Permophiles

International Commission on Stratigraphy

8th INTERNATIONAL
BRACHIOPOD CONGRESS

Brachiopods in a changing planet:
from the past to the future

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8th INTERNATIONAL BRACHIOPOD CONGRESS
Brachiopods in a changing planet: from the past to the future
Milano 11-14 September 2018

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CONGRESS MAIN PROGRAM

	am			LUNCH	pm			
	I	Coffee Break	II		III	Coffee break	IV	V
Sept 6-9th	Pre-Congress excursion							
Monday Sept 10th							Registration Ice Breaker Party	
Tuesday Sept 11th	Opening Cerimony Plenary Lars Holmer		Scientific sessions S1		Scientific sessions S1		Scientific sessions S6	Poster Wine and Cheese
	Registration							
Wednesday Sept 12th	Plenary Uwe Brand Scientific sessions S5		Scientific sessions S5		Scientific sessions S5-S4		Scientific sessions S4	Group photo Concert Gala dinner
Thursday Sept 13th	Free day or Mid-Congress excursions							
Friday Sept 14th	Plenary Elizabeth Harper Scientific sessions S3		Scientific sessions S3		Scientific sessions S3-S2		Scientific sessions S2	
Sept 15-18th	Post-Congress excursions							

Monday 10th September 2018

16:30-19:00 **REGISTRATION**

17:30-19:30 **ICE BREAKER PARTY**

Tuesday 11th September 2018

08:30-08:50 **OPENING CERIMONY**
Institutional greetings
Prof. E. Erba (Dipartimento di Scienze della Terra 'A. Desio' and Società Geologica Italiana)
Prof. G. Carnevale (Società Paleontologica Italiana)
Sig. G. Agostoni (Comunità Montana Valsassina, Valvarrone, Val d'Esino e Riviera)

08:50-09:40 **PLENARY LECTURE**
Moderator: **Posenato R.**
Holmer L. E., Zhang Z., Zhang Z., Brock G. A., Popov L. E.
Brachiopod phylogeny in the Cambrian

09:40-10:00 **COFFEE-BREAK**

SESSION 1 *Systematics and evolution*

Convenors: **Carlson S.**, **Alvarez F.** and **Jin J.**

10:00-10:25 *Keynote lecture*
Butler A. D., Eitel M., Wörheide G., Carlson S. J., Sperling E. A.
Phylogenomic analysis of Brachiopoda: revealing the evolutionary history of biomineralization with an integrated palaeontological and molecular approach

10:25-10:40 Kuzmina T. V., Malakhov V. V., Temereva E.
Support of the "brachiopod fold hypothesis" in Recent rhynchonelliformeans: a new view on the evolution of brachiopod life cycles

10:40-10:55 Madison A., Kuzmina T.
Fossil records of the evolution of brachiopod life cycles

10:55-11:10 Zhang Z., Popov L. E., Holmer L. E., Chen F., Zhang Z.
Earliest ontogeny of Early Cambrian acrotretoid brachiopods — first evidence for metamorphosis and its implications

11:10-11:25	Chen Y., Zhang Z., Zhang Z. **Geometric morphometric analysis reveals the ontogeny of Early Cambrian (Series 2) brachiopods *Eohadrotreta zhenbaensis* from Cigui, Hubei Province, South China**
11:25-11:40	Garbelli C. **Modelling the shape of brachiopod valves**
11:40-11:55	Liang Y., Zhang Z. **New data on shell structure in *Heliomedusa orienta*: taxonomic and phylogenetic implications**
11:55-12:10	Chen F., Zhang Z., Betts M. J., Zhang Z., Liu F. **First report on Guanshan Biota (Cambrian Stage 4) at the stratotype area of Wulongqing Formation in Malong County, eastern Yunnan**
12:10-12:25	Skovsted C. B., Liu F., Topper T. P., Zhang Z., Shu D. **Are hyoliths brachiopods?**
12:25-12:40	Lavié F., Serra F., Feltes N. **Microbrachiopods from the Las Aguaditas and Las Chacritas Formations (Middle Ordovician), Precordillera terrane of western Argentina: a preliminary taxonomic analysis**
12:40-13:50	**LUNCH**
13:50-14:15	*Keynote lecture* Stigall A. L. **Brachiopods as key to evolutionary theory: from foundational systematics and phylogenetics to speciation and biogeography**
14:15-14:30	Jin J. **Morphological plasticity in the early diversification of the post-extinction Silurian pentameride fauna**
14:30-14:45	Zhou H., Huang B. **Population analysis of the Silurian brachiopod *Atrypoidea foxi* Jones from Qujing, Yunnan Province**
14:45-15:00	Lü D., Ma X. **Small-sized brachiopods from the Upper Frasnian (Devonian) of central Hunan, China**
15:00-15:15	Qiao L. **Devonian brachiopod fauna from the Baoshan block in western Yunnan, China**
15:15-15:30	Wu H., Shi G. R., He W. **A quantitative taxonomic review of *Fusichonetes* and *Tethyochonetes* (Chonetidina, Brachiopoda)**
15:30-15:50	**COFFEE-BREAK**

SESSION 6 *Modern brachiopods*

Convenors: **Bitner M. A.**, **Cusack M.** and **Lüter C.**

15:50-16:15 *Keynote lecture*
Temereva E., Kuzmina T.
Organization of the lophophore in linguliform *Pelagodiscus atlanticus* (King) and the evolution of the lophophore in brachiopods

16:15-16:30 Lüter C., Furchheim N.
Light sensation in adult brachiopods

16:30-16:45 Simonet-Roda M., Milner Garcia S., Müller T., Griesshaber E., Jurikova H., A., Eisenhauer A., Harper D.A.T., Jansen U., Schmahl W. W.
The evolution of thecideide brachiopod shell microstructure from Triassic to modern times

16:45-17:00 Simon E., Motchurova-Dekova N., Mottequin B.
Diving into the morphology and ontogeny of the micromorphic rhynchonellide genus *Tethyrhynchia* Logan, 1994 in an attempt to elucidate a conflict between morphological and molecular phylogenies

17:00-17:15 López Carranza N., Carlson S. J.
Quantifying variability and understanding species delimitation: a case study integrating morphological and genetic datasets in terebratulide brachiopods

17:15-17:30 Carlson S. J., López Carranza N., Butler A. D., Sperling E. A.
Extant Terebratellidina phylogeny and homology of the long loop

17:30-17:45 Gaspard D.
Recent brachiopods of the French Insular Caribbean Region

17:45-18:00 Pakhnevich A. V., Galkin S. V.
New data on brachiopods at the underwater Piip Volcano (Bering Sea)

18:00-18.15 Bitner M. A.
Recent brachiopods from the Tonga Islands, SW Pacific: taxonomy and biogeography

18:15-18.30 Williams U. M., Robinson J., Lee D., Lamare M.
Investigating the ecology and environmental tolerance to sedimentation of the brachiopod *Calloria inconspicua* in Otago Harbour, New Zealand

