining segments are visible in C (arrows in the left), as well as a flange (right arrow). E-J. Protoconodont elements similar to *Protohertzina unguiformis*. E. Large specimen with pointed tip. MPCM-AB-0014a. F. Specimen with a lateral fringe (arrowed). MPCM-AB-0014b. G-J. Natural oblique sections of the protoconodonts: G. Image showing a central cavity filled with pale minerals, hints of concentric lamellae (left arrow), fine external ring-like grooves (right arrow), and a shred of the outer layer (above the scale bar). MPCM-AB-0026a. H. Another view of the same specimen. I. Tip of the broken specimen MPCM-AB-0026b, an almost longitudinal section, showing a whitish medullar cavity (arrow) and a fibrous texture. J. The other extreme of MPCM-AB-0026a, with crystalline matter in the central cavity, a shred of the organic outer layer, and very fine transversal striation in the surface (arrowed). K. *Vendotaenia antiqua* showing longitudinal striae and a right part with tubular structure. MPCM-AB-0027. L. Hollow tubular microfossil. MPCM-AB-0016.

the basal level is probably cut by a fault; the uncut development of this level eastwards reaches more than 50 m. Only the upper carbonates are figured in the geological map 1:50,000, being represented as a dolostone band (number 12 in the map legend). Apart from these two main levels, thin carbonate beds are also found sometimes in between. In this unit, the carbonates appear in beds of varying thickness, from about 1 to 50 cm, and they are usually very dark bluish limestones, with some beds of a similar dolostone of paler hue. Both types show abundant organic matter, frequent detrital layers, and wavy stratification.

The sandstones are the main detrital rocks within this unit, being mostly ochraceous, fine grained, and 5-30 cm thick. Some of them show lenticular stratification and others form quite regular alternations

with very thin beds of carbonate. Other detrital rocks observed in the unit are siltstones (similar to those of the previous unit), siliceous conglomerates (beds 30-70 cm thick, with a moderate fraction of reddish matrix and quartz clasts up to about 0.3-1.5 cm long), and quartz-arenites (light grey, beds 40-60 cm thick).

The best exposures of the unit are found between the Navezuelas and Hondón streams. Its characteristics indicate a depositional environment of higher energy than the previous one. Thickness is difficult to estimate with confidence, but it may be about 350 m between the Navezuelas and Hondón streams.

(III) Upper sandstone: this unit contains all the beds above the upper carbonate level of the previous one up to the detrital covering of the upper part of the Navezuelas stream. Carbonates disappear

completely, and the most characteristic lithology is a guide level of light bluish-grey quartz-arenite, about 3 m thick, in banks of up to 80 cm. Immediately below this level there are about 10 m of very hard ochraceous sandstones, 10–30 cm thick, overlying a quite monotonous sequence of grey-ochre siltstones in strata of 1–2 cm. Just above the upper carbonate level of the previous unit there are approximately 10 m of sandstones, hard and ochraceous.

Above the quartz-arenite level, a flysch-like alternation of dark siltstones and sandstones, in thin beds (1–5 cm), starts up until it contacts with a detrital covering derived from Lower Ordovician rocks (*raña*) in a parkland (*dehesa*). The thickness of this unit can be estimated with confidence to be close to 250 m in the Navezuelas stream. The sedimentary environment is interpreted to be a shallow siliciclastic platform, and the important presence of siltstones suggests energy not as high as in the previous unit.

According to these lithologies and the geological map 1:50,000, the lower and middle units correspond to the lower La Grajera-Cañuelo (Ortega Girones & Sánchez Vizcaíno, 1987), whereas the third unit, lacking carbonates, would belong to the upper part. The quite gradual changes of strikes and dips measured along the Navezuelas valley support that these three units form a relatively continuous sequence. It was interrupted by a fault that displaced about 150 m of the middle unit, but this missing record is preserved between the Navezuelas and Hondón streams, where no major faults were found between the lower and upper carbonate levels. Below, the lower siltstone starts with vertical to subvertical dips (Fig. 2) that gradually passes to the values typical of the basal carbonates, whereas the mean dip in this and the upper part of the sequence is the same, about 45°.

