Progress in echinoderm paleobiology

Samuel Zamora[1,2] and Imran A. Rahman[3]

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

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

[3]Oxford 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, which have an extensive fossil record that dates 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, in order 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, and 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 Paleobiology 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 focusses 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 later 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), and 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* 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 analysing 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 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 Thy (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.

Acknowledgements

The guest editors would like to thank A.B. Smith for all his support and advice throughout our careers. His legacy in the form of papers, monographs, and books serves as an ideal example of an outstanding career for future generations of palaeontologists. This special issue would never have been possible without the great efforts of all those who contributed papers. We also thank B. Hunda, J. Jin, B. Pratt, S. Marcus, and D. Davis for fantastic editorial support. We are grateful to the Palaeontological Association for providing financial support that enabled early-career researchers to attend the Progress in Echinoderm Palaeobiology meeting. S. Zamora was funded by a Ramón y Cajal Grant (RYC2012-10576) and project CGL2013-48877 from the Spanish Ministry of Economy and Competitiveness. I.A. Rahman was funded by an 1851 Royal Commission Fellowship.

References

Allaire, N., Lefebvre, B., Nardin, E., Martin, E.L.O., Vaucher, R., and Escarguel, G., 2017, Morphological disparity and systematic revision of the eocrinoid genus *Rhopalocystis* (Echinodermata, Blastozoa) from the Lower Ordovician of the central Anti-Atlas (Morocco): Journal of Paleontology.

Aronson, R.B., Moody, R.M., Ivany, L.C., Blake, D.B., Werner, J.E., and Glass, A., 2009, Climate change and trophic response of the Antarctic bottom fauna: PLoS ONE, v. 4, e4385.

Ausich, W.I. and Peters, S.E., 2005, A revised macroevolutionary history for Ordovician Early Silurian crinoids: Paleobiology, v. 31, p. 538–551.

Bauer, J.E., Sumrall, C.D., and Waters, J.A., 2017, Hydrospire morphology and implications for blastoid phylogeny: Journal of Paleontology.

Belaústegui, Z., Muñiz, F., Nebelsick, J.H., Domènech, R., and Martinell, J., 2017, Echinoderm ichnology: Bioturbation, bioerosion and related processes: Journal of Paleontology.

Cole, S.R., 2017, Phylogeny and morphologic evolution of the Ordovician Camerata (Class Crinoidea, Phylum Echinodermata): Journal of Paleontology.

Cole, S.R., Ausich, W.I., Colmenar, J., and Zamora, S., 2017, Filling the Gondwanan gap: Paleobiogeographic implications of new crinoids from the Castillejo and Fombuena formations (Middle and Upper Ordovician, Iberian Chains, Spain): Journal of Paleontology.

Deline, B. and Thomka, J.R., 2017, The role of preservation on the quantification of morphology and patterns of disparity within Paleozoic echinoderms: Journal of Paleontology.

Deline, B. and Ausich W.I., 2011, Testing the plateau: A reexamination of disparity and morphological constraints in Early Paleozoic crinoids: Paleobiology, v. 37, p. 214–236.

Ewin, T.A.M. and Thy, B., 2017, Brittle stars from the British Oxford Clay: Unexpected ophiuroid diversity on Jurassic sublittoral mud bottoms: Journal of Paleontology.

Gahn, F.J. and Baumiller, T.K., 2010, Evolutionary history of regeneration in crinoids (Echinodermata): Integrative and Comparative Biology, v. 50, p. 514a–514m.

Gale, A., 2015, The research contribution of Dr Andrew B. Smith, BSc, PhD, DSc, FRSE, FRS, *in* Zamora, S. and Rábano, I., eds., Progress in Echinoderm Paleobiology: Cuadernos del Museo Geominero, 19, Instituto Geológico y Minero de España, p. 13–16.

Grun, T.B., Kroh, A., and Nebelsick, J.H., 2017, Comparative drilling predation on time-averaged phosphatized and non-phosphatized assemblages of the minute clypeasteroid echinoid *Echinocyamus stellatus* from Miocene offshore sediments (Globigerina Limestone Fm., Malta): Journal of Paleontology.

Kammer, T.W., Sumrall, C.D., Ausich, W.I., Deline, B., and Zamora, S., 2013, Oral region homologies in Paleozoic crinoids and other plesiomorphic pentaradial echinoderms: PLoS One, v. 8, e77989.

Kroh, A. and Smith, A. B., 2010, The phylogeny and classification of post-Palaeozoic echinoids: Journal of Systematic Palaeontology, v. 8, p. 147–212.

