

**The  
Palaeontological  
Association**

**48th Annual Meeting  
17th–20th December  
2004**

*University of  
Lille*

**ABSTRACTS**



## The Palaeontological Association

# 48th Annual Meeting 17th–20th December 2004

## Laboratoire de Paléontologie et Paléogéographie du Paléozoïque (LP3), Université des Sciences et Technologies de Lille

On the following pages you will find the preliminary programme, schedule of events and abstracts (of the seminar talks, regular talks and posters) for the 48th Annual Meeting of the Palaeontological Association.

Following the suggestion of members, this year in Lille, as last year in Leicester, **no parallel sessions** are scheduled. All talks (except the seminar talks) are scheduled for 15 minutes, including discussion.

At the time of going to press more than **250 participants** are registered for the meeting, which will make the Lille meeting most probably the second largest Annual Meeting of the Association (the largest remains the 46th Meeting in Cambridge, 2002).

### *Confirmation of registration*

We are currently in the process of preparing booking confirmation letters, that will be distributed by mid-November together with arrival and hotel information.

If you have not heard from us and wish to confirm your registration, a list of registered participants will soon be available on the website <<http://www.palass.org/>>.

If you wish to attend but have not yet registered, the booking form will be available at the website <<http://www.palass.org/>> until Friday 3rd December 2004. Accommodation, participation in the seminar, and excursions can no longer be booked, however, once the deadline has passed.

Registered participants should note that it will not be possible to refund registration and accommodation fees for bookings cancelled after Friday 3rd December 2004.

### *Venue, Accommodation and Travel*

Detailed information will be sent to all registered participants before mid-November.

Lille is easily accessible from London by Eurostar high speed trains (appr. 1 hour 40 minutes). You can also come to Lille by using TGV high speed trains from Paris (1 hour) and Bruxelles (40 minutes), or other cities.

The seminar and icebreaker (Friday 17th) are in the city centre, the seminar will take place in the Musée des Beaux-Arts, the icebreaker in the Musée d'Histoire Naturelle.

The regular sessions, the Annual Address, Reception and Annual Meeting are taking place on the campus of the Université des Sciences et Technologies de Lille at Villeneuve d'Ascq, that can easily be reached by metro (underground train) in about 15 minutes from the city centre of Lille.

Sessions will take place in the Congress Centre MACC on the campus (five minutes' walk from the metro station «Cité Scientifique»). Lunches, Reception and the Annual Dinner take place in the University restaurant «Charles Barrois», just next to the metro station «Cité Scientifique» (about eight minutes' walk from the MACC).

Accommodation is organised in different hotels (IBIS hotels or other). Most participants stay at Villeneuve d'Ascq, in hotels located at some 15 to 20 minutes' walking distance from the MACC. Some other participants stay in the city centre of Lille (transport to the MACC by metro). Precise information will be sent individually to all participants before mid-November.

### *Registration*

A registration desk will be open for all participants who registered for the seminar in the afternoon of Friday 17th at the Beaux Arts Museum (1 pm to 5 pm). Registration will continue at the Natural History Museum (6 pm to 8 pm) the same day.

The registration desk will be placed in the entrance hall of the MACC on Saturday 18th and Sunday 19th.

### *Seminar*

A seminar on «palaeobiogeography» is scheduled for the afternoon of Friday 17th from 2pm to 5pm. The seminar will highlight the importance of fossils for the reconstruction of palaeogeographical maps, and the impact of changing palaeogeography on the dynamics of biodiversity in the past.

Confirmed speakers are **F. Cecca** (Paris), **R.A. Fortey** (London), **P. Neige** (Dijon), **B. Rosen** (London) and **C.R. Scotese** (Arlington, Texas).

The lecture hall in the Beaux Arts Museum is limited to 200 seats. Attendance at the **seminar is free** to conference participants, but only if **booked in advance** in due time.

For programme, speakers and abstracts see subsequent pages.

*See you in Lille !*

**Thomas Servais**

on behalf on the organising committee:

Sophie Beckary

Alain Blicck

Philippe Courville (field trip coordinator Boulonnais)

Catherine Crônier

Thomas Servais (chair)

Jacques Verniers (field trip coordinator Brabant)

# Schedule of events and timetable of oral presentations

## FRIDAY 17th December

**Registration** for those attending the Seminar from 1 pm in the Musée des Beaux Arts, Lille.

Otherwise in the Musée d'Histoire Naturelle from 6 pm.

### 2:00 to 5:00 Seminar: *Palaeobiogeography*

Oral presentations in the Amphithéâtre, Musée des Beaux Arts.

**Palaeobiogeographic Units: history, applications, recommendations, methods and drawbacks**

F. Cecca

**Palaeontological evidence bearing on Lower Palaeozoic continental reconstructions**

R.A. Fortey

**Palaeobiogeography and the macroevolutionary theory**

P. Neige

**Is the biogeographical past a key to distribution patterns of the present? Progress on scleractinian corals, and the case history of the staghorn coral, *Acropora***

B. Rosen

**Early Paleozoic Plate Tectonics, Paleogeography and Paleoclimate**

C.R. Scotese

**6:00 to 8:00 Icebreaker: Musée d'Histoire Naturelle**

## SATURDAY 18th December

Registration from 8am in the Congress Centre MACC, campus of the USTL, Villeneuve d'Ascq.

Oral presentations in the main lecture hall, MACC.

Poster presentations in the adjoining hall.

Book exhibitions in the entrance hall.

### 8:45 **Welcome**

### 9:00 **Evolution of polymorphism in colonial animals: differentiation of the earliest avicularian polymorphs in the Cretaceous cheilostome bryozoan *Wilbertopora***

*Paul D. Taylor, Alan H. Cheetham, Andrew N. Ostrovsky and JoAnn Sanner*

### 9:15 **Homology, shape and morphometric analysis of the conodont skeleton**

*David Jones, Mark Purnell, Peter von Bitter*

- 9:30 Echinoderm Palaeoecology from fragments: reconstructing salinity and substrate controlled faunas in the British Middle Jurassic**  
*Aaron W. Hunter*
- 9:45 Biotic recovery in the aftermath of the Late Permian mass extinction event: new data from the oceanic seamounts of SW Japan**  
*David Casenove, Richard J. Twitchett, and Tatsuo Oji*
- 10:00 From flying reptile to marine turtle : the «pterodactyl» from the Chalk of Lezennes-lez-Lille**  
*Eric Buffetaut*
- 10:15 The evidence for and implications of an invertebrate diet in Jurassic pliosaurs (Reptilia: Sauropterygia)**  
*Leslie F. Noè*
- 10:30 Coffee and posters**
- 11:00 A Silurian sea spider**  
*Derek J. Siveter, Mark D. Sutton, Derek E. G. Briggs, David J. Siveter*
- 11:15 Contrasting Late Miocene bryozoan faunas from the eastern Atlantic and western Mediterranean: implications for palaeoenvironmental reconstruction and the species concept in Bryozoa**  
*Björn Berning*
- 11:30 Eurypterid phylogeny and the origin of Arachnida**  
*O. Erik Tetlie*
- 11:45 The apparatus architecture of the prioniodinid conodont *Erismodus quadridactylus* (Stauffer) and its implications**  
*Rosie Dhanda*
- 12:00 Double-trouble in the Devonian – extinction and anoxia**  
*David Bond*
- 12:15 Exceptional Preservation in the Upper Carboniferous Coseley Lagerstätte**  
*Laura Braznell*
- 12:30 The first Danish dinosaur footprints!**  
*Jesper Milàn*
- 12:45 Lunch and posters**
- 14:00 Exploring an Early Palaeozoic Tropical Archipelago on the Shores of Hudson Bay**  
*Graham A. Young, Robert J. Elias, Godfrey S. Nowlan, David M. Rudkin, and Edward P. Dobrzanski*
- 14:15 A new test of the role of CO<sub>2</sub> in the late Ordovician glaciation**  
*Benjamin J. Fletcher, Charles H. Wellman and David J. Beerling*

- 14:30 Nitrogen and carbon isotopes in conodonts: Evidence of trophic levels and nutrient flux in Palaeozoic oceans**  
*Chris Nicholas, John Murray, Robbie Goodhue and Peter Ditchfield*
- 14:45 The «Avis event», a remarkable highstand at the end of the Tournaisian. Its influence on the global distribution and on the evolution of the Viséan rugose corals**  
*Edouard Poty*
- 15:00 Terrestrial Gastropods and the Perils of Palaeoclimate Studies, or When Size Does Matter (sample size that is)!**  
*Claire L. Pannell*
- 15:15 Neogene climates near the South Pole: evidence from fossil plants and climate-vegetation models**  
*Jane Francis, Alan Haywood, Allan Ashworth, Steven Roof, and David Cantrill*
- 15:30 Tea and posters**
- 16:00 A new genus of tetrapod from the Devonian of East Greenland**  
*Jennifer A. Clack, Per E. Ahlberg, Henning Blom*
- 16:15 The evergreen or deciduous habit of Cretaceous polar forests: Fossil data versus computer model predictions**  
*Melise Harland*
- 16:30 A null biogeographic model for quantifying the role of dispersal in shaping taxonomic richness and similarity patterns**  
*Noel A. Heim and Steven M. Holland*
- 16:45 A.G.M.**
- 17:15 Annual Address: 'Palaeontologia de profundis'**  
**Stefan Bengtson**
- 18:30 Members Reception (sponsored by Blackwell Publishing), University Restaurant Charles Barrois**
- 19:30 Annual Dinner, University Restaurant Charles Barrois**  
followed by Open Bar

## SUNDAY 19th December

Oral presentations in the main lecture hall, MACC.

- 9:00 Validating fossil bacteria: some cautionary tales from the Mid-Palaeozoic**  
*D. Edwards, L. Axe and R.J. Parkes*
- 9:15 How to make a Burgess Shale fossil: an experimental approach**  
*Lucy Wilson*

- 9:30 Tunnelling trilobites in Middle Ordovician *Thalassinoides***  
*Lesley Cherns, James R. Wheeley and Lars Karis*
- 9:45 Might machaeridians be molluscs?**  
*Liam Herringshaw, Alan Thomas and Paul Smith*
- 10:00 Functional and Adaptive Implications of Cryptic Speciation in Planktic Foraminifera**  
*Blair A. Steel, Michal Kucera and Kate F. Darling*
- 10:15 Molluscan diversity in deteriorating climate regimes: The Plio-Pleistocene of the southern North Sea Basin**  
*F.P. Wesselingh*
- 10:30 Coffee and posters**
- 11:00 Pollen abundance patterns: Neocological insights for palaeoecology?**  
*Guy J. Harrington*
- 11:15 Towards the development of a Palaeo UV-B proxy from fossil land plants**  
*B.H. Lomax, M.A. Sephton, T.V. Callaghan, C.H. Wellman and D.J. Beerling*
- 11:30 How to get a date in the Devonian of Bolivia**  
*Ian Troth, John Marshall and Andrew Racey*
- 11:45 In search of the earliest seed plants**  
*Christopher M. Berry, John E.A. Marshall, Alan R. Hemsley and Susan Hammond*
- 12:00 A new Upper Permian flora from the Middle East with typical Triassic Gondwana elements**  
*Hans Kerp, Abdallah Abu Hamad, Klaus Bandel, Birgit Niemann*
- 12:15 Plant and vertebrate fossil-lagerstätten from the Albian-Cenomanian of Charente-Maritime (Western France)**  
*Bernard Gomez, Didier Néraudeau, Romain Vullo, Blaise Videt, Vincent Perrichot, Véronique Daviero-Gomez, Frédéric Thévenard and Clément Coiffard*
- 12:30 Assessing the Evidence for Extensive Wildfires at the Cretaceous-Tertiary Boundary**  
*C.M. Belcher, M.E. Collinson, P. Finch and A.C. Scott*
- 12:45 Lunch and posters**
- 14:00 Influence of seawater saturation state on the Phanerozoic diversity of calcified marine algae and invertebrates**  
*Robert Riding*
- 14:15 The Galeropygidae: towards triumph or Disaster? A phylogeny of the basal irregular echinoids**  
*Colin Barras*

- 14:30 Graptogonophores, scopulae and *Dawsonia*: putative reproductive organs reconsidered**  
*Alex Page, Phil Wilby, Mark Williams and Jan Zalasiewicz*
- 14:45 Ray-finned fishes evolution and breakup of Pangaea**  
*Lionel Cavin and Peter L. Forey*
- 15:00 The systematic position of the Late Jurassic alleged dinosaur *Macelognathus* (Crocodylomorpha: Sphenosuchia)**  
*Ursula B. Göhlich, Luis M. Chiappe, James M. Clark and Hans-Dieter Sues*
- 15:15 Mid-Miocene latitudinal environmental gradient in western Europe: mammals and vegetation compared**  
*Loïc Costeur, Gonzalo Jimenez-Moreno*
- 15:30 Tea and posters**
- 16:00 Siliceous microfossils and biosiliceous sedimentation in the lowermost Cambrian of China**  
*Andreas Braun, Chen Jun-Yuan, Dieter Waloszek and Andreas Maas*
- 16:15 Inside the inside of a dendroid**  
*Kate Saunders and Denis Bates*
- 16:30 Functional morphology and light-gathering ability of podocopid ostracod eye**  
*Gengo Tanaka*
- 16:45 Discovery of Famennian and Early Carboniferous trilobite larvae: implications for the systematics and the evolutionary history of proetoids**  
*Lerosey-Aubril Rudy*
- 17:00 Substrate specificity of Auloporida (Tabulata) from the Devonian of the Holy Cross Mts., Poland**  
*Mikolaj K. Zapalski*
- 17:15 On convergent evolution in Nummulitidae with secondary chamberlets (Foraminiferida)**  
*Willem Renema and Peter Lunt*
- 17:30 Age assessment of Pleistocene and Holocene mammal bone**  
*Christina Karla Reimann and Christian Ostertag-Henning*
- 17:45 Announcement of prize winners and close**

## MONDAY 20th December

Field excursions (Boulonnais, Brabant)

Depart 8:00 am, return 5:00 pm approx.

# Abstracts of seminar presentations

## Palaeobiogeographic Units: history, applications, recommendations, methods and drawbacks

**Fabrizio Cecca**

*Université "Pierre et Marie Curie", Paris VI, CNRS-UMR 5143 "Paléobiodiversité et Paléoenvironnements", Tour 56-46, 5ème étage, case 104, 4, place Jussieu, 75252 Paris Cedex 05, FRANCE <cecca@ccr.jussieu.fr>*

Since the pioneering work of de Candolle (1820), who recognized 20 different botanical regions on the basis of the living floras, the practice of the definition of Province, Regions, Realms has been generalised to both Neo and Palaeobiogeography. As far as Mesozoic is concerned, Neumayr (1873) introduced the zoogeographic province, defined as a large area characterized by a common particular fauna and caused by geographic position (barriers, latitude, climate) but independent of facies. Uhlig (1911) introduced the more inclusive rank, the Realm and stressed the independence of facies. Thus, according to these original definitions, biogeographic units are based on endemism and should have an historical meaning. However, different definitions and concepts of biogeographic units have been proposed since.

There is no doubt that this notion has been extremely important in the history of biogeography because it highlights the importance of endemism and the idea of area relationship. Provincial schemes are applied to palaeogeographic reconstructions and also to the study of evolutionary patterns, which imply the relation between diversity and endemism.

Biogeographical units (or biochorema) have been created and defined with the application of different criteria, both qualitative and quantitative. The recommendations recently proposed in the framework of the informal group "Friends of Paleobiogeography" are presented and discussed.

A short review of the most used analytical methods in biogeography is presented. Provincial schemes based on different organisms may lead to provincial patterns which reflect ecological responses of individual groups thus making their historical meaning unclear. Subjectivity, due to the use of endemic species arbitrarily selected as "provincial markers," is strongly discouraged. The quantitative treatment of similarity coefficients ("phenetics") is a far less subjective approach but it must be conceptually clarified and its limits stated as biogeographical units cannot be always used as proxies of endemism. The comparison of results obtained with different analytical techniques, from phenetics to cladistics, are recommended in biogeography.

## Palaeontological evidence bearing on Lower Palaeozoic continental reconstructions

**Richard A. Fortey**

*Department of Palaeontology, The Natural History Museum, Cromwell Rd, London SW7 5BD, U.K., and Dept of Zoology, Oxford University <raf@nhm.ac.uk>*

Because of the difficulties in determining the disposition of continents in the Lower Palaeozoic, fossil evidence has played a crucial role in the definitions and position of palaeocontinents. The recognition of both Iapetus and Tornquist's was initially based largely on faunal evidence, often opposed at first by geologists from other disciplines. I shall describe something of the history of research on Lower Palaeozoic geography as deduced from fossil distributions. The original approach described 'faunal provinces' typified by widespread taxa. The recognition of benthic biofacies both rationalised and complicated the provincial picture. Integration of these data with plate tectonic models provided an initially satisfyingly simple picture of continental distributions, one that came to be progressively more complex as microcontinents and terranes were deduced to have had independent histories. Biofacies discrimination is a necessary prelude to interpreting the weight that can be placed on a single fauna. Various quantitative methods have been applied to continental reconstructions from faunal evidence—most show support for continental distributions arrived at from more subjective lines of evidence. Vicariance biogeographic methods are in their early days, largely because of the shortage of good phylogenetic analyses. Nonetheless, continental reconstructions are now sufficiently well-founded to plot range excursions of biota within them—for example, as evidence of a late Ordovician global warming that preceded the well-known glaciation.

## Palaeobiogeography and the macroevolutionary theory

**Pascal Neige**

*Centre des Sciences de la Terre & UMR CNRS 5561 Biogéosciences, Université de Bourgogne, 6 bd Gabriel, 21000 Dijon, France <Pascal.Neige@u-bourgogne.fr>*

Eldredge and Gould launched one of the earliest pragmatic criticisms of the modern synthesis with the publication of their punctuated equilibrium theory. This may be seen as a liberating concept allowing the development of a macroevolutionary theory whose main object is to explore large-scale patterns and processes. Even if the micro/macroevolutionary split is still subject to much debate, palaeontologists now possess different tools and concepts to explore and interpret large-scale data. Among them is the concept of morphological disparity, which entails investigating biodiversity through its morphological component alone, and which complements the taxonomic diversity measurement, which is now widely used to study increase and decline of morphologies over time at the macroevolutionary scale.

Surprisingly, the biogeographic (or palaeobiogeographic) impact on disparity fluctuations has largely been ignored by authors. However, seminal studies report large differences in disparity measurements with respect to geographical units. Here, this

geographical component of disparity is explored using two complementary examples: one on Recent cuttlefishes and the other on Jurassic ammonites. The first allows discussion of two distinctive geographical patterns (the East Indies and southern Africa) and the second, fluctuations in the diversity / disparity relationship through time and space.

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**Is the biogeographical past a key to distribution patterns of the present?  
Progress on scleractinian corals, and the case history of the staghorn coral,  
*Acropora***

**Brian Rosen**

*Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD*  
<B.Rosen@nhm.ac.uk>

Over-fishing, pollution and global warming are all concurrent threats to the ecology and biodiversity of the marine environment. Their destructive effects on corals and coral reefs worldwide is now well known to science and the wider public. Biologists are increasingly asking what the response of organisms in the past can tell us about the future of biodiversity (*sensu lato*). Their methods (*e.g.* cladistic, phenetic, and molecular), however, either concentrate entirely on, or are unavoidably restricted to, living taxa. The complementary study of fossil data provides insights that living taxa on their own cannot reveal, *e.g.* through the study of the history of regional taxonomic pools.

During the Cenozoic, zooxanthellate corals (*cf.* 'reef corals'), the warmer the climate, the higher the diversity, but this was modulated by historical patterns of suitable habitat. For example, the highly diverse fauna of Europe and the Mediterranean during the Paleogene declined to zero during the Miocene as climate cooled and geotectonic events isolated it (yet this history and its significance are beyond detection by study of modern taxa alone). However, the quality of palaeobiogeographical coral data is extremely uneven across different regional pools (*e.g.* much better in the Caribbean Neogene, than the Indo-Pacific Neogene). Collaboration with Carden Wallace (Museum of Tropical Queensland) has made it possible to concentrate, instead, on one well-studied, species-rich genus, the staghorn coral, *Acropora*. Very early in its history, this was a common coral in the mid Eocene of southern England and northern France. Their palaeolatitude (*c.* 50°N) is well beyond those of any zooxanthellate corals today (*c.* 30°N&S), suggesting that during such warm climatic times, zooxanthellate corals track warmer conditions into higher latitudes.

Understanding the effects of present global warming will increasingly dominate the scientific agenda, in step with social, economic and political agendas. In conclusion, I will suggest some implications for the future of palaeontology.

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**Early Paleozoic Plate Tectonics, Paleogeography and Paleoclimate**

**Christopher R. Scotese**

*PALEOMAP Project, Department of Earth and Environmental Sciences, University of Texas at Arlington, 500 Yates, Arlington, Texas, 76019* <chris@scotese.com>

Ten paleoreconstructions are presented, illustrating the plate tectonics, paleogeography and paleoclimate of the Latest Precambrian and Early Paleozoic. The time intervals chosen include two maps for the latest Precambrian (600 Ma and 570 Ma), maps for the Early and Late Cambrian, four maps for the Ordovician (early Tremadoc, early Arenig, Llandeilo/Caradoc, and Ashgill), as well as paleoreconstructions for the Early and Middle Silurian. The plate tectonic reconstructions show the probable location of active plate boundaries (subduction zones, island arcs and mid-ocean ridges). The paleogeographic maps illustrate the distribution of deep oceans, shallow shelves, lowlands and mountainous areas for each time interval. There are two versions of each paleogeographic map. One map shows the extent of maximum flooding during a period of high eustatic sea level. The second map shows the paleogeography during a time of minimum sea level corresponding to a major sequence boundary. In the final set of maps, climatically sensitive lithofacies such as evaporites, calcretes, bauxites, and tillites are plotted on the paleoreconstructions. Climatic zones are mapped based on the distribution of these climatically sensitive lithofacies.

# Abstracts of oral presentations

## The Galeropygidae: towards triumph or *Disaster*? A phylogeny of the basal irregular echinoids

**Colin Barras**

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One of the most rapid and most important morphological diversifications of echinoids occurred during the late Early and Middle Jurassic. It was during this period that the major lines of irregular echinoid became established, leading on the one hand to the Cassiduloids and on the other, ultimately, to the Holasteroids and Spatangoids. These two groups are now morphologically highly differentiated, but precisely how this was achieved remains poorly understood. It is generally supposed that a small group of late Early-early Middle Jurassic irregulars, the Galeropygidae, are basal to both clades. While the Cassiduloid fossil record can be traced back with confidence to the Galeropygidae, thanks to an excellent fossil record of intermediaries, the origins of the Holasteroid-Spatangoid body plan is less well understood, and they have traditionally been linked to the Galeropygidae through a morphologically rather diverse Jurassic group, the disasteroids. There have been few previous attempts to produce a phylogeny documenting this critical period of divergence among the irregular echinoids, and none that take into consideration all of the pertinent taxa. Here, a comprehensive study of relevant material, coupled with new plating diagrams of many of these taxa, has been used to generate a cladistic analysis of the early irregular echinoid genera. This has confirmed the Galeropygidae as basal to both the Clypeidae and the collyritid-disasterid complex.

## Assessing the Evidence for Extensive Wildfires at the Cretaceous-Tertiary Boundary

**C. M. Belcher<sup>1</sup>, M. E. Collinson<sup>1</sup>, P. Finch<sup>2</sup> and A. C. Scott<sup>1</sup>**

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<sup>2</sup>*Centre of Chemical Sciences, Royal Holloway University of London, Egham, Surrey, TW20 0EX* <p.finch@rhul.ac.uk>

Models of the Cretaceous-Tertiary impact at Chicxulub have suggested that the thermal radiation released by the impact would have been sufficient to ignite extensive wildfires. Eight non-marine K-T sequences stretching across North America have been studied in order to test this hypothesis. Multiple palaeowildfire proxies (charcoal, soot and polyaromatic hydrocarbons (PAHs)) have been used in combination to assess the extent of any biomass burning. Quantitative data from three different measures of charcoal abundance reveal that the K-T boundary rocks contain significantly less charcoal than is typical of the Cretaceous background of this area. The Cretaceous sedimentary rocks

contain between four and nine times (according to the measure used) more charcoal particles than the K-T sedimentary rocks. Furthermore non-charred plant remains are also abundant in the K-T rock layers. Re-assessment of the record of soot and PAHs reported in the K-T rocks suggests that the morphology of the soot and the signature of the PAHs is more consistent with them being sourced from the vaporization of hydrocarbon material rather than biomass burning. We conclude that there was no significant wildfire across North America as part of the K-T events and that the impact at Chicxulub did not deliver the high amounts of thermal radiation previously predicted.

## Contrasting Late Miocene bryozoan faunas from the eastern Atlantic and western Mediterranean: implications for palaeoenvironmental reconstruction and the species concept in Bryozoa

**Björn Berning**

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A comparative morphological study on bryozoan faunas from the Late Miocene of the eastern Atlantic and western Mediterranean has shown that there exist considerable differences in morphology within species. The presence of a great number of Mediterranean species in the eastern Atlantic Guadalquivir Basin (SW Spain) rendered it possible to compare directly morphological variation between these two regions. Measurements of zooid size yielded a general trend towards the existence of smaller zooids in specimens from the eastern Atlantic. Although it is well known that environmental factors can generate within-colony variations in morphology (*e.g.* there is an inverse relationship between zooid size and temperature), genotypic differences have as yet been found to be predominant in producing between-colony variations. However, the present study indicates that the environment might play a greater role in producing intraspecific morphological variation than previously recognised. This is exemplified by the extant, erect, cheilostome *Myriapora truncata* (Pallas) which shows intracolony, within-site and between-site variability in zooid size and branch diameter in both fossil and Recent assemblages. These findings suggest yet again that species discrimination purely based upon zooidal or colonial dimensions should be avoided in bryozoans. Furthermore, if the extrinsic controls on bryozoan morphology can be qualitatively and quantitatively ascertained, (palaeo)environmental information may be gained at various spatial and temporal scales.

## In search of the earliest seed plants

**Christopher M. Berry<sup>1</sup>, John E. A. Marshall<sup>2</sup>, Alan R. Hemsley<sup>1</sup> and Susan Hammond<sup>1</sup>**

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The appearance of seed plants in the Late Devonian is a critical episode in earth history. How seeds evolved is still an open question. Recently, in *Palaeontology*, Marshall

talks

talks



and Hemsley described *Spermasporites allenii* from a Middle Devonian lake on Ella Ø, East Greenland. *S. allenii* is a seed megaspore bearing at its apex not only three smaller aborted spores of the original tetrad, but also a cluster of microspores. This suggested a new path to seed evolution, where the seed megaspore is most likely to be fertilized by microspores from within the same sporangium but also allows for fertilization by microspores from another sporangium or individual. In order to determine the taxonomic affinity of the seed-megaspore bearing plant, CMB, JEAM, and AH mounted a NERC-funded expedition to Ella Ø (see poster) under the umbrella of CASP. Excavation of the layers in which the seed megaspores were concentrated yielded numerous partial specimens of the plant. Single megaspores are snugly contained in sporangia which are inserted erectly, singly and terminally on the end of an isodichotomous branching system. Association suggests that these were carried laterally on small sparsely dichotomously and trichotomously branching naked stems. This suggests morphology more similar to that of latest Devonian seed plants than to that of the contemporaneous advanced progymnosperm *Archaeopteris/Svalbardia* found elsewhere in the same lake, which may otherwise be an obvious candidate for ancestry of seed plants.

