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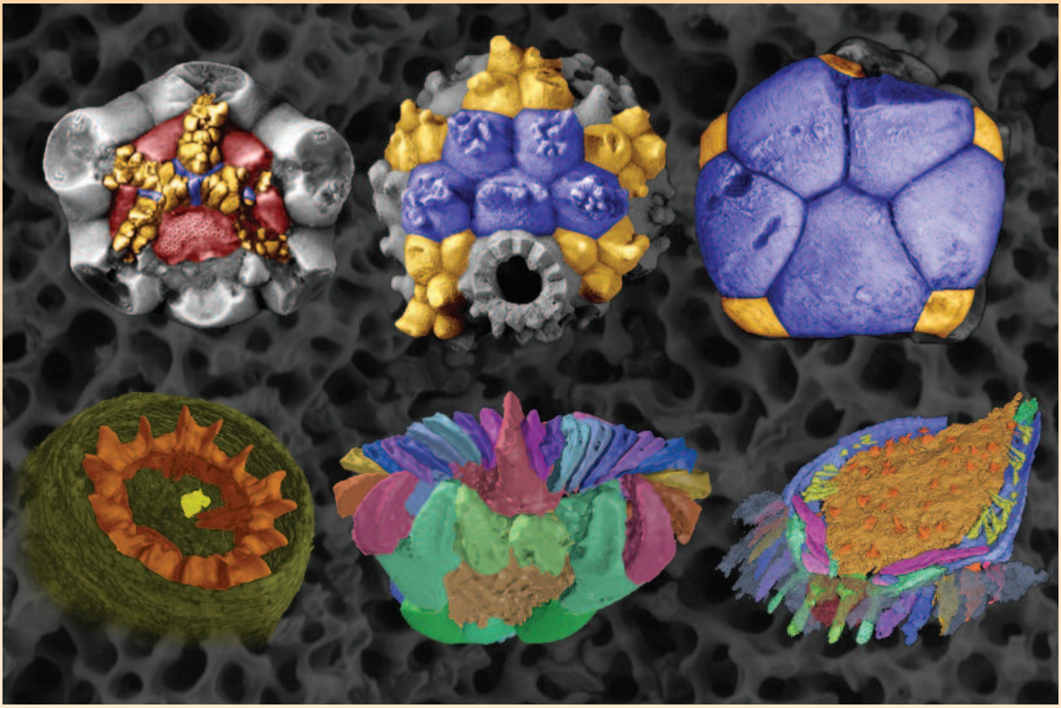
# PROGRESS IN ECHINODERM PALAEOBIOLOGY



Progress in Echinoderm Palaeobiology Spain'15

Editors: S. Zamora
I. Rábano

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# PROGRESS IN ECHINODERM PALAEOBIOLOGY

Edited by

**S. Zamora & I. Rábano**

Instituto Geológico y Minero de España
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Oral areas in the crinoids *Nuxocrinus* (upper left), *Collicrinus* (upper center) and *Neoplatycrinus* (upper right) (after Sumrall, this volume). Three dimensional computer reconstructions (CT-scans) of a holothurian (lower left, after Reich, this volume), ctenocystoid *Ctenocystis* (lower centre, courtesy of Imran A. Rahman) and the bilateral echinoderm *Ctenoimbricata* (lower right, after Zamora *et al*. this volume).

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# PREFACE

Echinoderms are an important group of animals that have been a major component of marine ecosystems from the Cambrian to the Holocene. Our understanding of this group requires not only the study of modern forms, but also investigation of their highly diverse fossil record. The five recent classes of echinoderms are just a small part of the group's wide disparity, which was largely restricted to the Palaeozoic. Throughout their existence, echinoderms have been strongly affected by major events in Earth and life history, including mass extinctions, climate change, sea level change and the rise and fall of important predators.

Because they possess a hard skeleton made of calcite plates, echinoderms are characterized by a relatively good fossil record, which allows us to reconstruct their diversity through geological time. Moreover, their complex skeleton offers palaeontologists a unique opportunity to assemble comprehensive phylogenetic datasets in order to address major macroevolutionary questions. Echinoderms are also good indicators of past environmental change, modifying their ecology and distribution in response to fluctuations in salinity, ocean acidity or temperature, for example. Taken together, all these aspects make echinoderms an ideal group for addressing fundamental questions about the history of life on Earth.

This book, "*Progress in Echinoderm Palaeobiology*", is divided into three main parts. The first part comprises a tribute to one of the most important echinoderm workers of the past 35 years, Dr Andrew Smith FRS FRSE, a researcher from the Natural History Museum, London, who recently retired after a career of outstanding work on echinoderms. The second part consists of a series of papers dealing with a wide range of echinoderm research topics, such as taphonomy, ecology and new technologies for their study. Lastly, the book ends with a very detailed field guide highlighting the most important echinoderm fossil sites from the Palaeozoic of North Spain, which represents the itinerary of the field trip. This book follows the path of previous important publications on echinoderms that have contributed to the understanding and discussion of this important group of animals, including *Geobiology of Echinoderms* (1997; Waters and Maples Eds.), *Echinoderm Phylogeny and Evolutionary Biology* (1988; Paul and Smith Eds.) and Echinoderm Paleobiology (2008; Ausich and Webster Eds.).

This book will serve as an indicator of the current state-of-the-art of echinoderm research, and will also highlight future lines of enquiry. The publication of this book would never have been possible without the assistance of a number of echinoderm researchers who have contributed major advances in echinoderm palaeobiology, as well as the tremendous efforts of the organizers of the field trip. The quality of the papers was ensured thanks to the detailed comments of the scientific board members.

The Spanish Geological Survey (IGME) was founded in 1849 and one of the current aims of the institution is to support research in the different fields of the Earth sciences. Thus, the publication of this book and the support of the PEP´15 meeting are a source of great pride. We acknowledge all the institutions and sponsors that have helped support the meeting, especially the Spanish Ministry of Economy and Competiveness, Government of Aragón (DGA), academic institutions such as Universities of Zaragoza, Oviedo and León, and the Palaeontological Association.

Jorge Civis
Director
Spanish Geological Survey (IGME)

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# A TRIBUTE TO THE CAREER OF ANDREW B. SMITH

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# THE RESEARCH CONTRIBUTION OF DR. ANDREW B. SMITH, BSC, PHD, DSC, FRSE, FRS

Andrew Gale

School of Earth and Environmental Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth PO1 3QL, UK.
andy.gale@port.ac.uk.

## BRIEF BIOGRAPHY

**Figure 1.** Andrew Smith working in his office, Natural History Museum (London, 1992).

Andrew Benjamin Smith was born in the town of Dunoon in Argyllshire, Scotland on 6th of February 1954. He grew up in Stonehaven, on the east coast of Scotland, south of Aberdeen, geologically famous for its exposure of the Highland Boundary Fault and a spectacular Devonian conglomerate. To describe the weather there as inhospitable is an understatement – it once snowed, heavily, on my field party in May; Andrew's disregard of ambient weather conditions in the field dates back to this period of his life.

Andrew first became interested in fossil collecting at age of 13 after a watching a UK children's TV program called "Blue Peter" on which it was promoted as a summer holiday activity, and he subsequently collected his first fossils from the Rhaetian Penarth Group at Watchet, Somerset when on holiday in 1967. The following year he collected a complete Devonian fish (*Dipterus valenciennesi* ) while on holiday in Shetland – the specimen was put on display at Lerwick museum.

Andrew studied geology at Edinburgh University from 1973-1976 during which he spent two summers mapping marine fossiliferous Jurassic outcrops on the Isle of Skye in the Inner Hebrides. After graduating, he received a Carnegie Award to study echinoid distribution in the Aalenian (Inferior Oolite) of the Cheltenham region of England, for a summer project, on the recommendation of Euan Clarkson, which led to his first paper (1978a) in *Lethaia*.

In 1976, Andrew moved to the Biology Department of Exeter University in order to research links between the skeletal histology and soft-tissue anatomy of echinoids for a PhD, under the supervision of David Nichols. This work involved use of the SEM, then relatively new, histological staining, sectioning and some *in vivo* work. The results of his PhD study were published as four major papers (Smith 1978b, 1980a-c) dealing with the microstructure and construction of the echinoid test, which paved the way to a new level of understanding of echinoid functional morphology.

Andrew moved to Liverpool University in 1980 as a research assistant to Chris Paul and with the aim of using stereom microstructure to understand the biology of Lower Palaeozoic echinoderms, especially the enigmatic and controversial carpoids. He produced a monograph of the cyclocystoids (Smith and Paul, 1980), a group which he still claims impossible to understand, and wrote *Echinoid Palaeobiology* (Smith, 1984). In 1982 he moved to London as a Scientific Officer at the Natural History Museum, then the British Museum (Natural History). On arrival, he discussed

**Figure 2.** Andrew Smith collecting echinoids in the Cretaceous (Spain, 2009).

the nature of his work with Dick Jefferies who told Andrew to look after "everything with pentameral symmetry" and he would do the rest! This arrangement held good until after Dick's retirement, when Andrew felt obliged to interpret the bilaterally symmetrical forms as echinoderms (Smith, 2005). Over this 30 year period at the Museum Andrew produced a vast body of research, including the 12 part *British Cretaceous echinoids* (Smith and Wright, 1989-2012) and numerous papers on echinoid and echinoderm taxonomy and phylogeny. Andrew retired from the NHM in 2012 at the age of 60.

## SCIENTIFIC WORK

Andrew's extensive research on echinoderm phylogeny, evolutionary relationships and systematics (see online CV) has changed the way we look at the phylum. It is important to note that all of his work is underpinned by thoroughly researched and beautifully illustrated taxonomic treatment. In addition, his research has made substantial contributions to the wider scope of palaeontology, including three areas are of outstanding importance.

(i) The extent to which the fossil record, and major events in it, such as extinctions are artefactual products of the rock record as it is preserved, where it is studied, and the taxonomic groups which we impose on the fossil groups. Patterson and Smith (1987, 1989) pointed out that large palaeontological databases include numerous non-monophyletic groups, which do not actually exist, and therefore skew any patterns which appear from analysis. He also addressed the importance of fossils in the reconstruction of phylogeny - Smith (1994), in *Systematics and the Fossil Record*, extensively discussed the relationships between the patterns of fossil distribution and analysis of their relationships, and established ground rules for the application of cladistics to phylogenetic reconstruction using fossils. He also argued (Smith, 2001; Smith *et al.*, 2001) that a significant part of what has been called "extinction" is actually just rapid facies change brought about by marine transgression – the "lost" shallow water taxa or their descendants, re-appear later in the record, often under different names. Latterly, Smith and McGowan (2008), McGowan and Smith (2008), Smith *et al.* (2012) and Vilhena and Smith (2013) investigated the relationship between patterns in the fossil record and potential sampling bias, and concluded that a large part of the "signal" is a product of sampling biases of various types, most notably plate tectonic history and sea level cycles which determine what is preserved where.

(ii)The integration of molecular and morphological phylogeny, and the significance and importance of fossils in the reconstruction of phylogeny. Many zoologists believe that reconstructing phylogeny simply involves sequencing a few genes and publishing the resultant tree as representing real evolution. Andrew and co-workers painstakingly developed congruent molecular and morphological trees for the echinoids, and used the fossil record to precisely calibrate this tree (Smith *et al.*, 2006; Kroh and Smith, 2010). This remains the most convincing integrated study of a branch of the tree of life.

**Figure 3.** Andrew Smith in Morocco on fieldwork (2012).

(iii)The ubiquity of the internet and its powerful communication potential were evident to Andrew early on, and he pioneered the development of a web-based approach to systematic zoology and palaeontology, in setting up, writing and editing the Echinoid Directory. This is a community-driven site, to which echinoid workers around the world contribute through a web interface. There are currently over 2000 species pages and 10,000 specimen illustrations, with the type species of all genera ever named now described, illustrated and on-line, fundamentally changing the way taxonomy of echinoids is approached. This should serve as a model for other groups of organisms, but in reality few groups have leading workers with Andrew's level of commitment and vision.

## AWARDS

Andrew's excellence as a scientist has resulted in numerous medals and awards, of which the following are a selection:

- Linnean Society Bicentennial Medal, 1993
- The Geological Society Bigsby Medal, 1995
- Elected a member of the Royal Society of Edinburgh, 1996
- The Geological Society Lyell Medal, 2002
- Elected a Fellow of the Royal Society, 2002
- The Palaeontological Association, Golden Trilobite Award, 2004 (Best website)
- The Linnean Society, Zoology Medal, 2005

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# PROGRESS AND PROSPECTS IN ECHINODERM RESEARCH

Andrew B. Smith

Department of Earth Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK.
a.smith@nhm.ac.uk

## INTRODUCTION

In the almost 40 years since I embarked upon my Ph D research enormous advances have been made in our understanding of echinoderms and their evolution, for the most part triggered by technological advances. The advent of personal computers and their ever increasing computational power has led to the routine assessment of phylogenetic relationships and evolutionary scenarios within a statistical framework placing both on a much more secure footing. The ability to sequence and read genes (initially small stretches of just a few hundred bases but now entire genomes) has unlocked a wealth of new comparative data, while technological advances in imaging and microscopy now allow us to study the echinoderm skeleton down to atomic level, document the variety of subcellular components, and build virtual models. Hand in hand with these advances has also come a remarkable growth in knowledge of the echinoderm fossil record, as detailed anatomical studies have been published and less well-documented parts of the world have been explored more thoroughly. Especially noteworthy is the increase in knowledge of early Palaeozoic echinoderms. Indeed new Cambrian records continue to accrue at a rapid rate and show no sign of plateauing. By comparison, echinoid diversity in the Mesozoic and Tertiary is now comparatively well-established and new genus-level discoveries are relatively uncommon arising principally from the reinterpretation of established species rather than new discoveries.

## CURRENT PROBLEMS

Despite having more, better quality information than ever before, there are several fundamental issues that remain poorly understood and which hamper progress in echinoderm research. I highlight here two that are of particular interest to me.

(i) The lack of robust, high-resolution (200+ taxa) phylogenetic trees of primitive fossil echinoderms uniting the various body plans is a major impediment. The most insightful science these days comes from tree-based analyses of patterns and the larger the tree the more powerful the statistical tests that can be applied. At the root of this difficulty, is the problem of establishing credible, reliable homologies across the wide diversity of disparate entities that comprise primitive echinoderms. Part of the problem stems from the surprising absence of intermediate taxa bridging the various echinoderm body plans (helicocystids and asterozoans being notable exceptions). However, a lack of early ontogenetic data and incomplete knowledge of internal plating organization due to the nature of the fossil record also hinders progress.

(ii) There is currently a worrying disagreement between morphology and molecular estimates of phylogeny, most notably in asteroids but to a lesser degree across all other groups. We need to understand the cause of this mismatch if we are to have any faith in using morphological traits alone in palaeontology. While more molecular data appears at first sight an advantage, more is not always better as it could simply be strengthening signal coming from inherent systematic biases. Much greater dissection and interrogation of the signal coming from molecular data is needed and more probability-based analyses of morphological traits to highlight where the problems lie and identify possible source of error.

## FUTURE OPPORTUNITIES

It is clear to all that better knowledge of the ontogeny, plate microstructure and plating organization of primitive echinoderms would be of great benefit, as would the discovery of new fossils – but these are serendipitous advances dependent on chance finds of specimens in the right state of preservation. Applying a systematic, comparative approach to existing data, however, can currently be done wherever you have a phylogenetic tree, and three specific questions seem ripe for tackling:

(i) While it is impossible to homologize specific skeletal elements between for example a cyclocystoid and a stylophoran, a detailed survey of growth strategies across the diversity of echinoderms might prove to be insightful. We already know some basic rules: In extant echinoderms plates are added at very specific zones and growth can be determinate or indeterminate. New elements are added at the tips of crinoid but proximally in its stem. A comparative analysis of how growth is achieved across extinct classes may help to identify homologous regions but will require the painstaking assembly of well-documented ontogenies.

(ii) A robust and comprehensive phylogeny of the Cambro-Ordovician clades will surely emerge in the next year or two, so there is huge scope for developing Bayesian or likelihood approaches to investigate rates and patterns of evolution, where uncertainties in the data are catered for in a statistically robust way. For example mapping out the evolution of feeding strategies in time and space could provide key data on the changing nutrient levels in early Palaeozoic oceans.

(iii) A phylogenetic-based comparative analysis of deep-sea echinoderms framed within a Bayesian analysis which looked at the fossil record of sister-groups will help solve the current uncertainties over when and how often echinoderms moved into the abyssal habitat and again will provide key information on nutrification levels in open oceanic environments.

# PAPERS

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# TAPHONOMY OF NEW *RHOPALOCYSTIS* ASSEMBLAGES IN THE LOWER ORDOVICIAN OF THE ZAGORA AREA (CENTRAL ANTI-ATLAS, MOROCCO)

Ninon Allaire[1,2], Bertrand Lefebvre[2], Emmanuel Martin[2], Elise Nardin[3] and Romain Vaucher[2]

[1] UMR CNRS 8198 EvoEcoPaleo, Cité Scientifique, bâtiment SN5, Université Lille 1, 59655 Villeneuve d'Ascq, France. ninon.allaire@ed.univ-lille1.fr
[2] UMR CNRS 5276 LGLTPE, Université Lyon 1, 2 rue Raphaël Dubois, 69622 Villeurbanne cedex, France. bertrand.lefebvre@univ-lyon1.fr, emmanuel.martin@univ-lyon1.fr, romain.vaucher@univ-lyon1.fr
[3] UMR CNRS-IRD-UPS 5563 Géosciences Environnement Toulouse, Observatoire Midi-Pyrénées, 14 avenue Edouard Belin, 31400 Toulouse, France. elise.nardin@get.omp.eu

**Keywords:** Anti-Atlas, eocrinoids, Morocco, Ordovician, *Rhopalocystis*, taphonomy.

## INTRODUCTION

*Rhopalocystis* is a Tremadocian (Early Ordovician) genus of eocrinoids (basal blastozoans), endemic to the Agdz-Zagora area in the central Anti-Atlas, Morocco. Isolated skeletal remains from the Valdemiedes Formation (Cambrian Series 2, Stage 4) of Spain were tentatively assigned to *Rhopalocystis* (Clausen, 2004). However, they more likely belong to a yet undescribed gogiid eocrinoid (S. Zamora, pers. comm., 2013). The morphology of *Rhopalocystis* is characterised by a mixture of plesiomorphic (e.g., epispires) and more advanced characters (e.g., theca organised into well-defined circlets of plates). Its phylogenetic position remains largely unresolved. *Rhopalocystis* was identified as a gogiid eocrinoid (Sprinkle, 1973; Broadhead, 1982), assigned to various groups of more derived blastozoans (e.g., Paul, 1988; Sumrall *et al.*, 2001; Nardin, 2007), or interpreted as a possible transitional form between blastozoans and crinoids (e.g., Ausich *et al.*, 2013; but see Ubaghs, 1963; Guensburg and Sprinkle, 2007).

Remains of *Rhopalocystis* were first collected in 1952 at Tansikht bridge (locality 1; Fig. 1A) during the field excursion of the 19th International Geological Congress (Ubaghs, 1963). However, specimens of *Rhopalocystis* from Tansikht bridge were not described by Choubert *et al.* (1953), who only reported on the presence of the associated glyptocystitid *Mimocystites* (= *Macrocystella*). Abundant specimens of *Rhopalocystis* were subsequently collected by Jacques Destombes (from 1959 to 1985) in several localities located E of the Jbel Bou Dehir, in Zagora area (localities 2, 3 and 5; Fig. 1A), W of Agdz (locality 4; Fig. 1A), and at Tansikht bridge (locality 1). This material was described in a series of papers by Ubaghs (1963), Chauvel (1971, 1978) and Chauvel and Régnault (1986). Ubaghs (1963) created the genus *Rhopalocystis* based on exquisitely preserved specimens collected at locality 2. All individuals were assigned to the type species, *R. destombesi*. Four additional species of *Rhopalocystis* were described by Chauvel (1971), based on new material collected at localities 2 (*R. grandis*, *R. zagoraensis*), 3 (*R.* sp. A), and 4 (*R. fraga*). Chauvel (1978) redescribed *R. zagoraensis* and identified three more species, based on new material from localities 1 (*R.* sp. C), 2 (*R. havliceki*), and 3 (*R.* sp. B). Finally, Chauvel and Régnault (1986) discussed the systematics of the different species assigned to *Rhopalocystis* and suggested the erection of two more taxa, based on new material from localities 2 and 5 (*R. dehirensis* and *R. lehmani*).

The aim of this paper is to describe three new *Rhopalocystis* assemblages (localities 6, 7, and 8) in the Lower Ordovician of the Zagora area and to discuss their taphonomy. Moreover, intensive field work conducted between 2012 and 2014 made it possible to obtain a detailed logging of the Lower Ordovician succession in the Zagora area, and to place all known occurrences of *Rhopalocystis* in this revised stratigraphic framework (Fig. 1B). The morphological disparity within the genus *Rhopalocystis* and the validity of its 10 described species will not be investigated here, but will be treated elsewhere.

## GEOLOGICAL CONTEXT

In the central Anti-Atlas (Morocco), the Lower Ordovician succession rests unconformably over the middle Cambrian sandstones of the Tabanite Group (Destombes *et al.*, 1985). In the Agdz-Zagora area, the Lower Ordovician sequence corresponds to a thick (1000 m), monotonous series of fine siltstones (Fezouata Shale, Tremadocian to late Floian), capped by the sandstones of the Zini Formation (latest Floian). In the last twelve years, successive field excursions in the Ternata plain (N. of Zagora) resulted in the detailed logging of the whole Lower Ordovician succession and the definition of a precise biostratigraphic framework based on both graptolites and acritarchs (Martin *et al.*, in press). All historical sites yielding remains of *Rhopalocystis* could be placed in this refined biostratigraphic framework: a late Tremadocian age (*A. murrayi* biozone) was confirmed for the three localities of the Ternata plain, E of Jbel Bou Dehir (localities 2, 3 and 5; Fig. 1B), and also for the two other sites, in the Agdz area (localities 1 and 4). Moreover, three new sites yielding abundant remains of *Rhopalocystis* (localities 6, 7, and 8; Fig. 1) were discovered in the Lower Ordovician of the Zagora area.

Locality 6 (Fig. 1) corresponds to a low cliff along the banks of a dry stream bed (oued), about 10 km NE of the small village of Beni Zoli and 21 km N of Zagora, in the western part of the Ternata plain (W of Jbel Bou Dehir). Laminated greenish siltstones have yielded a late Tremadocian assemblage (*A. murrayi* biozone) consisting in abundant remains of *Rhopalocystis* spp., associated with an extremely depauperate fauna comprising only rare specimens of the trilobite *Bavarilla* sp. In 2003, the exploitation of this site yielded 80 specimens deposited in the collections of Cadi-Ayyad University, Marrakesh (AA.TAM.OI.1-80).

Locality 7 (Fig. 1) is located 20 km NE of Zagora, in the eastern part of the Ternata plain (E of Jbel Bou Dehir). Abundant specimens of *Rhopalocystis* were collected in 2003-2004 by Roland and Véronique Reboul within large, massive lenses of bioclastic sandstones. No other faunal element was observed in these levels. The study material is deposited in the collections of the Musée des Confluences, Lyon (ML20.269379-382) and Lyon 1 University, Villeurbanne (FSL 711650, FSL 711160-163, FSL 712045). Locality 7 is indeed very close to Jacques Destombes' locality 1687 mentioned in Vidal (1998a, 1998b). Destombes' site corresponds to a distinct, concretion-bearing level occurring a few meters below, in the same area. The small alumino-siliceous concretions of locality 1687 have yielded an abundant and diverse assemblage comprising many bivalves (e.g., *Redonia michelae*), brachiopods, cephalopods (e.g., *Bathmoceras australe*, *Destombesiceras zagorense*, *Rioceras* sp.), conularians, echinoderms (e.g., *Anedriophus moroccoensis*, *Argodiscus espilezorum*, *Balanocystites primus*, *Balantiocystis regnelli*, *Lingulocystis* sp.), gastropods (e.g., *Carcassonnella courtessolei*, *Thoralispira* cf. *laevis*), graptolites, hyolithids (e.g., *Cavernolites senex*), machaeridians, trilobites (e.g., *Ampyx* sp., *Asaphellus fezouataensis*, *Basilicus* sp., cheirurids indet.) and other arthropods (e.g., *Eoduslia*, *Zagoracaris*). A mid to late Floian age has been generally assigned to this assemblage (Vidal, 1998a, 1998b; Van Roy, 2006; Sumrall and Zamora, 2011; Kröger and Lefebvre, 2012). However, the composition of the graptolite assemblage suggests that a latest Tremadocian age (*H. copiosus* biozone) is more likely (Martin *et al.*, in press). Consequently, a latest Tremadocian (or earliest Floian) age can be inferred for the overlying horizon yielding large *Rhopalocystis*-bearing concretions.

Locality 8 (Fig. 1) is located at the summit of a small hill, N of Jbel Tizagzaouine, about 2.2 km NE of locality 6 and 23 km N of Zagora, in the western part of the Ternata plain (W of Jbel Bou Dehir). Large fragments of massive lenses of bioclastic sandstones were collected in 2013-2014. They have yielded a late Tremadocian assemblage (*A. murrayi* biozone) comprising abundant specimens of *Rhopalocystis* spp., sometimes associated to large fragments of disarticulated trilobites. All available material is deposited in the collections of Cadi-Ayyad University, Marrakesh (AA.TISa.OI.1-24) and Lyon 1 University, Villeurbanne (FSL 712044).

## TAPHONOMY

Taphonomic features of *Rhopalocystis* assemblages in the late Tremadocian of the Agdz-Zagora area were thoroughly investigated and discussed by Ubaghs (1963), who identified two main kinds of preservation. The first one

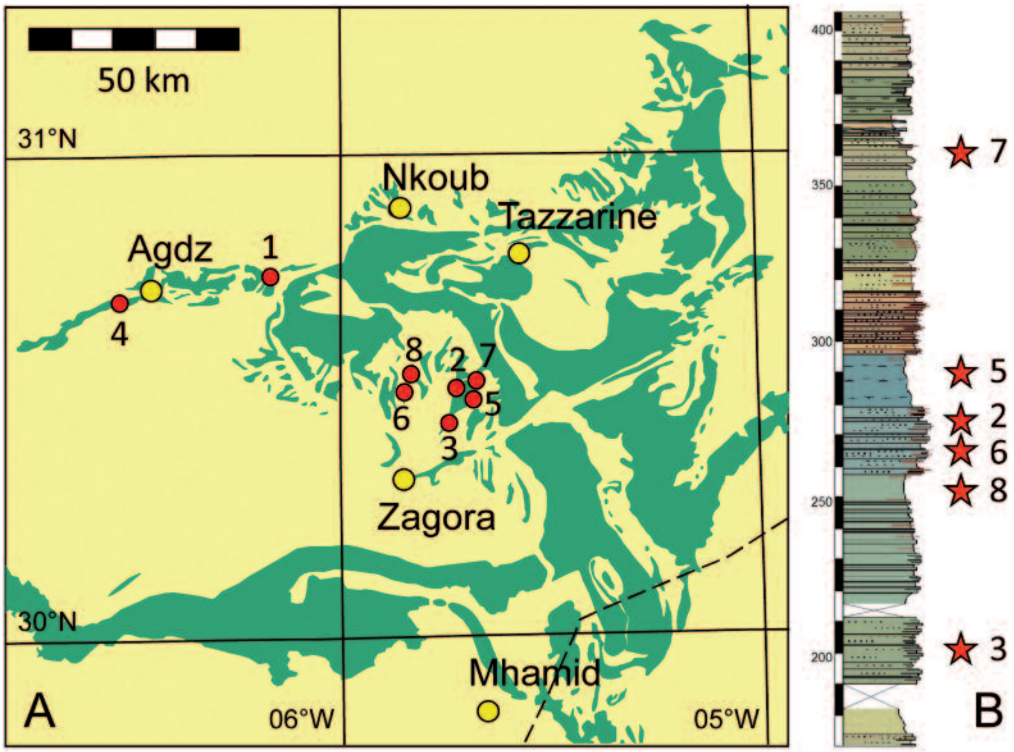

**Figure 1.** Location and stratigraphic position of *Rhopalocystis* assemblages. A. Simplified geological map of the central Anti-Atlas, Morocco. Ordovician outcrops are indicated in green. B. Partial log of the Lower Ordovician succession in the Zagora area (interval between 170 and 405 m above the unconformity between the Tabanite Group and the Fezouata Shale) showing the stratigraphic position of *Rhopalocystis* beds. Locality 1: Tansikht bridge (= Destombes locality 2082); locality 2: Jbel Bou Dehir (= Destombes localities 1157 and 1725); locality 3: Jbel Bou Dehir (= Destombes localities 1737, 1738 and 1750); locality 4: W. of Agdz (= Destombes locality 1773); locality 5: Jbel Bou Dehir (= Destombes locality 2367); locality 6: Tameraout, Z-F1; locality 7: Bou Chrebeb, Z-F25; locality 8: small hill, N of Jbel Tizagzaouine, Z-F12c.

corresponds to extremely dense accumulations of individuals in massive, bioclastic sandstones, and the second one, to more scattered individuals preserved in laminated siltstones. The three new *Rhopalocystis* assemblages confirm the existence of, at least, two main modes of preservation, but they also offer the opportunity to place them in their palaeoenvironmental context.

Both locality 7 and 8 have yielded type 1 assemblages of *Rhopalocystis* (Fig. 2A-F). They consist in densely packed accumulations of complete, fully articulated thecae in thick, lenticular beds of massive sandstones (Fig. 2C-F). Thecae do not exhibit any preferential orientation. Articulated portions of stems are sometimes preserved, either as isolated stumps, or still in connection with the theca (Fig. 2A, E). No distal extremities of stems have been observed. Brachioles are never preserved. In some other levels, complete thecae are less common and are associated with thousands of disarticulated thecal plates (Fig. 2B) and sometimes, large fragments of trilobites (Fig. 2A). In these levels, isolated skeletal elements consist almost exclusively of basal plates. Type 1 assemblages of *Rhopalocystis* are interpreted here as storm-generated levels of accumulation, resulting from the downslope transport and rapid burial of shallower communities. A similar interpretation was proposed by Vidal (1998a, 1998b) for the taphonomy of trilobite assemblages occurring (stratigraphically) a few meters above the *Rhopalocystis* horizon at locality 7.

The *Rhopalocystis* assemblage collected at locality 6 illustrates the second type of preservation (Fig. 2G-J) mentioned by Ubaghs (1963). Individuals are not preserved in clusters, but randomly distributed in fine, laminated

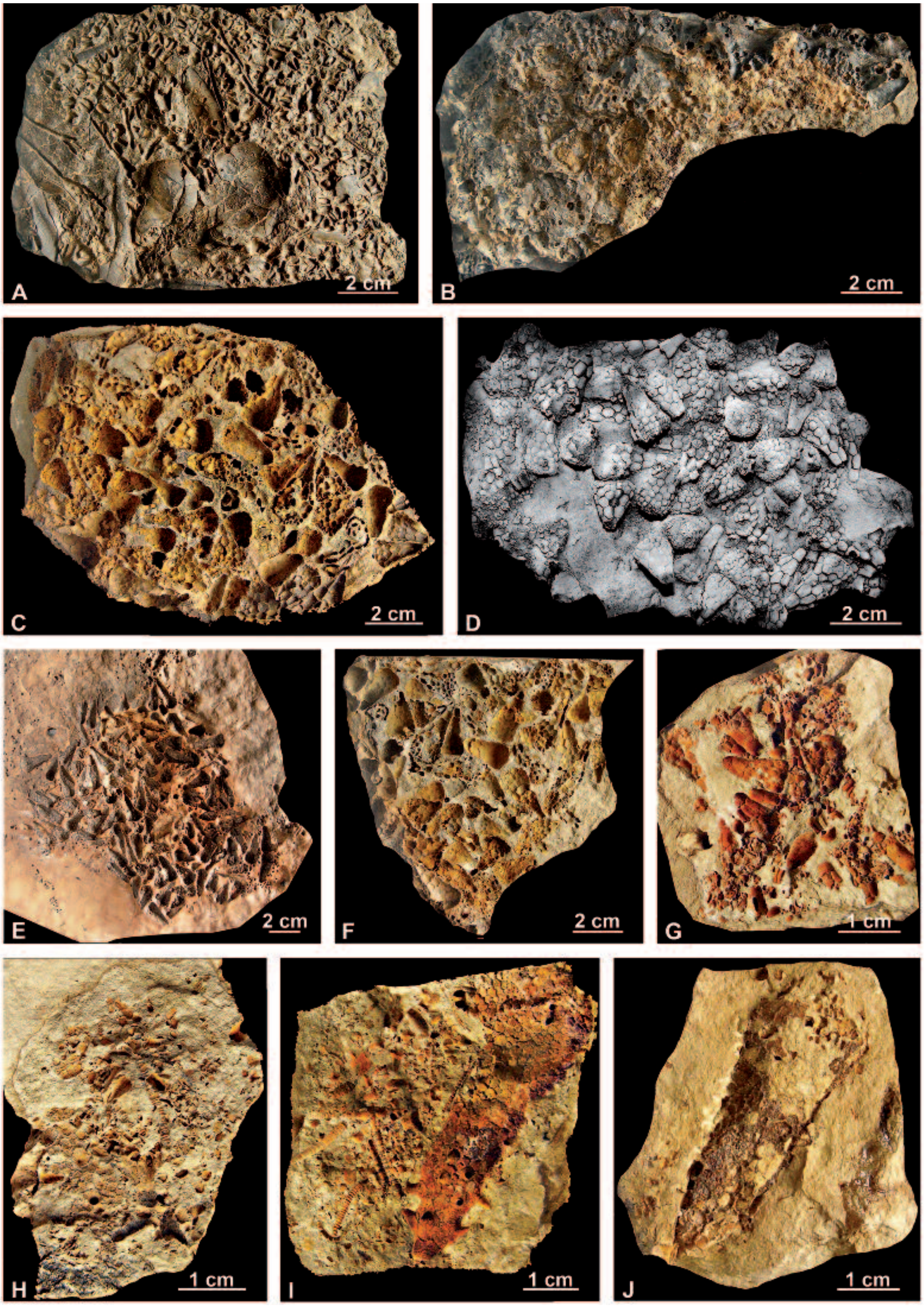

**Figure 2.**

siltstones (Fig. 2G). Their thecae are large to very large, but never complete, frequently slightly disarticulated and/or collapsed (Fig. 2I-J). Brachioles have not been observed. Fully articulated proximal parts of stems are often preserved in connection with the thecae. The siltstones also contain abundant disarticulated fragments of *Rhopalocystis* (different types of thecal plates, columnals and numerous smaller elements; Fig. 2H-I). Type 2 assemblages are here interpreted as distal storm-influenced deposits, resulting from the *in situ* disarticulation and slow burial of *Rhopalocystis*-dominated communities.

## CONCLUSIONS

The discovery of three new *Rhopalocystis*-dominated assemblages confirms the existence of widespread eocrinoid meadows in shallow environmental conditions in the late Tremadocian of the Agdz-Zagora area. The absence or extreme rarity of associated benthic fauna (e.g., molluscs, trilobites) is a characteristic feature also observed in many fossil and modern echinoderm dense beds (Fujita and Ohta, 1989; Lefebvre, 2007; Zatoń *et al.*, 2008). The abundant material collected at the new localities will offer the opportunity to reevaluate the systematics and morphological disparity within the genus *Rhopalocystis*.

## Acknowledgements

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**Figure 2.** Different types of preservation of *Rhopalocystis* spp., late Tremadocian, Zagora area (Morocco). All photographs show original specimens, with the exception of D (latex cast). A-F. Accumulations of *Rhopalocystis* spp. within lenses of bioclastic sandstones. A. Partially disarticulated thecae, portions of stems and isolated skeletal elements of *Rhopalocystis* sp., associated with large isolated pieces of trilobites, Z-F12c (AA.TISa.OI.10). B. Isolated plates and complete thecae of *Rhopalocystis destombesi*, Z-F12c (AA.TISa.OI.9). C, F. *Rhopalocystis destombesi*, Z-F25 (FSL 711650, part and counterpart). D. *Rhopalocystis destombesi*, Z-F25 (ML20-269382). E. *Rhopalocystis zagoraensis*, Z-12c (FSL 712044). G-J. *Rhopalocystis* spp. preserved in fine siltstones, Z-F1. G. Complete to slightly disarticulated thecae of *Rhopalocystis zagoraensis* (AA.TAM.OI.2). H-I. Part and counterpart of specimen AA.TAM.OI.21. H. Isolated skeletal elements of *Rhopalocystis* sp. I. Isolated plates of *Rhopalocystis* sp. and large complete theca of *Rhopalocystis havliceki*. J. Large complete theca of *Rhopalocystis havliceki* (AA.TAM.OI.13). Repositories: Université Cadi-Ayyad, Marrakesh, Morocco (AA), Université Lyon 1, Villeurbanne, France (FSL) and Musée des Confluences, Lyon (ML).

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# SUBSTRATE STABILITY: WHEN THE TROUBLES COME FROM THE BOTTOM

J. Javier Álvaro

Instituto de Geociencias (CSIC-UCM), José Antonio Novais 12, 28040 Madrid, Spain. jj.alvaro@csic.es

**Keywords:** benthos, echinoderms, microbial crusts, diagenesis, Cambrian.

## INTRODUCTION

Substrate stability was a key limiting factor that controlled the heterogeneous distribution patterns of benthic metazoans across the Ediacaran-Cambrian transition. The so-called Agronomic Revolution (Seilacher and Pfluger, 1994) and Cambrian Substrate Revolution (Bottjer *et al*., 2000) were linked to both diversification of burrowing metazoans and a switch from microbial mat-dominated to unconsolidated substrates. However, this "revolution" took place in a stepwise and progressive manner through Cambrian times due to the abiotic control on substrate replacement, mainly yielded by the availability of new kinds of substrates (Álvaro *et al*., 2013).

## TYPE OF SUBSTRATES

Soupgrounds (saturated in water and incompetent), firmgrounds (stable and nearly lithified) and hardgrounds (lithified) co-existed in the Cambrian although controlled by different factors, such as microbial and shelly carbonate production, and synsedimentary or earliest-diagenetic precipitation of apatite, calcite or iron oxy-hydroxides. In the absence of microbial crusts, interaction of early diagenetic precipitation of calcite, apatite or hematite/goethite occluding primary porosity and sedimentation rate yielded new available substrates for colonization by spiculate and non-spiculate (archaeocyathan) sponges, chancelloriids and new echinoderm clades. Their palaeogeographic distribution exhibits a microbial mat/epifaunal antagonistic relationship between microbial-dominated reefs and crusts vs. mud-sticker sessile metazoans.

## FINAL CONSIDERATIONS

Modification of shelly substrates (or shell pavements) through Cambrian times was related to thickness increase, shell content and composite development of hiatal surfaces, in some cases encrusted with microbial mats and biofilms. As a result, microbially induced precipitation of calcite on surfaces and occluding primary porosity available in shell-dominated sediments led to the progressive occurrence of firm-to-hardgrounds. Substrate stability was then not only yielded by scattered shells, but also by their earliest-diagenetic cementation (Zamora *et al*., 2010). Several carbonate hardground substrates were then occurring: (i) microbial-dominated reefs, mats and biofilms exhibiting stromatoid and thromboid fabrics; (ii) microbially influenced shell accumulations with hiatal interbed surfaces marked by development of microbial crusts; (iii) shell substrates with no macroscopic evidence of microbial evidence but earliest-diagenetic precipitation of calcite cements occluding primary porosity; and (iv) biofilms forming microbially induced sedimentary

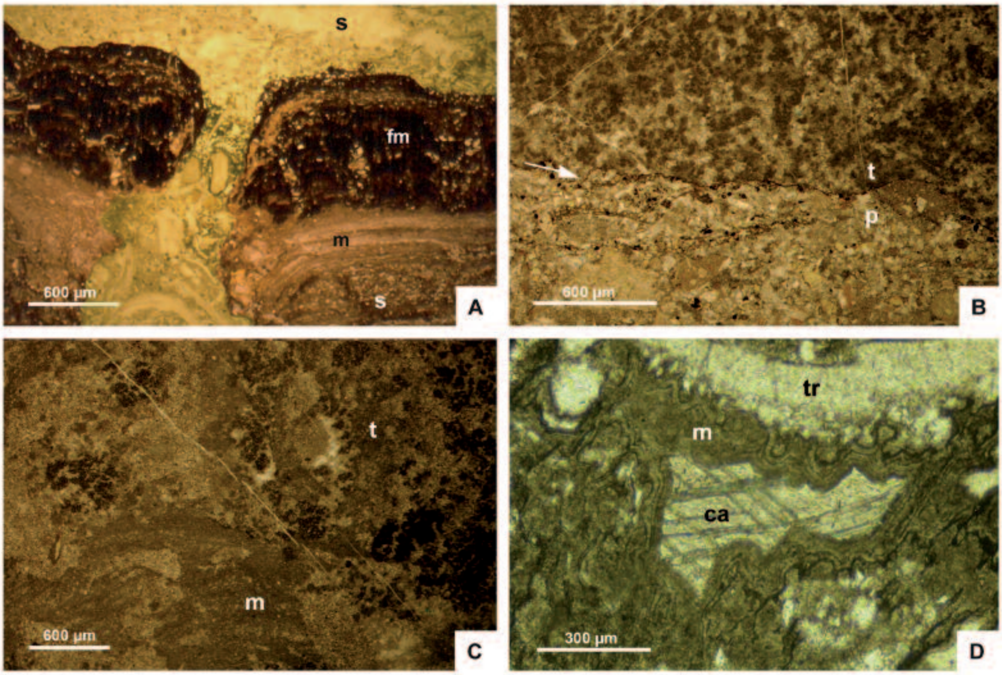

**Figure 1.** Thin-section photomicrographs of Cambrian carbonate and phosphate hardgrounds. A. Microbial laminae encrusting a shelly accumulation and eroded and partly infilled (false greenish colour) by overlying echinoderm-dominated packstone; Brèche à Micmacca Member, Anti-Atlas, Morocco. B. Pyroclastic substrate encrusted by thrombolitic crust (erosive contact arrowed); Lemdad Formation, High Atlas, Morocco. C. Stromatoid mat capped by thromboid crust; Lemdad Formation, High Atlas, Morocco. D. Interparticular porosity of a shelly pavement encrusted by phosphatized microbial mats and finally occluded with calcite; Thalis Member (Marcory Formation), northern Montagne Noire, France. Abbreviations: ca. calcite, fm. ferruginized microstromatolitic mat, m. microstromatolitic mat, p. pyroclastic substrate, s. shell accumulation, t. *Epiphyton*-dominated thrombolite, tr. trilobite sclerite.

structures (MISS) and yielding partial stability to clayey soupground substrates. These substrates played nucleation roles for colonization by the so-called chancelloriid-echinoderm-sponge (CES) community. The latter differed from: (i) the microbial-archaeocyathan (reefal) and microbially dominated, carbonate-hardground communities; and (ii) the (spiculate) sponge-thromboid phosphate-hardground communities.

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# TOWARD A PHYLOGENETIC CLASSIFICATION OF THE CRINOIDEA (ECHINODERMATA)

William I. Ausich[1], Thomas W. Kammer[2], David F. Wright[1], Selina R. Cole[1], Mark E. Peter[1] and Elizabeth C. Rhenberg[3]

[1] School of Earth Sciences, 125 South Oval Mall, Ohio State University, Columbus, OH 43210, USA. ausich.1@osu.edu, wright.1433@osu.edu, cole.678@buckeyemail.osu.edu
[2] Department of Geology and Geography, West Virginia University, Morgantown, WV U26506, USA. tkammer@wvu.edu
[3] Department of Geology, Earlham College, 801 National Road West, Richmond, IN 47374, USA. elicrhen@gmail.com

**Keywords:** Crinoidea, evolution, phylogeny, paleophyletic.

## INTRODUCTION

Several crinoid phylogenies have been proposed based either on genomic studies (Rouse *et al.*, 2013; Roux *et al.*, 2013) of crown group crinoids or on morphologic studies of fossil taxa (Simms and Sevastopulo, 1993; Brower, 1995; Ausich, 1998; Guensburg, 2012). Morphological studies were based on either inspection of morphology or on computational methods, and in some cases, they resulted in conflicting results. Since the publication of the *Treatise on Invertebrate Paleontology* (Moore and Teichert, 1978) (Fig. 1A), examples of crinoid Linnaean classifications include Ausich (1998) (Fig. 1B), Simms and Sevastopulo (1993) (Fig. 1C), and Hess and Messing (2011) (Fig. 1D). However, a phylogenetic classification has not previously been attempted. The recovered topology of Ausich *et al.*'s (2014) recent phylogenetic analysis of Ordovician crinoids is used herein to propose an informal phylogenetic classification for the Crinoidea. It is our hope that this classification will serve to inform and complement, rather than replace, the Linnaean classification of crinoids (e.g. Potter and Freudenstein, 2005). Following Wagner (2002), where we use Linnaean taxonomy (e.g., Cladida) formally, we are referring to taxa defined by other workers. The clade names we propose are informal and are used only to describe the phylogenetic structure of Ausich *et al.*'s (2014) analysis; therefore, this obviates the need to follow taxonomic rules (Wagner, 2002). Quotation marks are used where referring to clades rather than nominal Linnaean taxa.

## CRINOID EVOLUTIONARY HISTORY

From a Phanerozoic perspective, the Crinoidea is a bottom-heavy clade (Gould *et al.*, 1987) and relatively few taxa are encompassed within the single crinoid crown group, comprised of comatulids (including the bourgueticrinids), cyrtocrinids, hyocrinids, and isocrinids (Hess and Messing, 2011; Rouse *et al.*, 2013). In contrast, by the close of the Ordovician, six major crinoid lineages had emerged. The oldest crinoids are from the lower Tremadocian and include representatives of the Camerata, Protocrinida, Cladida (Dendrocrinida and Cyathocrinida), and Disparida. Thus, stratigraphic appearance of taxa offers little insight into ancestral-descendant morphologies among crinoids. The oldest member of the Hybocrinida is from the Floian and the oldest crinoid belonging to the Flexibilia is from the Sandbian.

- Class Crinoidea
  - Subclass Echmatocrinea
    - Order Echmatocrinida
  - Subclass Camerata
    - Order Diplobathrida
    - Order Monobathrida
  - Subclass Inadunata
    - Order Disparida
    - Order Hybocrinida
    - Order Coronata
    - Order Cladida
  - Subclass Flexibilia
    - Order Taxocrinida
    - Order Sagenocrinida
  - Subclass Articulata
    - Order Millericrinida
    - Order Cyrtocrinida
    - Order Bourgueticrinida
    - Order Isocrinida
    - Order Comatulida
    - Order Uintacrinida
    - Order Roveacrinida

**A**

- Class Crinoidea
  - Subclass Aethocrinida
  - Subclass Cladida
    - Order Dendrocrinida
    - Order Cyathocrinida
    - Order Poteriocrinida [1]
  - Subclass Flexibilia
    - Order Taxocrinida
    - Order Sagenocrinida
  - Subclass Articulata [2]
  - Subclass Camerata
    - Order Diplobathrida
    - Order Monobathrida
  - Subclass Disparida [3]
    - Order Eustenocrinida
    - Order Maennilicrinida
    - Order Tetragonocrinida
    - Order Homocrinida
    - Order Myelodactylida
    - Order Hybocrinida

**B**

- Class Crinoidea
  - Subclass Camerata
    - Order Diplobathrida
    - Order Monobathrida
  - Subclass Disparida
  - Subclass Cladida
    - "stem-group cladids"
    - Infraclass Cyathocrinina
    - Infraclass Flexibilia
  - "stem-group articulates" [1]
    - Infraclass Articulata
  - Incertae Sedis ("Subclass") Hybocrinida

**C**

- Class Articulata
  - Order Holocrinida
  - Order Encrinida
  - Order Isocrinida
  - Order Comatulida
  - Order Millericrinida
  - Order Hyocrinida
  - Order Cyrtocrinida
  - Order Roveacrinida

**D**

**Figure 1.** Proposed classifications for crinoids. A, Moore and Teichert (1978), note: coronoids are no longer considered crinoids; B, Ausich (1998), [1]acknowledged to be polyphyletic and requiring further study; [2]orders as in Moore and Teichert (1978); [3]partial list of orders; C, Simms and Sevastopulo (1993). [1]Added here to be consistent with Simms and Sevastopulo (1993, Text-fig. 1); D, Hess and Messing (2011), order-level classification of the Articulata.

Applying the Universal Elemental Homology scheme to radiate echinoderms suggests that blastozoans are the nearest sister group to crinoids (Kammer *et al*., 2013; Sumrall, 2014). With six blastozoans forming an outgroup (*Cheirocystis*, *Echinosphaerites*, *Eumorphocystis*, *Glyptocystella*, *Protocrinites*, and *Rhopalocysts*), the computational phylogenetic analyses of Lower and Middle Ordovician crinoids by Ausich *et al*. (2014) indicated that the "Camerata" was an early crinoid clade that radiated from a blastozoan-like ancestor and is a sister to the clade comprising all other crinoids. Similarly, the "Protocrinida" is sister to a clade comprising disparids, cyathocrines, hybocrinids, and dendrocrines. Interestingly, the "Disparida" forms a sister clade to members of the Cladida and Hybocrinida and, therefore, supports a refurbished resurrection of Wachsmuth and Springer's (1885) Inadunata. Combining the cladogram of Ausich *et al*. (2014) with topologies recovered from phylogenetic studies on younger taxa (Simms and Sevastopulo, 1993; Brower, 1995; Ausich, 1998), the phylogenetic classification herein includes the position of the Flexibilia, crownward dendrocrines, and the Articulata. Excluding the Articulata, clades comprised of all Linnaean ranks emerged before the close of the Ordovician. Protocrinids and hybocrinids went extinct during the Ordovician, but other

Paleozoic groups persisted into the Permian. The Articulata must have emerged during the latest Paleozoic (Webster and Jell, 1999), but a consensus of this history remains to be developed.

## PHYLOGENY

The overwhelming majority of Paleozoic clades are stem lineages with respect to the crinoid crown group, which makes a phylogenetic classification based on monophyletic clades challenging. One difficulty of reconciling a Linnaean *versus* a phylogenetic classification results from the extinction of major lineages. In order to recognize the importance of extinct stem lineages, we propose the term "paleophyletic", which describes the geologically transient temporal window in which a paraclade was monophyletic prior to giving rise to another nominal Linnaean taxon.

In the informal phylogenetic classification scheme proposed here, new monophyletic crinoid groups that are nested include the "Pan-Crinoidea", "Pan-Inadunata", "Pan-Cladida", "Eucladida", and the "Eucrinoidea". In this view, the phylogenetic structure of major crinoid clades was in place by the close of the Ordovician Period. The articulates emerged during the latest Paleozoic, but the details of early articulate radiation requires further refinement. Pan-crinoids include all taxa historically included in the Crinoidea (with the exception of coronoids). Pan-inadunates include all crinoids other than camerates and protocrinids. The pan-cladids are a diverse clade comprised of several Linnaean taxa including the Cyathocrinida, Hybocrinida, Dendrocrinida, Flexibilia, and the Articulata. The "Eucladida" include all dendrocrines crownward of their split with flexibles and their sister clade "Articulata". The articulates are split into the paleoarticulates and the eucrinoids, the latter of which is the crinoid crown group. The Paleoarticulata comprise several stem lineages including the encrinids, holocrinids, millericrinids, and roveacrinids.

The phylogeny presented here only attempts to delineate the branching order of the major groups of crinoids. Sampling more taxa would undoubtedly result in stem groups for each of these major lineages. Interestingly, historical crinoid subclasses and orders remain as either monophyletic or paleophyletic clades for most of the Paleozoic. For example, the Inadunata was first defined by Wachsmuth and Springer (1885) as a major group among crinoids (see Moore and Teichert, 1978) and used as a crinoid subclass until it was demonstrated to be polyphyletic (Kelly, 1982; 1986). However, the present view of the Crinoidea recognizes a clade that roughly corresponds to the Inadunata *sensu* Wachsmuth and Springer (1885). This clade is designated the "Pan-Inadunata", which is essentially all of the former Inadunata and all of their descendants.

## CONCLUSIONS

An informal phylogenetic classification is proposed for the Crinoidea that largely supports historic subdivision of crinoids into major lineages, while also encompassing inferred branching order based on cladistic analysis. The informal clade names "Pan-Crinoidea", "Pan-Inadunata", "Pan-Cladida", and "Eucrinoidea" are proposed as successive clades within the Crinoidea, with the pan-crinoids forming the total crinoid clade and the eucrinoids forming the crinoid crown group. It is hoped that the informal phylogenetic classification scheme presented herein will help provide guidance to crinoid workers interested in studying evolutionary patterns and processes in "real" biological entities (i.e., monophyletic groups, or once monophyletic groups = paleophyletic) rather than nominal Linnaean ranks.

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# CLASSIFYING BLASTOIDS THROUGH HYDROSPIRE MORPHOLOGY

Jennifer E. Bauer[1], Colin D. Sumrall[1] and Johnny A. Waters[2]

[1] Department of Earth and Planetary Sciences, University of Tennessee, Knoxville, Tennessee 37996-1410, USA.
jbauer5@vols.utk.edu, csumrall@utk.edu
[2] Department of Geology, Appalachian State University, Boone, North Carolina 28608, USA. watersja@appstate.edu

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## INTRODUCTION

Traditionally, blastoids have been separated into two groups: Fissiculata and Spiraculata based on details of the internal respiratory structure called hydrospires (Jaekel, 1918; Wanner, 1940; Beaver, 1967). Waters and Horowitz (1993) suggested that various clades of spiraculates are nested within a larger fissiculates group, indicating a paraphyletic Fissiculata and a spiraculate evolutionary grade rather than a clade. This hypothesis was supported by a recent phylogenetic analysis by Atwood *et al.* (in review), which discovered spiraculates appearing multiple times within the large clade of Blastoidea. As the hydrospires are internal organs, new visualization methodology had to be developed (Waters *et al.*, 2014) to digitally render and manipulate complete hydrospire structures. The primary objective of this project is to utilize internal character data to generate a refined phylogenetic hypothesis for Blastoidea and test Fissiculata and Spiraculata for monophyly.

Systematic revision of the group has been previously performed via observation and subjective analysis rather than phylogenetic methods. Utilizing phylogenetic methods allows for the discovery of synapomorphies, which are important in the evolution of the clade. A recent study by Atwood *et al.* (in review) generated a phylogenetic framework to describe the synapomorphies and group origination among blastoids. External morphological and homologous characters were successfully employed utilizing phylogenetic methods. Although the thecal morphology provided a robust data set, much is still unknown about the internal morphology (Bodenbender, 1995; Bodenbender and Fisher, 2001; Sumrall and Brochu, 2003; Atwood *et al.*, in review). The conclusions of the study suggest that the ordinal and familial blastoid classification scheme needs to be reanalyzed. The addition of internal characters and the inclusion of more taxa across all families will result in the inference of a more robust evolutionary hypothesis for blastoids.

The external expression of hydrospires forms the basis of differentiation between fissiculates and spiraculates (Beaver *et al.,* 1967). Consequently, it is critical that an in depth examination needs to be performed before these structures are incorporated into a phylogenetic analysis. Hydrospires, unlike other internal structures, are bounded by thin calcareous walls (Beaver, 1967) and are typically preserved within the theca. Preliminary work by Waters *et al.,* (2014) indicates that hydrospires occur in a variety of forms and are important for delineating familial relations. In addition to utilizing the evolutionary history of blastoids to further the understanding of echinoderm relationships, this project will emphasize the importance of incorporating internal characters into the reconstruction.

## MATERIAL AND METHODS

Thin sections and acetate peels of serial sections of thecae have previously been used to render hydrospire morphology in 2-D (Breimer and Macurda, 1972) as well as 3-D (Schmidtling and Marshall, 2010). This project digitally transforms these 2-D serial peels into a 3-D model of hydrospire morphology for examination and character coding. We have been scanning and gathering preliminary data (Waters *et al.*, 2014) from unpublished acetate peels reposited in the Naturalis Biodiveristy Center in Leiden, Netherlands, which is home to a large collection of blastoid peels from the late 1960s. Peels are scanned, resized, and compiled in Adobe Photoshop (Fig. 1A-C, E-F); next the hydrospires are located and traced on each of the peels of the individual specimen. Once completed, the original photos are hidden and what remains is a series of drawings that trace the hydrospire vertically through the theca. The image is then compressed and transferred into Rhinoceros, which is a design program to render 2-D images in 3-D. Within Rhinoceros, the images are connected to generate complete structures. Once the computer models have been generated, they can be enlarged and printed as ceramic models (Fig. 1D, H; Waters *et al.*, 2014). To date there have been six models completed, encompassing six genera within five previously identified families of Blastoidea.

## RESULTS

Two of the six completed models are within the same family, Orbitremitidae, and show variable hydrospire morphology (Fig. 2). *Ellipticoblastus* (Fig. 2A-B) has hydrospire fold pairs that begin nearly the same distance apart as those of *Monoschizoblastus* (Fig. 2C-D) but remain closer together as they extend vertically towards the spiracles. The paired hydrospire folds of *Monoschizoblastus* bow outward slightly prior to tapering nearer to the spiracle openings. The number of hydrospire folds in each group varies between families as *Diploblastus* and *Deltoblastus* show two folds within each group whereas both *Ellipticoblastus* and *Monoschizoblastus* both have a singular fold per suture. Reduction of hydrospire folds has been discovered in *Deltoblastus* (Fig. 1G-H). In the CD interray (anal side) bears a single hydrospire whereas in other rays hydrospires are paired. This reduction is not seen in either *Ellipticoblastus* or *Monoschizoblastus.* Hydrospires have been suggested to appear conjoined in some individuals (Breimer, 1988), which do not appear in any of the currently modeled specimens. These internal characters will help form the basis of hydrospire classification for subsequent use in a phylogenetic analysis.

Ideally, all of the taxa used to infer blastoid phylogeny would be represented by species for which there are both specimens to code external morphology and peel data to code internal morphology. The goal of the project is to gain a wide range of species to determine how the hydrospire structure varies not only between families but also within families, as the phylogeny generated by Atwood *et al.* (in review) suggests that the family level structure requires

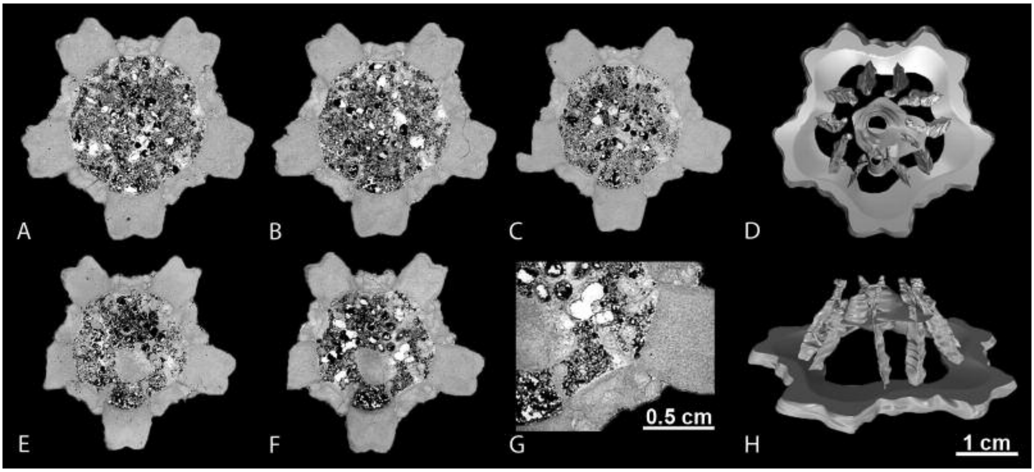

**Figure 1.** (A-C, E-F) Resized and reoriented serial sections of *Deltoblastus*; (G) Enlarged view of section F, depicting the reduction in hydrospire folds near the anal region compared to the two folds to the above right; (D) Aerial view of the reconstructed model of *Deltoblastus*; (H) Lateral view of the reconstructed model, same orientation as G, showing the single and double folds. Modified from work by Waters *et al.* (2014).

revision. Two genera, *Ellipticoblastus* (Fig. 2A-B) and *Monoschizoblastus* (Fig. 2C-D) are from the family Orbitremitidae and there is considerable variation in hydrospire structure between the two genera (Fig. 2). These preliminary results suggest that there is variation between and within families.

## FINAL CONSIDERATIONS

Our understanding of the systematics of echinoderms as a whole is still developing specifically with the Assembling the Echinoderm Tree of Life project. There is conflicting phylogenetic signal among datasets used to reconstruct echinoderm phylogeny, resulting from various interpretations of homology (Sumrall, 2010; Sumrall and Waters, 2012; Kammer, *et al.*, 2013). Once the hydrospire structures have been fully classified and coded, the reconstruction of blastoid relationships will provide a basis to support or reject the groupings of Fissiculata and Spiraculata as well as a framework for taxonomic revision. Relationships inferred by the Assembling the Echinoderm Tree of Life project suggests that modern crinoids have ancestry originating within the blastozoan group. Data derived from the evolutionary history of the blastoids can therefore be applied to other echinoderm groups to aid in inferring the true relationships among members of this diverse clade.

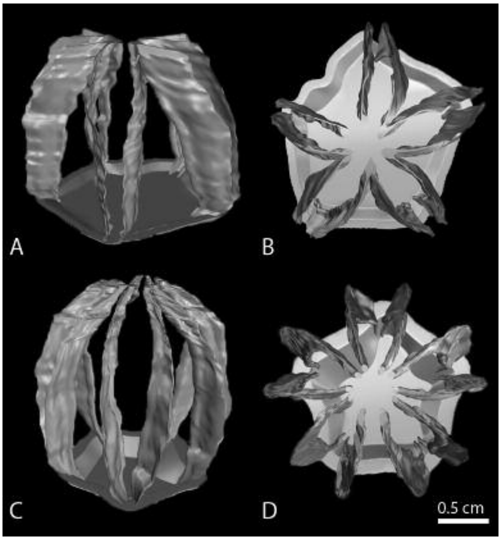

**Figure 2.** (A) Lateral view of *Ellipticoblastus* hydrospires; (B) Aerial view of *Ellipticoblastus* hydrospires; (C) Lateral view of *Monoschizoblastus* hydrospires; (D) Aerial view of *Monoschizoblastus*. Rhino models from work by Waters *et al.* (2014).

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# ECHINODERM ICHNOLOGY: A STATE OF THE ART

Zain Belaústegui[1], Fernando Muñiz[2,3], Rosa Domènech[1] and Jordi Martinell[1]

[1] IRBio (Biodiversity Research Institute); and Departament d'Estratigrafía, Paleontologia i Geociències Marines, Universitat de Barcelona, Martí i Franquès s/n, 08028 Barcelona, Spain. zbelaustegui@ub.edu; rosa.domenech@ub.edu; jmartinell@ub.edu
[2] Grupo de Investigación RNM 293 "Geomorfología Ambiental y Recursos Hídricos", Universidad de Huelva, 21071 Huelva, Spain. fmguinea@uhu.es
[3] Universidad Andrés Bello, Facultad de Ingeniería, Geología, Autopista Talcahuano, 7100, Concepción, Chile.

**Keywords:** Echinodermata, Bioturbation, Bioerosion, Trace Fossils, Neoichnology.

## INTRODUCTION

Several groups of echinoderms are among the most active and widespread bioturbators and bioeroders both in modern as well as in fossil marine environments. Burrowing and/or boring behaviours of regular and irregular echinoids, starfish, brittle stars and sea cucumbers are probably the best known in modern settings (Bromley, 1975; Bromley and Asgaard 1975; Martinell, 1981; Dashtgard and Gingras, 2012), and some of the resulting traces are well known in the fossil record. Other modern echinoderms, however, such as sand dollars or even crinoids, are able to leave different kind of traces on the sea floor, mainly superficial trails and trackways. These traces have received far less attention from an ichnological point of view and have not yet been identified in the fossil record. With respect to extinct echinoderms, most taxa exhibit sessile life-habits and no bioturbation or bioerosion structures have been associated to them. Among vagile forms, trace fossils associated to mitrate body fossils have, however, been described (Rahman *et al.*, 2009).

## TRACE FOSSIL RECORD

### Bioturbation structures

*Bichordites* and *Scolicia*, i.e. large meniscate backfill burrows bearing one or two drains respectively, are quite common in the fossil record (since the Jurassic). Detailed neoichnological studies, both from aquaria as from natural environments, have shown that these large meniscate traces result from backfilling activity of spatangoid echinoids ploughing through the sediment (e.g. Kanazawa, 1992; 1995) at least for Cretaceous and younger material. The presence of one or two drains is related to the subanal tuft spines and corresponding tube feet of the echinoid tracemaker. Among modern spatangoids, the traces produced by the so-called *Spatangus* group exhibit a double drainage, while those generated by the *Echinocardium* group have a single one (Plaziat and Mahmoudi, 1988). Ichnotaxa *Subphyllochorda*, *Taphrhelminthopsis* and *Taphrhelminthoida* were included in *Scolicia* by Uchman (1995). This author regarded *Subphyllochorda* as the sole expression of *Scolicia*, *Taphrhelminthopsis* as a cast of washed-out *Subphyllochorda*, and *Taphrhelminthoida* as having the same morphology as that of *Taphrhelminthopsis.* Uchman (1995) also considered the ichnogenus *Laminites* as a preservational expression of different types of traces (*Scolicia*, *Bichordites* and other non-echinoid Palaeozoic burrows), lacking diagnostic features and only useful in order to informally characterize a particular preservational variant. Smith and Crimes (1983) erected the ichnogenus *Cardioichnus* to describe ovoid to sub-quadrate, bilobate resting impressions preserved as convex hiporeliefs and occasionally continuous to *Scolicia* burrows; its range is from the Cretaceous to the Pliocene.

*Asteriacites*, *Arcichnus* and *Ophioichnus* have been interpreted as resting or locomotion traces produced by asterozoans, commonly preserved as convex hyporeliefs (Fig. 1A, B). The main morphology of *Asteriacites*, ascribed to asteroid or ophiuroid activity, consists of star-shaped traces with five or more rays, with bioglyphs (striae) attributed to the activity of digging tube feet, and occasional vertical repetition due to rapid sedimentation. It is recorded from Cambrian to Recent marine sediments (Häntzschel, 1975). Ichnogenera *Arcichnus* and *Ophioichnus* respectively consist of horseshoe- and hook-shaped traces interpreted as a trackway produced by a pair of arms of an ophiuroid (Sutcliffe, 1997; Bell, 2004). The great similarities between these two ichnotaxa suggest that *Ophioichnus* could be synonymous with *Arcichnus*, but a more detailed study is needed. *Arcichnus* and *Ophioichnus* have been described in Devonian and Cretaceous deposits respectively.

The ichnogenus *Artichnus*, interpreted as resulting from the burrowing activity of holothurians, consists of J- or 'test tube'-shaped, cylindrical and blind burrows with a thick laminated lining which may consist of retrusive spreiten (Zhang *et al.*, 2008; Belaústegui *et al.*, 2014). At the moment, its fossil record is limited to the Eocene of Poland and the Miocene of Spain.

Finally, and associated to body fossils of the Devonian stylophoran *Rhenocystis latipedunculata*, Rahman *et al.* (2009) described the ichnogenus *Vadichnites* as horizontal straight to curved traces with low relief protuberances or closely spaced fine ridges transversely oriented across a shallow groove. Some of these traces have been interpreted as non-directional agonic movements and provide new insights to interpret the mode of life of mitrates.

### Bioerosion structures

Ichnogenera *Gnathichnus* and *Circolites* are unique bioerosion structures attributed to echinoderms, in particular to regular echinoids (Fig. 1C, D; e.g. Bromley, 1975; Martinell, 1981). *Gnathichnus* correspond to bite traces produced by plucking and grazing (by using their jaw apparatus, and occasionally also their spines) on hard substrates (organic or inorganic). They are known from the Triassic and are very common in modern environments (Bromley, 2004). *Circolites* consists of bowl-shaped, hemispherical or deeper pits produced in rock surfaces and related to shallow water; its range is from the Jurassic to Recent (Bromley, 2004).

### Miscellanea

This section includes those traces not directly produced by echinoderms but closely related to them. Ettensohn (1981) erected the ichnogenus *Crininicaminus* to describe cylindrical burrows with a lining mainly composed of crinoid ossicles probably produced by tube-dwelling worms. Ichnogenus *Tremichnus* was erected by Brett (1985) to include simple circular-parabolic pits, with or without stereom swellings, produced on echinoderms (mostly crinoids) by parasitic organisms. Bohatý *et al*. (2012) propose the ichnogenus *Ostiocavichnus* to describe gall-like swelling on Palaeozoic crinoid pluricolumnals, distinguished by elliptical or subcircular concavities resulting from epizoozoan rugose corals encased by stereomic coating. These last two kinds of traces resulting from symbiotic relationships and skeletal accretion are known as bioclaustration structures or Impedichnia.

## NEOICHNOLOGY

Neoichnological studies provide a very large amount of information concerning the burrowing and boring behaviours of modern organisms. Related to echinoderms, there are many studies focused on this topic, as for example, those carried out by Seilacher (1979), Christensen and Colacino (2000), Baumiller and Messing (2007) or Ayranci and Dashtgard (2013) in which the burrowing behaviour of sand dollars, brittle stars, stalked crinoids and holothurians are described respectively. Since many of the structures described in these studies have not yet been identified in the fossil

**Figure. 1.** Comparative examples between fossil and modern bioturbation and bioerosion structures. A) *Asteriacites* resting traces from the Eocene of Tavertet (Barcelona, NE Spain). B) *Astropecten irregularis* burrowing in the Nueva Umbría Spit (Lepe, Huelva, SW Spain). C) *Circolites* from the Pliocene of Viladamat (Girona, NE Spain). D) Specimens of *Paracentrotus lividus* boring hemispherical pits in the rocky coast of Zumaia (Gipuzkoa, N Spain).

record, and in most fossil cases the tracemaker is not preserved, a detailed record of modern bioturbation and bioerosion structures is of great importance in order to find possible fossil analogues, and even to amend misinterpreted ichnotaxa.

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# PHYLOGENETIC ANALYSIS OF THE ORDOVICIAN DIPLOBATHRIDA (SUBCLASS CAMERATA, CLASS CRINOIDEA): IMPLICATIONS FOR EARLY CAMERATE EVOLUTION

Selina R. Cole and William I. Ausich

School of Earth Sciences, The Ohio State University, 125 South Oval Mall, Columbus, OH 43210, USA.
cole.678@osu.edu, ausich.1@osu.edu

**Keywords:** Phylogeny, systematics, crinoids, Echinodermata.

## INTRODUCTION

The subclass Camerata (Echinodermata) is a diverse group of evolutionarily and ecologically significant crinoids comprised of Orders Diplobathrida and Monobathrida. Recent analyses indicate Subclass Camerata was one of the earliest clades to diverge within the Crinoidea (Ausich *et al*., 2014). As a sister group to the rest of the Crinoidea, understanding the early morphologic evolution of Camerata is important for interpreting relationships at the base of the crinoid tree of life and the initial diversification of the class. Despite their prominent role in the early evolution and diversification of crinoids, phylogenetic relationships within the Camerata are poorly resolved, and the monophyly of many higher camerate taxa remains untested.

Camerates are united by the presence of rigidly ankylosed thecal and tegminal plates, fixed brachials and interbrachials incorporated into the calyx, subtegminal mouth, and typically additional plates in the posterior interray. The Diplobathrida are characterized by having two circlets of plates below the radial circlet, whereas the Monobathrida possess only one circlet of plates below the radial circlet (Ubaghs, 1978). Diplobathrids are the less abundant of the two orders, comprising roughly a quarter of the total diversity of camerates. However, during the Ordovician diplobathrids were a major component of the Early Paleozoic crinoid evolutionary fauna (Ausich and Deline, 2012) with nearly twice as many genera as the Monobathrida. This study performed a genus-level phylogenetic analysis of Ordovician camerates with an emphasis on the Diplobathrida to explore evolutionary relationships within the Camerata and to assess the monophyly of camerate taxa.

## CAMERATE PHYLOGENY

Recovery of evolutionary relationships at the base of the crinoid tree of life has been elusive for decades. Placement of the Camerata within the Crinoidea has varied between phylogenetic reconstructions based on differences in outgroup selection, ingroup taxa sampled, and homology schemes (Simms, 1993; Ausich, 1998a, 1998b; Guensburg, 2012). Early qualitative cladograms depicting inferred evolutionary trends of the Camerata broadly outlined the relative placement of suprageneric camerate taxa but made little attempt to infer the relationship between Camerata and the other crinoid subclasses (Moore, 1952; Ubaghs, 1978). A qualitative cladistic study by Simms (1993) inferred the Cladida to be the sister group to the rest of Crinoidea with Camerata and Disparida sharing a more recent common ancestor (Fig. 1A). A quantitative phylogenetic analysis by Ausich (1998a, 1998b) identified the Disparida as the first group to diverge from the Aethocrinea and the Camerata as a sister group to the Cladida (Fig. 1B). Guensburg (2012) performed a quantitative analysis that identified the Camerata as the first group to branch from the protocrinids, making Camerates the sister group to cladids and disparids (Fig. 1C). Most recently, a quantitative analysis by Ausich *et al*. (2014) placed the Camerata as the most basal clade within Crinoidea. Although the precise relationship of the Camerata with other crinoid subclasses has varied in these different analyses, most have shown consistent grouping of camerate taxa, supporting the monophyly of the subclass.

Evolutionary details within the Camerata remain largely unstudied, and our poor understanding of these relationships has been repeatedly acknowledged (Ubaghs, 1978; Simms, 1993). Early reconstructions of relationships within the Camerata were based purely on qualitative observations. Moore (1952) and Ubaghs (1978) produced inferred phylogenies of the Camerata that focused on family level relationships. Details of the divergence between Monobathrida and Diplobathrida were either left ambiguous (Fig. 2A) or shown as a simple, basal division between the orders (Fig. 2B). Simms (1993) produced a cladogram representing the inferred relationship between the Monobathrida and Diplobathrida as well as the relationships between major monobathrid suborders/superfamilies (Fig. 2C). The most comprehensive phylogeny of the Ordovician Camerata was performed by Ausich (1998b). This analysis considered 26 genera and provides the most detailed inference of evolutionary relationships to date among higher camerate taxa (Fig. 2D). This analysis, as well as that of Guensburg (2012), shows the Monobathrida originating from within the Diplobathrida, which may indicate the Diplobathrida are a paraclade. In addition, families lack coherence in these analyses indicating further studies to explore monophyly of subordinal taxa are in order.

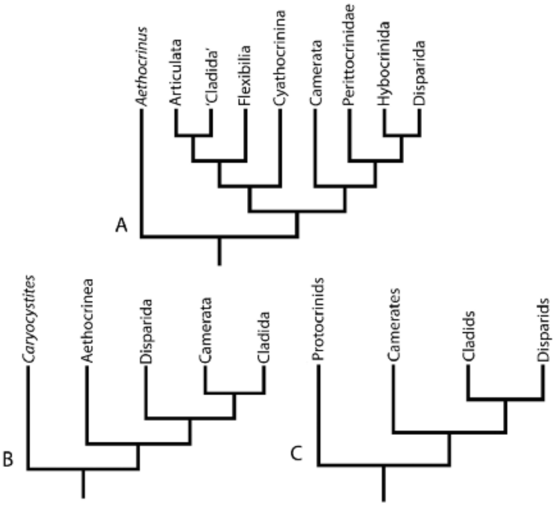

**Figure 1.** Simplified cladograms of evolutionary relationships within the Crinoidea highlighting the variable placement of the Camerata. A, modified from Simms (1993, fig. 4). B, modified from Ausich (1998a, fig. 7). C, modified from Guensburg (2012, fig. 2).

## PHYLOGENETIC ANALYSIS AND APPLICATIONS

To assess the evolutionary relationships within Camerata with an emphasis on the Diplobathrida, a quantitative genus-level phylogenetic analysis was performed. The analysis considered all currently named Ordovician camerate genera (31 diplobathrids and 18 monobathrids) and used over 100 discrete, multistate morphological characters inferred to be homologous (Foote, 1995; Ausich, 1996). A single representative species, typically the type species, was coded for each genus using museum specimens and primary taxonomic literature. Outgroups were selected based on recent analyses that have identified blastozoans (e.g., *Rhopalocystis*, *Echinosphaerites*) as the sister group to the Crinoidea (Sumrall, 2014).

This analysis is the first quantitative phylogenetic study that focuses on the Camerata during this significant period in their evolutionary history. The recovered phylogeny provides a framework for assessing the monophyly of camerate taxa and aids significantly in systematic revision of the group by helping to identify named higher taxa that are polyphyletic groups. For example, the veracity of diplobathrid suborders and superfamilies as representing true clades has been debated (Brower, 1973; Frest and Strimple, 1981), and grounds have been suggested for subdividing or synonomyzing many diplobathrid families (Brower and Veinus, 1974; Kolata, 1982; Ausich, 1986). In addition to informing systematic revision, the camerate phylogeny produced allows macroevolutionary patterns to be tested within the clade that have previously been impossible, such as the hypothesis that the number of circlets was plastic in some Camerate taxa (Sprinkle and Guensburg, 2013).

