

The Palaeontology Newsletter

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Reminder: The deadline for copy for Issue no 57 is 8th October 2004

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

Association Business

47TH ANNUAL GENERAL MEETING AND ANNUAL ADDRESS

Saturday 16th December 2004
University of Lille

AGENDA

1. Apologies for absence
2. Annual Report for 2003
3. Accounts and Balance Sheet for 2003
4. Election of Council and vote of thanks to retiring members

ANNUAL REPORT 2003

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 1,235 on 31 December 2003, an overall increase of 17 over the 2002 figure. There were 755 Ordinary Members, an increase of four; 140 Retired Members, an increase of eight; and 340 Student Members, an increase of five. There were 163 Institutional Members in 2003, a decrease of one from last year. Total Individual and Institutional subscriptions to *Palaeontology* through Blackwell's agency numbered 385. Subscriptions to *Special Papers in Palaeontology* numbered 151 individuals, an increase of 11 on last year, and 1,055 institutions, a decrease of two. Regular orders through Blackwell's agency for *Special Papers in Palaeontology* totalled 37 copies. Sales to individuals through the Executive Officer of current and back numbers of *Special Papers in Palaeontology* yielded £13,769. Income from sales of *Field Guides to Fossils* amounted to £9,399. Sales of "Fold out Fossils" totalled £107.

Finance. Publication of *Palaeontology* and *Special Papers in Palaeontology* is managed by Blackwell, 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 £4,770. The Association gratefully acknowledges the donations from Members to the Sylvester-Bradley Fund, which amounted to £358.

Grants from general funds to external organisations, for the support of palaeontological projects, totalled £12,573.

Publications. Volume 46 of *Palaeontology*, comprising six issues and 1,318 pages in total, was published at a cost of £72,291. *Special Paper in Palaeontology* 69 on the "Interrelationships and evolution of theropod Dinosaurs" was published in June and *Special Paper in Palaeontology* 70, papers from the International Trilobite Symposium, was published in October. These Special Papers were published at a cost of £18,275 and totalled 609 pages. A new series "Fold Out Fossils" was initiated with the publication of *Lower Carboniferous echinoderms of north-west England*. The Association published the joint venture book *Telling the Evolutionary Time: Molecular clocks and the fossil record* with the Systematics Association.

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 & Nick Stroud and Y Lolfa (printers) for assistance with the publication and distribution of *Palaeontology Newsletter*.

Meetings. Six meetings were held in 2003, and the Association extends its thanks to the organisers and host institutions of these meetings:

- a. Lyell Meeting.** 11th February. "The Application of Ichology to Palaeoenvironmental and Stratigraphic Analysis" was convened on behalf of the Association by Dr D. McLroy.
- b. Forty-Sixth Annual General Meeting** was held on 7th May at the Natural History Museum, London.
- c. Progressive Palaeontology.** 10th–11th June. The annual open meeting for presentations by research students was organised by Jennifer England at the University of Glasgow.
- d. 47th Annual Meeting.** 14th–17th December. The Annual Meeting was held in the Department of Geology, University of Leicester, organised by Dr Mark Purnell with much local support. The President's Award was made to Maria McNamara (University College Dublin). Council Poster Prizes were presented to Jennifer England (University of Glasgow) and James Wheeley (University of Cardiff). On the final day a field trip was undertaken to examine the Precambrian Biota of Charnwood Forest. The meeting was attended by 230 attendees.
- e. Systematics Association Biennial Meeting, Dublin. Palaeontological Association Symposium.** Was titled "Human Evolution" and organised by Dr Una Strand Vidarsdóttir.
- f. Review Seminar.** "British Dinosaurs" was organised by Dr M. Munt of the Isle of Wight Museum.

Awards. Sylvester-Bradley Awards totalling £6,856 were made to Hernandez Castillo, Lane, Joomun, Zuykov, Gladwell, Tetlie, Harrington and Broughton. No Mary Anning Award was made this year. 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 Charlotte Jefferies (University of Liverpool). Dr Stuart McKerrow was awarded Honorary Life Membership.

Council. The following members were elected to serve on Council at the AGM on 7th May 2003: Prof. D.E.G. Briggs (President), Prof. D.A.T. Harper (Vice President), Dr M.A. Purnell (from Internet Officer to Vice President), Dr P. Ahlberg (Editor), Dr P.J. Orr (co-opted as Book Review Editor), Dr L. Anderson (co-opted as an Editor) and Dr Jason Hilton (from Ordinary Member to Internet Officer). Dr P.C.J. Donoghue (Newsletter Editor) and Prof J. Hancock (Treasurer) agreed to stand for further terms. The following members stepped down from Council: Dr J. Clack, Dr S. Gabbott, Dr A.L. Johnson, Dr Milsom, Dr P. Orr, Dr I.J. Samson and Dr M.P. Smith. Dr T.J. Palmer continued to serve as the Executive Officer of the Association, and Prof. D.J. Batten (University of Wales, Aberystwyth) as the Editor in Chief.

Council is indebted to the Natural History Museum, London, the University of Leicester and the University of Glasgow 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.

Reserves. The Association holds reserves of £422,791 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 £81,003 in Designated Funds which enable the funding of the Sylvester-Bradley, Hodson and Mary Anning awards.

Council Activities. The Association continues to improve its administration with improvements to the *Newsletter* and the implementation of secure online membership renewal and sales. At an E.G.M. held on 15th December and through a postal ballot the membership agreed to move the A.G.M. to the Annual Meeting. It is hoped these changes will make the formal business of the Association more accessible to the wider membership. The Annual Address, given at the Annual Meeting and entitled "Palaeontology and the future of life on Earth," was presented by Prof. Mike Benton and was attended by 350 people. Further back issues of *Palaeontology* and out-of-print *Special Papers in Palaeontology* have been scanned and released in electronic version. The Association sponsored the Seventh International Congress on Vertebrate Morphology (ICVM-7; Boca Raton, Florida, July 2004). In a collaborative venture the Association sponsored a series of public lecture events organised by Durham County Council entitled "Jurassic." The Association continues as a Tier 1 sponsor of *Palaeontologia Electronica* and continues its membership of the International Palaeontological Association. Due to a funding shortfall for the *Treatise on Invertebrate Palaeontology* the Association offered financial support of \$5,000 per year for the next three years. Grants in aid were provided to: Dr Martill to assist the excavation of a giant pachycormid fish from the London Clay, and Dr P. Davies to run a steering group meeting for the authors of the proposed Field Guide to fossils of the Lias. The Sylvester-Bradley Fund continues to attract a large number of quality applications. Council agreed that under exceptional circumstances awards in excess of £1,000 should be considered. Typically these would aid pilot projects with an aim of supporting future applications to research councils. Council awards an undergraduate prize to each university department in

which Palaeontology is taught at a post-1st year level. Grants were also made to postgraduates attending and presenting at the Annual Meeting. A reduced subscription rate to *Lethaia* of \$75 for Association members has been negotiated. The Association held the Chair and Secretarial posts of the Joint Committee for Palaeontology. The Association continues to be proactive in generating publicity for palaeontology with major press initiatives and a continued high profile on the television.

Forthcoming plans. In 2004, a similar programme of meetings and publications will be carried out as in 2003, including sponsorship of the Lyell Meeting plus an annual symposium at the British Association for the Advancement of Science meeting. 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. Additional electronic versions of early volumes of *Palaeontology* and *Special Papers in Palaeontology* will be produced. It is intended that one new *Field Guide* will be published within the year. Forthcoming books include the "Fossils of the type Maastrichtian" by Prof. S. Donovan and "Early Vertebrates" by Dr P. Janvier. The Annual Meeting has continued to develop as one of the major international palaeontological meetings and will be held at the Université des Sciences et Technologies de Lille in 2004. During 2004 Blackwell will transfer distribution of their electronic publications from Ingenta to their own platform Synergy.

Nominations now being sought

Council

At the AGM in December 2004, the following vacancies will occur on Council:

Vice-President, Treasurer, two Ordinary members

Nominations are now invited for these posts. Please note that each candidate must be proposed by at least two members of the Association and that any individual may not propose more than two candidates. Nomination must be accompanied by the candidate's written agreement to stand for election and a single sentence describing their interests.

All potential Council Members are asked to consider that:

'Each Council Member needs to be aware that, since the Palaeontological Association is a Registered Charity, in the eyes of the law he/she becomes a Trustee of that Charity. Under the terms of the Charities Act 1992, legal responsibility for the proper management of the Palaeontological Association lies with each Member of Council.'

The closing date for nominations is **Friday, 26th September 2004**. They should be sent to the Secretary: Dr Howard A. Armstrong, Department of Earth Sciences, University of Durham, Durham DH1 3LE, e-mail <h.a.armstrong@durham.ac.uk>.

Hodson Fund

This 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, through the website, is preferred 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. **Deadline Friday 26th November 2004.**

Nominations for these Awards should be submitted to the Association Secretary, Howard Armstrong <secretary@palass.org>.

THE PALAEOLOGICAL ASSOCIATION Registered Charity No. 276369 STATEMENT OF FINANCIAL ACTIVITIES FOR THE YEAR ENDED 31st DECEMBER 2003

	General Funds £	Designated Funds £	TOTAL FUNDS £	TOTAL 2002 £
INCOMING RESOURCES				
Subscriptions	65,015	0	65,015	65,014
Sales:				
<i>Palaeontology</i>	116,543			
<i>Special Papers</i>	17,752			
Offprints	3,235			
Fossil Guides	9,399			
Postage & Packing	<u>1,028</u>			
Total Sales	147,957	0	147,957	149,293
Investment Income & Interest	13,454	2,713	16,167	15,602
Donations	1,090	1,192	2,282	3,584
Sundry Income	<u>3,206</u>	<u>0</u>	<u>3,206</u>	<u>1,784</u>
Total	230,722	3,905	234,627	235,277
RESOURCES EXPENDED				
Publications:				
<i>Palaeontology</i>	72,291			
<i>Special Papers</i>	18,275			
Offprints	3,717			
Fossil Guides	6,076			
Newsletters	18,971			
Carriage & Storage	1,345			
Management	<u>26,604</u>			
Total Publications	147,279	0	148,458	135,902
Scientific Meetings & Costs	6,615	0	6,615	2,932
Grants	<u>6,412</u>	<u>8,306</u>	<u>14,718</u>	<u>20,308</u>
Total Charitable Expenditure	160,306	8,306	168,612	159,142
Marketing & Publicity	2,640	0	2,640	3,252
Administrative Expenditure	<u>40,546</u>	<u>0</u>	<u>40,546</u>	<u>36,159</u>
Total	203,492	8,306	211,798	198,553
NET INCOMING RESOURCES	<u>27,230</u>	<u>-4,401</u>	<u>22,829</u>	<u>36,724</u>
INVESTMENT GAINS				
Realised Gain	543			
Unrealised Gain	<u>26,421</u>			
	26,964	0	26,964	-57,733
NET MOVEMENT IN FUNDS	<u>54,194</u>	<u>-4,401</u>	<u>49,793</u>	<u>-21,009</u>
BROUGHT FORWARD	368,597	85,403	454,000	475,009
CARRIED FORWARD	<u>422,791</u>	<u>81,002</u>	<u>503,793</u>	<u>454,000</u>

**THE PALAEOLOGICAL ASSOCIATION Registered Charity No. 276369
BALANCE SHEET AS AT 31st DECEMBER 2003**

2002		2003
£		£
	INVESTMENTS	
245,380	At Market Valuation	264,521
	CURRENT ASSETS	
191,175	Cash at Banks	243,982
22,842	Field Guide Stocks at Valuation	18,226
<u>31,235</u>	Sundry Debtors	<u>32,686</u>
245,252	Total	294,894
	CURRENT LIABILITIES	
17,730	Subscriptions in Advance	30,204
<u>18,902</u>	Sundry Creditors	<u>25,418</u>
36,632	Total	55,622
<u>208,620</u>	NET CURRENT ASSETS	<u>239,272</u>
<u>454,000</u>	TOTAL	<u>503,793</u>
	Represented by:	
381,833	GENERAL FUNDS	422,791
	DESIGNATED FUNDS	
49,966	Sylvester Bradley Fund	45,055
15,318	Jones-Fenleigh Fund	16,189
<u>20,119</u>	Hodson Fund	<u>19,758</u>
<u>85,403</u>		<u>81,002</u>
<u>454,000</u>	TOTAL	<u>503,793</u>

These financial statements were approved by the Board of Trustees on 17th March 2004.

D.E.G. Briggs

H.A. Armstrong

Notes to the Financial Statements for the year ended 31st December 2003

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 2003 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 2003 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.

1.2.1 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.

1.2.2 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.

1.3 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 2003	Total 2002
Publications	20,912	126,367	147,279	135,902
Scientific Meetings & Costs		6,615	6,615	2,932
Grants		14,718	14,718	20,308
Marketing & Publicity		2,640	2,640	3,252
Administration	<u>20,912</u>	<u>19,634</u>	<u>40,546</u>	<u>36,159</u>
	<u>41,824</u>	<u>169,978</u>	<u>211,798</u>	<u>198,553</u>

3. Staff Costs

	Salary	National Insurance	Pension Contrib'ns	Total 2003	Total 2002
Publications – 1 employee (2002 – 1)	16,848	1,537	2,527	20,912	19,205
Administration – 1 employee (2002 – 1)	<u>16,848</u>	<u>1,537</u>	<u>2,527</u>	<u>20,912</u>	<u>19,205</u>
	<u>33,696</u>	<u>3,074</u>	<u>5,054</u>	<u>41,824</u>	<u>38,410</u>

4. Trustees Remuneration and Expenses

Members of Council neither received nor waived any emoluments during the year (2002: nil).

The total of travelling and accommodation expenses reimbursed to 20 Members of Council amounted to £6,624 (2002: £3,800).

5. Costs of Independent Examiner

	<u>2003</u>	<u>2002</u>
Examination of the accounts	300	250
Accountancy and payroll services	<u>1,000</u>	<u>950</u>
	<u>1,300</u>	<u>1,200</u>

6. Stocks

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

7. Debtors – All Receivable within One Year

	<u>2003</u>	<u>2002</u>
Accrued income	32,686	31,235

8. Creditors – Falling Due within One Year

	<u>2003</u>	<u>2002</u>
Social Security Costs	3,340	3,022
Accrued Expenditure	<u>22,078</u>	<u>15,880</u>
	<u>25,418</u>	<u>18,902</u>

Independent Examiner's Report to the Trustees of the Palaeontological Association (Reg. Charity No 276369)

I report on the accounts of the Palaeontological Association for the year ended 31 December 2003, which are set out in the preceding pages.

Respective responsibilities of trustees and examiner

As the charity's trustees you are responsible for the preparation of the accounts; you consider that the audit requirement of section 43 (2) of the Charities Act 1993 does not apply. It is my responsibility to state on the basis of procedures specified in the General Directions given by the Charity Commissioners under section 43 (7) (b) of the Act, whether particular matters have come to my attention.

Basis of independent examiner's report

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 you as Trustees concerning any 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 view given by 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: (i) to keep accounting records in accordance with section 41 of the Act; and (ii) to prepare accounts which accord with the accounting records and to 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.

G.R. Powell B.Sc., F.C.A.

Nether House, Great Bowden, Market Harborough, Leicestershire.

3 March 2004

Membership subscriptions, 2004 – 2006

On 23rd June 2004 Council agreed the rates set out below for members' subscriptions in 2005 and 2006. The proposed changes are in line with recent Council practice to hold individual membership rates steady unless the income from this source is threatened by exchange rate perturbations, but also to apply a moderate but steady annual increase to institutional subscriptions.

At the AGM to be held at the Meeting in Lille in December 2004, members will be asked to approve changes as follows.

1. That the rates for 2005 are ratified as set out below;
2. That the rates for 2006 are set as set out below;
3. That if on 1st October 2005 the exchange rate of the pound against the dollar or the pound against the euro has fallen by more than 4% from the rate on 23 June 2004 (1.825 dollars to the pound; 1.510 euros to the pound), then all subscriptions priced in dollars or euros (as appropriate) shall be raised to yield the same pound sterling equivalents, rounded up to the nearest dollar or euro.

	2004	2005	2006	2004	2005	2006	2004	2005	2006
	£	£	£	\$	\$	\$	€	€	€
Ordinary Member	28	28	28	55	55	55	52	52	52
Retired Member	14	14	14	28	28	28	26	26	26
Student Member	10	10	10	20	22	22	22	22	22
Special Paper add-on	25	25	25	50	50	50	48	48	48
Institutional Member	130	140	150	255	265	275	235	245	255
SP freestanding sub	80	85	85	160	170	170	160	170	170

ASSOCIATION MEETINGS



48th Annual Meeting of The Palaeontological Association
Lille, France 17 – 20 December 2004

The 48th Annual Meeting of the Palaeontological Association will be held in the Congress Centre (MACC) of the Université des Sciences et Technologies de Lille (USTL), on its campus at Villeneuve d'Ascq near Lille. The opening session with a seminar on Palaeobiogeography will be held on Friday afternoon, 17th December, in the lecture hall of the Beaux Arts Museum in the centre of Lille. In the evening the Icebreaker Party will be held in the Natural History Museum of Lille, in the heart of the Capitale Européenne de la Culture 2004 (<<http://www.lille2004.fr/>>).

The technical sessions will consist of two full days of talks in the main lecture hall of the Congress Centre at Villeneuve d'Ascq on Saturday 18th and Sunday 19th December, with poster sessions in an adjoining lecture hall. Technical sessions are open to all aspects of palaeontology. All talks will be scheduled for 15 minutes including five minutes for discussion; there are no parallel sessions so it is possible that some proposed oral contributions will have to be rescheduled as posters. On Monday 20th December two geological excursions will be organised; one to examine the Mesozoic sediments on the coastal sections in the Boullonnais area, the other to the Palaeozoic (Cambrian-Devonian) rocks exposed in the Brabant Massif, Belgium.

Seminar : Palaeobiogeography

Friday, 17th December 2004 (part of the Annual Meeting)

For the second time, an afternoon seminar is added to the Annual Meeting. This afternoon of thematic talks and discussion will focus on palaeobiogeography and take place on Friday, 17th December 2004. The seminar will highlight the importance of fossils to understanding past and present palaeogeographical and biogeographical patterns. The seminar will include lectures by the following speakers:

- Fabrizio Cecca (Paléobiodiversité et Paléoenvironnements, Université Pierre et Marie Curie, Paris)
- Richard Fortey (Department of Palaeontology, The Natural History Museum, London)
- Pascal Neige (Biogéosciences, Université de Bourgogne, Dijon)
- Brian Rosen (Department of Zoology, The Natural History Museum, London)
- Chris Scotese (Department of Geology, University of Texas at Arlington)

Attendance at the seminar is free to conference participants, but only if booked in advance (limited number of seats available in the Musée des Beaux Arts Amphithéâtre). Please do not turn up on the day without informing the organisers.

Venue and Travel

Details about the City of Lille can be found on the website at <<http://www.mairie-lille.fr/>>. Lille is less than two hours from London by Eurostar (<<http://www.eurostar.com/>>), and tickets at reduced prices are available if you book some weeks in advance. Lille can also be reached easily from Paris and its airport Charles de Gaulle (about one hour) and from Brussels (about 40 minutes) by TGV high speed trains. The Congress Centre can easily be reached by Metro.

Accommodation

Accommodation will mostly be organised in hotels around the Congress Centre at Villeneuve d'Ascq. This is approximately 15 minutes' walk from the conference venue. Participants are free to book alternative accommodation at a wide range of prices. Please note that the strict deadline for reservation of accommodation through the organisers is **10th September**. After this date, accommodation must be arranged by the participants themselves.

Registration and booking

Booking for accommodation, field excursions and also abstract submission for the conference must be completed by **Midnight on Friday 10th September 2004**. After this date participants will have to organise their own accommodation in Lille in order to attend the meeting. After 10th September registration for the meeting is still possible but will incur additional costs. Final registration for the meeting will be Friday 3rd December.

Registration details and online registration

<<http://www.palass.org/forms/XAnnualRegistration.html>>

For the second time, registration, abstract submission and payment (by credit card) are by online forms at <<http://www.palass.org/>>.

Outline Programme:

Friday 17th December :

Afternoon seminar, Palaeobiogeography

Lecture hall of the Beaux Arts Museum, Lille

Icebreaker party

Natural History Museum of Lille

Saturday 18th December :

Scientific sessions, followed by :

Annual Address: *Palaeontologia de profundis* by S. Bengtson (NRM, Stockholm)

Congress Centre of the Université des Sciences et Technologies de Lille

Members reception & Annual Dinner

University Restaurant 'Charles Barrois'

Sunday 19th December :

Scientific sessions:

Congress Centre of the Université des Sciences et Technologies de Lille

Monday 20th December :

Post conference excursions

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

The Palaeontological Association runs a programme of travel grants to assist student members presenting talks or posters at the Annual Meeting. For the Lille meeting, grants of up to £100 (or the Euro equivalents) will be available to student presenters who are travelling from outside continental Europe. 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 at <palass@palass.org> once the organisers have confirmed that their presentation is accepted and before 10th December 2004.

Annual Address

This year's Annual Address of the Palaeontological Association will be given by Prof. Stefan Bengtson and will take place during the Association's Annual Meeting, on Saturday 18th December 2004, at the Congress Centre of the Université des Sciences et Technologies de Lille.

'Palaeontologia de profundis'

Stefan Bengtson

Swedish Museum of Natural History, Stockholm <Stefan.bengtson@nrm.se>

Palaeontology is about life in deep time. The deeper we go in palaeontological time, however, the more we encounter also other aspects of depth: the depth of our understanding, the depth of our convictions, and indeed the very foundations of our science and of science in general. Through recent work in the depths of palaeontological time, I have experienced various fascinating perspectives of *palaeontologia de profundis*, ranging from the joy of working with people, rocks and fossils Down Under to the despair at the depths of our pigheadedness when deep convictions seem violated. Scientific work needs creativity, scepticism, and even conviction, in a process that can be thought of as Darwinian, but the way we let these interact with each other decides how good our science will be. In addition to scientific examples, I will give a seasonable illustration from music: Arthur Honegger's *Une cantate de Noël* (A Christmas Cantata) opens with the ancient cry of despair *De profundis clamavi* (Out of the depths I cry), but the stunningly complex web of carols woven by Honegger later in the same cantata lifts the sense of despair by showing the beauty of multiple ideas in clashing harmony. Palaeontology arises out of the depths, and with the help of clashing opinions it flies. In the end, as every flyer knows, convection is better than conviction to keep you in the air.

Association event at the 2004 British Association Festival of Science

Fossils, fakes and fiction: scientific and public perceptions of extinct organisms

University of Exeter

6 September 2004, 13.00 – 16.00



As we did for the BA Festival of Science in Leicester, the Association is putting on a session at this year's Festival in Exeter. The half-day of talks and discussion on the subject of how fossils are interpreted and perceived is designed to complement the overall theme of the meeting, 'the responsibilities of being a scientist'. In summary, the issues to be addressed arise because extinct organisms make big

news, but media attention is generally focused on interpretations of fossils rather than the hard evidence of the palaeontological data. Interpreting fossils is a complex process, and this session will explore the difficulties in balancing the factual and the fanciful, and the ethical questions involved in bringing fossils to life. Presentations will be aimed at a general audience.

Attendance at this session is free to members of the Association, but you will need to book a ticket, and numbers are limited. See below for booking details.

Booking:

This event is part of the BA Festival of Science in Exeter, 4–11 September 2004. Thirty free tickets for the Palaeontological Association session are available to Association members; additional tickets are available on a B.O.G.O.F. basis (i.e. two for £5). Details of all events are available on the BA website, at <http://www.the-ba.net/festivalofscience>.

To book, call 020 7019 4941.

Programme:

Brian Gardiner (Linnean Society):

The Piltdown Forgery: a re-statement of the case against Hinton

The results of two separate analyses prove Hinton was the hoaxer. The first analysis was on material discovered above Hinton's NHM office, the second on a set of human teeth provided by his executor. The forger used two methods for staining his material, one involving decalcification, converting apatite into gypsum, the other which did not.

Henry Gee (Nature):

The Archaeoraptor Saga

Archaeoraptor was promised as a true missing link—a bird with a dinosaur-like tail. It turned out to have been an expensive fake. The saga of Archaeoraptor illustrates the extent to which science publishing is built on trust, and how easily that may be exploited.

John Martin (Haley Sharpe Design Ltd.):

How much is real, Mum?

When you visit the British Museum, you expect the Greek urns to be real. But fossils on display in museums are different—especially spectacular skeletons of dinosaurs. Improved, replicated, downright faked: how would you know, and would it matter? And how much of the science can you trust?

Paul Barrett (Natural History Museum):

The ethical difficulties of reconstructing long extinct organisms for entertainment

When dinosaurs and other extinct animals are portrayed on film, TV or other media, whether for the purposes of pure entertainment or education, what are the limits that should be applied to such reconstructions? Do different rules apply for different types of presentation, and how 'honest' should we be?

Mike Benton (University of Bristol):

Daring to walk with dinosaurs

'Walking with dinosaurs' showed dinosaurs going about their daily lives. I was intrigued to work as an advisor. The blurring of fact and fiction is an ethical problem, but we were doing what Sir Richard Owen did in 1854, but updated. I felt this was a good way to engage the public in science, and the result was the most spectacularly successful science documentary ever.

**Lyell Meeting 2005: Applied Phylogeny**

London 9 February 2005

The 2005 Geological Society of London Lyell Meeting, sponsored by the Joint Committee for Palaeontology, is to be organised by The Micropalaeontology Society (Joint Convenors Haydon Bailey and John Gregory). This prestigious one-day meeting will be held at Burlington House, London on 9th February 2005. It is intended that the meeting will comprise three sessions, arranged stratigraphically (Palaeozoic, Mesozoic and Tertiary), each session with an invited keynote speaker, with the opportunity to discuss a complete range of macrofossil and microfossil subject areas within the proposed theme.

Contributors are asked to consider a single phylogenetic lineage and to pursue its development and application, both stratigraphically, and to any other area of applied usage. It is intended to publish the proceedings of the meeting at the earliest possible opportunity as a Special Publication of the Geological Society (authors' notes will be distributed prior to the meeting).

Proposed titles and abstracts should be sent to Haydon Bailey either via e-mail, or to the address below, as soon as possible so that a complete programme can be drawn up. Further details of this meeting will be made available once an initial programme has been established. Details will also be posted on the TMS website at <<http://www.tmsoc.org/>>.

Haydon Bailey (Network Stratigraphic Consulting Ltd, Unit 60, The Enterprise Centre, Cranborne Road, Potters Bar, Hertfordshire <haydonbailey@btconnect.com>) and John Gregory (Kronos Consulting, 33 Royston Road, St Albans, Hertfordshire AL1 5NF <john@jgregory.demon.co.uk>)

**Rewriting the history of life: exceptionally well-preserved fossils and our understanding of evolution**

BA Festival of Science, Trinity College Dublin, Ireland 5 – 9 September 2005

Fossils are familiar objects to many people. The petrified remains of shells, bones and other rot-resistant hard-parts of organisms are the standard fare of museum displays and rock collections. But this view of fossils is misleading: looking only at hard parts gives a very distorted view of the history of life. This session will focus on recent discoveries of amazing fossils that preserve what normally rots away (dinosaurs with feathers, bizarre 500 million year old worms and other ancient oddities) and how they are reshaping our view of the evolution of life on Earth. Check out the BA website or contact the meeting organiser for further details: Dr Patrick Orr <Patrick.Orr@ucd.ie>, tel 00353 1 7162323, Department of Geology, University College Dublin.



news

**Workers on Chenjiang Biota win first prize from Chinese Academy of Sciences**

The First Prize of the National Award for Natural Sciences in 2003 goes to studies on Chengjiang Biota and the Cambrian Explosion, which were conducted by Chen Junyuan from the CAS Nanjing Institute of Geology and Palaeontology (NIGPAS), Hou Xianguang from Yunnan University, and Shu Degan from Northwest University. The announcement was made at the award ceremony held on 20th February in Beijing.

For many decades, palaeontologists have debated on the Cambrian Explosion, the sudden appearance of a majority of animal phyla nearly at the base of the Cambrian Period from 570 to 510 million years ago. The discovery of 530-million-year-old Chengjiang Biota throws light on the issue.

The Chengjiang Biota, which is brought to light in the east part of southwest China's Yunnan Province, is known worldwide for its exceptionally well-preserved soft-body fossils. It was first discovered by then NIGPAS researcher Hou Xianguang on 1st July 1984 when searching for a group of micro-arthropods called bradoriids on the west slope of Mt. Maotian, Chengjiang County.

The fossil evidence there reveals an assemblage of a fauna represented by more than 120 species, including, among others, sponges, cnidarians, ctenophorans, priapulids, arthropods, brachiopods, poronids, echinoderms and chordates. There are also a number of animal body plans at phylum or subphylum level that are extinct, including medusiform *Eldonia*, *Facivermis*, Tardipolyda, cancelloriids, *Dinomischus*, hyoliths, vetulicoliids, Opabinida and anomalocarids. The life forms from the Chengjiang assemblage indicate that the Cambrian Explosion really happened.

Over the past two decades, Chen, Hou, Shu and their colleagues have never stopped working at the Chengjiang Biota. They have explored the phylogenetic origins of vertebrates, euarthropods, crustacea, and proved that the existing phyla, subphyla and complicated ecosystem can be traced to the early Cambrian epoch. Their work also provides evidence for the top-down model of evolution theory. They have published more than 90 papers, 14 of them in *Nature* or *Science*.

Source: CAS website.

Geological Society Awards 2004

Wollaston Medal – Professor Geoffrey Eglinton

The Wollaston Medal, the Society's highest honour, first issued to William Smith in 1831, was this year awarded to Professor Geoffrey Eglinton of the University of Bristol, UK.

Geoff Eglinton is one of the founding fathers of modern organic geochemistry. He is responsible for many of the molecularly-based geochemical tools and concepts that Earth scientists today take for granted. His work has been characterised by three main elements—insight into big problems of global significance, the ability to bridge widely separate disciplines, and the skill to assemble groups of key scientists to solve the problems. His work has been of inestimable academic and practical value—for example, the invention of the petroleum geochemical biomarker maturity and facies assessment approach was a direct result of Geoff's pioneering work. Without it, modern petroleum biomarker geochemistry simply would not exist. Geoff and his colleagues have also given to Earth science molecular yardsticks for palaeoclimate study.

Lyell Medal – Professor Dianne Edwards

The Lyell Medal of the Geological Society this year went to Professor Dianne Edwards of the University of Cardiff, UK.

Dianne Edwards has been working for the past 40 years on one of the greatest evolutionary stories—the colonisation of the land by plants. Her magnificent preparatory work has helped her to show how some of the earliest land plants were indeed truly vascular. Much of her work has been done close to home, in Wales and the Welsh Borderland; however she has also collaborated with workers all over the world in amassing her publication list of over 125 papers as groundbreaking in their own way as the first land plants she has brought to light.

Dianne's reputation is truly worldwide, and her work a permanent monument that must be incorporated into all scenarios of terrestrialisation.

Lyell Fund – Michal Kucera

The Lyell Fund this year was awarded to Dr Michal Kucera (Royal Holloway, University of London, UK) for his outstandingly successful work on planktonic foraminifera, especially their evolution and use as palaeoproxies in palaeoclimatic reconstruction.

ICS Medal – Stephen Hesselbo

Dr Stephen Hesselbo (University of Oxford, UK) is to be awarded the IUGS International Commission on Stratigraphy ICS Medal at the opening ceremony of the 32nd International Geological Congress in Florence, Italy, this August. The ICS Medal is awarded to honour high quality research in stratigraphy, recognizing a singular achievement in advancing stratigraphical knowledge. The award to Stephen Hesselbo is in recognition of 'the quality and breadth of his research, in collaboration with others, on the Lower Jurassic of Britain'. Dr Hesselbo is graduate of the University of Aberdeen, UK (BSc 1983) and the University of Bristol, UK (PhD 1986). He is currently Lecturer in Stratigraphy at the University of Oxford, UK, and Secretary of the Stratigraphy Commission of the Geological Society.

Join the Paleobiology Database

The Paleobiology Database (<<http://paleodb.org/>>) welcomes all professional palaeontologists who wish to contribute to this collaborative, web-based, international project. The Database's mission is to provide a global, discipline-wide repository for taxonomic and palaeoecological data and a research tool for palaeontology in the 21st century.

The Database comprises taxonomic lists, abundance data, contextual information on fossil assemblages, ecological assignments of taxa, synonymies, classifications, and digital images. The Database spans the entire Phanerozoic and includes marine and terrestrial, plant and animal, and macrofossil and microfossil data. We encourage the participation of palaeontological colleagues from Europe and elsewhere around the globe.

Current contents of the database

The Database currently involves 89 data authorizers and 100 data enterers from 55 research institutions in ten countries. The Database includes accounts of 38,580 fossil collections, 400,450 occurrences of taxa in collections, authority data on 57,238 taxa, and 79,070 classification and synonymy opinions (including Jack Sepkoski's global compendia of marine invertebrate families and genera). The data are tied to 10,372 published references. Just over the past 12 months, 7,434 collections, 71,401 occurrences, and 1,982 references have been entered into the Database.

The Database includes working groups on marine invertebrates, palaeobotany, vertebrate palaeontology, taphonomy, and taxonomy, and involves participation from collaborative projects such as the Evolution of Terrestrial Ecosystems consortium, the Paleogeographic Atlas Project, and the Palaeoinformatic Approach to the Context of Earliest Human Dispersals, which is funded by the British National Research Council. Most of the fossil collections are split between marine invertebrates (55%), vertebrates (25%), and plants (18%).

A significant amount of data from across the globe already is included in the Database, with substantial information on Europe, Africa and Asia, and with 48% of our fossil collection records coming from elsewhere than North America. However, we seek to make the Database as inclusive as possible, and value not just European data but the taxonomic expertise of European researchers. We therefore encourage European palaeontologists to join with us in making the Paleobiology Database a data repository for the entire discipline.

How and why to join

Requirements for becoming a data contributor are minimal: contributors must have an advanced degree in palaeontology (normally a Ph.D.) and must intend to contribute a substantial amount of data. Simply send an e-mail to the Database coordinator (<alroy@nceas.ucsb.edu>) and state your academic background, planned focus on a time interval, geographic area, taxonomic group, and planned time frame for your project. Once you have received feedback from our 15-member Advisory Board, we'll set up an account for you and your students right away.

There are many advantages to joining the Database. You can reposit your data in a fully relational database with sophisticated, web-based data entry and analysis software. You won't need to design your own system, but you'll still have a full say in software development, and you will be using communally endorsed data definitions. Only you have the right to alter your data, and you can set aside data from being viewed for several years. You can download your data at any time, and the data are fully backed up at five different research institutions. You can form collaborations and share data with other Database members. The fact that you are repositing data in the world's largest palaeontology database may raise your profile with funding agencies. Finally, by repositing your data you create a permanent record of your work and help to create synergy throughout the discipline.

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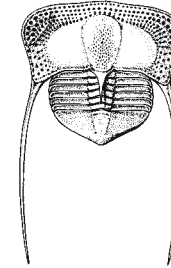
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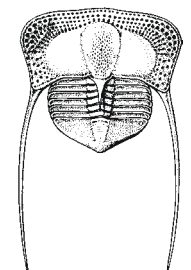
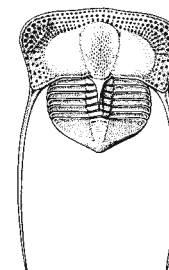
news



***Palaeontology:*
 CALL FOR SHORT PAPERS!**

From January 2005 *Palaeontology* will be published in A4 size with a new layout. In line with this development space will be 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 6 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).



—OBITUARY—

Sir Alwyn Williams

1921 – 2004

Alwyn Williams died peacefully of cancer on 4th April at Glasgow, aged 82.

He was a giant amongst brachiopod workers, being not only the editor and first author of the first brachiopod *Treatise on Invertebrate Palaeontology* (two volumes) in 1965, but fulfilled the same roles in the second edition, four volumes of which have been published (1997 to 2003), and there are another two in press. He successfully organised contributions from 43 co-authors for the second edition, an enormous political challenge which he tackled with a characteristic mixture of charm, tenacity and efficiency.



But the originality of his brachiopod work was also outstanding; he was the first to evaluate shell structure across the whole phylum through pioneer electron microscopy; he was amongst the first to undertake DNA studies; over his long career he published and refined many times the overall classification of the Brachiopoda, with the end product of a robust and well-known phylogeny that will probably require little future change.

His systematic work, although originally on Silurian faunas (he was the first to recognise and document the evolution of *Stricklandia*, a key zonal fossil) was chiefly concerned with the Ordovician. His substantial and painstaking memoirs and monographs on the Ordovician brachiopods of central and northern Wales, Shropshire, and Girvan, as well as many smaller papers, will stand for a long time. For many of these areas he also remapped the often difficult geology, and published correlation data. He was the lead author of the 1973 Ordovician correlation chart of Britain and Ireland, and the first Chairman of the IUGS Ordovician Subcommittee. He had many prizes, including the Murchison Medal of The Geological Society of London, and was a Fellow of the Royal Society. He was also knighted.

Alwyn was a keen supporter of the Association since its inception: he was a member of the very first Council in 1957, President from 1968 to 1970 and Vice-President from 1970 to 1971. He has published a great many papers, both alone and with a variety of co-authors, in *Palaeontology*, and was also the author of two *Special Papers*. It is fitting that one of the final honours of his long life was the award of the Lapworth Medal of the Association at the Christmas meeting in 2001.

He was, of course, a Welshman, born in Aberdare, as could be heard from his accent until the last, and did his first and second degrees at Aberystwyth. Whether or not that impressed O.T. Jones, then at Cambridge, is hard to say, but his geological ability certainly did, and he spent a year at Cambridge working on Jones' and new collections from the type Llandovery area, eventually producing the classic paper outlining the evolution of *Stricklandia*. This was followed by a very important two-year Harkness Fellowship to the Smithsonian, where he was able to study one of the world's great collections under the guidance of G.A. Cooper.