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### Double-trouble in the Devonian – extinction and anoxia

**David Bond**

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The extinctions at the Frasnian-Famennian (Late Devonian) boundary constitute one of the “big-five” crises of the Phanerozoic. Many faunal studies have been compiled, but these have never been properly integrated. A lack of high-resolution faunal range data has hindered our understanding of the extinction dynamics. Amalgamation of the faunal data available in the literature, at conodont-zone level, together with the author’s own findings from a variety of marine sections in Europe and the United States, has allowed recognition of the nature and timing of the extinction. In particular, the tentaculitoids, a group of small, conical animals which were locally abundant during the Frasnian, provide a detailed record of the extinction timing.

A number of questions, crucial to our understanding of the extinction, will be explored: did the F–F extinction actually occur? If so, when, and how suddenly did it occur? How selective was the extinction? What was the significance of sea-level change during the extinction?

There are a number of competing extinction mechanisms. The faunal range data has been correlated with the record of globally widespread anoxia, supported by a variety of geochemical and sedimentological techniques. This provides strong evidence of a causal link between marine anoxia and the extinction.

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### Siliceous microfossils and biosiliceous sedimentation in the lowermost Cambrian of China

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Clay-rich and siliceous sedimentary rocks of lowermost Cambrian age on the Yangtze Platform, China contain a large amount of siliceous microfossils. Based on their high content of siliceous hard parts, these rocks are in fact biosiliceous sediments. In more clay-rich lithologies, diagenetic dissolution processes however caused a removal of siliceous hard parts and led to “pure mudstones” and “silicified claystones,” being apparently devoid of siliceous microfossils. Abundant preservation as Fe-hydroxide pseudomorphs and in early diagenetic concretions however indicate a high biosiliceous content of the original sediments. Rocks investigated belong to the lowermost Cambrian (*Anabarites trisulcatus* – *Protohertzina anabarica* assemblage zone) and come from black-chert sequences (Kuanshuanpu, S.-Shaanxi province, *cf. Chen et al.* 2004; Fengkoushao, Yunnan province) as well as sequences of black shales (Nuititang formation, Songtao section, E Guizhou province; Niuitang formation at Mengdong train station, Hunan province). Lighter coloured clay-rich lithologies of equal age in Guizhou (Taozichong section, *cf. Wang et al.* 1984) have similarly yielded abundant siliceous hardparts.

The significant contribution of biosiliceous particles to early Cambrian sedimentation on the Yangtze platform, as well as to other occurrences in Kazakhstan and Europe, implies that silica-biomineralizing organisms have played a significant role in the geochemical cycling of silica in the oceans by the beginning of the Phanerozoic. The high abundance of sponge spicules in the sediments indicates that sponges (Porifera) played a major ecological role in the early Cambrian environment of the investigated areas. This is supported by findings of complete sponges and spicule clusters on bedding planes of clay rich sediments and black shales.

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### Exceptional Preservation in the Upper Carboniferous Coseley Lagerstätte

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The Late Carboniferous Coseley Lagerstätte of the West Midlands, UK, contains exceptionally preserved plant and animal fossils that occur as hard parts and mineralised soft tissues sealed within siderite nodules, which vary in size from 15–250 mm. The nodules are recovered from Westphalian B siltstones and mudstones that lie above the Thick Coal of the Coal Measure Group, and were abundant enough in these horizons to form commercial ironstone beds in the nineteenth century.

The Coseley fossils have been examined using various techniques, including scanning electron microscopy and electron microprobe analysis, that have revealed several distinctive phases of preservation. Soft tissues have been replicated by kaolinite and



pyrite, voids have been extensively filled with sulphide minerals, and all of these phases are encased in siderite. The growth of clay minerals on the surface of decaying soft tissues could have been controlled either by purely inorganic processes or through bacterially mediated biofilms. This growth was accompanied by early framboidal pyrite formation and closely followed by void-filling sphalerite, galena and pyrite precipitation. Siderite formation occurred both during and shortly after soft tissue preservation, producing a nodule that inhibited compaction of the tissues.

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### From flying reptile to marine turtle: the « pterodactyl » from the Chalk of Lezennes-lez-Lille

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In 1874, Charles Barrois reported a pterodactyl tibia, from the White Chalk (“Craie blanche”) which was then exploited in underground quarries at Lezennes (now in the suburbs of Lille). He referred it to *Pterodactylus giganteus*, a species from the English Chalk. Although no detailed description or illustration was provided, the occurrence of a pterodactyl in the Coniacian Lezennes Chalk was repeatedly mentioned in papers on local geology, as well as in lists of French pterosaurs.

A re-examination of the specimen (Musée d'Histoire Naturelle de Lille, MGL 4158) shows that it is an elongate, more or less cylindrical non-pneumatized bone with poorly differentiated articular ends, which bears no resemblance to pterosaur tibia, nor to any other element of a pterosaur skeleton.

Comparisons reveal that the so-called pterosaur tibia from Lezennes is in all likelihood a phalanx of a marine reptile. Among Late Cretaceous marine reptiles, plesiosaurs have proportionally much shorter phalanges. In mosasaurs, the phalanges are elongate but more hourglass-shaped than the specimen from Lezennes. The greatest resemblances seem to be with phalanges of marine turtles, which show a comparable degree of elongation and proximal and distal expansion. Incidentally, a turtle shell is known from the Lezennes Chalk.

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### Biotic recovery in the aftermath of the Late Permian mass extinction event: new data from the oceanic seamounts of SW Japan

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The Permian–Triassic interval witnessed the most severe mass extinction of the Phanerozoic. Despite its significance for the evolution of the marine biosphere, the subsequent recovery has attracted relatively little research effort. Recent work has demonstrated that the most rapid post-Permian recovery occurred in shallow, seamount



settings of Neotethys (Twitchett *et al.*, 2004, *Geology*, v. 32, pp. 805–808). Is rapid recovery typical of all Early Triassic seamounts, or only those in Neotethys?

To address this question we undertook palaeoecological analyses of limestones of the Lower-Middle Triassic Taho Formation of SW Japan, which were deposited in an oceanic seamount setting in Panthalassa. The fauna comprises gastropods, bivalves, brachiopods, echinoderms, foraminifera, ostracods and serpulids. Firstly, the abundance of the different taxa, from thin sections and acetate peels, was assessed. Secondly, the palaeoecological parameters of dominance, evenness and diversity were calculated.

From the Griesbachian to the Anisian, dominance decreases slightly (from 1.0 to 0.8) as diversity increases (from 0.4 to 1.0). This contrasts with results from a shallow seamount in Neotethys, where high diversity and low dominance assemblages occur in the middle and late Griesbachian. The Taho Formation seamount limestones show no rapid recovery in the Griesbachian, but, instead, much slower recovery typical of shelf settings worldwide (*e.g.* western USA, northern Italy). Levels of ecological recovery recorded in the Griesbachian seamount limestones of Neotethys are not recorded in the Taho Formation limestones until the Anisian.

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### Ray-finned fishes evolution and breakup of Pangaea

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During the Late Jurassic and throughout the Cretaceous, Pangaea fragmented to northern and southern continents, which became separated by a Western arm of the Tethys Ocean. During the Cretaceous further fragmentation took place between South America and Africa to form the South Atlantic, and inland seas were beginning to form in North America and in North Africa. These geological events may have had great significance on fish evolution by allowing more available coastline with increased habitat diversification to be colonised. The fragmentation of land masses also isolated freshwater basins from each other, with their contained fish assemblages. It is usual in vicariance biogeography studies to look at terrestrial and freshwater organisms because it is thought that their distributions are more closely constrained and more easily definable. However, it is equally true that the distributions of most marine coastal fishes are also tightly constrained either by substrate or temperatures, or both.

In this study we test the congruence between the phylogenetic splitting of seven clades of ray-finned fishes—pycnodontiforms, vidalamins, osteoglossomorphs, aspidorhynchiforms, ichthyodectiforms, paraclupeids, chanoids—with the fragmentation of Pangaea. The pattern of form (phylogeny) matches the pattern of space for most of the clades, suggesting a causal relationship, but there are discrepancies between phylogenetic and fragmentation of geographical areas for a few clades and for two geographical areas. The discrepancies can be explained by the dispersal ability and/or ecological differences of the fishes, or by poorly determined phylogenies or depauperate taxon sampling.

We discuss the results in the light of Hunn and Upchurch's chronobiogeographical paradigm (2001).

HUNN, C.G. and UPCHURCH, P. 2001. The importance of time/space in diagnosing the causality of phylogenetic events: towards a “chronobiogeographical” paradigm. *Systematic biology*, 50, 391–407.



### Tunnelling trilobites in Middle Ordovician *Thalassinoides*

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Articulated *Asaphus* (*A.*) *raniceps* body fossils are preserved within *Thalassinoides* branching burrow networks across an extensively exposed bedding surface of the Llanvirn Orthoceras Limestone in Jämtland, Sweden. Facultative tunnelling behaviour is interpreted for these trilobites, previously thought to be surficial dwellers. Diagenetic segregation of carbonate has enhanced burrows into a nodular semirelief 2D tier at a heterolithic limestone–black shale junction. Burrow interconnections are Y–T shaped, expanded at turning chambers. The diagenetic environment suggests originally shallow burrows where firmground transition layer carbonate mud enabled these trilobites to construct open domichnia. Vertical connection pipes to the palaeo-seafloor are not preserved so that depth of burrowing is unknown, and any original tiered 3D boxwork architecture, as reported for some early Palaeozoic *Thalassinoides*, is masked by the diagenetic nature of limestone beds. What was the advantage of an infaunal ethology to trilobites that were predators or scavengers? Tunnel networks would have provided protection from large carnivorous cephalopods at the top of the Ordovician food chain, while tunnel hydrodynamics likely aided breathing by drawing generally tranquil bottom waters across gill branches. The overlying black shale is the only physical evidence for the kill event, possibly anoxia, leading to preservation of the trilobites *in situ*. The intimate association of trilobites in *Thalassinoides* identifies this burrow geometry in the early Palaeozoic as arthropod prior to the decapod crustacean fossil record from the Devonian.

### A new genus of tetrapod from the Devonian of East Greenland

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A new genus and species of Devonian tetrapod has been identified from material collected in 1947 from the southern slope of Celsius Bjerg, Ymer Ø, East Greenland. The specimen preserves both lower jaws, partial palate, premaxillae and maxillae, with a natural mould of parts of the shoulder girdle. The new taxon shows many differences from both *Acanthostega* and *Ichthyostega*, though shows a closer resemblance to the latter. The dentition of *Ichthyostega* has also been reassessed in the light of fresh studies. Differences from *Ichthyostega* are most clearly seen in the dentition: tooth shape, number and proportions differ from that genus on all tooth-bearing bones. It also differs from *Ichthyostega* in skull ornamentation and lateral line expression. A cladistic analysis using characters of the palate, marginal bones, lower jaws and dentition shows that the specimen nests immediately below *Ichthyostega*, but above other Devonian tetrapods. Early and Late Carboniferous tetrapods stack robustly



above these and suggest progressive modifications to the lower jaw associated with changes to feeding modes. Nine sites yielding Famennian tetrapods have now been recognised worldwide, producing a complement of at least 17 separate tetrapod taxa.

### Mid-Miocene latitudinal environmental gradient in western Europe: mammals and vegetation compared

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The middle Miocene (16 to 11 My) is a key period in the Cenozoic climatic evolution. It represents the last warmest episode of the Tertiary (Miocene Climatic Optimum) in a general cooling trend and development of major permanent Antarctic ice sheets (Zachos *et al.*, 2001). In this context, terrestrial ecosystems evolved towards their present-day structure. We investigated how the western European middle Miocene vegetation and mammalian communities responded to this climatic evolution. We found that southwestern Europe (south and central Spain) was dominated by very arid environments and that progressively more closed and humid conditions were encountered going northward. The pollen grain contents of mega-mesothermic plants with higher water requirements increase and the mammalian communities body weight distributions progressively change from sub-desertic to closed and humid environments from central Spain to northeastern Germany. Thus a strong latitudinal environmental gradient already existed by mid-Miocene times and probably finds explanations in the global climatic and tectonic events that took place during this time-period.

### The apparatus architecture of the prioniodinid conodont *Erismodus quadridactylus* (Stauffer) and its implications

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Of the three major orders of denticulate conodont, the Prioniodontida, the Prioniodinida and the Ozarkodinida, there is an abundance of architectural data available for the feeding apparatuses of prioniodontid and ozarkodinid conodonts. Conversely, the apparatus composition and architecture of prioniodinid conodonts is poorly understood due to the shortage of assemblage data. The apparatuses of prioniodinid conodonts generally comprise very fluid element shapes, making it difficult to reconstruct apparatus plans from discrete element collections.

An excellently preserved natural assemblage of the prioniodinid conodont *Erismodus quadridactylus* (Stauffer), found in core borehole rock in North Dakota, USA, offers some significant insights into the apparatus architecture of the genus *Erismodus*. In particular, the assemblage allows specific element morphotypes to be assigned to a fixed position within a constrained architectural template. The assemblage also reveals that certain element morphotypes, traditionally considered to reside within the main

ramiform basket, lie elsewhere within the apparatus. Hence, this material allows for a near complete apparatus architecture to be constructed that is representative of basal prioniodinid conodonts. In addition the assemblage data provides a focal point for phylogenetic analysis of prioniodontid and prioniodinid relationships, and an insight into the evolution and diversity of conodont feeding mechanisms.

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### Validating fossil bacteria: some cautionary tales from the Mid-Palaeozoic

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Bacteria are very small, monotonously simple morphologically and very abundant throughout the biosphere. They may facilitate fossilization—but more frequently prevent it, e.g. destroying soft parts of plants and animals. Their own record is appalling, and its authenticity controversial. Just how does one identify a fossil bacterium? Spheres, rods and filaments of prokaryotic dimensions present on Silurian and Lower Devonian fossils offered the opportunity, courtesy of the NERC, to address this problem. We used SEM and TEM with elemental analyses, combined with experiments involving exposing fossil spores to an extant bacterial cocktail. We discovered that minerals, both naturally occurring and synthesised during extraction, are remarkably good at simulating coccoid and rod-shaped bacteria, even to the extent of producing tracks on spores. To our mortification, some mimicked tapetal residues associated with spore development. Biofilms contained more promising candidates for bacterial status, but when they first colonised the ‘fossils’ remains conjectural. Storage in hydrochloric acid immediately after collection was employed to avoid recent contamination, but water may have been seeping through those rocks for millions of years. These uncertainties have some relevance to those who seek to validate extra-terrestrial life. We, who now more fully appreciate what confronts them, wish them luck!

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### A new test of the role of CO<sub>2</sub> in the late Ordovician glaciation

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Glaciation in the late Ordovician caused the second largest mass extinction in the Phanerozoic, with 26% of families made extinct. It is thought that atmospheric CO<sub>2</sub>, a major control of climate, was very high during the Ordovician. There are currently two hypotheses vying to explain how such extensive glaciers formed under these conditions.

The productivity hypothesis suggests that increased phytoplankton growth drew down CO<sub>2</sub> during the Ordovician, leading to cooling. The weathering hypothesis suggests that after a lesser drop in CO<sub>2</sub>, caused by silicate weathering, CO<sub>2</sub> rose as the land was covered in ice, but that the increase in albedo was enough to maintain the cold temperatures. However, a deadlock remains due to the lack of proxy measures of CO<sub>2</sub> over this period.

Based on laboratory growth experiments, we report that the stable carbon isotope

composition of mosses and liverworts is very sensitive to atmospheric CO<sub>2</sub> levels. This finding indicates that fossil remains of Ordovician land plants can offer a means of reconstructing past CO<sub>2</sub> levels, with the exciting potential of resolving the role of CO<sub>2</sub> in the glacial event. Preliminary isotopic analysis of Ordovician mesofossils using an ion-microprobe mass spectrometer indicates high (10 x present) CO<sub>2</sub> levels before the glaciation when calibrated against modern plants.

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### Neogene climates near the South Pole: evidence from fossil plants and climate-vegetation models

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Since the initiation of glaciation in the early Oligocene the Antarctic ice sheets have been an important driver of our global oceanic and atmospheric systems. The ice sheets have been considered as inherently stable, keeping Antarctica in a state of deep freeze. However, the discovery of fossil plants and insects interbedded with glacial tillites of the Sirius Group at 85°S indicates that the climate must have warmed dramatically during the Neogene and caused the ice sheets to retreat. New fossil discoveries indicate that tundra vegetation of *in situ* dwarf beeches, cushion plants and moss, with beetles and molluscs, colonised periglacial landscapes only 300 miles from the South Pole. Palaeoclimatic analysis of the fossils suggests that the mean annual temperature was ~-12°C, with short Summers of temperatures up to +5°C and long freezing winters. Although the age of the Sirius Group is debated, climate-vegetation models using a global Pliocene database predict comparable tundra conditions at this locality. This implies that the Antarctic ice sheets are not stable but may respond to future climate warming more dramatically than once thought.

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### The systematic position of the Late Jurassic alleged dinosaur *Macelognathus* (Crocodylomorpha: Spheenosuchia)

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*Macelognathus vagans* was described by O.C. Marsh in 1884 on the basis of a mandibular symphysis from the Upper Jurassic Morrison Formation of Wyoming, USA.

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In the past, this taxon was often considered a dinosaur, but later was also tentatively referred to the Crocodylia. Its phylogenetic identity has until now been enigmatic and its determination was hampered by the fact that the taxon was represented only by a mandibular fragment.

Recently, some partial disarticulated skeletons, also from the Upper Jurassic Morrison Formation, but from a different locality, namely the Fruita Palaeontological Area, Colorado, have been studied and identified as sphenosuchians—an extinct sister-taxon of the Crocodyliformes (Crocodylomorpha). Two mandibles of this new material are morphologically identical with the holotype of *Macelognathus vagans*. On the basis of this new sphenosuchian material from the Fruita Paleontological Area it is possible for the first time to identify the enigmatic taxon *Macelognathus vagans* as a sphenosuchian crocodylomorph.

The new material of *Macelognathus vagans* augments our knowledge of the diversity of sphenosuchians and for the first time provides postcranial information of this taxon. In addition, the new material from the Upper Jurassic Morrison Formation of the Fruita Paleontological Area extends the known stratigraphic range of sphenosuchians and constitutes the youngest definitive occurrence of a sphenosuchian, previously known from the Late Triassic to the Middle or Late? Jurassic.

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### Plant and vertebrate fossil-lagerstätten from the Albian-Cenomanian of Charente-Maritime (Western France)

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Uppermost Albian and Lower Cenomanian limestones, sands and coaly clays were extensively deposited in the region Charente-Maritime of Western France. These fossil-lagerstätten are exposed locally at the lowermost parts of coastal cliffs and inland in sand quarries. They are of two types: (1) fossil-lagerstätten by preservation (e.g. plant beds at Puy-Puy), and (2) fossil-lagerstätten by concentration (e.g. sands bearing teeth and bones microremains at Les Renardières). They delivered very abundant and diverse palaeontological assemblages consisting of plants (leaf cuticles and wood of ferns, conifers, cycads and angiosperms), and vertebrates (bones and teeth of selachians, actinopterygians, turtles, crocodiles, snakes, pterosaurs, dinosaurs and mammals). From the palaeoenvironmental point of view, these settings represent transgressive deposits formed in an internal estuary and coastal lakes or lagoons, which were more or less continental (freshwater) or marine influenced. Interestingly, plants and vertebrates share palaeogeographical affinities with North America and North Africa.

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### The evergreen or deciduous habit of Cretaceous polar forests: Fossil data versus computer model predictions

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During the Cretaceous the polar regions were covered with dark dense forests. These forests would have significantly modified the climate both on polar and global scales, due to their low albedo and their effect on the land-surface heat budget and the hydrological cycle. The deciduous or evergreen habit of the conifers and the length of time they held their leaves would have played an important part in this feedback.

This project involves determination of the distribution of ancient polar forests and their deciduous or evergreen habit, to obtain data to be input into computer climate models. In previous studies the leaf habit of these trees has been determined by Nearest Living Relative analysis, a method that assumes the trees had the same leaf habit in the past as now. In this study, a new technique that quantitatively characterises the cell patterns within growth rings in fossil wood is used to determine how long the trees kept their leaves.

Analysis of Cretaceous fossil wood from the Arctic (Canadian Arctic and Svalbard) and the southern polar regions (Antarctica and Australia) indicates that the forests were composed of a mixture of both deciduous (e.g. *Laricioxylon*) and evergreen (e.g. *Protocedroxylon*, *Juniperoxylon*, *Piceoxylon*, *Araucariopitys*, *Cedroxylon*, *Glyptostroboxylon*, *Xenoxylon*) conifers in the northern polar regions but only evergreen conifers in southern high latitudes (e.g. *Podocarpoxylon*). The climate-vegetation models predict mixed deciduous and evergreen forests at both poles, which matches the fossil evidence for the north but not the southern polar region.

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### Pollen abundance patterns: Neocological insights for palaeoecology?

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Pollen grains are usually counted in discrete samples of ≈300 specimens which, allowing for taphonomic filtering, provide proxy data on both parent floral composition and taxonomic diversity. However, there are no taxonomically independent (i.e. neutral) ways to determine environment and climate based on pollen data. I present an attempt to extract information from the modern pollen record that ignores the assumed systematic affinity of the pollen grains. My approach centres on the abundance distribution of pollen grains within counted samples. I posit that the abundance distributions will reflect plant community (biome) characteristics and especially pollination syndromes; samples should have increasing equitability with increasing latitude. The data set is constructed from 48 eastern North American localities which are isotaphonomically sampled along a latitudinal transect from the subtropics to the tundra. Pollen composition, taxonomic richness and pollen co-occurrence patterns change significantly between biomes. Evenness metrics (including Hurlbert's PIE) indicate that equitability shows only minor changes from one biome to another—all localities have positively skewed, leptokurtic abundance patterns and conform to a truncated log-normal distribution. Hence, sampled pollen equitability can not determine parent communities and has few, if any, predictive powers.



## A null biogeographic model for quantifying the role of dispersal in shaping taxonomic richness and similarity patterns

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Diversity patterns in the fossil record are often interpreted as functions of only origination and extinction, while taxonomic dispersal among regions is rarely considered. We present a null biogeographic model of global diversity, that calculates taxonomic richness (S) and similarity (J), as measured by the Jaccard Coefficient. The model contains three regions, each initially containing a unique set of taxa. At each time step, each taxon is randomly allowed to go extinct, create a new taxon, disperse or remain unchanged. At the end of each time step, global S and mean global J are calculated. The probabilities for origination and extinction are set to be equal and the model was run with origination/extinction and dispersal probabilities that spanned over four orders of magnitude.

The model has two significant results. (1) If the probability of dispersal is sufficiently large relative to origination/extinction, regional and global richness increase exponentially. For non-negligible probabilities of origination, the combined effect of dispersal and origination exceeds the effect of extinction, causing the exponential increase in diversity. (2) If richness increases, global mean J will reach equilibrium ( $J_{eq}$ ). When plotted against the ratio of dispersal probability to origination/extinction probability,  $J_{eq}$  follows a sigmoidal curve.

This null biogeographic model is useful for predicting dispersal probabilities in the fossil record when origination and extinction probabilities are known. Taxonomic dispersal among regions has the potential to play a significant role in shaping diversity trends, and should be considered when analysing Phanerozoic diversity trends.

## Might machaeridians be molluscs?

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Machaeridians were elongate, slug- or worm-like organisms with an external skeleton of imbricating calcite plates (sclerites). Known only from Palaeozoic marine environments, three groups are recognized—plumulitids, turrilepadids and lepidocoleids—but their zoological affinities are enigmatic. Withers (1926) recognized that they formed a monophyletic group, but was uncertain of their systematic position. He did note similarities between the optical properties of machaeridian sclerites and echinoderm ossicles, leading many later workers to interpret machaeridians as aberrant members of the Echinodermata. However, Bengtson (1978) showed this to be erroneous, and subsequent studies have suggested variously that machaeridians are most closely related to arthropods, annelids or molluscs. Using specimens from the Much Wenlock Limestone Formation (Silurian) of England, new information is presented here that indicates machaeridians are molluscs, probably the sister-group of Polyplacophora + Conchifera.



BENGTSON, S. 1978. The Machaeridia – a square peg in a pentagonal hole.

*Thalassia Jugoslavica*, 12, 1–10.

WITHERS, T. H. 1926. *Catalogue of the Machaeridia (Turrilepas and its allies) in the Department of Geology*. British Museum (Natural History), London, XV+99 pp.

## Echinoderm Palaeoecology from fragments: reconstructing salinity and substrate controlled faunas in the British Middle Jurassic

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Research using bulk sampled sediments (of typically 10–40kg) from across the British Middle Jurassic (Bathonian), where the full spectrum of marine and marginal marine environments are represented, has demonstrated a distinct ecological zonation pattern in the crinoid groups characterised by at least two genera.

This research has been taken a stage further with its application to three more echinoderm groups (echinoids, asteroids and ophiuroids). Previously it was noted that lack of homology in the ossicles made identification beyond family level problematic; however, examination of complete specimens in museum collections has allowed the recognition of diagnostic ossicles that can identify tests, spines and marginal plates to generic level.

Results indicate a marked facies control on the distribution of groups influenced by factors including substrate and salinity. Groups such as echinoids inhabit ecosystems defined by facies belts; for example, *Hemipedina* inhabits normal marine settings, *Hemicidaris* is found in open shelf areas and *Acrosalenia* is found in lagoonal and restricted conditions. Such results are also mirrored in the asteroid and ophiuroid data.

This new data, combined with the previous findings on crinoid groups, has allowed the construction of a model for echinoderm palaeoecology across marginal marine environments. The application of this model to marine environments outside the British Jurassic, such as the Middle Jurassic of France and the Western interior, USA, has demonstrated that factors such as substrate and marine connection have a greater bias than geographical and stratigraphic controls.

## Early eukaryotes in Paleoproterozoic and Mesoproterozoic oceans

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Biomarker molecular fossils in 2770 Ma shales suggest that the Eucarya diverged from other principal domains early in Earth history. Nonetheless, at present, the oldest fossils



that can be assigned to an extant eukaryotic clade are filamentous red algae preserved in *ca.* 1200 Ma cherts from Arctic Canada. Between these records lies a rich assortment of potentially protistan microfossils. New microscopic study of late Paleoproterozoic shales from China (1800–1625 Ma Chuanlinggou Formation) and Australia (1650 Ma Mallapunyah Fm) permits the significant extension of the stratigraphic range of fossil evidence for early eukaryotes. Combined light microscopy, scanning electron microscopy, and transmission electron microscopy on fossils from the 1500–1400 Ma Roper Group, Australia, and broadly coeval rocks from China show that these intermediate assemblages do indeed include a moderate diversity of eukaryotic remains, although the observed diversity remains well below Neoproterozoic levels. In particular, preserved cell wall ultrastructure, observed using transmission electron microscopy (TEM), can help to bridge the current stratigraphic gap between the unambiguous eukaryotic morphologies of mid-Proterozoic assemblages and molecular biomarkers in much older rocks. Ongoing microchemical analyses (Micro-FTIR spectroscopy, Laser micro-Raman spectroscopy and Laser micro-pyrolysis-GC/MS) of individual microfossil walls may help us to place firmer constraints on phylogenetic interpretation.

