Instituto Juan March
de Estudios e Investigaciones

3

CENTRO DE REUNIONES
INTERNACIONALES SOBRE BIOLOGÍA

Lecture Course on

Palaeobiology: Preparing for the Twenty-First Century

Organized by

F. Álvarez and S. Conway Morris

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I N D E X

INTRODUCTION

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The purpose of this short publication is to make more widely available the lecture notes and other handouts used for the short course. The published version is modified in a number of ways, most notably the exclusion of some of the figures and other illustrative material. Nevertheless, it is our hope that this publication will provide easy access to the topics covered in the short course, and so by implication those areas that we believe are of special interest or value in making the science of palaeontology a continuing success in its own right and an important contributor to our understanding of natural sciences as a whole. It will be clear that there are many other topics that could have been covered, and even with these notes we would not wish to make any claim that the areas are dealt with in exhaustive detail.

We hope the success of the short course is reflected to some extent in these notes, and if they act as a guide or spur to those who were not able to attend, then their purpose will have been amply filled.

MOLECULAR METHODS IN PALAEONTOLOGY

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PART 1: MOLECULAR EVOLUTION

The molecules of life

In geological materials (minerals) covalent bonds extend in two or three dimensions (mica or quartz). In biological molecules, covalent bonds form the backbones of linear polymers and the bonds in other directions are weak. This explains the softness and flexibility of most biological materials. There are four common kinds of linear polymers:

- polypeptides (proteins) – linear polymers of amino acids
- polynucleotides (RNA and DNA) – linear polymers of nucleotides
- polysaccharides (carbohydrates) – linear polymers of sugars
- lipids – linear polymers of hydrocarbons

Linear polymers store information in a digital fashion. For example, the cadang-cadang coconut viroid genome consists of 246 DNA nucleotides, each being in one of four possible states (A, G, C or T). It therefore represents 984 "bits" of information and, theoretically, could code for 82 amino acids in each of six reading frames.

```
  1 CTGGGGAAAT CTACAGGGCA CCCCAAAAAC CACTGCAGGA GAGGCCGCTT GAGGGATCCC
 61 CGGGGAAACC TCAAGCGAAT CTGGGAAGGG AGCGTACCTG GGTCGATCGT GCGCGTTGGA
121 GGAGACTCCT TCGTAGCTTC GACGCCCGGC CGCCCCTCCT CGACCGCTTG GGAGACTACC
181 CGGTGGATAC AACTCACGCG GCTCTTACCT GTTGTTAGTA AAAAAAGGTG TCCCTTTGTA
241 GCCCCT

  1 LGKSTGHPKN HCRRGRLRDP RGNLKRIWEG SVPGSIVRVG GDSFVASTPG RPSSTAWETT
 61 RWIQLTRLLP VVSKKRCPFV AP (READING FRAME 1)
```

Molecular evolution

The family of proteins that includes the light-harvesting molecules called rhodopsins provides a straight-forward example of the way sequence information from proteins may be used for phylogenetic purposes. Rhodopsins have a secondary structure that is characteristic of many membrane proteins: all members of the family consist of seven lengths of alpha-helix connected by unstructured loops. Rhodopsins are ancient proteins which appear to have evolved in the Archean because similar molecules are found in the archaebacterium, *Halobacterium halobium*, various kinds of animals, and possibly a green alga. Rhodopsin sequences from archaebacteria, man (*Homo*), mouse (*Mus*), ox (*Bos*), sheep (*Ovis*), chicken (*Gallus*), lamprey (*Lampetra*), fruit-fly (*Drosophila*), squid (*Loligo*), and *Octopus* are available for analysis. This normally involves aligning the sequences, editing out regions where the aligments are ambiguous, translating from DNA or RNA to protein (or *vice versa*), removing third-position nucleotides, distinguishing transitions from transversions, constructing unrooted or rooted trees using parsimony or distance algorithms, and testing the trees for statistical significance by bootstrapping and other non-parametric methods.

Gene duplications complicate matters. Many genes belong to multigene families that are derived by successive duplications from a common source gene. For example, the human red, green and blue visual pigments are protein cousins of rhodopsin that share all of the basic properties and many of the same amino acid residues. In the case of these light-sensing proteins it is clear from sequence comparisons alone that the red and green pigments of the human eye are the result of a recent gene duplication event (they are only 4% different in amino acid sequence). In

contrast, the blue protein is approximately 60% different from the red and green proteins and all three are about 60% different from human rhodopsin. It is therefore necessary to know the history of any multigene family in order to avoid comparing paralogous genes rather than homologous ones.

Globins (haemoglobins and myoglobins) are the oxygen-transporting molecules of blood and muscle. The sequence (order and kind) of the amino acids is known as the primary structure of the protein. The globin molecule resembles a framework constructed from unequal lengths of pipe joined by U-pieces. The pipe-like parts are lengths of alpha-helix. As most of the haemoglobin molecule has this kind of structure, there are few constraints on the nature of many of the 140 or so amino acid residues. The "works" of the globin (the part that reversibly binds oxygen) is an iron-porphyrin complex not very different from the magnesium-porphyrin complex of the chlorophylls. Because the segments of alpha-helix (the secondary structure) are unequal in length, the protein "box" (the tertiary structure) is quite irregular in shape. The same irregular structure is present in globins from vertebrates, an annelid, a mollusc, an insect, and the root nodules of a legume plant. This is good evidence that all globins are are monophyletic. Myoglobins consist of a single 140-amino acid subunit. Haemoglobins may be composed of one, two, four, or many 140-amino acid subunits.

In all living vertebrates except the jawless fish, hemoglobin is a four-part molecule (tetramer) formed of two pairs of distantly related globins called the α and β subunits. The primordial alpha and beta haemoglobins were produced by a pair of identical genes that resulted from a duplication in the line leading from the jawless fish to all other vertebrates. This event

postdated the origin of the jawless fish in the late Cambrian or Ordovician, and it predated the evolution of other fish in the Silurian. It is therefore possible to use the fossil record of primitive vertebrates to date the gene duplication event. Once the duplication had occurred the α and β genes began to evolve independently. As a result, it is necessary to distinguish between the histories of genes and the histories of organisms when using molecules like the rhodopsins and the globins for phylogenetic purposes.

Dickerson, R.E. and Geis, I. 1983. *Hemoglobin: Structure, Function, Evolution and Pathology*. Benjamin and Cummings, Menlo Park, 176 pp.

Fryxell, K.J. and Meyerowitz, E.M. 1991. The evolution of rhodopsins and neurotransmitter receptors. *Journal of Molecular Evolution* **33**, 367-378.

Nathans, J., Thomas, D. and Hogness, D.S. 1986. Molecular genetics of human color vision: the genes encoding blue, green and red pigments. *Science* **232**, 193-202.

The polymerase chain reaction (PCR)

The introduction of PCR in 1985 has transformed molecular biology and has made molecular palaeontology, molecular archaeology, and molecular forensic science into rapidly developing fields. PCR works by amplifying DNA sequences between conserved or previously sequenced regions. It is a specific probe for a particular part of the genome and it may, in principle, be used to detected and amplify DNA from a single cell.

Erlich, H.A., Gelfand, D. and Sninsky, J.J. 1991. Recent advances in the polymerase chain reaction. *Science* **252**, 1643-1651.

PART 2: MOLECULAR EVIDENCE FOR THE HISTORY OF LIFE

Life on Earth probably originated during the final stages of the heavy bombardment of the inner solar system (3.5 to 4.0 Ga ago). As the flux of objects hitting the Earth declined, a point was reached where the planet could be continuously inhabited. Even so, occasional energetic impacts may have boiled parts of the oceans, with the result that thermophilic microorganisms would have had the best chance of surviving. Thus, one useful current speculation is that the last common ancestor of modern life was an extreme thermophile.

Following early ideas of A.I. Oparin and J.B.S. Haldane, and a classic experiment of Stanley L. Miller, it is now generally accepted that life originated spontaneously on Earth from precursor organic molecules which were synthesised abiotically. These are not preserved, but it is assumed that fresh carbonaceous meteorites (e.g., Murchison which fell in Victoria, Australia, on the 28th September, 1969) contain compounds like those delivered to Earth by early impacts. Other organic molecules were synthesized in the atmosphere by impact shocks, ultraviolet light and electrical discharges. These processes may be simulated in the laboratory.

Bada, J.L. 1991. Amino acid cosmochemistry. *Philosophical Transactions of the Royal Society of London* B **333**, 349-358.

Chyba, C. and Sagan, C. 1992. Endogenous production, exogenous delivery and impact-shock synthesis of organic molecules: an inventory for the origins of life. *Nature* **355**, 125-132.

Miller, S.L. 1992. The prebiotic synthesis of organic compounds as a step toward the origin of life. *Major Events in the History of Life*, J.W. Schopf (ed.), Jones and Bartlett, Boston, Massachusetts, pp. 1-28.

Sleep, N.H., Zahnle, K.J., Kasting, J.F., Morowitz, H.J. 1989. Annihilation of ecosystems by large asteroid impacts on the early Earth. *Nature* **342**, 139-142.

The first cells

It is not known how life originated on Earth, whether or not there were multiple origins of life, nor is it known what the first cells looked like. The recent discovery of catalytic RNAs has shifted attention away from proteins as the original components of living systems. In the "RNA World" RNA stored information and also built structures. These functions are now generally divided between DNA and proteins, respectively.

Cavalier-Smith, T. 1987. The origin of cells: a symbiosis between genes, catalysts and membranes. *Cold Spring Harbor Symposium on Quantitative Biology* **52**, 805-824.

Bacterial evolution

Woese *et al.* used 16S and 18S ribosomal RNA (rRNA or rDNA) sequences to determine the relationships of microorganisms. Their unrooted tree has three main branches: Eubacteria, Archaebacteria and Eukaryota (renamed recently the Bacteria, Archaea and Eucarya).

Pace, N.R., Olsen, G.J. and Woese, C.R. 1986. Ribosomal RNA phylogeny and the primary lines of evolutionary descent. *Cell* **45**, 325-326.

Woese, C. R. 1987. Bacterial evolution. *Microbiological Reviews* **51**, 221-271.

Woese, C.R., Kandler, O. and Wheelis, M.L. 1990. Towards a natural system of organisms: proposal for the domains Archaea, Bacteria and Eucarya. *Proceedings of the National Academy of Sciences U.S.A.* **87**, 4576-4579.

Rooting the Woese tree in the eubacterial branch has been possible because some conserved genes were duplicated prior to the existence of the last common ancestor of all living organisms. Trees constructed from unambiguously aligned, conserved parts of these genes may therefore be rooted at the gene duplication event. When this is done, it is seen that the topology on one side of the tree is the same as on the other side. In particular, the archaebacteria group with the eukaryotes rather than with the eubacteria on both sides of the tree.

Gogarten, J.P., Kibak, H., Dittrich, P., Taiz, L., Bowman, E.J., Bowman, B.J., Manolson, M.F., Poole, R.J., Date, T., Oshima, T., Konishi, J., Denda, K. and Yoshida, M. 1989. Evolution of the vacuolar H^+-ATPase: implications for the origin of eukaryotes. *Proceedings of the National Academy of Sciences U.S.A.* **86**, 6661-6665.

Iwabe, N., Kuma, K., Hasegawa, M., Osawa, S. and Miyata, T. 1989. Evolutionary relationship of archaebacteria, eubacteria and eukaryotes inferred from phylogenetic trees of duplicated genes. *Proceedings of the National Academy of Sciences U.S.A.* **86**, 9355-9359.

Iwabe, N., Kuma, K., Hasegawa, M. and Miyata, T. 1991. Evolution of RNA polymerases and branching patterns of the three major groups of Archaebacteria. *Journal of Molecular Evolution* **32**, 70-78.

Lake's view is that the Archaebacteria is not a monophyletic group. In his opinion, two of the three principal archaebacterial grroups, methanogens (methanobacteria) and halophiles (halobacteria) form a monophyletic clade; the third group, known either as eocytes or the sulfobacteria, are the sister of the eukaryotes. New evidence suggests that this interpretation is correct. It depends upon the recognition of a unique 11 amino acid insert in elongation factor (EF) proteins which is a synapomorphy of the sulfobacteria + eukaryotes. Conserved regions on either side of the insert enabled the critical part of the gene to be amplified by PCR from a variety of sulfobacteria.

Lake, J.A. 1988. Origin of the eukaryotic nucleus determined by rate-invariant analysis of rRNA sequences. *Nature* **331**, 184-186.

Rivera, M.C. and Lake, J.A. submitted. EF-1α sequences suggest eocytes are the closest prokaryotic relatives to eukaryotes.

Endosymbiotic origin of mitochondria and chloroplasts

One of the great triumphs of modern molecular biology has been the demonstration that the chloroplasts and mitochondria of eukaryotes are ultimately of endosymbiotic origin. This idea was championed by Lynn Margulis (*Origin of Eukaryotic Cells*, 1970) using cytological evidence, but it was the subsequently discovered sequence similarities between chloroplast and bacterial 16S rRNAs which confirmed the endosymbiont hypothesis. There is now equally good evidence for a distant relationship between mitochondria and purple bacteria, so this group of eubacteria is believed to be the source for the ancestral mitochondrion (or mitochondria).

Some living eukaryotes, such as the diplomonad *Giardia*, lack mitochondria. It was unclear whether this condition is primitive or secondary until the sequence of the 16S-like rRNA of *Giardia* became available. The new data indicate that diplomonads, microsporidians, and presumably most other amitochondriate protists are aerotolerant anaerobes which separated from the line leading to higher eukaryotes before the eukaryotes acquired their mitochondria. Thus the earliest eukaryotes did not require molecular oxygen for aerobic respiration.

Cavalier-Smith, T. 1987. The simultaneous symbiotic origin of mitochondria, chloroplasts and microbodies. *Annals of the New York Academy of Sciences* **503**, 55-71.

Kabnick, K.S. & Peattie, D.A. 1991. *Giardia*: a missing link between prokaryotes and eukaryotes. *American Scientist* **79**, 34-43.

Schwarz, Z. and Kössel, H. 1980. The primary structure of 16S rDNA from *Zea mays* chloroplast is homologous to *E. coli* 16S rRNA. *Nature* **283**, 739-742.

Sogin, M.L., Gunderson, J.H., Elwood, H.J., Alonso, R.A. & Peattie, D.A. 1989. Phylogenetic meaning of the kingdom concept: an unusual ribosomal RNA from *Giardia lambalia*. *Science* **243**, 75-77.

Radiation of the eukaryotes

Protein and rRNA sequence comparisons are being used to tease apart the order in which the numerous groups of living eukaryotes appeared. Unfortunately, the data are ambiguous because several major clades, including the animals, plants and fungi, originated at much the same time. It is therefore unknown whether plants, fungi, or plants + fungi constitute the

sister group of animals. Nevertheless, the main structure of the radiation is becoming clear as old misconceptions are laid to rest: the small subunit rRNA tree has a series of early branches leading to the diplomonads, microsporidians, euglenoids + kinetoplastids, amoebae, and the slime molds; higher up, a nearly polychotomous set of branches leads to the metazoa, the red algae, the sporozoa, the higher fungi, the ciliates, the green plants, and several minor protistan groups.

A minimum date for this radiation of the higher eukaryotes is given by the discovery of a well-preserved red alga in Arctic Canada. If the preferred age of 1.1-1.2 Ga is approximately correct, lineages leading to red algae, fungi, metaphytes and metazoans might well have diverged from each other more than a billion years ago.

Sequences of 16S rRNAs, DNA-dependent RNA polymerases, and the small and large subunits of ribulose-1,5-bisphosphate carboxylase/oxygenase (rubisco) show that the chloroplasts of *Euglena* and green plants are monophyletic, and should therefore have been present in the central branch of the unrooted tree: ((*Giardia*, *Euglena*) (*Petunia*, *Homo*)). The origin of the green chloroplasts is inseparable from the radiation that gave rise to the major groups of living cyanobacteria. It therefore probable that early Proterozoic eukaryotes housed green chloroplasts, which, like modern *Euglena*, used chlorophylls *a* and *b* as light-harvesting pigments.

Bhattacharya, D., Elwood, H.J., Goff, L.J. & Sogin, M.L. 1990. Phylogeny of *Gracilaria lemaneiformis* (Rhodophyta) based on sequence analysis of

its small subunit ribosomal RNA coding region. *Journal of Phycology* **26**, 181-186.

Butterfield, N.J., Knoll, A.H. & Swett, K. 1990. A bangiophyte red alga from the Proterozoic of Artcic Canada. *Science* **250**, 104-107.

Giovannoni, SA.J., Turner, S., Olsen, G.J., Barns, S., Lane, D.L. & Pace, N.R. 1988. Evolutionary relationships among cyanobacteria and green chloroplasts. *Journal of Bacteriology* **170**, 3584-3592.

Hendriks, L., De Baere, R., Van de Peer, Y., Neefs, J., Goris, A. & De Wachter, R. 1991. The evolutionary position of the rhodophyte *Porphyra umbilicalis* and the basidiomycete *Leucosporidium scottii* among other eukaryotes as deduced from complete sequences of small ribosomal subunit RNA. *Journal of Molecular Evolution* **32**, 167-177.

Valentin, K. & Zetsche, K. 1990. Nucleotide sequence of the gene for the large subunit of Rubisco from *Cyanophora paradoxa* – phylogenetic implications. *Current Genetics* **18**, 199-202.

Carbon isotopes

Carbon occurs as a mixture of two stable isotopes, "light" ^{12}C and "heavy" ^{13}C (plus trace amounts of radioactive ^{14}C). All common photosynthetic pathways discriminate against ^{13}C, mainly in the carbon-fixing reaction catalyzed by the enzyme rubisco. As a result, organic matter is lighter than sea water carbonate (~0 ‰) by about 25‰:

$$\delta^{13}C \approx -25‰_{PDB}$$

After burial in sediments, organic matter (kerogen) may preferentially lose hydrogen (measured by a decrease in H/C) as its temperature is increased. It may also lose ^{12}C thereby increasing $\delta^{13}C$. Generally speaking, kerogens with $H/C \geq 0.2$ are thought to retain their initial $\delta^{13}C$ values. The fact that

most kerogens with H/C ≥ 0.2 lie within the range –25‰ to –35‰ regardless of their age, is evidence that photosynthesis has been operating as it does now for the last 3.5 Ga years (and possibly for the last 3.8 Ga).

Exceptionally light carbon isotope ratios ($\delta^{13}C \leq -40‰_{PDB}$) obtained from organic matter from late Archaean and early Proterozoic rocks (2.1 and 2.7 Ga old) have been interpreted as evidence for the existence, at those times, of eubacterial methylotrophs which were using methane produced by archaebacterial methanogens.

Hayes, J. 1983. Geochemical evidence bearing on the origin of aerobiosis, a speculative hypothesis. *Earth's Earliest Biosphere. Its Origin and Evolution*, J.W. Schopf (ed.), Princeton University Press, Princeton, NJ, pp. 291-301.

Hayes, J.M., Kaplan, I.R. and Wedeking, K.W. 1983. Precambrian organic geochemistry, preservation of the record. *Earth's Earliest Biosphere. Its Origin and Evolution*, J.W. Schopf (ed.), Princeton University Press, Princeton, NJ, pp. 93-134.

Schidlowski, M. 1988. A 3,800-million-year isotopic record of life from carbon in sedimentary rocks. *Nature* **333**, 313-318.

Molecular fossils

Until recently, it was necessary to use the stratigraphic range of eukaryotic microorganisms as a proxy for the history of their membrane lipids. For example, it is believed that the last common ancestor of all living eukaryotes possessed the ability to manufacture sterols by the epoxidation of squalene.

This logic has been short-circuited by developments in analytical organic geochemistry. The introduction of metastable reaction monitoring as a refinement of computerized gas chromatography/mass spectroscopy (GCMS) has led to the detection of small quantities of modified sterols (steranes) in rocks as old as 1,690 Ma. Fossil compounds such as 5α(H)14α(H)17α(H)-cholestane from organic-rich shales of the MacArthur Basin, northern Australia, must have required free oxygen for their fabrication. They therefore provide direct evidence for the existence, some 1.7 Ga ago, of aerotolerant or aerobic eukaryotes and an atmosphere that contained, at the very least, about 0.3×10^{-3} PAL O_2.

Runnegar, B. 1991. Precambrian oxygen levels estimated from the biochemistry and physiology of early eukaryotes. *Palaeogeography, Palaeoclimatology, Palaeoecology* **97**, 97-11.

Summons, R. E., Powell, T. G. and Boreham, C.J. 1988. Petroleum geology and geochemistry of the Middle Proterozoic McArthur Basin, northern Australia: III. Composition of extractable hydrocarbons. *Geochimica Cosmochimica Acta* **52**, 1747-1763.

Summons, R. E. and Walter, M.R. 1990. Molecular fossils and microfossils of prokaryotes and protists from Proterozoic sediments. *American Journal of Science* **290-A**, 212-244.

Molecular clocks

The observed similarity between any pair of correctly aligned protein or nucleic acid sequences diminishes roughly in proportion to the evolutionary distance which separates each pair. It was this apparently regular decline in pairwise similarity – first observed in aligned protein sequences – which led

Zuckerkandl and Pauling to suggest that the rate of sequence evolution might be sufficiently constant for any given protein to function as a "molecular evolutionary clock". This fruitful idea has been applied to a variety of questions in historical biology, but it has also been roundly criticised, both for the unsupportable assumptions upon which its is based, and for the way in which it performs in cases where molecular dates may be compared with those derived directly from the fossil record. There are also internal tests of consistency which indicate that the molecular evolutionary clock is frequently imprecise and unreliable. Despite these shortcomings, molecular estimates of time may provide information about the history of life that is not available in any other way. This is particularly true for the Precambrian.

Doolittle, R.F., Anderson, K.L. and Feng, D.F. 1989. Estimating the prokaryote-eukaryote divergence time from protein sequences. *The Heirachy of Life*, B. Fernholm, K. Bremer and H. Jörnvall, (eds), Elsevier Biomedical Division, Amsterdam, pp. 73-85.

Jukes, T.H. (ed.) 1987. Special issue – molecular evolutionary clock. *Journal of Molecular Evolution* **26**, 1-171.

Runnegar, B. 1991. Nucleic acid and protein clocks. *Philosophical Transactions of the Royal Society of London* B **333**, 391-397.