He was subsequently appointed lecturer at Glasgow, where he was for four years before moving to Queen's University, Belfast, where he remained Professor of Geology for twenty years before moving on to the Lapworth Chair at Birmingham University in 1974. He then went on in 1976 to become Principal of Glasgow University, a job that for any normal person would have meant the cessation of geological research. Alwyn was not a normal person. He will be much missed.

He is survived by his wife Joan, whom he had met when they were both students at Aberystwyth and married in Canada in 1949; they had a daughter and a son.

Robin Cocks

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There will be a memorial meeting for Sir Alwyn on Saturday 2nd October 2004, in the Bute Hall, University of Glasgow, with a buffet lunch to follow. All are welcome to attend both. Anyone wishing to attend should, if possible, let Patricia Peters know in advance by e-mail to <ppeters@dcs.gla.ac.uk>, for catering purposes.

— OBITUARY —

Robert Milsom Appleby 1922 – 2004

Robert Milsom Appleby was born on 28th April 1922 at Denton, Manchester. As a boy he was interested in all things natural, including Geology. Another hobby of his was radio, which was to help him during his service in the Royal Navy during WWII. He attended Sir William Hulme's Grammar School in Manchester, amongst whose Alumni are included Sir Robert Mark, who was to become Commissioner of the Metropolitan Police. Robert then went to Manchester University to study Geology.



He completed his first year at Manchester University before volunteering along with a fellow student, Alan Warburton, to join the Royal Navy, and enlisted as a junior officer (Sub-Lieutenant) in the Royal Navy Secret Service working on radar. He served on several ships: HMS Bermuda (a light Cruiser), HMS Saumarez (a destroyer), and HMS Polomares (a corvette), and saw service on the Arctic convoy to Russia. It is worth mentioning here that HMS Polomares, as escort, was part of the disastrous convoy PQ17. The HMS Saumarez was sunk by mines laid by the Yugoslavians in the Corfu Strait in 1946, which led to a crisis between the two countries at the beginning of the Cold War era. Even in wartime, while stationed in Fair Isle (1944–45), he was able to make observations on the local geology (Appleby, 1961).

The author remembers one particular story Robert recounted about his time aboard ship. One day he was Officer of the Watch in charge of overseeing the issuing of the daily ration of rum (or 'grog' as it was known) to those on board. An exact amount of 'grog' for each person aboard ship was decanted into the barrel, and after each man had received his daily 'tot,' the officer of the watch would inspect the barrel from which the rum had been issued. To Robert's surprise there was some rum left over, and not knowing what to do, he placed the barrel under guard, while he went to look at Naval Regulations to find out what to do in such circumstances. Unfortunately, there was nothing in Naval Regulations to cover such an eventuality, so he then decided that the rum had to be disposed of, which he dutifully did, by having it poured over the ship's side.

During his time aboard ship, being a member of the Secret Service, he was unable even to tell the ship's Captain what he was doing, apart from the day-to-day duties of shipboard life during wartime. Much of what he did during the Second World War remains secret to this day, although the author suspects that it was more than just peering at a radar monitor. But it was during this time that an idea began to form in his mind, which was to come to fruition in years to come.

After his war service he demobilised with the rank of full Lieutenant, and returned to Manchester University to complete his degree, becoming interested in fossils in general, and trilobites in particular. After graduating BSc (hons) in 1949, he commenced work at Leicester City Museum and Art Gallery as assistant keeper in the Geology department. It was here that he compiled the catalogue 'Ophthalmosauridae In the Collections of Leicester and Peterborough Museums' (1958), a principal part of which was the 'matching' of a collection that had become separated, and reuniting disparate parts. This was his first contact with ichthyosaurs, which was to become a lifelong passion.

In 1954 he obtained the post of Lecturer in Palaeontology in the then University College of South Wales and Monmouthshire in Cardiff, in the somewhat cramped building on Newport Road. This was just as a new wing for the Department of Geology in Cathays Park was being designed, to which Robert had an input.

In 1964 Robert was one of the first to move into the new wing of the Main College building in Cathays Park, where he had designed a purpose-built tank room, complete with glass fibre tanks for the extraction of large fossils from matrix using acetic acid. About this time he published some articles on science and religion (and how they might mutually co-exist) in an Anglican magazine called 'Prism'.

While a lecturer in Cardiff he would run the Department's annual Easter Field excursion to Dorset for first year students, an event planned with military precision even down to prior inspection of the hotel rooms to be occupied by the students, and the menu that they would be provided with—long before the days of risk assessments and Health and Safety legislation. To the author's knowledge, there were never any 'incidents' or fatalities during some 25 years that the field trips were run under his leadership.

In 1965/66 he started, along with Mr Graham Jones, an electronics technician in the Faculty of Science Electronics workshop of Cardiff University, the first prototype of what was to become known as the Analogue Video Reshaper or AVR. This came from an idea he had while working with radar in WWII, and involved creating an electronic grid which could be deformed in two directions. This could thus deform or 'undeform' objects using an image superimposed onto a TV screen, and also allow for the comparison of two similar ones, by placing one image on top of another. It became a new tool for the palaeontologist. It was developed and received its Patent in 1968, the completed machine being shown in 1970 at the Physics Exhibition at Alexandra Palace, London, as well as being shown on the BBC's science programme 'Tomorrows World'. It was for this new invention that he was elected a member of The Royal Institution in 1974, the badge of which he always wore with pride. At this time, the Home Office became interested in what the AVR could do with fingerprints, helping 'unsquash' distorted ones. As a result of his involvement with this, he was unable to publish any work until 1979. There exists today in The Cardiff Earth Sciences Department archives a video (transferred from film) of the AVR and its capabilities.

Whenever one of Her Majesties Navy ships visited Cardiff, Robert would always be invited to attend a drinks reception given by the Commanding Officer for local dignitaries. He would politely decline these offers of “Drinks in the Wardroom” and would have much preferred instead to be invited to look at their ship’s radar.

He retired from Cardiff in 1981 to Healing, just outside Grimsby, South Humberside, where he planned to spend his time writing up his monograph on Ichthyosaurs, gardening, and playing Mozart on his violin. The 500 page monograph had only five pages left to be typed up when he died on 8th February 2003, after contracting pneumonia from a chest infection. Earlier this year, at the age of 81, he had been fitted with a pacemaker, which he told the author would not need to be replaced for ten years, when he would be 91! He is survived by his wife, Valerie, whom he met while working in Leicester’s New Walk Museum and Art Gallery, and married in 1956.

But what of Robert the man? The author, along with many of his former students, will remember him for his many acts of kindness and concern for their well-being.

The author first met him in 1967 upon joining the Cardiff Department as a Junior Technician, and remembers accompanying him on many field excursions. His brisk little walk, typical of a Naval Officer, on these excursions, would often be interrupted as he stopped and pointed out to the group the animal and plant interactions, and how the kind of trees and plants related to the underlying geology.

He was a quiet man, but with close friends had a lively humour and was an excellent raconteur. He had a fine mind and was a good scientist. The publication of his last work would be a fitting memorial for him.

Perhaps it would be fitting to close this tribute with the following, received from a former Ph.D. student of his, Edwin Willey, now in Australia:

“On the matter of truth, half truths and lies—my last contribution on this was rather close to his heart so to speak as it was on Ichthyosaurs. I was quite agitated, and I was sure that he would have been too had he heard an item on the ABC news some 18 months ago. It categorically announced that Ichthyosaurs were only found in Australia. Knowing another truth, which I believe Robert shared wholeheartedly, one had to consider how this happened. The original item might have said that ‘Ichthyosaurs of Genus x species y have only been found in South Australia.’ But this was too long, so some seemingly surplus words had to go, so ICHTHYOSAURS (of Genus x species y) ARE ONLY (been) FOUND IN SOUTH AUSTRALIA.”

The brief statement could have been most alarming as he was getting close to completing his life’s work on Ichthyosaurs elsewhere. He had his own tales on this theme.

To close, the author of this obituary, being born and bred in the South Wales Valleys, would like to quote a saying that we have about someone special in this part of the world: “He was a lovely man”. I for one feel privileged to have known him.

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Howard Bartlett

The School of Earth, Ocean, and Planetary Sciences, University of Cardiff

OBITUARY

Jake Hancock 1928 – 2004



With the death of Jake Hancock at the age of 75 on 4th March 2004, the Palaeontological Association has lost a distinguished member who contributed much to our development.

John Michael Hancock was born in Salisbury, Dorset, on 10th August 1928. He attended Dauntsey's School, Wiltshire, which unusually taught Higher Schools Geology, the subject to which he was to devote himself. Following National Service in 1947–1949, he went up to Cambridge with fellow pupil Richard Lambert (1928–1992), and met Michael House (1930–2002), forging two life-long friendships. Jake was a student of Queens' College, gaining a B.A. in geology and petrology in 1952. He lodged, as a graduate student, with the legendary Gertrude Elles, of who he had the fondest of memories: from cleaning fossils on her sitting room carpet, to his first and most disastrous encounter with the phylum Echinodermata. Miss Elles used only the best of the Sedgwick Museum's collection in her classes, including types. The fragmentary nature of some of the Cambridge Chalk starfish is (as Jake told it) due to his assistance in one of her practicals, during which he dropped the drawerful.

He was appointed to an Assistant Lectureship at King's College, London in 1955, and completed his doctorate in 1957, in which year he was appointed to a full Lectureship. Subsequent promotions were to Senior Lecturer (1970), and Reader (1977). He migrated to Imperial College, London, in 1986, and was awarded a full Professorship in that year, retiring in 1993, and moving to Shaftesbury in Dorset. Thereafter, he divided his time between Dorset and London, retaining a room at Imperial for the next decade. He continued to teach palaeontology and stratigraphy in retirement: his 2004 lecture series was to be on Cretaceous sea level changes.

Jake's research interests were wide, from the composition and sedimentology of the Chalk, to its significance as a hydrocarbon reserve in the North Sea. He was a regular contributor to seminars run by the Joint Association for Petroleum Exploration Courses, and the author of a series of reviews on the Cretaceous in the North Sea. A further area of interest was Cretaceous sea level changes, and the development of precise international correlation frameworks as a basis for determining their global synchronicity (or otherwise). It was precision of correlation by fossils that dominated his work as a palaeontologist.

His first publication was in 1954, with a paper in the *Geological Magazine* on 'A new Ampthill Clay fauna from Knapwell, Cambridgeshire', based on a collection of ammonites picked up on a cycling trip. One's first publication is very special. As he told it, it was a record of a lost age. Returning to the Sedgwick Museum, he took the specimens to W.J. Arkell (1904–1958) who had moved from Oxford to Cambridge in 1947. Arkell expressed interest in the fossils (he had monographed the

Corallian (Upper Oxfordian) ammonites between 1935 and 1948), and remarked they should be written up for publication, and would Jake mind leaving them with him (Arkell) for a few days? Returning a week later, Arkell presented him with the completed manuscript. A tale embroidered: perhaps? Apocryphal: no. Long gone, alas, is the age when a senior academic would write a paper for a young graduate; more likely now the mentor adds his name to the work of the pupil, I fear.

Doctoral fieldwork (for the most part by train, ferry, and bicycle) took him to the Western Isles, Ireland, and northern France, including Sarthe, which includes the type locality of the Cenomanian stage at Le Mans (Roman Cenomanum). His attendance at the 1959 Dijon Colloquium on the Upper Cretaceous Stages led (1960) to the first review of the ammonite faunas of that stage in its type area, upon which the later researches of Pierre Juignet and others is founded. At that same meeting, Jake Hancock was the only person present who had visited all of the type areas of the Upper Cretaceous stages. Later stratigraphic benchmark publications are on the Cretaceous System in Northern Ireland (1961), and on the Norfolk Chalk (with Norman Peake: 1961).

My own encounter with Jake Hancock began in 1961, as an undergraduate at King's College, London; thereafter he supervised my doctoral thesis (1964–1968), and forty years of research collaboration began. In 1965, he was awarded a NERC grant to visit sections in Algeria and Tunisia in order to investigate the ammonite succession across the Cenomanian-Turonian boundary. He purchased a long wheel-base Land Rover, and we drove there together (parenthetically, I should add that I rolled the vehicle in northern France, but that is another and long story). We collected ammonites by the thousand, a project that Andy Gale and I now intend to complete for publication. The following years saw fieldwork together in the U.K. and France, while we spent several months together in the field in North America, notably in Texas and Mexico. Subsequent research grants from NERC between 1977 and 1991 took us to the type areas of all of the Upper Cretaceous stages, to Spain, Germany, Portugal, back to Tunisia, to the USA, and to many, many museums. The results included a series of papers on subjects that ranged from the ammonite faunas of the type Turonian (with Willy Wright and Gordon Chancellor), to stratigraphic correlation of the mid-Cretaceous across the Atlantic, to work on potential stratotypes for a number of Upper Cretaceous stages.

Jake Hancock's continuing interest in Cretaceous stratotypes and stage definitions was reflected in his election to the Chair of the International Subcommittee on Cretaceous Stratigraphy (1984–1989), and his co-editorship of the 1996 Brussels volume on Cretaceous Stage boundaries (Rawson *et al.* 1998). At the time of his death he was coordinating a multidisciplinary project on the Santonian–Campanian boundary in north-central Texas.

In 1972–3, Jake spent a year in the United States, and, under the direction of Erle Kauffman, undertook a major tour of the Cretaceous of the Western Interior, from Kansas down to the Mexican border and beyond. A visit to the United States Geological Survey in Denver at this time led to 30 years of friendship and collaboration with Bill Cobban and the development of further areas of interest: transatlantic correlation by fossils, and late Cretaceous sea-level changes and shoreline positions. But it was the Chalk, where his researches built on the largely unpublished work of his mentor Maurice Black (Jeans & Rawson 1980), to which he constantly returned.

Hancock's teaching encompassed the predictable subject areas of stratigraphy, sedimentation, and palaeontology (especially of cephalopods). He also developed his graduate interest in heavy mineral studies, and taught not only practical sedimentary petrography, but also classes in igneous

and metamorphic petrology. He was deeply involved in adult education for the extra-mural departments of both London and Oxford universities, and with the London Working Men's College, where he taught evening classes in geology, chemistry and physics for many years.

His services to Cretaceous geology went far beyond chairing the subcommission: he served on the Editorial Board of *Cretaceous Research* from 1980 until his death, and chaired the international working group on the Campanian Stage from 1995 onwards. In the wider geological community, he served on committees of the Geological Society of London, International Geological Correlation Programme, International Subcommission on Geochronology, Natural Environmental Research Council, Systematics Association, and Palaeontographical Society. He served as Vice-President and then President of the Geologists' Association from 1985 to 1989, was Secretary and then Treasurer of the Palaeontological Association from 1967 to 1976, and Treasurer once more from 1999 to 2004. He had an abiding interest in money, especially other peoples'. Apart from advising an array of relatives and friends on their finances (and accumulating a series of stacks of copies of the *Financial Times* in his Shaftesbury study that must have totalled three metres—pink at the top and bleached white at the bottom—he made a major impact on the finances of our Association. In 1968, the year before he took over as Treasurer, our assets stood at £10,796, 17 shillings and 5 pence. At the end of 1975, his last full year in his first term as Treasurer, our assets stood at £21,589.99. The increase was a source of satisfaction to Jake, involving as it did both conventional and less conventional approaches to asset management.

His contribution to geology, and his excellence as a scientist, were recognised by the award of the Lyell Medal of the Geological Society of London in 1989. As he remarked on accepting the award, 'my first reaction on receipt of notification of the award was to check the list of previous recipients, to see who had *not* received it ...!'

Jake Hancock was an original. Geology was his great passion, and in the weeks before his death, which he approached with great calmness and stoicism, he reviewed papers for the Geologists' Association, worked on manuscripts on ammonites, and instructed us on how to deal with unfinished business, geology and wines at Coonawarra, the Albian-Cenomanian boundary in Texas, and unfinished work in North Africa, Cenomanian sea-levels, and his evolutionary studies on the Cenomanian ammonite genus *Schloenbachia*. But there were other interests: the growing of rare potato varieties, wine, and Help the Aged, were but three. That extraordinary profile, even more extraordinary laugh, ability to sleep under all circumstances (notably at conferences), that great kindness and generosity to the young, are what I recall. For more than forty years, at first in London, and thereafter in Dorset, he and Ray Parish, his companion of 42 years, wined, dined and helped young (and not so young) geological visitors. They provided accommodation for the impecunious young, and Jake purchased journal subscriptions for those without hard currency, found rare publications, and provided a guide to collections, field areas, and the mysteries of London's public transport system. And he gave me his friendship for forty years.

John Michael (Jake) Hancock, born Salisbury, Dorset, 10 August 1928, died Shaftesbury, Dorset, 4th March 2004.

Jim Kennedy
 University of Oxford, UK
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Jake Hancock Memorial Meeting
14th October 2004
The Geological Society (of London)
Burlington House, Piccaadilly, London, UK

Introduction; the life of Jake Hancock

W.J. Kennedy (University of Oxford, UK)

Jake Hancock at Imperial College (provisional title)

R.C. Selley (Imperial College London, UK)

The nature and characterisation of eustasy

A.S. Gale (University of Greenwich, UK)

Oil from North Sea Chalk

I.E. Oxnevad (BP Stavanger, Norway)

Nannofossils and the K-T boundary

*J.A. Lees and J.R. Young (University College London, UK;
 Natural History Museum, UK)*

Palaeoecology of chalk echinoids

A.B. Smith (Natural History Museum, UK)

Geochemistry and petrography of the Chalk

D.S. Wray (University of Greenwich, UK)

The Cenomanian Stage

W.J. Kennedy (University of Oxford, UK)

Palaeogeography of the Chalk Sea

J.C.W. Cope (Cardiff University, UK)

Geology and wine

J.M. Huggett

The meeting will begin at 10am, and will be followed by wine and nibbles at 5:30pm.
 Organiser: John Cope (Cardiff, UK)
 Further details: Lucy Kimber, Geological Society <Lucy.Kimber@geolsoc.org.uk>

PalAss vs. Paxman – the full story

The reputation of PalAss is intact. The Association has not been shamed. I just wish the same were true of myself.

In the last edition of the *Newsletter* I mentioned that a quartet representing the UK's finest fossiliferous organization had made it through to the televised rounds of *University Challenge: The Professionals*. I also declared that if the team—Tim Palmer, Norm MacLeod, Richard Fortey and myself—performed particularly badly members would hear nothing more about it. So from the existence of this piece you can make a reasonable deduction: we didn't get annihilated. But, although this article will tell the story of our adventures in TV-land, I shan't reveal the result of the match itself. For that you'll just have to wait until it goes on air later this Summer.

Unlike the regular, student version, *University Challenge: The Professionals* is not simply a tough TV quiz. It is also an opportunity for the various societies and august bodies who qualified to make themselves known to an audience of millions and explain a little about what they do. Hence, Granada Television, who produce the show, asked each team to choose a location that 'best reflects the traditions of your society' for a spot of introductory filming. Alehouses being ruled out, we selected a quarry on the Isle of Portland, and on a chilly Tuesday in February the four of us were to be found scrabbling about among blocks of Jurassic limestone, pursued by a camera crew.



Tim is being interviewed by the film crew, whilst Norm finds fossils for Philippa the researcher and Richard loses interest and wanders off.

This was fine in itself, but, almost inevitably, good specimens proved hard to come by and our cameraman became more interested in filming the various items of machinery in explosive action. Since relatively few palaeontologists collect samples by gunpowder, we were somewhat concerned of the impression this would give, so it was a relief when the quarrymen told us

they would not be using the equipment that day. However, when the camera was turned back on us our slightly uneasy feeling didn't dissipate. Being filmed 'finding' fossils we'd actually picked up earlier that morning wasn't too bad, but having to gaze blankly, smile, then laugh to camera, each time for a minute, was excruciating. I didn't get into palaeontology for its comedy potential, and I can't believe the Granada team, who were a pleasant bunch, thought the footage made for good viewing.

They seemed content enough with it all, though, and we were soon able to swap hardhats, wellies, and fluorescent jackets for a pub lunch. Richard and Norm departed immediately afterwards, but Tim and I stuck around to inspect the rest of the shoot. Having been unable to dig up any dazzling material, the crew wanted to film some fossils, and this necessitated the help of a local eccentric. In an old quarry building, assisted by a gang of servile men, she rambled incessantly at us about her plans for a combined art and geology theme park on the island. To say she had no understanding of geological science would be to besmirch the reputation of someone who has no understanding of geological science. When I mentioned fieldwork I'd done studying Jurassic oysters around Weymouth, she said "Oh yes! The oyster bed!" and gave me a book on the creation of the universe. But she did have some photogenic specimens and the team was able to film them unmolested. Eventually I told Tim I had a train to catch and we fled, wondering whether the 90-second introduction would accurately reflect either our day or our science.

The show proper was filmed a month later at the Granada Studios in Manchester. Having been repeatedly refused any information on our opponents, we arrived to find we were up against the Eden Project, in a Biology-v-Botany clash (of sorts). Their team included the project founder, Tim Smit, and whilst waiting for instructions on what to do and where to go, we had an entertaining discussion on how to make natural history attractive to the general public. Norm suggested that the NHM should invest in animatronic dinosaurs that devoured every 50th child, which would certainly add a new dimension to school trips. And if that thought didn't unnerve the Eden Project team sufficiently, Norm had another trick up his sleeve: our mascot, a rather malevolent-looking *Pteranodon* dubbed Terry.

Ours was the last of the first round matches to be filmed, so there was a fair amount of sitting around required. Watching the Welsh Assembly do battle with the Scottish Parliament killed some time, before we were led off to make-up and then for some food. As we walked into the canteen, the people already in there (presumably involved in some way with *Celebrity Stars In Their Eyes*, being filmed in the studio next door) turned and stared at us, trying to work out if we were famous. One small boy tugged his father's shirtsleeve.

"Look Dad!" he whispered, "it's the expert on late diagenetic carbonate cementation in the Mesozoic, Dr Tim Palmer!"

"Don't be daft, lad!" retorted his father. "That's Norm MacLeod, the leading authority on morphometric variability in planktonic foraminifera!" They returned to their dinner.

And finally it was time to get on with it. In the studio, a warm-up man whipped the audience into a sub-orgiastic frenzy as we waited in the wings and when we walked out into the bright lights it seemed the crowd was almost exclusively on our side. It turned out this was true,

as Paul Selden had persuaded a gaggle of Manchester University geology students to queue for tickets and join the various members of the Association already invited to attend. I was honoured to find myself seated closest to presenter Jeremy Paxman, thereby enabling me to hear the questions that vital fraction of a millisecond earlier than anyone else, although it did mean I couldn't see the scoreboard.

The make-up ladies gave our faces a final powdering, the soundmen did a few last tests, Sir Jezza of Paxo sauntered in, and we were ready to roll.



Nil points? They must be the Brits...

With it being the last match, we had the luxury (or misfortune) of knowing what score would take us through to the semi-finals: over 180 points and we'd claim a place. Inevitably, I can't remember many of the questions, but Tim correctly interrupted the first starter and off we went. Or at least we did until it came to the dreaded, inevitable, geological question, which went something like this: "Existing between 250 and 200 million years ago, what was the name of the only ocean of the time, taking its name from the Greek for 'everywhere' and 'sea'?" I thought of Tethys and Iapetus, knowing neither was right, and waited for one of my senior colleagues to buzz in with the answer. They didn't, so I took the plunge. "Thalassia?" I enquired. "No," responded Jeremy witheringly, turning to the Eden Project team for an answer. They gazed blankly back at him until he announced "Panthalassa," just after Norm had turned and whispered the same word to me. Oh dear, close, but still wrong. I might never live this down.

Thankfully my knowledge of pop music provided redemption of sorts, whilst our expertise on television superheroes amused Mr Paxman. The Eden Project, meanwhile, got lumbered with bonus questions on male reproductive organs. There were one or two incorrect interruptions, a

few educated guesses and a good deal of blank expressions, before Norm whispered 'We have to get this right,' as Jeremy prepared to read another starter for ten. He began, Richard pressed the buzzer, and was just about to give the right answer when the end-of-match gong rang. It was all over. I still couldn't see the score, but Jeremy commiserated us on a valiant effort and after one or two re-takes and a few gratuitous audience shots we trooped out.

Consolation came with free drinks in the legendary Green Room, this one even more legendary than usual, being the Rovers Return of *Coronation Street* fame. OK, so it was a mock-up, the real one being in a studio somewhere, but it was novel enough. And when the hospitality ran out, we went off to the hotel for dinner. Outside it was mildly disappointing not to be mobbed by the screaming hordes, especially since I'd suggested the Birmingham PhD posse should buy all of Richard's books and demand them autographed, but it wasn't too awful to rejoin the real world. Fifteen minutes of fame is quite enough for the time being.

University Challenge: The Professionals (Palaeontological Association v. Eden Project) is scheduled to be broadcast on Monday 2nd August at 8:30pm on BBC2 [subject to confirmation].

Liam Herringshaw

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From our Correspondents

Button counting: an advanced course

On this Christmas Day, his father said: "you have reclassified your buttons, I see."...

"The taxonomic principle being colour. The spectrum from left to right, with size the second principle of order."

"Yes, father."

"Very good" said Theophilus.

Peter Carey (1988). *Oscar and Lucinda*, p.10.

Figuring out how to classify things (including buttons and brachiopods, although to me these are rather similar) has always been a problem. As I mentioned in a previous column, Aristotle and Linnaeus thought you could do it simply by chopping up the world into convenient little pieces, each with its own unique characteristics. We managed like this in a perfectly satisfactory manner for several thousand years, but then someone had the disturbing thought that, in an evolutionary world, this might not do the job at all well. Despite the fact that the most famous publiciser of this problem, Hennig, looked specifically at palaeontological problems, and that his system of phylogenetic systematics was promulgated in the English-speaking world by palaeontologists such as Dick Jefferies and Colin Patterson, it took a long time for the palaeontological world to catch on to this. The idea that *general* similarity sometimes fails if you want systematics to capture or at least reflect evolution is still resisted by many palaeontologists. Indeed, if you are one of the many (including me) who are exasperated by the fanatics who insist on talking about "non-avian dinosaurs" or, if they use it all, always put the word fish in inverted commas, you are part of the resistance movement. And despite a flicker of interest in the subject at the beginning of the 1990s, it still strikes me as amazing how few talks based on cladistics are presented at the Annual Meeting every year. Of course, one reason that palaeontologists can't face cladistics is the horrific realisation of how many palaeontological systematics units would go to the wall if one wanted to be rigorous about its application. In a way, this is not the fault of palaeontologists past or present. After all, every paraphyletic group was once monophyletic. Silurian palaeontologists would have been able to talk about fish without any sort of added punctuation, after all, and mean exactly the same thing as we do today, if we are brave enough to say it. The fact that many of our morphogroups lived—and died—in the past is bound to lead to trouble once their broadly ancestral position is recognised.

Still, this column is not going to be dedicated to extolling the merits of cladistics. Rather, I want to recognise that palaeontologists have now in general accepted the principles behind it all. Ironically, several important revolutions in systematics are ongoing, some of which

address the issues that worried palaeontologists in the first place, and I want to point to some of them. At least I will not get the blame when palaeontologists are still arguing about them in twenty years time.

One of the canker worms at the heart of cladistics is the idea of parsimony: we "maximise character congruence" as the jargon goes, with the aim of ending up with as few character changes as possible. In other words, we explain the observed character distribution with the minimum number of postulated changes. The standard objection to this is that we all know Nature is not parsimonious, so why assume it to be in our systematics? To which the equally standard response is: Nature may or may not be parsimonious, but we should be. All very well, but the suspicion that our classification is then not mimicking nature creeps over you—the whole point of dumping eclectic systematics in the first place. This problem all boils down to the ludicrous idea embedded in classical cladistics that each "character" is of equal weight, and that it is just as parsimonious to lose as to gain them. We know that this assumption cannot possibly be true, not even approximately, but with morphology, we cannot do much about it. Placing weightings on characters before running the analysis simply fixes the analysis according to how one weights: and who gets to decide what the weights should be?

There are two related ways out of this fix, and both are being tried. The first is to ditch the parsimony claim, and have an explicit probabilistic model for how things should evolve. With molecules, one might think this is moderately straightforward. For example, Jukes and Cantor, in a classic paper way back in the 1960s, proposed a model for nucleotide substitutions (*i.e.* that the rate of substitution of each of the four nucleotides by any of the others was the same). With this as a basis, it was possible to compare one sequence with another and work out which ones were likely to be the most closely related to each other. This modelling relied on so-called *maximum likelihood*; which is a bit like probability, but in reverse. Maximum likelihood was in fact invented by one of the planet-brains of the 20th Century, Sir Ronald Fisher, who also did a fair amount of pretty reasonable genetics work as well. Whereas in modelling probability one takes certain parameters (such as the chance of being hit by a falling grand piano) and works out the expected outcome of those parameters (*e.g.* to work out how many times it will happen to you a year), in maximum likelihood analysis you already know the outcome, but want to know the underlying probabilities. Given that you have had the grave misfortune to be struck by a piano ten times this week, what is the most *likely* probability of being hit by a piano in a given year? In sequence analysis, Jukes and Cantor give us a probabilistic model for how sequences evolve, and we know what the final sequences look like, so one can use maximum likelihood analysis to marry the two together, to show which sequences are most likely to be most closely related to each other. As you might suspect, this is fiendishly expensive computationally, and makes parsimony analysis look like abacus work. The trouble is that you need in theory to look at all possible trees, and then see how each substitution site evolves through each one. Fortunately, there are various cunning short cuts (just as in parsimony analysis) that speed the whole thing up—somewhat.

I would guess that we palaeontologists have heard of maximum likelihood, although not having any explicit models for trilobite evolution has made it of curio value only, unless one wants to do things like compare phylogeny to stratigraphy. In any case, events have moved on to the latest craze, Bayesian analysis. Named after a 17th century clergyman, Bayesian analysis is the most controversial and most trendy method currently available. Here is an example of how it works. Suppose you had two huge drawers full of fossils; one (Drawer A) with a 50/50 split of trilobites and brachiopods, and the other (Drawer B) with a 70/30 bias in favour of trilobites—a situation devoutly to be wished for. Someone has selected two random fossils from one of the drawers; and—alas!—they are both brachiopods. What is the likelihood that the fossils come from drawer B? This seems a hard question to answer, but the Rev. Bayes made it easy. If both came from Drawer A, then the probability of getting two brachs is (basically) $0.5 \times 0.5 = 0.25$. And if they came from Drawer B, then the probability is $0.3 \times 0.3 = 0.09$. In other words, the ratio of the likelihoods is 2.78 in favour of the 50/50 drawer.

Bayes distinguishes between prior and posterior probabilities; *i.e.* between's one initial estimate of the probability and then one's altered estimate based on the actual outcome of the data. In this case, as there are two drawers to choose from, one might reasonably guess, "a priori," that there is a 50/50 chance of the fossils coming from either drawer. What posterior estimate do we get based on our two brachiopods?

Baye's formula says in this instance that:

$$p(\text{brachs from B}) = \frac{p(2 \text{ brachs from B}) \times \text{Prior (B)}}{p(2 \text{ brachs from A}) \times \text{Prior (A)} + p(2 \text{ brachs from B}) \times \text{Prior (B)}}$$

where $p(\text{brachs from B})$ is the probabilitiy we are trying to calculate: $p(2 \text{ brachs from A or B})$ are the probabilities of getting two brachs from either of these drawers (known to be 0.25 and 0.09 respectively) and Prior (A or B) is the prior estimate of the fossils coming from A or B respectively, which we've just guessed to be 0.5 for each. In other words, the formula expresses the posterior probability as the ratio of the likelihood times the prior probability to the summed (likelihoods times the prior probability) of all possible scenarios. Now we can calculate the posterior probability of both brachs coming from B: it is $(0.09 \times 0.5) / ((0.09 \times 0.5) + (0.25 \times 0.5))$, and this comes out at 0.28.

Seems slippery? It is. Obviously, one of the reasons this is controversial is that it allows you to insert a prior guess about the probability of a particular outcome into an analysis. But after all, why not? It seems that the results are not greatly sensitive to the prior probabilities, which can be and normally are all set to be equal.

This very simple example can be grotesquely expanded into phylogenies by substituting prior probabilities of a particular tree (usually regarded as equal for all) and the likelihood of a particular tree given the data. Unfortunately, the computation is typically mind-boggling because of the need to sum all possible likelihoods x priors, but several devious ways of speeding the thing up are now available.

The nice thing about Bayesian analysis is that everything is up for grabs (it has already been applied to the existence of God—answer: 67% likely—and the Cambrian explosion). One is not tied to the assumption that each morphological change is equally likely. Indeed, if you think that, say, evolving a backbone is somewhat less likely than evolving a nose, you can insert this guess or experience into the analysis as a prior. After all, even if your model is that each change is as likely as the next, this is still no worse than parsimony analysis, and you might be able to improve on this. Of course, this sort of use of guesstimate has been infuriating sober-minded mathematicians for centuries now; but palaeontology as a whole probably does that anyway.

To destroy a phrase of Bertrand Russell: the gateway to a golden age of morphological phylogeny is guarded by a dragon; and that dragon is parsimony. But these newly-resurrected flexible approaches to probability are exactly what palaeontology needs in order to utilise its knowledge base of qualitative and "silent" data that is hard to articulate. A colleague of mine was once amused to be told at a "Taxonomy & Evolution" meeting that "these are glorious times for systematics!". For palaeontologists as well as molecular biologists, this might finally be about to come true.

Graham Budd

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FURTHER READING

ARIS-BROSOU, S and YANG, Z.H. 2003. Bayesian models of episodic evolution support a late Precambrian explosive diversification of the Metazoa. *Molecular Biology and Evolution* **20**, 1947–1954.

HUELSENBECK, J.P., RONQUIST, F., NIELSEN, R. and BOLLACK, J.P. (2001). Bayesian Inference of Phylogeny and Its Impact on Evolutionary Biology. *Science* **294**, 2310–2314.

MrBayes: a program for inferring phylogeny using Bayesian analysis is available at

<<http://morphbank.ebc.uu.se/mrbayes/info.php>>

Epigenetics: The Context of Development

During the last six columns we have attempted to demonstrate why palaeontologists need developmental biologists, and *vice versa*. In this column we discuss epigenetics and why this concept should be of interest to those who study traces of organisms long since deceased.

Epigenetics is often confused with *epigenesis*. Epigenesis historically refers to the process of development by which a complex structure (embryo, organ or tissue) is produced from a single cell homogeneous starting point. In contrast to epigenesis is *preformation*, long debunked in its extreme form, which was that a tiny version of the adult was present in the gamete(s), and which grew only in size to produce the adult organism. In a less extreme form, we know that eggs inherit preformed structures such as mitochondria, ribosomes, nuclei *etc.* Indeed, the egg is inherited as a fully formed structure.

Waddington coined the term “epigenetics” to merge epigenesis with genetics, producing the notion that embryos, organs, tissues and cells develop under genetic control. Importantly, for Waddington the genetic control was not autonomous, but rather responsive to environmental signals, where the environment might be factors internal to the organism or external. However, epigenetics as used today has a second meaning that can be characterized as the “phenotype of the gene,” a concept that includes such processes as genetic imprinting and DNA methylation, which result in selection expression/repression of genes. Waddington’s definition and the new approach both highlight factors necessary for successful and selective transcription of DNA products and the interactions of these products in space and time. The environment of a cell provides the conditions necessary for the successful initiation of DNA transcription, whereas cell-cell interactions or physical factors such as temperature, pH and nutrition provide other conditions required for cell, tissue and organ differentiation (Robert 2004). Epigenetics then, recognizes that *context* is everything.

So why should palaeontologists be concerned with examples and details of epigenetics? The fossil record is depauperate (or completely lacking) in evidence of cell-cell interactions, let alone the ability to characterize the genetic code of the various study organisms, so epigenetics might initially seem to be of little interest to those who study hard tissue, or trace remains of long dead organisms. However, palaeontology in its most general sense is the study of ancient morphology and its evolution through time. Epigenetics reminds us that there is rarely a one-to-one coupling of gene mutation and morphological change. The evolution of morphology is not solely the product of heritable genetic mutations, but rather driven by a dynamic interplay of cellular components and tissues with their environments.

Internal Factors

The environment of a cell, its location and surroundings, are important epigenetic factors that influence the cell’s identity and activities. For example, osteoblasts remain as such until the bony matrix they secrete surrounds them and they become entombed as osteocytes. Along with position there are associated changes in cell shape and gene expression patterns.

As far as we know particular osteoblasts are not predetermined to become embedded and ultimately form osteocytes, the differentiation is apparently a consequence of position in relation to osteoid matrix.

Epithelial-mesenchymal tissue interactions are important epigenetic factors necessary for chondrogenesis (cartilage formation) and osteogenesis (bone formation) of the mandible of chicks and mice. While three types of epithelial-mesenchymal interactions are possible (cell-cell contact, diffusible factors from the epithelium, or matrix-mediated factors located in the basal lamina), factors located in the basal lamina have been demonstrated to be necessary for mouse mandibular skeletogenesis (Macdonald and Hall 2001). Due to differences in the timing and nature of neural crest migration, avian mandibular mesenchymal cells are chondrogenic prior to neural crest migration due to an interaction with cranial epithelium during neurulation; however mammalian mandibular mesenchymal cells also depend upon a later interaction with mandibular epithelium, perhaps because migration occurs prior to completion of neural tube folding and interaction with cranial epithelium. The ability for the matrix-mediated factors to be provided in spatially and temporally different patterns provides a means for heterochronic change. An awareness of epigenetics provides the context with which to interpret such features as: associations of the dermal skeleton with the epidermis; the functioning of odontodes, and the conditions underlying increase or decrease in skeletal elements, morphological changes in tooth patterns and tooth shapes, and so forth.

Embryonic induction and the competence of cells/tissues to respond to different inductive signals are also epigenetic interactions. They can be explained at both the cell and the tissue level (*e.g.*, at the level of the cell—development of the vulva in the nematode—precursor cells need to be competent to respond to the signal from the anchor cell; *e.g.* at tissue level—eye development—ectoderm overlying the optic vesicle needs to be competent to respond to the inductive signal from the vesicle in order to form a lens placode). Take a cell/tissue out of its usual context/environment and its fate can change (within limits). But first it must be *competent* to respond to the new environment (Dawid, 2004). The evolution of external cheek pouches in pocket gophers and kangaroo rats or the origin of the turtle shell are classic examples.

