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The Ediacaran-Cambrian Radiation of Animals within the Villuercas-Ibores-Jara UNESCO Global Geopark, Spain

Iván Cortijo[1,*], Teodoro Palacios[2], Sören Jensen[2], José María Barrera[1]

[1]Villuercas-Ibores-Jara UNESCO Global Geopark. Diputación de Cáceres. C/ Pintores nº 10, 10003 Cáceres, Spain

[2]Área de Paleontología, Faculta de Ciencias, Avenida de la Física s/n, 06006 Badajoz, Spain

Corresponding Author:
Iván Cortijo
Villuercas-Ibores-Jara UNESCO Global Geopark. Diputación de Cáceres. C/ Pintores nº 10, 10003 Cáceres, Spain
ORCID 0000-0002-6027-9002
Email: icortijo@dip-caceres.es

Abstract

Across the Ediacaran to Cambrian transition, some 541 Ma, the Earth's biosphere changed from one dominated by microbial organisms to one where multicellular organisms, including animals, rose to importance. Within a few tens of millions of years into the Cambrian Period an array of animal groups appeared, some extinct and others ancestral to modern groups, the Cambrian "explosion". Two key elements were the appearance of biomineralized hard parts and the rise of animal disturbance of the sea floor (bioturbation), which continued into the great Ordovician biodiversification event (GOBE). These events are well documented in the Villuercas-Ibores-Jara UNESCO Global Geopark (UGG) by trace fossils, carbonaceous compression fossils and fossils of some of the earliest skeletonized animals record. Simple to more complex trace fossils are evidence of the "Cambrian substrate revolution". Among carbonaceous compressions, sabelliditids provide evidence of tubular animals and vendotaenids possibly of algae. In addition, Villuercas-Ibores-Jara is the only UNESCO Global Geopark with *Cloudina*, the first described and best-known of the pioneering organisms in the acquisition of skeletons. Geosites, geological itineraries and interpretation centers in the geopark show visitors these exceptional fossils, including the holotype of *Cloudina carinata*.

Keywords: Biomineralization, *Cloudina*, Ediacaran–Cambrian transition, Sabelliditids, trace fossils, vendotaenids.

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The Ediacaran Period and the Ediacaran–Cambrian transition

The Ediacaran Period, approximately 635 to 541 Ma (Knoll *et al*. 2006; Cohen *et al*. 2013), followed some of the most severe glaciations in Earth history (Halverson *et al*. 2020), and it was the time when the first fossils of large, complex, organisms appeared. This includes the Ediacara biota, first appearing 575 Ma. Although probably including a range of organisms, they share the unusual fact of their preservation as casts and molds in sandstone and mudstone even though they had no hard parts. Their affinities have been a matter of much discussion but at least some probably were distant relatives of modern animals (e.g. Fedonkin *et al*. 2007; Xiao & Laflamme 2009; Budd & Jensen 2017; Darroch *et al*. 2018; Dunn *et al*. 2018).

Unicellular organisms dominated life on Earth for about 4 billion years. Suddenly, multicellular life (in the form of animals in relatively diverse ecosystems) made a vigorous entry at the end of the Ediacaran Period, including the first animals with a biomineralized shell and ever more diverse forms of animal interactions with sediments as seen in trace fossils (e.g. Muscente *et al.* 2018; Wood *et al*. 2019; Mángano & Buatois 2020). The reasons why animals diversified so dramatically at this time remain unsolved, although it might have been triggered by permissive levels of oxygen.

High levels of dissolved carbonate in the oceans close to the Ediacaran–Cambrian transition could have generated conditions enabling the appearance of skeletonized animals (Peters & Gaines 2012). Having to eliminate such a quantity of carbonates while filtering the water or sediments in search of food turned a waste product into a crucial tool for evolution: external and/or internal skeletons composed of mineralized tissue, a fundamental evolutionary innovation widely present in animals. Predation may also have played an important role in the origin of skeletons as an effective defense against becoming another animal's lunch (Bengtson & Zhao 1992).