Results

The fossil record of the area displayed in Fig. 2, along the sequence of Fig. 3, can be summarized as follows, from base to top. The points refer to those of Fig. 2.

(I) Lower siltstone: The siltstones and mudstones near the mouth of the Navezuelas stream contain abundant internal and external moulds of annulated tubular fossils (points 3 and 11, Fig. 4A–D).

These moulds depict an organism with a tubular funnel-in-funnel structure that is clearer in the specimen of Fig. 4A. These remains are *Cloudina* cf. *hartmannae* preserved in siliciclastics. In this basal sequence there are also some fine-grained sandstone beds with sinuous oxidized ribbons (points 1 and 2). The specimen of Fig. 4E shows very fine longitudinal striation (Fig. 4F, point 2), supporting identification as *Vendotaenia antiqua* (Gnilovskaya, 1971; see Hofmann, 1985; Cohen *et al.*, 2009).

(II) Middle carbonate: Acid digestion of the lower limestones of the Navezuelas stream valley (point 4) yielded phosphatized skeletons of *Cloudina* sp. (Fig. 5A–D) together with protoconodonts similar to *Protohertzina unguiformis* (Fig. 5E–J). Other microfossils from these lower limestones are *steinkerns* and hollow tubes of unidentified tubular organisms, may be *Cloudina* sp. (Fig. 5L), in phosphate and pyrite. There are also tiny specimens of *Vendotaenia antiqua*, preserved as flattened filaments of carbonaceous aspect, with fine longitudinal striation and hints of tubular structure (Fig. 5K). The upper carbonate level (point 6) provided fewer and more incomplete microfossils after acid maceration: fragments of hollow tubes, and vendotaenids. Both carbonate levels contain abundant organic debris, including soft sheets resembling algal remains.

In the sandy beds between the carbonates, some soles show small isolated semireliefs similar to *Palaeophycus* (Fig. 6B, point 5) that may be trace fossils or body fossils of tubular organisms. At about this level, a slab was found with trace fossils (Fig. 6F, point 10) interpreted as burrows of sediment feeders due to their form and compositional difference with the surrounding matrix of quartz-arenite. They are preserved as sinuous hyporeliefs, with ellipsoidal section and irregular constrictions (peristaltic movement?). The burrows are unlined, mainly horizontal, and sometimes show possible branching. All these features suggest the ichnogenus *Planolites*, but the irregular constrictions remind *Torrowangea* (Pemberton & Frey, 1982; Webby, 1970, Jensen & Palacios, 2016), so the ichnogenic assignment of these trace fossils is unclear.

(III) Upper sandstone: At the lowermost part of this unit, immediately above the upper carbonate level, there are thick sandstone beds where a