When inductive interactions between tissues are disrupted, “upstream” phenotypes can be altered or fail completely. The Mexican tetra *Astyanax mexicanus* has two forms—a surface form that is pigmented and a cave form that is eyeless and unpigmented. Cave fish may have exchanged sight—unnecessary in underground rivers—for more teeth and taste buds (see Vogel 2000; Jeffery *et al.* 2003). In normal eye development, the lens induces the optic cup to form the optic vesicle, composed of the inner and outer layers of the retina. The blind tetras initially form an optic primordium with a small lens but the eye subsequently degenerates. Jeffery and colleagues (2003) discovered differences in the expression of key eye genes (*Pax6*, *shh*) between the two morphs, with reduced *Pax6* expression in the lens placodes. The degenerated lens is incapable of setting up later inductions involved in further eye development, and the eye degenerates after subsequent programmed cell death of the lens. Current hypotheses suggest that adaptation to cave environments may have occurred either once or multiple times during the evolutionary history of this species.

External Factors

Whether maternal characteristics (extra-embryonic egg shell and contents or *in utero*) or characteristics of the physical environment, the external environment around an embryo can greatly influence the process of development and the resulting morphology. One can develop chicken embryos in shell-less culture (up to about 19 days out of 21 *in ovo* developmental period). In response to the reduction of the calcium reservoir, much of the cartilaginous skeleton of these chicks fails to ossify. Interestingly, in the American alligator, a similar semi-shell-less culturing technique has proven to be much less detrimental to the embryo (see Ferguson, 1981). Unlike birds (and turtles), alligators are more dependent on contents within the egg (and not the egg shell) as a calcium source. Indeed, semi-shell-less alligator egg cultures appear to develop normally, even to hatching (Ferguson, 1981). An adequate interpretation of palaeohistology requires recognizing the nuances of metabolic regulation of skeletal development.

Experimental work on mice and other rodents highlights the importance of hormonal exposure during prenatal development (see Vandenberg 2003). Testosterone levels increase within prenatal male mice, leading to sexually dimorphic characteristics such as increases in the size of the hypothalamus and anogenital distance; removal of the testosterone signal, either by surgery or pharmaceutical blockage, results in a pup exhibiting anatomical and behavioural female traits. Female pups located adjacent in the uterus to males are exposed to increased levels of testosterone from their brothers, and exhibit increased amounts of male sexual morphology and behaviour depending upon the amount of exposure (one adjacent male or two). The uterine environment has a measured affect on the adult morphology and variation within the litter.

Mechanical strain plays an important role in the development of bone morphology, processes, and remodelling. Strain is detected by osteocytes and is communicated via connections (cell processes) between osteocytes and osteoblasts on the bone surface, thereby modulating remodelling (Hall 2004).

The role of muscular activity on the growth of bones has been investigated in paralysed chick embryos (Hall and Herring 1990). Individual bones, or the elements of a single bone, vary in their dependence on muscle contraction for normal growth. As an example of a single bone, the development of the anterior portion of the mammalian dentary bone is influenced by the developing dentition but not by muscle action. Development of the posterior portion of the mammalian dentary bone is influenced by the muscle action but unaffected by the dentition. As an example comparing bones, the furcula is more dependent and the mandible less dependent on muscular activity for normal bone growth than the long bones, which showed a decrease in growth rate of about 52–63% of normal rate (this is comparable to overall reduction in embryonic growth). Not only does paralysis affect the growth rates but it can also stop some developmental processes. For example, in paralysed chick embryos, developmental arrest of fusion of the sternum, followed by its collapse and the displacement of the entire shoulder girdle was observed (also in Hall and Herring 1990). It was suggested that perhaps the sternum is incapable of resisting loads imposed on it because of the effects of paralysis on adjoining musculoskeletal elements (rib cage, muscle attachments to the sternum, *etc.*).

Temperature can affect pigment pattern and/or sex ratios (temperature-dependent sex determination) in some reptiles. The American alligator expresses an F:M:F ratio—below 31.5°C or above 35°C and all embryos are female (Western, 1999). The temperature sensitivity period of gonadogenesis occurs during days 32 to 42 (of a 70 day average) at an ambient temperature of 33°C.

The three-spined stickleback, *Gasterosteus aculeatus*, is distinguished by three individual spines on the back, close to the dorsal fin. This species shows great variation in the development of the series of bony plates along the sides of its body. In the past these variations were considered to constitute distinct and named forms or varieties of the one species. While variation in the development of these side plates has been considered a result of local habitat differences such as variation in temperature and particularly in salinity, as well as the sex and age of the fish (see Ahn and Gibson 2004, and Pelchel *et al.* 2001), increasing strides are being made on demonstrating how the morphological differences could be linked to gene regulation (Pennisi 2004). Hubbs (1922) and Lindsey and Arnason (1981) noted that modulation in the number of somites and hence number of vertebrae as a result of temperature most likely occurs in the posterior part of the body.

Newman and Müller (2000) propose that plasticity, extreme morphological variation that results from variations in the environment during development, may have been much more prevalent in the early evolution of multicellular life. For example, the fungal pathogen *Candida albicans* switches between very different forms such as budding cells, to thread-like hyphae, or strings of yeast-like cells with long septated filaments, with no apparent default morphology. They suggest that genetic integration, which limits the effect of environmental variability, is a highly derived condition and that epigenetic plasticity permitted rapid accommodation to highly variable conditions as well as a wider range of morphologies on which selection could act.

Considering the Fossil Record

Some of the cave fish forms of *A. mexicanus* have been described as belonging to a separate genus *Anoptichthys* (Wilkens and Strecker 2003). The eyed and eyeless form of *A. mexicanus* show morphological differences in their craniofacial skeletons, particularly in the circumorbital bones (Yamamoto *et al.* 2003). If these were found in the fossil record, the morphological differences may have led to misidentification (splitting into separate species)—but with our knowledge of developmental processes, we know they are the same species. The Mexican tetra example also demonstrates plasticity inherent in development, where loss of eyes occurred as well as increase in tooth and taste bud number. That is, there are different changes occurring in different tissues in the head region.

Examples initially known from the fossil record, but where our understanding has been expanded by incorporating studies on the epigenetics of development, include the transition from fins to tetrapod limbs, the origin of the mammalian middle ear ossicles, and the transformation of forelimbs to flippers in cetaceans.

- For fins to limbs we have: homology between the endoskeletal elements; knowledge of the expansion of domains of expression of Hox genes associated with the transition; models of altered timing (heterochrony) to explain the loss of the fin rays (Hall, 2004).

- For the middle ear ossicles we have: the evolutionary transition preserved in the ontogeny of marsupial embryos; an understanding of how the pharyngeal arches are patterned by Hox genes; knowledge of the major genes that initiate skeletogenesis; information on how groups of cells are specified and migrate within the embryo (Hall, 1999).
- For flippers we have: mutants that display various degrees of loss of paired appendages; knowledge of the contribution of somitic cells that maintain the specialized apical ectodermal ridge (AER) in limbed tetrapods, and whose premature death deprives the AER of the factors required to maintain it; knowledge of the specialized interactions between the AER and underlying mesenchyme required for outgrowth and patterning of limb rudiments (Fedak and Hall, 2004).

Epigenetic relationships identify factors and interactions important for hypotheses and studies of morphological evolution. Also, growing attention to plasticity in developmental systems, which produce extreme polymorphisms depending upon external environmental factors, suggest the fossil record may include an (irreconcilable) bias producing taxa-splitting in systematic studies, because the exact environmental variables during development for fossil specimens will always be unavailable. Furthermore, the hypothesis that genetic integration is a highly derived condition and that plasticity was the norm early in multi-cellular evolution provides important context for interpreting the significance of the earliest fossil record of multi-cellular life.

Some might suggest that epigenetics is a catch-all term to account for all variation 'noise' not accounted for by heritable changes of the genetic code that some still consider the primary, if not only, factor driving evolution. However, the 'code' is context-dependant, and there is much information available from considering the details of this non-genetic variation. Epigenetics and developmental plasticity remain fundamental developmental concepts of great relevance to the study of morphological evolution in the fossil record.

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Historical imagination, colonial theories and phylogenetic fashion

“The reach of the imagination is necessary to build the presence of the past with any kind of power and persuasiveness” Simon Schama.

Once upon a time fossils could be considered the “primary documents of the historians of life” (Simpson, 1951: p. 14). Times have changed rather a lot. To make such an apparently naive statement today would immediately elicit the scorn of many knowledgeable colleagues. In our enlightened age the evidentiary status of fossils has largely been reduced to being mere road-kills straddling the ditches alongside evolution’s highway. According to the new doctrine you will have about as much hope to shed light on the path of evolution by strictly studying the fossil record, as you would have understanding faunal dynamics in North America by studying dismembered racoons and flattened armadillos on the nation’s roads. If you consider this to be a perverse exaggeration, please consult Henry Gee’s book *Deep time: the revolution in evolution* (2000). In this popular work of a technical subject Gee introduces cladistics as the grim reaper that robbed fossils of their exalted status as beacons illuminating evolution’s pathways.

What has happened will undoubtedly be familiar to most readers. In a nutshell, the unique status of fossils as singular oracles telling the absolute truth about evolution was ‘officially’ demolished in an infamous lecture delivered by Gareth Nelson at the American Museum of Natural History in 1969, the integral text of which is for the first time published as an appendix to a paper by Williams & Ebach (2004). Nelson’s thesis—that fossils cannot directly illustrate ancestor-descendant relationships in a non-theoretical manner, but can only be systematised in the same way as living taxa in the reconstruction of sister group relationships—is well-known and widely accepted today. The only ancestors for which there is a place in cladistic logic are hypothetical ancestors. In Nelson’s own words: “In fact, looking for ancestors in the fossil record seems to be like looking for honest men: in theory they must exist, but finding them in practice, alas, is another matter.”

The nature of hypothetical ancestors may be reconstructed or inferred, but they can never be directly recognized. Ancestors will therefore forever remain empirically unknown and unknowable. So far so good. This much is widely, although by no means universally, accepted by biologists and palaeontologists. Moreover, since the habitats and habits of imperfectly preserved fossil taxa remain conjectural at best, such information for some becomes simply “quite irrelevant to retrieving the evolutionary history” of any taxon of interest (Gee, 2000: p. 185). Of course fossil taxa may attain cladistic importance in shedding light on evolution through their placement as basal stem taxa on the line to modern crown groups, but Gee concludes forcefully that “any concerns about adaptation or function” relating to taxa only known as fossils are “untestable and thus unscientific” (Gee, 2001: p. 192). Apparently, interpretation should be shunned at all costs if we are to reconstruct history objectively.

Similar sentiments about the character of historical scholarship can also be found in the works of phylogeneticists dealing strictly with living taxa. A recent paper by Giribet (2003: p. 315) provides a forceful illustration. Giribet is convinced that in order to reach a firm understanding of metazoan phylogeny “we will have to rely on observation *rather* than inference.” Furthermore Giribet considers the necessity to use ground patterns (the character states considered primitive for a taxon) for phylogenetics to “cause bias and subjectivity in phylogenetic analyses.” Again, we are advised to steer clear of mere inference in our quest to reconstruct deep history, even when fossils are not considered. But how can we possibly reconstruct history by relying on observation rather than inference, and without bias and subjectivity?

The short answer, of course, is that we can’t. It is simply impossible to reconstruct history, especially the deep past that reaches back multiple million years, by mere observation in a completely objective way, without relying on extensive inference. Although this column is scarcely the place to open such a can of worms as different perspectives on historical epistemology, we nevertheless need to dip ever so briefly into this topic to understand the opinions of Gee and Giribet. Simply put, Gee and Giribet fall on one extreme of a continuum in existing attitudes towards engaging the inherent uncertainties of historical inference. Gee and Giribet’s attitudes towards historical reconstruction place them squarely into a large faction of phylogeneticists that have formerly been labelled as pattern or transformed cladists (Hull, 1988), without implying, I hasten to add, that Gee and Giribet themselves would necessarily claim membership in this elusive group. The central commitment of these workers is to keep phylogenetic analysis as theory-free as possible. Cladistic analysis should strictly be concerned with the identification and evaluation of shared derived characters, on the basis of which taxa can be arranged in cladograms that express nothing but the relative branching order of sister groups. Under no circumstance are any considerations of unobserved evolutionary processes allowed in the reconstruction of phylogeny, neither in the form of differential character weighting (which amounts to *a priori* judgement of the phylogenetic value of characters), nor in the form of presumed selection pressures or functional scenarios that may be reflected in different relative probabilities of different character state transformations. Under this perspective, to infuse phylogeny reconstruction with any evolutionary process considerations is to commit the cardinal sin of putting the scenario in front of the cladogram.

At the other end of the continuum we find workers who do not adhere to the stance of agnosticism with respect to the evolutionary process as adopted by the pattern cladists. Realizing that historical inference unavoidably deals with uncertainties, they have chosen to engage these head on. Among the ingredients of their approach to phylogeny reconstruction we may find data quality evaluation prior to a phylogenetic analysis, for example on the basis of a comparison of the complexities of conflicting characters, attempts at *a priori* separation of good and bad characters, a concern for functionality of hypothetical ancestors implied by the combination of characters at internal nodes of cladograms, and a consideration of presumed selection pressures and the functional correlates of evolutionary changes in morphology. These workers might adopt as a fitting motto “it is because we see little, that we have to imagine much,” a phrase deriving from the Victorian playwright, actor and polymath



George Lewes. Lewes was deeply concerned about the role of imagination in the generation of scientific hypotheses (Carignan, 2003), and we will meet him again somewhat later in this essay.

Perhaps another way of conceiving this difference in historical epistemology is to decide what type of uncertainty one prefers: uncertainty of assumptions, or of results. Standard cladistic analysis maximizes its power to test competing hypotheses and objectivity by treating all characters equally and minimizing process assumptions. However, the results may not represent the true phylogeny if in fact different characters have different susceptibilities to convergence, for example. In contrast, other workers may want to incorporate their *a priori* suspicions about the evolutionary process that they initially developed independent of phylogeny into the reconstruction of phylogenetic hypotheses, no matter how conjectural the assumptions may be. Yet, if we are of the opinion that “systematics as a realist, truth-seeking activity is doomed” (Schram, 2004), and that the only true tree will forever remain unknowable in principle anyway, this appears to be nothing more than a difference in taste.

Unfortunately, although I believe the different perspectives really to be extremes of a continuum, to many, perhaps most others, it seems to be a difference in taste at least as fundamental and unbridgeable as whether you like to eat raw fish or not. It is striking to note that one person’s central epistemological commitments are an opponent’s gravest logical fallacies. The history of phylogenetics is a rich repository of debates between dogged epistemological fundamentalists who have engaged in round after round of notorious head butting. Familiar tales range from the battle between phenetics versus cladistics at the cradle of the discipline, parsimony versus likelihood approaches during most of the era of cladistics, and still continuing, and supermatrices versus supertrees as a relatively younger debate. Although such debates in general are a healthy sign of critical scrutiny of our conceptual instruments, the fundamentalist adherence to a single epistemological framework, without the willingness to consider seriously any results generated within different epistemological frameworks I think is reason for concern. Despite more than 20 years of attempts by different factions to bring the general phylogenetic populace to the equivalent of phylogenetic deism, opinions remain as divided as ever, and judging by the ongoing polemics in the professional literature, we have progressed towards a state of mutual understanding and respect about as far as religious fundamentalists have come towards ecumenical brotherhood.

To illuminate this issue from a different corner, and to redirect our course away from strictly phylogenetics towards historical narration in general, let us return to George Lewes and Victorian Britain. 19th century Britain witnessed many changes. At the end of the century the beginnings of both professional science and historiography were on firm footing. At this time Thomas Henry Huxley objected to being labelled as a mere ‘scientist’ with its connotations of narrow specialization and cultural impoverishment. Instead, he preferred to be referred to as a “man of science,” as he considered himself to be the proprietor not only of scientific expertise, but also of moral and religious gravity, an equal authority on matters of scientific and general interest (White, 2003). However, change was ineluctable, and Huxley’s plea for recognition became a fading cry. Somewhat earlier in the 19th century Huxley’s intellectual companions and friends George Lewes and his lover, the great novelist George Eliot, were



involved in the throes of another event of professionalization. By that time history had become a professional academic science in Oxford and Cambridge, largely by severing its maternal bond with literature. If history was to be an objective science, all elements of fiction were to be banned from its documents. Imagination, dramatization, and good story telling, however pleasing to the reader, must be avoided at all costs. It was against such views that Lewes and Eliot objected (Carignan, 2003). When Lewes wrote “it is because we see little, that we have to imagine much” he didn’t mean that we should simply fabricate or distort history, but that inferential imagination is essential for gaining historical knowledge. This postulate was central for George Eliot during the writing of her historical novels. She felt that imagination was essential for filling in inescapable gaps in our knowledge, and animating the narrative. The use of analogy was especially important for informed guesses, and in Victorian historical epistemology it was considered to be the next best thing after empirical induction (Carignan, 2003). Eliot held these convictions in opposition to the established norms of academic historical scholarship throughout her career. This attitude can of course be excused because Eliot was, after all, not an academic historian but a novelist. Yet, at the same time, she always remained loyal to the highest ideals of factual veracity to the point that she would postpone writing a historical work of fiction because she felt that she didn’t know enough about the time and place in which the fictitious story was to take place. Interestingly, Eliot’s almost compulsive attention to factual detail appears to have been inspired by a model of writing natural history with its emphasis on accurate and detailed observations (Carignan, 2003).

At this point we can see a parallel between the tension between the rise of an academic or scientific approach to historiography at the end of the 19th century and the resistance of Lewes and Eliot on the one hand, and the current tension between the two extremes to phylogeny reconstruction described above on the other hand. Some workers are loathe engaging the speculative, inferential aspect that attends deep history reconstruction, and instead restrict themselves to an ideal, formulaic approach to history reconstruction intended to yield maximally objective and repeatable results by straying only a minimal distance from pure observation. The apparent weakness of such an approach seems to be that so much is simply left unstudied. By contrast, workers at the other extreme have taken the approach of Lewes and Eliot at heart in choosing not to remain agnostic about the more uncertain aspects of the evolutionary process. They animate their writings with plausibility arguments, hypothesized selection pressures, functional assessments of hypothetical ancestors, and they posit explicit evolutionary processes such as heterochrony, to explain their observations. As with Eliot, these workers cannot be labelled as less concerned with factual veracity. However, as the historian Simon Schama said in a debate in the first issue of PEN America (2001): “historians use their imagination to tell the truth about the past.” The reception of Schama’s books by fellow historians potentially illustrates that the same extreme positions about the art of reconstructing the past exist today both in phylogenetics and history at large. Schama has received a fair share of flak for his willingness to employ his inventive faculty to draw vivid historical pictures. A good example of such imaginative writing is his masterful *Rembrandt’s eyes* (1999). In this book Schama paints a compelling picture of the life story of the great painter and his times. The book reads more like a novel than a work of historical scholarship,



but that reflects the book's great strength as much as any perceived weakness. Not shunning judgement, inference, and imagination, Schama has produced a lively synthesis that is utterly different from a dry historical chronicle. Schama animates and dramatizes the story with frequent citations from personal correspondence of the protagonists, and by projecting himself into the mental lives of the personae, and he speculates where speculation seems due. Among books in the history of science that I know, Adrian Desmond's fantastic two-volume biography of Thomas Henry Huxley, *Huxley: the devil's disciple* (1994), and *Huxley: evolution's high priest* (1997), has many of the same qualities. Yet, these books are all serious pieces of historical scholarship, certainly not fiction.

Such qualities as may be possessed by the books of Schama and Desmond are certainly absent from most of the professional literature that deals with the reconstruction of the deep history of the animal kingdom. And we are not talking literary style here. The theory and speculation-free ideal of cladistics has put a heavy stamp on the discipline, especially since computer-cladistics and molecular phylogenetics started their surge towards modern prominence in the late 1980s and early 1990s. Whereas the primary journals of the trade still displayed a certain amount of pluralism towards reconstructing animal phylogeny before this time, the literature has become much more homogenous nowadays. Today the majority of works dealing with animal phylogeny and body plan evolution are characterized by being almost entirely free of speculation. The almost universal adoption of standard cladistic analysis seems to have radically purged all impulses to theorize about animal evolution. To a degree I consider this to be a salutary effect, as it has put a stop on the generation of still more uncertain phylogenies, just-so adaptive stories, and untestable scenarios of events in deep history. However, it has also led to a literature that is, quite frankly, very boring. For intellectual enjoyment I'd much rather read an exciting, provocative, synthetic, yet speculative paper that presents an evolutionary scenario about imagined transformations in ancient animal body plans based on the thoughtful integration of disparate evidence, than a sterile cladistic paper solely concerned with clade support statistics, and presenting as the only discussion an uninspired list of synapomorphies based on a data matrix reported in an appendix at the end of the paper, or merely online.

Perhaps more important than a mere aesthetic preference for the 'old way,' seven years of studying animal phylogeny has led me seriously to doubt the exclusive superiority of adopting the cladistic straight and narrow. In particular, my recent conclusion that conflicting molecular and morphological signals for the phylogeny of the Metazoa can be more readily resolved by taking evolutionary process considerations explicitly into account, has for me cast some doubt on the justification of current cladistic hegemony. Therefore, in honour of epistemological pluralism, and a current minority perspective in studies of deep history, I want to use the rest of this essay to discuss the work of several biologists who have refused to be incarcerated in the strait jacket of cladistic consensus. Although the professional expertise of these biologists ranges across the Metazoa from platyhelminths to tardigrades and chordates, their work discussed here is focused on a single theme: to attempt to bridge some of the most conspicuous gaps in body plan organization in the animal kingdom by proposing coloniality as a stepping stone.



We start the story with the Austrian invertebrate zoologist Reinhard Rieger. From the 1970s onward Rieger profiled himself as an expert on the ultrastructural morphology of aquatic microscopic invertebrates, especially free-living platyhelminths or turbellarians. Rieger and colleagues, jokingly called the Austrian mafia by American colleagues (Morse, 1999), were among the first zoologists to start a fundamental reappreciation of our understanding of animal evolution on the basis of electronmicroscopical evidence. Among his other key achievements, Rieger co-edited and co-authored a wonderful and popular multi-author textbook on invertebrate zoology (Westheide & Rieger, 1996), which without question is one of the best textbooks on invertebrates available today, and he headed the writing of the most comprehensive synthesis of turbellarian ultrastructure published to date (Rieger *et al.*, 1991a).

Especially in the third quarter of the 20th century there were extensive debates about the nature of the bilaterian ancestor, a speculative but powerfully attractive topic that has recently regained its popularity around scientific coffee tables in the context of exciting findings in molecular developmental biology. Discussion focused in particular on four characteristics of Urbilateria. First, was it microscopical (mm-range) or macroscopical (cm-range)? Second, was it coelomate (possessing a body cavity lined by mesodermal epithelium) or non-coelomate? Third, did it move by ciliary or muscle action or was it sessile? And fourth, did it have direct development (no larva) or indirect development (larva present; also known as a biphasic life cycle)? Different authors defended different views. The majority of proposals assumed that the adult Urbilateria was a microscopical ciliated organism with direct development, but of rather uncertain general body organization. In a series of papers Rieger (1986, 1988, 1994a, b; Rieger *et al.*, 1991b) presented quite an ingenious solution to the problem of bilaterian origins by constructing a beautiful synthesis of evidence garnered from comparative morphology, embryology, life history, and ecology, and he animated his evolutionary scenario with heterochrony and functional considerations based on analogies with living phyla.

To bridge the major gap between the body plans of non-bilaterians and bilaterians Rieger first tried to make the gap as small as possible. On the basis of its existence in lower metazoans such as sponges and cnidarians, Rieger considered the biphasic life cycle with a microscopic ciliated larva and a macroscopic adult to be primitive for at least Eumetazoa (cnidarians + bilaterians). Moreover, on the level of the Eumetazoa Rieger also considered the adults to be primitively organized as colonies of polyps, such as may be found in anthozoan cnidarians. Starting with a body plan like this, a biphasic life cycle with a sessile macroscopical adult and a microscopical ciliated motile larva, the final step to the level of the Bilateria appears quite easy to achieve in Rieger's scheme. The ancestral colonial organization of the adult animal was retained to form a colony similar to those of ectoprocts or pterobranch hemichordates. The one major transformation would be the origin of a coelom in these animals. Not surprisingly, in line with ideas popular in the influential German school of evolutionary zoology, Rieger postulated the evolution of the coelom at the base of the Bilateria from the gastrovascular system of the cnidarian-grade polyps. He proposed that the origin of the coelom could be functionally explained by analogy with the functional morphology of colonial anthozoans and ectoprocts. Polyps in an anthozoan colony can be retracted and reversed at will. Pinching off a coelom from the gastrovascular cavity could lead to functional



dissociation of the process of zooid evagination from the function of the remainder of the gastrovascular space. Moreover, new ultrastructural data had shown a clear distinction between coelomate and non-coelomate organizations. However, rather than being two incompatible body architectures that could only be linked phylogenetically, Rieger recognized that a coelomate adult and non-coelomate larva could co-exist within a given biphasic bilaterian life cycle. This insight obviated a major problem of many previous theories that started with either a coelomate or a non-coelomate bilaterian ancestor, which by direct transformation had to give rise to descendants of fundamentally different body architecture. This often necessitated *ad hoc* explanations, for example for the reduction of coeloms in animals without any trace of them.

However, despite Rieger's important insight about the existence of two different types of body organization within a single life cycle of indirectly developing bilaterians, it still remains all too common in modern phylogenetic analyses of the Metazoa to code either the adult or the larval situation alone. The result is the postulation of linear evolutionary transformations between non-coelomate and coelomate organizations without even considering the possibility that heterochrony might be an equally or even more appropriate evolutionary mechanism to explain the diversity of bilaterian body architectures. By starting with an ancestral biphasic life cycle, Rieger could envisage within a single life cycle separate starting points for bilaterian evolution to follow along non-coelomate and coelomate lines, respectively. Using reasoning analogous to that explaining the reduction of coeloms in interstitial polychaetes on the basis of progenesis, Rieger proposed that the non-coelomate bilaterian phyla could be derived through progenesis from the non-coelomate larval form of Urbilateria, while the coelomate Bilateria could simultaneously radiate from individualized zooids of the ancestral colony. Thus Rieger's ingenious hypothesis at the same time explained the striking differences between larval and adult body organizations in the Bilateria, and the similarities between classic primary larvae and non-coelomate adults in terms of muscle systems, body cavities, excretory systems, *etc.*

In 1997, Rieger's papers inspired Thurston Lacalli to propose a different colonial theory, this time aimed at explaining the origin of the deuterostomes. Like Rieger, Lacalli is an expert on the ultrastructure of invertebrates, and he is especially recognized for his many meticulous studies of the ultrastructure of a wide variety of invertebrate larvae, in particular their nervous systems. The context in which Lacalli proposed his hypothesis for the origin of the deuterostomes was the beginning of a widespread reconceptualization of dorso-ventral body axis organization throughout the Bilateria that was initiated in the early 1990s by the discovery of a strikingly similar dorso-ventral patterning system that operates during the development of the insects and vertebrates. Lacalli simply extended Rieger's idea for a primitive colonial organization to the ancestor of the deuterostomes. Lacalli starts with a colonial organism that as an adult looks much like an anthozoan cnidarian, and which develops through a free-swimming planula-like larva with one opening to the gut. From this starting point a deuterostome-type of organization could result by the precocious budding of a zooid from the larva while it is still motile. Because the original larva and its budding sister-zooid share the same gut, but now with two instead of one opening to the outside, one of these openings could specialize as a mouth and one as an anus. Superficially this 'diplozoon'



would resemble something like a dipleurula larva, which is common in the life cycle of both echinoderms and enteropneusts.

However, Lacalli used this rather simple scenario only as a stepping stone for a much more elaborate and quite complex colonial theory. In the "stolon hypothesis," Lacalli (1999) used the pelagic colony-forming salps and pyrosomes as models from which to derive the more advanced chordates, *i.e.* the cephalochordates and vertebrates. Lacalli argues that the trunk-like reproductive stolons of salps, which are located roughly in the same place as the tails of ascidian larvae and the posterior trunk of vertebrates, could have been the evolutionary precursors of the tail and caudal trunk of advanced chordates. Specifically, the blastozooids forming alongside the stolon could act as morphological modules that could be independently moulded into new structures during evolution, such as vertebrate trunk somites. Although there is no space here to deal with the specifics of Lacalli's elegant and complex hypothesis, Lacalli explicitly recognized the importance of the colonial construction of salps with their modular blastozooids borne on a stolon as a source for evolving complex structures.

A final theory, which perhaps makes the ultimate heuristic use of colonial organization, was recently proposed by Ruth Ann Dewel (2000). Dewel is an expert on tardigrades, although her wide-ranging research ranges from arthropods to eukaryote phylogeny. In what is certainly the most entertaining, original, closely argued and elaborate scenario of the origin of the Bilateria that I know, Dewel integrates an impressive amount of morphological, fossil, and molecular evidence to support her thesis that Urbilateria was a macroscopic and morphologically complex animal with a well-defined head, trunk, and tail, and much internal complexity ranging from the presence of segments to a blood vascular system. The most striking aspect of Dewel's fantastic hypothesis is that the body of Urbilateria is derived from an entire colony of cnidarian-grade ancestors. The individuation of an entire colony at once creates a modular organism pregnant with evolutionary potential. Not surprisingly, Dewel argues that the modular construction of this versatile urbilaterian could be a partial explanation for the rapidity of the Cambrian diversification of bilaterians. Dewel's thesis is far too elaborate and complex to do justice to here, but I recommend all readers at least to read her enjoyable paper.

In this essay we have seen the great attraction of colonial organization for different theories that all attempt to explain the evolution of animal complexity. For Rieger, individual polyps or zooids could become independent from the colony to found the diverse lineages of coelomate bilaterians. Lacalli instead proposed that the fusion of two zooids provided the foundation for the evolution of the deuterostomes, or that entire pelagic urochordate colonies could become modified to form the single body of more advanced chordates. Finally, Dewel derived the body of Urbilateria from an entire colony of cnidarian-grade animals. Even if you consider these hypotheses as mere fantasy, they nevertheless deserve our attention and respect, for they are the brainchildren of some of our best and most daring thinkers, and the many issues they address are definitely worth pondering. At the very least, studying these works will allow us to appreciate ourselves better, as they reveal how our modes of thinking may affect our explanations of the evolutionary past.

However, we are missing a hypothesis that proposes the fusion of independent colonies to form one larger superstructure. Incidentally, the day on which I started to write this essay provides just such a fitting end. I started this essay on 4th July 2004, the day the United States of America celebrated its 228th birthday. On 4th July 1776, 13 colonies of the British Empire were officially united to become what is today the most powerful nation in the world. However, I finished this essay on 5th July, just before midnight, on the day that Ernst Mayr is celebrating his 100th birthday. Therefore, I dedicate this essay to Ernst Mayr, whose books I bought as an undergraduate, and who is therefore partly responsible for why I became a professional biologist.

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Palaeo-math 101: Regression 2

Last time we looked at a simple linear regression problem in descriptive morphology and found out that it wasn't so simple after all. In this essay I'd like to extend that analysis to consider the same problem from a slightly different angle in order to introduce another important consideration in designing such analyses, and another regression analysis method.

You will recall, our problem from the last issue was to characterise the relation between gross dimensions of the glabella for a suite of trilobite genera. Complications arose in choosing among the different ways deviations from the assumption of linearity could be calculated. Because, as is often the case with palaeontological data, no clear distinction could be drawn between glabellar length and width in terms of their dependency relations, we chose a model—the reduced major axis—that minimized the joint deviation of both variables from the model. So far so good. However, in order to determine the slope of the reduced major axis, we did something sneaky to the original length and width measurements. Something you might not have noticed, but something that changed the nature of these variables utterly and would not have been needed under the least-squares regression model. We standardized them. What is standardization? Why would you want to do it? When is it appropriate? And what effect does it have on regression analyses? Those are our questions for today.

Standardization is a procedure that allows us to compare quantitatively observations of different types. In effect, it's a technique statisticians use for comparing apples with oranges. Palaeontologists need to make such comparisons all the time. To illustrate this, let's consider an alternative variable in which the distinction between variable types is clear. Say we wanted to determine how the length of the glabella was related to its size and had decided to use area as a measure of glabellar size. Table 1 summarizes these data for our example set of trilobite genera.

The summary statistics at the bottom of the table reflect what's obvious after a moment's reflection. Even though the measures 'length' and 'area' are closely related, they are nevertheless variables of different kinds. In the table values this is expressed in the gross difference between the measurement ranges. The difference between the maximum and minimum length values covers a mere 17.74 units whereas the corresponding area range value is 304.71! This difference begs the question of whether 'length' and 'area' represent the same qualities, which they clearly do not. Glabellar length is measured in mm, whereas glabellar area is measured in mm². Because of this difference, I cannot easily construct a simple, consistently-scaled graph of both datasets because the scales along which the observations are arrayed are inherently different. This contrast between variable types renders direct comparisons between them difficult, even (as in this case) when the units associated with length and area exhibit a simple underlying unity.

Table 1. Trilobite Data

Genus	Length (mm)	Area (mm ²)
<i>Acaste</i>	5.10	23.61
<i>Balizoma</i>	4.60	17.40
<i>Calymene</i>	12.98	154.22
<i>Ceraurus</i>	7.90	51.22
<i>Cheirurus</i>	12.83	158.23
<i>Cybantyx</i>	16.41	270.65
<i>Cybeloides</i>	6.60	39.23
<i>Dalmanites</i>	10.00	67.40
<i>Delphion</i>	8.08	68.81
<i>Narroia</i>	15.67	127.67
<i>Ormathops</i>	4.53	14.85
<i>Phacopdina</i>	6.44	34.27
<i>Pricyclopyge</i>	21.53	250.70
<i>Ptychoparia</i>	12.82	109.40
<i>Rhenops</i>	22.27	319.56
<i>Sphaerexochus</i>	4.93	35.29
<i>Trimerus</i>	16.35	261.06
<i>Zachanthoides</i>	13.41	169.98
Minimum	4.53	14.85
Maximum	22.27	319.56
Range	17.74	304.71
Mean	11.25	120.75
Variance	32.16	9813.65
Standard Deviation	5.67	99.06

There are a number of ways to compensate for this difference and make the two variables more directly comparable. The easiest is to transform both variables so that they exhibit a common mean value. This has the effect of centring the distributions of observations on a joint, grand mean, the most convenient value for which is zero. Table 2 shows the data presented in Table 1 after mean centring, which is accomplished by subtracting the mean value of each variable from the observed value.

Table 2. Mean-Centred Trilobite Data

Genus	Length (mm)	Area (mm ²)
<i>Acaste</i>	-6.15	-97.14
<i>Balizoma</i>	-6.65	-103.35
<i>Calymene</i>	1.73	33.47
<i>Ceraurus</i>	-3.35	-69.53
<i>Cheirurus</i>	1.58	37.48
<i>Cybantyx</i>	5.16	149.90
<i>Cybeloides</i>	-4.65	-81.52
<i>Dalmanites</i>	-1.25	-53.35
<i>Delphion</i>	-3.17	-51.94
<i>Narroia</i>	4.42	6.92
<i>Ormathops</i>	-6.72	-105.90
<i>Phacopdina</i>	-4.81	-86.48
<i>Pricyclopyge</i>	10.28	129.95
<i>Ptychoparia</i>	1.57	-11.35
<i>Rhenops</i>	11.02	198.81
<i>Sphaerexochus</i>	-6.32	-85.46
<i>Trimerus</i>	5.10	140.31
<i>Zachanthoides</i>	2.16	49.23
Minimum	-6.72	-105.90
Maximum	11.02	198.81
Range	17.74	304.71
Mean	0.00	0.00
Variance	32.16	9813.65
Standard Deviation	5.67	99.06

Note this transformation makes it much easier to compare differences in the ranges of variables about their respective means, but leaves the range of the observations unchanged. However, there's still a problem. Because the nature of the differences between the variable types has also remained unchanged, we still can't easily portray both sets of observations on a single, consistently-scaled graph. In order to achieve true comparability we need to find some other, more standard way of describing the patterns of variation present in both variables.

The solution to our problem lies in a quantity called the *standard deviation*. Probably most of you have heard this term. Some may know that it can be calculated by taking the square-root of the sample or population variance. But what is standard about the standard deviation?

To understand the standard deviation we need to understand the variance, which is the average¹, squared deviation of all observations from the mean.

$$s^2 = \sum (x_i - \bar{X})^2 / (n - 1) \tag{1.1}$$

In this equation s^2 is the standard symbol for the sample variance, x_i is the i^{th} observation or measurement, \bar{X} is the sample mean, and n is the sample size. The sum of the squared deviations from the sample mean is used, rather than the more intuitively obvious sum of the deviations, because the quantity $\sum x_i - \bar{X}$ will always be 0.0 (see Table 2). Nevertheless, this sum still has a unit; and an odd unit at that. In our trilobite example, the variance of the length variable is expressed in the unit mm², and the variance of the area variable in the unit (mm²)²! Taking the square root of the variance returns these statistics to the units—or standard—of the original measurements.

$$s = \sqrt{\sum (x_i - \bar{X})^2 / (n - 1)} \tag{1.2}$$

Now for the trick that makes variables of fundamentally different types comparable. The significance of the standard deviation is that it tells you something about how your measurements are distributed about the mean. Because the magnitude of the standard deviation is related to the magnitude of the measurements, it's complex to assess the meaning of a standard deviation by itself. Regardless of this magnitude though, and regardless of the shape of the distribution, the manner in which the standard deviation is calculated ensures that at least 75.00 per cent of the observations will lie within two standard deviations of the mean, and 88.89 per cent will lie within three standard deviations. If the distribution of your observations follows the normal probability density function (= a normal distribution) these percentages rise to 95.46, and 99.73 respectively. So, in principle we can get an idea of whether glabellar length has a pattern of variability greater than, equal to, or less than glabellar area by comparing their standard deviations. Better still, we can use the standard deviation to scale the original measurements, thereby expressing both distributions, not in terms of their non-comparable original units (mm and mm²), but in terms of a common standard-deviation scale that is comparable directly for any set of variables, irrespective of their type or the character of their distribution. This operation is termed *standardization*, and the formula most often used to compute the standard normal form of a variable is:

$$z_i = (x_i - \bar{X}) / s \tag{1.3}$$

¹ For a sample this average is calculated by dividing the degrees of freedom ($n - 1$) into the sum of the squared deviations rather than the sample size, because the uncorrected average almost always underestimates the true population variance. See Gurland and Tripathi (1971) for discussion and an additional correction factor.