### Homology, shape and morphometric analysis of the conodont skeleton

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Conodonts possess an exceptionally good fossil record and occupy a key phylogenetic position within the vertebrate clade. Consequently, they represent an invaluable tool for understanding both evolutionary patterns and the acquisition of vertebrate characters. Correct identification of homology is vital in exploiting this potential. However, as with most vertebrates, conodonts are rarely preserved as articulated skeletons, where homology can be determined directly from topological relationships. Traditionally homology has therefore been identified exclusively through qualitative description of the morphology of disarticulated elements. Yet hypotheses of homology based on articulated skeletons may contradict those derived from the morphology of isolated elements alone. Here, quantitative morphometric analysis of both skeletons and isolated elements is used to determine rigorously whether element morphology is an accurate guide to element homology.

### A new Upper Permian flora from the Middle East with typical Triassic Gondwana elements

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Several species of *Dicroidium* are described from the Um Irna Formation (Upper Permian) of the Dead Sea region, Jordan. Plant remains are preserved as compressions with excellent cuticles. It is the earliest unequivocal record of *Dicroidium*, a genus that is typical for the Triassic of Gondwana and the northernmost occurrence of this genus that apparently originated in the Late Permian in the palaeotropics. Middle and Late Permian floras from the Arabian Peninsula show a remarkable mixture of elements from different floral provinces, *i.e.* Euramerica, Cathaysia and Gondwana. The climatic amelioration that has been reported for the Early Triassic of the Gondwana apparently enabled *Dicroidium* to migrate southward and finally colonize the entire Gondwana region. *Dicroidium* is one of the very few megaplant genera that was not affected by the biotic crisis at the Permian-Triassic transition.

### Discovery of Famennian and Early Carboniferous trilobite larvae: implications for the systematics and the evolutionary history of proetoids

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New silicified material from the Middle Famennian of Morocco, the Late Famennian of Germany, and the Early Carboniferous of France substantially increase our knowledge of proetoid larvae. Both anaprotaspides and metaprotaspides illustrate that proetoid trilobites possess a unique early ontogeny, remaining highly conservative from the Ordovician to the Early Carboniferous. Accordingly, they support the view that Proetida may be composed of two different clades. The new data also enable the evolution of anaprotaspis size in proetoids from the Ordovician to the Lower Carboniferous to be broadly depicted. In particular, two marked increases of larval sizes are recognised. The first one may have occurred around the Silurian/Devonian boundary, but its potential implication on proetoid evolutionary history is unknown. On the other hand, the substantial sizes reached by Late Famennian and Early Carboniferous anaprotaspides suggest the acquisition of an extended planktonic period in the early ontogeny of proetoids. The possible implications of this developmental strategy on the survivorship of these trilobites during the end Devonian Hangenberg biocrisis or, alternatively, on the colonization of deep water benthic habitats, are discussed.

### Towards the development of a Palaeo UV-B proxy from fossil land plants

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Changes in atmospheric oxygen, major volcanic eruptions and impact events have the potential to induce short- and long-term changes to the stratospheric ozone layer. However, detecting the interaction between these events and the expected increase in terrestrial UV-B flux has proved elusive.



Recent laboratory investigations suggest that the spores and pollen of land plants may respond to variations in the UV-B radiation by increasing investment in UV-B screening pigments. However, it is not known if this response is replicated in natural settings. Here, we report an increase in UV-B protecting pigments from the spores of plants growing in South Georgia (54° 20'S, 36° 40'W) and exposed to a progressive thinning of the Antarctic ozone hole since the 1950s. Our data records a strong three fold linear increase in the concentration of UV-B protecting pigments of *Lycopodium magellanicum* spores in response to a 14% thinning of the ozone column.

Our results were obtained using high temperature FTIR analysis of sporopollenin, a decay-resistant biomacromolecule readily preserved in the fossil record. Therefore, this newly identified response of extant plants to modern day climate change offers the exciting possibility for the development of a potential tool to investigate palaeo changes in stratospheric ozone layer and UV-B flux.

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### The first Danish dinosaur footprints!

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Remains of dinosaurs from Denmark have hitherto consisted of two teeth, one complete dromaeosaur tooth, and a toothcrown with possible Titanosaurid affinities. Both teeth are of Lower Cretaceous (Berriasian/Ryazanian) age and found on the Baltic island Bornholm. In May 2004 two large sauropod footprints and a smaller, possibly thyreophorean footprint were found in the Middle Jurassic (Tithonian/Bathonian) Bagå Formation, which is exposed on the north-west coast of Bornholm in the Hasle Klinkefabrik clay pit. The sauropod tracks are pes imprints, 70 cm long and 45 cm wide, pentadactyl, with the impressions of digits I-III being the most prominent. The small track is 25 cm long and 19.5 cm wide, pentadactyl, with short clawed digits and symmetrical along the length axis. The Bagå Formation consists of alternating layers of clay and coal with thick cemented fluvial sandstone beds. During quarrying for clay, the hard sandstone beds were broken up and dumped on the beach in front of the clay pit. Palynological investigations of clay preserved between the footprint casts will determine the exact stratigraphic position of the blocks. These are the first dinosaur footprints found in Denmark, and the first sauropod footprints recorded from the Scandinavian area.

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### Nitrogen and carbon isotopes in conodonts: Evidence of trophic levels and nutrient flux in Palaeozoic oceans

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Animals fractionate nitrogen and organic carbon isotopes during food digestion and preferentially excrete the lighter isotopes. New body tissues subsequently grown become about +3.4‰ more positive in  $\delta^{15}\text{N}$  than their food and about +1‰ more enriched in  $\delta^{13}\text{C}$ . This simple relationship between consumer and food means that the trophic level of organisms within the same ecosystem can be distinguished on the basis of their isotopic signature. This technique has been successfully applied to modelling trophic structure in present day and Neogene vertebrate ecosystems. But could original nitrogen and carbon isotopic ratios be preserved in much older fossil material?

Here we present the results of an initial attempt to investigate community structure in biotas where organisms are not only extinct but have no clear modern analogues. Conodont platform elements from two species, *Gnathodus bilineatus* and *Gnathodus girtyi*, display consistent and significantly different  $\delta^{15}\text{N}$  and organic  $\delta^{13}\text{C}$  signatures within the same sample. This isotopic discrepancy is consistent with data from modern marine organisms feeding at different trophic levels in the same ecosystem. These results not only extend the range of the nitrogen and carbon technique back a further 250 Ma than any previous studies, but they also raise the possibility of using fossil groups such as conodonts as tracers of nutrient flux in Palaeozoic oceans.

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### The evidence for and implications of an invertebrate diet in Jurassic pliosaurs (Reptilia: Sauropterygia)

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The Callovian pliosaurs found in the Peterborough Member of the Oxford Clay Formation are relatively poorly understood. New reconstructions of the key taxa *Peloneustes*, *Liopleurodon* and *Simolestes* show divergent cranial, mandibular and dental specialisations. The cranial morphology of *Peloneustes* is elongate, narrow and low; in *Liopleurodon* the skull is shorter and wider, but still relatively depressed; but in *Simolestes* the cranium is short, and exceptionally wide and deep. Comparison to modern analogues indicates diet varied between the pliosaurian taxa, with *Peloneustes* a piscivore, *Liopleurodon* a predator on large hard-boned prey (thus confirming previous suggestions), but that *Simolestes* should be reinterpreted as predominantly consuming invertebrates, probably cephalopods. However, the consumption of invertebrates, which impart a high salt load on the consumer, has important physiological implications for reptiles, which are unable to produce urine stronger than the blood plasma; indeed it has been suggested that life in water is impossible for reptiles that cannot solve the problem of salt. It is therefore suggested that large salt-secreting glands were present in *Simolestes* due to its predominantly invertebrate diet, and present but smaller in other pliosaur genera. Due to the close packing of the tooth bases ('roots') and other organs in the skull, the salt glands of pliosaurs were probably located within the orbits, as seen in modern marine turtles.





## Graptogonophores, scopulae and *Dawsonia*: putative reproductive organs reconsidered

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Putatively vesicular structures on graptolites, for example scopulae, tend to attract interest and debate. For most of the nineteenth century scopulae were considered to be reproductive organs, similar to those of modern hydrozoans, and termed graptogonophores. Despite the increasing acceptance of a hemichordate affinity for graptolites in the twentieth century, the proposed reproductive function remained largely unchallenged, and latterly overlooked. Similarly, disarticulated sclerites from the problematic fossil *Dawsonia* have been regarded as scopulae broken from graptolites.

This work reassesses these structures: morphometric analysis demonstrates that the similarity between scopulae and *Dawsonia* is superficial. Moreover, comparison with isolated graptolites and vesicular graptolitic tissues shows that scopulae are best considered to be two-dimensional paddle-like appendages. Their two-dimensional nature indicates their function is more likely hydrodynamic than reproductive, leaving the term graptogonophore obsolete. Scopulae are only known in biserial graptolites but have arisen independently on several occasions, though in each instance their fossil occurrence is extremely rare. This may be consistent with modification to inhabit an infrequent and probably marginal habitat.

## Terrestrial Gastropods and the Perils of Palaeoclimate Studies, or When Size Does Matter (sample size that is)!

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Terrestrial gastropods have been widely used to investigate palaeoclimates by measuring the stable isotope signals of  $\delta^{18}\text{O}$  Oxygen and  $\delta^{13}\text{C}$  Carbon bound up within the shell carbonate. These signals can act as proxies for the local precipitation and/or relative humidity and the vegetation from which the snail obtained its moisture and food, and thus can be used to infer the wider climate at the time of shell formation. Results will be presented to illustrate that all land snail shells are not equal; some shells demonstrate wide within-shell variation, and within-species variation is just as great. It will be shown that inadequate homogenization of the shell or measurement of only part of a shell could lead to highly erroneous conclusions. Even where homogenization is possible, the large intraspecific variation found in Canarian land snail shells requires that researchers ensure a sufficiently large sample size that takes into account the natural variation present.



## The « Avins event », a remarkable highstand at the end of the Tournaisian. Its influence on the global distribution and on the evolution of the Viséan rugose corals

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On the Namur-Dinant Basin platform (Belgium, north France), the top of the highstand system tract of the third-order sequence 4 corresponds to the Avins Member, a little lower than the Tournaisian-Viséan boundary, which is situated in the lower part of the transgressive system tract of the sequence 5. The Avins Member is characterized by the appearance, among others, of *Palaeosmia*, *Merlewoodia*, and *Amygdalophyllum*, which mark the base of the RC4b Subzone, and are the stock for typical Viséan genera and species.

It is remarkable that the Avins level can be traced throughout Eurasia, and as far as Australia. In some areas, the corresponding levels rest directly on an old basement and are the oldest Lower Carboniferous rocks recorded.

Such a very widespread coral assemblage is unusual for the Dinantian, during which most coral faunas are endemic, and shows that good connections between distant areas existed, confirming the very high sea level determined by sedimentological studies. The “Avins event” is followed by a strong fall in the sea level during which the common stock of corals gave rise by separate evolutions to endemic Lower Viséan coral assemblages, with basins becoming more or less isolated. The correlations between high-stand—widespread of fauna, and low-stand—endemism and evolution, can be extended to other radiations of corals during the Carboniferous.

## Age assessment of Pleistocene and Holocene mammal bones

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Palaeoenvironment, ecology and climate development reconstructions based on mammal bones need a palaeostratigraphic classification of the fossils. Too often this is not the case, especially with fossils from river currents out of highly reworked sediments.

A case study of about 5,000 mammal bones from a sandpit of a bayou of the River Ems, Münsterland, Germany, will help getting closer to that problem.

By the determination of archaeological troves from the mentioned sandpit the age of the fossils ranges from the Middle Palaeolithic up to the present day.

Because of their varying colours 16 different colour groups have been distinguished. Element analyses by REM indicate a possible influence of element inclusions on discolouration.

To look for more factors which could give a hint for the bones' age, thin sections have been investigated in terms of possible histological patterns.

Afterwards the age of the bones within the different colour groups was determined applying Amino-Acid-Racemization to check out a synchrony within the groups. If in fact the colour, microstructure or element-inclusions depend on the age of the bones, this would be a great tool for an easy age classification of fossils from one and the same location by only measuring the age of a few of the bones.

## On convergent evolution in Nummulitidae with secondary chamberlets (Foraminiferida)

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Recently molecular data have shown that extant nummulitid genera with secondary chamberlets are more closely related to *Operculina* than to each other. We discuss the palaeontological occurrence of nummulitids with secondary chamberlets and the implications for their phylogeny.

For the generic classification of Nummulitidae with secondary chamberlets we used the following characters:

1. Characters of the stolon system.
2. The presence and shape of secondary chamberlets in the first chambers.
3. The presence of lateral chamberlets (l.c.) and/or cubicalae. Cubicalae are shown to evolve into lateral chamberlets, with some specimens possessing cubicalae in the early whorls and l.c. in the latter.
4. The type of coiling (involute, maturo-evolute and evolute is regarded as less important. Not only is it not possible to use these characters in juveniles, but the presence of maturo-evolute specimens (*Heterostegina* cf. *depressa* of Tan Sin Hok, 1932) as intermediates between the *praecursor*-group and *Vlerkina* shows that this character state evolved more than once.
5. Additional characters can be found in the shape of the chamberlets (very narrow to as high as broad), the angle between the secondary and primary septa (rectangular vs. sharp angle).

Based on these characters we propose a simplified nomenclature for the groups included. *Heterostegina praecursor* and *H. bantamensis* will be included in *Cycloclypeus*, whilst *Tansinhokella* includes all Eocene species with lateral chamberlets or cubicalae and *Spiroclypeus* will include the Oligo-Miocene species.

## Influence of seawater saturation state on the Phanerozoic diversity of calcified marine algae and invertebrates

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Calcification in many marine algae and invertebrates is biologically induced rather than controlled. It can therefore be expected that secular variation in seawater saturation state for CaCO<sub>3</sub> minerals should have influenced the long-term history of organisms that biologically induce, rather than closely control, their calcification. Comparison of calculated seawater saturation state with patterns of marine calcified organisms during the Phanerozoic Eon suggests that the diversity of organisms with biologically induced calcification, such as chlorophytes, corals and sponges, increased during periods of

elevated saturation state and declined when saturation state was reduced. In contrast, organisms with relatively controlled calcification, such as molluscs, brachiopods, bryozoans, and echinoderms, appear to have been relatively unaffected by saturation state. This indicates that CaCO<sub>3</sub> availability—governed by saturation state—has significantly influenced the diversity of organisms with biologically induced calcification. This effect involves many tropical marine algae and invertebrates, especially those that are most involved in reef building. Thus, despite its apparent abundance, CaCO<sub>3</sub> has been so widely employed in biomineralization by aquatic organisms during the past ~550 million years that it has constituted a limiting resource, partitioned between organisms that biologically control and biologically induce their calcification, with the surplus being inorganically precipitated.

## Inside the inside of a dendroid

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*Desmograptus micronematodes* Spencer, from the lower dendroid bed at Thornton quarry, Cook Co., Illinois, USA (middle Wenlock or lundgreni Biozone) is remarkably preserved in relief, outlined in pyrite. The internal details of the thecae, and of the stolon system, examined using the SEM, enabled us to reconstruct the growth of a stipe. Autothecae have a proximal portion, the stolotheca, partially within the parent autotheca, containing a stolon; a central portion which has a branching node of the stolon succeeded by the internal portions of its daughter autotheca and bitheca; and a distal portion which is an open cup. The stolons and stolon nodes are formed of a dense crassal fabric, and are surrounded by a loose fabric of three-dimensional fibrils. The nodes have a complex structure of three boxes with proximal and distal nozzles. The base of a bitheca, and the base of each autothecal cup, has a central nozzle surrounded by a unique honeycomb fabric. Cortical and fusellar fibrils bear a surface structure of spiral ridges.

## A Silurian sea spider

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The Herefordshire (Silurian) Konservat-Lagerstätte in England yields remarkable, three-dimensional, non-biomineralized fossils in carbonate concretions hosted in a volcanoclastic deposit. Pycnogonids (sea spiders) have an extremely sparse fossil record, and are known globally from just four species based on a few tens of specimens from



two localities. A new, exceptionally-preserved sea spider from the Herefordshire deposit represents the oldest known adult by some 35 million years, the most completely known fossil species, and provides new insight into the early morphology of the Pycnogonida and its relationship to other arthropod groups. Cladistic analyses place the new species near the base of the pycnogonid crown group, implying that the latter had arisen by the Silurian. The morphology of this recently discovered form has been digitally reconstructed to produce a 'virtual fossil' in the round.

### Functional and Adaptive Implications of Cryptic Speciation In Planktic Foraminifera

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Cryptic species (genetically isolated and ecologically disparate sibling taxa) are seemingly common in the marine plankton, and both molecular clock and palaeontological methods suggest that some, if not many, of these diverged many millions of years ago. We have morphometrically analysed over 2,000 specimens of the common planktic foraminifers *Globigerinella siphonifera* and *Globigerinoides ruber*, extracted from well-dated ODP cores at two tropical sites (926A (Atlantic) and 806 (Pacific)). In both forms, DNA methods suggest the occurrence of deep (7–11 Ma) diverging cryptic species complexes and strong evidence of ecological specialisation—but with minimal concomitant morphological change. Our morphometric dataset (based on a suite of characteristics ranging from ultrastructural assays to multivariate analysis of whole-test form) suggests that the *Gl. siphonifera* sub-types are resolvable as fossils if the correct characters are extracted, but cryptic species of *Gs. ruber* appear to be almost entirely resistant to morphological division. In both cases, morphometric and/or molecular clock methods imply the long-term coexistence of ecologically discrete, but morphologically near-identical, reproductively isolated species. From a functional viewpoint, this finding is ambiguous; either very strong stabilising selection is acting to constrain morphological evolution (suggesting the adaptive primacy of test form), or the locus of selection is centred on other characters (implying that test form is of little or no adaptive significance). Resolving this paradox is of prime evolutionary importance, certainly amongst foraminifers, and potentially throughout the pelagic realm.

### Functional morphology and light-gathering ability of podocopid ostracod eye

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Optical features of lateral ocelli of the ostracod eye were examined in 29 species of the Podocopida using a theoretical morphological model. A cuticle lens–tapetum model was introduced for this purpose. The ray-tracing was simulated in each model, to assess light-gathering abilities of various forms of the eyes. The results of computer simulations and morphospace analyses indicate that the light-gathering ability is



dominantly affected by thickness and curvature of outer surface of the lens. On the basis of a combination of form and light-gathering ability, four categories were recognised in the podocopid eye. The results of the phototactic experiment were concordant with estimated scores on the light-gathering ability using the theoretical model. The present study also indicates that the light-gathering ability is related to development of surface ornamentation on the valve.

### Evolution of polymorphism in colonial animals: differentiation of the earliest avicularian polymorphs in the Cretaceous cheilostome bryozoan *Wilbertopora*

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In many colonial animals particular zooids perform different functions. This is usually reflected in their morphology, resulting in polymorphism. Darwin, during the voyage of the *Beagle*, observed the behaviour of non-feeding polymorphs called avicularia in cheilostome bryozoans. Avicularia are zooids with opercula enlarged to form mandibles or setae that are capable of functioning in defence and cleaning or, in rare instances, acting as locomotory appendages. Occurring in the majority of Recent and fossil cheilostomes, avicularia make their first appearance in the fossil record in the Cretaceous genus *Wilbertopora*. Scanning electron microscopy and morphometric studies of *W. mutabilis* Cheetham, 1954, from the Albian–Cenomanian of Texas and Oklahoma, have shown that this 'species' actually comprises eight different species distinguished most readily by their avicularia. Five of these species have well-differentiated avicularia resembling those found in many younger cheilostomes. However, in *W. mutabilis* s.s. and two new species, the avicularia are so similar to autozooids that they have been overlooked in the past. A series of morphological changes inferred from a cladistic analysis of the eight *Wilbertopora* species demonstrates the progressive differentiation of increasingly advanced avicularia.

### Eurypterid phylogeny and the origin of Arachnida

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The monophyletic Palaeozoic chelicerate order Eurypterida, contains around 65 genera and is the subject of the first large-scale phylogenetic analysis of the group (201 morphological characters for the entire Chelicerata). Many eurypterids are known from fragmentary remains, and the 40 best-known genera are included in this analysis.



The analysis suggests that the two previous models that divide Eurypterida into two suborders—Pterygotina *vs.* Eurypterina (large *vs.* small chelicerae) and Eurypterina *vs.* Stylonurina (sixth appendage developed into swimming legs *vs.* walking legs)—renders one suborder paraphyletic. The suborder concept is therefore abandoned, but a number of superfamilies and families are recognised. The position of Eurypterida within Chelicerata (excluding Pantopoda) was also analysed and the result suggests Xiphosura is the most basal taxon in Chelicerata. Chasmataspidida are sister-group to Eurypterida + Arachnida. The monophyletic Arachnida has Scorpiones as its most basal taxon, followed by Haploucnemata (Solifugae + Pseudoscorpiones). The remaining higher taxa form a clade where Opiliones is basal, followed by the extinct Phalangiotarbitida, Acaromorpha (Acari + Ricinulei), Palpigradi, Anthracomartida, Araneae, the extinct Haptopoda, Amblypygi, Thelyphonida and Schizomida.

### How to get a date in the Devonian of Bolivia

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During the Mid Palaeozoic Bolivia was part of the Malvinokaffric Province, a high-latitude southern hemisphere realm that had a highly endemic marine fauna. This makes dating and correlation with Euramerica by macrofossils difficult, but microfossils have proved more useful. A succession of microplankton ‘events’ has been recorded throughout the Devonian of Bolivia that comprise short-lived monospecific pulses of distinctive marine palynomorphs. Particular emphasis in this study has been placed on the *Evittia sommeri* event, dated by cosmopolitan chitinozoan and spore taxa as latest Emsian/early Eifelian. Sedimentology shows the *E. sommeri* event is associated with a major marine transgression that, based on the earliest Mid Devonian date, can be considered the Chotěc Event. This is the first time the Chotěc Event has been identified at high palaeolatitudes and its recognition has allowed a test of the Euramerican sea-level curve. Preliminary results of the Mid/Late Devonian in Bolivia show that the sea-level curve should be regarded with caution through this interval.

### Molluscan diversity in deteriorating climate regimes: The Plio-Pleistocene of the southern North Sea Basin

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After the catastrophic surge in the delta region of SW Netherlands in February 1953 an ambitious scheme of waterworks was erected, the deltaworks. The geological research preceding many of the new large infrastructural works resulted in a massive bore campaign. These so-called ‘Deltadienst boreholes’ cover SW Netherlands, and represent mainly Pliocene and Quaternary deposits, rich in fossil shells.



Ongoing research into the faunal successions provides a picture of molluscan diversity in the southern North Sea Basin during the Pliocene and Quaternary. In general a decline in species numbers is seen, with thermophile and endemic groups most affected. However, immigration events, especially of Arctic–Pacific species, from the Middle Pliocene onwards, have greatly influenced the faunal development of the North Sea.

The deltadienst successions, together with new successions described from the Antwerp (Belgium) Pliocene, will lead to an improved molluscan biozonation for the southern margin of the North Sea Basin.

### How to make a Burgess Shale fossil: an experimental approach

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The Burgess Shale fauna represents a taphonomic conundrum. A number of theories have been proposed to explain its preservation, ranging from a simple lack of bioturbation or increased anoxia to the heightened preservation potential by burial within sediments of particular physical or chemical properties, notably clay minerals. While several taphonomic experiments have been conducted with an aim to understand ‘soft-part’ decay and preservation, none have investigated the effect that different sediment properties have on taphonomy.

A series of experiments have thus been carried out looking at the preservation potential of four end-member sediment types. The results are certainly intriguing, and it appears that the non-smectite clay kaolinite has a preservation potential that far exceeds those of the other sediments, including montmorillonite. This reaffirms the idea that the presence of clay minerals may markedly enhance soft-part preservation, but suggests that the more reactive smectite clay minerals may not be responsible. This is supported by the suggestion that the premetamorphic sediment of the Burgess Shale was likely to have been an illite-smectite-kaolinite clay assemblage, with an absence of highly reactive species such as nontronite or Na-montmorillonite (Powell, 2003).

### Exploring an Early Palaeozoic Tropical Archipelago on the Shores of Hudson Bay

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A unique and spectacular Early Palaeozoic tropical archipelago is being unearthed near Churchill, Manitoba, Canada. Islands composed of Proterozoic quartzite are

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surrounded by shallow marine deposits of Late Ordovician and Early Silurian age. Field research since 1996 has revealed a total of 16 localities, representing shoreline and nearshore environments preserved both before and after the Late Ordovician mass extinction. The detailed data collected from surface outcrops were enhanced in 2003 by the extraction of drillcore from five sites, permitting three-dimensional interpretation.

Upper Ordovician (Richmondian) carbonates and sandstones were deposited in a variety of settings around quartzite islands: muddy bay, boulder beach, shallow-water sands, and a cove with restricted water circulation. They contain diverse biotas: trilobites, corals, brachiopods, cephalopods, gastropods, and conodonts. A claystone of undetermined age overlies the Ordovician rocks. Above this are Lower Silurian (lower Llandovery) deposits, consisting of poorly fossiliferous muddy dolostones overlain by coral-rich dolostones and by strata containing monospecific assemblages of the brachiopod *Virgiana decussata*. The unusual depositional settings represented by these rocks provide an excellent opportunity to improve our understanding of the Late Ordovician extinction and of Early Palaeozoic shallow marine ecosystems.

Data analysis and systematic description of the fossils are ongoing. Discoveries to date include: (1) records of environmental change through the extinction interval; (2) the largest known trilobite, *Isotelus rex*, and associated trace fossils; (3) unusual fossils including eurypterids and ophiuroids; and (4) diverse corals encrusting Ordovician shoreline boulders.

### Substrate specificity of Auloporida (Tabulata) from the Devonian of the Holy Cross Mts., Poland

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Brachiopods encrusted by various organisms (corals, bryozoans, crinoids) are common in the Devonian of Holy Cross Mts., Poland. Observations made on the material from the Skaly Fm. (Upper Eifelian-Lower Givetian) of two sections—Grzegorzowice-Skały and Świętomarz-Śniadka (northern region of the Holy Cross Mts.)—allowed recognition of substrate specificity of auloporids (Tabulata).