PART 3: BIOCHEMICAL FOSSILS

The four principal kinds of "biochemical" fossils are:

- proteins trapped in bone or shell
- DNA from mummified tissues
- biomarkers (biological marker compounds)
- stable isotopes of carbon, oxygen and sulphur

Biomarkers

Most biomarkers are derivatives of the structural components of cell membranes (lipids, steroids, hopanoids) or pigment molecules such as chlorophyll. They are studied by organic geochemists using computerized gas chromatography-mass spectroscopy (GCMS), now often enhanced by metastable reaction monitoring (MRM). Some biomarkers can be identified as the products of particular kinds of organisms (e.g., the dinoflagellate sterol "dinosterol"), but many are found throughout whole kingdoms of organisms. The "best" stable isotope biogeochemistry is now being done on individual biomarkers rather than on whole-rock kerogens.

Proteins from bones and shells

Broadly speaking, there seem to be two classes of proteins that participate in the production of mineral skeletons – those which form a primary structural framework and those which are attached to the framework in such a way as to control the site of deposition and the crystallographic orientation of the subsequently deposited mineral phase. The structural proteins are normally insoluble in water and rich in the amino acid glycine; the other kinds of proteins obtained by dissolving the shell or bone in a weak acid are often rich in negatively charged residues (aspartic or glutamic acids) which are assumed to interact with the cations of the mineral crystallites. For example, in vertebrate bone the structural framework is formed of collagen and a much smaller molecule, osteocalcin, it believed to be implicated in the deposition of hydroxyapatite. Most osteocalcins contain three residues of γ-carboxyglutamic acid per molecule, and each of these doubly negatively charged side chains is thought to bind Ca^{2+} ions in the apatite lattice.

Collagen from vertebrate bone of Quaternary age was first used to obtain conventional radiocarbon ages, but the usefulness of the technique was limited by the relatively large amounts of protein required and doubts about *post mortem* contamination. Conversion of the collagen to gelatin resulted in a purer product, but an even better procedure in which the carbon source is limited to the collagen-specific amino acid hydroxyproline, could not be implemented until accelerator mass spectrometry (AMS) became available some twenty years later. Collagen and osteocalcin are now routinely used as sources of carbon and nitrogen for stable isotope analysis and ^{14}C age determinations.

Proteins in well-preserved bones and shells are used for two other purposes – phylogenetics and amino acid racemization/epimerization dating. The former depends upon immunological methods and the latter on the fact that the symmetry bias seen in amino acids of biological origin diminishes with time and some other factors.

Fossil DNA

This is a hot topic at present because of the discovery that long sequences of chloroplast DNA may be obtained from Miocene fossil leaves at a locality near Clarkia, Idaho. Shorter sequences have also been obtained from Egyptian mummies, subfossil human brains, the skins of extinct mammals, forensic specimens, hams from the *Mary Rose*, and English civil war graves. A 1,320-long DNA sequence of the gene (*rbcL*) for the large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase (rubisco) from a Miocene

bald cypress (*Taxodium*) gives a direct measure of the rate of evolution of this molecule.

Eglinton, G. and Curry, G.B. (eds) 1991. *Molecules Through Time. Fossil Molecules and Biochemical Systematics*. Royal Society, London, 127 pp. (*Philosophical Transactions of the Royal Society of London* B **333**, 307-433).

Pääbo, S., Higuchi, R. and Wilson, A.S. 1989. Ancient DNA and the polymerase chain reaction. *Journal of Biological Chemistry* **264**, 9709-9712.

Runnegar, B. and Schopf, J.W. (convenors) 1988. Molecular evolution and the fossil record. *Short Courses in Paleontology* **1**, 167 pp.

Soltis, P.S., Soltis, D.E. and Smiley, C.J. 1992. An *rbcL* sequence from a Miocene *Taxodium* (bald cypress). *Proceedings of the National Academy of Sciences U.S.A.* **89**, 449-451.

Waples, D.W. and Machihara, T. 1991. Biomarkers for geologists. *AAPG Methods in Exploration* **9**, 1-91.

General reference:

Li, W. and Graur, D. 1991. *Fundamentals of Molecular Evolution*. Sinauer, Sunderland, MA, 284 pp.

BIOMINERALIZATION AND GROWTH

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BIOMINERALIZATION AND GROWTH

Processes of Biomineralization

Biomineralization refers to the processes by which organism form minerals. It is, therefore, by definition a true multidisciplinary field that spans both the inorganic and the organic world. The phenomenon is extremely widespread, and some 60 or so minerals are known to be formed by organisms under a wide variety of conditions. They are deposited at many different locations both inside and outside cells. Some biogenic minerals are formed on such a huge scale in the biosphere that they have a major impact in ocean chemistry and are important components of marine sediments and ultimately of many sedimentary rocks as well.

All five kingdoms contain members that mineralize and these are distributed among no less that 55 phyla. These organisms are capable of forming 60 different minerals and it is clear that the true diversity it is far from having been ascertained (Table I).

Biogenic minerals often have unique shapes and mineralogies, as well as an overprint of disequilibrium (with respect to the environment) chemical signatures. These proprieties may be exploited to provide a more complete picture of the evolution of biomineralization based in the fossil record.

Formation of new crystals from solutions, in which no such crystals existed previously, involves two phases: crystal nucleation and crystal growth. Nucleation is considered to be achieved by a stepwise addition of single molecules, atoms, or ions, and eventually a lattice is formed. Many of these nuclei are unstable and redissolve.

There are two types of biomineralization processes:

A) Biologically **induced** mineralization (Lowenstam 1981). Mineral formation in many aqueous environments in which organisms live is not inherently difficult to achieve. Even a relatively minor perturbation, such as the introduction of biologically produced metabolic end-products, the release of particular cations by the cell, or even the construction of a charged surface such as a cell wall, will under certain circumstances induce minerals to precipitate. The secondary precipitation of mineral as a result of the interactions between biological activity and the environment was termed **"Biologically induced mineralization"**. In this type, the biological

system exercises little control over type and habit of mineral deposited although biological surfaces may be important in the induction of mineral.

This process appears to be the predominant process among the monerans and fungi and it occurs fairly frequently in the protoctists and it is by no means uncommon among the animals.

B) Biologically **controlled** mineralization (Mann 1983). In this type of biomineralization, the genetically controlled matrix controls nucleation, growth and microarchitecture of the mineral deposited. The organism synthesizes a structural framework composed of organic macromolecules into which the appropriate ions are introduced, and then induced to grow. The structural framework determines, at least in part, the mineral phase to be formed, the orientation of its crystallographic axes and the final morphology of the individual microarchitectural units.

Our knowledge of mineralization processes is still rather limited, however it is already apparent that many organisms can combine different control processes and end up with an unique final product. If each of the large variety of minerals deposited by organisms are formed by a unique process, then the possibility of understanding the mechanisms by which these minerals are formed is remote. A more fruitful approach is to assume that the basic processes of mineral formation are common to all systems and that mineral formation by any individual biological system may diverge from the common pathway.

It is obvious that a precondition for mineralization is that the solution from which the mineral is to precipitate must be saturated and all the thermodynamic and kinetic considerations that apply to mineral formation from saturated solutions in a beaker also apply to the space delineated by organisms for mineralization.

The formation of the mother liquor in biologically controlled mineralization is dominated by the cell or cells responsible for orchestrating the entire mineralization process. Cells are equipped so that they can actively pump ions of choice into the mineralizing compartment or, when appropriate, allow passive diffusion of specific ions. The compositions of the ions that enter into the mineralization compartment is determined by the manner in which they are extracted from the environment, transported through the tissues, and introduced into the mineralization site. The facts are that many organisms are well equipped to determine which ions enter into the mineralization compartment.

There are examples of biogenic minerals formed by organisms that live in environments in which the same mineral would never form inorganically. One of the best

known is the protoctists Acantharia. These single celled marine animals form hard parts composed of celestite (strontium sulfate), mineral highly undersaturated in the oceans and, upon death, the shells rapidly dissolve (Lowenstam & Weiner 1989).

Nucleation, in general, represents an activation energy barrier to the spontaneous formation of a solid phase from a supersaturated solution. This kinetic constraint may be sufficient to offset the thermodynamic driving force for precipitation, resulting in a metastable solution which do not undergo phase transformations over a long period of time. In biological environments, the activation energy for nucleation can be reduced by lowering the interfacial energy and/or increase the supersaturation.

Two features of the organic matrix are essential on nucleation. First, organization of the organic matrix, through which they control the number of nucleation sites and second its molecular complementarity with the inorganic ions that results in the crystalochemical specificity in the mineral deposits.

The real world of biomineralization includes not only ions, macromolecules and minerals, but also the all important cells that orchestrate the whole phenomenon and coordinate their activities with the rest of the organism. They are usually responsible for the timing of mineralization processes and for determining the rates at which mineral will be deposited. They also coordinate this rate with the rest of organism growth.

There is evidence (isotopic composition of sulfide minerals) of biologically induced mineralization as far back as 2.7 Byr BP (Monster *et al.* 1979). However the oldest actual fossils that show direct evidence of biologicaly produced minerals are the manganese encrusting bacteria, present in deposits formed 1.6 billion years ago (Muir 1978). Biologically controlled minerals may have originated sometime in the Precambrian. Then, biomineralization products comprise single crystals, small crystal aggregates formed in spicules and so on.

The Precambrian appears to represent a period in which organisms produced minerals by the "biologically-induced" type mineralization process, and only towards the end of the Precambrian is more control exercised over the crystal growth processes and "matrix-mediated" mineralization evolved (Lowenstam & Weiner 1989).

One of the most significant events in the evolution of the biomineralization was the formation of large composite mineralized skeletons that took place 570 million years ago (Lowenstam & Weiner 1989). It is also significant that the first hard parts formed by organisms at or close to the Precambrian-Cambrian boundary already include carbonates, phosphates and silica.

During the Phanerozoic, biomineralization processes exhibited certain trends both with respect to mineral types utilized and complexity of organization. Just prior to the Cambrian period, all the known biogenic minerals were calcium-minerals and two thirds were composed of calcium phosphate. Within 40 to 50 mya, calcium carbonate became the dominant mineralization product and in the course of the Phanerozoic, many groups substituted aragonite for calcite in part or all of their mineralized hard parts. Another major development during the Phanerozoic, was the increasing utilization of amorphous silica by members of various eukaryotic phyla.

Most of the fossils with carbonate hard parts are from the Animalia or Protoctista, and, only a few from the Monera (Lowenstam & Weiner 1989). The other two kingdoms with very few exceptions do not have preserved fossils remains. As marine deposits are better preserved than continental ones, the record is also biased towards marine organisms.

Lightly calcified cyanobacteria, the first documentation of carbonate mineralization in the fossil record, are presents in rocks from 1,000 mya and through Vendian times (Riding and Voronova 1982, 1984). By the end of the Cambrian carbonate precipitating organisms dominated (Lowenstam & Weiner 1989).

The formation of biogenic carbonates in the marine environment increased almost expontentially during the Mesozoic and Cenozoic, what had a big impact on the chemistry of the present day oceans.

The fossil record of phosphatic hard parts begins at the end of the Vendian, some 570 to 580 mya, and is, to date, confined to the Animalia (Lowenstam & Weiner 1989).

The major part of the fossil record of phosphatic mineralizers in the Cambrian comprises problematica organisms, most of which became extinct by the end of the Cambrian. Is there any connection between their becoming extinct and their option for the use of phosphate for skeletal hard part formation?. Concentration of phosphate in sea water towards the end of the Vendian and the beginning of the Toomotian were relatively high (Cook & Shergold 1984) what could explain their initial selection.

Based in the fossil record, primary period of phosphatic biomineralization started in the late Vendian, peaked during the Cambrian, and by mid-Ordovician times was confined for the most part to the vertebrates (Lowenstam & Weiner 1989). Many Cambrian phosphate-bearing organisms apparently became extinct, whereas others started forming carbonate minerals.

The formation of siliceous skeletons is common and widespread in the kingdoms Protoctista and Plantae and in the animal Phylum Porifera. To date no Fungi or Monera are known to definitely form opal (Table I) (Lowenstam & Weiner 1989).

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The oldest known biogenic silica deposits are found at the base of the Cambrian, just above the Precambrian-Cambrian boundary, where siliceous spicules of hexactinellid sponges have been found in marine deposits (Sdzuy 1969). The mid-Ordovician, some 450mya, is the first time that extensive sedimentary accumulations of siliceous skeletal deposits occur (Lowenstam 1948). These are composed of radiolarian skeletons.

An addition to the spectrum of opal forming organisms occurred with the evolution of the diatomeans in the early Jurasic about 200 mya. They did not become quantitatively important constituents of the marine planktonic community until about 100 mya in the mid-Cretaceous (Tappan 1980).

The expansion of terrestrial angiosperm grasses in the mid-Cenozoic resulted in huge amounts of biogenic silica being formed in land. Expansions on land and in the ocean occurred more or less at the same time (Lowenstam & Weiner 1989).

Construction of mineral skeletons

Organism show four basic methods of skeletal growth:

- ***Accretion***: Growth is by addition of mineral material to the preexisting skeleton.
- ***Molting***: This growth form is restricted to arthropods. In molting, the skeleton is periodically discarded and a new, larger, and perhaps different shaped skeleton develops.
- ***Addition of skeletal elements***: The simplest example of this is the addition of spicules to a spicular skeleton (sponges, alcyonarians, holoturians). A more complex example is the equinoderm skeleton which is enlarged by the addition of new plates.
- ***Modification***: This method involves growth on all sides and even within the skeleton and resorption of material so that both the shape and size of the skeleton can change as needed. This method is used in the vertebrates.

The most widespread method is the first one, and we will use the brachiopods as an example of skeletal growth by accretion.

Although much research remains to be done on the fabric of the brachiopod skeleton, and fundamental changes in our views on the evolution of the structure of the calcareous shell may yet occur, studies of living and fossil calcitic-shelled Brachiopoda show that skeletal growth has never involved, more than a few secretory processes (Williams 1968a&b, 1971a&b, 1984, 1990; MacKinnon & Williams 1974). The

succession: periostracum (organic)-mineral primary layer-mineral organic fibrous secondary layer-[and in some stocks, mineral prismatic tertiary layer] is the common fabric throughout the evolutionary record of brachiopods. In living brachiopods, the skeletal fabric can be related to the external form and secretory activity of cells composing the outer epithelium of the mantle lining the shell. With growth, those cells that originated in the part of the generative zone away from the mantle margin move away remaining as part of the inner surface of the mantle. They have no role in the development of either the shell or the periostracum. On the contrary, cells proliferating on the opposite part of the generative zone are intimately involved in the secretion of the shell playing a complex and changing role in its development. During growth, each cell moves as in a conveyor belt pushed by the new cells proliferating behind it, at the generative zone. During this migration secretory activity of the cells change periodically. Each cell is responsible of the secretion of part of the periostracum, and part of each of the layers of the shell. The cells form organic periostracum as they move away from the generative zone until they reach the mantle margin. At this point secretory activity changes and cells begin to deposite mineralized shell on the inner surface of the periostracum. The calcite crystals initially formed, constitutes what it is known as **primary layer**. Thickness of the primary layer increases slightly towards the anterior. As the primary layer deposition is restricted to a small zone of the outer epithelium cells situated at the valve edge, this thickening could be due to the progressive increment in the number of cells of that epithelium involved in the secretion of the primary layer. On the other hand, the thickening of the primary layer, observed under growth lamellae, could be attributed to a diminution of the speed of migration of the outer epithelium cells during the readjustement of the mantle after the regression, together with the better preservation expected in the primary layer below lamellae, where it is less exposed to superficial abrasion (Alvarez *et al.* 1987; Alvarez 1990; Alvarez & Brunton 1990, 1991).

These cells, responsible of primary layer formation, secrete just calcite, but as the growing mantle margin moves away from a particular cell, its secretory activity change once again. Now, besides of the deposition of calcite, it lays down an organic membrane. Although shape of the organic membrane, and thus the resulting shell structure, change in the different brachiopod groups, this part of the shell formed by the calcite and the organic membrane it is called **secondary layer**. So far two main types of microstructures have been identified in the secondary layer: fibrous and laminar. A fibrous secondary layer is the most frequently found and apparently represents the primitive condition in the articulate brachiopods. It is found in the Cambrian articulate brachiopods, it is a persisting characteristic in many of the main lineages, and it is the

microstructure characteristic of most of the Recent articulates. During deposition of fibrous layer, each cell secretes a long rode of calcite with a characteristic shape. Epithelial cells are disposed in alternate rows, and only the posterior part of each cell deposite calcite, whereas the acute anterior part exudes an organic membrane, This membrane is fused with those of the adjacent cells, and together cover each calcite fibre. The shape and packing of the fibres of secondary layer depends initially on the spatial relationship between the outer epithelium cells and the inner surface of the shell. Secondary fibres appear as blades which gradually become wider towards the inner surface of the shell. In longitudinal section the fibres are obliquely sloping, from their origin under the primary layer anteriorly towards the inner surface of the shell, with an angle close to 10°. The shape and packing of the fibres has been observed in transverse sections. This kind of packing facilitates the overlapping of fibres during growth and provides a considerable consistency to the shell. The regular packing of the fibres ends at the internal surface of the valve forming a mosaic structure.

When the primary layer is removed it is possible to see that the secondary fibres are disposed radially, perpendicularly to the margin of the valve. However, this disposition may change during growth. At some distance from the valve margin the secondary fibres stop growing anteriorly in synchrony with the primary layer and reorientate in different directions. With this change in the growth strategy a strengthening and thickening of the valve wall is achieved. To allow the rotational movements of the secondary fibres, maintaining their compact packing, it is likely that the secretion of some fibres had to slow down or stop for a while. The rotation of groups of fibres requires a differential growth, being slower at the inner than the outer fibres of each group. All inner skeleton, including teeth, dental sockets, cardinalia and brachidium, are usually formed by secondary shell. Regularity of fibre stacking in those structures is usually interrupted due to resorption and development of new cells in the secondary generative zones.

During growth, brachiopods have to keep a delicate balance between **forward growth** of the margin of their valves and the **thickening** of the previously secreted valve. The secretion of **prisms of tertiary layer** seems to be a more efficient method of shell thickening than that the simple reorientation and crossing of secondary fibres described above. The thickness of this prismatic, or tertiary layer, is greatest in the posteromedian region of both valves but diminishes progressively to the anterior and lateral margins. The prisms of tertiary layer appear as consequence of a change in the carbonate secretion of the shell. At the same distance from the valve margin, the outer epithelium cells stopped migrating in the horizontal plane but continued secreting calcite

in the form of well defined prisms arranged perpendicular to the inner surface of the shell and in structural continuity with the underlying secondary layer fibres. In some instances it is possible to observe how every secondary layer fibre gives rise to a characteristic prism of tertiary layer (Alvarez *et al.* 1985; Alvarez 1990). The different orientations of the growth banding in the two layers results from the banding in the prisms no longer representing any growth in length but only vertical accretion of calcareous material.

During the process of secretion of the tertiary layer, the epithelial cells may have suffered a reversion to secrete secondary layer again, giving rise to small transgressions and regressions in the secondary-tertiary layer boundary (Alvarez 1990), possibly caused by fluctuations in the rate of growth of the specimen.

Detailed study of these prims has shown the sporadic presence of banding, of variable periodicity, parallel to the inside of the shell (Alvarez *et al.* 1985; Alvarez 1990). This banding is probably the result of small fluctuations in the physiological behaviour of the epithelial cells, possibly induced by environmental changes.

In the zones of attachment of the muscle bases, and in response to the need for maximum adherence between the shell and the outer epithelium, the typical mosaic of secondary layer is modified as an irregular deposit, the **myotest**. The modifications observed in secondary layer fibres are basically the fusion of adjacent fibres and the lost of their characteristic outlines (MacKinnon 1977; Alvarez 1990). In some longitudinal sections the transgressive disposition of the myotest fibres can be seen in both valves (Alvarez 1990).

The presence of cylindrical microscopic canals (puncta) in the calcareous shell of many brachiopods, implies that the growth pattern just described may show modifications (see for example Williams 1968:29). Function of these puncta and caeca (⇒ tubular multicellular outgrowths of the mantle) are discussed elsewhere.

Growth of endoskeleton structures such as the different types of brachidia, or external features such as lamellae or spines etc, also implies some modifications of the general secretive pattern described. Normal growth of the brachidium, for instance, implies a delicate equilibrium between resorption and secretion in the function of the mantle cells. The deposition and resorption processes by which the spiral cones expand continuously in the brachial cavity are rather complex, as the locations of the areas in which growth and resorption took place is very difficult.

Formation of spines, lamellae, and structures facilitating the tight closing of the commissure require complex transgressive and regressive movements of the mantle

affecting cells secreting both primary and secondary layers (see Alvarez *et al.* 1987; Alvarez & Brunton 1990, 1991). The shelly extensions of brachiopod valve surfaces were originated as a consequence of periodical fluctuations in the secreting behaviour of the marginal zones of the mantle. In general, the first stage in the formation of lamellae was the "elevation" of the plane of growth of primary shell away from the projected curve of the valve. Under this primary layer was secreted a series of secondary fibres whose number decreases progressively distally. Once the lamella was fully grown, there was an interruption in the secretion of primary and secondary layers followed by a regression of the epithelial cells that had secreted the lamella. The surface along which the normal shelly secretion was interrupted slopes posteriorly forming a variable angle with the inner surface of the shell depending on the species under consideration and the position of the lamellae according to their time of growth, during ontogeny. This surface, known as the regression plane, has two well differentiated regions: the distal part, principally associated with the underside of the lamellae, corresponds to the fibres most directly affected by the regression of the epithelial cells. In a radial section these fibres usually curve inwards towards the regression plane. In some species this distal zone of recurved fibres extends into the outermost layers of the valve itself. Thus while the distal part is principally external, in the sense of forming the underside of the lamella, a short section is internal, in the sense of being within the shell. Further into the shell is the proximal part of the regression plane. Mantle regression is marked mainly by flexure in the secondary fibres. Frequently at the inner part of the regression plane, a fine band of micritic-like material appears. On the anterior part of the regression plane, on the undersides of the lamellae in some genera, mantle cells secreted calcite accumulations. These "pads" are the material reflection of the reorganization of the epithelial cells as the started to regress from the lamellae. After this reorganization the normal growth of the shell was resumed. It is important to emphasize that during the development of these lamellae, the cells responsible for their secretion may have been exposed to the action of possible predators, since they lacked the shelter provided by the shell itself during normal shell secretion. The whole growth process of lamellaè may have been very rapid, taking only a matter of hours. In some genera however, the growth of lamellae may be expected to have taken longer, but vulnerability of the epithelial surfaces would have been reduced to that of normal valve growth by the way in which the dorsal and ventral lamellae grew parallel and close to each other, acting as temporary valve margins. Indeed, at the times of maximum regression the true valve margins would have been separated and free to grow towards one another at the start of the next transgression, forming U-shaped gutters (see Alvarez & Brunton 1991). These structures then became the functional valve margins, well posterior to the margins of the lamellae, in so doing providing

closure for the valves and sufficient opposed growth to separate the lamellae and increase the depth of the mantle cavity of the shell. This was followed by the growth of the next pair of lamellae. Initially the outer surfaces of each pair of lamellae diverged slightly, but as they grew, their inner surfaces became parallel to each other and took over the role of functional valve margins, augmenting or superseding the true valve margins, which by this stage were left behind internally. It seems that the nature of the lamellae is a more significant character than, for example, folding and sulcation, which altered during the ontogeny of the individual, but much research remains to be done on the fabric of the brachiopod skeleton. Comparative studies can show the possible changes in skeletal structure (and, by inference, in cell biochemistry) occurred during the history of the different orders, and the possible *post-mortem* alterations in the skeletal fabric induced by diagenesis and lithification.