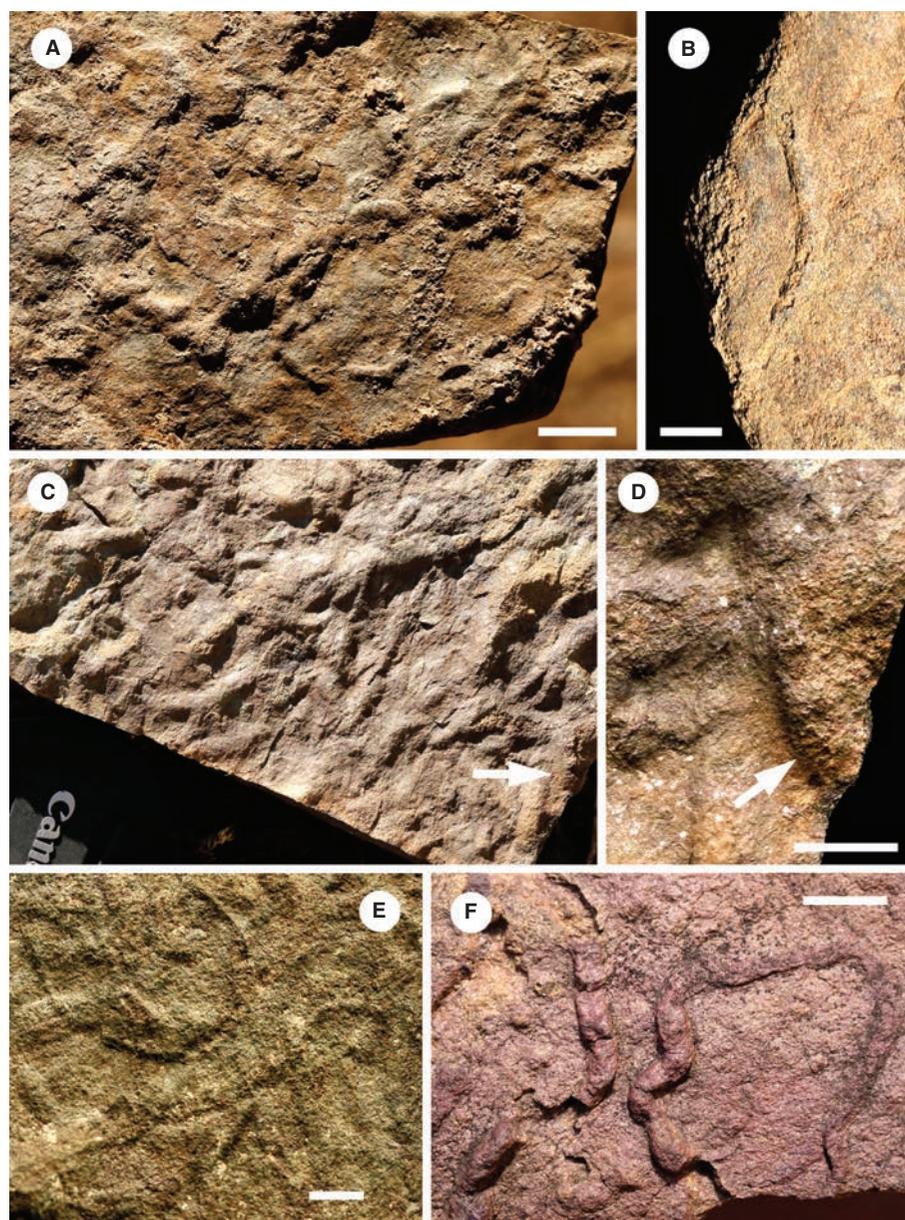


Figure 6.—A. *Treptichnus pedum* in positive hyporelief (MPCM-AB-0006). Point 7. Scale bar = 10 mm. B. Trace fossil resembling *Palaeophycus*, or body fossil of a tubular organism. Sole of a sandstone bed in point 5. Scale bar = 5 mm. C. Mass occurrence of burrows in positive hyporelief (MPCM-AB-0007). The arrow indicates the burrow illustrated in D. Point 9. Lens cap diameter = 58 mm. D. Detail of a burrow showing very fine transversal arcuate striations, being a possible *Psammichnites* in ventral preservation. Scale bar = 5 mm. E. Narrow meandering traces in positive hyporelief that could be a stretch of *Gordia*, due to the presence of loops, or body fossils of filamentous organisms preserved with the aspect of a trace fossil. MPCM-AB-0008. Point 9. Scale bar = 5 mm. F. Sinuous burrows preserved as full reliefs, interpreted as the record of sediment feeders. MPCM-AB-0025. From the sole of a sandy bed in point 10. Scale bar = 6 mm.

loose slab was found with the complex trace fossil *Treptichnus pedum* (point 7, Fig. 6A), developed as curved series of almond-shaped knobs. The *Treptichnus pedum* assemblage of trace fossils identifies the beginning of the Cambrian,

but the range of this trace fossil extends about 4 m below the Ediacaran–Cambrian boundary in Newfoundland, and similar treptichnids are also known from the latest Ediacaran (Gehling *et al.*, 2001; Seilacher, 2007).