18:30-20:30 **POSTER WINE AND CHEESE**

Wednesday 12th September 2018

8:45-9.35 **PLENARY LECTURE**
Moderator: **Angiolini L.**
Brand U.
Modern brachiopods: superheroes of archives

SESSION 5 *Biologic mineralization of natural functional materials and archives of geochemical proxies*

Convenors: **Griesshaber E.** and **Eisenhauer A.**

09:35-10:00 *Keynote lecture*
Ziegler A., Simonet-Roda M., Griesshaber E., Henkel D., Häusermann V., Eisenhauer A., Laudin J., Schmahl W. W.
Mechanisms of calcite fibre formation in *Magellania venosa*

10:00-10:15 Takayanagi H., Nishio T., Fujioka H., Yamamoto K., Endo K., Iryu Y.
A generalized monthly growth curve of modern brachiopod shells

10:15-10:30 Robinson J. H.
Drill-hole repair in Cenozoic and Recent brachiopods

10:30-10:45 Ye F., Angiolini L., Garbelli C., Shen S.
Evolution and fabric differentiation of Palaeozoic rhynchonelliformean brachiopod shells

10:45-11:05 **COFFEE-BREAK**

11:05-11:20 Mages V., Casella L., Simonet-Roda M., Ye F., Crippa G., E. Griesshaber, Angiolini L., Schmahl W. W.
The intermediate stages of diagenetic overprint deduced from hydrothermally altered and fossil brachiopod shells

11:20-11:35 Romanin M., Bitner M.A., Angiolini L., Gatta D. G., Brand U.
Cement-filled fossil brachiopod punctae and potential analytical bias in paleoenvironmental reconstructions

11:35-12:00 *Keynote lecture*
Rollion-Bard C., Milner Garcia S., Saulnier S., Burckel P., Vigier N., Angiolini L., Tomašových A., Henkel D., Jurikova H., Lécuyer C.
What can geochemical proxies tell about the biomineralization processes of brachiopods?

12:00-12:15 Bajnai D., Fiebig J., Tomašových A., Milner Garcia S., Rollion-Bard C., Raddatz J., Löffler N., Primo-Ramos C., Angiolini L., Henkel D., Brand U.
Assessing kinetic fractionation in brachiopod calcite using clumped isotopes

12:15-12:30 Smajgl D., Mandic M., Böhm F., Eisenhauer A.
New approach in stable isotope analysis of carbonates: isotope ratio infrared spectrometry

12:30-12:45	Jurikova H., Liebetrau V., Gutjahr M., Krause S., Büsse S., Gorb S. N., Henkel D., Hiebenthal C., Schmidt M., Leipe T., Laudien J., Eisenhauer A. **Major and trace element composition and microstructure of cultured brachiopods – new proxies?**
12:45-13:00	Nishio T., Takayanagi H., Asami R., Shinjo R., Yamamoto K., Iryu Y. **Variations in trace element concentrations of modern brachiopod shells**
13:00-14:10	**LUNCH**
14:10-14:25	Müller T., Tomašových A., Mikuš T. **Variation of Mg/Ca in brachiopod shell: expression of growth rate rather than temperature seasonality**
14:25-14:40	Fuchs R., Lazar B., Angiolini L., Crippa G., Felletti F., Fruchter N., Eisenhauer A., Stein M. **Reconstructing ^{87}Sr/^{86}Sr and $\delta^{88/86}$Sr in Pliocene-Pleistocene seawater by fossil brachiopods, bivalves, gastropods and foraminifera**
14:40-14:55	Wang W., Garbelli C., Shen S. **Permian strontium isotope stratigraphy based on brachiopod shells from South China**

SESSION 4 *Mass extinctions and recovery*

Convenors: **Shen S.**, **Baliński A.** and **García Joral F.**

14:55-15:20	*Keynote lecture* Vörös A. **Mass extinctions and fatal extinctions in the history of brachiopods: review and post-Paleozoic cases**
15:20-15:35	Hughes Z. E., Belben R. A., Johnson K. G, Twitchett R. J., Hughes C. **Brachiomatic: utilising new museum collections digitisation protocols to examine brachiopod size across extinction boundaries cases**
15:35-15:50	Chen D., Rong J. **The linguliform and craniiform brachiopods from the latest Ordovician *Hirnantia* fauna of South China and Myanmar**
15:50-16:10	**COFFEE-BREAK**
16:10-16:25	Huang B., Jin J., Rong J. **Diversification patterns of brachiopods after the end Ordovician mass extinction and its palaeobiogeographic significance**
16:25-16:40	Mottequin B., Bartzsch K., Simon E., Weyer D. **Evolution of the brachiopod assemblages at the Devonian–Carboniferous boundary (Hangenberg Crisis) in basinal facies from SE Thuringia (Germany)**

16:40-16:55 Jurikova H., Gutjahr M., Wallmann K., Flögel S., Liebetrau V., Posenato R., Angiolini L., Garbelli C., Brand U., Eisenhauer A.
Major marine carbon cycle perturbations during the Permian-Triassic mass extinction

16:55-17:20 *Keynote lecture*
Shen S., Ramezani J., Chen J., Cao C., Erwin D. H., Zhang H., Xiang L., Schoepfer S. D., Henderson C. M., Zheng Q., Bowring S. A., Wang Y., Li X., Wang X., Yuan D., Zhang Y., Mu L., Wang J., Wu Y.
A sudden end-Permian mass extinction in South China

17:20-17:35 Wang F., Chen J., Dai X., Song H.
A new Induan (Early Triassic) brachiopod fauna from South China and implications for biotic recovery after the Permian-Triassic extinction

17:35-17:50 MacFarlan D. A. B.
Early Jurassic terebratulide brachiopods from Zealandia

17:50-18:05 Piazza V., Aberhan M.
Selectivity of temperature-related stresses towards brachiopods across the Early Toarcian (Early Jurassic) extinction event in Neo-Tethys

18:05-19:00 **POSTERS**

19:00-20:00 **CONCERT**

20:00-23:00 **GALA DINNER**

Friday, 14th September 2018

08:30-09.20 **PLENARY LECTURE**
Moderator: **Brand U.**
Harper E. M.
Living brachiopods: hanging on or fit for a modern world?

