

Celebrating 25 years of advances in micropalaeontology: a review

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INTRODUCTION (F. JOHN GREGORY)

To commemorate the publication of the 25th Volume of the *Journal of Micropalaeontology*, the first issue of which came out in 1982, this celebratory review article was commissioned. Officers of each TMS Group (Ostracod, Foraminifera, Palynology, Nannofossil, Microvertebrate and Silicofossil) were requested to reflect over the last 25 years and assess the major advances and innovations in each of their disciplines. It is obvious from the presentations that all Groups report that research has moved on from the basic, but essential descriptive phase, i.e. taxonomy and establishing biostratigraphies, to the utilization of new technologies and application to issues of the day such as climate change and global warming. However, we must not lose sight of the fact that the foundation of micropalaeontology is observation and the building block for all these new and exciting innovations and developments is still good taxonomy. Briefly, the most obvious conclusion that can be drawn from this review is that micropalaeontology as a science is in relatively good health, but we have to ensure that the reported advancements will sustain and progress our discipline. There is one issue that has not really been highlighted in these contributions – we need to make sure that there are enough people being trained in micropalaeontology to maintain development. The last 25 years has seen a dramatic decrease in the number of post-graduate MSc courses in micropalaeontology. For example, in the UK, in the 1980s and early 1990s there were five specific MSc courses to choose from (Hull, Southampton, Sheffield, Aberystwyth and UCL) now there is just one left, run jointly by UCL and the Natural History Museum, in London. This decrease occurred for a variety of reasons but was related initially to fluctuations in oil price, leading to a lack of stability and confidence in the oil industry which used to attract many postgraduates. Fortunately, there has been a recent trend to try and bolster student numbers with the introduction of multi-disciplinary postgraduate courses which include an element of micropalaeontology, and there are more students entering the subject through PhD programmes than in the past.

I wonder what my successor as Editor will be able to report in 25, or even 50 years? The most significant factor then, is that oil – which has provided a good number of us with a career or funding to do academic research – will be entering its final phase. We will all need to be on the hunt for new horizons and this has already started, especially in the last 5–10 years, as illustrated in the following reports. My bet is that we will look back and see major advances based on further enhancements in biological and imaging technologies and an increase in integrated multi-disciplinary studies, with the inclusion of two or more microfossil groups (something that I feel has not really happened yet). Here's to the future.

Acknowledgement

FJG would like to thank Mark Williams (Leicester) and David Siveter (Leicester) for providing reviews of this article and also to members of the various TMS Groups who offered support and additional comments to several of the Group contributions.

OSTRACODS (IAN BOOMER, WITH CONTRIBUTIONS FROM THE OSTRACOD GROUP, TMS)**Introduction: from time markers to environmental indices**

The past 25 years have seen a number of advances in our understanding of the Ostracoda and their application to the earth and life sciences, with a marked shift in emphasis from their use in biostratigraphy to indicators of environmental change both faunally and geochemically. The first Stratigraphical Atlas published by The Micropalaeontology Society (Bate & Robinson, 1978), was the Ostracoda (the second edition of which will be published in 2007). Their application to the study of environmental change has been largely driven by technological advances and an increasing focus across the earth and environmental sciences on the global climate system and quantification of the rate and magnitude of past climate events. These changes have been mirrored in the decreasing call from oil

companies for ostracod workers but a continued presence within universities and research institutes, particularly those investigating climate change.

The fossil ostracod record continues to be a major focus for research and has led to some of the important advances, particularly in evolutionary biology, outlined below. In recent years a number of research groups, particularly in Europe and Japan, have concentrated on the ostracods as living organisms, leading to a greater understanding of the interaction between species and environment. Advances in the study of fresh-water faunas led to the establishment of regional ostracod databases, i.e. NODE, Non-marine Ostracod Distribution in Europe (Horne *et al.*, 1998) and NANODE, North American Non-marine Ostracod Database (Forester *et al.*, 2005).

The last 25 years has also seen advances in our knowledge of one of the most fundamental aspects of ostracod biology, the structure, composition and calcification process of the ostracod carapace (e.g. Keyser & Walter, 2004).

When is an ostracod not an ostracod? Cambrian ostracod record questioned?

Twenty-five years ago the fossil ostracod record extended from the Early Cambrian to Recent. Since then, our knowledge of fossil ostracods and their allies has been advanced significantly by the discovery and investigation of a number of Palaeozoic Lagerstätten. The lower Cambrian Chengjiang Lagerstätte has yielded the only known bradoriid with soft parts (Hou *et al.*, 1996), while the upper Cambrian 'Orsten' of the Baltic (e.g. Maas *et al.*, 2003) and the lower Cambrian of England (Siveter *et al.*, 2001) have yielded phosphatocopids with soft parts. These finds demonstrate that typical bradoriids lie outside the Crustacea *s.s.* and that phosphatocopids are the sister group to the Eucrustacea, thus debunking the Cambrian ostracod record. Some Cambrian bradoriids may yet prove to be true ostracods; however, without soft parts it is impossible to be certain. The earliest confirmed ostracods are now Early Ordovician.

A long history of sex – or celibacy

Perhaps most remarkable amongst these studies is the discovery of three-dimensional preservation of soft parts from the Silurian of the Welsh Borderlands. Using computer imaging, a Silurian myodocope with soft-part anatomy (Siveter *et al.*, 2003) has pushed back the earliest described evidence for ostracod soft-part anatomy by nearly 200 million years and provided unequivocal evidence for the occurrence of Ostracoda in the Palaeozoic. It also gave the earliest unequivocal testimony for male gender in any group of animals.

Non-marine darwinulid ostracods have achieved fame as an 'ancient asexual' lineage, confounding evolutionary theory by apparently surviving without sex since the beginning of the Mesozoic (Martens *et al.*, 2003). However, this has recently been called into question, although not totally disproved, by the discovery of elusive darwinulid males (Smith *et al.*, 2006).