Table I. Distribution of the more important compositional materials among various taxonomic groups.

		Monera	Protoctista	Fungi	Plantae	Porifera	Cnidaria	Platyhelminthes	Nemertina	Ectoprocta	Brachiopoda	Annelida	Mollusca	Arthropoda	Sipuncula	Pogonophora	Echinodermata	Chordata
CARBONATES	Calcite	x	x	x	x	x	x	x		x	x	x	x	x	x		x	x
	Aragonite	x	x		x	x	x			x		x	x	x	x			x
	Vaterita				x								x	x				x
	Monohydrocalcite	x	x										x					x
	Protodolomite																x	
	Hydroccerussite			x														
PHOSPHATES	Hydroxylapatite	x										x						x
	Octacalcium phosphate																	x
	Francolite	x									x		x					x
	Dahllite	x	x	x									x					x
	Whutlockite	x																
	Struvite	x																x
	Brushite												x					
	Vivianite	x																
HALIDES	Fluorite												x	x				
	Hieratite					x												
SULFATES	Gypsum		x				x											
	Celestita		x															
	Barite		x										x					
SILICA	Opal		x		x	x						x	x	x			x	
IRON OXIDES	Magnetite	x	x										x					x
	Goethite												x					x
	Lepidocrocite					x							x					
	Ferrihydrite	x											x					x
MANGANESE	Todorokite	x																
OXIDES	Birnessite	x																
SULFIDES	Pyrite	x																
	Hydrotroilite	x																
	Sphalerite	x																
	Wurtzite	x																
	Galena	x																
	Greigite	x																
	Mackinawite	x																
METALS	Sulfur															x		
CITRATE	Earlandite				x								x					
OXALATES	Whewellite				x		x							x				x
	Weddellite			x	x								x	x			x	x
	Glushinskite			x														

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ANIMAL PALAEOECOLOGY

It is clear for any observer that animals and plants are not uniformly distributed over the earth. We easily associate groups of organisms with each other and with particular environments: polar bears live in the artic and coral reefs in warm, shallow waters. Deserts are sterile and rain forests luxuriant. Somehow we are all ecologists because ecology tryes to explain the patterns in the distribution and abundance of organisms.

In **palaeoecology** we must determine the relationship between the fossil and the associated sediment, the relationships between the various taxa and the interactions that existed in ancient environments. Thus a good basis, not only in sistematic palaeontology, functional morphology and evolution, but also in sedimentology as well as in biology and chemistry is required in this **integrated approach** to the evolution of the biosphere.

The ecological use of body and trace fossils is of wider interest to geologists, and tries to answer questions related with its palaeophysiology, habitat and cummunity analysis as: How a fossil and where did it "live"?, how it once fed and on what?, how it respired, grew, reproduced, moved and protected itself? with what was it associated?. The answer of this questions is clearly related with the other main items of this course as the self-organizaton of morphologies, plant palaeoecology, funcional morphology and biomineralization and growth.

In a palaeocological analysis the **first questions to answer** are:

- is the fossil in the position in which it lived (**autochthonous**)?,
- has it been either disturbed (**parautochthonous**) or sorted?,
- has it been substantially removed, dispersed and/or transported (**allochthonous**)?.

The answer to these question is not always clear. The normal criteria used to determine autochthony and parautochthony, as the normal life attitude, size frequency distribution, completeness and sorting, shell breakage and damage, orientation among others, are not eassily used.

Besides of this, it is useful to remember the importance of the **local factors** and of past sea-levels and climate when making palaeoecological deductions based on ecological factors. In general, the precision with which various factors can be determined decreases with geological age.

Apart of the **depth** (light intensity), "**inshore** to **offshore**" (nutrient levels) and **latutudinal gradients, other ecological factors**, related with these three and that are of concern to palaeoecology **are**:

- **palaeobathymetry** (⇒ depth and light),
- **palaeotemperature** and **palaeoclimate** (⇒ seasonality, growth rings and banding),
- **type of substrate** (and how the benthos used it: attachment, protection, a source of food...)
- **salinity** and **oxygenation** [⇒ relationship between **oxygenation, benthos** (**nutrients**, degree of bioturbation), **and stratification**],
- **inter-relationship** (⇒ trophic structure, predation, symbiosis, commensalism, parasitism, overgrowth, fouling ...),
- **abundance** [⇒ frequency and **density**)(using, if possible, semiquantitative comparison diagrams)], **diversity** [⇒ **richness** (number of species present), and **evenness** (relative abundance of each species)] and **dispersion** (⇒ **spacing**),
- **population structure** and **dynamics**,
- **palaeobiogeography** (⇒ barriers, physical, chemical and biological limiting factors).

In the investigation of the palaeoecology of a fossiliferous site it is useful to attempt a pictorial reconstruction of the site as it was at the time of formation, the study of the association of organisms that, when alive, formed and interdependent association or **palaeocommunity**. Further discussion on palaeocommunties is beyond the scope of this course, but it is important to finish this section, remembering that before any attempt is made we must seriously considered that the **taphonomic loss** was probably greater than it appears to be ["it si the understanding and appreciation of taphonomy that distinguishes a palaeontologist from a biologist"].

It is generally accepted that hard parts and mineralized skeletons of organisms are preserved, whereas soft bodied organisms hardly have any fossilization potential. However this is not necessarily the case. Mineralized exoskeletons are also badly damaged on a considerably short period after organisms death, thus reducing in a great extent the number of organisms that are preserved in the fossil record and severely limiting palaeoecologicl tinterpretations.

Decay of Recent brachiopod shells could be a good example of the extent of taphonomic loss. **Four different types** of ***postmortem*** **behaviour** have been observed (Emig & Alvarez 1990) in **Recent brachiopods**:

- The **quitino-phosphatic shells** of the inarticulate genera ***Lingula*** and ***Glottidia*** suffer after death of the brachiopod, and within the sediment, a very rapid disaggregation from the borders of the valves to their central parts, that being the most mineralized are more resistant. This quick degradation of the valves, accelerated not only by the enzymatic actions of organisms but also by mechanical abrasion, causes the total disintegration of empty shells within 2 to 3 weeks (Emig 1981, 1983, 1990). So only **catastrophic events** may cause the taphonomic presence of *Lingulida* shells (Emig 1986).

- Organic matrix of **carbonate shells with two layers**, such as that of ***Terebratulina***, is degraded after the death of the organism what causes, first a general softening of the shell and then, and after a period of 6 or 7 month, its total disaggregation. This disaggregation results in the incorporation of numerous calcite fibres to the sediments (Collins, 1986). These fibre, usually long (15x5≥100μm), may dissolve and/or recrystallize thus loosing their characteristic shape.

  Other brachiopods with two layer shells such as *Terebratalia, Laqueus, Terebratella, Waltonia, Neothyris, Megerlia* etc. seem to undergo a similar softening process (Stewart 1981; Collins 1986).

- Some **rynchonelids such as *Notosaria***, although having a carbonate shells formed by two layers (primary and secondary) do not show any type of softening. This different behaviour can be due in one hand to the proteic characteristics of *Notosaria* shell, and in the other to lack of punctuation. Mechanical abrasion processes combined with the destructive action of the organisms seem to be the main cause for shell destruction.

- Brachiopods with carbonate **shell formed by three layers** have a bigger resistance against the destructive processes. However some processes facilitate shell fragmentation. Thus it is possible to observe how the three layers shell of ***Gryphus*** (see MacKinnon & Williams 1974 and Alvarez *et al.* 1985) suffers the alteration of the organic matrix of the secondary layer, alterations facilitate by the microorganisms action and the dissolution (and/or recrystallization) of the tertiary layer (see also Gaspard 1988). Mechanical fragmentation of *Gryphus* specially affects the anterior two thirds of the valve, whereas the thicker posterior part, remains longer in or over the sediment (probably several years).

So under normal environmental conditions taphonomic loss of brachiopod shells is caused by:

(1) Alteration of the organic matrix of the shell, directly related to its structure and composition.

(2) Dissolution and recrystallization of the mineralized parts of the shell, directly related to environmental conditions.

(3) Mechanical abrasion together with the destructive activity of different kind of organisms.

It seems evident that even in a group of invertebrates having what we consider an excellent representation in the fossil record, we are just considering a very partial scenario of benthic life.

As a consequence of our geological background, paleontologists tend to explain faunal changes and distributions relating them with changes in the physical conditions of the environment, ignoring or limiting the importance of biotic interactions.

The action of organisms has an effect **not only** on fossil preservation. **Biotic interactions** profoundly affect also **species composition and abundance**, of both hard and soft bottom communities.

In **terms of abundance** suspension feeding brachiopods were clearly successful occupants of soft substrata in the Palaeozoic, and the seemed to be exceptionally tolerant of turbidity. But during the Late Palaeozoic and Early Mesozoic their diversity and abundance declined to present relatively minor levels (Williams *et al.* 1965). But if they were so well adapted to the physical rigours of life on mud, why do they no longer live there? One answer appears to be a dramatic increase in biological disturbance of sediments (see Thayer 1983). With the increase of "bulldozing" there was a sharp reduction in the free-lying brachiopod genera. The less vulnerable groups (burrowing and cemented inarticulates) persisted (in number of genera) or increased, albeit modestly, in percentage of genera.

If ancient articulates had growth rate similar to modern shells [less than 1cm/year (Thayer 1981; Curry 1982)], a refuge-in-size from bulldozing was improbable. Thus lacking mobility, they were restricted to hard substrata, where they faced overwhelming competition from other organisms.

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FUNCTIONAL MORPHOLOGY

We notice that palaeontological research concentrated on fossil recognition up through the first third of the 20th Century. Then questions of palaeoecology, extinctions and evolution took over for a third, and now in the final third, we are in an era where many of the resources for palaeontological research are being spent to answer molecular questions. However, in spite of this trend, we must keep in mind that the organism is still our prime tool. The structure and function of the organism give context and perspective for the cellular and molecular approaches to the study of life.

The analysis of the skeletal structures in terms of simple functional morphology, although contributes to the palaeobiological knowledge of the studied forms, overlooks to a great extent the variability of the adaptative structures present in related organism and, therefore, do not allow to balance their possible biological and systematic significance. In the palaeoecological analysis is then necessary to study not only the individual functional morphology but also, and whenever possible, the structure at the population level of the different species in relation with the sedimentary context.

Of each structural feature we must ask: "what is its function and the mechanism by which it functions?", "what were the steps and causal mechanisms in its development?", "what were the steps and causal mechanisms in its evolutions?".

There are two simple questions that may guide us in our approach to functional morphology: "what do I have to know?", "what am I looking for?".

A short list of concepts can help us to answer these questions.

- What to know: Scales of size and time.
  Hierarchy.
  Permission, constraints and opportunities of function.
  Properties as descriptors of structure and function.
  Analogy and homology.
- What to look for: Pattern (polarity and symmetry).
  Dimensions that signify the size of the scale.
  Heterogeneity: Composite (aggregates and interfaces).
  Anisotropy resulting from preferred orientation of fibres and crystals.

This list of ideas is not an exhaustive one, but it is more than enough to introduce the study of form and function.

As in my previous contributions, I will use brachiopods to illustrate the subject. Although morphology of their shells is directly observable, functional analysis of some structures is difficult to conduct experimentally, not only due to material difficulties involved but also because such structures probably developed as a result of a balance between several tendencies, sometimes opposed, as can be to get a bigger protection of the organism and a diminution of its global weight in order to not be sunk in a muddy bottom. Growth, form and function must be rejoined in our studies by the application of effort, skill, and a good notion of the intact organism.

Structural features of organisms have three important biological contexts: **functional, developmental** and **evolutionary**. Thus any study of morphology must inevitably cope with the problem of assessing the relative importance of these factors (Fig. 1).

In order to understand better the morphology and characteristics of the brachiopd shell it is necessary to remember that morphology must satisfy the requests for protection, internal volume and stability continually posed by the organism.

The maintenance of an stable position is a priority for suspension feeding organisms such as brachiopods. There is good evidence for this requirement in the great variety of methods adopted by Recent brachiopods to guarantee a good attachment area for their various kinds of pedicles. (Bromley and Surlyk 1973; Richardson 1979, 1981; Curry 1981).

On soft bottoms, the areas available to the brachiopod larvae to attach were only shells, their fragments, crinoid columnals, small pebbles, etc.. Many of these objects were big enough to provide stability during the early stages of life of the brachiopods, but they were not sufficient as the brachiopod increased its size, so that in spite of keeping a functional pedicle, most of the adult specimens were lying free on the substrate.

The strategies followed by brachiopods to survive on these soft bottoms were varied (see Jaanusson 1979; Bassett 1984; Alvarez 1990 ...):

a) **Differential thickening of the shell in the posterior region** helping to keep the shell with the beaks close to or even buried into the sediment, its lateral commissure subperpendicular to the water-sediment interphase and the posterior

margin directed upwards, into clearer waters (cf. Ziegler *et al.* 1966). This kind of strategy is frequently associated with the appearance of free lying forms.

b) **Development of subtriangular cardinal areas** that would have served, together with the **acquisition of progressively more transverse shapes**, to distribute the weight of the shell over greater areas of the sediment and thus aid its stability while keeping the anterior margin in a relatively high position. The transverse development not only helps to solve the stability problems on soft substrates but, together with the type of folding also facilitates the expulsion of waste products, in the stagnant conditions normally associated with soft bottoms, as it provides the maximum separation between the inhalant and exhalant currents.

c) **Development of wide flat growth lamellae or long spines** helped to keep the shell in position on a soft surface and contributed, with the pedicle, to the anchorage of the shell. The presence of a median dorsal fold helped to raise the anterior commissure of the brachiopod above the sediment. The small size usually attained by brachiopods with this type of lamellae would have facilitate their "flotation" over soft substrates. On the other hand, the type of foramen usually observed, indicates the existence, through their lifes, of a small pedicle that may not have been strong enough to support the shell upwards but could acted as an anchor (cf. Brookfield 1973).

It is well known that most Recent brachiopods feed from a wide variety of food e.g. diatoms, dinoflagelates, organic molecules in solution they filter from the inhalant currents. Brachiopods get food and oxygen from the pumping and filtering action of the lophophore.

In general it is admitted that the filtering capacity of the brachiopods is a function of the area occupied by the lophophore filaments. The metabolic necessities of the organisms increase proportionally to the increase in body volume and these requirements are satisfied by an increase in size of the lophophore.

Influenced, to some extent, by their strategy to secure their stability, brachiopods followed, at least, two main lines to increase the surface, and thus the metabolic efficiency of the lophophore.

a) Increase in the basal diameter of the cones of the brachidium, associated with a progressive increase in shell convexity.

b) Increase of the conus height by the adquisition of forms increasingly wider.

The lophophore and all other soft parts of the body of brachiopods are protected by a calcareous exoskeleton, the shell. The closing of the shell would constitute the main defense of the organisms facing any external threat.

In Recent brachiopods the edge of the mantle is very sensitive to tactil stimulus. This sensibility is reinforced by the presence of projecting chitinous setae. These setae, as well as providing a sensitive or "warning" function, might also have formed, with the growth lamellae, in some cases spinose, a kind of filter or screen obstructing the passage of particles that could be a threat to the survival of the organism. The distribution of the setae could be particularly dense if the amount of particles in suspension was high.

Structures such as lamellae and spines have **different functions** in brachiopod shells. They could act as elements of **stabilization**, **filtration** and **flotation** over soft bottoms. It is possible that these structures could serve also as protection elements either directly acting as camouflage on the bottom or preventing the attachment of the larvae of other organisms. In some cases lamellae seem to have acted as very efficient deterrents to the colonization by epizoans, but in others have not been so efficient in preventing epizoan settlement. In these cases epizoans appear, however, to have been limited to settling on the lamellae rather than on the true valve surface below (cf. Alvarez & Taylor 1987).

During brachiopod life the **caeca** of punctate stocks could be considered as an important "instrument" for protection of the brachiopod shell. The caeca may also have a nutrient storage capacity, very important in environment with pronounced seasonal fluctuation in food availability (see Owen & Williams 1969; MacKinnon 1971 and Curry 1983). The possible advantage of endopunctate shells over the impunctate ones may explain the relative success of the Terebratulida from the Silurian to Recent (Williams *et al.* 1965).

Recent brachiopods tend to develop a wide tolerance to depth, with variations of even hundreds of meters. Thus, depth is not a determining factor of the distributions of these organisms. This does not mean that the depth and the nature of the substrate are not important data in understanding brachiopod distribution but that other ecological factors (oxygen abundance, nutrients, water circulation and turbulence, temperature, salinity, competitors, predators etc.), of course difficult to recognize in the stratigraphic column, often played important roles (some times decisive) in their surviving and expansion.

Why should we care about structure and function? It seems to me that it is all in aid of understanding the evolution of organisms. Functional morphology is not a subject into itself. It is just a point of view, like all the other points of view (ecological,

biochemical, behavioural, mathematical, etc). It is a tool that can help us to come to understand the origin, history, and continuation of life on Earth.

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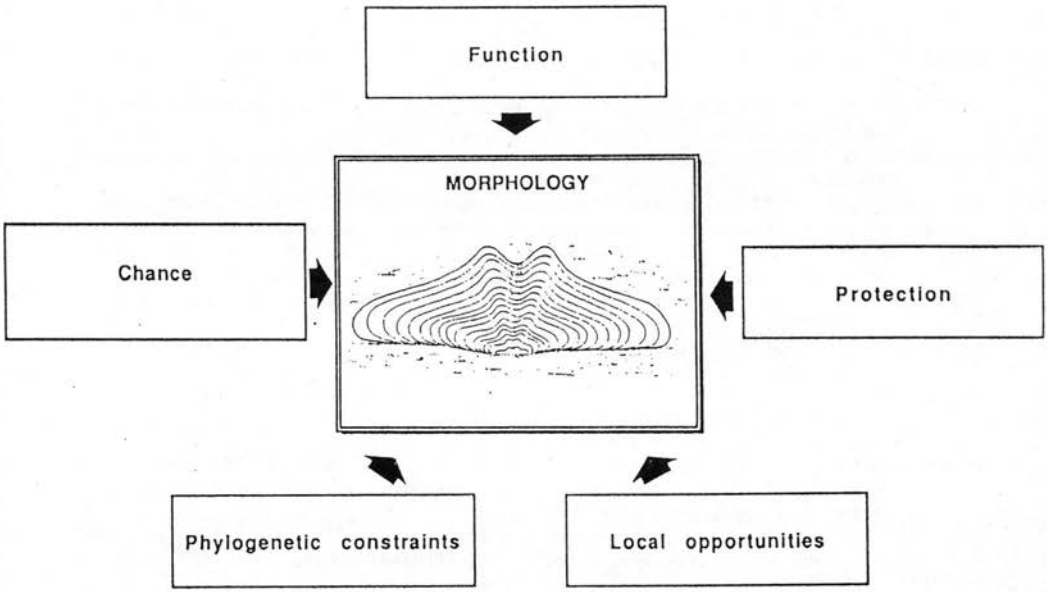

Fig. 1. Major factor influencing skeletal morphology.

VENDOBIONTA: STRANGEST ORGANISMS ON EARTH AND EVOLUTION OF TRACE FOSSILS

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Vendobionta: strangest organisms on Earth

Because of their size and regular organization, the Ediacara-fossils of the late Proterozoic were traditionally referred to soft-bodied ancestors of modern animal phyla (GLAESSNER 1984). Closer examination, however, reveals not only a unique kind of preservation, but also a strange organization unlike that of any modern counterparts. Instead, these organisms (Vendobionta) are interpreted as an independent group that reached large size not by multicellularity, but by subdividing a body through serial (segmental) or fractal quilting of a tough skin. This hydrostatic coenocytic construction also allowed them to maximize the body surface for photosymbiosis, chemosymbiosis or direct absorption of dissolved organics. While bilaterian animals were still small, worm-like and infaunal deposit feeders, whose activities are recorded by trace fossils, the Vendobionta became the rulers of Late Proterozoic sea bottoms. Like immobile soft bottom dwellers of later times, they developed flat recliners, erect elevators, or sediment stickers in different sedimentary environments. They always required extraordinary sedimentational events (tempestites, turbidites, inundites, ash layers) in order to be preserved. Such obrution lagerstätten provide "fossil snapshots" recording the topology, age structure and standing biomass of local communities. The Vendobionta and their "Garden of Ediacara" came to an end with the Cambrian revolution, in which the advent of hard jaws and skeletons started the Phanerozoic arms race.

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Fig. 1.

