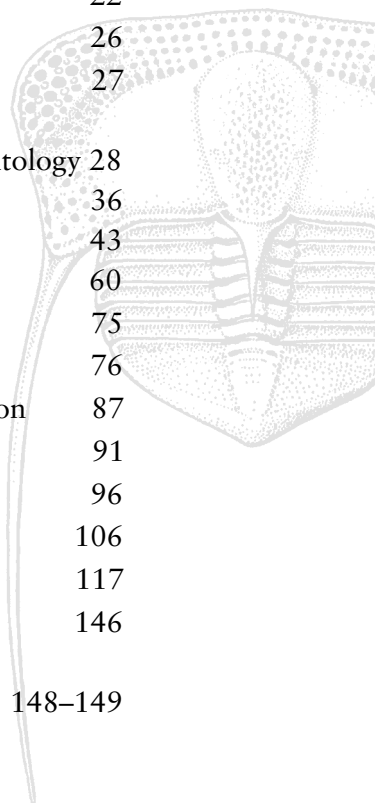


The Palaeontology Newsletter

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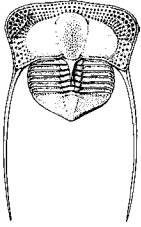


Reminder: The deadline for copy for Issue no 63 is 6th October 2006.

On the Web: <<http://palass.org/>>

ISSN: 0954-9900





50th Annual General Meeting and Annual Address

AGENDA

1. Apologies for absence
2. Annual Report for 2005
3. Accounts and Balance Sheet for 2005
4. Proposed changes to the Constitution
5. Election of Council and vote of thanks to retiring members.
6. Palaeontological Association Awards
7. Annual address

H. A. Armstrong
Secretary



Association Business

The Palaeontological Association Annual Report for 2005

Nature of the Association. The Palaeontological Association is a Charity registered in England, Charity Number 276369. Its Governing Instrument is the Constitution adopted on 27 February 1957, amended on subsequent occasions as recorded in the Council Minutes. Trustees (Council Members) are elected by vote of the Membership at the Annual General Meeting. The contact address of the Association is c/o The Executive Officer, Dr T. J. Palmer, Institute of Geography and Earth Sciences, University of Wales, Aberystwyth, SY23 3DB, Wales, UK.

Membership & subscriptions. Individual membership totalled 1,270 on 31st December 2005, an overall decrease of 15 over the 2004 figure. There were 775 Ordinary Members, a decrease of 16; 173 Retired Members, an increase of 15; 320 Student Members, a decrease of 20 and 2 honorary members. There were 142 Institutional Members in 2004, of which 62 also subscribe to *Special Papers in Palaeontology*. Total Individual and Institutional subscriptions to *Palaeontology* through Blackwell's agency numbered 378. Subscriptions to *Special Papers in Palaeontology* numbered 217 individuals (Ordinary, Retired and Student) and 142 institutional members. Regular orders through Blackwell's agency for *Special Papers in Palaeontology* totalled 39 copies. Sales to individuals through the Executive Officer of current and back numbers of *Special Papers in Palaeontology* (279 copies) yielded £8,499. Income from sales of *Field Guides to Fossils* amounted to £4,317. Sales of "Fold out Fossils" totalled £10.

Finance. Publication of *Palaeontology* and *Special Papers in Palaeontology* is managed by Blackwell's, who also make sales and manage distribution on behalf of the Association. In addition to the fee that they take directly from the subscribers, the Association paid them a further fee of £8,009. The Association gratefully acknowledges the donations from Members to the Sylvester-Bradley Fund, which amounted to £238. Grants from general funds to external organisations, for the support of palaeontological meetings and projects, totalled £11,430. Twenty-three grants-in-aid totalling £8,000 were provided to support postgraduate student attendance at the International Palaeontological Congress in Beijing. The Association continues its membership of the International Palaeontological Association and remains a Tier 1 sponsor of *Palaeontologia Electronica*. The Association continues to support the Treatise on Invertebrate Paleontology with financial support of \$5,000 per year.

Publications. Volume 48 of *Palaeontology*, comprising six issues and 1,427 pages in total, was published at a cost of £91,619. A new section of *Palaeontology* was dedicated to "Rapid Communications." *Special Papers in Palaeontology* 73 "Conodont biology and phylogeny: interpreting the fossil record" edited by M. A. Purnell and P. C. J. Donoghue was published at a cost of £7,745 and totalled 218 pages. *Special Papers in Palaeontology* 74: "Brachiopods from the Dashaba Formation (Middle Ordovician) of Sichuan Province, south-west China" by Zhan Ren-bin and Jin Jisuo was published at a cost of £2,239 and totalled 63 pages. There were no *Field Guides to Fossils* or *Fold-Out Fossils* for 2005. Digital files of published papers in *Palaeontology* and multi-authored *Special Papers in Palaeontology* are now given to authors in addition to free reprints.



The Association is grateful to the National Museum of Wales and the Lapworth Museum, University of Birmingham for providing storage facilities for publication back-stock and archives. Council is indebted to Meg and Nick Stroud for assistance with the publication and distribution of *Palaeontology Newsletter*.

Meetings. Three meetings were held in 2005, and the Association extends its thanks to the organisers and host institutions of these meetings.

The **Forty-ninth Annual General Meeting** was held on 18–21 December at Oxford University Museum of Natural History. Dr D. Siveter, with much local support, organised the meeting. The President's Award was made to Maria McNamara (University College Dublin). The Council Poster Prize was presented to Richard Callow (University of Oxford). On the final day field trips were undertaken to the Jurassic and Cretaceous of Oxfordshire. There were 300 attendees.

Progressive Palaeontology was held at the University of Leicester on 15th June. The annual open meeting for presentations by research students was organised by David Jones at the University of Leicester.

A **British Association Festival of Science Symposium** was held in Trinity College Dublin on 3–10 September, on "Rewriting the history of life: exceptionally well-preserved fossils and our understanding of evolution," organised by Dr Orr and Dr Manning.

Awards. The Lapworth Medal, awarded to people who have made a significant contribution to the science by means of a substantial body of research, was awarded to Prof. W. G. Chaloner. The Hodson Fund, for a palaeontologist under the age of 35 who has made an outstanding achievement in contributing to the science through a portfolio of original published research, was awarded to Dr P. C. J. Donoghue (University of Bristol). Prof. J. H. Callomon and Prof. C. H. Holland were awarded Honorary Life Membership. The Mary Anning award, for an outstanding contribution by an amateur palaeontologist, was made to Mr Andrew Yule and Mr Steve Etches. The Sylvester-Bradley Fund continues to attract a large number of high quality international applications and awards totalling £10,985 were made. Council awards an undergraduate prize to each university department in which palaeontology is taught at a post-first-year level. One new "Golden Trilobite" award was made, to <www.trilobites.info>, and links were made to the Association website.

Council. The following members were elected to serve on Council at the AGM on 19th December 2005: Dr Twitchett (Newsletter Editor), Dr Servais (Ordinary Member) and Dr Harper will stay on Council as a handling editor and Trustee. During the year Dr Sutton and Dr Wellman (as Annual meeting organiser for 2006) were co-opted as Ordinary Members. At the AGM the following members stepped down from Council: Dr Purnell (Vice-President), Dr Donoghue (retired as Newsletter Editor but stays on Council as a Vice-President) and Prof. Evans (retired as a Trustee but will remain as a handling editor). Dr T. J. Palmer continued to serve as the Executive Officer of the Association, and Prof. D. J. Batten (University of Manchester) as the Editor in Chief.

Council is indebted to the Natural History Museum, London, and the Universities of Leicester and Birmingham for providing meeting venues through the year.

Professional Services. The Association's Bankers are NatWest Bank, 42 High Street, Sheffield. The Association's Independent Examiner is G. R. Powell BSc FCA, Nether House, Great Bowden, Market Harborough, Leicestershire. During the year the Associations' investment portfolio was transferred



to Common Funds under the management of Morgan Stanley Quilter, St Helen's, The Undershaft, London EC3A 8BB. This will allow the account managers to deal on our behalf without the instruction of the Treasurer, being more efficient and saving on fees.

Reserves. The Association holds reserves of £532,408 in General Funds. These Reserves enable the Association to generate additional revenue through investments, and thus to keep subscriptions to individuals at a low level, whilst still permitting a full programme of meetings to be held and publications to be produced. They also act as a buffer to enable the normal programme to be followed in years in which expenditure exceeds income, and new initiatives to be pursued, without increasing subscription costs. The Association holds £69,955 in Designated Funds which contribute interest towards the funding of the Sylvester-Bradley, Hodson Fund and Mary Anning awards.

Council Activities. The Association continues to improve its administration with further improvements to the Newsletter and website. The Association continues to be proactive in generating publicity for palaeontology with major press initiatives and a continued high profile on the television. Primers on numerical analysis and cladistics in the Newsletter have been widely acclaimed. A highlight of the year has been the provision online of *Palaeontology* (back to volume 12) and further back issues of *Special Papers in Palaeontology*, free to the palaeontological community. A new Publicity sub-domain has been developed for the website. Further developments have been made to online purchasing of Association publications and meetings registration. Blackwell continue to provide additional services to the Association including, an e-alert service and a publicity service. The Annual Address, given at the Annual Meeting and entitled "William Buckland and the dawning of palaeoecology," was presented by Prof. W.J. Kennedy (Oxford University Museum of Natural History) and was attended by 300 people. The Association was represented during the year by Prof. Crane and Dr Lloydell on the Joint Committee for Palaeontology. The Association sponsored the development of a fossil display at the National Botanic Garden of Wales and "New discoveries in old collections" (Linnéan Society, Palaeobotany Specialist Group) and the following international symposia: "Pre-vertebrate to Vertebrate transition" (Charles University, Czech Republic), European Evolutionary Development Society and International Palaeontological Conference 2006, Beijing.

Forthcoming plans. Council will continue to improve its administration during 2006. A new "Conditions of Membership" will be prepared and revisions of the Constitution will be proposed to incorporate recent developments and policy changes. A new publishing contract with Blackwell will be negotiated in 2006 and will reflect new online and e-publishing activities. Council will continue to make substantial donations, from both Designated and General funds, to permit individuals to carry out research into palaeontological subjects and to disseminate their findings in print and at conferences. In 2006, a similar programme of meetings and publications will be carried out as in 2005, including sponsorship of the Lyell Meeting plus an annual symposium at the British Association for the Advancement of Science meeting. Additional electronic versions of early volumes of *Palaeontology* and *Special Papers in Palaeontology* will be produced. Online submission of manuscripts will be enabled early in 2006. Further developments will be made to the website including increasing online search functionality. It is intended that one new *Field Guide to Fossils* will be published within the year. The Annual Meeting has continued to develop as one of the major international palaeontological meetings and will be held at the University of Sheffield in 2006, celebrating the 50th Anniversary of the Association. A one-day symposium



entitled “Macroevolution,” a programme of internationally recognised speakers has been arranged, to celebrate the scientific activities of the Association. The proceedings will be published in a special issue of *Palaeontology*. Council has agreed substantial support for this meeting.

Howard A. Armstrong
Secretary

Nominations For Council

At the AGM in December 2006, the following will be nominated for Council:

President: Prof. M. G. Bassett
Vice President: Dr Wellman
Publicity: Dr Manning
Book Review Editor: Dr Orr
Web master: Dr Hilton
Ordinary Member: Dr Rasmussen

Honorary Life Membership

The following members have been elected Honorary Life Members:

Prof. W. G. Challoner
Prof. A. Hallam
Prof. Harry Whittington
Dr Robin Cocks

Awards and Prizes

Nominations are now being sought for the Hodson Fund, Mary Anning Award and Sylvester-Bradley Award.

Hodson Fund

This award is conferred on a palaeontologist who is under the age of 35 and who has made a notable early contribution to the science. Candidates must be nominated by at least two members of the Association and the application must be supported by an appropriate academic case. The closing date for nominations is **1st September**. Nominations will be considered and a decision made at the October meeting of Council. The Award will comprise a fund of £1,000, presented at the Annual Meeting.

Mary Anning Award

The Award is open to all those who are not professionally employed within palaeontology but who have made an outstanding contribution to the subject. Such contributions may range from the compilation of fossil collections, and their care and conservation, to published studies in recognised journals. Nominations should comprise a short statement (up to one page of A4)



outlining the candidate's principal achievements. Members putting forward candidates should also be prepared, if requested, to write an illustrated profile in support of their nominee. The deadline for nominations is **1st September**. The award comprises a cash prize plus a framed scroll, and is usually presented at the Annual meeting.

Sylvester-Bradley Award

Awards are made to assist palaeontological research (travel, visits to museums, fieldwork *etc.*), with each award having a maximum value of £1,000. Preference is given to applications for a single purpose (rather than top-ups of other grant applications) and no definite age limit is applied, although some preference may be given to younger applicants or those at the start of their careers. The award is open to both amateur and professional palaeontologists, but preference will be given to members of the Association. The awards are announced at the AGM.

Council will also consider awards in excess of £1,000, particularly for pilot projects which are likely to facilitate a future application to a national research funding body.

Electronic submission of applications is through the website and will comprise a CV, an account of research aims and objectives (5,000 characters maximum), and a breakdown of the proposed expenditure. Each application should be accompanied by the names of a personal and a scientific referee. Successful candidates must produce a report for *Palaeontology Newsletter* and are asked to consider the Association's meetings and publications as media for conveying the research results. The deadline for applications is **1st November**.

Golden Trilobite Award

Nominations are sought for the "Golden Trilobite Award" for prestigious websites.

This is awarded for the best institutional and amateur websites that promote the charitable and scientific aims of the Association, the promotion of palaeontology and its allied sciences. The award will take the form of a statement of recognition that can be posted on the winning sites. Nominations are

sought from the membership, and should be sent to the Secretary at <secretary@palass.org> by **1st September**. The websites will be judged by Council members.



Grants in Aid

Applications for sponsorship for scientific meetings should be sent to <secretary@palass.org>.

Funds typically will cover speaker expenses, attendance of students or scientists, who would normally be unable to attend meetings for financial reasons, and other expenses associated with the running of scientific meetings. Awards will be considered at a full Council meeting and will typically be up to £2,000.



Proposed changes to the Constitution

Council is recommending certain changes in the Constitution, and members will be asked to approve these at the AGM to be held at the Sheffield Conference.

The proposed changes are largely of a housekeeping nature. They include:

1. A rationalisation of the categories of individual membership. These include a restatement of the definition of Student Membership; expansion of the Retired Membership categories to include new members (as opposed to previous Ordinary Members of 15 years standing) who are over 60 and not in full-time employment; and formal inclusion of the category of Honorary Member.
2. A move to permit the Institutional Membership subscription to be decided by Council rather than be referred to the AGM. This permits easier integration with Blackwell's rates for full subscribers and more rapid response to currency fluctuations. Arrangements for the setting of subscriptions for individual members are unchanged.
3. Inclusion of information required to be consistent with recent changes in Charity law.

The wording of the existing and the proposed new Constitutions are given below.

Existing Constitution

1. *Name:* The name of the Association shall be '*The Palaeontological Association*'.
2. *Aims:* The aim of the Association is to promote research in Palaeontology and its allied sciences by (a) holding public meetings for the reading of original papers and the delivery of lectures, (b) demonstration and publication, and (c) by such other means as the Council may determine.
3. *Membership:* There shall be Ordinary Members, Institutional Members and Student Members. In addition there shall be Retired Members, who shall be Ordinary Members of not less than fifteen years standing and over the age of 60, who are not engaged in full time employment. The annual subscription for Retired Members shall be one half of that for Ordinary Members. Each subscriber shall be considered a member of the Association, but Institutional Members shall not be eligible to take part in the government of the Association. In addition there shall be Honorary Life Membership conferred on members who Council deems to have been significant benefactors and/or supporters of the Association. Recipients will receive free membership of the Association. Each subscriber shall be considered a member of the Association, but Institutional Members shall not be eligible to take part in the government of the Association.
4. *Subscriptions:* The annual subscriptions for individuals and institutions shall be determined by the members in General Meeting.
5. The business of the Association shall be undertaken by a Council and by committees of the Council. The Council shall consist of a maximum of twenty members. The Officers shall consist of a President and, at least, two Vice-Presidents, a Treasurer, a Secretary and an Editor, and such other Officers as the Council may from time to time determine. At any meetings of the Council six members shall form a quorum which shall always include the President, or a Vice-President or the Secretary. The committees of the Council may co-opt members of the



Association as non-voting committee members. Committees of Council shall be open to all members of Council.

Periods of service for Officers shall be flexible but should normally not exceed two years for President and Vice-Presidents, and five years for Secretary, Editors, and Treasurer. Total consecutive service as an Officer (excluding service as President) shall not exceed ten years. Other members of the Council shall be elected for a period of three years. All members of Council are Trustees of the Association in accordance with charity law.

Elections shall be held annually to fill vacancies on Council. The results of elections shall be announced at the Annual General Meeting. If nominations exceed vacancies a ballot shall be conducted at the meeting and provision shall be made for a postal ballot for members unable to attend the meeting. Nominations should be received by the Secretary not later than the Wednesday of the first full week in October preceding the Annual General Meeting.

6. The Annual General Meeting shall be held within 12 months of the end of the Association year. Other meetings shall be held as determined by Council.
7. The accounts of the Association shall be made up to 31st December in each year and shall be examined in accordance with the requirements of the relevant Charity Acts. Examined accounts shall be submitted to the Annual General Meeting.
8. No member is entitled to any distinct or separate share in the property or effects of the Association, and in the event of a dissolution of the Association such property or effects shall be disposed of by gift to one or more other charitable Societies or Associations which have for their objects the furtherance of palaeontology or its allied sciences, as shall be decided by a vote of a meeting called for the purpose.
9. No alteration of these rules shall be made except by a majority vote at a meeting of the Association held after one month's notice of the proposed alterations has been given by the Secretary to the Ordinary, Student and Retired Members.
10. Council may, as resources allow, employ the services of one or more paid officers, to be known as Executive Officers, to carry out a proportion of the tasks involved in the running of the Association. Paid officers will normally attend meetings of Council but shall not be entitled to vote and will not be Trustees. The appointments of all paid officers will be reviewed on an annual basis.

Wording of proposed new Constitution

1. *Name:* The name of the Association shall be '*The Palaeontological Association*'.
2. *Nature of the Association:* The Palaeontological Association is a Charity registered in England, Charity Number 276369. Its Governing Instrument is the Constitution adopted on 27 February 1957, amended on subsequent occasions as recorded in the Council Minutes. Trustees (Council Members) are elected by vote of the Membership at the Annual General Meeting. The contact address of the Association is that of The Executive Officer.



3. *Aims:* The aim of the Association is to promote research in Palaeontology and its allied sciences by (a) holding public meetings for the reading of original papers and the delivery of lectures, (b) demonstration and publication, and (c) by such other means as the Council may determine.
4. *Membership:* Membership of the Palaeontological Association is open to anyone who agrees with the charitable and scientific aims of the Association and who agrees to abide by the conditions of membership of the Palaeontological Association as set out below. Members fall into one of the following categories: **Ordinary members:** These are individual members of the Association who are neither students nor retired members. **Student members:** These are individual members who are registered members of a school, college or university; study towards a formal educational qualification is their full-time or principal occupation. **Retired members:** These are individual members over 60 years old and not in full-time employment. The annual subscription for Retired members is one half of that for Ordinary members. **Honorary members:** These are Retired members who have been elected to be Honorary members by Council, usually on account of substantial services that they have rendered to the Association at some former time. Recipients will receive free membership of the Association. **Institutional members:** Institutions that wish to obtain copies of *Palaeontology* and the Newsletter that may be consulted by multiple individuals should apply for Institutional Membership through the Executive Officer. Ordinary, Student, Retired and Honorary members shall be considered full members of the Association and eligible to take part in the government of the Association, but Institutional Members shall not be eligible to take part in the government of the Association.
5. *Subscriptions:* The annual subscriptions for individuals shall be determined by the members in General Meeting. The annual subscriptions for institutions shall be determined by Council.
6. The business of the Association shall be undertaken by a Council and by committees of the Council. The Council shall consist of a maximum of twenty members. The Officers shall consist of a President and, at least, two Vice-Presidents, a Treasurer, a Secretary, a Chair of the Publications Board, and such other Officers as the Council may from time to time determine. At any meetings of the Council six members shall form a quorum which shall always include the President, or a Vice-President, or the Secretary. The committees of the Council may co-opt members of the Association as non-voting committee members. Committees of Council shall be open to all members of Council.
7. Periods of service for Officers shall be flexible but should normally not exceed two years for President and Vice-Presidents, and five years for Secretary, Editors, and Treasurer. Total consecutive service as an Officer (excluding service as President) shall not exceed ten years. Other members of the Council shall be elected for a period of three years. All members of Council are Trustees of the Association in accordance with charity law.
8. Elections shall be held annually to fill vacancies on Council. The results of elections shall be announced at the Annual General Meeting. If nominations exceed vacancies a ballot shall be conducted at the meeting and provision shall be made for a postal ballot for members unable to attend the meeting. Nominations for all Council positions except President should be received by the Secretary not later than 1st June preceding the Annual General Meeting at which the elected Council member will start to serve. Nominations for President should



be received by the Secretary not later than 1st June in the year preceding the Annual General Meeting at which the elected President will start to serve.

9. The Annual General Meeting shall be held within 12 months of the end of the Association year. Other meetings shall be held as determined by Council.
10. The Annual Report and accounts of the Association shall be made up to 31st December in each year and shall be examined in accordance with the requirements of the relevant Charity Acts. Examined accounts and the Annual Report shall be submitted to the Annual General Meeting.
11. No member is entitled to any distinct or separate share in the property or effects of the Association, and in the event of a dissolution of the Association such property or effects shall be disposed of by gift to one or more other charitable Societies or Associations which have for their objects the furtherance of palaeontology or its allied sciences, as shall be decided by a vote of a meeting called for the purpose.
12. No alteration of these rules shall be made except by a majority vote at a meeting of the Association held after one month's notice of the proposed alterations has been given by the Secretary to the Ordinary, Student, Retired and Honorary Members.
13. Council may, as resources allow, employ the services of one or more paid officers, to be known as Executive Officers, to carry out a proportion of the tasks involved in the running of the Association. Paid officers will normally attend meetings of Council but shall not be entitled to vote and will not be Trustees. The appointments of all paid officers will be reviewed on an annual basis.



THE PALAEOONTOLOGICAL ASSOCIATION Registered Charity No. 276369
STATEMENT OF FINANCIAL ACTIVITIES FOR THE YEAR ENDED 31st DECEMBER 2005

	General Funds £	Designated Funds £	TOTAL FUNDS £	TOTAL 2004 £
INCOMING RESOURCES				
Subscriptions			65,646	66,164
Sales:				
<i>Palaeontology</i>	136,161			
<i>Special Papers</i>	14,268			
Offprints	2,275			
Fossil Guides	4,332			
Postage & Packing	<u>652</u>			
Total Sales	157,688		157,688	142,487
Investment Income & Interest	15,484	3,594	19,078	18,467
Donations		818	818	3,059
Sundry Income	1,515		1,515	<u>2,915</u> _n
Total	<u>240,333</u>	<u>4,412</u>	<u>244,745</u>	<u>233,092</u>
RESOURCES EXPENDED				
Publications:				
<i>Palaeontology</i>	68,128		68,128	
<i>Special Papers</i>	5,359		5,359	
Offprints	4,008		4,008	
Fossil Guides	2,204		2,204	
Newsletters	16,281		16,281	
Carriage & Storage	829		829	
Management	<u>42,189</u>		<u>42,189</u>	
Total Publications	138,998		138,998	149,572
Scientific Meetings & Costs	11,430		11,430	11,481
Grants	<u>7,739</u>	<u>10,985</u>	<u>18,724</u>	<u>16,040</u>
Total Charitable Expenditure	158,167	10,985	169,152	177,093
Marketing & Publicity	5,069		5,069	4,826
Administrative Expenditure	46,352		46,352	<u>40,470</u> _n
Total	<u>209,588</u>	<u>10,985</u>	<u>220,573</u>	<u>222,389</u>
				<u>n</u>
NET INCOMING RESOURCES	30,745	-6,573	24,172	10,703
INVESTMENT GAINS				
Realised Gain	2,784			
Unrealised Gain	<u>40,735</u>			
	43,519	0	43,519	<u>17,911</u> _n
NET MOVEMENT IN FUNDS	74,264	-6,573	67,691	28,614
BROUGHT FORWARD	455,880	76,528	532,408	<u>503,793</u> _n
CARRIED FORWARD	<u>530,144</u>	<u>69,955</u>	<u>600,099</u>	<u>532,408</u>



Notes to the Financial Statements for the year ended 31st December 2005

1. Accounting Policies

The principal accounting policies adopted in the preparation of the financial statements are set out below and have remained unchanged from the previous year and also have been consistently applied within the same financial statements.

1.1 Basis of preparation of financial statements

The financial statements have been prepared in accordance with the revised Statement of Recommended Practice published in October 2000 and include the results of all the charity's operations, all of which are continuing.

The effect of events relating to the year ended 31st December 2005 which occurred before the date of approval of the statements by Council have been included to the extent required to show a true and fair representation of the state of affairs at 31st December 2005 and the results for the year ended on that date.

1.2 Fund Accounting

General funds are unrestricted funds which are available for use at the discretion of the Council in furtherance of the general objectives of the charity and which have not been designated for other purposes.

Designated funds comprise unrestricted funds that have been set aside by Council for particular purposes. The aim of each designated fund is as follows:

- *Sylvester-Bradley Fund*: Grants made to permit palaeontological research
 - *Jones Fenleigh Fund*: Grants to permit one or more students annually to attend the meeting of the Society of Vertebrate Palaeontology and Comparative Anatomy (SVPCA)
- Hodson Fund*: Awards made in recognition of the palaeontological achievements of a worker under the age of 35.

1.3 Incoming Resources

The charity's income principally comprises subscriptions from individuals and institutions which relate to the period under review and sales of scientific publications which are brought into account when due.

1.4 Resources Expended

All expenditure is accounted for on an accruals basis and has been classified under the appropriate headings.

Charitable expenditure is that which is incurred in furtherance of the charity's objectives. Administrative costs are those incurred in connection with the administration of the charity and compliance with constitutional and statutory requirements.

1.5 Investments

Investments are stated at market value at the balance sheet date. The statement of financial activities includes net gains and losses arising on revaluations and disposals throughout the year.



2. Analysis of Financial Resources Expended

	Staff Costs	Other Costs	Total 2005	Total 2004
Publications	28,117	110,881	138,998	149,572
Scientific Meetings & Costs		11,430	11,430	11,481
Grants		18,724	18,724	16,040
Marketing & Publicity		5,069	5,069	4,826
Administration	<u>28,117</u>	<u>18,235</u>	<u>46,352</u>	<u>40,470</u>
	<u>56,234</u>	<u>164,339</u>	<u>220,573</u>	<u>222,389</u>

3. Staff Costs

	Salary	National Insurance	Pension Contrib'ns	Total 2005	Total 2004
Publications – 1 employee (2004: 1)	22,440	2,251	3,426	28,117	25,981
Administration – 1 employee (2004: 1)	<u>22,440</u>	<u>2,251</u>	<u>3,426</u>	<u>28,117</u>	<u>25,981</u>
	<u>44,880</u>	<u>4,502</u>	<u>6,852</u>	<u>56,234</u>	<u>51,962</u>

4. Trustees Remuneration and Expenses

Members of Council neither received nor waived any emoluments during the year (2004: nil).

The total of travelling expenses reimbursed to 20 (20) Members of Council amounted to £4,416 (2004: £4,075)

5. Costs of Independent Examiner

	<u>2005</u>	<u>2004</u>
Examination of the accounts	350	300
Accountancy and payroll services	<u>1,050</u>	<u>1,000</u>
	<u>1,400</u>	<u>1,300</u>

6. Stocks

Stocks of *Field Guides* have been included at the lower of cost or net realisable value.

7. Debtors

	<u>2005</u>	<u>2004</u>
Accrued income – receivable within one year	48,460	18,031
Prepayment re 2006 conference	<u>500</u>	<u>500</u>
	<u>48,960</u>	<u>18,531</u>

8. Creditors – Falling Due within One Year

	<u>2005</u>	<u>2004</u>
Social Security Costs	1,545	4,314
Accrued Expenditure	<u>36,162</u>	<u>23,845</u>
	<u>37,707</u>	<u>28,159</u>



BALANCE SHEET AS AT 31st DECEMBER 2005

2004		2005
£		£
	INVESTMENTS	
279,148	At Market Valuation	452,554
	CURRENT ASSETS	
268,670	Cash at Banks	153,893
14,897	Field Guide Stocks at Valuation	12,692
<u>18,531</u>	Sundry Debtors	<u>48,960</u>
302,098	Total	215,545
	CURRENT LIABILITIES	
20,679	Subscriptions in Advance	30,293
<u>28,159</u>	Sundry Creditors	<u>37,707</u>
48,838	Total	68,000
<u>253,260</u>	NET CURRENT ASSETS	<u>147,545</u>
<u>532,408</u>	TOTAL	<u>600,099</u>
	Represented by:	
455,880	GENERAL FUNDS	530,144
	DESIGNATED FUNDS	
38,294	Sylvester Bradley Fund	30,475
19,111	Jones-Fenleigh Fund	20,618
<u>19,123</u>	Hodson Fund	<u>18,862</u>
<u>76,528</u>		<u>69,955</u>
<u>532,408</u>	TOTAL	<u>600,099</u>

These financial statements were approved by the Board of Trustees on 15th March 2006.

P. Crane

J.C.W. Cope

H.A. Armstrong



Independent Examiner's Report on the Accounts of The Palaeontological Association for the year ended 31st December 2005 as set out on attached pages

Respective responsibilities of trustees and examiner

The charity's trustees are responsible for the preparation of the accounts. The trustees consider that an audit is not required for this year under section 43(2) of the Charities Act 1993 (the Act) and that an independent examination is needed.

It is my responsibility to:

- examine the accounts (under section 43(3)(a) of the Act);
- follow the procedures laid down in the General Directions given by the Charity Commissioners (under section 43(7) of the Act); and
- state whether particular matters have come to my attention.

Basis of independent examiner's statement

My examination was carried out in accordance with the General Directions given by the Charity Commissioners. An examination includes a review of the accounting records kept by the charity and a comparison of the accounts presented with those records. It also includes consideration of any unusual items or disclosures in the accounts and seeking explanations from the trustees concerning such matters. The procedures undertaken do not provide all the evidence that would be required in an audit and consequently I do not express an audit opinion on the accounts.

Independent examiner's statement

In connection with my examination, no matter has come to my attention:

(1) which gives me reasonable cause to believe that in any material respect the requirements:

- to keep accounting records in accordance with section 41 of the Act and
- to prepare accounts which accord with the accounting records and comply with the accounting requirements of the Act

have not been met; or

(2) to which, in my opinion, attention should be drawn in order to enable a proper understanding of the accounts to be reached.

Dated: 6 March 2006

G R Powell F.C.A.

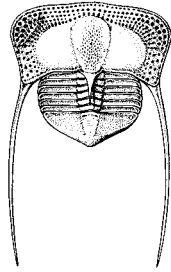
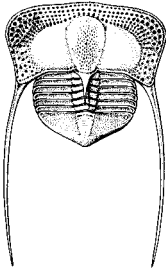
Nether House, Great Bowden, Market Harborough LE16 7HF



Nominal	Holding	Cost (bought pre 2005)	Value end 2004
£19,000	6 1/4% Treasury 2010	£17,580.14	£20,825.00
£4,700	Treasury 2.5% I/L Stock 2013	£10,145.15	£10,497.00
£13,000	Treasury 2.5% I/L Stock 2011	£32,947.71	£34,289.00
£18,029.71	COIF Charities Fixed Interest Fund	£25,000.00	£23,683.83
£46,146.75	COIF Charities Fixed Interest Fund		
2,800	Shell Transport & Trading Ord 25p shares	£4,671.00	£12,432.00
804	Royal Dutch Shell B shares		
825	BHP Billiton \$0.5 shares		
10,080	Legal and General Ordinary 25p shares	£4,213.00	£11,088.00
1,200	Electrocomponents Ordinary 10p shares	£2,817.00	£3,417.00
1,000	Lloyds TSB Ordinary 25p shares	£7,952.00	£4,730.00
925	HSBC Holdings Ordinary 0.5 US Dollar shares		
900	HBOS Ordinary 25p shares		
1,428	Unilever Ordinary 1.4p shares	£7,751.00	£7,304.00
2,400	Premier Foods Ordinary 1p shares		
1,055	Glaxo Smithkline Ordinary 25p shares	£16,608.00	£12,892.00
725	Smith & Nephew Ordinary £0.122 shares		
875	Cable and Wireless Ordinary 25p shares	£5,862.00	£1,041.00
780	BT Group Ordinary 5p shares	£4,787.00	£1,583.00
1370	BT Group Ordinary 5p shares		
780	MMO2 0.1p Ordinary shares	£162.00	£957.00
1750	Centrica Ordinary £0.0617 shares		
460	Pearson Ordinary 25p shares	£8,069.00	£2,891.00
1350	Prudential Ordinary 5P shares		
800	Resolution Ordinary 5P shares		
650	RIT Capital Partners Ordinary £1 shares		
750	JP Morgan Fleming Merc. IT Ordinary 25p shares		
1500	British Empire Sec & Gen Trust Ordinary 10p shares		
425	Findlay Park Partners US Smaller Companies		
4450	New Star European Growth Instl Acc Nav		
2300	Aberdeen Far Eastern Emerg Enons Trust		
3100	Capita Morant Wright Japan B Inc Nav		
1283.8	COIF Charities Investment Fund Acc Units		
5,720	M & G Charifund Units	£4,073.00	£64,526.00
1,775	SocGen Technology Units	£7,619.13	£1,887.00
1,450	Gartmore European Select Opps Fund	£8,006.31	£7,091.00
690	Baring European Growth Trust	£6,097.61	£3,679.00
5,000	Credit Suisse A UK Transatlantic Fund	£8,197.00	£6,043.00
15,000	Fleming Worldwide Zero Div Pref 25p shares	£9,914.95	£12,263.00
9,500	Inv Trust of Inv Trust Zero Div Pref shares	£9,936.46	£76.00
9,500	Europ Growth & Inc Trust Zero Div Pref 10p shares	£10,104.70	£2,019.00
42,500	M & G Equity Inv Trust Cap 1p shares	£9,579.73	£5,419.00
8,250	Martin Currie I & G Cap 25p shares	£9,861.82	£371.00
9,960	Utilico Inv Trust Ord 1P shares	£6,624.00	£13,172.00
7,003	Utilico Zero Div Pref shares 1.776 pounds	£2,634.00	£7,423.00
3,112	Utilico Inv Trust Wts	£386.00	£1,354.00
3,000	Edinburgh UK Small Co Trust 25p shares	£5,004.22	£6,195.00
Total		£246,603.93	£279,147.83
Total Investment Income			
Interest Receivable			
Total Investment Income & Interest			



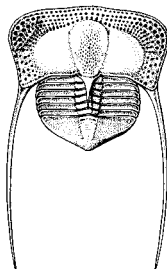
Proceeds (sold in 2005)	Cost (bought in 2005)	Gain realised during 2005	Value end 2005	Gain unrealised during 2005	Income in 2005
			£20,856.00	£31.00	£1,187.50
			£10,918.00	£421.00	£248.10
			£35,343.00	£1,054.00	£820.30
			£24,156.20	£472.37	£721.18
	£60,000.00		£61,827.42	£1,827.42	
£12,441.37		£9.37			£427.00
	£12,432.00		£14,938.00	£2,506.00	£253.51
	£5,969.54		£7,833.00	£1,863.46	£66.43
£11,078.43		-£9.57			£514.08
			£3,372.00	-£45.00	£220.80
£4,818.97		£88.97			£235.00
	£8,138.45		£8,630.00	£491.55	£72.98
	£7,913.49		£8,937.00	£1,023.51	£105.75
£7,992.54		£688.54			£183.07
	£8,136.48		£7,176.00	-£960.48	£114.00
			£15,498.00	£2,606.00	£443.10
	£4,011.14		£3,882.00	-£129.14	£15.23
£1,183.16		£142.16			£10.15
			£1,737.40	£154.40	£30.42
	£3,000.53		£3,051.60	£51.07	£139.75
£1,522.56		£565.56			£17.55
	£4,027.44		£4,458.00	£430.56	£54.25
			£3,163.00	£272.00	£118.22
	£7,063.25		£7,425.00	£361.75	£—
	£5,068.10		£5,184.00	£115.90	£—
	£4,903.90		£5,918.00	£1,014.10	£20.15
	£5,168.79		£6,735.00	£1,566.21	£63.76
	£5,005.61		£6,848.00	£1,842.39	£—
	£6,158.47		£7,301.00	£1,142.53	£—
	£6,079.59		£7,129.00	£1,049.41	£—
	£3,938.86	30.16	£5,058.00	£1,088.98	£37.00
	£5,170.11		£6,139.00	£968.89	£—
	£75,000.00		£86,015.88	£11,015.88	£—
			£73,025.00	£8,499.00	£3,107.46
£1,766.50		-£120.50			£—
£7,022.78		-£68.22			£—
£3,539.72		-£139.28			£—
£6,054.24		£11.24			£—
£12,156.22		-£106.78			£—
£47.50		-£28.50			£—
£2,054.92		£35.92			£—
£5,658.65		£239.65			£—
£214.16		-£156.84			£—
£14,115.01		£943.01			£—
£7,560.73		£137.73			£—
£1,642.63		£288.63			£—
£6,427.81		£232.81			£—
£107,297.90	£237,185.75	£2,784.06	£452,554.50	£40,734.76	£9,226.74
					£9,226.74
					£6,257.26
					£15,484.00



Palaeontology: **CALL FOR SHORT PAPERS!**

From January 2005 *Palaeontology* has been published in A4 size with a new layout. In line with this development, space is reserved for rapid publication of short papers on topical issues, exceptional new discoveries and major developments that have important implications for evolution, palaeoclimate, depositional environments and other matters of general interest to palaeontologists. Papers, which should not exceed six printed pages, should be submitted in the normal way, but they will be refereed rapidly and fast tracked, on acceptance, for publication in the next available issue.

Submission of longer review papers is also encouraged, and these too will be given priority for rapid publication. While *Palaeontology* maintains its reputation for scientific quality and presentation, these developments will ensure that the Impact Factor of the journal reflects its status as a leading publication in the field (rising to 1.19 in 2003).





SYNTHESYS

SYNTHESYS Project funding is available to provide scientists based in European Member and Associated States to undertake short visits to utilize the infrastructure at one of the 20 partner institutions for the purposes of their research. The 20 partner institutions are organised into 11 national Taxonomic Facilities (TAFs).

The 11 TAF institutions represent an unparalleled resource for taxonomic research offering:

- Collections amounting to over 337 million natural history specimens, including 3.3 million type specimens.
- Internationally renowned taxonomic and systematic skill base.
- Chemical analysis.
- Molecular and imaging facilities.

SYNTHESYS is able to meet the users' costs for research costs, international travel, local accommodation, and a *per diem* to contribute towards living costs.

Forthcoming deadlines: 15th September 2006
16th March 2007
14th September 2007
14th March 2008

For more information visit <<http://www.synthesys.info/>> or contact <synthesys@nhm.ac.uk>.



ASSOCIATION MEETINGS



50th Annual Meeting of the Association
Sheffield, UK 18 – 21 December 2006

The 50th Annual Meeting of the Palaeontological Association will be held at the University of Sheffield, under the auspices of the Department of Animal & Plant Sciences.

The meeting will begin on Monday 18th December with a special full-day symposium on “Macroevolution” (details below). This will be followed by an evening reception at the Sheffield Botanical Gardens. The technical sessions will consist of two days of talks on Tuesday 19th and Wednesday 20th December in the Auditorium located in the Students’ Union on the main campus, together with poster presentations situated adjacent to the lecture theatre. The talks and posters will be open to all aspects of palaeontology. The talks will be scheduled for 15 minutes inclusive of questions and there will not be parallel sessions. Depending on submissions for oral presentations, some talks may have to be re-scheduled as posters. On Thursday 21st December there will be a field excursion collecting Carboniferous plant fossils from a local opencast pit, and incorporating a visit to The National Coal Mining Museum for England, with a trip descending 140 m underground into Caphouse Colliery, one of Britain’s oldest working mines.

Venue and travel

Information about the University of Sheffield can be obtained at <http://www.sheffield.ac.uk/>. Sheffield is easily reached by road and rail links from London and all other major UK cities. The most convenient airport is Manchester, with a direct rail link to Sheffield (1 hour 15 minutes). Sheffield may be reached from London airports via underground plus overland rail links that take a minimum of 3 hours 30 minutes.

Accommodation

This will be at Tapton student hall of residence, which is situated 10–15 minutes walk (or a short bus ride) from the main University buildings. Details of how to get to the meeting venue on the main University campus and how to get to Tapton student hall of residence are available on the University website at <http://www.sheffield.ac.uk/travel/>. There will be a range of accommodation with different facilities and prices.

Registration and Booking

Registration and booking (including abstract submission) has commenced. Abstract submission will close on **Wednesday 13th September**. After this date abstracts will not be considered. Registration and booking after **Wednesday 13th September** will incur an additional administration cost of £15, with the final deadline on **Friday 24th November**. Bookings will be taken on a strictly first come, first served basis.

Registration, abstract submission, booking and payment (by credit card) is from online forms available on the Palaeontological Association website <http://www.palass.org/>.



Programme:

- Monday 18th December One day symposium on “Macroevolution” (details below).
Evening reception at Sheffield Botanic Gardens.
- Tuesday 19th December Scientific sessions followed by Annual Address (details below) at the Auditorium in the Students’ Union of the University of Sheffield.
Annual Dinner, the Cutlers’ Hall, Sheffield.
- Wednesday 20th December Scientific sessions at the Auditorium in the Students’ Union of the University of Sheffield.
Presentation of awards.
- Thursday 21st December Post-conference field excursion to an open cast coal pit and the National Coal Mining Museum.

Travel grants to help student members (doctoral and earlier) to attend the Sheffield meeting in order to present a talk or poster

The Palaeontology Association runs a programme of travel grants to assist student members presenting talks and posters at the Annual Meeting. For the Sheffield meeting, grants of up to £100 (or the Euro equivalent) will be available to student presenters who are travelling from outside the UK. The amount payable is dependent on the number of applicants. Payment of these awards is given as a disbursement at the meeting, not as an advance payment. Students interested in applying for a Palass travel grant should contact the Executive Officer, Dr Tim Palmer, by e-mail to <palass@palass.org> once the organisers have confirmed that their presentation is accepted, and before 8th December 2006.

Details of symposium

50th Palaeontological Association annual meeting
University of Sheffield
18th–21st December 2006

Special one-day seminar: Macroevolution (18th December 2006)

Macroevolutionary perspective

- Todd Grantham (College of Charleston, USA): *“How does philosophical work on mechanism and emergence bear on the relation between micro- and macro-evolution?”*

Species and Species Interactions

- Mark McPeck (Dartmouth College, USA): *“Phylogenetic patterns resulting from species interactions”*
- Richard Bambach (Harvard University, USA): *“Autecology, ecospace and change in the realized ecospace through the Phanerozoic”*



Tempo and Mode

- Kevin Peterson (Dartmouth College, USA): “*Tempo and the macroecological impact of early animal evolution*”
- Nic Butterfield (University of Cambridge, UK): “*Mode and the macroevolutionary history of metazoans*”

Diversity

- Brent Emerson (University of East Anglia, UK): “*Molecular phylogenetic approaches to understanding the origins and maintenance of community level species diversity*”
- Mike Benton (University of Bristol, UK): “*How did life get to be so diverse?*”

Disparity

- Mike Akam (University of Cambridge, UK): “*Is disparity just skin deep? A developmental perspective*”
- Doug Erwin (Smithsonian Museum of Natural History, USA): “*Why so many gaps? Morphologic disparity in the fossil record*”

Macroevolutionary Synthesis

- David Jablonski (University of Chicago, USA): “*Hierarchy and scale in macroevolution*”

Annual address

We are delighted to announce that this year’s annual address of the Palaeontological Association will be given by Professor Art Boucot, and will take place during the Association’s Annual Meeting on Tuesday 19th December at the University of Sheffield. Art, a member of the Palaeontological Association since its formation, will present an address on “What can be included in taxonomic descriptions?”; see next page.