SESSION 3 ***Ecosystems in time and space***
Convenor: **Harper D.A.T.**

09:20-09:45 *Keynote lecture*
Zhang Z., Holmer L. E., Brock G. A., Topper T. P.
Paleoecological complexities during Cambrian explosion: evidence from brachiopods

09:45-10:00 Topper T. P., Harper D. A. T.
Back to the beginning: the life and times of Cambrian brachiopods

10:00-10:15 Liu F., Zhang Z., Chen Y., Chen F.
A diverse fossil assemblage from a new section through the Shipai Formation (Cambrian Series 2, Stage 4) in western Hubei Province, South China

10:15-10:30 Pan B., Skovsted C. B., Li L., Li G.
The Cambrian Epoch 2 brachiopod fauna from the Xinji Formation, Shuiyu section of North China

10:30-10:50 **COFFEE-BREAK**

10:50-11:15 *Keynote lecture*
Harper D. A. T.
The rise of the rhynchonelliform brachiopods: the role of the great Ordovician biodiversification event

11:15-11:30 Candela Y., Harper D. A. T., Mergl M.
Early Ordovician (late Tremadocian – early Floian) brachiopods from the Fezouata Shale, Anti-Atlas, SE Morocco

11:30-11:45 Zhan R., Jin J., Rong J.
***Foliomena* fauna: Macroevolution of deep water benthic communities with the environmental changes**

11:45-12:00 Cocks L. R. M., Torsvik T. H.
Useful and useless – brachiopods and palaeogeogeography

12:00-12:15 Jansen U.
Evolution, stratigraphy and palaeobiogeography of late Pridolian–early Eifelian brachiopods from the Rhenish Massif (Germany)

12:15-12:30 Guo W., Sun Y., Nie T.
Facies control on the Lower Emsian (Lower Devonian) brachiopod faunas in South China

12:30-12:45 Balinski A., Halamski A. T., Racki G.
A diverse Early Frasnian brachiopod fauna from central Poland and its palaeoecological characteristics

12:45-13:00 Halamski A. T.
Palaeobiogeography and evolutionary affinities of the Early Frasnian brachiopod fauna from central Poland

13:00-14:00 **LUNCH**

14:00-14:15 Xu H., Zhang Y., Qiao F., Shen S.
A new Changhsingian (Late Permian) brachiopod fauna from the Xiala Formation at Coqen in the central Lhasa Block and its palaeogeographical implications

14:15-14:40 *Keynote lecture*
Twitchett R. J.
Brachiopods in post-Permian hothouse worlds

14:40-14:55 Kiel S., Peckmann J.
The ecology of brachiopods in ancient methane-seep environments

14:55-15:10 Dulai A., Özcan E., Less G.
Eocene brachiopods of the Thrace Basin (NW Turkey)

15:10-15:25 García-Ramos D. A., Zuschin M.
Cyclicity of *Terebratula* pavements in a mixed carbonate-siliciclastic prograding wedge: Early Pliocene of SE Spain

15:25-15:40 Buono G.
Brachiopods in Italy: a very long record and a new database

SESSION 2 *Taphonomy and Palaeoecology*

Convenors: **Pérez-Huerta A.** and **Tomašových A.**

15:40-16:05 *Keynote lecture*
Shiino Y.
Form and function of fossil brachiopods: insights into evolutionary morphology

16:05-16:20 Tomašových A., Kidwell S. M., Müller T.
Time averaging of brachiopods in the southern California bight: implications for paleoecology, taphonomy, and conservation paleobiology

16:20-16:35 **COFFEE-BREAK**

16:35-16:50 Cisterna G. A., Sterren A. F., Shi G.R.
Carboniferous-Permian glacial-deglacial events and their effects on the brachiopod faunas from Argentina and Australia

16:50-17:05 Yuan Z., Sun Y., Shen B.
An *in situ* preserved late early Carboniferous brachiopod fauna in southern Guizhou, China

17:05-17:20	Bahrammanesh M., Rezaee H., Mossadegh H. **Tournaisian (Mississippian) brachiopods from the Mobarak Formation, eastern Alborz (north Iran)**
17:20-17:35	Sun Y., Li T., Nie T., Shen B., Guo W. ***Dzieduszyckia* in southern China: morphological variation and population dynamics**
17:35-17:50	Sproat C. D., Zhan R. **A late Katian (Late Ordovician) low diversity and high dominance brachiopod fauna from the Tarim Basin in Northwest China**
17:50-18:05	Chen J., Song H., Wang F. **Size evolution of brachiopods from the Late Permian through the Middle Triassic in South China**

POSTERS

SESSION 1 *Systematics and evolution*

1 Bahrammanesh M., Zahabizadeh B., Alaeddini K.
Carboniferous brachiopods from NW Havir Lake (Damavand, N Iran)

2 Berrocal-Casero M., Barroso-Barcenilla F., García Joral F.
Micrornamentation and other external features as distinctive criteria for the Coniacian (Upper Cretaceous) terebratulides from Northern Spain

3 Buono G.
Famous brachiopods, part 1: brachiopods in lapidary stones

4 Buono G.
Famous brachiopods, part 3 – brachiopods in philately

5 Legrand-Blain M.
Gigantoproductid and allied brachiopods from "L'ardoisiere" (Visean), northern Massif Central, France

6 Leone M. F., Benedetto J. L.
Phylogenetic relationships of the Silurian Afro-South American Realm rhynchonellide brachiopods *Anabaia*, *Harringtonina* and *Clarkeia*: new insights from their ontogeny

7 Mottequin B., Lefèvre U., Cisterna G. A.
A review of the brachiopod subfamily Septosyringothyridinae (Spiriferinida) from the Carboniferous of Laurussia and Gondwana

8 Taddei Ruggiero E., Raia P.
The old, misnamed, misunderstood *Terebratula sinuosa*

SESSION 2 *Taphonomy and Palaeoecology*

9 Angiolini L., Banks V., Carniti A., Della Porta G., Stephenson M.
How mud mounds controlled brachiopod population growth and life-style in the Carboniferous: an example from the Viséan of Derbyshire, UK

10 Baliński A., Skompski S., Szulczewski M., Zawadzka I.
The origin of the Middle–Late Devonian brachiopod shell concentration within intrashelf basinal carbonates in the Holy Cross Mountains (central Poland)

11 Madison A., Kuzmina T.
The tube-like structures on the juvenile shells of strophomenids and billingsellids as evidence of their life cycles

12 Pakhnevich A. V.
Preservation of brachiopod soft tissues outside the Lagerstätte conditions

13 Pálfy J., Price G. D., Vörös A., Kovács Z., Johannson G. G.
Cold seep-related occurrence of the Early Jurassic rhynchonellid brachiopod *Anarhynchia* from the Canadian Cordillera

14 Paredes R., Comas-Rengifo M. J., García Joral F., Duarte L. V., Goy A.
Disparity and diversity in Early Jurassic first colonizing brachiopods of the Lusitanian Basin (Portugal)

15 Shiino Y., Tsuchida T.
A hydrodynamic approach to orthid brachiopod *Vinlandostrophia ponderosa*: reevaluation of zig-zag function

16 Sklenář J.
Brachiopods of the Late Turonian hemipelagic strata of the Saxo-Bohemian Cretaceous Basin (central Europe)

17 Stadtmauer D., Butts S.
Skeletal ultrastructure, ecology, and functional morphology of the Permian lyttoniid brachiopod *Pirgulia*

18 Viaretti M., Angiolini L., Heward A.
Lower to Middle Permian brachiopods from the Qarari Unit, Oman

19 Zhang Y., Zhan R., Huang B.
Late Ordovician brachiopods from Xichuan, southwestern Henan, central China and their implications

