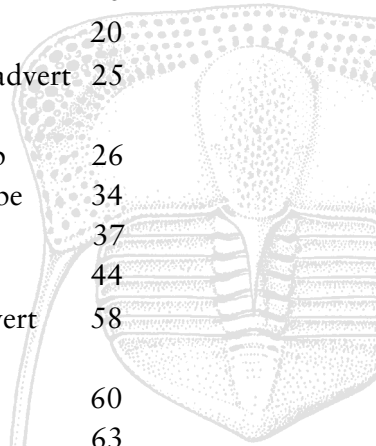


The Palaeontology Newsletter

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Reminder: The deadline for copy for Issue no 60 is 14th October 2005.

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

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Association Business

The Palaeontological Association: Draft Annual Report for 2004

Nature of the Association. The Palaeontological Association is a Charity registered in England, Charity Number 276369. Its Governing Instrument is the Constitution adopted on 27th 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 1,288 on 31st December 2004, an overall increase of 53 over the 2003 figure. There were 791 Ordinary Members, an increase of 36; 158 Retired Members, an increase of 18; 340 Student Members, a decrease of one; and one honorary member. There were 99 Institutional Members in 2004. Total Individual and Institutional subscriptions to *Palaeontology* through Blackwell's agency numbered 378. Subscriptions to *Special Papers in Palaeontology* numbered 182 individuals and 94 institutions, a decrease of 20. Regular orders through Blackwell's agency for *Special Papers in Palaeontology* totalled 41 copies. Sales to individuals through the Executive Officer of current and back numbers of *Special Papers in Palaeontology* yielded £9,148. Income from sales of *Field Guides to Fossils* amounted to £4,339. Sales of "Fold out Fossils" totalled £42.

Finance. Publication of *Palaeontology* and *Special Papers in Palaeontology* is managed by Blackwell's, who also make sales and manage distribution on behalf of the Association. In addition to the fee that they take directly from the subscribers, the Association paid them a further fee of £4,845. The Association gratefully acknowledges the donations from Members to the Sylvester-Bradley Fund, which amounted to £778. Grants from general funds to external organisations, for the support of palaeontological meetings and projects, totalled £16,779. The Association remains a Tier 1 sponsor of *Palaeontologia Electronica*.

Publications. Volume 47 of *Palaeontology*, comprising six issues and 1,653 pages in total, was published at a cost of £80,223. The number of pages for *Palaeontology* 47(2) – (6) was increased to 261, 347, 279, 263 and 315 respectively to assist in alleviating some of the backlog of manuscripts. *Palaeontology* 47(6) was dedicated to Prof. Jake Hancock. *Special Papers in Palaeontology* 71 on "Fossils of the Miocene Castillo Formation, Venezuela: contributions on neotropical palaeontology", edited by M.R. Sánchez-Villagra and J.A. Clack, and *Special Papers in Palaeontology* 72, on "Lower Jurassic floras from Hope Bay and Botany Bay, Antarctica," by P.M. Rees and C.J. Cleal, were published at a cost of £8,947 and totalled 202 pages. There were no Field Guides to Fossils or Fold-out Fossils for 2004.

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



Meetings. Three meetings were held in 2004, and the Association extends its thanks to the organisers and host institutions of these meetings.

- a. **Forty-Seventh Annual General Meeting** was held on 17th – 20th December. The Annual Meeting was held at the Université des Sciences et Technologies de Lille at Villeneuve d'Ascq. Dr Thomas Servais with much local support organised the meeting. The President's Award was made to C.M. Belcher (Royal Holloway). Council Poster Prizes were presented to J. Pollitt (University of Bath) and L. Muir (Natural History Museum). On the final day field trips were undertaken to Boulonnais and Brabant. There were 270 attendees.
- b. **Progressive Palaeontology.** 9th – 10th June. The annual open meeting for presentations by research students was organised by James Wheeley at the University of Cardiff.
- c. A symposium at the **British Association Festival of Science**, held in Exeter on 4th – 11th September, on “Fossil Fakes and Forgeries”, was organised by Dr Mark Purnell.

Awards. The Lapworth Medal, awarded to people who have made a significant contribution to the science by means of a substantial body of research, was made to Prof. J.W. Valentine. 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 H. Wilson (University of Yale). Dr Stuart McKerrow was awarded Honorary Life Membership. The Mary Anning award, for an outstanding contribution by an amateur palaeontologist, was made to Mr Bjørn Funke (Oslo) and Mr Phil Bennett (Bristol). Sylvester-Bradley Awards totalling £9,810 were made to Botting, Braznell, Ghobadipour, Harvey, Kubo, Miller, Moore, Nunn, Pollitt, Popov, Raisodissat and Wheeley. Two new “Golden Trilobite” awards, to recognise amateur and institutional websites that promote palaeontology, were presented and links were made to the Association website.

Council. Prof. Jake Hancock, a long standing member of Council, passed away during the year. The following members were elected to serve on Council at the AGM on 18th December 2004: Sir Peter Crane (President), Dr D. Loydell (Vice President), Prof. D.A.T. Harper (Chair of the Publications Board), Prof J.C.W. Cope (Treasurer), Dr M.P. Smith (Editor), Dr D. Siveter (co-opted, Annual meeting organiser 2005), and Dr N. Macleod (Ordinary Member). Drs Modesto and Rauhut were co-opted as editors and will not be Council members. At the AGM the following members stepped down from Council: Prof. Derek Briggs and Prof. P. Ahlberg. Dr Thomas Servais was co-opted to remain on Council to allow an overlap with Dr D. Siveter. 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 and the University of Lille 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 £455,880 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 £76,528 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 webpages. During the year it was agreed to establish a new position on Council, Chair of the Publications Board. This Board will be responsible for strategic issues, and policy development and evaluation. Prof. Harper (Chair), Prof. Batten, Dr Harper, Dr Smith, Iain Stevenson (External Consultant) and Miriam Maus (Blackwell) will act as the members of the Publications Board. Blackwell have provided additional services to the Association including an e-alert service and a publicity service including press releases. The new Blackwell online editorial system had proved satisfactory. A new format for *Palaeontology* and *Special Papers in Palaeontology* was established during the year and will be in place for the first issues of 2005. The Association continued to recognise the increasing numbers of members in Europe and held the Annual meeting at the University of Lille. The Annual Address, given at the Annual Meeting and entitled "Palaeontologica profundis", was presented by Prof. Stephan Bengston and was attended by 270 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 following international symposia: Evolution and development of the vertebrate dentition (University of London); 9th Symposium on Mesozoic Ecosystems and Biota (Manchester 2006); NAPC 2005 (Halifax, Nova Scotia); ICOS Symposium 2006 (Leicester); Fifth International Brachiopod Symposium; and British Association meetings in Exeter (2004) and Dublin (2005). The Association continues its membership of the International Palaeontological Association. The Association continues to support the *Treatise on Invertebrate Paleontology*, with financial support of \$5,000 per year for the next two years. The Sylvester-Bradley Fund continues to attract a large number of quality applications. 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. The Association held the Chair and Secretarial posts of the Joint Committee for Palaeontology during the year. The Association continues to be proactive in generating publicity for palaeontology with major press initiatives and a continued high profile on television. It is widely recognised that the success of the Association's team in *University Challenge* was a highlight of the year.

Forthcoming plans. In 2005, a similar programme of meetings and publications will be carried out as in 2004, 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. The Annual Meeting has continued to develop as one of the major international palaeontological meetings and will be held at the University of Oxford in 2005.

Howard A. Armstrong
Secretary

<secretary@palass.org>



Subscriptions Renewals

Annual renewal of subscriptions is currently by far the most time-consuming aspect of running the Pal Ass and we are constantly looking for ways to make it run more efficiently. We earnestly beg all members to pay when first asked to, so that we do not have to expend unnecessary effort and expense on follow-up mailings *etc.*

Currently, we follow slightly different procedures for members in different parts of the world, and we urge you to familiarise yourselves with these as they apply to you.

Members in the UK

The invoice goes out with the last Newsletter of the year, in November. The cheapest way for you to pay is by cheque. You can also use a Credit or Debit Card, either at the online secure payment site at <<http://palass.org/>> or by filling in the card details on the subscription form. If you pay using a card, the cost to you will be slightly greater because we pass on the processing costs. Many UK members now pay by Standing Order (the form is on the back of the subscription form) and you are encouraged to do this. Please inform us if your e-mail address changes. If you leave payment until after 1st January, then we charge an additional £1 late payment fee. A standing order avoids this.

Members in Europe (both within and outside the EU)

We will send you an invoice, as a separate mailing, at the beginning of November, priced in Euros. We will also give an equivalent price in GB pounds for people who want to pay by cheque drawn on a UK bank. People in Europe overwhelmingly pay by card, either by completing and returning the form or by using the online secure payment site at <<http://palass.org/>>. We convert this into GB pounds at the time of processing. We do not add anything further to cover the card processing costs. These, and the additional costs of mailing publications to Europe, are covered within the subscription price. However, we shall add a small additional supplement for late payment.

If you are an Ordinary or a Retired Member (not a student), we shall assume that we may keep your card details until the *following* year and then deduct your subscription again (assuming your card has not expired by then) in early November. There will be an opt-out box on the form that you can tick if you do not want us to do this. If we take a further subscription in this way, we will not send you another invoice, thus saving postage.

Members in the USA, Canada, and the Rest of the World

We will send you an invoice, as a separate mailing, at the beginning of November, priced in US Dollars (Pesos if you are in Argentina). We will also give an equivalent price in pounds for people who want to pay by a sterling cheque drawn on a UK bank. Most people outside the USA (and many within) pay by card, either by completing and returning the form or by using the online secure payment site at <<http://palass.org/>>. We convert this into GB pounds at the time of processing. We do not add anything further to cover the card processing costs. These, and the additional costs of mailing publications to the North America and the Rest of World postal zones, are covered within the subscription price. However, we shall add a small additional supplement for late payment (after 1st January). US members are welcome to pay by check in US Dollars drawn on a US bank.



If you are an Ordinary or a Retired Member (not a student), we shall assume that we may keep your card details until the *following* year and then deduct your subscription again (assuming your card has not expired by then) in early November. There will be an opt-out box on the form that you can tick if you do not want us to do this. If we take a further subscription in this way, we will not send you a further invoice in that year, thus saving postage.

The Secure Payment pages at <<http://palass.org/>>

Online payment saves postage, and is efficient. Only one person at the Association has the codes to decrypt and process your payments. In the three years that we have run this scheme, we have not had any security problems. There have been three minor problems: 1. If you are a new user of this system, you might get a non-recognition message from your computer that sounds rather threatening. We recommend that you ignore it and carry on. 2. Very occasionally, server problems at our end mean that messages don't reach us, or reach us blank (without indication of whom they are from). In this case (five cases in 500 last year) you will be unaware that your payment has failed until we contact you requesting payment. 3. Every time you hit Enter, we will get a copy of your payment details. The record so far is 12. Almost always we have managed to sort these out and take only a single payment.

Good subscribing...

Tim Palmer

Executive Officer

<palass@palass.org>

Nominations for Council

At the AGM in December 2005, the following vacancies will occur on Council:

Vice-President
Newsletter Editor
three handling editors
one Ordinary member

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. Nominations must be accompanied by the candidates' 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 **Monday, 3rd October 2005**. They should be sent to the Secretary: Dr Howard A. Armstrong, Department of Earth Sciences, University of Durham, Durham DH1 3LE, email <secretary@palass.org>.



Awards and Prizes

Nominations are now being sought for the Hodson Fund and Mary Anning Award.

Hodson Fund

This award is conferred on a palaeontologist who is under the age of 35 and who has made a notable early contribution to the science. Candidates must be nominated by at least two members of the Association, and the application must be supported by an appropriate academic case. Closing date for nominations is **1st September 2005**. 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 2005**. The award comprises a cash prize plus a framed scroll, and is usually presented at the Annual meeting.

Sylvester-Bradley Awards

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. The deadline for applications is **1st November 2005**.



THE PALAEOLOGICAL ASSOCIATION Registered Charity No. 276369
STATEMENT OF FINANCIAL ACTIVITIES FOR THE YEAR ENDED 31st DECEMBER 2004

	General Funds £	Designated Funds £	TOTAL FUNDS £	TOTAL 2003 £
INCOMING RESOURCES				
Subscriptions	66,164	0	66,164	65,015
Sales:				
<i>Palaeontology</i>	119,011			
<i>Special Papers</i>	13,325			
Offprints	4,512			
Fossil Guides	4,810			
Postage & Packing	<u>829</u>			
Total Sales	142,487	0	142,487	147,957
Investment Income & Interest	15,259	3,208	18,467	16,167
Donations	0	3,059	3,059	2,282
Sundry Income	<u>2,915</u>	<u>0</u>	<u>2,915</u>	<u>3,206</u>
Total	226,825	6,267	233,092	234,627
RESOURCES EXPENDED				
Publications:				
<i>Palaeontology</i>	80,223			
<i>Special Papers</i>	8,947			
Offprints	5,519			
Fossil Guides	2,398			
Newsletters	18,584			
Carriage & Storage	573			
Management	<u>33,328</u>			
Total Publications	149,572	0	149,572	148,458
Scientific Meetings & Costs	11,481	0	11,481	6,615
Grants	<u>5,298</u>	<u>10,742</u>	<u>16,040</u>	<u>14,718</u>
Total Charitable Expenditure	166,351	10,742	177,093	168,612
Marketing & Publicity	4,826	0	4,826	2,640
Administrative Expenditure	<u>40,470</u>	<u>0</u>	<u>40,470</u>	<u>40,546</u>
Total	211,647	10,742	222,389	211,798
NET INCOMING RESOURCES	15,178	-4,475	10,703	22,829
INVESTMENT GAINS				
Realised Gain	595			
Unrealised Gain	<u>17,316</u>			
	17,911	0	17,911	26,964
NET MOVEMENT IN FUNDS	33,089	-4,475	28,614	49,793
BROUGHT FORWARD	422,791	81,003	503,793	454,000
CARRIED FORWARD	<u>455,880</u>	<u>76,528</u>	<u>532,408</u>	<u>503,793</u>



Notes to the Financial Statements for the year ended 31st December 2004

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 2004 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 2004 and the results for the year ended on that date.

1.2 Fund Accounting

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

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

Sylvester Bradley Fund: Grants made to permit palaeontological research.

Jones Fenleigh Fund: Grants to permit one or more students annually to attend the meeting of the Society of Vertebrate Palaeontology and Comparative Anatomy (SVPCA).

Hodson Fund: Awards made in recognition of the palaeontological achievements of a worker under the age of 35.

1.3 Incoming Resources

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

1.4 Resources Expended

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

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

1.5 Investments

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



2. Analysis of Financial Resources Expended

	Staff Costs	Other Costs	Total 2004	Total 2003
Publications	25,981	122,994	149,572	147,279
Scientific Meetings & Costs		11,481	11,481	6,615
Grants		16,040	16,040	14,718
Marketing & Publicity		4,826	4,826	2,640
Administration	25,981	14,489	40,470	40,546
	<u>51,962</u>	<u>169,830</u>	<u>222,389</u>	<u>211,798</u>

3. Staff Costs

	Salary	National Insurance	Pension Contributions	Total 2004	Total 2003
Publications – 1 employee (2003 – 1)	20,334	2,597	3,050	25,981	20,912
Administration – 1 employee (2003 – 1)	20,334	2,597	3,050	25,981	20,912
	<u>40,668</u>	<u>5,194</u>	<u>6,100</u>	<u>51,962</u>	<u>41,824</u>

4. Trustees Remuneration and Expenses

Members of Council neither received nor waived any emoluments during the year (2003: nil).

The total of travelling expenses reimbursed to 12 Members of Council amounted to £4,075 (2003: £6,624)

5. Costs of Independent Examiner

	<u>2004</u>	<u>2003</u>
Examination of the accounts	300	300
Accountancy and payroll services	1,000	1,000
	<u>1,300</u>	<u>1,300</u>

6. Stocks

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

7. Debtors

	<u>2004</u>	<u>2003</u>
Accrued income – receivable within one year	18,031	32,186
Prepayment re 2006 conference	500	500
	<u>18,531</u>	<u>32,686</u>

8. Creditors – Falling Due within One Year

	<u>2004</u>	<u>2003</u>
Social Security Costs	4,314	3,340
Accrued Expenditure	23,845	22,078
	<u>28,159</u>	<u>25,418</u>



BALANCE SHEET AS AT 31st DECEMBER 2004

2003 £		2004 £
	INVESTMENTS	
264,521	At Market Valuation	279,148
	CURRENT ASSETS	
243,982	Cash at Banks	268,670
18,226	<i>Field Guide</i> Stocks at Valuation	14,897
<u>32,686</u>	Sundry Debtors	<u>18,531</u>
294,894	Total	302,098
	CURRENT LIABILITIES	
30,203	Subscriptions in Advance	20,679
<u>25,418</u>	Sundry Creditors	<u>28,159</u>
55,622	Total	48,838
<u>239,273</u>	NET CURRENT ASSETS	<u>253,260</u>
<u>503,793</u>	TOTAL	<u>532,408</u>
	Represented by:	
422,791	GENERAL FUNDS	455,880
	DESIGNATED FUNDS	
45,056	Sylvester Bradley Fund	38,294
16,189	Jones-Fenleigh Fund	19,111
<u>19,758</u>	Hodson Fund	<u>19,123</u>
<u>81,003</u>		76,528
<u>503,794</u>	TOTAL	<u>532,408</u>

These financial statements were approved by the Board of Trustees on March 16th 2005.

P. Crane

J.C.W. Cope

H.A. Armstrong



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 2004, 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.

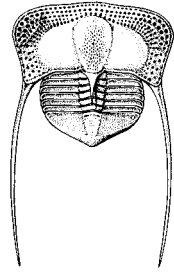
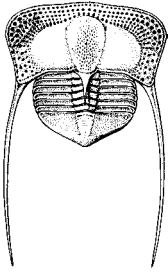
1 March 2005



THE PALAEOLOGICAL ASSOCIATION Registered Charity No. 276369

DESIGNATED FUNDS: INCOMINGS AND OUTGOINGS 2004

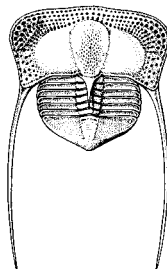
2003 £		Sylvester- Bradley	Jones- Fenleigh	Hodson	TOTAL
1,192.42	Donations	778.06	3,115.10	0	3,893.16
<u>2,713.12</u>	Interest Received	<u>1,784.18</u>	<u>641.05</u>	<u>782.40</u>	<u>3,207.63</u>
3,905.54	Total Incoming Resources	2,562.24	3,756.15	782.40	7,100.79
<u>8,306.00</u>	Grants Made	<u>9,324.00</u>	<u>0</u>	<u>1,417.95</u>	<u>10,741.95</u>
-4,400.46	Net Income before Transfers	-6,761.76	3,756.15	-635.55	-3,641.16
<u>0</u>	Transfer In	<u>0</u>	<u>0</u>	<u>0</u>	<u>0</u>
-4,400.46	Net Incoming Resources	-6,761.76	3,756.15	-635.55	-3,641.16
<u>85,403.25</u>	Brought Forward	<u>45,056.21</u>	<u>16,188.51</u>	<u>19,758.07</u>	<u>81,002.79</u>
<u>81,002.79</u>	Carried Forward	<u>38,294.45</u>	<u>19,944.66</u>	<u>19,122.52</u>	<u>77,361.63</u>



Palaeontology: **CALL FOR SHORT PAPERS!**

From January 2005 *Palaeontology* is 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 six printed pages, should be submitted in the normal way, but they will be refereed rapidly and fast tracked, on acceptance, for publication in the next available issue.

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





GOLDEN TRILOBITE AWARDS



Nominations are invited for this annual website award, instituted in 2004, for sites that promote palaeontology and its allied sciences.

There are two categories of award, professional and amateur.

Winners are announced at the AGM, on the Association's website, and in *Palaeontology Newsletter*.

Nominations must be received by the Secretary, Howard Armstrong <secretary@palass.org> by **1st November 2005**.

Last year's awards were made to:

- *The echinoid directory*
<<http://www.nhm.ac.uk/palaeontology/echinoids/>>
- *Fossils of the Gault Clay and Folkstone Beds of Kent, UK*
<<http://www.gaultammonite.co.uk/home.html>>



PALAEOBIOLOGICAL ILLUSTRATIONS by David Jones

High-detail reconstructions of extinct organisms in pencil and oil pastel, by commission.



David Jones is a Palaeobiology PhD researcher at The University of Leicester

email: <doj@le.ac.uk>



news



2005 Geological Society Awards

Palaeontologists have often done well in the Annual Awards of The Geological Society, and this year was no exception.

Prof. Mike Benton of Bristol University was awarded the prestigious Lyell Medal which is given to people who have made a significant contribution to the science by means of a substantial body of research.

This is what they had to say: "The Lyell Medal is awarded this year to Dr Mike Benton of Bristol University. Mike Benton is an extraordinarily energetic palaeontologist and science communicator. Mike's career began as a vertebrate palaeontologist. Mike has since broadened his studies to include major extinction events from the end of the Palaeozoic, showing that there were two distinct extinction episodes within the Triassic. In this broad work of synthesis, he has been helped by his enormous compilation *Fossil Record 2*, which involved the work of dozens of fellow specialists to compile a massive database of fossil occurrences that has proved a highly fruitful source of information about the nature of the fossil record, and patterns of evolution and extinction within it. In all his subsequent research he has displayed a flair for innovation that shows no sign of running out of steam."

The Prestwich Medal, which is awarded for having 'done well for the advancement of the Science of Geology', was awarded to Russell Coope (University of Birmingham). Russell is the founder and main exponent of the study of Pleistocene insect faunas, and now in his mid seventies he continues to research and publish actively.

Russell Coope's work has shown that insect species exhibit a remarkable degree of evolutionary stability throughout the Quaternary period in spite of the climate's instability at that time. He has demonstrated the usefulness of insect faunas in determining palaeoclimates, using large-scale changes in species distribution as indicators of frequent, rapid and intense climate changes. Together with his colleagues he has developed the 'Mutual Climatic Range' method of quantifying past thermal climatic conditions based on insect assemblages.

Coope's approach has always been staunchly multidisciplinary, and is now universally adopted as the norm. And, as the number of published insect faunas has increased, so has their utility in biostratigraphy, in which Coope has shown how they may be used to distinguish different interglacials. What has emerged from his work on the terrestrial record is a clearer impression of the complexity of the Pleistocene climate.



SYNTHESYS

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

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

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

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

Forthcoming deadlines: 16th September 2005
17th March 2006
15th September 2006

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



ASSOCIATION MEETINGS



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

BA Festival of Science, Trinity College Dublin, Ireland 8 September 2005

Sponsored and organised by the Palaeontological Association; 2pm–4pm.

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.

Speakers

Dr Philip Donoghue (University of Bristol, UK)

Fossil embryos: insights into evolution

The very existence of fossilized embryos is nothing short of miraculous. Goopy embryos are about as likely to be fossilised as snot and yet in the last few years an extensive fossil record has begun to appear providing new insights into the embryology, not just the anatomy, of long extinct organisms.

Dr Mark Sutton (Imperial College London, UK)

The Herefordshire Lagerstätte: a 3D glimpse of Silurian life

The spectacular fossils of the 'Herefordshire Lagerstätte', reconstructed using three-dimensional computer graphics, provide unprecedented information on soft-bodied Silurian invertebrate animals. Important finds of molluscs, arthropods, echinoderms and others have provided exciting new insights into the evolution of each group.

Dr Gareth Dyke (University College Dublin, Eire)

Feathered dinosaurs and birds: insights from fossils

Exceptional fossil discoveries over the last five years have solidified our understanding of birds as a living branch of the dinosaur family tree. Mostly from Asia (China and the Mongolian Gobi Desert) new records of dinosaurs with a variety of feather types include four-winged forms with feathered legs.

Dr David Martill (University of Portsmouth, UK)

Flying high in the Mesozoic: flight dynamics of pterosaurs from exceptional fossils

Fantastic new specimens of pterosaurs have recently been discovered that reveal details of the wing structure and provide insights into how the wings may have functioned during flight. Recent



discoveries of pterosaur eggs with fully developed embryos show that pterosaurs could probably fly shortly after hatching.

Dr Mark Purnell (University of Leicester, UK)

What's left of where we came from? The fossil record of early chordate evolution

As the phylum to which we belong, chordates attract more than their fair share of scientific attention. Yet understanding their origins and early evolution remains difficult because the organisms that arose during this crucial period of evolution almost never fossilized. New fossil discoveries, mostly from China, are challenging some long held views of our early relatives.

Local organiser: Dr Patrick J. Orr, Department of Geology, University College Dublin, Belfield, Dublin 4, Ireland, e-mail <patrick.orr@ucd.ie>, tel: 00353 1 716 2323, fax: 00353 1 283 7733.



49th Annual Meeting

Oxford, UK 18 – 21 December 2005

The 49th Annual Meeting of the Palaeontological Association will be held in the Oxford University Museum of Natural History, under the auspices of the University Museum and the Department of Earth Sciences.

Before the main meeting, on the afternoon of Sunday 18th December, there will be a seminar in the University Museum on Ediacaran biotas. This seminar will be free to conference participants. It will be followed on Sunday evening by a reception in the University Museum to welcome delegates. The technical sessions will consist of two days of talks on 19th and 20th December in the lecture theatre of the University Museum, together with poster presentations situated adjacent to the lecture theatre. The talks and posters will be open to all aspects of palaeontology. The talks will be scheduled for 15 minutes inclusive of questions and there will not be any parallel sessions. Depending on submissions for oral presentations, some talks may have to be re-scheduled as posters. On Wednesday 21st December there will be a field excursion to the Mesozoic of Oxfordshire.

Venue and travel

Information about the city can be obtained on <<http://www.oxfordcity.co.uk/>>, and about the University on <<http://www.ox.ac.uk/>>. Oxford is easily reached from London airports, as well as those of Birmingham, Bristol and many other regional centres. It has frequent transport services from central London, from where it is reached in about an hour by train, and about one and a half hours by coach.

Accommodation

This will be in St Anne's College, which is situated about five minutes' walk from the University Museum. There will be a range of accommodation with different facilities and prices.

Booking for accommodation, the field excursion and abstract submission must be received by **Friday 9th September 2005**. After this date abstracts will not be considered, and registration for the meeting will incur an extra administration cost of £15. The final deadline for registration and for booking accommodation is Friday 25th November. The maximum number of participants for the meeting is 300, and bookings will be taken on a strictly first come, first served basis.



Registration details and online registration

Registration, abstract submission and payment (by credit card) are by online forms at <<http://palass.org>>.

Outline programme

Sunday 18th December

Seminar: Ediacaran biotas, Oxford University Museum of Natural History. Talks will be given by:

Doug Erwin (Smithsonian Institution, Washington): *The origin and relationships of early animals.*

Guy Narbonne (Queen's University, Kingston): *Earth's earliest Ediacarans.*

Mary Droser (Riverside University, California): *Palaeoecology of the Ediacaran biota.*

Shuhai Xiao (Virginia Polytechnic Institute, Virginia): *Palaeobiology of the Doushantuo Formation: the first 80 million years of the Ediacaran Period.*

Martin Brasier (University of Oxford, UK): *Decoding the Ediacaran enigma.*

Evening reception: Oxford University Museum of Natural History

Monday 19th December

Scientific sessions, Oxford University Museum of Natural History

Annual address: *William Buckland and the dawning of palaeoecology*, by W.J. Kennedy (Oxford University, Museum of Natural History)

Reception, Blackwell's Bookshop, Oxford

Annual Dinner, Christ Church College

Tuesday 20th December

Scientific Sessions, Oxford University Museum of Natural History

Presentation of awards

Wednesday 21st December

Post-Conference field excursion to the Jurassic and Cretaceous of Oxfordshire

Travel grants to help student members (doctoral and earlier) to attend the Oxford 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 Oxford Meeting, grants of up to £100 (or the Euro equivalents) will be available to student presenters who are travelling from outside the UK. The amount payable is dependent on the number of applicants. Payment of these awards is given as a disbursement at the meeting, not as an advance payment. Students interested in applying for a Palass travel grant should contact the executive officer, Dr Tim Palmer, by email to <palass@palass.org> once the organisers have confirmed that their presentation is accepted, and before 9th December 2005.



Annual Address

This year's annual address of the Palaeontological Association will be given by Prof. Jim Kennedy and will take place during the Association's Annual Meeting on Monday 19th December 2005, at the Oxford University Museum of Natural History.

William Buckland and the dawning of palaeoecology

Jim Kennedy

Oxford University Museum of Natural History

<jim.kennedy@oum.ox.ac.uk>

William Buckland (1784–1858) was born at Axminster in Devon. He obtained a scholarship to Corpus Christi College in 1801, gained a BA in classics and theology in 1804, was elected to a fellowship in 1808, in which year he was ordained.

A childhood interest in natural history led him to attend lectures by John Kidd, Reader in Mineralogy, and in 1813 he was appointed Kidd's successor. In 1818 he added the newly created Readership in Geology to his portfolio. Buckland's 1818 inaugural address on election to the geology post was an affirmation of the reconciliation of geology and theology (and was largely written by his friend and colleague William Daniel Conybeare (1787–1857)). It gave little indication of what was to come.

In 1816 he went on a grand geological tour of Europe, with Conybeare and George Bellas Greenough (1778–1855); this included visits to Goethe in Weimer, Werner in Freiberg, and the famous bear's bone cave at Gailenreuth. Hearing of a Yorkshire bone cave in 1821, he visited Kirkdale Cavern, and from a careful analysis of fauna and context, interpreted it not as the debris swept in by the waning waters of the biblical flood, but as a pre-diluvial Hyaena's Den. The results were published in the *Transactions of the Royal Society* in 1822, and in his *Reliquiae Diluvianae* (1823). There was not only interpretation, but also experiment: the bones from the cave were compared to those gnawed by a hyaena borrowed from a travelling menagerie, and found to be identical, as were fossil and recent faeces. Buckland was awarded the Copley Medal of the Royal Society for this work, and he has been claimed as the first palaeoecologist, taphonomist, and founder of cave science. In 1824, he provided the first scientific description of what Richard Owen (1804–1892) would subsequently include in his *Dinosauria* in 1842. Buckland had obtained the bones of the great lizard of Stonesfield already in 1814, and the delay in describing them remains a puzzle. In 1829 he published a brief note on ichthyosaur faeces, ink associated with fossil coleoids, and a pterosaur from Lyme Regis.

The coprolite work was published at length in *Transactions of the Geological Society of London* for 1835, and coprolites described from the Rhaetic Bone Bed to diluvial caves. In his conclusion he wrote that "the general law of Nature ... bids all to be eaten in their turn ... the *Carnivoria* in each period of the world's history fulfilling their destined office, to check excess in the progress of life, and maintain the balance of creation."

The coprolite study was expanded in the *Bridgewater Treatise* (1836), involving the casting of the gut of a range of sharks and rays, to produce analogues of fossil faeces.



Fossil footprints were an area of fascination for Buckland, notably those from the New Red Sandstone, and here too, experiment prevailed in the form of the artificial production of trackways (by the family tortoise on fresh pastry), an experiment repeated before his peers.

Functional morphology also received attention, and ranged from an interpretation of the adaptations of the giant sloth to the workings of the chambered shell of cephalopods.

Experimentation and comparison of living animals and plants with their fossil representatives led Buckland to advances in taphonomy, cave science, ichnology and functional morphology, and reveal him as an innovator at the dawning of palaeoecology.

And then, there were the toads ...



Lyell Meeting 2006: Millennial-scale events

Burlington House, London, UK 15 February 2006

This prestigious one-day meeting – the 2006 Geological Society of London Lyell Meeting, sponsored by the Joint Committee for Palaeontology, organised by the Geological Society and convened by Maurice Tucker and Howard Armstrong – is currently being planned for 15th February 2006.

Millennial-scale events and cycles are being increasingly recognised in the Quaternary stratigraphical record and in much older strata. Repetitions of beds, horizons, particular facies, fossil/microfossil occurrences *etc.* on the scale of many hundreds to several thousand years record millennial-scale changes in the environment. In many cases these can be linked to changes in the climate, and in the Quaternary this is often related to changes in ice-cap volume or dynamics, which have knock-on effects on global temperature, wind regimes, oceanic circulation and sediment influx. Millennial-scale events are also recorded in strata deposited during greenhouse times, and here subtle changes in climate are again implicated.

This meeting is aimed at bringing together palaeoclimatologists, palaeontologists, Earth System scientists, modellers, sedimentologists, physical geographers, *etc.*, to discuss the evidence, the mechanisms and the processes involved in the recording of short-term climatic events in the sedimentary succession.

Proposed titles and abstracts should be sent to Howard Armstrong by email to <h.a.armstrong@durham.ac.uk>, as soon as possible so that a scientific programme can be drawn up. Posters can be displayed during the meeting.

Further details will be posted on <<http://www.geolsoc.org.uk>> and <<http://palass.org/>> once the scientific programme has been finalized.



Algorithmic approaches to the automated identification problem in systematics

A symposium on the theory, technique, technology, current application, and future potential of automated taxonomic identification.

19 August 2005

Flett Theatre

the Natural History Museum, London

Sponsors: The Systematics Association and the Natural History Museum

Organisers: Norman MacLeod, Keeper of Palaeontology, the Natural History Museum
Mark O'Neill, Centre for Neuroecology, University of Newcastle upon Tyne, Newcastle
Stig Walsh, Palaeontology Department, the Natural History Museum

http://www.nhm.ac.uk/hosted_sites/paleonet/aaips_symposium



Skeletal Biology in an Evo-Devo-Palaeo Lab

In our last column (58, 26–31, 2005) we continued our dialogue between development and palaeontology – a dialogue begun in 2002 (49, 41–42; 50, 29–32) – by discussing how, using knowledge from extant metazoans, modes of embryonic and larval development can be inferred from fossilized developmental stages of extinct metazoans. A year earlier (54, 16–21, 2004) we discussed vertebrate exo- and endo-skeletons and noted the existence of endo- and exo-skeletons in gastropods, ammonites, brachiopods and arthropods. Earlier we devoted two columns to the nature of bone – which may be cellular or acellular (53, 48–51, 2003; 55, 37–41, 2004) – and one to the nature of the sutures between skeletal elements in vertebrate and invertebrate taxa (52, 29–32, 2003). Given the disparate backgrounds of those in the lab – developmental, cellular and evolutionary biology, ichthyology, systematics, genetics, invertebrate zoology and palaeontology are represented currently – and our common interest in the development, palaeontology and evolution of skeletal tissues, I thought it would be appropriate to outline the approaches we are taking in our effort to understand skeletal development and evolution.

