Organ system development in recent lecithotrophic brachiopod larvae

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Published in:
Geological Society of Australia. Abstracts Series

Publication date:
2010

Document version
Publisher's PDF, also known as Version of record

Citation for published version (APA):
Altenburger, A., Martinez, P., & Wanninger, A. W. G. (2010). Organ system development in recent lecithotrophic brachiopod larvae. *Geological Society of Australia. Abstracts Series*, 3-3.

Geological Society of Australia

ABSTRACTS

Number

95

6th International Brachiopod Congress

Melbourne, Australia
1-5 February 2010

Geological Society of Australia
Abstracts 95

6th INTERNATIONAL BRACHIOPOD CONGRESS
2010 - Melbourne

Program & Abstracts

Editors: Guang R. Shi, Ian G. Percival,
Roger R. Pierson and Elizabeth A. Weldon

Geological Society of Australia Abstracts Number 95

6th International Brachiopod Congress, Melbourne, Australia, 1-5 February 2010
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ISSN 0729 011X

Recommended citation for this volume:

Shi, G.R., Percival, I.G., Pierson, R.R. & Weldon, E.A. (editors). Program & Abstracts, 6th International Brachiopod Congress, 1-5 February 2010, Melbourne, Australia. *Geological Society of Australia Abstracts* No. 95.

Example citation for papers in this volume:

Weldon, E.A. & Shi, G.R., 2010. Brachiopods from the Broughton Formation: useful taxa for the provincial and global correlations of the Guadalupian of the southern Sydney Basin, eastern Australia. In: *Program & Abstracts, 6th International Brachiopod Congress, 1-5 February 2010, Melbourne, Australia; Geological Society of Australia Abstracts* 95, 122.

Copies of this publication may be obtained from:

Geological Society of Australia
Suite 61, 104 Bathurst St
Sydney, NSW 2000, Australia
or online at: **www.shop.gsa.org.au**

Congress logo design: Ms D. Zhong and Dr. Z.Q. Chen
Printed by: Deakin University, Melbourne Campus, Burwood, Victoria 3125, Australia

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PREFACE

Welcome to the 6th International Brachiopod Congress (6IBC) being held at the Holmesglen Conference Centre from 1-5 February, 2010, in Melbourne, Australia. With over 90 scientists from around the world attending the congress, we are able to offer an exciting program including six special symposia each named after a distinguished brachiopodologist and one open session, six associated field trips, as well as an ice breaker and a congress dinner.

A total of 119 abstracts, submitted by 169 authors from 30 different nations, have been received and are included in this volume. The contributions highlight new and exciting discoveries, as well as theoretical and methodological advances that have taken place in the field of brachiopodology since the last International Brachiopod Congress held in Copenhagen in 2005. The abstracts for oral presentations are grouped in the six special symposia and one open session. Abstracts for posters have not been differentiated into specific sessions or themes to encourage broad viewing.

We are extremely grateful to our congress sponsors: Deakin University (especially its Faculty of Science and Technology and School of Life and Environmental Sciences), the Association of Australasian Palaeontologists (AAP), the Geological Society of Australia, the International Palaeontological Association (IPA), the Williams family (for the Alwyn Williams Fund), the Brunton/Cooper Family, and Mrs Linda Archbold. The generous support of the last three family sponsorships has enabled 10 brachiopod workers, mostly PhD students and early career brachiopodologists, to attend this congress.

Much appreciated has been the sustained enthusiasm and support of colleagues who have organised and convened the six special congress symposia and one open session, and those who have organised and lead the mid- and post-congress excursions in Australia and New Zealand (three one-day mid-congress excursions in Victoria; two week-long post-congress excursions in New South Wales, and one week-long field trip to New Zealand).

Numerous individuals (staff, students and friends) from Deakin University in the Melbourne Campus have provided great support to the organisation and successful delivery of the congress in many different ways: finances, communication and publicity, transportation, and assistance with visa application and itinerary booking.

As the 6IBC Convenor I would like to express my deep appreciation to all members of our Organising Committee and my co-editors of this volume, for their sustained support, timeless effort and immense personal support to me throughout the past 12 months. In particular, I feel deeply indebted and very grateful to Dr. Elizabeth (Liz) A. Weldon, our dedicated 6IBC Secretariat, and Mr. Roger Pierson, our Financial Manager, who have jointly carried and skilfully managed the most challenging aspects of the congress organisation.

Finally, I would like to thank all participants for your interest in and support for the congress. It is with great anticipation that I invite you all to peruse this volume and to enjoy the full range of activities, both technical and social, offered by the congress and its associated field trips.

Professor Guang R. Shi
Chair, 6th IBC Organising Committee
Deakin University, Melbourne, Australia

6th IBC Sponsors

Deakin University

Association of Australasian Palaeontologists (AAP)

Geological Society of Australia

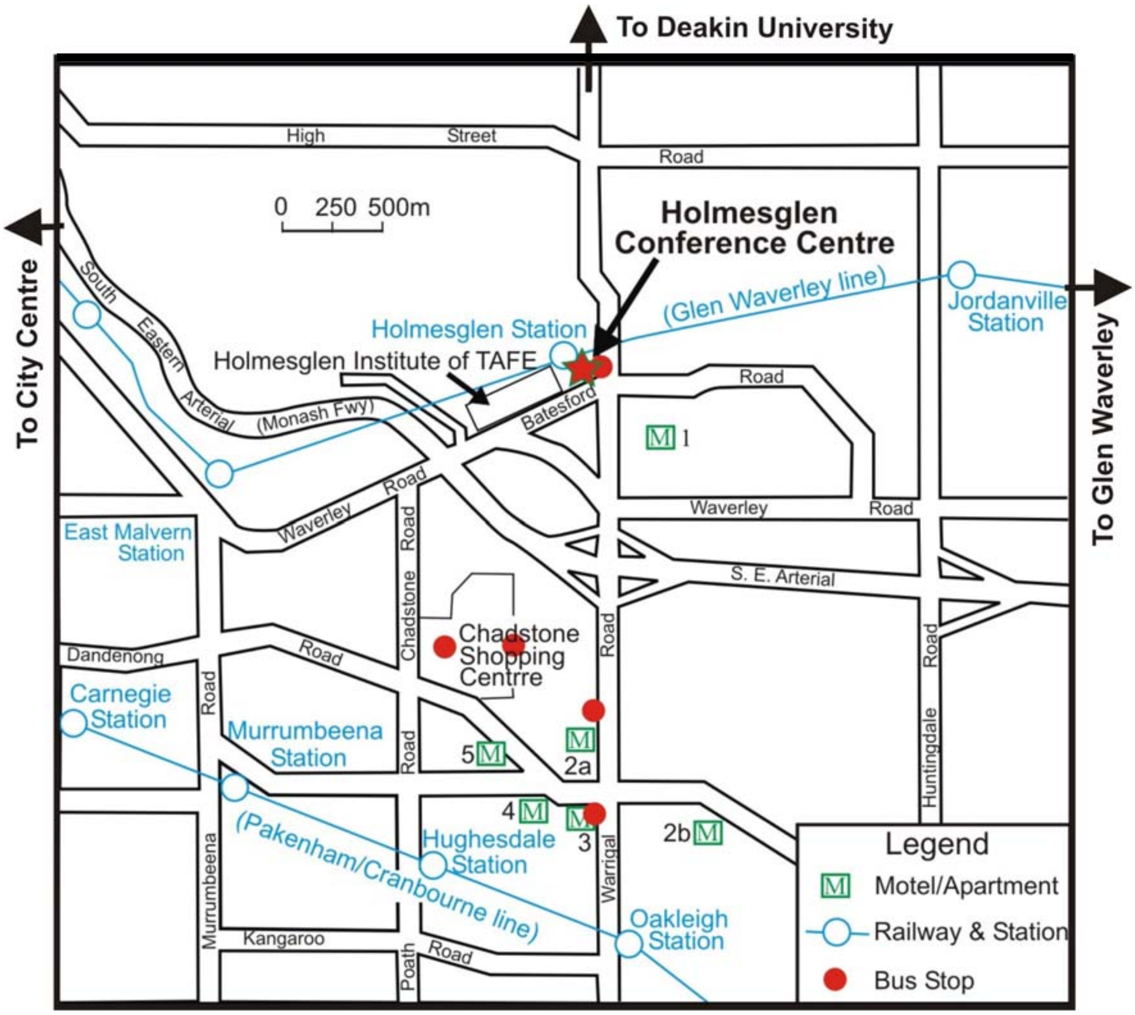
International Palaeontological Association (IPA)

Mrs Linda Archold **Brunton/Cooper Family**

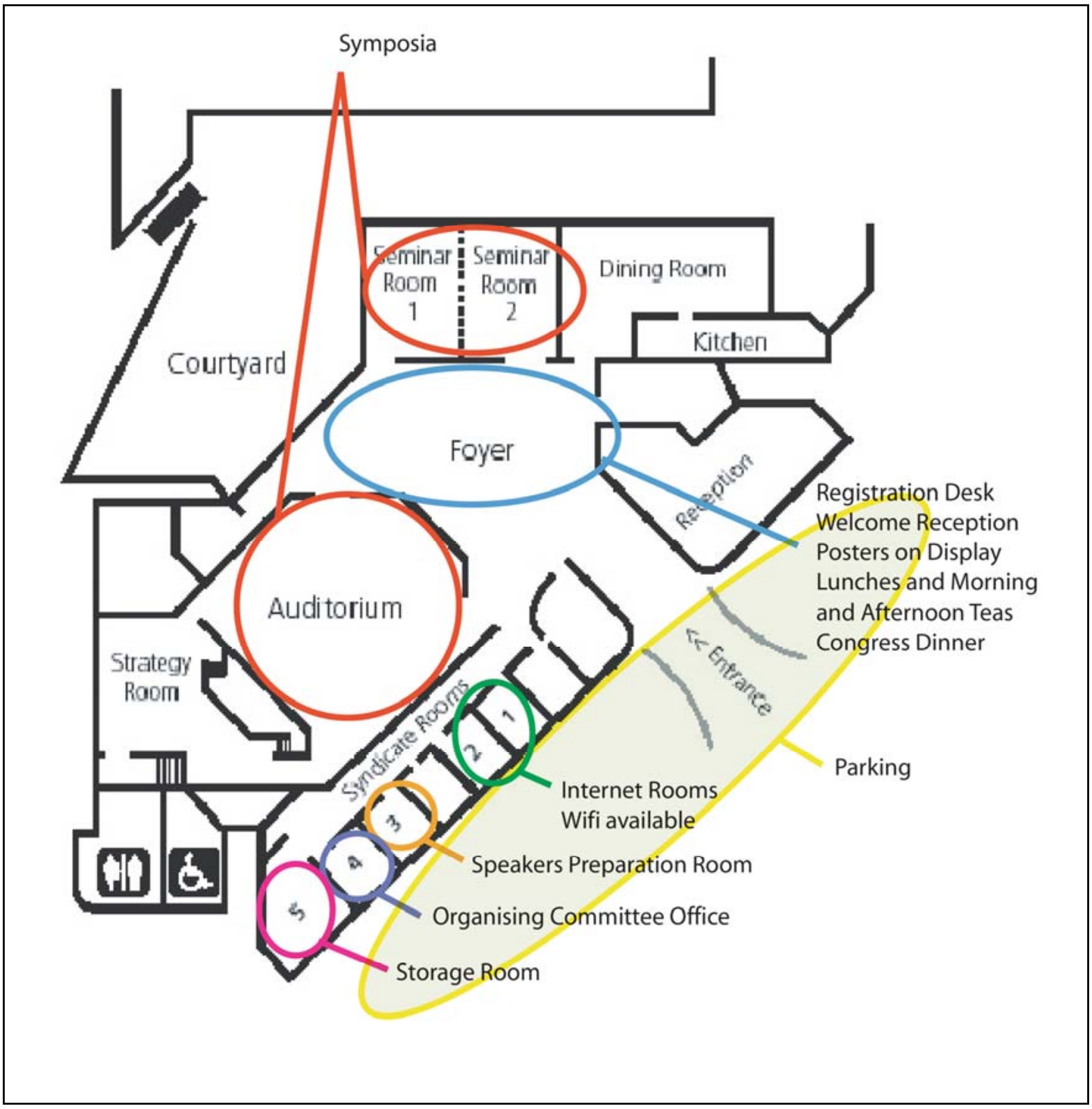
Alwyn Williams Family (Alwyn Williams Fund)

6th IBC Organising Committee

Prof. Guang Shi	Committee Chair, Deakin University, Australia
Dr Glenn Brock	Macquarie University, Australia
Dr Monica Campi	Geoscience Victoria, Melbourne, Australia
Dr Zhong-qiang Chen	The University of Western Australia, Australia
Dr Gordon Curry	'Alwyn Williams Fund' selection panel chair, University of Glasgow, Scotland
Dr Norton Hiller	Canterbury Museum, New Zealand
Mr Higo Jasser	Webmaster, Deakin University, Australia
Assoc. Prof. Daphne Lee	University of Otago, New Zealand
Dr Ian Percival	Geological Survey of New South Wales, Australia
Mr Roger Pierson	Finance Manager, Deakin University, Australia
Dr Mark Warne	Deakin University, Australia
Dr Elizabeth Weldon	Congress Secretariat, Deakin University, Australia



Map 1: Location of the Holmesglen Conference Centre, suggested accommodation and public transport.



Map 2: Floor map of the Holmesglen Conference Centre, showing location of rooms for the various congress activities.

THE VENUE

The Holmesglen Conference Centre is conveniently located just 30 minutes by train east of Melbourne's city centre (see Map 1 on page vi). The Centre provides all the amenities required for our congress activities (see Map 2 on page vii), please familiarise yourself with the location of rooms for the various congress activities.

REGISTRATION AND HELP DESK

Registration is to be held in the foyer of the Conference Centre (see Map 2) and will be open on Sunday 31 January 2009 between 6-8pm and again on the following Monday from 8.30-9.30am. **Mrs Robyn Cook** will be available at the registration desk throughout the congress to answer any questions in relation to the congress and other general inquiries.

Each registrant will be given a **named congress satchel** containing various items, including the combined congress Program and Abstracts volume, vouchers for drinks and the congress dinner, as well as tax receipts for your registration, depending on each participant's details of registration. Therefore, we advise that you check the name badge on the back side of the satchel to make sure you get the correct satchel and content.

To make contact with the IBC Secretariat directly please leave an email at 6IBC2010@gmail.com, or during business hours on 1-2 and 4-5 February please phone: +61 3 95648417. Alternatively a message may be left anytime from 1-5 February by contacting the Holmesglen Conference Centre Reception by phone: +61 3 95641500 or fax: +61 3 95641940 or email: confcentre@holmesglen.edu.au.

TRANSPORTATION TO THE HOLMESGLEN CONFERENCE CENTRE

Train: The Glen Waverley line, stopping at Holmesglen railway station and located adjacent to the Holmesglen Conference Centre (see Map 1 on page vi).

Car: Free car parking is available in front of the Conference Centre. Entry is via a boom-gate at Gate 1 on Batesford Road. Please contact the Secretariat in advance for the boom gate number if you will be using the car park.

NB: Bus and train timetables and fares are available from www.metlinkmelbourne.com.au

ORAL PRESENTATIONS

The duration of keynote presentations is 30 minutes, including questions and discussion time. All other presentations will be 20 minutes in length, including questions and discussion time. Presentations should be prepared in MS PowerPoint 2003 or newer versions. Only single screen projection is available. A data projector is also available. Please advise us in advance if you wish to use the data projector or require any other audio-visual equipment (e.g. a movie). Session Convenors are asked to keep strictly to time.

Syndicate Room 3 (see Map 2 on page vii) has been reserved as a **'speakers' preparation room',** with a technical assistant (**Mr Higo Jasser**) available for assistance and several computers available to check that your presentation works. We ask all speakers to preload, between 8-9am on each of the congress presentations days, their PowerPoint presentation file directly to the computer in your theatre assigned for your presentation, with a uniquely identified file name, which should include the speaker's last name, session/symposium number and time (e.g., **Jasser-T2-945am.PPT**).

POSTER PRESENTATIONS

All posters will be displayed throughout the congress in the foyer of the conference centre. Each poster has been given a number (see page xiv). We ask poster presenters to put up their posters between 8.30-9.30am in the morning of 1 February 2010. The posters should be mounted to the correct poster board, each of which has also been numbered to match the number of posters listed in page xvii of this volume.

Although posters can be viewed throughout the congress week especially during refreshment times, we have scheduled a **poster session** between 3-4.30pm on Thursday 4 February to encourage interactions between poster presenters and viewers. We therefore ask poster presenters to stand by your poster for at least half of this poster session. All posters should be removed between 3.20-3.40pm on Friday 5 February.

RECEPTION (ICE BREAKER)

The welcome reception will take place between 6-8pm on Sunday 31 January in the Foyer at the Holmesglen Conference Centre. Come along and catch up with old friends, make new acquaintances, and sample some Aussie beer and wine. The welcome reception is included in the registration fee. All registrants will be provided with two complementary drink vouchers that can be exchanged for a soft drink, a beer or a glass of wine at the bar. A cash bar will be available for the purchase of any additional drinks that you may require.

CONGRESS DINNER

At 7pm on Thursday 4 February a three course dinner will be held at the Holmesglen Conference Centre. Pre-dinner drinks will be served from 6.30pm. If you have paid for the congress dinner, please bring your dinner voucher enclosed in your registration satchel. Registrants for the dinner will each be provided with a complementary pre-dinner drink voucher which can be exchanged for a soft drink, a beer or a glass of wine at the bar. Drinks will also be served during dinner and a cash bar will be available for additional purchases. The dress code will be smart casual attire (shirt, no tie required).

Our special guest speaker for the Congress dinner is Professor David Harper, a well known brachiopodologist and also President of the International Palaeontological Association. Professor Harper's address is titled: "*30 years on: has the human face of the brachiopod changed?*"

REFRESHMENTS AND LUNCHES

Morning and afternoon teas as well as lunches are provided and will be held in the foyer at scheduled times.

PHOTOGRAPHY

A photographer will be at this event to take photographs for potential use in future Deakin University publications and promotional materials as well as for IBC materials. Please advise the Secretariat prior to the beginning of the Congress if you do not wish your photograph to be taken. Also at 10.10am on Thursday 4 February a group photograph will be taken at the Holmesglen Conference Centre, which we intend to include in the Congress Proceedings. Please wait for instructions from Deakin University's photographer in the foyer area.

COMMUNICATIONS SERVICES (PHONES, LAPTOPS AND INTERNET ACCESS)

Several computers with internet connections are available in Syndicate Room 2. In addition, WIFI wireless internet access is also available within the conference centre through self-paid online subscription. Please have your mobile phones switched off during sessions and refrain from using laptops in the conference rooms during sessions.

ASSOCIATED BUSINESS MEETINGS AND GROUP GATHERINGS

The Association of Australasian Palaeontologists (AAP) will hold its Annual General Meeting between 5.30-7.30pm on Tuesday 2 February in Seminar Room 1. All are welcome to attend. Coffee and tea will be provided.

EMERGENCY CONTACTS

If you require police, ambulance or fire brigade in an emergency, please phone: 000. If you require police, ambulance or fire brigade in an emergency and you are using a GSM digital mobile phone which is out of range of your service provider, displays a message indicating emergency calls only, or does not have a SIM card, try 112.

LITERATURE SALES AND EXCHANGE

For the duration of the Congress a table will be set up for reprint exchange. Please bring along items (including copies of your reprints, literature you no longer require, CDs containing pdfs, etc) that may be of interest to brachiopod workers

EDITORIAL CHANGES TO ABSTRACTS

As editors of this volume, we have carried out minimal but necessary editorial changes to ensure a consistent format and language standard.

DISCLAIMERS

Disclaimer 1: This publication is not valid for taxonomical and nomenclatural purposes (based on Recommendation 8E, of Article of 8.2 (Chapter 3), of the ICZN 4th Edition, available online: http://www.iczn.org/iczn/index.jsp).

Disclaimer 2: Neither the Holmesglen Conference Centre nor the organisers of the congress accept responsibility for injury, accident, illness or death to, or financial loss by, any person attending the congress or its associated field trips, whatever the reason. All insurance is the responsibility of individual registrants.

Congress Program

The Congress program is set out below. First authors' surnames are given. Where the presenting author differs from the first author, the presenter's name is given in brackets. Please note that there are two concurrent sessions on Monday 1 February and Thursday 4 February.

	Sunday 31 January
6.00 - 8.00pm	**Welcome Reception and Registration** **[FOYER]**

	Monday 1 February	
8.30-9.30am	**Registration (Display posters) [FOYER]**	
9.30-9.40am	**Opening Remarks: Prof. Guang R. Shi, Chair 6th IBC Organising Committee [AUDITORIUM]**	
9.40-10.00am	**Welcome: Prof. Lee Astheimer, Deakin University Deputy Vice Chancellor (Research) [AUDITORIUM]**	
10.00-10.10am	**Congress Logistics: Dr Liz Weldon, Secretariat 6th IBC [AUDITORIUM]**	
10.10-10.30am	**Morning Tea [FOYER]**	
10.30am-5.00pm	**T1: Neil Archbold Symposium** **CONVENOR: Prof. Shuzhong Shen** **[AUDITORIUM]**	**T3: G. Arthur Cooper Symposium** **CONVENORS: Prof Sandra J. Carlson and Assoc. Prof. Daphne E. Lee** **[SEMINAR ROOMS 1 & 2]**
10.30-11.00am	**Waterhouse (KEYNOTE):** *The origin and composition of Australian Permian brachiopods*	**Carlson & Lee (KEYNOTE):** *In the loop - 400 million years of Terebratulide evolution: a tribute to G. Arthur Cooper*
11.00-11.20am	**Shen:** *Palaeoclimatic fluctuations implied by faunal changes near the Permian-Triassic transition in the peri-Gondwanan region*	**Tomasovych:** *Evolutionary changes in brachiopod body size during the Mesozoic*
11.20-11.40am	**Shi:** *Neil Archbold: his contributions to brachiopodology and the studies of the global Permian System*	**Chen ZQ:** *Impact of Permian icehouse-greenhouse climatic changes on benthic ecosystems: Brachiopod's fossil record from high-latitude to tropic regions*
11.40-12.00am	**Angiolini:** *Guadalupian brachiopod faunas from Tunisia, Turkey and North Iran and their implications for correlations across the Neo-Tethys*	**Balthasar:** *Cambrian origins and transitions in the evolution of the brachiopod shell*
12.00-12.20pm	**Li WZ:** *Cancrinella and Costatumulus (Brachiopoda) from the Permian of South Mongolia and South China: their morphology, biostratigraphy and distribution*	**Bitner:** *Cave brachiopods from the Upper Oligocene of south-western France – a missing element in European Tertiary faunal history*
12.20-1.20pm	**Lunch [FOYER]**	
1.20-1.40pm	**He:** *Brachiopod miniaturization and productivity decline during the Permian-Triassic crisis in South China*	**Chen J:** *Brachiopod diversification during the benthic recovery following the end-Permian mass extinction*

1.40-2.00pm	**Cisterna:** *Permian brachiopod faunas of northern Chile*	**MacFarlan:** *A survey of the Mesozoic brachiopods of Misool Archipelago, eastern Indonesia*
2.00-2.20pm	**Pagani:** *The Cisuralian faunal succession in Patagonia*	**Manceñido:** *Late Triassic brachiopods from Western Argentina and their significance*
2.20-2.40pm	**Tazawa:** *Permian brachiopod faunas of the Mino Belt, Central Japan, and its provincial relationship with that of West Texas, USA*	**Mergl:** *The Poramborthis and Poramborthidae puzzle: new data*
2.40-3.00pm	**Chen ZQ:** *When did bivalves take over brachiopod's world? New observation to an old question*	**Dulai:** *Paleogene brachiopods from the Late Eocene of Austria and the Oligocene of Hungary*
3.00 - 3.20pm	**Afternoon Tea [FOYER]**	
3.20-3.40pm	**Zhang Y:** *Diversity variation of brachiopods from the Late Permian (Lopingian) deep-water facies of South China*	**Chen XQ:** *Late Devonian brachiopods from the Junggar Basin, northwest Xinjiang, China*
3.40-4.00pm	**Ganelin:** *Brachiopods in the Late Palaeozoic benthic biota of Northeast Asia*	**Chen ZQ:** *Permian-Triassic evolution of brachiopod faunas: mass extinction, recovery, body size dynamics, community structural changes, and climatic zone's controls*
4.00-4.20pm	**Weldon:** *Brachiopods from the Broughton Formation: useful taxa in the provincial and global correlation of the Guadalupian of the southern Sydney Basin, eastern Australia*	
4.20-4.40pm	**Mii:** *Carbon and oxygen isotope records of Permian brachiopods from the southern Sydney Basin and Tasmania in southeastern Australia and their palaeoenvironmental implications*	
4.40-5.00pm	**Biakov:** *Permian brachiopods and bivalves of Northeast Asia: a competition before the great end-Permian mass extinction*	
5.00pm	**Close**	

Tuesday 2 February	
9.00am-5.10pm	**T2: Howard Brunton Symposium [AUDITORIUM]** **CONVENOR: Dr A. Pérez-Huerta**
9.00-9.30am	**Angiolini (KEYNOTE):** *What the morphology and shell structure of Permo-Carboniferous brachiopods from the Western Palaeotethys/Neotethys can tell us about palaeoecology and palaeoclimate?*
9.30-9.50am	**Rong:** *Early evolution of eospiriferines through Late Ordovician and Early Silurian*
9.50-10.10am	**Popov (Holmer):** *New insights on the ontogeny of Early Palaeozoic rhynchonelliform brachiopods: implications for brachiopod phylogeny*
10.10-10.30am	**Schemm-Gregory:** *The phylogeny of delthyridoid spiriferids - a new interpretation*

10.30-10.50am	**Morning Tea [FOYER]**
10.50-11.10am	**Kuzmina:** *Periesophagal coelom: a new division of the coelomic system and a possible site of ultrafiltration in the articulate brachiopods*
11.10-11.30am	**Waterhouse:** *Ordinal classification for Brachiopoda*
11.30-11.50am	**Taboada:** *Taxonomic review and evolutionary trends of Levipustulini and Absenticostini (Brachiopoda) from Argentina: palaeobiogeographic and palaeoclimatic implications*
11.50am-12.10pm	**Cisterna:** *Morphology and systematics of Late Palaeozoic Syringothyrids from West-Central Argentina*
12.10-12.30pm	**Madison:** *Patterns of cardinal development of some Ordovician articulated brachiopods*
12.30-1.30pm	**Lunch [FOYER]**
1.30-1.50pm	**Malakhov:** *Brachiopods and phoronids are true metameric animals*
1.50-2.10pm	**Pakhnevich:** *Micro-CT investigations of recent and fossil brachiopods*
2.10-2.30pm	**Altenburger:** *Organ system development in Recent Lecithotrophic brachiopod larvae*
2.30-2.50pm	**Alvarez:** *Early Palaeozoic diversification of European "smooth" Athyrididines and their affinities*
2.50-3.10pm	**Carlson:** *Crowns and stems: defining Brachiopoda and Pan-Brachiopoda*
3.10-3.30pm	**Afternoon Tea [FOYER]**
3.30-3.50pm	**Mergl:** *Origin and Palaeozoic diversification of discinoids*
3.50-4.10pm	**Skovsted:** *The origin of brachiopod shells*
4.10-4.30pm	**Manceñido:** *A review of crural types, their relationship to shell microstructure, and significance among post-Palaeozoic Rhynchonellida*
4.30-4.50pm	**Hoffmann:** *An integrated approach towards the phylogeny of Recent thecideide brachiopods*
4.50-5.10pm	**Sperling:** *The phylogenetic position of the Brachiopoda and Phoronida: new evidence from nuclear housekeeping genes and microRNAs*
5.10-5.30pm	**Close**
5.30-7.30pm	**Association of Australasian Palaeontologists (AAP) Business Meeting [SEMINAR ROOM 1]**

Wednesday 3 February		
Departing time	**Mid-Congress Field Trips**	
8.00am	**Mid 3 - Tertiary and the Great Ocean Road** (LEADERS: Drs Mark Warne & Rolf Schmidt)	All departing from Holmesglen Conference Centre and returning approximately 6pm
8.30am	**Mid 1 - Siluro-Devonian & Healesville Sanctuary** (LEADER: Dr Monica Campi)	
8.30am	**Mid 2 - Permian in Bacchus Marsh** (LEADER: Mr Roger Pierson & Prof. Guang R Shi)	

Thursday 4 February		
9.00am-2.50pm	**T4: Joyce Richardson Symposium** **CONVENOR: Dr Norton Hiller** **[AUDITORIUM]**	**T5: Des Strusz Symposium** **CONVENOR: Dr Ian Percival and Dr Glenn A. Brock** **[SEMINAR ROOMS 1 & 2]**
9.00-9.30am	**Logan (KEYNOTE):** *Ontogenetic stages in Recent and Mesozoic thecideoids: an index of a common developmental pattern since the Jurassic*	**Harper DAT (KEYNOTE):** *Macroevolutionary patterns and trends in the rhynchonelliform brachiopods through the Ordovician – Silurian interval*
9.30-9.50am	**Harper EM:** *Establishing a modern baseline for shell damage and repair in rhynchonelliform brachiopods: assessing levels of durophagous predation*	**Gourvennec:** *Genus, species and authors: a dangerous inflation*
9.50-10.10am	**Brand:** *Brachiopods: proxies or imposters of seawater chemistry*	**Percival:** *Brachiopod-based biogeographic linkages between eastern Australia and South China in the Late Ordovician (Darriwilian-Katian)*
10.10-10.30am	**Group Photo [FOYER]**	
10.30-10.50am	**Morning Tea [FOYER]**	
10.50-11.00am	**Aldridge:** *Ontogenetic discontinuities in brachiopod populations: their detection and significance*	**Bassett (Holmer):** *Craniiformeans and their position within crown group Brachiopoda*
11.10-11.30am	**Schumann:** *Growth patterns in living brachiopod associations - shallow and deep*	**Wright:** *A new Late Devonian brachiopod fauna from New South Wales*
11.30-11.50am	**Hiller:** *Brachiopods in a Late Cretaceous oyster reef*	**Gourvennec:** *Diversity and survivorship of Siluro-Devonian brachiopods*
11.50am-12.10pm	**Aldridge:** *Brachiopod life histories from spiral deviations in shell shape*	**Reyes-Abril (Villas):** *Middle Ordovician harknessellids (Orthida, Dalmanellidina) from the Mediterranean margin of Gondwana*
12.10-12.30pm	**Rojas Briceño:** *Recent terebratulids (Brachiopoda) of San Bernardo, Caribbean Sea from Columbia*	**Brock:** *Taphonomy and palaeoenvironment of Early Cambrian stem group brachiopods from South Australia*
12.30-1.30pm	**Lunch [FOYER]**	

1.30-1.50pm	**Furchheim:** *The larval eyes of Brachiopoda*	**Huang:** *Can the Lilliput Effect be detected in the brachiopod faunas of Southeast China following the terminal Ordovician mass extinction?*
1.50-2.10pm	**Harper EM:** *Analysis of drill holes in Recent New Zealand brachiopods*	**Valentine:** *Early Silurian linguliform brachiopod biostratigraphy and oceanic turnover events*
2.10-2.40pm	**Lee D:** *A diverse brachiopod-dominated community on settlement plates from Doubtful Sound, New Zealand: a 'retrograde' lophorate community emulates Paleozoic seafloor* [2.10-2.40pm]	**Zhan (KEYNOTE):** *Brachiopod biogeographic change during the Early to Middle Orodvician of South China*
2.40-3.00pm	**Afternoon Tea [FOYER]**	
3.00-4.30pm	**Poster Session [FOYER]**	
4.30pm	**Close**	
6.30 - 7.00pm	**Pre-dinner drinks [FOYER]**	
7.00-10.00pm	**Congress Dinner [SEMINAR ROOMS 1 & 2]**	

Friday 5 February	
9.00am-12.20pm	**T7 (Open Session): Brachiopod biology, palaeobiology ecology and palaeoecology [AUDITORIUM]** **CONVENOR: Prof. Renbin Zhan**
9.00-9.30am	**Copper (KEYNOTE):** *From shallow to deep, hot to cold, and acme to crisis: brachiopod shelly communities from the Ordovician through Devonian*
9.30-10.00am	**Jin (KEYNOTE):** *Morphological cline, palaeogeographical gradient, and the evolution of the Late Ordovician brachiopod faunas of North America*
10.00-10.20am	**Zhang ZF:** *Life strategies of Early Cambrian brachiopods on mud substrate: inferences from the Chengjiang fauna of South China*
10.20-10.40am	**Butts:** *A reorganization of the North American Brachiopod fauna across the mid-Carboniferous boundary*
10.40-11.00am	**Morning Tea [FOYER]**
11.00-11.20am	**Sun:** *Palaeobiogeographical significance of new discovery of the Tournasian brachiopods in South China*
11.20-11.40am	**Lee SM:** *Palaeoecological variation of brachiopod assemblages in marginal marine environments: the Geumcheon-Jangseong Formation (Pennsylvanian), Taebaeksan Basin, Korea*
11.40-12.00	**Stigall:** *Application of niche modeling to analyze biogeographic patterns in Palaeozoic brachiopods: evaluating niche stability in deep time*
12.00-12.20pm	**Colás Gracia:** *Sporadic occurrence of Jurassic nucleatids in non-Alpine areas of Spain: palaeoecological and palaeobiogeographical significance*

12.20-1.30pm	**Lunch [FOYER]**
1.30-4.40pm	**T6: Alwyn Williams Symposium [AUDITORIUM]** **CONVENOR: Dr Uwe Balthasar**
1.30-2.00pm	**Cusack [KEYNOTE]:** *Brachiopod shells recording ambient water temperature while under strict biological control*
2.00-2.20pm	**Endo:** *Artificial fertilisation in Lingula anatina: a portal to brachiopod developmental genetics*
2.20-2.40pm	**Holmer:** *Ontogeny and phylogeny of Early Cambrian rhychonelliform brachiopods*
2.40-3.00pm	**Lüter:** *Protegular secretion in thecideide brachiopods - larval size matters*
3.00-3.20pm	**Pérez-Huerta:** *Comparison of material properties of fossil and Recent shells of Thecidellina*
3.20-3.40pm	**Afternoon Tea (Remove posters) [FOYER]**
3.40-4.00pm	**Lang:** *Nanostructures in Palaeozoic linguloid brachiopods*
4.00-4.20pm	**Madison:** *Shell structure of the smallerst rhynchonelliformean brachiopods from the Ordovician of the Leningrad region, Russia*
4.20-4.40pm	**Tuross:** *Environmental information in the* $\delta^{13}C$, $\delta^{15}N$, δD *and* $\delta^{18}O$ *of Lingula*
4.40-5.00	**Gaspard:** *Endoliths and bacterial activity in Cretaceous and Recent brachiopod shells - diagenetic consequences*
5.00-5.30pm	**Closing remarks and announcement of the host for the 7th IBC 2015 [AUDITORIUM]**
5.30pm	**Congress Close**

Posters

Posters are listed below and will be displayed all week during the Congress. First authors' names are given. Where the presenting author differs from the first author, the presenter's name is given in brackets.

Authors (presenter if different to primary author)	**Poster Titles**	**Poster Board Number**
Angiolini, L. et al.	*The internal morphology of fossil brachiopods under X-ray computerised tomography (CT)*	1
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ABSTRACTS

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Geological Society of Australia, Abstracts No. 95
6th International Brachiopod Congress, Melbourne, Australia, February 2010

ONTOGENETIC DISCONTINUITIES IN BRACHIOPOD POPULATIONS: THEIR DETECTION AND SIGNIFICANCE

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While measurements of shell length, width, and height are included in taxonomic studies, they rarely refer to population discontinuities in shape. Is this because such discontinuities are rare, or because we lack the methods to detect them? Evidence of abrupt shape change is not in question for individuals through crowding, or extreme events such as storms. Less often reported are abrupt shape changes that are size specific throughout a population. Such changes may be more common than previously expected.

Piecewise regression is utilised to detect and estimate these discontinuities as breakpoints in six Recent species. Both previously published studies and new measurements are investigated using piecewise regression on shell length, width and height. That is, the traditional measurements of shell shape are treated in different way to highlight important population features. Population shape breakpoints and their size related confidence limits are estimated, and then corroborated through changes in valve shape of individual brachiopods.

Breakpoints can occur at different sizes, and appear to be taxon and substrate specific. Where breakpoints exist, they occur at a constant size for habitat specialists, but at various sizes for generalist species. Not having a breakpoint, or breakpoint at a constant size, appears to be diagnostic of a specialist species.

Substrate relationships are the preferred, but not exclusive cause of discontinuities studied. Other population-wide causes are possible, but less likely: reproductive maturity, size limit, extreme temperature change, and crowding and storm events. However, general environment seems a most unlikely cause given the range distribution of species with parameters other than substrate.

Piecewise regression is a promising new way of identifying substrate relationships and behaviour from shell shape in articulate brachiopods. The method is suitable for both large and small samples. Spiral deviation analysis on individual valves provides additional confirmation of breakpoints. Such confirmation is important for small samples (less than ten brachiopods), where piecewise regression itself might not be statistically significant.

BRACHIOPOD LIFE HISTORIES FROM SPIRAL DEVIATIONS IN SHELL SHAPE

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Preliminary investigation of valve shape and section microstructure has been made for four individuals of extant genera. In each individual, valve shape follows closely that of a logarithmic spiral (R^2>98%). Deviations from spiral are non random and comprise periodic and aperiodic components that match known life history and growth.

One periodic component identifies annual growth. On a valve section, annual changes can be matched to growth breaks that extend into the secondary shell layer. While identified changes are not always visually clear on a shell, they can be highlighted using spiral deviations. The annual component of spiral deviations is distinguishable from components that are linked with major disturbances, and the more numerous growth lines.

Individual growth rates are estimated up to four years of age. When rates are included with a sigmoidal growth model, the age at death of each individual can be estimated. For the species studied we estimate adult ages of less than fifteen years. These results offer the opportunity to develop brachiopod chronologies that could test links with environmental variables such as average water temperature, depth and salinity over long periods of time.

Large, aperiodic deviations are assumed to link with already postulated causes of temperature extremes, storm events, crowding, and constraints of substrate size and mass. Smaller amplitude, periodic, high frequency deviations can be matched to the more regular growth lines on a shell. Identifying components of deviations about spiral shape is a nondestructive complement to conventional sectioning and microscope photography. The starting requirement is an accurate and precise outline in the sagittal plane for either ventral or dorsal valve. Digital photography now provides the means for such outlines. Further specimens and population studies are needed to confirm and extend our preliminary investigations.

