

Progress in echinoderm paleobiology

Samuel Zamora^{1,2} and Imran A. Rahman³

¹Instituto Geológico y Minero de España (IGME), C/Manuel Lasala, 44, 9ºB, 50006, Zaragoza, Spain (s.zamora@igme.es)

²Unidad Asociada en Ciencias de la Tierra, Universidad de Zaragoza-IGME, Zaragoza, Spain

³Oxford University Museum of Natural History, Parks Road, Oxford, OX1 3PW, United Kingdom (imran.rahman@oum.ox.ac.uk)

Echinoderms are a diverse and successful phylum of exclusively marine invertebrates that have an extensive fossil record dating back to Cambrian Stage 3 (Zamora and Rahman, 2014). There are five extant classes of echinoderms (asteroids, crinoids, echinoids, holothurians, and ophiuroids), but more than 20 extinct groups, all of which are restricted to the Paleozoic (Sumrall and Wray, 2007). As a result, to fully appreciate the modern diversity of echinoderms, it is necessary to study their rich fossil record.

Throughout their existence, echinoderms have been an important component of marine ecosystems. Because of their relatively good fossil record, researchers have been able to reconstruct echinoderm diversity through geological time (e.g., Smith and Benson, 2013). Moreover, the echinoderm skeleton is rich in characters for rigorous analyses of disparity, functional morphology, and phylogeny, providing the means to tackle large-scale evolutionary questions (e.g., Ausich and Peters, 2005; Gahn and Baumiller, 2010; Kroh and Smith, 2010; Deline and Ausich, 2011). Echinoderms are known to modify their physiology, ecology, and distribution in response to fluctuations in salinity, pH, or temperature, so fossil forms may be useful indicators of past and future environmental change (Aronson et al., 2009). Taken together, these aspects make echinoderms an ideal group for addressing fundamental questions about the history of life on Earth.

On June 15–16, 2015, around 50 echinodermologists (Fig. 1) from 12 different countries attended the Progress in Echinoderm Palaeobiology meeting in Zaragoza, Spain, which was hosted by the Geological Survey of Spain and the University of Zaragoza. This meeting was followed by a five-day field trip (June 17–21, 2015) that included stops at the most remarkable Paleozoic echinoderm localities in North Spain (Iberian Chains and Cantabrian Mountains) (Zamora et al., 2015). The conference celebrated the career of our colleague and friend Dr. Andrew Smith (Fig. 2), a world-renowned specialist in echinoderms, who retired in late 2012. Andrew spent the majority of his career at the Natural History Museum, London (1982–2012), where he carried out remarkable research on a diverse range of topics, including echinoid taxonomy, Phanerozoic marine diversity, and early fossil echinoderms (Gale, 2015). As a result of the meeting and scientific discussion that took place, we have prepared this special issue in which we combine a series of papers dealing with recent and fascinating advances in echinoderm paleobiology. The issue is divided into six major themes: homology, disparity, trace fossils, functional morphology, systematics, and phylogeny.

Universal elemental homology (UEH) has proven to be one of the most powerful approaches for understanding homology in early pentaradial echinoderms (Sumrall, 2008, 2010; Sumrall and Waters, 2012; Kammer et al., 2013). This hypothesis focuses on the elements associated with the oral region, identifying possible homologies at the level of specific plates. Two papers, Paul (2017) and Sumrall (2017), deal with the homology of plates associated with the oral area in early pentaradial echinoderms. The former contribution describes and identifies homology in various ‘cystoid’ groups and represents a seminal work for understanding homology among these fossil taxa. The latter paper carefully reviews recent advances in UEH and outlines how this can be applied to representatives of modern echinoderm groups. Both papers provide invaluable data for future research on the relationships of early pentaradial echinoderms.

Characterization of the influence of taphonomy on morphological diversity is crucial for studies that seek to use disparity to address macroevolutionary questions. Deline and Thomka (2017) examine the importance of preservation for quantifying the morphology of Paleozoic echinoderms. They find that estimates of blastozoan disparity are not greatly influenced by the loss of taphonomically sensitive characters, whereas the opposite pattern is seen in crinoids.

Since their early history, echinoderms have interacted with and influenced the sediment in which they lived (Rahman et al., 2009); they can also act as substrates for other organisms, even recording the signal of potential predators. Grun et al. (2017) provide a very detailed analysis of predator-prey interactions in various assemblages of the echinoid *Echinocyamus stellatus* (Capeder, 1906) from the Miocene of Malta. Their study of drilling predation provides critical information about the preferences of predators and serves as an excellent comparison with data obtained from modern ecosystems. Belaústegui et al. (2017) review the extensive record of traces associated with extant and extinct echinoderms. This sheds light on how echinoderm ecology has changed through the Phanerozoic.

Reconstructing the function of structures in extinct animals that lack a clear analogue among extant forms has been a major barrier in paleobiological studies. However, the development of methods for visualizing and analyzing fossils digitally and in three dimensions has transformed the field of functional morphology (Sutton et al., 2014). Waters et al. (2017) use computational fluid dynamics to recreate the function of



Figure 1. Participants at the Progress in Echinoderm Palaeobiology meeting, in front of the Earth Sciences building (University of Zaragoza).



Figure 2. Andrew and Mary Smith during the meeting.

hydrospires in extinct blastoids. This has significance for understanding the functional morphology of different blastoids and might explain why some groups of echinoderms were more successful than others in certain marine environments.

The description and interpretation of new groups or taxa is fundamental to the field of echinoderm paleobiology, and a series of papers in this special issue deal with taxonomy and systematics. Nardin et al. (2017) present a new ‘old weird’ echinoderm from the Cambrian of the Czech Republic that shows intermediate features between imbricate eocrinoids and more derived blastozoans. Allaire et al. (2017) revise the eocrinoid *Rhopalocystis*, informed by rigorous morphometric and cladistic analyses, and suggest that the genus contains five valid species. Cole et al. (2017) report a new diverse fauna of Ordovician crinoids (dominated by camerates) from Spain that fills an important gap in the history of this group in Gondwana. Reich et al. (2017) report the first complete cyclocystoid from the Ordovician of Gondwana, describing its morphology in great detail with the aid of X-ray computed tomography. Sheffield and Sumrall (2017) revise the *Holocystites* fauna from the Silurian of North America, suggesting that the plating of the oral area is more informative for taxonomic purposes than thecal morphologies. Thompson et al. (2017) describe an important echinoid assemblage from the Permian of Texas that is characterized by the presence of the earliest crown-group and latest stem-group echinoids. Ewin and Thuy (2017) review ophiuroids from the classic Jurassic London Clay deposits of England and describe new taxa.

Finally, there is a block of four papers dealing with echinoderm phylogeny. Wright (2017) uses a cutting-edge Bayesian approach to reconstruct the phylogenetic relationships of Paleozoic crinoids. Cole (2017) provides a new phylogenetic analysis for the early Camerata (a major subdivision of crinoids), thereby testing the monophyly of traditionally recognized higher taxa, including Monobathrida and Diplobathrida. Wright et al. (2017) present a phylogeny-based classification for crinoids, defining a number of major taxa (including several new clades) within the group. Bauer et al. (2017) describe the

hydrospires of several species of blastoids, using these data in a phylogenetic analysis that incorporates both internal and external morphological characters.

The collection of papers included in this special issue is intended to demonstrate not only the current state-of-the-art knowledge in echinoderm paleobiology, but also the potential of utilizing the phylum to address major evolutionary questions. We hope this will encourage future generations of researchers to study echinoderms in new and exciting ways, building on the great legacy of Andrew Smith's work.

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