Currently we are investigating the skeleton in the embryos of fish, frogs, chickens and alligators and in the ontogeny of prosauropod dinosaurs. I should really say *skeletons*, for vertebrates have both exo- and endo-skeletons that have existed side by side for almost 500 million years (*Newsletter*, 2004, 54, 16–21). Much of the endoskeleton is founded on cartilage as the embryonic skeletal tissue. Much of that cartilage is later replaced by bone, exceptions being the cartilages of our ears, noses, larynx and joints, and the cartilages of the cartilaginous fishes. The exoskeleton is based on bone and dentine, not on cartilage. Consequently, teeth are part of the exo-skeleton. With these different tissue compositions the two skeletons have had separate evolutionary histories, even when exo-skeletal elements have sunk inside and become associated with (and often assumed to be part of) the endo-skeleton, as is true for the incorporation of the exo-skeletal clavicle into what is otherwise an endo-skeletal pectoral girdle (Smith and Hall, 1990, 1993; Hall, 2001).

Evo-devo and developmental and evolutionary skeletal biology

Because of its fascinating evolutionary history and the evolution of an amazing diversity of skeletal tissues, elements and systems, we are as much interested in skeletal evolution as in skeletal development. *Developmental and Evolutionary Skeletal Biology*, the subtitle of a recent book (Hall, 2005a) captures this integrated approach for what is a subfield within evolutionary developmental biology or evo-devo (Hall, 2002, 2005b). As one illustration of the pursuit of these links in the lab, Matt Vickaryous is studying skeletogenesis in the American alligator *Alligator mississippiensis*. Why? Because alligators, like all crocodylians, are related to birds and their immediate ancestors (dinosaurs), and thus provide us with an opportunity to understand avian (and dinosaurian) skeletal development better, at the same time as we tease out the details of alligator skeletal development.



Development, palaeontology and evolution

Matt is one of four people trained in palaeontology currently in the lab; his special interest and background is in ankylosaurian dinosaurs (Vickaryous and Russell, 2003). The other three are Lisa Budney, Tim Fedak and Tamara Franz-Odenaal. Their backgrounds are very different (see below) and illustrate how different – and seemingly unrelated – approaches, training and backgrounds can be integrated in an ‘evo-devo’ lab.

Our column on exo- and endo-skeletons (Franz-Odenaal *et al.*, 2003) pursued an interest that goes back 30 years (Hall, 1975). That interest was developed most fully in a collaboration with the palaeontologist Moya Smith (Smith and Hall, 1990, 1993), building on a foundation that included a seminal paper by the late Colin Patterson (Patterson, 1977), a paper that contains an important evaluation of the exo- and endo-skeletons as well as cartilage, dermal and membrane bones from developmental and phylogenetic points of view.

Exo-skeletons

A major focus of our work on vertebrate skeletons has been on exo-skeletal development and evolution, especially the head (craniofacial) skeleton. To that end we integrate comparative and experimental studies of vertebrate embryos (developmental biology), with analysis of the dermal skeleton in extinct fish and reptiles (palaeontology) and evolutionary biology, to frame developmental questions in an evolutionary context and *vice versa*. A sign above the door of one of our labs reads *development evolves*, to which the caveat *unless it is constrained* has been added, both of which are pretty accurate statements of guiding principles of evo-devo (see the entries in Hall and Olsen, 2003).

Development and evolution of the exo-skeleton of the American Alligator

Analysis, using histology and immunohistochemistry of the development of the dermal skeleton of the American alligator, *Alligator mississippiensis*, combined with analysis of reptilian dermal skeletons (museum specimens) is being used to understand how these dermal bones form and to evaluate homology between dermal skeletal elements within Reptilia and between reptiles and mammals.

The exo-skeleton includes the majority of the skull, but also osteoderms (bony plates in the skin), gastralia (abdominal ribs), and the clavicles (collar bone). Osteoderms have an unusual taxonomic distribution among modern tetrapods, being present in crocodylians and turtles, some lizards, a few species of frogs, and armadillos. Of particular interest is that alligators and their ilk develop osteoderms and gastralia as a postcranial exo-skeleton, a skeletal system common among early fossil taxa but largely absent from modern forms. We want to understand how the exo-skeleton develops in living alligators and use that knowledge to understand skeletal development in extinct taxa. Matt Vickaryous has identified two distinct modes of osteoderm skeletogenesis. Among armadillos, osteoderms develop in a manner similar to other exo-skeletal bones such as the bony skull – bone-forming cells condense, lay down non-mineralized bone (osteoid) and ossify. In contrast, the development of alligator osteoderms more closely resembles the mineralization of tendons and ligaments, in that the osteoderms lack obvious osteoblasts and an osteoid phase (Vickaryous and Hall, 2004a,b; Vickaryous and Olson, 2005). Indeed it appears that a section of dense connective tissue in the skin transforms into bone.



The unusual taxonomic distribution and morphological variability of many exo-skeletal elements leads to questions of homology. The clavicles of reptiles and mammals have long been regarded as homologous with the furculae (wish bones, merry thoughts) of birds (Hall, 1981, 2001; Tran and Hall, 1989). Most reptiles, however, also have an unpaired mid ventral pectoral element known as the interclavicle. Data from alligator embryos are challenging the long-held homology of clavicles and furculae; a furcula–interclavicle homology is equally plausible (Vickaryous and Hall, 2003).

Development and evolution of scleral ossicles in reptiles (including birds) and teleosts

Scleral ossicles are bony plates in the sulcus of the eyes of fish and reptiles (including birds) that support and/or aid in accommodation of the eyes (Rowe, 2000). Little was known about the development and mode of ossification of ossicles in teleosts until Tamara Franz-Odenaal, a post-doctoral fellow, began to study them using a combined background in developmental biology and palaeobiology acquired in South Africa, where she studied expression patterns of genes involved in melanin production in the eyes of chick embryos and analyzed developmental tooth defects in fossil short-necked giraffes (*sivatheres*), which she related to defects to changing environmental conditions (Franz-Odenaal *et al.*, 2003). Tamara has undertaken a phylogenetic survey of the presence and number of scleral bones in teleost fishes, and an investigation of the homology of scleral ossicles across the vertebrates (Franz-Odenaal and Hall, 2005). Some teleosts such as tuna (*Thunnus* spp.) have two large ossicles forming a complete ring around the cornea. Others such as zebrafish (*Danio rerio*) have small anterior and posterior ossicles that fail to meet to form a ring.

These studies are coupled with an experimental analysis of the molecular basis of the induction of scleral bones in chick embryos. Initial studies indicate that extracellular matrix molecules such as tenascin play a role in ossicle initiation (Franz-Odenaal and Hall, 2004b) and that cell death (apoptosis) and cell proliferation are involved in shaping and removing the transient epithelial papillae that are responsible for ossicle induction.

Mutants can reveal much about normal development (Leroi, 2003; Hall, 2004). We anticipate that analysis of the *scaleless* mutant in domestic fowl will help us unravel ossicle development. *Scaleless* chick embryos, perhaps not surprisingly given the name, fail to form scales. More interestingly from our point of view, they only form one or two of the 13 scleral papillae that encircle the eye of wild type individuals and that induce, individually, the 13 scleral ossicles (Franz-Odenaal and Hall, 2004a,b; Hall, 2005a).

Endo-skeletons

Much of what we consider as the craniofacial endo-skeleton – the jaws and skull – consists of endo-skeletal cores onto which exo-skeletal elements have been applied – Meckel's cartilage and the dermal bones of the lower jaw; the chondro and osteocrania; the cranial base and osteocranium. Neely Vincent has just completed a Masters thesis on how (or whether) elements of the jaw skeleton in *Hymenochirus boettgeri*, the dwarf African clawed frog, respond to thyroid hormone during metamorphosis (Vincent, and Hall, 2004). *Hymenochirus* tadpoles are carnivorous, which may explain why elements of the lower jaw that depend on thyroxine for their development in taxa with herbivorous tadpoles, develop early and independently of thyroxine in *Hymenochirus*.



Pelvic fin position, transformation and loss in teleost fishes

Although homologous with the hind limbs of tetrapods as paired appendages, the pelvic fins of bony fishes (teleosts) are often found in front of (anterior to) the pectoral fins (which are homologues of tetrapod forelimbs), often attached to the skull and/or gill cover (Hall, 2005c). A Ph.D. student, Lisa Budney, is examining patterns in the placement of pelvic fins along the body in bony fishes in an effort to seek phylogenetic signals on how many times fins have moved along the body, and is examining functional correlates within the nervous or muscular systems associated with pelvic fins taking up a more anterior position. With a background in palaeontology from the University of Alberta, Lisa studied the shape of the digestive tracts of heterostracans and thelodonts for her B.Sc. Honours thesis, and described the tooth attachment histology of extant and extinct snake and lizard taxa for her M.Sc., concluding from the latter study that cement, periodontal ligament, and alveolar bone – tissues traditionally considered present only in mammals and crocodylians – attach snake and lizard teeth to the tooth bearing bones (Caldwell *et al.*, 2003).

Some fishes have lost their pelvic fins. We want to know how often loss has occurred, *i.e.*, how easy is it for a group of fish to lose this set of fins? Are there constraints that prevent or mechanisms that facilitate loss in some groups? In other groups of fishes, the pelvic fins have transformed into a single midline sucker on the ventral body surface. Patricia (Paty) Avendaño, a research assistant in the lab, with 22 years' experience with larval fish – much of it gained from the 110 cruises she has participated in – along with Lisa, is undertaking a comparative analysis of the transformation of pelvic fins to suckers in Atlantic lumpfish and in gobiid fishes. Such a transformation provides an ideal system in which to investigate issues of homology and modes of *developmental transformation*. The following project seeks *evolutionary mechanisms* of morphological change.

Mediation of phenotypic change by heat shock protein 90 (HSP-90)

Despite cryptic genetic variation for phenotypic variation, much phenotypic variation is buffered by processes such as canalization that stabilize and channel development (Hallgrímsson and Hall, 2005). It has long been known that repeated exposure to environmental stress can trigger phenotypic shifts in a population. In particular, extreme temperature or chemical stress can increase morphological variability, notably, in traits that normally show little phenotypic variation. Selection can then elicit the variation in the absence of the environmental stress, a process known as genetic assimilation, the Baldwin effect or organic selection (Weber and Depew, 2003). Coming to the lab with a background in genetics and development, having reared, crossed and bred fish since she was eight and then worked alongside a commercial fish breeder who specialized in mouth-brooding cichlids and various angelfish species, Michelle Connolly's studies indicate that fish skeletons show discrete and plastic development in response to embryonic heat-shock. These changes in both vertebrae number and shape are being traced to the activity of heat shock protein 90 (Hsp90).

Hsp-90 is a cytoplasmic chaperone protein that interacts with transcription factors, thereby suppressing and so mediating multiple developmental pathways. Suppression is released in the presence of heat shock and is followed by the appearance of a greater range of morphologies. Both in *Drosophila* and in plants, selection of such individuals leads to genetic assimilation of



the new features. Michelle, another Ph.D. candidate, is using *in situ* hybridization of an HSP-90 probe to trace patterns of HSP-90 expression in zebrafish embryos to see whether HSP-90 is modulating the heat-shock-induced changes in vertebral and tail skeletons. HSP-90 is localized to the somites and tail bud during early embryonic development but extends to adjacent regions in early embryos exposed to heat shock (Connolly and Hall, 2004).

Cephalopod and other invertebrate cartilages and echinoderm spicules

Our interest in endoskeletal development and evolution extends beyond vertebrates to invertebrates.

Invertebrate cartilages

While bone is only found in vertebrates, cartilage is found in several major invertebrate groups. The existence of such cartilages has been known since the 19th century – invertebrate cartilage was one of the tissues used by Theodor Schwann in formulating the cell theory (Schwann, 1839) – although the structure of these cartilages was not investigated until the 1960s and '70s (see Person, 1983, Cole and Hall, 2004a,b, and Hall, 2005b for reviews).

How any invertebrate cartilage develops was unknown until Alison Cole joined the lab to tackle this question. Alison arrived with a keen interest in comparative marine invertebrate biology and a background in invertebrate neural development from studies on cell lineage of the larval central nervous system in the ascidian *Ciona intestinalis* and neural development in pond snails (Cole *et al.*, 2002; Cole and Meinertzhagen, 2004). Alison completed her Ph.D. in August 2004, having investigated tentacular cartilages in polychaetes, odontophoral cartilages in gastropods, cranial and scleral cartilages in cephalopods, and the gill book cartilages of *Limulus* (Cole and Hall, 2004b). Alison identified the distinguishing features of invertebrate cartilage, estimated that invertebrate cartilage has arisen four times, provided detailed analyses of cephalopod and polychaete cartilages, identified major classes of modes of cephalopod cartilage development, and documented two major modes of chondrogenesis; see Cole and Hall (2004a,b).

Echinoderm spicules

With her background in marine, invertebrate and developmental biology obtained at Dalhousie, Jennifer Legere has initiated a study of the mechanisms of formation, growth, remodelling and resorption of the calcium carbonate skeletons of two larval echinoderms, the common sand dollar, *Echinarachnius parma*, and the green sea urchin, *Strongylocentrotus droebachiensis*, especially focusing on changes during metamorphosis. This topic arose from the interest of our German collaborator, P. Eckhard Witten, in resorption of bone in teleost fishes. Although many fish osteoclasts are mononucleated, bone in all fish is resorbed using the same enzymes and proton pumps that mammals use to resorb their bone (Witten *et al.*, 1999, 2000). Previous studies suggested that spicule resorption in echinoderm larvae may be a cell-mediated process as it is in vertebrates, although whether spicules are remodelled during growth or resorbed at removal is unknown (see Chia and Burke, 1978 and Dubois and Chen, 1988). For her M.Sc., Jen is assessing remodelling and resorption using light, Confocal, transmission and scanning electron microscopy, enzyme histochemistry (especially tartrate-resistant acid phosphatase or TRAP) and labelling with autofluorescent calcein (Legere *et al.*, 2004).

**Last but not least: fossils**

Tim Fedak's explicitly palaeontological project involves the analysis of patterns of growth of prosauropod dinosaurs. As many as five specimens of varying maturity have been collected from the Early Jurassic McCoy Brook Formation here in Nova Scotia; Tim will be co-leader of a field trip to the site during the North American Paleontological Congress in June. Analysis of the histology of the long bones (palaeohistology) allows Tim to determine specimen age and modes of bone development, approaches that dovetail with our overall interest in the biology, development and growth of bone.

Tim is an artist with a Bachelors degree in Fine Arts. His avocation for fossils began serendipitously when he went along as an assistant on a field trip. Finding himself able to recognize fossil skeletons within the marine strata on the beach, Tim was hooked. Practical training as a preparator at the Royal Ontario Museum in Toronto, and as manager of the research lab of the Fundy Geological Museum in Parrsboro Nova Scotia, led Tim to seek graduate training, which is how he now comes to be studying prosauropod dinosaurs in an evo-devo lab.

The evo-devo net is wide and deep; Tim has completed an analysis of cetaceans using developmental and palaeontological approaches in an integrated analysis of patterns and process of hyperphalangy or how extra segments form in existing digits (Fedak and Hall, 2004), a follow-up to an earlier study from the laboratory on limb loss in cetaceans (Bejder and Hall, 2002). Such are the approaches we are taking to understand skeletal development and evolution.

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Things ain't what they used to be

It's a dicey business, evolution. One has to tread very carefully, when using insights gleaned from the grand story of Life to explain the history and behaviour of our own very idiosyncratic species. Even now, Michael Ruse is berating the likes of Richard Dawkins for using evolution as a counter-productive stick to attack religious belief with, while in turn being berated by Eugenie Scott for providing ammunition to the Intelligent Designists.

One should therefore proceed nervously, aware that an incautious simile here, a misplaced analogy there, could precipitate a chain of events that might in future years enforce us all, by some Educational Decree or other, to give equal weighting to the theory that dinosaurs were Intelligently Designed (though, in the case of the duck-billed dinosaurs, perhaps Humorously Designed) and that the devil's toenail is no less than divinely encoiled. The temptation is, nevertheless, irresistible. So plunging on regardless, let's explore, with a quite gratuitous lack of intellectual rigour, some of the more dissonant ramifications of Darwin's dangerous idea.

Darwin of course termed it descent with modification, the changes in successive generations being driven by natural selection. And everything worked beautifully until the human race came along and complicated matters dreadfully. For the structure, functioning and behaviour of human communities have changed beyond recognition since our ancestors first abandoned their caves, and they're still changing, at even more dizzying speed than before. Can any of this be described in Darwinian terms?

It's been done, of course, perhaps most famously with Richard Dawkins' concept of the meme, the memory-bound equivalent of a gene, in which conservative behavioural elements of, say, culture, religion or football allegiance are passed down from generation to generation. Now, those memes which offer a more selective advantage to the community possessing them, such as increased social cohesion, will spread more widely as that community prospers and grows more



numerous at the expense of the hopelessly-adapted uncouth, ungodly or unsporting. That could, perhaps, be loosely regarded as a Darwinian process.

But then, there are aspects of culture that are anything but conservative. The appearance and spread, for instance, of the ever more sophisticated technology that envelops our lives and drives our behaviour (how many e-mails did *you* have to answer today?). This seems rather to represent the spread of characteristics which appeared and were acquired during one's lifetime. Is it, therefore, the shade of Jean-Baptiste Lamarck texting that particular message to us from the Great Beyond?

It's a species thing: human beings are remarkable in their capacity for their systematic accretion, through time, of a variety of behavioural adaptations. Other animals aren't anywhere near so adept at adapting their behaviour to keep up with changing circumstances, and then at passing on their adaptations to succeeding generations. Some of them, nevertheless, might be doing better than others. I've often wondered how Mister Crow has always managed to keep skipping nimbly out of the way of speeding automobiles, all the while snacking on the earthly remains of Brother Hedgehog, who, alas... hasn't.

There's another type of evolution within human culture, though, that might have puzzled both Lamarck and Darwin. It's the evolution of those baroque excrescencies of the human spirit, non-adaptive to a fault, the developmental pathways of humanity's artistic endeavours.

There's a funny thing going on here. One might, initially, attempt to treat CP Snow's two cultures quite equally, and envision a progression towards both increasing sophistication and narrative power. In the sciences, to be sure, our collective understanding grows progressively deeper. Standing on giants' shoulders, we probe ever farther into the lineaments of the observable universe, not least because of the seven-, then seventy-, and then seven-hundred-league boots of our ever-more-miraculous technology.

But is it so in the arts? Let's take music. Not all music, one hastens to add. We won't count, say, Showaddywaddy, which has become, at least in some quarters, both a deeply embedded meme and a category all of its own. But does a newly-commissioned twenty-first-century string quartet effortlessly reach previously unattained heights, its sinuous computer-aided harmonies relegating the fossilized efforts of long-dead composers to the status of musical Amstrads?

Well, strangely, no. The gigantic shoulders here seem to be an awful long way above the ground for those who would attempt to scramble up. But first, who were they, those giants? Who, can we say, represents the peak of evolution in serious music, and at what point would they make their grand entrance within the libretto of *Red Queen: The Opera*? Now *there's* a question to start a bar-room fight in the intervals between acts at La Scala.

Dodging the broken bottles and flying fists, one might take refuge behind an upturned table and there compare lists of the very greatest composers of all, quoted independently by the various but considerable figures of the late Bernard Levin, professional word-smith (bulk orders a speciality, but don't expect too many full stops) and lifetime worshipper at the feet of the Music Muse; and of Mitsuko Uchida, a pianist of such luminous touch that she has almost, almost tempted me to venture seriously into Arnold Schoenberg's alien musical landscapes. I recall Uchida interviewed on the radio saying how *most interesting* Schoenberg's work was but – and here she lowered her voice conspiratorially – she suspected that *he might not have been a very nice man*.



Four names appeared around the top of both lists, and they are absolutely unsurprising, which helps make the point. Bach; Mozart; Beethoven; and Schubert – the last of these featuring even despite his (relative) technical failings. That's four white central European males, their almost-overlapping working lives spanning not much more than a century. Bach started flexing his musical and other muscles about the early 1700s, with a street brawl as his emerging musical sensibilities were offended by a bassoonist whose efforts he compared to those of a nanny-goat. Mozart, born just six years after Bach's death, in 1756, had a precocious but ridiculously brief working life, not even coming close to seeing out the century. The last of them, Schubert, died in 1828, having been a torch-bearer at Beethoven's funeral the year before.

Remarkable, isn't it. This was when the world population was not a fifth of today's. When most of that population was uneducated, and most hardly ever left their towns and villages. When the female half of humanity was – how can one put it? – not *encouraged* in serious musical endeavour. When there was no radio, no phonographic records or compact discs by which people might easily listen to and assimilate the music of their peers. Those four men, often beset by worries over money or employment, nevertheless created music that, by general agreement, has not been surpassed.

When their work was finished, by the way, Charles Darwin was just eighteen years old, at Cambridge, in between the influences of Robert Grant and John Henslow and, incidentally, of the bewitching Fanny, Shropshire lass and daughter of Squire Owen. The *Beagle* was not to sail for another three years.

In the twentieth century, with five and then ten times as many people on the earth, with the works of these four composers, and of those almost of their stature, easily available for study, and performed by the finest artists (I have a 1904 recording by Caruso of Donizetti's aria *Una furtiva lagrima*; the book of words on these things says it's unforgettably perfect: a pretty fair assessment, to my ear). With all of these advantages, available now to an ever-greater proportion of an ever-growing, ever-richer and ever more-educated population on the planet, what was achieved?

Genius did burn, certainly, in Stravinsky and Debussy, Bartok and, yes, even (I understand in theory, so to speak) in Schoenberg. And, of course, it leapt, thrillingly, from the bars and bawdyhouses of New Orleans and the clubs of New York and Chicago, as Armstrong and Ellington, Hines and Hawkins improvised what might yet turn out to be the deepest musical footprint of the twentieth century.

But all this was not, certainly, the same thing. It's innovation that's been the key. New musical paths were carved out, but old ones were not extended towards ever-higher ground. It's almost as if the giants, while carving out their own path, left boulders in the path of those who would follow, preventing others getting as far as they did. *The Marriage of Figaro*, well past its two hundredth birthday, remains, to many, the greatest opera ever written (others disagree, and claim – just to labour the point – *The Magic Flute*). A century on, Guiseppe Verdi didn't attempt to compete with Mozart in the classical style, but struck out along a different path. His operas are miraculous, breathtaking: but the same degree of perfection is rarely claimed for them.

So, if it's a tree of cultural evolution, it's one where a highly successful branch doesn't lead to another one in a linear fashion, but almost forces a displacement into a different direction,



though, arguably, one that doesn't extend *quite* as far. It's the inevitable reaction to a punctured equilibrium, one might say, and one that was taken not so much out of a rejection of things past, but more in a kind of awed affirmation of what had been achieved in a particular idiom, and how hard it is to follow and then overtake a class act. Schoenberg said that he was a conservative who was forced to be a radical, while Stravinsky told students that they could be revolutionary, but not anarchists. Not even the *niciest* anarchists.

Enough! – things here have gone far too far. This kind of comparison is not homology, or even analogy, but something perilously close to scatology. It's not evolution Lite, but trite. I await, in trepidation, outraged letters from offended serialists, deeply offended late romantics, seething Wagnerians and incandescent punk rockers¹; not to mention from social, unsocial and downright antisocial Darwinists and unreconstructed Lamarckians. All the while, the neo-creationists will be rubbing their hands gleefully and waiting to pounce. A dreadful prospect. Still, if the result is that we become forced to promote evolution and Intelligent Design equally, then, perhaps music lecturers will also be made to allot equal time to the study of Mozart and Showaddywaddy. That, at least, would show a nice sense of symmetry.

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¹ The Editor, for instance, notes the unforgivable omission of the genius that is *The Flaming Lips*.

Meeting a nemertean Nemesis

In the last Newsletter I discussed the nemertean theory for the origin of the vertebrates as proposed in the late 19th century by the Dutch embryologist Ambrosius Hubrecht (1853–1915). Hubrecht proposed his theory in conscious contrast to the two leading hypotheses that derived the vertebrates either from an ascidian tadpole larva or from an annelid worm. By homologising the nemertean proboscis sheath (also known as the rhynchocoel) with the vertebrate notochord, and the nemertean proboscis with part of the pituitary gland, Hubrecht sought to determine the evolutionary origins of some of the most conspicuous chordate features, and at the same time reveal the evolutionary link between the invertebrate and vertebrate domains of the animal kingdom.

However, Hubrecht's theory never enjoyed the same popularity as the competing annelid and ascidian tadpole theories, even though Hubrecht's theory arguably necessitated less special pleading than the annelid theory, and represented a more penetrating analysis of the evolutionary origin of vertebrate characteristics than the mere comparison with other chordates would allow. But despite the absence of any significant following, the nemertean theory maintained a tenuous thread of continuity across three centuries through the works of three remarkable individuals who could not have been more different in professional orientation. This essay chronicles their advocacy of the nemertean theory, and shows how a once fruitful hypothesis about the evolution of animal body plans ultimately became transformed into a



sterile monstrosity that spent its last years of life within the confines of published or unpublished abstracts in conference proceedings, until it finally expired in the new millennium with the death of its last and most vociferous proponent.

As the 19th century drew to a close, efforts to reconstruct the nature of distant ancestors were increasingly regarded as sterile exercises in mental gymnastics, and concurrently the nemertean theory of vertebrate origins sank into quiet oblivion. However, after several decades of dormancy it was revived in no uncertain terms by an unlikely intellectual successor of Hubrecht. At the end of a productive career John Muirhead Macfarlane (1855–1943) published his book *The causes and course of organic evolution. A study in bioenergetics* [sic] (1918). Bestowing praise in no uncertain terms, Macfarlane credits Hubrecht's nemertean theory as "one of the most far reaching and brilliant steps ever taken in zoological science." Not surprisingly, Macfarlane was a botanist.

Born and educated in Scotland, Macfarlane occupied several different academic positions at the University of Edinburgh before he emigrated to the United States to assume a professorial chair at the University of Pennsylvania in 1893, which he held until retirement in 1920. Although he was primarily a botanist, Macfarlane's interests ranged widely, and in addition to the book mentioned above his other works included *The evolution and distribution of flowering plants (Apocynaceae. Asclepiadaceae)*, *The evolution and distribution of fishes, Fishes the source of petroleum*, and *The quantity and sources of our petroleum supplies*. Nevertheless, despite such an outpour of work, Macfarlane is certainly no household name in biology. His main source of fame is probably connected with his leading role in organizing and elaborating the botanical garden of the University of Pennsylvania. In the obituary for Macfarlane published in *Science* a colleague justly admired the "universality of knowledge" of "this beloved Scot" (Steckbeck, 1943) and it was therefore only fitting for Macfarlane to crown his career with *The causes and course of organic evolution* (1918), which was a wide ranging panoramic overview of the patterns and causes of animal and plant evolution. To celebrate his obvious admiration for Hubrecht's ideas, Macfarlane dedicated a significant portion of this book to discussing and elaborating the nemertean theory for vertebrate origins. His main goal was to fill in some holes in Hubrecht's scheme that Macfarlane thought would have led to a "rapid and wide acceptance" of Hubrecht's ideas, would Hubrecht have thought of them himself. Thus, Macfarlane enthusiastically set out to expand Hubrecht's list of possible homologies between vertebrate and nemertean structures, and he confidently pointed out the nemertean precursor structures of vertebrate teeth, eyes, ears, and even the uvula (proboscis stylet, eyes, cerebral organs, dorsal wall of proboscis, respectively).

However, far from smoothly extending Hubrecht's ideas, Macfarlane adopted a radically different strategy of evolutionary inference than Hubrecht had. Hubrecht had built his case according to the principles of evolutionary morphology, *i.e.* on the basis of a detailed study of pure comparative morphology, without much explicit attention to contextual information such as ecological factors, habits, possible selection pressures, the adaptive value of new features, *etc.* In sharp contrast, Macfarlane was very much concerned with the ecological and environmental context of evolutionary changes in body plans. However, rather than aiding the reception of his ideas, Macfarlane's consideration of contextual information may have contributed rather more to the rapid obsolescence of his book. The reason for this is that Macfarlane outlined his ideas within the conceptual framework of neo-Lamarckism at the eve of the terminal last phase of this evolutionary outlook on life. In the 1920s, the famous exposure of apparent fraud in



the work of neo-Lamarckian zoologist Paul Kammerer on midwife toads extinguished the last hopes for systematically sought experimental support for the inheritance of acquired characters, and it created a scientific scandal that ended with Kammerer shooting himself in the head on an Austrian mountain path. Although these events signalled the end of neo-Lamarckism in experimental zoology, certain palaeontologists and field naturalists relinquished their faith rather more slowly (Bowler, 1983). Macfarlane's 1918 book represents a prominent example.

Macfarlane's outlook on the evolutionary panorama was significantly influenced by ideas previously elaborated by the premier member of the first important American evolutionary school: the neo-Lamarckian Edward Drinker Cope (1840–1899). Specifically, reading Macfarlane's *The causes and course of organic evolution*, one cannot escape the conclusion that it owed an obvious debt to Cope's *The primary factors of organic evolution* (1896), in particular Cope's ideas about the importance of consciously chosen reactions of the animal to its environment, and his concept of "kinetogenesis" in determining the direction of evolutionary change. According to the first idea, animals adapt by consciously or protoconsciously reacting to changes in the environment, leading to the evolution of novel features. According to Cope's concept of kinetogenesis, motion could exert direct and inherited effects upon an organism's structure, a proposal explicitly accepted by Macfarlane (1918: 657). These concepts of the evolutionary importance of environmental change and the organism's direct and inherited response are reflected in Macfarlane's list of five "causes" of evolution, especially the second and the third: 1) heredity; 2) environment; 3) proenviron; 4) selection; 5) reproduction. Macfarlane proposed the second and third causes in conscious analogy to Newton's law of action and reaction; each action imposed by the environment (cause 2) upon the organism leads to an immediate and inherited reaction, or "proenviroal response" (cause 3) by the organism, thereby determining the direction of evolutionary change.

Given the great importance of the environment in stimulating organisms to change, Macfarlane thought the marine realm not to be challenging enough to drive significant evolutionary progress. Instead Macfarlane considered the "struggle for existence" to be much more severe in the more challenging terrestrial and fresh water environments. "Accordingly proenviroal response and selective survival act more sharply to evolve new types" in terrestrial and fresh water environments (Macfarlane, 1918: 408). As a result "the writer is forced to the conclusion that the main and dominant lines of animal evolution have all originated in fresh water or on land, and that only side lines have assumed a marine life." Macfarlane extended his heterodox ideas to the evolution of plants as well, and the main trunks of both plant and animal phylogenies in his book run through fresh water from root to crown.

Additionally, the concept of kinetogenesis leads one to envision nature as an ambitious sculptress who incessantly chisels away at the form of animals. In line with such brute mechanical forces operating upon the shape of organisms, Macfarlane therefore expected armoured animals to be relatively immune to rapid evolutionary change. Such could be expected, for example, for arthropods with hard exoskeletons (Macfarlane, 1918: 538).

Naturally, the soft-bodied and pliable nemerteans could scarcely be expected to put up a fight against the relentless action of the elements, and after their fresh water origin, they were quickly moulded into a multiplicity of forms, ranging from the lowly cyclostomes to our



exalted selves. Apparently, Macfarlane's ideas about the causes and course of animal evolution were not generally considered the stuff of textbooks, and a long period of silence followed his championing of the nemertean theory of vertebrate origins. However, the theory's mummified remains were once again disinterred in 1960, this time simultaneously and independently by an English cytologist specialized in tissue cultures, and an American comparative psychologist interested in the behaviour of *Paramecium*. However, these authors didn't built on Macfarlane's ideas, but rather were inspired more directly by the initial papers of Hubrecht.

In 1960 Edward Neville Willmer (1902–2001) was reader of histology at the University of Cambridge, and in his tissue culture laboratory he studied tissue growth and cell division with several collaborators, including the Nobel prize winner Peter Medawar. After Willmer had published previous books on tissue culture and the structure of the retina in relation to colour vision, he published the first edition of *Cytology and evolution*. In this textbook of comparative histology nemerteans only appear on page 334, to introduce a few pages dedicated to “the nemertine as prototype,” that is, as a prototype vertebrate. However, this situation changed dramatically with the publication of the second edition of Willmer's book in 1970. The nemerteans as a vertebrate prototype had been promoted from a cameo role to a leading character, and the nemertean theory of vertebrate origins functioned as the main organizing theme in the book. In the book and a 1974 paper, Willmer attempts to identify precursor cell types and tissues in nemerteans of as many vertebrate cell types, tissues and organs as he can, including chloride-secreting cells, the pineal organ, the urogenital system, and the liver. In addition, Willmer placed his study of comparative histology in the context of a functional evolutionary scenario that specifies the changes in habit and habitat accompanying the evolutionary transition of nemertean to vertebrate, in particular the evolution of filter-feeding and swimming that were concomitant with a proposed escape of the carnivorous nemerteans from the benthos into the pelagic realm of the ocean. Willmer also presented a consideration of the selection pressures potentially involved in this change in body plans. As an example of his approach, Willmer suggested that it would be beneficial for nemerteans to leave the benthos because overcrowding “with a probable plethora of floating eggs, larvae, and unicellular organisms, would make it advantageous to escape into the supernatant water-phase (just as the insects and birds have escaped into the air)” (Willmer, 1974: 328).