20 Zhang Z., Holmer L. E., Zhang Z., Chen F., Liang Y.
Brachiopods with soft parts from the Early Cambrian Wulongqing Formation (Series 2, Stage 4) of Yunnan, southern China

SESSION 3 *Ecosystems in time and space*

21 Baeza-Carratalá J. F., Dulai A., Giannetti A., Soria J. M., Tent-Manclús J. E.
A new Late Tortonian brachiopod assemblage from the Mediterranean-Atlantic seaway (Guadix Basin, SE Spain)

22 Vörös A., Escarguel G.
Brachiopod paleobiogeography in the western Tethys during the Early Jurassic taxonomic diversity maximum: identification of a new Pontic province

SESSION 4 *Mass extinctions and recovery*

23 Baeza-Carratalá J. F., Dulai A., Sandoval J.
First brachiopod diversification in the Early Jurassic of the Subbetic platform (South-Iberian Paleomargin, Spain)

24 Baeza-Carratalá J. F., García Joral F.
Adaptive response of brachiopod fauna to the environmental changes related to the Early Toarcian mass extinction event

25 Serobyan V., Grigoryan A., Crônier C., Mottequin B., Taniel D.
The brachiopod record around the Devonian–Carboniferous boundary: insights from the sedimentary sequences of Armenia

26 Vörös A., Dulai A., Főzy I.
Brachiopods and the Early Cretaceous Weissert event (Bakony Mountains, Hungary)

27 Zhang Y., Wu H.
Early warning signals of marine benthic ecosystem prior to the Permian–Triassic boundary mass extinction event in South China

SESSION 5 *Biologic mineralization of natural functional materials and archives of geochemical proxies*

28 Bruggmann S., Klaebe R., Frei R.
Chromium isotopes in brachiopods as a redox proxy

29 Füger A., Kuessner M., Rollion-Bard C., Leis A., Dietzel M., Mavromatis V.
The effect of pH and precipitation rate on $\delta^7Li_{solid-fluid}$ during the growth of calcite - an experimental approach

30 Fujioka H., Takayanagi H., Yamamoto K., Iryu Y.
Quantitative study of geochemically diagenetic impact on fossil brachiopod shells from northeastern Japan

31 Gaspard D.
Disorder introduced in the hierarchical architecture of selected fossil rhynchonelliform brachiopod shells

32 Gaspers N., Magna T., Tomašových A., Henkel D., Jurikova H.
Lithium in brachiopods – proxy for seawater evolution?

33 Isowa Y., Kito K., Endo K.
An immunological study of the shell matrix protein ICP-1 in brachiopods

34 Jurikova H., Liebetrau V., Gutjahr M., Rollion-Bard C., Hu M. Y., Krause S., Henkel D., Hiebenthal C., Schmidt M., Laudien J., Eisenhauer A.
Geochemical and physiological responses of brachiopods to ocean acidification – new insights from boron isotopes

35 Kocsis L., Dulai A., Yunsi M., Cipriani A.
Geochemical study of *Megathiris detruncata*, a brachiopod species known since the Eocene in Europe

36 Legett S. A., Rasbury E. T., Grossman E. L., Hemming N. G., Wright C. C.
Shelled archives: using brachiopods to reconstruct the seawater $\delta^{11}B$ record across the Late Paleozoic Climate Shift

37 Milner Garcia S. A., Rollion-Bard C., Burckel P., Müller T., Jurikova H., Tomašových A., Angiolini L., Henkel D.
Fossil brachiopod shell calcite: how well is the oxygen isotope composition and minor element ratios preserved within the shell microstructure?

38 Romanin M., Crippa G., Ye F., Bitner M. A., Gaspard D., Häussermann V., Laudien J., Brand U.
Trace elements, stable isotope composition and shell microstructure, defining the optimal sampling shell segment for geochemical analyses in five modern brachiopod species

39 Simonet-Roda M., X. Yin, Cross E., Harper E.M., Ziegler A., Schmahl W. W., Peck L., Griesshaber E.
Microstructure formation in the shell of the Antarctic brachiopod *Liothyrella uva* (Broderip 1833): transition from larval to juvenile stages

40 Twitchett R. J., Paulus C., Hughes Z.E., Brownscombe W.
Giants in the hot tub? Sclerochronology of Pliocene brachiopods of southeast UK

41 Ye F., Jurikova H., Angiolini L., Brand U., Crippa G., Henkel D., Laudien J., Hiebenthal C., Šmajgl D.
Variation in brachiopod microstructure and isotope geochemistry under low pH - ocean acidification – conditions

SESSION 6 *Modern brachiopods*

42 Bitner M. A., Romanin M.
Recent brachiopods from the South China Sea, NW Pacific

43 Bitner M. A.
The first recent record of the genus *Neobouchardia* (Brachiopoda: Bouchardiidae) from the Coral Sea, SW Pacific

44 Buono G., Davidde B., Sacco Perasso C., Ricci S.
“Famous brachiopods”, part 2 – brachiopods on archeological remains

45 Endo K., Motchurova-Dekova N., Suzuki N., Maekawa Y., Takayanagi H., Hirose M.
A new locality of a living platidiid in northern Japan observed by a remotely operated vehicle

46 Temereva E., Kuzmina T.
Spermatogenesis in the deep-sea brachiopod *Pelagodiscus atlanticus* (Brachiopoda: Linguliformea)

47 Posenato R.
A cancelled field excursion: Upper Permian to Middle Triassic brachiopod beds of the Dolomites (Italy)

ABSTRACTS

How mud mounds controlled brachiopod population growth and life-style in the Carboniferous: an example from the Viséan of Derbyshire, UK

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Mississippian carbonate platforms are predominantly ramps characterized by a widespread development of mud mound bioconstructions (e.g. Gutteridge, 1995; Lees & Miller, 1995). The Viséan carbonate platform of Derbyshire hosts several of these mud mounds, which are associated with rich brachiopod faunas. In particular, in Ricklow Dale (near the village of Monyash) brachiopods occur abundantly both in the mud mounds of the Monsal Dale Limestone Formation and in the overlying Eyam Limestone Formation. The Monsal Dale Limestone Formation mud mounds are in fact composite and complex structures, which originate from the juxtaposition of several smaller mounds and comprise a complex set of core-, flank- and intermound facies. Here, brachiopods are very diversified and occur as life assemblages in 'pockets' possibly scoured by storm currents in the core facies of the mounds (Gutteridge, 1995) as well as neighbourhood assemblages in the well bedded flank-facies, which are otherwise dominated by large crinoids; intermound-facies mainly comprise skeletal wackestone/packstone with diverse skeletal composition. Brachiopods from the core-pockets and from the flank facies are similar and comprise free-living seminfaunal productids, pedicle-attached terebratulids and rhynchonellids and free-living spiriferids. Seminfaunal productids are dominant and reach a larger size than the other taxa, suggesting food resources sparse or not abundant.