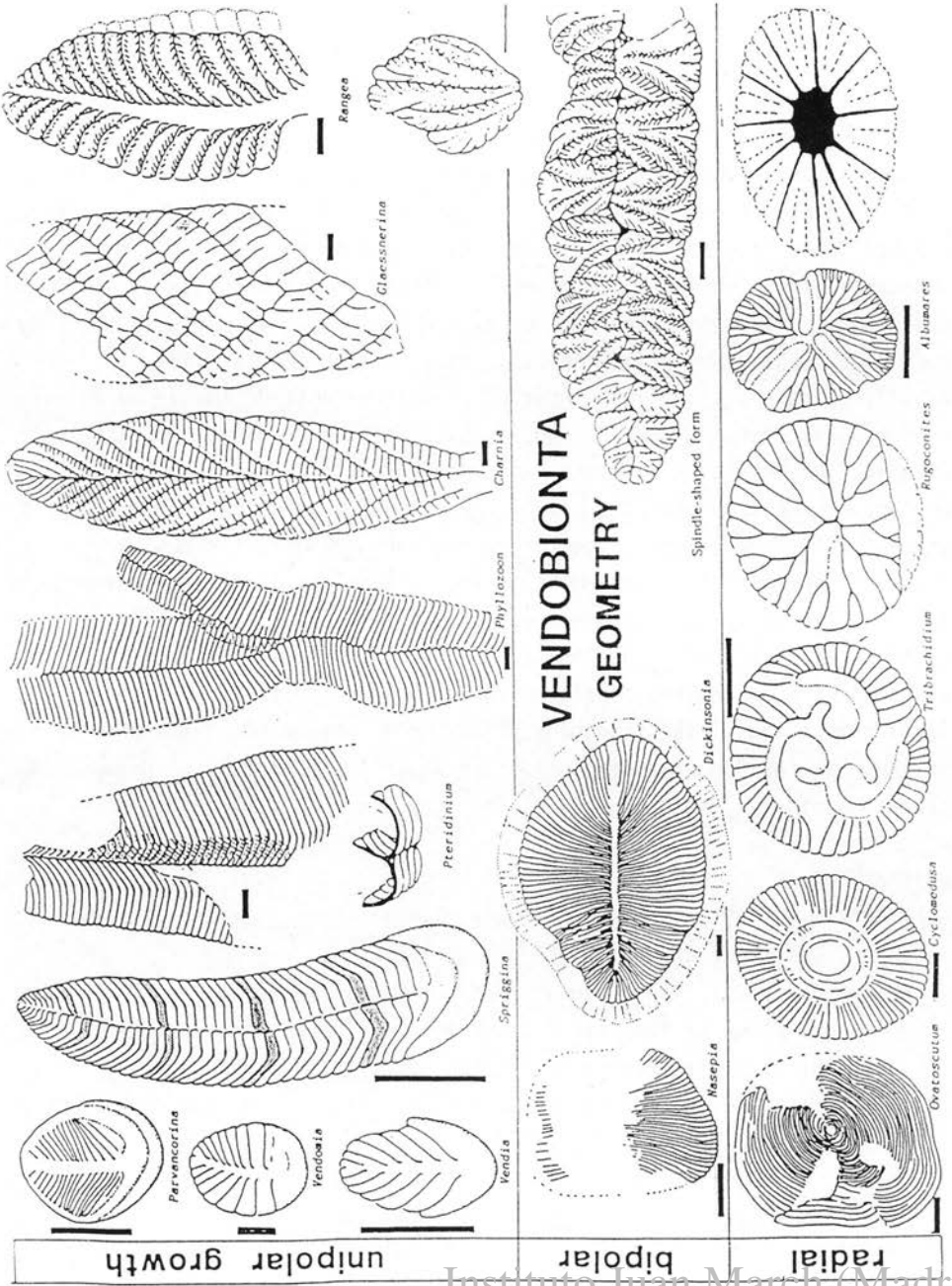

Fig. 2.

Fig. 3.

Fig. 1. Seen as animals, Ediacaran bodyplans would fall into disparate phyla (jellyfish, seapens, echinoderms, worms, arthropods). In the new interpretation, they represent an extinct group, probably non-cellular, one in which the protoplasm was compartmentalized by allometric quilting of a chitinous skin. In spite of their determination early in ontogeny, general symmetries would then be only subordinate features (modified from SEILACHER 1989).

Fig. 2. Vendobiontan life styles followed similar adaptational pathways as known from other immobile soft bottom dwellers. Carpet-like recliners transformed into erect elevators by differentiation of a stem and a self-implanting holdfast. In environments with a higher rate of background sedimentation, the margins of the carpets grew vertically up to form bag-like sediment stickers. According to new observations in Namibia, their growing margins did not emerge from the sediment, as shown here. This suggests a chemosymbiotic or fungus-like habit, while species living at the surface might have been photosymbiotic. Note parallel pathways in serially and fractally quilted groups (from SEILACHER 1992).

Fig. 3. Newfoundland Vendobionta have been smothered by episodic submarine ashfalls. Associated surges felled the erect forms in a downcurrent direction, but did not affect the recliners in spite of their highly orientable outlines. Folded-over spindleshaped forms show that upper and lower surfaces had the same shape. As the inverse relief of the stem parts suggests, they were filled with a different, more slowly decaying material. Figures drawn from silicon casts (positive hyporeliefs) (from SEILACHER 1992).

Evolution of trace fossils I: Trilobite burrows

By processing loose sediments for detrital food, trilobites produced undertracks that reflect the particular burrowing behaviour of the producers as well as distinctive fingerprints of their appendages. Although the trilobite species responsible can no more be identified, known Cruziana ichnospecies serve the stratigrapher as chronological, palaeoenvironmental and palaeogeographic indices.

On this basis, a Cruziana stratigraphy has been established that helps to correlate otherwise non-fossiliferous Palaeozoic sandstone sequences in now dispersed fragments of the Gondwana megacontinent. The recent discovery of seemingly Ordovician Cruziana species in the Lower Cambrian of the Canadian Rockies emphasizes that separate Cruziana statigraphies yet need to be worked out in other palaeocontinents. But we

also face the task to refine the stratigraphic resolution of these trace fossils by gauging them against body fossils in well explored Gondwana regions such as Spain.

In a palaeobiological sense, these trace fossils tell us much about form and function of trilobite appendages, which are bodily preserved in only a few and probably non-representative species. They also help to understand other trilobite features, such as terrace lines and the lack of mouth parts.

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Fig. 1. Trilobite dorsal skeletons, like those of limulids, form a low hood rather than an armour contouring the body. This suggests that they served primarily as a roof under which the legs could process the sediment. The extracted food particles were then transported along the mid-line to the backwardly directed mouth (asterisked). Trace fossils (*Cruziana*) record details of the burrowing process (medio-posterior digging of endites; longitudinal brushing of exopodites). While the trilobite makers are bodily preserved only in a very few cases, or impressions of pleurae, cephalic edges and pygidia in others, some *Cruziana* species may actually be the products of limulids or aglaspids with similar modes of life.

Fig. 2: Preservation and behaviour modify the shapes of *Cruziana* burrows, but only some of the variants are specific enough to justify taxonomic and biostratigraphic distinction (from Seilacher 1970).

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 3: Cruziana species based on process-related, rather than typological, distinction can be used as index fossils in clastic sequences that are devoid of body fossils. The present scheme applies only to areas that once belonged to the Gondwana supercontinent. They thus help also to reconstruct palaeogeography (note Gondwanan species in South China and their lack in Baltica). Equivalent schemes still have to be established for other palaeocontinents.

Evolution of trace fossils II: Worm burrows

Since the late Proterozoic, worm-like creatures of different affiliation have been browsing through sediments in search of food. The undertraces they left on bedding planes reflect differences in modes of infaunal locomotion and behavioural programs. Their transformation and optimization can be studied in evolutionary lineages, even though the taxonomic identity of the producers may forever remain unknown.

In contrast to trilobite burrows, most of these traces have time ranges too long to be helpful for stratigraphic correlation. They may be used, however, as almost ideal autochthonous facies fossils, because even in the cases of convergence, similar behaviour is likely to be environmentally controlled. Unfortunately, sloppy identification and nomenclature of many authors has made this tool next to useless. Therefore, a palaeobiological revision of published data in terms of uniformly defined ichnospecies, ichnogenera and ichnofamilies would be as important as the accumulation of new material. A second area that needs to be explored is the biomechanics of infaunal animals. Only with such knowledge can we hope to unravel the history of bilaterian animals before their Cambrian explosion, because in the Proterozoic trace fossils are their only available record.

In the meantime, the quantified study of "ichnofabrics" has been established as a new field. It avoids the difficulty of palaeobiological analysis and promises to become useful in the framework of sequence and event stratigraphy. Nevertheless it will remain true that the more we know about organisms, the better we can use their fossil records as biogeological tools.

Literature

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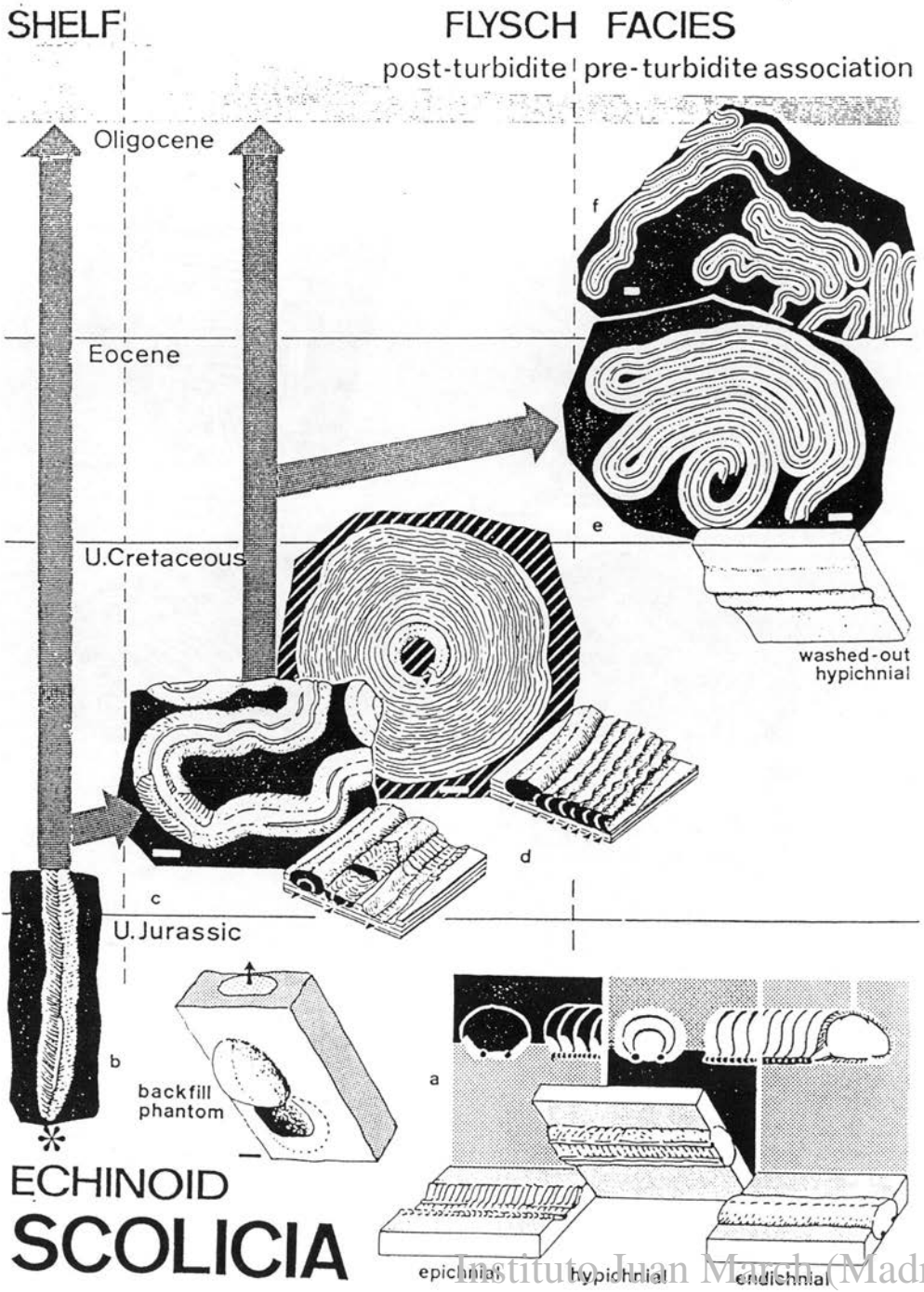
Fig. 1. The ichnogenus Scolicia reflects a mode of burrowing in which sediment is removed in front, passed along the sides of the body and deposited as meniscoid backfill structure behind. When the animal crosses a sand/mud interface, this process leaves a phantom of its body shape, which is longer in Palaeozoic than in post-Jurassic examples. The latter were probably produced by irregular echinoids (Spatangoidea). The trace fossil record reflects their immigration into deep sea environments, where they evolved meandering behaviours for more efficient exploration of the food-bearing sediment.
Note:
(d) This spiralling form violates the foraging paradigm by systematic double or triple reworking of the same sediment (Ectosymbiotic fermentation?).
(f) Improvement of the meander program (starter spiral no longer required) (from SEILACHER, 1986).

Fig. 2. The ichnogenus Nereites reflects the burrowing action of an unknown worm-like sediment feeder (enteropneust?) that processed the sediment at the head end before stowing it in lobes around the body. The cavity behind the body became backfilled with finer (presumably faecal) material that was deposited either as a continuous string, as a meniscoid structure or as serially or alternatingly arranged pellets. Different biostratinomic situations (epichnial, endichnial, hypichnial) lead to different preservational expressions of the trace fossil.
Assuming that this very specific behaviour marks one group of animals, the fossil record reflects its behavioural evolution through the Phanerozoic, particularly in deep sea environments. Note that the improvement of coverage is accompanied by a decrease in body size and that the Cambrian representative still had difficulties to execute the program: each turn was triggered by collision with the previous lobe. When this trigger failed (asterisked), the animal nevertheless produced a kink before turning (from Seilacher 1986).

Fig. 3. Graphoglyptid trace fossils are found on the erosional sole faces of flysch turbidites. In contrast to the burrows of true sediment feeders they lack backfill structures and avoid close contact with

previous parts of the system. Nevertheless programs and patterns are overly elaborate. Short cuts and preservational details also suggest that there must be open tunnel systems which became repeatedly revisited. Therefore it is assumed that the tunnels served as mushroom gardens for microbial symbionts that could draw nutrients from areas around the tunnels. Pattern diversity in this and other groups of graphoglyptids would then not express adaptational radiation, but character displacement in the sense of door keys, that is only open to utilization by a specific group.

Fig. 1.



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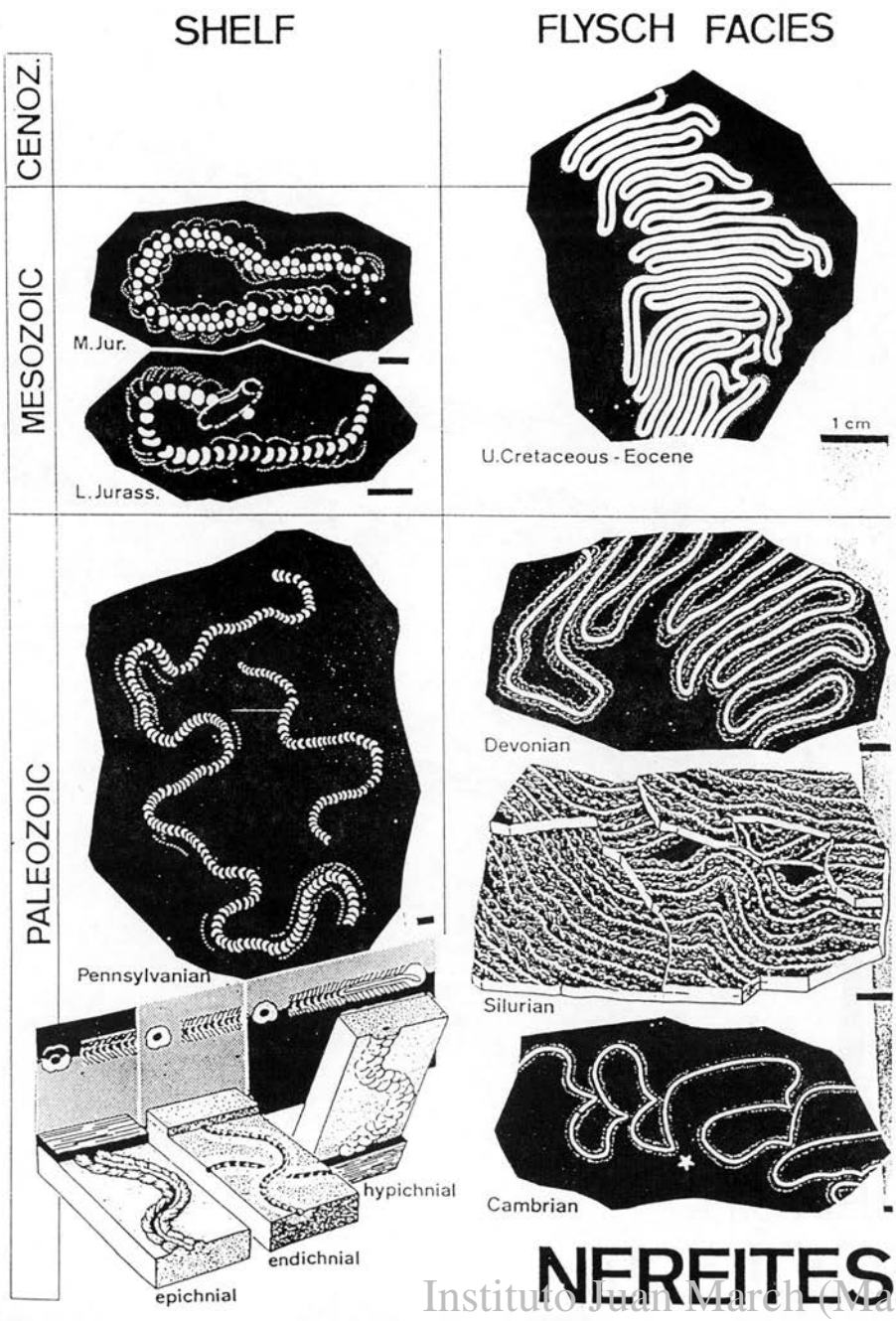

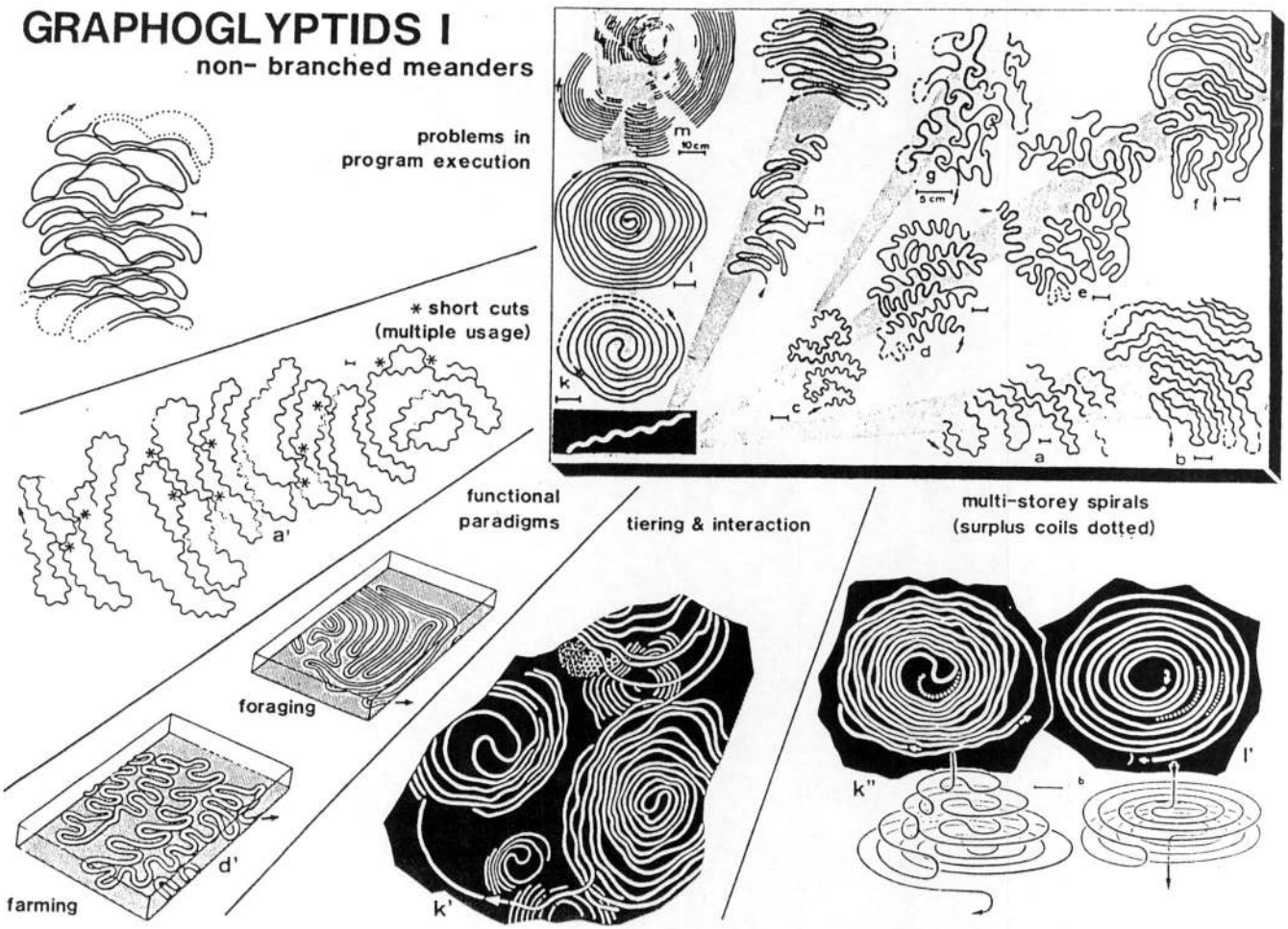

Fig. 3.

EARLY METAZOAN EVOLUTION: THE FIRST SKELETONS AND BURGESS SHALE-TYPE FAUNAS

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The main component of my lectures is to deal with the early evolution of metazoans. This is not only an area of rapidly growing research interest, perhaps not quite deserving the sought-after "band-wagon" status, but one where there are problems of considerable intrinsic interest. Of equal importance, however, is that the study of early metazoan evolution not only has a general relevance to many areas of palaeontology, but is also attracting the interest of other disciplines. Most notable in this respect are molecular and evolutionary biologists, but valuable co-operation is possible also with geologists, chemists and oceanographers.

