



UNIVERSIDAD DE EXTREMADURA



ESTUDIO DE LOS PRIMEROS METAZOOS MINERALIZADOS DEL REGISTRO GEOLÓGICO

TESIS DOCTORAL

**ESTUDIO DE LOS PRIMEROS METAZOOS
MINERALIZADOS
DEL REGISTRO GEOLÓGICO**

IVÁN CORTIJO SÁNCHEZ

**DEPARTAMENTO DE BIOLOGÍA VEGETAL,
ECOLOGÍA Y CIENCIAS DE LA TIERRA**

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DEPARTAMENTO DE BIOLOGÍA
VEGETAL, ECOLOGÍA Y CIENCIAS
DE LA TIERRA

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CERTIFICAN:

Que la presente Tesis Doctoral, titulada **“ESTUDIO DE LOS PRIMEROS METAZOOS MINERALIZADOS DEL REGISTRO GEOLÓGICO”** [**“STUDY OF THE FIRST BIOMINERALIZING METAZOA”**], de la que es autor IVÁN CORTIJO SÁNCHEZ, ha sido realizada bajo nuestra dirección en el Área de Paleontología del Departamento de Biología Vegetal, Ecología y Ciencias de la Tierra de la Facultad de Ciencias de la Universidad de Extremadura.

Que revisada la memoria presentada, los Directores del trabajo consideran que posee las condiciones requeridas para un Trabajo de Tesis Doctoral. Por todo ello

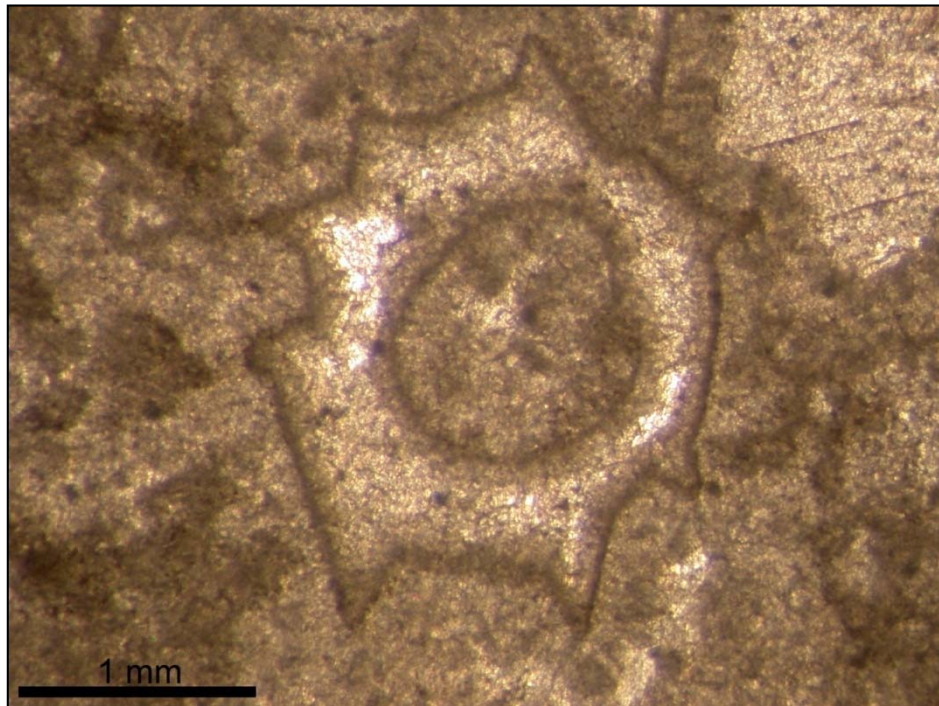
AUTORIZAN:

Su presentación y defensa pública ante el tribunal designado al efecto. Y para que así conste y surta los efectos oportunos expido el presente certificado en Badajoz a de de 2015.

Fdo. Rolf Sören Jensen

Fdo. Mónica Martí Mus

Fdo. Teodoro Palacios Medrano



"Consequently, if my theory be true, it is indisputable that before the lowest Silurian stratum was deposited, ... the world swarmed with living creatures." (Darwin, The Origin of Species, 1859).

"...porque cada mutación prepara el terreno para un nuevo cambio." (Maquiavelo, El Príncipe c. II p. 7, 1513).

Image: cross-section of a *Cloudina carinata* specimen in a thin section from El Membrillar locality. Image taken 03/03/2004. It was the beginning of all this...

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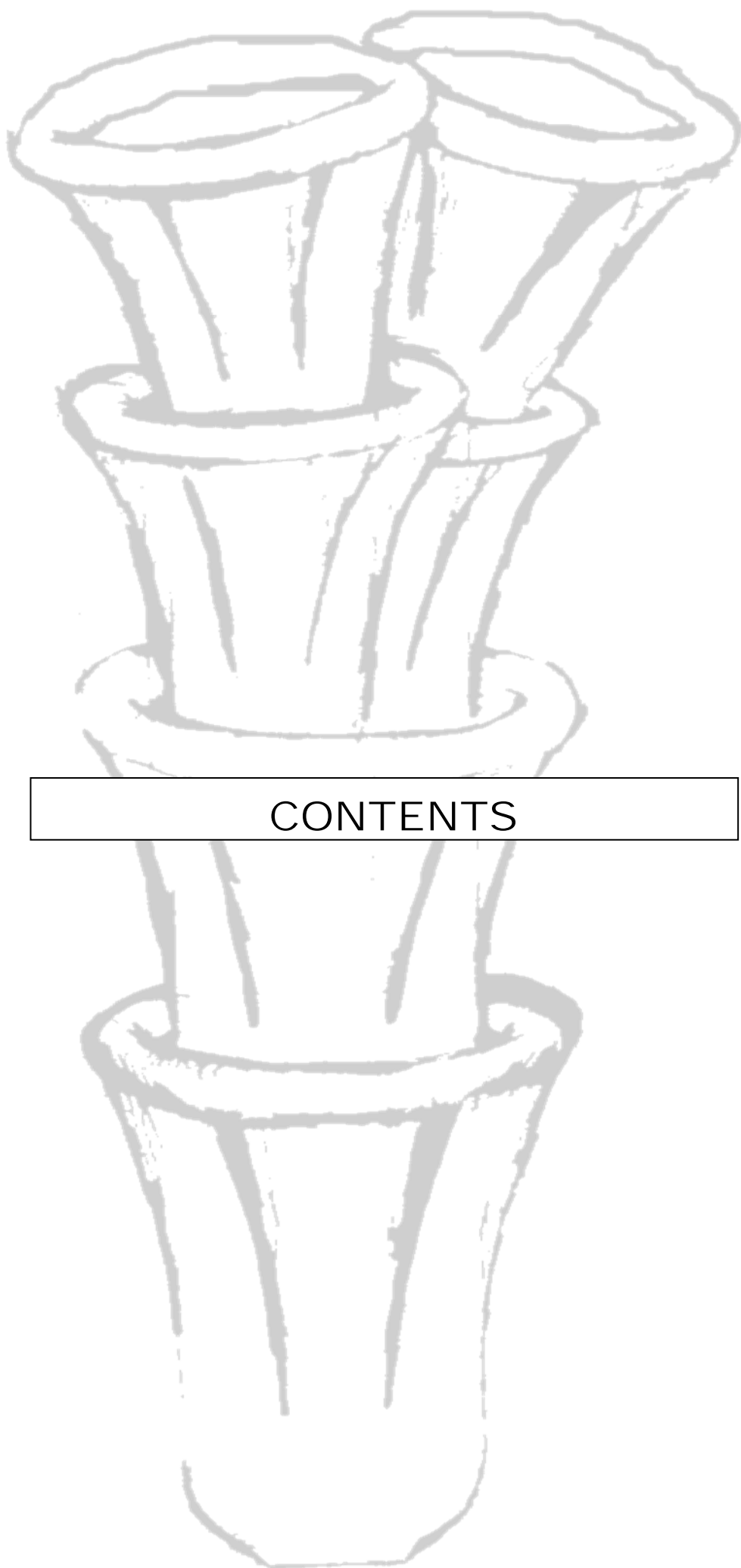
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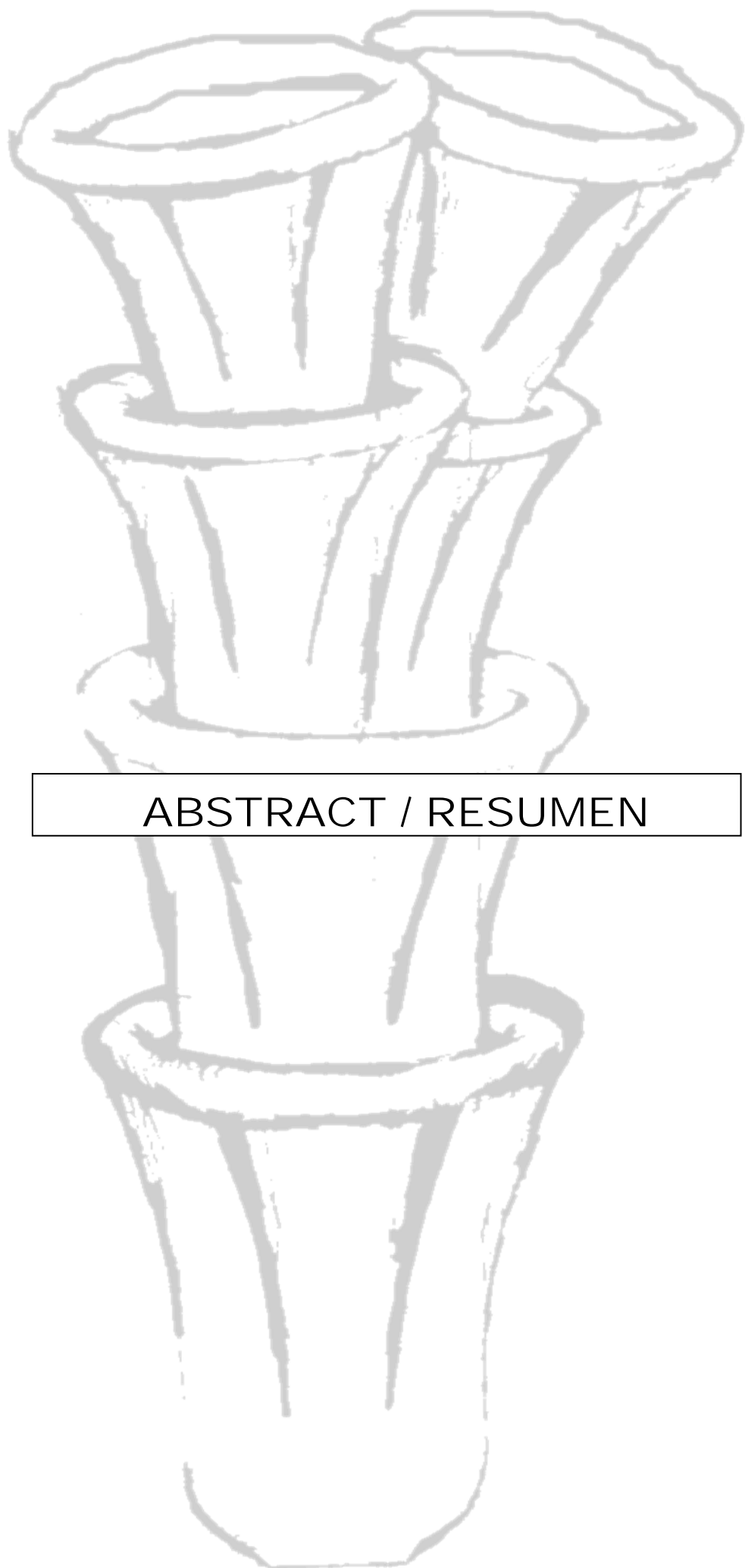


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ABSTRACT / RESUMEN

ABSTRACT

Over the last several decades mineralized fossils have been described from late Ediacaran rocks all over the world, and have been interpreted as the first metazoans capable of secreting a mineralized skeleton, which makes them highly significant from the standpoint of biological evolution. Several genera of these early biomineralizers have been described, the most abundant and widespread of them being the tubular *Cloudina* and *Sinotubulites* and the goblet-shaped *Namacalathus*.

In Spain Ediacaran skeletal fossils occur in association with a carbonate level of the Ibor Group (and a related olistostromic level of the Río Huso Group) which crops out in numerous localities in central Spain. Although the presence of *Cloudina* in some of these localities is known since the '80s, the fossils had never been studied in detail. This thesis represents the first in-depth study of the Ediacaran skeletal fossils in central Spain and includes a study of comparable fossils from South China.

Two previously known *Cloudina*-bearing localities of central Spain, Villarta de los Montes and El Membrillar (Badajoz Province), have been studied in detail during this thesis. They have yielded some of the best preserved early skeletal fossils worldwide, including a new species of *Cloudina*, *Cloudina carinata*. Additional outcrops of terminal Ediacaran carbonates (some within the Villuercas-Ibores-Jara Geopark) have been studied in search for fossils. A locality in the Arroyo del Cubilar area (Toledo Province) shares features in common with that from El Membrillar, including the presence of silicified specimens of *C. carinata*.

Cloudina carinata, like the type species, *C. hartmanae*, is a millimetric tubular fossil, consisting of several nested funnels, but has a distinct morphology characterized by external longitudinal crests and funnels with a thickened apertural rim and a basal, slightly constricted circular opening. Successive funnels appear less deeply imbricated than in the type species. The evidence of tube disarticulation in the studied material of *C. carinata*, particularly the abundance of loose funnels, indicates that *Cloudina* funnels were secreted as independent elements, not fused to the previous ones. However, they could become fused during the life of the organism through the precipitation of inorganic cements between their walls. *C. carinata* shows evidence of asexual reproduction by branching, a feature previously reported in the type species.

C. carinata has only been described from the Ibor Group and occurs both in El Membrillar and in Villarta de los Montes. It is the only species described in El Membrillar, but in Villarta it co-occurs with other skeletal fossils, in a diverse fossil assemblage dominated by both species of *Cloudina*, *C. hartmanae* and *C. carinata*. The multilayered tubular fossil *Sinotubulites baimatuoensis*, reported for the first time from Spain (and Northwestern Gondwana) is also abundant, as well as small, long, tubular fossils which show characteristic twists and constrictions along their length. These later tubes may represent a new taxon of Ediacaran skeletal fossils. A globular fossil that co-occurs with *Cloudina* and *Sinotubulites* in some localities of South China has also been found. The Villarta de los Montes assemblage most closely compares to that from the Dengying Formation of South China.

The Dengying Formation from South China, as it crops out in the Lijiagou section, has yielded some of the best preserved material of *Cloudina*. Previous studies on this material have shown that *Cloudina* tubes grow from a closed cone with a rounded base and that they occasionally branch. New material from the Lijiagou section has shown that some tubes have a pointed base instead of a rounded one. Comparisons of these specimens with newly formed branches suggest that they may represent branches that have detached from their parent tubes. This interpretation implies that *Cloudina* could disperse both through sexual and asexual reproduction.

RESUMEN

En las últimas décadas se han descrito en rocas del Ediacárico terminal de todo el mundo fósiles mineralizados que han sido interpretados como los primeros metazoos capaces de secretar un esqueleto mineralizado, lo que les convierte en muy importantes desde el punto de vista de la evolución. Varios géneros de estos primeros biomineralizadores han sido descritos, siendo los más abundantes y extendidos los tubulares *Cloudina* y *Sinotubulites* y el globular pedunculado *Namacalathus*.

Los fósiles esqueléticos ediacáricos en España aparecen asociados a un nivel de carbonatos del Grupo Ibor (y a un nivel olistostrómico relacionado del Grupo Río Huso) que aflora en numerosos yacimientos en el centro de España. Aunque la presencia de *Cloudina* en alguno de ellos es conocida desde la década de los 80, los fósiles nunca habían sido estudiados en detalle. Esta tesis representa el primer estudio en profundidad de los fósiles esqueléticos del Ediacárico del centro de España, e incluye el estudio de fósiles comparables de China.

Dos localidades con *Cloudina* previamente descritas en el centro de España, Villarta de los Montes y El Membrillar (en la provincia de Badajoz), han sido estudiadas en detalle en esta tesis. En ellas se han obtenido algunos de los fósiles esqueléticos tempranos mejor conservados del mundo, incluyendo una nueva especie de *Cloudina*, *Cloudina carinata*. Otros afloramientos de carbonatos del Ediacárico terminal (varios en el territorio del Geoparque Villuercas-Ibores-Jara) han sido estudiados en busca de fósiles. Un yacimiento en el área del Arroyo del Cubilar (provincia de Toledo) comparte características con el de El Membrillar, incluyendo la presencia de ejemplares silicificados de *C. carinata*.

Cloudina carinata, como la especie tipo *C. hartmanae*, es un fósil tubular milimétrico consistente en varios elementos en forma de embudo imbricados, pero tiene una morfología distintiva caracterizada por crestas longitudinales externas, elementos con el borde distal engrosado y un orificio circular ligeramente constreñido en la parte basal. Los sucesivos elementos están imbricados de forma menos profunda que los de la especie tipo. La evidencia de desarticulación en el material de *C. carinata*, especialmente la presencia de numerosos elementos aislados, indica que estos elementos eran secretados de forma independiente y no estaban fusionados a los anteriores. Sin embargo, podrían

haberse fusionado durante la vida del organismo mediante la precipitación de cementos inorgánicos entre las distintas paredes. *Cloudina carinata* muestra evidencias de reproducción asexual, algo descrito previamente en la especie tipo.

C. carinata sólo ha sido descrita en el Grupo Ibor y aparece tanto en El Membrillar como en Villarta de los Montes. Es la única especie descrita en El Membrillar, pero en Villarta aparece con otros fósiles esqueléticos en una asociación fósil diversa dominada por ambas especies de *Cloudina*, *C. hartmanae* y *C. carinata*. En esta asociación aparece también el fósil tubular multilaminado *Sinotubulites baimatuoensis*, descrito por primera vez en España (y en el noroeste de Gondwana), así como pequeños fósiles tubulares con curvas y constricciones características, que podrían constituir un nuevo taxón de fósiles esqueléticos ediacáricos. También ha sido encontrado un fósil globular que co-ocurre con *Cloudina* y *Sinotubulites* en algunos yacimientos de China. La asociación de fósiles de Villarta de los Montes es similar a la que se ha descrito en la Formación Dengying de China.

La Formación Dengying, sobre todo en la sección Lijiagou, ha dado algunos de los ejemplares mejor conservados de *Cloudina*. Estudios previos de ese material han mostrado que los tubos de *Cloudina* crecen a partir de un elemento cerrado de base esférica y que se ramifican ocasionalmente. Nuevo material de Lijiagou muestra que algunos tubos tienen una base puntiaguda en vez de redondeada. Las semejanzas entre estos ejemplares y aquellos formados durante la ramificación, sugieren que podrían representar “ramas” desprendidas del tubo original. Esta interpretación implica que *Cloudina* podría dispersarse tanto mediante reproducción asexual como mediante reproducción sexual.



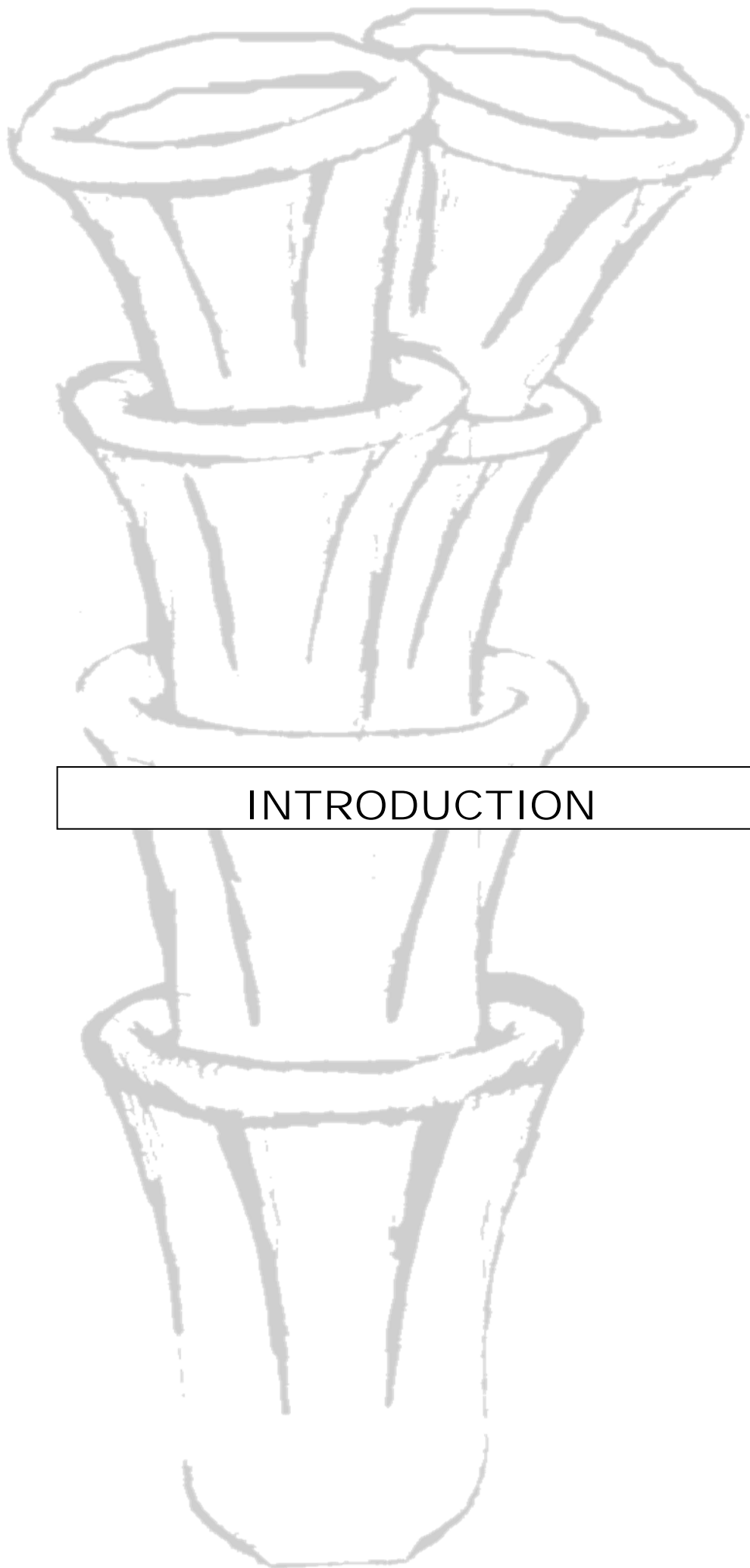
OBJECTIVES

OBJECTIVES

The aim of this thesis was the in-depth study of the first biomineralizing metazoans, focusing in those from the late Ediacaran Ibor Group, Central Iberian Zone, primarily within the area of Extremadura. The thesis also includes a study of comparable late Ediacaran skeletal fossils from South China.

The detailed objectives were:

- 1.- To study the late Ediacaran localities in the area of Extremadura, Spain, and their stratigraphic context.
- 2.- To study the diversity and morphology of the various late Ediacaran skeletal fossils found in the studied localities.
- 3.- To compare the Spanish fossils with those from other geographic areas, particularly with the exceptionally preserved material from South China.
- 4.- To explore the broader implications of the new findings.



INTRODUCTION

INTRODUCTION

The Ediacaran Period

Ratified in 2004 by the International Union of Geological Sciences (IUGS), the Ediacaran Period (ca. 635–542 Ma) is the latest official period added to the Geologic Time Scale, and the only one in more than a century. The period, named after the Ediacara Hills of South Australia, includes the last Ma of the Neoproterozoic Era, and precedes the Cambrian Period, and therefore the Phanerozoic Eon. Its lower boundary is identified worldwide by perturbations in C-isotopes and the occurrence of a unique “cap carbonate” precipitated as a consequence of the end of the global Marinoan glaciation. Its upper limit concurs with the base of the Cambrian system, defined on the trace fossil *Treptichnus pedum*, a somewhat complex trace fossil (Jensen et al., 2000; Knoll et al., 2004, 2006).

Life before this time was relatively elemental in its organization level: most organisms were simple and composed of individual cells, occasionally organized into colonies or filaments. The earliest known macroscopic, complex organisms appeared ca. 575 million years ago and are called “the Ediacaran biota”.

Ediacaran biota

It is believed that the Ediacaran sea-floor was dominated by microbial mats, and that there was a diversity of organisms associated with them: anchored and embedded in, grazing on or burrowing just under the mats. The Ediacaran biota comprises more than 100 genera which include enigmatic forms like the frond-shaped *Charnia*, *Charniodiscus* and *Rangia*, the discoidal *Ediacaria*, the sand-filled bag *Pteridinium*, and other fossils of uncertain interpretation like *Arkarua*, *Dickinsonia*, *Spriggina*, *Tribrachidium*, and *Parvancorina*. Other Ediacaran fossils have been interpreted as possible early members of living phyla, like the mollusk-like *Kimberella*. All these intriguing organisms are known thanks to the window to the past provided by exceptional preservation sites –*lagerstätten*–, among which are the following localities: Ediacara Hills (Australia), Mistaken Point (Canada), and localities in southern Namibia and the White Sea region (Russia).

Despite their diversity, all the organisms included in the so called “Ediacaran biota” have a common feature: they appear to have been soft bodied.

The Cambrian Explosion

The so called Cambrian Explosion consisted in the relatively sudden appearance of most major animal phyla, followed by their rapid diversification. New niches, like the infaunal realm (organisms began to burrow vertically) and the water column, were occupied for the first time by animals comparable to those of recent times (e.g. the arthropods *Marrella* and *Canadaspis*, brachiopods similar to *Lingula*, the polychaete worm *Canadia*, sponges like *Choia*, priapulids, etc.), and by others with no obvious modern relatives (problematic regarding their phylogenetic relationships, such as armored lobopods like *Hallucigenia*, the probable stem-group arthropods *Anomalocaris* and *Opabinia*, the likely early lophotrochozoan hyoliths and *Wiwaxia*, or the even more problematic *Eldonia*, *Pikaia* and *Nectocaris*). These organisms have been described from several *lagerstätten*, particularly those known as Chengjiang (China), Sirius Passet (Greenland) and Burgess Shale (Canada).

The Cambrian Explosion included a crucial event in the history of life: the acquisition of mineralized skeletons in many animal lineages. Shells, sclerites, thorns and plates became common in many groups of animals. It is hypothesized that the acquisition of hard parts provided some evolutionary advantage in the “new”, competitive Cambrian ecosystems.

The first biomineralizers

Although the Cambrian Explosion is characterized by the radiation of many biomineralizing lineages, the first biomineralizing metazoans appeared at the end of the Ediacaran Period. Mineralized tubes, basal supportive skeletons and stalked tests appeared during the last million years of this period (Bengtson, 2005).

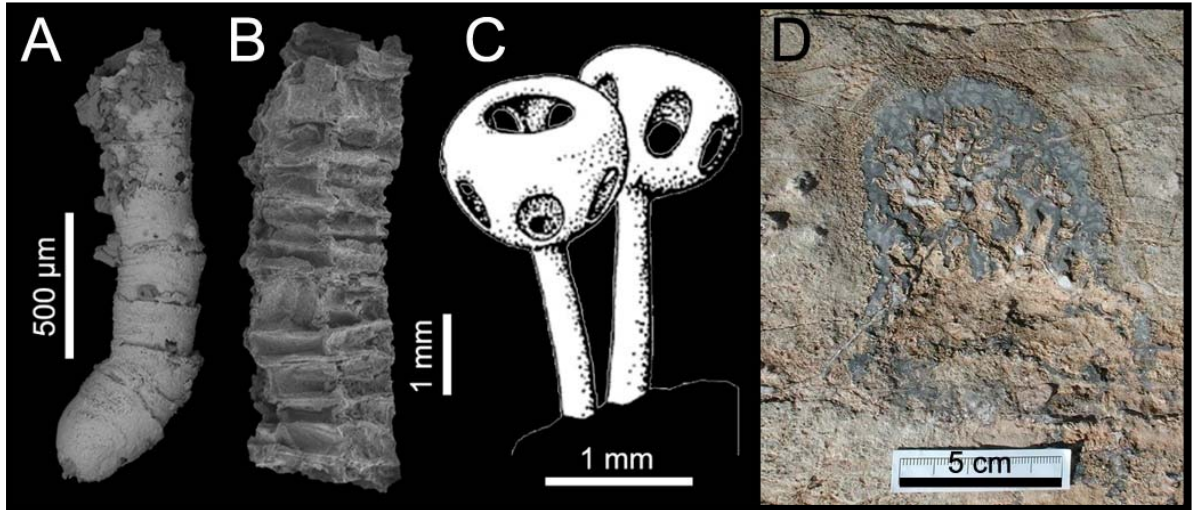


Fig.1. (A) *Cloudina* from China (modified from Cortijo et al., 2014). (B) *Sinotubulites* from China (modified from Sun et al., 2012). (C) Reconstruction of *Namacalathus* (modified from Seilacher et al., 2003). (D) *Namapoikia* from Namibia (modified from Wood et al., 2002).

Fossils older than the Ediacaran Period (~750 Ma) indicate that mineralization was probably present in small photosynthetic algae, presumably as a defense from single-celled eukaryotic predators (Cohen et al., 2011; Porter, 2011). However, uncontroversial biomineralized skeletons in animals first appear in the late Ediacaran (Fig. 1). Fossil genera

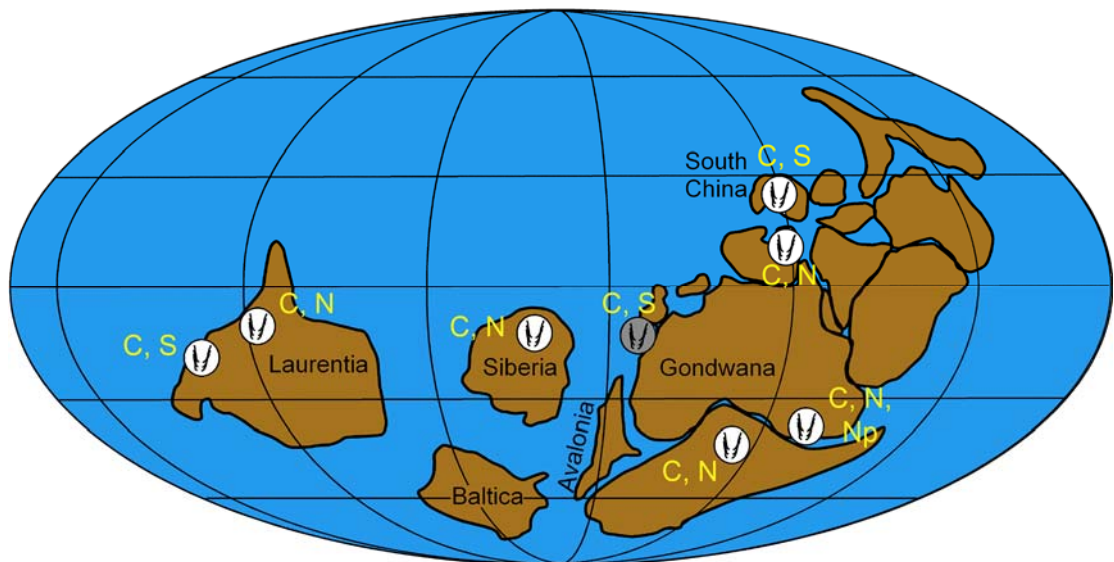


Fig. 2. Paleogeographical reconstruction of the late Ediacaran (based on McKerrow et al., 1992 fig.1) with reported occurrences of biomineralized fossils indicated (C – *Cloudina*, S – *Sinotubulites*, N – *Namacalathus*, Np – *Namapoikia*); symbol for Spain is shaded.

such as *Cloudina*, *Sinotubulites*, *Namacalathus* and *Namapoikia* (Figs. 1–2), are the pioneers (and may include the ancestors) of the diverse biomineralizing metazoans that radiated during the Cambrian Period. Although different genera and species of these first biomineralizers have been described, their detailed morphology, ontogeny, lifestyle, and many aspects of their diversity and phylogeny remain poorly understood.

Biomineralization and the importance of skeletons

As mentioned above, biomineralization is a critical evolutionary event, and all the major divisions of the animal tree, as well as many protists and algae, have groups with mineralized skeletons, therefore these are found “in an astounding range of grades of organization, body plan and function” (Murdock and Donoghue, 2011 p. 99).

The apparently sudden emergence of mineralized skeletons in the latest Ediacaran and their widespread presence in the Early Cambrian has been explained by different hypotheses including geochemical and physical changes in seawater, substrate colonization strategies (e.g. in shallow carbonate environments), defense against predators, support for increased body size, mechanical support, etc. (e.g., Valentine, 2002; Knoll, 2003; Bengtson, 2004, 2005; Hua et al., 2007; Porter, 2011; Wood, 2011). It is accepted that skeletons have evolved multiple times among animals, therefore the selective pressures favoring their evolution may have been different in different lineages. However, it may not be a coincidence that all the first biomineralizers, which hardened their skeletons with calcium carbonate, are supposed to have lived in shallow marine carbonate settings (e.g. Wood, 2011; Warren et al., 2011, 2013, 2014; Penny et al., 2014; Cai et al., 2014; Wood and Curtis, 2014). Also, although there are alternative ways to get a hardened skeleton (particularly agglutination and sclerotization of organic molecules), biomineralization is more effective for mechanical support, and biominerals are cheaper to produce, since they can be more or less directly absorbed from the environment (e.g. Bengtson, 1994).

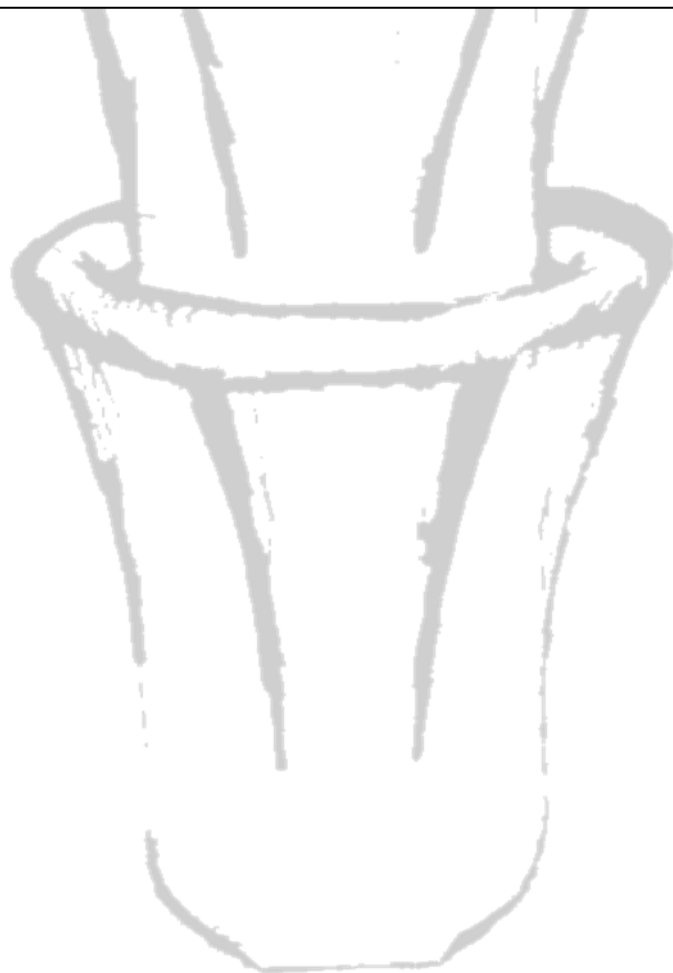
History of research on late Ediacaran skeletal fossils in central Spain

The earliest mention of Ediacaran skeletal fossils from Spain was a reference to tubular fossils from the locality Castañar de Ibor as “Calcareous microfossils related to annelid polychaetes... are the oldest record of skeletal metazoans in the Spanish Series”

(Liñán et al., 1984, p. 221). The first reference to *Cloudina* was in Palacios (1989), who described the fossils from the locality El Membrillar as tubular microorganisms with cross section consisting of eccentric layers that resemble the genus *Cloudina* (Palacios, 1989, p. 63; pl. 16 figs. 1–4). However, it was not until Grant (1990) that those same tubular fossils were confidently identified as belonging to the genus *Cloudina*. Grant (1990) also reported specimens of *Cloudina* with triangular ridges. Since then, and aside from the work compiled in this thesis, *Cloudina* has been reported and illustrated from the late Ediacaran localities Castañar de Ibor (Vidal et al., 1994; Fernández Remolar, 2001; Jensen et al., 2007) and Villarta de los Montes (Vidal et al., 1994; Jensen et al., 2007), in Extremadura; Abenójar (Vidal et al., 1994; Zhuravlev et al., 2012), in Ciudad Real Province; and Pastores (Vidal et al. 1994), in Salamanca Province. *Cloudina* has also been reported from northern Spain (Álvaro and Blanc-Valleron, 2002), but the fossils are likely not *Cloudina*, and of Cambrian age (Gámez Vintaned et al., 2012).



METHODS



METHODS

Samples from several Spanish localities were studied in the Área de Paleontología of the Universidad de Extremadura in Badajoz using different techniques according to their different lithologies and fossil preservation mode.

In addition to the Spanish material, samples from South China were studied in the Geosciences Department of Virginia Polytechnic Institute and State University in Blacksburg, Virginia (USA) and in the Área de Paleontología of the Universidad de Extremadura in Badajoz. Secondly phosphatized fossils were extracted from dolostone blocks collected by Profs. Shuhai Xiao, James D. Schiffbauer, Hong Hua and Yaoping Cai from the Beiwan Member in the Lijiagou section, Ningqiang County, Shaanxi province, South China.