Brachiopods were encrusted by *Aulopora* spp., *Aulocystis skalensis* (STASIŃSKA), *Aulocystis* sp. and *Pachyphragma* sp. (the latter one recognized in Europe for the first time).

*Kyrtatrypa* sp., a rare brachiopod in the Formation (under 5%), were the most often encrusted (63% of investigated specimens; N=31), while the most often occurring species, *Aulacella eifeliensis* (DE VERNEUIL) was nearly not encrusted. The majority of encrusted brachiopods were larger than 20 mm, while smaller brachiopods occur abundantly in the Formation. The substrate specificity has been caused mainly by the ornamentation of the host's shell, because in the Formation occur other big brachiopods with more delicate ribs (e.g. *Xystostrophia*). The position of corallites along the commissure of the brachiopod shell proves that auloporids often encrusted living hosts.

The epizoan probably used water currents produced by brachiopod's lophophore impoverishing the host's food composition; their relationship can therefore be described as scramble competition.



## Abstracts of poster presentations

### The rugose coral fauna from the Serpukhovian (Carboniferous) of the Ardengost Massif (Pyrenees, France) and its palaeobiogeographic implications

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The Ardengost Massif represents one of the rare occurrences of shallow-water carbonates from southern Armorica. Its microbial and bioclastic limestones of Serpukhovian age contain occasionally abundant coral faunas. Solitary forms dominate, but colonial forms are always present. The absence of non-dissepimented corals indicates non-stressed, shallow-water environments. Almost monospecific coral beds of *Kizilia*, *Dibunophyllum*, and *Palaeosmia* are characteristic for the Serre de Castets section.

The overall generic composition indicates some interesting palaeobiogeographic aspects for the European rugose coral province. It confirms the wide distribution of some classic Central European taxa, as e.g. *Dibunophyllum*, *Axophyllum*, *Palaeosmia*, and *Diphyphyllum*. However, *Kizilia* and *Melanophyllum* indicate an overlap with the coral fauna of Russia and Ukraine. Therefore, migration from Russia into Europe followed two different paths: one north of Armorica into Central Europe indicated by *Nemistium*, and a second along the southern margin indicated by *Kizilidae*.

However, the composition of the coral fauna along a single path may vary considerably. Although almost similar in age and depositional realm, the closely spaced Ardengost and Montagne Noire coral faunas show remarkable compositional differences. Taxa very abundant in the Central Pyrenees—e.g. *Dibunophyllum*, *Koninckophyllum*—are almost unknown in the Montagne Noire and vice versa, e.g. certain Lithostrotonidae.

### Morphology and Ultrastructure of a Lower Carboniferous Megaspore

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The majority of Palaeozoic megaspores were produced by free-sporing, heterosporous, lycopsids. The Early Carboniferous was marked by an increase in the abundance

and diversity of several megaspore genera, such as *Lagenicula*, that became dominant in the Upper Carboniferous. This rise in abundance/diversity probably reflects the development of forests dominated by large arborescent lycopsids. The study of the megaspore *Lagenicula variabilis* (Winslow, 1962) nov. comb. from the Lower Carboniferous of northeastern Ohio, U.S.A., utilizing LM, SEM and TEM analysis, has provided new information on its gross morphology, wall structure and wall ultrastructure. By comparing this spore with other fossil species of *Lagenicula* and the spores of extant lycopsids, it is possible to confirm its biological affinities with lycopsids. *In situ* *Lagenicula* (and related forms) from the Upper Carboniferous studies indicate that such megaspores derive from the Lepidocarpacea, that include many of the typical arborescent lycopsids that dominated the Euramerican Coal Measure forests. Although the specimens from the Lower Carboniferous of Ohio have not been recovered *in situ*, it seems likely that they derive from a similar source. This suggests that the arborescent lycopsids typical of the Upper Carboniferous were already present in the Lower Carboniferous, possibly forming forests in similar environments.

### Euconodont histology, modularity and the development of complexity

**Howard A. Armstrong**

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Higher organisms are incredibly complex systems and one of the outstanding questions of modern biology is, how does such complexity evolve? Modularity, the combinational assembly of elementary building blocks, allows for the generation of complexity, particularly if the building blocks are duplicated and modified during evolution.

The vertebrate oral skeleton is an example of a modular system, comprising in various manifestations dentine, enamel and enameloid tissues. Tooth structures among gnathostomes comprise two configurations (Carlson 1990). At its most primitive, in Cambrian euconodonts, teeth are formed from dentine capped by enamel; a configuration also found enigmatically in clades crownwards of the amphibians. In the Chondrichthyes and Osteichthyes teeth are formed from dentine capped by enameloid. This pattern raises the obvious questions as to the origin of enameloid, and why are different combinations of tissues expressed at different times and in different clades?

Recent work on the histology of *Panderodus*, a coniform euconodont, thought to have had a nektonic or pelagic mode of life, indicates a tooth structure comprising dentine and enameloid. This clade arose in the Tremadoc (*deltifer* biozone) and it would therefore appear that the dentine–enamel configuration, found in most euconodonts, has evolutionary primacy. A hypothesis is offered in which enameloid was derived from a modification of the “enamel genetic module” as an adaptive response to different structural demands on teeth. From the Tremadoc, enamel and enameloid modules became available for expression in different adaptive situations.

CARLSON, S. J. 1990. Vertebrate dental structures. In: Carter, J. G. (ed.) *Skeletal Biomineralization: Patterns and Evolutionary Trends, Volume 1*, 531–556. Van Nostrand Reinhold, New York.

### Biodiversity variations around the Triassic/Jurassic boundary: example of vertebrate remains from paralic environments

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Some new sections were studied in central and southern Burgundy (Eastern France), which exhibit continuous lithologic successions around the Triassic/Jurassic (T/J) boundary. Supposed to correspond to a major biological crisis, the T/J boundary is typically characterized in that area by siliciclastic facies, of proximal marine to paralic environments.

The Rhaetian typical facies is particularly enriched with vertebrate remains, mainly belonging to fishes (selachians and actinopterygians: *Acrodus substriatus*, *Hybodus cloacinus*, *H. minor*, *H. plicatilis*, *H. sublaevis*, *Lissodus minimus*, *Polyacrodus holwellensis*, *Pseudodalatias barnstonensis*, *Nemacanthus monilifer*, *Synechodus rhaeticus*, *Synechodus* sp., *Pseudocetorhinus pickfordi*, *Saurichthys longidens*, *Gyrolepis albertii*, *Birgeria acuminata*, *Colobodus* sp., *Sargodon tomicus*, *Lepidotes* sp., *Paralepidodus* sp., *Ceratodus kaupi*, C. sp.) or reptiles (*Ichthyosaurus* sp., *Rutiodon* sp.) and mammalian reptiles (*Pseudotricodon* sp., *Gaumia* sp.).

The Hettangian part of the sections only yielded poor or absent vertebrate associations, despite the absence of obvious lithological/environmental changes around the T/J Boundary.

Is such an observation reflecting a general change in the vertebrate content around the T/J limit, resulting from a real biological crisis? Or is it not simply related to some local, changing environmental conditions? Or is it simply due to the taphonomic and preservation contexts?

### Palaeoecology of Upper Eocene and Upper Oligocene larger foraminiferal and coralline algal dominated carbonates (north-eastern Italy)

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During the Cainozoic, two main extinction events of marine benthic taxa took place in the Indo-Pacific area: a broad interval from the Middle Eocene to Lower Oligocene and a shorter interval during the Late Oligocene to earliest Miocene. During these periods, coralline red algae and larger foraminifera were important sediment producers while corals play a subordinate role in the northern margins of the Tethys. Priabonian (Late Eocene) and Chattian (Late Oligocene) coralline algal facies are identified in an extensive geographic area in north-eastern Italy including the Colli Berici, Monti Lessini

area, the Piedmont Flexure, and Alpage area. These facies, found in both pure, shallow water carbonate as well as mixed siliciclastic-carbonate settings, are compared in terms of taxonomic diversity, coralline growth-forms, and taphonomic signatures. In the Priabonian the crustose coralline algal pavements are represented by a coralline crust bindstone and highly diversified nummulitid and orthophragminid foraminiferal fauna. Large rhodoliths occur commonly within this facies and are characteristically discoidal in shape. Chattian rhodolith pavements consist of a rudstone with a packstone matrix dominated by large spheroidal rhodoliths. These different biotic responses to ecological disturbances, probably due to increased rates of weathering and nutrient supply, associated with new trophic resources, promoted the flourishing of coralline algae rather than coral reefs.

### Larval shell morphology, geographic range and abundance in a species-rich gastropod radiation (Turridae: Polystira): Recent perspectives on its 30my history

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The turrid gastropod *Polystira* (Olig-Rec) is endemic to the subtropical/tropical Neotropics where it is among the most abundant and widely occurring marine molluscan genera (Recent and fossil) in 10–500m water depth. Accretionary growth leads gastropods to preserve their complete skeletal ontogeny, including the larval shell (protoconch) whose morphology reflects lifestyle. Analysis of protoconch morphology in *Polystira* show a bimodal distribution in form and individual morphospecies can be categorized as being either paucispiral (inferred non-planktotrophy) or multispiral (planktotrophic), the latter having greater dispersal potential.

*Polystira* represents a model marine invertebrate for examining the relationship between larval ecology and geographic range because it is; 1) exceptionally species-rich: 82 Recent Tropical Western Atlantic morphospecies; 2) well sampled: 770 mappable lots (>5,200 specimens), and 3) possible to map morphologies onto a robust molecular phylogenetic tree (16S, 28S, COI).

We have plotted the geographic ranges of each morphospecies within the TWA to test the extent to which inferred dispersal potential correlates with species distribution. Paucispiral taxa show uniformly restricted distributions as predicted by limited dispersal potential but perhaps surprisingly planktotrophic multispiral taxa appear to have more complex distributions including extremely wide and very narrow ranges.

The *Polystira* radiation demonstrates how patterns of abundance and distribution in Recent species have important consequences on our ability to estimate accurately macroevolutionary dynamics using the fossil record.

### A rolling stone gathers no moss animals!?

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Although bryozoans are well known to be part of the Recent rocky-shore boulder community, fossil assemblages are seldom recorded. Here we present a shallow-water bryozoan fauna with exceptional preservation from the Early Pliocene of the Carboneras Basin (Cabo de Gata, SE Spain). This small and shallow embayment of the Mediterranean Sea received, by means of intermittently shedding delta lobes, large amounts of coarse terrigenous material from the uplifting Sierra Cabrera to the north. These conglomerates host a diverse *barnamol* fossil assemblage dominated by large balanids, bivalves and bryozoans. The latter, of which some 35 species have been identified, are dominated by *Calpensia nobilis*, which frequently forms thick multilaminar crusts around the pebbles, and *Escharoides coccinea*. The excellent state of preservation of the pebble-encrusting fauna and the almost *in situ* conservation of most fossils imply an absence of strong turbulent currents, rapid burial and future exclusion from reworking. The considerable size reached by the encrusting barnacles and bryozoan colonies is further evidence for (occasionally perturbed) stability of the seafloor for several (tens of) years. Thus, although the proverb still holds true since these conglomerates were not rolling stones *sensu strictu*, this example shows that bryozoans can play an important role in contributing to the carbonate factory of shallow-water rocky shores.

### In search of the earliest seed plants: a geological expedition to East Greenland

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Recently, in *Palaeontology*, Marshall and Hemsley described a seed-megaspore, *Spermasporites alleni*, from the Middle Devonian of Ella Ø, East Greenland. This seed-megaspore is highly unusual as it bears at its apex not only three smaller aborted spores of the original tetrad, but also a cluster of microspores. This suggested a new path to seed evolution. But the seed-megaspore has only been found as isolated specimens with no evidence as to their parent plants. In order to determine the taxonomic affinity of the seed-megaspore bearing plant, a NERC-funded expedition was mounted to Ella Ø under the umbrella of CASP. This poster describes the expedition and illustrates some of the palaeontological findings. It complements the scientific results which are being presented in a separate talk (Berry *et al*). A short video is also available on request.



## Devonian Bryozoa from New Zealand

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As a whole Palaeozoic bryozoan fauna is scarce and poorly preserved in New Zealand. Some Devonian Bryozoa were described from two small areas of the South Island: Reefton and Baton River that belong to different structural units: Buller and Takaka terranes. The Reefton species were included into Cystoporata and Trepstomata. Recent collects yielded mainly Fenestrata, comparatively more abundant, but decalcification of the colonies prevents any determination at the specific level. The material was provided by the Lankey Limestone, Emsian in age. The Baton River species were almost exclusively attributed to Fenestrata. The shelly beds of the Baton River Formation are considered as Pragian/Emsian.

Low biodiversity of the Palaeozoic bryozoan fauna in New Zealand is confirmed with the Devonian forms. It differs widely from the nearest gondwanian domain, that is Australia, even though further studies have to be continued concerning the period. Therefore palaeobiogeographical links are not easy to establish.

## Evolutionary patterns for *Normalograptus persculptus* (Elles and Wood, 1907)

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Assemblages of *Normalograptus persculptus* (Elles and Wood), collected through the LATEST Ordovician *persculptus* zone and EARLIEST Silurian *acuminatus* zone of Cerig Gwynion Quarry and the associated Prys stream section and Ystraddfin sections of central Wales show: (1) a progressive delay in the insertion of the median septum, as originally identified by K.A. Davies IN 1929, representing a unidirectional microevolutionary trend within a lineage; (2) marked variability in morphology, particularly in rhabdosome dorso-ventral width, through time, producing alternate broader and narrower forms. New data indicate that these broad and narrow forms correspond to the species *Normalograptus persculptus* and *Normalograptus parvulus* (H. Lapworth), which are thus regarded as morphological end members within one variable species. We retain the name *N. persculptus* because of its historical stratigraphical importance, even though *N. parvulus* technically has priority.



## A Welsh Ordovician Hunsrück?

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Ordovician lagerstätten are extremely rare in comparison with the Cambrian, and known examples are severely restricted in the environment represented (Soom Shale) or the taxonomic range (Beecher's Trilobite Bed); the Arenig Fezouata Shale of Morocco yields more diverse organisms, but is at an early stage of investigation. This gives the impression, perhaps misleading, that the Burgess Shale-type communities are largely restricted to the Cambrian, despite some similar taxa in later deposits such as the Hunsrück Slate. The very recent discovery (Summer 2004) of a pyritised fauna in middle Ordovician black shales may help to resolve this issue. The associated, 'normal' fauna is dominantly graptolitic, with only very rare trilobite fragments; the pyritised components of the assemblage appear to be rapidly lost to weathering once exposed. Collections so far have been very restricted in view of the conservation needs of the material, and although soft tissue has not been definitively proven at the time of writing, the first fossils recovered strongly suggest exceptional preservation. The fauna already recovered is dominated by sponges and crinoids, but further organisms include a bivalved arthropod carapace, a partial asteroid (?), and apparently soft-bodied problematica, one of which is possibly a holothurian. The results of a more extensive investigation will be available by the time of the meeting.

## The Ontogeny of the Phacopid trilobite *Calyptaulax strasburgensis* (Ulrich and Delo, 1940) from silicified Middle Ordovician material

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The complete ontogeny of *Calyptaulax strasburgensis* is presented with both SEM images and diagrammatic reconstructions based on numerous silicified specimens of exceptional quality, originally collected by W.R. Evitt in the 1940s from Ordovician limestones of the Shenandoah Valley, Northern Virginia, USA. The exceptional state of preservation has allowed features on the smallest specimens to be preserved in sufficient detail for several noteworthy observations to be made. Photographic evidence is presented which shows common morphological features that confirm the link between minute (0.3mm diameter), presumably planktonic, bulbous protaspid larval forms with larger benthic protaspides. As recently as the latest *Treatise on Invertebrate Palaeontology* a discussion was had as to whether these bulbous forms represented a larval trilobite or an unidentified crustacean species. Changes in spinosity and tuberculation are documented throughout development and photographic evidence is presented to show the tubercles on the immature glabella are arranged in a spiral formation. Photographic evidence and discussion of the possible function of a unique bifurcating comb-like structure on the benthic protaspids is presented. A new related



species is presented which is an intermediate, not fitting into the current generic classification of the Pterygometopids. The need for further work and a taxonomic revision is suggested.

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### Standing up on its own two (dozen) legs: A new trilobite-like arthropod from the Lower Cambrian Sirius Passet fauna and its functional morphology

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A large arthropod from the exceptionally-preserved Sirius Passet fauna (Lower Cambrian, Buen Formation, North Greenland) is described. Unusually for the Sirius Passet fauna, external morphology including limbs is well preserved, and internal anatomy less-well preserved, although a series of small gut diverticulae are known. The cephalic segmentation and overall layout of the body are similar to that of trilobites and their close relatives, and the limbs bear a remarkable resemblance to those of the relatively basal trilobites *Olenoides* and *Eoredlichia*. The plesiomorphic nature of this limb type (it is shared by naraoiids and other trilobite-like taxa) suggests that the remarkable success of the trilobites in the Early and Middle Cambrian did not come about primarily through modification of their limb type.

The functional morphology of all these taxa remains problematic, with basic disagreements in the literature concerning how the limbs were attached and oriented, and how they could have functioned to produce the characteristic arthropod trace fossils *Rusophycus* and *Cruziana*. We tackle these problems through the use of computer reconstruction and animation of the limbs of the new arthropod. The limbs of this, and by extension those of the trilobites, cannot have functioned like those of the extant *Limulus*, and indeed the suspicion must be that, unlike modern arthropods, trilobites truly did “stand on their legs, and not hang down from them”—to reverse Manton’s crisp aphorism.

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### A multi-element radula-like structure from the Lower Cambrian Mahto Formation, Jasper National Park, Alberta, Canada

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Organic-walled microfossils isolated from locally bioturbated shelf-facies mud/siltstone of the Lower Cambrian (mid *Bonnia-Ollenelus* zone) Mahto Fm., south central Canadian Rockies, include a diversity of articulated and disarticulated tooth-like structures with marked similarities to more recent molluscan radulae. Such assignment is supported by a conspicuously fibrous microstructure, presumably reflecting growth via microvilli. This style of construction, however, is not limited to radulae, or indeed molluscs, and the occurrence of organic-walled, microvillar, multi-element jaw structures in other lophotrochozoan phyla may eventually frustrate definitive taxonomic assignment of these fossils. As a radula, however, it supports (and is supported by) the

interpretation of various early Cambrian SSF as crown-group molluscs. In any case, these structures clearly *worked* like a radula and document one of the earliest attempts to scrape out a living.

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### Late Ordovician Cool Water Bryozoan Mud Mounds From Libya

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Upper Ordovician bryozoan mud mounds are identified from subsurface of the Jifarah Formation of Tripolitania, NW Libya. These limestones form part of a much wider, high latitude belt of cool water carbonates across several hundred kilometres through NE Spain, Morocco, Algeria and western Libya, which lay on the NW margin of Gondwanaland. In the mud mounds, the diverse, trepostome-dominated bryozoan assemblage includes delicate and robust branching, encrusting and nodular bryozoan growth forms, but mounds lack organic framework and microbial fabrics. Regional geophysical data suggest rapid thickness changes, where mud mounds in complexes up to 100m thick had some topographic relief over the surrounding muddy sea floor. The Jifarah limestones, which are overlain by glaciomarine shales, have been interpreted as developing during an early Ashgill period of warmer climates, when coral–stromatoporoid reefs formed at low latitudes in areas of Laurentia and Baltica. It is proposed here that analogues of the Jifarah bryozoan mounds are represented from upper slope environments of the Quaternary of the Great Australian Bight by cool-water bryozoan mud mounds, which apparently flourished during the last glacial lowstand. This comparison suggests that the Jifarah mounds may have developed in slope/outer ramp environments at an early Ashgill lowstand, and in cool climates.

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### Palaeoenvironments of the Montceau-les-Mines freshwater biota (Upper Carboniferous, France): new data from the flora preserved in nodules

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Recent faunal studies of the Montceau Lagerstätte have considerably improved our knowledge of this exceptional Upper Carboniferous freshwater biota. However, there is still a lack of information concerning its exact palaeoenvironmental setting (hydrology, relief, climate, ecological niches) and the aquatic ecosystem (*e.g.* trophic links) in which these animals were living. The sideritic nodules that yielded most of

the fauna also contain a diverse and abundant flora. The composition of this flora is analyzed here and provides valuable information concerning the palaeoenvironment of the Montceau-les-Mines Lagerstätte. More than fifty species are recognized (*e.g. Annularia stellata, Pecopteris unita, Neuropteris cordata* are particularly abundant) that belong to groups typical of the Stephanian flora (lycophytes, sphenopsids, tree ferns and pteridosperms). Quantitative analyses indicate that arborescent sphenopsids and tree ferns were overwhelmingly dominant even though variations do exist between the floral composition of the different opencast mines studied at Montceau. At some localities, the flora may consist almost exclusively of pteridosperms or tree ferns. Taphonomical and sedimentological studies show that flora contained in nodules was autochthonous to parautochthonous. The three-dimensional preservation of plant remains indicate a rapid burial under presumably anoxic conditions. Nodules formed around plant remains through the precipitation of authigenic siderite, in the same way as in other Upper Carboniferous Lagerstätten such as Mazon Creek (USA), Coseley (UK) or Sosnowiec (Poland). A palaeoenvironmental reconstruction of the Montceau Lagerstätte is proposed, that displays a mosaic of environments (*e.g. deltaic lacustrine, paludal to fluvial*) colonized by plants in which a rich and diverse fauna (*e.g. aquatic crustaceans, insects, amphibians, fishes*) once flourished.

### Spiny trilobites from the Devonian of Morocco

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Morocco has become one of the great sites for discovering new fossils. Notable among these are a range of spiny Devonian trilobites from the Anti-Atlas Mountains that exhibit some of the most bizarre adaptations of an already diverse group. At least five different families have produced morphologies unparalleled in the history of trilobites—or, indeed, the arthropods. These include the genus *Walliserops*, which carries a trident on the front of the cephalon, and another with an anterior ‘spoon’. The functional explanations of these spines and projections have remained speculative but some have been postulated as defensive in nature. When some of these trilobites were enrolled the orientation of the spines would have presented predators with a particularly unappealing mouthful. One plausible functional explanation has been deduced for a structure associated with the eyes of a complete specimen of the phacopoid trilobite *Erbenochile erbeni* (Alberti). This trilobite has unique tower-like schizochroal eyes where the lenses are arranged in straight-sided columns and not in the usual spherical fashion. The palpebral lobe of each eye projects outwards over the visual surface so that light incident directly from above is prevented from reaching the lenses. This structure is thought to have acted as a visor or eyeshade.

### Wagner's Parsimony analysis of Mid-Cretaceous European vegetation

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The vegetation of Europe during the Mid-Cretaceous is poorly known (Kvaček, 2001, Uličný *et al.*, 1997). Nevertheless, numerous floristic lists have been published during the last century. A comparison of this database using the Wagner's Parsimony method (Coiffard *et al.*, 2004) results in the distinction of six plant associations.

Two associations are characterised by the dominance of gymnosperms *sensu lato* and represent estuary mouth and salt marsh deposits.

Three other associations are richer in pteridophytes, conifers and angiosperms, and correspond to levee, floodplain and probably swamp deposits.

The last association is characterised by three angiosperms, and characterises braided river deposits.

From the ecological and environmental points of view, gymnosperms *sensu lato* were still well-established in brackish, disturbed environments, while angiosperms dominated in freshwater, disturbed environments. This analysis provides important information for the understanding of the floristic turnover during the mid-Cretaceous times.

### Xenomorph growth in ostreids: an example from the middle Oxfordian of Burgundy (Dijon, France)

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Some attached marine molluscs rarely reflect the positive form of the substrate (xenomorphic sculpture) on the right (free) valve whereas the left one preserves the (negative) imprint of the substrate morphology. This phenomenon, called xenomorphism or previously designated as ‘pseudomorphose’ or ‘mimetism’, is observed more frequently in ostreids. Two xenomorph ostreids have been found in argillaceous limestones of the middle Oxfordian in the Dijon area (France). The attachment surfaces of both ostreids have preserved the imprint of an ammonite conch (*Perisphinctes* sp) while the right (upper, free) valve reflects perfectly its positive form. Any ammonite conch has been found in the same bed as the oysters, probably due to dissolution of the conch during diagenesis.

Image analysis indicates that the positive replica of the ammonite on the free ostreid valve is very accurate and preserves the most delicate morphological features. The ammonite conch is reflected by the young part of the free right valve. According to some authors, this could be explained by folding of the right mantle-edge parallel to

the left one, both being influenced by the relief of the substrate, according to which the valves are secreted. Xenomorphism can be due to biological mechanisms, ecological factors or both.

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### Biodiversity vs Preservation: example of a trilobite association (Middle Ordovician, Massif Armoricaïn, France)

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Middle Ordovician (Darrivilian = 'Llandeilo Auct.' pars.) outcrops were recently discovered in the Massif Armoricaïn (Manche, western France). The clay 'Formation d'Urville' yields numerous well-preserved macrofossils, mainly trilobites: Illaenidae (*Illaenus giganteus*, *Cekovia perplexa*), Calymenidae (*Salterocoryphe salteri*, *Neseuretus tristani*, *Colpocoryphe rouaulti*), Homalonotidae (*Kerfornella brevicaudata*), Dalmanitidae (*Dalmanitina actua*, *D. philippoti*, *D. bossei*, *Eodalmanitina chillonensis*, *E. henryi*, *E. destombesi*, *E. macrophthalma*, *Crozonaspis morenensis*, *C. rouaulti*), Asaphidae (*Isabelmia* sp.), Cheiruridae (*Eccoptychile* sp.), Lichidae (*Uralichas* sp.), Odontopleuridae (*Selenopeltis* sp.), etc. Poorly known or even unknown larval stages were collected for most species.

The high diversity may partly be the result of faunal-mixing, in a calm, deep/distal depositional environment (clay deposit). Whole individuals or moults of Dalmanitidae and Illaenidae, with abundant larvae, are considered as the autochthonous trilobite association. Opposite, *Neseuretus* may characterize shallower, proximal environments: good individuals, moults or larvae are generally rarer, except for destroyed pieces of cranidia or isolated segments.

In fact, two kinds of preservation coexist: 1, generally well-preserved autochthonous elements, inside sediment. Allochthonous forms are rare in such a condition, and may profit by currents to arrive regularly. 2, Storm-controlled, rhythmic surface-accumulations of debris (mainly *Neseuretus*), related to the destruction of exotic, proximal communities.

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### Brachiopods and chips

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The juvenile shell of Discinoid brachiopods is mineralised by a single layered mosaic of siliceous tablets prior to the formation of the apatite shell. The rhombic tablets have

a mean length, width and thickness of 1.3 µm, 0.7 µm and 100 nm respectively. The mosaic is bounded by a tablet-free ring of lamellae, separating it from the mature shell. The siliceous tablets are produced intracellularly within a vesicle and extruded onto the surface. Rhombic siliceous tablets and their imprints occur in extant *Disciniscia*, *Discina* and *Pelagodiscus*. Imprints of siliceous tablets have also been found on juvenile shells of the late Devonian *Schizobolus* and the late Silurian *Opatrilkiella*.