ORGAN SYSTEM DEVELOPMENT IN RECENT LECITHOTROPHIC BRACHIOPOD LARVAE

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Although most recent phylogenetic analyses include Brachiopoda within Lophotrochozoa, the brachiopod sistergroup relationships within this superclade remain unsettled. In order to shed more light on this issue we investigated the development of the musculature and the nervous system in lecitothropic larvae of rhynchonelliform and craniiform brachiopods. The results show striking differences in the muscle systems of rhynchonelliform and craniiform larvae, despite similarities in their overall gross morphology and probably also larval ecology. The nervous system of the craniiform *N. anomala* larvae, consisting of four apical flask shaped cells and two ventral nerve cords, shows resemblances to the neural anatomy of lecitotrophic larvae of spiralians, thus supporting the phylogenetic hypothesis that brachiopods are ingroup lophotrochozoans. We supplement our morphogenetic data with analyses of *Hox* gene expression to assess the genetic basis of body plan patterning in Brachiopoda.

EARLY PALAEOZOIC DIVERSIFICATION OF EUROPEAN "SMOOTH" ATHYRIDIDINES AND THEIR AFFINITIES

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During the process of reviewing the athyridide genera and their species for the revised edition of Part H, Brachiopoda of the *Treatise on Invertebrate Paleontology* we had the opportunity to study and discuss the classic collections housed in our own institutions, others on loan (e.g. the Verneuil Collection, now in Lyon), and new large collections from the Cantabrian Zone. This systematic revision facilitated increasingly detailed analyses of spatial and temporal changes of athyrididid diversity. The main objective of this paper is to analyse the distributional pattern of the commonly called "smooth" athyrididines of Silurian and Early Devonian age, in the Cantabrian Zone (NW Spain) and Baltica. As expected, in the smooth athyrididines with few (not always well preserved) external characters, with many variants and with rather complex, poorly known interiors, it was not easy to envisage spatial distributions and/or phyletic lineages. Besides this, similarities in some morphological characters could be accounted for by convergent or parallel evolution, and thus do not represent a real phylogenetic relationship. Therefore we still have incomplete knowledge of the morphological characters commonly used to describe these "smooth" athryididines, leading to problems and differences in taxonomic concepts as indicated by diagnoses and groupings of species and genera and possibly in assigned rank and distributions observed in the literature. However, it is clear that a clear increase of athyrididine diversification and dispersion took place especially in Baltica (northern Europe eastward to the Urals and Kara Sea), coinciding with the climate warming and transgression which occurs during the Early Silurian. Soon after, the general Late Silurian marine regression seems to have had a strong influence in the decrease of generic originations, and as a result, the Late Silurian was the time of the first substantial crisis of the group. This was followed by a period, in the Early Devonian, of high innovation and radiation rates, leading also to the rise of many endemic genera, particularly in Armorica regions as the Cantabrian Zone (NW Spain).

WHAT THE MORPHOLOGY AND THE SHELL STRUCTURE OF PERMO-CARBONIFEROUS BRACHIOPODS FROM WESTERN PALAEOTETHYS/NEOTETHYS CAN TELL US ABOUT PALAEOECOLOGY AND PALAEOCLIMATE?

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The life-long researches on the brachiopod phylum, for which Howard Brunton was and is universally known and acknowledged, range from the Palaeozoic to the recent, from taxonomy and evolution to functional morphology and palaeoecology. An invariable feature characterises his original work: the elegant style combined with a very subtle humour with which he has presented the excellent quality of his researches. Howard used to say (and also wrote about) that he had always been "interested in how brachiopods grew and in the possible functions for the observed morphologies"; so in this key-note talk to the session dedicated to him as a celebration to his work, the morphology and shell structure of some Carboniferous and Permian productids and spiriferinids will be discussed and related to their growth and possible relation with the environment.

Productida reached a peak in diversity in the Early Carboniferous, a time in which they represented nearly half of the total brachiopod fauna (Curry & Brunton, 2007). This success was accomplished by the great diversity of the available environments and the occurrence of major climate fluctuations with the beginning of the different phases of the Gondwana glaciations. Productida was still the dominant order in the Permian, even in the last pulses of the glaciations, but other groups such as the Spiriferinida assumed characteristic morphologies which reflect a different life-style on high energy mobile substrates. Besides their morphologies and their possible functions, the structure of their shells and the way they grew, is also discussed. Alvarez (1990) showed that the growth of the brachiopod shell is the result of the balance between forward growth of the margin and the thickening and strengthening of the already secreted shell. This can be accomplished by the secretion of the prismatic tertiary layer or by reorientation and convolutions of the secondary layer fibres. Both options have been tried with success by the brachiopods under study.

Firstly, the case of a large and thick shelled *Gigantoproductus* aff. *okensis* from bioclastic limestones of tropical shallow marine conditions in the upper Viséan (Mississippian) Monsal Dale Limestones of Great Britain is presented. This brachiopod assumed a concavo-convex bow-like shape (type 1 of Brunton, 1985) with the anterior margins mainly growing in an anterior direction. Its shape, postero-ventral shell thickening, ears and trails were adapted to free, semi-infaunal living on a mobile substrate in agitated waters at shallow depths. The specimen was cut along a longitudinal section and its shell structure was screened at SEM and then under cathodoluminescent microscope. The shell consists mostly of a very thick prismatic tertiary layer showing about twenty conspicuous growth lines. At these growth lines the fabric changes from calcite prisms to irregular laminae or granules, indicating periodical mantle reversal and reduction of growth rates caused by regular perturbations in the environmental conditions. Also, this change in secretion corresponds to the occurrence of luminescent lines under cathodoluminescent microscope. The number of growth lines suggests a life span of at least 20 years in agreement with the expected survival rates of extant brachiopods. The shell was sampled in great detail for geochemical analyses (both isotopes and trace elements) consecutively at 121 points across a ~20 yr period of growth lines along the preserved and mostly non luminescent shell interior. Isotope variation shows that growth and geochemistry is periodical, showing regular oscillation of about 1.1‰ for $\delta^{18}0$ and 0.5-1 for $\delta^{13}C$. $\delta^{18}0$ and $\delta^{13}C$ periodicity were correlated with growth lines and Fourier analysis showed that this periodicity is annual in form and thus seasonal, though other periodicity seems to be present also. The seasonal oscillation of about 1.1‰ for $\delta^{18}0$ may indicate sea surface temperature (SST) variation of ~ 5-6 ºC. Thus, the study of this productid shell revealed a high seasonal isotopic variation which may have been related both to strong monsoon circulation at time of high insolation during the austral summer, and to the growth of ice sheets of limited extent in Gondwana.

From the equatorial sea of the Early Carboniferous I will shift to Tethyan intermediate latitudes in the Early Permian aftermath of the Gondwanan glaciations, recorded by the Saiwan Formation of Oman. Here, free-living brachiopods displayed a different strategy of colonization of high energy mobile substrates, a strategy which still involved postero-ventral shell thickening, in this case accomplished by reorientation of secondary layer fibres in *Pachycyrtella omanensis.* This species is a free-living, biconvex spiriferinid characterised by a high, wide ventral interarea interiorly filled by a thick callus producing a posterior weighting, which stabilised the shell oriented with the ventral valve more or less vertical and the high and heavy ventral umbo partially buried in the mobile sandy substrate. It has a well developed interlocking articulation and a strongly fitting commissure with overlapping lateral and anterior margins which could have prevented coarse substrate particles from entering the shell. The deep ventral sulcus and high sulcate dorsal fold of *Pachycyrtella omanensis* provided an efficient separation between the inhalant and exhalant currents. Major growth lines of *P. omanensis* suggest fast growth rates, a maximum life-span of about 14 years, and an early achievement of sexual maturity. Its large biovolume implies greater storage capacities and high reproduction rates due to increase in the effective surface area of the lophophore conferring advantages in the physically stressed environment, characterised by high energy and high nutrient influx at the end of the Gondwanan deglaciation. Oxygen isotope ratios on *P. omanensis* shells ($\delta^{18}O$ of –3.7 to –3.1‰) indicate influx of glacial meltwater which periodically affected the environment.

No free-living productids co-occur with *P. omanensis*, but a strophalosiid, *Strophalosia ericinia,* has been found cemented by the umbo and creeping adherent spines to *P. omanensis* and to bivalves. Not only juveniles of *S. ericinia* have been found cemented to other shells, but also specimens with a relatively larger cicatrix are found attached at maturity and probably adopted for most of their life this strategy: the relationships to the substrate seem thus to be quite variable at maturity among individuals belonging to the same species.

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THE INTERNAL MORPHOLOGY OF FOSSIL BRACHIOPODS UNDER X-RAY COMPUTERISED TOMOGRAPHY (CT)

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The study of the internal morphology of fossil brachiopods has never been an easy task, except in those fortunate, but rare, cases in which the shells are silicified and contained in limestone or when finely preserved internal moulds are available. The study of the fossil brachiopod interiors is mostly based on serial grindings methods, which are time consuming, destructive and whose reliability has been questioned (Alvarez & Brunton 2008).

To test new solutions to reveal fossil interiors, twenty articulate specimens of Carboniferous and Permian brachiopods (Athyridida, Spiriferida, Spiriferinida) have been analysed using an X-ray computerised tomography, a new technique successfully used in other fields of Earth Sciences to investigate the internal structure of geological materials.

X-ray computerised tomography (CT) consists of a three dimensional reconstruction of the inside of a sample, obtained by the stacking of two-dimensional images. A CT image, called a slice, corresponds to a certain thickness of the sample and is thus composed of 3D volume elements, called voxels. The object being scanned reduces the X rays energy passing through, as a function of its density and atomic number. In CT slices the denser the scanned material the brighter the image.

A large spectrum of geological materials can be examined (soils, intact rocks, porous and fractured rocks, fossils, gems and pearls), providing a difference in density/X rays adsorption among different parts of the specimen exists.

The use of CT presents the main following advantages:

- it is a non destructive technique, leaving the specimen intact and available for further analyses.
- the samples do not need any particular preparation.

The industrial micro CT system used in this study is a BIR Actis 130/150, located at the University of Milano-Bicocca. In this system both generator and detector are fixed, while the sample rotates; the scanning plane is horizontal.

This device works with a polychromatic X rays generator (i.e. different energy X rays). X rays, passed through the sample, are collected on a detector, which converts them into light radiations. A digital camera transforms light radiations in raw data (sinograms) and send them to the computer, where they are processed as black/white 2D images. 3D images have been reconstructed both with Actis and Avizo-Fire (Visualization Science Group Inc.) softwares.

An energy of 120keV/100mA has been used to scan bigger brachiopods and that of 100keV/80mA to scan smaller ones. The dimensions of the voxel, corresponding to the resolution of the images, varies from 0.042x0.042x0.044 mm to 0.021x0.021x0.024 mm, depending on the brachiopod dimensions. To allow a detailed study of the umbonal region the fossils have been placed as near as possible to the X rays source, reconstructing slices up to 0,008x0,008x0,008 mm resolution.

Due to the intrinsic limit of the method based on density differences, only brachiopods filled with sandstone (*Pachycyrtella omanensis*) gave valuable CT images showing details of articulation, dental plates, muscle field, and spiralia. Out of the many micritic limestone, bioclastic limestone and marlstone filled brachiopods which have been scanned, only one (*Cleiothyridina kusbassica*) gave remarkable CT images, due to the presence of a thin void layer (dark grey in the images) between the internal structures and the micritic filling.

Even if still limited by the occurrence of a significant density contrast between the shell and the matrix, the method is very useful as it is non destructive and it provides high quality images of all possible sections of the interior along any orientation of interest. Also it allows 3-D reconstruction based on selected sections.

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GUADALUPIAN BRACHIOPOD FAUNAS FROM TUNISIA, TURKEY AND NORTH IRAN AND THEIR IMPLICATIONS FOR CORRELATIONS ACROSS THE NEO-TETHYS

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The Guadalupian was a period of climate change and plate tectonic reconfiguration. Climate changed from glacial conditions at the dawn of the Permian to warm conditions in the Guadalupian. The Cimmerian terranes migrated from southern Gondwanan palaeolatitudes in the Early Permian to subequatorial palaeolatitudes by the Middle-Late Permian as the result of the opening of the Neo-Tethys Ocean. This opening was asymmetrical, with higher seafloor spreading rates for the central Cimmerian terranes (central Afghanistan, Pakistan Karakoram) than for the western terranes (Iran), and it took place contemporaneously with the transformation of Pangea from an Irvingian B to a Wegenerian A-type configuration. During this Early to Middle Permian tectono-climatic transition, bioprovincial patterns evolved rapidly across the southern and northern margins of the opening Neo-Tethys Ocean, as testified by the rich fossil record.

Guadalupian (Wordian) brachiopod faunas from Jebel Tebaga de Medenine in Tunisia and from the Pamucak Formation in Turkey, both located in the palaeotropical zone along the Gondwanan margin, are well preserved and quite diverse. They have several taxa in common respectively with the Fusulina Limestone of Sosio (Sicily) and with the Khuff Formation of Oman allowing correlations along the western Gondwanan margin, correlations which are supported by the associated conodonts.

The Guadalupian Ruteh Formation in North Iran contain several taxa in common with Tunisia, Turkey, and also Oman along the Gondwanan margin, such as *Neochonetes (Nongtaia)*, *Entacanthadus, Spinomarginifera, Linoproductus, Vediproductus, Ombonia, Perigeyerella, Kotlaia, Squamularia*. As North Iran was part of the northward moving Cimmerian terranes at Middle Permian times, these taxa allow correlations across the Neo-Tethys shores and may bridge the gap between the Gondwana margin and the Cimmerian and Cathaysian blocks in the central and eastern Tethyan oceans.

ARTICULATED BRACHIOPODS: A NEW PROXY OF SEAWATER REE-CHEMISTRY AND NATURAL PROCESSES

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The ΣREE (rare earth elements) and shale-normalised (PAAS –Post-Archean Australian Shale) REE_{SN} trends of recent brachiopods (biogenic low-Mg calcite-bLMC) represented by several species from high- to low latitudes, from shallow- to deep waters and from warm- and cold-water environments define three major and distinct 'seawater' groups. The two largest groups, the warm- (256 ppb ΣREE) and cold-water (235 ppb) brachiopods define two statistically indistinguishable ($p<0.050$) populations that mimic open ocean seawater REE chemistry, exhibiting the typical La enrichment with a slight to marginal Ce anomaly followed by an otherwise invariant series. The third group, recent brachiopods from an essentially siliciclastic environment are distinct in both ΣREE (586 ppb) and REE_{SN} trends from the previous two populations, showing a slight enrichment in the MREEs (medium rare earth elements) and an increasing trend in the HREEs (heavy rare earth elements). Another group of recent brachiopods is characterised by elevated REE_{SN} trends relative to the 'major' group as well as by increased complexity of the series trend. The most characteristic feature is the decrease in the HREEs in brachiopods from areas of unusual productivity (i.e., locations of upwelling currents, fluvial input and aerosol dust deposition). Well-preserved brachiopods from the Eocene and Silurian exhibit REE_{SN} trends similar in configuration to that of 'open-seawater' recent brachiopods. However, their absolute ΣREE concentrations are enriched by approximately two and one order of magnitudes, respectively. Consequently, well-preserved calcitic brachiopods (bLMC) may be excellent proxies of original seawater REE composition and water masses but also an important tracer of natural processes.

Preservation of the biogenic low-Mg-calcite was tested by comparing its ΣREE content and REE_{SN} trend to that of altered brachiopods and enclosed fine-grained lime-mud. The altered material exhibits features of closed system diagenesis for the lime-mud and a partly closed one for the brachiopods. Despite these subtle diagenetic alteration features, their ΣREEs and REE_{SN} trends are significantly enriched relative to that of their coeval and preserved calcitic brachiopods and lend support to their previously assigned status of preservation with their original shell microstructures and geochemistry.

In contrast to these changes in ΣREE and REE_{SN} with subtle diagenetic carbonate alteration, are the comparable compositions of carbonates that experienced more severe degrees of diagenetic alteration as well as precipitation of late burial diagenetic cement. Their REE and REE_{SN} trends are significantly enriched relative to the best of the preserved calcitic brachiopods as well as to those components that only experienced closed and partly-closed system diagenetic alteration. Thus closed- to open-system carbonate diagenesis changes are documented by significant and increasingly larger shifts in their respective REE compositions and REE_{SN} trends.

CRURAL-BASE POSITION AS CRITERIA FOR GENERIC DIFFERENTIATION OF LOWER JURASSIC ZEILLERIIDAE (BRACHIOPODA, TEREBRATULIDA)

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Certain representatives of the Family Zeilleriidae Allan, 1940 such as *Zeilleria* Bayle, 1878, *Bakonyithyris* Vörös, 1983 and *Securina* Vörös, 1983, may be considered among the most abundant and characteristically Mediterranean genera within the Lower Jurassic associations of brachiopods of the Western Tethys. Traditionally, the systematic discrimination of these genera has been based on morphological external features, such as the presence of a dorsal sulcus in *Bakonyithyris*, or of an axiniform outline in *Securina*. The architecture of the brachidium in the cardinal region is proposed here as an additional criterion for this purpose.

Detailed analysis of serial sections prepared in specimens of eight different species from the Lower Jurassic of the Betic Cordillera (Baeza-Carratalá, 2008), *Bakonyithyris gastaldii* (Parona, 1880), *Zeilleria* aff. *venusta* (Uhlig, 1879), *Z. batilla* (Geyer, 1889), *Z. mutabilis* (Oppel, 1861), *Securina partschi* (Oppel, 1861), *S. plicata* (Geyer, 1889), *S. securiformis* (Gemmellaro, 1874) and *S. oxygonia* (Uhlig, 1879), has allowed recognition of the fact that the relative position of the crural bases follows different patterns and is useful as a method for generic discrimination. These different patterns confirm the generic attribution for most of the species included in our study, and in particular cases have allowed us to put forward some new combinations (e.g.: *Securina oxygonia*).

Thus, this study has led to the establishment of the following criteria as valid for generic differentiation:

Genus *Zeilleria*: the crural bases are located on the ventral region of the hinge plates, and do not develop dorsally until clearly individualised.

Genus *Bakonyithyris*: the crural bases are also located on the ventral part of the hinge plates, but begin to develop dorsally before being individualised from the hinge plates.

Genus *Securina*: the crural bases are located at the interior of the distal end of the hinge plates, and dorsal to the septalial plates.

By applying this additional diagnostic approach to other zeillerid genera such as *Neozeilleria, Cincta, Aulacothyris, Plesiothyris* or *Antyptychina*, more precise phylogenetic relationships should be obtained and the taxonomic position of some of their species might be better established.

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Poster

TOURNAISIAN (MISSISSIPPIAN) BRACHIOPODS FROM THE MOBARAK FORMATION, NORTH IRAN

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A very rich brachiopod fauna comprising 54 taxa has been found in the Tournasian (Mississippian) marly limestones and bioclastic limestones of the Mobarak Formation, Alborz Mountains, North Iran. It includes: *Leptagonia* cf. *L. analoga* (Phillips, 1836), *Caenanoplia* cf. *C. burlingtonensis* (Carter, 1968), *Geniculifera* sp., ?*Rhytiophora* sp., *Antiquatonia* sp., *Promarginifera* sp., Dictyoclostinae gen. et sp. indet., *Buxtonia* sp, *Marginatia vaughani* (Muir-Wood, 1928), *Marginatia* aff. *M. deruptoides* Sarytcheva in Sarytcheva, Sokolskaya, Beznosova & Maksimova, 1963, *Tomiproductus elegantulus* (Tolmatchoff, 1924), Tolmatchoffiini gen. et sp. indet., *Pustula* cf. *P. altaica* Tolmatchoff, 1924, *Pustula* sp., Pustulinae gen. et sp. indet., *Brochocarina* sp., Orthotetoidea fam. indet., *Schellwienella* sp., *Rhipidomella michelini* (Léveillé, 1835), *Schizophoria (Schizophoria) resupinata* (Martin, 1809), *Hemiplethorhynchus crassus* Gaetani, 1968, *Rossirhynchus adamantinus* Gaetani, 1964, *Paraphorhynchus* aff. *P. elongatum* Weller, 1905, ?*Athyris* sp., *Lamellosathyris lamellosus* (Léveillé, 1835), *Cleiothyridina kusbassica* Beznosova in Sarytcheva, Sokolskaya, Beznosova & Maksimova, 1963, ?*Cleiothyridina* sp., *Gerankalasiella* sp., *Carteridina* sp., *Composita megala* (Tolmatchoff, 1924), *Composita subquadrata* (Hall, 1858), *Composita* aff. *C. pentagonia* (Weller, 1914), *Composita* cf. *C. caimaensis* Chen, Tazawa, Shi & Matsuda, 2005, *Composita* sp., ?*Densalvus* sp., ?*Iniathyris* sp., Spirigerellinae gen. et sp. indet., Athyrididae gen. et sp. indet., *Kisilia* sp., ?*Tenisia* sp., *Ectochoristites* sp., *Parallelora* sp., *Unispirifer (Unispirifer) striatoconvolutus* (Benson & Dun in Benson, Dun & Browne, 1920), *Unispirifer* cf. *U. (Septimispirifer) septimus* (Thomas, 1971), *Unispirifer* sp., *Atylephorous* sp., Prospirinae gen. et sp., *Voiseyella* aff. *V. texana* (Carter, 1967), *Brachythyris* sp., *Kitakamithyris* sp., *Torynifer* sp., *Syringothyris carteri* (Hall, 1857b), *Syringothyris skinderi* Sokolskaya in Sarytcheva, Sokolskaya, Beznosova & Maksimova, 1963, and *Pseudosyrinx* sp.

The fauna has been collected bed by bed along two sections: Abrendan section and Simeh Kuh section, whose correlation has been attempted using quantitative biostratigraphy. Although mostly cosmopolitan, the brachiopods show closer affinity to North America, Western Europe and the Russian Platform than to cold-water Australian faunas, confirming the affinity of foraminifers and other biota. This seems to contradict Early Mississippian palaeomagnetic reconstructions placing the Alborz region at 45–50° South latitude. The answer to this discrepancy may lie in the circulation of Palaeo-Tethyan currents to the south along the Gondwanan shelf.

CAMBRIAN ORIGINS AND TRANSITIONS IN THE EVOLUTION OF THE BRACHIOPOD SHELL

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Brachiopods are among the first animal phyla to emerge from the Cambrian explosion and lack immediately compelling ancestral forms that might shed light on the origins of the body plans of the phylum and its constituent subphyla. In order to recognise the true phylogenetic significance of Cambrian brachiopods the crown and stem group principle must be applied. In a strict sense, a crown group is defined as the last common ancestor of all extant species and all of its descendents. Following this definition the crown groups of linguliforms, craniiforms, and rhynchonelliforms only appeared during the Ordovician. By implication, Cambrian taxa do not possess the complete sets of features that define the body plans of the respective subphyla. Instead the Cambrian brachiopod fauna holds the key to decipher how the distinctly different body plans of linguliforms, craniiforms, and rhynchonelliforms evolved from a common ancestor.

A particularly important feature in deciphering the origins of the phylum and subphyla is the shell composition and microstructure of Cambrian brachiopods. Recent work on the origins of the brachiopod shell has led to the hypothesis that the bivalved brachiopod body plan evolved through the successive reduction of the multi-element organophosphatic tubular skeleton of tommotiids, a group of early Cambrian small shelly fossils (Skovsted et al. 2008, 2009). This view is also supported by recent findings in microstructural similarities between tommotiids and paterinid brachiopods (Balthasar et al. in press). Microstructural comparison between tommotiid sclerites and paterinid shells also reveals a trend towards reduced mineral (apatite) density in brachiopods. This trend is further highlighted by the occurrence of several Cambrian 'soft'-shelled taxa that lack notable shell mineralisation (Balthasar & Butterfield 2009). The trend towards reduced apatite mineralisation probably reflects the challenge of maintaining a physiologically expensive phosphorous budget which could also explain the emergence of calcite in brachiopod shells. Recently discovered chemico-structural similarities between taxa that have previously been thought to be purely organophosphatic or calcitic indicate that calcitic shells might have evolved several times independently (Balthasar 2008; Holmer et al. 2009). The only way of testing these hypotheses is by means of cladistic analysis and a collective effort with various colleagues is currently under way to analyse Cambrian and Ordovician brachiopods including potential stem group forms.

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CRANIIFORMEANS AND THEIR POSITION WITHIN CROWN GROUP BRACHIOPODA

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As currently defined, the Subphylum Craniiformea is the smallest and probably the most conservative clade within crown group Brachiopoda, surviving from the Ordovician to Recent without significant morphological change. In detail, its phylogenetic relationships with two other major brachiopod clades, the Linguliformea and Rhynchonelliformea, remain controversial. Such characters as calcitic shell biomineralisation, a lecithotrophic larva, and a body wall lacking dermal muscles were formerly considered as synapomorphies with rhynchonelliforms, but biomolecular data derived from SSU (18S) and partial LSU (28S) sequences pointed towards craniiforms as being a sister group of linguliforms and phoronides. However, this brachiopod molecular phylogenetic model has since been challenged by further LSU and SSU data, suggesting that Brachiopoda, Phoronida, and Bryozoa are not a monophyletic entity. At the same time, it is becoming clear that lecithotrophic larva evolved independently in rhynchonelliforms. Additionally, the lecithotrophic nature of the larva in Palaeozoic craniiformeans has been subjected to question. However, current study of well preserved specimens of the Early Palaeozoic craniiform brachiopods *Orthisocrania* and *Craniops* gives clear evidence of a lecithotrophic larval stage, indicating the loss of planktotrophy early in their phylogeny. Recent studies of strophomenate brachiopods, siphonotretides and the enigmatic chileide-like *Salanygolina* show that the pattern of ontogenetic succession and larval body plan characteristic of Recent and extinct craniiforms exists also outside the Subphylum Craniiformea. Although all these Early Palaeozoic brachiopods most probably had a planktotrophic larva, they exhibit a remarkably similar pattern of metamorphosis after settlement, including the early loss of larval attachment on the posterior part of the body, replaced by adult attachment structures secreted by the ventral mantle, which are not homologous to the pedicle of rhynchonellates; there was no mantle reversion, while differentiation of the ventral mantle and secretion of the ventral valve took place later in metamorphosis. In paterinides and in early rhynchonelliforms typified by the orthides, the bivalve larval shell was probably formed prior to settlement and both valves underwent continuous peripheral growth. In this interpretation the delayed formation of the ventral valve in craniiforms and strophomenates can be interpreted as an apomorphic state.

ENDOPUNCTAE IN THE 'PLECTORTHOID' *FAMATINORTHIS* LEVY & NULLO (MIDDLE ORDOVICIAN, FAMATINA RANGE, ARGENTINA): IMPLICATIONS FOR EARLY DIVERSIFICATION OF DALMANELLIDINE BRACHIOPODS

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Famatinorthis Levy & Nullo is a distinctive orthide brachiopod from the Famatina Range of western Argentina, where it occurs in volcaniclastic rocks of Dapingian age (*navis* and/or *originali*s conodont zones). Its overall morphologic features (suboval, anteriorly raised ventral muscle field bounded by thickened ridges, well developed fulcral plates, bladelike brachiophores supported by medially converging plates to form a septalium, simple ridge-like cardinal process) led to it being referred to the superfamily Plectorthoidea. A new collection from the volcano-sedimentary La Escondida Formation yielded exceptionally well preserved ventral and dorsal internal moulds of *Famatinorthis turneri* on which silicified infillings of punctae are clearly visible. Previously, endopunctae were discovered in specimens of *Lipanorthis* Benedetto from the upper Tremadocian of NW Argentina, formerly attributed to the plectorthoids and subsequently transferred to the enteletoids (family Linoporellidae) by Harper et al. (2004). To date, *Lipanorthis* is the oldest known punctate orthide. Clearly, the less derived members of plectorthoids (plectorthids and giraldiellids) are so close morphologically to the earlier forms of enteletoids that their assignment to the suborder Orthidina or Dalmanellidina depends largely on the evidence of punctae. Preservation of the latter, however, is controlled by taphonomic factors, mainly the nature of the sediment (abundance of clay) and chemical environment (adequate supply of silica during early diagenesis), which may explain the apparent absence of punctae in most *Famatinorthis* and *Lipanorthis* specimens. This opens the possibility that punctae can be detected in other genera currently classified among the Plectorthoidea. Evidence from the siliciclastic successions of Central Andean basin of NW Argentina and Bolivia is critical to decipher the origin and early radiation of punctate orthides. In this poster, phylogenetic analysis is used to determine the evolutionary relationships of *Famatinorthis*, *Lipanorthis* and other Early-Middle Ordovician Gondwanan genera (*Nocturnellia*, *Atlantida*, *Apollonorthis*, *Paterorthis*, *Irhirea*, among others). The basal taxon from which some plectorthoid lineages evolved is the Late Cambrian *Protorthisina*, the oldest 'septalium bearer' plectorthoid from the Central Andean basin. Cladistic analysis supports the idea that at least some enteletacean clades (i.e. linoporellids and related forms) arose from a plectorthoid ancestor. Of special relevance is *Lesserorthis*, a late Tremadocian plectorthoid which probably gave rise to *Famatinorthis.* According to our phylogenetic hypothesis, *Paurorthis*, the oldest known dalmanelloid of Floian age, lies close to the ancestry of a quite different clade of punctate orthides, the dalmanellidines. As has been suggested, paurorthids may have evolved from a ranorthid-like clade of plectorthoids, but this possibility is not tested here. It seems that presence of endopunctae in the orthides does not necessarily indicate close phylogenetic relationships as it could have occurred at different times in different clades. If the homoplasic nature of endopunctae in the order Orthida is supported by further morphologic and phylogenetic studies, then the fundamental division of orthides in non-punctate (Orthidina) and punctate (Dalmanellidina) may need revision.

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PERMIAN BRACHIOPODS AND BIVALVES OF NORTHEAST ASIA: A COMPETITION BEFORE THE GREAT END-PERMIAN MASS EXTINCTION

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The Permian marks a dramatic stage in the development of Northeast Asia's benthic communities. During this time, bivalves almost completely displaced brachiopods and became dominant for the first time in deep-water benthic communities in Northeast Asia. Starting with the late Middle Permian (Capitanian), bivalves also dominated over brachiopods in shallow-water environments. This phenomenon is in sharp contrast with counterpart faunas in Tethyan and Gondwanan basins.

In the Early Permian (Asselian - Middle Artinskian), brachiopods dominated over bivalves, at least in their biomass, in all basins of Northeast Asia (the Omolon, Verkhoyansk, Okhotsk, and others). The situation changed dramatically during the Late Artinskian when *Inoceramus*-like bivalves invaded Northeast Asia (probably from Gondwanan basins) and occupied many ecological niches previously taken by brachiopods (mostly productids). Since this time *Inoceramus*-like bivalves become rock-forming organisms, forming the so-called "kolymic" ("atomodesmic") limestones. New data recently acquired show that rare *Inoceramus*-like bivalves of Gondwanan origin even appeared from the base of the Sakmarian (Dr. Kutygin, personal communication). However, these forms must have been individual invasive immigrants and never developed further.

The invasion and subsequent wide distribution of *Inoceramus*-like bivalves in Northeast Asia during the Late Artinskian was assisted by a major transgression. In addition, the wide spread of these bivalves must have also been promoted by the development and expansion of a deep-water basin system comprising, notably, the Oimyakon Basin, which has been considered a smaller ocean by some geologists. The new ecological niches, characterised by a significant flux of terrigenous material, with brachiopod communities subdued, were vacated. At the same time, these new niches were successfully populated by *Inoceramus*-like bivalves, accompanied by some nuculids (*Palaeoneilo*, *Phestia,* etc.) and gastropods (*Straparolus,* etc.). In shallow-water communities, especially those of the Omolon Basin, the dominance of brachiopods over bivalves continued to the end of the Wordian. Simultaneously, in basins where terrigenous sedimentation dominated (e.g. Verkhoyansk, Okhotsk, Balygychan, and others), even in relatively shallow-water facies brachiopods were suppressed by bivalves since the Late Artinskian, though in some facies brachiopods locally dominated and formed shell beds.

In the Early Capitanian, a large biotic crisis took place. Following that time, and especially throughout the Early Wuchiapingian mass extinction, brachiopods practically disappeared from all Northern Asian basins except for the Omolon. However, even in the Omolon basin the latest Permian brachiopod diversity was significantly lower than their coeval bivalve faunas. Apparently, one of the factors promoting brachiopod extinction was the complete disappearance of shallow-water biotopes.

The last brachiopod elements (spiriferids and productids) disappeared in the middle part of the *Intomodesma costatum* Zone (early Changhsingian), though Permian bivalves and gastropods survived in Northeast Asia's basins almost until the end of the Permian.

Acknowledgements: These studies have been financially supported by the Russian Foundation for Basic Research, Projects 08-05-00100 and 09-05-98518-r_vostok.

GEOBIOSPHERICAL EVENTS IN THE PERMIAN OF NORTHEAST ASIA

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The analysis of Northeast Asia's Permian bivalve faunas has revealed significant fluctuations in its species diversity (Biakov, 2008) (Fig. 1, next page). Firstly, we have determined four levels of sharp decrease in bivalve diversity: in the end of the Early Permian, Early Capitanian, Early Wuchiapingian, and in the Latest Changhsingian, respectively. Along with extinction events, several intervals of significant diversity increases and originations have also been distinguished: the Early Asselian, Middle Kungurian, Early Roadian, Late Wordian, and Early Changhsingian, respectively. Normally these origination events were followed by mass extinctions.

These events of extinctions and originations are also shown in other biotic (foraminifers, brachiopods, ammonoids); and, as a rule, can be correlated with changes in sedimentation, eustacy, isotope characteristics and other factors of the environment. Most of these geobiospherical events have been traced far beyond Northeast Asia, and many appear to have been of global scale and causes.

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Poster

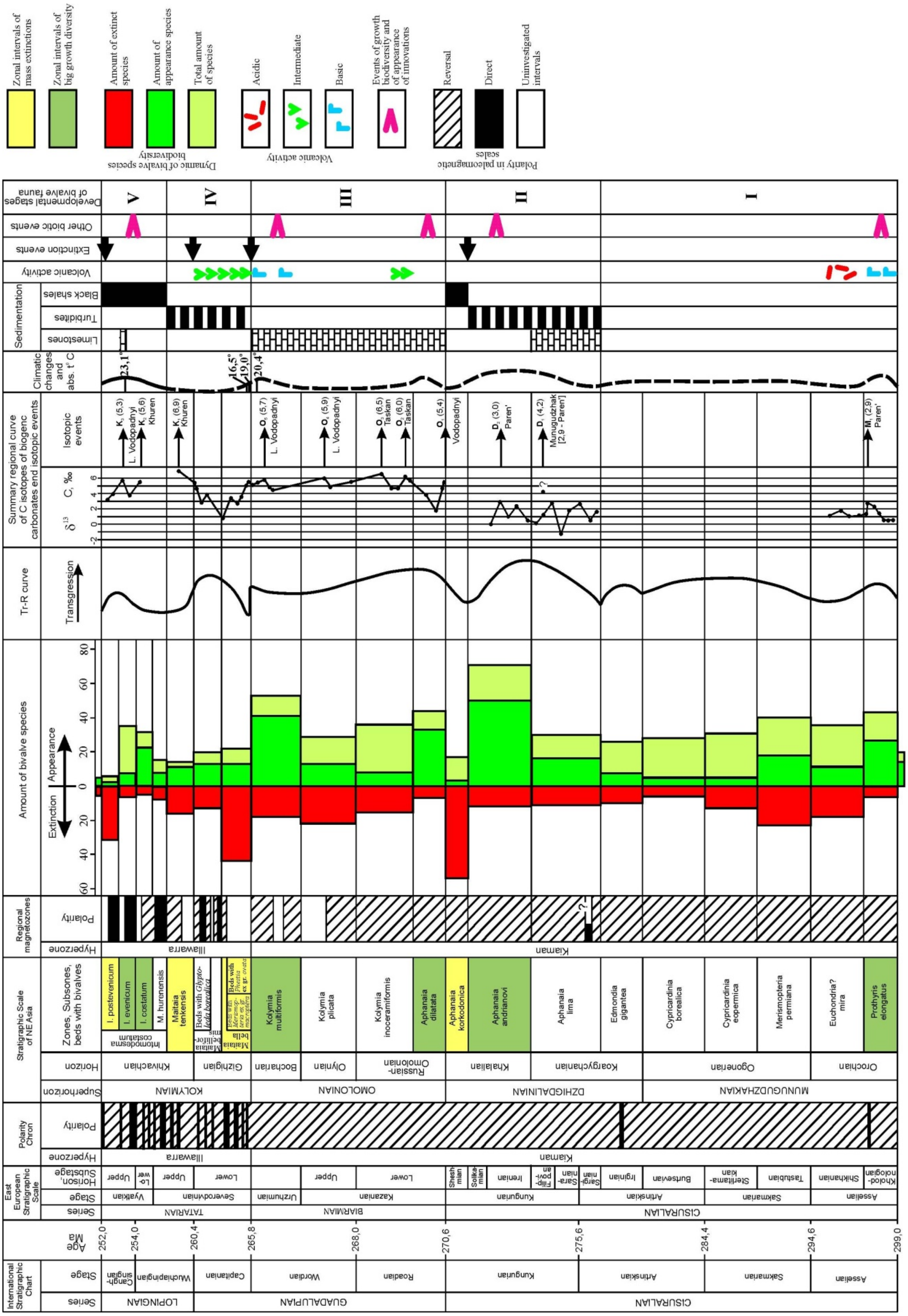

Fig. 1. Geobiospherical events in the Permian of NE Asia

CAVE BRACHIOPODS FROM THE UPPER OLIGOCENE OF SOUTH-WESTERN FRANCE – A MISSING ELEMENT IN EUROPEAN TERTIARY FAUNAL HISTORY

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Although in the Cenozoic brachiopods have lost importance and their taxonomic diversity is low, they represent a stable, locally even dominant, element of the benthic fauna in European Tertiary deposits. Eocene brachiopods are well known and described from the whole of Europe, and although their taxonomic composition in particular assemblages can differ significantly, many species have a very wide geographical distribution from Great Britain to Ukraine. Miocene brachiopods are also well known throughout Europe, being especially studied from the Paratethyan and Mediterranean provinces, and are predominantly micromorphic forms. On the other hand, very little is known about Oligocene brachiopods. The gap in this knowledge is now filled with a rich Upper Oligocene (Chattian) fauna, herein reported, from the Adour Basin, SW France that belongs to the Atlantic Province. The brachiopods, mostly excellently preserved with more than 1100 specimens, were recovered from 22 samples. These extremely fossiliferous deposits are interpreted, based on geological situation and associated faunas (Cahuzac *et al*. 1995, Lozouet 2004), as infillings of a submarine palaeocanyon with many small caves and crevices.

