THE SECOND INTERNATIONAL PALAEONTOLOGICAL CONGRESS
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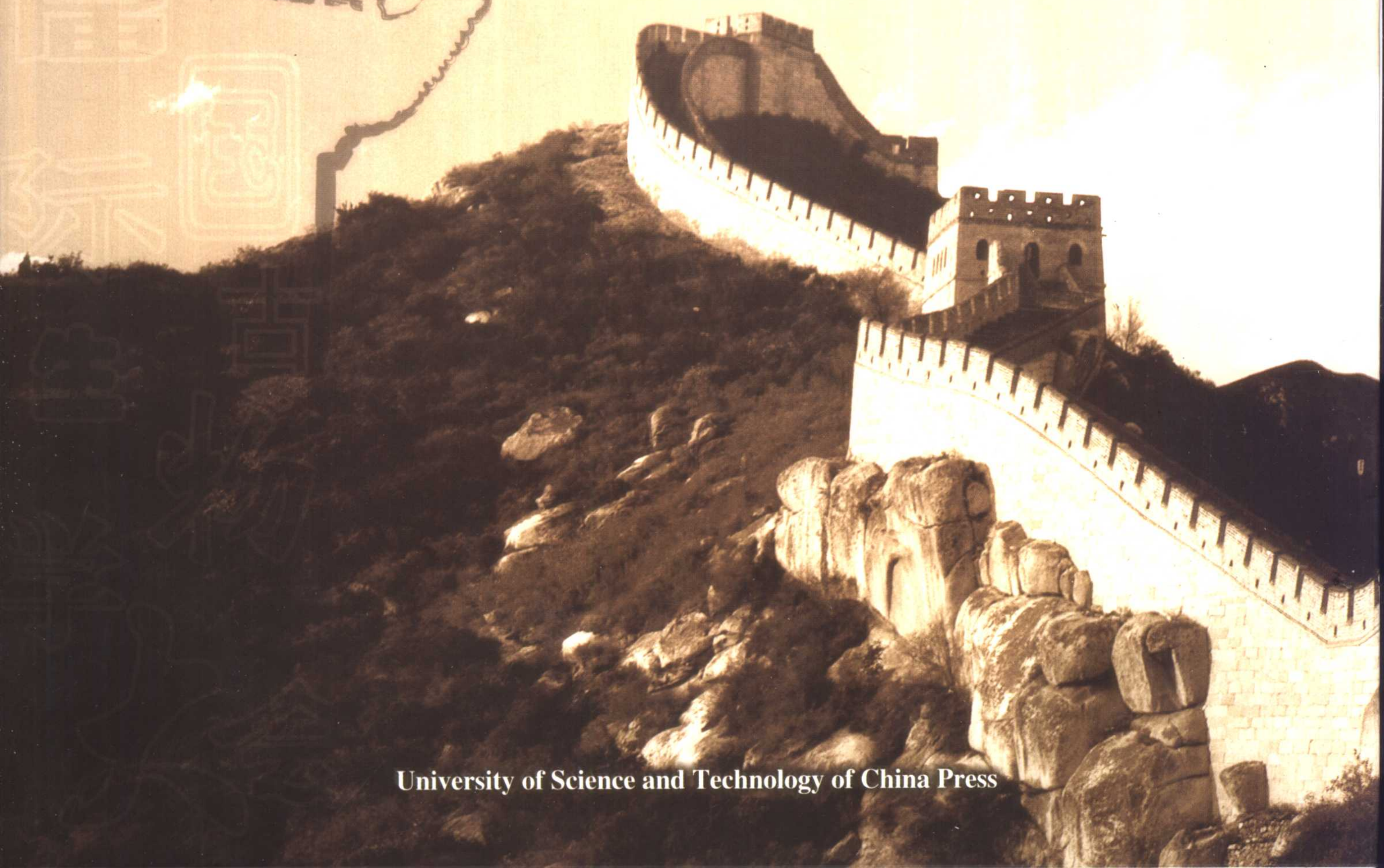
JUNE 17–21, 2006, BEIJING, CHINA

ANCIENT LIFE AND MODERN APPROACHES

ABSTRACTS OF THE SECOND INTERNATIONAL PALAEONTOLOGICAL CONGRESS

Editors
Qun Yang
Yongdong Wang
Elizabeth A. Weldon



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内容简介

本书收编了第二届国际古生物学大会（2006，北京）论文摘要 680 篇，作者来自全世界 50 多个国家。比较充分地反映了当前国际古生物学领域的最新学术动态、新发现和新的研究成果。适合于地球科学、生命科学、古生物专业和相关科研与开发人员及研究生等读者参考、阅读。

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—Abstracts of the Second International Palaeontological Congress

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FOREWORD

Yugan JIN

Convener, Second International Palaeontological Congress (IPC2006)
Vice President, International Palaeontological Association
Academician, Chinese Academy of Sciences

Following the success of the First International Palaeontological Congress (2002, Sydney), the Second International Palaeontological Congress (June 17-21, 2006, Beijing) - IPC2006 - has attracted even a larger group of palaeontologists and scientists of related disciplines from worldwide, thanks to the sponsorship of the International Palaeontological Association, the Palaeontological Society of China and relevant government agencies, to the hard work service provided by the Chinese Organizing and the Executive Committees, and to tremendous support from our colleagues worldwide. A number of national and regional academic organizations, including Europe, Japan and USA, have also provided financial support to encourage younger researchers to take part in IPC2006.

