



CrossMark  
click for updates

## Research

**Cite this article:** Thuy B, Kiel S, Dulai A, Gale AS, Kroh A, Lord AR, Numberger-Thuy LD, Stöhr S, Wisshak M. 2014 First glimpse into Lower Jurassic deep-sea biodiversity: *in situ* diversification and resilience against extinction. *Proc. R. Soc. B* **281**: 20132624. <http://dx.doi.org/10.1098/rspb.2013.2624>

Received: 5 October 2013

Accepted: 23 April 2014

### Subject Areas:

palaeontology

### Keywords:

evolution of deep-sea biota, onshore-offshore patterns, *in situ* diversification, resilience against extinction

### Author for correspondence:

Ben Thuy

e-mail: [nebyuht@yahoo.com](mailto:nebyuht@yahoo.com)

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2013.2624> or via <http://rspb.royalsocietypublishing.org>.



# First glimpse into Lower Jurassic deep-sea biodiversity: *in situ* diversification and resilience against extinction

Ben Thuy<sup>1</sup>, Steffen Kiel<sup>2</sup>, Alfréd Dulai<sup>3</sup>, Andy S. Gale<sup>4</sup>, Andreas Kroh<sup>5</sup>, Alan R. Lord<sup>6</sup>, Lea D. Numberger-Thuy<sup>1</sup>, Sabine Stöhr<sup>7</sup> and Max Wisshak<sup>8</sup>

<sup>1</sup>Natural History Museum Luxembourg, Department of Palaeontology, 24, rue Münster, Luxembourg 2160, Luxembourg

<sup>2</sup>Geoscience Centre, Geobiology Group, University of Göttingen, Goldschmidtstrasse 3, Göttingen 37077, Germany

<sup>3</sup>Hungarian Natural History Museum, Department of Palaeontology and Geology, 1431 Budapest, Pf. 137, Hungary

<sup>4</sup>School of Earth and Environmental Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth PO1 3QL, UK

<sup>5</sup>Natural History Museum Vienna, Department of Geology and Palaeontology, Burgring 7, Vienna 1010, Austria

<sup>6</sup>Senckenberg Research Institute, Micropalaeontology I, Senckenberganlage 25, Frankfurt 60325, Germany

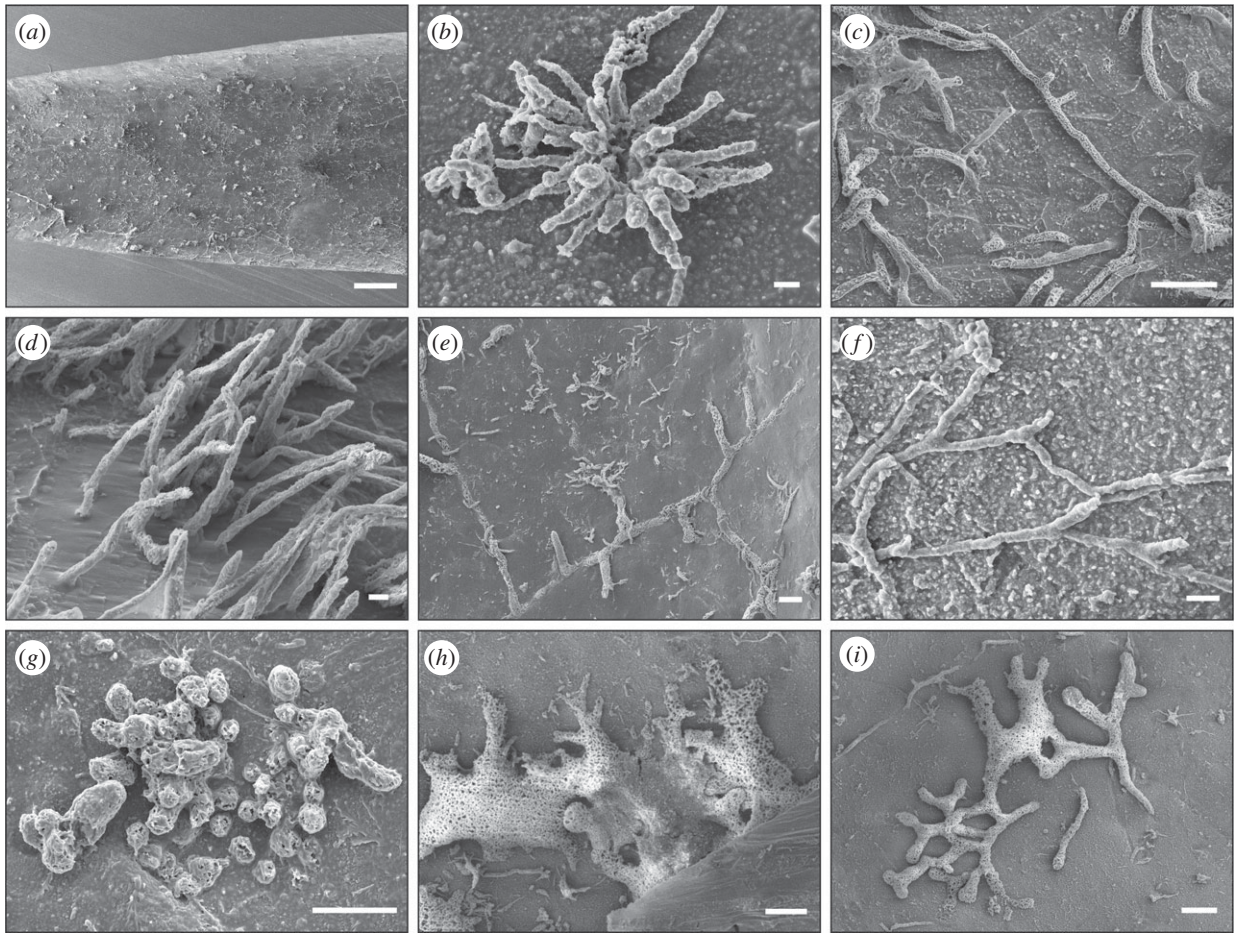
<sup>7</sup>Swedish Museum of Natural History, PO Box 50007, Stockholm 10405, Sweden

