FIELD TRIP:
PALAEOZOIC ECHINODERMS FROM NORTHERN SPAIN
**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 Døp, 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” holds attached to firmgrounds during the Cambrian. This provides important palaeoecological and evolutionary information, suggesting that the echinoderms with columnals and holdsfasts 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 barriosenis (Zamora and Smith, 2008) and the oldest columnal-bearing eocrinoid, Ubaghsiocyrtis segurae (Gil Cid and Dominguez, 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 Lucia 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 Agüión 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 monoclinal 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.
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 Valdemedes, Mansilla, Murero, Borobia and Valtorres formations (Fig. 2). The oldest echinoderm ossicles appear in the carbonate tempestites of the mixed (carbonate-siliciclastic) Valdemedes 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, stylorhaphs and stenocystoids (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 (Schröeder, 1973; Friedrich, 1993). The first rigorous study on Cambrian echinoderms from the Iberian Chains dates from the early 1970s, when Schröeder (1973) described new occurrences of Decacystis hispanica (currently Gyrocystis platessa) from the Cantabrian Mountains and a new species, Gyrocystis melendezii (currently Undatacinctus melendezii) 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 “Trilobe 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 Tabuenca (352).
Geological setting: Badules Unit (eastern Iberian Chain).
Main topic: faulted contact between the Palaeozoic and Mesozoic rocks.
**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 Tabuenca (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 Sdzuy, 1961, and the upper assemblage contains Kingaspis (Kingaspidoides) velata Sdzuy, 1961, and Redlichia sp. Sdzuy. 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 Tabuenca (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 dibrachycystid 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 stereomicrostructure in recrystallized calcitic plates that was invisible under conventional transmitted light or SEM (Gorzelak 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...
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 dibrachicystid 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 90º, 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 (Purujo Sa 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 Tabuenca (352).
Geological setting: Badules Unit (eastern Iberian Chain).
Lithostratigraphic unit: Murero Formation.
Age: Caesaraugustan (mid Cambrian).

Aims

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

Description

The Ctenoimbricata quarry (Fig. 6A) lies at the base of the Murero Formation in the Purujo Sa 6 section (Fig. 3, 4), which is mid Caesaraugustan 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 Purujo Sa in the most distal part of the Iberian Platform (a part of the Cantabro-Iberian Basin) favoured preservation of multiple obstruction 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 dibrachicystids (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
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 radiality (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 NH₄Cl 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: 41º40’11.77”N, 1º47’18.84”W
Geological map of Spain, 1:50.000, sheet of Tabuenca (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*, *Parabailella languedocensis*, *Cte noecephalus 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 M1l 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 stеле. Plate addition appears to be more prevalent in the ventral and possibly dorsal integums 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 NH₄Cl 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 Tabuenca (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 stylarhorans Ceratocyctis sp. (Fig. 11B), plus two different undescribed cothurnocystids, and the blastozoans Gogia gondi, Lichenoides sp. (Fig. 8I) and Dibrachicyctis purujoensis (Fig. 11A), polymerid trilobites (Eccaparadoxides pradoanus Fig. 11E, H, I, Conocoryphe heberti, Solenopleuropsis (Manublesia) thorali (Fig. 11J), S. (M.) ri beroi (=S. (M.) marginata), S. (M.) ver diagana, Schopfaspis? gracilis (Fig. 11C), agnostoids (Condylopyge sp., Peronopsis acacida, 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 Vizcaino, 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 Cambian 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 enrollment 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
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.) thorali*), 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 revaluation. 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 portioning 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 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 paradoxid *Eccaparadoxides pradoanus* (C).
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: 41º39’ 59.09”N, 1º47’43.99”W
Geological map of Spain, 1:50.000, sheet of Tabuenca (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, Torrijode 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 barrandeii (Fig. 12A, B). The upper level is more diverse and has provided isolated stylophoran plates, indetermined cinctans, the edrioasteroid Cambraster sp., and the ctenocystoid Etocenocystis (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 theoensis*. F. The ctenocystoid *Etocystocystis*. G, H. The edrioasteroid *Cambraster cannati*. I, J. An indeterminate cothurnocystid stylophoran. All photographs are from latex cast whitened with NH$_4$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 Tabuenca (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 obruption 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 3000 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
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 Castillejo Formation (Fig. 14), the local representative of the “Neseuretus shales and sandstones”, widespread throughout Iberia (Hammann et al., 1982). The Castillejo Formation can be correlated with most of the Darrwillian, although it probably overlies a stratigraphical gap corresponding to the lower Oretanian regional stage (equivalent to the British lower Aberediddian), 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 Darriwiliant 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 diamictites 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 Pridoli 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 aragonensis* 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 Nogueras (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 Triasicrocks. 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 murchisoni 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. murchisoni 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 “cambricensis” (P. tornemini) and Redonia sp. In the upper part of this member, the graptolites Gymnograptus innorsoni and Hustedograptus teretiusculus have been found (Hammann et al., 1982; Gutiérrez-Marco, 1986) as well as the trilobites Placoparia tornemini, Neseuretus tristani, Eodamanitina macrophthalma, Colpocoryphe rouaulti and Salterocoryphe salteri, the molluscs Sinuites hispanica and Redonia deshayesi (Hammann et al., 1982), and the brachiopods Heterorthina morgatensis, Aegiromena mariana and Crozonorthis musculosa; an assemblage of early Dobrotivian (late Darriwilian) age.
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 Eohomalonus sdzuyi 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 coquinooid bed probably of late Dobrotivian age (latest Darriwilian 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 Aristeocystitidae gen. et sp. indet. From the Castillejo Formation a complete specimen of the crinoid Heviacrinus sp. (Fig. 17) has also been collected.