The origin of pelagic ostracods: an ecological shift in the Silurian

Another important discovery from the Palaeozoic saw the development of a model that explained the timing and nature of the appearance of pelagic ostracods during the Silurian. Early

Silurian myodocope ostracods were benthic, living on well-oxygenated marine shelves. Myodocope ostracods appear to have undergone an ecological shift by the Late Silurian, an event that provides the best evidence for the earliest occurrence of pelagic ostracods in the fossil record (Siveter, 1984; Siveter *et al.*, 1987; 1991).

The rise of the machines: quantifying past environmental changes

Technological advances in analytical equipment have, in part, led to new applications for ostracods. The ability to analyse the isotopic and chemical composition of individual (or a very few) shells has provided the ability to **quantitatively** reconstruct past water temperature, solute and isotopic composition. This has brought ostracods to the fore in a number of fields, including palaeoclimatology, palaeoceanography and palaeolimnology.

Chivas *et al.* (1983, 1986a, b) did much to develop the ostracod shell-chemistry technique in non-marine systems, focusing on local and regional changes in hydrology, although debate continues as to the interpretation that may be drawn from such data. Von Grafenstein *et al.* (1999) demonstrated that the stable isotope geochemistry of benthic ostracods in southern European lakes could be correlated in detail with late Quaternary climate records from the Greenland ice-cores (see also reviews of applications by De Deckker (2002) and von Grafenstein (2002)).

Geochemical approaches have also been applied to the deep-sea record (e.g. Dwyer *et al.*, 1995, 2002; Cronin & Raymo, 1997), building upon the fundamental Deep Sea Drilling Project (DSDP) and Ocean Drilling Program (ODP) taxonomic work of Benson in the USA and the Aberystwyth School under the direction of Robin Whatley.

Genetics and taxonomy

The 'genetic revolution' in the biosciences has led to significant technical advances that have also benefited ostracod research. The development of DNA replication technologies has allowed the relatively small amount of DNA from ostracods to be analysed, advancing understanding of ostracod evolutionary biology.

Ostracod research is still underpinned by knowledge of taxonomy, ecology and geological processes. Although the number of scientists undertaking purely taxonomic work dwindles, that expertise continues to be fundamental to the applications outlined above and remains an important skill of all ostracodologists. Most workers today are indebted to the invaluable work of Kempf and his group (University of Köln), who continue to maintain an ostracod publication database, recording descriptions of new taxa in the 'Kempf Database on Ostracoda' (e.g. Kempf, 1996, 1997).

Despite the disappearance of the only serial publication dedicated to the Ostracoda, *A Stereo-Atlas of Ostracod Shells*, which ceased publication in 1998 after 25 years and the description of 720 fossil and living taxa, ostracod research is thriving today throughout the world.

FORAMINIFERA (DANIELA SCHMIDT & JOACHIM SCHOENFELD)

Introduction

Looking back over 25 years of foraminiferal research from a personal point of view is a daunting task. How do we

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quantify the importance of research? In particular since today's research of encompassing ecosystem analysis and multi-proxy approaches make it difficult to 'assign' it to foraminiferal research. In contrast, in the 1970s research focused more clearly on the organisms, with emphasis on the ecology and biology of planktonic (Bé, 1977) and benthic (Murray, 1973) foraminifers. Actualistic understanding of foraminiferal ecology provided the justification for use of their shells for stable isotope and trace metal analyses and changed the field of foraminiferal research. However, in the early 1980s, many researchers were convinced that the distribution of foraminifera was driven by single, physical or chemical parameters – for example, water depth, temperature or salinity. The mid- and late 1980s saw a profound widening of this scope due to many new insights and evidence that multiple environmental parameters and the physiology of foraminifers account and interact in a web of environmental forcings.

This new understanding of ecology and rapid innovation of computer technology resulted in dramatic changes for foraminiferal micropalaeontology: for example, the use of planktonic foraminiferal assemblages combined with multivariate statistics to reconstruct past sea-surface temperatures (CLIMAP Project Members, 1981). This gave way to the rise of palaeoceanography, the invention of astronomical age models, tracking ancient water mass distributions and the first numerical models (Imbrie *et al.*, 1984).

Stratigraphy

Since the early 1980s, foraminiferal biozonations have been available for most stages (e.g. various planktonic zonations contained within Bolli *et al.* (1985) for the Cretaceous to Recent). However, these schemes have been refined and revised using astronomical time-scales, which provide the means to date sediments with unprecedented accuracy, particularly for the Cenozoic to Recent (e.g. Shackleton *et al.*, 1990).

Refinement in palaeoecology

We have learned that the distribution of benthic foraminifera in the sea bed is structured into different microhabitats (Corliss, 1985) and that foraminifera respond rapidly to phytodetritus deposition, which turns the deep sea into one of the most seasonal environments on Earth (Gooday & Lambshead, 1989). The observation of salt-marsh foraminifera in tidal estuaries (Scott & Medioli, 1980) introduced a centimetre-precise sea-level gauge, applicable as far back in time as the Late Carboniferous. Studies of shape (Malmgren *et al.*, 1983) produced classic papers suggesting new microevolutionary models. The late 1980s and 1990s saw a merging of these new observations with statistics. Statistical methods were used to define species groups with similar ecological preferences and to link them to steering environmental parameters (Lutze & Coulbourn, 1984). As statistical results were often ambiguous, more detailed observations were necessary to make the next step forward. Food and oxygen were considered to be the most important environmental factors for foraminiferal distributions. Hence, it was attempted to use their abundance and species composition for estimates of primary production, oxygen content of bottom waters and the flux of particulate organic matter to the sea floor (Mix, 1989; Herguera & Berger, 1991; Kaiho, 1994). However, it was

difficult to discern the interfering influences of food flux and oxygen availability in pore waters below the sediment surface (e.g. Jorissen, 1999).

New technologies: impact

The rise of new biotechnology in the 1990s facilitated a sensible revision of the Kingdom Protozoa using molecular genetics (Cavalier Smith, 1993). The emerging field of foraminiferal molecular genetics (Darling *et al.*, 2000, 2004; de Vargas *et al.*, 2001) led to the discovery of cryptic species (Huber *et al.*, 1997), which will significantly improve our understanding of foraminiferal ecology and evolution. In recent years, stable isotopes and trace metals, in particular Mg/Ca for temperature estimates, have been the focus of current research and further the use of foraminifera as palaeoceanographic proxy carriers (Vincent *et al.*, 1981; Delaney & Boyle, 1987; Pearson & Palmer, 2000).