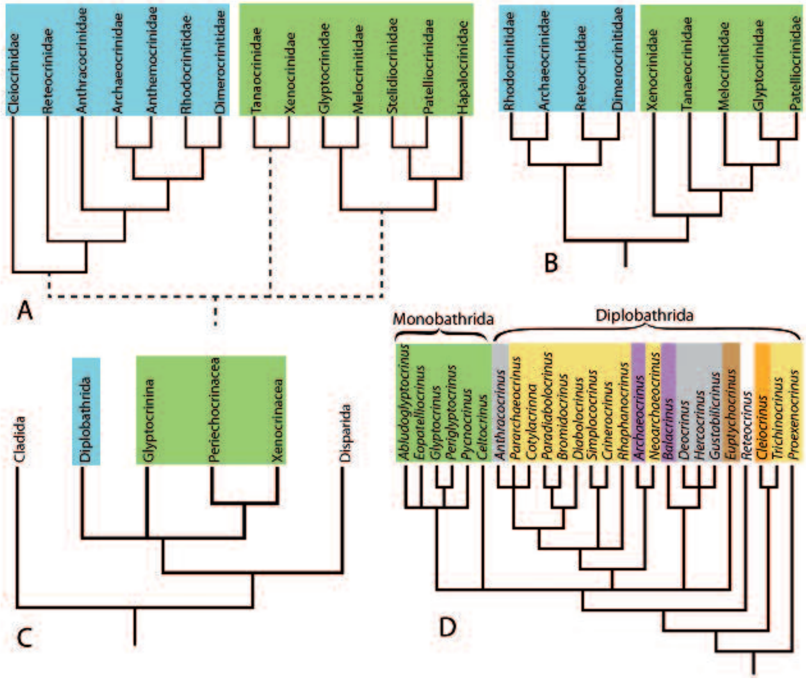

**Figure 2.** Simplified cladograms of relationships within the Ordovician Camerata (blue = Diplobathrida, green = Monobathrida). A, major camerate families, dotted lines represent ambiguous relationships, modified from Ubaghs (1978, fig. 208). B, major camerate families, modified from Moore (1952, figs. 8, 10-11). C, Diplobathrida and major monobathrid superfamilies, modified from Simms (1993, fig. 5). D, Arenig-Caradoc camerate genera, modified from Ausich (1998b, fig. 4.1) (green = monobathrids, grey = Anthracocrinidae, yellow = Rhodocrinitidae, purple = Archaeocrinidae, brown = Dimerocrinitidae, white = Reteocrinidae, orange = Cleiocrinidae).

## CONCLUSIONS

Understanding the phylogenetic relationships of crinoids is of particular importance during the Ordovician when most crinoid clades initially originated and diversified. Presently, the evolutionary relationships among camerates are poorly understood, and a phylogeny focusing on this clade will be a significant contribution to our understanding of the Crinoidea. In addition to informing potential systematic revision of Ordovician camerates, this phylogeny provides an evolutionary context for assessing the monophyly of Monobathrida, Diplobathrida, and their respective suprageneric taxa and will permit future studies of camerate diversity, disparity, morphology, and paleoecology within an evolutionary context.

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# QUANTIFYING MORPHOLOGICAL DIVERSITY IN EARLY PALEOZOIC ECHINODERMS

Bradley Deline

Department of Geosciences, University of West Georgia, 1601 Maple St, Carrollton, Georgia, USA. bdeline@westga.edu

**Keywords:** Disparity, Morphospace, Ordovician Radiation, Cambrian Explosion.

## INTRODUCTION

Morphological diversity (disparity) is a complex metric that can yield insight into evolutionary patterns and mechanisms. The examination of this metric is hindered by the inherent difficulty in accurately and thoroughly quantifying organismal morphology, particularly at higher taxonomic levels. The commonly hypothesized pattern of disparity through time is that of early morphologic diversification followed by stasis or contraction (Gould, 1989), which is consistent with early experimentation followed by ecological or genetic constraint. This is a common pattern at lower taxonomic levels (Hughes *et al.*, 2013), but has only been tested in a limited sense (comparing just Cambrian and Modern disparity) at the phylum-level (Briggs *et al.*, 1992, Wills, 1998).

Echinoderms have long been considered to follow this disparity pattern given their high class-level diversity during the Early Paleozoic (Valentine, 2004) as well as the morphologic patterns seen in analyses of echinoderm subphyla (Foote, 1992) and classes (Foote, 1994, 1995, 1999; Lefebvre *et al.*, 2006; Deline and Ausich, 2011). However, an analysis of echinoderm disparity through time has not been attempted and such a study would represent the first phylum-level disparity curve through the Early Paleozoic. The quantification of echinoderm disparity could also potential yield insights into the rates of convergent evolution, the ecological structuring of morphospace, the geographic distribution of anatomical features, and how disparity and morphospace occupation change during and after mass extinctions or through environmental fluctuations.

This current study lays the groundwork of quantifying echinoderm disparity by constructing a character set that encompasses the vast array of body plans and features found within Early Paleozoic echinoderms. We can then examine the effectiveness of this character set by determining if the resulting morphospace captures the morphological features that would be expected.

## METHODS

A novel character suite was constructed that encompassed the diversity of morphological features seen across echinoderms. Characters were added from a mixture of those modified from cladistic analyses, literature descriptions, and from discussions with experts in the different echinoderm classes. This character suite also incorporates the Universal Elemental Homology model to recognize similar morphology in very different organisms (Sumrall and Waters, 2012, Kammer *et al.*, 2013). Care was taken to avoid a pure phylogenetic signal, for instance the names of individual plates were often avoided in order to code based on body structure rather than jargon. This methodology also aims to code convergent features in a similar manner, which is a valuable feature in studying the functional evolutionary trends. The character suite also has additive properties (characters contingent on previous characters) and follows the character scheme of Deline and Ausich (2011) in which non-preserved and non-applicable data are treated differently.

The character suite contains a total of 419 binary and multistate characters covering morphology of the oral surface, aboral surface, appendages, respiratory structures, and attachment structures.

A total of 92 Early Paleozoic echinoderms from 25 classes were coded. The only class that was excluded was Holothuroidea, which lacks an adequate fossil record. The dataset was analyzed using gower's similarity metric and principal coordinate analysis. Disparity was calculated as the average squared distance between taxa in morphospace and all analyses were conducted using R 3.1.2 (R Core Team 2014).

## RESULTS

The resulting morphospace is shown in figure 1. The first two axes account for 31% of the variation in the dataset while the first five axes only account for 46% indicating a large amount of noise as would be expected with the variation present within the phylum. Analyzing the dataset using nonmetric multidimensional scaling, which allows the a priori choice in the number of axes produced, results in similar morphospace as that shown in figure 1 with a two axes solution.

The first axis largely differentiates the pelmatozoan body plan (pelma, theca, and feeding appendages) from that of the eleutherozoans (body plans dominated by the oral surface). The second axis differentiates these two largely pentaradial groups from the homalozoans, which have asymmetrical or bilateral body symmetry. Within the pelmatozoan group there is separation between the crinoids and blastozoans with eocrinoids occupying the largest area of any class within morphospace. The eleutherozoan group separates the attached forms (edrioasteroids, helicoplacoids, and cyclocystoids) from the mobile forms (echinoids and asterozoans). The homalozoans are split between two morphological subgroups, the first containing Ctenocystoidea, *Ctenoimbricata*, and Homostelea while the second is composed of Stylophora and Homoiostelea.

## DISCUSSION

The utility of morphologic data to address evolutionary and ecological questions hinges on whether it is able to accurately capture the features and body plans of organisms. The choice of characters and how those characters are applied to different organisms can greatly alter the resulting morphospace and subsequent analyses. Therefore, it is important to determine if a new attempt at quantifying morphology captures the features of a clade that have been previously documented or are obvious before using the dataset to assess broader questions. At the taxonomic level of this study, a surprising distribution of taxa within morphospace likely indicates a poor representation of the morphology. For instance, if animals with very different body plans plot together (e.g. asteroids and ctenocystoids) it would indicate issues with the coding structure.

The features that would be expected in a morphospace of Echinodermata would be some degree of phylogenetic structure. There are multiple methods to quantify morphology. Shape-based methods that quantify outline or the distribution of landmarks (e.g. Lefebvre *et al.*, 2006) are the most distinctive from phylogenetic signals, but are impractical at higher taxonomic levels. Character-based methods can show similar patterns to shape-based studies (Villier and Eble, 2004), but likely show a stronger relationship to character-based phylogenetic studies depending on the homology scheme used in the cladistics analysis. Other features that would be expected include morphologically intermediate forms between body plans, variable levels of plasticity between different classes, convergence between classes, and likely an increase in disparity from the Cambrian to the Ordovician.

The higher-level morphologic structure of echinoderms is recognized with delineation between the three major body plans. A clear distinction between groups is lost at a lower taxonomic level (e.g. class), which is consistent with the plasticity within echinoderms. Several Early-Middle Cambrian forms (e.g. *Helicocystis* and *Lepidocystis)* fall between the pelmatozoan and eleutherozoans and may represent transitional body plans. In addition, there is a large unoccupied gap between the pentaradial and non-pentaradial forms, which is consistent with an early divergence between these two groups as was proposed by Zamora *et al.*, 2012, but see David et al. (2000) for an alternative phylogenetic hypothesis.

There are several instances of convergence shown in the morphospace, these can be recognized when a later member of a class deviates from the centroid of its own class and converges on the body form of another. Edrioasteroids show multiple instances of convergence with pelmatozoans by either the development of stalks (e.g.

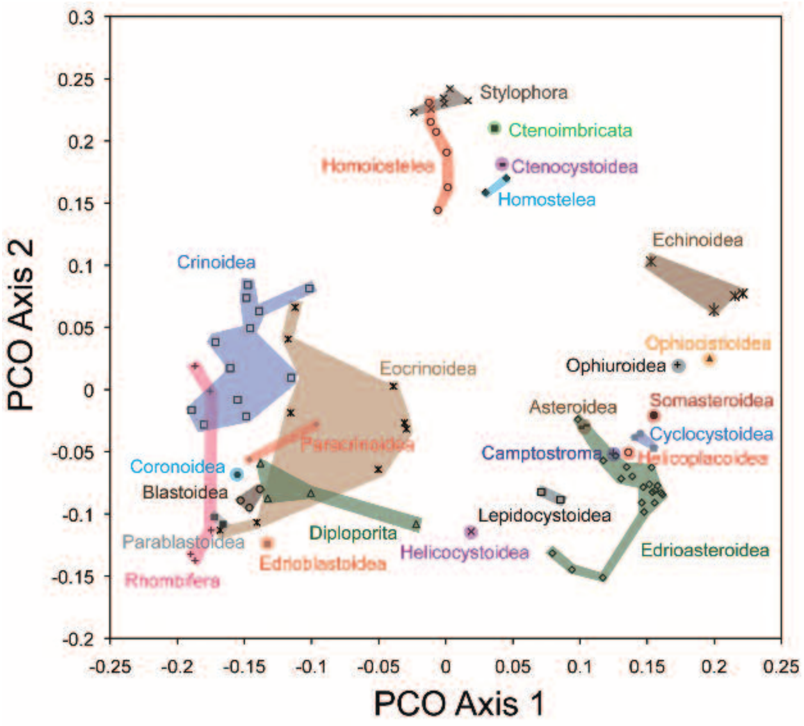

**Figure 1.** Morphospace including 92 Early Paleozoic echinoderms representing 25 classes.

*Archaepyrgus*) or prominent interradial plates (e.g. *Edrioaster).* Rhombiferians also show multiple instances of convergence by either developing crinoid characteristics such as complex feeding appendages and a tegmen (e.g. *Caryocrinites*) or homalozoan characteristics such as bilaterial symmetry and a flattened body plan (e.g. *Pleurocystities*). These examples often appear midway between the two classes within morphospace because they still retain most of the characters of their own class along with the addition of the convergent features. As more taxa are added to the analysis the degree of convergent evolution through time can be assessed.

Finally, previous disparity studies on echinoderms have indicated that several clades showed an increase in disparity from the Cambrian to Ordovician (Foote, 1992; Lefebvre *et al.*, 2006) or achieved their highest disparity soon after they originated in the Ordovician (Foote, 1999, Deline and Ausich, 2011). The results are tentative since the current study does not include a comprehensive sampling from both the Cambrian and Ordovician. However, based on the taxa currently included the Ordovician echinoderms (0.09, SE 0.005) show a 57% increase in disparity from those in the Cambrian (0.057, SE 0.006).

## CONCLUSIONS

The current study represents the foundation for future work examining the broad patterns of echinoderm morphology. The morphospace captures many aspects of echinoderm morphology and, therefore, is likely a good estimate of the distribution of animals within shape space and their relative degrees of morphological diversity. The quantification of morphology can yield insights into evolutionary dynamics, diversifications, extinctions, and ecology. With a more detailed sampling of Paleozoic echinoderms the current character suite will enable the testing of broad hypotheses regarding the history of echinoderms.

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# THE HEXAMER HYPOTHESIS EXPLAINS APPARENT IRREGULARITIES IN THE PLATING OF EARLY AND EXTANT CRINOIDS

Marc H.E. de Lussanet

Institut für Sportwissenschaft, Westfälische Wilhelms-Universität Münster, Horstmarer Landweg 62b, 48149 Münster, Germany.
lussanet@uni-muenster.de

**Keywords:** Early crinoids, fossil, embryology, Bauplan, evolution, Extraxial axial theory (EAT).

## INTRODUCTION

In 2011 I proposed a new hypothesis for the evolution and development of the five-rayed structure of echinoderms, the *Hexamer Hypothesis* (Lussanet, 2011). According to this hypothesis, the five-rayed structure develops by reduction from a six-rayed Bauplan. This six-rayed origin is reflected developmentally in the six coelomic spaces, which are, in the early larva, arranged symmetrically around the mouth and the larval mid-sagittal plane.

According to the new hypothesis the mouth and five Anlagen for rays migrate to the left side of the larval body, in a process well known as coelomic stacking. The sixth Anlage along with its coelom, the right hydrocoel either degenerates (for example, the dorsal sac in echinoids), or specializes into attachment structures. Meanwhile, the mouth and the surrounding ray-Anlagen turn in an anti-clockwise direction. Thus the missing ray, recognizable by the closure point of the hydrocoel crescent, becomes located towards the anus or periproct.

In the original presentation of the new hypothesis I tried to collect evidence from the extant echinoderm clades, and the main focus was on the developmental deformations and on morphological features, such as the Lovén's rule and symmetry planes. I showed that the missing ray originates from the CD interray (according to Mortensen's encoding of the rays), on the side of the C-ray. Accordingly, the bivium-trivium arrangement of rays, typical for early crinoids and other paleozoic clades, is derived from a bivium-quartium arrangement, with the D-E bivium being derived from the rostral larval side.

Echinoderms are a rich phylum with a rich fossil record reaching back into the Cambrian. Of this richness, only five classes survive to date, four of which belonging to the same subphylum, the Eleutherozoa, and the fifth, the crinoids, as extant representatives of the once much more diverse subphylum of Crinozoa. Crinoids are unique as the only extant clade with stalked representatives, reaching back at least to the early Ordovician. Their extraordinary rich fossil record and the known embryology of recent forms make them ideal to test the *Hexamer Hypothesis*. This was proposed to me by Michel Roux, and the discussions with him and Marc Eléaume led to the considerations presented in the following.

## EXISTING THEORIES

The extraxial-axial theory (EAT) refers primarily to the skeletal structures of the body wall and their patterns of development (David *et al.*, 1996). According to David and Mooi, the skeletal plating of all echinoderms can be distinguished in three classes by the developmental pattern. The axial skeleton is arranged around the mouth and can be very prominent (Echinoidea) or almost absent (Holothuria). The perforate extraxial skeleton forms the rest of the body whereas the imperforate extraxial skeleton is typically related to stalk structures. In crinoids (in contrast, e.g., to blastoids), the arms are formed of both, axial and extraxial elements. The EAT was originally developed for echinoids, and subsequently extended to eleutherozoans and other echinoderms. Although widely accepted for eleutherozoans, its validity for other clades of echinoderms is still disputed. As far as I am aware, the *Hexamer Hypothesis* is compatible with the EAT, although the nature of the imperforate extraxial is unsure.

The Universal Elemental Homology (UEH) model was developed for the plating of the oral region of blastozoan echinoderms (Sumrall, 2012), and has recently been applied to crinoids (Kammer *et al*., 2013). The plating of the mouth region is not focus of the present study.

## THE STALK

According to the *Hexamer Hypothesis*, the sixth ray was lost from the oral region to form attachment structures. Depending on the time of coelomic stacking, aboral plating regions may not be involved in the loss of the sixth ray and thus retain hexamery. Consequently, it is predicted that the plating of attachment structures, such as the crinoid stalk, resembles the axial growth pattern (so that the term „imperforate axial" might be more appropriate than imperforate extraxial).

A typical property of axial growth, as opposed to extraxial growth, is that new elements are added only behind a terminal end plate. Indeed, the stalk of crinoids does grow in such manner (Améziane and Roux, 2005; Breimer, 1978; Ubaghs, 1978). Interestingly, new plates are added on the proximal side of the stalk, so that the sixth ray in effect growth towards the body, pushing it up. This might be a crucial factor in the survival of crinoids, enabling the stalk to regenerate after loss. Also, the direction of growth appears consistent with an axial pattern, because the growth is directed towards the extraxial border as in the axial plating.

## THE CALYX

If the stalk is axial, we predict that the calyx is not reduced and therefore has six rays. The calix of crinoids is composed of circlets of plates (Ubaghs, 1978). For the present study, the plating of the calyx was reinterpreted on the assumption that each circlet is composed of exactly six plates at least during some stage in development, and that each plate can be associated with one of six columns each of which is associated with a ray.

The taxonomy of these circlets has caused ample controversy. For example, the circlets of the very early *Aethocrinus moorei* from the Cambrian/Ordovician transition have been revised at least four times (Ubaghs, 1969; Simms, 1993; Ausich, 1996; Ausich, 1998; Guensburg and Sprinkle, 2003). Indeed, the plating pattern appears quite irregular (Fig. 1). Indeed, *Aethocrinus* proved to possess one of the most complex plating schemas. The following five simple rules could be applied to a large number of early and recent crinoids.

First, it is hypothesized that each of the plates of a circlet also belongs to a columnar series. It is hypothesized that these columns tend to spiral in a leftward direction (when following the spirals in an upwards direction), as in the Cambrian helicoplacoids (Sprinkle and Wilbur, 2005), and as in the gut system of extant echinoderms (Breimer, 1978). Thus, starting from the lowest circlet, it is assumed that each column progresses into the left neighbor of the next circlet.

Second, that the sixth column is associated to the CD interray, according to the *Hexamer Hypothesis*.

Third, that the sixth ray, P, typically looses connection to the stalk and is therefore the source of perturbation in the plating pattern of the calyx. The rationale is that the sixth ray is involved in the formation of the stalk structures so that connection to the sixth column in the calyx may loose connection to the base of the stalk.

Finally, that each circlet is composed of exactly six plates. This may be impossible to prove in many-plated cups such as *Titanocrinus* (Guensburg and Sprinkle, 2003). Extant crinoids posses two circlets of calyx plates. The five radials are supplemented by a radianal plate (which is sometimes reduced in the adult). The circlet of basals seems to be formed of just five plates, but a sixth plate may be formed in early embryo.

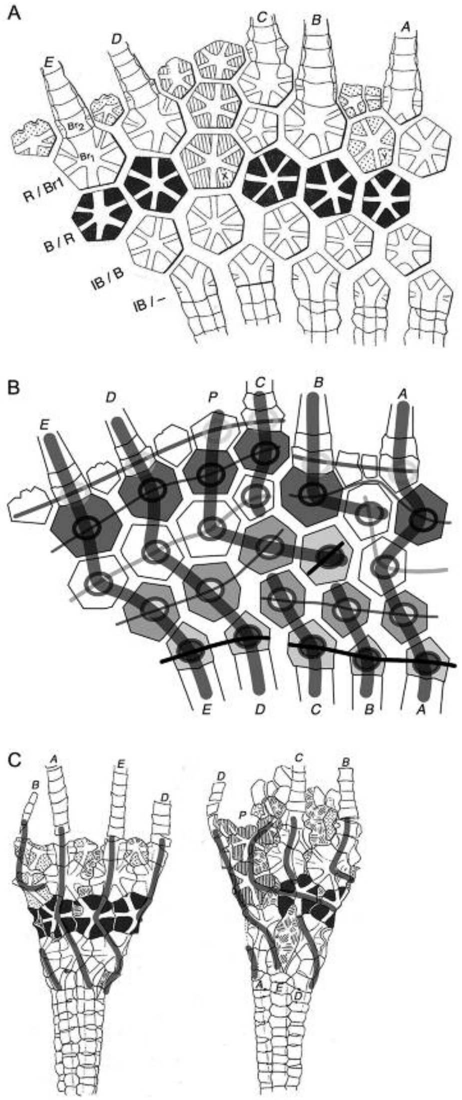

**Figure 1.** Application of the hexamer circlet rules to *Aethocrinus moorei*. A. Ubaghs' original interpretation (Ubaghs, 1969). Note the irregular „X" and „Y" plates. B. Hexamer circlet interpretation of the same schema and two views of the holotype (C). Columns are indicated by thick curves (P is the C-D interray). Circlets are connected by thin grey curves. The plates of each circlet are given the same grey tone. The brachials of the top circlet alternate with thecal plates. Note, that the P column has lost connection to the lowest circlet, and interrupts the C and B columns. Also, the C ray is moved up due to this interference.

## DISCUSSION

Crinoids are not the earliest stalked echinoderms. Crinoids have the advantage to have direct, extant ancestors. Moreover, already early crinoids are very well documented and have a rich fossil record. Potentially this study can be a starting point for investigating further and earlier clades of the earliest echinoderms.

The *Hexamer Hypothesis* gives an explanation for the origin of the stalk, and why it is consistently clearly set apart from the calyx. I argue that the stalk resembles an axial structure in its development, not only by having a single growth zone of plate addition, but also because this growth zone faces the extraxial plating of the calyx. There remains potential for speculation of the origin of holdfast structures which are manifold and which differ markedly from the stalk itself.

## CONCLUSIONS

The calyx plating of crinoids shows a clear and regular hexamery as predicted by the *Hexamer Hypothesis*. The axial region is clearly pentamer in structure, with one ray (P) missing in the CD interray. The axial elements of the P-ray seem to be not missing in crinoids but instead involved with the formation of the stalk.

## Acknowledgements

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# TWO NEW BRITISH MESOZOIC OPHIUROID LOCALITIES, PRELIMINARY OBSERVATIONS AND DETERMINATIONS

Timothy A. M. Ewin[1] and Ben Thuy[2]

[1] Department for Earth Sciences, The Natural History Museum, Cromwell Road, South Kensington, London, UK SW7 5BD, UK.
T.ewin@nhm.ac.uk
[2] Natural History Museum Luxembourg, Department of Palaeontology, 24 rue Münster, L-2160 Luxembourg-city, Luxembourg.
nebyuht@yahoo.com

**Keywords:** Ophiuroid, British, Oxford Clay, Callovian, Atherfield Clay, Aptian, Mesozoic.

## INTRODUCTION

Ophiuroids, like other echinoderms, have a skeleton composed of numerous ossicles held together by soft tissue that quickly breaks down after death and usually results in disarticulation of the ossicles. Thus, articulated fossil ophiuroids are rare and only preserved in exceptional circumstances, such as rapid burial. Therefore any new localities displaying articulated individuals are of importance. Two such new finds are reported here from the Callovian of Gloucestershire and the Aptian of the Isle of Wight. Ophiuroids from these ages are comparatively poorly known globally and so we here report some preliminary observations.

In the Oxford clay of the UK Ophiuroids are only previously known from Dorset, Wiltshire and Bedfordshire (Martill and Hudson, 1991). The Dorset material, from Weymouth is taxonomically relatively well known, being represented by numerous articulated specimens originally described as *Ophioderma weymouthiense* Damon, then revised in detail by Hess (1964) who transferred the species to *Ophiomusium*, and recently selected by Thuy (in press) as type species of the new genus *Enakomusium*. Forbes (1844) described two occurrences of ophiuroids from Wiltshire and assigned them to *Amphiura pratti*. These were tentatively transferred to *Ophiochiton*? by Hess (1964). Finally there is also an undescribed ophiuroid species from Stewartby in Bedfordshire, from the Medea Subzone of the Jason Zone (Duff, 1975; Martill and Hudson, 1991) but no further information is currently available nor are the published images of sufficient quality and orientation to permit assignation. Thus, British Oxford Clay ophiuroids are fairly poorly known and in need of review.

Ophiuroids from the Atherfield Clay of the UK are only reported from the Chale Clay Member, the Lower Lobster Bed Member and the Crackers Member of the Isle of Wight as "*Ophiura* sp. nov." in a faunal list by Simpson (1985) without further description or occurrence in the literature, nor reference to known public collections. Thus, British Aptian ophiuroids are poorly known. The Aptian was recently identified as one of the blank areas of the Mesozoic ophiuroid fossil record with, until recently, very few known species (Taylor, 1966; Smith and Crame, 2012; Thuy *et al.,* 2014). Thus, our new material contributes to a better knowledge of Lower Cretaceous ophiuroid diversity.

The discovery of these new localities is timely, as a great improvement of our understanding of Ophiuroid phylogeny is currently being made through the combined approach of molecular and taxonomical datasets (O'Hara, *et al.* 2014). New fossil data is crucial to this work to enable a better understanding of relationships in deep time and the emergence and distribution of lineages through time. We here briefly present two new occurrences of fossil ophiuroids that will be described exhaustively in future contributions.

## MATERIAL, METHODS AND LOCALITIES

The specimens were imaged with a Cannon 600D digital SLR mounted on a Nikon SMZ1000 light microscope. Scanning Electron Microscope (SEM) images were made using a Leo LV1455VP low pressure environmental SEM with uncoated specimens at 20KV and 20Pa. Terminology follows that of Stöhr *et al.* (2012) and higher-level classification follows O'Hara, *et al.* (2014).

Locality 1; Coln Quarry, Lechlade, Gloucestershire, UK 51.6951N, 1.7372W (Fig. 1). The specimens studied were collected from ex-situ material that had been extracted from a drainage trench in the base of the quarry. The fossils were from a fissile grey shaly clay from the Jason Zone, Peterborough Member, Lower Oxford Clay, Callovian, Upper Middle Jurassic. All material studied here was collected and donated by Ms Janet Whyman. Material includes 28 articulated specimens, numerous partially articulated arms and discs and numerous disarticulated arm ossicles. Specimens were extracted either by splitting the rock or bulk sieving in water using a 150um mesh. Specimens were further cleaned of adherent mud using an ultrasonic bath. All material is housed in the Natural History Museum London (NHMUK EE 15466).

Material is very well preserved with original stereom clearly visible. Most specimens display small localised growths of pyrite, particularly around the oral areas of the disks. Articulated specimens still adhered to the rock also show pyrite growths around the specimen creating a halo effect of darker matrix (Fig. 2A). Specimens are variously orientated with both ventral and dorsal surfaces visible, however most were orientated in life position.

Apart from unpublished observations and logs compiled by Dr N. Hollingworth (Science and Technology Facilities Council, Swindon, UK), the Oxford Clay at Coln Quarry is poorly known. Much is inferred by comparison with the better known type locality for the Peterborough Member, near Peterborough, Bedfordshire, which were heavily studied in the early 1990's (e.g. Hudson and Martill, 1994; Martill *et al.,* 1994 and MacQuaker, 1994). The Peterborough Member at Coln is comprised of a richly fossiliferous series of shales and calcareous mudstones, dominated by the ammonite *Kosmoceras* and by bivalves and gastropods (Hollingworth pers. comm. 15/03/2015) although contextual material collected along with the ophiuroids includes sharks teeth, crinoids, arthropods, brachiopods and belemnites. The environment of the Oxford Clay surrounding Coln Quarry has been interpreted as a warm shallow shelf sea with normal salinity with land probably lying close by, to the northeast, where marginal marine facies are seen in the East Midlands (Cox 2002). The bottom waters of the sea are suspected to have been euroxic with the high carbon content attributed to high productivity (MacQuaker, 1994 and Martill *et al.,* 1994).

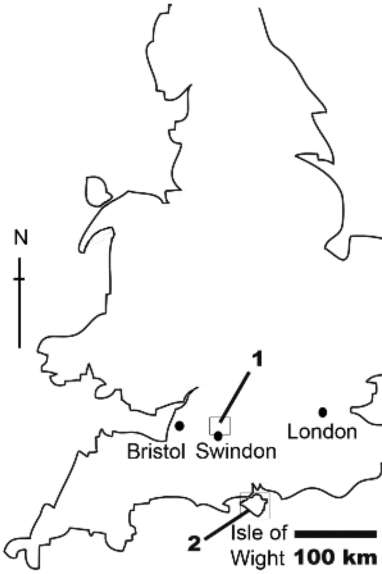

**Figure 1.** Map of England showing location of new Ophiuroid localities: 1. Coln Quarry. 2 Atherfield.

Locality 2; Atherfield, Isle of Wight, Hampshire, UK (Fig. 1). Material collected from ex-situ blocks on the beach consisting of hard, beige coloured, calcareous concretions ("doggers") composed of clayey sand of the Crackers Member, from the upper Atherfield Clay Formation, Lower Greensand Group, lower *Deshayesites callidiscus* Subzone, Lower Aptian, Lower Cretaceous. Material was collected and prepared using an air-abrasive by Mr John Quayle. A block containing two complete articulated specimens and numerous articulated arm fragments is housed at the Dinosaur Isle Museum (IWCMS: 1994.78). Another specimen associated with articulated arm fragments is lodged at the Natural History Museum London (NHMUK). Specimens are well preserved although many secondary ossicles have been lost and the fine detail of the plates blurred during preparation. Individuals are variously orientated with both ventral and dorsal surfaces visible.

The Crackers Member of the Isle of Wight is famous for its rich fossil content, particularly ammonites, gastropods, bivalves, sharks teeth and arthropods (Simpson, 1985; Casey *et al.,* 1998). Complete faunal lists for the Atherfield Clay Formation, including the Crackers Member, can be found in Simpson (1985). The Crackers Member consists of 8 m of clayey, coarsening-upwards sandstones which contain several layers of calcareous nodules. These nodules weather out and are the source of most of the well-preserved fossils (Simpson, 1985), including those studied here. The Crackers was deposited in a warm, shallow, stenohaline, well oxygenated sea which was affected by storms and represents a regressive sand with some fresh water influences (Ruffel and Wach, 1991, Insole *et al.,* 1998). Land was probably not far to the north and fossil wood is frequently found within the nodules (Simpson, 1985).

## DESCRIPTION OF THE NEW FINDS

The ophiuroids from the Oxford Clay (locality 1) are relatively small (disc diameter of 2.8 – 4.4 mm) and display a rather unusual combination of characters. The disc is covered by relatively thick scales and large radial shields, both devoid of granules or spines (Fig. 2B). The oral shields are conspicuously elongated and arrow-shaped (Fig. 2E). There are up to six lateral oral papillae varying in shape from pentagonal distally to leaf-shaped proximally, and up to two small conical apical papillae. The arms appear noded proximally as a result of the slightly constricted proximal lateral arm plates (Fig. 2E). There are large between-plate tentacle pores in the proximalmost five to seven segments (including those incorporated into the disc), followed by within-plate tentacles pores which rapidly decrease in size distally. The lateral arm plates have a coarsely meshed outer surface stereom with a furrow lining the proximal edge (Fig. 2C). The distal edge of the lateral arm plates bears up to five large spine articulations consisting of a large muscle opening proximally, tightly encompassed by thin ridge and distally separated from a small nerve opening by a large, strongly protruding ridge. Both ridges form a circle around the muscle opening. The arm spines are large, pointed, conical and longitudinally striated (Fig. 2L). The dorsalmost arm spines of the proximal segments are the longest and exceed one arm segment in length.

This combination of characters is most reminiscent of Jurassic *Ophiomusium*-like ophiuroids for which the new genus *Enakomusium* was recently introduced (Thuy, in press). The finds reported herein show striking similarities with the type species of the genus, *Enakomusium weymouthiense* from the British Oxford Clay, in particular with respect to the shape of the oral shields and the development of the tentacle pores. Differences mainly pertain to the shape of the distal-most lateral oral papillae and the length of the arm spines in proximal segments. Closest similarities in terms of lateral arm plate morphology are shared with *Enakomusium mammilatum* (Hess) from the Oxfordian of Switzerland and France, especially with respect to the large, protruding spine articulations. The specimens described herein, however, have fewer spine articulations and more finely meshed outer surface stereom. Preliminary observations suggest that the new finds belong to a new species to be described in a forthcoming contribution.

The specimens recovered from the Crackers Member (locality 2) shows relatively thick disc plates and scales with large, rounded triangular radial shields (Fig. 2M), leaf-shaped lateral oral papillae, second oral tentacle pores opening within the mouth slit (Fig. 2N), thick lateral arm plates with deep tentacle notches but devoid of a constriction, small spine articulations at the distal edge of the lateral arm plates composed of parallel, horizontal dorsal and ventral lobes (Fig. 2P), large, fan-shaped dorsal arm plates, no accessory dorsal arm plates (Fig. 2O) and wide ventral arm plates with deep lateral tentacle notches. The single, conical apical oral papilla, the leaf-shaped rather than opercular distalmost lateral oral papillae, the relatively high number of arm spines (four to five), and the absence of a triplet of disc plates distally bordering the radial shields favour assignment to *Eozonella* (Thuy *et al.,* 2013). If this preliminary assignment holds true, then these specimens represent the youngest record of the genus. On species level, similarities are greatest with the dissociated lateral arm plates from the Aptian of Spain recently described as *Ophiozonella eloy* Thuy *et al.*, 2014, in particular on account of the two spurs on the outer proximal edge and the small spine articulations. In the British specimens, however, lateral arm plates are larger and have an apparently more finely meshed outer surface stereo and spine articulations sunken into shallow depressions of the distal edge. They thus probably belong to a new species to be described in a more exhaustive study.

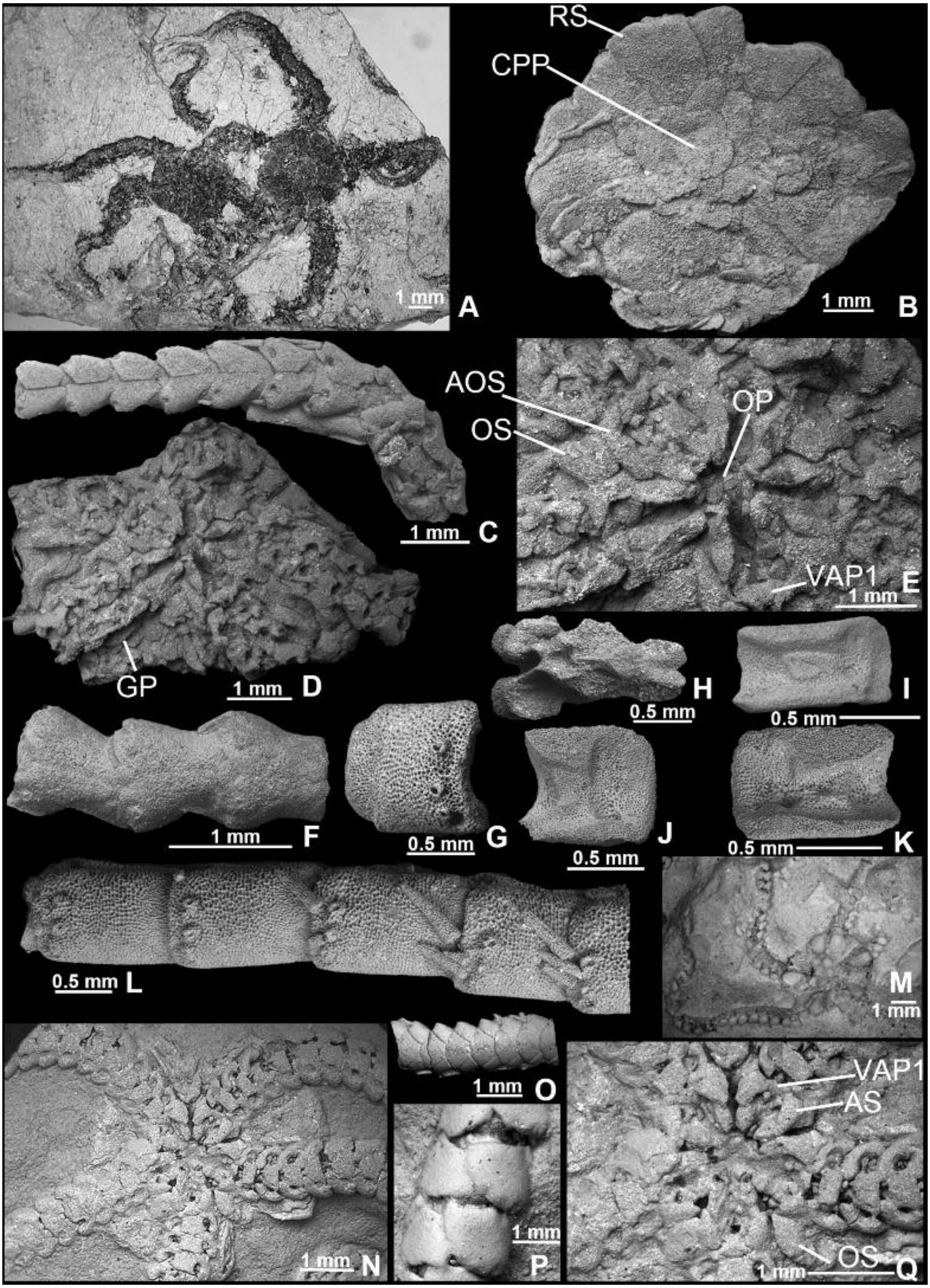
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**Figure 2.**

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**Figure 2.** A-M. *Enakomusium* n. sp., Coln Quarry, Lechlade, Gloucestershire, UK. A. Dorsal surface of two articulated specimens showing dark pyrite halo. B. Disk, dorsal surface, showing central primary plate (CPP) and radial shields (RS). C. Ventral surface of median arm fragment. D-E. Disk ventral surface showing genital plate (GP), oral shield (OS), Adoral shield (AOS), oral papillae (OP) and first ventral arm plate (VAP 1). F. Dorsal view of medial arm fragment. G. Lateral arm plate external surface. H. Arm vertebra. I-K. Lateral arm plate internal surface. L. Lateral arm plates in articulated median arm fragment (proximal segments to right). M-Q. *Eozonella* n. sp. Atherfield, Isle of Wight, Hampshire, UK. M. Disk dorsal suface. N. Disk, ventral surface. O. Dorsal surface of medial arm. P. Lateral arm plates. Q. Disk ventral surface detail.

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# HOMOLOGICAL AND PHYLOGENETIC IMPLICATIONS OF A DISPARID-LIKE POSTERIOR INTERRAY AMONG LOWER ORDOVICIAN CAMERATE CRINOIDS

Forest J. Gahn

Brigham Young University, Idaho, Department of Geology, ROM 150, Rexburg, Idaho, 83460-0510, USA. gahnf@byui.edu

**Keywords:** Paleozoic, Crinoidea, phylogeny, homology, evolutionary morphology.

## INTRODUCTION

The number and arrangement of plates in the posterior (or CD) interray of Paleozoic crinoids is of fundamental importance for the classification of the group (Moore and Laudon, 1943b; Ubaghs, 1978). Historically recognized clades such as camerates, cladids, and disparids have long been distinguished by the presence of distinctive posterior plating, and uncertainty in the homological relationships among these plates has hindered resolution of high-level crinoid phylogeny. Some researchers (e.g., Philip, 1964; Ubaghs, 1978; Guensburg and Sprinkle, 2003) have even speculated that CD plating might be nonhomologous within the Crinoidea, implying that camerates, cladids, and disparids could have independently acquired unique posterior plating from a shared common ancestor.

The literature is rife with debate on the inferred homology and evolutionary morphology of posterior plating in Paleozoic crinoids (Wachsmuth and Springer, 1897; Bather, 1900; Jaekel 1918; Moore and Laudon, 1943b; Philip, 1964; Ubaghs, 1978; Simms, 1993; Rhoznov, 2002; Webster and Maples, 2006). An incomplete early fossil record, in addition to crinoids' abilities to substantially modify their skeletons via plate resorption, fusion, and addition, frustrate attempts to weigh competing hypotheses of plate homology. Continuing efforts to sample the earliest fossil record of crinoids have resulted in the discovery of numerous new species and higher taxa (Guensburg and Sprinkle, 2003, 2009; Gahn *et al*. 2006; Sprinkle *et al*., 2008; Guensburg, 2010), many of which are still too obscured by matrix for proper study. Some of these new Lower Ordovician crinoids offer important new insights into the phylogeny, evolutionary morphology, and plate homology of Paleozoic crinoids. This is especially true of two undescribed camerate crinoids that possess a posterior morphology that is strikingly similar to that of some disparids (Fig. 1A; Fig. 2B-D).

## STANDARD POSTERIOR PLATING IN ORDOVICIAN CRINOIDS

Uncertain homology among the posterior plates of camerates, cladids, and disparids is reflected in differences in the standard terminology applied to each group (*sensu* Ubaghs, 1978). A single plate, the primanal, supports the CD interray of most Ordovician camerates (Fig. 1B). This plate may lie directly atop the suture shared by the C and D radials (as in *Glyptocrinus*) or between these plates, immediately above the CD basal (as in *Compsocrinus*). The primanal often supports a column of plates, the anitaxis, which forms the midline of a bilaterally symmetrical posterior interradius. In many Ordovician camerates (such as *Reteocrinus* and *Xenocrinus*), the anitaxis is morphological similar to adjacent brachial plates, including possession of a ridge that runs along the anitaxis like a brachial ray ridge.

Most early cladids (such as *Cupulocrinus* and *Dendrocrinus*) possess two plates in the C ray that consist of an underlying radianal and overlying radial (Fig. 1C). The oldest known crinoids with a cladid-like posterior morphology, *Apektocrinus* and *Aethocrinus*, possess a third plate, sometimes called the inferradianal, immediately below the (super)radianal; however, calyx plating in *Aethocrinus* has been subject to various conflicting interpretations (Ubaghs, 1969; Philip and Strimple, 1971; Ausich, 1996; Rozhnov, 2002; Webster and Maples, 2006; Guensburg and Sprinkle, 2010). The curiously named anal X typically rests on the upper right shoulder of the radianal between the C and D radials, directly above the CD basal. Anal X most directly supports the anal sac or the periproct in the majority of Ordovician cladids.

A two-plate sequence also characterizes C ray of many Ordovician disparids (such as *Ectenocrinus* and *Iocrinus*; Fig 1D). The lowermost of these plates is traditionally termed the inferradial, and the upper plate, the superradial. However, the uppermost of these plates has also been referred to as the anibrachial or aniradial (Ubaghs, 1978). The right shoulder of the superradial supports brachials of the C ray, and the left shoulder of the superradial supports the anal plates. In his discussion of *Alphacrinus*, the oldest described disparid, Guensburg (2010, p. 1209) suggested that the most diagnostic characteristic of the clade is a "ray-like anal series" that branches from the C ray. As discussed below, a similar structure is also present in some Ordovician camerates.

## POSTERIOR PLATING IN LOWER ORDOVICIAN CAMERATES

Some of the oldest known camerates, including *Eknomocrinus* from the Fillmore Formation of west-central Utah, possess typical posterior plating with a primanal that disrupts the radial circlet (Guensburg and Sprinkle, 2003; Fig 1B). However, two new camerates from the Lower Ordovician Garden City Formation of northeastern Utah deviate substantially from the standard plate arrangement (Fig. 1A; Fig.2B-D). These crinoids lack a plate in the CD interray that supports the anal series. Instead, an anitaxis branches from the left shoulder of the uppermost of two "radial" plates in the C ray (here collectively and tentatively called "biradials" following Ubaghs, 1978). The primibrachials of the C ray originate from the right shoulder of the same plate, the "superradial". This configuration is remarkably similar to that observed in early Ordovician and later disparids (Fig. 1D; Fig. 2A).

The posterior interadii of these early Ordovician camerates (Fig. 2B-D) and coeval disparids (Fig. 2A) are similar in the number and arrangement of plates in the C ray, and they also share anal plating with a similar orientation. Unlike most early camerates that bear a nearly vertical anal series, the anal plates of these crinoids angle from the lower right side of the C ray to the upper left side of the CD interray. A bilaterally symmetrical posterior is roughly present, but it slants strongly toward the D ray, generating an overall asymmetry in the calyx. Moreover, the stacked series of anal plates (anitaxis) is strongly differentiated from the other plates of the posterior interradius; they have the appearance of elongated brachials with a prominent ridge rather than the more equant, stellate plates that characterize adjacent calyx plates. In the new Garden City camerates, the anus opens directly through the tegmen at the distal end of the anitaxis as in reteocrinids and xenocrinids (see Kolata, 1975, pl. 8, figs. 1, 4).

## EVOLUTIONARY MORPHOLOGY OF THE CAMERATE POSTERIOR INTERRAY

The new Garden City crinoids presented here (Fig. 2B-D) possess many features that suggest they are basal camerates, including: 1) a polymeric stem; 2) five basals; 3) median ray and anitaxial ridges; 4) fixed brachials (at least five in the specimen figured in Fig2. C); 5) uniserial arms that lack pinnules; 6) numerous, irregularly arranged interradials; 7) a high, domed tegmen with plating that appears similar to that of the interrays; and especially, 8) a subtegmenal mouth. Although all early crinoids share many of these traits, the nature of the tegmen is apomorphic for camerates; thus, despite the morphology of the posterior interray, these new crinoids are not disparids. However, because these monocyclic camerates lack a plate that is unquestionably recognized as the primanal, they cannot be assigned to either of the major monobathrid suborders, Compsocrinina or Glyptocrinina, which are organized according to the position of that plate (see above). Assuming that the posterior morphology of these new camerates represents a basal configuration, an arrangement that is synapomorphic with disparids, an important question remains: How did the standard camerate interradius (Fig. 1B) arise from a disparid-like posterior (Fig. 1A)?

The most fundamental change that had to take place in the posterior interradius of more derived camerates is the displacement of the anitaxis from the C ray to the CD interray, which as mentioned previously, resulted in the reorientation of this structure from being tilted toward the D ray to being essentially vertical. This change would have necessitated the reorganization of the nervous and digestive systems, and it may explain the abrupt reversal in coiling direction of the camerate hindgut (Haugh, 1975b) and the "radial-like" anal nerves of the posterior interradius (Haugh, 1975a). There are several ways this change could have progressed, all of which must have occurred very early in development. Some developmental hypotheses for the posterior interray of camerates include the following (see Fig. 1):

- Hypotheses 1. The inferradial migrates into the CD interray to support the anitaxis, and the superradial supports the C ray arm only. Under this model, the inferradial is homologous with the primanal.
- Hypothesis 2. The superradial migrates into the CD interray, carrying with it the anitaxis and leaving the inferradial free to support the C ray arm only. Under this model, the superradial is homologous with the primanal.
- Hypothesis 3. Either the superradial or the inferradial is resorbed. The anitaxis migrates into the CD interray, and the remaining biradial supports the C ray arm only. Under either one of these models, the first plate of the anitaxis is homologous with the primanal.
- Hypothesis 4. The superradial and inferradial are both retained. The anitaxis migrates into the CD interray, and the superradial is repurposed as the proximal C ray primibrachial. Under this model, the first plate of the anitaxis is homologous with the primanal.

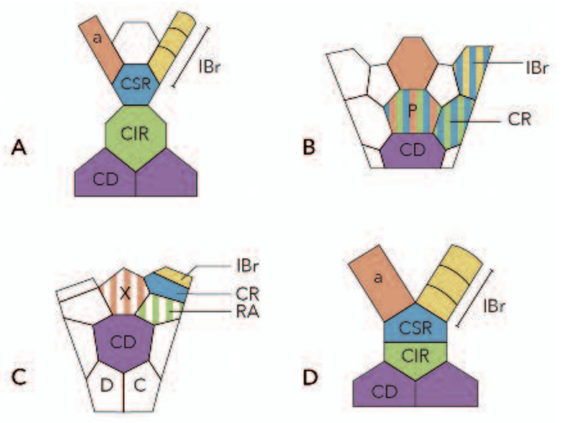

**Figure 1.** Posterior morphology of some Ordovician crinoids. A, posterior morphology of undescribed camerates from the Lower Ordovician Garden City Formation, Utah (Fig. 2B-D). Note that this morphology is essentially identical to the posterior morphology of the disparid in Fig. 2A. B, standard camerate posterior (after *Compsocrinus*). C, standard cladid posterior (after *Ottawacrinus*). D, standard disparid posterior (after *Iocrinus*). Letters refer to standard terminology for each group following Ubaghs (1978): a = first anal plate; CD = CD interray basal; CIR = C ray inferradial; CSR = C ray superradial; IBr = primibrachials; P = primanal; X = anal X, Similarly colored plates indicate inferred homology. Striped patterns indicate questionable homology. See text for discussion.

Although testing hypotheses of camerate posterior development is fraught with difficulty, the fossil record provides some discriminating evidence. Median ray and anal plate ridges mirror the underlying entoneural system of crinoids (Brower, 1973; Haugh, 1975a; Ubaghs, 1978). Therefore, this ornamentation can be used to delineate the changing positions of major radial and anal nerves through time. In *Pararchaeocrinus decoratus* Strimple and Watkins, 1955 from the Upper Ordovician Bromide Formation, ray and anal ridges converge in the C radial (Fig. 2E). The anitaxis is supported from the left shoulder of this plate, and the C ray arm is supported from the right shoulder as in the Garden City camerates. However, *P. decoratu*s lacks biradials, and the identity of the missing plate is uncertain. The superradial of earlier camerates supports a junction of radial and anal nerves; and therefore, it might be considered to be functionally significant and morphologically conservative. Thus, it seems reasonable to homologize the C radial of *P. decoratus* with the superradial of earlier camerates. An alternative explanation is that the junction of the radial and anal nerves migrated from the superradial downward behind the inferradial plate (which might be of even greater functional importance) and that the C radial of *P. decoratus* is homologous with the inferradial of earlier camerates.

At least two other camerates, both from the Middle Ordovician, bear a transitional posterior interradius like *P. decoratus*: *Trichinocrinus terranovicus* Moore and Laudon, 1943a from Newfoundland (see Ausich *et al*., 1998), and *Cefnocrinus samgilmouri* Botting, 2003 from Wales. In addition to possessing a C radial that supports both the anitaxis and an arm branch, all three species have a large plate positioned between the C and D radials, directly atop the CD basal. This plate is in the position of the camerate primanal, but it cannot be the first anal, which is articulated to the left shoulder of the C radial. One interpretation of this plate is that it is homologous with the inferradial of earlier camerates (see Hypothesis 1 above). It is probably not homologous with the superradial because Hypothesis 2 predicts that the superradial would migrate into the CD interray with the anitaxis, which is still attached to the left shoulder of the C radial. However, this large plate above the CD basal may be nothing more than a proximal interradial plate on the left side of the anitaxis.

*Retocrinus rocktonensis* Kolata, 1975 from the Upper Ordovician Guttenburg Formation of Illinois may preserve a final transitional stage in the evolution of a standard camerate posterior interradius (Fig. 1B). In *R. rocktonensis*, the C radial supports an arm as is typical, but there is an additional plate, probably the first anal plate (but see Hypotheses 1 and 2), articulated to its lower right side (see Kolata, 1975, fig. 12). Plate ridges indicate that a junction between the radial and anal nerves existed within the C radial as in earlier camerates, but the position of both the probable first anal plate and the nerve junction have migrated to the lower-left side of the C radial. Moreover, plate ridges suggest that there is an additional anal-brachial nerve junction within the CD basal as might be expected if the entire anitaxis migrated from the C ray in earlier camerates to the CD interray in later camerates.

Finally, recall that some camerates, such as basal Glyptocrinina, bear an anitaxis that although positioned directly above the CD basal, is still articulated to the left shoulder of the C radial. However, the right shoulder of the D radial equally supports the anitaxis in these taxa. This posterior arrangement is attainable through little more than reduction of the interradial plating surrounding the anitaxis. Thus, the Glyptocrinina is here considered to conserve a less derived posterior configuration than the Compsocrinina and all other camerates in which the primanal is no longer articulated to the left shoulder of the C radial.

## HOMOLOGY OF THE POSTERIOR INTERRAY AMONG PALEOZOIC CRINOIDS

Despite previous uncertainty regarding plate homology among Paleozoic crinoids (Philip, 1964; Ubaghs, 1978; Guensburg and Sprinkle, 2003), it is now difficult to overlook the similarities in anal plating among early camerates and disparids (Fig. 1A, D; Fig. 2A-D). A biradial C ray with the anus supported by the left shoulder of the superradial, and brachials supported by the right shoulder, is a probable synapomorphy that unites the two clades. Given its complexity, it is nonparsimonious to suggest that this radial-anal structure evolved independently in camerates and disparids, but this claim has yet to be tested within the framework of a proper phylogenetic analysis.

Homologizing the camerate-disparid posterior interray with that of cladids is more tenuous. The earliest cladids bear a "triradial" arrangement that has not been observed in camerates or disparids. Although it is tempting to homologize the radianal and C radial of cladids with the inferradial and superradial of camerates and disparids, this is by no means certain (see Fig. 1). Based on evidence from the development of living crinoids, functional morphology, and comparative anatomy and ontogeny of camerates, Brower (1973) argued that the primanal of camerates is homologous with the radianal of cladids. In living crinoids, two plates form in the C ray during early development (Springer, 1920). The lowermost of these plates, the radianal, migrates from under the C radial into the CD interray to support the anus, while the C radial supports an arm. Following the hypothesis for the evolutionary morphology of the camerate posterior interradius outlined above, support for the anus in some early camerates begins in the C ray (Fig. 1A) and later shifts into the CD interray (Fig 1B). If the lowermost plate of the C ray (inferradial) in early camerates migrates into the CD interray to support the anitaxis, as suggested by Hypothesis 1, then it would seem reasonable to homologize the primanal of camerates with the radianal of cladids.

## CONCLUSIONS

Many morphological similarities unite the oldest known camerates, cladids, and disparids. In fact, early crinoids are so similar that, upon initial discovery in the field, it is not always immediately obvious to which subclass a new specimen should be assigned. Traits that are common among the earliest representatives of each group suggest that their shared common ancestor bore an irregularly plated, pentameric stalk that was secured to a hard substrate via a polyplated, discoidal holdfast. It also likely possessed a calyx comprised of numerous, loosely organized stellate plates,

**Figure 2.** Posterior interradii of some Ordovician disparids and camerates. A, undescribed disparid (cf. *Alphacrinus*), Fillmore Formation (Floian), Millard, Co. Utah. B, undescribed camerate 1, Garden City Formation (Floian), Cache Co. Utah. C, undescribed camerate 2, Garden City Formation (Floian), Cache Co. Utah. The small specimen in the lower left is assumed to be a juvenile of the same species. D, magnified juvenile from C showing posterior morphology. E, *Pararchaeocrinus decoratus* Strimple and Watkins, 1955, Bromide Formation (Sandbian), Carter Co. Oklahoma. Similarly colored plates indicate inferred homology as in Figure 1. Striped patterns indicate questionable homology. See text for discussion.

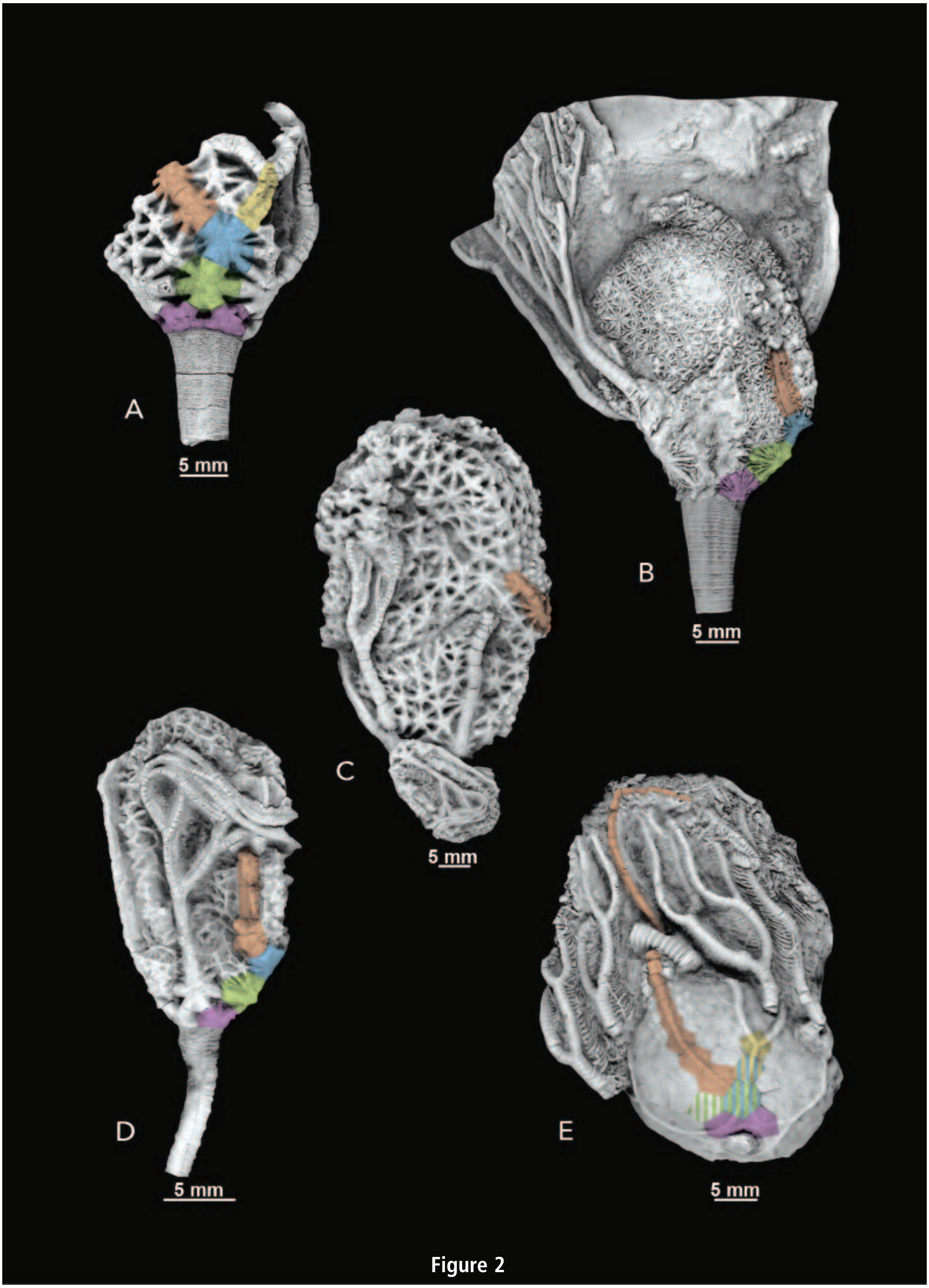

**Figure 2**

including fixed brachials and interradials. Fixed anal plates might have also generated an asymmetry in its calyx. The atomous arms consisted of uniserial brachials that lacked pinnules but possessed floor plates.

As camerates, cladids, and disparids diverged from such an ancestral population, they became increasingly distinct from one another. Whereas camerates retained many fixed plates in the calyx, cladids and disparids reduced fixed plating. In fact, cladids and disparids were long united under the Subclass Inadunata (Wachsmuth and Springer, 1885) until it was increasingly recognized that the inadunates were polyphyletic (Simms and Sevastopulo, 1993; Ausich, 1998a, 1998b). Not only does the discovery of a disparid-like posterior interray in basal camerates provide additional support for the polyphyly of the Inadunata, it suggests that Camerata and Disparida share a more recent common ancestor than either clade does with Cladida.

Early camerates and disparids supported the anus from the left shoulder of a "superradial" in the C ray, resulting in an assymetrical calyx. Such an asymmetry could negatively affect the hydrodynamic stability of the crown, generating selective pressure for increased cup symmetry over geologic time. Disparids appear to have solved this problem via paedomorphosis: They generally retained an arm-like anal structure, but it was displaced out of the calyx in concert with the reduction of fixed brachials and interradials. Camerates, on the other hand, enhanced their symmetry by shifting the anus from the C ray into the CD interray. Considering their early morphological similarity, and given that camerates and disparids are the most common crinoids in most Lower Ordovician strata, competition avoidance might explain why the two clades became so morphological distinct by the Middle Ordovician.

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# EVOLUTION OF THE ODONTOPHORE AND THE ORIGIN OF THE NEOASTEROIDS

Andrew Gale

School of Earth and Environmental Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth PO1 3QL UK.
andy.gale@port.ac.uk.

**Keywords:** Asteroid, evolution, odontophore, neoasteroid.

## INTRODUCTION

A small internal odontophore, positioned interradially between the inner surfaces of the paired oral ossicles, and separated from the inferomarginals by actinal ossicles is one of the defining characters of the post-Palaeozoic Neoasteroidea (Gale, 1987; 2011). Plesiomorphically, as in Paxillosida, the odontophore has a small external face. In Palaeozoic asteroids the homologue of the odontophore, sometimes called the axillary or axillary inferomarginal, is often a large ossicle, which proximally articulates with the interior of the paired oral ossicles, and distally with the two most proximal inferomarginals (e.g. *Calliasterella* Gale, 2011). This condition obtains also in the Permian *Monaster canarvonensis* Kesling, 1969 (Fig. 1E). In *Permaster grandis* Kesling, 1969, the external surface of the odontophore is reduced, but the plate remains in firm articulation with the first pair of inferomarginals (Fig. 1F).

## HOMOLOGIES

Spencer and Wright (1966) argued that the axillary is an unpaired interradial inferomarginal, which became intimately articulated with the oral ossicles, and was eventually occluded from the marginal frame. In some Palaeozoic asteroids such as *Schuchertia* and *Siluraster* (Shackleton, 2006 pl. 6 figs 7,10) the odontophore is an unpaired interradial inferomarginal which articulates with the oral ossicles (Fig. 1A). In more derived taxa, such as *Calliasterella mira*a (Trautschold) and neoasteroids, the articulation became complex, developing two specialized articulation surfaces, a keel and a muscle which ran from the inside of the oral to the lateral surface of the odontophore (Gale, 2011).

The intimate association between the odontophore and the inferomarginals limited expansion of the interradial disc. Only two small groups of Palaeozoic asteroids got round this problem, and they did so in different ways.

In the Devonian Xenasteridae, a double column of up to two pairs of inferomarginals became incorporated into the disc (e.g. *Agalmaster grandis,* Schondorf, 1909, pl. 9 fig. 5; Fig. 1B, C). Additionally, small irregularly arranged actinal plates are intercalated between the marginal pairs, and between the inferomarginals and the adambulacrals along the radius. These plates differ from true actinals, found in the neoasteroids which are arranged in regular rows, either parallel with the interradial arc (Marginal Row Pattern) or with the adambulacrals (Ambulacral Column Pattern-Hotchkiss and Clark, 1966; Blake and Hotchkiss, 2004).

In *Monaster clarkei* (de Koninck), a single column of four elongated interradial plates extend across the broad interradius from the paired interradial inferomarginals to the odontophore (Fig. 1G).

In all living asteroids, new inferomarginals and other serial ossicles are generated only at the contact betweeen the terminal ossicle and the last formed inferomarginal, such that inferomarginals can be numbered sequentially from the first formed in the interradius to the last formed, adjacent to the terminal, and the same applies to all other serial

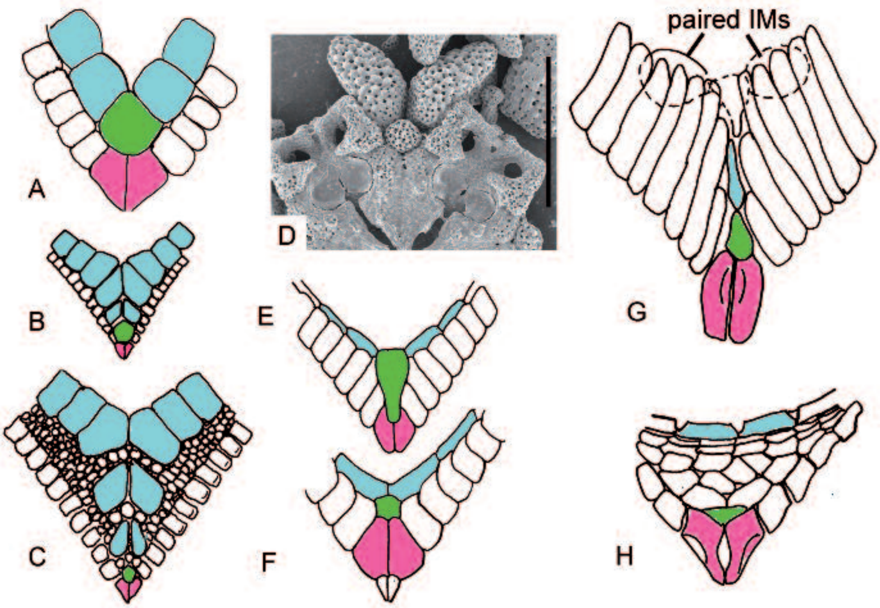

**Figure 1.** Actinal interradial views of asteroids. A, *Siluraster* sp., Ordovician; B, *Rhenaster* sp. C, *Xenaster* sp., both from the Devonian of Germany, after Schondorf 1909. D, *Echinaster* sp. Recent, Brazil. E, *Monaster canarvonensis*, F, *Permaster grandis*, both from the Permian of Western Australia, after Kesling 1969. G, *Monaster clarkei*, Permian, New South Wales. H, *Porcellanaster* sp., Recent. Oral ossicles red, odontophore green, inferomarginals blue. Actinal plates and adambulacrals are white. Scale bar 0.5mm.

ossicles. The signalling mechanism for the generation of plate rows is therefore positioned immediately proximal to the terminal as demonstrated in non-regenerating damaged individuals (Hotchkiss, 2009). Generation of intercalated plates in other sites requires mutation, and probably gene replication, which must have occurred in Xenasteridae, *Monaster* and neoasteroids, to permit intercalation of plates into the actinal interradius.

Accepting interpretation (Blake and Hotchkiss, 2004) of *Renaster schwerdi* Schondorf as a juvenile *Xenaster margaritatus* (Simonov) makes it possible to follow part of the ontogeny of xenasterids (Fig. 1B, C). The first formed three pairs of inferomarginals met over the interradius during growth, and the proximal pair was still in contact with the odontophore (Fig. 1B). At this point, very specific signalling was switched on, and actinal plate generation commenced, around the inferomarginal pairs, along the inner margin of the inferomarginals of the radius, and abradial to the adambulacrals, creating triangular interradial actinal zones. However, the odontophore:inferomarginal contact remained inviolate.

In *Monaster*, ontogeny is known from a juvenile individual from the Permian of Timor (Jell, 1999), which has three paired inferomarginals, and a large odontophore. With growth, three interradial plates were introduced of which the third from the odontophore was the smallest and therefore probably the last to form. In this case, a signalling site was located at the distal end of the odontophore adjacent to the first paired inferomarginals, and possibly between unpaired interradial ossicles 2 and 3. The articulation bond between the odontophore and the paired inferomarginals was finally broken, allowing the evolutionary pathway to neoasteroid expansion of the actinal interareas to open up – the next stage involved loss of the intermediate interradial ossicles, and extension of the signalling zone to the boundary between the adambulacrals and inferomarginals.

Early juveniles of living *Echinaster* at 50-150 days have, set between the oral ossicles, a relatively large, equilaterally rhombic odontophore, which has a large external surface, and articulates firmly with both the orals and first formed pair of marginal (Fig.1D). The juvenile thus closely resembles a Palaeozoic asteroid in shape, development and articulation of the unpaired interradial odontophore. During subsequent development, the odontophore separates from the inferomarginal ossicles, becomes internal, and actinal ossicles develop between the two (Fig. 1H). It thus appears that ontogeny accurately recapitulates the phylogeny of the neoasteroids from a Palaeozoic ancestor.

## Acknowledgements

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# SNEAKY SNAILS:
# HOW DRILLHOLES CAN AFFECT PALEONTOLOGICAL ANALYSES OF THE MINUTE CLYPEASTEROID ECHINOID *ECHINOCYAMUS*?

Tobias B. Grun and James H. Nebelsick

Department of Invertebrate Paleobiology and Paleoclimatology, Institute of Geosciences, University of Tübingen, Hölderlinstraße 12, 72074 Tübingen, Germany. tobias.grun@uni-tuebingen.de, nebelsick@uni-tuebingen.de

**Keywords:** Predation, Echinoids, Echinocyamus, Taphonomy, Drillholes.

## INTRODUCTION

Drilling in marine invertebrate shells is a common feeding strategy for a variety of predatory and parasitic gastropods. Naticids, muricids, capulids, nudibranchs, eulimids as well as the group of tonnaceans including cassids, cymatiids, tonnids, and some pulmonats are known drilling predators in marine environments (Bromley, 1981; Carriker, 1981; Kelley, 1988; Hoffmeister *et al.*, 2004). Most of these drilling gastropods predate on a restricted variety of prey. Naticids, muricids and capulids, cymatiids and some pulmonats drill in other mollusks or barnacles (Carriker and Yochelson, 1968; Bromley, 1981; Palmer, 1982; Kelley, 2001; Kelley and Hansen, 2006). Nudibranchs are known to drill in calcareous polychaete tubes (Young, 1969), while cassids and eulimids drill in echinoids (Hughes and Hughes, 1971, 1981; Warén and Crossland, 1991; Warén *et al.*, 1994). Drilling in shells leave predatory drillholes (Fig. 1A), which can be attributed to a specific predator due to characteristic morphological features. Drilling frequencies and the drillhole size can give detailed insights into fossil predator-prey interactions. Cassid gastropods are known predators of echinoids producing characteristic drillhole morphologies (Fig. 1B) and sizes (Hughes and Hughes, 1971, 1981). There has, however, been little study on the effects of taphonomic bias with respect to drillhole morphologies and preservation (Nebelsick and Kowalewski, 1999; Ceranka and Złotnik, 2003; Grun *et al.*, 2014).

This analysis includes numerous Recent and fossil tests of the clypeasteroid echinoid *Echinocyamus pusillus* from Recent nearshore environments around Giglio Island (Mediterranean Sea) and fossil specimens from Astrup and Doberg (northern Germany): with trace fossils (*Oichnus*) interpreted as drillholes. Tests were analyzed for: (1) drilling rates, (2) drillhole size, (3) size selectivity, (4) site selectivity, (5) drillhole morphology, (6) drilling based test-destructions, and (7) taphonomic alterations.

## STUDIED FAUNA

The genus *Echinocyamus*, a minute clypeasteroid echinoid, is used for analysis since it is easy to collect, abundant in a various habitats and occurs in Recent as well as in the Cenozoic fossil record. The behavior, morphology and predator-prey interactions of this genus has been described by several authors (Mortensen, 1927, 1948; Nichols, 1959; Ghiold, 1982; Telford *et al.*, 1983; Nebelsick and Kowalewski, 1999; Kowalewski and Nebelsick, 2003; Ziegler *et al.*, 2008; Grun *et al.*, 2014). *Echinocyamus* shows a wide distribution occurring in shallow waters down to 1250 m depth, burrowing in the sediment. The flattened calcareous test is oval to sub-elliptical in outline, up to 15 mm in length and

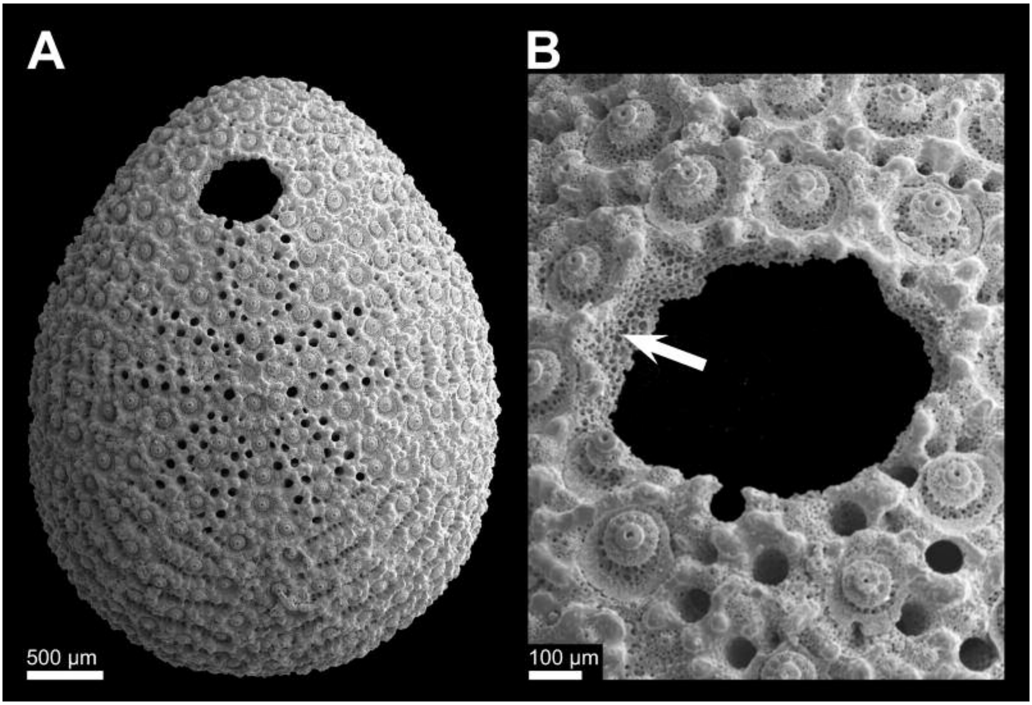

**Figure 1.** Photomicrographs of a Recent *Echinocyamus pusillus* test from nearshore environments around Giglio Island (Italy, Mediterranean Sea). (A) The elliptical test shows a drillhole in the anterior part. (B) In the detailed view the presence of microstructures (tubercles, knobs and pores in a ragged drillhole outline. The arrow indicates the concave cross-section of the drillhole.

entirely covered by minute spines. The aboral test side contains the apical disc and the petals; the oral test side is characterized by the slightly depressed peristome and periproct. The skeleton also features an internal support system which connects the oral and aboral sides of the test which leads to a high preservation potential.

## TAPHONOMY

Despite its high preservation potential, specimens of *Echinocyamus* are subjected to taphonomic effects which can dramatically bias Recent and fossil samples, depending on the environment in which the individuals occur. High energy environments with low sedimentation rates are more likely to result in test destruction than low energy environments associated with high sedimentation rates. Additionally, drillholes can be potentially affect the stability of the echinoid tests, especially when large drillholes occur in small individuals leading to a size bias of preserved specimens.

## MORPHOLOGY, FREQUENCIES AND TAPHONOMIC BIAS

Analyses of drilling frequencies show similar rates with 15 % for Recent samples around Giglio Island and for Oligocene samples from northern Germany. These drilling rates are in contrast to those found by Nebelsick and Kowalewski (1999) with a drilling frequency of up to 70 % for environments in the Red Sea. Analyzed tests show predominantly single drillholes. Predators do not seem to actively choose prey items by test size since correlations between tests length and drillhole length are absent or low. The distribution pattern of drillholes shows a high selectivity of the predator for the aboral side of the test, especially for the petal area which contains the respiratory tube feet. Predators do not prefer the anterior or posterior parts of the echinoids test as both show similar drilling frequencies. Drillhole morphology (Fig. 1B) is highly affected by the microstructure of the skeleton; the drillhole outline is irregular if drilled within pore rich areas or is smoother if the cassid drill into areas without pores. Drillholes are concave shaped in the cross-section which is due to stereom differentiation of the echinoid test plates (Figure 1B, arrow).

The lack of very small individuals with large drillholes may be indicative for a biased size distribution of Recent drilled tests due to handling effects of the predator. The test size distribution of drilled and undrilled tests suggests that drilled test do not seem to be subjected to preferential test destruction than non-drilled test. Further predation and drillhole based biases are discussed.

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# UPPER ORDOVICIAN ECHINODERMS FROM BUÇACO, PORTUGAL

Ana Filipa Montóia Jacinto[1], Juan Carlos Gutiérrez-Marco[2] and Samuel Zamora[3]

[1] Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, José Antonio Novais 12, 28040 Madrid, Spain.
ana.fm.jacinto@gmail.com
[2] Instituto de Geociencias (CSIC, UCM), José Antonio Novais 12, 28040 Madrid, Spain. jcgrapto@ucm.es
[3] Instituto Geológico y Minero de España, C/ Manuel Lasala 44, 9ºB, 50006 Zaragoza, Spain. s.zamora@igme.es

**Keywords:** Rhombifera, Diploporita, Crinoidea, Coronata, Katian, Portugal.

## INTRODUCTION

Echinoderms from the Ordovician of Portugal are poorly known. Delgado (1870, 1892, 1897, 1908) was the first author who recorded several cystoids, crinoids and coronates from Buçaco, Valongo and Amêndoa-Mação areas (Central Iberian Zone) but did not provide any description or illustration justifying his identification. Recent taxonomic studies focused only on Portuguese Middle Ordovician pelmatozoans, being the Upper Ordovician forms still undescribed. Here we present a review of the original collection from Delgado (1897, 1908), coming from three levels of Katian age in the Buçaco area, central Portugal. Delgado's collections are stored in Museu Geológico de Lisboa (Laboratório Nacional de Energia e Geologia); the echinoderm material is properly identified by its original labels that contain precise locality information from each specimen.

## MATERIAL

All the studied fossils come from the unit so-called "Schistos impuros diabasicos" by Delgado (1897, 1908), currently included in the Porto de Santa Anna Formation (Young, 1985, 1988). This formation consists of volcaniclastic sediments with some interbedded silicified limestones and tuffs that overlie a basal thick oolitic ironstone bed (Leira Má Member). The overlying sequence is composed by interbedded silicified limestones and thinly-bedded, fine-grained tuffs, culminating in a volcanic flow. The lower part of the Member Leira Má yielded an abundant assemblage of brachiopods, trilobites, bryozoans, cnidarians, molluscs and echinoderms, in part described by Ribeiro *et al.* (1853), Thadeu (1947), Young (1985) and Romano (1991). The upper part of the formation contains an unpublished fauna with brachiopod, bryozoans, echinoderms and rare trilobites (Young, 1988). Sá *et al.* (2011) assigned an upper Berounian (Katian 2) age to the Leira Má Member of the Porto de Santa Anna Formation, whose upper part reaches the Kralodvorian (Katian 3-4).