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, Jezerica 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 Ktoua 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 Mespiilocystites lemenii, Calix? cf. gutierrezi, Sphaeronitida fam. indet., Caryocrinites cf. rugatus, Hemicosmitida fam. indet., Heliocrinites sp. and Rhombifera bohemica.

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
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., Diploporein indet. and Mesilocystites lemeni. 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 camerate (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 Mesilocystites (Fig. 19E). Rhombiferans are also very conspicuous in the formation and we have found nearly complete specimens of Rhombifera bohemica (Fig. 19A) and Caryocrinites sp. (Fig. 19D), both preserving the stem. New unreported taxa include a fragment of an indeterminate asterozoan and the solutarian 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 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 Rebosilla Member. D. Bed plane containing several cystoids.
Figure 19. Echinoderms from the Fombuena Formation. A. Blastozoan *Rhombifera bohemica* preserving the stem. B. Cladid crinoid. C. Oral area of the diploporan *Codiacytis* n. sp. D. Blastozoan *Caryocrinites* sp. preserving part of the proximal stem. E. Coronoid *Mespliocystites 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 NH$_4$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 Rebollarejo 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 stromatoid-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-bryozoans meadows degraded by wave- and storm-induced processes (La Peña and Rebosilla 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, Eridolithis 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 or dovcius Zone where identified by Carls (1975) throughout the massive limestones of the Rebollarejo 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 sduz(Fig. 21A, B), Caryocrinites elongatus, Caryocrinites cf. crassus, Caryocrinites europaeus, Stichocystis unilineata, Heliocinites rouvillei (Fig. 21D), Heliocinites minuta (Fig. 21M), Heliocinites helmackeri, Heliocinites cf. saenzli), 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).
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 (Echinosphaerites, 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 (Cariocestites sp., Cariocestites? 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 Rebosilla 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 Bruteras.

Coordinates: 41º9'25"N, 1º7'47"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 Himantia 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 Dimocrinites aragonensis (Figs. 24A, B, E), are concentrated in some levels; although there are isolated columns from other species of crinoids (Fig. 24E) and rare ophiuroids (Fig. 24F). Le Menn (1985) was the first that mentioned Dimocrinites in those levels, although it was not until 2003 when he described Dimocrinites aragonensis Le Menn (in Le Menn et al. 2003). Dimocrinites 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 bryozoan marls and shales (d4aα), in which the lower boundary of the traditional German Emsian Stage is located (Carls, 1987, 1988). The submember d4aβ 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, tentaculitids, ostracods, crinoids and bivalves. The overlying submember (d4aγ) 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 dacroconarid 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 d4bα is 15 meters thick interval of limestones and shales with a rich fauna of trilobites, ostracods and brachiopods. The submember d4bβ is composed of 30 m of shales rich in fossils, mostly trilobites (Phacops), brachiopods, tabulate corals, tentaculitids and crinoids. Lastly the d4bγ 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 d3αβ. 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 NH4Cl sublimated.
PALAEZOIC 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 (Ustifluvent) 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 stabilised 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 Ovettian 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 chemostatigraphic 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, edrioasteroids 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 Lánycara 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 Lánycara Formation

**Location**

Road cut in the CL-626 below the old locality of Lánycara 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: Lánycara 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 Lánycara 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,
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 Láncara Formation but articulated specimens are rare and include only complete cinctans belonging to the genus Gyrocystis. 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 where pre-adapted to such settings. Stemmed eocrinoids
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 Barrrios de Luna village, near the Mora-Los Barrios de Luna road.