Final thoughts

Both, genetics and geochemistry heightened the demand for a sound and timely concept of foraminiferal taxonomy. Benchmark textbooks have aged (Morkhoven *et al.*, 1986; Loeblich & Tappan, 1987; Hemleben *et al.*, 1989; Jones, 1994) and new research is required because, ultimately, every conclusion is just as good as the taxonomy on which it is based. As a final thought, readers may be interested in the highest cited paper using foraminifers during the last 25 years. Some may think it unimportant, but for those of you who do consider it important – the winning paper, with 642 citations, is by Nick Shackleton and colleagues (1990) on the 'Astronomical calibration of the Lower Pleistocene Timescale based on ODP Site 677'. They dissolved foraminifers to analyse oxygen isotopes, resulting in the most accurate time-scale. Who would have thought about this in the 1940s when people started to date marine sediments with foraminifers?

PALYNOLOGY (IAN HARDING, WITH CONTRIBUTIONS FROM THE PALYNOLOGY GROUP; TMS)

Introduction

The last 25 years has witnessed the 'coming of age' of palynology: a dramatic and exponential maturing of the discipline, progressing from straightforward descriptions of new taxa and the development of biostratigraphic zonations to its current role as a fully integrated tool operating alongside complementary areas of research in the quest to understand complex geological problems, both in an academic and industrial context. The literature cited in this short review will, by necessity, be selective and examines a small spectrum of thematic areas of palynological research. However, an attempt has been made to include references from the various fields of dinoflagellate, spore, pollen, acritarch, chitinozoan and palynofacies studies, in addition to balancing academic and industrial facets of the subject.

The striking palynological advances that have been made in the past quarter of a century would have been impossible without such seminal works as those by Tappan (1980) and Traverse (1988). Both are landmark syntheses of information concerning a plethora of palynological groups, while the three-volume Jansonius & McGregor (1996) is still the most

comprehensive set of literature yet assembled that covers all aspects of palaeopalynology. The major tomes in the field of palynofacies analysis have been the publications of Traverse (1994) and, perhaps most notably, Tyson (1995). The latter is still a standard text and widely cited, together with Batten's (1996a, b) contributions. Jones & Rowe (1999) provided an exhaustive compilation of techniques related to fossil plants and sporomorphs.

The aquatic palynomorphs have perhaps seen the most significant gains in understanding, based on such works as the *Big Blue Book* (Evitt, 1985), perhaps one of the most significant tomes ever written on the dinoflagellates. This was a progenitor of the first widely accepted classification of modern and fossil dinoflagellates, by Fensome *et al.* (1993), itself now a classic work. Acritarchs have been reviewed by Strother (1996) and chitinozoa by Paris & Nölvak (1999). Other notable works have drawn together biostratigraphies for the various aquatic palynomorphs, in the forms of Williams & Bujak (1985) and Powell (1992) for dinoflagellates (the latter published under the auspices of this society), Downie (1984) for acritarchs and Verniers *et al.* (1995) and Paris *et al.* (2000) for chitinozoa.

Our understanding of several groups of organic-walled fossil microplankton would not be as advanced as it is today without the expertise of neontologists: collected works by Spector (1984) and Taylor (1987) provided thematic papers on dinoflagellates, while the pioneering work of Harland (1983), documenting the distribution of dinoflagellate cysts in modern oceans, has been built upon by such works those of Rochon *et al.* (1999) and Marret & Zonneveld (2003).

Eye of newt, toe of frog: demystifying palynomorph chemistry

Progress has been made towards understanding the structure, function, chemical diversity and diagenetic modification of palynomorph walls, furthered by such works as de Leeuw & Largeau (1993) and van Bergen *et al.* (2004). The important review by Versteegh & Blokker (2004) brought together compositional analyses of extant and fossil microalgae, illustrating biosynthetic pathways for the production of resistant biomacromolecules. Hemsley and co-workers have discussed self-assembly as an important process in wall formation (e.g. Gabarayeva & Hemsley, 2006, and references therein), whereas works such as that by Marshall *et al.* (2005, on Proterozoic acritarchs) demonstrate the role new analytical techniques can play in analysing palynomorph composition.

Several degradational and preservational pathways for organic matter in the fossil record have been proposed (e.g. Tissot & Welte, 1984; Sinninghe Damsté & de Leeuw, 1990) and a greater appreciation of these processes is required to assess fully the extent to which the geomacromolecules represent the original biomacromolecules, as palynomorph cell walls are modified readily by elevated temperature and pressure conditions (e.g. Aroui *et al.*, 2000) and oxygen concentrations (Versteegh & Zonneveld, 2002).

Taxonomy, morphological problems and evolution: the gene genie

There has been tremendous clarification of the taxonomy and systematics of most palynological groupings, assisted by such encyclopaedic data compilations as the Lentin & Williams

(1973) dinoflagellate index (culminating in Fensome & Williams, 2004) and Fensome *et al.*'s (1990) publication for the acritarchs. Chitinozoan workers have agreement on suprageneric classification (Paris *et al.*, 1999), but work remains to be done at a specific level. Digital databases and online resources now have a vital role to play in the global dissemination of such information (e.g. Achab *et al.*, 2000).

Laboratory cultures have proven to be of huge importance in clarifying planktonic life cycles and phylogenetic relationships (e.g. Kokinos & Anderson, 1995; Ellegaard *et al.*, 2003). They will increase in importance, given genomic investigations showing that unicellular organisms can demonstrate cryptic speciation, serving to further emphasize the precision with which morphotaxa must be circumscribed. New biogeochemical genetic and cladistic techniques have had a major impact on dinoflagellate phylogenetic studies (e.g. Fensome *et al.*, 1996; Moldowan & Talyzina, 1998; Saldarriaga *et al.*, 2004). However, the discovery of extra-thecal cysts of the dinoflagellate *Palaeoperidinium* (Evitt *et al.*, 1998) and the 'dinocasts' of Versteegh *et al.* (2004) illustrate that the fossil record will continue to divulge oddities.