Quite independent of whether one accepts Willmer's carefully crafted functional scenarios or not, his work represents the most comprehensive and detailed attempt to date to defend an evolutionary link between vertebrate characters and precursor structures present in nemerteans in terms of both the structure and function of cells. Willmer's ideas even stimulated some research into nemertean ultrastructure (e.g. Ling, 1969) to test the nemertean theory. It should be noted, however, that Willmer did not propose to derive extant vertebrates from extant nemerteans, but merely from some as yet unidentified extinct nemertean-like worm. As a result, when *Yunnanozoon* was described, Willmer was quite struck with its similarities to nemerteans, as he confided to fellow Cambridge-based nemertean worker Janet Moore. In fact, Willmer was not the only one with that idea. The palaeontologist Jerzy Dzik recently pointed to the similarities of nemerteans and fossils such as *Yunnanozoon* as perhaps providing tentative support for the “rather unorthodox” hypothesis that links nemerteans to chordates (Dzik, 2000: 139).



Willmer did not publish more work on the nemertean theory after the early 1970s. When he submitted a manuscript on this topic to be included in the proceedings of the meeting on “Recent advances in nemertean biology” to be published in 1988 in *Hydrobiologia*, nobody could be found to review it. The manuscript was never published. And when Janet Moore confronted Willmer with genetic data that might refute his ideas, Willmer simply responded that genes were recipes for the phenotype, and he wasn’t interested in recipes.

The last and in many ways the most extreme chapter in this story also opens in 1960. Two years after earning his PhD in comparative and experimental psychology for a thesis on “Behavioral effects of feeding, fission, and ultraviolet microbeam irradiation in *Paramecium aurelia*,” Donald D. Jensen published a short paper in *Nature* titled “Hoploneurians, myxinozoans and deuterostome origins” (Jensen, 1960). Inspired by Hubrecht’s ideas, and independently of Macfarlane and Willmer, Jensen elaborated a list of possible homologies shared between nemerteans and vertebrates. He proposed that the hoploneurians (a group of nemerteans possessing a proboscis armed with teeth) gave rise to early hagfishes. Hagfishes in turn formed the ancestral stock for all vertebrates, as well as all other deuterostomes, including tunicates, cephalochordates, hemichordates, and echinoderms, which arose by varying degrees of degeneration. One of the strikingly controversial aspects of Jensen’s theory was his derivation of all living deuterostomes from within the extant nemerteans. In his last contribution to the published literature, Jensen took this idea to its extreme. He in effect proposed that all bilaterians have evolved from within the nemerteans, with palaeoneurians representing the elusive Urbilateria, heteroneurians giving rise to protostomes, and hoploneurians evolving into the deuterostomes (Jensen, 1999). In summary, during a period of 40 years Jensen defended and elaborated his nemertean theory in publications that were without exception invited book chapters, conference proceedings, or abstracts (e.g. Jensen, 1963, 1983, 1988, 1990, 1999).

In the end the nemerteans became Jensen’s Nemesis. What had initially started out as a fruitful theory of animal body plan evolution in the late 19th century had become transformed into a personal dogma that was zealously advocated, and aggressively shielded from criticisms. Although Jensen was a good field naturalist and a very friendly colleague (Dr Janet Moore, pers. comm.), he was regarded as somewhat of an oddball in the nemertean community because of his rather heterodox ideas. As a result, and despite repeated airing of his ideas at seminars and meetings, his ideas mostly fell on deaf ears, and his theory was never critically discussed (Sundberg *et al.*, 1998 represents the only exception). The inability of either morphological or molecular evidence to support a close relationship between nemerteans and vertebrates effectively doomed Jensen’s ideas.

But Jensen never relented. Jensen ended his unpublished abstract for the 5th International Conference on Nemertean Biology in 2000 by writing “recent attempts by this writer to apply methods of biochemical systematics to available biochemical data will be discussed.” Unfortunately that was the last on nemerteans by Jensen. While teaching a course on scientific approaches to parapsychology, Jensen was hospitalised on Thanksgiving Day of 2003. He died three weeks later.

What can we learn from this nemertean affair? Should the opinions of Hubrecht, Macfarlane, Willmer and Jensen simply be dismissed with a chuckle as the misguided efforts of some feeble minds? Or can we learn something more instructive from the shared commitments over a period



spanning three centuries of a Dutch embryologist, a Scottish botanist, an English cytologist, and an American psychologist? I think we can, and we should. Hubrecht, Macfarlane, Willmer and Jensen all placed ancestors centre stage in their evolutionary epistemology, and this approach represents no oddity in evolutionary inference. As recently summarized by Mayr and Bock (2003: 175) “The study of phylogeny was traditionally considered to be, so to speak, a backward looking endeavour, the search for and study of common ancestors. The starting point in such an analysis is a particular taxon and the student of phylogeny attempts to infer the properties of its ancestors.” As Dayrat (2003) recently pointed out in a perceptive paper, this central role of ancestors in phylogeny reconstruction is strikingly illustrated in the work of the first great phylogenizer, Ernst Haeckel. The trunks of Haeckel’s trees represent a linear evolutionary succession of morphological stages exhibited by the species at the top of the trunk. This strategy necessitates one to make direct pronouncements about the nature of distant ancestors in order to explain the observed morphology of a chosen taxon. This backward looking approach to phylogeny reconstruction, this immediate infusion of the arrow of time into their evolutionary speculations, is exactly what unites the efforts of Hubrecht, Macfarlane, Willmer, and Jensen. This strategy of recovering the past by looking back really became only unpopular with the advent of cladistics. Ancestors have no central role in cladistics. They are merely the by-products of studies of comparative morphology, and they only vaguely flicker in ghostly outlines at the internal nodes of cladograms. The construction of a cladistic data matrix typically involves no assumptions at all about the arrow of time, just an assessment of organismic variation. Only when the cladogram is rooted do the hypothetical ancestors appear.

With the exception of the later papers by Jensen, the nemertean theory of vertebrate origins was defended before the cladistic revolution had gathered sufficient force. And Jensen himself had serious misgivings about cladistics. Both Willmer and Jensen can be criticized for ignoring conflicting evidence, or at least not being overly receptive to it. But their direct focus on ancestors was current practice for many systematic biologists for a very long time. I think that for most of us it just feels natural to include the arrow of time right from the beginning of our phylogenetic theorizing. That explains why we sometimes cannot help ourselves. Even the most devoted hardcore cladists sometimes let their intuitions take over, with the result that cells in a data matrix are filled with nothing more concrete than unsupported expectations and suspicions based on the acceptance of an *a priori* hypothesis about the pattern or process of evolution. The scoring of the presence of an orthogonal, or ladder-like nervous system for taxa that lack any trace of such a nervous system in morphological cladistic data matrices published over more than a decade is a revealing example (Jenner, 2004).

There are enough other examples that reveal our tenacious tendencies to infuse our thinking about evolution with time’s arrow to fill a sizeable book. Just consider the extremely common fallacy of equating character states in species-poor taxa as ancestral with respect to those found in its more species-rich sister group (Crisp and Cook, 2005). The prevalence of this nasty habit of thought recently inspired an editorial in *Systematic Entomology* (Krell and Cranston, 2004). Evidently, we haven’t cleaned up our acts as well as we should, yet...

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PalaeoMath 101

Principal Components Analysis (Eigenanalysis & Regression 5)

This time out we're going to take up a topic I've been looking forward to, and dreading, ever since Phil Donoghue invited me to consider writing this column. Principal components analysis (PCA)—or perhaps more correctly, the method of eigenanalysis on which PCA is based—is pre-eminent among the multivariate, numerical-analysis techniques used by palaeontologists to analyze all kinds of data. Both the theoretical and applied PCA literature are vast. Nevertheless, good explanations for a non-mathematical audience are rare; especially explanations that relate PCA to regression analysis (hence the hybrid title of this column) and that provide examples of its use in the context of morphological data analysis. A good discussion of PCA is also made challenging in that a number of the issues we've been discussing in previous columns need to be reviewed and combined with new material.

Table 1. Trilobite data

Genus	Body Length (mm)	Glabella Length (mm)	Glabella Width (mm)
<i>Acaste</i>	23.14	3.50	3.77
<i>Balizoma</i>	14.32	3.97	4.08
<i>Calymene</i>	51.69	10.91	10.72
<i>Ceraurus</i>	21.15	4.90	4.69
<i>Cheirurus</i>	31.74	9.33	12.11
<i>Cybantyx</i>	36.81	11.35	10.10
<i>Cybeloides</i>	25.13	6.39	6.81
<i>Dalmanites</i>	32.93	8.46	6.08
<i>Deiphon</i>	21.81	6.92	9.01
<i>Ormathops</i>	13.88	5.03	4.34
<i>Phacopidina</i>	21.43	7.03	6.79
<i>Phacops</i>	27.23	5.30	8.19
<i>Placopania</i>	38.15	9.40	8.71
<i>Pricyclopyge</i>	40.11	14.98	12.98
<i>Ptychoparia</i>	62.17	12.25	8.71
<i>Rhenops</i>	55.94	19.00	13.10
<i>Sphaerexochus</i>	23.31	3.84	4.60
<i>Toxochasmops</i>	46.12	8.15	11.42
<i>Trimerus</i>	89.43	23.18	21.52
<i>Zacanthoides</i>	47.89	13.56	11.78
Mean	36.22	9.37	8.98
Variance	346.89	27.33	18.27



Since this series is meant to focus on practical issues, the first thing to do is set up a problem. In the last column, on multivariate linear regression, we asked how we could use glabellar length and width measurements taken on a selection of trilobites to estimate overall body length of individuals. Our answer, somewhat surprisingly, was that both variables could be combined to yield quite an accurate estimate of individual body length. We also found, somewhat less surprisingly, that the longer measurement (glabella length) was the better, overall, body-length proxy. This data-analysis situation was predicated on a need to make the classic, least-squares distinction between an independent variable (body length) and a set of dependent variables (glabellar length and width).

Now, let's change this question slightly. Instead of wanting to know how best to estimate one variable in terms of others, suppose we wanted to (1) explore the relations between all three variables simultaneously and (2) use those relations to create new variables with more desirable statistical properties: such that (a) all these new variables are known to be independent of each other, (b) the relative relations between species in the sample are strictly preserved and (c) the geometric relations between the new variables and the old (measured) variables are both constant and easy to interpret in a meaningful, qualitative manner. That's a tall order, but it's precisely what is done by PCA. Indeed, PCA gives us this power and much more besides.

On to the data. For this discussion we'll use the same dataset we used in the last column (Table 1). A three-dimensional scatterplot of these data yields Figure 1.

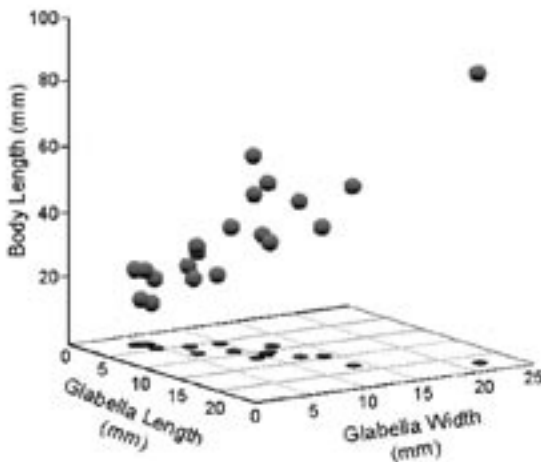


Figure 1. Scatterplot of Table 1 data in a Cartesian coordinate system.

While this is the standard way of representing data consisting of real numbers such as measurements, once you think about it, this Cartesian scatterplot makes an odd assumption about these data. Note the orientation of the three axes. They're all at right angles to one another—or, at least, they're supposed to look that way, this being a perspective drawing. In



mathematical terms, variable axes drawn this way would be taken to mean these variables are independent in the sense that the pattern of variation among measurements plotted along one variable axis would not be expected to be a good predictor of the pattern of other measurements plotted along another axis. The point is that these data themselves, the plot, and simple logic all tell us body length, glabella length, and glabella width are not independent of one another. We proved that result for this dataset last time.

What is the true relation between these variables? We've seen this before, too. The two most common ways to express inter-variable relations is through the covariance or correlation indices. If the variables are all measured in the same units, and if we wish to take the magnitude of the variables into consideration when expressing their relations, we should calculate the covariance between variables (see the Regression 2 column). The structure of covariance relations between multiple variables is usually expressed in terms of the pairwise covariance matrix (Table 2). Here the matrix's diagonal cells, or 'trace', is filled by variable variance values, and the off-diagonal cells filled by between-variable covariance values.

Table 2. Trilobite measurement covariance matrix

Variable	BL (x_1)	GL (x_2)	GW (x_3)
BL (x_1)	329.549	82.832	64.995
GL (x_2)	82.832	25.966	19.299
GW (x_3)	64.995	19.299	17.353

Alternatively, if the variables are measured in different units (*e.g.*, some in mm, some in inches², some in ml, some in degrees of arc) such that it makes no sense to compare them directly, or if we do not wish to take the magnitude of the variables into consideration when expressing their relations, we should calculate the correlation between them (see the Regression 2 and Regression 4 columns). The structure of correlation relations among multiple variables is usually expressed in terms of the pairwise correlation matrix (Table 3) in which the matrix's trace is filled by correlations of variables with themselves (= 1.000) and the off-diagonal cells filled by correlations between pairs of different variables.

Table 3. Trilobite measurement correlation matrix

Variable	BL (x_1)	GL (x_2)	GW (x_3)
BL (x_1)	1.000	0.895	0.859
GL (x_2)	0.895	1.000	0.909
GW (x_3)	0.859	0.909	1.000

Note: both matrices are symmetrical about their trace.

Now, let's talk geometry. We can model the distribution of the Table 1 data by enclosing our data points in a volume. The volume that makes the fewest assumptions about the shape of the underlying distribution from which our trilobite sample was drawn is a three-dimensional ellipsoid (Fig. 2).

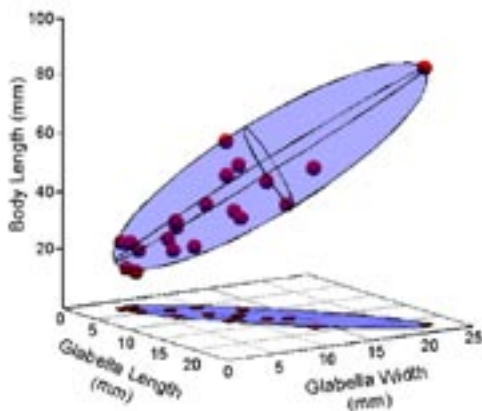


Figure 2. Model of the Table 1 data as a 3-dimensional ellipsoid.

If the three variables exhibited perfect covariance or perfect correlation with one another (e.g., columns 2 and 3 of Table 1 filled with the same values of column 1), the points in Figure 1 would fall along a perfectly straight line oriented at 45° to the three axes. In that case, the ellipse in Figure 2 would collapse to a straight line. By the same token, if the columns of Table 1 were filled with completely random numbers, the points would fill a space best represented by a sphere. The fact that our data represent a somewhat fat cigar shape indicates that their covariance-correlation structure lies somewhere between these two extremes. Observe that the true distribution of our data points in these figures has been systematically distorted because I've drawn the body length axis to be approximately the same length as the glabellar length and width axes. Given the interval over which body length values range, this axis really should be four times longer than it is. If I did that, the ellipsoid model would appear much thinner than it's portrayed. Thus, the true structure of covariance-correlation relations in our trilobite data is closer to being perfect than to being random.

Here's another way to make the same observation. Take a look at covariance and correlation matrices for those data (tables 2 and 3 respectively). The off-diagonal values are all relatively high, confirming our qualitative geometric intuition. Note also how much easier it is to get a sense of the geometry from looking at the correlation matrix as opposed to the covariance matrix.

In a qualitative sense, what PCA does is to create basic descriptive elements of the model shown in Figure 2. The nature of these descriptive elements is most simply illustrated in two dimensions, which would be analogous to the plot shown at the base of the coordinate systems in figures 1 and 2. Consider a graph of a simple ellipse (Fig. 3).

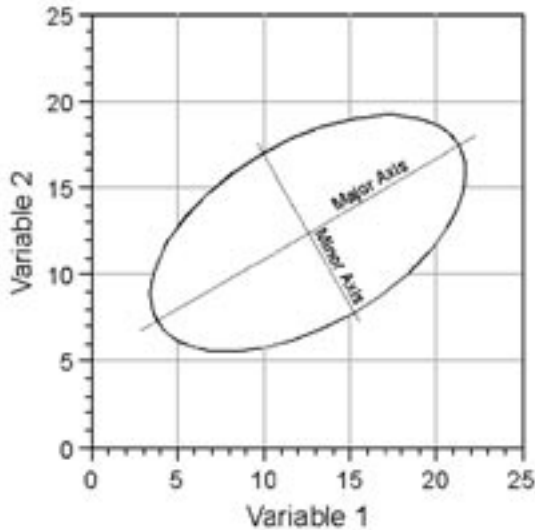


Figure 3. Descriptive elements of an ellipse.

Like a circle—which is a special case of an ellipse—the ellipse's position is established by its centre. Radiating from this centre are two axes: a long axis typically referred to as the major axis, and a shorter axis typically referred to as a minor axis (also referred to as the semi-major axis or semiaxis). Since these axes are described by two quantities, a length and a direction, they can be represented by vectors. In addition, the most efficient and conventional description of an ellipse requires that the major and minor axes (or vectors) be oriented at right angles to one another. Thus, the model ellipsoid drawn in the space between the three axes of Figure 2 can be characterized by a major axis, oriented along the ellipsoid's long axis, and two minor axes oriented at right angles both to the major axis and to one another, with each axis being a different length. The mathematical problem inherent in PCA is that of how to take the information embodied by the covariance or the correlation matrix of a sample, and estimate the geometry of ellipsoid model. The hope of PCA is that, by analyzing a sufficiently representative sample, you will be able to infer and/or quantify relations existing within the population from which the sample was drawn.

This is both easier and more difficult than it appears. Let's start off by simplifying our problem even further and only focus on body length and glabella length. We can graph the structure of covariance or the correlation relation directly. For this example we'll use the correlation matrix so the numbers won't be so large as to make the underlying geometry unclear. Figure 4A shows this graph. The two vectors represent the correlation between the two variables. One coordinate value represents the correlation of the variable with itself and the other represents its correlation with the other variable. Because the correlation matrix is symmetric, these two vectors are always symmetric about one axis of the ellipsoid model and lie on the same side of the other axis. In addition, because this is a representation of the correlation matrix, the origin of the coordinate system is always the centre of the ellipsoid model.



Once we know these quantities it is a relatively simple matter to calculate the model in Figure 4B, at least for the two-variable case. Indeed, we've already done this problem back in the Regression 3 column. There, I presented a series of somewhat complex, but tractable formulae that allow you to calculate the slope of a regression line passing through the centroid of a bivariate dataset such that the sum of the deviations of data points from a linear model, measured by distances oriented normal to the linear model, are minimized. That was called Major Axis Regression. The major axis linear regression model is the same thing as the major axis of the PCA ellipsoid model for a bivariate dataset. In this sense then, a PCA of a dataset containing more than two variables is the same as a 'Major-Axis Multiple-Linear Regression Analysis'.

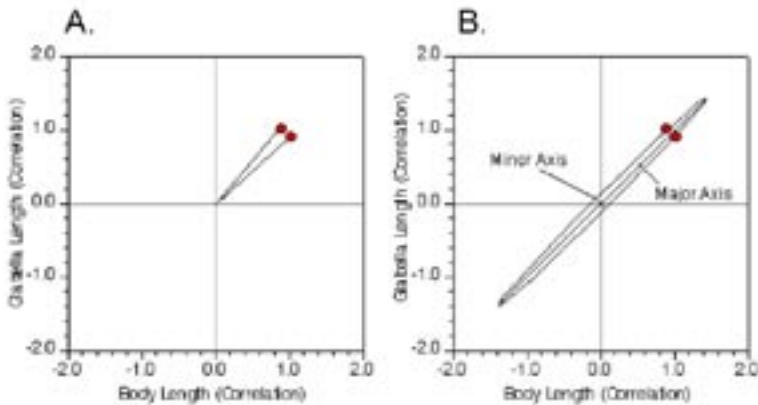


Figure 4. Conceptual diagram of a principal components analysis for two variables. See text for discussion.

OK. That's the concept bit. Now let's consider aspects of PCA mathematics. We're not going to derive PCA from first principles because (1) it's complex (literally), and (2) it's unnecessary if you understand the geometric concepts and have access to appropriate software. Nonetheless, there is a bit of terminology and conceptual material associated with the maths you do need to understand in order to set up and interpret the results of a PCA correctly.

Fundamental to understanding the maths behind PCA is the need to understand that the measurements you make on a specimen can be thought of as terms in an equation that, for the purposes of the analysis, represents the specimen. Take the first three specimens in Table 1. Those specimens are represented by three measurements. For the purposes of a PCA analysis, these measurements may be combined to give the following equations.

$$\begin{aligned}
 \textit{Acaste}: & \quad 30.41 = 23.14 + 3.50 + 3.77 \\
 \textit{Balizoma}: & \quad 22.37 = 14.32 + 3.97 + 4.08 \\
 \textit{Calymene}: & \quad 73.32 = 51.69 + 10.91 + 10.72
 \end{aligned}$$



Geometrically, perhaps the best way to think of equations like these is to consider the three measurements as specifying a vector that represents the object. The basis of PCA is a simple expansion of these equations. If x_1 = body length, x_2 = glabella length, and x_3 = glabella width, the fundamental equations of a three-variable PCA are as follows.

$$a_{11} x_1 + a_{12} x_2 + \dots + a_{1n} x_n = \lambda x_1 \quad 5.1$$

$$a_{21} x_1 + a_{22} x_2 + \dots + a_{2n} x_n = \lambda x_2$$

$$a_{31} x_1 + a_{32} x_2 + \dots + a_{3n} x_n = \lambda x_3$$

$$\vdots$$

$$a_{n1} x_1 + a_{n2} x_2 + \dots + a_{nn} x_n = \lambda x_n$$

What these equations mean is that there exist a series of coefficients (the a -values, think of them as weights) such that when they are multiplied by the object vector in the manner shown, the sums are equal to some constant value (the λ s) multiplied by the specimen vectors themselves.

The set of a -values are called eigenvectors. These are sets of weight coefficients or 'loadings' determined by iterative adjustment of the entire weight–vector system such that, when the first set of eigenvectors are multiplied by the original measurements, the variance of those sums across the entire sample is maximized. Subsequent eigenvectors are adjusted to achieve an identical maximum sum constraint for the residual data. Symmetrical matrices also yield eigenvectors with the desirable property of being oriented at right angles to one another. In terms of the ellipsoid model described above, the eigenvectors represent the orientations of the major and various minor axes oriented such that they are aligned with the major directions of variation in the sample and are perfectly uncorrelated.

The λ values are called the 'eigenvalues' or the 'latent roots'. When summed these roots are equivalent to the maximum variance or correlation uniquely associated with the sample. By convention they are subdivided into component roots assigned to each eigenvector. When the values of all the component eigenvalues are added together they equal the sum of the trace of the basis covariance or correlation matrix. There are as many positive component eigenvalues in a covariance or correlation matrix as there are independent dimensions of variation in these data. Usually, this means there are as many positive eigenvalues as there are measured variables. Symmetrical matrices, such as the covariance and correlation matrices, always produce real-number eigenvalues. Non-symmetric matrices produce complex-number eigenvalues. We don't want to go there just now. Where we do want to go is to think of the eigenvalues in terms of the ellipsoid model. As a set of constant scalars associated with the eigenvectors and reflecting the amount of variance they represent when combined with the original measurements, the eigenvalues are the lengths of the ellipsoid models' major and set of minor axes.

Decomposition of a covariance, correlation, or any other type of matrix into its eigenvectors and eigenvalues is called eigenanalysis. The basic method used today was developed by Hotelling in the 1930s but, because of the computation-intensive nature of the procedure, it wasn't often employed for data analysis until the advent of computers. Today, eigenanalysis is applied routinely in fields as disparate as theoretical topology and computer game programming (which, actually, are not as different as you might think). Many of the multivariate methods we'll be discussing in future columns will make use of eigenanalysis.



Now, on to illustrate these concepts with a few examples. To make the simplest possible illustration of PCA from a geometric point-of-view, let's continue with the analysis of body length and glabella length described in conceptual terms above. Remember, because that analysis was based on a decomposition correlation matrix we're not analysing the data presented in Table 1 (above), but rather those variables in their standardized form. Figure 5A plots the values of the two standardized variables while 5B plots the sums of the two PCA equations (see below) for the same data in the coordinate space formed by this sample's two principal component axes. These sums are called the 'scores' of the original measurements along the principal component (= eigenvector) variable axes.

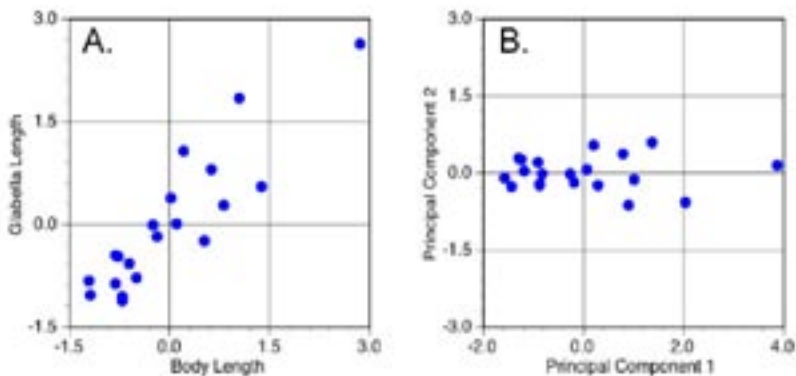


Figure 5. Scatterplots of standardized variables (A) and principal components variables (B) (see text for discussion).

There are several things to notice about this diagram. The most obvious is the alignment of the scores with the PCA plot axes. This alignment means that the PC1 and PC2 (eigen)vectors have been oriented such that their directions coincide with the directions of maximum variation in the original sample. In addition, note this realignment involved a rigid rotation of the original data in the sense that the position of each data point relative to every other data point has been preserved. Points that were close together in Figure 5A remain close together in Figure 5B and *vice versa*. Look even more closely and you'll see another interesting thing about the symmetry between these two graphs. The scores in Figure 5B are not only rotated rigidly from the positions of the original data points in Figure 5A, they're also reflected about the PC2 axis. The reason for this commonly-seen PCA phenomenon is that the direction of the principal component axes (= the eigenvectors) is arbitrary. This reflection is a consequence of the way these axes are calculated and the fact that, from a purely directional point of view, the vector 1, -1 is equivalent to the vector -1, 1. Finally, notice the difference in the scale of the two graphs. The points plotted in Figure 5A range over a little less than 4.5 standard deviation units along both axes. The scores plotted in Figure 5B range over a bit less than 6.0 standard deviation units along PC1, but just a little over 1.0 unit along PC2. This means the scale of the scores along PC1 and PC2 has been adjusted so as to provide a direct reflection of the sample variances represented by the associated eigenvectors.



Additional discoveries await inspection of the PCAs' numerical results. Equations for the two eigenvectors plotted above are shown below.

$$PC1 = 0.707 x_1 + 0.707 x_2$$

$$PC2 = 0.707 x_1 - 0.707 x_2$$

The numerical values of these equations are the weight coefficients or loadings of each principal component axis. These numbers accomplish everything we just described above. You can also think of these loadings as slopes of the multivariate major axis regression of body length and glabella length on a third variable, PC1 (or PC2) score. Remember, these scores are determined by substituting the values for standardized body length (x_1) and standardized glabella length (x_2) into these equations and calculating the result for every object in the dataset.

For this sample, the only difference between the PC1 and PC2 equations is a change in the sign of the second loading. This change in sign means the two principal component axes are oriented at right angles to one another. Consequently, the scatterplot shown in Figure 5B is a true representation of the dataset's inherent geometry, with both axes drawn in their correct relative positions. In contrast, Figure 5A portrays a biased geometry in which the data scatter appears larger than it really is because the Cartesian convention of drawing variable axes at right angles artificially inflates the distal portion of the true coordinate system.

Since the magnitude of the loadings for each variable are identical, the principal component axes lie at an equivalent angle to both the body length and glabella length axes. Because this is a correlation-based PCA, these loadings are the cosines of the angle between the original axis and the principal component axis. Thus, the angle between the body length axis and PC1 is the arccosine (cosine⁻¹) of 0.707, or 45°, a result that accords well with our observations of the data portrayed in Figure 5A.

Table 4. Trilobite measurement covariance matrix

Principal Component	Eigenvalue	% Variance	Cum. % Variance
1	1.895	94.75	94.75
2	0.105	5.25	100.00

Much good information is also contained in the eigenvalue results (Table 5). Recall, the eigenvalues represent the amount of variance assigned to each eigenvector. In the original correlation matrix for these data (Table 3), the variance is given by the sum of the values along the trace. Since this is a correlation matrix, both variables have been standardized to unit variance, and the sum of the trace is 2.0. However, even though standardized body length and standardized glabella length both exhibit variances of 1.0, the variance assigned to PC1 is 1.895; almost twice the variance of the original variables. This means that, in terms of between-object contrasts, PC1 represents 94.75 per cent of the information present in our sample, with the remaining 5.25 per cent being represented by PC2.

While this result is impressive, it should be taken with a pinch of salt when considering questions of biological interpretation. After all, variance is only one aspect of a dataset and there is no guarantee that dimensions of biological interest will coincide with directions of maximum



variance. In making interpretations of PCA results, it also pays to recall the regression-like character of PCA. For any sample, PC1 will always be the axis that represents a factor all individuals have in common. In our example, equality of the PC1 coefficients, and their common positive sign, identify it as an axis of isometric size change (albeit, one calculated from standardized data). In other words, the PCA has uncovered a pronounced tendency within this sample for a unit increase or decrease in standardized body length to be matched by a unit increase or decrease in standardized glabella length. Moreover, this factor, or component, of variation, accounts for almost 95 per cent of the observed variance.

Contrast this with the trend recovered by PC2, in which the coefficients exhibit the same magnitude, but opposite signs. Geometrically, this means there exists a subdominant tendency within this sample for a unit increase or decrease in standardized body length to be matched by a unit decrease or increase in standardized glabella length. This opposing trend is the signature of shape change. Although shape changes account for a relatively minor component of variation in this sample, if the character of shape change is what you're interested in, PC2 is where you have to go to study it, despite the low variance associated with this shape-change axis. The advantage of a PCA in this context is that, while both size and shape changes are confounded in the original body length and glabella length variables, the principal components representation of these data partitions size changes and shape changes cleanly and convincingly into mutually independent vectors or 'components'.

This two-variable system is very easy to deal with, so easy that analysis via PCA is a bit of overkill. Principal Component Analysis really comes into its own when analyzing multivariable systems, which is what we'll do now. For our final example, let's return to the question posed at the start of the column. This time we'll eschew geometric simplicity and go whole hog, setting up the PCA so that intrinsic differences in the magnitude of all variables are reflected in the results. This is accomplished by using the covariance matrix calculated from the raw data values as the PCA basis matrix (see Table 2). The sum of the trace of this matrix (392.492) quantifies the overall variance of the sample. Note that, like the correlation matrix (Table 3), the covariance matrix is symmetrical about the trace and so will have real eigenvalues along with eigenvectors oriented normal to one another.

The eigenvectors of this matrix are listed below and the table of eigenvalues below that.

$$\begin{aligned}
 \text{PC1} &= 0.951x_1 + 0.244x_2 + 0.192x_3 \\
 \text{PC2} &= 0.310x_1 - 0.700x_2 - 0.644x_3 \\
 \text{PC3} &= -0.023x_1 + 0.671x_2 - 0.741x_3
 \end{aligned}$$

Table 5. Eigenvalue and eigenvector results

Principal Component	Eigenvalue	% Variance	Cum. % Variance
1	383.08	97.60	97.60
2	7.46	1.90	99.50
3	2.00	0.50	100.00



As in the previous example, the first eigenvector contains all positive coefficients and so would be commonly interpreted as a size axis. But, this simplistic interpretation—that is to be found throughout the published literature whenever PCA is applied to morphological measurements—is misleading. Note that, contrary to the previous example, the PC1 coefficients are not equal. Since these coefficients express the rate of change in one variable relative to the others (= the slopes of the partial multivariate major axis regressions), this means that, for each unit change in PC1 score, body length change is, on average, much larger than changes in the glabellar measurements. In the previous, two-variable example, we used the term isometric size change to express the pattern of morphological deformation in which all variables increase or decrease in concert and at the same rate. This is the sort of change one sees when a shape drawn on a balloon increases in size as the balloon is blown up or (perhaps more commonly) when we increase the size of a computer graphic while holding the control key down that prevents distortion due to changes in the image's aspect ratio (Fig. 6). Isometric size change is *not* the type of morphological change indicated by our three-variable PC1 axis. Rather, along this axis the magnitude of the glabellar measurements is changing at a much slower rate than changes in body length. Moreover, the aspect ratio of the glabella is also changing slightly, as indicated by the difference between the glabellar measurement PC1 coefficients.

In effect, the dominant trend among these three variables is for the glabella of large-sized genera to be slightly narrower along the body axis, and the glabella of small-sized genera to be slightly broader at right angles to the body axis. This is allometric size change (Fig. 6), which is to say, size change within which a corresponding shape change is embedded. The condition of allometry is the sort of relation between size and shape change typically seen in biological systems (we'll discuss why this is so in a future column). Allometric size-shape change also, typically, accounts for the largest single between-object component of variation in morphological datasets. For this sample, allometric size-shape change accounts for more than 97 per cent of the measured variance.