<sup>8</sup>Senckenberg am Meer, Marine Research Department, Südstrand 40, Wilhelmshaven 26382, Germany

Owing to the assumed lack of deep-sea macrofossils older than the Late Cretaceous, very little is known about the geological history of deep-sea communities, and most inference-based hypotheses argue for repeated recolonizations of the deep sea from shelf habitats following major palaeoceanographic perturbations. We present a fossil deep-sea assemblage of echinoderms, gastropods, brachiopods and ostracods, from the Early Jurassic of the Glasenbach Gorge, Austria, which includes the oldest known representatives of a number of extant deep-sea groups, and thus implies that *in situ* diversification, in contrast to immigration from shelf habitats, played a much greater role in shaping modern deep-sea biodiversity than previously thought. A comparison with coeval shelf assemblages reveals that, at least in some of the analysed groups, significantly more extant families/superfamilies have endured in the deep sea since the Early Jurassic than in the shelf seas, which suggests that deep-sea biota are more resilient against extinction than shallow-water ones. In addition, a number of extant deep-sea families/superfamilies found in the Glasenbach assemblage lack post-Jurassic shelf occurrences, implying that if there was a complete extinction of the deep-sea fauna followed by replacement from the shelf, it must have happened before the Late Jurassic.

## 1. Introduction

Thanks to intense research efforts during the last few decades, it is now generally acknowledged that the deep sea supports one of the highest levels of biodiversity on Earth, while differing fundamentally from shallow marine and terrestrial ecosystems [1,2]. Yet, the evolutionary processes that have shaped the unique attributes of the deep sea are still controversial. Growing evidence that the deep sea was anything but stable and unchanging through time has challenged the initial concept of the deep sea as a refuge for ancient lineages excluded from shelf habitats. Debates have focused on the impact of variations in temperature, oxygenation and circulation mode on the colonization of deep habitats, and at least for the late Cenozoic, deep-sea sediment cores have provided extensive benthic foraminifer and ostracod microfossil evidence in this respect [3,4]. Biogeographic patterns and molecular clock estimates have yielded dates which predominantly converge to a latest Mesozoic or early Cenozoic origin of the modern deep-sea fauna [5–9]. Testing these hypotheses and exploring older deep-sea biodiversity using direct fossil evidence, however, has been hampered so far by the sparse record of



**Figure 1.** Scanning electron microscope images of microboring trace fossils (in order of abundance) prepared as epoxy resin casts from mollusc shells from the Sinemurian–Pliensbachian (Early Jurassic) of the Glaserbach section, Austria. (a) Semi-cylindrical resin cast of a belemnite rostrum exhibiting a large number of microborings; (b) the dominant fungal microboring *Polyactina araneola*, in modern seas produced by the fungus *Conchyliastrum*; (c) the aphotic index ichnotaxon *Orthogonum lineare*, producer unknown but most likely a fungus; (d) cluster of *Flagrichnus profundus*, produced by schizochytrid fungi; (e) *Orthogonum giganteum*, producer unknown; (f) *Saccomorpha* isp., presumed fungal trace; (g) *Podichnus centrifugalus*, attachment scar of a juvenile brachiopod pedicle; (h) *Platydendrina convexa*, producer unknown; (i) unknown dichotomously branching dendridic microboring with affinity to the ichnogenus *Abeliella*. Scale bars equal 1 mm in (a), 10  $\mu\text{m}$  in (b,d,f) and 100  $\mu\text{m}$  in (c,e,g–i).

