

FIELD TRIP:  
PALAEOZOIC ECHINODERMS FROM NORTHERN SPAIN





## FIELD TRIP: PALAEOZOIC ECHINODERMS FROM NORTHERN SPAIN

Samuel Zamora<sup>1</sup> (coord.)

José Javier Álvaro<sup>2</sup>, Miguel Arbizu<sup>3</sup>, Jorge Colmenar<sup>4</sup>, Jorge Esteve<sup>2</sup>, Esperanza Fernández-Martínez<sup>5</sup>, Luis Pedro Fernández<sup>3</sup>, Juan Carlos Gutiérrez-Marco<sup>2</sup>, Juan Luis Suárez Andrés<sup>6</sup>, Enrique Villas<sup>4</sup> and Johnny Waters<sup>7</sup>

<sup>1</sup> Instituto Geológico y Minero de España, Manuel Lasala 44 9ºB, 50006 Zaragoza, Spain. s.zamora@igme.es

<sup>2</sup> Instituto de Geociencias (CSIC-UCM), José Antonio Novais 12, 28040 Madrid, Spain. jj.alvaro@csic.es, jcgrapto@ucm.es, jorgeves@unizar.es

<sup>3</sup> Departamento de Geología, Universidad de Oviedo, Jesús Arias de Velasco s/n, 33005 Oviedo, Spain. marbizu@geol.uniovi.es, lpedro@geol.uniovi.es

<sup>4</sup> Área de Paleontología, Departamento de Ciencias de la Tierra, Universidad de Zaragoza, Pedro Cerbuna 12, 50009 Zaragoza, Spain. colmenar@unizar.es, villas@unizar.es

<sup>5</sup> Facultad de Biología y Ciencias Ambientales, Universidad de León, Campus de Vegazana, 24071 León, Spain. e.fernandez@unileon.es

<sup>6</sup> Soningo, S.L. PCTCAN, Isabel Torres, 9 P20. 39011 Santander, Cantabria, Spain. juan\_suarez@yahoo.es

<sup>7</sup> Department of Geology, Appalachian State University, ASU Box 32067, Boone, NC 28608-2067, USA. watersja@appstate.edu

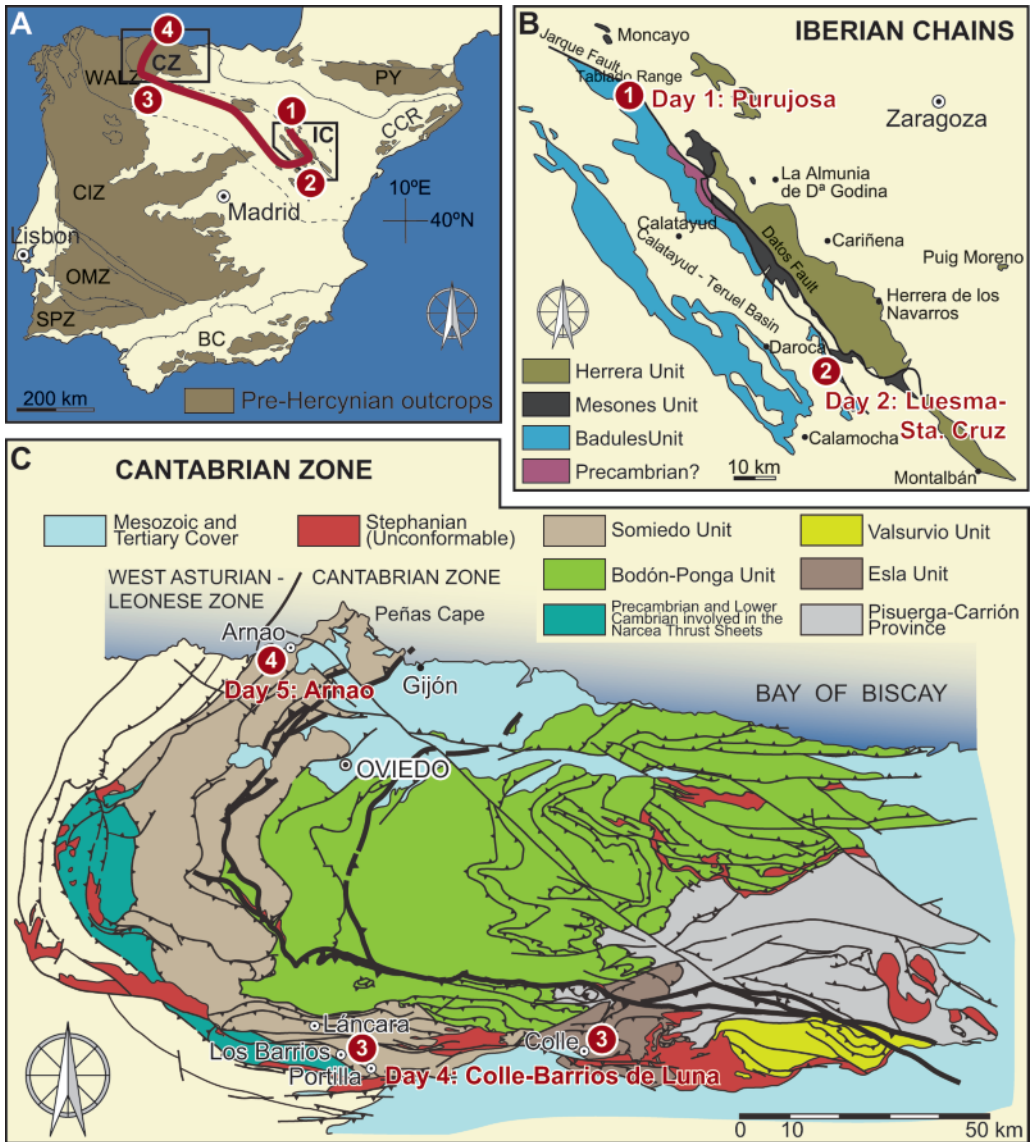
**Keywords:** Cambrian, Ordovician, Silurian, Devonian, echinoderms, environments, evolution.

### INTRODUCTION

Samuel Zamora

Spain contains some of the most extensive and fossiliferous Palaeozoic outcrops in Europe, including echinoderm faunas that are internationally significant in terms of systematics, palaeoecology and palaeobiogeography. This field trip will review some of the most remarkable Palaeozoic localities in North Spain. It will be divided into two different but related geological and geographical areas, the Cantabrian Zone in northern Spain and its southeastern prolongation, known as the Iberian Chains (Fig. 1).

Palaeozoic echinoderms have been known from northern Spain since De Verneuil (1850) who described the Devonian crinoid *Pradocrinus baylii*. Ten years later, Prado *et al.* (1860), reported the first Cambrian echinoderm, *Trochocystites bohemicus* ?, n. sp. (sic!), on the southern slope of the Cantabrian Mountains between Sabero and Boñar (León). Since then, numerous echinoderms have been described from the Cambrian of Spain, and some of the most important contributions include the works of Friedrich (1993) and Sdzuy (1993), who provided the most comprehensive work to date on cinctan systematics and stratigraphic distribution. In addition, the Spanish palaeontologist Prof. Bermudo Meléndez published a series of papers on Ordovician echinoderms from northern Spain (Meléndez, 1942–44, 1952, 1959; Meléndez and Hevia, 1947). The knowledge of Ordovician faunas was greatly improved by his work in collaboration with Jean Jacques Chauvel and Jean Le Menn (Chauvel *et al.* 1975), and more recently by Gutiérrez Marco *et al.* (1996a), who has collaborated with us in the preparation of this field guide. In



**Figure 1.** Itinerary followed by the field trip. A. Map of Spain showing Pre-Hercynian outcrops and tectonostratigraphic zones. Zones: CZ, Cantabrian; CIZ, Central Iberian; WALZ, West Asturian-Leonese; OMZ, Ossa-Morena Zone; SPZ, South Portuguese; BC, Betic Cordillera; IC, Iberian Chains; PY, Pyrenees. B. Geological map of the Iberian Chains with tectonostratigraphic units. C. Geological map of the Cantabrian Zone with indication of main geological units.



contrast, the Silurian faunas are poorly understood, partly because of their scarcity. Le Menn *et al.* (2003) described one of the few crinoid species known from the Silurian of North Spain. Devonian echinoderms have attracted much more attention. Spain has continuous fossiliferous sections with abundant and diverse echinoderms especially from the Lower and Middle Devonian. Unfortunately, there has been only limited work on this material: Breimer (1962) published on crinoid systematics, but other groups such as blastoids, edrioasteroids, echinoids and ophiuroids have received relatively little attention (Breimer, 1971; Breimer and Macurda, 1972; Breimer and Dop, 1975; Smith and Arbizu, 1987; Smith *et al.* 2013a; Blake *et al.* in press).

Although the main focus of my research over the past 10 years has been the study of Cambrian faunas, more recently, and in collaboration with other colleagues, I have begun to study Spanish echinoderms from other parts of the Palaeozoic – especially from the Ordovician, but also from the Silurian and Devonian. Because of these collaborations, we are now able to organize this field trip reviewing echinoderm communities from the Cambrian to the Devonian of North Spain.

During the first day of the field trip, we will visit Purujosa, one of the most interesting Cambrian sections in NE Spain (Zamora *et al.*, this guide). Large-scale excavations (with the help of students) over the past 10 years have allowed us to assemble an extensive collection of echinoderms and other fossils from the classic middle Cambrian Mansilla and Murero formations. This material is remarkable and includes some of the oldest representatives of major clades (Zamora, 2010), including the oldest cinctan (Rahman and Zamora, 2009), cothurnocystid stylophorans (Zamora, 2010) and isorophid edrioasteroids (Zamora and Smith, 2010), as well as taxa that fill important gaps in echinoderm evolution, such as the most primitive bilateral echinoderms (Zamora *et al.*, 2012) and arm-bearing “pelmatozoans” (Zamora and Smith, 2012).

For the second day of the field trip, Colmenar *et al.* (this guide) have provided an itinerary of the Iberian Chains reviewing important new and classic localities preserving echinoderm communities from the Ordovician to the Devonian. The Upper Ordovician faunas from the Fombuena and Cystoid Limestone formations were described in several seminal papers (Chauvel *et al.*, 1975; Gutiérrez Marco *et al.*, 1996a), and are associated with a dramatic change in global climate (the so-called Boda Event). These strata record the immigration of marine invertebrates against the backdrop of global warming. This will be followed with a visit to the Silurian represented by a low-diversity fauna of crinoids and ophiuroids. We will end the day with a short visit to the Devonian, where a recent road cut allows access to the Mariposas Formation (Emsian), which provides the only complete crinoids of this age in the Iberian Chains, and will serve as a comparison with a fauna of similar age from the Cantabrian Zone (that we are visiting in the following days).

The third day will cover the Cambrian to the Devonian at the southern slope of the Cantabrian Mountains. The chapter from Álvaro *et al.* (this guide) focuses on the lower Palaeozoic faunas (Cambro–Ordovician). The “griotte” facies of the Láncara Formation (dated as middle Cambrian) preserves the only worldwide examples of “pelmatozoan” holdfasts attached to firmgrounds during the Cambrian. This provides important palaeocological and evolutionary information, suggesting that the echinoderms with columnals and holdfasts cemented directly onto the substrate evolved first in Gondwana, spreading and diversifying in proximal environments from the Furongian onwards when hardgrounds started to become common (Brett *et al.* 1983). The Cambrian from Los Barrios de Luna is one of the most spectacular and continuous sections from northern Spain, and was first described by geologists in the 19th century. It preserves an interesting echinoderm fauna from the Oville Formation (middle Cambrian), including, among others, the very asymmetrical cinctan *Lignanicystis barriosensis* (Zamora and Smith, 2008) and the oldest columnal-bearing eocrinoid, *Ubaghsicystis segurae* (Gil Cid and Domínguez, 2002). Next, a short stop at Upper Ordovician outcrops recently discovered by Gutiérrez Marco *et al.* (1996b) will provide a unique example of echinoderm faunas from the latest Ordovician in the Cantabrian Zone. Fernández *et al.* (this guide) complete the third day with a visit to two Devonian localities. The classic locality of Colle (Valporquero Formation, Emsian) is spectacular in terms of both faunal diversity and preservation. Blastoids are more abundant here than in any other Lower Devonian locality worldwide (Waters and Zamora, 2010). During the visit we will discuss possible causes of this uniquely high abundance. Crinoids are also important and most of the type specimens from Breimer (1962) come from this locality. A short stop in an abandoned open quarry close to Los Barrios de Luna will illustrate more typical Devonian faunas preserved in a carbonate platform environment (Santa Lucía Formation) and dominated by crinoids.

The last day, Suárez-Andrés *et al.* (this guide) present the faunas from a very important fossil site close to the locality of Arnao at Cape La Vela (Asturias). Here, an interesting fauna from the Lower Devonian Aguión Formation

(upper Emsian) contributes to the understanding of the role of substrates in the distribution of echinoderms. Abundant fossils preserved *in situ* in both soft and hard substrates serve as a remarkable example of echinoderm anchoring strategies. This outcrop also preserves two echinoderms that were described by Andrew Smith, the only edrioasteroid known from the Devonian of Spain, *Krama devonica* (Smith and Arbizu, 1987), and the only echinoid known from the Palaeozoic of Spain, *Rhenechinus ibericus* (Smith *et al.* 2013a).

Although previous researchers have made important contributions to the understanding of Palaeozoic echinoderm faunas from Spain much more work remains to be done on Spanish echinoderm faunas. This field guide reviews the aforementioned works, but also identifies several new possible lines of enquiry. We hope that this field guide will drive future generations in the study of this enigmatic, sometimes difficult, but really interesting group of metazoans.

## PALAEOZOIC FROM THE IBERIAN CHAINS

J. Javier Álvaro

The pre-Variscan outcrops of the Iberian Chains constitute a relic of the deeply eroded Variscan orogen in NE Spain. These NW-SE-trending chains or ranges are longitudinally divided, by the Cenozoic Calatayud-Teruel trough, into the western and eastern Iberian chains (Fig. 1). Traditionally, the pre-Variscan outcrops have been further subdivided into three NW-SE-trending tectonostratigraphic units, bounded by major faults and mainly characterized by differences in the style of Variscan-dominated deformation. From southwest to northeast, they are named Badules, Mesones and Herrera units. The former comprises Ediacaran to Lower Ordovician rocks, and show monoclinial to thin-skinned geometries associated with folds and intersected by major nappe structures. The Mesones unit contains Ediacaran to middle Cambrian rocks, is bounded by the western Jarque and the eastern Datos faults, and is dominated by complex thrust systems and nappe structures. It is up to 12 km wide but, in some areas, they disappear due to the coincidence in surface of both faults. The Jarque fault, which longitudinally crosscuts the Paracuellos antiform, is considered as the prolongation of the contact that separates the Variscan Western Asturian-Leonese and Cantabrian Zones, which longitudinally traverses the Narcea Antiform (Gozalo and Liñán, 1988). Finally, to the NE of the Datos fault, the Cambrian-Carboniferous succession of the Herrera unit is deformed into a NE-directed fold and thrust system, in which many thrust faults are blind with tip lines within Ordovician to Devonian rocks.

The pre-Variscan basement of the Iberian Chains consists of a mosaic of crustal elements fragmented and structured during the Variscan and Alpine orogenies. These sediments were thrust northeastward during the late Carboniferous (post-Westphalian A) onto a Precambrian continental margin, named Cantabro-Ebroic Land Area (Carls, 1983; Álvaro *et al.*, 2000a), which lies at present-day under the Cenozoic Ebro valley. The Variscan structures of the Iberian Chains are attributable to three major deformational phases at least (Capote and González Lodeiro, 1983; Tejero, 1986; Tejero and Capote, 1987; Navarro Vázquez, 1991), which were developed under a low to very low grade of metamorphism (Bauluz *et al.*, 1998). A late-Variscan deformational regime reflects an evolution from reverse strike-slip tectonics to radial extension associated with the emplacement of Stephanian-Permian calc-alkaline dykes and sills. Finally, Alpine regional stress regimes affected pre-existing crustal discontinuities, reactivating both Variscan structures and discordant contacts of Precambrian/Lower Paleozoic rocks with Triassic (Morés trough) and Cenozoic (Calatayud-Teruel trough) rocks.

DAY 1: June 17<sup>th</sup> 2015

## CAMBRIAN ECHINODERMS FROM PURUJOSA, NORTHERN IBERIAN CHAINS

Samuel Zamora, J. Javier Álvaro and Jorge Esteve

## INTRODUCTION

As stated above, the Iberian Chains are two NW-SE-trending Palaeozoic ranges in NE Spain separated by the Cenozoic Calatayud-Teruel Basin (Lotze, 1929; Carls, 1983). The Cambrian of the Iberian Chains is a sedimentary succession, about 3000 m thick, containing lower Cambrian to Furongian volcanic-free formations (Fig. 2). Strata providing complete echinoderms in the Iberian Chains are conspicuous throughout the entire Cambrian, but they are especially abundant in the middle Cambrian formations, from bottom to top, the Valdemiedes, Mansilla, Murero, Borobia and Valtorres formations (Fig. 2). The oldest echinoderm ossicles appear in the carbonate tempestites of the mixed (carbonate-siliciclastic) Valdemiedes Formation (where lies the regional lower-middle Cambrian boundary), as a result of the influence of storm events in a mixed platform recording shallowing-upward cycles from upper offshore to peritidal environments (Álvaro *et al.*, 2013b). These faunas include benthic meadows dominated by chancelloriids, spiculate sponges (Álvaro and Vennin, 1996a, 1997), eocrinoids (gogiids) and edrioasteroids (?*Stromatocystites*) (Clausen, 2004; Álvaro *et al.*, 2013b). The Mansilla Formation comprises a 70-m-thick interval of reddish-to-purple limestone/shale couplets grading upsection into shales with interbedded carbonate nodules. Disarticulated ossicles are common in the lower part and complete echinoderms are scattered on top of the formation. The latter represent the oldest cinctan species reported up to now from Gondwana: *Protocinctus mansillaensis* (Rahman and Zamora, 2009). Traditional echinoderm faunas from the Spanish Cambrian come from the Murero Formation, interpreted as a clayey offshore-dominated unit punctuated by storm-induced shell beds. The formation has been properly sampled and has yielded abundant skeletonized faunas including trilobites, brachiopods, sponges and echinoderms. Several levels have provided a diversified fauna that includes cinctans, eocrinoids, edrioasteroids, stylophorans and ctenocystoids (Friedrich, 1993; Zamora, 2011). The Borobia Formation, up to 250 m thick and representative of prograding episodes of shoaling complexes, is episodically rich in echinoderms; several levels have yielded the same major taxonomic groups than the Murero Formation but represented by different species.

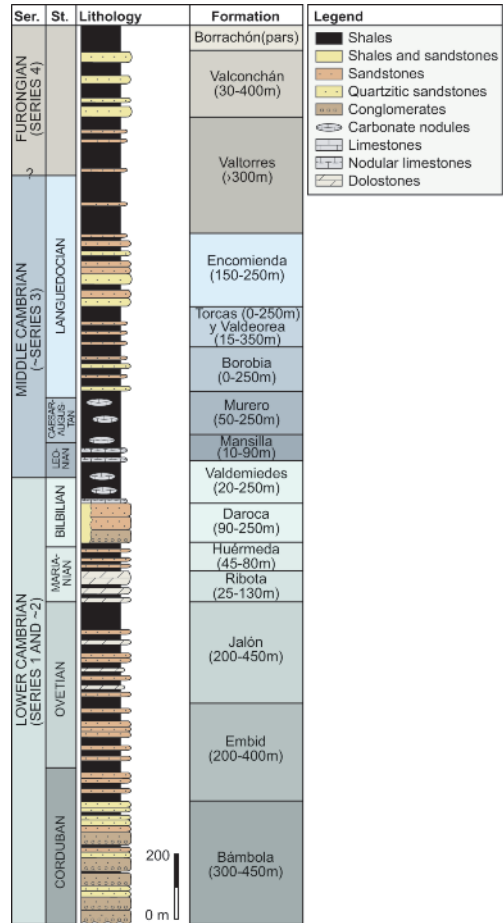


Figure 2. Synthesis stratigraphic log of Cambrian rocks in the Iberian Chains.

Echinoderms are very rare upsection and only become conspicuous again in the offshore-dominated Valtorres Formation (Shergold and Sdzuy, 1991). A new recently discovery echinoderm fossil assemblage in the vicinity of Ateca, probably Furongian in age, includes stylophorans, glyptocistitids and edrioasteroids.

Historically, the first Cambrian echinoderm in Spain was described from the Cantabrian Zone and is the cinctan *Trochocystites bohemicus*?, n. sp. (sic) Prado *et al.* (1860). Hernández-Sampelayo (1935) was the first to describe a Cambrian echinoderm from the Iberian Chains, in the classic locality of Murero, which was then reported as *Trochocystites*. Most of the echinoderms from the old literature were classified as *Trochocystites* or *Decacystis*, but they are currently included in the genus *Gyrocystis*, which is the most common cinctan taxon (Schröder, 1973; Friedrich, 1993). The first rigorous study on Cambrian echinoderms from the Iberian Chains dates from the early 1970s, when Schröder (1973) described new occurrences of *Decacystis hispanica* (currently *Gyrocystis platessa*) from the Cantabrian Mountains and a new species, *Gyrocystis? melendezi* (currently *Undatacinctus melendezi*) from Ateca (Iberian Chains) based on specimens collected by Master students from Münster University (Germany) and his own collections. The latter is the second echinoderm species cited in the Iberian Chains and the first ever reported from the Borobia Formation (Zamora and Álvaro, 2010). The monograph from Friedrich (1993) is the most complete synthesis of the Class Cincta and included several new taxa from the Iberian Chains. Based on specimens sampled in the Iberian Chains, he erected *Gyrocystis testudiformis*, *G. badulesiensis*, *G. erecta* and *Progyrocystis disjuncta*. Clausen (2004) provided the first evidence of echinoderms from the lower Cambrian Valdemiedes Formation, represented by a possible eocrinoid named *Rhopalocystis? mesonesensis*. Further work in these beds and new localities revealed that this is, in fact, a basal plate of a gogiid eocrinoid closely related to *Gogia*. Subsequently, Zamora (2009) carried an exhaustive work in both previously known and new localities from the Iberian Chains, reviewed all the previous works and situated the old samplings in a modern stratigraphic context. This work revealed that the Cambrian diversity of echinoderms in Spain was overlooked and described new taxa and major groups never reported from the Iberian Chains before, which include cinctans, stylophorans, edrioasteroids, several blastozoan groups and ctenocystoids (Zamora, 2010, 2011).

In the Iberian Chains, Purujosa (Fig. 1) is probably the best sampled outcrop and its faunas are relatively well known. The locality is situated in the northern edge of the eastern Iberian Chain, south of the Moncayo summit, the highest peak in the whole chain. One MSc and two PhD theses have been carried out in Purujosa for different purposes. Zamora (2005) was the first to describe in detail the stratigraphy of the area, mapped the different Cambrian formations and collected the first echinoderms. Zamora's (2009) work was focused on echinoderm faunas and recognized important fossiliferous levels in the middle Cambrian formations. Esteve (2011) focused his work in trilobites from the Murero Formation and sampled an amazingly rich echinoderm-trilobite interval from the top of the Murero Formation that, due to its wealth in complete enrolled trilobites, known as the "Trilobite Purujosa assemblage" (Esteve *et al.*, 2011). The rich echinoderm faunas from Purujosa provide important information about the chronostratigraphic and environmental distribution of several groups through the Cambrian. In addition, it includes several critical taxa that allow a better understanding of early echinoderm evolutionary patterns (Zamora *et al.*, 2012, Zamora and Smith, 2012; Zamora and Rahman, 2014).

The aim of the excursion is to visit different echinoderm intervals from the Mansilla, Murero and Borobia formations (Figs. 2, 3). This will offer a rather complete view of how Cambrian echinoderm faunas from Spain occur and how those faunas recorded important palaeogeographic shifts associated with environmental changes.

### STOP 1: Mesozoic/Palaeozoic contact – The Jarque Fault

#### Location

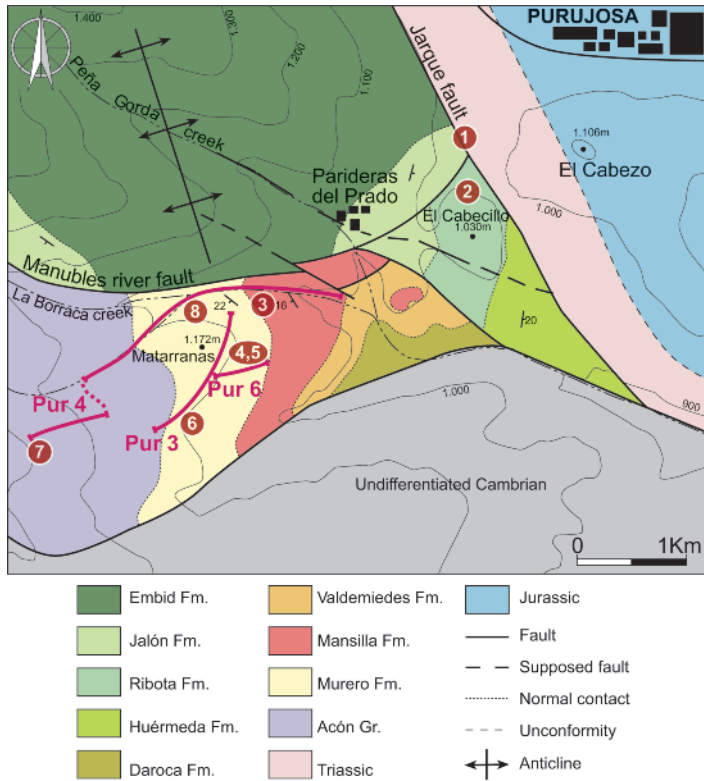
Main creek to the south of the Cabezo hill, in the main path going from Purujosa to Pomer villages (Fig. 3).

Coordinates: 41°40'37.19"N, 1°46'35.35"W

Geological map of Spain, 1:50.000, sheet of Tabuena (352).

Geological setting: Badules Unit (eastern Iberian Chain).

Main topic: faulted contact between the Palaeozoic and Mesozoic rocks.



**Figure 3.** Detailed geological map of the Purujosa area with indication of visited sections and situation of stops. Modified from Zamora (2005).

## Aims

Look at a thrust marking the Mesozoic/Palaeozoic contact.

## Description

As explained above, the pre-Variscan exposures of the Iberian Chains constitute a relic of the deeply eroded Variscan Orogen in NE Spain. Traditionally, their outcrops have been subdivided into three NW-SE-trending tectonostratigraphic units, bounded by the Jarque and Datos Faults. The western Badules Unit, limited to the east by the Jarque Fault, comprises Ediacaran(?) to Lower Ordovician rocks with monoclinal to thin-skinned geometries associated with folds and intersected by major nappe structures. (Álvaro and Blanc-Valleron, 2002; Álvaro *et al.*, 2008, and references within). The Jarque Fault and its associated Paracuellos Fault crosscut longitudinally the Paracuellos Antiform. The latter offers exposition of the oldest unit of the Iberian Chains, the uppermost Ediacaran-lowermost Cambrian Paracuellos Group. This antiform is considered as the lateral prolongation of the Narcea Antiform, which separates the Variscan Cantabrian and West Asturian-Leonese Zones in NW Spain (Gozalo and Liñán, 1988).

The Variscan Jarque Fault was reactivated during the Alpine Orogeny, as a result of which it is mapped as a thrust over Mesozoic strata. In the northwestern edge of the eastern Iberian Chain, the main Jarque Fault splits into two smaller thrusts, the western W-E-trending one is the so-called 'Manubles river' Fault (Fig. 3). The Purujosa study area occurs in the southern hanging fault block of the latter fault.

## STOP 2: Trilobites from the lower Cambrian Ribota Formation

### Location

Path crossing the Isuela river in the SW of Purujosa. Section between el Cabecillo hill and Parideras del Prado (Fig. 3).

Coordinates: 41°40'34,39"N, 1°46'40,68"W  
 Geological map of Spain, 1:50.000, sheet of Tabuena (352).  
 Geological setting: Badules Unit (eastern Iberian Chain).  
 Lithostratigraphic unit: Ribota Formation.  
 Age: Marianian (early Cambrian).

### Aims

Look at the faunas and lithology of a fossiliferous lower-Cambrian formation devoid of echinoderms. Equivalent levels in other Gondwanan areas have reported oldest echinoderms from Gondwana. Discuss the origin of first echinoderms faunas.

### Description

This outcrop provides one of the few places in the Iberian Chains where the Ribota Formation yields abundant and well preserved trilobites. The Ribota Formation is a 115 m thick succession composed of yellow-grey dolostones with interbedded shales, containing mainly trilobites, hyoliths and trace fossils. The dolostones are not fossiliferous but the shale interbeds bear two trilobite assemblages. The lower assemblage is characterised by *Lusatiops ribotanus* Richter and Richter, 1948, *Strenuaeva incondita* Szalay, 1961, and the upper assemblage contains *Kingaspis* (*Kingaspidoidea*) *velata* Szalay, 1961, and *Redlichia* sp. Szalay. Other undetermined redlichiid trilobites have been found in neighbouring localities. The trilobite fauna indicates a regional Marianian age that broadly correlates with the Botoman and the global Cambrian Age 3. Equivalent age levels in North America and Morocco have reported the oldest worldwide echinoderms, which have never been reported from the Iberian Chains.

## STOP 3: Echinoderms from the middle Cambrian Mansilla Formation

### Location

Following the aforementioned path the Mansilla Formation crops in both sides of the path. Just before the path crosses La Borraca Creek there is a well exposed outcrop to the left slope (Figs. 3, 4).

Coordinates: 41°40' 21,27"N, 1°47'16,78"W  
 Geological map of Spain, 1:50.000, sheet of Tabuena (352).  
 Geological setting: Badules Unit (eastern Iberian Chain).  
 Lithostratigraphic unit: Mansilla Formation.  
 Age: Leonian (mid Cambrian).

### Aims

Look at poorly diversified fauna from the Mansilla Formation consisting of cinctans and isolated plates belonging to dibrachicystid blastozoans. It is remarkable the different modes of preservation in the Mansilla Formation (as calcite ossicles) and in the Murero Formation (as natural moulds).

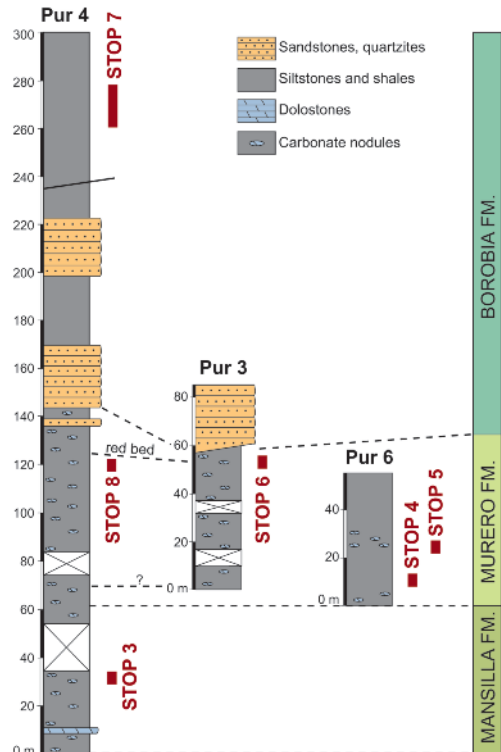


## Description

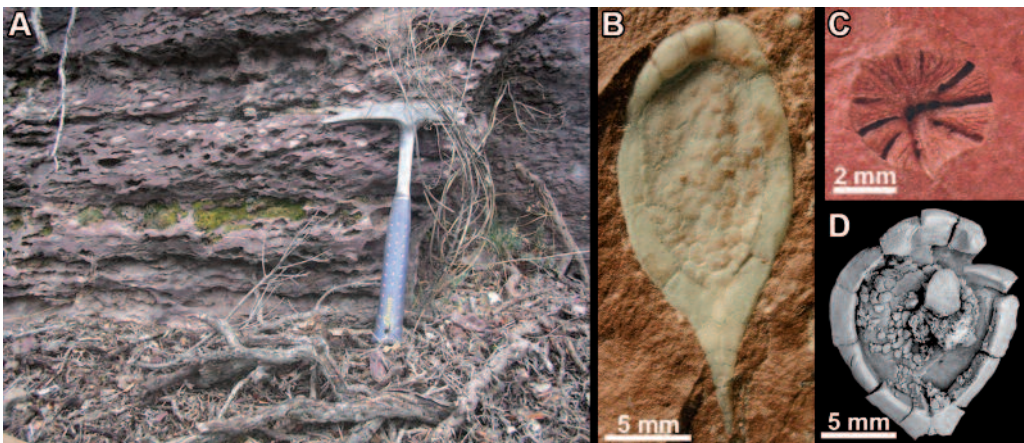
The Mansilla Formation in the study area comprises a 70 m-thick interval composed of red-purple shale/limestone couplets (the so-called 'griotte facies') passing upsection into shales with interbedded carbonate nodules (Fig. 5A). The upper part of the formation is more fossiliferous and dominated by shales. The formation shows a general transgressive trend from onshore to offshore deposits and, due to sharp changes in biozonal thickness, the formation represents episodic carbonate production on the top of palaeohighs surrounded by lows with mud-dominated sedimentation (Álvaro and Vennin, 1996b). Cinctans are very abundant through the section but complete specimens (Fig. 5B, D) have only been reported from the upper part of the formation, where they coexisted with dibrachicystid isolated plates (Fig. 5C), trilobites, brachiopods and molluscs.

In contrast to other formations from the area, echinoderms of the Mansilla Formation are preserved as calcite. Detailed studies of these specimens using cathodoluminescence revealed the original stereom microstructure in recrystallized calcitic plates that was invisible under conventional transmitted light or SEM (Gorzalak and Zamora, 2013).

Only the species *Protocinctus mansillaensis* (Fig. 5B) has been erected from these beds using CT-scan combined with traditional techniques (Rahman and



**Figure 4.** Stratigraphic sections from Purujosa with indication of the intervals visited in each stop. Modified from Zamora (2005) and Esteve (2011).



**Figure 5.** The Mansilla Formation and its echinoderm fauna. A. General aspect of the formation showing the typical griotte facies in which carbonate nodules intercalate with the reddish shales. B. The cinctan *Protocinctus mansillaensis* preserved in calcite. C. Isolated plate of a dibrachicystid blastozoan. D. The cinctan *Asturicystis* sp.



Zamora, 2009). The inclusion of this taxon into a cladistic analysis revealed its basal position within the sucocystid clade (Smith and Zamora, 2009), which is not unexpected if we consider the taxon as the oldest cinctan from Gondwana. Close to the Mansilla-Murero contact, Zamora (2009) reported *Asturicystis* sp. (Fig. 5D), a genus previously described in the Cantabrian Mountains and Czech Republic (Sdzuy, 1993; Fatka and Kordule, 2001). The presence of *Asturicystis* in Bohemia seems questionable based on the poor illustration and specimen morphology with ventral swellings in several plates and the length of food grooves. Moreover, those levels are rife of dibrachycystid isolated plates (Fig. 5C).

Based on trilobite content, those levels correspond with the regional *Eccaparadoxides asturianus* Zone, which is considered as late Leonian in age (Sdzuy *et al.*, 1999).

#### STOP 4: Echinoderms from the base of the middle Cambrian Murero Formation – The *Ctenoimbricata* quarry

##### Location

Follow the aforementioned path until it turns left 90°, and then abandon the path to the southeast slope of Matarranas hill arriving to a small ravine that comprises the top of the Mansilla Formation and most of the Murero Formation (Purujosa 6 section) (Figs. 3, 4).

Coordinates: 41°40' 11.70"N, 1°47' 16.91"W  
 Geological map of Spain, 1:50.000, sheet of Tabuena (352).  
 Geological setting: Badules Unit (eastern Iberian Chain).  
 Lithostratigraphic unit: Murero Formation.  
 Age: Caesarugustan (mid Cambrian).

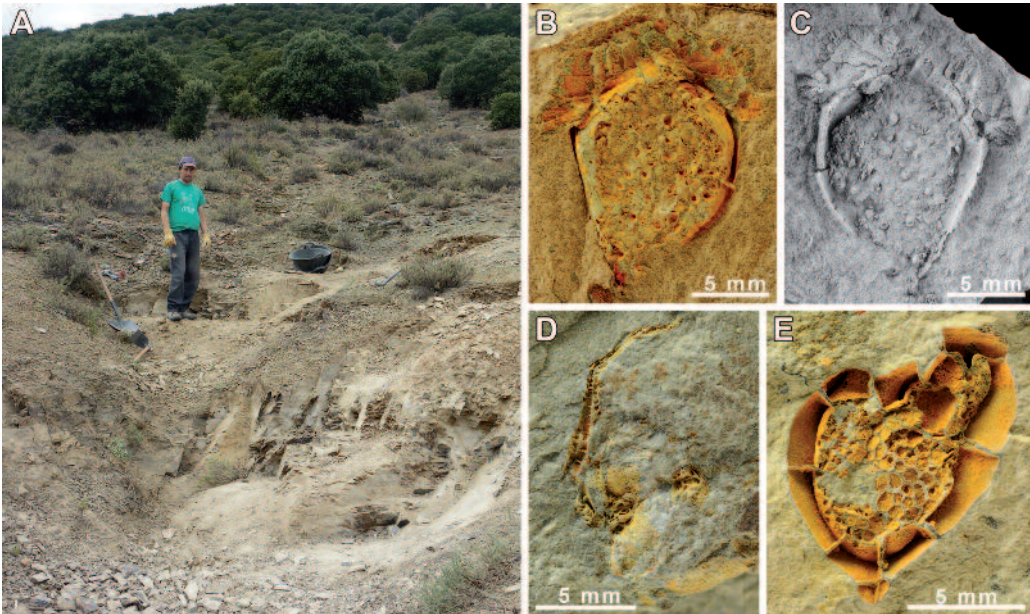
##### Aims

Look at a classic echinoderm assemblage with intermediate to high diversity from the Murero Formation consisting of cinctans, ctenocystoids, gogiids, dibrachycystids and stylophorans.