The evolution and phylogenies of the terrestrial plants have also been active areas for palynological contributions, notably for the angiosperms (e.g. Walker & Walker, 1984; Cornet, 1989; Hughes, 1994; Brenner, 1996; Hochuli & Feist-Burkhardt, 2004), while *in situ* studies of spores and pollen (e.g. Balme, 1995) have played a major role in understanding the early evolution of land plants (e.g. Wellman *et al.*, 2003) and thin-section studies (e.g. Batten & Dutta, 1997) have been useful for determining botanical relationships. This work helps to inform genetically and morphologically based cladistic analyses (e.g. Qiu & Lee, 2000), in combination with meso- and macro-fossil data (e.g. Friis *et al.*, 2006).

From qualitative to quantitative, isolation to integration

The emphasis placed on much palynological research has shifted from the descriptive and qualitative to more rigorous quantitative approaches, employing statistical and computational methodologies. Quantitative techniques applied in palynological contexts include a variety of multivariate statistical procedures (such as cluster analysis) and ordination methods, such as principal component analysis (PCA), correspondence analysis (CA) and detrended correspondence analysis (DCA) (e.g. Dale & Dale, 2002). In addition, sporomorph workers have developed methods, such as squared-chord distance dissimilarity coefficient (SCD), average pairwise dissimilarity and total variance, nearest living relative (NLR) and coexistence analyses (CoA) (e.g. Overpeck *et al.*, 1992; Mosbrugger & Utescher, 1997; Lupia, 1999; Liang *et al.*, 2003; Poole *et al.*, 2005). Although a common methodology employed by foraminiferal workers, transfer functions have not received the same attention from palynologists, excepting such work as that by Mudie (1992). Shaw's graphic correlation method has been utilized in the erection of biostratigraphies (Edwards, 1989; Eldrett *et al.*, 2004), as has automated correlation (D'Iorio, 1986).

Palynological investigations are now firmly embedded in multidisciplinary geological studies, from those of academic interest to those on an industrial and societal scale, such as global climate change. The last 25 years have seen the

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hydrocarbon exploration industry continue to provide major impetus to palynology, especially in the context of sea-level change and the development of sequence stratigraphy – with papers by Parry *et al.* (1981), Davies *et al.* (1991), Gorin & Steffen (1991), collected papers in Katz & Pratt (1993), Partington *et al.* (1993), Hart *et al.* (1994), Achab *et al.* (1997) and Winchester-Seeto *et al.* (2000) providing some notable contributions in the areas of palynofacies, dinoflagellates, chitinozoa and sporomorphs. Techniques for the determination of thermal maturity have also ‘matured’ over the past 25 years, with quantified studies examining spore colour (Marshall, 1991; Yule *et al.*, 2000), acritarch fluorescence (Obermajer *et al.*, 1999) and chitinozoan reflectance (e.g. Tricker *et al.*, 1992).

However, it is perhaps in the fields of palaeoecology, palaeogeography and climate change that palynology has made, and will continue to make, significant contributions to integrated research, especially concerning notable ‘boundary events’ such as the Cretaceous/Tertiary boundary (e.g. Tschudy *et al.*, 1984; Sweet, 1994; Nicholls, 2003) and the Paleocene/Eocene boundary (Wing *et al.*, 2005; Crouch & Brinkhuis, 2005; Sluijs *et al.*, 2006). By combining palynological research with sedimentology, stable isotope analysis, geochemistry, Milankovitch cyclicity and climate modelling (e.g. Versteegh, 1994; Pearson *et al.*, 2004), recent studies have demonstrated the potential of palynology. A variety of groups across a spectrum of depositional environments throughout the geological column have been examined (e.g. Huber *et al.*, 2004; Mullins *et al.*, 2004; Grice *et al.*, 2005; Brinkhuis *et al.*, 2006; Stricane *et al.*, 2006) – this is likely to be one of the main directions of palynological research over the next 25 years.

NANNOFOSSILS (JEREMY R. YOUNG & JENS O. HERRLE)

Taxonomy and biostratigraphy

Twenty-five years ago, the field was coming to the end of an intensive period of primary descriptive work, during which most of the obvious calcareous nannoplankton species had been described and the basic zonations we still use had been developed – at least for the Late Cretaceous and Cenozoic. Since then the most obvious development has been broadening of the scope of nannoplankton research beyond taxonomy and biostratigraphy, but there have also been major developments in these areas. The Jurassic and Early Cretaceous nannofloras have been monographed lovingly (e.g. Bown, 1987), Mesozoic and Cenozoic zonations have been calibrated against magnetostratigraphy (e.g. Monechi & Thierstein, 1985; Bralower *et al.*, 1995) and, more recently, cyclostratigraphy and finer resolution zonations have been developed (e.g. Varol, 1989; Burnett, 1998; Raffi *et al.*, in press) and, perhaps most importantly, the data have been synthesized accessibly. There are two obvious benchmark publications: first, the Bolli *et al.* (1985) ‘yellow book’, *Plankton Stratigraphy*, which includes a 250-page synthesis of nannofossil taxonomy by Katharina Perch-Nielsen; second, the Bown (1998) ‘black book’ *Calcareous Nannofossil Biostratigraphy*, a Special Publication of our society. The work has paid dividends, with nannofossils becoming one of the most widely used and reliable sources of biostratigraphic data. The good quality taxonomy, based largely on meaningful biomineralization-based characters

(Young *et al.*, 1992) and, more recently, on morphometry (Bollmann, 1997), has been vindicated by molecular genetic studies (e.g. Saez *et al.*, 2004).