Under the congress theme of *Ancient Life and Modern Approaches*, we have assembled more than 45 titles of special, general, topical symposia and workshops, organized by many active scientists from around the world. Chinese colleagues along with their collaborators from other countries have successfully organized about 10 pre-, mid- and post-congress field excursions, providing an opportunity for international delegates to examine some of the most exciting fossil sites in China, including the fantastically well preserved Neoproterozoic, Palaeozoic and Triassic fossil biota and stratigraphy in south and southwest China, Palaeozoic and Mesozoic sections in Tibetan Himalayas, terrestrial Mesozoic rocks and fossils in northwestern China's Xinjiang Uygur Autonomous Region, the famous Jehol Biota in northeast China's Liaoning Province, and Cenozoic fossil sites in Shaanxi Province and Nei Mongol (Inner Mongolia) Autonomous Region of north China. These carefully selected localities certainly represent a good sample of palaeontological and stratigraphic discoveries made by Chinese scientists in recent history.

There is no doubt that IPC2006 will greatly facilitate academic exchange among participants from different countries, promote research collaborations internationally, and provide an opportunity for worldwide delegates to better know China and its fossil treasures.

As the convener of IPC2006, I would like to extend my appreciation to all participants for their support and hope that every participant can use this opportunity for scientific exchange and future communication.

PREFACE

Ancient Life and Modern Approaches is a fitting theme for the 2 Second International Palaeontological Congress. The contributions to this volume highlight new and exciting discoveries, as well as theoretical and methodological advances that have taken place in palaeontological research in the four years since the 1st IPC in Sydney. But it is not only by the introduction of new techniques, such as obtaining 3-D images of fossils using X-ray computed tomography and the integrated evo-devo-palaeontology approach, that our field will advance over the next years. New initiatives such as Palaeoparks and Geo-biodiversity have the potential to capture the public's interest and carry our field into the future.

We hope that the abstracts presented in this volume offer a stimulating read and provide you with interesting ideas to further your own research. It is important to remember, as we broaden our horizons from ichthyosaurs to isotopes and from gingkos to glaciation, that at the base of our research is the ever present need for sound taxonomy. It is encouraging to note that many new species are proposed and described herein, further acknowledging this core aspect of our research. However, please note that this publication is not valid for taxonomical and nomenclatural purposes (based on Recommendation 8E, of Article 8.2 of the ICZN 4th edition, online). We look forward to the formal validation of these new species in future publications.

A total of 680 abstracts, submitted by participants from over 50 countries, are presented in this volume, a number far surpassing our expectations. They are grouped in the proposed congress session programme (i.e., Plenary, Special, General and Topical sessions). Although some of sessions may not run for oral presentations in the final congress programme, the session titles and their designated abstracts are retained in this book.

We heartily thank all the contributors, and in the short time available to us we hope that in this publication we have done justice to the effort you have put into your research. Please accept our apologies for any omissions or errors. Many of the abstracts were reviewed by session conveners and we would therefore especially like to thank them for this service.

We would also like to thank our colleagues and graduate students for their organisational and collative work. In particular, we are grateful to Yunbai Zhang and Zhefeng Gao for their professional assistance in editing. Special thanks are due to Caihua Lin, Longhua Deng, Sengui Zhang, Yan Shi, Peiyun Cong, Qing Ni and Kaijun Bao for their technical and editing assistances.

It is with great anticipation that we invite you to peruse this volume. We hope it generates new cooperative research projects that can be reported on at the next IPC in 2010.

Qun YANG and *Yongdong WANG*
Nanjing Institute of Geology and Palaeontology
Chinese Academy of Sciences

Elizabeth A. WELDON
China University of Geosciences, Wuhan

25th May, 2006

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Plenary Session

[PS-1]