What can be included in taxonomic descriptions?

A. J. Boucot

Department of Zoology, Oregon State University, Corvallis, OR 97331, USA

A case can be made for the expansion of the “routine” taxonomic description. A number of possibilities are readily available for many groups of organisms. Organisms, fossil and extant, are far more than their basic morphology, important as that may be. I am concerned here with the important possibilities inherent in documenting ontogenies in many groups where this has seldom been paid much attention for many higher taxa. Another potentially significant possibility is the documenting of behaviours. I’m thinking here of such things as larval substrate selection behaviour, preferring one substrate over another, as well as spacing in the sense of the spectrum from commonly solitary individuals to those that commonly aggregate together. Physiology is commonly thought to be beyond our grasp, but the relatively conservative substrate selection process is certainly a measure of certain physiological as well as behavioural properties. Evidence of disease, whether it be only teratological as contrasted with knowledge of the actual “cause,” can be extracted from the fossil record, particularly if samples are sufficiently large. Information about the diets of past organisms is in short supply. However, visceral region remains provide a fair source for well-preserved vertebrates. For most invertebrates dietary information is mostly absent. Community ecology, contrariwise, is a rich source of potentially useful taxonomic information. For the relatively stenotopic, uncommon to rare genera this is particularly true. The recognition and definition of community types is still in its infancy, despite its great taxonomic potential. Autecology of taxa with close modern relatives is fairly straight forward, but for organisms belonging to extinct higher taxa it is far more speculative, although sound functional morphological analysis is of assistance in some instances. Data on the relative abundances of taxa, high to low, is of great value, particularly since it commonly correlates with the stenotopy to eurytopy spectrum, as well as with the cosmopolitan to provincial spectrum. Counts of the numbers of taxa in each sample are then of great potential value although seldom published in the past. The definition of biogeographic units globally is still another valuable area where the differing degrees of provincialism can provide clues concerning stenotopy and eurytopy. One cannot overemphasize the importance of doing one’s best to obtain as large a sample as possible at each locality. Still another potentially valuable data source, particularly for some invertebrate groups, is careful study of shell structure down to at least the family level; its potential at the generic and specific levels is untested at this time. All of the above suggests that many more parameters may be included with profit in taxonomic descriptions.



LYELL MEETING 2007

**Early Palaeozoic peri-Gondwana terranes:
New insights from tectonics and biogeography**

21 February 2007

The Geological Society, Burlington House,
Piccadilly, London, W1J 0BG

Technical Convenor:

M.G.Bassett
National Museum of Wales

Late Cambrian
490 Ma



The meeting will form part of the 200th anniversary of the Geological Society and the 50th anniversary of the Palaeontological Association. Additional support from the National Museum of Wales will also recognise the 100th anniversary of the Museum.

In recent years there has been considerable emphasis in both palaeogeographical/palaeontectonic and palaeobiogeographical studies, with the emphasis on reconstructing ancient Palaeozoic continents. This meeting will focus specifically on the Cambrian to Silurian evolution of marginal terranes that form the periphery of Gondwana itself or that broke away from the main Gondwanan supercontinent at various intervals through the early Palaeozoic. Speakers are being invited from various parts of the world to present new insights into aspects of peri-Gondwanan terranes. An outstanding example of recent controversies now challenging what had become an accepted interpretation is the re-examination of the Argentinian Precordillera as a drifted segment from Laurentia.

Apart from examining the physical/tectonic composition of peri-Gonwanan terranes, there will then be regional analysis of Cambrian through Silurian biogeography, covering regions including Armorica/North Africa, Perunica, the Middle East, Kazakh terranes, Avalonia, Cetic oceanic terranes, Argentina/Bolivia and Australia/Antarctica. It is proposed that the proceedings of the meeting will be published as a Special Publication of the Geological Society of London and the programme will also represent a contribution towards IGCP Project No. 503 Ordovician Palaeogeography and Palaeoclimate.

For further details please contact Georgina Worrall, Conference Office, Geological Society, Burlington House, Piccadilly, London W1J 0BG. Email: georgina.worrall@geolsoc.org.uk or Tel: +44 (0)20 7434 9944

www.geolsoc.org.uk / www.palass.org



GEOBIOLOGY MSc



Cardiff University

School of Earth, Ocean and Planetary Sciences

Commencing September 2006

Cardiff University School of Earth, Ocean and Planetary Sciences is introducing a new one year taught MSc degree course in GEOBIOLOGY in September-October 2006.

Geobiology is a rapidly developing interdisciplinary and holistic approach to Earth and Life sciences. It explores the inter-relationships of life and environments on Earth and their significance for life elsewhere.

Cardiff is a friendly and vibrant capital city, and the School of Earth, Ocean and Planetary Sciences is a leading international centre for research and teaching. It has particular strengths in Geobiology and the course will emphasize – but not be limited to – Climate Change, Geomicrobiology, Palaeobiology and Palaeoceanography.

We welcome applications from graduate students with backgrounds in Earth, Environmental or BioSciences.

For further information please see our website: <<http://www.earth.cardiff.ac.uk/>>

And contact Emma Paris: <parisec1@cardiff.ac.uk>



From our Correspondents

On Cosmik Debris and Palaeontology

“Look here brother who you jiving with that cosmik debris?” Frank Zappa, *Apostrophe*, 1973.

Consider the following three pairs of statements.

1. “I don’t like to say bad things about palaeontologists, but they’re really not very good scientists. They’re more like stamp collectors” a Nobel laureate infamously remarked in an interview in the *New York Times* in 1988. In the same year at a meeting of the Society for the Study of Evolution a prominent biologist asked a younger colleague “How can someone who is able to solve integral equations, like you, waste his time on such non-sense as homology?” The first case elicited an international wave of indignation among palaeontologists, and before the year ended the perpetrator of this heinous statement was dead (no causal relation assumed here). In the second case, the biologist who posed the rude question lived on for another 26 years, and the question merely precipitated a bemused thought in the young biologist’s brain: “Needless to say, I took this as a compliment.” It is of course well known that Luis Alvarez uttered the first remark. In the second case, it was John Maynard Smith who asked Günther Wagner the impolite question (Wagner, 2006).
2. In 1990 Simon Conway Morris described a “bizarre metazoan” from the Carboniferous Bear Gulch Limestone of Central Montana (my own first publication was on stem group mantis shrimp from the same deposits) that he called *Typhloesus wellsii*. The name referred to its possession of a voluminous but blind gut with ample contents (from the Greek typhlo, for blind, and oesous, for glutton). This hallmark characteristic poses a serious challenge to the interpretation of the biology of *Typhloesus* because its general body shape and external anatomy suggest the animal was an active swimming predator or scavenger with a smooth streamlined body and a posterior fin presumably used for propulsion. Blind ending guts are typically restricted to either diploblasts, such as cnidarians, or sessile or low-activity bilaterians such as platyhelminths and articulate brachiopods. In speculating on the phylogenetic affinities of *Typhloesus*, Conway Morris (1990: 618) considered the “failure to identify any of the expected features such as a notochord, gills slits or myotomes” as ground for a “refutation that *Typhloesus* is a chordate.” In 1999 Geoffrey Fryer wrote a review of Conway Morris’ book *The crucible of creation*. In his review Fryer takes issue with several phylogenetic hypotheses of Cambrian metazoans reported in Conway Morris’ book. For example, Fryer deems the conclusion that *Anomalocaris* is “some kind of arthropod” to be severely compromised because “no indisputable arthropod has anything remotely like its circular jaw apparatus” (Fryer, 1999: 2).
3. In his important book *The evolution of developmental pathways*, Adam Wilkins concludes that new discoveries in molecular developmental biology necessitate “some changes in the ways in which we view, and use, the term ‘homology.’” The basic concept of shared possession of a trait through common descent remains intact, but the idea that the ‘same’



trait in two different organisms may actually exhibit more points of visible difference than of discernable identity seems counterintuitive, to put it mildly” (Wilkins, 2002: 167). In a paper published the next year, fellow newsletter correspondent Brian Hall devised a new classification for homological and homoplastic correspondences. Hall (2003: 409) concluded that “joint examination of nearness of relationship and degree of shared development reveals a continuum with an expanded category of homology, extending from homology → reversals → rudiments → vestiges → atavisms → parallelism, with convergence as the only class of homoplasy,” thus “seeing reversals, rudiments, vestiges, atavisms and parallelism as closer to homology than to homoplasy” (Hall, 2003: 426).

I expect that most readers will not immediately sense a uniting thread of logic that could bind these three pairs of statements into a coherent whole. Similarly, perhaps with the exception of the acrimonious statements by Alvarez and Maynard Smith, many readers may not identify anything obviously objectionable about the last two pairs of statements. In this essay I will show that all these statements are logically related to each other by continuing the metaphysical musings that I started in issue 60 of the newsletter. Specifically, I will present a brief ABC of the individuality thesis, which I believe is the logical foundation of the natural sciences and the conceptual key that is necessary for grasping the hidden bond between the above statements. Now, don't be alarmed. What follows is not particularly difficult, but it is without question one of the most fundamental topics you can think about. I guarantee that getting familiar with the individuality thesis could really change your perspective on science. Personally it helped me a lot. At the very least I hope this little exercise will provide some flesh on the bones of vaguely articulated intuitions that you might already have, and that it will spur you on to read more deeply into the literature. A proper grasp of the individuality thesis can provide you with the most broadly applicable intellectual tool you can wish for. For me it was a real eye-opener.

Before going into details, I want to try to pre-empt a response that certain readers inevitably have. This is *not* merely an issue of semantics! What comes is neither simply the juggling of words or an act of semantic sanitation, nor is it merely the pasting of imaginary labels on abstract mental constructs. Even though an armchair is really the only tool we need here, this essay deals with nothing less than reality at its most fundamental level. This is the sense in which metaphysics should be understood here. Michael Ghiselin (1997) goes so far as to include metaphysics within science, rather than considering it as the necessary context for science. It emphatically does not refer to new age wish-wash or other pseudoscientific pap. It is sometimes said that science is, or at least ought to be, metaphysics neutral. I vehemently disagree. Some people dismiss difficult or personally uncomfortable conceptual problems as ‘mere metaphysics.’ At best this is an attempt to neutralize deeply conceptual issues by exiling them from the realm of scientific responsibility to the no man's land of lawless speculation. At worst it is an act of intellectual cowardice. As we will see when we return to the statements posed above, turning a blind eye to metaphysics can only lead to confusion. Metaphysical commitments set the inescapable boundaries within which all scientific work attains its meaning, and it is irrelevant whether the commitment is conscious or not. By explicitly addressing metaphysics one can at least ensure that the elements of one's work exhibit logical coherence, as well as external consistency with the evidence and ideas of one's discipline outside of one's own personal research programme.



Most fundamentally and least controversially, scientific materialism is the metaphysical commitment that underpins all natural sciences. As discussed in the previous essay, it was his radical materialism that worried Charles Darwin greatly because it broke so sharply with tradition. In Ghiselin's (2005: 127) words "much as Copernicus had moved the sun to the center of the physical world, Darwin moved concrete particular things to the center of the metaphysical world." Materialism, or naturalism as it is also sometimes called, comes in two basic flavours. Methodological materialism (or naturalism) is a commitment to viewing the world as being governed by natural causes, and the scientific approach to obtaining knowledge can only address the materialist aspects of the world. It does not deny that the supernatural may exist, only that science is impotent in informing us about it. Metaphysical materialists (or naturalists) on the other hand commit to the view that the world is basically as we 'see' it. According to this perspective science is the only way to obtain knowledge about the world, with no place for the supernatural. Not surprisingly metaphysical materialists are typically atheists. Religious fundamentalists, including proponents of intelligent design, deny the validity of both methodological and metaphysical materialism (see Ruse, 2005a for an example). If you do not accept at least methodological materialism I respectfully say goodbye to you at this point. Our views of the world are so different that I cannot presume to be able to understand you, and *vice versa*. For the remaining readers, here is a very succinct summary of the core of individualism.

I consider the individuality thesis (IT hereafter) to be a logical corollary of materialism, which confers a particular shape or flavour upon it. This is what it tastes like. (The following is heavily indebted to the work of Michael Ghiselin, in particular his book *Metaphysics and the origin of species*. This is simply the most insightful book written by a biologist that I have read in many years, and its message is absolutely indispensable for any self-respecting biologist and palaeontologist).

The distinction between classes and individuals is the most fundamental ontological dichotomy within IT. Anything you can think of is either a class or an individual. The following distinctions are important:

1. Individuals are concrete and spatio-temporally restricted. Classes (including natural kinds) are abstract concepts outside of time and space.
2. Individuals, by virtue of being concrete, can partake in natural processes, while classes cannot.
3. The ontology of individuals is the part/whole relation, wherein high-level individuals are composed of low-level parts. Consequently, ontologically, the whole body of a multicellular organism *versus* its comprising parts (*e.g.* organs, cells) exhibit the same part/whole relation as a high-level monophyletic taxon *versus* its subclades or species. In contrast, the ontology of classes is the membership relation. As a result, and in contrast to individuals, classes can have members, examples, and instances.
4. Individuals do not have defining properties. They can undergo an indefinite amount of change, and still remain the same individual. A class has defining properties and can therefore not change indefinitely without becoming a different class.
5. Natural laws don't refer to any particular individuals. Laws can only be formulated for classes, of which individuals may be members.



These five stipulations leave no doubt: species and other monophyletic taxa are individuals. So are organisms, and the parts or characters that they are composed of. For me this understanding provided a hugely efficient broom that could sweep up the conceptual debris that had accumulated in the corners of my mind.

Before we take a look at how the logical implications of IT can help clean up the conceptual debris that contaminates the three pairs of statements posed at the beginning of this essay, you may find yourself still in doubt about IT. This would not be too surprising. Although the concepts of IT are not particularly difficult, they do deal with ultimate reality or at least with the ultimate insights about the world that science at its best can provide. Consequently it may take some time before you convince yourself about the compelling logic of IT. Please delve into the literature. Use the work of Michael Ghiselin and David Hull as starting points, and try to include some of the recent writings of Olivier Rieppel for a contrasting view. The issue is too important not to deal with explicitly at least once in your professional career. Yet, such an exercise may still not convince you. Although I think that the majority of biologists and palaeontologists accept IT, either implicitly or explicitly, there is no absolute consensus. Philosopher Michael Ruse, for example, labelled IT as “a good idea...that just did not work” (Ruse, 1998: 286). In the 1980s Ruse told Ernst Mayr in a discussion group at Harvard that he thought that the idea that species are individuals was nonsense. This triggered Mayr to cross the room towards Ruse, waving his finger, and yelling (Ruse, 2005b). After all, Ruse is a philosopher, not a biologist, so what does he know about species, right?

In my initial excitement about IT, I wrote a paper on the logical implications of embracing IT for current thinking in the field of evolutionary developmental biology or evo-devo (Jenner, 2006). The summarizing statement of one of the reviewer's reports gave me a taste of my own medicine (I recently found out that several of my colleagues have awarded me the dubious honour of making my name a verb. To 'Jennerize' has apparently come to mean to 'severely criticize'...): “this is a hopelessly lost treatment of an old problem, that does not appear to contribute anything useful to evo-devo thinking.” Luckily the other reviewer and the editors did not agree. See for yourself what IT can do for you.

Specifically, IT brings into plain view previously hidden traces of typological thinking that remain surprisingly prevalent in the literature. A hallmark of typological thinking is to consider taxa as classes rather than individuals, but surely modern biologists are not typologists? In the annual address of the Systematics Association in 2001 Norman Platnick said the following: “Now one thing I've learned from 30 years of watching biologists is that whenever you find one systematist calling another one an essentialist or a typologist, you can be 100% sure that the name-caller is purely, simply, and entirely, wrong, and is just creating a smokescreen to cover his or her tracks.” Two remarks are necessary here. First, Platnick is wrong. As I will show below and document in Jenner (2006), typological thinking is still prevalent, but its manifestations are more hidden than what you might expect from a cardboard 19th century pre-Darwinian. Which leads to the second remark: Platnick is right, but perhaps not in the way he intended. In his insightful book *The changing role of the embryo in evolutionary thought* Ron Amundson takes a critical look at the traditional historiography of evolutionary biology. He makes the critical observation that the widespread idea that many pre-Darwinian typologists were religiously deluded idealists, is based on the uncritical acceptance of what he calls Synthesis Historiography, of which Ernst Mayr was a major architect. What is wrong with this interpretation of history is that no distinction was made



between metaphysical typologists, who really interpreted real species as mere manifestations of eternal non-material types, and those who invoked typology more as a methodological precept, akin to methodological materialism among materialists as discussed above. Amundson's revised interpretation reveals that history is riddled with far fewer boneheaded metaphysical typologists than previously thought. Surely Platnick is right that today people so inclined are virtually non-existent among serious scientists. Yet, a typological undercurrent can still be diagnosed in the current literature, as we will see now when we turn to the three pairs of statements with which I began this essay.

The problems with the three pairs of statements become clear when we realise what implications the recognition of individuals can have for conclusions at different levels of generality. Pairs two and three are intuitively the easiest to grasp, and they can be united by the following aphorism: differences don't matter. IT stipulates that individuals can change indefinitely without compromising the identity of the individual. This may be counterintuitive, as the vernacular understanding of individuals hinges on their uniqueness. For example, Gould (2002: 602) wrote that "an individual may undergo some, even substantial, change during its lifetime, but not so much either to become unrecognisable or to encourage redefinition as a different thing." This is particularly ironic because throughout his career Gould explicitly endorsed IT for it constitutes the conceptual foundation for punctuated equilibrium. Yet, spatio-temporal continuity is all that an individual needs to stay the same individual, and nothing else. No change in the intrinsic characters or parts of an individual can negate individuality. Charles Darwin said as much for taxa as individuals without having explicitly worked out IT: "Let two forms have not a single character in common, yet if these extreme forms are connected together by a chain of intermediate groups, we may at once infer their community of descent" (Darwin 1859: 409). This reveals the error in thinking by Conway Morris and Fryers in the second pair of statements. The fact that *Typhloesus* seemingly does not possess "expected features" of chordates is no "refutation that *Typhloesus* is a chordate." Differences are impotent with respect to phylogenetic conclusions. Without going into character study, *Typhloesus* could in principle well be a chordate, which has lost many plesiomorphies. Differences are agnostic with respect to phylogenetic relatedness because evolution is "descent with modification" and no amount of modification can therefore erase common descent. Moreover, all that monophyletic taxa that are part of a higher-level individual (more encompassing clade) need to share is common ancestry. Just because a given taxon is related to another does not allow us to expect that they share particular traits. That is merely a matter of historical contingency, dependent on whether change has in fact occurred or not. Similarly, Fryer's conclusion that the possession of a distinctive autapomorphic circular jaw apparatus in *Anomalocaris* negates arthropodan affinities is flawed. These conclusions would only make sense if taxa are classes with particular definitions, by virtue of which one can extrapolate across members of the class based on the traits stipulated by the definition. In that case if a member does not possess a certain character required by the class' definition, such as a notochord or appendages as mouthparts, that member no longer fulfils the necessary membership criteria of the class and therefore is excluded from it. Applying such thinking to taxa is perniciously typological. The resolution provided by IT shows that no matter how much a part of an individual may change, in this case a species as part of a larger clade, this does not falsify it as a part of the higher-level whole. In other words, no degree of modification can negate a conclusion of common descent.



The same reasoning shows the problems with the third pair of statements. Homology is nothing more than a correspondence relation between homologues, based on shared common ancestry. Consequently, even if homologues change through time, no matter how much, they do not become less homologous. Fundamentally, it is a metaphysical impossibility for intrinsic properties (similarity) to influence decisions about relational properties (homology). The extraordinarily modified middle ear bones of extant mammals are not less homologous to the jawbones of their non-mammalian ancestors than those of the earliest mammals. Character similarity is merely a tool to help diagnose possible homologues, nothing more. The fact that Wilkins (2002) feels this is “counterintuitive, to put it mildly” shows that our intuition is a tool much too blunt to cut through conceptual Gordian knots. It scarcely provides a robust rationale for accepting partial homology, as advocated by Wilkins. A similar problem is inherent in the thinking of several other evo-devologists, including Brian Hall (2003), who attempt to mingle the mere diagnostic criterion of similarity of possible homologues with their proper definition as being simply a result of common descent. For the definition of homology an uninterrupted continuum of shared history is all that counts. I do appreciate the motivation for Hall’s attempted new classification of homology and homoplasy. He wants to express the important fact that even in cases of phenotypic homoplasy, conserved developmental mechanisms may be implicated. However, by arguing that reversals and atavism are “closer to homology than to homoplasy” Hall is likely to sow more confusion than enlightenment. Homology is an either/or issue. Homology does not come in shades or degrees. If corresponding parts and wholes are properly recognized, homology is either fact or fiction. Evolutionary retention of developmental mechanisms that later become active in the development of an atavism, for example, simply indicate non-homology of the phenotypic product with previous plesiomorphies and homology of continuously retained developmental mechanisms (see Jenner, 2006 for additional discussion).

The first pair of statements addresses the old issue of the status ranking of scientific disciplines. Even at this very general level IT can illuminate the problem. The snide remarks by Alvarez and Maynard Smith are unsurprising given a long history of classifying the sciences based on perceived worth along some scale of vague description. Without exception physics is placed triumphantly at the top of academic prestige, while the humanities, historical, and social sciences are frequently not even labelled as ‘science.’ I believe such conclusions at the same time represent the acme of academic arrogance, and a blatant display of metaphysical ignorance. A non-arbitrary classification of science distinguishes between the nomothetic, or law propounding, disciplines, and the idiographic disciplines that describe and explain contingent events. IT teaches us that laws of nature do not apply to particular individuals, and can only be formulated for classes, of which individuals may be members. Consequently, the nomothetic sciences are never concerned with investigating the properties or history of just single individuals, but always have a broader focus on a class that contains at least several individuals. Moreover, the nomothetic sciences are not concerned with the vicissitudes of contingent events, but with the predictable outcomes of natural laws. This means that any science that concerns itself with single individuals is idiographic, and therefore resides squarely in the domain of historical contingency. Such disciplines naturally lack in predictive ability, which is typically associated with the operation of natural laws that produce predictable regularities. It is important to note that the arrow of arrogance in the sciences unfailingly soars straight from the nomothetic arena to impale innocent idiographers. This is sad and ironic, because a full understanding of



the natural world is absolutely dependent upon the integrated efforts of both nomothetic and idiographic disciplines, and nomothetic sciences are incapacitated without idiographic data. Without a richly documented fossil record Luis Alvarez would never have been able to make his important contribution to our understanding of mass extinctions. And without the central role that homology has played in establishing the fact of evolution, and in providing the cornerstone of comparative biology, an aircraft engineer named John Maynard Smith would perhaps have never escaped his hangar.

Yet I think that the nomothetic sciences will always be considered as somehow superior to the idiographic. The prestige of precise predictions, the ideal of quantification, and the appeal of smooth extrapolation have a very strong attraction. Even such a staunch campaigner for disciplines with a strong idiographic tradition, including natural history and palaeontology, such as the late Stephen Jay Gould, could not entirely escape the beguiling glare of nomothetics. From his early days as a professor at Harvard, and most vociferously in the 1970s and 1980s, Gould laboured mightily at the cradle of palaeobiology (Sepkoski, 2005). Gould explicitly envisioned palaeobiology to be the nomothetic brethren to traditional idiographical palaeontology, and *Paleobiology* was to become the primary outlet for nomothetic approaches to the history of life. Nevertheless, I think that the message that Gould himself impressed most firmly in the minds of both lay and professional readers is that contingency rules the history of life. In contrast, it was Simon Conway Morris who effectively took advantage of the nomothetic realm in his last two books to present a view of the history of life that stands in almost complete opposition to Gould's view of life. Especially in *Life's solution*, Conway Morris catalogues an impressive array of examples of convergent and parallel evolution. Considering certain expected, perhaps universal boundary conditions, a broad predictability may characterise the history of life on Earth and possibly elsewhere. To be sure, the predictions will be very broad, but given the rules of competition for limited resources (economics in a very broad sense), and the physical rules that govern gas exchange and locomotion, for example, one may be led to expect certain characteristics. Similarly, closely related and similar organisms may repeatedly evolve the same adaptations or analogues based on constraints in their construction and faced with similar environmental challenges. Ultimately, we need both idiographics and nomothetics, individuals and classes, chance and necessity, contingency and law.

Before we conclude I want to return briefly to the question that I posed at the end of the previous essay. I agree with Ghiselin that IT is the proper conceptual basis of modern evolutionary biology. I think that accepting a Darwinian view of life logically engenders it, and that it is the core of the Darwinian revolution in thinking. Yet, the revolution has not yet been completed. Why could that be? I suspect the answer is not very ennobling. I believe that the individuality thesis, which was brought to general attention with Ghiselin's 1974 paper titled "A radical solution to the species problem," has simply suffered from scotoma born out of apathy. Less than two years ago I was not at all interested in metaphysics. This lack of interest was a simple result of ignorance. Even during my PhD training as a systematic biologist I cannot remember any serious attention being paid to IT. Maybe this is a result of the fact that in the Netherlands we don't have to take many courses, but the ones I have taken remained silent on this fundamental topic. I think that for many people IT simply doesn't pop up on their radar. Depending on your discipline, you may not have much daily use for it. If you are engaged in experimental work in



developmental biology, you may never have seriously to consider IT to be able to be successful. It is a very different matter in comparative and evolutionary disciplines. The extent to which one can extrapolate findings from one taxon to another, the value of similarities and differences for phylogenetics, and the relation of nomothetic and idiographic aspects in evolutionary biology, are all informed by IT. Ignore it at your peril.

Metaphysics is not a semantic sanitizer. Instead it is a most potent conceptual caustic soda that is able to dissolve through the most caked conceptual debris we may find before us. A substantial amount of this residue we find scattered in the literature is the conceptual contamination deposited by many decades of uncritical and outdated typological thinking. IT is a conceptual fractal that can shed equally illuminating light on thinking in evo-devo, palaeontology, and evolutionary biology. I leave it to you to diagnose and disinfect the remaining conceptual debris you may find on your way. Trust me, there is enough for everyone...

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REFERENCES

- AMUNDSON, R. 2005. *The changing role of the embryo in evolutionary thought*. Cambridge University Press, Cambridge.
- CONWAY MORRIS, S. 1990. *Typhloesus wellsi* (Melton and Scott, 1973), a bizarre metazoan from the Carboniferous of Montana, U.S.A. *Phil. Trans. R. Soc. Lond.* **B 327**: 595–624.
- CONWAY MORRIS, S. 2003. *Life's solution. Inevitable humans in a lonely universe*. Cambridge University Press, Cambridge.
- FRYER, G. 1999. Cambrian animals: evolutionary curiosities or the crucible of creation? *Hydrobiologia* **403**: 1–11.
- HALL, B. K. 2003. Descent with modification: the unity underlying homology and homoplasy as seen through an analysis of development and evolution. *Biol. Rev.* **78**: 409–433.
- GHISELIN, M. T. 1974. A radical solution to the species problem. *Syst. Zool.* **23**: 536–544.
- GHISELIN, M. T. 1997. *Metaphysics and the origin of species*. State University of New York Press, New York.
- GOULD, S. J. 2002. *The structure of evolutionary theory*. The Belknap Press of Harvard University Press, Cambridge.
- JENNER, R. A. 2006. Unburdening evo-devo: ancestral attractions, model organisms, and basal baloney. *Devel. Genes Evol.* (published online).
- RUSE, M. 1998. All my love is towards individuals. *Evolution* **52**: 283–288.
- RUSE, M. 2005a. Methodological naturalism under attack. *S. Afr. J. Philos.* **24**: 44–60.
- RUSE, M. 2005b. Ernst Mayr 1904–2005. *Biol. Philos.* **20**: 623–631.
- SEPKOSKI, D. 2005. Stephen Jay Gould, Jack Sepkoski, and the 'quantitative revolution' in American paleobiology. *J. Hist. Biol.* **38**: 209–237.
- WAGNER, G. P. 2006. How wide and how deep is the divide between population genetics and developmental evolution? *Biol. Philos.* (published online).
- WILKINS, A. S. 2002. *The evolution of developmental pathways*. Sinauer, Sunderland.



The curse of plenty

It's hard to recall, now, exactly which piece of music I first owned. In extreme youth, I laid claim to moral ownership of a few of the ragbag of odd 78s and 45s that formed part of the family treasure. The favourite was the theme tune to *The Legion's Last Patrol*, a B film of such profound anonymity that it underwent obtrusion¹ in Goldwyn's cellar or Mayer's attic, never to emerge into the weakly oxygenated bottom waters of late-night TV. The lead trumpet was undoubtedly a session musician playing stock banalities to pay the rent, but to my sub-teen sensibilities the music was stirring, heroic, elegiac. I played it over and over again. Mussorgsky's *Night on the Bare Mountain* (almost certainly the Stokowski version used by Walt Disney), too, was played pretty well to destruction; I can hear the tune in my head now as I write, resonating from almost half a century back.

Now this is thin stuff, artistically, and doesn't compare to the reminiscences of those urbane jazz sages of a certain age, as they recall awaiting, in their youth, the latest three-minute explosions of music from a still-youthful Armstrong or a sleek Ellington. Small rations of genius miraculously preserved on a fragile black disc, shipped from far transatlantic shores, listened to until the notes were burnt into memory. Then the notes haltingly, painfully, repeated, note for note, on a battered trumpet or borrowed saxophone, until those exotic musical memes from New Orleans have been implanted into the likes of (say) downtown Huddersfield.

Into my student years, recorded music became commonplace. Long-playing records could hold many songs, or an entire symphony. Costly, mind, on a student budget, when artistic needs had to be balanced against those of beer and other bare necessities, but nevertheless a modest and not entirely infrequent luxury. Then, with middle age and careworn employ, that brief, brutal putsch as laser technology ousted vinyl. As we approach the close of this reign, entry to the musical cosmos can be had for almost nothing. The local supermarket or remainder bookshop will, for a pound or two, provide triple CDs of Schubert or Sinatra or, if you are favoured by the random currents of fortune, Showaddywaddy. Even that is passé, now. Plugging into the information superhighway, you can download a thousand tunes on to a matchbox-sized iPod (that will seem absurdly bulky a year or two hence), to mix and match melodies at will.

One could, at this point, make deeply meaningful analogies with the course of Darwinian evolution in the natural world, of whatever shade of tooth and claw, or with the shifting of zoogeographic provinces in a rapidly changing climate. But my immediate reaction to this accelerating transmigration is visceral rather than analytical. The embarrassment of riches has become a tsunami and, rather than simply revelling in limitless cultural possibilities, one feels a little overwhelmed by it all. When every kind of music is instantly available, what does one choose, what can one settle on, focus on?

The contemporary superabundance of riches isn't confined to music. There's a little of the same feeling confronted with the row upon row of palaeontological volumes produced by the august organization producing this newsletter and by many others, in any academic library, or the

¹ Almost instantaneous deep burial, as in that moment in the career of any palaeontologist when they disappear beneath the mass of their own half-finished manuscripts.



thousands of articles thrown up by a Google search. There's just so much information, so much accumulated description. And in palaeontology, of course, this information doesn't become obsolete. That is unlike the case of, say, that groundbreaking geochemical paper that can quietly be forgotten when, after a decade or so, it is entirely outdated by data from the latest glitzy atom-counting machine. The most humble description of the most humdrum fossil in the least prestigious of local journals will, in synonymy lists, join the creations of Linnaeus and d'Orbigny and Barrande and keep on turning up for ever. In the science of dead things, the descriptions themselves will – to compensate for mere physical mortality – stay emphatically undead.

In this growing mass of accumulated knowledge there are, of course – to use that contemporary icon of forced optimism – opportunities. Of those more anon, perhaps. But I'm increasingly drawn to those early days of the science, when the subject was young and uncluttered, just as I have a weakness for the early days of recorded music when listening to the disembodied voices of Caruso or Ponselle, conjured up by a steel needle from a revolving disc, must have seemed miraculous.

I caught a minuscule glimpse into the early days of the earth sciences a month or two back, via the standard operation of chance and serendipity and those notorious temporal trouser-legs. In the corner of the entrance hall to the museum at Wrocław's Institute of Geological Sciences there is a bust of a middle-aged man with a determined cast to his eye. The label said this is the likeness of one Carl Ferdinand Roemer, director of that museum (in what was then Breslau) between 1855 and 1891.

The name rang a bell, and detonated the tiniest amount of inquisitiveness in my head, just enough to prevent the natural course of events from bringing on that tiny, blessed increment of amnesia that smoothes most random thought from the memory. That idle question, with all the unstoppable momentum of that notoriously overworked butterfly wing at loose somewhere in China, provoked the necessary minimum of activity that leads one to enquire: who he?

For lodged well back in those increasingly chaotic memory banks is a picture of graptolite of robust, almost Schwarzeneggerian (relatively speaking, of course) demeanour from the interminable Ludlow turbidites of east-central Wales. This graptolite bears the name *Saetograptus roemeri*. Was this the same Roemer, and, if so, just what was he doing attached to a Gallic hemichordate?

My hosts at Wrocław, better-read than I, provided material on this (Voelkel, 2002; Grodzicki, 2003). Roemer, it transpires, was by general agreement the most energetic and able geologist and palaeontologist ever to have settled in Wrocław, with a formidable reputation as a teacher, researcher and administrator. It wasn't a role that he was destined for. He had been meant to go into the family business of lawyering. But some unspecified political difficulties and a weakness for natural history saw him slide sideways into studying the infant science of geology in Berlin.

He seems to have been an adventurous soul. He travelled widely, including a year in north America in his youth to become, rather improbably, the 'father of Texan geology'. The biography sketched out the main events of his life, though without providing much enlightenment as regards his character, except that sheer bloody-minded determination must have figured largely. But it was the list appended to this story that really struck me.



Now, lists are not usually thought of as riveting reading. An occasional challenge, perhaps, as Rossini demonstrated in his boast of being able to set a laundry list to music (though for him that was shooting fish in a barrel: a good laundry list can contain better-rounded characters than many the libretto to a baroque opera). One of the funniest books I have ever encountered was essentially a list: the first edition of the Greater Slovene-English dictionary, a list of words assembled with a delicate creativity with the English language that would have had Groucho Marx raise his hat as to a master (the second and completely revised edition, alas, has impeccably correct translations throughout²).

The list here, though, was that of Roemer's publication, arranged by date. It's remarkable stuff. The first reference is his doctoral thesis, published in 1842. It's titled *De Astartarum genere et speciebus quae et saxis iurassicis et cretaceis proveniunt*. Scholarship then being proper scholarship, it was written entirely in Latin, a barrier to scientific communication perhaps roughly on a par with those currently embodied within modern computer drawing programs³.

After that, thankfully, he abandoned classical discourse, and became increasingly prolific. He helped Heinrich Bronn, for instance, compile the third edition of the *Lethaea Geognostica*, an ambitious attempt to show all fossils then known in stratigraphical order.

The publications of the year 1855, the year he came to Wroclaw, give an idea of Roemer's range. Twelve published papers, not far off the average of his half-century career. There is taxonomy, ranging over two kingdoms and four phyla: echinoids, vertebrates both limbed and limbless, cephalopods, plants. There is an article on anthracite, and one on an iron meteorite from the Atacama desert. There is stratigraphy, Cretaceous and Devonian, and biography (of Angelin). There is – anticipating H.G. Wells – a paper on the egg and metatarsal of the fabled *Aepyornis*. It's as much fantasy science as the stuff of solid description. Here be dragons, indeed, their claws and teeth carefully measured and their scales counted.

But where from the Barrande connection? For there were no graptolites obviously described by Roemer in those early years, nor any obvious reference to them in the list of his publications until 1865, and even then it is quite obvious that these fossils formed only the tiniest part of Roemer's output (a character flaw if ever I saw one). Barrande had described *roemeri* way back in 1850, based on Bohemian material; his description of that species is simply that: a description; he makes no comment on the derivation of the name. So why Roemer?

The plot thickens a little on considering Ethel Wood's history of nineteenth-century graptolite research in the redoubtable 'Monograph of British Graptolites' – a century on and still the entirely indispensable 'Elles & Wood' (no further qualifier needed, for graptolite workers). A few pages after a glowing encomium to Barrande's work ('epoch-making', 'brilliant' and so on), she notes, rather sniffily, some descriptions by the 'German palaeontologist Roemer' of material from the Harz Mountains. This includes four new species, including the magnificently-monikered *Monograpsus oblique-truncatus*, all of which instantly sank without trace, because the drawings were 'so poor that it is impossible to identify the species'.

² The original was introduced to me by its reviser, the late, irreplaceable and irrepressible Dr Harry Leeming, of the School of Slavonic and East European Languages in London. More than any other single person, he influenced my understanding of what scholarship is, or should be.

³ Cladistics doesn't enter my mind at this point at all, honest.



Miss Wood was being a bit harsh. The drawings are certainly of their age, but not much worse than, say, the cave art graptolite simulacra of Rudolf Ruedemann a century later. The paper itself, though, did not appear to be on the Roemer publication list. I tracked it down. It is by one 'Fr. Ad. Roemer', from Clausthal. Thus, not our Carl Ferdinand. The culprit was Friedrich Adolph, an older brother, head of the Mining Academy in Clausthal, and obviously another spare-time palaeontologist. (As was, in fact, the middle brother Hermann, who didn't manage to escape the family legal traditions, but nevertheless amassed a large geological collection and co-founded the Roemer-Museum in Hildesheim.)

So, Barrande might have had more than one Roemer on his mind when he named his species. My money, though, is still on Carl Ferdinand, for the ascent of his reputation in his youth seems to have been meteoric⁴. After all, he had been urged into his explorations in north America by no lesser figures than Leopold von Buch, who in the opinion of Louis Agassiz was the greatest geologist of his age, and Alexander von Humboldt, whose name would surely go into the hat in any competition to choose the greatest scientist of all time.

Some of the parallels of Roemer with Humboldt are striking. Both were explorer-scientists, travelling literally into the perilous unknown, and both published prolifically across a range of disciplines. If Roemer's was remarkable, Humboldt's was breathtaking, as geographer, meteorologist, zoologist, geologist and stratigrapher. The year of his birth, 1769, he shared with both Napoleon and Wellington (and with Cuvier, too), in an age when the national governments were based upon the divine right of kingly possession. In the upheavals during his lifetime that changed the world's political landscape, he was a committed republican and wrote trenchantly against slavery⁶.

If one is to believe Agassiz, Humboldt virtually invented biogeography, and, as minor footnotes in his career, drew the world's first geological cross-section in Mexico in 1804, anticipating William Smith's justly renowned Snowdon-to-London cross-section by thirteen years⁷; introduced that 'happy expression' of 'geological horizon', and first recognised the Jurassic (sic) 'formation'.

Curiously, although Agassiz drops many illustrious names in his account of Humboldt's life, there is no mention of Darwin, even though it was written in 1869, a decade after the *Origin of Species* had appeared and ignited the varied disputatiousness that goes on to this day. But phylogeny does appear via Goethe, who had 'declared the unity of structure in the bony frame of all Vertebrates'. This had provoked a cause célèbre of its day, with some arguing passionately for this idea – notably Geoffroy St. Hilaire – and some against. The opposing camp included, bizarrely, Cuvier, by then near the end of his life. Cuvier, in a succession of public lectures, weighed in vigorously against St. Hilaire's 'brilliant generalizations'.

⁴ A fine adjective in the grand tradition of the English language, being wonderfully ambiguous in its own literal terms. For meteors can travel upwards, sideways or downwards⁵, or can come crashing down to earth. Or the word might just mean very wet. In the case of Roemer, though, normal connotations apply.

⁵ I am quite aware that there is no up or down in space. But in matters of idiomatic meaning one is surely free to specify one's vectors.

⁶ 'While we maintain the unity of the human race, we at the same time repel the depressing assumption of superior and inferior races of men'. That and more in that vein in Humboldt (1848, pp. 368–9).

⁷ Disputable, this. John Strachey could well have the honours here (Fuller, 1992), working, as chance would have it, in Smith's future back yard.



This was special pleading, albeit based on the technical objections that can be drawn from a lifetime's anatomical study, and Humboldt, sitting in the audience with Agassiz, recognised this. In whispered asides, he made clear his view that whatever problems there might be with the idea that vertebrates are united, this idea clearly must be true, and Cuvier should recognise this and support it instead of being the standard-bearer for the opposition.

Humboldt supported and promoted many young scientists, just as he supported Agassiz in the latter's impecunious early years. Roemer, in the year of his Texan adventure, must have been one of quite a number so encouraged, for Humboldt was then in his late seventies, renowned, laden with honours and – for all his republican leanings – attached to the court of the King of Prussia.

Today, attempting a Humboldtian or even Roemerian range isn't possible. With a million or so published fossil species, the most obvious way to cope is to focus, and most palaeontologists stick to one fossil group, as the most sensible way to cope with the ever-growing pile of literature. What to do with this ever-growing heap, the sheer abundance of information, in which one can lose oneself quite as effectively as one can drown in the myriad musical possibilities of the iPod and its like?

Within it, we have a pretty fair census of the common, easily fossilizable organisms of the Phanerozoic, and a smattering of the uncommon ones. The boundless, unexplored taxonomic jungles that Roemer and his colleagues so delighted in are no more. But there is another horizon that still seems to be on the horizon, as it were. That is, the interaction between that long-departed biota and the world around it.

Now, yes, of course, fossils do make wonderful climate and environmental proxies, to be sure. There's palaeosalinity from bivalves and gastropods, and, after a fashion, water depth from trace fossils, and a host more such examples in the textbooks. But there's a world of difference between drawing more or less obvious conclusions from any given fossil assemblage, and getting answers to the questions that one would like to ask.

It seems to me now that there is no larger question scientific today than just how the Earth has managed to regulate its climate and environment to render it consistently habitable for life for in excess of three billion years. And, as a corollary of considerable personal importance to us all, of *precisely* how, when the system is perturbed, it reacts before some sort of equilibrium is restored, a few million years down the line.

Life itself is a large part of this insanely complex equation, governing everything from atmospheric composition and albedo to (on the wilder shores of speculation, admittedly) the production of granite melts (Rosling *et al.* 2006). Hence from the patterns of life of the past there will emerge some skeletal outline of Earthly life support system. Ergo, there's a hell of a lot of work out there for palaeontologists to do.

There has been progress made. I'm as impressed as the next person with the ingenuity with which, say, microscopic shells, once the property of sundry amoeboids, have been used to reconstruct the twists and turns of Quaternary climate. But even here there's a long way to go as to quite *how* all this has worked.



That's in the sunlit slopes of the near-recent, with familiar creatures and familiar oceans. Deep in the Palaeozoic, it feels like an entirely different world. Looking at graptolites, the only group to which I can claim any faint vestigial expertise, the overwhelming feeling I have is of how obscurely they reflect the changing states of their strange ocean-realm.

It's not altogether because of lack of evidence. There are longish sections of early Palaeozoic strata in the Welsh Basin, say, where pretty well every century (and many of its component decades) seems to have left some sort of imprint in those laminated hemipelagic mudrocks. The book of the past here has entire chapters that are more or less complete. And in those one can even see, quite clearly, oscillations of ocean state that periodically turned that Welsh sea floor into a dead zone for bottom-living animals and simultaneously a pickling jar for the mortal remains of the graptolites.