The outcrops of the Eyam Limestone Formation at Ricklow are mostly inner to middle ramp facies without the development of mud mounds, but characterized by the occurrence of massive shell beds dominated by large and thick-shelled seminfaunal species of *Gigantoproductus* (Nolan et al., 2017 and references therein). Many authors have previously considered these assemblages as part of the mud mound deposits. Yet they represent distinct life to neighbourhood assemblages developed at times of mud mound inactivity, onlapping the flanks of the mound and its top. Even if successive to the growth of the mound, their relict morphology provides sheltering for the pioneer *Gigantoproductus* palaeocommunities, allowing their development and success.

The few-tens of metres thick succession at Ricklow Dale discloses a neat and sharp faunal change from the high diversity and spatially restricted mud mound adapted brachiopod communities to the low diversity widespread *Gigantoproductus* shell beds.

View of the Ricklow mud mound with core-pockets brachiopods and the two onlapping *Gigantoproductus* beds.

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A new Late Tortonian brachiopod assemblage from the Mediterranean-Atlantic seaway (Guadix basin, SE Spain)

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The paleogeography of the Late Neogene Atlantic-Mediterranean seaway via the Betic-Rifean Domain is quite complex due to the presence of several marine corridors. The study of transitional basins in this seaway and its benthic biota is crucial to understand the configuration and evolution of the Mediterranean-Atlantic inter-connection during a key timespan involving critical (bio)events such as the well-known Messinian Salinity Crisis Event. In this context, a mixed skeletal-siliciclastic sandy/calcarenite succession located in one of these transitional areas (Guadix Basin, Southern Spain) and dated within the MMi12b Subchronozone of the Late Tortonian was studied from a comprehensive palaeontological standpoint focused on the main benthic communities.

Brachiopods are mostly represented by the *Aphelesia-Gryphus* assemblage. The outcrop studied is the most prolific locality comprising the genus *Aphelesia* (225 individuals) in the Betic-Rifean Domain, constituting the 94.5% of the individuals; the genus is represented mainly by *Aphelesia bipartita*, with a high range of variability. The monotypic character of the assemblage, with *A. bipartita* as the single faunal constituent, is predominant in the lower part of the stratigraphical section. In the upper part, the assemblage shows greater taxonomic diversity. An *Aphelesia* stock with pyriform dorsal outline and true costate shells in the anterior margin can be assigned to *A. margineplicata*. Terebratulids are recorded in this upper part as well, mainly represented by *Gryphus miocenicus* and *Gryphus* sp., this latter morphotype is more triangular in dorsal outline and with a much higher degree of uniplication. Occasional occurrences of the large-sized *Terebratula* cf. *calabra* are recorded in the uppermost level of the section. Overlying this sandy-calcarenite succession, a marly interval barren in brachiopod fauna crops out, giving rise, upwards, to the Gilbert-type delta depositional environment where Reolid et al. (2012) identified thick shell-beds monospecific accumulations assigned to *Terebratula terebratula* forming densely-packed skeletal concentrations.

Palaeoecological data gathered from foraminifers, brachiopods, and trace fossil assemblages (*Ophiomorpha-Bichordites,* and *Macaronichnus* ichnoassemblages) revealed habitats integrated in an open platform located in the outer neritic-upper bathyal bathymetric range.

Excluding micromorphic forms, Miocene brachiopods are relatively scarce (especially in the late Tortonian) when compared with the Pliocene assemblages that profusely occur in the European region, and particularly in the South-Iberian basins, following the well-known Messinian Salinity Crisis Event (Toscano-Grande et al., 2010). Miocene brachiopod assemblages with macromorphic forms are patchily-distributed, marked by the *Aphelesia/Terebratula/Gryphus* association (the latter occurs more sporadically) as the prevailing taxa in Mediterranean assemblages. In the Betic-Rifean domain, this assemblage is more prolific in Pliocene deposits (e.g., Bitner and Martinell 2001; Bitner and Moissette 2003, García-Ramos 2006; Toscano-Grande et al., 2010). However, these brachiopods, displaying a Mediterranean palaeobiogeographic affinity, are constrained in the Late Tortonian to the restricted basins of the Betic-Rifean corridor (such as the Guadix basin), being subsequently prolific in the earliest Pliocene in both Mediterranean- and Atlantic-type basins of the Betic Domain. Thus, the location of the Guadix Basin in the central part of the Betic Corridor contributed to the Mediterranean-Atlantic faunal inter-connection through the Betic-Rifean Corridor, making feasible effective faunal dispersal across the Mediterranean-Atlantic seaway system in the Late Tortonian, no longer a faunal filter-barrier for the benthic biota. As results of this free connection during the Late Tortonian, brachiopod assemblages have been recorded in several Atlantic-type basins in the earliest Pliocene (Bitner and Martinell 2001; Bitner and Moissette 2003, Toscano-Grande et al. 2010) revealing clear affinities with the Mediterranean bioprovince and contributing therefore to the expansion of this Mediterranean biochorema.

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First brachiopod diversification in the Early Jurassic of the Subbetic platform (South-Iberian Paleomargin, Spain)

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Lower Jurassic brachiopods are widely known in the External Betic Zones (SE Spain) of the Betic Range. Their occurrence was so far virtually restricted to the easternmost Subbetic Zone where they underwent a diversity burst and radiation event during the Late Sinemurian–Early Pliensbachian interval, leading to a bloom in brachiopod diversity from the Early Pliensbachian onwards, up to their sudden decreasing in the Early Toarcian Mass Extinction Event (Baeza-Carratalá, 2011, 2013; Baeza-Carratalá et al., 2015). Taxonomical and paleobiogeographical analyses performed in a newly recorded assemblage from the most offshore areas of the Subbetic basin (Granada province, Spain) reveals that this diversification event occurred earlier than expected hitherto, in the Turnieri–Obtusum chronozones, as similarly took place in the most intra-Tethyan basins such as the Northern Calcareous Alps and the Transdanubian Ranges (Siblík, 1999; Böhm et al., 1999; Dulai, 2001; Vörös and Dulai, 2007), thus typifying the recovery of the background conditions for the establishment of diversified brachiopod communities after the end-Triassic extinction event.

The studied assemblage recorded in the Internal Subbetic Domain, partly agrees with the diversity pattern estimated by Sandy (1995) for the earliest Jurassic post-extinction fauna. Sandy (1995) recognized in this interval assemblages dominated by generalist species belong to *Calcirhynchia, Zeilleria*, and *Lobothyris*, together with spiriferinids such as *Spiriferina walcotti*, representing a low-diversity fauna. In the Internal Subbetic assemblage, spiriferinids are completely absent and rhynchonellids are the predominant group in species diversity. There are seven rhynchonellid species from six different genera (*Cuneirhynchia* aff. *cartieri*, *Prionorhynchia* cf. *polyptycha*, *Calcirhynchia hungarica, Calcirhynchia* aff. *rectemarginata, Cirpa subcostellata, Salgirella albertii*, and *Alebusirhychia* nov. sp). Short-looped terebratulids are scarce and they are represented by two species of *Lobothyris* (*Lobothyris*? *sospirolensis* and *Lobothyris* gr. *punctata*) while long-looped zeilleriids are overrepresented in individuals (31.3%) but they are only typified by a single species (*Zeilleria venusta*).