Coccolithophore biology and ecology

In the early 1980s coccolithophore biology and ecology was as woefully a neglected field as that of any microfossil group and, as with other groups, this led palaeontologists to undertake new research on their taxonomy, biogeography and ecology, with outstanding PhD studies (for example, by Mara Cortés, Ali Haidar, Ric Jordan and Annelies Kleijne). For coccolithophores, however, this general pattern was reinforced by a number of special factors. First, coccolithophore blooms provided some of the most dramatic features seen in satellite images of the oceans (Holligan *et al.*, 1983). Secondly, coccolithophores were adopted as model organisms for biomineralization study, especially by Peter Westbroek’s group. Thirdly, coccolithophore-derived alkenones proved invaluable biomarkers and palaeothermometers (Brassell *et al.*, 1986). Fourthly, development of sediment traps and interest in the carbon cycle stimulated extensive research on coccolith fluxes (Ziveri *et al.*, 1995). All these factors would certainly have led to widespread research on coccolithophores, but the field was stimulated immensely by Peter Westbroek’s dream to integrate everything through multi-disciplinary research on *Emiliania huxleyi* to make it the *Escherichia coli* of the ocean, i.e. a model organism to understand marine biogeochemistry (Westbroek *et al.*, 1993). This dream led to a succession of interdisciplinary workshops hosted by Jan van Hinte in the Chateau de Blagnac. These, in turn, spawned a series of multi-national projects and have indeed made *E. huxleyi* one of the most widely studied marine protists (and its genome is close to being sequenced). More broadly, our knowledge of coccolithophore life cycles, ecology, biomineralization biochemistry, molecular biology and biodiversity has changed beyond recognition. Key syntheses of this work include *Coccolithophores* (Winter & Siesser, 1994), *Coccolithophores – from molecular processes to global impact* (Thierstein & Young, 2004) and the pioneering work on *E. huxleyi* of Eystein Paasche, John Green and William Balch, summarized excellently by Paasche (2002).

Coccolithophore palaeobiology, palaeoceanography and global change

Of course, in parallel with this biological work, the agenda of micropalaeontological research was shifting to palaeoceanography and global change, and this has certainly been reflected in nannofossil research. An early highlight was extensive research on the mid-Cretaceous Oceanic Anoxic Events (e.g. Bralower *et al.*, 1994; Erba, 1994), the K/T boundary (e.g. Pospichal, 1994), followed more recently by much work on the PETM (e.g. Gibbs *et al.*, 2006). Broader palaeoceanographic studies have been hampered by difficulties in developing reliable quantitative palaeoproxies, reflecting the rapid evolution of coccolithophores and the tendency for assemblages to be dominated by a narrow range of eutrophic/mesotrophic species. However, for the Mesozoic, one of the most important and fundamental ecological and palaeoceanographic studies goes back to Roth & Krumbach (1986), introducing for the first time a preliminary toolbox for semi-quantitative nannoplankton-based proxies for

reconstructing Mesozoic palaeoceanographic changes. Prime examples for using coccolithophores as quantitative proxies in the field of palaeoceanography are the development of *Florisphaera profunda* as an indicator of water column stratification and oligotrophy (e.g. Molino & McIntyre, 1990; Beaufort *et al.*, 1997) and the *Gephyrocapsa*-palaeothermometer (Bollmann *et al.*, 2002). In general, however, coccolithophores have probably not yet come near to realizing their potential in palaeoceanography. This seems to be changing fast as the results of biological research are applied to nannofossil research, resulting in new biotic proxies based on more refined species concepts (e.g. Bollmann, 1997). Of equal importance are new geochemical proxies based on the refined understanding of coccolith chemistry (Dudley *et al.*, 1986) and on new techniques for separating nannofossil assemblages into narrow size fractions, as introduced by Paull & Thierstein (1987) and recently improved by Minoletti *et al.* (2005), enabling high quality geochemical data to be extracted from the nannofossil record.

Final thoughts

It is always dangerous to attempt predictions, but our suspicion is that two emerging trends will lead nannofossil research over the next few years. First, automated methods will allow rapid generation of data from normally preserved assemblages and methods are in progress (Beaufort & Dollfus, 2004; Bollmann *et al.*, 2004). Secondly, detailed analysis of exceptionally preserved assemblages will enable us to provide a much more meaningful picture of the phylogeny, palaeobiodiversity and evolutionary development of coccolithophores in relation to long-term global environmental change.

MICROVERTEBRATES (HOWARD A. ARMSTRONG)

Introduction

The Microvertebrate Group includes researchers interested in the Palaeozoic fossil record of vertebrates as revealed by their tiny scales, teeth and bone fragments extracted from rock samples. Such 'micro-remains' are derived from a variety of animals and have important applications in biostratigraphy, palaeoecology, palaeobiogeography, anatomy and phylogeny. The thelodonts and conodonts, extinct jawless vertebrates, are the most widely studied 'micro-vertebrates'. Commonality is also found in that the fossil record of both of these groups is dominated by collections of discrete skeletal elements and our understanding of their palaeobiology has undergone revolutionary change in the last 25 years.

Conventionally thelodonts have been perceived as dorso-ventrally compressed fish-like animals, with unsupported pectoral flaps, dorsal and anal fins, and a hypocercal tail (Turner, 1991). However, whilst this body plan may apply to most thelodonts, the recently discovered *Furcacaudiformes* (Wilson & Caldwell, 1998) are characterized by a deep, hump-backed and laterally compressed body, approximately symmetrical tail and lack the anal fins of dorso-ventrally compressed thelodonts (Wilson & Caldwell, 1993, 1998; Caldwell & Wilson, 1995). Thelodonts characteristically possess a dermal skeleton composed of thousands of microscopic scales that are commonly dispersed after death. Recent description of the full anatomy of *Turinia pageni* (Powrie), the holotype, has resolved the mor-

phology, anatomy and phylogenetic relationships of at least one of the groups, the thelodonts. Phylogenetic analysis resolves *T. pageni* (and likely all thelodonts) and the Galeaspidia as sister-taxa, comprising a sister group to the Osteostraci plus jawed vertebrates (Donoghue & Smith, 2001).

Since the 1930s conodonts have become the premier microfossils for dating Palaeozoic shallow-marine carbonates and they have been used widely in palaeoecological and biogeographical studies. Conodonts are now the microfossil group of choice for biostratigraphical work of Late Cambrian to Triassic age. Graphical correlation has been used to constrain taxon ranges through much of the Ordovician and Silurian (Kleffner, 1995; Sweet, 1995), parts of the Devonian (Klapper, 1989) and the lower part of the Triassic (Sweet, 1989) and composite standards compiled graphically have been used in the analysis of mass extinction (Armstrong, 1995, 1999). Work progresses on developing a composite standard for the rest of the Palaeozoic and Triassic. Attempts to date conodonts using radiometric and other methods have proved successful but give large error bars (Sachs *et al.*, 1980; Ueki & Sano, 2001). Conodont colour alteration (CAI) has been extended to indicate a range of temperatures from 25°C to 600°C and has been applied widely in the interpretation of basin histories, regional metamorphic studies and in the search for hydrocarbons and minerals.