But those chapters are huge; the Silurian alone could fit almost a dozen Quaternaries within it. And to begin to consider the Silurian in Quaternary terms, and dissect those ocean-states in any half-way sophisticated manner, one should think millennial-scale, think global and be terribly careful as regards both the stratigraphic location and the morphological description of those fossils.

There are hundreds of thousands of graptolites from those rocks in UK collections, and millions of their kin in museums around the world. The vast majority are unpublished. Many have some sort of name attached to them, though a lot of them do not. Their localization, stratigraphic and geographic, ranges from just-adequate (to the task envisaged) to appalling. As to each of these species names ... well, anyone who has ever laboured in the salt mines of systematic palaeontology will know them to be a more or less disputable shorthand for phylogenetic position, a feast so moveable it should be put on wheels. Even when those taxon names seem respectable, there's always the threat of those sibling taxa insinuating themselves into one's carefully shepherded assemblage. And if those systematic perils are avoided, the taxon names bear almost no information on, say, the state of preservation or specimen dimensions or ecophenotypic variation. And that's just graptolites. There are all those other fossil groups to apply this treatment to...

This line of thought isn't in the least original. There are not a few palaeontologists out there trying to amass the kind of data to tackle such questions. This does need finding effective ways of dealing with the amount of information to hand, of coping with the curse of plenty. But the size of the current effort seems to me entirely dwarfed by the scale – and the importance – of the problem. Even the largest of these exercises, such as the Chronos project⁸, will always hang on the uncertain thread of continued funding.

On the scale of global science, stratigraphy and palaeontology are cottage garden industries, with funding almost invisible by comparison with the megabucks swallowed up by particle physics, say, or by space science. Even in the latter, the money is currently being siphoned away from the science – and particularly from earth observation – for the staging of that ultimate reality TV show of sending a human to Mars, on the grounds that such a spectacle will add excitement to Science and succour the body politic. The Emperor Nero, if I recollect aright, had a similar appreciation of the value of bread and circuses.

⁸ www.chronos.org



We are – and this is really a point that should not need to be emphasized – living on what is by far the most complex, intricate, fascinating and (not to put too fine a point on it) habitable astronomical body for (at the very least) four light-years in any direction. It's a Fabergé egg amid limitless amounts of nothing, with just a standard-issue medium-sized thermonuclear oven and a scattering of planetary rubble for local company. Its singular properties and their subtle modulation through time are a direct result of its evolving freight of living matter. Understanding this phenomenon should be high on any agenda.

For all kinds of reasons, we could do with a significantly improved historical perception of cause-and-effect in the only planet that really counts⁹. In that sense, we are where Roemer and Humboldt were, a century and more ago: on the cusp of a new level of understanding. We should all perhaps be somewhat more forthright about the importance of our science to this endeavour. For this, we might borrow a little of Humboldt's vigorous republicanism. *Aux armes, citoyens, et vive la Revolution!*

Jan Zalasiewicz

27/6/2006

REFERENCES

- AGASSIZ, L. 1869. *Address delivered on the centennial anniversary of Alexander von Humboldt*. Boston: Society of Natural History.
- BARRANDE, J. 1850. *Graptolites de Bohême*. Prague.
- FULLER, J.G.C.M. 1992. The invention and first use of stratigraphic cross-sections by John Strachey, F.R.S. (1671–1743). *Archives of Natural History*, **19**, 69–90.
- GRODZICKI, A. (ed), 2003. *Historia nauk geologicznych na Uniwersytecie Wroclawskim 1811–2003*. Wydawnictwo Uniwersytetu Wroclawskiego, Wroclaw, 320 pp.
- HUMBOLDT, A. 1848. *Cosmos: A sketch of the physical description of the universe*. Vol. 1. London: Henry G. Bohn.
- ROSLING, M.K., BIRD, D.K., SLEEP, N.H., GLASSLEY, W. and ALBAREDE, F. 2006. The rise of continents – An essay on the geologic consequences of photosynthesis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **232**, 99–113.
- VOELKEL, H. 2002. *Mineralogen und Geologen in Breslau. Geschichte der Geowissenschaften an der Universitaet Breslau von 1811 bis 1945*. Bode Verlag, Haltern, 223 pp.

⁹ Within four light-years, that is. One should always be precise about one's extravagant claims.



Tree building

In this article I will explore the ways in which cladograms/trees are constructed from the data matrix by the parsimony programs. I should point out that when cladistics first started (pre-computer) Hennig argumentation was used: that is, groups were constructed solely upon the evaluation of what were judged *a priori* to be apomorphic character states (details of the argumentation can be seen at <<http://research.amnh.org/~siddall/methods/day2.html>>).

From cladogram/tree construction I will detail how we use the PAUP* program in order to read the data matrix, set various starting conditions and any assumptions that we may wish invoke to build the tree, as well as actually building the tree. We will then deal with the tree output but leave the meanings of all the optimisation and tree statistics until the following article when you have refreshed your batteries from this battery. This is not intended as a manual, but it may speed up the inevitable learning curve that we all experience confronted with a new program. I will deal with the Macintosh version of PAUP*. For those with a PC version then I do have a help sheet on request.

The scale of the problem

There is no theoretical reason why we have to use computers. It is just the scale of the task that makes it a practical necessity. The problem is that with increasing numbers of taxa to be evaluated then the number of possible trees that must be considered in order to find the most parsimonious is staggering (Figure 1). Therefore we need computers. Even then it turns out that the problem is currently beyond the technology.

The tree building algorithms used in PAUP* fall into two main methods: Exact and Heuristic. All of them construct unrooted trees/cladograms which are then rooted according to the criteria that you set (see later).

number of taxa	Number of rooted fully bifurcating trees	Number of unrooted fully bifurcating networks
1	1	-
2	1	1
3	3	1
4	15	3
5	105	15
20	8,200,794,532,673,891,559,375	221,643,095,476,699,771,875

Figure 1. The number of possible cladograms/trees increases alarmingly with increase in number of taxa. If we were to allow polytomies as well the number increases even more. Hence, we need computers.



Exact methods

These are guaranteed to find the shortest tree(s) – remember there may be more than one.

The *Exhaustive Search* routine is the simplest (Figure 2). In this routine three taxa are taken (usually the first three in the data matrix) and a fourth is added to all possible positions to give three possible paths; then to each of these a fifth taxon is added in all five possible positions on each path, followed by a sixth *etc.* until all taxa have been added and *all* possible networks have been generated. Then the lengths (numbers of steps) of *all* the cladograms are evaluated and the shortest chosen. Given the astonishing number of possibilities (Figure 1) the Exhaustive search is usually only practicable for about ten taxa.

EXHAUSTIVE SEARCH

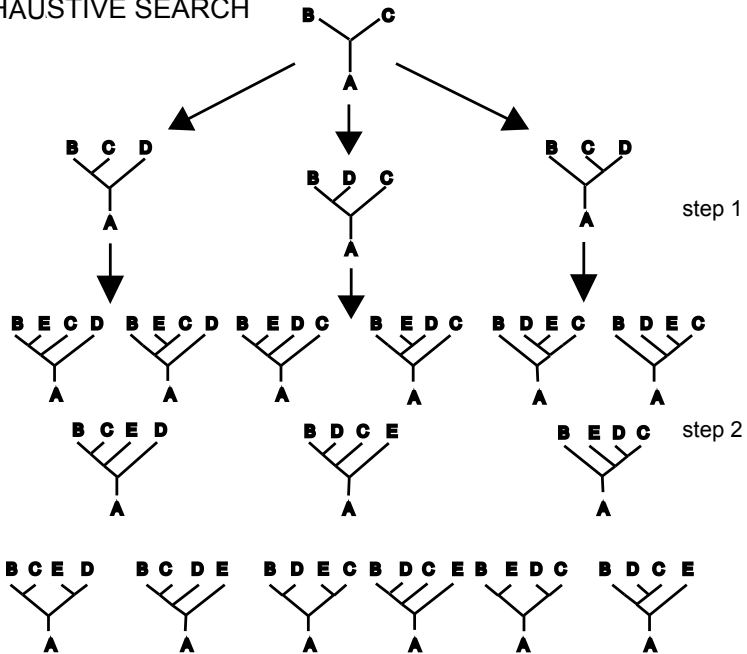


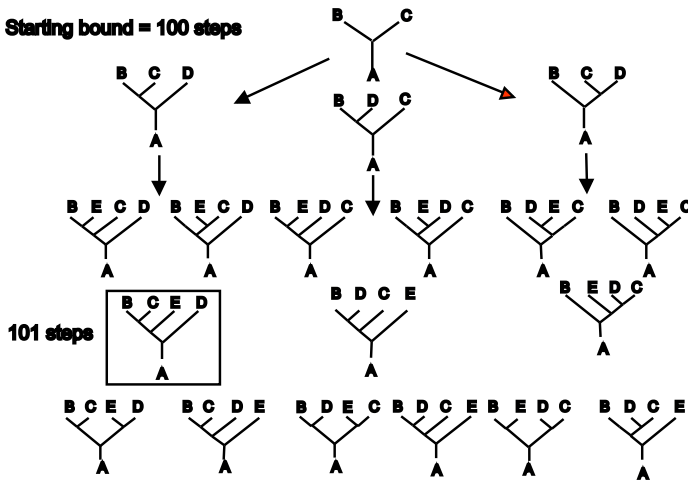
Figure 2. In the exhaustive search routine the first three taxa are chosen. A fourth is added to all possible positions in the network (step 1). Then a fifth is added to all possible positions (step 2) until all taxa have been added in all positions. The lengths of the trees are then calculated.

A compromise on this method is provided by *Branch and Bound* (Figure 3). This is a technique that does not require *every* possibility to be examined individually. In this method a cladogram is constructed for all the taxa using one of the Heuristic techniques that we will come onto later. The length of this cladogram is stored in the memory and it is called the ‘upper bound’. Then, the Branch and Bound method proceeds as in the Exhaustive Search routine. As each of the paths is followed, the lengths of the partial cladograms (those in which not all taxa have been yet added) is calculated. As soon as the length of a cladogram in any path is longer than the upper bound, that entire path is abandoned – because the addition of more taxa can only increase

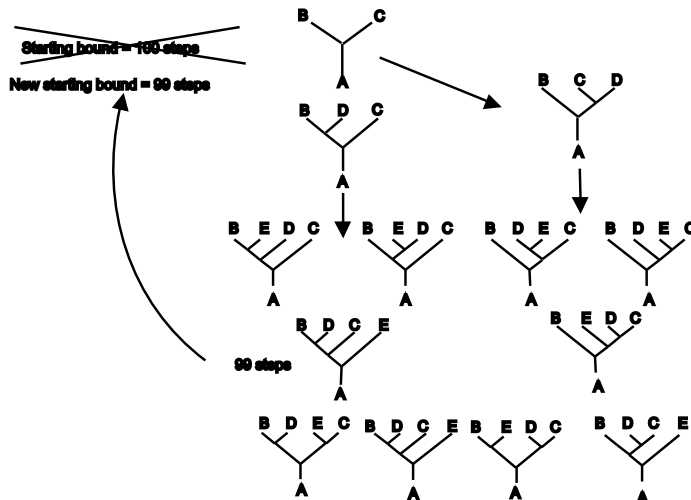
Figure 3.

Branch & Bound

Starting bound = 100 steps



Branch & Bound proceeds by calculating the shortest tree length using a simple heuristic algorithm. Then it continues as an exhaustive search. If a longer tree is encountered then the whole branch is abandoned and trees deleted from memory.



If a shorter tree is found, then this becomes the new upper bound and the process continues. In this way the number of trees to be evaluated is drastically reduced.

the length of the cladogram further. If one of the paths is completed and a shorter cladogram is found, this becomes the new 'upper bound'. By this method the number of cladograms that have to be evaluated is drastically reduced. Even so, *Branch and Bound* usually begins to creak at about 15 – 20 taxa (it very much depends on how clean the data is).

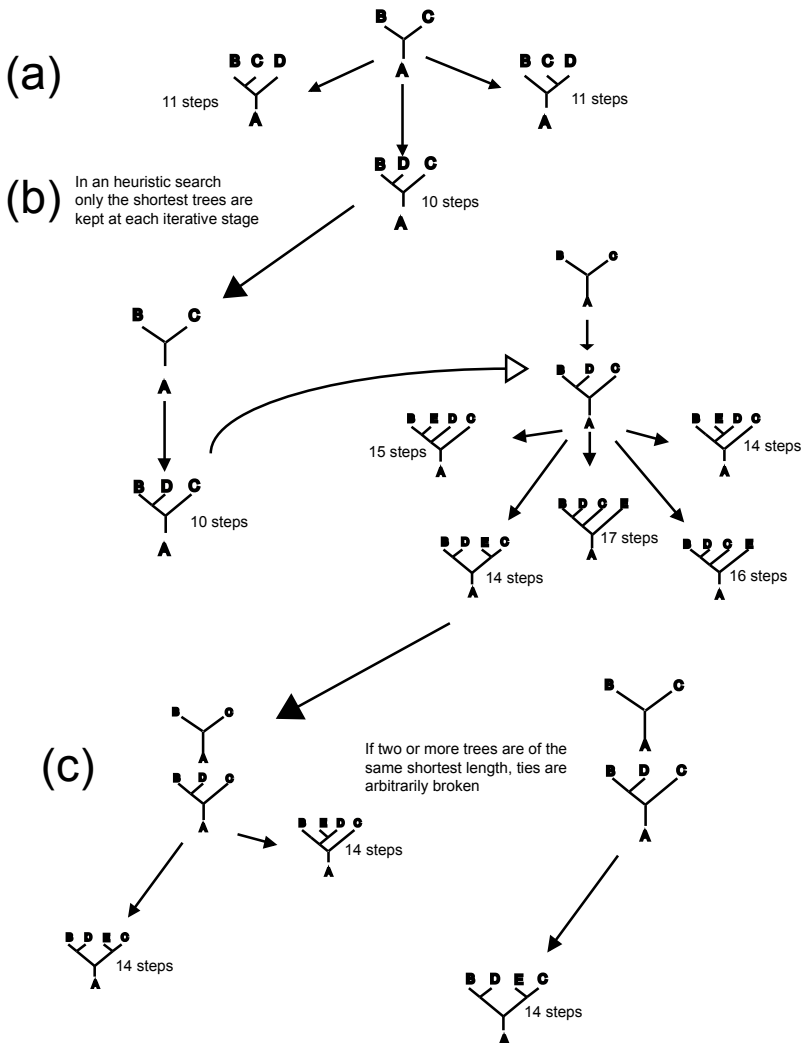


Heuristic methods

Ideally one would like to use one of the exact methods. However, because we usually have more than twenty taxa or because we have messy data (lots of homoplasy, question marks *etc.*) we are forced to use heuristic (trial and error) methods. Do not despair! Heuristic methods do have a number of short cuts and slick moves that usually enable us to find the shortest cladograms. But let's start with the pitfalls.

The heuristic method, pure and simple, starts with the first three taxa in the data matrix (Figure 4a). It then adds the fourth taxon, calculates the lengths, and discards all but the shortest

Figure 4. Heuristic Searches



(Figure 4b). This means that even if the addition of the next taxon to one of the cladograms now discarded should turn out to yield trees shorter than those retained it will never be considered – it has already gone down the drain because of the inferiority of its antecedent cladograms. The situation is worse because, if there is a tie in the lengths of the cladogram one will arbitrarily be discarded (Figure 4c). So, it is possible that by discarding paths of cladogram building so early we are forced onto a path that may lead to a less than optimal cladogram length. We are, effectively, being forced onto an island where we may never find the shortest tree. At the risk of stretching the metaphor – we don't always get the coconut! This is called the 'Island of trees problem'.

We might explain this another way using the analogy of a hill climber wishing to reach the 'highest peak', which in our case is the shortest cladogram. The cartoon in Figure 5 is meant to illustrate the dilemmas. In this cartoon each of the mountains represents a path of cladogram construction. If we happened to start on any mountain but "Mount C" we would never reach the optimal solution. But, of course, having started to climb a particular mountain (started to go down a path of tree building) we cannot go back. There are two things that we could do. First we

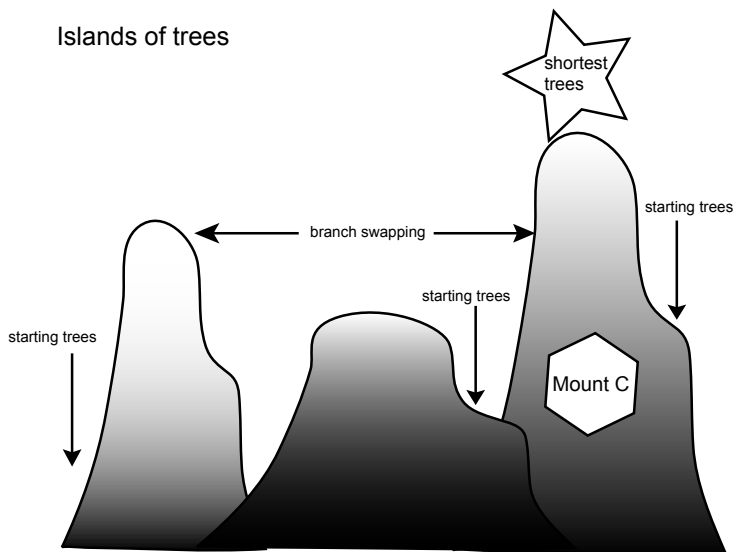


Figure 5. Heuristic metaphor. Given a total landscape of hills that represent piles of trees of different lengths, it depends on which hill we start as to how high (nearest the shortest trees) we will get. The starting trees are the particular taxa that we use to start tree building. If we started on the left hand hill we would reach a local optimum but it would not be the shortest of all trees. These are to be found on the right hand hill. We could choose to start somewhere else (on another hill). Or, having started to climb we could jump horizontally from one hill to another in the hope of landing on a more promising hill. Both tactics are invoked in the heuristic algorithm.



could change the trees/cladograms that we start with: in other words we could change the order in which we add the taxa. This may allow us to start on another mountain. Second, we could try to jump from one mountain to another in the hope that we land on “Mount C” and eventually reach our nirvana.

The heuristic algorithm in PAUP* has alternatives for specifying the order in which taxa are to be added into cladogram building (starting on different mountains), and it has alternatives for branch-swapping (jumping from one mountain to another). The order in which taxa are to be added to the heuristic search is called STEPWISE ADDITION and is an attempt to start on different mountains. PAUP* provides four options that are explained in Figure 6. The most frequently used are ‘Random addition’ and ‘Closest’. For branch swapping (jumping from

Addition sequence

ASIS - taxa are added in the order in which they appear in the matrix

Taxon A 0 1 1 0 0 1 1 0
Taxon B 0 1 0 1 1 0 0 1
Taxon C 1 1 0 0 1 1 1 0
Taxon D 0 0 1 0 0 1 0 0 4th
Taxon E 1 0 1 0 0 1 0 1 5th
Taxon F 0 1 1 0 1 1 1 0 6th

RANDOM - taxa added in random sequence and the procedure is repeated many times

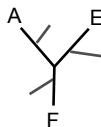
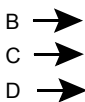
Taxon A 0 1 1 0 0 1 1 0
Taxon F 0 1 1 0 1 1 1 0
Taxon B 0 1 0 1 1 0 0 1
Taxon C 1 1 0 0 1 1 1 0 4th
Taxon D 0 0 1 0 0 1 0 0 5th
Taxon E 1 0 1 0 0 1 0 1 6th

SIMPLE - Reference taxon chosen; then taxa added in order in which they deviate.

reference taxon	Taxon A 0 1 1 0 0 1 1 0		Taxon A 0 1 1 0 0 1 1 0
	Taxon B 0 1 0 1 1 0 0 1 5th		Taxon F 0 1 1 0 1 1 1 0
	Taxon C 1 1 0 0 1 1 1 0 3rd	→	Taxon D 0 0 1 0 0 1 0 0
	Taxon D 0 0 1 0 0 1 0 0 2nd		Taxon C 1 1 0 0 1 1 1 0
	Taxon E 1 0 1 0 0 1 0 1 4th		Taxon E 1 0 1 0 0 1 0 1
	Taxon F 0 1 1 0 1 1 1 0 1st		Taxon B 0 1 0 1 1 0 0 1

CLOSEST - initial triplets are compared to find the shortest cladogram, the remaining taxa are added in turn to find the shortest tree and the procedure continued until all taxa are used.

ABC ACD ADE **AEF** ABD ABE ABF ACE ACF
ADF BCD BCE BDE BDF BEF CDE CEF CDF DEF



remaining taxa tried in alternative positions to find shortest trees

Figure 6. There are various ways in which taxa can be sequentially added (stepwise addition) to the heuristic tree building program.



mountain to mountain) there are three options but only one is really effective – tree bisection and reconnection, or ‘TBR’ (Figure 7); this is the default in PAUP* so I suggest that you leave well alone. By using a combination of stepwise addition and branch swapping the heuristic algorithm more than likely will find the shortest tree(s). The trick is to repeat the heuristic searches several times until both the topology and the length of the trees stabilise. The combination of random addition sequence and TBR is usually sufficient.

Tree bisection and reconnection (TBR)

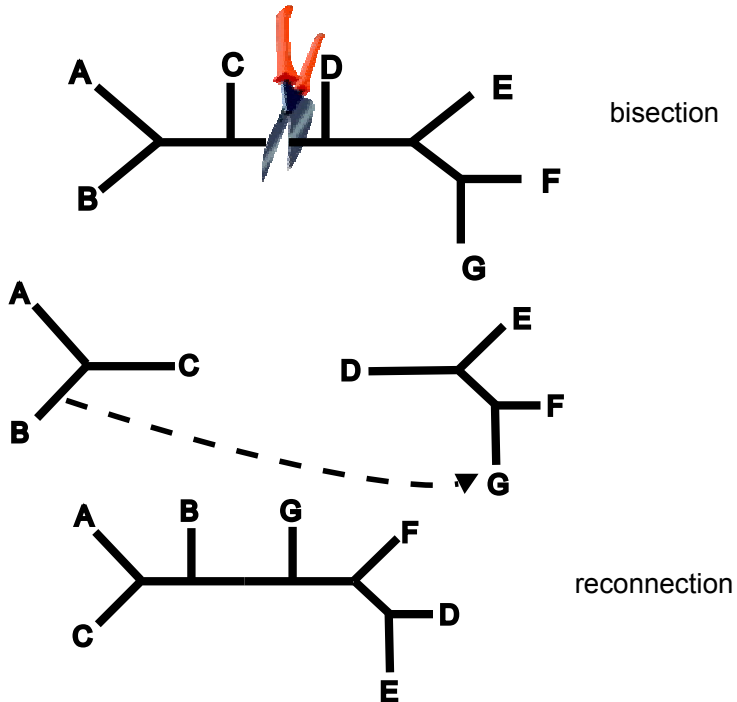


Figure 7. Branch swapping using TBR. Here the network cladogram is broken into two subcladograms. One is then regrafted (reconnected) on to various parts of the other until the shortest network is found.

Having dealt with the theory we can now look at the computer screens and see what it actually looks like. I will follow through a sequence of screen dumps as you may see them when carrying out an analysis. In all of what follows there are many more options. For simplicity, I will deal only with those usually used.



Figure 8 is the opening screen that you get after reading the matrix. It tells you that the matrix has been read successfully. If there are errors it specifies the problem. If you use NDE or MacClade to construct the data matrix you should have no problems because you would not be able to save those files successfully. If you write your own matrix from scratch then the normal sources of errors are mismatches between the numbers of taxa and/or characters specified and those actually recorded.

```
File Edit Options Data Analysis Trees Window Help
PAUP- 4.0b10 (PPC)
Total memory available: 30671K Largest free block: 30666K

P A U P *
Version 4.0b10 for Macintosh (PPC)
Thursday, February 10, 2000 3:57 PM

This copy registered to: 7500
Paleontology, BPHH
(serial number = 0400999)

-----NOTICE-----
This is a beta-test version. Please report any crashes,
apparent calculation errors, or other anomalous results.
There are no restrictions on publication of results obtained
with this version, but you should check the IAGLR site
frequently for bug announcements and/or updated versions.
See the README file on the distribution media for details.
-----

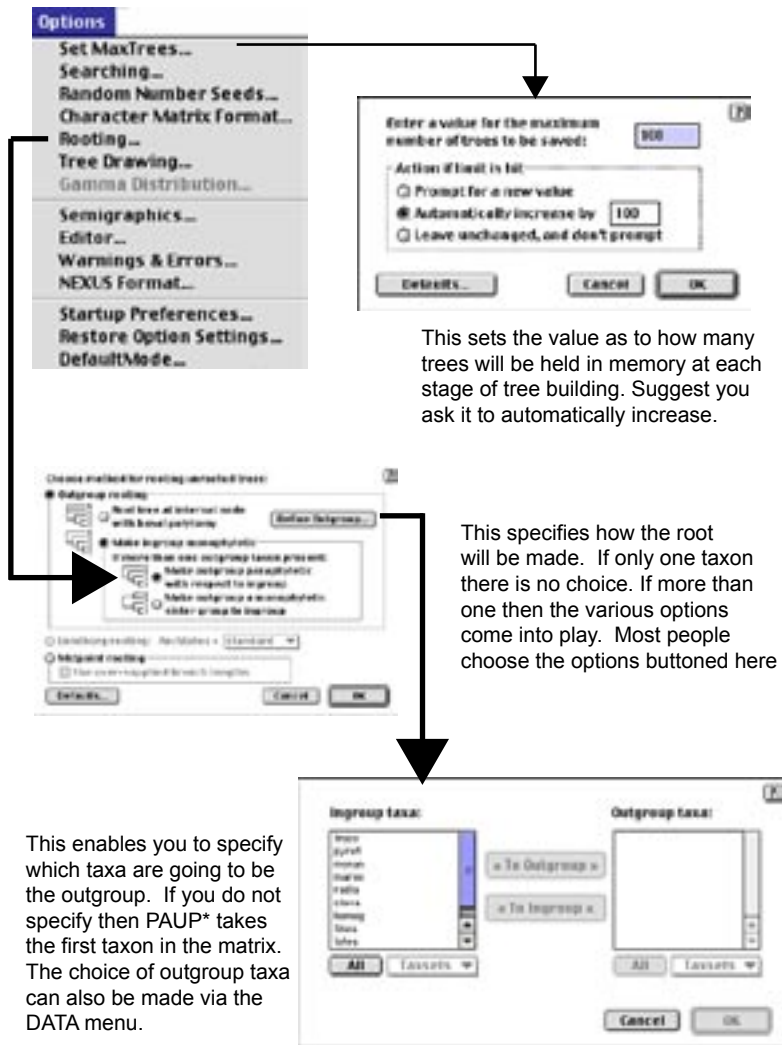
Processing of file "Anacyclus" begins...
Chris Rumphries' Anacyclus data
Character 47 not in original data set (added later by Rumphries)
Data matrix has 10 taxa, 47 characters
Valid character-state symbols: 0123
Missing data identified by '?'
Processing of file "Anacyclus" completed.
```

Figure 8. Having opened up PAUP* and opened (executed) the data file the program should read the file and present you with this screen, showing the name of the file, how many taxa and characters are in the file and what kinds of codes have been used for the character states.

At the bottom of the screen there will be a narrow, full width window in which you can type commands instead of using the pull down menus. In the Macintosh version there is probably no point in doing this. In the PC version it is the only way!

In the next stage is the **OPTIONS** menu (Figure 9) where we would set the Maxtrees. This sets a value of the number of trees to be held at each iterative stage of the tree building process. The usual setting is "automatically increase by 100". The next job under the options menu is to set the outgroup and how that outgroup is to be represented. The computer actually builds an unrooted network but then roots the tree(s) using your specification of outgroup. This action will polarise the characters (see previous article). The screens should be self explanatory.

The **DATA** menu (Figure 10) is very useful. Options here allow you to include or exclude characters, include or exclude taxa, and to set the type of character to behave under alternative parsimony theories (we will deal with these in another article). Normally you may wish to set a particular multistate character to be ordered or unordered, but there are other options such as



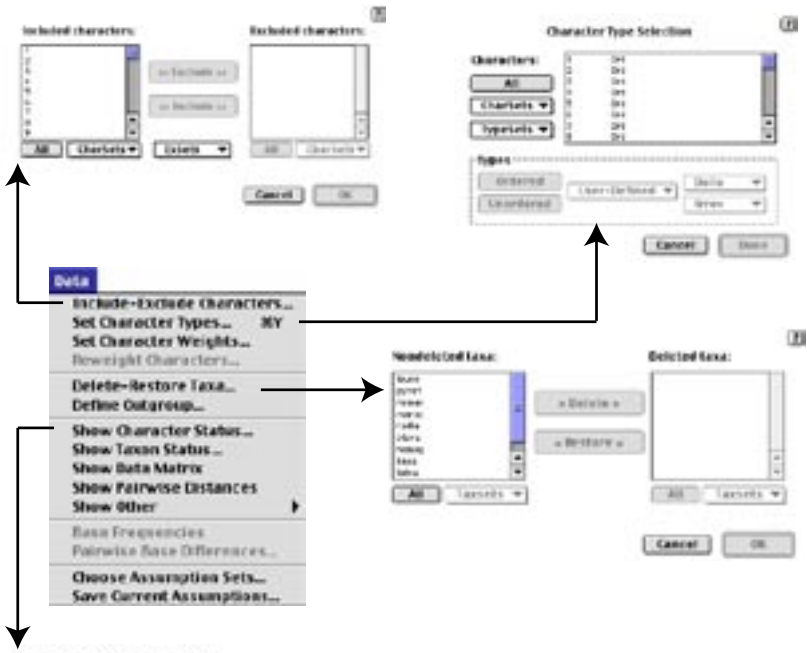
This sets the value as to how many trees will be held in memory at each stage of tree building. Suggest you ask it to automatically increase.

This specifies how the root will be made. If only one taxon there is no choice. If more than one then the various options come into play. Most people choose the options buttoned here

This enables you to specify which taxa are going to be the outgroup. If you do not specify then PAUP* takes the first taxon in the matrix. The choice of outgroup taxa can also be made via the DATA menu.

Figure 9. The first thing you would do is to set the Maxtrees and to specify the outgroup and how the trees are to be rooted.

Dollo and irreversible (Camin-Sokal parsimony). You may also change the weight of a particular character, but I'm not encouraging you to do this!! What this means is that you are saying that character A is x times more important than character B. What actually happens is that the computer rewrites the data matrix including that character several times, and consequently



Character-status summary:
 Current optimality criterion = parsimony
 No characters are excluded
 Of 47 total characters:
 All characters are of type 'ond' (logner)
 All characters have equal weight
 2 characters are constant
 24 variable characters are parsimony-uninformative
 Number of parsimony-informative characters = 21

Current status of all characters

Character	Type	Status	Weight	States
1	ond	U	1	01
2	ond	U	1	01
3	ond	U	1	01
4	ond	U	1	01
5	ond	U	1	01
6	ond	U	1	01
7	ond	U	1	01
8	ond	U	1	01
9	ond	U	1	01
10	ond	U	1	01
11	ond	U	1	01
12	ond	U	1	01
13	ond	U	1	01
14	ond	-	1	01
15	ond	U	1	01
16	ond	U	1	01
17	ond	-	1	01
18	ond	-	1	0123
19	ond	-	1	01

The character status window is useful to check where you are at any time. In this table it shows you that characters 1-13, 15 and 16 are parsimony uninformative and will not contribute anything to tree building (they would be autapomorphies). Character number 18 is a multistate character with four states.

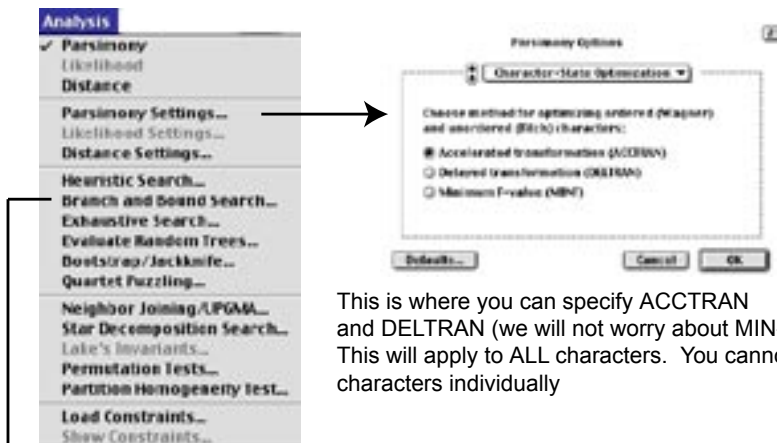
Figure 10. The DATA menu

'loads the dice'. So if you set character 2 to have a weight of four then the matrix would include character 2 four times. How you justify this with morphological data *a priori* I do not know!! There are, however, perfectly good reasons for doing so with molecular data.



The **ANALYSIS** menu (Figure 11) is where you set the conditions of tree building just before you hit the button. Here, there are a number of tree-building options. We are only interested in Parsimony (the others are appropriate for molecular data). Under Parsimony there are three options: Exhaustive, Branch & Bound, and Heuristic. The screens for Exhaustive and Branch & Bound are straightforward and do not need any explanation. Most people just hit the ‘search’ button. I have included the Branch & Bound screen (bottom of Figure 11) because, like screens under the other parsimony options, you can ask the computer to save all trees that are X steps and less. This can be useful when we compute Bremer Support for the trees (article 5).

Figure 11. Trees searches. Make sure **Parsimony** is ticked.



This is where you can specify ACCTRAN and DELTRAN (we will not worry about MIN-F). This will apply to ALL characters. You cannot set characters individually

For exhaustive and Branch & bound searches the options are straightforward. Shown below is the screen for B & B. Probably best to leave as default. But, when you progress through an analysis you may like to enter a number in the **keep trees** box so that you save some of the near optimal trees as well as the optimal. This box will be relevant when we come to apply Bremer Support to nodes (Article 5).





For **HEURISTIC** searches then we have options of stepwise addition and branch swapping to take into consideration (Figure 12). The common thing to do here is to hit the 'random' button under "Stepwise addition" and put in a number of replications.

Heuristic searches

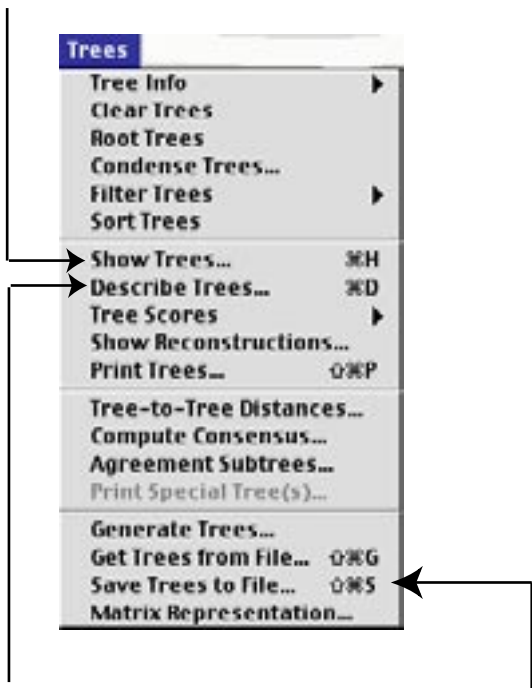
Figure 12. Under the heuristic search you have at least two options to set the stepwise addition and branchswapping. You find each of these under General Search options menu.

Under any of these parsimony algorithm screens we hit the 'SEARCH' button.

Once the trees have been built under one of the tree search options you then have to examine the tree(s). This is found under the **Tree** menu (Figure 13). It is here that you could save your tree into a file for use later.

Figure 13. The TREE menu

This command will simply show the shapes of the trees that you ask for



This command will show the trees as well as describing character output and a host of other things. You would usually use this command (Fig. 16)

This command saves the trees that you specify for use later

The trees are saved in parenthetic notation. You may wish to save the trees to import into MacClade and manipulate characters Alternatively, you may wish to optimise someone else's characters against your tree.



Usually you would want to describe the trees using the **Tree Description** menu (Figure 14), asking for certain pertinent pieces of information. Here there are a number of options indicated on the menu. Normally, you would ask for the list of changes and the list of apomorphies.

Figure 14. The tree description menu

Make sure the 'cladogram' and 'label interior nodes' are checked. Also, you will usually want to check the 'f-value'. This gives you all the stats that we will examine in the next article.

This allows you to select the trees you want to examine. Usually, only the optimal trees are shown here. But if you had entered a tree length to save (Fig. 11) then more than just the optimal trees will be shown here.



Check this to get a list of all character changes that take place node by node (Fig. 16)

Check this to get a list of changes, character by character

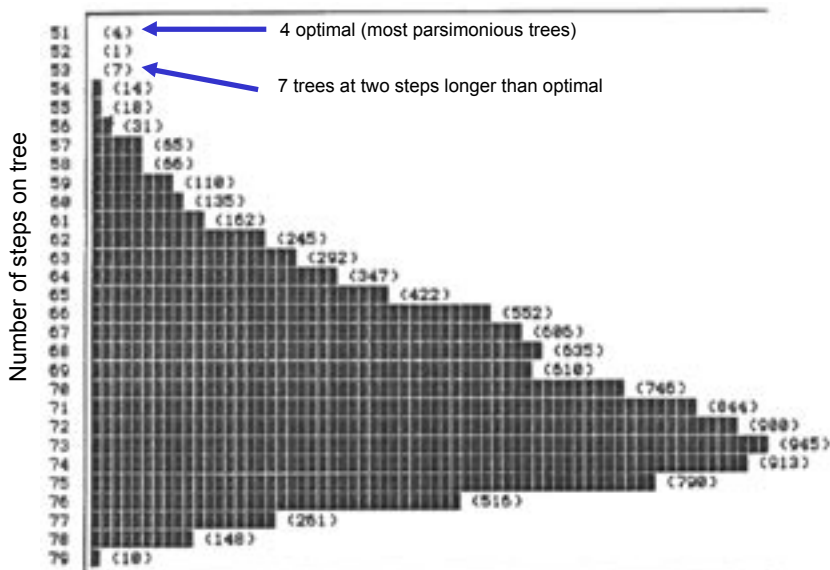
At last you will be able to see your tree(s). As a slight diversion: when you carry out an Exhaustive Search (and only when you do this) a graph will automatically scroll past (Figure 15). This gives you a tree length distribution of all trees examined. It can be very useful.

When you hit the 'Describe' button a lot of information will scroll past (Figure 16). This will take some digesting. Much of it we will deal with in the next article. For now, let's look at the basics. The first thing to scroll past is a paragraph giving you details of tree length, consistency indices *etc.* The second is the tree itself, with terminal taxa numbered and the internal nodes numbered (you asked for this). When there are multiple trees each will have the same output format, so the screen could scroll past for some time (there is a buffer limit and therefore if you ask for the output for many trees it could be that the operation will be cut short – if this happens then just ask for the output for some of the trees, say trees 1 – 20).

If you have asked for the changelist and the apomorphy list you will get a table under each heading. The same information is conveyed in both but in a different format. Under the changelist each character is taken in turn and certain facts are displayed. The headings are character

Figure 15. When you ask for a tree description after carrying out an Exhaustive Search you automatically get this graph of tree length distributions. It can be useful as it tells you immediately how many near rival trees there are and how many steps longer they are. There is also a string of stats at the bottom. The only one of interest is the 'g1' value as it tells you how skewed your data is. This is basically a measure of the strength of the hierarchical signal because it signifies how far your data is removed from random data. It does not mean that it is the correct signal!! You only get this with Exhaustive Search.

Frequency distribution of tree lengths



Mean=69.844156 sd=4.775776 **g1= -0.664305** g2=0.029334

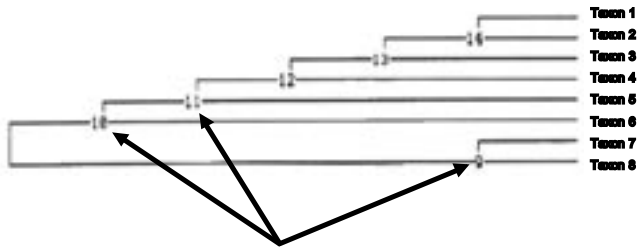
number, consistency index of that character on that particular tree (next article), the number of steps that character has (if a binary character it will be 1 step, if a multistate such as a 0, 1, 2 character it will be 2 – an earlier screen in Figure 10 bottom has shown you this), and the actual change that the character has made on that particular tree. So, character 1 (binary character) has changed from the '0' state to the '1' state along the internode numbered 13 to 14. So the '1' state would be interpreted as a synapomorphy supporting the group Taxon 1 + Taxon 2. Character 2 (also a binary character) has actually changed twice on the tree, in each case from the '0' state to the '1' state, once along the branch from node 13 leading to taxon 3 and again from node 14 to taxon 1. This would be interpreted as a parallel change (a homoplasy). Character 3 (a multistate of three states) has also changed twice on the tree but the state changes have been different: from the '0' state to the '1' state from node 11 to node 12 and then from the '1' state to the '2' state from node 13 to node 14.



Figure 16. On hitting the describe tree button some statistics and the tree will scroll past. If asked for you will also get character output in either or both change lists and apomorphy lists

Tree number 1:

Tree length - 23
 Consistency Index (CI) = 0.698
 Homoplasy Index (HI) = 0.304
 CI excluding uninformative characters = 0.667
 HI excluding uninformative characters = 0.333
 Retention Index (RI) = 0.562
 Rescaled consistency index (RC) = 0.391



Nodes numbered following on from highest taxon number

CHANGELIST

Character	CI	Steps		Changes
1	1.000	1	node 13	0 \Rightarrow 1 node 14
2	0.500	1	node 13	0 \rightarrow 1 taxon 3
		1	node 14	0 \rightarrow 1 taxon 1
3	1.000	2	node 11	0 \Rightarrow 1 node 12
			node 13	1 \Rightarrow 2 node 14
4	1.000	1	node 9	0 \Leftrightarrow 1 node 10

APOMORPHY LIST

Branch	Character	Steps	CI	Change
node 9 \rightarrow node 10	4	1	1.000	0 \Leftrightarrow 1
node 11 \rightarrow node 12	3	2	1.000	0 \Rightarrow 1
node 13 \rightarrow node 14	1	1	1.000	0 \Rightarrow 1
	3	2	1.000	1 \Rightarrow 2
node 13 \rightarrow taxon 3	2	1	0.500	0 \rightarrow 1
node 14 \rightarrow taxon1	2	1	0.500	0 \rightarrow 1

You will also notice that there are different kinds of arrows between the state changes. There are two variations; single- or double-headed, single or double lines. The double-headed arrows mean that the change has happened between the outgroup (in this case Taxon 7 + Taxon 8) and the ingroup. The double line means that the change is unambiguous on that tree (it cannot be



interpreted any other way). The single-lined arrow means that the change is ambiguous on this particular tree. As explanation look at character 2. The '1' state is present in taxon 1 and taxon 3. On this particular tree there are two explanations for this distribution: either it has been gained twice – once in Taxon 1 and again in Taxon 3; or it has been gained at node 13 and lost along the branch leading to Taxon 2. If you cast your mind back to article 1, this is the difference between DELTRAN and ACCTRAN. So this particular optimisation is not the only one possible.

The apomorphy list is the same information but it takes the tree node by node; so this gives you an instant read out of what characters are supporting what nodes (the usual piece of information that we need to know).

We will deal with the 'ci' value next article.

Happy Summer!