Table 3 shows the trilobite glabellar length and area data in their standardized form and Figure 1 compares the scatterplot of these raw (Table 1) and standardized data.

Table 3. Standardized Trilobite Data		
Genus	Length (mm)	Area (mm ²)
<i>Acaste</i>	-1.08	-0.98
<i>Balizoma</i>	-1.17	-1.04
<i>Calymene</i>	0.31	0.34
<i>Ceraurus</i>	-0.59	-0.70
<i>Cheirurus</i>	0.28	0.38
<i>Cybantyx</i>	0.91	1.51
<i>Cybeloides</i>	-0.82	-0.82
<i>Dalmanites</i>	-0.22	-0.54
<i>Delphion</i>	-0.56	-0.52
<i>Narroia</i>	0.78	0.07
<i>Ormathops</i>	-1.19	-1.07
<i>Phacopdina</i>	-0.85	-0.87
<i>Pricyclopyge</i>	1.81	1.31
<i>Ptychoparia</i>	0.28	-0.11
<i>Rhenops</i>	1.94	2.01
<i>Sphaerexochus</i>	-1.11	-0.86
<i>Trimerus</i>	0.90	1.42
<i>Zachanthoides</i>	0.38	0.50
Minimum	-1.19	-1.07
Maximum	1.94	2.01
Range	3.13	3.08
Mean	0.00	0.00
Variance	1.00	1.00
Standard Deviation	1.00	1.00

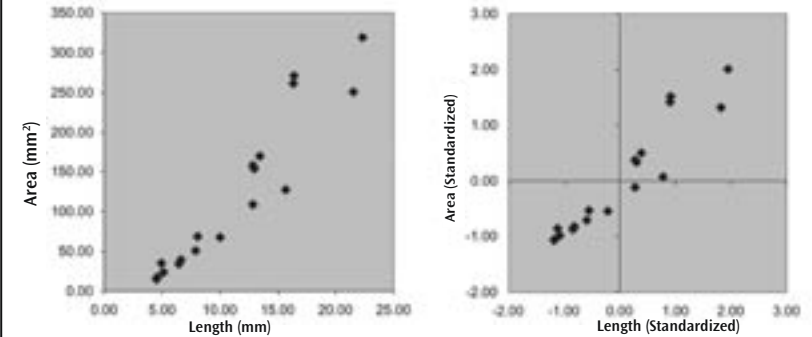


Figure 1. Scatterplots of raw (left) and standardized (right) trilobite glabellar data. Note how the standardization procedure shifts the placement and the scaling of the variables, but does not alter the positions of points relative to one another.

Where does this leave us in terms of our regression problem? As you'll recall from last time, reduced major axis (RMA) regression calculates the regression slope as the ratio of two standard deviations. This is equivalent to performing the analysis on standardized variables. Indeed, another name for RMA regression is standard major axis regression (Jolicouer 1975). From what I've said above you might have the impression that it's always best to standardize your data before analysis, in which case RMA regression would be a simple alternative to least-squares regression analysis. But recall that the example we used above for exploring standardization was a comparison between glabellar lengths and areas; two very different types of variables. In our example from last time, the variables were glabellar length and width, two variables whose distributions differ in terms of their means, variances, and standard deviations, but whose units are identical. In cases like this is it appropriate to standardize the variables and then use RMA to model their linear relationship? Or should they be left in their raw states, in which case another type of regression method will be needed?

The answer to this question is by no means straightforward, and disagreements between competent practitioners continue to surface every now and then in the technical literature. The advantage of standardization is that, through its application, non-comparable variables, or comparable variables with non-identical distributions, can be compared with the assurance that variable type and/or distributional differences are not influencing the result. The price paid for this assurance, though, is that one is no longer analyzing the variables that were measured, but a transformation of those variables in which differences in the scale and magnitude of the original observations have been, in effect, thrown away. When dealing with different types of variables this is not such a problem because it is unlikely that these qualities will be important to the comparison. After all, if one wanted to focus on issues like differences between the scale and magnitude of observations it would hardly be logical to reference those observations to variables whose scaling and magnitude are different intrinsically. In the case of variables that are measured in the same units, however, this idea of throwing away any information is troubling. Fortunately, an alternative regression method is available that allows users to minimize the joint deviation of observations from a linear model while, at the same time, preserving the flexibility to undertake their analysis on either standardized or unstandardized

variables. Unfortunately, discussions of this method are even less common than those of RMA regression. The method is called major axis (or principal axis) regression analysis.

Recall that RMA regression minimized the product of the deviations from the regression line across both the x and the y variables. This is geometrically equivalent to minimizing the area of a set of triangles in which the trace of the regression slope forms the hypotenuse (see Figure 4 from the Regression 1 essay). The triangle approach is a workable, but somewhat counterintuitive, minimization strategy that has the saving grace of being very simple to implement computationally, providing you are comfortable standardizing your variables. A more generalized approach would be to minimize the simple sum of the squared deviations of observed points from the model. This is geometrically equivalent to minimizing the squared deviations drawn perpendicular to the trace of the regression slope (Figure 2).

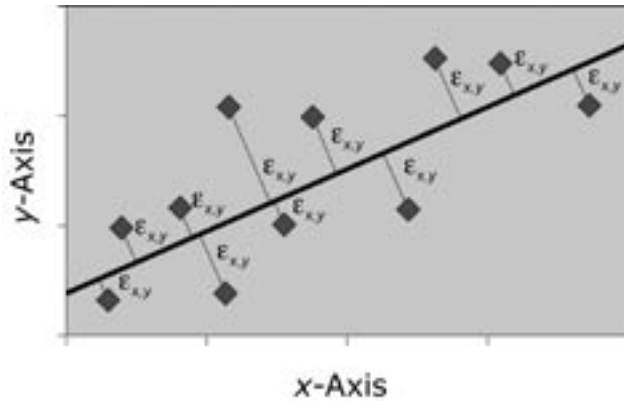


Figure 2. Geometric representation of the error-minimization model used by major axis regression analysis. In the actual calculations the sum of the squares of these distances is what is being minimized.

The line, passing through the bivariate centroid (\bar{X} , \bar{Y}), whose slope minimizes the sum of these perpendicular deviation lines across the entire dataset, represents not only an intuitively reasonable trendline, but arguably the trendline we instinctively try to estimate through qualitative—or ‘eyeball’—inspection.

Calculations involved in estimating the major axis slope of a bivariate dataset are more complicated than those for the reduced major axis, but the necessary equations can be programmed into Excel easily. The equations given below are for reference only. They are implemented for the example trilobite data from last time in the Regression 2 worksheet that can be downloaded from this column’s webpage at <<http://www.palaeomath101.html>>.

In order to understand the calculation better we need to deconstruct it into its parts. The first quantities needed are the variances of the two variables. These are most often calculated using an equation that is algebraically equivalent to equation 1.1, but more efficient computationally.

$$s^2 = \left(\sum x_i^2 - \left(\left(\sum x_i \right)^2 / n \right) \right) / (n - 1) \quad (1.4)$$

Next we need a single measure of the proportion of variance the two variables have in common, which is termed the *covariance*. Think of the variance as being a one-dimensional measure of the distribution of observations about the mean (e.g., Figure 1). The covariance is a two-dimensional measure of the spread of two variables around their joint mean (Figure 3).

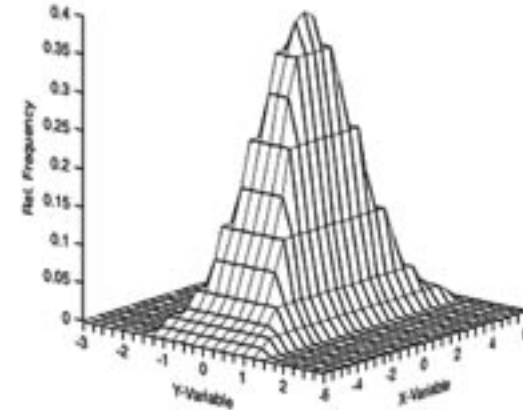


Figure 3. Joint probability distribution of two variables; x (mean = 0.0, std. deviation = 1.0) and y (mean = 0.0, std. deviation 0.5).

The covariance is calculated by first computing the sums of products for all paired observations.

$$s_{x,y} = \left(\sum x_i y_i - \left(\left(\sum x_i \right) \left(\sum y_i \right) / n \right) \right) / (n - 1) \quad (1.5)$$

Once these values have been found an intermediate quantity must be calculated as follows.

$$\lambda_i = 0.5 \left(s_x^2 + s_y^2 + \sqrt{(s_x^2 + s_y^2)^2 - 4(s_x^2 s_y^2 - s_{xy}^2)} \right) \quad (1.6)$$

Calculation of the major axis slope is then given by a simple equation:

$$b = s_{x,y} / (\lambda_i - s_y^2) \quad (1.7)$$

Once the major axis slope value is in hand, the y -intercept of a line with this slope passing through the bivariate centroid is calculated in the manner described in the previous essay. Once again, these are somewhat involved formulae, but a worksheet is available (1) to illustrate the calculations and (2) to enable you simply to copy your data into the example table, in which case the worksheet will calculate the major axis slope and intercept for you.

How does this method perform on our example trilobite data? Figure 4 summarizes the results obtained for four different regressions.

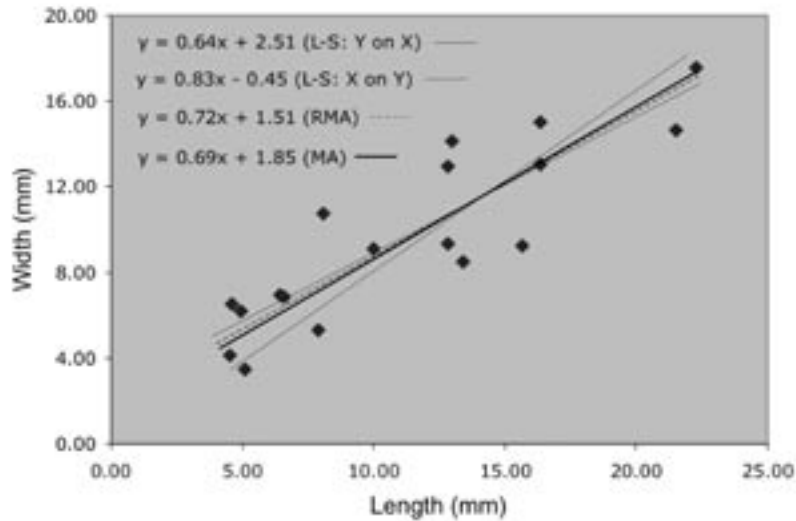
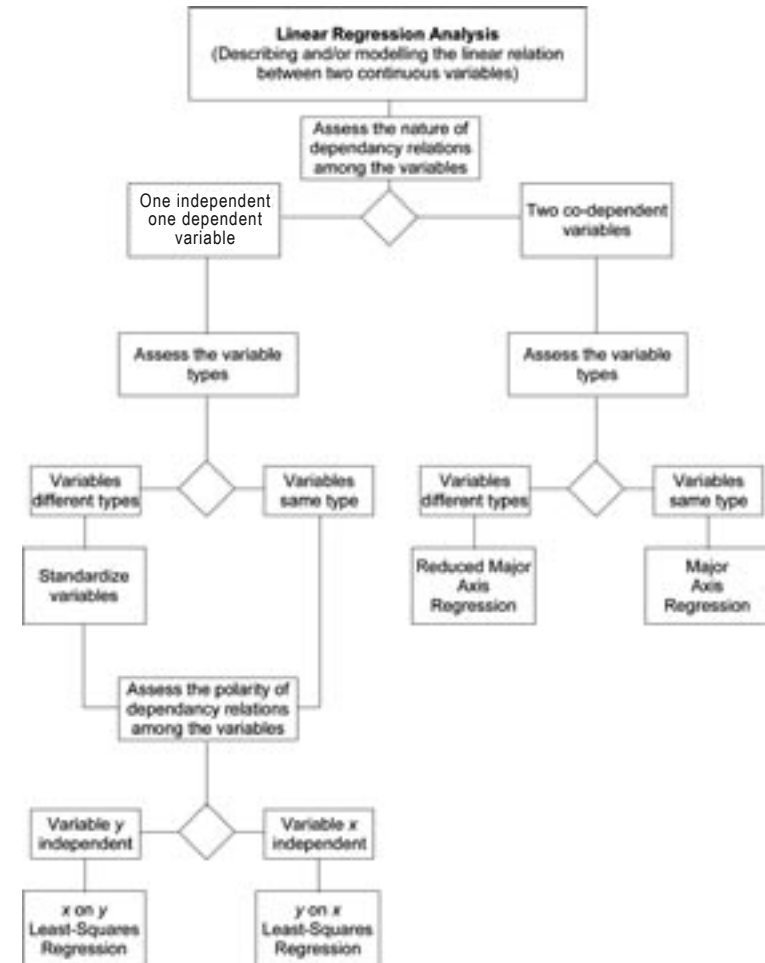


Figure 4. Alternative linear regression models for the trilobite glabella length and width data used to demonstrate reduced major axis regression.

The **y on x** and **x on y** least-squares regressions form an envelope within which the RMA and major axis (MA) models are contained. In data more symmetrically distributed about the linear trend, the RMA model usually bisects this envelope. The MA model exhibits a slightly lower slope than the RMA model because it is being ‘pulled’ in that direction by the greater variance associated with the length axis.

Which model is right? They all are. Each model minimizes a different aspect of variability about the linear trend. The answer to the more important question—“Which model is most appropriate for my data?”—depends, as always, on the goal of the analysis. If your goal is to estimate the magnitude of one variable based on the value of another (e.g., body weight based on body length) least-squares regression offers the best option because it minimises the estimation error. Alternatively, if you’re trying to quantify the pattern of linear covariation between gross dimensions measured in the same types of variables (e.g. linear distances between reference points), major axis regression would be the preferred choice because it (1) minimizes the joint deviations from the assumption of linearity in an intuitively reasonable manner and (2) takes differences in the scaling and magnitude between the variables into consideration. As for reduced major axis regression, I’d reserve this for situations in which you need to quantify the pattern of linear covariation between variables of intrinsically different types. Of course, these rules of thumb can be elaborated to cover a variety of situations. For example, what method would be most appropriate for estimating the magnitude of one variable based on the value of another when the two variables are of intrinsically different types? The following decision tree should help you make decisions regarding use of these models in your own work.



As I alluded to above, discussions of major axis regression are even rarer in statistical textbooks than discussions of reduced major axis regression. This is because the mathematics associated with major axis regression are necessarily bound up with the subject of eigenvalues—that ‘intermediate quantity’ we calculated in equation 1.6. This is one of the more complex concepts in linear algebra and one that is usually introduced in the context of matrix algebra. Sokal and Rohlf (1995) present the most complete discussion of the major axis approach in the context of regression of which I am aware. Davis (2002) mentions it under the name *principal axis regression* in his section on regression analysis, but refers the reader to his discussion of eigenvalues for computational details. Neither Swan and Sandilands (1995) nor Zar (1999) make any mention of major axis regression.

Readers' Comments

Since this column is intended to encourage discussion of quantitative data analysis topics, I'll try to include a discussion/response to at least some of the comments and questions received from readers. Two comments stood out from your responses to the first essay. The first, from Andy L.A. Johnson of the University of Derby, takes me to task for a mistake.

"One small correction for you to perhaps mention in your next piece: the critical 'slope' value which determines whether change in one variable is greater than that in the other is unity not 0.5 (see p. 30)."

Andy is correct. The sentence should read:

'Slope values of less than 1.0 (< 1.0) mean that a unit change in the x variable engenders a less than unit change in the y variable. Slope values greater than 1.0 (> 1.0) mean that a unit change in the x variable engenders a greater than unit change in the y variable.'

This has been corrected in the on-line version of the Regression 1 essay. The error was typographical, but nevertheless my responsibility. The slope 1.0 has a special significance in studies of allometry (the study of the biological consequences of size change) where it corresponds to the limiting condition of perfect geometric scaling, and is used to mark the interface between size/shape-change models that denote localized size changes that take place at a greater rate than overall size change (= positive allometry, $\beta > 1.0$) from those models that denote localized size changes that take place at a lesser rate than overall size change (= negative allometry, $\beta < 1.0$). In terms of ontogenetic allometry these models also have implications for morphogenic processes associated with the evolution of developmental programmes. We'll be returning to these topics in future essays.

Claire Pannell of The University of Glasgow also wrote in, with a warning about MS-Excel:

"I would like to add a cautionary note on the use of Excel for statistics as I believe that Excel is at best unreliable and at worst incorrect in many of its formulae calculations. Excel is a good spreadsheet tool but not a statistical package and its algorithms are often unstable. There have been many criticisms about Excel voiced by many statisticians, which have never been resolved by Microsoft."

Claire too is correct. Excel is not an adequate substitute for a generalized statistical software package, though, as we have seen, these are by no means complete in terms of their respective approaches to, say, regression models. Excel's problems appear to arise from some unfortunate choices in terms of the algorithms used to calculate various statistics. The problems are reasonably well known (e.g., statisticians delight in pointing them out), also exist in some dedicated statistical software packages (e.g., few packages implement Gurland and Tripathi's 1971 correction factor for unbiased estimation of the standard deviation), and tend only to become noticeable when the magnitude of the numbers one is analysing becomes very large. Like all software, Excel is a tool and, like all tools, there are jobs for which it is sensible and jobs for which it is not. My preference for using Excel as a basis for exploring the methods discussed stems not from any inherent love of Excel as a computation

platform (I much prefer *Mathematica*), but rather from the practical expectation that few people will run out and purchase dedicated computational/statistical software just to follow this column. Interestingly, Excel's well-known deficiencies have opened up the market for many third-party suppliers of statistical plug-ins, macros, virtual basic routines *etc.* designed to extend and correct the program's capabilities. Many of these are inexpensive ways to get high-quality stats capability on your computer. Sadly though, none includes the regression methods we have been discussing. Regardless, Excel's errors need to be watched out for, so Claire's advice is timely as well as correct. For those interested in learning more about what Excel can—and cannot—be expected to do, here are a few urls that will provide entry into this literature.

HELSEL, D.R. 2002. Is Microsoft Excel an adequate statistics package?

<<http://www.practicalstats.com/Pages/excelstats.html>>

GOLDWATER, E. 1999. Using Excel for statistical data analysis.

<<http://www-unix.oit.umass.edu/~evagold/excel.html>>

Pottel, H. 2002. Statistical flaws in Excel

<<http://www.mis.coventry.ac.uk/~nhunt/pottel.pdf>>

Excellent comments. Thanks to both Andy and Claire, and keep those e-mails coming.

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FURTHER READING

DAVIS, J.C. 2002. *Statistics and data analysis in geology* (third edition). John Wiley and Sons, New York. 638 pp.

GURLAND, J. and TRIPATHI, R.C. 1971. A simple approximation for unbiased estimation of the standard deviation. *American Statistician* **25**, 30–32.

JOLICOUER, P. 1975. Linear regressions in fishery research: Some comments. *Journal of the Canadian Fisheries Research Board* **32**, 1491–1494.

SOKAL, R.R. and ROHLF, F.J. 1995. *Biometry: the principles and practice of statistics in biological research* (third edition). W.H. Freeman, New York. 887 pp.

SWAN, A.R.H. and SANDILANDS, M. 1995. *Introduction to geological data analysis*. Blackwell Science, Oxford. 446 pp.

ZAR, J.H. 1999. *Biostatistical analysis*, Fourth Edition. Prentice Hall, Upper Saddle River, New Jersey. 663 pp.

Don't forget the PalaeoMath 101 web page at:

<<http://www.palass.org/pages/Palaeomath101.html>>



Correspondence with Correspondents

Rocks and the music of time

We must of course have sympathy with colleagues, including perhaps the members of the Stratigraphy Commission of the Geological Society of London, who struggle with difficult concepts and who, to judge by the poetic exposition of its Chairman (*Palaeontology Newsletter* 55, p.41), are more confused at the end than they were at the beginning. Happily, help is at hand.

For those readers of our Newsletter who may still feel unsure in their minds as to the differences between rock and time, between time (of which there is only one kind) and time-scales (of which there are many), between the chronology of events (geo- or any other) and the chronometry of their dates; between biostratigraphy and chronostratigraphy (palaeontologists: be particularly alert); between chronostratigraphy and standard chronostratigraphy and its scales; between primary and secondary standards and their units: there is a simple D-I-Y kit to be found in the *Proceedings of the Geologists' Association* of last year (114, 263-69), specially designed to meet these needs. It includes the references to the other two members of the kit, published by the Geological Society in the last ten years and seemingly unknown to its Stratigraphy Commission. It also includes a reference to Hedberg 1954, an illuminating report apparently also not looked at by the Commission, rather than to his much-vaunted publication of 1973. It does not include any reference to "time-rock" because the author had never heard of this before and has difficulty in trying to think what it could mean (- as opposed to "hard-rock", or "soft-rock", or "not-time-rock"?). Even less, "the stratigraphy of time", "simplified" or otherwise. It concludes by re-emphasizing the continuing need to pay attention to the meaning of words and rigorously to separate interpretation from observation, in geology as in any other branch of science—in geology, particularly the distinction between rock and time. And the good news is that provided we do this, it is all very simple.

Of course, in practice it often does not much matter whether we describe rocks in terms of their ages (Devonian Period) or their stratigraphical positions (Devonian System), for the context usually leaves no doubt as to what is meant. And so yes, we find them used interchangeably and nobody dead. And those who find the distinctions intellectually altogether too challenging may privately abolish them in their own personal use. But principles are principles, and I should warn its Chairman that attempts by the Stratigraphy Commission officially to codify its proposals formally to abolish our venerable standard chronostratigraphic geological column will serve only to make the edicts of that Commission look even more ridiculous than they are already, at least in the eyes of some of us. It all seems so unnecessary. The time would be better spent in sorting out some of those textbooks.

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Time: stolen or regained?

Dear Jan,

I enjoyed your essay, *Stealing Time*, and it got me thinking even harder about the time and time-rock issue. I have been able to resolve it to my satisfaction and I have come to the place where I think you are right on some matters (*e.g.*, no Upper January or Upper Silurian) but that perhaps you have missed an important point (the need for specific types of chronostratigraphic units). To me chronostratigraphy (delineating and correlating time surfaces and their enclosed units) is a valid stratigraphic methodology, just like lithostratigraphy, biostratigraphy and sequence stratigraphy *etc* are, and each stratigraphic methodology results in real, physical units specific to that methodology (*e.g.* formation for lithostratigraphy, sequence for sequence stratigraphy *etc*). We can go stand on the Jurassic System and the Jameson Bay Formation in the Sverdrup Basin and bang on each of them with our hammers. There is no doubt that the boundaries of chronostratigraphic units are more interpretive than say formations, but that does not detract from their "realness". It just makes their boundaries somewhat more uncertain and open to debate.

So what are the units of chronostratigraphy? A reasonable hierarchy of chronostratigraphic units including system, epoch and stage *etc* as well as a more general chronozone have all been defined and accepted by most. To me, as long as we accept chronostratigraphy as an acceptable stratigraphic methodology and go about recognizing such physical units in our stratigraphic successions, we will always need names for the chronostratigraphic units we delineate and map (and stand on). Of course the general unit names such as 'system' and 'stage' need modifiers to name a given chronostratigraphic unit specifically (*e.g.* a given stage). For lithostratigraphic units the convention is a geographic place name. For chronostratigraphic units the convention is that the time unit that corresponds to the chronostratigraphic unit is used as part of the name. Notably many workers (including myself) do the same for sequence stratigraphy. Because many major unconformities correspond reasonably closely (for historical reasons) to Age boundaries (*e.g.* base Rhaetian and base Hettangian), the dominant age of the sequence is sometimes used in the sequence name (*e.g.* Rhaetian sequence).

Now here is where you are spot on. When we name a chronostratigraphic unit, we use a combination of the unit type (System) and the appropriate time unit name (Cretaceous) giving us Cretaceous System as an acceptable chronostratigraphic unit name. The Cretaceous System that I map and hammer away on in my study area is not the abstract Cretaceous Period. So far so good. You have correctly pointed out that the terms 'upper' and 'lower' have no place in time unit names and, because it is the time unit names that are being included as part of the chronostratigraphic unit names, these terms have no place in chronostratigraphic names. This is where the illogical bust is. When one realizes that time unit names are being used as part of the chronostratigraphic unit names then it becomes clear that the modifiers 'Early' and 'Late' have to be used, and *not* 'Upper' and 'Lower'.



In summary, we need both time units and chronostratigraphic units, and they are completely different conceptual entities and have different unit names. Time unit names are used as part of chronostratigraphic names (as geographic names are for lithostratigraphic units) and thus we can have the 'Late Cretaceous Series' and the 'Early Albian Substage'. Terms such as 'Upper Cretaceous Series' and 'Lower Albian Substage' are not logical and, as you note, make as much sense as 'Upper January' and 'Lower Tuesday'.

Time unit names also can be used informally as modifiers of other unit descriptions. For example we can have a late Albian sandstone unit. Again the informal term 'upper Albian sandstone' is not acceptable even if the person meant to say the upper part of the Albian sandstone. Unit names and their modifiers are one thing and the relative position in them is another.

To me it is no big deal and totally logical that we can have a Rhaetian Age, a Rhaetian Stage, a Rhaetian sequence and a Rhaetian sandstone. Time units are fundamental and, although they may have been originally derived from stratigraphic studies, they can be applied to all geological disciplines. In stratigraphy they are simply used as part of, or modifiers of, formal and informal unit names for various types of stratigraphic units (chronostratigraphic unit, sequence unit, lithologic unit *etc.*).

I emphasize that I am most concerned about the usage of chronostratigraphy for layered rocks (sedimentary and volcanic) to which the law of superposition can be applied. The export of chronostratigraphy to non-layered rocks to me is not appropriate in part for the reasons you have mentioned, and chronostratigraphic units always have, and hopefully always will, refer to the depositional units (*i.e.* the buildup of the layered succession) and not subsequent to diagenetic modifications. That is how we derived the time scale in the first place through the law of superposition. Time terms can be applied to a diagenetic event, but this has nothing to do with the chronostratigraphic unit (*e.g.* an Early Jurassic cement in the Rhaetian Stage delineated at X locality).

I agree with you, therefore, that chronostratigraphy should be restricted to layered rocks in which we draw unit boundaries on the basis of interpreted time surfaces (of deposition). You can't do that with a non-superimposed layered rock. The use of time terms for non-layered rocks is best as an informal modifier (*i.e.* not part of the formal name which presumably uses a combination of lithology and a geographic name—Kalamazoo Granite). Thus we can have the Rhaetian Kalamazoo Granite although it is essential to discuss somewhere what part of the history of the formation of the granite that Rhaetian refers to. Perhaps it intrudes into the Late Norian X Formation and is overlain by the Hettangian Y Formation. I would again emphasize that the time term is not part of the formal name of the granite (or the X Formation for that matter) and that this is *not* a chronostratigraphic unit (a lithodemic one). To me the bottom line is that chronostratigraphic units are useful units for the stratigraphic analysis of a sedimentary basin (just as formations, sequences and biostratigraphic zones are) and they are not applicable to non-layered rocks. I hope we get a chance to discuss this further in Florence.



The bottom line is we need to retain the terms 'system', 'series', 'stage' because they are acceptable general unit types of an acceptable stratigraphic discipline. It is the modifiers 'lower' and 'upper' that have no place in stratigraphic unit names. 'Upper' and 'lower' of course can be used as a modifier when referring to the position in a given stratigraphic unit (*e.g.* upper part of the Late Cretaceous Series in the X Basin, the lower part of the Rhaetian sequence in the Y Basin, the lower part of the Late Cretaceous Frontier Formation at Cody Wyoming).

I'd be interested to hear what you have to say about the above, especially the need for chronostratigraphic units, which, unlike time units, are real physical units which one can map and have lunch on. The boundaries of your Arenig Series may not be the same as my boundaries for the Arenig Series in a given basin, resulting in two different Arenig Systems in the same basin despite the fact there is only one Arenig Epoch.

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Dear Jan,

Zalasiewicz *et al.* (2004; *Geology*, no. 1) and Jan Zalasiewicz in his recent thought-provoking text "Stealing time" propose dropping chronostratigraphic division and using only temporal scale/terms (geochronology). Although the concept of "dual usage" of geological time-related units may indeed lead to some confusion, nevertheless the rejection of the dual classification may cause serious problems. After having read your remarks and the paper "Stealing time" I still have objections as to dropping chronostratigraphic division and using only temporal scale/terms (geochronology) and thus avoiding "dual usage". I will try to present my objections as clearly as I can, although I realise that my English may not be perfect here,

I will further refer only to sedimentary rocks with which I am most familiar and which, I think, pose most practical problems with the dual usage.

From my perspective the most common confusion encountered in my editorial or reviewing work is when authors refer to purely temporal phenomena (such as "episodes of sedimentation") and use terms 'lower' and 'upper' (*e.g.* Upper Devonian depositional event, Lower Devonian basin development *etc.*). Also, some authors refer to the position of a rock unit in a section and at the same time use geochronological terms, *e.g.* they provide a lithological log "calibrated" with terms such as Early Devonian or Late Carboniferous, though it is more or less obvious they do not mean nor consider in fact the time when a particular rock was formed.

As far as I understand the idea behind the proposal by Jan Zalasiewicz and his colleagues, they would say that: in both cases temporal terms are OK, perhaps with a slight modification in the second instance (Early Devonian deposits, Late Carboniferous sediments). However, this 'slight modification' has important consequences as it adds a genetic aspect to the

term. I do not think—and I will return to this point a bit later—that we can simply neglect this consequence by saying that *e.g.* “by convention” we can assume that age of a rock is equal to the time of deposition. At this point, I would like to make an observation that an author/geologist may not want to go into any kind of genetic implications. In many cases of geological reports there is no need to refer to processes (such as sedimentation), and it is absolutely sufficient simply to refer to the position in the section and thus use the mixed “spatial-temporal” approach typical for chronostratigraphy applied to sedimentary rocks.

Furthermore, in many cases it may appear very difficult, or impossible, to infer unequivocally about the rock-forming processes or events. In my earlier comment I used the example of burial lithification of deep water carbonate oozes transforming (after, say, 10 million years) into chalk and then into dense hard limestone. Strictly speaking (and it is always better to be strict about what we mean in science) we cannot name the lithified Late Cretaceous coccolith ooze as a Late Cretaceous limestone unless we can prove that this particular compact limestone was formed before the Tertiary. The same problem occurs *e.g.* with clays vs. shales: again if we weight our words we cannot say (in Poland at least) that “shales are deposited” as they are a product of later—how much later?—diagenesis of clays or muds. If you are not convinced by my examples, please consider a secondary dolomite. One has usually no problem when placing such a rock in a stratigraphical column as *e.g.* Lower Carboniferous dolomite. But if we try to avoid the “dual approach” and use a temporal term then we may encounter serious problems. If we will say “Early Carboniferous” dolomite, this clearly implies (at least in Polish) deposition (or early replacement of calcareous sediment) during the Early Carboniferous (and thus probably early diagenetic) origin of this particular rock/sediment. However, after more careful study, it may in fact appear that we are dealing with a product of the Late Carboniferous burial replacement of an Early Carboniferous limestone. In this particular case we again need to have a reliable genetic interpretation to use a temporal term. Of course the same argument may be applied to dolomite, anhydrite or chert, which all may be late diagenetic rocks.

In other words: applying temporal terms to sedimentary rocks is always associated with a genetic context. Only sometimes the problem is trivial and further discussion may not be necessary, or it may quickly end with a statement that age of the rock that we see is more or less equal to the time of its deposition. However, there are situations (not uncommon, I think) when we have to undertake or refer to more or less sophisticated interpretations (the conclusions of which may not be that certain). But for a geologist it is not always necessary to have to (or not always in a position to) be involved in a genetic discussion of rock genesis or implications. Sometimes he or she needs simply to place a geological (physical) object in a stratigraphical column or to present mappable chronostratigraphic units (it is difficult to imagine a geological—though not *e.g.* a palaeogeographical—map with subdivisions such as Late Devonian or Early Triassic).

In the text by Jan Zalasiewicz and his colleagues you have a very useful distinction between a conceptual and a practical need for the dual terminology. My perception of both these needs is as follows:

- (1) *Conceptually* chronostratigraphy is different from geochronology as the first term is mixed time-rock, and refers to the relative position of rocks in a stratigraphic column; it is more empirical, and devoid of genetic burden, whereas the second one, by contrast, is purely temporal and is thus involved in genetic problems including the recognition (and dating) of rock-forming processes and events.
- (2) *Practically* the distinction is useful as it appeals to different needs in practical stratigraphic applications (as I have tried to show above). Using only a temporal (geochronological) approach would make our language poorer. We would get into trouble in cases when we are not interested in processes but simply in a statement about the relative position of rocks (as we see them now) against the geological time-scale.

What is, though, very valuable in the approach presented by Jan Zalasiewicz is that it draws attention to the complexity of temporal aspects of rocks. For me personally, the conclusion from these ideas about the pitfalls of “dual usage” is that when applying geochronological terms to rocks we have to be very careful and more strict. We should clearly define which rock-forming or rock-shaping event or process we have in mind. This may be not so obvious, and may indeed be very difficult sometimes, but it clearly deserves attention because it leads to better understanding of the temporal aspects of rock origin, of “absolute” ages of particular diagenetic or metamorphic events, of rates of the geological processes involved and so on. Therefore, I would foresee that this approach has a big future in forthcoming decades. Having said that, I would still argue that we also need the less interpretative chronostratigraphic approach (terminology).

P.S. As far as I understand Hedberg’s reply (cited in the Zalasiewicz paper) he is not denying (or even doubting) the “conceptual need for the dual time-scale.” He only sees no problem with replacing names of chronostratigraphic or geochronological units by the terms “rock” or “time,” respectively. This means (for me at least) that the distinction between time-rock units and time units is still useful for him and that only terminology may be “simplified” by dropping either ‘periods,’ ‘ages’ *etc.* or ‘systems,’ ‘stages’ *etc.* and replacing them by adding either the word “time” or “rocks”.

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Jan replies...

Is the Stratigraphy Commission (in bulk, so to speak) deeply confused and thus in need of deep sympathy? Speaking purely personally, I'm happy to accept all the sympathy that's going, and as to the charge of confusion about difficult concepts—well, guilty as charged, m'lud. A lifetime of uncertainty has always seemed to me an inevitable corollary to a career in geology, an occupational hazard, as it were. But one way to gain a little illumination—even if illusory—is simply, collectively, to try to think some things through a little. Fellow mortals and I on said Commission did, indeed, try to think through the relation between time and rock. Having come to some interim conclusions (Zalasiewicz *et al.*, 2004), we then, as Søren Jensen (2004) precisely noted, offered these *for discussion*.

The discussion duly arrived, detailed on the accompanying pages and elsewhere (Pratt, 2004; Bassett *et al.*, in press; Heckert *et al.*, in press; Gong *et al.*, in press; Zalasiewicz *et al.*, in press). It might be said to involve some principles of geology, but the questioning of principles is still, fortunately, permissible in science. Of course, if the principles survive the questioning they emerge strengthened, the stratigraphic column—in this case—safely grows more venerable, and the questioners then pick egg off their faces (this last activity falling within, I've always thought, the 'inevitable corollary' category also).

Was all this unnecessary? Well, the responses to our suggestions have spanned a gamut well beyond Dorothy Parker's A to B. It's obvious that there's a wide variety of opinion among geologists about the relations between time and rock, which either means that there are a lot of very misguided people out there, or that there is genuine room for discussion.

The discussion essentially encompasses two questions. Firstly, is there an absolute philosophical need for the dual classification of time, a logical necessity to have both Ordovician Period and Ordovician System? And secondly, even if this absolute need doesn't exist, does the dual classification nevertheless serve a purpose useful enough for it to be retained?

Now that the dust has settled a little from the shot and shell, here are a couple of interim conclusions. The answer to the first question is (I think) still no. We don't expressly need both Ordovician Period and Ordovician System. Just one of these will do. Nothing I've seen in the various critiques, John Callomon's toolkit included, has made (to me) a convincing case.

As an example (and to extend the discussion a little outside these pages) let's take Lucy Edward's pithily posed critique of our ideas (quoted, indeed headlined, in Pratt, 2004), that "1957 is a year. A 1957 Chevy is a car. Why should I say cars and years are the same?"

Of course they are not the same. A car is a car. A year is a year. A 1957 Chevy is a car, manufactured in the year 1957. That's all you need to say (just as a Silurian shale is a shale deposited in the Silurian Period). Modern historians don't need a timescale on the one hand, and a parallel Chevy-scale on the other. They would, though, try to fit collections of antique Chevys in chronological successions. They could also classify Chevys not simply by year of assembly but by engine size, colour or shape of chassis. They might even use Chevys to put

other cultural objects, such as jukeboxes or television sets, into a chronological context. And they would also realise that a particular Chevy had a history of design going back years, a chronology of the manufacture of components and their assembly; and a chronology of sale, use, resale, head-on collision, botched repair, further re-sale, brief re-use and final abandonment. They might well take the timing of assembly of components as reflecting any Chevy's 'age' (just as geologists, by convention, take the timing of deposition of sedimentary particles as reflecting the 'age' of strata) but they would be aware of the longer histories contained within each car.

To brass tacks. Marek Narkiewicz and Ashton Embry, in these pages, have provided admirably well-thought-out critiques of our idea that one relative time-scale will suffice for geologists. Food for thought, indeed. They mainly focused on the second point (the idea that the dual time-scale is useful in practice), and they both considered (Ashton more expressly) time-rock classification as being applied just to stratified rocks. To Marek, though, the usefulness of time-rock classification comes close to necessity, given the distinctions he wishes to make.