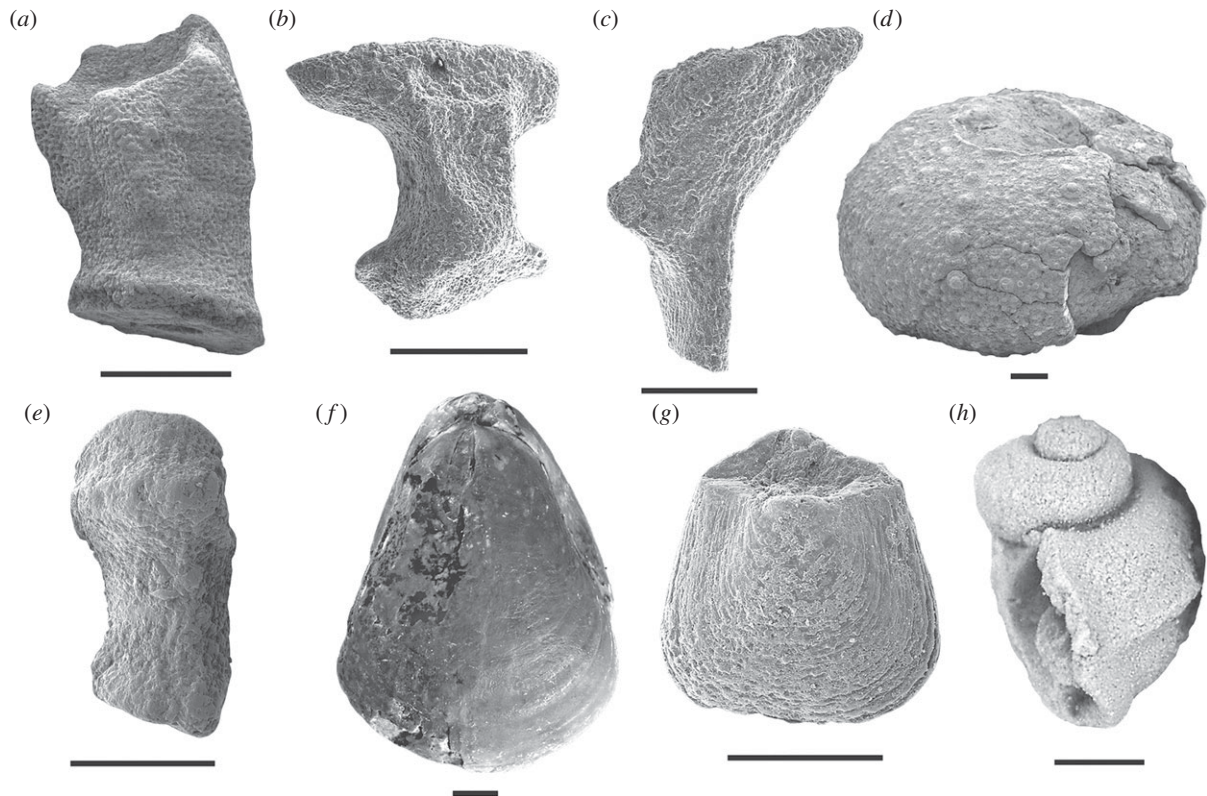
deep-sea faunas older than the Late Cretaceous [6]. The recent discovery of a modern-type echinoderm assemblage from Lower Cretaceous bathyal deposits of the subtropical north Atlantic [10] demonstrated that direct fossil evidence of deep-sea biodiversity exists in sediments beyond Late Cretaceous age and showed that the origin of at least some modern deep-sea groups is to be sought in even older strata.

## 2. Geological context

We here present fossil remains of a newly discovered diverse deep-marine assemblage retrieved from marls of the Kehlbach and Scheck Members (informally known as ‘Hauptknollenbrekzie’) within the Adnet Formation, exposed in the Glaserbach Gorge, south of Salzburg in the northern Calcareous Alps, Austria. These sediments are interpreted as a giant slump deposit derived from the slope of a submarine high in the former northern Tethys Ocean, and their ammonite fauna indicates an Early Jurassic age (from the late Sinemurian *Echioceras raricostatum* Zone to the late Pliensbachian *Amaltheus margaritatus* Zone) [11,12]. Palaeo-depth reconstructions suggest at least 1000 m for the slump components, based on subsidence models of the area, sedimentological comparisons with present-day