The function of the siliceous tablets is unknown and very little is known about the formation of the tablets. Silicon isotope measurements have been used to determine the extent to which marine invertebrates fractionate silicon from seawater, shedding light on the much neglected silicon cycle in modern and ancient oceans. Preliminary silicon isotope measurements of the silicon chips of *Disciniscia tenuis* suggest that brachiopods fractionate silicon to a lesser extent than do diatoms and siliceous sponges.

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### The ctenocystoids seen as stem-group hemichordates (not echinoderms) and their position within the deuterostomes

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Molecular methods show that the cladogram for the deuterostomes is: ((echinoderms + hemichordates) chordates).

The ctenocystoids (Cambrian – Ordovician) have a skeleton of monocrystalline calcite plates. Such a skeleton is diagnostic of echinoderms in the extant fauna, but not among fossils, since many Palaeozoic fossils with such a skeleton are not echinoderms but chordates. The cladogram therefore implies that the latest common ancestor of the deuterostomes would also have had a calcite skeleton and is therefore diagnostic, not of echinoderms, but of deuterostomes. For deciding the systematic position of a fossil within the deuterostomes, a calcite skeleton is irrelevant.

The ctenocystoids are probably hemichordates. This is suggested, in the first place, by their almost perfect bilateral symmetry and the presence of a posterior opening, probably a combined gill slit and anus, giving a general resemblance to an enteropneust hemichordate. Of particular interest is a still unpublished cylindrical ctenocystoid covered by a "fleece" of thin recurved spines. By annelid comparisons, these spines imply fossoriality, as in extant enteropneust hemichordates. If hemichordates, the ctenocystoids belong to the stem group, not to the crown group of the phylum, since they lack two important features (absence of calcite skeleton, presence of muscular protosome) which the latest common ancestor of extant hemichordates would have possessed.

In this light, we shall briefly discuss the systematic position of the other carpod groups.



### Lower Cretaceous swimming theropod trackway from La Virgen del Campo (La Rioja, Spain)

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A major question concerning the behaviour of dinosaurs is whether or not they were able to swim. The Lower Cretaceous locality «La Virgen del Campo» (La Rioja, Spain) has yielded a new trackway that was made under water. The 15 m trackway consists of a series of 12 consecutive ichnites, each of which is a set of two or three long and slender well-impressed grooves. They are interpreted as being the result of scratches made on the sediment by the distal parts (claws or toe-tips) of digits II and III or II, III and IV. The long wispy sinuous scratching form of the footprints, and the variation in their length, clearly indicate their under water formation and thus the swimming ability of the trackmaker. The presence of NE–SW oriented ripple marks and the very marked S-shape of the right footprints points to the presence of a current at a 45 degree angle to the animal's direction. The peculiar form and digit marks associations (2 or 3) of the footprints as well as the type of locomotion inferred from the tracks reveal that the trackmaker probably was a bipedal carnivorous dinosaur. This is the first definitive evidence for active swimming in a theropod dinosaur.

### New insight into Palaeozoic charophytes using high-resolution X-ray Synchrotron microtomography

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Recent findings on the nature of the fructification in Palaeozoic forms bring a new understanding of the early stages of charophyte evolution. Examination of Palaeozoic charophyte fructifications, using resources of high-resolution X-ray Synchrotron microtomography and microscopy, has revealed that most of them are provided with a utricle constituting a supplementary calcified cover around the gyrogonite. According to this new evidence, we assign all taxa with utricles to the Sycidiales. Indeed, they exhibit common features, such as a multilayered wall and an internal vesicle, but the different families can be distinguished by the diversity in orientation of external cells,



complexity of the utricle wall and in the presence or absence of antheridia. The solidly packed structure of the utricle is regarded as an organ of protection of the zygote against desiccation. We interpret the morphological similarities between Palaeozoic Sycidiales and Mesozoic Clavatoraceae, which both possess a utricle, as homoplasous rather than the expression of a true phylogenetic relationship. Our findings suggest that some Umbellids might correspond to utricles of charophytes.

### Different modes of spine development in the pygidium of Devonian scutelline trilobites

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Styginid trilobites are characterized by their large pygidium with an entire margin. This general configuration is modified in specialized Early and Middle Devonian scutellines where evolutionary trends towards spine development on the pygidial margins occur. Besides denticles and short spines, which are apparently unrelated to pleural segmentation, there are cases where segmental spines extend beyond the margin of the pygidium. Such modifications of the pygidium follow three different modes:

*Thysanopeltella* mode: size and shape remain unchanged, except that pleurae continue into free segmental spines.

*Weberopeltis* mode: overall size is maintained, but shape changes result from regression of interpleural fields leaving the pleural ribs as free spines.

*Kolihapeltis* mode: both size and shape are modified by lateral compression resulting in complete obsolescence of pleural fields.

Whereas in the first two modes spine development may occur iteratively, in the *Kolihapeltis* mode there is evidence of gradual evolution within a single lineage. New investigations of all forms with the *Kolihapeltis* mode shows shared characteristic traits of cephalic and thoracic sclerites. The acquisition of extremely reduced adaxial pleural fields in the thorax, along with the compressed pygidial configuration that differs from all other styginids, may be an adaptation to a mesopelagic life-style.

### The ancestry of the Echiura. Early soft bodied preservation from the Cambrian of the Welsh Basin

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The phylogenetic positioning of the Echiura, Sedwick 1898, has been disputed many times. Members of this phylum share many homologous characters with Annelida. The argument for maintaining them within a phylum rests upon the lack of segmentation within the body cavity or other structures. Studies of the development of the nervous system of the extant *Bonellia viridis* suggest it is descended from a segmented ancestor (Hessing & Westheide, 2002, *J. Morphology*. 252(2)). A fossil Echiuria recovered from the Welsh basin, near Harlech, is remarkably well preserved in three dimensions and demonstrates the presence of segmentation towards the anterior end. The existence



of this fossil supports the proposal by Hessing & Westheide that the Echiuria should be included within the Annelida and also illustrates the presence of a lagerstätte of remarkable 3D softbody preservation.

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### Rates of fish evolution during the breakup of Pangaea

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The rise of halecomorph and teleost fishes was co-incident with the breakup of Pangaea. During this time continents and seas became increasingly provincialised and the fishes responded, marine and freshwater alike. There were discernable and consistent patterns in the rates of morphological evolution of different fish groups, most of which showed initial bursts contemporaneous with the major continental reorganisations followed by decline in successive time bands. However, the nature of the changes was very different for different groups.

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### The Bjørkåsholmen Formation (Tremadoc): a homogenous distribution of trilobites throughout the Baltoscandian platform

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The Lower Ordovician succession of Baltoscandia is initiated by extensive carbonate deposition forming the Tremadoc Bjørkåsholmen Formation, formerly the Ceratopyge Limestone, a distinctive unit corresponding to the trilobite zone of *Apatokephalus serratus*. The limestone succession has a broad regional distribution and its associated sediments were deposited across the Baltoscandian platform in a shallow water epicontinental sea. Similar depositional conditions are not known today. The unit is remarkable in its near homogenous facies, lithologic and faunal composition throughout the platform. This is clearly demonstrated in the present study, where sequences at Ottenby and Degerhamn on southern Öland, Sweden, were logged and compared for trilobite biostratigraphy. In both investigated localities the resulting trilobite abundance distributions are very consistent. The trilobite fauna from the Bjørkåsholmen Formation in the Oslo Region, Norway, and Öland are composed of the same typical Ceratopyge assemblage. Trilobite abundance data from both areas are nearly identical and demonstrate an upward declination of trilobite specimens. Comparison across the Baltoscandian platform between the westernmost occurrences in the Oslo Region and the easternmost outcrops on Öland therefore suggests widespread stable conditions of the Ceratopyge fauna during the sedimentation of the Bjørkåsholmen Formation.




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### Using Geometric Morphometrics to Examine Lipotyphlan Relationships

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Morphological phylogenies coded with discrete characters reconstruct the 'Lipotyphla' as a monophyletic group. In contrast, molecular analyses divide the group into two—a rump Eulipotyphla, and the Tenrecoidea which are nested in Afrotheria. We have looked at this problem from a third perspective by using the continuous quantitative characters in a geometric morphometric analysis.

A dataset of 19 cranial landmarks on members of all extant 'lipotyphlan' families, plus the fossil taxa *Apternodus*, *Oligoryctes* and *Nesophontes*, had been previously collected in order to study functional relationships. A series of Maximum-Likelihood trees were constructed from these data. These consisted of an unrooted tree; trees rooted with erinaceids in order to reflect traditional morphological hypotheses of relationships; trees rooted with tenrecoids in order to reflect molecular hypotheses of relationships; and a tree rooted with the non-'lipotyphlan' taxon *Didelphis*.

The analysis failed to recover either the morphological or molecular hypotheses of relationships. Nevertheless, there was greater resolution at lower taxonomic levels. The Soricidae was recovered as a monophyletic group and the tenrecines Tenrec and Setifer grouped as sister taxa, although the other tenrecid in the analysis, *Oryzorictes*, grouped with the mole *Talpa* instead. This suggests that the strongest phylogenetic signal in the data was roughly at the level of families, but that only weak hierarchical structure existed for higher level groupings.

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### The evolution of the post-Palaeozoic Neoasteroidea

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The evolutionary relationships, and therefore the classification, of the monophyletic post-Palaeozoic Neoasteroidea have been controversial, and recent molecular phylogenies have all provided highly divergent results. A morphological investigation of the skeletons of examples from 25 extant asteroid families, using progressive denudation of soft tissues and SEM imaging of 15 ossicle types, provides information for a new character set. Cladistic analysis of this database, using two Carboniferous and Permian outgroups, generated a single most parsimonious tree with an unexpected topology, implying that two of the widely recognised ordinal level neoasteroid groups are paraphyletic. This analysis supports the basal position of the Order Paxillosida, and the highly derived condition of the Forcipulatida (like the modern *Asterias*). Fossil taxa from the Jurassic and Cretaceous provide evidence of the evolutionary origins of many modern families, illustrated by the ancestry of the deep sea Pterasteridae. An entirely new classification of the Neoasteroidea is proposed. The new phylogeny has important implications for the origins of deep sea and tropical shallow marine asteroid families in particular.



## New Early to Mid Ordovician trilobite faunas of Iran and their biogeographical significance

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New, biogeographically important trilobite faunas have been discovered recently in two Lower to Middle Ordovician sections in Iran. The outer shelf Tremadoc to early Arenig trilobite assemblages of the Eastern Alborz are dominated by cosmopolitan or pan-Gondwanan genera, such as *Geragnostus*, *Asaphellus*, *Apatokephalus* and *Conophrys*, but also contain *Asaphopsis*, *Dactylocephalus* and *Psilocephalina* which suggest affinity to the faunas of South China. *Taihungshania* appears in the Eastern Alborz at about the same time as in Armorica and in the Turkish Taurides. The Tremadoc to Lower Arenig fauna from the Derenjal Mountains, Central Iran is of low diversity and includes such cosmopolitan taxa as *Shumardia* and *Proteuloma*. The upper Arenig to lower Llanvirn trilobite assemblage contains *Paraonychopyge*, *Nileus*, *Parabasilicus* and *Illaenus*. The youngest trilobite assemblage from the Derenjal Mountains is dated as upper Llanvirn to Early Caradoc. It contains *Neseuretinus*, *Ovalocephalus*, *Birmanites* and *Liomegalaspides*, as well as asaphids, cheirurids, lichids and trinucleids. It shows a close similarity to the contemporaneous trilobite faunas of Sibumasu, South China and South Uzbekistan. This study suggests that the Alborz was probably a separate microplate, situated between South China and the Turkish Taurides during the Early Ordovician. The palaeogeographical position of the Central Iranian plate is less certain, and it may have been a part of Gondwana at that time.

## Exceptionally preserved Upper Silurian echinoderms from submarine channel deposits, Welsh Borderland

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The Upper Silurian submarine channel deposits at Leintwardine in the Welsh Borderland provide a unique palaeoenvironmental setting and contain a diverse range of predominantly fully articulated echinoderms, namely starfish, crinoids, echinoids and ophiocistioids, within so-called starfish beds. Some specimens are semi-articulated, for example starfish may have disarticulated arm portions, and the crinoids do not retain their distal holdfast structures. The starfish are the most abundant group and are ophiuroid-dominated. Crinoids are less common, whilst the echinoids and ophiocistioids are rarer still. Various biostratigraphic and palaeoecological criteria are used to assess whether the biota was indigenous to the channels, as in some Recent submarine canyon settings. Echinoderm thanatocoenoses are generally not preserved and transportation is variable both between and within species. The echinoderms are interpreted to have been predominantly parautochthonous to allochthonous and may have been indigenous to the channel area including the immediately surrounding shelf. The relatively unbioturbated nature of the enclosing sediment may suggest that the channel facies was oxygen-restricted; complete bottom-water anoxia is unlikely, as rare surface bioturbation has been documented. The other major faunal groups of the channels, namely the arthropods and brachiopods, are also likely to have undergone transportation.



## Unique microbiota from the Early Neoproterozoic of Yakutia (Eastern Siberia)

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In the early 1980s a diverse and well preserved microphytofossil assemblage was discovered in a series of boreholes that crossed Precambrian strata in the Nepa-Botuoba anticline (Yakutia), eastern Siberia. This assemblage was characterized by a high number of various acanthomorph acritarchs which were interpreted as being distinctive for the Early Cambrian (Rudavskaya, 1985, 1989). However, on the basis of subsequent taxonomical studies and of similarities with Australian microfossils from the Ediacaran Pertatataka Formation a Neoproterozoic (Vendian) age was suggested for the eastern Siberian assemblage (Moczydlowska *et al.* 1993).

In the present work the material from the Parshino Formation of the Nepa Horizon of Yakutia (boreholes Ozernaya-761, Zapadnaya-742 and Talakanskaya-841) has been reinvestigated, and a complete description of the exceptionally preserved Neoproterozoic microbiota is provided. The material includes distinctive taxa, such as *Ericiasphaera spjedaesii* Vidal, *E. magna* (Zang) Zang *et al.*, *Meghystrichosphaeridium densum* (Kolosoვა) Zang *et al.*, *M. magnificum* Zang *et al.*, *M. perfectum* (Kolosoვა) Zang *et al.*, *Tanarium acuminatum* Kolosoვა, *T. conoideum* Kolosoვა, *T. tuberosum* Moczydlowska *et al.*, *Talakania obscura* Kolosoვა, *Obruchevella* sp., *Polytrichoides lineatus* Herman and others, which are common in the assemblages from the Chinese Doushantuo Formation and the Australian Pertatataka Formation. Numerous vase-, ring-, dumb-bell shaped problematical forms and multicellular algae also occur in the investigated microbiota. Its stratigraphical position can be correlated precisely in the Early Neoproterozoic.

## Role of palaeo-environment in ammonite distribution: a Late Cretaceous example from Tunisia

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Tunisia yields many interesting Upper Cretaceous sections, including the GSSP for the K/P boundary at El Kef. In three areas, large quantities (>100 for each area) of ammonite specimens were collected from the Upper Maastrichtian part of the El Haria Formation. All three areas are situated in the same sedimentary basin, but in different palaeo-environmental settings, which allows us to investigate the role of the palaeo-environment (especially depth) in the distribution of the different suborders, families, genera and species.

In all three areas, the ammonite fauna is dominated by the Scaphitidae Gill genus *Indoscaphites* Forbes (Ancyloceratina Wiedmann). This dominance ranges from 45–75% over the three areas. Other Ancyloceratina Wiedmann like the Diplomoceratidae Spath compose up to 18.5%, the Desmoceratidae Zittel (Ammonitina Hyatt) up to 29%, and the Tetragonitaceae Hyatt up to 6% of the fauna. Phylloceratina Arkell are extremely rare (>1%).

Distinct abundance shifts of the different suborders, families, genera and species could be linked to the palaeo-environmental differences (depths) for the three areas. Scaphitidae appear to prefer a shallower habitat than Desmocerataceae and Tetragonitiaceae, providing an example of depth control in the distribution of Late Cretaceous ammonite species.

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### A new approach to studying microevolution in the fossil record

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We cannot measure microevolutionary rates or patterns directly in the fossil record, we can only measure morphological features on fossils preserved in stratigraphic sections (stratophenetic series). Analysis and interpretation of stratophenetic data depend on assumptions about the fossil organism and about the geological deposits yielding the fossils. Inference of evolutionary tempo and mode from fossil data thus depends on an underlying model, and the analysis of stratophenetic data is necessarily an inverse problem: given observed data, our knowledge of basin-fill and fossils, and a model mapping evolutionary to stratophenetic patterns, what is the most plausible evolutionary model supported by the available data? This involves a fundamental two-level problem: how do we fit unknown quantities to the data, and how many unknowns should we fit? Although theoretically analogous, the latter is more complicated in practice. In both cases, however, we seek quantitative measures of non-uniqueness, that is how much the model may vary while fitting the data. Here, I present a method that is designed to let the geological and palaeontological data justify our choice of evolutionary model and to quantify the associated uncertainty. Rather than a single 'best-fit' solution, a large number of solutions forms the basis for inference.

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### Diversity fluctuations in the Cenozoic brachiopod faunas of the greater Caribbean region

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A compilation of new and existing brachiopod data from the Caribbean islands of Antigua, Barbados, Carriacou, Cuba, Curacao, Dominican Republic, Haiti, Jamaica, Puerto Rico, St. Bartholomew and Trinidad together with Costa Rica, Panama, Venezuela and SE USA has established some clear biotic patterns within the Cenozoic rocks of the Caribbean basin. The data for some 80 rhynchonelliformean species are of variable quantity and quality, nevertheless diversity apparently peaked during the Eocene and to a lesser extent during the Miocene; both events were dominated by terebratelloid and terebratuloid species. These diversity peaks are coincident with marked facies variations, particularly in deeper-water environments, across the basin and optimal climatic conditions. The more monotonous lithologies of the Oligocene have yielded few brachiopod taxa. Following a significant drop in diversity during the

cooler climates of the late Miocene, diversity remained low during the Pliocene and Pleistocene. Throughout the Cenozoic cemented forms (thecideids) maintained a low but consistent background diversity at a range of depths; fluctuations are most marked amongst the larger pedunculate taxa.

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### Metazoan buildups on the Early Mid-Ordovician carbonate platform in NE Greenland: radiation of stromatoporoid mounds and substrates

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The Albert Heim Bjerge region exposes the higher parts of the Ordovician succession of NE Greenland. The upper Cape Weber, Narwhale Sound and Heim Bjerge formations range in age from late Arenig to Lanvirn (Whiterock) and display a wide range of nearshore to midshelf carbonate environments with a locally abundant macrofauna of low diversity: cephalopods and gastropods are common at a few levels but the more typical members of the Paleozoic Evolutionary fauna, the brachiopods and trilobites, are rare, restricted mainly to deeper-water facies. Marked, however, is the sudden dominance of stromatoporoids in the inshore environments of the upper Cape Weber Formation, in contrast to the spectacular microbial mounds in the lower part of the succession. Within this early Whiterock interval a variety of growth strategies are developed, including both domical and laminar forms. This early stromatoporoid diversification provided a new carbonate factory, a variety of different substrates and a new and hitherto unfamiliar seascape during the early stages of the Ordovician radiation in NE Greenland.

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### Using Carboniferous palynomorphs to monitor temporal changes in vegetation

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A detailed palynological and sedimentological analysis has been undertaken through an 11m thick succession of fine-grained sediments from the Marsdenian Stage, Upper Carboniferous, exposed at Pule Hill, near Marsden, Lancashire, UK (Ordnance Survey grid reference: SE 0320 1000). This well-exposed section of predominantly marine sediments deposited in the Pennine Basin contains two, possibly three, 'marine bands': strata deposited during periods of sea level rise that contain a distinctive fossil assemblage important in local and regional correlation. Forty-seven samples were collected for palynological analysis and the occurrence of the marine macrofauna (goniatites and bivalves) was also noted. The distribution and abundance of the spores, pollen and marine microphytoplankton (possibly reworked) have been documented and the terrestrial palynomorphs have been assigned to their palaeobotanical and palaeoecological groupings. Statistical analyses will be carried out on these data to

establish any significant trends within the section. The results of this research will be placed within a wider context through comparison with previous studies on similarly aged, near-shore, deltaic sediments that have yielded significant, systematic changes in the terrestrial palynomorph assemblages related to sea level fluctuation.

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### The Dennis Curry Collection at the Natural History Museum, London

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Dennis Curry was a highly successful businessman becoming Chairman of the family business, Currys, in 1967. He was also a distinguished geologist, making his name in diverse fields and publishing widely. He won many medals and awards for his science and was appointed Visiting Professor of Marine Geology at University College, London, in 1971.

The Natural History Museum, London, first acquired some of Curry's material in 1961, with the majority of his collection arriving between 1998 and 2001. The collection is large (a conservative estimate of the number of molluscs alone stands at 90,000 specimens), and represents sixty years of prolific collecting. The majority of the collection falls into three categories: Mollusca, micropalaeontological, and sieved residues. Curry was a pioneer in sieving his samples and collecting the "total mollusc fauna" including the small species. There are also other macrofossils, including a small amount of vertebrate material. The collection comes mainly from south east England and the Paris Basin, but includes material from numerous other European countries and the rest of the world. The majority is of Palaeogene and Neogene age, and there are also a number of Chalk samples.

The size of the collection means that curatorial work is currently ongoing. This paper will serve as a snapshot into the scientific value and potential of a unique collection.

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### The ancestry of modern Priapulidae traced back to the Early Cambrian: new fossil evidence from China

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The small ecdysozoan phylum Priapulida consists of only 18 described living species in present-day marine environments. The family Priapulidae accommodates six living species distributed in three genera (*Priapulus*, *Acanthopriapulus*, *Priapulopsis*). Eleven species of conclusive priapulid worms are described from the Lower Cambrian Maotianshan Shale and reveal the high diversity of the group in the early stages of its evolutionary history. At least five species from the Maotianshan Shale are recognized as possible representatives of the extant family Priapulidae. They possess most of the diagnostic features of modern priapulids.

1, *Xiaobeiqingella*: Swollen introvert covered with 25 longitudinal scolid rows anteriorly, a circle of circumoral scalids present; neck as a contraction; annulated trunk evenly wide, without subdivisions; a caudal appendage rather thin and elongate.

2, *Yunnanpriapulus*: Swollen introvert covered with 25 longitudinal scolid rows anteriorly and with scattered scalids further back, a circle of circumoral scalids present; neck area relatively well defined; trunk divided into an anterior annulated section and a posterior swollen section armed with ring-papillae; a caudal appendage very short.

3, Double tailed "*Xiaobeiqingella*": Swollen introvert covered with 25 longitudinal scolid rows anteriorly and with small scattered scalids further back; neck as a contraction; annulated trunk with its posterior section slightly swollen and armed with ring-papillae; a pair of broad and elongate caudal appendages with tapering shape.

4, *Paratubiluchus bicaudatus*: Swollen introvert covered with 25 longitudinal scolid rows anteriorly; neck area as a contraction probably; trunk rather smooth, with no subdivisions; a pair of relatively short caudal appendages with tapering shape.

5, A new type: Swollen introvert covered with 25 longitudinal scolid rows anteriorly and with larger scattered scalids further back, a circle of circumoral scalids present; neck as a contraction; trunk rather smooth with ring-papillae posteriorly; two caudal appendages thin and elongate.

This set of fossil evidence (five different forms) shows that the body plan of modern Priapulidae was already established in the Early Cambrian. These remarkable fossils also bring detailed evidence of morphological stasis over extremely long periods of time (more than half a billion years).

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### The paleokarst of Ohain Sandpit. A geological site to protect

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The sandpit of Ohain is located in the north of France, Avesnois. This geological site belongs to the south-western part of synclorium of Dinant; we can see it in two different parts, as follows. The bottom of the quarry is composed of Eifelian reef limestone and shale, with many builders: stromatoporoids, tabulate and rugose corals associated with crinoids and some brachiopods. The surface of this limestone has been weathered and hill shaded in palaeokarst. In the dip between the plurimetric high "dome" created by phenomenon of karstification are deposited Ypresian sandstone, of which exploitation finished in the 1980s. This geological feature, uncommon in France, is similar to the large karst massives that we can observe in South China, Guangxi Province around Guilin city along the Lijiang river.

Actually this geological site is threatened with the creation of a rubbish dump. The aim of this work is to try with different partners: municipality, nature protection organisations, university ..., to include the palaeokarst of Ohain sandpit into the France geological patrimony.



## Redescription of Ishijima's types of coralline algal species (Corallinales, Rhodophyta)

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The taxonomy of living species of coralline red algae (Corallinales, Rhodophyta) has undergone marked changes since 1960. The group is now treated as a separate order of Rhodophyta and it is considered to represent a major evolutionary line within the red algae. Concepts of families, subfamilies, genera, and species have changed as a result of extensive new information. These developments have significant implications for the taxonomy of fossil coralline red algae.

From 1935 to 1979 W. Ishijima published several papers on the taxonomy of fossil calcareous algae of diverse ages from the large geographic area including Japan, Philippines, Malaysia, and Indonesia. Among many other taxa, Ishijima described fourteen new species which he attributed to the Corallinales (Corallinales, Rhodophyta). The study of this collection highlights the importance of re-documentation of type material of fossil taxa defined decades ago with descriptions and illustrations focused on characters different from those considered diagnostic in modern taxonomy. Re-examination of the species types from a modern perspective of coralline algal taxonomy shows that all the species have been validly published. Among them, five species are confirmed to be valid, six species are assigned to different genera, one species is re-named, and two species are of uncertain circumscription within the Corallinales as their recognisable features do not warrant confidently delimiting the genera.

## Taxonomy, biostratigraphy and ecostratigraphy of Ordovician (Arenigian) megistaspid trilobites from Western Russia

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Approximately seven thousand trilobites have been sampled bed-by-bed in the Putilovo quarry and Lynna River section east of St. Petersburg, Russia. Here the middle to upper Arenigian carbonate succession spans the upper part of the Billingen, Volkhov and most of the Kunda stages. The large trilobite material has been registered, facilitating a preliminary biofacies investigation and recognition of biozones. The aim of the present study is to undertake a taxonomic revision of the stratigraphically important megistaspid group, which is represented by several hundreds of specimens belonging to the subgenera *Megistaspis*, *Paramegistaspis*, *Rhinoferus* and *Megistaspidella*. The chronostratigraphic zonation of the Billingen and Volkhov stages of Scandinavia is based on the distribution of megistaspids, but the eastern Baltic faunas are rather different and provide only few ties for correlation across Baltoscandia. However, at local level a very detailed correlation can be based on megistaspids. Correlation between Putilovo quarry and the Lynna River section, located 70 kilometres further east, indicates that the latter section is thicker but stratigraphically less complete. An important faunal shift from dominance of *Rhinoferus* to dominance of *Megistaspidella* occurs in the upper part of

the Volkhov Stage. The distribution of *Megistaspis* and *Paramegistaspis* indicates that the representatives of these taxa preferred somewhat deeper water environments by comparison with representatives of *Rhinoferus* and *Megistaspidella*.