For instance, he proposes that a distinction should be retained between:

- a Late Cretaceous limestone, *i.e.* where the whole rock-forming event (*i.e.* the deposition plus the main phase of diagenesis) occurred in the Late Cretaceous; and
- an Upper Cretaceous limestone, *i.e.* one deposited some time in the Late Cretaceous time interval, but in which diagenesis (that is to form a rock from the sediment) might have taken place, say, in the Tertiary.

I'm not sure, that, at least in the UK, these distinctions are made in practice (or theory): particularly the concept that a limestone could "be" upper Cretaceous but not simultaneously late Cretaceous in age. Trying to make, or introduce, such a distinction here would, I think, almost certainly increase the amount of confusion concerning these terms, as the vast majority of geologists, in their everyday work, would not pick up the subtle difference implied. Further, in most limestones, diagenesis takes place as several phases, often over a long time interval (and with modification by recent weathering), and this diagenesis is often patchily distributed. So, to say that a limestone is 'Late Cretaceous' in the meaning above would always be an approximation.

However, these distinctions can easily be achieved simply by spelling out just *what* processes happened *when*. For instance, that deposition took place over a particular span of Late Cretaceous time, while episodes of diagenesis took place slightly later in the Late Cretaceous, and also in the Tertiary and Quaternary. The rock itself does not have to 'be' any particular age, but all the important events governing its composition and fabric can be simply and effectively placed within a single reference framework of time.

My interpretation of a Late Cretaceous limestone, for instance, or a Late Cretaceous shale, is that these rocks were deposited as sedimentary particles in the Late Cretaceous, and I (and incidentally Ashton Embry, too: see above) then take it as read that there will have been greater and lesser amounts of subsequent diagenesis (for rocks may be buried, but they certainly don't become geologically dead). This is convention in the UK, at least in the

circles where I've worked (though it may not be in Poland and some other countries, giving an international twist to the whole wider discussion). With dolomites and anhydrites, the amount of diagenesis has simply been greater rather than lesser. Showing them on a map and generalized vertical section, it would again be the depositional age (by this convention) that I would be referring to, while in any written account one can spell out, again with reference to a single time-scale, that deposition took place in the Late Cretaceous with subsequent diagenesis, say, in the early Palaeogene.

Ashton Embry also precisely found the nub of the argument, though from a slight different angle. He states essentially that there is a good case to be made for classifying sedimentary strata by their age, and that such a classification is as valid a methodology as any. He would now, though, take the fruits of this time-rock classification, the systems, series and so on, and qualify them as Early or Late, rather than Lower and Upper.

That latter point came as a rather unexpected angle to me (that confusion kicking in again, obviously) but it does, in that scenario, seem to make logical sense. Upper/Lower qualifiers are appropriate for lithostratigraphic units, but in an implied time classification depending on order of superposition, anything that's 'lower' must be therefore also 'earlier'.

But I'm not sure that the time-rock terms represent a methodology exactly. They do seem more to be temporal descriptors, and their definition and identification is the end result of the various methodologies (palaeontological, isotopic, palaeomagnetic and so on) applied to the rock successions as we attempt to correlate them. I guess that takes us back, yet again, to the irreducible question: would, in the long run, a unified system allow us to say the same things more simply, if not always more concisely, and (without the use of the time-rock shorthand to fall back upon automatically) in a more precise and considered fashion? I wonder—particularly as the pre-, syn- and post-depositional histories of strata are increasingly being considered in geological studies—whether the time-rock shorthand is an invitation to the kind of inevitable sloppiness that are the bane of an editor's life. The use of a unified system might—and I simply throw this out as an untested suggestion—encourage geologists to be more precise about what they are implying (and what they are not) about a rock as they are describing it.

There is also the point that strata, amazing palaeoenvironmental archives that they are, do not represent the whole of geology. There are also those igneous and metamorphic rocks: these do not submit at all easily to time-rock classification, though particular events which have shaped them can be sensibly placed within a relative time framework (and such rocks may even be considered to have golden spike potential: witness Euan Nisbet's 1982 suggestion that the cooling age of the Great Dyke of Zimbabwe be used to define the Archaean/Proterozoic boundary)

So one resultant stance might be to devise a scheme by which there was one primary and overarching time-scale (of time units) that everyone could use, and also to have an optional means of classifying strata by the time of their deposition for those geologists who found this helpful. A wish to retain chronostratigraphic (time-rock) units, as well as time units, seems here to depend upon the discipline studied by the geologist. Some geologists working on

strata find these a handy and pragmatic way of labelling those strata (though as a geologist working on strata myself, I'm curious as to whether the habit can be kicked). And for geologists working on metamorphic core complexes within orogenic belts, time-rock units are largely or wholly irrelevant.

The trick would be to leave a dual option open in such a way as not to clutter up the lives of those scientists who did not need to, or wish to, use and be confused by the time-rock classification. And that balancing act will need a wiser head than mine, certainly at this time of night. Perhaps some sort of half-sensible resolution might be dreamed up at the International Geological Congress meeting at Florence this year. Here's hoping for an end to confusion.

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Meeting REPORTS



Progressive Palaeontology 2004
Cardiff University 9 – 10 June 2004

Some 40 postgraduate palaeontologists attended the Progressive Palaeontology meeting held at Cardiff's School of Earth, Ocean and Planetary Sciences on the 9th and 10th of June. Professor Dianne Edwards, Head of School, welcomed our delegates and stressed the importance of our research not only for the palaeontological community but also for contributing to the present day global picture of changing ecologies and climates and for understanding the interaction of biology, geology and chemistry.

The first session of our varied programme, chaired by James Wheeley, began with **Lucy Wilson** who told us about how she is using optimal digestion theory to investigate the feeding ecologies of Burgess animals. Previously feeding strategies of Burgess animals have been elucidated from external functional morphology. **David Jones** followed with a description of morphometric analysis of the conodont apparatus, which will ultimately clarify the taxonomy of species and allow testing of evolutionary models. **Jessica Pollitt** then outlined her cladistic analysis into the systematics of the Trilobita, presenting a well resolved tree for the family Lichidae Hawle and Corda, 1847. We then moved on to vertebrates, and **Marc Jones** demonstrated the unexpected variation in skull evolution in the Rhynchocephalia, using Morphologika, a geometric morphometric programme for his investigations. To end the first session **Rosemary Stephens** gave us a detailed outline of her work on the palaeoclimatic, biogeographic and evolutionary significance of the conifer dominated flora collected from the Antarctic Peninsula. The flora is so well preserved that it will allow her to reconstruct CO₂ values for the Eocene.

After refreshments, our second session chaired by Susannah Moore kicked off with **Elizabeth Nunn** telling us more about high latitude late Jurassic and early Cretaceous climates which she will investigate with an array of geological data from localities in Northern Europe, Siberia and Svalbard by logging and macrofossil collection. We were then introduced to the systematics and phylogeny of *Stegosauria* by **Susannah Maidment**, who is reviewing known material to carry out a cladistic analysis to improve the understanding of interrelationships within this clade. **Susannah Moore** outlined her project on the perispore of fossil and extant pteridophytes, telling us more about problems in terminology for this outer spore wall layer, the fossil record of the perispore as well as latest findings on its chemical composition in extant spores. After this short excursion into the world of plants we returned to the dinosaurs with **Richard Butler** giving us new information on the ornithischian dinosaurs of the Elliot Formation of Southern Africa, which he gained from revising material of the NHM, London and various South African collections. The last talk of this session was presented by **Rachel Moore** on the taphonomy of new Silurian xiphosurans from Iowa and their implications for the phylogeny of the synziphosurines, a rarely understood stem-group of the xiphosurans. A buffet lunch for omnivores was attended by the group at a local pub in order to be revitalised for the afternoon.



Progressive Palaeontology delegates exploring the fossils of the High Tor Limestone (Carboniferous), Ogmore by Sea, South Wales. Photographer: Lucy Wilson (University of Cambridge, UK)

Susan Hammond chaired our third session, following lunch, that began with **Laura Braznell** talking on her taphonomic investigations of the Coseley Lagerstätte. Laura has identified a complex kaolinite–sulphide mineral preservation of late Carboniferous plants and animals in siderite concretions. **Robert Raine** then informed us on how he is deciphering the biostratigraphy of the Durness Group using conodont data that will give a much higher resolution for the ages of the different formations within the group. Continuing with conodonts, **Rosie Dhanda** spoke on the apparatus architecture of *Erismodus quadridactylus* and its implications for the evolution of the prioniodinids. To finish up the third session, **Erik Tetlie** told us about a new eurypterid fauna from Norway revealing a new species of *Eurpaterus* and a possible new species of *Pterygotus*. Erik then told us about the first parsimony analysis of eurypterids, recognising a number of monophyletic superfamilies and families.

Our final session chaired by Christian Baars started with **Alexander Page** entertaining us with the reproductive organs of graptolites, which according to his study are two-dimensional paddle-like appendages of hydrodynamic function. **David Hone** informed us about the comparison of two cladistic methods (Supertree and Total-Evidence methods) using basal Diapsids and the positions of the Prolacertiforms and Pterisaurus therein. Both methods need to be treated cautiously but on the other hand can give valuable results. **Nicholas Minter** then explained what one of the most diverse ichnofaunas in the world can tell us. New reports include fish and amphibian trails as well as insect jumping traces and full body imprints. Nicholas is planning more field work in New Mexico this Summer. **James Wheeley** told us about his plans to investigate the missing

molluscs phenomenon in the Silurian of the Prague Basin, funded by a Sylvester Bradley Award. Abstracts for all these talks can be found at <www.palass.org>.

The group then attended a reception at the National Museum and Galleries of Wales and was guided through the Evolution of Wales Exhibition by **Caroline Butler**, the museum's conservator. We finished off the day with a group meal at a local Italian.

The 10th turned into a sunny day after a cloudy start as we explored the fossiliferous Carboniferous, Triassic and Jurassic of the Glamorgan Heritage Coast at Ogmere by Sea, Southerndown and Bendrik Rock, Barry.

We are extremely grateful to our sponsors, namely: The Palaeontological Association, Blackwell's Earthpages (<www.earth-pages.com>), the Alden Group (<www.alden.co.uk>)—typesetters of *Palaeontology*, The Geology Department, National Museum and Galleries of Wales, Cardiff and the School of Earth, Ocean and Planetary Sciences, Cardiff University (<www.earth.cardiff.ac.uk>).

Susannah Moore, James Wheeley

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Progressive Palaeontology 2005 will take place at the Department of Geology, University of Leicester, UK, on 15–16 June. For further details contact the meeting organiser, David Jones, at <doj2@leicester.ac.uk>.

THE MYSTERY FOSSIL

Mystery Fossil Numbers Two to Four still remain a mystery.



Mystery Fossil Five comes from our very own Executive Officer, Tim Palmer. Tim took these pictures of a large vertebrate drag trace in Madagascar in 1984. The trace is on the surface of what appears to be an emergent carbonate mud bank, which also has dinosaur footprints. The sediments are certainly Middle Jurassic, probably Bajocian. Tim has no idea whether the mystery trace represents some sort of 'normal' behaviour of something dragging itself across the surface (turtle? other marine reptile?) or the 'abnormal' (injured) behaviour of something else. He thinks that the former is more likely as the trace is symmetrical. The kink at one end is where the beast swivelled and changed direction.


Take this opportunity of one-upmanship on the Association's Executive Officer. Explanations in an email to <c.little@earth.leeds.ac.uk>.




Cris Little

School of Earth Sciences, University of Leeds, UK
<c.little@earth.leeds.ac.uk>

>> **Future** Meetings of Other Bodies



32nd International Geological Congress
Firenze, Italy 22 – 28 August 2004



Computer techniques in the modelling and analysis of biological form, growth and evolution

This is the first of the general symposia planned in section G17 (Palaeontology) of the Congress, and will encompass the following five topics:

- Theoretical morphology of biological skeletons: This topic includes all techniques for generating and displaying models of biological skeletons. Different approaches will aim at modelling morphology alone, or at modelling the growth and constructional processes that govern skeletal morphology.
- Morphogenesis of colour, relief and structural patterns: Unlike the foregoing topic, which has long been the domain of palaeobiologists, this aspect has been largely studied by biologists. It deals with smaller-scale patterns on or within skeletal parts. Of special interest to palaeobiologists are the modelling of morphogenetic programmes producing surficial patterns on shells that grow by marginal accretion, and the modelling of the genesis of microstructures in these shells.
- Modelling of evolutionary processes: This is a little developed area of computerized modelling but one that has a high potential. It embraces all aspects of the modelling of evolution, and contributions integrating evolutionary and morphological modelling will be especially welcome.
- Computer-assisted statistical and morphometric techniques: This topic is concerned with applications of geometric morphometrics to problems in the analysis of shape-variation in organisms, though with particular emphasis on advances in Geometric Morphometrics in the spirit of Bookstein, Dryden, Kendall, Kent and Mardia.
- Computer-assisted imaging techniques applied to palaeobiology: This topic will embrace applications of results accruing from image-analytical aspects of morphometrics. Although connected to the foregoing topic, this field involves a different area of expertise.

The symposium will take place over half a day, and will consist of approximately six to eight oral contributions, some from invited speakers. A poster session in connection with the symposium is possible, and can be used to host contributions that cannot be accommodated in the oral part of the symposium.

Since the International Geological Congress is very large, funds will not be available to subsidise symposium organisers and invited speakers. However, a Geohost program will be available, mainly to help individual scientists from developing countries to help cover their attendance costs. Information on this will be available on the Congress website at <<http://www.32igc.org/home.htm>>. Contact the organizers for more information: Enrico Savazzi (Uppsala University <enrico.savazzi@pal.uu.se>) and Richard A. Reymont (Swedish Museum of Natural History <richard.reymont@pal.uu.se>).



Chemosynthetic communities through time (32nd IGC) Session T-18.4 at the International Geological Congress

The aim of this session is to gather together researchers interested in the evolution of chemosynthetic faunas, both microbial and macrofaunal. The convenors are Crispin Little <c.little@earth.leeds.ac.uk>, Roberto Barbieri <barbieri@geomin.unibo.it> and Kathy Campbell <ka.campbell@auckland.ac.nz>.

The session will have a half-day duration, and will include up to ten standard oral presentations (including invited presentations). Standard oral presentations have a 15 minute duration, including time for questions. Invited speakers include Crispin Little (Leeds University), Jack Farmer (Arizona State University), Lisa Levin (Scripps Institution of Oceanography), Antje Boetius (Alfred Wegener Institute for Polar and Marine Research) and Marco Taviani (Consiglio Nazionale delle Ricerche). Deadline for submission of abstracts and initial registration is 10th January 2004.

Through the generous sponsorship of NASA Astrobiology Institute the registration cost (€430) will be covered for up to six individuals whose submitted abstracts are selected by the convenors to give oral presentations. Costs will be reimbursed after the conference.

The second circular for the 32nd IGC is now available on the Web at <<http://www.32igc.org/home.htm>>. This lists registration details and deadlines for submission of abstracts and various payments for the Congress. The circular also has details of a post-congress fieldtrip P 07 – Fluid expulsion and authigenic carbonates in Miocene foredeep and satellite basins (northern Apennines) that may be of interest (see <http://www.32igc.org/circularN-field05_1.asp>). The Organizing Committee will help individual scientists mainly from developing and East-European Countries to attend the Congress by partially subsidizing their expenses via the GeoHost Program <<http://www.32igc.org/circular-gen07.htm>>.



Paleobiodiversity and major biotic changes in Earth History (Session G-17.3, International Geological Congress)


Palaeontological research on biodiversity has concentrated on global-scale patterns of diversity of taxa and of broad ecological groups, especially with respect to mass extinctions. However, biodiversity was originally defined to include all biological levels from genetics to ecosystems and landscapes. Here we invite papers that address any biodiversity level, or relationships between levels, with an emphasis on radiations and background trends through time.

Palaeontology provides historical perspectives from long-term patterns, and therefore complements studies of living biodiversity. After several decades of research however, there is still no satisfactory universal model for taxonomic biodiversity that integrates ongoing ('maintenance') and historical processes. Therefore we particularly encourage papers that identify problems which currently hinder our progress towards an integrated theory of biodiversity and suggest ways forward.

Papers may be based on any group(s) of organisms. Possible subjects include: measurement and analysis of biodiversity; development of open-access databases; sampling controls; phylogenetic constraints, including molecular vs palaeontological patterns; modelling (e.g. causal links


between earth system processes and life processes); methods for investigating controlling factors; problems of scale (e.g. relative importance of ecological, regional and global factors); roles and relative importance of tectonic, eustatic, climatic, oceanographic and biogeochemical factors; proxies for, and possible roles of, nutrients; Adaptive innovations, including role of symbioses.

For further information feel free to contact the conveners: Francesca Bosellini <frabos@unimore.it>, Gian Luigi Pillola <pillolag@unica.it>, or Brian Rosen <B.Rosen@nhm.ac.uk>.




10th Meeting of PhD students in Evolutionary Biology
 Preston Montford Field Centre, Shropshire, UK 29 August – 3 September 2004

The meeting will bring together PhD students from all over Europe to discuss current topics in evolutionary biology. Students are encouraged to present their research, which can be at any stage. The conference is open to 100 PhD students and registration has begun. Topic sessions will include: Palaeobiology, Experimental and Microbial Evolution, Population Genetics and Genomics, Phylogenetics, Coevolution, Life-history Evolution, Behavioural Ecology, and Ecology and Conservation. Please see our website <<http://students.bath.ac.uk/bspgh/>> or contact Jessica Pollitt <bspjrp@bath.ac.uk> for further details.




4th International Bioerosion Workshop (IBW-4)
 Prague, Czech Republic 30 August – 2 September 2004

The aim of the workshop series is to combine the knowledge of biologists (working mainly in reef ecosystems) with the experience of palaeontologists interested in bioerosion of all types of substrates (reefs and other calcareous matters, wood, bone, etc.). All participants should communicate their results or problems as talks, posters or presentations of specimens. The workshop will be held at the Czech National Museum in Prague. Several additional days of field trips are planned during and prior to the meeting (e.g., Devonian and Jurassic reef facies, Cretaceous and Miocene rockgrounds and hardgrounds, Miocene bored mollusc deposits, recent wood borings). For information please contact: Dr Radek Mikuláš, Institute of Geology, Czech Academy of Sciences, Rozvojová 135, CZ-165 00 Praha 6; e-mail <mikulas@gli.cas.cz>.



13th Symposium of Palaeontological Preparation and Conservation
 Leicester, UK 6 – 7 September 2004



52nd Symposium of Vertebrate Palaeontology and Comparative Anatomy
 Leicester, UK 8 – 11 September 2004

The SVPCA 52/SPPC 13 will be hosted by the University of Leicester and Leicester City Museums Service. As usual, the SVPCA will comprise three days of formal talks, poster sessions and

post-meeting activities, followed by a field trip. The SPPC will comprise a day of talks, and an afternoon of tours/demonstrations. Talks and poster sessions will be held in the Department of Geology, University of Leicester. Accommodation will be at the University Halls of Residence, located some 3.5 km from the main campus. Leicester is centrally located and easily accessible. There are direct and frequent rail services to and from London St Pancras, and international airports with good transport links include Nottingham East Midlands, Birmingham, and London Stansted.


Communications for this meeting will be online this year, and more information can be found on the websites. Booking and submission of presentation abstracts will be by online form. Booking is available from 1st June 2004 until 31st July 2004. (The deadline for submission of abstracts was 30th June 2004.) For further details please visit the meeting websites: SVPCA <<http://www.svpca.org/>>; SPPC <<http://www.preparator.org/>>, e-mail <leicester2004@svpca.org>, or write to SVPCA, Mark Evans, New Walk Museum, 53 New Walk, Leicester, LE1 7EA, United Kingdom.



2004 UK Evolutionary Developmental Biology Meeting
 Oxford, UK 13 September 2004


This year's meeting will be held at the Department of Zoology, University of Oxford, and the scheduled speakers are Detlev Arendt (EMBL, Germany), Michalis Averof (IMBB, Greece), Graham Budd (Uppsala, Sweden), Peter Holland (Zoology, Oxford), Jane Langdale (Plant Sciences, Oxford), Tim Littlewood (NHM, London) and Adam Wilkins (BioEssays). Registration and coffee will begin at 10am, talks 10:30–5:30. Lunch will be provided. £10 registration fee (pay at the door).

Please notify David Ferrier if you will be attending the meeting. Posters are welcome (please notify in advance if you will be bringing a poster). Enquiries to <david.ferrier@zoo.ox.ac.uk> or <peter.holland@zoo.ox.ac.uk>.



64th Annual Meeting of the Society of Vertebrate Paleontology
 Denver, Colorado, USA 3 – 4 November 2004

The Meeting will be held at the Adam's Mark, Denver, and the Denver Museum of Science and Nature. For further details visit the website: <<http://www.vertpaleo.org/meetings/>>.



Geoscience in a Changing World
 Colorado Convention Center, Denver, USA 7 – 10 November 2004

Details of the 2004 GSA Annual Meeting & Exhibition are on the conference website at <<http://www.geosciety.org/meetings/2004/>>.



Society of Integrative and Comparative Biology
San Diego, California 4 – 8 January 2005

See <<http://www.sicb.org/meetings/2005/index.php3>>. The following two items are part of this meeting.



Symposium on Terminal Addition, Segmentation, and the Evolution of Metazoan Body Plan Regionalization

Recent insights into the developmental basis of body plan specification provide a new perspective upon major patterns of Metazoan diversification. Terminal addition, a process by which the body of bilaterian animals grows at a posterior growth zone that is most clearly displayed in segmented animals, is a common condition found among disparate metazoan groups. Terminal addition is both a morphologic and a developmental phenomenon. Consequently, it can be examined through the study of development of modern organisms where molecular tools are available for the comparison of developmental process among taxa. The symposium aims to balance discussion of developmental mechanisms against historical evidence chronicled in the phylogenies of both living and fossil groups. We hope that it, and the resultant volume, will play a significant role in emphasizing the strengths of an integrated approach to the evolution of posterior body patterning. Sponsored by: SICB Divisions of Evolutionary Developmental Biology, Systematic Biology, Vertebrate Morphology and Invertebrate Zoology, the Paleontological Society and the Palaeontological Associations. Organizers: Nigel Hughes <nigel.hughes@ucr.edu> and David Jacobs <djacobs@ucla.edu>.



Evolution and Development of the Vertebrate Dentition

The programme includes the following speakers: Moya Smith (KCL, UK: *Developmental models for the origin of vertebrate dentitions*), Philip Donoghue (Bristol, UK: *Evolution and development of the skeleton in the earliest vertebrates*), Anne Huysseune (Ghent, Belgium: *Patterning of development in tooth replacement in osteichthyan dentitions*), Robert Reisz (Toronto, Canada: *Origin of dental occlusion in tetrapods, signals for terrestrial vertebrate evolution*), Tim Mitsiadis (KCL, UK: *Recovery of teeth in birds*), Renata Peterkova (Czech Republic: *Phylogenetic memory of developing mammalian dentition*), Todd Streebman (New Hampshire, USA: *Genetics and development of the cichlid dentition*), Ken Weiss (Penn State, USA: *Evolutionary genetics of dental development*), Paul Sharpe (KCL, UK: *Development and evolution of dental pattern*), and Jukka Jernvall (Helsinki, Finland: *Mammalian dental diversity*). Sponsored by SICB Divisions of Evolutionary and Developmental Biology, Vertebrate Morphology, Cell Biology, and Systematic and Evolutionary Biology (primary). Organizer: Moya Smith <moya.smith@kcl.ac.uk>.



4th International School on Planktonic Foraminifera: Oligocene to Middle Miocene Planktonic Foraminifera
Perugia, Italy 14 – 18 February 2005

The course will include lectures (taxonomy, biostratigraphy and palaeoceanography) on Oligocene to Middle Miocene Planktonic Foraminifera and practical sessions studying washed assemblages. For further details, please contact Dr Roberto Rettori, Dipartimento di Scienze della Terra, Piazza Università, 1, I-06100 Perugia, Italy <rrettori@unipg.it>, tel 00390755852664, fax 00390755852603, website <<http://www.unipg.it/~denz/>>.



Geologic problem solving with microfossils
Rice University, Houston, Texas, USA. 6 – 11 March 2005

The aim of the meeting is to draw together a diverse array of geoscientists to showcase the problem-solving power of microfossils in a variety of geologic settings. Call for abstracts via the website from 1st April to 14th October 2004. Registration begins 6th September 2004, via the website. For further details visit the conference website at <<http://www.sepm.org/microfossils2005.htm>>, or contact <garry.jones@unocal.com>.



Tracking Dinosaur Origins: the Triassic/Jurassic terrestrial transition
Dixie State College of Utah, St. George, Utah 22 – 24 March 2005

(Followed by the Utah Friends of Paleontology Annual Meeting, 25–26 March). The Triassic/Jurassic transition is a critical time in Earth history, recording the origins and early radiation of dinosaurs, pterosaurs, crocodylians, mammals, and several other significant Mesozoic vertebrate clades. Additionally, a major interval of faunal stepwise extinction is recorded in both the marine and terrestrial environments that may be linked to impact events, setting the stage for the ascendance of dinosaurs to a position of dominance for the remainder of the Mesozoic. Current research in this area is dynamic, with important implications for a number of areas in palaeobiology and geology. A number of recently discovered fossil localities in a little researched area of southwestern Utah preserves a thick sequence of rocks spanning the Triassic/Jurassic interval. These localities are proving to be a catalyst for new studies on this time period. Many of these studies have centered on the basal Jurassic St. George Dinosaur Tracksite at Johnson Farm. This remarkable new site preserves an extraordinary series of track levels along the margin of a Hettangian lake ("Lake Dixie"); associated fossil plants, invertebrates, fish, and dinosaur remains make it particularly significant. These discoveries, along with a new interpretive centre slated to open in the Summer of 2004, provide an impetus to bring scientists together to discuss terrestrial faunas across the Triassic/Jurassic transition in a dramatic geologic setting unfamiliar to most attendees. A proceedings volume to be published by the New Mexico Museum of Natural History and Science, and a full colour overview volume, are planned by the Utah Geological Survey for initial



distribution to attendees at the conference. This volume will include short review papers on areas of critical interest regarding the Triassic/Jurassic terrestrial transition in various areas of the world, summary papers on these rocks, and their preserved fossils in southwestern Utah. Preliminary programme: March 22 – plenary papers; 23 – general conference papers; 24 – field trip: Triassic/Jurassic geology and palaeontology in the St. George and Zion National Park areas. Conference participants may fly into St. George, Utah directly, or speakers may fly into Las Vegas, Nevada and then be transported by volunteers to St. George. Conference participants are invited to remain for the Utah Friends of Paleontology Annual Meeting, which will include additional afternoon field trips on March 25 and 26. Information on the St. George tracksite may be viewed starting on page 4 of Survey Notes v. 34, no. 5, at <<http://geology.utah.gov/surveynotes/snt34-3.pdf>>.



10th Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics (CAVEPS)

Naracoorte Caves World Heritage Area, South Australia 29 March – 2 April 2005

The 10th CAVEPS will be held at the World Heritage listed Naracoorte Caves National Park and nearby Naracoorte township, approximately 360 km SE of Adelaide (capital city of South Australia), in the Limestone Coast region of South Australia. The Limestone Coast is well known for its Pleistocene vertebrate sites, with the most significant of these within the Naracoorte Caves World Heritage Area (serial nomination with Riversleigh, Queensland). The region is also famous for its high quality wine, wetlands and significant karst and geological features. CAVEPS is a biennial meeting of vertebrate palaeontologists from around Australia and overseas. CAVEPS 2005 will consist of three days of general sessions including papers on all aspects of vertebrate palaeontology, culminating in a two-day symposium which will focus on Quaternary extinctions and dating applications. Included in the general sessions will be a special session on cave palaeontology which will be held in the historic Blanche Cave. In addition to the main sessions, a student forum is also proposed where students can present their project proposals or work in progress and benefit from professional input. The conference will be held during the AVCC (Australian Vice Chancellors Commission) common vacation week and will commence on Tuesday 29th March (Monday 28th is Easter Monday), and culminate on Saturday 2nd April. For further details: <<http://www.environment.sa.gov.au/parks/naracoorte/events.html>>, contact Liz Reed <liz.reed@flinders.edu.au> or Steven Bourne <Bourne.Steven@saugov.sa.gov.au>, or write to CAVEPS 2005 c/- Naracoorte Caves National Park, PO Box 134, Naracoorte South Australia 5271, Australia.



Devonian vertebrates of the continental margins, IGCP 491 meeting

Yerevan, Armenia 22 – 27 May 2005

The meeting will be dealing with all aspects of taxonomy, biostratigraphy, palaeoecology and biogeography of early vertebrates as listed in the scopes of IGCP 491: “Middle Palaeozoic Vertebrate Biogeography, Palaeogeography and Climate”. Special focus will be on the neritic



to hemipelagic vertebrate faunas of the Middle to Upper Devonian on the northern edge of Gondwana and their relationships to contemporaneous faunas of Laurasia and the rest of Gondwana. IGCP 491 business meeting and a post-conference field trip to Armenian Devonian –Carboniferous sites are also planned. The meeting will be hosted by the Institute of Geological Sciences, National Academy of Sciences, Marshall Baghramian Ave., Yerevan, Armenia on 22–27 May 2005. The scientific sessions are planned for 23–25 May. A post-conference field trip in two days is proposed, on 26–27 May, to visit four Upper Devonian–Lower Carboniferous sections (Erdich and Noravank in the east of Armenia; Sevakavan and Khor Virap in the west). The approximate cost for the field trip is about US\$70. For further details, please contact the organisers, Dr Araik Grigoryan (Institute of Geological Sciences, Armenia), Dr Michal Ginter (University of Warsaw, Poland) <fiszbit@uw.edu.pl>, or Vachik Hairapetian (Islamic Azad University, Iran) <vachik@khuisf.ac.ir>, <vh_hai@yahoo.com>.



TAPHOS-05

Barcelona, Spain 16 – 18 June 2005

The Facultat de Geologia of the Universitat de Barcelona and the Museu de la Ciència (Fundació La Caixa) are pleased to announce the celebration of the 4ª Reunión de Tafonomía y Fossilización / 2nd International Meeting TAPHOS-05 that will take place in Barcelona between June 16th and 18th, 2005. The Reunión de Tafonomía y Fossilización will be celebrated for its fourth time, after the success of previous meetings in Madrid (1990), Zaragoza (1996) and Valencia (2002). The growing number of participants in previous meetings and their variety of countries of origin show the increasing interest in this science and its utility in very different fields. The aim is to provide a periodically updated vision of the state of knowledge on the topic, which is achieved in two parallel ways: invited lectures by outstanding researchers and poster/oral contributions by the rest of participants. In this meeting it is planned to give a great weight to participants' contributions through the organization of topic sessions coordinated by a specialist in the topic. Young researchers working in or having finished their Ph.D. concerning taphonomic aspects are particularly encouraged to participate. To register for circulars concerning this meeting send an email to <rosa.domenech@ub.edu> with the message 'preinscription Taphos05' in the 'subject' field of the email and including your name and complete postal address. Otherwise, further information on the meeting can be obtained by contacting the meeting secretary, Rosa Domènech <rosa.domenech@ub.edu>.



American Association of Petroleum Geologists Annual Convention

Calgary, Canada 19 – 22 June 2005

At this meeting, the North American Micropaleontology Section of SEPM (NAMS) will sponsor a poster session on the 'Integration of Micropaleontology and Petroleum Exploration.' This session falls within AAPG Meeting Theme 5: 'Depositional Systems in Time and Space.' The NAMS session will be co-chaired by Dave McNeil (Geological Survey of Canada, Calgary) and Pete McLaughlin



(Delaware Geological Survey/University of Delaware, NAMS President), who extend an open invitation to micropalaeontologists to submit an Abstract for consideration and come to Calgary to attend this major international conference. Our AAPG 2005 session topic was chosen so that virtually any aspect of micropalaeontology within any hydrocarbon basin from around the world could be included. The deadline for Abstract submission is 12th November 2004. We encourage you to present your data and interpretations, which we feel are important to understanding 'Depositional Systems in Time and Space.' Please note that last-day traffic for submissions is heavy and can cause 'gridlock.' If at all possible, don't procrastinate—submit before the last day! Visit the meeting website for further details, at <<http://www.aapg.org/calgary/index.cfm>>



North American Paleontological Convention

Dalhousie University, Halifax, Nova Scotia, Canada 19 – 26 June 2005

The meeting will include field trips to Horton Bluff (Dev/Carb boundary—early tetrapod trackways), Wassen's Bluff (Tri/Jur—link fossil between dinosaurs and mammals), Joggins (Carboniferous—world heritage site), and Arisaig (a world class Silurian invertebrate site). Major field trips will include the Gaspé Peninsula (Quebec).

The local organizer is David B. Scott (Centre for Environmental and Marine Geology, Dalhousie University, Halifax, Nova Scotia B3H3J5 Canada).

The meeting website is at <<http://www.dal.ca/~es/staff/dbscott/scott.htm>>.



Fourth International Symposium on the Cambrian System

Nanjing, China 18 – 24 August 2005

More than thirteen years after the successful *Third International Symposium on the Cambrian System* in Novosibirsk, former Soviet Union (1990), the time has come to focus on a new target and to create a platform for all scientists working on the Cambrian to meet and calibrate their information. This meeting will accumulate not only the most influential colleagues but create the intellectual guidelines for the next decades. The symposium will focus on (i) meetings to discuss latest research findings relating to the System, especially in the global context, (ii) discussions and workshops of the IUGS Subcommittee of Cambrian Stratigraphy and related geosciences, and (iii) field trips to examine the best exposed Cambrian rocks in China and South Korea. Further details can be found on the symposium website at <<http://www.nigpas.ac.cn/cambrian-conference.htm>>.



6th Baltic Stratigraphic Conference

St. Petersburg, Russia 22 – 26 August 2005

The Conference will be held at the A.P.Karpinsky All-Russian Geological Research Institute (Sredniy prospect 74) and St. Petersburg University (Universitetskaya nab. 7/9 and 16 Liniya 29). The scientific sessions and workshops are planned on 23–25 August. Pre-conference field trips (Lower Paleozoic and Carboniferous) will take place on 19–21 August, post-conference field trip (Devonian) on 26–28 August. In parallel with the scientific session, a business meeting of the ICGP 491 Project 'Middle Palaeozoic Vertebrate Biogeography, Palaeogeography' will be held. The main issue of the Conference will be every kind of problem relating to the sedimentary basin stratigraphy of Baltic and neighbouring regions. The number of sessions and topics of symposia could be specified according to the preferences of registered participants. Participants are invited to submit abstracts of both oral and poster presentations that will be published in a special issue. For further details please contact Andrey Zhuravlev <stratigr@mail.wplus.net> or Alexander Ivanov <aoi@AI1205.spb.edu>.



15th International Symposium on Ostracoda

Berlin, Germany 12 – 15 September 2005

The First Circular can be downloaded from the symposium website <<http://www.palaeo.de/iso15>>. The deadline for pre-registration is 31st July 2004. We will offer a number of field trips with various contents (stratigraphically and ecologically), each also including an extensive touristic and cultural program. Please have a look at our website at regular intervals <<http://www.palaeo.de/iso15>>. We are perpetually updating and extending these pages, in order to inform you about congress, programme, excursions, accommodation possibilities *etc.* to be as complete and up-to-date as possible.



9th Symposium on Mesozoic Terrestrial Ecosystems

Manchester, UK July 2006

The 9th Symposium on Mesozoic Terrestrial Ecosystems (sponsored by the Palaeontological Association) will take place at the University of Manchester in July 2006. The scientific programme will run over three days, with a short pre-conference field trip to Lower Cretaceous localities on the Isle of Wight, and a longer post-conference field trip to explore the Mesozoic succession of southern England. Preliminary enquiries can be made to <ucgasue@ucl.ac.uk>.

Please help us to help you! Send announcements of forthcoming meetings to <newsletter@palass.org>.

Sylvester-Bradley AWARDS 2003–4

This year the Association received 27 applications for Sylvester-Bradley Awards requesting a total of £23,821.33. Once again the Association was impressed by the high standard shown in the applications, and appreciated the diversity of projects submitted.

Applications originated from researchers currently based in six countries including the United Kingdom (18), Canada (3), Iran (2), Norway (1), United States of America (1) and Russia (1), and represented different levels of palaeontological experience ranging from current Masters (4) and PhD students (15), post-doctoral scientists (2), museum-based researchers (2), university-based researchers (2) and retired palaeontologists (1).

After evaluation by a body of four palaeontologists selected from different fields within palaeontology, 12 Sylvester-Bradley Awards have been made this year with a total value of £9,310.00. Financially this represents approximately 39% of the total amount requested and represents 44% percent of applications being successful. The demographic breakdown of the awards includes two Masters and six PhD students, one post-doctoral scientist, two museum-based researchers and one university-based researcher.

The following Awards have been made:

- *Joseph Botting* (Cambridge University, UK). Exploratory investigation of Arenig (Lower Ordovician) echinoderms and sponges near Zagora, Morocco.
- *Laura Jane Braznell* (University of Birmingham, UK). Modes of Exceptional Preservation in the Mazon Creek Lagerstätte.
- *Mansooreh Ghobadipour* (University of Esfahan, Iran). Early Ordovician Thysanotos brachiopod assemblage and associated trilobites from north-central Iran.
- *Tom Harvey* (University of Bristol, UK). The cuticular ultrastructure and systematics of palaeoscolecsids.
- *Tai Kubo* (University of Bristol, UK). Limb posture of basal archosaurs.
- *Randall F. Miller* (New Brunswick Museum, Canada). A study of Early Devonian pterygotid eurypterids of eastern Canada and Scotland.
- *Jason Moore* (University of Cambridge, UK). Biodiversity into the fourth dimension—Calculating percentage abundance in vertebrate palaeoecosystems.
- *Elizabeth Nunn* (University of Plymouth, UK). High Latitude Cretaceous Climates.
- *Leonid Popov* (National Museums and Galleries of Wales, UK). Middle to Late Ordovician brachiopods of Central Kazakhstan, biofacies analysis and biogeographical significance.
- *Jessica R. Pollitt* (University of Bath, UK). The Phylogeny of the Corynexochida.
- *Seyed Naser Raisosadat* (Birjand University, Iran). Isotope signature of early Cretaceous belemnites from the Kopet Dagh Basin (Iran): A record for a low latitudinal Aptian-Albian succession.
- *James R. Wheeley* (Cardiff University, UK). Bohemian bivalves: a taphonomic investigation.