##### Description

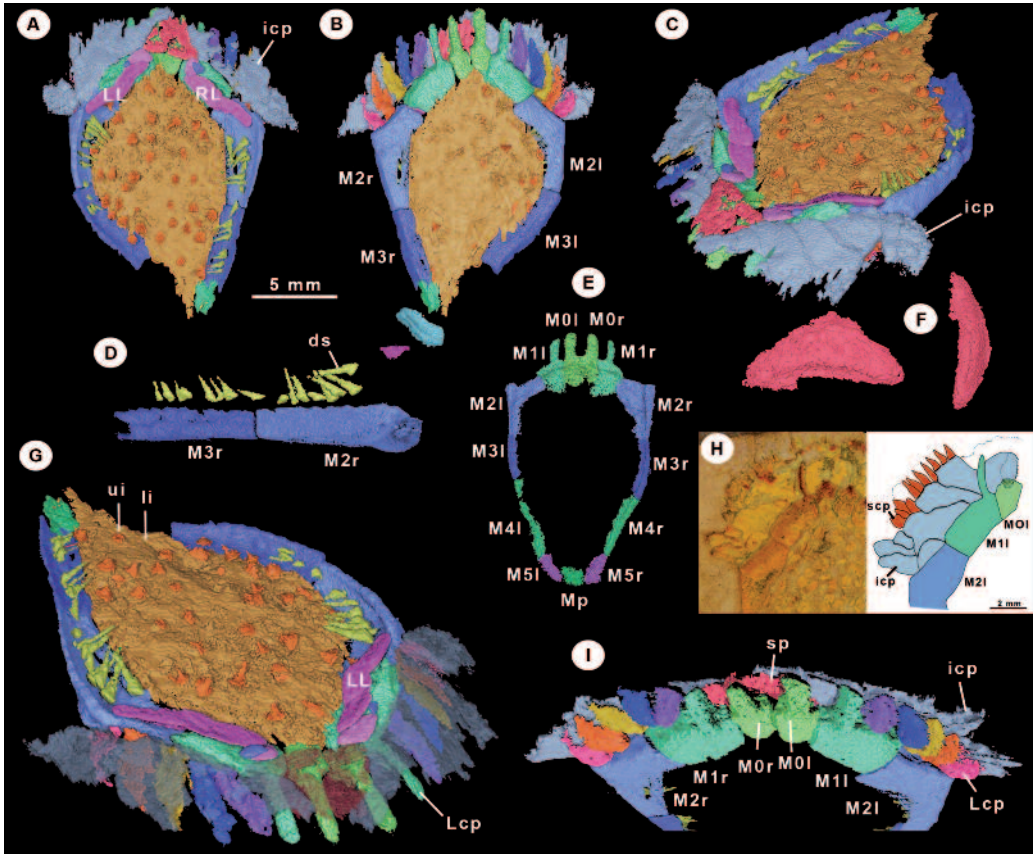
The *Ctenoimbricata* quarry (Fig. 6A) lies at the base of the Murero Formation in the Purujosa 6 section (Fig. 3, 4), which is mid Caesarugustan in age. The Murero Formation is a 80 meters thick shale succession with some carbonate nodules deposited during transgressive conditions in an offshore-dominated environment. The palaeogeographic position of Purujosa in the most distal part of the Iberian Platform (a part of the Cantabro-Iberian Basin) favoured preservation of multiple orobruption events in which articulated echinoderms and complete trilobites are common. The quarry has yielded two specimens of *Ctenoimbricata spinosa* (Fig. 6B, C, 7), one specimen belonging to the ctenocystoid *Courtessolea* (Fig. 8E, F), several specimens of *Ceratocystis* sp. (Fig. 6D), the eocrinoid *Gogia* sp., the cinctan *Graciacystis ambigua* (Fig. 6E) and isolated plates of dibrachycystids (Zamora, 2010, 2011; Zamora *et al.*, 2012, 2013a).

*Ctenoimbricata* (Fig. 7) is a very important fossil and requires further attention. It is a small (20 mm), disc-like animal with a clearly defined anterior–posterior axis and with skeletal elements arranged bilaterally and symmetrically along that axis. A uniserial marginal ring of stout plates frames the body, comprising four elements at the anterior forming part of the ctenidium, four on either side plus a single posterior element (plate Mp). Dorsal and ventral plated membranes cover the centre of the disc. At the anterior part, there is a wide opening framed by marginal plates and covered dorsally by a sheet of imbricate plates. This dorsal roof is formed by several superimposed series of thin, flat plates that imbricate posteriorly. A row of very small spinose plates forms the outermost dorsal row. The dorsal



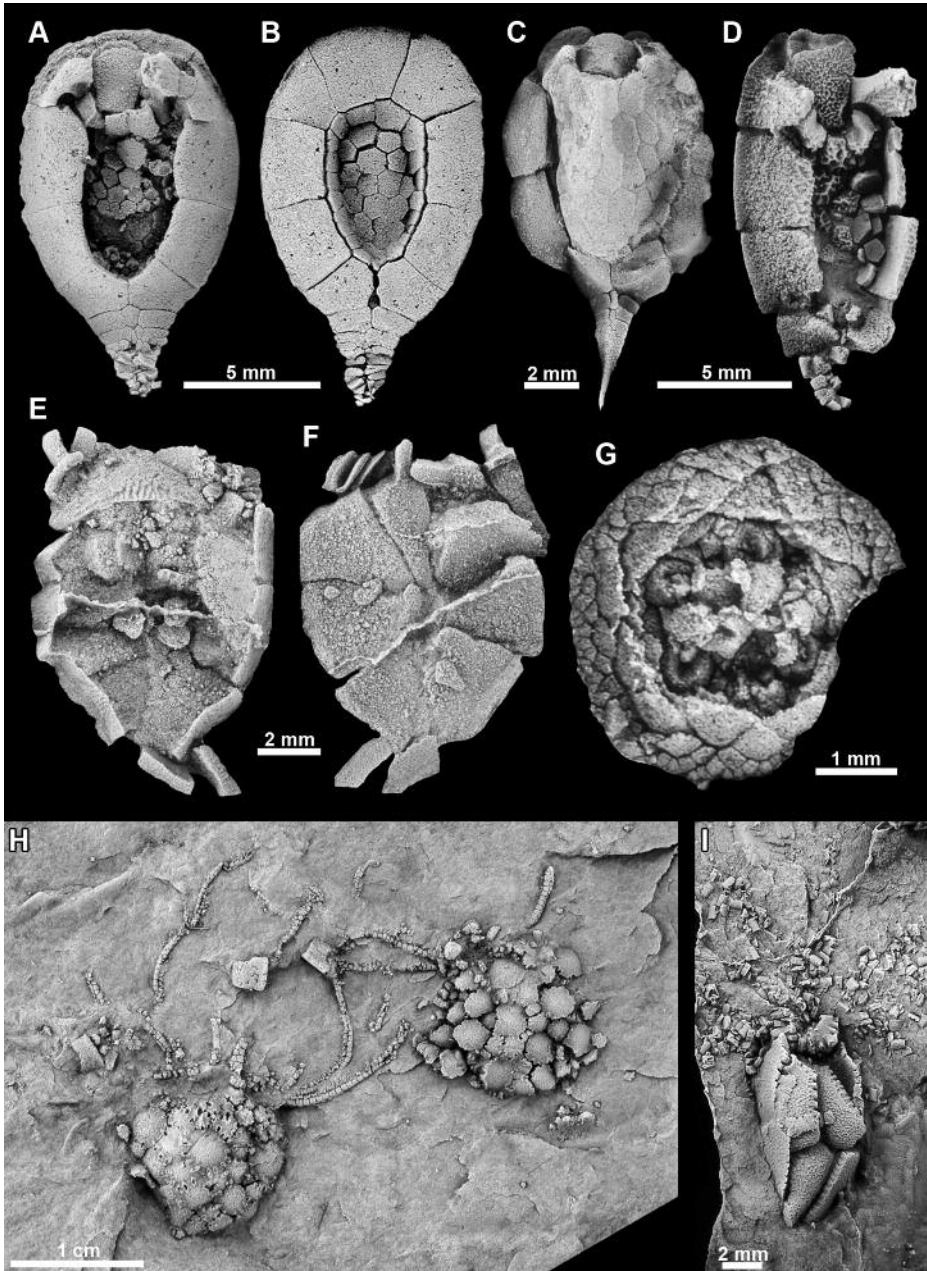
**Figure 6.** A. General view of the *Ctenoimbricata* quarry in levels from the base of the Murero Formation. B, C. *Ctenoimbricata spinosa* preserved as natural mould (B) and latex cast from the same specimen (C). D. The stylophoran *Ceratocystis* preserving a complete feeding appendage. E. The cinctan *Graciacystis ambigua*.

ctenidium formed a single unit with limited flexibility. Ventrally, the opening is lined anteriorly by 14 spinose elements. The four median ones are anterior extensions of marginal frame plates M0 and M1. The remaining 10 are free elements that articulated with the outer edge of marginal plates. Distally, these plates taper, becoming knife-like in outline, and overlap from posterior to anterior. The periproct is not seen but certainly does not pass through the marginal ring, as this is unbroken. It must therefore be situated in the dorsal membrane, and the only part of that structure missing from our specimen is the very posterior. By comparison with the closely related genus *Courtessolea*, the periproct should have opened in the posterior part of the dorsal membrane, close to plate Mp. *Ctenoimbricata* is an important taxon deciphering echinoderm basal relationships, and was interpreted as a basal echinoderm based on its bilateral morphology and absence of radially (Zamora *et al.*, 2012).



**Figure 7.** CT scan images of *Ctenoimricata spinosa*. Computer models (A–G, I) and photograph with interpretive camera lucida drawing (H). A, B. Dorsal and ventral views. C. Oblique left view. D. Lateral view of two marginal plates showing the articulation of the spines. E. Marginal frame plates after correction of plate orientations. F. Suroral plate in dorsal and lateral aspect. G. Oblique right view with the dorsal ctenidium partially transparent to show the ventral ctenidial plates. H. Left anterior part of the theca showing the arrangement of the dorsal ctenidial plates. I. Frontal view. Abbreviations: ds, dorsal spines; icp, imbricate ctenidial plates; Lcp, lower ctenidial plates; LL, adoral left plate; M, marginal plate; RL, adoral right plate; scp, spiny ctenidial plates; sp, suroral plate; ui, li, upper and lower integuments.





**Figure 8.** Echinoderm faunas from the Murero Formation at Purujosa. A, B. Dorsal and ventral view of the cinctan *Gyrocystis platessa*. C. Dorsal view of the cinctan *Gyrocystis testudiformis*. D. Dorsal view of the cinctan *Gyrocystis erecta*. E, F. Dorsal and ventral view of the ctenocystoid *Courtessolea* sp. G. Oral view of the isorophid edrioasteroid *Protorophus hispanicus*. H. Two specimens of the eocrinoid *Gogia parsleyi*. I. The eocrinoid *Lichenoides* sp. All photographs are from latex cast whitened with  $\text{NH}_4\text{Cl}$  sublimated.

## STOP 5: Cinctan ontogeny based on *Graciacystis*

### Location

Follow the previous ravine. New levels of the Murero Formation appear while ascending in the series up to the next small excavation (Fig. 3).

Coordinates: 41°40'11.77"N, 1°47'18.84"W  
 Geological map of Spain, 1:50.000, sheet of Tabuena (352).  
 Geological setting: Badules Unit (eastern Iberian Chain).  
 Lithostratigraphic unit: Murero Formation.  
 Age: Caesaraugustan (mid Cambrian).

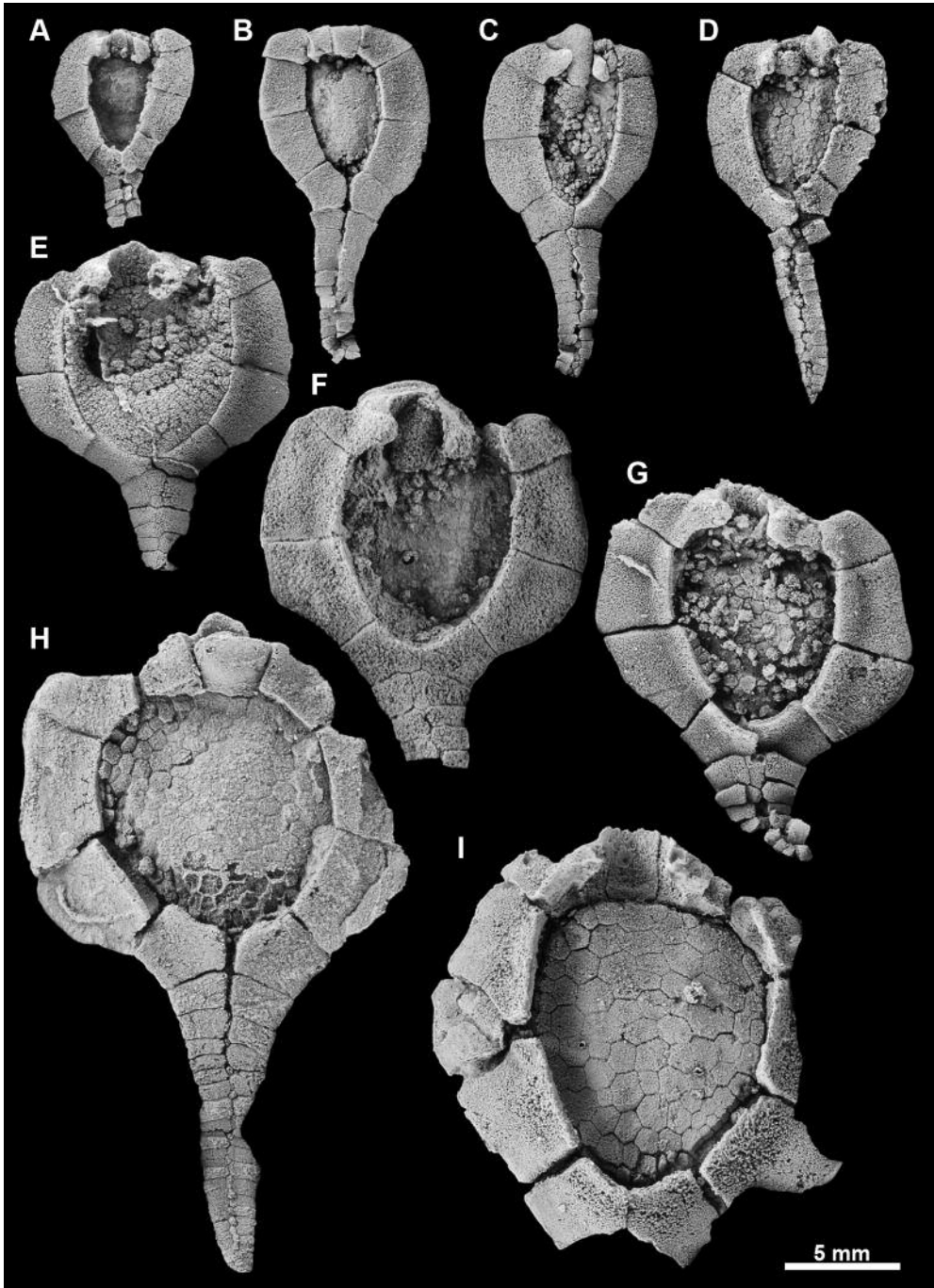
### Aims

Show a level dominated by cinctans from different ontogenetic stages that probably represent a single population. Discuss cinctan ontogeny base on the genus *Graciacystis*.

### Description

A second quarry ascending the Purujosa 6 section (Fig. 4) has provided a rich assemblage of cinctans. Although *Graciacystis ambigua* was originally collected between 5 and 25 m above the base of the Murero Formation, most of the specimens come from the visited quarry (25 m above the base of the Murero Formation) and appear associated with a single specimen of *Vizcainoia moncaiensis* and the trilobites *Badulesia tenera*, *Pardailhania hispida*, *Pardailhania multispinosa*, *Eccaparadoxides sequeirosi*, *Parabaillella languedocensis*, *Ctenocephalus antiquus* and *Peronopsis acadica* (Zamora and Smith, 2012; Zamora *et al.*, 2013a). The associated trilobite assemblages indicate its belonging to the *Pardailhania multispinosa* Zone, which is indicative of a mid Caesaraugustan age.

Zamora *et al.* (2013a) provided the complete ontogeny of the genus *Graciacystis* (Fig. 9), based on specimens ranging from 6.4 to 14.5 mm in thecal length. The thecal shape is very variable, with the central body cavity ranging from elongate and narrow to broad and shield-shaped. The shape is predominantly elongated in juveniles and shield-shaped in adults. Although the shape of the theca is rather variable, the construction of the theca is highly conserved through later ontogeny. The number of plates in the cinctus is very consistent; all known specimens have 10 marginal plates with the exception of one which displays an extra-plate in the left side. This suggests that plate number was established at a very early stage in development and did not vary during growth. The length and number of plates forming the stele is also very similar throughout growth. Plates were likely added to the stele through intercalation rather than at the distal end. The number of plates forming the ventral membrane remains more or less constant through growth. Ontogenic addition of plates was done by intercalation. The relative length of food grooves remained constant throughout the ontogeny, with the left food groove always extending to M11 and the right food groove to M2r. This is one of the most conservative characters in cinctans and thus taxonomically very important, as has been suggested in many previous studies (Ubaghs, 1968; Friedrich, 1993; Smith and Zamora, 2009). One significant change that does occur during ontogeny is the development of a ventral swelling on the anterior cinctus plates. Juveniles with a thecal length of 6 mm lack a ventral swelling (Fig. 9B), whereas it is always present in adults (Fig. 9H). It first appears in individuals about 12 mm in size and becomes progressively more prominent in larger individuals. Based on the data presented above, the cinctans seem to have been very conservative in their growth patterns. Growth was largely achieved through the enlargement of the plates that were formed early in ontogeny rather than by the addition of new plates, at least for the cinctus and stele. Plate addition appears to be more prevalent in the ventral and possibly dorsal integuments although plate growth remains predominant. Although the ontogenetic series of *Graciacystis ambigua* shows the growth for just one species of cinctans, the fundamentally similar construction of other species points that all followed a similar growth strategy.



**Figure 9.** Ontogenetic series of the cinctan *Graciacystis ambigua*. A, C-G, I are dorsal views and B, H are ventral views. All photographs are from latex cast whitened with  $\text{NH}_4\text{Cl}$  sublimated.

## STOP 6: Red beds from the upper part of the middle Cambrian Murero Formation – a 'hot spot' of enrolled trilobites and echinoderms

### Location

Ascend the previous aforementioned ravine until we reach the main path, and then turn left until the path crosses the red beds forming the top of the Murero Formation. Then abandon the main path to the south reaching a big quarry in which red beds have been excavated (Fig. 3).

Coordinates: 41°40'7.37"N, 1°47'23.79"W  
 Geological map of Spain, 1:50.000, sheet Tabuena (352).  
 Geological setting: Badules Unit (eastern Iberian Chain).  
 Lithostratigraphic unit: Murero Formation.  
 Age: Languedocian (mid Cambrian).

### Aims

Look at one of the most important Cambrian assemblages from Spain consisting in highly diversified echinoderms and abundant trilobites. Discuss the peak in Cambrian echinoderm diversity from Gondwana based on a single outcrop with highly diversified echinoderms comprising eight different taxa.

### Description

The red beds that appear in the upper part of the Murero Formation in the study area (Fig. 10) have been excavated through more than eight years for detailed taphonomic and taxonomic studies (Fig. 10D, E). They include a thin layer (< 1m thick) of weakly bioturbated shale (ichnofabric index 1–2 of Droser and Bottjer, 1986) that stands out from adjacent beds by an abrupt change in colour: beds immediately overlying and underlying the layer are green-grey. The associated fauna includes echinoderms (the edrioasteroid *Protorophus hispanicus* (Fig. 8G), the cinctan *Gyrocystis platessa*, the stylophorans *Ceratocystis* sp. (Fig. 11B), plus two different undescribed cothurnocystids, and the blastozoans *Gogia gondi*, *Lichenoides* sp. (Fig. 8I) and *Dibrachicystis purujoensis* (Fig. 11A), polymerid trilobites (*Eccaparadoxides pradoanus* Fig. 11E, H, I, *Conocoryphe heberti*, *Solenopleuropsis (Manublesia) thorali* (Fig. 11J), *S. (M.) riberoi* (= *S. (M.) marginata*), *S. (M.) verdiagana*, *Schopfaspis? graciai* (Fig. 11C), agnostoids (*Condylopyge* sp., *Peronopsis acadica*, *P. ferox*, *Pleurocterium* sp., and *Megagnostus* sp. Fig. 11D), and both orthid (Fig. 11F) and lingulid brachiopods (Fig. 11G) (Zamora, 2009, 2010; Esteve, 2011; Esteve *et al.* 2011; Mergl and Zamora, 2012). The FAD of the trilobite *Solenopleuropsis (M.) thorali* marks the base of the regional Languedocian Stage (*sensu* Álvaro and Vizcaïno, 1998).

These beds are unusual in two aspects: (i) their high diversity patterns of echinoderms by comparison with coeval occurrences; and (ii) the large number of trilobites preserved in enrolled position and comprising different taxa.

The assemblage of enrolled trilobites was described by Esteve *et al.* (2011) and occurs throughout the bed. The trilobite fossils recovered at Purujosa are likewise notably diverse, but the bed is even more important as the world's oldest assemblage containing abundant enrolled trilobites (Esteve *et al.*, 2011). Until the discovery of the Purujosa assemblage enrolment was considered rare among Cambrian trilobites, a notion supported by the fact that it was structurally impossible for some early forms (Whittington, 1990), even some enrolment styles (e.g. sphaeroidal or discoidal) were unable to fulfill by Cambrian trilobites. Purujosa shows that, a wide variety of trilobite body plans common in the Cambrian could enrol, prompting a fundamental reevaluation of the evolution of trilobite enrolment (Esteve *et al.*, 2011). The abundance of these enrolled trilobites at Purujosa allowed Esteve *et al.* (2011) to assess modes of enrolment among these early trilobites. It is noteworthy that each of the classical enrolment types (i.e. spiral enrolment and sphaeroidal and subtypes; see Esteve, 2013 for more details) are represented in the Purujosa assemblage. Furthermore, two or more of these enrolment types are represented within the genera *Solenopleuropsis* and *Conocoryphe*. The importance of this result is twofold. First, it demonstrates that several modes of enrolment were



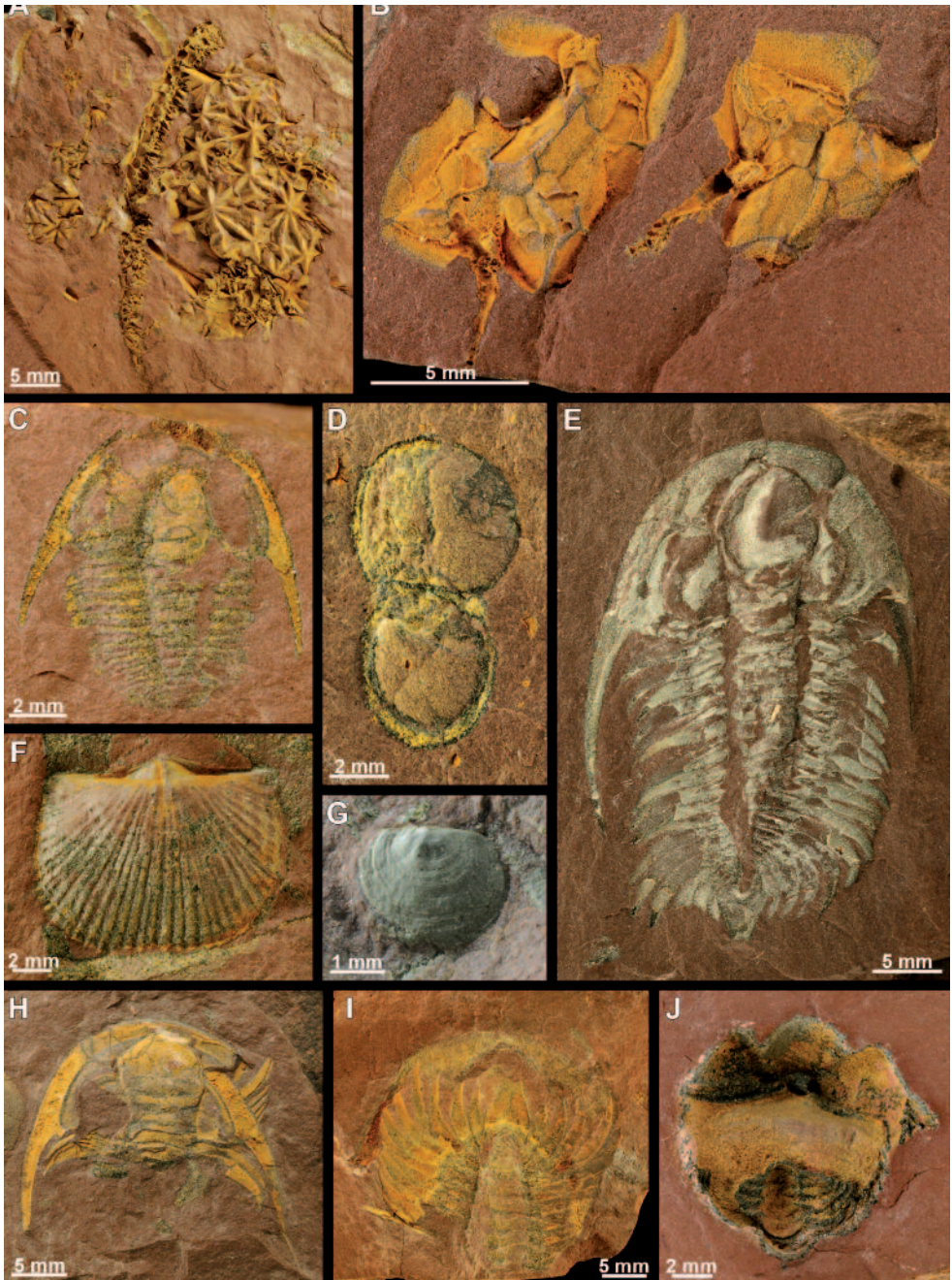


**Figure 10.** Red beds from the upper part of the Murero Formation excavated in a relatively big quarry (A, B) for both taxonomic and taphonomic purposes (D, E). Trilobites are very abundant, specially the paradoxidid *Eccaparadoxides pradoanus* (C).

available to contemporaneous individuals belonging to the same Cambrian genera. Second, it is noticeable that closely related individuals, sometimes even belonging to the same species (e.g., *Solenopleuropsis (M.) thoralis*), may differ in manner of enrolment. On the other hand, this assemblage shows the importance of enrolment for the evolution of the post cephalic segmentation in trilobites since enrolment plays an important role of selective pressure favouring the caudalization process, which is the allocation of an increased proportion of the post cephalic segments to the holaspid pygidium (Esteve *et al.* 2013).

Echinoderms are here more diverse than in any other Cambrian deposits with the exception of a recently discovered level in Morocco (Smith *et al.*, 2013b) that still is in need of further reevaluation. From the total sampling (150 complete specimens), only one specimen is a 3 mm-long isorophid edrioasteroid that corresponds to the oldest record of this group (Zamora and Smith, 2010). There are also two specimens of cothurnocystids belonging to two different species that represent the oldest record of such a clade in Gondwana (Zamora, 2009, 2010, 2011). Other echinoderms, such as cinctans, armoured stylophorans and blastozoans are more abundant. This informs about how rare some groups were in the Cambrian and the type of methodology needed to collect those groups. The presence of eight different taxa in the same bed indicates that niche partitioning was already established by mid Cambrian times. In fact, these species are very different in their mode of feeding and attachment as revealed by their different morphology.





**Figure 11.** Fossils collected from the red beds of the Murero Formation. A. The blastozoan *Dibrachicystis purujoensis*. B. the stylophoran *Ceraticystis* sp. C. The trilobite *Schofaspis? graciai*. D. The agnostoid *Megagnostus* sp. E. The trilobite *Eccaparadoxides pradoanus*. F. The rhynchonelliformean brachiopod *Brahimorthis alvaroi*. G. lingulid brachiopod *Micromitra* sp. H, I. Enrolled specimens

**STOP 7: Trilobites and echinoderms from the middle Cambrian Borobia Formation****Location**

Following the main path to the west for almost one kilometer until it turns right. The Borobia Formation is well exposed on both sides of the path (Fig. 3).

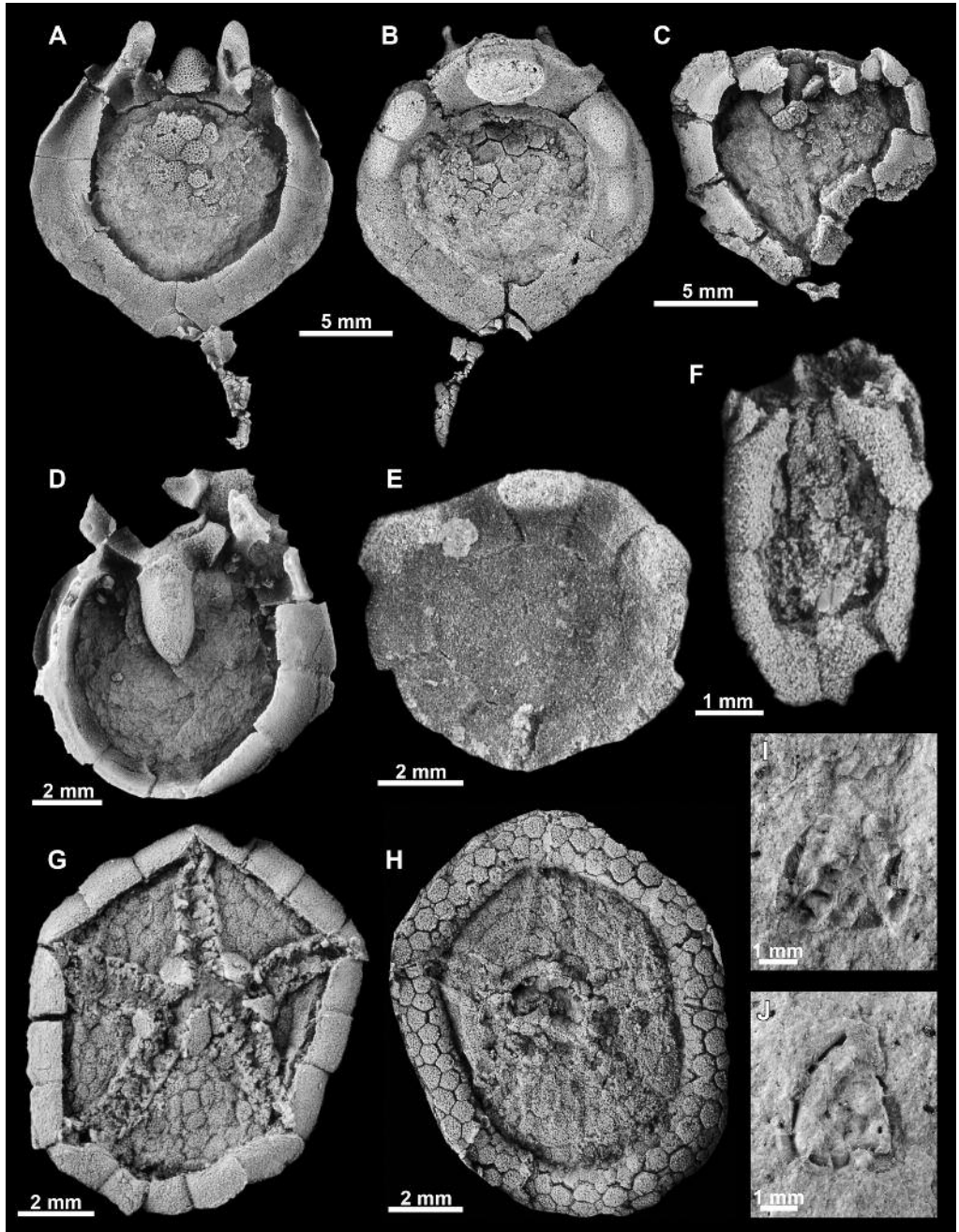
Coordinates: 41°39' 59.09"N, 1°47'43.99"W  
Geological map of Spain, 1:50.000, sheet of Tabuena (352).  
Geological setting: Badules Unit (eastern Iberian Chain).  
Lithostratigraphic unit: Borobia Formation.  
Age: Languedocian (mid Cambrian).

**Aims**

Look at the echinoderm faunas from the Borobia Formation. Based on taphonomic and sedimentologic features, they are interpreted as living in more energetic substrates than those of the Murero Formation.

**Description**

In the study area, the Borobia Formation comprises up to 350 m of interbedded shale and sandstone, in which fossils are restricted to certain shaly horizons. The alternations are arranged in shallowing- and coarsening-upward cycles, less than 2.8 m thick, ranging from offshore to shoreface (shoal) intervals. The Borobia Formation has been studied in Purujosa and coeval localities, such as Jarque, Torrijo de la Cañaba, Borobia and Villalengua (see Zamora and Álvaro, 2010; Zamora *et al.* 2013b) and has revealed a rich assemblage of echinoderms that varies in composition depending on the locality. In Purujosa, three levels from the lower part of the formation have provided complete echinoderms, not yet described. In this stop, we will visit the intermediate level (Fig. 4) that has provided only the cinctan *Elliptocinctus barrandei* (Fig. 12A, B). The upper level is more diverse and has provided isolated stylophoran plates, indeterminated cinctans, the edrioasteroid *Cambraster* sp., and the ctenocystoid *Etoctenocystis* (Fig. 12F). In contrast, other localities of the Iberian Chains have been more investigated and have reported several species of cinctans, including *Lignanicystis* sp. (Fig. 12C), *Sucocystis theroensis* (Fig. 12D, E), the edrioasteroid *Cambraster cannati* (Fig. 12G, H), the eocrinoid *Gogia gondi*, and the stylophorans *Ceratocystis* sp. and *Cothurnocystid* indet (Fig. 12I, J).



**Figure 12.** Echinoderms collected in the Borobia Formation at Purujosa (A, B, F) and coeval localities like Jarque (C), Torrijo de la Cañada (D, E, I, J) and Villalengua (G, H). A, B. The cinctan *Elliptocinctus barrandei*. C. the cinctan *Lignanicystis* sp. D, E. The cinctan *Sucocystis theroensis*. F. The ctenocystoid *Etectenocystis*. G, H. The edrioasteroid *Cambraster cannati*. I, J. An indeterminate cothurnocystid stylophoran. All photographs are from latex cast whitened with  $\text{NH}_4\text{Cl}$  sublimated with the exception of I and J.



**STOP 8: *Gyrocystis platessa*-*Gogia parsleyi* level (Murero Formation, middle Cambrian)****Location**

Ascending la Borraca creek abandoning the main path, the Purujosa 4 section shows the top of the Mansilla Formation and the entire Murero Formation (Fig. 4). The top of the Murero Formation is exposed just at the intersection of la Borraca creek with a small ravine. The *Gyrocystis platessa*-*Gogia parsleyi* level appears just 1 m below the red beds at the top of the Murero Formation (Fig. 3).

Coordinates: 41°40'19.41"N, 1°47'34.64"W

Geological map of Spain, 1:50.000, sheet of Tabuena (352).

Geological setting: Badules Unit (eastern Iberian Chain).

Lithostratigraphic unit: Murero Formation.

Age: Caesaraugustan (mid Cambrian).

**Aims**

Discuss an example of a typical eocrinoid-cinctan assemblage in which specimens are very abundant. Look at different states of preservation within a single bed.

**Description**

The *Gyrocystis platessa*-*Gogia parsleyi* level only occurs in this part of the section and corresponds to a thin (50 cm) bed of green-grey claystones with common complete echinoderms. There is a unique example of complete and very abundant echinoderms and lack of almost any other fossil, with the exception of trilobite fragments. One day sampling can provide approximately twenty complete specimens which is very unusual for a Cambrian locality. From those, the cinctan *Gyrocystis platessa* (Fig. 8A, B) and the eocrinoid *Gogia parsleyi* (Fig. 8H) are the most abundant. We have found a single specimen of an indeterminate isorophid edrioasteroid and isolated plates belonging to *Ceratocystis* sp. (Zamora *et al.*, 2009; Zamora and Smith, 2010). Both eocrinoids and cinctans appear in different ontogenetic stages and are well preserved. This bed probably corresponds to a classic orobruption event that preserved complete echinoderms belonging to contemporaneous populations. *Gyrocystis platessa* also occurs in the red beds that appear overlaying the *Gyrocystis platessa*-*Gogia parsleyi* level, but just 3-5 m above another level that has yielded the cinctan *Gyrocystis erecta* (Fig. 8D). Echinoderms are absent from the rest of the formation until they appear again at the base of the Borobia Formation, coinciding with another transgressive pulse.