The brachiopod fauna contains eight, exclusively micromorphic, species belonging to seven genera, i.e. *Novocrania anomala* (Müller, 1776), *Terebratulina retusa* (Linnaeus, 1758), *Megathiris detruncata* (Gmelin, 1791), *Joania cordata* (Risso, 1826), *Argyrotheca cunaeta* (Risso, 1826), a new species of *Argyrotheca*, *Megerlia truncata* (Linnaeus, 1767), and *Lacazella mediterranea* (Risso, 1826). *M. detruncata* and *L. mediterranea* constitute more than 80% of the material. The least frequent species are *N. anomala* and *M. truncata*, each being represented by only a few specimens.

The species of *Argyrotheca* recognised as new is very thin-shelled, subtriangular in outline, with a smooth, coarsely punctate surface. In outline the new species resembles *J. cordata* but differs strongly by the lack of marginal tubercles and a much less strongly defined cardinal process.

There are several peculiarities of this Upper Oligocene fauna. For example, *Lacazella mediterranea* reaches a very large size up to 9 mm long, being even more than twice as long as today. The occurrence in the studied assemblage of *Terebratulina retusa*, *Joania cordata*, *Argyrotheca cuneata* and *Megerlia truncata* extends the stratigraphical range of these taxa from the Miocene to the Oligocene. In taxonomic composition the brachiopod fauna from the Adour Basin differs strongly from any other Oligocene assemblage and displays low affinity with European Eocene faunas. Surprisingly, there is a great resemblance to the Miocene faunas of the Mediterranean Province and Paratethys. The dominance of micromorphic megathyridids and thecideids is characteristic of cryptic habitats such as submarine caves and/or crevices, thus supporting the previous interpretations of the whole faunistic assemblage as a cave biocenosis. These new data allow us to present a more complete picture of the history of European Tertiary brachiopods.

Acknowledgements: This research is supported by the grant No. N N N307 129837 from the Ministry of Science and Higher Education (Poland).

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BRACHIOPODS: PROXIES OR IMPOSTERS OF SEAWATER CHEMISTRY

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Many biogenic allochems and whole rock are used as proxies of original seawater chemistry for the geologic past. Common proxies are conodonts, whole rock, brachiopods, mollusks and forams. All of them have different geologic ranges, mineralogy and some have extant representatives. All, except for the conodonts, have modern representatives for modeling the modern oceans and seas as baseline parameters, and most importantly for serving as 'keys' to decipher the evolution of the hydrosphere during the geologic past. Conodonts consist of apatite, a calcium phosphate; whole rock is usually diagenetic low-Mg calcite altered from different original carbonate mineralogy; articulated brachiopods secrete low-Mg calcite shells; mollusks depending on group/species, etc may secrete shells of aragonite, low-Mg calcite or mixtures of carbonate minerals; and forams secrete test of various mineral compositions.

The group with the greatest biostratigraphic acuity is the phosphatic conodonts, with a resolution that is far superior to that of all the other groups. In addition they possess distribution characteristics for superior identification of ambient environmental settings. Brachiopods have less acuity but are usually widespread and abundant in Phanerozoic rocks, and subject to few environmental restrictions.

Diagenesis is the great nemesis of all these allochems, and in many instances the fossil remains are not preserved in their original composition. Thus, the composition of many of these fossils instead of being representative of the original and ambient seawater, reflects the composition of the diagenetic fluid and the character of the diagenetic microenvironment (water/rock ratio system). Some believe that conodonts preserve their original seawater chemistry for both Sr and O isotopes, however, this concept is challenged due to the paucity of test methods proving their preservation. Furthermore, it is assumed by some researchers, that fine-grained carbonates, altered in diagenetic closed systems, have retained their carbon isotopic composition, although scientific evidence is generally lacking. In contrast, brachiopods secrete shells consisting of low-Mg calcite that resist diagenetic alteration and it may be preserved as old as Ordovician. State of preservation is based on results from multiple tests including visual, optical, microstructural, nanoarchitectural examination, and trace chemistry, cathode luminescence, stable isotopes, radiogenic isotopes and REE evaluation. Thus based on ALL the available information of fossil and present representatives, articulated brachiopods are judged to be the most suitable proxy of original seawater chemistry.

TAPHONOMY AND PALAEOENVIRONMENT OF EARLY CAMBRIAN STEM GROUP BRACHIOPODS FROM SOUTH AUSTRALIA

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There is now compelling morphological, scleritome and ultrastructural evidence to root the ancestry of organophosphatic brachiopods within eccentrothecamorph and tannuoliniid tommotiids. Analysis of biostratinomic processes such as disarticulation, re-orientation, sorting, fragmentation, and nesting provide important clues about the sedimentary facies (= depositional environments) associated with these fixed-sessile filter-feeding organisms. All disarticulated sclerites and complete scleritome material of *Eccentrotheca* n. sp. and *Paterimitra pyramidalis* occur in direct association with archaeocyathid-microbial-sponge bioherms and boundstones which developed in high energy, shallow water, inner carbonate shelf environments best represented in the upper half of the lower Wilkawillina Limestone, Arrowie Basin. The complex niches associated with these calcareous build-ups include numerous voids, internal cavities with ceilings and irregular crypts (now filled with secondary spar). The irregular shape of the attachment disc (apical perforation) and variable inclination of the tubular scleritome suggests that *Eccentrotheca* n. sp was probably attached to the lateral sides of large archaeocyaths-spongiomorphs and/or as fixed pendant forms on the uneven surfaces common to ceilings, overhangs and walls of cavities in these cryptic environments. The contemporaneous pedunculate stem group brachiopod *Paterimitra* occurs in the same type of sedimentary facies as *Eccentrotheca*, though it may also have used post mortem shells of large trilobite, brachiopod and mollusc as suitable substrates. Both *Eccentrotheca* and *Paterimitra* are also common in slightly deeper intrashelf depressions (produced by syndepositional faulting) dominated by archaeocyath-hexactinellid build-ups in the Ajax Limestone, Mt Scott Range.

The taphonomic signature for the bivalved tannuoliniid tommotiid *Micrina etheridgei* and the paterinid (cryptotretid) brachiopod *Askepasma toddense* is slightly different. These forms are invariably recovered in huge numbers (often representing thousands of individuals) as disarticulated valves in moderate to high energy skeletal grainstones deposited between individual build-ups. The sclerites/valves of these taxa commonly occur as cross-bedded, chaotically oriented, coquinas or as "nested" to fragmentary bioclastic debris in synsedimentary "neptunian dykes" which pervaded some parts of the shallowest carbonate platform. Available evidence suggests that *Micrina* and *Askepasma* may have selectively inhabited the fringes or channels between archaeocyathid-microbial-sponge build-ups. The variation in mitral:sellate sclerite ratios for *M. etheridgei* across the carbonate platform range from highly skewed in high energy, shallow water reefal facies to almost 1:1 in slightly deeper, subtidal (outer shelf) and lower energy carbonate environments. This range of ratios is closely comparable to typical pedicle: brachial valve ratios recorded in a number of post-Cambrian crown group brachiopod assemblages from similar environments.

Poster

TOARCIAN BRACHIOPOD ASSEMBLAGES

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The Toarcian is a key period in Earth history because it is characterised by intense tectonic activity that directly or indirectly led to numerous changes in palaeogeographic, palaeoceanographic and sedimentological settings. These changes had major repercussions on marine ecosystems, culminating in a 2nd order mass extinction and subsequent faunal turnovers. In this contest, brachiopod assemblages underwent complex reorganization and extinction-survived taxa show several radiations that led them to have wide areal colonizations.

Here we take into consideration different Toarcian brachiopod assemblages and discuss them from palaeoecological, biostratigraphical and palaeogeographical points of view, giving particular attention to the following aspects:

- the frequent turnover linked to the eustatic changes,
- the distribution in different micro-environments of Tethyan carbonate platforms,
- the occurrences of disaster forms linked to the 2nd order extinction,
- the blooming of species belonging to long-lived taxa,
- the chance to build a detailed brachiopod based biostratigraphical zonation,
- the discrimination of palaeobiogeographical provinces.

Poster

EARLY TRIASSIC BRACHIOPODS FROM OMAN

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The first description of brachiopods (rhynchonellids and spiriferids) from the Lower Triassic (Lower Induan, *isarcica-carinata* zones) Al Jil Formation in the Wadi Wasit area of Oman is presented here. These small brachiopods belong to a diverse, partially silicified fauna including micro-gastropods, echinoderms, bivalves, and ostracods (see Krystyn et al. 2003).

The brachiopods have been assigned to *Orbicoelia extima* (Grant) and ?*Lissorhynchia* n.sp, and each species has been analyzed taxonomically and biometrically. Moreover this association has been examined from a palaeobiogeographical and palaeoecological point of view and the most important results of this analysis are:

- Both species show a micromorphic look, following the general trend of many Permian/Triassic boundary marine invertebrates, possibly because of productivity decrease.
- *Orbicoelia* survived the end-Permian mass extinction due to a number of survival mechanisms/strategies, such as opportunism, generalism, eurytopy, widespread and rapid biogeographical distribution, and chance/luck. This was an unspecialised and morphologically simple dysaerobic genus, able to withstand both low and well oxygenated environments.
- The presence of *?Lissorhynchia* in the lower Induan (upper Griesbachian) could represent the oldest record of this genus previously known from the upper Induan (Dienerian). Moreover this new species seems to have intermediate characteristics between *Prelissorhynchia* to *Lissorhynchia.*

Krystyn, L., Baud, A., Richoz, S. & Twitchett, R.J., 2003. A unique Permian-Triassic boundary section from Oman. *Palaeogeography, Palaeoclimatology, Palaeoecology* 191, 329–344.

A REORGANIZATION OF THE NORTH AMERICAN BRACHIOPOD FAUNA ACROSS THE MID-CARBONIFEROUS BOUNDARY

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Previous research has noted a coincidence between the onset of the late Palaeozoic ice age (LPIA) and a minor global extinction event. Brachiopod faunas were particularly hard hit in some regions and post-extinction faunas exhibit profound shifts in their latitudinal distributions as compared to pre-extinction faunas. Herein, we investigate the response of North America brachiopod faunas to global climate changes in the Carboniferous, in particular, across the mid-Carboniferous boundary.

As in the rest of the world, Late Serpukovian rock units in North America, just prior to the mid-Carboniferous boundary, record the transition from global greenhouse to icehouse climate. Published carbon isotope curves record the onset of glaciation as early as the Kinderhookian (Tournaisian), with increasingly higher frequency and amplitude $\delta^{13}C$ values through the second half of the Chesterian (roughly Serpukovian) and significant positive C isotope excursions across the mid-Carboniferous boundary. One consequence of the shift from global greenhouse to icehouse conditions is a transition of depositional regimes from massive thick-bedded carbonates (relative sea level stability) to mixed carbonate-siliciclastic deposition recording high-amplitude, high-frequency sea level changes associated with polar ice cap volume fluctuations.

The exact link between the greenhouse-icehouse transition and the reorganization of North American brachiopod faunas is unclear. We note that generic diversity of several brachiopod orders shows a decline just prior to the mid-Carboniferous boundary and coincident with carbon isotope fluctuations. In this study we evaluate the effect that the climatic transition has on brachiopod faunas in light of three distinct, although not necessarily mutually exclusive hypotheses. First, we note that icehouse times are characterised by compartmentalised marine biotic environments, a result of high-frequency and –amplitude oscillations in sea level. This compartmentalization could lead to less cosmopolitan faunas in the late Carboniferous. Second, we evaluate the substrate affinities of genera in our database because widespread carbonate deposition is uncommon in Late Carboniferous icehouse environments. If many early Carboniferous genera show a preference for carbonate substrate this could help to explain the observed faunal reorganisation. Finally, we evaluate the geographic ranges of several common genera to determine if high-latitude genera preferentially survived the extinction event.

CROWNS AND STEMS: DEFINING BRACHIOPODA AND PAN-BRACHIOPODA

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The designation of "stem-groups" requires the definition of the crown clade to which they refer, as well as the total clade that encompasses both. We recently defined the crown clade Brachiopoda (the most recent common ancestor of all living brachiopods and all its descendants) and the total clade Pan-Brachiopoda (Brachiopoda and all organisms that share more recent common ancestry with Brachiopoda than with any other mutually exclusive crown clade) in the Companion Volume to the *PhyloCode* (Cantino & de Queiroz, 2007) that aims to name clades in explicit reference to phylogeny. The node-based definitions we adopted for the purposes of compositional stability do not easily accommodate recognition of the phylogenetic location of more than 99% of extinct species in Brachiopoda and Pan-Brachiopoda, so we have reevaluated the morphological "synapomorphies" that have defined Brachiopoda in the Linnaean system, in view of these node-based definitions.

Much attention has focused recently on: (1) reconstructing patterns of phylogenetic relationship among lophotrochozoan crown clades using several different lines of molecular evidence, and (2) describing and identifying as putative brachiopod stem-group members several Early Cambrian fossils. In order to investigate the intersection of these two disparate lines of research, we combined our morphological and molecular data sets, gathered and refined over two decades, to analyse patterns of phylogenetic relationships among the major clades of brachiopods plus phoronids, using polyplacophorans, polychaetes, and nemerteans as outgroups, as in various molecular analyses of lophotrochozoan relationships. Preliminary analyses yield results that place phoronids either as the sister group of brachiopods or in a basal polytomy with inarticulated and articulated clades. We will discuss the implications of these, and later, "total evidence" results for hypotheses of lophotrochozoan morphological character evolution. We will show how different interpretations of the composition of crown and stem lead to different evolutionary interpretations of the morphology and evolution of brachiopods and putative brachiopod stem-group fossils.

IN THE LOOP — 400 MILLION YEARS OF TEREBRATULIDE EVOLUTION: A TRIBUTE TO G. ARTHUR COOPER

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In this special symposium honoring Gustav Arthur Cooper, it is fitting to focus attention on the terebratulide brachiopods. Over the course of Cooper's long and remarkable career, as he worked systematically on brachiopod faunas from Cambrian to Recent, the later years of his life were occupied largely by terebratulides, since they make up approximately two thirds of extant brachiopod generic diversity. The tradition, which Cooper exemplified, of studying brachiopod faunas time-period by time-period is necessary and invaluable in order to document morphological diversity. However, to investigate questions of evolution and identify patterns of change in morphology over long periods of time, a longitudinal, phylogenetic approach, in addition to a horizontal, stratigraphic approach is necessary to utilise all sources of informative data that exist, to understand more completely the 400-million year history of terebratulide brachiopods.

Terebratulida is a clade that shares ancestry with retziid athyridids and, more distantly, with atrypids, evolving sometime in the latest Silurian. The Palaeozoic terebratulide fauna is notably different from the post-Palaeozoic terebratulide fauna: all Palaeozoic terebratulides have only short loops; post-Palaeozoic terebratulides include short-loop lineages, but are particularly distinguished by the origin and striking diversification of long-loop morphologies. Both genetic and morphological phylogenetic analyses indicate that short-loop and long-loop forms are sister groups. Because representatives of both loop-types are extant, it is necessary to embrace molecular (e.g., Cohen 2007) and morphological (e.g., Lee et al. 2006) data, as well as ontogenetic data (e.g., MacKinnon & Lee 2006) to begin to understand the evolutionary dynamics behind the major transition from Palaeozoic to post-Palaeozoic terebratulide faunas. Under what circumstances did the long-looped clade evolve when it did? Why did the short-looped clade persist? We will discuss several unresolved issues regarding terebratulide morphological evolution, including: the origin of long-looped terebratulides; patterns of loop development and evolution in short-looped forms; and the most effective way to fully incorporate molecular evidence into the body of traditional, morphological evidence used to reconstruct terebratulide evolutionary history. Finally, we will present an overview of the morphological diversity of modern short and long-looped terebratulide morphology and attempt to explain why terebratulides are the dominant brachiopod clade 400 million years after they first appeared in Palaeozoic oceans.

BRACHIOPOD DIVERSIFICATION DURING THE BENTHIC RECOVERY FOLLOWING THE END-PERMIAN MASS EXTINCTION

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Global statistical studies show that the final recovery of benthos after the end-Permian mass extinction occurred in the Anisian (early Middle Triassic). Anisian radiation of benthos is well indicated by faunas uncovered from the Qingyan Formation of Guiyang, Guizhou Province, southwest China, from which, so far, more than 300 species including 15 leading fossil groups such as the Ammonoida, Annelida, Anthozoa, Bivalvia, Brachiopoda, Bryozoa, Cnidaria, Crinoidea, Echinoidea, Foraminifera, Gastropoda, Nautiloidea, Ostracoda, Porifera, and Scaphopoda have been reported. Of these, brachiopods are extremely abundant and numerically dominate the level-bottom marine communities. They comprise 23 species in 18 genera in sharp contrast to the mere total of four species in four genera known from the entire Early Triassic in South China, and thus mark the recovery/radiation of this clade following the Permian-Triassic crisis. However, the Qingyan Formation is an 880-m-thick succession, with a depositional duration of ~5 million years, and most of Anisian fossils are yielded from the Leidapo Member, the upper part of the formation. Thus, this study attempts to assess the diversification mechanism and process of the brachiopod faunas during the Anisian on the basis of a quantitative analysis. Seven brachiopod communities are recognised throughout the entire Anisian. Their substratum types vary from thin-bedded muddy limestone, medium-bedded limestone to massive bioclastic limestone. When compared with the late Anisian faunas, the early Anisian communities have the similar abundance but are obviously less diversified. Community replacements throughout the Anisian may have been controlled by environmental disturbances.

LATE DEVONIAN BRACHIOPODS FROM THE JUNGGAR BASIN, NORTHWEST XINJIANG, CHINA

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Late Devonian sediments, well exposed in northern Xinjiang were formerly referred to as the Hongguleleng Formation, a unit whose stratotype is located about 3 km west of Boulongour Reservoir, and 30 km north of Hoxtolgay in the Hoboksar Autonomous Mongolian County. On the basis of sedimentary characteristics two units can be readily discriminated. Unit one, about 64 m thick, consists of bedded limestones (sedimentation commencing in latest Frasnian) with, at the base, brachiopod-rich beds with subordinate bryozoans, ostracods and crinoid ossicles. Unit two is 30 m in total thickness and consists of flaggy limestone interbedded with mudstones. Above the Hongguleleng Formation s.s. is the Somontoma Formation, consisting principally of 100 m of pink and green shales; it has a much lower diversity of brachiopods compared with the Hongguleleng Formation s.s.

The abundant and highly diverse Hongguleleng faunas consist of brachiopods (Chen et al. 2002; Chen & Liao 2006), bryozoans (Xia 1997), crinoids and blastoids (Lane et al. 1997; Waters et al. 2003) and conodonts (Xia et al. 1997; Mawson et al. unpub.) with subordinate tabulate and solitary rugose corals (Pickett unpub.), ostracods (Xia 1997), trilobites and fish micro-remains (Xia 1997). Gastropods, bivalves and sponges are rare; trilobite diversity is conspicuously low. The 32 presently-known brachiopod genera (Chen unpub.) are assigned to 12 families. Beds teeming with small chonetids are common at the base of the formation, especially in the Boulongour and Genaren sections. Rhynchonellids are prominent, notably *Sinotectirostrum*, *Ptychomaletoechia*, *Ripidiorhynchus,* *Cyphoterorhynchus*, *Evanescirostrum*, *Eoparaphorhynchus*, *Rugaltarostrum*, *Planovatirostrum*, *Megalopterorhynchus* and *Nayunnella*. Spiriferids, the group of second importance, is characterised by *Palaeospirifer*, *Uchtospirifer*, "*Cyrtospirifer*" and "*Mucrospirifer*". Athyrids are significant but are notably less diverse that the rhynchonellids and spiriferids, e.g. *Athyris* and *Cleiothyridina*. Productids are represented mainly by *Productella* and *Productellana*. Schizophoriids are occasional especially in the Qiligoa Section and in unit two of the stratotype Boulongour Section.

Chen Xiuqin, Zhang Zixin & Jin Yugan, 2002.The discovery of the genus *Yunnanella* Grabau, 1923 from northern Xinjiang. *Alcheringa* 26(3), 451-458.

Chen Xiuqin & Liao Zhuoting, 2006. The palaeoecological characters of the brachiopod genus *Planovatirostrum* Sartenaer, 1970. *Acta Palaeontologica Sinica* 45(1), 77-82.

Lane, N.G., Waters, J.A & Maples, C.G., 1997. Echinoderm faunas of the Hongguleleng Formation, Late Devonian (Famennian), Xinjiang-Uygur Autonomous Region, People's Republic of China. *Paleontological Society Memoir* 47, 43 pp.

Waters, J.A., Maples, C.G., Lane, N.G., Marcus, S., Liao Zhuoting, Liu Lujun, Hou Hongfei & Wang Jinxin, 2003. A quadrupling of Famennian pelmatozoan diversity: New Late Devonian blastoids and crinoids from northwest China. *Journal of Paleontology* 77(5), 922-948.

Xia Fengsheng, 1997. Marine microfaunas (bryozoans, conodonts and microvertebrate remains) from the Frasnian-Famennian interval in northwestern Junggar Basin of Xinjiang in China. *Beiträge zur Paläontologie* 22, 91-207.

WHEN DID BIVALVE TAKE OVER BRACHIOPOD'S WORLD? NEW OBSERVATION TO AN OLD QUESTION

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The Permian-Triassic mass extinction fundamentally redirected the macroevolution of both brachiopod and bivalve faunas and precipitated the governorship changeover in marine ecosystems between these two fossil groups. The phyletic switch from rhynchonelliform brachiopods to bivalves across the P/Tr boundary and the causes have long been discussed. Most authors attempted to answer the "brachiopod-bivalve question" by comparing these two clades in terms of functional ecology and physiologic advantages and disadvantages to adapt the stressed environments. More recently, Fraiser and Bottjer (2007) quantitatively assessed the bivalve ecologic takeover and concluded that, as an ecological dominant, bivalve replaced rhynchonelliform brachiopods at the P/Tr boundary. The study of 23 P/Tr communities from platform to basin settings enables us to look closely the roles that these two clades played in marine communities over this critical period. Thus, this study presents the first data demonstrating when and where bivalves took over brachiopod's governorship in marine communities. Preliminary study shows that the governorship switch from brachiopods to bivalves in marine communities has been facilitated by two pulses of the end-Permian mass extinction and the whole takeover process took about 200 ka cross the P/Tr boundary. Bivalve ecological takeover initially occurred immediately after the first P/Tr extinction in shallow water habitats and was eventually completed in all niches after the second P/Tr event. In addition, the bivalve-brachiopod change-over event is also assessed in a large scale from high-latitude regions to tropic areas in light of macrofaunal assemblage successions throughout the P-Tr transition

Fraiser, M.L. & Bottjer, D., 2007. When bivalves took over the world. *Palaeobiology* 33(3), 397–413.

IMPACT OF PERMIAN ICEHOUSE-GREENHOUSE CLIMATIC CHANGES ON BENTHIC ECOSYSTEMS: BRACHIOPOD'S FOSSIL RECORD FROM HIGH-LATITUDE TO TROPIC REGIONS

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The Permian witnessed the most dramatic climatic change in our planet during its Phanerozoic history. The Late Carboniferous to earliest Permian glaciation resulted in huge ice sheets covering much of the Gondwana continent in the south and also cooled vast Boreal regions in the north. The integration of palaeogeographical, biogeographical and geochemical data show that the glaciation terminated in late Sakmarian (Early Permian) and from then the Earth's climate evolved to a greenhouse regime towards the end-Permian. The global warming trend also appears to have accelerated during the Late Permian, and in particular prevailed on a global scale throughout much of the Permian-Triassic transition. Thus, the extreme climates also tested benthos' adaptation tolerance during Permian times. The impact of climatic changes, particularly during the Late Permian global warming, on marine benthos is here assessed by analysing the Permian fossil records of brachiopod faunas from both south and north high-latitude regions (Western Australia and Greenland-Spitsbergen) to tropic region such as South China. Brachiopod faunas are mostly sessile organisms and thus sensitive to climate change. The assessment of the Permian brachiopod assemblages from these regions shows that the icehouse-greenhouse climatic switch triggered a significant increase in biodiversity in low-latitude regions, whereas the global warming resulted in a decrease in biodiversity and body sizes in the high-latitude regions. Both the Gondwana and Greenland faunas were characterised by cold-water brachiopods during the Early Permian, some of which invaded some temperate-subtropical to even tropical habitats in the Middle-Late Permian. In contrast, the palaeoequitorial Tethyan faunas were mixed with some Gondwanan elements during the Early Permian, dominated by the tropic elements in the Middle-early Late Permian, and then, curiously, were invaded by several distinct cold-water brachiopod species in the latest Permian. The late Permian global warming may have destroyed most of the cold-water brachiopod habitats. As a result, on one hand, some relatively adaptable cold-water elements migrated involuntarily to the hospitable deep-water niches of the low-latitude region due to collapse of their original habitats. On the other hand, some Tethyan elements inhabiting tropical zone expanded their niches to the relatively high-latitude regions due to increase in water temperature. In addition, as a possible consequence of the late Permian global warming, some shallow-water brachiopods were forced to settle in the relatively hospitable deep-water settings in the low-latitude region.

PERMIAN-TRIASSIC EVOLUTION OF BRACHIOPOD FAUNAS: MASS EXTINCTION, RECOVERY, BODY SIZE DYNAMICS, COMMUNITY STRUCTURAL CHANGES, AND CLIMATIC ZONE'S CONTROLS

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The Permian-Triassic transition witnessed the most important evolutionary stage of brachiopod faunas since their rise 540 million years ago. The end-Permian mass extinction destroyed most of the brachiopod-dominated ecosystems in the Permian oceans. Since then, brachiopods lost their dominance in most of the Triassic and younger marine communities. Our earlier study focused on the short interval of the end-Permian mass extinction and brachiopods' responses to the ecologic crisis as well as their rebounds in the Early Triassic oceans. Surprisingly, brachiopods were actually the second largest fossil group surviving the first episode of the P-Tr crisis, although most of them were wiped out in the second episode of the same catastrophic event. Brachiopod's recovery was profoundly delayed. The normalised community did not recover until late Anisian, approximately 10-11 million years after the P-Tr event. In the present study, we undertake analysis of brachiopod's body size changes throughout the Late Permian to Late Triassic based on the newly established global P-Tr brachiopod database. Body size dynamics reflected the collapse and rebuilding of the brachiopod communities during the P-Tr transition. As part of our P-Tr benthic community database, a large quantity of brachiopod communities from both side of the P-Tr boundary has been analysed. The new study shows that brachiopod community structures changed significantly from the latest Permian to Early-Middle Triassic times. In addition, brachiopod's mass extinction and recovery are re-assessed based on numerical data from various climate zones. The potential climatic factors affecting brachiopod's extinction and recovery are also discussed in a global scale based on the global distribution pattern.

MORPHOLOGY AND SYSTEMATICS OF LATE PALAEOZOIC SYRINGOTHYRIDS FROM WEST-CENTRAL ARGENTINA

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The syringothyrids constitute an interesting group of spiriferinid brachiopods whose generic diagnoses are based mainly on their ventral interior features. Study of abundant well-preserved specimens of syringothyrids from the late Palaeozoic marine sequences of the central western Argentinean basins allowed us to evaluate the importance of the small changes in the syrinx, delthyrial plate and median septum for generic recognition, as well as their temporal implications. Also, the review of Argentinean species previously described by other authors indicates that several external features used in their definition are widely variable through ontogeny reflecting intra-specific variations lacking systematic significance.

Syringothyrids from the low diversity Early Carboniferous (Tournasian-Visean) faunal assemblages from the Río Blanco basin are herein assigned to a new (?) Septosyringothyridinae genus which could be also present in equivalent sequences from northern Chile. Although the studied material is scarce, internal moulds show a conspicuous delthyrial plate slightly below the plane of interarea and a distinctive incomplete wedge shaped syrinx connected to the valve floor by a median septum, that suggest a possible new genus.

In the Late Carboniferous (Late Serpukhovian-Bashkirian) and Early Permian (Asselian-Sakmarian) intervals, the Argentinean syringothyrids are mainly represented by septosyringothyrids which have been usually assigned to the genus *Septosyringothyris* Vandercammen, whose occurrence in Argentina would constitute the only record for Gondwana. Restudy of the Carboniferous species *Septosyringothyris keideli* (Harrington) from its type locality of the Leoncito Formation, and *Septosyringothyris* sp. aff. *S. keideli* from the Las Juntas Formation confirms their inclusion in the genus *Septosyringothyris*, although the typical median septum connecting the syrinx to the floor of valve appears to be shorter in the Argentinean species. However, most of the septosyringothyrids studied from the Permian sequences of the Paganzo, Río Blanco and Calingasta-Uspallata basins (Tupe, Río del Peñon, Quebrada Larga, Del Salto and Agua del Jagüel formations) bear a large syrinx inserted between a very short delthyrial plate (not completely included in the delthyrial plate as in *Septosyringothyris*) and a distinctive median septum, which becomes more conspicuous in mature specimens. These features allow us to reassign the Permian Argentinean septosyringothyrid species (*Septosyringothyris jaguelensis* Lech, *Septosyringothyris* sp. aff. *S. jaguelensis*, *Septosyringothyris globosa* Lech and, probably, *Septosyringothyris feruglioi* (Amos) and *Septosyringothyris* sp. aff. *S. feruglioi*) to a new genus.

The Early Permian Argentinean syringothyrids are more diversified than in the Carboniferous *Levipustula* faunal assemblages developed under glacial conditions. This is consistent with the important Permian climatic amelioration recorded in the central western Argentinean basins at that time.

PERMIAN BRACHIOPOD FAUNAS OF NORTHERN CHILE

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Brachiopod assemblages from the Permian carbonate sequences of northern Chile have been studied in different localities (Cerros de Cuevitas (Salar de Navidad area), Cerro El Árbol and Cerro 1584 (Augusta Victoria area) and Cerro Juan de Morales in the Iquique area). These assemblages can be integrated into a highly diversified fossil fauna composed of bryozoans, crinoids, bivalves and gastropods.

A preliminary study suggests that the brachiopod faunal assemblages identified are typically dominated by large shells of two productid genera: *Kochiproductus* and *Waagenoconcha*. However, *Waagenoconcha* appears restricted to the northernmost part of the studied area (Juan de Morales Formation), where it is associated with Artinskian-Kungurian foraminifera. *Kochiproductus*, accompanied by a more diversified brachiopod fauna (mainly species of the genera *Kozlowskia*, *Cleiothyridina*, *Composita, Neospirifer*, *Hustedia*), is the dominant and common element in the rest of the localities studied. The age of these localities, bearing *Kochiproductus*-dominated brachiopod fauna, appear to be slightly older than the Juan de Morales Formation.

The brachiopod faunas from northern Chile show clear affinities with those from the Copacabana Formation of Perú and its equivalents in Bolivia, as well as sharing some common elements with faunas from the northwestern Argentina (Arizaro Formation). *Kochiproductus* is also known from Permian clastic sediments in central western Argentina (Río Blanco and Paganzo basins), where it occurs in mixed faunas with boreal and Tethyan elements.

Geological Society of Australia, Abstracts No. 95
6th International Brachiopod Congress, Melbourne, Australia, February 2010

Poster

MORPHOMETRIC ANALYSIS OF *SOARESIRHYNCHIA BOUCHARDI* (DAVIDSON, 1852): TAXONOMICAL AND PALAEOECOLOGICAL IMPLICATIONS

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Soaresirhynchia bouchardi (Rhynchonellida, Basiliolidae) is the only *Soaresirhynchia* species recorded in the Iberian Chain (northeastern Spain). In this region and other areas around the Iberian massif (Portugal, Algeria, Morocco), this species shows a great polymorphism during the lower Toarcian (Lower Jurassic). A large number of morphotypes have been defined, some of them considered sometimes as nominal species. The morphometric analysis carried out in this work is an attempt to clarify their taxonomical status.

The studied sample has been collected from the Strangewaysi Subzone (lower Serpentinum Zone) in the Toarcian of Calanda (Teruel, Spain). 17 numerical variables and 17 morphometric indices (ratios between numerical variables) have been considered. A preliminary univarate analysis shows that distribution of values of different variables fits with an expected unimodal pattern. Such distribution allows us to consider the sample as representative of a monospecific population. Two types of principal components analysis (PCA), one with the numerical variables and the other with the morphometric indexes, have been carried out. In both cases the scatter diagrams obtained for the first three principal components show a homogeneous dispersion area with high individual density in the central zone and lower density in the peripheral area, so the distribution seems to fit with a normal pattern. In these diagrams the dispersion areas of the different morphotypes recognised in the sample appear poorly differenciated with a great superposition and very close position of their mean values. Both unimodality of variable values and the poorly differentiated distribution of the morphotypes in the multidimensional space prove the continuity of the morphological variability within the studied sample. It could be considered as representative of that recorded in near areas because of its size and similarity in the different morphotype proportions. Consequently the consideration of different morphotypes as separate nominal species may be neglected.

The occurrence of *S. bouchardi* at the Iberian Basin marks the recovery phase after the extinction event that took place at the Tenuicostatum-Serpentinum Zones boundary. Firstly it is the only brachiopod recorded at the basin, but later it is associated with the taxa that characterise the Spanish Bioprovince of brachiopods (*Homoeorhynchia, Choffatirhynchia* and *Telothyris*). The existence of changes in the morphological variability of *S. bouchardi* related with the co-occurrence of these taxa has been evaluated. With this aim the variation in the distribution ranges of the PCA scores across the stratigraphical section was analysed. A trend toward overall size reduction is generally recognised. Also a reduction in the dispersion of the values can be observed at the uppermost part of the section, where the new taxa are recorded, whereas the distribution amplitude is greater at the lower part. These variability and size reduction is accompanied by a decrease in the number of morphotypes recognised.

The higher morphological variability at the lower part of the section, where *S. bouchardi* is the only brachiopod taxon recorded, reflects its pioneer nature and opportunism in the colonization of the vacant niches after the Tenuicostatum–Serpentinum Zones extinction event. The decrease in the morphological variability at the uppermost part of the section, related to the occurrence of new taxa, could reflect a niche reduction caused by ecological competence during the colonisation of these taxa.

The conclusions of this preliminary study should be confirmed with similar analysis of samples from other localities both at the Iberian Chain and other areas around the Iberian massif, were high morphological variability in *S. bouchardi* has also been reported.

SPORADIC OCCURRENCE OF JURASSIC NUCLEATIDS IN NON-ALPINE AREAS OF SPAIN: PALAEOECOLOGICAL AND PALAEOBIOGEOGRAPHICAL SIGNIFICANCE

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Nucleatids (Superfamily Dyscolioidea, Family Nucleatidae) are a well-defined group of Jurassic terebratulids. They display a very conservative morphology characterised by moderately to strongly unisulcate shells. This morphology is recorded repeatedly from Sinemurian (Lower Jurassic) to Cenomanian (Upper Cretaceous) showing a wide palaeobiogeographical distribution across the so-called Mediterranean Province of the Tethyan Realm. There is a general agreement in assuming that, during the Mesozoic this province represented deeper environments than the Northwestern European Province.

Representatives of this group have been recorded sporadically at shallower proximal areas. Two case-studies of this situation from East Iberian platform (northeastern Spain) are presented. The first case comprises one single specimen of *Linguithyris nepos* (Canavari) collected from the Upper Aalenian of the Catalonian Coastal Range. This record is related to an episode of relatively free communication with open seawaters. The second case consists of a population composed by both juvenile and mature individuals of *Linguithyris bifrons* (Oppel). The material has been collected from the Lower Callovian of the Iberian Range from a single bed that marks a regional transgressive maximum. This finding agrees with other sporadic records reported from Portugal and Algeria, which are also related to a generalised flooding event of wide areas across epicontinental seas of the Western Tethys. Other reports of Jurassic Nucleatidae recorded outside the Mediterranean Province are entirely similar in terms of their sporadic occurrences and lack of lasting settlement.

Adaptation of nucleatids to deep, more stable and quiet environments with low food supply is suggested by their morphological stasis and highly discontinuous record in shallow waters. Therefore, the repeated occurrence of representatives of nucleatids at discrete moments during the Jurassic can be interpreted as revealing recurrent intervals of special environmental conditions, which would allow the dispersion of such forms in the platforms. As environmental conditions turn back to the normal situation at the platforms, they would become harsh environments for these nucleatids, hence making adaptation and evolution of the group unlikely in shallow platform environments. Such environments would become evolutionary dead-ends for this deep-environment group.

FROM SHALLOW TO DEEP, HOT TO COLD, AND ACME TO CRISIS: BRACHIOPOD SHELLY COMMUNITIES FROM THE ORDOVICIAN THROUGH DEVONIAN

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Concomitant with the spectacular expansion of shelly lophophorate communities on the global seafloor in the Mid- to Late Ordovician (the great "Ordovician explosion'), brachiopods sought out niches from the shallow nearshore to the deeper ocean, and the equator to the cool temperate settings. The prime eco-setting of mid- to late Ordovician brachiopods appears to have been on relatively shallow, stable, equatorial carbonate shelves particularly favoured by some orthides, pentamerides and atrypides. Large shell sizes exceeding 2 cm were rare in early taxa prior to the Katian, at which time seafloor-covering brachiopod shellbeds evolved. Roughly equal numbers of brachiopods moved from deep to shallow environments during their history, as the converse pattern from onshore to offshore. Very few early brachiopod genera seem to have been adapted to high latitude, cool temperate climates in the Cambro-Ordovician. From an early diversity acme in the Late Ordovician, during which most of the Palaeozoic brachiopod orders had evolved and expanded, the first diversity crash occurred around the Ordovician/Silurian boundary glaciation events. Early Llandovery revival favoured pentameride and spire-bearer communities that came to dominate the Siluro-Devonian shelly biota in size and number. The Siluro-Devonian saw a peak in both brachiopod diversity and equatorial reef expansion, with concomitant new niches available. By the Early Devonian some brachiopod groups shifted towards high latitudes, e.g., the Malvinokaffric realm: these included strophomenides, orthides, rhynchonellides, spiriferides and terebratulides (the last may well have originated in cool settings and maintained that ever since). The Frasnian-Famennian stepped extinctions, matched by global cooling, saw the total elimination of the atrypides and pentamerides: for some 27 myr, the global reef ecosystem collapsed completely. From then on in the Palaeozoic, niches were occupied by rhynchonellides, productides, orthides, spiriferides and athyridides.