The appearance of biomineralization among animals in the terminal Ediacaran was one of the most important innovations in the history of life, showing coevolution of geosphere and biosphere with evidence from bio-, litho-, and chemostratigraphy (e.g., Cui *et al*. 2019). The origin of skeletons, something that perhaps may seem unimportant to the general public, caused crucial changes in biogeochemical cycles (Cappellen 2003) and sedimentological regimes (Warren *et al*. 2013) and was a driving force behind the increased complexity of benthic ecosystems (Wood & Zhuravlev 2012; Penny *et al*. 2014; Wood & Curtis 2015) and ecological interactions (Bengtson & Zhao 1992; Schiffbauer *et al.* 2016; Becker-Kerber *et al*. 2017) .

Villuercas-Ibores-Jara UNESCO Global Geopark / geological setting

The Villuercas-Ibores-Jara UNESCO Global Geopark is located in south-central Spain, in the Community of Extremadura, Province of Cáceres. Geologically, it belongs to the Central Iberian Zone of the Iberian Massif (Fig. 1). During the Cadomian orogeny (ca. 630–550 Ma), lithospheric convergence along western Gondwana resulted in the formation of an orogenic belt flanked by adjacent fore- and back-arc basins (Sánchez-García *et al*. 2019; Álvaro *et al.* 2019). In the back-arc basin a several kilometers thick succession of deep-water shale and sandstone deposits formed, which forms the basement of the territory of the geopark, including some of the oldest sedimentary rocks of the Iberian Peninsula. Progressive collision of the arc with the margin of Gondwana from 570–535 Ma led to closure of the back-arc basin and deposition of more shallow water sediments deposits, including late Ediacaran carbonates of the Ibor Group. The remaining Cadomian suture was reactivated during the Variscan (Hercynian) and Alpine orogenies.