We wish every success to those undertaking projects this year, and look forward to hearing about them in future issues of the *Palaeontology Newsletter*.

Sylvester-Bradley REPORTS

Ordovician sponges, echinoderms and oddities of Morocco

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Moroccan fieldwork is an experience to remember. On the one hand, there is the spectacular scenery, extraordinary exposure and singularly worthwhile fossils, and on the other there's the fossil dealer network. Mercifully for me, most of the logistics were organised by Morocco veteran Peter van Roy (University of Ghent), who led the expedition; the other members were Thijs Vandembroucke, Dirk and Kay van Damme, and two all-terrain Fiat Unos (Fig. 1). The trip was based in Zāgora, in the Anti-Atlas, and working primarily in the Vallé du Draa, where outcrops of the 2 km-thick, Tremadoc-Arenig Fezouata Shale occur over several hundred square kilometres.



Figure 1. Typical exposure and scenery, at a site dominated by a large dendroid graptolite, 10 km northeast of Zāgora. The distant mountains show the rest of the Ordovician above the Fezouata Formation.

The most frustrating aspect of Moroccan fieldwork is that you have to accept that the commercial network is in control. They have a large number of agents, who scour the desert for sites, and they are fed in turn by the nomads and desert villagers, who are continually searching

for fossils to supplement their income from goat herding. Some of the agents are reputable and helpful, particularly higher in the hierarchy; others can be highly obstructive. But that's the way it is, and given that the entire economy of places like Erfoud is based on the fossil and mineral industry, it is unlikely to change soon. When the less helpful agents produce fossils for you to examine, they are adept at spotting even involuntary signs of interest; at that point, the price will rocket, and the locality will become secret. For a fee (trivial or extortionate), they will show you some localities, but you can never be certain that they are not showing you poor sites in the same general area as the true locality. With this in mind, and appreciating the vast area of desert that needs to be searched, the approach is normally to obtain as much information as possible from the agents, and then explore the surrounding square kilometres for variations and signs of previous workings. The desert is public land, so there are no issues with access, or permission to collect. Gradually, it is possible to build up an idea of the sedimentological and palaeontological variations in the Formation, which helps to refine the search process further.

The Fezouata shale is divided into Upper and Lower units, with the Upper much more widely exposed. The Lower F. S. is a pale blue siltstone that yields locally abundant *Rhabdinopora* spp. with occasional shelly fossils. Nothing of particular note was recovered, although it is likely that much remains to be found. The Upper F. S. is rather different. The basic lithology is a homogeneous green mudstone to siltstone, gradually coarsening upwards to fine-medium sand in the upper Middle Arenig. Throughout the sequence are thin (up to 50 cm) bands of dark limestone with cone-in-cone structures and peculiar, abundant faunas. Thirty centimetre-long asaphid trilobites are common, sometimes near-complete, and in the central part of the sequence, where the limestones are most abundant, there are frequent complete specimens of *Clonograptus*, also up to 30 cm diameter. The remainder of the fauna varies according to which precise band you examine, but normally consists of a very dense accumulation of one or more of the following: small bivalves, gastropods, articulate brachiopods, phosphatic brachiopods (acrotretids?), trilobites, edriasteroids (*Pyrgocystis*) or diploporite cystoids. *Pyrgocystis* is a very rare, columnar edriasteroid; they were collected on only one small slab that, ridiculously, preserves over a hundred specimens.

The siltstones yield the most interesting material, however, from what appear to be three-dimensional annelids (alas, no setae), to Peter van Roy's cheloniellids (see his abstract, PalAss 2003). Preservation of these soft-tissue traces (and other possible examples, but sadly nothing truly conclusive) is as iron minerals, with at least some relief, and may result from early pyritisation. There is also locally abundant articulated material of fragile skeletons, including echinoderms and sponges.

Echinoderms

Alas, no definite crinoids. I am unreliably told that Arenig crinoids exist in the area, but no one was willing to show me where. However, we uncovered a total of perhaps fifteen species of cystoids and asterozoans, from several localities, and some are very peculiar indeed. The bulk of the material is still in transit, but among the highlights are a ?cystoid theca with triradial symmetry, a large villebrunasterid somasteroid, and an unidentified asteroid(?) with some possibly somasteroid characteristics. Carpoids also fall out of the rocks at the mere sight of a hammer. Described faunas from the Arenig and higher are dominated by cystoids and

carpoids, unlike the Avalonian faunas where both are rare. Bohemian communities may represent a mixed assemblage, and further analysis of the echinoderm faunas should yield clear palaeobiogeographical signals.

Sponges

Unfortunately, we found only a few isolated spicules. However, I have specimens from the formation supplied by local agents, of *Choia* and *Pirania*. These two demosponges are known from Burgess Shale-type localities in the Cambrian, but with the exception of two *Pirania* specimens from the Caradoc Llanfawr Quarries of Wales, they are not known from younger deposits. On the slab with *Pirania* (the specimen closely resembles the type species, *P. muricata*) are fragments of at least two other species of sponge, including what seems to be a vauxiid (another Cambrian leftover). Outside lagerstätten, the record of non-lithistid demosponges from the Ordovician–Silurian is almost non-existent. The *Choia* specimens are from a coarser lithology that closely matches the upper part of the sequence; a dozen specimens are densely packed onto two small slabs.

The most surprising aspect of the sponge fauna is that there is no evidence of hexactinellids. These are more easily preserved than non-lithistid demosponges, with more distinctive spicules, and dominate most Ordovician siliciclastic sponge faunas elsewhere. Their absence here suggests a genuine ecological distribution, whether due to water depth, unusual chemistry or biogeographic aspects, but the patchy distribution of all groups in the U. F. S. makes any positive statement premature. Continued work on the formation will almost certainly yield further sponges, probably including hexactinellids.

Oddities and potential

There is clear evidence of soft tissue preservation in the U. F. S., from arthropods (cheloniellids and aglaspidids). The possible annelids are remarkably preserved in three-dimensions, apparently through pyritisation, and other, fainter traces are suggestive of additional groups of worms. There are also unsubstantiated rumours of starfish with tube-feet. Combined with the presence of exceptionally-preserved sponges and echinoderms, this indicates obrution deposits with occasionally rapid mineralisation. The result is preservation that, at its best, looks similar to Chengjiang. As yet, such soft tissue traces are extremely rare. However, the formation is very thick, with extremely patchy faunal distribution. I would be rather surprised if it doesn't yield a true lagerstätte in the next ten years.

This expedition was largely exploratory, as proposed, but at least two papers should emerge from it directly. Although it failed to yield Arenig crinoids, the unusual faunas leave tantalizing questions related not only to the fossils themselves, and the potential for lagerstätten, but also for the composition of these faunas from the perspective of the Ordovician Radiation. Much of the faunal development and diversification seen in Avalonia, Baltica and Laurentia during the Lower and Middle Ordovician seems to be absent here, with more 'primitive' groups dominating. One day, there may be an interesting story of ecological migration out of diversification centres to be explored.

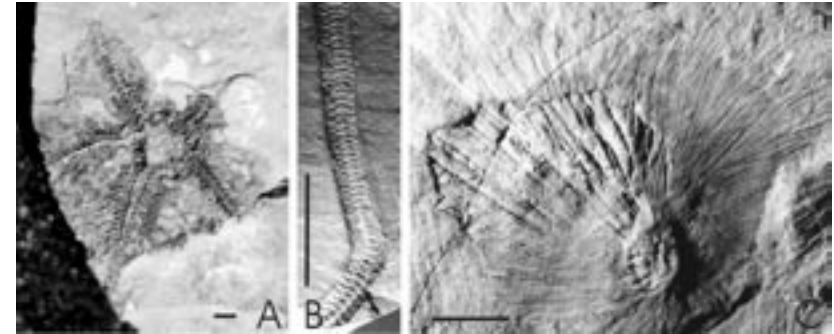


Figure 2. Fossils of the Upper Fezouata Formation: A, vellebrunasterid somasteroid; B, possible three-dimensionally preserved worm; C, the Burgess Shale demosponge *Choia* sp., recorded for the first time above the Cambrian. Scale bars 5 mm.

Taxonomic reevaluation and systematics of primitive conifers from Euramerica

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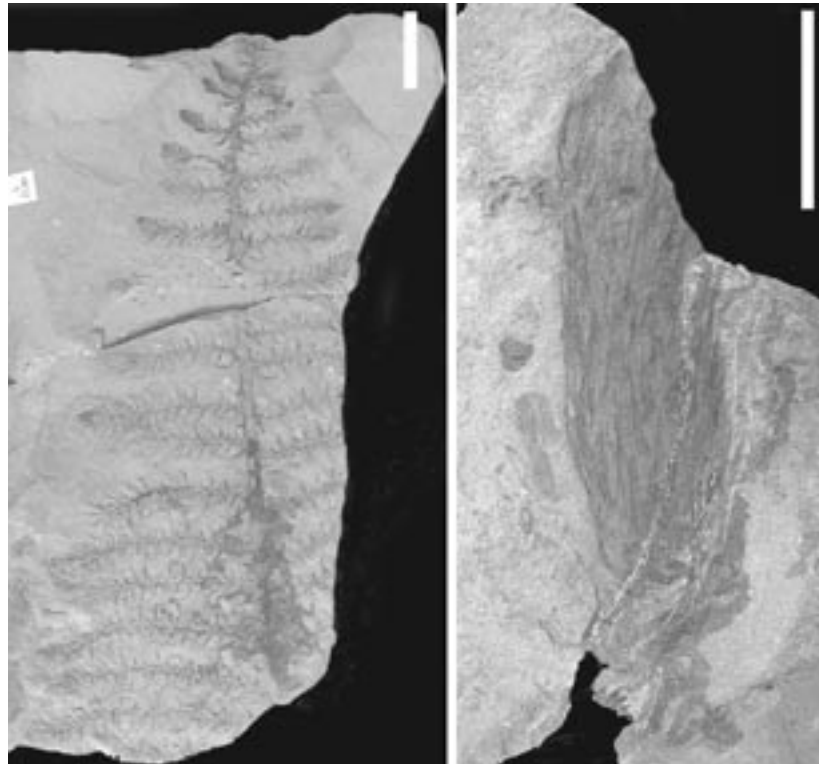
The fossil record of primitive conifers is characterized by fragmentary lateral vegetative and fertile branching systems (Florin 1938–45, Clement-Westerhof 1984, Kerp *et al.* 1990, Mapes and Rothwell 1991). Commonly, these fossil conifers are preserved as compressions and/or impressions that display morphological and sometimes epidermal features of leaves. Current species concepts are based on characters of these branches and similarities of the epidermal cells on their leaves (Florin 1938–45). However, leaf size and shape among vegetative branches in different species overlap considerably, making species identification extremely difficult. Moreover, epidermal characters used to associate these branches cannot always be used because not all primitive conifers have similar vegetative and fertile leaves on the same plant (Hernandez-Castillo *et al.* 2001). Consequently, most newly discovered specimens cannot be assigned to a species with confidence.

A new approach has been proposed to reevaluate the taxonomy of these primitive conifers based on the analysis of ranges of variation among lateral branches (Hernandez-Castillo *et al.*, 2002). This approach includes the use of multivariate analyses such as Principal Components Analysis (PCA), among others, to create whole plant reconstructions. These reconstructions will serve as the basis of new species concepts. According to previous analyses (Florin 1938–45, Lausberg 2002, Hernandez-Castillo *et al.* 2003), primitive conifers have similar tree architecture to juvenile trees of *Araucaria heterophylla* (Salisb.) Franco (Norfolk Island pine). This living tree is being used to compare and contrast tree architecture of fossil and living conifers. Preliminary results indicate that ontogenetic differences among lateral branches can be recognized and then used to differentiate conifers in the fossil record.

This Sylvester-Bradley Award enabled a trip to examine Florin's figured specimens (1938–45) and other relevant material such as the earliest conifer remains (Scott and Chaloner 1983, Galtier

et al. 1992) housed in several collections in England (Royal Holloway, University of London), France (Muséum National d'Histoire Naturelle, Paris, Université de Montpellier II, Montpellier), Germany (Paläontologisches Museum, Nierstein), and Sweden (Naturhistoriska Riksmuseet). Most specimens examined belong to the LodPve (France), Fischbach-Niederwörresbach, Goldlauterer, and Oberhöfer localities (Germany).

At the same time, more than 300 digital pictures were taken to record specimen morphology, as well as the number of specimens per species at each locality. Digital images have been used to assess 14 morphological characters of lateral branches to be compared with North American species, and lateral branches of *A. heterophylla*. Results of these multivariate analyses will be used for a publication on the affinities of Upper Paleozoic conifers of Euramerica. Comparisons to North American species include the Upper Pennsylvanian conifers *Thucydia mahoningensis* Hernandez-Castillo, Rothwell and Mapes, a long-needled conifer and two short-needled conifers from the Hamilton Quarry, Kansas. The Kansas species are now being reconstructed in order to be compared as whole plants to the European specimens.



Walchian conifers. Left: Lateral branch of *Walchia* (*Ernestiodendron?*) *arnhardtii* Florin. Figured in plate CXLIII/CXLIV, fig. 11 (Florin 1936–45). Specimen number: 1937-3, Naturhistoriska Riksmuseet, Sweden. Right: Pollen cone of *Lebachia piniformis* (Schloth.) Florin. Specimen number: 1928-13, Naturhistoriska Riksmuseet, Sweden. Scale: 2cm.

Closer examination of these specimens helps to test the validity of taxa such as *Gomphostrobus* Marion, *Ernestiodendron* Florin, and several species of *Lebachia* Florin. Morphological characters of penultimate and ultimate shoots, as well as leaf position and shape (*e.g.*, simple vs. forked), will aid in our understanding of plant architecture. Whole plant reconstructions and tree architecture of these European specimens will be assessed and compared to those of North American conifers, and a newly reconstructed conifer from the Saar-Nahe-Becken (Lausberg 2002).

Ovulate and pollen cones from different localities need to be reinvestigated and their affinities reevaluated. For example, not all specimens described as ovulate cones are indeed ovulate cones, and some of them seem to have a more complex cone organization. Excellent specimens of these cones can be found at the Muséum National d'Histoire Naturelle, Paris, and the Université de Montpellier II, Montpellier. Use of maceration techniques will be required to corroborate cone organization and cuticular features of microsporophylls. These cuticles then need to be compared to previously described cuticles by Florin (1938–45) in order to reevaluate their taxonomic affinities.

This trip to Europe using funds from the Sylvester-Bradley Award was very important in my research and help me truly to understand the current status of the Upper Palaeozoic European walchian conifers. The only way to create whole plant reconstructions of these conifers is by careful on-site reevaluation. This is due to the large number of specimens (housed at different museums) and the time consuming techniques needed. Resulting whole plant reconstructions and new species concepts will be added to an ongoing study that will incorporate similar results from North American species. New species concepts resulting from these plant reconstructions will be used to assess systematic relationships of Euramerican walchian conifers by means of cladistic analyses.

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Fossil spearing and smashing stomatopods

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Stomatopods, or mantis shrimps, are malacostracan crustaceans. These “lean, mean, killing machines” (Watling *et al.*, 2000) are highly specialized marine predators, characterised by having enlarged second thoracic appendages which form powerful raptorial claws. Modern stomatopods are divided into two broad functional groups based on the shape and usage of their raptorial claws, namely ‘spearing’ and ‘smashing’ forms (Caldwell and Dingle, 1976).

Spearing forms are found in each of the seven stomatopod superfamilies (see Ah Yong and Harling, 2000; Ah Yong, 2001) and spear their prey, which is usually soft-bodied, with the spined terminal forelimb segment (dactyl) of the raptorial claw. The strike, made with the dactyl open, is completed within four to eight milliseconds at a velocity of over 10 metres per second; it is one of the fastest known animal movements (Caldwell and Dingle, 1976).

Smashing forms are only found within four families within the superfamily Gonodactyloidea (although the family Coronodidae within the superfamily Lysiosquilloidea has adaptations for both spearing and smashing). These stomatopods feed mainly on armoured prey such as crabs and gastropods. They strike with a closed dactyl and smash their prey’s shells by using the inflated base of the dactyl. Some species are even capable of smashing their way out of glass aquaria (Caldwell and Dingle, 1976).

There has been a large body of work on the taxonomy, functional morphology and behaviour of extant stomatopods. However, the fossil record of this group is poor; while at least 450 extant species are known (Ah Yong, 2001), less than 30 fossil species from the Mesozoic and Tertiary, and only four from the Palaeozoic, have been described (see Hof and Briggs (1997); Jenner *et al.* (1998)). The occurrence of any new fossil material is therefore significant as it contributes important new data to elucidate the evolutionary history of the group. In particular, important information can be gained regarding the evolution of spearing and smashing raptorial claws.

This Sylvester-Bradley Award enabled the sparse stomatopod fossil record to be extended with the description of four new specimens. One specimen is from the Miocene of California; the remaining three are from the Oligocene of northern Italy.

The single Californian specimen was described as a new genus and species within the superfamily Squilloidea (Cunningham *et al.*, in preparation). Incorporation of this new taxon into Ah Yong and Harling’s (2000) cladistic matrix of stomatopod genera confirmed that this new genus lies within the Squilloidea, however missing data meant that its precise position within this clade could not be fully resolved. Reduced consensus methods (Wilkinson, 1994) allowed its position to be limited to five possible positions within the clade, with the relationships of the other taxa being fully resolved. The application of a ‘fossil friendly’ approach (*cf.* Dunlop and Braddy, 2001) did not change the relationships among the Squilloidea. This suggests that those characters that are abundant in extant taxa, but are unlikely to be fossilised, were not biasing this analysis.

The Sylvester-Bradley Award made it possible to visit the Zoological Museum in Amsterdam in order to study well-preserved stomatopod specimens from the Oligocene of northern Italy. Three specimens were described, all belonging to the superfamily Gonodactyloidea. Two of the specimens belong to the family Gonodactylidae and represent the oldest members of this family. One of these specimens preserves smashing raptorial claws and is the second oldest smasher to be described.

The internal structure of the claws is visible in the fossil; examination of the claw structure of a modern smasher revealed a similar two-layer structure. This specimen therefore provides important information on the early evolution of smashing claws, suggesting that the structure of smashing claws has remained conservative since soon after they first appeared. Material believed to represent the earliest example of a spearing stomatopod was also examined, however, detailed examination revealed that this material was very poorly preserved, and most likely not a stomatopod.

ACKNOWLEDGEMENTS

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Upper Silurian starfish from Leintwardine, Herefordshire

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Fossils of intact Palaeozoic starfish are rare and very few Palaeozoic “starfish beds” are known from Britain (Goldring and Stephenson 1972). The systematics of fossil starfish of Ludlow Series, Upper Silurian age form a major component of my ongoing Ph. D. studies on an exceptionally preserved biota from submarine channel deposits of the Welsh Borderland. These fossiliferous channel deposits (earliest Ludfordian in age) are unique in the British Silurian, due to their remarkable exceptionally preserved fauna and the unusual palaeoenvironmental setting (Siveter 2000). Six shelf-edge channels, interpreted to be submarine canyon heads, have been mapped in the area (Whitaker 1962), around the Herefordshire village of Leintwardine. The channel fill is a calcareous laminated siltstone and contains an abundant and diverse fauna. Along with typical Silurian fossil representatives such as brachiopods, graptolites and trilobites, a diverse rarer fauna is also present. Echinoderms are relatively abundant, comprising asteroid and ophiuroid starfish, echinoids, crinoids and ophiocistioids. Arthropod fauna is represented by ostracod and phyllocarid crustaceans, and eurypterid and xiphosuran chelicerates. Conulariids, rare palaeoscolecid worms and heterostracan fish components have also been recorded.

Extensive pre-existing and newly collected specimens of complete, articulated starfish (figure 1) from a number of the fossiliferous channel localities have provided a unique opportunity to re-assess the systematics and palaeoecological setting of these rare echinoderms. A wide-ranging assessment of existing collections of Upper Silurian starfish from the Welsh Borderland localities has been undertaken; all major UK collections, many of which were collected in the 19th Century, have been re-examined. Excavation of the major starfish-bearing channel deposit has yielded many new *in situ* specimens, which are vital in unravelling the taphonomic history of the deposits; a major limitation of the pre-existing collections is the lack of precise details of their stratigraphic provenance.



Figure 1. Ophiuroids recovered from the Channel fill, showing the typical intact state and fine preservation (specimen NHM E 13131, The Natural History Museum, London).

Extensive taxonomic study of these Ludlow Series ophiuroids and asteroids from Leintwardine has been undertaken. Funding from the Sylvester-Bradley Award has allowed thorough study of collections of the Leintwardine starfish held at the Queensland Museum, Brisbane, Australia. A substantial amount of material collected from the Welsh Borderland sites during the late 1800s was gifted to the Museum. This collection may well contain original missing holotypes of selected ophiuroid taxa, although this cannot be confirmed from comparison with the original descriptions and figures of Salter (1857). Due to the mouldic nature of the material, study was based on silicone casts. This is the first detailed review of the Leintwardine asterozoans undertaken since Spencer’s (1914–1940) classic work of the last century; one of the limitations of which was that much of his study was based on a limited amount of cast material (pers. com. Dr Peter Jell). As part of my study, a major review of all relevant literature of the group was undertaken, and where possible type specimens have been located and restudied.

The starfish are the most abundant and diverse group of echinoderms recorded from the localities of the submarine channels. The ophiuroids comprise the most diverse group of Leintwardine asterozoans, consisting of eight species assigned to seven genera. Many of the genera are monospecific. The asteroids comprise four species and genera, and form an extremely rare and limited component of the biota. Higher-level taxonomy of the Palaeozoic ophiuroids is somewhat problematic and is in need of revision, and is beyond the scope of my current studies. Based on existing higher-level classification (Spencer and Wright 1966) the greatest number of the studied ophiuroid taxa (five species) belong to the Order Stenurida Spencer, 1951; the remainder belong to the Order Oegophiurida Matsumoto, 1915. Preliminary study of contemporaneous Silurian Australian species, also held at the Queensland Museum, reveal that some do indeed show close similarities with the UK material (pers. com. Dr. Peter Jell).

Only with proper taxonomic revision can the palaeoecology and physical taphonomy of the channel deposits be accurately assessed (studies in progress). Combined with study of the

other faunal element of the channel localities (including ophiocistioids, echinoids, crinoids, eurypterids, xiphosurans and palaeoscolicid worms) a more complete understanding of all of the biota and its relationship to the channel deposits themselves is emerging.

ACKNOWLEDGEMENTS

I gratefully acknowledge the Palaeontological Association for granting me a Sylvester-Bradley Award, without which my studies in Australia would not have been possible. Many thanks are also due to Peter Jell and to all at Queensland Museum for invaluable advice and support during my research visit.

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Spatial-temporal characterization of subtropical vegetation change in the Initial Eocene Thermal Maximum

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The Palaeocene–Eocene boundary has attracted much interest because it represents a period of rapid climate warming in Earth history only paralleled by present-day warming. This brief warm interval at the Palaeocene–Eocene boundary is termed the Initial Eocene Thermal Maximum or IETM for short. Research into changes in plant records across the boundary have lagged well behind other fossils groups because geological sections are rare that (a) contain plant remains, (b) have independent age constraint, and (c) can yield a carbon isotope signature, which is an important indicator of the IETM. Plant records are important because plants have complex reciprocal interactions with the carbon cycle and the distribution of plants is strongly influenced by climate.

Climate change should result in major alterations in plant communities. But the picture obtained so far is that plant communities do not change significantly during the event (e.g. Crouch and Visscher 2003; Wing *et al.* 2003). The early Eocene vegetation type after the IETM is slightly different from the Palaeocene but the causes of this are unclear (Wing and Harrington 2001; Harrington 2001; Harrington *et al.* 2004). The Sylvester-Bradley Award allowed me to undertake fieldwork in North Dakota and sample a set of different sections from a geographically defined area across the Palaeocene–Eocene boundary. In collaboration with a group from the University of Wisconsin, Madison, we collected pollen samples and organic carbon samples. The western interior USA is an ideal place to collect plant fossils because the terrestrial sediments are well known and the mammalian chronology well established in the basins in Wyoming and Montana, and the exposures are generally good. Unlike the Bighorn Basin, which contains no plant records from within the IETM (Wing and Harrington 2001), or the Powder River Basin which has only one confirmed plant bearing boundary section (Wing *et al.* 2003), the Williston Basin in North Dakota has the potential to yield multiple IETM plant bearing sections.

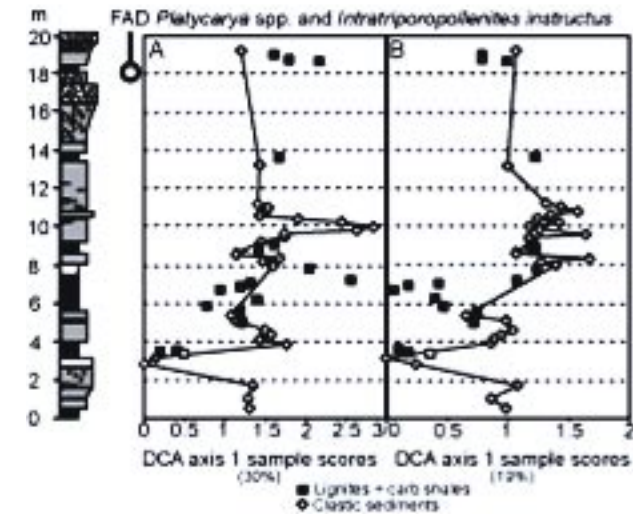


Figure 1: Sampled 20 m section through the upper Fort Union Formation and Golden Valley Formation, Williston Basin, North Dakota USA. Composition change is illustrated by (A) Detrended correspondence analysis (DCA) of axis 1 sample scores plotted against measured section for relative abundance pollen data, and (B) DCA on presence-absence pollen data. In both ordinations, clastic samples are plotted as open diamonds, and lignites and carbonaceous sediments are plotted as black squares. The first occurrence of Eocene indicator taxa (Platycarya and Intra-triporopollenites instructus) are noted at the top of the section and after any obvious vegetation change of range-through taxa at ≈7 m.

The composition change throughout the best sampled section is picked out on Figure 1 by detrended correspondence analysis of both relative abundance and presence-absence pollen

data—the trends and first occurrence patterns of the Eocene immigrants *Platycarya* and *Intratropipollenites instructus* are the same as those from other Palaeocene–Eocene transition sections in North America (Wing and Harrington 2001; Wing *et al.* 2003). The pollen floras change from typically Palaeocene to typically Eocene, and at no stage is there a flora that is warmer in aspect than either the Palaeocene or the early Eocene; the vegetation type shifts from one state to another. Our results will be enhanced with the results from other sections that we have studied and will allow us to build up a picture of local and eventually regional scale changes in vegetation during the IETM.

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Feeding Preferences and Trophic Structure of Late Jurassic Fishes

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The Late Jurassic is an important time in the development of the actinopterygians. Many of the lineages first appeared at this time, most notably those leading to modern teleosts. This is seen in the extensive, exceptionally preserved Kimmeridgian and Tithonian fish faunas of Solnhofen in Southern Germany, which were deposited in an anoxic lagoonal environment surrounded by coral and sponge reefs. During the Late Jurassic the climate was in a Greenhouse phase and its effect on fish palaeoecology (*e.g.* trophic relationships) has relevance with regard to the ecology of the present time. A study of the ecological changes and their influences over 10 million years would aid in the understanding of the ecological and climatic changes relating to global warming effects (*e.g.* El Niño).

The taphonomic conditions during the formation of the Solnhofen Limestones allowed the preservation of the digestive tracts of the fish and their content. This provides direct evidence of the feeding preferences of the fish of Solnhofen. Comparisons can therefore be made with

trophic studies based on the analysis of gut contents of modern fish (*e.g.* Stergiou and Karpouzi 2002). Previous studies on Solnhofen fish have, however, only concentrated on examples of piscivorous fish (Viohl 1990) or on the gut contents of a specific taxonomic group (Kriwet 2001). Fish were found to be the most common item of prey, however a few examples of other prey items including crustaceans (Resch and Lehmann 1994) and bivalves and echinoid spines (Kriwet 2001) have also been recorded.

Where the gut content of the fish is unknown, functional morphological analysis can be used to determine a likely feeding method and therefore possible prey types.

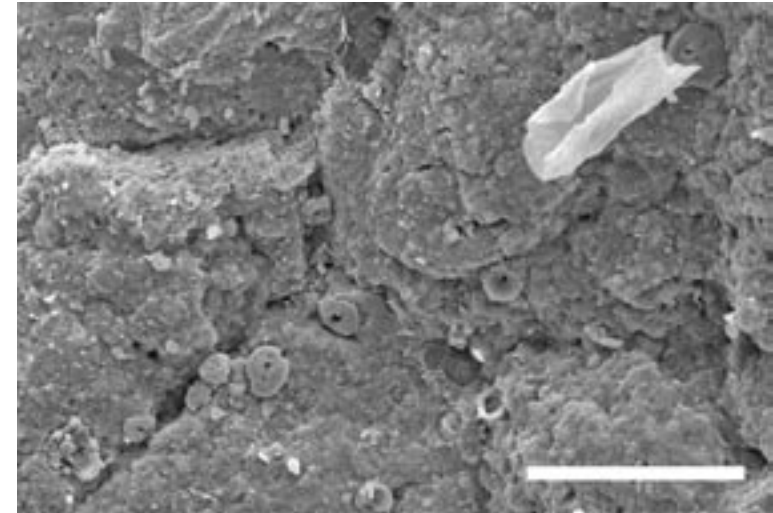


Figure 1. Coccoliths found in the gut of *Tharsis dubius* (MB.f.3039). Scale bar represents 20 μ m.

The Sylvester-Bradley Award enabled a visit to be made to the Museum für Naturkunde in Berlin, to examine their collection of Solnhofen fish, looking particularly for preserved digestive tracts and gut contents. 42 Solnhofen fish from the Museum showed evidence of preservation of the digestive tract or its contents. Small samples from 17 of the best-preserved guts were removed and examined using the scanning electron microscope for possible gut contents and remains of the soft tissue. (EDAX analysis of the chemical composition was also carried out and cross sections through some of the guts were examined.)

A species-level database of all the actinopterygian fish from Solnhofen was created based on the faunal composition described in Lambers (1999). It contained the locality (from detailed horizon studies *e.g.* Röper 1997), frequency of occurrence and additional information required to reconstruct the feeding preferences of each fish. Direct evidence from the gut content (from this and other studies) was combined with functional morphological analysis of the size, dentition and the shape of the body, fins, head and jaw. These data were used to determine the life habit and feeding mechanism and to assign a trophic guild to each fish. As a result food webs were reconstructed for the Kimmeridgian and Tithonian of Solnhofen.

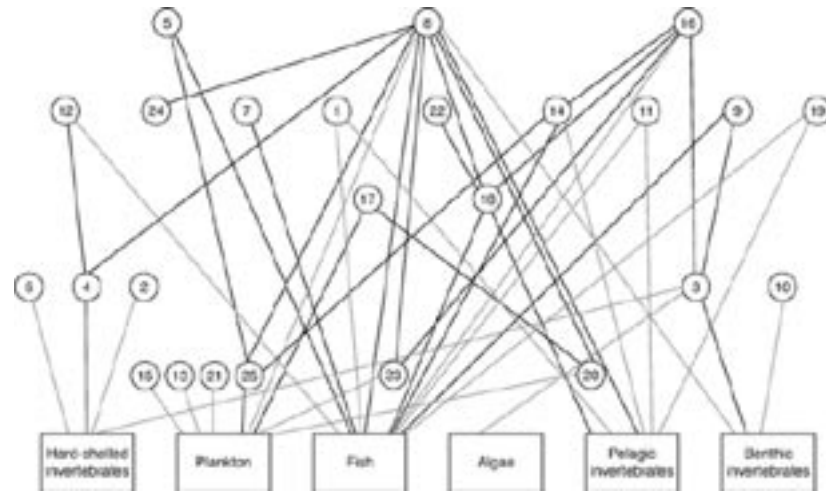


Figure 2. Food web for Solnhofen fish from the Late Jurassic. (1) Coccolepis, (2) Semionotidae, (3) Macrosemiidae, (4) Pycnodontiformes, (5) Pachycormidae, (6) Heterostrophus, (7) Amiidae, (8) Caturidae, (9) Ionoscopidae, (10) Ophiopsidae, (11) Furidae, (12) Brachyichthys, (13) Callopterus, (14) Pholidophoridae, (15) Pleuropholidae, (16) Aspidorhynchidae, (17) Allothrissopidae, (18) Anaethalionidae, (19) Elopidae, (20) Orthogonikleithridae, (21) Tischlingerichthys, (22) Daitingichthys, (23) Eichstättia, (24) Ascalabos and (25) Tharsis. Black links indicate direct evidence and grey links indicate inferred evidence.

The guts of *Tharsis dubius* and *Allothrissops salmoneus* contained planktonic organisms (including coccoliths, coccoid cyanobacteria and enigmatic spherical objects). This study therefore shows the first occurrence of direct evidence of planktivory in these species. The guts of *Tharsis dubius* and an unidentified teleost contained structures, which may represent small arthropod remains. The known piscivore *Aspidorhynchus acutirostris* had a mass of fish bones in its gut and highly digested coprolitic material without preserved structures was found near the anal opening indicating complete digestion of bony material.

A number of specimens displayed the striated texture of the soft tissue of the gut wall. Muscle fibres were preserved on the surface of the gut wall of *Solnhofenamia elongata*. Some fibres were preserved in three dimensions, emerging from the edge of the sample and others showed striations. Muscle fibres have been reported previously from Solnhofen vertebrates and the preservation observed in this study is similar to that of the fish fossils of Cordillera de Domeyko, Chile (Schultze 1989).

The EDAX analysis confirmed that the gut contents and the gut tissues themselves are preserved as apatite.

This study has shown that fish are not the only gut content preserved in the Solnhofen fishes and that there is direct evidence of planktivory. The gut wall and three-dimensional muscle fibres show the detail of preservation possible in this taphonomic environment.

The food web for Solnhofen has more than half its links supported by direct evidence. It is predator-heavy, with a high proportion of piscivorous forms and few herbivorous taxa (contrary to earlier assumptions); this is due to the preservation potential of the different food types.

There were more trophic guilds in the biologically productive Kimmeridgian than in the Tithonian, where the guilds were dominated by pelagic food sources due to the hostile benthic environment. More data on the occurrence in time of particular species are required in order to make significant conclusions about changes in the environment and faunal composition through the Late Jurassic.

ACKNOWLEDGEMENTS

The Sylvester-Bradley Award is very gratefully acknowledged. I would like to thank my supervisors Dr Jürgen Kriwet and Prof. Mike Benton for their support during this project and also the Institut für Paläontologie, Museum für Naturkunde, Berlin for permission to remove samples from the fossil specimens.

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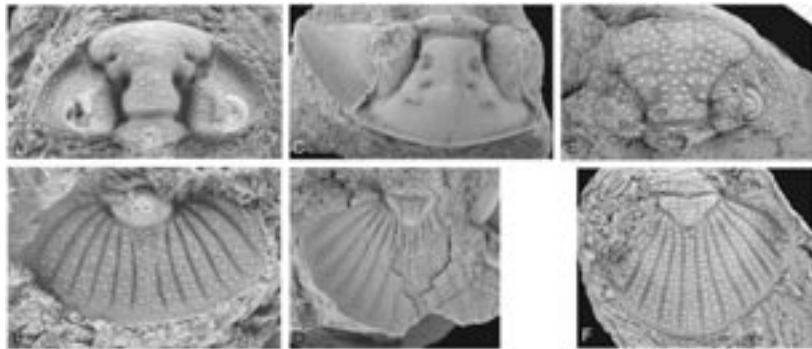
The Silurian carbonate mound trilobite faunas of central western New South Wales

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A research project to describe the above trilobite faunas in collaboration with David Holloway has been underway in earnest since 1993, when I first spent a period at Museum Victoria, Melbourne. On this occasion, we sorted and prepared material which had been collected by David Holloway over a number of years, and also made additional collections. The existence

of trilobites in the Silurian of the Orange district of New South Wales has been known since de Koninck (1876) identified '*Illaeus wahlenbergi*', '*Bronteus partschi*' and '*Harpes unguis*' from strata which are now assigned to the Borenore Limestone. Since then a few contributions have been published (e.g. Etheridge 1909; Etheridge and Mitchell 1917; Fletcher 1950; Sherwin 1968, 1971a) but the contribution on the effaced 'styginids' (Holloway and Lane 1998) was the first extensive study on the trilobites of the area. In preparing the large volume of material for the description of the effaced forms, a large number of 'scutelluids' were noticed, and selected for the next contribution. Members of many other trilobite groups are present, and whilst Proetida are the most taxonomically diverse group present, in descending order of occurrence, members of the Cheiruridae, Encrinuridae, Odontopleuridae, Harpetidae, Lichidae, rare calymenids and very rare phacopids (one pygidium!) also occur.



Silurian trilobites from New South Wales; A–B, *Australoscutellum* sp. nov.; C–D, *Decoroscutellum* sp. nov.; E–F, *Eoscutellum* sp. nov.

The purpose of the work funded by the Sylvester-Bradley Award was twofold. First, it was planned to extend the search for trilobite faunas to other limestones of Silurian age in a greater geographical area than that covered in the first publication (Holloway and Lane 1998, text-fig. 1), and in other (possibly allochthonous) limestones which had been mapped in the original area (e.g. Limestones L and K; Sherwin 1971b, figs 7, 15). The as-yet-uncollected (by us) Molong and Nandillyan limestones (Joplin *et al.* 1952; Adrian 1971) in the areas around Molong to the north and north-east of the initial area were to be prospected; second, selected localities in the previously collected area were to be re-collected in the hope of adding material of rare taxa to the collections.

The first objective proved as spectacularly unproductive as the second proved rewarding.