Just below the guide level of quartz-arenites, there are hard sandstones (point 9) with abundant trace fossils that look very similar to the assemblage described by García-Hidalgo (1993) at the top of the Hondón stream beds. The commonest trace fossils are simple burrows that frequently cross themselves, sometimes to the extent that it is difficult to follow individual traces (Fig. 6C). On some bed soles there are isolated burrows, about 4 mm wide, with very fine transversal striation (Fig. 6D). This is typical of the ventral surface of the ichnogenus *Psammichnites*, but identification of these specimens as *Psammichnites* is uncertain, according to Mángano *et al.* (2002), since the emended diagnosis they proposed depends on the upper surface. Most of the burrows around these particular ones may be *Palaeophycus* if their lack of striation was an original feature, which is not clear since preservation is not optimal.

Other fossils in the same sandstone exposure are simple, unbranched and thin traces, approximately 1.5 mm wide, that describe very tight curves and loops in the bedding plane (Fig. 6E). They could be ascribed to *Gordia*, but the possibility exists that they are fossils of filamentous organisms preserved with the aspect of traces (Jensen *et al.*, 2006; Cohen *et al.*, 2009). Possible bilobed furrows occur isolated or in the mass occurrences of intercrossing burrows (point 8), but it can't be ruled out whether they are just random juxtapositions of unilobed burrows.

Systematic paleontology

Incertae sedis

Family Cloudinidae Hahn & Pflug, 1985

Genus *Cloudina* Germs, 1972

Remarks: *Cloudina* was one of the earliest animals with a biomineralized skeleton, and it occurs almost worldwide in late Ediacaran carbonates (Grant, 1990; Zhuravlev *et al.*, 2012, Cortijo, 2015; Cai *et al.*, 2017). It has been found in several sites of the Central Iberian Zone (Vidal *et al.*, 1994; Cortijo *et al.*, 2015), including the Abenójar anticline (Zhuravlev *et al.*, 2012), but few of these occurrences shows unambiguously the diagnostic characters of this genus (Vidal *et al.*, 1994). The affinity of *Cloudina* is uncertain, with available evidence suggesting a polypoid cnidaria or annelid-grade

bilaterian (Hua *et al.*, 2005; Cortijo, 2015, Cai *et al.*, 2017), but the structure and development of the skeleton support a cnidarian rather than annelid affinity (Vinn & Zaton, 2012). *Cloudina* was previously thought to have disappeared in a mass extinction at the end of the Proterozoic (Amthor *et al.*, 2003), but this idea would require revision after the finding of *Cloudina* with typically Cambrian microfossils by Yang *et al.* (2016) and the present work.

Cloudina cf. *hartmannae* Germs, 1972 (Fig. 4A–D)

Material: tens of specimens collected in siltstone or shale slabs, found *in situ* or loose near the outcrops; numerous smaller or less complete specimens were examined in the field. Sampling points 3 and 11 in Fig. 2. Accession codes: MPCM-AB-0009 to 0012, MPCM-AB-0021, MPCM-AB-0022 and MPCM-AB-0024.

Description: Cylindrical to gently conical tubes, preserved as external and/or internal moulds, with the surface divided into segments by grooves or rims. The best preserved specimen (Fig. 4A), found by splitting siltstones in the exposure of point 3, display an external mould with flanges (see the arrows) that suggest a funnel-in-funnel structure, with transversal irregular wrinkles on the outer surface of the funnels (Fig. 4A, below the scale bar; Fig. 4B). Some specimens start as quite horizontal tubes (Fig. 4D) that bend towards the bed top (MPCM-AB-0009). Tube width ranges from about 0.5 to 3 mm, with a length from approximately 3 to 17 mm. No biomineralization is apparent, being the fossils preserved in what appears to be limonite.