A total of 235 echinoderm specimens have been studied from the original collection of Delgado (1897, 1908) coming from three different localities placed on the Porto de Santa Anna Formation. They are mainly preserved as external and internal moulds occurring in decalcified yellowish volcaniclastic marls. Among the studied material, the rhombiferans are the most abundant and are dominated by the cariocystitoid *Heliocrinites* (Fig. 1D, E, H, I), that includes at least two different species ((*Heliocrinites* cf. *rouvillei* von Koenen and *H. helmhackeri* (Barrande)) and

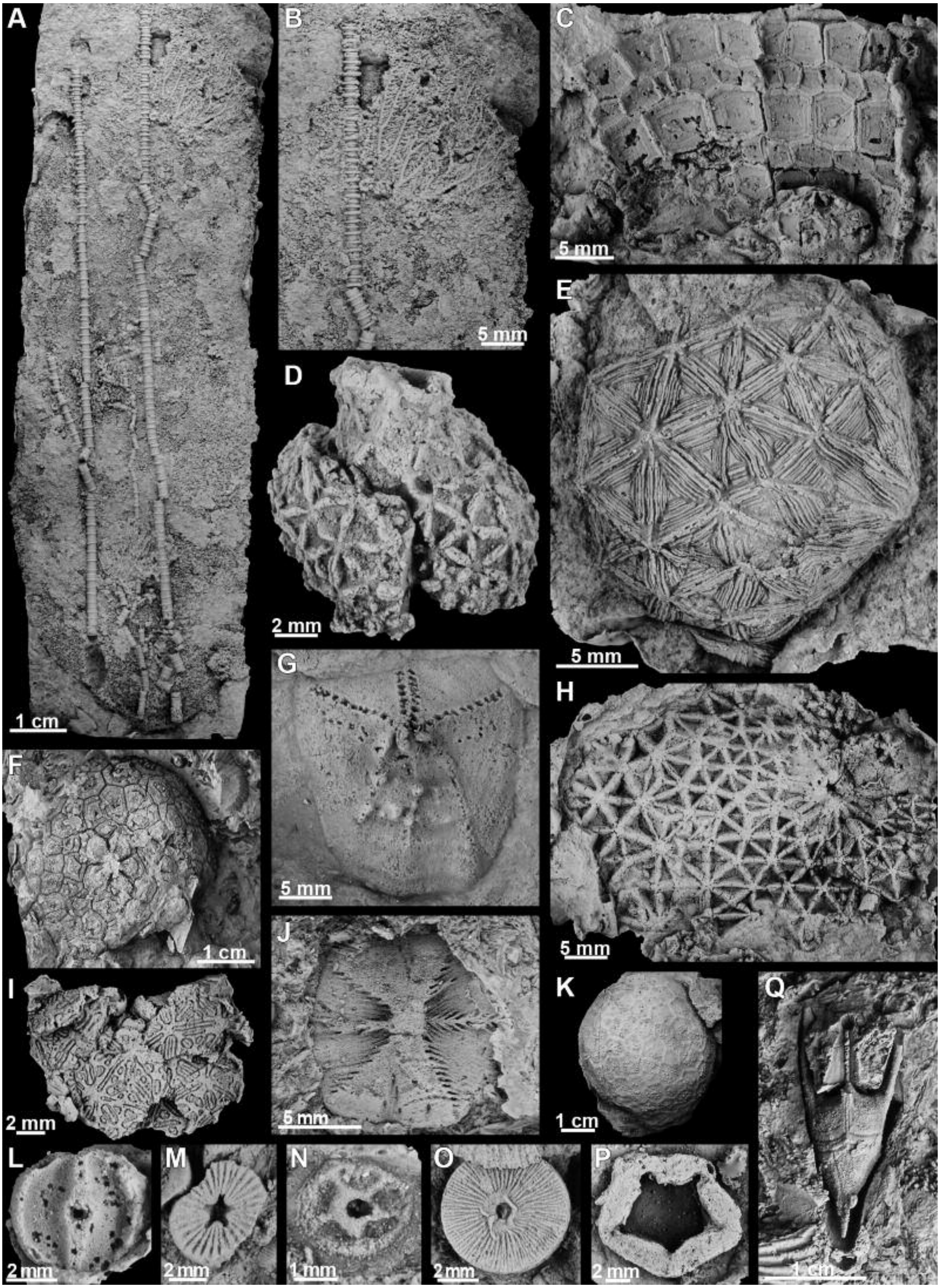
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**Figure 1.**

"*Echinosphaerites*" sp. (Fig. 1K). There are isolated plates belonging to two other groups of rhombiferans and assigned to Hemicosmitida indet. (Fig. 1G, J) and Glyptocystitida indet. Diploporans are the second group in order of abundance and include Sphaeronitida indet. and Aristocystitida ? indet. (Fig. 1C). Complete thecae of coronoids are also present including the single taxon *Mespilocystites* sp. (= *M. bussacensis* Delgado, *nomen nudum*) (Fig. 1Q). Lastly, several isolated columnals with possible crinoid affinities have been identified (Fig. 1L-P) including *Conspectocrinus* (col.) *celticus* Le Menn, *Ristnacrinus* (col.) cf. *cirrifer* Le Menn, *Cyclocharax* (col.) *paucicrenellatus* Le Menn and a nearly complete specimen assigned to Crinoidea indet. (Fig. 1A, B).

## CONCLUSIONS

The review of the echinoderm fauna reported by Delgado (1897, 1908) from the Porto de Santa Anna Formation of the Buçaco syncline, resulted in the identification of a relatively diverse assemblage dominated by cariocystitoid rhombiferans, that belongs to the "Heliocrinites Fauna" (*sensu* Gutiérrez-Marco, 2001) known from middle Berounian to Kralodvorian strata of France, Spain, Italy, Serbia, Bohemia, British Isles and North Africa. Although *Heliocrinites* is a widespread genus, according to Paul (1997), this genera appears to have been adapted to both tropical and cold polar latitudes during the Ordovician, occurring also in association with a rich shelly fauna in Baltica, Britain, Belgium, Myanmar and China, ranging from upper Arenigian to Hirnantian rocks.

The "Heliocrinites Fauna" of Buçaco occurs in upper Berounian and Kralodvorian rocks, partly contemporaneous of its Kralodvorian occurrences from the Pyrenees, southern Cantabrian Zone, Iberian Ranges and the southern Central Iberian Zone; and provides critic palaeobiogeographic information to understand the patter of echinoderm distribution at such interval.

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**Figure 1.** Echinoderms from the Upper Ordovician of Portugal. A, B. Specimen of Crinoidea indet., preserving articulated stem and part of the arms (MG92.5.1). C. Aristocystitida? indet., showing details of primary and secondary thecal plates (MG3236). D. Partially articulated theca of *Heliocrinites* sp. (MG3371). E. External mould of *Heliocrinites* cf. *helmhackeri*. (MG3128). F. Echinosphaeritida indet. (MG3368). G, J. Isolated thecal plates of Hemicosmitida indet. (MG92.5.14). H. Partially articulated theca of *Heliocrinites* cf. *rouvillei* showing the aboral pole (MG3232). I. Canals in rhombs of *Heliocrinites* sp. (MG3372). K. Internal mould of an articulated theca of "*Echinosphaerites*" sp. (MG3129). L. *Ristnacrinus* (col.) cf *cirrifer* (MG3241). M. *Cyclocharax* (col.) *paucicrenellatus* (MG92.6.6). N. *Conspectocrinus* (col.) *celticus* (MG3245). O. "Pelmatozoan" (col.) indet. (MG3135). P. "Pelmatozoan" (col.) indet. (MG3384). Q. Specimen of *Mespilocystites* sp., showing the internal mould of the theca and coronal processes (= *M. bussacensis* Delgado, *nomen nudum*) (MG3382).
Specimens A, B, C, E, F, G, H, I, J, L, M, N, O and P are latex casts whitened with MgO.

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# PALEOECOLOGY OF CRINOIDS FROM THE UPPER CRETACEOUS COLD SEEP DEPOSITS OF CENTRAL UNITED STATES AND JAPAN: WERE THEY CHEMOSYNTHETIC COMMUNITY MEMBERS?

Moe Kato[1] and Tatsuo Oji[2]

[1] Department of Earth and Environmental sciences. Graduate school of environmental Studies, Nagoya University, Fro-cho, Nagoya 464-8601, Japan. katou.moe@d.mbox.nagoya-u.ac.jp
[2] Nagoya University Museum, Fro-cho, Nagoya 464-8601, Japan. oji@num.nagoya-u.ac.jp

**Keywords:** paleoecology, crinoids, cold seep, chemosynthetic community.

## INTRODUCTION

A cold seep is a place where reduced substances (mainly sulphur and methane) emerge from seafloor sediments without any appreciable temperature rise and is known as one of the extreme environments where special fauna called "the chemosynthesis community" inhabits. Echinoderms were thought to be rare in a cold seep environments and had not been considered as a member of the chemosynthetic community until recent years (Grassle, 1985; Laubier, 1989; Desbruye`res, *et al*. 2006), whereas echinoderms are one of the main groups in marine invertebrates especially in deep sea. In the last 10 years, some species of echinoderms have been reported as a member of the modern chemosynthetic community (Stöhr and Segonzac, 2005; Pawson and Vance, 2003). However ecology of these echinoderms and the process of adaptation to environments of cold seep still remain to be clarified. The purpose of this study is i) to clarify the process of adaptive evolution of echinoderms associated with a cold seep environment and ii) to discuss to what extent the life of the echinoderms was related to reducing substances from cold seeps, based on the carbon isotopic data.

## GEOLOGICAL SETTINGS AND MATERIALS

Fossil echinoderms from carbonates associated with cold seeps are extremely rare, but have recently been reported from some localities (Gaillard *et al.*, 2011; Landman *et al.*, 2012). Fossils from two coeval formations (Upper Campanian), the Pierre Shale in South Dakota, USA and the Osoushinai Formation in Hokkaido, Japan, have been studied to compare the influence of cold seeps to echinoderms, and the factor associated with such interaction. At least five species of echinoderms from the Pierre Shale have been collected comprising mainly specimens of a crinoid and irregular echinoids with cold seep endemic species such as lucinid bivalves and tube worms. Ophiuroids and one specimen of asteroid are less abundant, and were also collected from carbonate mounds in the same area. The Osoushinai Formation has reported only one species of isocrinid crinoid. The seep carbonates are found as boulders and include tube worms and crinoid columnals.

The crinoid from the Pierre Shale has been studied separately, and it has some unique morphological characteristics absent in any living crinoids (Fig. 1). These crinoids probably adapted to a cold seep environment (Hunter *et al.*, in progress). The crinoid from the Osoushinai Formation is assigned to the family Isocrinidae, which is very common in "normal" non-seep environments. Thus, Isocrinids do not display any special feature as an adaptation to cold seeps.

## STABLE CARBON ISOTOPES

To discuss the degree of linkage between the crinoids and methane released from cold seeps, the stable carbon isotope ratios ($\delta^{13}C$) of crinoid skeletons were measured. Because methane released from a cold seep is characterized by the extremely light $\delta^{13}C$ values (Roberts *et al.*, 1989), it is expected that $\delta^{13}C$ values of fossil crinoid skeletons were affected by that of cold seep methane and were lighter than echinoderms living in normal conditions. Before analyzing $\delta^{13}C$, the microstructure of echinoderm skeletons was observed with a polarizing microscope to estimate the degree of diagenesis, and spots of less diagenetically affected skeletal parts were measured. As a result, $\delta^{13}C$ values of crinoids from the Pierre Shale was from -31.1 to -11.1‰ (n =20, mean -20.9‰), and that of crinoids from the Osoushinai Formation was -39.8 to -38.4‰ (n = 2). $\delta^{13}C$ values of seep carbonates (matrix) from the Pierre Shale was from -46.1

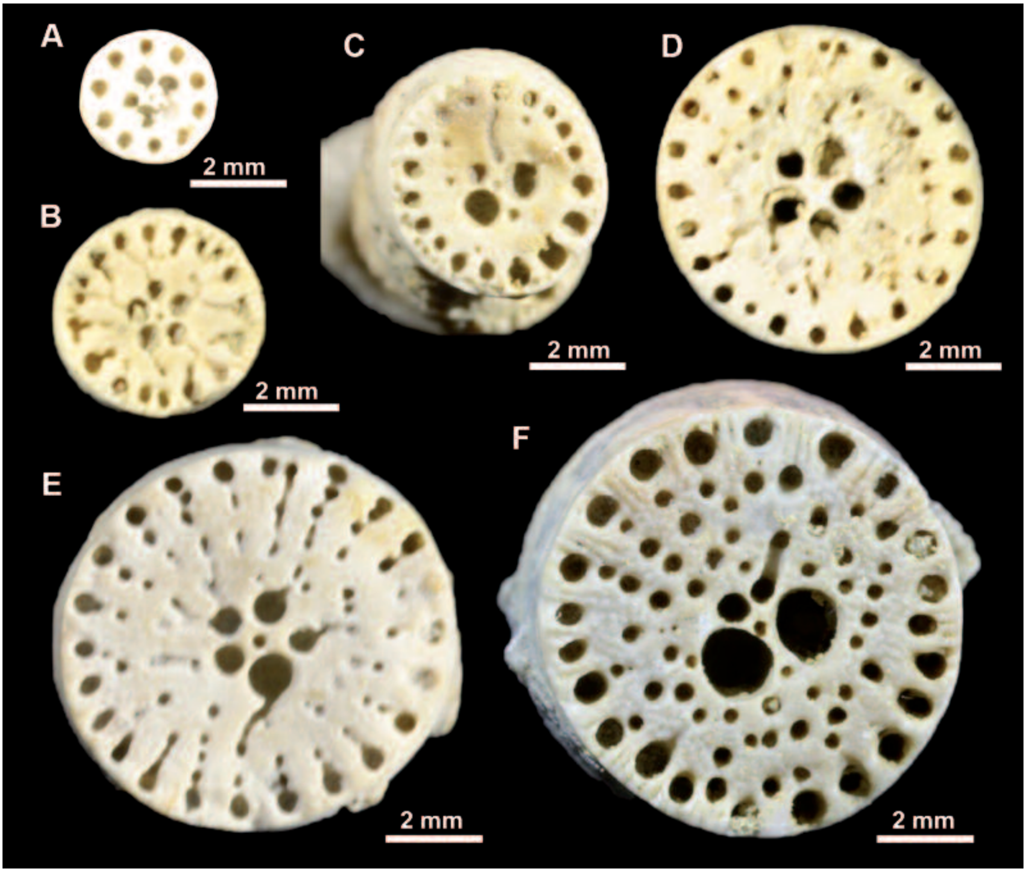

**Figure 1.** A-F. Columnals of crinoid from cold seeps in the Pierre Shale with many large tubulis which vary in size. All specimens are deposited in AMNH (American Museum of Natural History).

to -9.9‰ (n = 12, mean -21.5‰), and that of seep carbonates from the Osoushinai Formation was from -46.5 to -21.4‰ (n = 27, mean -35.2‰). The crinoids from both the Pierre Shale and the Osoushinai Formation showed $\delta^{13}$C values comparable to those from seep carbonate matrix around the fossils. These results suggest that the crinoids from both localities lived close in cold seep environments and they were ecologically under close relationship with cold seeps.

## CONCLUSIONS

Fossil echinoderms were discovered in cold seep carbonates from the Upper Campanian of United States and Japan. The crinoid from the Pierre Shale has a unique morphology and low $\delta^{13}$C values suggesting adaptation to cold seep environments. The isocrinoid from the Osoushinai Formation has typical morphology, and the skeleton shows low $\delta^{13}$C values. The isotopic data suggest that the Isocrinid from the Osoushinai Formation lived close to cold seeps but did not change its morphology notably. Carbon isotope data of the crinoid skeletons from the Osoushinai are not greatly variable, and thus suggests that they were not influenced by the diagenetic alteration. Additional measurements of carbon isotope ratios from the normal (non-seep) isocrinid skeletons and the comparison of data from both seep and non-seep crinoids may clarify whether the Osoushinai crinoid adapted to the seep environment.

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# WHAT CAN *AGANASTER* VERTEBRAE TELL ABOUT ITS ECOLOGY?

Aleksandr Kokorin

Paleontological Institute RAS, 117647, Profsouznaya st. 123, Moscow, Russia. korveng@gmail.com

**Keywords:** *Aganaster*, ecology, ophiuroidea, carboniferous.

## INTRODUCTION

*Aganaster* is a rather widespread Late Paleozoic brittle star, with occurrences in the USA, China and Europe. It is one of the first so-called modern-type Paleozoic ophiuroids. Despite its age, *Aganaster* has many features typically found in recent brittle stars, such as fused vertebrae and a disc which is completely covered by plates. Formerly it was placed in the families Ophiuridae, Aganasteridae and Ophiolepididae (Spencer and Wright, 1999; Jell, 1997; Hotchkiss and Haude, 2004), but at present the position of the genus is unclear; it might be close to the ophiuroid crown-group ancestors (O'Hara *et al.*, 2014). Considering the importance of *Aganaster* for the understanding of ophiuroid evolution and its wide geographical distribution in the Late Paleozoic, knowledge on the possible mode of life of this genus is of interest. I tried to reveal some features of the autecology of *Aganaster* on the basis of the functional morphology of the vertebrae (axial ray ossicles).

## MATERIAL

The material was collected in Upper Carboniferous sediments of the Moscow Basin (Kasimovian and Gzhelian stages). There are five articulated specimens of ophiuroid, thought to be a new species of *Aganaster*. Additionally, a lot of isolated ophiuroid remains were found at the same and similar localities (22 in total) using chemical etching of clays. Isolated ossicles were correlated with complete specimens on the basis of lateral arm plate morphology and according to X-ray microtomography data. Ossicles were sorted under the stereomicroscope, and vertebrae were studied using scanning electron microscopy.

## RESULTS

Vertebrae morphology of brittle stars correlates with their ecological specialization. Food-gathering behavior of ophiuroids consists mostly of different arm movements, and intersegmental arm flexibility seems to be determined by the shape of vertebrae articulating surface (although in some works this last statement is challenged (LeClair and LaBarbera, 1997). Different ecological groups of brittle stars show significant differences in morphology of vertebrae (Litvinova, 1989).

*Aganaster* vertebrae have zygospondylous articulation but unlike the "normal" articulation present in most modern brittle stars. The median process on the distal surface is strongly reduced (Fig. 1a), and the corresponding median socket on the proximal surface is reduced too. The median process provides horizontal flexibility of the arm.

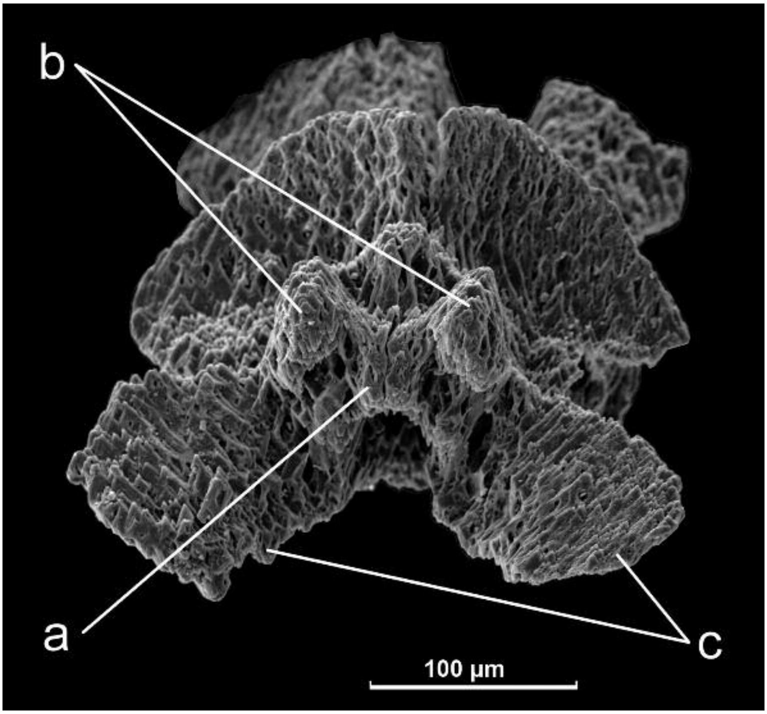

**Figure 1.** *Aganaster* sp., distal view of isolated vertebra under SEM. Moscow Region, Kasimovian stage. Explanations: a – median process, b – dorsal processes, c – ventro-distal muscule attachment areas.

For example, vertebrae of the small boreal brittle star *Stegophiura nodosa* (Lütken, 1855), in which the arms are bending mostly in horizontal plane, has a very well-developed median process. On the contrary, the dorsal processes on the distal surface of *Aganaster* vertebrae are well-developed and widely spaced (Fig. 1b), forming the horizontal axis of rotation. Hence it can be assumed that the horizontal flexibility of the arms of *Aganaster* was limited, and that they bent mainly in vertically. Since brittle stars use horizontal arm movements rather than their tube feet for locomotion, *Aganaster* was probably not a good runner.

Another interesting feature of the vertebrae is the position of the ventro-distal muscle attachment areas (Fig. 1c). In fact, since they are almost horizontal, they probably limited ventralward arm bending.

Litvinova (1989) described this type of vertebrae as aberrant. According to her paper, several recent ophiuroids have similar morphology of articulating surface, for example *Ophiotholia* and *Ophiomyces*. Both of these genera have an unusual appearance: sack-like shape and upward directed arms (Litvinova, 1992; O'Hara and Stöhr, 2006) and are probably burrowers (Litvinova, 1994).

## CONCLUSIONS

The specific structure of *Aganaster* vertebrae and in particular its articulation surface morphology suggest that this brittle star was a slow-moving species; it possibly lived slightly burrowed in the sediment with the oral side facing down and the arms directed upward to intercept detritus in transport.

It is interesting that a very similar mode of life is assumed for early stem-group ophiuroids with discrete ambulacra and petaloid-like rays, such as *Stenaster* (Dean, 1999). This similarity is surprising because the compact, fused, cylindrical vertebrae of *Aganaster* should give an advantage in mobility. In all probability, *Aganaster* has secondarily adopted such an ecological role at the cost of mobility.

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# BODY WALL HOMOLOGIES IN BASAL BLASTOZOANS

Bertrand Lefebvre[1], Elise Nardin[2] and Oldrich Fatka[3]

[1] UMR CNRS 5276 LGLTPE, Université Lyon 1, 2 rue Raphaël Dubois, 69622 Villeurbanne cedex, France.
bertrand.lefebvre@univ-lyon1.fr
[2] UMR CNRS-IRD-UPS 5563 Géosciences Environnement Toulouse, Observatoire Midi-Pyrénées,
14 avenue Edouard Belin, 31400 Toulouse, France. elise.nardin@get.omp.eu
[3] Charles University, Institute of Geology and Palaeontology, Albertov 6, 128 43 Prague 2, Czech Republic. fatka@natur.cuni.cz

**Keywords:** Cambrian, Blastozoa, Extraxial-Axial Theory, Echinodermata, Homology.

## INTRODUCTION

When echinoderms first appeared in the fossil record in Cambrian Series 2, they were already diverse and widespread (Smith *et al.*, 2013; Zamora *et al.*, 2013a). The initial stages of their diversification are relatively well documented in both Laurentia and Gondwana (Lefebvre and Fatka, 2003; Smith *et al.*, 2013; Zamora *et al.*, 2013a). These two regions have yielded assemblages consisting exclusively of radially symmetrical forms: blastozoans (gogiid eocrinoids and lepidocystids), edrioasteroids and helicoplacoids. The later appearance (Cambrian Series 2 - 3 boundary) of echinoderm taxa with asymmetrical, flattened body plans (cinctans, ctenocystoids, solutans, stylophorans) coincides with a major ecological turnover (Dornbos, 2006). Finally, representatives of the five extant classes of echinoderms are not documented before the Ordovician (Paul and Smith, 1984; Guensburg and Sprinkle, 2001; Lefebvre *et al.*, 2013).

In Cambrian Series 2 and 3, the extremely wide morphological disparity exhibited by the earliest echinoderms is puzzling (e.g., spiral, pentaradiate, bilateral, asymmetric body outlines). This initial disparity can result either from a long unrecorded evolution, or from an extremely rapid diversification into highly specialised ecological niches (Ubaghs, 1975; Lefebvre and Fatka, 2003; Smith *et al.*, 2013). Whatever its origin, the wide original disparity of the oldest echinoderms makes it particularly difficult to identify overarching homologies in all Cambrian taxa and thus, to elucidate their evolutionary relationships.

In most recent phylogenies including basal echinoderms, character coding is largely dependent on theoretical assumptions and much emphasis is placed on the symmetry of body outlines (Smith, 2005, 2008; Zamora *et al.*, 2012; Smith and Zamora, 2013; Zamora and Rahman, 2014). Non-radiate taxa are considered as necessarily primitive and forced down the trees, simply because of the choice of bilaterally symmetrical outgroups (e.g., hemichordates). The elaboration of a formal, robust cladistic analysis of early echinoderms urgently requires the identification of a set of objective characters based on well-defined homologies. In this context, the aim of this paper is to identify and discuss body wall homologies in the earliest blastozoans, based on both the now widely accepted extraxial-axial theory (EAT) and the report of a new "transitional" form from the Jince Formation (Cambrian Series 3) of Bohemia, Czech Republic.

## THE EXTRAXIAL - AXIAL THEORY

The extraxial-axial theory (EAT) is a model providing keys to identify body wall homologies in both extant and extinct echinoderms. This model was initially defined mostly on ontogenetic and architectural criteria (Mooi *et al.*, 1994; Mooi and David, 1998). In recent years, the validity of the EAT -at least in the five extant classes of echinoderms- was confirmed by both embryologic data (David and Mooi, 1996, 1998) and Hox cluster analyses (Mooi *et al.*, 2005; Mooi and David, 2008; David and Mooi, 2014). The EAT is now almost universally acknowledged as a robust framework for skeletal homologies in echinoderms (Peterson *et al.*, 2000; Sprinkle and Guensburg, 2001; Hotchkiss, 2012; Sumrall and Waters, 2012; Smith and Zamora, 2013).

The EAT identifies two main regions in the body wall of echinoderms: the axial and extraxial regions. In ontogeny, the axial region (AR) of the body wall derives exclusively from the larval rudiment. It is associated with the mouth and the water vascular system. The extraxial part of the body derives from the non-rudiment part of the larva. It forms the rest of the body wall, and can be subdivided into two parts: (1) the perforate extraxial region (PER), which contains several primary body openings (anus, gonopore, hydropore); and (2) the imperforate extraxial region (IER), without any primary opening. In primitive echinoderms, new extraxial elements can be added almost anywhere during growth.

In recent years, a well-defined set of skeletal homologies (Universal Elemental Homology, UEH) was defined for individual plates associated with the peristomial border in derived blastozoans (Sumrall and Waters, 2012). The UEH model is largely based on axial elements and certainly provides a powerful tool to identify individual plate homologies within closely related taxa. Similar models of individual plate homologies have been proposed in other groups of Palaeozoic echinoderms. For example, homologies of individual skeletal elements of the PER were thoroughly investigated in stylophorans (Lefebvre and Vizcaïno, 1999). The identification of homologous individual skeletal elements is pivotal for inferring phylogenetic relationships among closely related taxa. However, this identification largely depends upon similarities of positions. Consequently, it cannot provide a robust framework for the comparison of the morphologically extremely diverse plate patterns of early echinoderms.

## LEPIDOCYSTIDS

Lepidocystids (or imbricate blastozoans) are almost universally considered as basal-most blastozoans (Sprinkle, 1973; Ubaghs, 1975; Broadhead, 1982; Paul and Smith, 1984; David *et al.*, 2000; Zamora and Smith, 2011). Lepidocystids have been documented in Cambrian Series 2 and 3 of Laurentia (*Kinzercystis*, *Lepidocystis*; Durham, 1968; Sprinkle, 1973; Paul and Smith, 1984), European peri-Gondwana (*Vyscystis*; Fatka and Kordule, 1990) and West Gondwana (unnamed form from Morocco; Smith *et al.*, 2013).

All lepidocystids share the same basic organisation, consisting in a flat to slightly domed oral surface, and an elongate cone-shaped aboral region (Fig. 1A; Sprinkle, 1973; Ubaghs, 1975; Paul and Smith, 1984). The oral surface of lepidocystids contains all main body orifices (anus, gonopore, hydropore and mouth), as well as the ambulacra (flooring plates and associated sheets of cover plates). Ambulacra regularly branch into free, erect portions (brachioles), which can be either straight (*Kinzercystis*, *Lepidocystis*) or coiled (*Vyscystis*). Polyplated interambulacral areas consist in numerous, tessellate plates bearing epispires. The aboral part of the body is entirely made of small, scale-like, imbricate plates. In both *Kinzercystis* and *Vyscystis*, the aboral region is relatively large and cone-shaped. In *Lepidocystis*, it is differentiated into (1) a short, expanded proximal part forming the cup-like, aboral portion of the bud-shaped test; and (2) a long, almost cylindrical, polyplated, distal stalk-like appendage.

The morphology of lepidocystids can be readily interpreted using the EAT framework of body wall homologies (Fig. 2A). The oral surface of lepidocystids contains both the axial (cover plates, flooring plates, mouth) and perforate extraxial (interambulacral plates, anus, gonopore, hydropore and epispires) regions. The imbricate aboral sac, which contains neither any body orifice, nor any ambulacral element, can be identified as the IER of the body wall. The body plan of lepidocystids is indeed very close to that of other basal, pentaradial echinoderms (e.g., *Camptostroma*, *Stromatocystites*). The main difference with Cambrian edrioasteroid-like taxa consists in the presence of brachioles (apomorphy of blastozoans) in lepidocystids (Sprinkle, 1973; Ubaghs, 1975; Paul and Smith, 1984; David *et al.*, 2000; Nardin *et al.*, 2009a).

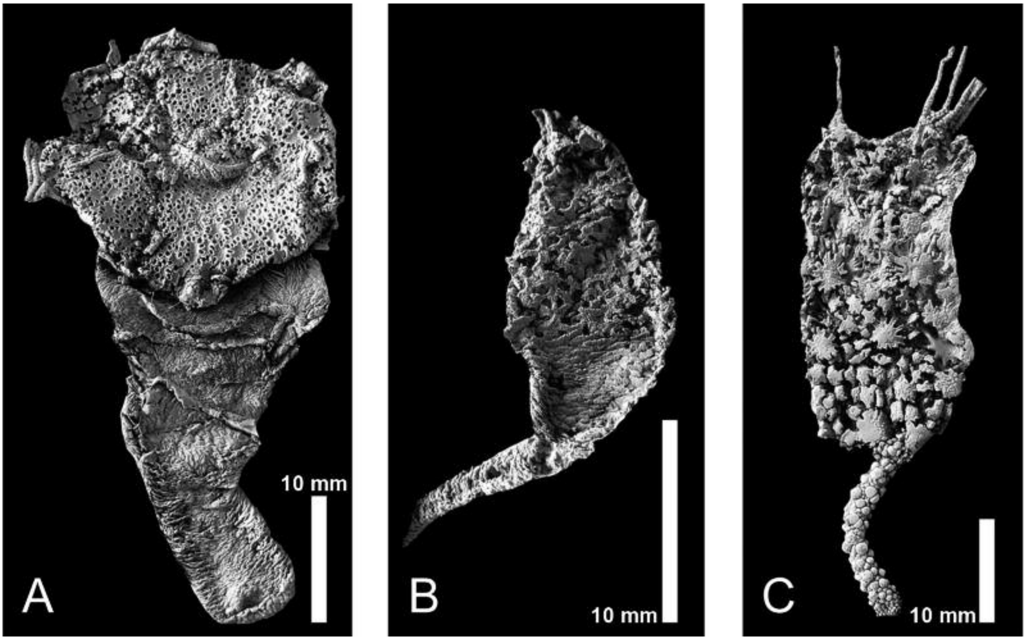

**Figure 1.** Basal blastozoans (latex casts of original specimens). A. *Kinzercystis durhami* Sprinkle, 1973, Kinzers Formation, Pennsylvania (holotype, MCZ 581). B. Undescribed transitional form between lepidocystids and gogiids, nov. gen., nov. sp., Jince Formation, Czech Republic (SZ 349). C. *Gogia palmeri* Sprinkle, 1973, Spence Shale, Langston Formation, Idaho (holotype, USNM 165418). Repositories: MCZ, Museum of Comparative Zoology, Harvard University; SZ: Narodni Museum, Prague; USNM: U.S. National Museum, Washington.

## GOGIID EOCRINOIDS

Gogiids are universally considered as the most primitive representatives of the class Eocrinoidea (Sprinkle, 1973; Broadhead, 1982; Zamora and Smith, 2011). Eocrinoids are a paraphyletic assemblage uniting non-imbricate, basal blastozoans (Ubaghs, 1975; Smith, 1984; Paul, 1988; David *et al*., 2000; Nardin *et al*., 2009a; Zamora and Smith, 2011). The stratigraphic range of gogiid eocrinoids is restricted to the Cambrian Series 2 and 3 (Zamora *et al*., 2013a) of Laurentia (e.g., *Gogia*; Ubaghs, 1968, 1975; Sprinkle, 1973; Nardin *et al*., 2009b), European peri-Gondwana (e.g., *Acanthocystites*, *Akadocrinus*, *Alanisicystis*, *Luhocrinus*; Prokop, 1962; Fatka and Kordule, 1984, 1990; Prokop and Fatka, 1985; Ubaghs and Vizcaïno, 1990), West Gondwana (*Alanisicystis*; Smith *et al*., 2013) and South China (e.g., *Balangicystis*, *Guizhoueocrinus*, *Sinoeocrinus*; Zhao *et al*., 1994; Parsley and Zhao, 2006).

The globular test of gogiids is entirely made of numerous, irregularly arranged tessellate plates (Fig. 1C). In most taxa (e.g., *Alanisicystis, Gogia, Sinoeocrinus*), ambulacra are short and restricted to the upper-most region of the test. Each ambulacral ray typically leads to a small group of free, erect brachioles occurring on the summit of a small, spout-like projection (e.g., *Gogia parsleyi*, *Sinoeocrinus*). In gogiids, brachioles can be either straight (e.g., *Akadocrinus*, *Gogia palmeri*) or spirally coiled (e.g., *Gogia spiralis*, *Guizhoueocrinus*). The location of the anal pyramid, although variable, frequently occurs in lateral position on the test. The other main body orifices have been seldom documented in eocrinoids (e.g., hydropore in *Alanisicystis*; Ubaghs and Vizcaïno, 1990). Epispires can occur all over the test (e.g., *Alanisicystis*, *Gogia spiralis*), or they can be restricted to its upper half (e.g., *Gogia kitchnerensis*). However, the description of ontogenetic sequences in several gogiids suggests that the extension of epispires over the test is indeed variable during growth (Parsley and Zhao, 2006; Parsley, 2012; Zamora *et al*., 2013b; Nohejlová and Fatka, 2014). In most gogiids, the boundary between the test and the aboral appendage is relatively sharp. The morphology of the appendage is variable. In some taxa, it corresponds to a short, inflated, polyplated aboral sac (e.g., *Alanisicystis*). In most taxa, the appendage is a narrow, cylindrical, stem-like structure (stalk) made of numerous, irregularly arranged plates (e.g., *Balangicystis*, *Gogia longidactylus*). In *Akadocrinus*, the aboral appendage corresponds to a holomeric stem, made of homeomorphic columnals (Prokop, 1962; Sprinkle, 1973; Fatka and Kordule, 1991).

The test of gogiids contains various structures indicating both axial (embedded parts of ambulacra) and perforate extraxial (e.g., anus) affinities (Fig. 2C; Mooi and David, 2008; Nardin *et al.*, 2009a; Smith and Zamora 2013). This interpretation is supported by the extension of epispires all over the test in some taxa, and by the variable location of the anus. The aboral, stalk-like appendage of gogiids contains neither any primary body opening, nor elements associated with the water-vascular system. Consequently, this region is probably made of imperforate extraxial skeletal elements. If these identifications are correct, then (1) the flat to slightly domed oral surface of lepidocystids is homologous to the entire test of gogiids; and (2) the imbricate aboral sac of lepidocystids is equivalent to the stalk-like appendage of gogiids. This implies that the tests of lepidocystids and gogiids are not homologous structures.

## INTERMEDIATE, SEMI-IMBRICATE BLASTOZOANS

The Jince Formation (Cambrian Series 3, Drumian) of Bohemia (Czech Republic) yielded recently several exquisitely preserved specimens of basal blastozoans displaying a unique body plan organisation. Their globular, elongate test shows two clearly distinct regions (Fig. 1B). The upper two-thirds of the test are entirely made of numerous, adjacent plates bearing sutural epispires. At least two main body orifices (mouth and anus) occur in this region. Brachioles and ambulacral rays are mounted on a narrow spout-like oral surface. The presence of brachioles supports the identification of these fossils as blastozoans. The lower third of the test is entirely made of imbricate skeletal elements, without any epispire or any other body orifice. The aboral, imbricate part of the test is in physical continuity with the underlying, elongate, polyplated, imbricate stalk-like appendage.

The unique body plan of the new blastozoan from the Jince Formation can be interpreted with the EAT (Fig. 2B). The upper (adoral) part of its test contains structures typical of both the AR (ambulacra, mouth) and the PER (anus, epispires). The lower (aboral) part of the test and the stalk-like appendage, which contain no main body orifice and no ambulacral (axial) elements, are both probably made of imperforate extraxial plates. If these identifications are correct, the aboral, imbricate portions of the new blastozoan (i.e., lower third of the test and stalk-like appendage) can be considered as homologous to both the elongate, aboral sac of lepidocystids and the stalk-like appendage of gogiids. The upper two-thirds of the test of the new form are thus equivalent to both the oral surface of lepidocystids and to the whole test of gogiids. Consequently, the morphology of the new Jince blastozoan appears in many respects as intermediate, transitional between lepidocystid and gogiid body plans. This new fossil strongly supports the view that the globose test of gogiids results from the complete devagination of the flat to slightly domed oral surface of lepidocystids. It also suggests that, correlatively, the contribution of the IER is dramatically reduced in gogiids (stalk-like appendage) compared to the situation in lepidocystids (lateral walls of the test and aboral stalk).

## CONCLUSIONS

The EAT provides a powerful tool to investigate body wall homologies in Early Palaeozoic echinoderms. The EAT indicates that the tests of lepidocystids and gogiid eocrinoids are not homologous, and should be assigned different names. Following Nardin *et al.* (2009a), the term "calyx" is proposed here for body capsules comprising a flat to slightly domed oral surface (or tegmen) and a large, cone-shaped aboral cup. The possession of a calyx possibly represents the plesiomorphic condition in early echinoderms, as it occurs in both basal edrioasteroid-like taxa (e.g., *Camptostroma*, *Stromatocystites*) and in basal blastozoans (lepidocystids). Following Nardin *et al.* (2009a), the term "theca" is proposed here for body capsules corresponding to fully devaginated tegmens. The possession of a theca is an apomorphy of non-imbricate blastozoans (gogiids and all more derived blastozoan taxa; David *et al.*, 2000; Nardin *et al.*, 2009a). The new Jince blastozoan represents a transitional form between lepidocystids and more derived blastozoans. This interpretation is based on its unique, intermediate body organisation, resulting from the partial devagination of the oral surface. The test of the Jince blastozoan cannot be identified as a calyx, because of the devagination of the tegmen, which constitutes not only the roof, but also a significant portion of the lateral body walls. However, the test of the Jince blastozoan cannot be identified as a theca, because contrary to the situation in gogiids,

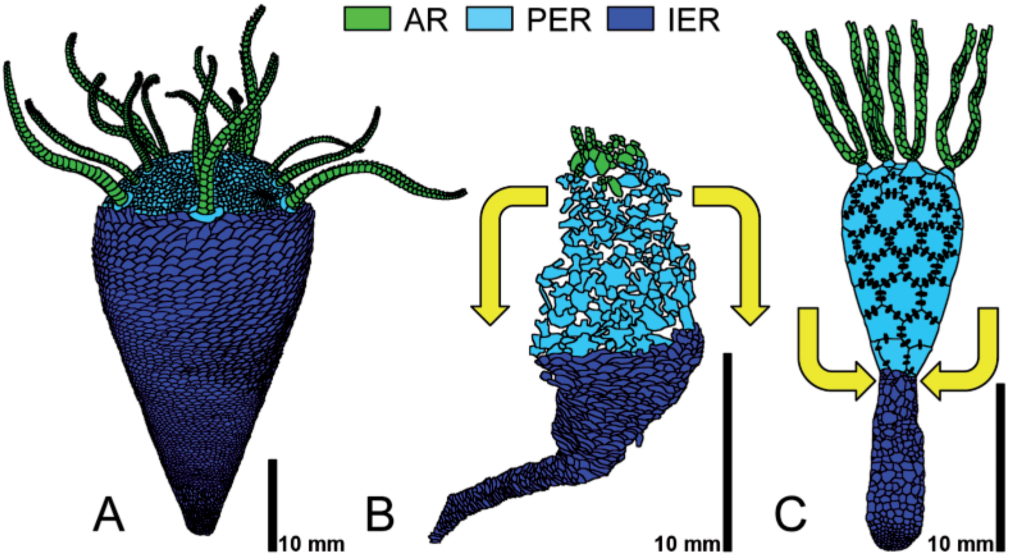

**Figure 2.** Progressive devagination of oral surface in basal blastozoans. A. *Lepidocystis wanneri* Foerste, 1938, Kinzers Formation, Pennsylvania (reconstruction modified from Durham, 1968). B. Undescribed transitional form between lepidocystids and gogiids, nov. gen., nov. sp., Jince Formation, Czech Republic (camera-lucida drawing of specimen SZ 349). C. *Gogia spiralis* Robison, 1965, Wheeler Shale and Marjum Formation, Utah (reconstruction modified from Robison, 1965). Repository: SZ: Narodni Museum, Prague. Abbreviations: AR, Axial Region; PER: Perforate Extraxial Region; IER: Imperforate Extraxial Region.

the devagination of the tegmen is only partial, and the aboral cup still contributes to a large part of the test. Consequently, the term "prototheca" is coined here, to describe tests characterised by a partial devagination of the tegmen and thus, intermediate in morphology between a calyx and a theca.

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# TAPHONOMY OF A STYLOPHORAN-DOMINATED ASSEMBLAGE IN THE LOWER ORDOVICIAN OF ZAGORA AREA (CENTRAL ANTI-ATLAS, MOROCCO)

Emmanuel Martin, Bertrand Lefebvre and Romain Vaucher

UMR CNRS 5276 LGLTPE, Université Lyon 1, 2 rue Raphaël Dubois, 69622 Villeurbanne cedex, France. emmanuel.martin@univ-lyon1.fr, bertrand.lefebvre@univ-lyon1.fr, romain.vaucher@univ-lyon1.fr

**Keywords:** Anti-Atlas, cornutes, Morocco, Ordovician, stylophorans, taphonomy.

## INTRODUCTION

Echinoderms are a major component of benthic communities in the Lower Ordovician of central Anti-Atlas (Noailles *et al.*, 2010; Van Roy *et al.*, 2010). In the Fezouata Shale (Tremadocian-late Floian), stylophorans (cornutes and mitrates) are the most diverse group of echinoderms (24 taxa). Until recently, however, stylophorans were considered as extremely rare fossils in the Lower Ordovician of this region. From 1959 to 1991, a single specimen was collected, despite intensive fieldwork performed by Jacques Destombes. This specimen was found at Destombes' locality 1685 (Fig. 1; latest Tremadocian to earliest Floian) and described by Chauvel (1971) as the holotype of *Thoralicystis zagoraensis*. This cornute was associated to a diverse benthic assemblage dominated by bivalves, gastropods and trilobites (e.g., *Asaphellus fezouataensis, Colpocoryphe thorali*), associated with brachiopods (e.g., *Paurorthis tadristensis*), conularians, crinoids (*Ramseyocrinus* sp.), glyptocystitid rhombiferans (*Macrocystella bohemica*), and hyolithids (Chauvel, 1969; Havliček, 1971; Donovan and Savill, 1988; Vidal, 1998).

In the last twelve years, successive field campaigns in the Lower Ordovician of the Zagora area confirmed that stylophorans are a minor component of high-diversity benthic assemblages dominated by arthropods and molluscs. Stylophorans, however, also occur in mass occurrences in densely packed, low-diversity assemblages, within some well-defined, thin horizons (Lefebvre, 2007; Lefebvre and Botting, 2007). For example, Lefebvre (2007) figured a slab containing numerous specimens of the cornutes *Cothurnocystis* sp. and *Galliaecystis* sp. (locality Z-F3, late Tremadocian, *A. murrayi* biozone; Fig. 1). Two distinct stylophoran beds were reported by Lefebvre and Botting (2007) at locality Z-F2(1) (late Tremadocian, *A. murrayi biozone*; Fig. 1): a *Thoralicystis*-dominated horizon and, about two meters above it, a *Peltocystis*-dominated level. Lefebvre (2007) suggested that stylophoran beds observed in the Fezouata Shale of Zagora area were showing taphonomic features characteristic of taphofacies E as defined by Brett *et al.* (1997) for echinoderms, and were thus associated with relatively deep environmental conditions (outer shelf, slope; see also Van Roy *et al.*, 2010). In contrast, Lefebvre and Botting (2007) suggested that stylophoran beds were possibly associated with much shallower environmental conditions, closer to normal wave base (echinoderm taphofacies C).

The aims of this paper are to describe a new stylophoran-dominated assemblage in the Lower Ordovician of the Zagora area and to discuss its associated palaeoenvironmental context. A taphonomic classification dedicated to stylophorans is proposed here for the first time thus describing the taphonomy of the new assemblage. Finally, all published occurrences of stylophorans in the Lower Ordovician of Zagora area (central Anti-Atlas, Morocco) are replaced in a new, refined biostratigraphic framework (Fig. 1B), based on field campaigns achieved in 2012-2014 (Martin *et al.*, in press).

## GEOLOGICAL CONTEXT

The Fezouata Shale (Tremadocian-late Floian) represents the basal member of the Outer Feijas Group (Tremadocian-mid Darriwilian), which corresponds to a shale-dominated interval comprised between the sandstones of the middle Cambrian Tabanite Group and the sandstone-dominated units of the First Bani Group (late Darriwilian-early Sandbian; Destombes *et al.*, 1985; Gutiérrez-Marco *et al.*, 2003). In Zagora area, the Fezouata Shale corresponds to a 1000 m-thick, monotonous succession of fine-grained siltstones. In this area, a detailed logging of the Fezouata Shale and of the overlying Zini Formation (latest Floian) was achieved through a series of field campaigns organized between 2012 and 2014. Sedimentary structures typical of storm deposits (e.g., ripple marks, hummocky cross-stratification) were observed repeatedly, at different scales in all parts of the Lower Ordovician succession (Martin *et al.*, in press). Consequently, the general depositional context of the Fezouata Shale more likely corresponds to relatively shallow conditions (lower shoreface), at or above storm-wave base (Lefebvre and Botting, 2007; Martin *et al.*, in press), rather than to a deep, outer shelf setting (Lefebvre, 2007; Van Roy *et al.*, 2010; Gaines *et al.*, 2012).

Moreover, the detailed analysis of both graptolite and acritarch assemblages collected in the last twelve years in Zagora area offered the opportunity to better constrain the biostratigraphic framework of the Fezouata Shale (Martin *et al.*, in press). In this revised biostratigraphic scheme, most deposits formerly interpreted as early to mid Floian in age are now assigned to the *Hunnegraptus copiosus* biozone (latest Tremadocian). In Zagora area, all described occurrences of stylophoran-dominated beds in the Fezouata Shale are restricted to the *A. murrayi* biozone (late Tremadocian; Fig. 1B).

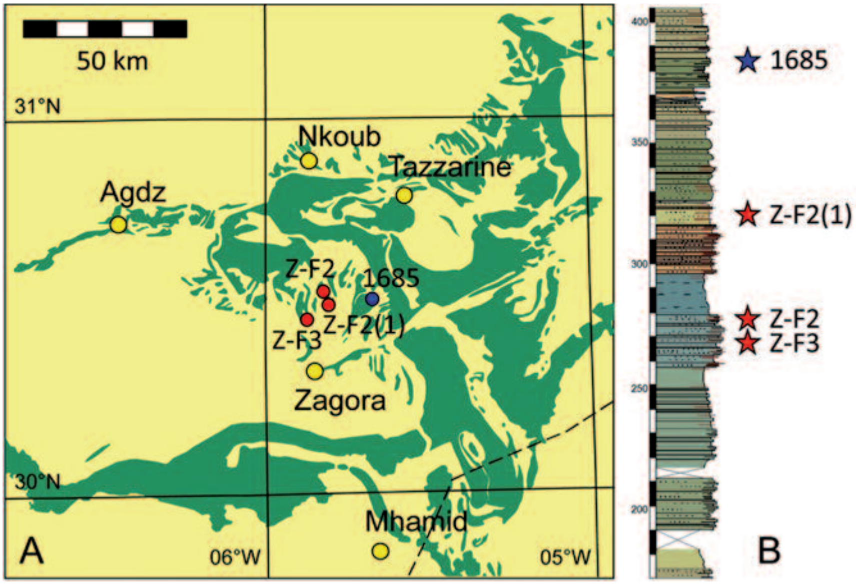

**Figure 1.** Location and stratigraphic positions of all stylophoran occurrences described in the Lower Ordovician of Zagora area. A. Simplified geological map of central Anti-Atlas, Morocco. Ordovician outcrops are indicated in green. B. Partial log of the Lower Ordovician succession in Zagora area (interval comprised between 170 and 405 m above the unconformity between the Tabanite Group and the Fezouata Shale) showing the stratigraphic positions of stylophoran beds (in red) and stylophorans occurring within diverse benthic assemblages (in blue). Z-F3: locality NE of Beni Zoli village (Lefebvre, 2007); Z-F2: Jbel Tizagzaouine (new assemblage); Z-F2(1): locality S of Jbel Tizagzaouine (Lefebvre and Botting, 2007); 1685: type-locality of *Thoralicystis zagoraensis* (Chauvel, 1971).

The new stylophoran-dominated assemblage reported here was collected from a single, thin, lens-shaped layer of beige siltstones at locality Z-F2, along the very steep slopes forming the eastern flank of Jbel Tizagzaouine. This site is located about 11 km NE of the village of Beni Zoli and 21 km N of Zagora, in the western part of the Ternata plain (W of Jbel Bou Dehir; Fig. 1A). The stylophoran bed was entirely quarried out in 2002-2003. This small lens yielded extremely abundant specimens of cornutes (over 500 individuals), all of them belonging to the same, yet undescribed species. One specimen of this large cornute from Jbel Tizagzaouine was reported as "undescribed Tremadoc boot-shaped form" and figured by Ware and Lefebvre (2007, p. 784, fig. 5.1-2). In Z-F2, the monospecific stylophoran assemblage is associated to a low diversity, depauperate fauna comprising fragments of large trilobites (Fig. 2H), along with rare articulate brachiopods, relatively common graptolites (e.g., *Paradelograptus norvegicus*) and, locally, clusters of tiny gastropods (Fig. 2C). The graptolite assemblage observed in locality Z-F2 suggests a late Tremadocian age for this level (*A. murrayi* biozone; Fig. 1B).

## MATERIAL AND METHODS

The excavation of the Z-F2 stylophoran bed in 2002-2003 yielded 300 specimens (rock samples) containing more than 500 individuals belonging to the same undescribed species of large cornute (Fig. 2). Study material is deposited in the collections of the following public institutions: Cadi-Ayyad University, Marrakesh, 190 specimens (AA.JTZ.OI.1-6, AA.JTZ.OI.11-194), Musée des Confluences, Lyon, 9 specimens (ML20.269238-246), and Muséum d'Histoire naturelle, Nantes, 101 specimens (MHNN.P.045197-297). During fieldwork, sampling was performed as exhaustively as possible: all fossiliferous pieces of rock were collected, even those containing fragmentary, disarticulated material. A sampling bias towards better-preserved, fully articulated specimens is, however, likely. Indeed, minute isolated skeletal elements are less eye-catching, and the possibility that they were under-sampled cannot be excluded.

## TAPHONOMY

Five taphonomic groups are defined here for stylophorans, based on the quality of preservation of the specimens. Similar taphonomic classifications have been already proposed for helicoplacoids (Dornbos and Bottjer, 2001) and ophiuroids (Zatoń *et al.*, 2008).

Group 1 includes all cornute specimens with (1) their distal aulacophore preserved, with cover plates articulated (or in close contact) to underlying ossicles; (2) their proximal aulacophore; and (3) a complete to slightly disarticulated theca. Cover plates are extremely delicate skeletal elements protecting the food groove of stylophorans (Ubaghs, 1968; Lefebvre, 2003). In cornutes, their preservation requires the rapid burial of live, *in situ* organisms (Lefebvre, 2007). Unlike cornutes, mitrates had the possibility to flex their distal aulacophore, so as to close their cover plates and thus protect their food groove in case of physical disturbance and/or danger (Parsley, 1988; Lefebvre, 2003). In mitrates, the recurved, distress position of the aulacophore greatly enhances the preservation potential of cover plates. Consequently, group 1 only includes mitrates preserved in life position, i.e. with their distal aulacophore held in extended position, over the sea floor (see e.g., Parsley and Gutiérrez-Marco, 2005; Lefebvre and Botting, 2007).

Group 2 corresponds to cornutes with (1) only their brachials (stylocone, ossicles) preserved (cover plates absent); (2) their proximal aulacophore; and (3) a complete to slightly disarticulated theca. In mitrates, group 2 includes all specimens with their distal aulacophore (brachials and cover plates) preserved in flexed, distress position.

Group 3 comprises stylophorans with (1) no distal aulacophore; (2) a complete or more or less dissociated proximal aulacophore; and (3) a complete to partly disarticulated theca.

Group 4 is defined for more or less strongly disarticulated stylophoran thecae, with no aulacophore articulated to them.

Group 5 is proposed for dissociated skeletal elements.

## TAPHOFACIES

Three distinct types of preservation (taphofacies) can be identified in the stylophoran bed of locality Z-F2. The first taphofacies is restricted to the lowermost part of the lens, which consists in a thin, irregular layer (0-3 mm in thickness) of coarse siltstones. This level contains abundant isolated skeletal elements of cornutes (taphonomic group 5; Fig. 2G-

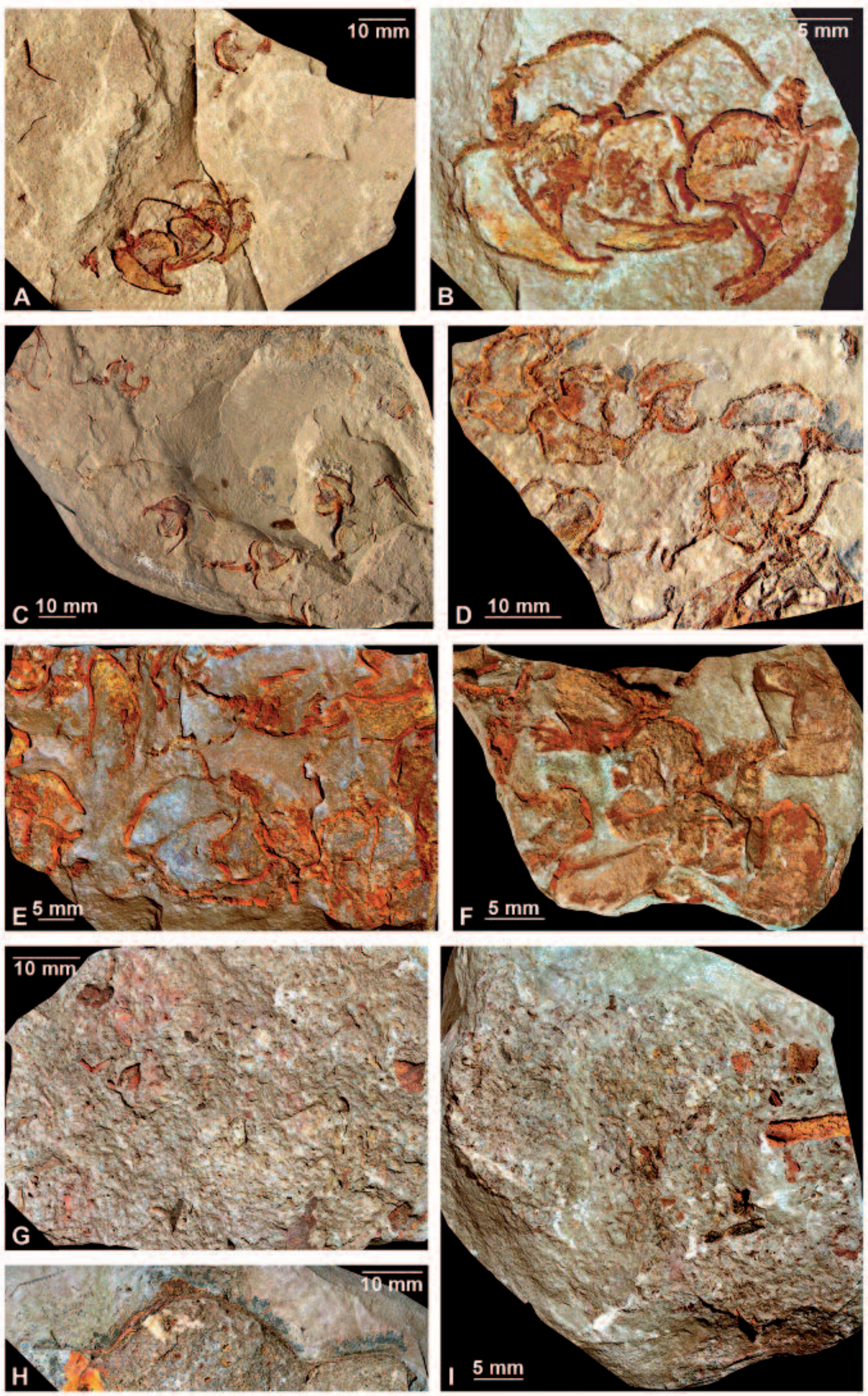

**Figure 2.**

I), sometimes sheltered under large pieces of disarticulated trilobites (Fig. 2H). The second taphofacies is observed in the overlying, thicker, irregular layer (2-5 mm in thickness) of finer siltstones. This horizon corresponds to a dense accumulation of hundreds of cornutes, piled on top of each other (Fig. 2D-F). In this level, individuals do not exhibit any preferential orientation, and about half of the specimens are upside-down. Most cornutes can be assigned to taphonomic group 2, although some individuals belonging to groups 1 and 3 are also present. The third taphofacies occurs in the overlying, thick, upper part of the stylophoran bed (10-30 mm in thickness), which consists in very fine siltstones. This level has yielded scattered, well-preserved specimens of cornutes, frequently associated with graptolites and clusters of tiny gastropods (Fig. 2A-C). In this layer, most individuals belong to taphonomic group 2. Specimens do not show any preferential orientation, and only a few cornutes are upside-down (Fig. 2B).

## CONCLUSIONS

In their taphonomic classification of echinoderms, Brett *et al*. (1997) identified three main groups, based on the resistance of their skeleton to disarticulation. In this scheme, stylophorans belong to type 1 echinoderms (i.e., taxa characterized by loosely articulated skeletal elements; Brett *et al*., 1997; Lefebvre, 2007). Experimental taphonomic studies on extant type 1 organisms (e.g., ophiuroids) indicate that their skeleton entirely disarticulates within a few days after death (Schäfer, 1972; Allison, 1990; Donovan, 1991). Freshly killed specimens of type 1 echinoderms, however, can endure high-energy conditions without severe disarticulation (Kerr and Twitchett, 2004; Gorzelak and Salamon, 2013). Consequently, the preservation of hundreds of exquisitely preserved specimens of cornutes in locality Z-F2 requires exceptional environmental conditions. The available sedimentological evidence (e.g., scoured bioclastic lag at the base of the lens, fining upward lithology) and the geological context of the Fezouata Shale (shallow deposits at or above storm wave base) both strongly suggest that the stylophoran bed of Jbel Tizagzaouine represents a storm deposit (taphofacies IIC of Brett *et al*., 1997). The local accumulation of hundreds of specimens of cornutes very likely results from distal storm scour and redeposition of a para-autochtonous, monospecific community.

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**Figure 2.** Different types of preservation in the stylophoran bed of locality Z-F2 (Jbel Tizagzaouine, Zagora area), Lower Ordovician (late Tremadocian, *A. murrayi* biozone). All photographs show original specimens. A-C. Isolated cornutes in uppermost part of fossiliferous layer. A-B. MHNN.P.045281. A. Large slab showing four complete individuals and a few isolated skeletal elements. B. Cluster of three specimens: two of them are in lower aspect, one is in upper aspect. C. Large slab showing six complete individuals (all in lower aspect), associated with portions of other specimens, isolated plates, and numerous poorly preserved tiny gastropods, MHNN.P.045296. D-F. Accumulation layer full of complete cornutes. D. AA.JTZ.OI.5. E. AA-JTZ-OI-50. F. AA-JTZ-OI-14. G-I. Bioclastic lag at base of stylophoran bed. G. AA-JTZ-OI-50. H. MHNN.P.045295. I. AA-JTZ-OI-34. Repositories: Cadi-Ayyad University, Marrakesh (AA), Muséum d’Histoire naturelle, Nantes (MHNN).

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# ACROTHORACIANS BARNACLES ON PENNSYLVANIAN CRINOIDS FROM THE MOSCOW REGION

Georgy V. Mirantsev

Borissiak Paleontological Institute, Russian Academy of Sciences, 117647, Profsoyuznaya st. 123, Moscow, Russia.
gmirantsev@gmail.com

**Keywords:** Acrothoracica, crinoids, paleoecology, Carboniferous, Moscow Region.

## INTRODUCTION

Traces of acrothoracian barnacles are generally preserved on various fossil marine invertebrates (molluscs, corals, echinoderms) and are easily identified by their characteristic elongated, oval to pear shape borings. The Mesozoic records of acrothoracian borings on echinoderms are well known in the literature. In most cases, however, these borings are post-mortem and represent the traces of bioerosion in dead skeletons (e.g. Zamora *et al.*, 2008; Wilson *et al.*, 2014). Seilacher (1969) proposal that some acrothoracian borings in irregular echinoids associated with ambulacral pores demonstrate a commensal association has been viewed with scepticism in later publications (Bromley, 1970; Donovan and Jagt, 2013). The Paleozoic records of acrothoracian borings on echinoderms, in particular on crinoids, are rare and have not been published in detail. Acrothoracian borings on Permian crinoid stems from the Cis-Ural region of Russia were mentioned by Arendt (1970, 1985) but not figured. Rozhnov suggested that the ornamentation in *Pisocrinus ornatus* could be the post-mortem settlement of acrothoracid barnacles (Rozhnov, 1981). Finally, Chesnut and Ettensohn (1988) figured some borings on wing plates of the Mississippian crinoid *Pterocrinus*, also suggesting that these borings were post-mortem in origin.

Reliable evidence of relationships between living crinoids and acrothoracian barnacles in the Palaeozoic is still lacking in the literature. The newly collected specimens of crinoids from the Upper Carboniferous (Pennsylvanian) deposits of the Moscow region presented here shows evidence of live crinoid-acrothoracid interactions.

## DESCRIPTION OF THE SPECIMENS

Both studied specimens belong to the same genus and species of an undescribed advanced cladid crinoids belonging to the family Graphiocrinidae Wachsmuth and Springer, 1886. The specimens were collected in the middle member of the Neverovo Formation (Kasimovian, Pennsylvanian) at the Afanas'evo quarry, Moscow Region (Goreva *et al.*, 2009).

The first specimen (PIN Nº 5450/44) is a cup with proximal parts of arms (Fig. 1). There are numerous (more than 80) borings on the preserved portions of arms. The borings are situated on brachials only; there are no traces of borings on cup plates. All borings are small, oblong, oval, show a length range from 0.29 to 0.43 mm and width range from 0.09 to 0.17 mm; some borings are slightly round. The second specimen (PIN Nº 5450/50) is more complete (only the distal parts of arms are missing). There are considerably fewer borings and the borings are less pronounced than in the first specimen. The borings are also situated in all rays, mostly on the lateral surface of brachials (primibrachials and proximal secundibrachials).

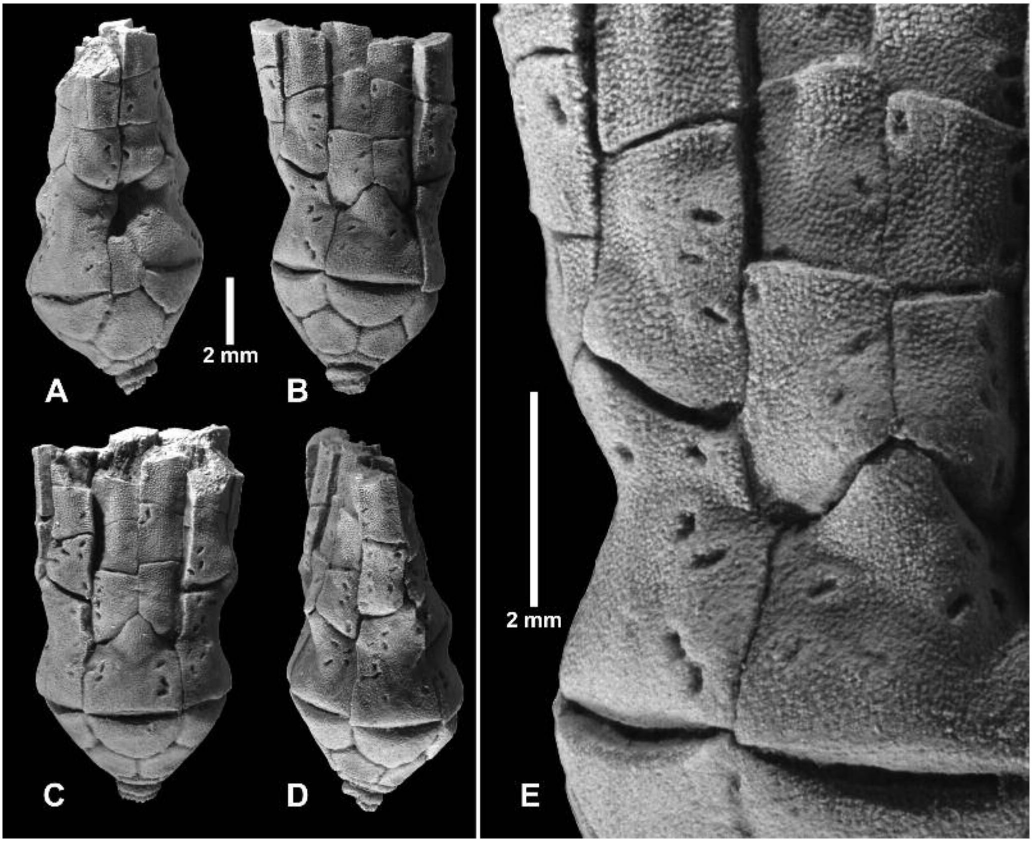

**Figure 1.** Crown of an undescribed graphiocrinid crinoid with a numerous borings of acrothoracian barnacles (PIN Nº 5450/48). A. CD-view; B. B-ray view; C. E-ray view; D. A-ray view; E. close up of b, showing the details of acrothoracian borings. Neverovo Formation (Kasimovian, Pennsylvanian), Afanas'evo quarry, Moscow Region.

## DISCUSSION

The evidence of living crinoid-acrothoracian interactions in these specimens is provided by the location of borings around the whole crown in all rays and in all preserved brachials, and by the stereom "blisters" near the borings. In addition, the specimens were found in a tempestite layer as the articulated brachials indicate that both specimens were buried alive.

Both specimens show similar arrangement of borings; near the lateral surface of brachials. Some borings are located directly on the outer edges of arms. This arrangement of holes could explain the nature of these crinoid-acrothoracian interactions. It seems that acrothoracians were commensals of crinoids and exploited the benefit of their position. Thus food particles coming from the water current to the aboral side of crinoid filtration fan were captured partly by crinoid tube feet and partly by barnacles.

The taxonomic position of these borings is uncertain. Various authors attributed Paleozoic acrothoracian borings to different ichnogenera including *Bascomella* (Alekseev, 2001), *Rogerella* (Sumrall *et al.*, 2006), *Zapfella* (Baird *et al.*, 1990) and others. All of these ichnogenera, however, do not differ significantly from each other and could be synonymised in the future. Unlike most other Carboniferous acrothoracian borings, the borings in the studied specimens are proportionally shorter and three to four times smaller. These specific size relationships could be explained by the small size of host.

Besides these two specimens, there are no further traces of acrothoracian borings among the numerous specimens of Pennsylvanian crinoids from this and other formations in the Moscow Region. It is interesting that in both cases the borings were associated with the same species of crinoid.

The borings of acrothoracian barnacles were also observed on brachiopods and corals (Alekseev, 2001) and also common in euomphalids and *Platyceras* from the Upper Carboniferous deposits of the Moscow Region. Some bored specimens of *Platyceras* are attached to crinoid *Cromyocrinus simplex* and were buried alive. This indicates that acrothoracian borings in these cases were made during the life of the gastropod. Many specimens, however, lack traces of "healings" of these borings. Thus the shells of *Platyceras* were bored during their settlement on a crinoid. Clear traces of acrothoracian borings are absent on dorsal cups of *Cromyocrinus*. Sometimes there are some poorly defined traces of borings with an acrothoracian like shape on cup plates near *Platyceras* attachment. Such peculiar acrothoracian-platyceratid associations were described by Baird *et al*. (1990). The absence of borings in *Cromyocrinus* and presence on the shells of attached *Platyceras* could be explained by the presence of a crinoid epidermis which prevented the settlement of acrothoracian larvae. Nevertheless, in some small crinoids with a thin epidermis such as in the described graphiocrinids, acrothoracians could still easily settle.

## CONCLUSIONS

The first reliable association of acrothoracians with echinoderms are described. Studied specimens strongly support the previously proposed idea that acrothoracian barnacles could bore into the skeletal of living hosts (e.g. Seilacher, 1969). These associations can thus be considered as an example of commensalism.

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# REGENERATION IN PENNSYLVANIAN CRINOIDS FROM THE MOSCOW REGION

Georgy V. Mirantsev

Borissiak Paleontological Institute, Russian Academy of Sciences, 117647, Profsoyuznaya st. 123, Moscow, Russia.
gmirantsev@gmail.com

**Keywords:** Crinoids, regeneration, Carboniferous, Pennsylvanian, Moscow Region.

## INTRODUCTION

Crinoids, as well as most other echinoderms, have a high regenerative potential. The fossil record of crinoid regeneration has been recently summarized by Baumiller and Gahn (2003), Gahn and Baumiller (2005, 2010), and Oji (2001). Specimens with regenerating body parts have been identified among numerous Upper Carboniferous (Pennsylvanian) crinoids from the Moscow Region. Here, some new data on the regenerative abilities of some of the Moscow Region crinoids are presented.

## ARM REGENERATION

Arm regeneration has been found in nearly all species of Pennsylvanian crinoids from the Moscow Region that are preserved with complete or nearly complete crowns. These include cladid taxa, such as *Aesiocrinus*, *Apographiocrinus*, *Cromyocrinus*, *Mooreocrinus*, *Moscoviocrinus*, *Pegocrinus*, *Trautscholdicrinus*, *Ulocrinus*, and the flexible *Neotaxocrinus*. It is difficult to give any data about the regeneration frequency (as it was given for Mississippian Le Grand crinoid community; Gahn and Baumiller 2005) because complete crowns of Pennsylvanian crinoids are rare. However, the detailed analysis of some particular Pennsylvanian crinoid communities in the Moscow Region with common nearly complete crinoid crowns (e.g. Myachkovian assemblages) can provide data about regeneration frequency.

Regenerated arms are easily recognized by their smaller size and shape (Fig. 1A), although complete regeneration makes them indistinguishable from non-regenerated arms. In most of the studied specimens that show regeneration, regeneration characterizes multiple, adjacent arms. Some specimens show arm regeneration from the most proximal brachials or even from the radial plate facets, and in these specimens adjacent arms may show no traces of regeneration. In one specimen of *Aesiocrinus* sp. (PIN, Nº 3678/517; Fig. 1B, C), all 10 arms are regenerating and all do so at the same level from IIBr-4; Baumiller (2008) figured a similar example which also belongs to the same genus. These specimens suggest that the predatory attack may have occurred while the crinoid crown was in cone-like, non-feeding posture, with all arms closed over the tegmen.

## REGENERATION OF THE ANAL SAC

Lane (1984) proposed that large anal sacs found among some cladid crinoids served to accommodate gonads. Regenerated anal sacs may thus represent evidence of predation on crinoid gonads. In one adult specimen of a cladid crinoid *Parasciadiocrinus lancetospinosus* (PIN, Nº 5450/244) one half of the anal sac is regenerated. Large

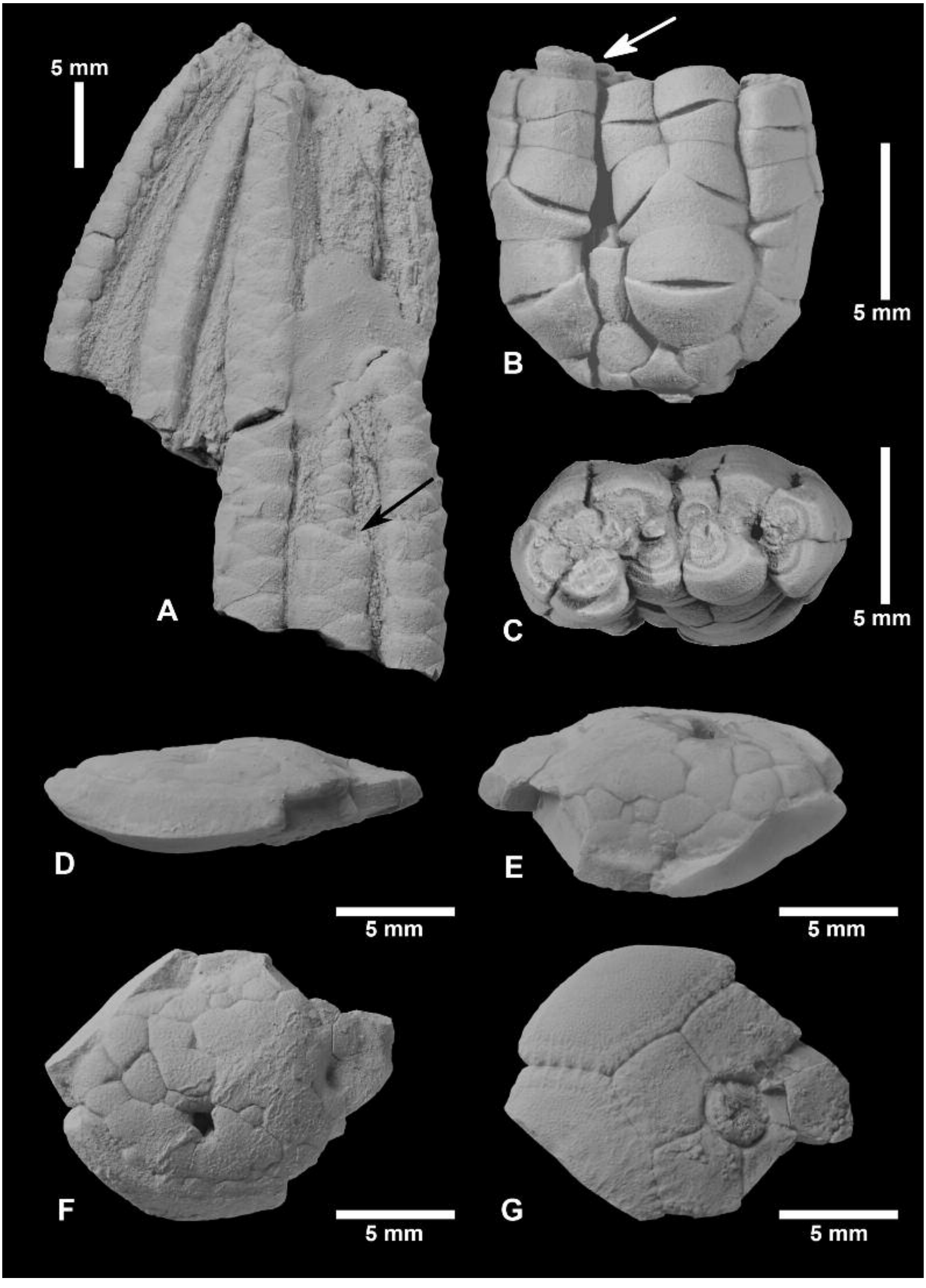

**Figure 1.**

hypertrophied mushroom-shaped anal sacs are typical for this species. Although the *P. lancetospinosus* specimen is slightly deformed, regeneration can be identified by presence of smaller tegmen plates in the regenerated area as well as by small marginal spines in the peripheral ring that are not laterally compressed as in the normal part of the tegmen.

## FILLING PLATES

A partly preserved cup of *Dicromyocrinus subornatus* (PIN, Nº 5362/80) illustrates the process of the filling plate recovery (Fig. 1D-G). This non-regenerative repair was previously reported in various Paleozoic crinoids by Gahn and Baumiller (2010). However in the previously described cases of such recovery, most of the crown was intact, whereas in this example of *D. subornatus* all arms as well as radials, anal plates and most of basal plates are missing, perhaps removed by the predator. Both of the preserved basal plates were broken off and their edges were healed (Fig. 1D-E) and the oral side of the cup is covered by numerous small polygonal filling plates. The positioning of the plates is highly irregular. There may have been a small cavity between cup plates and filling plates; a small opening can also be seen in the center on the oral side of the cup. It is interesting to note that previous examples of crinoids with nearly the same lost parts have been published (Springer, 1920; Amemiya and Oji, 1992) and they suggest crinoids may be capable of regenerating the whole crown.

## CONCLUSIONS

The described specimens expand our knowledge of regeneration in Palaeozoic crinoids. It seems that various groups of Paleozoic crinoids had different regenerative abilities. Differences in the possibilities of the crown regeneration described here and stem regeneration (see regeneration in articulate crinoids and in a flexible crinoid *Euonychocrinus simplex* (Strimple and Frest, 1979) and filling plates on a cladid *Ancyrocrinus bulbosus* (McIntosh and Schreiber, 1971)) show that with similar injuries modern articulate crinoids and even Paleozoic flexible crinoids could able to regenerate more body parts than cladid crinoids. It seems that most of the described specimens of crinoid regenerations are associated with predation.