The following preparation techniques were used:

- Dissolution

Secondarily phosphatized and pyritized fossils have been isolated from the carbonate matrix using acetic acid maceration techniques (Jeppsson et al., 1999). Rock fragments were immersed in buffered acetic acid. Residues were retrieved regularly, after 3–4 days of reaction, filtering the solution through a set of sieves of different mesh-size (1 mm, 0'45 mm, 0'2 mm). Microfossils were handpicked using a stereoscope.

- Thin sections

Thin sections of selected blocks were prepared.

- Epoxy cubes

Selected isolated silicified specimens were embedded in epoxy resin to form small cubes which were gradually polished with carborundum and serially photographed to reveal the internal morphology of the fossils.

- Latex casts

Latex casts of the specimens preserved as molds were produced to obtain positive replicas. For photography, latex casts were coated with ammonium chloride sublimate.

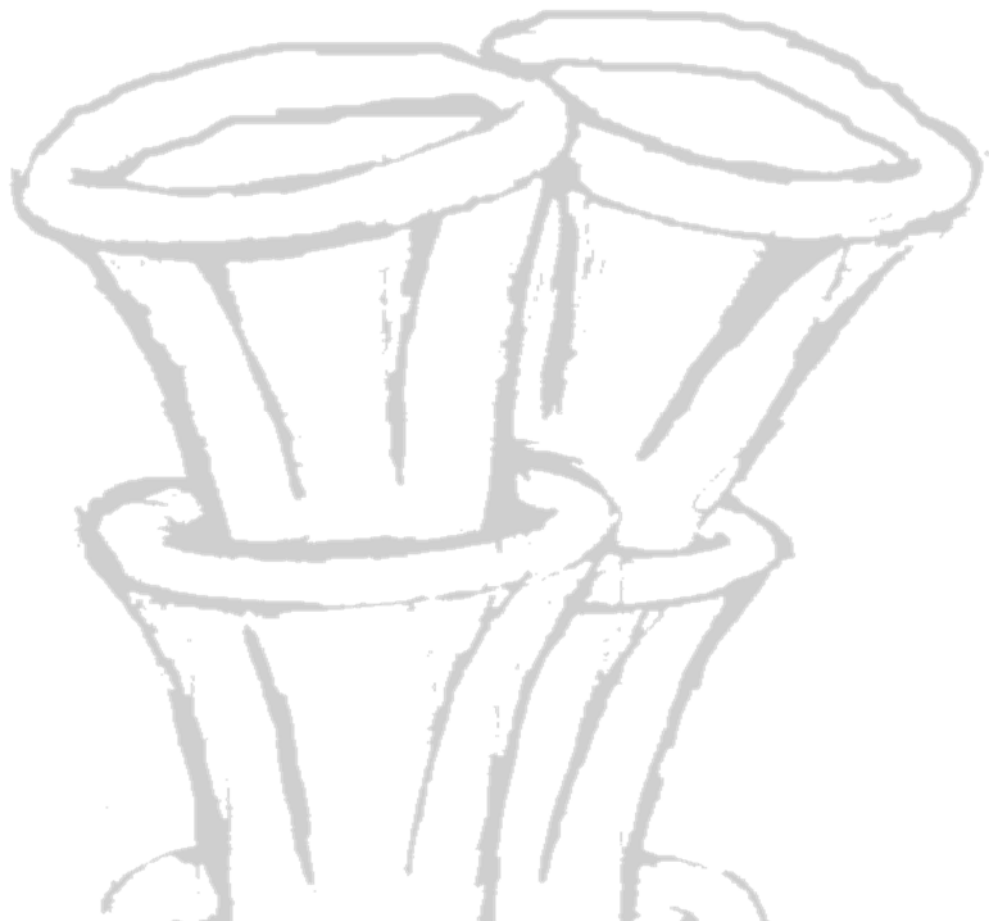
- Digital photography

Depending on size, specimens were photographed using a digital camera with a 50 mm macrolens attached, or a stereoscope with a digital camera attached.

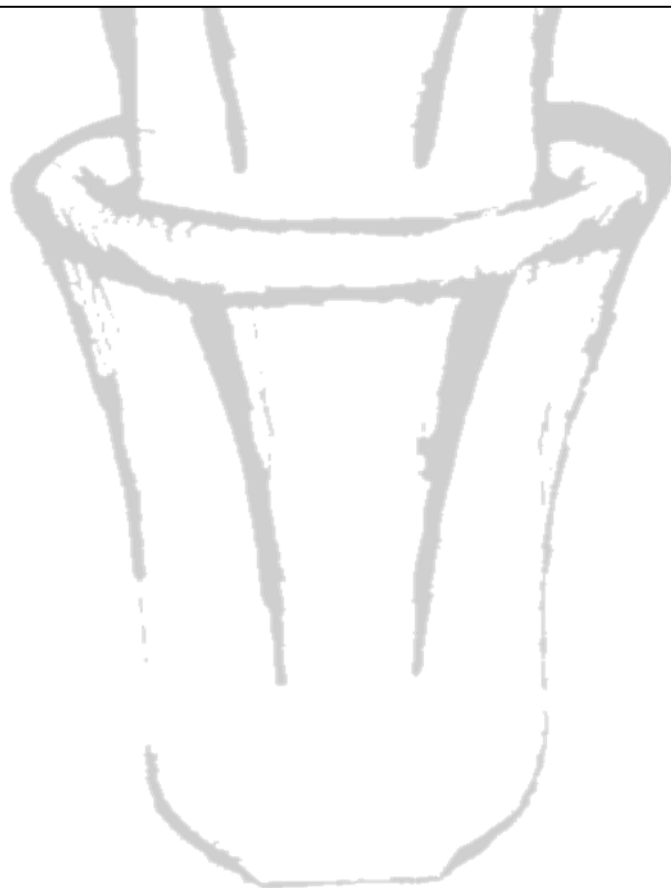
- Scanning electron microscopy (SEM)

Selected microfossils were mounted on aluminum stubs for scanning electron microscopy (SEM). Different equipment was used in four different institutions:

- ZEIS SUPRA 35VP equipped with a Robinson BSE detector and an EDAX Genesis 40000 Cryospec at Evolutionary Biology Centre, Uppsala University, Sweden.
- Hitachi S-4300 at Department of Palaeozoology, Naturhistoriska riksmuseet (Swedish Museum of Natural History), Stockholm, Sweden.
- FEI Quanta 600F at Nanoscale Characterization and Fabrication Laboratory, Institute for Critical Technology and Applied Science (ICTAS CRC), Virginia Polytechnic Institute and State University, Blacksburg, VA, USA.
- Hitachi S-4800II at Servicio de Análisis y Caracterización de Sólidos y Superficies (Service for Analysis and Characterization of Solids and Surfaces), Universidad de Extremadura, Badajoz, Spain.



LATE EDIACARAN SKELETAL
FOSSILS FROM CENTRAL
SPAIN AND SOUTH CHINA





LATE EDIACARAN ROCKS IN CENTRAL SPAIN

Ediacaran sedimentary rocks of the Central Iberian Zone consist of a thick succession of siliciclastic rocks, mainly greywacke and mudstone deposited by turbidites, attributed to the Domo Extremeño Group (Palacios et al., 2013). Although the base of this succession has not been observed and the maximum age is unknown, trace fossils and detrital zircons show that most is younger than ca. 570 Ma (Jensen et al., 2007; Pereira et al., 2012). The Ibor Group appears discordantly overlying this succession. Carbonates in the Ibor Group are an important reference level for latest Ediacaran–Lower Cambrian rocks in the Central Iberian Zone since, over 400 km in length, this carbonate level extends from the south of the Salamanca Province to the Ciudad Real Province in a northwest-southeast stretching band, intermittently outcropping across Extremadura (Fig. 3). The Ibor Group carbonates were deposited in relatively shallow waters (as indicated by the local presence of oolites, probable stromatolites, and the evidence for storms), on a mixed platform that opened to the sea in a northeast direction, where there is evidence of a deeper depositional environment with olistostromes (mixture of carbonate blocks and siliciclastic rocks). The olistostromes occur in the base of the Río Huso Group, a likely lateral equivalent of the Ibor Group although higher in the succession, the Río Huso Group contains a typical Early Cambrian fauna, especially “small shelly fossils” and ichnofossils (Brasier et al., 1979; Palacios, 1989; Vidal et al., 1994, 1999; Jensen et al., 2007).

The presence of *Cloudina* and other late Ediacaran skeletal fossils provides biostratigraphic evidence for a late Ediacaran age for the carbonate-bearing part of the Ibor Group. A late Ediacaran age for the carbonates is also consistent with the finds of vendotaenids and other filaments, particularly abundant in siliciclastics directly overlying the carbonates, and the first regional appearance of Cambrian-type trace fossils in overlying strata (e.g. Jensen et al., 2007). Also consistent with a late Ediacaran age are delta carbon ($\delta^{13}\text{C}$) values around positive 2 from the lower part of the *Cloudina*-bearing carbonates at Villarta de los Montes (unpublished results), in agreement with the $\delta^{13}\text{C}$ signatures of *Cloudina*-bearing rocks from Namibia, South China and Oman. The above *Cloudina*-bearing strata have been age-constrained, by Pb/U or Pb/Pb dated zircons, between 550 and 542 Ma (Grotzinger et al., 1995; Condon et al., 2005; Bowring et al., 2007). Therefore, taking all these data into account, a late Ediacaran age, between 550 and 542 Ma, can be assigned with some confidence to the *Cloudina*-bearing carbonates of the Ibor Group.

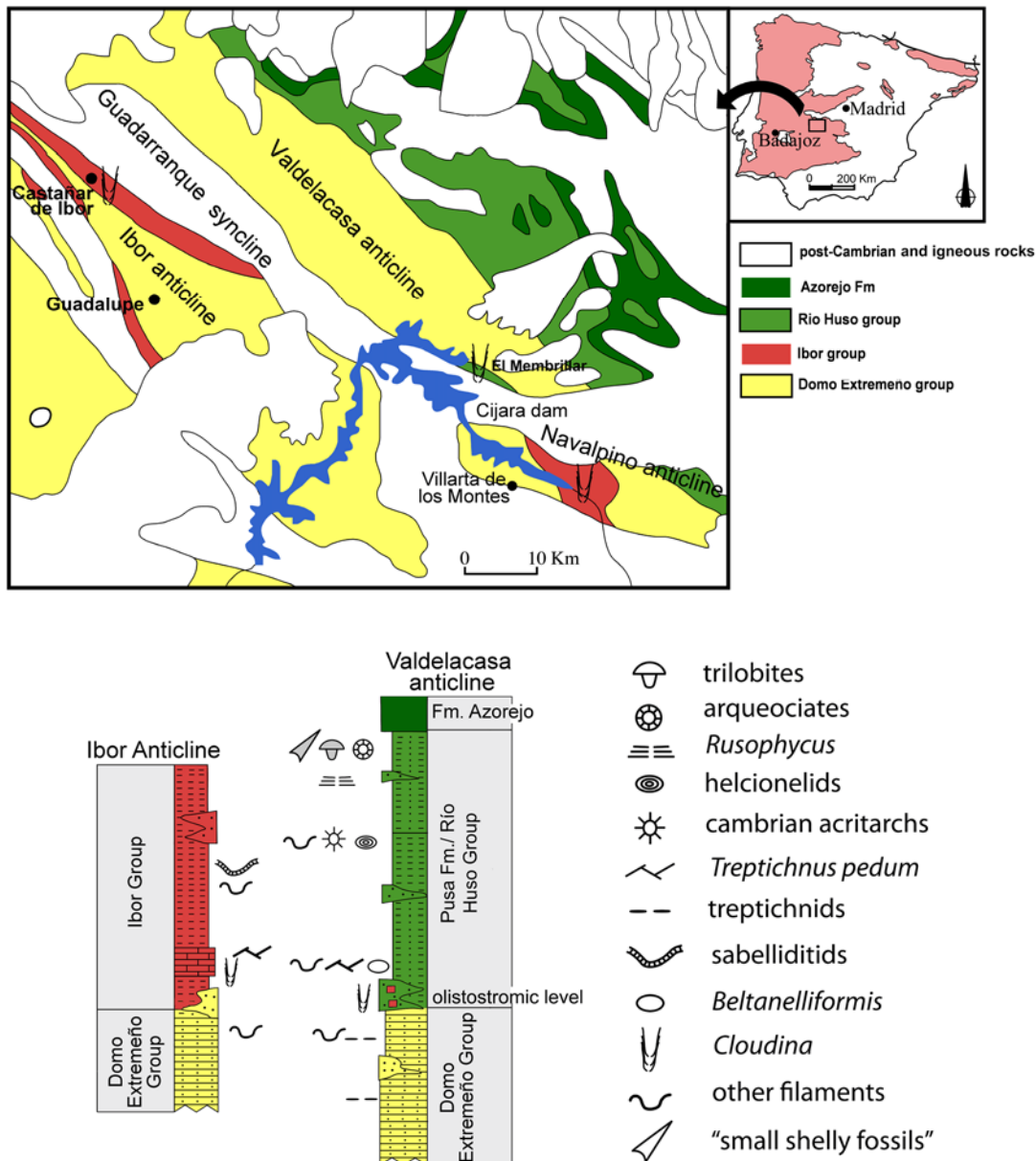


Fig. 3. Location map of the three main studied localities and general stratigraphic columns.

Three localities from the Ibor Group (marked in Fig. 3) have been studied during this PhD thesis because they represented the best known *Cloudina* localities in central Spain. Two of them, El Membrillar and Villarta de los Montes, have been studied in detail because they have the best preserved material. An additional locality with *Cloudina* in central Spain is reported here for the first time (Arroyo del Cubilar). The locality, recently discovered, is situated close to the village La Nava de Ricomalillo, in the Toledo Province.

- Castañar de Ibor

The outcrop (Fig. 4) is located along the road between Castañar de Ibor and Robledollano villages, in Cáceres Province (UTM (EUR50): 30S 0290793, 4388856; Fig. 3; Palacios et al., 2004; Cortijo et al., 2010a, b). The *Cloudina*-bearing carbonates are intercalated with siliciclastic sediments in a 15 m thick sequence overlaid by a shale-dominated unit with abundant filamentous fossils, including sabelliditids, which could indicate a Cambrian age. Carbonates of this site are altered by dolomitization and recrystallization and fossil preservation is not good.



Fig. 4. View of the Castañar de Ibor outcrop.

- Villarta de los Montes

Carbonates of the Ibor Group (also called Ibor-Navalpino Group in this area) crop out on both sides of the Guadiana River, northeast of the Villarta de los Montes village, Badajoz Province (Fig. 3), where they receive the local name of Villarta limestone (Fig. 5). In this area, carbonates reach a thickness of 300 m and present evidence of synsedimentary displacement. The principal outcrop examined in this study is to the east of the hillock “El Tamujoso”, along the watershed “Vertiente de Tamujillo” (UTM (EUR50): 30S 0350734,

4342415), where fossils are found below the main carbonate levels in fine-grained laminated siliciclastics and in dark-grey carbonate beds with phosphatic clasts.



Fig. 5. General view of one outcrop in the Villarta de los Montes area (left). Details of the carbonate (upper right) and siliciclastic (lower right) levels.

Accumulation of fossils can be naturally observed on the rock surfaces. Fossils appear as molds in the siliciclastic levels and with a carbonatic preservation (presumably preserving the original skeletal composition, although they appear recrystallized), or secondarily mineralized (pyritized or phosphatized) in the carbonate blocks.

- Olistostromic levels from El Membrillar

The El Membrillar locality (UTM (EUR50): 30S 0341717, 4358665; Fig. 6) is located in El Membrillar property, in Helechosa de los Montes village, Badajoz Province. Fossils occur in carbonate blocks which are part of the El Membrillar olistostrome, located on the southern flank of the Valdelacasa anticlinorium at the tail end of the Cíjara dam, near the mouth of Estena River (Fig. 3). The level is about 300 m thick and comprises several types of gravitational deposits, including olistostromes and debris flows, with siliciclastic and carbonate blocks up to 100 m in length (Moreno, 1975; Palacios, 1989; Santamaría and

Pardo, 1994). The olistostrome rests on a succession of sandstone and greywacke (interpreted as turbidites and tempestites from the slope) and is situated below strata assigned to the Pusa Formation (also called Río Huso Group), a unit dominated by shale that crops out extensively in the northern flank of the Valdelacasa anticline (Fig. 3).



Fig. 6. General (right) and detailed (left) view of El Membrillar outcrop. Note the orange carbonate blocks.

El Membrillar olistostrome is located northeast of the Ibor Group platform carbonates, which are the most likely origin of the carbonate blocks in the olistostrome. It is interpreted as the result of a huge slide, probably caused by collapse of the distal platform associated with a submarine canyon (Moreno, 1974; Capote et al., 1977; Palacios, 1989; Vidal et al., 1994). The selective silicification of carbonates in this site has resulted in exceptionally preserved fossils: secondarily silicified fossils are three-dimensionally exposed on the rock surface owing to differential dissolution caused by weathering (Cortijo et al., 2010b).

- Arroyo del Cubilar

In the locality Arroyo del Cubilar (Fig. 7), close to the village of La Nava de Ricomalillo (Toledo Province, Spain), carbonate blocks of the Ibor Group are included in the Fuentes olistostrome. Fossils are abundant in some blocks and have been identified in two different areas:

- At the top of the Cerro Zahabón (UTM (EUR50): 30S 325115, 4391800): fossiliferous carbonate blocks crop out at the top of the hill, but fossils appear poorly preserved.
- Along the Arroyo del Cubilar (UTM (EUR50): 30S 325074, 4391729): accumulation of fossils occur in carbonate blocks that crop out along the stream bank. Some tubes show successive funnels and longitudinal crests, which identify them as *Cloudina carinata*.



Fig. 7. Arroyo del Cubilar outcrop. (A) General view of Cerro Zahabón. Carbonates crop out at the top of the hill and at the base, along the river bank. (B) Detailed view of the carbonates at the stream bank.

LATE EDIACARAN SKELETAL FOSSILS IN CENTRAL SPAIN

Three species corresponding to two biomineralizing fossil genera, *Cloudina* and *Sinotubulites*, have been identified in the late Ediacaran of central Spain. Additionally, small tubes of uncertain assignation and a flask-shaped fossil similar to *Protolagena* have been found together with *Cloudina* and *Sinotubulites* in one of the localities.

CLOUDINA

Cloudina is a millimetric tubular fossil consisting of a succession of imbricated funnel-shaped elements. Its name honors the 20th century geologist and paleontologist Preston E. Cloud (1912–1991). The type species, *C. hartmanae* (Germs, 1972; Grant, 1990; spelling of the species follows recommendation made by Glaessner, 1976, p. 266), is globally distributed, while a second species, *C. carinata* (Cortijo et al., 2010a, b, in review), is present only in Spain (doubtful specimens have been reported from Siberia –Terleev et al., 2011 fig. 38F). The distinctiveness of other proposed species (*C. riemkeae*, *C. luciano*i, *C. sinensis*, and *C. latilabrum*) is controversial since they differ mainly in size.

Cloudina is the most common and best known of the first biomineralizers and appears in all late Ediacaran localities with mineralized fossils (Fig. 2). The fact that no *Cloudina* fossils have been found in Cambrian (or younger) sediments, as well as its wide geographic range (Fig. 2), makes it an index fossil for the late Ediacaran–Early Cambrian transition (Grant, 1990). It was first described in 1972 from the Nama Group in Namibia (Fig. 8; Germs, 1972), but has since been reported from many localities all around the world: in the Ara Group from Oman (Grant, 1990; Conway Morris et al., 1990; Amthor et al., 2003), in the Gaojiashan and Beiwan Members of the Dengying Formation from South China (Figs. 1A, 9, 10D, 18–19; Conway Morris et al., 1990; Bengtson and Yue, 1992; Bengtson, 1994; Hua et al., 2003a, b, 2005a, 2009; Chen et al., 2001; Cai et al., 2010, 2014; Cortijo et al. 2014), in the Miette Group from eastern British Columbia in Canada (Hofmann and Mountjoy, 2001), in La Cienega Formation from Mexico (Grant, 1990; McMenamin, 1985; Sour-Tovar et al., 2007), in the Deep Spring Formation from California and Nevada, in USA (Signor et al., 1983, 1987; Grant, 1990; Hagadorn and Waggoner, 2000), in the Siberian platform in Russia (Gámez Vintaned et al., 2007; Terleev et al., 2011; Zhuravlev et al., 2012), in the Arroyo del Soldado Group from Uruguay (Gaucher and Sprechmann, 1999;

Gaucher and Germs, 2009), in the Itapucumí Group from Paraguay (Boggiani and Gaucher, 2004; Warren et al., 2011), in the Tamengo Formation (Grant, 1990; Gaucher et al., 2003) and in the Sete Lagoas Formation (Warren et al., 2014) in Brazil. *Cloudina* has also been reported from the Shackleton Glacier area in Antarctica (Yochelson and Stump, 1977) and Sierras Bayas Group in Argentina (Yochelson and Herrera, 1974; Gaucher et al., 2005; Warren et al., 2014), but the specimens are problematic.

In Spain, *Cloudina* occurs in several localities of the Iber Group (e.g. Vidal et al., 1994; Palacios et al., 2004; Palacios, 2005; Jensen et al., 2007; Cortijo et al., 2010a; Zhuravlev et al., 2012) and these are the only *Cloudina*-bearing localities in Europe.

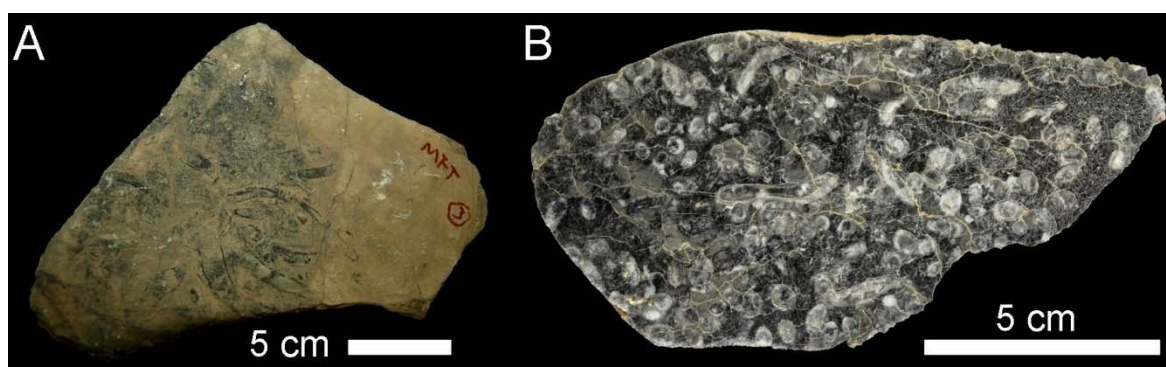


Fig. 8. *Cloudina* fossils from Namibia. (A) Block with multiple *Cloudina hartmanae* specimens (dark) from the Mooifontein Member; collection of Prof. Shuhai Xiao (Department of Geosciences at Virginia Tech). (B) Polished block with multiple *Cloudina hartmanae* from the Omkyk Member; sample courtesy of Prof. Joachim Reitner.

Cloudina has been interpreted as the builder of the first metazoan reefs (Penny et al., 2014; Wood and Curtis, 2014), which gave rise to the first skeletal packstones/grainstones known in the geological record (Wood, 2011). However, material from China suggests that *Cloudina* lived in a microbially bound carbonate substrate but where biostromes and bioherms were absent (Cai et al., 2014). In some localities, *Cloudina* co-occurs, or has a successive occurrence, with some non-biomineralized fossils such as *Corumbella* (Warren et al., 2011, 2012, 2014) and, especially, *Conotubus*, which appears to have had a very similar ontogeny and mode of life (Cai et al., 2011). This suggests that *Conotubus* could be a preservational variant of *Cloudina* in a different taphofacies. Holes in *Cloudina* shells from the Lijiagou section have been interpreted as the oldest case of predation in the fossil record (Bengtson and Yue, 1992).

Description of the shell

Exceptional, three-dimensionally preserved, specimens from South China and central Spain (Hua et al., 2005a; Cortijo et al., 2010b, 2014; Cai et al., 2014) have allowed a precise reconstruction of *Cloudina*. The skeleton of *Cloudina* is formed by the stacking of two types of elements (Figs. 1A, 9):

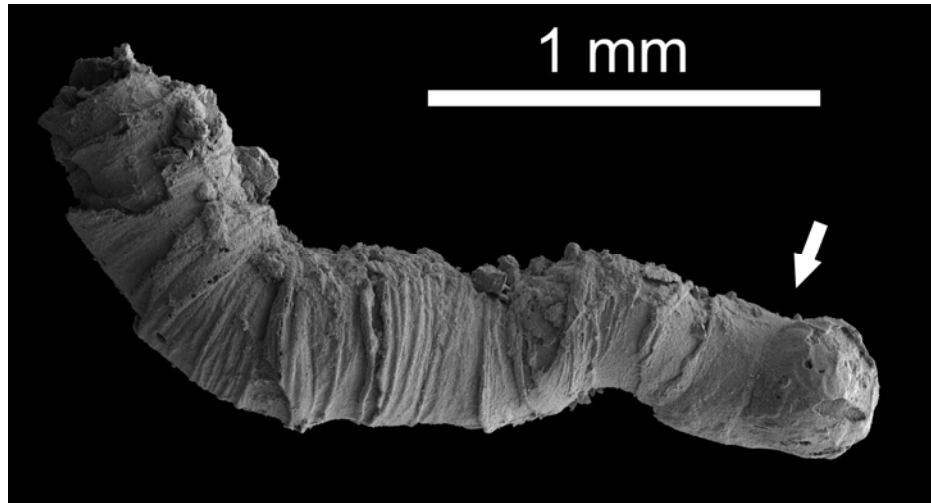


Fig. 9. *Cloudina hartmanae* specimen from the Lijiagou section, China. Note the cone with the hemispherical end (arrow) and the successive funnels with undulating ornamentation.

- Cone: the basal element and the only one different from the rest of skeletal elements (Fig. 1A; arrowed in Fig. 9). It has a conical shape closed at one end, with a generally hemispherical base (Bengtson and Yue, 1992; Chen and Sun, 2001; Hua et al., 2005a; Chen et al., 2008; Cai et al., 2014; Cortijo et al., 2014). Its surface is usually smooth both internally and externally. These elements are scarce among *Cloudina* fossils and have only been found in material from South China. Even rarer are the cones with a pointed closed base (Fig. 23), first described in Cortijo et al. (2014).
- Funnels: form the rest of the tube and are funnel-shaped units opened at both ends. Their inner surface is smooth, while the outer surface usually shows different ornamentation patterns such as undulations, wrinkles, folds, etc. These are the most commonly found elements. The tube resulting from the succession of funnels has a continuous inner space,

which likely was the living space of the *Cloudina* individual (Hua et al., 2005a; Cortijo et al., 2010b).

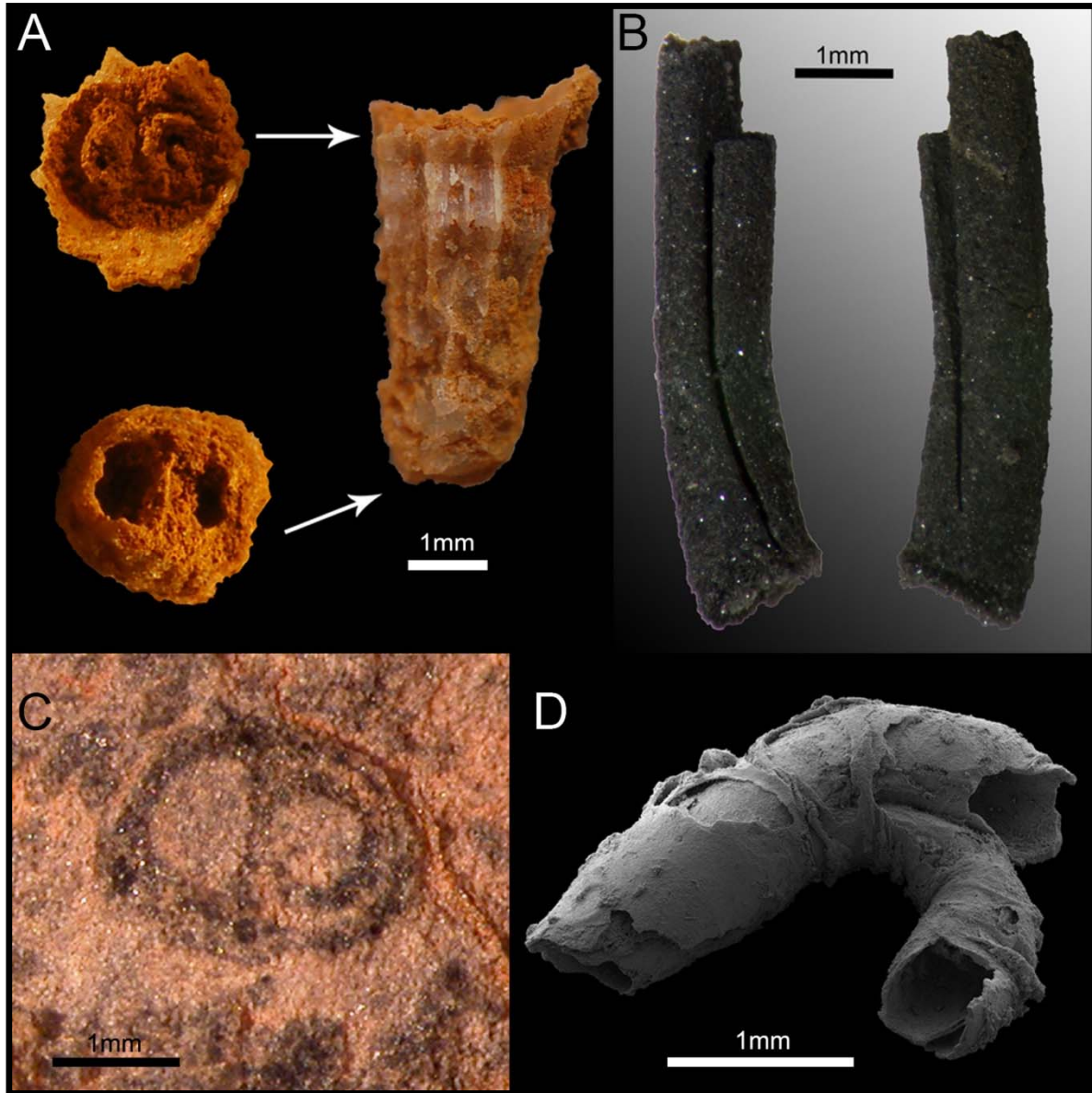


Fig. 10. Evidence of asexual division: branching *Cloudina* fossils. (A) Secondary silicified specimen of *C. carinata* from El Membrillar. (B) Secondary phosphatized specimen from Villarta de los Montes. (C) Specimen preserving its carbonatic composition from a carbonate block from Villarta de los Montes. (D) Secondary phosphatized specimen of *C. hartmanae* from the Lijiagou section. Note the different sizes of the resulting daughter tubes.

Some specimens show both signs of plastic deformation and brittle breakage suggesting that the funnels were originally flexible, and hardened during the life of the organism (Grant, 1990; Hua et al., 2005a; Cortijo et al., 2010b).

The oldest evidence of asexual division in metazoans has been described in *Cloudina* fossils from China (Hua et al., 2005a; Cortijo et al., 2014) and Spain (Fig. 10; Cortijo et al., 2010b). It consists of branching specimens where the original tube (mother tube) contains two smaller tubes (daughter tubes) of different diameter –since one is always smaller than the other (Cortijo et al., 2010b; Vinn and Zatoń, 2012; Cortijo et al., 2014).

Biological affinities

Although *Cloudina* was first described as an algae (*Aulophycus lucianoï*, in Beurlen and Sommer, 1957, from Brazil), and it is similar to the Early Cambrian calcareous algae *Proaulopora rarissima* Vologdin (Fig. 11; e.g. Luchinina and Terleev, 2004 pl. 1 figs. 3–6;

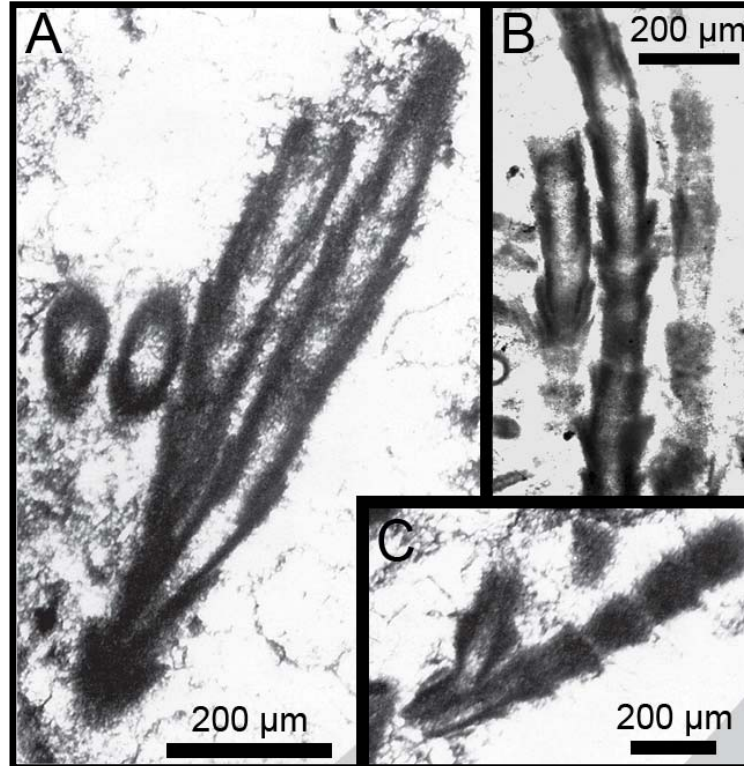


Fig. 11. *Proaulopora rarissima* fossils in thin section. (A, C) Modified from Luchinina and Terleev, 2004. (B) Modified from Luchinina, 2013. Note its similarity with *Cloudina*.

Luchinina, 2013 pl. 5 figs. 1–5), it is generally interpreted as the external skeleton of a sessile, gregarious, filter feeding (Grant, 1990), and perhaps modular (as suggested by the occurrence of asexual division) metazoan. However, its precise phylogenetic position remains unclear.

New insights into the morphology and development of *Cloudina* (Cai et al., 2014; Cortijo et al., 2014) and recent phylogenetic data on the early evolution of metazoans makes it possible to revisit the discussion on the position of *Cloudina* within the metazoa.