BRACHIOPOD SHELLS RECORDING AMBIENT WATER TEMPERATURE WHILE UNDER STRICT BIOLOGICAL CONTROL

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The strict biological control exerted in the formation of Rhynchonelliform brachiopod shells is evident in many aspects of their ultrastructure and crystallography. Atomic force microscopy (AFM) highlights the fact that the calcite fibres comprise large numbers of nanogranules. These nanogranules are added incrementally as fibres grow yet electron backscatter diffraction (EBSD) indicates that the fibres are effectively single crystals or mesocrystals with the calcite *c*-axis perpendicular to the fibre axis. Punctae permeate the calcite fibres of the secondary layer, and indeed the primary layer. X-ray tomography reveals the 3-D complexity and striking uniformity of the punctae distribution and growth which again requires superb biological control.

It is within this context of exquisite biological control that we must consider the possibility that brachiopods record environmental conditions such as seawater temperature. With their long geological history and stable low magnesium calcite, Rhynchonelliform brachiopods are attractive sources of such environmental data.

In most species of Rhynchonelliform brachiopods, the outer primary layer of acicular calcite is isotopically light in both $\delta^{18}O$ and $\delta^{13}C$ while the secondary layer calcite fibres are in oxygen isotope equilibrium with ambient seawater. Thus the calcite of the secondary layer fibres records the ambient water temperature despite the obvious biological control exerted in fibre formation. In addition to isotopic composition, the primary and secondary layers differ in magnesium content. The primary layer contains more magnesium than the secondary layer. Magnesium concentrations tend to be fairly constant throughout the inner half of the secondary layer where the magnesium concentration reflects the ambient temperature. X-ray absorption near edge spectroscopy (XANES) at the Mg-K edge confirms that magnesium is a true lattice component in brachiopod shell calcite and thus ideal substitution of calcium by magnesium has been confirmed opening up the possibility of using the Mg:Ca ratio in brachiopod calcite as another proxy for water temperature.

Although there remains much to be understood about how this precise biological control is achieved, the recording of ambient water temperature by brachiopod shell calcite, while under such strict biological influence, is counter-intuitive.

PALAEOGENE BRACHIOPODS FROM THE LATE EOCENE OF AUSTRIA AND THE OLIGOCENE OF HUNGARY

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Eocene brachiopods have been published from several areas of Europe but until now they were unknown from Austria. Recently I have studied 54 Late Eocene (Priabonian) samples from two boreholes of the Upper Austrian Molasse Zone (Helmberg-1 and Perwang-1) and a surface locality of the Waschberg Zone (Reingruberhöhe). All samples were collected by Kamil Zágoršek for Bryozoa studies. As he used a chemical method and treated the samples in acetic acid for several weeks, the preservation of brachiopods is very good even in the case of the smallest juvenile specimens. The three localities yielded altogether more than 2500 micromorphic specimens (Helmberg-1: 568, Perwang-1: 1457, Reingruberhöhe: 536). The taxonomic composition of Perwang-1 and Helmberg-1 samples is very similar: dominant taxa are *Orthothyris pectinoides* (66.2% and 42.4%, respectively) and *Terebratulina tenuistriata* (10.21% and 33.3%, respectively). The small and smooth terebratulides (e.g. "*Terebratula*" *italica*) are relatively frequent in Perwang samples (17.9%), while *Platidia* sp. is moderately common in Helmberg samples (9.7%). All the other genera (*Argyrotheca*, *Megathiris*) are less significant in both localities. However, Reingruberhöhe samples show significantly different taxonomic composition. The most frequent taxa are *Argyrotheca* (65.3%) which is not significant in the boreholes and *Lacazella mediterranea* (25.7%), which is completely missing at the former two localities. Small and smooth terebratulides (5%), *Megathiris* (2.8%) and *Terebratulina* (0.9%) are less important faunal elements at Reingruberhöhe. On the basis of his bryozoan studies, Zágoršek interpreted Helmberg-1 and Perwang-1 samples as belonging to a cool water and/or deep-water basin with active upwelling of cold water (at least 200 m and perhaps as much as 500 m depth). According to him, the Reingruberhöhe fauna originally lived in a shallow environment and has been re-deposited in more deep-water sequences. These interpretations are confirmed by brachiopod results. The taxonomic composition of the Late Eocene shallower and deeper water brachiopod faunas is similar to Recent Mediterranean ones (Logan 1979) where *Argyrotheca*, *Megathiris* and *Lacazella* dominate in shallow waters (ranging down to about 200 m), while *Gryphus*, *Terebratulina*, *Platidia* and *Megerlia* characterise the eurybathic species, which are more typical of the bathyal zone. It suggests that more or less the same depth differentiation among Recent brachiopod genera was already present in the Late Eocene seas.

Oligocene brachiopods of the Central Paratethys are very poorly known. Báldi et al. (1961) mentioned some *Megathiris decollata* and *Terebratula* sp. from the glauconitic sandstone of Nyárjas Hill at Noszvaj (North Hungary). Recently I have found dozens of *Megathiris* and *Argyrotheca* from the Lepidocyclina Marl of the same locality in the collection of Natural History Museum in Vienna, and subsequently I have washed a sample (8-10 kg) from this level. The brachiopod fauna of the Lepidocyclina Marl is surprisingly rich both in specimen number (more than 2000) and in diversity (10 species of 9 genera). Five-eighths (62.5%) of the specimens belong to *Megathiris detruncata*. *Argyrotheca* is represented by two species (18.1%): more frequent is *A. cuneata* but *A. cordata* is also present. Until now, both species were known to occur only from the Miocene deposits of the Central Paratethys, and the same is true for *Terebratulina retusa* (8.6%). *Megerlia* sp. is the first occurrence in the Oligocene not only for the genus, but also for family Kraussinidae and superfamily Kraussinoidea. *Gryphus* (2.1%) is represented by small specimens of *G. miocenicus*. *Orthothyris*? sp. (3.5%) is known from the Cretaceous to the Eocene, but the Hungarian Oligocene specimens are different from *O. pectinoides* occurring in the Eocene of Italy, Hungary and Austria. *Platidia*? sp. is present only as a small juvenile specimen. Inarticulated brachiopods are represented by *Novocrania*. A single juvenile *Aphelesia*? sp. is the only rhynchonellide. The taxonomic composition of this Oligocene material is very similar to that of the Miocene to the Recent brachiopod faunas in the Mediterranean and Central Paratethyan faunas, but *Orthothyris*? may be a survivor of the earlier Tethyan fauna.

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ARTIFICIAL FERTILIZATION IN *LINGULA ANATINA*: A PORTAL TO BRACHIOPOD DEVELOPMENTAL GENETICS

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Early development is a key to understanding evolution of not just shells but also other body plan components in brachiopods. To observe the processes repeatedly and carry out embryological experiments routinely, it is desirable to have a model system from which embryos are obtained by artificial fertilization. Such a system has been developed for *Lingula anatina* collected from Amami Island, southern Japan. Monthly measurements of gonad index and inspection of plankton hauls for a year indicated that natural breeding takes place in middle September in this population of *Lingula*. For artificial fertilization, mature individuals were collected in early September and reared in an aquarium. Injection of dibutyryl cAMP into the main body cavity, a method pioneered by Freeman (1994), proves to be effective in the induction of spawning. The eggs mixed with sperms that had been activated by ammonia treatment fertilised normally, allowing us to observe embryogenesis until the larval stage of three pairs of cirri (p.c.). Observation of segregated chromatids in unfertilised oocytes revealed a karyotype of 2n = 20, a chromosome number different from that reported for *L. anatina* of mainland Japan (2n =16). Embryonic shells are formed 10 hours after fertilization at the stage of 1 p.c. Three days after fertilization, embryos at 3 p.c. are hatched to become free swimming larva. Larval shells are observed in the larva later than 4 p.c. that were collected by a plankton net. Both the embryonic and larval shells are birefringent under polarised light, suggesting that they are crystallised. However, SEM-EDS and TEM-EDS analyses demonstrated that even the larval shells contain no Ca nor are they crystallised. In situ hybridization analysis using an engrailed gene fragment as the probe has been unsuccessful so far, due both to high background reactions and to opaqueness of the embryos. Among various methods to solve the latter problem, treatment of the embryos with a KOH solution appears to be most effective.

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A *SPHRIGANARIA* (TEREBRATELLIDINA, ZEILLERIOIDEA) COMMUNITY (JURASSIC, UPPER BATHONIAN) FROM NORTHERN SINAI

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A *Sphriganaria* community has been recognised from Gebel El-Maghara, a breached anticline in northern Sinai consisting of Pliensbachian-Oxfordian strata 2000 m thick (33°20’00’’; 34°40’00’’). The section lies at the junction of the Indo-African and Tethyan faunal realms on the Sinai Peninsula. The lithology from which the fossils were extracted consists of interbedded to micro-oncolitic, friable limestones and shales of the Upper Bathonian Kehailia and Safa formations. Alternating sequences of clastics and carbonates were deposited in a peritidal setting by continually shifting river systems that drained the Arabo-Nubian shield. Locally, the depositional environment was low-energy, mid-neritic with a relatively slow sedimentation rate. The fauna is dominated by brachiopods (*Sphriganaria*) and bivalves (*Eligmus*, *Grypheligmus* and *Africogryphaea*) that inhabited a muddy substrate. In this community *Sphriganaria* represents the trophic nucleus; however, a rare smooth terebratulid (*Ptychtothyris*) is also present. The brachiopods, low-level suspension feeders, are followed in abundance by bivalves, also low-level suspension feeders, occasional gastropods (*Purpuroidea*; browsers? scavengers? collectors?), cephalopods (oxyconic ammonites; predators) and rare echinoderms (regular echinoids; predators, scavengers). The five different trophic groups recognised here as well as the relatively high diversity is indicative of a low-stress offshore environment; however, the fact that bivalves are in a number two biovolume dominance position suggests a position closer to shore. Mesozoic workers are generally of the opinion that the common European zeillerid brachiopod genus *Eudesia* King, 1850 also occurs along the southern Tethyan margin. Recent research in the Jurassic Ethiopian Province of Jordan, Israel and Saudi Arabia, however, indicates that Cooper’s (1983) genus *Sphriganaria* has been misidentified over past decades as *Eudesia*. *Eudesia* is a strictly European taxon that, according to Muir-Wood (1965), has a cardinal process that is complicated in structure, hollow, with two small cavities, trilobed, prominent, and elevated above fused thickened hinge plates that are commonly pierced by 3 small cavities. *Sphriganaria* does not have a cardinal process but superficially resembles *Eudesia*.

THE LARVAL EYES OF BRACHIOPODA

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We here present the first detailed description of light sensitive organs in brachiopods and illustrate their unique architecture among lophotrochozoan larvae. In the laqueoid brachiopod *Terebratalia transversa* up to 16 epidermal eyes are embedded in the apical lobe of the three-lobed larva. Expression of *Pax-6* supports the “eye-nature” of the examined cells. Each eye consists of two specialised epidermal cells, a lens cell and a shading pigment cell, both with sensory functions. Proximally, both eye-forming cells have a cytoplasmatic process, an axon, which runs towards the larval neuropile, potentially connecting both photoreceptor cells with the larval nervous system. The light-percepting structures of both cells are cilia with enlarged ciliary membranes, which form large membrane stacks within the optical cavity. Presence of a ciliary opsin as photopigment was documented by *in-situ* hybridizations, showing c-opsin expression in the larval eyes of *T. tranversa*. With the overall presence of *Pax-6* several studies have provided strong evidence for a monophyletic origin of eyes within Metazoa. Ciliary as well as rhabdomeric photoreceptors were hypothesised for the last common ancestor of Bilateria. The ciliary design of the photoreceptors of *T. transversa* is in conflict with the general assumption of rhabdomeric photoreceptors within Protostomia. However, the evolution of eyes has been widely discussed and is still far from being resolved. Further studies of the ultrastructural eye-architecture of various bilaterian taxa are essential to clarify the evolution of eyes within Bilateria.

BRACHIOPODS IN THE LATE PALAEOZOIC BENTHIC BIOTA OF NORTHEAST ASIA

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The Late Palaeozoic basins of Northeast Asia are a large palaeogeographic element in a system of Carboniferous-Permian basins surrounding the Recent Arctic Ocean. They represented the autonomous Taimyr-Kolyma palaeogeographic region. Since the middle of the Early Permian, the latter belonged to a spacious Circum-Arctic system of basins: the Biarmian realm (Ganelin and Kotlyar, 1984). Tectonic reorganizations determined changes in ecological-palaeogeographic settings, which were responsible for successive development of five different types of faunas (benthic formations): East Siberian, Taimyr-Kolyma (Magar), Verkhoyansk, Pechora-Kolyma, Kolyma-Omolon.

Communities of the East Siberian type characteristic of the Tournaisian–mid-Visean were widespread through the entire East Siberia, where they were confined to epiplatform carbonate basins. They were most cosmopolitan and diverse. Brachiopods were represented by ~100 genera belonging to >30 families with Echinoconchidae, Tolmatchoffiidae, Dictyoclostidae, Syringothyridae, Spiriferidae*,* and others being dominant.

Communities of the Magar type, corresponding to the development stage from the mid-Visean to mid-Bashkirian, reflect the onset of a major palaeogeographic reorganization resultant from the destruction of epiplatform settings and the initiation of a system of deep troughs instead of former basins. This process was accompanied by formation of a thick sequence of terrigenous sediments on the Angarida margin and reduction of shelves with carbonate accumulation, which led to the decrease in taxonomic diversity of benthic communities and increase in their endemism. Brachiopods were represented by ~40 genera: mainly endemic *Balkhashiconcha, Buxtoniella, Praehorridonia, Bailiena, Sajakella, Verkhotomia,* and *Orulgania.*

Communities of the Verkhoyansk type characteristic of the mid-Bashkirian to mid-Early Permian correspond to the terminal stage of the above-mentioned palaeogeographic reorganization, which was marked by basalt volcanism. Deep basins with sharply reduced shelves accumulated largely black shales, while carbonate sedimentation completely ceased at that time. Such changes resulted in a major biotic crisis reflected in the extinction of high-rank taxa. Brachiopods included approximately ten mostly endemic genera: *Verkhojania, Jakutoproductus, Lanipustla, Jakutella, Taimyrella,* and *Costatumulus.* Their ecological analogs in Gondwana are represented by the *Levipustula–Verkhojania–Costatumulus* fauna known from Australia and Patagonia.

Communities of the Pechora-Kolyma type, peculiar of the mid-Artinskian–Kungurian ages, correspond to the onset of a transgression, which enhanced palaeogeographic connections. Preceding dominant taxa disappeared, reducing endemism of communities and increasing the number of taxa shared between North Urals, Pechora and Northeast Asia. Brachiopods were represented by ~25 genera, including, notably, *Waagenoconcha, Anidanthus, Megousia, Striapustula, Rhynchopora, Neospirifer, Crassispirifer, Attenuatella,* and to a lesser extent, Chonetidae, Horridoniidae and Licharewiidae families. This stage was culminated with a biotic crisis coeval with the development of the uniform *Kolymaella-Bocharella* fauna.

Communities of the Kolyma-Omolon type, typical of the Roadian (Kazanian)-terminal Permian stage, was developed against the background of a spacious transgression during the second half of the Permian. The communities populated usually moderate uplifts and their slopes, which received peculiar H_2S-saturated carbonates ("*Kolymya-Atomodesma* limestones"). Relatively diverse communities (~30 genera) were dominated by thin-striate and phylogenetically related Linoproductidae genera: *Terrakea, Omolonia, Magadania, Cancrinelloides,* and *Stepanoviella,* replacing each other in time. They are accompanied by common Chonetidae *(Komiella),* Strophalosiacea *(Mongolosia, Marginolosia, Wyndhamia),* Rhynchonellida-*Rhynchopora (Rhynoleichus),* Licharewiida *(Kungella, Tumarinia, Olgerdia, Penzhinaella).* Ecological analogs of such communities are widespread in Gondwana and they exhibit also notable morphological similarities at the generic and specific levels with coeval assemblages from Australia and New Zealand. It is remarkable that sequences of H_2S-saturated carbonates ("*Atomodesma* limestones") developed in New Zealand are similar to their counterparts in the Kolyma-Omolon region.

Acknowledgements: This work was supported by the Russian Foundation for Basic Research (project no. 08-05-00155) and Presidium of the Russian Academy of Sciences (program no. 15).

ENDOLITHS AND BACTERIAL ACTIVITY IN CRETACEOUS AND RECENT BRACHIOPOD SHELLS - DIAGENETIC CONSEQUENCES

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Investigations on natural surfaces and in sections of Recent and Cretaceous brachiopod species from various locations have highlighted the presence and activity of algae, fungi and bacteria in shells. These marine benthic organisms are found in both shallow and even deep waters and, in the fossil records, sampled from limestone or marly-limestone.

The organo-mineral exoskeleton, a structural low magnesium calcite combined with a small amount of organic matrix is in main cases perforated by caecal punctae. It provides many locations where endoliths and bacteria can operate.

In some cases, just an association is observed (see for example: *Gryphus vitreus* (Born) invaded by *Ostreobium queketti*; this symbiosis takes place without microstructural modification. The SEM reveals opposite cases with beginning modifications of the microfabric induced by branched or segmented endoliths in the primary and above all in the secondary shell layers. In this case the calcite granules are secondarily transformed, (cf. in *Stenosarina*, among examples). This modification leads to a progressive disorganisation of the organic sheaths around the fibres (cf. in *Frenulina* for explanation), even its disappearance. Therefore, the state of softening and maceration is introduced.

In addition, consequences of bacterial activity are more obvious with the presence of bacterial mats or maceration, while bacteria use the organic matrix as a food supply leading to an early diagenesis in recent shells. This aspect is also observed in Cretaceous species. In counterpart, the fossil records reveal cases of strengthening while the fibrous elements, after the disappearance of their organic sheath, become coalescent to form silicified or secondary calcite nodules in the shells. Many other cases could be discussed.

Two problems are evoked: after the setting of the biomineralisation process, what is relevant to diagenetic modifications, and what mechanisms are involved in the aspects recorded?

DIVERSITY AND SURVIVORSHIP OF SILURO-DEVONIAN BRACHIOPODS

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Using the data of the recently revised Treatise on Invertebrate Palaeontology (Part H) and the databases available on the Web, this work is an attempt to investigate the diversity of the brachiopod genera during the Siluro-Devonian period. As shown by some recent studies, the generic level is well adapted for a detailed observation of the diversity and abundance and is preferable to the family level used in former studies that tends to cause excessive smoothing of the diversity peaks. In some peculiar cases (e.g. the lower Eifelian), results concerning appearances/disappearances can be inverted, depending on whether genera or families are considered. For a more efficient approach, we worked at the substage level for the Devonian period, but this was not possible for Silurian, due to lack of confident data.

Brachiopods as a whole were relatively poorly affected by the different "crises" known during this period (e.g. the Frasnian-Famennian crisis) and show a good ability to recover, although it is necessary to distinguish between Linguliformea and Craniiformea on one hand and Rhynchonelliformea on the other hand. The first ones undergo little or no perceptible changes during this period, following a major crisis at the Ordovician-Silurian boundary. Concerning the Rhynchonelliformea, the diversity and abundance show a regular increase during the entire lower Devonian, reaching a maximum during the Emsian, as mentioned in the Treatise (463 genera present in upper Emsian).

The main period of crisis for Siluro-Devonian brachiopods occurs at the Ordovician-Silurian boundary (one of "Big Five"), during the Pridoli and principally at the Emsian-Eifelian transition where 25 % of the genera disappear, constituting a major crisis for the brachiopods, possibly in relation with the "Chotec Event". After this crisis brachiopods regularly decline until the upper Devonian; at the end of the Famennian they reach an abundance ratio equivalent to that of the basal Devonian. The so-called Frasnian-Famennian crisis is in fact effective as soon as the basal Eifelian for brachiopods, whatever the orders considered. During the Devonian, while the appearances / disappearances follow more or less identical curves, the Linguliformea and Craniiformea abundance seems to follow an opposite tendency compared to that of the Rhynchonelliformea.

Contrary to some recent studies, our results show that the time range of a genus (and thus its survivorship capacities) depends on its number of species and on its geographical distribution (endemic vs. cosmopolitan genera): the more species-rich a genus and the wider its geographical distribution, the longer its life expectancy and the higher its chances of survival at a system, series or stage boundary.

GENUS, SPECIES AND AUTHORS: A DANGEROUS INFLATION

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The building of a database may lead to unexpected concerns. The collection of data on Siluro-Devonian brachiopods shows that 388 authors are responsible for more than 1800 genera since the 19th century. Among them, 35 authors (9% of the total) have erected 1086 genera (58% of the total). These numbers are respectively 1036 genera and 55.5% if we consider only publications as first authors. Curiously, in the case of multi-authorship, "prolific" authors tend to associate *inter se*.

The mean number of genera erected by an author is 5, but the 35 above mentioned authors have erected 15 genera or more (mean = 31), with a (unbeatable?) record of 200 genera for a single author! If these authors are excluded, the mean number of erected genera becomes 2 per author.

This results in a dangerous inflation of the monospecific genera: since the year 1950, these "prolific authors" have erected 918 genera - among them 390 are monospecific, 170 include 2 species, 111 genera include 3 species, etc. Up to the 1950s, a relative equilibrium was maintained between mono- and multispecific genera. The incursion of monospecific genera begun in the 1960s and drastically increased in the 1970s; this tendency is still present and becomes worse with the virtual disappearance of genera with more than 5 species. Since the mid-1950s there has been a complete inversion of the proportion of monospecific vs. multispecific genera.

The message that can be extracted from these data is that authors should be careful when erecting a new genus: a monospecific genus is of poor interest both in terms of systematics and in terms of palaeogeography. Such genera are almost necessarily (or statistically) endemic and will have a poor value for correlations and comparisons. Alternatively, this could be interpreted as the evidence that all the brachiopods are endemic. We know from experience that this is not the case, and many evidences show the contrary (although this fact depends on the period and many other elements). Nevertheless it seems that there is a problem of methodology and, before erecting a new genus, authors should seriously consider the eventuality of an emendation of existing genera.

MACROEVOLUTIONARY PATTERNS AND TRENDS IN THE RHYNCHONELLIFORM BRACHIOPODS THROUGH THE ORDOVICIAN – SILURIAN INTERVAL

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During the Great Ordovician Biodiversification Event the rhynchonelliformean (articulated) brachiopods dominated the benthos in an interval when more modern biodiversity levels, climate conditions and trophic structures were initiated. Apart from marked increases in biodiversity at the species, genus and family levels, major changes in the rhynchonelliforms were associated with the establishment of well-defined and dynamic provincialism (gamma diversity), bicomplexity in community structures with expansions into deeper water and around and within carbonate buildups (beta diversity) together with the canalization of niches (alpha diversity). Innovations associated with hinge structures and lophophore supports dominated the evolutionary agenda while a range of megaguilds, that included the orthides (attached low and erect) and the strophomenides (reclining), may be further divided into 1, strongly biconvex pedunculate, 2, strongly biconvex alate pedunculate, 3, planoconvex to weakly biconvex pedunculate, 4, relatively flat free-lying and 5, inflated free-lying types. Such eco-diversity generated narrower niches and a mechanism to increase alpha diversity. Moreover during the period the individuals of many groups progressively increased in size. Multivariate analysis of Ordovician brachiopod-range data indicates two evolutionary faunas; a Tremadocian-Floian fauna dominated by the orthidines and syntrophiidines and a Dapingian-Hirnantian fauna dominated by orthides and strophomenides. Although the end Ordovician extinctions numerically devastated brachiopod faunas, ecological structures within the suspension-feeding benthos survived but with a marked takeover of communities by the cyrtomatodonts (e.g., athyridides, atrypides and spiriferides) together with the advanced deltidiodonts (pentamerides).

TROPIDOLEPTUS (BRACHIOPODA): NEW ORDER FOR AN UNUSUAL DEVONIAN TAXON

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The phylogenetic placement of *Tropidoleptus*, a common and distinctive genus of articulated brachiopod has proved difficult. *Tropidoleptus* has, for example, been related to the orthides, strophomenides and terebratulides. In the first edition of the Treatise, the genus was assigned to the Enteletoidea, largely on the basis of its general shape and the presence of punctation. The cyrtomatodont dentition, however, and complex cardinalia with crurae, apophyses and a median septum are more typical of some of the more unusual rhynchonellides, for example the Uncinuloidea and more specifically the Eatoniidae. A punctate shell condition, none the less, has not been reported in that group. It is argued that *Tropidoleptus*, although sharing many of its features with a number of rhynchonellate orders, has characteristic and unique features justifying the elevation of the Tropidoleptidae to ordinal status, occupying a basal position in the rhynchonellate stem-group.

ESTABLISHING A MODERN BASELINE FOR SHELL DAMAGE AND REPAIR IN RHYNCHONELLIFORM BRACHIOPODS: ASSESSING LEVELS OF DUROPHAGOUS PREDATION

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There are conflicting hypotheses concerning how important predation might have been in the evolution of rhynchonelliform brachiopods. In particular, questions have been raised as to whether their post-Palaeozoic diversity and distribution might, at least in part, be shaped by the increase in predation pressure associated with the Mesozoic Marine Revolution, and alternatively whether brachiopods are such unfavourable prey, when compared with bivalve molluscs, that they would have been virtually immune to such pressures.

One of the problems with testing such hypotheses has been the lack of modern baseline data for shell damage and repair levels in modern brachiopods. In common with bivalves, there are real problems in trying to ascribe damage to particular causes (whether biogenic or physical). But I shall also argue that both the quality and type of data available for brachiopods and bivalves are, at present, so different that they prevent meaningful comparison.

In this talk I attempt briefly to pull together the scattered information we do have on predation on modern brachiopods and to indicate areas where data may be profitably collected to assist with testing the above hypotheses and integrating it with data from the fossil record.

Although it is known that predators which either swallow their prey whole or prise them apart do, at least on occasion, attack brachiopods (whether accidentally or deliberately), they leave no diagnostic traces. As a result death or fossil assemblages do not allow for quantification of these types of predation and thus hypotheses concerning the importance of such activities (e.g. Donovan & Gale, 1990) must remain fundamentally untestable. Whereas the study of drill holes in both brachiopods and bivalves is relatively tractable and comparatively advanced, that of crushing predation is less frequently studied in post-Palaeozoic and modern assemblages and much more difficult to interpret. I present data for modern brachiopods from a wide range of geographic areas and environments in order to assess frequency of breakage and repair and examine criteria by which to differentiate between breakage caused by predators and physical processes (Harper *et al.* 2009) and discuss the significance of repair frequencies.

Donovan, S. K. & Gale, A.S., 1990. Predatory asteroids and the decline of the articulate brachiopods. *Lethaia* 23, 77-86.

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ANALYSIS OF DRILL HOLES IN RECENT NEW ZEALAND BRACHIOPODS

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Small circular perforations are not infrequently reported in brachiopod shells. These are often interpreted as the work of mistaken or confused predatory gastropods (Kowalewski et al., 2005; Simões et al., 2007). This 'unfocussed', low frequency collateral damage is therefore not likely to be of any real consequence in terms of selection. This may be a fair interpretation where frequencies of drill holes are very low, and in particular in habitats where perhaps more rewarding prey (notably molluscs) co-occur. However, in recent years there have been a number of papers providing data for Cenozoic brachiopod samples that show remarkably high incidences of drill holes (e.g. Baumiller & Bitner, 2004; Baumiller *et al*., 2006; Tururua *et al.,* 2008) that suggest that drilling may be an important agent of death at least locally. One of the problems in interpreting such cases has been a dearth of information about drilling predation experienced by modern brachiopods.

We present results of an analysis of drilling predation recorded in six lower taxon collections from five modern brachiopod death assemblages from around the South Island, New Zealand. In particular we test the hypothesis that drilled individuals were attacked occasionally by predators that were unfamiliar with them. In this case, we might anticipate drill holes to be randomly located, no evidence of selectivity of prey size, and a high incidence of either incomplete drill holes or repair of complete ones. At each of our sites, there is statistically significant evidence that drill holes are associated either with particular valve regions, or that there is prey size selection by the driller, or both. It is of note that the preferred drilling site differs between the prey taxa. The incidence of incomplete drill holes is low and there is no evidence that complete drill holes are repaired if the attack is abandoned. Together these observations suggest that in these particular habitats sampled predatory drillers are familiar and experienced with brachiopod prey.

Additionally, we report on aquarium observations of a variety of New Zealand brachiopods maintained with potential gastropod predators.

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Kowalewski, M., Hoffmeister, A.P, Baumiller, T.K. & Bambach, R.K., 2005. Secondary evolutionary escalation between brachiopods and enemies of other prey. *Science* 308, 1774-1777.

Simões, M.G., Rodrigues, S.C. & Kowlewski, M., 2007. Comparative analysis of drilling frequencies in Recent brachiopod-mollusk associations from the Southern Brazilian Shelf. *Palaios* 22, 143-154.

Tururua, M.E., Baumiller, T.K. & McNamara, K.J., 2008. Drill holes in Australian Cainozoic brachiopods. *Historical Biology* 20, 203-212.

BRACHIOPOD MINIATURISATION AND PRODUCTIVITY DECLINE DURING THE PERMIAN-TRIASSIC CRISIS IN SOUTH CHINA

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Body size is often affected by environmental stresses and the study of size change through mass extinction intervals is of particular importance in understanding the biotic responses of organisms to global-scale climatic and environmental changes. The Late Permian mass extinction event was the most severe biotic crisis of the Phanerozoic, and body size fluctuated greatly in this crisis, typically in the Early Triassic, including a post-extinction Lilliput effect. Here, based on high resolution, quantitative size data of rhynchonelliform brachiopods from the uppermost Permian to lowermost Triassic sequences of a section in South China, we discovered that all four studied taxa record size decreases during the late Changhsingian. Following extinction of several taxa, the two most extinction-resistant species underwent significant size increase in the latest Changhsingian. Subsequently, body size underwent a more prominent decrease towards the earliest Triassic. In order to better determine whether there is a directional, 'active' trend or whether the differences are due to passive mechanisms, we used the statistical analyses of the methodology of Jablonski (1996). The statistical results also suggest, in general, most of the changes in body size recorded in our study are the result of directional trends, rather than simply passive changes in variance.

In order to evaluate whether palaeoproductivity and/or anoxia caused these size changes, we assessed the abundances of trace elements, acritarchs and rare earth elements from the same section. Our results demonstrate that significant size reductions typically correspond to declines in productivity rather than changes in oxygen levels, and a single episode of size increase late in the extinction interval in the more extinction-resistant taxa may be related to decreased interspecific competition for scarce food resources.

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BRACHIOPODS IN A LATE CRETACEOUS OYSTER REEF

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Investigations of exposures of the *Ostrea* Bed at the top of the Broken River Formation in North Canterbury, New Zealand have revealed the presence of two species of brachiopods among the abundant molluscan remains. One of these is a rhynchonellide, whose occurrence in this unit was noted as long ago as 1920. The other is a terebratellidine of unclear affinities, which is reported for the first time.

The *Ostrea* Bed is a 2-5 m thick, medium to coarse-grained calcareous quartz sandstone packed with fossil oyster shells. It rests on a sequence of mudstones and quartz sandstones with thin coal seams and locally developed conglomerates. It is taken to mark the beginning of the transgressive marine sequence deposited during the gradual floundering of the Zealandia fragment of Gondwana in Late Cretaceous to mid-Oligocene times.

The stratigraphic position, sedimentology and palaeofauna all point to a very shallow water origin for the *Ostrea* Bed. Apart from the oyster shells, seven other species of bivalves and three species of gastropods are present, all usually associated with shallow marine environments. In addition, numerous examples of the flask-shaped boring *Gastrochaenolites* are present in the oyster shells. A high density of trace fossils of this type indicates very shallow conditions, perhaps only a few metres of water.

The evidence suggests that the *Ostrea* Bed could be interpreted as an oyster reef, thus allowing some inferences to be made regarding the palaeoecological conditions under which it developed. Modern oyster reefs, such as those of the southern United States, occur in near shore areas but grow especially vigorously near estuarine river mouths where waters are brackish and less than 10 m deep. As successive generations of oysters settle and grow, reefs become highly complex, with many structural irregularities that can provide a wealth of microhabitats for many different species of animals.

In such a setting, the *Ostrea* Bed was probably subject to quite vigorous environmental conditions. The brachiopods therefore must have been able to withstand these circumstances. Certainly the markedly attrite beak and large foramen of the new taxon suggests it attached very closely to a hard substrate, probably the large oyster shells. The rhynchonellide, likely occupied more cryptic situations among the oyster shells, sheltered from high energy water movements. In such a setting, these species may have been tolerant of fluctuations in salinity.

AN INTEGRATED APPROACH TOWARDS THE PHYLOGENY OF RECENT THECIDEIDE BRACHIOPODS

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Thecideide brachiopods are an enigmatic group of small-bodied brachiopods living in cryptic habitats of coral reefs and volcanic islands. Recent representatives are known from only two thecideide families, Lacazellinae Backhaus and Thecidellininae Elliot. There is an ongoing debate on the phylogenetic position of thecideides within brachiopods and their ingroup relationships.

In this comprehensive study an integrated approach of both molecular and morphological methods was carried out to reveal the phylogeny of Recent Thecideoidea.

Adult shell characters and shell development patterns were intensively studied using SEM. Thus a set of relevant taxonomic and phylogenetic characters could be established for both lacazellines and thecidellinines. Whereas the diversity of species in each of the three lacazelline genera is very low, the thecidellinine genus *Thecidellina* is much more species-rich. This is reflected by a high degree of plasticity in shell morphology either resulting from similar traits in shell development or representing convergent traits. Besides the cryptic genus *Minutella* was discovered, characterised by a very small body size and a well-defined pseudodeltidium. The position of *Kakanuiella*, a genus with hitherto uncertain affiliation, was re-evaluated on the basis of morphological characters, e.g. shell development and brooding habit, revealing a sistergroup relationship to all other Recent lacazellines.

The comprehensive investigation of different ribosomal and nuclear markers led to a first molecular based phylogeny of Recent thecideides. The molecular data suggest monophyly of Thecideoidea and its subfamilies Thecidellininae and Lacazellininae. Furthermore, the lacazelline genera *Lacazella* and *Pajaudina* seem to be more closely related to each other than to the genus *Ospreyella*, which corresponds with their geographic distribution. High genetic diversity is characteristic for *Thecidellina* in the West Pacific. This consolidates the results of the comprehensive morphological studies. The cryptic genus *Minutella* is highly supported by molecular data and is closely associated with the thecidellinine genus *Thecidellina*, also corresponding with the morphological data. The comparison of thecideide 18S rRNA data with other available brachiopod sequences confirms the unique status of Thecideoidea within the articulated brachiopods.

ONTOGENY AND PHYLOGENY OF EARLY CAMBRIAN STEM RHYNCHONELLIFORM BRACHIOPODS

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The ontogeny of fossil and recent brachiopods has been of great importance in deciphering phylogenetic relationships of the clade. However, the ontogeny of many early Cambrian brachiopods remains poorly known, which has impeded understanding of key groups; one such group is the enigmatic early Cambrian Order Chileida, which has been considered to belong within the calcareous-shelled crown group Rhynchonelliformea in the Class Chileata. The chileids are amongst the earliest known brachiopods with a calcareous and strophic shell, but as they are known mostly from rather coarsely silicified shells, their early life history has been largely unknown. A unique find of well preserved phosphatised material of a chileid from the Flinders Ranges, South Australia, shows that their early ontogeny closely parallels that of the aberrant early Cambrian paterinate-like *Salanygolina* from Mongolia. In both *Salanygolina* and the new chileid, the anterior margin of the well defined ventral larval shell is indented by an unrestricted notch that, through later ontogeny, develops into an umbonal perforation, directly anterior to the umbo. In subsequent ontogenetic development, this subtriangular perforation is enlarged by resorption and covered posteriorly by the colleplax - a triangular plate - in the umbonal perforation. The colleplax structure was first described from the equally enigmatic Palaeozoic Order Dictyonellida (Rhynchonelliformea, Chileata); the colleplax in *Salanygolina* is considered to be homologous with that of the chileates. As proposed in the original description, the foramen and colleplax clearly represent integral parts of an attachment structure that developed early in the ontogeny and was retained in the adult. This type of colleplax holdfast cannot be considered homologous with the pedicle of the Cambrian paterinids, such as *Micromitra*, which are famously found still-attached to sponges in the Burgess Shale. However, it is possible that the earliest larval attachment of the chileids and *Salanygolina* can be compared with the paterinid pedicle, emerging between the valves; we infer that the first larval pedicle was thus homologous to the adult pedicle of paterinids

Uniquely preserved scleritomes of early Cambrian tommotiids from South Australia show that they represent sessile stem brachiopods. Study of the early ontogeny of the derived tommotiid *Paterimitra* shows that its early life history closely parallels that of the brachiopods; it has a brachiopod-like bivalved larval shell, which is also provided with a colleplax structure, here considered to be homologous with that of *Salanygolina* and the chileids. However, in *Paterimitra* the colleplax-structure does clearly not function as an adult holdfast.

We propose that *Salanygolina* and the chileids, as well as the tommotiid *Paterimitra* belong to the stem of the crown group Rhynchonelliformea.

APPLICATION OF DISCRIMINANT ANALYSIS TO A STUDY OF ORDOVICIAN-SILURIAN BRACHIOPOD GENUS *KATASTROPHOMENA*

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In the traditional systematic palaeontology of brachiopods, methods of comparison for two similar genera are usually qualitative and intuitive rather than quantitative. Discriminant Analysis (DA) is an important technique of classification analysis, and forms a statistical basis for the taxonomy of modern biology, but the method has drawn less attention in palaeontology.

The two Strophomenidae genera, *Katastrophomena* and *Strohpomena,* have been assigned to Furcitellinae and Strophomeninae respectively. But, the characters of these two genera are so close that there exist many different opinions on their taxonomic assignments (Cocks, 1968; Rong and Yang, 1981; Sheehan, 1987; Cocks and Rong, 2000; Cocks, 2008).

In order to differentiate these two genera quantitatively, 31 species assigned to *Katastrophomena* and *Strophomena* are examined. There are 52 specimens (including 7 holotypes, 23 paratypes, 6 hypotypes, and 4 lectotypes) compared. Having measured the known specimens in length and width of the valves and the ventral muscle fields, the analysis of covariance (ANCOVA, see Huang, 2007) was performed. The result shows a significant difference (p=0.002) between *Katastrophomena* and *Strophomena* which is represented by length ratio of ventral valve and muscle field. The discriminant function is built through the DA processed and its validity is tested. The significant validity (p=0.03) of the function indicates that the function can be used to differentiate *Katastrophomena* from *Strophomena*.