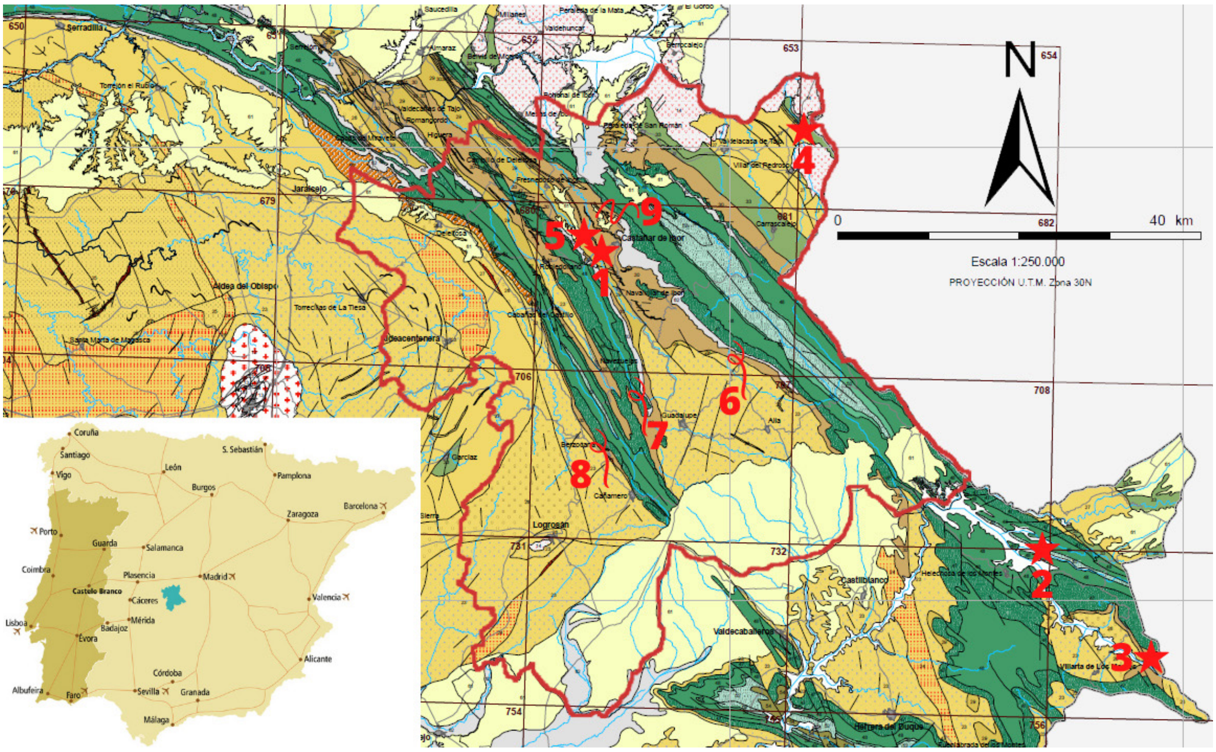

Figure 1. Location of selected fossils outcrops in the Villuercas-Ibores-Jara UNESCO Global Geopark and surroundings related with the Edacaran–Cambrian transition: *Cloudina* (Stars 1–5), carbonaceous fossils (Ribbons: 6–8) and trace fossils (Waves: 9). Geology based on "Mapa Geológico de Extremadura a escala 1:250.000". The stratigraphic units can be consulted at: http://sigeo.juntaex.es/portalsigeo/web/guest/geologia-de-extremadura

Uplift and erosion led to a significant gap in the preserved younger pre-Ordovician sedimentary record, which left us without rocks of much of the Cambrian (c. 541–486 Ma) within the territory of the geopark. However, there are small exposures of Lower Cambrian rocks within the geopark (e.g., Jensen *et al.* 2019) and well-preserved material of *Treptichnus pedum*, a trace fossil with a first appearance in the Cambrian are known from areas immediately adjacent to the geopark (Jensen & Palacios 2016).

Carbonaceous Compression Fossils

The soft tissues of organisms are made largely of organic carbon compounds (especially if the organism lacks a hard skeleton). When organic material is buried under many layers of sediment, pressure increases and heat and force gases and liquids from the organism during diagenesis. The result is a thin film of carbon residue, forming a silhouette of the original organism, called a carbonaceous film. Two types of fossils generally preserved as carbonaceous compressions in the Villuercas-Ibores-Jara UNESCO Global Geopark are vendotaenids and sabelliditids (Vidal *et al*. 1994). Vendotaenids (Fig. 2A), which to the naked eye are featureless strings, and have been interpreted as either algae or of bacterial origin. They are particularly common in late Ediacaran rocks and are known from numerous outcrops in the geopark including localities 6–8 in Figure 1, one of which has been designated a geosite (Fig. 1, locality 7, 4F). Sabelliditids are tubular fossils sometimes with a transverse external wrinkling. They may originally have had a chitinous composition and are interpreted as animals, possibly annelids (Moczydłowska *et al*. 2014). Several genera are known from upper Ediacaran and basal Cambrian sedimentary rocks. From the Villuercas-Ibores-Jara geopark are known *Sabellidites* and *Saarina* (Vidal *et al*. 1994; Jensen *et al*. 2007; Fig. 2B), with important localities at La Calera and Berzocana (Fig. 1, localities 8, 9).

Trace Fossils and Bioturbation

Trails, burrows and other types of animal-sediment interactions (bioturbation) modify the sediment (e.g. Meysman *et al*. 2008; Tarhan 2018; Darroch *et al*. 2021). Primary depositional structures are disrupted, and selective grain-size feeding generate new layering. In the absence of bioturbation oxygen is depleted a short distance below the surface, but with the presence of tubes and other forms of bioturbation, a more complex ecosystem is created with oxygen piped into the sediment. This leads to deeper colonization of micro-organism in the sediment providing a new food source for animals. In the absence of bioturbation, microbial mats form on the sediment surface, and so-called matgrounds were prevalent before the appearance of sediment disruption by animals. The increase of bioturbation from approximately 541 Ma had far-reaching impact on sediment properties and benthic ecology, termed the "Cambrian Substrate Revolution" and "Agronomic revolution", an early example of ecosystem engineering (e.g., Herringshaw *et al*. 2017).