A new multicostate rhynchonellid species is found among the ten different taxa recorded for the first time in this area. The diagnostic external features and the distinctive internal structure (very short dorsal median septum, crural bases incipiently with dorsal orientation, developing raduliform crura) allows for its arrangement into the genus *Alebusirhynchia*, which seems to be endemic to the Subbetic area.

This assemblage represents the first step on the evolutionary diversification of the Mediterranean Lower Jurassic brachiopods in the Betic Ranges and the recovery of the background conditions for the establishment of diversified brachiopod communities after the end-Triassic mass extinction event in the External Betic Zones, since is the oldest assemblage recorded into the Sinemurian with several genera occurring together, after the Euro-Boreal monotypic assemblage reported by previous authors in the earliest Sinemurian.

The Mediterranean affinity of this assemblage, recorded in the more offshore areas of the Betic Domain closer to the proto-Atlantic seaway, reveals that the onset of the Mediterranean/Euro-Boreal bioprovinciality (*sensu* Vörös et al., 2016) and the initial brachiopod diversification in the pre-Pliensbachian Internal Subbetic platform took place earlier than expected.

Consequently, a remarkable speciation and radiation episode is documented as precursor of the peak of brachiopod prosperity reported in the latest Sinemurian–earliest Pliensbachian in the Subbetic Domain as a whole (Baeza-Carratalá, 2013). This diversification was probably related with the incipient pre-rifting stage of the westernmost Tethyan platform system (Vera, 1998), interpreted as the first tectonic pulses in the Sinemurian (Ruiz-Ortiz et al., 2004), thus diversifying the ecological niches and facilitating the establishment of steady brachiopod communities in the South-Iberian Paleomargin.

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Adaptive response of brachiopod fauna to the environmental changes related to the Early Toarcian mass extinction event

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The Early Toarcian Mass Extinction Event (ETMEE) was one of the most critical Mesozoic biotic crises having a significant impact on the brachiopod fauna. This crisis has been recently explained as a multi-phased interval (so-called "Extinction interval") with episodes of changing environmental conditions, whose onset is detected from the Elisa–Mirabile subzones up to the extinction boundary within the lower Serpentinum Zone. The virtually continuous and well calibrated record of brachiopod communities developed in a mosaic of ecospaces from the Lower Jurassic peri-Iberian platform system is a suitable tool to analyze the different adaptive strategies underwent by the diverse brachiopod clades affected by the interplay of several ecological factors that lead to the ETMEE in the westernmost Tethys Ocean.

The orders Spiriferinida and Athyridida became extinct in the ETMEE boundary (Vörös 2002, Baeza-Carratalá et al., 2015, Vörös et al., 2016) but prior to their definitive extinction, they carried out different adaptive strategies. The koninckinids (last recorded group of the order Athyridida) experienced a migration process from the intra-Tethyan to the NW-European basins (Vörös 2002, Baeza-Carratalá et al., 2015). A first phase of this dispersal coincides with the onset of a progressive warming episode in the Pliensbachian–Toarcian transition and triggered a koninckinid fauna exodus stage from the eastern/central Tethys areas toward the westernmost Mediterranean margins where they found a suitable habitat to colonize. This migratory episode did not involve changes in the oxygen-supply conditions of the seafloor and do not imply important changes in morphology or size. A second stage shows an adaptive response to more adverse conditions in the marginal Tethyan basins (North-Africa). This turnover represented a replacement of species implying a decrease in size and diversity loss. Finally, an escape and extinction phase is detected in the Atlantic areas from the mid-Tenuicostatum Zone onwards up to their global extinction in the lower Serpentinum Zone. This migration pattern is independent from the bioprovinciality and unrelated to a facies-controlled pattern. The anoxic/suboxic conditions only is considered as a minor factor of partial control since well-oxygenated habitats are noted in the intra-Tethyan basins and this factor is only noticeable in the second migratory stage (with dwarf and oligotypical taxa).

Order Spiriferinida becomes extinct in the ETMEE as well, but without significative decrease in diversity in the extinction interval. Several new evolved species appear in the Tenuicostatum/Polymorphum Zones in the peri-Iberian basins, including representatives of the *Calyptoria* community which undertook a considerable dispersal episode from their Arab-Madagascan homeland along the North-Gondwana paleomargin into the peri-Iberian epicontinental platform system, coincident with the thermal maximum of seawater temperature recorded prior to the ETMEE. This adaptive strategy carried out by *Calyptoria*, consisted of a sudden and long, practically synchronous spreading without outstanding morphological changes, showing a latitudinal-controlled distribution between 0-30º on both hemispheres. This dispersal episode is facies-dependent due the settlement of this community predominantly in epicontinental areas (Baeza-Carratalá et al., 2018). On the other hand, it seems that the aforementioned thermal maximum episode prior to the super-warming event occurred in the ETMEE contributed to the opportunistic occurrence of Thecideides, with *Eudesella mayalis* as prevailing species, typifying a pre-ETMEE marker horizon ("thecideid beds") which enables correlation among the Lower Jurassic outcrops of the Iberian Range (Baeza-Carratalá et al., 2016) and higher palaeolatitude areas (South England/Normand basins).

The Order Rhynchonellida suffered an entire renewal. Both epicontinental and epioceanic pre-extinction taxa, clearly discriminated in the Mediterranean/Euro-Boreal bioprovinces, gave rise in the early Serpentinum Chronozone to the record of monospecific populations of the opportunistic *Soaresirhynchia bouchardi*, with high intraspecific variability, regarded as the Western Tethys brachiopod colonizer aftermath the extinction, and the subsequent dominance of the "Spanish Fauna of brachiopods" (e.g., García Joral & Goy 2000; García Joral et al., 2011) typifying the return to the background conditions in the Serpentinum-Bifrons chronozones.

The Order Terebratulida remain quite unaffected (Vörös 2002; García Joral et al., 2011; Baeza-Carratalá et al., 2015; Vörös et al., 2016) likely due to the long-term steady communities established in the peri-Iberian margins.

Regarding the spatial distribution of the brachiopod fauna in the extinction interval, the pre-extinction dwarfing abovementioned in the koninckinid fauna through a spatial gradient in the westernmost Tethys is also detected in the peri-Iberian basins in the other groups. All of them show a trend to diminishing size, from shallow and well oxygenated areas to the oxygen-depleted and argillaceous bottoms that do not derives from the miniaturization of the species, but affected the taxonomic composition of the assemblages, with bigger species in the East and smaller ones to the North and West. In parallel to this trend, other of size increasing in the Semicelatum Subzone is observed in some species in all the peri-Iberian basins. This increase is independent from the standard size of the species, affecting both big spiriferinids in the more favorable conditions on the Iberian Basin, and small rhynchonellids and koninckinids in the less favorable habitats in the Cantabrian and Lusitanian basins. The first trend of decreasing size can be explained as a response to the environmental stress associated with deeper and more turbid bottoms, whereas species more resilient or better adapted to the degrading environmental conditions increased in size probably as a response to the decrease in diversity and the lack of competition pressure for food.