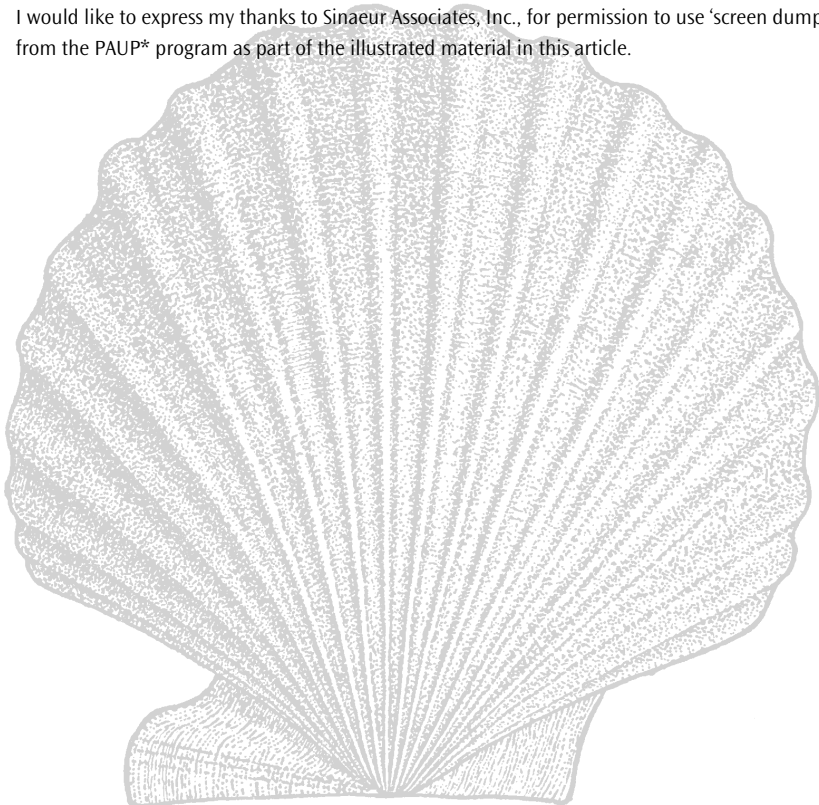
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ACKNOWLEDGEMENTS

I would like to express my thanks to Sinaeur Associates, Inc., for permission to use 'screen dumps' from the PAUP* program as part of the illustrated material in this article.





PalaeoMath 101

Rs and Qs II: Correspondence Analysis

Last time we took a look at how we might want to approach the quantitative analysis of measured 'objects' (e.g., specimens, localities, samples in a section or core) as opposed to variables, and drew a useful distinction between *R*-mode and *Q*-mode analyses. No doubt you noticed over the past several essays that, despite our geometric approach to the analysis of any data matrix, we're really interested in both quantities. You may have even asked yourself, "isn't there anything that does both?". There is, and we'll spend this essay discussing one of the most popular ways to do so. Along the way we'll compare and contrast this new method to some of our old friends and (hopefully) gain a bit deeper insight into what multivariate analysis is all about.

Correspondence analysis (CA) grew from the ground prepared by Pearson's (1901) early work on what came to be known as principal components analysis (PCA) and Spearman's (1904) work on the original factor analysis (FA) model. Both these approaches were concerned with the decomposition of similarity matrices into components or factors that represented a more complex, underlying structure. Their success implied that it might be possible to do the same thing with any table of data. By 'any table of data' I don't mean a data table of any size or shape. That situation can be handled by PCA and FA as you already know them. Rather, this statement refers more to different types of data.

Since CA derives much of its power from being able to handle different types of data, a brief digression is called for here. We touched on this last time in our discussion of *Q*-mode similarity coefficients. There, we said different similarity coefficients were needed because a variety of data can be collected from objects. Now it's time to come to grips with this topic in a more systematic manner.

Quantitative data come in four basic types: nominal, ordinal, interval, and ratio. The difference between these is the manner in which they incorporate the concept of scale.

- **Nominal data** are simply number names for different, mutually exclusive groups of objects (e.g., 1 = dog, 2 = cat, 3 = horse). These data contain no scale information and are most frequently represented as contingency tables.
- **Ordinal data** represent observations that can be ranked with reference to some external scale (e.g., 0 = small, 1 = medium, 2 = large). These data embody information about the rank order of the categories, but nothing else.
- **Interval data** have a true scale, in the sense that the magnitudes of the numbers express important information. The classic example of an interval-scale variable is temperature expressed as °F or °C. In both those scales the difference between 2.4° and 1.1° is the same as the difference between 3.7° and 2.4°, but the zero point of both scales is set arbitrarily.
- **Ratio data** have equivalent steps in magnitude and true zero points. Lengths are typical examples of ratio-scale variables.



The regression and component-factor analysis methods we've discussed previously have, for the most part, assumed interval or ratio-scale data. Of course, our trilobite data matrix is composed entirely of ratio-scale variables. Correspondence analysis was originally developed to provide an eigenanalysis-based means for analyzing nominal and ordinal scale variables, though it can, just as easily, analyze interval or ratio-scale variables and/or data matrices that mix different variable types. Not only that, it scales these data such that relations between objects and variables can be graphed on the same ordination plot and used to refine the interpretation of those data. All in all it's a neat trick, and there's little wonder you are seeing more correspondence analyses appearing in the palaeontological literature.

We'll begin our presentation with a classical CA of ordinal-scale data.

Table 1. Trilobite frequency data (X matrix)

Genus	Paralic Shale	Shoal Lmstn.	Upper Lmstn..	Mid. Lmstn.	Phant. Lmstn.	Org. Siltstn.	Black Shale	Row Total
<i>Acaste</i>	8	5	3	10	4	5	1	36
<i>Balizoma</i>	6	6	5	10	2	3	1	33
<i>Calymene</i>	8	7	7	13	2	2	1	40
<i>Ceraurus</i>	10	1	1	10	10	11	4	47
<i>Cheirus</i>	10	9	1	14	13	19	2	68
<i>Cybantyx</i>	9	3	1	9	8	10	3	43
<i>Cybeloides</i>	5	4	1	7	6	9	3	35
<i>Dalmanites</i>	6	4	1	7	5	7	2	32
<i>Deiphon</i>	9	7	3	12	4	5	1	41
<i>Ormathops</i>	9	5	1	10	8	10	2	45
<i>Phacopidina</i>	5	3	2	6	3	4	2	25
<i>Phacops</i>	9	7	3	12	5	6	1	43
<i>Placoparia</i>	6	6	2	8	5	7	2	36
<i>Pricyclopyge</i>	3	1	0	3	8	9	8	32
<i>Ptychoparia</i>	10	9	2	14	9	13	2	59
<i>Rhenops</i>	6	1	1	6	5	5	3	27
<i>Sphaerexochus</i>	7	2	2	8	4	5	2	30
<i>Toxochasmops</i>	7	5	4	10	3	3	1	33
<i>Trimerus</i>	2	2	2	3	2	2	4	17
<i>Zacanthoides</i>	4	4	1	5	10	14	5	43
Column Total	139	91	43	177	116	149	50	765

Here we are looking at a hypothetical distribution of trilobite genera among different environmental facies representing a peritidal-bathyal transect. This is a typical contingency table. The numbers are occurrence frequencies of the different genera among the environments. Our



problem is to infer the character of faunal similarity relations among environments (*R*-mode analysis of the matrix columns) and the character of environmental-preference similarities among the genera (*Q*-mode analyses of the matrix rows), simultaneously. Since there are seven variables and twenty objects, a premium will also be placed on dimensionality reduction so we can summarize the greatest amount of information in the lowest number of composite variables. In the end we want a single plot, or set of plots, that will tell us everything we need to know about this system of variables and objects.

Our first problem is the fact that the sums of the matrix rows and the columns are numbers of characteristically different magnitudes. This is the typical situation. The methods we've discussed previously (PCA, FA, PCoord) finesse this issue because they focus on analysing only one type of similarity relation, either that among variables (PCA, *R*-mode FA) or among objects (*Q*-mode FA, PCoord). Correspondence analysis considers the matrix from both points of view. Accordingly, this discrepancy must be corrected. Otherwise, the scale of the resulting composite variables will not be comparable.

In order to render the scales comparable we divide each element of the matrix by the grand sum of the matrix, which is the sum of the sums of rows (or the sum of the sums of columns).

$$b_{ij} = \frac{x_{ij}}{\sum_{i=1}^n \sum_{j=1}^p x_{ij}} \quad (8.1)$$

Dividing a frequency observation by the total number of times the observation has occurred provides an estimate of its proportion of the total occurrence pattern. This proportion is also an estimate of the probability of finding the observation at that locality, horizon, genus, *etc.* Accordingly, the matrix resulting from this scaling operation is an expression of the joint probabilities genera will be found in specific environments and specific environments will contain genera.

In Table 2 (opposite), the row totals ($B_{i\cdot}$) represent the marginal probabilities of each genus occurring in any environment. Similarly the column totals ($B_{\cdot j}$) represent the marginal probabilities that specific environments will contain any trilobites. Naturally, both groups of marginal probabilities sum to 1.000.

Now comes the first complex part. If the trilobite faunas of two environments are similar we would expect to find similar patterns of variation in the proportion of trilobite genera in each column. If the environments differ in terms of their trilobite fauna, the joint probabilities should be different. This holds for the rows too. Thus, we should be able to come up with an index to express the similarities between rows and columns.



Table 2. Trilobite frequency data (B matrix of joint and marginal probabilities)

Genus	Paralic Shale	Shoal Lmstn.	Upper Lmstn.	Mid. Lmstn.	Phant. Lmstn.	Org. Siltstn.	Black Shale	$B_{i\cdot}$
<i>Acaste</i>	0.010	0.007	0.004	0.013	0.005	0.007	0.001	0.047
<i>Balizoma</i>	0.008	0.008	0.007	0.013	0.003	0.004	0.001	0.043
<i>Calymene</i>	0.010	0.009	0.009	0.017	0.003	0.003	0.001	0.052
<i>Ceraurus</i>	0.013	0.001	0.001	0.013	0.013	0.014	0.005	0.061
<i>Cheirurus</i>	0.013	0.012	0.001	0.018	0.017	0.025	0.003	0.089
<i>Cybantyx</i>	0.012	0.004	0.001	0.012	0.010	0.013	0.004	0.056
<i>Cybeloides</i>	0.007	0.005	0.001	0.009	0.008	0.012	0.004	0.046
<i>Dalmanites</i>	0.008	0.005	0.001	0.009	0.007	0.009	0.003	0.042
<i>Deiphon</i>	0.012	0.009	0.004	0.016	0.005	0.007	0.001	0.054
<i>Ormathops</i>	0.012	0.007	0.001	0.013	0.010	0.013	0.003	0.059
<i>Phacopidina</i>	0.007	0.004	0.003	0.008	0.004	0.005	0.003	0.033
<i>Phacops</i>	0.012	0.009	0.004	0.016	0.007	0.008	0.001	0.056
<i>Placoparia</i>	0.008	0.008	0.003	0.010	0.007	0.009	0.003	0.047
<i>Pricyclopyge</i>	0.004	0.001	0.000	0.004	0.010	0.012	0.010	0.042
<i>Ptychoparia</i>	0.013	0.012	0.003	0.018	0.012	0.017	0.003	0.077
<i>Rhenops</i>	0.008	0.001	0.001	0.008	0.007	0.007	0.004	0.035
<i>Sphaerexochus</i>	0.009	0.003	0.003	0.010	0.005	0.007	0.003	0.039
<i>Toxochasmops</i>	0.009	0.007	0.005	0.013	0.004	0.004	0.001	0.043
<i>Trimerus</i>	0.003	0.003	0.003	0.004	0.003	0.003	0.005	0.022
<i>Zacanthoides</i>	0.005	0.005	0.001	0.007	0.013	0.018	0.007	0.056
$B_{\cdot j}$	0.182	0.119	0.056	0.231	0.152	0.195	0.065	1.000

Fortunately, there is such an index. The derivation is a tad complicated and I won't go into it in detail. Good—though somewhat mathematical—discussions of this index can be found in the references listed at the end of this column. Effectively what the mathematics does is scale the transformed data (B) by the reciprocal of the square root of the marginal row and column probabilities ($B_r^{-1/2}$ and $B_c^{-1/2}$, respectively). In matrix notation the equation is as follows.

$$H = B_r^{-1/2} B B_c^{-1/2} \tag{8.2}$$

In order to make this calculation, the $B_r^{-1/2}$ and $B_c^{-1/2}$ matrices need to be arranged so that the marginal probabilities are located in the matrix diagonals with all off-diagonal values set to 0.0 (see the *PalaeoMath 101: R&Qs II* worksheet for details of the calculations). This calculation estimates the conditional probabilities specific genera will be found in specific environments and *vice versa*. Another way of thinking about this calculation is that it's scaling, or weighting, the column values by the reciprocal of the row sums (and so forming a weighted average) and scaling the row values by the reciprocal of the column sums. This, in turn, leads to the other name for CA, 'reciprocal averaging' or 'reciprocal averaged PCA'. As a by-product, this weighted averaging also helps equalize the scales within the rows and between columns, but it does not enforce equal scaling (as does correlation-based PCA or *R-mode* FA).



The H matrix of conditional probabilities for our trilobite frequency analysis is listed below.

Table 3. Trilobite frequency data (H matrix of conditional probabilities)

Genus	Paralic Shale	Shoal Lmstn.	Upper Lmstn.	Mid. Lmstn.	Phant. Lmstn.	Org. Siltstn.	Black Shale	Row Total
<i>Acaste</i>	0.113	0.087	0.076	0.125	0.062	0.068	0.024	0.556
<i>Balizoma</i>	0.089	0.109	0.133	0.131	0.032	0.043	0.025	0.561
<i>Calymene</i>	0.107	0.116	0.169	0.154	0.029	0.026	0.022	0.624
<i>Ceraurus</i>	0.124	0.015	0.022	0.110	0.135	0.131	0.083	0.620
<i>Cheirus</i>	0.103	0.114	0.018	0.128	0.146	0.189	0.034	0.733
<i>Cybantyx</i>	0.116	0.048	0.023	0.103	0.113	0.125	0.065	0.594
<i>Cybeloides</i>	0.072	0.071	0.026	0.089	0.094	0.125	0.072	0.548
<i>Dalmanites</i>	0.090	0.074	0.027	0.093	0.082	0.101	0.050	0.517
<i>Deiphon</i>	0.119	0.115	0.071	0.141	0.058	0.064	0.022	0.590
<i>Ormathops</i>	0.114	0.078	0.023	0.112	0.111	0.122	0.042	0.602
<i>Phacopidina</i>	0.085	0.063	0.061	0.090	0.056	0.066	0.057	0.477
<i>Phacops</i>	0.116	0.112	0.070	0.138	0.071	0.075	0.022	0.603
<i>Placoparia</i>	0.085	0.105	0.051	0.100	0.077	0.096	0.047	0.561
<i>Pricyclopyge</i>	0.045	0.019	0.000	0.040	0.131	0.130	0.200	0.565
<i>Ptychoparia</i>	0.110	0.123	0.040	0.137	0.109	0.139	0.037	0.694
<i>Rhenops</i>	0.098	0.020	0.029	0.087	0.089	0.079	0.082	0.484
<i>Sphaerexochus</i>	0.108	0.038	0.056	0.110	0.068	0.075	0.052	0.506
<i>Toxochasmops</i>	0.103	0.091	0.106	0.131	0.048	0.043	0.025	0.548
<i>Trimerus</i>	0.041	0.051	0.074	0.055	0.045	0.040	0.137	0.443
<i>Zacanthoides</i>	0.052	0.064	0.023	0.057	0.142	0.175	0.108	0.621
Column Total	1.891	1.514	1.098	2.130	1.700	1.910	1.203	11.446

Now most of the hard work is done. As before, genera (rows) and/or environments (columns) that are similar to one another should exhibit similar patterns of values. Drawing on analogy with previous multivariate methods, we now need to summarize this between-rows and between-columns similarity with a numerical index. We can do this in a couple of different ways. The method most similar to PCA, FA, and PCoord is to calculate the covariance between columns of the H matrix. Because of the probability calculations we have performed, this quantity (d) represents the product of two χ^2 values, and is sometimes referred to as a χ^2 'distance'. Once you have obtained the H matrix the easiest way to calculate the matrix of χ^2 distances (D) is as follows.

$$D = H' H \quad (8.3)$$

In this equation H' is the transpose of the H matrix and the matrix multiplication is equivalent to calculating the sum of squares and cross products between all pairs of columns. Since we had



previously designated the columns of X to contain our variables, D is analogous to an R -mode distance matrix. The D matrix for our trilobite frequency data set is listed below.

Table 4. R-Mode χ^2 distance matrix (D)

	Paralic Shale	Shoal Lmstn.	Upper Lmstn.	Mid. Lmstn.	Phant. Lmstn.	Org. Siltstn.	Black Shale
Paralic Shale	0.191	0.148	0.107	0.214	0.159	0.179	0.097
Shoal Lmstn.	0.148	0.138	0.098	0.176	0.120	0.140	0.069
Upper Lmstn.	0.107	0.098	0.094	0.131	0.068	0.075	0.048
Mid. Lmstn.	0.214	0.176	0.131	0.245	0.173	0.196	0.104
Phantom Lmstn.	0.159	0.120	0.068	0.173	0.170	0.193	0.115
Organic Siltstn.	0.179	0.140	0.075	0.196	0.193	0.222	0.126
Black Shale	0.097	0.069	0.048	0.104	0.115	0.126	0.111

Note this matrix is symmetric about its diagonal or trace. An eigenanalysis of the D matrix yields the following eigenvalues, which express the character of between-facies biotic similarity relations.

Table 5. Eigenvalues of D matrix (W matrix)

	Eigenvalue	% Variation	Cum. % Variation
1	1.000	85.412	85.412
2	0.117	10.022	95.435
3	0.036	3.090	98.524
4	0.014	1.159	99.683
5	0.003	0.270	99.953
6	0.000	0.026	99.979
7	0.000	0.021	100.000

In CA the first eigenvalue is usually 1.000. Obviously the first three eigenvalues represent the overwhelming majority of the variation. Arguably the first two do, but you'll see why I'm going to interpret three in a moment. Eigenvector 7 is going to be 0.0 (save for rounding error) because we've scaled the data and so removed a component of variation. Eigenvector 6 exists (0.0003) but is too small to show up in a report to three decimal places.

These eigenvalues correspond to the eigenvectors of the D matrix, which are what we will use to produce an ordination plot of the similarity relations between environments. To do so these values are first scaled by the square roots of the eigenvalues in a manner identical to the one we



used in PCoord Analysis (see previous *PalaeoMath 101* column: *Minding your Rs and Qs*). Then, in order to make it possible to plot both the *R*-mode and *Q*-mode loadings in the same coordinate space, these scaled values are scaled again by the square roots of the *Q*-mode conditional probabilities (= column sums) of the *B*-matrix, as follows.

$$A_{r-scaled} = B_c^{1/2} A_r \tag{8.4}$$

The results of these calculations are shown below.

Table 6. Eigenvectors and scaled, R-mode correspondence axis loadings (A_r) of the *D* matrix

R-Mode Eigenvectors			
Environments	1	2	3
Paralic Shale	0.426	0.166	0.102
Shoal Lmstn.	0.345	0.310	0.127
Upper Lmstn.	0.237	0.491	-0.479
Mid. Lmstn.	0.481	0.328	0.062
Phantom Lmstn.	0.389	-0.381	0.139
Organic Siltstn.	0.441	-0.429	0.324
Black Shale	0.256	-0.447	-0.784
Singular Value-Scaled Eigenvectors			
Environments	1	2	3
Paralic Shale	0.426	0.057	0.019
Shoal Lmstn.	0.345	0.106	0.024
Upper Lmstn.	0.237	0.168	-0.091
Mid. Lmstn.	0.481	0.112	0.012
Phantom Lmstn.	0.389	-0.130	0.026
Organic Siltstn.	0.441	-0.147	0.062
Black Shale	0.256	-0.153	-0.149
Cond. Probability (Q)-Scaled Eigenvectors			
Environments	1	2	3
Paralic Shale	0.182	0.024	0.008
Shoal Lmstn.	0.119	0.037	0.008
Upper Lmstn.	0.056	0.040	-0.022
Mid. Lmstn.	0.231	0.054	0.006
Phantom Lmstn.	0.152	-0.051	0.010
Organic Siltstn.	0.195	-0.065	0.027
Black Shale	0.065	-0.039	-0.038

The resulting plots of the similarity structure among environments for the first three correspondence axes (Fig. 1) present the data at the bottom of Table 6 graphically.

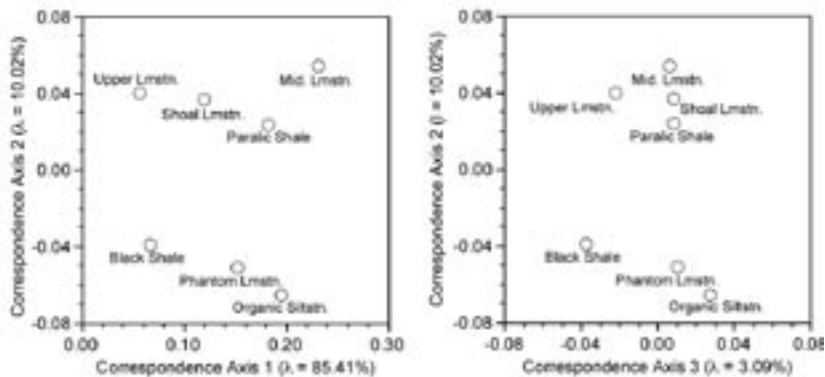


Figure 1. Scaled R-mode loadings on the first three trilobite frequency data correspondence axes.

These ordination plots are deceptively simple. As always, care needs to be taken with their interpretation. The clearest substructure among environments is the separation of shallower facies (Paralic Shale, Shoal Limestone, Middle Limestone, Upper Limestone) from the deeper-water facies (Phantom Limestone, Organic Siltstone, Black Shale). However, that separation occurs along the second correspondence axis, which represents only 10 percent of the overall variation (Table 5). The environment (facies) points are spread out along the first CA axis with no obvious clustering. What aspect of the original data matrix \mathbf{X} is this pattern expressing?

When in doubt, return to the basis matrix (in this case the R-mode χ^2 'distance' matrix, Table 4) and the original data (Table 1). Everything there is to see in the data should be visible there, especially if your eye has been clued in by seeing the ordination of R-mode loadings. The Black Shale and Upper Limestone facies plot low along CA-Axis 1. Inspection of Table 4 shows the 'biotic distance' between these facies is the lowest in the table. They should be close to one another along the predominant eigenvector. The pattern at one end of CA-Axis 1 should then be compared with that at the other end: the Organic Siltstone and Middle Limestone facies. Both are located at a relatively large distance from the Black Shale and Upper Limestone facies, and this is borne out by their distances from these facies in Table 4. This gives us confidence that the plot is a faithful picture of relations within the R-mode χ^2 'distance' matrix and encourages us to look further, to the original data. Take a look at Table 1 now and see whether you can find the pattern responsible for the distribution of facies along CA-Axis 1.

Did you find it? It's a bit subtle but it's there. If you didn't see it don't give up (and don't be lazy). Go back and look for it. No pain no gain and all that. Here's a hint: Think about the bottom line of any matrix-based data analysis. Of course, I'm stalling a bit here so the answer is buried in the text. If you're going to undertake multivariate analyses you need to develop a skill at looking for and finding the geometric patterns you see in the ordination plots within tables of numbers. But if you took that 'bottom line' bit to heart you now know that the distribution of points along CA-Axis 1 represents a measure of the relative frequency of trilobite occurrence in each of the



facies. In retrospect, this is perfectly understandable. Those 'bottom line' numbers summarize a dominant pattern among facies created by considering the data across all trilobite genera.

Many CA practitioners will tell you the best practice is to interpret only the correspondence axes that have eigenvalues less than 1.000 and term the first axis a 'trivial' or 'nuisance' factor (see Manley, 1994). After all, we already extracted that information during our scaling operations (it's the B_c matrix). This sort of CA-Axis 1 result doesn't show up in every CA analysis, but it's not uncommon. Some describe it as a trivial or 'nuisance' factor since it really doesn't tell us much about the relation between genera and facies we didn't already know without having dragged all the complex mathematical machinery of a full-blown correspondence analysis out of the closet. Still, 'trivial' and 'nuisance' are relative terms. It all depends on what you're looking for.

We now have interpretations of correspondence axes 1 and 2. What about CA-Axis 3? As with CA-Axis 1, we see the Black Shale and Upper Limestone facies form a group on the low end of that axis while the other four facies cluster together at the high end. Is the interpretation the same? Not quite. The ordination of facies along CA-Axis 1 is not clustered to the same degree and represents a pattern strictly controlled by the trilobite relative occurrence frequency. Not so with CA-Axis 3. Inspection of Tables 1 and 4 doesn't reveal an obvious pattern and, owing to the small amount of variance expressed on this axis, we really wouldn't expect them to. But there must be a reason for it.

Here is where the power of CA reveals itself. What we need is an explanation of the ordination pattern of facies along CA-Axis 3 in terms of the pattern of trilobite occurrences. In effect, we need to relate patterns of between-columns variation to patterns of between-rows variation. That's what CA does, and does more effectively than any of the methods we've discussed thus far. So how do we perform the Q -mode analysis in the context of CA? Best to go through the same set of calculations we did before, but this time focus on comparisons between rows rather than columns.

A couple of convenient mathematical theorems make this Q -mode analysis a snap. The first and most important of these is the Eckhart-Young Theorem which we've already met informally in the guise of Gower's (1966) proof that a PCoord analysis of a Q -mode squared Euclidean distance matrix is an exact mirror, or 'dual', of the covariance-based R -Mode PCA for the same data (see previous *PalaeoMath* 101 column: *Minding your Rs and Qs*). Eckhart and Young theorized that any real matrix X is equivalent to the product of three matrices, V , W , and U such that ...

$$X = VWU' \quad (8.5)$$

Matrix V is the set of Q -mode eigenvectors. Matrix U' is the transpose of the R -mode eigenvectors. Matrix W is the diagonalized matrix of 'singular values' that are equivalent to the square roots of the eigenvalues. Note here that all those times I've been asking you to multiply or divide matrix values by the square root of the eigenvalues in the previous PCoord analysis and above, I've really been asking you to make use of the data matrix's singular values. Goulub and Reinsch (1971) devised a method for finding these matrices directly and their method (with improvements) is now called singular value decomposition or SVD. The important result of the Eckhart and Young Theorem we need to make use of now is that, for real matrices such as the one we've transformed our trilobite frequency data into, the R -mode and Q -mode eigenvalues are the same (because the singular values of these matrices are the same). That means we don't



have to recalculate the Q-mode eigenanalysis. We've already determined the eigenvalues of both analyses (see Table 5).

Since we already have the *W* matrix we can easily use that to calculate the Q-mode CA loadings we need using the following equations.

$$A_q = H A_r W^{-1} \tag{8.6}$$

$$A_{q\text{-scaled}} = B_r^{1/2} A_q \tag{8.7}$$

This is equivalent to scaling each of the Q-mode eigenvector loadings by the corresponding singular value and the scaling by the R-mode conditional probabilities (= square roots of the row sums of the B-matrix). Results of this calculation for the first three correspondence axes (= eigenvectors) are shown below.

Table 7. Scaled Q-mode correspondence axis loadings (A_q-matrix)

Genus	Q-Mode Correspondence Axis Loadings		
	1	2	3
<i>Acaste</i>	0.047	0.013	0.001
<i>Balizoma</i>	0.043	0.024	-0.007
<i>Calymene</i>	0.052	0.035	-0.012
<i>Ceraurus</i>	0.061	-0.018	0.002
<i>Cheirurus</i>	0.089	-0.014	0.023
<i>Cybantyx</i>	0.056	-0.011	0.004
<i>Cybeloides</i>	0.046	-0.010	0.001
<i>Dalmanites</i>	0.042	-0.003	0.003
<i>Deiphon</i>	0.054	0.018	0.003
<i>Ormathops</i>	0.059	-0.005	0.010
<i>Phacopidina</i>	0.033	0.003	-0.004
<i>Phacops</i>	0.056	0.015	0.004
<i>Placoparia</i>	0.047	0.003	0.002
<i>Pricyclopyge</i>	0.042	-0.035	-0.018
<i>Ptychoparia</i>	0.077	0.001	0.013
<i>Rhenops</i>	0.035	-0.007	-0.004
<i>Sphaerexochus</i>	0.039	0.002	-0.002
<i>Toxochasmops</i>	0.043	0.019	-0.004
<i>Trimerus</i>	0.022	-0.003	-0.016
<i>Zacanthoides</i>	0.056	-0.028	-0.001



Plotting axes 2 and 3 in the same coordinate system as the *R*-mode loadings gives us the following diagram.

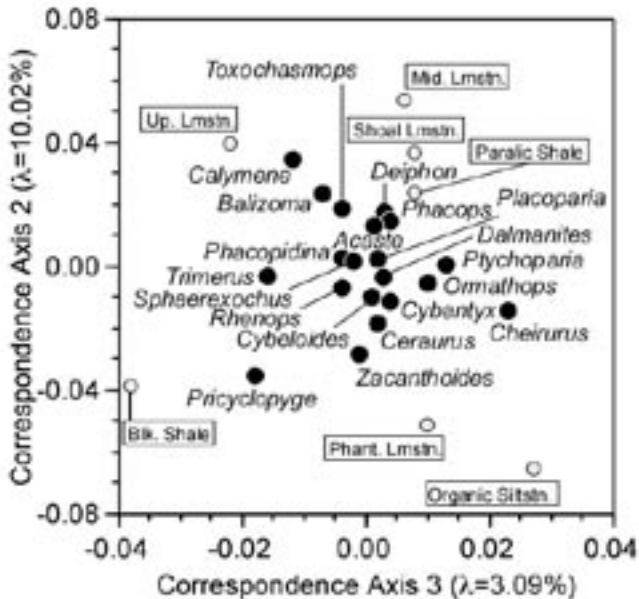


Figure 2. Q-mode loadings on the correspondence axes 2 and 3.

Comparison of figures 1 and 2 now reveals why the Black Shale and Upper Limestone facies are being pulled down along the third axis. *Pricyclopyge* exhibits a unique deep-water distribution and its relatively high abundance in the Black Shale facies is differentially affecting the placement of that facies. Similarly, the Upper limestone facies is being pulled down by the shallow-water occurrence pattern of *Calymene* and, to a lesser extent, *Balizoma*. Both these patterns are further reinforced by the unusual distribution of *Trimerus*. Note that the combined plot of the scaled *R*-mode and *Q*-mode loadings is also conveniently centred on the centroids of both datasets.

The ability of CA to handle simultaneous *R*-mode and *Q*-mode analyses in a manner that really improves the interpretation of data matrices and ordination plots is a big plus in the technique's favour. So is its similarity to PCA and FA, both of which have proven their usefulness in many different data analysis contexts. But there is another advantage possessed by CA that needs brief discussion: flexibility.

Recall that PCA is used to conduct *R*-mode analyses of data matrices composed of real numbers with no missing values. *R*-mode factor analysis can be used in the same manner, but is built on a different mathematical model than PCA. Principal Coordinates–*Q*-mode factor analysis can handle a variety of different data types, but only if you select an appropriate similarity/dissimilarity index. Correspondence analysis combines the best parts of all these methods and, as a bonus, can be used to analyse almost any type of data. In the example above we used it to

analyse occurrence frequencies. Because of the scaling calculations inherent in CA, this would be possible even if a large number of cells in the X matrix were occupied by zeros (= no observations or missing data). But while CA was originally developed to handle the case of contingency-table data, it is not restricted to analyzing nominal or ordinal data. It can handle interval and ratio data just as easily. To demonstrate this, here's a CA ordination of the original trilobite body and glabellar length data we've used throughout this series.

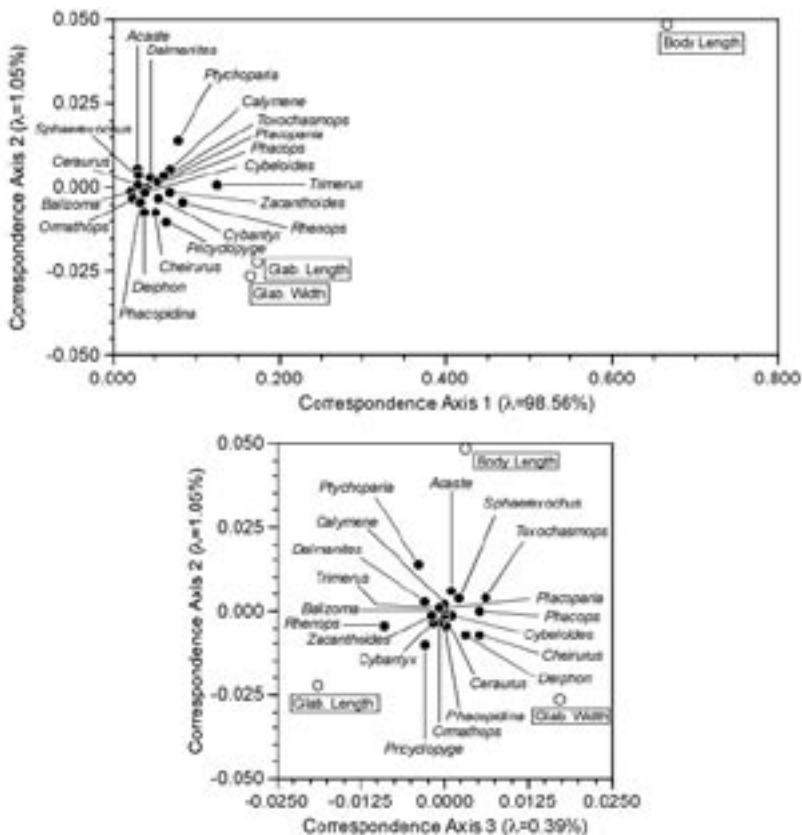


Figure 3. R-mode (hollow circles) and Q-mode (solid discs) correspondence axis scores for axes 1 and 2 (upper) and 2 and 3 (lower) of the trilobite body and glabellar size data.

Comparing these plots to Figure 7 of the PCA column (Newsletter vol. 59) shows that, with minor changes in relative point spacing (brought about as a result of the scaling calculations), the ordinations are very similar, with all outlying points in comparable relative positions. In that previous column recall we had to jump back and forth between the table of eigenvectors (shown just above Table 5 of the PCA column) and the plots in order to develop a sense of the geometric meaning of the PCA subspaces. We still need the eigenvectors to interpret the CA subspaces. But it's much easier and intuitive to develop these interpretations when a representation of the eigenvector 'positions' can be graphed on the same diagram.



The method I've illustrated above scales the results in terms of the B matrix. One can easily preserve the scale of the original X matrix by conducting all weighting operations using the original X matrix along with the row and column sums from that matrix. The singular values, eigenvalues, and eigenvectors will be the same, but the magnitudes of the H matrix, and D matrix, along with the various row matrices, column matrices, and eigenvector loading (= score) matrices, will be larger. The relative placement of points within the ordination diagrams should remain unchanged.

I appreciate this has been the most complex mathematical presentation of the series (thus far) and both thank and congratulate you if you've stuck with me to this point. As you can probably imagine there's much more to the mathematics of CA than I've presented here. What I've tried to do is give you enough maths to understand what CA is about, how to interpret CA results, how CA relates to the methods we've discussed previously. The *PalaeoMath 101* spreadsheet for this column contains a complete worked example of the trilobite frequency analysis. Look to that to clarify details of the calculations.

Correspondence analysis is a newer data analysis method and is being included in more high-end multivariate statistical analysis packages these days (*e.g.*, SPSS, SAS, Multitab, Statistica, GenStat). Not everyone has access to such packages, however, and it is expensive to acquire personal copies. Among the less expensive commercial software packages, XLStat (<<http://www.xlstat.com/en/home/>>) has a good implementation, as does CANOCO (<<http://www.pri.wur.nl/uk/products/canoco/>>). With a bit of practice and access to public-domain Excel routines like PopTools (<<http://www.cse.csiro.au/poptools/>>), though, you can easily make up an Excel spreadsheet that will perform simple CA analyses.

Sometimes you will see reference to a variant of CA termed 'detrended correspondence analysis' or DCA. This is a standard CA to which a post-processing step has been added in order to remove the possibility of generating ordinations that look like a parabola or a wave (also called the 'arch effect', horseshoe effect', 'Guttman effect'). Such results are usually obtained when analysing datasets in which there is strong gradient. Those who perform Q -mode analyses of any sort on a routine basis run into such results sooner or later. They are especially common in ecological analyses because one often runs into gradient-like structures in ecological data. Despite looking rather strange when you first encounter one, there's nothing wrong with an analysis that produces such a result. All it really means is that an important aspect of your data's variation is organized or patterned in a non-linear manner.

'Detrending' such plots sounds like a grand thing to do. Usually it's not. The most popular detrending algorithm arbitrarily subdivides the range of the data along one CA axis (usually CA-Axis 1) into a set of n bins and centres the data falling into each bin about 0.0. This removes the trend and 'linearizes' the data. But other than responding to an aesthetic desire to remove non-linearities from the CA scores, there seems little justification either for applying this method of *post hoc* data 'correction' or preferring it to other conceivable methods (*e.g.*, applying a curvilinear regression or spline function and representing the data along the CA-Axis 1 as residuals from the regression or spline axis). Indeed, such *ad hoc* manipulations can destroy aspects of the data's pattern that are important for its correct interpretation (see Watenberg *et al.* 1987 for a critical review). The safest course of action is always to try to stay as close to the raw data as possible.



My advice is not to correct any analytic result for what amounts to aesthetic reasons. If you find a horseshoe in your results it's telling you something about your data (presence of a gradient or some other source of non-linear signal). Use that information to understand how the pattern relates to your hypothesis test. Good discussions of, and further references to, the horseshoe effect can be found in Greenacre (1989), Reyment (1991) and Reyment and Joreskog (1993). Early and ecological practitioners of CA—and those influenced by them—often advocate detrending (*e.g.*, Pielou 1984, Hammer and Harper 2006). More recent commentators, especially those concerned with applications in the geological sciences, have been decidedly more sceptical as to the technique's value. Certainly the application of such 'corrections' to data in which there is no non-linear trend (see examples above) is entirely unnecessary and indefensible.

The methods on which modern approaches to CA are built are among the most powerful in the entire field of linear algebra. We'll encounter them again when we discuss how patterns of variation in one set of variables can be related to those on other sets of variables. Looking back though, CA is perhaps best understood as a generalization of PCA. Anything you can do with PCA you can do with CA. The main difference between the methods is that PCA allows you to choose whether to retain the original scale of the data (unstandardized, covariance-based PCA) whereas CA, of course, requires the data be normalized to 'correct for' scaling differences. The ability of CA to handle more different types of data is a product of its attention to scaling issues, and a clear advantage in terms of the number of different types of data analysis situations it can cope with. It is possible to scale PCA and FA results to portray both eigenvector loadings and the scores of objects on the same PCA/FA axis, using methods developed in the context of CA. I can present those variations on PCA/FA analyses if there's any interest.

Finally, a word about where CA leads us. There is a school of thought in multivariate data analysis that focuses on dimensionality reduction of complex numerical data and the production of graphs that express 'relations' between 'entities' in a low-dimensional space. This is the field of multidimensional scaling. Most often the purpose of these methods is simply to produce a picture of the data with little or no interest in the parameters of the data that control the graphical representation. The methods of PCA, PCoord, and CA are members of this family of data analysis techniques, and can be collectively referred to as classical approaches to the multidimensional scaling problem. There are other approaches (*e.g.*, non-metric multidimensional scaling) that are even more generalized than CA. What I've tried to do here is show that the classical scaling methods can not only be used to produce the picture of your data. They can also help you understand it. That's the ultimate plus in my book.

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REFERENCES

- DAVIS, J. C. 2002. *Statistics and data analysis in geology (third edition)*. John Wiley and Sons, New York. 638 pp.
- GOLUB, G. H. and REINSCH, C. 1971. Singular value decomposition and least squares solutions, 134–151. In WILKINSON, J. H. and REINSCH, C., eds). *Linear algebra: computer methods for mathematical computation*, v. 2. Springer-Verlag, Berlin.



- GOWER, J. C. 1966. Some distance properties of latent roots and vectors used in multivariate analysis. *Biometrika*, **53**, 588–589.
- GREENACRE, M. J. 1984. *Theory and applications of correspondence analysis*. Academic Press, London. 364 pp.
- HAMMER, Ø. and HARPER, D. 2006 (actually 2005). *Paleontological data analysis*. Blackwell Publishing, Oxford, UK. 351 pp.
- JACKSON, J. E. 1991. *A user's guide to principal components*. John Wiley & Sons, New York. 592 pp.
- MANLEY, B. F. J. 1994. *Multivariate statistical methods: a primer*. Chapman & Hall, Bury St. Edmunds, Suffolk. 215 pp.
- PEARSON, K. 1901. On lines and planes of closest fit to a system of points in space. *Philosophical Magazine*, **2**, 557–572.
- PIELOU, E. C. 1984. *The interpretation of ecological data*. John Wiley & Sons, New York. 263 pp.
- REYMENT, R. A. 1991. *Multidimensional paleobiology*. Pergamon Press, Oxford. 539 pp.
- REYMENT, R. A. and JÖRESKOG, K. G. 1993. *Applied factor analysis in the natural sciences*. Cambridge University Press, Cambridge. 371 pp.
- Spearman, C. 1904. 'General intelligence', objectively determined and measured. *American Journal of Psychology*, **15**, 201–293.
- WARTENBERG, D., FERSON, S., and ROHLF, F. J. 1987. Putting things in order: a critique of detrended correspondence analysis. *American Naturalist*, **129**, 434–448.

Don't forget the *Palaeo-math 101* web page, now at a new home at:

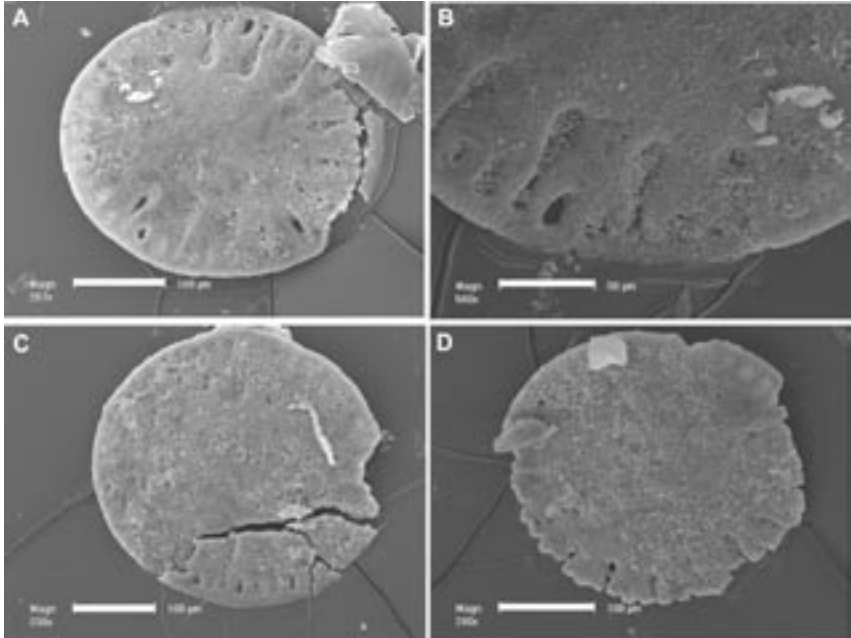
<http://www.palass.org/modules.php?name=palaeo_math&page=1>

Original article:

MACLEOD, N. 2006. Rs and Qs II Correspondence Analysis. *Palaeontological Association Newsletter*, **62**, 60–74.