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Geological Society of Australia, Abstracts No. 95
6th International Brachiopod Congress, Melbourne, Australia, February 2010

GIGANTOPRODUCTINAE (CARBONIFEROUS BRACHIOPODA) OF JAPAN AND ITS PALAEOBIOGEOGRAPHICAL SIGNIFICANCE

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As large-sized Carboniferous brachiopods, the Gigantoproductinae is a subfamily belonging to Order Productida (Sarytcheva and Sokolskaya, 1959). Gigantoproductinae brachiopods are known from the Akiyoshi Limestone and Omi Limestone in Akiyoshi Belt, the Hikoroichi Formation in South Kitakami Belt and the Ichinotani Formation in Hida Gaien Belt in Japan. But the number of described species was low until several years ago.

In recent years, some Gigantoproductinae brachiopods have been described and figured from the South Kitakami Belt, Hida Gaien Belt and Akiyoshi Belt in Japan, including *Gigantoproductus* cf. *okensis* from the Lower Carboniferous (Upper Visean) Onimaru Formation in South Kitakami Belt (Tazawa and Miyake, 2002), *Gigantoproductus* cf. *crassiventer* Prentice, 1949 and *G*. cf. *latiexpansus* Sarytcheva in Sarytcheva and Sokolskaya, 1952 from the Lower Carboniferous (Lower Visean) Hikoroichi Formation in South Kitakami Belt (Tazawa and Ibaraki, 2009), *Gigantoproductus meridionalis* (Legrand-Brain, 1973) and *G. tujucsuensis* Gladchenko, 1955 from the Lower Carboniferous (Namurian) Tsuchikurazawa Limestone, Akiyoshi Belt (Ibaraki et al., 2008), *Gigantoproductus sarsimbaii* (Sergunkova, 1935) from the Lower Carboniferous (Upper Visean) Ichinotani Formation in Hida Gaien Belt (Ibaraki et al., 2009).

In this presentation, I will summarise the classification, stratigraphical and geographical distribution of Gigantoproductinae brachiopods from Japan, and consider their palaeobiogeography, especially the palaeo-positions of the South Kitakami Belt, Hida Gaien Belt and Akiyoshi Belt during the Carboniferous.

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MORPHOLOGICAL CLINE, PALAEOGEOGRAPHICAL GRADIENT, AND THE EVOLUTION OF THE LATE ORDOVICIAN BRACHIOPOD FAUNAS OF NORTH AMERICA

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During the Late Ordovician (mid to late Katian) greenhouse episode and sea level highstand, the palaeocontinent of Laurentia was covered largely by shallow tropical epicontinental seas, in which evolved a fairly homogeneous but highly endemic benthic shelly fauna on a continental scale. At the generic level, most brachiopods that dominated in epicontinental seas had their respective ancestral stocks in continental-margin seas within Laurentia. At the faunal level, epicontinental brachiopod faunas (EBF) generally have a considerably lower species diversity and higher dominance than continental margin brachiopod faunas (CMBF). Some common genera of CMBF rarely invaded epicontinental seas, especially the palaeoequatorially located Hudson Bay and Williston basins towards the centre of Laurentia (e.g. *Platystrophia*, *Hebertella*, *Dalmanella*, *Onniella*, *Tcherskidium*, *Proconchidium*, *Rhynchotrema*, *Rostricellula*). On the other hand, EBF genera can usually be traced to CMBF, represented by the same or different species. Among several discrete evolutionary lineages, several common trends of morphological modification are recognisable when the ancestral forms are compared to their descendants in epicontinental seas. 1) Increase in shell size, shell-wall thickness, and shell globosity is prevalent in some lineages of orthides (*Plaesiomys*, *Platystrophia*), strophomenides (e.g. *Strophomena*, *Nasutimena*, *Tetraphelerella*, and *Rafinesquina*), and rhynchonellides (*Hiscobeccus* and *Lepidocyclus*). 2) Conspicuous rugosity developed independently in stocks that do not have a close phylogenetic relationship (e.g. *Nasutimena*, *Hiscobeccus*). 3) In some orthide lineages, there was a tendency of evolutionary convergence for epicontinental taxa to evolve a larger, trilobed cardinal process from its ancestral counterpart that lived in continental-margin seas and possessed a small, bilobed cardinal process (e.g. *Dalmanella* compared to *Paucicrura* and *Diceromyonia* in the superfamily Dalmanelloidea, or various species of *Plaesiomys* in the superfamily Orthoidea). 4) The predominant dalmanelloid shells in epicontinental seas have prominent aditicules and unusually large punctae, marked by a dorsal medial costa (e.g. *Paucicrura*, *Diceromyonia*); whereas these characters are absent or poorly developed in continental-margin dalmanelloids of cool-water origin (*Dalmanella*, *Onniella*). Such evolutionary trends may have been related to several palaeoecological and palaeogeographical factors: a) the warmer water mass with increased supersaturation of Ca^{2+} and CO_3^{2-} in the palaeoequatorial epicontinental seas facilitated the growth of large and thick shells; b) episodic invasion and isolation of brachiopods in inland seas during sea-level fluctuations favoured opportunistic explosion of a specialised, endemic fauna of relatively low diversity. Such a fauna was also more susceptible to extinction than CMBF.

Poster

SOME STRUNIAN BRACHIOPODA FROM THE KHOSHYYLAGH FORMATION IN THE MEYGHAN SECTION (NE SHAHRUD, EASTERN ALBORZ OF IRAN)

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The Khoshyylagh Formation is widespread in the eastern Alborz of Iran, especially in the Shahrud region. The Formation is highly fossiliferous, including brachiopods, corals, trilobites, Mollusca, foraminifera and fish remains. In the Meyghan section (30 km NE of Shahrud in the eastern Alborz), the Mila Formation (Cambrian- Ordovician) is faulted against the Khoshyyagh Formation, which is conformably overlain by the Mobarak Formation (early Carboniferous). The Khoshyyagh Formation is mostly composed of limestone, marly limestone, sandstone and shale, with a thickness of about 400 meters. The Brachiopoda at the top of the Khoshyylagh Formation in the Meyghan section include the following species: *Schizophoria impressa, Aulacella interlineate, Leptagonia* sp., *Schellwienella* sp., *Mesoplica praelonga, Semiproductus* aff. *irregularicostatus, Spinocarinifera* sp., *Sentosia* sp., *Centrorhynchus charakensis, Centrorhynchus touranica, Araratella dichotomians,* Rhynchonellid indent., *Paurogastrorhynchus bikniensis, Athyris tau, Lamellosathyris* sp., *Dichospirifer piriformis, Prospira lapparenti, Prospira struniana, Rigauxia crassiplicatus, Eobrachythyris* sp., and *Toryniferella echinulata*.

Based on the above mentioned Brachiopoda a Strunian (late Famennian) age can be determined for the top of the Khoshyyagh Formation in the Meyghan section.

LATE DEVONIAN BRACHIOPODA FROM THE DAMGHAN REGION (EASTERN ALBORZ, IRAN)

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Late Devonian sediments of the Khoshyylagh Formation are widely distributed in the Damghan region (Eastern Alborz). This formation in the north of the Damghan region (Namakeh section) is 450 m thick, and is mostly composed of limestone, marly limestone and shale. The Brachiopoda of the Khoshyylagh Formation in the section were studied and the following taxa are recognised: *Schizopohoria impressa*, *Aulacella interlineata*, *Leptagonia* sp., *Schellwienella* sp., *Schuchertella* sp., *Mesoplica praelonga*, *Buxtonia* sp., *Sentosia* sp., *Avonia* sp., *Megalopterorhynchus chanakchiensis*, *Centrorhynchus charakensis*, *Evanescirostrum* sp., *Paurogastroderhynchus nalivkini*, *Athyris tau*, *Athyris* sp., *Lamellosathyris* sp., *Cleiothyridina coloradensis*, *Composita globosa*, *Cyrtospirifer semibugensis*, *Dichospirifer piriformis*, *Dichospirifer thylakistoides,* *Prospira lapparenti*, *Prospira struniana*, *Cyrtiopsis lapparenti*, *Rigauxia crassiplicatus*, *Rigauxia cyrtinaeformis*, *Syringospira* cf. *prima*, *Dimitria seminoi*,

Based on the biostratigraphical value of the above mentioned Brachiopoda, the age of the Khoshyeilagh Formation in the Namakeh section is Middle-Late Famennian, being equivalent to Biozones 9, 10 and 11 of Brice (1977) in Afghanistan. Also, the Khoshyylagh Formation in the Namakeh section is equivalent to the upper part of the Koshyylagh Formation in the type section (northeast of Shahrud- Eastern Alborz).

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PERIESOPHAGAL COELOM: A NEW DIVISION OF THE COELOMIC SYSTEM AND A POSSIBLE SITE OF ULTRAFILTRATION IN THE ARTICULATE BRACHIOPODS

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Traditionally, it is accepted that the coelomic system of articulate brachiopods is composed of the perivesceral cavity, forming an extension to the mantle, and the canal system of the lophophore (Hyman, 1959). The lophophore contains the coelomic canals: great and small brachial canals. In Linguliformea the coelomic spaces were described in the esophagus connective tissue (Pross, 1980). In *Novocrania anomala,* a central coelomic canal surrounds the esophagus and connects with the small brachial canals (Blochmann, 1892). Until now, there has been no information as to whether any related cavities are present in articulate brachiopods.

Detailed investigation of the coelomic system in *Hemithyris psittacea* revealed that articulate brachiopods possess a periesophagal coelom that surrounds the esophagus. It is isolated from the perivisceral cavity but connects with the small brachial canals. The periesophagal cavity is crossed by irregular septa. The lining of the periesophagal coelom includes cells of two types: epithelial and myoepithelial cells. Both are monociliary. Some epithelial cells have long processes extending along the basal lamina. Perhaps these cells function as podocytes. The myoepithelial cells have the basal myofilaments.

The periesophagal coelom forms protrusions penetrating the connective tissue of the body wall above the mouth and the connective tissue surrounding the esophagus. The coelomic lining of the canals above the mouth consists of flattened epithelial cells. The canals of the esophagus connective tissue form a three-dimensional network. Three types of canals are distinguished. The external canals are close to the cavity of the periesophagal coelom. Their coelomic lining consists of the epithelial cells and the podocytes. The wall of the middle deep canals is formed by both epithelial and myoepithelial cells with the smooth muscle fibers running along the longitudinal axis of the esophagus. The deepest canals lose the lumen; they are filled with the muscle cells surrounded by basal lamina. Their smooth muscle fibers are circular.

What is the function of the complicated system of canals in the connective tissue of the esophagus? The canals perform a dual function, the first of which may be excretion. The podocytes have not been found in brachiopods before, so the site of ultrafiltration has been uncertain. The gut of brachiopods is surrounded with a thick layer of loose semi-fluid connective tissue, which plays the role of the blood sinus. At the same time, the coelomic lining of the periesophagal coelom contains the podocyte-like cells. So, the ultrafiltration may take place in these very areas. Articulate brachiopods lack an anus, hence antiperistalsis is necessary for the release of faecal pellets through the mouth. Perhaps the thickened muscle wall formed by the middle deep and the deepest canals may serve this purpose.

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Geological Society of Australia, Abstracts No. 95
6th International Brachiopod Congress, Melbourne, Australia, February 2010

STRUCTURE OF THE RETICULATE GONAD OF THE ARTICULATE BRACHIOPODS

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Gonads of the articulate brachiopods are located in the mantle. Chuang (1983) identified four main types of such gonads: unbranched, arborescent, reticulate and ovoid. The reticulate gonad is formed by a network of the outgrowing blood vessels, pierced by the connective tissue pillars. They are the most enigmatic structures of such gonads, and some authors have interpreted them as short muscles that participate in releasing gametes (Hancock, 1859). James et al. (1991) proposed that these pillars are supporting columns and not contractile. We studied the microscopical anatomy of the ovary of *Hemithyris psittacea* by light and transmission electron microscopy with special reference to the connective tissue pillars.

The gonads lie in the broad proximal mantle coelomic sinuses. Its walls are formed by the mantle epithelium: the inner mantle wall covers the mantle cavity; the outer mantle wall underlies the valve. The inner mantle wall consists of the epidermis covering the inner side of the mantle cavity, and the coelomic epithelium covering the inner side of the coelomic sinus. The connective tissue matrix lies between the basal laminae of both epidermis and coelomic epithelium. The amoebocytes and the globular cells occur among the connective tissue fibres. The globular cells are oval. Their cytoplasm is filled with numerous electron-dense membrane-free globules and large membrane-bound homogenous inclusions of moderate electron density. The globular cells perhaps take part in the storage of nutrients. The coelomic sinus is lined by the myoepithelial cells.

The connective tissue pillars have a wine-glass form and consist of two parts: a column, attached to the inner mantle wall, and a broader part attached to the outer mantle wall. The coelomic epithelium, which is a continuation of the coelomic epithelium of the inner mantle wall, covers the connective tissue pillars. The connective tissue matrix is enclosed within the columns. The coelomic epithelium of the columns contains myofilaments forming the smooth muscles that are orientated across the gonad cavity. The broad part of the connective tissue pillars contains the parenchymal tissue of oval or polygonal cells. Numerous profiles of rough endoplasmic reticulum, which accompany the nucleus and enmesh with irregular-shaped membrane-bound inclusions of different dimension, are characteristic of these cells. The inclusions (from 1 to 8 µm diameter) contain homogenous material of moderate electron density, bearing ribosomes in its membrane. Probably, these inclusions are expanded profiles of rough endopalsmic reticulum. The unique parenchymal tissue has not been described before for the brachiopod gonads. It is possible that this tissue plays a role in the nutrition of the developing gametes.

Thus the connective tissue pillars contain both connective tissue, and muscle fibres in the myoepithelial coelomic cells. Therefore, these pillars could perform a dual function: supporting and contractile. The pillars may prevent the collapse of the gonad during gametogenesis but contract to facilitate spawning.

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NANOSTRUCTURES IN PALAEOZOIC LINGULOID BRACHIOPODS

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Preservation of shell structure elements of nanostructure scale (0.1-100 nm) is quite rare in fossil brachiopods. Our studies of untreated non-coated fracture sections of Cambrian and Devonian linguloid brachiopods by means of an environmental scanning electron microscope (ESEM) with back-scattered electron detector in a low-vacuum regime revealed phosphatised fibril-like nanostructures interpreted as compounds of early stages of baculi.

The nanofibrils observed in *Obolus ruchini* Khazanovitch & Popov from the Cambrian of the Leningrad district, NW Russia and in *Bicarinatina bicarinata* (Kutorga) from the Devonian of Estonia (Lang & Puura, 2009, Fig. 3F) are flexible strands, 70-100 nm in diameter, and resemble the structures observed by Schmahl et al. (2008, Fig. 5e) in a modern linguloid *Discradisca stella* (Gould). We conclude that the nanofibrils observed in Cambrian and Devonian linguloid brachiopods are phosphatised polymers that supported the apatite mineralization from the early stages of the formation of baculi. Williams & Cusack (2007) have suggested that in modern linguloids with baculate structure, these axial organic strands are composed of specific proteins that are yet to be identified.

Alongside the different stages of mineralisation of the baculi, the observed nanostructures are instructive for understanding biomineralisation and taphonomic processes shaping the shell structures. The use of non-destructive ESEM studies of fracture surfaces of lingulate brachiopod valves may lead to further discoveries of these fragile structures.

Acknowledgements: We acknowledge the consultations of Dr. Aivo Lepland at the Norwegian Geological Survey concerning the ESEM studies and the support of the Alwyn Williams Fund, Kristjan Jaak Foundation (to LL) and research grants SF180051s08 and ETF8049 for supporting this research and participation in the 6th Brachiopod Congress.

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A DIVERSE BRACHIOPOD-DOMINATED COMMUNITY ON SETTLEMENT PLATES FROM DOUBTFUL SOUND, NEW ZEALAND: A 'RETROGRADE' LOPHOPHORATE COMMUNITY EMULATES A PALAEOZOIC SEAFLOOR

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New Zealand is a recognised centre for modern brachiopod biodiversity, with nearly 20% of the extant global brachiopod fauna living in the New Zealand biogeographic region. Brachiopods are key species in many environments including those of the South Island fiords, and the diverse fiord communities provide an ideal opportunity to investigate aspects of brachiopod recruitment, settlement and ecology in shallow-water, temperate, mid-latitude sites. In Doubtful Sound, as in other New Zealand fiords, normal salinity marine conditions exist beneath a 2-5 m deep, humic-acid-rich low salinity layer (LSL) below which light levels are much reduced. Water temperatures vary between 11-15˚C, and suspended sediment is low. The shallow epifaunal communities are dominated by mussels, barnacles, and algae, while those between 3-6 m are dominated by bryozoans, hydroids and mussels. Mussels are restricted to the LSL because low salinity water inhibits their stenohaline predators, mainly echinoderms. Below ~6 m, low light levels, lack of sedimentation, and reduced macroalgal competition allow lophophorates such as brachiopods, bryozoans, sponges, serpulids, ascidians, and solitary corals to dominate the fiord walls.

In this study, we analysed brachiopod settlement and recruitment patterns at 5 sites in Doubtful Sound, Fiordland, New Zealand. Recruitment plates (slate tiles) with various treatments (caged, fenced, open) to examine the effects of predators and grazers were attached to near-vertical fiord walls at depths of 10-20 m. The 33 settlement plates retrieved after 12, 22 and 32 months, and ~10 years were colonised by a wide range of mainly lophophorate epibionts, including >5000 brachiopods belonging to 5 species: the rhynchonellide *Notosaria nigricans,* the short-looped terebratulid *Liothyrella neozelanica,* the long-looped terebratellids *Calloria inconspicua, Terebratella sanguinea,* and the micromorphic *Neoaemula vector.* Only 2 bivalve species were present on the tiles: bysally attached anomiids, and mobile scallops that became trapped in the cages. Brachiopod recruitment was high (up to 8,000 individuals per square metre) in contrast with results from earlier studies of colonization and growth on artificial substrata in polar seas which recorded no recruits after 3 years despite the close proximity of adult brachiopods. In our study, few brachiopods survived for more than 2 years, but the few brachiopods to reach adult size may be long-lived.

The principal determinants of the density and species richness patterns of the brachiopods appear to relate to the length of time the tiles were deployed (for one or many spawning cycles), and the diversity and density of brachiopod species on adjacent fiord walls. Water depth, substrate differences, and predator/grazing exclusion factors appear less significant. Growth rates of up to 5 mm/year were observed for several species. This study provides insights into the recruitment and ecology of a diverse, brachiopod-dominated community that is the closest living example of the rich and diverse assemblages that dominated the Palaeozoic, and to a lesser extent, the Mesozoic sea floor.

PALAEOECOLOGICAL VARIATION OF BRACHIOPOD ASSEMBLAGES IN MARGINAL MARINE ENVIRONMENTS: THE GEUMCHEON-JANGSEONG FORMATION (PENNSYLVANIAN), TAEBAEKSAN BASIN, KOREA

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The upper Palaeozoic Pyeongan Supergroup in the Taebaeksan Basin, mid-eastern Korea comprises largely a siliciclastic succession (ca. 1700 m thick) deposited in marginal marine and non-marine environments. The Geumcheon-Jangseong Formation representing the lower part of the supergroup has yielded a relatively diverse marine invertebrate fauna consisting of brachiopods, molluscs, echinoderms, corals, fusulinids, and conodonts. The brachiopod assemblages are represented by 23 species in 20 genera. A study of the palaeoecology of these brachiopod species indicates that they play an important role in understandings the significance of the environmental control on biotic distribution in marginal marine environment.

In the Geumcheon-Jangseong Formation three brachiopod assemblages, all of late Moscovian (Pennsylvanian) age, are recognised based on species composition, associated fossils and character of certain key species, namely the *Choristites*, *Rhipidomella*, and *Hustedia* assemblages. The *Choristites* assemblage includes relatively large brachiopods represented by *Derbyia*, *Choristites*, and *Stenoscisma* and may have inhabited in open marine to partly restricted marine environments, whereas the *Rhipidomella* and *Hustedia* assemblages consist mostly of small-sized brachiopods interpreted to have lived in lagoonal environments.

A REVISION OF *KANINOSPIRIFER* KULIKOV AND STEPANOV, 1975 AND RELATED TAXA

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Since *Kaninospirifer* Kulikov and Stepanov was first proposed by Stepanov et al. (1975), several species from around the world have been assigned to the genus by subsequent researchers. However, there remains considerable confusion and uncertainties about the systematics and stratigraphic and palaeogeographic distributions of this genus and allied genera. The main source of current confusion appears to have stemmed from the fact that the internal structures were not adequately documented nor figured in the original study by Stepanov et al. (1975); this has then led to many different interpretations of the genus and its relationships with allied genera. This situation has prompted us to conduct a thorough review of the genus and other genera on the basis of collections from Spitsbergen, northwest Russia (Pechora Basin), Mongolia, Russian Far east and northeast China.

In this review we have carefully reassessed the type species of *Kaninospirifer*, *Spirifer* (*Spirifer*) *kaninensis* Likharev (1943), based on the original material and descriptions of the species by Kalashnikov (1996, 1998) and also the recent study by Grunt and Afanasieva (2006) featuring their new collections from the type area (Kanin Peninsula). In this process of taxonomic revision, we have also taken the opportunity to review the phylogeny and palaeobiogeography of *Kaninospirifer*. We provisionally suggest that a subfamily, Kaninospiriferinae, which was originally proposed by Kalashnikov (1996) but has been ignored in the revised brachiopod treatise, would be revived. The subfamily is characterised by several genera representing parallelism in high latitude of both hemispheres, and it is thought that they would have evolved from *Neospirifer* Fredericks, 1924. However, more detailed phylogenetic analysis is required for understanding the whole phylogeny between genera related to *Neospirifer*.

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INTERNAL STRUCTURE AND LIFE STYLE OF *TRIPLESIA ANTICOSTIENSIS* (EARLY SILURIAN) FROM ANTICOSTI ISLAND, EASTERN CANADA

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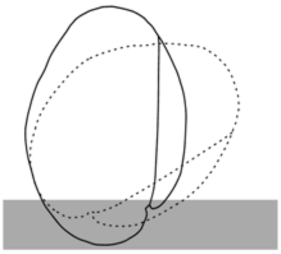
Little work has been done on *Triplesia anticostiensis* since its definition by Twenhofel in 1914 (then as a new variety of *T. insularis*) and there has been no examination of its internal structure. A collection of 744 specimens from the Goéland, Richardson, and Cybèle members of the Lower Silurian Jupiter Formation were examined. Six specimens of different sizes from different horizons were serial sectioned for investigation of the internal features. Internally, no variations were observed. The cardinal process, with cowl and keel developed, is long (ranging from 10-15% of the shell length) and fork-like. Before bifurcating, the cardinal process extends upward from its point of origin, then bifurcates and curves ventral-anteriorly before the prongs of the cardinal process project posteriorly into the ventral umbo but do not protrude beyond the hingeline. Brachiophores are short and confine the sockets with the shell wall. Divergent dental plates extend shorter than the cardinal process prongs.

Previous sedimentological and palaeoecological studies showed that *T. anticostiensis* lived in a relatively deep water setting. The water depth and the smooth shell surface of this genus may not favour the settlement of epibionts on the shells. Nevertheless, six specimens of *T. anticostiensis* were found encrusted by *Cornulites* sp. and reptant bryozoans (Figs. A, B). *Cornulites* sp. was observed to attach to the flanks of dorsal fold or in the ventral sulcus with its aperture opened towards the anterior of the brachiopod commissure but not crossing the commissure. Bryozoans tended to encrust on the dorsal valve although attachment to the ventral valve was observed as well. When bryozoans were on ventral valves, they usually attached to the sulcus or close to the anterior commissure. Both the location of the epibionts and their orientation on the brachiopod shells indicate a possible symbiotic relationship between the epibionts and their hosts. Such relationship and the preference of epibionts on the dorsal valve or, in some cases, on anterior part of the ventral valve, may indicate the life style of this brachiopod genus. It is proposed that the genus may have had a vertical to oblique living position. When in oblique position, the dorsal valve points upward away from the substrate and the umbonal region partially sinks into the soft fine-grained substrate (Fig. C). Observations of shells preserved on slabs, presumably representing original living positions, statistically support the proposed living positions. Whether other brachiopod groups with similar shell morphology have similar life style will require further investigation.

A, x2

B, x1.5



C

CANCRINELLA AND *COSTATUMULUS* (BRACHIOPODA) FROM THE PERMIAN OF SOUTH MONGOLIA AND SOUTH CHINA: THEIR MORPHOLOGY, BIOSTRATIGRAPHY AND DISTRIBUTION

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Two brachiopod genera, *Cancrinella* Fredericks and *Costatumulus* Waterhouse, are studied from Permian of South Mongolia and South China. Many of the specimens previously described as *Cancrinella* in fact belong to *Costatumulus*. The new data presented in this paper indicates that despite their crude morphological similarities, the two genera can be distinguished by features such as ornamentation, spinosity and internal details. Several species of both genera are described here, providing critical new information on the morphology and taxonomy of *Cancrinella* and *Costatumulus*. Also, the reported biostratigraphical information reveals that species of *Cancrinella* are present in the Lower Carboniferous (Tournaisian) through to Upper Permian (Changhsingian), whilst species of *Costatumulus* are mostly restricted to the Permian. From a palaeogeographical/palaeobiogeographical viewpoint, both *Cancrinella* and *Costatumulus* were very widely distributed, but there are some differences: *Cancrinella* appears to occur more frequently in the Northern Transitional Zone and Boreal Realm, whilst *Costatumulus* is mostly, though not exclusively, distributed in the Southern Transitional Zone and Gondwanan Realm.

ONTOGENETIC STAGES IN RECENT AND MESOZOIC THECIDEOIDS: AN INDEX OF A COMMON DEVELOPMENTAL PATTERN SINCE THE JURASSIC

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Brachiopod workers since the time of Thomas Davidson have used information derived from studies on modern brachiopods to help reconstruct the anatomy, shell morphology, reproduction, palaeoecology and phylogeny of fossil relatives. While this is certainly the case in the thecideoids, detailed ontogenetic studies in this group have, until recently, been rare.

Now discoveries of new modern-day occurrences of thecideoids from a wide variety of localities, mainly in shallow cryptic environments, together with their very early juvenile stages, have established virtually complete ontogenies for the internal skeletal elements of dorsal valves of the Recent lacazellines *Lacazella caribbeanensis* (Bahamas), *Pajaudina atlantica* (Canary Islands) and *Ospreyella palauensis* (Palau, Pohnpei) and the thecidellines *Thecidellina congregata* (Saipan*), Thecidellina* aff. *blochmanni* (Europa Island) and a new form from Grand Cayman. Comparison of ontogenetic stages between species within and between these two subfamilies reveals a recurring similarity which can also be recognised in their Mesozoic ancestors, reinforcing the idea of a developmental pattern common to thecideoids from the Middle Jurassic to the present day (Baker & Logan, in press). The nature of the delthyrial cover in thecideoids varies from a flat impunctate striated plate contiguous with the ventral interarea in *Thecidellina* to an upraised, triangular, centrally-placed endopunctate structure in the lacazellines and in a certain group of thecidellines also. Research with Peter Baker into the nature, development and taxonomic significance of this delthyrial cover in both modern and fossil thecideoids is ongoing.

PROTEGULAR SECRETION IN THECIDEIDE BRACHIOPODS - LARVAL SIZE MATTERS

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Calcitic first formed shells ('protegula') of rhynchonelliform brachiopods are built by the outer mantle epithelium during or immediately after metamorphosis. Ultrastructural observations of very young post-metamorphic stages of recent thecideide species revealed unexpectedly large protegular sizes (width up to 580 µm in *Thecidellina meyeri*), despite the fact that thecideide larvae are lecithotrophic. The size of the first formed shell seems to correlate directly with the size of the larva. Thecideides, being rather small with regard to absolute shell size, produce only few larvae per individual female, i.e. per-larva investment is high, resulting in relatively large offspring. Ventral and dorsal protegula of the examined thecideide post-larvae are equally sized and secreted simultaneously. *In-vitro* observation of metamorphosing *Pajaudina atlantica* showed that shell material secretion (formation of the first formed shell) happens within seconds after attachment and subsequent contraction of the animal. Post-attachment contraction flattens the animal, leading to a 'virtually' enlarged surface of its outer mantle, which then secretes the first formed shell. Although the morphological and genetic processes behind protegulum formation in brachiopods are far from being fully understood, we conclude that the size of rhynchonelliform brachiopod protegula only depends on the size of the outer mantle of the attached post-larva irrespective of parental and/or larval life history traits.

A SURVEY OF THE MESOZOIC BRACHIOPODS OF MISOOL ARCHIPELAGO, EASTERN INDONESIA

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The Misool archipelago in eastern Indonesia lies in the Seram Sea, about 80 km west of the "Birds Head" of New Guinea. The Mesozoic brachiopod fauna of Misool is described from material collected in 1981 by a joint Geological Research and Development Centre/Australian Bureau of Mineral Resources party. Ten species of brachiopod have been recognised from these collections, which also include a diverse bivalve, gastropod, ammonoids, belemnite and annelid fauna. Microfossils include forams and dinoflagellates. Dating is based mainly on ammonoids, belemnites, bivalves and the microfauna. Lithologies present include limestone, calcareous sandstone and calcareous mudstone.

One species, the Late Triassic athyrid *Misolia misolica*, has previously been described. A lectotype is designated, and the three forms recognised by von Seidlitz (1913) are synonymised. A second Late Triassic athyrid with strong, opposed costae is assigned to the genus *Pentactinella*, previously described from the European Alps and Southern Europe.

Four rhynchonellides are present. Two from the Late Triassic are left in open nomenclature. A new species of the genus *Aucklandirhynchia* is described from the middle Jurassic. This genus is present in the Early to Middle Jurassic of New Zealand, and the middle to Late Jurassic of the Antarctic Peninsula, and appears to be an Austral form. The Late Jurassic to Early Cretaceous Pacific genus *Ptilorhynchia* is represented by a new species from the Early Cretaceous.

A new species of the widespread Pacific or Perigondwanan genus *Zugmayerella* is present in the Late Triassic.

Three terebratulids are present. A single specimen which appears to be *Terebratulina* is present in the Late Jurassic. An early Cretaceous zeilleriid is left in open nomenclature. From the Late Cretaceous, a new species of *Prochlidonophora* is described. This genus has previously been described from the Early Cretaceous of the Antarctic Peninsula. Serial sections of the Misool species show a loop with fused crural processes, suggesting that the genus should be reassigned to the subfamily Cricosiinae.

PATTERNS OF CARDINALIA DEVELOPMENT OF SOME ORDOVICIAN ARTICULATED BRACHIOPODS

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Separate valves of Middle Ordovician articulated brachiopods from the Leningrad Region beginning with the size of 0.3-0.4 mm were studied. The material was obtained by the washing of clays. The study was conducted separately for orthid-like brachiopods and for strophomenids. In orthids, we observed the order of appearance of cardinalia structures. In strophomenids, we studied the peculiarities of development of the cardinal process and socket ridges.

In all studied orthid dorsal valves, the first structures to appear were rod-like socket ridges, or brachiophores. At this stage the valve is about 20 µm thick (the shell consists of one layer of fibers directed subperpendicular to the valve surface) and the sockets are absent. The valve surface between the brachiophores is smooth or with a pit, which may be where the diductors attach. The cardinal process is absent at the stage of the dorsal interarea appearance (1.2 mm), but it appears shortly thereafter at the size of 1.3-1.4 mm.

The valves of juvenile strophomenids are very thin; most valves are partly or completely broken in washing, and thus the smallest observed are 1.5 mm wide whereas the smallest studied orthid valves are considerably smaller. Though the material is scanty, the main trends in formation of the complicated cardinal process were observed. It was previously supposed that trilobed and undercut processes of strophomenids developed in the following order: simple → trilobed (by appearance of two small lateral lobes) → undercut (high median lobe is supported by lateral lobes and does not make contact with the valve bottom anteriorly). The present taxonomy of the order is based on this scheme, and the type of the cardinal process is a feature of the superfamily rank (Cocks and Rong, 1989). We studied dorsal valves from different families at different developmental stages and found that the trilobed cardinal process is formed at the base of the bilobed process by addition of the third small lobe on two closely set lower lobes. The undercut process formed in a similar way, but its lower lobes consist of posteriorly accreted socket ridges; two smaller upper lobes grew from their inner lateral surfaces. Then upper smaller lobes also accreted, turned back, resembling a curved lingua with a groove in the middle. Thus the undercut process is possibly not a real cardinal process, as at the early developmental stages the cardinalia of these strophomenids consisted only of socket ridges; the additional upper lobes possibly did not serve as a place for muscle attachment and were utilised for closing the pedicle opening. If it were so, then the muscles attached to the hollow between the socket ridges as seen in the genus *Ujukella*, whose cardinalia consists only of socket ridges bearing rudimentary crural processes. Therefore, some plectambonitoids possibly evolved from those strophomenoids with bilobed cardinal process, and hence subdivision of the Strophomenida into the superfamilies Plectambonitoidea (simple, trilobed, and undercut cardinal process) and Strophomenoidea (bilobed cardinal process) (Cocks and Rong, 1989) is possibly incorrect, as the trilobed process is formed on the base of the bilobed, and the undercut process is possibly not a real cardinal process.

Acknowledgements: This study was supported by the Russian Foundation for Basic Research, project no. 08-04-01347-a.

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Geological Society of Australia, Abstracts No. 95
6th International Brachiopod Congress, Melbourne, Australia, February 2010

SHELL STRUCTURE OF THE SMALLEST RHYNCHONELLIFORMEAN BRACHIOPODS FROM THE ORDOVICIAN OF THE LENINGRAD REGION, RUSSIA

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It is now considered to be proved that all three brachiopod subphyla Linguliformea, Craniiformea, and Rhynchonelliformea had planktotrophic larvae in the Early Palaeozoic. This feature is preserved only in the development of those brachiopods with phosphatic shells whereas brachiopods with calcareous shells evolved to develop lecithotrophic larva. In the latter, the umbonal region is usually smooth and comparable with the egg size (up to 175 µm wide). In brachiopods with planktotrophic larva the first-formed shell is from 225 to 3000 µm wide (Freeman and Lindelius, 2005) with relief that may follow the larval structure.

We obtained orthid-like brachiopods 200 to 500 µm wide from the Middle Ordovician of the Leningrad Region by washing and sieving soft clays. The sizes of shells testify that the juvenile brachiopods died at the age of 1-4 days. The preservation of the material is almost perfect, with shell structure well preserved in most cases. The central smooth umbonal region is 100-200 µm wide and consists of the microgranular primary layer. The outer part of the shell is composed of thick fibres about 20 µm long that look like ribs at high magnification. Thus the valves are not ornamented and only the brephic shell is developed. These first-formed shells may be regarded as a real protegulum formed by the whole mantle surface just after the metamorphosis; the larvae were probably lecithotrophic. The largest shells have the largest protegula. Ventral valves bear a small collar surrounding the pedicle opening and are composed of fibres 15-20 µm long and 5-7 µm thick.

Some orthids are known to have planktotrophic larva, which are preserved as well developed imprints of larval shells generally about 600 µm wide on the umbonal regions (Madison, 2004). Sometimes the microstructure of their surfaces is seen to be composed of well developed fibres with a visible length up to 100 µm. Thus well preserved small specimens of orthid-like brachiopods differ in the size, relief, and microstructure of the first-formed shell and therefore in the type of the larval development. Absence of the microgranular layer on the surfaces of larval shell imprints may be explained not only by the type of preservation but also by strong differences in the structures of both types of the larvae and thus by differences in the first secretory activity of the mantle. The inner surface of small valves (about 300 µm wide) is also composed of the microgranular layer; with fibres developed only along the valve margins. Of inner structures, the area with teeth and rodlike socket ridges are formed first (the sockets are absent), and a small depression may be developed between the “brachiophores” in the position of the cardinal process.

Acknowledgements: This study was supported by the Russian Foundation for Basic Research, project no. 08-04-01347-a.

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BRACHIOPODS AND PHORONIDS ARE TRUE METAMERIC ANIMALS

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Traditionally, Lophophorata were considered as archicoelomate animals and a sister group to Deuterostomia. However, according to more recent molecular phylogenies, the brachiopods together with phoronids and, possibly, bryozoans form a common clade with the protostome coelomates in possession of a trochophore larva, which is called the Lophotrochozoa. Molecular phylogeny suggests the close relation between Trochozoa and Lophophorata, but this grouping is weakly supported by the classical morphology. Metamery is common for Trochozoa, but Lophophorata are rather regarded as archimeric than metameric.

On the other hand, true metamery can be found among the brachiopods and phoronids. For instance, the larva of the brachiopod *Neocrania* has metameric organization. This larva possesses three pairs of chaetal sacks corresponding to three pairs of coelomic compartments in the trunk (plus an unpaired preoral coelom). During metamorphosis, larva of the craniid brachiopod *Neocrania* literally folds onto its ventral side, so that the anterior portion of the larval body becomes the dorsal side of the adult, while the posterior end becomes the ventral side. Do adult brachiopods retain the metamery? The majority of brachiopods possess two pairs of lateral mesenteries called gastro-parietal and ileo-parietal. If we assume that *Neocrania* metamorphosis accounts for the formation of the adult body plan in all brachiopods, the nature of their lateral mesenteries becomes apparent. The lateral mesenteries are perpendicular to the bent longitudinal axis that enables us to regard them as dissepiments between the trunk segments. Primitive articulate brachiopods Rhynchonellida possess two pairs of nephridia. One pair opens on gastro-parietal mesenteries, whereas the other opens on ileo-parietal mesenteries. This fact suggests that lateral mesenteries of brachiopods originated from the dissepiments between trunk segments. Thus, adult brachiopods possess three trunk coelomic segments in addition to the well developed lophophoral coelom and reduced epistome coelom.

During phoronid metamorphosis, the larval dorso-ventral axis becomes the adult antero-posterior axis, as the larval dorsal side shrinks and a protrusion on the larval ventral side makes up the majority of the adult body. As the ventral protrusion becomes larger, the midgut is drawn into it bringing the mouth and anus together at the anterior end of the adult body. In addition to the dorso-ventral mesentery, adult phoronids possess one pair of lateral mesenteries. These are perpendicular to the primary longitudinal axis and bear nephridial funnels that let us regard them as the dissepiment between two trunk segments. Phoronids have only two trunk coelomic segments in addition to the lophophoral coelom and reduced epistome coelom. Thus the number of trunk segments in phoronids is two, compared to the three in brachiopods.

Our hypothesis concerning metameric ancestors of Lophophorata supports the concept of the Lophotrochozoa. Annelida, the central group of the Trochozoa, possess a strongly pronounced metamery. Remnants of metamery are apparent in molluscs and echiurids, being exhibited in the metameric organisation of the larval nervous system and repetitive structures of polyplacophoran and monoplacophoran molluscs. The remnants of metamery in phoronids and brachiopods support the view that the common ancestor of the Lophophorata was also metameric. Thus, metamery is a plesiomorphic feature of all lophotrochozoans.

