

## Chapter 1

### Early Palaeozoic biogeography and palaeogeography: towards a modern synthesis

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The benchmark volume edited by Christopher Scotese & Stuart McKerrow (1990), the so-called 'Green Book', marked a turning point in Palaeozoic biogeography and geography. The 40 papers in that volume included substantial new data and important syntheses on palaeoclimatology, palaeomagnetism and the distribution of climatically sensitive sediments, but the majority of contributions were on Palaeozoic biogeography. Since 1990 there have been major advances in the taxonomy of Early Palaeozoic organisms, the correlation of Lower Palaeozoic rocks together with numerical methods for the analysis of fossils and their distributions. Moreover and most significantly there has been a quantum leap in the accuracy and precision of palaeogeographic reconstructions, reconciling in many cases palaeomagnetic data and the distribution of fossil organisms.

The Early or (Lower) Palaeozoic was an interval characterized by a major radiation of marine life, including not only the 'Cambrian Explosion', but also the 'Great Ordovician Biodiversification'. An International Geoscience Programme (formerly International Geological Correlation Programme, IGCP) was dedicated to the Great Ordovician Biodiversification Event (IGCP 410, 1997–2002). This programme focused on the Ordovician, but it also analysed the roots of the Ordovician biodiversification in the Cambrian, the first big mass extinction at the end of the Ordovician, and the Silurian recovery. A subsequent programme, the IGCP 503, 'Ordovician Palaeogeography and Palaeoclimate', followed from 2004 to 2009. Several special issues and review papers resulted from this programme, including special issues on Lower Palaeozoic palaeoenvironments (Servais & Owen 2010) and Lower Palaeozoic sea-level and climate (Munnecke *et al.* 2010).

The papers presented here originated from the 'Absolutely Final Meeting of IGCP 503: Ordovician Palaeogeography and Palaeoclimate' in Copenhagen, September, 2009 (see Harper *et al.* 2011). That symposium focused especially on the palaeogeographical dimension of the Cambrian–Ordovician marine radiation; the current volume critically uses the available world pre-drift maps for the Early Palaeozoic, many presented in Copenhagen, to plot and analyse fossil distributional data and further develop the relationship of biogeography to major biotic events, such as extinctions and radiations. In contrast to Scotese & McKerrow (1990), this volume covers only the Early Palaeozoic, but looks in significantly greater detail at current ideas on the biogeography and biodiversity of a much wider range of fossil groups, albeit through a shorter time interval. Twenty-five papers are devoted to faunal and floral data, after introductory papers on palaeogeographic reconstructions and biotic provinces, together with overviews of Cambrian Lagerstätten and trace fossils.

Following this concise introduction, **Torsvik & Cocks (2013)** describe and illustrate their state-of-the-art palaeogeographic maps for the Early Palaeozoic. Many authors have mapped their data onto these reconstructions, although some have used others, and some have used the BugPlates software to accurately plot

their biotic data. **Servais *et al.* (2013)** present an analysis of the use and abuse of biogeographical and tectonic terrane terminology. Interrogation of Cambrian Lagerstätten (**Hendricks 2013**) suggests that clades with Precambrian origins have more widespread distributions, whereas arthropods were less widely distributed and persistent than other groups (Hendricks 2013). Cambrian trace fossil distributions, like individual animals, are both endemic and cosmopolitan, with the deep-sea *Oldhamia* generally having a wide distribution during the Early Cambrian but with some species describing more restricted distributions in shallower water (**Jensen *et al.* 2013**). The subsequent chapters document a very diverse range of fossil organisms, their palaeobiogeography and in many cases their palaeobiodiversity through much of the Early Palaeozoic. Biogeographical patterns and trends show some contrasts across the different groups of mobile and sessile benthos, and pelagic and planktonic organisms; and many authors have used their data to test the available palaeogeographic reconstructions.

The sponges, including the archaeocyathans and stromatoporoids together with the rugose and tabulate corals, were the major metazoan reef-building organisms during the Early Palaeozoic. The archaeocyathans, exclusively a Cambrian group of fossil sponges, have been used to constrain correlations and palaeogeographic constructions through analyses of a new online database (**Kerner & Debrenne 2013**). The Ordovician stromatoporoids initially displayed high levels of endemism during the late Mid-Ordovician, but individual groups became more widespread later in the Ordovician and into the Silurian, with some provincialism returning during the Ludlow (**Nestor & Webby 2013**). The remaining sponge groups show little provincial differentiation during the Cambrian and a broad restriction to low latitudes during the Ordovician (**Muir *et al.* 2013**), while Silurian distributional patterns remain poorly known. Late Ordovician corals in Laurentia were distributed across four provinces within the equatorial belts of this ancient continent (**Elias *et al.* 2013**), originating during the Great Ordovician Biodiversification Event (Harper 2006; Servais *et al.* 2010), and terminated during the end Ordovician mass extinction (Harper *et al.* 2013b).