Figure 6. Illustration of the difference between pure or isometric size change and allometric size change, which is accompanied by a change in the specimen's shape.



If quantifying dominant, generalized linear trends within a dataset were all PCA had to offer the palaeontological data analyst it would be well worth the effort. But, as alluded to at the beginning of this column, there's much more. Let's move on to an interpretation of PC2. Here we see a contrast between the positive, middle value of the body length loading, and the high negative loadings of the glabellar measurements. The contrast in signs between PC2 and PC1 assures us that the morphological trend represented by the former is uncorrelated with the sample's allometric size trend. The values of the PC2 loading coefficients show that the second most dominant component of variation in this system is a tendency for individuals with long body lengths to have disproportionately small glabellas. Interpretation of PC3 proceeds in the same way. Once again, the unique pattern of signs assures us that the morphological trend captured by PC3 is uncorrelated with both of the previous principal components. Here, the loading coefficient associated with body length is so small as to be practically negligible. Instead, the equation of this axis reveals a strong contrast between glabellar length and width. Consequently, genera with high scores on PC3 are characterized by a glabella that is strongly elongated in the direction of the body axis.

Since PC2 and PC3 only capture 2.5 per cent of the measured variance, you might suspect that these can be effectively ignored and such may well be the case. In fact, one of the routine uses of PCA is to reduce the dimensionality of a variable system. It is often the case that a large number of variables can be reduced to just two or three principal components while still preserving a very high percentage of the measured variation. However, when dealing with so few variables it's always a good idea to make the most of what you've got, even if this might turn out not to be significant statistically later on. As a last exercise then, I'll summarize the distribution of objects in a size-shape space defined by our principal component axes and relate those ordinations to the interpretations I've outlined above.

Figures 7A and 7B illustrate the locations of all genera within our three-dimensional principal components system. Note again the similarity of the ordination in Figure 7A to that obtained from the two-variable analysis (Fig. 5B).¹ This is due to the relatively small amount of additional variance contributed by glabellar width (see Table 2). To get a sense of the three-dimensional structure of the PCA scores, in your mind's eye hinge Figure 5B up, out of the plane of the paper about the common axis (PC2) so that it forms a right angled plane with respect to Figure 5A.

¹ Don't be fooled by distortions induced, this time, by drawing the axes to the same physical size, but different scale ranges.

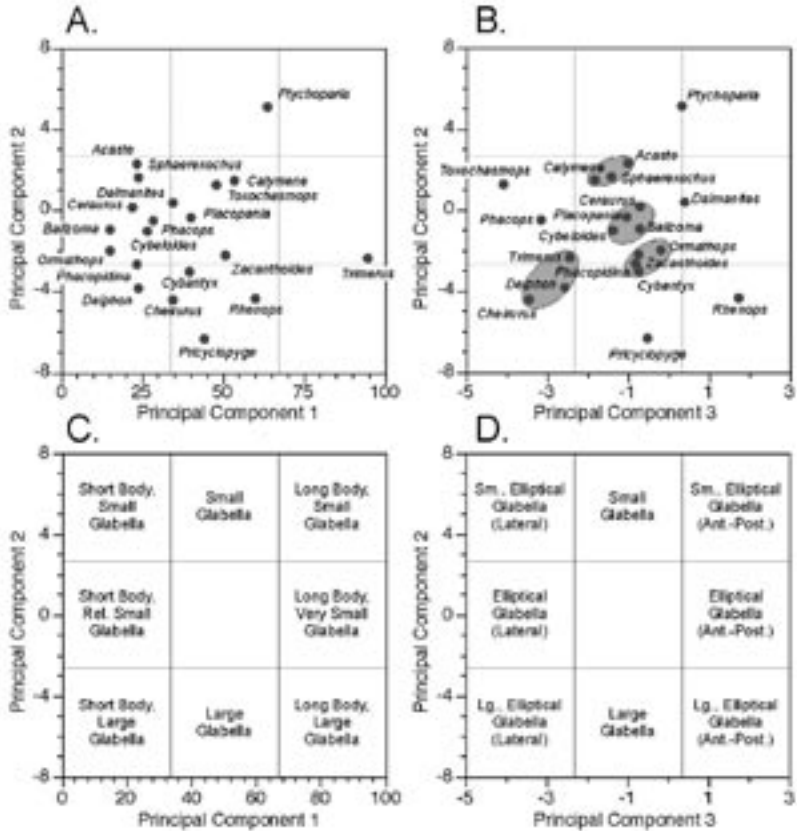


Figure 7. Scatterplots (A-B) and morphological interpretations (C-D) of principal component scores along planes defined by PC-1 and PC-2 (A, C) and PC-2 and PC-3 (B, D). See text for discussion.

Figures 7C and 7D assign relative morphological characteristics to regions of the score scatterplots based on our previous interpretations of the principal component axes. Genera whose projected score positions lie within regions so delimited would be assigned to their corresponding broad morphological categories. Of course, it's an open question as to whether the specimens I've chosen to represent these genera truly are representative. Nevertheless, the analysis could, in principle, be repeated on a larger, more representative sample and these provisional morphological category assignments confirmed or revised. Also note how the score ordinations tend to resolve themselves into subgroups and outliers separated by gaps (some of the more obvious of these are indicated in Fig. 7B). These gaps may reflect consistent and interpretable aspects of the morphological system (e.g., species boundaries, functional constraints) whose morphological character can be inferred from the geometric interpretation of the principal component axes, despite the fact that no specimen representing this morphology was included in the sample.



Principal components analysis—and the eigenanalysis technique upon which it is based—is a powerful data analysis tool. It can be treated as a method in its own right or used as a component part of more complex methods. While PCA is often used as a ‘black box’, the time taken to understand this method’s geometry will be more than repaid in better data analytic designs and better interpretations. All that’s left for me is to close with a few comments about calculating your own PCAs.

Unfortunately, MS-Excel does not provide a routine for determining eigenvalues or eigenvectors within its data analysis library.² It is possible to program MS-Excel to perform the necessary calculations, but doing so is not a trivial undertaking. The spreadsheet accompanying this column takes these externally computed eigenvalues and eigenvectors and shows how they can be combined with the original data to yield the PCA scores and plotted in MS-Excel. Those wishing to perform PCA on their data have a variety of options. One can simply obtain a specialized multivariate data analysis package that includes or supports eigenanalysis. Such packages are available as freeware (e.g., PAST, <<http://folk.uio.no/ohammer/past/>>) or commercial software (e.g., Statistica™, Systat™, MatLab™, Mathematica™). Alternatively, one can obtain software add-ons to MS-Excel that extend its data analysis toolkit to cover eigenanalysis. There are many of these as well, including freeware (e.g., PopTools, <<http://www.cse.csiro.au/poptools/>>) and commercial packages (e.g., XLStat, StatistixL). New software tools for performing the necessary calculation are also appearing daily on various web search engines. Given this range of alternatives, there is an eigenanalysis/PCA package out there that is right for your needs, computer system, budget, expertise, and level of interest.

The references listed below contain descriptions of principal components analysis I’ve found useful over the years, and discuss some of its variants/extensions in more detail than I’ve had an opportunity to do here.

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Don’t forget the *Palaeo-math 101* web page at <<http://www.palass.org/pages/Palaeomath101.html>>

² The basic eigenvalues and eigenvector results shown in this column’s accompanying spreadsheet were preformed in Mathematica™.



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Electronic submission of applications to the Secretary <sll@nhm.ac.uk> 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 name and contact details of a scientific referee. Successful candidates must produce a short illustrated report for the Palaeontological Association's *Newsletter* and are asked to consider publication of their research results in the Palaeontographical Society's monograph series. The deadline for applications is **1st November 2005**.

Dr Sarah Long

*Secretary, Palaeontographical Society,
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The Palaeontographical Society



'Everyone who has collected Sessile barnacles must have perceived to what an extent their shape depends on their position and groupingthus I have seen a strongly-ribbed species and a nearly smooth species closely resembling each other and both having a peculiar appearance, owing to their having been attached to a pecten.'

Charles Darwin's observations are as true today as they ever were. We cannot hope to reconstruct the past biosphere unless we understand the basic building blocks, the fossils themselves.

He was a member, shouldn't you be!

From Charles Darwin's barnacles to the Cycadales of the Wealden, for 150 years the Palaeontographical Society of Great Britain has published the highest quality monographic works detailing the whole range of invertebrate, vertebrate and plant fossil records of the British Isles. The society typically publishes two monographs per year. Details of our catalogue and instructions to authors are available through the website at: http://www.nhm.ac.uk/hosted_sites/palsoc/. We publish papers quickly and without cost to the authors. For an individual membership fee of just £33 per annum, members receive two monographs per year and full access to the extensive back catalogue at a much-reduced cost. For details about membership please download the membership form from the website, or contact Dr Sarah Long at the Natural History Museum, Department of Palaeontology, Cromwell Road, South Kensington, London SW7 5BD.



LEFT Charles Darwin, *A Monograph on the Fossil Balanidæ of Great Britain*. London, Printed for the Palaeontographical Society, 1 8 5 4 .

RIGHT Joan Watson & Helen Cusack, *A monograph on the Cycadales of the English Wealden*, London, Printed for the Palaeontographical Society, 2 0 0 5 .





— OBITUARY —

Stuart McKerrow **1922 – 2004**

William Stuart McKerrow – Mac – died suddenly at the age of 81 on 12th June 2004. From 1947 to 1989, he was the person who gave the first taste of real geology – rocks in the rain – to generations of Oxford geologists. It will have begun with a week in Arran, usually in the rain, at first with Mac and J.V. Harrison, then with others, notably Brian Atkins. In some years it would be followed by a visit to a marine biology lab, and even more traumatic encounters with the denizens of the slimy deep. Thereafter, the interminable journey back to Oxford.



With Trinity Term of that first year came days out around Oxford, to quarries, most now long-vanished: Long Hanborough, Kirtlington, Headington, Wheatley. At the end of the Long Vacation, Mac, sometimes accompanied by his wife Jean, drove south to Weymouth, with or without a van load of the young. Who can forget the awfulness of some of those hotels? Long days on the beach, walking most of the way from Lyme Regis to Bridport, before the Nanny State clad us in hard hats, goggles, dayglow jackets, and the rest of it as we strode past near-naked holidaymakers sunbathing at the foot of shale cliffs too dangerous for mere geologists to approach?

And there were those tutorials and practicals, and the mythology of that list of 492 fossils you had to know to get a degree in the golden age, before they divided seconds, an age when geology and theology fought it out to retain the honour of the lowest percentage of firsts in the University.

Mac was an Oxford and a geological institution, with a life and career of distinction: a D.S.C. in World War II at the age of 21, and an Oxford D.Sc. 25 years later.

Stuart McKerrow was born in Glasgow on 28th June 1922. He attended the Glasgow Academy, and Abbotsholme School in Derbyshire, before entering Glasgow University in 1940. Having completed two years at university, he was called up in 1942, and commissioned as Sub-Lieutenant. Following general induction, he joined the river clan frigate H.M.S. Tay, on convoy escort duty in the North Atlantic, working as a high frequency direction-finding expert. It was during extreme bad weather that Stuart discovered his receiver – a yard-square cube, weighing a hundredweight or so – was damaged, and its direction finding abilities impaired. As U-boats remained submerged during bad weather, he had himself and the receiver secured with ropes, and held steady by a suitably robust seaman, spent six hours with a soldering iron carrying out repairs that would normally take ten minutes on land. After some further hours' work, the receiver was reassembled and switched on. A U-boat was immediately detected on the surface, and thereafter destroyed.



In mid-May 1943, his escort group joined SC130 in thick fog east of Newfoundland, and proceeded north-eastward. As the fog cleared, the convoy changed course, and around 20 U-boats surfaced and radioed Germany to report the course change. Repeated course changes on Stuart's advice led to repeated surfacing and radio traffic, and detection of the position of the submarine pack. Five of the six escorts were placed in the same quarter, repelling U-boat attacks with great success: the convoy arrived at Londonderry without loss of a single merchantman. Such was the confidence of Commander John Gretton in his High Frequency Direction-Finding team.

From Londonderry, Stuart was summoned to the Admiralty, and driven north towards Bletchley, where he gave the third lecture of his life, to around twenty mathematicians and code breakers at Bletchley Park, who wanted to know why U-boat radio transmissions had been so unusual in the previous week. It was for these two examples of "outstanding skill and duty" that his D.S.C. was awarded.

In March 1944, his then Escort Group (B7) was disbanded, and the ships reassigned to assist in the Normandy landings of 6th June 1944. When Germany surrendered on 7th May 1945, U-boats in the North Atlantic were ordered to proceed to Loch Eriboll on the north coast of Scotland. The 21st Escort Group (to which Stuart was now attached) was sent to greet them, and boarding parties sent to remove small arms, torpedo detonators, and all alcohol. Much time was devoted to harvesting mussels and winkles from the shore of the Loch to go with the recently acquired German wines.

Stuart finished his war in Australia. He was demobbed on Friday 16th November 1945, and started geology classes back at Glasgow University three days later, on Monday 19th November. As a result, he graduated in 1947, when qualified geologists were in great demand. Offered four posts, he accepted an offer from Oxford University, where he remained until retirement, marrying his fellow Glaswegian Jean Stark Brown in 1949.

His Oxford appointment arose from a telephone conversation between E.R. Trueman and J.A. Douglas, the latter seeking a promising young palaeontologist. Two days later, Stuart was on the night train to Oxford. Douglas met the train with his car. Driving out of the station, he turned right, away from the city, and stopped under the railway bridge for about twenty seconds, and then drove on for a further 250 or so yards, stopping again on the bridge over the Thames. As he told it, Stuart then remarked to Douglas that "They must have quite good pumps under the railway bridge to keep the road dry." Douglas responded that this was indeed the case, and that it was one of the best tank traps around Oxford. He then explained that he had been the commanding officer of the Oxford Battalion of the Home Guard. There then followed a tour of the defences of Oxford, dinner with Douglas and his wife, the offer of a job, and no further reference to geology. It was, Stuart believed, his observations on pumps alone that got him the job, and the magnificent starting salary of £450 per annum, compared to the £300 per annum offered by the Universities of Cardiff and Birmingham, and the Geological Survey of Great Britain and Northern Ireland.

It was on this same day that Stuart was introduced to W.J. Arkell – Jurassic Arkell – who asked him what topic he intended to pursue for his doctoral research. Given the Glasgow training, and a course in statistics, his reply was to work on variation in some group of local Jurassic fossils. Arkell responded "you may work on any group you like except ammonites. Ammonites don't vary". In September of that year, Arkell proposed a study of the brachiopods of the Fuller's Earth Rock in the Middle Jurassic of Somerset and South Gloucestershire. They drove to Chipping Sodbury,



with Stuart's bicycle in the boot of Arkell's car. After viewing a few localities, and agreeing a list of twenty more, Arkell left Stuart and his bicycle to their own devices. In the course of eight days collecting (with only one minor accident) enough brachiopods were amassed for the thesis. This was eventually published in the *Quarterly Journal of the Geological Society* (one of the few UK journals of standing where palaeontology appeared in print in those days). The discussion published after the paper reveals much of the philosophy of the times, with Helen Muir-Wood very much on the side of the splitters.

Stuart McKerrow followed a distinguished career as an academic – as Stuart to his colleagues – and as Mac to the 42 generations of students he taught, and the 20 doctoral students he supervised. It was, he said, his students who gave him the ideas and inspiration. He was the author of more than 120 books and articles on a wide range of topics, from the fossils of the Jurassic rocks of southern England to the reconstruction of the configuration of ancient continents and oceans through the last half billion years of earth history. His collaborations with Colin Campbell, John Dewey, Stephen Moorbath, Fred Ziegler, Robin Cocks, Chris Scotese, Art Boucot and others reached a wide audience. His last publication, with Tony Watts, and his last research student, was on the landscape evolution of south-central England, a topic that had fascinated him for more than thirty years, and always came up as we drove northwards from Oxford and observed the dramatic increase in valley incision in the few miles between the Department and the valley of the Glyme just to the north of Woodstock.

He was a founding member of the Palaeontological Association, the society that led to the renaissance of the study of fossils in the United Kingdom. The background to that foundation extends perhaps as far back as the three-week field trip organised by the Geological Society of London in 1946. One or two students from each University Geology department travelled from Girvan to Oxford, examining the rocks along the way. Nearly all of the first officers of the Association were on the bus. When our Association was founded in 1957, Stuart was the first Treasurer.

Stuart's contributions to science were recognised by the award of the degree of Doctor of Science by Oxford University in 1977, the Lyell Medal of the Geological Society of London in 1981, the Clough Medal of the Geological Society of Edinburgh in 1988, the Fournier Medal of the Geological Society of Belgium in 1995, and the T.N. George Medal of the Geological Society of Glasgow in 1997. He served as Vice-President of the Geological Society, and President of the Palaeontological Association.

Stuart's contribution to the world of teaching and research extended beyond his subject. In the mid-1960s he found himself a member of the increasingly large number of University Lecturers in Oxford who lacked college fellowships. Seven of these 'non-fellows', of whom he was one, met informally in the Spring of 1961 to discuss what should be done to prevent the creation of a second-class society in Oxford. A few months later they met formally, and the group was enlarged and became a committee. Thereafter, on every possible occasion, they brought their position to the attention of the University. The outcome was that in 1965, two new postgraduate colleges, St Cross and Iffley College, were created. Stuart, together with 35 others, became a Fellow of Iffley College. They asked Isaiah Berlin to lead the new college. His response was to approach the Ford Foundation and the Wolfson Foundation, whose generous benefactions enabled Iffley College, now renamed Wolfson College, to become the largest graduate college in the University. Stuart became chairman of the Academic Planning Committee, which defined the academic structure of the College, its functions and connections with the outside world. He also served on the Building Committee. Stuart was not



only a Founding Fellow of Wolfson, he was also in part responsible for its conception. Later, over an unbroken period of 39 years, he contributed much to its growth and development, and to the ethics of a society he helped to create. Furthermore, he was an important focus of stability in the College. His forthright, no-nonsense manner ensured that when problems arose, they were quickly dealt with, and soon forgotten. He served as Senior Tutor, and as Vicegerent.

Stuart retired in 1989, continuing to lunch in College most days, a familiar figure in the Upper Common Room (when not obscured by clouds of pipe smoke – at least until such pleasures were forbidden him), wrestling with a crossword with his fellow addicts. He was College Archivist at the time of his death.

Stuart was an elder of St Columba's United Reform Church in Oxford, where he worshipped for nearly 50 years. He thought long on the matter, and successfully reconciled his deeply held Christian beliefs and his science.

Stuart McKerrow died on 12th June 2004. He is survived by his wife, Jean, and their three sons.

Jim Kennedy

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— OBITUARY —

Georges Ubaghs 1916 – 2005

With the death of Professor Georges Ubaghs, aged 88, on 31st January 2005, the palaeontological community has lost one of the greatest specialists of fossil echinoderms (particularly Palaeozoic forms) of the 20th century. His most important legacy is probably his major contribution to the *Traité de Paléontologie* (1953) and to the *Treatise on Invertebrate Paleontology* (1966–1978), in both of which he was – by far – the main contributor to chapters devoted to echinoderms, with



respectively 199 pages (54%) and 516 pages (22%). Moreover, all the people who had the chance to meet and know him personally will regret not only the great scientist, but also the man. Everybody will remember his extreme courtesy and kindness, his discretion, his modesty, and his great open-mindedness. For these two reasons, the whole echinoderm community feels a bit orphaned.

Georges Jean Charles Ubaghs was born in Angleur (Liège, Belgium) on 29th February 1916. After brilliant studies at the University of Liège, Georges Ubaghs obtained a PhD in Zoological Sciences in 1939. He had not yet performed his national service when World War II began. For this reason, he was not mobilized and did not participate in the dramatic



battles that took place in Belgium in May 1940. His very first scientific contribution dealt with dendroid graptolites from the Lower Carboniferous of Belgium. However, his centre of interest rapidly moved on to echinoderms, and especially Palaeozoic crinoids. During war time, he produced his first echinoderm paper (devoted to the anatomy and systematics of *Mespilocrinus*, a Lower Carboniferous crinoid of Belgium), but he was also involved in several contributions dealing with regional geology and Famennian outcrops of the Liège region.

Immediately after the end of the war, Georges Ubaghs was nominated as Professor of Palaeontology at Liège University (1945). This extremely rapid promotion was largely the consequence of the arrest of Charles Fraipont, former Professor of Palaeontology in Liège, for “incivic behaviour” (collaboration) during the war. From 1945 to the late 1950s, Georges Ubaghs was involved in two main projects. The first one concerned Palaeozoic crinoids, with several key papers devoted to the description of various forms from the Devonian of Belgium, France, Germany and Bohemia, and from the Silurian of Gotland and Germany. These contributions (as well as later ones) are remarkable for the quality and accuracy of both observations and hand-drawings. Very rapidly, Georges Ubaghs became one of the best specialists of Palaeozoic crinoids, and it was wholly logically that he was asked by Jean Piveteau to write the chapter dealing with crinoids in the third volume of the French *Traité de Paléontologie* (1953). However, the contribution of Georges Ubaghs to the *Traité* is not limited to crinoids, as he was also in charge of two other chapters devoted to “stelleroids” (sea-stars and ophiuroids), and ophiocystioids (a group of Palaeozoic echinoderms related to both echinoids and holothurians). During the 1950s, Georges Ubaghs was also involved in an eight year project devoted to the stratigraphy of foraminiferans collected from cores made in Angola by the oil company Petrofina (modern Total). His works for this private company have not been published.

The year 1959 was pivotal in the scientific career of Georges Ubaghs, with the beginning of the re-examination of “carpoid” echinoderm faunas from the Lower Ordovician of Montagne Noire (southern France). “Carpoids” are flattened Palaeozoic echinoderms, with no sign of five-fold symmetry (e.g. cinctans, solutes, stylophorans). The exquisite preservation of the Montagne Noire material (within silico-aluminous concretions) and the elaboration of a new technique of casting (using latex) allowed him to observe numerous previously undocumented aspects of carpoid morphology, and to propose new interpretations of their anatomy. For example, Georges Ubaghs demonstrated that *Lingulocystis* and *Rhipidocystis*, two forms long interpreted as “carpoids”, were indeed eocrinoids. Later on, he began to investigate the atypical morphology of stylophorans (cornutes, mitrates), with the description of the Montagne Noire mitrate *Chinianocarpus thoralii*. In his first paper on stylophorans, Georges Ubaghs followed their traditional interpretation as bizarre, stemmed, asymmetrical echinoderms. However, soon after, new observations made on the Montagne Noire cornute *Phyllocystis blayaci*, as well as his great knowledge of the anatomy of both crinoids and “stelleroids”, led him to propose a new interpretation for the articulated appendage of these fossils. He suggested that it was not a stem made of columnals, but rather that it corresponds to a feeding device bearing a single ambulacral groove protected by two series of movable cover plates: the “aulacophore”. Later on, the description of new cornutes and solutes from the Upper Cambrian of Nevada allowed him to support the view that the long, articulated appendage of solutes was probably not homologous with that of stylophorans.

After these major advances in the knowledge of carpoid and eocrinoid anatomy, almost all papers produced by Georges Ubaghs focused on Cambro-Ordovician echinoderms, and he rapidly became one of the leading specialists in the field. During the 1960s and 1970s, he produced



several key papers on the morphology and systematics of various eocrinoids, “carpoids”, and primitive crinoids. However, during these years, most of his energy was devoted to the *Treatise on Invertebrate Paleontology*. He contributed to all three volumes of the echinoderm *Treatise*, as he was in charge of the chapters dealing with ophiocistioids (volume “U”; 1966), general characters of echinoderms, eocrinoids, stylophorans, cinctans, and “haplozoans” (volume “S”; 1967), and finally skeletal morphology and origin of crinoids, camerate crinoids, and classification of echinoderms (volume “T”; 1978). His enormous contribution to the *Treatise on Invertebrate Palaeontology* probably represents his major legacy and scientific achievement. The *Treatise* provided Georges Ubaghs a powerful agent for the expansion of his new interpretations (otherwise poorly known, as most of his papers were written in French): not only those concerning the anatomy of the various groups of “carpoids”, but many other key advances, such as the evidence – for the first time – of the fundamental difference between “arms” (as in crinoids) and brachioles (as in blastoids, cystoids and eocrinoids).

When he retired in 1984, Georges Ubaghs was nominated Honorary Professor at Liège University. He then had plenty of time to devote to the study of Early Palaeozoic echinoderms. His last contributions were greatly enhanced by two very fruitful collaborations. The first one, with R. Robison (Lawrence, Kansas), provided him the opportunity to describe beautifully-preserved Middle Cambrian faunas of both “carpoids” (solutes, stylophorans) and eocrinoids from Utah. The second collaboration was with Daniel Vizcaïno (Carcassonne, France), and concerned Cambro-Ordovician echinoderm faunas from Montagne Noire and Spain. He was strongly affected by the death of his wife in March 1999, but he survived her by five years. He died peacefully on 31st January 2005 in Liège.

The legacy of Georges Ubaghs to our knowledge of echinoderms (and especially crinoids, eocrinoids, and “carpoids”) is invaluable. The exceptional quality of his work was recognized by several distinctions: he was appointed Member of the Royal Academy of Belgium and Commander of the Order of the Crown. His absence will be all the more felt in that he did not transmit his great experience and knowledge of echinoderms to any PhD student. However, in a certain way, the contribution of Georges Ubaghs has influenced so deeply our current knowledge of various groups of echinoderms that, even if his work has left few traces in his own country, his ideas – often ahead of their time – are more alive than ever in the worldwide echinoderm community.

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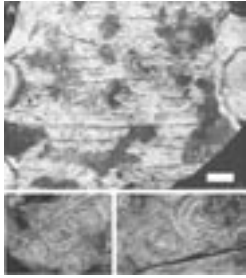
Edouard Poty

Université de Liège, Liège (Belgium)



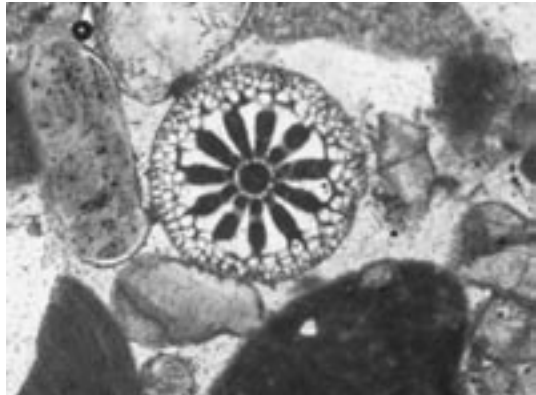
MYSTERIOUS FOSSILS

Mysteries no more:



Brian Pratt of the University of Saskatchewan suggests that the Mystery Fossil Number Two is not a *Rhysonetron* trace, but is more like ripple trough syneresis cracks called *Manchuriophycus*, which he has argued in a 1998 *Sedimentary Geology* paper are earthquake-induced shrinkage and dewatering features. So now you know. Unless you know different, of course.

Mystery Fossil Number Seven has attracted a small flurry of e-mail activity. John Hampton at Edinburgh identified it as a very nearly horizontal section of a holothurian wheel sclerite, while Steve Donovan at the Nationaal Natuurhistorisch Museum, Leiden identified it as two fossils, with the spoked centre being a transverse section through an echinoid spine, most probably from a diadematoïd, and the surrounding outer 'vesicular' structure being



a possible algal coating on the spine. A third party was called in to adjudicate (David Pawson at the Smithsonian) and he sided with Steve's identification. David states that the fossil is not a holothurian ossicle, firstly because it seems to have an unadorned central cavity, secondly because the rim area (with or without algae) is unlike holothurian wheels. Finally, present-day holothurians with 11-spoked wheels (Family Myriotrochidae) live mostly in bathyal/abyssal depths in the central Atlantic region; in the Arctic, one or two species venture into shallower depths. Perhaps three western Atlantic shallow-water species have wheel ossicles, and in these all of the wheels have six spokes. Echinoderms seem to be quite popular!

Mystery Fossil Number Eight comes from the Chrysospilitotissa outcrop of the Pliocene–Pleistocene Nicosia Formation, Cyprus and was found by a Leeds University final year undergraduate in 2004. This is a slightly tapering cylindrical tube with an odd-shaped 'foot' formed of a number of much smaller radiating tubes, one of which bifurcates. Both the large tube and the small 'foot' tubes are formed of a thin layer of calcium carbonate. The Nicosia Formation at Chrysospilitotissa consists of muddy fine sands and contains in addition to the mystery fossil a diverse range of shallow marine fossils, including many non-cemented serpulid tube fragments. Best guess is that the mystery fossil

is also a serpulid, but on the very large side, with the 'foot' being an attachment onto a cluster of pre-existing thinner serpulid tubes.

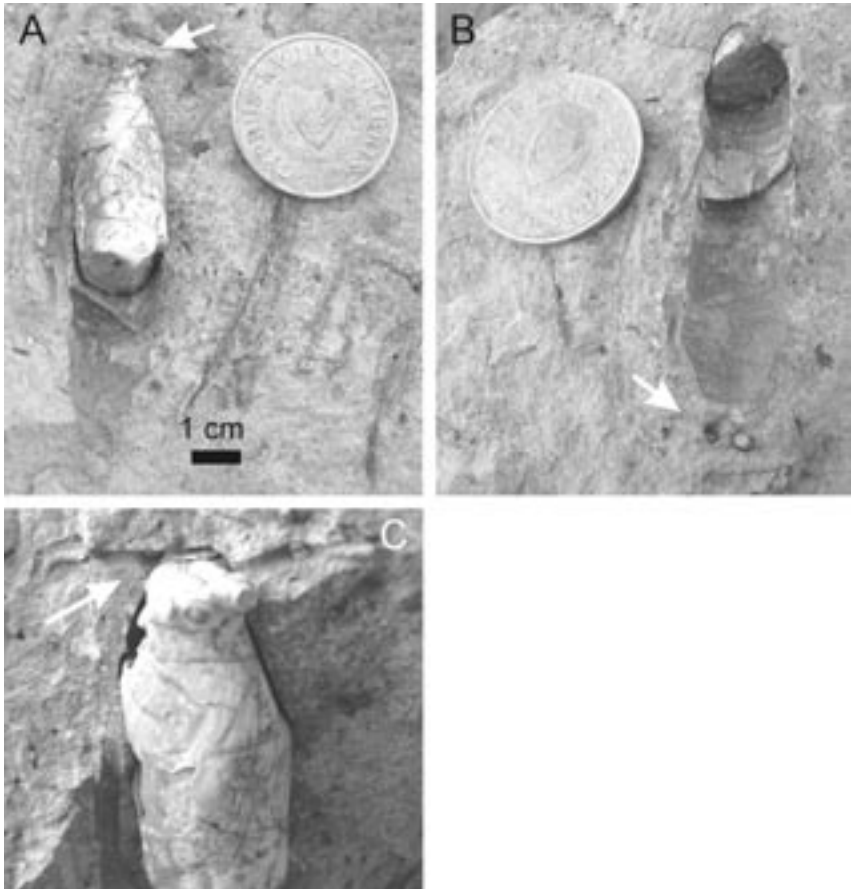


Image A: mystery fossil with 'foot' at top (white arrow). B: counterpart of mystery fossil (inverted compared to A). C: detail of 'foot'.

What do you think? Answers in an email to Cris Little at the address below.

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Meeting REPORTS



2nd International Biogeography Society Meeting

National Conservation Training Center, Shepherdstown, WV, USA

5 – 9 January 2005

The International Biogeography Society (IBS) was founded in 2000. Given the long history of biogeography as a discipline, and its importance in the development of ideas about evolution, speciation and adaptation, IBS is a surprisingly young society. The IBS website (<<http://www.biogeography.org/>>) explains that the IBS was established with three main goals in mind:

- To improve communication and collaboration among researchers in disparate fields who are working on biogeographic questions.
- To raise awareness of the utility and contributions of biogeography to both the scientific community and among the general public.
- To promote the training and professional development of biogeographers to aid the study and conservation of life on Earth.

The website is also a superb resource for information on biogeographic publications, phylogenetic and statistical software, and publicly available data sets.

The second meeting of IBS was held in January in West Virginia, in the sylvan setting of the National Conservation Training Center (NCTC), which has a variety of roles. The NCTC uses a lot of eco-building techniques, and the accommodation was plush to say the least. NCTC was an apt setting for a meeting that had conservation biogeography as its theme.

The conference opened with a one-day workshop on Historical Biogeography, organized by **Dan Brookes** (University of Toronto). Dan gave a talk in which he outlined the search for explanatory models that successfully predicted the distribution of organisms, adaptations, and communities in space. He ranged from the roots of the discipline in the work of Wallace and Darwin, covered the importance of island biogeography theory in converting biogeography into a quantitative, predictive science, and covered Hubbell's Neutral Theory of Biogeography and Biodiversity.

Maggie Wojcicki (University of Toronto), an undergraduate computer scientist, worked with Dan to develop a new program, Phylogenetic Analysis for Comparing Trees (PACT). The inspiration for PACT came from methods used in the analysis of historic manuscripts, and it relies on inputting the Venn diagram strings for trees, rather than presence/absence matrices. Despite scaring most of the workshop participants with the words "I'll just let you see the (program) code," she explained PACT with admirable clarity. Maggie has moved to Australian National University to study for a Ph.D. in computing science, but hopefully she will continue to contribute to phylogenetic computational methods.

Brett Riddle (University of Nevada, President of IBS) works primarily as a phylogeographer, comparing molecular phylogenies among populations to their geographic distributions. As benefits



the president of a society that aims to encourage interdisciplinary studies, Brett urged closer cooperation between historical biogeographers and their colleagues working on extant biotas. He emphasized the contributions that an understanding of extinction, missing data, and geodispersal could make to unravelling apparently contradictory or unresolved area relationships in the modern world, and how population thinking in a spatial framework might help palaeobiogeographers.