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**Figure 1.** A-C. Arm regeneration, arrow indicate regenerated arms (A, *Ulocrinus neverovoensis* (PIN, Nº 137/29); B, C. *Aesiocrinus* sp. (PIN, Nº 3678/517) side and top view); D-G. *Dicromyocrinus subornatus*, filling plate recovery (PIN, Nº 5362/80), D, E. Leteral views; F. Oral view; G. Aboral view.

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# PALAEOECOLOGY OF *ASCOCYSTITES*-DOMINATED ASSEMBLAGES (ECHINODERMATA, BLASTOZOA, EOCRINOIDEA) FROM THE UPPER ORDOVICIAN OF THE MOROCCAN ANTI-ATLAS

Elise Nardin[1] and Serge Régnault[2]

[1] Geosciences Environnement Toulouse, Observatoire Midi-Pyrénées, CNRS, 31400 Toulouse, France. elise.nardin@get.omp.eu
[2] Muséum d'Histoire naturelle, 12 rue Voltaire, 44000 Nantes, France. serge.regnault@mairie-nantes.fr

**Keywords:** Blastozoa, Eocrinoidea, Ascocystites, palaeoecology.

## INTRODUCTION

The strata of the Ouine-Inirne and Izzeguirene formations (1st Bani Group, Mid-Upper Ordovician) from the Tizi n'Tanekfoult area (central anti-Atlas, Morocco) and the Jbel Tijarfaïouine (eastern Anti-Atlas Morocco), respectively, have yielded abundant material of echinoderms, conularids, eldonioids, palaeoscolecid worms, cheloniellid arthropods, and trilobites (Samuelsson *et al.*, 2001; Gutiérrez-Marco *et al.*, 2003; Lefebvre *et al.*, 2007, 2008, 2010; Régnault, 2007; Hunter *et al.*, 2007; Corbacho, 2011; Sumrall and Zamora, 2011; Gutiérrez-Marco and García-Bellido, in press). The two formations show successive units composed of intercalations between silty mudstones, fine- to medium-grained muddy sandstone beds and coarse-grained sandstones (Destombes *et al.*, 1985). In the Jbel Tijarfaïoune locality (Izzeguirene Formation), each sand unit show erosive bases, indicating abrupt channel infillings topped by fine-grained ripples-marked sandstones beds and mudstones deposited in lower energy environment (Corbacho, 2011). In the Tizi n'Tanekfoult locality, similar but coarser alternations occur in the Ouine-Inirne Formation (Marante, 2008). Fossiliferous accumulations are found in the sandstones units in both sites. Fossiliferous slabs show no apparent bioturbation and are composed of alternations of pinkish coarse- and greyish fine-grained laminas. Depositional environment of fossiliferous beds seems to correspond to a low-energy wave-dominated mid to proximal ramp.

Eocrinoid ascocystitids are typical for the Mid-Upper Ordovician of the Mediterranean Province (Barrande, 1887; Régnault, 1990, 2007; Young and Donovan, 1993; Lefebvre *et al.*, 2007, 2008, 2010; Makhlouf *et al.*, 2014). This genus is characterized by robust brachioles borne by curved ambulacra embedded in the thecal surface. The theca is composed of hundred of small polygonal plates showing varied ornamentation, such as small granules, longitudinal ridges or star-like network of ridges (Fig. 1B, D). The holomeric stem is proximally bimorphic and becomes unimorphic and slender distally (Fig. 1B).

The abundant Moroccan material is composed of specimens of varied sizes and preservation states. In addition to the opportunity to precise the morphology and biogeography of *Ascocystites*, the study of the Moroccan material will provide information about the growth and the ecology of well-preserved assemblages. The purpose of this contribution is to distinguish the modes of preservation of the different assemblages and their ecology.

The material referred to in this paper is deposited in the following public institutions: Muséum d'Histoire naturelle de Marseille (MHNM), Muséum d'Histoire naturelle de Toulouse (MHNT), Université Claude Bernard – Lyon 1 (FSL).

## PRESERVATION AND TAPHOFACIES

The abundant available material from the Jbel Tijarfaïouine has been collected in several levels. It mostly corresponds to (pluri)decimetric slabs, allowing the investigation of both the preservation of each individual and the organisation of the specimens on the slab. All specimens are preserved horizontally to the bedding plane. The classification of the different preservation state of crinoids and blastoids, proposed by Meyer *et al.* (1989), has been adapted for the Moroccan eocrinoids material:

i. Complete theca with brachioles and column attached (Fig. 1D).
ii. Complete theca with brachioles and only proximal stem attached (Fig. 1B).
iii. Fragmented theca with brachioles but no column attached (Fig. 2B, D).
iv. Fragmented theca with (partial) column attached and no brachioles (Fig. 2A).
v. Fragmented and disarticulated theca with brachioles but no column attached (Fig. 1C).

Preservation patterns (taphofacies) for the Jbel Tijarfaïouine material can be established based on the observation of both the preservation of individual specimens (articulation, fragmentation, abrasion) and the assemblage characteristics (size sorting, orientation):

Taphofacies A. Isolated specimens (juvenile-like or adult-like size) in at least a 100cm$^2$ surface. Specimens are flattened or slightly compressed, mostly complete (Fig. 1D), and show various preservation states (mostly state I, but also states iii and v; Fig. 1C).

Taphofacies B. Bunches of small and/or large specimens at a concentration of at least 10 small and 5 large specimens over a 100cm$^2$ surface. Specimens tend to be flattened, abraded, superimposed and randomly distributed (Fig. 2B-C). Their preservation state ranges from state i to state iv. Sandstone grain-size ranges from fine to moderate.

Taphofacies C. Clusters of specimens in loose concentration (no or slight superimposition). Specimens are in majority adult-sized but few juvenile-size specimens can also co-occur. All specimens are relatively well preserved

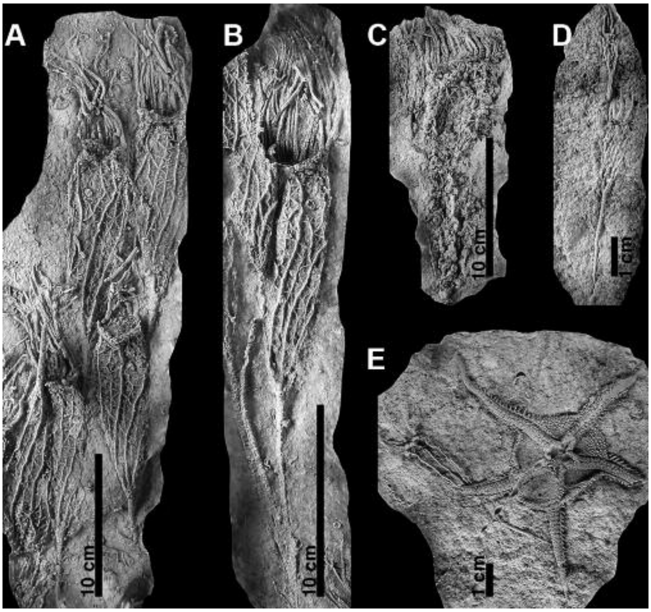

**Figure 1.** Photographs from latex casts of *Ascocystites* sp. (Izzeguirene Fm, Upper Ordovician; Bou Nemrou, Morocco). A. Concentration of aligned specimens (MNHT-PAL-2014-2a-e). B. Complete adult-like specimen (MHNT-PAL-2014-2-f). C. Slightly disarticulated specimen (MHNM-15406.32). D. Juvenile-like specimen (MHNM.15406.31). E. Example of co-existence of an ophiuroid sp. indet. and a juvenile-like specimen of *Ascocystites* (MHNM-15406.20). Casts are whitened with $NH_4Cl$.

(states i to iii), aligned according two directions (with an angle less than 30°). Associated fauna corresponds to ophiuroids with arms mostly complete and sometimes aligned in the same direction as the eocrinoids (Fig. 2D).

Taphofacies D. Aggregations of specimens in relatively high concentration. Specimens slightly compressed, not abraded, unidirectionally aligned and partially superimposed (Fig. 2A). They are distributed in two ranges of size, adult-size (longer than 10 cm) or juvenile-size (less than 5 cm). They are well preserved in majority (state i and sometimes state ii). The large specimens show exquisite morphological details, such as the anal pyramid and various types of ornamentation (from granules to tertiary ridges). Associated fauna can be composed of mitrates with outstretched aulacophore or ophiuroids with complete arms (Fig. 1E). Some specimens show apparent complete stem (with distal ossicles less than half millimetre in diameter). Flattened and abraded specimens can also occur within these aggregations, but they differ in their orientation. A variation of this taphofacies is composed of loosely concentrated small specimens (4-7 specimens per 100cm$^2$), with the same characteristics.

Material from the Tizi n'Tanekfoult area available for this study is less abundant, mostly fragmented. It is composed of juvenile-size and flattened specimens, showing details on the anal pyramid or the internal side of the oral surface. The patterns of preservation might be associated to the taphofacies C or D as defined on the material from the Jbel Tijarfaïouine (preservation states i to ii).

## BIOSTRATINOMIC PROCESSES

Due to the fragility of its thecal plating, *Ascocystites* is be classified among the type 1 echinoderms, as well as the associated mitrates and ophiuroids (Brett *et al.*, 1997). The theca of *Ascocystites* is composed of dozens to hundreds of weakly articulated embedded within the epidermis. Brachioles are robust and large, whereas the stem ossicles are thin. The propensity to decay and post-mortem disarticulation of *Ascocystites* would lead to their rarity in normal burying condition or after long transportation in relatively high-energy conditions (Brett *et al.*, 1997). Recent experimental study of Gorzelak and Salamon (2013) suggests the initiation of partial disintegration of distal ophiuroid arms and of dismemberment of distal crinoid arms as pinnules after few hours corresponding to a short transport. Abrasion starts after ~36 km of transportation while arm/disc disarticulation and split amplify though time/distance (up to 192h, ~96km). Complete disintegration of ophiuroid disc and disarticulation of crinoid cup occur much later (360h, ~180km).

The different states of preservation found in the Moroccan material of *Ascocystites* can reveal information about the biotratinomic processes affecting them, and their palaeoecology. Taphofacies A and B can be considered as allochtonous. They show evidence of moderate to long post-mortem exposure on the sea bottom and then rapid burial and turbulent transportation. The taphofacies C shows aligned well-preserved specimens in relatively poor concentration, suggesting relatively short transportation of moderate energy. The fossil assemblage C might be considered as para-autochtonous to allochtonous. The taphofacies D shows exquisitely preserved complete specimens, organised in high concentration. No echinoderm holdfast has been identified close to the specimens. The absence of bioturbation and the excellent preservation (no abrasion, skeletal completeness etc.) of the eocrinoids, mitrates, and ophiuroids specimens suggest a rapid burial and/or a transport either absent or limited to a short distance (less than 2 hours according to the study of Gorzelak and Salamon (2013)). Therefore the taphofacies D might be considered as autochtonous, formed by obrution deposits, *sensu* Brenchley and Harper (1998) and those aggregations may not be a simple taphonomic artefact, as already suggested by Lefebvre *et al.* (2008, 2010) for some slab samples.

## PALAEOECOLOGICAL SIGNIFICANCE

Co-existence of numerous aggregated well-preserved specimens in the taphofacies D (and in a minor extent in the taphofacies C of the Jbel Tijarfaiouïne and of the Tizi n'Tanekfoult localities) would suggest that the *in situ* populations of *Ascocystites* sp. experimented gregarious settlement, before transportation (Fig. 1A). Joint presence of young and adult individuals might suggest that gregariousness may have provided advantages for breeding and/or for the protection of the post-larval growing individuals (Pawlik, 1992).

No particular structure seems to occur at the end of the stem. Moreover the small diameter of the distal stems might indicate that the presence of an anchoring structure in *Ascocystites* is unlikely. *Ascocystites* individuals probably rested standing up, with the stem partly inserted in the soft substrate. In addition the robustness, the curvature and

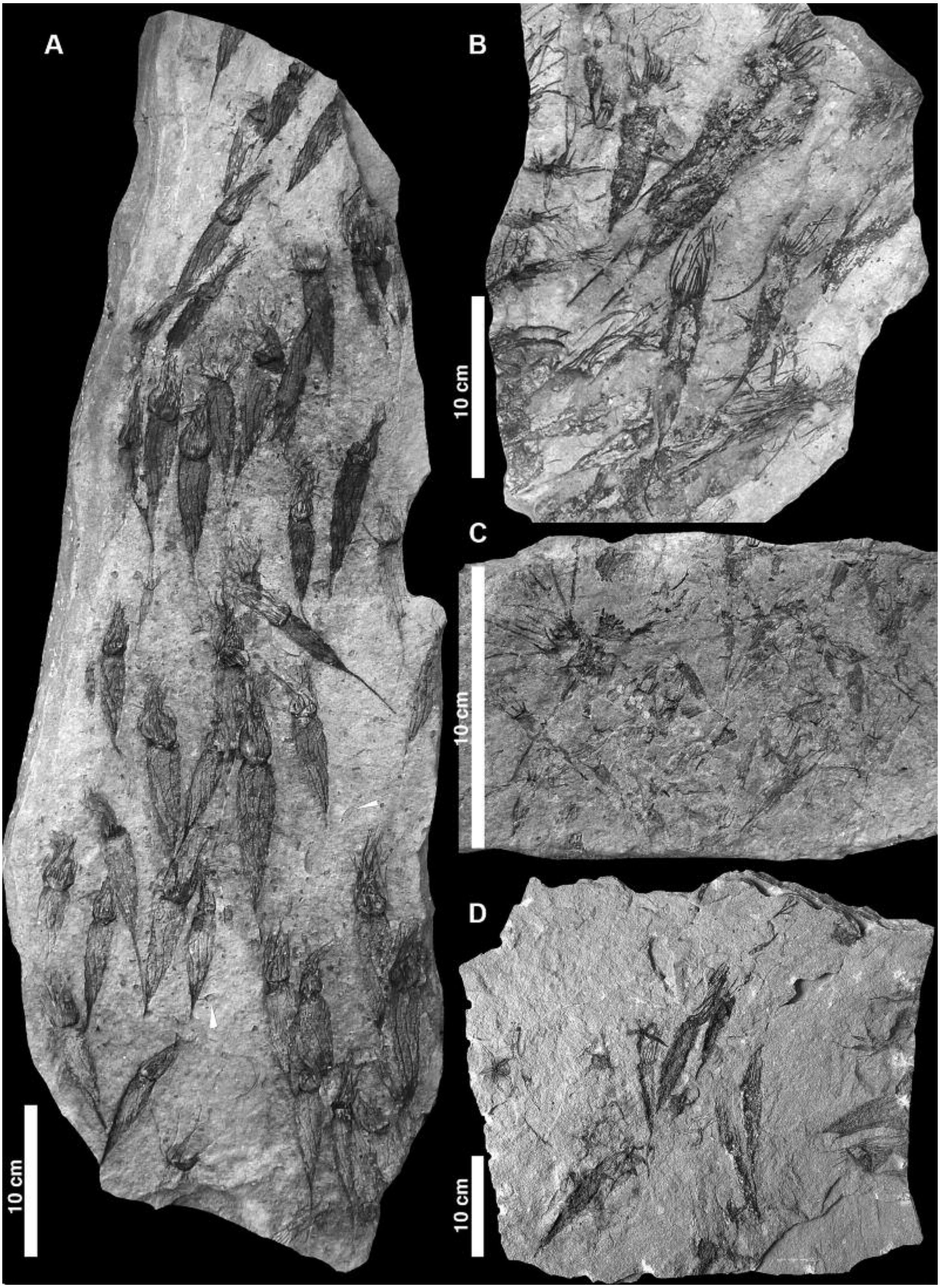

**Figure 2.**

the flexibility of the proximal brachiolar plates may suggest that they might have been able to crawl to escape predation or environmental disturbance (Baumiller and Messing, 2007).

Mitrates, ophiuroids and eocrinoids are epibenthic feeders, occupying different tiering and trophic levels. The filter-feeder *Ascocystites* ranges up to 30 cm above the sediment-water interface, whereas the two others represent the lowest tiers (<2cm). The three groups seem to occupy various ecospace poles and therefore prevent direct competition. However the frequent close association between large ophiuroid and juvenile-like *Ascocystites* individuals (Fig. 1E) may suggest of a predatory behaviour of the ophiuroids on the eocrinoids.

## Acknowledgements

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**Figure 2.** Photographs of fossiliferous slabs (Izzeguirene Fm, Upper Ordovician; Bou Nemrou, Morocco). A. Aligned well-preserved specimens coexisting with mitrate stylophorans (arrows) (MHNT-PAL-2014-2). B. Disorganised combination of juvenile-like and adult-like specimens (MHNT-PAL-2005-0-159). C. Unorganised accumulation of badly preserved juvenile-like specimens (FSL-424-873). D. Association of well-preserved ophiuroids, juvenile-like and adult-like specimens organised in two preferential directions (MHNM-15406-39-2).

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# ECHINOID ASSEMBLAGES FROM THE MIOCENE OF SARDINIA: A TOOL FOR RECOGNIZING FAUNAL DIVERSITIES, DEPOSITIONAL ENVIRONMENTS AND PRESERVATION POTENTIALS

James H. Nebelsick[1] and Andrea Mancosu[2]

[1] Institut für Geowissenschaften, Universität Tübingen, Sigwartstraße 10, D-72076 Tübingen, Germany.
nebelsick@uni-tuebingen.de
[2] Dipartimento di Scienze Chimiche e Geologiche, Università degli studi di Cagliari, Via Trentino 51, 09127 Cagliari, Italy.
andrea.mancosu@gmail.com

**Keywords:** Echinoids, Palaeoecology, Taphonomy, Miocene, Sardinia.

## INTRODUCTION

Echinoids provide excellent possibilities for applying the functional morphology of skeletal features to interpret modes of life within different environments. This is due to the numerous skeletal features at different hierarchical scales ranging from stereom differentiation to complete skeletons, their unique adaptations to specific modes of life on and within various sediment types, and finally the high diversity of extant taxa allowing for actualistic observations of life styles to be applied to the interpretation of fossil taxa.

Miocene sediments from Sardinia contain a rich echinoid fauna from different depositional environments ranging from the shoreface to the deeper shelf. These faunas can thus be used as a case study for recognizing how: 1) faunal distributions are influenced by sediment types, 2) preservation potentials vary among taxa as well as sedimentary environments, 3) both depositional environments and taphonomic pathways determine faunal diversities along geographic and temporal gradients.

## PREVIOUS STUDIES

This presentation is based on a number of recent studies on echinoids faunas from Sardinia as well as on new data. These studies include 1) investigating multiple routes to mass accumulations of clypeasteroid echinoids (predominately *Parascutella* and *Amphiope*) ranging from well-preserved autochthonous assemblages to multiple *in situ* reworked accumulations (Fig. 1A, Mancosu and Nebelsick, 2013); 2) comparing assemblages dominated by the genus *Clypeaster* from different shelf settings allowing test morphotypes to be correlated to specific environments (Fig. 1B, Mancosu and Nebelsick, in press); and 3) the origin of well preserved monotypic shell beds of both regular echinoids and spatangoid remains from deeper water, siliciclastic environments (Fig. 1E, Mancosu *et al.*, 2014).

At each locality detailed studies were made on the stratigraphy, sedimentology, palaeontology and taphonomy in both the field and in the laboratory. Detailed facies analyses were made from vertical sections observing the composition, diversity and abundance of fossils. Taphonomic signatures recorded for the echinoids included rates of disarticulation, fragmentation, abrasion, encrustation and bioerosion. The fabric of the accumulations was recording including the orientation of fossil material relative to the bedding plane both in plan and in cross section.

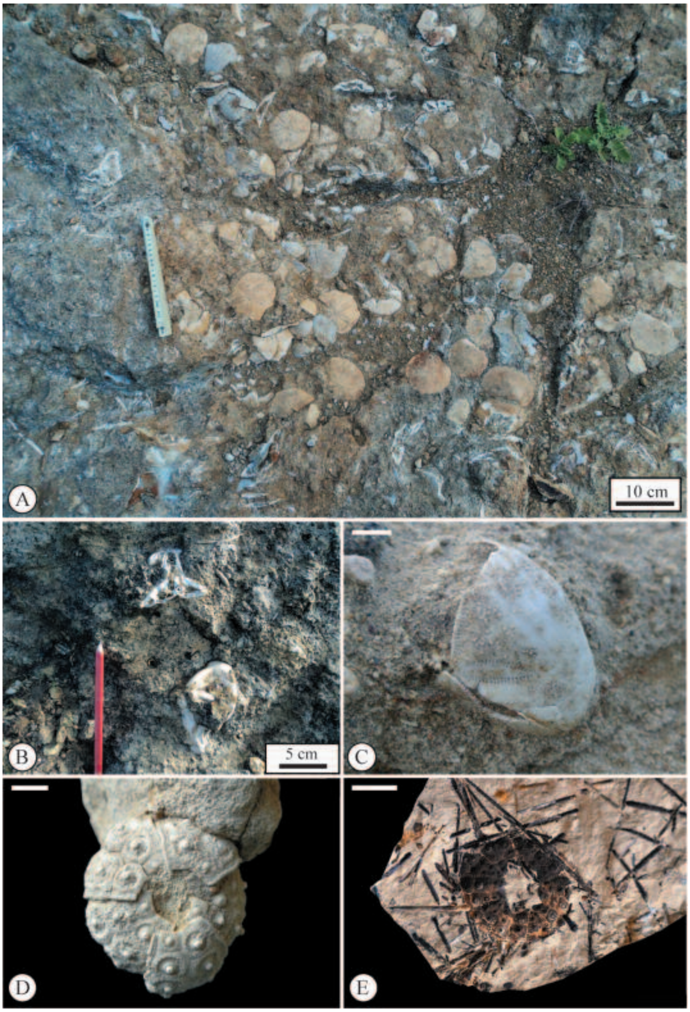

**Figure 1.** Examples of echinoid assemblages from the Miocene of Sardinia ranging from shoreface to offshore habitats (scale bar = 1 cm if not otherwise indicated). A. Clypeasteroid mass accumulation of the Duidduru section (Genoni) dominated by chaotically distributed *Parascutella* with subordinate *Clypeaster* and bivalves. The denuded echinoid remains include both complete tests and variously sized test fragments. This assemblage is interpreted as a proximal storm deposit (Mancosu and Nebelsick, 2013). B. Complete tests of obliquely oriented, highly domed *Clypeaster* specimens from the clypeasteroid-dominated deposit of the Ittiri Section. This is interpreted as resulting from multiple *in situ* reworking in a moderate to low energy sublittoral environment (Mancosu and Nebelsick, in press). C. Fragmented specimen of *Spatangus* from the Colonia Sartori (Funtanazza) section representing shallow sublittoral environment with moderate energy. D. A denuded tests of the cidaroid *Tetrocidaris* from the Colonia Sartori (Funtanazza) section. These echinoids are found in relatively deeper water environments with low to moderate energy conditions and fine-grained soft substrates. E. Specimen of a monospecific phymosomatid echinoid assemblage from a single bedding plane from Gennas (Villanovaforru). Complete test are very well preserved; long primary spines are not attached to the test. This assemblage is interpreted to have been generated in deeper, distal, offshore environments characterised by rapid influx of very fine-grained sediments without subsequent winnowing and reworking (Mancosu *et al.*, 2014).

## NEW MATERIAL

New data is provided from a lower Miocene (Aquitanian to early Burdigalian) sedimentary sequence cropping out at Funtanazza (middle-western coast-line of Sardinia) shows a wide range of highly fossiliferous facies with macrofossil assemblages characterized by echinoids, mollusks, corals and bryozoans. Eleven genera of echinoids were recognized which occur in four different echinoid assemblages suggesting a wide variation of environments, energy conditions and substrates.

Assemblage 1 is characterized by a high degree of fragmentation, affecting camarodont and cidaroid echinoids as well as clypeasteroids, cassiduloids and spatangoids, and represents a shallow water, shoreface environment with high energy conditions. Assemblage 3, with the presence of the cassiduloid *Conolampas*, the spatangoid *Spatangus* (Fig. 1C), the clypeasteroid *Echinocyamus* and the camarodont *Genocidaris*, point to a shallow sublittoral environment with moderate energy, slightly deeper than the those represented by the Assemblage 1, including soft bottoms, secondary hardgrounds and possibly seagrass patches. Assemblage 2 and 4 are characterized by well-preserved spatangoids and cidaroids (Fig. 1D) respectively, and represent relatively deeper water environments with low to moderate energy conditions and fine-grained soft sediment substrates which enabled both infaunal spatangoid echinoids and epifaunal cidaroid to flourish.

## CONCLUSIONS

Previous studies on the Miocene echinoids fauna from Sardinia as well as newly present data suggest that the differences of diversity and preservation between the echinoid assemblages can be correlated to an interplay of ecological factors (both abiotic and biotic), skeletal architectures and taphonomic bias, determining the preservation potential of echinoid test. A model is given which suggest how faunal diversities and preservation potentials change along an ecological gradient from shoreface to deeper water conditions.

### Acknowledgements

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# BLASTOZOAN ECHINODERMS FROM THE CAMBRIAN OF THE BARRANDIAN AREA (CZECH REPUBLIC)

Martina Nohejlová and Oldřich Fatka

Charles University, Faculty of Science, Institute of Geology and Palaeontology, Albertov 6, Praha 2, 12843, Czech Republic.
martina.nohejlova@natur.cuni.cz, oldrich.fatka@natur.cuni.cz

**Keywords:** Echinodermata, Blastozoa, Cambrian, Barrandian area.

## INTRODUCTION

Blastozoans belong to one of extinct groups of Palaeozoic invertebrates. Fossils of these ”pelmatozoan” echinoderms are well known from the early Cambrian to the late Permian marine associations (Sprinkle, 1973; Zamora *et al.*, 2013). Although disarticulated blastozoan plates are abundant in Cambrian sediments of the Příbram–Jince and Skryje–Týřovice basins of the Barrandian area (Prokop, 1960; Chlupáč *et al.*, 1998), articulated specimens are rare and restricted to very specific strata (Fatka *et al.*, 2004).

Cambrian material housed in the Paleontological Department of National Museum Prague and in the Czech Geological Survey Prague contains more than one hundred articulated blastozoans. These specimens have been collected from about ten outcrops and sections in the Jince Formation of the Příbram–Jince Basin, and from three restricted outcrops and one section in the Buchava Formation of the Skryje–Týřovice Basin. Stratigraphic ranges of blastozoan echinoderms from the Buchava and Jince formations are compiled in figure 1.

Cambrian blastozoans of the Barrandian area display a mosaic of morphologies and can be assigned to three major groups, (1) imbricate eocrinoids (= lepidocystids), (2) gogiid eocrinoids including the family Lichenoididae Jaekel, 1918, and (3) early rhombiferans. Eocrinoids from the Barrandian area comprise eight species classified within five described and one undescribed genera (see Barrande, 1846, 1887; Prokop, 1962; Fatka and Kordule, 1984, 1990, 1991; Parsley and Prokop, 2004; Lefebvre *et al.*, this volume). From those the presence of early rhombiferans has been recently documented by Fatka and Szabad (2014b). The aim of the current manuscript is presenting a brief summary of Cambrian blastozoans from the Barrandian area highlighting the most important morphological information and future lines of research.

## IMBRICATE EOCRINOIDS

Two different imbricate eocrinoids appear in the Barrandian area. *Vyscystis* Fatka and Kordule, 1990 was the first described and is characterized by a slightly domed oral surface and slightly elongate cone-shaped aboral region and represents the only imbricate eocrinoid described from peri-Gondwana. Compared with other imbricate eocrinoids (ii e. *Kinzercystis*, *Lepidocystis*) it is the only taxa with coiled brachioles. Articulated specimens are attached by its aboral region to large skeletal debris (i. e. cephalic shields of conocoryphid and paradoxidid trilobites). A second, yet undescribed, occurrence of an imbricate eocrinoid represented by several exquisitely preserved specimens of a basal

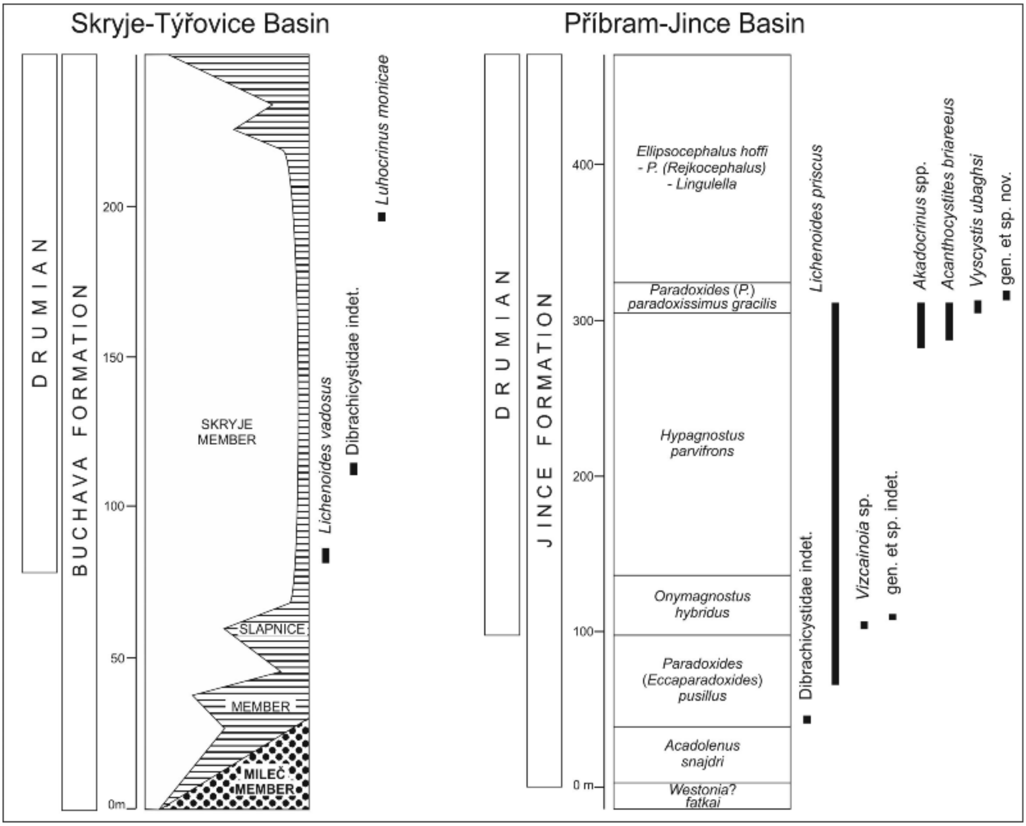

**Figure 1.** Lithostratigraphic subdivision of Cambrian rocks in the Skryje–Týřovice Basin (modified after Fatka *et al*., 2011) and biostratigraphy of the Jince Formation of the Příbram–Jince Basin (after Fatka and Szabad, 2014b), with stratigraphic ranges of blastozoan echinoderms.

blastozoans displaying a unique body plan organisation (Fig. 2D), that has been collected from the Jince Formation. It displays a unique combination of characters including an imbricate aboral region, which occupies the lower third of the test. The upper two-thirds of the theca are entirely made of numerous, adjacent plates bearing epispires (more information in Lefebvre *et al*. this volume).

## GOGIID EOCRINOIDS

Gogiid eocrinoids are the most diverse group in the Barrandian area. Three genera, *Acanthocystites* Barrande, 1887; *Akadocrinus* Prokop, 1962 and *Luhocrinus* Prokop and Fatka, 1985 share common features like a bottle-shaped theca composed of numerous, irregularly arranged plates, with or without epispires, straight, numerous biserial brachioles arranging from the summit and aboral holomeric stem with a distal, polyplated attachment disc (Fig. 2C, E).

The stem-less *Lichenoides* Barrande 1846 Fig. 2B) has been found in both Cambrian basins. It displays a quiete organize theca in three circlets plus an indeterminate number of small plates in the aboral part (Ubaghs, 1953; Sprinkle, 1973, Parsley and Prokop, 2004).

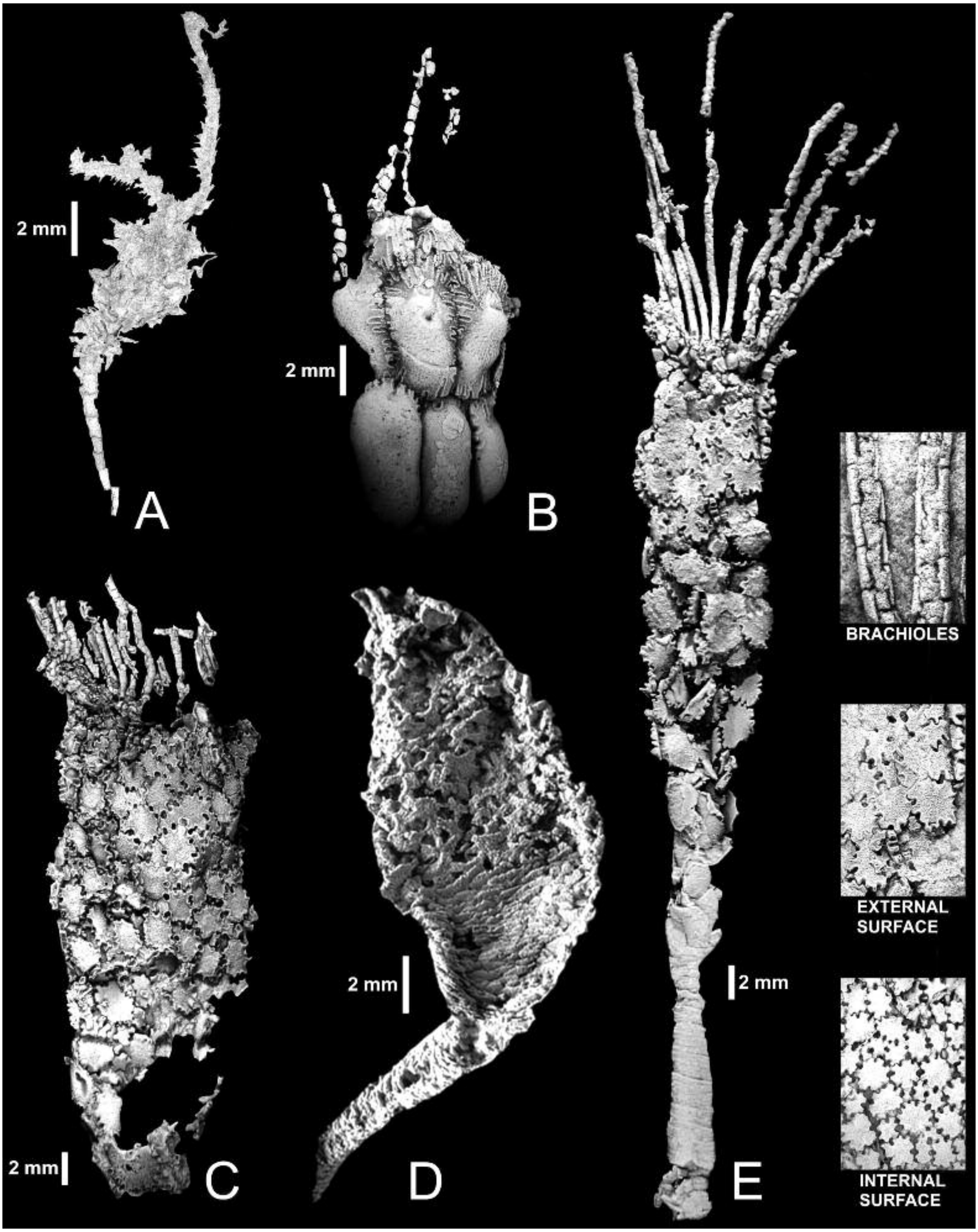

**Figure 2.** Cambrian blastozoans, Jince Formation of the Příbram–Jince Basin (A - natural mould, all other are latex casts). A. *Vizcainoia* sp., Vinice slope near Jince locality,outcrop behind the house of Baborský (CGS SZ 359). B. *Lichenoides priscus* Barrande, 1846, locality unknown (NM L42961). C. ?*Acanthocystites briareus* Barrande, 1887, locality unknown (NM L42228).D. Undescribed transitional form between lepidocystids and gogiids, nov. gen., nov. sp., Rejkovice, (SZ 349). E. *Akadocrinus jani* Prokop, 1962, locality unknown (NM L42223). Detail brachioles – NM L42226. Detail of external surface – NM L42223. Detail of internal surface – YA1193. Repositories: CGS, Czech Geological Survey Prague; NM SZ and NM L, Paleontological department of National Museum Prague.

## EARLY RHOMBIFERANS

Zamora and Smith (2012) recently classified a group of blastozoans from Gondwana as early rhombiferans. Those taxa were originally described base on isolated plates known in the literature as "*Eocystites*". Based on complete specimens from Spain displaying a unique morphology that include a polyplated theca with two complex arms arising as body extensions, and a tripartite stem composed with a flexible proximal part, cone-shaped intermediate plate and a distal stiff part composed with columnals; a new group of blastozoans known as Dibrachicystidae was erected, that includes two genera *Dibrachicystis* and *Vizcainoia*. Occurrence of a nearly complete specimen of *Vizcainoia* Zamora and Smith, 2012 (Fig. 2A) has been recently documented in the Jince Formation; and isolated plates at different levels of the Jince and Buchava Formations have been reassigned to Dibrachicystidae gen. et sp. indet. (see Fatka and Szabad, 2014b).

## DISCUSSION AND FINAL REMARKS

All the studied material appears in siliciclastic sediments that base on the trilobite content are considered Drumian in age (Fig. 1). Some specimens are excellently preserved and provide the opportunity to describe even the finest morphological details like internal and external surface of thecal plates (see Fig. 2) or the arrangement of oral areas. A number of taxa are known from several tens of specimens providing important information on the ontogeny of those groups. The presence of several blastozoan taxa coexisting in the same layers require future investigation, but probably indicate that those groups were specialize to very specific conditions (tiering, attachment strategies, substrate adaptations), indicating that niche portioning within blastozoans was already established by the Drumian.

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# PLIOCENE DEEP-SEA OPHIUROIDS FROM THE MEDITERRANEAN WITH WESTERN ATLANTIC AFFINITIES

Lea D. Numberger-Thuy and Ben Thuy

Natural History Museum Luxembourg, 24, rue Münster, L-2160 Luxembourg. lnumberger@gmx.de, nebyuht@yahoo.com

**Keywords:** Ophiuroidea, extra-Mediterranean taxa, Pliocene, deep sea.

## INTRODUCTION

The present-day Mediterranean deep-sea fauna is strongly impoverished compared to its Atlantic equivalents, with low diversities and only few strictly bathyal species (Emig and Geistdoerfer, 2004). This is generally assumed to be the result of the unusual oceanographic conditions prevailing in the Mediterranean, with warm, oligotrophic and high-salinity deep waters separated from the Atlantic deep water masses by the relatively shallow Gibraltar Sill. Plio-Pleistocene bathyal sediments, however, have produced fossil evidence for much more diverse ancient deep-sea communities in the Mediterranean (e.g. Roux *et al*., 1988; Gaetani and Saccà, 1984; Di Geronimo and La Perna, 1997; Marsili, 2007). Most of the species which lived in the Plio-Pleistocene Mediterranean deep sea have strong affinities with Atlantic relatives, which is not surprising considering that the Gibraltal Sill was the only gate for faunal exchange following the Messinian crisis (Harzhauser *et al*., 2007) when the Mediterranean underwent a near-complete desiccation.

These so called extra-Mediterranean deep-sea species are of particular interest since a detailed assessment of their distribution in the ancient Mediterranean and their affinities with present-day relatives provides insights into the evolutionary history of a modern deep-sea fauna under changing environmental conditions. We here present new finds of deep-sea ophiuroid fossils from the Late Pliocene (Piacenzian-Gelasian) of Punta Mazza at Capo Milazzo, Sicily, Italy, and discuss their affinities with modern relatives.

## MATERIAL AND METHODS

The material presented herein consists of dissociated skeletal plates retrieved from sieving residues of marly sediments washed over a 0.063 mm screen using regular tap water. Ophiuroid remains were picked under a dissecting microscope, mounted on aluminium stubs and gold-coated for scanning electron microscopy. Systematic morphological assessment was based on the lateral arm plates using the characters highlighted by Thuy and Stöhr (2011) and Martynov (2010). Modern lateral arm plates for comparison were extracted from complete skeletons macerated in household bleach and rinsed in distilled water.

## RESULTS

Of the several hundred ophiuroid lateral arm plates that were retrieved from the sieving residues, thirteen turned out to have strong affinities with the lateral arm plates of the closely related extant genera *Ophiodoris* Koehler, 1904

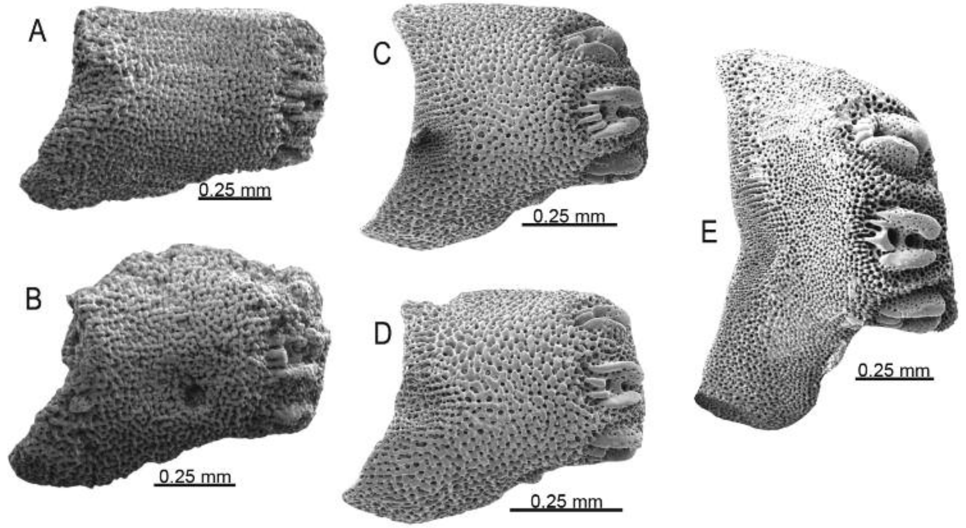

**Figure 1.** A-B. Median to distal lateral arm plates assignable to *Ophiodoris* or *Ophioplax*, Late Pliocene (Piacenzian-Gelasian) of Punta Mazza, Capo Milazzo, Sicily, Italy. C-D. Proximal (C) and median (D) lateral arm plates of *Ophiodoris malignus* Koehler, 1904, recent, New Caledonia. E. Proximal lateral arm plate of *Ophioplax lamellosa* Matsumoto, 1915, recent, Australia.

and *Ophioplax* Lyman, 1875. The general morphology of the fossil lateral arm plates with a strongly protruding ventral portion, the outer surface ornamentation consisting of small tubercles, the large tentacle notch, and the ridge on the inner side with the widened dorsal tip and the sharp kink between the dorsal and ventral portions all favour assignment to either of the two genera which share very similar lateral arm plate morphologies. The most decisive character, however, is the shape of the spine articulations, consisting in nearly parallel, horizontal dorsal and ventral lobes proximally separated by small, slightly elongated knobs. This effectively excludes assignment to the closely related genus *Ophiochiton* Lyman, 1878.

*Ophiodoris* includes four currently accepted extant species occurring in the Indo-West-Pacific from Japan to La Réunion (Stöhr *et al.*, 2014). Of the eight currently accepted species of *Ophioplax*, four are found in the Indo-Pacific and the other four live in the western Atlantic (Stöhr *et al.*, 2014). The latter are of particular interest here since they are most likely the closest extant relatives of the Pliocene fossils from the Mediterranean, given the Atlantic origin of most of the post-Messinian Mediterranean deep-sea fauna. With the exception of a rare species found along the coast of central Brazil, the Atlantic occurrences of *Ophioplax* are centred on the Caribbean.

Interestingly, modern species of both *Ophiodoris* and *Ophioplax* live at sublittoral to shallow bathyal depths, down to approximately 1000 m, but most commonly between 100 and 300 m. Thus, they are part of the deep-sea fauna but by no means qualify as strictly cold-adapted deep-water taxa. As a result, the occurrence of *Ophiodoris*-*Ophioplax* fossils in the Pliocene of the Mediterranean challenges the generally acknowledged hypothesis that the post-Pleistocene impoverishment of the Mediterranean deep-sea fauna was mainly controlled by warming of deep water masses (e.g. Marsili, 2007).

## CONCLUSIONS

The finding of lateral arm plates in bathyal sediments of Pliocene age from Sicily assignable to the ophiuroid genera *Ophiodoris* or *Ophioplax* adds to the record of extra-Mediterranean Plio-Pleistocene deep-sea taxa with very probable western Atlantic, and more specifically Caribbean, affinities (e.g. Borghi, 2014). In contrast to previous reports, however, the ophiuroid evidence does not support a selective expulsion from the Mediterranean of strictly cold-adapted deep-sea species and thus favours factors other than temperature to explain the post-Pleistocene impoverishment of the Mediterranean deep-sea fauna.

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# THE STYLOPHORAN AULACOPHORE (*SENSU* UBAGHS) REVISITED

Ronald L. Parsley

Professor Emeritus, Department of Earth and Environmental Sciences, Tulane University, New Orleans, Louisiana, 70118, USA. [Current address and Research Lab., 81 Beaumont Drive, Hendersonville, NC 28739, USA] and Research Associate, Department of Paleobiology, Smithsonian Institution, Washington, DC 20560 USA. parsley@tulane.edu

**Keywords:** Stylophora, aulacophore, Cambrian, feeding structures.

## INTRODUCTION

As aptly stated by Clausen and Smith, 2005, p.351: "One of the most enduring problems in deuterostome phylogeny has been the position of a peculiar group of asymmetric fossils named Stylophora". Most of the discussion has centered on the homology and function of the elongated and differentiated appendage. The appendage was commonly interpreted to be a locomotor/orienting non-attaching stem in the nineteenth and first sixty years of the twentieth century (e.g. Barrande, 1887; Haeckel, 1886; Zittel, 1903; Kirk, 1911; Chauvel, 1941; and post 1961; Phillip, 1979; Kolata and Jolie, 1882; Clausen and Smith, 2005). Ubaghs, 1961 first introduced the interpretation that the appendage, the aulacophore, was a feeding structure. Accordingly, the small biserial series of plates on the dorsal surface were movable cover plates that roofed over a food groove. Also, impressions on the upper surface of the large distal uniserial plates were, in addition to the food groove, that of ampulae and radial canals of the water vascular system. This interpretation has been defended by numerous papers (e.g. Ubaghs, 1967, 1971, 1975; Parsley, 1988, 1991; Lefebvre, 2000, 2003). Jefferies, 1967 rejected the echinodermal affinities of stylophorans and placed them into an ancestral chordate lineage, the Calcichordata. Despite numerous papers defending the concept (e.g. Jefferies, 1968, 1969b, 1986) it has few adherents and will not be discussed further here.

The purpose of this paper is to reevaluate the aulacophore interpretation as proposed by Ubaghs, to discuss a modification of it, and how its reevaluation relates to early history of the Echinodermata.

## AULACOPHORE STRUCTURE REVISITED

Whatever interpretation of the stylophoran appendage is adhered to, all agree on the three basic elements of its construction. For ease of interpretation Ubaghs', 1967 terminology will be used. Adjacent to the theca there is the proximal aulacophore, a multi-segmented hollow structure, each segment made up of multiple meres, or in more advanced forms, each segment is made up of four elements (most common in mitrates). Distal to the proximal aulacophore the aulacophore necks down to a single element that is either cone shaped, the stylocone, (most common in cornutes) or has ventrally directed cusps or laterally and ventrally directed flanges, the styloid (It serves to anchor into the substrate and is most common in mitrates). The upper surface is excavated and in the depression is a longitudinally bisecting ridge bearing a shallow rounded groove. The distal element is a uniserial series of ossicles each with a flattened upper surface. This surface is longitudinally bisected by a continuation of the grooved ridge present in the stylocone/styloid. On either side of the grooved ridge is a longitudinal depression that is continuous with adjacent plates. Along the outer edge of the flattened upper surface there is a ridge that is broken by transverse depressions. The top of each high point of the outer ridge is an articulating surface for a long slender cover plate. These cover plates are quite similar to those of gogiid eocrinoids. The cover plates broaden above the articulating surface and partially overlap the cover plate distal to it. They can stand vertically, even past vertical in cornutes to expose the elevated central grooved ridge. When closed the cover plates form a vault. The cover plates, as viewed by proponents of the appendage (aulacophore) being a stem or tail, are fixed and immovable (e.g. Clausen and Smith, 2005; Jefferies, 1969a). With the Ubaghs' interpretation cover plates are movable and open sufficiently to expose the food groove (Ubaghs, 1961, 1967, 1975).

Where I differ from Ubaghs is that the longitudinal depressions on either side of the grooved ridge and the transverse depressions in the outer ridges are not occupied by a water vascular system (Clausen and Smith, 2005; Parsley, 2009). Supposed depressions for vascular canals and side-branched depressions occupied by ampulae were instead occupied by muscular tissue which opened, closed, and rotated the cover plates. Without a water vascular system the simplified morphology of the upper surface of the distal aulacophore and stylocone/styloid consists of muscular depressions, a food groove, movable cover plates, and ample surface area for ciliary-mucoid entrapment of food particles and bespeaks of a brachiole-like subvective system that is functionally similar to those of eocrinoids and solutes. Despite the nature of the stereom (Clausen and Smith, 2005) the preponderance of evidence indicates the appendage is a feeding structure and not a stele. This paper is based primarily on a reexamination of specimens of *Ceratocystis perneri* Jaekel, 1901 in the Barrande Collection, as well as, other material of this species, in the National Museum in Prague (Fig. 1). Also see papers by Ubaghs (1967) and Jefferies (1969a) based on much of the same material. With a uniserial arm-like structure it is shares little in homology with other nearly bilaterally symmetrical echinoderms (Homalozoa and essentially bilateral eocrinoids). The aulacophore is probably an independently evolved structure as is the feeding structure of a solute. Critics of the aulacophore as a subvective organ point out that the cover plates in mitrates are usually preserved in place and interpret them as incapable of opening (outwardly along the longitudinal axis). Preservational evidence clearly shows that they could open in the cornutes and most of the cover plate movement in mitrates may have been rotational on the bases of the cover plates so that a between-cover-plate (upper limit food size) sieve was created. Additional space between cover plates was created by convexly arching the distal aulacophore away from the substrate (Parsley, 1988). Preservational evidence clearly suggests that this arched posture was common (also see Parsley and Gutierrez-Marco, 2005). Ciliary-mucoid currents generated on the inner surfaces of the cover plates brought food into a "leaky vault" formed by the cover plates and conveyed it to the food groove (Parsley, 1988). The aulacophore in mitrates also serves as a locomotor organ. The distal aulacophore in mitrates is narrowed (compressed) relative to that in the cornutes and in my interpretation moved the organism, theca end first, by propulsive sine waves moving down the length of the structure generated by lateral, wagging motion, of the proximal aulacophore. Mitrates probably wriggled along the bottom in a manner similar to that of a tadpole (Parsley, 1988).

## CONCLUSIONS

The aulacophore is interpreted as a feeding structure without an accompanying water vascular system and functionally resembles that of solutes or gogiid eocrinoids. Whether the feeding structure is primarily uniserial (Stylophora), biserial with a hollow lumen (Soluta) or biserial without a lumen (Gogiids and other blastozoans) the soft tissue structure on top of the exothecal supporting plates and roofed over by cover plates appears to be that of a brachiole. These animals seem to share a simple extension of a very similar food gathering ciliary mucoid system out onto different exothecal extensions of the oral plates. Stylophorans apparently had a water vascular system restricted to the theca just as it probably was in the other homalozoan groups (Soluta, Ctenocystoidea and Cincta). All of these groups appear to be evolutionary dead ends within the echinoderm stem- group and the water vascular association with the ambulacral system is linked with pre- (2-1-2) and true pentaradiality. This interpretation also simplifies the stem-group grouping of the Echinodermata.

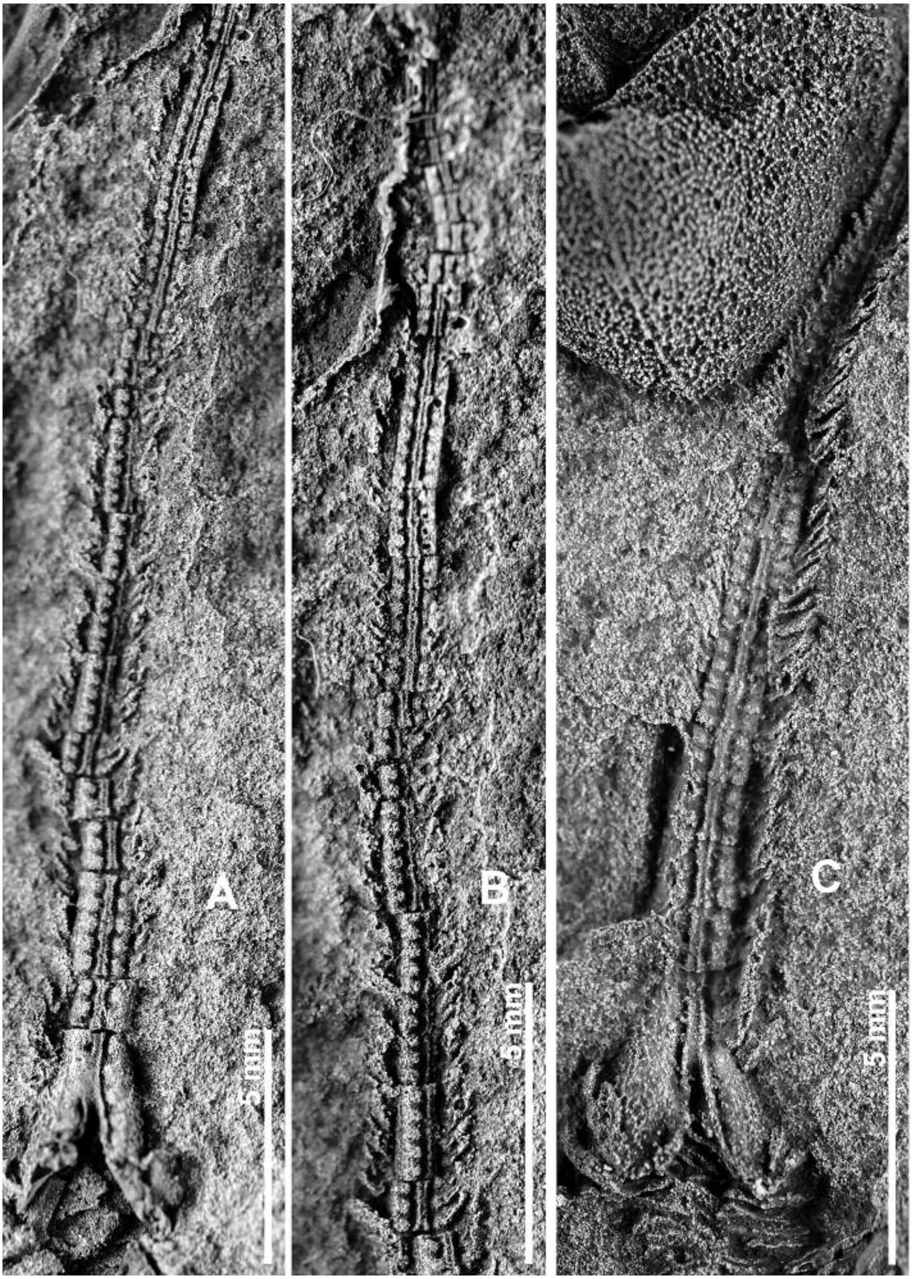

**Figure 1.** *Ceratocystis perneri* Jaekel, 1901. Specimens are from the 'middle' Cambrian Skryje Shale, Skryje, Czech Republic and are part of the Barrande Collection, National Museum, Prague (NM). A, Stylocone and upper surface of a distal aulacophore; food groove and tall movable opposed cover plates are well developed (NM 221123, lectotype). B, Middle and distal parts of distal aulacophore in Fig. A. C, Stylocone with well-developed food groove and upper surface of an aulacophore with displaced cover plates proximally; distally, cover plates are essentially in place and standing nearly vertically (NM 28257, lectotype). Specimens are latex casts whitened with sublimate of NH4Cl.

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# ECHINOID DIVERSITY THROUGH TIME

Bruno C. Pereira

School of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, U.K. and GeoBioTec, Dept. Earth Sciences, Fac. de Ciências e Tecnologia, U.N.L., Portugal; Museu da Lourinhã, Portugal. glbmcp@bristol.ac.uk

**Keywords:** Echinoidea, Palaeodiversity, evolution, biogeography.

## INTRODUCTION

For quite some time, there has been a debate about the trustworthiness of the diversity signal extracted from the fossil record, because it is commonly accepted that not all organisms are preserved. The diversity curves obtained from the fossil record do not correspond to the true biological signal, being inherently biased by taphonomic, geological and sampling factors. The aim of this work is to investigate echinoid diversity through time, seeking to interpret and test the signal for possible bias. Focusing on a single group generally implies similar taphonomic conditions and a better chance to fully comprehend its evolution. Echinoids were chosen as the study group for their wide abundance and diversity in the past and present seas. They are presumed to have originated in the Early Ordovician, 475 Myr ago (Pisani *et al.*, 2012), and diversified and expanded through many remarkable stages before the present.

The diversity signal from different continents was compared to assess the possibility of sampling bias. The fossil record has been studied for much longer in Europe and North America compared with other continents, which could imply that the global diversity signal would be driven by these areas rather than being truly global. Therefore, the diversity signal needs to be tested to address this issue. If significant differences between the diversity patterns from different continents are found to exist, it could indicate such bias. Another way to test the relevance of the diversity curves extracted from fossil counts is to correct the raw diversity signal for ghost lineages, by rectifying the taxon range for lineages that missing in the fossil record, against time-calibrated phylogenetic trees. With that objective, three independent echinoid datasets were compared to understand the changes in diversity. Two of them are commonly used to perform such studies and are based on the data gathered by Sepkoski (2002), obtained through bibliographic search, and the Paleobiology Database (2014), depending on the input of numerous collections and occurrences. The third dataset was built for this study, based on the information in Smith and Kroh (2011), which provides a reliable source of information for echinoids, with the data being frequently reviewed and updated.

## METHODS

The echinoid information based on Sepkoski's dataset was obtained from the FossilPlot 1.1 Excel file, provided by Tapanila at Idaho State University. From this dataset, we retained the generic information as well as the age range of each genus. The information from the Paleobiology Database (PBDB) was extracted from their website, using the filter tools that it provides. Again, the genera and age range information was retained. To build the third dataset, families, genera and species age ranges were extracted from Smith and Kroh's (2011) webpage, as well as occurrence regions. When needed, different subdatasets were created, for example to compare the evolution of the different echinoid orders. The third dataset was corrected for such lineages, at family level, through the use of the most recent time-calibrated phylogenetic tree of the group (Kroh and Smith, 2010). Unfortunately, this latter study focused only the post-Palaeozoic families and, consequently, such corrections could not performed for the Palaeozoic period.

For a visual comparison, the alpha diversity curves were calculated and plotted in RStudio (2014), using the script published by Pereira *et al*. (2015). This script divides the time frame under study into equal length time bins, and calculates the number of taxa present in each one. The time bin length here used is 1.5 Myr, spanning from the beginning of the Cambrian (541 Myr) to the present, comprising 60 time bins in all.

## RESULTS

Sepkoski's dataset comprises 728 genera, while the dataset based on the PBDB contained notably less (447 genera). The observation of the two datasets revealed some genera present in one and not in the other. Meanwhile, the dataset based on Smith and Kroh (2011) resulted in 867 genera, being significantly higher than the two previous ones, even after merging the first two. Most of genera in this last dataset are not monospecific. The plot of the three palaeodiversity curves shows a similar pattern. Echinoid diversity is far from having been stable since its origin (Fig. 1). Instead, the diversity curve based on occurrences shows an increasing global trend, towards the present day. Two datasets (Sepkoski and PBDB) show an apparent stabilisation in diversity during the Quaternary, after a decrease at the end of the Neogene. This decrease period in diversity is an artefact resulting from lack of genera with no fossil record. Due to its higher accuracy, the subsequent analyses performed in this study focused on the dataset built from Smith and Kroh (2011).

Diversity comparisons between continents reveal clear differences in the number of genera found on each, but with a similar pattern. Europe is the continent that constantly yields the highest number of genera. During most of the Palaeozoic, North America had a similar generic number to Europe, decreasing significantly after that. In contrast, the Antarctic continent has the smallest number of genera across most time periods. Although some continents appear to be undersampled compared with others, the comparison between the combined European and North American echinoid diversity (NAE) and the rest of the world (RW) curves shows a similar pattern. Until the Late Cretaceous, the NAE shows higher diversity, while the RW curve has higher number of genera from this point onwards. These results imply that both curves are undersampled at different time periods. Nevertheless, the diversity patterns are consistently rather similar, providing some confidence in the global palaeodiversity curve.

The ghost lineages corrections extended the appearance of several families back in time, and added many missing tree branches that had not yielded any fossils. In general, the corrected curve shows a very analogous trend to the uncorrected one, with the corrected one showing systematically higher numbers of families, from the Permian until the present day. This demonstrates the existence of a gap in knowledge of the diversity extracted from the fossil record. Although this gap exists, it remained relatively stable, since the Permian, permitting analyses of the uncorrected diversity curve.

The uncorrected echinoid alpha diversity curve can be split into two parts (Fig. 1). The first segment extends from the appearance of the group (Early Ordovician) until the Middle Triassic, with palaeodiversity relatively stable at around 30 genera. This low diversity number could be interpreted in two ways: (1), the echinoids were actually not very diverse; or, (2), it is a taphonomic and/or sampling bias. The echinoid representatives that lived during most of this period were different from the post-Palaeozoic forms. They possessed flexible tests, which were probably more likely to completely disarticulate after death than younger forms. Therefore, the fossil record of these echinoids is taphonomically and sampling biased, since they are hard to see in the field after complete disarticulation and frequently impossible to identify from loose material. The appearance of suckered aboral tube feet and small spines that covered the entire aboral surface appears during the Early Carboniferous. It probably conferred the ability to cover tests with debris, which may have increased the preservation potential and explain the diversity rise during this time interval.

The second part of the curve shows a significant global trend of diversification since the Late Triassic, with the acquisition of new significant morphological changes. In the Carnian (Late Triassic), a series of changes in echinoid tests led to a stronger and more robust morphology, such as: fusion of plates, which bear the tubercle; and longer and more robust spines. Also in the Carnian, the irregular echinoid clade emerged and slowly diversified, according to

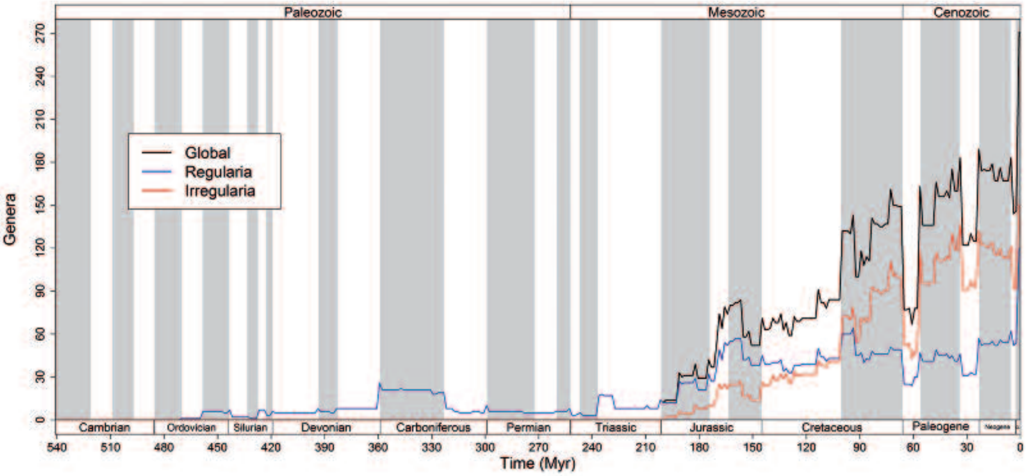

**Figure 1.** Global alpha echinoid diversity, based on Smith and Kroh's (2011) dataset. The black line represents the echinoid diversity curve, the blue line the diversity of regular echinoids, the red line the diversity of irregular echinoids.

molecular clock estimates and phylogenetic inferences. This clade could have originated from regular echinoids that experienced a reduction in test thickness and armour, through the colonization of soft bottoms. In contrast, the Jurassic showed an important increase in echinoid diversity, possibly linked with the establishment of new marine conditions in the Tethys area. Cidaroids, the most diverse group during this time period, evolved towards the thickening of test, and larger and thicker spines. Other regular echinoids persisted with relatively small tests and spines, and acquired higher ambulacral plating complexity. The irregulars underwent a rapid diversification, with a similar trend to the regulars (Fig. 1) and echinoid diversity continued to increase in the Cretaceous. The irregular echinoids were responsible for the overall increase in diversity of the echinoid clade, while the number of regular echinoid genera remained rather constant. The transition between Early and Late Cretaceous marks a shift in echinoid diversity. From this point onwards, regular echinoids became less diverse than irregulars, due to the great diversification of spatangoids and holasteroids. The beginning of the Cenozoic is marked by a significant decrease in diversity and test size. Contrasting with their Mesozoic ancestors, most post-Mesozoic regular echinoids possessed thinner tests and spines, possibly from a lack of nutrients (Smith and Jeffery, 1998). After this initial decrease, a new echinoid diversification occurred at the Paleocene/Eocene boundary. This increase in diversity is seen in both regular and irregular echinoids, more substantially on the latter. The camarodonts become the most diverse regular echinoids during the Cenozoic, while the second most diverse, the cidaroids, had a tenuous increase. The clypeasteroid lineage, which diverged from its sister group in the Early Cretaceous, greatly diversified during the Cenozoic and became the second most abundant irregular group, after the spatangoids. At the present, irregular echinoids are slightly more diverse than irregulars, contrasting with the more recent geologic record. This difference might be explained through taphonomic differences between the two groups, where irregular echinoids live a great part of their life buried and, possibly, increasing their rates of preservation.

These major post-Palaeozoic diversification events are associated with a significant increases in the rates of morphological evolution, namely during the Jurassic and the Paleocene/Eocene. Regular echinoids have not changed much in morphospace, implying that they experienced very little change through time. On the other hand, the irregulars became separated into two major groups, the Neognathostomata and Atelostomata, diverging and spreading in morphospace (Hopkins and Smith, 2015). This pattern of morphospace occupation might explain the reason why the regular echinoid diversity has been more or less stable, while the diversity of irregulars increased substantially. Despite this general trend of diversity increase, some drops in diversity stand out from the general pattern, such as during the Late Jurassic, the Turonian, the end of the Cretaceous and the Oligocene. These drops can be observed in the diversity pattern of both regular and irregular echinoids. Some of these drops are associated with global extinction events, such as the Cretaceous/Paleogene and the Eocene/Oligocene transitions.

## CONCLUSIONS

Echinoid diversity has risen and fallen over time. Plotting the diversity from different continents and correcting for ghost lineages generate similar patterns to the global diversity curve, implying some degree of confidence in the pattern obtained. For about the first half of their history, echinoids had relatively low and constant diversity. It is during the Late Triassic that the group experienced a major diversification event, which significantly increased its diversity until they reached present numbers. Diversity did not increase constantly. Periods of considerable decrease in diversity can be observed and, in some cases, are associated with global extinction events.

## Acknowledgements

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# DIFFERENT PATHWAYS IN EARLY EVOLUTION OF THE HOLOTHURIAN CALCAREOUS RING?

Mike Reich

SNSB - Bavarian State Collection for Palaeontology and Geology (BSPG) Munich and
Ludwig-Maximilians University Munich, Department of Earth and Environmental Sciences, Section of Geobiology and
Palaeontology, Richard-Wagner-Str. 10, 80333 München, Germany. m.reich@lrz.uni-muenchen.de

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## INTRODUCTION

A uniting synapomorphy of all sea cucumbers (Echinodermata: Holothuroidea) is a structure of calcified elements, which surrounds the mouth (pharynx) internally, called the calcareous ring (Kerr and Kim, 2001; Smith and Reich, 2013; Fig. 1A, D, F, H). This structure is one of the most important systematic characters within the Holothuroidea (e.g., Becher, 1908; Heding, 1933, 1935; Pawson and Fell, 1965; Kerr, 2001; Smirnov, 2012), therefore it is strange that holothurian calcareous rings have rarely been the subject of more than passing interest to zoologists and palaeontologists. Although this structure is also present in the fossil record (e.g., Gilliland 1993; Reich, 2001, 2013), the pharyngeal calcareous ring remains one of the least-studied structures among holothurian anatomy. With a few exceptions (Ludwig, 1889-1891: 79ff.; Hyman, 1955: 138ff.), no general overview of this structure has been undertaken since the initial descriptions and monographs of modern holothurian faunas in the late 19th and early 20th centuries, and the three-dimensional anatomy and organization of the calcareous ring (Fig. 1A, D, F, H) remains unclear in nearly all recent sea cucumber species (Reich and O'Loughlin, 2010). In the last few decades, this gap in knowledge has resulted in anatomical misinterpretations in modern species (e.g., Gage and Billett, 1986), as well as misinterpretations and/or incorrect reconstructions of fossil holothurian material (e.g., Haude, 1992, 1997; Boczarowski, 1997, 2001; Jell, 2010).

## MORPHOLOGY AND FUNCTION OF CALCAREOUS RINGS

Within the calcareous ring (CR) of Holothuroidea, 5 equal formed radial elements (radials; R) typically alternate with 5 interradial elements (interradials; IR) (Fig. 1A). The individual CR elements are bound to each other either firmly or loosely by means of connective tissue. The CR narrows anteriorly or posteriorly (Fig. $1A_2$), or is equal at both ends. Furthermore, the structure is not always symmetrical (Fig. 1A); bilateral symmetry occurs in members of the Dendrochirotida and especially in apodid holothurians (Synaptacea). The length of the CR is normally proportional to the total length of the animal. This total length of the CR ranges between less than 1 mm and more than 10 cm, varying within different sea cucumber groups. Within representatives of the Synaptacea, the CR length is usually only a few percent of the total length of the specimen, whereas in representatives of the Dendrochirotida and Molpadiida (Holothuriacea), the CR length can cover up to one third of the total holothurian length.

The CR is of great importance as a support for the pharynx and tentacles, water vascular system and radial nerve ring, as well as a point of insertion for the longitudinal and/or retractor muscle bands.

The size and shape of the elements forming the CR vary greatly, but are distinct for each holothurian group. IR are generally smaller (i.e., shorter and narrower; Fig. 1F) than R, only in apodid (Synaptacea) holothurians R and IR are of equal size (almost square-like; Fig. 1A). The anterior end of the R is perforated (Fig. 1A) or notched for the passage of the radial nerve (and radial water channel; depending on the sea cucumber group) and a single/double process (e.g., Synaptacea) or up to three processes (in fossil forms) can be formed. At the posterior end of the R (and sometimes also in IR) a short to long forked process can be shaped (Holothuriacea; Fig. 1F). At the outer surface of R there are also depressions (or fossae and ledges; Fig. 1A) depending on the respective group, where the longitudinal and (if present) retractor muscle bands as well as tentacular bases/ampullae insert. The inner side of the R reveals in some groups (e.g., Molpadiida and Dendrochirotida) branching grooves for the tentacle canals and a single posterior groove for the radial canal (Fig. 1F). The front end of IR normally also has a single process (Fig. 1F) that can be reduced in apodid holothurians (Synaptacea; Fig. 1A). Each CR element may be a single solid piece, or in some groups of the Holothuriacea (especially in the Dendrochirotida), a mosaic of individual segments.

An increase in the total number of CR elements is only known from aberrant dendrochirote forms (e.g., Ludwig, 1886: 6x R + 6x IR) and from derived members of the Synaptacea (Chiridotidae, Synaptidae), in which only further IR were implemented in addition to the already available 5 IR and 5 R (Fig. 1A). The often mentioned and specified reduction (e.g., Kerr and Kim, 2001) of the IR within the Elpidiidae (Elpidiacea; only 5 R present) in my opinion is a misinterpretation. All CR elements (Fig. 2B-D), as well as outer test scales or plates (Fig. 2A) of holothurians, show distinct types of stereom structures, whereas only in elpidiid sea cucumbers no stereom can be observed in CR. The latter therefore indicating a condition found in all other 'normal' microscopic body-wall ossicles ('juvenile' stage after Seilacher, 1981).

## EARLY PALAEOZOIC CALCAREOUS RINGS

Articulated or partly articulated calcareous ring material from Early Palaeozoic strata (Ordovician, Silurian, Early Devonian) is only known from a few localities worldwide: (1) New South Wales, Australia (Přídolí; e.g., Jell, 2010), (2) Hunsrück area, Germany (Emsian; e.g., Seilacher, 1961; Reich and Smith, 2010), (3) Precordillera (San Juán Province), Argentina (Emsian; Haude, 1995). Unfortunately, most of the described material is based on internal and external moulds (Australia, Argentina) or diagenetically changed (pyritized and/or silicified) fossils (Germany), in which the microstructures have not always been well preserved. Unravelling the early fossil record and evolution of Holothuroidea is hence problematic, largely due to the scarcity of well preserved specimens. Therefore, the combination of macro- and micropalaeontological methods (cf. Reich and Smith, 2009), offering well-preserved microstructures (cf. Smith *et al.*, 2013), is more promising.

In the last 15 years, more than 2.000 isolated holothurian CR elements from Ordovician, Silurian and Early Devonian strata were collected and investigated in detail. Most of the isolated CR elements studied come from the Silurian of the Isle of Gotland, Sweden: the Telychian (Llandovery) (1) *Lower Visby Formation*; the Sheinwoodian (Wenlock) (2-4) *Upper Visby* and *Högklint Formations,* as well as the *Slite Group*; the Gleedonian (Wenlock) (5-6) *Halla* and *Klinteberg Formations*; the Gorstian (Ludlow) (7) *Hemse Group*; the Ludfordian (Ludlow) (8-11) *Eke*, *Burgsvik*, *Hamra* and *Sundre Formations*. In addition, material from the Early Devonian of the Barrandian area (Czech Republic),

**Figure 1.** Three-dimensional computer reconstructions of the holothurian calcareous ring (CR) based on X-ray µCT (A, D, F, H) compared to 'normal' (formerly) published two-dimensional drawings (B, C, E, G). A-C, *Chiridota gigas* (Apodida: Chiridotidae), oblique view ($A_1$), anterior view ($A_2$), posterior view ($A_3$); B, lateral outer view, from Dendy and Hindle (1907), modified; C, lateral outer view, from Hickman (1962), modified. D-E, *Ocnus planci* (Dendrochirotida: Cucumariidae), lateral view (D), including cut body wall; E, lateral outer view, from Panning (1971), modified. F-G, *Molpadia* spp. (Molpadida: Molpadiidae), F, *M. musculus*, oblique anterior view including cut body wall; G, *M. arctica*, lateral outer view, from Heding (1935), modified. H, *Elpidia heckeri* (Elasipodida: Elpidiidae), posterior view including cut body wall.
Note that the calcareous ring (reddish) contains much more information (e.g., anchor points of muscle bands, grooves for the water vascular system on the inner side etc.) than the simple drawings previously suggested.

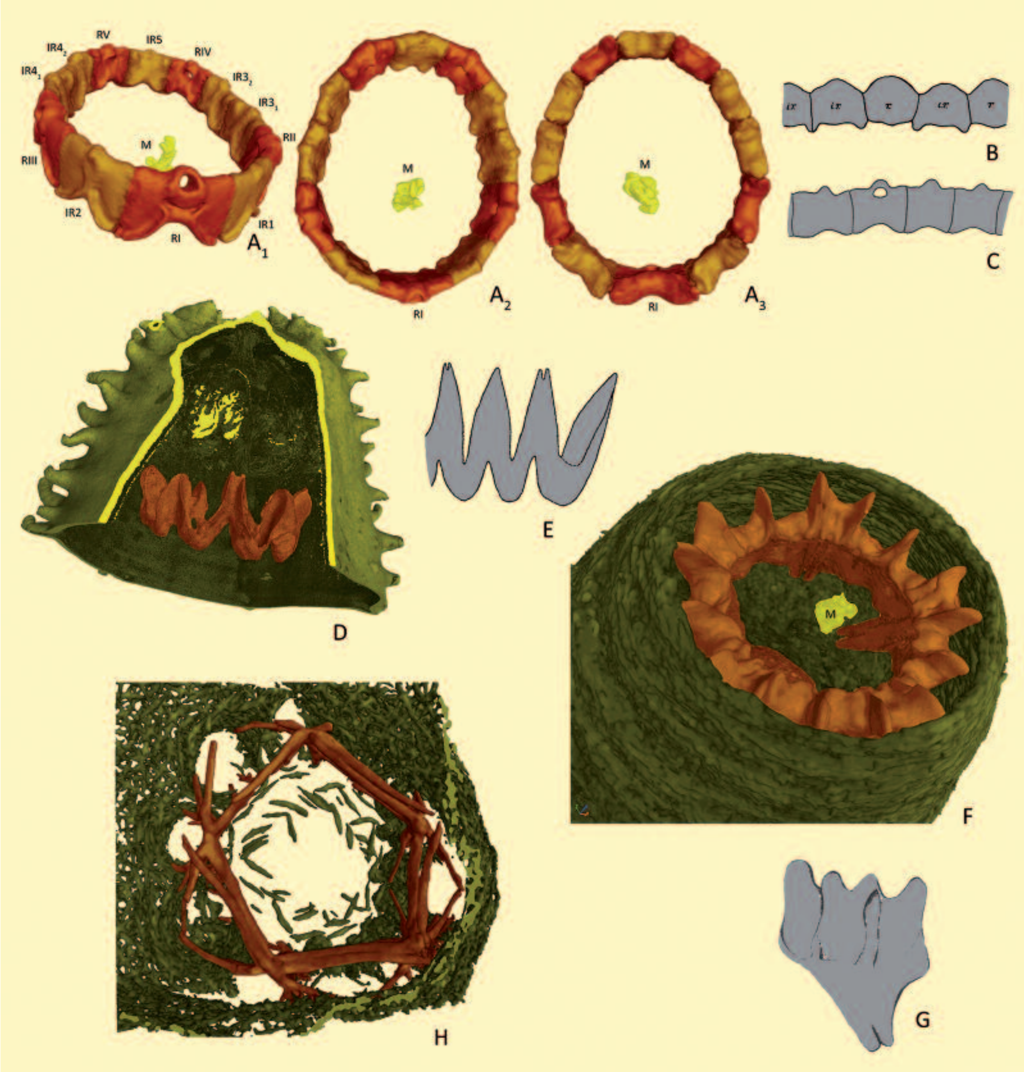


**Figure 1.**

*Provenience:* A, Western South Pacific, Tasmania, rocky shallows, CR Ø ~ 4 mm; D, western Mediterranean Sea, near Banyuls-sur-Mer, 85 m water depth, CR Ø ~ 12 mm; F, eastern Indian Ocean, western Australia, 373-382 m water depth, CR Ø ~ 6 mm; H, North Atlantic Ocean, south off Greenland, ~ 1,500 m water depth, CR Ø ~ 2 mm [all MR].
*Abbreviations:* RI-RV + IR1-IR5 Ludwig (1889) letters for designation of radial (R) and interradial (IR) calcareous ring elements; M = Madreporite. MR = coll. M. Reich, SNSB - BSPG Munich; SMNH = Swedish Museum of Natural History, Stockholm.
*Methods:* The figured material was investigated by high resolution computed tomography (µCT) and scanned with the v|tome|x s 240D (GE Sensing and Inspection Technologies GmbH phoenix|x-ray) at the Steinmann Institute of Geology, Mineralogy and Palaeontology, Bonn University, Germany. The voltage and current values commonly used for the present material were in the range of 120 kV/120 µA to 150 kV/150 µA. A series of 1,000 to 1,500 projections were made of the specimens; the single images have a voxel size between 0.012 x 0.012 x 0.012 and 0.019 x 0.019 x 0.019 mm. Visualization etc. were realized with the software VGStudio Max2.2 (Volume Graphics GmbH, Heidelberg, Germany) with additional processing of images using Adobe Photoshop CS2 and CS6.]