Cloudina has been usually compared either with cnidarians (e.g. Knoll, 2003; Vinn and Zatoń, 2012; Zhuravlev et al., 2012) or with tubiculous annelids, especially serpulids (Glaessner, 1976; Hua et al., 2005a; Cai et al., 2014). Being gregarious, sedentary and having a modular growth, are common features of basal metazoans, including the Porifera and Cnidaria, although they are also present, as secondary adaptations, in various bilaterians (e.g. serpulid and siboglinid annelids). *Cloudina* seems to share more features in common with cnidarians (Fig. 12A–C) than with annelids (Vinn and Zatoń, 2012), and recent findings of the possible stem-group cnidarian *Cambroctoconus* (Park et al., 2011, 2014; Geyer et al., 2014) which shows some similarities with *Cloudina* (especially *C. carinata*), support a cnidarian affinity for *Cloudina*. A close phylogenetic relationship between *Cloudina* and annelids would imply a reevaluation of the current view of metazoan evolution. Both molecular clocks and the fossil record suggest that crown group annelids are no older than Late Cambrian–Ordovician (Sperling et al., 2009), while the oldest stem group annelid has been recorded from the Early Cambrian (Parry et al., 2014). *Cloudina* tube morphology, growth pattern, branching, and mode of life closely resemble those of some serpulid annelids, such as *Salmacina* and *Filograna* (Fig. 12E–F). *Cloudina* also closely resembles siboglinid annelids (note the similarities between *Cloudina* –especially *C. carinata*– and *Riftia* or *Lamellibrachia* tubes; Fig. 12D), and *Cloudina* ontogeny is also reminiscent of that of siboglinid worms (Knoll, 2003). According to some interpretations, the comparison of *Cloudina* and siboglinids could also be extended to their environment owing to the similarities between the *Cloudina*-mound environment and some modern hydrothermal seepage vents (Reitner and Wörheide, 2002). The most problematic aspect of these comparisons is that both serpulids and siboglinids are derived within the Annelida. The first serpulid fossils are from the Mid-Triassic (Parry et al., 2014). Regarding siboglinids, molecular clock estimates suggest that they are Mesozoic or younger, although

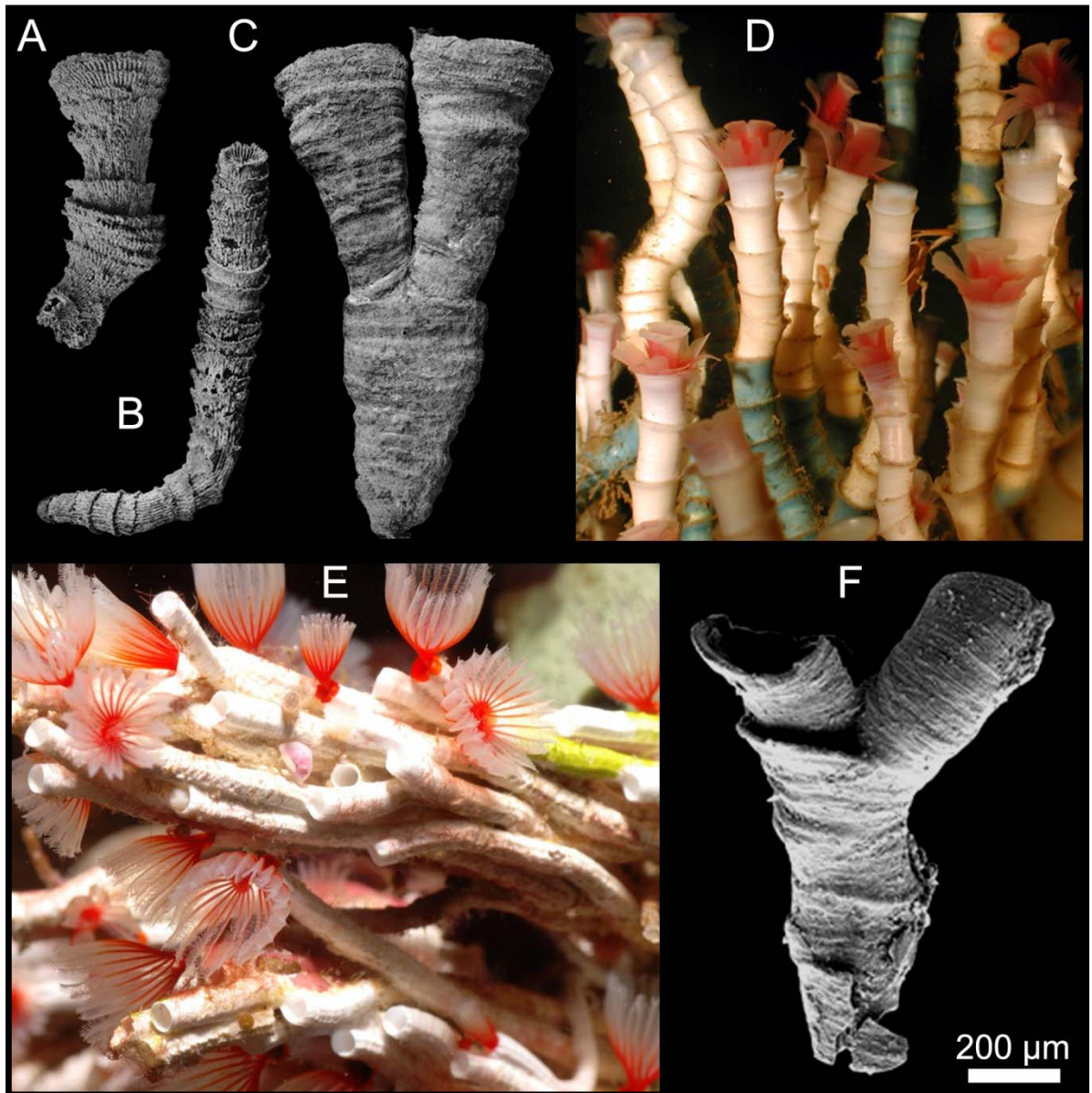


Fig. 12. Cnidarians and annelids that resemble *Cloudina*. (A–C) Cnidarians (modified from Davis, 1885: (A), (C) pl. 88, (B) pl. 100). (A) *Cyathophyllum detextum*. (B) *Blothrophyllum cinctutum*. (C) *Cyathophyllum multigemmatum*. (D) The siboglinid *Lamellibrachia luymesii* (Photo by Charles Fisher in Boetius, 2005). (E–F) Serpulids. (E) *Filograna elatensis* (Photo by Raja Ampat). (F) *Salmacina dysteri* (modified from Hua et al., 2005a).

there are possible fossils from the Silurian (Parry et al., 2014). However, the above groups could represent good modern analogues of *Cloudina* (Hua et al., 2005a; Cai et al., 2014). *Cloudina* has also been compared with the chitinous tubes of sabellid polychaetes, and with the fossils *Sabellidites*, *Saarina* and *Calyptrina*, long organic tubes which have themselves been compared with various annelid groups including sabellid and siboglinid polychaetes (Grotzinger et al., 2000; Fedonkin, 2002; Xiao et al., 2002; Moczyłowska et al., 2014).

Despite the above mentioned similarities between recent metazoan groups and *Cloudina*, based on the current knowledge of the fossil record and molecular phylogenetic analysis of metazoans, a more basal position for *Cloudina* within the Eumetazoa, for example in the stem group of Eumetazoa (Cnidaria + Bilateria), Bilateria or Cnidaria, is perhaps more likely (Fig. 13; Cortijo et al., 2010c; Wood, 2011).

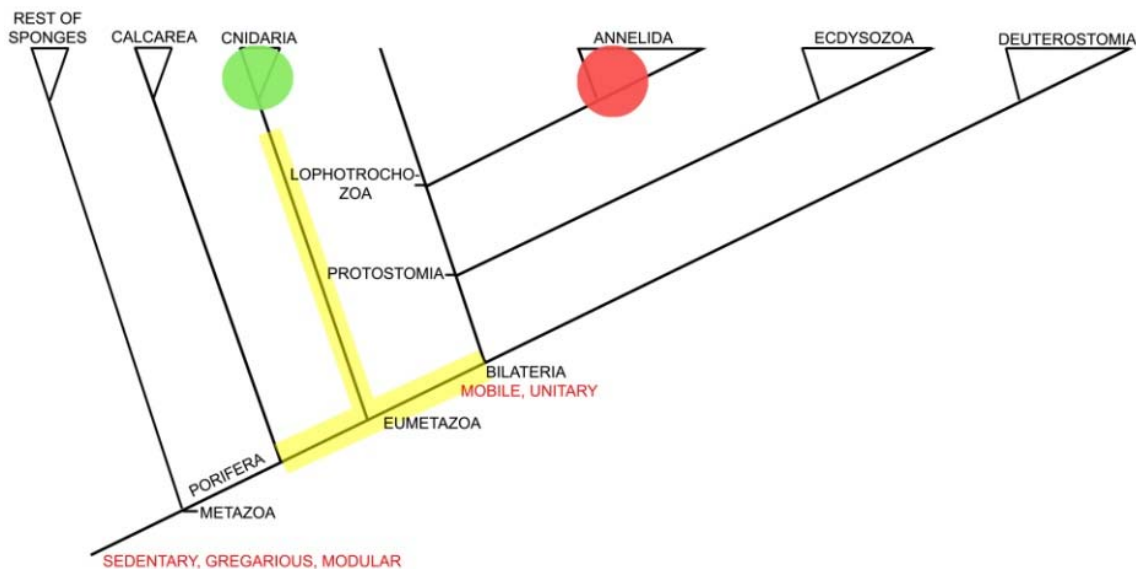


Fig. 13. Phylogenetic tree (based on Sperling et al., 2007) showing previous interpretations of the phylogenetic position of *Cloudina*, as cnidarians (green) or as tubicolous annelids (red). In yellow is marked a possible, more basal interpretation of the phylogenetic position for *Cloudina*.

***Cloudina* in central Spain**

Although the presence of *Cloudina* in central Spain had been previously reported, the fossils had never been studied in detail. The work compiled in this PhD thesis represents the first detailed study of *Cloudina* in central Spain.

- Castañar de Ibor

The fossils in Castañar de Ibor (Fig. 14) are poorly preserved and have only been studied in polished rock surfaces. Although fossil identification is not obvious, cross sections typical of *Cloudina*, showing eccentrically nested rings, are abundant (Cortijo et al., 2010a).





Fig. 14. Polished surface of a carbonate block from Castañar de Ibor. Note large accumulation of *Cloudina* fossils in different orientations.

- Villarta de los Montes

Both siliciclastic and carbonate levels yield *Cloudina* fossils in different preservation modes (Fig. 15; Cortijo et al., 2010a, b, in review). *Cloudina* occurs as molds in the siliciclastic levels (Fig. 15 right) and preserves its carbonatic composition or is secondarily mineralized in the carbonate blocks (Fig. 15 left). *C. carinata* is abundant in the siliciclastic level, but no *C. hartmanae* specimens have been identified. On the other hand, both species are present in the carbonate level, although *C. hartmanae* predominates.



Fig. 15. Surfaces of carbonate (left) and siliciclastic (right) blocks. Note large accumulation of fossils. Coin is 16 mm in diameter. Scale divisions in millimeters.



Fig. 16. Block (left) and detailed view of the surface (right) from El Membrillar. Note large accumulation of fossils showing exceptional, three-dimensional preservation.

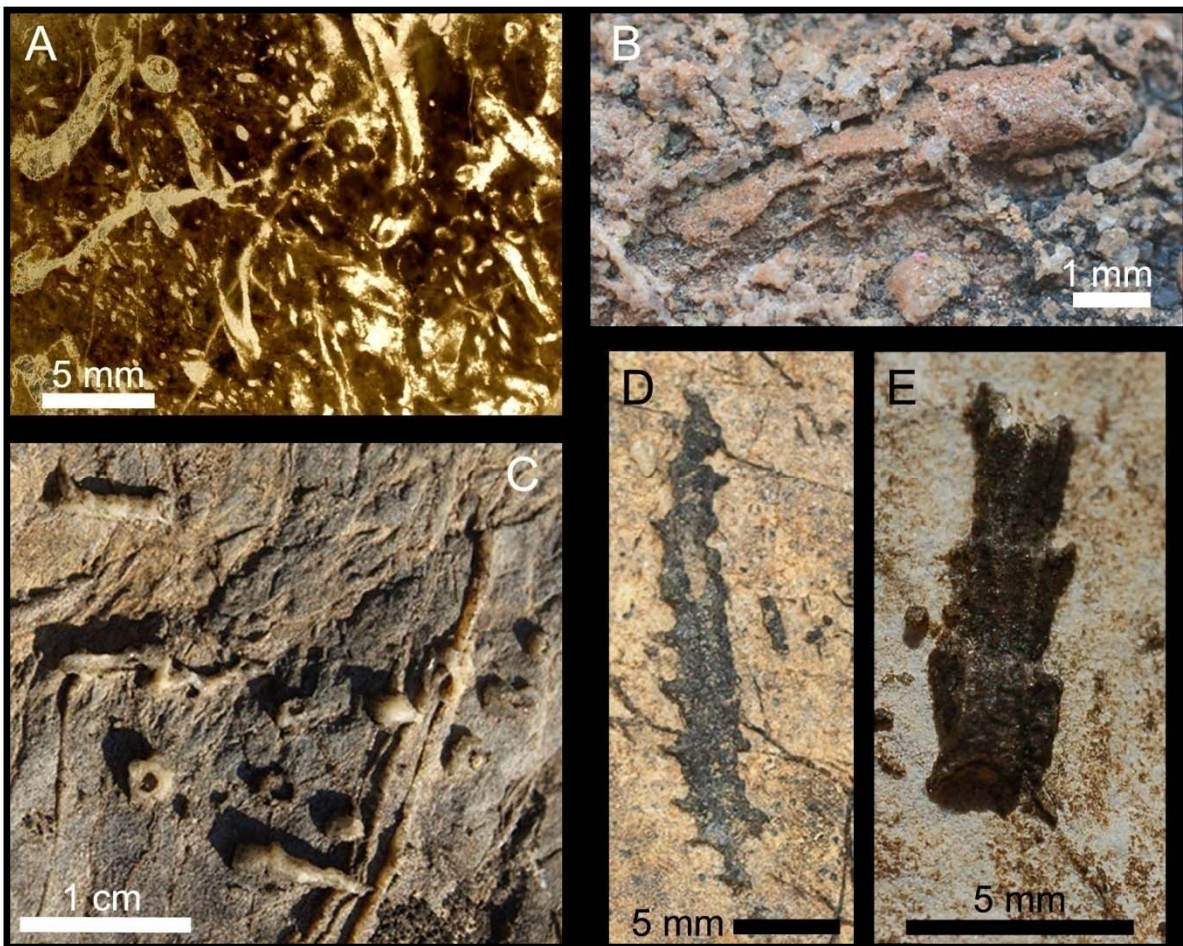


Fig. 17. Fossils from Arroyo del Cubilar. (A) Thin section from a block from the top of Cerro Zahabón. Note fossils sectioned in different orientations. (B) Detailed view of a *Cloudina* specimen from the top of Cerro Zahabón. Note the different layers. (C) Detail of a naturally weathered block surface from the stream area. Note the silicified *Cloudina* fossils, some with several funnels (upper left) or with a polygonal cross section (middle-bottom left). (D) Side view of a *Cloudina* specimen from the stream area with clear funnel-in-funnel construction. Note the empty central canal. (E) Side view of a *Cloudina carinata* specimen from the stream area. Note the prominent longitudinal crests.

- El Membrillar

Some of the carbonate blocks from the olistostrome contain silicified, exceptionally preserved *Cloudina* fossils (Fig. 16; Cortijo et al., 2010a, b). Silicification has allowed a three-dimensional preservation of the fossils. An exceptional example is one block (Fig. 16 left) recovered from the locality and deposited in the University of Extremadura. About 100x100x60 cm in size, its surface abounds in three-dimensionally preserved *C. carinata* specimens.

- Arroyo del Cubilar

Well preserved *Cloudina* specimens (Fig. 17) appear secondarily silicified, similarly preserved to those from El Membrillar (Fig. 16 right; Cortijo et al., 2010a, b). Both *C. hartmanae* and *C. carinata* (Fig. 17E; note the longitudinal crests) seem to be present. Dissolution of the carbonates has made possible the observation of fossils in weathered surfaces.

Description of a new *Cloudina* species, *C. carinata*

Cloudina carinata Cortijo, Martí Mus, Jensen and Palacios, 2010, has been described from El Membrillar and Villarta de los Montes (Figs. 10A, 15–16, 17E, 18).

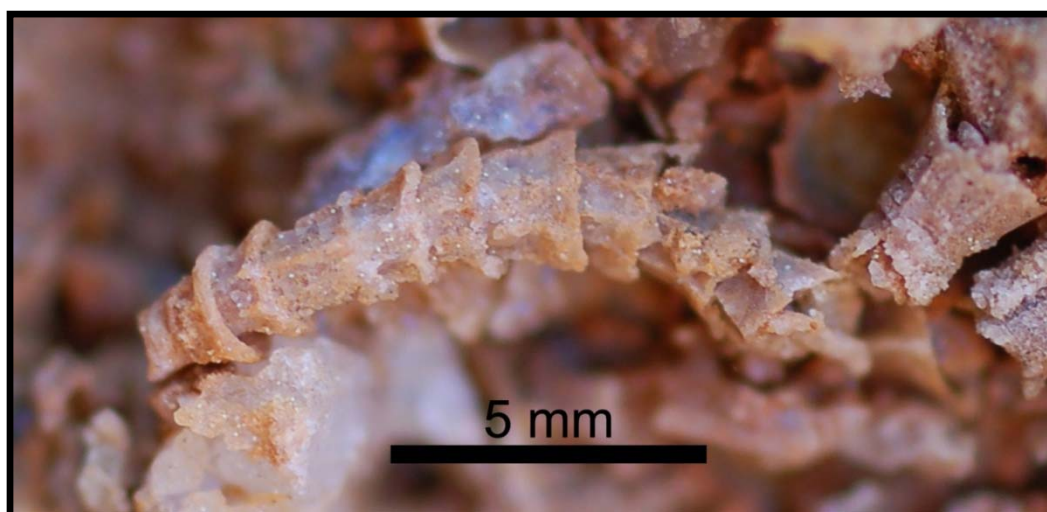


Fig. 18. *Cloudina carinata* holotype from El Membrillar. Note the thickened apertural rims and the longitudinal ridges.

C. hartmanae and *C. carinata* differ in some features of the shell (Cortijo et al., 2010b), particularly, the presence of prominent external longitudinal ridges in *C. carinata*. Other differences are the thickened apertural rims, a basal, slightly constricted circular opening, and the less deep imbrication of the funnels in *C. carinata*. The evidence of tube disarticulation in the studied material of *C. carinata*, particularly the abundance of loose funnels, indicates that *Cloudina* funnels were secreted as independent elements, not fused to the previous ones. However, they could become fused during the life of the organism through the precipitation of inorganic cements between their walls. *C. carinata* shows evidence of asexual reproduction by branching, a feature previously reported in the type species.

SINOTUBULITES

Sinotubulites (Figs. 1B, 19) is the third most common of the biomineralized metazoans of the late Ediacaran, after *Cloudina* and *Namacalathus*. It was first described from China, in the Yangtze Gorges area (Chen et al., 1981; Ding et al., 1985, 1993; Hua et al., 2003a; Chen et al., 2008; Cai et al., 2010, 2015), and has also been found in the upper part of the Dengying Formation in southern Shaanxi Province (Hua et al., 2000; Zhang and Hua, 2000; Chen and Sun, 2001; Chen et al., 2008; Sun et al., 2012). Outside China, *Sinotubulites* has been described from Mexico and Nevada (Signor et al., 1983; McMenamin, 1985). Although *Sinotubulites* has been recently reported in the Ibor Group at the Abenójar Anticline, Ciudad Real Province, Spain (Zhuravlev et al., 2012), the description is based on two poorly preserved specimens (only one illustrated), and assignation to the genus is problematic.

Sinotubulites is a tubular fossil which ranges between 1.5 and 6 mm in diameter and between 3 to 28 mm in length. It is thought to be open at both ends and is often polygonal in cross section. The structure of *Sinotubulites* has been described as a tube-in-tube construction and consists of several concentric thin walls. The external surface is markedly wrinkled with longitudinal ribs and irregular annulations. The ornamentation of the wall was reported to be gradually weaker towards the inner layers (e.g. Chen et al., 2008, fig. 3C–D), but a more detailed study of the fossils has shown that the walls can be divided into two blocks, an inner block consisting of smooth walls and an outer block with walls prominently ornamented (Cai et al., 2015; Cortijo et al., in review). The walls of *Sinotubulites* seem to



have been thin and flexible, which suggests they were of organic-dominated composition with limited mineralization (Chen et al., 2008). *Sinotubulites* is interpreted as an epibenthic organism, with unknown affinities.

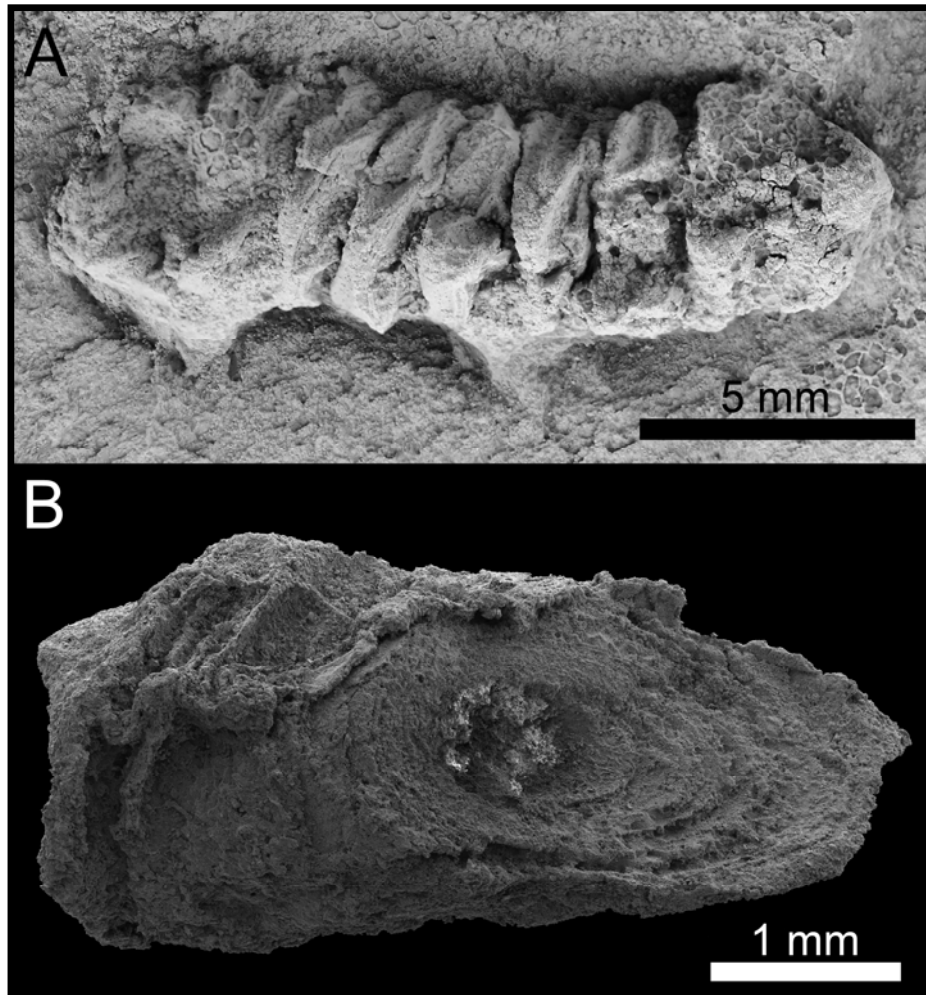


Fig. 19. *Sinotubulites baimatuoensis* from Villarta de los Montes. (A) Latex cast of a specimen from the siliciclastic level. (B) SEM image of a specimen from the carbonate level. Note the ornamented external wall and the tube-in-tube construction.

***Sinotubulites* in central Spain (Villarta de los Montes locality)**

Although less abundant than *Cloudina*, fragmentary but well preserved *Sinotubulites* specimens have recently been found in the Villarta de los Montes section (Fig. 19). They show the typical tube-in-tube construction of the genus, the polygonal cross section and the corrugated external surface with longitudinal ridges and transversal annulations. The largest specimens of *Sinotubulites* have been found preserved as molds in siliciclastics (Fig. 19A).

Secondarily mineralized specimens of *Sinotubulites* have also been recovered from carbonate blocks (Fig. 19B).

OTHER FOSSILS FROM VILLARTA DE LOS MONTES

In addition to the two different *Cloudina* species and *Sinotubulites*, other fossils have been recovered from the Villarta de los Montes locality.

?*Protolagena*

A single flask-shaped specimen was isolated from a carbonate block (Fig. 20). The specimen has a rounded body with a constricted neck and a flaring aperture and resembles *Protolagena* Zhang and Li, 1991, a calcareous microfossil which co-occurs with *Cloudina* and *Sinotubulites* in the Beiwang Member in the Lijiagou section. *Protolagena* also occurs in the Gaojiashan Member of the Dengying Formation and in the Doushantuo Formation of South China (Zhang and Li, 1991; Li et al., 2008; Hua et al., 2010; Cai et al., 2010). Unlike *Protolagena*, the Villarta de los Montes specimen is flattened and has a granular wall. Also, the size is relatively larger than the usual size of *Protolagena*.

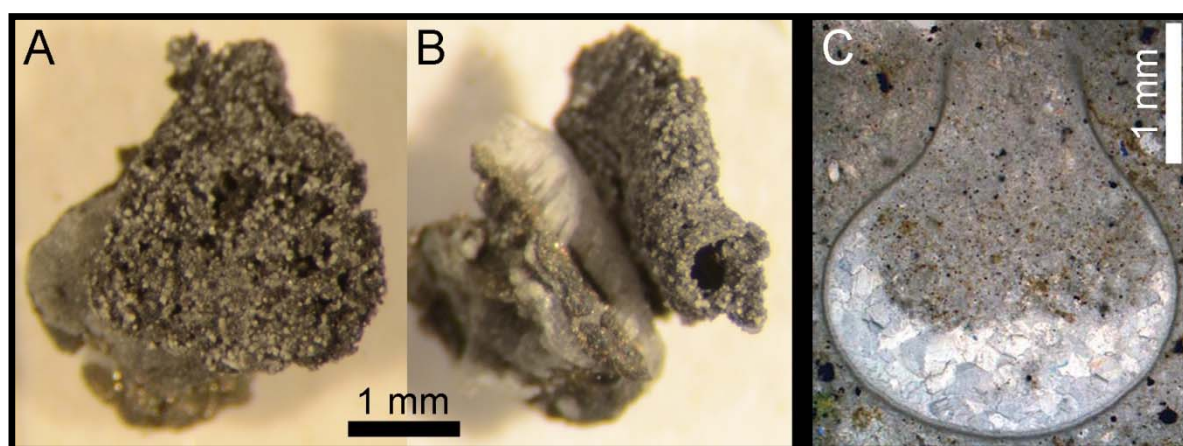


Fig. 20. (A–B) Different views of the *Protolagena* specimen from Spain. Note the flask-shaped body and the constricted neck. (C) *Protolagena* specimen from China (modified from Cai et al., 2010 fig. 4K).

Titanotheca coimbrae, a problematic rutile-agglutinated form from the Ediacaran of Uruguay (Gaucher and Sprechmann, 1999 pl. 6 and text-fig. 9), is also somewhat similar to

the Villarta de los Montes specimen. Both *Protolagena* and *Titanotheca* have been compared with foraminifera (Gaucher and Sprechmann, 1999; Hua et al., 2010).

Small tubular fossils

Co-occurring with the above fossils there is a heterogeneous group of small tubular fossils (Fig. 21). They occur (mostly phosphatized, but also pyritized) in the carbonate level (Fig. 21B–E), where they represent a heterogeneous assemblage. They can be more or less straight, curved or sinuous. These tiny tubular fossils have a diameter less than 500 μm (usually, 250–300 μm) and some are longer than 1 cm. Most of the mineralized specimens are solid cylindrical forms, but there are empty tubes with a smooth thin wall (Fig. 21B) and

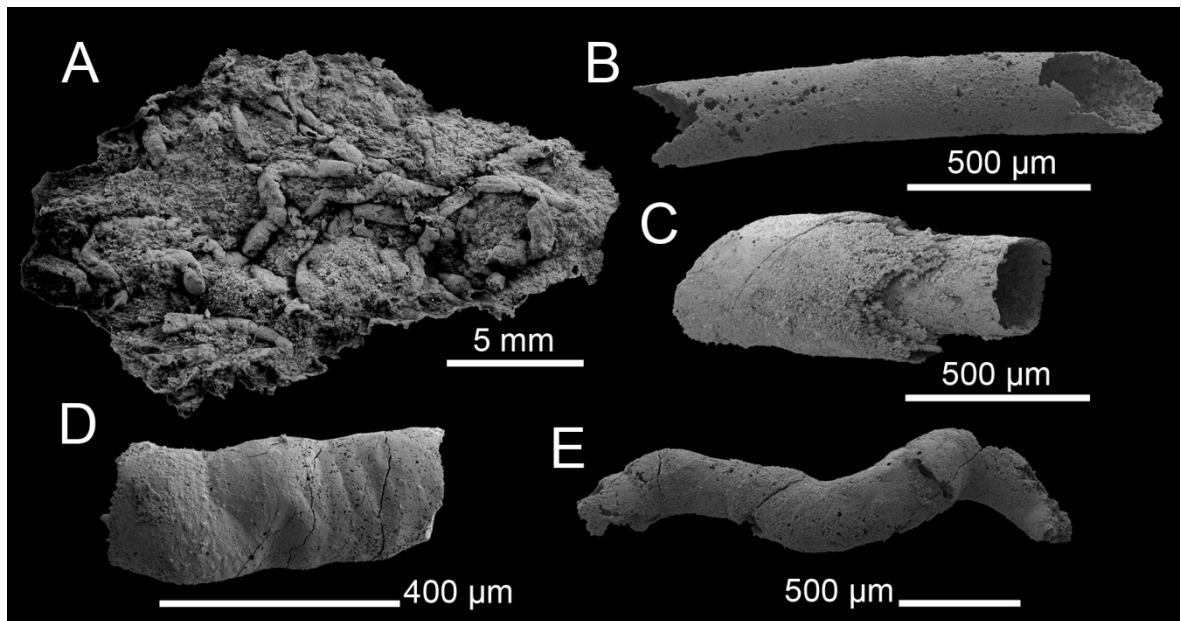


Fig. 21. Small tubular fossils from Villarta de los Montes. (A) Latex cast from the siliciclastic level. Note the accumulation of fossils. (B–E) SEM images of fossils from the carbonate level. (B) Straight tube with thin wall. (C) Specimen with a tube-in-tube construction. (D) Tube with several constrictions. (E) Twisted tube. Note the similarities between (A) and (D–E).

others that show signs of several walls (Fig. 21C). Many of these specimens seem to be fragments of larger fossils (e.g. molds of the internal lumen of *Cloudina* or isolated internal tubes of *Sinotubulites*). However, one of the types (which occurs as well in the siliciclastic level in large “monospecific” accumulations; 21A) may represent a taxon of its own. The

tubes are long, curved to sinuous, and show characteristic twists and constrictions (Fig. 21D–E).

Similar small tubular fossils co-occur with *Cloudina* and other biomineralizers at different localities: Namibia (Grotzinger et al., 2000 fig. 14D), Mexico (McMenamin, 1985 fig. 5.1, 5.4), Siberia (Kontorovich et al., 2011 fig.13C1–G2) and China (Hua et al., 2005b pl. 1; personal observation). Although these small fossils seem to be a common component of late Ediacaran skeletal assemblages (e.g. more than a 10% of the total in the Nama Group in Namibia; Grotzinger et al., 2000), they have never been properly described or illustrated.

CLOUDINA FROM SOUTH CHINA

Cloudina has been described in carbonates from the upper part of the Ediacaran Dengying Formation, in the Gaojiashan (Gaojiashan section) and Beiwan (Lijiagou section) Members. *Cloudina* fossils occur calcified in the microbial limestones of the Gaojiashan section and exceptionally preserved by secondary phosphatization in dolostones of the Lijiagou section (Figs. 1A, 9, 10D, 22, 23; e.g. Cai et al., 2010, 2014; Cortijo et al., 2014).

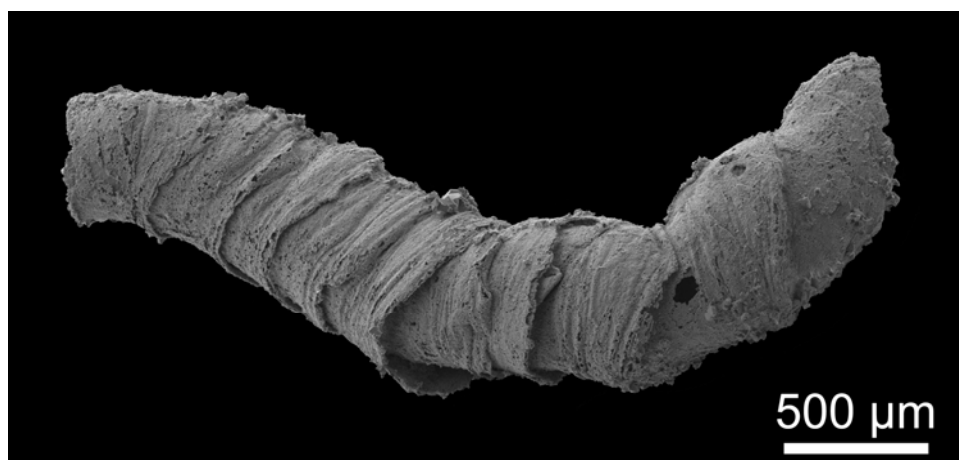


Fig. 22. *Cloudina hartmanae* specimen from the Lijiagou section, China.

The study of the exceptionally preserved *Cloudina* fossils from the Lijiagou section has yielded abundant information about this early biomineralizers, such as the hemispherical (Figs. 1A, 9; Bengtson and Yue, 1992; Chen and Sun, 2001; Hua et al., 2005a; Chen et al., 2008; Cai et al., 2014) and pointed bases (Fig. 23; Cortijo et al., 2014) of *Cloudina* tubes, the existence of branching specimens (Hua et al., 2005a; Cortijo et al., 2014), and the presence of possible predatorial borings in the shells of *Cloudina* (Bengtson and Yue, 1992). All this information has lead to novel hypothesis regarding the development, mode of life and dispersal strategies of *Cloudina* (Hua et al., 2005a; Cai et al., 2014; Cortijo et al., 2014).

Ontogeny and dispersal of *Cloudina*

Previous reports have shown that *Cloudina* tubes grew from a basally closed cone, and that they occasionally branch. However, specimens with developed branching have not



been observed, suggesting that branching tubes may eventually detach from the original tube. New material from the Beiwan Member in the Lijiagou section, includes two distinct morphotypes, tubes with rounded versus pointed apices (Fig. 23). Since in branching specimens one of the daughter tubes has a conical apex (Cortijo et al., 2014, fig. 3A), the

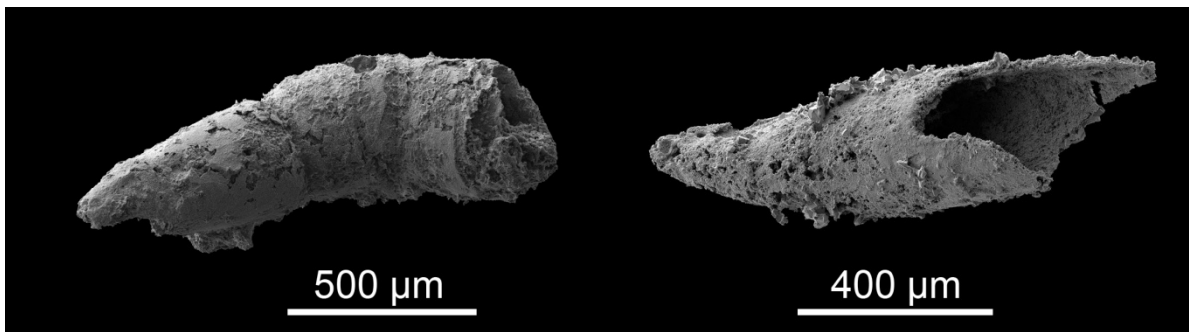


Fig. 23. *Cloudina* specimens from China with a pointed closed cone (modified from Cortijo et al., 2014 fig. 2). Note the smooth surface.

loose specimens with pointed apices have been interpreted as propagules originated by asexual division. Spherical structures, similar in both morphology and dimensions, to the bases of the hemispherical cones of *Cloudina* occur as well in the samples and have been interpreted as embryonic shells of *Cloudina* resulting from sexual reproduction. These interpretations lead to the following reconstruction: cloudinids with a spherical apex were derived from sexual reproduction, with their spherical termination deriving from spherical embryonic shell, whereas those with a conical apex are branches originated through asexual reproduction and detached from their parent tubes. These interpretations imply that *Cloudina* could disperse both through sexual and asexual reproduction, producing spherical embryos and conical propagules, respectively (Fig. 24).

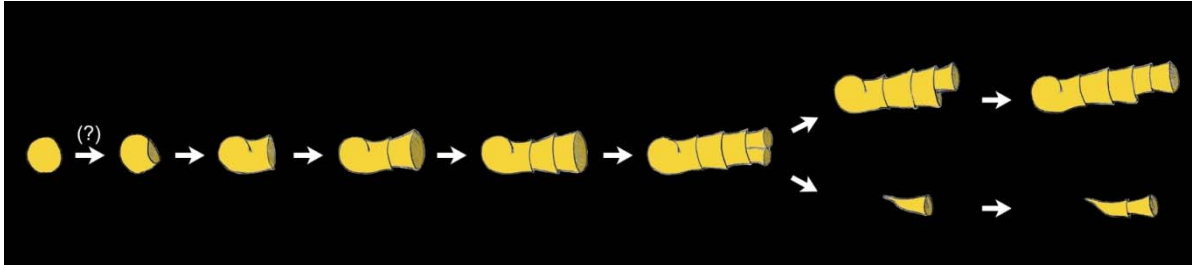
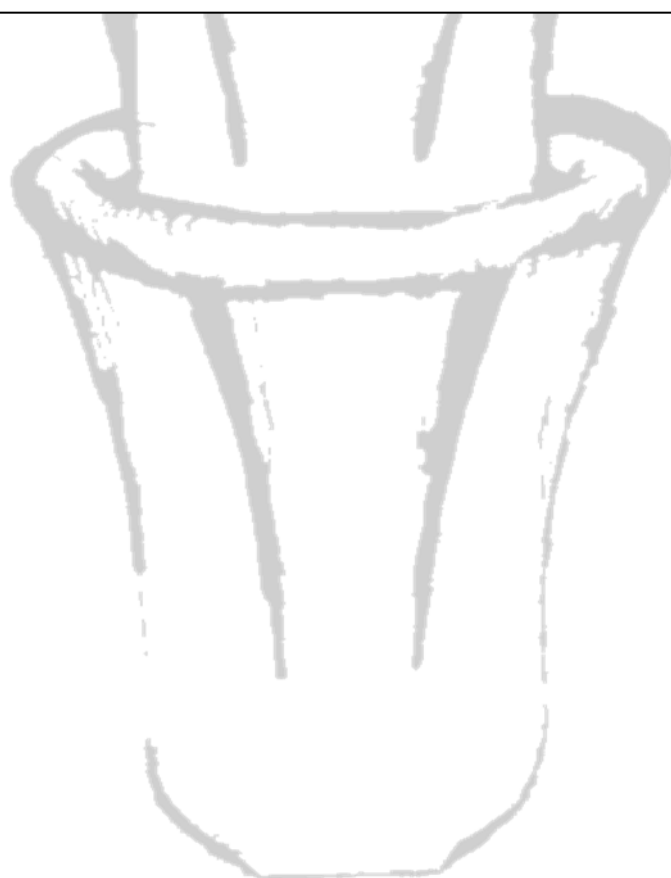


Fig. 24. Interpretive diagram showing the proposed ontogenetic sequence of *Cloudina* (modified from Cortijo et al., 2014 fig. 5). From a possible spherical embryo, the tube grows by adding successive funnels, divides by branching at some time and the daughter propagule is later released, giving rise to two distinct individuals.