Bruce Lieberman talked about his recent work on the application of Geographic Information Systems (GIS) to palaeobiogeographic problems, particularly those of range sizes in the fossil record. A tremendous amount of work has been done on range sizes and extinction risk in present day organisms, and some work has been done on Pleistocene taxa. Palaeontologists have tremendous amounts of data on extinction, but our focus tends to be on the temporal patterns. Bruce demonstrated the power of GIS tools for adding the spatial dimension to the study of speciation and extinction in the geological record.

Dan Brooks bookended the session with another talk, this time on Terry Erwin's Taxon Pulse Hypothesis (TPH) that originated at about the same time as the vicariance model, but has been ignored. Dan has been involved in analytical biogeography for many years, developing Brooks Parsimony Analysis (BPA), and variants on that method. Some readers will be familiar with the maximum vicariance biogeography model, which developed in close association with maximum parsimony cladistics. For those unfamiliar with it, vicariance models simply state that differences in fauna or flora between areas are the result of climatic and geographic splitting of taxon ranges. This view of biogeography grants almost no explanatory power to other processes, such as dispersal of organisms, extinction, or the problems faced by parsimony-based methods when previously isolated areas come into secondary contact. TPH explains biogeographic distributions, and speciation, in terms of range expansions and contractions. A consensus was definitely emerging among meeting participants that richer models that incorporated a wider number of parameters provided significantly better fits to observed distributions of organisms.

The rest of the conference was organized around five symposia spread across two days. In between symposia talks a large number of posters were displayed, with the posters changing each day.

Biogeographic Responses to Global Change

David Currie and his research group are assessing the relative impacts of global change and local habitat loss on biodiversity. The outcome of this work indicates that habitat loss is currently the more significant factor. **Felisa Smith** gave a presentation on the range of adaptive responses exhibited by mammals to climate change in North America after the last deglaciation. **Jim Clark** discussed the important task of predicting future changes in range and migration routes of bird species responses, testing his models with historical data. **Lesley Hughes** examined the potential impacts on Australian fauna and flora of a range of climate change scenarios. **Camille Parmesan** examined whether there was evidence of biased poleward shifts in species ranges. She explained how her work contributes to IPCC Group II: Impacts, adaptation, and vulnerability, which attempts to make testable predictions about the effects of global change, and suggests ways to mitigate those effects. So IPCC is not just temperature curves and sea-level rise!

Geography of Parasites and Infectious Diseases

This was topical session, given current concerns about avian flu, which examined the role of spatial structure in understanding the evolution and transmission of parasites and diseases. **Dan Brooks**



started this session with a talk that reminded the audience of the close parallels between historical biogeography and host-parasite work. **Eric Hoberg** discussed host-switching in the context of geographic populations of host organisms and how this influences the diversity of host-parasite interactions. **Leslie Real** demonstrated the power of GIS tools for understanding the spread of rabies. The UK model was a hypothetical case, but the US study used historical data in a GIS framework to identify dispersal routes (in one case racoons inside dustbin lorries that dumped their rubbish at a central location was a key 'jump dispersal' event). **Uriel Kitron** specializes in vector-borne diseases, diseases that need an intermediate host, and explained how spatial information about carriers and susceptible hosts can be used to break the life cycles of such diseases. **Jean Francois Guegan**, in a similar vein, covered the influence of spatial and seasonal cycles in the spread of diseases in human populations.

Geography of Extinction: From Palaeo to Recent Periods

Spatial patterns and influences on extinction at a range of time scales from the Mesozoic to the Recent were examined in this session. **Rob Channell** examined patterns of range contraction in threatened species, and showed that in many cases range contraction does not result as a steady retreat to the centre of a species range, but tends to leave populations at the edge(s). The edge of a species range is often the most marginal areas for a population to be viable in, increasing the risk of extinction. **Gerardo Ceballos** looked at the structure of population extinctions among mammals around the world, and the problems presented by different modes of population extinction present to developing conservation strategies. One strategy does not fit all cases was the simple point of the talk. **Sandy Harcourt** examined the relationship between spatial distribution and abundance among primates, and how different abundance/density relationships can enhance the risk of extinction of some primate groups relative to other primates. **Harmut Walter**, a veteran conservation biologist, gave an overview of his experiences over the last forty years. **David Jablonski** examined the role of geographic range in survival and recovery patterns from mass extinctions in the marine fossil record.

Biogeography and Ecological Impacts of Human Civilizations

Rob Whittaker assessed the progress that conservation biogeography has made since it established itself as a separate aspect of biogeography. **Stuart Pimm** argued that biogeography should be used as part of evidence-based conservation efforts, using the Atlantic Coastal forest of Brazil as one of his examples. This small fragment of forest, a hotspot of endemic bird biodiversity, has been reduced dramatically in size over the past century. The research found that all bird populations in the forest were equally likely to go extinct, whether or not they could exploit secondary habitats. **Terry Root** presented the case for climate change being the most pressing environmental problem currently facing conservation biologists, using phenological data. She also discussed explaining the 'ecological economics' of environmental degradation to policy makers and the wider public. **Mark Ritchie** examined the potential changes in nitrogen fixation in grassland ecosystems. About 50% of earth's land area currently consists of ecosystems that are managed for grazing by large mammals, and Mark considered how climate change might affect nitrogen fixation, a critical biogeochemical process, in these ecosystems. **John Terrell**, an anthropologist, made novel use of Powerpoint by presenting an almost silent slideshow on the evolving biogeographic patterns of human occupation in Papua New Guinea, and discussed the resistance to viewing humans as animals subject to the rules of ecology and biogeography within some areas of anthropology.



Biogeography of Exotic Species

Invasive species are a key area of concern in conservation biology, and it was fitting that a session was devoted to this field at a conservation biology themed meeting. **Dov Sax** has studied the introduction of exotic species to oceanic island biotas, and how this altered the net biodiversity, rather than focusing simply on whether native taxa were displaced or driven extinct. **Matt McGlone** discussed the problems of invasive species in New Zealand, comparing the changes in invasion patterns and processes between historical invasions and the current ongoing wave of human-mediated introductions. **Peter Pysek** examined the stages of naturalization of plants, and how geographic factors influence whether a plant becomes naturalized, and demonstrated that even centuries after introduction some plants continue to have more rapid range expansion rates than native species. **Julian Olden** addressed the problems that biotic homogeneity present for conservation biology efforts, as well-differentiated regional biotas are replaced by cosmopolitan communities at continental scales. Julian touched on the social/aesthetic impacts of the loss of localized biotas, reminding us that one of the intangible 'ecosystem services' of biodiversity is the pleasure it gives us. **George Gilchrist** presented his work on how invading species' evolutionary patterns and rates vary along different parts of the invasion track from the point of initial introduction to the leading edge of range expansion.

The poster sessions gave a much wider sample of the vast range of techniques, disciplines, scales, and questions that fall under the category 'biogeography'. Everything from using truck-mounted radar to produce incredibly detailed images of Wicken Fen, a nature reserve near Cambridge, to the importance of the maximum vicariance model in driving the questions that have led to the richer view of the number of processes involved in generating spatial patterns.

The poster sessions were allotted generous amounts of time in the schedule, and the practice of isolating the conference in a location where everything the participants could need was close at hand created an environment that was conducive to interaction. For instance, I ended up speaking at length to two researchers from the University of Virginia who were interested in how the shape of reserves, rather than the size or distance between reserves, affected the success of conservation efforts. Having some background in morphometrics, I was able to discuss outline analysis techniques and free software packages, which they have since been able to implement.

If your interest in biogeography has been piqued, you should be aware of two meetings coming up in the next 18 months. IBS is backing two meetings in Europe, as they are keen to avoid becoming a dominantly North American society. **Claire Slater** (Natural History Museum, London/University of Cambridge), **Paul Upchurch** (University College London), and myself (Natural History Museum, London) are organizing a four-day meeting, "Palaeogeography and Palaeobiogeography: Biodiversity in Space and Time", to be held at the National Institute for Environmental e-Science, Centre for Mathematical Sciences, University of Cambridge in early April 2006. We hope this meeting will help to strengthen links between palaeontologists and biogeographers working on the recent biota. We also hope to attract delegates from the wider earth science community, and remind them of the value of their data, whether climatic, palaeogeographic or palaeontological, for interpreting and testing biogeographic patterns and processes.

The next meeting of the IBS will be held in the Canary Islands in January 2007: details have just been announced on the IBS website.

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International Symposium on Triassic Chronostratigraphy and Biotic Recovery
Chaohu, China 23 – 25 May 2005

The Triassic, bookended as it is by two of the major Phanerozoic biotic crises, witnessed important changes in the Earth's biosphere. It is also a geological period of note in that, to date, relatively few of its stage boundaries have been formally skewered with a 'golden spike'. To address both issues was the ambitious goal of this three-day conference in Chaohu, organised by the China University Geosciences, with sponsorship from the ICS subcommissions on Permian and Triassic stratigraphy, IGCP-467 (*Triassic Time and trans-Panthalassan Correlation*) and the NSF-CHRONOS project (more of which later!) to name but a few. Full details of the conference presentations, and the pre- and post-symposium excursions, have been published in *Albertiana*, volume 33 <<http://www.bio.uu.nl/~palaeo/Albertiana/Albertiana01.htm>>.

The conference began with a two day pre-symposium excursion to a couple of Permian-Triassic boundary sites (including the base-Triassic GSSP and the proposed base-Changhsingian GSSP, both at Meishan) and a brief visit to the Nanjing Institute of Geology and Paleontology to view, somewhat incongruously given the meeting's theme, a new display of Chengjiang fossils. I have to confess that this fieldtrip, scientifically but not gastronomically, was probably the only slight disappointment of the whole conference. Due to a combination of events both outside of, but also under, the fieldtrip leader's control, including the living hell that is China's road network (justifiably listed by the WHO as among the most deadly in the world, and with new roads being constructed at such a frenetic pace that getting lost is, apparently, all too easy), we ended up spending precious little time actually on the rocks: a mere 20 minutes at Meishan. The lack of on-site discussion time was particularly frustrating given the breadth and depth of expertise present and the fact that for many, myself included, this was our first visit to the Meishan sections. The second stop at Hushan the following day was better, but still too short.



The Meishan P/Tr GSSP is a wonder to behold!



The Meishan P/Tr GSSP itself is a wonder to behold! The quarry (Meishan D) has been paved, landscaped, and set about with flowerbeds, sculptures and information boards, all of which are kept scrupulously clean. Only a souvenir stand is missing. A short stairway takes you up from the viewing platform to the famous “Bed 27”, containing the FAD of the base Triassic index conodont *Hindeodus parvus*. The outcrop itself is completely inaccessible, covered as it is by thick netting, but one is allowed to get close to – even touch! – a short section of Bed 27. The beautiful environs of the Meishan D quarry are in stark contrast to the distinctly unlandscaped villages we passed through to get there, so perhaps it is not surprising that whenever our driver had to stop to ask directions to the ‘golden spike locality’, the locals all knew precisely what he was talking about. Would the same happen, I wonder, if one were to stop residents of West Somerset in the street and ask them the way to the “base Sinemurian GSSP”?



Bed 27, containing the GSSP of the base Triassic, peeking out from its protective netting.

The conference itself took place in the excellent facilities of the Tang Shan Hotel, in Chaohu City, Anhui Province. Apart from the first day, and the last afternoon, the talks were mostly presented in two parallel sessions, which, unfortunately, means that I am unable to report on all presentations, so only a partial list is included here. For further details, and extended abstracts, please refer to *Albertiana* 33, pp. 6–115.

After the mandatory group photo, the sessions began with **Yin Hongfu** (Wuhan) giving a comprehensive overview of the end-Permian mass extinction event and the subsequent recovery. **Bruce Wardlaw** (USGS, Reston) then followed with an introduction to CHRONOS <<http://www.chronos.org/>>, and particularly to the flagship Permian–Triassic time slice project. This represents a major initiative (investment) by NSF and is worth a look. Through the Paleostrat data entry system <<http://www.paleostrat.org/>> everyone is welcome to input and store their own data, whether it



be stratigraphic sections, range data, facies data, geochemistry, geochronology, digital images (of thin sections, localities, specimens) *etc.* Storage space is, apparently, unlimited. Whoever owns the data then has the option of making it freely available to anyone, limiting access to a few good mates or keeping it absolutely private. The CHRONOS system can then be employed to number-crunch and produce graphic correlations, for example, using any and all of the available data you care to include. Even if you view such databases with a high degree of suspicion and/or scepticism they should not be completely ignored. I can guarantee that you will see data published in the future that derive from CHRONOS or Paleostrat, so understanding their uses and limitations is important. Have a look for yourself.



Meishan A quarry adjacent to Geopark showing the P-Tr transition. Leo Krystyn (scale!) is stooping over collecting samples of the uppermost horizon of the Late Permian Chanxing Formation.

Following Bruce's talk, **Aymon Baud** (Lausanne) gave an overview of the anachronistic carbonate facies (stromatolites, flat pebble conglomerates and such like) that occur in many sections, local environmental conditions permitting, at different times during the Early Triassic. **Manfred Menning** (Potsdam) then presented his new estimates of the duration of the Early Triassic, based on analysis of sedimentary cycles in the Germanic basin, which, if Milankovitch-driven, must represent 100 kyr eccentricity cycles. If the underlying assumptions are correct, then the duration of the entire Early Triassic is *ca.* 5.2 Myr, with the Induan being just 1.4–1.5 Myr, and the Olenekian *ca.* 3.7 Myr. This significantly reduces the duration of the post-Permian recovery interval, which is perhaps not as anomalously lengthy as we have previously supposed.

After yet another fantastic lunch (all the meals were first class), the afternoon session began with **Mike Orchard's** (GSC, Vancouver) presentation on the radiation of Early Triassic conodonts, based on reassessment of their affinities and taxonomic relationships through analysis of multi-element assemblages. Gone are the days of erecting new taxa and relationships on minor blemishes of the Pa element! Conodonts, even biostratigraphically useful ones, were real animals too.



There then followed a series of talks, with the exception of **Yuri Zakharov's** (Vladivostok) discussion of an Olenekian–Anisian succession from Primorye, focused on the task of choosing a GSSP for the Induan–Olenekian (I–O) boundary. As the leading candidate section is in Chaohu itself, the Chinese scientists were out in force to present their case, led by **Tong Jinnan** (Wuhan) and **Zhao Laishi** (Wuhan). **Charles Henderson** (Calgary) also added his weight to the Chaohu proposal, by pointing out the ease of correlation between Chaohu and NW Canada. Only a single voice (seemingly) stood against the tide: **Leo Krystyn** (Vienna) presented data from the Muth section of the Spiti Valley. Less work has been done on this section in comparison to Chaohu, but it has one advantage in containing a better ammonoid fauna above and below the proposed boundary.

The following morning, bright and early, we all had the chance to visit the Chaohu sections. To say that GSSPs in particular, and geology in general, are big news in China would be an enormous understatement. At the West Pingdingshan section (proposed I–O GSSP locality), hoards of paparazzi, local TV crews and members of the general public who had come to view the spectacle were there to greet us. The following day our pictures were liberally splashed over the front – yes, the FRONT – pages of the local papers, accompanied by details of the conference and the arguments for and against Chaohu and Spiti as GSSP localities. We often bemoan the lack of geological knowledge among the general public in the UK, or wonder how we can promote the geosciences or explain what we do without resorting to mentioning dinosaurs and volcanoes. Maybe we could learn a thing or two from the Chinese.

Talks resumed with **Chris McRoberts'** (Cortland) discussion about the Permian–Triassic evolution of the Myalinidae: a familiar tale of ecological and taxonomic diversity in the Permian, succeeded by a few survivors of simple morphology in the Early Triassic. This was followed by **Shen Shuzhong's** (Nanjing) discussion of the Selong Xishan section in Tibet, where he noted that, in contrast to some recently published work by UK geologists, the timing and pattern of extinction matches very closely with that observed in Meishan and elsewhere. **Yang Wan** (Wichita) then described the facies and inferred climatic changes of a beautifully exposed terrestrial Permian–Triassic section from the Bogda Mountains of NW China. My own presentation followed: a discussion of the Permian–Triassic size change and the Lilliput effect. Next, **Wang Yongbia** discussed the Early Triassic calcimicrobialites that sit atop the Permian reefs of South China. Finally, **Oliver Weidlich** (Royal Holloway) presented some good arguments and novel data in support of his reinterpretation of the Early Triassic 'lacustrine' oolites and stromatolites of the Germanic basin: are they really marine as he suggests?

The final day began with a host of eagerly awaited presentations, beginning with **Chen Zhongqiang** (Perth) on the post-Permian recovery of articulate brachiopods. This was followed by **Tyler Beatty** (Calgary) who gave an excellent presentation on the Permian–Triassic trace fossil records of a broad swathe of northwestern Pangaea, from the Sverdrup Basin, through NW Canada to Idaho. **He Weihong** (Wuhan) used her slot to give two short presentations: the first on radiolaria, showing that peaks in abundance and diversity at Meishan cluster around maximum flooding surfaces; the second on size reduction in articulate brachiopods through the Late Permian extinction event, caused by progressive loss of larger taxa. **Demir Altiner** (Ankara) then presented evidence from Turkey that all Middle Triassic and later calcareous foraminifera are ultimately derived from Late Permian forms that were surviving, somewhere, as Lazarus taxa, during the Early Triassic.



Greeted by local TV cameras and journalists at the proposed GSSP of the Induan–Olenekian boundary in Chaohu!

The final session kicked off with **Dave Bottjer** (USC), who treated us to an authoritative history of Phanerozoic and Triassic trace fossil studies. **Jin Yugan** (Nanjing) followed, with a detailed and well-illustrated account of the sedimentology of the Permian–Triassic succession at Meishan, including wonderful cut and polished sections of ‘Bed 27’: the P/Tr boundary coincides with a well-developed firmground surface and the sediments of the latest Permian and earliest Triassic are thoroughly bioturbated. **Yukio Isozaki** (Tokyo) then reviewed the facies, faunal and environmental changes associated with the end-Guadalupian and end-Permian extinction events as recorded in the oceanic sediments (deep sea cherts and shallow seamount limestones) of Japan. Next up, **Vladimir Davydov** (Boise) gave us another opportunity to hear more details of the Paleostat and the CHRONOS initiative (see above). **Peng Yuanqiao** (Wuhan) then tried to convince us that he could correlate between marine and terrestrial sections based on ‘eventostratigraphy’. Finally, last slot was given over to **Dan Lehrmann** (Wisconsin) who took us through the Permian–Triassic strata of the isolated carbonate platforms of Guizhou. This presentation was an introduction to a post-symposium fieldtrip that was scheduled to begin the following day, and which, unfortunately, I was unable to attend.

Overall, then, it was a thoroughly enjoyable meeting with excellent and stimulating presentations throughout and much food for thought. The organizers are to be congratulated that, during the conference at least, all ran smoothly and we all enjoyed first rate hospitality. China is such an interesting place for obvious reasons other than geology and palaeontology. The next major conference there will be the IPC meeting in Beijing in June 2006 <<http://www.ipc2006.ac.cn/>> and I hope to see you there!

Richard Twitchett

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**Progressive Palaeontology 2005**

University of Leicester 15 – 16 June 2005

On a rainy Wednesday morning in June, around forty postgraduates assembled at the Department of Geology at the University of Leicester for *Progressive Palaeontology 2005*. The meeting opened with a welcome from Prof. Dick Aldridge, who emphasised the importance of this annual conference in providing a forum for more relaxed scientific discussion amongst young researchers.

Alas, the morning proved to be anything but relaxed. Things started well, with **Nicolas Minter** (University of Bristol) walking us through the locomotary behaviours of extant basal insects, and illustrating how these can be used to interpret the trackways left by their early representatives in the Lower Permian of New Mexico. **Rowan Whittle** (University of Leicester) was the first of the home team, introducing us to Fred, Roger and Bert – a.k.a. her Soom Shale enigmatic fossils – and the evidence for her interpretations of them. **Alex Page** (University of Leicester) was next up, but unfortunately, the computer refused to recognise his USB stick (those cursed devices that I've yet to see function properly at a conference). Undaunted, we attempted a direct hook-up to his laptop, which promptly crashed the whole system.

At this juncture, it was decided that an early tea break should be called, while we engaged the system in a battle of wills. Twenty minutes and much computer jiggery-pokery later, we triumphed, but by now time was short, so while the system completed its tectonically slow start-up, Alex started his talk with the Jackanory-approach, considering the connection between graptolite-bearing shales and the Silurian oceanic system. Up to that point I'd not really registered the large hook at the end of our improvised pointing stick, but Alex, having abandoned his crutches (see PalAss 2004 review for non-locomotary use of these) in favour of this new gesticulatory appendage, proceeded to give the hook a whole new aspect of menace.



Delegates at the wine reception in the New Walk Museum. Photo: David Baines.



A gratifyingly un-lacerated projector screen awaited **Tom Dunkley Jones** (University College London) who showed how biotic changes in nanofossils from a Tanzanian section might be used as a proxy for elucidating the global environment during the climatically turbulent Eocene–Oligocene boundary. **Alexei Rivera** (University of Bristol) gave us a review of the evidence for metazoan origins, addressing particularly how the quality of the fossil record affects the utility of its contribution to the debate. His method of assessment using random resampling of the record showed that it can indeed be considered germane to the arguments (phew). **Jonathon Antcliffe** (University of Oxford) asked what makes an arthropod an arthropod, or a mollusc a mollusc? Such questions need answering, he argued, in order to characterise higher taxa such as phyla so as to deal with their evolution and inter-relationships, and he presented his approach to do just that.

A buffet lunch followed at a local pub, after which the remainder of the day went far more smoothly. Postponed from the morning, **Rosie Stephens** (University of Leeds) presented the fantastic floras of Eocene Antarctica (some of them visualised spectacularly in 3D using the new technique of neutron tomography) and their utility in tracking the evolution and biogeography of the species preserved, and in elucidating the climate of the continent at that time. An inexplicably distracted **David Jones** (University of Leicester) then presented a morphometric approach to investigate element homology with the conodont skeleton. **David Baines** (University of Leicester) illustrated how tooth microwear in the extant three-spined stickleback can correlate with feeding strategy and hence be used to investigate resource-driven speciation within the fossil record of teleosts. **Mark Evans** (University of Leicester) showed how a veritable perfusion data could be obtained from very fragmentary material (heart-warming for vertebrate palaeontologists everywhere), using suture patterns in a plesiosaur skull to extrapolate the stress patterns it had



evolved to tolerate. There followed another plesiosaur talk: **Adam Stuart Smith** (University College Dublin) drew our attention to the important plesiosaurs of the National Museum of Ireland (Natural History), and their unfortunate neglect, as a potentially important contribution to understanding plesiosaur palaeontology.

Michael P. Taylor (University of Portsmouth) explained why Godzilla was biomechanically untenable based on analysis of limb-bone cartilage, and showed how analysis of this hitherto little considered limiting factor to maximum body weight could also be extended to look at really large dinosaurs. Raising the conference to international status, **David J. Allen** (Northern Illinois University) stepped up to introduce a sixth sense in extant crocodylians: probable mechanoreceptors known as Integumentary Sense Organs, and their evolution in extinct crocodylomorphs.



Laura B. Porro (University of Cambridge) used Finite Element Analysis to investigate feeding in the phylogenetically indecisive (more on that in a bit) ornithopod *Heterodontosaurus tucki*, specifically to assess the various hypotheses of feeding in this species. Immediately afterwards, *Heterodontosaurus tucki* was phylogenetically problematic no more, as **Richard Butler** (University of Cambridge) presented a new, well supported cladistic analysis of the Ornithischians, slotting it securely at the base of the clade, and resolving many of the other relationships within the group.

An over-arching theme of the day, mentioned by many, was the inevitable discovery that things are far more complex than a blasé PhD project outline would suggest, leading to the realisation that dawns on all of us when we progress with our research: that there are very good reasons why this has never been done before. A wine reception in the Geology gallery of the New Walk Museum, followed by an evening meal at (predictably) a curry house, rounded the day off.

The field trip the following day had somewhat poor attendance: three in fact. Undeterred by the great emptiness behind us, myself, David Baines (our driver) and Rowan Whittle took our empty sixteen-seater minibus on a jolly across east Leicestershire to Ketton Quarry; once there, we were shown around by Andrew Swift (University of Leicester) and Bill Learoyd (Stamford and District Geological Society), collecting a good haul of fossils along the way; all the more for us.

Thanks go to the Geology Department at the University of Leicester, The Palaeontological Association and the New Walk Museum for their support of the conference, to our guides for the field trip, and to the palaeobiology PhD students at Leicester for their help in the organisation.



The few, at Ketton Quarry. Photo: Andrew Swift.

David Jones

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>>**Future** Meetings of Other Bodies



The Seventh International Congress on Rudists

Austin, Texas 5 – 11 June 2005

The International Congress on Rudists calls together Cretaceous sedimentologists, palaeontologists, stratigraphers, and explorationists every three years to pursue research goals set forth in 1988 by the Cretaceous Resources, Events and Rhythms project of the Global Sedimentary Geology Program. The 2005 Congress theme is “Cretaceous Rudists and Carbonate Platforms: Environmental Feedback”. This theme will be developed in three sessions, “Depositional Environments of Cretaceous Carbonates”, “Origins, Events, and Demise of Rudist Paleocommunities”, and “Towards Rudist Taxonomy, Biogeography, and Phylogeny”. Oral and poster sessions are planned.

Before the meeting participants will enjoy a one-day field trip to see the Texas Hill Country geology. Following the meeting a three-day excursion will give participants the opportunity to examine rudist-bearing outcrops and collect from classic middle Cretaceous carbonate buildups. The Texas Memorial Museum has developed a new exhibit of Cretaceous life, and the museum will give access to its extensive and important collections of Cretaceous fossils for qualified specialists.

The University of Texas and the University of Tulsa will co-sponsor this seven-day conference and field trip. The John A. and Katherine G. Jackson School of Geosciences has made a very generous grant to the Congress, and the Department of Geosciences of Tulsa University is providing financial and logistical support.

To register and submit abstracts contact Debra Sue Trinke, Treasurer, 7th International Congress on Rudists, PO Box B, Austin TX 78713-8901, USA, or see the meeting website at <<http://www.tmm.utexas.edu/npl/rudist2005/>>.



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 4^a Reunión de Tafonomía y Fossilización / 2nd International Meeting TAPHOS-05 that will take place in Barcelona between 16th and 18th June 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 the 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. Visit the meeting website for further details, at <<http://www.aapg.org/calgary/index.cfm>>.



North American Paleontological Convention (NAPC 2005)
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 B3H 3J5 Canada). The meeting website is at <<http://www.dal.ca/~es/staff/dbscott/scott.htm>>.



The Fifth International Brachiopod Congress
Natural History Museum of Denmark, Copenhagen 4 – 8 July 2005

The Copenhagen conference follows the successful meetings in Brest (1985), Dunedin (1990), Sudbury (1995) and London (2000). The main events, lectures and posters will be held in the Geological Museum of the University of Copenhagen. The Museum has a strong tradition in palaeontological research, particularly in the Arctic and Baltic regions. The Congress is being organised by David Harper (Chair), Lars Holmer, Sarah Long, Claus Nielsen and Nina Topp. There



will be a pre-congress field excursion to Gotland and two post-congress field excursions, one to Jutland and one to Estonia. For more details visit the meeting website at <<http://www.nathimus.ku.dk/geomus/>> or e-mail <dharper@savik.geomus.ku.dk>.



Sixth International Crustacean Congress

University of Glasgow, Scotland, UK 18 – 22 July 2005

The conference is organised on behalf of the International Crustacean Council by The Institute of Biomedical and Life Sciences, University of Glasgow. The Meeting will also host the 5th European Crustacean Conference, the 4th Crustacean Larval Conference, and the 2005 Summer Meeting of the Crustacean Society. For more details see the meeting website at <<http://www.gla.ac.uk/icc6/>>.



II Latin American Congress of Vertebrate Paleontology (II CLPV)

Rio de Janeiro 10 – 12 August 2005

The MUSEU NACIONAL/UFRJ will host the event. For further information, see the meeting website at <<http://acd.ufrj.br/mndgp/2clpv/en/>>.



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>>.



Algorithmic Approaches to the Identification problem in Systematics

The Natural History Museum, London 19 August 2005

The automated identification of biological objects (individuals) and/or groups (e.g., species, guilds, characters) has been a dream among systematists for centuries. Despite much preliminary work in the 1950s and '60s, progress in designing and implementing practical systems for fully automated



object identification has proven frustratingly slow. However, recent developments in computer architectures, as well as innovations in software design, have finally placed the tools needed to make the development of generalized, automated, specimen- and/or group-identification systems a practical reality.

In order to summarize the current state-of-the-art in automated group-recognition systems, and assess their potential to make practical contributions to systematics and taxonomy both now and into the future, the Systematics Association and The Natural History Museum, London have agreed to sponsor a free, one-day symposium, to be held in the Flett Theatre of The Natural History Museum, London on 19th August 2005. The purpose of this symposium is to provide leaders of research groups, researchers, post-doctoral research assistants, and students working or studying in any area of systematics with an opportunity to (1) learn about current trends in quantitative approaches to the group-recognition problem, (2) become familiar with the capabilities of various software systems currently available for identifying systematic objects/groups, and (3) evaluate various applications of this technology to present and future systematic problems. Special attention will be paid to showing how different approaches to automated identification can be applied to various organismal groups and in various applied research contexts (*e.g.*, biodiversity studies, biostratigraphy, conservation, agriculture, curation). Ample programme time will also be provided for discussions of issues relating to how these approaches and technologies can play a larger role in meeting the needs of current and future systematists.

This free symposium is being held in association with the Biennial Meeting of The Systematics Association which begins on Monday, 22nd August 2005 at the University of Cardiff. Attendees of the Systematics Association meeting are encouraged to include attendance at this symposium in their Biennial Meeting plans. If you would like to attend this symposium, provide a demonstration or contribute a chapter to a book of collected technical articles, please send your contact details to Norman MacLeod, Palaeontology Department, The Natural History Museum, Cromwell Road, London SW7 5BD, e-mail <N.MacLeod@nhm.ac.uk>, tel +44 (0)207 942 5204/5295, fax +44 (0)207 942-5546. The Symposium website is at <http://www.nhm.ac.uk/hosted_sites/paleonet/aaips_symposium/>.

Sponsors: The Systematics Association and The Natural History Museum, London.



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 Palaeozoic and Carboniferous) will take place on 19–21 August, a post-conference field trip (Devonian) on 26–28 August. In parallel with the scientific session, a business meeting of the IGCP 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>.



**IGCP 491 meeting: Middle Palaeozoic vertebrates of Laurussia:
relationships with Siberia, Kazakhstan, Asia and Gondwana**
St. Petersburg University, Russia 22 – 26 August 2005

This meeting is being held in conjunction with the 6th Baltic Stratigraphical Conference, and will deal with any aspect of research on Middle Palaeozoic vertebrates (taxonomy, morphology, palaeogeography, palaeoecology, biostratigraphy), with a focus on the vertebrate fauna of Laurussia and its relationship to the faunas of other palaeogeographic provinces. Participants are invited to submit abstracts for both oral and poster presentations (details below). An abstract volume will be published as a Special Publication of Ichthyolith Issues.

The IGCP meeting is organised by the Department of Palaeontology, St. Petersburg University. For further details, contact Dr Alexander Ivanov, Department of Palaeontology, St. Petersburg University, e-mail <aoi@AI1205.spb.edu>.



7th International Symposium on the Cretaceous
Neuchâtel, Switzerland 5 – 9 September 2005

The meeting will be held in the University of Neuchâtel. For more details see the meeting website at <<http://www.unine.ch/geologie/isc7/>>.



15th International Symposium on Ostracoda
Freie Universität Berlin 12 – 15 September 2005

The First Circular can be downloaded from the symposium website at <<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 programme. Please have a look at our website at regular intervals. 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.



**IV International Symposium ProGEO on the Conservation of
the Geological Heritage**

Braga, Portugal 13 – 16 September 2005

For further details see <<http://www.dct.uminho.pt:16080/cct/progeo2005/frames.html>>.



The London Evolutionary Research Network (LERN): Third Annual Conference

Natural History Museum, London 16 September 2005

Call for talks and posters from postgraduate and postdoctoral research students.

Each year we celebrate the range of evolutionary research taking place in London. The conference is a friendly venue where young scientists can gain experience giving presentations in a conference setting, as well as networking with other researchers. We would like to promote appreciation for all disciplines, and facilitate lateral thinking and synthesis of different disciplines. Therefore, we invite students from any discipline working on any aspect related to evolutionary biology to participate.

For more information please contact Nehal Saleh (e-mail <n.saleh@qmul.ac.uk>) or visit our website at <<http://www.anat.ucl.ac.uk/research/lern/>>.

The deadline for registration and abstract submission is **31st July 2005**.



The American Association of Stratigraphic Palynologists (AASP)

2005 meeting

Radisson Hotel, St. Louis, Missouri, USA 18 – 21 September 2005

For further details see <<http://dce.umn.edu/NonCredit/Conference/AASPMeeting2005.html>>.



Development and Phylogeny of Arthropods

Museum National d'Histoire Naturelle, Paris 23 – 24 September 2005

Comparative Developmental Genetics (so-called 'evo-devo') is currently renewing Comparative Anatomy, which has been the ground on which animal phylogeny was established during the last two centuries. The meeting will try to show, from examples taken in arthropods, the interplay between organisms' evolutionary history (phylogeny) and ontogenetic history (development). What are (or could be) the respective contributions of developmental studies to Phylogeny and of phylogenetic analyses to Developmental Biology? Invited speakers: David Cribbs (Toulouse, France); Wim Damen (Cologne, Germany); Jean Deutsch (Paris, France); Cyrille D'Haese (Paris, France); Ronald Jenner (Amsterdam, Netherlands); Michael Manuel (Paris, France); Alessandro Minelli (Padova, Italy); Éric Quéinnec (Paris, France); Gerhard Scholtz (Berlin, Germany); Patricia Simpson (Cambridge, UK); Angelika Stollewerk (Cambridge, UK); Michel Veuille (Paris, France). Further details are provided at <<http://ifr-bi.snv.jussieu.fr/>>.