equivalents and the presence of very similar lithologies directly overlying both oceanic and deeply submerged continental crust in the Jurassic of the north Atlantic [11,13], as well as the absence of light-dependent benthic organisms even on the submarine tops of the source area of the slumping mass [12]. These estimates are supported by our palaeobathymetric analysis using microbioerosion trace fossils in 15 bivalve and brachiopod shell fragments and belemnite rostra. Not a single unequivocal trace of a phototrophic chlorophyte or cyanobacterium, which could indicate a photic environment, was found. Rather, all identified traces are produced by heterotrophic organisms (mostly marine fungi) and are typical constituents of aphotic trace fossil assemblages (figure 1) [14]. Thus, the material studied herein must have been deposited at a palaeo-depth exceeding the lower limit of sunlight influence in the water column, which, in the present case (low palaeo-latitude sea with low water turbidity, deduced from the low sedimentation rate [11]), was between 150 m (deepest regular phototrophic records during settlement experiments [15]) and 370 m (deepest known occurrence of phototrophic microendoliths [16]), and thus well below regular palaeo-shelf depths.

Further evidence supporting a bathyal palaeo-depth is provided by the ostracod assemblage of the Glaserbach fauna, which includes only forms lacking eyes or other signs of



**Figure 2.** Representatives of modern deep-sea groups from the Sinemurian–Pliensbachian (Early Jurassic) of the Glaserbach section, Austria. (a) *Eudesicrinus cuneatus* (Eudesicrinidae, Crinoidea), cup in lateral view; (b) Benthopectinidae (Asteroidea) new genus and species, ambulacral in actinal view; (c) Pterasteridae (Asteroidea) genus and species indeterminate, ambulacral in actinal view; (d) Aspidodiadematae (Echinoidea) new genus and species, test in latero-oral view; (e) Ophiomycetidae (Ophiuroidea) new genus and species, lateral arm plate in external view; (f) *Securithyris adnethensis* (Dyscolioidea, Rhynchonellata), in dorsal view; (g) *Zellania* sp. (Gwynioidea, Rhynchonellata), in dorsal view; (h) Pleuromarioidea (Gastropoda) genus and species indeterminate. Scale bars equal 500  $\mu\text{m}$  (a–d, f–g), 200  $\mu\text{m}$  (e) and 1000  $\mu\text{m}$  (h).

photoreception. In addition, it almost exclusively consists of members of the extant eurybathic Bairdioidea, and thus fundamentally differs from all known coeval ostracod assemblages from shelf depths [17,18] and instead resembles a coeval assemblage found in slope deposits from Turkey [19]. The Glaserbach assemblage thus provides a unique window into Early Jurassic deep-sea biodiversity and predates the late Mesozoic oceanic anoxic events commonly considered to have triggered extinction in the deep sea and subsequent replacement from the shelf.

### 3. Material and methods

Specimens were collected in the field or picked from washed residues. Figured specimens were deposited at the Natural History Museum in Vienna. Families and, where applicable, superfamilies were chosen as basis for the faunal analyses because they were found to represent a compromise between taxonomic resolution and comparability with modern communities. Identifications of dissociated echinoderm plates followed latest taxonomic recommendations [20–22].

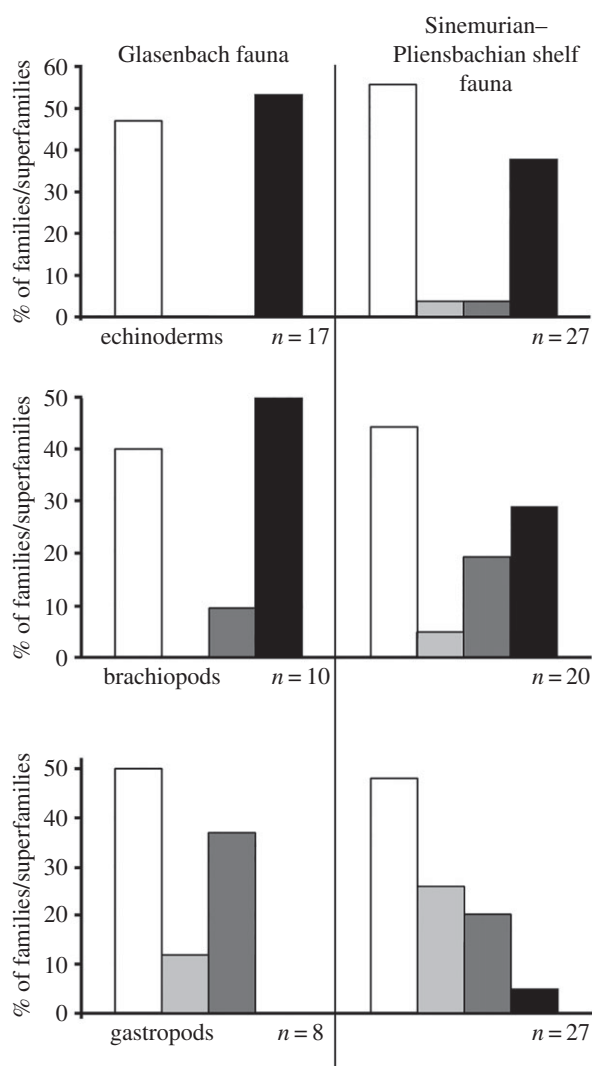
To assess the origin, resilience and bathymetric range shifts of the deep-sea fauna, we classified the families/superfamilies of the Glaserbach assemblage as well as coeval shelf (less than 200 m palaeo-depth) faunas [20,21,23–36] as extinct, or extant and, according to their present-day bathymetric distribution, typically deep, typically shallow, or without depth preference (eurybathic) (figure 3; electronic supplementary material, table 1). Our bathymetric classification was based on the averaged mean depth distribution of the extant species of the families/superfamilies (calculated by averaging the upper and lower distribution