MYSTERY FOSSIL 10



Mystery (Micro) Fossil number 10 was discovered by two students, Ania Witek and Iwona Jableka, of the University of Silesia while picking through sieved residues of Campanian age rocks from the Miechow area of southern Poland. John Jagt (Natuurhistorisch Museum Maastricht) and Elena Jagt-Yazykova (Uniwersytet Opolski) passed the SEM images on and say that the specimens have so far eluded definitive identification, with guesses so far ranging from holothurian ossicles, through coelenterates to octocorals. Three specimens are shown (A, C, D) and one detail (B) of the edge of specimen A. Scale bars: A, C, D = 100 microns, B = 50 microns.



Update on previous Mystery Fossils. Phil Hadland (Bristol University) suggests that the weird traces shown in Mystery Fossil 5 were caused possibly by a tetrapod with a hip pathology dragging its splayed hind quarters forward using only its forelimbs in a shuffling motion. Intriguing, but perhaps untestable?

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Meeting REPORTS



INYS International Networking for Young Scientists

Biodiversity: perspectives from deep time

Stockholm, Sweden 22 – 24 March 2006

In March, the Swedish Natural History Museum in Stockholm hosted the fourth International Networking for Young Scientists (INYS) workshop entitled *Biodiversity: perspectives from deep time*. The INYS is an initiative run by the British Council to support young researchers to build international connections and encourage exchange of ideas for future collaborations. Together, the British Council Sweden, David Cantrill and Jane Francis organised this workshop, making it an all round success.

The event brought together twenty-six scientists from the UK, Scandinavia and America to discuss aspects of biodiversity change seen in the past. Researchers were specialists in a range of areas from palaeobotany, palaeoclimatology and palynology to invertebrate and vertebrate evolution and mass extinctions. The three-day workshop was packed full of keynote lectures, round table discussions and poster presentations, as well as the obligatory evening social events. There was even time to squeeze in a tour of the Swedish Natural History Museum Palaeobotany and Palaeozoology stores.

The first keynote lecture was delivered by **Kirk Johnson** from the Denver Museum of Nature & Science, entitled: “The fossil record of hyperdiverse angiosperm forests and multiple origins of the tropical rainforest biome”. Kirk examined hypotheses of the radiation of angiosperm diversity. This involved highlighting the differences in species diversity and leaf characteristics between tropical and temperate forests and how this is used in understanding the fossil record.

The lecture was followed by several short poster presentations giving participants an insight into each poster topic. **Thomas Denk** (Swedish Museum of Natural History) presented a poster on plant diversity in the Cenozoic and problems of distinguishing species due to the presence of morphotypic variability. Next **Caroline Strömberg** (Swedish Museum of Natural History) examined grass evolution and the use of indirect fossil evidence to explore the spread of grasslands in the Late Miocene. Then **Guy Harrington** (University of Birmingham) discussed the paratropical floral extinction in the Late Palaeocene–Early Eocene. **Hervé Sauquet** (Swedish Museum of Natural History) reported palynological data on extant Banksieae (Proteaceae) and the use of diporate palynomorphs and serrate leaves as calibration points in molecular dating techniques.

The first round table discussion started with the topic “How good are our estimates of taxic diversity,” with various people commenting on their experience with their particular interest groups, from foraminifera and brachiopods to vertebrates. It was interesting to gain different perspectives on the same problem. The second round of poster presentations started with **Michael Hautman** (University of Bristol) explaining the reconstruction of species diversification patterns of bivalves and their use in analysing existing theories on biodiversification. **Daniela Schmidt** (University of Bristol) discussed the evolutionary history of calcification in planktic foraminifers and its influence on the global



Delegates enjoying a champagne reception [photo C. McDonald]

carbon cycle. **Mark Purnell** (University of Leicester) ended the day by presenting the difficulties in analysing historical aspects of diversity using vertebrate body plans to highlight the problems.

The second day was full of promise to deliver an interesting and thought-provoking array of presentations, even after a champagne reception the previous night with the British Ambassador to Sweden, Anthony Joyce Cary. The first lecture of the day was given by **David Harper** of the Geological Museum at the University of Copenhagen, entitled “The Ordovician biodiversification: setting an agenda for marine life.” The significant changes in biodiversity and complexity of marine species during this time were examined in terms of what drives the changes and the use of models to explain the relationship between ecology, environment, geography and adaptive strategy during them. The morning session ended with more poster presentations, with **Jan Ove Ebbestad** (Uppsala University) giving an introduction to gastropod biodiversity, biogeography and ecology in the lower Palaeozoic. **Jesper Hansen** (Tromsø University Museum) presented the influence of sea level oscillations and immigration of brachiopod taxa on an epicontinental brachiopod fauna in the Oslo Region. **Christian Rasmussen** (Natural History Museum of Denmark) examined the increase in brachiopod diversity in three case studies in the lower Palaeozoic.

The next speaker was **Vivi Vajda** from the Department of Geology at the GeoBiosphere Science Centre at Lund University in Sweden. The lecture was entitled: “Palynological diversity patterns: long term vs. short term ecological crises in Earth History.” The responses of different plant families to the Cretaceous/Palaeogene (K–T) boundary and Permian–Triassic (P–Tr) transition mass extinction events were documented. The second discussion session was centred on common patterns associated with diversification events and recoveries after mass extinctions. This resulted in various topics being talked about from carbon isotope shifts and radiation of the angiosperms to latitudinal effects and dating techniques.

The final lecture of the day was given by **Michael Foote**, entitled “Current Progress in the study of taxonomic rates of evolution.” The relationship between diversification, origination and extinction



was highlighted and the problems of taxonomic bias and variation in sampling quality were discussed. The next group session followed on from the lecture as it focused on evolutionary rate variations which brought up cladistic analysis, molecular dating and phylogeny calibrations. Poster presentations ended the second day with **Richard Twitchett** (University of Plymouth) commenting on Phanerozoic diversity and ecological functioning after mass extinction events. **Mats Eriksson** (Lund University) then highlighted polychaete radiation and diversification and the problems working with fragmented fossil evidence. Lastly, **Howard Falcon-Lang** (University of Bristol) introduced the topic of obtaining global climate data from analysis of growth rings in woods, and how it can be used in palaeoclimate studies.

The final day of the workshop began with **Alistair Crame** from the British Antarctic Survey, UK, giving a presentation entitled “Latitudinal gradients in taxonomic diversity: a perspective from deep time.” The pattern of higher diversity at low latitudes and tropical areas than at high latitudes and poles is documented. Evidence for an increase in taxonomic diversity, especially at the tropics – just as global climates were cooling – was also discussed. Then it was time for more posters with **Gary Mullins** (University of Leicester) presenting work on the phytoPal project which was set up to improve our understanding of how the diversity of phytoplankton changed through the Palaeozoic. **Anne Sørensen** (University of Copenhagen) described ongoing work on the diversity and variety of life forms from different areas on a transect from a Late Cretaceous rocky shore to deep water carbonate oozes. Finally, **Claire McDonald** (University of Leeds) reported on the variety of insect trace fossils found on Eocene fossil leaves from Antarctic and their implications. The last item on the agenda was a discussion on contrasting diversity patterns between marine and terrestrial realms where plant, animal and insect diversification was talked about.

It is therefore evident that the workshop covered a wide range of issues and brought specialists in different areas together to discuss such an important topic.

Claire McDonald

University of Leeds



Palaeogeography and Palaeobiogeography: Biodiversity in space and time.

Centre for Mathematical Sciences, Cambridge 10 – 13 April 2006

The meeting started on Monday 10th April at 1pm. I had just returned from the European Geophysical Union meeting in Vienna, where I had been presenting, listening and discussing, doing lots of sitting and walking around, and picking up many pieces of information, which I thought I needed to incorporate into my research. Now, I was back in Cambridge and a bit tired. Fortunately, there was a welcoming lunch buffet before the talks started.

I spend most of my research life dwelling into the Quaternary, where tectonic effects are negligible. I had concentrated my efforts examining a single group of organisms (planktonic foraminifera), studying the deep-sea North Atlantic sediments to infer high-frequency past climatic and oceanographic changes. Difficult to say what I was expecting from the meeting, except the opportunity to listen to something different.



The launch of the meeting was a welcome address by **Claire Slater** and **Stuart Ballard** from the National Institute for Environmental e-Science (NIEES). Professor Brett Riddle's introduction outlined the purpose of the meeting as being an invitation for people of various research backgrounds to listen to each other and exchange ideas. The Monday afternoon session chaired by Claire Slater was devoted to three exciting one hour-long keynote lectures.

Prof. Brett Riddle (University of Nevada) took us to the Neogene of Baja California. He explained how the unique geography of the 1,000 km long peninsula may have interacted with complex tectonic activity and sea-level changes triggering a series of vicariance events among both terrestrial and marine taxa during the late Neogene. The results were intriguing, especially for a palaeoceanographer; the vicariance events implied the existence of seaways for which no geological evidence has yet been discovered. My recent research on the Panama closure from palaeoceanographic and palaeoclimatologic perspectives made me think that examining deep-sea sediments to extract some clue about the history of this seaway could help with this intriguing biogeographic puzzle.

Dr Paul Upchurch (University College London) then gave a presentation entitled "What is wrong with palaeogeography?". First, the controversial and confused aspect of the subject was stressed and then the theoretical and practical problems exposed. Paul defined much of the terminology relating to palaeobiogeography and what palaeobiogeographers do, or rather as I understood it, what they aim to do. In particular, the reconstruction of the history of taxa and the detection of cyclical, climatically driven events, which can result in repeated area relationships. He told us about jump dispersal and geodispersal, the first acting as a "noise" in cladistic biogeographic analyses, while the second might be a source of signal. Paul then stressed that in the concept of area fragmentation and vicariance, if the barrier is geological it is assumed that this will leave a clear phylogenetic signal in the evolutionary trees of the taxa affected. However, the fossil record is very fragmentary or incomplete making palaeobiogeography very difficult and leading to an ontological dilemma. The evolutionary history of a particular group may have been congruent with other groups, but missing data or differential responses to vicariance may block this signal. Paul emphasized the need for more knowledge of the geological background including climate and ocean history. It emerged that biogeography has still many unresolved challenges, and there is a growing realisation that palaeobiogeography needs to be more analytical and less narrative, and needs to make use of databases, because in many cases the link between palaeogeography and palaeobiogeography is not straightforward.

The third keynote lecture was from **Dr Alan Smith** (University of Cambridge). Alan presented an animated set of global reconstructions through geological time and pointed out their uncertainties. From the onset Alan urged us to consider the reliability of different types of data used in palaeogeographic reconstructions through time. No undeformed Palaeozoic seafloor remains, and because most is remagnetized, not much can be reconstructed with certainty within the Palaeozoic era. After introducing plate tectonics, Alan underlined the need for palaeolatitudinal estimates to be constrained by precise palaeomagnetic data. Alan presented case studies of the complexity of crustal extension, which accompanies the creation of rifts, and the breaking-up of the crust into several pieces. Problems arise with fine detail, as in the case of the opening and closing of oceanic "gateways". As the oldest unsubducted oceanic crust is Callovian in age, for periods younger than this the magnetic strips recorded in the oceanic crust are being used to aid plat reconstructions. The



sediments covering the sea floor can also provide independent dating, which explains why Mesozoic age reconstructions are more precise. However, despite the possible use of complementary methods such as radar altimetry, which unmasks the topography of ocean floor in great detail, continental reconstruction still poses problems in areas where major deformation has taken place, such as the collision of India and Asia.

Then Alan explained the importance of hot spots as initiating the crust break up, and therefore creating gateways, giving the example of the opening of the north Atlantic during the Palaeogene thermal maximum. He stressed that the activity of hot spots as recorded by basalt-trap formation released a lot of SO₂ which, in turn, affects the climate and is associated with large biotic changes or even mass extinctions. Finally, according to Alan, additional problems in the field of palaeogeography include the lack of a good model for hotspot evolution; the lack of knowledge about the past height of mountains, which is very important for palaeoclimate modellers; and, to a lesser extent, the fact that in the past, although rare, the geomagnetic field could have been quadrupole or octopole.

Dr David Norman (Sedgwick Museum) introduced the evening social with an interesting historical account of the creation of the Sedgwick Museum, and how the magnificent collections were built up. There were drinks and nibbles as we congregated in the Museum. Very well attended, this was a very successful social event where people were exchanging ideas and commenting on the three keynotes of the day as well as admiring the beautiful collection on display. This was truly an enjoyable evening for all participants.

The next day, Tuesday 11th, was entirely devoted to invited talks, with the sessions being organised in a loose 'stratigraphic' order.

The first talk was by **Dr Robin Cocks** (Natural History Museum, London) about terrane recognition through the Phanerozoic. Robin explained that prior to 170 Ma palaeomagnetism of continental crust provides palaeolatitudes but is unable to provide palaeolongitudes, making terrane positioning subjective. While climatically significant sediments can help with latitude reconstruction, only key benthic organisms can help with specific terrane recognition. Robin presented the examples of the role of Ordovician trilobites and Silurian brachiopods in helping to refine terrane positioning.

Dr Malte Ebach (Université Pierre et Marie Curie, Paris) discussed the systematics of biogeography. First we heard that biogeography has both systematic and evolutionary aspects. Malte discussed how early phytogeographers defined regions (areas of endemism) as early as in the map of "la Flore Française" published by Lamarck and Candolle (1805). Most importantly he pointed to the crucial need for biogeography to adopt a more systematic approach to using biogeographic classification and diagnosis.

Prof. Alycia Stigall (Ohio University) examined the considerable potential for combining GIS and phylogenetics in palaeobiogeography better to understand extinction and origination patterns. The basic steps for GIS-based range reconstruction are database assembly (including taxonomy, geography, and stratigraphy) for specimens and the mapping of localities onto modern maps. The results of GIS analyses of species ranges coupled with phylogenetic analyses were used to examine faunal dynamics of the Late Devonian mass extinctions, using brachiopods and bivalves. This showed that a pattern of reduced vicariance could be recovered, which may relate to the reduction



in speciation rate observed during this interval. If Late Devonian species invasions and range expansions contribute to reduced vicariance, then modern species invasions may depress speciation rate among the modern biota as well.

Paul Upchurch chaired the second session of the morning, on Mesozoic palaeobiogeography.

Dr Wolfgang Kiessling (Humbolt–Universität zu Berlin) presented his latest research on geographical range and extinction risk: lessons from ancient marine benthic organisms. Geographical range is a key determinant of extinction risk today. Wolfgang used data on Middle Triassic to Late Jurassic benthic marine species occurrences to test for positive correlation between geographic range and species longevity. He found similarities between the extinction patterns of wide-ranging *versus* geographically-restricted taxa and common *versus* rare taxa. But narrow distributed, rare taxa had a significantly higher per-stage extinction rate than widely distributed and common taxa.

Dr Roy Livermore (British Antarctic Survey) presented a talk about Mesozoic palaeogeography: methods, limits and uncertainties. He summarized the development of methods of palaeogeographic reconstruction, from the earliest computer-based reconstructions of the continent to the latest GIS-based models that can incorporate information on palaeovegetation or palaeodrainage.

Dr David Cantrill (Swedish Museum of Natural History) closed the second session with a presentation on Southern Hemisphere biogeography with reference to the fossil record of Antarctica. He opened with a discussion of vicariance patterns across the Ethiopian Rift. As a full ocean has not developed yet, he used this as an example of a confirmed set of vicariance events that would not have a geological signal associated with them. This served as a segue into his work on angiosperm dispersal in the Mesozoic, which stressed the need for detailed palaeogeographic reconstructions to help discriminate between dispersal versus vicariance events.

After lunch we heard about Cenozoic palaeobiogeography and palaeogeography in a session chaired by Dr Malte Ebach.

The session started with a two-part talk entitled “Towards a specimen-based biotic history of Indo-West Pacific Cenozoic corals”: **Dr Brian Rosen** (Natural History Museum, London) presented the story to date. Brian outlined the importance of understanding the biotic recovery of coral reefs through time for conservation work in the face of human impact on reef ecosystems. Today corals are at their highest species richness and species abundance in the Indo-West Pacific (IWP), while there is only one genus in the Mediterranean Sea. However, it is important to understand how old this pattern is and what controls it. Brian put a Neogene age on the establishment of the pattern, and reported that during the Palaeogene the highest diversity was in the Atlantic. Brian also discussed the poor fit between coral diversity and climate curves, except in Europe.

Dr Kenneth Johnson (Natural History Museum, London) followed on with the second part of the presentation on the future research directions they had planned. Ken’s analyses were obtained using a specimen-based compilation of the distribution of scleractinian corals. Age assignments for each locality were based on planktonic and large benthic foraminiferal biostratigraphy. One important result of the study was a Pliocene diversity peak.



Prof. Isabel Sanmartín (Uppsala University) discussed new analytical methods in biogeography. Isabel stressed the need to understand the relative importance of vicariance and dispersal processes in the generation of biogeographic patterns.

Prof. Robert Hall (Royal Holloway) gave the final talk in this session, on the geological, oceanographic and climatic controls on the Wallace Line. This line, possibly the best-known biogeographic boundary, is located between Borneo and Sulawesi. As early as 1858 Wallace recognised the biological significance of this divide. The area is part of an active tectonic regime, with a fast active convergence zone. During the past 55 Ma a lot of crust has been subducted and mountain-building has occurred. This made the straits very narrow and shallow. This has influenced regional oceanography, forcing the Indonesia through-flow to parallel the Wallace line. The shallowing of the straits enhances the potential for small absolute changes in sea-level to drive major changes in the through currents, which could in turn have major influences on regional monsoon patterns and even global ocean circulation.

The last oral session of the conference, was devoted to recent biogeography and geography, and was chaired by Professor Brett Riddle.

Prof. Pascal Neige (University of Dijon) spoke on the use of disparity as a complementary diversity metric among extant cuttlefish. Pascal has studied 111 species within 17 biogeographic units. Pascal's results showed that along the western African coast high morphological disparity is associated with low species richness, whereas in eastern regions species richness is high, but disparity is low.

The second talk, Phylogenetic methods in Palaeobiogeography: closing the Gap between “Is” and “Ought”, was presented by **Dr Daniel Brooks** from the University of Toronto. Daniel opened with a discussion of the evolution of human pattern analysis behaviour, which explored the reasons why humans fear complexity and tend to retreat into simplification and generalization, even when such explanations ignore much of the evidence. When applying analytical methods one must weigh parsimony against simplicity and only simplify when such choices can be supported by data. Dan stressed the likelihood that reticulated area relationships are the rule and not the exception in biogeography, and our efforts should be directed at explaining ALL the observed data.

Dr Emma Telling (University College Dublin) presented a truly fascinating piece of research on “Bat biogeography as revealed by molecular phylogenetics”. Bats are the only mammal flyer. With more than 100,000 species they are only absent in the polar regions, despite some species being very endemic, and appeared 55 Ma ago. But the fossil record is very fragmentary, and it is difficult to quantify the fraction of missing fossil history because of the lack of a robust phylogeny. Emma presented us with the first well-resolved molecular phylogeny her results supported: the hypothesis that mega bats are nested within microbats and the latter are divided into four major lineages. Divergence time estimates indicate that each of the microbat lineages began to diversify in the early Eocene coincident with a global warming and increase in plant diversity and abundance, and the zenith of Tertiary insect diversity. Parsimony ancestral reconstructions refute a southern origin for bats and instead suggest that bats originated in Laurasia, possibly in North America. Three of the major microbat lineages are Laurasian in origin whereas the fourth is Gondwanan.

Prof. Peter Allison (Imperial College) talked on the application of the Imperial College Ocean Model to his research on “Tidal range and its palaeoenvironmental implications in ancient epicontinental



seas: the use of finite-element modelling to understand non-uniformitarian systems". Peter started with the observation that most of the marine sedimentary rock record is from shallow epicontinental seas. Tidal range is likely to have been a major influence on the hydraulic behaviour of these seas, particularly in the control of water column stratification. Peter presented some model simulation outputs showing that during the Late Carboniferous the epicontinental sea covering much of NW Europe would have had a cm-scale tidal range. This equatorial seaway would have been more susceptible to thermal and salinity-driven stratification, which would have in turn controlled factors such as oxygenation and carbon sequestration. Tidal range appears to be an unrecognised but important factor influencing the geological records of epicontinental seas.

The two final days were taken up by workshops, rather than talks. One of the advantages of the CMS site was access to a computer lab, which allowed a 'hands-on' component to some of the workshops, which was a success, and allowed considerable feedback and discussion during the remainder of the meeting.

The morning workshop on day three focused upon palaeogeography, with a demonstration of TimeTrek by **Alan Smith** and his colleagues Colin Reeves and Lawrence Rush. During the first hour of their session they showed some of TimeTrek's capabilities. The animations were particularly impressive. You can examine the range of palaeogeographic mapping tools the group has developed at <<http://www.the-conference.com/CPSL/>>.

Allister Rees (University of Arizona) ran the afternoon session dealing with various on-line data bases. Allister and the TimeTrek group were able to integrate data sets and display various palaeontological and climate-sensitive sediment data sets on the animations. Allister's work and links to data sets can be found at <<http://www.geo.arizona.edu/~rees/>>.

The second day of workshops concentrated on analytical tools.

Malte Ebach (Université Pierre et Marie Curie, Paris) gave a command performance on the chalk boards to discuss some of the theoretical issues he has had to grapple with during the development of his program '3Item,' which is a consensus-based methodology for phylogenetic reconstruction that he is working on extending to biogeographic problems.

Trying to keep delegates awake through the final afternoon, **Paul Upchurch** and **Al McGowan** presented the (almost) finished version of Simulation Program for Area-Taxon Analysis (SPARTA) that we presented a poster about at the 2005 Annual Meeting in Lille. We have been able to start using simulated data from SPARTA to begin to assess the ability of various biogeographic methods to recover a signal from known data. Some additional software tools for processing biogeographic data have also been developed.

The workshop days also allowed some exploration of Cambridge by the non-residents. One botanist managed to fit in a pleasant trip to the Cambridge Botanic Gardens. Other people took the opportunity to have more extended discussions about topics they were particularly interested in. CMS is an excellent facility for this purpose, as the building has many subdivided areas for small group discussion, as well as a large canteen area.

We must thank the National Institute for Environmental e-Science (NIEeS), who helped with a great deal of the logistical and computing support for the meeting. Quantifying and Understanding the



Earth System (QUEST) provided substantial funding to help support the meeting. The Geologists' Association, International Paleontological Association, Cambridge University Press, Blackwells and Taylor & Francis all made contributions that helped to make the meeting possible.

The Systematics Association, another major sponsor of the meeting, will be handling the publication of a special volume based on the meeting through CRC Press. A special issue of 'Historical Biology' will be coming out in 2007 with some papers from poster presenters. To whet your appetite until then, the meeting abstracts are available from the meeting website <<http://www.tethys.org.uk/biogeography>> as a PDF.

We will be migrating the meeting website to a permanent on-line archive soon, and will make as many of the speakers' presentations available as possible. Anyone who is interested in copies of the software and resources that were distributed at the meeting should contact Al McGowan by email (<a.mcgowan@nhm.ac.uk>).

Maryline Vautravers

British Antarctic Survey



Deep Time in Lyme

Impressions by Robert Ward (14) and Andrew Ward (11)

Lyme Regis, Dorset, UK 28 – 30 April 2006

Last year, over the Easter Weekend, our parents were invited by the Natural History Museum (NHM) to help with the first Lyme Regis Fossil Festival. We helped with their activity, and were involved in sieving and identifying sharks' teeth from the Abbey Wood Shell Bed. Our activity, and the whole Fossil Festival, was such great success that we were invited back this year, in our own right.

This year, the festival took place over the Spring Bank Holiday. It was extended from two to three days. As last year, we were in a marquee on the sea front close to the Marine Theatre, with the other Natural History Museum activities. The first day (Friday) was "Schools Day" when hundreds of school children visited the marquee. My parents said that they were dreading it, but it was not too bad, because the schoolchildren were very well behaved. The other two days were open to the public and we were so busy the memory is just a blur.

In our opinion, other than ours, the best activity was run by the NHM Palaeontology Conservation Unit (PCU). It involved building a dinosaur limb out of dog biscuits on a bed of clay, then covering it with more clay. Millions of years of time and erosion were simulated by hitting the clay a few times with a large hammer. The children then had to excavate the now-not-so-whole bones from the clay, without damaging them further. It was a chance for everyone to get their hands really mucky and have a lot of fun.

In contrast, the fossil casting activity was a model of precision, tranquillity and concentration. You were told how fossils were formed and you had the opportunity to make a plaster cast of a shark's tooth, an ammonite, a trilobite, fossil shrimp or sea urchin.



Rob excavating dog biscuit bones

People with special fossils, or things they found during the guided beach walks, were enthusiastically pounced on and had their finds identified by a flock of distinguished Natural History Museum experts.

A microfossil activity allowed you to search for microscopic fossils using a microscope and a brush. You could identify and keep the fossils you found, taking them home in a microscope slide.

The PCU demonstrated their drills and chisels. In this activity, James Fletcher showed me how to repair a broken dog biscuit from the Digging for Dinosaurs Activity. Useful.

There was also a book stall which was very successful, selling all kinds of very interesting books on fossils and minerals.

Our parents' activity involved sieving for fossil shark teeth. In this activity people got a cupful of Eocene Abbey Wood Shell Bed, and sieved it. You were left with what looked like just shells but if you look closely there were sharks' teeth dotted in the tray. Once you had sorted what teeth and shells you wanted, they were identified and labelled.

Overall we think the Festival was a huge success and I do hope there will be another next year.

Lyme Links

If you would like to know more about Lyme Regis and fossil hunting on the Jurassic Coast Dorset and East Devon World Heritage Site, you can find out more at the following websites:



Andrew and friends casting fossils

- Deep Time in Lyme: <<http://www.deeptimeinlyme.com/info.htm>>
- Jurassic Coast Dorset and East Devon World Heritage Site: <<http://www.jurassiccoast.com/index.jsp>>

If you are a young person interested in geology and palaeontology, you may be interested in joining Rockwatch, who will be able to put you in touch with local geological societies, as well as organising special events around the country. Their website address is: <<http://www.rockwatch.org.uk/>>.

Robert Ward

Andrew Ward



Barrington Pit Ichthyosaur excavation: from the Greensand to the galleries

Between July and September 2005 the Palaeontology Conservation Unit (PCU) of the Natural History Museum (NHM) led an excavation of an ichthyosaur specimen at Barrington Pit near Cambridge, owned by CEMEX. The ichthyosaur was exposed during routine excavation work at Barrington Pit, and John Drayton, the quarry manager, was notified. English Nature had to be consulted before the excavation could go ahead, as the site is a Site of Special Scientific Interest (SSSI). The exposure was of particular importance, as no fresh exposures of the Cambridge Greensand have been available for over one hundred years, and field collection techniques for vertebrate material have changed dramatically in that time.

The Cambridge Greensand, from which the ichthyosaur was recovered, was a major source of vertebrate and invertebrate fossils during the 19th century. Like the ichthyosaur at Barrington Pit, these fossils were discovered because of commercial activities. While Barrington is largely involved in the extraction of material for the construction industry, the earlier excavation of the Cambridge Greensand was related to agriculture. Phosphate fertilizers were derived from coprolites (fossil faeces), which can be thought of as a Mesozoic guano deposit. These coprolite layers were very



Scott Moore-Fay of the Palaeontology Conservation Unit (PCU) of the Natural History Museum (NHM) with part of the reconstructed dentary of the specimen.



A selection of teeth from the specimen.

distinctive, and commercial exploitation involved little more than strip-mining the coprolite levels. Cambridge and the surrounding area is dotted with old coprolite workings. Coldham's Common, which is about a mile from where I live, was one such site. Many of the Cambridge colleges owned the mineral rights to the areas that were mined, and made considerable sums of money from this industry.

The initial work was carried out by a large group of NHM personnel (Scott Moore-Fay, Andy Ross, Paul Barrett, Andy Carrant, Felicity Bolton, Lu Allington, James Fletcher and Jackie Skipper) during the week of 18–22 July. In addition to the obvious work of recording, preserving, and lifting the ichthyosaur remains, the stratigraphic and palaeoenvironmental context of the remains had to be established. Such data are as important as anatomical data that can be collected from the specimen, and the scientific value of any fossil is increased by the collection and accurate recording of the location, rock type, and other data relating to recovery of the fossil. Work on the site indicated that the stratigraphy consisted of underlying Gault Clay, followed by the Greensand. The Cambridge Greensand is an Upper Cretaceous (Upper Albian) unit. The top surface of the Gault was very uneven, and it appeared the carcass of the ichthyosaur had rolled around, depositing fragments in a variety of orientations. The Cambridge Greensand is a reworked deposit, so it was not unexpected that the ichthyosaur was somewhat disarticulated.

After the initial work in July, there was a need to return to the site to try to retrieve all other large fragments of the skeleton before the site became unworkable in the Autumn and Winter rains. As I live nearby, I went out with Scott Moore-Fay over 28–29 September. This was my first experience of a detailed vertebrate excavation, and it had much more in common with an archaeological dig



than my previous palaeontological field experiences. The site already had a reference grid laid out to record the position of the ichthyosaur elements and associated information. Scott had already decided which squares were the most likely ones to contain further remains, and which ones we needed to excavate to rule out as containing any further pieces of the specimen. Our main tools were a builder's trowel, dustpan and brush, rather different from my usual computer, camera and callipers. With these tools we carved our way through our grid squares down to the junction between the Gault and the Greensand.

We did recover more of the specimen, including a number of teeth, parts of the jaw, pieces of rib, and parts of the vertebral column. These materials had to be consolidated before they could be lifted and taken back to the PCU lab for further preparation work. A major aspect of the PCU is to develop and apply good conservation practice in the field and within the NHM collections. The consolidant that we used on the dig was conservation grade adhesive called Paraloid B72 dissolved in acetone. This adhesive does not yellow with age, cross-link or become brittle, so is widely (almost exclusively) used in the museum industry. By dissolving the consolidant in differing quantities of acetone the adhesive can be thinned so that it penetrates into the bone and all cracks. This is especially important on specimens riddled with cracks or fractures and specimens that are very friable.

An associated fauna was collected from the site as well. The taxonomic list included bivalves, brachiopods, sponges, fish teeth and centra, large numbers of shark teeth and several shark centra, gastropods, small fragments of fossil wood, belemnites, bryozoa, and a turtle. Amber pieces, some clear with air bubbles and some cloudy, were also found.



Figure 3. Elements of the associated fauna.



A recent visit to the PCU allowed me to see the material after some reconstructive work and preparation. Many fragmentary pieces of bone had been reunited and pieced together. The practice of mapping the position of each fragment, and assigning each fragment a unique ID number based on its grid square, made the task of uniting parts of the same bones much easier. A tentative identification of *Platypterygius sp.* has been made for the ichthyosaur, and preparation and restoration work continue on the specimen. The fauna found associated with the ichthyosaur is now under study by a number of people. Hugh Owen and I are identifying the ammonites that were recovered from the excavation. As a Triassic ammonoid worker I am a bit out of my field, and I found a display in the public galleries in the Sedgwick Museum in Cambridge very helpful, both as a starting point for identifications and for background to this article, as it dealt with both the coprolite workings and the detailed ammonite biostratigraphy of the area around Cambridge. CEMEX have donated the specimen to the NHM, so hopefully it will make it all the way from the Greensand to the NHM galleries for all to view in the future.

Al McGowan

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What a long strange trip it's been...

Ten years ago, when our second child was born and Anita's career began to defy gravity, I decided to quit a career in palaeontology so that I could help out more at home. It wasn't an easy decision, nor was it made in a hurry. At first I kept my options open. A career break, originally intended to last for only a year, stretched out to five years before the resignation letter was finally posted, and the Rubicon crossed.

Beyond the point of no return, the process of packing away the ephemera of one life to make way for another began. The files, the reprints, the projects in progress, the unfinished papers, all packed in anonymous cardboard boxes and consigned to the loft. And the specimens, so many specimens, each with a memory attached, a time, a place, a feeling, and the promise of a story still to tell, banished to the barn to continue their journey through deep time beneath new strata of dust and swallow guano, half way to the dump.

Yes, it has been hard to let go. I am a life-long addict of all things fossiliferous. I know that now. I do not have the strength of mind, or character, to make a clean break. Somehow, I never managed to allow my membership of Pal. Ass. to lapse. I still dissect lasagne layer by layer. I still rubberneck at the tiniest hint of roadside outcrop whilst zipping along country lanes, and I still annoy the family by insistently correcting the TV for its factual lassitude. Sometimes months can pass without me picking up a geological hammer, but I always know exactly where it is. Then there is the lure of the beach.

Our farm snuggles in a hollow between two hills, each carved from black basalt flows of the Antrim Lava Group. Step out of the back door, and it's only a two minute walk down the track to the shore. As beaches go, it's not exactly holiday brochure material. Behind the raised beach, a steep slope of gorse and hawthorn marks a degraded cliff line, cut into the red Mercia Mudstone that occupies the hollow. Below the raised beach, a narrow belt of shingle and cobbles gives way to a wide expanse of rounded basalt boulders and weed at low tide. A most unpromising scene for any palaeontologist, but things are not entirely as they seem.

Things never are around here, but this part of the world does not give up its secrets lightly. The Mesozoic geology has a character all of its own. Deep basins, initiated in the Permian, preserve thick sequences, which have more in common with the offshore basins to the North and West of Ireland than with the classic successions of southern Britain. These basins are poorly known and little studied. Veiled by a thousand metres of dense, geophysics-frustrating, plateau basalts, a generous helping of glacial till, grass, and cows, the Mesozoic peeps coyly. No wonder, then, that the North of Ireland has failed to attract the attentions of Mesozoic specialists, and that even those few based here have been largely distracted by the more brazenly exhibited charms of strata across the water. The politics of this land have not been conducive to the advancement of science either. A land that time simply gave up on, Ulster sits physically and psychologically isolated on the northwest frontier of Europe. Dependant for so much upon mainland Britain, yet shunned by its populace as the black



sheep of the family. I may have a soft spot for the place now, but I do remember having very mixed feelings when offered a job here many years ago, and I do understand that when given a choice between fieldwork in Ulster or, say, Afghanistan, most UK based palaeontologists would choose Afghanistan on the grounds that it has better exposure and doesn't rain as much.

Our beach isn't mentioned in the survey memoirs, it's not mentioned in the literature, and in fact it's not mentioned anywhere. There is apparently nothing at all of geological interest here. The locals call it the Backshore. In times gone by, the Backshore bustled with activity, for those who didn't farm on the island fished for their livelihood, and many did both. A fleet of small wooden boats plied the inshore kelp beds for blocken and lithe, for hern, mackerel, and in Winter, for cod. Lacking anything resembling a harbour, the boats could only be beached on the shingle at high tide, except at the 'ports', places where the boulders had been cleared from the foreshore by the labour of men and horses, and one suspects, the odd stick of dynamite, in a strip five yards wide, for as much as a hundred yards down to the low water mark.

For a palaeo-addict in recovery, the Backshore should have provided a safe haven, a fossil-free zone where I could be distracted by the seals, the choughs, or the occasional cetacean, whilst the kids do the things kids do with crabs, and sand, and seaweed. Instead, it has proved to be my downfall, for the boulder-strewn expanse of the backshore was formed from eroded remnants of the lateral moraine of the Irish Sea Glacier, that vast relentless conveyor of exotica from the Firth of Clyde, from Ayrshire, and from all points north. I may have been able to resist the temptation to jump in the car and go fossil hunting, but when nature conspires to bring miscellaneous petrifications to you, and dumps them on your doorstep, what can a poor addict do?

Most of the fossiliferous blocks are, of course, of more local derivation, carried down along the Antrim coast upon the broad shoulder of the glacier. Hunt around among the boulders, and it soon becomes apparent that some of these are not as randomly distributed across the shore as one might expect, but tend to occur in discrete concentrations. Dig away the sand and gravel from below the boulders, and another secret is revealed, for parallel to the strand line, an unseen and uncharted fault has downthrown Rhaetian and Hettangian strata against the Mercia Mudstone, to subcrop just below the beach deposits and the last remaining smears of till. For a while I was in clover. The resistant limestone blocks yielded a prolific fauna, and allowed my cravings to be sated on a regular, but not inconvenient, basis; methadone for the junkie. Alas, it could not last. A finite resource and the law of diminishing returns were beginning to result in lean pickings. My forays took me ever further afield, until, a few months ago, I fetched up, five hundred metres south, in the dark shadow of Muldersleigh Hill, at Cloghfin Port.

At Cloghfin Port, also known locally as the Stinking Port, because mounds of decaying kelp accumulate on the strand line in this corner of the bay, my fate was sealed, and any hope of recovery finally abandoned. There was something just too tempting to be left alone. It started harmlessly enough. A few loose blocks of sandstone from the Penarth Group with vertebrate bits and pieces; nothing fancy. Then the trace fossils started accumulating, then the bivalves. Before I knew it I was completely hooked again, an obsessive-compulsive rock-chipper. What a waste. None the less, this lot was going to need writing up. The loft was raided, back issues of journals recovered, and a frantic search for more recent related literature initiated. In the intoxicated euphoria of a true backslider, I even put some limestones in acid to see if any conodonts would



drop out. Meanwhile, e-mails were sent requesting reprints, and the task of mapping and logging the fiendishly obscure mosaic of tiny outcrops amongst the boulders began in earnest.

As it happens, Cloghfin Port does get an honourable mention or two in the literature, but most attention has been directed at the well exposed Upper Cretaceous and Palaeogene (basalt) sequences at this locality. Generations of Queen's University undergraduates, and their lecturers (and yours truly!), have stomped and stumbled across the scrappy outcrops of the late Triassic, with only a passing nod in their direction, *en route* for the Hibernian greensand, that quintessentially Irish formation with facies quite distinct from the correlative chalks of southern England. It is a curious feature of Irish Mesozoic stratigraphy, but perhaps not a surprising one given the geopolitical and historical context within which the science was carried out, that the Irish Mesozoic has been treated as a mere appendage of the British Mesozoic. From the early work of Portlock onward, correlation with the established English sequence was the aim, and similarities were naturally emphasised over differences to support those correlations. This resulted in the wholesale application of British lithostratigraphic terminology to the Irish sequences (again emphasising the correlations), and the implication that the Irish Mesozoic is basically the same as the British, but much more poorly exposed. Consequentially, if you were to conduct a literature survey of the Irish Mesozoic, you might well come to the conclusion that it is 'known'. In actuality, this is far from the case, but the illusion has had the unfortunate effect of stifling research effort.

Cloghfin Port provides a graphic, and somewhat ironic, example of this effect. The literature relating to the late Triassic portion of the locality amounts to two sketch maps (which differ in so many respects that you might be forgiven for thinking that they are not of the same locality), and



Rockhounds in the foreground; Cloghfin Port and Muldersleigh Hill in the background



a few lines of vague description, in publications of the Geological Survey. There is not the slightest hint that Cloghfin might be an exceedingly interesting site, which has a lot to say about late Triassic events and stratigraphy (it is, and it does), in fact the literature gives quite the opposite impression. Of course, it's not the job of the Survey exhaustively to document every outcrop in the land, and I intend no criticism of any previous work. My point is that the literature on the Triassic and Jurassic of the North of Ireland is so scant that it implies that there is nothing of interest for specialists to look at. Had the literature even mentioned trace fossils at Cloghfin Port, then I am sure Tony Wright and Mike Benton (both then at QUB, just a few miles down the road) would have found and written up that excellent assemblage, saving me from my current predicament, and a deal of disapproval from the wife, in the process. As it transpires, their work on Westbury Formation material from *Staffordshire* remains the only comprehensive description of a Penarth Group trace fossil assemblage.

The postman left a steady trickle of brown paper packets at the door as the reprints started to arrive (thanks to all of you who responded). It quite soon became apparent that most of the work relating to the Penarth Group that has been published over the past ten years was carried out in the context of studies of the Triassic–Jurassic boundary interval. This was all new to me, a past patron of Devonian deltas and Carboniferous swamps, Mr. How-many-hairs-on-the-scorpion's-foot (well it takes all sorts). This was all mass extinctions, and sea level change, and cosmic cannon balls, and something called CAMP. Not really my thing at all. I was, however, surprised to learn that there is a global shortage of good continuous marine sections through the critical interval. I suppose it was the old 'familiarity breeds contempt' thing at work, but somehow it had completely failed to occur to me, while I was busy counting those scorpion hairs, that the rocks I walk over every day might actually be rather special in a global context; that their significance might extend beyond 'good spots to find nice ammonites'. And then I realised what a first class pillock I had been. English Andy has been sleepwalking over the geology of Ulster for the last fifteen years, lulled into a drugged soporific state by the subtle cultural imperialism that insists all roads lead to Rome, or, in this case at least, to the Glorious Jurassic Coast and its green and pleasant hills. The scientist within was finally awakening.

Around about this time, whilst trawling the Internet for all things Rhaetian, I came across the website of the International Commission on Stratigraphy, and discovered the reason why so much attention had been focused on the Triassic–Jurassic boundary interval; the base of the Jurassic system has still not been defined by a GSSP. There are several candidate stratotype sections under consideration by the Subcommittee on Jurassic Stratigraphy, including the section at St. Audrie's Bay in north Somerset, generally regarded as the best (most 'expanded') section available in Britain. A lot of effort has been concentrated on St. Audrie's Bay in recent years by numerous workers, documenting the sedimentology, biostratigraphy, isotope stratigraphy, magnetostratigraphy, sequence stratigraphy, *etc.* Going through the various accounts of St. Audrie's Bay, I started to feel a little uneasy. For an 'expanded' section, St. Audrie's Bay looks significantly less complete than the sections I am familiar with in the Larne Basin, particularly the excellent foreshore exposure on the outskirts of Larne. Why on earth had no one come over here to take a look?

I can only surmise that the 'literature effect' has struck again; that it has been assumed the Irish Mesozoic basins are just poor reflections of the British 'type areas'; that there is nothing to merit further investigation. In time, of course, this erroneous impression can be corrected. I, for one,



will do my bit, and make sure that the work on the Rhaetian succession of the Larné Basin gets published, but time is in shorter supply than good T–J boundary sections, for the ISJS has stated its intent to complete GSSP proposals for all remaining Jurassic stages in time for the Jurassic Congress in September this year. The selection of GSSPs ought to be based upon the best available scientific evidence, but we all know that science, the art of getting things right, is in a perpetual dynamic tension with politics, the art of getting things done. I would argue that, in the case of the base Jurassic GSSP, it is more important to get it right than to get it done according to a politically convenient timetable, even if that means delaying a recommendation on the GSSP so that the merits, or otherwise, of alternative sections can be properly assessed, which need not take a great deal of time.

Of course the ISJS has an unenviable task. The end-Triassic ‘mass extinction’ is a diffuse affair, and, compared with other mass extinction events, still not understood very well. There is every possibility that, as research continues, new sections will be found which shed more light on this intriguing interval. This raises the question of whether it is still too early formally to define the base of the Jurassic system, or whether it is better to establish a GSSP now, even though it may be necessary to revise the GSSP in the light of ongoing research, as has happened with other GSSPs. There can be no doubt that the work of the ICS, and particularly its efforts to define global chronostratigraphic units, has focused minds and research effort on some particularly thorny problems. The T–J boundary has proved to be one of these, and in some respects, the intensified research has only served to highlight how little we know. Inevitably, as a political entity, the ICS wishes the job to be done within a reasonable timeframe, and as a scientific entity, it must anticipate some slippage to ensure due rigor. Is this not a dilemma that we all face in our individual research? I hear through the grapevine that a new T–J boundary section in Austria is to be proposed as a candidate GSSP at the forthcoming Congress, so perhaps the slippage has started. Let’s hope that the research momentum generated as a result of the boundary issue does not dissipate once the job is judged done.

I am not privy to the discussions and thinking of the Subcommittee, or the appropriate working group, so I don’t know which of the candidate sections they currently favour, nor do I particularly care, as long as it is the section which best meets the scientific criteria. I do, however, care that the process for identifying and selecting candidate sections, which I don’t doubt was rigorously carried out, has failed to recognise the very good boundary sections in the Irish basins as worthy of further investigation. If this rigorous process has failed to flag up the Irish basins, then we do indeed have a serious problem with the literature, and if it can happen here, where else?