CLOSING THE GAP: INTERMEDIATE CHARACTER SUITES AND LIFESTYLES AT THE FISH-TETRAPOD TRANSITION

P. E. AHLBERG

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It is now 19 years since the discovery of articulated *Acanthostega* material in East Greenland sparked off a new wave of research on the earliest tetrapods and their fish ancestors (Clack, 2002). During that time the subject has changed beyond recognition, with a wealth of new data leading both to the stabilisation of the large-scale phylogenetic framework and to the framing of ever more precise evolutionary questions. There is now a robust consensus that the tetrapods are monophyletic; that the lower part of the tetrapod stem group is composed of "osteolepiform" fishes; that the most crownward of these fishes are the "elpistostegids" such as *Panderichthys* and *Tiktaalik* (Daeschler et al., 2006; Shubin et al., 2006); and that all known Devonian tetrapods belong to the stem group rather than to the crown Tetrapoda. Because osteolepiforms, elpistostegids and Devonian tetrapods all appear to be paraphyletic segments of the tetrapod stem group rather than "side branch" clades, character change along the stem lineage can now be investigated in remarkable detail. Perhaps the single most important conclusion is that of elpistostegid paraphyly, with *Elpistostege* and *Tiktaalik* located crownward to *Panderichthys*, as this defines a suite of transitional characters for a short segment of the tetrapod stem. These include a body form that is tetrapod-like but retains the short tail and small pelvic fins of fishes, a shoulder girdle with an expanded coracoid plate pierced by a large foramen, a humerus that is tetrapod-like but with a narrower entepicondyle, a robust tapering radius, and a short, wide spiracular tract bounded posteriorly by a hyomandibula that has lost its distal half compared to that of osteolepiforms. These morphologies must be directly antecedent to those of the earliest tetrapods, but in some instances the gap is still very wide. This is particularly so in the limb, where even *Tiktaalik* presents no wholly convincing digit homologues. The evolution of the wrist and ankle from the earliest tetrapods to the base of the crown group indicates that an important boundary exists between the centrals and distal carpals/tarsals, at which new elements differentiate in a distal direction from the limb skeleton and in a proximal direction from the digits. This suggests that the digits are in origin semi-independent structures, not simply distal outgrowths of the preexisting limb skeleton. The pectoral fin radials of the Recent lungfish *Neoceratodus* originate separately and attach themselves to the fin axis in a comparable manner; similarities in gene expression suggest this process may have a level of homology with tetrapod digit development. Closing the gap between elpistostegids and tetrapods will require further fossil discoveries, but precisely targeted comparisons with the most primitive known tetrapods, such as *Ventastega*, will also be highly informative.

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Shubin, N.H., Daeschler, E.B., Jenkins Jr, F.A., 2006. Nature, 440: 764–771.r

[PS-2]

MOLECULAR TAPHONOMY

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The bulk of the fossil record consists of biomineralised remains, but deposits that preserve soft-bodied organisms also provide critical evidence of the history of life. Preservation of labile tissues like muscle requires replication by authigenic minerals, whereas more recalcitrant materials, such as the cuticle of eurypterids and insects, graptolite periderm, leaves and woody tissues, form organic fossils. The preservation of such organic remains was long considered to be primarily a product of decay resistance (selective preservation) but recent investigations have shown that the process is more complicated. This change in our understanding is a result of the investigation of ancient biomolecules in identifiable organic remains (e.g. leaves and insect fossils). This is a different approach to the usual application of biomarkers in organic geochemistry: for example, to determine the origin of sedimentary organic matter and kerogen, and to provide evidence of early life in Archaean and Proterozoic rocks. In situ biomolecules (those in identifiable organic remains) can provide chemosystematic and phylogenetic data and yield environmental indicators. Coupled with isotopic analyses (compound specific carbon and hydrogen isotope signatures) they provide a tool for investigating ancient CO_2 concentrations, temperature and precipitation patterns, and ancient physiological adaptations. In situ biomolecules also allow the calibration of organic maturity and diagenetic processes, because the original composition of the fossil material can be inferred by comparison with modern organisms, allowing diagenetic changes to be reconstructed. Most organic remains of identifiable fossil organisms (e.g. insects, leaves) are preserved as biopolymeric materials that are insoluble in organic solvents. Analysis using Pyrolyis-Gas Chromatography/Mass Spectroscopy shows that their composition is usually aliphatic. Their preservation has been explained by the presence of similar aliphatic components in living organisms: cutan in leaves, for example. This can not explain the preservation of insects, however, as insect cuticles do not contain a decay-resistant aliphatic component; recent work has also shown that cutan is not widespread in leaf cuticles. It appears that the fossilisation of organic material often involves the transformation of the original composition by a process of in situ polymerisation. Investigation of this diagenetic process involves a variety of methods: the analysis of living organisms; decay experiments to determine the loss of molecular components; electron microscopy to document the nature of material and changes in its structure with time; analysis of a sequence of young to progressively older fossils to show changes with time; laboratory maturation experiments to explore the result of varying starting materials and temperatures and duration. Fossils are analysed using a range of methods, some of which involve chemical degradation (thermochemolysis, oxidation). These different approaches are yielding a clearer understanding of the processes leading to the preservation of organic fossils, particularly leaves and arthropod cuticles. They are also revealing the nature of biases in the fossil record of terrestrial plants and insects. In addition, this research provides insights into the formation of Type I/II kerogens, which are similar in composition to the fossils.

Keywords: ancient biomolecules, cuticle, diagenesis, taphonomy

[PS-3]

THE GREENING OF EARTH AND ITS CONSEQUENCES

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The early and mid Palaeozoic colonisation of land surfaces by plants was accompanied by ever-increasing diversity and complexity in vegetation and ecosystems, by transformation of landscapes, and by changes in lithosphere and atmosphere. This lecture will trace the early records of interactions between terrestrial plants, invertebrates and fungi and show how they contributed to the evolution of a series of novel habitats at the interface between rock and air with profound consequences for both chemical weathering and atmospheric composition.