## DAY 2: June 18th 2015

## ORDOVICIAN TO DEVONIAN ECHINODERM FAUNAS FROM THE IBERIAN CHAINS

Jorge Colmenar, Enrique Villas, Juan Carlos Gutiérrez-Marco and Samuel Zamora

## INTRODUCTION

A complete Ordovician to Devonian succession crops out in the vicinity of Fombuena, Luesma and Santa Cruz de Nogueras (Fig. 13), in the eastern Iberian Chain. The Ordovician is nearly 4000 m thick, composed primarily of siliciclastic rocks, with the only exception of 40 m of upper Katian limestones, and up to 8 m of upper Sandbian bryozoan marlstones (Fig. 14). The thicknesses of the different Ordovician stages change greatly, with the Tremadocian to Dapingian being more than 3.000 m thick, and the Darriwillian to Hirnantian less than 500 m thick. Lotze (1929) described the stratigraphy with refinements by Carls (1975), Wolf (1980), Villas (1983) and Hammann (1992). Modern

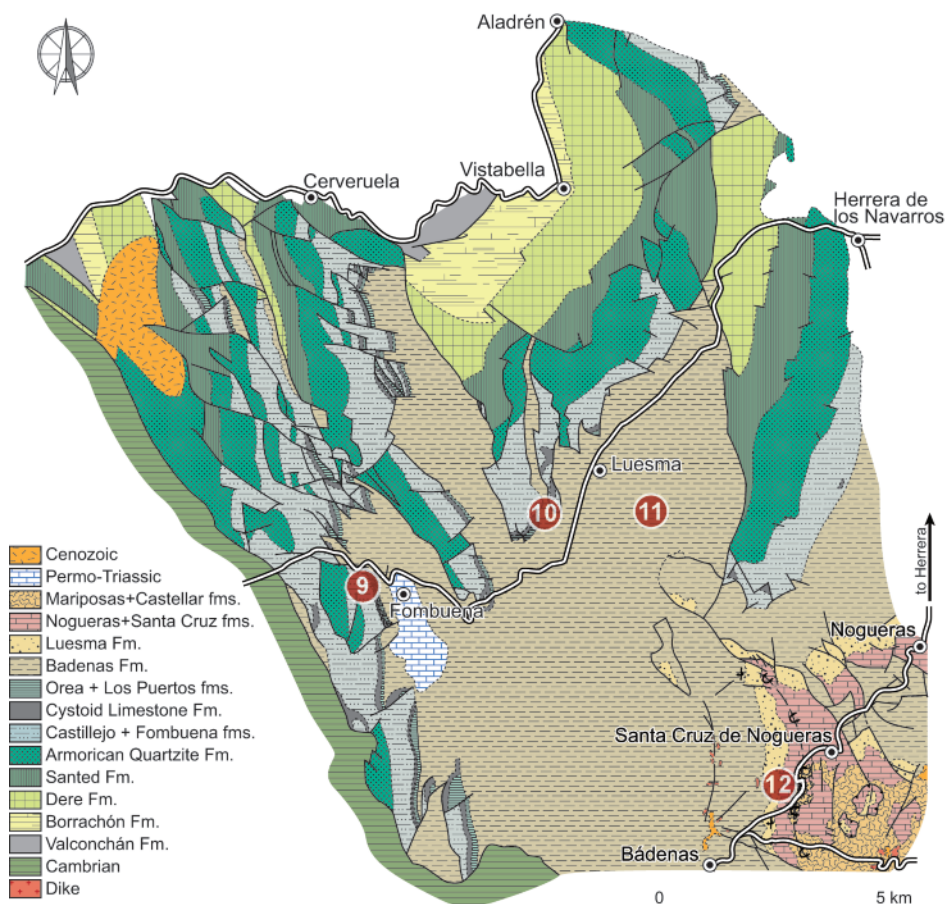
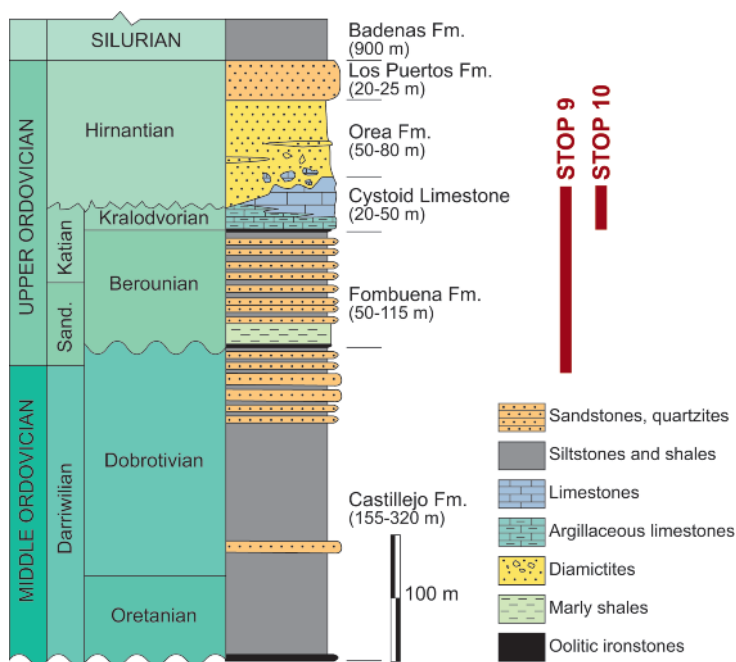


Figure 13. Geological map of the surroundings of Luesma with indication of stops. Modified from Hammann (1992).



**Figure 14.** Schematic stratigraphic column of the Ordovician (pars.) of the Eastern Iberian Chain, with the correlation between the Ordovician Global Series and Stages and the Ordovician Mediterranean Stages. Note the stratigraphic position of different stops.

stratigraphic reviews have also been made by Sarmiento (2002) and Gutiérrez-Marco *et al.* (2002, 2005). Liñán *et al.* (1996) contained a thorough palaeontological synthesis of the Ordovician of the Iberian Cordillera.

The thick Lower and lower Middle Ordovician succession has been divided into four formations, two of them mainly silty and shaly, the Borrachón and Santed formations, and the other two mainly quartzitic, the Dere and Armorican Quartzite formations. Although the quartzitic formations display a rich ichnofossil record, shelly fossil occurrences are sparse in the four units. As a result, the position of the Cambrian-Ordovician boundary remains controversial. It was considered to lie within the thickly bedded quartzites with shaly intercalations of the Valconchán Formation, just below the Borrachón Formation (Havlíček and Josopait, 1972; Wolf, 1980). More recently the Cambrian-Ordovician boundary has been changed to the middle-upper part of the Borrachón Formation, based on the occurrence in its basal part of trilobite assemblages close to late Furongian ones from Mexico and the Central Andean Cordillera (Shergold and Sdzuy, 1991; Gutiérrez-Marco *et al.*, 2002). The Armorican Quartzite is the local representative of the typical Armorican sandy facies that characterizes the Floian and earliest Dapingian in a great part of Iberia and Armorica. Its original name, given by Dereims (1898), was maintained by Wolf (1980) when defined formally the formation.

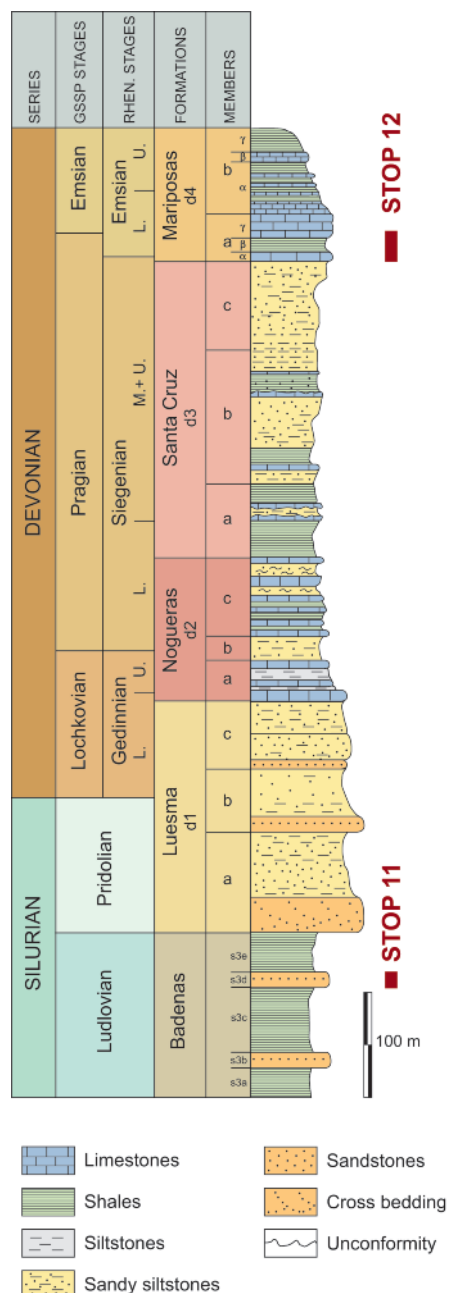
An oolitic ironstone, overlying the Armorican Quartzite, marks the base of the sandy and shaly Castillojo Formation (Fig. 14), the local representative of the "Neseuretus shales and sandstones", widespread throughout Iberia (Hammann *et al.*, 1982). The Castillojo Formation can be correlated with most of the Darrivillan, although it probably overlies a stratigraphical gap corresponding to the lower Oretanian regional stage (equivalent to the British lower Abereiddian), since the lowest graptolites found in the formation belongs to the *D. murchisoni* Zone (Gutiérrez-Marco, 1986). Trilobites (Hammann, 1983) and brachiopods (Villas, 1985) are relatively abundant in its upper part, of Dobrotivian (latest Darrivillan to basal Sandbian) age.

The Upper Ordovician is represented in the region by the upper Sandbian to middle Katian (Sa2-Ka2; "Caradoc-Ashgill") alternating siltstones and sandstones of the Fombuena Formation (Fig. 14) overlain by the upper Katian (Ka3-Ka4) Cystoid Limestone Formation, the Hirnantian diamicrites of the Orea Formation and the quartzites of the Los Puertos Formation, the latter mainly of Hirnantian age. These units are well exposed in the localities we will visit in this first excursion day, and their most outstanding features are introduced below.

The Silurian succession (Fig. 15) probably begins near the top of the Los Puertos Formation, which in the Hesperian Chains bears some shaly intercalations with Rhuddanian and Aeronian graptolites (Gutiérrez-Marco and Štorch, 1998). This quartzite is followed by the Bádenas Formation, a thick (900-1400 m) sequence of black shales with nodules and sandstone intercalations, especially abundant in the upper part. The massive black shales have yielded sparse graptolite horizons indicating that the formation spans from the basal Telychian *Rastrites linnaei* Zone up into the basal Ludfordian *Saetograptus leintwardinensis* Biozone (Wehner, 1984). The black shales and nodules also contain brachiopods, bivalves, cephalopods, eurypterids, phyllocarids, tentaculitids, trilobites and conodonts. Thin sandstone beds of the upper part of the formation yield shallow water brachiopods, echinoderms, molluscs, conodonts and trilobites (Carls, 1974; Gandl, 1972; Sarmiento *et al.*, 1998; Le Menn *et al.*, 2003). The Bádenas Formation is overlain by the Luesma Formation, a sandstone unit about 200 m thick that towards its upper part has provided successive assemblages of Pridolian brachiopods and Lochkovian conodonts and brachiopods (Carls, 1977).

The complete Devonian thickness is about 4000 m (Fig. 15), 95% of which is composed of siliciclastic rocks, but due to a complicated tectonics a complete Devonian section is lacking. Carls (1965) was a pioneer in describing the Devonian strata in detail, mapping the areas and providing information on biostratigraphy. German and Spanish disciples of Carls have been working in the area from the last half century and demonstrated the worldwide importance of Devonian strata around the axial depression of the Cámaras River. There the best sequence of Rhenish faunas is known from the early Devonian (Carls and Valenzuela Ríos, 2002).

The field excursion allows us to visit several echinoderm communities from the Upper Ordovician, Silurian and Devonian outcrops (Fig. 13). Upper Ordovician echinoderms are the most diverse and a complete stratigraphic section displaying the Castillejo, Fombuena and Cystoid Limestone formations will allow us to analyze the replacement of echinoderm communities related with the type of substrate and the Boda Event (Fig. 13, stop 9). Correlated beds at La Rebosilla (Fig. 13, stop 10) will show a different type of preservation of echinoderms from more proximal facies of the Cystoid Limestone. This will be completed with a visit to the Silurian Bádenas Formation in which the crinoid *Dimerocrinites argonensis* is very abundant and



**Figure 15.** Stratigraphic column of the Silurian and Lower Devonian in the Eastern Iberian Chain (Spain). Note the position of the stops. Modified from Carls (1987). Abbreviations: L: Lower, M: Middle, U: Upper.

appears associated with rare ophiuroids (Fig. 13, stop 11). At the end of the excursion we will be visiting the Mariposas Formation (early Devonian) in the vicinity of Santa Cruz de Noguerras (Fig. 13, stop 12) that show a really nice section in which only crinoids have been found.

## STOP 9: Late Ordovician Echinoderms from La Peña del Tormo section

### Location

The section crops out in a road cut of the A-1506 road in its passage through the Peña del Tormo stream (Figs. 13, 16).

Coordinates: 41°8'53"N, 1°12'16"W

Geological map of Spain, 1:50,000, sheet of Daroca (465).

Geological setting: Badules Unit (eastern Iberian Chain).

Lithostratigraphical units: Castillejo, Fombuena and Cystoid Limestone formations (Fig. 14).

Age: Sandbian-latest Katian (Late Ordovician).

### Aims

Show general aspects of the Upper Ordovician succession in the Iberian Chains. Discuss a typical example of benthic echinoderm community replacement related with changes of substrate. Discuss the effect of the global warming Boda event to the echinoderms.

### Description

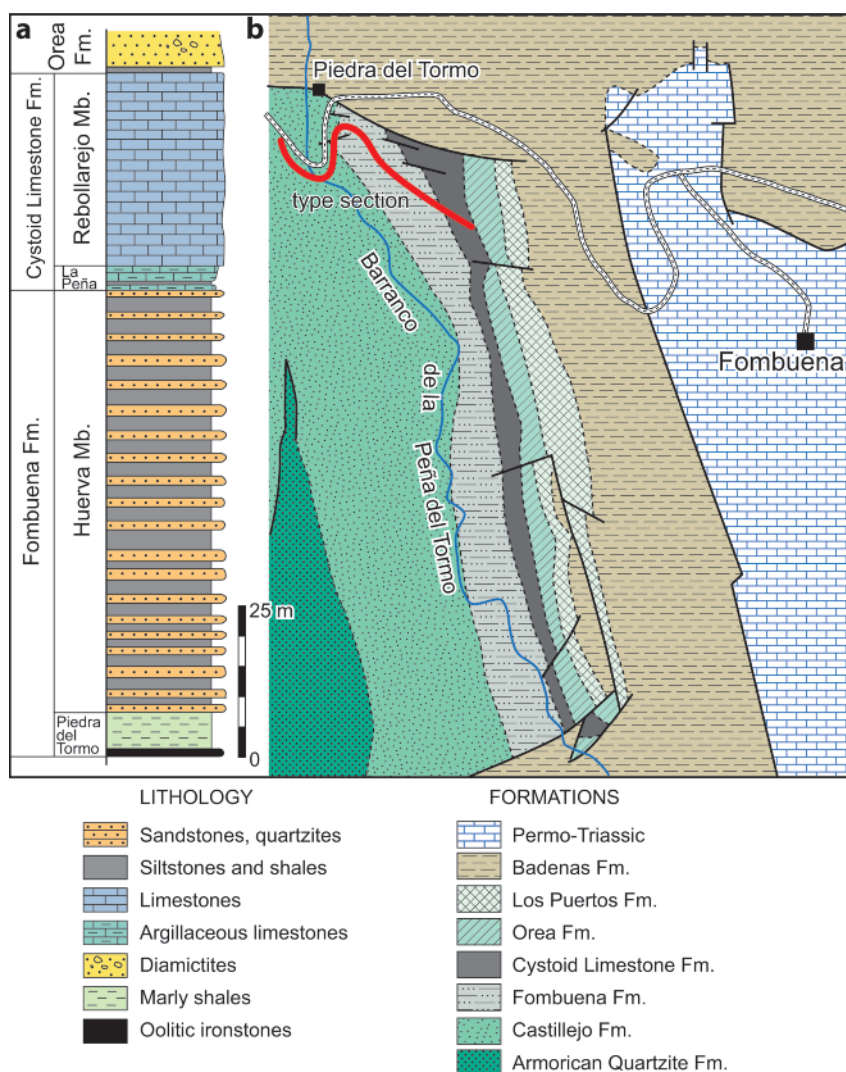
In this section there is an almost continuous exposure from the top of the Castillejo Formation, Darriwilian in age, to the base of the Bádenas Formation, lower Silurian. The outstanding Peña del Tormo (Tor Rock), a faulted white quartzite block of the Los Puertos Formation, gives name to the stream where the section begins. The locality is about 1 km west of the small village of Fombuena ("good fountain" in old Spanish), built on Triassic rocks. The section starts in the eastern bank of the road Bádules-Fombuena where the boundary between the Castillejo and Fombuena formations is well exposed.

### The Castillejo Formation

The Castillejo Formation paraconformably overlies the Armorican Quartzite and contains three members. The basal Marité Member displays a variable thickness, from one meter in its type section up to 40 meters in the Marité Mine (Carls, 1975). It is composed of ferruginous shales that locally comprise up to three oolitic ironstone beds. Several authors (Kolb, 1978; Wolf, 1980; Gutiérrez-Marco, 1986) indicate the presence of graptolites belonging to the *Didymograptus muchisoni* Zone (late Oretanian).

The middle Alpartir Member (110-200 m thick) is composed mainly of shales with some intercalations of sandstones and siliceous and ferruginous nodules. Last graptolites of the *D. muchisoni* Zone have been found 25-30 m above the base of the member (Gutiérrez-Marco, 1986). In equivalent levels, Kolb (1978) reported *Neseuretus tristani*, *Placoparia "cambriensis" (P. tournemini)* and *Redonia* sp. In the upper part of this member, the graptolites *Gymnograptus linnarssoni* and *Hustedograptus teretiusculus* have been found (Hammann *et al.*, 1982; Gutiérrez-Marco, 1986) as well as the trilobites *Placoparia tournemini*, *Neseuretus tristani*, *Eodalmanitina macroptalma*, *Colpocoryphe rouaulti* and *Salterocoryphe salteri*, the molluscs *Sinuities hispanica* and *Redonia deshayesi* (Hammann *et al.*, 1982), and the brachiopods *Heterorthis morgatensis*, *Aegiromena mariana* and *Crozonorthis muscolosa*; an assemblage of early Dobrotivian (late Darriwilian) age.

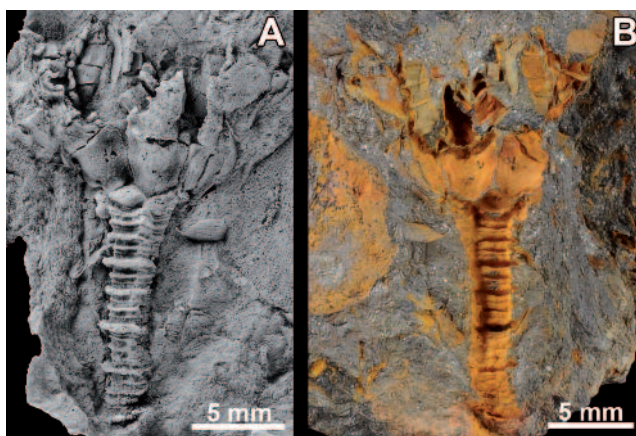




**Figure 16.** Geological map and lithological column of the Peña del Tormo locality. Modified from Hammann (1992). Itinerary marked with a red line.

The upper Sierra Member displays a variable thickness decreasing towards the northwest from 150 to 10 m (Villas, 1983). It is characterized by alternating shales and sandstones and frequently by highly fossiliferous sandstone lenses with calcareous cement. Hammann *et al.* (1982) cited the trilobites *Neseuretus henkei*, *Crozonaspis incerta*, *Crozonaspis armata*, *Phacopidina micheli* and *Eohomalonotus szuyi* as well as gastropods, bivalves and rostroconchs. The brachiopod content is very similar to that of the underlying member, except for the replacement of *H. morgatensis* by *H. kerfornei*. Sarmiento *et al.* (1995) also reported some conodonts (*Distomodus? tamarae*, *Icriodella aff. praecox*, *Drepanoistodus* and *Amorphognathus?*), occurring in a single coquinoïd bed probably of late Dobrotivian age (latest Darrivilian to earliest Sandbian).

Echinoderms from the Castillejo Formation are rare. Carls (1975) was the first to report echinoderms from this formation. These were later assigned to *Calix* sp. by Kolb (1978). Gutiérrez-Marco (pers. obs. see Gutiérrez-Marco *et al.*, 1996a) revised the original collection made by Carls and considered those specimens as *Calix rouaulti*. Gutiérrez-Marco *et al.* (1996a) confirmed the presence of *Calix rouaulti* in those levels and also reported fragments of Aristocystitidae gen. et sp. indet. From the Castillejo Formation a complete specimen of the crinoid *Heviacrinus* sp. (Fig. 17) has also been collected.



**Figure 17.** The crinoid *Heviacrinus* sp. from the Castillejo Formation. A. latex cast whitened with  $\text{NH}_4\text{Cl}$ . B. Natural mould coated with iron oxides.

### The Fombuena Formation

The Fombuena Formation is divided in two members (Fig. 16). The lower Piedra del Tormo Member overlies the alternating sandstones and siltstones of the Castillejo Formation. It has a one meter thick ooidal ironstones in its base which can be easily correlatable with a similar ooidal ferruginous horizons throughout SW Europe and North Africa. The ironstone is overlain by 8 meters of marly shales and marlstones, rich in bryozoans and some brachiopods, gastropods, benthic graptolites and echinoderms (Fig. 18A). The ironstone is always present at the base of the formation throughout the eastern Iberian Chain, but the bryozoan marls are restricted to the vicinity of Fombuena. In the northeastern margin of the chain, the basal ironstone is already overlain by the alternating sandstones and shales that characterize the rest of the formation. Brachiopod associations throughout the formation are of low diversity, and composed with up to 5-6 taxa. Some of the brachiopods recorded in the ironstone and the overlying marls, as *Aegiromena aquila intermedia*, *Gelidorthis meloui*, *Jezerzia chrustenicensis*, *Reuschella herreraensis*, *Rostricellula ambigena* and *Svobodaina armoricana*, allow correlating the base of the formation with distant units in Iberia, such as the ferruginous horizon at the lower part of the "Cantera Shales" (Corral de Calatrava, Central Spain) or the Favaçal Bed at the base of the Louredo Formation (Buçaco, Portugal). They also allow a correlation with the chloritic ooidal ironstone occurring about 100 m above the base of the Vieille-Cour Formation in Normandy and with the Zdice-Nucice iron ore horizon at the base of the Vinice Formation (middle Berounian) in Bohemia (see Villas, 1992). Some elements from this brachiopod assemblage have also been recently identified in the upper part of the Lower Ktaoua Formation in the Moroccan Anti-Atlas, and a correlation with the former unit has been suggested (Villas *et al.*, 2006). All of them can be also correlated with the Longvillian (upper Burrellian stage of the British Caradoc) based by the chitinozoans found in the Portuguese and Armorican units (Paris, 1979, 1981). In terms of the global scale, a late Sandbian to earliest Katian (Sa2-Ka1) age is assigned to the middle part of the Berounian regional stage.

The basal Piedra del Tormo Member of the Fombuena Fm. is very fossiliferous. The first echinoderms, *Heliocrinites? sampelayanus* and *Heliocrinites? Isabellae*, were described by Meléndez (1944a, 1944b) based on poorly preserved specimens. Gutiérrez-Marco *et al.* (1996a) did an extensive sampling in those levels and provided a relatively diverse echinoderm fauna that includes *Mespilocystites lemenni*, *Calix? cf. gutierrezzi*, Sphaeronitida fam. indet., *Caryocrinites cf. rugatus*, Hemicosmitida fam. indet., *Heliocrinites* sp. and *Rhombifera bohémica*.

The marly horizon is overlain by the Huerva Member of the same Fombuena Formation, mostly composed of sandstones with interbedded sandy shales. A single fossiliferous horizon (Fig. 18B), 20 m above the base of the unit, has yielded a typical Berounian brachiopod assemblage, dominated by *Svobodaina havliceki*, *Gelidorthis meloui*, *Rafinesquina pomoides*, *Triplesia iberica* and *Rostricellula ambigena*. Brachiopods occur there besides bryozoans, disarticulated echinoderms and scarce trilobites. The occurrence of *Dalmanella unguis unguis*, in the middle horizons of this formation, close to this section, suggests a correlation with the Marshbrookian (upper Cheneyan stage of the British Caradoc). The lower half of the Fombuena Formation can then be correlated with the upper Sandbian. The upper



**Figure 18.** Field aspect of the Fombuena Formation (A, B) and the Cystoid Limestone (C, D). A. Briozoan marlstones from the Piedra del Tormo Member. B. Fossiliferous sandstones from the Huerva Member. C. Limestone beds from the Rebovilla Member. D. Bed plane containing several cystoids.

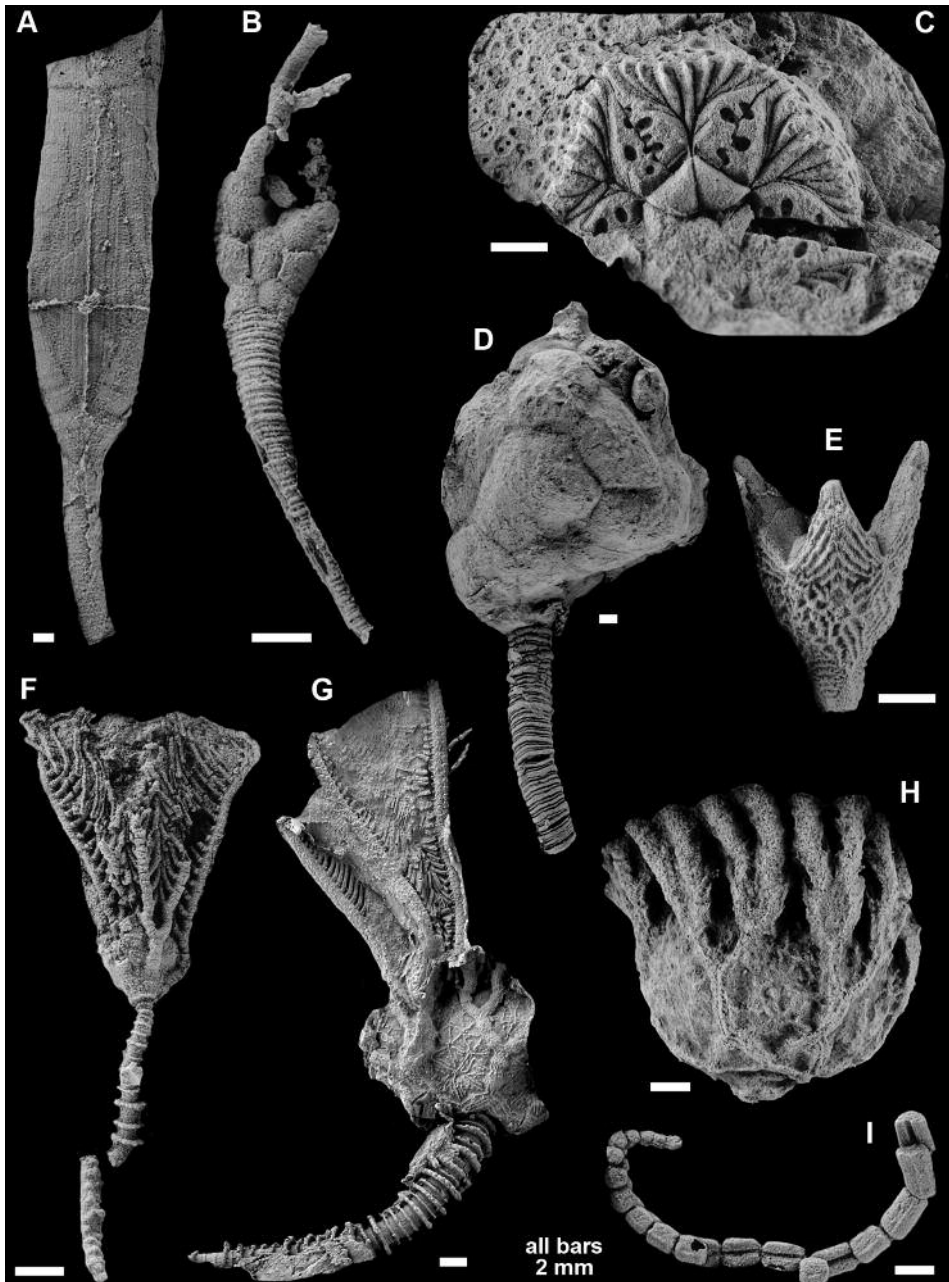
half must represent the Katian 2 substage (Caradoc-Ashgill boundary), according to the occurrence of a low diversity brachiopod assemblage known in the Bancos Mixtos from Central Spain and the base of Porto do Santa Anna Formation in Portugal (Villas, 1995).

The single fossiliferous level from the Huerva Member varies in its position within the unit, but its fossil content is almost identical in all localities. The first echinoderms from this level were described by Gutiérrez-Marco *et al.* (1996a), who reported *Rhombifera* sp., *Diploporita* indet. and *Mespilocystites lemenni*. New samplings in the La Peña del Tormo section and surrounding localities of Fombuena have yielded a remarkably well-preserved echinoderm fauna (Zamora *et al.*, 2014) that includes three crinoid taxa, three different types of camerates (Fig. 19F-H) and a new cladid (Fig. 19B). The blastozoan fauna is mainly dominated by the diploporan *Codiacystis?* nov. sp. (Fig. 19C) and the coronoid *Mespilocystites* (Fig. 19E). Rhombiferans are also very conspicuous in the formation and we have found nearly complete specimens of *Rhombifera bohémica* (Fig. 19A) and *Caryocrinites* sp. (Fig. 19D), both preserving the stem. New unreported taxa include a fragment of an indeterminate asterozoan and the solutan carpoid *Dendrocystites* sp. (Fig. 19I).

### The Cystoid Limestone Formation

The Cystoid Limestone Formation is the local representative of the carbonate sedimentation that took place during late Katian times (Ka3-4: early-mid Ashgill) on the high-latitude shelf bordering the southern (palaeogeographically) Gondwana margin as a consequence of the global warming Boda event (Fortey and Cocks, 2005). It displays strong





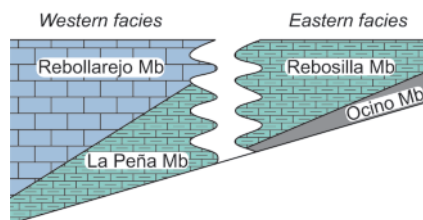
**Figure 19.** Echinoderms from the Fombuena Formation. A. Blastozoan *Rhombifera bohémica* preserving the stem. B. Cladid crinoid. C. Oral area of the diploporan *Codiacystis?* n. sp. D. Blastozoan *Caryocrinites* sp. preserving part of the proximal stem. E. Coronoid *Mespilocystites lemenni*. F. Camerate crinoid preserving part of the stem and arms. G. Camerate crinoid preserving an almost complete theca, arms and proximal part of the stem. H. Camerate crinoid. I. Distal stele part of the solutan *Dendrocystoides* sp. All photographs are from latex cast whitened with  $\text{NH}_4\text{Cl}$  sublimated.

lateral facies changes, with massive limestones in the western part of its outcrop area. The Cystoid Limestone has been divided in this western area into two units: the La Peña Member (Fig. 16), made up by 2 m of marly limestones, with abundant pelmatozoans, bryozoans and brachiopods, and the overlying Rebolarejo Member, up to 40 m thick, characterized by the occurrence of mud-mound complexes (Vennin *et al.*, 1998). The complexes are up to 10 m high and 300 m wide, and comprise individual lenticular mounds. Mounds are up to 2 m thick and 6 m wide, and form flattened carbonate lenses embedded in bioclastic facies. The main carbonates within the mound cores are bafflestones with in situ preserved sessile biota and stromatolite-rich cementstones. Mud-mound complexes developed at various sites on the outer ramp, being influenced by weak to moderate turbulence. The small size of the mounds and the geometry of the mound complexes reflect a limited accommodation space (Villas *et al.*, 2011). The mud-mound complexes pass shoreward to pelmatozoan-bryozoan meadows degraded by wave- and storm-induced processes (La Peña and Rebolarejo members) (Fig. 20). Within these units pelmatozoan-rich packstones are frequent.

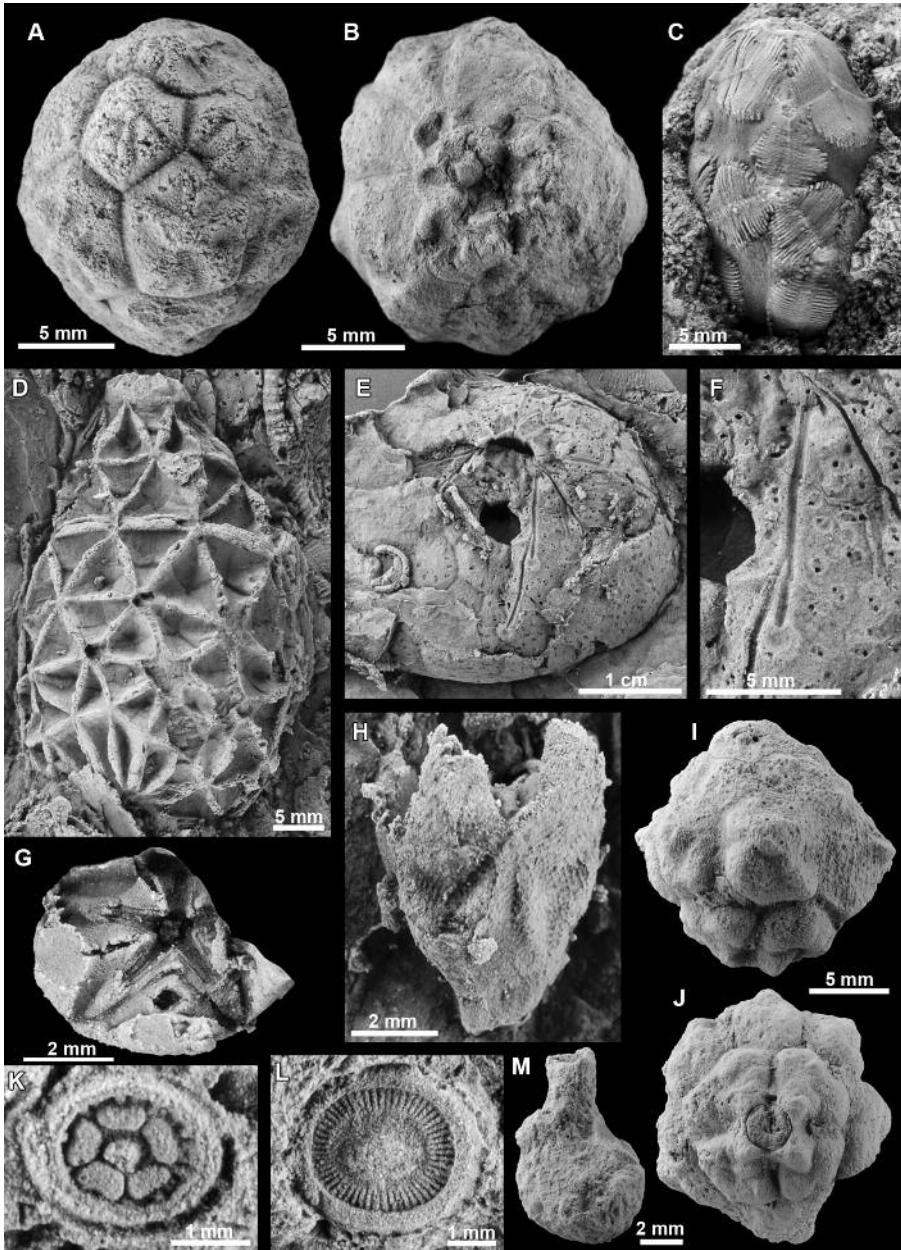
Brachiopod diversity (up to 28 different taxa) is significantly higher than in the underlying siliciclastic formations. The brachiopods found in the Cystoid Limestone are elements of the *Nicolella* Community including *Nicolella*, *Iberomena*, *Eoanastrophia*, *Dolerorthis*, *Porambonites*, *Eridorthis* and *Eoplectodonta* (*Kozlowskites*), among others. Brachiopods are very strongly related to the environmental conditions in which they live (Colmenar *et al.*, 2014) and are consequently very sensitive to changes in the environmental parameters of their habitat. The low diversity brachiopod associations endemic to the Mediterranean region during the early Late Ordovician, were replaced by immigrants (*Nicolella* Community) from low latitude palaeocontinents (Baltica-Avalonia), better adapted to the environmental changes accompanying the Boda event. Larvae of these organisms arrived to the Mediterranean region presumably favoured by the eastward and poleward warm-water currents of the temperate zone (Colmenar, *in press*).

Conodonts characteristic of the *Amorphognathus ordovicicus* Zone where identified by Carls (1975) throughout the massive limestones of the Rebolarejo Member. All the conodont taxa reported by Carls were reinterpreted by Sarmiento (1993) in terms of multielemental taxonomy. Sarmiento (2002) and Del Moral González (2008) summarized the main features of the association.