At the same time, occasional deeper habitats in the south-Iberian paleomargin operated as long-term resilient reservoirs where the evolutionary lineages of several smooth brachiopods entailed an *in situ* diversification in these deeper habitats and posterior radiation. The high evolutionary stability of these resilient environments enabled that new latest Pliensbachian-Lower Toarcian smooth morphotypes (*Atychorhynchia falsiorigo* and *Koninckodonta sumuntanensis* in a wider smooth assemblage) withstood several perturbation peaks within the extinction interval. They not only survived the main TOAE event in this restricted semi-graben areas, but also developed new evolutionary lineages during the extinction interval, but not reaching the repopulation interval (Baeza-Carratalá et al., 2017). The super-warming episode of the early Serpentinus Chronozone seems to have been unbearable even for these resilient taxa.

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Tournaisian (Mississippian) brachiopods from the Mobarak Formation, Eastern Alborz (North Iran)

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A rich brachiopod fauna of 176 specimens belonging to 30 taxa of Strophomenida, Productida, Orthida, Orthotetida, Rhynchonellida, Athyridida, Spiriferida, Spiriferinida and Terebratulida has been found in the Tournaisian (Mississippian) Mobarak Formation at the Shotorgardan section (Fig. 1). Most of the brachiopod species here described were obtained from the middle and upper parts of the Mobarak Formation: *Leptagonia analoga* Phillips, *Buxtonia* sp. ind., *Marginatia* sp. ind., *Marginatia vaughani* (Muir-Wood), *Tomiproductus* sp. ind., *Tomiproductus elegatulus* (Tolmatchoff), *Tomiproductus* cf. *vaughani* (Muir-Wood) *Schellwienella* sp., *Rhipidomella michelini* (Leveille), *Hemiplethorhynchus* aff. *H. crussus* Gaetani, *Septemirostellum*? aff. *S. tereticostu* Roberts, *Rossirhynchus adamantinus* Gaetani, ?*Athyris* sp. ind., *Lamellosathyris lamellose* (Leveille), *Cleiothyridina* sp. ind., *Cleiothyridina kusbassica* Beznosova in Sarytcheva, Sokolskaya, Beznosova and Maksimova; *Cleiothyridina* aff. *C. obmaxima* (McChesney), *Gerankalasiella* sp. ind., *Composita* sp. ind., ?*Densalvus* sp. ind., ?*Martinia* sp. ind., *Parallelora* sp. ind., *Unispirifer* spp. ind., *Unispirifer* (*Unispirifer*) aff. *U. striatoconvolutus* Benson and Dun in Benson, Dun and Brown, ?*Atylephorus* sp. ind., *Tylothyris* aff. *T. transversa* Roberts, *Torynifer* sp. ind., *Syringothyris carteri* (Hall), *Cranaena* sp. ind. This brachiopod assemblage is characteristic of the Tournaisian of the eastern Alborz.This age determination is reinforced by the associated foraminifer fauna (Figs 1-2).

The brachiopods here described are mostly cosmopolitan with only a few species endemic to Iran and show a close relationship with those of North America, Western Europe and the Russian Platform rather than with the ‘cold-water’ Gondwanan faunas. In fact, provincialism was not strongly developed during the Tournaisian and Viséan, but became very distinct in the Paleotethys subsequently, during the Serpukhovian (Qiao and Shen, 2014).

Previous studies of foraminifera and algae from the Mississippian of the Alborz have been performed by Bozorgnia (1973), Maisami et al. (1978) and Brenckle et al. (2009). These studies, as well as data from brachiopods (Bahrammanesh et al. 2011), suggest warm and sub-tropical settings of Paleotethyan affinity. On the other hand, the Alborz region is part of the North Iran block and it was located at or near the peri-Gondwanan region at Tournaisian times, at about 45° to 50° S (e.g. Torsvik & Cocks, 2004; Zanchi et al., 2009).

Paleocurrent reconstructions, however, may solve this conundrum, providing an explanation for the biotic affinities between the northern Paleotethys and Iran. A counterclockwise warm current flowing around the Paleotethyan Ocean and southeasterly along the Gondwanan margin could have promoted brachiopod larval dispersal and thus explain similarities between European and North American faunas and Iranian ones.

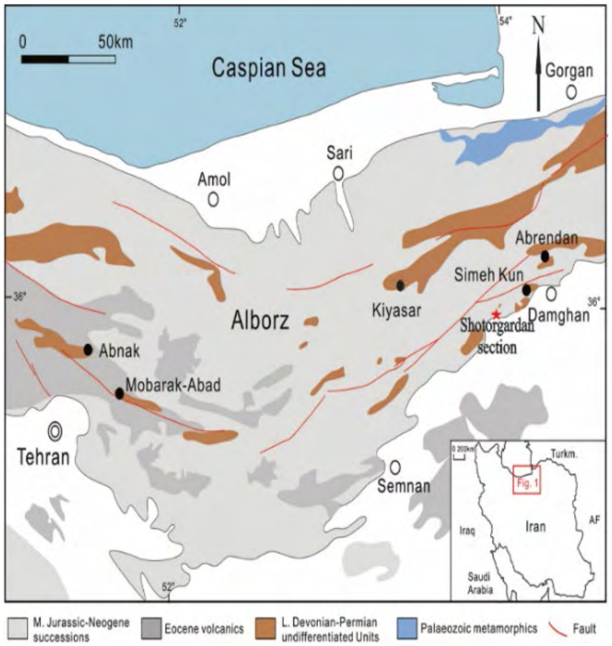

Figure 1. Simplified geological map of central and eastern Alborz Mountains. The black circles indicate key sections of Mobarak Formation.

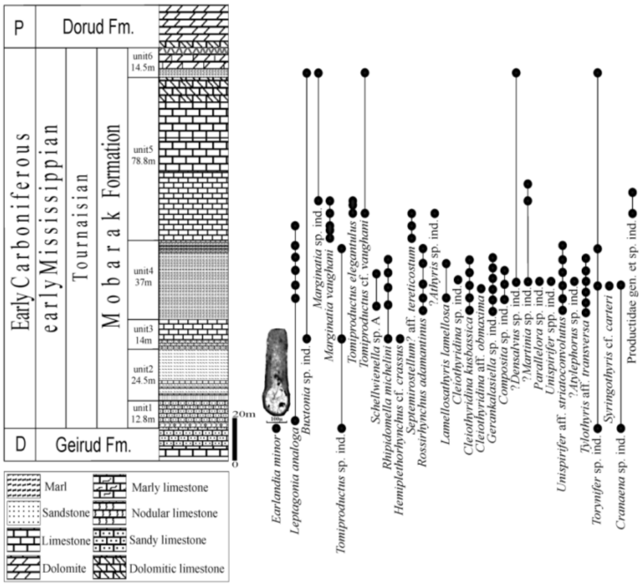

Figure 2. Stratigraphic log of the Mobarak Formation at the Shotorgardan section.