[PS-4]

THE CAMBRIAN RADIATION

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The origin and diversification of the metazoan is one of the major evolutionary transitions in the history of life. Over the past two decades paleontologists and others have produced a remarkably robust picture of the geological, geochemical and biological events during the late Neoproterozoic, enabling the testing of a variety of hypotheses about driving forces behind this diversification. Geochronologists have produced a highly resolved temporal framework, demonstrating that the Ediacaran Fauna is more closely associated with the Cambrian explosion than previously believed, establishing the ages and estimating the durations of several of the major Neoproterozic glaciations, and constraining the pattern of changes in carbon and other stable isotopes. Recent work on sulfur isotopes is beginning to constrain apparent increases in atmospheric oxygen that occurred at this time. Other aspects of the geochemical record are now known in far greater detail, and improved correlations have established how changes in stable isotopes relate to paleontological and geological events. The fossil record of this event has been enormously enriched with the discovery and continuing description of the widespread Chengjiang fauna of Yunnan Province, the continuing investigations of the Doushantuo fossils, and new work on the Middle Cambrian Kali biota. Paleontologists have been enormously fortunate that biologists have greatly contributed to this field through the introduction of molecular data and phylogenetic techniques for the reconstruction of metazoan phylogeny, and the wealth of data on developmental evolution which has arisen through comparative evolutionary developmental biology.

The principle questions about the Cambrian Radiation are: Why did it occur when it did, rather than earlier or later? And, What was responsible for the extraordinary rapidity and morphologic breadth of this event? Attempts to answer these questions fall into four different areas: 1) Environmental triggers, including the late Neoproterozoic glaciations, changes in ocean chemistry and an increase in atmospheric oxygen; 2) developmental and genetic factors, including the introduction of new families of transcription factors which increase the potential range of morphologies which can be produced by metazoans; 3) ecological factors, ranging from predation to the construction of new niche relationships; and finally, 4) suggestions that various aspects of the Metazoan radiation are artifacts. While environmental factors seem increasingly likely as triggers for the event, there is no logical explanation of how they could have been responsible for the rapidity or the breadth of the diversification of metazoans. As more and more taxa have been analyzed developmentally, it is becoming increasingly clear that much of the developmental complexity of metazoans was present in cnidarians, with few obvious innovations at the base of the Bilateria, eliminating developmental innovation as an explanation. Artifacts of various kinds can also be excluded. The generation of new ecological interactions thus seems the most likely explanation of the breadth of the metazoan diversification, probably through positive feedback effects.

Keywords: Cambrian, Metazoan diversification, evolution and development, paleoecology

[PS-5]

SECRETS OF CRETACEOUS FLOWERS UNRAVELLED BY X-RAY TOMOGRAPHY

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Exquisitely preserved flowers from the Cretaceous have been studied for more than 25 years. The flowers are typically minute and charcoalified, preserving the 3-dimensional shape and an amazing degree of structural detail. Many of the flower types occur in great numbers in the fossil assemblages, and reconstructions of external and internal features have been made by combining information from scanning electron microscopy (SEM) and serial sectioning. Mechanical sectioning or opening of the minute and often brittle fossil flowers is, however, no trivial task, and many flowers have been destroyed during the preparation process without providing the information that was sought. Further, even among more abundantly occurring floral structures, specimens with more or less complete preservation of organs are not common, and many taxa are known only from a single or a few specimens. Retrieving information on internal structures from such flowers has typically required mechanical dissection of unique specimens. This has been done, for instance, for the Early Cretaceous flower *Teixeiraea* described recently from Portugal based on a single flower. The flower had the staminate organs clearly exposed, but stamens obscured the centre of the flower. The only way to establish sexuality was to remove parts of the androecium to expose the central region of the flower. This was done successfully in the sense that it could be documented that the flower was unisexual without remains of pistillate organs, but after the dissection the specimen now consists of several fragments instead of a single flower, and further analyses of floral organisation is strongly limited.

Synchrotron-radiation X-ray tomographic microscopy (SRXTM) applied to these charcoalified flowers shows that destruction of specimens is no longer necessary to retrieve information on internal structures. The method has already been applied to a variety of microfossils, including Cambrian embryos. To test the method on fossil flowers we selected a number of taxa for which external morphology and internal structures were relatively well known. Information retrieved from traditional mechanical sectioning and SEM was compared with the results obtained from the SRXTM studies. We selected several simple floral structures as well as a more complex flower. The simple flowers show adaptation to wind-pollination with a single whorl of perianth parts and one or a few ovules. They are assigned to the Normapolles complex, an extinct group of plants related to the eudicot order Fagales. Internal structures such as organisation, number and position of ovules are crucial for the systematic assessment of these fossils. We also studied the more complex flowers of *Scandianthus costatus,* which is an extinct form with characters indicating insect pollination. *Scandianthus* was chosen to investigate the degree of resolution of, for instance, vascularisation of the tissues and ovary structure in a flower with more floral organs.