Echinoderms from the Cystoid Limestone in the Peña del Tormo section are very abundant and well preserved in the lower La Peña Member. The most comprehensive papers on the echinoderms from these levels were published by Chauvel *et al.* (1975) and Chauvel and Le Menn (1979) who reported a diversified fauna of rhombiferans (*Corylocrinus melendezi*, *Caryocrinites szdzy* (Fig. 21A, B), *Caryocrinites elongatus*, *Caryocrinites cf. crassus*, *Caryocrinites europaeus*, *Stichocystis unilineata*, *Heliocrinites rouvillei* (Fig. 21D), *Heliocrinites minuta* (Fig. 21M), *Heliocrinites helmhackeri*, *Heliocrinites cf. saenzi*), diploporans (*Eucystis cf. angelini*, *Proteocystites hispanica* Fig. 21E, F), coronoids (*Mespilocystites tregarvanicus* Fig. 21G, H) and columnals belonging to several pelmatozoan genera (*Cyclocharax paucicrenellatus*, *Malovicrinus* sp., *Ristnacrinus cf. cirrifer*, *Conspectocrinus cf. celticus* Fig. 21K).



**Figure 20.** Relationship of facies and lithostratigraphic units of the Cystoid limestone Formation in the eastern Iberian Chain. Modified from Hammann (1992).



**Figure 21.** Echinoderms from the Cystoid limestone Formation. Specimens A-H, K, L come from the Rebovilla Member in Herrera de los Navarros (A-C) and Luesma (D-H, K, L). Specimens I, J, M come from La Peña Member in Fombuena. A, B. Lateral and oral views of *Caryocrinites sdzuyi*. C. Internal rhomb structures of *Caryocrinites cf. rouvillei*. D. Lateral view of *Proteocystites hispanica* and detail showing diplopores, food grooves and facets for brachioles insertion (F). G, H. Oral and lateral views of *Mespilocystites tregarvanicus*. I, J. Lateral and aboral views of *Caryocrinites* sp. K. Isolated columnal of *Conspectocrinus celticus*. L. Isolated columnal of *Aonodiscus cf. spinosus*. M. Lateral view of *Heliocrinites minuta*. Specimens D-H are latex casts whitened with NH<sub>4</sub>Cl sublimated.

## STOP 10: Late Ordovician Echinoderms from La Rebosilla section

### Location

This section is located in an arable land located about 1.5 km. South-West Luesma village, in a place so-called La Rebosilla.

Coordinates: 41°9'28"N, 1°9'40"W.

Geological map of Spain, 1:50,000, sheet of Moyuela (466).

Geological setting: Badules Unit (eastern Iberian Chain).

Lithostratigraphical unit: Cystoid Limestone Formation (eastern facies, Rebosilla and Ocino members) (Figs. 13, 22).

Age: Katian 3-4 (Late Ordovician).

### Aims

Look at the echinoderm faunas from the Cystoid Limestone in the eastern facies and comparing with those from the western facies.

### Description

Moving eastwards from the former locality, the Cystoid Limestone Formation displays its typical eastern facies (Fig. 20). It is characterized by basal calcareous siltstones to claystones, up to 5 m thick, called the Ocino Member, and alternating marly shales and limestones, nearly 20 m thick, above them. This upper part of the unit is known as the Rebosilla Member, and is considered to represent the same environmental setting than that of the La Peña Member, visited in the former stop (Fig. 22).

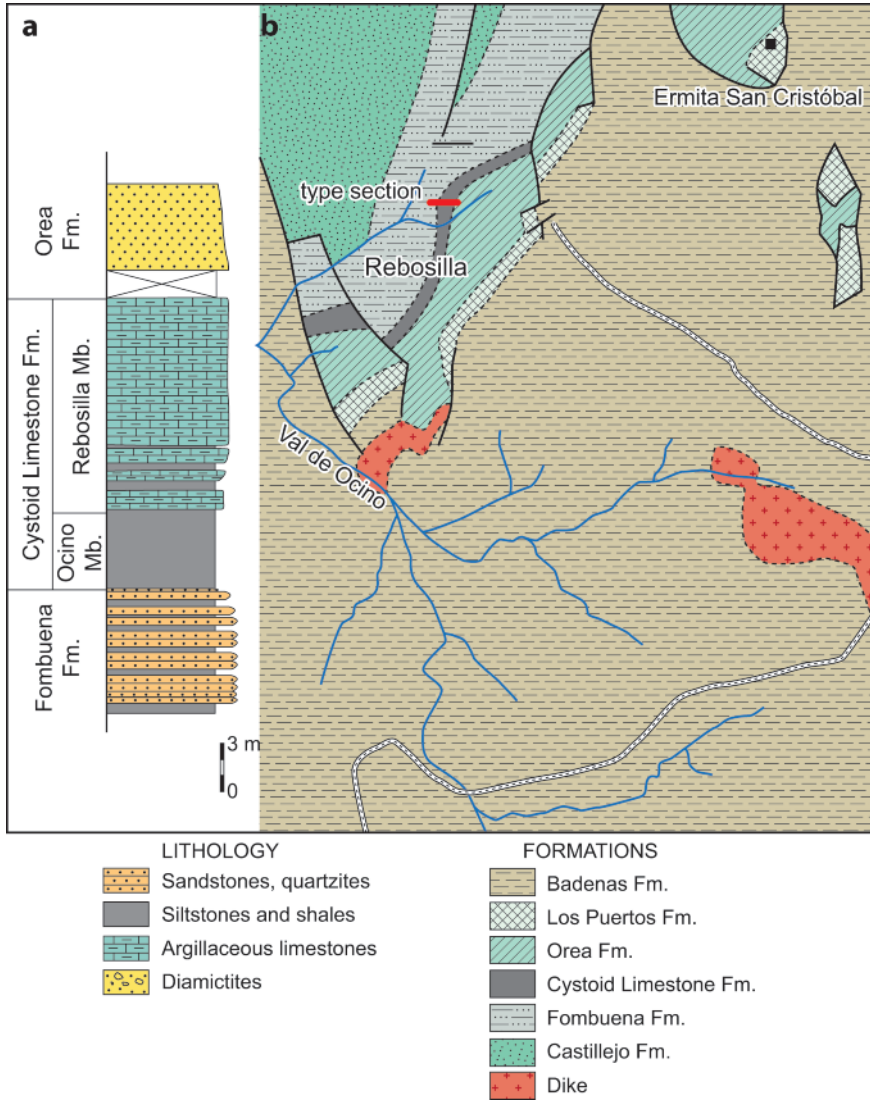
A taphonomic study of skeletons by Vennin *et al.* (1998) showed vertical changes on a decimeter-scale, where erosive bases are paved by abraded shell layers that pass gradually upward into skeletal elements that show a greater degree of articulation and larger size. Complete articulated skeletons of pelmatozoans and fragile dendroid/ramose bryozoans overlie these storm-induced deposits and are interpreted to represent quiet episodes that favoured episodic development of pelmatozoan and bryozoan meadows. Therefore, sediments of the Rebosilla Member can be attributed to open-sea conditions in an offshore environment, which experienced quiet deposition punctuated by storm events.

First echinoderms from this section were reported by Dereims (1898) who compared the fauna with "*Orthis actoniae*" and cystoids (*Echinospaerites*, *Caryocrinites*) with that of the Upper Ordovician described by v. Koenen (1886) from the Montagne Noire (France). Meléndez (1944a, 1944b, 1959) and Meléndez and Hevia (1947) gave first descriptions of echinoderms from La Rebosilla section and considered them Ashgillian. The most recent compilation of those faunas comes from Chauvel *et al.* (1975) and Chauvel and Le Menn (1979) who provided several species of rhombiferans (*Cariocystites* sp., *Cariocystites? saenzi*, *Heliocrinites* cf. *rouvillei*, *Heliocrinites* aff. *helmackeri*, *Heliocrinites pacheco*) and isolated columnals (*Conspectocrinus celticus*, *Ristnacrinus* cf. *cirrifer*, *Cyclocharax paucicrenullatus*, *Trigonocyclicus* cf. *vajgatchensis*, *Aonodiscus spinosus* Fig. 21L).

All the studied specimens from this section come from the Rebosilla Member.

The echinoderm faunas from the Cystoid Limestone need a revision because some genera (i. e. *Caryocrinites*, *Heliocrinites*), include several species based on poorly preserved specimens or discrete morphological characters. Some of the differences between species are better explained in terms of ontogenetic development, intraspecific variation and taphonomy.





**Figure 22.** Geological map and lithological column of the La Reboquilla locality. Modified from Hammann (1992). Type section indicated with a red line.



**STOP 11: Silurian crinoid-ophiuroid assemblage from Luesma****Location**

This section is located in a small hill about 1.7 km. South-East Luesma village, in a place so-called Las Bruterias.

Coordinates: 41°9'25"N, 1°7'47"W.

Geological map of Spain, 1:50,000, sheet of Moyuela (466).

Geological setting: Badules Unit (eastern Iberian Chain).

Lithostratigraphical unit: Bádenas Formation, s3d member (Fig. 15).

Age: Ludlow (Silurian).

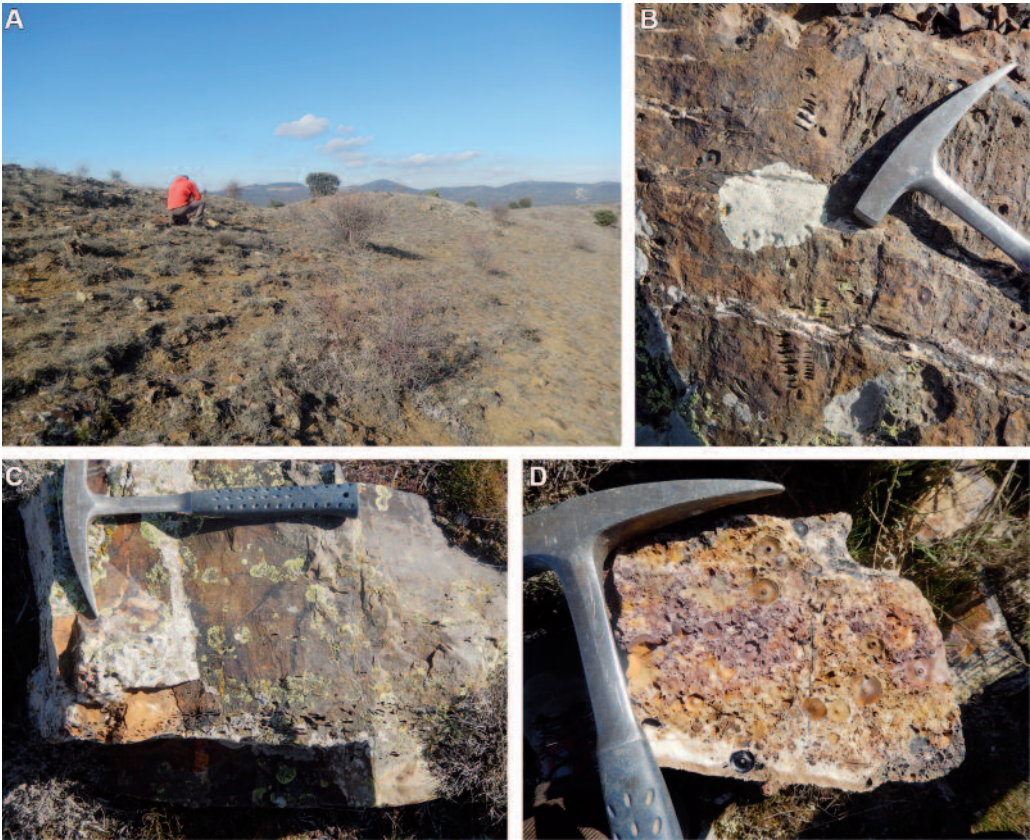
**Aims**

Visit one of the few Silurian outcrops in Spain that has provided very abundant complete crinoids. Look at the different sedimentary structures associated with the crinoid beds. Discuss the possible environment based on fossil preservation and sedimentary structures.

**Description**

The Ordovician-Silurian boundary in the Iberian Cordillera lies in the uppermost quartzites of the Los Puertos Formation (20-40 m), where recent sampling has resulted in the discovery of some brachiopods (*Plectothyrella crassicosta chauveli* and *Eostropheodonta* sp.) typical of the *Hirnantia* fauna. The overlying Bádenas Formation comprises mostly shales with sandstone intercalations (900-1400 m). Carls (1965) studied the stratigraphy of this formation and subdivided it into five members from s3a to s3e: s3a, s3c and s3e are mostly composed of shales while the other two members (s3b, s3d) are mostly quartzitic. The s3d member close to Luesma is approximately 43 meters thick (Carls, 1965) and is very fossiliferous containing a rich assemblage dominated by chonetid and rhynchonellid brachiopods, gastropods, bivalves, trilobites, tentaculitoids and echinoderms (Fig. 23). These faunas have not been studied in detail. Carls (1965) favoured an undetermined late Wenlock-early Ludlow (Homerian to Gorstian) age for this s3d sandstone member of the Bádenas Fm.

Crinoids, especially *Dimerocrinites aragonensis* (Figs. 24A, B, E), are concentrated in some levels; although there are isolated columnals from other species of crinoids (Fig. 24E) and rare ophiuroids (Fig. 24F). Le Menn (1985) was the first that mentioned *Dimerocrinites* in those levels, although it was not until 2003 when he described *Dimerocrinites aragonensis* Le Menn (in Le Menn *et al.* 2003). *Dimerocrinites* has a heteromorphic stem composed by extremely large nodals and small internodals, associated with large articular facets. The Iberian species has global affinities with several species from the Silurian of Gotland, Wales and New York (Le Menn *et al.*, 2003).



**Figure 23.** Field views of the Bádenas Formation. A. General view. B. Bed plane containing several stem fragments of *Dimerocrinites aragonensis*. C. Bed section showing a tempestite level at the base. D. Several columnals of *Dimerocrinites aragonensis* preserved as natural moulds.

## STOP 12: Early Devonian echinoderms from Santa Cruz de Nogueras

### Location

The section crops out in a new road cutting of the TE-V-1521 road from Santa Cruz de Nogueras to Bádenas villages (Fig. 13).

Coordinates: 41°6'31"N, 1°5'57"W.

Geological map of Spain, 1:50,000, sheet of Moyuela (466).

Geological setting: Badules Unit (eastern Iberian Chain).

Lithostratigraphical unit: Mariposas Formation (meaning Butterflies Formation) (Fig. 15).

Age: early Emsian (Devonian).

### Aims

Visit a lower Devonian (late Pragian to early Emsian) succession and compare with the rocks we will visit in the Cantabrian Mountains.

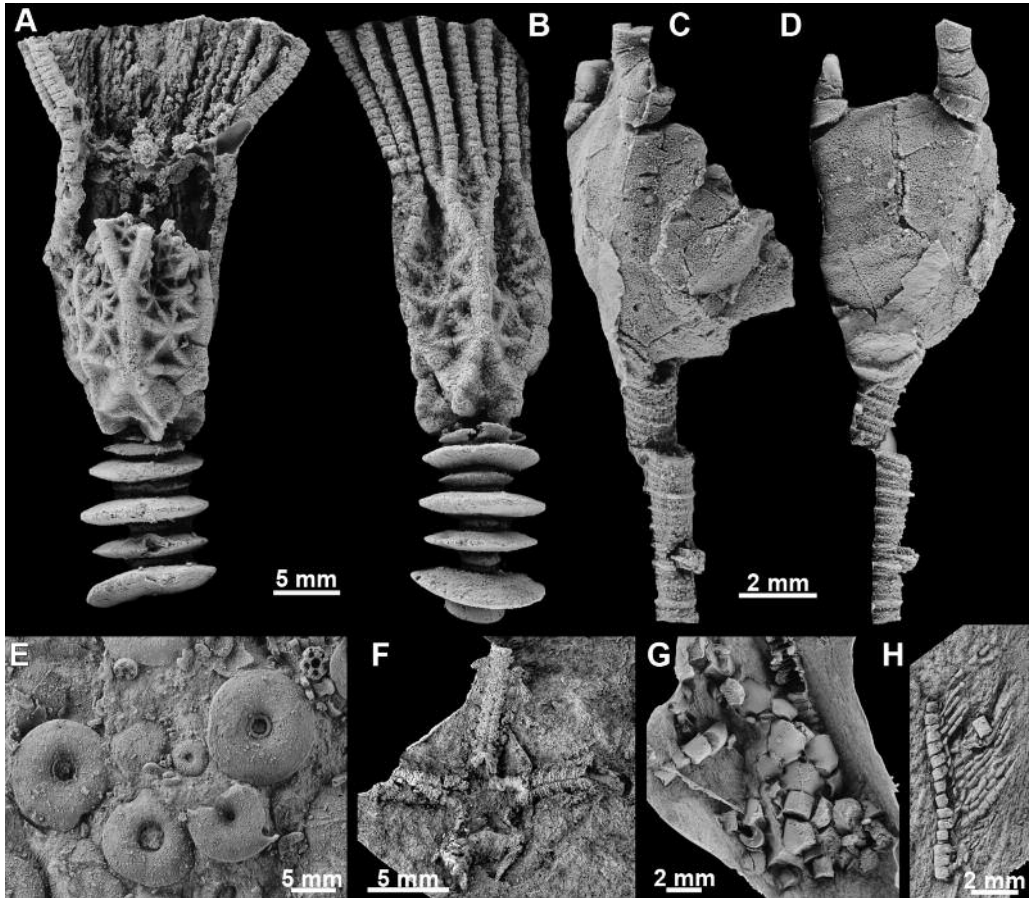
### Description

The Mariposas Formation is one of the most fossiliferous Devonian units in the Iberian Cordillera. It consists of a 200 m-thick interval dominated by shales and carbonates. The faunas change from typical Rhenish facies of shallow water to Hercynian hemipelagic biofacies. The Mariposas Formation is subdivided into two members (d4a and d4b) (Fig. 15).

Carls and Valenzuela (2002) provided a synthesis of the Devonian sequence from the Iberian Cordillera and indicated that the Mariposas Formation starts with a 8 m-thick alternation of shelly limestones and bryozoans marls and shales (d4a $\alpha$ ), in which the lower boundary of the traditional German Emsian Stage is located (Carls, 1987, 1988). The submember d4a $\beta$  is 20 m thick and contains Rhenish brachiopods, trilobites and endemic conodonts of the genus *Icriodus*. There are rare *Otarion* and proetid trilobites, solitary rugose corals, thamnoporid and michelinid tabulate corals, tentaculitoids, ostracods, crinoids and bivalves. The overlying submember (d4a $\gamma$ ) is 15-20 m thick, and consists of a shelly crinoidal limestone and contains similar fauna than the previous units but also includes abundant atrypid brachiopods and some dacryoconarid tentaculitoids and trilobites (scutellids and *Phacops*).

According to Carls and Valenzuela (2002), Rhenish faunas practically disappear at the beginning of the d4b Member except for few trilobites (*Asteropyginae*) and brachiopods (*Arduspirifer*). The submember d4b $\alpha$  is 15 meters thick interval of limestones and shales with a rich fauna of trilobites, ostracods and brachiopods. The submember d4b $\beta$  is composed of 30 m of shales rich in fossils, mostly trilobites (*Phacops*), brachiopods, tabulate corals, tentaculitids and crinoids. Lastly the d4b $\gamma$  member is a 20 m thick barren interval composed of black marly shales.

Crinoids from this formation (Fig. 24C, D, G, H) are abundant in the outcrops from both sides of the road that we are going to visit (Fig. 13) but they apparently show low diversity compared to assemblages from the Cantabrian Zone where the fauna appears associated with reef episodes. Articulated specimens are rare (Fig. 24C, D) and were mostly collected when the road was opened giving access to big blocks of rock of unknown exact stratigraphic position. They are concentrated in the shaly intervals of the submember d3a $\beta$ . Detailed taxonomic work on those faunas is pending further work.



**Figure 24.** Silurian (Bádenas Formation) and Devonian (Mariposas Formation) Echinoderms. A, B. The crinoid *Dimerocrinites aragonensis*. C, D. Diplobathrid camerate crinoid. E. Crinoid columnals of at least two different taxa, *D. aragonensis* and an indeterminate crinoid. F. indeterminate ophiuroid. G. Fragment of a crinoid theca. H. Pinnulate arm of an indeterminate crinoid. All specimens are latex casts whitened with NH<sub>4</sub>Cl sublimated.

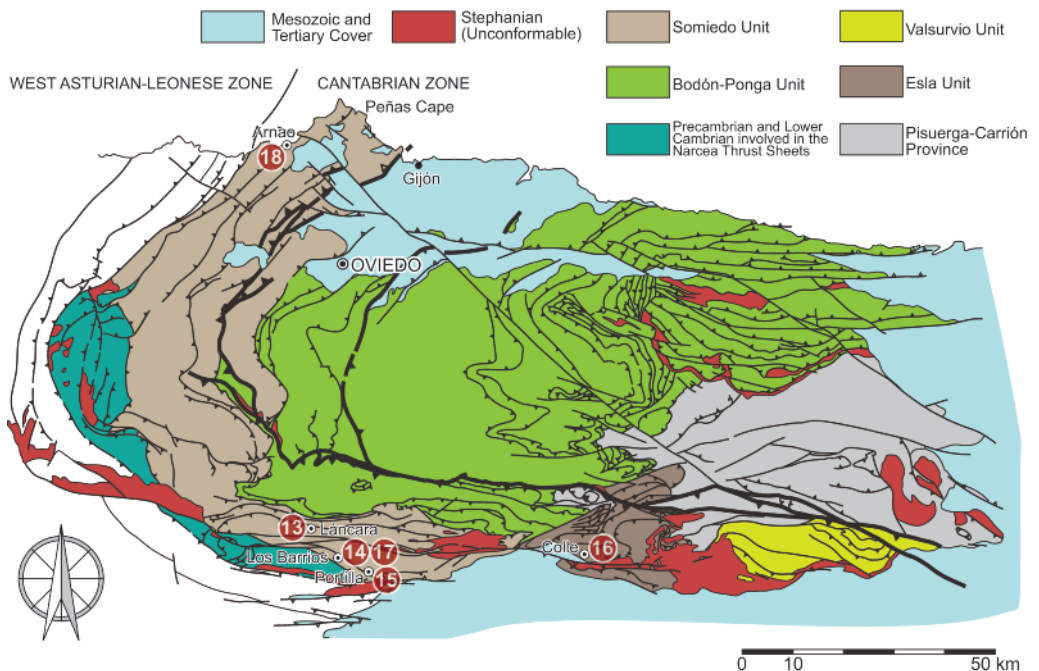
## PALAEOZOIC FROM THE CANTABRIAN ZONE

Esperanza Fernández-Martínez

The Cantabrian Zone represents the most external part of the Variscan Iberian Massif in the northwestern part of the Iberian Peninsula (Fig. 1) and is mainly composed of pre-Mesozoic sedimentary rocks. Its Palaeozoic succession unconformably overlies Precambrian rocks, which mark the boundary between the West-Asturian Leonese and Cantabrian Zones (Figs. 1, 25). According to its relationships with the Variscan orogeny, the Palaeozoic succession of the Cantabrian Zone is usually divided into a pre-orogenic sequence and a syn- to post-orogenic sequence (Fig. 26) (Aller *et al.*, 2002).

The pre-orogenic sequence displays a wedge shape, thinning out eastward, where the basin margin was located and from where sediments were fed. It is characterized by an incomplete Cambrian-Ordovician interval, a thin Silurian package, and a mixed carbonate and siliciclastic Devonian succession of variable thickness (Aramburu *et al.*, 2002, 2004). In a broad sense, the pre-orogenic succession consists of an alternation of carbonates and siliciclastics laid down in mainly shelfal to coastal environments. Siliciclastic sediments dominated during Early Palaeozoic times and were mostly replaced by Lochkovian to Upper Devonian carbonates (Keller and Grötsch, 1990; García-López, 2002). Up to seven reefal episodes have been recorded in the Devonian rocks of the Cantabrian Zone (Méndez-Bedia *et al.*, 1994).

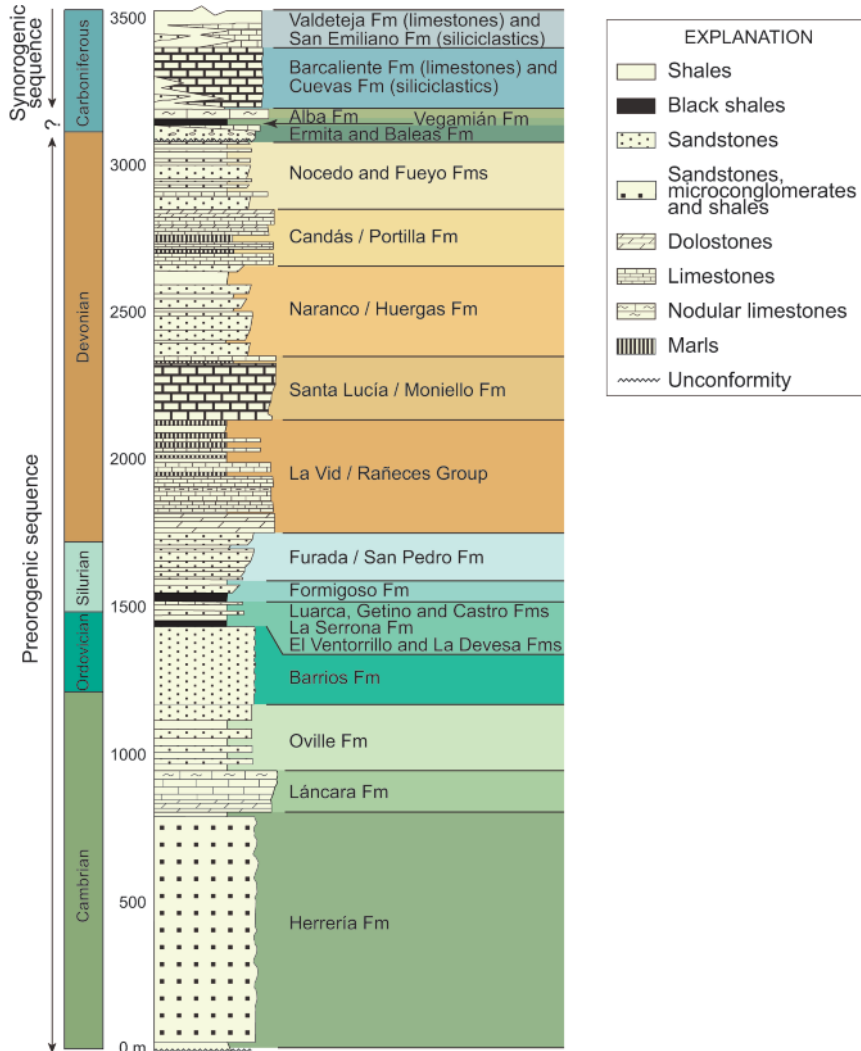
The Carboniferous succession starts with a condensed interval that has been interpreted as recording the inversion to the synorogenic stage. The remaining succession is a thick, mainly clastic interval, which represents the infill of a foreland basin formed in front of the advancing orogen. These sediments were supplied from the growing mountain chain and faced a mainly carbonate province located in the distal parts of the basin (Colmenero *et al.*, 2002; Fernández *et al.*, 2004).



**Figure 25.** Geological map of the Cantabrian Mountains with indication of different domains and situation of different stops. Modified from Alonso *et al.* 2009.



From a tectonic point of view, the Cantabrian Zone is characterized by the occurrence of a thin-skinned deformation, represented by thrusts and related folds, almost lacking metamorphism, which is of a very low grade condition where it occurs (Aller *et al.*, 2002).



**Figure 26.** Synthetic generalized stratigraphic column of the Cantabrian Zone showing the pre-orogenic sequence and the lower part of the synorogenic sequence. Stratigraphic intervals visited in each stop are indicated on the right. Modified from Alonso *et al.* 2009.

DAY 4: June 20th 2015

## EARLY PALAEOZOIC ECHINODERM FAUNAS FROM THE LUNA VALLEY

J. Javier Álvaro, Juan Carlos Gutiérrez-Marco and Samuel Zamora

## INTRODUCTION

The Cantabrian Zone, one of the Variscan tectonostratigraphic units of the Iberian Peninsula, comprises the proximal part of a platform whose distal counterpart is at present exposed in the West Asturian-Leonese Zone (to the west). The continental source neighbouring the Cantabrian Platform, the so-called Cantabro-Ebroan Land Area, lies actually in the subsurface of the Ebro basin (Aramburu *et al.*, 1992). The platform was attached to this relic of Gondwanaland, which followed a poleward drift during Cambro-Ordovician times, crossing low- and mid-latitude settings and recording the Hirnantian glaciation in subpolar palaeolatitudes (Álvaro *et al.*, 2000a, 2003a; Gutiérrez-Marco *et al.*, 2010).

The Cambro-Ordovician succession of the Cantabrian Zone (see Fig. 26) represents a thick (ca. 1500 m), siliciclastic-dominated interval mainly representative of marine conditions. Tectonic activity controlled episodically the basin geometry, marking some distinct basin rearrangements during the record of the lowermost Cambrian (post-Cadomian) molasses (lower member of the Herrería Formation) and the lower-middle Cambrian boundary interval (transition across the lower/upper members of the Láncara Formation).

Two Early Palaeozoic episodes of carbonate production are recognized. The oldest took place across the lower-middle Cambrian transition and is lithostratigraphically identified as the Láncara Formation. The lower Cambrian Herrería and Láncara formations record the influence of subtropical conditions, marked by the presence of lateritic (Ustifluent) paleosols, microbial mats, archaeocyathan-microbial patch reefs, ooidal shoal complexes associated with phosphorites, and evaporite pseudomorphs (Zamarreño, 1972; Álvaro *et al.*, 2000a,b, 2003b, in press; Perejón and Moreno-Eiris, 2003; Perejón *et al.*, 2012). The second episode of carbonate production is recognized in the Katian 3-4 La Devesa Formation, reflecting development of echinoderm-bryozoan meadows, although only reaching up to 13 m in thickness (Gutiérrez-Marco *et al.*, 2006; Toyos and Aramburu, 2014). Finally, the formation of subglacial tunnel valleys and fluvial incised valleys during the Hirnantian has been reported by Gutiérrez-Marco *et al.* (2010) and Toyos and Aramburu (2014), respectively.

From a palaeobiogeographic point of view, Cambrian trilobites exhibit a typical West Gondwanan affinity, belonging to the so-called Acado-Baltic Province *sensu* Sdzuy (1972), a mid-Cambrian biogeographic unit that included the Mediterranean region (from Morocco to Turkey), Avalonia and Baltica (for a synthesis, see Álvaro *et al.*, 2013a). Ordovician shelly faunas belong to the "Calymenacean-Dalmanitacean" trilobite assemblage (Mediterranean or "Selenopeltis" provincial faunas), characteristically developed on the shallow peri-Gondwanan shelves lying at high south Polar Palaeolatitudes. The area was affected by the warm climatic "Boda event" at the end of the Katian, and also by the close proximity to the African ice sheet during Hirnantian glaciation.

At the end of the Cadomian Orogeny marine conditions were established and several pulses of faunal immigration were recorded in the Cantabrian Platform. The oldest occurrence of trilobites in the Herrería Formation marks the base of the regional Ovetian Stage (after Oviedo, capital of Asturias; Palacios and Vidal, 1992; Liñán *et al.*, 1993), broadly correlatable with the Russian Atdabanian or the global Cambrian Stage 3. The overlying peritidal carbonates of the lower member of the Láncara Formation, are succeeded by a series of Bilbilian (Toyonian), stepwise transgressive pulses associated with extensional tectonic episodes, which led to the immigration of non-spiculate sponges (archaeocyaths), which locally form patch reefs in the uppermost part of the lower member, associated with a new shelly assemblage that includes new trilobite families, brachiopods, hyoliths and skeletonized microfossils (Clausen and Álvaro, 2006; Álvaro, 2007; Álvaro *et al.*, 2013b). However, it is another tectonic pulse, recorded by the regional unconformity of the lower-middle Cambrian boundary (Álvaro *et al.*, 2000b; for a chemostratigraphic analysis, see Wotte *et al.*, 2007), the responsible of a major immigration event that led to the development of chancelloriid-echinoderm-(spiculate) sponge meadows (the so-called CES community) on tilted palaeohighs, preserved in the upper member of the Láncara Formation. The final flooding of the upper member deposits blanketed the previous palaeotopographies by clay

deposits episodically punctuated by prograding sand shoal complexes. After a long time span extremely poor in shelly fauna, a final episode of shelly immigration was controlled by the onset of the Hirnantian glaciation.

The echinoderm faunas of the Lower Palaeozoic of the Cantabrian Zone provide important information to better understand the evolution of the taxon in two important time intervals, the mid Cambrian and the Late Ordovician. Mid Cambrian echinoderms are relatively diverse and include cinctans, eocrinoids, stylophorans, edriasteroids and ctenocystoids. Some of the taxa (i.e., cinctans, lichenoidid eocrinoids and armoured stylophorans) reflect biogeographic connections with other Gondwanan areas, but some endemic taxa, such as the columnal-bearing eocrinoid *Ubaghsicystis segurae*, provide important evolutionary information about how pelmatozoans developed stems with true holomeric columnals. More important is the presence of different environments, high-energy onshore to offshore Lánara Formation (stop 13) vs calm water offshore-dominated Oville Formation (stop 14) that directly influenced in the palaeoecological distribution of benthic communities. Another important feature is the diachronic nature of the Oville Formation (Zamarreño, 1972; Sdzuy and Liñán, 1993) that permits a chronostratigraphic control on the replacement of echinoderms communities led by modifications from high-energy (shelly) carbonate to calm clayey substrates.

A very small pre-Hirnantian (Upper Ordovician) outcrop from Portilla de Luna (stop 15) is the unique reference we have in the area about the echinoderm communities that colonized the Cantabrian Platform during the so-called Boda warming event. This recent finding represents an intermediate (palaeogeographic) setting linking other Katian fossiliferous areas, such as the Armorican Massif, the Central Iberian Zone and the Iberian Range, providing key palaeobiogeographic information.

### STOP 13: Echinoderm communities from the middle Cambrian of the Lánara Formation

#### Location

Road cut in the CL-626 below the old locality of Lánara de Luna.

Coordinates: 42°54'34.19"N, 5°55'25.67"W.

Geological map of Spain, 1:50.000, sheet of Los Barrios de Luna (102).

Geological setting: Southern slope of the Cantabrian Zone, Somiedo Unit.

Lithostratigraphical unit: Lánara Formation.

Age: Caesaraugustan (mid Cambrian).

#### Aims

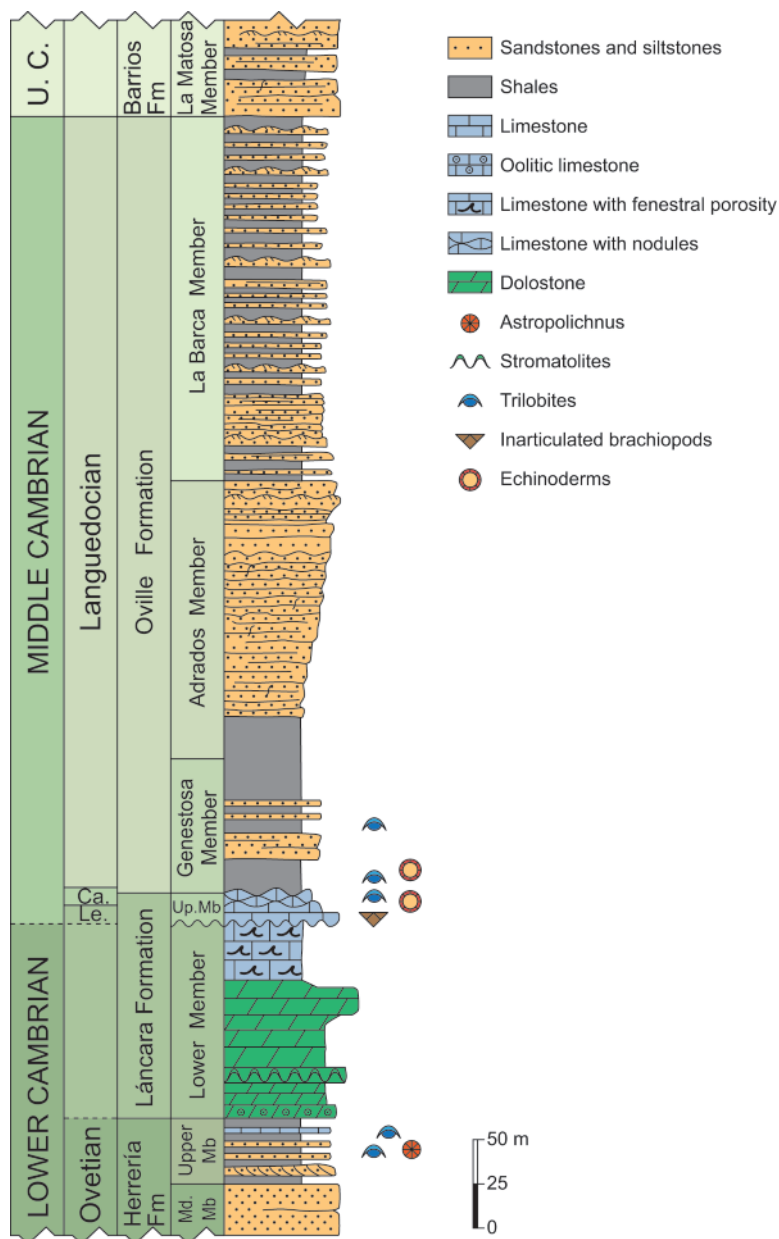
To examine echinoderm faunas (mostly cinctans and eocrinoids) associated with high energy environments. Discuss the substrate control on which the earliest pelmatozoans attached on firmgrounds.