Several days spent collecting in the Molong and Nandillyan limestones produced almost nothing of interest to the project and, incidentally, proved almost trilobite-free. For instance, on the first day, the area of Molong Limestone north of the town was covered. Large numbers of stromatoporoids and colonial corals, very large bivalves and some brachiopods were seen, but the only arthropods collected were two trilobite cranidia (one a fragmentary lichid and the other a *Sphaerexochus*) and two beyrichiacean ostracods. On that day, the only thing of value that was collected was a 'stash of loot' (\$A281 + \$NZ2 in coins), possibly left for later collection by local

felons; the local constabulary was not amused at having to count and provide a receipt for this bonanza. The re-collection of targeted localities, however, provided the sort of material we had hoped. From processing the c.150 kg of limestone collected, in the following month we were able to add significantly to the collections, and the taxonomic results are listed below.

From the excellently preserved material, we have been able to clarify the concepts of the previously poorly known genera *Australoscutellum*, *Eoscutellum*, and *Illaeoscutellum*. Also present in the fauna are several new species of *Japonoscutellum*, a genus that previously was not well known and recorded only from Japan. Additionally, we have described new species of *Kosovopeltis* and *Decoroscutellum*, and a new genus.

This award also allowed a brief meeting with Peter and Joan Sylvester-Bradley's youngest son Ben, Professor of Psychology at Charles Sturt University at Bathurst.



Collecting the Silurian limestones above Borenore Caves, near Orange, NSW. David Holloway sensibly in the shade in the foreground. Lower Silurian limestones in middle and far distance.

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The genitalia of *Jaekelopterus rhenaniae* and its phylogenetic position

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Eurypterids are Palaeozoic predatory, aquatic chelicerates. The pterygotid eurypterids have attracted attention as they are the largest arthropods, attaining lengths of at least 230 cm, excluding chelicerae (Chlupáč 1994a), and undescribed material suggests even larger. Pterygotids are a monophyletic group united by the following synapomorphies: enlarged chelicerae with denticles (“teeth”) adapted to crush or cut prey, non-spiniferous appendages II-V and a postlaterally expanded pretelson with a median dorsal keel (Plotnick & Baumiller 1988; Dunlop *et al.* 2002).

It is important to resolve the phylogeny of pterygotids, as they were top predators in the Silurian and Lower Devonian, at the same time some vertebrates developed armour, possibly in response to pterygotid predatory pressure. Establishing a reliable phylogeny for pterygotids is an important first step to test the possible “arms race” between pterygotids and early vertebrates, and the timing of acquisition of key adaptation in these two groups.

Jaekel (1914) described *Pterygotus rhenaniae* from the Emsian of Overath, Germany based on an isolated pretelson. Størmer (1936) described the species in more detail, and suggested the genital appendages of both females and males as three-segmented. Waterston (1964) reviewed the morphology of pterygotids and erected the new genus *Jaekelopterus* for the German species. Based on the three-segmented genital appendages, *J. rhenaniae* was placed as a sister-taxon to the remaining pterygotids, which are known to have undivided appendages (Plotnick & Baumiller 1988; Dunlop *et al.* 2002).

During review of the entire Pterygotidae, it became clear that there were problems with this interpretation. First, the segmentation could not be seen on the original photos of the type A (female) appendage (Størmer 1936, pl. 6, fig. 4); only two dashed lines divided the appendages in Størmer’s interpretative drawing. The same was true for the type B (male) appendage. Secondly, one would expect the most plesiomorphic pterygotid to be older than more derived taxa, but *J. rhenaniae* is actually the second youngest pterygotid, after removing specimens that should be assigned to phyllocarids (Chlupáč 1994b) and the enigmatic *Angustidontus* (pers. obs. 2003; R. Feldmann pers. comm. 2003).

The original specimens of Jaekel (1914) and Størmer (1936) were studied in the Museum für Naturkunde, Berlin. MB.A.7 is the original type A appendage prepared by Størmer to show the dorsal and internal structures of the genital appendage. MB.A.10 is another type A appendage showing the unprepared ventral surface. MB.A.4 and MB.A.21 are two type B appendages, both distally incomplete and showing the dorsal (internal) part of the appendages; the latter also shows a pair of oval openings on the dorsal side of the appendage.

The type A appendages are both quite short, only extending slightly longer than the genital operculum (*i.e.* two anterior fused sternites). It is obvious that both the dorsal and ventral side are an undivided appendage, not divided into three as suggested by Størmer (1936, fig. 4). A pair of internal canals on the type A appendage is interpreted as the appendages of the median opercular plate (*sensu* Størmer 1973, figs. 29–36), what I would call the furca (but not in the sense used by Braddy & Dunlop 1997). The opening described by Størmer (1936, fig. 4b “ap”) is clearly a preparation mark. If there ever was an opening, its existence has been destroyed by preparation. On the ventral side, the appendage has a median ridge, unknown in any other pterygotid. The outline of the appendage is also less broad distally (*i.e.* less “spoon-shaped”) than other pterygotids, but more so than was indicated in Størmer (1936, figs. 4a, b).

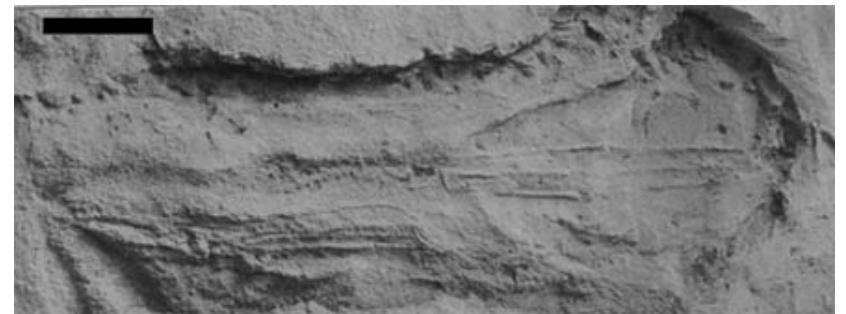


Figure 1: The prepared type A appendage of *J. rhenaniae*, with no sign of segmentation. Scale bar is 5 mm.

The type B appendages are also devoid of segmentation, not divided into three as suggested by Størmer (1936). No trace of internal canals are present in the type B appendage, suggesting that the furca are not preserved or raising the possibility that pterygotid males (*sensu* Braddy & Dunlop 1997) did not possess furca, but independent evidence from other pterygotids is needed to demonstrate the latter. However, two large oval openings described by Størmer as

oviducts are evident internally on the dorsal surface of the appendage. If oviducts, this would require a reversal of the sexual determination compared to *B. tetragonophthalmus* (see Braddy & Dunlop 1997). Alternatively, they can be interpreted as genital ducts, being larger in males than females, or muscle attachment sites of the appendage, although these should be more visible dorsally than ventrally on the dorsal surface. The outline of the type B appendage is also different from other pterygotids.

A very obvious character present on the genital appendages of both sexual dimorphs in *J. rhenaniae* are prominent lateral processes resembling 'hilts' or 'hand guards' on swords, on the posterior part of the anterior triangular plate of the genital appendages. If these could be found in either *Pterygotus* or *Acutiramus*, it would be a useful character to help resolve the phylogeny of the part of the clade containing these taxa, but the reconstructions of Waterston (1964) only indicate small processes in these taxa. They are not present in the outgroup *Slimonia acuminata*, and are present but very small in *Erettopterus bilobus*.

Other morphological characters were examined in Berlin; the chelicerae of *J. rhenaniae* have a curved distal 'tooth' on the free ramus and an angular distal 'tooth' on the fixed ramus, (characters shared with *Pterygotus*), and a principal angular 'tooth' in the fixed ramus (a character shared with *Acutiramus*), but without the serrations found in *Acutiramus*. An apomorphy for the genus appears to be a triangular, paddle-shaped telson, not seen in any other pterygotid genus, and the shape of the genital appendages discussed above. Therefore *Jaekelopterus* remains a valid genus even though the genital appendages are not divided. The phylogeny of the group will be dealt with in detail in a later publication, but in light of these findings, two most parsimonious trees are likely: ((*Erettopterus* + *Truncatiramus*) + (*Acutiramus* (*Pterygotus* + *Jaekelopterus*))) or (*Jaekelopterus* (*Pterygotus* (*Acutiramus* (*Erettopterus* + *Truncatiramus*))))). The former hypothesis is more consistent with the stratigraphical distribution of the genera.

I would like to acknowledge the Palaeontological Association for awarding me the Sylvester-Bradley Award making this study possible, Dr Jason Dunlop and others at the Museum für Naturkunde, Berlin for providing facilities and hospitality, and Dr Simon J. Braddy (University of Bristol) for providing helpful discussion on this report.

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Brachiopods of the Family Porambonitidae from the Middle Ordovician of the East Baltic

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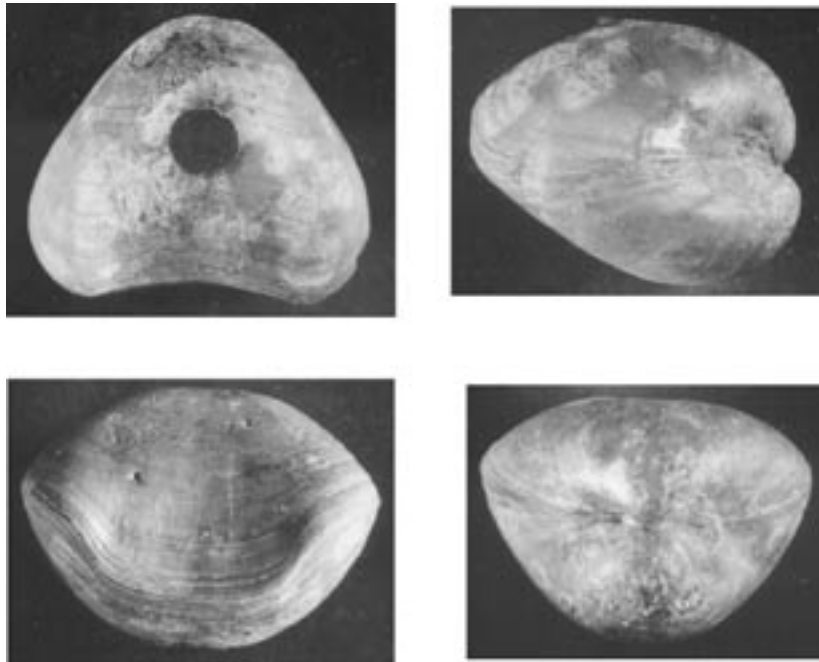
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This report presents preliminary results of the study of the Baltoscandian taxa usually assigned to *Porambonites* under the research project supported by one year's Sylvester-Bradley Award. The primary objective for the study was morphological and taxonomical definition of *Porambonites* from the East Baltic in order to answer the question "what can be referred to *Porambonites*?".

Activities related to the project include field work in the St. Petersburg region and subsequent laboratory work. More than 400 specimens of *Porambonites* from the newly assembled collection and specimens deposited in the museums in St. Petersburg (Tschernyshev Central Geological Research and Exploration Museum and Geological Museum of Mining Institute) were studied. This material, in particular, includes specimens from the Popovka River which was the type locality for many species described by Pander (1830). A revision of the Teichert's collection housed in Berlin, Museum of Natural History of Humboldt University was also conducted. New specimens were collected from the Middle Ordovician deposits (Volkhov to Kunda regional stages) of St. Petersburg region (list of the localities includes Putilovo quarry, Lava River, Volkhov River). The specimens of unique preservation of interior morphology were collected from the lower Caradoc deposits in the western part of St. Petersburg region, in particular in the Klyasin quarry (Zuykov & Terentiev 1997).

Preliminary results of the study show convincingly that a group of species presently assigned to *Porambonites* represents in reality an assemblage of several related and unrelated genera. Subgenus *Porambonites* (*Noetlingia*) has a distant relationship both to *Porambonites* and the family Porambonitidae and it may represent a senior synonym of *Punctolira*. The stratigraphic range of *Noetlingia* is entirely confined to the Aseri Regional Stage (middle Llanvirn), but not to the lower Silurian (Llandovery-Wenlock) as it was reported in the new edition of the brachiopod volume of *Treatise on Invertebrate Paleontology* (2002). Overall the stratigraphical

range of the family Porambonitidae does not exceed the lower boundary of the Hirnantian Stage. *Porambonites* and related genera are usually regarded as rather typical Ordovician syntrophiidines; however, existing evidence on the affinity of *Porambonites* to the order Pentamerida are relatively weak and include mostly a presence of the astrophic shell and characteristic, long brachiophore plates. However the presence of extraordinarily long and almost discrete dental plates without tendency to form any kind of spondylial structures at least in the early species is quite unusual for pentamerides. Dorsal adductor scars of the early species of *Porambonites* are weakly impressed, but they were more likely situated within the space enclosed by very long brachiophore plates and not in front of them as in syntrophiidines. At the same time the ventral muscle field of *Porambonites* has a remarkable similarity to the ventral muscle field of *Lycophoria*, which is also characterised by the astrophic shell. It is possible that these two brachiopod genera are related and both represent an aberrant group within orthides. However knowledge of morphology and shell structure of *Porambonites* remains inadequate and any attempt to define its affinities could be only tentative.



Porambonites aequirostris (Schlotheim). Middle Ordovician, East Baltic. Original specimen from the collection by E. Schlotheim; Museum of Natural History of the Humboldt University, Berlin, Germany. Photos were made by Carola Radke.

The family Porambonitidae is one of the most distinctive groups of Baltic brachiopods, but it has not been the subject of any comprehensive study since that of Teichert (1930). However, identification of the taxa described by Pander (1830) is difficult; the location of the original collection that forms the basis of his study is unknown for more than 150 years (for more details see Lamansky 1905; Jaanusson and Bassett 1993). Type species of the genus *Porambonites*, *P. intermedius*, is known only from the original paper by Pander (1830) and was not revised subsequently, whereas morphology and stratigraphic ranges of most of the species are known from the very generalised descriptions in the papers of 19th and early 20th centuries. It is important, that *P. intermedius* belongs to a group of smooth porambonitids and differs markedly from the taxa traditionally referred to the genus. The nature of this poorly known taxon which was subsequently designated by Hall and Clarke (1894, p. 226) as the type species of the genus, becomes certain only after a revision of new materials from the Billingenian and Volkhovian deposits of the St. Petersburg region. It shows that generic attribution of the majority of species assigned to *Porambonites* by (Teichert 1930) must be reconsidered.

The main problem which concerned the external morphology of Porambonitidae is evaluation of the taxonomical significance of finely fenestrate external surface ornament which is a highly variable but characteristic feature of most of the species previously assigned to the genus. *Porambonites intermedius* apparently lacks this ornament. '*Porambonites*' *latus* Pander, possibly the earliest species of the family Porambonitidae, has a finely multicostellate radial ornament without distinctive pitting between ribs, whereas in '*Porambonites*' *reticulatus* Pander fenestrate ornament is one of the most distinctive features. These two species are considered (Popov *et al.* in press) as not to be congeneric with the type species of the genus that lacks completely any surface ornament. One of the most distinctive features of most of the species once referred to *Porambonites* (*sensu lato*) is very long, subparallel dental plates enclosing a narrow and strongly elongated ventral muscle field. However, there is no indication of any spondylial structures, and the dental plates remain discrete throughout their length. In *Porambonites* (*sensu lato*) the brachiophores are supported by long, divergent brachiophore plates. They do not converge anteriorly and are not fused with a median septum, notwithstanding the diagnosis of the genus provided by Biernat *in* Moore (1965). There is also no record of a dorsal median ridge or septum in the Early Ordovician species of the genus. In the course of the subsequent study diagnosis of the genus *Porambonites* and family Porambonitidae must be emended and neotypes of some species must be selected. Results of the work on the project are now being prepared for publication. Collected specimens will be deposited in the Geological Museum of the Department of Palaeontology, St. Petersburg State University, St. Petersburg, Russia.

ACKNOWLEDGEMENTS

I am grateful to the Palaeontological Association for granting me a Sylvester-Bradley Award. I would like to thank Dr Martin Aberhan for organization of work in the Museum of Natural History of the Humboldt University, Berlin. The fieldwork in the glacial deposition in Berlin district was organised by a group of amateur palaeontologists and fossil collectors under the advice of Ms Edith Fritsch (Natural Sciences Collections, the Museum of Berlin). I am greatly indebted to Prof. Anthony Wright and Dr Leonid Popov for their advice and valuable discussions.



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Book Reviews

The cruise of the Betsy

Or, A summer ramble among the fossiliferous deposits of the Hebrides with

Rambles of a geologist

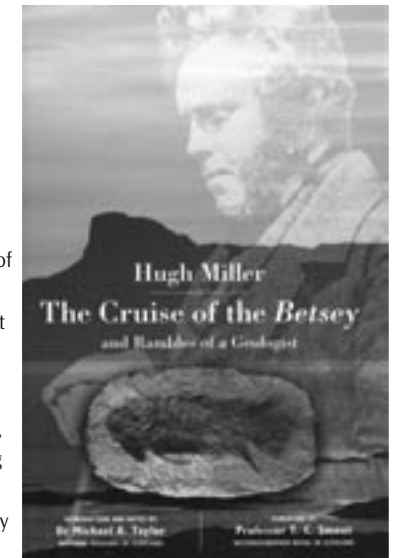
Or, Ten thousand miles over the fossiliferous deposits of Scotland

Hugh Miller. Facsimile of text first published in 1858. Introduction and notes by Michael A. Taylor; Foreword by T.C. Smout; National Museums of Scotland, 2003, 468 pp. + A1–A64 and B1–B36, ISBN 1-90663-54-X (pbk), £20.

Hugh Miller was quintessentially a Victorian: hard-working, self-made, proud of his country, and a staunch supporter of the church, in his case the Free Church of Scotland. He is remembered by inhabitants of the Black Isle, north of Inverness, as a famous man who once lived in their midst, and he is known, at least by name, to generations of geology students at Scottish universities as one of the pioneers of the subject. Until the appearance of this facsimile edition of the 'Cruise' with 'Rambles', his published work had, however, been out of print for more than a century.

As Michael Taylor notes in his interesting and informative introduction, the first part of the book, the 'Cruise', is devoted to Miller's travels, beginning in July 1844, to the islands of Mull, Eigg, Rùm and Skye, then across the Scottish mainland to Cromarty and the Moray Firth region. It also includes an 1845 detour to Eigg on his way home after attending the General Assembly of the Free Church in Inverness. The second part, the 'Rambles', covers his trips in 1846 and 1847 to Caithness and Orkney and from Aberdeen to the Black Isle and Strathpeffer.

Miller originally published articles on these journeys in *The Witness*, a newspaper of which he was founding editor that supported the evangelical wing of the Church of Scotland. He intended to edit them into books but committed suicide in 1852, apparently because he was having hallucinations and believed he was going mad. In his memory, his widow Lydia started overseeing the posthumous publication of some of his writings, with considerable support in due course from the Reverend William Symonds, a well-known Herefordshire geologist and author of popular natural history books. The 'Cruise' with 'Rambles' went through numerous 'editions', with the last known printing being in 1897.



Miller's geological writings formed only a fraction of his output, which also covered literary, political and religious themes. They appealed to Victorians because being out in the field looking at rocks and collecting fossils was regarded as constructive recreation for self-improvement, providing excellent exercise for body and mind in fresh air. Miller was regarded as a great popularizer of geology, his influence extending to the English-speaking world far beyond Scotland and encouraging others to take a scientific interest in their surroundings. Among those he inspired were Archibald Geikie, who went on to become Director-General of the Geological Survey and President of the Royal Society, and John Muir, an expatriate Scot who pioneered the conservation movement in North America. His important fossil collection is now mostly housed in the National Museums of Scotland.

The fact that many of Miller's observations and conclusions were not recorded in formal 'scientific' journals was to his disadvantage in the long term because he has not necessarily been given credit where this was due. On the other hand, it has been difficult to determine which of the observations made were his own and which were derived from the work of others because he did not provide detailed references to the literature. As today, this was considered unnecessary in articles aimed at the general populace. It is, however, clear that he made a substantial contribution to the discovery of fossiliferous sites and their interpretation. His observations on the fish-bearing Old Red Sandstone of Devonian age were of particular importance at a time when questions were being asked about the diversity of living things and how this might have arisen.

Both the 'Cruise' and 'Rambles' are not, however, just about geology. As a Lowlander, he found much to enjoy and celebrate in the natural environment of the Highlands and Islands, and its inhabitants and folklore. He was very involved in the political and religious controversies of the day. He was a social commentator, especially on the injustices of the Highland Clearances and poverty. All of these interests are apparent in his writing, and are put into perspective by Michael Taylor.

Although aware of the importance of stratigraphic correlation and the palaeoenvironmental implications of his discoveries, Miller's observations on, and conclusions drawn about, these matters were sometimes mistaken. This was inevitable at such an early stage in the development of geological interpretation. There is a useful short section and table at the end of the volume on the terms and deposits he mentions and their modern nomenclature. There is also a glossary that includes explanations of obsolete geological terms and translations of words in Scots dialect which are not covered in the footnotes that have been added to the facsimile text.

For anyone with an interest in the geology, history and landscape of Scotland, this is a delightful book. Miller's early experiences as a stonemason and quarry worker, and later as an author, journalist and newspaper editor combined with his interest in, and enthusiasm for, the world around him shine through his prose. It is travel writing at its best.

David J. Batten

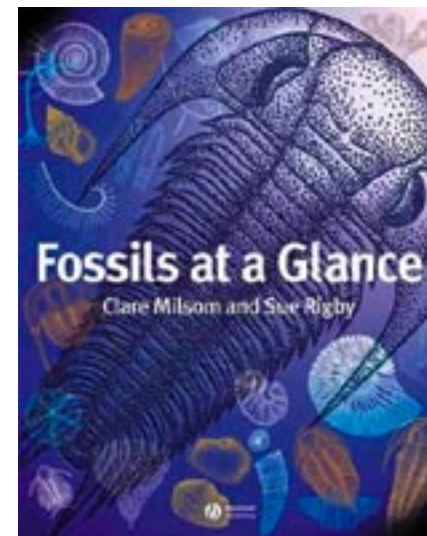
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Fossils at a Glance

Milsom, C. and Rigby, S. 2003. Blackwell Science, Oxford. ISBN 0632060476 (paperback). 168pp. £19.99

With regularity akin to that of the leaves turning to myriad hues of gold and orange, and the first Christmas displays appearing in the local shopping centre, each Autumn a new intake of undergraduate students start asking about textbooks (in particular "the ones that will give me what I need to pass the exams"). Until a few years ago, recommending textbooks for palaeontology was simple. There were relatively few options on the market, and with few exceptions these concentrated entirely on the main macroscopic invertebrate groups. In most cases it was good enough to recommend "the most recent edition of Clarkson that you can get, or if you get one of the other books around cheap enough, that will do fine". Latterly, there have been changes to palaeontology teaching, with many institutions cutting hours devoted to palaeontology to make way for other, expanding, fields of geology, and a common move towards a more holistic approach to the subject, where invertebrate macrofossils are increasingly seen as just one element. These changes have been associated with the release of several new text books and the re issue of at least one other. At the same time, increasing demands on the dwindling finances of students (including the mature students that I work with; the pressures may be different from those of younger undergraduates, but they are still there) has started to make the buying of any but the most essential of books appear more of a luxury than a necessity. Suddenly, the recommendation of course books became far more complicated.

It is into this arena that *Fossils at a Glance* was released. This is a book with a lot of promise. It has a wide-ranging coverage, concentrating on invertebrate macrofossils but also including other groups and topics, and a very clear style. Unfortunately, I feel that it is this clarity that is the problem. For undergraduate teaching, even at first year level, this book is simply too basic. Within the eleven lectures that I teach invertebrate palaeontology to first year students,



there are aspects of every group that I cover that are not in this book (I admit that I am being rather self-indulgent here by saying what I do, but that is what I know best and would form the best basis to compare this book against). Admittedly, there are things in this book that I do not mention, but this still means that this book does not cover all of the lectures I give, let alone provide additional input. The bottom line for any textbook is whether it helps students learn. The style of this will certainly help some students, but can only take them to a certain level. There would probably not have been enough background information here for my students (if they had used just the notes they were provided with and this book) to

have been able to achieve marks high within the first class bracket for some of the examination questions they were set last year. Please don't get me wrong, I am not saying that this book is without considerable merit, more that the claim on the back cover suggesting that this is for "students taking an introductory level course in palaeontology" is wrong. I can see few occasions where a palaeontology course (as opposed to elements of palaeontology within a more wide ranging course) that has not been written to mirror this book's contents would be adequately backed up by this publication. So where does this book's niche lie? I can see several cases where it would be excellent. I can see it having great potential as a reference text book for schools where a little palaeontology is covered within an A level or equivalent course. Likewise, it could prove an invaluable resource for degree level courses introducing basic geology as a whole (what a colleague in America unflatteringly called "rocks for jocks"). The heavy reliance on clear line illustrations may also make this book ideally suited for having as a reference book within laboratories where palaeontology practical classes are carried out.

Any comments on the various biases in the coverage of this book, and of its layout, are obviously more heavily influenced by personal preferences than anything else. I like the general format with large pages and the glossaries at the end of each chapter, which is a great boost to this book's utility as a reference source. The illustrations are clear and well chosen (although there seems to be a general trend for pictures I cannot recall having seen before, and presumably new for this publication, being less good). In places I feel that more diagrams of representative taxa would have been useful, especially within the diverse echinoderms and molluscs, and drawings of some common trace fossils would have also been useful. There are a few poor diagrams or misrepresentations. This is especially true of the diagram of graptolite faunas on page 82 (which is disappointing; I have a soft spot for graptolites and was expecting good things here). This is badly drawn and not aligned, with no clear indication to where the system boundaries should be. In addition, the graptolite diversity curve bears only a very crude resemblance to reality (for example, where did that mass extinction in the mid Ordovician come from?). Other diagrams are misleading in other ways. The diagram of foram occurrence has drawings of benthic taxa where planktic ones should be, whilst the drawing of the possible life occurrences of ammonite morphotypes seems to contradict itself, with similar numbers of forms stated to be either planktic or benthic being in both settings.

That said, this Autumn, as with last and the one before that, I shall be sending my palaeontology students to the library to get their books, but this year there will probably be a couple of copies of *Fossils at a Glance* on the shelves.

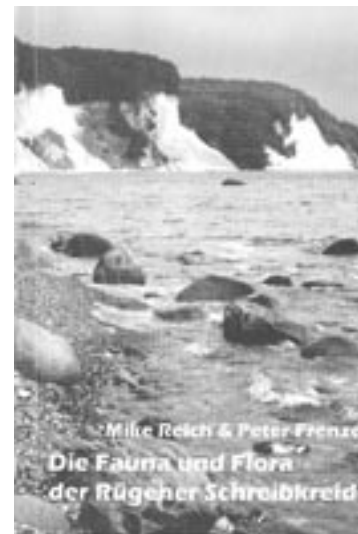
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Die Fauna und flora der Rügener Schreibkreide [The fauna and flora of the Rügen Chalk]

Reich, M. and Frenzel, P. 2002. *Archiv für geschichtliche Geologie* 3 (2/4): 73-284, 55 Taf., 9 abb., 2 Tab., Hamburg. ISSN 0936-2967.



This is an extremely useful well-illustrated and comprehensive guide to the fossils of the (Lower Maastrichtian) Chalks of the Island of Rügen, North Eastern Germany. It is intended as both an identification guide and an introduction to the geology of Rügen. The first part of the guide illustrates the history of the study area, looking at the individuals who have made major contributions to this locality, figuring some of their monographs and their rather illustrious portraits. This is followed by a brief account of the geology of the chalks and the macro structure found within them, including flint formation and ichnology. As this guide is intended to be used in the field, detailed cliff sections and a locality map are included; this, plus a summary log, provide a good all round introduction to the region, where few other similar works exist.

The overall perspective of the book is to look at the diversity and palaeoecology of the Rügen chalks. This ranges from the microbenthos through to the macrobenthos and the infaunal organisms to the large nekton such as mosasaurs. For the most part the book is a summary monograph or guide constructed from both collections and bulk sampled residues. The notable distinction of this publication is that it utilises all of the fossils including the fragments from numerous residues (residues typical of the chalks from around Baltic region). The authors have used this feature of the chalk rubble faunas to a great extent, showing photographs of typical residues that can be produced, including large accumulations of brachiopods and bryozoans.

The guide includes illustrations of all the main fossil groups expected to be encountered by both collector and specialist. These comprise of calcareous nannofossils through to invertebrates, micro and macro vertebrates and finally trace fossils. The identification section aims to be comprehensive in its treatment of the fauna and flora, so that as well as illustrated guide sections, there are long faunal lists showing all of the fossils noted from the localities; these are clearly sourced to publications where they were first described. This aspect is one of the highlights of the book. At the end of this section the data is brought together in two forms: firstly the distribution of groups across the localities is mentioned, and secondly there are illustrated reconstructions of different parts (e.g. macrobenthos) of the Rügen chalk habitat, giving an overall picture of the diversity of this type locality. Although on a single type locality, this book is of great interest to anyone working on the chalk facies in northern Europe, including myself.

With such a great range of fossil groups there are places where the scope has allowed for some mistakes in specimen identification, particularly in groups not specialised in by the authors. This is especially true of the vertebrates, which fall outside the normal field of interest of the authors. Firstly, it was noted that the species list of the sharks contains genera that do not appear until after the Cretaceous (*Carcharhinus*, *Otodus* and *Sphyrna*). In addition, there are several misidentifications amongst the figured specimens, whilst several species shown in an original figure by von Hagenow are not included. Of the figured specimens on Plate 46, Fig. 3 shows a tooth of a Placoidschuppe? that is more likely to be a *Chiloscyllium* sp.; Fig. 4 appears to show a lower tooth of *Proetmopterus hemmoorensis* (Herman 1982), identified as *Centroscymnus*; Figs 5–6 show a scyliorhinid, possibly of an unnamed genus, but not *Scyliorhinus*; and Fig. 7 identified also as *Centroscymnus* appears to be a lower tooth of *Eoetmopterus supracretaceus* Müller and Schöllmann 1989. In addition, the original plate of von Hagenow appears to show specimens of *Cretalamna* gr. *appendiculata* (Agassiz 1843), *Squalicorax kaupi* (Agassiz 1843) and an indeterminate odontaspid or mitsukurinid not shown here.

Echinoderms are a group on which one of the authors is a known authority, and as a result such mistakes are few, although some of the ossicles shown do not exhibit key features; for instance the *Nielsenicrinus* lacks the diagnostic ornament to distinguish it from *Isocrinus*, and the asteroid plates lack close-up images of the marginal plates essential for identification. However, it is noted that groups common in Maastrichtian chalks are not shown, but rather confusingly, they appear in the images of residues shown in the book. In part this demonstrates the difficulty of including all the fragments found in a locality. The authors have overcome these inaccuracies by including the faunal lists and a reference section to ease further identification, thus it is important to stress that this book should be used as a starting point for identification and subsequent research.

As the title suggests, this guide is written in German. Although this would encourage local collectors (and it is envisaged that this was the original purpose of the book) it could inhibit its usefulness to the wider audience, particularly around the Baltic region. Although an English abstract is provided, the usefulness and international appeal of this guide would be greatly increased with English figure captions and summary sections. On the whole, guides that endeavour to include all of the fossils, including fragments, are rare, and although it is important to encourage collectors to find complete specimens this publication allows confident identification of fragmentary specimens. This feature is not included in many fossil guides, including those on other chalk localities in Europe. Despite the inaccuracies that may result from such a wide approach, an attempt to produce a guide of this type is a very important step indeed.

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African Dinosaurs Unearthed: the Tendaguru Expeditions

Maier, G. 2003. Indiana University Press. ISBN 0-253-34214-7 (hardback). 380pp. £37.95.

Few people who have opened a dinosaur book will be unfamiliar with the image of the giant African *Brachiosaurus* skeleton displayed at Berlin's Museum für Naturkunde. It stands about

12 m tall, is something like 23 m long, and represents an animal that would have weighed between 28 and 47 tons, depending on whose estimate you believe (Colbert 1962; Paul 1988; Seebacher 2001). It is surrounded by other dinosaurs: the diplodocoid sauropod *Dicraeosaurus*, the stegosaur *Kentrosaurus*, the ornithopod *Dysalotosaurus* (= *Dryosaurus*) and the archaic theropod *Elaphrosaurus*. The importance of the Jurassic dinosaurs of Tendaguru (Tanzania), which include these five taxa, for our understanding and perception of dinosaur diversity, evolution, biogeography and palaeobiology cannot be overstated: it is no exaggeration to say that Tendaguru is one of the most important Mesozoic fossil sites in the world.

In *African Dinosaurs Unearthed*, Gerhard Maier presents the full, detailed story of the Tendaguru excavations, from the discovery of the site by Bernhard Sattler in 1906 to the most recent works of 2001. Historical reviews of Tendaguru have been published before (e.g., Zils *et al.* 1995), but nothing as detailed as this. The volume will certainly be the standard reference on the history of Tendaguru from here on, and while it would prove enjoyable reading to anyone interested in historical palaeontology, or indeed the history of colonial Africa, it is also almost a technical volume with meticulously detailed source notes and a complete bibliography. The volume combines biography, historical narrative and scientific discovery, all set against the socio-political events of the 20th century.

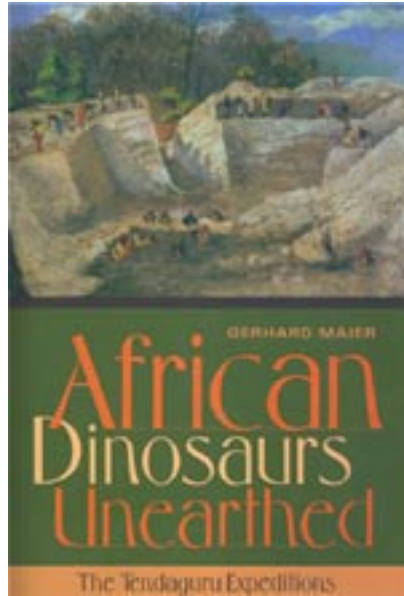
Maier makes it clear early on that this book is not really about the scientific discoveries made at Tendaguru; it is instead concerned with the expeditions, the procurement and preparation of the fossils, and the people involved. Edwin Hennig and Werner Janensch are well known for their connections to Tendaguru, but some of the other expedition leaders based there over the years include Hans Reck, William Cutler, Frederick Migeod (apparently pronounced mee-zhoh) and John Parkinson. Some people that worked at Tendaguru later became better known for work elsewhere in the palaeontological world. Louis S. B. Leakey worked at Tendaguru during 1924 and Francis Rex Parrington was there in 1930. William Swinton was due to work at Tendaguru in 1926 but dropped out due to health reasons. When you add to all this the names of the other palaeontologists, native workers, financial backers, museum preparators, administrative staff and military personnel involved, the number of people that need to be kept track of is considerable and I could forgive myself for getting confused at times. A huge amount of biographical work is included on most of these people; in many cases, more than has been published in any single work before.

Maier's coverage is so thorough that he discusses far more than just the dinosaurs. Invertebrates, fish, squamates, pterosaurs and mammals have been described from Tendaguru, and he also covers the extensive debates that arose concerning the stratigraphy and age of the deposits. Palaeontological and geological collection was not the only aim of work at Tendaguru and literally thousands of modern plant and animal specimens were collected. Many points stuck in my mind. The (likely apocryphal) story of Sattler's discovery of the site is intriguingly similar to the (also likely apocryphal) story of Walcott's discovery of the Burgess Shale. Sattler alerted the director of his firm, Wilhelm Arning; Arning notified the Commission for the Geographical Investigation of the Protectorates; and in August 1907 Eberhard Fraas arrived at Tendaguru, the first of so many scientists to do so. There followed the outstandingly successful 1909, 1909–10, 1911 and 1912–13 expeditions of Janensch, Hennig and Reck.

Following the end of WWI Germany lost her colonies to the Allied powers, and what had been Deutsch Ostafrika now belonged to Britain. The geologist and engineer Charles Hobley had clearly been keeping close tabs on Tendaguru for as early as 1918 he urged Arthur Smith Woodward to exploit the site, the result being successive expeditions led by the British Museum (Natural History) to Tendaguru from 1919 to 1930. As Maier explains, the British approach to Tendaguru was rather different from the German one, though ultimately both were extremely successful. This has always been less obvious for the British discoveries, given that the British Museum (Natural History) did not publish its results.

The hardships endured in the field were clearly considerable at times and included shortages of food and material, wildfires, flooding, disease and sickness, difficulties with post and transport, the dangers posed by man-eating lions, and an absence of outcrops. British expeditions in particular suffered from lack of funding. Cutler paid the ultimate personal price at Tendaguru, his premature death (at age 47) from malaria being exacerbated by other health problems. As for technical difficulties with the fossils themselves, Migeod suffered from a lack of experience in palaeontological identification and was without assistance, despite requests for such. Consequently he made a number of interesting mistakes, (mis)identifying plesiosaurs, giant birds, horned dinosaurs and pterosaur skulls from the bones of other animals. Unlike Migeod, Parkinson was a trained geologist and provided a new perspective on the stratigraphy and palaeoenvironment of Tendaguru. One interesting fact that Maier does not note is that Parkinson was a fan of Hay and Tornier's idea that sauropods walked in a sprawling lizard-like posture (Parkinson 1930). And while on the subject of sprawling sauropods, I was fascinated to learn that in 1912 Tornier managed to get permission from Kaiser Wilhelm II to remount the Berlin *Diplodocus* cast in the belly-dragging pose that he advocated. Needless to say this never occurred.

Germany's contribution to the Tendaguru excavations may have come to an end for the time being, but a new part of the story was to begin: the between-the-wars reconstructing and mounting of the dinosaurs at the Museum für Naturkunde. Against the background of riots, strikes, and an unbelievable economic slump (at the height of which, one US dollar was equivalent to 4.2 trillion marks), Berlin's museum curators were dedicated enough to continue the preparation of the Tendaguru dinosaurs. The stegosaur *Kentrosaurus* was first to be mounted (1924) and Maier's description of the techniques used prove that the Germans faced and overcame the problems encountered by museum technicians today.