The suspension-feeding, sessile benthos of the Palaeozoic Evolutionary Fauna included the brachiopods, bryozoans and echinoderms in addition to the reef-building corals and sponges. The linguliform and craniiform brachiopods were widely distributed in marginal environments across the deep shelves of most of the major continents during the Ordovician, but nevertheless show some distinctive biogeographical patterns during the period (**Popov *et al.* 2013**). The rhynchonelliform brachiopods show marked provincialism during the Ordovician that can be related to the diversity and phylogeny of the group (**Harper *et al.* 2013a**). The bryozoans diversified during the Ordovician, displaying an initial provincialism that decreased during the Ordovician, appearing again in the Llandovery to subsequently decline during the Wenlock (**Buttler *et al.* 2013**). Some provincialism is

apparent in the Ludlow and Pridoli. Cambrian echinoderms show distinctive biogeographic patterns. Critically the appearances of echinoderm ossicles predate the first occurrences of their associated articulated specimens, and thus provide key data on first appearances and the biogeographical distributions of these taxa in the fossil record (Zamora *et al.* 2013). During the Ordovician the six major echinoderm clades permit the definition of six provinces during the period and the authors relate the bio-diversification in these groups to the dispersal of the palaeocontinents (Lefebvre *et al.* 2013).

The mobile benthos was dominated by the trilobites. Cambrian trilobite distributions, analysed by Parsimony Analysis of Endemism, have distinguished a number of palaeobiogeographic units, not all conforming to conventional biogeographic units (Alvaro *et al.* 2013). Controls such as palaeoclimate and oceanic current circulation patterns are apparent from the careful analyses of this rich source of new and existing data. During the Ordovician a new species relational database reveals that generic endemism in the trilobite faunas peaked in most places during the Floian and declined afterwards (Adrain 2013). Ordovician ostracodes, analysed for two time slices (earliest Late Ordovician and terminal Ordovician), are apparently more related to palaeocontinents than palaeolatitude (Meidla *et al.* 2013). During the Silurian provinciality is recognized in the three major ostracode groups, describing in broad terms European and North American biogeographic units with oceans providing major barriers to migrations (Perrier & Siveter 2013).

Within the molluscs, the gastropods, monoplacophorans and mimospirids present clear biogeographic signals differentiated into distinct provinces associated with the various palaeocontinents and terranes (Ebbestad *et al.* 2013). The bivalves were cosmopolitan during the Cambrian. The initial Ordovician radiation of the class was confined to Gondwana but migrated elsewhere during the period within mainly siliciclastic facies (Cope & Kříž 2013). Silurian taxa were generally more cosmopolitan. The Rostronchia show some provinciality, particularly at low latitudes, during the Ordovician but are markedly more provincial during the Silurian and later (Amler & Rogalla 2013). The polychaetes, recorded by their scolecodont jaw apparatus, peaked in generic diversity during the early Mid-Ordovician. The species-rich groups were widespread during the Ordovician, becoming increasingly cosmopolitan during the Silurian (Eriksson *et al.* 2013).

Within the plankton the acritarchs and associated taxa formed the phytoplankton and displayed varying degrees of provinciality through the Early Palaeozoic (Molyneux *et al.* 2013). This was most marked during the early stages of the Great Ordovician Biodiversification Event and the terminal Ordovician extinctions. The distributions of Late Ordovician zooplankton, particularly the chitinozoans, map out climate belts following water masses controlled by sea surface temperatures (Vandenbroucke *et al.* 2013). The radiolarians, despite a paucity of data, formed a coherent tropical province during much of the Ordovician (Danielian *et al.* 2013).