THE
VILLUERCAS-IBORES-JARA
GEOPARK



THE VILLUERCAS-IBORES-JARA GEOPARK

A Geopark is a unified area with a geological heritage of international significance. Geoparks use this heritage to promote awareness of key issues facing society in the context of the dynamic planet we all live on. The Global Geoparks Network, established in 1998, is supported by United Nations Educational, Scientific and Cultural Organization –UNESCO (unesco.org).

The Villuercas-Ibores-Jara Geopark (Fig. 25) is a mountainous massif that covers 2,544 km² and includes 19 municipalities with about 15,000 inhabitants. It is located in the south-east of the province of Cáceres (Extremadura, Spain), between the Tajo and Guadiana rivers. It was approved as a Geopark on the 17th of September 2011 (geoparquevilluercas.es). It is composed by a system of quartzite sierras and shale valleys aligned in parallel in a northwest-southeast direction. They are crossed by faults, which have given rise to a fractured landscape. This landscape is mostly formed by rocks dated from the Ediacaran to the Silurian, although younger rocks (20 to 1.8 Ma) are also present.

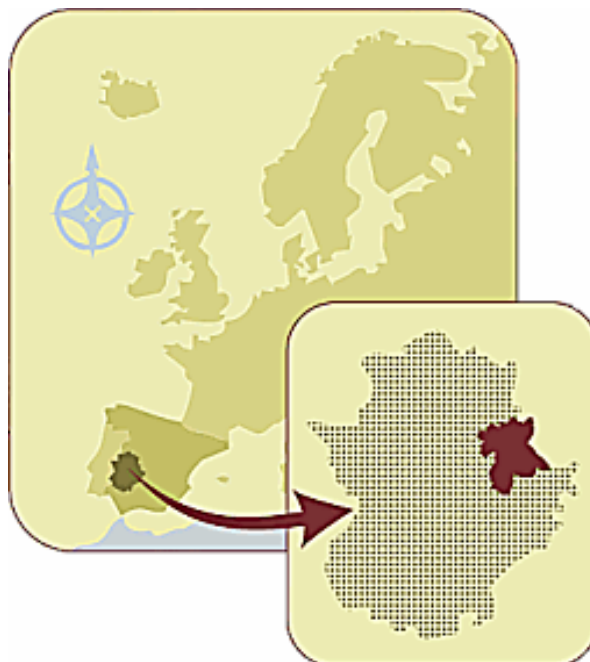


Fig. 25. Geopark location map (geovilluercas.com).

The geopark is essential for the development of the area, due to the lack of industries or other sources of employment besides agriculture. Tourism is growing, especially ecotourism and wildlife-related tourism (bird watching, hiking, etc.), and the geopark has a crucial role promoting this type of tourism.

Among the forty-four geosites that comprise the Geopark (including ridges, faults, river valleys, caves, prehistoric paintings, old mines, etc.), paleontological localities are highly relevant, particularly the *Cloudina*-bearing locality in Castañar de Ibor, numbered as Geosite 39 and called “Yacimiento paleontológico del Arroyo de las Fuentes” (Arroyo de las Fuentes paleontological site; Figs. 3–4; Cortijo et al., 2010a, b). The Villuercas-Ibores-Jara Geopark is currently the only geopark worldwide that includes localities with *Cloudina*, and this represents a paleontological heritage of singular importance.

During this PhD thesis, several outcrops of carbonates of the Ibor Group (usually associated with old carbonate quarries) within or close to the Villuercas-Ibores-Jara Geopark, were examined for skeletal fossils. In most of them fossils have not been found to date:

- Roturas: carbonates crop out along road CC-121, about 2 km NW of the village of the same name (UTM (EUR50): 30S 0285390, 4382563). No fossils were identified.
- La Calera: carbonates crop out about 400 m W of the small village La Calera, close to Alía (UTM (EUR50): 30S 305962, 4376275). This outcrop yields problematic fossil-looking fragments, but positive identification has not been possible.
- Navalvillar de Ibor: carbonates crop out in several old quarries about 5.5 km SE of the village Navalvillar de Ibor (close to the CC-20 road from Guadalupe to Navatrasierra; UTM (EUR 50): 30S 297296, 4381150) and also 3.5–4 km SE of the same village (close to the EX-118 road from Navalvillar de Ibor to Guadalupe, around La Cereceda area; UTM (EUR 50): 30S 295382, 4381952, 295401, 4381827 and 296004, 4381272). No fossils were identified.
- Río Fresnedoso: small carbonate blocks crop out on the banks of the Fresnedoso River, about 5 km NW of Anchuras, Ciudad Real Province (UTM (EUR 50): 30S 339247, 4376210). No fossils were identified.

- Calera de la Ermita de Mirabel: carbonates crop out in an abandoned quarry close to the Chapel of Mirabel, about 3.5 km SW of Guadalupe (UTM (EUR50): 30S 296621, 4368019). No fossils were identified.
- Arrocampo: carbonates crop out in the north bank of the Tajo River, close to the Arrocampo dam, about 7 km SW of Almaraz (UTM (EUR50): 264733, 4407045). No fossils were identified.
- Río Frío: carbonate blocks crop out on the banks of the Frío River where it is crossed by a narrow road from La Estrella to Sevilleja de la Jara, about 4.5 km SW of La Nava de Ricomalillo, Toledo Province (UTM (EUR 50): 30S 328051, 4386617). No fossils were identified.
- Arroyo del Pedroso: an olistostrome similar to that of Fuentes or El Membrillar occurs in the northeastern part of the Villuercas-Ibores-Jara Geopark, in the Arroyo del Pedroso area close to the EX-387 road about 6 km SW of Puente del Arzobispo (UTM (EUR50): 30S 312541, 4402602); Fig. 26), within the same area as Geosite 42. Although the sedimentary rocks are affected by a nearby granite intrusion and visibility is limited by soil and vegetation cover, the olistostrome can be readily observed here. Preliminary investigations suggest the presence of *Cloudina* in the olistostrome (Fig. 26B–C).

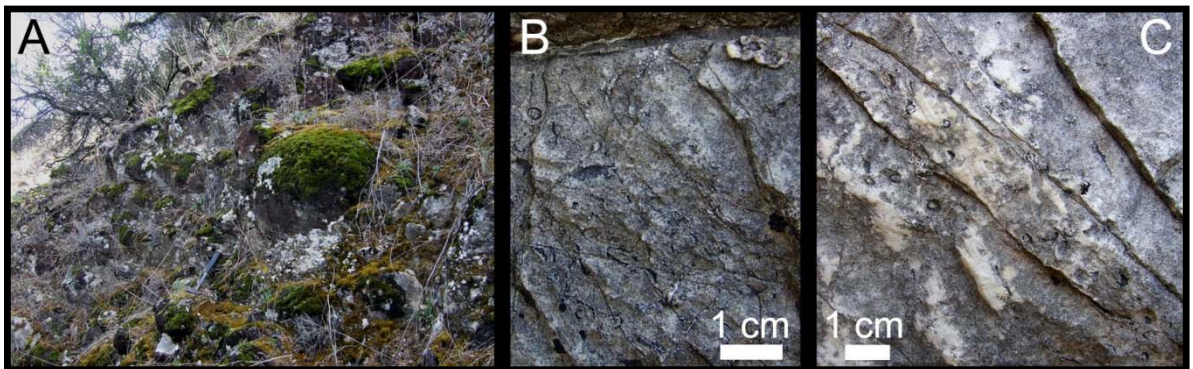


Fig. 26. Arroyo del Pedroso locality. (A) View of the olistostrome. (B–C) Detail of a carbonate block with circular and tubular forms. Note the similarity with *Cloudina* fossils in comparable surfaces (e.g. compare with Fig. 15 left).

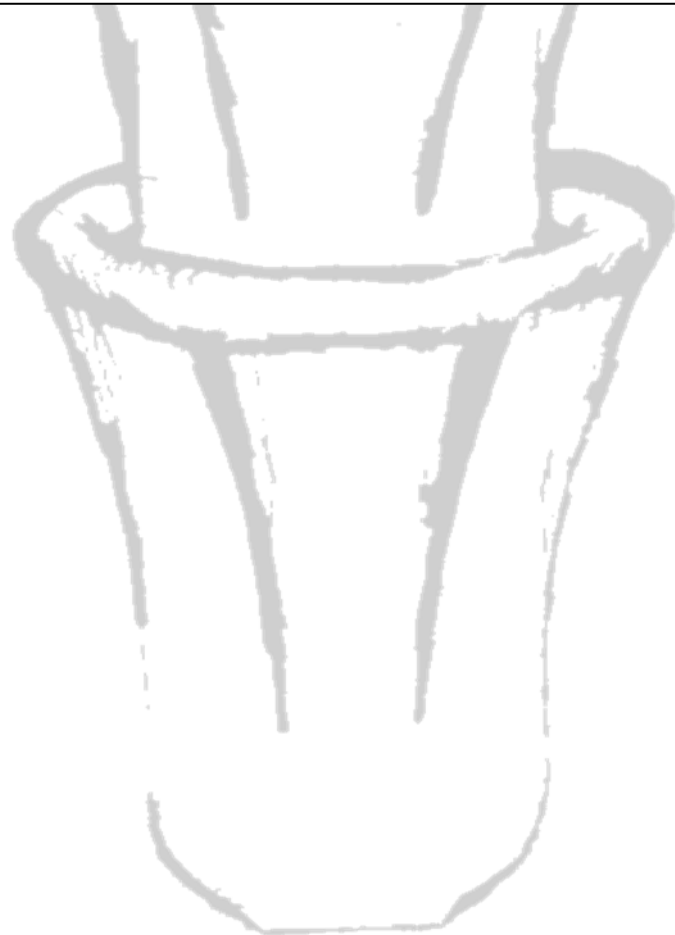
- Area of Garganta Honda: in the road CC-20 from Guadalupe to Navatrasierra, about 11.5 km SW of Navatrasierra (UTM (EUR50): 30S 297627, 4380964) there are siliciclastic levels with tubular, fossil-like molds (Fig. 27). Some of these (Fig. 27 right) show the typical funnel-in-funnel structure of *Cloudina* or a constricted appearance similar to that of the small tubes from Villarta de los Montes (see Fig. 24). Fossils from this locality were reported as “Less well preserved specimens” of *Cloudina* in Vidal et al., 1994 (fig. 11; locality 10 called “Hospital del Obispo section; road cut”).



Fig. 27. Area of Garganta Honda. View of the outcrop (left) and detail of possible *Cloudina* fossils (right). Note the transversal ornamentation that could represent the funnel-in-funnel construction.



CONCLUSIONS /
CONCLUSIONES



CONCLUSIONS

- From the previously known late Ediacaran localities from central Spain, two of them, Villarta de los Montes and El Membrillar, both in the Badajoz Province, have yielded exceptionally preserved early skeletal fossils.
- *Cloudina* is the most abundant late Ediacaran skeletal fossil in the Spanish localities.
- Two *Cloudina* species have been identified from central Spain, the type species, *Cloudina hartmanae* Germs, 1972, and the new species *Cloudina carinata* Cortijo, Martí Mus, Jensen and Palacios, 2010, characterized among other features by prominent longitudinal crests and funnels with a thickened apertural rim.
- *Cloudina* funnels were secreted as independent elements not fused to the previous ones.
- The Villarta de los Montes locality has yielded a diverse skeletal fossil assemblage, including *Cloudina hartmanae*, *C. carinata*, *Sinotubulites*, a flask-shaped form comparable to *Protolagena*, and long sinuous tubular fossils. The Villarta de los Montes assemblage most closely resembles that from the Dengying Formation of South China.
- The presence of *Sinotubulites baimatuoensis* is confidently reported for the first time in Spain and represents the first report of the genus outside China and America.
- *Cloudina* tubes with pointed basal elements have been reported from the Dengying Formation in the Lijiagou section, South China, and have been interpreted as detached branches (propagules) originated by asexual reproduction, which implies that *Cloudina* could disperse both through sexual and asexual reproduction.
- A new *C. carinata*-bearing locality has been described in the Arroyo del Cubilar area (Toledo Province).
- The Villuercas-Ibores-Jara Geopark (UNESCO) is the only geopark with fossils of late Ediacaran biomineralized metazoans. One geosite located close to Castañar



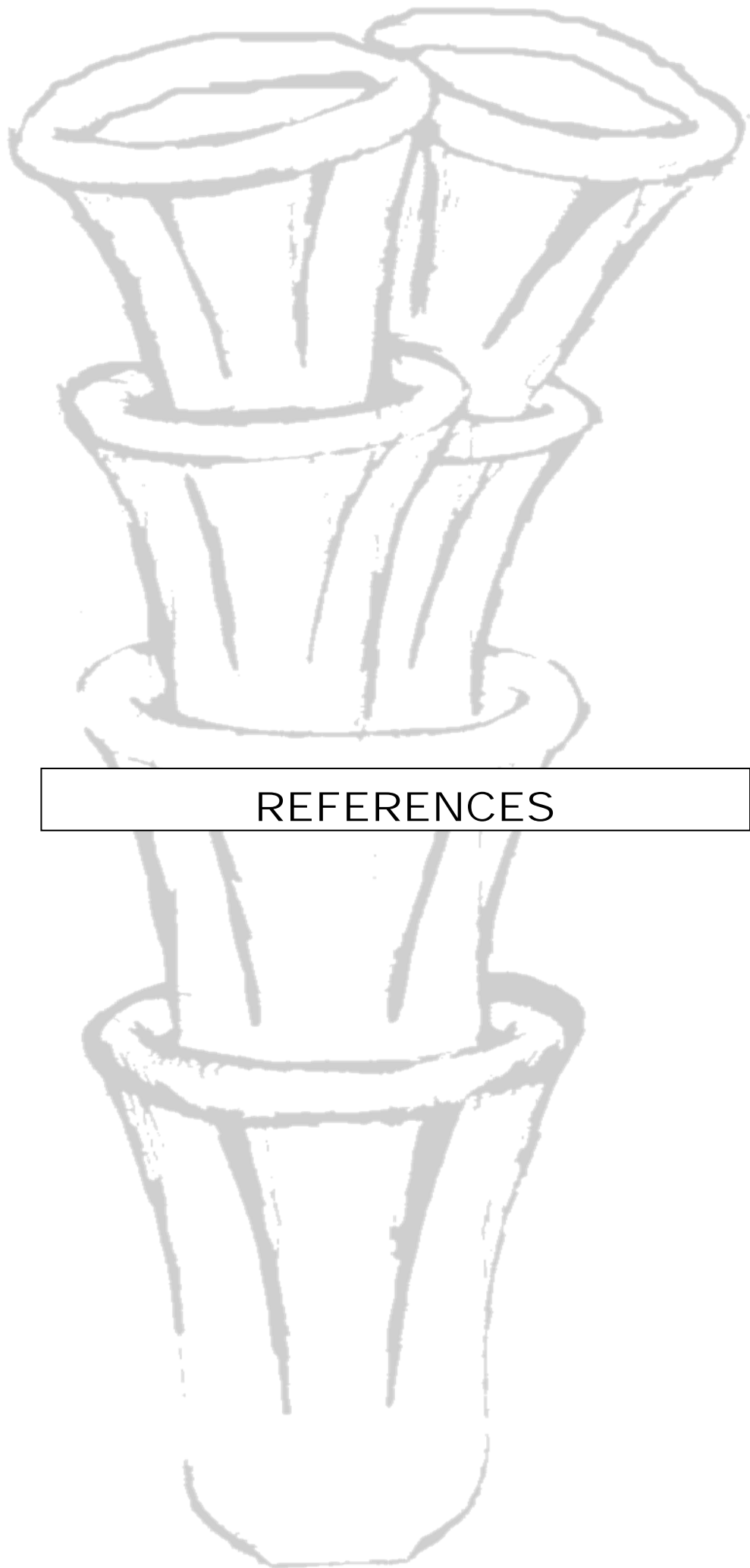
de Ibor is an outcrop of the Ibor Group carbonates with *Cloudina*. Two possible additional occurrences of skeletal fossils have been found in the geopark, in outcrops along Arroyo del Pedroso and Garganta Honda.

CONCLUSIONES

- De los yacimientos del Ediacárico terminal previamente conocidos en España central, dos de ellos, Villarta de los Montes y El Membrillar (ambos en la provincial de Badajoz) contienen fósiles esqueléticos tempranos excepcionalmente preservados.
- *Cloudina* es el fossil esquelético del Ediacárico terminal más abundante en los yacimientos españoles.
- Dos especies de *Cloudina* han sido identificadas en España central, la especie tipo, *Cloudina hartmanae* Germs, 1972, y la nueva especie *Cloudina carinata* Cortijo, Martí Mus, Jensen and Palacios, 2010, caracterizada entre otras cosas por unas prominentes crestas longitudinales y elementos con bordes distales engrosados.
- Los sucesivos elementos de *Cloudina* eran secretados de forma independiente y no estaban fusionados a los anteriores.
- El yacimiento de Villarta de los Montes contiene una diversa asociación fósil que incluye *Cloudina hartmanae*, *C. carinata*, *Sinotubulites*, un fósil con forma de botella comparable a *Protolagena* y pequeños fósiles tubulares. Esta asociación fósil es similar a la que aparece en la Formación Dengying del sur de China.
- Se confirma por primera vez la presencia de *Sinotubulites baimatuoensis* en España, siendo la primera cita del género fuera de China y América.
- Tubos de *Cloudina* con elementos basales cónicos aparecen en la Formación Dengying, en la sección de Lijiagou, en el sur de China. Estos tubos han sido interpretados como propágulos desprendidos del tubo principal de *Cloudina* tras su ramificación, lo que implicaría que *Cloudina* se dispersaba tanto sexual como asexualmente.
- Un nuevo yacimiento con *C. carinata* ha sido descrito en el área del Arroyo del Cubilar (provincia de Toledo).
- El Geoparque Villuercas-Ibores-Jara (UNESCO) es el único con fósiles de metazoos biomineralizados del Ediacárico terminal. Un geosítio cercano a



Castañar de Ibor es un yacimiento de carbonatos del Grupo Ibor que contienen *Cloudina*. Otros dos posibles yacimientos de fósiles esqueléticos han sido encontrados en el geoparque, en las áreas del Arroyo del Pedroso y de la Garganta Honda.



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Speculative reconstruction of the sea-floor in central Spain in the late Ediacaran Period (modified from an illustration by **Antonio Gragera**). A shallow marine carbonate platform dominated by stromatolitic structures, where *Cloudina* and other organisms (sabelliditids, vendotaenids, etc.) were common.

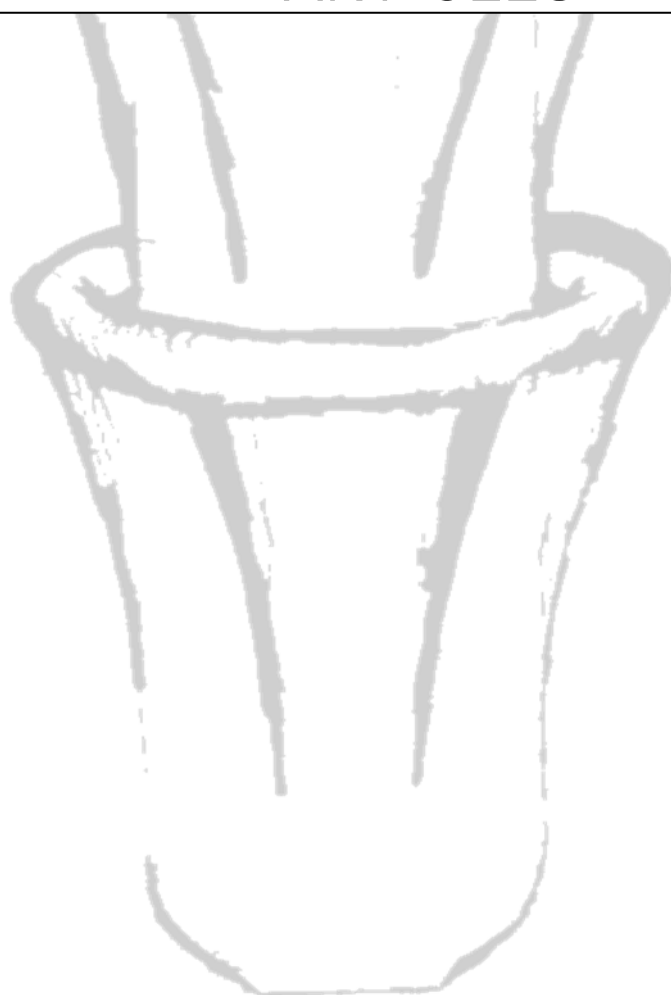


Cloudina by **Luisa Torrejón Morales**. 1st prize in the Villuercas-Ibores-Jara Geopark Pet Scholar Award. Note the friendly face and the controversial arms.



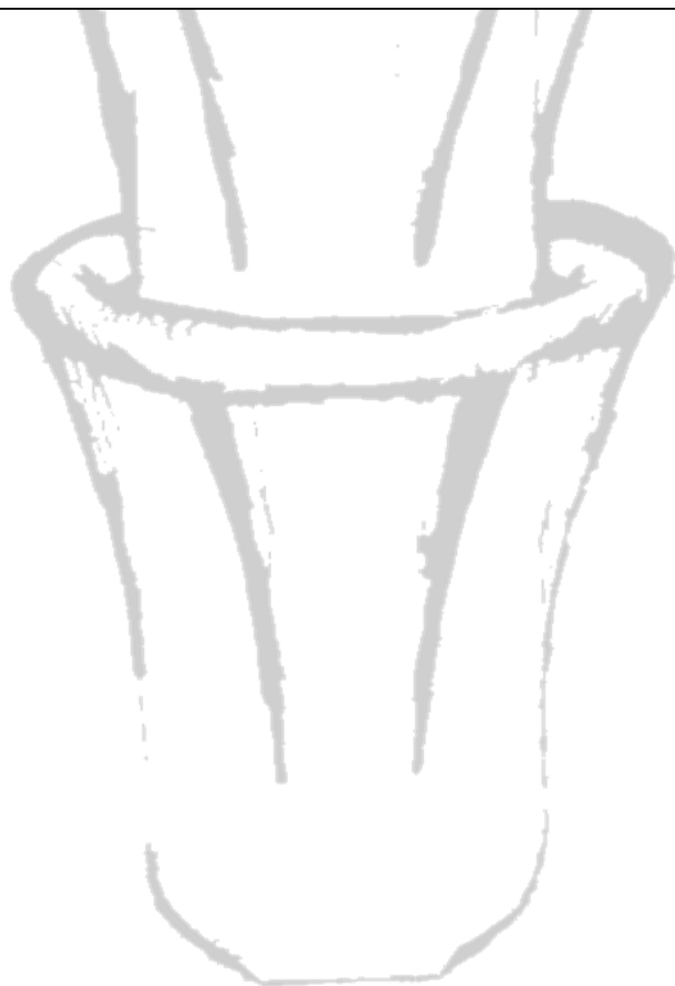


ARTICLES





ARTICLE I



YACIMIENTOS EXCEPCIONALES EN EXTREMADURA DE LOS PRIMEROS METAZOOS MINERALIZADOS DEL EDIACÁRICO

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Resumen: Durante las últimas décadas se han descrito varios fósiles mineralizados del Ediacárico terminal que quizá constituyan los ancestros de los diversos metazoos biomineralizadores surgidos durante la subsiguiente "explosión cámbrica", hace unos 530 Ma. Estos fósiles se interpretan como los primeros metazoos capaces de secretar un esqueleto mineralizado, lo que les confiere una gran importancia desde el punto de vista de la evolución biológica. El primero de ellos en ser descrito, y quizás el mejor conocido, es *Cloudina*, un fósil de pequeño tamaño y aspecto tubular con una estructura muy característica, ya que está formado por una sucesión de elementos individuales con forma de embudo encajados uno dentro de otro. *Cloudina* se considera un fósil índice del Ediacárico terminal, por lo que, además de su gran interés paleontológico, posee un gran valor bioestratigráfico. Actualmente se conocen varios yacimientos de *Cloudina* en España, en la zona Centro Ibérica, que constituyen los únicos en Europa. Tres de ellos están en Extremadura: uno en Castañar de Ibor, Cáceres; otro en Villarta de los Montes, Badajoz; y un tercero en la finca El Membrillar, en Helechosa de los Montes, Badajoz. Los fósiles de estos yacimientos presentan una gran variedad de modos de preservación, algunos excepcionales, así como cierta diversidad morfológica, incluyendo la presencia de la nueva especie *Cloudina carinata* Cortijo *et al.*, 2010, hasta ahora exclusiva de Extremadura. Todo esto convierte a los yacimientos extremeños, en especial el de El Membrillar (donde muchos fósiles aparecen secundariamente silicificados), en yacimientos ediacáricos de gran importancia a nivel mundial.

Palabras clave: *Cloudina*, Ediacárico, Extremadura, Metazoos mineralizados, Yacimientos excepcionales.

Exceptional outcrops of the first mineralized Ediacaran metazoans in Extremadura

Abstract: Over the last decades, several mineralized fossils have been described from the terminal Ediacaran which may include the ancestors of the diverse biomineralizing metazoa that emerged during the "Cambrian Explosion", ca. 530 Ma ago. These fossils are interpreted as the first metazoans capable of secreting a mineralized skeleton, which makes them highly significant from the standpoint of biological evolution. The first of these fossils to be described, and perhaps the best known, is *Cloudina*, a small, tubular fossil with a characteristic structure consisting of a succession of stacked funnel-shaped elements.

Cloudina is considered an index fossil of the terminal Ediacaran and therefore, in addition to its paleobiological interest, has a high biostratigraphic value. Several *Cloudina*-bearing outcrops are known in Spain, in the Central Iberian zone, and they represent the only known occurrences of *Cloudina* in Europe. Three of them are in Extremadura: one in Castañar de Ibor, Cáceres province; another in Villarta de los Montes, Badajoz province; and a third one in El Membrillar property, in Helechosa de los Montes, Badajoz province. Fossils from these outcrops occur in a variety of preservational modes, some exceptional, and show a considerable morphological diversity, including the presence of the new species *Cloudina carinata* Cortijo *et al.*, 2010, until now only known in Extremadura. For these reasons, the *Cloudina*-bearing outcrops in Extremadura, especially the one in El Membrillar (where some specimens are secondarily silicified), are of great importance on a global scale.

Key words: *Cloudina*, Ediacaran, Extremadura, mineralized metazoans, exceptional outcrops.

INTRODUCCIÓN

Hasta el periodo Cámbrico (hace aproximadamente 543-490 Ma.) no aparecen en el registro fósil diversos y abundantes metazoos con esqueletos mineralizados, como parte de la radiación evolutiva conocida como "explosión cámbrica". Sin embargo, durante las últimas décadas se han descrito varios fósiles esqueléticos algo más antiguos (del final del periodo Ediacárico) que se interpretan como los primeros metazoos biomineralizadores. En concreto, se trata de los géneros *Cloudina*, *Namacalathus*, *Sinotubulites* y *Namapoikia*, quizá los ancestros de la subsiguiente radiación de animales biomineralizadores del Cámbrico (McMenamin, 1985; Grant, 1990; Grotzinger *et al.*, 2000; Hofmann y Mountjoy, 2001; Wood *et al.*, 2002; Hua *et al.*, 2005).

Cloudina fue el primero de estos fósiles en ser formalmente descrito (en sedimentos ediacáricos de Namibia; Germs, 1972) y es el mejor conocido y quizá el más abundante, ya que también se ha encontrado en Omán (Conway Morris *et al.*, 1990), el sur de China (Hua *et al.*, 2005), el sureste de los Estados Unidos (Signor *et al.*, 1987), Méjico (McMenamin, 1985; Sour-Tovar *et al.*, 2007), la Columbia Británica, Canadá (Hofmann y Mountjoy, 2001), Siberia (Kontorovich *et al.*, 2008) y España (Palacios, 1989; Vidal *et al.*, 1994). Sin embargo, aunque los yacimientos de *Cloudina* están universalmente distribuidos, son escasos y resultan siempre de gran interés paleontológico (Grant, 1990).

Dataciones U-Pb de circones en Namibia y Omán sitúan la edad de *Cloudina* entre 550 y 543 Ma. (Grotzinger *et al.*, 1995; Amthor *et al.*, 2003) y el contexto bio y quimioestratigráfico de los otros registros de *Cloudina* (en especial los de Estados Unidos, Méjico, Columbia Británica y China; Corsetti y Hagadorn, 2003), sugieren una edad comparable. Por lo tanto, estos datos indican que *Cloudina* podría constituir un fósil índice del Ediacárico terminal (Grant, 1990).

Cloudina es un fósil de pequeño tamaño (unos milímetros de diámetro) y aspecto tubular, consistente en una serie de embudos de pared delgada imbricados de forma excéntrica. Las dos especies de *Cloudina* más estudiadas y citadas, *C. hartmannae* Germs, 1972, y *C. riemkeae* Germs, 1972, difieren principalmente en el tamaño y posiblemente sean sinónimas (Grant, 1990; Hua *et al.*, 2005). Otras especies de *Cloudina* han sido descritas posteriormente, especialmente en China, pero sus características distintivas no están claras (Steiner *et al.*, 2007) y es posible que todos los ejemplares hasta ahora descritos pertenezcan a la especie tipo *C. hartmannae*.

Aunque las afinidades biológicas de *Cloudina* son inciertas, se le ha considerado un animal de, al menos, "grado de cnidario" (Grant, 1990) y ha sido relacionada principalmente con anélidos serpúlidos y cnidarios (Glaessner, 1976; Grant, 1990; Hua *et al.*, 2005). A pesar de no tener claros descendientes en el periodo Cámbrico, su importancia a la hora de entender la evolución temprana de los metazoos y del proceso de biomineralización son indiscutibles.

YACIMIENTOS DE *CLOUDINA* EN EXTREMADURA

Cloudina fue encontrada en España en la década de los ochenta (Palacios, 1989) y actualmente se conocen varios yacimientos de este fósil en la zona Centro Ibérica (Fig. 1) que constituyen los únicos en Europa (Vidal *et al.*, 1994; Jensen *et al.*, 2007). Los fósiles de *Cloudina* en España aparecen asociados a un nivel de carbonatos que constituye un importante nivel guía dentro de una potente sucesión de rocas del Ediacárico tardío-Cámbrico inferior en la Zona Centro Ibérica. Este nivel de carbonatos se extiende en dirección noroeste-sudeste formando una banda que abarca desde el sur de la provincia de Salamanca, atravesando la parte noreste de Extremadura, hasta Ciudad Real. Los carbonatos afloran en varias localidades a lo largo de esta banda, donde reciben distintos nombres locales. Esta banda de carbonatos se depositó en aguas relativamente poco profundas (como indican la presencia local de oolitos y probables estromatolitos, y la evidencia de tormentas) y se piensa que se formó en una plataforma carbonatada que se abría al mar en dirección noreste. Hacia el suroeste la presencia de carbonatos se reduce y dominan los sedimentos siliciclásticos de aguas someras. Al nordeste de la banda de carbonatos hay evidencias de un ambiente de deposición más profundo. Entre estas evidencias están los ejemplos de colapso a gran escala de la plataforma, quizá debidos a la influencia de terremotos o a bajadas del nivel del mar. Estos colapsos han dado lugar a sedimentos caóticos, denominados olistostromas, formados por bloques de carbonato mezclados con distintas rocas siliciclásticas (Moreno, 1975). Algunos de los ejemplares mejor preservados de *Cloudina* se encuentran en los bloques de carbonato de estos olistostromas.

El nivel de carbonatos al que se asocian los fósiles de *Cloudina* forma parte del Grupo Ibor, dominado en general por rocas siliciclásticas de grano fino, pero que también contiene areniscas y conglomerados. El Grupo Ibor se sitúa sobre el Grupo Domo Extremeño, que contiene lutitas, grauvacas y conglomerados. El Grupo Domo Extremeño se caracteriza por la presencia de facies turbidíticas y representa una deposición en aguas más profundas que el Grupo Ibor (Vidal *et al.*, 1994).

Algunos de los mejores (sin duda, los mejor conocidos) yacimientos de *Cloudina* de España están en Extremadura (uno en Castañar de Ibor, Cáceres; otro en Villarta de los Montes, Badajoz; y un tercero en la finca El Membrillar, en Helechosa de los Montes, Badajoz). Entre los fósiles de estos yacimientos existe cierta diversidad morfológica, hallándose representantes de más de una especie, incluyendo la nueva especie *Cloudina carinata* Cortijo *et al.*, 2010 (por ahora sólo descrita en Extremadura), y abundantes tubos sencillos no descritos previamente. Un aspecto importante de los distintos yacimientos de *Cloudina* en Extremadura son los diversos modos de preservación que muestran los fósiles, lo que ha facilitado el empleo de numerosas técnicas de preparación que permiten la obtención de información morfológica diversa y complementaria.

El yacimiento de Castañar de Ibor (Fig. 2) se encuentra cerca del pueblo, a lo largo de la carretera entre esta localidad y Robledollano (Palacios *et al.*, 2004a). En este yacimiento los carbonatos a los que se asocian los fósiles de *Cloudina* se encuentran intercalados con sedimentos siliciclásticos en una sucesión de aproximadamente 15 m de potencia (Fig. 2A-B). Siguiendo la carretera Castañar de Ibor-Robledollano en

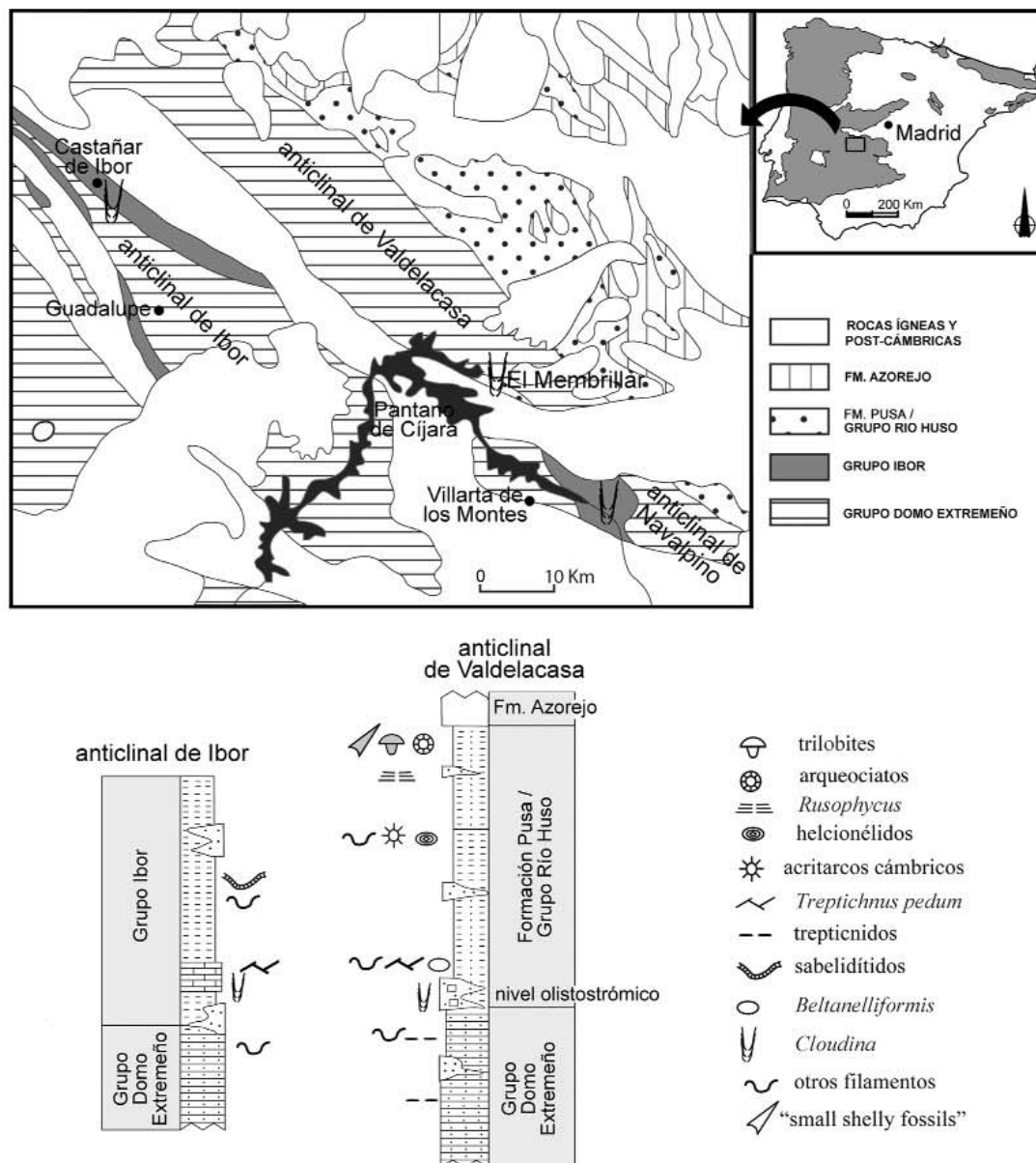


Figura 1. Localización y contexto geológico de los yacimientos de *Cloudina* en la zona Centro Ibérica. La columna estratigráfica del anticlinal de Navalpino es comparable a la del anticlinal de Ibor (basado en Vidal *et al.*, 1999 y Jensen *et al.*, 2010).

Figure 1. Location and geological context of *Cloudina*-bearing outcrops in the Central Iberian zone. The stratigraphic column of the Navalpino anticline is comparable to that of the Ibor anticline (based on Vidal *et al.*, 1999 and Jensen *et al.*, 2010).

dirección suroeste afloran los sedimentos (principalmente grauvacas, aunque existen niveles conglomeráticos) que se encuentran por debajo del nivel carbonatado. Por encima de los carbonatos se dispone una unidad dominada por lutitas donde aparecen, en distintos yacimientos de esta región, abundantes fósiles filamentosos, incluyendo sabelidítidos que podrían indicar una edad cámbrica para estos sedimentos. Los carbonatos de este yacimiento están muy alterados por dolomitización y la preservación de los fósiles no es buena (Fig. 2C).