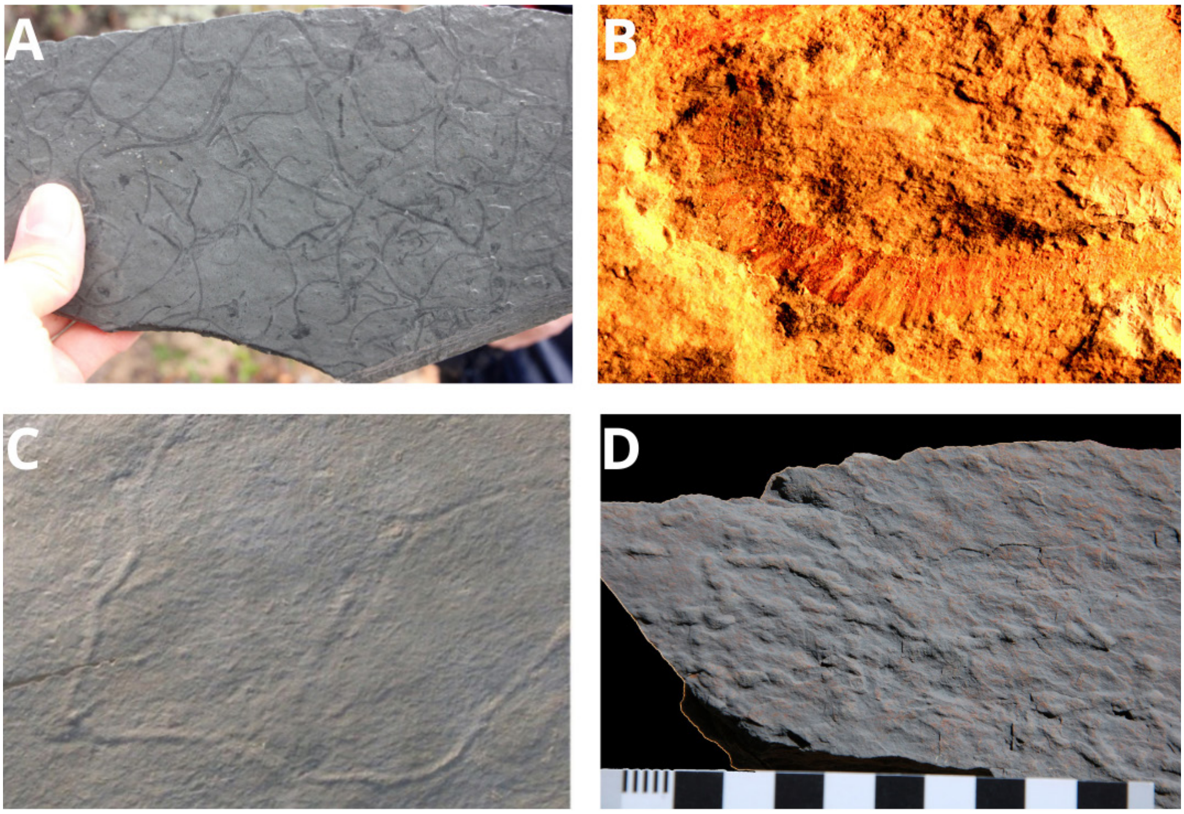

Figure 2. Carbonaceous compression fossils and trace fossils: A) Fresh sample with vendotaenids and possible sabelliditids. Image taken during the pre-conference field trip of the International Meeting on the Ediacaran System and the Ediacaran–Cambrian Transition, at geosite in La Villuerca geological itinerary (locality 7 in Fig. 1; 4F). B) Portion of a weathered sabelliditid with characteristic transverse wrinkles. The fossil is approximately 2 mm wide. Locality 6 in Fig. 1. C) Simple horizontal trace fossils, approximately 2 mm wide, from late Ediacaran rocks near Navalvillar de Ibor. D) *Treptichnus pedum*, a typical Cambrian trace fossil with probe-like branching from the Fortunian Arrocampo Formation (Ibor Group), adjacent to the geopark.

Trace fossils provide the earliest widely accepted evidence for animals with bilateral symmetry, found in sedimentary rocks from about 560 Ma onwards (Budd & Jensen 2017). Late Ediacaran trace fossils are simple horizontal superficial forms extending at the most a few millimeters into the sediment. Observed in vertical section there is no real sediment disruption. In the Villuercas-Ibores-Jara UNESCO Global Geopark this type of trace fossil is rarely seen in the Ibor Group (Fig. 2C). In rocks of Cambrian age infaunal activity is more prominent, with the appearance of more complex branching burrow systems, vertically orientated burrows and relatively large trace fossils, some more than a centimeter wide. In the Villuercas-Ibores-Jara UNESCO Global Geopark such trace fossils have been observed in Cambrian sandstone at north of Castañar de Ibor (locality 9 in Fig. 1; Jensen *et al*. 2019), and particularly well-preserved material is known from adjacent areas (Fig. 2D). The Villuercas-Ibores-Jara geopark offers the possibility to compare the modest sediment disturbance in lower Cambrian rocks with the much more dramatic exploitation of the sediment seen in Ordovician rocks (see Neto de Carvalho *et al*. 2021 in this volume).