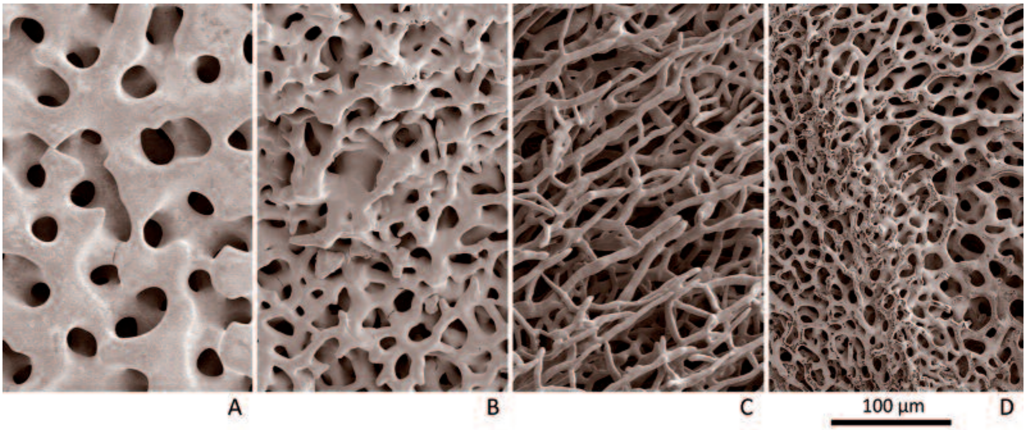


**Figure 2.** Different types of stereom microstructure in modern holothurians (A-D). A, Irregular perforate stereom, forming the outer surface of an (outer) test scale of *Psolus fabricii* (Dendrochirotida: Psolidae); B, Dense labyrinthic stereom forming the inner surface of a radial calcareous ring element of *Molpadia borealis* (Molpadiida: Molpadiidae); C, Sparse (maze-like) labyrinthic stereom forming the inner surface of a radial calcareous ring element of *Laetmogone violacea* (Elasipodida: Laetmogonidae); D, Medium to fine labyrinthic stereom forming the inner surface of a radial calcareous ring element of *Myriotrochus rinkii* (Apodida: Myriotrochidae); [all SMNH].

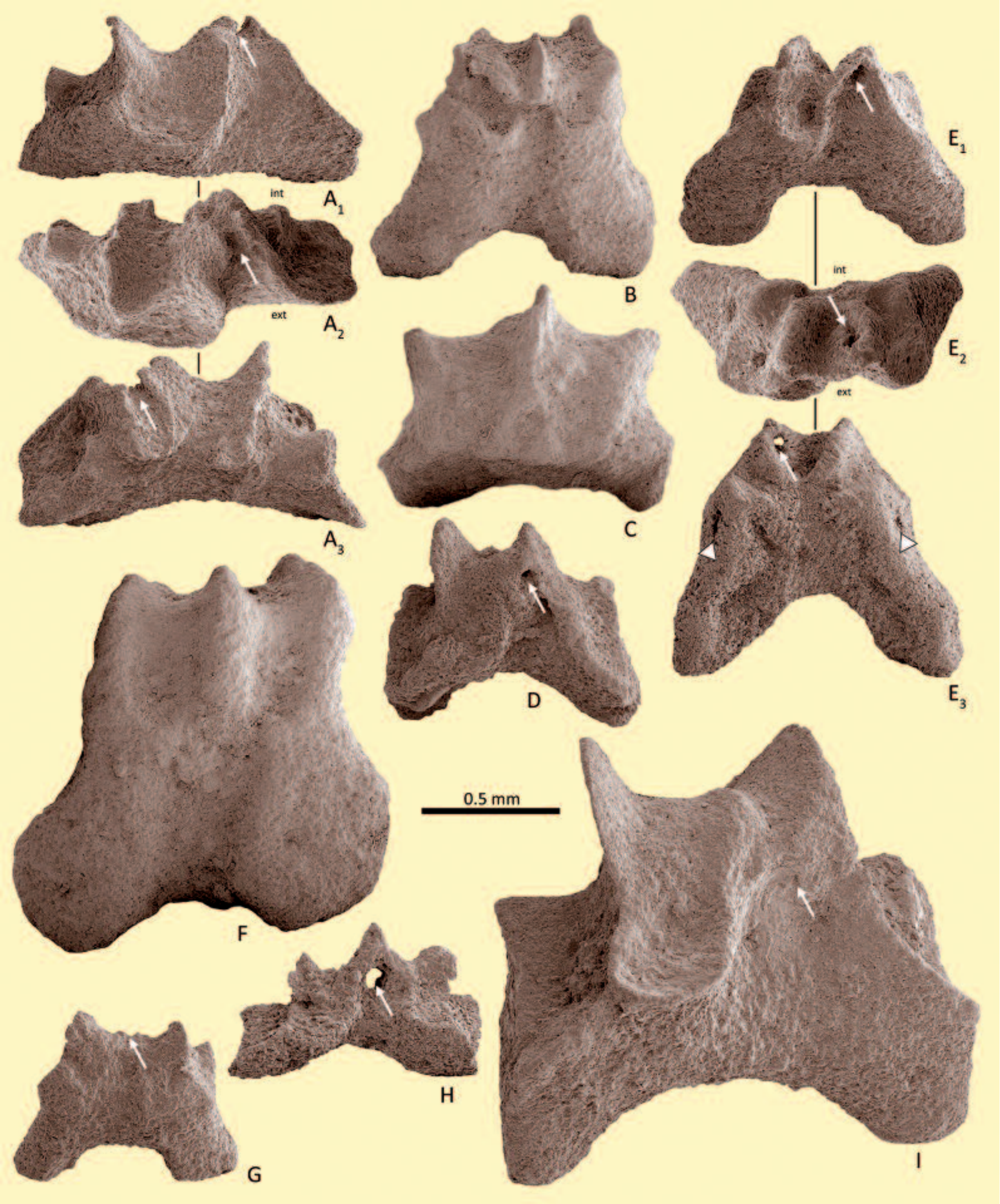
especially the Lochkovian (12) *Lochkov Formation* (Kotýs Limestone); the Pragian (13) *Praha Formation* (Koněprusy Limestone, Slivenec Limestone, Loděnice Limestone, Dvorce-Prokop Limestone); and the Emsian (14-15) *Zlíchov* (Zlíchov Limestone) and *Daleje-Třebotov Formations* (Třebotov Limestone) were investigated.

Furthermore, a few specimens were obtained from the Darriwilian (Middle Ordovician) (16) *Upper Red Orthoceratite Limestone* of Sweden, the Sheinwoodian/Homerian (Wenlock) (17) *Coalbrookdale Formation* (Shropshire, UK), and the Ludfordian (Ludlow) (18) *Kopanina Formation* (Czech Republic).

Most of the investigated material (> 1,800) can be assigned to the Apodida (?Myriotrochidae and stem-group apodids; Fig. 3A, D) and to two new extinct holothurian groups (Fig. 3B, C, F), in which combined characteristics of modern groups are shown (cf. Reich 1999, 2010; Smith et al., 2013). Only a few specimens (< 100) belonging to the Aspidochirotida (Mesothuriidae or stem-group Mesothuriidae; Fig. 3G) and Elasipodida (?'Pannychiidae' / Laetmogonidae; Fig. 3H) were found. There is, in addition to the other previously mentioned groups, a supplementary number of distinct R, which have been perforated or holed at the lateral faces (Fig. 3E), and hence show features hitherto unknown in modern sea cucumber taxa.

Early members of Holothuroidea (Darriwilian and Telychian) exhibit the standard architecture of the CR (5 R and 5 IR), with 3 anterior processes in all R, and thus 20 tentacles can be assumed. The earliest apodid representatives, on the other hand, show evidence for 15 tentacles (i.e., all R have 2 anterior processes).

**Figure 3.** Isolated radial CR elements from different Silurian strata of the Isle of Gotland, Sweden. A, undescribed gen. et sp. nov. (Apodida: ?stem myriotrochid), $A_1$, outer view, $A_2$, anterior view, $A_3$, inner view; B, undescribed gen. et sp. nov. (new order), outer view; C, undescribed gen. et sp. nov. (new order), outer view; D, *Nudicorona* sp. nov. (Apodida: ?Myriotrochidae), outer view; E, undescribed gen. et sp. nov. (new order), $E_1$, outer view, $E_2$, anterior view, $E_3$, inner view; F, undescribed gen. et sp. nov. (new order), outer view; G, undescribed gen. et sp. nov. (Aspidochirotida: ?stem mesothuriid), outer view; H, undescribed gen. et sp. nov.



(Elasipodida: ?'Pannychiidae'), outer view; I, '*Achistrum*' sp. nov. (Apodida: ?Myriotrochidae), outer view.
*Provenience:* A, Nyhamn - Lower Visby Fm (Llandovery: Telychian; ~ 435 Ma); B, C, F, G, H, Petsarve - Eke Fm (Ludlow: Ludfordian; ~ 424 Ma); D, E, Mästermyr - Hemse Group (Ludlow: Gorstian; ~ 426 Ma); I, Svarvare - Slite Group (Wenlock: Sheinwoodian; ~ 432 Ma) [all MR].
*Abbreviations etc.:* CR = calcareous ring, ext = outer side, int = inner side (A, E); the passage (notch or perforation) for the radial nerve is indicated by an arrow (A, D, E, G, H, I); perforated or holed positions at the lateral faces are indicated by small triangles (E only).

## EVOLUTIONARY TRENDS

### What is known about the number of holothurian tentacles during the Phanerozoic?

The results listed above contrasts with formerly proposed data concerning the tentacle number in the earliest holothurians: 10 (e.g., Ludwig, 1891, 1892; Becher, 1907, 1908) or 12 (Haude 1992; Smirnov 1999). Östergren (1907) was the only person to have left an open discussion regarding this, and suggested 20 or probably 10 tentacles. Pawson (1980) proposed for the (stem-group) holothurian *Palaeocucumaria* (Emsian; Hunsrück Slate of Germany) 20 tentacles; however, Smith (1988) and Smith and Reich (2013) confirmed that in this fossil form the tentacles were plated and numerous (40-50) as well as arranged in 5 lobe-like clusters, which is unknown in recent forms.

The 'basic condition' of 20-15 tentacles in holothurian representatives remained in (early) fossil Apodida and in modern (and probably also fossil) Elasipodida (Deimatidae, Laetmogonidae, 'Pannychiidae', Pelagothuriidae, Psychropotidae), Aspidochirotida (Holothuriidae, Mesothuriidae, Stichopodidae, Synallactidae), Gephyrothuriida (Gephyrothuriidae) and Molpadiida (Caudinidae, Eupyrgidae, Molpadiidae) with a few exceptions in caudinid, holothuriid, synallactid, and psychropotid sea cucumbers.

By reducing the number of anterior processes in the R of apodids, most members of modern Apodida (Myriotrochidae, Chiridotidae, Synaptidae) bear 10-12 tentacles. In more advanced apodids (species in which the anterior processes of R are reduced; Chiridotinae, Synaptidae) the number of tentacles is often secondarily increased as mentioned above. However, due to a paedomorphic status of the CR in the Elpidiidae, consisting of 5 R only (as described above), a low number of tentacles, 10-(12), can also be found in one group of the Elasipodida.

The highest diversity related to the tentacle number (and arrangement) can be found within the Dendrochirotida. Most modern representatives of the Placothuriidae, Heterothyonidae, Psolidae, Ypsilothuriidae, Cucumariidae, Sclerothyoninae [Sclerodactylidae], Thyoninae [Thyonidae] bear 10 or 12 (Paracucumidae, Cucumellidae) or rather 15-20 tentacles (Thyonidiidae, Cladolabidae, Phyllophoridae, Vaneyellidae, Rhopalodinidae, and Semperiellinae [Thyonidae]). Only a few spezialised dendrochirote species are slightly different in having 25 or 30 tentacles (e.g., some phyllophorids, thyonidiids and rhopalodinids). Additionally, tentacles in members of the Dendrochirotida are furthermore often arranged in 2(-3) nested circles.

### How has the calcareous ring changed through time?

There seem to be a few main morphological trends through time in the evolution of the holothurian groups still known today. First, in apodids (or in holothurians without radial canals) there is a reduction and partial loss of anterior processes as well as an opening of radial nerve perforations (in R). A second general process is that of increasing of the length of the CR (Apodida → Elasipodida → Aspidochirotida/Gephyrothuriida → Molpadiida/Dendrochirotida), especially well known from holothuriacean species (e.g. molpadiid and dendrochirote forms), with posterior prolongations formed as solid pieces or as a mosaic of individual segments. An equivalent morphology was also developed secondarily in highly advanced Apodida by prolonging (and partial covering) of the CR with a cartilaginous ring (Synaptinae). Another trend is that of bilaterally symmetrical CRs, for instance in apodids (Myriotrochidae and Synaptidae), where anterior processes in R were partially reduced to show dorsal/ventral differences. Otherwise, in Molpadiida/Dendrochirotida, there is also a strong trend in anterior process size, such that the muscular process was enlarged in comparison to the non-muscular process.

## CONCLUSIONS AND PERSPECTIVES

One of the most important features in distinguishing the Holothuroidea is the CR, which is present in (nearly) all fossil and living sea cucumbers. The discovery of fossil isolated CR elements and CR *in situ* in early Palaeozoic strata promises to improve our knowledge of the early evolution of holothurians. Although the dating and detailed steps in the early diversification of fossil sea cucumbers remain problematic, by combining investigations on macro- and micropalaeontological holothurian material, it is possible to answer some unsolved questions.

Based on articulated and isolated microscopic or mesoscopic CR material, with the exception of Early Palaeozoic members (or stem-group members) of the Apodida, Elasipodida and Aspidochirotida, there is evidence for at least 2-

3 other extinct groups, showing, in part, unusual features that are currently unknown in modern holothurians. The ~ 465-400 Ma (Middle Ordovician to Early Devonian) interval remains critical for understanding the early holothurian evolution and phylogeny. The apparent constancy in the CR patterns, at least from the early Mesozoic until the present, suggests that a more detailed study of extant sea cucumbers may help to interpret their affinities with fossil forms. It is to be hoped that the existing gaps in our knowledge will be filled, especially for articulated material, although this is extremely rare. In the future, the classification of the modern and fossil groups of the Holothuroidea has to be reorganised in a few respects concerning the CR.

While this brief summary of holothurian CR evolution and early diversity is far from complete or conclusive, there appears to be substantial evidence for the existence of several separate, divergent phylogenetic lineages within fossil and extant Holothuroidea.

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# ON THE PARACRINOID-LIKE ECHINODERMS *ACHRADOCYSTITES* VOLBORTH, 1870 AND *HECKERITES* ROZHNOV, 1987 FROM THE ORDOVICIAN OF BALTICA

Sergey V. Rozhnov

Borissiak Paleontological Institute, Russian Academy of Sciences, 117647, Profsoyuznaya st. 123, Moscow, Russia
rozhnov@paleo.ru

**Keywords:** Paracrinoids, morphology, arms, brachioles, morphogenesis, Ordovician, Laurentia, Baltica.

## INTRODUCTION

Paracrinoids are a characteristic group of the Ordovician echinoderm fauna of Laurentia. Two endemic genera tentatively assigned to paracrinoids found in the Ordovician of Baltica are also found outside Laurentia. These are two very different genera, *Achradocystites* Volborth, 1870 and *Heckerites* Rozhnov, 1987 from the Upper Ordovician (Katian) of northern Estonia. Here, I do not discuss Baltic cryptocrinids, rhipidocystids, or similar North American taxa, which may be related to paracrinoids (Sprinkle, 1973), but are not very similar and need to be considered separately. Typical paracrinoids from Laurentia have uniserial exothecal, often recumbent "arms", with uniserial "pinnules". The Baltic *Achradocystites* and *Heckerites* have many features similar to North American paracrinoids, including the food-gathering system, but differ in the biserial "arms" and biserial "pinnules". A detailed study of their food gathering systems, evaluation of the possibility of biserial appendages becoming uniserial, and possible mechanisms for such transformations, are required to substantiate the unification or separation of the two Baltic genera from the North American paracrinoids. The food-gathering system of *Heckerites* has been studied in detail (Rozhnov, 2012). Until recently, the morphology of the brachioles of *Achradocystites* was only known from isolated brachials found separate from the theca (Hecker, 1958; Stukalina and Hints, 1989). New material, part of the theca with three "arms", two of them well preserved, allows detailed description of the "arm" morphology (Fig. 1). I use here the paracrinoid terminology although the "arms" with "pinnules" of *Achradocystites* are very similar with the "ambulacral trunks with brachioles" of some eocrinoids and other blastozoans (Sprinkle *et al.*, 2011). I suppose that paracrinoid and eocrinoid terminology can be combined in the future because the eocrinoid "biserial trunks with brachioles" could be ancestral for the paracrinoid "uniserial arms with pinnules". Both these exothecal structures appeared independently with true endothecal arms and pinnules of crinoids although the pattern of "pinnulation" is very similar in all these cases.

## MORPHOLOGY OF BRACHIOLES OF *ACHRADOCYSTITES*

Each of three "arms" (A, C, and E) extends from a pair of large plates of the pre-oral field. The "arms" are long, ca. 50 mm, which is slightly shorter than the theca. The "arms" are biserial gradually decreasing distally. The "arm" width is 6 mm proximally and 4 mm distally. The height of the brachials is 3.5 mm proximally and 2.5 mm distally. Each segment had a semi-circular slightly depressed crested facet for "pinnular" attachment and is mounted on a

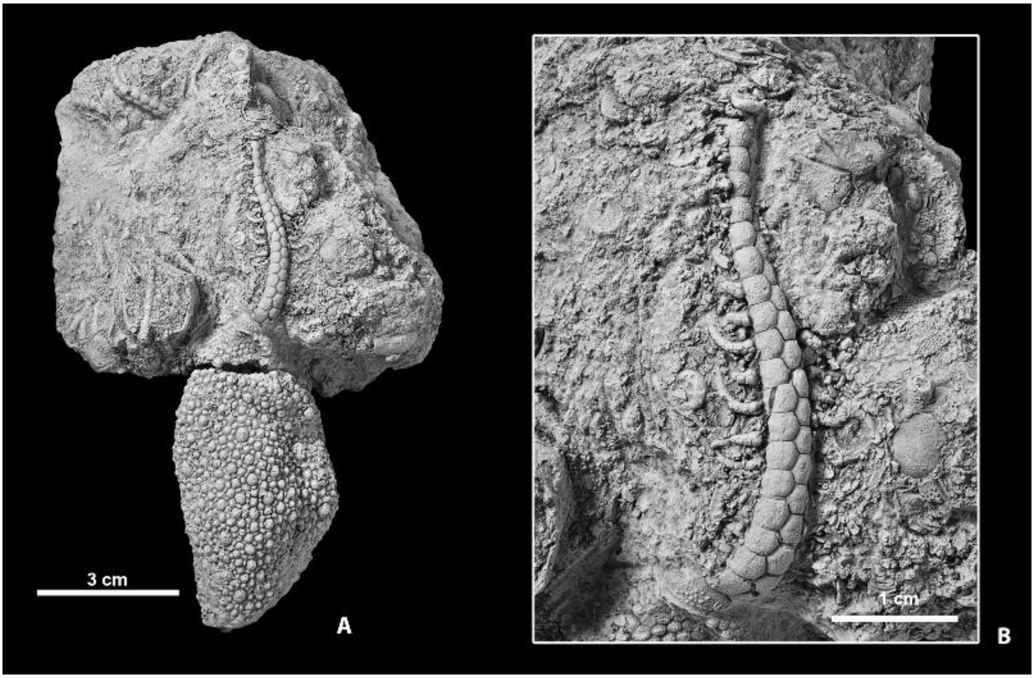

**Figure 1.** Theca of *Achradocystites* sp. with biserial "arms" and "pinnules", PIN 4125/909, general view (A) and detail of the "arm" (B). Vasalemma Formation, Keila regional stage, Katian. Upper Ordovician, quarry near Vasalemma, North Estonia.

small pedestal. The ambulacral canal is deep, V-shaped, branching in the middle of each brachial, approaching the facet and running further, into the "pinnule". Biserial "pinnules" arise from each plate beginning from the proximal; they are 10-12 mm long, each composed of 8-10 pairs of plates, rapidly narrowing and forming a dense meshwork on the right and left of the ambulacrum. The gradual narrowing and lowering of the plates of the main branch and "pinnules" shows that the new plates were added terminally.

## DISCUSSION

The complex morphology of "pinnule"-bearing "arms" of *Achradocystites* suggests that the ambulacral groove included, apart from the ambulacral canal and ciliated epithelium, other organ systems necessary for the function and growth of the food-gathering system, i.e., mesoderm for formation and growth of the calcite skeleton, neural system for coordination of the movements of the ambulacral appendages, and blood circulatory system and/or coelomic canal system necessary for feeding this food-gathering system. Therefore, despite the exothecal characters of biserial "arms" in *Achradocystites* and uniserial arms in typical paracrinoids, coeloms and their derivatives continued into the ambulacral canals (at least the left coelom). The biserial terminal growth model of the flooring plate series and the cover plates is strikingly similar to that of the development and growth of radial ambulacral canals of extant crinoids and other echinoderms. This model can be characterized as a terminal growth with serial branching on the right and left alternating ambulacral appendages. Therefore the hydrocoel and its derivatives, primarily radial ambulacral canals, can be considered as inductors of successive events, including skeleton development. This is analogous to the dorsal blastopore lip and its derivatives, the chord and prechordal mesoderm in vertebrates. Growth and branching of radial ambulacral canals can be considered as a model inducing a similar model first in the development of the axial skeleton, and later in some parts of the extraxial skeleton (in the terminology of David and Mooi, 1998). As the autonomy of the skeleton of the food-gathering appendages increased, the model of alternating biserial terminal growth could apparently be simplified to uniserial, terminal growth. This process could have followed a pattern, which can be reconstructed by comparing brachiole morphology in different rhipidocystids. Initially, the brachiolars of adjacent series were shifted to the same level to form paired plates. This corresponds to a change in growth from alternating terminal biserial to simultaneous biserial. Later, the fusion of paired plates resulted in uniserial terminal growth. In paracrinoids with arms arising from the theca, the transition from uniserial to biserial growth could have followed this rhipidocystid pattern. In genera with recumbent arms, the transition from biserial to uniserial brachioles was probably more complex. This can be inferred from the morphology of the ambulacra in *Heckerites*. Biserial flooring plates in this genus are at the same time thecal plates covering the thecal interior, similar to edrioasteroids. However, in contrast to the ambulacra of edrioasteroids, at least one of the two ambulacra of *Heckerites* terminates with a terminal plate. This terminal plate is probably equivalent to the ocular plate in echinoids and the terminal plate in starfish, which limits the terminal growth of an ambulacrum to the theca. In comparison, in the North American paracrinopid genus *Platycystites,* only the most proximal plates of the uniserial recumbent arm directly cover the thecal interior, and later the plates of the theca become fused, so a lumen expanded proximally and decreasing distally is developed between the arm ossicle and thecal callus (Parsley and Mintz, 1975). There is no terminal plate, and the ambulacrum growth is not limited to the theca and sometime continues much further down to the stem.

## CONCLUSIONS

The biserial skeleton of the food-gathering appendages of the Baltic genera *Achradocystites* and *Heckerites* could transform into uniserial arms and pinnules characteristic of the North America paracrinoids, following the rhipidocystid pattern. Therefore the biserial pattern in the Baltic genera does not contradict their placement within paracrinoids but suggests that they separated from the main stalk of paracrinoids of Laurentia at the early stages of its development, probably beyond the realms of both Laurentia and Baltica.

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# THE DISPARID FAMILY ALLAGECRINIDAE (CRINOIDEA): PROBLEMS IN SYSTEMATICS AND PHYLOGENY

George D. Sevastopulo

Department of Geology, Trinity College Dublin, Dublin 2, Ireland. gsvstpul@tcd.ie

**Keywords:** Allagecrinidae, Disparida, Crinoidea, ontogeny, systematics, phylogeny.

## INTRODUCTION

Recent treatments of crinoid taxonomy recognize a monophyletic clade Disparida - as an Order in the Treatise on Invertebrate Paleontology (Moore and Teichert, 1978) or as a Subclass in Ausich (1998); Ausich *et al*. (2014); and Ausich *et al*. (this volume). Ausich (1998) carried out a phylogenetic analysis of all Ordovician crinoids, and recognized seven orders of disparids. However, he did not analyze post-Ordovician taxa, which, with the exception of the Order Calceocrinida, have not been subjected to comprehensive phylogenetic analysis. The Calceocrinida contains several relatively character-rich genera and appears amenable to phylogenetic analysis (Harvey and Ausich, 1997). However, even in this case, homoplasy appears to have been rife and Harvey and Ausich used stratigraphic information to reduce the very large number of equally parsimonious trees generated in their analysis. In contrast to the Calceocrinida, many of the post-Ordovician families within the Disparida recognized in the Treatise (to which the reader is referred for details of authorship of taxa) contain few genera or only a single genus: examples are Anamesocrinidae (monotypic), Haplocrinitidae (monotypic) and Pygmaeocrinidae (*Pygmaeocrinus* and *Storthingocrinus*, the latter clearly not related to the former following the comprehensive description by Bohatý *et al*., 2014). The family Allagecrinidae, like the Calceocrinida, contains several genera, but individual genera are generally character-poor, and to date have not been subjected to phylogenetic analysis.

## THE FAMILY ALLAGECRINIDAE

A typical allagecrinid has a small theca (many are so-called microcrinoids) consisting of three circlets of plates. There are competing hypotheses regarding the homology of the circlets of the aboral cup with those of other crinoids. For the purposes of this discussion, the terminology proposed by Ausich (1996) is adopted; irrespective of what terminology is used, there is no suggestion that the three circlets making up the theca are not homologous in all allagecrinids. The theca consists of lintels, five arm-bearing infrabasals and five primary peristomial cover plates (Kammer *et al*., 2013), formerly referred to as oral plates; these may be lacking in mature individuals of some genera. The infrabasals may be axillary, each bearing from two to more than 11 uniserial arms. The infrabasal in the C ray in some genera bears an arm-like anal series on its left shoulder. The column consists of a distally tapering proxistele, formed of columnals with a distinctive architecture of the articular surface with a narrow crenulate rim and a central raised, nodose areola (Lane and Sevastopulo, 1981; 1982), which may possibly a synapomorphy for the clade, and a dististele, which is poorly known for most genera. The character that is diagnostic for identification of the Allagecrinidae and particularly for distinction from the Catillocrinidae, with which they are grouped in the superfamily Allagecrinacea in the Treatise, is the distribution of arms on the infrabasals. The allagecrinid genera recognised in the Treatise have either five or fewer arms, or three axillary infrabasals (A, B and D); in the catillocrinid genera recognized, only two infrabasals are axillary (A and D). Exceptions within the allagecrinids are *Thaminocrinus* (C infrabasal axillary) and *Wrightocrinus* (only A and D infrabasals axillary) and within the catillocrinids *sensu* the Treatise, *Allocatillocrinus* (A, B and D infrabasals axillary), *Isocatillocrinus* (all infrabasals axillary), *Neocatillocrinus* (A, B and D infrabasals axillary), *Xenocatillocrinus* (A, B, C and D infrabasals axillary).

## *ALLOCATILLOCRINUS*

The case of *Allocatillocrinus* is instructive. The type species, *A. carpenteri*, is from the Mississippian (late Viséan) of the USA. It has been possible to trace its ontogenetic history using several well preserved crowns on shale surfaces with portions of stem still attached, individual thecae and disarticulated plates washed from shales (Sevastopulo, 2008). The smallest individuals are armless. As the theca grew, arms were added in the order C, E, B, D, A - the pattern common to all the genera of the Allagecrinidae investigated to date (Sevastopulo and Lane, 1988). At this five-armed stage of development, the thecae are morphologically similar to species of the genus *Litocrinus* (Lane and Sevastopulo, 1981). After the five-armed state was achieved the anal tube developed. Thereafter, new arm facets were added to the B, D, and A infrabasals. Large individuals bore as many as 30 arms. Larger specimens of the theca lack primary peristomial cover plates. The absence of peristomial cover plates commensurate in size with the large thecae in washed residues is interpreted as reflecting their resorption, because the residues do contain isolated large axillary infrabasals and lintels. *Allocatillocrinus* differs from *Allagecrinus*, the type genus of the Allagecrinidae, only in the larger number of arms present, and consequently the width of arm articular facets in thecae of comparable height, and possibly also in the stage in development at which the peristomial cover plates were resorbed (later, or not at all, in *Allagecrinus*). *Allocatillocrinus* clearly is a member of the Allagecrinidae. Moore (1940) suggested that it was derived from *Allagecrinus* and placed it in a subfamily Allagecrininae; its inclusion in the Catillocrinidae (Catillocrininae in Moore, 1940) in the Treatise reflects a later pre-occupation with symmetry of the aboral cup.

Gutschick (1968) described two species, assigned to *Allagecrinus*, from Chesterian rocks of southern Illinois, USA. One of these, *A. coronarius*, can be shown to be based on specimens of *Allocatillocrinus carpenteri* that are not fully mature, because topotype material of the former includes disarticulated axillary infrabasals closely comparable in size and number of arm articular facets to the holotype of the latter. Similarly, Lane and Sevastopulo (1982) showed that microcrinoids named by Weller (1930) as *Kallimorphocrinus*, and described by him as being five-armed, having peristomial cover plates and lacking an anal tube, are immature examples of a mature microcrinoid which had axillary infrabasals and an anal tube and lacked peristomial cover plates. This necessitated the introduction of a new genus, *Litocrinus*, to accommodate species that had five arms, no anal tube and retained the peristomial cover plates at maturity.

The examples above illustrate that in order to characterize an allagecrinid species completely and to assign it to a genus, the full growth history needs to be established. Because the early stages of ontogeny are similar in disparid families that are not closely related, an immature specimen with the characters of *Litocrinus*, for example, might not even be an allagecrinid. Moore and Ewers (1942) and Koenig (1956) described the ontogeny of two species of disparid, each of which was assigned to *Synbathocrinus*. The generic assignment of the juveniles has been disputed by Marcus (2000) but is endorsed here. Immature thecae of *Synbathocrinus* are similar to those of *Litocrinus*. The majority of species of allagecrinids have been described on the basis of small numbers of specimens. Consequently, their generic assignment may be incorrect with the consequence that the stratigraphical ranges of many genera based on published records are suspect.

## EVOLUTION OF *ALLOCATILLOCRINUS* AND RELATED FORMS

*A. carpenteri* from the USA, and the closely similar *A. scoticus* from Scotland, are the stratigraphically oldest (late Viséan) species recognised to date. They are most probably derived from *Allagecrinus* through increase in the number of arms on the A, B, and D infrabasals. The largest number of arms in the stratigraphically older known species of

*Allagecrinus* (*A. americanus* from the late Famennian (Devonian) of the USA; *A. mccraneyensis*, *A. rowleyi* and *A. sculptus*, all from the Tournaisian of the USA) is 14 and they are all slender, like those of *Allocatillocrinus*, in contrast to the relatively stout arms in the type species of *Allagecrinus*, *A. austinii*. Moore (1940) described a complete growth series of *Allocatillocrinus rotundus* from the Bashkirian (early Pennsylvanian) of the USA. This included the smallest individuals with two arms; larger individuals with five arms, which without additional information, would be assigned to *Litocrinus*; and larger individuals similar to *Allagecrinus*. Mature specimens bore up to 42 slender arms and the theca was substantially wider than high, on which basis the species was placed in a new genus, *Gongrocrinus*, by Burdick and Strimple (1983). The stratigraphically youngest taxon that has been assigned to *Allocatillocrinus* is *A. rarus*, described by Arendt (2007) from the early Permian (late Artinskian) of Russia. The largest specimen bore 27 arms and the aboral cup is substantially wider than high. If the genus *Gongrocrinus* is to be retained, *A. rarus* should be transferred to it.

The morphological changes observed in the evolutionary history outlined above are: an increase in the ratio of the width to height ratio of the aboral cup; an increase in the number of arms; and the resorption of the primary peristomial cover plates in mature individuals of stratigraphically younger taxa. It is also notable that the size of mature specimens is generally larger in stratigraphically younger taxa (Table 1).

| Taxon | Stratigraphical age | Max height (mm) | Max width (mm) |
|---|---|---|---|
| *Allagecrinus americanus* | Late Famennian | 1.7 | 1.1 |
| *Allocatillocrinus carpenteri* | Late Viséan | 2.8 | 4.6 |
| *Gongrocrinus* [*Allocatillocrinus*] *rotundus* | Bashkirian | 6 | 11.7 |
| *Gongrocrinus* [*Allocatillocrinus*] *rarus* | Late Artinskian | 6.1 | 8.5 |

**Table 1.** Maximum height and width of the aboral cup recorded for different taxa of allagecrinids of different stratigraphical ages. Note that *G. rarus* is known from only 7 specimens (Arendt, 2007).

It could be argued that many of the morphological changes seen in the evolution of these taxa, for instance the increase in the number of arms, are correlated with increase in size for obvious functional reasons, but it is worth noting that one of the smallest specimens of *A. rotundus* described by Moore (1940, fig. 6a, b) has only two arm facets, yet is not much smaller (approximately 1.4mm high and 1.4mm wide) than the largest mature *A. americanus*. It would be worth enquiring whether *Neocatillocrinus* from the Permian of Timor, which shares the same pattern of distribution of arms on the infrabasals as *Allocatillocrinus*, should be transferred to the Allagecrinidae.

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# CAMPANIAN HOLASTERID ECHINOIDS *GALEOLA* AND *OFFASTER* FROM THE KOPET DAGH BASIN, NE IRAN

Hossein Kamyabi Shadan[1], Amir Mohammad Jamali[1], Roghayeh Ghorbanverdi[2] and Mohammad Reza Asnafi[1]

[1] Exploration Directorate, National Iranian Oil Company, Tehran, Iran.
kamiabi1356@yahoo.com, amjgeo@yahoo.com, M.asnafi@hotmail.com
[2] Faculty of earth science, Shahid bahonar university, Kerman, Iran. R.ghorbanverdi@yahoo.com

**Keywords:** Holasteroid Echinoid, Campanian, Abtalkh Formation, Kopet Dagh, Northeast Iran.

## INTRODUCTION

Two well preserved small and domed shape Holasterids *Galeola papillosa* and *Offaster pillula* are reported from the Campanian deposits (AbTalkh Formation) of northeast Iran. *Offaster* and *Galeola* are widespread Late Cretaceous genera of holasterid echinoids whose earliest occurrence has been recorded in the Campanian and its latest one (*Galeola*) in the Maastrichtian (Smith and Jeffery, 2000; Smith and Wright, 2003). *Offaster* and *Galeola* are very similar in shape but *Galeola* differs from *Offaster* by having lower position of the periproct and by lacking a fasciole. The present work reports these taxa from the Campanian Abtalkh Formation in the Kopet Dagh Basin, NE Iran.

## GEOLOGICAL SETTING AND STRATIGRAPHY FRAMEWORK

The paper describes the holasterid echinoids belonging to Galeola and Offaster from two sections (Padeha and Aitamir). These sections are part of the Kopet Dagh Basin in the northeast of Iran. The Padeha section is approximately located 80 km away from southwest of Serakhs City at latitude 36° 30′ 5″ N and longitude 15° 44′ 60″ E and the Aitamir Syncline section is positioned 45 km away from southwest of Maraveh-Tappeh City at latitude 37° 47 ′69″ N and longitude 55° 33′ 38″ E.

Echinoid specimens were sampled from the base of Abtalkh Formation. The Abtalkh Formation has 1650 m thickness in the Aitamir section. The formation rests on the marly and chalky limestone of the Abderaz Formation, and is overlain by the thick-bedded and riffal limestones of the Kalat Formation The dominant rock facies are silty and grey to blue calcareous marl (Afsharharb, 1994; Fakouri, 1996). According to Afshar harb (1994) age of the base of the Abtalkh Formation is Campanian.

## SYSTEMATIC PALEONTOLOGY

The systematic classification follows the Smith and Wright (2003) and all linear measurements are given in millimeters (taken with Vernier Caliper).

*Abbreviations:* L: test length; W: test width; H: test height; $L_{ap}$: Length of the apical disc; $W_{ap}$: width of the apical disc; $L_I$: length of the posterior paired ambulacra (I or V); $L_{II}$: length of the anterior paired ambulacra (II or IV); $L_{III}$: length of ambulacrum III; $L_{pc}$: length of the periproct; $W_{pc}$: width of the periproct; $L_{pr}$: length of the peristome; $W_{pr}$: width of the peristome.

The studied specimen, are housed in the Mr. Hooshang Dashtban personal collection, in Tehran.

Class Echinoidea Leske, 1778
Cohort Irregularia Latreille, 1825
Order Holasteroida Durham & Melville, 1957
Family Holasteridae Pictet, 1857
Genus *Offaster* Desor, 1858
*Offaster pillula* Lamarck, 1816
Fig.1E-H, Table 1

1816 *Ananchytes pillula* Lamarck, p. 27.
2003 *Offaster pilulla* Lamarck; Smith and Wright, p. 550, pl. 175, figs. 5-19; pl. 176, figs. 1-4.[cum syn.]

Material: There were two specimens gathered from Abtalkh Formation, the Padeha section, (RGOf,1&2).

Description: Small globular holasteroids with domed shape test.Oral face is weakly convex and periproct is positioned at mid-height on posterior face. Marginal fasciole weakly distinct.

Occurrence: Upper Cretaceous (Campanian-Maastrichtian), Europe, Former Soviet Union (Smith and Wright, 2003) and the Campanian of Padeha section, NE of Iran.

Family Incertae sedies
Genus *Galeola* Quenstedt, 1874
*Galeola papillosa* Leske, 1778
Fig. 1A-D, Table 1

1778 *Echinocorys minor* var. *papillosa* Leske, p. 183, pl. 16, figs C,D.
2003 *Galeola papillosa* Leske; Smith and Wright, p. 554, pl. 176, figs. 5-16.

| *OFFASTER* and *GALEOLA* | Parameter/Species no. | RGOf-1 | RGOf-2 | HKGp-1 | HKGp-2 |
|---|---|---|---|---|---|
| | **L** | 20.8 | 14.3 | 33.5 | 32.3 |
| | **W** | 18.7 | 13.05 | 30.05 | 28 |
| | **H** | 15.5 | 13.2 | 20.6 | 21.1 |
| | **W/L** | 0.90 | 0.91 | 0.90 | 0.87 |
| | **H/L** | 0.75 | 0.92 | 0.61 | 0.65 |
| | $L_{ap}$ | 4.5 | 3.9 | 6.6 | 5.4 |
| | $W_{ap}$ | 2.6 | 2.2 | 3 | 2.8 |
| | $L_I$ | 14.1 | 10 | 19.8 | 20.6 |
| | $L_{II}$ | 14 | 10.3 | 18.6 | 19.5 |
| | $L_{III}$ | 13.1 | 10 | 18.6 | 18.7 |
| | $L_{pc}$ | 3.6 | 3.1 | 4 | 4 |
| | $W_{pc}$ | 2.9 | 2.7 | 4 | 4.1 |
| | $L_{pr}$ | 2.6 | 2.4 | - | 4.2 |
| | $W_{pr}$ | 2.7 | 2.4 | - | 4.35 |

**Table 1.** Quantitative description of the test shape variations in *Offaster pillula* and *Galeola papillosa*.

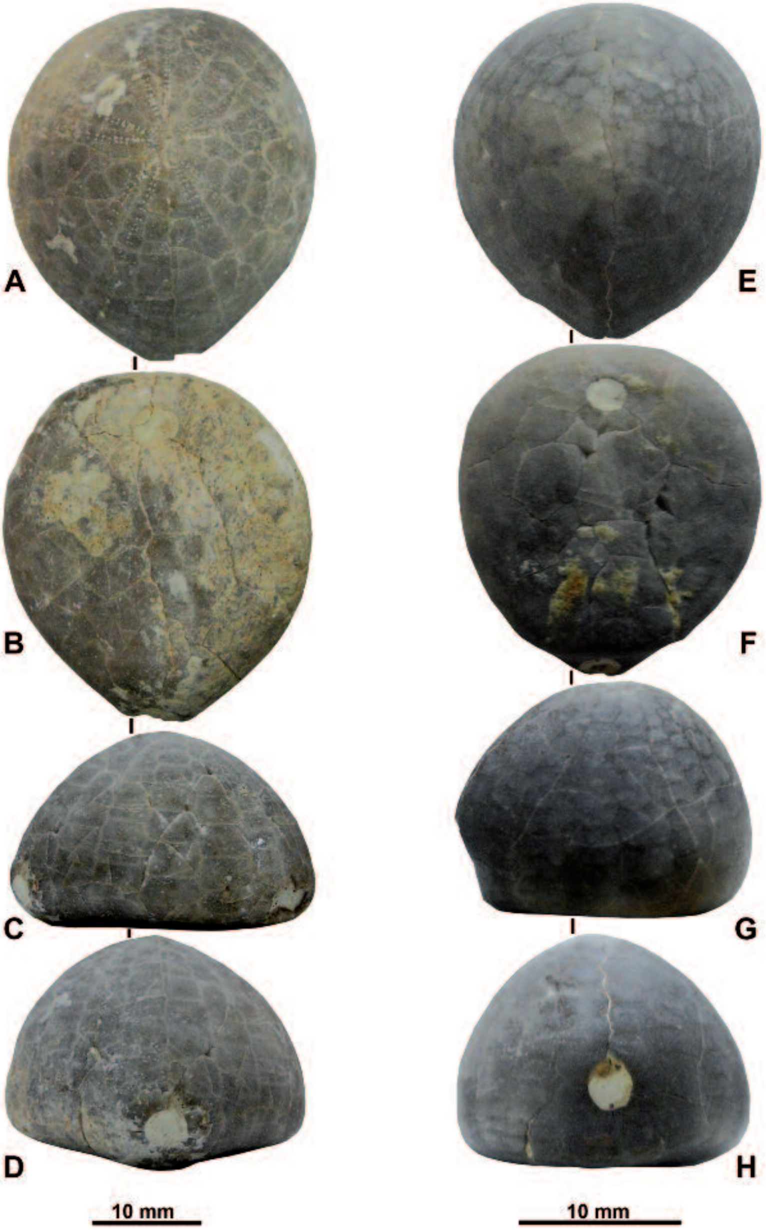

**Figure 1.** A-D. *Galeola papillosa* Leske,1778.Campanian, Abtalkh Formation, Aitamir section. Specimen HKGp. 2; A. apical view, B. oral view, C. Lateral view and D. Posterior view. E-H. *Offaster pillula* Lamarck, 1816.Campanian, Abtalkh Formation, Padeha section. Specimen RGOf. 1; E. apical view, F. oral view, G. Lateral view and H. Posterior view.

Material: There were two specimens gathered from Abtalkh Formation, the Aitamir section, (HKGp.1&2).

Description: Small Holasteroids with subconical to slightly domed shape test without anterior sulcs. Oral face is flat to slightly convex and periproct is positioned inframarginally to marginally at low-height on posterior face. There is no fasciole.

Occurrence: Upper Cretaceous (Campanian), Europe, and England (Smith and Wright, 2003) and the Campanian of Aitamir Syncline section, NE of Iran.

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# A NEW INTERPRETAION OF THE ORAL PLATING PATERNS OF THE *HOLOCYSTITES* FAUNA (DIPLOPORITA, ECHINODERMATA)

Sarah L. Sheffield and Colin D. Sumrall

Department of Earth and Planetary Sciences, The University of Tennessee, 1412 Circle Dr., Knoxville, TN 37996, USA.
ssheffi2@vols.utk.edu, csumrall@utk.edu

**Keywords:** *Holocystites*, diploporitan, oral plating, homology.

## INTRODUCTION

The *Holocystites* Fauna of North America presents a rare window into Silurian-age North American diploporitans, which have been found almost exclusively within the Wenlock (middle Silurian) of the midwestern portion of the continent (Paul, 1971; Frest *et al*., 2011). As such, a number of studies have been undertaken to understand the paleoecology and evolutionary relationships of this group of organisms, which encompasses the overwhelming majority of all non-gomphocystitid diploporitan taxa described from North American. In fact, *Gomphocystites* (widely distributed in middle Silurian strata of the midcontinent) is the only Silurian North American diploporitan not included within the *Holocystites* Fauna (Bockelie, 1984; Frest *et al.,* 2011).

Very few studies have been done to reevaluate the taxa that have been erected; those studies have typically erected more genera and species from within the original collections (Paul, 1971; Frest *et al.,* 2011). Two studies have involved the taxonomic makeup of the *Holocystites* Fauna, one that was purely systematic (Paul, 1971) and one that was quasi-phylogenetic (Frest *et al.,* 2011). The *Holocystites* Fauna were split amongst newly erected genera based on major differences in their thecal shape and ambulacral system. Genera included within the *Holocystites* Fauna are: *Holocystites* Hall 1861 (Fig. 1A); *Pentacystis* Paul 1971 (Fig. 1B); *Osgoodicystis* Frest and Strimple 2011 (Fig. 1E); *Trematocystis* Miller 1878 (Fig. 1G); *Paulicystis* Frest and Strimple 2011 (Fig. 1I); *Pustulocystis* Miller 1891; and *Brightonicystis* Paul 1971. However, much of this work should be re-evaluated using modern homology and phylogenetic methods.

A common problem across a number of fossil groups is that the identification of morphological features is often based on location or function rather than homology within an evolutionary lineage. This problem is especially highlighted in the echinoderms, where plates associated with the peristome are given different names in each clade, based on location with respect to the ambulacra and peristomial opening (Sumrall, 2010). However, analysis of a number of stemmed echinoderms shows that the peristomial bordering plates of different echinoderm groups are derived from common ancestry. By not recognizing homologous elements, the evolutionary relationships between these groups are often poorly understood. Universal Elemental Homology (Sumrall and Waters, 2012; Kammer *et al.,* 2013) is an attempt to correctly identify the homologous elements across echinoderm clades.

It was previously unrecognized that members of the *Holocystites* Fauna had a conservative peristomial border plate system that was modified among the genera involved. All taxa bear the plesiomorphic seven oral plate configuration characteristic of derived stemmed echinoderms (Sumrall, this volume). Orals 1, 6 and 7 lie in the CD interray with O7 precluded from the peristomial opening by O1 and O6. Oral 7 also uniformly is in contact with the periproct. The remaining oral plates lie interradially and bear the proximal food grooves along their adjacent sutures (Fig. 1D).

Seven facetals form a plate circlet distal to the oral plates (Fig. 1D). Five plates of this circlet lie radially and bear large facets for erect feeding appendages. These are labeled A-E in relationship to the ambulacra they support. Two additional facetals (labeled L) do not bear appendage facets are positioned in the lateral position between the B and C and the D and E ambulacra. Oral 7 is positioned in this circlet between plates C and D resulting in the facetal circlet to be open. It is an important distinction that this plate series is not part of the ambulacral system but rather thecal plates that have ambulacra supported upon them epithecally.

Previous studies of the *Holocystites* Fauna have been flawed by a lack of understanding of this basic structure. This resulted in a complicated and confused narrative, with resulting from changes in the number and positions of oral and facetal plates surrounding the peristomial opening. Careful analysis of type specimens from various museum collections show that some of the taxa have been erected from differences that are purely taphonomic, rather than intrinsic to the taxa involved. For example, *Pentacystis gibsoni* Paul 1971 (Fig. 1B, C) was erected, in part, based on the number of oral plates surrounding the peristome; the holotype of the genus shows only O7, located above the periproct. The lack of O1-O6 around the peristome caused it to be distinguished from other genera in the fauna; upon closer analysis, attachment surfaces from oral plates O1-O6 can be seen and it is evident that the loss of these plates is only a taphonomic artifact (Fig. 1C). When *Pentacystis* is compared with *Osgoodicystis bissetti* Frest and Strimple 2011 (Fig. 1E, F), a species here shown to have seven oral plates, it is clear that these two taxa show identical plating of the ambulacral plate series and are congeneric.

## DIFFERENTIATION OF GENERA

*Holocystites* has the stereotypical arrangement for the peristomial border (Fig. 1A, D). All five ambulacra lead to scars that are partly positioned on the oral plate series and the facet-bearing facetal circlet. The positioning of the facets is looser than other taxa often spread across edges of more than one facetal. The species currently described within *Holocystites* show high variability with one another. *H. scutellus* exhibits proportionately small and bulbous thecal plates with sunken plate sutures and the distal end of the theca narrows to an almost stem-like distal region below a globular upper region. Other species are represented by a number of different thecal shapes, plate forms, and by makeup of the distal portion of the theca.

*Pentacystis* bears the stereotypical arrangement for the holocystitid border (Fig. 1B, C). All five ambulacra lead to large facets for erect appendages that are wholly supported on the facet bearing plates of the facetal series. Plates of the oral series are narrow and confined to the peristomial depression except for O7, which is large. The facetals are large and form a spout-like protuberant summit structure. Each of the appendage facets is confined to the center of the facet bearing plates. The lateral facetals are not depressed. The thecal plates are large and flat without sunken sutures. The theca is elongate and globular, narrowing toward the base without a constricted distal portion like *Holocystites*. Thecae are often preserved missing O2-O5 or O1-O6 causing confusion in the peristomial border designations in the past. *Osgoodicystis* is a junior synonym of *Pentacystis*.

*Trematocystis* (Fig. 1G, H) bears the stereotypical holocystidid oral plating, except that the A ambulacrum is missing via paedomorphic ambulacral reduction (Sumrall and Wray, 2007). Large facets for the B-E erect ambulacra are centered in the facet bearing facetals and the lateral facetals and A facetal are sunken. Oral 7 is relatively small as compared to other taxa. The thecal plates are large and flat without sunken sutures. The theca is squat and globular and has a relatively wide cementation disk.

*Paulicystis* (Fig. 1I, J) bears the stereotypical holocystidid oral area except that the A ambulacrum is missing by paedomorphic ambulacral reduction (Sumrall and Wray, 2007). The remaining ambulacra rather than being in the form of erect appendages are recumbent on the thecal surface beginning with scars on the facet bearing facetals. The lateral and A facetals are sunken with respect to the other facetals. O7 is smaller than other taxa and is similar to that seen on *Trematocystis*. The thecal plates are small and bulbous with sunken sutures. The theca is squat and globular with a relatively wide cementation disk.

Neither *Brightonicystis* Paul 1971 nor *Pustulocystis* Miller 1878 was examined for this study based on a lack of preservation in available specimens.

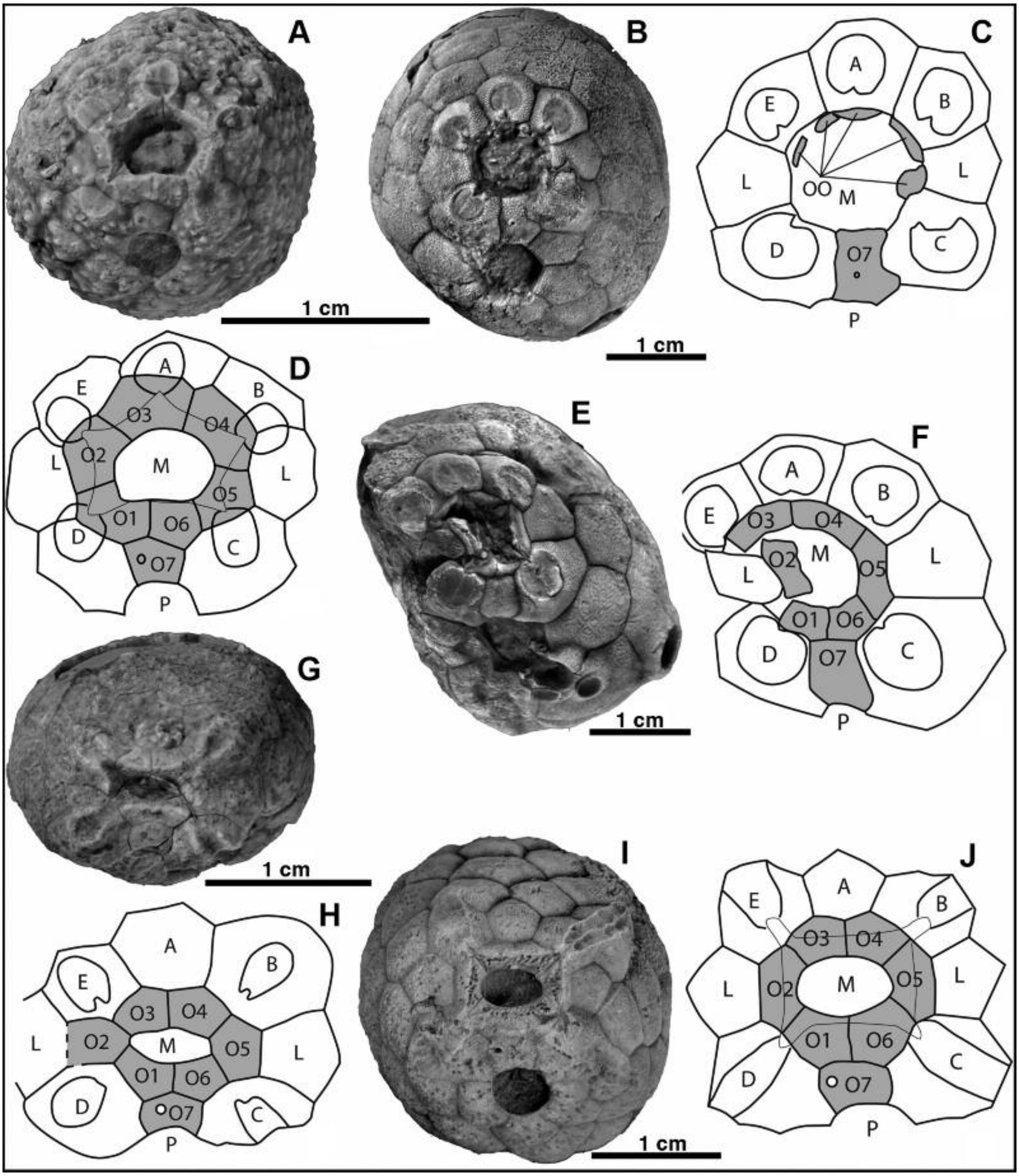

**Figure 1.** A, D. *Holocystites scutellus* (SUI48183)*;* ambulacral scars are positioned on both facetal and oral plates. B, C. *Pentacystis gibsoni* (SUI48170); ambulacral scars positioned completely on facetal plates. E, F. *Osgoodicystis bissetti* (SUI48166)*;* considered to be a junior synonym of *Pentacystis gibsoni* (openings in lower hemisphere parasitic embedment structures, *Tremichnus* (Brett, 1985)). G, H. *Trematocystis magniporatus* (SUI48198)*;* A ambulacrum is missing due to paedomorphic ambulacrum reduction. I, J. *Paulicystis densus* (SUI48164); A ambulacrum missing due to paedomorphic ambulacral reduction and ambulacra are recumbent. M=mouth; L=non appendage bearing facetals; P=periproct; O=oral plate. Scale bars=1cm.

## FINAL CONSIDERATIONS

The revision of the phylogenetics of the *Holocystites* Fauna is part of a much larger effort to better understand the evolutionary relationships of the larger diploporitan group, which has been long since described as polyphyletic (Paul, 1971; Sumrall *et al.,* 2009; Lefebvre *et al.,* 2014). At present, there is only one potential synapomorphy for the group, the presence of diplopore respiratory structures (Sprinkle, 1973). However, based on the different constructions of these respiratory structures and a host of other differences in the construction of the feeding ambulacral system, attachment structures etc., it is likely that the diploporitans do not represent a monophyletic group, and a phylogenetic analysis will test this. This work will place diploporitans into a testable evolutionary framework and will determine if the three groups of diploporitans represent a monophyletic evolutionary group or are dispersed in the echinoderm evolutionary tree. Ultimately, the diploporitans will be placed into the context of the larger echinoderm tree of life.

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# COMPUTED TOMOGRAPHY (CT) SCANS OF A NEW ORDOVICIAN CYCLOCYSTOID FROM MOROCCO AND ITS ORIENTATION AND LIFE MODE

James Sprinkle[1], Mike Reich[2] and Bertrand Lefebvre[3]

[1] Department of Geological Sciences, Jackson School of Geosciences, University of Texas, 1 University Station C1100, Austin, TX 78712-0254, USA. echino@jsg.utexas.edu
[2] SNSB – Bayerische Staatssammlung für Paläontologie und Geologie München and Ludwig-Maximillians-Universität München, Department für Geo- und Umweltwissenschaften, Sektion Geobiologie und Paläontologie, Richard-Wagner-Strasse 10, 80333 München, Germany. m.reich@lrz.uni-muenchen.de
[3] UMR CNRS 5276 LGLTPE, Université Lyon 1, 2 rue Raphaël Dubois, 69622 Villeurbanne cedex, France. bertrand.lefebvre@univ-lyon1.fr

**Keywords:** Cyclocystoid, Morocco, Ordovician, morphology, orientation, life mode.

## INTRODUCTION

Cyclocystoids are a relatively small extinct class of circular, flattened echinoderms that have been known for about 155 years. Twenty genera and about 40 valid species have been named, ranging from the Middle Ordovician to the Early Carboniferous (Smith and Paul, 1982; Ressmeyer and Frest, 1983; Berg-Madsen, 1987; Haude and Thomas, 1994; Boczarowski, 2001; Reich and Kutscher, 2010). Most specimens come from Laurentia and Baltica (Lefebvre *et al.*, 2013), but a few are known from Avalonia and Laurussia. However, our new material represents the second report (and first articulated material) of this echinoderm group from Gondwana. Their morphology has been controversial because well-preserved specimens that show all parts of the animal are rare, and several different interpretations have been proposed (Salter and Billings, 1858; Foerste, 1920; Sieverts-Doreck, 1951; Kesling, 1966). However, Smith and Paul (1982) produced a comprehensive monograph of the class using a large number of well-preserved museum specimens and established six new genera. We agree with many of their conclusions involving systematics, biostratigraphy, morphology, diversity, phylogeny, and biogeography, but disagree with their interpretation of orientation and feeding mode. The recent discovery of a new cyclocystoid from the Middle and Late Ordovician of Morocco shows somewhat different morphology and additional evidence about the likely living orientation of cyclocystoids.

## MATERIAL AND OCCURRENCE

Six specimens of this new cyclocystoid from SE Morocco are known: two were in a private collection for about five years until donated recently to the palaeontological collections of Lyon 1 University, Villeurbanne, France (FSL) for study and description; one was sold at the 2013 Tucson Fossil Show to a private collector (we have only photographs of this concretionary specimen); Sprinkle purchased another concretionary specimen at the 2014 Tucson Fossil Show, perhaps from the same vendor, and deposited it in the Non-vertebrate Paleontology Laboratory (NPL), University of Texas, Austin; and two other partial concretionary specimens were found by or given to Samuel Zamora in 2014 and have been borrowed from the Natural History Museum, London, UK. All six specimens are preserved as external molds either on slabs of fine-grained siliciclastic matrix or in siderite-encrusted siliciclastic concretions. Most specimens (including the NPL one) come from the Taddrist Formation (Darriwilian, upper Middle Ordovician), but one is reported to be from an Upper Ordovician formation.

## X-RAY COMPUTED TOMOGRAPHY SCANS

Because the fragile molds in the NPL concretion (Fig. 1A-B) had not previously been cast in latex (the standard technique for studying moldic specimens), they were submitted for possible scanning at the University of Texas at Austin High-Resolution X-ray Computed Tomography (CT) Facility. We hoped that the reassembled concretion with its internal air-filled cyclocystoid mold could be differentiated from the enclosing siliciclastic matrix encrusted by siderite. This technique has recently been used to scan molds of arthropods and a few echinoderms in a variety of sedimentary rocks and concretions (Rahman *et al*., 2012; Sutton *et al*., 2014). The non-destructive results of this scan were excellent, producing numerous cross sectional views through the concretion, usable top, side, and bottom views of the void space representing the reconstructed specimen (Fig. 1C-F), and a rotating model that eliminated part of the enclosing concretion matrix.

## MORPHOLOGY

Like most other cyclocystoids, the new specimens are nearly circular in top or bottom view, and flattened vertically along the axis. A slightly domed central disk of small, thin plates is surrounded by a ring of large, thick, marginal ossicles, which in turn are surrounded by elongate frontal plates and a peripheral skirt of tiny imbricate plates (Smith and Paul, 1982). The marginal ossicles have either one or two pores penetrating them radially. The upper side is domed with V-shaped notches between ossicles; the lower side is nearly flat with tightly sutured ossicles. No cupules are present on the outer edge of the marginal ossicles (Fig. 1C-E), only elongate, trough-shaped, frontal plates attached to the lower edge. In the NPL specimen, a 2-3 plate segment of the marginal ring is shrunken with numerous small ossicles (Fig. 1A, right; Fig. 1C, top), perhaps from an early injury. The central disk is circular, domed in the concretion, very thin and apparently double-layered, with pores alongside radiating grooves that appear to be covered food grooves (Fig. 1C-D). No mouth or anal opening is visible in the central disk of this specimen. The peripheral skirt is relatively wide, extends between and beyond the frontal plates, and is slightly raised in the concretion. It has numerous diagonal rows of small-to-tiny imbricate plates decreasing in size outwards (Fig. 1C-D). The interior of the domed central disk has no basal plated surface extending in from the marginal ossicle ring in CT scan cross sections (Fig. 1F).

## ORIENTATION AND LIFE MODE

Most earlier authors who named and studied cyclocystoids (Salter and Billings, 1858; Foerste, 1920; Kesling, 1966 [Fig. 2A], and Kolata, 1975 [Fig. 2B]) reconstructed them as small-particle suspension feeders living with the flattened ventral side recumbent on or attached to the sea floor. Most later authors (starting with Nichols, 1969; but especially Smith and Paul, 1982 [Fig. 2C]; Berg-Madsen, 1987; Rowe, 1988; and Glass *et al*., 2003) reconstructed cyclocystoids as mobile, small-particle, deposit-feeders with the convex surface down with no large body cavity. Our interpretation (Fig. 2D) mostly uses the morphology of the later authors, but returns to the inferred orientation and life mode of the earlier authors.

The circular flattened shape of this new cyclocystoid, the domed central area, and the lack of an enclosed body cavity containing the soft parts of the animal (digestive system, gonads, water-vascular system, other structures) indicate to us that cyclocystoids lived with their flat surface downward, sitting on or attached to the sea floor like most post-Cambrian domal edrioasteroids (Guensburg, 1988; Sumrall, 1994). The elongate frontal plates, convex marginal ossicles, and domed central disk with its radiating grooves were upward-facing regions where food particles were first collected and then transported to a central mouth. The body cavity below the domed central disk sat directly on the sea floor without an underlying plated surface. The flat side of the marginal ring plates and especially the surrounding

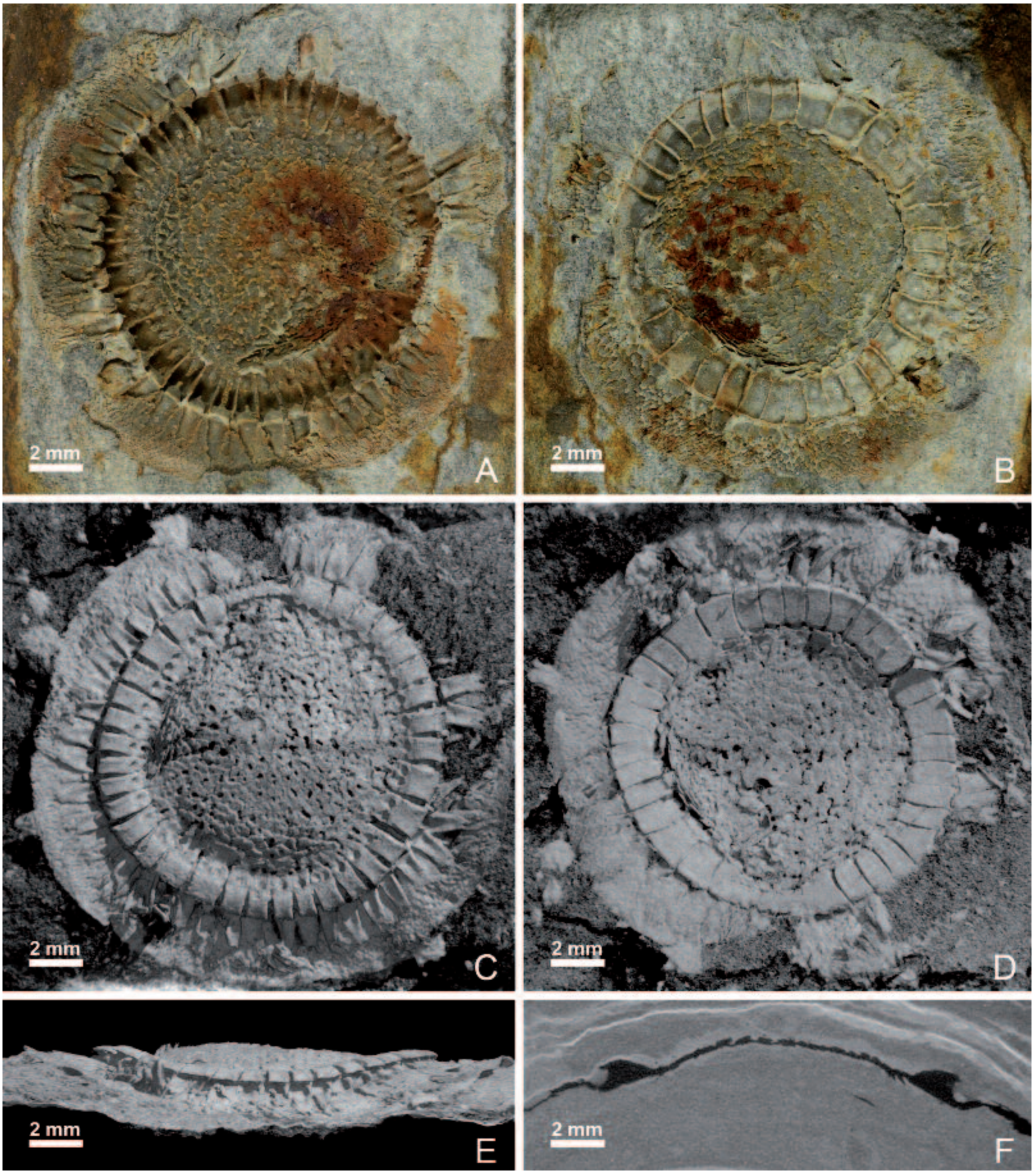

**Figure 1.** New cyclocystoid specimen NPL 62451A&B (Middle Ordovician) from SE Morocco. A-B. Top and bottom counterpart molds in siderite concretion (red staining) showing small-plated central disk, high-relief marginal ossicle ring (note shrunken segment at right of A), elongate frontal plates just outside ring (note disrupted plates), and 2/3-complete, tiny-plated, peripheral skirt; C-D. Frames 0000 and 0043 of reconstructed CT-scanned model (top and bottom views) showing convex central disk with pores, domed and flat sides of marginal ossicle ring (note shrunken segment at top of C), elongate frontal plates, and wide peripheral skirt; E, Frame 0067 of reconstructed CT-scanned model (side view looking toward lower edge of C) showing domed central disk and marginal ossicles overhanging elongate frontal plates; elongate, white, digitally-cut margin in left-front matrix digitally removed; F. Slice 36 through center of cyclocystoid molds showing thin, domed, central disk, thick marginal ossicles with flat bottoms and distal overhangs, and surrounding thin frontal and skirt plating; concretion cracked open just beyond right edge.

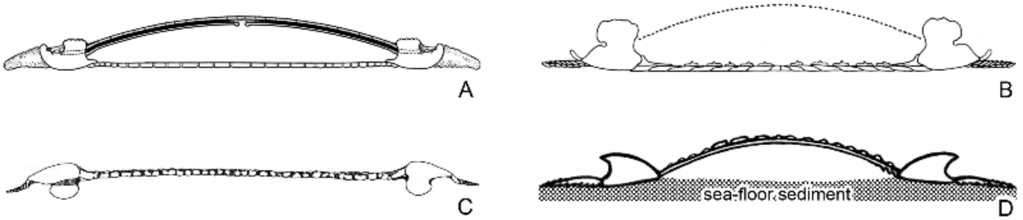

**Figure 2.** Unlabeled cross-sectional reconstructions of cyclocystoid morphology and inferred living position by recent authors. A. Modified Kesling (1966) reconstruction showing two plated central disks, one domed above soft parts, one flat on sea floor; B. Modified Kolata (1975) reconstruction showing single central disc flat on sea floor; C. Modified Smith and Paul (1982) reconstruction showing cyclocystoid inverted with nearly flat marginal surface above and feeding central disk below; D. Our cyclocystoid reconstruction showing nearly flat marginal ossicles on sea floor and domed central disk above internal soft parts, also on sea floor.

imbricate peripheral skirt held the cyclocystoid down on the sea floor using the weight of the thick marginal ossicles, perhaps aided by suction or bioglue, or actual cementation to a firm or lithified substrate. Our largest FSL specimen from Morocco is sitting on a yellowish-brown slab that may have been a hardground. Cyclocystoids are sometimes found on carbonate hardgrounds in Laurentia, where cementation was more common (Wilson *et al.*, 1992), and they are predominantly flattened-side down (Kolata, 1975; Tom Guensburg, pers. comm.).

## CONCLUSION

This Moroccan cyclocystoid appears to represent a new family, genus, and species because it lacks cupules on the outer edge of the marginal ossicles, and has elongate-trapezoidal, trough-shaped, frontal plates instead (Fig. 1C). It will be described in a separate longer publication (Reich *et al.*, in preparation).

We disagree with Smith and Paul (1982) about the inferred orientation of cyclocystoids such as this new taxon from Morocco. The nearly flat sides of the marginal ossicles, the frontal plates, and the peripheral skirt are very similar to the large-to-tiny peripheral rim plates in domal edrioasteroids, which are interpreted to have been attached to the substrate using their flat lower surface around an unplated central area. Although the overall thecal shape appears to have been very similar in cyclocystoids and many domal edrioasteroids, other oral surface, ambulacral, and marginal ring features had become very different, indicating that these classes had either converged because of similar life modes, or were only distantly related sister groups.

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We thank Jessica Maisano for scanning and reconstructing the sections of this NPL cyclocystoid in its concretion at the High-Resolution X-ray Computed Tomography Facility, University of Texas at Austin, using funding provided by NSF Grant EAR-1258878; Angie Thompson, NPL, for digitally photographing the concretion halves using a camera purchased through NSF Grant DBI-0646468; Moussa Minerals & Fossils and Kendal Martyn for their help in acquiring the NPL cyclocystoid for research; Diana Sprinkle, Austin, TX, for setting up digital photos and drawings in figures 1 and 2; and Timothy Ewin, Andrew Smith, and Samuel Zamora for access to the newly collected cyclocystoids housed at the Natural History Museum, London. Samuel Zamora and William Ausich reviewed this PEP Proceedings manuscript and made several helpful suggestions for improvements. The Geology Foundation, University of Texas at Austin, provided funds to acquire the NPL cyclocystoid, and travel funds to attend the PEP Symposium. This paper is also a contribution to Project RALI (Rise of Animal LIfe).

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# UNDERSTANDING THE ORAL AREA OF DERIVED STEMMED ECHINODERMS

Colin D. Sumrall

Department of Earth and Planetary Sciences, The University of Tennessee, 1412 Circle Dr., Knoxville, TN 37996, USA.
csumrall@utk.edu

**Keywords:** Echinodermata, Peristome, Homology, Blastozoa, Crinoidea.

## INTRODUCTION

One of the great challenges encountered while inferring the phylogenetic relationships of echinoderms is an accurate understanding of the homology of skeletal elements across clades. Recently, new insights into homology of elements around the peristome via the universal elemental homology model (UEH) have shown promise for the identification of individual elements associated with the mouth region (Sumrall, 2010; Sumrall and Waters, 2012; Kammer *et al.*, 2013). With this model, evolved differences in plate relationships, morphology, and presence / absence can be identified with high precision and utilized in the construction of characters for use in phylogenetic inference. Here, I will illustrate various taxa of derived stem-bearing echinoderms and show how UEH can be used to describe characters, within this high-resolution framework.

Within derived stemmed echinoderms, the peristomial area is constructed by four plate series. The peristomial opening is bordered by oral plates that are positioned interradially and bear proximal ambulacral food grooves that follow their adjacent sutures. The CD interray bears three orals in most taxa that are associated with the hydropore and gonopore (Sumrall, 2010). The peristome is covered by interradially positioned primary peristomial cover plates (PPCP) that roof the peristome and form the center of the cover plate series. Ambulacral floor plates are positioned perradially and bear the food grooves and brachioles. Ambulacral cover plates mount directly to the oral plates and floor plates covering the ambulacral system. Aligning these plate types to the underlying ambulacral designations allows individual plates to be precisely identified and traced phylogenetically (Sumrall and Waters, 2012).

## DERIVED BLASTOZOAN PERISTOMIAL BORDER CONFIGURATIONS

A common expression of the UEH model is seen in glyptocystitoid rhombiferans and forms the archetype for the model (Fig. 1A). Seven oral plates are positioned around the peristome with O1, O6 and O7 lying in the CD interray and O2-O5 positioned interadially around the peristome clockwise from O1. The 2-1-2 ambulacral symmetry of Sprinkle (1973) is well developed such that O2 and O5 do not touch the peristomial opening. Instead, the shared ambulacra lie on the O4/O6 and O3/O1 sutures. The PPCPs are small and separated. Double biserial floor plates extend from the oral plates and are covered by undifferentiated cover plates. Similar morphologies are seen in the diploporitan *Protocrinites* (Fig. 1C), although the cover plate system is poorly documented.

Some taxa, such as *Rhopalocystis*, show a simplification of this pattern by bearing shorter shared ambulacra. As a result, O2 and O5 share in the peristomial border and consequently, no sutures are seen between O4/O6 and O3/O1 (Kammer *et al.*, 2013). This type of shared ambulacral reduction is common in derived stemmed echinoderms and variations are seen in coronates (Fig. 1G), blastoids (Fig. 1H), plesiomorphic crinoids (Fig. 2A), and several of the diploporitan clades.

Is some diploporitans, such as *Glyptosphaerites,* the oral plates are rotated 36˚ with respect to the ambulacra (Fig. 1E). Here, the main food grooves lie atop the oral plates, rather than along the adjacent sutures, and extend distally, irregularly down the theca. Because the floor plates are lost phylogenetically in this group, the distal food grooves and brachiole facets are borne directly atop the thecal plating. The oral plates are clearly diagnosable despite their radial position by the presence of the plesiomorphic seven-plate oral configuration condition with O1, O6 and O7 positioned in the CD interradius where they are associated with the hydropore and gonopore (Fig. 1E). The PPCPs, however, retain the plesiomorphic interradial position.

Holocystitid diploporitans are highly modified, but retain the plesiomorphic seven oral plate condition (see Sheffield and Sumrall, this volume). Generally, extremely short food grooves extend along oral plate sutures epithecally to large appendage facets mounted on differentiated thecal plates (facetals). Earlier confusion of this peristomial configuration largely resulted from taphonomic issues among poorly preserved specimens (Sheffield and Sumrall, this volume).

Paracrinoids show considerable variation in oral plate arrangement. *Columbocystis* has the plesiomorphic condition with large appendage facets mounted along the oral plate sutures (Kammer *et al*., 2013). In *Bistomiacystis* (Fig. 1B) the oral area has been greatly modified to bear two peristomial openings connecting the BC ambulacra on the right and the ED ambulacra on the left. The A ambulacrum is absent via paedomorphic ambulacral reduction (Sumrall and Wray, 2007). O1, O3, O4 and O6 are roofed over the centrally located common peristome. The hydropore and gonopore are associated with O1, O6 and O7 in the CD interray. Elongated O1, O2, O4 and O5 form the food groove where they suture with right side floor plates of the ambulacral system (Sumrall and Deline, 2009). The diploporitan *Tristomiacystis* is similar but the A ambulacrum has a separate peristomial opening and plate O7 is absent (Fig. 1D) (Sumrall *et al*., 2009).