Los carbonatos del Grupo Ibor (también denominado Grupo Ibor-Navalpino en la zona del anticlinal de Navalpino) afloran a ambas orillas del río Guadiana al noroeste del pueblo de Villarta de los Montes y reci-



Figura 2. Yacimiento de *Cloudina* en Castañar de Ibor. A-B, vistas generales del yacimiento donde se aprecia el nivel de carbonatos. C, ejemplares de *Cloudina* en la superficie pulida de una muestra de Castañar de Ibor.

Figure 2. *Cloudina*-bearing outcrop in Castañar de Ibor. A-B, general view of the outcrop with the carbonate level. C, specimens of *Cloudina* on a polished surface of a sample from Castañar de Ibor.

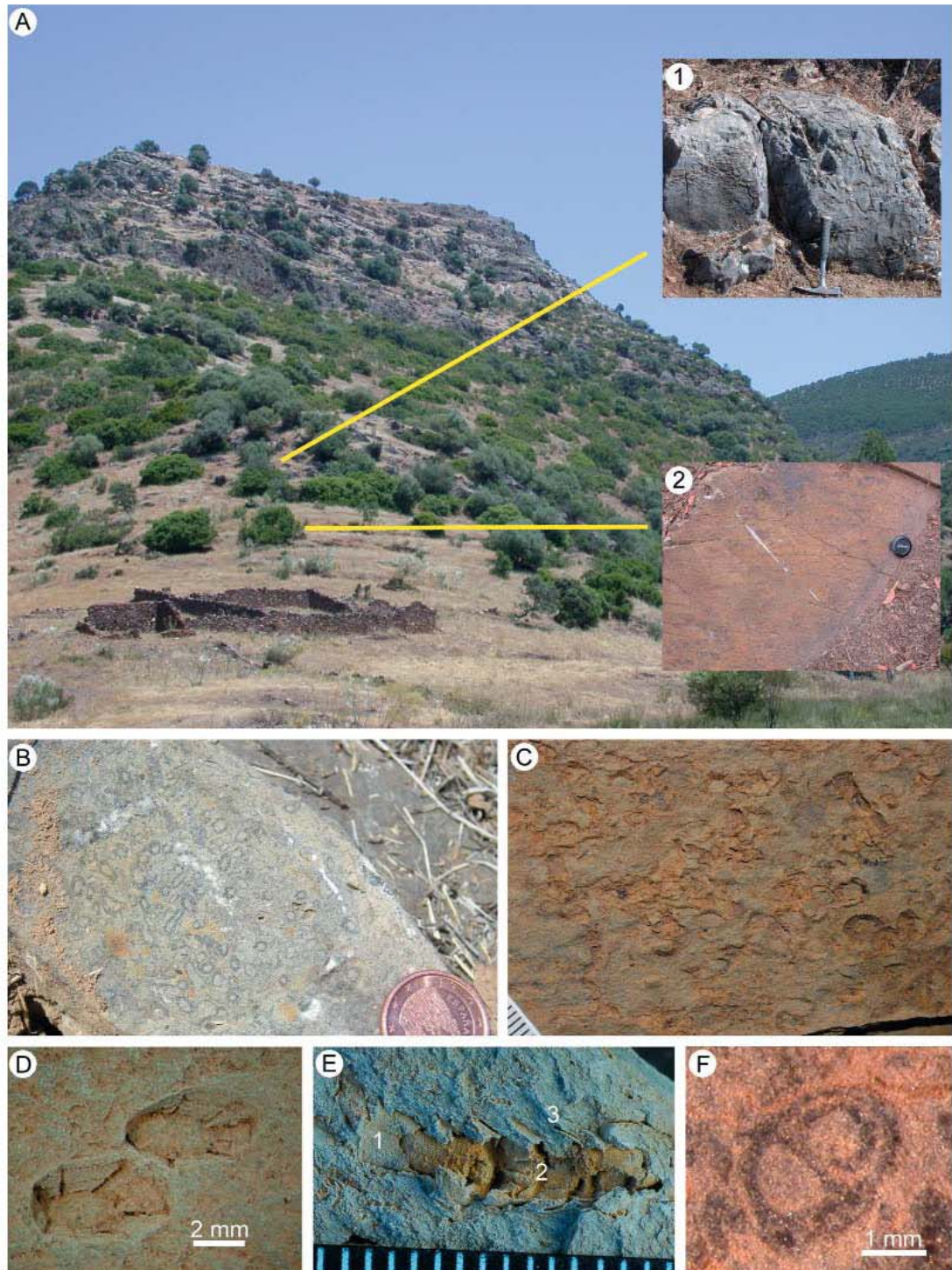
ben el nombre local de "calizas de Villarta" (Fig. 3). En este área los carbonatos alcanzan 300 m de potencia y presentan evidencias de desplazamientos sinsedimentarios. Los fósiles de *Cloudina* son abundantes en los niveles masivos de carbonatos (Fig. 3A-1), pero también inmediatamente debajo, en sedimentos siliciclásticos (que también contienen carbonatos lenticulares, Fig. 3A-2). En los niveles carbonatados la mayoría de los fósiles tienen composición carbonatada (Fig. 3B, F), pero también hay ejemplares secundariamente mineralizados. En los niveles siliciclásticos los fósiles de *Cloudina* están preservados como moldes (Fig. 3C-E).

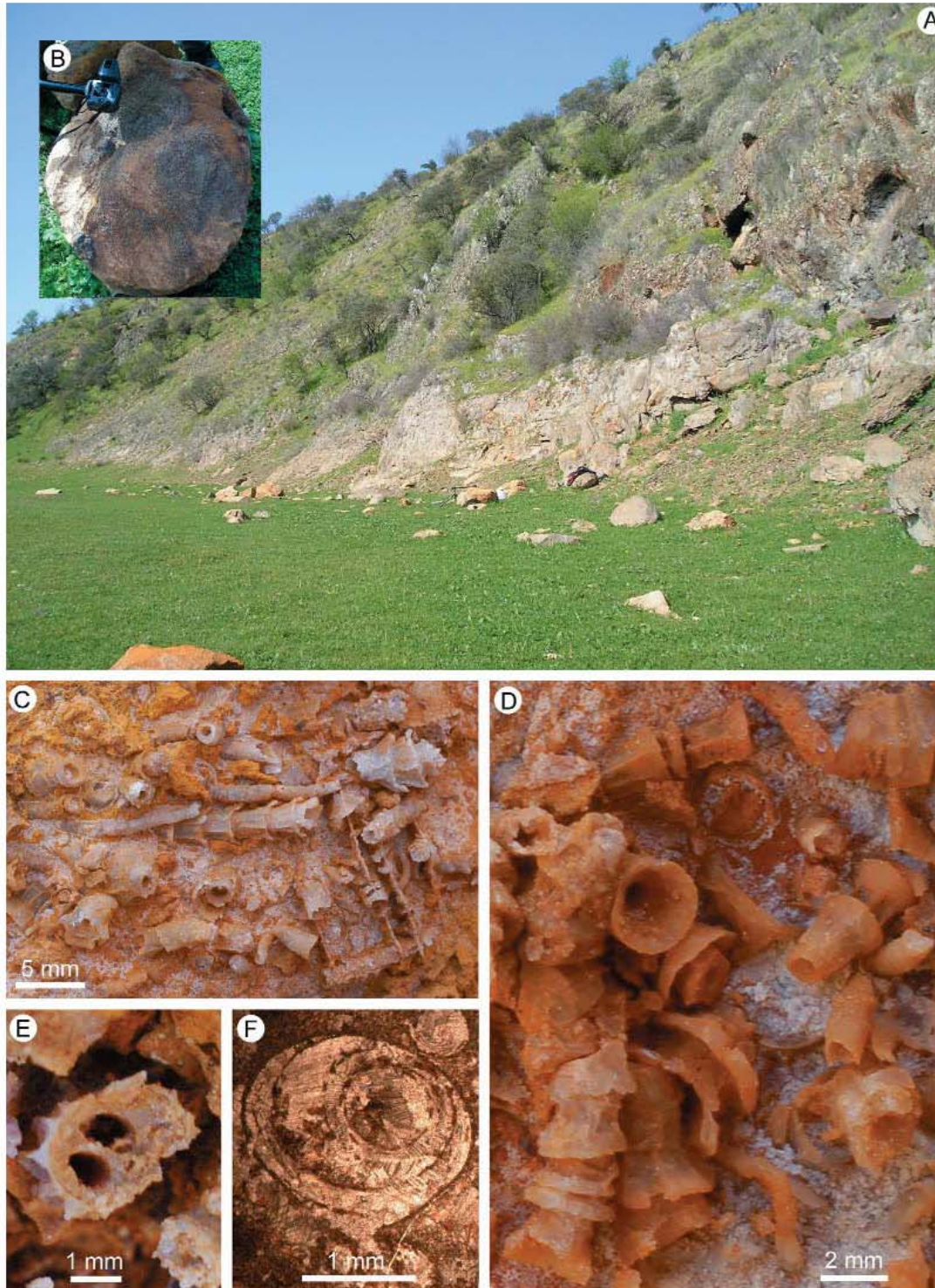
El tercer yacimiento de *Cloudina* está situado en la finca de El Membrillar, en el término municipal de Helechosa de los Montes (Fig. 4). Los fósiles aparecen en bloques de carbonato que forman parte del Olistostroma de El Membrillar (Fig. 4A-B). El Olistostroma de El Membrillar está situado en el flanco sur del anticlinorio de Valdelacasa, en la cola del embalse de Cijara en la desembocadura del río Estena, al este de la provincia de Badajoz. El nivel tiene unos 300 m de potencia y comprende varios tipos de depósitos gravitacionales, incluyendo olistostromas y debritas (depósitos gravitacionales desorganizados o "debris flows") con bloques siliciclásticos y carbonatados de hasta 100 m de longitud (Moreno, 1975; Palacios, 1989; Santamaría Casanovas y Pardo Alonso, 1994). El Olistostroma de El Membrillar descansa sobre una sucesión de areniscas y grauvacas (interpretada como tempestitas y turbiditas de talud) y está situado debajo de estratos asignados a la Formación Pusa (también llamada Grupo Río Huso), una unidad dominada por lutitas que aflora extensamente en el flanco norte del anticlinal de Valdelacasa. Esta unidad contiene una fauna típicamente cámbrica, particularmente "small shelly fossils" e icnofósiles (Vidal *et al.*, 1994, 1999; Jensen *et al.*, 2007; Jensen *et al.*, 2010). El Olistostroma de El Membrillar está situado al nordeste de los carbonatos de plataforma del Grupo Ibor, que son el origen más probable de los bloques de carbonatos del olistostroma, ya que éste se interpreta como el resultado de un gran deslizamiento, probablemente causado por un colapso de la plataforma distal asociado a un cañón submarino (Moreno, 1975; Palacios, 1989; Vidal *et al.*, 1994). En este yacimiento muchos fósiles aparecen secundariamente silicificados y se encuentran naturalmente expuestos en tres dimensiones debido a la disolución selectiva de la roca por meteorización (Fig. 4C-E).

Tanto en Villarta de los Montes como en El Membrillar, además de aparecer la especie tipo *C. hartmannae* (Fig. 4F), aparece la nueva especie *C. carinata* (aunque no se han observado coexistiendo en los mismos bloques en ninguno de los dos yacimientos). *C. carinata* posee una morfología distintiva caracterizada por la presencia de crestas longitudinales externas que confieren al tubo una sección transversal poligonal irregular (Figs. 3D, E, 4C-E). Los elementos individuales (embudos) de *C. carinata* están imbricados de forma menos profunda que en *C. hartmannae* (Figs. 3E, 4C, D) y poseen un anillo terminal engro-

Figura 3. Yacimiento de *Cloudina* en Villarta de los Montes. A, vista general del yacimiento donde pueden distinguirse los niveles de carbonato (1) y los siliciclásticos (2). B, F, ejemplares de *Cloudina* sp. en los niveles carbonatados. C-E, ejemplares de *C. carinata* conservados como moldes en los niveles siliciclásticos. D, moldes externos en vista superior donde se aprecian las crestas longitudinales que caracterizan a *C. carinata*. E, molde compuesto de un ejemplar articulado de *C. carinata* en vista longitudinal. F, ejemplar de *Cloudina* con evidencias de reproducción asexual; nótese la presencia de dos conos hijos dentro del cono original. La moneda en B tiene 16 mm. de diámetro.

Figure 3. *Cloudina*-bearing outcrop in Villarta de los Montes. A, general view of the outcrop; note the carbonate (1) and siliciclastic (2) levels. B, F, specimens of *Cloudina* sp. in the carbonate levels. C-E, specimens of *C. carinata* preserved as moulds in the siliciclastic levels. D, top view of two external moulds showing the external crests that characterize *C. carinata*. E, composite mould of an articulated specimen of *C. carinata* in lateral view. F, specimen of *Cloudina* showing evidence of asexual reproduction; note the two daughter cones inside the original one. The coin in B has a diameter of 16 mm.





sado (Figs. 3E, 4D) y un orificio circular basal (Fig. 4D). Tanto en el material de El Membrillar como en el de Villarta existen abundantes ejemplares de *C. carinata* que muestran evidencias de reproducción asexual (Figs. 3F, 4E), algo sólo descrito antes en ejemplares de *C. hartmannae* de China (Hua *et al.*, 2005).

La excepcional preservación y diversidad fósil presente en los yacimientos extremeños de *Cloudina* (Palacios, 1989; Vidal *et al.*, 1994, 1999; Grant, 1990; Cortijo *et al.*, 2006, 2010; Jensen *et al.*, 2007) hace que, además de figurar entre los más destacables de todos los yacimientos paleontológicos de Extremadura (por su gran interés científico e importancia educativa y cultural), se encuentren entre los yacimientos de *Cloudina* más importantes del mundo junto con los de China y Namibia (Grant, 1990; Hua *et al.*, 2005). Por todo ello, se ha propuesto que el yacimiento de El Membrillar, actualmente el mejor conocido y el que muestra una mejor preservación de los fósiles, sea declarado como "Lugar de Interés Científico" (Palacios *et al.*, 2004b, Martínez Flores y Muñoz Barco, 2005).

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Figura 4. Yacimiento de *Cloudina* en El Membrillar. A, vista general del yacimiento donde se pueden apreciar los bloques del olistostroma. Los bloques de carbonato tienen color anaranjado por su contenido en óxidos de hierro. B, bloque de carbonato que ha sufrido silicificación diferencial y que presenta gran cantidad de ejemplares de *C. carinata*. C-E, ejemplares silicificados de *C. carinata* expuestos en la superficie del bloque ilustrado en B. C, en el centro de la imagen se observa un ejemplar articulado con crestas alineadas en los sucesivos conos; en la parte derecha se observan algunas de las múltiples venas silíceas que recorren todo el bloque. D, varios ejemplares de *C. carinata* donde pueden apreciarse algunas de las características distintivas de la especie, particularmente el borde engrosado en la parte superior de los embudos y el orificio central en la parte inferior de los mismos. E, ejemplar mostrando reproducción asexual; las crestas se ven claramente como engrosamientos triangulares de la pared. F, lámina delgada de una muestra de El Membrillar (perteneciente a un bloque de carbonato distinto al ilustrado en las demás imágenes de la figura) con un ejemplar de *C. hartmannae* en vista transversal; nótese la imbricación excéntrica de los conos.

Figure 4. *Cloudina*-bearing outcrop in El Membrillar. A, general view of the outcrop; note the large olistostromic blocks. Carbonate blocks have an orange hue due to iron oxides. B, carbonate block from the olistostromic unit with numerous specimens of *C. carinata* and evidence of selective silicification. C-E, naturally exposed silicified specimens of *C. carinata* on the surface of the block illustrated in B. C, note articulated specimen with aligned crests in the center of the image and the presence of multiple silica veins across the block. D, specimens of *C. carinata* showing some of the distinctive characteristics of the species, particularly the thickened apertural rim of the funnels and the central hole at their base. E, specimen showing asexual reproduction; longitudinal crests are seen as triangular thickenings of the wall. F, thin section showing a specimen of *C. hartmannae* in cross section; note the excentric imbrication of the cones (specimen comes from a different carbonate block than the one illustrated in A-E).

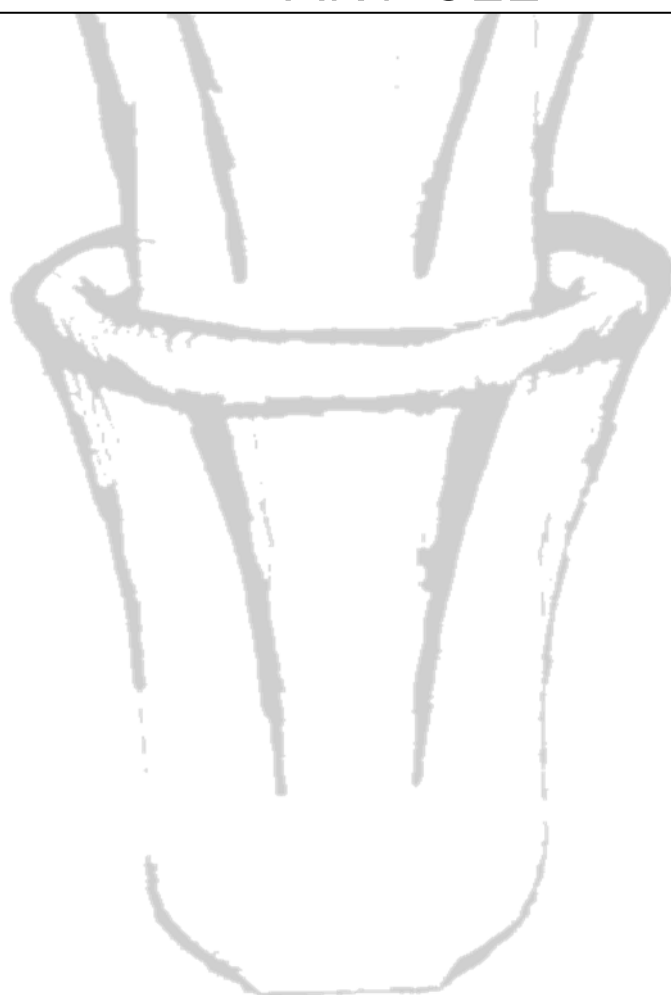
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ARTICLE II





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A new species of *Cloudina* from the terminal Ediacaran of Spain

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ABSTRACT

The terminal Ediacaran genus *Cloudina* includes some of the earliest biomineralized fossils. It consists of a tube formed by stacked funnel-shaped elements, and is usually interpreted as the external skeleton of an early metazoan. Although a number of species have been described within this genus, their distinctiveness remains unclear and they may all belong to the type species, *Cloudina hartmannae* Germs, 1972. Here we describe the new species *Cloudina carinata*, from central Spain. *C. carinata* n. sp. has a distinct morphology characterized by external longitudinal crests, which confer on the tube an irregular polygonal cross-section. The funnels have a thickened apertural rim and a basal, slightly constricted circular opening. Successive funnels appear less deeply imbricated than in previously described material of *Cloudina*. The evidence of tube disarticulation in the material studied, particularly the abundance of loose funnels, indicates that funnels were secreted as independent elements, not fused to the previous ones. However, they could become fused during the life of the organism through the precipitation of inorganic cements between their walls. Several specimens of *C. carinata* n. sp. show evidence of asexual reproduction.

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1. Introduction

Animals with mineralized skeletons appeared during the last 10 million years of the Ediacaran. Their earliest diversity was summarized by Bengtson (2005, p. 105) as consisting of mineralized tubes, basal supportive skeletons, spicules, and stalked tests. By far the best known of these early skeletons is *Cloudina*, a genus characterized by stacked funnel-shaped elements. It was first described from the Nama Group of Namibia (Germs, 1972; Grant, 1990), and has subsequently been reported globally from late Ediacaran carbonates, including Oman (e.g., Conway Morris et al., 1990), south China (e.g., Hua et al., 2005), southeastern USA (Signor et al., 1987), Mexico (McMenamin, 1985; Sour-Tovar et al., 2007), British Columbia (Hofmann and Mountjoy, 2001), Siberia (Kontorovich et al., 2008), and Spain (Palacios, 1989; Vidal et al., 1994).

Waggoner (2003) noted that the palaeogeographical distribution of *Cloudina* was centred on the equator, a pattern strengthened by the recent discovery of *Cloudina* in Siberia (Kontorovich et al., 2008). Although the Spanish *Cloudina* were not included in Waggoner's (2003) analysis, widely used palaeogeographic reconstructions, such as that of McKerrow et al. (1992), place the Iberian peninsula in a position compatible with an equatorial distribution pattern (Fig. 1; however, in alternative reconstructions Iberia is located between 30° and 50° S for the late Ediacaran; e.g., Cocks and Torsvik, 2006).

In Namibia and Oman, U–Pb zircon dating constrains the occurrences of *Cloudina* to between ca. 548 Ma and 542 Ma (Grotzinger et al., 1995; Amthor et al., 2003), and the biostratigraphical and chemostratigraphical contexts of other occurrences, particularly those from southeastern USA, Mexico, British Columbia, and south China (e.g., Corsetti and Hagadorn, 2003; Steiner et al., 2007), suggest a comparable latest Ediacaran age. Therefore, *Cloudina* is currently considered a late Ediacaran index fossil (Grant, 1990).

Grant (1990) showed that the skeleton of *Cloudina* had a characteristic structure which consisted of numerous, thin-walled, eccentrically nested cones. According to that author (Grant, 1990), each cone was an entire element with an independently secreted wall and a closed base. Therefore, *Cloudina* was reconstructed (Grant, 1990, fig. 9) as a curving tube with a complex wall consisting of several layers (each belonging to one of the deeply nested cones) and successive flaring flanges. Secondly phosphatized material from south China (Bengtson and Yue, 1992; Hua et al., 2000, 2005) has confirmed the basic structure of *Cloudina* and provided further morphological detail, such as the presence of corrugations on the outer surface of the walls (Hua et al., 2005) and the occurrence of dichotomous branching of the tubes (Hua et al., 2005). It has also contradicted some aspects of earlier interpretations (see Grant, 1990, fig. 9), presenting evidence that the individual elements (excluding the basal one) had an open base (Hua et al., 2005). The shell shows both signs of brittle breakage and plastic deformation suggesting that the funnels were originally flexible, and hardened during the life of the organism (Grant, 1990; Hua et al., 2005).

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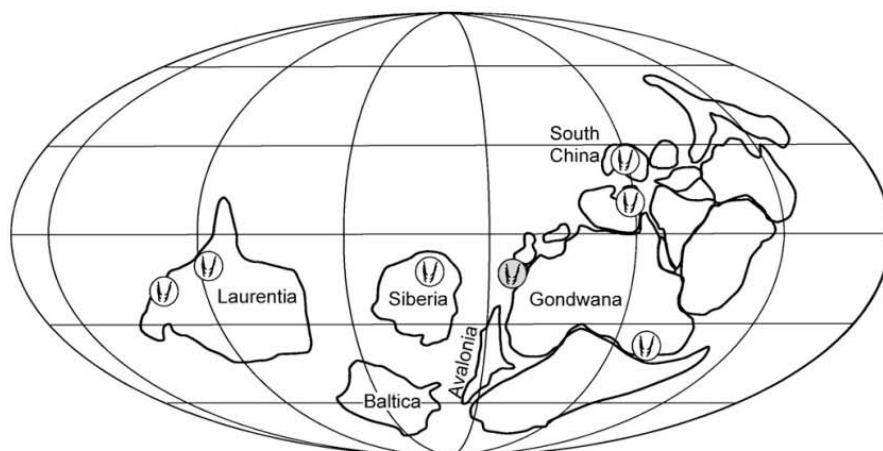


Fig. 1. Palaeogeographical reconstruction of the late Ediacaran (based on McKerrow et al., 1992, fig. 1) with principal reported occurrences of *Cloudina* indicated; the *Cloudina* symbol situated on Iberia is shaded.

Cloudina has been considered an animal of “cnidarian grade” or higher (Grant, 1990), the most frequent comparison being made with tubicolous annelids (e.g., Glaessner, 1976; Hua et al., 2005). Its phylogenetic affinity, however, remains unknown and there are no obvious Cambrian descendants. The two most widely reported species, *Cloudina hartmannae* Germs, 1972, and *C. riemenkae* Germs, 1972, differ mainly in size and are possibly synonymous (Grant, 1990; Hua et al., 2005). Several additional species of *Cloudina* have been described, especially from China, but the distinctiveness of these taxa remains unclear (Steiner et al., 2007). Also a matter of discussion is the relationship of *Cloudina* with somewhat similar, co-occurring taxa such as the mineralized tube *Sinotubulites* (see below) and the non-mineralized tubes *Conotubus* (Hua et al., 2007) and *Saarina* (e.g., Grotzinger et al., 2000).

Cloudina has been found in several localities in the Central Iberian zone (CIZ in Fig. 2A), Spain, as reviewed by Vidal et al. (1994). Among the material illustrated by Vidal et al. (1994) were specimens with a polygonal cross-section thought to be a possible new species (Vidal et al., 1994, p. 755, fig. 12c and d). Here, on the basis of three-dimensionally preserved, secondarily silicified specimens, we substantiate the presence of this new species of *Cloudina*, characterized by prominent exterior longitudinal crests. A further notable feature of this material is that it includes specimens showing evidence of asexual reproduction.

2. Geological setting and age constraints

The majority of the material described here is preserved on a large carbonate block from the Membrillar olistostrome, located in the lower reaches of the Estena River, in the northeastern part of the province of Badajoz, central Spain (Fig. 2A–C). The Membrillar olistostrome (Fig. 2E) is about 300 m thick and comprises various types of gravity deposits including debris flows with blocks of reworked graywackes and carbonates, the latter up to 100 m long (Moreno, 1975; Palacios, 1989; Santamaría Casanovas and Pardo Alonso, 1994). It overlies a thick succession dominated by sandstone and graywacke, which has been interpreted as slope and outer platform turbidites and tempestites (Cijara Formation of Palacios, 1989; Fig. 2E). The contact between the Membrillar olistostrome and the underlying strata has been variously interpreted as an angular unconformity with tectonic folding prior to the deposition of the Membrillar olistostrome (Santamaría Casanovas and Pardo Alonso, 1994), or a surface of essentially synsedimentary deformation. Moreno (1975) interpreted the Membrillar olistostrome as the

result of outer platform collapse along a fault scarp associated with a submarine canyon, and a similar view was favoured by Vidal et al. (1994). The Membrillar olistostrome is overlain by (the contact does not crop out) strata that have been assigned to the Pusa Formation (also referred to as the Rio Huso group), a siltstone-dominated unit that crops out extensively in the northern flank of the Valdelacasa anticline (Fig. 2B and C, E).

The most likely source of the carbonate blocks of the Membrillar olistostrome are platform, and possibly slope apron, carbonates of the Ibor Group (Fig. 2B). The Ibor Group stretches in a NW–SE trending band for at least 400 km, and can be traced SE to the Navalpino anticline (where it is known as the Ibor/Navalpino Group), close to the Membrillar area. Although dominated by dark, laminated siliciclastic sediments, the Ibor Group contains one (or perhaps several) carbonate level up to 200 m thick, which has been interpreted as formed on a carbonate platform opening to the NE and therefore located on the inboard side of the olistostromes. This carbonate level crops out in a number of sections, some of which contain *Cloudina* (Vidal et al., 1994). Near the Membrillar area, in the Navalpino anticline (Fig. 2B, F), it is known as the Villarta limestone (e.g., López Díaz, 1995), and contains abundant and well preserved, although apparently non-silicified, material of *Cloudina* (Vidal et al., 1994, fig. 12C). *Cloudina* also occurs immediately underneath the massive Villarta limestone, in siliciclastic sediments which also contain lenticular carbonates. In these siliciclastic sediments, *Cloudina* specimens are preserved as moulds.

The Membrillar olistostrome lines up along the strike with less potent conglomeratic/debris flow units with carbonate clasts in the nearby Estomiza and Estenilla Rivers (Fig. 2C), which probably represent lateral equivalents to the Membrillar olistostrome (Moreno, 1975; Palacios, 1989). There are simple trace fossils above and below the conglomeratic levels at the Estenilla River (Palacios, 1989; Jensen et al., 2007, fig. 2b; Fig. 2C and D), and here we report the first finds of trace fossils below the Membrillar olistostrome (Fig. 2C and E), which consist of simple looping rows of discontinuous ridges (Fig. 3). Based on the current knowledge of the age of the oldest trace fossils (e.g., Jensen, 2003), the occurrence of these simple traces demonstrates that the strata underlying the *Cloudina* beds are no older than late Ediacaran and therefore cannot be substantially older than the Membrillar olistostrome. The organic-walled microfossil *Sphaerocongregus variabilis* occurs in the Membrillar olistostrome and in the probable lateral equivalents at Estenilla River, and the upper part of the Cijara Formation at the Estenilla River yielded *Palaeogomphos-*

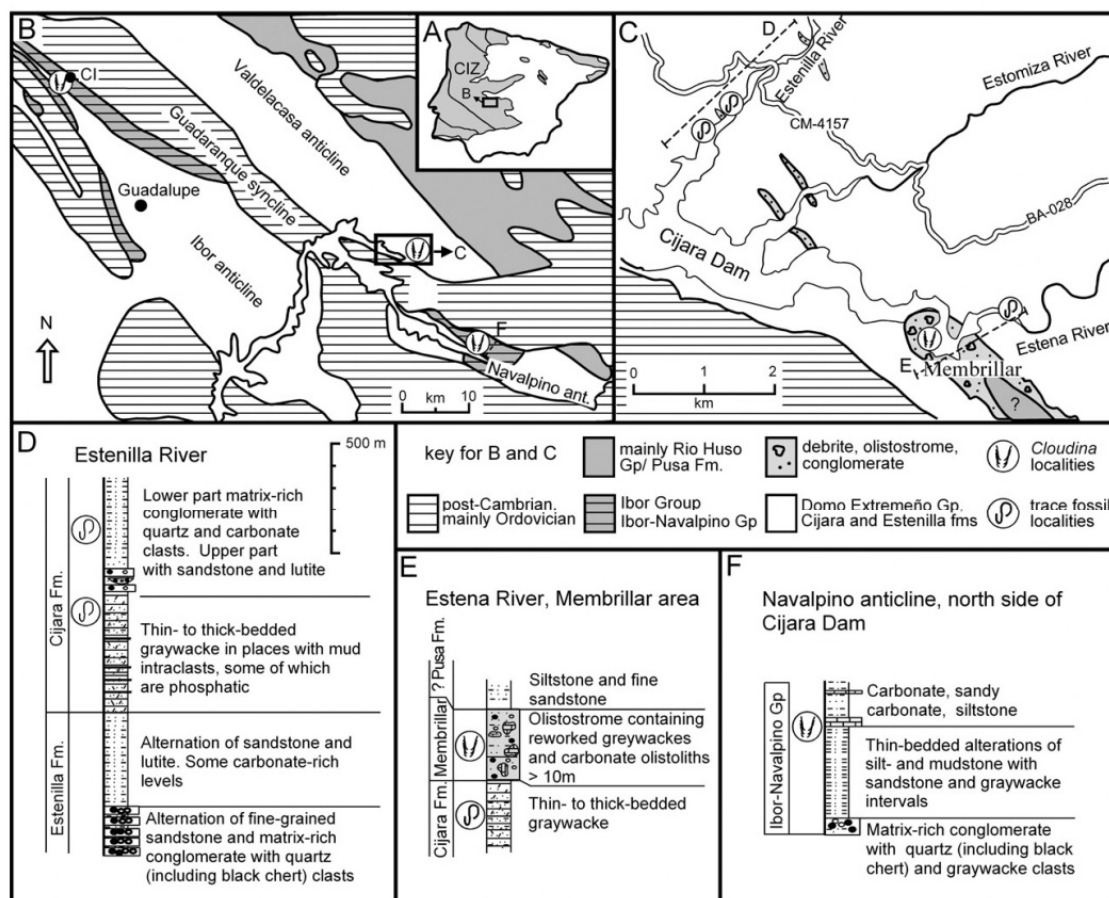


Fig. 2. (A–C) General geological setting and location map for *Cloudina carinata* n. sp. (A) Sketch of Iberian peninsula with location of study area within the southern portion of the Central Iberian Zone (CIZ); shading indicates pre-Mesozoic sediments. (B) Location of *Cloudina* localities in the western part of the Montes de Toledo/Guadalupe area; Cl, Castañar de Ibor. (C) Map showing location of the *Cloudina*-bearing carbonate blocks in the Membrillar olistostrome. (D–F) Simplified logs showing the stratigraphical and sedimentological context of *Cloudina* and trace fossils. All sections are to the same scale. Based on Palacios (1989) and additional observations.

phaeria cauriensis (Palacios, 1989). These probably bacterial forms do not provide biostratigraphical information, but are indicative of comparable depositional environments. The overlying Pusa Formation (Fig. 2C and E) contains a Lower Cambrian fauna in other areas of the Valdelacasa anticline, including small shelly fossils and trace fossils (Vidal et al., 1994, 1999; Jensen et al., 2007; Martí Mus et al., 2008). Taken altogether, the biostratigraphical data are coherent with the Ediacaran to Cambrian succession in this area being more

or less continuous, but affected by tectonic instability as a result of differential block movements resulting in local deformation and collapse.

Additional possible age constraints on *Cloudina carinata* n. sp. come from chemostratigraphic analysis of the aforementioned carbonates of the Ibor Group, in the Pastores section, south of Salamanca (about 200 km northwest of Membrillar). Valladares et al. (2006) identified a sharp negative carbon isotope excursion in the Pastores section, and suggested that this peak correlates to a globally recognized negative excursion close to the Ediacaran–Cambrian transition. These data are consistent with the carbonates of the Ibor Group, including the *Cloudina*-bearing section in the Navalpino anticline (Fig. 2B and F) and the Pastores section, being broadly correlatable and of the latest Ediacaran age.

3. Material, methods, and preservation

Most of the studied specimens are naturally exposed on the weathered surface of a large (about 1 m × 1 m × 0.6 m), somewhat ferruginous, dolomitized limestone block from the Membrillar olistostrome. This large block is particularly rich in three-dimensionally preserved tubes, which stand out from the rock surface (Figs. 4–6, 8 and 9). Other fossiliferous blocks from Membrillar were also studied, mostly in thin section. Morphologically similar specimens, but preserved as moulds, have also been studied

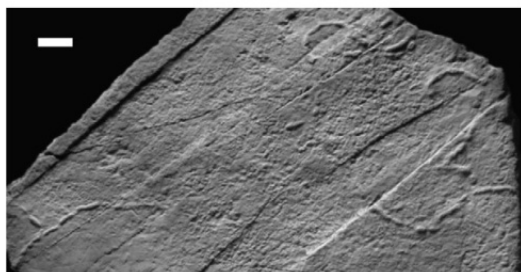


Fig. 3. Trace fossils preserved on lower bedding surface from the Cijara Formation in the Membrillar area (locality indicated by trace fossil symbol along the Estena River in Fig. 2C). It is unclear whether the beaded or segmented appearance of the traces is a primary feature or formed in connection with deformation; for this reason, no ichnogenetic assignment is given. Scale bar represents 10 mm. UEXP709Me1:001.

for comparison. These come from siliciclastic sediments immediately underneath the massive carbonate banks of the Villarta limestone, in the nearby locality in the Navalpino anticline (see above).

The specimens from the large block are secondarily silicified and often coated with a ferruginous rind. The silicification seems to be related to the presence of fine silica veins that cross the block (Fig. 4A). The timing and conditions of this selective silicification process is not as yet understood, and it is also unclear whether it affected other carbonate blocks from Membrillar. The *Cloudina* specimens from the large block are concentrated in irregular but clearly defined bands, probably representing original bedding. None of the tubes is obviously *in situ* and their distribution is likely the result of the accumulation of transported tubes.

Specimens were cleaned with dilute hydrochloric acid (about 5%) sprayed over the block surface, and photographed with a digital

camera with a 50 mm macrolens attached. A few loose specimens from the block were studied under scanning electron microscopy (SEM), and a few others were embedded in resin and gradually ground to observe their internal organization (Fig. 9). Thin sections were prepared from different blocks of the Membrillar olistostrome and studied using transmitted light microscopy and SEM. Energy dispersive X-ray spectroscopy (EDS) and back-scattered electron (BSE) imaging were used to analyse the elemental composition of selected fossils. SEM imaging and EDS were carried out at the Evolutionary Biology Centre, Uppsala University (Sweden), using a ZEISS SUPRA 35VP equipped with a Robinson BSE detector and an EDAX Genesis 40000 Cryospec. The variable pressure chamber (VP) allowed the imaging and analysis of uncoated samples.

All illustrated fossils are housed in the collections of Área de Paleontología, Universidad de Extremadura, Badajoz.