General texts and monographs

Not surprisingly, there is no general text that covers the entire area of this course. Of some relevance are the following:

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The four lectures will address the following points and problems:

1. Early metazoan evolution: the first skeletons

The objective record, to deal with the variety of biominerals (following on from the previous lectures by Fernando Alvarez) and the fossil evidence. This will begin with Cloudina and the calcareous algae in the late Precambrian and then proceed to review the evidence of a wide variety of skeletal taxa during the early Cambrian.

What mechanisms were responsible for this irruption in the Cambrian? Here we contrast the known changes in the environment, involving possible changes in ocean chemistry and atmospheric composition, with biological changes, especially the rise of predators. Disentangling these two is not easy, but the weight of evidence in favour of predation hypotheses is growing.

There is no doubt that the widespread onset of biomineralization was polyphyletic, but just how many times it evolved is uncertain for two reasons. First, the early stages of metazoan evolution are only just beginning to be understood in any detail, a topic which is returned to below. Second, although the mechanisms of biomineralization, including the nature of the organic templates, are beginning to be documented, very little is known yet about the gene sequences that underlie the entire process. When such data are available, we may find that seemingly unrelated groups share common genetic mechanisms for biomineral secretion.

Many of these questions are still unanswered, but in respect of our knowledge of early skeletal faunas there has been quite considerable

improvement in understanding because of extensive documentation of various Lower Cambrian fossil assemblages. Much of the initial credit must go to Russian and Chinese palaeontologists, who provided initial documentation of richly fossiliferous strata, especially in Siberia and south China. However, insufficient appreciation of taphonomic variants, and more importantly that many skeletons were originally composite with a single species of organism bearing numerous skeletal elements (spicules, sclerites), often showing a variety of morphologies, led to some confusion. These problems are partly, but by no means entirely, resolved. What is possible, however, to identify a number of major clades, whose place in the grand scheme of metazoan phylogeny will be returned to below. In brief, the principle clades that can be recognized are as follows:

Molluscs (especially monoplacophorans), brachiopods and "pseudobrachiopods", sponges (and archaeocyathids), echinoderms, arthropods (especially bradoriids), chaetognaths (as protoconodonts), priapulids (as palaeoscolecidan sclerites), anabaritids, carinachitiids, tommotiids, coeloscleritophorans (halkieriids, sachitiids, siphogonuchitiids, chancelloriids), cambroclaves; to which could be added a number of taxa whose assignment to any higher taxon remains problematic.

A detailed review of these groups is neither possible, nor probably desirable. Rather three aspects will be emphasized:

(a) What was the original disposition of the soft-parts, especially in sclerites that originally formed a scleritome?

(b) What was the original mineralogy and ultrastructure of these early skeletons? Recrystallization and replacement of primary biominerals has confused the picture, but study of polished and etched sections can be highly informative. In addition impression of skeletal ultrastructure on steinkern surfaces and casts of endolithic borings are a valuable source of

information. It is also clear that many supposedly phosphatic skeletons owe their composition to diagenetic replacement. However, it is still very difficult to assess whether the use of phosphatic biominerals was unusually prevalent in the Cambrian.

(c) What are the wider relationships of some of these early skeletal groups? The main purpose of this discussion is not to add to the roster of extinct Cambrian phyla, but to place these groups into the framework of metazoan phylogeny.

Early metazoan evolution: the first skeletons

The physical environment

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2. Early metazoan evolution: trace fossils, soft-bodied faunas and the Burgess Shale

It is the pursuit of this major question that leads on to the documentation of the soft-bodied and lightly skeletalized component of Cambrian faunas. In normal circumstances of fossil preservation the only

avenue to documenting this area is via trace fossils. Despite the inherent difficulty in their study, especially linking maker to trace, the importance of ichnological data for understanding early metazoan evolution should not be underestimated. Most obvious is the dramatic increase in trace fossil diversity close to the Precambrian-Cambrian boundary, coincident with or perhaps slightly preceding the widespread appearance of skeletons. Why Ediacaran ichnotaxa are largely two-dimensional i.e. no vertical burrows and simple is difficult to understand in the absence of information of body fossils. What is clear from the Cambrian record is that styles of behaviour and sophistication of activity changed substantially. As yet no serious attempt has been made to put these data into the context of metazoan evolution, especially with regard to anatomy, e.g. morphology of burrowing organ, walking appendage and associated neural connections.

The so-called "Cambrian explosion" would, therefore, have been entirely apparent from the trace-fossil record alone, self-evident even if skeletons had never evolved.

Information on the soft-bodied animals from the Cambrian is, nevertheless, an essential part of the story. The principal source is, of course, the Burgess Shale fauna from the Middle Cambrian of British Columbia, close to the town of Field. Two other more recently-discovered faunas are adding invaluable new information. Both are from the Lower Cambrian, and comprise the Chengiang fauna from the Chiungchussu Formation, Yunnan Province, China and the slightly younger Sirius fauna from the Buen Formation of Peary Land, Greenland. In addition there are more than 30 Lower and Middle Cambrian faunas that have yielded elements of Burgess Shale-type taxa. Of these localities in Utah, USA are most prolific, but search strategies for new occurrences suggest that many more Burgess Shale-

type faunas should be discovered.

These remarkable faunas allow inspection and discussion of a number of important topics.

(a) Are Burgess Shale-type faunas representative of Cambrian marine life as a whole? In general, the answer seems to be yes, because if it is hypothesized that only well-skeletalized taxa had survived (i.e. trilobites, brachiopods, hyoliths, molluscs) then the impoverished assemblage is indistinguishable from a "normal" Cambrian fauna. This is certainly true of the Burgess Shale itself, but the Sirius fauna, for example, may be more peculiar.

(b) What is the palaeobiogeography of these faunas? Strong similarities between the Burgess Shale and Chengjiang, located on separate cratons, can be explained by a simple oceanographic model. The Sirius fauna, however, which shares a Laurentian location with the Burgess Shale, is somewhat less similar. Why?

(c) What is the taxonomic profile of Burgess Shale-type faunas? They share an abundance of arthropods, and are also characterized by priapulid worms, sponges and a wide variety of seemingly miscellaneous forms. Taxa with robust hard-parts form an insignificant proportion both in terms of number of genera and individuals.

(d) The relative completeness of these faunas allows more reliable inferences on palaeoecology, especially with regard to life position and feeding habits. In the latter category we observe an abundance of predators.

(e) There now seems to be good evidence that a number of taxa in Burgess Shale-type faunas are closely related to forms hitherto thought to be restricted to Ediacaran assemblages. Such "Ediacaran survivors" may help to resolve some of the controversies that surround the Vendobionta.

(f) The exceptional taphonomic conditions of Burgess Shale-type preservation result in preservation of not only soft-parts, but also articulated scleritomes. Most spectacular in this context is the recent discovery of articulated halkieriids from the Sirius fauna, which complements earlier descriptions of wiwaxiids and chancelloriids from the Burgess Shale itself. In addition recognition of *in situ* plates of *Microdictyon*, in association with early onychophores has led to several radical revisions, including the hitherto enigmatic *Hallucigenia*.

(g) The most important aspect of these faunas, however, is that relevance to understanding early metazoan evolution. It is convenient to subdivide this question into two topics, albeit somewhat arbitrarily separated.

(i) Within well documented clades, such as the arthropods and priapulids, documentation of taxa is invaluable to establishing possible phylogenies.

(ii) Of possibly greater significance is understanding the supposedly problematic taxa, some with seemingly bizarre morphologies e.g. *Hallucigenia*, *Eldonia*, *Anomalocaris*, *Opabinia*. It is now clear that the way is open, at least in principle, to integrating these data into the scheme of metazoan phylogeny.

All this information and discussion is merely designed, however, to think how best to address some of the major problems of palaeobiology, those for the 21st century.

(a) Are the mechanisms of evolution operating during the Cambrian explosion different from those at other times? Is the undoubted increase in range of morphologies and behaviour over a relatively short period of geological time a product of novel evolutionary processes?

(b) What will the emerging story from developmental biology tell us about the organization of morphology, especially at a basic level such as

segmentation. What relevance do these studies have to understanding the Cambrian diversifications?

(c) Is there any useful way we can address the problem of how much morphospace or morphovolume was occupied during this initial radiation? Objective data strongly suggests that at least some groups occupation of morphospace (or disparity) increases through geological time. This may well hold for Cambrian faunas as a whole when compared with younger assemblages. Is there any sense in which there is a limit to morphospace occupation, towards the notion of a set of "ideal morphologies"?

(d) Does the much-vaunted notion of contigency as an historical process in evolutionary radiations have any bearing on our understanding of the "Cambrian explosion"?

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SELF-ORGANIZATION OF MORPHOLOGIES

A. Seilacher

Self-organization of morphologies I: Morphodynamics

In the reductionist stance of modern biology we have learned that all features of organisms are written down in the genome and that all of them have a biological function. The coming of chaos theory now makes the other, holistic approach acceptable again. In a world full of non-deterministic systems it makes sense to search for self-organizing mechanisms in morphogenesis and evolution, and to treat them as quasi-independent entities that first occur randomly, then get genomically adopted and eventually become tamed towards functions that Darwinian selection happens to discover. This principle is most obvious in repetitive patterns such as zebra lines, fractal leaf and wing venations and reticulate bone sculptures, where configurations vary not only between individuals, but also between right and left sides of the same specimen. In accretionary skeletons the autonomy of pattern formation is also expressed by repairs, in which untamed versions re-occur.

In the old concept of constructional morphology, processes of this kind figured in the fabricational corner. In its expanded version ("morphodynamics"), the inclusive organism is viewed as a dynamic system, of which the "effective environment" forms an integral part. Taphonomy extends this view into the post-mortem history of organisms, when the carcass becomes the passive object of a non-specific environment.

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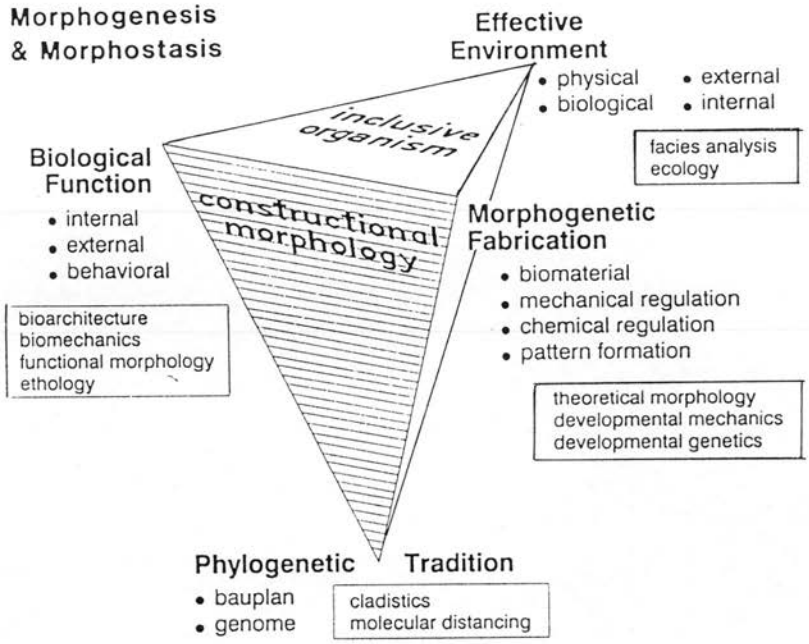
Fig. 1. In the morphodynamic view biological form is never static, but either in the state of buildup, maintenance, or decay. Given structures and their changes in ontogeny, evolution can be understood in the constraining frame of tradition, function and fabrication, with addition of the effective environment as a fourth corner. Change in any of the top three corners may cause an evolutionary transformation.
Death puts an end to the feedback system of the inclusive organism. Nevertheless the entropic recycling of the carcass is not always complete

but may be stopped at any stage by fossilization. Singular events, such as bacterial mineralization, prefossilization and selective weathering (shaded areas) may upgrade, rather than dilute, the information during taphonomic history.

Fig. 2. The autonomy of pattern-forming processes is expressed by different printouts on the two sides of bilateral organisms. Zebra patterns involve a critical distance between colour bands or ribs. In accretionary skeletons they transform into divaricate chevrons or radial ribs. The apparent violation of this asymmetry in the stegocephalian skull resulted from the reconstruction of the shaded areas by an over-enthusiastic preparator. In all cases the right side of the same specimen is shown as mirror image (from Seilacher 1991).

Fig. 3. The intricate meshwork of a dragonfly wing can be simulated by placing soap bubbles between a wire frame copying the pattern of the primary ribs. This (and the right/left asymmetry in actual wings) suggests that a similar process is involved in morphogenesis. In the "walking leaf", Phyllium, the low-order reticulation shows acute angles that are in conflict with the soap bubble model. Obviously, the mimetics resulted not from copying, but from using a similar morphogenetic process as underlies the leaf venation of dicotyledon angiosperms. The latter resembles a bubble float in advanced forms, although there is an excessive number of four-way crossings. High magnification (in Castanea) and comparison with more primitive groups reveals that the meshwork arises from dendroid fractals "sprouting" into higher order meshes of the expanding leaf. Only branches that approach higher-order veins in the right loci (middle between branching points) are allowed to link and establish new meshes.

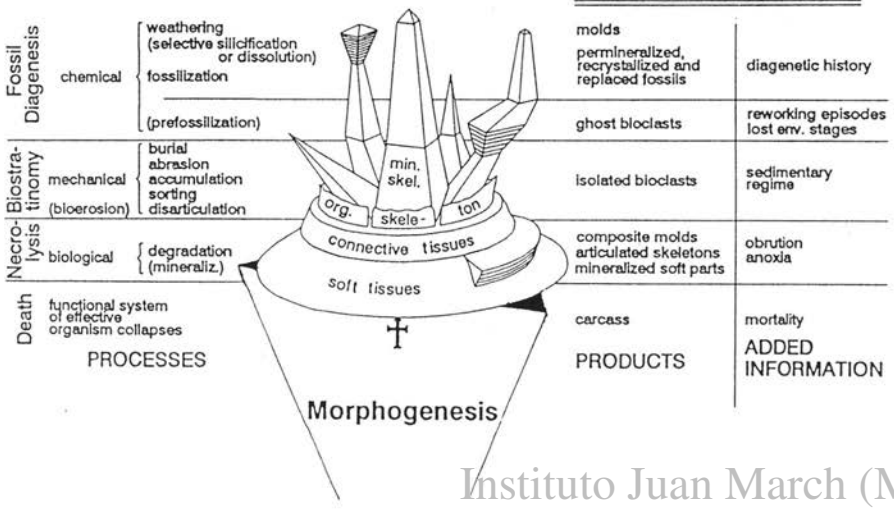
MORPHODYNAMICS I :



MORPHODYNAMICS II :

Taphonomy (Morpholysis)

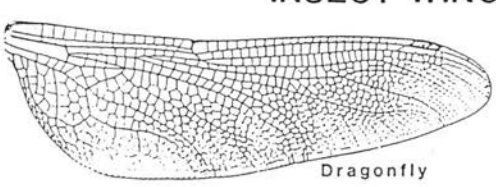
(= passive degradation by any environmental agent and non-linear preservational events)



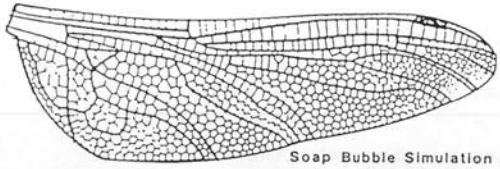
ZEBRA PATTERNS:

Bilateral Asymmetry

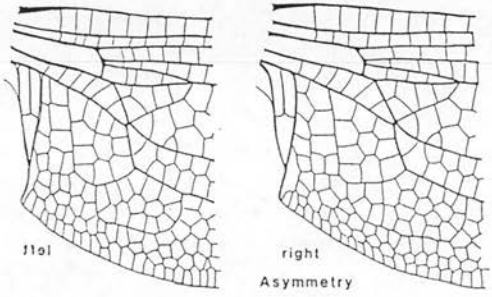
INSECT WING PATTERNS



Dragonfly



Soap Bubble Simulation



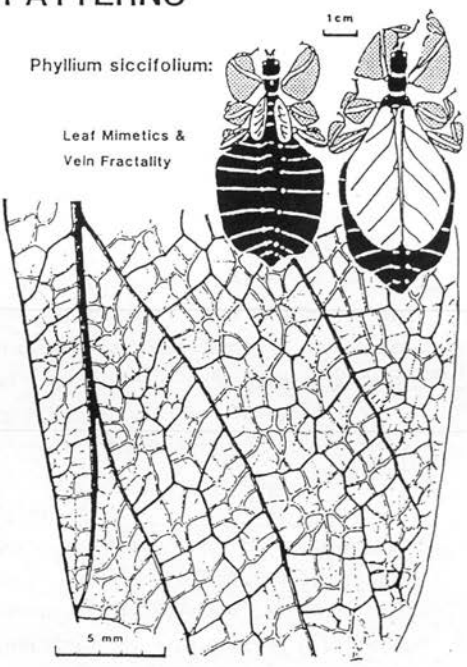
left

right

Asymmetry

Phyllium siccifolium:

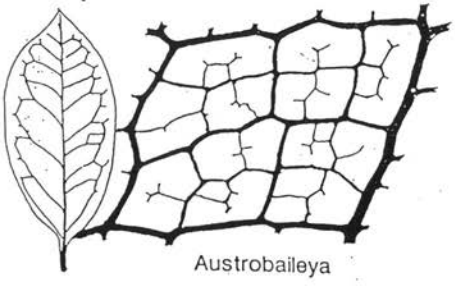
Leaf Mimetics &
Vein Fractality



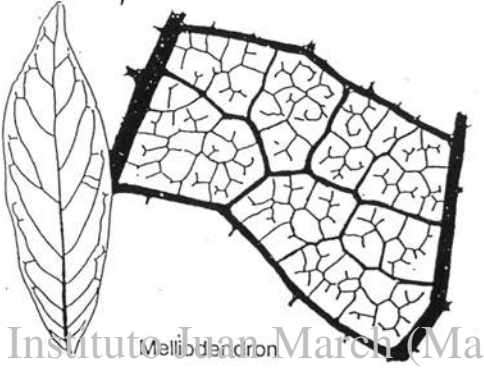
Fractal Dicot. Venation

Cinnamodendron.

Castanea



Austrobaileya



Melliodendron

Self-organization of morphologies II: Accretionary shells

Theoretical morphology has taught biologists that few informational and no vitalistic forces are required to generate seemingly complex and pleasing shell geometries. These computer-based studies can now be complemented by a very simple candle experiment, in which growth lines and remarkably naturalistic shell shapes result from the mutual interaction of a soft and a stiff stage in a self-organizing feedback system. Thus, it becomes possible to single-out the signals of adaptational taming from the background of fabricational noise in real shell forms. But we can also learn how different fabricational processes (logarithmic shell growth, rib intercalation, spine generation) interact to create hierarchical systems of morphological information. In some cases (muricid varices, ammonite sutures), this morphogenetic memory becomes reactivated only at rhythmical intervals (spine production, coordinated "crawling" of tie points).

As a yet more general conclusion, hard parts are not mere additions to pre-existing soft-bodied constructions, but act as chief modifiers of organismic bauplans. Therefore it was possibly the adoption of biomineralized skeletons that caused the sudden emergence of new bilaterian phyla during the Cambrian explosion.