#### Description

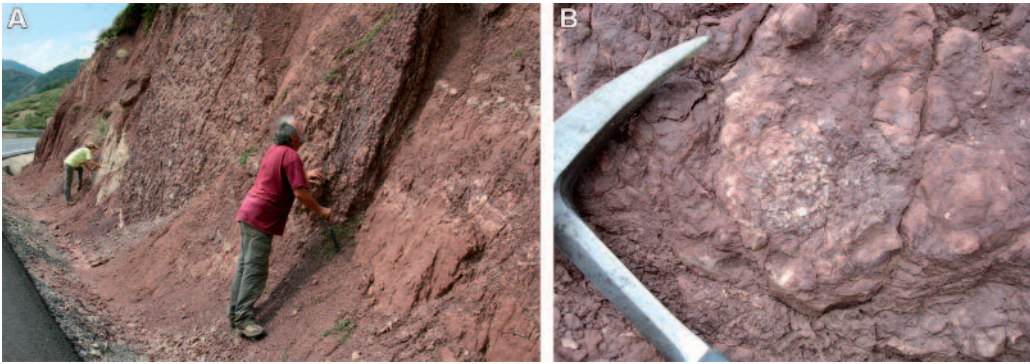
The Lánara Formation (Fig. 27) comprises two members. The lower one, 100-225 m thick, consists of yellow-weathering dolostones, commonly rich in ooids, peloids and stromatolitic crusts. Some areas, such as the Esla nappe, display a distinct facies association of ooidal shoals locally punctuated by archaeocyathan-microbial patch reefs (Álvaro et al., 2000b; Perejón and Moreno-Eiris, 2003; Perejón et al., 2012) dated as Bilbilian in age. The lower/middle member contact is an erosive unconformity that marks the Bilbilian/Leonian or regional lower-middle Cambrian boundary. Zamarreño (1972) subdivided the upper member into two facies, the so-called Beleño and Barrios facies. The former is a grey-to-pinkish, glauconitic limestone, 1-40 m thick, dominated by echinoderm-dominated packstones representative of low-angle shoal complexes. The upper member (also known as "griotte"/cherry-coloured facies by comparison with the same facies association in Montagne Noire, France), is up to 30 m thick, and consists of



centimeter-scale, reddish-to-purple, bioclastic limestone/shale couplets (Fig. 28), deposited on the top of tilted palaeohighs. Deepening-upward sequences are recognized in the griotte facies, where skeletons exhibit stepwise, upward modifications from echinoderm- to brachiopod/trilobite-dominated associations reflecting changes in depth,



**Figure 27.** Stratigraphic column from the Cambrian in Barrios de Luna (after Zamarreño, 1977 and Aramburu, 1989).

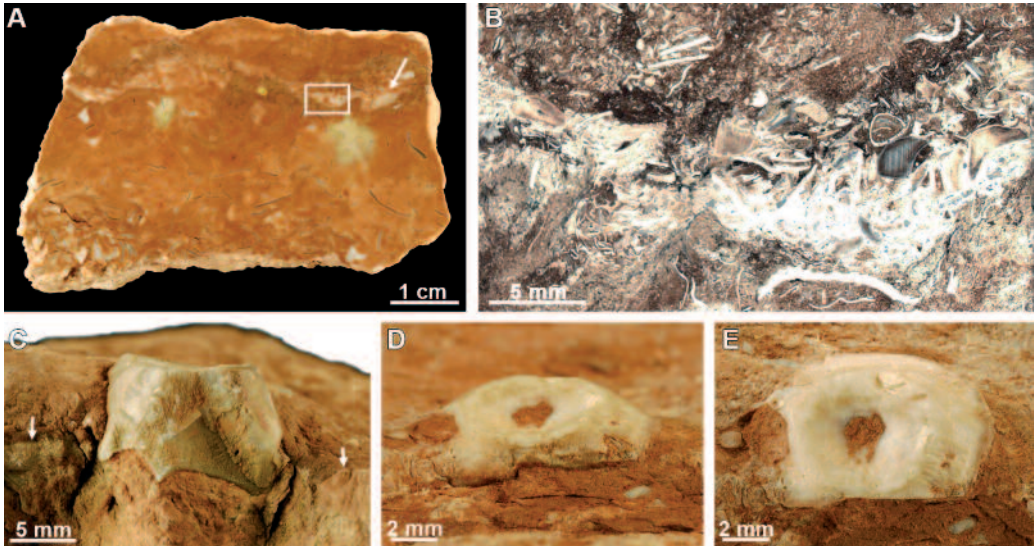


**Figure 28.** A. Bedding planes of the Lánacara Formation. B. Accumulation of echinoderm plates in the Lánacara Formation.

substrate stability and guild strategies of benthic communities (Álvaro *et al.*, 2000b; Wotte, 2005, 2006; Wote *et al.*, 2004; Wote and Mergl, 2007; Barragán *et al.*, 2014). Sealing of this palaeotopography was diachronous, ranging from late Leonian to early Languedocian times (Sdzuy, 1968; Zamarreño, 1972).

Echinoderms are abundant in the Lánacara Formation but articulated specimens are rare and include only complete cinctans belonging to the genus *Gyrocyrtis*. One of the most interesting faunal elements from this facies is the preservation of holdfasts directly attached to firmground carbonate substrates (Fig. 29). They are abundant in the Barrios/griotte facies, where they are preserved in life position. Based on facies and isopach studies, the griotte facies has been interpreted as the progressive drowning of a mixed (carbonate-siliciclastic) platform, in which carbonate production was restricted to tectonically induced palaeohighs that recorded a Milankovich-like cyclicity (Zamarreño, 1972; Álvaro *et al.*, 2000a,c). Early-diagenetic calcite cementation in the bioclastic packstone to wackestone textures that formed the substrate was restricted to intraparticle skeletal pores, syntaxial overgrowths, and occlusion of shelter porosity underlying trilobite sclerites and brachiopod valves. Centimeter-thick tempestites show high densities of skeletons, where the cementation process developed matrix-poor layers that episodically acted as firm substrates (Fig. 29). The effects of late diagenetic compaction, both mechanical and chemical, were concentrated at the limestone/shale contacts, leading to fitted fabrics and solution seams (Álvaro *et al.*, 2000b). As a result, the holdfasts are found attached to undulating bedding surfaces with their attachment surface clearly following local microtopographic irregularities (Fig. 29). While the holdfasts are unambiguously associated with bedding plane surfaces, where the porosity was occluded with earliest diagenetic calcite cements, there is no evidence of either boring or grain truncation at these levels. Consequently, the surfaces are best referred to carbonate firmgrounds rather than true hardgrounds (Zamora *et al.*, 2010).

Echinoderms probably always needed to attach at some stage in their development, and the great majority of pelmatozoans simply retained this attachment phase into adulthood. For the earliest pelmatozoans living in soft-bottom offshore meadows, attachment opportunities were limited to microtopographic hardgrounds provided by skeletal debris. Gogiids are a typical example of eocrinoids living attached to skeletal fragments, as trilobite moults and brachiopod shells in soft muddy environments (Sprinkle, 1973; Ubaghs, 1987; Lin *et al.*, 2008; Zamora *et al.*, 2009). Their stalk was no more than a loosely plated tube and their attachment a small terminal zone of tiny plates (Sprinkle, 1973). This mode of attachment, however, had distinct disadvantages. Firstly, it limited the size to which adults could grow, and secondly it restricted echinoderms to low-current habitats where small pieces of skeletal debris provided sufficient anchorage. In order to successfully colonize moderate- to high-energy environments, pelmatozoans had to shift to larger, more secure, firm- or hardgrounds and develop biomechanically stronger stalks reinforced with collagen fibers. Both of these attributes had evolved in echinoderms by the early mid Cambrian suggesting that a shift to higher energy environments was already well underway. The first encrusting and discoid holdfasts described here, and the earliest holomeric columnals with long stereom galleries for collagen fibers (Clausen and Smith, 2008) both come from Gondwanan shallow-water settings. When first true carbonate hardgrounds started to be common in the geological record by the Furongian (Brett *et al.*, 1983), echinoderms were pre-adapted to such settings. Stemmed eocrinoids



**Figure 29.** Polished slab (A) and thin section (B) of the griotte facies that contains the holdfast. Arrow indicates the undulating firmground horizon to which the pelmatozoan attached. C-E. Two specimens of holdfasts from the Cantabrian Mountains. Arrows indicate the surface where the specimen was attached. Note the microfractures that flank the holdfast produced after differential compaction of limestone and claystone layers.

with cemented holdfasts were among the first skeletonized metazoans to colonize these hardgrounds (Guensburg and Sprinkle, 2001), but the fossil record of Gondwana suggests that immigration into shallow-water settings started earlier, by the basal mid Cambrian (Álvaro *et al.*, 2013b).

## STOP 14: The middle Cambrian Oville Formation and the most diversified echinoderm fauna from the Cantabrian Mountains

### Location

Creek 500 m to the southeast of Los Barrios de Luna village, near the Mora-Los Barrios de Luna road.

Coordinates: 42°50'31.26"N, 5°51'22.46"W

Geological map of Spain, 1:50.000, sheet of Los Barrios de Luna (102).

Geological setting: Southern slope of the Cantabrian Mountains, Somiedo Unit.

Lithostratigraphical unit: Láncara and Oville Formations.

Age: Caesaraugustan-Languedocian (mid Cambrian).

### Aims

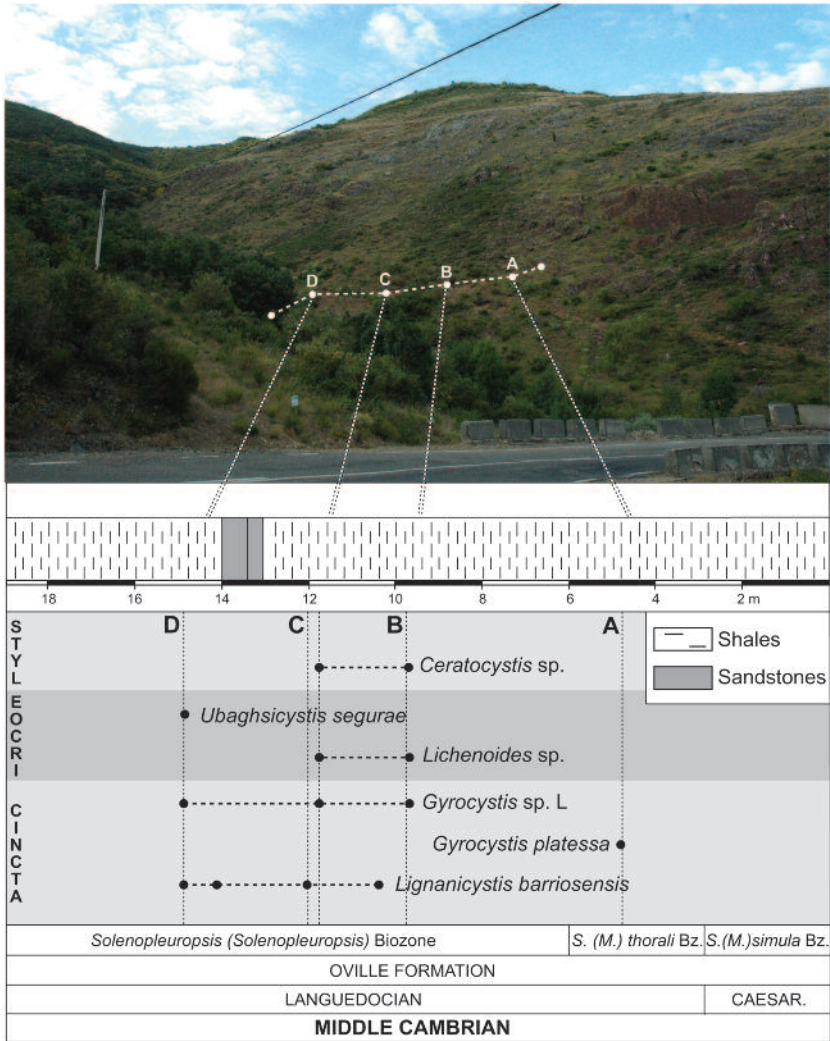
Look at the most diversified level of echinoderms from the Cantabrian Mountains that include representatives of cinctans, eocrinoids and stylophorans preserved on relatively soft substrates.

### Description

The Oville Formation (Fig. 27) is a siliciclastic succession, subdivided, from base to top, into (1) the lower Genestosa Member (traditional "Paradoxides Beds"), 15-100 m thick, and dominated by homogeneous green shales locally interrupted by sandstone levels; (2) the Andrados Member, 50-160 m thick, marking the presence of sandstone-dominated shoals; and (3) the La Barca Member, 8-20 m thick, dominated again by homogeneous green shales (Aramburu *et al.*, 1992).

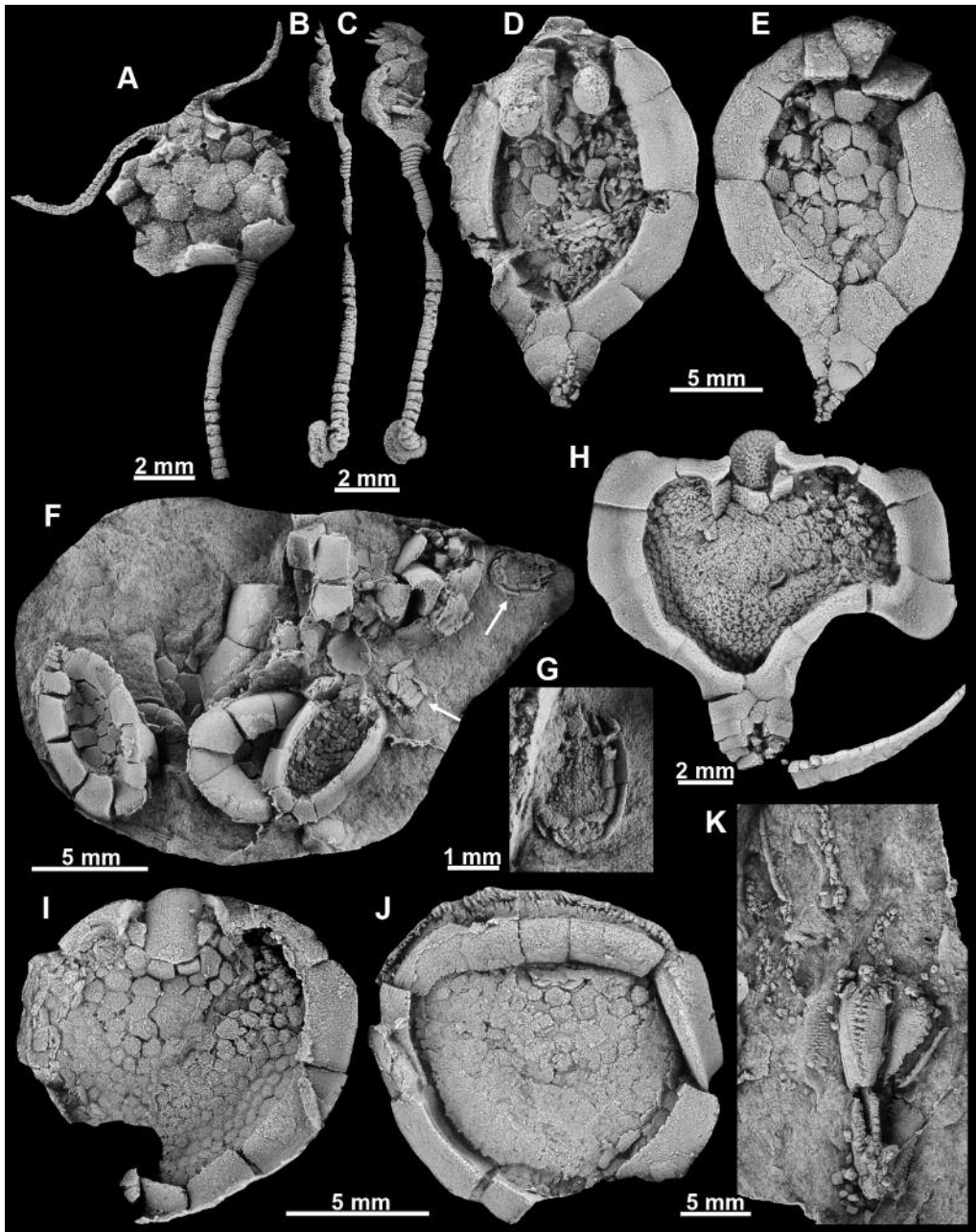
The Genestosa Member comprises the highest diversity of trilobites and echinoderms in the Cantabrian Zone. The diachronous character of the Láncara/Genestosa contact, ranging from late Leonian to early Languedocian in age (Sdzuy, 1968; Zamarreño, 1972) directly affected peaks of diversity both on trilobites and cinctans (Zamora and Álvaro, 2010). As a consequence, this diachronous modification of the seafloor allows us to analyse the evolution of mid Cambrian benthic communities on both carbonate and clayey substrates. The oldest echinoderms from the Genestosa Member were sampled in the Porma section, where Sdzuy (1993) described the cinctan *Asturicystis?* sp. considered as Leonian in age. Early Caesaraugustan echinoderms are relatively common in Soto de Caso locality, from which the same author described the cinctans *Sotocinctus ubaghsi* and *Asturicystis jaekeli*. Further work during the PhD of Zamora (2009) resulted in the discovery in the same section of indeterminate ctenocystoids and stylophorans belonging to *Ceratocystis*.

The Barrios de Luna section (Fig. 30) provides a relatively complete log from the upper Caesaraugustan-lower Languedocian. In the upper Caesaraugustan, only the cinctan *Gyrocystis platessa* has been reported. In the lower Languedocian strata echinoderms are more diverse and include the cinctan *Gyrocystis* sp. L (Zamora *et al.*, 2007) (Fig. 31D, E) and *Lignanicystis barriosensis* (Zamora and Smith, 2008) (Fig. 31H, 32A), a new eocrinoid related to *Lichenoides* (Fig. 31K), the columnal-bearing eocrinoid *Ubaghsicystis segurae* (Gil Cid and Domínguez Alonso, 2002; Zamora *et al.*, 2010) (Fig. 31A-C, 32B), and the stylophoran *Ceratocystis* (32C). A section of similar age in the vicinity of Ciñera has also provided some ctenocystoids similar to *Ctenocystis* (Fig. 31F, G). The diachronic nature of the base of the Oville Formation allows the study of echinoderms from similar environment but different ages, while the faunas are relatively young in Los Barrios de Luna section (*Solenopleuropsis* (*M.*) *thorali*-*Solenopleuropsis* (*S.*) Zones) they are older in the vicinity of Soto de Caso locality. In the later a quiet peculiar echinoderm fauna from the *Badulesia tenera* Zone was first reported by Sdzuy (1993), who described the cinctan species *Sotocinctus ubaghsi* (Fig. 31I, J) and *Asturicystis jaekeli*. Further work in such section has provided *Ceratocystis* sp. and a new ctenocystoid similar to *Courtessolea*.

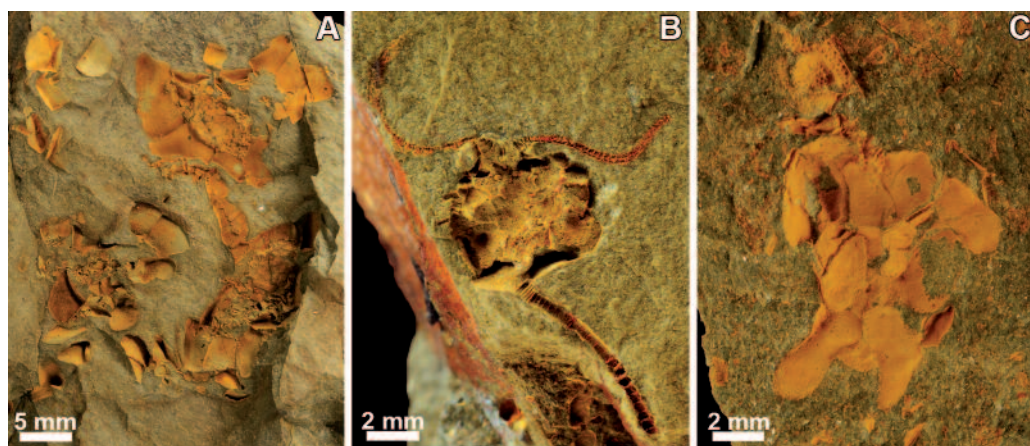


**Figure 30.** Detailed stratigraphic section of Genestosa Member (Oville Formation) in Barrios de Luna with the distribution of echinoderm taxa.





**Figure 31.** Cambrian Echinoderms from the Oville Formation at various localities. Specimens A-E, H, K come from Los Barrios de Luna; F, G from Ciñera and I, J from Soto de Caso. A-C. The eocrinoid *Ubaghsicystis segurae* with a columnal bearing stem and a distal holdfast. D, E. The cinctan *Gyrocystis* sp. F, G. The cinctan *Gyrocystis platessa* and a new ctenocystoid closely related with *Ctenocystis*. H. The cinctan *Lignanicystis barriosensis*. I, J. The cinctan *Sotocinctus ubaghsi*. K. The eocrinoid *Lichenoides* sp. All specimens are latex casts whitened with NH<sub>4</sub>Cl sublimated.



**Figure 32.** Cambrian Echinoderms from the Barrios de Luna section (Oville Formation). A. three specimens of the cinctar *Lignanicystis barrioiensis*. B. The eocrinoid *Ubaghiscystis segurae*. C. The armoured stylophoran *Ceratocystis* sp.

### STOP 15: Late Ordovician Echinoderms from Portilla de Luna

#### Location

Crossroad close to Portilla de Luna, approximately 1 km before getting to the village on the left.

Coordinates: 42°49'26.32" N, 5°49'06.47" W

Geological map of Spain, 1:50,000, sheet 129.

Geological setting: Southern slope of the Cantabrian Zone, Somiedo Unit.

Lithostratigraphical unit: upper part of "El Ventorrillo beds" and La Devesa Formation.

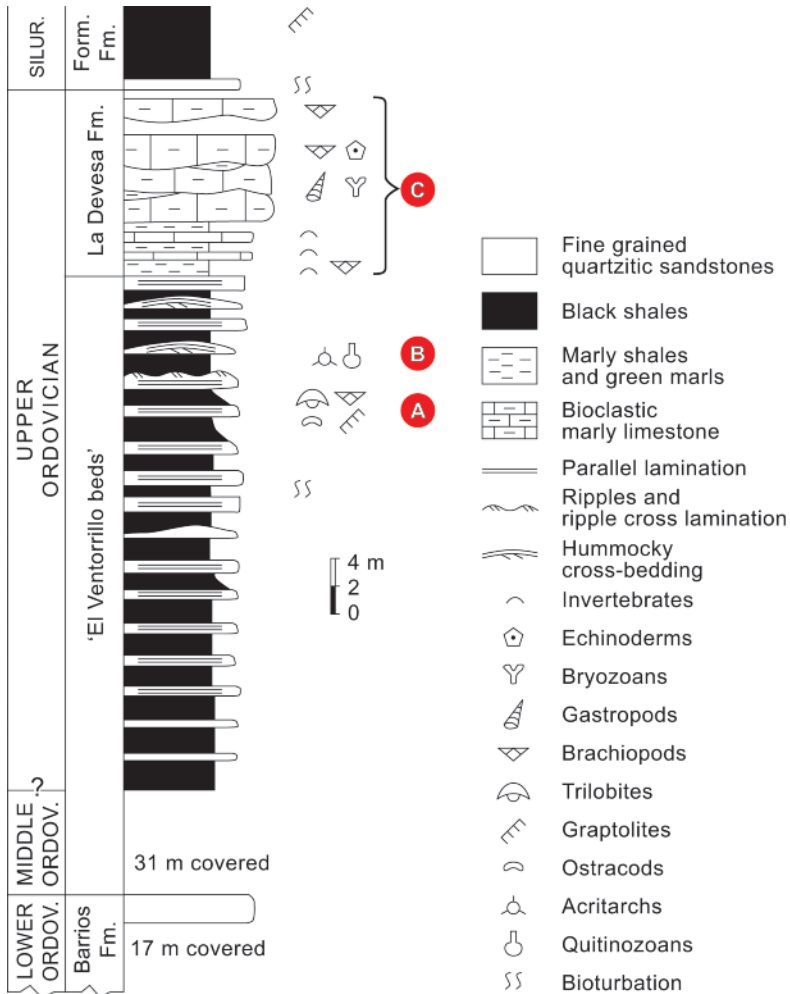
Age: Katian (Upper Ordovician).

#### Aims

Show general aspects of the Upper Ordovician succession in the Cantabrian Zone. Comparison with previously observed successions from the Iberian Chains. Look at the echinoderm faunas mostly composed of blastozoans and small crinoid fragments.

#### Description

The road to Portilla de Luna village provides a very complete Lower Palaeozoic section, complementary to the main Luna river section. The road starts at the Precambrian-Cambrian angular unconformity and the first kilometers offer a good succession including the La Herrería, Lánacara and Oville formations, all Cambrian in age, as well as the Cambro-Ordovician Barrios Formation and the Middle to Upper Ordovician "El Ventorrillo beds" and La Devesa Formation. Overlying the thick quartzite strata of the Barrios Formation (Fig. 33), a partially covered interval ca. 75 m thick reaching the base of the Silurian will be visited. It displays two different units, a lower siliciclastic "El Ventorrillo beds" and an upper calcareous La Devesa Formation (*sensu* Toyos and Aramburu, 2014).



**Figure 33.** Stratigraphic column from the lower Palaeozoic succession in Portilla de Luna (adapted from Gutiérrez-Marco *et al.* 1996). A-C indicate fossiliferous levels.

### “El Ventorrillo beds”

It is a 60-65 m-thick succession of black and green shales and fine sandstones, following two thickening and coarsening-upward sequences placed towards the upper half of the unit. Sandstone strata exhibit parallel lamination that change upsection into hummocky cross-stratified sets with some trace fossils. This interval was deposited in a marine environment affected by storms.

Fossils from the examined section are rare and only two horizons have provided some remains. Level A (see Fig. 33) has yielded trilobites (*Scotiella?* cf. *taouzensis*, Homalonotidae indet.), ostracods (*Vogdesella* sp.) and brachiopods (*Rafinesquina* sp.) that suggest a Berounian (Katian 1-2) age. Ordovician acritarchs and chitinozoans have been

sampled from Level B (M. Vanguetaine pers. com. 1985 in Gutiérrez-Marco *et al.*, 1996b). The lower half of the “El Ventorrillo beds” in its type section, here represented by a covered interval, provided a different assemblage of trilobites, graptolites, ostracods, brachiopods, molluscs, rare echinoderms (an ophiuroid arm and a single plate of *Anatifopsis* sp.) and some chitinozoans reassigned by Gutiérrez-Marco *et al.* (1999) to a late Oretanian (Darrivilian 2) age.

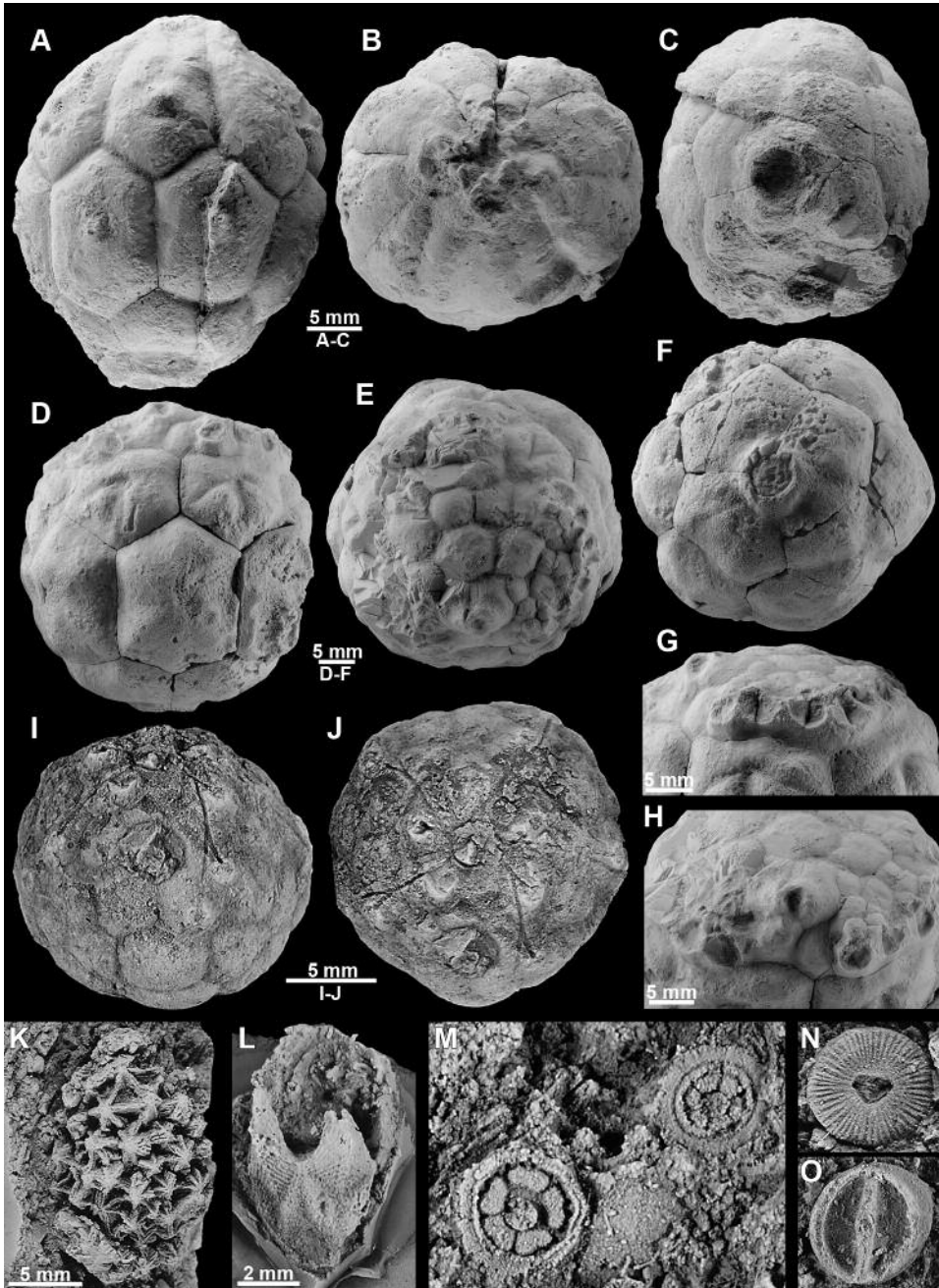
### La Devesa Formation

This interval is 13.5 m thick and comprises bioclastic carbonates with interbedded marlstones and shales. The top is marked by a 80 cm-thick burrowed sandstone. Overlying the sandstone level appears a 30 m-interval of black shales with Telychian graptolites belonging to the Silurian Formigoso Formation.

Fossils are common in this interval (Level C in Fig. 33) and include abundant echinoderms, brachiopods, bryozoans and scarce trilobites, machaeridians, gastropods and conodonts (Leyva *et al.*, 1984; Aramburu, 1989; Aramburu *et al.*, 1992; Gutiérrez Marco *et al.*, 1996; Del Moral, 2003). Brachiopods include at least 18 species: *Nicolella actoniae*, *Dolerorthis aberensis*, *Schizophorella* sp., *Skenidioides* sp., *Epitomyonia* sp., *Saukrodictya* sp., *Bicuspina armoricana*, *Oxoplecia* cf. *luesmae*, *Leangella* (L.) *anaclya*, L. (*Leptestiina*) *prantli*, *Aegironetes?* sp., *Eoplectodonta* (*Kozlowskites*) *ichnusae*, *Iberomena sardoa*, *Longvillia* sp., *Hedstroemina* sp., *Porambonites* (P.) *magnus* and *Eoanastrophia pentamera*. Echinoderms are a major component of the shelly assemblage but complete specimens including determinable taxonomic characters are rare. Blastozoans are the most common elements and include rhombiferans (*Heliocrinites rouvillei* Fig. 34K, *Caryocrinites* sp. Fig. 34D-H and *Hemicosmites* sp. Fig. 34A-C), diploporans (*Eucystis* n. sp. Fig. 34I, J and *Aristocystidae?* gen. et sp. indet.) and coronoids (*Mespilocystites* sp. Fig. 34L). Columnals belonging to both rhombiferans and crinoids are very abundant and include the following parataxa: *Trigonocyclicus* (col.) *vajgatschensis* Fig. 34N, *Aonodiscus* (col.) *spinusus*, *Conspectocrinus* (col.) *celticus* Fig. 34M, *Cyclocharax* (col.) *paucicrenellatus*, *Hexagonocyclicus* (col.) sp., *Pentagonocyclicus* (col.) spp., *Trilobocrinus* (col.) spp., *Cyclocyclicus* (col.) sp., *Pentagonopentagonalis* (col.) sp. and *Ristnacrinus* sp. Fig. 34O. Trilobites include *Ovalocephalus* cf. *tetrasulcatus* and *Cekovia?* sp. Finally, conodonts include *Amorphognathus ordovicicus*, *Amorphognathus* sp. A, *Scabbardella altipes*, *Birksfeldia* sp., *Icriodella* sp., *Dapsilodus* sp., *Panderodus* sp. and a single eocarnioniform element.

The above-reported fossil assemblage suggests a Katian 3-4 (Kradlovorian or Rawtheyan-Cautleyan Ashgill) age for this unit (Gutiérrez-Marco *et al.*, 1996b; Del Moral, 2003).





**Figure 34.** Echinoderms from the Upper Ordovician of Portilla de Luna. A-C. *Hemicosmites* sp. D-H. *Caryocrinites* sp. I, J. *Eucystis* sp. K. *Heliocrinites rouvillei*. L. *Mespilocystites* sp. M. *Conspetrocrinus* (col.) *celticus*. N. *Trigonocyclicus* (col.) *vajgatschensis*. O. *Ristnacrinus* (col.) sp. Specimens I-O are latex casts whitened with NH<sub>4</sub>Cl sublimated.



## DEVONIAN ECHINODERMS FROM THE SOUTHERN CANTABRIAN ZONE: BLASTOID VS CRINOID COMMUNITIES

Esperanza Fernández-Martínez, Luis Pedro Fernández, Johnny Waters and Samuel Zamora

### INTRODUCTION

During the Devonian times, Iberia was situated in the northwestern margin of Gondwana and separated from Laurussia by a narrow NE-trending Rheic Ocean. As the rest of Gondwana, Iberia moved northward, reaching about 35°S in Givetian times (Scotese, 2000, 2001; Nance *et al.*, 2012). Thus, the Devonian sediments were deposited in subtropical seas.

The localities visited in this field trip belong to the Asturian-Leonese facies Domain (Brouwer, 1964), which comprises an alternation of siliciclastic and carbonate formations bearing benthic fauna and deposited in a shallow-marine platform. The rocks of the Asturian-Leonese facies, which crop out in Asturias and León provinces, contrast with those from the Palentine Domain (Palencia province), which exhibit characteristics typical of a relatively deep but still neritic environment.

Two formations will be visited during this field trip: 1) the Valporquero Formation (Upper Emsian) at Colle locality (stop 16), and 2) the Santa Lucía Formation (Upper Emsian-Lower Eifelian) near Los Barrios de Luna locality (stop 17).

Devonian echinoderms from the Cantabrian Mountains, specially the crinoids, are well documented and the first species were described by De Verneuil in the 19th century (De Verneuil, 1850). Several authors have described crinoids from this area (Oehlert, 1896; Schmidt, 1931; Almela and Revilla, 1950; Sieverts Doreck, 1951), but the first comprehensive monograph on Spanish crinoids comes from Breimer (1962). He described five new genera, sixteen new species and fourteen previous unreported taxa in this area, most of them coming from the Lower and Middle Devonian. He also described a small number of Carboniferous species. Since then, only a few species have been reported (Webster, 1976; Pidal 1984, 2008; Kammer, 2001). Blastoids are also very common in this area, especially from the Lower Devonian and have been described by Etheridge and Carpenter (1883, 1886), Breimer (1971), Breimer and Dop (1975), and Waters and Zamora (2010). Other echinoderms from the Devonian of the Cantabrian Mountains include the rare echinoid *Rhenechinus* (Smith *et al.* 2013a), the edrioasteroid *Krama* (Smith and Arbizu, 1987) and a new ophiuroid (Blake *et al.* in press).

## STOP 16: Colle locality

### Location

Colle is on the left side of the regional road LE-3143 from Boñar to Sabero. The section to be visited lies at a hill, where the main church is situated (Figs. 35, 36A).

Coordinates: 42°50'38.06"N, 5°15'5.10"W

Geological map of Spain, 1:50.000, sheet of Boñar (104).

Geological setting: Southern slope of the Cantabrian Mountains, Esla Unit.

Lithostratigraphical unit: La Vid Group. Upper part of Valporquero Fm (Vilas Minondo, 1971; Vera de la Puente, 1989) or Sagüera Member of the Esla Fm. (Keller, 1988) (Fig. 37).