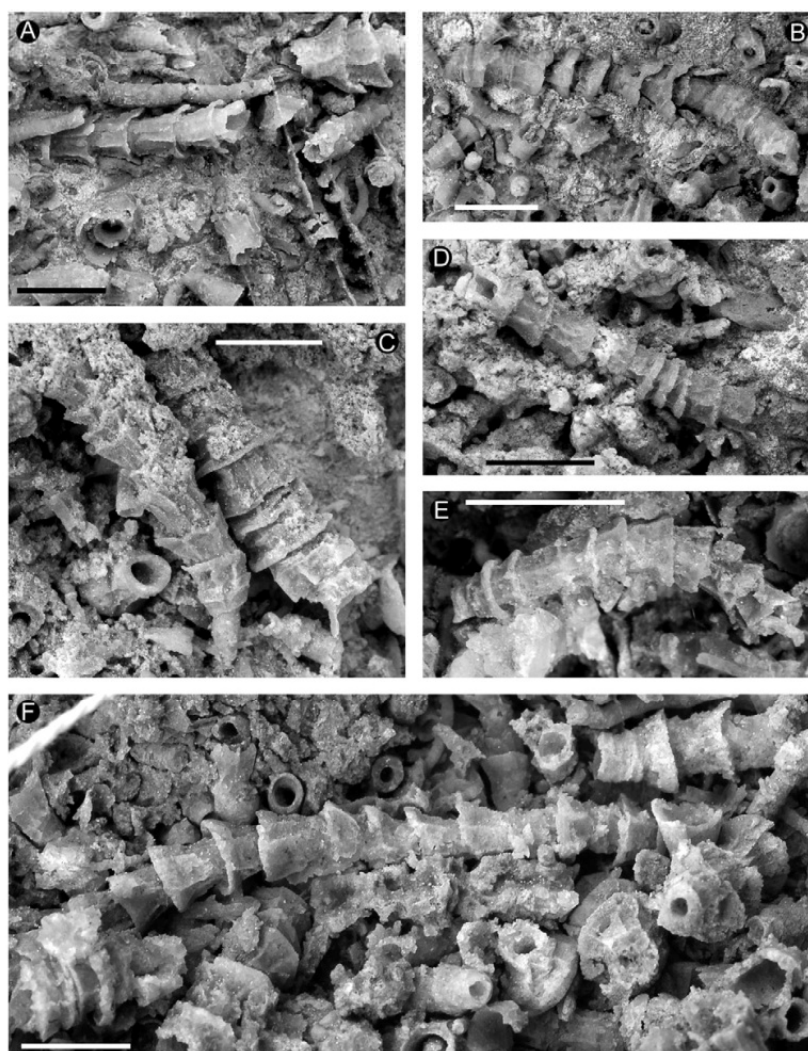


Fig. 4. Naturally exposed specimens of *Cloudina carinata* n. sp. on the weathered surface of a large limestone block from the Membrillar olistostrome; specimens display the characteristic features of the species, such as funnels possessing longitudinal crests and thickened apertural rim; note different degrees of tube curvature. (A) Specimen with sharply defined aligned crests; note thin silica veins cutting through the specimens (bottom-right corner of image). UEXP709Me2:001 (B) Specimen with a relatively smooth, flange-free portion (right of image) as part of a tube with the typical funnel-in-funnel structure; note how flanges close to the “smooth” portion are broken and cracked. UEXP709Me2:002. (C and D) Specimens showing variation in distance between successive funnels, C, left of centre: UEXP709Me2:003; C, right of centre: UEXP709Me2:004. D, UEXP709Me2:005. (E) Holotype of *C. carinata* n. sp. UEXP709Me2:006. (F) One of the longest specimens among the studied material. UEXP709Me2:007. Scale bars represent 5 mm.

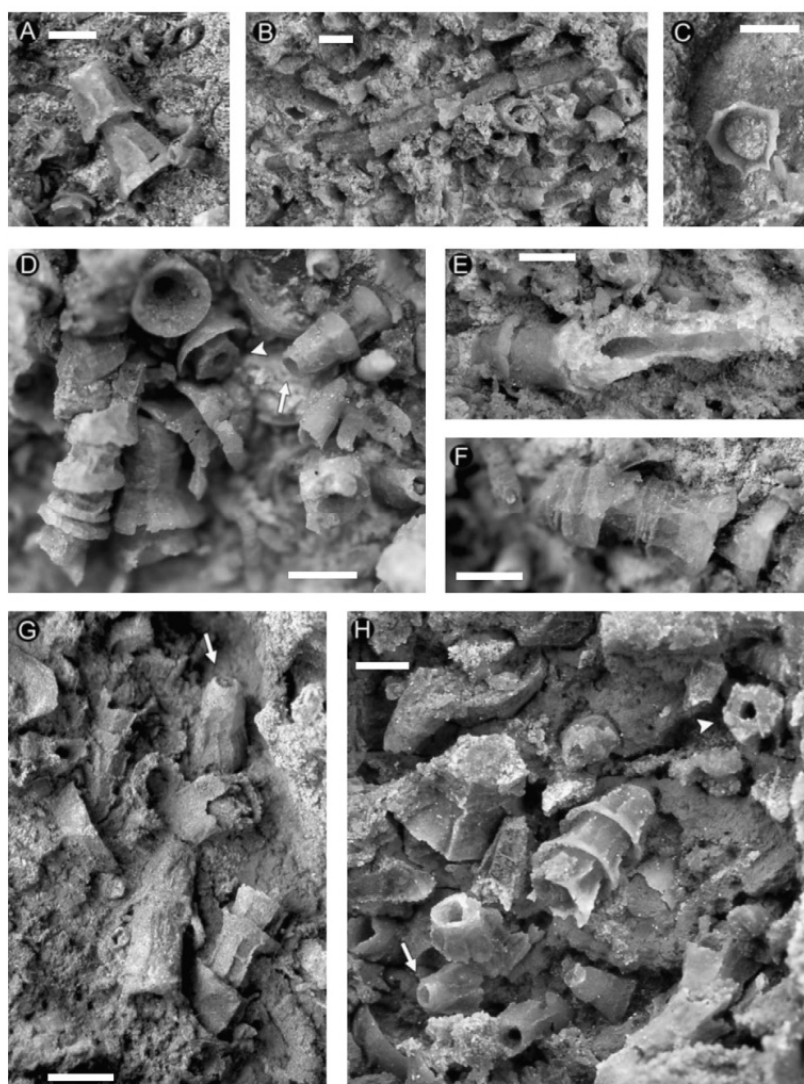


Fig. 5. Naturally exposed specimens of *Cloudina carinata* n. sp. on the weathered surface of a large limestone block from the Membrillar olistostrome; specimens display the characteristic features of the species, such as funnels possessing longitudinal crests and thickened apertural rim; note the abundance of disarticulated funnels and specimens consisting of only a few elements. (A) Specimen consisting of two almost disarticulated funnels. UEXP709Me2:008. (B) Articulated funnels with a narrow, elongated morphology which departs from the typical bell shape seen in most specimens. UEXP709Me2:009. (C) Upper view of a funnel with crests that appear formed by folding of the wall. UEXP709Me2:010. (D, G and H) Specimens showing various degrees of disarticulation; arrows indicate basal openings of funnels (basal opening in (D) is slightly broken; UEXP709Me2:027); arrowheads point to broken specimens showing apparently thick wall; specimen at bottom-left in (D) shows variation in distance between successive funnels; UEXP709Me2:011; largest specimen in (D) (centre-left of image) appears dislocated; UEXP709Me2:012; short articulated specimens in (G and H) shows sharp, aligned crests (UEXP709Me2:017 and UEXP709Me2:013 respectively). (E) Broken specimen showing apparently thick wall and empty, well-defined central canal. UEXP709Me2:014. (F) Close-up of specimen in Fig. 4B showing transversally oriented wrinkles. Scale bars represent 2 mm.

4. Systematic paleontology

Genus Cloudina: New species *C. carinata*, Figs. 4–10.

Synonymy: ?*Cloudina* sp.—Grant, 1990, fig. 7c.

Cloudina sp.—Vidal et al., 1994, fig. 12c.

?*Cloudina* sp.—Vidal et al., 1994, fig. 12d.

C. carinata n. sp.—Cortijo et al., 2009, pp. 175–176, fig. 1 (nomen nudum).

Etymology: *carinata*, from Latin *carina*, keel, in reference to the shape of the longitudinal crests.

Holotype: Specimen illustrated in Fig. 4E, UEXP709Me2:006.

Type locality and strata: Lower reaches of the Estena River on the Membrillar property (Fig. 2C), northeastern Badajoz, south-central

Spain. 39°21'42"N, 4°50'16"W. Carbonate blocks in the Membrillar olistostrome.

Diagnosis: A species of *Cloudina* characterized by prominent external, longitudinal crests. Funnels have a basal, slightly constricted circular opening, and a thickened apertural rim.

Description: *C. carinata* n. sp. is a tubular fossil formed by a series of imbricated, identical funnels with a basal opening, a thickened apertural rim, and a marked external ornamentation in the form of longitudinal crests (Fig. 4). The longest specimens consist of 9–12 stacked funnels and reach a length of ca. 25 mm (Fig. 4C–F). Shorter tubes (Figs. 4A, 5A and B, D, G and H), and specimens showing evidence of disjunction (Fig. 5A) or dislocation (Fig. 5D) abound in the sample. Isolated funnels (Figs. 4C, F, 5C, G and H, 6A and B, D and E)

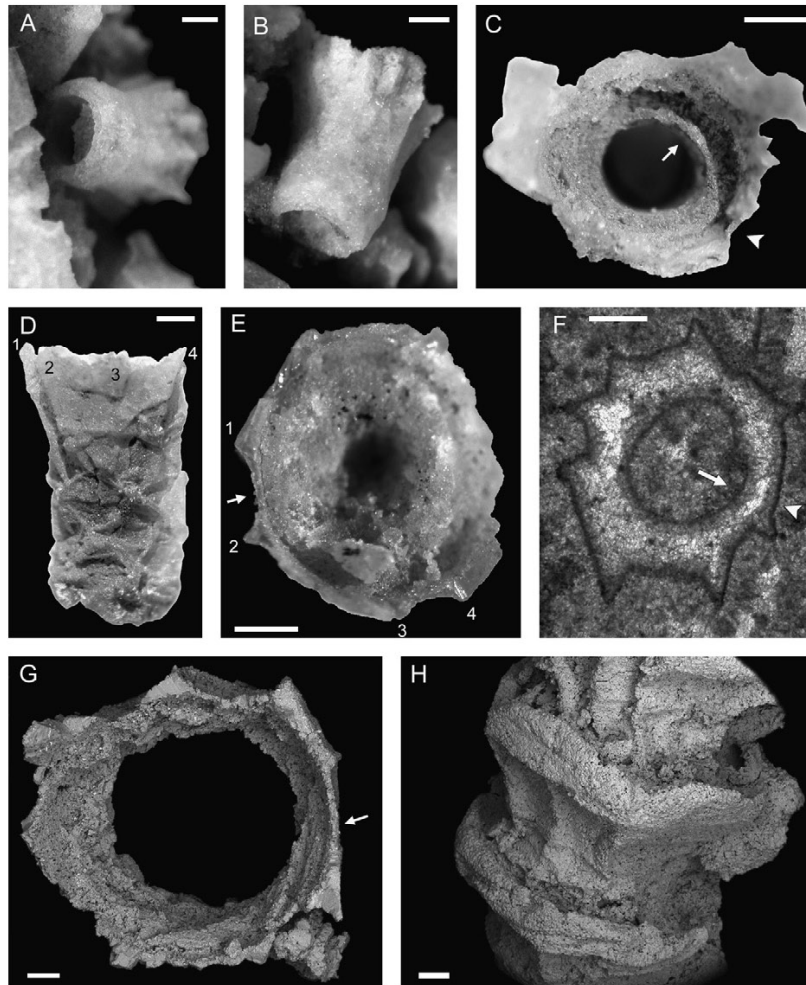


Fig. 6. *Cloudina carinata* n. sp. from the Membrillar olistostrome. (A and B) A loose funnel in basal (A) and lateral (B) views; note constricted circular opening and crests on the flaring portion. UEXP709Me2:015. (C and F) Apertural view (C) and cross-section (F) of two different specimens with articulated (imbricated) funnels; the “outer” wall (arrow heads) represents the flaring portion of the embracing funnel; the “inner” wall (arrows) represents the imbricated funnel sectioned at the level of its proximal, conical portion; note the cemented space between the walls and the empty central cavity (filled with sediment in (F)); note the polygonal irregular outline of the “outer” wall in (F) and the smooth outline of the “inner” walls in (C and F) indicating that crests are only expressed in the flaring portion of the funnels. Observation of various specimens indicates that the darker laminae seen in (F) do not represent the original walls (at least not the complete walls). Instead, the wall is likely represented by the grayish band adjacent to the laminae (although these bands are not clearly differentiated from the cement between them). C, UEXP709Me2:016; F, UEXP709Me3:001. (D and E) A loose funnel in lateral (D) and upper (E) views; note the wrinkled pattern on the external surface of the funnel (D) and the crests representing triangular thickenings of a thin wall (arrowed in E); the funnel is filled with cement, except for a rounded central cavity (it is unclear whether this cavity reflects the previous presence of an imbricated funnel in the manner seen in (C and F)). UEXP709Me2:018. (G and H) BSE images of two different specimens: (G) broken funnel showing that crests represent triangular thickenings of a thin wall (arrowed). UEXP709Me2:019; (H) articulated specimen (three funnels are seen) showing crests in lateral view and thickened apertural margin. UEXP709Me2:020. Scale bars represent 500 μm in (A–F), 200 μm in (G) and 300 μm in (H). Specimens in (A–E, G and H) come originally from the large limestone block from the Membrillar olistostrome; the specimen in (F) comes from a smaller carbonate block from the same area.

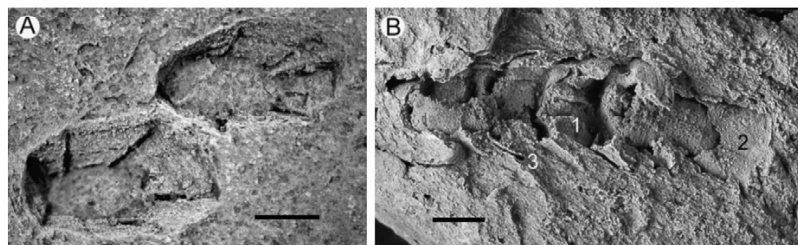


Fig. 7. *Cloudina carinata* n. sp. from siliciclastic sediments a short distance below massive carbonate banks of the Villarta limestone, from the Navalpino anticline. Specimens are preserved as moulds. (A) External moulds of the flaring portion of two funnels; note the crests preserved as longitudinal grooves. Specimen on the left, UEXP734Vi2:001; specimen on the right, UEXP734Vi2:002. (B) Composite mould (preserved partly as an external and partly as an internal mould) of articulated specimen in lateral view; note crests as grooves (1) and thin wall with thickened apertural rim (3) in a portion preserved as an external mould; note as well the smooth internal surface of a funnel in a portion preserved as an internal mould (2). UEXP734Vi2:003. Scale bars represent 2 mm.

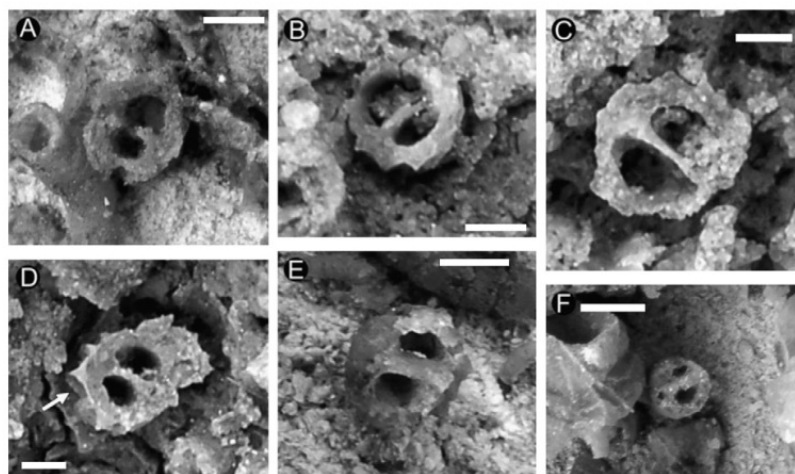


Fig. 8. Naturally exposed specimens of *Cloudina carinata* n. sp. on the weathered surface of a large limestone block from the Membrillar olistostrome. All specimens show evidence of asexual reproduction; note how each parent tube contains two daughter tubes of unequal size; note as well (in D) how the space between parent and daughter walls is filled with cement whereas the interior of the daughter tubes is empty (compare with Fig. 6C); parent tube in (D) shows crests representing triangular thickenings in an otherwise thin wall (arrowed). A, UEXP709Me2:021; B, UEXP709Me2:022; C, UEXP709Me2:023; D, UEXP709Me2:024; E, UEXP709Me2:025; F, UEXP709Me2:026. Scale bars represent 1 mm.

are also abundant and are interpreted as disarticulated elements of originally articulated tubes. Broken specimens and shell fragments are also present in the sample. The evidence of disarticulation, as well as the absence of differentiation between funnels in articulated specimens, suggests that most specimens are fragmentary to some degree, and in any case make it impossible to determine if any of them represents a complete skeleton. Attachment structures were not observed in any of the specimens. Tube diameter ranges from 1 to 4 mm, and appears constant through the preserved length of each specimen. In most articulated specimens each funnel is nested only within the previous one and embraces only the immediately following, therefore forming a series of imbricated, but not deeply nested funnels (Fig. 7B). The distance between two successive funnels is not constant, varying within a single tube (Figs. 4B–D, 5D) and from one tube to another. Crests appear often aligned along

the length of the tube (Figs. 4A, 5A, H). In a few specimens, there are portions of the tube where flaring rims are missing and the surface appears annulated or wrinkled (Fig. 4B), therefore resembling that of the genus *Sinotubulites* (see Grant, 1990, p. 281–282, and discussion below).

Although there is considerable morphological variation among funnels, the same basic design is repeated in all of them (for this description “proximal” will refer to the narrower end of the funnel, presumably the base, while “distal” will refer to the wider, apertural, end). The length of individual funnels ranges from 1 to 4 mm. Longitudinally, each funnel can be divided into two distinct portions: a proximal cylindrical portion and a flar-

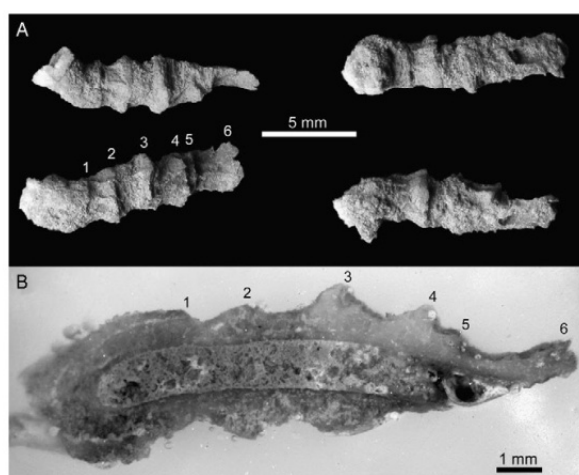


Fig. 9. Articulated specimen of *Cloudina carinata* n. sp. (originally from a large limestone block from the Membrillar olistostrome). (A) Specimen illustrated from different angles, all in lateral view. (B) Same specimen in longitudinal cross-section; note the presence of a well delimited central canal (see text for details). Numbers indicate successive apertures of the articulated funnels.

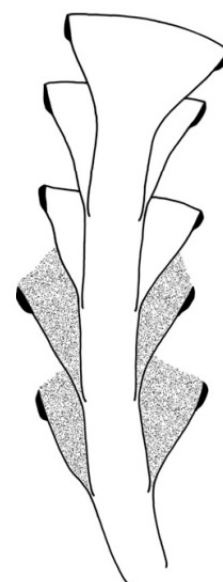


Fig. 10. Schematic reconstruction of a cross-sectioned tube of *Cloudina carinata* n. sp.; note some of the characteristic features of the species such as the relatively superficial imbrication, and the morphology of the funnels with a basal opening and an apertural thickening. Shading indicates spaces filled with early cements.

ing distal one that terminates in a wide aperture (loose funnels in Figs. 5G and H, 6B show this pattern clearly). Thus the diameter of the funnels increases from 1.5–2.1 mm at the base to 2–4 mm at the aperture. Proximally, funnels have a slightly constricted, circular opening (0.2–1.2 mm in diameter) with a smooth, sharply defined rim (Fig. 5G and H, 6A and B). Distally, the flaring portion of the funnels ends in a roundish aperture with a thickened margin (Figs. 4B, D–F, 5A, D, F–H, 6H). Funnels seem to articulate by their conical portions, the base of each fitting tightly (but not deeply) into the conical portion of the previous (Fig. 7B). Above this joining point, the walls of the successive funnels separate gradually as the proximal funnel flares. Some specimens suggest that each funnel starts to flare where the previous one terminates (e.g., Fig. 7B), implying that the conical portions are always shielded within the flaring portions of the preceding funnels. One illustrated specimen (Fig. 5B) departs somewhat from the described general morphology, particularly in the funnels being almost cylindrical, showing very little or no flaring; crests and thickened margin are visible, identifying this small specimen as belonging to *C. carinata*.

The inner surface of the funnels seems relatively homogeneous and smooth (Figs. 6A, C, F and G, 7B; however this surface is only incompletely exposed in a few specimens and the details of its relief remain unknown). Apart from the presence of the crests, the outer surface may be relatively smooth (Fig. 6A and B) or show wrinkles, which may form a polygonal pattern (resembling the type of folding characteristic of paper; Fig. 6D) or a series of transverse folds (as if caused by vertical collapse of a cone made of a thin, plastic material; Fig. 5F). The longitudinal crests occur only in the flaring distal portion of the funnels (Figs. 5G, 6B, F). They start to develop with the flaring, and continue until the aperture, where they merge with the thickened margin (Figs. 5A, G, 6H). Although a few specimens suggest that crests could form by the folding of the wall (Fig. 5C), most of them show that they represent thickenings of the wall and therefore are expressed only externally (Figs. 6E, G, 7B, 8D). In cross-section, the crests are somewhat triangular (Figs. 6E, G, 8D). The precise morphology and spacing of the crests is highly variable within a single funnel, but the resulting irregular polygonal pattern is remarkably constant within the species (e.g., Fig. 6E–G). The number of crests seems somewhat variable (the precise number of crests is difficult to determine in most specimens, mostly because of incomplete exposure on the rock surface or partial breakage of the specimens), but many specimens seem to have 7 or more crests (Figs. 6E–G, 7A). In lateral view the crests give the impression of having been formed by the pinching of a plastic material (Fig. 6H). The crests are apparent in most silicified specimens (Figs. 4A, C–F, 5A–D, F–H, 6A and B, D–H, 8B, D) and are also obvious in the specimens preserved as moulds (Fig. 7), which indicates that they represent a biogenic feature rather than a preservational artefact.

Many silicified specimens appear to have a robust wall (up to 1 mm thick; e.g., Figs. 4F, 5D and E, H) unlike that seen in other occurrences of *Cloudina* (Grant, 1990; Hua et al., 2005). However, this “wall” is in reality a composite, formed by the original (but secondarily silicified) wall plus a cement (also siliceous) which occupies the space between nested funnels (Figs. 6C, F, 8D) or within the funnel cup (Fig. 6E). In many specimens the original wall can be easily distinguished as a thin (40–60 µm thick at the portions where crests are not developed, and 3–4 times thicker at the crest’s axis) and transparent layer adjacent to the more opaque cement (Figs. 6C, E, 8D). Specimens preserved as moulds confirm that the original wall of *C. carinata* was thin, and thickened slightly to form the apertural rim (Fig. 7B). A significant feature of the preservation of the silicified specimens is that, although the space between successive funnels is usually silicified, most tubes have a rounded, smooth central canal which is not silicified but either filled with

carbonate sediment or empty (in the specimens exposed to weathering; Figs. 5D and E, H, 6C, F, 9).

Finally, in some specimens (ca. 10), two smaller tubes can be seen within a larger funnel (Fig. 8), which often displays clear crests on its outer surface (Fig. 8B and D). The daughter tubes are of unequal size, one being always slightly larger than the other (Fig. 8). Both are almost oval in cross-section, but with flattened facing sides. Particularly well preserved specimens (Fig. 8D) show that the daughter funnels are not formed by a septum dividing the parent funnel, but instead represent smaller, complete funnels with their own walls. Specimens showing daughter tubes are not uncommon in the studied material, suggesting that branching may have been common among the tubes. However, the specimens are incomplete, and the development of the daughter tubes could not be observed.

Discussion: In consisting of stacked, funnel-shaped elements, this material is assignable to *Cloudina*. However, it differs from previously described material of *Cloudina* in a few features. These features are consistently expressed (allowing for natural intraspecific variation) both in the silicified specimens and in those preserved as moulds. Perhaps the most conspicuous of these features is the presence of longitudinally aligned crests on the external surface of the tubes. Somewhat comparable longitudinal ridges (and irregular polygonal cross-sections) have been reported on some latest Ediacaran tubular fossils (e.g.; McMenamin, 1985; Hua et al., 2000; Chen and Sun, 2001; Chen et al., 2008) usually assigned to *Sinotubulites* (but see Hua et al., 2000; Chen and Sun, 2001, for some discrepancies about the systematics of some of these tubular specimens). *Sinotubulites* has been distinguished from *Cloudina* in consisting of a column-in-column rather than funnel-in-funnel structure (e.g., Hua et al., 2000), but it also appears to have a distinct wall structure consisting of multiple, characteristically folded layers (Chen et al., 2008). It is regularly noted (e.g., McMenamin, 1985; Chen et al., 2008) that the presence of longitudinal ridges in *Sinotubulites* is a further character that distinguishes it from the usually smooth or annulated *Cloudina*. However, the inclusion of a new species in the genus *Cloudina* necessarily extends the range of features observable in this genus and warrants a reconsideration of the characteristics which distinguish it from other genera. Although Chen et al. (2008) have convincingly shown that *Sinotubulites* is a distinct and well-defined genus, a few specimens of our material show a transition from a funnel-in-funnel structure to a *Sinotubulites*-like one (or vice versa; Fig. 4B). It is unclear if these *Sinotubulites*-like portions reflect an original structure in any of the specimens, but some appear to be portions of *Cloudina* tubes denuded (through breakage) of the flanges (see Grant, 1990, p. 281–282). The specimen in Fig. 4B illustrates clearly this second possibility, showing how the flanges closest to the “smooth” portion are cracked and partly broken.

Other distinguishing traits of *C. carinata* are the imbrication of the articulated funnels, which seems generally less deep than in other material of the genus (but see Germs, 1972; pl. 1, figs. 8, 10 and 11; fig. 3D, for similarly nested specimens), and (probably in part as a result of this) the presence of abundant loose, disarticulated funnels. A further notable feature of *C. carinata* is that the funnels have a slightly constricted, circular opening at their base. There has been some conflicting evidence as to whether *Cloudina*’s funnels had a closed base (Grant, 1990) or were fully open proximally (Hua et al., 2005). *C. carinata* clearly shows a somewhat intermediate situation, in being open but slightly constricted at the base. Whether this particular organization is exclusive of the species or can be extrapolated to other material of *Cloudina* is unclear.

The material of *C. carinata* represents the second population, in addition to that from the Dengying Formation of south China (Hua et al., 2005), in which there is evidence for asexual reproduction (Fig. 8). Budding has been reported also from Namibian *Cloudina* (Germs, 1972, p. 754), but the evidence is inconclusive.

Although *C. carinata* co-occurs with *C. hartmannae* both in the Membrillar olistostrome (Palacios, 1989, pl. 16, figs. 1 and 2; Vidal et al., 1994, fig. 12a and b) and in Villarta de los Montes (personal observations) we have not observed them together in the same sample. Particularly, no specimens of *C. hartmannae* have been observed in the large olistostromic block which is the main focus of this study. No intermediate morphotypes between *C. hartmannae* and *C. carinata* were observed and therefore we consider them two clearly recognizable morphospecies.

5. Palaeobiological implications

Some morphological traits of *C. carinata* n. sp. have particular biological implications, which are also relevant for other species of the genus as closely related organisms. One such characteristic is the propensity of the tubes to disarticulate yielding individual, entire funnels. This is coherent with the idea that the growth of *Cloudina* was episodic and that the funnels were built as independent units, articulated, but not fused. Since the observed disarticulation is likely post-mortem (as illustrated by specimens in the process of disarticulation, e. g. Fig. 5A and D), it also suggests that the soft parts of the organism played a role in keeping the funnels together (but see below). The particular, relatively superficial, imbrication of the funnels which characterizes *C. carinata* allows the possibility of a mobile articulation (particularly if the funnels were held together by the soft parts), and may be related to the apparent ease with which individual funnels disarticulate.

Also of biological relevance is the base of the funnels, with a slightly constricted, sharply defined, circular opening. The presence of this basal opening accords broadly with the latest reconstruction of *Cloudina* (based mostly on Chinese material; Hua et al., 2005), which depicts the interior of *Cloudina* as a continuous tube. However, the funnels of *C. carinata* cannot be described as “truncated” proximally (as those from the Chinese material have been; Hua et al., 2005) since they do not terminate abruptly, but end smoothly forming a slightly constricted opening. This again emphasizes the individuality of the funnels.

Some preservational features of the silicified material may also be biologically relevant. Many specimens show an empty, or matrix filled, central canal (since the matrix is partly carbonatic and has gradually dissolved during weathering, we interpret the empty internal canals as originally filled with sediment). In contrast, the numerous spaces between nested shell layers are often filled with siliceous cement. This suggests that when the skeletons of *C. carinata* were entombed within the sediment, the central canal was fully accessible, but some of the spaces between shell layers were already occluded by the precipitation of early (likely carbonatic in origin) cements. Grant (1990), observing the presence of early cements both between shell layers and within the central cavity of the tubes, suggested that inorganic precipitation of calcareous cements between shell laminae may have occurred during the lifetime of the organism, conveying robustness to the *Cloudina* tubes. Our observations support this hypothesis, suggesting that the precipitation of interlayer cements must have pre-dated the filling of the central canal with sediment and therefore the burial of the tubes.

Other features of the species, such as the presence of crests and a thickened apertural rim, indicate that the skeleton of *C. carinata* had a relatively elaborate design. These thickened areas occur only on the flanges and only on the external surfaces, which suggests that they may reflect particular adaptations to the substrate.

All considered, we can envision the skeleton of *C. carinata* as a (possibly branching) tube formed by the imbrication of morphologically elaborate, originally loosely articulated elements (funnels; Fig. 10), that likely fused during the life of the organism by the pre-

cipitation of early inorganic cements between their walls (whether the animal exerted any control over this process is unknown). The animal lived in the last secreted funnel, but likely extended its soft parts through a canal formed by the joined conical portions of the successive funnels forming the tube. This canal was “protected” externally by the “abandoned” ornamented flanges, which formed a kind of second (with respect to the central canal), discontinuous wall. The empty space between the two walls was eventually occluded (at least in some specimens) by the aforementioned cements.

Cloudina is generally regarded as a eumetazoan, with the most frequent comparison being made with cnidarians and tubicolous annelids (e.g., Glaessner, 1976; Grant, 1990; Hua et al., 2005). Independent fossil evidence, particularly the presence of trace fossils attributable to at least stem group bilateria (Budd and Jensen, 2000), is consistent with the interpretation of *Cloudina* as a eumetazoan. However, to interpret *Cloudina* as an annelid would imply that metazoan evolution had proceeded to a considerable degree by the latest Ediacaran times, and that the split between Spiralia and Ecdysozoa, plus a significant diversification of both branches, had already taken place. Although a few Ediacaran fossils have controversially been attributed to bilaterian phyla (notably *Kimberella* to the Mollusca), there is no convincing independent fossil evidence that Spiralia had diversified until the early Cambrian. Instead *Cloudina* could occupy a relatively more basal position within the eumetazoa, for example in the stem group of Eumetazoa, Cnidaria + Bilateria, or Cnidaria.

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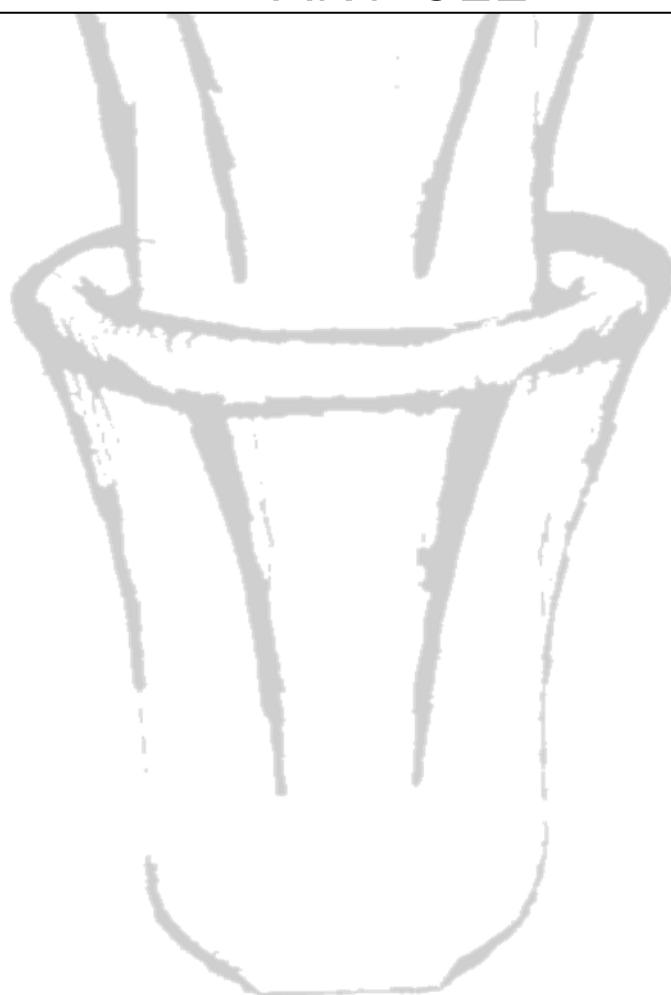
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ARTICLE III



Late Ediacaran skeletal body fossil assemblage from the Navalpino anticline, central Spain

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ABSTRACT

Among late Ediacaran biomineralized metazoans *Cloudina* has a cosmopolitan distribution, whereas other genera show a more restricted distribution. Thus, *Sinotubulites* and *Namacalathus* are not known to co-occur. Here we report the first well-preserved material of *Sinotubulites baimatuoensis* from northwestern Gondwana in material from the Ibor Group of Villarta de los Montes of the Central Iberian Zone, Spain. These are found with *Cloudina hartmanae* and *Cloudina carinata*. Also found are small tubular fossils and a flask-shaped form comparable to *Protolagena*. Among previously described assemblages of late Ediacaran skeletal fossils, the Villarta assemblage, unique in Europe, most closely compares to that from the Dengying Formation of South China.

Keywords: Ediacaran, biomineralization, Spain, *Sinotubulites*, *Cloudina*.

1. Introduction

The acquisition in metazoans of biomineralized hard parts was an important step in early metazoan evolution, allowing new, competitive substrate strategies (particularly in carbonate platforms), defensive strategies, and the evolution of a



whole host of body designs. The first evidence of metazoan biomineralization comes from the late Ediacaran (ca. 551–541 Ma), predating by several million years the radiation of biomineralizing metazoans that took place during the Cambrian (e.g., Maloof et al., 2010). *Cloudina* Germs, 1972, is the most commonly reported and widespread of these early skeletal fossils with a cosmopolitan late Ediacaran distribution, and it is considered an index fossil for the latest part of this period (e.g., Grant, 1990; Narbonne et al., 2012). Other late Ediacaran biomineralized macroscopic fossils include *Namacalathus* Grotzinger, Watters and Knoll, 2000, and *Sinotubulites* Chen, Chen and Qian, 1981. While *Cloudina* is known from all sites with late Ediacaran biomineralized fossils, the occurrences of *Namacalathus* and *Sinotubulites* appear to be mutually exclusive. *Namacalathus* is found in Namibia, British Columbia, Oman and Siberia, while *Sinotubulites* is known from South China, Mexico and western USA. The reason for this is not known and in general the life styles and phylogenetic affinities of these fossils remain under discussion. *Cloudina* has been interpreted as a sessile and gregarious epibenthic suspension feeder living either partially buried in the sediment or attached to biostromes/bioherms (Germs, 1972; Glaessner, 1976; Grant, 1990; Seilacher, 1999; Hua et al., 2005; Warren et al., 2011; Vinn and Zatoń, 2012; Cai et al., 2014) and was the component of the first skeletal packstones/grainstones known in the geological record (Wood, 2011). There is evidence that at least some *Cloudina* were active in the formation of reefs (Penny et al., 2014; Wood and Curtis, 2014), whereas others may have been adapted to life on soft or microbially bound substrates (Hua et al., 2007; Cai et al., 2014). *Conotubus* from the late Ediacaran of South China, similar to *Cloudina* except that it probably was not biomineralized, had its apex anchored into muddy substrates (Cai et al., 2011). Chen et al. (2008) suggested that the polygonal cross-section and



longitudinal crests of *Sinotubulites* could have been an adaptation to life as epibenthos lying on the sea floor. Although traditionally compared with annelids and cnidarians, biological affinities of *Cloudina*, and its probable relatives *Conotubus* and *Sinotubulites*, have not been unambiguously resolved.