SRXTM yields 3-dimensional information providing the traditional longitudinal, transverse and tangential sections as well as a direct means of linking external features with the internal structures. Flowers may be reconstructed in exact detail for visualisation purposes. Rather than piecing together information from sections or pieces of different flowers, we can now gather comprehensive information on the full anatomy of individual specimens. The SRXTM scans have also revealed astonishingly fine details at the cellular level. SRXTM is clearly a very powerful tool for retrieving maximum information from charcoalified fossil flowers.

Keywords: anatomy, fossil flowers, non-destructive method, X-ray tomography

[PS-6]

THE END-PERMIAN MASS EXTINCTION: PROGRESS AND PERSPECTIVES FROM CHINA

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The end-Permian mass extinction has been unanimously ranked as the greatest mass extinction during the Phanerozoic, eliminating about 95% of all the species in the world's ocean and also heavily affected terrestrial ecosystems (e.g. Erwin, 2006). Although it has been extensively studied, its causes remain a mystery. In China, intensive investigations have taken place in high-resolution biostratigraphy (Sheng et al., 1984), analytic palaeobiology and computer modeling (Jin et al., 2000), microstratigraphy and sedimentology, geochemistry (Cao et al., 2002) and geochronology (Bowring et al., 1998). These investigations have occurred in different facies and different palaeogeographical settings including southeast China, southwest China, Tibet and northwest China.

Careful analyses show that the widely perceived end-Permian mass extinction actually consisted of two phases, one at the end-Guadalupian which is either called the pre-Lopingian crisis or the end-Guadalupian mass extinction (Jin et al., 1994; Stanley and Yang, 1994; Wang and Sugiyama, 2000; Shen and Shi, 2002; Yang et al., 2004) and another at the close of the Changhsingian (Jin et al., 2000). Relatively little is known about the first phase in comparison to the second. What has been recognised however, is that the pre-Lopingian crisis is much less pronounced than the second extinction event (Shen and Shi, 2002), and it is taxonomically selective and possibly palaeobiogeographically different in severity (Wang and Sugiyama, 2000; Shen and Shi, 2002; Yang et al., 2004). Corals and fusulinids experienced significant decline, brachiopods, foraminifera, bivalves and gastropods, however, did not show distinctive changes (Jin et al., 1994; Shen and Shi, 2002). The crisis was associated with a major global regression. A dramatic $\delta^{13}C_{carb}$ depletion was recognised at the Guadalupian-Lopingian boundary (Wang et al., 2004; Kaiho et al., 2005). Although the pre-Lopingian crisis may be consistent in timing with the Emeishan igneous province in South China, the cause-effect links between them remain unclear.

Detailed statistical analyses based on high-resolution biostratigraphy and geochronology suggest that the effects of the end-Changhsingian mass extinction were rather rapid or even catastrophic, and probably lasted less than a couple of hundred thousand years or possibly even less than tens of thousands of years (Bowring et al., 1998; Jin et al., 2000; Xie et al., 2005). The sudden disappearance of fossil groups happened in various depositional environments from terrestrial to marine, from littoral, carbonate platform, reef, slope to basinal facies. It is also comparable in timing and pattern to the extinction event in the peri-Gondwanan region of southern high palaeolatitudes (Shen et al., 2006). A rapid climatic warming event is indicated by the southward invasion of various warm-water faunas in the peri-Gondwanan region. Rugose corals, brachiopods, fusulinids, ammonoids, etc. all turned out to be the victims of this bioevent. Recent investigations into the terrestrial alluvial, marine/nonmarine transitional and littoral Permian-Triassic boundary (PTB) sequences in southwest China also reveal a rapid climatic drought and deforestation of the tropical *Gigantopteris* megaflora which is synchronous with the mass extinction of marine organisms. The end-Changhsingian event was associated with a sharp negative drop of both $\delta^{13}C_{carb}$ and $\delta^{13}C_{org}$, which occurs slightly below the PTB in both marine and terrestrial sequences. A rapid transgression also began in the latest Changhsingian, frequent volcanic activities indicated by multiple ash beds occur near the Permian-Triassic boundary, and widespread anoxic conditions prevailed during the extinction and its aftermath intervals (Grice et al., 2005; Xic et al., 2005).