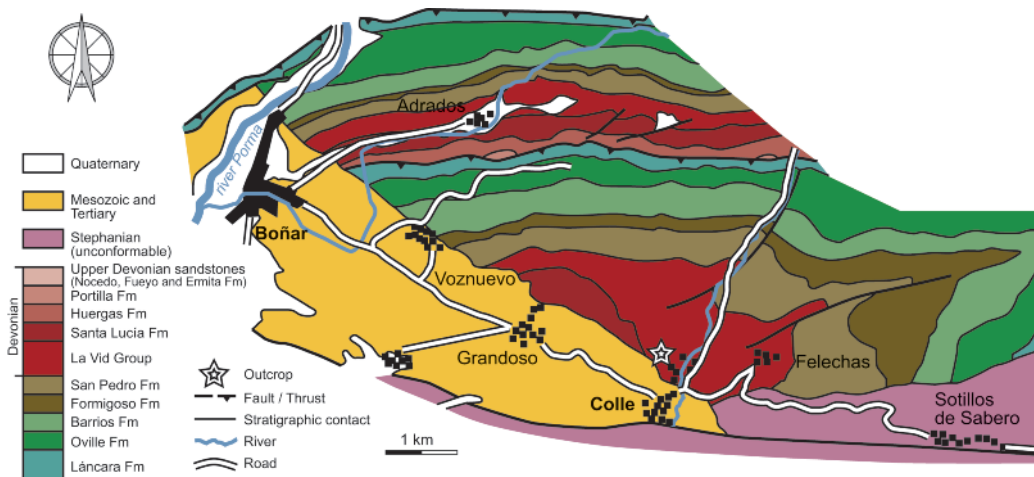
Age: Early Devonian, late Emsian.

### Aims

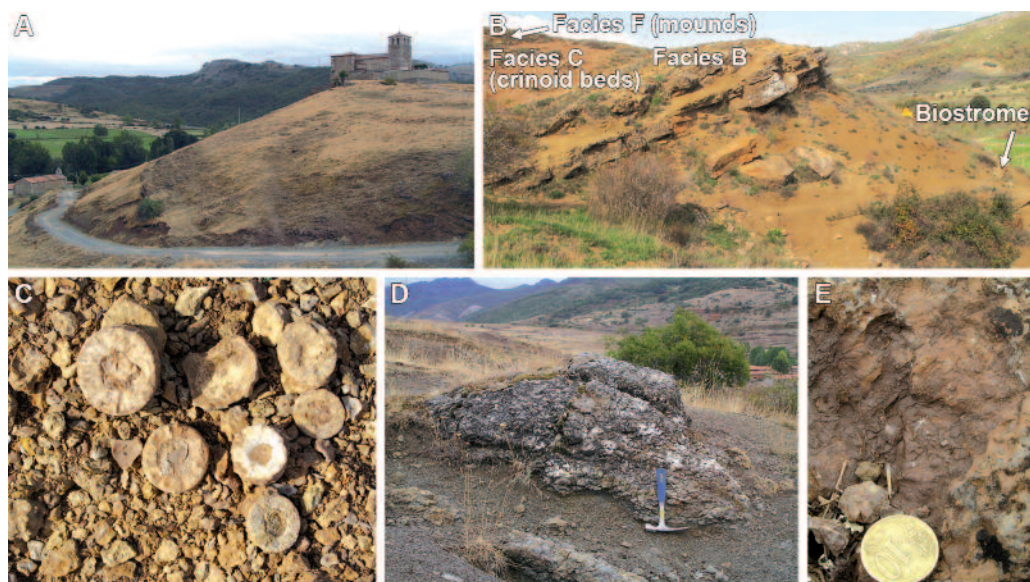
Compare two different beds with echinoderms. The lower bed (*Trybliocrinus* bed) is dominated by crinoids. *Pentremitidea* and rare specimens of other blastoid genera are found in the *Trybliocrinus* beds as a part of a typical Middle Palaeozoic Echinoderm Community. The upper bed (mud mounds bearing blastoids) has abundant blastoids belonging mostly to *Cryptoschisma* and *Pentremitidea*. The main goal of the stop is understand the causes that lead to the distribution of echinoderms.

### Description

Since the 19<sup>th</sup> century, Colle has been a well-known palaeontological site due to the quality and wealth of its fossils, which are usually known in ancient literature as "Sabero fossils". Most of them came from a red limestone and marlstone unit that crops out in the upper part of a hill located north of the village. Among these fossil taxa, the most



**Figure 35.** Simplified geological map of the Esla nappe near Colle showing the location of the study area. Modified after Fernández *et al.* 2006.



**Figure 36.** Field aspects of the Valporquero Formation in the vicinity of Colle. A. General view of the section. B. Detail of the section with indication of biostromes and crinoids bed and mud mound interval. C. Columns from the camerate crinoids *Trybliocrinus*. D. General aspect of a mud mound. E. Detail of a mud-mound.

relevant are brachiopods, corals, stromatoporoids, trilobites, bryozoans, nautiloids, gastropods, bivalves, ostracods, tentaculitoids, conodonts and abundant crinoids and blastoids.

This outcrop consists of a marly interval with limestone intercalations that caps a thick and rather monotonous shaly unit. This interval is important because of the occurrence of 1) several beds with a diverse fauna of crinoids and 2) an interval bearing mud-mounds with a very abundant, low diversity blastoid fauna.

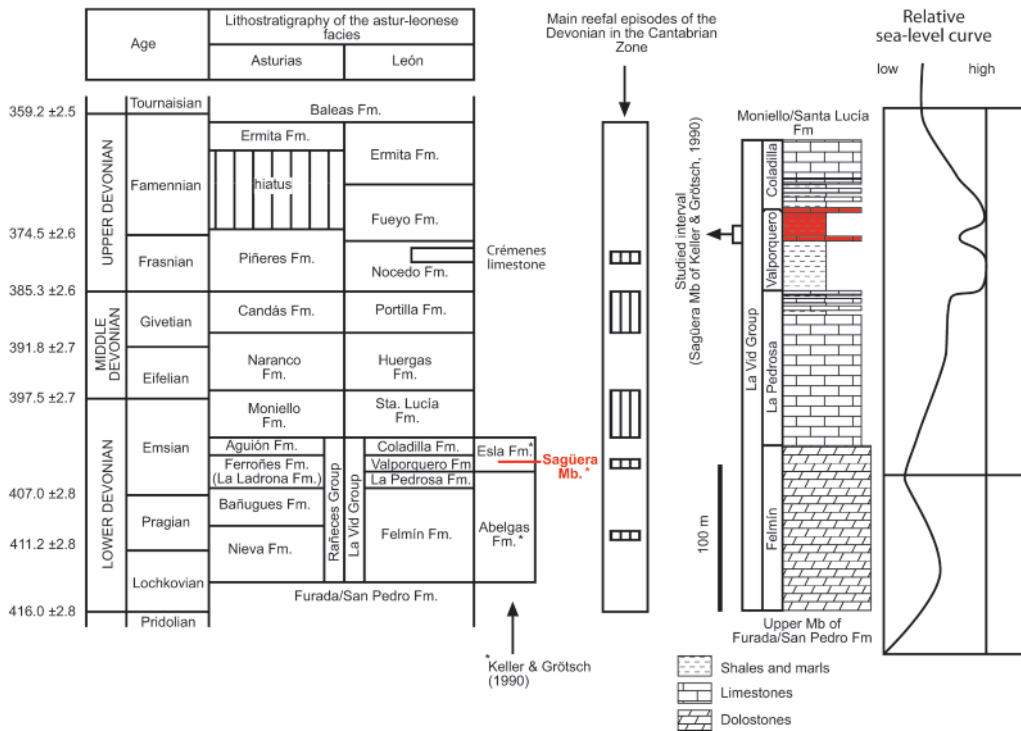
Lithostratigraphically, the interval exposed at Colle belongs to the Lower Devonian La Vid Group. In detail, it is located in the upper part of the Valporquero Formation (Vilas Minondo, 1971 and Vera de la Puente, 1989), forming the Upper Limestone Member of Leweke (1982). This interval has also been named as the Sagüera Member of the Esla Formation by Keller (1988) (Fig. 37). These beds have been dated as late Emsian by means of brachiopods and conodonts (García-Alcalde, 1987; García-López and Sanz-López, 2002).

The La Vid Group was deposited on a carbonate ramp, which underwent terrigenous incursions (Valporquero Shales). According to Vera de la Puente (1988), Keller and Grötsch (1990) and Keller (1997), the La Vid succession is tied to two 3<sup>rd</sup> order transgressive-regressive cycles. In this framework, the shales, marls and limestones of the Valporquero Fm. are thought to record the highstand deposits of the upper 3<sup>rd</sup> order cycle. (Fig. 37) In the following notes we will summarize the facies descriptions and interpretations after Fernández *et al.* (2006).

### *Trybliocrinus* bed

These beds mainly correspond to the facies C and B of Fernández *et al.* (2006). Both facies are similar but differ in the colour of the mudstones/marlstones, reddish in the case of facies C and greenish-gray in the case of facies B, and in their fossiliferous content, higher in the case of facies C (Figs. 36B, 38).

They are made of fossiliferous, shales/marlstones with alternations of cm-thick tabular beds of grey skeletal limestones. These limestones are packstones to wackestones with a matrix of argillaceous micrite to marlstone; limestone beds usually pinch out laterally passing into the surrounding muddy rock due to mixing by burrowing. The



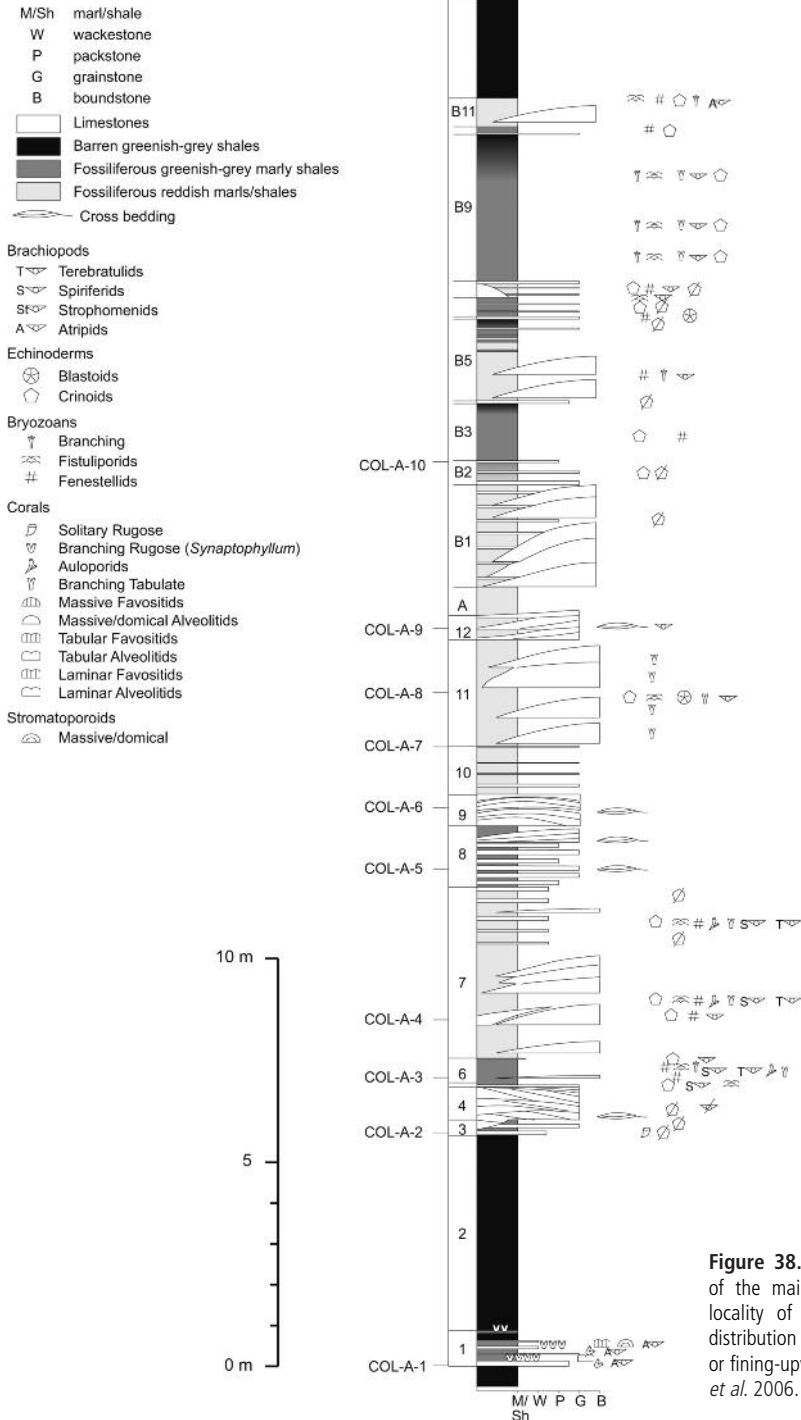
**Figure 37.** Chronostratigraphic chart showing the Devonian lithostratigraphic units of the Astur-Leonese facies that have been defined in the political regions of Asturias (northern part of the Cantabrian Zone) and León (southern part of the Cantabrian Zone) and the distribution of the reefal episodes. Absolute ages based on Gradstein *et al.* (2004). The stratigraphic subdivision of the La Vid Group is that of Vilas Minondo (1971) and Vera de la Puente (1989), but subdivisions by Leweke (1982) and Keller (1988) are also shown. Note that, contrary to other authors, Leweke (1982) treats La Vid Group as a formation made up of members. The log on the right depicts the interpreted relationships between the general stratigraphy of the La Vid Group and the sea-level curve (based on Keller and Grötsch 1990) and shows the location of the studied interval of the Valporquero Formation. After Fernández *et al.* 2006.

shales/marlstones contain abundant macrobiota of disintegrated echinoderm plates (mainly crinoids and blastoid ossicles) although some complete specimens may be found (Fig. 36D). Bryozoans are dominant in some beds. Bioclasts are variably bioabraded and/or iron stained.

The fossil content is similar in the limestones and marlstones/shales and is dominated by the following:

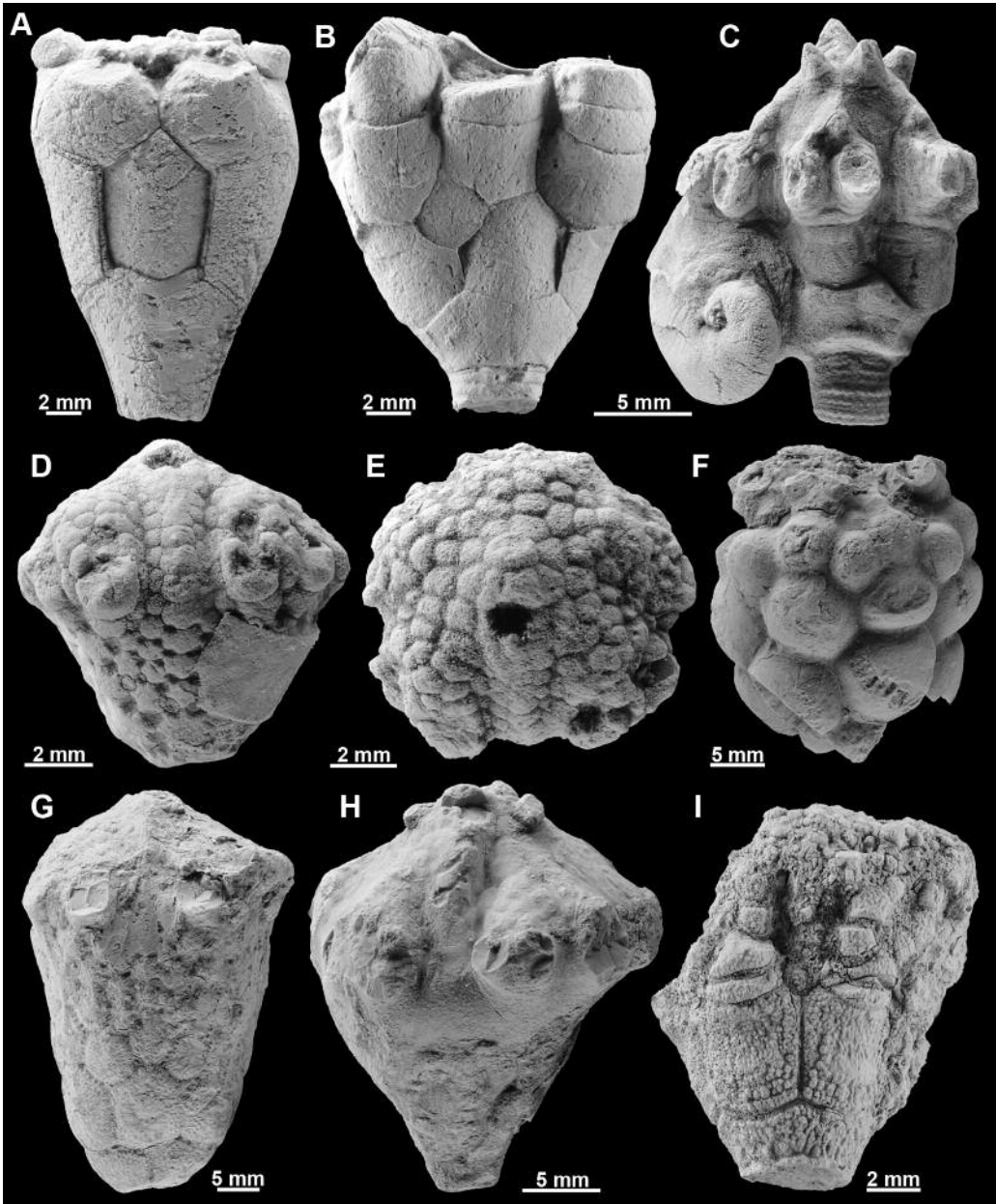
- echinoderms (crinoids and subordinate blastoids)
- bryozoans (fenestellids, mushroom-shaped fistuliporids and occasional ramose forms)
- brachiopods (spiriferids and terebratulids)
- diverse but small tabulate corals, such as ramose favositids (*Crenulipora*, *Thamnoptychia*, *Dendropora*) and auloporids (*Schlueterichonus*, *Cladochonus*, *Bainbridgia*).

The shales/marlstones were deposited in a low-energy marine environment with a background sedimentation dominated by clay fallout from suspension. The muddy water did not prevent colonization by benthic faunas. This environment was occasionally swept by currents that laid down the skeletal limestone beds. The complete fossils occurring in these beds are interpreted as infauna and epifauna that colonized the granular substrate after its deposition. The recorded burrowing activity would also account for the bedding destruction and mixing of the granular beds with the underlying muddy sediment. Nevertheless, it cannot be precluded that some skeletal limestone beds

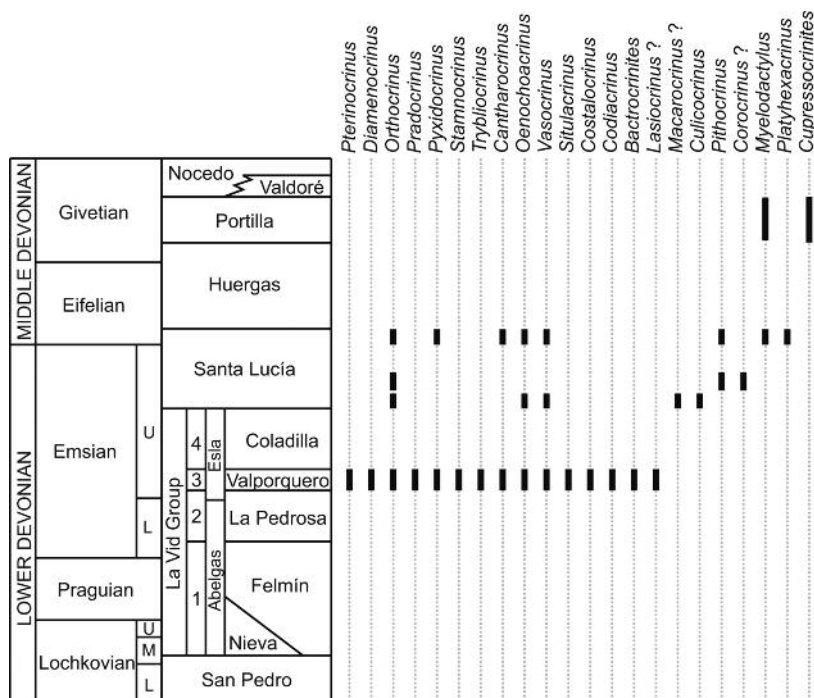


**Figure 38.** Simplified stratigraphic log of the main section described in the locality of Colle, showing the facies distribution and the coarsening-upward or fining-upward trends. After Fernández *et al.* 2006.





**Figure 39.** Crinoids from the Valporquero Formation of Colle (A, B, D, E, G, I), San Emiliano (H); and Santa Lucía Formation of Barrios de Luna (F); León. A. *Bactocrinites* sp., B. *Lasiocrinus?* sp. C. *Oenochoacrinus princeps*. D, E. *Pradocrinus baylii*. F. *Orthocrinus robustus*. G. *Pradocrinus baylii*. H. *Pyxidocrinus collensis*. I. *Hexacrinites* sp.



**Figure 40.** Stratigraphic distribution of crinoids from the Devonian of León. Based in data from Breimer (1962).

could represent “condensed” intervals, in which diminished rate of clay fallout could have resulted in a deposit enriched in skeletal components and lime mud.

Thus, as a whole, both facies would represent a shelf environment close to or above the storm wave base. The higher faunal content of facies C is interpreted to record a diminished clay input rate. Also, the reddish colour of the shales/marlstones of facies C is likely a syndimentary feature, generated by bacterial activity in the marine environment (see Bourque and Boulvain, 1993; Preat *et al.*, 1999; Boulvain, 2001). The vertical relationships between the reddish- and greenish-grey shales/marlstones intervals suggest that their apparition and vertical replacement by one another was controlled by allocyclic, long-term factors.

Crinoids from those beds are very abundant and show a high diversity (Figs. 39, 40). *Trybliocrinus* (Figs. 36C) is a very large camerate crinoid that developed an extensive root system for anchoring itself in the soft substrates of the maroon shales. Ruhrmann (1971) excavated a specimen in life position and determined that the roots penetrate more than 20 cm vertically into the sediment. Horizontal roots to neighboring individuals allowed for additional stabilization (Seilacher and Macclintock, 2005). Other crinoids from Colle (sensu Breimer, 1962; with updated information from Kammer, 2001) include *Diamenocrinus*, *Orthocrinus*, *Pradocrinus*, *Pyxidocrinus*, *Stammocrinus*, *Cantharocrinus*, *Oenochoocrinus*, *Vasocrinus*, *Situlacrinus*, *Costalocrinus*, *Codiocrinus*, *Bactrocrinites* and *Lasiocrinus?*. Unfortunately there is not information about the detailed stratigraphic distribution of taxa, and we can not discern whether those species occur in the *Trybliocrinus* bed or in the mud mounds.

### Mud-mounds bearing blastoids

These mud mounds belong to facies F of Fernández *et al.* (2006). They are small (0.3–0.8 m thick and 1–4 m wide) mounds or bed-like bodies, which display ragged margins (Fig. 36D) and occur encased in facies C (described above). The mounds mostly consist of a reddish and greenish micrite containing a relatively abundant macrobiota (<25%)

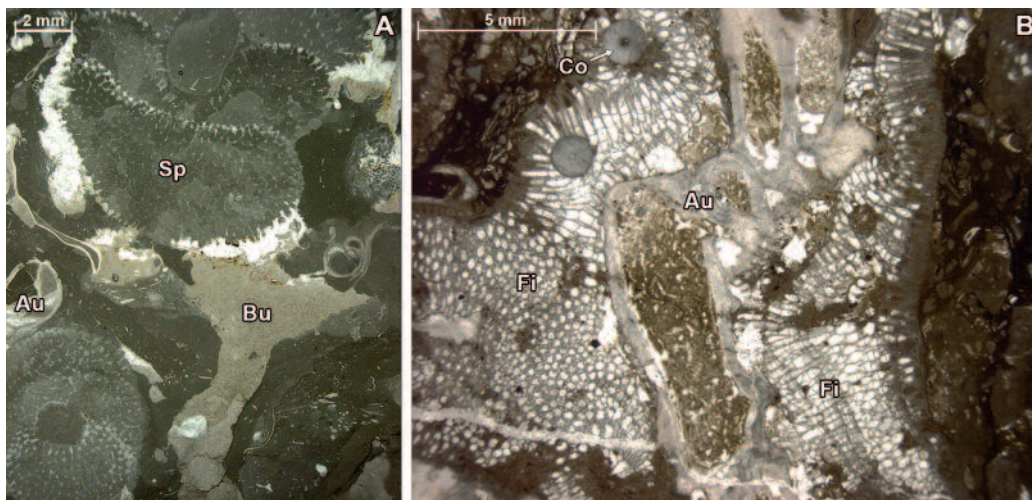
(Figs. 36E, 41). The micrite groundmass is structurally heterogeneous, with several sediment generations (polymuds of Lees and Miller, 1985) revealed by differences in colour or texture and displays different types of submillimetric to millimetric cavities (cf. Schmid *et al.*, 2001).

Under the microscope, three types of carbonate sediment are distinguished. Type 1 is a dense and dark micrite, with a homogeneous appearance, although it is locally peloidal (Bathurst, 1975). It is interpreted to result from cyanobacterial activity. Type 2 micrite is a lighter coloured, homogeneous micrite. It is thought to represent sediment deposited mechanically. This type of sediment likely originated within the mud mound proper, given the terrigenous mud-rich environment of the mounds. Type 3 is a microsparitic material with scarce minute bioclastic fragments. Cross-cutting relationships show that types 1 and 2 are coeval, but type 3 is a later sediment.

The rock contains three different types of millimetric cavities. None of them can be considered as typical stromatactis porosity and they are interpreted as resulting from burrowing processes partially modified by dissolution. Type A cavities are elongated pipe-like, occur in the micrite of types 1 and 2, and are filled by the type 2 micrite (Fig. 41A). They are thought to result from burrowing in soft sediment. Type B cavities comprise elongate or more irregular pores in type 1 and 2 micrites, sealed by type 3 sediment (microsparitic material) which completely fills the pores or just floors them giving rise to geopetal structures. The elongate pores are burrow-like, whereas the irregular cavities are larger (up to 1 cm) and display scalloped margins that truncate older sediment (micrite types 1 and 2) suggesting an origin by, at least partially, dissolution (cf. Lees and Miller, 1995). Nevertheless, scalloped margins have also been interpreted as indicative of sponge-boring activity (Schmid *et al.*, 2001, see their Fig. 17). Type C cavities are elongate burrow-like pores in type 3 sediment filled with the same type of sediment being only distinguished by subtle variations in colour.

Three generations of cement are found in the cavities of this facies. The first generation started growing during the final stage of the microsparite sedimentation and continued after its end. The second generation is found in some intraparticle pores and in type B porosity. The third generation is poorly developed and occludes the remnant voids in intraparticle and type B porosity.

The textural features and geometry of these mounds are comparable to those of mud mounds formed of microbial boundstones (see Lees and Miller, 1995; Monty, 1995; Pratt, 1995). Apart from the microbial communities, fenestellids and fistuliporids (Fig. 41B) played a significantly active role in the mud-mound stabilization by binding one another,



**Figure 41.** Detailed view of a mud mound. A. Microbial boundstone showing the complex relationships between sediment generations and pores. Note the burrow (type A cavity, Bu) in type 1 micrite and filled by microsparitic material. Skeletal components in this picture include sponges (Sp), partially bored auloporids (Au) and small bioclasts mainly corresponding to sponge spicules (tiny light coloured spots). B. Skeletal components in a mud mound. A small colony of auloporids (Au) surrounded by a fistuliporid bryozoan in which at least two columnals have been caught. Note the numerous bioclasts in the matrix around the fistuliporid.

the microbial micritic masses, diverse bioclasts, and the available sediment. In some instances, these bryozoans are found to be roofing type-B cavities, which suggests that they might have encrusted a soft body that later disappeared, although, in some of these cases, it seems that the bryozoans could have grown downwards from the cavity roof. The other organisms, chiefly crinoids and blastoids, are thought to have mainly played a passive role by providing grains, i.e., their complete or disarticulated skeletons, to the deposit (Fig. 41B). The small number of coral colonies suggests that they did not exert a significant baffling or binding role. The described biota is fairly similar to that of Devonian examples from Algeria (Wendt *et al.*, 1997), Kess-Kess mounds of Morocco (Brachert *et al.*, 1992). The suggested encrusting role of bryozoans has also been claimed in Early Devonian examples from the Clifton Saddle (west-central Tennessee, USA; Gibson *et al.*, 1998).

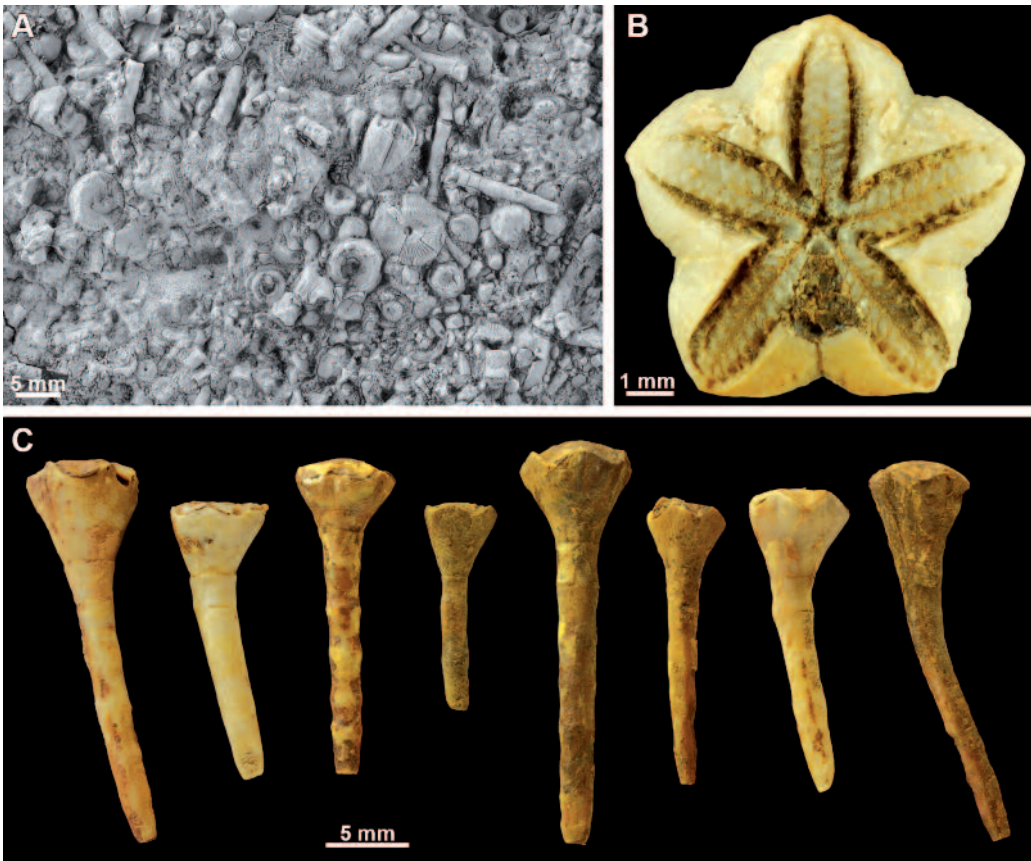
The macrobiota of the mud-mound facies does not differ significantly from that of the reddish marlstones and shales (see the previously described facies C) and shows a variable degree of bioabrasion (microborings). The most prominent organisms are:

- fenestellids and platy fistuliporids (Fig. 41B), usually encrusted by type 1 micrite masses and, in turn, encrust the micrite types 1 and 2 and the grains.
- branching bryozoans
- tabulate corals (Fig. 41B)
- tiny brachiopods or their disarticulated valves
- sponges (Fig. 41A)
- blastoid thecae and disarticulated plates of crinoids and blastoids (Fig. 42A)

Blastoids occur rarely in the maroon shales between the mud mounds or in areas where the mounds are absent. However, shales adjacent to the mud mounds contain an abundant echinoderm fauna dominated by the blastoid *Cryptoschisma* (Fig. 42C). Although population density varies considerably, blastoid abundance reached 1000 individuals per square meter in one sample. The vast majority of the individuals were *Cryptoschisma*. The remainder belong to *Pentremitidea* (Fig. 42B). Blastoids typically possess a long, somewhat flexible stalk, attached to a conical theca, and with long slender brachioles extending two or three times the height of the theca. The stem of *Cryptoschisma* consists of long cylindrical stem plates, which could not have produced a flexible stem common in most blastoids. The apparent rigidity of the stem suggests that it functioned more as a column, supporting the crown a short distance above the sea floor in a rigid position. *Cryptoschisma* shows no evidence of a root system or even an aboral tip of the stem which expanded into an attachment disk. The aboral tip of complete stems forms a point similar to the point of a pin. This attachment configuration is similar to the sediment sticker model of attachment seen in many Early and Middle Cambrian echinoderms, which are interpreted to have lived on substrates that included microbial mats. Although we have no direct evidence for microbial mats in the maroon shales adjacent to the mudmounds at Colle, *Cryptoschisma* would not have been able to support itself in the soupy substrates implied by the maroon shales without such mats. The stem of *Cryptoschisma* and its mode of life are in stark contrast to *Tribliocrinus* with its long stem and complex root system with long roots penetrating deeply into similar facies in shallow water presumably without microbial mats. We interpret *Cryptoschisma* as a Cambrian style sediment sticker living in a restricted environment in the Early Devonian.

The mud-mound facies was deposited in a low energy, relatively deep-water environment although absolute depth of sedimentation is difficult to assess. The blastoid populations at Colle are the oldest occurrence of truly abundant blastoids so the anachronistic sediment sticker mode of life for *Cryptoschisma* is significant. Although other blastoid genera are found in moderate abundance in shallow water environments within the La Vid Formation, *Cryptoschisma* is not. This pattern of relatively modest blastoid abundance in shallow water crinoid-dominated faunas versus blastoid domination of deep-water echinoderm faunas is repeated in the Famennian in the Hongguleleng Formation in China and in various faunas in the Mississippian. The pattern is often associated with significant biotic turnover in echinoderm faunas and was most noticeable in the Middle Mississippian extinction event (Ausich *et al.* 1988).





**Figure 42.** Blastoids from the Valporquero Formation at Colle. A. Detail of a tempestite with several fragments of blastoids and crinoids. D. *Pentremitidea* collected from the mud mounds. C. Different specimens of *Cryptoschisma* showing the complete stem. Specimens were collected from the shale intervals around the mud mounds.



## STOP 17. Crinoids and blastoids from the Santa Lucía Formation (Barrios de Luna locality)

### Location

This outcrop is a quarry placed near the town of Miñera de Luna, in the local road CL-626 between La Magdalena and Villablino localities. The access to this quarry is a trail that goes right across from the yacht club placed on the shore of the Luna reservoir (Fig. 43).

Coordinates: 42°52'36.00"N, 5°50'31.70"W

Geological map of Spain, 1:50.000, sheet of Los Barrios de Luna (105).

Geological setting: Southern slope of the Cantabrian Mountains, Somiedo Unit.

Lithostratigraphical unit: Santa Lucía Formation.

Age: Early Devonian, late Emsian to Mid Devonian, early Eifelian.

### Aims

Observe several species of crinoids and blastoids appearing in some calcareous beds of the Santa Lucía Formation.

### Description

A quite complete and well-exposed Palaeozoic succession overlying a Precambrian substratum crops out in the surroundings of Los Barrios de Luna locality. Because of it, this site has the status of Global Geosite, it is to say a geological site of international interest. In this stop, a quarry recently excavated in limestones belonging to the Santa Lucía Formation (Comte, 1936) (Figs. 26, 43A) is visited. This formation (and the Moniello Fm, its equivalent in the northern slope of the Cantabrian Mountains) consists of ca. 250 m of grey limestones and argillaceous limestones interbedded with thin shaly intervals.

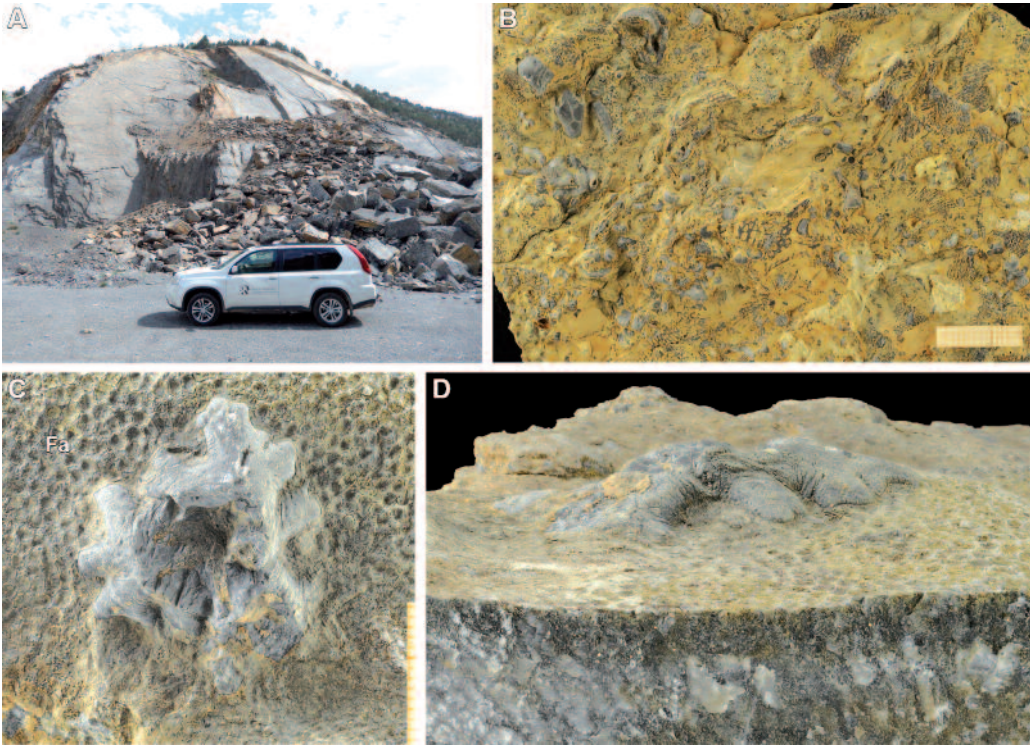
Most of the Santa Lucía Formation is Emsian, being the Emsian/Eifelian boundary marked by the first occurrence of *Icriodus retrodepressus* and *Arduspirifer intermedius*, which occurs within the upper part of the formation (García-López and Sanz-López, 2002).