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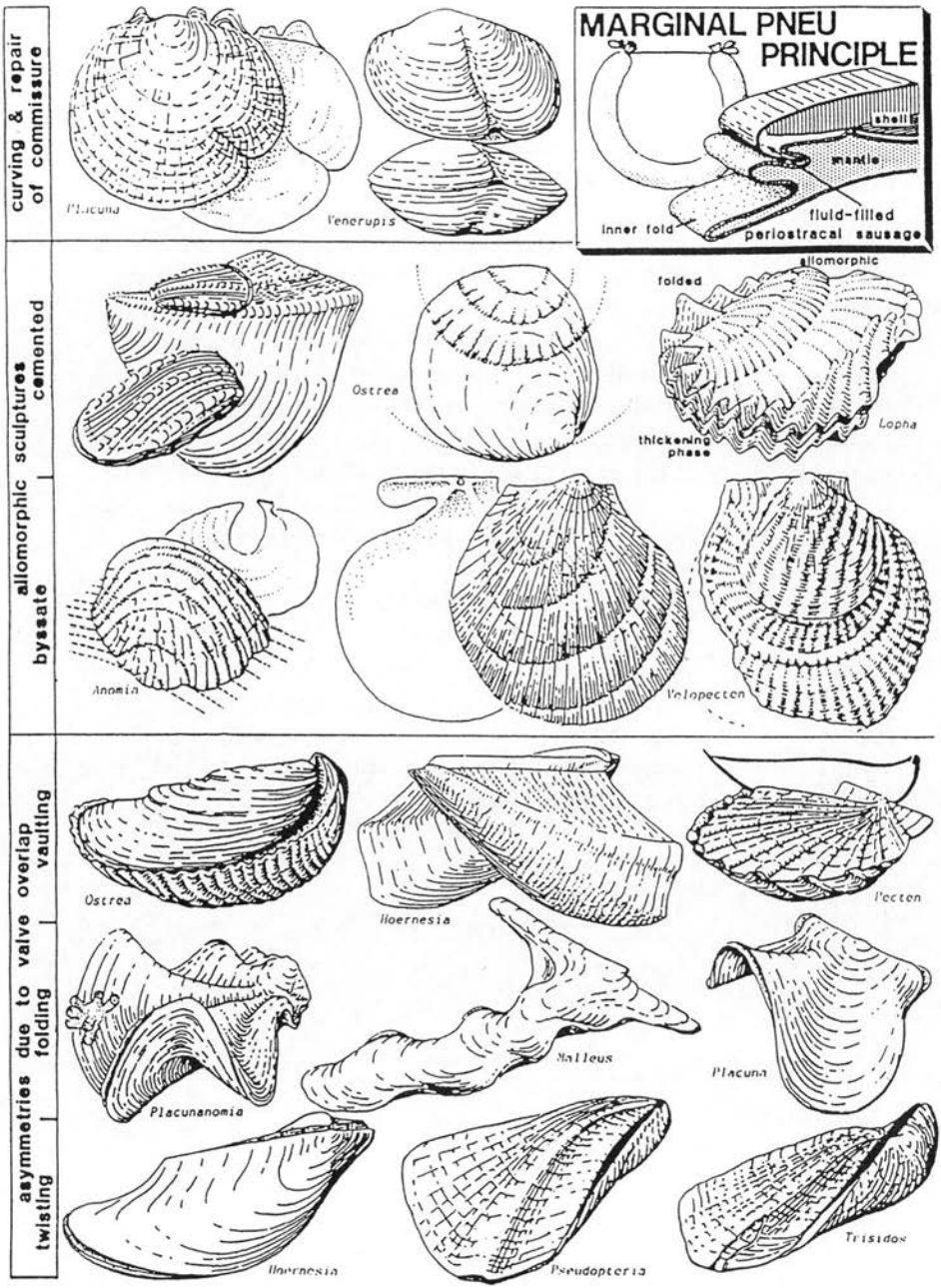
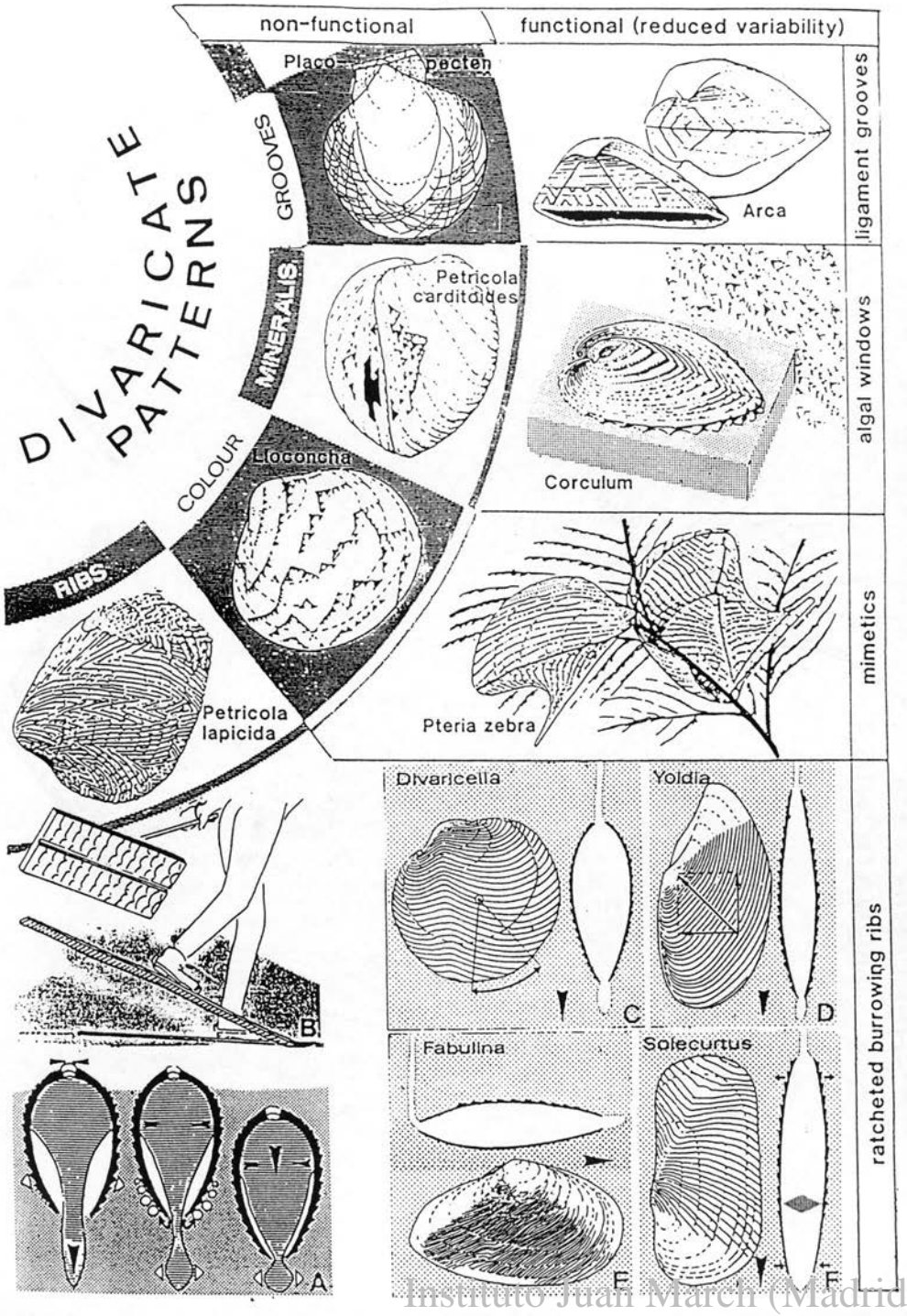
Fig. 1. Accretionary shells reflect a hierarchy of self-organizing mechanisms. The basic process is the addition of new calcified growth rings inside a sausage-like hydrostatic structure formed by the mantle margin and the as yet uncalcified periostracum. The shapes of these increments are controlled (1) by the tension of the marginal pneu, (2) by the shape of the previous calcified growth ring (including occasional bite marks) and (3) in bivalves or attached forms by the shape of a hard counterpart, to which the marginal pneu is appressed. The latter control may lead to allomorphic sculptures that render a distorted, but otherwise exact replica of the substrate. Another possibility is that the two valves do not exactly occlude at the commissure. The consequences are

equivalveness with regard to vaulting and sculpture, or the development of twisted or folded shells.

Fig. 2. Shell ribs (in contrast to shell folds; Fig. 1) tend to be negatively allometric. During growth, their number increases by intercalation of new ribs, whose hierarchy can be used to regulate other morphogenetic differentiations (e.g. hierarchically sized and distanced spines). In Murex pecten, varix spines respond to one signal, but in hierarchic succession. Thus their angular positions change so much that around the siphonal tube a cage is formed for prey catching. Haustorium (upper left) forms a free inner lip (to be resorbed before growth can continue) at each varix position. Since this part lacks the information of spiral ribs, a divaricate program is used instead. Spondylus ribs produce spines of varying size and distances according to their hierarchic order. In Spondylus mirabilis (lower right) "enslaved" lower order ribs adjust spine distances to those of their larger neighbours, but locally distort the resulting tridents by falling back into their own rhythm.

Fig. 3. Divaricate patterns come in different morphological or structural expression. In all four expressions we find species in which the pattern is still chevron-like, highly variable, and has no obvious function. They are interpreted as having serendipitously "adopted" the pattern-forming process. As soon as selection discovers a functional use, these self-organized patterns become "tamed" into shapes conforming to the new paradigm (modified from SEILACHER 1972).





FRONTIERS IN PALAEOBOTANY

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Introduction

The study of plants past and present is a key element in understanding all aspects of Earth systems processes. Green plants are of fundamental importance to all life on Earth. They trap solar energy and convert and store it in a form usable by all ecosystem components, they determine the environment within which most animals exist, co-evolutionary factors between plants and animals have shaped the form and relationships within both kingdoms, and land plants in particular have an intimate relationship with the atmosphere which strongly influences both atmospheric composition and climate. Moreover the plant fossil record is a rich one in both marine and non-marine environments. It preserves the most fundamental elements of the history of life at a variety of temporal and spatial scales, and records in considerable detail climatic changes over the past 400 million years. Plants affect erosion and sedimentation rates and future palaeobotanical research will also have a bearing on crustal dynamics.

The fossil record provides the only perspective against which present and future changes in biological, physical, and chemical changes in the Earth system may be assessed. For the foreseeable future palaeobotanical research is likely to be, and should be, providing long term perspectives of global change from which predictive tools and safe future global management practices may be derived.

Plant Taphonomy

Plants rarely if ever fossilise as whole organisms and most plant fossils represent indeterminate numbers of isolated organs, shed periodically or continually, throughout the lifetime of a plant. The fragmentary nature of the plant fossil record has led to the development of a system of taxonomy and nomenclature rather different to that for animals. For example it is not unusual for a single fossil plant to be represented by an array of generic and species names (fig. 1) (see papers in Spicer and Thomas, 1986).

Some organs such as pollen grains, spores, or seeds have special morphologies that enhance transport away from the site of growth while others such as stems or roots have limited transport potential. Some plant parts are inherently robust, are slow to decay, and have high reworking potential (eg pollen/spores, logs) while others such as leaves are usually destroyed when reworked (e.g. leaves and flowers) and therefore provide high temporal resolution for community reconstruction.

The planar nature of many plant organs (e.g. leaves) and variable submerged densities produced by progressive saturation and decay confound the theoretical modelling of their fluid dynamic properties. Nevertheless empirical approaches have demonstrated that fall velocities (a common component of most fluid dynamics equations) of leaves lie within narrow and predictable ranges (figs. 2 & 3). This results in consistent patterns of distribution by wind and successful modelling of the behaviour of populations of leaves under a variety of flow regimes in water. Plant taphonomic studies have shown that the processes that form allochthonous leaf assemblages, far from destroying ecological information, can preserve spatial, temporal and even structural details of the source vegetation (e.g.. Spicer, 1981; Burnham and Spicer, 1986; Spicer, 1989). Biostratinomic sorting has profound implications for assemblage formation particularly regarding palaeoclimatic interpretations, but it is clear that many of the biases are predictable and may be overcome by applying environment-specific algorithms or by sampling assemblages from a range of sedimentary facies and taphofacies.

Comparatively few studies of pollen/spore taphonomy have been undertaken but those that have (e.g.. Holmes, 1990) have shown the dangers of simplistic interpretation based on single cores or sections. Far more research is needed regarding palynomorph reworking on a variety of temporal scales, and the relationships between the broad range of palynological organic matter (pollens, spores, and fragments of cuticle, wood tissue, resins and charcoal) that comprise palynofacies.

Molecular studies are beginning to show important differences in the durability of plant components. In particular analysis of plant cuticles have shown them to be more complex than previously thought and that preservation potential is strongly dependant upon the relative proportions of the polymers cutin and cutan (Tegelaar et al. 1991).

Plant Palaeoecology

For many years plant palaeoecology was largely based on taxonomic lists and little more than informed imagination. It was not unusual for ancient communities to be reconstructed by direct analogy with Present communities: an approach that invited a static view of vegetation and denied evolution of the community in spite of evolution of the individual elements. The influence of greater taphonomic insight has led to more rigorous assessments (both qualitative and quantitative) of plant assemblages and their

relationships to their entombing sediments. Quantitative sampling involving the concept of the sedimentation unit, rarefaction curves to determine sample size, and multivariate statistics to detect patterns are now commonly used in plant palaeoecology (e.g.. DiMichele and Wing, 1988; Farley, 1990).

The most detailed windows on the past are inevitably provided by autochthonous or parautochthonous assemblages and recently great strides have been made in our understanding of Carboniferous mire vegetation by detailed excavations of forest floor sites (DiMichele and DeMaris, 1987; Gastaldo, 1987).

In general most palaeoecological information resides in allochthonous assemblages but to date few studies have been carried out where detailed community structure has been determined from specific taphonomic "corrections" applied to single sites. A more practical approach has been to sample a wide range of assemblages from a variety of sedimentary facies within a basin. In this way consistent community associations with respect to specific depositional environments may be identified and regional dominants that may be under-represented in any single assemblage may be identified from their ubiquitous occurrence (Spicer and Parrish, 1986; Spicer, 1987; Spicer and Parrish, 1990) (fig. 4).

As plant material is transported it is fragmented by both biological and physical processes into ever smaller particles. Not surprisingly much of this material goes unrecorded but it can contain considerable palaeoecological information primarily relating to the less robust elements of the source vegetation. At present it is impossible to make generalisations regarding taphonomic factors or plant palaeoecology based on such fragmentary material and clearly more research is required in this field (Kerp, 1990, etc.). At a more microscopic scale still are the organic particles that comprise palynofacies. Here instead of examining the traditional pollen and spore preparations where other biologically derived material is oxidised away, all organic debris is examined. At present little is known regarding the relationship between palynofacies and source vegetation or depositional environments but it has been well demonstrated that such relationships exist (Lorente, 1990).

The move to study populations of whole and fragmented plant parts inevitably results in a taxonomic "log jam": far more fossil material is recovered than can be given a formal taxonomic treatment. Consequently there have been several calls for computer-based data acquisition and recording systems. The most radical proposal is that of Hughes (1990) who makes a strong case for abandoning the Linnean binomial system and moving to a "biorecord" or palaeontological data handling system that would operate in parallel with conventional systematics while still enabling data recording and communication. Similar revisions of classification systems are underway with respect to "palynological organic matter" that comprise palynofacies.

Plants and Biogeography

Studies of plant palaeobiogeography based on taxon distributions provide a vital framework for plant evolutionary studies. Increasingly however the emphasis will be towards global palaeovegetation modelling because of the fundamental role that plants play in determining atmospheric composition, erosion and sediment deposition, faunal food and ecospace, and the fluxes in the hydrologic cycle. Photosynthetic land plants are spatially fixed post-germination and to produce food they process water from the substrate and the gases CO_2 and O_2 from the atmosphere. They have to do this as efficiently as possible under the conditions they are exposed to and in the course of evolution both vegetational communities and their component plants have developed morphologies and architecture that are characteristic of particular environmental conditions. By studying these features and their patterns of distribution in both space and time global environmental change can be studied through extreme greenhouse and icehouse conditions: information that is vital to our understanding of the operation of global systems for future planetary management.

Silurian and Devonian

Early land plants in the Silurian and early Devonian typically consisted of leafless stems no more than a metre in height with rather simple vascular systems, stomatal organisation, etc. This early simplicity (a function of their evolutionary novelty) conferred a degree of xeromorphy that potentially enabled them to occupy a wide range of environments. Their homosporous reproductive system was also rather simple and because each spore was able to produce a new plant by selfing at the gametophyte stage rapid geographic spread was facilitated. This simplicity, however, introduces considerable difficulties in taxonomic assignment and phytogeographical analysis, but some distinct floral provinces are detectable by both subjective and statistical methods (Raymond et al. 1985; Edwards, 1990).

Carboniferous

Phytogeographical differentiation becomes more pronounced in the Late Devonian and Carboniferous and is a function of increasing niche partitioning and concomitant increases in morphological specialisation (Raymond et al. 1985). Variety of morphological complexity also allows higher resolution taxonomic treatment. The record of Carboniferous plant communities is dominated by that derived from the specialised coal-forming mires but even here we see evidence for temporal (apparently climate driven) community change (Phillips and Peppers, 1985).

Permian

Climate change, sea-level rise, and monsoonal circulation developed as Pangea assembled symmetrically about the equator. This is associated with a significant loss of mire communities in the Permian. By analogy with modern vegetation/climate biomes Ziegler (1990) produced maps of Early and Late Permian vegetation showing considerable geographical differentiation (fig. 5).

The Mesozoic

In stark contrast the to Late Carboniferous and Early Permian most plant productivity was at high latitudes throughout the Mesozoic and low latitudes became seasonally arid. It appears that at times of global warmth widespread tropical rain forests do not exist and areas of productivity maxima shift poleward: an observation that has profound implications for the Present world.

Phytogeographic patterns for the Triassic when global monsoonal circulation was at its maximum (Kutzbach and Gallimore, 1989) are currently being assembled, but data are rather thin compared to the Jurassic and Cretaceous. Notwithstanding continuous land connection between the northern and southern hemispheres, phytogeographic differentiation into Laurasian and Gondwanan provinces was strong.

For some time it has been believed that Jurassic vegetation was globally uniform but we now know that this is a false interpretation borne of taxonomic lumping with the well-documented floras of Yorkshire, UK. Taxon-based studies of Jurassic floras even at sub-continent scales show a strong pattern of differentiation with respect to climate and can even demonstrate anomalies resulting from the movement of allochthonous tectonic terranes. High latitude floras from the Jurassic and Early Cretaceous exhibit broad leaves and a high frequency of deciduousness associated with a strongly seasonal growth pattern. This is also reflected in characteristic tree ring patterns. Typical high latitude taxa include ginkgophytes, ferns, and conifers. At low latitudes the Cheirolepidiaceae, an extinct family of conifers, predominated (Vachrameev, 1978). While morphological variation within this family was high, possibly reflecting an array of specialised environmental adaptations, the group as whole was well suited to seasonally arid conditions (Alvin, 1982).

This general floristic and climatic pattern extended into the Late Cretaceous but with global cooling and competition from flowering plants the low-latitude cheirolepidiaceous forests waned. At high latitudes in both hemispheres cool temperate rain forests predominated, but with moderate taxonomic differentiation between north and south. Angiosperms in particular seemed to have experienced few barriers to migration and expanded from a low-latitude possibly western gondwanan origin in the Early Cretaceous to Arctic and Antarctic sites by the latest Early Cretaceous.

Tertiary

The potential for detailed phytogeographic studies in the Tertiary is enormous and some attempts have already been made. However several problems complicate the issue.

1) The similarity of many plant organs to living taxa has encouraged the application of modern names to fossil taxa: in some instances this might be justified but often it is not. Similarity between single organs does not establish identity of the whole plant or imply the same ecology.

2) Many fossil floras survive that were laid down at altitude. This introduces a range of floristic heterogeneity not encountered in older rocks.

3) To disentangle the complex patterns produced by 1 & 2 high resolution stratigraphy is required.

Computer databases of fossil occurrences are being developed for pre-Tertiary and Quaternary material but the same approach is most urgently required for the Tertiary. In North America phytogeographic patterns produced in association with biotic and environmental change at the Cretaceous/Tertiary boundary are evident but the data need refining and the approach extrapolated to other regions where ecological trauma at the boundary is not so well pronounced.

Future Developments

Most phytogeographic studies have been, and no doubt will be, taxon-based because such data are to be found in existing literature. However from this type of minimal information multivariate statistical techniques can extract surprisingly detailed phytogeographic patterns. Subjective assessments of biomes as demonstrated by Ziegler have a strong future if only because they have an inherent link with climate, but care has to be exercised to avoid circularity of argument. New assemblages obviously should be investigated with vegetation reconstruction in mind and previously known assemblages will need to be re-investigated from a taphonomic viewpoint to achieve such aims. Studies iteratively coupling phytogeographic patterns and palaeoclimate modelling would seem to have considerable potential as the "spotty" spatial resolution of the fossil record could be interpolated and the performance of the climate models enhanced.

Plants and Climate

The morphology and anatomy of land plants reflect climate in a more or less direct manner. Plants ill-suited to a particular environment are quickly eliminated thus both the features of individual plants and of the vegetative community as a whole will equilibrate to the environment. This is easily demonstrated in the close similarity in appearance and structure (physiognomy) of taxonomically quite unrelated plant communities growing under

similar climatic conditions. Many plant parts also have a high preservation potential due either to robustness, abundance or both and thus the plant fossil record provides a sensitive long term (up to 400my) record of global environmental change.

Studies of the Quaternary have traditionally centred on simple temporal extrapolation of climatic tolerance windows of living taxa and recently more sophisticated methodologies have been developed (e.g. the Australian BIOCLIM project (Kershaw and Nix, 1988), and Response Surfaces, (Huntley, in press)) based on this assumption. This approach is clearly inappropriate for older assemblages because evolutionary change in climatic tolerance is likely to have occurred although it is not unusual for Nearest Living Relative (NLR) techniques to be applied to Tertiary material (Axelrod and Bailey, 1969; Axelrod, 1987).

Functional simplicity (efficiency constraints) and direct exposure to the atmosphere have resulted in the repeated evolution of unique solutions to given environmental (especially climatic) constraints. Thus it is possible by examining foliar physiognomy (leaf size, shape, margin type), stem anatomy (vascular system organisation, growth rings), and cuticle features (thickness, stomatal organisation and density) to derive quite precise and accurate qualitative and quantitative measures of climatic parameters that are taxon independent and therefore applicable to pre-Quaternary deposits (Spicer, 1989).

Plant form is inevitably a comprise between conflicting constraints so some plant features are difficult to ascribe to singular climate elements such as temperature, precipitation, etc. However modern vegetation occupies distinct thermal domains from which Mean Annual Temperature (MAT) and Mean Annual Range of temperature (MART) can be obtained (Fig. 6) and because many taxa are involved this approach is evolutionarily robust. Quantitative temperature estimates are most easily obtained from the leaves of woody angiosperms and by using a newly developed multivariate statistical method called CLAMP populations of fossil leaves can be used to determine MAT to within 1°C, as well as cold month mean temperatures (and from these data MART and Warm month mean temperatures), mean annual precipitation and mean precipitation during the growing season (Wolfe, in press)(figs 7-13).

One of the major controversies in geology revolves around the processes governing changes in land surface height. Rates in surface height change are dependant on the process and properties of the crust. Furthermore topography has a profound effect on climate both regionally and globally. No method in current use provides palaeo-surface height data unambiguously (England and Molnar, 1990) but by using CLAMP, appropriate taphonomic considerations, and lapse rates it should be possible to determine surface height at which an assemblage was formed to within ± 250m for any time within the past 90 my.

Armed with such a powerful climatic tool it will soon be possible to effectively evaluate and constrain global numerical climate models (particularly general circulation models - GCMs) (see Crowley and North, 1991) and to this end Oxford and Reading

Universities are constructing global Mesozoic sedimentological and palaeobotanical databases as part of an exercise to improve the performance of GCMs for "greenhouse world" conditions. Further research of this type is inevitable when coupled ocean/atmosphere models come on stream.

Part of the concern for the future is the role of the carbon cycle, particularly atmospheric CO_2 in determining global climate. Both qualitative and quantitative data suggest the Mesozoic had higher CO_2 levels than present and in particular it appears the Cretaceous witnessed values between 2 - 4 x Present and possibly as high as 11 x Present (Arthur et al. 1991). Changes in atmospheric CO_2 lead to changes in stomatal density (preserved in the fossil record) the productivity, water relations and distribution of plants with different photosynthetic pathways (C_3 and C_4) and evapotranspiration (Moore, 1983, 1989; Woodward, 1987) (table 1). The earliest anatomical evidence for C_4 photosynthesis in the Pliocene but isotopic evidence suggests C_4 systems may have evolved much earlier. To date no comprehensive surveys of carbon isotopes in individual plants has been undertaken but such a study is necessary to understand more fully ancient carbon fluxes, the hydrological cycle and inter-plant competition.

Extinctions

The susceptibility of plants to environmental variables has led to the evolution of a variety of mechanisms for overcoming temporary adverse conditions. From Devonian times onwards the evolution of dormancy mechanisms involving seeds, underground stems and deciduousness, coupled with adventitious growth patterns, provided a degree of robustness to seasonal climate change. These mechanisms undoubtedly also proved useful in enhancing plant survivorship during the short-term ecosystem trauma that characterises some extinction events: episodes that decimated more susceptible elements of the global biota (e.g.. many animals). It is not surprising therefore that the plant record in relation to extinctions is rather different to that of animals.