Cloudina **and the Appearance of Animal Hard Parts/Skeletons**

The appearance of hard parts played an important role in the Cambrian diversification of animals (e.g., Wood *et al*. 2019). Hard parts serve a variety of functions, such as protection against predation and ambient conditions, attachment and sites of muscle leverage. The appearance of biomineralized hard parts also increased the likelihood of animal fossil preservation and provided a new source of material for the formation of sediments. Cambrian carbonate rocks often contain a great diversity of tubes, spines and other hard parts. Among the rich diversity of late Ediacaran mineralized, weakly mineralized or non-mineralized tubular fossils cloudinomorphs share a construction of repeated nested units (Selly *et al*. 2019). The best known of the mineralized cloudinomorphs is *Cloudina*, a millimetric tubular fossil composed of weakly mineralized (high-Mg calcite, Wood & Zhuravlev 2012) stacked funnel-shaped elements. *Cloudina* has been found in late Ediacaran (about 550–539 Ma) rocks from Namibia, South China, Oman, Siberia and several localities in North and South America. In Europe *Cloudina* is known from Spain only, including localities in the Villuercas-Ibores-Jara Geopark (Cortijo *et al*. 2010a,b, 2015a; Fig. 1, localities 1 and 5) and surrounding areas (Fig. 1, localities 2, 3). The species *C. carinata* was first described on material from Spain (Cortijo *et al*. 2010a) but was later reported from Brazil (Adôrno *et al*. 2019) and, more controversially, Siberia (Terleev *et al*. 2011).

Cloudina fossils from China and Spain have yielded the oldest evidence of asexual reproduction (e.g., Cortijo *et al*. 2010a, b, 2015a, b), and fossils from China the proposed oldest reconstructed ontogeny (Cortijo *et al*. 2015b). *Cloudina* from China and Brazil with circular perforations have been interpreted as evidence of early predation (Bengtson & Zhao 1992; Hua *et al*. 2003; Becker-Kerber *et al*. 2017). Putative evidence for the earliest known guts has been found in cloudinids from western USA (Schiffbauer *et al*. 2020). *Cloudina*, and cloudinids, have generally been interpreted as cnidarians, but recent data suggest they might be basal annelids (Schiffbauer *et al*. 2020; Yang *et al*. 2020).

Cloudina, and other early biomineralized fossils, were usually found with different kinds of microbialites (e.g., Hofmann & Mountjoy 2001; Grotzinger *et al*. 2005; Warren *et al*. 2011; Cai *et al*. 2014; Becker-Kerber *et al*. 2017; Álvaro *et al*. 2020). The intimate association between *Cloudina* and biofilms, together with the deposition of early cements inside the flanges of *Cloudina* (Grant 1990; Cortijo *et al.* 2010a; Becker-Kerber *et al.* 2017) possibly also influenced the construction of the ancient metazoan-built reefs, with *Cloudina* as a frame-work builder, from Namibia and Spain (e.g., Penny *et al*. 2014; Álvaro *et al*. 2020). The