In *Hemicosmites* the oral area is greatly reduced by paedomorphic ambulacral reduction to include only the A, shared BC, and shared DE ambulacra (Sumrall and Wray, 2007; Sumrall, 2008). Consequently, the lateral oral plates O2 and O5 do not develop. Enlarged oral plates O7, O3, and O4 occupy the interradial areas of the remaining ambulacra. O1 and O6 are extremely small and lie between O7 and the oral area (Fig. 1F). Paired, likely fused, plates derived from the ambulacral floor plates are positioned perradially along the three ambulacra with small first left floor plates ("wedge plates" of Bockelie, 1979) lying along the left edge of the ambulacral groove proximally.

Blastoids (Fig. 1H) and coronoids (Fig. 1G) have similar oral areas owing to their close phylogenetic relationship (Brett *et al*., 1983; Donovan and Paul, 1985). Oral plates are the deltoids whose adjacent sutures form the proximal food grooves. These taxa show almost no hint of 2-1-2 symmetry, except in the configuration of the primary peristomial cover plates (Fig. 1G) and in most blastoids a slightly wider than high peristomial opening (Fig. 1H). The CD interray bears two dominate plates, likely O1 and O7, and in blastoids may include accessory plates (Ctyptodeltoids etc.). Ambulacral floor plates form erect, brachiole bearing appendages in coronoids (Brett *et al*., 1983) and recumbent, epithecal ambulacra in blastoids (Sumrall and Waters, 2012).

## CRINOID PERISTOMIAL BORDER CONFIGURATIONS

Crinoids show several peristomial configurations that transition between a fairly standard oral plate-dominated summit to a plated over tegmen. In taxa bearing an oral plate dominated summit such as *Nuxocrinus* (Fig. 2A), the five interradial fields are occupied by oral plates. The CD interray is unusual because it bears a single oral plate that appears to be O1 (Kammer *et al*., 2013). All five ambulacra enter the peristome via food grooves that mark the sutures between the five oral plates. The arms attach to radial plates across coelomic canals that pierce the summit at the aboral edge of the oral plates. Primary peristomial cover plates are poorly differentiated and plates 1, 3, and 4 articulate over the peristome (Fig. 2A). Plates 2 and 5 mark the bifurcation of the lateral ambulacra. Ambulacral cover plates cover the food groove and remainder of the peristomial cover.

More derived crinoids, such as monobathrids, have no visible oral plates and these plates are either internal or uncalcified (Kammer *et al*., 2013). Instead, the summit is covered by a tegmen, with many of the plates derived from the peristomial and ambulacral cover plate systems (Fig. 2B, C). In plesiomorphic taxa, the PPCPs lie centrally and in contact with the 2-1-2 symmetrical arrangement (Fig. 2B). Cover plates extend radially towards the arms in a biserial arrangement. Spaces between the arms are filled with tegmen filling plates of uncertain origin. More derived taxa, such as *Neoplatycrinus*, greatly enlarge the PPCPs that dominate the tegmen (Fig. 2C).

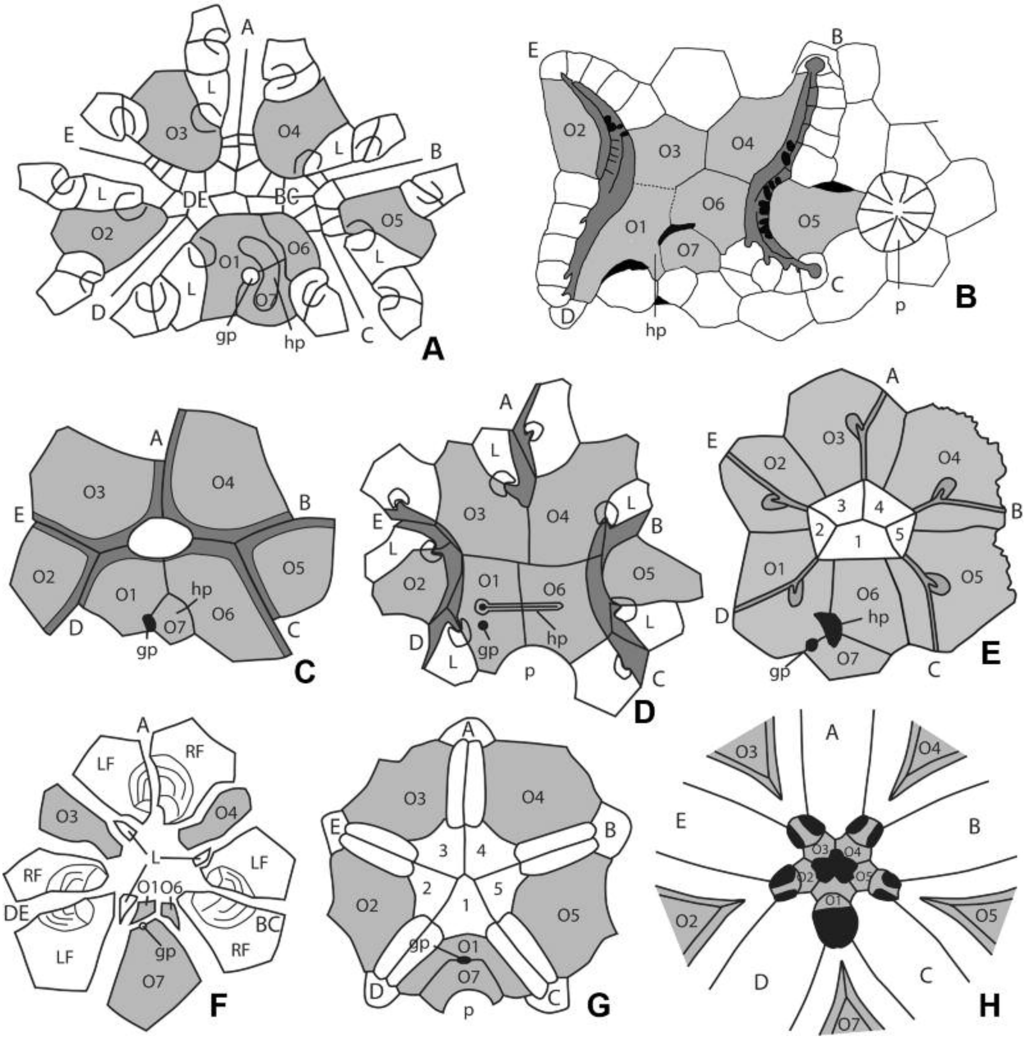

**Figure 1.** Peristomial bordering plate configurations across derived blastozoans. A, the glyptocystitoid *Lepadocystis*; B, the paracrinoid *Bistomiacystis*, C, the diploporitan *Protocrinites*; D, the diploporitan *Tristomiacystis*; E, the diploporitan *Glyptosphaerites*, F, the hemicosmitoid *Hemicosmites*, G, the coronate *Stephanocrinus*, H, the blastoid *Pentremites*, A-E = ambulacral designations, O1-O7 = oral plates (shaded), 1-5 = primary peristomial cover plates, L = first left floor plate, hp = hydropore, gp = gonopore, p = periproct. A, C, F after Sumrall (2009), B after Sumrall and Deline (2006), D after Sumrall *et al.*, (2009), G, H after Sumrall and Waters, 2012.

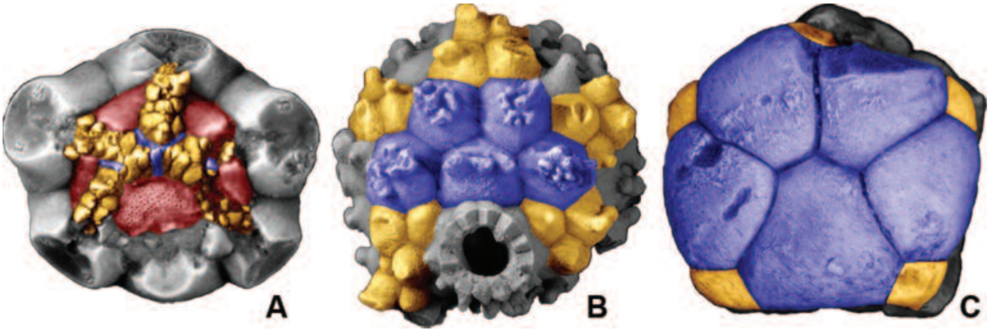

**Figure 2.** Peristomial modification in Crinoidea. A, the cladid *Nuxocrinus* showing the food groove roofed by cover plates (yellow) atop the oral plates (red). Blue are the PPCPs. B, *Collicrinus* showing enlarged PPCPs with biserial cover plates over the subtegmal ambulacra. C, *Neoplatycrinus* showing the tegmen dominated by the PPCPs. Images after Kammer *et al*. (2013).

## CONCLUSIONS

The common morphology seen in the peristomial border of derived stemmed echinoderms indicates that these structures result from a deep-seated homology. Different expressions of these morphologies among subsets of taxa, provide data for phylogenetic inference. The often-confusing nature of peristomial plate names found across stemmed echinoderms typically results from concentrating on differences, rather than the overarching similarity among taxa. It is, therefore, critical that before coding characters, the oral areas of taxa be interpreted using the UEH model to avoid the pitfalls of coding non-homologous elements simply based on position, or possessing the same name as an historical artifact.

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# NEW DATA ON LATE ORDOVICIAN (KATIAN) ECHINODERMS FROM SARDINIA, ITALY

Colin D. Sumrall[1], Bradley Deline[2], Jorge Colmenar[3], Sarah L. Sheffield[1] and Samuel Zamora[4]

[1] Department of Earth and Planetary Sciences, University of Tennessee, Knoxville 37996, USA.
csumrall@utk.edu, ssheffi2@vols.utk.edu
[2] Departamento de Ciencias de la Tierra (Área Paleontología), Universidad de Zaragoza, Pedro Cerbuna 12, E-50009 Zaragoza, Spain. colmenar@unizar.es
[3] Department of Geosciences, University of West Georgia, 1601 Maple St, Carrollton, Georgia, USA. bdeline@westga.edu
[4] Instituto Geológico y Minero de España, Manuel Lasala 44, E-50006 Zaragoza, Spain. s.zamora@igme.es

**Keywords:** Glyptocystitida, coronoids, Blastozoa, crinoids, Boda event.

## INTRODUCTION

Late Ordovician echinoderm faunas from Sardinia, Italy remain poorly documented. Previous investigations have yielded largely fragmentary material belonging to several clades of blastozoans and crinoids (Maccagno, 1965; Botquelen *et al.*, 2006; Touzeau *et al.*, 2012). Although several echinoderm taxa had previously been named, few were based on articulated thecae, most of which were internal molds, and feeding appendages were unknown. New collections from the Upper Ordovician (Katian) Portixeddu Formation at various localities near the towns of Portixeddu and Fluminimaggiore, southwestern Sardinia, Italy (Fig. 1) contain numerous complete specimens including previously unknown taxa.

## MATERIAL

The Portixeddu fauna has a rich taxon diversity including brachiopods, bryozoans, gastropods, bivalves, and echinoderms. All fauna were preserved as both internal and external molds in siltstone and studied using latex casts. Most of the echinoderm material was well-preserved with fully articulated thecae, although typically somewhat compacted. A few specimens preserved articulated feeding appendages and stems.

Echinoderms were common and diverse at localities near the town of Portixeddu and included hemicosmitoids, coronates, and diploporitans, but relatively few crinoids and glyptocystitoids. In contrast, echinoderms collected near the town of Fluminimaggiore included numerous crinoids (including cladids, disparids, and camerates), hemicosmitoids and coronoids, but relatively few diploporitans and glyptocystitoids. Based on associated brachiopods, the difference in relative abundances of echinoderm taxa likely reflects slight differences in water depth. In both areas, echinoderms were associated with root-like holdfasts suggesting that at least some of the taxa were autochthonous. Several specimens are preserved with intact oral areas and feeding appendages, which are significant for clarifying the phylogenetic positions of these taxa.

Two hemicosmitoid species were found. These taxa were detailed from internal molds by Maccagno (1965) and largely over split. "*Corylocrinus*" (Fig. 2B) bears a finely pustulose surface ornamentation, poorly defined cryptopores

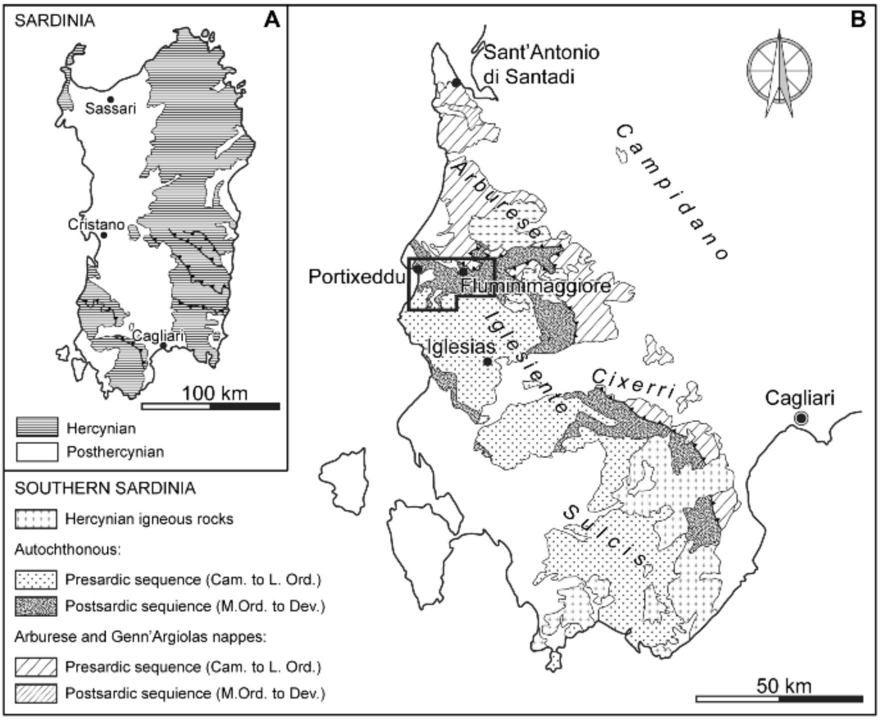

**Figure 1.** Geological map showing the Upper Ordovician (Katian) Portixeddu Formation deposits of southeastern Sardinia, Italy. After Hammann and Leone (2007).

on the exterior surface of the theca, and three facets for erect ambulacra. "*Oocystis*" (Fig. 2A) has a network of stellate ridges, well-defined cryptopores, and multiple facets for erect ambulacra. Two different morphotypes of hemicosmitoid erect ambulacra were also collected from the Portixeddu Formation, but it is unclear which appendage goes with each theca. Both appendage types conform well to those described by Sprinkle (1975) for *Caryocrinites ornatus* from North America. Both types bear double biserial floor plates with biserial brachioles arising from every other plate.

Thecae of the coronate *Mespilocystites tregarvanicus* (Fig. 2C) are common in the Portixeddu Formation as described by Botquelen *et al.* (2006), but no feeding appendage or stems as described by Brett *et al.* (1983) were recovered. These specimens provide views of the oral area from both the interior and exterior, adding new understanding to the nature of the gonopore. They also preserve details of the nature of the respiratory coronal canals.

Several other blastozoan clades are represented in the collections by relatively few specimens. A single specimen of the eocrinoid *Bockia* sp. (Fig. 2F) is notable for the spout-like oral area bearing large, well-developed oral plates. These plates bear large facets for erect feeding appendages that are not preserved. One species of the caryocystitoid *Heliocrinites* (Fig. 2G) was collected, though incompletely preserved lacking details of the oral area. Diploporitans are represented by two species. One has affinities to *Codiacystis* (Fig. 2D) and is represented by fragments and partial

**Figure 2.** A, the hemicosmitoid *Oocystis* showing well developed radial ridges; B, the hemicosmitoid *Corylocrinus* showing pustular ornamentation; C, the coronate, *Mespilocystites*; D, a fragmentary specimen of the diploporitan cf. *Codiacystis*; E, the diploporitan cf. *Tholocystis*; F, the eocrinoid *Bockia*; G, the caryocystitoid *Heliocrinites;* H, the echinosphaeritid *Echinosphaerites* showing well developed heumatorhombs; I, a single thecal plate of the glyptocystitoid rhombiferan *Rhombifera*. All figures are whitened latex casts of natural molds.

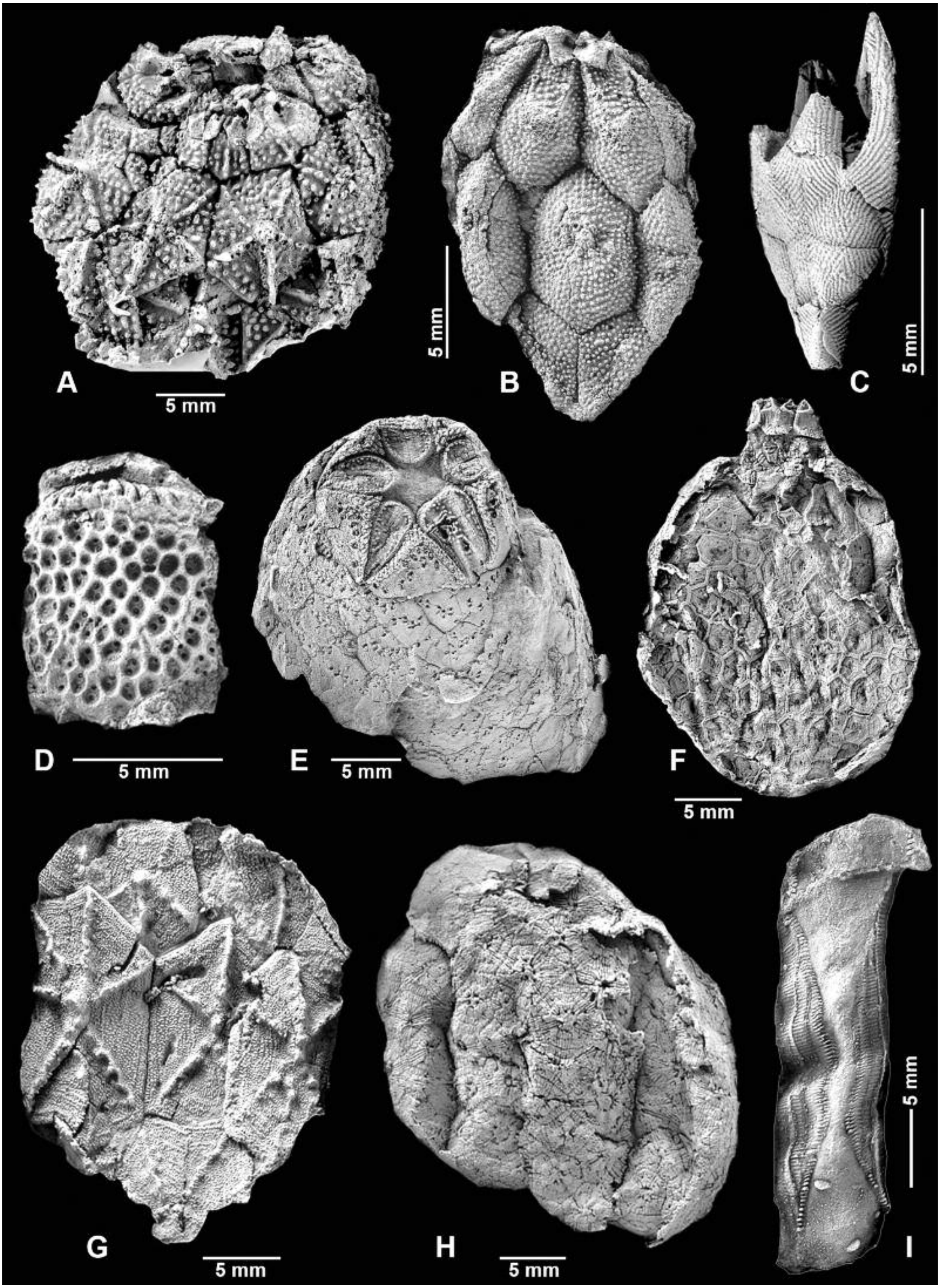

Figure 2.

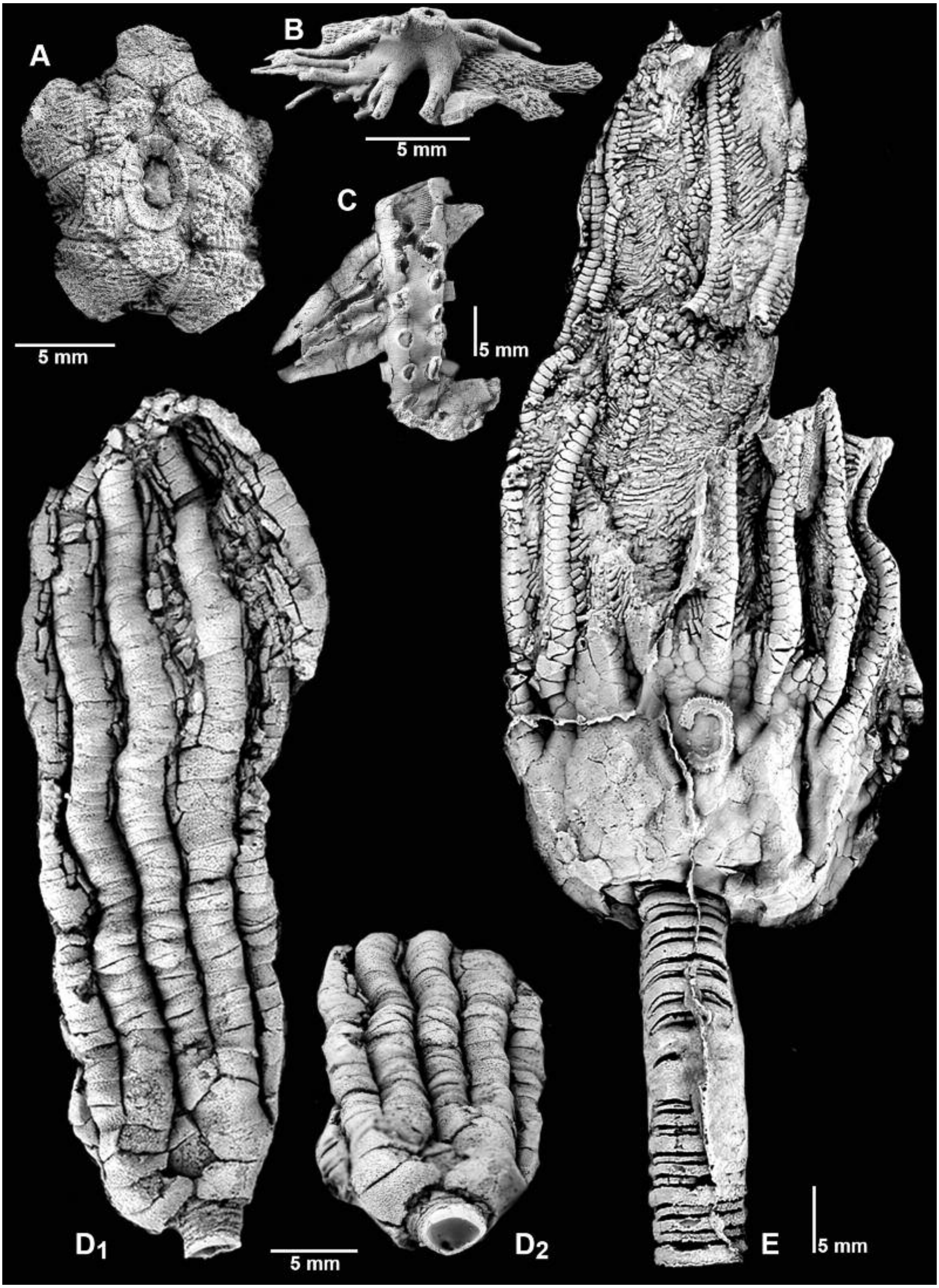

Figure 3.

thecae. The second has affinities with *Tholocystis* (Fig. 2E) is represented by a well-preserved theca from both internal and external mold. Echinosphaeritids are represented in the collection by a single partly crushed theca that has the theca covered by humatirhombs (Fig. 2H). Glyptocystitoids are represented in the collection by a small number of very large thecal plates assignable to *Rhombifera* sp. (Fig. 2I).

Crinoids are common in the sections near Fluminimaggiore but were nearly absent in the sections near Portixeddu (Figs. 3A, D, E). Previous collections included only columnals that were assigned to form taxa (Botquelen *et al*., 2006). Current collections have not been thoroughly analyzed, but include dendrocrinid cladids, homocrinid and maennilicrinid disparids, and anthracocrinid and rhodocrinitid diplobathrids. Most of these species are known from only a few specimens suggesting that the taxonomic diversity is fairly high. This is supported by previous and now lost collections by Hammann that included several taxa that were not recovered during the present study. There are also several fragmentary specimens that have yet to be identified.

Two types of holdfasts were found in the sections near Fluminimaggiore; type 1 holdfasts have dendritic radices that likely belong to one of the hemicosmitid species (Fig. 3B). Type 2 rhizoidal holdfasts likely belong to one of the crinoid species Fig. 3C). Morphologically, both are adapted for attachment on an unconsolidated substrate.

## FINAL CONSIDERATIONS

Taphonomic, sedimentologic, and palaeontologic data suggest that the fauna colonized the upper offshore soft substrates from the Mediterranean margin of Gondwana during the first pulses of the mid-late Katian global warming Boda Event. The Sardinian echinoderm fauna shows a stronger affinity to coeval Iberian communities (Chauvel and Le Menn, 1979; Gutiérrez Marco *et al*., 1996; Zamora *et al*., 2014) than Moroccan communities (Hunter *et al*., 2010; Lefebvre *et al*., 2013). Specimens are preserved as natural moulds in siltstones and some specimens are slightly strained by weak tectonic overprinting. Fossils accumulated in obrution deposits resulting from storm events favoring the preservation of delicate structures.

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**Figure 3.** A, the cup of an Rhodocrinitacea diplobathrid crinoid; B, type 1 holdfast likely belonging to a hemicosmitoid; C, type 2 holdfast likely belonging to a crinoid; D, the crown of a Maennilicrinidae disparid crinoid in normal ($D_1$) and basal ($D_2$) views; E, the crown of a large Anthracocrindae crinoid. All figures are whitened latex casts of natural molds.

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# PALAEOENVIRONMENTAL CONTROLS ON THE DISTRIBUTION OF CARBONIFEROUS ECHINOIDS

Jeffrey R. Thompson and David J. Bottjer

Department of Earth Sciences, University of Southern California, Zumberge Hall of Science, 3651 Trousdale Pkwy, Los Angeles, CA 90089-0740, USA. thompsjr@usc.edu, dbottjer@usc.edu

**Keywords:** Palaeozoic Echinoids, Carboniferous, Palaeoenvironment.

## INTRODUCTION

Echinoids are a diverse and abundant clade occupying a range of habitats in both modern and ancient ecosystems (e.g. Kier and Grant, 1965; Nebelsick, 1996; Schneider, 2008). Echinoids in modern oceans tend to occupy different substrates dependent upon their life mode (Nebelsick, 1996) and many echinoids have evolved to live on or in certain substrates. For example, the atelostomates are specifically adapted to life in fine-grained substrates, and have evolved specialized tube feet to allow for feeding in these sediments (Smith, 1984; Barras, 2008). Little is known about echinoid substrate affinities in the Palaeozoic, and rigourous testing of hypotheses regarding substrate affinities has never been undertaken. In the Palaeozoic, echinoids are first reported in rocks of Ordovician age (Smith and Savill, 2001; Reich and Smith, 2009), and reach their peak diversity in the Mississippian (Kier, 1965; Smith, 1984). Six families of echinoids are known from the Mississippian, the archaeocidarids, echinocystids, lepidocidarids, lepidesthids, proterocidarids, and palaechinids. These different families exhibit an array of diverse morphologies, likely representing different life modes and ecologies. The taxa comprising these families are known globally, however, due to poor sampling and the distribution of fossiliferous Paleozoic strata, are most well known from North America and Europe. Most of the fossil record of echinoids in the Mississippian can be attributed to a number of localities in North America and Western Europe that preserve numerous *in situ* echinoderm communities. These localities have long been sampled for their diverse and abundant crinoid "gardens" and have provided the data sets by which numerous hypotheses regarding crinoid diversity and abundance in the Mississippian have been tested (e.g Ausich and Kammer, 2006, 2013; Kammer and Ausich, 2007). Echinoids present from these localities and others have long been ignored except for their initial systematic identifications. Because echinoids reach their peak Palaeozoic diversity in the Carboniferous, it is the ideal interval of geologic time, in which to test for preferences in palaeoenvironmental setting.

## METHODS

As most of the specimens used in these analyses were collected in the 1800's without precise stratigraphic data at the bed or parasequence scale, it is typically not possible to place them within a sequence stratigraphic framework as advised by Patzkowsky and Holland (2012). Because this precise stratigraphic data is lacking, it is also important to note that the analyses performed herein are not an attempt to understand these echinoids as parts of communities, as it is impossible to tell whether or not any of these specimens were living together or were deposited on the same bedding plane. Nevertheless, we attempt to understand the substrate and environmental affinities of echinoids in a given locality and to gain insights into echinoid diversity at given localities in given periods of time.

In order to understand the factors controlling the distribution of different taxa, we applied multivariate statistical techniques to our data in order to find underlying patterns present. Non-metric multidimensional scaling (NMDS) was used to determine if certain environmental variables affect the distribution of certain taxa. NMDS ordinations were performed on generic level abundance data, with the number of species of a given genus recorded. A Euclidean similarity measure was used. Assemblages were compiled for eight Carboniferous localities including: Crawfordsville, Indiana; Hook Head, Ireland; Clitheroe, England; Lake Brownwood, Texas; Dineé, Belgium; Gilmore City, Iowa; Sloans Valley, Kentucky; and Lake Cumberland, Kentucky.

## RESULTS AND DISCUSSION

Preliminary results of NMDS are shown in Figure 1. The NMDS of the taxonomic and assemblage data reveal some interesting pattens. When assemblages are plotted with respect to generic composition (Fig 1.), one tight grouping is present consisting of Lake Brownwood, Gilmore City, Lake Cumberland and Sloan’s Valley, while Crawfordsville groups alone, and Dineé, Hook Head, and Clitheroe group in the same general area, though not tightly together. The localities appear to be separated out along a gradient based upon biogeographic differences, with North American localities grouping towards the left of the NMDS space and European localities grouping together towards the right (Fig. 1). European localities are, in all cases, more diverse than the North American localities, and this is likely also responsible for the separation of the taxa along this gradient. The tight grouping of Lake Brownwood, Gilmore City, Lake Cumberland and Sloan’s Valley may also be related to their lower alpha diversities, relative to other localities. Broadly, separation in the vertical direction appears to be related to the abundance of archaeocidarids in each locality. Localities with numerous archaeocidarid taxa plot towards the top of the coordinate space, while those without archaeocidarids, or with archaeocidarids, but only as accessory members of the assemblages, plot towards the bottom. This archaeocidarid related separation appears not to be related to bathymetric differences, as Clitheroe and Lake Cumberland record similar deep mud-mound depositional environments and plot apart on the coordinate space (Fig. 1). The NMDS (Fig. 1) furthermore shows no sign of differences in assemblage composition due to differential siliciclastic or carbonate depositional environments. The three siliciclastic localities herein discussed, Lake Brownwood, Dineé, and Crawfordsville show no systematic positioning relative to each other as dictated by assemblage composition (Fig. 1).

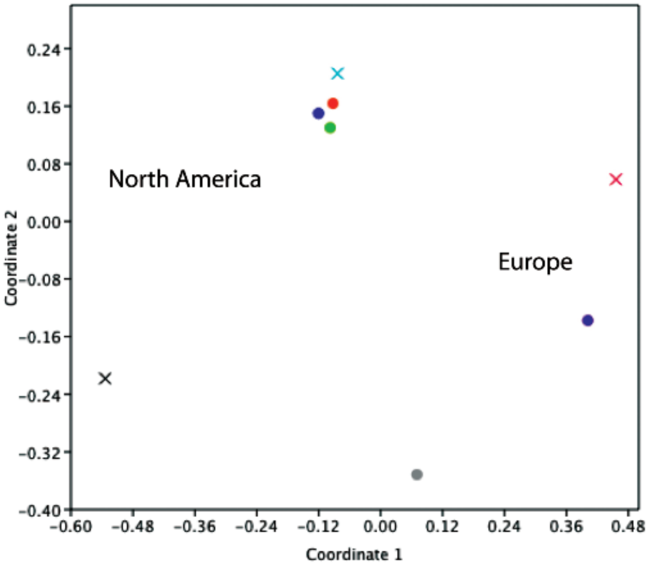

**Figure 1.** NMDS of Carboniferous localities with abundant echinoids. Ordination based upon the generic level assemblage compositions of localities. Black=Crawfordsville, Blue=Lake Cumberland, Turquoise=Lake Brownwood, Orange=Gilmore City, Green=Sloan’s Valley, Grey=Clitheroe, Red=Dineé, Purple=Hook Head. North American localities are on the left side of the ordination space while European localities plot toward the right. Siliciclastic localities indicated with an X and carbonate localities with a dot.

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# UNRAVELLING THE ORIGIN OF THE EURYALID BRITTLE STARS: A PRELIMINARY REPORT

Ben Thuy

Natural History Museum Luxembourg, 24, rue Münster, L-2160 Luxembourg. nebyuht@yahoo.com

**Keywords:** *Aspiduriella*, Euyalids, evolution, Jurassic, Ophiuroidea, Triassic.

## INTRODUCTION

Euryalids are among the most distinct extant brittle stars, including very large forms with strongly branched arms and epizoics with strongly reduced external skeleton tightly coiled around corals. Morphologically, they differ so markedly from other ophiuroids that, in the past, they were mostly placed in a group of their own (e.g. Mortensen, 1927; Fell, 1960; Smith, *et al.*, 1995), prompting the subdivision of ophiuroids into euryalids on the one hand and non-euryalids on the other. A close relationship between euryalids and the Ophiomyxidae as suggested by other authors (e.g. Matsumoto, 1915; Murakami, 1963), was recently challenged on the basis of micro-morphological evidence (Martynov, 2010).

Palaeontological evidence has been of little help in clarifying the systematic position of the euryalids so far, with only very sparse irrefutable remains reported from latest Cretaceous to Neogene strata (e.g. Jagt, 2000; Kroh, 2002). In spite of superficial similarities, the Paleozoic genus *Onychaster* Meek and Worthen, 1868 was conclusively discredited as a potential early representative of the euryalids (Hotchkiss and Glass, 2012).

The latest molecular phylogeny of the Ophiuroidea by O'Hara *et al.* (2014) provided fundamentally new perspectives: first, it unprecedentedly found close phylogenetic ties between the euryalids and the Ophiuridae which form a group sister to all remaining extant ophiuroids; second: it endorsed the significance of previously underexplored micro-morphological features to trace phylogenetic relationships between ophiuroid groups. Since the Ophiuridae and the euryalids must have had diverged by the early Mesozoic (O'Hara *et al.*, 2014), euryalid fossils older than the latest Cretaceous are to be expected.

On these grounds, the fossil record of the ophiuroids was thoroughly re-assessed, taking into account the vast array of dissociated skeletal parts retrieved from sieving residues, in order to unravel the evolutionary history of the euryalids. The present short paper presents preliminary results of this quest.

## THE JURASSIC RECORD – NEW AND REVISED REPORTS

To date, no Jurassic fossils have been unambiguously assigned to euryalids. Given the predicted early Mesozoic origin of the euryalids, the lack of Jurassic reports is surprising considering that the ophiuroid fossil record of that period is probably the best known (e.g. Thuy, 2013). Thanks to the recent findings on the diagnostic relevance of microstructural features pertaining to lateral arm plate morphology, in particular arm spine articulations (Martynov, 2010; Thuy and Stöhr, 2011), the ophiuroid fossil record was systematically re-assessed in order to identify possible euryalid remains.

Indeed, several records of dissociated ophiuroid lateral arm plates, including both previously described and novel occurrences, were found to have strong euryalid affinities. Lateral arm plates from the Toarcian/Aalenian (Early to Middle Jurassic) of Germany (Fig. 1A-B) (Kutscher, 1996) and the Toarcian (Early Jurassic) of France (Kutscher and Villier, 2003) erroneously assigned to *Sigsbeia*? *lunaris* (Hess, 1962) turned out to display the highly distinctive spine articulation morphology typically found in euryalids and consisting in large, vertically elongate muscle and nerve openings widely separated by a vertical ridge. In addition, the overall lateral arm plate morphology is strongly reminiscent of that found in extant *Gorgonocephalus* Leach, 1815 (Fig. 1D), with a large, protruding ventral portion of the plate and the lack of ornamentation on the outer surface. The vertebrae associated with the lateral arm plates in question show typical hourglass-shaped articulation pegs (Fig. 1C). Thus, there is strong morphological support for an assignment of the material to the euryalids. The shape of the ridge on the inner side implies that the lateral arm plates most probably held a lateral rather than ventral position with respect to the vertebra, suggesting a basal position within the euryalids. The material belongs to a new genus to be formally described in a forthcoming study.

Previously undescribed lateral arm plates showing strong similarities with the above-mentioned ones from the Toarcian and Aalenian were retrieved from sieving residues of Bajocian (Middle Jurassic) coral reef sediments from Luxembourg and France (Fig. 1E), and from Callovian (Middle Jurassic) erratic boulder sediments of Germany. They show the same diagnostic characters supportive of an assignment to the euryalids as their Toarcian/Aalenian equivalents, including associated vertebrae with hourglass-shaped articulation pegs in the case of the Luxembourgian material.

Interestingly, the currently known Mesozoic euryalid record completely lacks vertebrae suggestive of arm branching (i.e. with double-headed distal articulation pegs). The oldest known record of arm branching in euryalids is of Miocene age (Kroh, 2002). Further research is needed to test if branched arms are, indeed, a relatively young phenomenon in euryalids.

## TRACING THE EURYALIDS INTO THE TRIASSIC

While the above-described reports from the Jurassic are rather clear in terms of euryalid affinities, identification of possible Triassic relatives is more complicated. Intriguingly, the lateral arm plates which show the greatest similarities with those assigned to Jurassic euryalids are found in *Aspiduriella streichani* (Kutscher, 1987) from the Anisian (Middle Triassic) of Germany (Kutscher, 1987) (Fig. 1F). In terms of general morphology, *Aspiduriella* Bolette, 1998 is anything but euryalid-like, with a strongly developed rather than reduced external skeleton and short, broad arms with single dorsal arm plates, which is why the possibility of euryalid affinities has never been considered before. Microstructural features, however, in particular those pertaining to the shape of the lateral arm plates, the spine articulation morphology and the presence of hourglass-shaped vertebral articulation pegs (Fig. 1G) bear clear euryalid traits. Interestingly, the young postlarvae of the extant euryalid *Asteronyx loveni* Müller and Troschel, 1842 (Stöhr, 2005) show a number of features which, indeed, favour closer phylogenetic ties with an *Aspiduriella*-like ancestor, including short, broad arms, lateral arm plates wrapped around the arm rather than holding an exclusively ventral position, and a large and entirely contiguous primary rosette.

Among all currently known representatives of *Aspiduriella*, *A. streichani* is the most euryalid-like. The other species also display spine articulations reminiscent of those found in modern euryalids and, at least in some cases, hourglass-shaped vertebral articulation pegs, but at a much more reduced level in favour of a more compact skeleton. The morphological evidence at hand leaves no doubt as to the position of *Aspiduriella* close to the base of the euryalids, as already sketched by O'Hara *et al.* (2014), but further research is necessary to clarify its position in the ancestry of the group. In particular, the euryalid clade will have to be put on solid grounds defining meaningful synapomorphies and thus enabling distinction between stem group and basal crown group members.

In addition to the new findings concerning *Aspiduriella*, dissociated lateral arm plates from sieving residues of Carnian (Late Triassic) age from Italy (Fig. 1H) were found to show similarities both with the above-described Jurassic euryalid lateral arm plates, in particular with respect to the spine articulations, and with the lateral arm plates of *A. streichani* in terms of overall shape of the plate. These lateral arm plates thus seem to bridge *Aspiduriella* and the Jurassic euryalids both morphologically and stratigraphically, contributing to a first sketch of the early euryalid evolution.

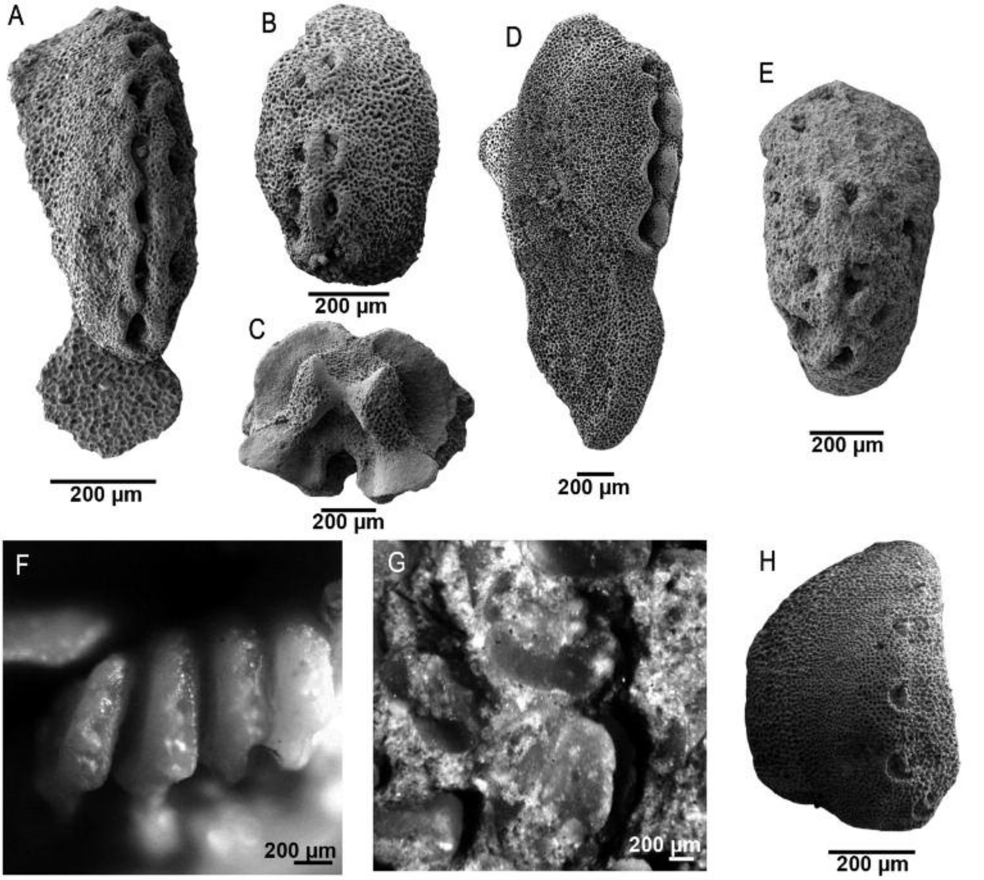

**Figure 1.** A-C. Unnamed euryalid from the Toarcian/Aalenian (Early/Middle Jurassic) of Quedlinburg, Germany; proximal (A) and median (B) lateral arm plates in external view, vertebra (C) in distal view. D. *Gorgonocephalus caputmedusae*, recent, median lateral arm plate in external view. E. Unnamed euryalid from the Bajocian (Middle Jurassic) of Rumelange, Luxembourg; median lateral arm plate in external view. F-G. *Aspiduriella streichani* from the Anisian (Middle Triassic) of Rüdersdorf, Germany; lateral arm plates in external view (F), dissociated vertebrae (G). H. Unnamed probable euryalid from the Carnian (Late Triassic) of Cortina d'Ampezzo, Italy; proximal lateral arm plate in external view.

## CONCLUSIONS

So far, disentangling the evolutionary history of the euryalids was hampered by the lack of irrevocable fossils older than the latest Cretaceous. Thanks to recent findings on phylogenetically informative characters pertaining to the microstructure of lateral arm plates, the quest for previously overlooked euryalid fossils could be raised to an unprecedented level. Preliminary results show that unquestionable euryalids can be traced at least to the Early Jurassic, with several undescribed species most probably holding a basal position with the euryalids.

With the new insights on Jurassic euryalids at hand, it was possible to identify the middle Triassic *Aspiduriella streichani* as the most probable oldest member of the euryalid ancestry. At present, however, it remains unclear whether *Aspiduriella* is a member of the euryalid stem group or a basal crown group representative.

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# THE EVOLUTIONARY PALEOECOLOGY OF THE BLASTOIDEA: WHAT HAVE WE LEARNED IN THE PAST 29 YEARS?

Johnny A. Waters

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

**Keywords:** Blastoids, history, evolution, fissiculate, spiraculate.

## INTRODUCTION

In December 1986, Chris Paul and Andrew Smith hosted a conference on echinoderm phylogeny and evolutionary biology in London and I presented a summary of the evolutionary paleoecology of the blastoids (Waters, 1988). It seems appropriate some 30 years later at a conference celebrating the career of Andrew Smith to address the question of what have we learned about blastoids in the interim and where studies in blastoids are heading in the near future. Blastoids are an extinct class of blastozoan echinoderms ranging in age from Upper Ordovician to the Upper Permian. They have been reported from every continent except Antarctica, although the North American and European faunas are much better known than faunas from other parts of the world. One hundred fifteen genera of blastoids are currently recognized although not all have been formally described. Historically, blastoids were divided into two orders, the Fissiculata and the Spiraculata, by the presence or absence of exposed hydrospire slits and spiracles. Horowitz *et al.* (1986) concluded that the Spiraculata was polyphyletic and Waters and Horowitz (1993) revised the Spiraculata by dividing it into five orders, Troosticrinida, Nucleocrinida, Pentremitida, Granatocrinida and a fifth unnamed order. Recent (but currently unpublished) cladistic studies support the hypothesis of a polyphyletic Spiraculata, but were not comprehensive enough to confirm the revised ordinal scheme of Waters and Horowitz (1993).

The typical blastoid genus is monospecific, relatively short lived, relatively rare in terms of abundance, and geographically restricted to one depositional basin. Many are known from a single locality. Historically blastoids were considered part of shallow water crinoid dominated communities. Often they were, but blastoids also occur in deeper water communities where they dominate local echinoderm communities. Blastoids have an evolutionary history of local explosions of abundance and diversification with later rapid declines. Often blastoids become more diverse taxonomically and morphologically as well as the numerically dominant echinoderm after a major perturbation in the crinoid community.

## THE EVOLUTIONARY PALEOECOLOGY OF BLASTOIDS

Blastoids are the longest-lived and most diverse members of Blastozoa, a major component of the Great Ordovician Biodiversification Event (Sprinkle and Guensburg, 2004). Blastozoan clades diversified through the Lower and Middle Ordovician replacing low diversity Cambrian echinoderm communities (Lefebvre *et al.*, 2013). In contrast, blastoids first appeared in the Late Ordovician. The oldest blastoid genus, *Macurdablastus*, is found only in the Benbolt Formation in Tennessee (Broadhead, 1984) but occurs with a number of other blastozoan taxa. Blastoids are noticeably absent from diverse Ordovician echinoderm communities such as the Bromide Formation of Oklahoma, which contains over 11000 complete specimens belonging to 61 genera and 13 classes occurring in a variety of depositional environments (Sprinkle, 1982). The extremely endemic distribution of blastoids in the Late Ordovician is in stark contrast to the distribution of other blastozoan clades. By the Late Ordovician, blastozoan biogeography had transitioned from provincial to more geographically complex exchanges across geographic and latitudinal regions (Lefebvre *et al.*, 2013). Although the limited Late Ordovician blastoid distribution is not likely the result of taphonomic bias relative to other blastozoans, few alternative hypotheses exist.

Silurian blastoids are geographically restricted, but locally are reasonably abundant members of echinoderm communities. Assuming *Macurdablastus* is a fissiculate blastoid, the first transition from a fissiculate to a spiraculate order (Troosticrinida) occurred in the Silurian. Silurian blastoids from the Czech Republic occur in the Slivenec Limestone, which was deposited in relatively deep water in dysaerobic to anoxic conditions (Mamet, 1997). The Slivenec Limestone contains facies with significant microbial communities and hypothesized microbial mats and biofilms (Mamet, 1997). Blastoids are unknown from some of the best documented Silurian shallow water echinoderm communities (e.g., the Wenlock faunas from the U.K.).

Devonian blastoids radiated biogeographically and taxonomically. Locally, they dominate echinoderm communities. Emsian blastoids are well known from a variety of localities and generally yield faunas with multiple co-existing genera for the first time. Spanish Devonian blastoids form the only more or less coherent blastoid fauna from the Lower Devonian in the world. These blastoids occur in two distinct communities – a typical shallow water Middle Paleozoic crinoid dominated community associated with reefal buildups and a deep water community reminiscent of Cambrian echinoderm communities. *Cryptoschisma* lived in deep water (below storm wave base) associated with microbially mediated mud mounds. Blastoid communities containing *Cryptoschisma* show high levels of abundance reaching 990 individuals per square meter in one sample. *Cryptoschisma* is a sediment sticker blastoid that occupied an anachronistic environment. Previously Cambrian-style echinoderms with a sediment sticker attachment strategy have only been reported from Early and Middle Cambrian ecosystems. Although other blastoid genera are found in moderate abundance in more typical shallow environments in the Lower Devonian in Spain, *Cryptoschisma* is not. Emsian blastoids from Bolivia and South Africa are notable because the Emsian continental reconstructions place them in very high latitudes. Middle Devonian blastoids are abundant, diverse and have a worldwide distribution. Most are associated with shallow water crinoid dominated echinoderm communities. Phylogenetically, the Middle Devonian is important because of the three separate transitions from fissiculates to spiraculate orders, the Nucleocrinida, the Pentremitida, and the Granatocrinida. Of these, only the transition to the Pentremitida is reasonably well documented. Breimer and Dop (1974) concluded that *Pentremitidea* (a fissiculate) was ancestral to *Hyperoblastus* (a spiraculate in the Pentremitida) with *Conuloblastus* as an intermediate. As presently understood, all the genera in this transition from one order to another were part of shallow water communities.

Blastoids suffered a major extinction event at the Givetian/Frasnian boundary as do other echinoderm clades and bryozoans. Frasnian blastoids are rare globally. Although the Frasnian/Famennian Extinction Event was not as severe for blastoids and crinoids as the Givetian/Frasnian event, rebound faunas containing both groups appear very quickly after the Frasnian/Famennian Extinction in a shallow marine setting associated with an oceanic island arc complex in the Central Asian Orogenic Belt (CAOB). These faunas span the interval between the Late Frasnian Kellwasser Event and the Late Famennian Hangenberg Event. The rebound fauna immediately after the Frasnian/Famennian Extinction Event occurred in shallow water and is dominated by crinoids but blastoids are diverse and relatively abundant. Echinoderm communities from later in the Famennian lived in deep water and are associated with maroon and green shales and radiolarian cherts. These faunas are numerically dominated by blastoids. Crinoids are less abundant but contain numerous flexibles. They are morphologically advanced showing many thecal characters rare in Devonian faunas, but common in the Mississippian. The rebound fauna was concentrated in CAOB particularly for echinoderms and we can conclude that the Age of Crinoids encompassed the Famennian in addition to the stages of the Mississippian.

The Mississippian is characterized by abundant and diverse echinoderm communities that became dominant carbonate producers after the demise of coral stromatoporoid communities in the Famennian. Major changes in dominance and diversity of blastoids, particularly in North America and Europe, accompanied fundamental shifts in the sedimentation patterns and major reorganizations in the echinoderm communities during the Mississippian. In North America, Kinderhookian (Tournaisian) faunas are known from shallow water carbonates and deeper water facies associated with the Waulsortian buildups. During the Osagean (Late Tournaisian; Early Visean) of North America, blastoids continued to occur in deep water facies, but became very diverse in shallow water facies. Monobathrid camerate crinoid communities reached a zenith on the broad shallow water carbonate platforms such as the Burlington Shelf and correlatives. Blastoids were an integral part of this community and attained their maximum diversity (17 genera) in the Burlington. During the latest Tournaisian and Lower Visean, buildups of the Walsortian facies were widespread across Europe. Blastoids are commonly found in the flank facies associated with diverse crinoid communities. A major blastoid extinction event (Ausich *et al*., 1988) occurred in the Early Visean. Both in North America and Western Europe, significant blastoid extinctions accompanied the virtual elimination of blastoids from shallow-water habitats. The shift in blastoid habitat preference to deeper water settings lasted only a few million years. By the end of the Visean, blastoids had reinvaded the full spectrum of shallow-water habitats and numerically dominated many echinoderm communities in North America and Europe.

Although Mississippian blastoids had a worldwide distribution, by the Serpukhovian (Pennsylvanian) the biogeographic center of the blastoid occurrences had shifted eastward toward the Paleo-Tethyan seaway and away from North America and Europe (Waters and Webster, 2012). Pennsylvanian blastoids tended to be small and occurred in localized faunas often in clastic settings, but they set the stage for the final radiation of blastoids in the Permian of Southeast Asia. In contrast to the short duration of the typical blastoid genus, three Pennsylvanian genera (*Pentremites*, *Angioblastus*, and *Orbitremites*) averaged generic longevity of 50 million years. Paleo-Tethys was a refugium for blastoids during the Pennsylvanian. Large-scale reorganization of Paleozoic echinoderm communities and changing sedimentological regimes caused by Gondwanan glaciation and the emergence of the Appalachian orogen were likely contributing factors for the major biogeographic shift during this time.

Permian blastoids are widespread outside North America and Europe but the most diverse faunas are found in southeast Asia and Australia. The fissiculates are the most cosmopolitan, with *Angioblastus* occurring in Bolivia, the Urals, and Indonesia. Blastoids from Timor are well known from museum collections, but their palaeoecology and stratigraphic relationships are very poorly understood. Fissiculates are more diverse (14 genera) in the Timor faunas but spiraculates dominate in terms of abundance. *Deltoblastus* is known from tens of thousands of specimens. Australian Permian faunas are similar in age to the Timor faunas and occur in both eastern and western regions of the continent. Elements of the Timor blastoid fauna have recently been found in Oman.

## CONCLUSIONS

In the past thirty years we have learned the following about blastoids. Even though they are the most successful of the blastozoan clades, they basically missed the Great Ordovician Biodiversification Event. Blastoids are not just minor elements of shallow water crinoid communities, but are often found in deep water. Major events in blastoid evolution are tied to changes in crinoid community structure. They underwent a major biogeographic shift in the Late Paleozoic. Many of these changes may be climate driven, but viable alternative hypotheses exist. Major questions about the earliest and latest blastoid faunas remain poorly understood.

In the coming years we will see a major effort to better characterize the internal anatomy of blastoids by producing virtual 3D models using state of the art synchrotron imaging as well as legacy collections of acetate peels. These models should provide additional morphological characters to produce a phylogenetically sound classification, which is currently lacking. These models will also allow us to finally address fundamental questions about blastoid morphology such as the functional significance of the fissiculate and spiraculate condition as it relates to fluid flow through the hydrospires. Finally, we will see an increase in blastoid diversity coming from Central Asia as echinoderm workers there further explore the vast areas covered in Palaeozoic sedimentary rocks.

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# ADVANCING PHYLOGENIC INFERENCE IN THE BLASTOIDEA (ECHINODERMATA): VIRTUAL 3D RECONSTRUCTIONS OF THE INTERNAL ANATOMY

Johnny A. Waters[1], Colin D. Sumrall[2], Lyndsie E. White[3], and Bonnie K. Nguyen[4]

[1] Department of Geology, Appalachian State University, Boone, NC 28608, USA. watersja@appstate.edu
[2] Department of Earth and Planetary Sciences, University of Tennessee, Knoxville, TN 37996, USA. csumrall@utk.edu
[3] Department of Industrial Design, Appalachian State University, Boone, NC 28608, USA. white.lyndsie@gmail.com,
[4] Department of Health and Exercise Science, Appalachian State University, Boone, NC 28608, USA. nguyenbk@appstate.edu

**Keywords:** Blastoidea, Echinodermata, virtual palaeontology, 3D reconstructions.

## INTRODUCTION

Recent studies by Sumrall (2010); Sumrall and Waters (2012) and Kammer *et al*. (2013) demonstrate that external morphology and homology of fossil echinoderms can be reconciled across clades and used to score characters for phylogenetic inference. Blastoids are the longest-lived and most diverse members of the Blastozoa, a group within which the ancestry of modern crinoids is rooted. Thus testing hypotheses of the phylogeny of extant crinoid clades requires a firm understanding of the phylogeny of extinct clades, particularly the Blastozoa. Blastoid thecae are data rich and well understood from the exterior. However, the internal construction of the mouth frame, reproductive structures, and respiratory structures are also vitally important for understanding blastozoan phylogeny. Here we compare destructive and non-destructive methodologies for reconstructing the internal anatomy of blastoid species using data sets gathered from acetate peels and from the Swiss Light Source Synchrotron.

Virtual Paleontology studies fossils through digital visualization of the three dimensional morphology (Sutton *et al*., 2013). The raw data for virtual 3D reconstructions usually involve tomographs, a series of two-dimensional parallel slices, of a specimen that are gathered either by destructive and non-destructive methodologies (see Cunningham *et al*. (2014) for a comprehensive review). Historically, tomographic data consisted of thin sections or acetate peels (Sollas, 1903; Stensio, 1927; Muir-Wood, 1934; Stewart and Taylor, 1965) collected through destructive techniques such as serial grinding, sawing, or slicing. Until the advent of high speed computing and 3D reconstruction software, individual tomographic slices provided the morphologic information required to taxonomic delineation. These tomographic slices were often coarsely and unequally spaced. Three-dimensional reconstructions were rare, time consuming and accomplished via the construction of physical models (e.g., Sollas, 1903; Jarvik, 1944). Jefferies and Lewis (1973) and Schmidting and Marshall (2010) are examples of echinoderm reconstructions using serial sections. Acetate peels were widely used to interpret the internal morphology of brachiopods (e.g., Copper, 1967; Posenato, 1998; Schemm-Gregory, 2014), corals (e.g., Wang *et al*., 2013), and many other fossil groups including blastoids (Breimer and Macurda, 1972).

Modern non-destructive methodologies include X-ray tomography, magnetic resonance imaging, or neutron tomography (Cunningham *et al.,* 2014). Modern techniques produce high-resolution 2-D images that can be reconstructed as three-dimensional computer models using appropriate visualization software. X-ray tomography is capable of micron scale resolution, and facilities are increasingly available at academic institutions; hence, the technique is commonly used in palaeontology. In contrast, MRI and neutron tomography have not been widely used as they are much less accessible and typically restricted to lower resolutions than X-ray tomography. X-ray tomography works well when the internal structures being imaged and the material filling the voids have significant density contrast (Abel *et al.*, 2012) or when specimens are preserved as molds. These techniques are not as successful in specimens showing little density contrast between internal structures and the void filling because materials with similar densities attenuate X-rays to similar degrees, and so are not clearly differentiated in the resulting slice images. This situation commonly occurs in some fossil echinoderm clades, such as blastoids.

Many 3D reconstruction software alternatives are available to transform tomographic datasets into 3D reconstructions (Cunningham *et al.,* 2014). SPIERS (Serial Palaeontological Image Editing and Rendering System) is a widely used, freely available package of three programs for the reconstruction and visualization of tomographic datasets (http://www.spiers-software.org). Using SPIERS to construct 3D visualizations from serial sections and acetate peels is challenging if the serial sections are not equally spaced and if fiduciary markings to aid alignment are not present. Although most modern datasets from serial sections do not suffer these problems, many legacy datasets from serial sections, including ours, do have these issues.

We have developed a visualization workflow based on Rhinoceros software, which is a NURBS-based 3D computer graphics and CAD software that produces mathematically precise representations of curves and freeform surfaces. Because Rhino is widely used in in rapid prototyping, computer aided design and manufacturing, and graphic design, it easily interfaces with a variety of other 3D visualization software packages and 3D printers. Rhino makes no assumptions about vertical spacing of tomographic slices and the user can interactively edit the vertical spacing as the model is reconstructed.

## DATA FROM ACETATE PEELS

Internal structures of blastoids historically have been characterized using thin sections or acetate peels of serial sections (e.g., Breimer and Macurda, 1972). The Naturalis Biodiversity Center in Leiden, Netherlands, houses a legacy collection of acetate peels of blastoids produced in the late 1960s (Breimer and Van Edmond, 1968). Although the peels are an important source of detailed information about the internal morphology of blastoids, information in the vast majority of the peels has never been published. Waters was awarded a Temminck Fellowship at Naturalis in 2012 to digitize and scan these peels. The peels were scanned with a Braun slide scanner at 7200 dpi and 8 bit grayscale. Even though the acetate peels were expertly prepared, they have flaws such as wrinkles, tears, and bubbles, which contribute to information loss. Typical results are shown in Figures 1, 2.

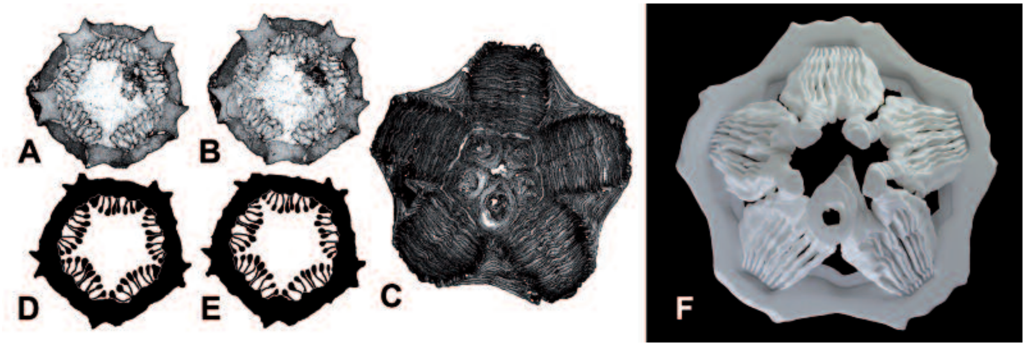

**Figure 1.** Reconstruction of *Pentremites godoni* from acetate peels. The peels lack homologous points of reference, and must be manually realigned using Photoshop. Once peels are digitized (A, B) and registered, the specimen outline is clipped from the background and stacked into different layers to virtually recreate the blastoid that had been destroyed through serially sectioning (C). Segmentation of morphologic characters, characterized as Regions of Interest (ROI), can begin as soon as registered composites of individual taxa have been completed. In order to three-dimensionally view these segments, the images are exported into Illustrator, where they can be converted into an Auto-CAD drawing file (D, E). The ROI's are lofted into 3D models that can be viewed electronically or converted to physical models by 3D printing (F). Not only can these segments now be viewed more accurately, but they provide quantitative data on surface area and volume and can be used as input into fluid flow software.

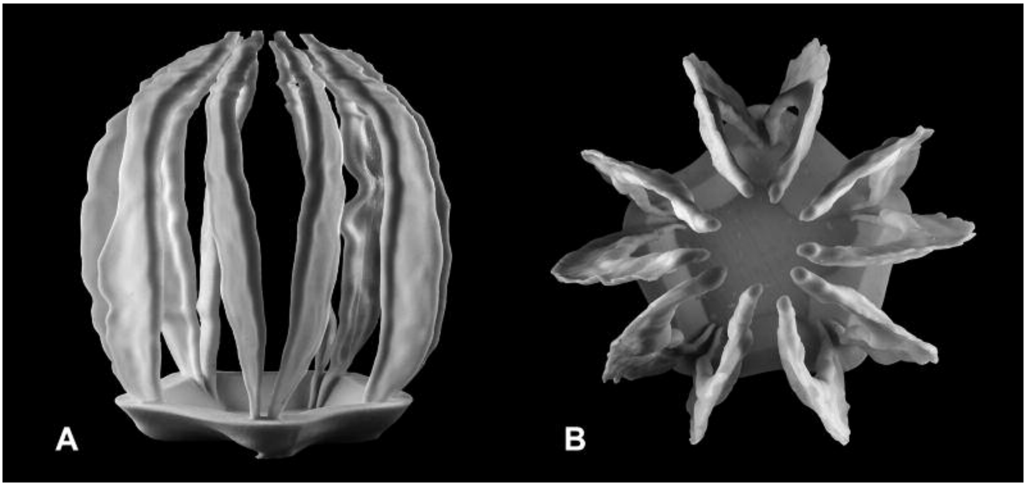

**Figure 2.** Individual hydrospire groups from *Monoschizoblastus rofei* have been segmented using Rhino 3D reconstruction software and are shown here as photographs of physical 3D models in lateral (A) and oral views (B) respectively.

## DATA FROM SYNCHROTRON IMAGING

Detailed 3D reconstructions can be produced via synchrotron imaging. However, synchrotron and similar non-destructive imaging techniques depend on density differences between the fossil and matrix to successfully segment targeted morphologies. Although conventional X-ray attenuation-based imaging does not clearly resolve samples lacking internal density contrast, as is the case for many three-dimensionally fossil echinoderms (including blastoids), the TOMCAT beamline at the Swiss Light Source uses phase contrast imaging to enhance subtle density differences. In spite of contrast subtleties, we were able to successfully segment internal organ systems in blastoids imaged at the SLS. We used SPIERS to segment the ROIs and produce the 3D reconstructions.

Datasets from the SLS are much more precise than the datasets taken from acetate peels and the specimen is not destroyed during the imaging process. Imaging is rapid but segmentation and interpretation of the morphology can be lengthy due to the large size of the datasets. Synchrotron imaging produces very large datasets ranging from 5 GB to 17 GB with 500 - 2000 projections. Although this is one of the most advanced visualization techniques currently available, the scans have significant noise and artifacts. Initial on-site post processing of the images by SLS personnel removed artifacts using proprietary software. Depending on the density differences between internal structures and the infilling matrix, morphologic information can be difficult to extract from the specimen.

## CONCLUSIONS

We have successfully produced 3D reconstructions of the internal anatomy of blastoids using both legacy acetate peels and synchrotron based non-destructive imaging. Synchrotron imaging successfully imaged remnant soft tissue structures, but was less successful in imaging lightly calcified internal structures such as hydrospires and elements of the reproductive system because of subtle density differences between the blastoid stereom and void filling calcite cement. Waters spent six weeks digitizing the Breimer peel collection at Naturalis and will reposit the digitized files there at the end of the project. The workflow to produce a 3D model from a series of peels is very tedious and time consuming. We estimate about 80 hours to complete an average reconstruction. The reconstruction in Figure 1 took more than 150 hours to complete. The workflow to produce a reconstruction from synchrotron based imaging is similarly tedious and time consuming. Data acquisition at the synchrotron is rapid, but competition for instrument time is intense. We estimate 40 - 60 hours to complete an average reconstruction of a synchrotron dataset, but the time decreases with experience. Work continues to produce 3D models across the taxonomic spectrum of blastoids for

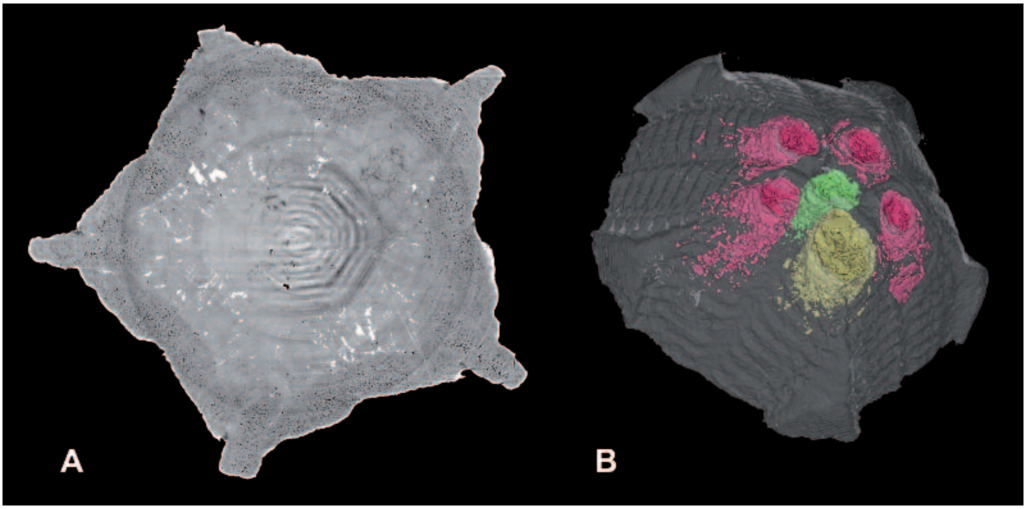

**Figure 3.** Tomographic image of blastoid specimen imaged at the Swiss Light Source and reconstruction using SPIERS. A. Image of the *Pentremites clavatus* with hydrospires visible but obscured by lack of density differentiation and artifacts. B. Reconstruction using SPIERS showing the spiracles, anispiracle and mouth. Hydrospires could not be segmented in this specimen. Compare these images to Fig. 1 which shows acetate peels of hydrospires in a different species of *Pentremites* and reconstructions using Rhino.

inclusion into phylogenetic analyses. We plan to continue reconstructions of the legacy set of acetate peels from Naturalis, and will likely make serial sections of additional taxa to fill in the taxonomic gaps in the data set.

## Acknowledgements

Waters thanks Imran Rahman for introducing him to virtual paleontology and allowing Waters to participate in his grant to image echinoderms at the Swiss Light Source in March 2015. Nguyen expresses her gratitude to Rahman for his encouragement and advice on the process of segmentation and visualization using SPIERS. Funding for this research came from ROA grants to Appalachian State University from NSF DEB 1036260, Assembling the Echinoderm Tree of Life through the University of Tennessee.

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# FROM THE STEM TO THE CROWN: PHYLOGENY AND DIVERSIFICATION OF PAN-CLADID CRINOIDS

David F. Wright and William I. Ausich

School of Earth Sciences, The Ohio State University, 275 Mendenhall Laboratories, 125 South Oval Mall, Columbus,
Ohio 43210, USA. wright.1433@osu.edu, ausich.1@osu.edu

**Keywords:** Phylogenetics, systematics, cladistics, Crinoidea, Cladida.

## INTRODUCTION

Knowledge of phylogenetic relationships among pan-cladid crinoids is fundamental to understanding geologic patterns of crinoid taxonomic diversification, morphologic evolution, and the evolutionary origin of extant crinoids. Cladids differ from other crinoids in (ancestrally) possessing a dicyclic aboral cup with arms free above the radial plates. When discussing the systematics and evolutionary history of this group, it is necessary to make a distinction between "pan-cladids" and members of the crinoid subclass Cladida. The Cladida has long been known to be paraphyletic (Springer, 1920; Moore and Laudon, 1943; Moore *et al.*, 1978) and suprageneric phylogenetic analyses of Crinoidea do not support the strict monophyly of the subclass Cladida (Simms and Sevastopulo, 1993; Ausich, 1998). Thus, the informal name 'Pan-Cladida' used herein refers to the common ancestor of all species included within the sublcass Cladida and all of its descendants, regardless of taxonomic rank in the Linnaean hierarchy.

The Pan-Cladida is the most taxonomically diverse and long-lived clade in the geologic history of crinoids, spanning most of the Phanerozoic Eon (Ordovician – Recent) and comprises three Linnaean subclasses: (1) Cladida, (2) Flexibilia, and (3) Articulata. The Cladida are a paraphyletic group, having given rise to the presumably monophyletic Flexibilia and Articulata (Simms and Sevastopulo, 1993; Ausich, 1998; Webster and Jell, 1999).

Although the Flexibilia likely originated from one species belonging to Cladida during the Ordovician (Springer, 1920; Brower, 1995; Ausich, 1998), it is less clear whether the Articulates originated before or after the Paleozoic and which lineage(s) within the Cladida is ancestral to the Articulata (Moore and Teichert, 1978; Simms and Sevastopulo, 1993; Webster and Jell, 1999). A summary of previous classifications of pan-cladid crinoids is presented in Fig. 1.

## PROBLEMATIC PALEOBIOLOGY OF CLADID CRINOIDS: MAXIMUM DIVERSITY AND MINIMUM PHYLOGENY

The subclass Cladida comprises the greatest number of genera in any crinoid subclass yet is the least understood in terms of evolutionary relationships. The Paleozoic diversity of the Cladida is depicted in Fig. 2. Cladid taxonomic richness steadily increased approximately in a linear pattern throughout the Paleozoic and reached maximal generic diversity during the Pennsylvanian as cladids became ecologically dominant constituents of the Late Paleozoic Crinoid Macroevolutionary Fauna (Ausich *et al.*, 1994).

Unfortunately, problematic classifications arising from unknown and/or questionable phylogenetic relationships prevent any fine-scale dissection of the taxonomic diversification patterns observed at this coarse level. Following the

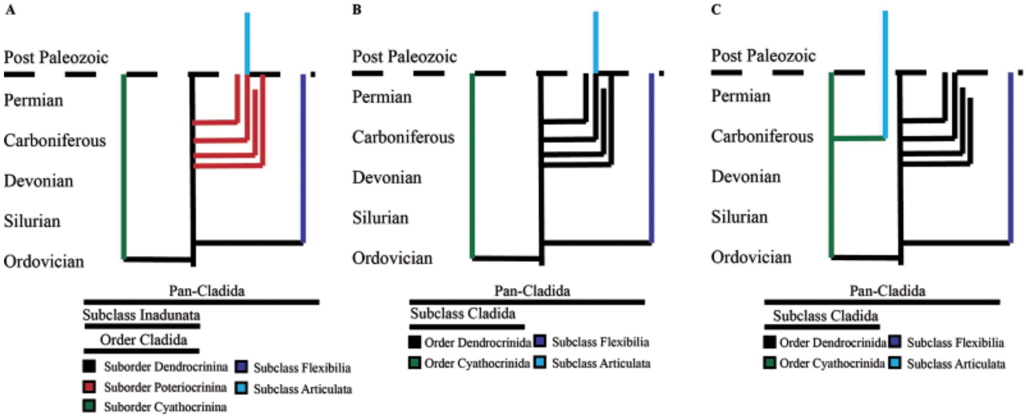

**Figure 1.** Summary of previously proposed phylogenetic relationships of pan-cladid crinoids. A. Phylogeny and classification of pan-cladid crinoids from the *Treatise of Invertebrate Paleontology* based on Moore and Teichert (1978) and Moore *et al.* (1978). B. A revised phylogeny and classification based on Simms and Sevastopulo (1993), Ausich (1998). C. Phylogenetic relationships of pan-cladid crinoids according to Webster and Jell (1999).

*Treatise of Invertebrate Paleontology* (Moore *et al.*, 1978), Ausich (1998) recognized three orders within the Cladida: the Dendrocrinida, Cyathocrinida, and the Poteriocrinida. However, the validity of these orders has been questioned (McIntosh, 2001; Simms and Sevastopulo, 1993; Kammer and Ausich, 1996). The Dendrocrinida is paraphyletic, having given rise to the Flexibilia (Springer, 1920; Moore and Laudon, 1943; Moore and Teichert, 1978; Brower, 1995; Ausich, 1998), and potentially the Cyathocrinida (Kammer and Ausich, 1992; Simms and Sevastopulo, 1993; Ausich, 1998) and Poteriocrinida. Because the Poteriocrinida is depicted in the *Treatise* as polyphyletic (Moore *et al.*, 1978, fig. 412), paleobiologists and paleoecologists have heuristically adopted concepts of evolutionary grades and informally referred to pinnulate cladids as "advanced" and non-pinnulate forms as "primitive" (Kammer and Ausich, 1992; 1996). Many crinoid taxonomists have followed McIntosh's (2001) suggestion that all advanced cladids be placed within the Dendrocrinida (Webster, 2012), but this practice has not been universally followed.

The current status of suprageneric classifications described above obfuscates any inference of macroevolutionary patterns among and within the major clades of pan-cladid crinoids. Thus, the current status of knowledge is problematic for testing hypotheses regarding character evolution and prevents further testing of any evolutionary hypotheses requiring an auxiliary hypothesis of genealogical relationships among taxa. Although a quantitative phylogenetic analysis of cladid crinoids would provide considerable insight into resolving suprageneric evolutionary relationships among higher taxa and provide a template for testing macroevolutionary hypotheses, no previous investigation has utilized a combined cladistic and computational phylogenetic approach. Family-level phylogenies for cladids were presented in Moore and Laudon (1943) and Moore *et al.* (1978), but these were inferred without a cladistic perspective and did not use rigorous computational methods for phylogenetic inference. Previous quantitative phylogenetic analyses involving

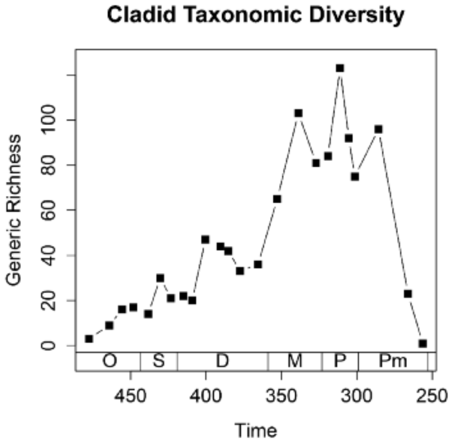

**Figure 2.** Genus-level diversity curve of Paleozoic crinoids classified within the subclass Cladida. Data compiled from Webster (2013).

relationships among cladid crinoids either only consider Ordovician taxa (Brower, 1995; Ausich, 1998) or were conducted on species within a single genus or related genera (Gahn and Kammer, 2002).

## A STEP TOWARDS PAN-CLADID PHYLOGENY

A quantitative phylogenetic analysis of pan-cladid crinoids was conducted, with emphasis on resolving relationships within the Cladida. Pan-cladid taxonomic diversity was formidably high for data collection to conduct a comprehensive generic or species-level analysis. For example, the subclass Cladida alone comprises some 505 nominal genera (Webster, 2013) (Fig. 2). Therefore, the analysis was conducted by examining phylogenetic patterns at the family-level. Sampling taxa at the family-level may better approximate the overall "big picture" structure of character evolution and morphological variability within the Pan-Cladida as a whole, thereby reducing phylogenetic noise from rampant character reversals/convergences within subclades and minimize the effect of sampling biases present at lower taxonomic levels (Wagner, 2000).