boundaries for each species and by computing the arithmetic mean of the obtained values for each family/superfamily): typically deep—averaged mean depth greater than 500 m; typically shallow—averaged mean depth shallower than 200 m; eurybathic—averaged mean depth between 200 and 500 m. The upper boundary of the deep sea is commonly set between 200 and 500 m, in line with the fading of seasonal variations in physical parameters (e.g. temperature) and of the influence of sunlight [2,6,37–39]. We adopted a conservative approach using the 500 m boundary to minimize the impact of potential outliers from shelf depths. Microbioerosion trace fossils were analysed by applying the vacuum cast-embedding method and scanning electron microscopic imaging to visualize the delicate microborings in decalcified polymer-resin casts [14]. Statistic tests were performed using the software package PAST v. 2.13 [40].

### 4. Results and discussion

Among the several thousand available specimens, we distinguished at least 68 species belonging to four different phyla, i.e. echinoderms (ophiuroids, asteroids, echinoids and crinoids), molluscs (gastropods), brachiopods and crustaceans (ostracods) (figure 2 and electronic supplementary material).

This assemblage includes the extant, typically deep ophiomycetid ophiuroids, basal pterasterid asteroids and gwynioid brachiopods. These fossils predate the hitherto oldest record of these groups from Middle Jurassic shallow-water deposits by more than 25 Myr [20,21,23,24]. In addition, four extant deep-sea groups present in the Glaserbach assemblage, namely benthopectinid asteroids, eudesicrinid crinoids and



**Figure 3.** Percentages of extinct, modern shallow, modern eurybathic and modern deep families/superfamilies of echinoderms, brachiopods and gastropods in the Sinemurian–Pliensbachian Glasenbach fauna and coeval shallow-water (less than 200 m) communities. White, extinct; light grey, extant typically shallow; dark grey, extant eurybathic; black, extant typically deep.

aspodiadematid as well as extinct stem-group irregular echinoids, either coincide with, or slightly predate, the oldest known occurrences at shelf depths [20,21,25], depending on whether the Glasenbach assemblage is considered as late Pliensbachian or late Sinemurian in age. A deep-sea origin or at least an immediate expansion to the deep sea following a shallow origin must be assumed for these groups, suggesting that *in situ* origination of family/superfamily-level diversity in the deep sea, as opposed to colonization by taxa from the shelf, played a greater role in shaping modern deep-sea biodiversity than previously thought. This highlights the potential of deep-sea environments to produce and export higher taxonomic diversity [41,42], and suggests that at least some fossil shelf occurrences of modern deep-sea groups may be temporary expansions into shallow water rather than indicators of an onshore origin.

Both the Glasenbach assemblage and the coeval shelf faunas contain a similar percentage of extinct taxa (figure 3). This intuitively suggests similar resilience against extinction in both shallow and deep-water habitats, but it does not take differential bathymetric range shifts between the two environments into account. To test for such diverging evolutionary

dynamics, we compared the number of extant families/superfamilies in the Glasenbach assemblage and in coeval shelf faunas that retained their Early Jurassic depth preference until today versus those that did not. In the case of the Glasenbach assemblage these are the typically deep and eurybathic groups and in the case of the shelf fauna, the typically shallow and eurybathic groups. Among the echinoderms, significantly more deep-sea inhabitants retained their Early Jurassic depth preference to the present day than did coeval shelf inhabitants (Fisher's exact test,  $p = 0.0002$ ); among gastropods, these proportions are indistinguishable. Although more deep-sea brachiopods retained their Early Jurassic depth preference than those in shallow water, this difference is not statistically significant (Fisher's exact test,  $p = 0.1$ ), possibly because many extant brachiopods are most common at depths between 100 and 300 m [23] and are thus classified as eurybathic rather than typically deep according to the criteria applied here. Thus, depth-related turnover, reflecting how many extant groups have undergone shifts in their preferred depth distribution since the Early Jurassic, was higher at shallow depths than in the deep sea among echinoderms and probably in brachiopods, but not among gastropods. These results call for caution when using a single taxonomic group as a model to explore evolutionary patterns controlling deep-sea biodiversity.