Limestones in this outcrop correspond to subtidal facies (Moniello succession type) and have been described as fossiliferous limestone with a small amount of corals and without stromatoporoids (Méndez-Bedia, 1976). This petrographic type is usual in the lower and upper members of the subtidal successions of the Santa Lucía Formation.

According limestone classification of Folk, they are biomicrite and biopelsparite types, being the crinoids and locally the bryozoan the most important sources of the bioclasts, whose size is quite diverse. Quarry works have exposed several bed planes, containing complete brachiopods (*Paraspirifer*, *Euryspirifer*, *Athyris*, *Uncinulus* and *Athyris*, among others), large fragments of bryozoans, common crinoids and subsidiary blastoids. Fragments of trilobites, ostracods, corals and sponges also occur in these beds.

These crinoidal bars are usually interpreted as open-marine facies. They acted as hard substrates for the setting of diverse opportunistic faunas (mostly brachiopods, bryozoan, corals and other crinoids), which eventually would give place to the development of biostromes and bioherms. In the visited outcrop, no reefal limestone has been observed but some beds contain on the top abundant massive and branched tabulate corals (favositids, alveolitids, caliaporids and thamnoporids).

Crinoids from the Santa Lucía Formation are very abundant (Figs. 39, 40) and several complete specimens have been collected from this outcrop (Fig. 39F). Interesting is the fact that some crinoids attached their holdfast on large living corals (Fig. 43C, D). Blastoids occurring in the Santa Lucia Formation, although very rare, include *Pentremitidea archiaci*, *Conuloblastus malladai* and *Hyperblastus wachsmuthi* (Etheridge & Carpenter 1886). Santa Lucia blastoids are very important in the phylogenetic history of the group because they illustrate one of five ordinal transitions of a fissiculate ancestor to a spiraculate descendent (Waters and Horowitz, 1993). Based on the detailed morphological work by Breimer and Dop (1975), the transition from *Pentremitidea archiaci* (a fissiculate) to *Hyperblastus wachsmuthi* (a spiraculate in the Order Pentrematida) through the intermediate species, *Conuloblastus malladai*, is



**Figure 43.** Santa Lucía Formation at Barrios de Luna. A. Detail of the Santa Lucía Formation in the visited quarry. B. General aspect of facies with abundant echinoderm remains. Note an almost complete blastoid in the upper left side of the photograph. C, D. Crinoid holdfast attached to the upper part of a tabular colony of the tabulate coral genus *Squameofavosites*.

well documented. Details of the other four transitions await new phylogenetic analysis. Unlike the La Vid Formation which had shallow- and deep-water echinoderm communities, all the echinoderms in the Santa Lucia belong to a shallow-water community.

DAY 5: June 21<sup>th</sup> 2015**DEVONIAN ECHINODERMS FROM ARNAO (ASTURIAS): CLAY VS HARD-GROUND PELMATOZOAN COMMUNITIES**

Juan Luis Suárez Andrés, Miguel Arbizu, Johnny Waters and Samuel Zamora

**INTRODUCTION**

The Devonian succession of the northern slope of the Cantabrian Zone is an alternation of clastic and carbonate units, up to 2000 m thick, deposited on a shallow marine platform within a general regressive context. The benthic fauna is both diverse and abundant across the whole series and up to seven reefal episodes can be differentiated (Méndez-Bedia *et al.* 1994). The foundations of Devonian stratigraphy in the northern slope were first described by Barrois (1882) in his study of the coastal outcrops, though several formations have been redefined thereafter. The currently accepted units are described in figure 26 together with the laterally equivalent formations from the southern slope. Comte (1959), Radig (1962), Arbizu (1972), Julivert (1976), Méndez-Bedia (1976), Truyols and Julivert (1976), Arbizu *et al.* (1979), Vera de la Puente (1989) and García-Alcalde (1992), among others, have discussed the stratigraphy and structure of the Devonian succession in Asturias.

The Lochkovian-Emsian Rañeces Group is 400 to 600 m thick and subdivided into four formations, named Nieva, Bañugues, La Ladrona and Aguión, primarily consisting of limestones and dolostones with marlstones and shales. Most of the succession represents a shallow-platform facies sequence, with terrigenous sediments increasing eastwards, where the source area was placed during the Early Devonian. The fauna is dominated by diverse brachiopods, rugose and tabulate corals, echinoderms, bryozoans, trilobites, but conodonts, ostracods, bivalves and tentaculitids are also present.

The oldest two reefal episodes were localized in the basal Pragian and the Pragian-Emsian transition of the Nieva and Bañugues formations. The third episode occurred throughout the basin at the beginning of the Late Emsian and is found in the Aguión Formation in Asturias and the Valporquero Formation in León. Along with reefal fauna, communities from lower energy environments flourished during the Late Emsian. The Aguión Formation contains abundant, diverse and well-preserved benthic communities of crinoids, corals, brachiopods and bryozoans. Reefal and low energy communities exposed in Arnao were described by Álvarez-Nava and Arbizu (1986), Arbizu *et al.* (1993) and Arbizu *et al.* (1995). Breimer, (1962) completed a systematic study of Devonian echinoderms, mostly crinoids, from Asturias. Other echinoderms, including blastoids, echinods, edrioasteroids and asterozoans, also have been described (Breimer, 1971; Breimer and Macurda, 1972; Macurda, 1983; Smith and Arbizu, 1987; Smith *et al.* 2013a; Blake *et al.* in press).

Although previous studies are limited, the excellent exposures of the Aguión Formation in Arnao provide an opportunity for detailed analysis of echinoderm palaeobiology and palaeoecology. Arbizu *et al.* (1993, 1995) described four different faunal communities with increasing turbidity and interpreted that *Trybliocrinus* flourished in low diversity, high turbidity environments. Smith *et al.* (2013a) concluded that specimens of the echinoid *Rhenechinus* found in the shallow marine beds of the Aguión Formation in Arnao should be considered as autochthonous. Pelmatozoans are abundant in the outcrop and bedding planes provide a unique opportunity to study the modes of attachment in Devonian pelmatozoans. The field excursion will focus on several bedding planes of Emsian red and green marls exposed along the rocky shore westward of Arnao beach. The cliffs were quarried and a railway laid over the soft, roughly horizontal marly beds of the Aguión Formation. Erosion of those beds has exposed numerous macrofossils including many pelmatozoan holdfasts preserved *in situ*.





**Figure 44.** A. Panoramic view of Arnao site. Outcrop indicated with an arrow. B. Detail of the succession that alternate red marls and limestones. C. Aboral view of a complete cup from the crinoids *Trybliocrinus flatheanus*. D. Complete crinoid *Pterinocrinus decembrachiatus* preserving a complete cup and pinnulate arms. E. Proximal view of the *Trybliocrinus flatheanus* roots preserved *in situ*. F. Lateral view of the *Trybliocrinus flatheanus* roots.

## STOP 18: Arnao

### Location

The Arnao Platform is located in a series of old quarries between La Vela Cape and Arnao beach. (Figs. 44A, 45).

Coordinates: 43°34'44.6"N, 5°59'02.2"W

Geological map of Spain, 1:50.000, sheet of Avilés (13).

Geological setting: Northern slope of the Cantabrian Zone, Somiedo Unit.

Lithostratigraphical unit: Aguión Formation (Fig. 46)

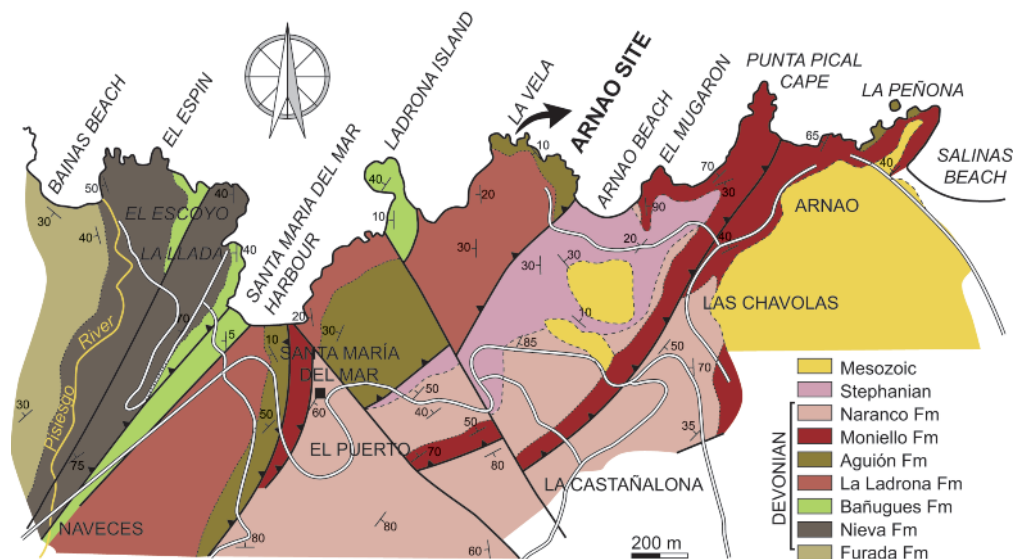
Age: Early Devonian, late Emsian

### Aims

Compare the attachment strategies and holdfast morphologies of different crinoids regarding the type of substratum; red marls correspond to soft substrates whereas yellow carbonate levels correspond to hard ground substrates. Alternating red marls and bryozoan pavements offered suitable firm ground for pelmatozoan attachment. Discuss the environment in which Devonian echinoids lived.

### Description

Arnao is a small village in the central coast of Asturias (Fig. 45) located in a complex geological setting. The Devonian succession is unconformably overlain by a small Stephanian basin. The entire sequence was deformed during the Variscan Orogeny and is capped by Mesozoic terrigenous deposits. The Arnao thrust outcrops west of the beach placing the Lower Devonian Aguión Formation over the Stephanian sandstones and siltstones. Arnao and its surroundings

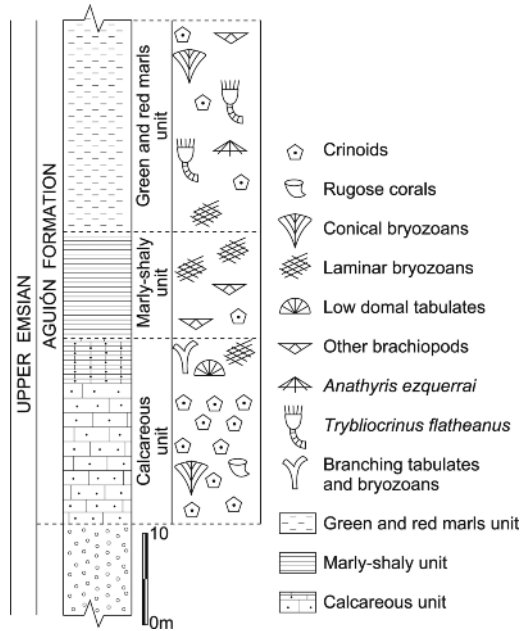


**Figure 45.** Map showing the geological setting of the Aguión Formation and the situation of Arnao fossil site. Modified from García-Alcalde (1992).

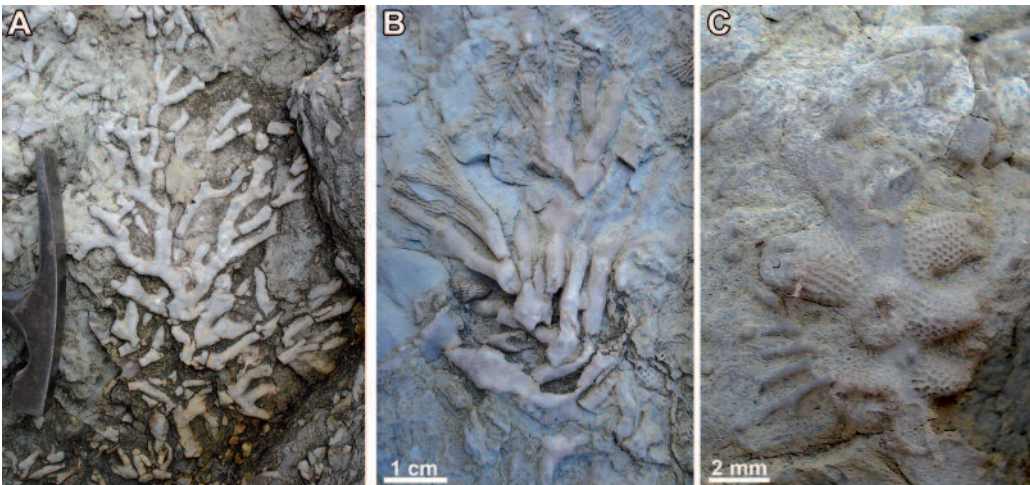


possess a remarkable geological and historical heritage due to the diversity of stratigraphic, palaeontological, geomorphological and structural features as well as preserved historical facilities of the mining industry that benefited from the Stephanian coal deposits (Arbizu and Méndez-Bedia, 2006; Arbizu *et al.*, 2012).

The Arnao platform is one of the most spectacular Palaeozoic fossil localities in northern Spain. In this area a Lower Devonian (upper Emsian) succession crops out in a series of quarried cliffs between La Vela Cape and Arnao beach. Here, the lower 60 m of the Aguión Formation are exposed and have been informally divided into three lithostratigraphic units by Álvarez Nava and Arbizu (1986). These units were subsequently used by Arbizu *et al.* (1993, 1995, 2012) in their description of the fossil communities of the outcrop (Fig.46). The lower calcareous unit is about 22 m of bioclastic limestones ranging from encrinitic grainstones to wackestones interpreted as bioclastic bars. Reefs developed on these bars by the successive colonization of domal, branching (Fig. 47A) and bilaminar tabulates. Bryozoans and crinoids are accessory faunal elements for which skeletal remains were the most common substrates. The middle unit is 12 m of grey argillaceous marlstones and shales with very abundant fenestrate bryozoans. The fauna also includes other bryozoans,



**Figure 46.** Stratigraphical succession of the Aguión Formation at Arnao Platform showing lithological units, their faunal composition and types of communities. From Arbizu *et al.* (1995).



**Figure 47.** A. Branching tabulate coral *Platyaxon* from the calcareous unit. B. Composite tubular colony of the fenestrate bryozoan *Bigeyina* from the red and green marls unit. C. The rare fenestrate bryozoan *Ernstipora* encrusting an unidentified lacy bifoliate bryozoan from the red and green marls unit.

solitary rugose corals, crinoids, the easily identifiable brachiopod *Anathyris* and other large brachiopods. Fenestrate and foliaceous bilaminar bryozoan colonies reached sizes up to 20 cm. Ephemeral, non-skeletal biota constituted suitable substrates for encrusting forms, as evidenced by hollow, pseudobranching bryozoans. The upper unit is 24 m of red and green argillaceous marls with interspersed red and yellowish limestones. This unit contains a rich fauna in which pelmatozoans, bryozoans and brachiopods are dominant, but sparse rugose corals, tabulates and bivalve molluscs are also present. Crinoids are diverse and sometimes very common, especially *Trybliocrinus flatheanus* (Fig. 44C) and to a lesser extent *Pterinocrinus decembrachiatus* (Fig. 44D), *Orthocrinus* sp. and *Stammocrinus intrastigmatus* (Schmidt 1931; Breimer 1962). Blastoids (Fig. 48C) include *Pentremitidea lusitanica*, *P. pailletti*, *P. archiaci*, *Pleuroschisma verneuili*, and *Metablastus? hispanica*. Articulated specimens of the echinoid *Rhenechinus* (Fig. 48G) come from a horizon towards the top of the upper unit, although isolated plates are found throughout. The most common brachiopod is *Anathyris* but atrypids, orthids and strophomenids can also be found. Bryozoans are abundant and diverse; fenestrates are the most conspicuous group but trepostomes, fistuliporids, rhabdomesid and ptilodictid cryptostomes also occur. Bryozoans in this unit developed a variety of growth habits ranging from different erect unilaminar forms (fenestrates, dendroid cryptostomes), to delicate erect lacy bifoliate colonies and a range of encrusting morphologies, the latter indicating colonization of ephemeral and skeletal substrates as well as the soft sediment. The abundance and preservation of delicate erect bryozoan forms indicates that these communities flourished in a low energy environment. The most representative fenestrate bryozoan in the red and green marls of Arnao is *Bigeyina* (Fig. 47B) which frequently developed tubular composite colonies, a growth habit very abundant in this outcrop but extremely uncommon among fenestrates elsewhere (Suárez Andres and McKinney, 2010). The outcrop of the Aguión Formation in Arnao is the type locality of *Ernstipora* (Fig. 47C), a singular fenestrate that encrusted fenestrate fragments and crinoids (Suárez Andrés and Wyse Jackson, 2014).

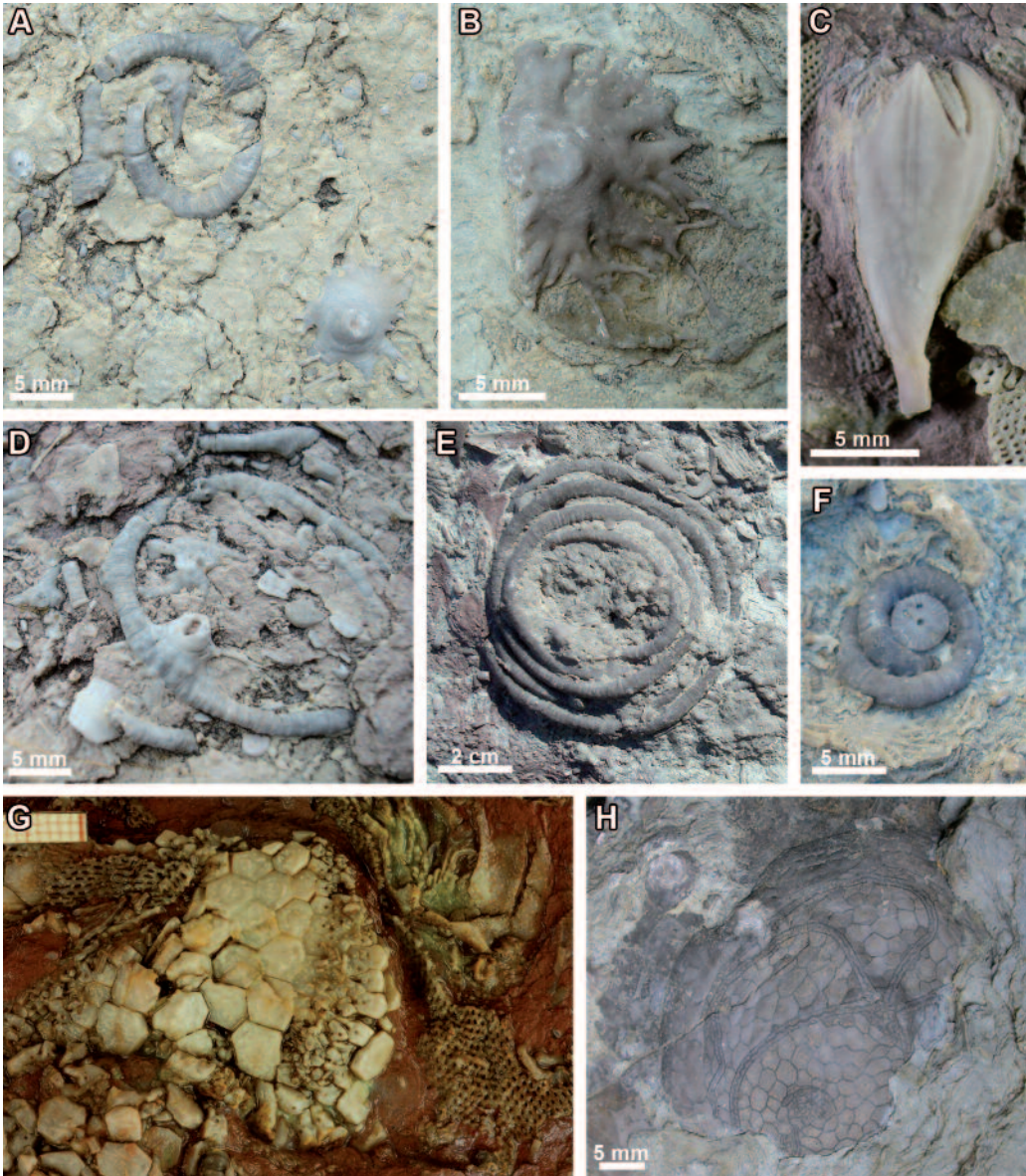
Argillaceous sediment content varies significantly within the upper unit of the Aguión Formation. Arbizu *et al.* (1995) suggested this was a major factor in controlling the different fossil assemblages found here. Levels in which the crinoid *Trybliocrinus* is common probably represent turbid palaeoenvironments where there was abundant mud in suspension, whereas the level with echinoids has abundant fenestrates and other crinoids (e.g., *P. decembrachiatus*) and appears to have been deposited in a well-oxygenated and relatively tranquil environment. Arbizu *et al.* (1995) interpreted the entire unit as having been deposited in a typical platform environment with highly variable rates of terrigenous supply. The presence of marl-rich beds with well-preserved echinoderm specimens alternating with encrinitic tempestite beds suggests an offshore setting above the storm wave base level, sporadically affected by storm events.

Different levels within Aguión Formation show differences in substrate consistency. The red marls represent a soft substrate in which the crinoid *Trybliocrinus* developed large stout cirri (Figs. 44E, F; 49) on large rhizoid holdfast. The terminal stem has a large lumen widened by resorption into a cavity that reaches half of the stem diameter (Seilacher and Macclintock, 2005) and cirri appear on polynodal articular facets. Those cirrials spread several centimeters through the substrate, up to 20 cm in depth, and are distally branched.

In contrast, yellowish carbonates display hard ground surfaces in places that are colonized by different types of holdfasts. The most abundant type are discoid holdfasts with lobate margins (Fig. 48A). Those are small (2 cm on length) and their distal part follows the hardground surface. Second in order of abundance are coiled distal stems with stereomatic outgrowths of columnals (Fig. 48E). They are several centimeters long and the coil is made with up to four loops of the distal stem. There is even possible to reconstruct the sequence of hardground colonization because there are some specimens overlapping previous developed holdfast (Fig. 48D).

Bioclastic firm ground substrates also offer an appropriate surface for pelmatozoan attachment. In those surfaces radix-like holdfast colonizing bryozoan pavements are very abundant (Fig. 48B). They show several centimeters in diameter and radicles branch distally. Minor components in those pavements are distal coil of stems growing around other crinoid stems (Fig. 48F).

The study of holdfast morphology and distribution in Arnao is still very preliminary but environmental factors, mostly substrate consistency, played an important role. Soft ground substrate dominated by *Trybliocrinus* was a principal environment in the Aguión Formation and its lateral equivalent in the southern slope of the Cantabrian Mountains, Valporquero Fm. (see stop 16). Hardground surfaces were more limited and the possible causes of their genesis have not yet been clarified. Those surfaces were colonized by pelmatozoans displaying discoidal holdfast and distal coiled stems with stereomatic outgrowths.



**Figure 48.** Echinoderms from the Aguión Formation in Arnao. A. Hardground preserving a discoidean holdfasts with lobate margins and a partially disarticulated distal coiled stem. B. Radix-like holdfast attached to a bryozoan pavement. C. The blastoid *Pentremitidea pailletti*. D. Discoidean holdfast overlapping a coiled distal stem. E. Coiled distal stem with stereomatic outgrowths of columnals. F. Distal coil of stem growing around other crinoid stem. G. The echinoid *Rhenechinus ibericus*. H. The edrioasteroid *Krama devonica*.



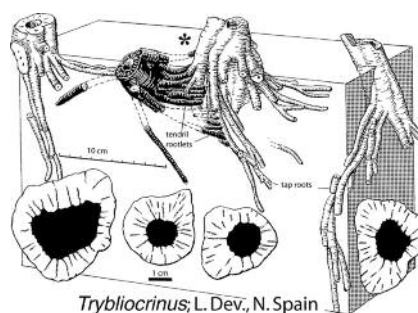
Regional criteria consistent with general structural features seem to indicate that the Devonian succession in Arnao is overturned, as represented by Álvarez-Nava and Arbizu (1986) and thereafter by García-Alcalde (1992, Fig. 1), Arbizu *et al.* (1995, 2012) and Arbizu and Méndez-Bedia (2006). Contrary to these regional criteria, the distribution of upright crinoid holdfasts preserved *in situ* in the Aguión Formation points to a normal polarity of the section. Palaeontological features may help elucidate the polarity of problematic sections, particularly if it can be stated that remains of benthic fauna are found preserved *in situ*. The geological structure of Arnao is complicated, as evidenced in the map and sections carried out by García-Alcalde (1992); detailed local structural, stratigraphical and palaeontological observations of this section should be performed in search of a better understanding of the geology of this area.

### Acknowledgements

Isabel Pérez (Zaragoza University) provided excellent assistance preparing most of the figures included in this field guide. This is a contribution to the projects CGL2012-39471, CGL2013-48877 and CGL2011-24775 of the Spanish Ministry of Economy and Competitiveness. JW was supported by a Research Opportunity Award to NSF Grant DEB-1036260 through the University of Tennessee. This is a contribution to IGCP 596. SZ was funded by a Ramón y Cajal Grant (RYC-2012-10576). We appreciate discussions with Bill Ausich (Ohio State University) and Tom Kammer (University of West Virginia) on some of the crinoid species. Silvia Menéndez (Museo Geominero) for access to the Devonian crinoid collection. J. L. S. and M. A. thank the Council of Castrillón for giving facilities during the study of Arnao.

### REFERENCES

- Aller, J., Bastida, F. and Rodríguez-Fernández, L.R. 2002. Cantabrian Zone: general geological features. In García-López, S. and Bastida, F. (Eds.), *Palaeozoic conodonts from Northern Spain*. Instituto Geológico y Minero de España, serie Cuadernos del Museo Geominero, 1, 3-33.
- Alonso, J.L., Marcos, A. and Suárez, A. 2009. Paleogeographic inversion resulting from large out of sequence breaching trusts: The León Fault (Cantabrian Zone, NW Iberia). A new picture of the external Variscan thrust belt in the Ibero-Armorican Arc. *Geologica Acta*, 7, 451-473.
- Álvarez-Nava H. and Arbizu M. 1986. Composición y desarrollo de un arrecife emsiense en la Plataforma de Arnao (Asturias, NO de España). *Memorias I Jornadas de Paleontología*, 33-51.
- Álvoro, J.J. 2007. New ellipsocephalid trilobites from the lower Cambrian member of the Láncara Formation, Cantabrian Mountains, northern Spain. *Memoirs of the Association of Australasian Palaeontologists*, 34, 29-41.
- Álvoro, J.J. and Blanc-Valleron, M.M. 2002. Stratigraphic and structural framework of the Neoproterozoic Paracuellos Group, Iberian Chains, NE Spain. *Bulletin de la Société géologique de France*, 173, 219-227.
- Álvoro, J.J. and Vennin, E. 1996a. Spicules d'éponges et Chancelloriidae cambriens des Chaînes Ibériques, NE Espagne. *Revue de Micropaléontologie*, 39, 293-304.
- Álvoro, J.J. and Vennin, E. 1996b. Tectonic control on Cambrian sedimentation in south-western Europe. *Eclogae Geologicae Helveticae*, 89, 935-948.
- Álvoro, J.J. and Vennin, E. 1997. Episodic development of Cambrian eocrinoid-sponge meadows in the Iberian Chains (NE Spain). *Facies*, 37, 49-64.



**Figure 49.** Drawing of cirral roots of *Trybliocrinus* from the Lower Devonian of northern Spain. From Seilacher and Macclintock, 2005.

- Álvaro, J.J., Ahlberg, P., Babcock, L.E., Bordonaro, O.L., Choi, D.K., Cooper, R.A., Ergaliev, G.K., Gapp, I.W., Ghobadi Pour, M., Hughes, N.C., Jago, J.B., Koronikov, I., Laurie, J.R., Lieberman, B.S., Paterson, J.R., Pegel, T.V., Popov, L.E., Rushton, A.W.A., Sukhov, S.S., Tortello, M.F., Zhou, Z. and Žylińska, A. 2013a. Global Cambrian trilobite palaeobiogeography assessed using parsimony analysis of endemism. In Harper, D.A.T. and Servais, T. (Eds.), *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoir, 38, 269-292.
- Álvaro, J.J., Bauluz, B., Gil Imaz, A. and Simón, J.L. 2008. Multidisciplinary constraints about Cadomian compression and early Cambrian extension in the Iberian Chains, NE Spain. *Tectonophysics*, 461, 215-227.
- Álvaro, J.J., Elicki, O., Geyer, G., Rushton, A.W.A. and Shergold, J.H. 2003a. Palaeogeographical controls on the Cambrian trilobite immigration and evolutionary patterns reported in the western Gondwana margin. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 195, 5-35.
- Álvaro, J.J., Rouchy, J.M., Bechstädt, T., Boucot, A., Boyer, F., Debrenne, F., Moreno-Eiris, E., Perejón, A. and Vennin, E. 2000a. Evaporitic constraints on the southward drifting of the western Gondwana margin during Early Cambrian times. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 160, 105-122.
- Álvaro, J.J., Shields, G.A., Ahlberg, P., Jensen, S. and Palacios, T. in press. Ediacaran-Cambrian phosphorites from the western margins of Gondwana and Baltica. *Sedimentology*.
- Álvaro, J.J., Van Vliet-Lanoë, B., Vennin, E. and Blanc-Valleron, M.M. 2003b. Lower Cambrian paleosols from the Cantabrian Mountains (northern Spain): a comparison with Neogene-Quaternary analogues. *Sedimentary Geology*, 163, 67-84.
- Álvaro, J.J., Vennin, E., Moreno-Eiris, E., Perejón, A. and Bechstädt, T. 2000b. Sedimentary patterns across the Lower-Middle Cambrian transition in the Esla nappe (Cantabrian Mountains, northern Spain). *Sedimentary Geology*, 137, 43-61.
- Álvaro, J.J., Vennin, E., Muñoz, A., Sánchez-Valverde, B. and Ojeda, J.L. 2000c. Interplay of orbital forcing and tectonic pulses in the Cambrian Iberian platform, NE Spain. *International Journal of Earth Sciences*, 89, 366-376.
- Álvaro, J.J., Zamora, S., Clausen, S., Vizcaino, D. and Smith, A.B. 2013b. The role of abiotic factors in the Cambrian Substrate Revolution: A review from the benthic community replacements of West Gondwana. *Earth-Science Reviews*, 118, 69-82.
- Aramburu, C. 1989. *El Cambro-Ordovícico de la Zona Cantábrica (NO de España)*. University of Oviedo, Ph.D. thesis, University of Oviedo, 530 p. (unpublished).
- Aramburu, C. and García-Ramos, J.C. 1993. La sedimentación cambro-ordovícica en la Zona Cantábrica (NO de España). *Trabajos de Geología*, Universidad de Oviedo, 19, 45-73.
- Aramburu, C., Arbizu, M., Bernárdez, E., Gozalo, R., Gutiérrez-Marco, J.C. and Liñán, E. 2006. *Paleontología y Estratigrafía del Paleozoico Inferior en Los Barrios de Luna*. XXII Jornadas de la Sociedad Española de Paleontología, Guía de Campo de la Excursión B. Universidad de León, 75 p.
- Aramburu, C., Méndez-Bedia, I. and Arbizu, M. 2002. The Lower Palaeozoic in the Cantabrian Zone (Cantabrian Mountains, NW Spain). In García-López, S. and Bastida, F. (Eds.), *Palaeozoic conodonts from Northern Spain*. Instituto Geológico y Minero de España, serie Cuadernos del Museo Geominero, 1, 35-49.
- Aramburu, C., Méndez-Bedia, I., Arbizu, M. and García-López, S. 2004. Zona Cantábrica: Estratigrafía: La secuencia preorogénica. In Vera, J.A. (ed.), *Geología de España*. Madrid, SGE-IGME, 27-34
- Aramburu, C., Truyols, J., Arbizu, M., Méndez-Bedia, I., Zamarreño, I., García-Ramos, J.C., Suárez de Centi, C. and Valenzuela, M. 1992. El Paleozoico Inferior de la Zona Cantábrica. In Gutiérrez Marco, J.C., Saavedra, J. and Rábano, I. (Eds.), *Paleozoico Inferior de Ibero-América*. Universidad de Extremadura, 397-421.
- Arbizu, M. 1972. El Devónico inferior de la costa asturiana entre la Punta de Narvata y la Ensenada de Moniello. *Breviora Geologica Asturica*, 3, 33-39.
- Arbizu, M. and Méndez-Bedia, I. 2006. El Patrimonio Natural y Cultura de Castrillón (Asturias): Geología, Fósiles e Historia Minera. *Trabajos de Geología Universidad de Oviedo*, 26, 73-91.
- Arbizu, M., Álvarez-Nava, H., Méndez-Bedia, I. and García-López, S. 1993. Las comunidades bióticas de las "Capas con Trybliocrinus" (Devónico Inferior) en la Plataforma de Arnao (Asturias, Noroeste de España). *Revista Española de Paleontología*, n. extr., 71-77.
- Arbizu, M., García-Alcalde, J.L., García-López, S., Méndez-Bedia, I., Sánchez de Posada, L.C., Soto, F.M., Truyols, M., Truyols, J., Álvarez, F., Méndez, C. and Menéndez, J.R. 1979. Biostratigraphical study of the Moniello Formation (Cantabrian Mountains, Asturias, NW Spain). *Geologica et Palaeontologica*, 13, 103-124.
- Arbizu, M., Méndez-Bedia, I. and Soto, M. 1995. Fossil communities in the Aguión Formation (Lower Devonian) of the Arnao Platform (Asturias, NW Spain). *Geobios*, 28, 567-571.



- Arbizu, M., Méndez-Bedia, I., Busquets, P., Pérez-Estaun A., Álvarez-Laó, D.J., Turrero, P. 2012. El patrimonio natural y cultural de Arnao (Castrillón): geología, fósiles e historia minera. In Bahamonde Rionda J.R., Cuesta Fernández A., Fernández-González M.A., Fernández-González L.P. y Colombo Piñol F. (Eds.), *Geo-Guías del Instituto Geológico y Minero de España, 9, Excursiones VIII Congreso Geológico de España*, 9-38.
- Ausich, W.I., Meyer, D.L. and Waters, J.A. 1988. Middle Mississippian Blastoid Extinction Event. *Science*, 240, 796-798.
- Barragán, T., Esteve, J., García-Bellido, D., Zamora, S. and Álvaro, J.J. 2014. New mid-Cambrian palaeoscolecid sclerites of *Hadimopanella oezgueli* from the Cantabrian Mountains, northern Spain. *GFF*, 136, 22-25.
- Barrois, Ch. 1882. Recherches sur les terrains anciens des Asturies et de la Galice. *Mémoires de la Société Géologique du Nord*, 2, Lille, 1-630 pp.
- Bathurst, R.G.C. 1975. Carbonate sediments and their diagenesis. *Developments in Sedimentology*, 12. Elsevier Science Publ. Co., New York, 658 pp.
- Bauluz, B., Fernández Nieto, C. and González López, J.M. 1998. Diagenesis-very low grade metamorphism of clastic Cambrian and Ordovician sedimentary rocks in the Iberian Range (Spain). *Clay Mineral*, 33, 373-393.
- Blake, D., Zamora, S. and García-Alcalde, J. in press. A new Devonian asteroid-like ophiuroid from Spain. *Geologica Acta*.
- Boulvain, F. 2001. Facies architecture and diagenesis of Belgian Late Frasnian carbonate mudmounds. *Sedimentary Geology*, 145, 269-294.
- Bourque, P.A. and Boulvain, F. 1993. A model for the origin and petrogenesis of the red stromatolite limestone of Paleozoic carbonate mounds. *Journal of Sedimentary Petrology*, 63, 607-619.
- Brachert, T.C., Buggisch, W., Flügel, E., Hüßner, H.M., Joachimski, M.M., Tourneur, F. and Walliser, O.H. 1992. Controls of mud mound formation: the Early Devonian Kess-Kess carbonates of the Hamar Laghdad, AntiAtlas, Morocco. *Geologische Rundschau*, 81, 15-44.
- Breimer, A. 1962. A monograph on Spanish Paleozoic Crinoidea. *Leidse Geologische mededelingen*, 27 (2), 190 pp.
- Breimer, A. 1971. Nota previa sobre los blastoideos del Devoniano de la Cordillera Cantábrica (España). *Boletín del Instituto Geológico y Minero de España*, 82 (2), 157-171.
- Breimer, A. and Dop J.A. 1975. An anatomical and taxonomic study of some lower and middle Devonian blastoids from Europe and North America, I and II. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, Series B 78, 39-61.
- Breimer, A. and Macurda Jr., D.B. 1972. *The phylogeny of the fissiculate blastoids*. Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afdeling Natuurkunde, Eerste Reeks. 26 (3), 390 pp.
- Brett, C.E., Liddell, W.D., and Derstler, K.L. 1983. Late Cambrian hard substrate communities from Montana/Wyoming: the oldest known hardground encrusters. *Lethaia*, 16, 281-289.
- Brouwer, A. 1964. Devonian biostromes and bioherms of the southern Cantabrian Mountains, Northwestern Spain. In Straaten, L.M.J.U. van (Ed.), *Deltaic and Shallow Marine Deposits*. Devonian Sedimentology. Elsevier Amsterdam 1, 48-53.
- Capote, R. and González Lodeiro, F. 1983. La estructura herciniana en los afloramientos paleozoicos de la Cordillera Ibérica. In Comba, J.A. (Ed.), *Contribuciones sobre temas generales*, IGME, Libro Jubilar J.M. Ríos, 3, 11-32.
- Carls, P. 1965. *Jung-silurische und unterdevonische Schichten der Östlichen iberischen Ketten (NE-Spanien)*. Inaugural-Dissertation Würzburg, 155 pp.
- Carls, P. 1974. Die Proschizoporiinae (Brachiopoda, Silurium-Devon) der Östlichen Iberischen Ketten (Spanien). *Senckenbergiana lethaea*, 55, 153-227.
- Carls, P. 1975. The Ordovician of the Eastern Iberian Chains near Fombuena and Luesma. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 152, 127-146.
- Carls, P. 1977. The Silurian-Devonian boundary in northeastern and central Spain. In: The Silurian-Devonian boundary. *International Union of Geological Sciences, Series A*, 5, 143-158.
- Carls, P. 1983. La Zona Asturoccidental-Leonesa en Aragón y el macizo del Ebro como prolongación del Macizo Cantábrico. In Comba, J.A. (Ed.), *Contribuciones sobre temas generales*, IGME, Libro Jubilar J.M. Ríos, 3, 11-32.
- Carls, P. 1987. Ein Vorschlag zur biostratigraphischen Redefinition der Grenze Gedinium/Siegenium und benachbarter Unter-Stufen. *Courier Forschung-Institut Senckenberg*, 92, 77-121.
- Carls, P. 1988. The Devonian of Celtiberia (Spain) and Devonian Paleogeography of SW Europe. In McMillan, N.J., Embry, A.F. and Glass, D.J. (Eds.), *Devonian of the World*. Canadian Society of Petroleum Geologists, Calgary, Memoir 14 (1), 421-466.
- Carls, P. and Valenzuela-Ríos, J.I. 2002. Devonian-Carboniferous rocks from the Iberian Cordillera. In: García-López, S. and Bastida, F.