## Kangerlussuaq and the latest Cretaceous ammonite faunas of East Greenland

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Hitherto the latest described Cretaceous ammonite fauna from eastern Greenland was D.T. Donovan's Campanian *Scaphites greenlandicus* assemblage from Traill Ø and Geographical Society Ø. Further collections by CASP also show better preserved but slightly older Campanian with *Scaphites ikorfatensis* and *Pseudophyllites skoui*. However, in the Kangerlussuaq Basin, south Blosseville Kyst, the late Jake Hancock first indicated the presence of the Maastrichtian, by an unfigured record attributed to *Pachydiscus gollevillensis* which was collected by Jack Soper. New collections from the basin by CASP and GEUS (Geological Survey of Denmark and Greenland) demonstrate the presence of rich Maastrichtian ammonite faunas. Most abundant is the heteromorph *Diplomoceras cylindraceum*, which reaches over 600 mm length. Other taxa recognised include *Neophylloceras groenlandicum*, *Anagaudryceras politissimum*, *A. cf. lueneburgense*, *Saghalinites wrighti*, *Pachydiscus (Pachydiscus) sp.*, *Baculites sp.*, *Acanthoscaphites tridens*, and *Hoploscaphites angmartussutensis*, many taxa similar to those described by Tove Birkelund from West Greenland. Dinoflagellate associations indicate the presence of both Early and Late Maastrichtian. The importance of these new collections is their use with other molluscs, palynology and micropalaeontology to provide a new detailed integrated Cretaceous biostratigraphy for eastern Greenland. CASP and GEUS are currently collaborating in preparing a detailed Kangerlussuaq Basin memoir, including lithostratigraphy and biostratigraphy. The Kangerlussuaq Basin together with the Traill Ø to Hold with Hope region are of major importance to the hydrocarbon exploration industry in the northern North Atlantic region, containing the only onshore exposures of Late Cretaceous sedimentary rocks.

## A new systematic subdivision for the Class Palaeoscolecida Conway Morris and Robison, 1986

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We try to provide some insights into the phylogeny of the Palaeoscolecida. A review of body fossils, isolated material and published information leads to a systematic subdivision based on a biological approach and allows us to recognize certain evolutionary steps. Palaeoscolecidan cuticle possessed up to three sclerite types which can be found isolated.

Our phylogenetic concept is based on the relationships of tubercles (plates) and platelets relative to their position to the epidermal layer. We distinguish four different families. Tubercles and platelets are regularly arranged in the family Palaeoscolecidae. Their sclerites were partly embedded within the epidermis, sitting at the outermost epidermal layer; only their upper central and sculptured part was uncovered. At the lateral-basal part of hadimopanellid tubercles “microwrinkles” display the cover of a soft-tissue. Utahphosidae split off the Palaeoscolecidae and bear similar *Hadimopanella*-like plates, but the amalgamated tubercles form extended conical structures without platelets between the rounded tubercles. In the Verrucotuberculidae sclerite morphologies and irregular platelet arrangements relative to the plates are unique. Basal portions of plates and platelets were above the surface bearing the microplates which was covered by epithelial cells. The Plasmoscolecidae have only larger plates and microplates which were fully uncovered and arranged in two parallel rows per annulum.

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### Difficulty in identifying mass extinctions among tetrapods (Late Permian Early Jurassic)

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The Late Permian to Early Jurassic transition is the most important in tetrapod history, and incorporates two or three posited extinctions; at the end-Permian, end-Carnian (possibly) and end-Triassic. However, because of small sample sizes, these events are hard to establish when the data are inspected closely. Two datasets, one of 814 genera and the other of 208 families, were compiled from the literature and each taxon assigned to categories of body size, diet, habitat and geographic range. Traditional metrics of diversity, extinction and origination failed to produce convincing evidence of mass extinction. However, where stage-crossing taxa alone were considered the two major events (end-Permian and end-Triassic) become more prominent (the postulated end-Carnian event could not be delineated). Chi-square tests compared survivorship and pre- and post-extinction faunas, although the former were plagued by low sample sizes. The most significant ecological changes are associated with the end-Permian event. Jablonski’s model of alternating macroevolutionary regimes is weakly supported, but not contradicted. Similarly differences between extinction events seem to support their contingency.

Further analysis of the datasets included, 1) Pearson chi-square tests of variable independence, 2) measures of endemism using Jacquard’s coefficient of similarity, and 3) comparisons between the two datasets. These results suggest that, 1) the selected ‘characters’ are mostly redundant due to significant levels of association, 2) faunas became more endemic throughout the Triassic (prior to Pangean breakup), and 3) neither genus- nor family-level data is the ideal taxonomic rank in tetrapod macroevolution. Although this study has mostly negative ramifications for future research a possibly rewarding line of enquiry is suggested.

### Soft tissue preservation in Mesozoic gastropods: Image capture and 3D reconstruction

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Only rarely is molluscan soft tissue preserved during fossilisation. However, Jurassic–Cretaceous nerineoidean gastropods possess a complex internal morphology in which the body cavity is constricted by a series of folds of shelly material. The soft tissue comprises a number of lobes constrained and defined by the characteristic internal morphology. Post-mortem this internal morphology facilitated fine sediment ingress in association with soft tissue decay. The sediment enveloped and supported the ducts of the presumed digestive gland/gonad in the body during lithification and diagenesis. In axial section these duct systems are now preserved as distinctive calcite “dots” within the lobes of what was the labile soft tissue in the spire. In three dimensions, it comprises helically coiled calcite rods.

A selection of nerineoidean gastropods preserved in fine sediment (mostly peloidal micrites) were ground axially producing serial sections at 500µm intervals. These were then digitally photographed. Using ‘Corel Draw 9.0’ the calcite “dots” were selected according to their position in the lobes of the soft tissue and copied onto a blank image. Each resulting image was imported into ‘Discreet 3D Studio Max 5.1’ in the corresponding position of the original fossil. The “dots” acted as 3D coordinates which were connected in a helical fashion to make a 3D reconstruction of the duct systems in each specimen.

This method of data analysis has revealed that nerineoidean gastropods possessed at least five individual duct systems presumed to be the preserved duct systems of the digestive gland/gonad.

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### *Oelandocaris oelandica*, the possible earliest stem-lineage crustacean

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*Oelandocaris oelandica* Müller, 1983 was originally described from a single limb-less fragment found in ‘Orsten’ limestones of Upper Cambrian age from the Isle of Öland, Sweden. It has been affiliated with the Crustacea on the basis of its general design, particularly the shallow head shield with a frontal rostrum but short lateral and no posterior extensions. Six additional specimens with preserved appendages discovered subsequently permit a detailed reconstruction of this approximately one millimetre long arthropod. The most significant features of *Oelandocaris* are: a shallow long hypostome with a pair of lobes anteriorly; a huge antennula subdivided into three long,



spine-bearing outgrowths; two subsequent limbs differing from the series of posterior limbs in having segmented exopods. The three anterior appendages were likely involved in food gathering and intake, while the six posterior limbs may have served mainly for swimming. The hypostome with exposed mouth, lack of a labrum and lack of fine setulation in the mouth area suggest a position of *Oelandocaris* in the stem lineage of Crustacea. The characteristic proximal endite, one of the autapomorphies of Crustacea, is developed only in the third limb. *Oelandocaris* may, hence, be regarded as the earliest representative of stem-lineage crustaceans. The striking similarities to the anterior three appendages of the co-existing *Agnostus pisiformis* (Wahlenberg, 1818) raises again the question if the specialisation of these appendages characterize an early phase in the evolution of Crustacea, which would bring the agnostids closer to the crustaceans.

### A new tool for the Gardener of Ediacara

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A major problem in the analysis of extinct non-skeletalised taxa is the lack of life-orientation and taphonomic data. Such information may be obtained through analogue modelling of scaled replicas. Here, a method is proposed for the construction of density compensated, liquid-filled, silicone rubber scale models of creatures which originally lacked true mineralised skeletons. This method was used to model a previously proposed reconstruction for *Ediacaria booleyi*, an enigmatic Cambrian discoidal fossil, of reputed Ediacaran affinity, from Co. Wexford. The reconstruction was modelled initially in self-hardening clay. Once hardened, both surfaces were then cast in clay, creating a two-part external mould, to which the fine ornament was added. A smaller clay insert was constructed, matching the profile of the external mould, so that the model could be created with a hollow interior. RTV 420 Silicone was then poured into each of the half-moulds and the inserts pushed into place. Once set, the silicone was peeled from the mould and the two counterparts joined with a strong adhesive. A particular strength to this approach lies in the fact that the density of the creature being modelled can be finely adjusted by filling the hollow interior with varying proportions of oil and water.

### Preliminary comparative analysis of large and small European neogene mammals: two different diversity dynamics

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The mammalian fossil record is very rich for the European Neogene. A database of more than 1,600 localities that yielded large and small mammals has been built in order to understand better the evolution of mammals' biodiversity, biogeography and communities structure. Throughout the Neogene, important environmental and climatic fluctuations are documented but the link between them and the diverse changes recognized in the faunas stays unclear. The dynamics of extant large and



small mammals' biodiversity exhibits different reactions to the various environmental constraints. Bearing this in mind, our preliminary palaeoecological approach compares the dynamics of Neogene large (ungulates) and small (rodents and lagomorphs) mammals' biodiversity at the regional scale. This spatial scale has proven to be ecologically relevant and enables a reliable estimation of the palaeobiodiversity thanks to the good fossil record available (*i.e.* several localities in each region).

The analyses undertaken involve for both groups of mammals:

- Basic diversity estimators (familial and species richness)
- Equitability measurements (species richness within families and Pielou's index)
- Palaeobiogeography computations (relationships between regions at the continental scale: Raup and Crick similarity index, 1979)

RAUP, D.M. and CRICK, R.E., 1979. Measurement of faunal similarity in paleontology. *Journal of Paleontology*, 53, 1213–1227.

### Unravelling fish swimming trails: a review of the ichnogenus *Undichna*

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Fish swimming trails, assigned to the ichnogenus *Undichna* currently comprise 13 ichnospecies, each consisting of various combinations of sinusoidal waves of differing complexity. Indeed, some of the more complex ichnospecies are made up of elements of the simpler forms. Such ichnospecies could therefore represent undertrails of the more complex forms. Potential taphoseris relationships (*i.e.* preservational variants that reflect, for example, undertrails) between the various ichnospecies are proposed, however, the naming of such simpler ichnospecies is valid if they represent a recurrent morphology. Suggested systematic revisions reduce the number of ichnospecies in *Undichna* to eight. *U. radnicensis*, a highly variable ichnospecies, is a synonym of *U. britannica*, based on material from China that demonstrates they can intergrade. *U. tricosta* and *U. prava* are based upon limited material. *U. tricosta* falls within the minimum diagnosis of *U. simplicitas*, whilst *U. prava* is a partial *U. tricosta*; both are regarded as subjective junior synonyms of *U. simplicitas*. *U. gosiutensis* is based upon a single specimen and is regarded as a junior subjective synonym of *U. quina*. *U. westerbergensis*, attributed to a crossopterygian fish and demonstrating that they used tetrapod-like gaits, is regarded as synonymous with *Lunichnium rotterodium*, which was originally erected for an amphibian swimming trackway.



### Devonian stromatoporoids, tabulate corals and brachiopods from the Northeast Thailand

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In 1928 Bourret observed isolated Devonian deposits for the first time in Thailand. Devonian rocks are exposed both in Northeastern and Western Thailand, but only Northeastern Thailand outcrops provided rich fossiliferous limestone facies. Material collected by Fontaine, Salyapongse and others in several isolated localities is here investigated. In spite of bad preservation and dispersed outcrops, precise determination is sometimes questionable but the fauna appears to be highly diversified. Biostratigraphic consequences and some palaeobiogeographical affinities are attempted.

Stromatoporoids are numerous and well diversified. Dendroid forms are the most representative, with several species of *Amphipora*, *Stachyodes* and some *Vacuostroma*, a genus known until now only from the Devonian of Vietnam and France (Boulonnais). Other recognized genera are *Hermatostroma*, *Clathrocoilon*, *Salairella*, and probably also *Atelodictyon*, *Coenostroma* and *Hermatoporella*.

Tabulate corals are also numerous with predominance of branching forms. Preliminary study allowed recognition of genera *Favosites*, *Echyropora*, *Alveolites*, *Crassialveolites*, *Calipora*, and various indetermined thamnoporids and auloporids.

Brachiopods belong probably to genera *Macropotamorhynchus* (rhynchonellid usually present in Lower Carboniferous), and Devonian *Desquamatia* (atrypid), *Athyris*, *Meristelloides* (athyrids), *Reticulariopsis* (spiriferid).

The stratigraphic range of the investigated fauna is estimated from the Middle Devonian (Givetian) up to locally the Lower Carboniferous.

The domination of dendroid stromatoporoids and branching tabulates indicate a rather calm depositional environment. However, some localities provided debris-like samples, which may indicate a slightly higher energetic environment than the previous one.



### Some data on the Upper Devonian succession of the Shaogun quarries, North Guangdong, South China

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Devono-carboniferous limestones are exploited in quarries near Shaoguan (South China, North Guangdong). These quarries were visited during fieldwork, in August 2002. Some new observations are presented.

In this area, two formations, Shetianquiao and Xikuanshan Fm, are exposed.

The lower (Shetianquiao) formation consists of thick-bedded metric grey dark limestone, sometimes argillaceous and bioclastic, with thinner shale beds.

The upper (Xikuanshan) formation consists also of thick-bedded (0.5 – 2 m) limestone but grey-yellow, micritic and lithographic, with frequent laminations, some oncolitic and bioclastic beds. Fossil traces are frequent, indicating near shore or tidal environments.

Classically, the Frasnian–Famennian boundary is placed at the limit between the two formations, but in this section, this boundary is faulted.

The two formations are poorly fossiliferous but some bioclastic beds provided fossils. The Shetianquiao Fm. has yielded remains of brachiopods (atrypids), associated with rugose (Disphyllid) and tabulate (Syringoporids) corals presumed Frasnian in age. The Xikuanshan Fm. has yielded rare other brachiopods (*Cyrtospirifer* e.g. *brodi* and *Nayunella*) giving a Famennian age.

Near the top of the Shetianquiao Fm., a 0.65 m thick dark shaly bed constitutes a guide level. According to its situation, it could correspond to the Kellwasser event. Samples collected just below and above this level contain Amphiporids. Comparisons are proposed with the Xichun section in Guangxi.

### The Ediacaran phytoplankton and cyanobacteria diversity – a recovery after the Snowball Earth glaciations

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Global radiations of phytoplankton (algal acritarchs) and benthic cyanobacteria are recognized in the Ediacaran Period, preceding the appearance of bilaterian metazoans. The Ediacaran large ornamented acritarchs are morphologically innovative and complex and are known from Australia, China and Siberia, showing a worldwide distribution in a relatively short time interval of ca. 20 Ma. The radiation of more than fifty species of acritarchs at ca. 570 Ma occurred while the Earth experienced severe climatic and environmental changes in the aftermath of the Snowball Earth glaciations and marine anoxia. The records of cyanobacteria are fragmentary and stratigraphically discontinuous, but the occurrence of certain diagnostic species pre- and post-dates the

global glaciations. The Ediacaran diversification may be interpreted as a recovery of marine microbiota after a major extinction caused by the global glaciations. However, the evidence of some persisting taxa, both of planktonic acritarchs and benthic cyanobacteria, speaks against the radical version of the Snowball Earth hypothesis assuming that oceanic photosynthesis and bioproductivity in the ocean collapsed for millions of years because of the ice cover blocking out sunlight.

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### Late Frasnian Atrypida (Brachiopoda) from the Ardenne shelf (southern Belgium)

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In southern Belgium, the atrypid brachiopods were decimated well below the Frasnian–Famennian boundary (Upper Devonian). Within the Late Frasnian formations of the Ardenne shelf, the following genera and subgenera have been recognized: *Costatrypa*, *Desquamatia* (*Desquamatia*), *D.* (*Seratrypa?*), *Pseudoatrypa*, *Radiatrypa*, *Spinatrypa* (*Spinatrypa*), *Spinatrypina* (*Spinatrypina?*), *Spinatrypina* (*Exatrypa*), *Waiotrypa*, and *Iowatrypa*. Their representatives are particularly abundant in the reefal environments. Godefroid & Helsen (1998) noted that their extinctions were linked to diachronous regional facies changes. Indeed, their demise occurred first within the Lower *Palmatolepis rhenana* conodont Zone (top of the Neuville Formation) on the southern flank of the Dinant Synclinorium, and in the Upper *P. rhenana* Zone (top of the Les Valisettes Formation) in the case of the Philippeville Massif. In these areas, the last atrypids have been collected just below the dark limestone bed(s) marking the base of the essentially shaly Matagne Formation expressing hypoxic bottom conditions during sedimentation. Additional data from the northern border of the Dinant Synclinorium and from the Vesdre Nappe showed that the atrypids vanished within the Lambermont Formation (Upper *P. rhenana* Zone), below a level of dark shales formerly included in the Matagne Formation by some authors. In the famous Hony section (northern border of the Dinant Synclinorium), the last occurrence of atrypids is ±9 m below the first Famennian limestone bed of the Early *P. triangularis* Zone.

GODEFROID, J. & HELSEN, S., 1998. The last Frasnian Atrypida (Brachiopoda) in southern Belgium. *Acta Palaeontologica Polonica*, 43, 241–272.

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### Biodiversity and paleogeography of Middle Jurassic ammonites (Upper Aalenian to Middle Bathonian)

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The break up of the Pangea takes place in the Jurassic; the palaeoceanographic consequences are the opening of seaways, particularly at the place of the future Atlantic and Indian oceanic areas. Near the end of the Aalenian, the Ammonitina sub-order undergoes a strong faunal turnover. The last Hammatocerataceae, a well known and diversified Liassic superfamily, gives birth to three distinct superfamilies which will

dominate among others till the end of the Jurassic: Stephanocerataceae, Perisphinctaceae and Haplocerataceae. The analysis of the worldwide corresponding radiation of these three major taxa puts in light differences and similarities between the biogeographic provinces usually recognised.

The counting of the species of each subfamily within the several palaeobiogeographic provinces emphasises faunal similarities in terms of total biodiversity between the several provinces. The North-Western Tethyan provinces share strong similarities between them and with the provinces of the South-West Tethyan margin. The Circum-Pacific provinces gather themselves, underlining their great faunal similarities.

The total time variation of the diversity is expressed by the counting of species in each biozone from the Late Aalenian to the Middle Bathonian. The primary and global signal of the diversity evolution obtained is then independently related to each palaeobiogeographic province. The comparison between the two signals shows the differences of the time evolution of the diversity in the several provinces. The maximum of diversity are often diachronous in the several listed provinces: Early Bajocian in North America; Late Bajocian on the North-West European platforms.

Finally, the palaeogeographic distribution of each ammonite subfamily is used to emphasise the evidence of the several seaways that would exist between the several provinces. The maps which has been constructed for the considered ammonite taxa show that peculiar seaways like the « Hispanic corridor » (Caribbean Tethys), the « South Gondwana » (South Pacific Sea) and the « North Laurasia » (Boreal Sea) bypasses could have been used by ammonites to invade several provinces.

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### Sponging off the poriferans: complex Ordovician ecosystems reliant on spicule-rich sediments

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For understanding the history of life, the development of complex shallow-water ecosystems during the Ordovician is one of the most critical areas in Palaeozoic palaeontology. Siliciclastic sediments often have a very intermittent record in shallow water, with poorly preserved and mixed fossil assemblages, and little lateral continuity. A study of the ecological patterns in well-preserved, shallow-water Llanvirn siliciclastics from the Builth Inlier volcanic island complex, central Wales, has revealed that the distribution of diverse communities is closely linked to the presence of abundant sponges. The gregarious hexactinellids *Brevicirrus*, and especially *Pyritonema*, modified the sediment by producing vast quantities of relatively large spicules (hexactines in *Brevicirrus*, monaxons in *Pyritonema*). These authigenic particles are often larger than the background sediment particles, and would have significantly stabilised the substrate; a similar phenomenon is known in modern polar deep sea floors. In some cases, bryozoans grew immediately around isolated spicules, and a variety of similar interactions are also preserved among other organisms. Further sediment-stabilising strategies followed, including monospecific crinoid thickets and substrate-encrusting bryozoans. The abundant faunas sometimes resulted in local bioclastic limestones. The

development of complex Ordovician shallow-water communities, possibly including the later coral-stromatoporoid carbonate community, was facilitated by the onshore migration of spicular sponges during the Lower Ordovician. The rise of the dominantly sessile, suspension-feeding Palaeozoic Evolutionary Fauna would have been difficult to achieve before this occurred.

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### Exploring the Radiolarian biotic response to the Late Cenomanian Oceanic Anoxic Event (OAE-2) in the tropical Atlantic (offshore Surinam)

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OAEs reflect relatively short periods of environmental perturbations which affected ocean chemistry and productivity, through changes in global climate. Improved understanding of the ecological disruption induced by OAEs to pelagic ecosystems may be obtained by studies of the biodiversity and abundance of planktonic organisms, especially those capable of generating biogenic sediments.

Radiolaria occur rather frequently throughout the Late Cenomanian-earliest Turonian part of finely laminated black shales drilled recently on Demerara Rise (ODP Leg 207) and they are often well-preserved. The observed faunas are of a remarkably low diversity, with a maximum of 14 species per sample and about 40 species in total for the entire Late Cenomanian interval. Assemblages are equally represented by Nassellarians and “Spumellarians”. The presence of six species unknown in time-equivalent diversified Tethyan assemblages is worth noting.

Unlike the sedimentary record of some Tethyan basins, radiolarian abundance not only fails to pick during the OAE-2 event, but with the exception of its initial phase, Radiolaria appear to be entirely absent in this interval. The biogenic silica record of Demerara poses many challenges to biogeochemical models suggested for the OAE-2, involving either volcanically-induced iron fertilisation of oceans or improved recycling of phosphorus following widespread anoxia.

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### Biotic response of Radiolaria during climax of Permian/Triassic Oceanic Anoxic Event

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According to the studies of deep and distal oceanic sedimentary facies, e.g. radiolarites in Japan, the Permo-Triassic time is significantly characterized by the presence of the longest oceanic anoxic event in the Phanerozoic, around P/T boundary. This remarkable

event began in Late Permian and persisted into Triassic, with the climax during early/middle Changshingian to late Induan (e.g. Kajiwaru *et al.*, 1994; Isozaki 1997). In such series, the observed radiolarian biodiversity suggests a rapid change of fauna after the boundary, with obviously observed extremely low faunal diversity in most of the lowest Triassic strata. The origin of this change is still debated; many possibilities can be proposed: a real low diversity, or poor faunal preservation related to sedimentary facies change and/or to oceanic water chemistry change, or the absence of radiolarians in the deposit environment, *etc.*?

The present study is mainly based on two fundamental possibilities: the environment, during this period, generated biomass extinction and/or only the increase of faunal diversity since late Early Triassic time when sufficiently oxygenated oceanic water has been recovered. Comparisons of radiolarian fauna between distal oceanic series (radiolarites) from Thailand and Japan and platform series (shallow siliceous deposits) from South China, focused on Late Permian and Early Triassic radiolarian assemblages, give an attempt to answer this question. Geochemical and physical analyses of these sediments are being studied in order to understand or at least to compare these different palaeoenvironmental rock facies.

Isozaki, Y.(1997) “Permo-Triassic Boundary Superanoxia and Stratified Superocean: Records from Lost Deep Sea”. *Science*, 276, 235–238.

Kajiwaru, Y., Yamakita, S., Ishida, K., Ishiga, H., & Imai, A., (1994) “Development of largely anoxic stratified ocean and its temporary massive mixing at the Permian/Triassic boundary supported by the sulfur isotopic record”. *Palaogeography, Palaeoclimatology, Palaeoceanography*, 111, 367–379.

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### Devonian pelagic bivalves – forgotten and misunderstood

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The Devonian pelagic facies (Bohemian or Hercynian facies) is rich in peculiar bivalves. Despite their great quantity in several different horizons, neither their life habits nor their correct stratigraphic range are well understood. Additionally, no systematic concept is available for classification and phylogenetic development.

Our current knowledge dates back to Münster (1840), Barrande (1881) and Clarke (1904) who erected most of the taxa from the Bohemian and the Laurussian region. But apart from the introduction of names, no details of the internal morphology or species concepts have been presented yet. Since that time, relationships between both the pelagic Bohemian and the nearshore Rhenish faunas also remain virtually unknown.

A characteristic example for these bivalves is the genus *Loxopteria*, erected for three species in the Late Devonian cephalopod limestones from Germany. Members of *Loxopteria* occur in the eastern North American Late Devonian and seem to be present in the Devonian of Bohemia. Morphological characteristics include strongly inequivalve shells with prosogyrate umbos and its bauplan seems to be analogous to species related to *Exogyra* and *Pseudomonotis*. Without bivalved specimens, correlation of right and

left valves remains almost impossible. This feature, however, has caused nomenclatural confusion as left and right valves have often been regarded as separate taxa. Fortunately, several well-preserved specimens offer many details of external and internal morphology including soft tissue attachment. It is expected to get more information on possible life habits of these bivalves in the near future.

Barrande, J. (1881): *Système silurien du centre de la Bohême*. v. 6: published by the author and editor, Prague, Paris.

Clarke, J.M., (1904): *Naples fauna in western New York*, Pt. 2: N.Y. State Museum, Mem.6, Albany.

Münster, G., Graf zu; (1840): *Die Versteinerungen des Übergangskalkes mit Clymenien und Orthoceratiten von Oberfranken*: Beitr. Petrefactenk., 3: 33–121, Bayreuth.

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### Revision and stratigraphical importance of “*Spirifer julii*” Dehée, 1928, a typical spiriferid species from Uppermost Devonian

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In 1929, Dehée created the new species “*Spirifer julii*” to design specimens collected in the “zone d’Etrœungt” of Avesnois by Gosselet, 1880 and called after Dehée by error, “*Spirifer distans*” Sowerby, 1840. Since then, this species has been found in Upper Devonian of many places in the world. In this paper, we revise “*Spirifer julii*”:

- with re-examination of type material kept in the Musée Gosselet, Lille France,
- with study of new material collected in the type locality and stratum typicum in Avesnois,
- with examination of material of different collections coming from neighbouring Belgian and German areas.

This revision led us to adopt, for the moment, the generic assignment of *Sphenospira* Cooper, 1954 to *julii*, already given by some authors. We have effectively observed the presence of remains of frills (one of the characteristics of the genus) in some specimens. However, none of the specimens we have studied shows the delthyrial covering (stegidium) given as another important feature of *Sphenospira* by Cooper. We suggest it could be a problem of preservation.

Finally, we examine critically the citations of *Sphenospira julii* in Uppermost Devonian of varied countries (western Europe, ex USSR territories, North Africa), to show its stratigraphical importance as brachiopod marker.