**Joint Meeting With The Marine Studies Group of The Geological Society
Biogeochemical Controls on Palaeoceanographic Proxies
Burlington House, Geological Society, London 3 – 4 October 2005**

Convenors: Dr Rachael James (Open University), Dr Bill Austin (St Andrews), Dr Leon Clarke (School of Ocean Sciences, Wales) and Dr Ros Rickaby (Oxford).

The aim of this meeting is to bring together palaeontologists, geochemists and palaeoceanographers who can contribute evidence that must be considered together, better to constrain proxies that are used for palaeoclimate reconstruction. The information that is provided by these proxies is crucial for the evaluation of climate models. As these models are the ultimate tool for predicting climate response to greenhouse gas build-up, a meeting that will help to elevate confidence in them is imperative.

The meeting will consist of three sessions.

- (1) **Palaeontological studies.** The aim of this session is to focus on the link (ecology–palaeoecology) between modern and fossil organisms – how well do we understand the modern biology and how does an improved understanding aid interpretation of the palaeo-record? Speakers include Joan Bernhard (WHOI), Kate Darling (Edinburgh), Andy Gooday (SOC) and Jeremy Young (NHM, London).
- (2) **Biom mineralization.** This session aims to develop a mechanistic understanding of the “vital effects” imposed upon trace metal and isotopic proxies captured in biogenic carbonates. Speakers include Colin Brownlee (Plymouth) and Bob Williams.
- (3) **Constraining proxy relationships.** This session will focus on experimental (field and laboratory) and theoretical studies of those factors that influence elemental and isotopic proxies, *i.e.* temperature, salinity, carbonate ion *etc.*, as well as assessment of the impacts of post-depositional dissolution and diagenesis on primary proxy relationships. A key element will be validation of novel proxies. Speakers include Anton Eisenhower (GEOMAR), Harry Elderfield (Cambridge), Andreas Mackensen (Alfred Wegner Institut), Paul Pearson (Cardiff) and Ann Russell (UC Davis).

Contact: Dr Bill Austin (St Andrews) for further information, e-mail <wena@st-andrews.ac.uk>.



**GANJ XXII: Geological Association of New Jersey 2005 Annual Meeting:
Geology of the Central Newark Basin – the view from the 21st Century
College of New Jersey, Trenton, New Jersey, USA 7 – 8 October 2005**

For further information see <<http://www.ganj.org/2005/2005mtg.htm>>.



IGCP 469: "Late Westphalian terrestrial biotas and palaeoenvironments of the Variscan foreland and adjacent intramontane basins"

Bucharest, Romania 7 – 13 October 2005

In October 2005, for two days, the IGCP 469 meeting will be held in Bucharest, hosted by the Faculty of Geology and Geophysics, University of Bucharest. The meeting will include presentations, collection surveys and a practical workshop attended by Romanian students in Geology. A field trip in the South Carpathians, to visit Upper Paleozoic formations of the Resita, Sirinia and Presacina Basins, is scheduled after the talks in Bucharest.

For further information, please see the University of Bucharest website at <<http://www.unibuc.ro/en/home/>> or the Faculty of Geology and Geophysics website at <http://www.gg.unibuc.ro/index_main.html>.



Paleontological Society Annual Short Courses at GSA 2005

Salt Lake City, GSA 16 – 19 October 2005

Paleobiogeography: Generating New Insights into the Coevolution of the Earth and its Biota.

Organiser: Bruce Lieberman. For further information see the meeting website at

<<http://www.paleosoc.org/futureprograms.html>>.



The 65th Annual Meeting of the Society of Vertebrate Paleontology

Phoenix Marriott Mesa, Mesa, Arizona, USA 19 – 22 October 2005

Further information is available from the vert-palaeo website at

<<http://www.vertpaleo.org/meetings/>>. To submit abstracts please go to

<<http://www.vertpaleo.org/abstracts/index.htm>>.



9th Meeting of the European Elasmobranch Association (EEA)

Oceanographic Museum of Monaco, Monaco 23 – 26 November 2005

For further details see <<http://www.oceano.mc/>>.



Journées Georges UBAGHS

Dijon, France 30 – 31 January 2006

The research team Biogéosciences (Dijon), the French Palaeontological Association (APF), and the French Palaeozoic Working Group (GFP) are very pleased to invite you to a two-day scientific meeting at Dijon University (Burgundy, France) in tribute to the late Prof. Georges UBAGHS (1916–2005), who was one of the greatest specialists of fossil echinoderms.



Contributions (oral presentations and posters) dealing with any aspect of fossil echinoderms (especially Palaeozoic forms), and/or the life and main scientific achievements of Georges UBAGHS are welcome. For further details, please contact Dr Bertrand Lefebvre, e-mail <bertrand.lefebvre@u-bourgogne.fr>, or visit the meeting website at <<http://www2.u-bourgogne.fr/BIOGEOSCIENCE/P1T.html>> (If you do not get direct access to the meeting web page, please click on "Actualités" and then "Colloques".)



Palaeobotany Specialist Group of the Linnean Society of London,
Spring Meeting 2006: a life of ferns and seed ferns
Montpellier, France *April 2006 (provisional)*

This is the initial announcement for a meeting to be held in Montpellier, the city where Jean Galtier has spent his academic life. Presentations will be on topics of special interest to Jean, specifically the early radiations of ferns and seed ferns. The meeting will [hopefully] be accompanied by an excursion visiting famous fossil plant localities in the south of France. Additional details will be made available shortly. Meeting organisers: Brigitte Meyer-Berthaud (e-mail <meyerberthaud@cirad.fr>) and Nick Rowe (e-mail <nrowe@cirad.fr>) (Montpellier, France).



IPC 2006: The Second International Palaeontological Congress
Beijing, China *17 – 21 June 2006*

Following the successful IPC 2002 in Sydney, the Second International Palaeontological Congress will be hosted in Beijing. The conference theme is 'Ancient Life and Modern Approaches', and there will be a wide variety of plenary sessions, general and topical symposia, short courses, workshops and special group meetings. The programme will also feature field excursions to the fossil sites that have helped Chinese palaeontology to grab so many headlines in recent years.

The deadline for returning reply forms for the first circular is 1st June 2005.

For further details visit the website at <<http://www.ipc2006.ac.cn/>>



9th Symposium on Mesozoic Terrestrial Ecosystems
Manchester, UK *27 – 29 June 2006*

The 9th Symposium on Mesozoic Terrestrial Ecosystems and Biota (sponsored by the Palaeontological Association) will take place at the University of Manchester, England, with optional field trips before and after the scientific meeting.

Full details, key dates, contacts, and a pre-registration form can be found on the MTE website at <<http://homepage.mac.com/paulselden/MTE/>>.



Fourth International conference on Trilobites and their relatives
Queensland Museum, Brisbane, Australia 10 – 14 July 2006

Following the successful meeting at Oxford in April 2001 it was thought a good idea to spread the sequence of these gatherings to the Southern Hemisphere. Accordingly you are now invited to the Fourth International Meeting on Trilobites and their Relatives to be hosted in the Queensland Museum, Brisbane, Australia. The Queensland Museum dates from the 1860s. Although it had an emphasis on vertebrate palaeontology until the 1970s it has recently become home to the large earth sciences collections of the University of Queensland and the Geological Survey of Queensland. Most significant among its holdings is the very large amount of Cambrian trilobite material collected by Frederick William Whitehouse during the 1920s–1940s.

The Geosciences Programme is housed in an offsite annex near the airport, whereas the Museum building is in the Queensland Cultural Centre at SouthBank adjacent to the city centre. The programme will entail four days of formal presentations at the Museum and a day at the annex among the collections, and other activities. Papers on any aspect of the conference title will be most welcome as will poster presentations.

A social programme including a conference dinner will be organised for participants during their time in Brisbane.

Field trips will be available before and after the meeting but numbers may be limited due to the logistics of remote field sites. The pre-conference field trip will visit Ordovician to Devonian sites in central New South Wales and the post-conference trip will be to the Lower Cambrian sequence of the Flinders Ranges, South Australia.

The conference proceedings will be published in the Memoirs of the Queensland Museum as soon as practicable after the meeting. If possible papers for the Proceedings should be submitted at the meeting so the review process can begin immediately.

Organising Committee

Greg Edgecombe, Australian Museum
David Holloway, Museum of Victoria
Jim Jago, University of South Australia
Peter Jell, Queensland Museum
John Laurie, Geosciences Australia
Ken McNamara, Western Australian Museum
John Paterson, Macquarie University
Andrew Sandford, University of Melbourne
Tony Wright, Wollongong University

If you wish to receive the second circular please contact Peter Jell at the Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia, e-mail <peter.jell@qm.qld.gov.au>.



International Conodont Symposium: ICOS 2006
University of Leicester, UK 17 – 21 July 2006

For further details, see <<http://www.conodont.net/>>.



7th International Congress on the biology of fish
St John's, Newfoundland, Canada 18 – 22 July 2006

During the next International Congress on the Biology of Fish, there will be a symposium on **Biom mineralisation in Fish Bones and Teeth: from Microscopy to Design of Materials**.

This symposium will discuss all aspects of biomineralisation of the hard tissues of fish, including bone, enamel, enameloid, dentine, calcified cartilage, otoliths and scale tissues. The processes involved in biomineralisation are known in part in some mammals, but little understood in fish. Studies on immunodetection of the proteins involved in the mineralization processes of hard tissues in fish are not very widely used, and the genes coding for these proteins are not always identified. That the fine structure of fish teeth shows an enormous diversity has been known since the early studies of Owen in the nineteenth century, but little of this diversity has been studied with modern techniques of microscopy. Specific adaptations of the ultrastructure of fish dentitions, in relation to stress induced during use of the teeth, have implications for biomaterials research and for the design of more effective machinery for industrial processes. Equally, analysis of the fine structure of bone has implications for biomechanics. Improved understanding of all of these aspects of fish hard tissues also has phylogenetic implications, especially for the relationships among problematic groups of fishes, or between fish and other vertebrates. This symposium will bring together ideas from different fields, in biochemistry, genetics, developmental biology, biomaterials and microscopy, and assist in the development of productive new ideas.

For more details see <<http://www.mun.ca/biology/icbf7/>>.

Biom mineralisation symposium organizers: Anne Kemp (University of Queensland) and Gilles Cuny (Geological Museum, University of Copenhagen).



3rd Workshop on Ichnotaxonomy
Prague, Olomouc and Brno (Czech Republic) 4 – 9 September 2006

For further details see

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



Carboniferous meeting “From Platform to Basin”: A field and research conference sponsored by SEPM-CES
University of Cologne, Germany 4 – 10 September 2006

The Carboniferous Conference Cologne 2006 will take place at the Institute of Geology and Mineralogy of the University of Cologne. The heading of this SEPM-CES research and field conference “From Platform to Basin” links a wide range of topics from very different disciplines in Earth Sciences. Field-trips to Belgium and Germany will follow a transect from the inner platform to the deeper basin. Full details, key dates, contacts, and a pre-registration form can be found on the



conference website at <<http://www.ccc2006.uni-koeln.de/>>. Please have a look at the website at regular intervals for updates and new information.

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



The 7th European Paleobotany–Palynology Conference (EPPC)

Prague, Czech Republic 6 – 11 September 2006

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



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

Albany Museum/Rhodes University, South Africa

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

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

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

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



FORAMS 2006: International Symposium on Foraminifera

Natal, Brazil 10 – 15 September 2006

Register now to ensure your participation on field trips, workshops, and other events. Updated meeting information (Scientific Programme for Technical Sessions and Workshops, and much more), online registration forms, and information for the submission of abstracts are available now at the FORAMS 2006 websites so you may register at any time.

The Web addresses are:

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

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Please note that the final acceptance of abstracts for all presentations depends upon full payment of the registration fees, which will be opened in July 2005 and should be received by 30th June 2006. Only registered participants will be allowed to attend the meeting.



The International Symposium on Foraminifera (FORAMS 2006)

Piramide Palace Hotel, Natal 10 – 15 September 2006

Technical sessions will consist of four days of talks and posters (11–12, 14–15 September), supplemented by social events.

For further information, see the meeting website at
<<http://www.labgis.uerj.br/forams2006/general.htm>>.



66th Annual Meeting of the Society of Vertebrate Paleontology

Ottawa, Canada 18 – 21 October 2006

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

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



International Federation of Palynological Societies

Bonn, Germany August 2008

The next International Palynological Congress will be in August 2008, in Bonn, Germany (see <http://www.uni-bonn.de/en/The_University.html>). For further details please refer to <<http://www.geo.arizona.edu/palynology/ifps.html>>.

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Sylvester-Bradley REPORTS

Exceptional preservation in Late Carboniferous siderite hosted Lagerstätte

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The Mazon Creek Lagerstätte of Illinois, USA, exhibits exceptional preservation of mineralised soft tissues sealed within siderite nodules that are found within mudstones and muddy siltstones that in turn occur within a series of coal-bearing sedimentary rocks. The palaeoenvironment of Mazon Creek was one of a river-influenced coastal system. Due to its unique position, two different environmental habitats existed: the freshwater to minimally brackish water Braidwood habitat; and the brackish to marginally marine Essex habitat, each with their own distinctive biotas. The Braidwood habitat developed along the estuary margins and further inland in river channel waterways and coal swamps, whereas the brackish to marginally marine Essex habitat occurred in a euryhaline prodeltatic setting that formed as the result of marine inundation of the delta-dominated coast (Baird *et al* 1985).

The Mazon Creek Braidwood biota is dominated by an allochthonous association of plant debris that represents a typical coal measure flora (Baird 1997). The plant component is dominated by seed ferns but also includes lycopsids and sphenopsids. The Braidwood animal component includes a sparse low diversity fauna of fresh to brackish water and terrestrial organisms including hexapods, arachnids, millipedes, bivalves, xiphosurans and crustaceans, along with rarer vertebrates including lungfish scales, xenocanth teeth and amphibian and reptile remains (Fig 1). The Essex biota, in contrast, is characterized by an abundant high diversity assemblage of marginal marine organisms, many of which are soft-bodied, including polychaete worms, holothurians, cnidarians, echiuroid worms, bivalves and crustaceans, with a small washed-in freshwater and terrestrial component (Baird 1997).

A British equivalent to Mazon Creek is the Coseley Lagerstätte from the coal measures of the West Midlands. The Coseley Lagerstätte is Upper Carboniferous Westphalian B (early Moscovian) in age and is found within the Coal Measure Group sediments of the Southern Pennine Basin from Coseley and surrounding areas of the South Staffordshire Coalfield. The palaeoenvironment for the Coseley Lagerstätte was one of a lacustrine delta complex where delta plains were dissected by meandering river channels. These were



An example of a Braidwood arthropod. Eubleptus danielsi Handlirsch, 1906. (PE 40223) from the Field Museum of Natural History, Chicago, Illinois.



in turn constrained by high banks, and the levee-bounded areas between the distributary channels formed low-lying flood basin plains. This would have been similar to the more inland coal swamp area of the Braidwood habitat. The Coseley Lagerstätte closely resembles the Braidwood biota in that it is also dominated by an allochthonous assemblage of plant debris that is dominated by seed fern pinnules along with lycopsids, sphenopsids and ferns. The animal component comprises a diverse assemblage of arthropods including xiphosurans, arachnids, crustaceans, millipedes and hexapods along with fresh water bivalves and fish.

The main aim of this project is to develop an integrated model for the taphonomic processes that operated within the Coseley Lagerstätte and led to soft tissue preservation and siderite concretion growth. Detailed petrographic studies have been carried out on the Coseley material using transmitted and reflective light microscopy, scanning electron microscopy, element mapping, electron microprobe analysis and cathodoluminescence to reveal a complex taphonomic and paragenetic history involving several phases of preservation. The analysis has identified several phases of preservation, including very early clay authigenesis, framboidal pyrite formation and the growth of the siderite concretions. It is possible from the analysis to determine the mineral paragenesis, clay formation occurs very early on closely followed by siderite formation. The preservation of organic material must have occurred during very early diagenetic processes before significant decay had occurred either by bacterially-mediated authigenesis, chemically-mediated colloidal mineralization or a combination of the two processes. This was closely followed by framboidal pyrite formation and siderite concretion formation. The concretions began to develop early as an open framework that was strong enough to withstand enclosing pressure from the surrounding sediment and prevent compaction of the fossil (Fisher *et al.* 1998). Void-filling sulphides and carbonates formed sometime afterwards.

Identification of the taphonomic and paragenetic sequences in the Coseley Lagerstätte leads to the question as to whether this style of preservation was limited to Coseley or was a more common process occurring elsewhere, such as in the Mazon Creek Lagerstätte. This award has enabled me to carry out a detailed study of the Mazon Creek material at the Field Museum in Chicago, Illinois, USA. The Mazon Creek fossils, in particular the Braidwood component, show a similar mode of preservation to Coseley: they show a multi-phase mode of preservation including early authigenic clay mineralization, sulphide mineralization and concretion growth. The fossils vary from preserving three-dimensionality to the destruction of internal soft tissues but with the preservation of more refractory tissues and tissue outlines (Alison and Briggs 1991). Most importantly the identification of kaolinite within the Mazon Creek fossils indicates that early authigenic kaolinite mineralization within siderite concretions is likely to be a more common process than originally thought; it also indicates that soft tissue clay mineralization can occur in a wider range of environmental habitats, both marine and freshwater. and hopefully with continued investigation this study may enable the identification of other such modes of preservation elsewhere in the fossil record.

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Posture change within basal archosaurs

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Archosauria is the group that contains all descendants of the most recent common ancestor of birds and crocodylians. Morphological studies of limb and pelvis elements suggest that the posture of archosaurs changed from sprawling to erect during the Triassic (Bonaparte 1984, Parrish 1986). The current consensus is that (i) the erect posture of archosaurs evolved within both the crocodylian and bird (dinosaur) lineages and (ii) possibly more than once in the crocodylian lineage and (iii) that modern crocodylians attained their semi-erect posture as a secondary adaptation.

This research aimed to assess a locomotion change on basal archosaurs by applying a biomechanical model that estimates the magnitude of stresses on the femur in different postures.

The biomechanical model used by Blob (2001) was applied. This model was established following experiments with iguanas and alligators that calculated bending and compressive femoral stresses. Among living tetrapods, the magnitude of limb bone loads differs with limb posture. Mammals with large body sizes mitigate the size-correlated increases of the load on limb bones by changing their postures to more upright and placing their limbs closer to the vector of ground reaction force (Biewener 1990). In contrast, data from alligators and iguanas show that an increase in some of the limb bone stresses occurs with more upright posture (Blob and Biewener 1999). These results suggest that tetrapods use the posture in which they suffer the least limb bone stresses. Therefore, if the bone stresses in various postures are calculated for extinct taxa, it helps in the reconstruction of their probable posture.

Stresses due to curvature of the femur, ground reaction force and knee extensor musculature were calculated to derive estimates of the maximum and minimum tensile and compressive stresses at the midshaft of the femur. If the femur does not rotate about its long axis, the femoral stresses take a value close to the maximum estimate. If it rotates, as it does in modern crocodylians and iguanas, the stresses take a value close to the minimum estimate. In the calculation, postures are represented by the angles between the longitudinal axis of the femur and the direction of the



ground reaction force. A smaller angle means a more upright posture and a larger angle means a more sprawling posture.

The Sylvester-Bradley Award allowed me to visit museums in Germany, (the Paleontological Museum, Tuebingen, and the Staatliches Museum für Naturkunde, Stuttgart), in order to measure anatomical data that cannot be measured from the literature. Five specimens were examined, two of which belonging to the sister group of archosaurs and others, are members of the crocodylian lineage.

Results are shown in Figure 1. Femur stresses of *Stenaulorhynchus*, the most basal taxon, increase with a more upright posture and suggest their sprawling posture (smaller x-axis value in the graph) whereas femur stresses of *Terrestriisuchus*, the most advanced taxon, decrease with a more upright posture that suggest their erect posture. In the other three taxa maximum stress estimates decrease with a more upright posture, whereas minimum stress estimates increase with a more upright posture. Thus, it is difficult to infer plausible posture from only this information.

Stress estimates of some taxa, namely *Erythrosuchus* and *Batrachotomus*, are relatively very high compared with living animals. These high stresses might constrain their posture and imply that the animals had an erect gait. This supposition is consistent with Bonaparte (1984), who indicates that the heavy weight of basal archosaurs is a cause of their graviportal erect posture.

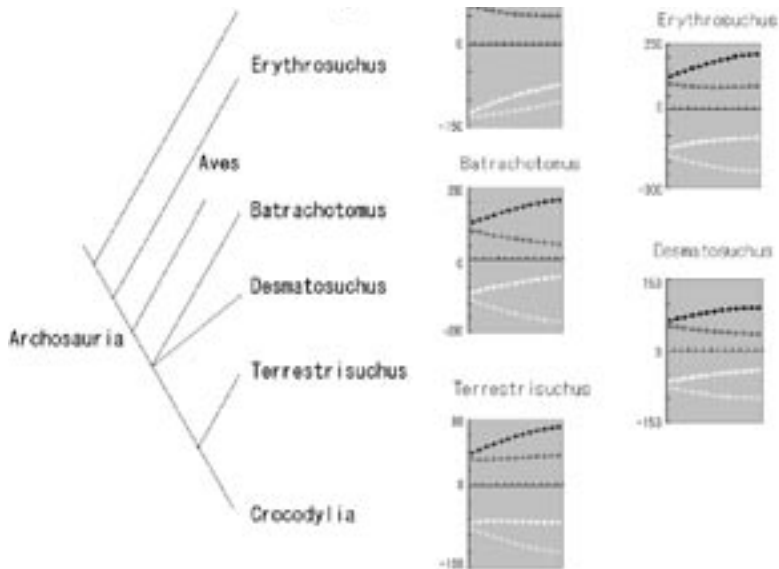


Figure 1. Graphs of posture-related changes in femur stresses, calculated by the biomechanical model and phylogenetic relationship of studied specimens. Smaller values of X-axis indicate a more upright posture and larger X values represent a more sprawling posture. From upper to lower, lines indicate values of maximum estimated peak tensile stress, minimum estimated peak tensile stress, minimum estimated peak compressive stress and maximum estimated peak compressive stress (in MPa).



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Biodiversity into the fourth dimension— calculating percentage abundance in vertebrate palaeoecosystems

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The science of palaeoecology is notoriously difficult to quantify. Not only do we have to deal with the legion complexities of a biological system which cannot be observed whilst functioning, but also with the interactions between this system and the geosphere over the large time periods between the preservation of the fossils in question and the present day (Behrensmeyer *et al.*, 2000). My particular interest in this field, and the focus of my Ph.D., concerns the quantification of the magnitudes of the taphonomic biases that control the preservation of percentage abundance in the fossil record. Were we able to determine with confidence that a fossil ecosystem contained 50% of taxon A, 30% of taxon B and 10% of each of taxa C and D then it becomes possible to describe the palaeoecosystem not simply in terms of species richness (how many different taxa are preserved), but also species evenness (how the individuals are distributed between the preserved taxa). From this we can then calculate biodiversity, which opens up new avenues of research into, for example, community change across major climatic or geological perturbations.

After developing methodology to address this problem, it was necessary to collect real data on which to test this methodology. This would ideally come from an ecosystem which is comparable with modern ecosystems, but has still been subject to a significant range of taphonomic



modifications. With this in mind, and after consultation with a number of those more familiar with the diversity of fossil assemblages preserved around the world, I settled on the White River Group of North America. These early Cenozoic formations contain some of the most abundant and well-preserved fossil mammalian faunas in the world. Among the best known exposures of these formations are those at Badlands National Park in South Dakota.



Badlands topography near Badlands National Park, South Dakota. Shows Scenic Member (lower, rounded outcrops) and Poleslide Member (upper, heavily incised outcrops) of the Brule Formation.

A brief field season during the Summer of 2003 working on one of the existing projects in the park gave me invaluable insight into the geology and palaeontology of the area, as well as some idea of the demanding logistics which lay ahead of me. One of the most important choices to be made was the exact stratigraphic interval which I would be sampling. This had to be of a geologically short duration and also not have been worked previously, so that the abundances of fossils in the collection that I was making were not biased by collection from two or more faunas or uncontrolled removal of specimens from the potential sample. With the help of Dr Emmett Evanoff (University of Colorado, Boulder) I was able to settle on a short interval around the Saddle Pass Marker within the Scenic Member of the Oligocene Brule Formation. The vast majority of specimens which have previously been collected from the Scenic Member come from the highly fossiliferous lower portion of the Member (known as the “Turtle-Oreodon Beds”) and little work has been carried out to characterise the fauna of the upper half, which includes the Saddle Pass Marker. The Scenic Member is composed of a mixture of volcanic ash deposits and sporadic, sand dominated channel intervals (Clark *et al.*, 1967). The ash deposits, which contain the vast majority of the vertebrate material, demonstrate a variety of degrees of reworking and are in general heavily overprinted by palaeosol formation (Metzger *et al.*, 2004). Radiometric dating of several horizons within the White River Group and comparison of sedimentary rates with similar



deposits elsewhere indicates that the interval from which I collected lasts in the order of 100ka (E. Evanoff, *pers. comm.*). Armed with all of this knowledge and having acquired the requisite permits to work on, and remove fossils from a National Park, I began preparations for the 2004 field season.

I put together a field crew of ten members who would rotate through the 12 weeks planned for the season. Fieldwork in the badlands can be quite harsh (during the 2003 season we had experienced temperatures in excess of 50°C) but the terrain, in addition to the fossils, more than make up for this (see figure 1). The Summer of 2004 turned out to be a particularly mild one, so for the most part avoiding sun burn, rather than death due to dehydration or heat exhaustion, was the main climatic concern, although a couple of large thunderstorms added occasional excitement. Although I had initially planned to collect from five or six different sites throughout the park, as usual, this plan disintegrated on first contact with the enemy. In this case the enemy was the huge abundance of vertebrate material preserved in the Saddle Pass Marker interval. The collection protocol required for this study meant that every scrap of bone, even if it was unidentifiable, had to be collected. While this did not make for the most exciting time for the field crew, the data that this has generated is proving most insightful, even at these early stages of the analysis. The number of sites worked was thus rapidly revised down to three and then two.



Bone bed below Saddle Pass Marker. Visible are Stylemys carapace (upper left) and Hyracodon skull (nasals pointing forward, lower right).

In the end, we collected about 3,000 individual specimens (about 500 of which were identifiable to generic level), which represents the largest accession of field material to the Sedgwick Museum in recent history. Each specimen was located to within a few centimetres using differential GPS equipment, so that any preservational patterns could be accurately analysed in 3D. The



sample comprises at least 22 species, ranging in size from shrew-sized insectivores through to large rhinocerotids and hyracodontids. For large animals (over 1kg body mass) the collection is dominated by the equid *Mesohippus* and two chelonians; *Stylemys* and *Testudo*. While the numbers of preserved equids may represent an underlying ecological pattern, early analysis indicates that the abundance of the chelonians is a taphonomic artefact due to the high preservation potential of turtle shell. Carnivores form the expected low proportion of the sample (eight identified specimens), represented entirely by the nimravids *Eusmilus* and *Hoplophoneus*. The small mammal fauna is diverse, making up at least half of the total number of species. This portion of the sample is dominated by the rodent *Ischyromys* and the lagomorph *Palaeolagus*, and, to a lesser extent, the rodent *Eumys*. However this dominance relates almost entirely to the relative sizes of these animals rather than any community structure.

Several articulated specimens were collected, including the anterior portion of a *Mesohippus* and the rib cage and hind limbs of a *Hyracodon* (with associated skull), however probably the most exciting find of the field season was that of a multispecific bonebed. In the course of unbiased collection protocols, we had been walking past this site for many days, but when we finally opened a quarry there, the finds were worth the wait (figure 2). We were presented not only with skulls of six different taxa (the “rhino”, *Hyracodon*, the oreodont, *Merycoidodon*, the equid, *Mesohippus*, the artiodactyl, *Leptomeryx*, the chelonian, *Stylemys* and a nimravid), but also jaws from 25 further individuals and a large assortment of postcrania. A total of 300 elements were collected from an area of 6m². With the exception of one articulated limb, every element in the bone bed was disarticulated. The distribution of sizes, elements and taxa found in the bone bed suggests an attritional accumulation, rather than a mass mortality event, but more detailed analysis of this will have to wait for preparation of all of the collected material. The sedimentology and taphonomy of the bone bed has already been the subject of a research project. This supports the attritional nature of accumulation and demonstrates that the bone bed formed as a lag in a palaeotopographic low, and has been subject to modification by soil formation (T.F. Russon, *pers. comm.*).

While complete analysis of the data collected from this fauna is still in progress, initial analyses suggest that these data will provide significant insight into the magnitudes of the taphonomic biases which control the preservation of abundance in the vertebrate fossil record. In combination with the other methodology devised during the course of my Ph.D., this will hopefully allow for the analysis of fossil vertebrate faunas using techniques which are much more similar to those currently only used in the modern realm.

ACKNOWLEDGEMENTS

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the support I have received from the Sedgwick Museum. The last thanks must go to my field assistants, without whose long hours of crawling on hands and knees picking up “just another tiny piece of crap” this fieldwork would have been much less productive and much more tedious.

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High latitude Cretaceous climates

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The Cretaceous Period has long been considered a time of great warmth, where high temperatures prevailed over both equatorial and polar regions. Elevated atmospheric CO₂ levels and a low global temperature gradient have commonly been postulated for this time (e.g. Frakes 1979). However Mutterlose and Kessels (2000) provide evidence for the existence of distinct climatic belts throughout parts of the early Cretaceous, whilst further studies have revealed that the eustatic changes illustrated in the Exxon sea level curve could in all probability not have occurred without a glacio-eustatic causal mechanism (e.g. Stoll and Schrag 1996). Evidence presented by Price (1999) in a review of high latitude glacial deposits, although equivocal, can be integrated with these and other studies to infer that an ice-house phase with the existence of limited polar ice was possible, particularly in the early Cretaceous.

Unfortunately, such evidence is both spatially and temporally limited, with a particular emphasis of current work on Southern high latitudes. This scarcity of data is particularly significant, as it is generally acknowledged that global climate is defined to a considerable degree by the prevailing conditions at polar latitudes. The major purpose of my current research is therefore to assemble an array of palaeontological and other geological data from biostratigraphically constrained localities in Northern Europe, Siberia, and Svalbard, which will be used to generate new evidence for the patterns and consequences of changes in early Cretaceous oceans, sea-level and climate.

Key fossils for this study (principally belemnites) are abundant throughout much of the Cretaceous Boreal Province, and specimens have already been collected from the Isle of Skye, Pechora River (Northern Russia) and the Boyarka River (Northern Central Siberia) in relation to this study. Belemnites have been proved through various studies to be eminently suitable recorders of palaeoceanographic and climatic change. The isotopic trends observed from the collected belemnites will be correlated with known climatic parameters and additional climate proxies (e.g. nannofossil variation and glendonite occurrence) to reconstruct high latitude



Cretaceous climates. This will then be used to test and validate both existing and impending climate models.

Receipt of a Sylvester-Bradley Award made it possible to undertake a preliminary research trip to Svalbard in July 2004. Svalbard is a small archipelago north of Norway, on the edge of the Arctic Ocean, and at a latitude of 78°N it is well within the Arctic Circle. Importantly, it would also have occupied a high palaeolatitude during the Cretaceous. Two locations in Svalbard were examined, Janusfjellet and Festningen, which together provide an almost complete stratigraphy from the Middle Jurassic to the Lower Cretaceous. The Janusfjellet subgroup of Bathonian to Hauterivian age is well exposed at both of these locations (with Janusfjellet being the type section for the subgroup). The subgroup can be easily correlated between the two sites by means of several prominent marker beds, the most suitable of which is the Myklegardfjellet Bed of Ryazanian age which divides the Bathonian–Volgian Agardhfjellet Formation from the Valanginian–Hauterivian Rurikfjellet Formation (Nagy and Basov 1998). The Myklegardfjellet Bed is described by Dypvik *et al.* (1991) as consisting of “several decimetres thick sub-units of white to yellow, soft plastic clays” which differs significantly from the shallowing upwards black shale interval below, and the light grey clays above (Nagy and Basov 1998).

Belemnites are common throughout much of the Janusfjellet subgroup, but are particularly dominant at several important horizons. Other fossils were also identified and examined, including ammonites, bivalves and gastropods. Phosphatised belemnites were also observed to be relatively common in places, although these are less suitable for isotopic analysis. The data collected from this fieldwork will provide a framework that will be used in comparisons with other Northern high-latitude sites and will also form the basis for further research in this area.



Myself and Dr Gregory Price with our method of transport whilst in Svalbard. This is us arriving at the Festningen section.



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The phylogeny of the trilobite suborder Illaenina Jaanusson, 1959

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The first phylogenetic study involving trilobites was published nearly thirty years ago (Eldredge 1977). Since then, there have been some fifty phylogenies conducted: many of those at generic- or familial-level (see references within Fortey 2001). Few focus on ordinal-level analyses and there is still much contention surrounding the phylogenetic relationships of trilobite orders, as well as between lower-level clades. Some orders have been studied quite comprehensively (e.g. the Phacopida), while others have been the subject of virtually no phylogenetic studies: the Corynexochida being a notable example of the latter.

The Corynexochida is thought to consist of the suborders Corynexochina, the Leiostegiina and the Illaenina; all three taxa show the conterminant hypostome condition and similar protaspid morphologies (Fortey 1990). The Illaenina comprises the Styginidae, Illaenidae and Thysanopeltidae.

The phylogenetic placement of the illaenine family Illaenidae is contentious: it seems to share some characters with the asaphid family Nileidae and may not be, as is generally accepted, closely-related to the Styginidae (Whittington 2000). Both groups have been well studied



morphologically (e.g. Lane & Thomas 1983; Whittington 1997, 1999). However, the generic-level phylogeny of the Illaenina is not well understood.