The Glasenbach assemblage lacks extant shallow-water families/superfamilies, except for a single gastropod superfamily (Neritoidea). Thus, it seems that once families/superfamilies had colonized the deep sea, they either remained there or became extinct. This implies first that deep-sea environments provide higher evolutionary stability than shallow-water environments, and second that bathymetric shifts, in contrast to bathymetric extensions, from the deep sea to shallow waters are unlikely. Many extant deep-sea families/superfamilies present in the Glasenbach assemblage occur also in Early Jurassic shallow-water settings. Their restriction to the deep sea today thus results from a restriction of their once broad bathymetric range. This loss of shallow-water representatives among the once eurybathic groups seems to be a continuous process through geological time [43], as suggested by the last shelf occurrences of some of the Glasenbach families/superfamilies: e.g. Eudesicrinidae in the Late Jurassic [21], Zeillerioidea in the Early Cretaceous [23], and Pleurotomarioidea in the Cenozoic [44].

Several present-day deep-sea families, including Benthoplectinidae, Aspidodiadematidae, Eudesicrinidae and Ophiomycetidae, lack a post-Jurassic fossil record at shelf depths but were already present in the Early Jurassic Glasenbach deep-sea assemblage. Had there been a complete extinction of the deep-sea fauna followed by recolonization from shelf seas since the Early Jurassic [1,5], it must have happened before the Late Jurassic. This further highlights the resilience of the deep sea against major palaeoceanographic perturbations and sheds further doubt on the global extent and/or devastating nature of the so-called anoxic events during the late Mesozoic [10,45–47].

## 5. Conclusion

In summary, our results imply that two macroevolutionary processes have concurrently contributed to deep-sea biodiversity since the Early Jurassic: the potential to generate higher-level taxonomic diversity and resilience against major palaeoceanographic perturbations. We show for the first time, to our

knowledge, that higher level taxa can originate in the deep sea, expand to shelf depths and survive in the deep sea even after having gone extinct in the shallow seas again. We speculate that the resilience of the deep sea results from the sheer size of the environment combined with the great dispersal potential of the deep-sea benthos, increasing the chance for taxa to survive in deep-sea refuges and to subsequently re-expand. The potential to generate diversity might result from the many unique attributes of the deep-sea environment [2], which require unique adaptations that can only evolve *in situ*. Whatever the causes, our results shed new light on the role of the deep sea as a macroevolutionary source and reservoir of biodiversity, as well as on its potential to contribute to shallow-water diversity.