### Major changes in the early ontogeny of molluscs across the Cambrian/Ordovician boundary

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Minute mollusc steinkerns are abundant in Early Paleozoic small shelly assemblages. These steinkerns represent casts of mollusc protoconchs or early juveniles. Generally, such casts are useless for taxonomic or systematic purposes. However, the size of these natural casts reflects the size of the hatching animal and the amount of yolk within the egg. Therefore, such steinkern faunas can reflect the ontogenetic development of molluscs. Size and shape of mollusc protoconchs from small shelly assemblages across the Cambrian/Ordovician boundary indicate a major evolutionary change in ontogenetic strategies. During the Cambrian, characteristic limpet shaped or coiled molluscs (e.g. *Pelagiella*, *Aldanella*, *Anarbarella*, *Latouchella*) have relatively large, undifferentiated initial parts which indicate non planktotrophic (lecitotrophic or direct) ontogeny. In the Early Ordovician, various forms of gastropod larval shells appear for the first time. The size of the initial part of many of these larval shells suggests planktotrophy. The gastropod protoconchs display a high number of different shapes and many of them are indeed openly coiled. The greater variation of gastropod protoconch morphology reflects the tremendous Ordovician radiation of the Gastropoda and the size indicates that planktotrophy has been acquired at the same time.

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### Phylogeny of early Caenogastropoda: Formation of a superclade

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The Caenogastropoda are one of the most diverse metazoan groups. Anatomical characters form a robust argument for the monophyly of the crown-group caenogastropods. However, the systematic placement of Palaeozoic members is more problematic. New protoconch data suggest that planktotrophic larval shells are shared with the Naticopsidae, a diverse Palaeozoic group which is assigned to the Neritaomorpha. This and the lack of nacre obstruct a clear differentiation between fossil neritaemorphs and caenogastropods. A sister-group relationship seems to be possible which would be in conflict with analyses based on anatomical characters. Openly coiled protoconchs are present in possible Palaeozoic stem-groups of the caenogastropods. This feature was increasingly abandoned during the Palaeozoic and is absent in the Mesozoic. This macroevolutionary loss of openly coiled larval shells in various clades shows that this character cannot be used as an apomorphy. The presence of slits in several Palaeozoic caenogastropods sheds light on the evolution of the mantle cavity. However, a previously suggested relationship to pleurotomarioideans is not supported by protoconch and shell structure data. Ongoing phylogenetic analyses of the Late Palaeozoic and Early Mesozoic caenogastropods show a poor resolution (basal multifurcations) but several clades can be recognized and possible links with Recent gastropods are suggested.

### Cathodoluminescence-spectroscopy of extant and fossil brachiopod shells

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Cathodoluminescence (CL)-microscopy is used for qualitative assessment of diagenetic alteration of fossil shells. CL-spectroscopy provides quantitative analyses. Combined with microprobe elemental analysis, CL-spectroscopy can determine which elements are contributing to luminescence. CL-spectroscopy is, therefore, an extremely powerful tool with which to assess alteration of fossils. CL-microscopy and CL-spectroscopy are applied to extant and fossil brachiopod shells. A detailed assessment of the conditions required for a linear CL response is determined using extant shells before applying CL-spectroscopy to fossils. In CL-microscopy, no luminescence is detected from *Terebratulina retusa* while *Novocrania anomala* emits orange-red luminescence as does *Crania quadrata* (Carboniferous) and *Crania craniolaris* (Cretaceous). In CL-spectroscopy, a 20nA current, applied as a 5µm diameter beam, results in extant *T. retusa* generating almost five times as much luminescence as *N. anomala*. While CL-microscopy displays orange luminescence from both *Crania quadrata* and *Crania craniolaris*, CL-spectroscopy reveals that *Crania quadrata* emits luminescence at 560 nm (yellow) and *Crania quadrata* at 406 nm (blue).

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### Originations and Extinctions of Pennsylvanian Brachiopods: Response to palaeogeographic and climatic changes

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Originations and extinctions of brachiopod faunas have been reported across the Mid-Carboniferous boundary and within the Pennsylvanian in response to palaeogeographic and climatic changes during the Late Palaeozoic. Previous studies were mainly based on analyses of global databases and, therefore, little is known about how the palaeoenvironmental changes affect the faunas regionally. Using a newly compiled 30 Myr record of Pennsylvanian brachiopods from the Great Basin (USA) the following matters are addressed: 1) Examination of species-level origination and extinction patterns; 2) The importance of changing palaeogeography in brachiopod origination events; 3) Causes of long-term extinction of brachiopod faunas.

The results show an extinction event at the Desmoinesian-Missourian boundary and three origination events: at the Mid-Carboniferous boundary, the Missourian-Virgilian boundary, and in the Desmoinesian. The extinction event at the end of the Desmoinesian is related to a warming episode. The appearance of new brachiopod faunas is likely related to migration in response to oceanic currents. The oceanic currents developed during the Pennsylvanian as a result of palaeogeographic changes

that accompanied the formation of Pangea toward the end of the Palaeozoic. These extinctions and originations represent long-term biotic responses to climatic and paleogeographic changes during the Pennsylvanian.

### Silurian midwater communities dominated by ostracods: evidence from fossil assemblages in France and Bohemia

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Much of our information about Palaeozoic marine life is known from shallow water benthic assemblages typically dominated by arthropods (e.g. trilobites, podocope and palaeocope ostracods), molluscs and brachiopods. By contrast, information concerning midwater communities is sparse and fragmentary. In recent years, the study of particular depositional environments such as deeper water black shales has yielded information on possible pelagic inhabitants of the water column, in addition to the ubiquitous planktonic graptolites. This is the case for Cambrian bradoriids (Vannier *et al.* in progress), Early Ordovician phyllocarid crustaceans and Late Silurian myodocope ostracods. Nevertheless, the assumed pelagic Silurian ostracod faunas of Europe (e.g. Great-Britain, France, Sardinia, Bohemia) and Morocco lack detailed studies.

The preliminary results presented here concern two myodocope-dominated assemblages from “black-shale” type deposits: one in Brittany (La Cultais, Armorican Massif, France; Late Wenlock, *Colonograptus ludensis* Biozone); the other from Bohemia (Holy Hill near Lounín, Prague Basin, Bohemia; Mid Ludlow, *Monograptus fritschi linearis* Biozone). At both localities, myodocopes occur with graptolites, nektobenthic cephalopods, phyllocarids and bivalves (epibenthic, nektonic or adapted to oxygen deficient waters). Bottom conditions (disoxyic to anoxic) were unsuitable for benthic faunas. At La Cultais, the most common myodocopes (size from *ca.* 5 to 15 mm) are *Bolbozoe bohémica*, *Bolbozoe anomala*, and cyprinidids. At Holy Hill, *Bolbozoe bohémica*, cyprinidid and *Entomis migrans* (ostracods with a finger-print ornament) are dominant. These ostracods had a non-mineralized, light carapace and external ornament (e.g. reticulated, corrugated, finger-print) typical of some present-day pelagic crustaceans (e.g. halocypridid myodocope ostracods). They were clearly adapted to a free-swimming lifestyle. The composition of modern midwater communities is strongly influenced by environmental parameters (sea temperature, bathymetry, light, food availability). Similarly, some of the differences observed between the French and the Czech assemblages may result from environmental factors. For example, *Entomis migrans* is frequent at Holy Hill and in more proximal settings of the Bohemian Basin (calcareous rocks with abundant bivalves, trilobites and gastropods) but is absent at La Cultais. This would suggest that *Entomis* may have been epipelagic whereas bolbozoids had ecological preferences for deeper (colder) water masses.



**The systematics of the trilobite family Lichidae Hawle & Corda, 1847****J. R. Pollitt<sup>1</sup>, M. A. Wills<sup>1</sup> and R. A. Fortey<sup>2</sup>**<sup>1</sup>*The Department of Biology & Biochemistry, The University of Bath, Claverton Down, Bath BA2 7AY <bspjrp@bath.ac.uk>, <bssmaw@bath.ac.uk>*<sup>2</sup>*The Natural History Museum, Cromwell Road, London SW7 5BD <r.fortey@nhm.ac.uk>*

The first cladistic and Bayesian analyses of the trilobite family Lichidae Hawle & Corda, 1847 are presented. Thirty lichid genera and five lichakephalid outgroup taxa were coded for forty-nine characters using published descriptions. Two methods of phylogenetic inference were adopted: (1) the more traditional maximum-parsimony approach (MP); and (2) the newer Bayesian approach (BI). The majority-rule consensus trees from the MP and BI analyses were topologically similar, but differed principally in the deeper branches (the relationships between major clades). The Lichidae is monophyletic with respect to the Lichakephalidae in both analyses. The Trochurinae (Holloway & Thomas 1988) is well supported by both analyses. Other groups are also supported (*i.e.* Tetralichinae, Echinolichinae and Platylichinae); two, however, are not (*i.e.* Homolichinae, Lichinae). The level of homoplasy found in the dataset (CI=0.4778) is comparable to that found in similar-sized trilobite datasets.

**Deep-oceanic conodonts: are they different?****Carine Randon<sup>1</sup>, Nutthawut Wonganan<sup>1,2</sup> and Martial Caridroit<sup>1</sup>**<sup>1</sup>*UMR-CNRS 8014 (LP3), UFR des Sciences de la Terre, Université des Sciences et technologies de Lille, France <carine.randon@ed.univ-lille1.fr>*<sup>2</sup>*Department of Geological Sciences, Chiang Mai University*

In northern Thailand, radiolarites deposited from Devonian to Triassic times. These continuous, siliceous and biogenic sediments are the witness of an oceanic realm that must have been opened between the Shan-Thai and the Indochina continental terranes and whose size must have been rather large and deep to avoid important detritic and/or carbonaceous sedimentation (at least several hundred of kilometres as the present Red Sea, and several thousands of kilometres during Carboniferous and Permian). Many conodonts were found from these radiolarites and so they are one rare witness of a deep-oceanic conodont fauna. The study focuses on Upper Devonian–Lower Carboniferous conodonts. This oceanic fauna has several features. The elements found are similar to the ones from pelagic limestones (deposited on the continental slope). But they seem to be smaller than the ones from limestones. Are conodont animals from the oceanic environment smaller? Or is this the result of a preferential transportation of smallest elements in the distal area? The study of this oceanic conodont fauna, and its comparison with the ones from limestone deposits, gives a new clue for the understanding of conodont palaeoecology.

**Early Mid Ordovician (Kundun) brachiopods from the Eastern Baltic: Biostratigraphy, palaeogeography and palaeoecology****Christian Mac Orum Rasmussen and David A. T. Harper***Geological Museum, University of Copenhagen, Denmark <c@orum.dk>, <dharper@savik.geomus.ku.dk>*

The Ordovician brachiopod fauna of the East Baltic is abundant, diverse and generally well preserved (Hints & Harper 2003). Whereas the Early Ordovician faunas show strong Gondwanan affinities, the early Mid Ordovician faunas reflect a major biotic turnover in the Baltic palaeobasin. Distinctive brachiopod groups, like the clitambonitoids, which are almost exclusively found in Baltoscandia (Vinn & Harper 2003) are more and more diverse, suggesting the increasing independence of the Baltic fauna during this interval.

New collections based on bed by bed sampling of calcareous tempestites from five localities in Northern Estonia and Western Russia along the Baltic–Ladoga Klint, in the *Asaphus expansus* trilobite zone (Upper Arenig), have yielded a very diverse although not particularly abundant brachiopod fauna. Especially striking are the diversifications amongst the clitambonitides, plectambonitoids and porambonitoids. These groups, together with the orthides, characterize the typical Baltic brachiopod province.

This pattern apparently also continues through the overlying Lower Llanvirn trilobite zones, *Asaphus raniceps*, *A. minor* and *A. pachyophthalmus*, based on detailed sampling in Putilovo Quarry, Western Russia.

Palaeoecological investigations suggest a wide range of ecospace utilization both in marl and limestone facies. Furthermore a series of depth related brachiopod associations are established along the sampled localities.

Hints, L. & Harper, D.A.T. 2003: Review of the Ordovician rhynchonelliformean Brachiopoda of the east Baltic: their biostratigraphy and biofacies. In Harper, D.A.T. & Stouge, S. (eds): *Studies in Ordovician geology: the Baltoscandian region. Bulletin of the Geological Society of Denmark*, 50, 29–43

Vinn, O. & Harper, D.A.T. 2003: Diversification patterns in the clitambonitoid brachiopods of the Ordovician of Baltoscandia. In Harper, D.A.T. & Stouge, S. (eds): *Studies in Ordovician geology: the Baltoscandian region. Bulletin of the Geological Society of Denmark*, 50, 55–61.

**Cut- and Bite-marks on Pleistocene and Holocene mammal bones****Christina Karla Reimann<sup>1</sup> and Manfred Schlösser<sup>2</sup>**<sup>1</sup>*Geologisch-Paläontologisches Institut der Universität Münster, Corrensstr. 24, 48149 Münster, Germany <reimi@uni-muenster.de>*<sup>2</sup>*Westfälisches Museum f. Naturkunde, Sentruperstr. 285, 48161 Münster*

In an old oxbow of the Ems river close to the city of Greven, Münsterland, Germany, a huge amount of Pleistocene and Holocene mammal bones have been found. Many of these different taxa from warm and cold periods show striking bite- and gnaw-marks, as well as cut- and hit-grooves. The marks can be recognized both on domestic animals and on bones of wild forms.

As one source of these marks the proven carnivores (*Crocuta spelaea*, *Panthera leo spelaea*, *Lynx lynx*, *Canis lupus*, *Canis familiaris*, *Vulpes vulpes*, *Felis silvestris*) can be assumed.

The trove of more than 50 human remains and the existence of a mediaeval settlement very close to the sandpit explain the different cut- and hint-marks.

The bone fragments are of great value, as no fossil record has been reported in the archaeological excavations that took place.



### Exceptional three-dimensional preservation in Triassic ostracods

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The exceptional preservation of small Triassic myodocope ostracods from Spitzbergen, first described by W. Weitschat in the 80s, is re-examined here in the light of new SEM studies and microprobe analysis. In addition to fine details of the exoskeleton and carapace structure, Triadocypris displays a wide range of remarkably preserved soft tissues such as appendages (e.g. 5th and 7th limbs bearing setae), appendage and adductor muscles, lateral eyes, gills, cluster of eggs and even ciliate parasites attached to the appendage cuticle. The extremely fine preservation of the soft anatomy of Triadocypris is due to apatite early mineralization. Three different types of microfabrics (see Wilby and Briggs 1997) are recognized: 1) substrate microfabric (apatite microspheres, diameter < 50nm), 2) intermediate microfabric (microspheres between 100nm and 1µm) and 3) microbial microfabric (microspheres < 150nm, preserved bacteria). Experimental taphonomy (E. Renvoisé, in progress) with Recent ostracods is aimed at bringing new knowledge on the processes and environmental parameters involved in the early mineralization of such small crustaceans.

Wilby, P. R. and Briggs, D. E. G. 1997. Taxonomic trends in the resolution of detail preserved in fossil phosphatized soft tissues. *Geobios Mémoire Spécial*, 20, 493–502.

### Distribution of Permian Fishes of Brazil and their palaeoenvironments

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Permian fishes are known from two epeiric basins in Brazil, the Parnaíba and the Paraná basins. During the Early and Late Permian, shallow neritic environments prevailed in northern and north-eastern Brazil, whilst interglacial/periglacial sequences were deposited in the southern states. The climate changed during the Late Permian in the whole of Brazil, with rapid continentalization of the intracratonic basins and shallowing of its aquatic environments. The Asselian-Ufimian Pedra de Fogo Formation (Balsas Group) of Maranhão yielded the lower actinopterygian *Brazilichthys macrognathus* Cox & Hutchinson, the oldest known xenacanthus sharks, namely *Xenacanthus tocaninensis* and *X. maranhensis* Silva Santos, a chimeroid, *Itapyrodus punctatus* Silva Santos and the eugeneodontid *Anisopleurodontis pricei* Silva Santos. From tempestites in the State of Tocantins come new ctenacanthid sharks, comprising spines, teeth and calcified cartilage. A marine sequence ('Budó' beds, Itararé Group, Paraná Basin) in the State of Rio Grande do Sul, considered Late Carboniferous/Early Permian, has yielded symmorid shark teeth and lower actinopterygian remains. Sakmarian marine black shales of the Rio do Sul Formation in Santa Catarina contain palaeoniscid fishes (*Santosichthys mafrensis* Malabarba, *Irajapintoseidon uruguayensis* Beltan, *Daphnaechelus* sp A Richter and others), together with *Coelacanthus* sp. Overlying the Itararé, the Guatá Group contains the actinopterygian *Tholonosteon santacatarinae* Beltan. The Passa Dois Group yielded the most diversified assemblages of fossil fishes in the Paraná Basin, containing the palaeoniscid *Tholonothus brazilensis* Dunkle & Schaeffer, *Rubidus pascoalensis* Richter, a platysomid, xenacanth sharks ('*Xenacanthus*'

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*santosi* Würdig-Maciel, *Xenacanthus pricei* Würdig-Maciel; *Triodus* sp.) and Acanthodidae, hybodontiforms, eugeneodontiforms, petalodontids (Holocephali) and dipnoans (e.g. Gnathorhizidae).

### The true identity of the supposed giant fossil spider *Megarachne*

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*Megarachne servinei* Hünicken, 1980, from the Permo-Carboniferous Bajo de Véliz Formation of San Luis Province, Argentina, was described as a giant mygalomorph spider ('tarantula') and, with its body length of 339 mm, the largest spider ever to have lived on Earth. The interpretation was based on: the carapace shape, position of the eye tubercle, interpretation of the carapace anterior protrusion with median ridge as a pair of chelicerae, and a posterior, circular structure as the abdomen. Morphology hidden in the matrix was suggested by x-radiography: cheliceral fangs, sternum, labium and coxae; and so a reconstruction of *Megarachne* as a giant spider was presented. Difficulties with the interpretation (unusual cuticular ornament, suture dividing the carapace, and spade-like anterior border of the chelicera), together with non-preservation of synapomorphies of Araneae, provoked debate about its interpretation as a spider. Now, the holotype and a new specimen have become available for study. *Megarachne* is not a giant fossil spider; its true identity will be revealed!

### A new Eocene conifer flora from Seymour Island, Antarctica

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Exceptionally well preserved plant material has been collected from new floras in Eocene strata (approximately 50Ma) on Seymour Island, Antarctic Peninsula. The plants are preserved in concretions within the La Meseta Formation, in sediments that formed in a marine shallow shelf environment.

The flora is dominated by well preserved conifer branches, preserved in three dimensions with their leaves still attached. The leaves are often replicated by delicate layers of calcite, which display cellular detail and stomata. The conifers are members of the Araucariaceae and are represented in this flora by intact branches, isolated leaves and cone scales. Several types of angiosperm leaves are also present, but are fragmented and not as well-preserved as the conifer material.

The excellent preservation of the plant material may allow computer-generated reconstruction of the conifers to be made. The fine detail preserved in this araucarian

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flora will provide new information about the biogeography and evolution of these Gondwanan plants, and data collected from the material can be used to infer palaeoclimate and palaeoenvironment in the Antarctic Peninsula region during the late-Early Eocene. This poster outlines conclusions drawn from initial data collection as part of an ongoing PhD project.

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### The Brach Pack: a composite brachiopod fossil from the Silurian Herefordshire Lagerst tte

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Articulate brachiopods are among the most familiar of fossils, but their soft-part record is almost non-existent. No unequivocal fossilised articulate pedicle, for example, has been reported previously, and the soft-parts of major extinct brachiopod clades are known only from analogy and inference. We present here a three-dimensionally preserved strophomenid from the Herefordshire Lagerstätte (Wenlock Series) that provides direct data on the soft-parts of an extinct brachiopod. The specimen probably represents a new genus, and is a juvenile. Its pedicle is robust and nearly as long as the valves, with prominent sub-transverse ridges; it terminates in an array of rootlets attached to a tubular structure in the sediment. The lophophore is a zygalophore, with thickened connective tissues forming prominent lateral lobes fringed by lophophore tentacles. Details of the mantle and canals are also preserved. Small articulate brachiopods are attached to both valves of the strophomenid; two preserve pedicles, and one, probably an atrypid, also bears marginal setae. Other epibionts of uncertain affinity are attached to the dorsal valve. The distribution of this demonstrably *in vivo* epifauna, together with the form and attachment of the pedicle, imply a near-vertical orientation of the commissure, supporting existing models of juvenile strophomenid ecology.

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### Endosymbiosis in corals and stromatoporoids: a new lingulid with preserved pedicle and its trace from the Ordovician and Silurian of eastern Canada

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A new species of the lingulid *Rowellella?* is preserved with a probable pedicle inside the cavities of Trypanites borings, which penetrate tabulate corals and stromatoporoids. The earliest known record of lingulid-coral associations is described from Ashgill tabulate corals preserved on Manitoulin Island, Ontario. Lingulid infestation of

tabulate corals and stromatoporoids is also locally abundant in Ashgill and Llandovery limestones on Anticosti Island, Québec. In all examples, lingulids appear to nestle in previously formed *Trypanites*, likely in a dead host coral or stromatoporoid. In some instances, regeneration of host growth while infested by lingulids is evidenced by a new type of compound trace fossil. Similar endosymbiotic relationships previously observed in Silurian corals from Wales and Sweden suggest that the lingulid association with tabulate corals and stromatoporoids was widespread in shallow marine settings of the Iapetus Ocean.

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### DNA, shell morphology and clades: palaeontological implications of delimiting biospecies in a species-rich radiation of Neotropical snails (Turridae: Polystira)

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Palaeontologists parcel their organisms into species yet there are only a handful of studies that analyse how well morphologically based 'palaeospecies' correspond to Recent species within closely related metazoan clades. How often is membership of palaeospecies liable to be conceptually equivalent to extant species ... occasionally, sometimes, or never? Combined genetic (DNA) and morphological studies of extant species-rich clades can provide clues.

The morphologically unspectacular marine snail *Polystira* ranges through the Late Oligocene to Recent of the American subtropics and tropics and comprises at least 82 living and narrowly separable (semi-cryptic) morphospecies in the Atlantic and Caribbean alone, and probably a hundred or more known extinct species.

Phylogenetic analyses of three gene fragments (16S, 28S, COI) for 25 Recent species produced trees showing almost perfect congruence between genetic clades and independently delimited morphospecies, despite them having been split as finely as possible. Doing so we uncovered many previously unnoticed species that had been concealed by ineffective taxonomy.

Clearly gastropod shell morphology can provide as good resolution of species level clades as DNA sequence. In these cases it will be possible to identify fossils that are conceptually equivalent to Recent biospecies. For *Polystira* this opens the possibility of examining meaningful species diversification dynamics through its fossil record.

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### Reorientation ability in modern and fossil brachiopods: predictions from dorsal pedicle muscle scars

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Size and shape variation of pedicle muscle scars in brachiopods can be used to infer their ability to reorient to ambient currents. Reorientation ability may also help



in competition for space and overgrowth inhibition and in keeping stable position on sediment-water interface. This project is focused on morphometric analysis of dorsal pedicle muscle scars in modern and fossil rhynchonelliform brachiopods. As hypothesized in earlier studies, the size and the inter-scar distance of dorsal pedicle muscle scars should be good indicators of their reorientation ability. Due to a marked decrease in the reorientation ability during ontogeny, modern brachiopod *Terebratalia transversa* provides a potential test of these hypotheses. As follows from this project, *T. transversa* exhibits 1) significantly positive allometry in the inter-scar distance of dorsal adjustors (the distance between adjustor scars becomes relatively larger than the size of cardinalia with growth), and 2) significantly negative allometry in the size of dorsal adjustor scar during ontogeny (adjustor scars become relatively smaller than the size of cardinalia with growth). Therefore, these trends are in accord with the predicted trends which would be expected if there is a decrease in reorientation behaviour during ontogeny. Pedicle scars of several Mesozoic brachiopods are analyzed and compared with these predictions.

#### Diachronous ecosystem recovery after the Late Permian mass extinction event

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In terms of global diversity, the recovery interval after the Late Permian mass extinction event is the longest of all post-extinction recoveries in the Phanerozoic. However, recent, detailed studies indicate that the recovery was a complex affair, with ecosystems in different regions recovering at different rates. Based on their work in the Cretaceous, Kauffman and Harries (1996, *Geological Society Special Publication* 102, pp. 15–39) predicted that post-extinction recovery should be faster at higher latitudes. Is a similar pattern observed after the Late Permian event?

Quantifying biotic recovery is not straightforward. Approaches based on simply counting shelly taxa face the obvious problems of fossil preservation. Also, an increase in diversity does not necessarily equate with an increase in the level of recovery, as alpha diversity may actually increase through the extinction interval with the appearance of numerous, short-lived, pioneering species. Instead, a semi-quantitative 'recovery scale' based on ecological parameters such as tiering, organism size, the dominance and evenness of fossil assemblages, and the presence or absence of specific ichnotaxa was used to assess levels of ecosystem recovery. The fastest initial recovery is recorded in shallow settings of western Neotethys, at tropical southern palaeolatitudes. However, outside Neotethys, in the northern hemisphere, rates of recovery appear to follow the predicted latitudinal pattern, with fastest rates at higher palaeolatitudes.

#### SPARTA (Simulation Package for Area-Taxon Analysis): A tool for testing the relative performance of cladistic biogeographic methods

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Over the past 30 years, numerous analytical biogeographic methodologies have been



devised. The robustness of these methodologies has received limited study, and data on the performance of the techniques are critical in selecting appropriate method(s) for future biogeographic studies. SPARTA (Simulation Package for Area-Taxon Analysis) is a computer simulation that generates coupled area-taxon evolutionary histories. Many user-variable geographic and biological parameters have been incorporated into the model to make it applicable to fields ranging from host-parasite co-evolution to historical biogeography. Rapid generation of large numbers of replicate data sets is a major advance over 'hand-built' data sets. SPARTA can also degrade data to simulate sampling problems associated with the fossil record. A program implementing the modified version of Brooks Parsimony Analysis proposed by Lieberman has also been written, to allow detailed analysis of the performance of this relatively new technique. Trial versions of both freeware programs will be presented at the meeting. Comparative tests of the ability of the various cladistic biogeographic methods to recover accurately "known" area-taxon histories generated by SPARTA are now underway. The outcome of these tests will provide clear guidance as to which method(s) are optimal for particular classes of evolutionary problems.

#### Chitinozoans from historical type areas and key sections in the UK: Towards a biozonation for the Upper Ordovician on Avalonia

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Working towards an Upper Ordovician chitinozoan biozonation for Avalonia, several historical type areas and other UK key sections were investigated. These include the Onny Valley, Shelve Inlier, Cautley district (type Ashgill area), Pus Gill, Greenscoe and Cardigan area (see poster Vandenbroucke & Williams) sections. Preliminary data from the Whitland section will be included. Eleven biozones are recognised, reflecting Baltoscandic, Gondwanan and endemic Avalonian affinities. The recognition of the Baltoscandic *Fungochitina fungiformis* Zone in the Onnian and Pusgillian of the Pus Gill section, and in the Pusgillian to lowermost Cautleyan of the Cautley district is of particular interest, allowing a tight correlation between both areas and demonstrating that the base of the Ashgill Series lies within the *F. fungiformis* Zone, rather than in the stratigraphically higher *Tanuchitina bergstroemi* Zone, as previously assumed. The Baltoscandic chitinozoan biozones are consequently better tied to the British chronostratigraphy. In addition, the co-occurrence of the *F. fungiformis* biozone (Van Nieuwenhove *et al.*, in prep) with the *Amorphognathus superbus* conodont biozone (Smith, 1999) in the Greenscoe road cutting fits with the records from the Cautley district (Orchard, 1980). The Pus Gill Onnian below the FAD of *F. fungiformis* is correlated with the topmost Onnian in Onny Valley.