Within present-day Europe, the only finds of late Ediacaran biomineralized fossils come from carbonates and associated siliciclastics of the Ibor Group of the Central Iberian Zone of central Spain (e.g. Palacios, 1989; Vidal et al., 1994; Cortijo et al., 2010; Zhuravlev et al., 2012). Paleogeographically, this area was located along the northwest margin of Gondwana, adjacent to northwest Africa, with a somewhat uncertain paleolatitude usually given as about 40° South (e.g. Cocks and Torsvik, 2006). The best known biomineralized fossil in the Ibor Group is *Cloudina*, which has been found in the provinces of Salamanca, Badajoz, Cáceres and Ciudad Real (Palacios, 1989; Vidal et al., 1994; Cortijo et al., 2010). This includes the new species *C. carinata*, characterized by prominent longitudinal external crests (Cortijo et al., 2010). Less is known about other biomineralized fossils in the Ibor Group. Zhuravlev et al. (2012) reported two small skeletal fragments from the Ciudad Real Province as *Sinotubulites* sp. Here we present new information of a moderately diverse skeletal fossil assemblage from the Ibor Group in the area of Villarta de los Montes, eastern Badajoz Province, Spain. The assemblage includes two species of *Cloudina* (*C. hartmanae* and *C. carinata*) and the first well-preserved material of *Sinotubulites* from Spain, which can be assigned to *S. baimatuoensis*. Co-occurring with these well-characterized forms are small, winding tubular fossils, and a flask-shaped fossil similar to *Protolagena* sp.



2. Geological setting

Late Proterozoic sedimentary rocks of the Central Iberian Zone consist of a thick succession of siliciclastic rocks, in great part consisting of greywacke and mudstone interpreted as turbidites, generally attributed to the Domo Extremeño Group. The base of this succession has not been observed, and the maximum age is not known, but trace fossils and detrital zircons show that most is younger than ca. 570 Ma (Jensen et al., 2007; Pereira et al., 2012). The overlying Ibor Group shows considerable lateral variations but is predominantly siliciclastic encompassing one or several carbonate levels. Intermittent outcrops of the Ibor Group extend for more than 400 km in a NW-SW trending band that stretches from the Salamanca to the Ciudad Real provinces and across the Extremadura Community (Fig. 1). *Cloudina* provides biostratigraphic evidence for a late Ediacaran age for the carbonate-bearing part of the Ibor Group, also consistent with locally abundant vendotaenids, particularly rich in siliciclastics directly overlying the carbonates, and the appearance of Cambrian-type trace fossils in higher portions of the stratigraphy (e.g. Jensen et al., 2007). A late Ediacaran age, between 550 and 542 Ma can then be assigned with some confidence. The Ibor Group carbonates were deposited in relatively shallow waters (as indicated by the local presence of oolites, probable stromatolites, and the evidence for storms), on a carbonate platform that opened to the sea in a northeast direction, where there is evidence of a deeper depositional environment with olistostromes consisting of a mixture of blocks of carbonate and siliciclastic rocks. To the southwest, the presence of carbonates is reduced, and shallow water siliciclastic sediments dominate.

The present study is based on material from a locality in the NE portion of the Badajoz Province, near the Villarta de los Montes village. Details of the Ibor Group in

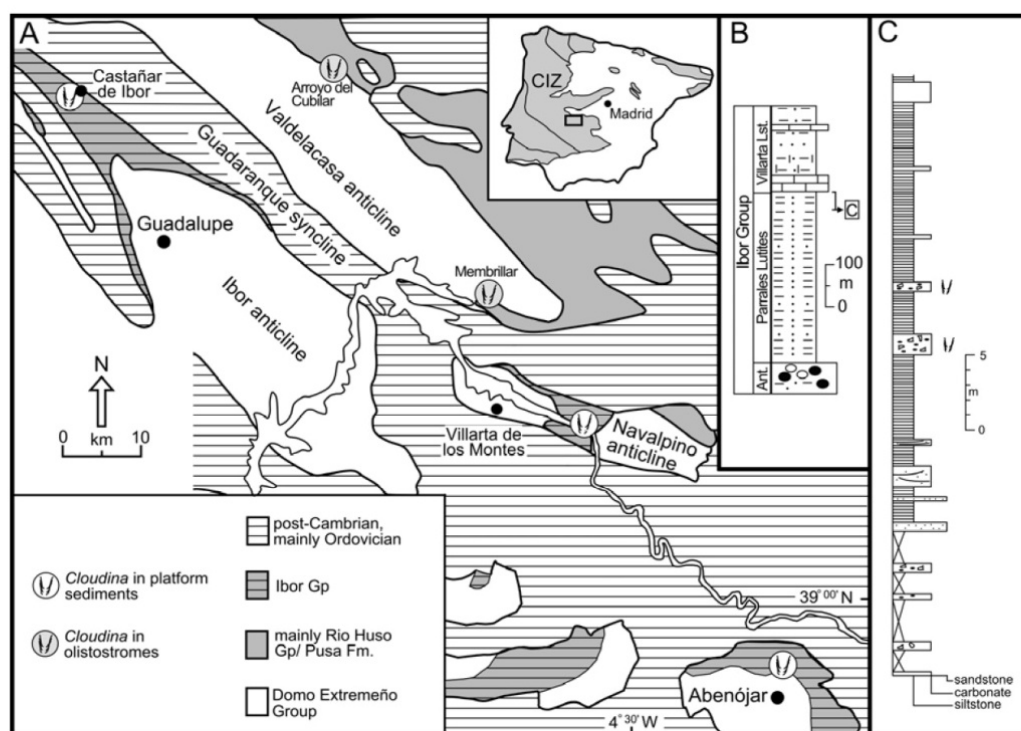


Fig. 1. (A) General geological setting of principal *Cloudina*-bearing outcrops in south-central Spain. The present study is based on material from the Navalpino anticline in the Ibor Group. Inset shows location within the Iberian Peninsula. CIZ, Central Iberian Zone (B) Generalized stratigraphical column of the Ibor Group in the Navalpino Anticline. Ant., Antigua Conglomerate. (C) Stratigraphical log of the fossil-bearing section of this study from the upper part of the Parrales Lutites.

this area can be found in San José (1980), López Díaz (1993, 1994, 1995), Monteserín López et al. (2008) and Palacios et al. (2013). Carbonates of the Ibor Group (the Ibor Group is also known as the Ibor-Navalpino Group in the Navalpino Anticline area; see Fig. 1), which here receive the local name of Villarta Limestone, crop out along both sides of the Guadiana River. In this area the base of the Ibor Group consists of a conglomerate (the Antigua Conglomerate) that rests unconformably on the Domo Extremeño Group, which here shows an abundance of large-scale syndimentary slumping. The following, lower part of the Ibor Group, referred to as the Parrales Lutites, consists of lutite with thin beds of siltstone and

some thicker sandstone beds. The only fossils recorded from this lower part of the Ibor Group in this area are *Sphaerocongregus variabilis*, a probably bacterial organic-walled microfossil without stratigraphic significance (Palacios et al., 2013). The transition to the Villarta carbonates is gradual with the appearance of carbonate lenses, conglomeratic beds including carbonate clasts, and thin carbonate beds. Phosphatic rims are present in the Parrales unit and there are phosphatic clasts in the conglomerates.

The studied material comes from a section located east of the hillock “El Tamujoso”, along the watershed “Vertiente de Tamujillo”. The principal outcrop (UTM ED-50, 30S 0352312, 4343088) consists of fine-grained sediments with interspersed beds of sandstone, greywacke, conglomerate, and carbonate (Fig 1C), belonging to the upper part of the Parrales Lutites. Beds are tabular at outcrop scale. The carbonate beds contain phosphatic clasts and quartz pebbles. These beds are interpreted as material shed down the foreslope. Accumulations of fossils can be observed on the naturally weathered rock surfaces. Fossils preserved as moulds were recovered in a near-by outcrop of laminated fine-grained siliciclastics (UTM ED-50, 30S 0352185, 4343085; Fig. 2A). Phosphatic rims are developed on some levels and there is evidence for former carbonate cement. Structural complications and lack of continuous outcrop does not allow the stratigraphic position of this material to be placed with precision relative to the previously described section, although it is obvious that it belongs to the Parrales Lutites.

3. Material, preservation and methods

Fossils occur as moulds (mostly external empty moulds, but also composite moulds including external and internal moulds) in the fine-grained siliciclastic beds



(Fig. 2A). Most of the fossils in the carbonate blocks are carbonatic, presumably preserving the original skeletal composition, although they appear recrystallized. However, a few are secondarily mineralized, pyritized or phosphatized. Most of the secondarily mineralized fossils appear to be either internal moulds or casts (defining cast as a positive replica formed having an external mould as a template), but they are generally difficult to interpret taphonomically, mostly because the layered structures of *Cloudina* and *Sinotubulites* do not define simple spaces. Finally, a few fossils appear to preserve the original wall replaced in phosphate.

Latex casts were produced of some of the external moulds from the siliciclastic levels to obtain positive replicas. Secondarily mineralized fossils were isolated from the carbonate matrix using the acetic acid maceration technique described in Jeppsson et al. (1999). Larger specimens were coated with ammonium chloride sublimate and photographed with a digital camera. To overcome limitations of depth of field, image stacks were fused with the software CombineZP. Smaller specimens were gold-coated and imaged using scanning electron microscopy (SEM). Energy dispersive X-ray spectroscopy (EDS) was used to analyze the elemental composition of selected fossils. SEM and EDS were carried out on a Hitachi FE-SEM S-4800II at “Servicio de análisis y caracterización de sólidos y superficies de la Universidad de Extremadura, Badajoz” and on a Hitachi FE-SEM S-4300 at the Swedish Museum of Natural History, Stockholm. All illustrated fossils are housed in the collections of Área de Paleontología, Universidad de Extremadura, Badajoz.

4. Description of *Cloudina* and *Sinotubulites*

Genus *Cloudina* Germs, 1972

Introductory remarks: *Cloudina* is a millimetric tubular fossil consisting of stacked funnel-shaped elements. Exceptional three-dimensionally preserved specimens from South China (e.g. Bengtson and Yue, 1992; Hua et al., 2005; Cortijo et al., 2014) and central Spain (Cortijo et al., 2010) have allowed a relatively complete reconstruction of the morphology of *Cloudina*. The growth of *Cloudina* was episodic, starting with a closed unit (cone) to which successive funnel-shaped elements (funnels) were eccentrically stacked. Funnels are open at both ends, forming an open central canal which could have accommodated the soft parts of the organism (Hua et al., 2005; Cortijo et al., 2010). Nested funnels show different degrees of imbrication, and the general tube morphology can range from more or less straight to strongly curved or sinuous (Cai et al., 2014). The occurrence of dichotomous branching in *C. hartmanae* (Hua et al., 2005; Cortijo et al., 2014) and *C. carinata* (Cortijo et al., 2010) has been interpreted as the earliest evidence of asexual reproduction in metazoans. Tube walls are thin and often show signs of plastic deformation, suggesting funnels were secreted as a flexible cuticle (e.g. Cortijo et al., 2010). Since there is also evidence that the skeleton was originally mineralized, it may have incorporated its mineral component during the life of the organism.

Presently there are two clearly distinct *Cloudina* species: the type species, *C. hartmanae* (Germs, 1972) and *C. carinata* (Cortijo et al., 2010). They differ both in funnel morphology and imbrication pattern. While other species have been described within the genus, their distinctiveness remains unclear (Grant, 1990; Hua et al., 2005; Steiner et al., 2007; Meira, 2011).

Both *Cloudina* species are present in the Villarta de los Montes material (Figs. 2–5). In the siliciclastic levels (Fig. 2A) moulds of *C. carinata* (Fig. 2B–C) are



abundant, but *C. hartmanae* has not been recognized. Conversely, *C. hartmanae* is abundant in the carbonate levels (Figs. 3–4), in which only one pyritized specimen of *C. carinata* has been unambiguously identified (Fig. 2D–E). A few specimens showing dichotomous branching have been identified in the carbonate levels (Fig. 5).

Cloudina hartmanae Germs, 1972

Figs. 3, 4

The Villarta de los Montes material of *C. hartmanae* shows the characteristic features of deeply imbricated, often eccentrically stacked funnels (Figs. 3A–D, F, I–J; 4A–C). Funnels are often ornamented, either with wide transverse undulations or with fine transverse lines (Figs. 3K–L; 4A–H). Longitudinal ornamentation is rare (Fig. 4D–E). Individual funnels have a long tubular base and a shorter flaring aperture. Some fragmentary specimens (Fig. 3A–B) preserve an incomplete flaring aperture, embracing the long tubular portion of the following funnel. Wall ornamentation is visible both in the external flaring portion and in the embraced tubular fragment.

Cloudina carinata Cortijo, Martí Mus, Jensen and Palacios, 2010

Fig. 2 B–E

C. carinata is distinguished from *C. hartmanae* by relatively short, bell-shaped funnels with prominent longitudinal crests and a thickened apertural rim, and by a relatively shallow imbrication of the funnels (Cortijo et al., 2010). In the Villarta de los Montes section *C. carinata* is particularly abundant in the siliciclastic levels.



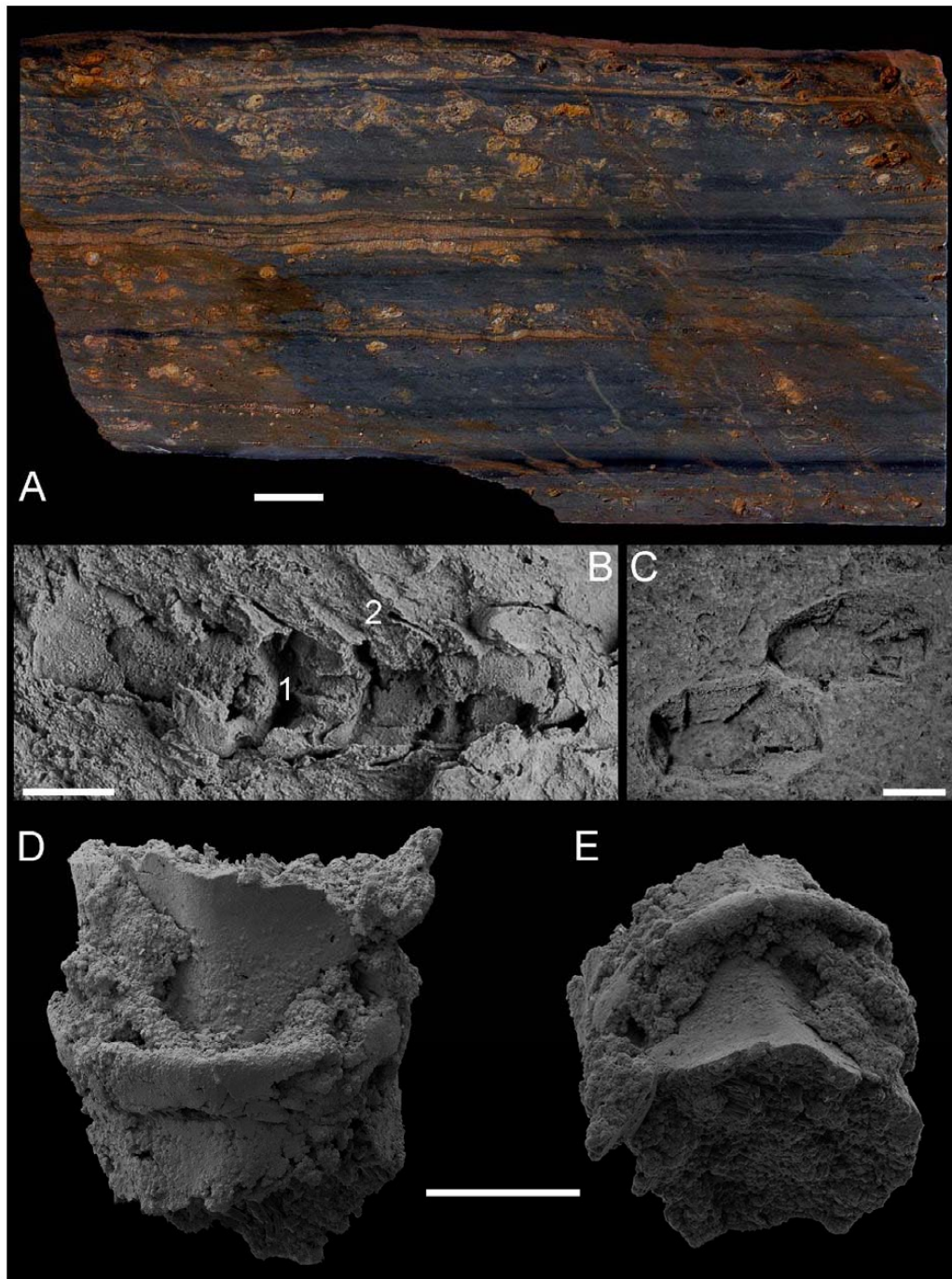


Fig. 2. (A) Polished slab showing dark- and light-grey-colored mudstone beds intercalated with lighter brown/orange fine sandstone beds. The darkest zones correspond to phosphatic rims. Skeletal fossils are seen as empty voids or as variously shaped sediment filled areas. (B-E) *Cloudina carinata*. (B-C) Specimens preserved as moulds from the siliciclastic levels (specimens illustrated in Cortijo et al., 2010). (B) Lateral view of an articulated specimen preserved as a composite mould; note

the crests preserved as grooves (1) and the flaring walls with thickened rims (2). (C) External moulds of two funnels viewed from above; note the crests preserved as grooves. (D–E) SEM images of the same articulated specimen, in lateral (D) and apertural (E) view, from the carbonate levels; note the typical features of the species, the longitudinal crests and the thickened apertural margin. Scale bars represent 1 cm in (A), 1 mm in (B–C) and 500 µm in (D–E).

Contrary to the claim of Zhuravlev et al. (2012) that this species should be assigned to a genus different from *Cloudina*, we maintain the species in *Cloudina* as it possesses the genus-diagnostic, stacked, funnel-shaped elements (Germs, 1972). The species was first described based on material from the El Membrillar olistostrome and from Villarta de Los Montes sections described here (Cortijo et al., 2010; Fig. 1). In the El Membrillar outcrop, *Cloudina* is found secondarily silicified in carbonate olistoliths. More recently, *Cloudina carinata* has also been found similarly preserved in the Fuentes olistostrome in the Arroyo del Cubilar section, in the Toledo Province (unpublished observations) (Fig. 1A). *C. carinata* has also been reported from Siberia (Terleev et al., 2011, fig. 38F), although the illustrated specimen (photographed from a rock thin section) is too poorly preserved to be unambiguously identified.

Genus *Sinotubulites* Chen, Chen and Qian, 1981

Introductory remarks: *Sinotubulites* is a millimetric tubular fossil with an irregular, polygonal cross-section, composed of several concentric, thin walls. Its structure has been described as a “tube-in-tube” construction (e.g. Hua et al., 2003; Chen et al., 2008; Cai et al., 2010, 2015; Sun et al., 2012). Specimens described to date are open at both ends, but are likely fragmentary. The external wall is wrinkled with marked longitudinal folds and irregular transverse annulations and folds. Ornamentation is prominent only on the outer walls, while the inner layers are

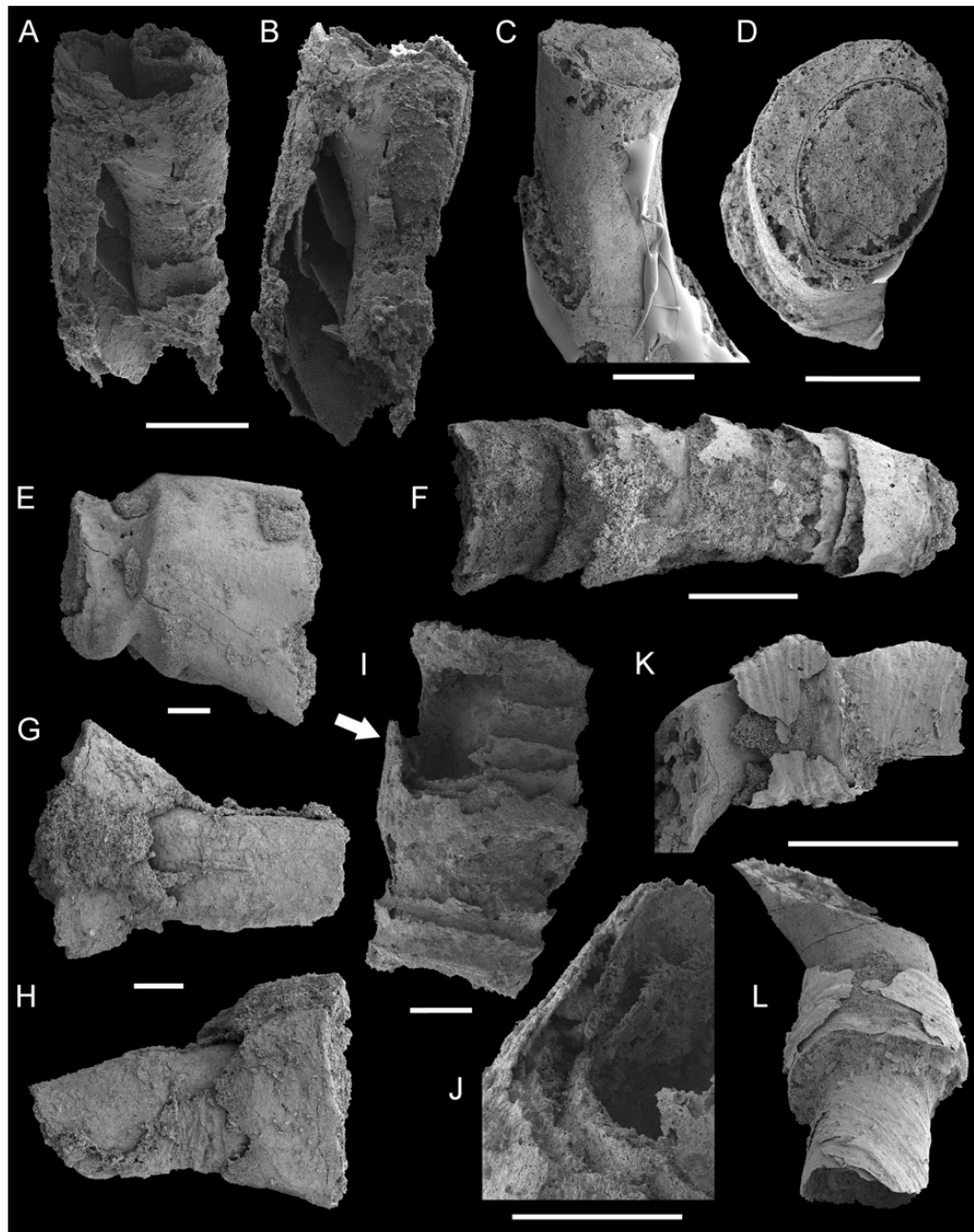


Fig. 3. SEM images of secondarily phosphatized specimens of *Cloudina* (A–D, I–L) *Cloudina hartmanae*. (A–B) Same specimen in lateral view; note the presence of at least 5 eccentrically nested, thin-walled, deeply imbricated funnels; note as well the pronounced flaring of the funnels. (C–D) Lateral (C) and apertural (D) view of a specimen preserved as an internal mould showing 3 eccentrically nested, thin-walled (the wall is preserved as a narrow empty space) funnels. (I–J) Specimen in lateral view showing deeply imbricated funnels. (J) Enlargement of area arrowed in (J). (K–L) Small specimen in lateral (K) and oblique (L) views; the specimen illustrates the flaring portion of a funnel embracing the cylindrical portion of the

subsequent one; the specimen is mostly preserved as a phosphatized internal mould, but note the fragments of ornamented, thin walls preserved surrounding the moulds; ornamentation is more pronounced in the flaring, embracing funnel. (E-H) *Cloudina* specimens preserved as internal moulds, specific characters are not obvious. (E) Single funnel in lateral view showing possible plastic deformation. (F) Articulated specimen; note smooth internal surface preserved in the basal funnels. (G-H) The specimen is similar to that illustrated in (K-L); the flaring portion of a funnel embraces the cylindrical portion of the subsequent one; only a fragment of the wall is preserved in the cylindrical fragment. Scale bars represent 500 μm .

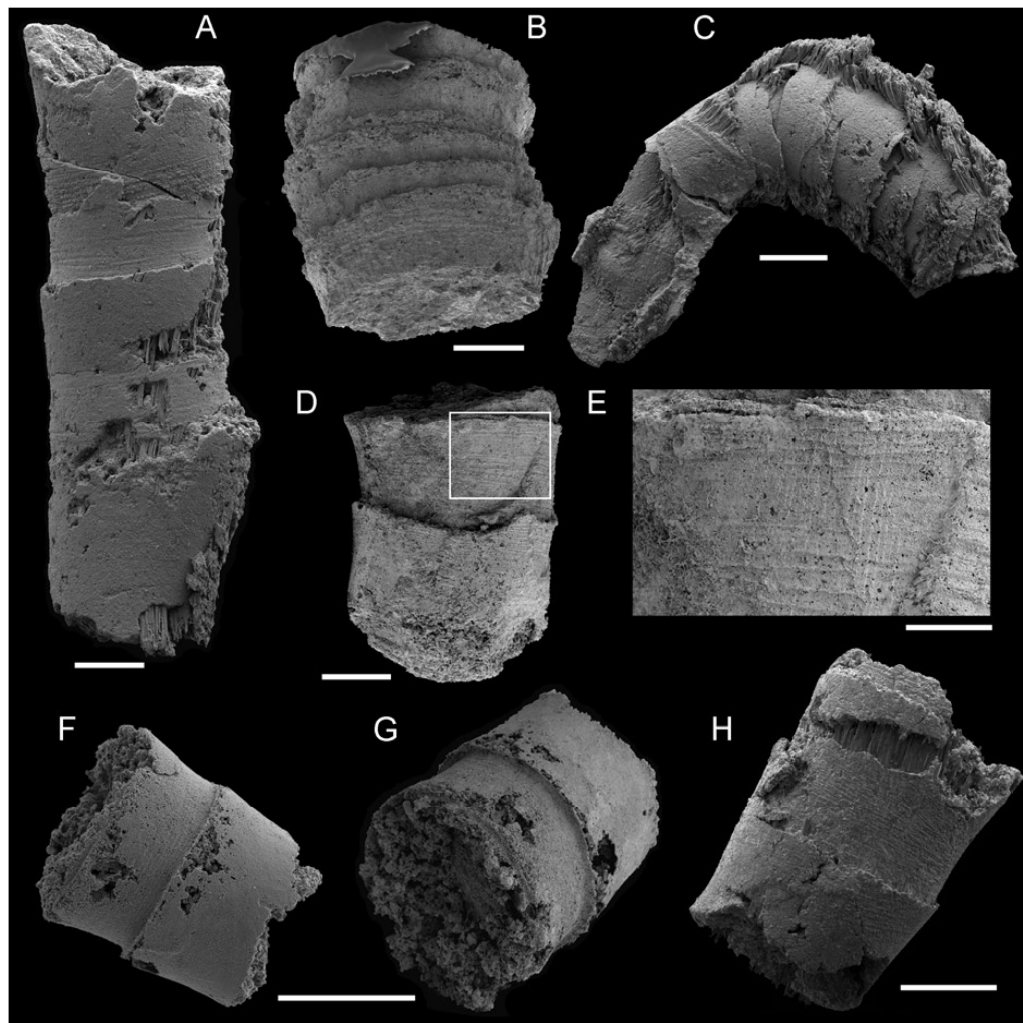


Fig. 4. SEM images of articulated, secondarily pyritized (A, C, H) and phosphatized (B, D–G), specimens of *Cloudina hartmanae*. All specimens appear to represent casts preserving a fine external ornamentation, mostly in the form of closely spaced transverse annulations. (A) Relatively long, straight specimen showing several funnels with fine transverse annulations. (B) Specimen showing at least 5 deeply nested, finely ornamented funnels. (C) Curved specimen with several, relatively smooth nested funnels. (D–E) Specimen showing a reticulated ornamentation. (E) Enlarged view of area framed in (D). (F–H)

Specimens consisting of two nested funnels showing fine transverse annulations. (F-G) Same specimen in different view. Scale bars represent 500 μm in (A-D, F-H) and 200 μm in (E).

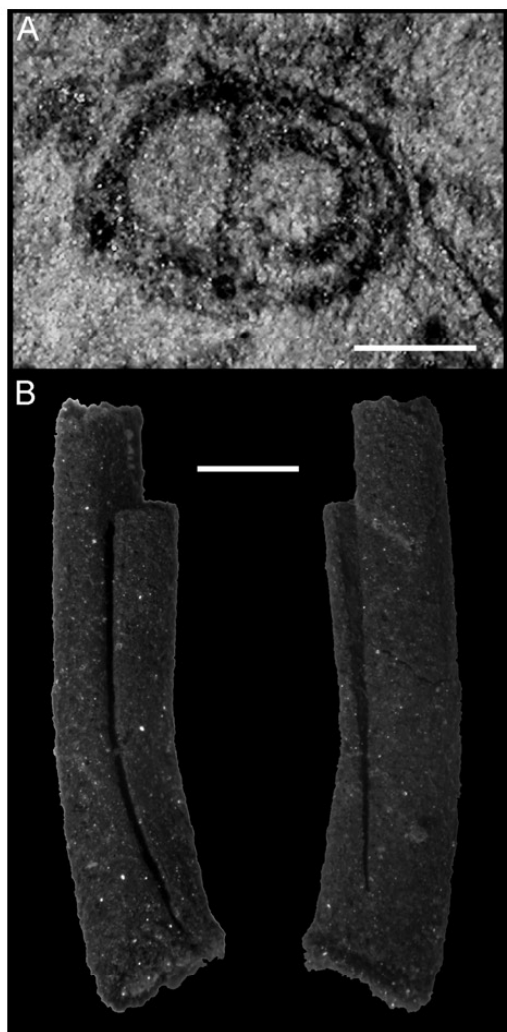


Fig. 5. *Cloudina* specimens showing evidence of asexual reproduction. (A) Specimen of *C. hartmanae* naturally exposed on the surface of a carbonate block from the carbonate levels. (B) Phosphatized internal mould of a branching ?*Cloudina* specimen isolated from the carbonate levels. Note the different size of the daughter tubes on both specimens. Scale bars represent 1 mm.

relatively smooth (Chen et al., 2008; Cai et al., 2015). The layers of this characteristic tube have been interpreted as originally thin and flexible, and therefore it has been suggested that *Sinotubulites* had organic-dominated walls with limited mineralization (Chen et al., 2008). Occurrences of *Sinotubulites* are relatively rare and always associated with *Cloudina*. Until now *Sinotubulites* had been found in two areas: 1) in South China, in several localities of the Dengying Formation (Chen et al., 2008; Cai et al., 2015; see below), and 2) in south-west North America, in the Deep Spring Formation at Mount Dunfee, Nevada (Signor et al., 1983, 1987), and in the La Cienega Formation, Sonora, Mexico (McMenamin, 1985). *Sinotubulites* has been

recently reported from the Ibor Group in the Abenójar Anticline, Ciudad Real Province (Zhuravlev et al., 2012). The report is based on two specimens, only one of which is illustrated (Zhuravlev et al., 2012, fig. 5). The illustrated specimen (described as an inner mould) is a very small fragment showing what appear to be closely spaced annulations. However, the specimen does not show the diagnostic tube-in-tube structure and a tube diameter of ca. 0.25 mm contrasts with a tube diameter of 1.5–6 mm in *Sinotubulites*. For the above reasons unambiguous identification of the Abenojar material as *Sinotubulites* is questionable. Although several species of *Sinotubulites* have been erected to date, their distinctness is unclear. Specimens from the localities in the Yangtze Gorges area in China (Chen et al., 1981; Ding et al., 1985, 1993) and from the American localities (Signor et al., 1983, 1987; McMenamin, 1985) are generally poorly preserved and relatively uninformative regarding morphological details. The best preserved material to date comes from the localities in the Shaanxi Province, China (Hua et al., 2000; Chen et al., 2008; Cai et al., 2010, 2015; Sun et al., 2012), and illustrates a highly variable species, particularly regarding the ornamentation of the outer wall. As the range of morphological and taphonomical variation of *Sinotubulites* becomes better known, it appears that all described specimens could probably be accommodated in the type species *S. baimatuoensis*.

Sinotubulites baimatuoensis Chen, Chen and Qian, 1981

Fig. 6

The Villarta de los Montes material of *Sinotubulites* (Fig. 6) is well-preserved and morphologically comparable to that from Shaanxi Province, China (see above). The largest and most complete specimens are those preserved as external moulds



in the siliciclastic levels (Fig. 6A–B), reaching ca. 20 mm in length (Fig. 6A–B) and ca. 5 mm in diameter (Fig. 6A). Secondly mineralized specimens from the carbonate levels (Fig. 6C–H) are generally smaller and more fragmentary. However, they are more informative in showing the typical tube-in-tube layered structure of the skeleton. Concentric layers are clearly visible in some specimens (Fig. 6E–H), as well as the polygonal cross-section (Fig. 6D, F) and the characteristic contrast between the ornamented external layers and the smooth central tubes (Fig. 6E–F). All specimens show the strongly and irregularly folded external surface.

5. Other fossils

In addition to *Cloudina* and *Sinotubulites* other fossils have been recovered from the Ibor Group in the Villarta de los Montes area that will be briefly described here.

A single flask-shaped fossil (Fig. 7) isolated from a carbonate block shows similarities with *Protolagena* Zhang and Li, 1991, a fossil from the Dengying Formation of South China which there co-occurs with *Cloudina* and *Sinotubulites* (see Hua et al., 2010 for a review of Ediacaran flask-shaped fossils). Like *Protolagena* (Zhang and Li, 1991; Li et al., 2008; Hua et al., 2010), the Villarta specimen has a rounded body, a constricted neck, and a flaring aperture. Unlike *Protolagena* (which is three-dimensionally preserved), the Villarta specimen is flattened and has a granular wall. The Villarta specimen is also somewhat similar to *Titanotheca coimbrae*, a problematic rutile-agglutinated form from the Ediacaran of Uruguay. Both *Protolagena* and *Titanotheca* have been compared with foraminifera (Gaucher and Sprechmann, 1999; Hua et al., 2010).



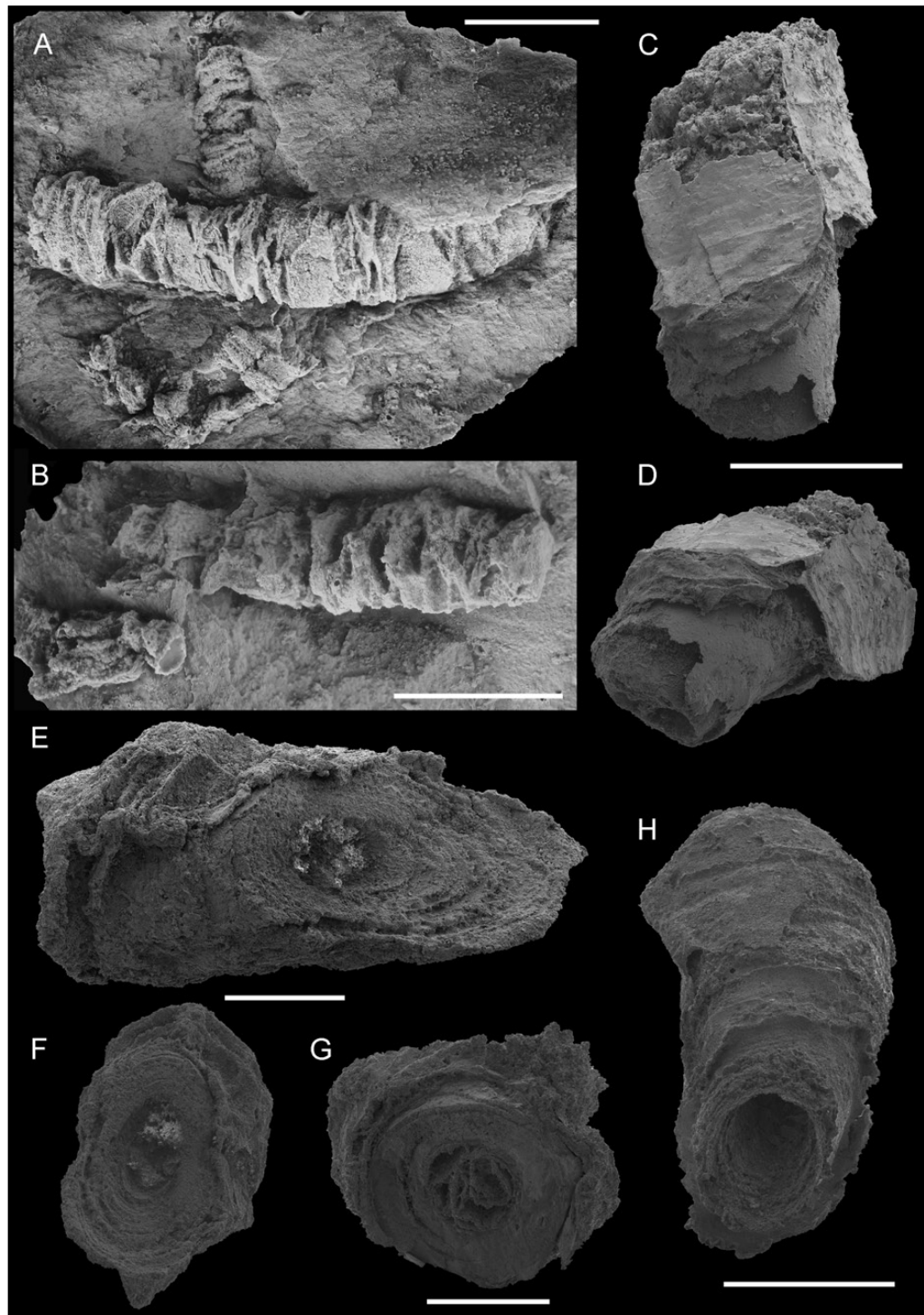


Fig. 6. *Sinotubulites baimatuoensis*. (A–B) Latex casts of relatively large specimens preserved as external moulds in siliciclastic sediments. Note the wrinkled surfaces with irregular transverse folds and short longitudinal ridges. (C–H) SEM images of

phosphatized specimens. (C–D) Same specimen in lateral (C) and oblique (D) view; note the multilayered structure of the tube and the marked longitudinal folds of the thin external wall; a central, narrow cylindrical tube can be seen in (D). (E–F) Same specimen in lateral (E) and frontal (F) view; note the folded outer wall, the smooth inner concentric walls and the polygonal cross-section. (G) Small, fragmentary specimen showing the contrast between the wrinkled external surface and the internal circular walls. (H) Oblique view of a specimen showing numerous, concentric thin walls. Scale bars represent 5 mm in (A–B) and 1 mm in (C–H).