General patterns of diversity and extinction are difficult to analyse in the plant fossil record due to the peculiarities of palaeobotanical systematics and mosaic evolution (heterobathmy) where individual plant organs have their own distinct evolutionary trajectory. Nevertheless both palynological and megafossil data consistently show originations of new taxa precede extinctions. This pattern occurs irrespective of, and unconnected with, extinctions (periodic or otherwise) observed in the faunal record and seems to indicate that in the plant world extinctions are most commonly caused by inter-plant competition and not short-term ecosystem disturbance (Boulter et al. 1988). If environment does have a role to play in causing plant extinctions it is in influencing longer term evolutionary trajectories.

There is now overwhelming evidence that the Cretaceous/Tertiary (K/T) boundary is characterised globally by a geochemical signature indicative of at least one extra-terrestrial bolide impact: an event originally proposed by Alvarez et al. (1980). Initially this event was regarded as the causal agent for the extinction of a variety of organisms including dinosaurs, marine planktonic forms, a range of marine invertebrates and even some plants. From a palaeontological perspective however this simplistic scenario was always rather suspect, but it provided a focus for concerted research effort. A rather different picture is now emerging as the result of that effort - much of which was undertaken at microstratigraphic scales.

The K/T boundary event has to be viewed against a background of a rapidly changing, heterogeneous and perhaps somewhat unstable global climate and a concomitant reduction in the diversity of a range of organisms - including dinosaurs. Beginning in the early Late Cretaceous global average temperature declined throughout the remainder of the Cretaceous (e.g.. Spicer and Parrish, 1990 and references therein). In the Maastrichtian however climate trends in different parts of the world show conflicting signals and although the precise timing is still controversial large scale vulcanism, particularly the Deccan Trapps may have strongly influenced global climate at this time. In Western North America the boundary itself is marked by an iridium-enriched boundary clay containing shocked quartz. Detailed analysis of this layer complex and the overlying sediments has led to the suggestion that there were probably two impacts (Wolfe, 1991). At least one of these impacts was close to the western US (probably near to what is now the Yucatan Peninsula, Gulf of Mexico) (Sigurdsson et al. 1991) and could have caused atmospheric fall-out and short term temperature fall beginning in June and lasting several months (Wolfe, 1991). Ecological trauma was felt throughout the main body of the North American continent but the biological effects elsewhere, and particularly in the southern hemisphere, were minimal (see review in Spicer, 1989). In eastern Russia floristic change was greater at the beginning of the Maastrichtian that at its end. There was no global conflagration at the K/T boundary (cf. Wolbach et al, 1988), but there was a post impact chill thereafter the Late Cretaceous deterioration in global climate was reversed, temperature and precipitation increased (Wolfe, 1990), and vegetation, particularly in the northern hemisphere, was restructured into something resembling its present form (Wolfe 1987; Wolfe and Upchurch, 1986).

Linkage between the reversal of the Late Cretaceous climatic trend and the impact(s) remains problematical. It is unfortunate that many people view the K/T boundary event as due to one of either a bolide impact or vulcanism. Patterns of extinction and ecological trauma in both plants and animals are consistent with both causal mechanisms. Although responsible for stimulating microstratigraphic multidisciplinary geologic research one wonders if the "Impact Scenario" has also resulted in some misdirection of research effort.

Extinctions quite naturally attract interest because of the opportunity to invoke dramatic causal mechanisms and because we are currently witnessing a global extinction event comparable to anything in the past due to human activity. Given that repeated mass extinctions in the geologic record appear to have no demonstrable common cause it seems likely that interest will and should be directed more to understanding the dynamics of post-extinction recovery as this will provide valuable perspectives for future global management.

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Legends (R.A. Spicer).

Fig. 1 Generic names of different organs of a Carboniferous arborescent lycopod.

Fig. 2 Time for a free fall in still air measured for a number or artificial leaves with the same area (56 cm^2) but different shapes (Ferguson, 1985).

Fig. 3 Fall velocities of fully saturated leaves in still water at 20°C.

Fig. 4 Reconstruction of Late Cretaceous vegetation of Northern Alaska at palaeolatitude 75°N based on plant megafossils collected in sedimentary facies context.

Fig 5 Early Permian vegetational biomes reconstructed from plant fossil data.

Fig. 6 Thermal domains of living forest types based on SE Asian data of Wolfe (1979).

Fig. 7 CLAMP multivariate analysis (correspondence analysis) of modern vegetation sites based on the leaf characters shown in figure 13. Axis 1 (the axis of greatest variation) shows a strong correlation with mean annual temperature but leaves from cold sites tend to plot anomalously due to reduction of leaf size and concommittant loss of characters (based on Wolfe, in press). Axes 1 and 2 in figures 8, 10 and 13 account for nearly 70% of the total variation.

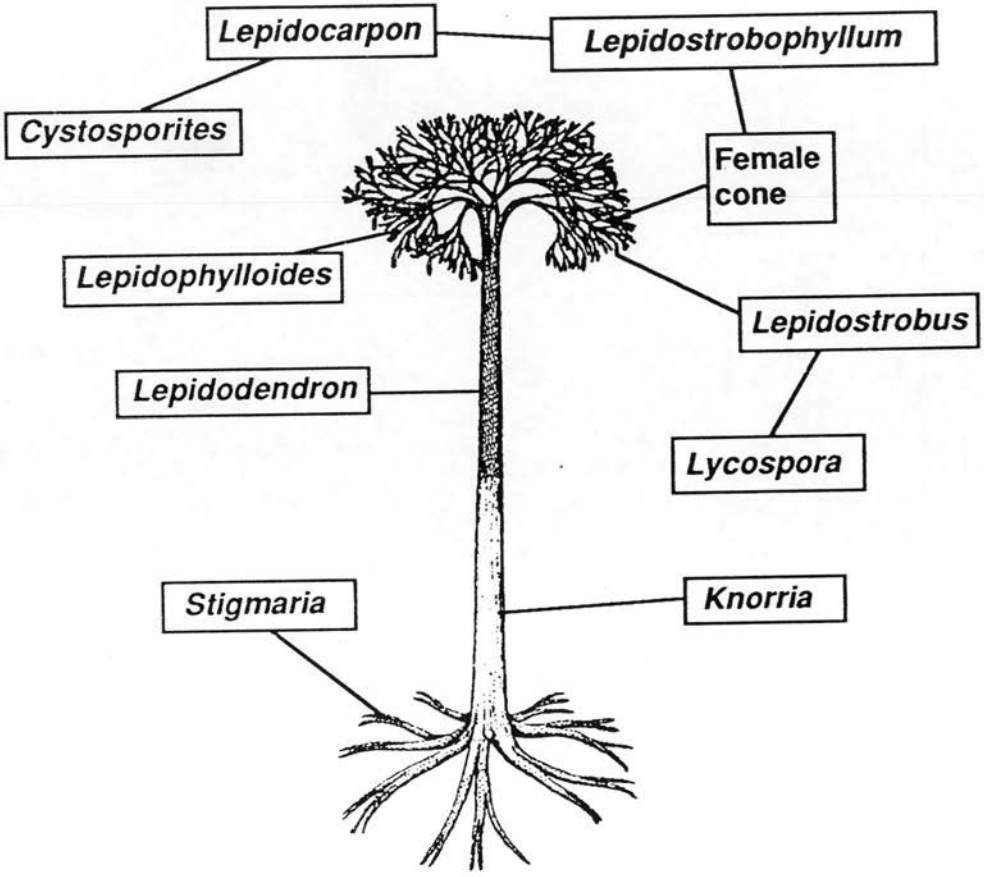
Fig. 8 Regression of mean annual temperature against axis 1 scores. Data as in figure 7.

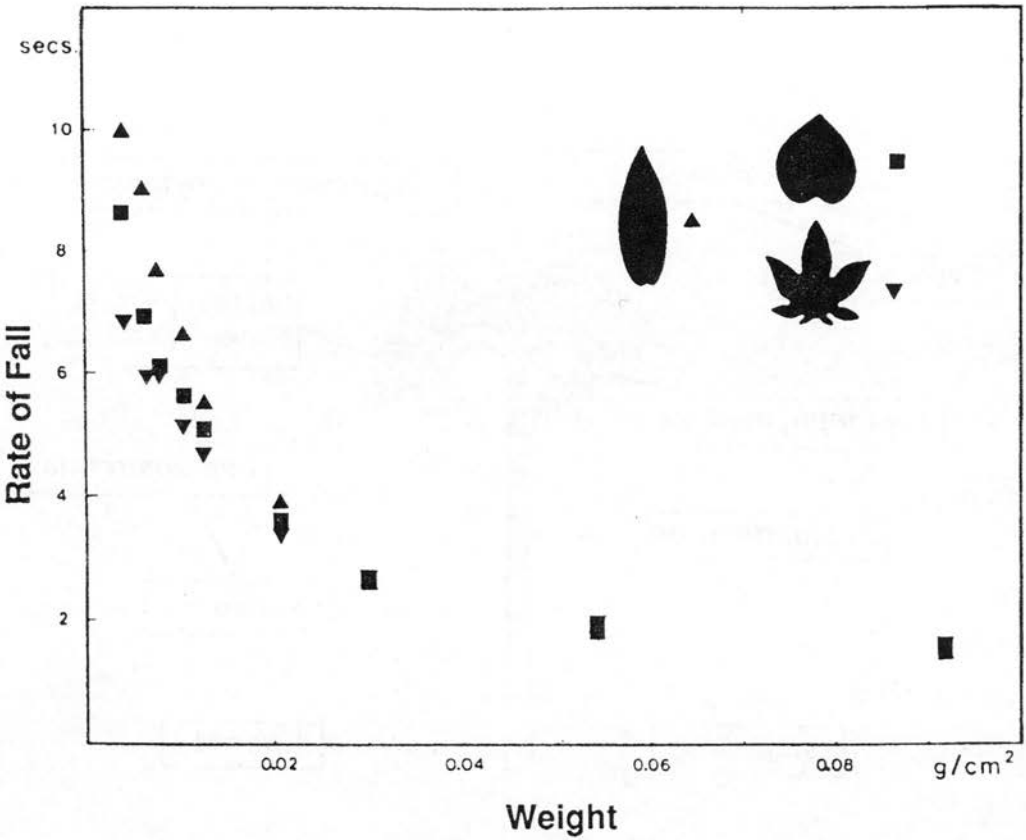
Fig. 9 Regression of mean annual temperature against axis 1 with anomalous sites removed.

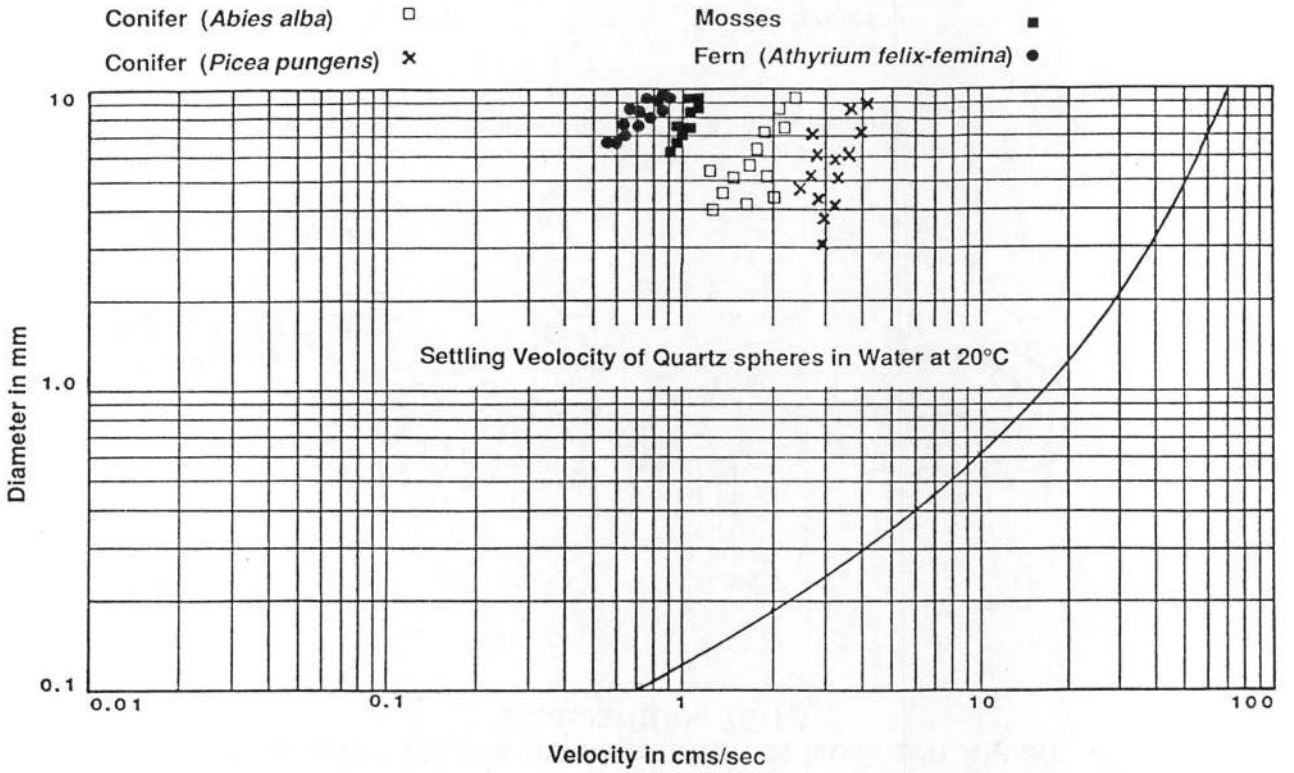
Fig. 10 CLAMP plot showing the distribution of sites in relation to mean annual precipitation. There is some correlation with axis 2 which as shown in figures 11 and 12 but again Arctic and alpine sites show some anomalies.

Fig. 13 CLAMP character plot. Axis 1 shows a strong trend in relation to leaf margin characters (teeth versus no teeth) while axis 2 shows a relationship with leaf size.

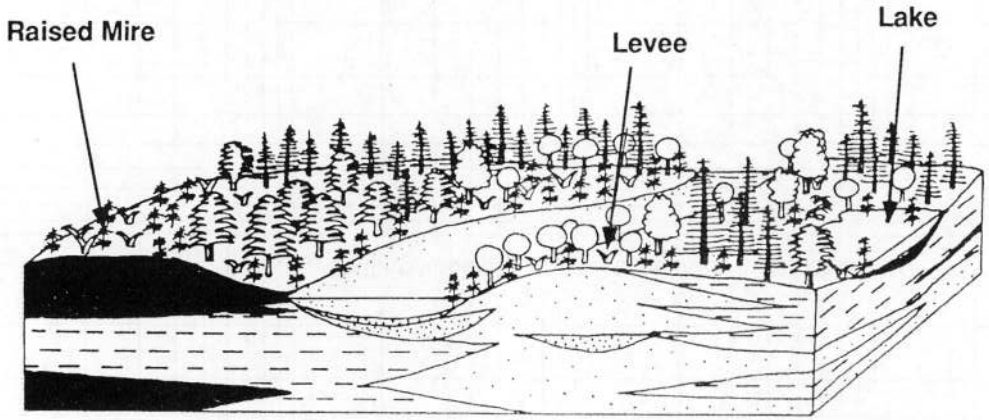
Table 1 Comparison of the characteristics of C_3 and C_4 photosynthetic pathways.







Early Late Cretaceous Vegetation of Northern Alaska (Palaeolatitude 75°N)



Podozamites

Taxodiaceous conifers

Angiosperms

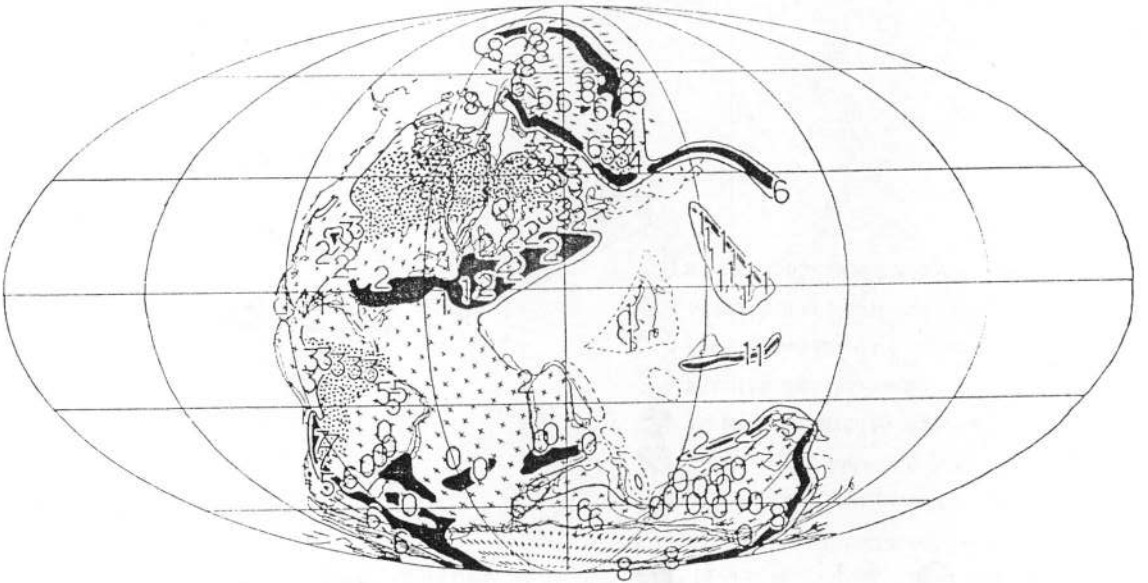
Cycads (*Nilssonia*

Ginkgophytes

Ferns

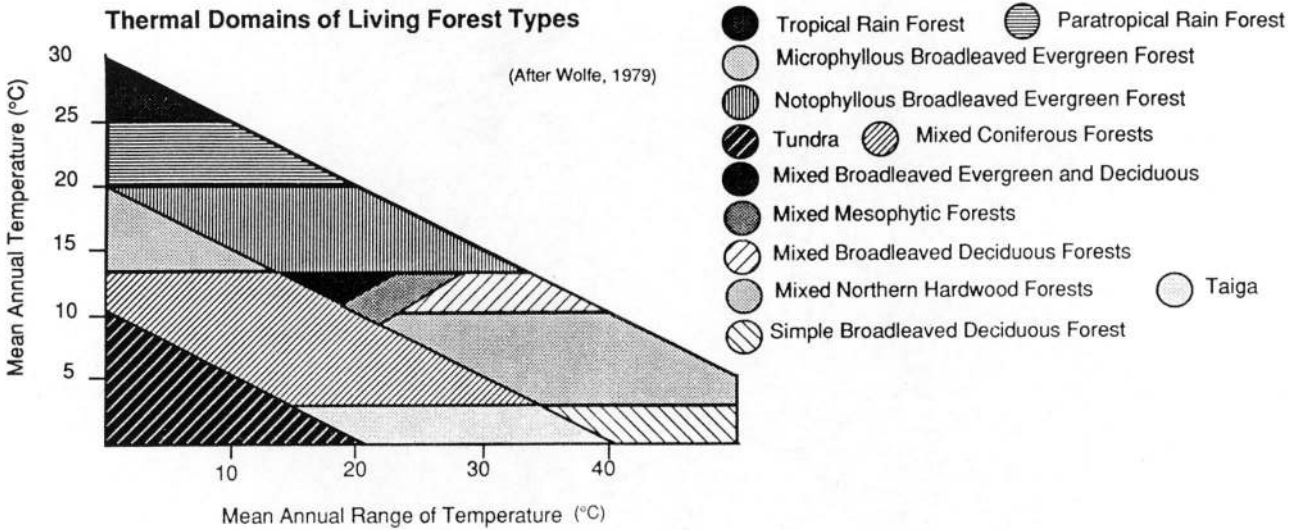
Equisetites

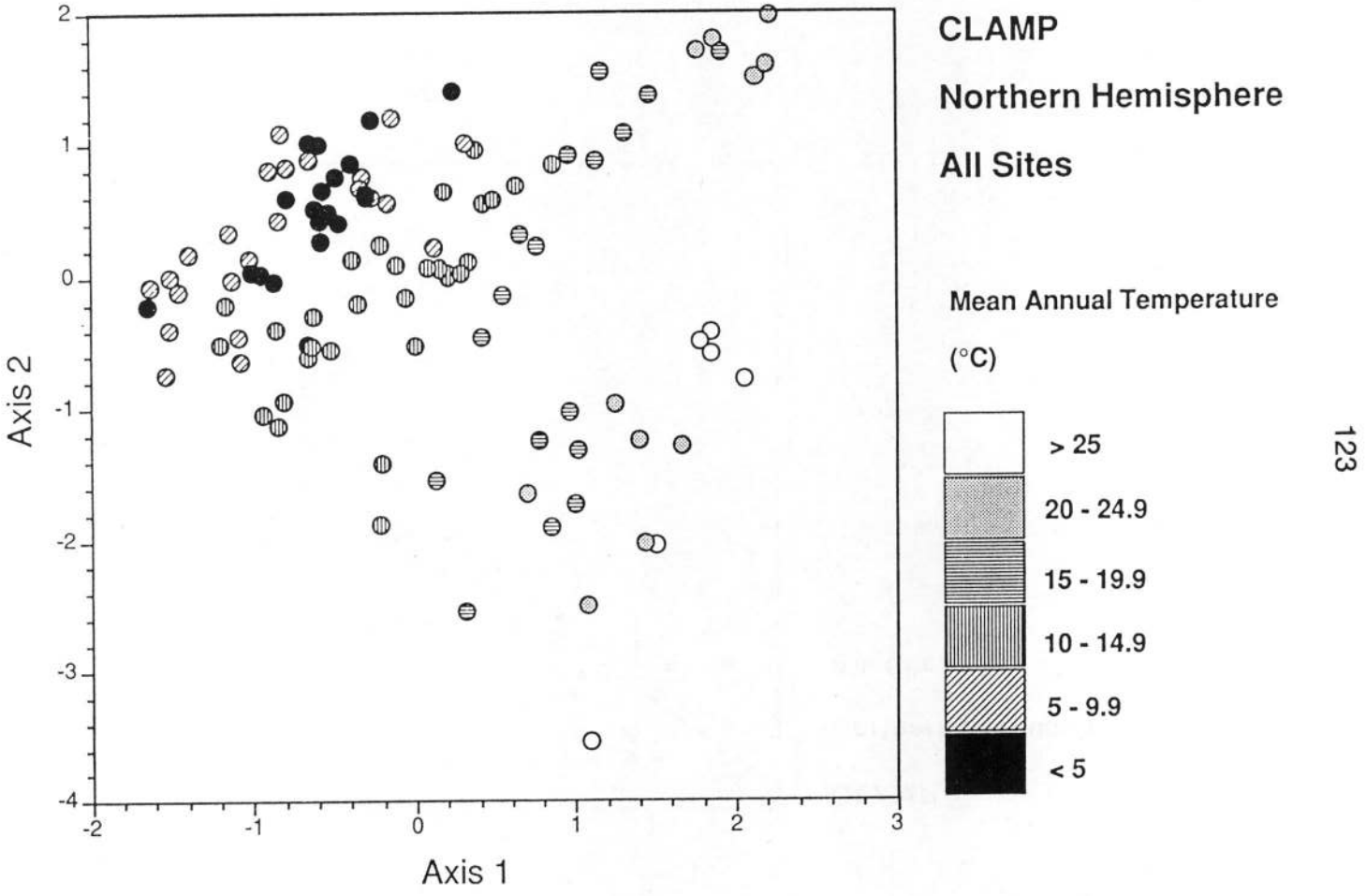
Early Permian (270ma) Vegetational Biomes