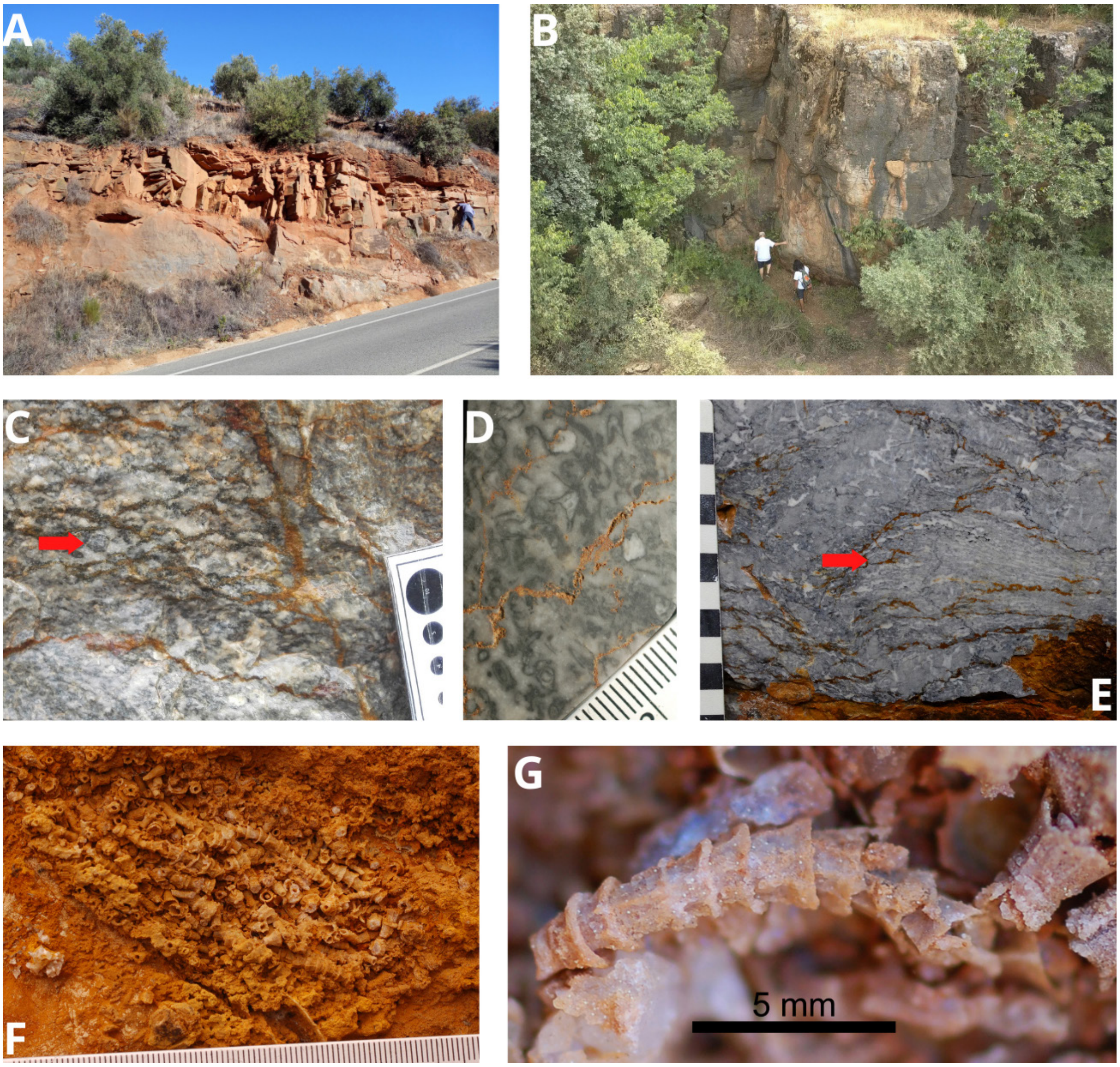

Figure 3. *Cloudina*-bearing outcrops and specimens: A) View of the classical *Cloudina* locality within the geopark, not safe for geotourism due to the busy road. B) Drone image of the new *Cloudina* geosite at Cerro La Mina. C) Fresh surface of the road-side outcrop showing accumulation of *Cloudina* shells; note the polygonal *C. carinata* specimen (arrow). D) Polished section of block from the road-side outcrop with abundant diverse sections through *Cloudina*. E) Polished surface in the new geosite showing accumulation of shells and stromatolitic structure (arrow). F) Detail of a surface of large carbonate block exposed in the Geopark Visitors' Reception Centre in Cañamero village (see Fig. 4B).G) *Cloudina carinata* type specimen from the same block.

mode of feeding of these animals is not known but they plausibly were suspension-feeders. As such they would have exploited plankton and the rise of suspension-feeders would have had a strong impact on early ecosystems by strengthening the planktic-benthic energy flow (Wood & Curtis 2015).

In addition, *Cloudina* has been proposed as a latest Ediacaran index fossil, with an age between 550 and ~539 Ma (e.g., Grant 1990; Linnemann *et al*. 2019), although there is growing evidence for earliest Cambrian cloudinids.

Villuercas-Ibores-Jara is the only UNESCO Global Geopark with *Cloudina*, which makes it a unique destination. These fossils, in addition to the Appalachian relief and the Natural Monument of the Castañar de Ibor Cave, are three of its main geological attractions.