The study of conodonts was advanced greatly in 1983 by the discovery of complete conodont animals in the Carboniferous Granton Shrimp Bed near Edinburgh (Briggs *et al.*, 1983). The excellent preservation of the material has provided detailed information on the anatomy of conodont animals, including sclerotic eye cartilages, notochord and chevron muscle blocks that have indicated a chordate affinity for the group (Aldridge *et al.*, 1986, 1993). A further animal of lower Silurian age (Mikulic *et al.*, 1985; Smith *et al.*, 1987) and giant conodont animals of Upper Ordovician age (Aldridge & Theron, 1993; Gabbott *et al.*, 1995) have since been discovered. The Ordovician animals differ from the Granton animals in the architecture of the apparatus, the size of the elements and the overall size of the animal, which could have reached 1 m in length. A single specimen preserves extrinsic eye musculature and the trunk muscles that show details of rod-like muscle fibres, myofibrils and possibly sarcomeres (Gabbott *et al.*, 1995). These indicate that conodont animals were sprinters, not marathon runners. A morphologically distinct conodont animal, *Panderodus unicostatus*, has been discovered in lower Silurian strata (Mikulic *et al.*, 1985). This animal is poorly preserved, but appears to be dorso-ventrally compressed; importantly, the head contains well-preserved coniform conodont elements (Smith *et al.*, 1987).

The anatomy of these animals, plus ultrastructural studies of the elements (Sansom *et al.*, 1992), have placed the conodonts firmly within the Chordata. The conodont element is the primitive product of vertebrate tissue mineralization and consists of a denticle formed from a lamellar crown composed of an enamel homologue and dentine basal body (Sansom *et al.*, 1992; Donoghue & Sansom, 2002). Derived conodonts grew by appositional growth that may have been entrained by tidal, lunar or seasonal cycles (Zhang *et al.*, 1997; Donoghue, 1998; Armstrong & Smith, 2001; Armstrong, 2005).

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Functional modelling (Aldridge *et al.*, 1987; Purnell & Donoghue, 1998), growth studies (Armstrong & Smith, 2001; Armstrong, 2005) and the discovery of microwear facets (Purnell, 1995) on the denticles of some elements support a grasping and processing function for the apparatus. The reconstruction of the *Panderodus* apparatus (Sansom *et al.*, 1994) suggests a similar function for this group of 'coniform' conodonts. If conodonts represent a monophyletic group then it is likely only a small number of apparatus baupläne existed, in much the same way as only a few basic dentitions, relating to feeding style occur in mammals.

Advances in classification

The suprageneric classification of conodonts (Aldridge & Smith, 1993; Sweet, 1988) is, at best, considered provisional and has many limitations, not least that the apparatuses of many taxa are incompletely known, that almost all have not been proven in natural assemblages and that the scheme is not based upon cladistic or other classificatory methods. Under this scheme the Conodonta would appear to be a grade of organization acquired independently in the ancestral Upper Cambrian *Teridontus* and *Proconodontus* lineages (Sweet & Donoghue, 2001). Cladistic analysis of primitive vertebrates indicates conodonts are best considered monophyletic stem group gnathostomes, though they lacked jaws (Donoghue *et al.*, 2000).

Advances in palaeoecology, palaeobiogeography and palaeoclimate

Conodonts were exclusively marine, occurring in a wide range of habitats from hypersaline to bathyal, even abyssal. The group underwent rapid ecological and phylogenetic differentiation during the Early Ordovician (Smith *et al.*, 2002). Recent work on the distribution of Middle and Upper Ordovician conodonts supports ecological differentiation into continental-shelf communities – largely nektonic – and oceanic communities, dominated by epipelagic taxa. There is no simple correlation between continental-shelf shelly and conodont biofacies and the primary ecological controlling factors of these conodonts remain unclear. But the fact that conodonts show marked provincialism at various times in their history suggests they were sensitive to temperature. Fundamental distinctions in these communities occur at the order level, suggesting differences in apparatus architecture and element morphologies reflect differences in habitat and mode of life (Armstrong & Owen, 2002). Species within the oceanic realm apparently show depth stratification and/or adaptation to specific water masses (Armstrong & Owen, 2002).

High resolution conodont element geochemistry (trace element and stable isotopes) is being used increasingly to parameterize Palaeozoic climate and oceanography models (e.g. Wright *et al.*, 1984; Keto & Jacobsen, 1987; Holmden *et al.*, 1996; Veizer *et al.*, 1986, 1997, 1999; Joachimski & Buggisch, 2002; Wright & Barnes, 2002; Joachimski *et al.*, 2006).

The new research frontiers lie in the areas of palaeobiology, phylogeny, the testing of evolutionary hypotheses and Palaeozoic environmental change. We should not forget, however, that these areas are entirely reliant upon sound alpha taxonomy based on painstaking collecting and description; we are as '*pigmaei gigantum humeris impositi plusquam ipsi gigantes vident*'.

SILICOFOSSILS (DAVID LAZARUS & RAINER GERSONDE)**Radiolaria: introduction (David Lazarus)**

Radiolarian research includes basic work on their taxonomy and biology and application of this knowledge to problems in stratigraphy, tectonics, palaeoceanography and understanding biological evolution. Recent reviews of radiolarian research include those by Casey (1987), De Wever *et al.* (2001) and Lazarus (2005, in press). Radiolarian research grew rapidly in the late 1970s/early 1980s, from c. 50 titles per year in the mid-1970s and earlier to c. 100 titles annually by the early 1980s.

Output has remained steady at this level ever since. The Mesozoic receives the most attention (46% of published papers¹), followed by the Cenozoic (32%), Palaeozoic (17%) and Recent (5%). All major topics were well established by 1980, but how much progress has there been in each area?