LATE TRIASSIC BRACHIOPODS FROM WESTERN ARGENTINA AND THEIR SIGNIFICANCE

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Marine Triassic deposits were long thought to be absent from the Argentine territory (cf. Stipanicic, 2002). However, in recent years, as a result of detailed stratigraphical studies in the Atuel river area (southwestern Mendoza Province), an interesting faunal assemblage was discovered in the lower and middle part of the Arroyo Malo Formation (Riccardi *et al*. 1997a, b). Such an important finding revealed the occurrence of invertebrate fossils of Rhaetian age (Riccardi *et al*., 1997a, b, 2004; Riccardi & Iglesia-Llanos, 1999; Riccardi, 2008), which include cephalopods, bivalves, gastropods, cnidarians and brachiopods. Among the latter, *Zugmayerella*? cf. *koerneri* Sandy shows strong similarity with a species known from Peru and Chile; *Sakawairhynchia marokopana* MacFarlan is indistinguishable from a species recorded in New Zealand and New Caledonia, whereas a probable new species of *Bolilaspirifer* suggests relationships with a stock from Tibet. With regard to the palaeobiogeographical affinities, in spite of its relatively low diversity, this brachiopod association shows close links with the Maorian (or Notal) biochorema, albeit with clear (mainly East) Pacific influences also (Manceñido, 2002). From the biostratigraphical viewpoint the assemblage as a whole exhibits close correspondence with the local Otapirian stage of the New Zealand succession (Murihiku terrane), thus providing useful evidence to help improve correlations among various regions that once formed part of the margins of Gondwana. In addition, since the overlying interval of the Arroyo Malo Formation has also yielded ammonites indicative of an early Hettangian age, and the sedimentary record does appear transitional and continuous (Riccardi *et al*., 2004; Lanés, 2005; Riccardi, 2008), this important section may become significant for a better understanding of faunal turnover among brachiopod taxa from the southern Hemisphere across the Triassic / Jurassic boundary.

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A REVIEW OF CRURAL TYPES, THEIR RELATIONSHIPS TO SHELL MICROSTRUCTURE, AND SIGNIFICANCE AMONG POST-PALAEOZOIC RHYNCHONELLIDA

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This overview deals with certain key morphological features that appear crucial to the advancement of knowledge about relationships between macro- and micromorphology of the rhynchonellide brachiopod shell. Briefly reviewed are relevant aspects that may hinder description, comparison and/or interpretation of morphological skeletal structures of rhynchonellides when studied by means of serial grinding techniques. Firstly, the types of crura, traditionally regarded of paramount taxonomic importance, are currently placed into four main cognate groups: *septifal*, *arcual*, *radical* and *ensimergal* (Manceñido *et al.*, 2007). Constituent types are characterised, and likely transformation series among them are also outlined. The value of crural types and their groupings within the systematic and evolutionary framework currently applied to post-Palaeozoic Rhynchonellida is corroborated, as is the significant role of heterochronic processes in the development of evolutionary novelties or in the recovery from a severe biotic crisis (Manceñido & Owen, 2002). Therefore, further studies of the ontogenetic development of crura should be encouraged. Secondly, the main kinds of microstructural patterns of the secondary shell layer as seen in cross section are summarised and illustrated. The *leptinoid* pattern, typically displaying finer, anisometric, fibres with an anvil-like or halberd-like outline is contrasted with the *eurinoid* type, characteristically having coarser, isometric fibres with a predominantly diamond-shaped cross section (Manceñido *et al.*, 2007; Radulović *et al.*, 2007). A close correspondence is established between leptinoid shell microstructure and superfamilies with crura of the radical and ensimergal groups (such as hemithiridoids, rhynchonelloids, rhynchotrematoids, dimerelloids) on the one hand, and between the eurinoid shell pattern and superfamilies with crura of the septifal and arcual groups (e.g. pugnacoids, wellerelloids, norelloids) on the other vindicates the prevailing classificatory scheme (Manceñido & Owen, 2002; *et al.*, 2007). Finally, some broad variations of the basic configurations in mantle canal patterns are outlined, confirming the merit of jointly analyzing multiple morphological characters and of applying a variety of techniques. All these may lead towards a stronger, more stable and predictive, classification of Rhynchonellida in which there is potential for reconsidering the suitability of proper subordinal divisions.

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THE *PORAMBORTHIS* AND PORAMBORTHIDAE PUZZLE: NEW DATA

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Poramborthis is a problematic genus, referred by Havlíček (1949) to the order Orthida. This concept was accepted by subsequent authors, and also in the new edition of *Treatise* by Williams and Harper (2000). The family Poramborthidae comprises only the nominal genus. *Poramborthis* has a typically Gondwanan distribution, being reported from Spain, Bavaria and Bohemia, with a Tremadocian to Floian range. New well preserved material indicates that *Poramborthis* shares many features with the early porambonitoids: the same gross morphology, distinct ventral interarea, wide hinge line, pinnate ventral vascular canal system, weak cardinal process and capillate radial ornament with radial rows of small pits. Its morphology is similar to other porambonitoids, especially to *Tetralobula* (Tetralobulidae) and also to *Rhabdostrophia* (Huenellidae). Therefore, re-assignment of *Poramborthis* to Porambonitoidea seems well based. This re-assignment indicates that endemicity of shelly fauna along the Gondwanan periphery in the Early Ordovician is not so prominent as formerly suggested.

ORIGIN AND PALAEOZOIC DIVERSIFICATION OF DISCINOIDS

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Discinoids are one of two recent clades of lingulate brachiopods, with several taxa having invariably convexo-planar shells. They live as epibenthos, often in clusters, from intertidal rocky shores to abyssal depths, always attached to any hard substrate. They always were hard-bottom dwellers. Their initial appearance in the Lower Ordovician was probably the result of a shift from a semi-infaunal to epibenthic habitat, as a response to a higher amount of skeletal debris in sediments. The pedicle foramen moved to the centre of the ventral valve, and the dorsal valve had the form of an operculum. The initial slow diversification of discinoids during the Ordovician was followed by a rapid spread of morphological disparity in Silurian and Devonian times, representing separate clades. The micromorphous discinoids appeared, copying the shape of acrotretoids or dwarf obolids; moderately-sized discinoids occupied semi-infaunal habitats in biodetrital sands; large convexoplanar discinids were fixosessile to large shells and skeletal remains. Various shapes of pedicle openings and ornament appeared in the Silurian and Devonian. This disparity disappeared in the Carboniferous and a uniform "body plan", with planar ventral and broadly conical dorsal valves, persisted from this time to the present.

Poster

DISTRIBUTION OF LINGULATE BRACHIOPODS IN A TRANSECT FROM REEF TO BASIN IN THE LOWER AND EARLY MIDDLE DEVONIAN OF BARRANDIAN, CZECH REPUBLIC

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A preliminary study of the distribution of lingulate brachiopods along a transect from reef to basin environments indicates a clear dominance of micromorphous and epibenthic species above infaunal and large ones. Lingulates are rare in reef environments, with a few large-shelled epibenthic discinoid taxa. Micromorphous genera are much abundant on the perireefal environment. There are small conical discinoid genera *Chynithele*, *Acrosaccus*, *Opatrilkiella*, and *Schizotreta,* all having rather large feeding cavity inside the shell. These are associated with dwarf obolids *Kosagittella* and *Microbolus*. A deeper environment is characterised by lingulates with small, weakly convex shells represented by small *Praeoehlertella* and other poorly known taxa, high conical and smooth shelled micromorphous biernatid *Opsiconidion* and very rare siphonotretaceans. A biernatid *Havlicekion* is more frequent in crinoidal sand. True deep water lingulates are represented by genera *Careniellus*, *Lochkothele* and *Paterula*, sometimes accompanied by small *Opsiconidion*. Dysaeroby has positive effect on the distribution of lingulates, but this is probably a result of low competition with rhynchonelliformeans. General absence of burrowing lingulates is obvious in this transect, indicating that calcareous mud and biodetridal sand could not be used as substrate for infaunal burrowers.

CARBON AND OXYGEN ISOTOPE RECORDS OF PERMIAN BRACHIOPODS FROM THE SOUTHERN SYDNEY BASIN AND TASMANIAN IN SOUTHEASTERN AUSTRALIA AND THEIR PALAEOENVIRONMENTAL IMPLICATIONS

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Fossil brachiopods have been widely used in reconstructing palaeoenvironments. In this study we have carried out 638 isotopic analyses of Permian brachiopod samples collected from Wasp Head Formation (WH; Sakmarian), Pebbly Beach Formation (PB; Artinskian), Snapper Point Formation (SP; Artinskian), Lower Wandrawandian Siltstone (at Warden Head, WarH; Rodian), Upper Wandrawandian Siltstone (at Penguin Head, PH; Wordian), and Broughton Formation (at Black Head, BH; Wordian), southern Sydney Basin; and also 15 fossil brachiopods from the Berriedale Limestone (BL; Artinskian), Tasman Basin in Tasmania. All samples were thin-sectioned and examined under the petrographic and cathodoluminescence microscopes for evaluating shell preservation. Elemental compositions of selected brachiopod samples were measured using electron probe microanalysis to further evaluate the preservation of shells.

Based on the different extent of luminescence, 344 isotopic analyses from the best preserved shelly materials (non-luminescent; NL) were found suitable for inferring palaeoenvironments. All of the average carbon isotope values of these NL shells from all stratigraphic intervals examined are greater than 5.1‰ with the highest value of 7.0‰ at the Warden Head (WarH) locality. Most of these carbon isotope values are comparable with those of tropical eastern Pangea (Russian Platform) but greater than those of contemporaneous western Pangea (North America).

The overall mean oxygen isotope values of NL shells (-1.0 to -0.2‰) are greater than those of Pangea except for those of PB (-2.9‰) and SP (-2.7‰). Assuming the oxygen isotope value was -1‰ for Permian seawater, the calculated oxygen isotope temperatures were for 13°C, 24°C, 23°C, 16°C, 12°C, 14°C, and 21°C forWH, PB, SP,WarH, PH, BH, and BL, respectively. These low isotopic temperatures are consistent with southeastern Australia’s high latitude setting during the Permian, whereas the warmer isotopic temperatures for the Artinskian PB, SP, and BL localities may indicate a combination of warming and input of melted glacial water.

SYNCHROTRON RADIATION X-RAY TOMOGRAPHIC MICROSCOPY (SRXTM) OF BRACHIOPOD SHELL INTERIOR FOR TAXONOMY: PRELIMINARY REPORT

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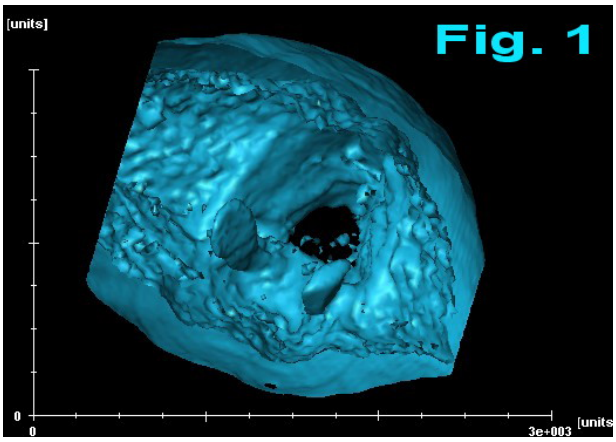
Brachiopods are one of the prime examples among all animal phyla in which the morphology of the shell interior has proved crucial for the classification and understanding of their phylogeny. In order to reveal the internal structures of fossil brachiopods with a consolidated internal matrix, destructive serial sectioning has most commonly been applied. In several cases, this technique is the only way to reveal the important internal morphological features of fossil taxa. The advantage of such destructive techniques is that they are usually relatively cheap and efficient. However, they have several disadvantages, for example: (i) destruction of the specimen, (ii) providing a poor volumetric representation of the internal structures and (iii) time and labour consuming. Many of the taxa investigated with this technique were based on a very small number of specimens (sometimes only one specimen), thus only parts of the internal morphology of some new genera were studied and/or open nomenclature was applied more often than desirable.

Here we report some pilot studies using a novel and quite advanced method to reveal the cardinalium of fossil brachiopods. Synchrotron radiation X-ray tomographic microscopy (SRXTM) is a non-destructive technique for investigation and visualizing the internal features of solid opaque objects which allows reconstruction of a complete three-dimensional image of the internal structures by observation and recording of the differences in the effects on the passage of waves of energy reacting with those structures. It uses a synchrotron, a form of particle accelerator, as a bright monochromatic X-ray source. SRXTM can produce tomographic data of exceptional resolution and clarity (Sutton, 2008). We have applied SRXTM for three-dimensional records of the internal morphology of two brachiopod taxa: (i) the rhynchonellide *'Rhynchonella' flustracea* Schlotheim from Faxe Quarry, Danian of Denmark and (ii) the terebratulide *Terebratulina imbricata* Owen from the Lower Cenomanian in northern Bulgaria. These analyses were performed at the Swiss Light Source, Paul Scherrer Institut, Villigen, Switzerland. In *'Rh.' flustracea* it was possible to observe the shape of the crura (Fig. 1) that helped to confirm our hypothesis that this species belongs to a new basiliolide genus (to be formally erected elsewhere), while in *T. imbricata* we observed the details of the tetebratulide loop forming a ring.



SRXTM was previously used to obtain three-dimensional information from Recent brachiopods to ascertain the function and growth of punctae in the shell and increase understanding of the role of cell biology in the context of biomineralisation (Pérez-Huerta et al., 2009). Here we report encouraging results from the use of the SRXTM for purely taxonomic purposes - to study the internal morphology of fossil brachiopods. Alvarez and Brunton (2008) noted that very often, due to the scarcity of well-preserved specimens and the destructive nature of the technique, some authors chose the worst specimens for serial sectioning, keeping the best preserved material for the holotype. In future, holotypes may be preferentially subjected to this mode of analysis in order to check their conspecificity with the sectioned paratypes. The SRXTM provides an opportunity to study the interiors of many taxa established only on exteriors, confirming or otherwise their taxonomic placement.

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CAN 3D "MODELISATION" BE A TOOL FOR RECONSTRUCTION OF INTERNAL STRUCTURES OF BRACHIOPOD SHELL?

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Descriptions of brachiopod shells in systematic studies require an exact examination of external features (e. g. size, shape, ornamentation) as well as internal structures of the ventral (e. g. articulation system, muscular scars) and dorsal valves (e. g. brachidium). Such structures can be directly observed if both valves are separated and free of sediment. In general, however, serial thin sections are needed when the valves are connected. Such sections give two-dimensional view on the shell at different planes.

Our aim is to reconstruct one of these structures in three dimensions using pictures given by serial sections with 3R-SOM software analysis.

A first trial has been made on the shells of *Cyrtospirifer syringothyriformis* (Paeckelmann, 1942), a Frasnian spiriferid from northern France. The dental plates were studied. They extend the teeth, support the shell and separate the central apical cavity from the lateral apical cavities.

Preparation of the three-dimensional model of discussed structures consists of the following steps: 1. preparation of the serial thin sections; 2. drawing and scanning of the serial thin sections; 3. approximating the 3D model by a cloud of points; 4. data processing with the 3D-SOM software; 5. modelisation using a grid of neurons; 6. correcting biases; and 7. final surfacing model.

The obtained 3D reconstruction needs to be improved. The first results, however, are promising. In our opinion this method may be applied to studies of dental plates in other species or in other internal structures of brachiopod shell. Such a tool may be very useful in giving more precise shell descriptions and completing species diagnoses.

THE CISURALIAN FAUNAL SUCCESSION IN PATAGONIA

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Marine lower Permian deposits bearing the brachiopod genus *Costatumulus* Waterhouse (in Waterhouse *et al.,* 1983) are known from the Tepuel-Genoa basin, located in the Patagonian region (Chubut Province) of southern Argentina. The basin enclosed a wide embayment open to the Panthalassic Ocean at the southwestern border of Gondwana, and was infilled by a nearly 7000m continuous sequence (Tepuel Group) of clastic sediments from the early Carboniferous (late Tournaisian) to the Early Permian (Artinskian). Earliest Permian faunas were recognised in the upper part of the Pampa de Tepuel Formation, but the first record of a *Costatumulus*-like faunal assemblage starts at the lower section of the overlying Mojón de Hierro Formation and ends at the uppermost Río Genoa Formation. *Costatumulus* was first recognised in the early Permian of the Calingasta-Uspallata subbasin, western Argentina (Precordillera), with the species *C. amosi* Taboada (1998), formerly *Cancrinella* cfr. *farleyensis* (Etheridge & Dun) Amos (1960). Recently, refined lithostratigraphy and biostratigraphy of the Mojón de Hierro and Río Genoa formations has allowed us to extend the stratigraphic range for the *Costatumulus* Biozone within the Tepuel-Genoa basin (Taboada & Pagani, 2009). New material collected from different localities and fossiliferous horizons throughout this basin suggests a greater number of species than previously thought (previously, only *Costatumulus* and an allied genus *Magniplicatina* Waterhouse were known from this biozone). Such adjustment in the taxonomic composition of the *Costatumulus* Biozone permits the recognition of six different and successive faunal assemblages within the basin. These are, in ascending order: the *Cimmeriella* fauna (~late Sakmarian) bearing *Costatumulus* sp. 1 (formerly *Cancrinella* cf. *farleyensis* of Amos, 1960); the newly recognised *Costatumulus-Kochiproductus* (~latest Sakmarian-earliest Artinskian) assemblage bearing *Costatumulus* sp. 2, recovered from the upper section of the Mojón de Hierro Formation; the *Costatumulus-Tivertonia* assemblage (~early Artinskian) from the lower Río Genoa Formation containing *Costatumulus* sp. 3, and the *Jakutoproductus* (~early late Artinskian), *Piatnitzkya* (~ early late-middle Artinskian) and *Magniplicatina* sp. (~middle Artinskian) assemblages from the uppermost section of the Río Genoa Formation. The taxonomic composition of the *Costatumulus* Biozone faunal succession in Patagonia appears to suggest strong faunal links with western Australia, Cimmeria (south and southeast Asia) and Siberia-Arctic and also, albeit subordinate, links with eastern Australia.

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MICRO-CT INVESTIGATIONS OF RECENT AND FOSSIL BRACHIOPODS

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X-ray microtomography is used in different spheres of the sciences and allows investigations of internal structures of small objects. One can apply this method for the research of brachiopods. Internal structures of many brachiopods have a three-dimensional construction. They are important for the determination of systematic characteristics as they carry supraspecific characters. A traditional method of investigation by using the sections of the shell is labour-intensive and resulted in destruction of the specimen. However, there is an opportunity of using a non-destructive method of x-ray microtomography for research into this important group of marine invertebrates. An x-ray microtomograph Skyscan 1172 is used for the investigation. Five recent species (13 specimens) and 100 fossil species (330 specimens) of brachiopods were studied. The research consisted of three stages: x-ray scanning, preparing slices, and creation of a 3D-model. Useful information may be obtained at every stage of the work. Slices with a pixel size of 34.1 µm and less in many cases replace sections. An opportunity to create 3D-reconstructions of internal structures is possible with the new method. In this case the shell of the holotype remains safe, and its internal structure can be studied. Research was carried out on holotypes of Upper Devonian – Lower Carboniferous brachiopods of the Kuznetsk Basin. Internal structures for 6 of these species were previously unknown, and for 8 species were not illustrated. This method is useful for rare museum objects, and also for fragile recent specimens. For example, a specimen of a micromorphic Recent brachiopod *Eucalathis murrayi* was investigated, and 3D-reconstructions of the brachidium throughout the development of the Recent brachiopod *Macandrevia cranium* were obtained. Micro-CT may be useful for the research of shell microstructures. Sometimes one can observe in slices with large magnification isolated fibers, for example in *Richthofenia* sp. Best of all in slices one can find punctation. Pseudopunctae of a diameter 100-140 µm are noted in the shell of the brachiopod *Semiplanus semiplanus*. Endopunctae in the shells of *Phragmophora* sp., *Isorthis* sp. and *Levenea depressa* are found. It was noted that destruction of valves of *Rhipidomella altaica* and *Eumetria* sp. took place according the punctation. Distinctive punctae, their density, and embranchment are noted in the Jurassic brachiopod *Russiella* sp. 3D-reconstruction of internal micro-ornamentation of a brachial valve beak of *Semiplanus semiplanus* was obtained by using micro-CT. Mantle spicules of *Terebratulina retusa* also can be observed. The effectiveness of the micro-CT technique depends on mineral composition of brachiopod shells and of the surrounding rock. For example, silicified, ferruginised, or pyritised shells are well contrasted in a carbonate rock. Calcite shell in phosphorite rocks and dolomitised shells in carbonate rocks are not contrasted. Thus, by using micro-CT Skyscan 1172 one can research the punctation and micro-ornamentation of brachiopod shells, spicules, fragile specimens, shells of holotypes, various internal shell structures and also different stages of their development. In some cases the slices replace sections, and 3D-models allow reconstruction of some internal structures.

FINDING OF TYPE SPECIMENS OF A RECENT BRACHIOPOD *DIESTOTHYRIS FRONTALIS* (MIDDENDORFF, 1849)

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Travelling in Siberia and the Far East of Russia, Aleksander F. Middendorff described in 1849 a new Recent brachiopod species *Terebratula frontalis* from the Sea of Okhotsk. The type material was found in August 1844 in the southern part of the Sea of Okhotsk, probably near the island of Bol`shoy Shantar. For a long while the storage place of the type specimens was not known, but these have now been located at the Zoological Institute of RAS in Saint-Petersburg. At first an original label of A.F. Middendorff was found, and then a type specimen (№ 141-1) with a copy of this label was located. E.D. Konzhukova (1957, p. 69) mentioned this specimen in amongst material of series 141. According to the International Code of Zoological Nomenclature, a specimen which an author has indicated as original may be accepted as a holotype. Some specimens of *D. frontalis* were figured in a paper by Middendorff (1851). Judging by the size of the newly-found specimen, it conforms to form A` as selected by the author. Its length is 14.6 mm, and its age as determined by the growth rings is 8 years. One can comment about a brachidium only based on the original drawing, as it is destroyed in the holotype. A column of a septum is preserved. Besides this specimen, another shell and 2 brachial valves of the brachiopod *D. frontalis* are found in the collection of A.F. Middendorff, earlier indicated by E.D. Konzhukova under numbers of a series 142 (№142-1, 142-2, 142-3). Another specimen with number 138 apparently belongs to the collection of Middendorff.

In August 1978 the scientific ship 'Poseidon' using a mass probe collected 553 live brachiopods and 4 empty shells of the brachiopod *D. frontalis* at a depth 23 m near Bol`shoy Shantar island in the Sea of Okhotsk. Their size and age distributions are bimodal, with both juveniles and adult brachiopods represented. Density of settlement of the brachiopods is 644 specimens per square metre. I.G. Zaks (1929) indicated that brachiopods are the leading group in communities at a depth about 30-35 m near Bol`shoy Shantar.

Four specimens of the Recent brachiopod *Hemithyris psittacea* are also stored in the collection of Middendorff. They were collected in 1840 in the region of the Barents or White Seas during K.M. Bar`s Lapland expedition. This collection has undoubtedly great historical significance.

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BRACHIOPOD-BASED BIOGEOGRAPHIC LINKAGES BETWEEN EASTERN AUSTRALIA AND SOUTH CHINA IN THE LATER ORDOVICIAN (DARRIWILIAN-KATIAN)

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Brachiopod faunas spanning the late Darriwilian to late Katian interval (late Middle and Late Ordovician) are represented in Eastern Australia from Tasmania and central New South Wales. The tectonic settings of these areas are dissimilar, with the Tasmanian succession developed as predominantly shallow water carbonates on the Delamerian margin of Gondwana, whereas in New South Wales contemporaneous brachiopods are preserved in limestones and deeper-water clastic rocks fringing volcanic islands of the Macquarie Arc, which is interpreted as having formed offshore to the continental margin. Biogeographic similarities between Eastern Australia and the various Ordovician terranes comprising Kazakhstan have been recognised for many years. Palaeogeographic reconstructions which place South and North China and the Tarim block off the coast of the Western Australian craton, between Eastern Australia and the Kazakhstan terranes, therefore suggest that considerable faunal linkages should exist between Eastern Australia and South China. During the Ordovician South China consisted of a passive margin setting comprising the Yangtze Platform, Jiangnan Slope and Zhujiang Basin. Although the tectonic setting of South China bears some resemblance to the Delamerian margin in Tasmania, biogeographic analyses of the South Chinese Late Ordovician brachiopods have disclosed greater similarities with the island arc faunas of central New South Wales than to the Tasmanian faunas. For example, the trimerellide brachiopod *Belubula* (first described from New South Wales) only occurs otherwise in Jiangxi Province of South China, where it is represented by its junior synonym *Zhuzhaiia*, and the plectambonitoids *Metambonites* and *Synambonites* which are quite restricted in their distribution are present in both New South Wales and South China. Furthermore, despite their apparently closer proximity in the later Ordovician, the brachiopod faunas of New South Wales (based on a database comprising 80 genera) and Tasmania (including 23 genera) share surprisingly few close biogeographic similarities.

In order to more precisely analyse biogeographic linkages between Eastern Australia and South China, the stratigraphy of each has been as finely subdivided as is practicable using graptolite and conodont zones, and each fossiliferous horizon has been assigned to a Benthic Assemblage (BA). The latter is especially significant in biogeographical analysis as most brachiopod species in the Macquarie Arc are restricted to generally one and rarely two adjacent BAs. Initially only contemporaneous faunas inhabiting comparable water depths were analysed, using the computer program PAST, in order to provide a geologically-'instantaneous' view of faunal affinity. Grouping several biostratigraphic zones, and then comparing brachiopod faunas inhabiting identical BAs may enable recognition of origination centres and migration pathways where the same genera appear in separate regions at slightly differing times. However, comparison of entire faunas from different areas with little regard for similarity of water depth habitat or contemporaneity runs the risk of smearing the result, leading to vague or erroneous biogeographic linkages.

COMPARISON OF MATERIAL PROPERTIES OF FOSSIL AND RECENT SHELLS OF *THECIDELLINA*

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Calcium carbonate biomineral structures, due to their abundance, diversity and unique material properties, are frequently analysed in materials science. Shells of marine invertebrates represent excellent examples of optimised composite biomaterials, mainly because of the interplay between the organic and inorganic components of biominerals. Brachiopod shells, particularly those of calcitic composition, have in fact been studied previously in terms of material properties (e.g. Pérez-Huerta et al. 2007; Pérez-Huerta et al. 2008; Goetz et al. 2009). Results have indicated that brachiopod shells are hierarchically structured biominerals with interesting material characteristics related to their microstructure, crystallography and ecology. However, the effects of diagenesis on the material properties of brachiopod shells have, to date, not been established. *A priori* assumptions would suggest a homogenisation of shell properties, associated with those of inorganic minerals (e.g. calcite), because of the loss of organic components throughout the process of fossilisation. To assess the influence of fossilisation, measurements of hardness and elastic modulus by nanoindentation were carried out on fossil shells of *Thecidellina* collected from a Pleistocene reef setting at Willemstad Harbor (Curaçao). Results were compared with material properties analysed in Recent specimens of the same genus from Jamaica. A comparison of material properties of fossil and Recent shells of *Thecidellina* will be presented as well as an analysis of the effect of fossilisation on the characteristics of calcite biominerals.

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NEW INSIGHTS ON THE ONTOGENY OF EARLY PALAEOZOIC RHYNCHONELLIFORM BRACHIOPODS: IMPLICATIONS FOR BRACHIOPOD PHYLOGENY

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All Recent rhynchonelliform and craniiform brachiopods possess lecithotrophic larvae. However, there is growing evidence that the larva in a significant number of Early Palaeozoic rhynchonelliforms was planktotrophic, with a prolonged free swimming stage. The larval trophic mode of extinct brachiopods can been revealed indirectly not only from the relative size of the embryonic and metamorphic shell, as expressed through growth marks, but most importantly from characters of secretion of the primary and secondary shell fabric, as well as from the loss of larval setae and formation of adult setae along the shell margin.

The metamorphic shells of Early Palaeozoic rhynchonelliforms with inferred planktotrophic larva usually vary in size from 350 µm to 700 µm, which significantly exceeds the documented maximum egg size in Recent brachiopods. Known Early Palaeozoic metamorphic shells consistently preserve two pairs of inflated lobes on the dorsal valve, most probably corresponding to the position of two pairs of larval setal sacs; they also preserve a rounded posterior mound, up to 170 µm wide, interpreted as the rudiment of an embryonic or metamorphic protegulum, which formed prior to the settlement of the larva. The metamorphic shell surface exhibits various minor deformations that suggest it was flexible and probably entirely organic in composition. Shell mineralisation started at the end of metamorphosis with the secretion of an irregular mosaic of tablets in the secondary shell layer along the entire surface of the outer epithelium. The regular laminar or fibrous pattern of the secondary shell fabric appears outside the halo, marking the outer boundary of the metamorphic shell.

There is a considerable difference in ventral metamorphic shell formation between the rhynchonellate and strophomenate clades. In the orthidines (typified by *Notorthis* and *Paralenorthis*) and some clitambonitidines (*Oslogonites*), the dorsal and ventral metamorphic shells were most probably secreted simultaneously, and with the pedicle emerging between valves. The metamorphic larval shell in these groups shows distinct similarity to that of paterinides.

In the strophomenates there was a significant delay in the ventral mantle differentiation and secretion of the ventral valve, which occurred only after settlement, while adult attachment structures were secreted by the ventral mantle, rather than representing a definitive pedicle formed from a posterior lobe as in rhynchonellates. Thus, the characters of larval development and early shell formation of the strophomenates do not correspond to the patterns of rhynchonelliforms as presently defined, but are shared with some linguliforms (siphonotretides and the enigmatic *Salanygolina*) as well as the craniformeans. This suggests that the lecithotrophic larva of Recent Craniiformea is derived and may be homologous with the Early Palaeozoic 'strophomenate-type' planktotrophic larva.

The lecithotrophic larva most probably evolved independently in the clitambonitidines (*Arctohedra*) by the Mid Cambrian and in the rhynchonellides by the Mid Ordovician. In both these groups, the dorsal and ventral protegulum is mineralised and secreted simultaneously shortly after settlement.

MIDDLE ORDOVICIAN HARKNESSELLIDS (ORTHIDA, DALMANELLIDINA) FROM THE MEDITERRANEAN MARGIN OF GONDWANA

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The family Harknessellidae Bancroft, 1928 (Orthida, Dalmanellidina) was erected to embrace an assemblage of species referred till then to *Harknessella*, including five genera mainly known from the Middle and Upper Ordovician of Britain. Subsequently only three new genera have been provisionally included within the family. It is characterised by a frequently mucronate hinge line, fulcral plates usually present and a rudimentary notothyrial platform, anteriorly excavated by posterior adductor scars. Variable shell profile, radial ornamentation and ventral muscle fields, allow a ready distinction of its genera. The earliest record of the family is from the upper Middle Ordovician, but most of its genera are restricted to the Upper Ordovician, with only one possible record from the Lower Silurian (Harper, 2000).

Herein we suggest assigning to the family also the genus *Cacemia* Mitchell, 1974, widespread in the middle Darriwilian (upper Middle Ordovician) of the Iberian and Armorican massifs, as well as in northeast Algeria. Since its erection *Cacemia* was placed among the dalmanellidin heterorthids, in spite of its strongly mucronate hinge line, absolutely unusual within this Mediterranean family. Supporting this assignment was the erroneous inclusion within *Cacemia* of an indeterminate species of the heterorthid *Tissintia* (Mitchell, 1974). Nevertheless, the outline and main internal features of *Cacemia* are more typical of the family Harknessellidae, of which it would be the oldest known representative.

From the upper Darriwilian beds of the Central Iberian Zone (Central Spain) a new harknessellid genus and species has been identified. Although close to *Horderleyella*, based on its strongly fascicostellate radial ornament and obtuse cardinal angles, its convexoplane to convexoconcave profile allows discrimination from the typically dorsibiconvex *Horderleyella*.

A phylogenetic analysis of the family, performed with PAUP and PAST programs, places *Cacemia* and the new genus in basal positions of the resulting cladograms, in good agreement with their early stratigraphic record. Based on our study, the family Harknessellidae seems to have originated in the high latitude Mediterranean margin of Gondwana during the late Mid Ordovician, from where it soon spread into Avalonia, shortly after the detachment of this palaeocontinent from Gondwana. The family reached its highest diversification in Avalonia throughout the Late Ordovician, keeping connections with the Mediterranean and Proto-Andean margins of Gondwana, as well as with the mid latitude palaeocontinents of Baltica and South China.

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LOWER CRETACEOUS BRACHIOPODS FROM COLOMBIA

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Very few studies have been carried out on the fossil record of brachiopods from Colombia. The lower Cretaceous of Colombia, however, has abundant and well-preserved brachiopod assemblages. Reported lower Cretaceous brachiopods include the terebratulids *Arenaciarcula beaumonti* and *Gemmarcula* cf. *menardi* deposited in the d`Orbigny Collection without accurate data field and *Sellithyris sella* reported as *Terebratula haueri* (Karsten, 1958) and *Terebratula sella* (Dietrich, 1938) from Zapatoca, Santander Province, in central Colombia. We studied a section, 200 km south of Zapatoca, in the upper Upper Rosablanca Formation from Santa Sofia-Boyacá that contains a well preserved assemblage dominated by *Sellithyris* aff. *sella* and other unidentified terebratulids. This new record suggests that *Sellithyris* was widely distributed during Late Valanginian–Hauterivian in the Andean realm. A Fourier analysis on these brachiopod shells was conducted to evaluate the relationship between Andean and Tethyan forms. There are extensive outcrops of shallow marine, lower Cretaceous sediments in the eastern Andes of Colombia, which have not been explored despite their high potential for yielding rich brachiopod assemblages.

RECENT TEREBRATULIDS (BRACHIOPODA) OF SAN BERNARDO, CARIBBEAN SEA FROM COLOMBIA

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Several specimens collected during the INVEMAR-MARCORAL cruise in the Island of San Bernardo in the Caribbean coast of Colombia were preliminarily examined. The brachiopods are associated with a deep-water reef community (120 -180 m) comprising marine algae, mollusks (snails, bivalves and tusk shells), echinoderms (stars and sea lilies), bryozoans, and decapod crustaceans. The brachiopods were collected from a wide range of sediments (mud to gravel-sand). The material includes terebratulids: *Argyrotheca* cf. *cuneata*, *Argyrotheca* sp.1, *Argyrotheca* sp.2, *Terebratulina* sp. and *Tichosina* sp. The fauna is dominated by *Terebratulina* and *A.* cf. *cuneata* which are represented by small shells with a bathymetric distribution from 100 to 170m; *Tichosina* includes 7 complete or near complete shells of adults and 1 juvenile. The relationships between body size, abundance, deep and sediment facies are described.

EARLY EVOLUTION OF EOSPIRIFERINES THROUGH LATE ORDOVICIAN AND EARLY SILURIAN

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Spiriferids, one of the major groups among the calcareous-shelled brachiopods that survived three mass extinctions during the Palaeozoic, include two suborders: Spiriferidina and Delthyridina. The Delthyridina contains two superfamilies, Delthyridoidea and Reticularioidea with the earliest known genera being *Howellella* and *Spirinella*, both recorded first from Telychian, Upper Llandovery strata (Johnson *et al.*, 2006). The earliest clade of the Spiriferidina is the eospiriferine *Eospirifer*, recorded first from the upper Katian (Upper Ordovician) of E China (Rong *et al.*, 1994) and possibly Kazakhstan (Sapelnikov & Rukavishnikova, 1975).

Eospirifer survived two phases of the end Ordovician mass extinction but is not encountered in the interval between these two phases. New investigations show that it is associated with constituents of the *Hirnantia* Fauna and the trilobite *Dalmanitina* (*Songxites*) from the Kuanyinchiao beds (early-mid Hirnantian) at Shanwangmiao, Honghuayuan, Tongzi County and Shichang'ao, Ganxi, Yanhe County, northern Guizhou, SW China. Moreover, *Eospirifer* has been recorded from the upper Hirnantian of SE China (Rong *et al.* 2008) and Tasmania (Sheehan and Baillie, 1981), the lower Rhuddanian of northern Guizhou, SW China (Rong *et al.* 2003a) and western Zhejiang, SE China (Rong and Zhan, 2006), and the upper Rhuddanian of northern Guizhou and western Zhejiang, S China (Rong and Yang, 1981; this paper), Ningxia (N China), western Tarim (NW China) (Rong and Chen, 2003; Cocks and Rong, 2008), and Chu-Ili, S Kazakhstan (Modzalevskaya and Popov, 1995).

In addition to *Eospirifer*, there occurred another two eospiriferine genera, *Yingwuspirifer* and *Striispirifer*, that both originated from *Eospirifer* during late Rhuddanian time. *Yingwuspirifer* seems to be an unsuccessful offshoot of the eospiriferines, characterised by possessing smooth lateral slopes, a uniplicate ventral sulcus and a grooved dorsal fold, whereas *Striistpirifer* (including *Hedeina*) can be considered a successful stock distinguished by plicate flanks and no ribs in the sulcus. *S. acuminiplicatus*, from the upper Rhuddanian of northeastern Guizhou, SW China, and *S. orbiplicatus*, most likely from the upper Rhuddanian of Ningxia, N China, are the two earliest known species of *Striispirifer*. *Espella* among the eospiriferines first occurred in Kazakhstan. Some of the species of this genus appeared in Tuva (Kulkov *et al.*, 1985), Central Asia (Zeravshano-Gissar), and Kazakhstan during the Aeronian. Other species at this time were confined mainly to east and central Asia. Eospiriferines were unable to spread to Siberia, Laurentia, Baltica, Avalonia, Southern Europe, North Africa, and South America until the Telychian, suggesting that the distribution of the eospiriferines in these regions during the Early-Mid Llandovery is of biogeographic significance.

Fundamental characters (such as a spiriferid shell form and laterally directed spiralia) were established in the earliest spiriferids in the late Katian (Late Ordovician) but this major group underwent an initial morphological diversification during the Rhuddanian and Aeronian (Early Silurian), indicating early evolutionary experiments that resulted from variations in environmental conditions. Spiriferids subsequently flourished through the rest of Palaeozoic. It is noted that the development of a ctenophoridium (=striated cardinal process) is known to occur in some eospiriferid genera, such as *Eospirifer*, *Striispirifer*, and *Xinanospirifer* of South China in Telychian, Late Llandovery and Ludlow-Pridoli time. Thus the establishment of a new family based only on this character within the superfamily Cyrtioidea is probably inappropriate.