Remarks: The funnel-in-funnel structure is diagnostic of the family Cloudinidae. The transversal wrinkles of the funnels and the lack of conical shape in long specimens (Fig. 4B) support its assignation to *Cloudina* instead of *Conotubus* (Hahn & Pflug, 1985; Cai *et al.*, 2011, 2017), and the lack of longitudinal crests rules out *C. carinata* (Cortijo *et al.*, 2010). The specimens resemble *C. hartmannae*, but preservation is not good enough to identify the species unambiguously since it depends on fine details of the external surface of the funnels (Cai *et al.*, 2017).

Comparable fossils of *Cloudina* in fine-grained siliciclastics have been reported in the Navalpino

anticline (*Cloudina carinata*), well below a carbonate level with phosphatized *Cloudina* (Cortijo *et al.*, 2010; 2014; 2015). Fossils resembling moulds of cloudinids in siliciclastics were also found in the area of Garganta Honda (Cáceres province, see fig. 27 in Cortijo, 2015). The unmistakable crests of *C. carinata* are very clear in the material from the Navalpino anticline, demonstrating that *Cloudina* fossilized not only in carbonates but also in siliciclastics, preserved as moulds lacking carbonate. This makes fuzzy the difference between *Conotubus* and *Cloudina*, because the fossils assigned to *Conotubus* differ from *Cloudina* mainly in their restriction to siliciclastics and lack of carbonate (Cai *et al.*, 2011). Although some specimens of *Conotubus* are more conical, overall the genus seems morphologically almost identical to *Cloudina* (Wood *et al.*, 2017).

In spite of the many tubular body fossils that have been described from the latest Ediacaran and earliest Cambrian, only *Cloudina* meets the characteristics of the present specimens. Anabaritids and *Cambrotubulus* (Matthews and Missarzhevsky, 1975; Yang *et al.*, 2016; Zhu *et al.*, 2017), *Gaojiashania* (Cai *et al.*, 2013), *Multiconotubus* (Cai *et al.*, 2017), *Platysolenites* (McIlroy *et al.*, 2001), *Rugatotheca* (Yang *et al.*, 2016), *Shaanxilites* (Meyer *et al.*, 2012), *Sinotubulites* (Cai *et al.*, 2015) and *Wutubus* (Chen *et al.*, 2014) do not have a funnel-in-funnel structure. The cloudinid *Rajatubus* differs in its quite regular collars flaring almost perpendicularly to the tube (see Yang *et al.*, 2016).

Cloudina sp. (Fig. 5A-D)

Material: several phosphatized specimens obtained from acid maceration of the limestones of point 4 (Fig. 2), including MPCM-AB-0013 (Fig. 5A-D), which comes from a hand sample that provided protoconodonts. Lower carbonates of the Navezuelas stream.

Description: The best preserved specimen consists on two nested phosphatic tubes, circular to elliptical in section, and quite separated. The external tube is a hollow and multilayered structure, 1.5 mm long, showing fine annulations in its inner surface and a smooth but slightly irregular outer surface (Fig. 5A-D). One extreme has a flaring border (Fig. 5A, D) with hints of division into segments

(Fig. 5D). The other extreme displays two annulations defining large segments (Fig. 5C, left arrows) and a small flange (Fig. 5C, right arrow). Taken together, these characteristics suggest a tubular skeleton made by stacked funnel-like segments with flaring borders.

Remarks: The morphology of this skeletal fossil is only compatible with *Cloudina* among the late Ediacaran and early Cambrian fossil record (Yang *et al.*, 2016; Cai *et al.*, 2017). The funnel-in-funnel disposition diagnostic of this genus can originate a tube-in-tube arrangement when the funnel flanges bend forming an outer wall, as describe Hua *et al.* (2005). The resulting structure, observed in phosphatized remains of *Cloudina* from the Dengying Formation (China), is illustrated in the figure 1C of Hua *et al.* (2005), which resemble the present specimen. The lack of regularly spaced collars projecting quite perpendicularly from the tube rules out the early Cambrian cloudinid *Rajatubulus* (Yang *et al.*, 2016). In the present material, deficient preservation impedes identification at the species level, but they could be *C. hartmannae* or a very similar species (*sensu* Cai *et al.*, 2017). *Cloudina* was capable of asexual reproduction by budding, and in fact the relative width of the outer and inner tubes of the specimen here described reminds a budding *Cloudina* without one of the tubes (see for example fig. 3C in Cortijo *et al.*, 2015).