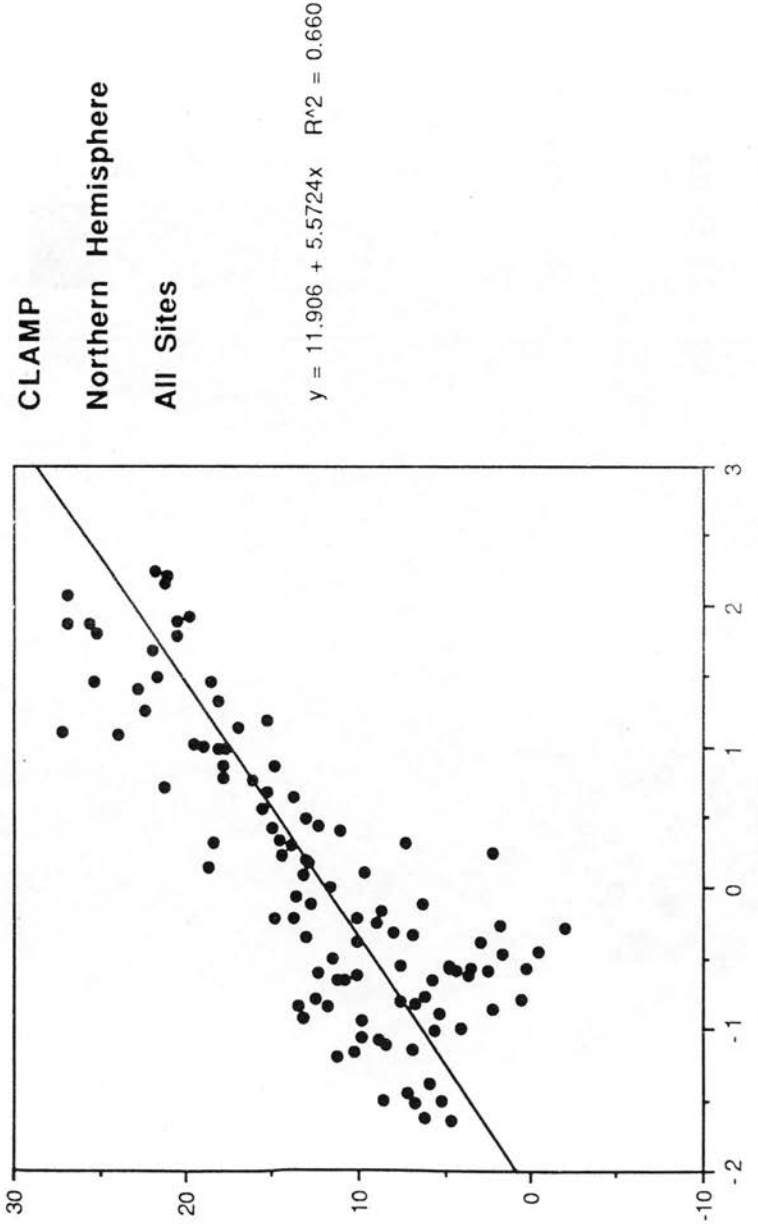


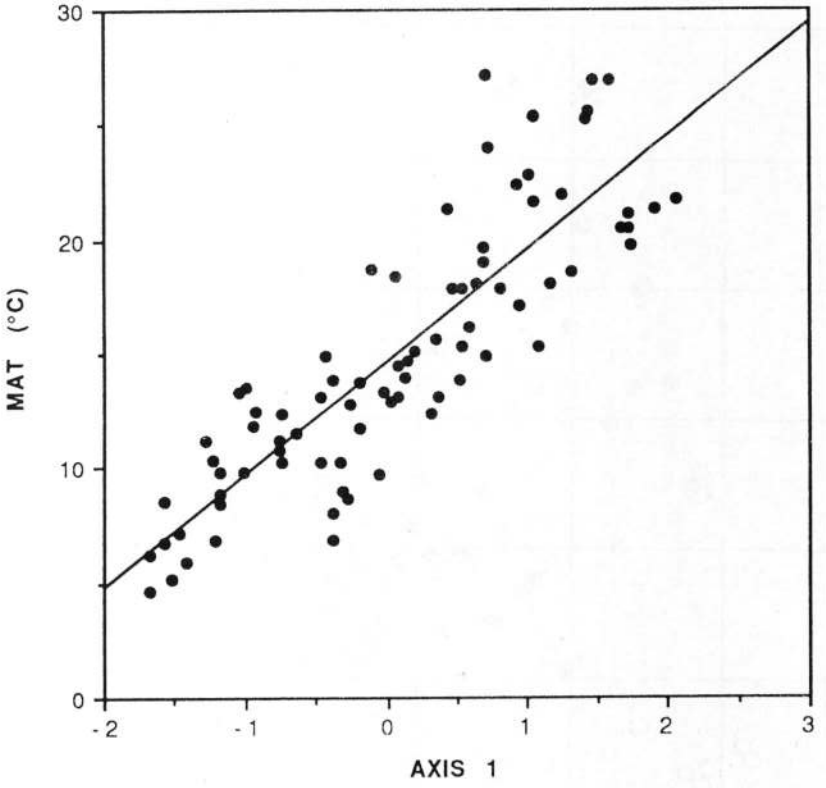
1 Equatorial and tropical everwet
2 Tropical and paratropical summerwet
3 Coastal and inland tropical desert
4 Winterwet
5 Western and eastern warm temperate
6 Western and eastern cool temperate
7 Midlatitude desert
8 Cold temperate
9 "Arctic"
0 Glacial

(Ziegler, 1990)







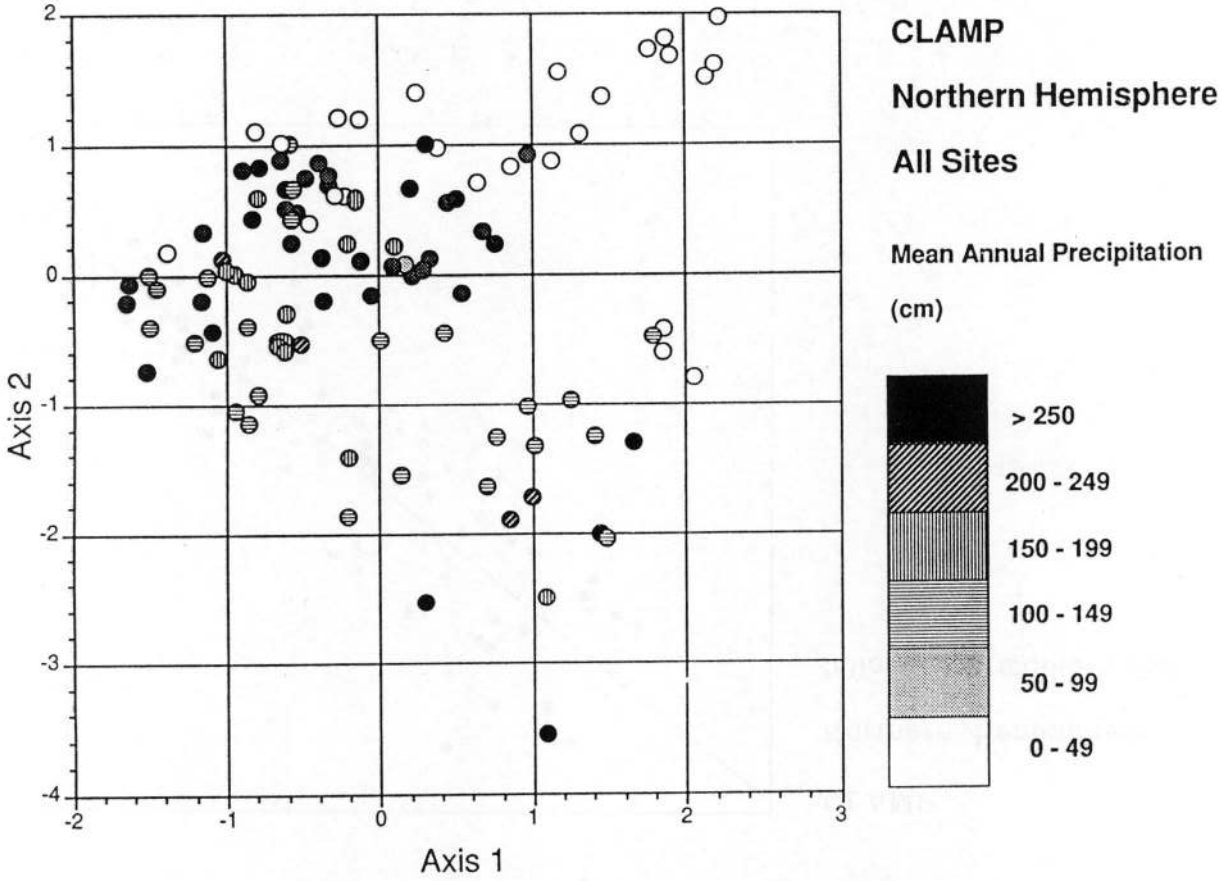


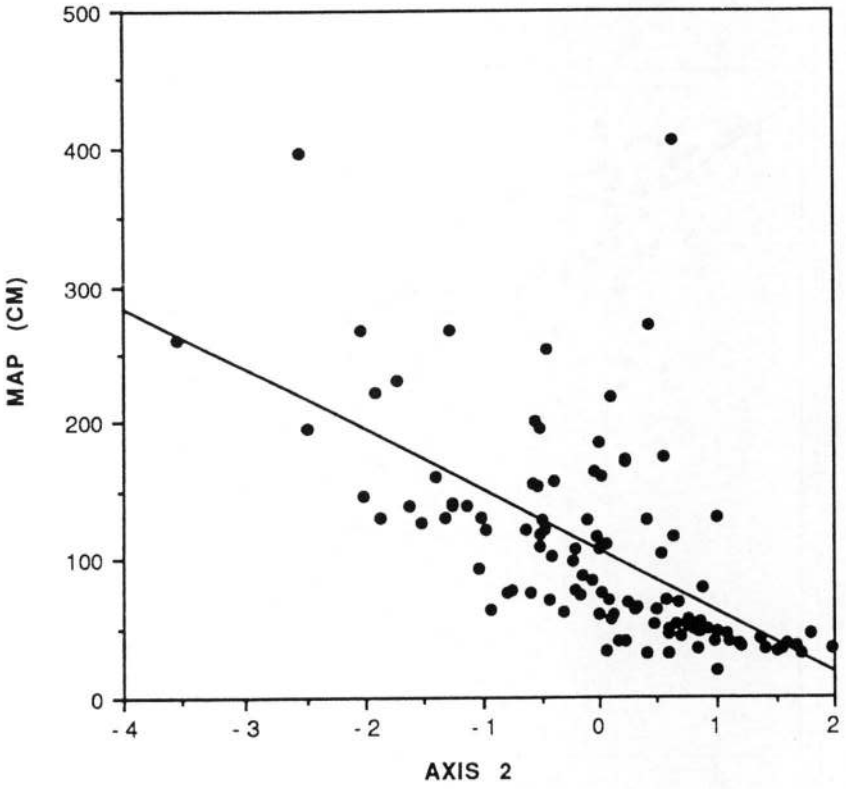
CLAMP

Northern Hemisphere

Inliers and Outliers Removed

y = 14.580 + 4.9309x R^2 = 0.745



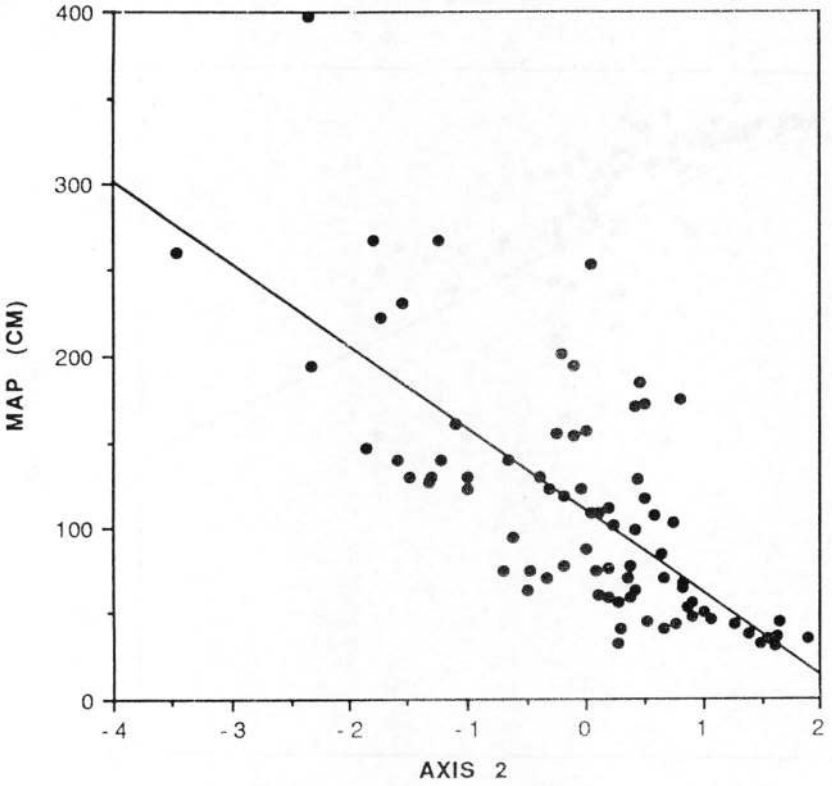


CLAMP

Northern Hemisphere

All Sites

$y = 105.91 - 44.479x \quad R^2 = 0.381$

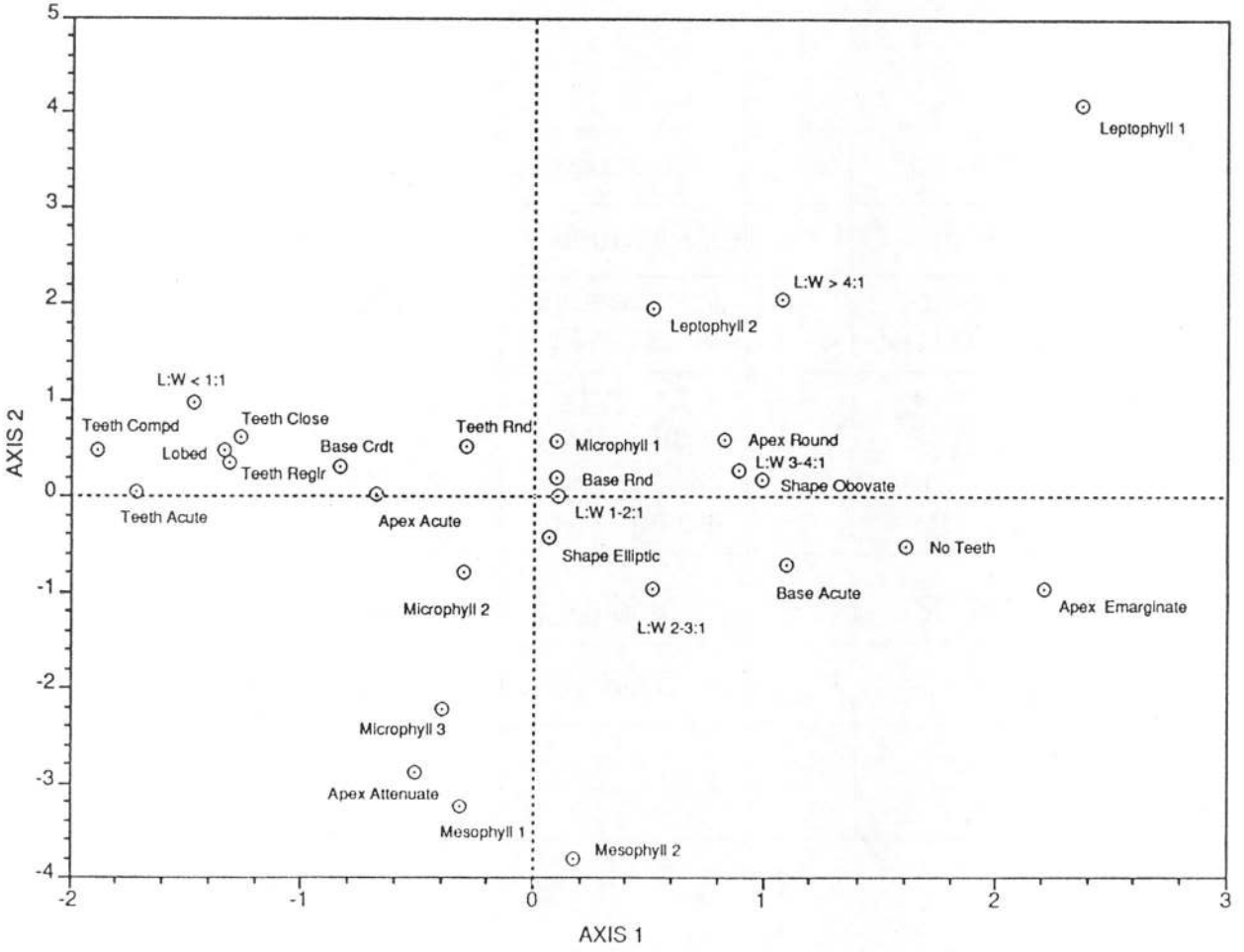


CLAMP

Northern Hemisphere

Inliers and Outliers Removed

y = 109.97 - 47.759x R^2 = 0.514



Variable	C_3	C_4
Temperature optimum	20-25°C	30-35°C
CO_2 optimum in stomatal chamber	220 ppm	120 ppm
Quantum yield (carbon per fixed unit of energy)	> C_4 below 30°C < C_4 above 30°C	> C_3 above 30°C < C_3 below 30°C
$\delta\ ^{13}C$ per mil $= \left[\frac{(^{13}C : ^{12}C)\ \text{sample}}{(^{13}C : ^{12}C)\ \text{standard}} - 1 \right] \times 1000$	Low, -22 to -33 (mean -27)	High, -10 to -18 (mean -14)
Water use efficiency	generally low	higher than C_3
Salinity tolerance	variable	generally high

ANIMALS AND MASS EXTINCTIONS

S. Conway Morris

Animals and mass extinctions

The renewed interest in mass extinctions is little short of remarkable if one considers the doldrums of neo-catastrophist speculation in the fifties and sixties. The renaissance is very largely due, of course, to the detection of anomalous levels of iridium at the Cretaceous-Tertiary boundary (K/T) by the Alvarez group, a result that was rapidly confirmed at many K/T sites around the world. The evidence of at least one impact is now overwhelming and includes not only candidate craters in Yucatan and Iowa, but a variety of related observations, e.g. shocked mineral grains, melt droplets, high pressure silica polymorphs, microdiamonds, extraterrestrial amino acids and wildfire soot. The strength of this evidence should not obscure, however, two important aspects.

(a) Why, seemingly do major meteorite/comet impacts normally fail to trigger mass extinctions? It still remains possible that the other Phanerozoic mass extinctions (late Ordovician, late Devonian, end Permian and Eocene/Oligocene events) were due to impacts, but as yet evidence in inconclusive.

(b) The correlation between episodes of flood basalts and massive volcanism and mass extinctions is not well established, but the apparent coincidence of the Deccan flood basalt effusions and the K/T event is notable.

Can the two opposing camps of thought, supporting either massive volcanism or catastrophic impact, be reconciled so that both mechanisms are necessary to account for the K/T extinctions? This is possible, but at the moment it may be better to seek further evidence for extra-terrestrial influences. New evidence suggests that the Earth could have been subject to a short-lived but intense episode of meteorite bombardment. It is not

impossible that at least five craters are of K/T age, and more may be found or alternately impacted areas of the ocean now subducted. Did a large body break up in the vicinity of the Earth, leading not only to a series of impacts but also infall of dust particles with the extraterrestrial amino acids?

What palaeontological information can help us to understand mass extinctions and their underlying mechanisms? Here are some of the questions we should ask:

(a) Why are extinctions selective? What renders some taxa and environments almost immune, whereas others appear to be devastated?

(b) Is the fossil record ever adequate to distinguish between gradual and abrupt extinction?

(c) What are the refugia in mass extinctions?

(d) Why is recovery in some post-mass extinction events so slow, and what processes operate in post-disaster faunas?

Mass extinctions

The literature on this topic continues to grow at an enormous rate, and the subject is still moving so quickly that reviews and text-books are rapidly out-dated. Literature, of course, appears in a very wide range of journals, but the most interesting results are often reported in Nature, Science (which has frequent updates in its Research News section) and Geology.

Recent volumes that bring together much useful information include:

DONOVAN, S.K. (ed) 1989. Mass extinctions: processes and evidence. Belhaven.

KAUFFMAN, E.G. & WALLISER, O.H. 1990. Extinction events in Earth history. Lecture Notes in Earth Sciences 30. Spring-Verlag.

RAUP, D.M. 1991. Extinction. Bad genes or bad luck? Norton.

LISTS OF INVITED SPEAKERS AND PARTICIPANTS

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PALAEOBIOLOGY: PREPARING FOR THE TWENTY-FIRST CENTURY

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