Apart from the phyto- and zooplankton, the water column was populated by partially automobile organisms such as the graptolites together with active swimmers, for example the predatory cephalopods and some groups of fishes. During much of the Ordovician the graptolites displayed strong provinciality traditionally partitioned into Atlantic and Pacific provinces, but their biogeography was probably controlled by surface water temperature and their positions in the water column (Goldman *et al.* 2013). However, provinciality also played an important role in the evolution of the group with some taxa originating offshore in deeper-water habitats and others in the shallow water of the Atlantic Province. The cephalopods appeared first on the carbonate platform of the North China palaeoplate, dispersing globally by the Late Cambrian. Throughout the Ordovician, however, associated with the expansion of niches, the class was characterized by larger numbers of cosmopolitan taxa and less endemism (Kröger

2013). During the Ordovician the fishes occupied two main provinces, the Gondwana and Laurentia–Siberia–Baltic realms while during the Silurian the many more fish-bearing localities have allowed a definition of a greater number of biogeographical units (Žigaitė & Blicek 2013).

On land the earliest vegetation is assessed through both megafossil and spore data, pinpointing with some accuracy the timing of the adaptive radiation and dispersal of land plants in quantitative terms (Wellman *et al.* 2013).

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## References

- ADRAIN, J. M. 2013. A synopsis of Ordovician trilobite distribution and diversity. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 297–336. <http://dx.doi.org/10.1144/M38.20>
- ÁLVARO, J. J., AHLBERG, P. *ET AL.* 2013. Global Cambrian trilobite palaeobiogeography assessed using parsimony analysis of endemism. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 273–296. <http://dx.doi.org/10.1144/M38.19>
- AMLER, M. R. W. & ROGALLA, N. S. 2013. Biogeographical distribution patterns in early Palaeozoic Rostronchia (Mollusca). In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 243–263. <http://dx.doi.org/10.1144/M38.17>
- BUTTLER, C. J., WYSE JACKSON, P. N., ERNST, A. & MCKINNEY, F. K. 2013. A review of the Early Palaeozoic biogeography of bryozoans. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 145–155. <http://dx.doi.org/10.1144/M38.12>
- COPE, J. C. W. & KŘÍŽ, J. 2013. The Lower Palaeozoic palaeobiogeography of Bivalvia. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 221–241. <http://dx.doi.org/10.1144/M38.16>
- DANIELIAN, T., NOBLE, P., POUILLE, L. & MALETZ, J. 2013. Palaeogeographical distribution of Ordovician Radiolarian occurrences: patterns, significance and limitations. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 407–413. <http://dx.doi.org/10.1144/M38.25>
- EBBESTAD, J. O. R., FRÝDA, J. *ET AL.* 2013. Biogeography of Ordovician and Silurian gastropods’ monoplacophorans and mimospirids. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 199–220. <http://dx.doi.org/10.1144/M38.15>
- ELIAS, R. J., YOUNG, G. A., LEE, D.-J. & BAE, B.-Y. 2013. Coral biogeography in the Late Ordovician (Cincinnatian) of Laurentia. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 97–115. <http://dx.doi.org/10.1144/M38.9>
- ERIKSSON, M. E., HINTS, O., PAXTON, H. & TONAROVÁ, P. 2013. Ordovician and Silurian polychaete diversity and biogeography. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 265–272. <http://dx.doi.org/10.1144/M38.18>
- GOLDMAN, D., MALETZ, J., MELCHIN, M. J. & JUNXUAN, F. 2013. Graptolite palaeobiogeography. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 415–428. <http://dx.doi.org/10.1144/M38.26>
- HARPER, D. A. T. 2006. The Ordovician biodiversification: setting an agenda for marine life. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **232**, 148–166.