Coordinates: 42º50'31.26"N, 5º51'22.46"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 Ge nestosa 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; Zamarréno, 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 Sotode 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 the 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 Ubaghscystis segurae (Gil Cid and Dominguez 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 (Solenopleuroeopsis (M.) thorali-Solenopleuroeopsis (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 Courtesseola.
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 *Ubaghsia cystis segurae* with a columnar bearing stem and a distal holdfast. D, E. The cinctan *Gyrocytis sp.* F, G. The cinctan *Gyrocytis 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 NH4Cl sublimated.
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 Herreria, Lán cara 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).
"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. Vanguêstaine 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 (Darriwilian 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: *Nicoleta actoniae*, *Dolerorthis aberensis*, *Schizophorella* sp., *Skenidioidea* sp., *Epitomyonia* sp., *Bicusponia armoricana*, *Oxoplecia* cf. luesmae, *Leangella (L.) anaclyta*, *L. (Leptestiina) prantli*, *Aegironetes?* sp., *Eoplectodonta* (Kozlowskites) *ichnusae*, *iberomena sardoa*, *Longvillia* sp., *Hedstroemia* 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 (*Mesilocystites* sp. Fig. 34L). Columnals belonging to both rhombiferans and cirinoïds are very abundant and include the following parataxa: *Trigonocyclicus* (col.) vaigatschensis Fig. 34N, *Aonodiscus* (col.) *spinosus*, *Conspectocrinus* (col.) celticus Fig. 34M, *Cyclocharax* (col.) paucicrenellatus, *Hexagonocyclicus* (col.) sp., *Pentagonocyclicus* (col.) spp., *Cyclocyclicus* (col.) sp., *Pentagonopentalgonalis* (col.) sp. and *Ristnacrinus* sp Fig. 34O. Trilobites include *Ovalocephalus* cf. tetrusulcatus and *Cekovia?* sp. Finally, conodonts include *Amorphognathus ordovicicus*, *Amorphognathus* sp. A, *Scabbradella altipes*, *Birkfeldia* sp., *Icriodella* sp., *Dapsilodus* sp., *Panderodus* sp. and a single eocarnioniform element.

The above-reported fossil assemblage suggests a Katian 3-4 (Kradlovian or Rawtheyan-Cautleyan Ashgill) age for this unit (Gutiérrez-Marco et al., 1996b; Del Moral, 2003).
Specimens I-O are latex casts whitened with NH4Cl 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-Leonesian 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-Leonesian 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 19th 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.
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 3rd 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 3rd 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 Asturo-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. Bactocrinus sp., B. Lasiocrinus? sp. C. Oenochoacrinus princeps. D, E. Pradocrinus baylii. F. Orthocrinus robustus. G. Pradocrinus baylii. H. Pyxidocrinus collensis. I. Hexacrinites sp.
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 synsedimentary feature, generated by bacterial activity in the marine environment (see Bourque and Bouplin, 1993; Preat et al., 1999; Bouvain, 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 alloyclic, 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. Ruhmann (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 *Diademocrinus, Orthocrinus, Pradocrinus, Pyxidocrinus, Stamnocrinus, Cantharocrinus, Oenochoacrinus, Vasocrinus, Situlacrinus, Costalocrinus, Codiacrinus, Bactocritides 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%)
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,
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. B. 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 Lucía Formation, although very rare, include Pentremitidea archiaci, Conuloblastus malladai and Hyperoblastus wachsmuthi (Etheridge & Carpenter 1886). Santa Lucía 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 descendant (Waters and Horowitz, 1993). Based on the detailed morphological work by Breimer and Dop (1975), the transition from Pentremitidea archiaci (a fissiculate) to Hyperoblastus wachsmuthi (a spiraculate in the Order Pentrematida) through the intermediate species, Conuloblastus malladai, is
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.
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, echi noids, 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 decembrachius 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
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 *Bigepina* 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 crinoids are dominant, but sparse rugose corals, tabulates and bivalve molluscs are also present. Crinoids are diverse and sometimes very common, especially *Trybliocrinus flateanetus* (Fig. 44C) and to a lesser extent *Pterinocrinus decembrachiatus* (Fig. 44D), *Orthocrinus* sp. and *Stamnodes intrastigmatus* (Schmidt 1931; Breimer 1962). Blastoids (Fig. 48C) include *Pentremitidea lusitania*, *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, rhabdometids and ptilodictid cryptostomes also occur. Bryozoans in this unit developed a variety of growth habits ranging from different erect unilaminate forms (fenestrates, dendroid cryptostomes), to delicate erect faceted 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 Andrés and McKinney, 2010). The outcrop of the Agüión 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 Agüión 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 the upper unit show differences in substrate consistency. The red marls represent a soft substrate in which the crinoid *Trybliocrinus* developed large stout cirri (Figs. 44E, 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 MacIntock, 2005) and cirri appear on polynodal articular facets. Those cirri 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 stereometric outgrowths of columnals (Fig. 48E). They are several centimeters long and the coil is made 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 Agüión 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 stereometric outgrowths.
Figure 48. Echinoderms from the Aguión Formation in Arnao. A. Hardground preserving a discoid holdfasts with lobate margins and a partially disarticulated distal coiled stem. B. Radix-like holdfast attached to a bryozoan pavement. C. The blastoid Pentremites pailletti. D. Discoid 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.

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