Ideally, any effort to accurately represent character variation needs to score character combinations present in "real" taxa and not nominal Linnaean ranks (Wiens, 2000). This problem was addressed by using representative species as proxies for family-level traits. Species were selected as exemplars based on the degree to which their character distributions reflect those of its higher taxon and were typically species from the type genus. Additional species were sampled when type species were poorly preserved or otherwise unavailable. Data was collected by examining museum specimens and primary taxonomic literature using characters from a comprehensive list of pan-cladid crinoid morphological characters and character states (107 total characters, >316 character states). Phylogenies inferred from these data will serve as a template for future macroevolutionary analyses dissecting patterns of phenotypic and taxonomic evolution among pan-cladid subclades.

### Acknowledgements

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# PALAEOBIOLOGICAL IMPLICATIONS OF A MASS-MORTALITY ASSEMBLAGE OF CINCTANS (ECHINODERMATA) FROM THE CAMBRIAN OF SPAIN

Samuel Zamora[1] and Imran A. Rahman[2]

[1] Instituto Geológico y Minero de España, Manuel Lasala 44 9ºB, 50006 Zaragoza, Spain. s.zamora@igme.es
[2] School of Earth Sciences, University of Bristol, Life Sciences Building, 24 Tyndall Avenue, Bristol BS8 1TQ, UK.
imran.rahman@bristol.ac.uk

**Keywords:** Cincta, Echinodermata, Cambrian, feeding, ontogeny.

## INTRODUCTION

Recent work on cinctans has provided valuable insights into the taxonomy, stratigraphic distribution, mode of life and phylogeny of this extinct group of echinoderms (Friedrich, 1993, 1995; Sdzuy, 1993; Zamora and Smith, 2008; Rahman and Zamora, 2009; Smith and Zamora, 2009; Zamora and Álvaro, 2010; Zamora *et al.*, 2013a). Despite these important advances, some fundamental aspects of cinctan palaeobiology remain contentious or poorly understood, in particular feeding and ontogeny. This is due in part to the absence of an unambiguous modern analogue, but another significant issue is the lack of data on living communities of cinctans. Here, we report a new mass-mortality assemblage of the cinctan *Elliptocinctus barrandei* that consists of 38 exceptionally well-preserved specimens. This is interpreted as a life assemblage of juvenile individuals, and it serves to shed light on the feeding mode and development of cinctans.

## GEOLOGICAL SETTING

The studied material was collected from the locality of Villalengua (western Iberian Chains, province of Zaragoza, Spain; Fig. 1). In this area, road cuts and farming activities, such as the ploughing of fields and excavation of irrigation pools, have yielded large amounts of rock that are rich in trilobites and echinoderms. These rocks belong to the Borobia Formation, which preserves a diverse echinoderm fauna, including the cinctans *Elliptocinctus barrandei* and *Sucocystis theronensis*, the edrioasteroid *Cambraster cannati*, the eocrinoid *Gogia gondi* and the stylophoran *Ceratocystis* sp., plus abundant trilobites and linguliformean brachiopods (Zamora and Álvaro, 2010; Zamora *et al.*, 2013b). In the Iberian Chains, the Borobia Formation is up to 250 metres thick; only the lower part is well exposed in the study area, comprising alternating beds of shale and sandstone, with fossils restricted to certain shaly horizons. The alternations are arranged in shallowing- and coarsening-upward cycles, ranging from offshore to shoreface (shoal) facies. Based on the trilobite content, these levels correspond to the *Solenopleuropsis* Assemblage Zone, which is lower Languedocian (upper mid-Cambrian) in age.

## MATERIAL AND METHODS

The fossils occur on a slab of yellowish grey shale, preserved as moulds on a single bedding plane (Fig. 2A). A latex cast was prepared in order to study the anatomy of the specimens in detail (Fig. 2B, C). This cast was whitened with

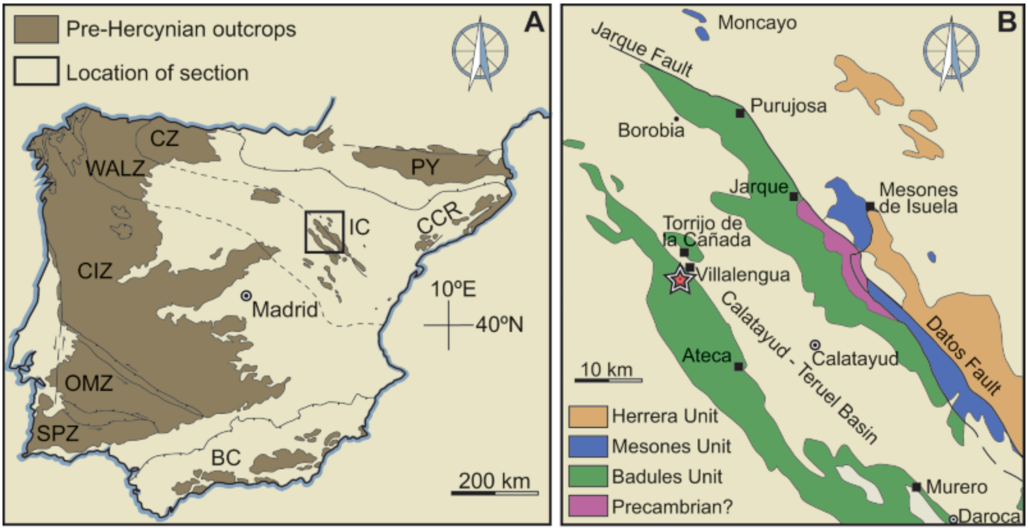

**Figure 1.** Geological setting with the study site marked. A. Map of Spain showing the position of the Iberian Chains. B. Geological map of the Iberian Chains indicating the locality where the slab was collected.

ammonium chloride sublimate prior to photography. The slab is currently housed in the Museo de Ciencias Naturales de la Universidad de Zaragoza, Spain.

## RESULTS

A total of 38 specimens of *Elliptocinctus barrandei* are preserved, ranging from 4–6 mm in width. They are aligned in a row that is around 10–13 mm in width and 14 cm in length (Fig. 2A, B). All but one of the fossils are oriented dorsal surface up, and many of the specimens are preserved articulated and complete, including delicate structures such as the dorsal integument and the stele (Fig. 2B, C). Some fossils are partly disarticulated, but the disarticulated elements show little displacement from their original position (Fig. 2C). The specimens do not show a preferential orientation.

## DISCUSSION

The cluster of cinctans described herein most probably represents a life assemblage, with fossils preserved in the position they occupied in life. Nearly all of the specimens are oriented with the dorsal surface facing upwards, which differs from the typical situation in transported associations, where fossils are also preserved overturned (Zamora, pers. obs.). Additionally, a life assemblage is suggested by the presence of numerous complete articulated specimens; even in the few cases where fossils are partly disarticulated, the plates are not substantially displaced from the original position (Fig. 2C), indicating no or minimal transport. Nevertheless, a few individuals overlap with one another (Fig. 2C) and one specimen is preserved overturned, and this suggests there may have been very limited post-mortem transportation prior to or during burial.

Cinctans are aligned in a row that is clearly differentiated from the rest of slab, characterized by sediment with a finer grain size than that of the surrounding rock. The specimens do not show any sort of preferential orientation and, assuming this represents their life position, this indicates that they were capable of surviving in a range of orientations to the current. This has implications for their likely mode of feeding; such a position is not compatible with passive suspension feeding in an environment with a unidirectional current, where individuals rely on the ambient flow to bring them nutrients, and can therefore be expected to align themselves normal to the current to enhance feeding

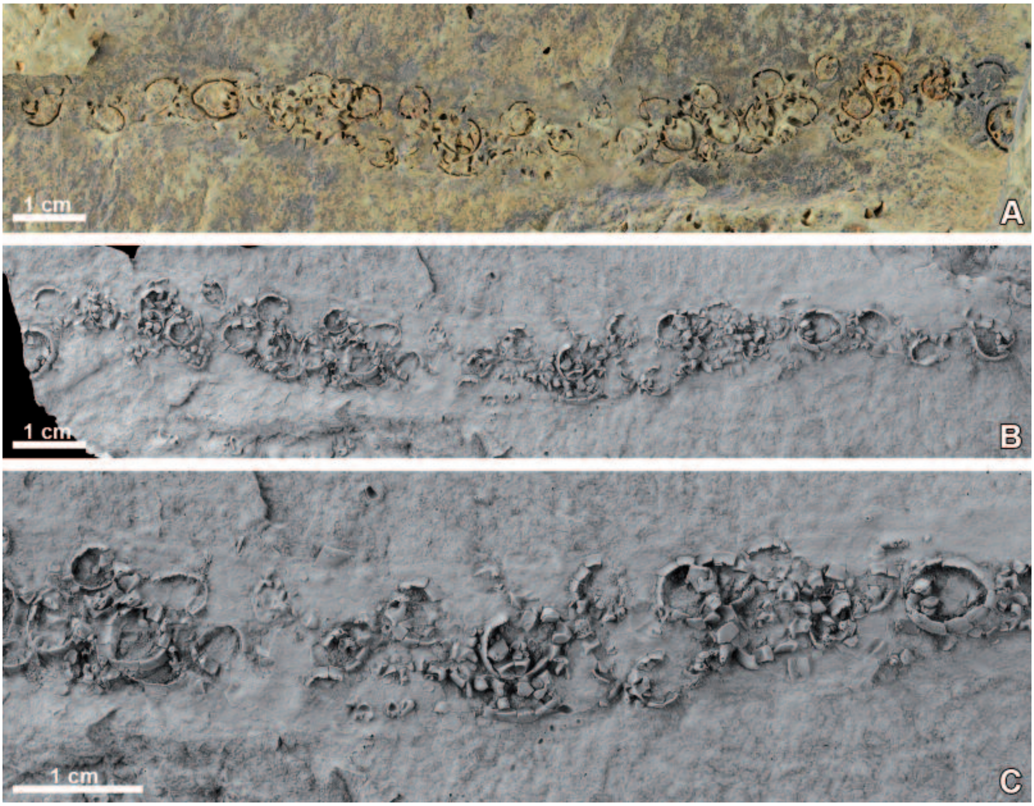

**Figure 2.** Slab preserving a mass-mortality assemblage of 38 articulated specimens of the cinctan *Elliptocinctus barrandei* from the Borobia Formation (Villalengua, Zaragoza, Spain). A. Fossils preserved as natural moulds in a yellowish grey shale. Note that all the specimens are preserved in a clearly demarcated row. B. Latex cast of the fossils. C. Close-up of the latex cast showing articulated specimens preserving delicate structures such as the upper integument and stele.

(Vogel, 1981; LaBarbera, 1984). Instead, the absence of a preferential orientation is more suggestive of active suspension feeding, with the animals creating an inhalant flow to transport food particles into the mouth, and hence not being greatly reliant on the ambient flow direction.

The studied specimens of *Elliptocinctus barrandei* are very small compared to previously described individuals, which can reach up to 17–20 mm in width (Friedrich, 1993; Zamora and Álvaro, 2010). This strongly suggests that they are juveniles. Because all the individuals are approximately the same size and are inferred to represent a life assemblage, this indicates that they belong to a single age class. The close association of numerous juveniles might be the product of settlement in a nursery area, as has been reported in modern asteroids (e.g. Chia *et al.*, 1984).

## Acknowledgements

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# FIELD TRIP:
# PALAEOZOIC ECHINODERMS FROM NORTHERN SPAIN

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Cuadernos del Museo Geominero, 19. Instituto Geológico y Minero de España, Madrid. ISBN: 978-84-7840-961-7

# FIELD TRIP:
# PALAEOZOIC ECHINODERMS FROM NORTHERN SPAIN

**Samuel Zamora[1] (coord.)**

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

[1] Instituto Geológico y Minero de España, Manuel Lasala 44 9ºB, 50006 Zaragoza, Spain. s.zamora@igme.es
[2] Instituto de Geociencias (CSIC-UCM), José Antonio Novais 12, 28040 Madrid, Spain. jj.alvaro@csic.es, jcgrapto@ ucm.es, jorgeves@unizar.es
[3] Departamento de Geología, Universidad de Oviedo, Jesús Arias de Velasco s/n, 33005 Oviedo, Spain. marbizu@geol.uniovi.es, lpedro@geol.uniovi.es
[4] Área de Paleontología, Departamento de Ciencias de la Tierra, Universidad de Zaragoza, Pedro Cerbuna 12, 50009 Zaragoza, Spain. colmenar@unizar.es, villas@unizar.es
[5] Facultad de Biología y Ciencias Ambientales, Universidad de León, Campus of Vegazana, 24071 León, Spain. e.fernandez@unileon.es
[6] Soningeo, S.L. PCTCAN, Isabel Torres, 9 P20. 39011 Santander, Cantabria, Spain. juanl_suarez@yahoo.es
[7] Department of Geology, Appalachian State University, ASU Box 32067, Boone, NC 28608-2067, USA. watersja@appstate.edu

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

## INTRODUCTION

### Samuel Zamora

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

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

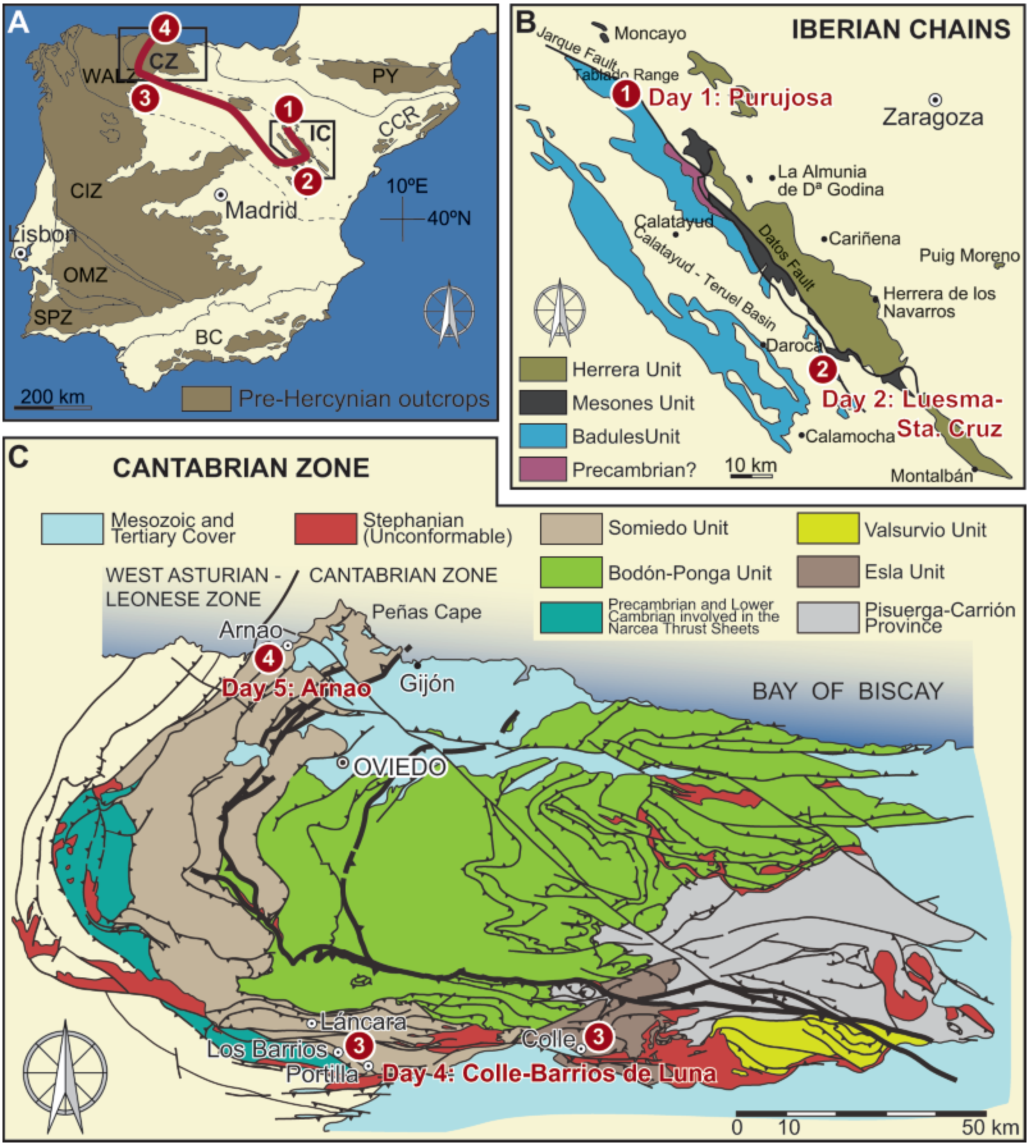

**Figure 1.** Itinerary followed by the field trip. A. Map of Spain showing Pre–Hercynian outcrops and tectonostratigraphic zones. Zones: CZ, Cantabrian; CIZ, Central Iberian; WALZ, West Asturian–Leonese; OMZ, Ossa–Morena Zone; SPZ, South Portuguese; BC, Betic Cordillera; IC, Iberian Chains; PY, Pyrenees.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

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

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

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

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

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

The last day, Suárez-Andrés *et al*. (this guide) present the faunas from a very important fossil site close to the locality of Arnao at Cape La Vela (Asturias). Here, an interesting fauna from the Lower Devonian Aguión Formation (upper Emsian) contributes to the understanding of the role of substrates in the distribution of echinoderms. Abundant fossils preserved *in situ* in both soft and hard substrates serve as a remarkable example of echinoderm anchoring strategies. This outcrop also preserves two echinoderms that were described by Andrew Smith, the only edrioasteroid known from the Devonian of Spain, *Krama devonica* (Smith and Arbizu, 1987), and the only echinoid known from the Palaeozoic of Spain, *Rhenechinus ibericus* (Smith *et al*. 2013a).

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

# PALAEOZOIC FROM THE IBERIAN CHAINS

J. Javier Álvaro

The pre-Variscan outcrops of the Iberian Chains constitute a relic of the deeply eroded Variscan orogen in NE Spain. These NW-SE-trending chains or ranges are longitudinally divided, by the Cenozoic Calatayud-Teruel trough, into the western and eastern Iberian chains (Fig. 1). Traditionally, the pre-Variscan outcrops have been further subdivided into three NW-SE-trending tectonostratigraphic units, bounded by major faults and mainly characterized by differences in the style of Variscan-dominated deformation. From southwest to northeast, they are named Badules, Mesones and Herrera units. The former comprises Ediacaran to Lower Ordovician rocks, and show 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.

## DAY 1: June 17th 2015

## CAMBRIAN ECHINODERMS FROM PURUJOSA, NORTHERN IBERIAN CHAINS

Samuel Zamora, J. Javier Álvaro and Jorge Esteve

### INTRODUCTION

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

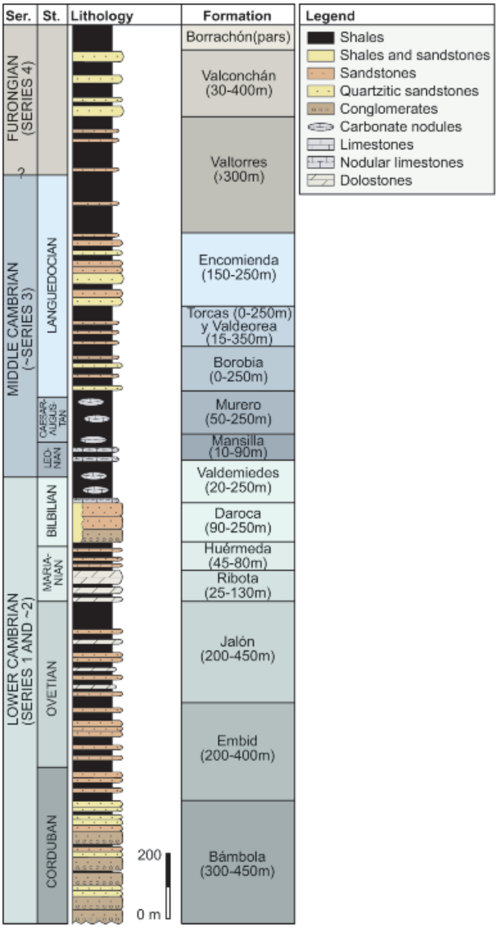

**Figure 2.** Synthesis stratigraphic log of Cambrian rocks in the Iberian Chains.

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

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

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

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

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

### Location

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

Coordinates: 41º40'37.19"N, 1º46'35.35"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.

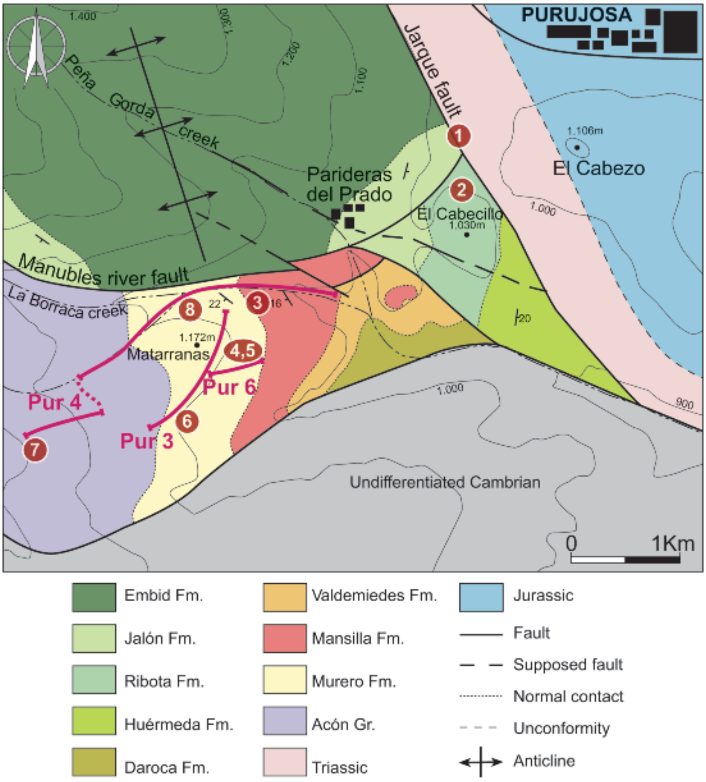

**Figure 3.** Detailed geological map of the Purujosa area with indication of visited sections and situation of stops. Modified from Zamora (2005).

## Aims

Look at a thrust marking the Mesozoic/Palaeozoic contact.

## Description

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

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

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

### Location

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

Coordinates: 41º40’34,39”N, 1º46’40,68”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 fossilifierous 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: 41º40’ 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 dibrachicystid isolated plates (Fig. 5C), trilobites, brachiopods and molluscs.

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

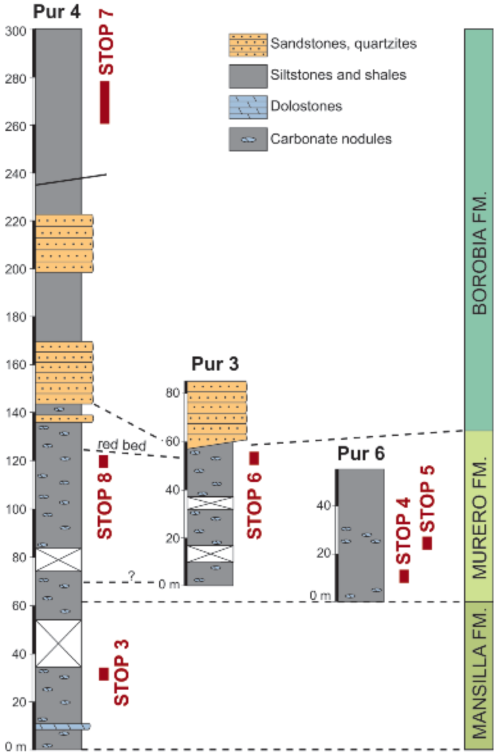

**Figura 4.** Stratigraphic sections from Purujosa with indication of the intervals visited in each stop. Modified from Zamora (2005) and Esteve (2011).

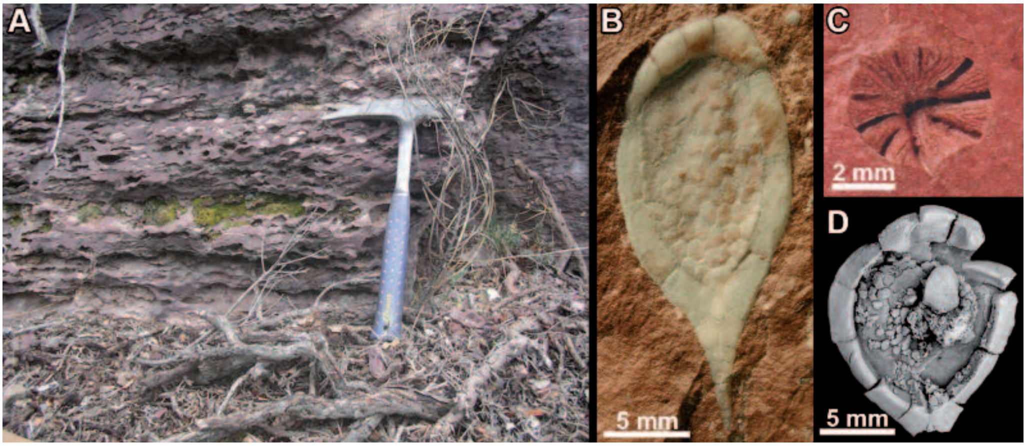

**Figure 5.** The Mansilla Formation and its echinoderm fauna. A. General aspect of the formation showing the typical griotte facies in which carbonate nodules intercalate with the reddish shales. B. The cinctan *Protocinctus mansillaensis* preserved in calcite. C. Isolated plate of a dibrachicystid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

Zamora, 2009). The inclusion of this taxon into a cladistic analysis revealed its basal position within the sucocystid clade (Smith and Zamora, 2009), which is not unexpected if we consider the taxon as the oldest cinctan from Gondwana. Close to the Mansilla-Murero contact, Zamora (2009) reported *Asturicystis* sp. (Fig. 5D), a genus previously described in the Cantabrian Mountains and Czech Republic (Sdzuy, 1993; Fatka and Kordule, 2001). The presence of *Asturicystis* in Bohemia seems questionable based on the poor illustration and specimen morphology with ventral swellings in several plates and the length of food grooves. Moreover, those levels are rife of 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 (Purujosa 6 section) (Figs. 3, 4).

Coordinates: 41º40’ 11.70”N, 1º47’16.91”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 hight diversity from the Murero Formation consisting of cinctans, ctenocystoids, gogiids, dibrachicystids and stylophorans.

### Description

The *Ctenoimbricata* quarry (Fig. 6A) lies at the base of the Murero Formation in the Purujosa 6 section (Fig. 3, 4), which is mid 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 Purujosa in the most distal part of the Iberian Platform (a part of the Cantabro-Iberian Basin) favoured preservation of multiple obruption 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

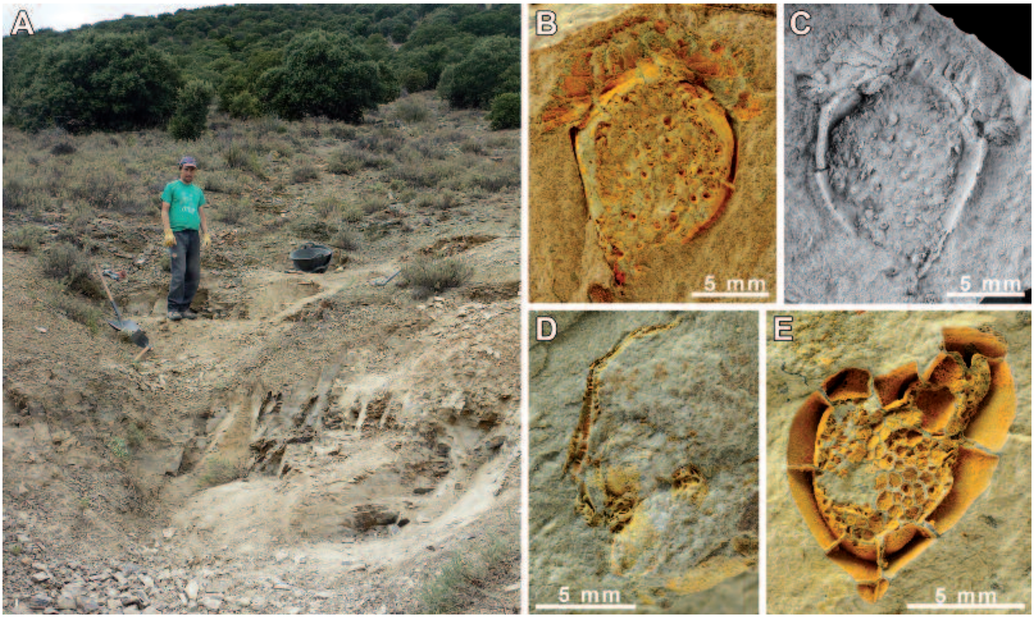

**Figure 6.** A. General view of the *Ctenoimbricata* quarry in levels from the base of the Murero Formation. B, C. *Ctenoimbricata spinosa* preserved as natural mould (B) and latex cast from the same specimen (C). D. The stylophoran *Ceratocystis* preserving a complete feeding appendage. E. The cinctan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

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

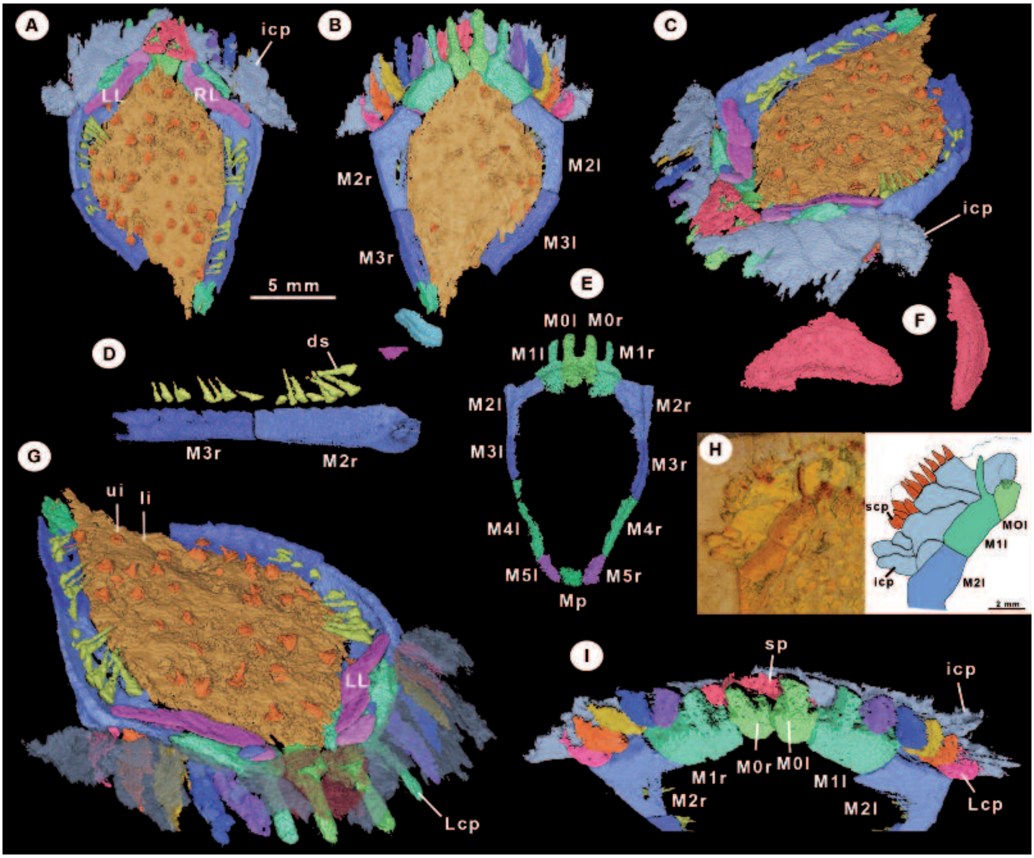

**Figure 7.** CT scan images of *Ctenoimricata spinosa*. Computer models (A–G, I) and photograph with interpretive camera lucida drawing (H). A, B. Dorsal and ventral views. C. Oblique left view. D. Lateral view of two marginal plates showing the articulation of the spines. E. Marginal frame plates after 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.

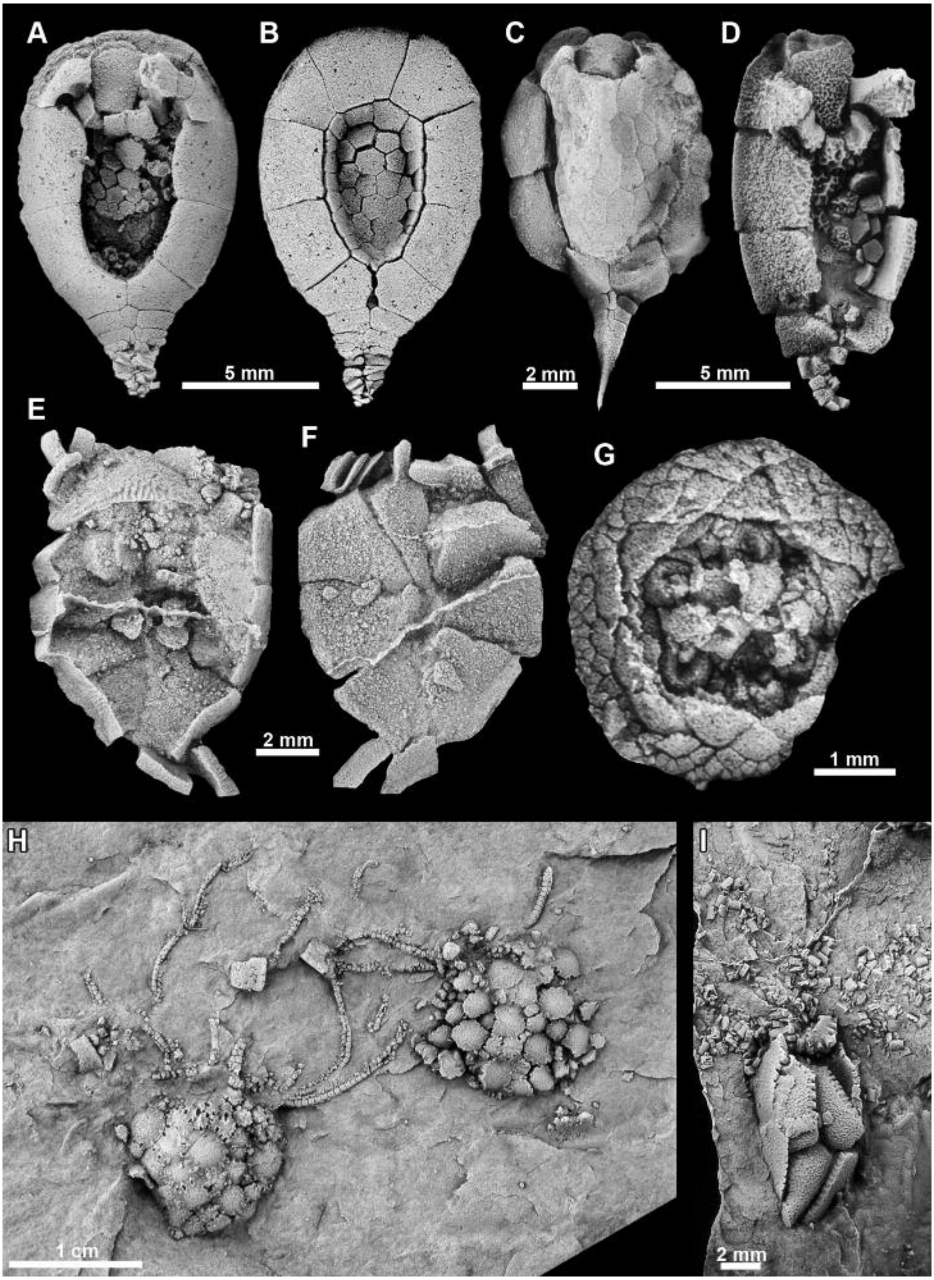

**Figure 8.** Echinoderm faunas from the Murero Formation at Purujosa. A, B. Dorsal and ventral view of the cinctan *Gyrocystis platessa*. C. Dorsal view of the cinctan *Gyrocystis testudiformis*. D. Dorsal view of the cinctan *Gyrocystis erecta*. E, F. Dorsal and ventral view of the ctenocystoid *Courtessolea* 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 $NH_4Cl$ 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*, *Ctenocephalus antiquus* and *Peronopsis acadica* (Zamora and Smith, 2012; Zamora *et al*., 2013a). The associated trilobite assemblages indicate its belonging to the *Pairdailhania 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 stele. Plate addition appears to be more prevalent in the ventral and possibly dorsal integuments although plate growth remains predominant. Although the ontogenetic series of *Graciacystis ambigua* shows the growth for just one species of cinctans, the fundamentally similar construction of other species points that all followed a similar growth strategy.

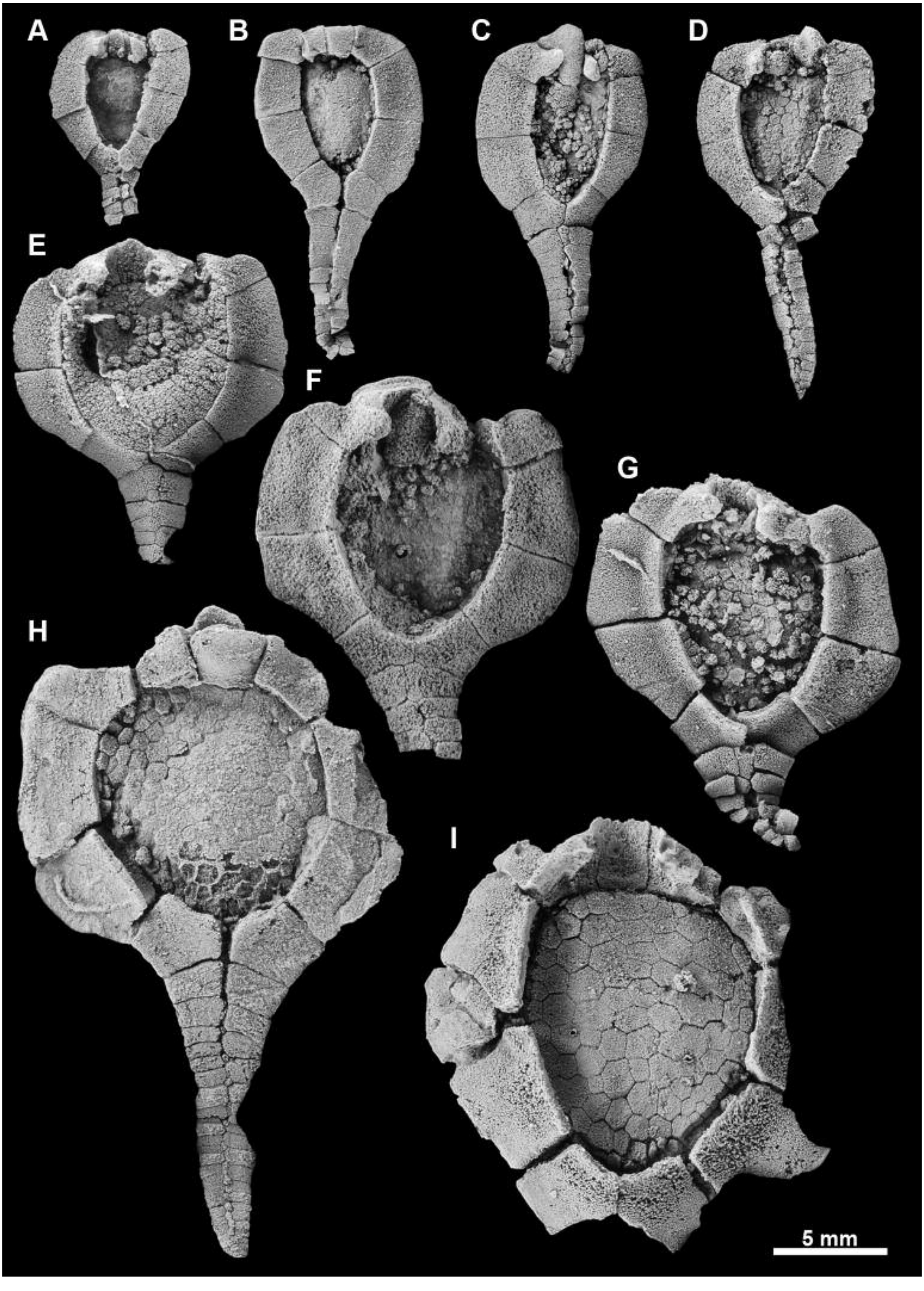

**Figure 9.** Ontogenetic series of the cinctan *Graciacystis ambigua*. A, C-G, I are dorsal views and B, H are ventral views. All photographs are from latex cast whitened with $NH_4Cl$ sublimated.

## 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: 41º40'7.37"N, 1º47'23.79"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 stylophorans *Ceratocystis* sp. (Fig. 11B), plus two different undescribed cothurnocystids, and the blastozoans *Gogia gondi*, *Lichenoides* sp. (Fig. 8I) and *Dibrachicystis purujoensis* (Fig. 11A), polymerid trilobites (*Eccaparadoxides pradoanus* Fig. 11E, H, I, *Conocoryphe heberti*, *Solenopleuropsis* (*Manublesia*) *thorali* (Fig. 11J), *S.* (*M.*) *riberoi* (=*S. (M) marginata*), *S.* (*M.*) *verdiagana*, *Schopfaspis*? *graciai* (Fig. 11C), agnostoids (*Condylopyge* sp., *Peronopsis acadica*, *P. ferox*, *Pleurocterium* sp., and *Megagnostus* sp. Fig. 11D), and both orthid (Fig. 11F) and lingulid brachiopods (Fig. 11G) (Zamora, 2009, 2010; Esteve, 2011; Esteve *et al*. 2011; Mergl and Zamora, 2012). The FAD of the trilobite *Solenopleuropsis* (*M.*) *thorali* marks the base of the regional Languedocian Stage (*sensu* Álvaro and Vizcaïno, 1998).

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

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

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

available to contemporaneous individuals belonging to the same Cambrian genera. Second, it is noticeable that closely related individuals, sometimes even belonging to the same species (e.g., *Solenopleuropsis* (*M.*) *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 11.** Fossils collected from the red beds of the Murero Formation. A. The blastozoan *Dibrachicystis purujoensis*. B. the stylophoran *Ceratocystis* sp. C. The trilobite *Schofaspis*? *graciai*. D. The agnostoid *Megagnostus* sp. E. The trilobite *Eccaparadoxides pradoanus*. F. The rhinchonelliformean brachiopod *Brahimorthis alvaroi*. G. lingulid brachiopod *Micromitra* sp. H, I. Enrolled specimens

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

### Location

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

Coordinates: 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, Torrijo de la Cañaba, Borobia and Villalengua (see Zamora and Álvaro, 2010; Zamora *et al. 2013*b) and has revealed a rich assemblage of echinoderms that varies in composition depending on the locality. In Purujosa, three levels from the lower part of the formation have provided complete echinoderms, not yet described. In this stop, we will visit the intermediate level (Fig. 4) that has provided only the cinctan *Elliptocinctus barrandei* (Fig. 12A, B). The upper level is more diverse and has provided isolated stylophoran plates, indeterminated cinctans, the edrioasteroid *Cambraster* sp., and the ctenocystoid *Etoctenocystis* (Fig. 12F). In contrast, other localities of the Iberian Chains have been more investigated and have reported several species of cinctans, including *Lignanicystis* sp. (Fig. 12C), *Sucocystis theroensis* (Fig. 12D, E), the edrioasteroid *Cambraster cannati* (Fig. 12G, H), the eocrinoid *Gogia gondi*, and the stylophorans *Ceratocystis* sp. and Cothurnocystid indet (Fig. 12I, J).

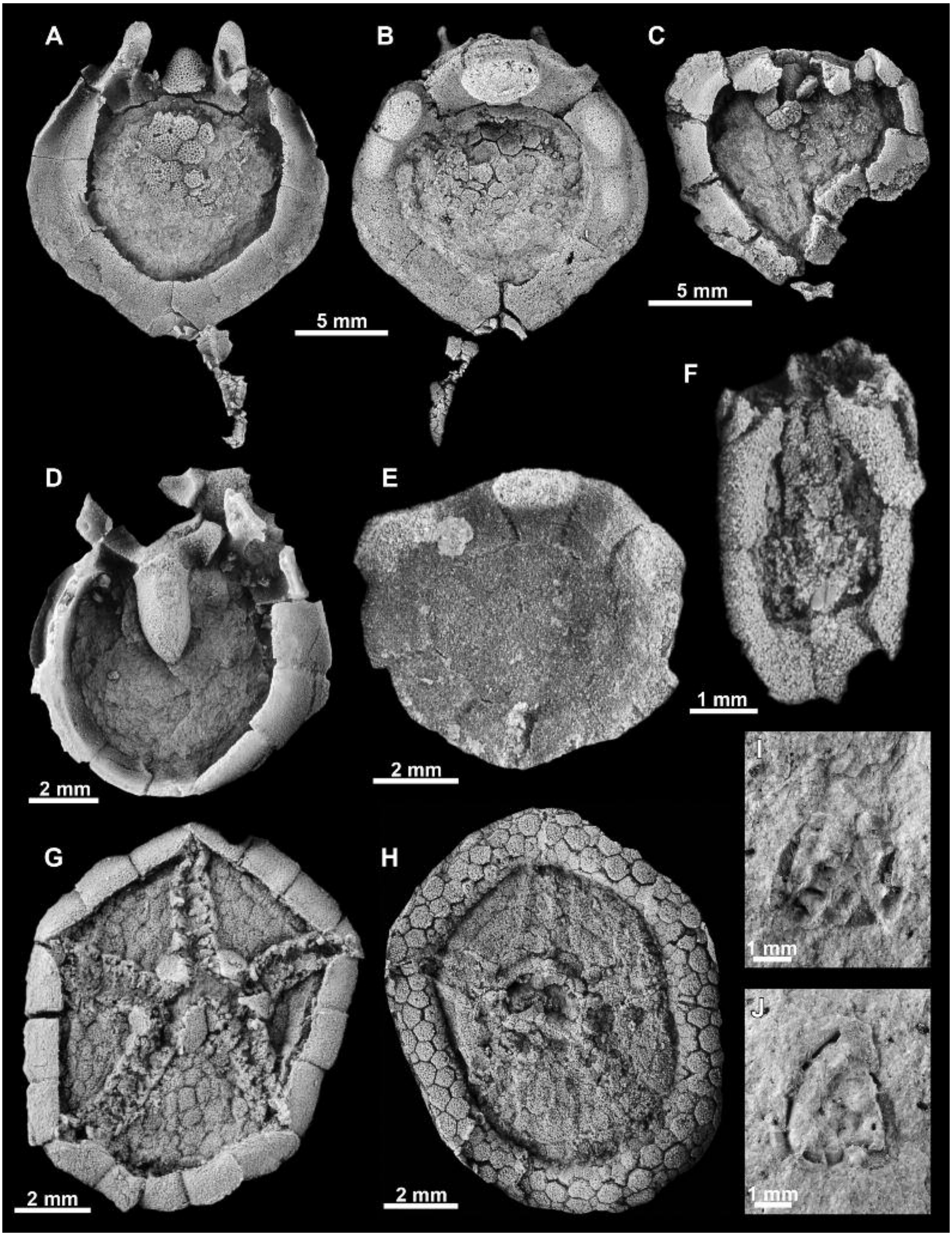

**Figure 12.** Echinoderms collected in the Borobia Formation at Purujosa (A, B, F) and coeval localities like Jarque (C), Torrijo de la Cañada (D, E, I, J) and Villalengua (G, H). A, B. The cinctan *Elliptocinctus barrandei*. C. the cinctan *Lignanicystis* sp. D, E. The cinctan *Sucocystis theroensis*. F. The ctenocystoid *Etoctenocystis*. G, H. The edrioasteroid *Cambraster cannati*. I, J. An indeterminate cothurnocystid stylophoran. All photographs are from latex cast whitened with $NH_4Cl$ 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 pasleyi* level appears just 1 m below the red beds at the top of the Murero Formation (Fig. 3).

Coordinates: 41º40’19.41”N, 1º47’34.64”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 *Gyrocytis platessa* (Fig. 8A, B) and the eocrinoid *Gogia parsleyi* (Fig. 8H) are the most abundant. We have found a single specimen of an indetermiate 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 3.000 m thick, and the Darriwillian to Hirnantian less than 500 m thick. Lotze (1929) described the stratigraphy with refinements by Carls (1975), Wolf (1980), Villas (1983) and Hammann (1992). Modern

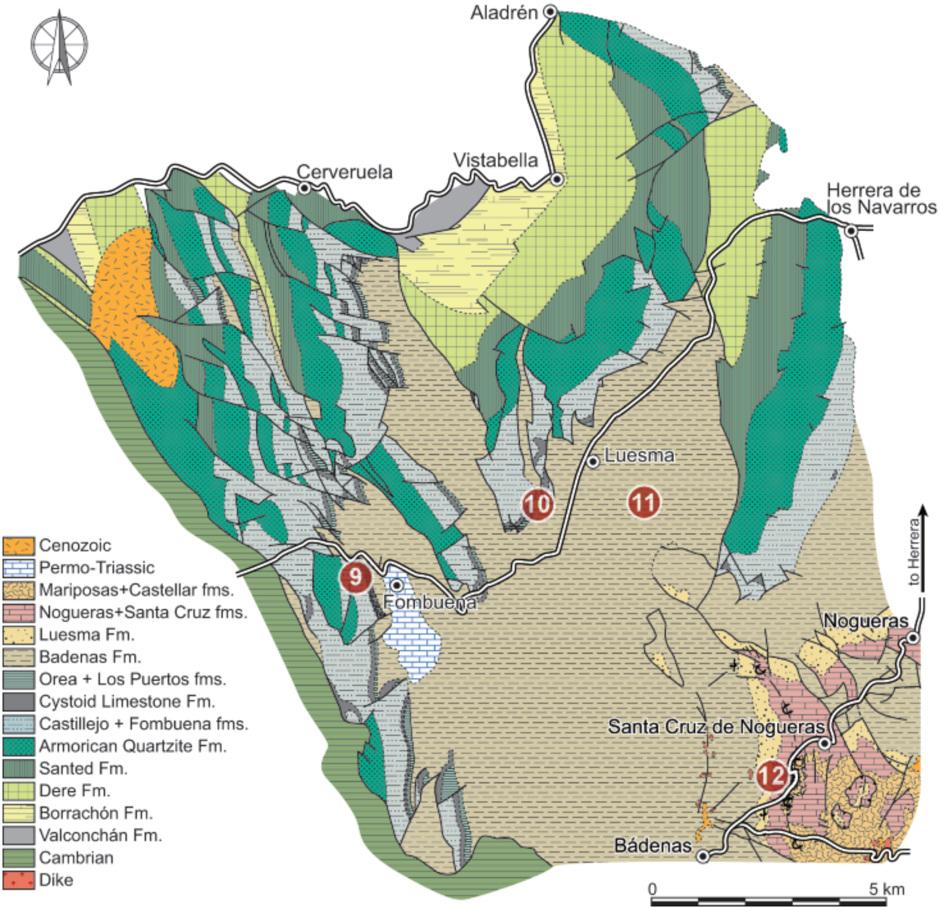

**Figure 13.** Geological map of the surroundings of Luesma with indication of stops. Modified from Hammann (1992).

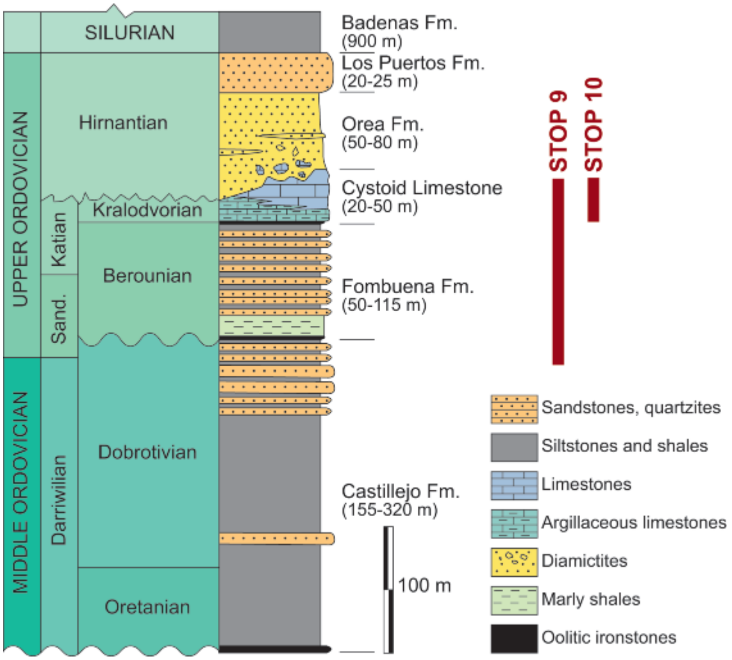

**Figure 14.** Schematic stratigraphic column of the Ordovician (pars.) of the Eastern Iberian Chain, with the correlation between the Ordovician Global Series and Stages and the Ordovician Mediterranean Stages. Note the stratigraphic position of different stops.

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

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

An oolitic ironstone, overlying the Armorican Quartzite, marks the base of the sandy and shaly 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 Darriwilian, although it probably overlies a stratigraphical gap corresponding to the lower Oretanian regional stage (equivalent to the British lower Abereiddian), since the lowest graptolites found in the formation belongs to the *D. murchisoni* Zone (Gutiérrez-Marco, 1986). Trilobites (Hammann, 1983) and brachiopods (Villas, 1985) are relatively abundant in its upper part, of Dobrotivian (latest Darriwilian 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

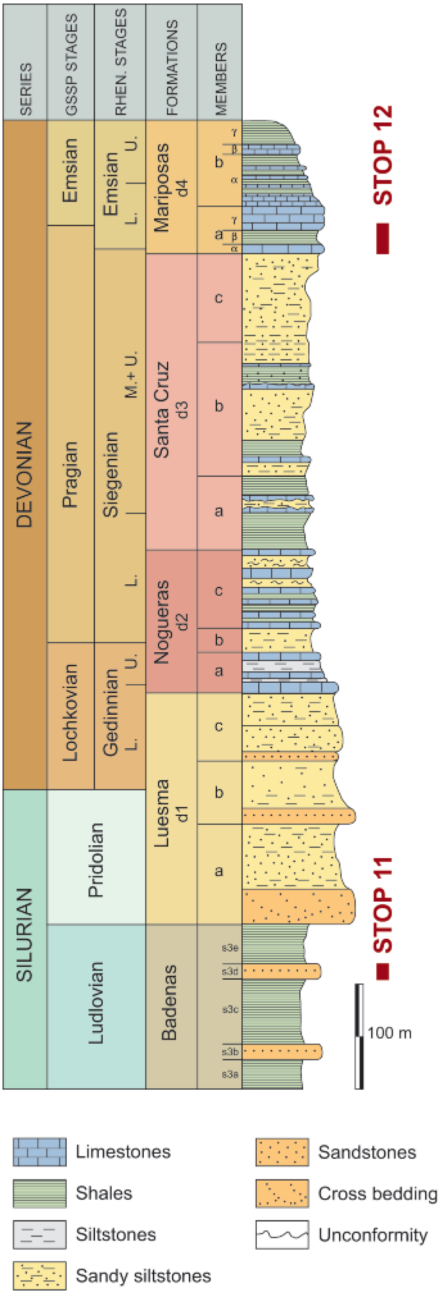

**Figure 15.** Stratigraphic column of the Silurian and Lower Devonian in the Eastern Iberian Chain (Spain). Note the position of the stops. Modified from Carls (1987). Abbreviations: L: Lower, M: Middle, U: Upper.

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: 41º8’53”N, 1º12’16”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 Triasic rocks. The section starts in the eastern bank of the road Bádules-Fombuena where the boundary between the Castillejo and Fombuena formations is well exposed.

#### The Castillejo Formation

The Castillejo Formation paraconformably overlies the Armorican Quartzite and contains three members. The basal Marité Member displays a variable thickness, from one meter in its type section up to 40 meters in the Marité Mine (Carls, 1975). It is composed of ferruginous shales that locally comprise up to three oolitic ironstone beds. Several authors (Kolb, 1978; Wolf, 1980; Gutiérrez-Marco, 1986) indicate the presence of graptolites belonging to the *Didymograptus 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 “cambriensis”* (*P. tournemini*) and *Redonia* sp. In the upper part of this member, the graptolites *Gymnograptus linnarssoni* and *Hustedograptus teretiusculus* have been found (Hammann *et al.*, 1982; Gutiérrez-Marco, 1986) as well as the trilobites *Placoparia tournemini*, *Neseuretus tristani*, *Eodalmanitina macrophtalma*, *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.

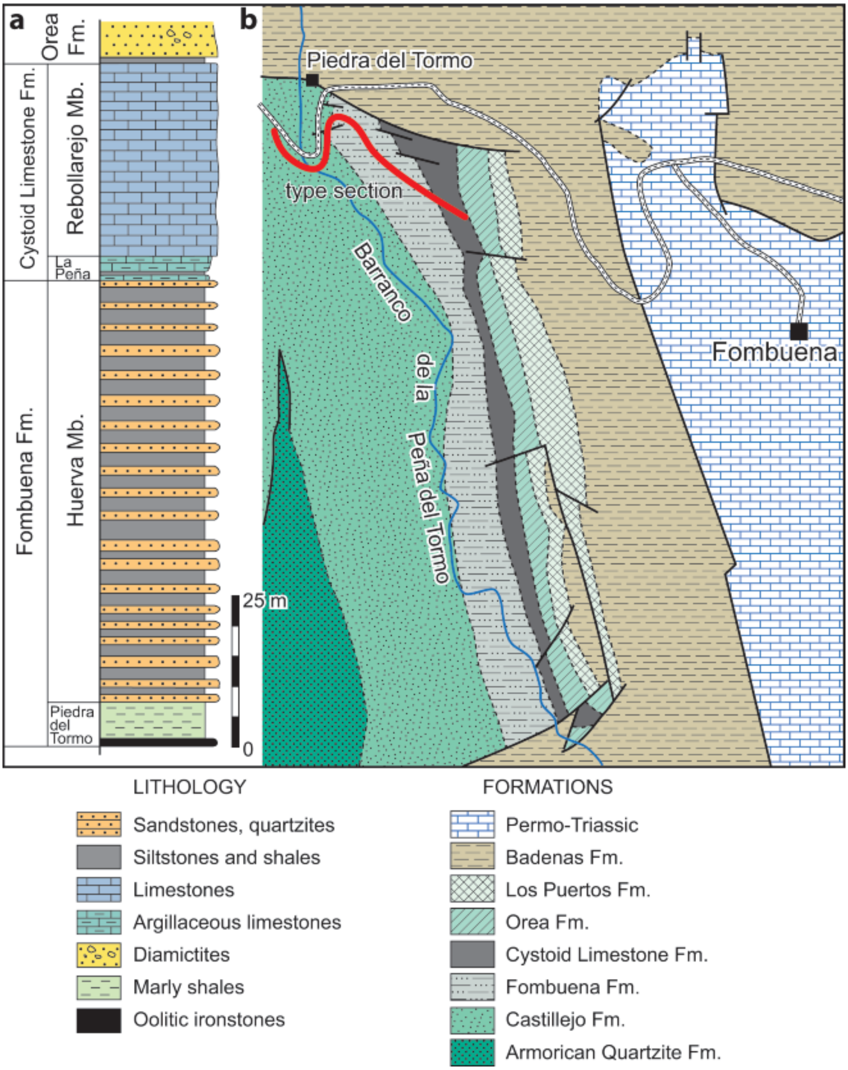

**Figure 16.** Geological map and lithological column of the Peña del Tormo locality. Modified from Hammann (1992). Itinerary marked with a red line.

The upper Sierra Member displays a variable thickness decreasing towards the northwest from 150 to 10 m (Villas, 1983). It is characterized by alternating shales and sandstones and frequently by highly fossiliferous sandstone lenses with calcareous cement. Hammann *et al.* (1982) cited the trilobites *Neseuretus henkei, Crozonaspis incerta, Crozonaspis armata, Phacopidina micheli* and *Eohomalonotus 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 coquinoid 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 Aristocystitidae gen. et sp. indet. From the Castillejo Formation a complete specimen of the crinoid *Heviacrinus* sp. (Fig. 17) has also been collected.

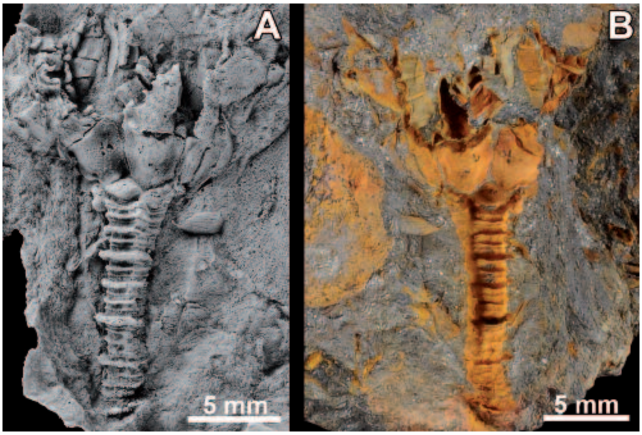

**Figure 17.** The crinoid *Heviacrinus* sp. from the Castillejo Formation. A. latex cast whitened with $NH_4Cl$. B. Natural mould coated with iron oxides.

### The Fombuena Formation

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

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

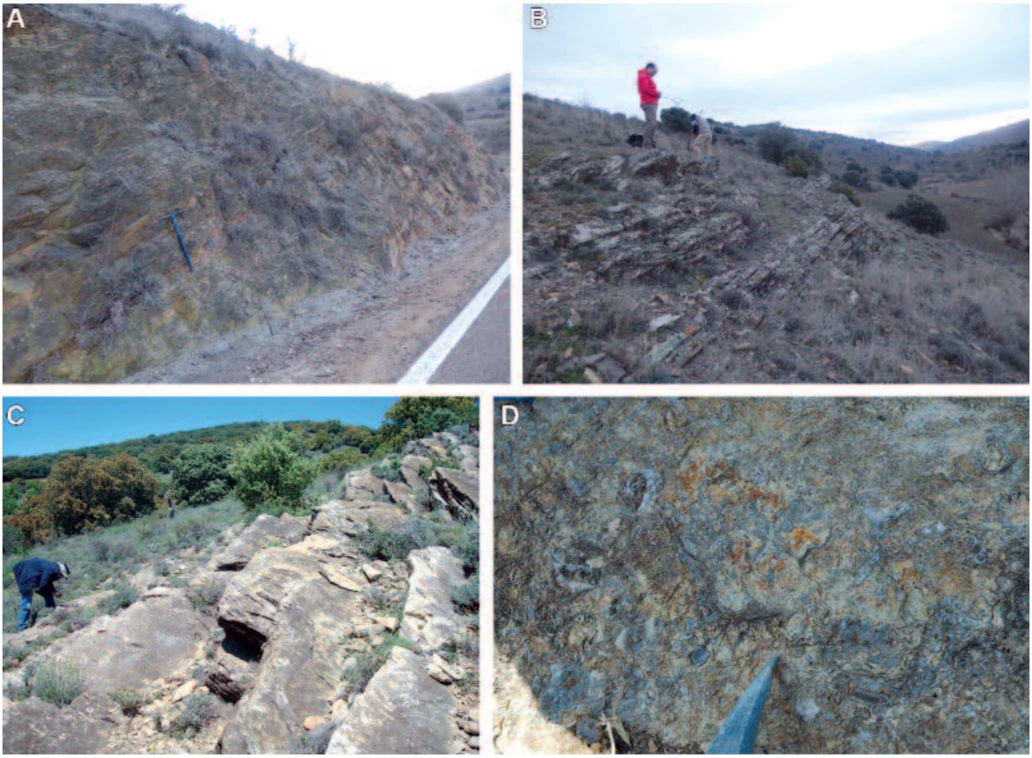

**Figure 18.** Field aspect of the Fombuena Formation (A, B) and the Cystoid Limestone (C, D). A. Briozoan marlstones from the Piedra del Tormo Member. B. Fossiliferous sandstones from the Huerva Member. C. Limestone beds from the Rebosilla Member. D. Bed plane containing several cystoids.

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

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

## The Cystoid Limestone Formation

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

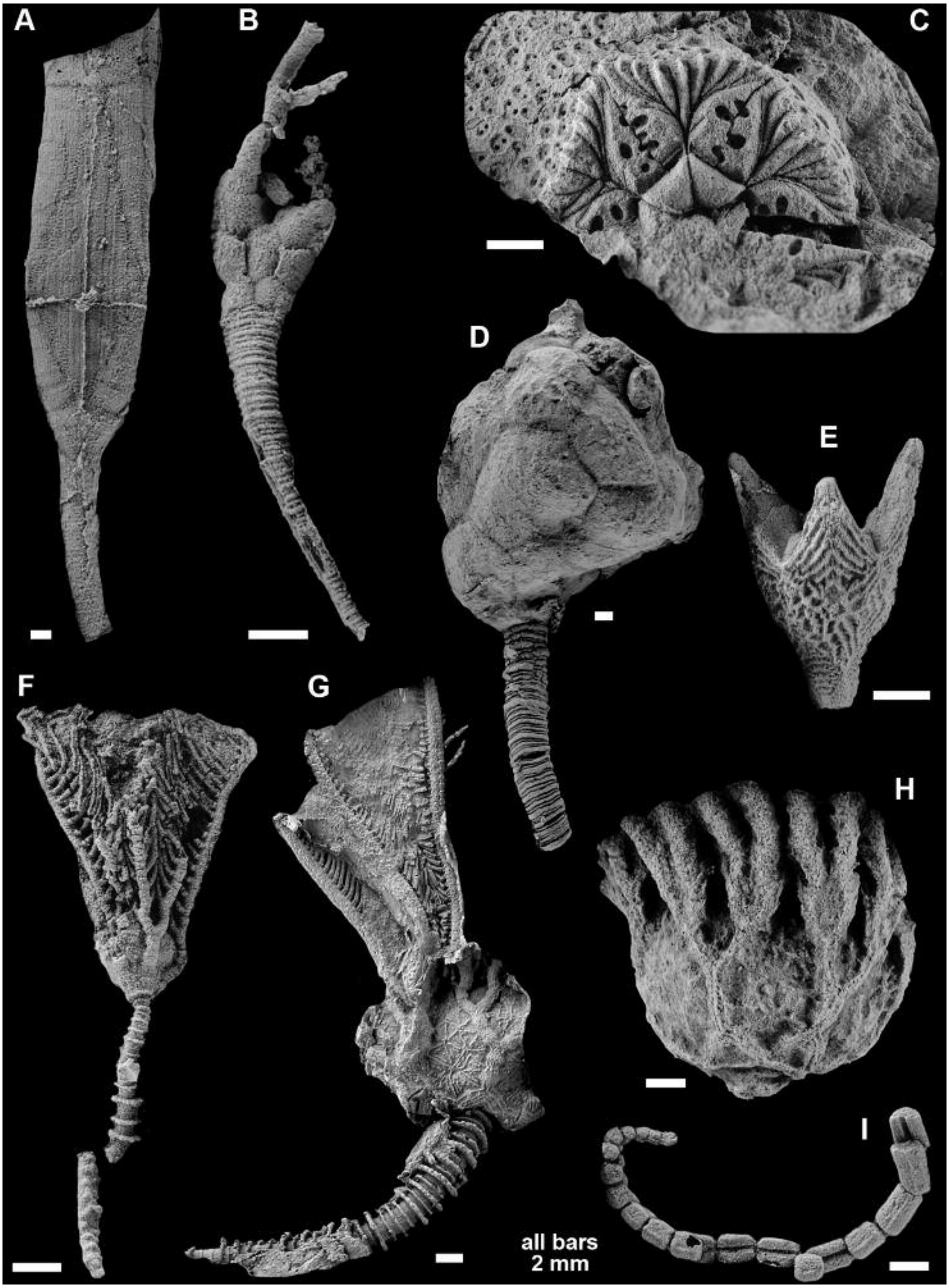

**Figure 19.** Echinoderms from the Fombuena Formation. A. Blastozoan *Rhombifera bohemica* preserving the stem. B. Cladid crinoid. C. Oral area of the diploporan *Codiacystis*? n. sp. D. Blastozoan *Caryocrinites* sp. preserving part of the proximal stem. E. Coronoid *Mespilocystites lemenni*. F. Camerate crinoid preserving part of the stem and arms. G. Camerate crinoid preserving an almost complete theca, arms and proximal part of the stem. H. Camerate crinoid. I. Distal stele part of the solutan *Dendrocystoides* sp. All photographs are from latex cast whitened with $NH_4Cl$ sublimated.

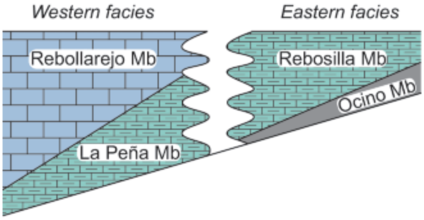

**Figure 20.** Relationship of facies and lithostratigraphic units of the Cystoid limestone Formation in the eastern Iberian Chain. Modified from Hammann (1992).

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 stromatactoid-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, Eridorthis* and *Eoplectodonta* (*Kozlowskites*), among others. Brachiopods are very strongly related to the environmental conditions in which they live (Colmenar *et al.*, 2014) and are consequently very sensitive to changes in the environmental parameters of their habitat. The low diversity brachiopod associations endemic to the Mediterranean region during the early Late Ordovician, were replaced by immigrants (*Nicolella* Community) from low latitude palaeocontinents (Baltica-Avalonia), better adapted to the environmental changes accompanying the Boda event. Larvae of these organisms arrived to the Mediterranean region presumably favoured by the eastward and poleward warm-water currents of the temperate zone (Colmenar, *in press*).

Conodonts characteristic of the *Amorphognathus ordovicicus* Zone where identified by Carls (1975) throughout the massive limestones of the 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 sdzuy* (Fig. 21A, B), *Caryocrinites elongatus*, *Caryocrinites* cf. *crassus*, *Caryocrinites europaeus*, *Stichocystis unilineata*, *Heliocrinites rouvillei* (Fig. 21D), *Heliocrinites minuta* (Fig. 21M), *Heliocrinites helmhackeri*, *Heliocrinites* cf. *saenzi*), diploporans (*Eucystis* cf. *angelini, Proteocystites hispanica* Fig. 21E, F), coronoids (*Mespilocystites tregarvanicus* Fig. 21G, H) and columnals belonging to several pelmatozoan genera (*Cyclocharax paucicrenellatus*, *Malovicrinus* sp., *Ristnacrinus* cf. *cirrifer*, *Conspectocrinus* cf. *celticus* Fig. 21K).

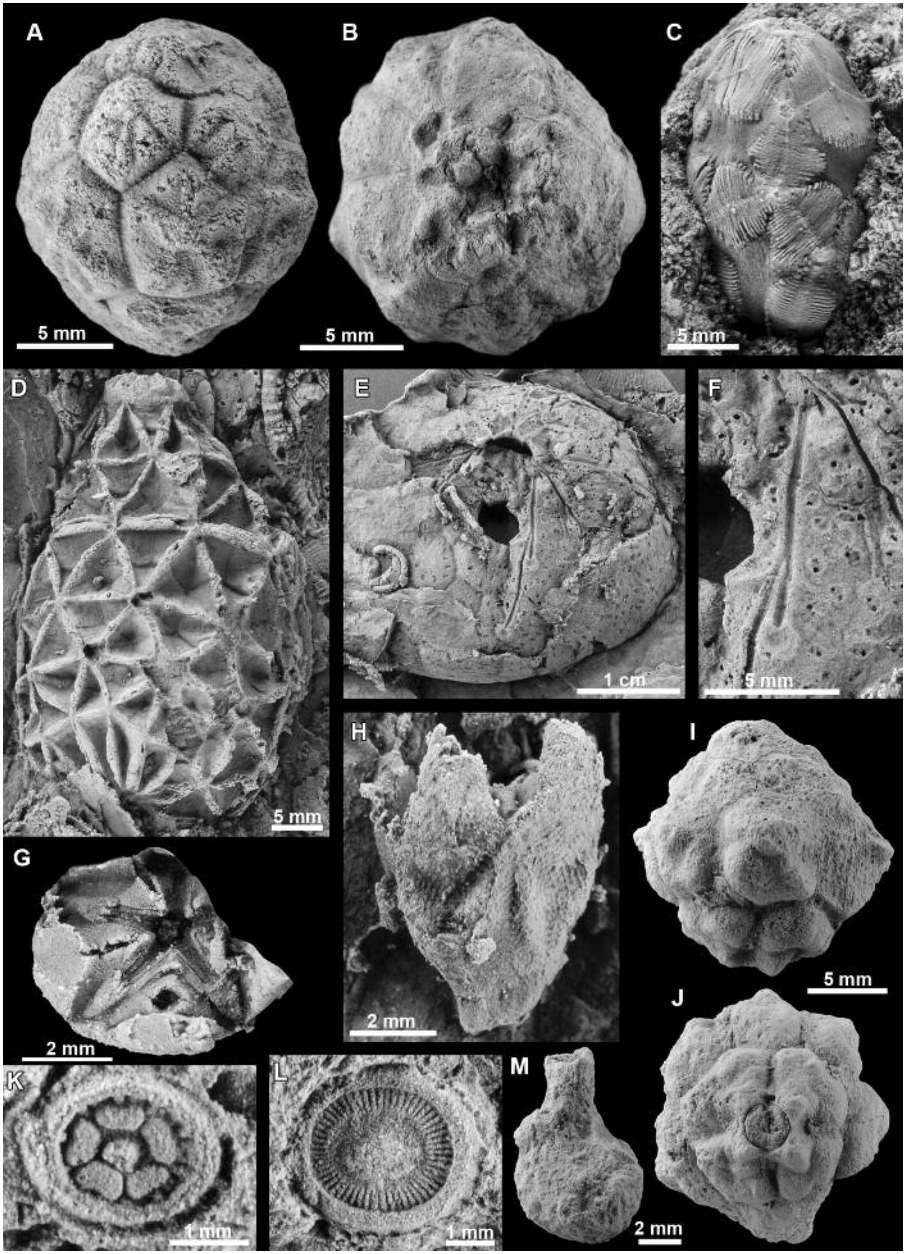

**Figure 21.** Echinoderms from the Cystoid limestone Formation. Specimens A-H, K, L come from the Rebosilla Member in Herrera de los Navarros (A-C) and Luesma (D-H, K, L). Specimens I, J, M come from La Peña Member in Fombuena. A, B. Lateral and oral views of *Caryocrinites sdzuyi*. C. Internal rhomb structures of *Caryocrinites* sp. D. Lateral view of *Heliocrinites* cf. *rouvillei*. E. Oral view of *Proteocystites hispanica* and detail showing diplopores, food grooves and facets for brachioles insertion (F). G, H.Oral and lateral views of *Mespilocystites tregarvanicus*. I, J. Lateral and aboral views of *Caryocrinites* sp. K. Isolated columnal of *Conspectocrinus celticus*. L. Isolated columnal of *Aonodiscus* cf. *spinosus*. M. Lateral view of *Heliocrinites minuta*.
Specimens D-H are latex casts whitened with NH4Cl sublimated.

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

### Location

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

Coordinates: 41º9’28”N, 1º9’40”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 (*Cariocystites* sp., *Cariocystites*? *saenzi*, *Heliocrinites* cf. *rouvillei*, *Heliocrinites* aff. *helmackeri*, *Heliocrinites pachecoi*) 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.

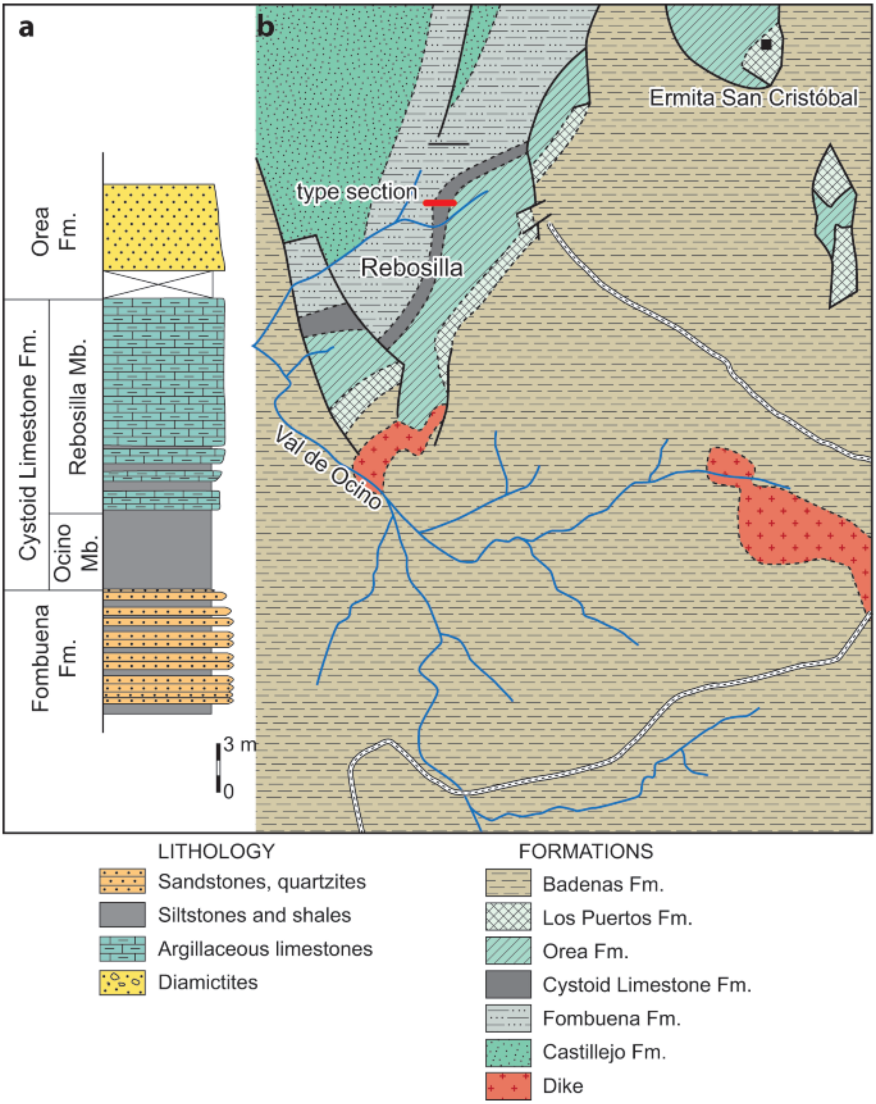

**Figure 22.** Geological map and lithological column of the La Rebosilla locality. Modified from Hammann (1992). Type section indicated with a red line.