ORCHARD, M. J. 1980. Upper Ordovician conodonts from England and Wales. *Geologica et Palaeontologica*, 14, 9–44.

SMITH, C. J. 1999. Evolutionary palaeobiology of deep water conodonts. Unpublished PhD thesis, University of Durham.

## Upper Ordovician chitinozoan biostratigraphy of the Cardigan area, southwest Wales

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The Caradoc rock succession between Fishguard and Cardigan has been remapped (Davies *et al.*, 2003) and studied for graptolites (Williams *et al.*, 2003). Thirty-five samples have been studied for chitinozoans. Although not extremely well preserved or rich, the chitinozoan assemblages have good potential for correlation with the Baltoscandian biozonation, and with several assemblages from northern England. Occurrence of the index fossil of the Baltoscandic *Cyathochitina reticulifera* chitinozoan Subzone, within the Newport Sands section (*clingani* graptolite Biozone, *morrisi* Subzone), together with *Spinachitina ?coronata*, *Lagenochitina baltica* and *Lagenochitina prussica*, indicate the *F. fungiformis* chitinozoan Biozone, although the index fossil itself has not been reported from Wales. The latter biozone has been reported from northern England, where it spans the base of the Ashgill.

Higher in the Cardigan stratigraphy, *Tanuchitina ?bergstroemi*, the index fossil of the eponymous Baltoscandic chitinozoan biozone overlying the *F. fungiformis* biozone, is reported from Frongoch (SN 0749 4108), at the level of the *Pleurograptus linearis* graptolite Biozone. The *bergstroemi* Biozone can tentatively be correlated with post-*fungiformis* levels in the Type Ashgill area. Preliminary chitinozoan-based correlations suggest that the base of the Ashgill in the Cardigan area is slightly lower in the rock succession than suggested by the graptolites.

DAVIES, J. R., WATERS, R. A., WILBY, P. R., WILLIAMS, M. & WILSON, D. 2003. The Cardigan and Dinas Island district – a brief explanation of the geology. 1:50 000 Series England and Wales Sheet 193 (including part of sheet 210). Keyworth: British Geological Survey.

WILLIAMS M., DAVIES J. R., WATERS R. A., RUSHTON A. W. A. & WILBY P. R. 2003. Stratigraphical and palaeoecological importance of Caradoc (Upper Ordovician) graptolites from the Cardigan area, southwest Wales. *Geological Magazine*, 140, 549–571.

## Tuzoia: a giant bivalved arthropod of the Cambrian seas

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The external morphology and soft anatomy of *Tuzoia* are interpreted in the light of new observations of specimens from both the Middle Cambrian Burgess Shale (British Columbia, Canada) and Kaili (Guizhou, China) Lagerstätten. *Tuzoia* was a very large (up to 180 mm long) bivalved arthropod with a non-mineralized dome-like carapace often strengthened by prominent pointed features (cardinal angles, posteroventral spines) and flanked by a long lateral ridge bearing a spiny frill. Huge stalked, spherical eyes protruded through the anterior notch. Other information on its soft anatomy (e.g. gill-like structures) indicate that *Tuzoia* had possible flap-like (not leg-like) trunk appendages. The reticulate ornament of *Tuzoia* is comparable with that of present-day crustaceans (e.g. myodocope ostracods) and may have been produced through epidermal cells underlying the cuticle. Reticulation is interpreted as a structural compromise between exoskeletal lightness and high resistance to mechanical stress. This ornament may have improved the hydrodynamics of the animal in water (e.g. swimming, sinking). *Tuzoia* typically occurs as laterally (lc) or dorsoventrally (dvc) compressed carapaces or single valves. Each type (lc or dvc) emphasizes particular aspects of the morphology (e.g. spiny lateral ridge, ventral margin) that were often mistakenly interpreted by former authors, leading to numerous unnecessary taxa and taxonomic confusion. A revision of *Tuzoia* is proposed with nine different species instead of 21. *Tuzoia* sp. nov. is described from the Burgess Shale. *Tuzoia* is tentatively placed within a group of large bivalved arthropods along with *Isoxys* and *Zhenghecaris*, that may have affinities with thylacocephalans (Lower Cambrian-Upper Cretaceous). In the Middle Cambrian, *Tuzoia* distributes across Laurentia, South and North China and the peri-gondwanan area (Bohemia) within a narrow transequatorial belt indicating high dispersal capabilities and latitudinal control, presumably related to sea temperatures. Functional morphology and distributional pattern both suggest that *Tuzoia* was a free-swimming arthropod.

**Konservat-Lagerstätten from the Arenig (Early Ordovician) of Morocco****Peter Van Roy<sup>1</sup>, Joseph P. Botting<sup>2</sup>, Thijs Vandenbroucke<sup>1</sup>, Dirk Van Damme<sup>1</sup> and Kay Van Damme<sup>3</sup>**<sup>1</sup>*Department of Geology & Soil Science, Ghent University, Krijgslaan 281/S8, B-9000 Ghent, Belgium* <peter.vanroy@ugent.be>, <thijs.vandenbroucke@ugent.be>, <dirk.vandamme@ugent.be><sup>2</sup>*Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, UK* <joseph00@esc.cam.ac.uk><sup>3</sup>*Department of Biology, Ghent University, K.L. Ledeganckstraat 35, B-9000 Ghent, Belgium* <kay.vandamme@ugent.be>

Exceptional fossil deposits preserving labile tissues are of primary importance for understanding ancient ecosystems and metazoan evolution. These “Konservat-Lagerstätten” have an irregular temporal distribution, being most common during the Cambrian and Jurassic. Ordovician labile tissue preservation is exceedingly rare; only two major occurrences have been described: Beecher’s Trilobite Bed (U.S.A.), and the Soom Shale (Republic of South Africa), respectively of Caradoc and Ashgill (Late Ordovician) age. Here we report the discovery of labile tissues in several outcrops of Arenig (Early Ordovician) mud- to fine sandstones of the Upper Fezouata Formation northeast of Zagora, Morocco. Most fossils are of benthic organisms preserved essentially *in situ*. A rich classical shelly fauna, including abundant articulated echinoderms, is complemented by several elements that are usually not preserved: articulated specimens of typical Burgess Shale-type sponges like *Choa*, *Pirania* and *Hamptonia*; soft-bodied vermiform organisms, including probable annelids and a possible planarian; a cheloniellid arthropod; a *Tremaglaspis*-like arthropod; large bivalved arthropod carapaces; an articulated plumulitid machaeridian; and a tuboid graptolite and perhaps *Clonograptus* preserving soft tissues. Also noteworthy are “wrinkled” trilobites, co-occurring with undeformed specimens, and probably representing freshly moulted, soft individuals. Although labile-tissue preservation is not abundant in the area, it is widespread, suggesting it may occur through the entire formation. The Moroccan Konservat-Lagerstätten are not only important because of the general rarity of Ordovician labile-tissue preservation; they significantly pre-date the two previously described major occurrences, providing an improved view of early Ordovician faunas, and significantly reducing the large temporal gap between Cambrian and Ordovician Konservat-Lagerstätten.

**A Late Ordovician aglaspidid arthropod from Morocco****Peter Van Roy***Department of Geology & Soil Science, Ghent University, Krijgslaan 281/S8, B-9000 Ghent, Belgium* <peter.vanroy@ugent.be>

Aglaspidids are a group of predominantly Cambrian arthropods. The Order Aglaspidida is rather poorly defined, but the possession of a paired post-ventral plate is generally regarded as a unique character identifying this clade. The systematic placement of aglaspidids is problematic. Here, a possible aglaspidid from a sandstone outcrop in the Ashgill (Late Ordovician) of the Ktaoua Group east of Erfoud, Morocco is discussed. Although disarticulated, the single specimen provides enough information to reconstruct the exoskeleton. The wide prosoma carries a pair of eyes and exhibits a faint glabella



area. A median notch divides the anterior prosomal doublure and accommodates the anterior part of a hypostome-like plate bearing a pair of large lateral wings. The faintly curving tergites are arranged parallel to each other and the body terminates in a relatively short tail spine. Below the posterior tergites and the base of this tail spine, a paired post-ventral plate is located. In general appearance, the prosoma of the new fossil somewhat resembles that of the problematic Caradoc arthropods *Zonozoe* and *Zonoscutum*. While considered to be a typical trilobite character, a hypostome-like plate was also described in the Tremadoc (Early Ordovician) aglaspidid *Tremaglaspis*. However, the anterior plate of the Moroccan fossil most strongly resembles that of the problematic Early Cambrian arthropods *Kodymirus* and *Kockurus*. A structure similar to the aglaspidid post-ventral plate is also present in the Middle Cambrian arthropod *Emeraldella*. It is apparent that, in order clearly to define Aglaspidida and to establish aglaspidid relationships, a revision of all relevant taxa is needed.

**How small mammal fossils accumulate: an example from the Late Eocene of the Isle of Wight****Katerina Vasileiadou<sup>1</sup>, Jerry Hooker<sup>2</sup> and Margaret Collinson<sup>3</sup>**<sup>1</sup>*Royal Holloway University of London, Dept. of Geology, Englefield Green, Surrey TW20 OEX, UK* <k.vasileiadou@gl.rhul.ac.uk><sup>2</sup>*Natural History Museum, Department of Palaeontology, Cromwell Road, London SW7 5BD, UK* <j.hooker@nhm.ac.uk><sup>3</sup>*Royal Holloway University of London, Dept. of Geology, Englefield Green, Surrey TW20 OEX, UK* <m.collinson@gl.rhul.ac.uk>

Micromammalian fossils have been collected from the Osborne Member, Headon Hill Formation, Late Eocene, NW Isle of Wight, and their taphonomic history is being studied. The cheek teeth of the theridomyid rodents *Isoptychus* and *Thalerimys* are described in terms of postmortem modifications shown on their enamel and dentine (*e.g.* etching, cracking, scratching). More than half of both the *Isoptychus* and the *Thalerimys* teeth show etching of the enamel attributable to digestion. The distribution of the teeth in etching groups shows different patterns for the two genera. Furthermore, 42% of the *Isoptychus* teeth and 31% of the *Thalerimys* teeth show cracking of the dentine (on occlusal surface and/or roots) attributable to sub-aerial weathering. No substantial skull elements were found and none of the teeth of either genus show polishing or rounding.

The likely process for the accumulation of most, if not all, of the *Isoptychus* and *Thalerimys* remains is predation by an avian or mammalian carnivore. It is possible that the predator is different for the two genera. Much of the material was exposed on the surface for some time before being incorporated into the sediments. The remains may have been subjected to trampling by other animals but have not been transported for long distances by water. Thus, the two theridomyid rodents belong to the local micromammalian community.



## Complex dynamics and Self-Organized Criticality might describe biodiversity patterns of Palaeozoic marine microphytoplankton

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Classic interpretations of marine microphytoplankton biodiversity patterns in the Phanerozoic emphasize the importance of external causes («environmental pressures») on the shaping of diversity curves, tending to find *ad hoc* cause-effect explanations for any given specific bio-event. Marine transgressions are generally believed to promote diversity increase among the microphytoplankton, and the opposite is assumed for regressions. Glaciations are causally associated with extinction events. Catastrophes such as bolide impacts have been invoked to explain inferred (but not adequately documented) microphytoplankton «mass extinction» events for example at the Ordovician–Silurian transition.

Analyzing the Palaeozoic fossil record of the acritarchs, I demonstrate that such kinds of “regular” relationships are not so obvious as normally considered.

I then test the hypothesis that the fossil record of marine microphytoplankton reflects the evolution of a highly connected natural system which has reached a state of Self-Organized Criticality (SOC), and that diversity fluctuations might result also from spontaneous generations of patterns independently from external physical controls. The quasi-linear power-law distributions of extinction/origination events and of species life spans of Ordovician acritarchs supports the SOC hypothesis which also may constitute the ground for explaining the observed decoupling between acritarch and marine invertebrate diversities and the enigmatic “Carboniferous phytoplankton blackout”.

## Occurrence of the trilobite *Taihungshania* on the North Gondwana margin during Lower Ordovician

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The trilobite genus *Taihungshania* is known to occur in South China, Iran, Turkey (Taurides), Sardinia (Italy), Montagne Noire (southern France) as well as in its western prolongation in Aquitaine basin (cored well samples). The terrigenous nature of deposits and associated sedimentary structures give evidence of an open platform depositional environment, between the median part of upper offshore up to proximal part of lower offshore in Sardinia, Montagne Noire and Iran.

According to recent studies about the larval development of *T. miqueli* (Bérard *et al.* 2000), it is expected that *Taihungshania* had a planktic mode of life during protaspid stages—which could represent a relatively short period of larval dispersion—and then adopted a benthic mode of life at the transition protaspid/meraspid period.

The specific habitat and inferred short period of larval dispersion of *Taihungshaniids* confirm close palaeogeographic relationships between South China, Iran, Turkey,



Sardinia, Montagne Noire and Aquitaine basin during Lower Ordovician. Moreover, stratigraphic and systematic comparisons show the precise migration route of this fauna along the North Gondwana margin.

## The Lower Cambrian *Halkieria* is a mollusc

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The Lower Cambrian *Halkieria evangelista* Conway Morris and Peel, 1995 was in its final description interpreted as part of the brachiopod stem group, and a link between the brachiopods and annelids, as sister groups, was suggested.

Although a number of authors have indicated molluscan affinities of *Halkieria*, none (apart from Runnegar 2000 and 2002) has systematically examined the halkieriid characters and compared them to those of living molluscs.

We have compared all the preserved morphological details of *Halkieria* with those of living molluscs, especially polyplacophorans. We have also tried to deduce the growth manner of the halkieriid scleritome by comparing smaller and larger specimens.

We have found agreement in almost all important details. The combination of a dorsal integument and shells growing by marginal accretion, together with spicules being replaced as well as being arranged in the marginal zones of similar morphology, are consistent with the interpretation of *Halkieria* as a mollusc. The spicule and shell mineralogy in the halkieriids has been argued for by previous workers as being aragonitic; this further supports a molluscan relationship.

## Affinities of Ordovician conulariid faunas from Central Anti-Atlas (Morocco) and Barrandian area (Czech Republic)

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Close affinities of the Ordovician conulariid fauna were observed in the North Gondwana (Central Anti-Atlas, Morocco) and peri-Gondwana (Barrandian area, Bohemia) regions. Both regions are assigned to the EAP (*Exococonularia-Archaeoconularia-Pseudoconularia*) cool-water conulariid province (Van Iten-Vyhlasová, 2004) which confirms current palaeogeographical reconstructions of the Ordovician period.

The study was based on the set of 124 specimens from Anti-Atlas (Morocco) and more than 600 specimens from the Barrandian area (Czech Republic). The following species were identified to be identical in both areas: *Pseudoconularia grandissima*, *Exococonularia consobrina*, *Conularia (Archaeoconularia) insignis*, *Metaconularia imperialis*, *Metaconularia anomala*.

A very favourable preservation of the specimens from Central Anti-Atlas allowed us to identify new morphological features; e.g. first observation of the sculptured periderm on the surface of the species *Anaconularia anomala* is new proof for its classification among the genus *Metaconularia*. Newly studied morphological characteristics combined with the micromorphological analysis can help to improve the systematics of this group.

Brabcová, Z., Van Iten, H. (2004): Conulariids. pp.119–123. – In Barry D. Webby, Florentin Paris, Mary L Droser, and Ian G. Percival: *The Great Ordovician Biodiversification Event*. Columbia University Press, New York. 484 pp.

### Ordovician conulariid diversity in the periGondwana and Baltica regions – a summary with a special view to the Ordovician of Barrandian

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High biodiversity of the suborder *Conulariina* Miller and Gurley, 1896 is exhibited globally at the Middle-Upper Ordovician. In contrast to the Cambrian from which no genera is described, first occurrences of eight genera are documented from the Middle-Upper Ordovician of the periGondwana and Baltica regions.

The Perigondwana is characterised by the cool-water EAP (*Exoconularia-Archaeoconularia-Pseudoconularia*) conulariid province (Van Iten – Brabcová, 2004) typical of the following other species: *Anaconularia*, *Conularia*, *Conulariella*, *Eoconularia* and *Metaconularia*. Host rocks of these genera are usually fine-grained sandstones, shales, exceptional preservation is in iron ores. All the forms are medium to big conulariids with well-developed sculpture. The genus *Conulariella*, typical for its rectangular cross-section and smooth transversal ribs, is characteristic only for the Arenigian of Bohemia. The EAP Province includes France, Bohemia, Thuringia, Sardinia, Morocco, Turkey and, probably, Jordan.

The palaeocontinent Baltica is assigned to the warm-water CC (*Conularia – Climacoconus*) conulariid province with the following other representatives: *Archaeoconularia*, *Conularina*, *Ctenoconularia*, *Eoconularia*, *Exoconularia*, *Glyptoconularia*, *Metaconularia* and *Pseudoconularia*. Host rocks are most often carbonates or cratonic basin shales. The CC province representatives are small to medium conulariid forms characteristic for its simple sculpture.

Brabcová, Z., Van Iten, H. (2004): Conulariids. pp.119–123. – In Barry D. Webby, Florentin Paris, Mary L Droser, and Ian G. Percival: *The Great Ordovician Biodiversification Event*. Columbia University Press, New York. 484 pp.

### New fossil arthropods and the evolution of the cephalic feeding system of arthropods and crustaceans

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New information brought up from the Upper Cambrian ‘Orsten’ stem-lineage crustacean *Oelandocaris oelandica* Müller, 1983, and of several Lower Cambrian Arthropoda s. str. from the Chengjiang biota in China aided to enlighten the evolutionary path of the feeding system in the head of Arthropoda and toward the crown group of Crustacea in particular. We suppose that from a rather simple mode of food intake by the first antenna, a first significant change occurred by the formation of a rigid but flat basipod for proximal food manipulation towards the mouth at the rear of the hypostome. In the stem lineage of Crustacea, the two post-antennal limbs and associated structures modified in a special way in two major steps: 1) inwardly oriented exopod setation; lobe-shaped ‘proximal endite’ medially and basally to the basipod; 2) enlargement of ‘proximal endite’ into a ‘coxa’ portion proximal to the basipod in antenna and mandible in the Labrophora. This significant step was coupled with: development of a fleshy labrum at the rear of the hypostome; recession of the mouth in an atrium oris; fusion of the sternites of the post-oral head segments (= sternum); paragnaths on the mandibular sternite; fine setulation on all structures around the mouth. This concentrated food intake and manipulation to this region.

### Faunal, sedimentological and geochemical indicators of dysoxia in Cretaceous marine sediments

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Cretaceous marine sediments worldwide are characterised by the occurrence of ‘Oceanic Anoxic Events’—periods of widespread dysoxia during which organic matter was extensively deposited in ‘black shale’ facies on the shelves and ocean basins. These events are of considerable importance as some are major source rocks for hydrocarbons. Although many Cretaceous black shales have been characterised in terms of their organic geochemistry and carbon isotope stratigraphy, little work has been undertaken on the palaeoenvironmental signatures of dysoxia, and the recognition of grades of dysoxygenation.

Although diverse criteria for the recognition of low oxygen levels have been described, both at present and in the geological record, these have not been fully calibrated against each other. Initial work on the Folkestone Gault Clay is presented, where faunal indicators of palaeo-oxygenation are compared with sedimentological and geochemical proxies for dysoxia. Conclusions are drawn on the applicability and resolution of such palaeoenvironmental indicators with reference to their potential use in quantifying grades of dysoxia within Cretaceous marine shales.





## Embryonic development of the priapulid worm *Priapulus caudatus* L. and its phylogenetic significance

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Stem group members of the Priapulida are known from the early Cambrian. Today the phylum is classified as a member of the group Cycloneuralia (Ehlers *et al.* 1996) together with nematodes, kinorhynchans, loriciferans and nematomorphs. The embryonic development of *Priapulus caudatus* has been monitored from the first cell stage until the “loricate” larva stage for the first time. Priapulids are the only cycloneuralians that are likely to have a primitively large body size, and potentially at least, a relatively unmodified development. They may thus help us to resolve the early evolution of Ecdyzoa (cycloneuralians plus arthropods). One particularly important question that can be addressed with the help of this study is whether or not the segmental and coelomate features of the arthropods have been lost in the cycloneuralians or have been secondarily gained in the arthropods themselves. Resolving these questions would have an important bearing on our views of the bilaterian ancestry of these important morphological features, and thus on our understanding of the early fossil record of animals.

## Enigmatic fossils from the Soom Shale lagerstätte, South Africa

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The Soom Shale Lagerstätte from South Africa is the only known Ordovician deposit with exceptional preservation equivalent to Cambrian occurrences at Chengjiang in China and the Burgess Shale of Canada. The horizon is located within the Cedarberg Mountains and is one of the most fossiliferous units in the Table Mountain Group. Organisms found to date include eurypterids, conodonts, orthocones, brachiopods, algae and a multitude of enigmatic forms. Soft tissues have been replicated by clay minerals and a high level of detail has been preserved. Examples include eurypterid musculature and respiratory structures, orthocones with radulae, brachiopods with pedicles and conodonts with preserved features of the head and trunk. In this study the documentation, analysis and identification of the enigmatic forms from the Soom Shale is bringing to light evidence of a greater diversity of organisms from this lagerstätte. Currently analysis is being focused on several arthropod like forms. Results test whether enigmatic features recognised in some Cambrian fossils persisted into Ordovician times.

## Using guano as a tool in unravelling Cambrian palaeoecology

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Defaecation is an essential part of most animals' alimentary process. As such, when preserved, it provides us with important information about who was eating whom in an



ecosystem. An exceptionally well-preserved faecal pellet assemblage from the Middle Cambrian Mount Cap Formation in Canada shows a wide diversity in faecal pellet forms. Analyses of their morphology and contents allow deductions to be made about the producer and the food consumed, respectively, and shows that the complexity of the Cambrian ecosystem was already well developed. Thus we have a novel approach for gaining insight into the Cambrian ecosystem and this highlights the potential of using faecal pellets as a tool to help determine the palaeoecology of other systems.

## Late triassic radiolarian from northern Thailand and its bearing on the palaeogeographic interpretation

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Excellent preserved Carnian and Norian (Late Triassic) radiolarians have been discovered from the bedded chert and siliceous–argillitic limestone sequences exposed at north of Mae Sariang city, westernmost of northern Thailand. The radiolarian assemblage including *Multimonilis* YEH has been reported from Norian in East Central Oregon of North America. These taxa are the characteristic species of the *Corum Parvum* assemblage and can be correlated to a biostratigraphic position of *Xipha straita* subzone. Therefore this assemblage is considered to be early to middle Norian (but not younger than late middle Norian) age. The presence of the faunas of the same assemblage in two different sedimentary facies in the area suggests the lithological transition of the sequence of the Late Triassic sediment reflects the change from deep to shallow marine environments or the narrowing of the ocean. Moreover, the occurrence of the Carnian to Norian radiolarian assemblages from these distal and proximal oceanic facies shows that the closure of the Palaeo-Tethys Ocean between the Shan-Thai and Indochina allochthonous continental terranes in this area was not prior the middle Norian time. And the similarity of fauna of Tethyan affinity to those of European Tethys and North American and Japanese oceans also suggests that this ocean was connected to the other oceans (at least by seaway). Based on our newly obtained data the closure of this ocean may have started during Late Permian or Early Triassic and the definitive closure was after middle Norian time. Owing to this very important palaeontological information the palaeogeographic scene of the palaeo-ocean between the two main continental terranes at late stage, which formed Southeast Asian mainland today, is now very much understandable.

## Wallowaconcha in the United Arab Emirates – a Late Triassic bivalve a long way from home

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Enigmatic fossils were discovered during recent fieldwork by the British Geological Survey (BGS) in the northern United Arab Emirates (UAE). The material consists of shells of the bivalve *Wallowaconcha*, a large Late Triassic bivalve with highly specialised morphology. *Wallowaconcha* is characterised by large size, thick shell and large wing-like folds of the shell wall extending from an inflated body chamber. The wings consist of parallel surfaces linked by vertical plates and were used by the animal as stabilisers for a reclining life habit on the sediment surface. 'Wing' fragments are the most common fossils found in the UAE deposits, but a few more complete valves have been found. The material occurs at three separate localities within the Ghalilah Formation (Elphinstone Group) in the UAE, dated as Late Triassic (Norian) on the basis of bivalve and brachiopod faunas. Hitherto, *Wallowaconcha* has only been recognised in displaced island arc terranes with North America tectonic affinities located in eastern Panthalassa, a palaeogeographically distant area from central Tethys in the Late Triassic.

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### Parasitism in favositids (Tabulata)

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Organisms described by Sokolov as genera *Chaetosalpinx*, *Camptosalpinx*, *Phragmosalpinx* and one genus described by Oekentorp, *Helicosalpinx*, of unknown taxonomical position, were considered in the literature as commensal organisms of favositids.

On account of the following characters:

- position between corallites,
- sometimes present in the lumen of corallites,

it seems that these organisms must have perforated the soft body of favositid colony. Such perforation probably enabled an interaction between the host and the perforating organism that was negative for the host (because of perforation and perhaps also metabolic interaction) and positive for the perforating organism (in other cases this organism would not perforate). Their relationship can therefore be described as parasitism.

The character of the relationship between other organisms known concurring with favositids (e.g. genera *Asterosalpinx* Sokolov, *Actinosalpinx* Sokolov) and their hosts remains unknown.

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### Radionuclides within shell of freshwater mollusc

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Radioactive elements are among commonly detected components of the shell material in any group of modern shelly fauna due to bioaccumulation from the environment.

However, their concentrations in the samples are usually extremely low, therefore information on the distribution and behaviour of radionuclides within shell matrix of hydrobionts cannot be obtained from the samples collected from the natural environment even in highly polluted areas. However, such knowledge is important and could be applied in neontology, palaeontology, and biomineralogy. In this presentation we show results of the study of the <sup>241</sup>Am-doped shell material of the bivalve freshwater mollusc *Dreissena polymorpha* after contamination through the water pathway in controlled laboratory conditions. The aim of the study is to trace a distribution of this radionuclide within the shell of the mollusc using a cathodoluminescence analysis. Our data suggest a high capacity for incorporation of this radionuclide in mollusc shells in laboratory conditions. The cathodoluminescent images of Am-doped shells (containing about 0.00005 wt.% of Am) in transverse sections were characterized by light bands of blue-green colour which are parallel to the shell surface and corresponded to different shell layers. Maximum intensity corresponds to the mineralized layers boundaries containing membranes and therefore characterized by high organic content. However, there is still some uncertainty in the discrimination of the Am separately from organic and mineral components of mollusc shells, which is the subject of further investigations.