The purpose of the work undertaken here was, therefore, twofold: to elucidate the phylogenies of the suborder Illaenina and to establish whether or not the illaenids are related to the styginids or the Nileidae.

Many illaenids and styginids are much effaced and character states often cannot be recognized from study of published material. The Smithsonian National Museum of Natural History, Lund University and the Swedish Museum of Natural History house important types of illaenid and styginid taxa (see Appendix). Visits to study the material directly allowed the construction of a much more comprehensive dataset than the literature allowed, and aided the development of some original characters. This, in turn, allows for more effective analysis and a probable lower yield of equally parsimonious phylogenetic trees (see Wilkinson 1995).

Data on the more obscure taxa are still being collected so further work is needed to be confident in generic-level relationships. However, preliminary analyses suggest that the Illaenidae is monophyletic and the illaenids and styginids arise from the Thysanopeltidae, which forms a paraphyletic basal grade. The Illaenidae seems to have many characters common to the Styginidae but the next phase of this work is to factor the Nileidae into the analysis: this will help to elucidate which family the illaenids are more closely-related to.

Acknowledgements

Many thanks are due to Drs Jann Thompson and Dan Levin for all their help with the NMNH trilobite collections (Smithsonian National Museum of Natural History, Washington D. C.). I am greatly indebted to Professors Per Ahlberg (Lithosphere and Biosphere Science, Lund) and Jan Bergström (Swedish Museum of Natural History, Stockholm) for their valuable advice and time. Thanks also go to Professors Stefan Bengtson and Christina Franzén (Swedish Museum of Natural History) and also to my doctorate supervisors, Dr. Matthew Wills (University of Bath, UK) and Professor Richard Fortey (NHM, UK). This work could not have been undertaken without a Sylvester-Bradley Award from the Palaeontological Association and a Systematics Research fund from the Systematics Association. Both grants aided different aspects of the project and both are gratefully recognized.

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Appendix: Institute; Taxa available for study (published references relating to taxa and specimen numbers available on request to JRP)

Smithsonian National Museum of Natural History: *Bronteopsis*, *Bumastus* (*Bumastus*), *Harpillaenus*, *Hyboaspis*, *Raymondaspis*.

Lund University: *Bronteopsis*, *Illaeus*, *Panderia*, *Phillipsinella*.

Swedish Museum of Natural History: Many species described in Jaanusson 1954.

Middle to Late Ordovician brachiopods of central Kazakhstan: biofacies analysis and biogeographical significance

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The palaeobiogeography and biofacies relationships of mid to late Caradoc brachiopod faunas of Kazakhstan have been discussed briefly by Popov *et al.* (2002) and Fortey and Cocks (2003). However, information on late Arenig to early Caradoc brachiopods from the region remains rather limited. The Chu-Ili Range and the west Balkhash region are the most convenient areas for such studies, because the geology there is quite well known and understood. General characters of the Late Ordovician brachiopod faunas are known from several recent publications and the major fossil localities are only a little bit over 400 km away from Almaty and are therefore relatively easily accessible.

The main objectives of the project were: (1) taxonomic revision of late Arenig to early Caradoc (*Nemagartus gracilis* Biozone) brachiopod faunas of the Chu-Ili Range and west Balkhash Region and from the Sarybidaik Formation of the Ekibastuz region; (2) study of brachiopod biofacies differentiation, which required additional sampling and sedimentological observations in the field; (3) biogeographical analysis of the brachiopod faunas.



Figure 1. View of Mirnyi, formerly a mining town, but now a ghost town located about 40 km west of Lake Balkhash. Despite clear signs of decline, which is also evident in the surrounding Kazakhstania province, it still provides shelter and infrastructure for fieldwork.

My task was completed and expenses were reduced significantly because of the kind help of my colleagues and old friends Evgenii Alperovich and Elena Vinogradova, who still live in the area. Both are leading members of a small geological exploration team working in the West Balkhash region. They are based in the town of Mirnyi about 40 km from the western coast of Lake Balkhash. This settlement was once a prosperous mining town on the southern margins of the Betpak-Dala desert. Prosperity came from the uranium and molybdenum mines. These mines were abandoned soon after the collapse of the USSR and nowadays Mirnyi is a ghost town. The population has been reduced more than tenfold, down to 800 people, nearly all services are gone, and even a water pipe that supplied inhabitants with fresh water from the river Chu about 80 km away was sold. Nowadays it is still possible to buy a hard drink in the local shop, but if you are seeking some water to make tea or simply to wash your hands, it is available only from the railway station ten kilometres away. There is a well in the town, which is the only source of brackish water, rich in heavy metals. Miraculously this water can still be converted into milk. As a result, the number of cattle has increased significantly during the last ten years, but life expectancy of these poor animals is well below the average.

Two weeks' somewhat surrealistic life in the area was well rewarded because of the outstanding Lower Palaeozoic geology. Extensive exposures of Ordovician rocks just 20–30 km south-west of Mirnyi became the main object of my fieldwork. Lower to Middle Ordovician sediments developed in the area were formed along the active margin of a small crustal terrane known as the Chu-Ili plate (Popov *et al.* 2002; Fortey and Cocks 2003). Subduction and associated island arc volcanism began sometime in the early Arenig and terminated at the beginning of the Late Ordovician. The subduction–accretion complex exposed just 15 km north of the studied sections includes radiolarian cherts of the Upper Cambrian to Middle Ordovician Burubaital Formation, well dated by conodonts (Tolmacheva *et al.* 2004). The last slabs of oceanic crust subducted under the Chu-Ili microplate can be dated as latest Darrivilian (*Pygodus anserinus* Biozone). The studied Ordovician section begins in alternating tuffs, siliceous and black graptolitic shales, with some units of volcanic mass flow deposits of the lower Darrivilian Balgozha Formation



formed in a fore-arc basin. The overlying Alakul Limestone was probably formed on the rim of the growing accretionary wedge. It contains small mud mounds, abundant stromatolites and stromatoporoids. Rhynchonelliform brachiopods from this unit are currently under study and some are partly published by Popov *et al.* (2001). However, more attention was paid to the sampling of poorly known brachiopod faunas from the uppermost Darriwilian Oisaksaul Formation. The depositional environment suggests a complicated bottom topography with strong biofacies differentiation. There are two low diversity brachiopod associations characteristic of shallow shelf (BA2): one was dominated by the primitive early rhynchonellide *Ancistrothynga*, and the other by strophomenoids and *Hesperorthis*. The latter, otherwise widespread genus, is reported for the first time from the Middle Ordovician of Kazakhstan. Remarkably, rhynchonellide and strophomenoid dominated brachiopod associations are not characteristic for the early to mid Caradoc of the Chu-Ili plate (Popov *et al.* 2002), but proliferated during the late Caradoc–early Ashgill. There is also an association dominated by the plectambonitoids *Acculina* and *Ishimia*, which may represent an early analogue of the *Acculina*–*Dulankarella* association of Popov *et al.* (2002). Limestone units with abundant dasyclad algae and *Girvanella* contain the endemic plectambonitoid *Bandaleta*, ribbed camarellides, and early smooth spire-bears, possibly *Rozmanospira*. There is a general impression that the late Darriwilian brachiopod faunas of the Chu-Ili plate already contain nuclei of the shallow shelf brachiopod associations that spread widely across the Chu-Ili plate during the Caradoc, but there is relatively little relationship with the early Darriwilian brachiopod associations.



Figure 2. Northerly view of exposures of the Middle Ordovician Oisaksaul Formation 7 km south-west of Alakol Lake, West Balkhash region.

Rapid subsidence of the area took place at the beginning of the Late Ordovician, resulting in deposition of black graptolitic shales and mass flow deposits containing large olistoliths of algal and bioclastic limestone. The black shales contain a distinctive East Gondwanan trilobite association with *Ampyxinella*, *Taklamakania* and *Telephina*, whereas the brachiopods are represented by a new endemic plectambonitoid genus. During the Caradoc this basin was filled mainly with clastic deposits.

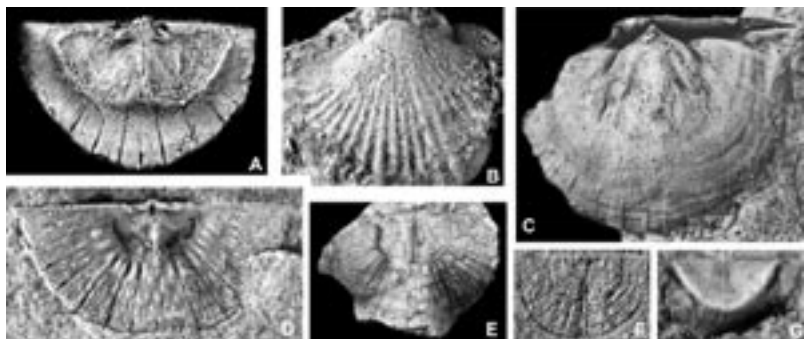


Figure 3. Selected brachiopod taxa from the Middle Ordovician Oisaksaul Formation of the West Balkhash region: A, dorsal valve interior of *Acculina rgaitensis* Nikitina; B, ventral valve exterior of *Ancistrorhyncha modesta* Popov; C, ventral internal mould of *Ishimia* sp.; D, dorsal valve interior of *Chonetoidea* sp. nov.; E, dorsal valve of *Esilia* sp.; F, dorsal valve exterior of new plectambonitoid genus; G, dorsal valve exterior of *Synambonites?* sp.

The overlying upper Caradoc to Lower Ashgill clastic deposits of the Dulankara Formation retain nearly horizontal stratification. They formed presumably in a tide-dominated environment and contain abundant coquinas of gastropod and bivalve molluscs, as well as plant remains, but this part of the sequence was outside the scope of this study because of the lack of time. On the return journey to Almaty there was a visit to the section of the lower Darrivilian Uzunbulak Formation exposed on the eastern side of the Kopalysai river in the Chu-Ili Range. Brachiopods from this area and unit have been under study for several years, but new sampling made a good contribution to the already assembled material. In addition to brachiopods, the new collection includes *Annamitella* and some other associated trilobites.

Significant additional material of Middle Ordovician brachiopods from the old collections together with associated geological documentation, was obtained in Almaty. It includes a valuable collection from the Sarybidaik Formation (*Hustedograptus teretiusculus*-*Nemagraptus gracilis* biozones) south of Ekibastuz in north-eastern Central Kazakhstan. The Middle Ordovician fauna of that part of Kazakhstan remains very poorly known. My visit to Almaty was also rewarded with Cambrian brachiopod and rock samples collected by a local geological mapping team around the former Semiplatinsk nuclear testing field in eastern Kazakhstan.

A preliminary review of the new collections from Kazakhstan shows that major features of biofacies differentiation of the brachiopod assemblages known from the Caradoc were already established in the late Darrivilian. The early Darrivilian brachiopod faunas remain known mostly from the Chu-Ili plate. They contain a large proportion of endemic genera and show little in common with contemporaneous faunas of Baltica and Siberia.

I greatly acknowledge the Sylvester-Bradley Award from the Palaeontological Association, which made it possible for me to visit and work once again in the West Balkhash region and in the Chu-Ili Range. My thanks are also due to Igor Nikitin for his helpful advice and support during my work on the project in Almaty.



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Early Ordovician *Thysanotos* brachiopod assemblage and associated trilobites from north-central Iran

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In 2002 there was a brief visit to a spot on the southern slopes of the Simeh-Kuh Mountain, north-west of Damghan, northern Iran, which was known for some time as an isolated Lower Ordovician trilobite locality surrounded by outcrops of mainly upper Palaeozoic rocks. It was immediately clear that there is a continuous, Upper Cambrian to Ordovician fossiliferous section. There were numerous trilobites in shales and some limestone beds useful for conodont dating. Just below the limestone unit there were sandstones containing unusually large, black oboloid shells with spinose growth lamellae. Later they were identified as *Thysanotos*. The lingulide brachiopod *Thysanotos* was widespread in the late Tremadoc and early Arenig of Baltica (Estonia, Poland and South Urals) and some peri-Gondwanan terrains (Czech Republic and southern Germany), but its first occurrence on mainland Gondwana was reported by Bassett *et al.* (1999) from the Shirgesht Formation of the Derenjal Mountains, north of Tabas in eastern Central Iran, where it co-occurs with the brachiopod *Protambonites*. Thus *Thysanotos* is also present in the Lower Ordovician of the Eastern Alborz.

The Simeh-Kuh section is situated only 13 km from Damghan, but there is 3 km of mountainous terrain from the road nearby. There is no water and no place for camping. Therefore a good vehicle and a team are needed to collect fossils and conodont samples and to ship them back to Esfahan more than 600 km south-west. Thanks to the Sylvester-Bradley Award all problems related to logistics and transportation were successfully resolved. It is a good foundation for the successful and extremely productive fieldworks of 2004.



Figure 1. Northern view of the Ordovician exposures in the Simeh-Kuh section. Hills in the far side were built of the Upper Cambrian limestone of the Mila Formation containing numerous *Billingsella* shell beds.

Field observations reveal a presence of the continuous sequence of the Cambrian to Middle Ordovician sediments south-east of the Simeh-Kuh Mountain assignable to the Lalun, Mila and Lashkarak formations. Discovery of abundant trilobite faunas of the *Asaphellus-Dactylocephalus* and *Psilocephalina* associations in the lowermost part of the Lashkarak Formation, which was previously considered as a barren interval, allows the more precise definition of the age of that part of the formation and a probable position of the Cambrian–Ordovician boundary, which, like in South China, can be placed closely to the first appearance of the trilobite *Asaphellus inflatus*. However in the absence of diagnostic conodonts, definition of the base of the Ordovician System in the Eastern Alborz Mountains requires further study. An observed pattern of the faunal replacement in the Lashkarak Formation is caused in significant part by a succession of depth-related trilobite associations which belong to the nileid, raphiophorid and *Neseuretus* biofacies. Numerous occurrences of conodonts recovered for the first time from the upper Tremadocian to lower Darriwilian part of the Lashkarak Formation give a good time constraint for precise dating of the observed faunal and environmental changes.

The age of the *Thysanotos* brachiopod assemblage was recently a subject of debate in the palaeontological literature. Popov and Holmer (1994) suggested the Hunnebergian age (*Paroistodus proteus*–lower *Prioniodus elegans* conodont biozones) of this assemblage, whereas Mergl (1997) argued that it is diachronous, and had evolved in western peri-Gondwana by the mid Tremadoc. The study of the faunas from the Iranian sections, which contain diverse trilobite assemblages, as well as conodonts, can be very helpful in resolving these debates. Conodonts of the lower *Paroistodus proteus* and distinctive trilobites *Taihungshania miqueli* previously known from the lower Arenig of Southern France and Turkey were found just below the first occurrence of *Thysanotos siluricus*, whereas conodonts *Trapezognathus diprion* suggesting the upper *Oepikodus evae* Biozone appear in the lower part of the overlying carbonates. Thus



in the Eastern Alborz the *Thysanotos* Brachiopod Association occupies precisely the same stratigraphical position as in Baltoscandia. Another similarity is that, both in the East Baltic and in the Eastern Alborz, first appearance of *Thysanotos* occurred just prior to the onset of a storm-generated carbonate sedimentation characteristic of temperate latitudes in the early to early middle Ordovician. An unusual feature of the *Thysanotos* association is that in the Eastern Alborz it co-occurs with bryozoans, which can be considered as one of the oldest in the World. In Baltoscandia the earliest bryozoans appear later, since the Billingenian (upper *Prioniodus elegans* to *Oepikodus evae* biozones) (Pushkin and Popov 1999). There is however an important difference. The Early Ordovician trilobite faunas from the Eastern Alborz retain strong affinities to the contemporaneous faunas of South China and there is no sign of a close link to Baltica.

Results of fieldworks exceed significantly primary goals of the project. Not only was the stratigraphical position of *Thysanotos*-bearing beds defined, but significant trilobite and conodont collections were assembled and important data on trilobite biostratigraphy, palaeoecology and biogeography were obtained. I greatly acknowledge the Sylvester-Bradley Award from the Palaeontological Association which made this work possible. I thank my friends Vachik Hairepetian, and Mehrosadat Hosseini who helped me in the field and with processing of the rock samples for conodonts, which were later identified by Dr Oliver Lehnert from the University of Erlangen.

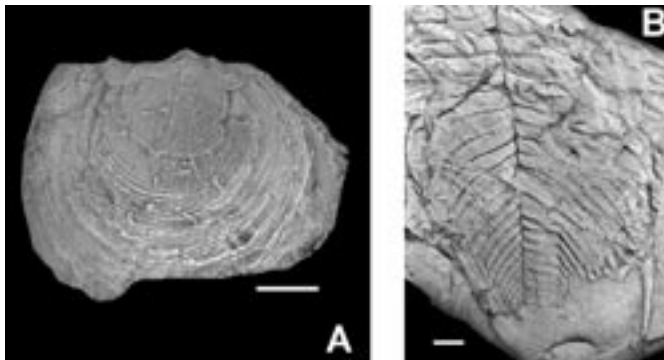


Figure 2. Fossils from the Lower Ordovician part of the Lashkarak Formation:
A: valve of *Thysanotos siluricus* incrustated with bryozoan colonies;
B: pygidium of trilobite *Taihungshania miqueli*. Scale bars 5 mm.

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Bohemian bivalves: a taphonomic investigation

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Comparison of silicified with non-silicified Silurian and Jurassic carbonate faunas has highlighted previously unrecognised catastrophic loss of aragonitic shallow infaunal bivalves during very early shallow burial diagenesis (Cherns and Wright 2000; Wright *et al.*, 2003). Mollusc liberated carbonate is a likely source of diagenetic carbonate cement in limestone-shale sequences ('black hole' facies of Wright and Cherns 2004). The spatial and temporal extent of the 'missing molluscs' phenomenon and their contribution to diagenetic limestone formation are not well quantified but consensus is that effects are extensive. Where evidence of shallow infaunal aragonitic bivalves does occur, it has to be asked, what arrested the well understood processes of early shallow carbonate dissolution (*e.g.* Sanders, 2003), and led to their entry into the fossil record?

The Silurian and Devonian of the Prague Basin, Bohemia, have a taxonomically and palaeoecologically well documented bivalve fauna (*e.g.* Kříž, 1999). The Wenlock–Lochovian, in particular, has abundant shallow infaunal originally aragonitic bivalves in biodetrital (BT), biomicritic (BM), and micritic (M) limestones, interbedded with shales (Kříž, 1999), that also contain diagenetic limestone nodules (*e.g.* Šrámek 1974; Kukul 1975).

A Sylvester Bradley Award made it possible for me to visit Bohemia for ten days in summer 2004 to address some of the issues mentioned above. Jirí Kříž and Štěpán Manda (Czech Geological Survey) showed me the Silurian and Devonian limestones in the field. Carbonate nodules collected in the field reveal bivalves as internal and external moulds. Bivalves are seemingly missing from the intervening calcareous shales, and evidence of their dissolution comes from external moulds (also of gastropods and cephalopods) on the exterior of nodules. In the nodules the presence of recrystallised aragonitic bivalves, sometimes also pyritised, indicates nodule formation acted to capture the remnants of the original aragonitic fauna, in the way that has been described for the Upper Cretaceous of Morocco (El Albani *et al.*, 2001). Petrographic analysis of nodules shows that they contain juvenile cephalopods, bivalves and gastropods (less than ~2 mm), that would be expected to dissolve easily and quickly, suggesting also that nodule formation was rapid. The presence of pyrite and sulphurous smell when the limestone is broken suggests formation in a reduction zone, in the shallow subsurface, and for nodules in shales this is confirmed by flattened-elongate nodule shape (Šrámek, 1974). Two of the controls on the extent of the 'missing mollusc' phenomenon then seem to be the rapidity and redox conditions under which dissolution-reprecipitation occurs.

Wright *et al.* (2003) demonstrated for Jurassic limestone a facies control on mollusc distribution. Higher energy grainy facies (Sutton Stone Formation of South Wales) contain mouldic preservation of aragonitic taxa – thought to be a result of its originally poor organic content/well-washed/oxygenated character. By contrast, offshore Blue Lias facies are dominated by biminerals taxa with loss of aragonitic taxa – thought to be the result of originally high organic content causing carbonate dissolution.



Can a similar facies control be tested on Bohemian bivalves? The division of the Silurian–Devonian limestones into BT, BM and M facies can be compared to the Jurassic example, with BT originally the least prone facies to dissolution, M the most, and BM intermediate. Tallies of infaunal aragonitic bivalve genera from Kříž (1999), show that there are a higher number of infaunal aragonitic genera in BT facies (14 genera known) than M facies (six genera known) for Silurian and Devonian localities of the Prague Basin. Is this purely an ecological distribution? The low number of shared genera between the facies (three between BT and BM; four between BT and M; none between BM and M) (Table 1), indicates there is a strong palaeoecological control on generic distribution. However, total abundance of valves for the shared genera between facies may hint at a taphonomic gradient overprinting a palaeoecological one. BT facies generally has a higher number of valves for shared genera than BM and M facies (Table 1). Exceptions are values for *Praecardium* and *Snoopyia*, suggesting that the distribution pattern is more complex than originally thought. Further in-depth study is needed on facies control of molluscan preservation.

Facies→ Shared genera↓	BT	BM	M
Neklania	23	16	–
Modiolopsis	46	7	–
Panenka	22	1	–
Praecardium	10	–	59
Cardiolinka	421	–	181
Snoopyia	24	–	31
Dualina	324	–	207

Table 1. Abundances of valves for shared genera between facies BT: biodetrital; BM: biomicritic; and M: micritic. Compiled from data in Kříž (1999).

Finally, the Sylvester Bradley Award has instigated an international research and technical collaboration between myself and Štěpán Manda (Czech Geological Survey); we plan to work together in the future on new cephalopod-rich Silurian–Devonian boundary sections in the Prague Basin.

ACKNOWLEDGEMENTS

I thank Jirí Kříž and Štěpán Manda for kindly hosting our (James Wheeley and Lesley Cherns) stay in Bohemia, and accompanying us in the field. I thank Susan Kidwell for discussions on bivalve mineralogy.



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Book Reviews

Macroflora Liasică din România, cu privire specială asupra Pădurii Craiului

Zoltán Czier (2000). Editura Imprimeriei de Vest, Oradea, Romania, ISBN 973-9329-89-6 (paperback). No price stated. Obtainable from the author at Str. Doina nr. 14, Bloc C 71, Ap. 10, 410326 Oradea, Jud. Bihor, Romania (e-mail <drcziergeol@freemail.hu>)

Although published several years ago, this volume is not widely known. It deals with the Lower Jurassic macroflora of Romania, with emphasis on five palaeobotanical sites in the King's Forest area around the mining town of Șuncuiuș on the Transylvanian Massif. As Zoltán Czier indicates in the three-page English summary, it is the first guide to the Liassic macroflora of Romania and the first synthesis of the King's Forest assemblage.

The volume deals with its subject matter in a logical fashion. A list of the geographical locations of 42 Lower Jurassic plant-fossil sites in Romania is followed by a review of past palaeobotanical work on the succession, notes on the geological setting and stratigraphic succession, and a list of most of the taxa that have been recorded, the localities at which they have been found, and the number of specimens recovered. Fifty-three pages of taxonomic descriptions follow, accompanied by line drawings and references to many of the 58 plates that are bound together at the end of the volume. No new taxa are described.

Consideration of the overall composition of the rich flora recovered from Hettangian–Sinemurian deposits and of the impoverished Pliensbachian assemblage (there is no Toarcian material) leads to discussion of the composition of the vegetation at the time, and chapters on taphonomy, palaeoecology, biostratigraphy, palaeogeography, palaeoclimate and palaeophytogeography.

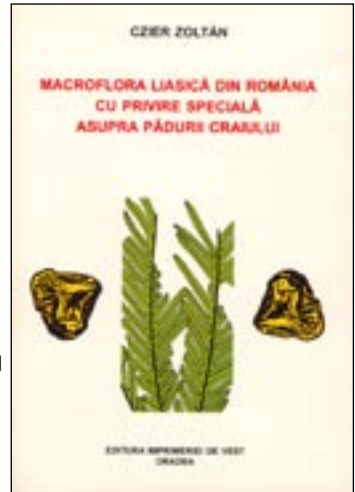
The first ten plates include photographs of several of the fossiliferous sites. Most of the remainder are of macrofossils, the exceptions illustrating a few spores recovered *in situ* and details of cuticles. Unfortunately the quality of reproduction of the plates is not as good as one might wish (some are very 'muddy' with details difficult to discern), but most are useful.

Although written in Romanian, it is possible to follow much of the general thrust of the work without knowledge of the language owing to the plethora of accompanying figures and tabulated data. The volume will be of interest to palaeobotanists and those concerned with Mesozoic phytostратigraphy and terrestrial environments.

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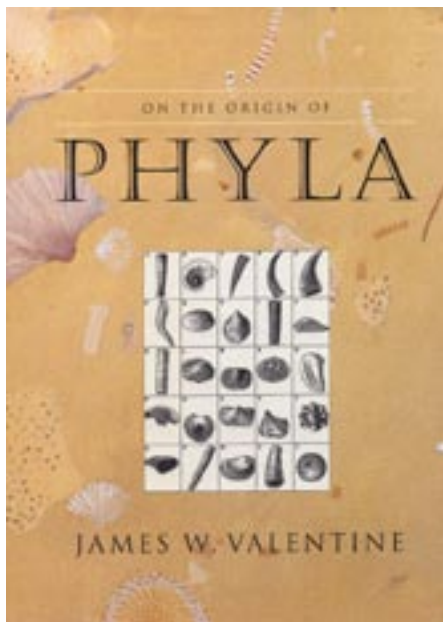
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On the Origin of Phyla

James W. Valentine (2004). The University of Chicago Press.
ISBN 0-226-84548-6. \$55.00. £38.50 (cloth).



For many years there has been much debate as to the mode of macro-evolutionary change and its patterns over time. As Darwin was methodical in approach and wide-ranging in scope with his *Origin of Species*, Valentine treats phyla in much the same way, (excepting that only the metazoa are covered). An interdisciplinary approach is brought to bear on the question of how phyla originated, are interrelated, and how the seemingly huge gulfs between distant clades can be crossed. It is one thing to try and explain how two different “species” of finch or stickleback diverged, (Schluter 2001), but here we are dealing with how very different divisions such as Mollusca and Annelida went their separate ways. The text is clear and concise, and if readers find themselves overwhelmed by jargon there is a comprehensive glossary at the back of the book. This is important because the book covers a range of subject

areas that will not be familiar to every reader. Many diagrams and photographs complement the text; some figures are taken from other publications so the quality can be variable, but generally they are clear and illustrate the point, or organism under discussion. All illustrations are in black and white, which along with the non-glossy paper contribute to making this an inexpensive book.

The book is composed of three sections dealing with: 1) *Evidence of the Origins of Metazoan Phyla*; 2) *The Metazoan Phyla* and 3) *Evolution of the Phyla*. As well as the fossil record, Valentine shows in the first section what evidence Developmental Biology and Genetics can offer by way of characterising the divergence amongst phyla. Each of these disciplines is reviewed, highlighting what they can show us, as well as their failings and drawbacks, but also how they agree with or contradict one another. An important theme in this book is the central role played by hierarchies: whether it is the traditional taxonomic nomenclature, the sequence of gene expression and regulation in the developing embryo, or the structure of the book itself.

After analysing and describing the evidence for their origins in the first section, part two takes us through the metazoan phyla. Grand alliances, such as Ecdysozoa and Enterochozoa are dealt with separately in their own chapters with their cargo of phyla described individually. This may seem like a huge task (and I am sure it is), but not all smaller individual crown groups are covered. Only the basic body-plans are dealt with; for example, the arthropod body-plan is discussed generally but no study of the relationships and origins of derived groups such as insects are covered, this book is aimed at the level of phyla. Valentine here is concerned with stem taxa, how they diverged and



acquired characteristics diagnostic of the later crown phyla: the point being that stem taxa need not look like their crown group descendants and may even resemble the stem groups of other phyla as there has been less time since divergence. From a zoological standpoint, I found this section particularly satisfying, seeing how wide the diversity of metazoan life is. A biology teacher of mine once said that she felt teaching the diversity of life was dull; I was gob-smacked, and thought it a wonderful interlude to investigating the osmotic capabilities of bits of potato! If you too feel this way, skip to section three which brings all the threads together in an explanation of how the phyla may have diverged in the late Neoproterozoic and early to mid-Cambrian and beyond. The Cambrian explosion is taken here as a true event rather than an accident of preservation that may not go down well with everyone. A comprehensive picture is built up showing us how the phyla diverged and evolved over time. Valentine has dealt elsewhere with why he thinks no new phyla have emerged since the Cambrian, favouring the filling up of ecological niches by body-plans and pre-empting the evolution of any new ones, rather than any inflexibility in developing genomes (Valentine 1995).

Unlike the *Origin of Species*, this work is a review of current ideas that tries to bring them all together to answer the question of the origin of phyla, rather than a proposal of any new grand theory. Of course scientific investigation continues and ideas may change, Valentine himself saying that the time never seemed right to publish and that a line had to be drawn in the sand sometime. I am sure this book will become a “classic” in this field leading to further editions in the future. So will we see the *Origin of Classes*, *Orders* etc, or is there any need? With ideas about taxonomy and systematics constantly being in a state of flux perhaps it is the processes that are important and need understanding, and the labels of intermediate stages in the hierarchy less important. This book will certainly provide fresh perspectives on these debates for most of its readers.

What we have here is a very scholarly piece of work, which may in the future become a classic of evolutionary biology, if not so already. There are a number of books already on the market covering the story of life, intended for the popular science market, but I do not think this is one of them. Despite its clear text, no prisoners are taken when it comes to pushing on and getting down to technical details. By the numbers of colleagues offering ideas for this review it seems a lot of people already own a copy and don't need convincing. This book will appeal and be of use to any academic working in any field of evolutionary biology, not just palaeontology; moreover the cost is not unreasonable and will not be beyond the reach of PhD and MSc students and senior undergraduates. Hopefully there will be an even cheaper softback edition to follow.

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Feathered Dragons: studies on the transition from dinosaurs to birds.

Philip J. Currie, Eva B. Koppelhus, Martin A. Shugar and Joanna L. Wright (eds) (2004). Indiana University Press, Bloomington, Indiana. ISBN 0-253-34373-9 (cloth: alk. paper), UK £37.95, US \$49.95, EUR €65.10

In this – one of the ‘Life of the Past’ series by Indiana University Press – Currie, Koppelhus, Shugar and Wright edit (what is essentially) a series of papers not only on dinosaur–bird transitions, but also concerning other important topics linked with the title area, such as: the K–T extinction event; dinosaur eggs and nesting; the origin of flight feathers; the reproductive physiology of *Troodon formosus*; as well as detailed descriptions of the anatomy of *Bambiraptor feinbergi*, the braincase of *Velociraptor*, and a new dromaeosaurid – *Atrociraptor marshalli*. With papers and essays by such names in palaeontology as: Bakker; Chiappe; Currie; Makovicky; Norell; Novas and Varricchio (to name but a few), surely this has to be an auspicious book?

Introducing *Feathered Dragons* we have Robert Bakker with an interesting and entertaining account of the early research on the links between dinosaurs and birds. We are informed that in the 19th Century whilst European palaeontologists were ‘committing anatomical malpractice’ the first director of the Massachusetts Geological Survey – the Reverend Edward Hitchcock – was reconstructing ‘true dinosaur posture and gait’. Bakker goes on singing Hitchcock’s praises throughout the introduction and credits him with being a century or so ahead of others in the field at the time in identifying that theropod dinosaurs (the term was not yet invented, but he was referring to the animals which we now know as members of the Dinosauria) basically possessed avian limbs and an avian body plan.

The rest of *Feathered Dragons* is set out in three sections: section one is concerned with setting the scene at the end of the Cretaceous; the second section includes papers on dinosaur–bird osteology



and ichnology; and the final section is everything else (feathers and flight, nests and eggs). Perhaps the most interesting paper in the first section is by Gregory Retallack, regarding selective extinction mechanisms between avian and non-avian dinosaurs during the end-Cretaceous. Retallack outlines his theory that acid rain resulting from bolide shock, burning vegetation and/or volcanic activity would have provided the mechanism for the selective extinctions at the K–T boundary. Essentially, the acid rain would have killed off enough plants to pose a serious problem for herbivorous dinosaurs, and therefore for the larger theropods relying on them for food. The suggestion is that this lack of vegetation would have affected birds and mammals to a lesser extent as they were mainly insectivorous and detritivorous at the time. Of course, this is not merely an unsubstantiated theory; Retallack backs up his hypothesis with some rather



complicated evidence concerning the chemistry of palaeosols *etc.* (which is not exactly easy reading, especially if you are used to less chemically orientated traditional palaeontology).

Within the osteology section (essentially a sequence of descriptive papers) there are chapters regarding the braincase of *Velociraptor mongoliensis*, a dromaeosaur sternal plate which exhibits several avian features, a new dromaeosaurid from the Upper Cretaceous of Canada, and a long-awaited detailed description of *Bambiraptor feinbergi*. As you may expect, many of the features described within these papers are a mixture of avian and non-avian characteristics, adding further weight (if any was needed?) and understanding to the argument that the bird clade is nested (no pun intended!) within the Dinosauria. David Burnham's section, describing *Bambiraptor*, deserves particular attention: with attractive anatomical illustrations and reconstructions (including a reconstructed endocranial cast), full measurements, explanations of the geology, taphonomy and preservation of *Bambiraptor*, descriptions of the sub-adult features of the holotype (of obvious importance when describing a species from juvenile specimens), not to mention the full colour photographic plates and plethora of different feathering reconstructions, there can be little doubt that Burnham has cut no corners here (perhaps a luxury of publishing in a book rather than in a journal with limited space and lack of colour pages?).