Well that’s my story, and what a long strange trip it has been. It seems I am a *bona fide* palaeontologist again, complete with works in progress, new piles of fossils, new files of reprints, and new sets of administrative headaches as I try and persuade my new-found colleagues to do things I know they really don’t want to do. I’m beginning to remember why it wasn’t so difficult to give up all this in the first place. Maybe I’ll give it another try, for the sake of the family, or maybe I’ll just slip back into those nice quiet backwaters of the Carboniferous. In the meantime, I have to keep reminding myself; don’t neglect what’s right on your doorstep, and *never* trust the literature when you can check it out for yourself.

Andy Jeram

Mullaghdubh House, 27 Gobbins Path, Islandmagee, Co. Antrim BT40 3SP
e-mail: <anitajeram@aol.com>



>> **Future** Meetings of Other Bodies

Please find below a list of known meetings from other bodies. Help us to help you! *Send announcements of forthcoming meetings to:* Meetings co-ordinator (<meetings@palass.org>).

The Palaeontological Association Future Meetings website is updated regularly; it is at <<http://www.palass.org/modules.php?name=palaeo&sec=meetings&page=55>>.



11th Chilean Geological Congress Antofagasta, Chile 7 – 11 August 2006

The 11th Chilean Geological Congress organized by the Department of Geological Sciences of North Catholic University (Universidad Católica del Norte) will be held between 7th and 11th August 2006, and will be dedicated to the memory of Mr Renato Fernández Flores, the geologist who contributed significantly to the formation of the Geology programme of this university. The official headquarters of the congress is Universidad Católica del Norte, Antofagasta, 2nd Region, Chile. The official language of the Congress is Spanish, but publications and presentations will also be accepted in English. The programme of the Congress includes: Thematic Sessions, Symposia, Invited Conferences, Scientific Poster Sessions, Field Excursions, Special Meetings, Technical Exhibitions, and Social and Cultural Activities. For further information, including instructions for abstract submission, please visit the congress website at <<http://www.congresogeologico2006.cl>>.



IGCP Project 503: Changing Palaeogeographical and Palaeobiogeographical Patterns in the Ordovician and Silurian Glasgow, Scotland, UK 30 August – 1 September 2006

This is the third Annual Meeting of IGCP 503, Ordovician Palaeogeography and Palaeoclimate, which aims to develop a better understanding of the environmental changes that influenced the Ordovician biodiversification, the end-Ordovician extinction and the Silurian radiation. It will focus on the changing palaeogeographical and palaeobiogeographical patterns in the Ordovician and Silurian, but contributions on any topic relevant to the aims of IGCP 503 will be welcome.

The main part of the conference will comprise two and a half days of lecture and poster presentations (30th August to 1st September), a half-day local mid-conference excursion, and various social events including a whisky tasting. There will also be a pre-conference day excursion to the Scottish Southern Uplands, including the Ordovician–Silurian boundary stratotype section at Dob's Linn (29th August), and a three day post-conference trip to the classical Ordovician and Silurian successions in southern Scotland at Girvan and in the Pentland Hills (2–4 September). Further details can be obtained from the IGCP 503 website at <<http://sarv.gi.ee/igcp503/>> or from the conference organiser, Alan Owen, e-mail <a.owen@ges.gla.ac.uk>.

**The Sauropterygia: The first European Association of Vertebrate Palaeontology (EAVP) Themed Symposium**

Karlsruhe, Germany 4 – 8 September 2006

The Sauropterygia will be the first international conference devoted exclusively to all aspects of sauropterygian palaeontology. Organised and run under the auspices of the European Association of Vertebrate Palaeontology (EAVP), The Sauropterygia will be a wide-ranging, cross-disciplinary summary of all the latest and most exciting research into the sauropterygian reptiles, ranging from historical perspectives and current successes, to future prospects.

Olivier Rieppel (Chicago), Nathalie Bardet (France) and Zulma Gasparini (Argentina), have agreed to act as keynote speakers, and will give a truly international flavour to The Sauropterygia. Abstracts will be published in *Oryctos*, and it is anticipated the conference will be followed by publication of a longer, high-quality peer-reviewed volume.

The language of the conference will be English; however, members of the organising committee are also native speakers of German, French and Spanish, and questions can be answered in these languages if required. The first point of contact is via the EAVP website (<<http://eavp.alettra.de/>>), or alternatively contact: Dr Leslie Noè (e-mail <noe01@esc.cam.ac.uk>), The Sedgwick Museum, University of Cambridge, Cambridge, United Kingdom.

**3rd Workshop on Ichnotaxonomy**

Prague, Olomouc and Brno (Czech Republic) 4 – 9 September 2006

For further details see

<http://www.gli.cas.cz/GLU_AV/WIT_2006/3rd_workshop_on_ichnotaxonomy.htm>.

**Carboniferous meeting “From Platform to Basin”: A field and research conference sponsored by SEPM-CES**

University of Cologne, Germany 4 – 10 September 2006

The Carboniferous Conference Cologne 2006 will take place at the Institute of Geology and Mineralogy of the University of Cologne. The heading of this SEPM-CES research and field conference “From Platform to Basin” links a wide range of topics from very different disciplines in Earth Sciences. Field-trips to Belgium and Germany will follow a transect from the inner platform to the deeper basin. Full details, key dates, contacts, and a pre-registration form can be found on the conference website at <<http://www.ccc2006.uni-koeln.de/>>. Please have a look at the website at regular intervals for updates and new information.

Organisers: Hans-Georg Herbig and Markus Aretz (e-mail <markus.aretz@uni-koeln.de>).



The 7th European Paleobotany–Palynology Conference (EPPC)

Prague, Czech Republic 6 – 11 September 2006

For further information, see the circular which is on the meeting website (in PDF format) at <<http://www.natur.cuni.cz/eppc2006/circular.pdf>>.

Register now to ensure your participation on field trips, workshops, and other events



4th London Evolutionary Research Network Student Conference

Institute of Zoology, London 8 September 2006

Call for abstracts (talks and posters) and registration (Admission free). Open to all postgraduate and post-doctoral students working on evolutionary research. Primarily aimed at students associated with a London teaching institution. Abstracts should be 150 words long or less.

For further details contact Emily Hornett (e-mail <e.hornett@ucl.ac.uk>) or Victoria Herridge (e-mail <v.herridge@ucl.ac.uk>)

View the LERN website at <<http://www.anat.ucl.ac.uk/research/lern/>>



PSSA 2006: Biennial Meeting of the Palaeontology Society of South Africa

Albany Museum/Rhodes University, South Africa 8 – 12 September 2006

Every two years a meeting of the Society is arranged at a different venue in Southern Africa. The format of the meetings, usually over a five day period, is three days of conference proceedings (papers and posters, *etc.*) and the Biennial General Meeting of the Society. The last two days are devoted to a field trip to sites of palaeontological interest in the district.

If you would like to attend the PSSA'2006 meeting at Rhodes University and the Albany Museum in Grahamstown, please contact Dr Billy de Klerk (e-mail <b.deklerk@ru.ac.za>) or Dr Rose Prevec (e-mail <rose.adendorff@ru.ac.za>) for more details.

Billy de Klerk, Curator: Earth Sciences, Albany Museum, Somerset Street, Grahamstown, 6139, South Africa, tel (046) 622-2312, fax (046) 622-2398, e-mail <b.deklerk@ru.ac.za>.

For further information see <<http://www.ru.ac.za/affiliates/am/pssa/pssameet.html>>.



FORAMS 2006: International Symposium on Foraminifera

Natal, Brazil 10 – 15 September 2006

Register now to ensure your participation on field trips, workshops, and other events. Updated meeting information (Scientific Programme for Technical Sessions and Workshops, and much more),



online registration forms, and information for the submission of abstracts are available now at the FORAMS 2006 websites so you may register at any time.

The Web addresses are:

New address: <http://www.fgel.uerj.br/forams2006/>

Mirror site: <http://forams2006.micropress.org/>

Please note that the final acceptance of abstracts for all presentations depends upon full payment of the registration fees, which should have been received by 30th June 2006. Only registered participants will be allowed to attend the meeting.



16th International Meeting on Natural Science in the New World:

The Descriptive Enterprise

Montreal, Canada 21 – 24 September 2006

Further information on this meeting can be obtained from Ingrid Birker (<e-mail ingrid.birker@mcgill.ca>, Paleontology Curator, Redpath Museum), Victoria Dickenson (e-mail <victoria.dickenson@mcCORD.mcgill.ca>, Director, McCord Museum) and Johanne Landry (e-mail <johanne_landry@ville.montreal.qc.ca>, Directrice, Insectarium de Montréal). Registration \$175 CAD; additional charges for banquet and field trips.



17th International symposium “Biodiversity and Evolutionary Biology”

Bonn, Germany 24 – 28 September 2006

The conference will take place in Bonn-Poppelsdorf, where many of the institutes of the Friedrich-Wilhelms University of Bonn – including the Nees Institute, the Botanical Gardens and the Poppelsdorf Palace – are located. The registration will be at the conference office in the Foyer of the Anatomical Institute, Nußallee 10, where also the lecture programme will take place. Conference languages are English and German but contributions in English are encouraged. Registration is open until 30th June 2006, and the registration form is available on the symposium website from 1st May 2006 onwards. The deadline for the submission of abstracts for both papers and oral presentations was 31st May 2006. For further information please visit the conference website at <<http://www.nees.unibonn.de/symp17/>>.



Biennial Meeting of the Palaeontology Society of South Africa: PSSA'2006

Grahamstown, South Africa 13 – 17 October 2006

Every two years a meeting of the society is arranged at a different venue in Southern Africa. The format of the meetings, usually over a five-day period, is three days of conference proceedings (papers and posters, *etc.*) and the Biennial General Meeting of the Society. The last two days are devoted to a field trip to sites of palaeontological interest in the district.



If you would like to attend the PSSA'2006 meeting at Rhodes University and the Albany Museum in Grahamstown, please contact Dr Billy de Klerk or Dr Rose Prevec for more details.

Billy de Klerk (e-mail <b.deklerk@ru.ac.za>), Curator: Earth Sciences, Albany Museum, Somerset Street, Grahamstown, 6139, South Africa, Tel: (046) 622-2312; Fax: (046) 622-2398,

For further information see <<http://www.ru.ac.za/affiliates/am/pssa/pssameet.html>>



16th Canadian Paleontology Conference
Montreal, Canada 13 – 17 October 2006

Each year the Paleontology Division of the Geological Association of Canada holds a scientific meeting at a selected location in the country. The 16th Canadian Paleontology Conference (CPC) will be held on 13–17 October 2006, at the Redpath Museum / McGill University in Montreal. Co-organized with the Musée de Paléontologie et de l'Evolution / Museum of Paleontology and Evolution (MPE), the meeting consists of a Friday night Icebreaker followed by a weekend of paper and poster sessions. A post-conference two-day field trip to Quaternary (Champlain Sea) sites and collections in Ottawa, Montreal and Quebec City is co-organized with the Society of Vertebrate Paleontology. The conference may also feature a Plenary session on Patrimoine Paléontologique du Québec and possible Workshops on Quantitative Paleontology and/or Taphonomy.

Accommodation: Our official conference hotel, the Days Inn, is located just off campus, about a 15 minute walk from the Redpath Museum. Blocks of rooms have been reserved at a rate of \$95.95 per day, single or double occupancy, taxes not included (\$15 per additional person). Two small hotel-style / B&Bs close to the Museum offer rates of \$70 – \$115 for double accommodation: the Hotel Manoir Armor Sherbrooke (<<http://www.amormanoir.com/>>) and the Manoir Ambrose (<<http://www.manoirambrose.com/>>).

Registration fees for CPC 2006 are \$100.00 for professionals, \$75.00 for amateurs and \$50.00 for students. All fees will go up \$15.00 after 1st September 2006. The fees include the Icebreaker, the Health Breaks, and a copy of the Programme with Abstracts booklet. The Banquet and post-conference field trip are a separate fee from the registration. For further information contact Ingrid Birker (e-mail <ingrid.birker@mcgill.ca>), Redpath Museum / McGill University, 859 Sherbrooke St. West, Montreal, QC, H3A 2K6. tel: 514/398-4086 ext. 4094#.



66th Annual Meeting of the Society of Vertebrate Paleontology
Ottawa, Canada 18 – 21 October 2006

Location: Marriott Ottawa Headquarters Hotel (<<http://www.marriott.com/>>) and Crowne Plaza (<<http://www.crowneottawa.ca/>>), Ottawa.

For further information, see the vert-palaeo website at <http://www.vertpaleo.org/meetings/future_meetings.html>.



The Plant Taphonomy Workshop of 2006

Cardiff, UK 27 – 29 October 2006

Provisional schedule and events

Friday 27th 16:00 – 19:00 Registration.
18:00 – 20:00 Reception, School of Earth Ocean and Planetary Sciences

Saturday 28th 10:00 – 11:00 Talks
11:00 – 11:30 Coffee
11:30 – 12:30 Talks
12:30 – 14:00 Lunch
14:00 – 15:30 Talks
15:30 – 17:00 Talks
17:00 – 18:00 Discussion session
19:30 – Workshop Dinner (venue to be arranged)

Sunday 29th 09:30 – 16:30 Field excursion to the Devonian and Carboniferous of South Wales.

Oral contributions will be of 15 minutes duration including time for questions. We will require titles and abstracts (a maximum of 250 words) before 1st September 2006. Slots will be allocated with the arrival of abstracts and cannot be reserved.

Fees (payable on arrival, dinner is not included): Attendance and Field Excursion £20
Student attendance and Field excursion £15
Attendance only £10
Student attendance £5

We will provide further information on accommodation in Cardiff for anyone responding to this flyer. A variety of accommodation is available. Please enquire if you have specific requirements. We cannot assist with the booking of accommodation after 1st October 2006.

Professor Dianne Edwards and I very much look forward to hosting this annual event and will gladly do our best to make you welcome in our vibrant city. There are now many direct flights each day from Amsterdam hub to Cardiff and there is always the Channel tunnel for those of you who prefer travel on, or underground. Please ask if there are any points on which you need clarification or if you need advice on travel.

Please address written correspondence to: Dr A.R. Hemsley, School of Earth, Ocean and Planetary Sciences, Cardiff University, Park Place, Cardiff, CF10 3YE, UK. E-mail: <hemsleyar@cf.ac.uk>.

Please put Taphonomy Workshop in your subject line to avoid spam filters. Fax: + 44 2920 874326



5th International Bioerosion Workshop

Erlangen, Germany 29 October – 3 November 2006

The aim of the bioerosion workshop series is to provide an interdisciplinary platform bringing together ichnologists dealing with bioerosion processes from the Proterozoic to the Recent and biologists studying various aspects of the hard substrate degrading mode of life.

The workshop comprises talks, poster sessions and field trips. In addition, all participants are strongly encouraged to bring along samples, outcrop images, SEM images, reprints *etc.* for lively discussions.

For further information please visit <<http://www.pal.uni-erlangen.de/index.php?id=79>>.



International Conference on Changing Scenario in Palaeobotany and Allied Subjects

Lucknow, India 15 -17 November 2006

An International Conference on “Changing Scenario in Palaeobotany and Allied Subjects” is planned during 15–17 November 2006 to mark the occasion of the Diamond Jubilee year of the Birbal Sahni Institute of Palaeobotany.

The Conference aims to stimulate and disseminate new information/ideas in palaeobotanical research. The emphasis will be on the applied aspects of palaeobotany, palynology and related subjects. The scientific deliberations to be held during the conference would be useful in identifying future trends in palaeobotanical and palynological research.

This Conference will deal with the following major themes:

- Origin and evolution of early life
- Biodiversity through time
- Gondwana floristics and biostratigraphy
- Patterns of Angiosperm origin and early evolution
- Quaternary Palaeoclimate and Palaeobotanical proxies
- Palynology and fossil fuel exploration
- Archaeobotany and Anthropogenic activities
- Mass extinctions, time boundaries and fossil record
- Applications of modern tools/techniques in palaeobotanical research
- Geochronometry

The official language of the Conference is English. Each participant will be allowed 10 minutes for oral presentation and 5 minutes for discussion. The proceedings of the conference will be published in the regular volume of the journal “The Palaeobotanist” after proper refereeing.

A Pre-Conference field trip to Garhwal & Himachal Himalaya showing Neoproterozoic successions of Krol-Tal is proposed for 5–13 November, and a post Conference field trip of 3–5 days covering



Gondwana and Tertiary localities of Central India from 18th November. The organization of field trips will depend upon the availability of participants.

The venue is the Birbal Sahni Institute of Palaeobotany, about 9 km from Lucknow railway station and about 18 km from the airport. The city is well connected with New Delhi, the Capital of India, by air, rail and road. Please contact the organizers for further details.

The fee for Indian participants is Rs. 5000/-, and for foreign participants, US\$ 500; for Accompanying Members it is Rs.1000/- or US\$ 300. Charges for pre- and post-conference field trips are, for Indian Participants Rs. 10,000/- (each trip), and for foreign participants US\$ 1000 (each trip). Registered delegates will be provided all conference material including abstract volume, breakfast, tea in between the sessions, lunch and dinner *etc.* during the conference. Delegates will be accommodated in Hotels and Guest Houses located in the city on payment basis. Details of charges will be provided later. If there is sufficient interest, special city tours, shopping programmes, etc. will be arranged for the spouse and other accompanying members.

Interested persons are requested to register online.

Contact information: The Director, Birbal Sahni Institute of Palaeobotany, 53, University Road, Lucknow 226 007, India. Tel: 0091-522-2740008/2740011/2740399/2740413. Fax: 0091-522-2740098/2740485. Website: <<http://www.bsip.res.in/>>. E-mail: <director@bsip.res.in> or <djconfsect@yahoo.co.in>.



First Mediterranean Herpetological Congress (CMH1)

Marrakech, Morocco 16 – 20 April 2007

This meeting is also devoted to palaeontologists interested in palaeobiodiversity and evolution of Amphibians and Reptiles, and the dynamics of palaeo-environments in the Mediterranean-type regions. Our principal aim is to promote the conservation of present and past herpetofauna as an integral part of the natural heritage of the Mediterranean-type regions.

For more information, please see the first circular on the meeting's website at <<http://www.ucam.ac.ma/cmh1>>, or contact the meeting organizer, Prof. N. E. Jalil (e-mail <cmh1@ucam.ac.ma>).



The Global Triassic

Albuquerque, New Mexico, USA 23 – 25 May 2007

This international symposium will be devoted to all aspects of the Triassic System, with particular focus on the Triassic timescale and Triassic biotic events. It will be an official meeting of the IUGS Subcommittee on Triassic Stratigraphy, and a final meeting of IGCP 467 on *Triassic Time and Correlation*. The meeting will be three days of talks and posters at the New Mexico Museum of Natural History in Albuquerque. Planning for pre-meeting and post-meeting field trips is underway, and the trips will be announced in the second circular. They will afford an opportunity to visit several classic marine sections including Fossil Hill (A–L), South Canyon (L–C), and New York Canyon (T–J), as well as



classic nonmarine Triassic sections in New Mexico–Arizona. For further information please contact Spencer G. Lucas, New Mexico Museum of Natural History, 1801 Mountain Road N.W., Albuquerque, NM 87104, tel: 505-841-2873, fax: 505-841-2808, e-mail <spencer.lucas@state.nm.us>.



40th Anniversary Symposium on Early Vertebrates/Lower Vertebrates
Uppsala, Sweden 13 – 16 August 2007

In August 2007, Uppsala University will be hosting the Symposium on Early vertebrates/Lower Vertebrates, the latest in a series of meetings initiated in Stockholm in 1967 by the Fourth Nobel symposium, “Current Problems of Lower Vertebrate Phylogeny”. The meetings are not linked to any society, but have been hosted by institutions in different countries on a running 3–4 year rotation. In 2004, the symposium was held in Gramado, Brazil; previous symposia have included Paris 1995, Miguasha (Québec) 1991 and Beijing 1987.

The Symposia on Early Vertebrates/Lower Vertebrates are the only recurring international meetings targeted specifically at the Palaeozoic vertebrate research community. As such, they draw a broad international field of very high profile speakers, including most of the acknowledged leaders in early vertebrate research. The meetings are friendly and informal, usually with no more than about 100 delegates, making them outstanding venues for young researchers to meet the established figures in their fields and build up contact networks.

Poster and platform presentations are accepted on an open competitive basis (there is usually room for all the posters); there are normally no invited speakers. Topics of presentations usually range from the earliest chordates, through Palaeozoic agnathans and fishes, up to the origin and early radiation of tetrapods. Platform presenters are invited, but not required, to contribute papers to a symposium volume. Past volumes such as “Current Problems of Lower Vertebrate Phylogeny” (ed. Ørving, 1968), “Early Vertebrates and Related Problems of Evolutionary Biology” (eds. Chang, Liu & Zhang 1991) and “Studies on Early Vertebrates” (eds. Arsenault, Lelièvre & Janvier 1995) have all become major landmarks in this area of palaeontology.

2007 is not only the 40th anniversary of the first Symposium, but also the 300th anniversary of the birth of Linnaeus – Professor of Botany at Uppsala University and one of the most influential biologists of all time. In this jubilee year, we are delighted to invite you to Uppsala, to attend what we hope will be an outstanding meeting on the early evolution and palaeontology of the Vertebrata.

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Sylvester-Bradley REPORTS

Carpal anatomy of fossil Diprotodontia: comparison against a large sample of extant taxa

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Anatomical studies of marsupials enjoy a long tradition, but comparative postcranial anatomy of both recent and fossil marsupials has been little studied in either functional or evolutionary contexts. The Australasian marsupial order Diprotodontia is particularly suitable for such study of the postcranials, as the clade is the most speciose and diverse extant marsupial order, and is also represented in a large fossil record extending back into the late Oligocene (Archer *et al.* 1999).

The comparative anatomy of Australian fossil marsupials has to date lacked in-depth comparisons with recent species, largely because little is known about the anatomy of the recent taxa. Thus, there is no base for comparing fossils to a comprehensive set of extant species to detect functional correlations and convergence. This is particularly obvious in the anatomical literature on the large, mainly extinct radiation of vombatiform marsupials. These have only been compared in detail with their three extant members (wombats and the koala) or the brushtail possum, *Trichosurus vulpecula*, because the latter species has been traditionally assumed to be plesiomorphic within Diprotodontia (Finch and Freedman 1988; Munson 1992).

Results of a study on wrist anatomy in a large sample of extant Diprotodontia as part of my PhD (Weisbecker and Sánchez-Villagra, in press) indicate that carpal anatomy varies in several details across the major diprotodontian clades. Much of the diversity is connected to locomotory habit, particularly arboreality or terrestriality. One important result is that the wrist anatomy of the terrestrial wombats and kangaroos is convergent in many aspects, which seem directly related to terrestriality. Because of the large sample of Diprotodontia used in that study, which includes two arboreal and two terrestrial radiations, I have a good base for comparing fossil diprotodontian wrist anatomy. In addition to this, my results from a recently finished study on finger morphometrics in a similarly large sample of diprotodontians could be applied. These results indicated that single phalangeal element proportions are reliable indicators of arboreal versus terrestrial locomotion (Weisbecker and Warton, submitted).

The funds from the Sylvester-Bradley foundation enabled me to travel through Australian fossil collections located in Melbourne, Adelaide, Alice Springs, and Brisbane to examine the wrist bones and fingers of various diprotodontian species. The objective of the project is to investigate the diversity of autopodial anatomy among fossil Diprotodontia in terms of its phylogenetic and functional implications based on the knowledge gained from extant species.



There were two main difficulties in the search of hand and foot remains. Firstly, the collections abound with traysfuls of postcranial material, but because teeth and skull elements are more easily identified and crucial for inferring phylogenetic relationships, little effort went into assigning postcrania to species. Sadly, many beautifully preserved specimens therefore had to be ignored. Secondly, there is little material containing complete and associated wrists so that many observations were made only on parts of the hands or feet of various specimens belonging to one species. To deal better with the single carpals, I created a photo catalogue of various carpals of recent Diprotodontia to compare with the fossil ones, which turned out to be very helpful for quick reference. When working with assembled casts there was an additional difficulty: some originals have been wrongly assembled so that the casts offered no help at all!

I managed to obtain information on hands and feet of 18 species overall, some from relatively recent times (such as the giant *Macropus titan* of the Pleistocene) and some dating back to the late Oligocene, such as *Muramura williamsi* (Pledge 1987). Most species are from the radiation of Vombatiforms, of which only wombats and the koala survive, but I also managed to examine an array of extinct kangaroos, most notably the lineage of sthenurines. No species which have been identified as completely arboreal were found in the collections.

While a formal analysis of observations and data is still in progress, preliminary results regarding functional anatomy are mostly in line with those from the study of recent species. The vombatiforms represent a largely terrestrial radiation whose representatives appear to show adaptations to terrestriality and graviportality to various degrees (Munson 1992). This I found reflected in their relatively "stiff" wrists which do not appear to be conducive to sideways motility, and which display signs of reduced grasping abilities. The fact that single phalanges of the hand can be used for a morphometric assessment of locomotion (Weisbecker and Warton, submitted) turns out to be helpful to confirm locomotory habits of many of the less complete specimens.

Comparison of extinct and extant vombatiforms to the more distantly related kangaroos considerably enhanced the scope within which the evolution of wrist anatomy could be interpreted. For example, the presence of distally flattened metacarpals, a broad and short hamatum/capitatum complex (Fig. 1), and a flat scaphoid appear to be convergences between the two clades, which could be related to the load-bearing function of the hand. The various extinct vombatiforms sampled display different combinations of these states. Superimposed on the (albeit very uncertain) phylogeny of diprotodontoids, a tendency towards a graviportal function of the hand is recognizable within the clade.

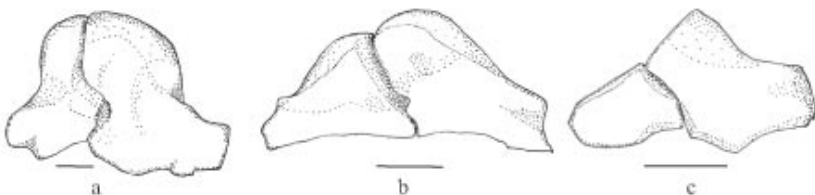


Figure 1: Dorsal view drawings of the articulated hamatum/capitatum complex of a) *Ngapakaldia tedfordi*, b) *Lasiorhinus latifrons* (hairy-nosed wombat), c) *Wallabia bicolor* (swamp wallaby). Scale = 5 mm.

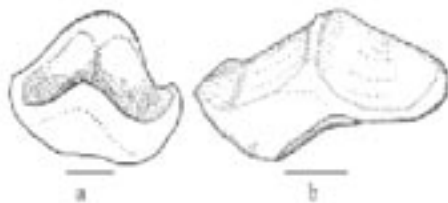


Figure 2. Drawings of the proximal facets of the triquetra of a) *Protemnodon* spp. (an extinct kangaroo) and b) *Thylacoleo carnifex* (vombatiform marsupial lion). Scale = 5 mm.

Some of the observed anatomy was also useful in terms of phylogenetic information. Vombatiforms are unique in sharing a peculiar facetation of the scaphoid, and the proximal facets of their triquetrum differ from others by being divided by a high ridge which rises above the rims of the facetial surfaces (Fig. 2).

In summary, the comparison of fossils with a large sample of extant relatives proved extremely useful for a broader view of Diprotodontian autopodial anatomy, in both systematic and functional aspects. The results demonstrate the value of crossing the boundary between extinct and extant mammals for a better understanding of anatomy and phylogenetic relationships.

ACKNOWLEDGEMENTS

I would like to thank the Palaeontological Association for providing me with the means to travel through the museum collections. For their generous help and access to collections I would like to thank: H. Dermot and D. Pickering, Museum Victoria; N. Pledge and M. Lee, South Australian Museum; R. Wells, Flinders University; D. Megirian, Northern Territory Museum; S. Hocknull, Queensland Museum. Particular thanks go to N. Pledge for generously allowing me access to undescribed specimens of *Muramura*.

REFERENCES

- ARCHER, M., ARENA, R., BASSAROVA, M., BLACK, K., BRAMMALL, J., COOKE, B. M., CREASER, P., CROSBY, K., GILLESPIE, A., GODTHELP, H., GOTT, M., HAND, S. J., KEAR, B. P., KRIKMANN, A., MACKNESS, B., MUIRHEAD, J., MUSSER, A., MYERS, T., PLEDGE, N. S., WANG, Y. and WROE, S. 1999. The evolutionary history and diversity of Australian mammals. *Australian Mammalogy*, **21**, 1–45.
- FINCH, M. E. and FREEDMAN, L. 1988. Functional morphology of the limbs of *Thylacoleo carnifex* Owen (Thylacoleonidae: Marsupialia). *Australian Journal of Zoology*, **36**, 251–272.
- MUNSON, C. J. 1992. Postcranial descriptions of *Ilaria* and *Ngapakaldia* (Vombatiformes, Marsupialia) and the phylogeny of the vombatiforms based on postcranial morphology. *University of California Publications in Zoology*, **125**, 1–99.
- PLEDGE, N. S. 1987. *Muramura williamsi*, a new genus and species of ?Wynyardiid (Marsupialia: Vombatoidea) from the middle Miocene Etadunna formation of South Australia. 393–400. In ARCHER, M. (ed.) *Possums and Opossums: Studies in Evolution*. Surrey Beatty & Sons and the Royal Zoological Society of New South Wales, Sydney.



Early cornulitids from the Ordovician of China

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The exact biological affinities of cornulitids are unknown. New data obtained by Vinn and Mutvei (2005) on the shell structure of the Silurian genera *Cornulites* and *Conchicolites* revealed a great diversity of shell ultrastructures. Regularly foliated shell structure and pseudopunctae, as well



as the ontogenesis of *Cornulites*, affiliates this genus to bryozoans and brachiopods, and even more closely to the tentaculitids (Vinn and Mutvei 2005). The earliest cornulitids appeared in the Middle Ordovician (Caradoc) of Baltica (Fig. 1). They became abundant in the Late Ordovician of North America and Baltica and range up to the Carboniferous (Richards 1974). Cornulitids of the other palaeocontinents have not been well studied, even though they were apparently part of the great Ordovician biodiversification event and may have appeared already by the Early Ordovician.

Figure 1. *Cornulites semiapertus* Öpik 1930 (Holotype), Upper Ordovician (Caradoc) oil shale from Estonia.

Several invertebrate fossil groups from the Ordovician of China are well studied (e.g. brachiopods, corals, cephalopods). However there has been hitherto no record of cornulitids from the Palaeozoic rocks of China. This could be explained either by palaeobiogeographic differences among Early Palaeozoic faunas, or by limited attention being paid to these small, encrusting worm fossils.

Large collections of various Early Palaeozoic invertebrates are deposited at the Nanjing Institute of Geology and Palaeontology in China (Fig. 2). Several fossil invertebrates such as the brachiopods, gastropods, crinoids and corals are known to be common substrates for encrusting cornulitids (Morris and Rollins 1971, Richards 1974, Morris and Felton 1993, Morris and Felton 2003). In order to search for encrusting cornulitids I have examined several thousand brachiopods from South China. Not surprisingly, brachiopods encrusted by cornulitids were discovered among rhynchonellids of Upper Ordovician (Middle Ashgill) age. According to preliminary identifications, these cornulitids belong to the genus *Conchicolites*, but a detailed study of their shell structure is required to confirm this. My search for cornulitids in the Lower



Figure 2. Nanjing Institute of Geology and Palaeontology in China.

Ordovician of China ended with the inconclusive find of an internal mould of a probable cornulitid attached to a cephalopod. Further evidence is needed to prove the occurrence of Lower Ordovician (Arenig) cornulitids in South China. New searches for early cornulitids from China will be carried out in cooperation with scientists from the Nanjing Institute of Geology and Palaeontology. A short paper on the ecology and taxonomy of Ordovician cornulitids from the Ashgill of South China is in an advanced state of preparation, co-authored by Prof. Renbin Zhan (Nanjing Institute of Geology and Palaeontology).

Successful completion of my early cornulitid project in China benefited greatly from the scientific and logistic support provided by my host Dr Mao-yan Zhu at the Nanjing Institute of Geology and Palaeontology. He also kindly introduced me to fossils of probable lophophore-bearing worms from the Chengjiang fauna (Early Cambrian) of China, which could well be the ancestors of cornulitids. Dr Gua-xiang Li enabled me to study a large collection of the Early Cambrian problematic tubicolous fossils. Some of the Cambrian tubicolous problematic fossils may represent the ancestors of cornulitids, and a comparison of their shell structures is planned for the future. I am grateful to the Palaeontological Association for a Sylvester-Bradley Award covering travel costs to the Nanjing Institute of Geology and Palaeontology in China.

REFERENCES

- MORRIS, W. R. and ROLLINS, H. B. 1971. The distribution and palaeoecological interpretation of *Cornulites* in the Waynesville Formation (Upper Ordovician) of Southern Ohio. *The Ohio Journal of Science* **71**, 159–170.



- MORRIS, R. W. and FELTON, S. H. 1993. Symbiotic association of crinoids, platyoceratid gastropods, and *Cornulites* in the Upper Ordovician (Cincinnatian) of the Cincinnati, Ohio region. *Palaios*, **8**, 465–476.
- MORRIS, R. W. and FELTON, S. H. 2003. Paleoecologic Associations and Secondary Tiering of *Cornulites* on Crinoids and Bivalves in the Upper Ordovician (Cincinnatian) of southwestern Ohio, southeastern Indiana, and northern Kentucky. *Palaios*, **18**, 546–558.
- RICHARDS, P. R. 1974. Ecology of the Cornulitidae. *Journal of Paleontology* **48**, 514–523.
- VINN, O. and MUTVEI, H. 2005. Observations on the morphology, and affinities of cornulitids from the Ordovician of Anticosti Island and the Silurian of Gotland. *Journal of Paleontology*, **79**, 725–736.
- VINN, O. 2005. A new cornulitid genus from the Silurian of Gotland, Sweden. *GFF*, **127**, 205–210.

A Tournaisian (Lower Carboniferous) vertebrate fauna from the Albert Formation of New Brunswick, Canada

Martin D. Brazeau

The Horton Bluff Formation of Nova Scotia is known for a well-represented Tournaisian vertebrate fauna. It is also the oldest Carboniferous locality that yields tetrapod remains and is consequently the source of growing data on tetrapods from 'Romer's Gap' (Clack and Carroll, 2000). Unfortunately, the vertebrates from the Horton Bluff Formation are invariably disarticulated; associated remains are uncommon. The site has been known for over 100 years, with frequent field parties visiting from the Redpath Museum (McGill University). The site is only now beginning to build its potential to a degree where we can understand members of the fauna with a more focused taxonomic emphasis (e.g. Brazeau, in press; Anderson *et al.* 2005).

Despite intense interest in Horton Bluff, an adjacent and coeval vertebrate fauna in the Albert Formation of southern New Brunswick has received comparatively little attention. More surprisingly, the classic Albert Mines locality has been known for nearly a century to produce articulated actinopterygian ('palaeoisoid') remains (Lambe, 1910). The Albert Formation is a lacustrine sequence with associated alluvial fan deposits (St. Peter, 1993). It outcrops in a southwest to northeast-running belt across southeastern New Brunswick. Newer outcrops have been exposed during recent road building. These will become the focus of subsequent field studies.

The Albert Formation has likely been ignored due to a low level of interest in the 'palaeoisoids' (which tend to be poorly preserved, along with the colossal confusion of Carboniferous actinopterygian systematics). Greiner (1977) reported a fauna of osteolepidid sarcopterygians from a locality near Irishtown, New Brunswick, suggesting a greater diversity of vertebrates in the formation. He described a disaggregated skeleton, jaws, and a partial braincase of an osteolepidid. In this paper, he noted the presence of acanthodian spines and a jaw possibly belonging to an onychodont. These latter specimens were never figured, nor given any collection numbers. All efforts to locate them have been in vain.



The Sylvester-Bradley Grant was awarded to me to study the Albert Formation in greater detail. The goal was to invest the first intensive effort in collecting vertebrate fossils from this formation. The results will provide the basis for continued, long-term studies on Albert Formation vertebrates. I assembled a field team to invest approximately one month of effort in the Albert Formation. The goal was to exploit the quarry near Moncton, New Brunswick, where Greiner had collected the material reported in 1977. In addition to this quarry, other nearby quarries and outcrops along road cuts were prospected. The results of this effort showed that, in Greiner's original quarry, the fossils appear to be restricted to an interval of approximately 20m in thickness. The highest concentrations of fossils were restricted to two beds of yellow-weathering dolostone.

The collection amounted to 163 specimens, dominated largely by osteolepidid (*cf. Megalichthyidae*) remains. However, we have obtained evidence of rhizodontids, acanthodians, as well as lungfish. Lungfishes are otherwise unreported in the Horton Group, and this occurrence provides important palaeoecological data on lungfish distribution in post-Devonian times. Horton Bluff lacks any evidence of the cosmine-covered bones and scales of osteolepidids. There is thus an emerging picture of faunal provinciality. Additionally, no successful field expedition would be complete without a few large mystery bones, which in our case included some unidentified braincase material.

A partial articulated rhizodontid skull was collected and awaits trimming and preparation. Articulated rhizodontid remains (particularly skulls) are exceedingly rare. New, well-preserved material from rhizodontids is therefore a very welcome and valuable find. Additional rhizodontid



The quarry where the fossil vertebrate fauna was discovered. The author (right) and Matt Friedman (photo by D. Snitting).



remains from the site include a dentary, premaxilla, and a partial cleithrum. The remains compare favourably with a new rhizodontid taxon described from the Horton Bluff formation (Brazeau, In press).

The specimens gathered during this investigation offer a wealth of new data on the palaeofauna of the Albert Formation. What was once thought to be a depauperate fauna of 'palaeoniscoids' can now be seen to be a relatively rich community of Carboniferous vertebrates. The quality of preservation of this material will permit detailed investigations of the fauna and allow comparisons with a neighbouring fauna from Horton Bluff. This may help us understand patterns of faunal 'provinciality' in the Early Carboniferous, as well as provide better data on faunal associations. Moreover, the formation clearly offers potential for continued work.

ACKNOWLEDGEMENTS

My thanks go first and foremost to my collaborator Randy Miller (New Brunswick Museum), who has supported and encouraged the Albert Formation project since the beginning. The dedicated and hard-working crew were: Catherine Boisvert (Uppsala U.), Krista-Lee Christensen, Matt Friedman (U. Chicago), Robert Godfrey, Patricia Hall (Norther Arizona U.), Jared Hoag (Dartmouth), Daniel Snitting (Uppsala U.), and Anne Warren (La Trobe). I thank the Bulmer Family (Indian Mtn. New Brunswick) for access to quarries on their land. Finally, I acknowledge the support from the Palaeontological Association's Sylvester-Bradley Award, and the New Brunswick Museum's G.F. Matthew Grant.

REFERENCES

- ANDERSON, J. S., MANSKY, C., WOOD, S., GODFREY, R., and CARROLL, R. L. 2005. New tetrapod fossils from the Lower Carboniferous of Blue Beach (Horton Bluff Formation), Nova Scotia. *PaleoBios* **25**: 13–14.
- BRAZEAU, M. D. In press. A new genus of rhizodontid (Sarcopterygii, Tetrapodomorpha) from the Lower Carboniferous Horton Bluff Formation of Nova Scotia and the evolution of the lower jaws in this group. *Canadian Journal of Earth Sciences*.
- CLACK, J. A., and CARROLL, R. L. 2000. Early Carboniferous Tetrapods, p. 1030–1043. In HEATWOLE, H. and CARROLL, R. L. (eds.), *Amphibian Biology*. Volume 4: Palaeontology. Surrey Beatty & Sons, Chipping Norton, NSW, Australia.
- GREINER, H. 1977. Crossopterygian fauna from the Albert Formation, New Brunswick, Canada, and its stratigraphic–paleoecologic significance. *Journal of Paleontology*, **51**(1): 44–56.
- LAMBE, L. 1910. Palaeoniscid fishes from the Albert Shales of New Brunswick. Contributions to Canadian Palaeontology. *Geological Survey of Canada Memoire* **3**.
- ST. PETER, C. 1993. Maritimes Basin evolution: key geologic and seismic evidence from the Moncton Subbasin of New Brunswick. *Atlantic Geology* **29**: 233–270.



The cuticular ultrastructure and phylogenetic affinities of palaeoscoleoids

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Palaeoscoleoids are an extinct group of worms that ranged from the Early Cambrian to the Late Silurian. For a long time they had nothing more to define them than a distinctive surface ornament of rows of 'papillae' on each of a large number of body annulations, and their phylogenetic affinities remained obscure. However, the application of latex peel and scanning electron microscope techniques to exceptionally preserved specimens from the Czech Republic (Kraft and Mergl 1989) brought about a revolution: the surface ornament was created by the regular arrangement of precisely sculpted plates set into the cuticle, and these plates had been known for years, in the form of phosphatic microfossils such as *Hadimopanella* and *Milaculum* (Hinz *et al.* 1990).

The subsequent discovery of palaeoscoleoids from the Early Cambrian of China provided vital further data: these specimens had heads! They showed clearly that palaeoscoleoids bore spiny proboscises – introverts – and demonstrated a phylogenetic link with the five extant introvertan phyla: priapulids, kinorhynchs, loriciferans, nematodes and nematomorphs (Hou and Bergström 1994).

Aside from nematodes, these 'minor phyla' received little attention until they were thrust into the limelight in their glittering roles in the New Animal Phylogeny as the non-arthropod ecdysozoans (Aguinaldo *et al.* 1997). However, interrelationships of these diverse groups are poorly known. Both morphological and molecular datasets are characterized by gaps: the embryology of kinorhynchs and loriciferans is virtually unknown, and few genes have been sequenced outside of the genomically idiosyncratic nematodes. Consequently, phylogenetic trees are unstable. A good bet is that priapulids, kinorhynchs and loriciferans form a clade (Scalidophora), as do nematodes and nematomorphs (Nematoida). Molecular data (mostly) resolve nematoids as the sister group to arthropods *s.l.*, rendering Introverta paraphyletic. But what of the (revived) tardigrade-nematode similarities, and was *Ursalidophora* meiofaunal, or big and penis-like? These are more important phylogenetic questions than most, considering that the arthropod *Drosophila* and the nematode *Caenorhabditis* are major model organisms of developmental genetics.

Suddenly, palaeoscoleoids take on a great importance: potentially, they could be close both temporally and phylogenetically to major cladogenesis events within Ecdysozoa. The aim of my project was to address the phylogenetic position of palaeoscoleoids, which has been rather vague, through the resolution of their cuticle ultrastructure in combination with observations of their gross morphology. A Sylvester-Bradley Award allowed me to visit important collections in Prague, Czech Republic and Bonn, Germany.

The compressed body fossils from the Czech Republic represent giants among palaeoscoleoids. There is some interesting taphonomy here, which deserves a far more detailed consideration, but the end result is an astoundingly faithful mouldic preservation, so that silicone rubber peels examined using scanning electron microscopy reveal structures to a resolution of a few



microns. Part and counterpart sometimes split through subsurface cuticle layers which must have experienced soft-tissue preservation shortly after burial. Recognised by Kraft and Mergl (1989), this subsurface cuticle is of great significance in light of the subsequent discoveries: a cross-wise arrangement of large fibres underlies the surface pattern of tessellating biomineralised and non-biomineralised elements. Such fibres are unknown from other modes of articulated cuticle preservation, but are evident from the basal layers of some isolated palaeoscolecid plate morphologies (e.g. *Milaculum*, *Kaimenella*).