- (Eds.), *Palaeozoic conodonts from Northern Spain*. Instituto Geológico y Minero de España, serie Cuadernos del Museo Geominero 1, 299-333.
- Chauvel, J. and Le Menn, J. 1979. Sur quelques Echinodermes (Cystoïdes et Crinoïdes) de l' Ashgill d' Aragon (Espagne). *Geobios*, 12 (4), 549-587.
- Chauvel, J., Meléndez, B. and Le Menn, J. 1975. Les Echinodermes (Cystoïdes et Crinoïdes) de l'Ordovicien supérieur de Luesma (Sud de l' Aragon, Espagne). *Estudios Geológicos*, 31, 351-364.
- Clausen, S. 2004. New Early Cambrian eocrinoids from the Iberian Chains (NE Spain) and their role in nonreefal benthic communities. *Eclogae geologicae Helveticae*, 97, 371-379.
- Clausen, S. and Álvaro, J.J. 2006. Skeletonized microfossils from the Lower-Middle Cambrian transition of the Cantabrian Mountains, northern Spain. *Acta Palaeontologica Polonica*, 51, 223-238.
- Clausen, S. and Smith, A.B. 2008. Stem structure and evolution in the earliest pelmatozoan echinoderms. *Journal of Paleontology*, 82, 737-748.
- Colmenar, J. in press. The arrival of brachiopods of the Nicolella Community to the Mediterranean margin of Gondwana during the Late Ordovician: palaeogeographical and palaeoecological implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*.
- Colmenar, J., Harper, D.A.T. and Villas, E. 2014. Morphofunctional analysis of *Svobodaina* species (Brachiopoda, Heterorthidae) from South-Western Europe. *Palaeontology*, 57, 193-214.
- Colmenero, J.R., Fernández, L.P., Moreno, C., Bahamonde, J.R., Barba, P., Heredia, N. and González, F. 2002. Carboniferous. In Gibbons, W. and Moreno, M.T. (Eds.), *The Geology of Spain*. Geological Society, London, 93-116.
- Comte, P. 1936. La série dévonienne du León (Espagne). *Comptes Rendus de l'Académie des Sciences de la Terre et des Planètes, Paris*, 202, 337-339.
- Comte, P. 1959. Recherches sur les terrains anciens de la Cordillère Cantabrique. *Memorias del Instituto Geológico y Minero de España*, 60, 1-440 pp.
- Del Moral González, B. 2008. *Conodontos y microfácies del Ordovícico Superior de la Cordillera Ibérica y Sierra Morena Oriental*. Universidad Complutense de Madrid (Unpublished PhD Thesis), 427 pp.
- Del Moral, B. 2003. Primeros conodontos kralodvorienses (Ordovícico Superior) de la Zona Cantábrica, Portilla de Luna, León (España). *Revista Española de Micropaleontología*, 35, 275-283.
- Dereims, A. 1898. *Recherches géologiques dans le Sud de l'Aragon*. Université de Lille, Unpublished PhD, 199 pp.
- Droser, M.L. and Bottjer, D. J. 1986. A semiquantitative field classification of ichnofabric. *Journal of Sedimentary Petrology*, 56, 558-559.
- Esteve, J. 2011. Sistemática, biostratigrafía y aspectos paleobiológicos de los trilobites del Caesaraugustiense medio-superior y Languedociense inferior de las Cadenas Ibéricas y Zona Cantábrica (Norte de España). *Unpublished PhD*, 393 pp.
- Esteve, J. 2013. Revision of enrolled Cambrian trilobites from Spain and its implications in trilobite evolution. *Estudios Geológicos*. 69, 165-181.
- Esteve, J., Hughes, N. and Zamora, S. 2011. The Purujosa trilobite assemblage and the evolution of trilobite enrollment. *Geology*, 39 (6), 575-578.
- Esteve, J., Hughes, N. and Zamora, S. 2013. Thoracic structure and enrolment style in middle Cambrian *Eccaparadoxides pradoanus* presages caudalization of the derived trilobite trunk. *Palaeontology*, 56, 589-601
- Fernández, L.P., Bahamonde, J., Barba, P., Colmenero, J.R., Heredia, N., Rodríguez-Fernández, L.R., Salvador, C., Sánchez de Posada, L.C., Villa, E., Merino-Tomé, O. and Motis, K. 2004. La Zona Cantábrica. Secuencia sinorogénica. In Vera, J.A. (Ed.), *Geología de España*. SGE-IGME, Madrid, 34-42.
- Fernández, L.P., Nose, M., Fernández-Martínez, E., Méndez-Bedia, I., Schröder, St. and Soto, F. 2006. Reefal and mud mound facies development in the Lower Devonian La Vid Group at the Colle outcrops (León province, Cantabrian Zone, NW Spain). *Facies*, 52 (2), 307-327.
- Fortey, R.A. and Cocks, L.R.M. 2005. Late Ordovician global warming - The Boda event. *Geology*, 33, 405-408.
- Friedrich, W.P., 1993. Systematik und Funktionsmorphologie mittelkambrischer Cincta (Carpoidea, Echinodermata). *Beringeria*, 7, 1-190.
- Gandl, J. 1972. Die Acastavinae und Asteropyginae (Trilobita) Keltiberiens (NE-Spanien). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 530, 1-184.
- García-Alcalde, J.L. 1987. North Gondwanan Emsian events. *Episodes*, 20, 241-246.

- García-Alcalde, J.L. 1992. El Devónico de Santa María del Mar (Castrillón, Asturias, España). *Revista Española de Paleontología*, 7 (1), 53-79.
- García-López, S and Sanz-López, J. 2002. Devonian to Lower Carboniferous conodont biostratigraphy of the Bernesga valley section (Cantabrian Zone, NW Spain). In García-López, S. and Bastida, F. (Eds), *Palaeoic conodonts from Northern Spain*. Instituto Geológico y Minero de España, serie Cuadernos del Museo Geominero, 1, 163-194.
- García-López, S. 2002. A stratigraphic overview of the Cantabrian Devonian (NW Spain). In García-López, S. and Bastida, F. (Eds), *Palaeoic conodonts from Northern Spain*. Instituto Geológico y Minero de España, serie Cuadernos del Museo Geominero, 1, 51-59.
- Gibson, M.A., Clement, C.R. and Broadhead, T.W. 1998 Bryozoan-dominated carbonate mudmounds in a cratonic setting from the basal Devonian of southeastern United States. In McMillan, N.J., Embry, A.F. and Glass, D.J. (Eds.), *Devonian of the World*. Canadian Society of Petroleum Geologists, Memoir 14, 541-552.
- Gil Cid, M.D. and Domínguez Alonso, P. 2002. *Ubaghsicystis segurae* nov. gen. y sp., nuevo eocrinoide (Echinodermata) del Cámbrico Medio del Norte de España. *Coloquios de Paleontología*, 53, 21-32.
- Gozelak, P. and Zamora, S. 2013. Stereom microstructures of Cambrian echinoderms revealed by cathodoluminescence (CL). *Paleontologia Electronica*, 16 (3), 32A.
- Gozalo, R. and Liñán, E., 1988. Los materiales hercínicos de la Cordillera ibérica en el contexto del Macizo Ibérico. *Estudios Geológicos*, 44, 399-404.
- Guensburg, T.E. and Sprinkle, J. 2001. Ecologic radiation of Cambro-Ordovician echinoderms, in Zhuravlev, A.Yu. and Riding, R. (Eds.), *The Ecology of the Cambrian Radiation*. Columbia University Press, New York, 428-444.
- Gutiérrez-Marco, J.C. 1986. *Graptolitos del Ordovícico español*. Universidad Complutense de Madrid (unpublished PhD thesis), 3 vol., 701 pp.
- Gutiérrez-Marco, J.C. and Štorch, P. 1998. Graptolite biostratigraphy of the Lower Silurian (Llandovery) shelf deposits of the Western Iberian Cordillera, Spain. *Geological Magazine*, 135, 71-92.
- Gutiérrez-Marco, J.C., Aramburu, C., Arbizu, M., Méndez-Bedia, I., Rábano, I. and Villas, E. 1996b. Rasgos estratigráficos de la sucesión del Ordovícico Superior en Portilla de Luna (Zona Cantábrica, noroeste de España). *Geogaceta*, 20, 11-14.
- Gutiérrez-Marco, J.C., Chauvel, J. and Meléndez, B. 1996a. Nuevos equinodermos (cistideos y blastozoos) del Ordovícico de la Cordillera Iberica (NE España). *Revista Española de Paleontología*, 11 (1), 100-119.
- Gutiérrez-Marco, J.C., Aramburu, C., Arbizu, M., Bernárdez, E., Hacar Rodríguez, M.P., Méndez-Bedia, I., Montesinos López, R., Rábano, I., Truyols, J. and Villas, E. 1999. Revisión bioestratigráfica de las pizarras del Ordovícico Medio en el noroeste de España (Zonas Cantábrica, Asturoccidental-leonesa y Centroibérica septentrional). *Acta Geologica Hispanica*, 34, 3-87.
- Gutiérrez-Marco, J.C., Ghienne, J.F., Bernárdez, E. and Hacar, M.P. 2010. Did the Late Ordovician African ice sheet reach Europe? *Geology*, 38, 279-282.
- Gutiérrez-Marco, J.C., Herranz, P., Pieren, A., Rábano, I., Sarmiento, G.N., San José, M.A. de, Barnolas, A. and Villas, E. 2005. El margen pasivo Ordovícico-Silúrico. In Vera, J.A. (Ed.), *Geología de España*. SGE-IGME, Madrid, 473-475.
- Gutiérrez-Marco, J.C., Robardet, M., Rábano, I., Sarmiento, G.N., San José Lancha, M.Á., Herranz Araujo, P. and Pieren Pidal, A.P. 2002. Ordovician. In Gibbons, W. and Moreno, M.T. (Eds.), *The Geology of Spain*. Geological Society, London, 31-49.
- Hammann, W. 1983. Calymenacea (Trilobita) aus dem Ordovizium von Spanien; ihre Biostratigraphie, Ökologie un Systematik. *Abhandlungen der Senckenbergischen naturforschenden Gesellschaft*, 542, 1-177.
- Hammann, W. 1992. The Ordovician trilobites from the Iberian Chains in the province of Aragón, NE Spain. The trilobites of the Cystoid Limestone (Ashgill Series). *Beringeria*, 6, 1-219.
- Hammann, W., Robardet, M. and Romano, W. 1982. The Ordovician System in southwestern Europe (France, Spain, and Portugal): Correlation chart and explanatory notes. *IUGS Publications*, 11, 1-46.
- Havlíček, V. and Josopait, V. 1972. Articulate brachiopods from the Iberian Chains. Northeast Spain (Middle Cambrian-Upper Cambrian-Tremadoc). *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 140, 238-353.
- Hernández-Sampelayo, P. 1935. El Sistema Cambriano. Explicación del nuevo mapa geológico de España. *Memorias del IGME*, 1, 291-518.
- Julivert, M. 1976. La estructura de la region del Cabo Peñas. *Trabajos de Geología Universidad de Oviedo*, 8, 203-309.
- Kammer, Y.W. 2001. Phenotypic bradytely in the Costalocrinus-Barycrinus lineage of Paleozoic cladid crinoids. *Journal of Paleontology*, 75 (2), 383-389.

- Keller, M. 1988. Die La-Vid-Gruppe - Fazies, Palaögeographie und synsedimentäre Tektonik im Unterdevon des Kantabrischen Gebirges (NW-Spanien). *Erlanger Geologische Abhandlungen Heft*, 115, 77-154.
- Keller, M. 1997. Evolution and sequence stratigraphy of an Early Devonian carbonate ramp, Cantabrian Mountains, Northern Spain. *Journal of Sedimentary Research*, 67, 638-652.
- Keller, M. and Grötsch, J. 1990. Depositional history and conodont biostratigraphy of the Lower Devonian La Vid Group in the Luna area (Cantabrian Mountains, NW Spain). *Neues Jahrbuch für Geologie und Paläontologie - Monatshefte*, 3, 141-164.
- Koenen, A., von 1886. Über neue Cystideen aus den Caradoc-Schichten der Gegend von Montpellier. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, 2, 246-254.
- Kolb, S. 1978. *Erläuterungen zur geologischen Kartierung des Gebietes S. Cerveruela in den Östlichen Iberischen Ketten (NE-Spanien)*. Diplom-Arbeit Universität Würzburg (unpublished), 122 pp.
- Le Menn, J. 1985. Les crinoïdes du Devonien inférieur et moyen du Massif armoricain. *Memoires de la Société géologique et minéralogique de Bretagne*, 30, 1-268.
- Le Menn, J., Gourvenec, R., Pizarra, J.M. and Robardet, M. 2003. Mid-Paleozoic dimerocrinitid crinoids from North Gondwana: evolution, biostratigraphy and paleobiogeography. *Revista Española de Paleontología*, 18 (1), 49-60.
- Lees, A. and Miller, J. 1995. Waulsortian banks. In Monty, C.L.V., Bosence, D.W.J., Bridges, P.H. and Pratt, B.R. (Eds.), *Carbonate Mud-Mounds: their origin and evolution*. International Association of Sedimentologists Series, Special Publication 23, 191-271.
- Leweke, B. 1982. The transition from sandy to carbonate sedimentation in the Lower Devonian of the southern Cantabrian Mountains (La Vid Formation). *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 163, 188-192.
- Leyva, F., Matas, J., Rodríguez Fernández, L.R., García-Alcalde, J., Arbizu, M., García-López, S. and Lorenzo Arias, P. 1984. *Mapa y Memoria explicativa de la Hoja nº 129 (La Robla) del Mapa Geológico de España E 1:50.000 (2ª serie MAGNA)*. Instituto Geológico y Minero de España, Madrid, 98 p.
- Lin, J.P., Ausich, W. and Zhao, Y.L. 2008. Settling strategy of stalked echinoderms from the Kaili Biota (Middle) Cambrian, Guizhou Province, South China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 258, 213-221.
- Liñán, E., Perejón, A. and Sdzuy, K. 1993. The Lower-Middle Cambrian stages and stratotypes from the Iberian Peninsula: a revision. *Geological Magazine*, 130, 817-833.
- Liñán, E., Villas, E., Gámez Vintaned, J.A., Alvaro, J., Gozalo, R., Palacios, T. and Sdzuy, K. 1996. Síntesis paleontológica del Cámbrico y Ordovícico del Sistema Ibérico (Cadenas Ibéricas y Cadenas Hespéricas). *Revista Española de Paleontología*, nº extr, 21-32.
- Lotze, F. 1929. Stratigraphie und Tektonik des Keltiberischen Grundgebirges (Spanien). *Abhandlungen der Gesellschaft für Wissenschaften Göttingen, math.-phys. Kl., n.F.*, 14 (2), 1-320.
- Macurda Jr., D.B. 1983. Systematics of the fissiculate Blastoida. Museum of Paleontology. *Papers on Paleontology*, 22, 1-291.
- Meléndez, B. 1942-1944. Contribución al estudio del Paleozoico aragonés. Trabajos del Instituto de Ciencias Naturales José de Acosta, Serie Geológica 3(1), 31-66.
- Meléndez, B. 1944a. Nuevos datos para la estratigrafía del Paleozoico aragonés. *Boletín de la Real Sociedad Española de Historia Natural*, 42 (1-2), 129-150.
- Meléndez, B. 1944b. Contribución al estudio del Paleozoico aragonés. *Trabajos del Instituto de Ciencias Naturales "José de Acosta", Serie Geológica*, 3 (1), 1-149.
- Meléndez, B. 1946. Cistídeos de España. *Las Ciencias*, 9 (2), 275-285.
- Meléndez, B. 1952. Los Carpoideos de España. *Las Ciencias*, 17 (4), 497-516.
- Meléndez, B. 1959. Los *Echinosphearites* del Silúrico de Luesma (Zaragoza). *Estudios Geológicos*, 15, 269-276.
- Meléndez, B. and Hevia, I. 1947. La fauna ashgillense del Silúrico aragonés. *Boletín de la Universidad de Granada*, 19, 247-259.
- Méndez-Bedia, I. 1976. Biofacies y litofacies de la Formación Moniello-Santa Lucía (Devónico de la Cordillera Cantábrica, NW de España). *Trabajos de Geología Universidad de Oviedo*, 9, 1-93.
- Méndez-Bedia, I., Soto, F., Fernández-Martínez, E. 1994. Devonian reef types in the Cantabrian Mountains (NW Spain) and their faunal composition. *Courier Forschungsinstitut Senckenberg*, 172, 161-183.
- Mergl, M. and Zamora, S. 2012. New and revised occurrences of rhynchonelliformean brachiopods from the middle Cambrian of the Iberian Chains, NE Spain. *Bulletin of Geosciences*, 87 (3), 571-586.
- Monty, C.L.V. 1995. The rise and nature of carbonate mud-mounds: an introductory actualistic approach. In Monty, C.L.V., Bosence, D.W.J., Bridges, P.H., Pratt, B.R. (Eds.), *Carbonate Mud-Mounds: their origin and evolution*. International Association of Sedimentologists Series, Special Publication 23, 11-48.

- Nance, R.d., Gutiérrez-Alonso, G., Keppie, J.D., Linnemann, U., Murphy, J.B., Quesada, C., Strachan, R.A. and Woodcock, N.H. 2012. A brief history of the Rheic Ocean. *Geoscience Frontiers*, 3 (2), 125-135.
- Navarro Vázquez, D. 1991. Cabalgamientos hercínicos en la Unidad de Herrera (Rama Oriental del Macizo Paleozoico de la Cordillera Ibérica). *Boletín Geológico y Minero*, 102, 830-837.
- Palacios, T. and Vidal, G. 1992. Lower Cambrian acritarchs from northern Spain: the Precambrian-Cambrian boundary and biostratigraphic implications. *Geological Magazine*, 129, 421-436.
- Paris, F. 1979. Les Chitinozoaires de la Formation de Louredo, Ordovicien Supérieur du Synclinal de Buçaco (Portugal). *Palaeontographica A*, 164, 24-51.
- Paris, F. 1981. Les Chitinozoaires dans le Paléozoïque du Sud- Ouest de l'Europe (Cadre géologique-Etude systématique-Biostratigraphie. *Mémoires de la Société Géologique et Minéralogique de Bretagne*, 26, 1-496.
- Perejón, A. and Moreno-Eiris, E. 2003. Arqueociatos del Bilbiliense (Cámbrico Inferior) del manto del Esla, Cordillera Cantábrica, Norte de España. *Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica)*, 98, 51-71.
- Perejón, A., Moreno-Eiris, E., Bechstädt, T., Menéndez, S. and Rodríguez-Martínez, M. 2012. New Bilbilian (early Cambrian) archaeocyath-rich thrombolitic microbialite from the Láncara Formation (Cantabrian Mts., northern Spain). *Journal of Iberian Geology*, 38, 313-330.
- Prado, C. de, Verneuil, E. de and Barrande, J., 1860. Sur l'existence de la faune primordiale dans la chaîne cantabrique. *Bulletin de la Société géologique de France*, 2<sup>ème</sup> serie, 17, 516-554.
- Pratt, B.R. 1995. Origin, biota and evolution of deep-water mud-mounds. In Monty CLV, Bosence DWJ, Bridges PH, Pratt, B.R. (Eds.), *Carbonate Mud-Mounds: their origin and evolution*. International Association of Sedimentologists Series, Special Publication 23, 49-123.
- Preat, A., Mamet, B., Bernard, A., Gillan, D. 1999. Bacterial mediation, red matrices diagenesis, Devonian, Montagne Noire (southern France). *Sedimentary Geology*, 126, 223-242.
- Radig F. 1962. Zur Stratigraphie des Devons in Asturien (Nord-Spanien). *Geologische Rundschau*, 51, 249-267.
- Rahman, I.A. and Zamora, S. 2009. The oldest cinctan carpoid (stem-group Echinodermata) and the evolution of the water vascular system. *Zoological Journal of the Linnean Society*, 157, 420-432.
- Ruhrmann, G. 1971. Riff-ferne Sedimentation unterdevonischer Krinoidenkalke im Kantabrischen Gebirge (Spanien) *Neues Jahrbuch für Geologie und Paläontologie - Monatshefte*, 4, 231-248.
- Sarmiento, G.N. 1993. *Conodontos ordovícicos de Sierra Morena (Macizo Hespérico meridional)*. Universidad Complutense de Madrid (unpublished PhD thesis), 600 pp.
- Sarmiento, G.N. 2002. Lower Palaeozoic of the Iberian Cordillera. In García-López, S. and Bastida, F. (Eds.), *Palaeozoic conodonts from Northern Spain*. Instituto Geológico y Minero de España, serie Cuadernos del Museo Geominero, 1, 281-297.
- Sarmiento, G.N., Gutiérrez-Marco, J.C. and Rábano, I. 1995. A biostratigraphical approach to the Middle Ordovician conodonts from Spain. In: Cooper, J.D., Droser, M.L. and Finney, S.E. (Eds.), *Ordovician Odyssey*. Pacific Section Society for Sedimentary Geology, Book 77, Fullerton, 61-64.
- Sarmiento, G.N., Sanz-López, J. and García-López, S. 1998. Silurian conodonts from the Iberian Peninsula - an update. *Temas Geológico-Mineros ITGE*, 23, 119-124.
- Schmid, D.U., Leinfelder, R.R. and Nose, M. 2001. Growth dynamics and ecology of Upper Jurassic mounds with comparison to Mid-Palaeozoic mounds. *Sedimentary Geology*, 145, 343-376
- Schmidt, W.E. 1931. Crinoiden und Blastoiden aus dem Jüngsten Unterdevon Spaniens. *Palaeontographica*, 76, 1-33.
- Schroeder, R. 1973. Carpoideen aus dem Mittelkambrium Nordspaniens. *Palaeontographica, Abteilung A*, 141, 119-142.
- Scotese, C.R. 2000. PALEOMAP Project. <http://www.scotese.com>
- Scotese, C.R. 2001. Atlas of Earth History, Volume 1, Paleogeography, PALEOMAP Project, 1, 1-52.
- Sdzuy, K. 1968. Trilobites del Cámbrico Medio de Asturias. *Trabajos de Geología*, Universidad de Oviedo, 1, 77-133 .
- Sdzuy, K. 1972. Das Kambrium der Acadobaltischen Faunenprovinz - Gegenwärtiger Kenntnisstand und Probleme. *Zentralblatt für Geologie und Paläontologie*, 2, 1-91.
- Sdzuy, K. 1993. Early Cincta (Carpoidea) from the Middle Cambrian of Spain. *Beringeria*, 8, 189-207.
- Sdzuy, K. and Liñán, E. 1993. Rasgos paleogeográficos del Cámbrico Inferior y Medio del norte de España. *Cuadernos del Laboratorio Xeolóxico de Laxe*, 18, 189-215.



- Sdzuy, K., Liñán, E., and Gozalo, R. 1999. The Leonian Stage (early Middle Cambrian): a unit for Cambrian correlation in the Mediterranean subprovince. *Geological Magazine*, 136, 39-48.
- Seilacher, A. and Macclintock, C. 2005. Crinoid anchoring strategies for soft-bottom dwelling. *Palaios*, 20 (3), 224-240.
- Shergold, J.H. and Sdzuy, K. 1991. Late Cambrian trilobites from the Iberian Mountains, Zaragoza Province, Spain. *Beringeria*, 4, 193-235.
- Smith, A.B. and Arbizu M.A. 1987. Inverse development in a Devonian edrioasteroid from Spain and the phylogeny of the Agelacrinitidae. *Lethaia*, 20, 49-62.
- Smith, A.B. and Zamora, S. 2009. Rooting phylogenies of problematic fossil taxa; a case study using cinctans (stem-group echinoderms). *Palaentology*, 52 (4), 803-821.
- Smith, A.B., Reich M. and Zamora S. 2013a. Morphology and ecological setting of the basal echinoid genus *Rhenechinus* from the early Devonian of Spain and Germany. *Acta Palaentologica Polonica*, 58 (4), 751-762.
- Smith, A.B., Zamora, S. and Álvaro, J.J. 2013b. The oldest echinoderm faunas from Gondwana show that echinoderm body plan diversification was rapid. *Nature Communications*, 4, 1385.
- Sprinkle, J. 1973, *Morphology and Evolution of Blastozoan Echinoderms*. University Museum of Comparative Zoology, Harvard, Special Publication, 283 p.
- Suárez Andrés J.L. and McKinney F.K. 2010. Revision of the Devonian fenestrate bryozoan genera *Cyclopelta* Bornemann, 1884 and *Pseudoisotrypa* Prantl, 1932, with description of a rare fenestrate growth habit. *Revista Española de Paleontología*, 25 (2), 123-138.
- Suárez Andrés J.L. and Wyse Jackson P.N. 2014. *Ernstipora mackinneyi*, a new unique fenestrate bryozoan genus and species with an encrusting growth habit from the Emsian (Devonian) of NW Spain. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 271 (3), 229-242.
- Tejero, R. 1986. Tectónica de los macizos paleozoicos al NE de Calatayud. Rama Aragonesa de la Cordillera Ibérica (Prov. Zaragoza). Universidad Complutense (PhD thesis), 300 pp.
- Tejero, R. and Capote, R. 1987. La deformación hercínica de los macizos paleozoicos nororientales de la Cordillera Ibérica. *Estudios geológicos*, 43, 425-434.
- Toyos, J.M. and Aramburu, C. 2014. El Ordovícico en el área de Los Barrios de Luna, Cordillera Cantábrica (NW de España). *Trabajos de Geología*, Universidad de Oviedo, 34, 61-96.
- Truyols J. and Julivert, M. 1976. La sucesión paleozoica entre Cabo de Peñas y Antromero (Cordillera Cantábrica). *Trabajos de Geología Universidad de Oviedo*, 8, 5-30.
- Ubaghs, G. 1968. Homostelea. In: *Treatise on Invertebrate Paleontology. Part 5, Echinodermata 1 (2)* (Moore, R. C. Ed.). The University of Kansas and the Geological Society of America, S565-S581.
- Ubaghs, G. 1987. Echinodermes nouveaux du Cambrien moyen de la Montagne Noire (France). *Annales de Paléontologie*, 73, 1-27.
- Vennin, E., Álvaro, J.J. and Villas, E. 1998. High-latitude pelmatozoan-bryozoan mud-mounds from the late Ordovician northern Gondwana platform. *Geological Journal*, 33, 121-140.
- Vera de la Puente, C. 1988. Estratigrafía, Sedimentología y Paleogeografía de los grupos Rañeces y La Vid en la Cordillera Cantábrica (Asturias y León). Universidad de Oviedo, Unpublished PhD, 653 pp.
- Vera de la Puente, C. 1989. Revisión litoestratigráfica y correlación de los Grupos Rañeces y La Vid (Devónico Inferior de la Cuenca Astur-leonesa). *Trabajos de Geología Universidad de Oviedo*, 18, 53-65
- Vilas Minondo, L. 1971. *El Paleozoico Inferior y medio de la Cordillera Cantábrica entre los ríos Porma y Bernesga (León)*. Memorias del Instituto Geológico y Minero de España, 80, Madrid, 169 pp.
- Villas, E. 1983. Las formaciones del Ordovícico Medio y Superior de las Cadenas Ibéricas y su fauna de braquiópodos. *Estudios Geológicos*, 39, 359-377.
- Villas, E. 1985. *Braquiópodos del Ordovícico Medio y Superior de las Cadenas Ibéricas Orientales*. Memorias del Museo Paleontológico de la Universidad de Zaragoza, 1 (1-2), 223 pp.
- Villas, E. 1992. New Caradoc brachiopods from the Iberian Chains (Northeastern Spain) and their stratigraphic significance. *Journal of Paleontology*, 66 (5), 772-793.
- Villas, E. 1995. Caradoc through early Ashgill brachiopods from the Central-Iberian zone (Central Spain). *Geobios*, 28 (1), 49-84.
- Villas, E., Vennin, E., Jiménez-Sánchez, A., Álvaro, J.J., Zamora, S. and Gutiérrez-Marco, J.C. 2011. *Ordovician of the Iberian Range (NE Spain)*. Post-symposium field trip. 11th International Symposium on the Ordovician System. ISOS-ICS-IUGS. 31 pp.

- Villas, E., Vizcaíno, D., Alvaro, J.J., Destombes, J. and Vennin, E. 2006. Biostratigraphic control of the latest-Ordovician glaciogenic unconformity in Alnif (Eastern Anti-Atlas, Morocco) based on brachiopods. *Geobios*, 39, 727-737.
- Waters, J.A. and Zamora, S. 2010. *Cryptoschisma* (Blastoidea): A Cambrian-style sediment sticker echinoderm from the Lower Devonian of Spain. *Geological Society of America Abstracts with Programs*, 42 (5), 633.
- Wehner, G. 1984. *Graptolithen aus der Bâdenas-Formation, NE-Spaniens*. Diplomarbeit Universität Würzburg (unpublished), 52 pp.
- Wendt, J., Belka, Z., Kaufmann, B., Kostrewa, R. and Hayer, J. 1997. The world's most spectacular carbonate mud mounds (Middle Devonian, Algerian Sahara). *Journal of Sedimentary Research*, 67, 424-436
- Whittington, H.B. 1990. Articulation and exuviation in Cambrian trilobites. *Philosophical Transactions of the Royal Society of London, Series B*, 329, 27-49.
- Wolf, R. 1980. The lower and upper boundary of the Ordovician system of some selected regions (Celtiberia, Eastern Sierra Morena) in Spain. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 160 (1), 118-137.
- Wotte, T. 2005. Facies distribution patterns and environment reconstruction of the upper member of the Láncara Formation in the Somiedo-Correcilla unit (Lower-Middle Cambrian, Cantabrian Zone, NW Spain) with special respect to biofacial investigations. *Geosciences Journal*, 9, 173-186.
- Wotte, T. 2006. New Middle Cambrian molluscs from the Láncara Formation of the Cantabrian Mountains (north-western Spain). *Revista Española de Paleontología*, 21, 145-158.
- Wotte, T. and Mergl, M. 2007. Brachiopods from the Lower-Middle Cambrian Láncara Formation of the Cantabrian Mountains, Northwest Spain. *Memoirs of the Association of Australasian Palaeontologists*, 33, 101-122.
- Wotte, T., Álvaro, J.J., Shields, G.A., Brasier, M. and Veizer, J. 2007. C-, O- and Sr-isotope stratigraphy across the Lower-Middle Cambrian transition of the Cantabrian Mountains (Spain) and the Montagne Noire (France), West Gondwana. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 256, 47-70.
- Wotte, T., Elicki, O., Perejón, A. and Moreno-Eiris, E. 2004. Facies distribution patterns and environment interpretation of the Upper Láncara Formation in the Esla Nappe (Cantabrian zone, NW Spain) by quantitative microfacies analysis. *Freiberger Forschungshefte, C502, Paläontologie, Stratigraphie, Fazies*, 12, 101-118.
- Zamarreño, I. 1972. Las litofacies carbonatadas del Cámbrico de la Zona Cantábrica (NW España) y su distribución paleogeográfica. *Trabajos de Geología*, Universidad de Oviedo, 5, 1-118.
- Zamora, S. 2005. Equinodermos en el Cámbrico de la Sierra de Tablado (Provincia de Zaragoza). *Unpublished Master thesis*, 97 pp.
- Zamora, S. 2009. Equinodermos del Cámbrico medio de las Cadenas Ibéricas y la Zona Cantábrica (Norte de España). *Unpublished PhD*, 307 pp.
- Zamora, S. 2010. Middle Cambrian echinoderms from North Spain show echinoderms diversified earlier in Gondwana. *Geology*, 38, 507-510.
- Zamora, S. 2011. Equinodermos del Cámbrico de España: Situación actual de las investigaciones y perspectivas futuras. *Estudios Geológicos*, 67 (1), 59-81.
- Zamora, S. and Álvaro, J.J. 2010. Testing for a decline in diversity prior to extinction: Languedocian (latest mid-Cambrian) distribution of cinctans (Echinodermata) in the Iberian Chains, NE Spain. *Palaeontology*, 53 (6), 1349-1368.
- Zamora, S. and Rahman, I. 2014. Deciphering the early evolution of echinoderms with Cambrian fossils. *Palaeontology*, 57 (6), 1105-1119.
- Zamora, S. and Smith, A.B. 2008. A new Middle Cambrian stem-group echinoderm from Spain: Palaeobiological implications of a highly asymmetric cinctan. *Acta Palaeontologica Polonica*, 53 (2), 207-220.
- Zamora, S. and Smith, A.B. 2010. The oldest isorophid edrioasteroid (Echinodermata) and the evolution of attachment strategies in Cambrian edrioasteroids. *Acta Palaeontologica Polonica*, 53 (3), 487-494.
- Zamora, S. and Smith, A.B. 2012. Cambrian stalked echinoderms show unexpected plasticity of arm construction. *Proceedings of The Royal Society B*, 279, 293-298.
- Zamora, S., Clausen, S., Álvaro, J.J. and Smith, A.B. 2010. Pelmatozoan echinoderms colonized carbonate firmground substrates in high energy environments since the basal Middle Cambrian. *Palaos*, 25, 764-768.
- Zamora, S., Colmenar, J. and Ausich, W.I. 2014. The echinoderm faunas from the Fombuena Formation (Upper Ordovician, Iberian Chains, Spain). In Royo-Torres, R., Verdú, F.J. and Alcalá, L. (Coord.), *XXX Jornadas de Paleontología de la Sociedad Española de Paleontología*. Fundamental!, 24, 257-259.

- Zamora, S., Gozalo, R. and Liñán, E. 2009. Middle Cambrian gogiids (Eocrinoidea, Echinodermata) from Northeast Spain: Taxonomy, palaeoecology and palaeogeographic implications. *Acta Palaeontologica Polonica*, 54, 253-265.
- Zamora, S., Liñán, E., Gámez Vintaned J.A., Domínguez Alonso, P. and Gozalo, R. 2007. Nuevo carpoideo de la clase Cineta Jaekel, 1918 del norte de España: inferencias sobre la morfología funcional del opérculo. *Ameghiniana*, 44, 727-738.
- Zamora, S., Rahman, I.A. and Smith, A.B. 2012. Plated Cambrian bilaterians reveal the earliest stages of echinoderm evolution, *PLoS One*, 7 (6).
- Zamora, S., Rahman, I.A. and Smith, A.B. 2013a. The ontogeny of cinctans (stem-group echinodermata) as revealed by a new genus, *Graciacystis*, from the middle Cambrian of Spain. *Palaeontology*, 56, 399-410.
- Zamora, S., Sumrall, C.D. and Vizcaino, D. 2013b. Morphology and ontogeny of the Cambrian edrioasteroid (Echinodermata) *Cambraster cannati* (Miquel) from western Gondwana. *Acta Palaeontologica Polonica*, 58 (3), 545-559.