Phylum *Chaetognatha* Leuckart, 1854
aff. *Protohertzina unguiformis* Missarzhevsky,
1973 (Fig. 5E-J)

Material: four fragments obtained from acid digestion, all from *Cloudina*-bearing samples from point 4 of Fig. 2. Lower limestone level of the Navezuelas stream valley. Accession codes MPCM-AB-0014 (specimens from the same hand sample that yielded the *Cloudina* fossil of Fig. 5A-D) and MPCM-AB-0026.

Description: Slender structures of ellipsoidal to flattened section. They are glossy, dark brown, with very chitinous aspect, composed mostly of a fibrous and ductile organic material that reminds chitin, with phosphate. The largest specimen (Fig. 5E) is a scimitar-like spine with pointed tip and flattened section. It is slightly curved and thins towards the inner side.

The other specimens are more incomplete, and one of them shows a lateral ridge (Fig. 5F, arrow). All of them are about 0.2 mm wide and up to approximately 2 mm long. They have a narrow central cavity running longitudinally almost up to the tip, filled with pale crystalline matter (Fig. 5G–J). Some similar crystals are present out of the cavity within the main wall (Fig. 5H). The texture of this wall is fibrous in longitudinal direction (Fig. 5I). Well preserved specimens show an external surface with a pattern of fine transversal striae (Fig. 5G, right arrow; Fig. 5J, arrow). Hints of concentric layers are visible in section (Fig. 5G, left arrow). The outer layer is very thin and it lacks visible crystals like those of the wall and medullar cavity.

Remarks: The shape of the specimens, the presence and nature of the internal cavity, the organic-rich wall (Szaniawski, 1983), and the pattern of the external surface suggesting stacked lamellae (Fig. 5G and 5J) are diagnostic elements of the structure and composition of protoconodonts (see fig. 1 in Szaniawski, 1983), specifically type I protoconodonts such as *Protohertzina* (Müller & Hinz-Schallreuter, 1998). The material here described is similar to *Protohertzina*, the earliest form of protoconodonts (Kouchinsky *et al.*, 2012). The elements here found lack the characteristic inner ridge that runs longitudinally in that genus, although the specimen in Fig. 5E has a sharp inner flank that may be related to this feature, like the keel of Fig. 5F. The very elongated shape suggests *P. unguiformis* (Missarzhevsky, 1973; Matthews & Missarzhevsky, 1975; Bengtson, 1982; Bengtson *et al.*, 1990), rather than *P. anabarica* or other protoconodonts or conodont-like genera from the lowermost Cambrian (see Yi *et al.*, 2004; Bengtson, 1982). *Protohertzina* occurs almost worldwide in lowermost Cambrian sequences, in the Siberian Platform, Kazakhstan, Mongolia, India, Iran, Australia, and Canada (Yi *et al.*, 2004; Kouchinsky *et al.*, 2012). In western Europe, this genus has been cited from English trilobitic beds (Cobbold, 1921; Hinz, 1987).

This is the first time that protoconodonts are found associated to an Ediacaran–Cambrian transition in Europe. Protoconodonts are typical members of the low diversity assemblage of small skeletal fossils of the earliest Cambrian (*Anabarites trisulcatus*–*Protohertzina anabarica* Zone, Nemakit-Daldynian,

lower Fortunian, see Yang *et al.*, 2016). The discovery of protoconodonts co-occurring with *Cloudina* and other cloudinids in the Yangtze Platform led Yang *et al.* (2016) to distinguish a new subzone of small shelly fossils at the very beginning of the Phanerozoic, the *Ganloudina symmetrica*–*Rugatotheca typica* Subzone.