Taxonomy (30% of published papers)

Despite numerous good studies in the last 25 years, taxonomy is still very incomplete and unclear. Most Cenozoic radiolarian species are still not described, although plenty of well-preserved material is available. More complete description of faunas is still hindered by the lack of comprehensive catalogues and by Haeckel's largely unrevised highly artificial generic framework, despite progress at individual genus-level groups. Mesozoic and Palaeozoic workers have not had such a difficult historical legacy. However, these faunas are also incompletely described due to incomplete and highly variable preservation, and by taxonomic losses from common lab preparation techniques (Blome & Reed, 1993). Catalogues for Mesozoic–Palaeozoic forms are better developed (e.g. Baumgartner *et al.*, 1995) and, although not comprehensive, they have improved the quality and efficiency of taxonomic work. The outlook for taxonomy in the next decades depends on the development of better tools – large taxonomic databases (Neptune: Lazarus, 1994; Radworld: Caulet *et al.*, 2006) and improving communication between workers via the Internet. Also important will be re-examination of the historic Ehrenberg and Haeckel collections (Suzuki *et al.*, 2006), access to which has improved dramatically since the late 1990s (Lazarus, 2000). The higher-level systematics of radiolarians is still largely unknown, although the extreme disparity in baupläne morphologies in radiolarians allows reasonable suppositions about most family-level taxa (e.g. De Wever *et al.*, 2001). We still lack any real knowledge of the biological basis of morphological characters, which is needed to develop robust higher-level systematic hypotheses. Genetic studies of radiolarians have begun to appear (Amaral-Zettler *et al.*, 1999; Yuasa *et al.*, 2006) and should hopefully in the next years provide a solid foundation on which to base higher-level radiolarian taxonomy and systematics.

¹Numerical analysis of literature based on Sanfilippo *et al.* (2000) and keyword classification given there. Individual papers with multiple theme assignments treated as multiple papers for calculations, total for papers since 1980 is 1545; unclassified/other theme papers (c. 40% of total, mostly non-English publications) excluded from totals. Geological time interval percentages calculated separately. More recent literature lists from www.radiolaria.org and its Interrad newsletter archive were examined to check for any changes in trends; none were noticed.)

Stratigraphy (plus tectonics, 47% of published papers)

Major stratigraphical advances have been made over the last 25 years. In 1980, a complete Cenozoic low-latitude zonation existed (Riedel & Sanfilippo, 1978; Sanfilippo *et al.*, 1985); but only partial zonations for most other time intervals or regions. In 2006 we now have an almost complete zonation for the entire Phanerozoic, much of it based on global markers and, in some cases (e.g. Cenozoic), also with additional regional markers and moderate-good calibration to geochronology (see summary in De Wever *et al.*, 2001). The next 25 years should yield additional resolution from the use of more species as markers and better calibration to geochronology. Diachroneity and limits to taxonomic precision will eventually, however, limit further increase in the precision or accuracy of zonations. Many stratigraphical studies will continue to be combined with tectonics to help understand the origin of complex terranes.

Palaeoceanographic research (12% of published papers)

In the Quaternary there has been continued use of quantitative calibration of assemblages to modern ocean conditions for palaeotemperature estimation (e.g. Pisias *et al.*, 1997; Abelson *et al.*, 1999), but the number of such studies was not very high. Future Quaternary palaeoenvironmental studies may also focus on using radiolarians to estimate other ocean characteristics, particularly productivity. A low-latitude upwelling index was developed in the 1990s (Caulet *et al.*, 1992; Nigrini & Caulet, 1992) and current work on a water-depth ecology ('WADE') method (Lazarus, 2005; Lazarus *et al.*, 2006) may be applicable more generally. Pre (late) Neogene palaeoenvironmental work is still limited by the lack of direct ecological information for extinct taxa and our inability, due to our lack of basic biological knowledge, to estimate the ecology of extinct species from their taxonomy and morphology. A few qualitative studies using radiolarian biogeography as water-mass tracers were, however, published (Pessagno & Blome, 1986; Lazarus & Caulet, 1994; Kiessling, 1999).

Biology (7% of published papers)

Biological knowledge of radiolarians has improved greatly in the last 25 years. Anderson (1983) provided a landmark summary of his research group's study of radiolarian biology. Water column studies have provided at least preliminary information on the depth ecology for many modern taxa (e.g. Boltovskoy & Riedel, 1987; Abelson & Gowing, 1996; Yamashita *et al.*, 2002) and more information on how taphonomy affects the fossil record (Takahashi, 1991; Welling & Pisias, 1998); while continued laboratory studies have added more information on basic cell behaviour. There is still, however, very much more to do in all of these areas and, in particular, on the functional ecology (especially the shell) of both taxonomic groups and individual species. Given that such knowledge would yield major benefits to palaeoenvironmental studies, particularly for extinct species, hopefully this topic will be better developed in coming decades. Methods, however, are still needed to maintain radiolarians in continuous culture and a long-term programme to study the ecology of individual specimens in the water column is required as well.

Evolution (4% of published papers)

Microevolution (speciation) case studies, begun in the 1970s, have continued (e.g. Lazarus, 1986) and contributed, albeit in a minor way, to the great 'punctuated equilibrium' debate in the early 1980s. Further advances in speciation research, however, will require better knowledge of species concepts (particularly in light of potential cryptic species, widely documented in other plankton groups) and the ecology of the studied taxa. Macroevolution research largely has not yet been carried out for radiolarians, despite a superb record of evolutionary change that can be compared accurately to coeval environmental history. Stratigraphic work has already shown distinctive patterns of radiolarian response to mass-extinction events at both the KT (Hollis, 1997) and PT boundaries (Kamata *et al.*, 2006). As tools such as databases and higher-level taxonomy improve, understanding the evolutionary mechanisms behind macroevolutionary patterns will be a major opportunity for new research in the next decades.