Elaphrosaurus was next, being mounted in 1926, and was followed by *Dicraeosaurus* (1930/1). As Maier explains, the mounted dicraeosaur was a composite, and not just of more than one individual, but of both dicraeosaur species. I was also interested to learn that the characteristic neck and skull pose of the skeleton (much copied in artwork and even in other mounted dicraeosaur skeletons) was not the planned pose but a compromise resulting from distortion. These dinosaur skeletons were, however, small jobs compared to the mounting of SII, the famous *Brachiosaurus* skeleton. The original plan was actually to mount a full-sized replica. The swastika banners that hung from behind the brachiosaur skeleton at its unveiling in August 1937 heralded the horror to come. What happened to Berlin and London during WWII, discussed here in depth, makes the book essential reading to anyone interested in the wartime history of museum collections.

Little would have happened at Tendaguru were it not for the manpower supplied by native Africans, and indeed one of the few constant presences throughout the book is the African guide and supervisor Boheti bin Amrani. Maier explains how various expedition leaders differed in their opinions of the Africans and their abilities, but it is clear that many native workers became skilled at preparation and osteological identification. A few interesting diversions link Tendaguru to other major areas of palaeontological discovery, including the Karoo, Olduvai Gorge and Kadzi. Maier concludes the book with the Tendaguru research renaissance of recent years and with a chapter on recent and current technical work on the Tendaguru fossils. Plates include most available photos of the relevant persons, the quarries and exposed bones, and of the Berlin dinosaur skeletons during the various stages of preparation and mounting. One thing I would have liked to have seen was a 20th century timeline illustrating the chronology of events at Tendaguru. As with other IUP books the standard of editing is very high: a few technical names are spelt wrongly in the last chapter of the book but that's about it.

I thoroughly enjoyed *African Dinosaurs Unearthed* and recommend it to anyone interested in the history of research on Mesozoic fauna. As a story of personal toil in the African bush, as a detailed source on Hennig, Janensch, Cutler and other palaeontologists, as a story of palaeontological discovery, and as a meticulous documentation of the history and discoveries of Tendaguru, it exceeds expectations and sets a high standard.

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The Great Rift Valleys Of Pangea In Eastern North America.

LeTourneau, P.M. and Olsen, P.E. 2003. (Eds), Columbia University Press, New York. Hard cover, two volumes. Vol. 1 ISBN 0-231-11162-2, 240 p., US \$79.50 / £55. Vol. 2 ISBN 0-231-12676-X, 248 p., US \$89.50 / £62.



The central Atlantic margin (CAM) rift province (Olsen, 1997) had a palaeolatitudinal extent of more than 45°, with a regional span covering much of the proto-Atlantic realm from South America to Greenland, and records much of Late Permian to Jurassic time. In North America, the CAM comprises a series of at least fifteen outcropping and sub-surface Mesozoic rift basins that run down the east coast, from Nova Scotia in the north to Florida in the south. These North American basins have been the focus of

much prior work. Lorenz (1988) provided an excellent overview of the historical research in the northerly basins, of which the initial studies took place almost 200 years ago. Froelich & Robinson (1988) and Manspeizer (1988) both published volumes collating recent work on the CAM system. Since 1988, there has been an increase in research on the subject of the North American Triassic–Jurassic rift system, although, until now, aspects of these studies had not been brought together within an up-to-date volume.

This two-volume thematic set is the product of a conference on ‘*Aspects of Triassic–Jurassic Rift Basin Geoscience*,’ held in 1996 at Dinosaur State Park, Connecticut. The conference was the fruit of a period of exceptionally productive 1990s research into the Triassic–Jurassic aged continental rift basins that are located around the central Atlantic margin, not least in part due to the acquisition of new datasets such as the National Science Foundation-funded Newark Basin Coring Project (NBCP), which complemented previously acquired industry core and seismic data. As such, and with a slight narrowing of the original focus of the conference, these volumes represent a collection of state-of-the-art papers covering a broad range of subjects related to the series of Pangaean rift basins that run up the eastern coast of North America.

Each volume is sub-divided into two separate sections, with each section addressing a different aspect of these CAM rift basins, from tectonics and volcanism in Volume One to stratigraphy and palaeontology in Volume Two. Discounting the preface and editorial introduction, which are included in both volumes, there are a total of thirty separate contributions. Each section begins with an introductory chapter, followed by several relevant papers.

Volume One (*Tectonics, Structure, and Volcanism*) provides detail on recent advances in tectonics and structure of supercontinent breakup (Part 1) and the Central Atlantic Large Igneous Province (Part 2). Part 1, containing seven chapters including introduction, deals with both large- and small-scale aspects of the structural evolution of these basins. At the large-scale, Kent & Muttoni detail the likely tectonic configuration and evolution of Pangaea from Permian to Middle

Jurassic time, using palaeomagnetic data. They then apply modern-day climatic zonal models to these reconstructions, based upon relative differences in evaporation and precipitation, in order to demonstrate the existence of an equatorial humid belt during the Triassic. *Schlische* presents an overview of the basin evolution and tectonic history of the North American CAM basins, and reviews the outcrop and sub-surface evidence for changing stress regimes through time, syn- vs. post-depositional structure, post-rift shortening and inversion, and stratigraphic vs. tectonic (or climatic) causes of transitions within basin-fill sequences. Papers by *Altamura, Malinconico, Goldberg et al.* and *Ackermann et al.* focus on studies relating to individual basins within the CAM system. *Altamura* examines evidence for embryonic rifting in southeast Connecticut, using tectonic and radiometric data from the silicified Lantern Hill fault zone. This fault zone, which has the same regional extension direction as the nearby Hartford Basin, developed during the Middle Triassic, approximately 23 Ma before initial syn-tectonic deposition within the Late Triassic Hartford Basin, and earlier than other basins in the CAM system. *Malinconico* uses vitrinite reflectance data to estimate the amount of structural inversion of the Taylorsville Basin in Virginia. VR samples taken from core and well-cuttings indicate a maximum of 2,600 m of inversion-related erosion of the syn-rift sediments. The erosion estimates are used to determine the duration of syn-rift sedimentation, which ended just before the Triassic–Jurassic boundary, and adds to the evidence of a diachroneity in the cessation of rifting between the southern and northern CAM basins. *Goldberg et al.* study core and down-hole data from the NBCP to examine extensional and contractional stress regimes within the Newark Basin of New Jersey. Two separate orientation populations are identified as being consistent with the principal stress directions formed during Late Triassic extension (steeply-dipping fractures) and Early Jurassic compression and inversion (subhorizontal fractures). *Ackermann et al.* examine extensional fractures from quarry outcrops in the Dan River–Danville Basin, Virginia–North Carolina. The fractures are divided into two subsets, based upon length and spatial distribution within the rock volume. The larger subset of structures form master faults and have stress reduction shadows around them; the smaller set of structures exhibit an anticlustering with respect to the larger set as a result of this stress reduction.

Over five chapters, including introduction, Part 2 of Volume One deals with the volcanism of the Central Atlantic Magmatic Province (CAMP), possibly the largest Large Igneous Province (LIP) on Earth (Marzoli *et al.*, 1999). *McHone & Puffer* review the stratigraphic distribution and setting of CAMP lavas, and indicate the widespread environmental consequences of such a series of eruptions over such a brief period of time, with their possible relation to the Triassic–Jurassic mass extinction. *Puffer* uses a global geochemical database to compare and contrast the origin of Pangaean and Rodinian continental flood basalts, identifying two geochemically distinct flood basalt populations. *Ragland et al.* examine a series of olivine–tholeiitic diabase dykes from the southeastern United States, finding a geographically-related trend in concentrations of MgO-standardised oxides. This trend is interpreted to be related to either variation in the depth of melt generation or progressive enrichment of a mantle-sourced melt. *De Boer et al.* use magnetic fabric analysis to investigate magma flow directions within feeder-dyke segments in New England. They indicate that the majority of the flow is along the dyke, with vertical flow only occurring where there is an abrupt change in dyke trend, and use this as evidence to support a plume model for the magma source.

Perhaps of more interest to members of the Palaeontological Association, Volume Two (*Sedimentology, Stratigraphy, and Paleontology*) focuses on the stratigraphic evolution of the basins during, and subsequent to, breakup. This volume is dedicated to John F. Hubert, who has done much to forward the sedimentological knowledge of the Newark Supergroup system, and a short biography is provided. In Part 1, each of the nine contributions focuses on sedimentology and stratigraphic architecture of a different CAM basin. *LeTourneau* provides a detailed study of the auto- and allocyclic controls on stratigraphic architecture in the Taylorsville Basin of Virginia-Maryland. He presents data from released oil-industry boreholes and seismic profiles, together with outcrop information; the dataset includes a technique of using well cuttings to provide a complete picture of gross basinal sedimentology where core is absent. He recognises two tectonostratigraphic cycles for the evolution of this basin, and correlates basinal stratigraphy to the Newark Basin using magnetostratigraphy. In an appendix, he revises and formalises the stratigraphic nomenclature for the Taylorsville Basin. *Tanner & Brown* present a comparison of the tectonostratigraphy of two basins onshore (Fundy Basin) and offshore (Orpheus Graben) eastern Canada. *Gilmer et al.* and *Coffey & Textoris* both present studies of the Durham Sub-basin, in North Carolina. *Gilmer et al.* carry out a provenance study of Upper Triassic fluvial sandstones, using compositional data from the sandstones and lithic grains and pebbles within the sandstones, isolating specific source terranes. *Coffey & Textoris* use changes in palaeosol development in ten outcrop sections to document climate change during basin deposition, showing a transition from humid to arid conditions throughout the time of basin fill. They include outcrop localities and descriptions as an appendix. *McInerney & Hubert* document meandering river facies over a 150 m thick sequence in the earliest sediments of the Hartford Basin, Connecticut, and identify four sedimentation megacycles that may be attributable to precession cyclicity. Like *Coffey & Textoris*, *Tanner* uses palaeosol morphology, including stable isotope data, to infer palaeoclimate in the Fundy Basin of eastern Canada. *Dickneider et al.* examine the organic geochemistry of Lower Jurassic lacustrine black shales in the Hartford Basin, in an attempt to determine the origin of the organic matter, and relate this to depositional environment or palaeoclimate. They show that there is an increase in total extractable organic material in shales before deposition of turbidites, which they interpret as being compatible with a sub-tropical, monsoonal-type climate for Pangaea at this time.

Part 2 of Volume Two comprises ten chapters that focus on Triassic–Jurassic assemblages and faunal change. The Newark Supergroup has long provided a wide selection of both vertebrate and invertebrate tracks (e.g. Hitchcock, 1836), and this section provides new data and interpretations regarding Triassic and Early Jurassic body fossils of tetrapods and insects, as well as reptilian ichnotaxa, from the CAM system. *Lucas & Huber* carry out a review of Pangaeian continental vertebrates, and propose a new biostratigraphic correlation of Late Triassic and Early Jurassic continental rocks across Pangaea based upon tetrapod assemblages. Two chapters, *Fraser & Grimaldi* and *Huber et al.*, examine insect assemblages. *Fraser & Grimaldi* present data on Late Triassic faunal change, using exceptionally preserved insects from a fossil Lagerstätte in the Solite Quarry of the Danville Basin (the same quarry examined by *Ackermann et al.* in Volume One). This extremely rich and diverse faunal assemblage has led to the extension of a number of extant insect families and orders, including thrips and water bugs, back into the Triassic, and provides the first North American record for several others. *Huber et al.* describe a small faunal assemblage in shallow- to ephemeral-lacustrine strata in the Early Jurassic of

three of the northerly CAM basins (Newark, Hartford and Deerfield Basins). This assemblage predominantly comprises beetles in both larval and adult forms and, excepting a single taxon from the southwestern U.S., constitutes the only record of Jurassic insects from North America. The last six chapters concentrate on vertebrate footprints and trackways. Somewhat tenuously linked with other chapters in this section, *Guinness* presents a history and overview of the “brownstone” industry in the Hartford Basin of Connecticut. This Early Jurassic arkosic sandstone from the Portland Formation has been quarried from the mid-seventeenth century to the present day for construction purposes. As a result of the quarrying, numerous reptile tracks from several genera were discovered, of which many are now lost. *Farlow & Galton* also examine dinosaur trackways from the Early Jurassic of Connecticut, this time originating from Dinosaur State Park. These trackways were probably created by a single species of theropod, with stride being short in comparison to the size of the trackmaker; however, it is not possible to tell whether solitary animals or groups made the tracks. *Szajna & Hartline* report on a new vertebrate footprint locality from the Late Triassic of the Newark Basin in Pennsylvania. This locality has furnished tracks that are rarely found in the early Rhaetian section of the Passaic Formation. The assemblage shows few differences from Carnian and Norian localities within the same basin, but fills an important gap in the biostratigraphy of the Newark Basin, enabling constraints to be placed on the timing of major changes in vertebrate footprint assemblages. Both *Smith & Farlow* and *Weems* determine trackmaker type for several ichnogenera using pedal anatomy. *Smith & Farlow* compare phalangeal and digit lengths for theropods, prosauropods and ornithopods. They apply the results to three tridactyl ichnotaxa of the Newark Supergroup, placing them all (and re-interpreting one) as resulting from theropod trackmakers. *Weems* uses a reconstructed foot of the Late Triassic prosauropod *Plateosaurus*, plus footprint measurements, to propose a single trackmaker for two separate ichnotaxa, the tridactyl *Eubrontes* and the tetradactyl *Gigandipus*. Whilst *Plateosaurus* was a tetradactyl dinosaur, the pedal reconstruction indicates that the first digit was highly specialised, extremely flexible, and could be carried out of the way during walking, resulting in a tridactyl footprint. *Olsen & Rainforth* undertake a detailed Pangaea-wide review of an early Jurassic ornithischian ichnogenus, *Anomoepus*, and recognise only the type ichnospecies *A. scambus* among several synonymous forms within the CAM basins of eastern North America. Two appendices are included, the first detailing the complex synonymy presented in the chapter, whilst the second provides a data table of osteometric measurements used in the study.

Each volume is well presented, with the papers split into related sections, followed by a list of contributors and an index. The editorial introduction is reproduced in both volumes, which can be purchased separately. The introduction for each of the four sections provides a concise description of their contents. The papers themselves are well laid out, with the figures, tables and photographic reproduction generally being of high quality. Few errors seem to have slipped through the editing process, although in this copy the first three figures of *Kent & Muttoni* (chapter 3, Volume One) have incomplete captions, and the very first reference in the editorial introduction (a paper by one of the editors, no less) is cited incorrectly in both volumes.

Several of the contributions and methods discussed therein have applications outside of this system of Triassic–Jurassic basins. Many of the structural concepts in the review by *Schlische* can be applied to other extensional settings: *de Boer et al.*'s use of magnetic fabric analysis

is regularly applied to examine flow directions in both igneous and sedimentary rocks, *LeTourneau's* technique of using well-cuttings to examine the fill of continental basins has been modified and applied to the Triassic of the Northern North Sea (Tomasso *et al.*, 2002), whilst several of the osteometric techniques used by authors in the last section of the book have applications to all studies of vertebrate footprints.

Whilst a book on the central Atlantic margin basins of North America must cover all available topics, the recent volume by Hames *et al.* (2003) covers the CAMP volcanism in much more detail, with many of the same authors providing contributions. Having said that, although these volumes appear to have been in limbo for several years, they still represent a comprehensive overview of up-to-date knowledge of the CAM basins in eastern North America. As such, they are worthy complements to earlier compilations such as Froelich & Robinson (1988) and Manspeizer (1988), and worth further investigation.

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Evolution and Palaeobiology of Pterosaurs

Buffetaut, E. and Mazin, J-M. 2003. Geological Society Special Publication 217. ISBN 1-86239-143-2 (hardback). 347 pp. £85.00/US\$142.00. (Reduced prices: GSL £42.50/US\$71.00; AAPG/SEPM/GSA £51.00/US\$85.00)

After dozens of books devoted to dinosaurs, or some subset thereof, it is a pleasure to come upon a book about a different group of fossil reptiles. The pterosaurs were the leathery-winged flyers that flitted over the heads of the dinosaurs from the Late Triassic to the end of the Cretaceous. This book stems from a meeting 'Two hundred years of pterosaurs' held in Toulouse in 2001.

When I come across a multi-authored book that arises from a meeting, my heart usually sinks. In many cases, the only reason for the book is that a number of authors met on a particular day, or days, and presented a mish-mash of papers, that are then gathered together. Fortunately, this book about pterosaurs has a function separate from the meeting. Indeed, the editors rejected many of the papers that were presented, and sought others from people who had not attended the meeting. There are twenty chapters, of which eight present new specimens, two offer original cladistic analyses, four concern function, four describe pterosaur tracks, and two present histology of pterosaur bones.

Among the new pterosaur taxa are two startling specimens from the Santana Formation of Brazil. Eberhard Frey and colleagues describe the ornithocheirid *Ludodactylus*, with a small parietooccipital crest, and a new species of *Tapejara* with a vast, high helmet-shaped crest sticking straight up above its head. These add to the already extensive new knowledge of bizarre, crested pterosaurs from Santana, a diversity and range of form that was not suspected before 1970. In describing a new azhdarchid pterosaur from Romania, *Hatzegopteryx*, Eric Buffetaut and colleagues indulge in a little sizemanship: no pterosaur paper is complete without estimates of giant size, even if the remains are limited. Here, based on some skull and humerus fragments, we appear to have a pterosaur with a skull from 2.9 to 4 metres long. These lengths are larger than any other known head, even than the large ceratopsians *Triceratops* and *Torosaurus*, whose skulls measure up to 2.4 metres long. Doubtless, of course, the head of *Hatzegopteryx* was extremely lightweight, but such a size defies belief. The wingspan is estimated as close to the magical 11–12 metres, the size predicted for *Quetzalcoatlus* from Texas, and numerous other recently reported giant pterosaurs. I don't doubt the estimates—after all, with an aerodynamically efficient organism, wings and body masses must be in proportion, so it is meaningful to make such estimates. It is interesting that all giant pterosaur sizes converge on a maximum wingspan of 11–12 metres, larger than any known bird, but perhaps the absolute maximum limit for any flying vertebrate.



The most important papers in the volume are the two original cladistic analyses of pterosaur relationships, by Alexander Kellner and David Unwin. Both authors had begun trailing their phylogenies as long ago as 1995 (Kellner) and 1992 (Unwin), so it is good to see the end results. Both analyses use the same taxa, and many of the same characters, which is inevitable, and the broad pattern of relationships that emerges is similar in both cases. However, there are differences in the placements of *Anurognathus*, species of *Ornithocheirus*, *Pteranodon*, and *Tupuxuara*, and someone will have to make a further analysis to determine which is closer to the truth. From the two presentations, Unwin's analysis appears more thorough, and he has based it almost entirely on first-hand observations of virtually every pterosaur specimen in museums around the world.

The palaeobiological chapters include a remarkable review by Eberhard Frey and others of soft-part preservation in pterosaurs. The wing membranes, supposed hair, and other structures are well enough known, but Frey and colleagues report a wing of *Rhamphorhynchus* with its blood vessel system preserved, and other specimens with claw sheaths, webbing between the toes, and soft-tissue head crests. The head crests of Santana pterosaurs show a toughened leading edge, and a fibrous zone at the bottom, with a thick pennant of skin and other soft tissues behind forming, in some cases, a massive rudder-like structure on top of the head. All of these fossils prove, if any more proof were required, that the pterosaur wing was deep, extending back to the hindlimb, that there was a broad flight membrane between the hindlegs, and that pterosaurs lurched about on all fours when walking.

The renaissance in the study of pterosaurian tracks is well represented. The paper by Jean-Michel Mazin and colleagues is important as the first serious account of the spectacular Crayssac site, discovered in the early 1990s. They describe thirty separate trackways, each showing quadrupedal locomotion—the hindlimbs some distance apart, in John Wayne posture, and the hands touching down even further out to the side.

Keen pterosaur spotters will be aware of the spectacular growth in knowledge of the group since 1970. The number of species described has doubled since then, with particularly important additions to knowledge from Santana and China. Debates about palaeobiology have focused on aerodynamics and walking: pterosaurs were sexed up in the 1970s and 1980s, when a new model was presented of sleek, narrow-winged albatross-like animals that soared and swooped at speed, and that ran about as efficient little bipeds on the ground. Close study of the fossils have shown that both assumptions, sadly, were wrong. Soft tissue remains in so many specimens have confirmed that the wing membranes were extensive, and skeletal anatomy, wing membranes, and especially fossilized trackways, have confirmed that ground locomotion was awkward. This debate is now roundly resolved, and the present book gives a mature state-of-the-art presentation.

The book is attractively presented. The editors have clearly worked well to exclude waffle and poor presentation, and the Geological Society Publishing House has made a good job of presenting a great deal of material in a compact book. The images are generally well reproduced, although the printing quality detracts a little from some of the photographs of

soft tissues. The only thing missing perhaps is a definitive catalogue of all valid pterosaurian taxa, and their distributions in time and space, but that is admirably fulfilled by the pterosaur database website, at <<http://www.pterosaur.co.uk/>>.

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Catalogue of the Marine Gastropod Family Fascioliidae

Snyder, M.A. 2003. Academy of Natural Sciences, Philadelphia, Special Publication 21. ISBN 0-910006-57-1 (paperback). 431pp. US\$38.50

Without the benefit of omniscience, it is difficult to review a catalogue of a taxonomic family. This extremely comprehensive work covers the nomenclature and synonymies for all 5,600 fossil and recent species of Fascioliidae, a family of carnivorous whelks dating from the early Cretaceous (110 MYA). This is the first attempt since the 18th century to deal with the nomenclature of this group. Although Snyder makes no attempt to present a new phylogenetic treatment of the family, it is an important addition to other taxonomic works.

The bulk of the text is organised alphabetically by species-groups. For each name the original genus and bibliographical reference are listed, with geographic and/or stratigraphic distribution, as well as a complete synonymy; each synonym has its own taxonomic, bibliographical, and distributional information. In addition, there is a similarly sized section organised into 18 'functional groups' by stratigraphic or generic affinities. Snyder stays on the fence about whether these are subfamilies, families, tribes or whatever; however, this abbreviated index may improve utility for specific projects. The third major section of the text is the 106-page bibliography, which is of immense value in itself.

Reading this book back-to-front, I was quickly able to grasp the organisation and structure of the catalogue, without depending on technical instructions for use. (The author does include methodological remarks at the beginning of each section, which are of supplementary use.) My only minor disappointment was that the species entries do not refer to where type material is deposited, but that is a point understandably outside the scope of this edition.

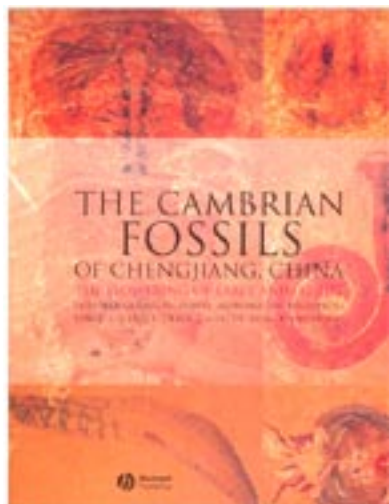
This is purely a catalogue; the lack of figures makes it useful for looking things up, but not for identifying species. The contents are straightforward, with a concise discussion of the biology of the group. The book is well worth the price for the bibliography alone, and it is a valuable addition to any malacological library.

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The Cambrian fossils of Chengjiang, China. The flowering of early animal life

Hou, Xian-Guang, Aldridge, R.J., Bergström, J., Siveter, David J., Siveter, Derek J. and Feng, Xiang-hong. 2004. Blackwell Science, Oxford. ISBN 1-4051-0673-5 (hardback). 233pp. £64.00.



Exceptional faunas have been well served by publications in recent years with a number of volumes treating either a series of faunas or single examples thereof. This book is an addition to the latter, devoted to illustrating and providing brief descriptions of selected fossils from the Chengjiang exceptional fauna, a wonderful example from the Lower Cambrian of eastern Yunnan, China. Remarkable progress has been made in our understanding of this fauna since its discovery at Maotianshan shortly after 3pm on Sunday 1st July 1984, although the same locality had yielded the appendages of a bivalved arthropod previously (see discussion in Zhang *et al.* 2001). Much of the research since has been undertaken by a series of Chinese research teams and their collaborators, the

leader of one of which, and the discoverer of the fauna, is the senior author of this book.

There is a voluminous set of primary literature about the Chengjiang fauna in Chinese. Literature published in English includes the monographic treatment of certain groups (*e.g.* arthropods, Hou and Bergström 1997) and some general papers on the fauna as a whole, but predominantly comprises descriptions and interpretations of individual taxa. A feature of the latter has been the often contradictory interpretation of the affinities of certain taxa by different research groupings each using a subset of the total material available. Compounding this confusion, new finds have been reported at an amazing rate. Illustrating the latter point, a note on p. 217 indicates that while this book was in press nine new species were described in a single paper. Clearly, a review volume of this kind, acting as some sort of interim report, is extremely welcome. The extended review by Chen and Zhou (1997) and shorter reviews by Bergström (2001) and Hagadorn (2002) are in English, but volumes such as this have, however, only been published previously in Chinese.

The enthusiastic foreword by Richard Fortey summarises the scope, and potential audience, of this latest contribution. He encourages the reader to view the book as “a field guide to the Chengjiang fauna, ... the equivalent of one of those manuals people take to the Great Barrier Reef to identify the marine life,” but emphasises that despite “the aesthetic qualities of the images” it is “more than a picture gallery”; it’s a stocktake of our current knowledge of certain aspects of the Chengjiang fauna. There is a useful general introduction to the geology of the fauna, a well-referenced review of selected taxa, and, as an added bonus, a series of outstanding colour photographs. The complex (weathered) mineralogies, with the specimens picked out

in shades of reds, browns, silver and black stand out against the homogenous buff, yellow and white tones of the matrix. Digital enhancement of an image of *Myllokunmingia fengjiaoa* (Figure 19.1a and b) hints at the potential this technique may have in future study of this and similar faunas; see also Bengtson (2000).

Those familiar with books such as that by Briggs *et al.* (1994) on the Burgess Shale fossils will recognise the structure and style of this contribution to the genre. In the first part (Chapters 1–6) there is a brief introduction to the geological context of the Chengjiang fauna, followed by short (1–2 page) summaries covering its evolutionary significance, discovery, initial study, geographic distribution, geological setting, taphonomy and palaeoecology. These are accompanied by a nice set of colour photographs, largely of the scenery and specific localities, plus colour illustrations of stratigraphical columns and palaeogeographic and locality maps. These sections are general in their nature, and aspects—notably the taphonomy and palaeoecology—have yet to be researched fully; the listing of the various localities that have yielded soft-bodied faunas and the summary of the lithostratigraphy are particularly useful. Remarkably, as Figure 4.4 illustrates, soft-bodied organisms are now known from at least 19 separate localities in the Kunming to Chengjiang area, distributed over an area of circa 3,500km²; other outlying localities extend this area to 20,000 km² (Zhang *et al.* 2001). The section on the discovery of the fauna includes a brief summary of the results of Hou Xian-guang’s ten weeks of fieldwork in 1984: ‘the collection of abundant well-preserved bradoriid specimens’, his finding the oldest trilobites at various localities, and, oh yes, I nearly forgot, ‘the discovery and collection of many fossils with preserved soft parts’ at various localities in Yunnan province (so just an average season then). The section includes images of Hou Xian-guang at the locality where he first discovered soft-bodied fossils and, a nice touch, also of the relevant pages of his field diary and field notebook complete with thumbnail sketches of some of the fossils—clear echoes of the reproduction by Briggs *et al.* (1994) of the relevant pages of Walcott’s notebook detailing his discovery of the Burgess Shale fauna.

The second, longer, part describes selected taxa for the following groups: Algae, Porifera, Cnidaria, Ctenophora, Nematomorpha, Priapulida, Hyolitha, Lobopodia, Anomalocarididae, Arthropoda, Brachipoda, Vetulicolia, Chordata and enigmatic animals; in all 92 taxa are described in Chapters 7–20. As in Briggs *et al.* (1994) two facing pages are devoted to each taxon. The left hand provides a summary of its anatomy, affinities, ecology, and global and temporal distribution, and, in some cases, an artist’s reconstruction of the living animal; the authors of key references are listed. The right hand page provides at least one photograph of a representative specimen; often there are several.

As the authors note in the preface (p. xi) “It was not intended that every known species should be treated herein,” and, of course, the rarity of specimens of some taxa means aspects of their anatomy and mode of life remain unknown. Nevertheless, and my only quibble with this book, the basis for the inclusion of some taxa (and, by extension, the exclusion of others) is, in a few cases, not obvious. *Yunnanocaris megista* is known only from two bivalved carapaces. Two pages are devoted to the single specimen of the arthropod *Dongshanocaris foliiformis*, which by the authors’ admission is “poorly preserved,” its morphology “difficult to discern” and its mode of life “uncertain.” Yet *Ercaia minuscula*, the small (2–4mm long) arthropod (a possible crustacean),

is mentioned only in Chapter 21, a listing of species recorded from the Chengjiang biota; this is despite the implications this taxon may have for the evolution of a specific group within the Arthropoda, and, given its size, the insight it provides into the fossil record of 'meiofaunal' animals. It makes me wonder about the relative importance of some of the other taxa treated only in the species list. Ultimately the specimen of *Dongshanocaris foliiformis* may tell us more about the taphonomic history of the fauna than its palaeobiology. What is presumably the carapace cuticle is defined in white, yet that covering the series of appendages is preserved in a red mineral; relative to the long axis of the carapace the appendages are progressively displaced laterally towards the anterior.

Both the palaeogeographic and temporal separation of the Burgess Shale and Chengjiang faunas are pronounced, and each was preserved in a different environment, particularly given the suggestion (p. 21) that the 'claystones' containing the Chengjiang fossils may have accumulated in waters "that were ... below normal salinities." Yet the line-up of taxa described by Hou and his colleagues includes some 'familiar faces' from the Burgess Shale—at least at the generic level—*Leptomitrus*, *Dinomischus*, *Eldonia*, *Canadaspis*, *Leanchoilia*, *Waptia* and possibly *Odaraia*. *Naraoia* is present (the holotype of the Chengjiang species, *N. longicaudata*, was among the first specimens to be recovered on the first day of excavation). These similarities with the Burgess Shale fauna are intriguing. Is it more than a function of looking through the same taphonomic window? There are various small Chengjiang arthropod taxa; the examples *Kunmingella* and *Occacaris* are described in this book. What significance do we attach to the absence in the Burgess Shale of arthropods of an equivalent size? What about the various taxa with possible/probable/definite* hemichordate/chordate/craniate* affinities (*delete according to personal preference): how will these various 'new signings' to the squad of Cambrian fossils shape up after a few seasons; has their taxonomic diversity been increased artificially in the Chengjiang fauna by the vagaries of the preservational processes? This book is an excellent introduction for anyone interested in the palaeobiology of not only Cambrian ecosystems but also exceptional faunas in general. It is a platform from which to follow discussion on topics such as these, reports of new forms and re-interpretations of those known already, in the coming years. It will be interesting to see what the contents of a similar book will be in 20 years' time: Chengjiang fossils, much done—more to do.

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Patrick J. Orr

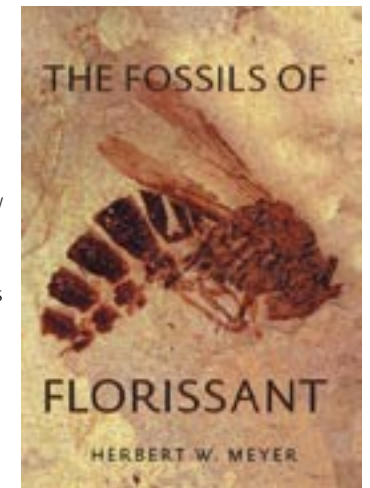
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The fossils of Florissant

Meyer, H.W. 2003. Smithsonian Books, Washington and London, ISBN 1 58834 107 0 (hardback). xiii + 258 pp. £30.00.

The attractive dust-cover of this book is sufficiently enticing to make any fossil enthusiast want to look inside, and he/she will not be disappointed. The Eocene rocks of Florissant, Colorado, have long been known to contain a wealth of fossils, but in no previous publication has their beauty and variety been so well illustrated. What is more, although a few parts might be a little hard going for non-scientists, in general the accompanying text is written in such a way as to appeal to both professional palaeontologists and interested members of the public. Use of both common and Latin names for the fossil groups discussed and figured helps in this respect.



The book stems from a major compilation of data by Meyer and colleagues on the fossils that have been recorded. These are housed in many museum and university collections, mainly in the USA but also in the UK (the largest of which is in The Natural History Museum, London). The database is maintained by the (US) National Parks Service and is available on the Web. The numerous illustrations in colour are of some of the finest examples of the fossils that have been described previously. They represent only a small fraction of the material that Meyer has examined.

The first two chapters set the scene by discussing the current location of the Florissant Formation, high in the Rocky Mountains, and the 130-year history of scientific investigation of the lacustrine and volcanic deposits from which more than 1,700 fossil species have been described. A chapter on the geological setting of the formation and taphonomic processes follows. This helps to put the sedimentary succession and its fossils into context, paving the way

for an important chapter in which an attempt is made to describe the scene around ancient Lake Florissant about 34 million years ago. The climate and vegetation, the complex of habitats represented, the impact of volcanic eruptions near-by and, on a smaller scale, plant-insect relationships (of which there is much evidence in the form of galls and feeding traces on leaves) are all discussed.

It is unfortunate that vertebrate remains apart from fish are rare and usually fragmentary. There is clearly a taphonomic bias in favour of plants and invertebrates. This missing evidence of animal life does not, however, prevent the Florissant assemblage being regarded by Meyer as the best example known to date of a latest Eocene upland ecosystem, immediately preceding a global cooling of the climate, although not all authors accept his high-elevation estimate.

Two lengthy chapters on the plants (53 pp.) and invertebrates (47 pp.), a shorter section on the vertebrates (12 pp.), and a brief epilogue (2 pp.) comprise the rest of the text. The chapter on plants includes illustrations of stumps of giant petrified *Sequoia* (redwood), of which, sadly, only a small proportion remains, the site having been plundered by tourists and others, especially during the late 1800s, until 6,000 acres (2,428 hectares) of the fossil beds were established as a National Monument in 1969. Most of the remains are, however, much smaller in that they consist largely of leaves, fruits and other parts of plants delicately preserved in fragile paper-shales. Among the illustrations are thin sections of fossil wood, gymnosperm foliage, cones and seeds, a wealth of angiosperm leaves and fruits, the remains of flowers and, on a microscopic level, examples of some of the pollen grains and diatoms that have been extracted from the deposits.

The invertebrates include spiders, millipedes, insects, ostracods, bivalves and gastropods. The huge number (more than 1,500) of species of spiders and insects that have been described may be larger than the true representation (their taxonomy is in need of revision) although, as now, both groups were extremely diverse during the Eocene. Among the insects discussed and illustrated are mayflies, damselflies, dragonflies, grasshoppers, termites, lacewings, beetles, weevils, midges, flies, wasps, bees, moths and butterflies.

There are two appendices. The first (42 pp.) is a complete list of the fossils that have been found in the formation. The second (just over 3 pp.) contains notes on museums with important collections of Florissant material. There are also two sets of references: one is a short list of titles that provide relevant general information; the other is a 16-page bibliography of nearly all the publications that pertain to Florissant.

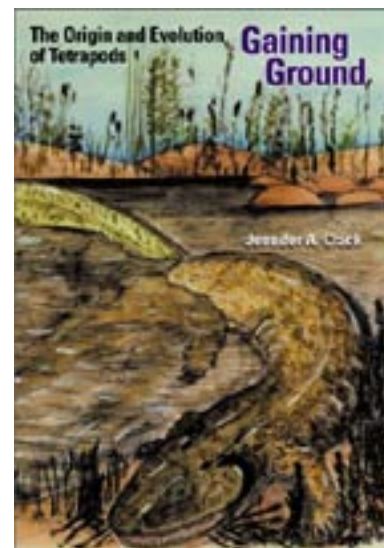
I recommend this book especially to palaeobotanists and palaeoentomologists, but anyone with an interest in what the world was like in the geological past would find much between its covers to feed the imagination.

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Gaining Ground: The Origin and Evolution of Tetrapods

Clack, J.A. 2002. Indiana University Press, Bloomington. ISBN 0-253-34054-3 (hardback) 369pp. £37.95.



I was really looking forward to reading this book. Thinking back to vertebrate palaeontology, I have always found the origin of tetrapods to be a confusing field. At one point, I had devised pneumonics to help me remember the monikers of the important fish-like amphibians and amphibian-like fish (*Panderichthys* and *Eusthenopteron*, *Balanerpeton* and *Crassigyrinus*). The recent literature in major scientific journals testifies to just how topical is the subject of the origin and evolution of tetrapods. However, this subject mostly demonstrates the impossibility of a comprehensive work at this stage in the field. Nevertheless, in *Gaining Ground* Clack presents a thorough if somewhat personal review of this controversial and dynamic subject in early vertebrate evolution.

As a teaching aid, I have found the bibliography to be potentially the most valuable product of this work—Clack reviews the major relevant literature from the 1930s to present. (Just two or three papers from earlier than this get a look in.) Figures, largely reproduced from cited works, add to the text but are not always satisfactory representations. These let the book down—nicely prepared specimens, bad illustrations.

Among the many topics covered in *Gaining Ground*, Clack's interesting discussions and expansions of individual characters and their dynamics through the span of tetrapod evolution are highlights. A good number of taxa, and several of their diagnostic features, are presented with reference to trees. These, also, are well discussed and presented, but do not always contribute in an holistic sense to answering what, exactly, the book is about. Early Tetrapods, of course, are known from a number of particular key localities; sometimes, it is hard to view these crucial early faunas in the wider context they deserve.

Despite my early excitement, I finished *Gaining Ground* with mixed feelings; although I did learn a lot about tetrapods, I feel little closer to a thorough understanding of the fauna. Altogether Clack has produced a stab at an impossibly large and difficult topic—containing a great deal of information of both scientific and more general interest, in the end this book does not succeed in what it set out to do. A satisfactory synopsis of this research field (addressed at either an academic or popular audience) is still lacking.

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