Opening the 'Eggs, Nests, Feathers and Flight' section Gerald Grellet-Tinner and Luis Chiappe outline their work on coding phylogenetic characters from eggs using extant reptiles and birds as well as dinosaurian eggs where the taxon is known *i.e.* by looking at the embryos inside. Through studying electron micrographs of sections of eggshells as well as nest morphologies, supposed brooding behaviour and egg laying intervals, Grellet-Tinner and Chiappe identify 11 discrete characters useful in cladistic analyses and propose a phylogeny based on eggs, nests and brooding behaviour alone. Perhaps, not surprisingly, the results of these analyses show that birds are nested within Theropoda 'on the basis of five unambiguous synapomorphies', and that an additional seven steps would be required to support a sister-group hypothesis between birds and crocodiles for instance.

Another paper in this section worth noting is Chapter 11: 'Dinosaur Brooding Behavior and the Origin of Flight Feathers' by Thomas Hopp and Mark Orsen. With no intermediate specimens and difficulties in recognising selection pressures for the stages before avian flight evolved, there have been a number of hypotheses put forward as means of explanation. Insect trapping (Ostrom, 1979), water and heat repellence (Dyck, 1985 and Regal, 1975 respectively) and display (Mayr, 1960) have been suggested in the past, but Hopp and Orsen explore brooding behaviour as a medium for lengthening forelimb and tail feathers enough to be a useful precursor for flight. Chiefly using oviraptorosaurs in comparison with modern birds as their examples, Hopp and Orsen eloquently summarise how postures very similar to those that modern birds use whilst brooding would have exposed oviraptorid eggs to the elements unless long feathers were possessed on the forearms and tail. Assuming that this state is primitive, this seems like a good, if not better, theory than most for explaining the driving force behind the evolution of flight feathers in birds.

Overall, *Feathered Dragons* is a very well written compilation of up to the minute research on dinosaur-bird transitions and connected areas of science. It will be useful for those working in either avian or dinosaurian Palaeobiology, and students wishing to find out more on the subject (although, probably only recommended for the most keen amateurs, as a lot of this book is dry, science writing as opposed to 'sexed up' popular science!). Incidentally, it is worth taking a look at



some of Robert Bakker's cartoons in the book; particularly, what can only be described as David Letterman being stalked by five dinosaurs, a turtle, a tortoise, several small mammals and a giant lungfish – which is biting his knee (find the picture in the book and it will all make perfect sense!).

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Fossil plants

Paul Kenrick and Paul Davis (2004). Natural History Museum, London. ISBN 0-565-09176-X. £16.95 (softback).

This is the latest in the Natural History Museum's *Living Past Series* that aims to bring fossils to life by examining the origins of these once-living organisms and making comparisons with their living relatives. Like others in the series (*Fossils: The Key to the Past* by Richard Fortey; *Ammonites* by Neale Monks and Philip Palmer), this is an easily read book that is well presented and includes information that will appeal to non-specialists and specialists alike. Considering the broad aims of the *Living Past Series*, it might at first seem uncertain who the target audience is for this publication. In order to answer that, this review has been undertaken by a fossil plant researcher (JH), a botany graduate now researching fossil plants (LJS), and an undergraduate student in Geology and Archaeology with a general interest in fossils (SJG).

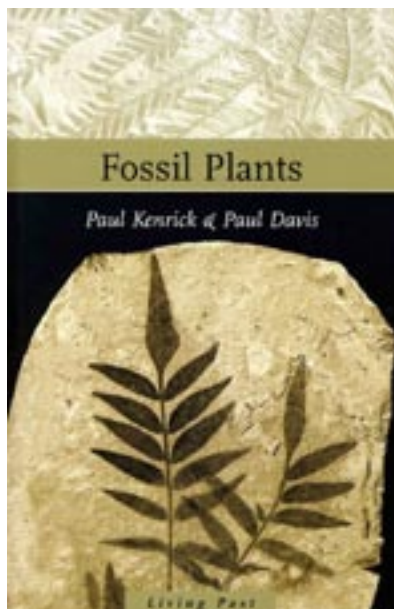
The book consists of nine concise and well-illustrated chapters that collectively span the life history of plants. The order is broadly stratigraphical, but in many parts the logic breaks away from being simply a list of occurrences and their implications into a more synthetic and process-driven account, and this works well. In Chapter 1, a comprehensive review of the earliest evidence of plant life is presented, including important evidence about past environments in which the earliest plants were living. The emphasis is not just on what plants had to tolerate but clearly identifies the role of plants in facilitating environmental change over geological time. Integration of examples from the fossil record with the underlying biological processes is generally seamless, and considering space constraints in the book, this works well.

Terrestrialisation spans chapters 1 and 2, and this is where the book starts to include some of the more interesting insights offered by the authors based on their research experience. Information not only includes examples of the earliest fossil evidence on land, but also develops to consider an overview of early terrestrial environments and the adaptations of plants to life out of water. Here the authors introduce the origins of ferns and fern allies (clubmosses, horsetails), and progress through progymnosperms and seed plants, in each case showing what these groups look as well as



identifying key features to allow their recognition. The illustrations match the text well, and with the exception of having to jump to the colour section in the middle of the book in some instances, flow well and come in a logical order.

Arborescence is the culmination of chapter 2 and the main focus of chapter 3 that examines forests and forest development over geological time. This mixes palaeobotanical specimens with botanical processes, and succeeds in showing that the diversity of plants we see around us today has a long and extensive fossil record. Coal is considered in detail in chapter 4, letting coal-forming plant communities take centre stage. This coverage is impressive and up to date; the ecological information presented and the synthesis of coal swamp diversity and distribution is especially noteworthy. Accounts of coal balls and other concretions bearing anatomically preserved plants are provided and shown to be important information sources for concepts such as palaeogeographic patterns and processes. In this section integration with the geological record is especially good.



Chapter 5 deals with the use of fossil plants in measuring past climates and environments, and although brief, is covered much better than in a number of other established text-books. This includes methods of analysis as well as examples from the fossil record, and provides a comprehensive introduction to this field. In Chapter 6 evolution and extinction are considered in detail, and biogeographical processes and patterns elaborated. Plant:animals relationships are considered in chapter 7, ranging from early terrestrial ecosystems to modern day studies. Dinosaurs have sneaked into the book (dinosaurs eating plants and not *vice versa*, sadly), but insects and mammals also get their place and tie in well with the botanical theme of the book.

The final two chapters become more synthetic and introduce modern floras and the origin and radiation of flowering plants, and finally in chapter 10, a brief summation section. This is worth reading, and sends you home with a happy, warm feeling.

On a more general note, the book is well produced, the quality of the text and illustrations are good. The inclusion of high-quality colour images makes the book stand out. A number of conceptual diagrams are included in addition to illustrations of fossil taxa, and these are comprehensive and well constructed. The subject index is good, but a real problem for the book is the lack of references, with only a handful of general reading sources provided. Individual ideas or concepts are not referenced, and as such, less informed readers would undoubtedly face problems locating additional reading materials should they be required.

For beginners in palaeobotany, the book makes a good read in the 'general interest' category, but you would at least have to like plants! The book clearly succeeds in communicating difficult



subjects, and makes the important transition from merely being an introduction to providing the essential background on the subject. The widespread use of similes assists explanations and succeeds in creating memory aids that are hard to dislodge. Although lots of terminology is used in the book, this is not done in a frightening way, and the text is accessible to all. Our conclusion is that this book gets the thumbs up for interested amateurs and undergraduates interested in palaeontology, botany and terrestrial ecology. For current research students the book also provides a good read and includes comprehensive synthesis of various different disciplines associated with the study of fossil plants. Linking of subjects is particularly impressive, providing a whole-system approach for issues that are all too often considered in isolation. The clear explanations, comprehensive use of simplified terms and also the construction of a matching glossary all add to the appeal of the book. As such this book also gets the thumbs up for research students in palaeobotany, botany, palaeontology and terrestrial ecology.

Finally, for the expert? Well, as it keeps all the other categories happy, that in itself is a good thing. Before this book there was an obvious gap in the market for an accurate short introductory book that can be recommended to others of various levels who are interested in the field. This book fills that niche, and does it well. Importantly, the concepts presented are not dated, and few cringe-worthy ideas have permeated its pages. As such, it can be recommended to a broad diversity of readers, but, to re-iterate, readers would at least have to like plants to open the pages. After reading this book, however, it is clear that palaeobotany still lacks a decent, comprehensive and recommendable student text (existing palaeobotany text books have various combinations of the following problems, being inadequate, inaccurate, dated, or out of print), and this hole in the market still exists. Notwithstanding, the *Living Past Series* never sets out to fill this gap, and *Fossil Plants* by Kenrick and Davis clearly achieves the aims of the Series. This book is important as it not only shows that fossils are interesting but also emphasises their importance to a diversity of other issues such as evolution, climate change, ecology and natural resources to name but a few. Worthy of adding to your collection, whoever you are, and hopefully will draw more people in to the subject. Well done to the authors, and it is clearly a publication that the Natural History Museum can be proud of.

On a final note, the addition of this title to the *Living Past Series* requires the Natural History Museum to modify the remit blurb for the series (see NHM website for details), adding fossil plants as well as fossil animals, or being all encompassing and changing the wording to cover 'fossil organisms'. After all, plants are rather nice and scientifically important as this book succeeds in telling us.

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Mammals from the Age of Dinosaurs. Origins, evolution, and structure

Zofia Kielan-Jaworowska, Richard L. Cifelli, and Zhe-Xi Luo. (2004). Columbia University Press, New York. ISBN 0-231-11918-6. \$195.00. £126.00 (hardback)

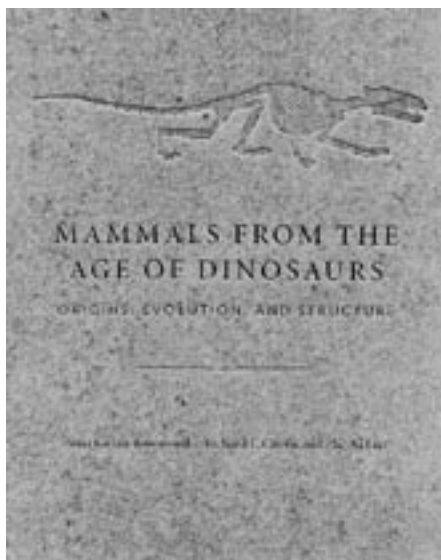
This book is a triumph; a magnificent summary and update of new knowledge about early mammals. Having made my view plain, I can now spend the rest of this review describing the book and encouraging you to ensure that your library has a copy, even if you are not personally entranced by early mammals. If you are looking for controversy, you are reading the wrong review.

The progenitor of this new volume was published a quarter of a century ago (Lillegraven *et al.* 1979) and much has changed. The fossil record on Mesozoic mammals has expanded by orders of magnitude, with discoveries pouring in from around the world. The results of new applications and techniques has also been dramatic. The field is changing so rapidly that the authors note that as soon as a chapter was drafted, a new discovery or phylogenetic analysis would require its complete revision.

Mesozoic mammals today, although still rare, are recognized as significant, rapidly-evolving constituents of their ecosystems. To quote the authors, "Mesozoic mammals have come into their own as an important, rich source of information for evolutionary biology in general ... they provide key information on the morphological transformations that led to modern mammals, including our own lineage of Placentalia." However, despite this wealth of new material, the times and origins of almost all major groups are still unknown. One of the most valuable functions of a compendium of this sort is therefore to draw attention to these gaps in our knowledge.

Unlike many previous compendium volumes, *Mammals from the Age of Dinosaurs* does not consist of chapters written by a variety of different experts in the field. Instead, this book was written entirely by the three authors, with separate chapters focusing on each different major group of Mesozoic mammals. This works very well, giving a useful consistency to a reference work of this scope. The information in the book, with minor exceptions, is based on published references, and the authors clearly note when they are expressing their own viewpoint. There are 15 chapters. The first three are of a general nature, followed by 11 chapters covering the different groups in detail. The concluding chapter is a general discussion of Mesozoic mammals and their relationships, followed by an appendix of cladistic characters and an extensive bibliography.

The introduction summarises major recent discoveries and the subsequent evolutionary bush of Mesozoic mammalian clades, with successive diversifications from the Late Triassic. The recent shift in thinking about Mesozoic mammal evolution is emphasised, with the understanding that the greatest





taxonomic diversification and morphological divergence tends to appear in the earlier periods of each major clade. The following chapter is titled “Distribution: Mesozoic Mammals in Space and Time”. This is a necessary update of that in the earlier compendium (Lillegraven *et al.* 1979), covering the geographical regions where important finds have been made, from the late Triassic through the Cretaceous. It is thorough and up to date, with clearly annotated maps, faunal lists and descriptions of sites. The third chapter deals with the biological characters associated with the origin of mammals. Inevitably this focuses on cranial and dental evolution, but the authors note that this does not merely reflect the paucity of postcranial remains as much as the relatively few derived postcranial skeletal characters diagnostic for mammals. Many functionally important features for modern mammals originated among mammaliaforms and are primitive for mammals.

The next 11 chapters each cover a different group of early mammals in detail, with a historical summary of work on the group, detailed discussions of anatomy, and sections on palaeobiology and systematic palaeontology. All these chapters follow the same convenient formula which allows easy reference and obviates any need for a detailed contents page. The systematic section is similarly well organised with a thorough compilation of known taxa and a useful source of references. Following diagnosis, taxa and distribution is a comments section, with notes on species or discussion of ambiguities with the referral of specimens. I feel there is a very even-handed treatment of the inevitable controversial specimens.

The final chapter deals with the major mammalian clades and their interrelationships. The challenge of compiling a comprehensive phylogeny that combines characters from different anatomical areas is a large one for early mammals, because many taxa are represented only by dental characters. A collateral study was therefore undertaken for the book (Luo *et al.* 2002) and a proposed phylogeny is adopted from this. The chapter also has a discussion of the inclusion of paraphyletic taxa used for historical reasons. The authors have adopted a broad-based definition of Mammalia that includes some extinct groups which lie outside the crown clade formed by monotremes, marsupials and placentals. This includes groups such as sinoconodontids, morganucodontids and docodontans on the basis that they are crucial to the interpretation of early mammals, regardless of whether they lie outside a definition restricting Mammalia to the mammalian crown group (Rowe, 1988; McKenna and Bell, 1997). I feel this is a very reasonable decision and characterises the common sense approach of this book. Commonly understood, although paraphyletic, groups such as “Symmetrodontans,” “Eupantotherians” and “Tribotherians” have therefore been included as separate chapters. There is, however, cross referencing of the placement of mammals of uncertain affinities, such as the Kuehneotheriidae.

The writing is admirably clear and precise, and the illustrations are well chosen with no obvious omissions. The illustrations are a mixture of diagrams from published work, original drawings from other workers or new artist reconstructions. They are all in black and white, as they are mainly from published work. A lack of colour illustrations is not an issue in this case, and has presumably helped to keep down the cost of the book. The index is thorough, and has not yet let me down in a search.

The book's one major drawback is its high price (\$195), but this is not unexpected for a technical book of this magnitude. The binding is good, as would be expected, and the book opens fully, showing no sign of pages coming adrift. I should have liked to have a dust cover, as the light brown cover marks very easily, but perhaps this should be seen as a rite of passage for a well used book.



A book with a similar title has been published hot on the heels of *Mammals from the Age of Dinosaurs*. This is *The Origin and Evolution of Mammals* by Tom Kemp (2005), which is an update on his 1982 *Mammal-like reptiles and the origin of mammals*. Kemp acknowledges that Professor Zofia Kielan-Jaworowska gave him access to the MS of *Mammals from the Age of Dinosaurs*, so there has been collaboration, not rivalry, between the authors. Kemp's book is organised according to a lecture series given to students at Oxford and differs in emphasis and scope (and also price, with a soft cover edition at £37.50!). There is a greater emphasis in Kemp's book on the evolution of the mammal-like reptiles and the radiation of mammals after the end of the Cretaceous, including molecular evidence. The section on Mesozoic mammals covers their diversity but also addresses their general biology. It is an excellent text and is a complementary, not alternative, volume to *Mammals from the Age of Dinosaurs*.

Mammals from the Age of Dinosaurs is a must-have for all workers on early mammals, and an essential reference for many others. It is appropriate for both advanced undergraduate and graduate students and any library serving vertebrate palaeontologists should have a copy. *Mammals from the Age of Dinosaurs* does an admirable job of presenting a clear picture of the current understanding of Mesozoic mammals. The book had a five year gestation, and the effort lavished on it is evident in its comprehensive coverage. To have brought together this wealth of up-to-date knowledge of early mammals within the covers of a single book is an impressive achievement.

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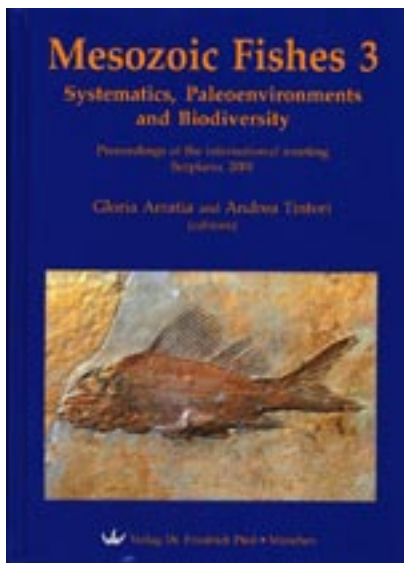


Mesozoic Fishes 3. Systematics, Paleoenvironments and Biodiversity Proceedings of the International meeting – Serpiano, 2001

Gloria Arratia, Andrea Tintori (editors) (2004). 649 pp., 19 colour and 277 b&w illustrations, Verlag Dr. Friedrich Pfeil. Hardcover ISBN 3-89937-053-8. [English]. €240.

This massively informative book contains 33 richly illustrated papers presented by 44 authors at a meeting in Serpiano in 2003. These contributions deal with various aspects of the palaeontology and evolution of all the major groups of gnathostom or jawed fishes that lived chiefly between 250 and 65 million years ago. Many papers also include accounts on the morphology and interrelationships of some living species of ray-finned and cartilaginous fishes, which makes this publication a valuable resource for both palaeontologists and biologists.

Two sister-books on Mesozoic fishes preceded this one (Arratia & Viohl, 1996; Arratia & Schultze, 1999) and the resulting trilogy has rapidly become a classic, a 'must have' series of publications in any good natural history library at universities and museums. Altogether, the three books in this series contain 1,828 pages, and many authors have contributed papers in two or three of these books.



This is a specialist publication, aimed primarily at the comparatively small world of fish palaeontologists, ichthyologists interested in biological evolution, and post-graduate students pursuing a career in palaeontology and phylogenetic systematics of lower vertebrates.

This is not an easy-reading textbook for undergraduates and the layman. At the cost of approximately £160, you will not see this publication in many private libraries, and it is not available in paperback. On the bright side, the editorial standards are topmost.

As with its predecessors, the book principally covers fish faunas from the northern hemisphere. Large gaps in palaeontological knowledge about the fish faunas of this geological era outside Europe and North America was pointed out by various authors in this book. There is, however, a

fair coverage of the geological record of Mesozoic fish faunas and characteristics of all major groups of Mesozoic fishes in five continents. It does not primarily provide updates on the geochronological and stratigraphic distribution of all Mesozoic fishes at genera and species level.

The impressively productive fish palaeontologist Gloria Arratia has obviously been the powerhouse behind the making of all the three volumes in this series. In her introduction to *Mesozoic Fishes 3*, she points out that the Mesozoic is when the modern fish fauna was established and during this Era the super continent Pangaea broke up. By the end of the Cretaceous, the distribution of land



and oceans originated the continental pattern familiar to us today. Strong evidence derived from vicariance biogeography indicates that the radiation of all the major lineages of continental fish faunas right through the Mesozoic and Early Cainozoic was influenced by the continental drift (e.g. Lundberg, 2000)

The predominant themes in *Mesozoic Fishes 3* are morphology and systematics, followed by descriptions of fish faunas and their putative palaeoenvironments as well as descriptions of new fossil taxa. Papers on bony fishes (Osteichthyes) predominate slightly over cartilaginous fishes (Chondrichthyes) in *Mesozoic Fishes 3*. None of the papers in this trilogy reports on any Mesozoic records of jawless vertebrates, which is not surprising since no post-Palaeozoic fossils of agnathan have ever been reported (see Halstead, 1993).

This book was dedicated to the late Barbara Jaffe Stahl, who contributed a chapter on the structure of the early chimaeroid (Holocephali) dentition.

Recently, there have been some criticisms of the uneven breadth and depth of the papers coming out in the proceedings of international conferences (e.g. Coates & Friedman, 2005). A feature of these volumes is that the precise nature and contents of the successive chapters cannot be predicted, unless papers are to be commissioned beforehand. It is indeed evident that, compared with the average contributions, some papers in this book as well as in its predecessors stand out as being more encompassing in terms of taxonomic and biostratigraphic coverage.

What are, then, the main specific themes explored by the various authors in *Mesozoic Fishes 3*?

In her paper about chimaeroid early dentitions, Barbara Stahl argues that the earliest securely identified fossils of this group of marine chondrichthyans come from the Early Jurassic, and the origin of the Holocephali is likely to be in the Triassic. Consequently, this would indirectly exclude the Late Palaeozoic Petalodonta from Holocephali, contrary to the view of some earlier authors (e.g. Zangerl, 1981). Stahl favours the elasmobranchs as the rootstock of all holocephalans and follows Patterson (1965) in considering the group monophyletic.

Maisey, Naylor & Ward focused on Mesozoic elasmobranchs, neoselachian phylogeny and the rise of modern elasmobranch diversity, suggesting that extinction has played an important role in the early stages of evolution of this group. They also found that there continues to be non-congruence between phylogenies based on molecular and morphological data of fishes of this clade. They predict that this conflict between results produced by genomics and phylogenies deduced from morphological characters will remain and proliferate in the future. This is because different genes “yield different signals from one another” and the “independent morphological characters will be found to be affected by developmental mechanisms” (p. 46). This stance may help reconcile the apparently discrepant methodological outcomes, since we know virtually nothing about the phenotypic plasticity of the genome throughout the geological time. They advise against combining results from these distinct methodologies, suggesting instead that a potentially more informative approach would be to investigate how each molecular dataset behaves when it is adjusted to the alternative phylogenetic trees and then try to determine what biological processes may be causing the distinct results.

Maisey *et al.* compared six hypotheses of neoselachian phylogenies and demonstrated that they heavily influence estimates of taxon longevity. They also argue that hybodontiformes and



neoselachians are probably monophyletic groups and that the former is the extinct sister-group of the neoselachians; furthermore, that together they constitute the monophyletic group of the elasmobranchs.

Several authors dealt with rays. Kriwet investigated the phylogenetic position of Cretaceous sclerorhynchid sawfishes, providing a comprehensive historical background and re-evaluation of their taxonomic characters. He concluded that Sclerorhynchidae is a monophyletic batoid group and created the order Sclerorhynchiformes. A new genus of platyrhinid ray from the Cretaceous of Italy was described by Carvalho, who points out that the Nardò deposits are the only Tethian deposits of Campanian/Maastrichtian age where articulated remains of fishes have been found to date. He provides excellent anatomical comparisons with extant species of *Platyrhina*.

The systematic position of Lebanese Rhinobatoidea from the Cretaceous, on the other hand, was investigated by Brito & Dutheil, and their analysis suggests that these fishes, together with the rajids, are the sister group of the torpediniforms, but the affinities between these fishes remain unresolved.

Underwood & Ward tackled the environmental distribution of Bathonian neoselachians in southern England. Their study – which includes data on Palaeospinaciforms, Hexanchiformes, Heterodontiformes, Orectolobiformes, Carcharhiniformes and Protospinaciformes – throws light on the distribution of neoselachian remains from fully marine through lagunal facies. This distribution possibly reflects their palaeoecological preferences.

Some papers concentrated on morphological and anatomical issues. Grande competently dwelled on distinctions between different kinds of morphological characters. He categorized them into taxonomic, ontogenetic and individual variations, concentrating on the latter. He exemplified the matter with characters in *Amia*, *Polyodon* and extinct genera. Micklich & Klappert exploited the putative intra-specific variations of two Middle Eocene fishes from Messel, and concluded that at least one new genus and species can be safely distinguished. However, most of the specimens ascribed to *Thaumaturus* and *Atractosteus* coming from that site are better understood as part of morphotype complexes.

Poplin revisited the problem of nomenclature and homology of the dermal skull of early actinopterygians, focusing on the dermosphenotic. She suggested that three main, non-random morphological patterns for this bone could be found among the 83 genera considered in her paper. Two of these patterns show ten topologically-defined differences. Some of them, at least, are apparently congruent with the distribution of those genera within higher taxonomic ranks as defined by recent authors.

Lombardo & Tintori gave a detailed description of a new deep-bodied Perleidiformes from the Triassic of Germany, and Mutter critically re-evaluated the family Colobodontidae emending its diagnosis. The morphology of another lower actinopterygian fish, namely *Coccolepis bucklandi* Agassiz from Solnhofen, was assessed in very great detail by Hilton, Grande & Bemis, who reviewed the diagnosis of the species emphasizing the striking presence of posteriorly-directed dermal denticles on various exo-skeletal elements of this fish.

Halecostom osteichthyans were discussed by many of the authors. Bürgin described a new Triassic semionotiform fish from the Triassic of Switzerland and Gallo & Brito gave an overview of the Brazilian semionotiforms, pointing out the abundance of remains of this group of fishes in Western



Gondwanan rocks of both marine and continental origins. Gonzalez-Rodriguez and Reynoso report on a new species of macrosemiids from the Albian of Mexico. It belongs to *Notogogus*, a genus previously described from Europe, which suggests that the group enlarged its palaeogeographic distribution following the aperture of the northern part of the Atlantic Ocean.

Arratia provided an in-depth evaluation of Mesozoic halecostoms' systematics and the early radiation of teleosts, and showed that there is still wide fluctuation in the position occupied by major actinopterygian groups in different phylogenetic schemes proposed recently. Furthermore, she has shown that the results of the analyses are highly sensitive to the choice of taxa. The data gathered by that author also suggests that there was apparently constant replacement of teleostean fish faunas since their humble appearance in the Late Triassic.

Nursall & Capasso went on presenting an extremely odd-looking new deep-bodied bony fish from the Cenomanian of Lebanon. A good palaeobiological account is given, together with a cladistic analysis of the new taxon.

Poyato-Ariza & Wenz reported on yet more deep-bodied fishes, this time from the Lower Cretaceous of Spain. Their morphological description of the new genus *Turbomesodon* is very detailed and richly illustrated, supporting their phylogenetic analysis of 89 characters for 23 ray-finned taxa.

Liston provided an historical view on the knowledge about the huge pachycormiform *Leedsichthys* and Zaragüeta Bagils explored the phylogeny of ellimmichthyiform teleosts.

The detailed three-dimensional structure of the skull of a primitive herring-like fish from Lebanon was presented by Forey, who also assessed the interrelationships between ellimmichthyiforms and clupeiforms, specially considering the development of the accusticolateralis system in both groups.

Grande & Pinna provided a richly illustrated account of the Weberian apparatus of teleosts, and brought new interpretation of homologies of bones within this bony complex. They discuss the phylogenetic implications of these new interpretations.

A new teleost from the Albian of Canada was described by Hermus, Wilson & Macrae. The fish is enigmatic in bearing mid-lateral scutes. Wilson & Bruner also gave a comprehensive review of Mesozoic fish assemblages of North America.

Schultz gave an excellent overview of the distribution and distinctive features of the only two groups of sarcopterygian fishes, namely Actinistia and Dipnoi, which survived into the Mesozoic and beyond. Cavin & Forey, on the other hand, described a new actinistian fish from Morocco.

A 'Purbeck-Wealden' type of ichthyofauna from Denmark was presented by Bonde, and Karatajute-Talimaa & Katinas developed a stratigraphic correlation scheme of Triassic formations in the Baltic region of Germany, Poland and neighbouring areas based on microvertebrates.

Asian faunas from the Mesozoic were dealt with by Chang & Miao in a very informative paper focusing on the most productive localities in China and other countries. Yamagishi reported on microvertebrate remains from the Lower-Middle Triassic of Japan.

Gondwanan fish faunas from the Mesozoic (except Madagascar and India) were presented by López-Arbarello, whilst Mesozoic fishes from India were reported by Prasad, Manhas & Arratia.



The possible feeding modes of Mesozoic fishes are explored by Belwood & Hoey using analyses of functional morphospace and implications for the radiation of fishes.

The last thing to say about *Mesozoic Fishes 3* is that it will not be the ultimate book on Mesozoic Fishes for much longer. It needs to be seen in perspective, as it is only the latest issue in this already classic series of publications, the natural follow up to *Mesozoic Fishes* (Arratia & Viohl, 1996) and *Mesozoic Fishes 2* (Arratia & Schultze, 1999). As you read this review, fish palaeontologists around the globe will be finishing writing up their contributions to the 4th Meeting on Mesozoic Fishes to take place in Spain in August this year. A new volume of this series is therefore bound to appear in the near future. It is in the nature of this series of books to be varied in contents, to be highly regarded scientifically and to be very well produced.

We can be certain to continue to find in books of this series a wealth of new palaeontological information, visually appealing illustrations and a lot of conflicting or unresolved phylogenies for a long time to come. Long live the *Mesozoic Fishes* series!

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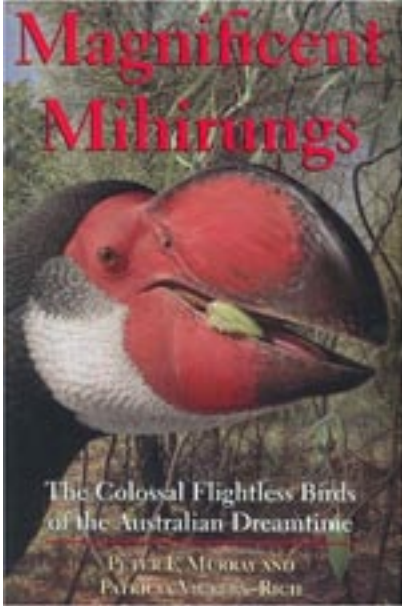
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Magnificent Mihirungs. The Colossal Flightless Birds of the Australian Dreamtime

Peter F. Murray and Patricia Vickers-Rich. 2004. Indiana University Press, Bloomington, Indiana. 410 pp. ISBN 0253342821. £57.00



This is an excellent book – a great read that will surely become a classic in the palaeontological literature, especially if your interests lie in fossil birds or generally in anatomy, systematics and the evolution of terrestrial ecosystems. The illustrations are excellent and the book is well-produced throughout; well-recommended! What's it all about?

In *Magnificent Mihirungs* Murray and Vickers-Rich provide a comprehensive survey of Dromornithidae, an extinct group of flightless birds known from the Eocene to Pleistocene of Australia (including Tasmania). This group includes some of the very largest birds that ever lived (like the massive, 570 kg *Dromornis stirtoni*); bizarre and mysterious fast-running browsing herbivores that roamed Australia's forests until forced to extinction in the Pleistocene, about 50,000 years ago, by human interference and forest fires. One reason that dromornithids are

fascinating is that prior to the appearance of this book, very little information was available about them – as noted by Murray and Vickers-Rich, a large proportion of the previous literature pertaining to these birds was published between 1896 and 1913 by the Australian palaeontologists Stirling and Zietz. Happily for us, many of the superb illustrations originally presented by these workers are reproduced in *Magnificent Mihirungs*, the originals not being widely available, at least in Europe.

Another cause of 'dromornithid fascination' (at least for me) is the issue of their evolutionary relationships. For more than 100 years – these birds were originally described by Richard Owen in 1874 – mihirungs were considered to be palaeognaths, putatively related to emus and cassowaries. Indeed, the colloquial name 'mihirung', first used by Rich (1979), is based on the Aboriginal word for emu. Skull material described in the 1990s, however, led to the alternative hypothesis that dromornithids are Anseriformes (see also Olson, 1985), giant representatives of the group that also includes the living screamers, ducks and geese. This is the reason that Murray and Vickers-Rich refer to dromornithids throughout the book as 'giant geese', an unfortunate and misleading simplification. This issue of relationships is one great unanswered question that *Magnificent Mihirungs* does not confidently address – one is left with little more understanding than readings of the earlier literature. I concur with Olson (2005): what's the evidence for the anseriform affinities of these birds? More importantly, I was left unconvinced that the monophyly of Dromornithidae can be demonstrated convincingly on the basis of the known material.



One giant quibble with this book – before coming back to the meat of the text – is that Murray and Vickers-Rich now consider the anseriform affinities of these birds to be self-evident; a fact that surely should have been noted by earlier anatomists such as Owen, Stirling and Zietz (!?). Quotes to this effect on pages 59–60 make it clear that Murray and Vickers-Rich cannot believe that the relationships of these ‘giant geese’ were not noticed earlier, even though it was the work of Rich (1979) that continued to perpetuate this hypothesis.

Magnificent Mihirungs is well-organised and, as I have mentioned, very well-executed. There are four large sub-sections: “Discovery” deals with the collection history of these birds subsequent to the 1870s; “Systematics and Morphology” deals with the morphology and evolutionary relationships of these birds (as well as their palaeontology); “Paleobiology” deals with inferences of dromornithid functional morphology, body-mass estimation and biomechanics; and “Paleoecology”, a section that discusses, in some detail, the fauna presumably associated with these birds, and their history in the context of the palaeoecology of Australia since the Eocene.

The idea to write this book was a great one – dromornithids are little known and Murray and Vickers-Rich’s *Magnificent Mihirungs* is an invaluable addition to the field. Of the questions raised, however, many are open-ended, although an exhaustive compendium of these birds would have been too much to expect. A work in progress. I echo the sentiments of Olson (2005) with a direct quote: “my sincere hope is that, in another decade, knowledge of dromornithids will have advanced so far as to merit a reissue of this work in which all the new information can be incorporated and all the flaws of the present edition corrected. This might then become one of the great classics in both ornithology and paleontology”. There is no better way to put it. I’d love to live in Australia just to get the chance to work on these birds!

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