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THE PHYLOGENY OF DELTHYRIDOID SPIRIFERIDS - A NEW INTERPRETATION

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In the recent years a new systematics of the Delthyridoidea has been established which is introduced here. During this study, delthyridoid brachiopod faunas from different regions of today's world, representing different palaeobiogeographical units, are compared side-by-side to investigate their phylogenetic relationships and to improve, in a second step, the palaeobiogeography from Late Silurian to Early Eifelian times. During this time span delthyridoid spiriferids are characterised by a global abundance and fast evolution, and, therefore, are used as important biostratigraphical and palaeobiogeographical tools. The new systematics is mainly based on direct comparison of articulated and isolated brachiopod shells, external and internal moulds, as well as latex casts and serial sections. Brachiopods, especially type material, from collections of different institutions and museums were studied as well as personal material, whenever possible collected from topotype outcrops. The specimens consist of externally very similar spiriferids which have been identified as the same genera, species, or even subspecies in earlier times. However, careful comparison has shown that under the same genus several new taxa were hidden. In total, 9 new families have been established: Australospiriferidae, Filispiriferidae, Multispiriferidae, Murchisonispiriferidae, Orientospiriferidae, Otospiriferidae, Patriaspiriferidae, Rostrospiriferidae, and Trigonospiriferidae; 1 new subfamily: Multiplicatispiriferinae; 10 new genera, and an additional 2 in open nomenclature: *Cyclopterospirifer*, *Frequentispirifer*, *Hallispirifer*, *Leonispirifer*, *Multiplicatispirifer*, *Murchisonispirifer*, *Ovetensispirifer*, *Parlinispirifer*, *Shujiapingensispirifer*, *Turcispirifer*, gen. nov. A, and gen. nov. B; and 12 new species, 3 of them in open nomenclature: *Filispirifer hamadae*, *Leonispirifer leonensis*, *Multiplicatispirifer foumzguidensis*, *Murchisonispirifer feldmani, Ovetensispirifer novascotianus*, *Patriaspirifer merriami*, *Patriaspirifer johnsoni*, *Quiringites arensentiae*, *Turcispirifer turciae*, and *Multiplicatispirifer* cf. *foumzguidensis*, *Quiringites* cf. *arensentiae*, and ?*Turcispirifer* sp. A; 1 taxon is defined as nomen nodum: *Orientospirifer nakaolingensis wani*. These forms are considered as 6 distinct morphotypes *Howellella-*, *Arduspirifer-*, *Acrospirifer-*, *Euryspirifer-*, *Paraspirifer-*, and *Multiplicatispirifer*-morphotypes, that occur in all palaeogeographic units. The new systematics consists of different and independent clades: the European/North African delthyridoid spiriferid clade, the North American delthyridoid spiriferid clade, the Asian delthyridoid spiriferid clade, the Malvinokaffric delthyridoid spiriferid clade, and the delthyridoid multiplicated spiriferid clade. Their phylogenetic relationship reflects a tendency for increasing endemicity until the end of the Early Emsian, which is interrupted by short term regional faunal exchange within a province or within a realm, followed by a loss of endemicity resulting from global distribution of brachiopod genera until the end of Givetian time. The Old World Realm is subdivided into the European Realm, consisting of the Gondwanan and Avalonian provinces, and the Asian Realm, consisting of the Siberian, Sinic, and Mongolian provinces.

Acknowledgements: This study is part of the DFG-Project JA 987/6-1: "Biohistoric evolution of spiriferid brachiopods: A model study of a globally distributed Devonian clade".

A NEW LIFE HABIT OF *CYRTINA* IN THE ORISKANY SANDSTONE (BRACHIOPODA, NORTH AMERICA, LOWER DEVONIAN)

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The brachiopod fauna of the Oriskany Sandstone of Cumberland/Maryland (USA) is characterised by silicified articulated shells. During the revision of "*Spirifer*" *intermedius* small cyrtinid specimens, probably or closely related to *Cyrtina rostrata*, have been found attached with their high ventral area to the shell of the spiriferid, either on the wings or on the flanks of the sulcus. This is interpreted as the cyrtinid brachiopod using the spiriferid shell as a hard substrate for attachment, profiting from the inhalant/exhalant current system initiated by the delthyridoid spiriferid. It is remarkable that this cyrtinid-brachiopod life habit has never been described before and that it is so far only reported in these two species in the Oriskany Sandstone (middle Lower Devonian). Due to the silicification of the shell material the surface shell structure is destroyed and further pedicle attachment marks are not recognisable. The question of whether this represents a new life habit of cyrtinid brachiopods or just a freak of nature cannot be answered at present.

NEW IMPLICATIONS ON THE INHALANT/EXHALANT CURRENT SYSTEM OF THE *PARASPIRIFER*-LIKE MORPHOTYPE

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A *Paraspirifer*-like morphotype is represented by delthyridoid spiriferid brachiopods characterised by medium to large specimens with a strong dorsibiconvex curvature and thick development of secondary shell material in the apical region. Within the Delthyridoidea these forms are represented mainly by the Early to Middle Devonian *Paraspirifer* in Europe and North America, and new genus (in press) that has been identified in northern Spain and in the Siegenian of Morocco (both Emsian, Early Devonian). Representatives of the new genus, *Paraspirifer cultrijugatus*, and partly the group including *Paraspirifer bownockeri* occur in a clear water carbonate facies which was probably poor in nutrients and required new life strategies by the brachiopods. A reconstruction is introduced of the life habit with special attention to the filter feeding system of the lophophores of *Paraspirifer* and the new genus.

Accretion of secondary shell material in the apical region of the ventral valve of both genera causes the shell to lie at an angle on the seafloor such that the dorsal valve is above the ventral valve. In this position, the anterior margin of the sulcus tongue is the highest point of the brachiopod so guaranteeing separation of the inhalant current from the exhalant current which is ejected at the sulcus tongue. In this way the inhalant current through the lateral commissure assures a maximum influx of nutrients.

A 3D reconstruction of the new genus shows that the spiralia were orientated in a posterior direction reaching almost to the hinge line, with spirals that were very small in diameter and extended to half of wing length in transverse cross section. It is suggested that very long tentacles were attached to the lophophore that could reach far into the suspension cloud to enhance the capture of nutrients. The large free part of the mantle cavity was needed to store the tentacles when the shells were closed.

Another possibility is that the brachiopod opened and closed the valves more frequently than in other taxa. The tentacles were probably of short to moderate length, and in a closed shell stage caused a vortex inside each flank of the mantel cavity for filtering the water. The exhalant current was ejected at the sulcus tongue as soon as the valves opened and produced the inhalant current entering from the side until the shells closed again. An advantage of this method would be that there is no nutrient competition during the filtering time because the inhalant water is protected within the shells against other nutrient competitors. In each vortex the water would have flowed in an anterior direction from smallest to largest spiral and the nutrients would have been transported along the food grove to the mouth while tentacles kept the vortex flow moving. In the lateral parts of the mantel cavity, the water current flowed in an opposite or posterior direction. The strategy of orientation of the brachidium in a posterior direction is only known from the new genus, and does not seem to have been successful as this evolutionary branch became extinct during the late Early Devonian.

The orientation of the brachidium in *Paraspirifer bownockeri* was in a lateral direction, which means that ecological parameters during the life of *Paraspirifer bownockeri* were different from the time interval in which the new genus has lived. Due to the mouldic preservation of European late Early Devonian *Paraspirifer* taxa the brachidia of these forms are unknown.

Acknowledgements: This study is part of the DFG-Project JA 987/6-1: “Biohistoric evolution of spiriferid brachiopods: A model study of a globally distributed Devonian clade”.

GROWTH PATTERN IN LIVING BRACHIOPOD ASSOCIATIONS - SHALLOW AND DEEP

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An association of living *Waltonia inconspicua* from Portobello (South Island, New Zealand) is compared with an association of *Chlidonophora chuni* which was dredged south of the Maldives in 1899 by the German Valdivia-Expedition.

The shells of *W. inconspicua* were collected directly on the shore line, they were marked with a pair of fine tweezers and replaced exactly in their living place. After 413 days they were collected again and measured.

It appeared that the growth rate can be very different within a very limited area of 25 by 25 cm. It was expected that small individuals (probably juvenile) would have a higher growth rate than bigger specimens (probably adult shells). Surprisingly this is not a strict rule. There are also small individuals with a low growth rate and large specimens with high growth rates.

Obviously this depends of the specific place of settlement. The larvae of *W. inconspicua* (as do probably most brachiopod larvae) prefer a quiet place. Probably the growth rate correlates with a “disturbance rate”. In comparison with suboptimal places, individuals living in less disturbed environments are able to feed more successfully. In this way large and small individuals of the same age are found living together in a relatively confined neighbourhood.

The *Chlidonophora chuni* specimens were dredged from a depth of 2,900 m in February 1899. All shells show very regular, uniform growth lines. This implies an ecologically stabile environment.

Whereas in *Waltonia* the growth rates could be determined quantitatively, those of *Chlidonophora* are speculative. *Waltonia* from the tidal zone shows a heterogeneous, irregular growth pattern; in contrast the growth of *Chlidonophora* in deep water is very regular.

Poster

A COMPARATIVE HISTOLOGY OF LARVAL BROODING IN THECIDEOIDEA

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There are significant differences in the morphology of brooding structures between the two recent sistergroups Lacazellinae and Thecidellininae within the monophylum Thecideoidea. Consequently, we investigated the brooding apparatus of four species in three different genera (*Minutella, Lacazella* and *Pajaudina*). Although there are major differences in their anatomy, histological studies reveal a common origin (homology) of the brood pouches. Lacazelline brachiopods possess the most complex brooding apparatus of all brachiopods. The larvae are attached to two specialised tentacles, which pass through the marsupial notch of the brachial bridge and reach into the median brood pouch in the inner mantle of the ventral valve. Brood pouch and specialised tentacles are derivatives of the lophophor epithelium. In contrast to that, species of Thecidellininae brood their larvae in two brood pouches that are located in the brachial lobes of the dorsal valve. Specialised tentacles are absent. However, the brood pouches are also derived from the lophophor epithelium. The origin of the brood pouches is similar in both groups and can be seen as a synapomorphic character of Lacazellinae and Thecidellininae.

PALAEOCLIMATIC FLUCTUATIONS IMPLIED BY FAUNAL CHANGES NEAR THE PERMIAN-TRIASSIC TRANSITION IN THE PERI-GONDWANAN REGION

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The peri-Gondwanan region in south and southeast Asia was located in a mesothermal temperate zone. As such, this region was more sensitive to climatic changes than the palaeoequatorial and polar settings. As predicted by some models, when the Earth became globally warmer, tropical temperatures changed little, but mesothermal and high-latitude temperatures became warmer, which normally would have favored the pole-ward spread of life from lower latitudes. In this report, we document distinct palaeoclimate fluctuations across the Permian-Triassic transition based on a few sections with mixed warm- and cold-water faunas including brachiopods, corals and conodonts in the Asian peri-Gondwanan region.

The faunal successions across the Permian-Triassic transition in the peri-Gondwanan region of Tibet and Himalaya indicate that the Late Guadalupian (Middle Permian) and the whole Wuchiapingian (Early Lopingian) contain highly diverse compound rugose corals such as *Waagenophyllum* and *Ipciphyllum*, and brachiopods dominated by the Tethyan elements such as *Enteletes tschernyschewi*, *Edriosteges* cf. *poyangensis*, *Richthofenia sinensis*, *Permophricodothyris elegantula*, *Transennatia gratiosa* etc., therefore indicating a relatively warm condition. However, early and late Changhsingian brachiopods became less diverse and dominated by cool-water Gondwanan/bipolar elements such as *Costiferina indica*, *Waagenoconcha purdoni, Aurilinoproductus alatus* and compound rugose corals disappeared, and conodonts are absent or characterised by typical cold-water elements such as *Vjalvognathus* and *Merrillina* (e.g. Wardlaw and Mei, 1999; Kozur, 2005; Shen et al., 2006). The above-mentioned change of faunal assemblages may suggest a cool climatic condition prevailing in the early and late Changhsingian in the Tibetan-Himalayan region. This cool condition was then followed by a rapid warming event in the latest Changhsingian just prior to the end-Permian (end-Changhsingian) mass extinction (Shen et al., 2006), as indicated by a highly diverse brachiopod fauna including many typical warm-water elements such as *Leptodus, Richthofenia, Tethyochonetes* and *Enteletes* (Shen et al., 2000), and compound corals and sudden occurrences of highly abundant conodont faunas just below the Permian-Triassic boundary in the peri-Gondwana region (Shen et al., 2006).

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NEIL ARCHBOLD: HIS CONTRIBUTIONS TO BRACHIOPODOLOGY AND THE STUDIES OF THE GLOBAL PERMIAN SYSTEM

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Neil Archbold had lived a short but remarkably successful academic life, characterised by an output of 222 professional publications (including co-authored full papers and abstracts) (Talent and Campi 2008), averaged at 8.54 publications per academic year (academic years used here are the total number of years since Neil's first scientific paper published in 1979 until his death in 2005), nine Australian Research Council competitive research grants and proposition and formal documentation of 174 new taxa, including 6 new subfamilies, one of which had been subsequently elevated to family rank, 37 new genera, 5 new subgenera and 178 new species (Campi 2008). All Neil's new taxa proposed prior to 2004 have been recognised in the revised Treatise on Brachiopoda. Neil has also been honored with his name associated with four new genera (*Archboldina* Waterhouse, 2001, *Archboldevia* Angiolini and Long, 2008, *Neilotreta* Waterhouse, 2008 and *Archboldiella* Winkler Prins, 2008) and five new species. Although most of Neil's taxonomic works were focused on the Permian brachiopod faunas of Western Australia, his taxonomic enterprise had extended well beyond state and national boundaries, as evident from his extremely productive research collaborations with colleagues of Argentina, China and India and several other countries.

Apart from a passionate interest in brachiopod taxonomy, Neil also contributed substantially to the improvement of Permian regional and global biostratigraphy and correlations and to the understanding of Permian regional and global biogeography and palaeogeography. The former includes the recognition and documentation of a succession of eighteen Permian brachiopod zones in Western Australia and another three macro-invertebrate (gastropod, bivalve, brachiopod) assemblage zones from the Lower Permian of eastern Australia. By publishing an article in 'Nature' in 1982, Neil was among the earlier workers who recognised and documented the then highly controversial Permian palaeobiogeographic and, by implication, palaeogeographic relationships between Australia and Southeast Asia. Neil's approach to Permian biostratigraphy and global correlations was characterised by detailed and robust taxonomy, with appropriate consideration for biogeographic provincialism and hence the need for regional biostratigraphic schemes and alternative correlation tools like the "biostratigraphic gateway" technique. Neil was not a great supporter for a globally unified Permian timescale because he believed that it was simply not tenable, either in theory or practice.

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FUNCTIONAL INNOVATION OF SPIRIFERIDE WING FORM: EXPERIMENTAL AND SIMULATED APPROACHES TO THE GENERATION OF PASSIVE FEEDING FLOWS

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The functional property of wing form in spiriferide brachiopod *Cyrtospirifer* was examined in terms of the generation of passive feeding flows. The flow structure around the shell of *Cyrtospirifer* was analysed using flume experiment and computational fluid dynamics simulation of the hollow *Cyrtospirifer* model. In the flume experiments, when the ventral or dorsal valve faces upstream direction, the experimental results showed that outflows were intermittently generated through lateral gapes of the shell, and those passive internal flows inside the models inevitably moved as a gyrating behavior which is effective for spiriferide feeding because of its alignment on their spiral lophophore (Fig. 1; Shiino et al., 2009; Shiino, 2009). Similar conditions were implemented for the fluid dynamics simulations. The velocity distribution along the gape and the visualised streamlines around the shell suggest that the lateral parts of the gape do not show constant area of inflow or outflow, which is concordant with the experimental results. Given the comparable results obtained for both experiment and simulation, it is likely that the hydrodynamic instability along the wing form of spiriferides could produce a random inflow or outflow along the gape as observed in the typical cavity flows. Using the functional property of wing form, spiriferides could increase their filtration rate, resulting in their morphological diversification during the Palaeozoic.

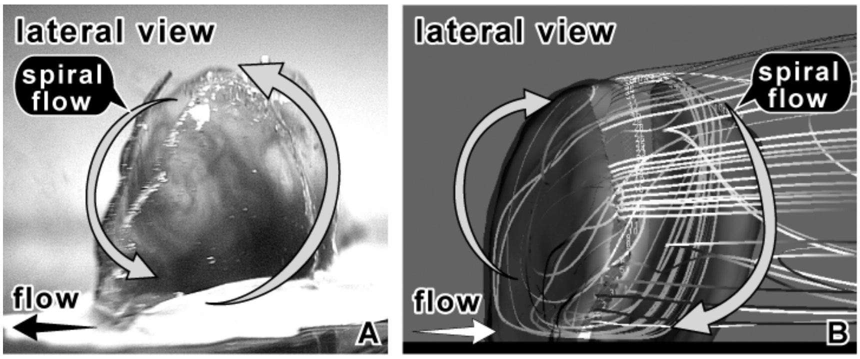

Fig. 1. Visualized flows around *Cyrtospirifer* model.
Lateral view of experimental (A) and simulation (B) results.

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EARLY PERMIAN BRACHIOPODS FROM THE NAGAIWA-SAKAMOTOZAWA AREA, SOUTH KITAKAMI BELT, NORTHEAST JAPAN

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The Sakamotozawa Formation is the regional standard of the Lower Permian chronostratigraphic subdivisions of Japan. Kanmera and Mikami (1965) subdivided the Sakamotozawa Formation into four submembers, and recognised five fusuline biozones in its upper three members. Ueno *et al*. (2007) described Fusuline fauna from the Yubanosawa Sandstone Member and concluded that the basal part of the Sakamotozawa Formation is correlated with the Sakmarian. However, there has been no study of brachiopods in the type area of the Sakamotozawa Formation.

42 species in 28 genera of Early Permian brachiopods are classified from the basal part of the Sakamotozawa Formation in the Nagaiwa-Sakamotozawa area. They occur from three horizons; 20, 28, 39 m from the base of the Sakamotozawa Formation, respectively. This fauna includes the following species; *Rugosochonetes* sp., *Avonia* sp., *Juresania juresanensis* (Tschernyschew), *Waagenoconcha* sp., *Cancrinella* sp., *Linoproductus cora* (d'Orbigny), *Scacchinella* cf. *gigantea* Schellwien, *Richthohofenia* sp., *Derbyia dorsosulcata* Liu and Waterhouse, *Schuchertella* sp., *Orthotetina* sp., *Meekella nodosa* Nakamura, *Streptorhynchus* sp., *Schizophoria* sp., *Hustedia* sp., *Rhynchopora* sp., *Phricodothyris* sp., *Spiriferellina* sp., *Parachoristites* sp., *Brachythyrina* sp., *Gypospirifer* sp. Especially, *Derbyia* are very abundant. *Waagenoconcha*, *Cancrinella*, *Rhynchopora* and *Gypospirifer* are Boreal-type genera, whereas *Richthofenia*, *Meekella* and *Orthotetina* are Tethyan-type genera. Consequently, the Sakamotozawa fauna represents a Boreal-Tethyan mixed fauna.

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RECENT RHYNCHONELLIFORM BRACHIOPODS FROM THE BRAZILIAN CONTINENTAL MARGIN, WESTERN SOUTH ATLANTIC

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Until now our knowledge of the taxonomy and distribution of the Recent rhynchonelliform brachiopods of the Brazilian continental margin (western South Atlantic) has been based largely upon the occurrences along the southeastern shelf of Brazil. Based on the data gathered from several oceanographic surveys (Revizee, Biota/FAPESP, Geomar, and Remac) we are now able to demonstrate that living brachiopods are not only confined to waters of the southern portion of the Brazilian shelf and continental slope. For this study, a collecting program included 409 oceanographic stations in continental shelf and slope bottoms, encompassing the entire latitudinal range (South, Central, Northeastern, North sectors) of the Brazilian continental margin was undertaken. The south sector from Chuí Creek (Rio Grande do Sul State, near 33ºS) to Cape São Tomé (Rio de Janeiro State, near 22ºS) is dominated by sands and muds and biodetritic sediments. Oceanographic conditions are complex, and governed by the tropical waters of the Brazil current with oligotrophic conditions. Southwards of the Doce River between 24ºS to 23ºS mesotrophic conditions are recorded due to the seasonal upwelling of cold, nutrient-rich waters of the South Atlantic Central Water masses (SACW). In this area, the fauna includes *Bouchardia rosea, Terebratulina* sp., *Argyrotheca* cf. *cuneata, Platidia anomioides*, *Dyscolia wyvillei* and *Macandrevia bayeri*. Bottoms of the Central sector (from São Tomé Cape to Salvador, 12ºS) are dominated by sands, fluvial muds, and carbonate banks. *A.* cf. *cuneata* is the most widespread species, also occurring in the vicinities of the volcanic islands of the Vitória-Trindade alignment. Southwards, near 14ºS scattered occurrences of *Dyscolia wyvillei* and *Terebratulina* sp. are also assigned in siliciclastic bottoms. The northeastern sector (from Salvador to Parnaíba river delta, near 2ºS) is influenced by the tropical climate, negligible siliciclastic sedimentation and the dominance of biogenic carbonate deposition. Of the 49 sampling stations in this sector, only one yielded brachiopods [*A.* cf. *cuneata* in biodetritic (coralline algae) bottoms, 45m of depth at 9ºS]. Finally, in the north sector (from Parnaiba River delta to Orange Cape, 4ºN) muddy, sandy and bioclastic bottoms dominate. Brachiopods are rare and only represented by *A.* cf. *cuneata* and *Terebratulina* sp. which are found in the Manuel Luiz reef, near the Equator.

Based on the available data we can highlight that: a- brachiopods are distributed over the latitudinal range of 33˚23'S (Chuí creek, near the Plata river mouth) to 00°30'S (Manuel Luis reef); b- brachiopods are mainly found in shallow water settings (<200m) although some occurrences are recorded in bottoms as deep as 1980m; c- the fauna is patchy-distributed, locally abundant and dominated by small specimens (<2mm); d- brachiopod diversity is generally low, with the majority of sites yielding one or two taxa only. The exception is in the shelfal zone and continental slope around 24 °S to 23 °S where nutrient-rich water masses of the SACW are recorded. There, the fauna is much abundant and diverse with at least six genera (*Bouchardia, Argyrotheca, Terebratulina, Platidia*, *Macandrevia* and *Dyscolia*); d- In that zone, *D. wyvillei* and *M. bayeri* were also documented for the first time for the western South Atlantic Ocean. The bathymetric distribution of *D. wyvillei* encompasses the depth range of 58.5 to 500m, whereas *M. bayeri* is recorded at the continental slope (450m of depth); e- *A.* cf. *cuneata* is the most widespread species in the Brazilian continental margin (latitudinal range of 32˚14'S to 00˚30'S), and the distribution of the endemic species *B. rosea* is confined to waters of 33˚23'S (Chuí creek) until 22° 31'9"S (Cape São Tomé); f- finally, the Brazilian brachiopod fauna shares similarities with those from the Atlantic and Indian shelves of southern Africa, and also from the Caribbean and Mediterranean waters. Hence, the Recent brachiopods of the western South Atlantic Ocean are much more diverse and cosmopolitan than previously thought, and their Cenozoic palaeobiogeographic history has to be reconsidered from that perspective.

Poster

DEAD-LIVE FIDELITY OF BRACHIOPOD ASSEMBLAGES IN THE BRAZILIAN SHELF: IMPLICATIONS TO LATE HOLOCENE PALAEOECOLOGY AND CONSERVATION PALAEOBIOLOGY

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Dead-live faunal comparisons can provide insights into the fidelity of the fossil record and may also offer us powerful data to detect natural or human-induced population changes in the late Holocene. Here we document dead-live comparisons for brachiopod-rich assemblages (*Bouchardia rosea*) found in nearshore environments (5 to 45 meters of depth) of the coast of the State of São Paulo, Brazil. This area is part of the Southeast Brazilian Bight Marine Province, and influenced by warm waters of South Brazil Current. Collecting program (2000 to 2003) included 30 stations (14 at Ubatuba Bay/UBA, 16 at Picinguaba Bay/PIC, 23° - 24° S/44° - 46° W), both sampled via Van Veen grab sampler (1/40 m^2), and dredging. Hence, the samples primarily represent the uppermost several centimetres of bay sediments (mainly sands). The fidelity estimates were obtained by direct comparisons of live biota with dead shells. Of 30 stations, 22 (72.4%) yielded brachiopod shells, 11 from UBA, and 11 from PIC. A total of 6627 *B. rosea* shells were recovered, 5339 (80.6%) from UBA, and 1288 (19.4%) from PIC. Shells were found at all sampling stations in the UBA Bay, except for two stations at 15 metres of depth. In the PIC Bay shells were not found at the shallowest sites (5 metres of depth). Out of 5339 shells found in UBA, 61% (n=3259) are small shells (2 mm), and the remaining are shells in 6 mm (28.9%, n=1542) and 8 mm (10.1%, n=538) fractions. A similar pattern is also observed in the samples from the PIC Bay, where 74% (n=953) are small (2 mm) shells, and 124 (9.6%) and 211 (16.4%) are shells in the 6mm and 8 mm fractions. Despite the *Bouchardia*-rich accumulations live specimens of *B. rosea* were not found in the Ubatuba Bay area throughout the entire sampling program. This absence is striking given the widespread and persistent occurrence of *Bouchardia*-rich death assemblages in this bay. When data are combined across both embayments, out of 6627 shells recovered, 6621 (99.9%) were dead shells and only 6 (0.1%) were found alive. Intriguingly, all six specimens found alive came from three adjacent sites located in the outer part of the Picinguaba Bay, three recovered in the 8mm fraction, two in the 6 mm fraction, and one in 2 mm fraction. These data point to a high dead-live disagreement (a low dead-live fidelity) in all sampled environments, at all sampled depths, and for all sieve sizes. These results suggest extremely poor dead-live compositional fidelity for *B. rosea* assemblages. This dead-live discordance seems to be a result of combined processes: spatial and temporal mixing, *taphonomic inertia*, and past and Recent environmental changes. Indeed, (a) temporal mixing of *B. rosea* shells in those accumulations is on the order of 10^2-10^4 years (mean shell age of 674 years BP), (b) shell ultrastructure and qualitative shell layer composition analysis (SEM/EDS) of specimens from the Ubatuba bay, at 10 metres of depth, near a small harbor, recorded heavy metals (Copper) in the primary shell layer of *B. rosea* shell. In this site heavy metals were also recorded in the bottom sediments; (c) intra-shell isotope ($\delta^{18}O$-$\delta^{13}C$) variation for Recent (rare specimen collected alive) and old (~20,000 years BP) shells indicate differences in $\delta^{18}O$ ratios. The old shell shows more positive isotope ratios than the Present-day specimen, indicating that they grew in waters cooler and/or more saline than those of today. Given these observations, it seems plausible that those assemblages of *B. rosea* are cumulative *in situ* records of past populations that have become locally scarce or extinct in recent years.

Geological Society of Australia, Abstracts No. 95
6th International Brachiopod Congress, Melbourne, Australia, February 2010

Poster

TAXONOMICAL POSITION OF CRETACEOUS BRACHIOPODS DEVELOPING A MOSAETHYRIDID BRACHIDIAL STRUCTURE

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A taxonomical problem subsists for some Cretaceous brachiopods which have a trabecular loop and which never possess dental plates at adult stage or through ontogeny.

The family Mosaethyrididae Simon, 2005 includes the genera *Kingenella* Popiel-Barczyk, 1968 and *Mosaethyris* Simon, 2005. In *Kingenella*, outer and inner hinge plates are fused to produce a platform attached to the median septum. This cardinal structure, in transverse section, appears as a W- platform. Two angular deep troughs are developed on each side of the median septum.

In *Mosaethyris*, a genus homeomorphous of *Kingenella*, the platform resulting from the fusion of the outer and inner hinge plates is more regular. Outer hinge plates are less developed. But in both *Kingenella* and *Mosaethyris* the crural bases acutely divide the platform formed by outer and inner hinge plates. The median septum is posteriorly very strong and divides the cardinal platform.

Several other Cretaceous brachiopods also exhibit a mosaethyridid loop structure. *"Magas" nilssoni* Lundgren, 1885 from the Swedish Campanian has cardinalia with each pair of fused outer and inner hinge plates forming a deep trough. Moreover the inner hinge plates are medially fused together giving a roof-shaped structure. These cardinalia are of the same type as those of Kingenella but these original characters are still more exaggerated. Katz (1974) described as *Kingenella nilssoni* (Lundgren, 1885) a brachiopod collected from the Maastrichtian of South-East Ukraine which has a cardinal platform drawn in the same way. Moreover, among a rich brachiopod fauna discovered in the Bulgarian Santonian, a specimen devoid of dental plates, presents a similar structure of cardinalia as those observed in *"Magas" nilsonni* and its perfectly intact loop is trabecular.

All these Cretaceous brachiopods cover nearly the whole European geographical area and their wide stratigraphical range extends from the Campanian to Upper Maastrichtian. The original structure of the cardinalia excludes that these brachiopods could be placed neither in the Terebratellidae nor in the Dallinidae *sensu stricto*. The Terebratellidae is a family present in the southern hemisphere. Inner hinge plates are uniting with median septum to form a septalium. The loop is passing trough all phases from axial to haptoid and trabecular. The Dallinidae is a family observed in the northern hemisphere but it could be found in the southern hemisphere (Pacific Ocean and Pacific-Antarctic ridge). A septalium (Dallininae) or a deep V-shaped trough (Nipponithyridinae) is formed by the inner hinge plates.

To find a right taxonomical place for Mosaethyridid brachiopods remains thus a problem.

Terebratellidina may have arisen from the family Angustothyrididae in the Dielasmatoidea (early Triassic). In this group the loop ontogeny is complex and always involves the median septum and/or septal pillar (MacKinnon & Lee, 2006). When considering the Dielasmatoidea, a comparison between the structures of the cardinalia in *Coenothyris* (Dielasmatiidae) with those observed in Mosaethyridid brachiopods is interesting. A septalium is present but the general structure of these cardinalia consists in a platform resulting of the fusion of outer and inner hinge plates. In transverse section, the cardinalia of *Coenothyris* is remembering the platform of *Kingenella* because it exhibits a W-structure. Those brachiopods as the Terebratellid and the Dallinid brachiopods seem to arise from a similar stock. A possible interpretation could be that these brachiopods such as *Kingenella* may have arisen from a similar early Triassic stock and that they could represent a distinct branch inside the Terebratelloidea. In this case the Mosaethyridid brachiopods should be placed in a new family within the Terebratelloidea near the Terebratellidae and the Dallinidae.

Another interpretation could lead us to create a new superfamily near the Terebratelloidea. But such a high taxonomical level seems not appropriate. The plasticity observed inside the cardinalia of the Dielasmatoidea illustrates a high potential of variations. In this way, terebratellid, dallinid and mosaethyridid cardinal structures arose probably from a common stock and they have developed their own brachidial structures independently.

The mosaethyridid structure was present in brachiopods of all European seas from the Campanian to the end of the Maastrichtian but they do not survive over the K/T boundary. Dallinid and terebratellid brachiopods continue their development till the Holocene.

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THE IMMENSE VARIABILITY – ENCRUSTING CRANIIDS OF THE ROCKY-COAST FACIES (UPPER CRETACEOUS, BOHEMIAN CRETACEOUS BASIN)

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The Upper Cenomanian/Lower Turonian rocky-coast facies of the Bohemian Cretaceous Basin (BCB) represents a highly agitated, oxygen-rich environment of the shore/near-shore nature. Sediments of its outcrops show diverse oryctocenoses of invertebrate fauna dominated by suspension feeders such as bivalves and spongies. Encrusters (oysters, spondylids and atretids, hexactinellid and demospongid spongies, octocorals, worms, bryozoans etc.) create a large portion of the association.

Brachiopods in general are well represented. Apart from relatively abundant cancellothyrids, terebratulids, sellithyrids and megathyrids, i.e. forms attached by their pedicle, encrusting brachiopods are also present. Nekvasilová (1964, 1966) published detailed papers on thecideides, their systematics, variability and palaeoecology. However craniids have not been treated in detail by this author.

Although craniid remains are a considerably common part of washings from some of rocky-coast localities they are still rather rare in general. Isolated dorsal valves and their fragments prevail – more than 500 exemplars have been gathered from nine localities. The domination of the dorsal valves is probably a result of taphonomical separation: washed sediments come from rock-depressions while ventral valves often rested on the elevations above, exposed to erosion. Rare ventral valves and one complete specimen are attached to hard, coarse and rather exposed substrates such as gneiss rocks and a sponge skeleton. The secretion of the ventral valve floor is rather suppressed and adductor scars are not incised, but the limbus of all the preserved specimens is rather thick. The low secretion rate, which may be controlled by the character of the substrate, is probably another reason for that the number of ventral valves is very low. Despite an enormous variability in scale as well as external and internal morphology most of the specimens show characters of the *Ancistrocrania* Dall. However a large amount of them show ribs on part of their surface at least and the anterior adductor scars are not raised or distinctly separated in many of them. Internals of larger number of specimens resemble rather those of *Neocrania* Lee & Brunton but transitional forms can be found. This evokes a question of a close relationship between both genera.

Due to their extensive variability any taxonomical studies are very difficult for the encrusting craniids in the fossil record. A detailed research on variability is essential in recent craniid populations particularly in relation to environmental conditions such as, among others, the substrate.

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Geological Society of Australia, Abstracts No. 95
6th International Brachiopod Congress, Melbourne, Australia, February 2010

THE ORIGIN OF BRACHIOPOD SHELLS

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The bivalved body plan of the Brachiopoda evolved very early on in the Cambrian, and the brachiopod crown group was probably established by the second stage of the period (Adtabanian), making the Brachiopoda one of the oldest of all modern phyla. The origin and early evolution of the Phylum Brachiopoda has long been shrouded in mystery. The 'Brachiopod Fold Hypothesis', contends that the bivalved condition arose through ventral folding of an elongated animal with two dorsal shells. This hypothesis gained support with the discovery of the articulated halkieriid animal (*Halkieria evangelista*), which exhibits two brachiopod-like shells in addition to numerous spine-like calcareous sclerites. However, new fossil discoveries have recently demonstrated that brachiopods evolved from tubular tommotiid ancestors.

Tommotiids are one of the most conspicuous organophosphatic components of the Cambrian 'small shelly fossils'. Their small cone or cap-shaped sclerites are among the first skeletal fossils to appear in the lowermost Cambrian. Until recently, tommotiids have only been known from disarticulated material and the gross morphology of the animal, the structure of the skeleton and the phylogenetic position has been subject to speculation. Tommotiids have usually been reconstructed as slug-like animals with a dorsal cover of imbricating sclerites. However, the first articulated tommotiids were recently found in South Australia, and these exhibit a radically different body plan.

The scleritome of *Eccentrotheca* is a slowly expanding cone with circular cross section, composed of a multitude of irregular cap-shaped sclerites arranged in vertically stacked rings. The tubiform skeleton displays wide variation in form but was attached to hard substrates via organic structures at the perforated apex, and the animal was likely a sessile filter feeder. A second tommotiid scleritome, *Paterimitra*, exhibit a modified version of the tubular model, with a multitude of *Eccentrotheca*-like sclerites surrounding two unequal, bilaterally symmetrical sclerites defining a tubular 'pedicle' opening.

The proposed link between brachiopods and tommotiids was originally based on similarities in shell composition and microstructure, in particular the shared presence of shell-penetrating setae in the Cambrian brachiopod *Mickwitzia* and the tommotiid *Micrina*. However, we now also know that tommotiids, like most brachiopods, were sessile filter feeders, and that they attached to the substrate via a pedicle-like organic structure.

The transition from a multiplated tommotiid tube to the bivalved brachiopod shell required a numerical reduction of skeletal components coupled with the evolution of bilateral symmetry in the remaining shells. Evidence from fused sclerites from a broad selection of tommotiids show that sinistral and dextral variants of asymmetrical sclerites occurred in pairs, together forming a bilaterally symmetrical composite. Early ontogenetic fusion resulted in fully symmetrical sclerites in a number of lineages and the scleritome of *Paterimitra* shows that bilateral symmetry evolved within the tubular tommotiid skeleton.

We can identify how the two opposing shells of brachiopods evolved from cap-shaped sclerites through a series of intermediate steps. The irregular basal sclerites of *Eccentrotheca* gave rise to the symmetrical sclerites of *Paterimitra* through numerical reduction and specialisation of function of sclerites in the basal sclerite ring. Reduction in tube height through loss of sclerite rings led to a simplified scleritome with 3 or 4 sclerites (*Tannuolina*) and paired fusion of the remaining sclerites resulted in an effectively bivalved scleritome (*Micrina*).

THE PHYLOGENETIC POSITION OF THE BRACHIOPODA AND PHORONIDA: NEW EVIDENCE FROM NUCLEAR HOUSEKEEPING GENES AND microRNAS

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Knowledge of the phylogenetic relationships between modern organisms allows the reconstruction of morphological characters shared by the last common ancestor of the crown group. With this knowledge, fossils can be correctly placed along the stem-lineage, thereby giving insight into the order of character acquisition during the evolution of that clade. Of particular importance for understanding brachiopod evolution, especially the evolution of biomineralisation, is the correct position of the phoronids. We have sequenced a new dataset consisting of seven nuclear housekeeping genes and analyzed these data in conjunction with 18S and 28S ribosomal DNA. Contrary to several recent multi-gene phylogenetic analyses that place phoronids within the Mollusca or Annelida, but consistent with hypotheses derived from morphological cladistic analyses, we find Phoronida as sister group to the Linguliformea + Rhynchonelliformea (Brachiopoda herein). Brachiopoda + Phoronida is found to be the sister taxon of Mollusca (but with weak support), and these three phyla are then the sister group of annelids with respect to nemerteans and platyhelminths.

We then tested the phylogenetic hypotheses arising from our analyses using an independent dataset, the presence and absence of specific microRNAs, which are ~22 nucleotide noncoding RNA genes that hold strong promise for phylogenetic reconstruction. MicroRNAs possess three properties that give them tremendous potential as phylogenetic markers: (1) new microRNA families are continually being incorporated into metazoan genomes through time; (2) they show only rare instances of secondary loss, and only rare instances of substitutions occurring in the mature gene sequence; and (3) they are almost impossible to evolve convergently. We have sequenced microRNA libraries using next-generation 454 sequencing from the brachiopods *Terebratalia transversa* and *Glottidia pyramidata* as well as the phoronid *Phoronis architecta*. These two brachiopods share at least one microRNA not found in the phoronid or any other lophotrochozoan library or genome investigated to date. This supports the monophyly of Brachiopoda, consistent with our sequence-based analysis. Intriguingly, the molluscs, annelids and brachiopods are all demonstrably monophyletic based on the presence of phylum-specific microRNAs, but there are no microRNAs shared between any two of the three phyla. This mirrors the low statistical support found in the sequence based analysis and raises the possibility that the radiation of these phyla represents a true polytomy.