Protoconodonts are the first fossils that can be attributed to predatory animals up to date, since there is compelling evidence that they are grasping spines of chaetognaths (arrow worms). *Chaetognatha* is an early branching phyla of bilateral animals with chitinous grasping spines, being important predators in marine plankton today (Szaniawski, 2002; Vannier *et al.*, 2007). The commonness of protoconodonts during the beginning of the Phanerozoic suggests a substantial diversity and ecological role of chaetognaths at the beginning of the Cambrian radiation (Szaniawski, 2002), although it is unclear whether they were crown-group or stem-group forms. The large morphological variation recorded within the genus *Protohertzina* is probably because the spines of the grasping apparatus of an individual chaetognath can have quite different shapes, so *P. unguiformis* may be synonymous with *P. anabarica* (McIlroy & Szaniawski, 2000). Clusters of protoconodonts forming apparatuses are known from the lower Cambrian (McIlroy & Szaniawski, 2000) and have been found in the head of exceptionally preserved fossils of arrow worms (Vannier *et al.*, 2007).

During the reviewing of this manuscript it was suggested that the specimens here described may be modern arthropod appendages due to contamination. This possibility is rejected due to the following reasons: First, the procedure of extraction of these microfossils ruled out external contamination: they were obtained after a sequential acid digestion of the corresponding sample, in closed vessel, involving respectively five and four rounds of extraction of the digested sediment, each one followed by washing the container and the etched rock fragments in tap water before adding new buffered acid. As a result, not a single particle attributable to a modern origin was detected in the sediment of the specimens, since they came from perfectly clean rock fragments and vessels. Second, the following characteristics of these microfossils support they are not modern arthropod appendages: (a) the very thick wall, compared to

the very thin cuticle of an arthropod leg of this size (personal observations); (b) the crystalline filling of the central cavity and the presence of crystals within the wall; and (c) the transversal grooves suggesting a kind of growth different from that of an arthropod leg, whose cuticle is secreted by the epidermis as layers of chitin that are continuous and so lack the striated pattern observed in the specimens.

Discussion

The fossil record of the Navezuelas sequence and the surrounding area suggests that it crosses the Ediacaran–Cambrian boundary. The co-occurrence of *Cloudina* and protoconodonts in the lower carbonate level of the sequence indicates a latest Ediacaran or lowermost Cambrian age. Thus, the lower siltstone (Fig. 3), extending more than 200 m below, could be terminal Ediacaran. At the other extreme of the succession, the upper sandstone contains examples of intense bioturbation (Fig. 6C) and trace fossils supporting a Cambrian age. *Treptichnus pedum* (Fig. 6A) may be terminal Ediacaran or Cambrian (Seilacher, 2007), but ornamented burrows like the possible *Psammichnites* of Fig. 6D are unknown from the Ediacaran (Mángano & Buatois, 2016). So this trace fossil assemblage probably indicates a Lower Cambrian age.

In the middle part of the sequence, the presence of *Cloudina* and protoconodonts implies either the youngest Ediacaran or the oldest Cambrian age, and there are no compelling reasons for choosing one or the other with our current knowledge about the biostratigraphy of this interval worldwide. This ambiguity should be accepted in the present case because of the following considerations. First, cloudinids were previously considered as index fossils of the latest Ediacaran, but this was quickly challenged since the stratigraphic range of *Cloudina* was found to overlap with that of *Anabarites trisulcatus*, which appeared at the very beginning of the Cambrian (Vidal *et al.*, 1994). On the other hand, the first protoconodonts belong to the *Protohertzina anabarica* - *P. unguliformis* group and appear in the oldest zone of small shelly fossils of the Lower Cambrian (Kouchinsky *et al.*, 2012). Yang *et al.* (2016) assigned to the lowermost Cambrian the level with *Cloudina* and *Protohertzina unguliformis*