Nardin, E., Lefebvre, B., Fatka, O., Nohejlová, M., Kašička, L., Šinágl, M., and Szabad, M., 2017, Evolutionary implications of a new transitional blastozoan echinoderm from the mid Cambrian of the Czech Republic: Journal of Paleontology.

Paul, C.R.C., 2017, Testing for homologies in the axial skeleton of primitive Echinoderms: Journal of Paleontology.

Rahman, I.A., Jefferies, R.P.S., Südkamp, W.H., and Smith, R.D.A, 2009, Ichnological insights into mitrate palaeobiology: Palaeontology, v. 52, p. 127–138.

Reich, M., Sprinkle, J., Lefebvre, B., Rössner, G.E., Zamora, S., 2017, The first Ordovician cyclocystoid (Echinodermata) from Gondwana, and its morphology, paleoecology, taphonomy, and paleogeography: Journal of Paleontology.

Sheffield, S. and Sumrall, C.D., 2017, Generic Revision of the Holocystitidae of North America (Diploporita: Echinodermata) based on universal elemental homology: Journal of Paleontology.

Smith, A.B. and Benson, R.B.J., 2013, Marine diversity in the geological record, its relationship to surviving bedrock area, lithofacies diversity and original marine shelf area: Geology, v. 41, p. 171–174.

Sumrall, C.D., 2008, The origin of Lovén's Law in glyptocystitoid rhombiferans and its bearing on the plate homology and the heterochronic evolution of the hemicosmitid peristomal border, *in* Ausich, W.I. and Webster, G.D., eds., Echinoderm Paleobiology. University of Indiana Press, p. 228–241.

Sumrall, C.D., 2010. A model for elemental homology for the peristome and ambulacra in blastozoan echinoderms, *in* Harris, L.G., Böttger, S.A., Walker, C.W., and Lesser, M.P., eds., Echinoderms: Durham. CRC Press, London, p. 269–276.

Sumrall, C.D., 2017, New insights concerning homology of the oral area and ambulacral system plating of pentaradial echinoderms: Journal of Paleontology.

Sumrall, C.D. and Waters, J.A., 2012, Universal Elemental Homology in Glyptocystitoids, Hemicosmitoids, Coronoids and Blastoids: Steps Toward Echinoderm Phylogenetic Reconstruction in Derived Blastozoa: Journal of Paleontology, v. 86, p. 956–972.

Sumrall, C.D. and Wray, G.A., 2007, Ontogeny in the fossil record: diversification of body plans and the evolution of "aberrant" symmetry in Paleozoic echinoderms: Paleobiology, v. 33, p. 149–163.

Sutton, M.D., Rahman, I.A., and Garwood, R.J., 2014, Techniques for Virtual Palaeontology. Wiley, Oxford, 208 p.

Thompson, J.R., Petsios, E., and Bottjer, D.J., 2017, A diverse assemblage of

Permian echinoids (Echinodermata: Echinoidea) and implications for character evolution in early crown group echinoids: Journal of Paleontology.

Waters, J.A., White, L.E., Sumrall, C.D., and Nguyen, B.K., 2017, A new model of respiration in blastoid (Echinodermata) hydrospires based on CFD simulations of virtual 3D models: Journal of Paleontology.

Wright, D.F., 2017, Bayesian estimation of fossil phylogenies and the evolution of early to middle Paleozoic crinoids (Echinodermata): Journal of Paleontology.

Wright, D.F., Ausich, W.I., Cole, S.R., Peter, M.E., and Rhenberg, E.C., 2017, Phylogenetic taxonomy and classification of the Crinoidea (Echinodermata): Journal of Paleontology.

Zamora, S. and Rahman, I. A., 2014, Deciphering the early evolution of echinoderms with Cambrian fossils: Palaeontology, 57:1105–1119.

Zamora, S., Álvaro, J.J., Arbizu, M., Colmenar, J. Esteve, J., Fernández-Martínez, E., Fernández, L.P., Gutiérrez-Marco, J.C., Suárez Andrés, J.L., Villas, E., and Waters, J., 2015, Field trip: Palaeozoic echinoderms from northern Spain, *in* Zamora, S. and Rábano, I., eds., Progress in Echinoderm Paleobiology: Cuadernos del Museo Geominero, 19, Instituto Geológico y Minero de España, p. 209–288.

Figure captions

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

Figure 2. Andrew and Mary Smith during the meeting.

399x194mm (300 x 300 DPI)

238x296mm (300 x 300 DPI)