Preserved quite differently in diagenetic phosphate, the three-dimensional, microscopic palaeoscolecids from the Middle Cambrian of Australia (Müller and Hinz-Schallreuter 1993) rival the Orsten arthropods in being the most spectacular products of this taphonomic mode. The associated microfauna is diverse and exquisitely preserved, with almost everything phosphatized and three-dimensional (trilobites, brachiopods, bradoriids, hyoliths, cancelloriids, wiwaxiids, halkieriids, sponges, arthropod larvae, embryos...); this makes for fun picking. Many unfigured palaeoscolecid specimens were available for examination, and some show the aboral end in considerable detail. Some show bizarre structures whose identity is unresolved. Importantly, no further specimens show anything like the trunk 'protuberances' figured by Müller and Hinz-Schallreuter (1993). Despite being superficially similar to lobopodous appendages, these structures are perhaps better interpreted as sensory/secretory organs; this further distances the homonomously annulated, non-appendage-bearing palaeoscolecids from lobopods.

Palaeoscolecids do not fit within the crown group of any introvertan phylum. Their large adult body size combined with an eversible introvert prompts immediate comparison to priapulids; this relationship is borne out by detailed examination of palaeoscolecid sensilla (of two, perhaps three, distinct types). These and other characters decide the outcome of any formal cladistic



A palaeoscolecid stares back. Actually, this is the aboral end. Specimen from the Middle Cambrian of Australia, body diameter approximately 200 μ m.



analyses – palaeoscolecid group with stem-group priapulids. However, palaeoscolecid cuticle bears a basal layer of large, helically wound cross-wise fibres, unknown among scalidophorans but readily comparable to those of many nematoids. Such fibres have convergently evolved in cylindrical structures across many phyla, and are always constructed of collagen. Palaeoscolecid fibres could very plausibly have evolved independently in the stem lineage of priapulids. Alternatively, such fibres, or at least a collagenous endocuticle as possessed by nematoids, could be plesiomorphic for introvertans, and by implication (if following the paraphyletic-Introverta tree) plesiomorphic for Ecdysozoa and hence the ancestral state for the eponymous moulting cuticle.

Progress has been made, but a more secure phylogenetic position for palaeoscolecids will emerge with increased understanding of ecdysozoan character evolution. This can only be achieved through the combined efforts of evolutionary development, molecular genetics and palaeobiology.

ACKNOWLEDGEMENTS

Many thanks to Oli Lehnert and Petr Kraft (Charles University, Prague) and Georg Heumann and Martin Sander (University of Bonn) for their extensive hospitality, and loaning of material. The project was supervised by Phil Donoghue (University of Bristol).

REFERENCES

- AGUINALDO, A. M. A., TURBEVILLE, J. M., LINFORD, L. S., RIVERA, M. C., GAREY, J. R., RAFF, R. A. and LAKE, J. A. 1997. Evidence for a clade of nematodes, arthropods and other moulting animals. *Nature*, **387**: 489–493.
- HINZ, I., KRAFT, P., MERGL, M., and MÜLLER, K. J. 1990. The problematic *Hadimopanella*, *Kaimenella*, *Milaculum* and *Utahphospha* identified as sclerites of Palaeoscolecida. *Lethaia*, **23**: 217–221.
- HOU, X.-G. and BERGSTRÖM, J. 1994. Palaeoscolecid worms may be nematomorphs rather than annelids. *Lethaia*, **27**: 11–17.
- KRAFT, P. and MERGL, M. 1989. Worm-like fossils (Palaeoscolecida; ?Chaetognatha) from the Lower Ordovician of Bohemia. *Sbornit Geologických Vedeckých Rada P: Paleontologie*, **30**: 9–36.
- MÜLLER, K. J. and HINZ-SCHALLREUTER, I. 1993. Palaeoscolecid worms from the Middle Cambrian of Australia. *Palaeontology*, **36**: 549–592.

Book Reviews

Evolving Form and Function: Fossils and Development

Proceedings of a symposium honoring Adolf Seilacher for his contributions to palaeontology, in celebration of his 80th birthday

Derek E.G. Briggs (ed.) (2005). Special Publication of the Peabody Museum of Natural History, Yale University. ISBN -10: 0-912532-72-6 \$59.00 (paperback).

In April of 2005 a symposium was held at Yale University celebrating the scientific life of Dolf Seilacher on the occasion of his 80th birthday. That symposium formed the basis for the papers included in this book. Seilacher's contributions to palaeontology are legendary, and have come in three major areas (Figure 1). However, the contents of the symposium and this book concern primarily one of these broad areas of research emphasis – the interacting role of functional morphology and development in evolution. This reviewer was able to attend the stimulating Yale symposium, and the contributions in the resulting volume, edited by Derek Briggs, reflect that success.

Dolf Seilacher of course has utilised powerful observational skills to focus on “key” unique fossils and morphologies to make breakthroughs on how animals have evolved to changing environments. The first paper in the book, by Derek Briggs, sets the stage for this viewpoint, by outlining a wide-ranging summary of Seilacher's many contributions

in the field of functional morphology. When all is said and done perhaps Dolf Seilacher's most important contribution to the science of form will be judged to be the stimulus that he provided the field of early animal evolution through his shocking analyses of the morphology of fossils from the Ediacara biota. It has long been acknowledged that this led to the re-invigoration of this field, much as the “hot-blooded dinosaur” controversy led ultimately to the current boom in dinosaur studies.

Thus studies on the form and evolution of early animals constitute one of the major emphases of this book. It begins with the first of two contributions by one of the foremost teams of Ediacara biota workers, in a paper by Jim Gehling, Mary Droser, Sören Jensen and Bruce Runnegar. Here they show the very important role of context that is required in understanding the mode of life of





Ediacara fossils. Through analysis of bedding planes with numerous fossils and associated biogenic features they are able to conclude that *Kimberella* was a grazing bilaterian, and that *Dickinsonia* and *Yorgia* were mobile bilaterians that absorbed nutrients through a “digestive foot”. The message that one takes home is that you need to look at more than just the specimens to unravel the Ediacara biota mystery. In another contribution by Droser, Gehling, and Jensen, these authors take a new look at the study of Ediacaran trace fossils, using in detail the broad evidence that has developed for the existence of microbial mats on normal marine Precambrian seafloors.

Doug Erwin has had a long and significant interest in understanding how early animals evolved. In a penetrating analysis he outlines the role of invention and innovation in the evolutionary origin of metazoans. One of Erwin’s key points is that the necessary genetic and developmental inventions evolved before the Cambrian explosion, but that environmental and ecological factors spurred the innovations that characterize this remarkable radiation. Among the innovations of the Cambrian explosion are mineralized skeletons that form the record of small shelly fossils, which have long been a staple of early animal evolution studies. In a synthetic paper Stefan Bengtson extensively reviews coelosclerites, one of the types of small shelly fossils, and what they might tell us about the origin of the bilaterians.

The discovery of the Doushantou phosphatized animal embryos is one of the major achievements of late 20th century palaeontology. Phil Donoghue and Xiping Dong consider the significant record of Ediacaran and early Cambrian embryos that has emerged since. One might wonder if this record of phosphatized embryos could be observed in younger strata. However, they conclude that a taphonomic window from the Ediacaran into the early Ordovician, due to favourable ocean chemistry, led to their preservation and that this window has been closed since then.

The continued elaboration of morphological diversity among the eukaryotes in the Phanerozoic presents numerous opportunities to understand development and what it can tell us about evolution. A number of excellent examples of such evo-devo contributions are found in this volume and reflect the vibrancy of this field. The first paper on this broad topic is a view on morphology and development from the plant world by Karl Niklas, which provides a thorough overview of how environmental stresses, particularly mechanical perturbation, affect plant development and form. In another stimulating contribution Nigel Hughes outlines how variations in trilobite segments can be used to understand developmental processes in this extinct clade. Matthew Giorganni

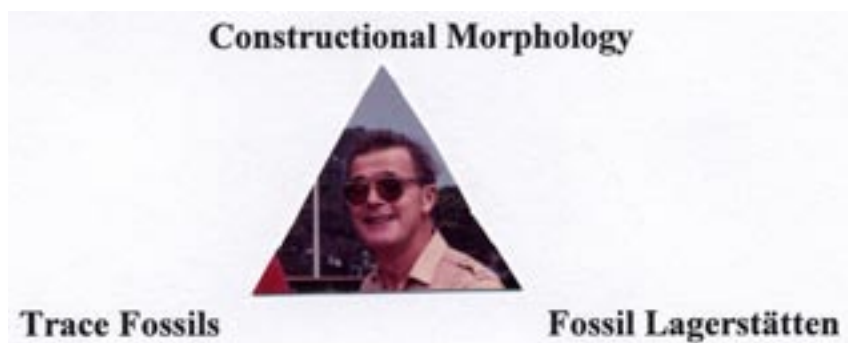


Figure 1. The dynamic triangle of Dolf Seilacher’s scientific life.



and Nipam Patel continue with this arthropod theme in a clear and concise review of arthropod appendages in modern organisms and how evolution and development have interacted to produce such an amazing diversity of appendages in these fascinating animals. Andrew Smith contributes a detailed analysis of echinoid plate development and growth and how variation and innovation in this system shaped Palaeozoic and post-Palaeozoic echinoids very differently. In a later paper Richard Prum provides an overarching discussion on the origin and evolution of feathers using a developmental approach, with data from modern and fossil feathers.

Evolutionary analyses of morphological and functional trends form another major thrust of this volume. In a novel presentation Geerat Vermeij synthesizes the very common phenomenon in molluscs of internalization of the shell – shell envelopment – and how this phenomenon evolved repeatedly in this clade. Jenny Clack provides a critical analysis of the evidence that is available on how tetrapods emerged onto land, the understanding of which has been further enhanced by the recent discovery of *Tiktaalik* from the Canadian Arctic (Daeschler *et al.*, 2006). Providing a fitting conclusion to this volume, Dolf Seilacher renders a marvellous synthesis of the phenomenon of secondary soft-bottom dwellers.

This truly outstanding volume not only honours the work of Dolf Seilacher but very much points the way to the future for studies of form and development as a way to answer a variety of the most significant problems of evolution. In many ways it may prove as inspirational to the nascent evo-devo field as the landmark “Models in Paleobiology” (Schopf, 1972) was to the then young field of palaeobiology, or the timeless “Biotic Interactions in Recent and Fossil Benthic Communities” (Tevesz and McCall, 1983) was to the first generation of evolutionary palaeoecologists.

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REFERENCES

- DAESCHLER, E. B., SHUBIN, N. H. and JENKINS, F. A. 2006. A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. *Nature*, **440**, 757–763.
- SCHOPF, T. J. M. (ed.). 1972. *Models in Paleobiology*, Freeman, Cooper & Company, San Francisco.
- TEVESZ, M. J. S. and MCCALL, P. L. (eds). 1983. *Biotic Interactions in Recent and Fossil Benthic Communities*, Plenum Press, New York.

Starring T. Rex – Dinosaur Mythology and Popular Culture

José Luis Sanz (2002). Indiana University Press, Bloomington and Indianapolis. 153pp. ISBN: 0253341531 \$17.95, currently on special offer: \$4.00 (paperback).

My enthusiasm for dinosaurs as a child and teenager (and adult) is evidenced today by a collection of scale models and posters, a worn out VHS cassette of Jurassic Park, and an ongoing Ph.D. in vertebrate palaeontology. So, as a self-confessed dinosaur fan, I was looking forward to reading *Starring T. Rex – Dinosaur Mythology and Popular Culture*. The book is easy to read (it was translated by Philip Mason) and well illustrated throughout with many black and white photos, movie posters,



and illustrations. Unfortunately, for a topic with so much apparent potential, it came as a bit of a disappointment in the end.

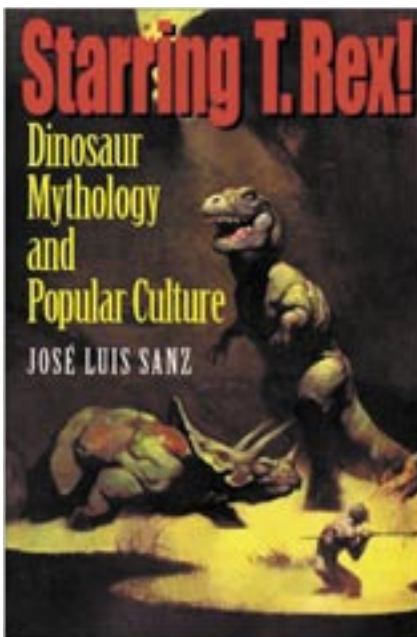
Starring T. Rex is structured in two parts (totalling 26 short chapters). The first part describes the process by which dinosaurs came to be cultural icons. This is achieved through a review of the history of dinosaur palaeontology, beginning with the first discoveries of dinosaurs in the 1800s, and ending with an overview of the current phenomenon known as ‘dinomania’. The second part of the book establishes the nature of dinosaur mythology. In general, this second section takes restorations of dinosaurs from movies, TV and literature, assessing and discussing their scientific accuracy.

Chapters 1–8 review the history of the discovery of dinosaurs and their first appearances in popular culture. Chapters 9–15 are enjoyable – they outline the various ways in which dinosaurs and humans are brought into contact in the fictional realm. This is achieved by a number of explanations (some obvious, others fantastical) involving the misportrayal of the prehistoric world (caveman living alongside dinosaurs), discovery of lost worlds, thawing out of frozen dinosaurs, time travelling, the reappearance of dinosaurs through evolution in the future or on different planets, and finally via genetic recreation. This section boils down to a list of fictional works – essentially movies, books, and television series, with a brief outline of the various dinosaur related action.

Chapter 16, ‘The extinction of the dinosaurs’, is a mishmash – the first third is pure popular science – how did dinosaurs become extinct? This is followed by some (not-so) popular culture concerning dinosaur extinction, (1) denial that they went extinct at all, and (2) fictional explanations that aliens were responsible, or at least interacted with dinosaurs. Point one brings us nicely to the next chapter...

As a plesiosaur researcher, I was particularly interested in chapter 17 – ‘Nessie and friends’. Throughout the book, a general theme is presented – that of popular culture mirroring science. This struck me as a way of dispelling cryptozoological myths. After all, if an early 20th century description of, say, a living sauropod in the Congo matches the erroneous early 20th century vision of sauropods as sluggish sea-weed munching aquatic monsters, surely the sceptic emerges victorious? The scope of this topic, and its relationship with certain religious beliefs (fundamentalist belief in recent living dinosaurs), seemed to me very worthy of deeper investigation.

Chapter 18, ‘Intelligent dinosaurs’, looks at the myth of brainy (and not so brainy) dinosaurs. Dale Russell’s infamous dinosauroid (if dinosaurs had continued to evolve to the present day, this is what they would supposedly look like – more or less a human) makes an inevitable cameo appearance,





alongside a few reviews of cartoon and TV series. Chapter 19 returns to the issue of coexistence between humans and dinosaurs. Chapters 9–15 investigated *how* the co-existence was reached; now their happy co-existence is reviewed. Following on this theme, chapter 20 investigates the nature of conflicts between humans and dinosaurs in movies. Chapter 21, 'Dinosaurs and Terror', explores the iconic scary dinosaur (in five paragraphs). We are reminded that dinosaurs are usually portrayed as monsters, but while this is, of course, a myth, this is not made clear or clarified – another under-explored chapter.

In Chapter 22, Sanz analyses the mechanical processes traditionally and currently used by movie-makers to re-create dinosaurs. The resulting dino-creations are classified into two groups – real dinosaurs and dinosauroids. The latter is subdivided into paradinosaurs (half sauropods, half theropods), sauriodynaminosaurs (living lizards decorated in plastic spines and sails), and dragodinosaurs (*e.g.* Godzilla). A clever approach to circumventing the subtleties of scientific accuracy in movie restorations is to make up fictional dinosaurs, as executed in the newest version of the movie *King Kong* (2005). The 'Venatosaurus', a slightly modified theropod, and the 'Ferrucutus', a modification on a ceratopsid dinosaur, provide examples. However, slightly modified real dinosaurs, such as these, do not fit happily into Sanz's classification of movie dinosaurs (of course, this version of the movie was released after the publication of the book). I suppose these dinosaurs fit under 'paradinosaurs', although strictly this is restricted to half-sauropod, half-theropod creatures, such as the 'Rhedosaurus' from *The Beast from 20,000 Fathoms* (1953). Appeasing the myth of the 'ferocious giant dinosaur', filmmakers combined the giant body of a sauropod with the toothy maw and vicious habits of a theropod. This is one of a frequent number of interesting tidbits throughout the book. Going back to *King Kong* these two chapters also seemed a suitable place to discuss the influence of the false myth of gorillas as ferocious monsters (not strictly dinosaur culture, I know).

Finally, Chapters 23–26 give us a peek at Godzilla and the like, explore the true myth of dragons and their possible relationship to dinosaur fossils (good stuff), and the behaviour of dinosaurs in movies (they all live in caves).

In addition to movies, which are well covered in this book, documentaries also (often inadvertently) contribute to myths surrounding dinosaurs. A most notable recent example omitted by Sanz is the BBC series *Walking with dinosaurs*. And so much other dinosaur culture seems to be missing from the book. There is no mention of dinosaurs in comic strips. Gary Larson's *The Far Side* and Bill Watterson's *Calvin and Hobbes* (there are many others), often take dinosaur myths and run with them; although one cartoon is figured, this is another missed opportunity for discussion. There is no discussion of toys or action figures. For example, I remember being appalled as a child when each dinosaur toy, carnivore and herbivore alike, possessed a mouth full of sharp bloodied fangs – such blatant (and probably intentional?) dinosaur myths result from existing ones, but also serve as a catalyst, exasperating and spreading the myth. Yet toys remain completely overlooked by Sanz. There is even no mention of *The Flintstones* or 'dino' the pet dinosaur, either in the analysis of synchrony between humans and dinosaurs in prehistoric times (chapter 9), or in the discussion of the co-existence of dinosaurs and humans (chapter 19, where pets are mentioned specifically).

One interesting point raised by Sanz is the relationship between science and 'dinomania' (chapter 8). For palaeontologists this is important because public interest fuels funding (p. 48). But, again, the surface is only scraped, leaving a number of unasked questions regarding the nature of 'dinomania'.



For example, why did dinosaur-mania blossom and not, for instance, plesiosaur-mania, mammoth-mania, or *Hallucigenia*-mania? Or does dino-mania include all these prehistoric organisms too? Or just the big ones? Or just the 'unusual' ones? Or just the Mesozoic ones? Alternatively dinomania may simply be a recurring fad as suggested by Gould (1996) – purely the result of commercialism? I don't know, and I was hoping *Starring T. Rex* would explore the subject.

At the risk of appearing pedantic, I have a few niggling points too. The figures are not linked specifically to the text, and are sometimes inexplicably cryptic. There is no distinction between the term 'reconstruction' (which applies to skeletons only) and 'restoration' (the presentation of animals as living organisms). There is an over-frequent use of wording such as 'without a doubt', 'it is clear that', 'of course', and 'obviously' throughout the book, often in cases when it doesn't (to me at least) seem quite as certain as implied. For example, on the topic of hunting for mythical monsters: "without a doubt, the search for fame has been one of the *most obvious* driving forces behind the huge amount of research carried out in Loch Ness, although, *of course*, we must also include those of human curiosity for the marvellous" [my italics]. I wonder if some of this may stem from the translation from Spanish to English. Also, a separate index or list of movies *etc.* would have been nice, maybe even with a review?

In conclusion, determining to whom this book would appeal is difficult. It raises some interesting points and discusses intriguing issues, but all too often cuts itself short. Anyone with a genuine interest in dinosaur mythology and culture (myself included) may be disappointed by the fleeting movie synopses and cultural analyses. Dinophiles may in all probability just be confirmed of what they already know. If you are looking for a review of dinosaur movies, you could preferably consult a more dedicated volume; Steven Jones' (1993) *The Illustrated Dinosaur Movie Guide* comes to mind. Plus, history of palaeontology is covered in more detail elsewhere. I'm ashamed to say I probably judged this book by its cover so my disappointment may come from my expectations. Nevertheless, I may still flick through *Starring T. Rex* on a rainy day, after I reorganise my collection of dinosaur stamps.

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REFERENCES

- GOULD, S. J. 1996. *Dinosaur in a Haystack: Reflections in Natural History*. Three Rivers Press, 496pp.
- JONES, S. 1993. *The Illustrated Dinosaur Movie Guide*. Titan Books, 128pp.

The Carnivorous Dinosaurs

Kenneth Carpenter (2005). Indiana University Press, Bloomington and Indianapolis, 371pp. ISBN 0-253-34539-1, \$49.95 (hardback).

Given their popularity, both within our field and among the public, it seems surprising that this special volume on theropods was not the first Indiana University Press dinosaur book to be published. Hot on the heels of Tidwell and Carpenter's *Thunder-Lizards: the Sauropodomorph*



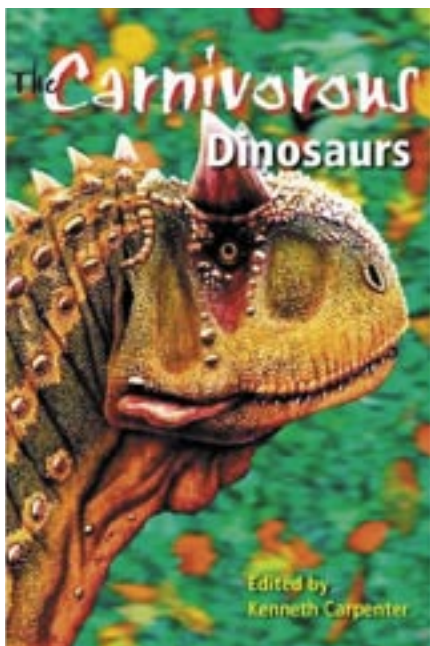
Dinosaurs (2005), *The Carnivorous Dinosaurs* is a slimmer but altogether similar volume, featuring 18 stand-alone contributions from various authors on theropod systematics, morphology and palaeobiology. At the risk of sounding tediously repetitive, I would make the same general point on this book as I would for the others in the series: for those with a serious academic interest in theropods, there are enough good contributions in the book to make it worthy of ownership and use. Some may doubt, however, whether all the articles in the volume can be rightly described as ‘exciting new research’ (as it states on the back cover).

Section I (‘Theropods old and new’) consists of descriptions and redescriptions, and reports on new faunal assemblages. Section II (‘Theropod working parts’) includes contributions on tooth microstructure, bite mechanics, body posture, and pectoral and forelimb morphology. Finally, in section III (‘Theropods as living animals’), various authors look at sexual dimorphism, gregarious behaviour, evidence for predator-prey interactions, and palaeopathologies.

Section I begins with Galton and Molnar’s article on English theropod tibiae. The first part of this article describes a 46-mm-long fragment of distal tibia from the Taynton Limestone Formation (consistently termed ‘Taunton Limestone Formation’ by the authors), while the second part reinterprets BMNH R186 from the Isle of Wight’s Wessex Formation. The *raison d’être* of the second section is to show that Naish *et al.* (2001) erred in their interpretation of this specimen, describing it as a left tibia instead of a right, and interpreting the cranial surface as the caudal one. The idiots. Or, rather, “idiot”, as my co-authors were not responsible for this travesty. While Naish *et al.* (2001) published only 43 words on the erroneous reinterpretation of this specimen, Naish (1999: unpublished thesis) contains a whole 17-page chapter on it. So, for Galton and Molnar to discuss in detail why Naish screwed up, they had to cite, discuss and critique an unpublished chapter from an unpublished thesis. Hold on: is that ethical?

Everyone I’ve asked agrees that it wasn’t. Maybe the crass errors I made explain why I never published that chapter.

Moving on, the section also includes redescriptions of the allosauroid *Erectopus* (by Allain), the small coelurosaurs *Ornitholestes* and *Coelurus* (by Carpenter *et al.*) and the ornithomimosaur *Harpymimus* (by Kobayashi and Barsbold). All of these have been long awaited: Ostrom was promising a redescription of *Coelurus* in 1980 and *Erectopus* hasn’t been properly described since 1882. Unfortunately, the photographic figures included in these articles are often blurred and too pale, making it highly difficult to examine the details. A reasonably good description of a new small Morrison Formation coelurosaur, *Tanycolagreus topwilsoni*, is also provided by Carpenter





et al. but feels incomplete in lacking a systematic interpretation of the taxon. Kirkland *et al.* report a braincase of *Nothronychus*, Sankey *et al.* describe the theropod tooth assemblage from Big Bend National Park (Texas), and Coria and Salgado describe isolated theropod elements from the Patagonian Allen Formation. The remains described by the latter authors are tantalising, indicating the presence of several unnamed taxa that do not belong to either Abelisauroida or Carcharodontosauridae (the two theropod clades that are best represented in South American Cretaceous faunas). Finally, at last, the etymology of *Quilmesaurus* Coria, 2001 is resolved: it was not named for a brand of beer after all, but after the Argentinian Quilmes people.

Section II begins with Stokosa's overview of enamel microstructure in Upper Cretaceous theropods. Using studies of modern reptile enamel as a bench-mark, Stokosa shows that at least some genera can be distinguished on the basis of enamel microstructure alone. In the longest article in the book, Therrien *et al.* use beam theory to provide a biomechanical analysis of theropod jaws, incorporating a diverse range of small and large taxa. There is much of interest in this study, and most of their conclusions agree with those of other workers who have looked at theropod skull mechanics. The data indicates that the large-skulled abelisauroids and allosauroids had bites several times more powerful than those of living alligators, while in the biggest tyrannosaurids bite force was an incredible 16 times greater than that of an alligator. Some of these figures suggest substantially more powerful bite forces than those estimated by other studies. Velociraptorine bite forces appear weak compared to those of the more robust-jawed *Dromaeosaurus* and many other theropods, an observation consistent with use of the pedal sickle claws as the primary weapons of these animals. These conclusions are in contradiction to those of Manning *et al.* (2006) who argued that sickle claws were not used as lethal weapons but for climbing the bodies of their prey, and that velociraptorines would have killed prey with their jaws. Even intuitively this appears unlikely given that these theropods had slim, gracile and rather fragile-looking skulls, and that climbing tetrapods invariably employ lots of claws, not just one big one.

By comparing juveniles with adults, Therrien *et al.* also include observations on ontogenetic changes seen among theropods. With ontogenetic data from extant carnivores in mind, the jaw morphology of juvenile tyrannosaurids indicates that they were catching and handling live, struggling prey by themselves, and thus perhaps going without extended parental care. An ontogenetic increase in the rigidity of the rostral end of the jaws in *Allosaurus*, however, indicates that juveniles did not feed in the same way as adults. So were babies hunting small prey, were their parents killing their prey for them, or were they killing large prey, but doing so by using a killing technique that did not require rigidity at the mandibular extremity (by employing slashing bites, for example)?

Paul's article on body and tail postures was written in response to the entertaining claim by Carrier *et al.* (2001) that large theropods would have minimised rotational inertia by running with their trunks and tails as near to vertical as possible, resulting in a sort of bizarre jack-knife posture. There isn't anything new in Paul's article – he repeats arguments that semi-vertical postures would overstretch certain muscles – but the points are worth making. Paul could not have incorporated the arguments used by Henderson and Snively (2004) on the same subject (his paper was in press when Henderson and Snively's was published): they also challenged Carrier *et al.*'s (2001) argument, using computer modelling to show that body shape in theropods changed as size increased, such that the effects of rotational inertia were minimised. Theropods would have been highly agile even at large sizes, without resorting to the employment of maladaptive postures.



Finally in this section, Larson and Rigby describe a new furcula of *Tyrannosaurus* and Lü *et al.* describe the pectoral girdle and forelimb of the Chinese oviraptorosaur *Heyuannia*, focusing in particular on the similarities present between members of this group and birds. Their opinion is that oviraptorosaurs are not basal maniraptorans, as most phylogenetic studies conclude, but actually basal members of Aves. These authors aren't the first to propose this idea, and indeed two parsimony analyses have supported it. However, a check of the characters and taxa used in these two studies reveals problems: Maryańska *et al.* (2002) only included *Archaeopteryx* and *Confuciusornis* among the avian taxa they coded. Why is this a problem? Well, most of the characters that pulled oviraptorosaurs towards *Confuciusornis* in their study involved jaw morphology and, uniquely among Mesozoic birds, confuciusornithids had rather oviraptorosaur-like, toothless jaws. Lü *et al.* (2003) also found oviraptorosaurs to be basal birds, but only because they excluded *Caudipteryx* (well supported as a basal oviraptorosaur) from Oviraptorosauria. It possessed only one of the 11 characters they used to support the oviraptorosaur-bird clade, the obvious conclusion being that it is only derived oviraptorosaurs that are bird-like. Several of these 11 characters are erroneous anyway, incidentally.

In this new article, Lü *et al.* now argue that the laterally directed humeral glenoid, partially fused metacarpus, and acute angle between the manus and forearm make *Heyuannia* more like a bird than other maniraptorans. However, these characters are either more widely distributed than implied here, or – again – absent in basal oviraptorosaurs and birds, thereby indicating convergence between derived birds and derived oviraptorosaurs. Convergences and reversals appear so rampant within maniraptorans that just about any possible relationship could be proposed if one were to pick and choose from just a few select characters, as has been done here.

The final section of the book opens with Gay's analysis of variation in *Dilophosaurus*, the conclusion being that, in contrast to its putative relatives the coelophysids, *Dilophosaurus* does not preserve evidence for sexual dimorphism. Molnar reviews evidence for sexual dimorphism in theropods and provides a thorough and useful discussion of the literature on this subject. While many authors have compared the distinction between the gracile and robust morphs seen in some theropod species with the size dimorphism present in many extant taxa, Molnar points out that theropods may have been unique in exhibiting 'a dimorphism of bone robustness, a kind apparently unknown in modern tetrapods' (p. 308). Currie *et al.* describe a *Daspletosaurus* bonebed (an intriguing discovery, as it is not the first multi-individual association of tyrannosaurid specimens). Carpenter *et al.* describe and interpret specimens indicating predator-prey interactions between Morrison Formation stegosaurs and allosaurs, and Rothschild and Tanke review theropod palaeopathologies.

As with the previous IUP dinosaur books, the editing of *The Carnivorous Dinosaurs* is mostly good but a few clangers have made it through. What is 'ontogeny' (pp. 277, 282) and who, exactly, is Bob Baker (p. 254)? And why is *Phorusrhacos* referred to by the incorrect 'Phororhacos' (p. 262)? Mis-spellings of generic names are sprinkled throughout the text, and in one case a female researcher is accidentally referred to as a 'he'. Luis Rey's cover-art (depicting *Carnotaurus*) has a washed-out look compared to his original, yet a garish blurry background. It also looks odd in that the animal has what looks like a piece of dead liver hanging from the back of its mouth.

In its inclusion of thoughtful, data-heavy studies such as that by Therrien *et al.*, and for the new information provided on taxa such as *Tanycolagreus* and *Harpyimimus*, this volume will be of great



interest to those working on theropods. Overall it seems too specialised to be of much use to others however, and, ultimately, the claim that it contains 'exciting new research' is arguable at best.

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REFERENCES

- HENDERSON, D. M. and SNIVELY, E. 2004. *Tyrannosaurus* en pointe: allometry minimized rotational inertia of large carnivorous dinosaurs. *Proceedings of the Royal Society of London B*, 271, S57–S60.
- LÜ, J., DONG, Z., AZUMA, Y., BARSBOLD, R. and TOMIDA, Y. 2002. Oviraptorosaurs compared to birds. 175–189. In ZHOU, Z. and ZHANG, F. (eds). *Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution*. Science Press, Beijing.
- MANNING, P. L., PAYNE, D., PENNICOT, J., B ARRETT, P.M. and ENNOS, R. A. 2006. Dinosaur killer claws or climbing crampons? *The Royal Society, Biology Letters*, 2, 110–112.
- MARYAŃSKA, T., OSMÓLSKA, H. and WOLSAN, M. 2002. Avialan status for Oviraptorosauria. *Acta Palaeontologica Polonica*, 47, 97–116.
- NAISH, D., HUTT, S. and MARTILL, D. M. 2001. Saurischian dinosaurs 2: Theropods. 242–309. In MARTILL, D. M. and NAISH, D. (eds). *Dinosaurs of the Isle of Wight*. The Palaeontological Association, London.

Extinction: how life on Earth nearly ended 250 million years ago

Douglas H. Erwin (2006). Princeton University Press, New Jersey. 306pp.
ISBN-13 978-0-691-00524-9, \$24.95 / £15.95 (hardback).

For some time now review articles and books about mass extinctions have tended to be organised along the lines of a mystery story. The crime scene is surveyed, background material discovered and presented, suspects identified, evidence collected, and, in one of the later chapters, the suspects gathered together so the culprit can be revealed in a suitably dramatic manner. I suppose this is natural. The causes of mass extinctions are indeed mysterious, and their identification requires the objective evaluation of largely forensic evidence. But there is a moral dimension to real mystery stories that's missing from attempts to fit scientific reviews into this structure. It's emotionally satisfying to see how disparate and seemingly unrelated facts can be fitted together to reconstruct a violent death and, more importantly, identify the criminal so that justice may prevail (and usually save the falsely accused maiden). Science isn't like that, and extinction science is especially not like that. The clues are few, far between, and usually don't add up to a coherent picture of events. The clues also tend to be complex and prone to ambiguity; not the sorts of subtle but obvious things that can be noted and passed over so one can return to the main betrayal and redemption story without upsetting that story's momentum. Finally, there is no moral dimension. The culprits are not people driven by jealousy or avarice, but natural processes, no more emotionally driven than gravity or ontogeny. Knowing who (or what) did the deed in a scientific mystery doesn't result in a sense that the natural order has been restored. Usually it's just the opposite, because the science addresses itself to a 'natural order' that is unnaturally small, big, or of exceedingly long duration.



Doug Erwin has written such a mystery book about the Late Permian extinction(s). This volume updates Doug's 1993 book on the same topic and covers essentially the same ground as Mike Benton's *When Life Nearly Died: The Greatest Mass Extinction of All Time* (2003, reviewed in vol. 54 of this Newsletter). The book will undoubtedly sell well to the general public who have a consistent interest in palaeontology, a growing concern over modern biodiversity crisis, and whose appetites have been whet by the media's continuing obsession with the K–T extinction story. Doug's book has already been reviewed favourably by the *Washington Post*, *Science*, *New Scientist*, *Science News*, etc. But what of the palaeontological community? What does the book have to offer us and how should it be used?

I found Doug's book curious for two reasons. First and less importantly, Doug has already been here before. His 1993 book *The great Paleozoic crisis: life & death in the Permian* was an excellent summary of the relevant data to that date and posited a causal scenario that tried to account for the event in light of those data. In 1993 Doug believed all the suspects had a hand in the deed (volcanism, anoxia, sea-level change, methane, impacts) and, in keeping with his mystery-book metaphor, dubbed this the Murder on the Orient Express scenario. Subsequent commentators referred to this as 'Erwin's Kitchen Sink hypothesis'. Since 1993 though, there has been a tremendous amount of work done on the Permian extinction, in no small part driven by a sense that the K–T extinction controversy has run its course, and determining whether the Permian extinction was similar to, or different from, the K–T was the next most pressing issue for palaeontological extinction studies. Building on his previous Permian work, Doug continued to be among the foremost Permian extinction researchers. The results Doug, his collaborators, and others achieved in the decade since 1993 are certainly noteworthy, and deserving of a popular description. However, their assembly here leads to the second curious aspect of the book; Doug Erwin is apparently much less sure of what caused the Permian extinction(s) in 2006 than he was in 1993. Doug gets this revelation out of the way early in the book by stating, 'The simple truth is that we do not know what caused these twin extinctions. Or at least I don't know.' (p. 9). But is there really that much difference between claiming that everyone – or to be precise, everything – was to blame in 1993 and suggesting the causes are uncertain in 2006?

Extinction is organised into ten chapters, including a presentation of background material (chapters 1 and 2), a summary of new geochronological data (chapter 4), overviews of the taxonomic and stratigraphic character of the extinction in marine and terrestrial habitats (chapters 5 and 6), a review and discussion of stable isotope data (Chapter 7), and the inevitable drawing room scene (Chapter 8). This is followed by two small and somewhat unfocused chapters, on the Triassic recovery (Chapter 9), and on the meaning of it all (Chapter 10). Interspersed within these largely factual and/or interpretational sections are two extended travelogues in which stories of field work in China (Chapter 3) and South Africa (first part of Chapter 6) are recounted.

What about the factual material? Generally speaking all the pertinent facts are mentioned in one way or another. The two most significant developments over the last ten years have been high-resolution radioisotope dates from the Meishan section in China and the recovery of high-quality $\delta^{13}\text{C}$ isotopic profiles from a globally distributed series of marine and terrestrial cores and sections. These data have been brought together to make a convincing case that a strong but progressive decrease in the global $\delta^{13}\text{C}$ ratio occurred throughout the Changhsingian whose duration is not on the order of a few million years as was thought previously, but rather a few hundred thousand years, possibly shorter. This interval also coincides with the disappearance of over 300 marine species in the Meishan section and is included within the interval during which the Siberian volcanic



province was erupted. Along with these data and inferences Doug reviews ancillary developments in a wide variety of areas, including a complete review of alternative P–Tr extinction cause models (excellent), atmospheric chemistry and the carbon cycle (a good layman’s explanation), discussions of the causes and effects of flood basalt volcanism (excellent), the search for P–Tr impact debris (little evidence found to date), identification of a fungal spike at the P–Tr boundary (many reports, one interesting alternative explanation), the importance of stratigraphic confidence intervals and the Signor-Lipps Effect (an incomplete and misleading discussion in my view), and so forth.

The care with which this material is put together, however, is mixed, and this is the area where I found myself being most frustrated. Naturally Doug uses the K–T extinction as a device with which to compare and contrast biotic patterns and physical evidence found close to the P–Tr boundary. That’s fine. But in Doug’s haste to present the Changhsingian event as different from the Maastrichtian he presents a one-sided, and so overly simplistic, caricature of the latter. Not only is this incorrect, it’s at odds with the main thrust of his own P–Tr story. According to Doug, the Maastrichtian extinction was caused by the Chicxulub impact because there’s copious evidence for impact debris at the K–T boundary. The Changhsingian event is probably not impact-related because such physical evidence has, for the most part, not been recovered. Leaving aside the logical gap between an impact event having occurred and it being linked to particular species extinctions, if the similarities between these two extinction intervals ended there few could argue with Doug that the two events are different. But the similarities (or lack thereof) don’t end there.

Doug spends a lot of time talking about a sea-level regression near the P–Tr boundary. A sea-level regression occurred at or just before the K–T boundary too, but you wouldn’t know that from Doug’s book. Doug also spends considerable time talking about flood basalts and even uses the Deccan volcanic province as an example to make some of his points regarding flood basalts in general. But he evidently believes Deccan played no role in the K–T extinctions because in several critical passages he neglects to mention Deccan took place coincident with the Maastrichtian extinction and the Chicxulub impact. One is left with the very distinct – but erroneous – impression the P–Tr interval has essentially nothing in common with the K–T interval and, of course, there are differences. But not as many as parts of Doug’s book suggest.

Why the, in my view, inappropriate distinction? Doug is no friend of impacts as a general cause for elevated extinction intensity. He does not dismiss the possibility of P–Tr impact out of hand, but he reviews the meagre evidence for such an event in detail and quite critically. To some extent





I believe it's the result of a philosophical stance. Toward the end of the book (p. 210) he states 'I think we would learn more about how the earth operates if the [mass] extinctions had different causes'. Though he doesn't acknowledge the link, this stands in opposition to a favourite Dave Raup quote of mine 'There is no way of assessing cause and effect [in historical data] except to look for patterns of coincidence – and this requires multiple examinations of each cause-and-effect pair. If all extinction events are different the deciphering of any one of them will be next to impossible.' (Raup 1991, p. 151). I'm definitely a Raupian on this one. If there's no consistent effect resulting from a given cause there's no way to identify the cause. Looking for consistency between cause and effect is what science is all about. This is implicitly understood by Doug insofar as he refers to his dislike of (usually impact-related) arguments based on coincidence in several passages. The way out of this for extinction studies is to follow Raup's advice and undertake a serious examination of comparable extinction events looking for commonalities. That is what Vincent Courtillot has done for flood basalts. That is what Tony Hallam and Paul Wignall have done for anoxia.

That is also what drives those who favour the impact-centred cause for extinction events to scour those boundary sections in excruciating detail. Along these lines I've always found it interesting that the three largest extinction events of the past 250 million years all took place when the emplacement of a major flood basalt volcanic province coincided with a major sea-level regression – not enough of a coincidence to be statistically significant but a perfect score nevertheless (see MacLeod 2004a, b for a set of, albeit crude, statistical tests of various more complex association models). So, looking for similarities and suspecting arguments based on non-repeated coincidences is what we have done and must continue to do. What is not acceptable in trying to make a case, or review the pertinent data, however, is to misrepresent the complexity of a comparator event by failing even to mention critical similarities.

On the more positive side Doug publishes the argument that has been made for some time skewering the old Jablonski (1985) idea that sea-level regressions cannot have played a major role in mass extinction events because the Pleistocene sea-level drop did not result in extinctions. The two regressions are not comparable in their ecological effects because sea-level already stood low in the Pliocene. The Pleistocene drop did not result in wholesale draining of the continental platforms with consequent effect on habitat areas as did the Permian regression (along with the K–T). In places Doug also exhibits an admirable care not to over-interpret his data (*e.g.*, he readily acknowledges that the turnover pattern in the Meishan section cannot be extrapolated over the entire globe). In other passages, though, caution is thrown to the winds, such as his presentation of conclusions based on unreferenced observations (*e.g.*, biogeographic differences between the end Guadalupian and Changhsingian extinction on p. 115.), loose use of the term 'catastrophe' (compare his fossil insect 'catastrophe' which took 40 million years to play out (p. 150) with his repeated insistence throughout the text that catastrophic change means less than 1 million years), selective or incomplete presentation of evidence (Doug's Fig. 8.1 shows an excellent correlation between flood basalt eruptions and six extinction-intensity peaks, whereas Courtillot 1999 shows the same figure with an essentially perfect correlation between ten flood basalt-extinction couplets – effectively the entire flood-basalt-extinction peak record) and many internal inconsistencies in his arguments (*e.g.*, describing an extinction that takes a 'few hundred thousand years' to occur as 'rapid' in an ecological sense).

When all has been said and done, Doug likes the correlation between the Changhsingian extinction and the Siberian flood basalts, but is at a loss about the precise mechanism whereby flood basalts



per se induce extinctions globally. He's attracted by the idea that those eruptions may have heated the carbon-rich Tuguskskaya Series sediments above 100°C to produce enough methane and so account for the P–Tr $\delta^{13}\text{C}$ isotopic anomaly by driving global warming, but there's no direct evidence this happened. Similarly, he doesn't like marine anoxia because he doesn't see a mechanism for that phenomenon to release carbon in sufficient quantities to account for the isotopic shift, but he would allow anoxia to be an effect of the global warming. He doesn't like clathrates any more, but only because he doubts they would supply enough methane to the atmosphere, though the warming would surely have melted those that were around at the time. He doesn't like impacts (see above) and he doesn't describe any mechanism by which an impact could produce the isotopic shift – especially the gradual shift documented by the many isotopic curves he reproduces, though in the end he hedges his bets by noting 'it is possible that an impact occurred as the Siberian flood basalt erupted.' (p. 205). Last, but not least, he appears to side with his old 1993 stance in the several places where he alludes to multiple-cause scenarios (e.g., p. 217), but he takes pains to distance himself from that work and never expounds on this eminently common-sense idea, much less attempts a credible test. In the end I was left with the impression that, while some solid progress had been made during the last decade in understanding what the thing we call the end-Permian mass extinction is, surprisingly little progress has been made toward determining its cause. Reading between the lines Doug thinks we're approaching the whole question too simplistically. I agree.