Organizational aspects

The last 25 years saw dramatic improvements in the social aspects of radiolarian research. In the 1980s the international radiolarian community coalesced into the Interrad Society, with regular congresses and an annual newsletter. Radiolarian workers also enjoy one of the best community websites in micropalaeontology at www.radiolaria.org (Dolven & Skjerpen, 2000–2006). Radiolarian workers, however, are still somewhat under-represented in other micropalaeontology societies, such as TMS, which recognized this fact and founded the Silicofossil Group in 1997.

Personalia/teaching/training

Many of the pioneers of modern radiolarian research, who in the 1950s and 1960s helped develop the field, have now retired, but their students are still active and continue to train new workers. Teaching continues to be done mostly by the relatively small number of radiolarian workers holding university teaching posts. Radiolarian specialists continue to be under-represented in academic departments, as micropalaeontology positions are still often combined with carbonate geochemistry (e.g. foraminifera and stable isotopes). One can only hope that more teaching positions will be filled by radiolarian workers. There are still many more opportunities to use radiolarians to solve important geological and biological problems than there are radiolarian workers to use them!

Fossil diatoms: introduction (Rainer Gersonde)

The 25 last years, which followed the introduction of marine and fresh-water diatoms as stratigraphical and palaeoenvironmental markers since the mid-1950s, have seen consolidation and further improvement, as well as development of new methods for extracting information from fossil diatoms. Much of the marine work has been accomplished on diatom records recovered with the drillship, *JOIDES Resolution*, within the Deep Sea Drilling Project (DSDP) (1968–1983) and Ocean Drilling Program (ODP) (1985–2003).

Biostratigraphy

Advanced coring techniques available since the late stage of DSDP provided sediment sequences at high recovery rates,

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permitting remarkable detailing of Cenozoic diatom species ranges and stratigraphical zonations for the North and Equatorial Pacific (Barron, 1980, 1981, 1985a; Gladenkov & Barron, 1995; Maruyama, 2000), the Atlantic (Baldauf, 1984, 1987; Fenner, 1984; Koc *et al.*, 1999) and the Southern Ocean (Gersonde & Burckle, 1990; Harwood & Maruyama, 1992; Censarek & Gersonde, 2002; Zielinski & Gersonde, 2002). The quality of the sediment cores further allowed the linking of diatom stratigraphies to geomagnetic and oxygen isotope stratigraphies. Such absolute dating of diatom ranges has provided the baseline for palaeoceanographic interpretation of the spatial distribution of diatom species and improved our understanding of Cenozoic diatom evolution and the mechanisms related to it.

Origin and evolution of diatoms

The recovery of extraordinarily well-preserved Early Cretaceous diatom assemblages (*c.* 110 Ma) on the Antarctic margin (ODP Site 693) provided the first comprehensive view of critical steps of early diatom evolution (Gersonde & Harwood, 1990; Harwood & Gersonde, 1990). These include the transformation of valve shape from cylindrical to discoid, and of the outline from circular to bipolar, and the development of specific structures (processes, protulae) that replace heavily silicified linking structures used for chain formation. Diatom evolution before 110 Ma and during the Late Cretaceous still remains largely unknown. Late Cretaceous (after 90 Ma) and Paleocene diatoms have been reported only from a few sites to date (e.g. Barron, 1985b; Harwood, 1988; Dell'Angelse & Clark, 1994; Tapia & Harwood, 2002). Because of the limited number of records the effect of the asteroid impact at the Cretaceous–Tertiary (KT) boundary (65 Ma) on diatom evolution remains unresolved. While Harwood (1988) concluded that 84% of the species survived the KT, Chambers (1996) estimated the survival rate to be only about 37%. Extensive documentation of diatom evolution considering the fossil record and molecular biological evidence has recently been presented by Sims *et al.* (2006) and Kooistra *et al.* (in press).

Diatom palaeoecology and isotope studies

During the past 15 years, major progress has been made in the application of diatoms to estimate past marine and fresh-water environmental conditions. This includes demonstrating the utility of diatoms as indicators of environmental parameters, including temperature, salinity, productivity regimes, sea ice, water chemistry and water level, and developing extensive reference datasets supporting quantitative reconstructions via transfer functions techniques (e.g. Gasse *et al.*, 1995; Pienitz *et al.*, 1995; Bigler & Hall, 2002; Fallu *et al.*, 2002; Andersen *et al.*, 2004; Crosta *et al.*, 1998; Zielinski *et al.*, 1998). Quantitative palaeoenvironmental estimations from fresh-water deposits have been focused on documenting the past 20 000–30 000 years (e.g. Barber *et al.*, 1999; Chalié & Gasse, 2002; Heiri & Lotter, 2005). Reconstructions of the marine surface water properties (e.g. temperature, sea ice) include the study of specific time slices (e.g. the Last Glacial Maximum, Gersonde *et al.*, 2005), as well as Quaternary and Tertiary time series studies at various different temporal resolutions and time series that document surface water parameters at various ranges of time resolution from Quaternary and Tertiary records (e.g.

Cunningham *et al.*, 1999; Lange *et al.*, 1999; Koizumi *et al.*, 2004; Bianchi & Gersonde, 2004; Domack *et al.*, 2005)

New stable isotope methods utilizing geochemistry on diatom opal ($\delta^{30}\text{Si}$, $\delta^{30}\text{O}$) and organic matter trapped within ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) have been established during the past decade. They serve as proxies for nutrient utilization or surface water temperature or salinity (e.g. melt-water input or moisture balance (Shemesh *et al.*, 1994; De La Rocha *et al.*, 1998; De La Rocha, 2006; Rietti-Shati *et al.*, 1998; Sigman *et al.*, 1999; Barker *et al.*, 2001). The longest record showing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements, together with diatom-derived surface temperature and sea ice estimates, covers the past 650 000 years in the Southern Ocean (Schneider-Mor *et al.*, 2005).

What next?

Future efforts in diatom research should consider further developments in diatom-based proxies for the description of past environmental development, using species composition and biometry, as well as geochemical and stable isotope composition. Taxonomic, stratigraphical and autecological information on diatoms should be collected and disseminated via international data repositories to avoid loss of information gathered in the past 50 years in a scientific environment that increasingly relies on electronic media.

Manuscript received 1 May 2006

Manuscript accepted 1 August 2006

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