The temporal coincidence between the extinction event and the flood basalt in Siberia (Renne et al., 1995), and evidence of climatic warming (greenhouse effect) possibly derived from carbon dioxide released from frequent volcanic eruptions suggest that volcanism is probably the most plausible causal links between the eruptions and the mass extinction. This scenario is also supported by widespread multiple ash beds or tuffs near the PTB in South China. However, the China ash beds are from pyroclastic volcanism, probably from northern Vietnam or southern China, rather than from the Siberian flood basalts based on the presence of bi-pyramidal quartz, which is associated with subduction-related volcanism. Therefore, to establish a close cause-effect link between volcanism and mass extinction remains a task for future multidisciplinal research (Erwin et al., 2002). The geochronogical and statistical evidence of a catastrophic extinction at the close of the Changhsingian continues to activate the scenario of an extraterrestrial impact as the cause of the extinction. The most suggestive evidence of this scenario is the presence of helium and argon trapped in a variety of fullerences (Becker et al., 2001). However, experimental results of Becker et al. (2001) were not validated by the subsequent study. Microspherules possibly related to volcanism or impact have been widely reported from the PTB sections in south China (Yang et al., 1991). However, sources of the PTB microspherules remain unclear in terms of their chemical composition and abundance. Sedimentological evidence of anoxia advanced by Wignall and Hallam (1992) has been widely recognised in South China based on the lithologic and community shift, frequent occurrences of framboidal pyrite and a biomarker of Chlorobiaceae across the PTB (Wignall and Hallam, 1992; Grice et al., 2005; Xie et al., 2005). However, the evidence for anoxia could reflect extinction rather than anoxia (Erwin et al., 2002).

In order to unravel the cause(s) of the end-Permian mass extinction, a detailed working plan was made recently. Two wells were drilled in 2004 at a quarry near the PTB GSSP section in Changxing, Zhejiang Province, SE China. A total thickness about 340 m of the cores was collected. In addition, large quantities of very fresh samples from the quarry at Meishan have been accomplished by blasting quarry faces. Research programs including an integrated succession for the Lopingian Series, timing of the end-Permian event, a blind test for the suggested extraterrestrial event, organic geochemical evidences and co-evolution in the

Permian-Triassic terrestrial and marine ecosystems are suggested.

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[PS-7]

MOLECULAR EVIDENCE FOR RADICAL CHANGES IN OCEAN CHEMISTRY, GLOBALLY, ACROSS THE PERMIAN TRIASSIC BOUNDARY

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The Late Permian mass extinction was most extensive in Earth's history, resulting in around 90% of marine animal species, and many terrestrial taxa, becoming extinct. Shallow and deep water anoxia, euxinia, global warming, Siberian Trap volcanism, collapse and oxidation of methane hydrates, sea level change and bolide impact are among the proposed causes of the extinction event.

Samples from outcrop, and from a new core drilled through the Permian-Triassic (P-Tr) Boundary at the type marine section at Meishan, have been examined for biomarker and isotopic evidence of environmental and associated biotic change. Late Permian sediments from Meishan Beds 22-30 are characterized by indicators of anoxia including low Pr/Ph ratios and abundant aryl iosprenoids and isorenieratane derived from the precursor carotenoid isorenieratene. These latter biomarkers, derived from brown species of green sulfur bacteria (Chlorobiaceae), are considered reliable indicators of euxinic water columns where hydrogen sulfide extends into the photic zone. Highest abundances of Chlorobiaceae biomarkers occur through Beds 24 to 27 and so bracket the major extinction horizon evident in ash Bed 25. Additional sub-maxima of Chlorobiaceae biomarker abundances, at Beds 30, 35 and 37 in the early Triassic and coincident with monotonous bivalve debris suggestive of mass extinction, indicate that pulses of photic zone euxinia occurred well after the Permian and may have caused the biodiversity recovery to be protracted.

The prevalence of aryl isoprenoids and isorenieratane is also recorded in a recently cored borehole, Hovea-3, of the Perth Basin, Western Australia (Grice et al., 2005). Other, well-established, boundary sections in Tibet and at the Great Bank of Guizhou, had similar biomarker patterns as did two sections outside the Tethys realm, in Western Canada and at Kap Stosch in East Greenland. In fact, the presence of biomarkers for Chlorobiaceae at six separate locations, worldwide, indicates that water column euxinia was pervasive during and after the extinction event and suggest that sulfide may have been a key toxic agent, as is supported by the photochemical modeling studies of Kump et al. (2005). Widespread outcropping of anoxic sulfidic waters onto continental shelves compromised aerobic habitats and might ultimately have allowed a hydrogen sulfide plume to influence continental regions and compromise terrestrial organisms (Kump et al., 2005). Further evidence for widespread euxinia comes from $\delta^{34}S$ isotope studies on sulfate and sulfide minerals at P-Tr sections from numerous locations worldwide (e.g. Nielsen and Shen, 2004).

At Meishan, a pronounced negative C-isotopic excursion of around 4 per mil for kerogen is evident reaching a maximum near the top of bed 26 (black shale layer). This, and roughly parallel shifts in carbonate $\delta^{13}C$, have been observed in other P-Tr sections worldwide. The carbon isotopic excursions, and accompanying anomalies in nitrogen and sulfur isotopes, indicate there was a major reorganisation of the global carbon cycle over the P-Tr Boundary. Biomarker and isotopic anomalies found for Meishan have much in common with those observed in black shales deposited during the early Aptian, late Cenomanian and late Frasnian oceanic anoxic events. This suggests globally pervasive euxinia is not a rare phenomenon and may explain many of Earth's major mass extinctions.