- HARPER, D. A. T., LI, J., MUNNECKE, A., OWEN, A. W., SERVAIS, T. & SHEEHAN, P. M. 2011. Concluding IGCP 503: towards a holistic view of Ordovician and Silurian Earth systems. *Episodes*, **43**, 32–38.
- HARPER, D. A. T., RASMUSSEN, C. M. Ø. *ET AL.* 2013a. Biodiversity, biogeography and phylogeography of Ordovician rhynchonelliform brachiopods. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 127–144. <http://dx.doi.org/10.1144/M38.11>
- HARPER, D. A. T., HAMMARLUND, E. U. & RASMUSSEN, C. M. Ø. 2013b. End Ordovician extinctions: a coincidence of causes. *Gondwana Research*, in press. <http://dx.doi.org/10.1016/j.gr.2012.12.021>
- HENDRICKS, J. R. 2013. Global distributional dynamics of Cambrian clades as revealed by Burgess Shale-type deposits. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 35–43. <http://dx.doi.org/10.1144/M38.4>
- JENSEN, S., BUATOIS, L. A. & MÁNGANO, M. G. 2013. Testing for palaeogeographical patterns in the distribution of Cambrian trace fossils. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 45–58. <http://dx.doi.org/10.1144/M38.5>
- KERNER, A. & DEBRENNE, F. 2013. The role of Archaeocyatha in Cambrian biostratigraphy and biogeography. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 59–66. <http://dx.doi.org/10.1144/M38.6>
- KRÖGER, B. 2013. Cambrian–Ordovician cephalopod palaeogeography and diversity. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 429–448. <http://dx.doi.org/10.1144/M38.27>
- LEFEBVRE, B., SUMRALL, C. D. *ET AL.* 2013. Palaeobiogeography of Ordovician echinoderms. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 173–198. <http://dx.doi.org/10.1144/M38.14>
- MEIDL, T., TINN, O., SALAS, M. J., WILLIAMS, M., SIVETER, D., VANDENBROUCKE, T. R. A. & SABBE, K. 2013. Biogeographical patterns of Ordovician ostracods. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 337–354. <http://dx.doi.org/10.1144/M38.21>
- MOLYNEUX, S. G., DELABROYE, A., WICANDER, R. & SERVAIS, T. 2013. Biogeography of Early to Mid-Palaeozoic (Cambrian–Devonian) marine phytoplankton. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 365–397. <http://dx.doi.org/10.1144/M38.23>
- MUIR, L. A., BOTTING, J. P., CARRERA, M. G. & BERESI, M. 2013. Cambrian, Ordovician and Silurian non-stromatoporoid Porifera. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 81–95. <http://dx.doi.org/10.1144/M38.8>
- MUNNECKE, A., CALNER, M. & HARPER, D. A. T. (eds) 2010. Early Palaeozoic sea level and climate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **296**, 213–413.
- NESTOR, H. & WEBBY, B. D. 2013. Biogeography of the Ordovician and Silurian Stromatoporoidea. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 67–79. <http://dx.doi.org/10.1144/M38.7>
- PERRIER, V. & SIVETER, D. J. 2013. Testing Silurian palaeogeography using ‘European’ ostracod faunas. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 355–364. <http://dx.doi.org/10.1144/M38.22>
- POPOV, L. E., HOLMER, L. E., BASSETT, M. G., GHOBADI POUR, M. & PERCIVAL, I. G. 2013. Biogeography of Ordovician linguliform and craniiform brachiopods. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 117–126. <http://dx.doi.org/10.1144/M38.10>
- SCOTESE, C. R. & MCKERROW, W. S. (eds) 1990. *Palaeozoic Palaeogeography and Palaeobiogeography*. Geological Society, London, Memoirs, **12**.
- SERVAIS, T. & OWEN, A. W. (eds) 2010. Early Palaeozoic palaeoenvironments. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **294**, 95–247.
- SERVAIS, T., OWEN, A. W., HARPER, D. A. T., KROGER, B. & MUNNECKE, A. 2010. The Great Ordovician Biodiversification Event (GOBE): the palaeoecological dimension. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **294**, 99–119.
- SERVAIS, T., CECCA, F., HARPER, D. A. T., ISOZAKI, Y. & MAC NIUCAILL, C. 2013. Palaeozoic palaeogeographical and palaeobiogeographical nomenclature. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 25–33. <http://dx.doi.org/10.1144/M38.3>
- TORSVIK, T. H. & COCKS, L. R. M. 2013. New global palaeogeographical reconstructions for the Early Palaeozoic and their generation. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 5–24. <http://dx.doi.org/10.1144/M38.2>
- VANDENBROUCKE, T. R. A., ARMSTRONG, H. A., WILLIAMS, M., PARIS, F., SABBE, K. & ZALASIEWICZ, J. A. 2013. Late Ordovician zooplankton maps and the climate of the Early Palaeozoic Icehouse. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 399–405. <http://dx.doi.org/10.1144/M38.24>
- WELLMAN, C. H., STEEMANS, P. & VECOLI, M. 2013. Palaeophytogeography of Ordovician–Silurian land plants. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 461–476. <http://dx.doi.org/10.1144/M38.29>
- ZAMORA, S., LEFEBVRE, B. *ET AL.* 2013. Cambrian echinoderm diversity and palaeobiogeography. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 157–171. <http://dx.doi.org/10.1144/M38.13>
- ŽIGAITĚ, Ž. & BLIECK, A. 2013. Palaeobiogeography of Early Palaeozoic vertebrates. In: HARPER, D. A. T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs, **38**, 449–460. <http://dx.doi.org/10.1144/M38.28>