APPLICATION OF NICHE MODELING TO ANALYZE BIOGEOGRAPHIC PATTERNS IN PALAEOZOIC BRACHIOPODS: EVALUATING NICHE STABILITY IN DEEP TIME

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The geographic area inhabited by a species is constrained by its ecological niche, which is determined by the multidimensional set of environmental variables that determine where members of a species can survive and maintain viable populations. The ecological niche of a species can be estimated from a set of species occurrence points in concert with data about the environmental conditions associated with those locations using a method known as ecological niche modeling (ENM). If environmental conditions are known across a study area, it is possible to estimate the geographic distribution of the same species based on the niche model. This technique has been most widely employed with modern continental organisms, although there have been a few studies on marine animals.

One potential use of niche modeling is to analyse changes in the parameters of a species' niche through time. This can be done by comparing the estimated geographic range for a species modeled for a time slice with the projected range of the species if the niche model developed for an earlier time slice were projected onto the environmental parameters of the same later time slice. If a species maintains an identical ecological niche over time (= niche conservatism) then that species should exhibit habitat tracking between successive time slices. Conversely, if a species adapts to changing environmental conditions (=niche evolution), then there should be disagreement between the geographic range exhibited by the species and that predicted based on its niche during an earlier time slice.

Neontologists have used this technique to examine possible range shifts following global climate change. The fossil record documents a series of environmental changes through time. Similar analyses using fossil organisms provide a framework to test hypotheses of niche stability over longer time scales. For ENM analyses of fossil organisms to be successful, studies should focus on common taxa deposited in sedimentary sequences characterised by a detailed stratigraphic framework that outcrop widely.

In this study, the relative stability of ecological niches of Late Ordovician (Katian) brachiopods of the Cincinnati Arch of eastern North America is assessed. A detailed sequence stratigraphic framework exists for these strata. Outcrops are abundant within the region, and the highly fossiliferous strata are dominated by articulate brachiopods and bryozoans. Biogeographic ranges of brachiopods from three depositional sequences, the C3, C4, and C4 sequences, are analysed in this study. C3 taxa are largely endemic to eastern North America. A significant faunal immigration event of taxa from palaeoequatorial waters, known as the Richmondian Invasion, occurred during the C4 sequence. This immigration event, which has been linked to palaeo-oceagraphic changes, resulted in significant faunal turnover during the C4 sequence and establishment of a new community structure in the C5 sequence. The transition from the C3 through C5 sequence, therefore, provides an opportunity to examine whether brachiopod species altered the parameters of their ecological niche to accommodate these environmental and biotic changes. Several hypotheses are addressed in this study: Is the degree of niche stability constant through time? Does niche evolution increase following the Richmondian Invasion compared to that of the C3 sequence? Does the degree of niche stability vary between native vs. immigrant species? Is there a discernable difference between the degree of niche stability of generalist vs. specialist species?

To analyze niche stability in these brachiopods, each depositional sequence is divided into three time slices resulting in nine total time slices for the study interval. Ecological niches of eight brachiopod species are modeled based on environmental parameters estimated from the sedimentary record. Environmental parameters included are inferred water depth, lithology, bedding thickness, bedding style, and physical sedimentary structures. Species modeled included those that persisted throughout the entire study interval (*Hebertella occidentalis, Dalmanella meeki, Rafinesquina alternata)*, species that become extinct at the onset of the invasion (*Platystrophia laticosta, P. cypha)*, and immigrant species new to the basin (*Leptaena richmondensis, Rhynchotrema dentatum, Glyptorthis insculpta*). Species ecological niches are modeled for each time slice in which they were extant. Then the amount of niche evolution is assessed by projecting the modeled niche of a species from one time slice onto the immediately successive time slice. The percent overlap between the original and forward geographic range projection is calculated. Species with 100% overlap are interpreted to exhibit complete niche conservatism, while 0% overlap is interpreted to indicate complete niche evolution. This procedure is repeated until niche evolution is assessed between all time slices.

Analytical results indicate that the degree of niche stability differs between times slices and groups of Cincinnatian brachiopods species. Niche conservatism is highest during the C3 sequence, prior to the Richmondian Invasion, and during the C5 sequence, after the establishment of the post-invasion ecosystem. Stenotopic species exhibit higher levels of niche evolution than eurytopes. No significant difference was recovered, however, between native and immigrant species. Studies, such as this, which analyse long term trends (a total of ~3 million years here) over intervals of short duration (approximately 300,000 years per time slice in this study) can potentially provide insight into the long term patterns expected following the current changes in the global ecosystem from both climatic shifts and invasive species.

Geological Society of Australia, Abstracts No. 95
6th International Brachiopod Congress, Melbourne, Australia, February 2010

THE SUCCESSION OF BRACHIOPODS IN THE SILURIAN OF THE CANBERRA-YASS REGION, SOUTHEASTERN AUSTRALIA

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The existence of fossiliferous Silurian strata in the Canberra-Yass region has been known since the middle of the nineteenth century (Clarke, 1848). The first brachiopods to be published from Yass were figured by Jenkins (1879), and from Canberra by Mahony & Taylor (1913), in both cases without description. Elements of the Yass fauna were described in a series of papers between 1892 and 1923 by R. Etheridge jr, W.S. Dun and J. Mitchell, and in a few short later papers, but much remained undescribed. Some Canberra brachiopods were illustrated in Townley & Veevers (1966), but the first formal descriptions were those of Strusz (1982).

The poster brings together in one chart the stratigraphic distribution of the new and revised species of Rhynchonellata published or in press since 1980, in the papers listed below. Sixty-seven taxa are now known, of which almost 60 are shown on the chart - another 9 or 10 are too poorly known to be included. Their systematics have been brought up to date following publication of the revised Treatise on Brachiopoda.

The oldest taxa are in the Canberra Formation, of probable Sheinwoodian or possibly earliest Homerian age (neither graptolites nor conodonts are available for age determination). The fossiliferous succession in the Canberra area, which is dominated by silicic volcanism, ends with the Yarralumla Formation. This is a lateral equivalent of the Yass Formation, which is sandwiched between the Hawkins (below) and Laidlaw Volcanics. From a re-examination of the conodonts of the Yass sequence described by Link & Druce (1972), Simpson (1995) has argued strongly that the Yass Formation and possibly the basal Silverdale Formation (above the Laidlaw Volcanics) are most likely to be of Homerian age. The youngest '*in situ*' brachiopods at Yass are from Mitchell's "Upper Trilobite Bed", probably in the lower Elmside Formation of latest Přídolí *Monograptus transgrediens* Zone age (Rickards & Wright, 1999), although a few reworked specimens occur in the Lochkovian Sharpeningstone Conglomerate.

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PALAEOBIOGEOGRAPHICAL SIGNIFICANCE OF A NEW DISCOVERY OF THE TOURNASIAN BRACHIOPODS IN SOUTH CHINA

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Much of previous work on the Tournaisian brachiopod fauna in South China was mainly focused on the wide-spread shallow-water carbonate platform facies which lead to an opinion that the Tournaisian brachiopod fauna in South China was mainly characterised by some endemic forms (such as *Yanguania*, *Eochorisitites*, *Martiniella*, *Ptychomaletoechia*) and cosmopolitans (such as *Schuchertella*, *Athyris*, *Cleithyridina*, *Shizophoria*, *Spirifer*) with relatively low generic diversity. However, a recent discovery from several localities in South China reveals that the Tournaisian brachiopod fauna from deep-water facies (slope to basinal) is much more diversified than that from the neritic carbonate platform facies, with more than sixty genera, including 4 chonetid, 15 productid, 5 orthotetoid, 13 rhynchonelid, 7 athyrid, and 12 spiriferid genera. Many of them show a close biogeographical relationship to those from Europe, North America and Australia.

TAXONOMIC REVIEW AND EVOLUTIONARY TRENDS OF LEVIPUSTULINI AND ABSENTICOSTINI (BRACHIOPODA) FROM ARGENTINA: PALAEOBIOGEOGRAPHIC AND PALAEOCLIMATIC IMPLICATIONS

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The tribe Levipustulini has been recorded abundantly in Argentina and a great number of genera are represented, including *Bulahdelia, Levipustula, Lanipustula, Verchojania, Jakutoproductus* and *Piatnitzkya*. A review of some key genera and species has allowed the recognition of *Levipustula levis* Maxwell and a new species of the Absenticostini *Absenticosta* Lazarev in western Argentina, as well as confirming the presence of *Lanipustula patagoniensis* Simanauskas and a new species of *Lanipustula* in Patagonia.

Levipustulini commonly exhibit antitropical distribution but some of the genera from this tribe are shared only between Siberia and Patagonia. *Lanipustula*, *Verchojania* and *Jakutoproductus*, with *Absenticosta* interpreted as their common ancestor, together constitute a phylogenetic lineage, which we consider as having undertaken parallel evolution in the high latitudes of both hemispheres during the Late Palaeozoic. If this scenario is accepted, the parallel evolution must have commenced during the late Viséan at a time when the Earth was experiencing a global cooling phase allowing the trans-oceanic and global dispersal of some cool-water tolerant brachiopod genera (e.g. *Absenticosta*) from lower to higher latitudes. At this time, Patagonia would have been separated from western Argentina and was progressively drifting toward southern higher latitudes. Thus, the isolation of Patagonia, coupled with its southward drift toward a colder climate, could have triggered the parallel evolution of the Levipustulini lineage between Patagonia in southwestern Gondwana and Angaraland in Northeast Asia.

Since Bashkirian times, warm ocean currents invaded western Argentina, and these currents were warm enough to build a thermal barrier between Patagonia and western Argentina, effectively restricting biotic interchanges between them and also between Gondwana and Eurasia. Under such a palaeogeographically and palaeobiogeographically isolated setting, Patagonia progressively became a sanctuary for the development of a highly endemic but locally abundant marine fauna, which persisted until the earliest Cisuralian.

The weak glacial record since Bashkirian times in western Argentina contrasts sharply with widespread evidence in Australia indicative of several main episodes of glaciation extending from late Mississippian till late Permian. The asymmetrical climatic pattern between Argentina and Australia reflects the clockwise rotation of Gondwana resulting in the consequent migration of western Argentina to lower latitudes and the drift of eastern Australia toward the South Pole. Patagonia, located in an intermediate palaeogeographic position between these two regions, was also rotated and displaced across latitudes, but must have been shifted to lower latitudes later and more slowly than western Argentina.

A thalassocratic regime during the late Asselian-Sakmarian and a global climatic amelioration since late Sakmarian could explain the fast recovery of migration pathways for the biotic interchange between Patagonia and other Gondwanic regions, including Western Australia and the Cimmerian regions now stretching from the Middle East to Southeast Asia.

PERMIAN BRACHIOPOD FAUNA OF THE MINO BELT, CENTRAL JAPAN, AND ITS PROVINCIAL RELATIONSHIP WITH THAT OF WEST TEXAS, USA

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Thirty-one species of Permian brachiopods have been described from limestone-basalt blocks embedded in the Jurassic melanges within the Mino Belt of Central Japan: 6 species in 6 genera from Akasaka (Hayasaka, 1932; Tazawa et al., 1998; Shen et al., 1999, 2006), being *Scacchinella gigantea* Schellwien, *Leptodus nobilis* (Waagen), *Coscinophora magnifica* Cooper and Grant, *Geyerella* sp., *Enteletes suessi* Schellwien, and *Peltichia akasakensis* (Ozawa); 13 species in 12 genera from Hiyomo (Tazawa and Shen (1997), being *Chonetinella* cf. *costellata* Cooper and Grant, *Calliprotonia* sp., *Ametoria* cf. *residua* Cooper and Grant, *Compressoproductus* sp., *Glyptosteges*? sp., *Eolyttonia* sp., *Enteletes* sp., *Cenorhynchia*? sp., *Martinia semiplana* Waagen, *Martinia* sp., *Cartorhium coristum* Cooper and Grant, *Lepidospirifer miyakei* Tazawa and Shen, and *Anomaloria hiyomoensis* Tazawa and Shen; and 12 species in 12 genera from Hatahoko (Shen et al., under review), being *Echinauris lateralis* Muir-Wood and Cooper, *Horridonia* sp., *Rugaria* sp., *Chonosteges variabilis* (Cooper and Grant), *Institella leonardensis* (King), *Acritosia teguliferoides* (King), *Eolyttonia* sp., Permianellids gen. et sp. indet., *Orthothetina* sp., *Goniarina permiana* (Stehli), *Enteletes costellatus* (Cooper and Grant), and *Acosarina rectimarginata* Cooper and Grant.

The Mino fauna is overwhelmingly dominated by species and genera with affinities of the West Texas fauna, and associated with some Tethyan elements and few very rare Boreal elements. The specific and generic composition of the fauna suggests that the Mino reef-seamount complexes were located within the equatorial mid-Panthalassa during the Permian. At that time, the warm-water palaeocurrent transported the West Texas fauna excluding Boreal-type species, from east to west. Consequently, the Mino fauna came to be a mixture of the Tethys and the West Texas faunas, without Boreal elements. This reconstruction of the Permian palaeobiogeography of the Panthalassa is consistent with the palaeomagnetic data obtained from Permian basaltic rocks of the Mino Belt, which indicate 3.5 ° N (Hattori and Hirooka, 1979), and palaeocurrent data for the Permian Panthalassa (Archbold and Shi, 1996), which indicate a westward ocean current in the equatorial region.

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EVOLUTIONARY CHANGES IN BRACHIOPOD BODY SIZE DURING THE MESOZOIC

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Understanding the long-term variations in diversity, abundance and body size of rhynchonelliform brachiopods requires integration of multiple tools, including distribution and macroecological models, macroevolutionary diversification models, phylogenetic models, and functional and morphometric models. Here, to assess the temporal changes in the shape of body size-frequency distributions of brachiopod assemblages during the Mesozoic and to evaluate the effects of mass extinctions on the body size patterns and their size-selectivity, I evaluate changes in body size-frequency distributions of brachiopod assemblages at global and regional scales, starting in the Middle Triassic. Preliminary analyses indicate that the Triassic/Jurassic boundary mass extinction substantially affected brachiopod body size-frequency distributions at genus and species levels. Based on resampled data (i.e., the number of taxa is kept constant in pairwise analyses), median size of Rhaetian brachiopod genera (20.1 mm) is significantly larger than median size of Hettangian brachiopod genera (14.9 mm) (Wilcoxon test, $p = 0.001$). All other consecutive stage pairs in the Late Triassic and Early Jurassic do not differ in median body size. Most distributions are left-skewed (the Norian, Rhaetian, Sinemurian, and Pliensbachian assemblages are significantly skewed), but Hettangian distribution is almost lognormal (skewness = -0.04). Size-frequency distributions resampled to equal number of taxa also show that the Hettangian distribution significantly differs from the Rhaetian distribution in terms of its shape (KS test, $p = 0.007$) and has also lower variance (Bartlett test, $p = 0.002$). Rhaetian victims are slightly larger than survivors, and survivors are slightly larger than Hettangian originators. However, body sizes of Rhaetian victims and survivors do not differ significantly (Kolmogorov-Smirnov test, $D = 0.27$, $p = 0.46$, Wilcoxon rank sum test, $p = 0.07$), similarly as body sizes of survivors and originators (Kolmogorov-Smirnov test, $D = 0.37$, $p = 0.46$, Wilcoxon rank sum test, $p = 0.8$). Therefore, extinction and origination patterns at the end of the Triassic are not strictly size selective (although taxonomic richness is low and the test power is thus limited). However, based on resampled data, size-frequency distribution of originators has lower variance than distribution of survivors (Bartlett test, $p = 0.01$) and median size of victims is significantly larger than median size of originators (Wilcoxon test, $p = 0.026$) – i.e., distributions of originators are restricted to narrow size range. The lack of small shells in the aftermath of the T/J mass extinction can partly be a consequence of the lack of poorly lithified or silicified rocks in the Hettangian and due to the presence of some Lazarus taxa that do not occur in the Hettangian. However, the lack of large shells in the Hettangian probably represents a true signal.

Using log of geometric mean size as a measure of body size, size-frequency distributions of the Triassic and Jurassic brachiopods at global scales are left-skewed, similarly as size-frequency distributions of present-day bivalve regional assemblages. Although small-sized species are frequently undersampled, size-frequency distributions at large spatial scales are probably less affected by biases favoring preservation and sampling of large-sized taxa than assemblages sampled at small (bulk-sample) scales because silicified and poorly lithified deposits that contain juveniles are available for many Mesozoic stages. Interestingly, multiple clades with small-sized micromorphic brachiopods originated during the Late Jurassic and Cretaceous (leading to high abundance of small-sized brachiopods in some environments), implying a potential shift in the shape of body-size frequency distributions towards right-skewed shapes with many small-sized taxa.

ENVIRONMENTAL INFORMATION IN THE δ^{13}C, δ^{15}N, δD AND δ^{18}O OF LINGULA

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Three collections of the inarticulate brachiopod, *Lingula*, were made in the Ariake Bay, Japan, Kanaohe Bay, Hawaii, USA, and Townsville, Queensland, Australia. An extensive light stable isotope (carbon, nitrogen, hydrogen and oxygen) study of these brachiopod populations revealed strong environmental effects on all four of the isotopic pairs in both organic and inorganic Lingula sources. The stable carbon and nitrogen (δ^{13}C and δ^{15}N) isotopic values of the lophophore and shell chitin have significantly different values in all three populations collected in Hawaii, Japan and Australia. The patterns in δ^{13}C and δ^{15}N likely reflect the differential input of marine and terrestrial nutrient sources that are recorded in both the variability and absolute isotopic tissue values. The organic δD and δ^{18}O lophophore values are also distinct among the populations and these data are consistent with significant terrestrial inputs at Ariake Bay, Japan. Surprisingly paired $\delta^{18}O_{organic}$ and $\delta^{18}O_{phosphate}$ covaried in the three populations, and resident sea water temperatures cannot be recovered from these values with current models. By adding an estimate of the oxygen isotopic values in precipitation runoff into seawater, a reasonable estimate of environmental sea water temperature can be determined from either organic or inorganic oxygen isotopic values.

EARLY SILURIAN LINGULIFORM BRACHIOPOD BIOSTRATIGRAPHY AND OCEANIC TURNOVER EVENTS

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As many as ten oceanic turnover events have been recognised as occurring during the Silurian, each marked by an extinction event. Six of these, the Sandvika Event (Aeronian), the "Utilis subzone" Event (Telychian), the Ireviken Event (Telychian-Sheinwoodian), the Boge Event (Sheinwoodian), the Valleviken Event (Sheinwoodian-Homerian) and the Mulde Event (Homerian), occurred during the Early Silurian (Jeppsson, 1998). The model developed by Jeppsson (1997) to explain these events postulates that variations in atmospheric and oceanic concentrations of carbon dioxide produced regular shifts between specific climatic and oceanic circulation states referred to as 'primo' and 'secundo' episodes. These events, and their associated biocrises, have been attributed to periods of oceanic turnover, as the system shifted from one state to the other. Fine resolution sampling by Jeppsson (1997, 1998) has demonstrated that each event is composed of a number of 'subevents', each marked by an extinction plane (or datum point).

These events appear to have primarily affected pelagic taxa, like conodonts and graptolites, to a greater extent than benthic taxa, like brachiopods (Jeppsson 1997, 1998). However, until now, little data on the impact of these events on benthic taxa has been available to support this claim. Analysis of Early Silurian linguliform brachiopod faunal turnover from a number of sections in the Orange area of central-western New South Wales, Australia, indicates linguliform brachiopod diversity is unaffected by these oceanic turnover events. Each species immediately present prior to the initiation of an event also occurs after it has ended. In fact, most species pass through multiple events. This is in stark contrast to conodonts which display an ~80% reduction in diversity worldwide during the Ireviken Event (Jeppsson 1997). However, whilst linguliform diversity is unaffected, their abundance is substantially reduced, particularly during the Ireviken Event. Some taxa even completely vanish during these events, only to reappear unchanged as Lazarus taxa once the biocrisis has ended.

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THE ORIGIN AND EVOLUTION OF AUSTRALIAN PERMIAN BRACHIOPODS

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An expert on brachiopods from the northern hemisphere must find Australian Permian brachiopods just as strange as zoologists of Victorian vintage found the Australian platypus. Especially brachiopods from eastern Australia, where faunas are dominated by *Terrakea, Echinalosia, Plekonella, Ingelarella, Aperispirifer – Trigonotreta, Fletcherithyris* – none other than *Echinalosia* found in the northern hemisphere. Furthermore, many more northerly families are missing, with no Echinoconchidae, Richthofeniidae, lyttoniids to mention a few: the unusual brachiopods reflect the unusual conditions of cold waters and high palaeolatitudes, where tillites, glendonites and drop stones were common.

The origins of many genera remain obscure: few appear to have persisted or evolved from local Carboniferous genera that also dwelled in glacigene surrounds: almost 20% originated from northeast Asia, from Omonlon or Verchoyansk, and another 20% from South America, south Asia, and even Europe. About half remain of uncertain origin and appear to have evolved de novo in migrant streams from either South America or more likely southeast Asia.

But evolution did not proceed steadily through the period. There were episodes of very low diversity, probably due to severe cold, when only the most Australian of genera survived – six episodes in all, three in the Cisuralian, two in the Guadalupian and one in the Lopingian. There were intervals by contrast when genera especially from southeast Asia, Himalaya and Arctic, involving such genera as *Azygidium, Stenoscisma, Coledium, Attenuatella,* neospiriferids *and Spinomartinia*, entered east Australia and the "cold-water" genera diminished or even disappeared. Five to seven such intervals are recognised as zones, three-four in the Cisuralian and three in the Lopingian. As well, lengthy stable biozones developed, dominated by Australian dominants, with many species and a number of genera shared with Western Australia. Western Australian brachiopods are less exceptional than those of the east, and show strong ties with those of southeast Asia and Himalaya, especially in Guadalupian time (15-20%), rising to 30% during Lopingian time. During the late Cisuralian (Baigendzinian, early Kungurian) and Lopingian, ice melted from east Australia and the crust rebounded, leading to terrestrial deposits, including coal. Marine biota survived by moving to New Zealand.

It is clear that the reiterated shifts in climate and habitat encouraged proliferation throughout east Australia. Some of the evolved genera penetrated south Asia, a few reached Siberia, and rarely, a few reached the mid-Permian of the Glass Mountains, Texas, where *Terrakea* and a trigonotretid have been recognised. Well adapted to cold conditions, no species survived the late Permian extinction shock, except for the dielasmatid *Fletcherithyris*. By contrast, bryozoans, scyphozoans and bivalves from east Australia and New Zealand proved more robust.

ORDINAL CLASSICATION FOR BRACHIOPODA

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The recently concluded Treatise series on the phylum Brachiopoda offers a fine and comprehensive overview of classification, and forms the basis for suggestions for further refinement. Of course there may be some who regard the Treatise as inviolate, but if brachiopodology is to remain a frontier science, we must continue to assess possible change. Here are some issues for discussion.

In the brachiopod Treatise, authorship is as a rule assigned to whoever proposed the particular category, at suborder, or order. One person advocates a suborder: he is author. A second elevates to full order, he authors the full order – usually, although not in all cases. Assessments of rank probably will change through time. Should we grant authorship at all ordinal ranks, just as for family group authorship? The system has worked well for family groups – so why not for ordinal groups? A second matter arises, that of technical adjustment. We tolerate deviation in endings, rightly so, and anyway the International Commission for Zoological Nomenclature has not provided a formal guide. But what are of slightly larger issues? Williams proposed Oldhaminoidea as a suborder in 1953. In 2000 Lyttoniidina was proposed and authored by Williams, Harper and Wardlaw. That seems to me a technical adjustment, and I would like to see Lyttoniidina (and at any ordinal level) remain attributed to Williams 1953. Moore in 1952 came close as well, but more contentiously, in proposing Order Rostrospiracea, for what was later called Suborder Athyrididoidea by Boucot, Johnson & Staton, later elevated to order by Dagys 1972, but attributed to Boucot et al. On the one hand, Moore used a non-generic root, like it has to be said, many bivalve studies. But to my mind, granting authorship to Moore is made even more difficult by his failure to clearly indicate that he was proposing a new entity, and I think we should retain Boucot and colleagues as authors.

Now for more contentious issues. For some reason, nowhere explained to my knowledge, and not consistent with any specified ICZN rules, or even their own practice in other of their studies, workers have attributed the authorship of some ordinal groups to an author, such as Schuchert, who in fact proposed only a family group name, placed in a different order. Such attributions are not correct, have not been explained, and appear to need adjustment. For example, Protorthida was first published by Williams & Harper (2000, p. 709). The authorship was attributed to Schuchert & Cooper (1931, p. 242), but they had treated protorthids as a family. I cannot see why the concept of Protorthida should not be attributed to Williams & Harper.

There may be some advantage in recognising for brachiopods the category of superorders, just as done for Bivalvia. We could gather closely related orders into a few larger categories, with authorship attributed to the author of the first named of the constituent orders. For example, Superorder Productiformii Waagen, 1883, for order Productida Waagen, 1883 and Chonetida Muir-Wood, 1955, and perhaps Lyttoniida Williams,1953. And superorder Spiriferiformii Waagen, 1883 for Order Spriferida Waagen, 1883 and Order Spiriferidina Ivanova, 1972.

These are matters for discussion: ultimately of course we await decision from the ICZN.

BRACHIOPODS FROM THE BROUGHTON FORMATION: USEFUL TAXA IN THE PROVINCIAL AND GLOBAL CORRELATION OF THE GUADALUPIAN OF THE SOUTHERN SYDNEY BASIN, EASTERN AUSTRALIA

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The Guadalupian (Middle Permian) Broughton Formation is located on the east coast of Australia in the southern Sydney Basin. The Formation is represented by shallow marine volcaniclastic sandstone members and latite members that accumulated in the final regressive marine sequence in the southern part of the Basin prior to the deposition of the Illawarra Coal Measures. The sandstone members contain an abundant but low diversity, cool water invertebrate fauna.

Many of the brachiopod faunas found in the southern Sydney Basin, during the Guadalupian, are endemic at a species level to the Basin or at a generic level to the Austrazean Province. In the Broughton Formation a few taxonomic elements illustrate antitropical distribution (e.g. *Terrakea* and *Fusispirifer*) and provide some correlation to the Boreal Realm and some other elements represent links to faunas of Gondwanan affinity in south and south-east Asia (e.g. *Sulciplica*). These faunas, used in conjunction with bivalve faunas, magnetostratigraphic and small foraminiferan data, are significant aids in correlation because they provide useful links to the international time scale at other localities during a time of strong provincialism. The ability to use brachiopod fauna for correlation is particularly important in eastern Australia during the Permian because the subdivision of the international time scale is primarily based on conodont faunas which are absent from this region during this time.

The brachiopod fauna of the Broughton Formation has been assigned to the *Echinalosia ovalis* Zone, of Wordian age (Waterhouse 2002). Significant brachiopod taxa occurring in the Broughton Formation include: *Echinalosia wassi* Briggs, 1998; *Terrakea brachythaera* (Morris, 1845); *Fusispirifer avicula* (Morris, 1845); *Sulciplica transversa* Waterhouse, 1968; *Ingelarella ingelarensis* Campbell, 1960 and *Johndearia* cf. *isbelli*.

In the Austrazean Province, there is a close correlation of the fauna from the Broughton Formation with fauna from the Muree Sandstone and Mulbring Siltstone in the northern Sydney Basin, the Malbina Formation (Member E) in Tasmania; the Flat Top, middle Blenheim and upper Peawaddy (Mantuan Member) formations in the Bowen Basin and the Mangarewa Formation (Units 6 and 7) in New Zealand. On a global scale the Broughton Formation can be correlated to the *Sulciplica occidentalis* Zone in the Westralian Province (Foster & Archbold 2001), and the Omolonsk Horizon, in the Kolyma-Omolon area of Siberia.

Foster, C.B. & Archbold, N.W., 2001. Chronologic anchor points for the Permian and Early Triassic of the Eastern Australian Basins. In: *Contributions to geology and palaeontology of Gondwana in honour of Helmut Wopfner,* Weiss, R.H. (ed.), Geological Institute, University of Cologne, Cologne, pp.175-197.

Waterhouse, J.B., 2002. The stratigraphic succession and structure of Wairaki Downs, New Zealand, and its implications for Permian biostratigraphy of New Zealand and marine Permian of eastern Australia and Gondwana. *Earthwise* 4, 1-260.

A NEW LATE DEVONIAN BRACHIOPOD FAUNA FROM NEW SOUTH WALES

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Late Devonian strata of the Lachlan Fold Belt of New South Wales belong almost exclusively to the widespread Lambie Facies, which typically consists of a molasse-like association dominated by sandstone, shale and conglomerate and was deposited mainly in an array of near-shore marine to fluvial environments. The Lambie facies marine strata normally yield a low-diversity invertebrate fauna dominated by brachiopods commonly referred in the past to '*Cyrtospirifer*' and '*Rhynchonella*', with few other taxa having been recorded. Not only has their often indifferent preservation in coarse, sandy, sometimes highly deformed rocks retarded and discouraged their study, but the domination of these faunas by such relatively difficult types of brachiopods has resulted in a marked, possibly justified, lack of enthusiasm for faunal studies. Most taxonomic identifications were considered suspect by Roberts et al. (1972).

A few species of strophomenate brachiopods, including a single chonetid, and perhaps two productids, are here recorded from the Late Devonian Lambie Facies of central western New South Wales. Cyrtospiriferid and rhynchonellid brachiopods occur as well but have not been studied.

The occurrence of these strophomenates in both the Gibbons Creek Sandstone of the Ilford-Running Stream district and the Bumberra Formation of the Mudgee-Cudgegong district suggests that the formations are correlatives. The presence of an atrypid brachiopod in the Lawsons Creek Shale, which overlies the Bumberra Formation east of Mudgee, indicates a Frasnian (early Late Devonian) age for the lower formations. This strophomenate fauna represents a new biofacies for the Lambie Group sediments, and a pteriomorph appears to be a common member of the biofacies. These faunas will be illustrated, and correlations of the fossiliferous units will be suggested.

No conodont data are available as limestone is not known from the Lambie Facies in the area. The two known occurrences of Late Devonian conodonts from limestones in the Lachlan Fold Belt in N.S.W. are Frasnian (Ettrema Limestone), and Famennian (Coffee Creek Member).

Roberts, J., Jones, P.J., Jell, J.S., Jenkins, M.A., Marsden, M.A.H., MeKellar, R.G., McKelvey, B.C. & Seddon, G., 1972. Correlation of the Upper Devonian rocks of Australia. *Journal of the Geological Society of Australia* 18(4), 467-490.

Poster

NEW INSIGHTS INTO THE LARVAL DEVELOPMENT OF *MACANDREVIA CRANIUM* (MÜLLER, 1776) (BRACHIOPODA, RHYNCHONELLIFORMEA)

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The terebratulid brachiopod *Macandrevia cranium* (Müller, 1776) is widespread in boreal waters of the northern hemisphere. In Europe shallow water populations of *M. cranium* are easily accessible along the Swedish coastline, which makes this species an ideal candidate for developmental studies. However, little is known about the embryology and the larval development of *Macandrevia*.

In order to obtain reproducible results we used a strict protocol of artificial fertilization under controlled temperature conditions as a basis for our morphological study. Sampling embryos or developing larvae at frequent intervals led to a comprehensive collection of preserved developmental stages, ranging from the early zygote to late three-lobed stage larvae. SEM-studies of all these stages showed that the development of *M. cranium* is similar to that of other terebratulid brachiopods. This includes the presence of four bundles of larval setae in three-lobed stage larvae. Our results contradict earlier observations of *M. cranium* development and show that this species exhibits more typical features of articulate brachiopod development than previously thought.

BRACHIOPOD BIOGEOGRAPHIC CHANGE DURING THE EARLY TO MIDDLE ORDOVICIAN OF SOUTH CHINA

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The Lower to Middle Ordovician sequence of South China is complete, well developed and exposed at many localities. Lithofacies and biofacies change substantially from the Yangtze Platform through the Jiangnan Slope to the Zhujiang Basin, and vary laterally between different localities on the platform. Six classical Lower to Middle Ordovician sections, mainly on the Yangtze Platform, were carefully measured and about 35,000 fossils collected, amongst which brachiopods (>80%), graptolites and trilobites are the major groups represented. On the basis of this extensive palaeontological database, a new chronostratigraphic framework has been established for each section measured, enabling precise correlation both within South China and internationally. So, for the first time, α-diversity and β-diversity changes can be discussed within the precise biostratigraphic context of graptolite biozones, and study of γ-diversity change also becomes possible.

Biogeographic analysis of the Early-Mid Ordovician brachiopod faunas of South China has been undertaken, utilizing each graptolitic biozone from the early Tremadoc to the Darriwilian. Preliminary results show that the South China brachiopod fauna was closely related to that of Laurentia during the Tremadoc, but the faunal affinities gradually shifted to Baltoscandia, Avalonia, Sibumasu and Kazakhstan from Floian (late Early Ordovician) to Darriwilian (Middle Ordovician) times. Palaeobiogeographically, a major change of brachiopods in South China happened at the very beginning of the Floian, in the *Tetragraptus approximatus* Biozone, thus occurring much earlier than that of α- and β-diversities. The first acme of brachiopod α-diversity change occurred in the *Didymograptellus eobifidus* Biozone (mid Floian), which was manifested by the rapid increase of regionally distributed genera concurrently with expansion of cosmopolitan forms at familial rank. There are nearly 20 brachiopod genera having their earliest occurrences in South China, suggesting this region may have served as a “cradle” for brachiopod biodiversification during the Early to Middle Ordovician.

DIVERSITY VARIATION OF BRACHIOPODS FROM THE LATE PERMIAN (LOPINGIAN) DEEP-WATER FACIES OF SOUTH CHINA

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During the Permian-Triassic crisis, brachiopods were severely affected and they have been extensively studied. The deep-water Changhsingian brachiopod faunas from South China, however, have been relatively under-studied. In this study, two deep-water sections were selected (Majiashan section in Chaohu City, Anhui Province and Rencunping section in Sangzhi County, Hunan Province), and 3810 fossils were collected, representing 17 species and 13 undetermined species in 17 genera. Based on our primary examination of these deep-water brachiopods, the changes of brachiopod diversity from these two sections can be divided into two phases. During the first phase, brachiopod diversity maintained relatively high or even increased slightly: from 5 genera and 12 species upwards to 7 genera and 12 species at the Majiashan section; from 3 genera and 3 species upwards to 7 genera and 8 species at the Rencunping section. This phase corresponds to the ammonites *Tapashanites-Shevyrevites* Zone (lower Changhsingian) and the lower part of *Pseudotirolites-Rotodiscoceras* Zone (lower upper Changhsingian) at the Majiashan section, and the *Sinoceltites* Zone (lower Changhsingian) to the lower part of *Pseudotirolites-Rotodiscoceras* Zone (lower upper Changhsingian) at the Rencunping section. During phase 2, brachiopod diversity distinctly declined, and then kept in lower diversity. The diversity decreased from 7 genera and 12 species to 1 genus and 2 species at the Majiashan section, and from 7 genera and 8 species to 1 genus and 1 species at the Rencunping section. This phase is equivalent to the upper part of ammonite *Pseudotirolites-Rotodiscoceras* Zone (and even up to the lowest Triassic *Ophiceras* Zone at the Majiashan section).

The main decline (or extinction event) of brachiopod diversity occurred just below the claystone layer at both deep-water sections. This horizon is approximately equivalent to bed 24 of the Meishan section, supported by ammonite assemblages and claystone layers. Nevertheless, the main extinction event occurred from bed 26 to bed 27 in the Meishan section (Chen et al., 2005). This implies that the most distinctive decline of brachiopod diversity in deep-water facies occurred earlier than in the shallow-water facies. Furthermore, this may suggest that the deterioration of the ecosystem in deep-water environment commenced earlier than in shallow-water settings during the Late Permian crisis. Additionally, the marine productivity of one of the two studied sections was reconstructed using geochemistry and quantitative fossil plants. In the Majiashan section, the marine productivity remained high during the early Changhsingian but became very low during the late Changhsingian. This change of marine productivity was then compared with the curve of brachiopod diversity. The comparison indicates that the most distinct decline of the end-Permian brachiopod diversity might have been affected by the decline of marine productivity.

Chen, Z.Q., Kaiho, K. & George, A.D., 2005. Survival strategies of brachiopod faunas from the end-Permian mass extinction. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology* 224, 232-269.

LIFE STRATEGIES OF EARLY CAMBRIAN BRACHIOPODS ON MUD SUBSTRATE: INFERENCES FROM THE CHENGJIANG FAUNA OF SOUTH CHINA

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Brachiopods, a group of benthic ciliary suspension-feeding marine bivalved invertebrates, were an important component of the Early Palaeozoic marine communities. The earliest brachiopods were known from the Lower Cambrian Meishucunian Stage. The Chengjiang Lagerstätte, commonly considered to correlate with the Lower Cambrian Late Atdabanian Stage, has been celebrated for yielding abundant soft-bodied fossils. This mud-dominated deposit contains abundant brachiopods including varieties of linguliforms and one genus of rhynchonelliform, often with fine preservation of soft parts, notably pedicles. The finding of soft tissues is of key importance to understanding the life style of brachiopods in the Early Cambrian.

Based on observations of a number of specimens of 8 genera, the life strategies of Early Cambrian brachiopods on muddy substrate were inferred. The Chengjiang brachiopods show several types of relationship with the soft substrate where they inhabited, including pedicle-anchoring, free-lying, cemented epifaunal, semi-infaunal. An analysis of the structure of fossil brachiopod communities in the Chengjiang soft-muddy substrate demonstrates that the Chengjiang brachiopod taxa, although inhabiting the same environment, could have occupied quite distinct tiers of space and ecological niches: *Diandongia* had a semi-infaunal mode of life, with its pedicle buried in sediment, and ventral valve lay on the sea bottom, and *Heliomedusa* was free-lying, but the coeval brachiopod genera *Xianshanella* and *Longtancunella* and *Kutorgina* tended to elevate their feeding structure through their stout pedicle to a higher level above the sea bottom. At the same time, the *Lingulellotreta* and *Linguella* were possibly suspended above the sediment-water boundary. In addition, some cementing small forms of brachiopods were ordinarily discovered to cement along the commissure of *D. pista* and on variable heights of large algae. Nonetheless, attachment by a pedicle was probably the most common relationship of Cambrian brachiopods with the substrate where they inhabited.

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