Keywords: Permian, extinction, biomarkers, euxinia

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[PS-8]

NEW DISCOVERIES FROM THE JEHOL BIOTA: BIOLOGICAL AND GEOLOGICAL IMPLICATIONS

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The Early Cretaceous Jehol Biota from Liaoning Province and neighboring areas in northern China has yielded, in the past two decades, a plethora of exceptionally preserved fossils such as birds, dinosaurs, mammals, pterosaurs, lizards, aquatic reptiles, amphibians, fish, insects and plants, which have helped to revolutionize our views on the origin and early evolution of birds, the radiations of dinosaurs, pterosaurs, early mammals and flowering plants *etc*. Many of the vertebrate fossils were also preserved with skin, scales, fibers, feathers, hairs and other integumentary structures, as well as stomach contents such as gizzard stones, seeds, leaves, and mammal, lizard, dinosaur and fish remains. These fossils have proven to be critical for reconstructing paleobiological features.

New taxa from the Jehol Biota continue to be discovered at an enormous pace. Vertebrates comparable to those from Liaoning are now being recovered from Gansu Province, the westernmost margin of the Jehol distribution. Bird footprints of similar age were reported from Shandong Province in eastern China. Further, discoveries concerning the diet, habit, development and behavior of Jehol vertebrates are receiving more attention thanks to the extremely complete preservation of specimens in this Early Cretaceous lagerstätten, which is comparable to the Late Jurassic Solenhofen lagerstätten. In particular, the first pterosaur embryo and the earliest avian embryo strongly suggest that both pterosaurs and early birds were precocial in their developmental mode. In addition, many three dimensional specimens are preserved (in mainly tuffaceous sediments), such as a troodontid theropod found in sleeping posture, a congregation of 34 juvenile and one adult individuals of the ceratopsian *Psittacosaurus* (indicating the presence of parental care), and the largest known Mesozoic mammal *Repenomamus*, which contains baby dinosaurs in its stomach, constituting the first evidence for mammals eating dinosaurs.

Several recent ^{40}Ar-^{39}Ar dates obtained from feldspars of the interbedded tuffs of the Jehol Group, which comprises, from the bottom up, the Dabeigou (131Ma), Yixian (125Ma) and Jiufotang (120Ma) formations, have provided the most direct age for these fossil-bearing sediments. Combining these chronological results, we estimate that Jehol Biota existed for at least 11 Ma. The evolutionary radiations of the Jehol Biota, which can be roughly divided into three stages, corresponding to the three Jehol formations, are characterized by fossil assemblages of variable abundance and diversity, and with a trend of progressively expanding geographic distribution and an increasing percentage of cosmopolitan taxa present.

The evolution of the Jehol Biota occurred against the backdrop of a global geological background of high tectonic activity, strong volcanic activity, and increasing atmospheric CO_2 and paleotemperature. Evidence of frequent volcanic eruptions is lavishly recorded in the Jehol sediments in nearly all stratigraphic horizons. The recognition of seasonal diet switching in birds is consistent with the occurrence of large seasonal variation in temperatures during the Early Cretaceous. Local geology in Liaoning reflects the impact of increasingly active West Pacific tectonics on northeast China during the Early Cretaceous.

Discovery of Jehol fossils in such abundance and diversity, as well as an understanding of their geological background, enables us to understand their evolution in an ecological perspective. The active volcanic eruptions could have led to the frequent turnover of the ecosystems and speeded selection and hence speciation processes. Further, our current knowledge of various animal and plant groups enables us to reconstruct a preliminary image of the food chain of the Jehol ecosystem. Interactions among various groups are better understood thanks to the new information uncovered from recently discovered fossil evidence. For example, the two competing flying vertebrate groups, birds and pterosaurs, could have contributed significantly to the geographic dispersal of plants. Considering the appearance of various biological taxa with a modern appearance or connection, the Jehol Biota can probably be regarded as a prelude to the emergence of modern terrestrial ecosystems.

Keywords: Jehol Biota, Early Cretaceous, evolutionary radiation, geological background

S1. Palaeoembryology and developmental biology in Earth history

[S1-1]