Within the Villuercas-Ibores-Jara UNESCO Global Geopark *Cloudina* is found in the Ibor Group, which stretches in a NW–SE trending band for at least 400 km in the Central Iberian Zone (Fig. 1). Although dominated by dark, laminated siliciclastic sediments, the Ibor Group includes two carbonate levels (Cortijo *et al*. 2010a, b, 2015a; Álvaro *et al*. 2019, 2020). These shallow water carbonates were the source for blocks of carbonates in olistostromes, which have yielded some of the best-preserved material of *Cloudina* (Fig. 3F, G). An olistostrome is found in the geopark at Arroyo Pedroso (Fig. 1, locality 4). Fossils are poorly preserved in this olistostrome but it is important in broadening the inventory of sedimentary deposits that can be observed in the geopark. The classic locality for *Cloudina* in the geopark is along road EX-386, which is the "Yacimiento del arroyo de la Fuente – deposit of the Fuente stream site" (Fig. 1, locality 1; 3A, C, D). A geosite known as Cerro de la Mina, more appropriate for visitors has been developed in an outcrop along a dirt road leading north off EX-386 (Fig. 1, locality 5; 3B). Several areas of the carbonate "wall" at this site have been polished, which facilitates observation of different sections through *Cloudina* (Fig. 3C, D) and sedimentary features such as stromatolites (Fig. 3E). *Cloudina* generally is not a spectacular fossil when observed in section and the visitor is therefore provided with information that helps relate what is seen to that of three-dimensionally preserved material (Fig. 3F). A particularly impressive example of 3D *Cloudina* through secondary silica impregnation can be observed in the Geopark Visitors' Reception Centre in Cañamero village (Fig. 4B). This unique block also contains the holotype of *Cloudina carinata* (Fig 3G).

The Villuercas-Ibores-Jara UNESCO Global Geopark, Witness of the Evolution of Life

UNESCO Global Geoparks seek to tell the history of our planet through their rocks, minerals, fossils, landscapes, etc. The fossils described above make the Villuercas-Ibores-Jara UNESCO Global Geopark a unique place in which to understand two key early evolutionary steps: the appearance of multicellular organisms and their acquisition of skeletons, closely related with the Cambrian "explosion", and the "Cambrian substrate revolution" and the later Ordovician radiation that forged modern biodiversity.

From a scientific point of view, these fossils make the geopark a highly interesting place for research and events such as meetings. In 2019 the International Meeting on the Ediacaran System and the Ediacaran–Cambrian Transition was held in Guadalupe village (Fig. 4A, B). It was organized by the geopark, together with the University of Extremadura, the IGEO (Institute of Geosciences, Madrid), and the International Commission on Stratigraphy. Over eight days, 105 researchers from universities and research centers from 18 countries participated in field trips, conference presentations and discussions. The most recent advances on sedimentology, geochemistry, paleomagnetism and paleontology of the Ediacaran System and its boundaries were presented (meeting proceedings are open access in *Estudios Geológicos* vol. 75(2) http://estudiosgeol.revistas.csic.es/index.php/estudiosgeol/issue/view/101) while the participants enjoyed the unique fossils of the geopark (Fig. 4B), and they learned about the cultural and natural heritage of the area. The geopark was chosen for this meeting for the exceptional nature of the outcrops of the Ediacaran Period, including the Ediacaran–Cambrian transition, and the importance of the fossils.

These fossils allow to the educational project of the geopark ("Geocentros") to use them as a tool to give school pupils the opportunity to learn about these events in a privileged way. *Cloudina*

Figure 4. Paleontology of the Ediacaran–Cambrian transition in the geopark's infrastructures and activities: A) Poster of the International Meeting on the Ediacaran System and the Ediacaran–Cambrian Transition held in the geopark in 2019; note the logo of the meeting and the main image showing a *Cloudina*. B) Participants of the meeting admiring carbonate boulder with three-dimensionally preserved *Cloudina* exposed in the Geopark Visitors' Reception Centre in Cañamero village. C) The Timeline wall Edusite in the Fausto Maldonado Primary School of Cañamero village. D) Detail of the wall with a student talking about *Cloudina* in an activity. E) A student acting as *Cloudina* during a function in the Geoconvivencia. F) Rock with vendotaenids installed in geosite in La Villuerca geological itinerary so that visitors can safely observe the fossils. G) Panel installed in Cerro La Mina geosite with the interpretation of *Cloudina* and the Ediacaran–Cambrian ecosystem of the geopark. H) Advertising poster for the premiere of the documentary film *The Importance of Being Hard* (artwork by Manuel García). I) The *Cloudina* card game, an example of educational material (artwork by Jesús Vázquez).