## References

- Rex MA, Etter RJ. 2010 *Deep-sea biodiversity: pattern and scale*. Cambridge, MA: Harvard University Press.
- Ramirez-Llodra E *et al.* 2010 Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. *Biogeosciences* **7**, 2851–2899. (doi:10.5194/bg-7-2851-2010)
- Yasuhara M, Hunt G, Cronin T, Okahashi H. 2009 Temporal latitudinal-gradient dynamics and tropical instability of deep-sea species diversity. *Proc. Natl Acad. Sci. USA* **106**, 21 717–21 720. (doi:10.1073/pnas.0910935106)
- Kawagata S, Hayward BW, Grenfell HR, Sabaa A. 2005 Mid-Pleistocene extinction of deep-sea foraminifera in the North Atlantic Gateway (ODP sites 980 and 982). *Palaeogeogr. Palaeoclim. Palaeoecol.* **221**, 267–291. (doi:10.1016/j.palaeo.2005.03.001)
- Jacobs DK, Lindberg DR. 1998 Oxygen and evolutionary patterns in the sea: onshore/offshore trends and recent recruitment of deep-sea faunas. *Proc. Natl Acad. Sci. USA* **95**, 9396–9401. (doi:10.1073/pnas.95.16.9396)
- Smith AB, Stockley B. 2005 The geological history of deep-sea colonization by echinoids: roles of surface productivity and deep-water ventilation. *Proc. R. Soc. B* **272**, 865–869. (doi:10.1098/rspb.2004.2996)
- Strugnell JM, Rogers AD, Prodöhl PA, Collins M, Allcock AL. 2008 The thermohaline expressway: the Southern Ocean as a centre of origin for deep-sea octopuses. *Cladistics* **24**, 853–860. (doi:10.1111/j.1096-0031.2008.00234.x)
- Williams ST *et al.* 2013 Cenozoic climate change and diversification on the continental shelf and slope: evolution of gastropod diversity in the family Solariellidae (Trochoidea). *Ecol. Evol.* **3**, 887–917. (doi:10.1002/ece3.513)
- Vrijenhoek RC. 2013 On the instability and evolutionary age of deep-sea chemosynthetic communities. *Deep-Sea Res. II* **92**, 189–200. (doi:10.1016/j.dsr2.2012.12.004)
- Thuy B, Gale AS, Kroh A, Kucera M, Numberger-Thuy LD, Reich M, Stöhr S. 2012 Ancient origin of the modern deep-sea fauna. *PLoS ONE* **7**, e46913. (doi:10.1371/journal.pone.0046913)
- Bernoulli D, Jenkyns HC. 1970 A Jurassic basin: the Glaserbach Gorge, Salzburg, Austria. *Verh. Geol. B.-A.* **1970**, 504–531.
- Böhm F. 2003 Lithostratigraphy of the Adnet Group (Early to Middle Jurassic, Salzburg, Austria). In *Stratigraphia Austriaca* (ed. WE Piller), pp. 231–268. Österr. Akad. Wiss., Schriftenr. Erdwiss. Komm. 16.
- Bernoulli D, Jenkyns HC. 2009 Ancient oceans and continental margins of the Alpine-Mediterranean Tethys: deciphering clues from Mesozoic pelagic sediments. *Sedimentology* **56**, 149–190. (doi:10.1111/j.1365-3091.2008.01017.x)
- Wisshak M. 2012 Microbioerosion. In *Trace fossils as indicators of sedimentary environments. Developments in Sedimentology, issue 64* (eds D Knaust, R Bromley), pp. 213–243. Amsterdam, The Netherlands: Elsevier.
- Vogel K, Gektidis M, Golubic S, Kiene WE, Radtke G. 2000 Experimental studies on microbial bioerosion at Lee Stocking Island, Bahamas and One Tree Island, Great Barrier Reef, Australia: implications for paleoecological reconstructions. *Lethaia* **33**, 190–204. (doi:10.1080/00241160025100053)
- Lukas KJ. 1978 Depth distribution and form among common microboring algae from the Florida continental shelf. *Geol. Soc. Am., Abstr. with Progr.* **10**, 448.
- Boomer I, Ainsworth NR. 2009 Lower Jurassic (Hettangian-Toarcian). In *Ostracods in British stratigraphy* (eds JE Whittaker, MB Hart), pp. 175–197. London, UK: The Micropalaeontological Society.
- Lord AR. 1988 Ostracoda of the Early Jurassic Tethyan Ocean. In *Evolutionary biology of Ostracoda* (eds T Hanai, N Ikeya, K Ishizaki), pp. 855–868. Tokyo, Japan: Kodansha.
- Lord AR, Lambourne DC. 1991 Lower Jurassic ostracods from the western Pontides, Turkey. *Geol. Rom* **27**, 381–387.
- Gale AS. 2011 The phylogeny of post-Palaeozoic Asterioidea (Neoasteroidea, Echinodermata). *Spec. Pap. Palaeontol.* **85**, 5–112.
- Hess H. 2011 Treatise on invertebrate paleontology. Part T, revised, Echinodermata 2, volume 3, Crinoidea Articulata. Lawrence, KS, USA: KU Paleontological Institute, The University of Kansas.
- Thuy B, Stöhr S. 2011 Lateral arm plate morphology in brittle stars (Echinodermata: Ophiuroidea): new perspectives for ophiuroid micropalaeontology and classification. *Zootaxa* **3013**, 1–47.
- Williams A *et al.* 1997–2007 Treatise on invertebrate paleontology. Part H, revised, Brachiopoda, volumes 1–6. Lawrence, KS, USA: KU Paleontological Institute, The University of Kansas.
- Thuy B, Meyer CA. 2012 The pitfalls of extrapolating modern depth ranges to fossil assemblages: new insights from Middle Jurassic brittle stars (Echinodermata: Ophiuroidea) from Switzerland. *Swiss J. Palaeontol.* **132**, 5–21. (doi:10.1007/s13358-012-0048-5)
- Kroh A, Smith AB. 2010 The phylogeny and classification of post-Palaeozoic echinoids. *J. Syst. Palaeontol.* **8**, 147–212. (doi:10.1080/14772011003603556)
- Conti MA, Szabó J. 1989 A revision of the Jurassic gastropod fauna from Cape San Vigilio (S-Alps, Italy), published by M. Vacek (1886). *Fragmenta Mineral. Palaeontol.* **14**, 29–40.
- Gatto R, Monari S. 2010 Pliensbachian gastropods from Venetian Southern Alps (Italy) and their palaeobiogeographical significance. *Palaeontology* **53**, 771–802. (doi:10.1111/j.1475-4983.2010.00961.x)
- Gründel J. 1999 Gastropoden aus dem höheren Lias von Grimmen, Vorpommern (Deutschland). *Archiv. Geschiebekde.* **2**, 629–672.
- Gründel J. 2001 Gastropoden aus dem Jura der südamerikanischen Anden. *Freiberger Forschungsh. C* **492**, 43–84.
- Gründel J. 2003 Gastropoden aus dem Unteren Lias (Ober-Hettangium bis Unter Sinemurium) Südwestdeutschlands. *Stuttgart Beitr. Naturkde. B* **340**, 1–55.
- Gründel J. 2007 Jurassische Gastropoden aus der Betakalkbank (oberes Sinemurium, obere *Obtusum-*