CAMBRIAN FOSSIL EMBRYOS FROM HUNAN, SOUTH CHINA

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Palaeoembryology was preceded by the discovery of fossilised embryos of Middle Cambrian (Zhang and Pratt, 1994). This discovery was quickly followed by two more exciting reports, i.e. Bengtson and Yue (1997) and Xiao et al. (1998), which led several international research groups to focus on recovering animal embryos of the Ediacaran and the earliest Cambrian rather than those of Middle Cambrian. Consequently, important new finds and controversial interpretations of fossil embryos were published (for references, see Chen, 2004; Donoghue and Dong, 2005). In contrast to fossil embryos of the Ediacaran and the earliest Cambrian, little attention has been paid to those of Middle and Late Cambrian age. We began to do field work, focusing on recovery of fossil embryos in August, 1999 in the Middle and Upper Cambrian, western Hunan, south China. As compared with the countless eggs and embryos recovered from the Ediacaran Doushantuo Formation and the Kuanchuanpu Formation of the early Cambrian, the abundance of eggs and embryos of the Middle and Upper Cambrian in western Hunan is very low, but the embryos recovered from Hunan are much better in terms of preservation. So far, we have processed more than 8,000 kg of limestone and recovered about five thousand eggs and embryos ranging from 236 to 462 μm in diameter, as well as lifelike, three-dimensional fossils of typical Orsten-type preservation represented by Phosphatocopida, Skaracarida and unnamed larvae (Dong et al., 2005a). Recently, we published a preliminary report on the initial collections of *Markuelia* from the Middle and late Cambrian of Hunan, south China (Dong et al., 2004). Unlike the above-mentioned papers on fossil embryos, which all lack phylogenetic constraint, our cladistic analysis suggests a stem Scalidophora (phyla Kinorhyncha, Loricifera, and Priapulida) affinity. More recently, we provided a more complete description of *Markuelia*, including the detailed comparison between *Markuelia hunanensis* and *Markuelia secunda*, based on the later collections. The available evidence supports stem-Scalidophora affinity, leading to the conclusion that scalidophorans, cycloneruallians, and ecdysozoans are primitive direct developers, and the likelihood that scalidophorans are primitively metameric (Dong et al., 2005b). Since February, 2004, an international synchrotron group including the present first three authors, led by Phil Donoghue has been doing the analysis of embryonic morphological features that are not exposed on the surface, by the method of Synchrotron radiation X-ray tomographic microscopy (srXTM). The srXTM analysis reveals the pentameric arrangement of the circumoral and pharyngeal spines in *Markuelia*, which is shared by scalidophorans (priapulids, loriciferans and kinorhynchs), but not nematodes and nematomorphs, interprets the lumen at the posterior terminus as a digestive tract opening to a terminal anus, and confirms that the introvert is capable of inversion. Concomitantly, a more precise phylogenetic analysis has been made (Donoghue et al., in prep). In light of this, along with more exquisitely preserved embryos we have recovered, the developmental sequence of *Markuelia*, from the earliest stage when the scalids only took shape to the latest stage (just about hatching), could be established. Only in the last decade, the fossil embryos of Late Neoproterozoic and Cambrian have been discovered in different continents (also cf. Donoghue et al., 2005). This is a remarkable event, not only because it introduced convincingly new evidence into the early history of metazoans , but also opened an entirely new window on to the evolution and development of animals. Apart from others, the discovery and study of fossilised embryos of Middle and Late Cambrian recovered from Hunan, south China is a paradigm especially for the latter. All the absolutely necessary data for phylogenetic constraint, anatomical analysis and for srXTM are available from the embryos of pre-hatchling stages of Middle and Late Cambrian of Hunan. It may demonstrate that the fossil embryos of Middle and Late Cambrian are as important as those of Ediacaran and the earliest Cambrian in Palaeoembryology and developmental biology.

Keywords: Cambrian, fossil embryos, *Markuelia*, Hunan

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[S1-2]

DECODING THE FOSSIL RECORD OF ANIMAL EMBRYONIC DEVELOPMENT

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The discovery of fossilized embryos contemporaneous with the emergence of metazoan diversity has provided radically new kinds of insight into the embryology of early animals. There is now a basis for testing long cherished hypotheses on the roles of developmental and life history evolution in the establishment of phyla. More than a decade has passed since the first discovery of fossilized embryos, and in the intervening years numerous localities, horizons and types of embryo have been recovered. The growing database appears so far to be dominated by the embryos of direct developing organisms. To some, this provides the final piece of evidence to reject the classical view that metazoans evolved from ancestors that underwent maximal indirect development, achieving adulthood only after undergoing a catastrophic metamorphosis from an earlier larval stage. However, the fossil record of embryos, like that other groups, should not be read literally. It exhibits many obvious biases, some of which are specific to individual deposits, such as the preponderance of early or late stage embryological stages (Donoghue and Dong, 2005). The fossil record of embryos is also very obviously biased in its stratigraphic extent. Palaeoembryology is a young subject and yet phosphatic microfossils have been sampled throughout the Phanerozoic for many decades. No recognisable embryos have been recovered beyond the Early Ordovician and it is likely that their absence from younger strata reflects both diminishing phosphate within the World's oceans and an expansion in activities of bioturbating organisms (Donoghue et al., 2006). Less obvious are biases in the preservation of stages and organisms according to their life history strategies, in part because there have been no experimental analyses of the relationship between embryology and taphonomy. From the first of these experiments (Raff et al. 2006), the implications for interpreting the palaeoembryological record are stark: under conditions that promote embryo preservation embryos can undergo aberrant patterns of cleavage, blastomeres can disaggregate, inflate and reorganise into unrepresentative arrangements; blastocoels collapse. Perhaps most worrisome is the observation that even under optimal conditions the primary larvae of indirect developers decay to amorphous organic matter within a matter of hours. More experiments are required to determine how these observations vary from group to group; these are underway. The message from such experiments appears to be that the record should be interpreted with great caution. At best, the record provides us with a direct insight into the certain stages of development of certain organisms and biases inherent in the record may be so limiting that it may never be possible to test directly such overarching hypotheses as the relationship between life history evolution and the divergence of