is one of the geopark's milestones and is represented in the first "Edusite": the Timeline wall in the school playground of the Fausto Maldonado Primary School of Cañamero village (Fig. 4C, D). This Edusite combines urban art, attractive for students, with the dissemination of geosciences. It was the result of activities carried out over three months by teachers, students and the parents' association (AMPA). Students (and all the educational community) learn about the history of our planet and they in turn pass this on to other students who visit their school (Fig. 4D). *Cloudina*, and fossils in general, are also a recurring subject in the Geoconvivencia, a daylong celebration activity that brings together all the Geocentros (and eventually educational centers of other geoparks) every year during European Geoparks Week. It consists of educational activities and a seminar in which students share their knowledge about the geological, natural and cultural heritage of the geopark through performances, videos, and large format publications – even dressing up as *Cloudina* (Fig. 4E). Several educational resources have been developed and produced by the Educational and Scientific Committee and the Geocentros Educational Working Group, including books and fossil replicas. Among the most successful are card games for the youngest pupils (Fig. 4I) by which they become familiar with fossils and their importance.

Touristically and promotionally speaking, fossils are a valuable attraction. As an example, *Cloudina* from the geopark had a key role in the documentary film *The Importance of Being Hard* made by the Spanish film company Libre Producciones with the support of Villuercas-Ibores-Jara and Naturtejo UNESCO Global Geoparks. The premier of this documentary was held in 2019 in the Museo Nacional de Ciencias Naturales (National Museum of Natural Sciences) in Madrid. The documentary is about the evolutionary implications of mineralized skeletons, but also about the Cambrian "explosion", the Ordovician radiation and also the Anthropocene (Fig. 4H).

Visitors to the geopark can observe and learn about these fossils in the interpretation centers of the geopark, especially in the Geopark Visitors' Reception Centre in Cañamero village, where a block with silicified specimens of *Cloudina*, including the holotype of the species *C. carinata* is exposed, allowing for an easy observation (Figs. 3 F, G, 4B). Fossils can also be seen in the Fossil Interpretation Center in Navatrasierra village and in the Vicente Sos Baynat geo-mining museum in Logrosán village. Several of the geological itineraries and touristic routes of the geopark include, or pass close to, the outcrops. The La Villuerca geological itinerary includes the vendotaenid Geosite (Fig. 4F). *The Bridge over the Armorican Quartzite* touristic route, anchored in the geological heritage but also the natural and cultural heritage of important natural areas of high scenic value within the Naturtejo and Villuercas-Ibores-Jara UNESCO Global Geoparks, the Canchos de Ramiro and the Sierras of Cañaveral Natura 2000 sites, and the Monfragüe and Tejo-Tajo International Transboundary Biosphere Reserves, includes an alternative itinerary to the Castañar de Ibor cave and the Cerro La Mina Geosite (Figs. 3B, E, 4G). Some stages of the route, which transects the geopark from east to west include this and other geosites or outcrops. The interpretation panels offer visitors accessible information about these fossils with eye-catching illustrations bringing to life diverse ancient ecosystems (Fig. 5), in addition to informing about basic rules for the conservation and preservation of outcrops and geosites (Fig. 4G). Prepared rock samples (e.g., polished surfaces; Fig. 3E) or mounted material (Fig. 4F) make it easy for visitors to observe the fossils without any risk.

The presence of these fossils makes the Villuercas-Ibores-Jara UNESCO Global Geopark a unique place in which to learn about this fundamental stage of our planet and the evolution of life on it. Geosites, routes, interpretation centers and educational materials ensure that experts and the general public can enjoy its exceptional paleonto-

Figure 5. Palaeontology of the Ediacaran–Cambrian transition in the geopark's infrastructures and activities: Detail of the reconstruction of the Ediacaran–Cambrian ecosystem of the Geopark used in panels, leaflets, etc.; stromatolites –right back, vendotaenids –center, sabelliditids –right front, and *Cloudina* –left (artwork by Antonio Grajera).

logical heritage, which has become a valuable tool for developing the territory through education and geotourism.

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Conflict of Interest

The authors have no known conflict of interest.

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