of the Yangtze Platform, due to the presence of typical Cambrian small shelly fossils. The same reason would imply a lowermost Cambrian age for the level where *Protohertzina unguliformis* and cloudinids (probably *Cloudina*) co-occur in the Siberian Platform, but Zhu *et al.* (2017) considered that its age is not Cambrian on the basis of chemostratigraphy, because these beds are only at the very beginning of the isotopic change that will lead to the basal Cambrian $\delta^{13}\text{C}$ excursion, just above the late Ediacaran $\delta^{13}\text{C}$ positive plateau. Thus these authors refused to assign an Ediacaran or Cambrian age for this level, and concluded that the biological Ediacaran–Cambrian transition was much more gradual than previously thought, lacking any major extinction event. This conclusion is strengthened by the coexistence of *Cloudina* and protoconodonts here described, since this is the third time that both are found together worldwide.

The Navezuelas sequence is the second possible Ediacaran–Cambrian transition found in the Iberian Massif, being the first one the Río Uso section in the Valdelacasa anticline (Fig. 1). This classical sequence of the Iberian geology is very different from the present one in lithostratigraphy and fossils (Brasier *et al.*, 1979; Palacios, 1989; Vidal *et al.*, 1994; Gámez-Vintaned, 1996; Gámez-Vintaned & Liñán, 2007). However, there are some problems with the widespread idea that it records the Ediacaran to Cambrian transition (see Jensen & Palacios, 2016). The Ediacaran–Cambrian boundary was proposed to be in the lower part of the Pusa Formation, approximately 250 m above the base of this fine-grained siliciclastic unit. The biggest problem is the lack of unambiguous Ediacaran fossils below the supposed boundary down to the base of the underlying unit, the Fuentes Olistostrome (“Nivel de Fuentes”), a megabreccia which lies unconformably above the Domo Extremeño Group. Between this unconformity and the proposed boundary, the fossils found could be either terminal Ediacaran or lowermost Cambrian, but no exclusively Ediacaran forms have been reported. The lower part of the Pusa Formation, between La Nava-Fuentes station and tunnel 9, has *Chuarialike* carbonaceous discs, found also around the station among beds with Cambrian trace fossils such as scratch marks (*Monomorphichnus*, Vidal *et al.*, 1994). The Fuentes Olistostrome contains carbonate

pebbles and boulders with *Cloudina* in the neighboring area of the Arroyo del Cubilar (Cortijo, 2015), but these carbonates may have fallen to the sequence at Cambrian times, and *Cloudina* itself may be of lowermost Cambrian age, as discussed above. Thus at present there is no positive evidence that the lower Pusa Formation records the Ediacaran to Cambrian boundary. In the Navezuelas section, the Ediacaran age of the lower siltstone is also uncertain but seems more likely, due to the presence of *Cloudina* in beds that do not represent an olistostromic event of uncertain timing and were deposited hundreds of meters below the level where *Cloudina* co-occur with protoconodonts, since they indicate an age very close to the Ediacaran to Cambrian boundary. Further work would be desirable to characterize the fossil record and time relationships in this area as well as in the Río Uso section.

Conclusions

A transitional Ediacaran–Cambrian biota is present in the Navezuelas stream area, with the early skeletal organism *Cloudina* co-occurring with protoconodonts similar to *Protohertzina unguiformis*. The coexistence of cloudinids and protoconodonts is here documented for the third time worldwide and implies an age very close to the Ediacaran to Cambrian boundary.

This transitional fauna suggests the biological change from the Ediacaran to the Cambrian was more gradual than previously thought, blurring the notion of a dramatic faunal boundary between Ediacaran and Cambrian times.

The Navezuelas sequence possibly records an Ediacaran–Cambrian transition, since its base contains *Cloudina* hundreds of meters below the level with protoconodonts, thus suggesting an Ediacaran age, whereas its top has Cambrian-type trace fossils, well above the protoconodonts.

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