- Zone) Südwestdeutschlands. *Stuttgart. Beitr. Naturk. B* **370**, 1–29.
32. Hess H. 2006 Crinoids (Echinodermata) from the Lower Jurassic (Upper Pliensbachian) of Arzo, southern Switzerland. *Schweizer Pal. Abh.* **126**, 1–143.
  33. Schubert S, Gründel J, Nützel A. 2008 Early Jurassic (Upper Pliensbachian) gastropods from the Herforder Liasmulde (Bielefeld, Northwest Germany). *Paläontol. Z.* **82**, 7–30. (doi:10.1007/BF02988430)
  34. Thuy B, Gale AS, Reich M. 2011 A new echinoderm Lagerstätte from the Pliensbachian (Early Jurassic) of the French Ardennes. *Swiss J. Pal.* **130**, 173–185. (doi:10.1007/s13358-010-0015-y)
  35. Szabó J. 2002 A new euomphalomorph gastropod genus in the faunula, listed by Vadász (1915) from Alsórákos (Persani Mts, Romania, ?Early Jurassic). *Fragmenta Palaeontol. Hungarica* **20**, 61–67.
  36. Thuy B. 2013 Temporary expansion to shelf depths rather than an onshore-offshore trend: the shallow-water rise and demise of the modern deep-sea brittle star family Ophiacanthidae (Echinodermata: Ophiuroidea). *Eur. J. Taxon.* **48**, 1–242. (doi:10.5852/ejt.2013.48)
  37. Gage JD, Tyler PA. 1991 *Deep-sea biology: a natural history of organisms at the deep-sea floor*. Cambridge, UK: Cambridge University Press.
  38. UNESCO. 2009 *Global open oceans and deep seabed (GOODS) – biogeographic classification*. Paris, France: UNESCO-IOC.
  39. Glover AG, Higgs N, Horton T. 2014 World register of deep-sea species. (<http://www.marinespecies.org/deepsea> accessed on 25 February 2014).
  40. Hammer Ø, Harper DAT, Ryan PD. 2001 PAST: palaeontological statistics software package for education and data analysis. *Palaeontol. Electr.* **4**, 1–9.
  41. Lindner A, Cairns SD, Cunningham CW. 2008 From offshore to onshore: multiple origins of shallow-water corals from deep-sea ancestors. *PLoS One* **3**, e2429. (doi:10.1371/journal.pone.0002429)
  42. Pante E, France SC, Couloux A, Cruaud C, McFadden CS, Samadi S, Watling L. 2012 Deep-sea origin and *in-situ* diversification of chrysogorgiid octocorals. *PLoS ONE* **7**, e38357. (doi:10.1371/journal.pone.0038357)
  43. Jablonski D. 2005 Evolutionary innovations in the fossil record: the intersection of ecology, development, and macroevolution. *J. Exp. Zool.* **304B**, 504–519. (doi:10.1002/jez.b.21075)
  44. Hickman CS. 1976 *Pleurotomaria* (Archaeogastropoda) in the Eocene of the Northeastern Pacific: a review of Cenozoic biogeography and ecology of the genus. *J. Paleontol.* **50**, 1090–1102.
  45. Little CTS, Vrijenhoek RC. 2003 Are hydrothermal vent animals living fossils? *Trends Ecol. Evol.* **18**, 582–588. (doi:10.1016/j.tree.2003.08.009)
  46. Kiel S, Little CTS. 2006 Cold seep mollusks are older than the general marine mollusk fauna. *Science* **313**, 1429–1431. (doi:10.1126/science.1126286)
  47. Kiel S, Wiese F, Titus AL. 2012 Shallow-water methane-seep faunas in the Cenomanian Western Interior Seaway: no evidence for onshore-offshore adaptations to deep-sea vents. *Geology* **40**, 839–842. (doi:10.1130/G33300.1)