This book can be read with profit by those who are interested in a knowledgeable insider's account of the more recent conceptual, radioisotope and stable isotopic work on the Permian extinction boundary. Doug's writing style is informal – often self-deprecating – and some of the travelogue passages are very effective at capturing the feeling of fieldwork and characters you meet when doing it. The text is relatively free of mis-statements, abounds with the sort of bad metaphors some find endearing, and Doug has opted to flesh out some of the points he makes in the text with footnotes. An unusually short and person-dominated (as opposed to topic-rich) index to the text is also included.

It's a nice book. A worthy book. It has some interesting insights. But in my view it contains too many inconsistencies and oversimplifications to qualify as a comprehensive overview of the current state-of-the-debate, either for the Permian event in particular or for the phenomenon of mass extinction in general. Hallam and Wignall's (1997) much more comprehensive review is still top of that heap for me, though of course it doesn't contain some of the more recent Permian material Doug's book includes. This is a popular account of one researcher's efforts to understand the Permian extinction event. It both benefits and suffers from being that sort of book. It should be read by professionals who want an update and students looking for ideas, though hopefully not in isolation from other, less idiosyncratic treatments.

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REFERENCES

- BENTON, M. J. 2003. *When Life Nearly Died: The Greatest Mass Extinction of All Time*. Thames & Hudson, Ltd., London, 336 pp.
- COURTILLOT, V. 1999. *Evolutionary catastrophes: the science of mass extinction*. Cambridge University Press, Cambridge, 173 pp.



- ERWIN, D. H. 1993. *The great Paleozoic crisis: life & death in the Permian*. Columbia University Press, New York, 327 pp.
- HALLAM, A. and WIGNALL, P. B. 1997. *Mass extinctions and their aftermath*. Oxford Science Publications, Oxford, 328 pp.
- JABLONSKI, D. 1985. Marine regressions and extinctions: a test using the modern biota, 335–354. In VALENTINE, J. W. (ed.) *Phanerozoic Diversity Patterns: Profiles in Macroevolution*. Princeton University Press, Princeton.
- MACLEOD, N. 2004a. Identifying Phanerozoic extinction controls: statistical considerations and preliminary results, 11–33. In BEAUDOIN, A. B. and HEAD, M. J. (eds). *The palynology and micropaleontology of boundaries*. Geological Society of London, Special Publications, London.
- MACLEOD, N. 2004b. A statistical evaluation of the association between LIP volcanism and extinction-intensity peaks over the last 250 m.y. 32nd International Geological Congress, Abstracts Volume, 1, 798.
- RAUP, D. M. 1991. *Extinction: bad genes or bad luck*. W. W. Norton and Co., New York, 210 pp.

The Origin and Evolution of Mammals

Thomas S. Kemp (2005). Oxford University Press, Oxford. 341pp.
ISBN 0198507611, £39.95 (paperback).

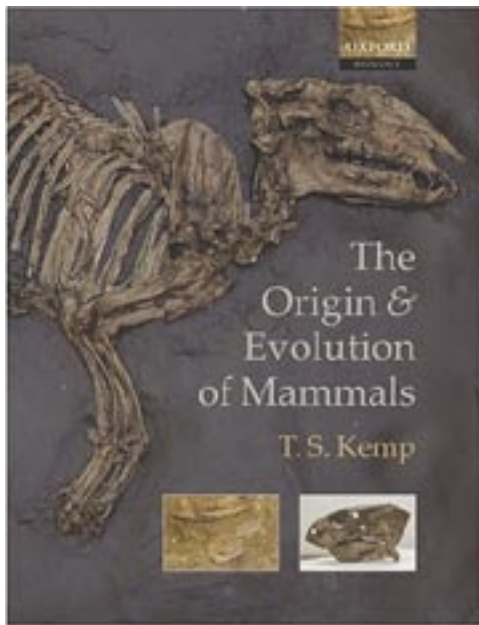
More than 24 years ago, Kemp produced his classic book *Mammal-Like Reptiles and the Origin of Mammals* (Academic Press, London, 1982). This new book is an update and expansion of the previous work, hence the more inclusive title. Like Kemp's 1982 book, this edition has many of the same strengths: the writing is clear and concise, the illustrations are nicely redrawn from numerous sources, giving the book a very consistent look that is helpful in understanding the anatomy of these creatures, and the book is carefully referenced and generally up-to-date. However, throughout the book there are surprisingly outdated notions and terminology that mar what is otherwise a very modern approach.

The biggest 'hang-up' is the difficulty that Kemp and many other palaeontologists have encountered when they must 'unlearn' terminology that has become obsolete or misleading. The classic example is the misnomer "mammal-like reptiles" (which is no longer in the title, but used widely in the text). As Kemp clearly understands, the synapsid lineage branched off at the same time in the early Carboniferous as the true 'reptile' lineage (the clade that includes all living reptiles), and the two are sister-groups. At no time was a primitive synapsid ever a "reptile"! All of the so-called "primitive reptiles" are either members of synapsid lineage or the reptile lineage. Unfortunately, this misleading term has been so widely used for generations that many scientists simply cannot expunge it from their minds. Consequently, we still find it in books like this, even though the term has completely vanished from the professional journals and from the meeting programme of groups such as the Society of Vertebrate Paleontology. Call them "protomammals" if you will, but never "mammal-like reptiles"! Likewise, Kemp uses many other groups that he admits are paraphyletic wastebaskets, yet the outdated terminology persists out of habit. The "Eupantotheria," for example, have long been abandoned as useless; they are better described by their monophyletic components, dryolestids and paurodonts, but not "pantotheres." Likewise, "Condylarthra" has vanished in favour of the less misleading term "archaic ungulates," but it reappears in this book. Kemp has accepted



and understood cladistics since before his 1982 book, but clearly the continued usage of misleading paraphyletic groups doesn't bother him (even though these names have virtually vanished from professional use).

The book begins with a general introduction to the mammals, outlining the approach used in the text, and follows with a second chapter on geologic time and classification. Even in these general introductory chapters, however, we can pick up the tension between Kemp's more traditional views and the newer approaches as he struggles valiantly to explain and defend the "crown-group" definition of Mammalia versus his more traditional Simpsonian ideas based on a particular suite of characters and adaptive niche. In addition, Kemp still uses the outdated term "absolute" dating, when most geological societies and stratigraphic codes (such as the 1983 North American Stratigraphic Code) have replaced it with the more accurate and less misleading "numerical dates."



Chapters 3 and 4 are by far the longest in the book, and are basically an updated version of his extended treatment of non-mammalian synapsids from his 1982 book. As in that previous edition, he espouses his own views of the synapsids without really addressing the contrary opinions of other authorities (e.g., James Hopson). Each of the major groups of synapsids is described in detail, with detailed drawings of the anatomy of key taxa, and their relationships and palaeoecology are discussed. Kemp shows generalised cladograms of these taxa on occasion, but unfortunately the cladograms are simple branching diagrams completely stripped of any character information, so the reader has no way to determine on what data the topology is based. By contrast, other recent summaries of vertebrate evolution for the general audience and college market (e.g., Benton, 2005; Pough *et al.*, 2004) have managed to squeeze in a condensed caption with the major synapomorphies labelled at each node, so at least the interested student and professional can get some sense of the character evidence for the cladogram, and not have to dig up the original sources.

Chapter 5 gives an overview of Mesozoic mammals, a field that has transformed dramatically in the past 20 years with dozens of new taxa, more complete specimens, fossils from previously unsampled regions, and especially new hypotheses and character analyses. The gold standard on this subject is Kielan-Jaworowska *et al.* (2004), which summarised and updated all of the new discoveries. Kemp was apprised of most of the developments in that book, so his coverage is consistent with the new discoveries. Kemp also briefly summarizes the K/T debate, and fortunately does not present a simplistic 'rocks from space' scenario but instead discusses the complexity of the palaeobiological data that supports a gradual extinction scenario with only a minor role for impacts (a position consistent with the majority opinion among vertebrate palaeontologists; see Brysse, 2004).



Chapters 6 and 7 are the major new additions not found in the 1982 book, which originally ended with the beginning of mammals in the Triassic. Chapter 6 summarizes marsupial evolution, with excursions into the many bizarre extinct groups of Australia and South America, and an extended discussion of Australia's oldest marsupials and a possible placental from the Eocene Tingamarra local fauna. In this chapter, the molecular data enter the discussion for the first time, although Kemp does not propose any resolution of the many conflicts that currently exist between morphological and molecular approaches.

The most disappointing section is Chapter 7. After such detailed summaries of nearly every family of non-mammalian synapsid, Mesozoic mammal, and marsupial, the huge diversity of placental mammals is dispensed with in fewer than 60 pages of a 330-page book! Clearly, the placentals are far from Kemp's specialty of the non-mammalian Synapsida, but this summary is so short that it leaves out nearly everything that readers might find interesting about mammal evolution, from gigantic indricothere rhinos to fascinating evolutionary stories of horses and camels, to the diversification of whales, to the origin and evolution of various groups of carnivores. The problems begin with Kemp's wholehearted adoption of the newly-proposed molecular classification of placentals without really giving any of the caveats or reservations about taxa such as "Afrotheria," "Boreoeutheria," "Lauriasiatheria" *etc.* Even those who advocate the molecular classifications are aware that they seriously conflict with the morphological data, yet Kemp cites none of this contradictory evidence. One needs only to think back to the embarrassing molecular papers that claimed that guinea pigs were not rodents to recognize that molecular data can also be misleading. The molecular classifications may eventually be corroborated (especially if the morphological data are reanalyzed and combined with molecular data to generate "total evidence" cladograms), but that consensus is not yet achieved, and Kemp misleads the reader by presenting only one set of hypotheses. Kemp concludes his too-short discussion of placentals with a brief summary of the conflict over the timing of the Cretaceous placental radiation (again, molecular vs. palaeontological data), Beard's "Garden of Eden" hypothesis, and a brief summary of Cenozoic geological and biotic events in the history of the mammals. The chapter concludes with a discussion of the Pleistocene megafaunal extinctions. Once again, Kemp is not seduced into the simplistic "black-or-white" thinking of the overkill advocates, but lays out the complex evidence that does not support any single hypothesis after 30 years of debate.

Covering all of the evolution of non-mammalian synapsids and mammals in a single relatively short book is indeed a difficult task, but I would still expect a little better balance between the huge diversity and complex history of Cenozoic placentals in relation to the less complete record of Permian and Mesozoic non-mammalian synapsids and mammals. Kemp clearly emphasizes what he knows best, but the result is uneven and not much use to those who are interested in the latter half of mammalian history. On the whole, most of the chapters are well written and illustrated, and will be very useful to the graduate student or professional palaeontologist who needs a brief introduction or update on the evolution of synapsids or Mesozoic mammals. The writing, however, is far too detailed for most undergraduates (at least in my experience in American colleges). Unfortunately, there is still no up-to-date single source on the evolution of Cenozoic placental mammals available for the student or professional, although Janis *et al.* (1998), Prothero and Schoch (2003), Rose and Archibald (2005), and Prothero (2006) provide part of the picture.

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REFERENCES

- BENTON, M. J. 2005. *Vertebrate Palaeontology* (3rd ed.) Blackwell, Malden, Massachusetts, 455 pp.
- BRYSSSE, K. 2004. *Off-limits to no one: vertebrate paleontologists and the Cretaceous–Tertiary mass extinction*. Unpubl. Ph.D. dissertation, University of Alberta, Alberta, Canada.
- JANIS, C. M., SCOTT, K. M. and JACOBS, L. L. (eds.). 1998. *Evolution of Tertiary Mammals of North America. Vol. 1. Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals*. Cambridge University Press, Cambridge, 691 pp.
- KIELAN-JAWOROWSKA, Z., CIFELLI, R. L. and LUO, Z.-X. 2004. *Mammals from the Age of Dinosaurs*. Columbia University Press, New York, 630 pp.
- POUGH, F. H., JANIS, C. M. and HEISER, J. B. 2004. *Vertebrate Life* (7th ed.). Prentice-Hall, New York, 752 pp.
- PROTHERO, D. R. 2006. *After the Dinosaurs: The Age of Mammals*. Indiana University Press, Bloomington, Indiana, 300 pp.
- PROTHERO, D. R. and SCHOCH, R. M. 2003. *Horns, Tusks, and Flippers: The Evolution of Hoofed Mammals*. Johns Hopkins University Press, Baltimore, Maryland, 311 pp.
- ROSE, K. D. and ARCHIBALD, J. D. (eds.). 2005. *The Rise of Placental Mammals*. Johns Hopkins University Press, Baltimore, Maryland, 259 pp.

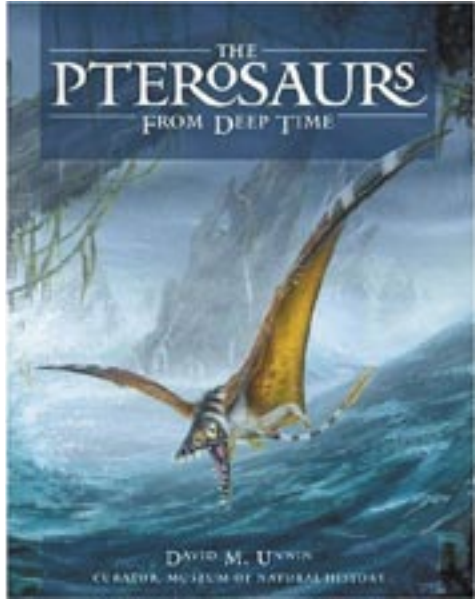
The Pterosaurs from Deep Time

David M. Unwin (2005). Pi Press, New York. 347pp, ISBN 0 13 146308 X, £28.99 (hardback).

Pterosaurs are enigmatic flying reptiles that lived alongside the dinosaurs for much of the Mesozoic. Despite a long and distinguished history of study, one of Dave Unwin's opening sentiments in his new book is particularly apt – for some reason 'pterosaurs are really hard to understand'. Or at least that's how it has proved, at least in popular culture: asked to name their favourite dinosaurs, most people would come up with 'a pterodactyl' as part of the list. These reptiles are superficially well known, but one has to delve deep into the primary literature to find out about their relationships and palaeobiology. Sadly, until now, few accessible accounts that deal with the diversity and biology of pterosaurs were available; Unwin's *The Pterosaurs from Deep Time* was long awaited and fills this most obvious of gaps in the popular vertebrate palaeontological literature. This book was years in the pipeline, long talked about at conferences and on discussion lists, and has been billed as a successor to Peter Wellnhofer's classic 1991 *Illustrated Encyclopedia of Pterosaurs*.

Pterosaurs are weird, one of only three vertebrate groups to have evolved flapping flight. Unlike their counterparts, the birds and bats, these reptiles supported a stretched wing membrane along a super-elongated 4th finger, just one aspect of their anatomy that is complex and unusual. Coupled with the fact that their light and hollow bird-like bones have rendered their preservation as fossils frequently poor, pterosaurs have been subject to a variety of reconstructions and interpretations since their discovery in 1784. Although anatomical studies of these beasts have always trundled along in the background, thanks to Dave Unwin and colleagues 'pterosaurology' has undergone somewhat of a renaissance in recent years.

Unwin’s choice of pterosaurs as the subject of this book is therefore not unsurprising given that he is among the foremost experts on these reptiles, and probably has seen more of their fossil remains than anyone else in the world. Nevertheless, pterosaurs are an ambitious choice for a popular book – compared to many other fossil groups, their anatomical complexities are beyond what would normally have to be explained to a lay audience. Pterosaurs also have unusual preservation and are of completely uncertain origin – we know that they comprise a clade within reptiles, but beyond this no one knows much more. Unwin is to be congratulated; tricky areas of pterosaur biology and anatomy are covered in this book in enough detail for the reader to get to grips with the subject, but without getting bogged down in any nasty specifics that might bore or confuse. Avoiding nasty details while summarising information is certainly no mean feat. This is a coffee table book.



Unwin’s style is delightful and easy to read throughout *The Pterosaurs from Deep Time*. For the more interested or serious researcher, some 35 pages of footnotes are available, which give details of individual specimens and other researchers as well as the odd anecdote. 18 pages of references and a complete list of all known pterosaurian taxa are also provided. Unwin’s chatty style is supported by a wealth of high quality photographs and figures throughout; these do allow insight into a number of rare and important specimens, several not illustrated before. The text is complemented by renditions of ‘living’ pterosaurs by artist Todd Marshall, the highlight of the book.

The Pterosaurs from Deep Time was much hyped; alas, there is still much to do, and much to learn about these fascinating Mesozoic beasts. Although this book attempts to bring the reader up to date with the latest theories, discoveries and research, many important questions are left unanswered. As Unwin aptly quotes from Sir Winston Churchill “...this is not the end. It is not even the beginning of the end. But it is, perhaps, the end of the beginning”. There are probably another two centuries of work ahead of Unwin’s “pterosaurologists”; this book is certainly one place to start.

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An Introduction to Astrobiology

Iain Gilmour and Mark A. Sephton (Eds) (2003). Cambridge University Press, Cambridge. 364pp. ISBN 0-521-54621-4, £30.00 (paperback).

Astrobiology is an emerging, interdisciplinary field of science that has been described as the study of the origin, evolution, distribution and future of life in the Cosmos. The nascent field was given major impetus with the establishment of the NASA Astrobiology Institute in the Spring of 1998. Since that time the field has continued to expand with the establishment of new academic programmes at many universities and research institutions around the world. Not surprisingly, the number of graduate and undergraduate level college courses being offered has also grown, with the need for textbooks to provide an introduction to the field. Gilmour and Sephton's *An Introduction to Astrobiology* is one of several texts that have appeared recently, which aim to meet this need. Here I briefly review this text, including perceived strengths and weaknesses based on my personal experiences teaching upper division and graduate courses in Astrobiology at Arizona State University.

The question of the existence of life beyond our home planet holds universal appeal for humankind and has fascinated us for millennia. Many educational institutions have embraced the new field of Astrobiology as a way to engage the innate scientific curiosity of students. And the good news is, we are living at a unique and important time in the history of science when many once disparate disciplines are finding ways to interact and hopefully one day, answer this question.

In my experience, the question of life elsewhere is, simply put, fascinating to most students, most of the time. My classes typically include students from fields as diverse as geology, microbiology, biogeochemistry, astronomy, engineering – even literature and human history. Most of these students arrive with limited scientific experience, beyond their major field of study. In fact, the principal challenge I have faced in the classroom is how to teach such a highly interdisciplinary field to what basically amounts to a 'specialist' audience. Gilmour and Sephton have helped me 'level the playing field' by providing basic introductions to many of the key concepts important for understanding this field.

The level of presentation and topical coverage of *An Introduction to Astrobiology* is targeted for advanced undergraduates. The writing style is simple and free of jargon. Most sections are regularly punctuated by 'pause and think' questions, answers and comments being provided in a section at the back of the book. Also included in the Appendix is a tabular summary of useful planetary data, a table of selected physical constants and unit conversions, a table of elements with estimated cosmic abundances and an abbreviated glossary of terms. There is also a list of recommended readings, which I find too abbreviated to be useful.

For my graduate level courses, I recommend the book as background reading. Based on class evaluations, the majority of students find the text a useful framework for understanding the field. However, to bring our classroom discussions to the right level for the graduate course, I have found that chapters from the textbook need to be supplemented with papers from the peer-reviewed literature. Most of the ideas covered in this book are not traced to their originators, which I see as a weakness. I believe it is important that students of science understand where and how ideas originate.



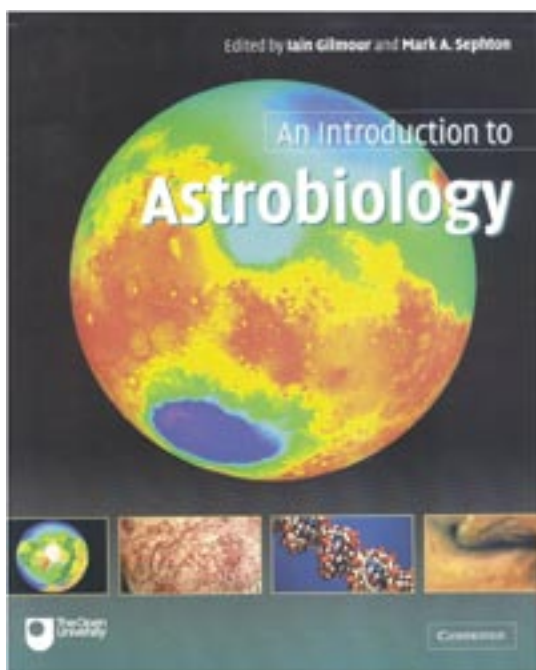
Astrobiology is a rapidly advancing, vibrant field. There have been many discoveries since the publication of this book, creating a need to supplement and update through lectures, homework assignments and targeted readings. For example, the spectacularly successful Mars Exploration Rover (MER) mission, the amazing images and data provided by the Cassini-Huygens probe, both during and following its successful descent to the surface of Titan, and the equally surprising discovery of geysering water fountains on Enceladus, to mention a few, have all happened since the book was published.

There are certainly many ways one can approach teaching a course in Astrobiology. In general, however, I find the organization and flow of ideas in *An Introduction to Astrobiology* to be appealing in their logic and simplicity. The book can be divided into three major sections: (1) the nature of terrestrial life and habitability, (2) exploring for habitable planets and moons in our Solar System, and (3) exploring for habitable worlds and intelligent life beyond our Solar System. Multiple chapters cover each of these areas and each includes a well-written summary at the end.

Chapter 1 (by Sephton) focuses on how we recognize life, what it requires, its environmental extremes and aspects of its evolutionary history, while Chapter 2 (by Gilmour) examines the concept of planetary habitability and how environments have changed over Earth history to create new evolutionary opportunities. Chapter 1 also includes useful boxed discussions about natural selection and Darwinian evolution, DNA hybridization, RNA, retroviruses and panspermia. Chapter 2 provides discussion boxes about the Snowball Earth, sources of Earth's water, distinguishing fossils from inorganic artefacts and the use of carbon isotopes as biosignatures. I find these boxed discussions, along with the embedded questions, to be very useful for generating classroom discussions.

Chapter 1 does a particularly good job with its coverage of the basic organic building blocks of life, the nature of biomolecular systems and hypotheses for the origins of complexity, leading to life's origin. However, there are weaknesses. In the discussion of life's requirements, there is a curious omission of the varied ways that life derives energy from its environment and what this suggests about habitability and the potential for life elsewhere. Also, the origin of the biologically important elements is given sparse attention, which would admittedly require the introduction of additional page filling concepts on nucleosynthesis and stellar evolution.

In the second section of the text,





there are chapters that deal with Mars (Chapter 3) and Titan (Chapter 5; both written by John Zarnecki) and the outer Solar System icy satellites (Chapter 4, by David Rothery). These chapters provide good, basic introductions to the potentially habitable planets and moons in our Solar System. The Mars chapter includes a summary of the ALH84001 (Martian) meteorite controversy and introduces the concept of planetary protection (with an emphasis on forward contamination, to the near exclusion of back-contamination issues). These chapters are well illustrated and also include boxed discussions of several important concepts, such as how to read a phase diagram, basics of oxidation–reduction reactions, internal tidal heating of moons, water radiolysis and photolysis and Lake Vostoc (largest of the sub-glacial lakes in Antarctica). What is missing is coverage of the previously mentioned discoveries in our Solar System that have occurred since the book was written.

The third section of the text deals with the exploration for life beyond our Solar System. Exoplanetary research is a particularly active area of Astrobiology and one that has seen numerous advances since the book was published. As with the previous section on the Solar System, there is a particular need to update this material with new discoveries. The exoplanet section kicks off with a discussion of the famous Drake Equation (Chapter 6, written by Andrew Conway) and what actually goes into calculating a probability for extraterrestrial life. I find this an especially helpful concept and great discussion organiser which I introduce early in the semester, revisiting it again near the end. This discussion is followed by sections (Chapter 6) and subsequent chapters (Chapters 7 and 8, both written by Barrie Jones) that deal with the methods used to detect planets around other stars, the nature of exoplanets, including approaches to the search for exoplanetary biosignatures. Included are boxed discussions covering astronomical magnitude, stellar classification, calculating angular distances and spatial resolution, planet formation and the use of emission/absorption lines in stellar spectra to identify the elemental composition of atmospheres

The book wraps up with a discussion of the exploration for intelligent life beyond Earth (Chapter 9, also written by Andrew Conway). This chapter includes a brief history of the search for intelligent life, with discussions of SETI (Search for Extraterrestrial Intelligence) and CETI (Communication with ET Intelligence). The chapter summary concludes with: “Encounters between terrestrial civilisations of different technological advancement provide an interesting, and perhaps worrying precedent for the arrival of a more advanced alien civilization at the Earth.” I have found that this particular topic engenders a great deal of interest and discussion with students, including many references to the range of potential outcomes suggested in such science fiction thrillers as *War of the Worlds*, *Mars Attacks*, *Alien*, *Predator* and *Contact*. It’s a good way to end a course!

In summary, *An Introduction to Astrobiology* lives up to its title by providing an interesting overview of this developing field. I recommend it both as a primary text for upper division courses that aim to introduce undergraduate students to science and as a supplementary (background) text for graduate level courses that explore more focused themes of this fascinating field of science.

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Biostratigraphy – Microfossils and Geological Time

Brian McGowran (2005). Cambridge University Press, Cambridge.
ISBN 0-521-83750-2. 459 pp. £50.00 / US\$85.00 (hardback).

Recently-trained palaeontologists and biostratigraphers, such as myself, who routinely use fossils to correlate sediment sequences and interpret palaeoenvironments, are spoilt with quite well developed frameworks of taxonomy and biozonation for a host of different vertebrate and invertebrate groups. It is all too easy for us to forget, therefore, the principles on which biozonations and classifications were founded, because we were not involved in their making (although possibly in their refinement).

Biostratigraphy – Microfossils and Geological Time by Brian McGowran takes a close look at these principles, *i.e.* the role of evolutionary theory at the core, the strength and weaknesses of different types of bio-event, the spatial limitation of biozones and the long process of acceptance of zonation schemes by communities through practical testing and refinement. It is an interesting book that breathes life back into biostratigraphy. Written solely by McGowran, the book is a synthesis that follows the development of biostratigraphy from classical origins into petroleum exploration and deep-ocean drilling. It explores the three-way relationship between species of microorganism, their environment and their evolution through time as expressed in skeletons preserved as fossils. McGowran provides a commentary on historical and biohistorical developments, extracting opinion and conceptual arguments from the confusion of stratigraphical and palaeontological literature. It is substantiated with example chronologies, biostratigraphic correlations and environmental trends together with summary figures that integrate biostratigraphic procedure from the micropalaeontology and (sometimes) broader palaeontological and stratigraphical literature. There is a focus on marine microfossils, especially foraminifera, because of their high quality fossil record, extensive use in industry and palaeoclimate studies and the author's own expertise, but it is not restricted to them, and there are attempts to bridge to the terrestrial realm with examples from records of fossil mammals where appropriate.

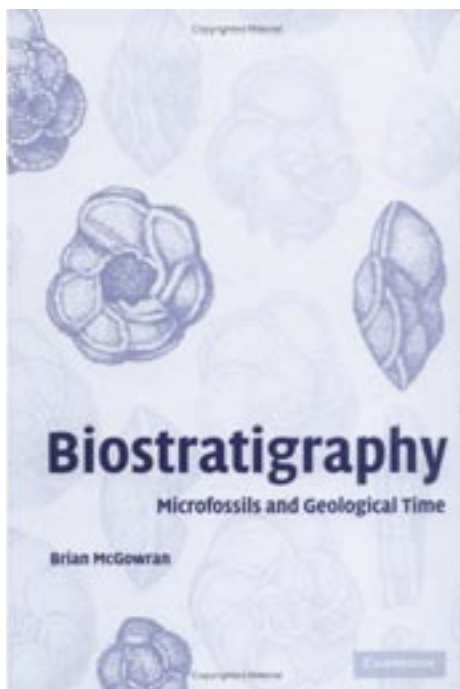
The book is organised into eight chapters. All are interesting and relevant, but some more coherent than others. The first four represent fairly cohesive treatments of the classical development of biostratigraphy, including the conceptual evolution of biozones with respect to microfossils, integration of biostratigraphy into modern geochronology (including magnetic reversal stratigraphy, radiometric dating and cyclostratigraphy), and the role of evolutionary theory. This includes a review of quantitative-morphological, palaeoecological and molecular studies of microfossil evolution in the context of defining 'species' for biostratigraphic purposes. McGowran's accounts are confusing in parts and it is sometimes difficult to follow exactly who said what and when. McGowran also writes with a gentlemanly modesty, his personal statements often qualified with a parenthesised "(I think)", which left me wondering what he really thought and whether the compiled material had been fully digested. For example, the discussion on event/datum diachronism is useful but somewhat confusing because it flips back and forth between opinions for and against first appearance datums as the most reliable zonal boundaries, leaving the reader slightly confused as to the author's conclusion. Despite these problems, McGowran has successfully extracted a history that reveals the development of biostratigraphy as a science, emphasizing the principle at the core, *i.e.* that organisms evolve, new species originate and go extinct. This emphasis reminds the reader how difficult it must have been to develop a science based on what was back then a very controversial idea.



The middle two chapters are less traditional in their approach and more difficult to follow. Chapter five takes biostratigraphy beyond its classical outline into the realm of system stratigraphy and sequence stratigraphy. Here McGowran attempts 'ecostratigraphy', fitting classical concepts of zones and datums into the epipelagic realm where sea-level driven reversible events and biofacies shifts prevail. For the sequence stratigraphy novice this is harder going but represents an important cross over between pelagic and epicontinental marine environments that forces closer examination of palaeoecology and changes in sediment in terms of environmental change, especially sea-level driven cycles. This is in part because many of the figures used to illustrate key concepts include numerous acronyms that are not explained fully in the abbreviated figure captions. Chapter six, 'Biohistory and biohistorical theory II: carving Nature at the joints' is a loosely bound chapter that attempts to integrate the somewhat woolly concepts of fossil 'communities' and 'ecological succession' on large (10^5 and 10^6 years) time scales. This scale of interpretation is ambitious. Knowing one group – the Eocene planktonic foraminifera – very well myself, I don't think that McGowran goes into enough detail at the ecosystem level. For example, the role of symbiosis as an ecological strategy in the radiation of Palaeocene 'muricate' planktonic foraminifer and subsequent sudden disappearance at the end of the middle Eocene is a classic example of an ecological response signalling environmental change, but somehow this was overlooked.

The penultimate chapter returns to a more structured look at specific problems in synthesizing stratigraphic procedure and bio-event correlation at key stratigraphic horizons, *i.e.* the Cretaceous/Tertiary and Eocene/Oligocene. The final chapter is a philosophical synthesis of all the material in the book, with the goal of outlining where McGowran feels biostratigraphy is or should be going in the future. He just about achieves this but it is sometimes tricky to identify the boundaries between this final chapter and the preceding ones.

Overall, I enjoyed this book although I think it could have been better organized in parts (especially the figure captions), and McGowran's own voice is sometimes difficult to find among the extensive historical accounts. However, it is thoroughly researched, broad and (mostly) sufficiently detailed, and makes a valuable contribution to the field. As a reference text for all biostratigraphers it might be a little too advanced, but for the expert and enthusiast, or a beginner looking to understand how the science of biostratigraphy evolved, this is a useful work. It might be a little pricey at £50, but will have a place in the lab and the graduate-level classroom. Reading the book cover





to cover made me reflect on my own understanding of biostratigraphy, forcing me to think about biozonation, and the key units, *i.e.* environmentally sensitive evolving species, within a broader palaeobiological framework. It also broadened my mind into other areas of stratigraphy that I am less familiar with, which, as McGowran hoped, has expanded my “biostratigraphic tool kit”.

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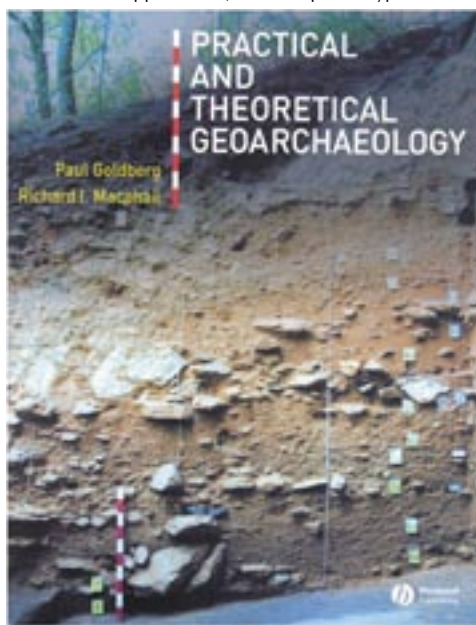
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Practical and Theoretical Geoarchaeology

Paul Goldberg and Richard I. Macphail (2006). Blackwell Science Ltd., Oxford. 454pages. ISBN 0-632-06044, £34.99 (paperback).

This book is attractively presented and considerably longer than its main competitor texts (French, 2002; Rapp & Hill, 1998). The book is divided into three parts. Part 1 comprises eight chapters on the depositional settings and processes that feature in the remainder of the book. These range from general descriptions of soils, sediments and stratigraphy, through to specific hydrological (slopes, rivers, lakes), aeolian and caves/rockshelter environments. The choice of which environments to include was presumably based on the availability of literature. This has the unfortunate effect of making this part of the book similar to both French (2002) and Rapp & Hill (1998) in concentrating on soil studies: it also precludes the interesting discussion of unusual archaeological environments where geoscience has proven essential in understanding archaeological context and planning excavation; marine and cold-climate (ice) archaeology are two environments that have abundant case-studies. Part 2 comprises six chapters that deal with applications, both to specific types of sites (cleared forest) as well as various occupation deposits. The latter leads nicely on to a chapter on experimental geoarchaeology, human materials and applications of the author's view of geoarchaeology to forensic science. Part 3 is essentially a methods section, made up of four chapters, on field, laboratory and reporting techniques. The conclusion chapter (two pages) is included in Part 3 for convenience, although it covers some aspects raised throughout the book.

The preface and introduction to a textbook are usually the sections that are ignored or quickly scanned by the reader who wishes to get to the guts of the book. In the case of this book however, comparison of these sections to the content of the book provides an insight into what our view of Geoarchaeology is. Goldberg and MacPhail





decide to base their work on the concept of site-forming processes, in a similar manner to French (2002) and Rapp & Hill (1998). This results in a strong reliance on evidence from soils and surficial sediments: of over 180 figures, more than 47 comprise photomicrographs or drawings of soil and sediment micro-textures. This 'illustrates' (no pun intended) what can be seen from the overall content of the book, that Geoarchaeology in this work follows that of others in concentrating on the depositional context of archaeology. The book does however begin to embrace an alternative definition of Geoarchaeology (which we prefer) as the application of geoscience techniques to archaeology. This latter definition is typified in Pollard (2000) and can be seen in Chapters 15 and 16: we congratulate the authors on their inclusion of analytical methods. The practising archaeologist could perhaps have benefited from expansion of these sections, and their inclusion earlier in the text, balanced by case studies from a wide range of environments, and less detail on each site. The chapters on forensic applications and reporting and publishing are welcome innovations. The latter could actually have been expanded and connected to the forensic aspects in terms of legal questions of preparing material for court and on the ethics of certain excavations.

Palaeontologists will probably already have textbooks that cover Parts 1 (sedimentology and soils) and 2 (techniques) of this book. There remain the case studies, reporting and forensic aspects, all of which will prove interesting. In this case, libraries with archaeological and palaeontological collections will benefit from purchase of this text: students and consultant archaeologists will find it a useful resource in writing-up their work. However, hard (igneous/metamorphic) rocks are also important in geoarchaeological research (e.g. sourcing of stone axes and Roman granite columns as well as the lithic materials at important sites such as Stonehenge, Newgrange and Easter Island). A little more on hard-rock geoarchaeology could have benefited the reader.

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REFERENCES

- FRENCH, C. 2002. *Geoarchaeology in Action: Studies in Soil Micromorphology and Landscape Evolution*. Routledge, 320pp.
- POLLARD, A. M. 2000. (ed.). *Geoarchaeology*. Geological Society Special Publication, Geological Society Publishing, 184pp.
- RAPP, G. and HILL, C. L. 1998. *Geoarchaeology: The Earth-Science Approach to Archaeological Interpretation*. Yale University Press, 286pp.

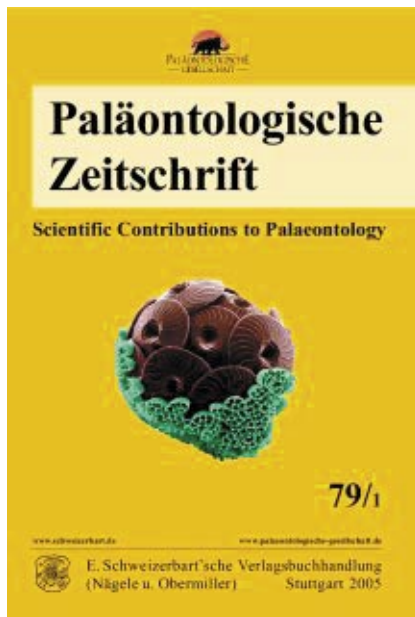


Marine plankton – a proxy for the understanding of Recent and fossil environments

Jörg Mutterlose (ed.) (2005). *Paläontologische Zeitschrift*, Vol 79/1, Schweizerbart'sche Verlagsbuchhandlung, Stuttgart. 200 pp. €30.00

Paläontologische Zeitschrift vol 79/1 is a proceedings volume of the session 'Marine Plankton als Umweltindikator für rezente und fossile Lebensräume' at GEO 2002, the joint meeting of thirteen German Geological Associations in Würzburg, 2002. The aim of this issue is to summarise 'the state of the art' in fossil microplankton research, giving an overview of *Bolboforma*, calcispheres, organic-walled dinoflagellate cysts, planktic foraminifera, calcareous nannofossils and radiolarians in ten articles.

At the beginning I was slightly puzzled about the book's remit to show "recent trends in marine plankton research, in particular from a German perspective" and questioned myself, had I been invited to comment on this because of my own "Germanness"?! I was pleased to see the broad range of articles summarising the current state of knowledge in most of the important modern plankton groups, though, sadly, no article on diatoms is included in this compilation.



Matthiessen *et al.* present a detailed and well balanced overview of organic-walled dinoflagellate cysts as palaeoenvironmental indicators in the Arctic Ocean. The chapter covers taxonomy, terminology, ecology, biogeography, preservation, and potential palaeoenvironmental applications. It represents a great introduction for students and non-specialists. The figures provide a good start for anyone preparing micropalaeontology lectures. The comprehensive reference list emphasises the broad selection of publications on which the article is based. This chapter is supplemented with a short contribution by Pross & Brinkhuis on the application of dinoflagellate cysts to palaeoenvironmental questions in the Palaeogene. The major highlight of this chapter is an amended version of the beautiful Brinkhuis (1994) cartoon on factors influencing distribution of Palaeogene dinoflagellates as well as species indicative for certain environmental conditions. A much more detailed review of this topic, including the same authors, was published recently in *Earth-Science Reviews* (Sluis *et al.*, 2005). This chapter would have been better incorporated into the Matthiessen chapter to avoid redundancies.

Zonneveld *et al.* discuss the environmental significance of modern calcareous dinoflagellate cysts whereas Kohring *et al.* focus on the evolution of the group and its palaeoecological significance. Although the review is based on the geographical focus of the authors' previous work and focuses on



the South Atlantic, the palaeoecology section provides a good overview of the most important species and their environmental preferences. The use of calcareous dinoflagellates as palaeoenvironmental proxies is demonstrated using a well illustrated example of the changes in dinocyst accumulation in association with Heinrich events. There might be some doubt however, if the 20 stable isotope measurements in dinocysts explain their potential as another palaeotemperature proxy adequately. The contribution by Kohring *et al.* has a very different angle by focusing on character traits in calcareous dinoflagellates with a view to elucidating genetic versus ecological influences on morphology. Kohring *et al.* have produced beautiful SEM pictures to illustrate character variability, for example wall thickness or morphological diversity. Their comprehensive introduction to terminology is very helpful for those less experienced with dinoflagellates. Once again, the two chapters are not integrated well; for example, both explain the crystallographic ultrastructure of the cyst wall.

The second half of the issue focuses on more conventionally used microfossil groups. Baumann *et al.* introduce coccolithophores as proxies for water masses, temperature and productivity. The chapter covers their biology, *e.g.* new knowledge on their life cycle. They provide a beautiful example illustrating the importance of sedimentological alterations of microfossil communities. The detailed study shows how different living communities (liths and spheres) compare to sediment traps and regional geographic variability. This contribution continues with palaeoceanographic reconstructions, ranging from conventional alkenone proxies to recent new approaches, and a discussion on changes in carbonate production by haptophytes. Some figures in this chapter would have benefited from a different grey scale selection. The evolutionary part of the nannofossil discussion is covered by Mutterlose *et al.* Their chapter focuses mainly on Mesozoic nannofossils; it introduces their morphology and systematics, evolutionary patterns, stratigraphy, and palaeobiology.

Modern planktic foraminifera are discussed by Schiebel & Hemleben and fossil species by Spezzaferri & Spiegler. Schiebel & Hemleben concentrate on the biological and physiological aspect of planktic foraminifers supported by excellent illustrations. This gives hope that the senior author might update his famous textbook. They have put their discussion on the ecology of foraminifers into the framework of influences on palaeoproxies. They touch on ecological stimuli, such as the season of test production, as well as physiological influences on isotope incorporation. Spezzaferri & Spiegler concentrate on the systematics and stratigraphy of planktic foraminifers with beautiful plates illustrating the most important species for each geological System discussed. Given the previous chapter, the rather general discussion of palaeoecology and palaeoceanography is largely redundant, and would have profited from examples of palaeoceanographic reconstructions of Cretaceous or Palaeogene age, along the lines of the chapter by Mutterlose *et al.*

Spiegler & Spezzaferri provide an overview of the *Bolboforma* biozonation. The chapter provides an overview of species using beautiful plates, but speculations on palaeoceanographic implications of this still enigmatic microfossil group are rather short.

The last chapter comprises Lazarus's review of radiolarians and is unfortunately the only chapter on siliceous microfossils. Lazarus provides an overview of their biology, ecology, taxonomy, and evolution. He discusses the significant influences of variable preservation on microfossil assemblages, and includes a brief paragraph on preparation. The focus is on stratigraphy with an overview on radiolarian zonation. The chapter closes by introducing palaeoenvironmental reconstructions, mainly palaeoproductivity.



After reading these 200 pages, I am still intrigued how one can treat microfossils from a national perspective. Besides the editorial, this is a well balanced compilation of our present understanding of their ecology and palaeoecology. Its contents embrace evolution, ecology, taxonomy, and explores the form and function of these important repositories of palaeoclimatic information. Better co-ordination of the “recent” versus “palaeo” chapters on a fossil group would have improved the overall quality of the issue. Though several microfossil groups are missing – most importantly one on diatoms – I recommend this overview to students of micropalaeontology and everyone using these microfossils as an introduction to ecology and its applications. This compilation is much more useful than some textbooks carrying micropalaeontology in their title, especially considering the modest price.

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REFERENCES

- SLUIJS, A., PROSS, J., and BRINKHUIS, H. 2005. From greenhouse to icehouse; organic-walled dinoflagellate cysts as palaeoenvironmental indicators in the Palaeogene. *Earth-Science Reviews*, **68**, 281–315.
- BRINKHUIS, H. 1994. Late Eocene to early Oligocene dinoflagellate cysts from the Priabonian type-area (northeast Italy); biostratigraphy and palaeoenvironmental interpretation. *Palaeogeography, Palaeoclimatology, Palaeoecology* **107**, 121–163.



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