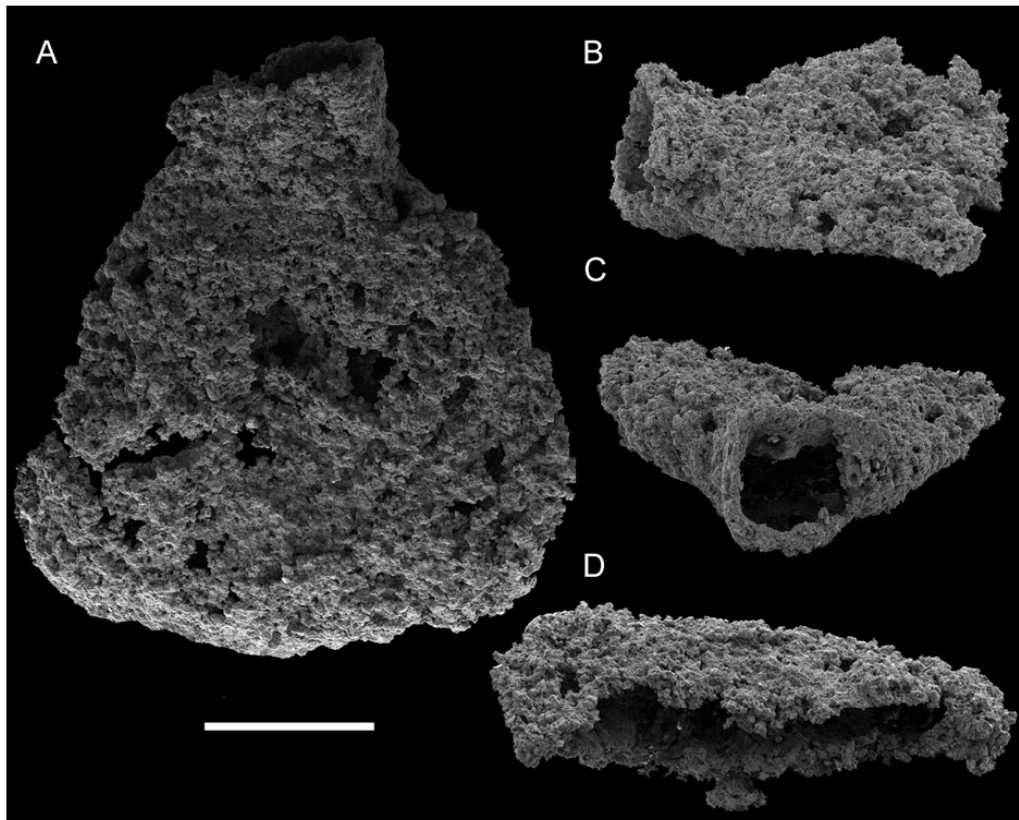


Fig. 7. SEM images of single flask-shaped specimen similar to *Protolagena*. The specimen broke during the process of mounting it to the SEM stub. (A) Reconstruction of the complete specimen. (B) Lateral view of apertural fragment. Note the constricted neck and the circular aperture. (C) Anterior view of the specimen showing the flattened body and the aperture. (D) Posterior fragment showing the empty inner space. Scale bar represents 1 mm.

The Villarta assemblage also contains an abundant and heterogeneous collection of small tubular fossil (Fig. 8). Many of them are likely fragments of larger fossils, particularly internal tubes of the multilayered *Sinotubulites*. However, there is

a distinct group of winding, relatively long tubes, which may represent a taxon of its own (Fig. 8A). They are curved to sinuous, showing characteristic twists and constrictions along their length, and tangle in relatively large accumulations where they represent the only fossils. Specimens longer than 1 cm are apparent, with diameters under 1 mm (mostly 500–250 µm).

Although still largely undescribed or poorly characterized, small tubular fossils may be a common component of late Ediacaran assemblages. Grotzinger et al. (2000; fig. 14D) stated that some 10 % of the skeletal fossils found in the Nama Group cannot be ascribed to *Cloudina* or *Namacalathus* and belong to one or more still undescribed taxa of small tubular fossils. The Namibian specimens show a “gentle curvature”, are typically 1–2 mm wide, with segments up to 3 cm long have been observed (“maximum lengths are harder to estimate because the fossils are almost always broken”) and sometimes “monospecific tube assemblages occur in micritic carbonates that accumulated on level bottoms” (Grotzinger et al., 2000, p. 346).

6. Conclusions

Late Ediacaran skeletal assemblages are not common in the fossil record, but may be of crucial importance to understand the acquisition of hard parts by metazoans. The Ibor Group of central Spain provides the only information on Ediacaran biomineralized skeletal fossils in Europe. The diverse and exceptionally preserved Villarta de los Montes assemblage includes *Cloudina hartmanae*, *C. carinata* and *Sinotubulites baimatuoensis*. Small, winding, tubular fossils are also an important component of the assemblage. It represents the only example of two co-





Fig. 8. Tubular problematica. (A) Latex cast of a surface from the siliciclastic level showing an accumulation of relatively long twisting tubes. (B-S) SEM images of a heterogeneous collection of secondarily mineralized tube fragments. (B-F, R) Empty cylindrical tubes, which may represent internal tubes of *Sinotubulites*; note the possible presence of concentric layers in (E, R-S). (G-J, O-P) Fragmentary internal moulds showing characteristic twists and constrictions similar to those observed in the more complete specimens illustrated in (A). (K) Small specimen showing fragment of ornamented wall. (L, N, Q, S) Internal moulds

showing evidence of layering or imbrication; they likely represent fragments of larger fossils, maybe internal portions of *Cloudina* tubes. Scale bars represent 5 mm in (A) and 500 μ m in (B–S).

occurring well differentiated *Cloudina* species and the first undoubted occurrence of *Sinotubulites* outside China and America.

The fact that biomineralized fossils appear in two different and exceptional preservational modes (which complement each other regarding the type of information they provide) is a particularly noteworthy feature of the Villarta assemblage.

A similar fossil assemblage has been described from the upper Ediacaran Dengying Formation (Beiwan Member) at the Lijiagou section, Shaanxi Province, South China (Cai et al., 2010). The finding of a single specimen of a flask-shaped fossil similar to *Protolagena* (a common fossil in the Dengying Formation) among the Villarta fossils strengthens the similarities between both assemblages.

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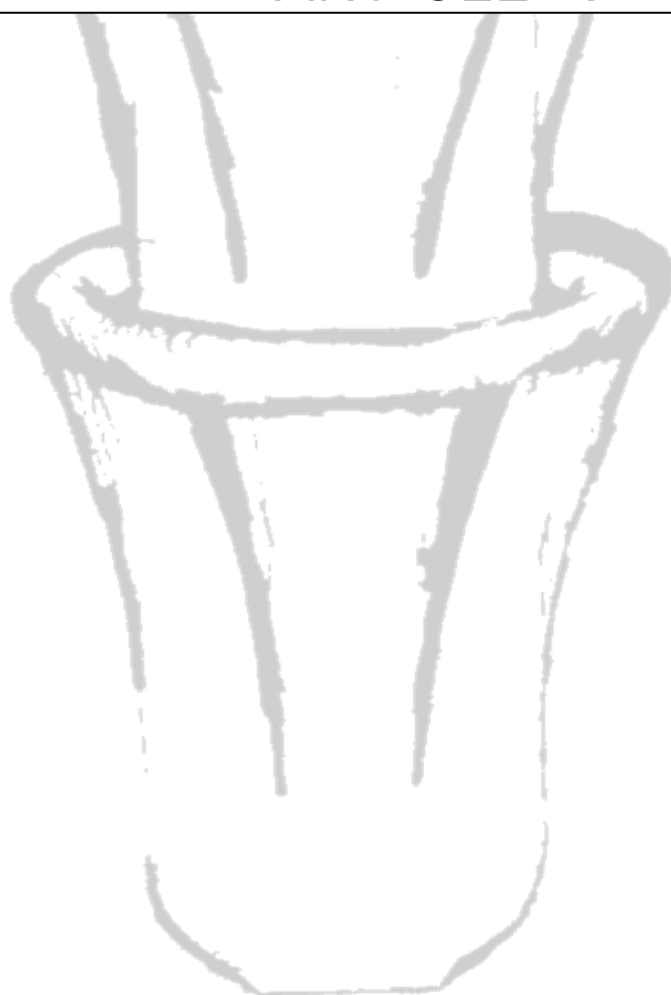
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Life history and autecology of an Ediacaran index fossil: Development and dispersal of *Cloudina*

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ABSTRACT

Cloudina is the best-known biomineralizing metazoan and a potential index fossil in the late Ediacaran Period, yet many aspects of its biology remain poorly understood. Previous reports have shown that *Cloudina* tubes grow from a basally closed funnel (or apical element), with occasional dichotomous branching. New material from the Ediacaran Beiwang Member of the Dengying Formation, South China, includes two distinct morphotypes—tubes with rounded versus pointed conical apices. In branching specimens, one of the daughter branches tends to have a conical apex. It is hypothesized that cloudinids with a spherical apex were derived from sexual reproduction, with their spherical termination representing the embryonic shell, whereas those with a conical apex are daughter branches detached from their parent tubes through asexual reproduction. These interpretations imply that *Cloudina* could reproduce both sexually and asexually, producing spherical embryonic shells and conical propagules, respectively. This strategy may have served to enhance dispersal, which was critical for the ecological success of early gregarious and sedentary animals such as *Cloudina*.

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1. Introduction

One of the most evolutionarily important events in the early Cambrian was the widespread acquisition of biomineralized skeletons across numerous metazoan groups. The seemingly synchronous rise of biomineralization across multiple animal phyla and involving multiple minerals (calcium carbonate, calcium phosphate, silica) indicates that the genetic toolkit and biomolecular machinery for biomineralization have earlier phylogenetic roots and that the Cambrian radiation of biomineralizing animals was driven by ecological and environmental factors (Knoll, 2003). The Cambrian radiation of biomineralizing animals was, however, preceded by a small number of late Ediacaran skeletal animals, including *Cloudina*, *Sinotubulites*, *Namacalathus*, and *Namapoikia* (Grant, 1990; Grotzinger et al., 2000; Wood et al., 2002; Hua et al., 2005). Of these Neoproterozoic biomineralizers, *Cloudina* is the first described and perhaps best known, with a wide geographic distribution in Namibia, Oman, South China, Siberia, Mexico, southeast USA, British Columbia, Brazil, Paraguay, and Spain (see Cortijo et al.,

2010; Warren et al., 2011) but with a restricted stratigraphic range between 549 Ma and 541 Ma (Grotzinger et al., 1995; Amthor et al., 2003). As such, *Cloudina* is a valuable terminal Ediacaran index fossil (Grant, 1990; Hua et al., 2005); but perhaps equally as important, the presence of biomineralizing metazoans, while restricted to only a few taxa, within the last few million years of the Ediacaran Period indicates the evolutionary emergence of mineralized skeletons prior to their phylogenetically widespread appearance in the Cambrian Period (Hua et al., 2003; Xiao and Laflamme, 2009; Peters and Gaines, 2012).

Cloudina is a small tubular fossil characterized by a succession of stacked funnel-shaped elements and interpreted as the biomineralized exoskeleton of an early metazoan (Germs, 1972; Grant, 1990). While widely accepted to have grown by episodic addition of new funnel-shaped elements from an apically-closed basal element, little is known about the early ontogeny of *Cloudina*, perhaps as a result of the susceptibility of *Cloudina* tubes and apices to fragmentation. Some Chinese *Cloudina* specimens, however, are preserved with complete apices, and therefore present an opportunity to examine the ontogenetic growth sequence of this important index fossil (Fig. 3A and 3C in Bengtson and Yue, 1992; plate 1 and Fig. 6 in Chen and Sun, 2001; Fig. 1A–B and 1F in Hua et al., 2005; Fig. 6.4 in Hua et al., 2007; Fig. 2D in Chen et al., 2008).

Dichotomous branching has been reported in both Chinese (Hua et al., 2005, 2007) and Spanish *Cloudina* specimens (Cortijo et al.,

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2010). Interpreted as asexual division, a general feature of cloudinid dichotomous branching is that it is irregular, with daughter tubes of different diameters being produced. One of the daughter tubes is always significantly smaller and narrower than the other. Furthermore, when dichotomy starts to develop, the combined diameter of the two daughter tubes is no greater than that of the parent tube, implying that the parent tube embraces both daughter tubes (Cortijo et al., 2010; Vinn and Zatoń, 2012). Most reported specimens show an early stage of division, but little is known about the developmental initiation and ontogenetic fate of daughter branches. To address unresolved questions about the life history of *Cloudina*, we examined new material collected from the late Ediacaran Dengying Formation of South China, with a focus on evidence of sexual and asexual reproductive strategies, and the inferred implications for ecological dispersal.

2. Geological setting

The fossils described here were collected from the upper Ediacaran Dengying Formation at the Lijiagou section, near the town of Kuanchuanpu, Ningqiang County, Shaanxi Province, South China (Fig. 1A). The Dengying Formation at Lijiagou is divided in three members (Fig. 1B; Hua et al., 2007): the Algal Dolomite Member (thick-bedded peritidal dolostone), Gaojiashan Member (thin-bedded calcareous siltstone, mudstone, and limestone), and Beiwan Member (a light gray, thick-bedded, peritidal dolostone). Although some authors regard the Beiwan Member as a part of the Gaojiashan Member (Chen and Sun, 2001; Hua et al., 2003, 2005; Chen et al., 2008; Cai et al., 2014), we follow Hua et al. (2007) in separating the upper dolostone unit because it is lithostratigraphically similar to the Beiwan Member and distinct from the more silty and argillaceous Gaojiashan Member at the type section near the Gaojiashan village (Cai et al., 2010; Meyer et al., 2012). The Beiwan Member at Lijiagou section, ca. 20 km WNW of the Gaojiashan section, has yielded abundant secondarily phosphatized *Cloudina* (Bengtson and Yue, 1992; Hua et al., 2005) as well as other fossils, including *Sinotubulites*, “vase-shaped microfossils” or protolagenids, branched tubular fossils and spherical structures of unknown affinities (Hua et al., 2003, 2007; Chen et al., 2008).

3. Material, methods and preservation

The material reported here was extracted from several dolostone blocks collected from the Beiwan Member in Lijiagou. More than a thousand secondarily phosphatized *Cloudina* tubes, the vast majority of which are fragmented and poorly preserved, were isolated from the carbonate matrix using acetic acid maceration techniques described in Jeppsson et al. (1999). Selected specimens were imaged using scanning electron microscopy (SEM; FEI Quanta 600F and Hitachi S-4800; backscattered electron imaging mode). Illustrated specimens are deposited at the Virginia Polytechnic Institute Geosciences Museum (VPIGM).

4. Description and morphological reconstruction

4.1. General description

Cloudina fossils from the Lijiagou section display a relatively wide range of size and morphology, but always fall within the typical range of the genus (Grant, 1990). Tube diameters range from 100 µm (Fig. 2H) to more than 2 mm (Fig. 3A), and the lengths are up to 5 mm in the longest but still incomplete specimens (Figs. 2B, 3A). Cloudinid tubes are constructed by a series of repetitive and successively-stacked funnel-shaped units. Together, these funnel-in-funnel tubes taper only slightly from their aperture to the basal apex, maintaining a largely consistent tube diameter through their overall length (Hua et al., 2005; Cortijo et al., 2010; Cai et al., 2014). As opposed to the open-ended repetitive funnel units, the apical element is basally closed (Chen and Sun,

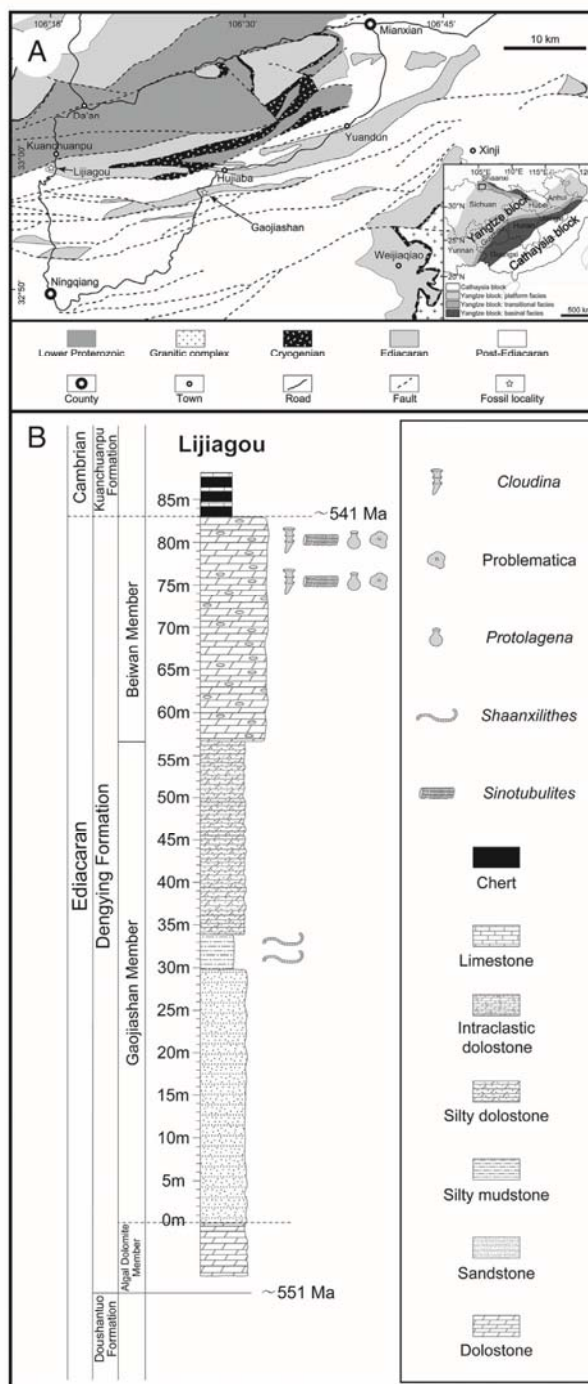


Fig. 1. (A) Geological map (modified from Cai et al., 2014) of the Ningqiang area, southern Shaanxi Province, South China, showing the locality of the Lijiagou section. Rectangle in inset map shows the location of the Ningqiang area in the northwestern margin of the Yangtze Platform. (B) Litho- and bio-stratigraphy of the Dengying Formation at Lijiagou (modified from Cai et al., 2014). The upper unit of the Dengying Formation is here recognized as the Beiwan Member (Hua et al., 2007), rather than as part of the Gaojiashan Member (Cai et al., 2014).

2001; Hua et al., 2005; Chen et al., 2008; Cai et al., 2014). Rarely, cloudinid tubes show dichotomous branching into two smaller tubes from the larger antecedent tube (Hua et al., 2005; Cortijo et al., 2010).

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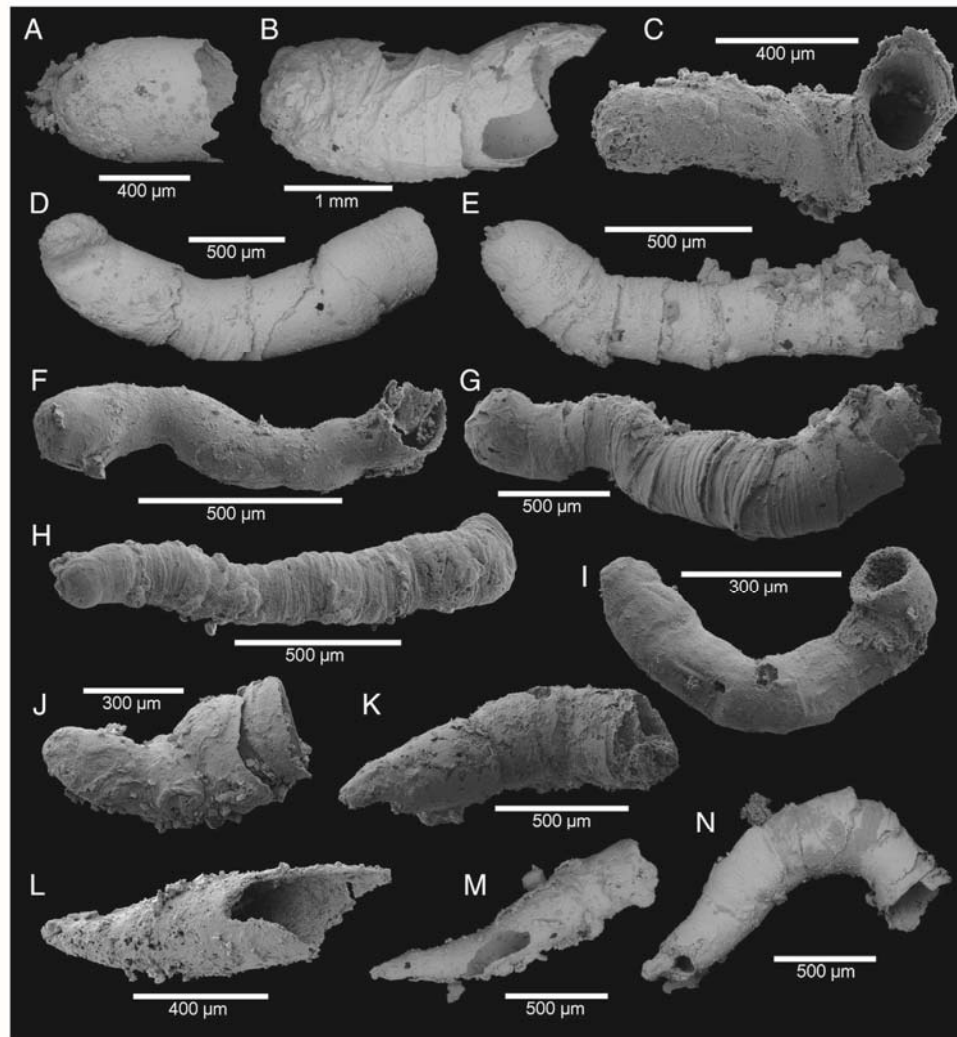


Fig. 2. SEM images of *Cloudina* fossils with preserved basal elements. (A–H) Specimens with a hemispherical basal element. This is the most common morphotype in our collection. (F) Specimen apparently with a continuous cylindrical test, rather than a series of nested funnel elements. (D, E, G, H) Specimens with a constriction separating the hemispherical base and subsequent funnel elements. (I–J) Specimens with a conical basal element but a blunt apex. (I) Specimen with a continuous cylindrical test rather than a series of nested funnel elements. (K–N) Specimens with a conical base and a pointed apex.

4.2. Apical element morphology

The Lijiagou *Cloudina* fossils show two distinct morphotypes, and a third less categorizable morphology, of the closed basal element (Fig. 2A–N). In most of the specimens, the basal end is hemispherical and shows no sign of attachment scars or anchoring structures (Fig. 2A–H). The hemispherical basal elements range from 100 µm (Fig. 2H) to 1.5 mm (Fig. 2B) in diameter, and from 200 µm (Fig. 2H) to more than 2 mm (Fig. 2B) in length in well preserved specimens, although some may be incomplete. The exterior surface texture of the basal elements may be smooth (Fig. 2A, C, F, G), wrinkled (Fig. 2B), or exhibit smooth undulations (Fig. 2D, E, H). These surface features have been commonly observed in non-basal *Cloudina* funnels. The basal element has approximately the same diameter as successive funnel-shaped elements in most of the tubes, with a largely consistent, or marginally widening, diameter along the length of the tube, a feature which seems to be a characteristic of *Cloudina* tubes (Cortijo et al., 2010). The best preserved specimens consistently show a fold, or

partial constriction, occurring just above the hemispherical base (Fig. 2D, E, G, H).

Previously unreported among *Cloudina* fossils are tubes with a pointed, or more conically-shaped, closed base (Fig. 2K–N). This conical morphotype is less abundant than the hemispherical base, with only approximately 10% of the best preserved specimens showing this apical morphology. The length of pointed basal elements ranges from 500 µm (Fig. 2K) to more than 900 µm (Fig. 2L, an incomplete specimen), and its maximum diameter is consistent between 250 µm (Fig. 2K) and 300 µm (Fig. 2L). The exterior surface of the conical basal elements appears smooth, contrasting with the wrinkled or undulated wall of most hemispherical basal elements.

Some specimens show a basal element that is less easily ascribed to either of the above morphological categories (Fig. 2I–J). These basal elements seemingly appear crushed or flattened, showing similarities to conical apices but with a blunt base. The maximum diameter of the blunt basal elements ranges from 150 µm (Fig. 2I) to 350 µm (Fig. 2J), and their maximum length may exceed 600 µm (Fig. 2J). Like the conical

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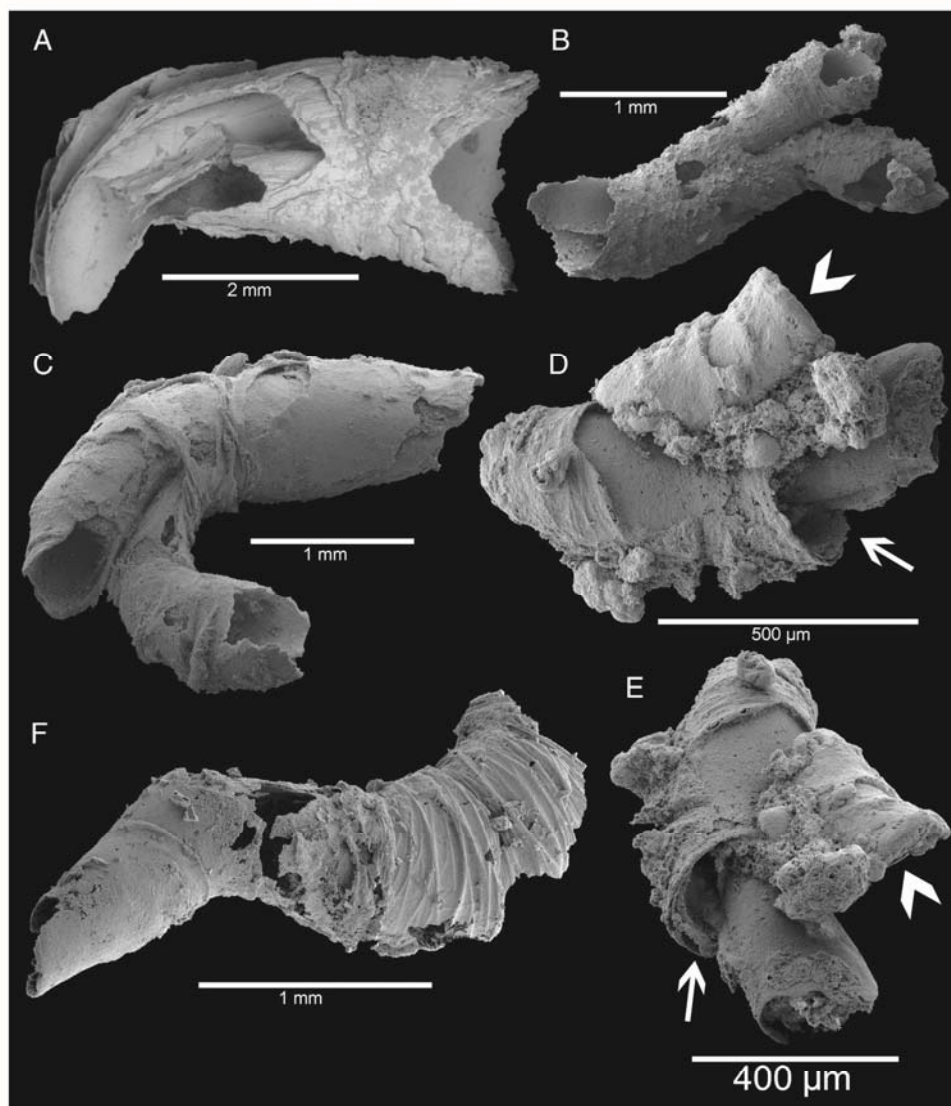


Fig. 3. SEM images of *Cloudina* fossils with dichotomously branching tubes. (A) Initial branching that produces a larger and a smaller daughter tubes, both nested within the parent tube. (B–C) Specimens with daughter tubes diverging and curving from each other as soon as they emerge from the parent tube. (D–E) Different views of the same specimen, showing dichotomous branching, with one of the daughter tubes released, leaving a wedge-shaped gap in the parent tube (arrows). A poorly preserved tube (arrowheads) is fortuitously attached to the parent tube. (F) Specimen showing the β stage (from Fig. 5) of the proposed *Cloudina* life cycle; note the different ornamentation patterns in the shell, smooth in the basal region and wrinkled in early growth funnels.

basal elements, the blunt basal elements also exhibit a smooth exterior surface.

4.3. Branching specimen morphology

Branching specimens are very rare in the Lijiagou samples. A total of 7 of > 1000 specimens analyzed show signs of branching, with the three best preserved illustrated in Fig. 3A–C. The specimen illustrated in Fig. 3A shows the beginning of the branching process inside the parent tube, with daughter tubes arising from within the narrow portion of the parent funnel. The larger daughter tube appears to have an open, relatively wide base, while the smaller one shows a narrow, conical, basally tapered apex. It is unclear whether the tapered base is closed or has a narrow opening. Beyond the point of division, the smaller daughter

tube expands rapidly (within $\sim 500 \mu\text{m}$ of tube length) to reach the diameter of the original parent tube. In most instances, branching is associated with a pronounced curvature of the tube, where both parent and daughter tubes may be involved in the curvature (Fig. 3A–C). Once they have extended beyond the parent funnel, the daughter tubes tend to diverge markedly from each other (Fig. 3C; also see Fig. 1M–P of Hua et al., 2005, and Fig. 6.5 of Hua et al., 2007).

4.4. Isolated spherical structures

Although not abundant (about 25 specimens in our collection), several spherical forms with a diameter of $\sim 300\text{--}400 \mu\text{m}$ have been found in the Lijiagou material (Fig. 4A–C). These spheres are mineralogically comparable to the cloudinid tubes as indicated by comparable

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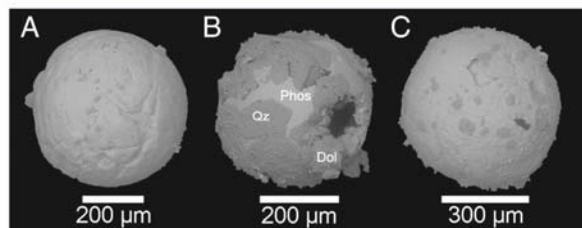


Fig. 4. SEM images of spherical fossils interpreted as possible embryos. Note that their size and compositions (as indicated by backscattered electron grayscale) are comparable to the *Cloudina* specimens with a hemispherical basal element (Fig. 2A–H). Phos: phosphate; Qz: quartz; Dol: dolomite.

grayscale observed in backscattered electron imaging. Some of these spheres have a smooth surface marked by scars (Fig. 4A), whereas others show an orange peel-like siliceous texture and secondary dolomite (respectively, dark-colored patches and rhombohedra in Fig. 4B). Although no obvious intermediate stages have been found, the morphology and physical dimensions of these spheres are similar to the spherical basal elements of *Cloudina*.

4.5. General autecology

Cloudina has been compared to both cnidarians and annelids (Germs, 1972; Glaessner, 1976; Grant, 1990; Hua et al., 2005; Vinn and Zatoń, 2012; Cai et al., 2014). With a lack of preserved soft-tissues, however *Cloudina* has not been yet confidently positioned phylogenetically. However, morphological and ecological studies have at least reconstructed *Cloudina* as a sessile, epibenthic, and colonial filter feeder (Grant, 1990; Warren et al., 2011; Cai et al., 2014), potentially with the apical end of the tube embedded within the substrate or containing soft-tissues within the apertural end of the tube, as suggested from preferential positioning of predatory borings (Hua et al., 2003). Likely contributing to their cosmopolitan distribution, *Cloudina* shows an apparent plasticity in the types of substrates it can inhabit within shallow marine ecosystems, having been shown in association with matgrounds, biostromes, and bioherms in various localities (Germs, 1972; Warren et al., 2011; Cai et al., 2014). External molds of cloudinid apical elements at the point of substrate attachment (Fig. 9A of Cai et al., 2014) in addition to preservation of clustered tubes (Fig. 9B of Cai et al., 2014) have bolstered the interpretation of aggregated *Cloudina* populations as gregarious colonies.

5. Interpretations and implications

The range of morphologies observed in the Lijiagou material permits the proposal of an ontogenetic growth series for *Cloudina*. We propose that *Cloudina* started its development from a spherical embryo (Fig. 5A). Although admittedly speculative, this spherical embryo stage

was possibly similar to, or even potentially represented by, the isolated spherical structures illustrated in Fig. 4. A spherical embryo would subsequently develop into an embryonic test with a hemispherical base (Fig. 5B, C). If the life mode of *Cloudina* is assumed to be analogous to that of *Conotubus* (Cai et al., 2011, 2014), the fold or constriction that appears directly subsequent to the hemispherical basal element (Fig. 2D, E, G, H) may be interpreted as positional adjustment of the emerging animal to the sea-floor. Following these early ontogenetic stages, funnel-shaped elements were successively added during the growth of the animal (Fig. 5D–E). The tube may occasionally divide into two daughter tubes, interpreted here as asexual paratomic reproduction by dichotomous branching (Fig. 5F). During division, two different daughter funnels would develop, a smaller one (Fig. 5α) with a conical and closed base, and a larger one with an open base contiguous to the parent tube (Fig. 5G). The new individuals would continue developing as described above (Fig. 5H, β), by adding new funnels to their tubes to accommodate increased body volume.

We also propose that the rarity of branching *Cloudina* tubes in the fossil record may be due to the release of the smaller “bud” from the parent tube. The reported specimens with a conical base represent the smaller daughter tubes that had originated through asexual paratomy and were then released from the parent tube. The specimen illustrated in Fig. 3D–E shows a wide empty space to the side of the last funnel (arrows); this space may represent a gap that had been occupied by a daughter tube, which had since been released as a propagule. The specimen illustrated in Fig. 3F may represent a released daughter propagule. As can be seen in this and other similar specimens, the conical basal element has a smooth external surface, and the lack of ornamentation may reflect the development of this part of the shell within and under the protection of the parent tube. Distal funnels, on the other hand, show wrinkled walls. These wrinkles may be related to deformation of the flexible organic substrate developing outside the parent tube by water current shearing, suggesting that the shell was weakly mineralized. There is also an abrupt change in orientation between the conical base and subsequent funnels (Fig. 3F); this change is consistent with the divergence of daughter tubes after they emerge from the parent tube (e.g., Fig. 3C). Thus, the two specimens illustrated in Fig. 3D–F provide strong support to the ontogenetic stages represented in Fig. 5G and β.

Given its global geographic distribution and wide environmental distribution, *Cloudina* must have been able to disperse across large expanses of the oceans, particularly if it lived a gregarious and sedentary life. The afore described propagule stage (Fig. 5β) may have served to facilitate the ecological dispersion during the cloudinid life cycle, although claims as to passive (density independent) or active (density dependent) dispersal are only speculative without an understanding of either the soft-tissues or phylogenetic affinity of *Cloudina*. With that said, however, the asexual paratomic reproduction of *Cloudina* seems likely to have served as an adaptation for density dependent dispersal in order to relieve pressure of high local population density, limited availability of habitat space, and competition for resources. Regardless of the dispersal mode, the paratomic reproductive strategy of *Cloudina*, as

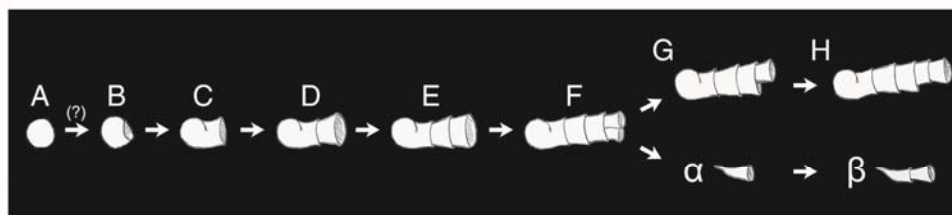


Fig. 5. Interpretive diagram showing the proposed ontogenetic sequence of *Cloudina*, from the putative spherical embryo (A) to the hemispherical basal apex (B), through funnel additions (C–E), dichotomous branching (F), and continued growth (G–H) after release of the daughter propagule (α–β).

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well as its plasticity of substrate type attachment, more than likely promoted its worldwide paleobiogeographic range.

6. Conclusions and summary

From the new cloudinid material of the Ediacaran Beiwan Member, Dengying Formation, South China, we have documented two distinct morphotypes of the cloudinid apical element—hemispherical and pointed conical apices. We interpret the hemispherical apices as incipient *Cloudina* derived from the embryonic shell. On the other hand, *Cloudina* tubes that exhibit a conical apex are paratomically-grown daughter branches detached from their parent tubes. The proposed life cycle, supported by surficial textures of these apical element morphotypes and individuals demonstrating dichotomous branching, suggests that *Cloudina* reproduced both sexually and asexually. Its asexually produced propagules could have assisted in ecological dispersal, therefore facilitating the global distribution of *Cloudina*.

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