## 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 *Hirnantia* fauna. The overlying Bádenas Formation comprises mostly shales with sandstone intercalations (900-1400 m). Carls (1965) studied the stratigraphy of this formation and subdivided it into five members from s3a to s3e: s3a, s3c and s3e are mostly composed of shales while the other two members (s3b, s3d) are mostly quarzitic. The s3d member close to Luesma is approximately 43 meters thick (Carls, 1965) and is very fossiliferous containing a rich assemblage dominated by chonetid and rhynchonellid brachiopods, gastropods, bivalves, trilobites, tentaculitoids and echinoderms (Fig. 23). These faunas have not been studied in detail. Carls (1965) favoured an undetermined late Wenlock-early Ludlow (Homerian to Gorstian) age for this s3d sandstone member of the Bádenas Fm.

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

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

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

### Location

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

Coordinates: 41º6’31”N, 1º5’57”W.
Geological map of Spain, 1:50,000, sheet of Moyuela (466).
Geological setting: Badules Unit (eastern Iberian Chain).
Lithostratigraphical unit: Mariposas Formation (meaning Butterflies Formation) (Fig. 15).
Age: early Emsian (Devonian).

### Aims

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

### Description

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

Carls and Valenzuela (2002) provided a synthesis of the Devonian sequence from the Iberian Cordillera and indicated that the Mariposas Formation starts with a 8 m-thick alternation of shelly limestones and bryozoans marls and shales (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, tentaculitoids, 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 dacryoconarid tentaculitoids and trilobites (scutellids and *Phacops*).

According to Carls and Valenzuela (2002), Rhenish faunas practically disappear at the beginning of the d4b Member except for few trilobites (Asteropyginae) and brachiopods (*Arduspirifer*). The submember 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 d3aβ. Detailed taxonomic work on those faunas is pending further work.

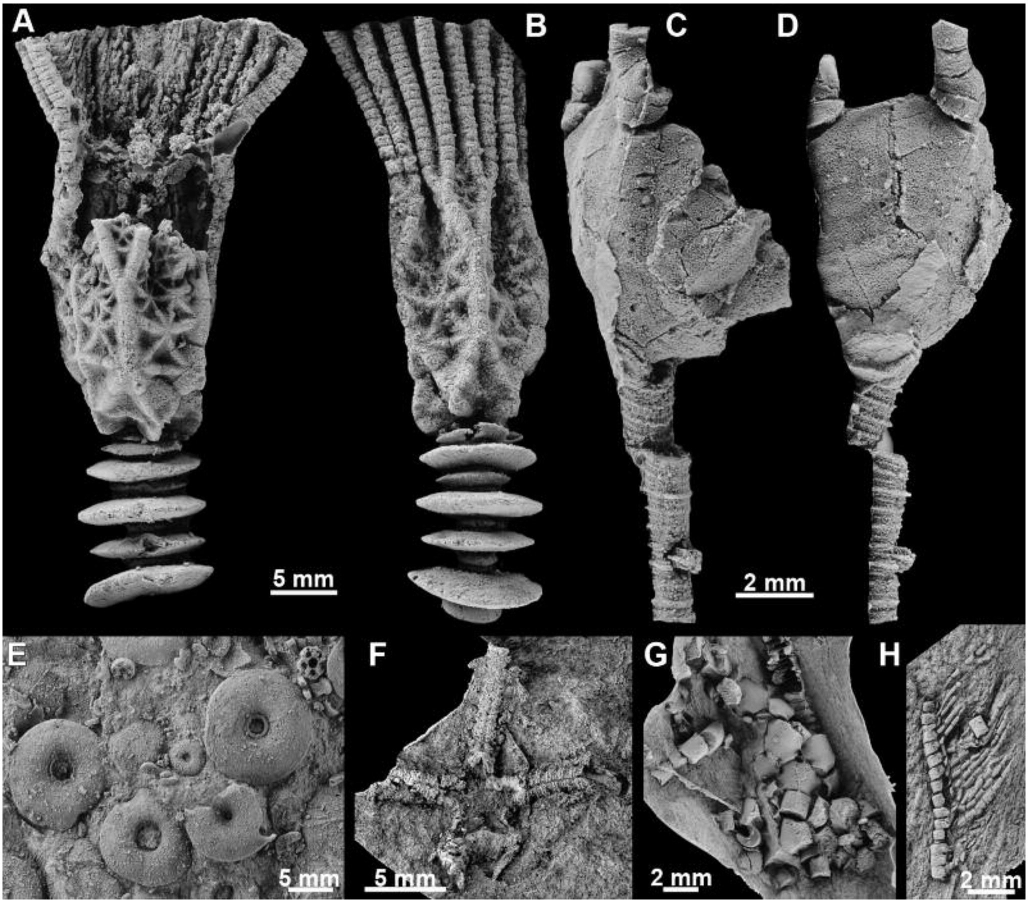

**Figure 24.** Silurian (Bádenas Formation) and Devonian (Mariposas Formation) Echinoderms. A, B. The crinoid *Dimerocrinites aragonensis*. C, D. Diplobathrid camerate crinoid. E. Crinoid columnals of at least two different taxa, *D. aragonensis* and an indeterminate crinoid. F. indeterminate ophiuroid. G. Fragment of a crinoid theca. H. Pinnulate arm of an indeterminate crinoid.
All specimens are latex casts whitened with NH4Cl sublimated.

## PALAEOZOIC FROM THE CANTABRIAN ZONE

Esperanza Fernández-Martínez

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

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

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

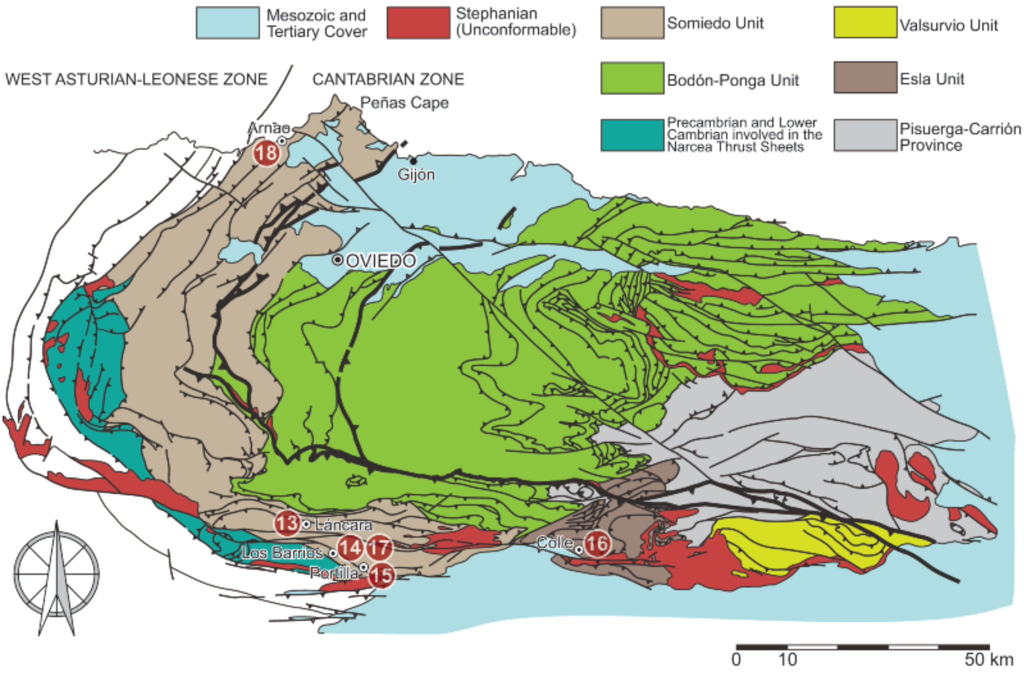

**Figure 25.** Geological map of the Cantabrian Mountains with indication of different domains and situation of different stops. Modified from Alonso *et al*. 2009.

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

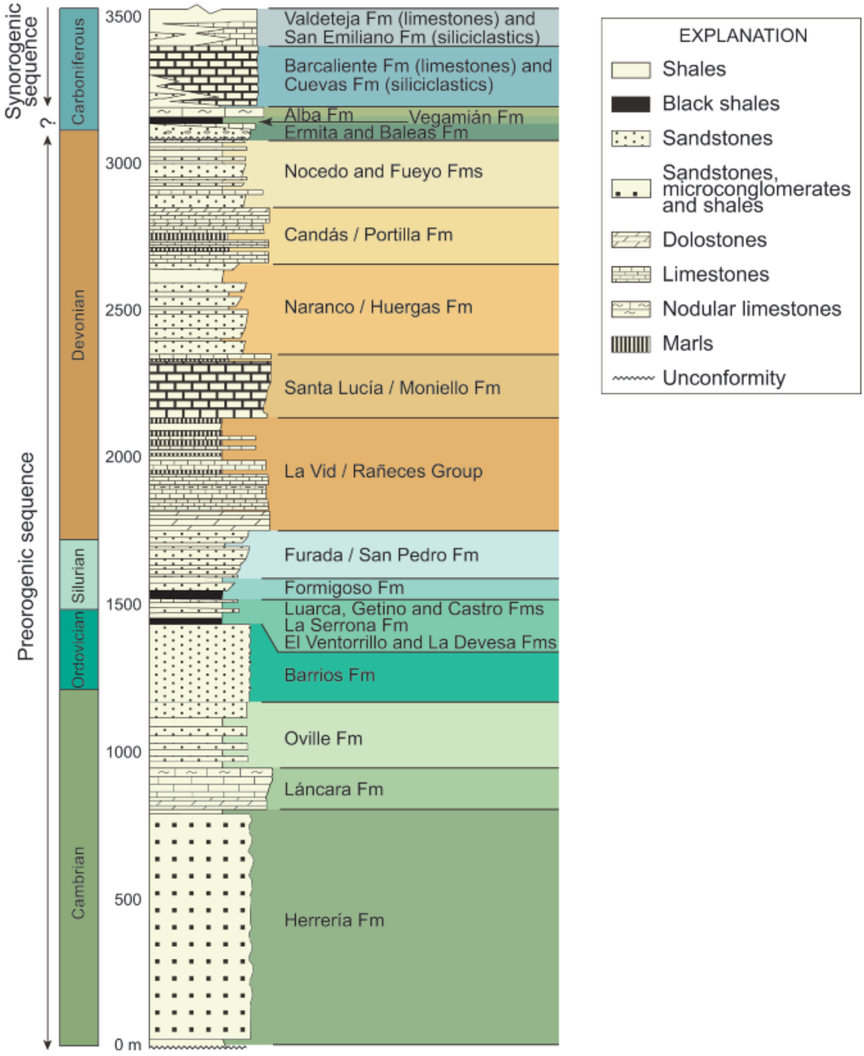

**Figure 26.** Synthetic generalized stratigraphic column of the Cantabrian Zone showing the pre-orogenic sequence and the lower part of the synorogenic sequence. Stratigraphic intervals visited in each stop are indicated on the right. Modified from Alonso *et al.* 2009.

## DAY 4: June 20th 2015

# EARLY PALAEOZOIC ECHINODERM FAUNAS FROM THE LUNA VALLEY

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

## INTRODUCTION

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

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

Two Early Palaeozoic episodes of carbonate production are recognized. The oldest took place across the lower-middle Cambrian transition and is lithostratigraphically identified as the Láncara Formation. The lower Cambrian Herrería and Láncara formations record the influence of subtropical conditions, marked by the presence of lateritic (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 stablished and several pulses of faunal immigration were recorded in the Cantabrian Platform. The oldest occurrence of trilobites in the Herrería Formation marks the base of the regional Ovetian Stage (after Oviedo, capital of Asturias; Palacios and Vidal, 1992; Liñán *et al*., 1993), broadly correlatable with the Russian Atdabanian or the global Cambrian Stage 3. The overlying peritidal carbonates of the lower member of the Láncara Formation, are succeded by a series of Bilbilian (Toyonian), stepwise transgressive pulses associated with extensional tectonic episodes, which led to the immigration of non-spiculate sponges (archaeocyaths), which locally form patch reefs in the uppermost part of the lower member, associated with a new shelly assemblage that includes new trilobite families, brachiopods, hyoliths and skeletonized microfossils (Clausen and Álvaro, 2006; Álvaro, 2007; Álvaro *et al*., 2013b). However, it is another tectonic pulse, recorded by the regional unconformity of the lower-middle Cambrian boundary (Álvaro *et al*., 2000b; for a chemostratigraphic analysis, see Wotte et al., 2007), the responsible of a major immigration event that led to the development of chancelloriid-echinoderm-(spiculate) sponge meadows (the so-called CES community) on tilted palaeohighs, preserved in the upper member of the Láncara Formation. The final flooding of the upper member deposits blanketed the previous palaeotopographies by clay deposits episodically punctuated by prograding sand shoal complexes. After a long time span extremely poor in shelly fauna, a final episode of shelly immigration was controlled by the onset of the Hirnantian glaciation.

The echinoderm faunas of the Lower Palaeozoic of the Cantabrian Zone provide important information to better understand the evolution of the taxon in two important time intervals, the mid Cambrian and the Late Ordovician. Mid Cambrian echinoderms are relatively diverse and include cinctans, eocrinoids, stylophorans, 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 Láncara 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 Láncara Formation

### Location

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

Coordinates: 42º54’34.19”N, 5º55’25.67”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: Láncara 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 Láncara Formation (Fig. 27) comprises two members. The lower one, 100-225 m thick, consists of yellow-weathering dolostones, commonly rich in ooids, peloids and stromatolitic crusts. Some areas, such as the Esla nappe, display a distinct facies association of ooidal shoals locally punctuated by archaeocyathan-microbial patch reefs (Álvaro et al., 2000b; Perejón and Moreno-Eiris, 2003; Perejón et al., 2012) dated as Bilbilian in age. The lower/middle member contact is an erosive unconformity that marks the Bilbilian/Leonian or regional lower-middle Cambrian boundary. Zamarreño (1972) subdivided the upper member into two facies, the so-called Beleño and Barrios facies. The former is a grey-to-pinkish, glauconitic limestone, 1-40 m thick, dominated by echinoderm-dominated packstones representative of low-angle shoal complexes. The upper member (also known as “griotte”/cherry-coloured facies by comparison with the same facies association in Montagne Noire, France), is up to 30 m thick, and consists of centimeter-scale, reddish-to-purple, bioclastic limestone/shale couplets (Fig. 28), deposited on the top of tilted palaeohighs. Deepening-upward sequences are recognized in the griotte facies, where skeletons exhibit stepwise, upward modifications from echinoderm- to brachiopod/trilobite-dominated associations reflecting changes in depth,

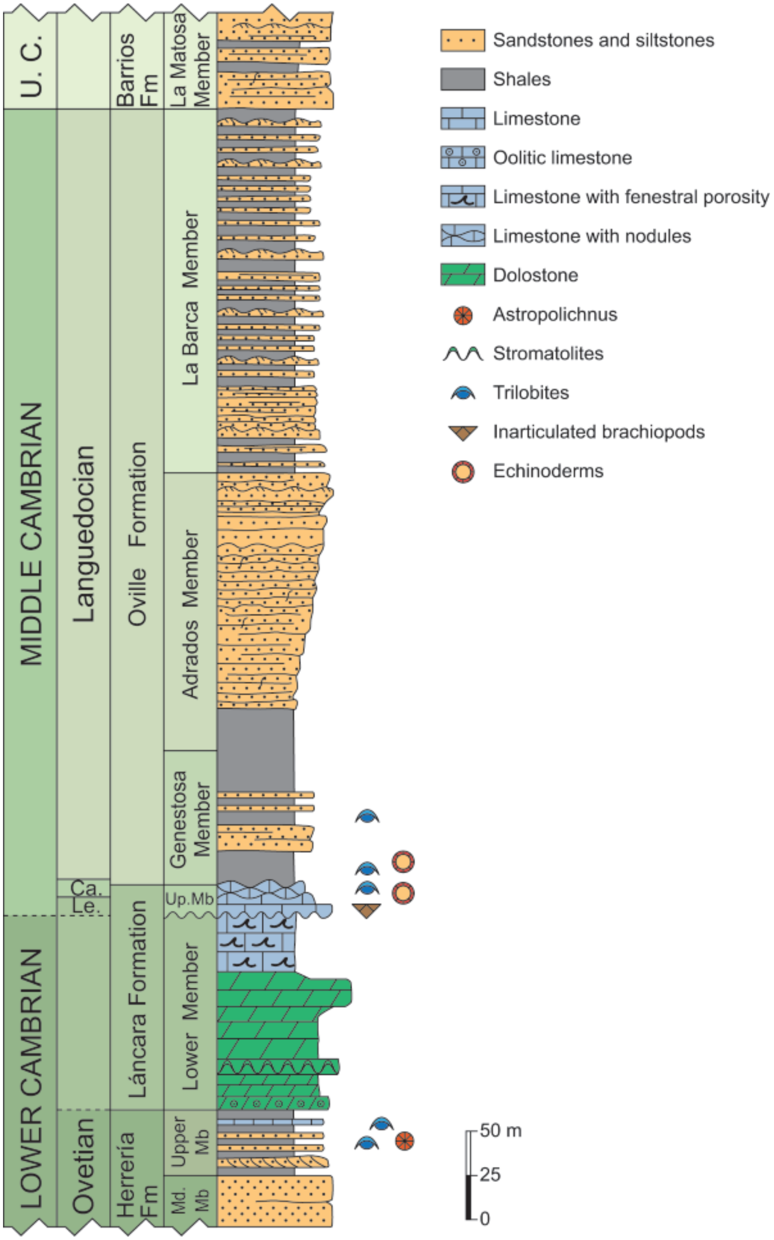

**Figure 27.** Stratigraphic column from the Cambrian in Barrios de Luna (after Zamarreño, 1977 and Aramburu, 1989).

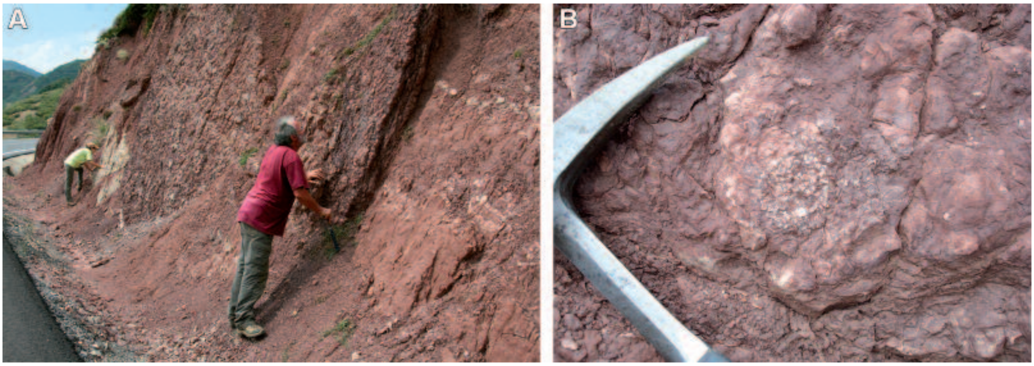

**Figure 28.** A. Bedding planes of the Láncara Formation. B. Accumulation of echinoderm plates in the Láncara Formation.

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

Echinoderms are abundant in the 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

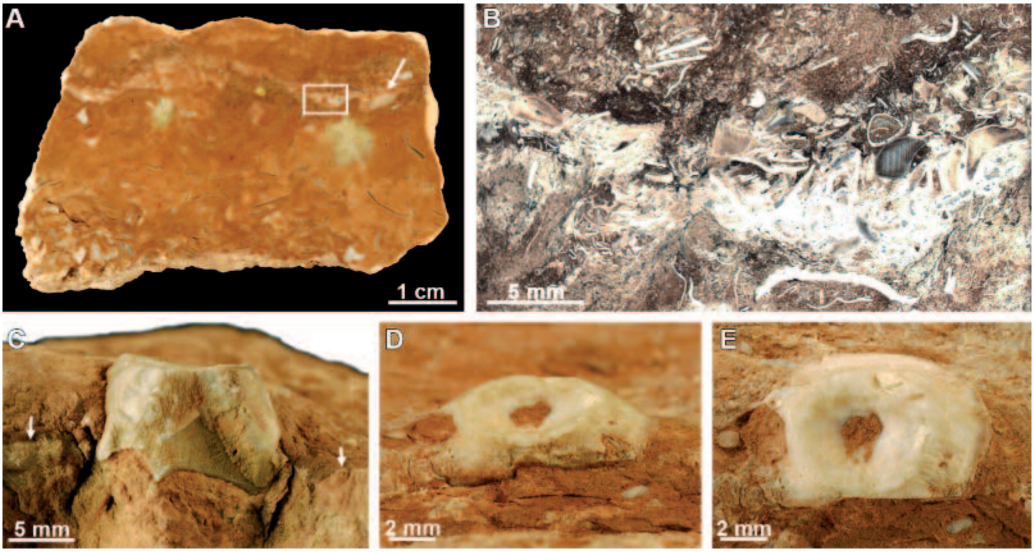

**Figure 29.** Polished slab (A) and thin section (B) of the griotte facies that contains the holdfast. Arrow indicates the undulating firmground horizon to which the pelmatozoan attached. C-E. Two specimens of holdfasts from the Cantabrian Mountains. Arrows indicate the surface where the specimen was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

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

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

### Location

Creek 500 m to the southeast of Los 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 Genestosa Member comprises the highest diversity of trilobites and echinoderms in the Cantabrian Zone. The diachronous character of the Láncara/Genestosa contact, ranging from late Leonian to early Languedocian in age (Sdzuy, 1968; Zamarreño, 1972) directly affected peaks of diversity both on trilobites and cinctans (Zamora and Álvaro, 2010). As a consequence, this diachronous modification of the seafloor allows us to analyse the evolution of mid Cambrian benthic communities on both carbonate and clayey substrates. The oldest echinoderms from the Genestosa Member were sampled in the Porma section, where Sdzuy (1993) described the cinctan *Asturicystis*? sp. considered as Leonian in age. Early Caesaraugustan echinoderms are relatively common in Soto de Caso locality, from which the same author described the cinctans *Sotocinctus ubaghsi* and *Asturicystis jaekeli*. Further work during the PhD of Zamora (2009) resulted in the discovery in the same section of indeterminate ctenocystoids and stylophorans belonging to *Ceratocystis*.

The Barrios 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 *Ubaghsicystis segurae* (Gil Cid and Domínguez Alonso, 2002; Zamora *et al.*, 2010) (Fig. 31A-C, 32B), and the stylophoran *Ceratocystis* (32C). A section of similar age in the vicinity of Ciñera has also provided some ctenocystoids similar to *Ctenocystis* (Fig. 31F, G). The diachronic nature of the base of the Oville Formation allows the study of echinoderms from similar environment but different ages, while the faunas are relatively young in Los Barrios de Luna section (*Solenopleuropsis* (*M.*) *thorali*-*Solenopleuropsis* (*S.*) Zones) they are older in the vicinity of Soto de Caso locality. In the later a quiet peculiar echinoderm fauna from the *Badulesia tenera* Zone was first reported by Sdzuy (1993), who described the cinctan species *Sotocinctus ubaghsi* (Fig. 31I, J) and *Asturicystis jaekeli*. Further work in such section has provided Ceratocystis sp. and a new ctenocystoid similar to *Courtessolea*.

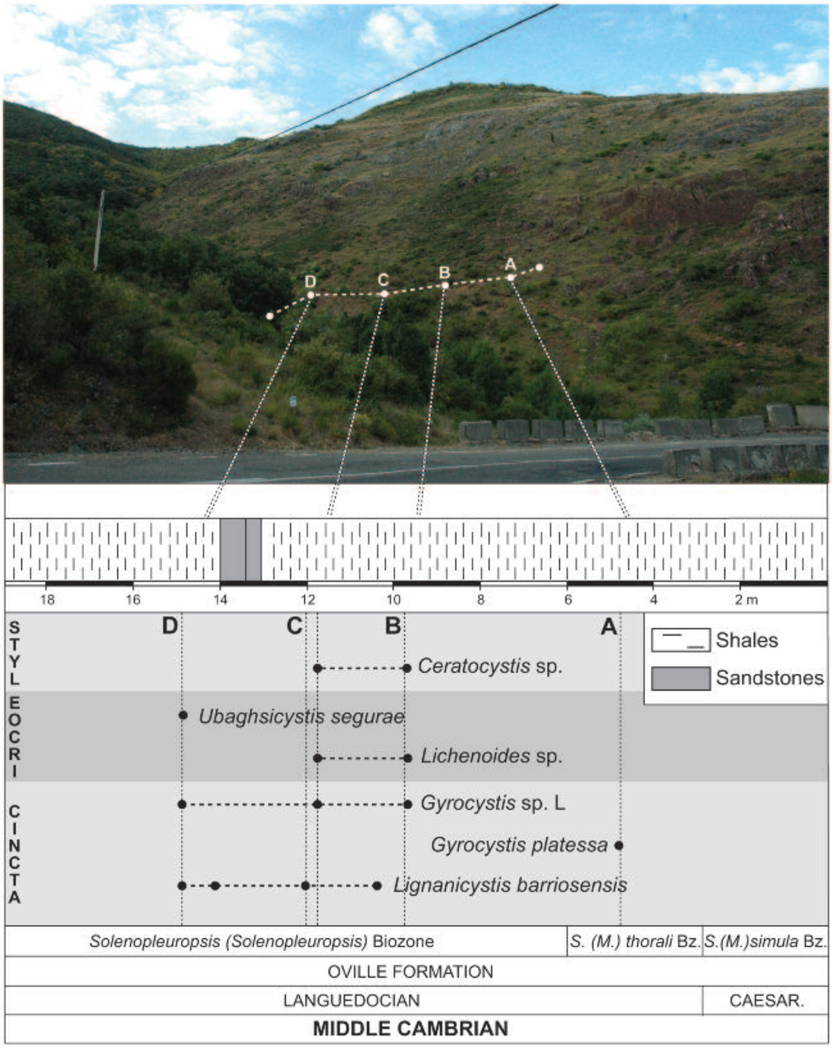

**Figure 30.** Detailed stratigraphic section of Genestosa Member (Oville Formation) in Barrios de Luna with the distribution of echinoderm taxa.

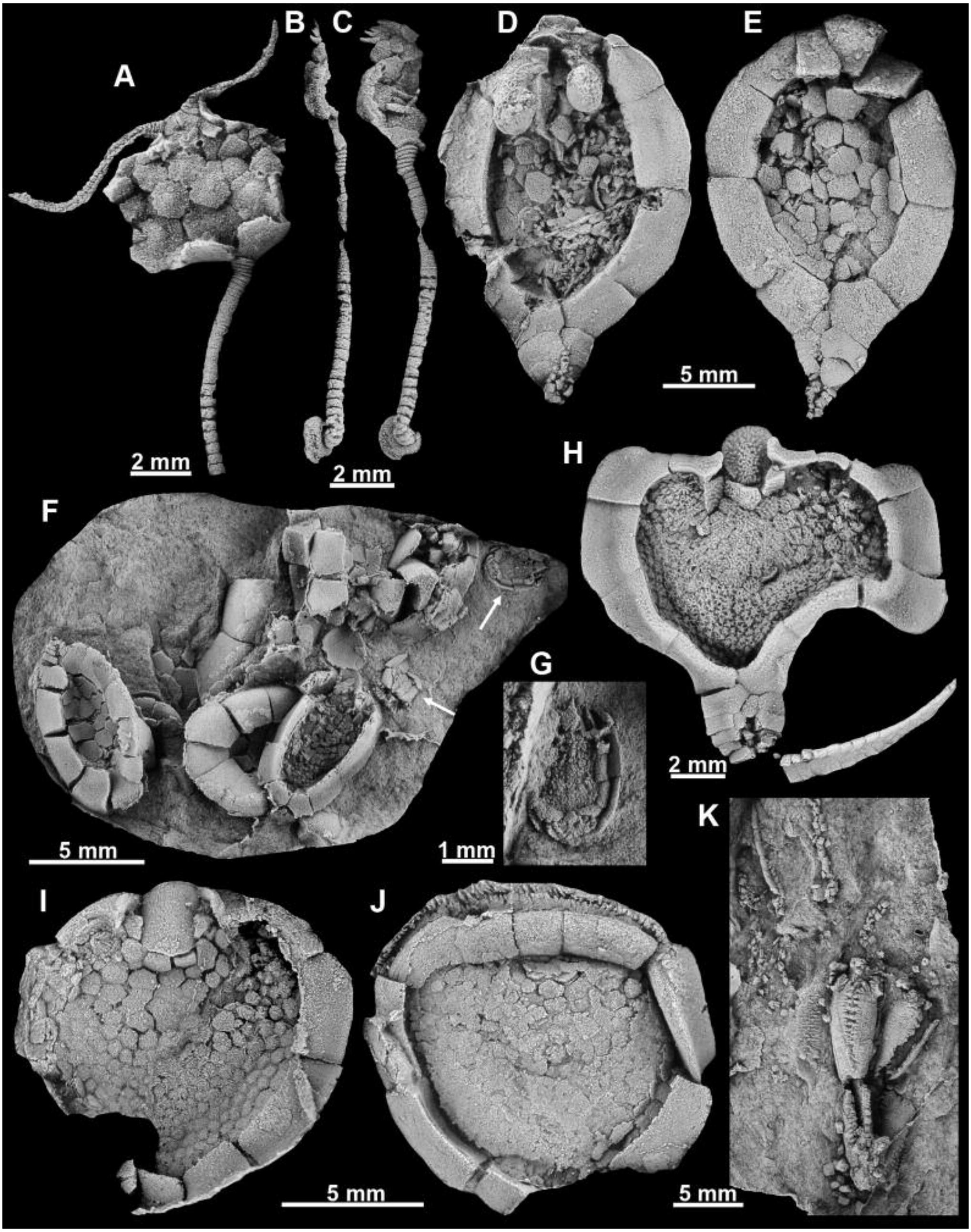

**Figure 31.** Cambrian Echinoderms from the Oville Formation at various localities. Specimens A-E, H, K come from Los Barrios de Luna; F, G from Ciñera and I, J from Soto de Caso. A-C. The eocrinoid *Ubaghsicystis segurae* with a columnal bearing stem and a distal holdfast. D, E. The cinctan *Gyrocystis* sp. F, G. The cinctan *Gyrocystis platessa* and a new ctenocystoid closely related with *Ctenocystis*. H. The cinctan *Lignanicystis barriosensis*. I, J. The cinctan *Sotocinctus ubaghsi*. K. The eocrinoid *Lichenoides* sp.
All specimens are latex casts whitened with NH4Cl sublimated.

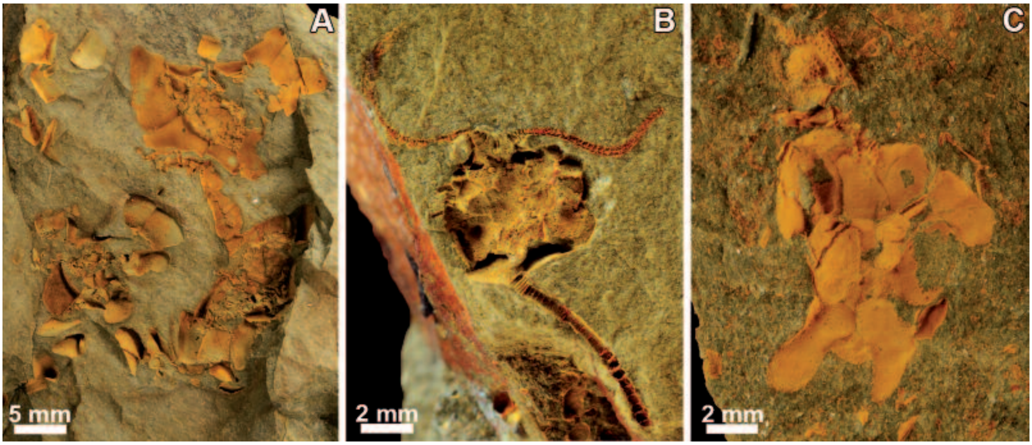

**Figure 32.** Cambrian Echinoderms from the Barrios de Luna section (Oville Formation). A. three specimens of the cinctan *Lignanicystis barriosensis*. B. The eocrinoid *Ubaghsicystis segurae*. C. The armoured stylophoran *Ceratocystis* sp.

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

### Location

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

Coordinates: 42º49'26.32" N, 5º49'06,47" 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 Ventorrilo beds" and La Devesa Formation.
Age: Katian (Upper Ordovician).

### Aims

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

### Description

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

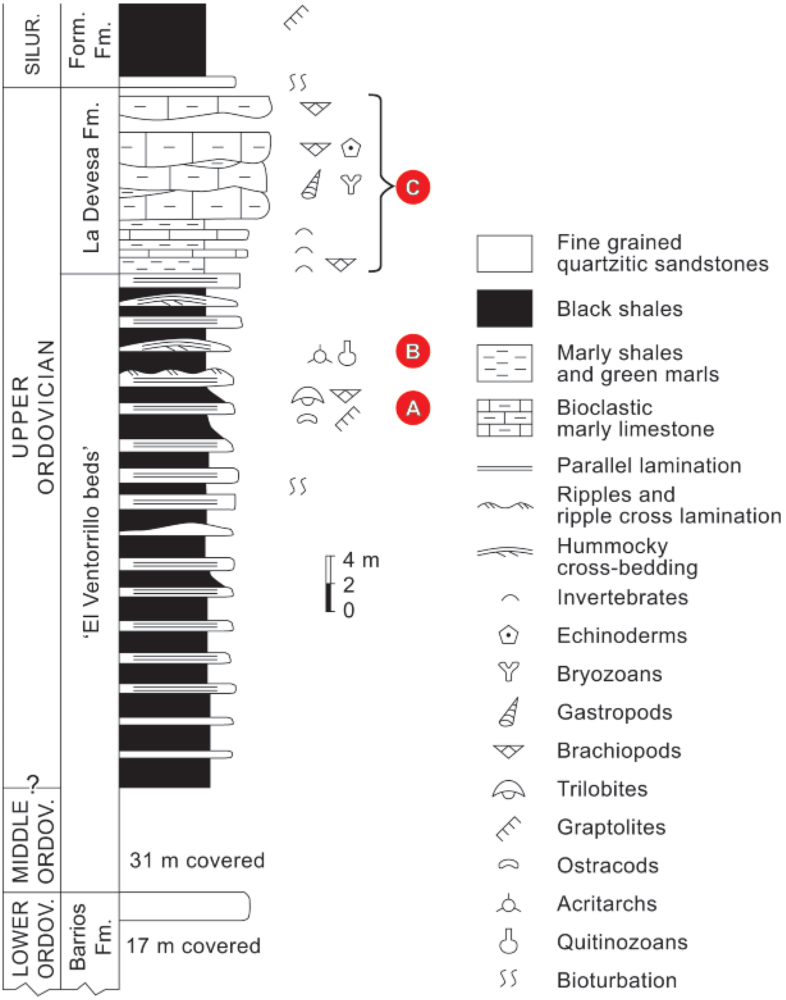

**Figure 33.** Stratigraphic column from the lower Palaeozoic succession in Portilla de Luna (adapted from Gutiérrez-Marco *et al.* 1996). A-C indicate fossiliferous levels.

## "El Ventorrillo beds"

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

Fossils from the examined section are rare and only two horizons have provided some remains. Level A (see Fig. 33) has yielded trilobites (*Scotiella*? cf. *taouzensis*, Homalonotidae indet.), ostracods (*Vogdesella* sp.) and brachiopods (*Rafinesquina* sp.) that suggest a Berounian (Katian 1-2) age. Ordovician acritarchs and chitinozoans have been sampled from Level B (M. Vanguestaine 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: *Nicolella actoniae*, *Dolerorthis aberensis*, *Schizophorella* sp., *Skenidioides* sp., *Epitomyonia* sp., *Saukrodictya* sp., *Bicuspina armoricana*, *Oxoplecia* cf. *luesmae*, *Leangella* (*L.*) *anaclyta*, *L.* (*Leptestiina*) *prantli*, *Aegironetes*? sp., *Eoplectodonta* (*Kozlowskites*) *ichnusae*, *Iberomena sardoa*, *Longvillia* sp., *Hedstroemina* sp., *Porambonites* (*P.*) *magnus* and *Eoanastrophia pentamera*. Echinoderms are a major component of the shelly assemblage but complete specimens including determinable taxonomic characters are rare. Blastozoans are the most common elements and include rhombiferans (*Heliocrinites rouvillei* Fig. 34K, *Caryocrinites* sp. Fig. 34D-H and *Hemicosmites* sp. Fig. 34A-C), diploporans (*Eucystis* n. sp. Fig. 34I, J and Aristocystidae? gen. et sp. indet.) and coronoids (*Mespilocystites* sp. Fig. 34L). Columnals belonging to both rhombiferans and crinoids are very abundant and include the following parataxa: *Trigonocyclicus* (col.) *vajgatschensi*s Fig. 34N, *Aonodiscus* (col.) *spinosus*, *Conspectocrinus* (col.) *celticus* Fig. 34M, *Cyclocharax* (col.) *paucicrenellatus*, *Hexagonocyclicus* (col.) sp., *Pentagonocyclicus* (col.) spp., *Trilobocrinus* (col.) spp., *Cyclocyclicus* (col.) sp., *Pentagonopentagonalis* (col.) sp. and *Ristnacrinus* sp Fig. 34O. Trilobites include *Ovalocephalus* cf. *tetrasulcatus* and *Cekovia*? sp. Finally, conodonts include *Amorphognathus ordovicicus*, *Amorphognathus* sp. A, *Scabbardella altipes*, *Birksfeldia* sp., *Icriodella* sp., *Dapsilodus* sp., *Panderodus* sp. and a single eocarnioniform element.

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

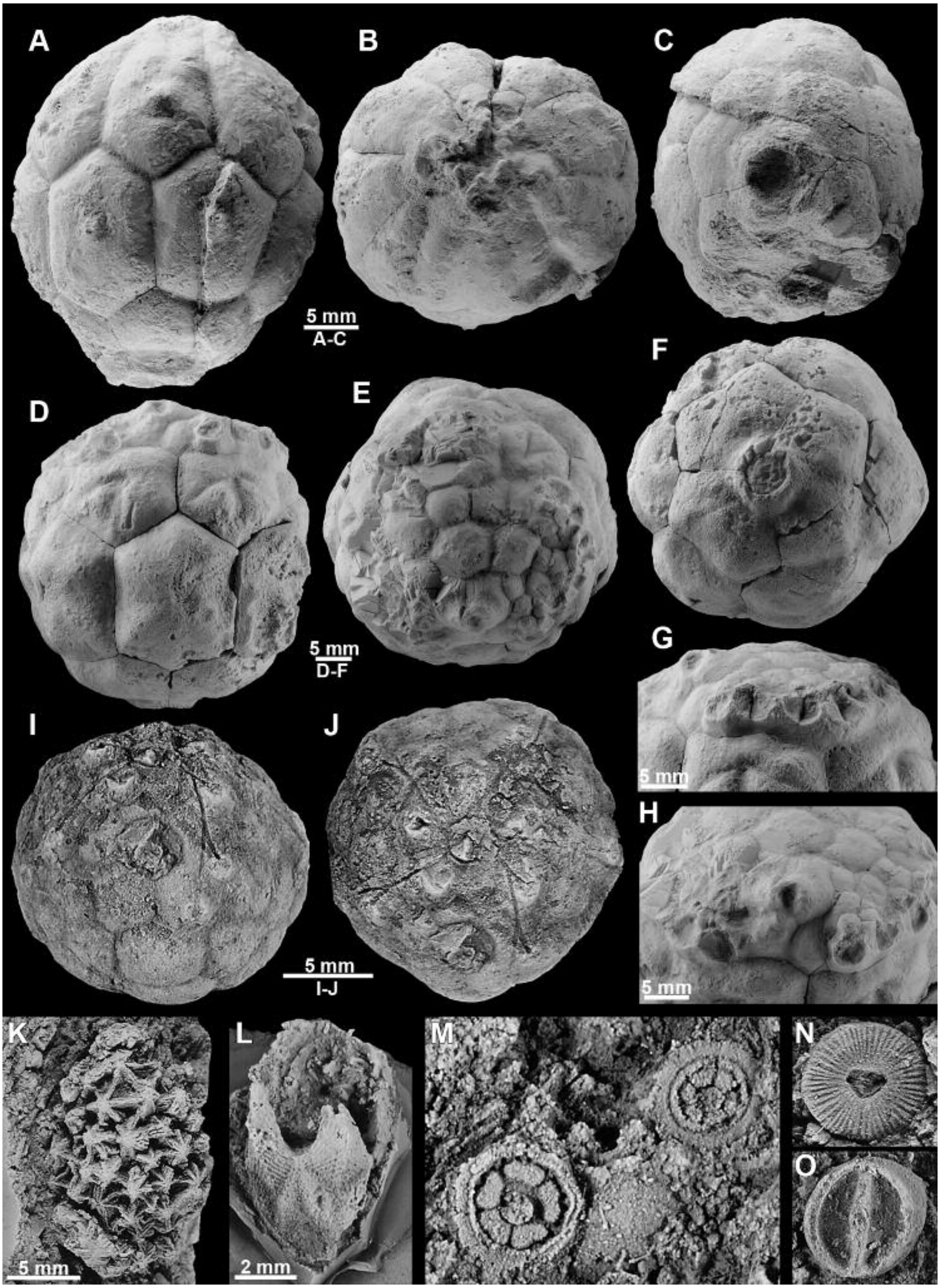

**Figure 34.** Echinoderms from the Upper Ordovician of Portilla de Luna. A-C. *Hemicosmites* sp. D-H. *Caryocrinites* sp. I, J. *Eucystis* sp. K. *Heliocrinites rouvillei*. L. *Mespilocystites* sp. M. *Conspectocrinus* (col.) *celticus*. N. *Trigonocyclicus* (col.) *vajgatschensis*. O. *Ristnacrinus* (col.) sp.
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 35ºS in Givetian times (Scotese, 2000, 2001; Nance *et al.*, 2012). Thus, the Devonian sediments were deposited in subtropical seas.

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

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

Devonian echinoderms from the Cantabrian Mountains, specially the crinoids, are well documented and the first species were described by De Vernuil 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: 42º50’38.06”N, 5º15’5.10”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

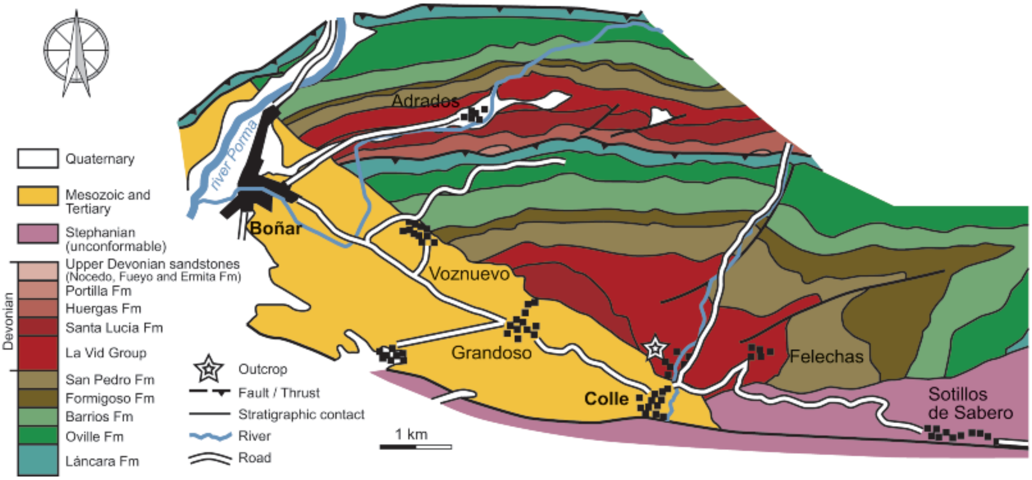

**Figure 35.** Simplified geological map of the Esla nappe near Colle showing the location of the study area. Modified after Fernández *et al.* 2006.

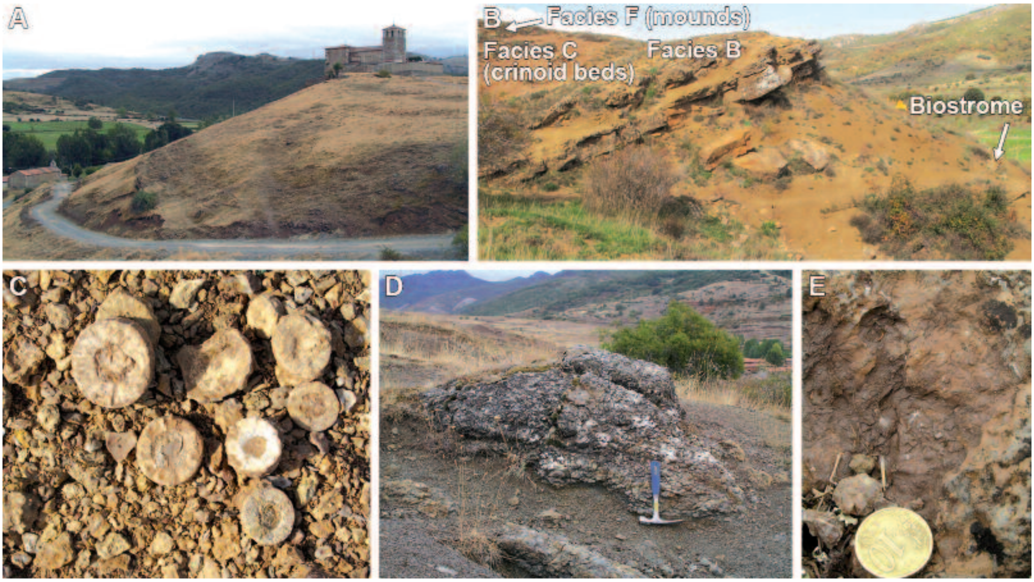

**Figure 36.** Field aspects of the Valporquero Formation in the vicinity of Colle. A. General view of the section. B. Detail of the section with indication of biostromes and crinoids bed and mud mound interval. C. Columnals from the camerate crinoids *Trybliocrinus*. D. General aspect of a mud mound.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

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

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

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

The La Vid Group was deposited on a carbonate ramp, which underwent terrigenous incursions (Valporquero Shales). According to Vera de la Puente (1988), Keller and Grötsch (1990) and Keller (1997), the La Vid succession is tied to two 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 wakestones 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

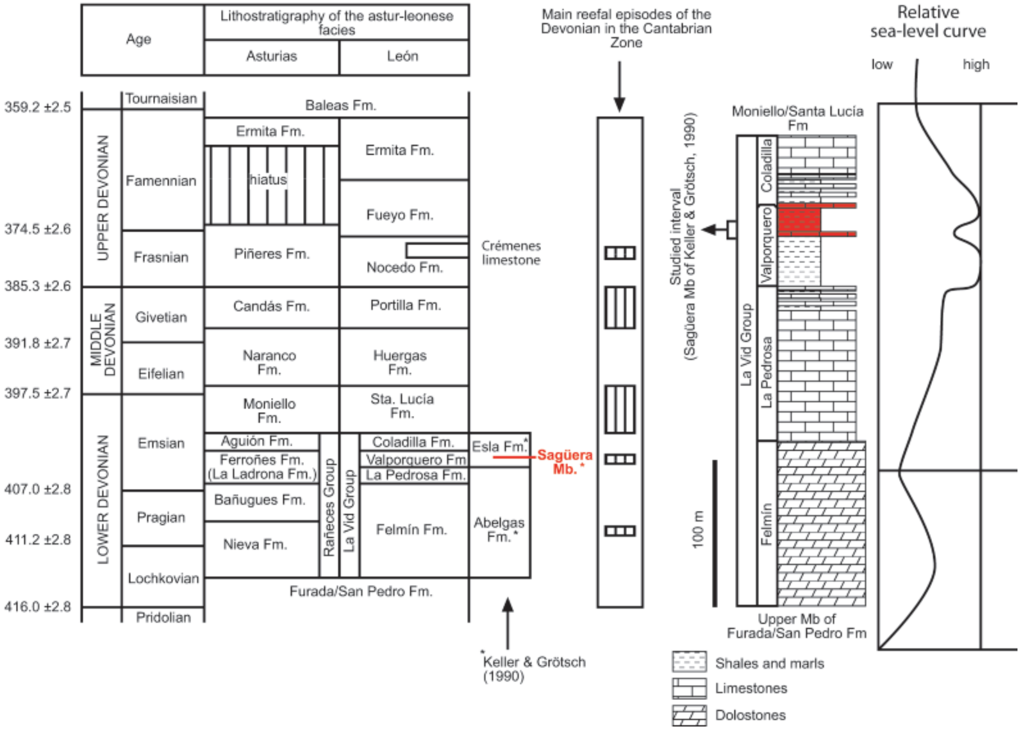

**Figure 37.** Chronostratigraphic chart showing the Devonian lithostratigraphic units of the Asturo-Leonese facies that have been defined in the political regions of Asturias (northern part of the Cantabrian Zone) and León (southern part of the Cantabrian Zone) and the distribution of the reefal episodes. 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

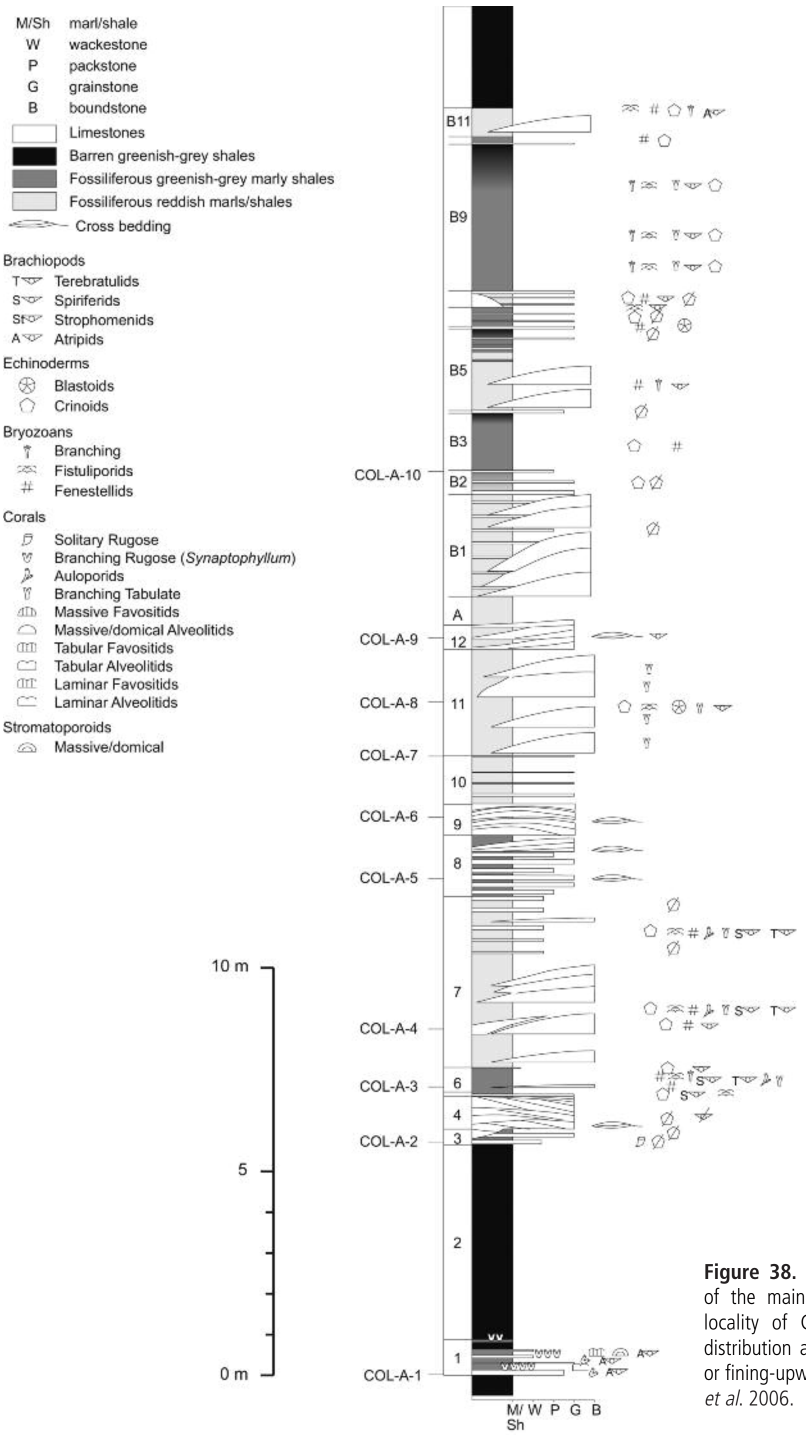

**Figure 38.** Simplified stratigraphic log of the main section described in the locality of Colle, showing the facies distribution and the coarsening-upward or fining-upward trends. After Fernández *et al*. 2006.

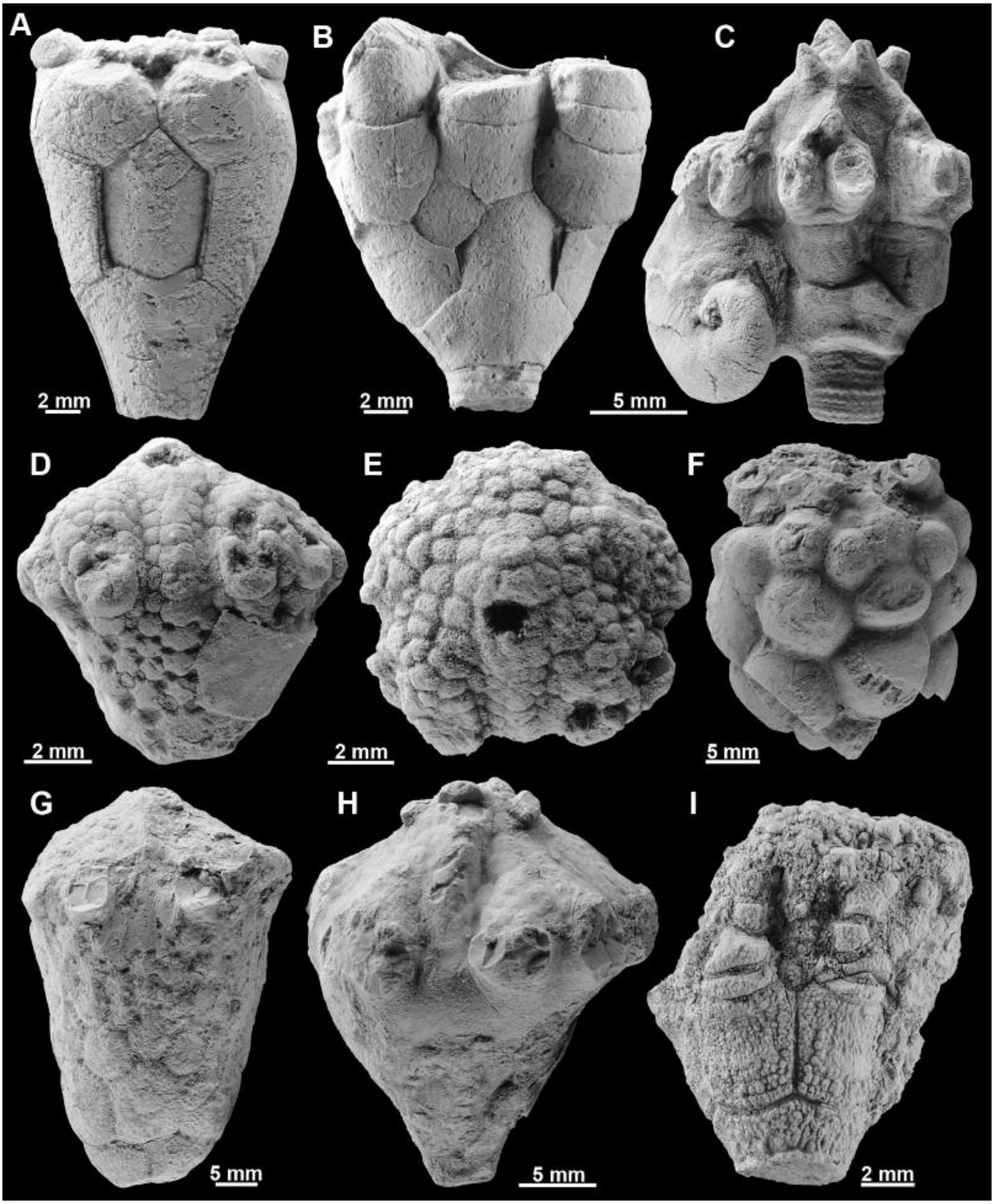

**Figure 39.** Crinoids from the Valporquero Formation of Colle (A, B, D, E, G, I), San Emiliano (H); and Santa Lucía Formation of Barrios de Luna (F); León. A. *Bactocrinites* sp., B. *Lasiocrinus*? sp. C. *Oenochoacrinus princeps*. D, E. *Pradocrinus baylii*. F. *Orthocrinus robustus*. G. *Pradocrinus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

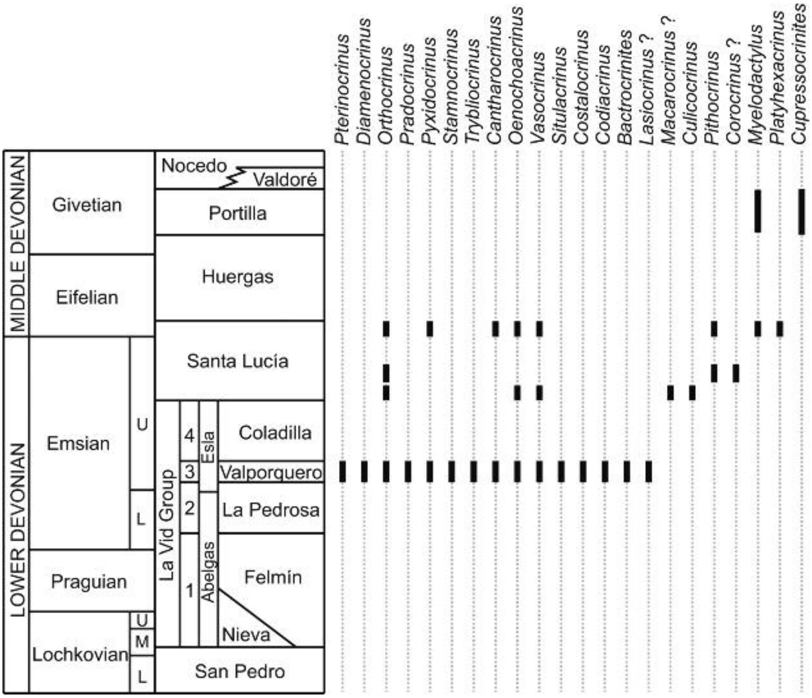

**Figure 40.** Stratigraphic distribution of crinoids from the Devonian of León. Based in data from Breimer (1962).

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

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

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

## Mud-mounds bearing blastoids

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

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

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

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

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

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

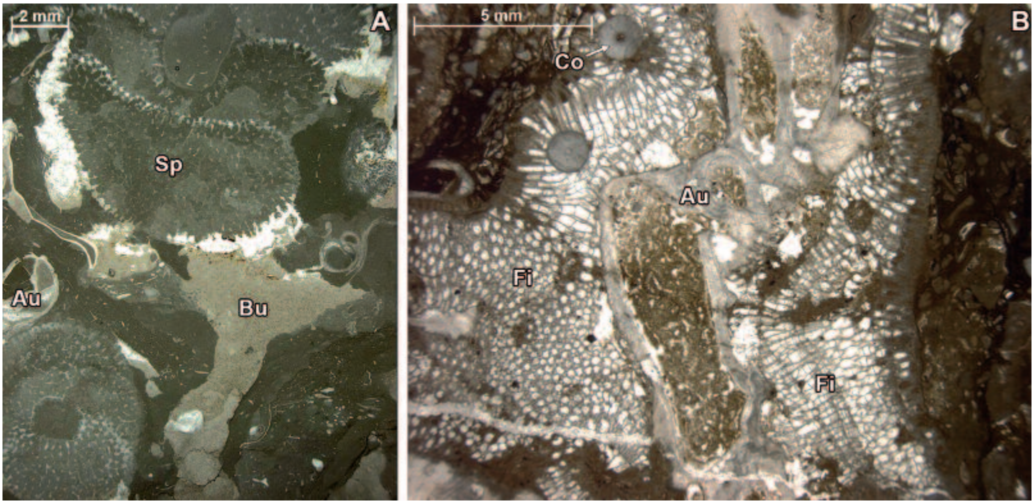

**Figure 41.** Detailed view of a mud mound. A. Microbial boundstone showing the complex relationships between sediment generations and pores. Note the burrow (type A cavity, Bu) in type 1 micrite and filled by microsparitic material. Skeletan components in this picture include sponges (Sp), partially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

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

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

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

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

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

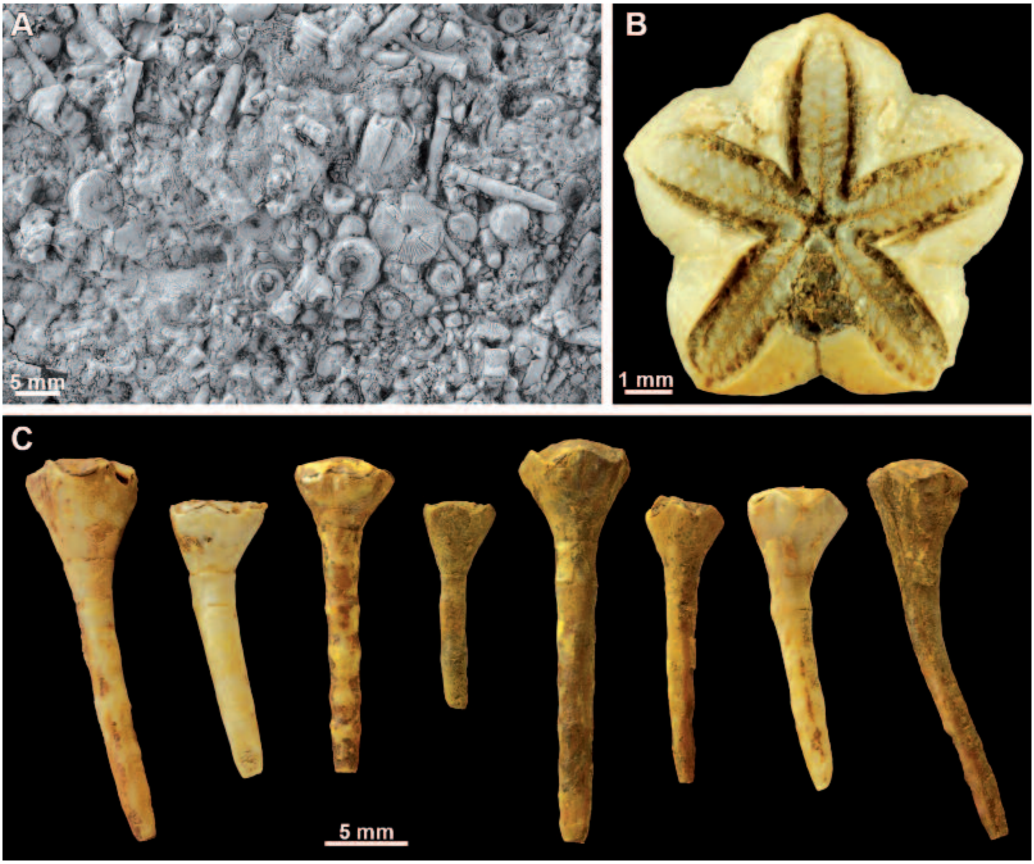

**Figure 42.** Blastoids from the Valporquero Formation at Colle. A. Detail of a tempestite with several fragments of blastoids and crinoids. D. *Pentremitidea* collected from the mud mounds. C. Different specimens of *Cryptoschisma* showing the complete stem. Specimens were collected from the shale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

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

### Location

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

Coordinates: 42º52’36.00”N, 5º50’31.70”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 fossilifeous limestone with a small amount of corals and without stromatoporoids (Méndez-Bedia, 1976). This petrographic type is usual in the lower and upper members of the subtidal successions of the Santa Lucía Formation.

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

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

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

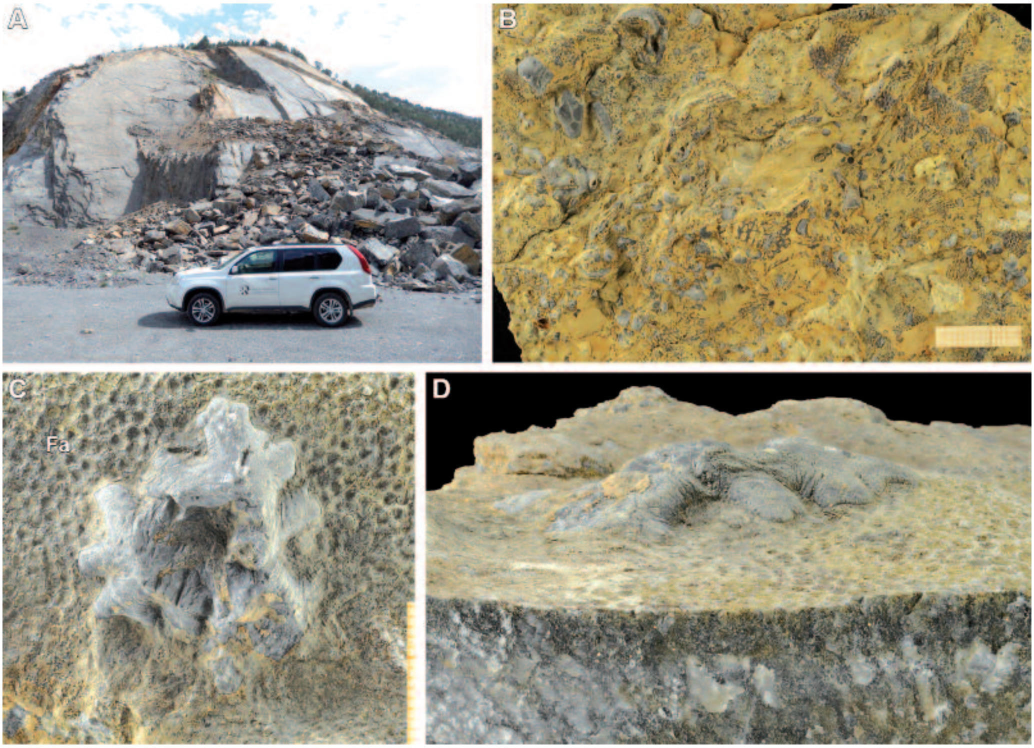

**Figure 43.** Santa Lucía Formation at Barrios de Luna. A. Detail of the Santa Lucía Formation in the visited quarry. B. General aspect of facies with abundant echinoderm remains. Note an almost complete blastoid in the upper left side of the photograph. C, D. Crinoid holdfast attached to the upper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

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

## DAY 5: June 21th 2015

# DEVONIAN ECHINODERMS FROM ARNAO (ASTURIAS): CLAY VS HARD-GROUND PELMATOZOAN COMMUNITIES

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

## INTRODUCTION

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

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

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

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

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

## STOP 18: Arnao

### Location

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

Coordinates: 43°34’44.6”N, 5°59’02.2”W
Geological map of Spain, 1:50.000, sheet of Avilés (13).
Geological setting: Northern slope of the Cantabrian Zone, Somiedo Unit.
Lithostratigraphical unit: Aguión Formation (Fig. 46)
Age: Early Devonian, late Emsian

### Aims

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

### Description

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

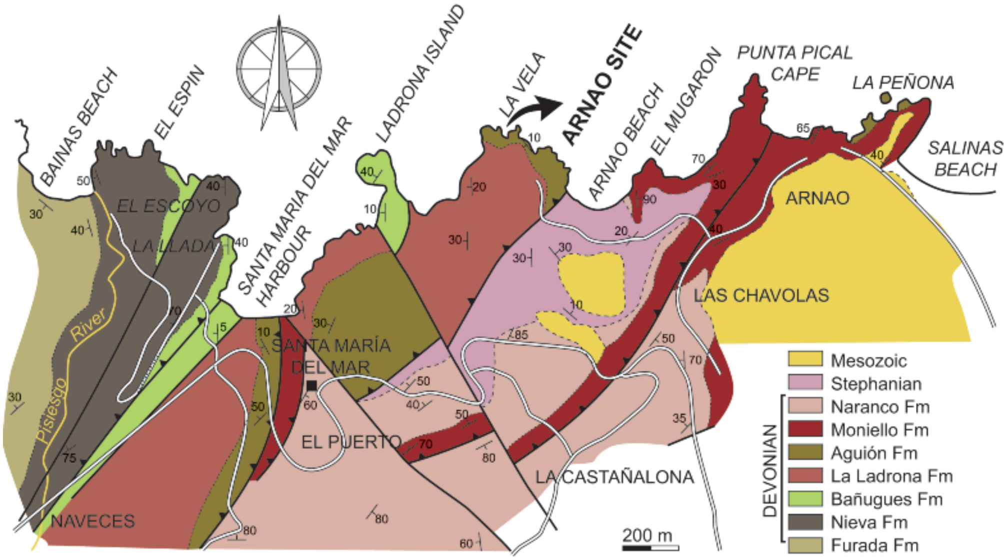

**Figure 45.** Map showing the geological setting of the Aguión Formation and the situation of Arnao fossil site. Modified from García–Alcalde (1992).

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

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

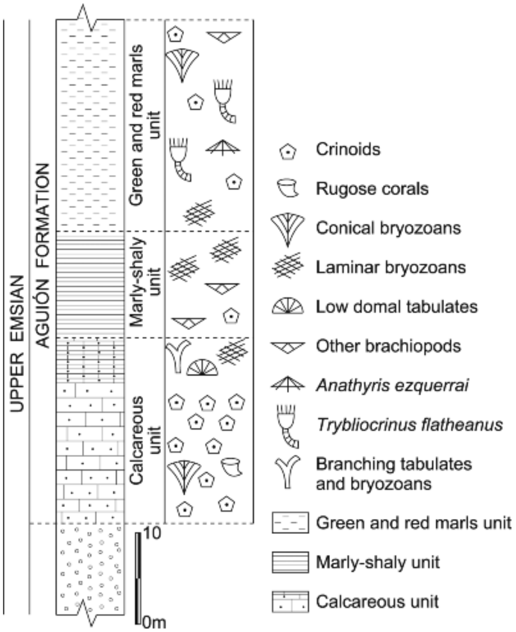

**Figure 46.** Stratigraphical succession of the Aguión Formation at Arnao Platform showing lithological units, their faunal composition and types of communities. From Arbizu *et al.* (1995).

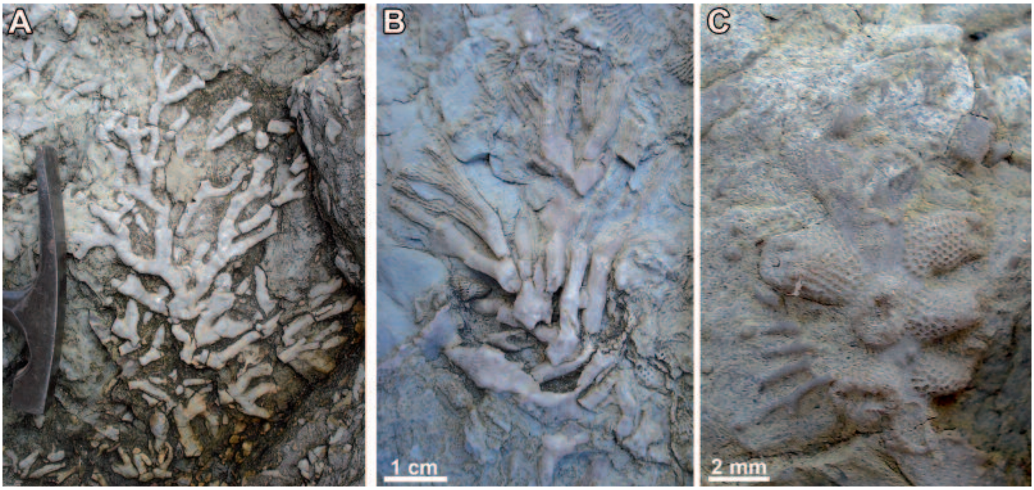

**Figure 47.** A. Branching tabulate coral *Platyaxon* from the calcareous unit. B. Composite tubular colony of the fenestrate bryozoan *Bigeyina* from the red and green marls unit. C. The rare fenestrate bryozoan *Ernstipora* encrusting an unidentified lacy bifoliate bryozoan from the red and green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

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

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

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

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

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

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

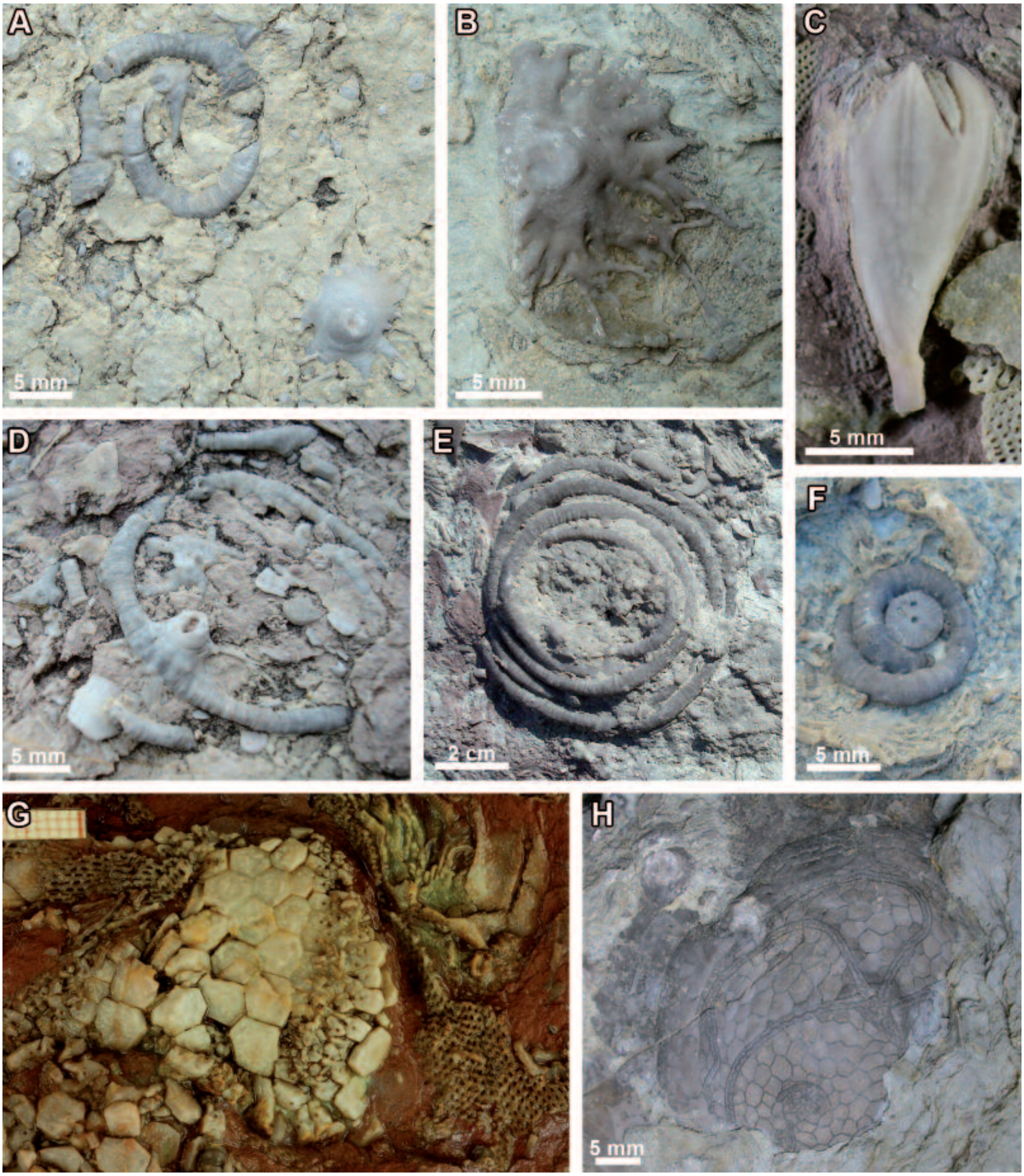

**Figure 48.** Echinoderms from the Aguión Formation in Arnao. A. Hardground preserving a discoid holdfasts with lobate margins and a partially disarticulated distal coiled stem. B. Radix-like holdfast attached to a bryozoan pavement. C. The blastoid *Pentremitidea pailletti.* D. Discoid holdfast overlapping 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.

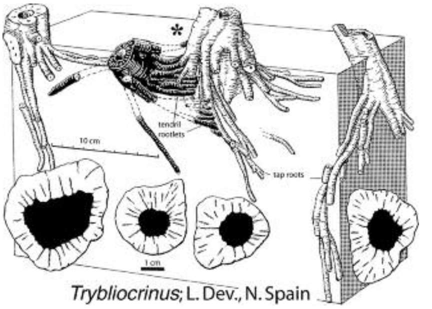

**Figure 49.** Drawing of cirral roots of *Trybliocrinus* from the Lower Devonian of northern Spain. From Seilacher and Macclintock, 2005.

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