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Carboniferous Brachiopods from NW Havir Lake (Damavand, N Iran)

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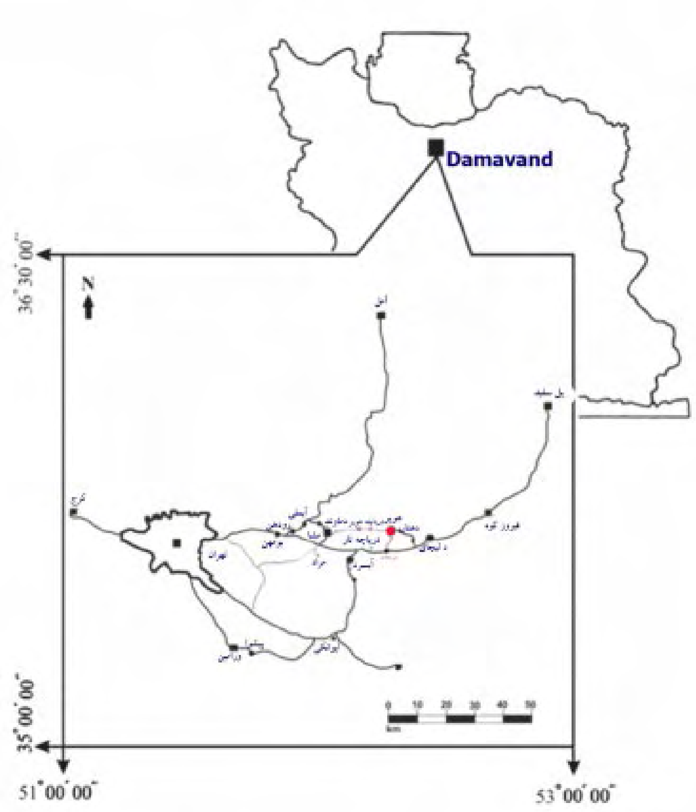
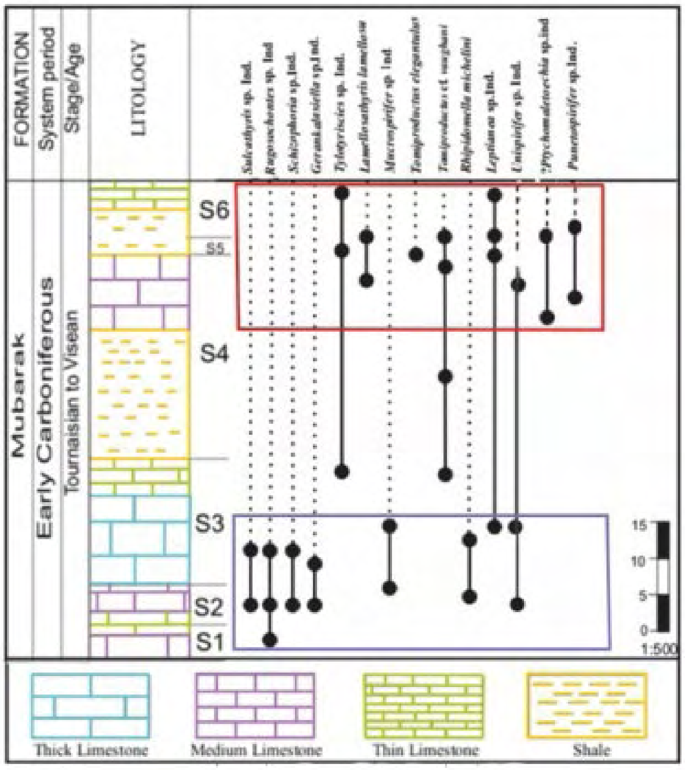
The Mississippian Mobarak Formation crops out into large parts of Central Alborz, N Iran. It is well exposed in the western section of Havir Lake, located 30 km north-east of Damavand city (52° 13´ 34.4" E, 35°44′12.5″ N). The lower part of the formation consists of thin layers of shales and limestones, gradually passing upward to thick limestone beds.

Here, we describe a very rich brachiopod fauna comprising 19 taxa, which have been found in the marly limestones and bioclastic limestones of the Mobarak Formation. The fauna comprises: Chonetoidea gen. et. sp. ind., *Delepinea* cf. *comoides* (Sowerby, 1822), Productidae gen. et. sp. ind., *Marginatia* sp. ind., *Marginatia vaughani* (Muir Wood, 1928), *Marginatia elegantulus* (Tolmachev, 1924), *Schellwienella* sp. ind., *Rhipidomella* sp. ind., *Rossirhynchus adamantinus* Gaetani, 1964, *Sulcathyris* cf. *campomanesii* (Verneuil & Archic, 1845), Spiriferidae gen. et. sp. ind., *Spirifer missouriensis* Swallow 1860, *Spirifer* sp. ind., *Ectochoristites* sp. ind., *Paralellora* sp. ind., *Unispirifer (Unispirifer)* cf. *striatoconvolutus* Benson & Dun & Browen 1920, *Unispirifer* sp. ind., *Eospiriferina* sp. ind., *Syringothyris* sp. ind. Also, three biozones have been distinguished in this section of Tournaisian to Visean age. The sedimentological study of this section allowed three facies to be described and a facies model of an open marine platform with a low gradient ramp to be reconstructed for this section.






Mobarak Formation

Assessing kinetic fractionation in brachiopod calcite using clumped isotopes

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Brachiopod shells are widely used to reconstruct palaeoclimatic variations based on their oxygen and clumped isotopic compositions (Veizer & Prokoph, 2015). However, it is not conclusive whether brachiopods precipitate their shells in thermodynamic equilibrium. Previous works have postulated that brachiopods secrete their shells in clumped isotopic equilibrium, even though the only brachiopod-based calibration (Came et al., 2014) is discrepant from the theoretical (Passey & Henkes, 2012) and mollusc-based (Henkes et al., 2013; Wacker et al., 2014) calibrations. No clear explanation has yet been given for this disagreement.

In this study, we investigated the significance of kinetic controls on brachiopod shell Δ47 and $\delta^{18}O$ values. For this purpose, we analysed modern brachiopods with independently-known growth temperatures and water $\delta^{18}O$ values for their bulk and clumped isotopic compositions and magnesium content. For the clumped isotope analyses, homogenised carbonate powder was reacted at 90°C with >105% phosphoric acid using a fully automated gas extraction and purification line.

Most specimens exhibited deviations in measured Δ47 and $\delta^{18}O$ values from predicted equilibrium. These observed departures from equilibrium correlate with each other and with brachiopod growth rates. Thus, we conclude that the oxygen and clumped isotope composition of modern brachiopod shells is affected by growth rate-induced kinetic effects. The most likely source of the kinetic effects is the incomplete hydration and/or hydroxylation of $CO_{2(aq)}$ at higher growth rates. Based on our findings, information about taxon-specific growth rate and kinetics involved in calcite precipitation would be essential whenever constraining seawater temperatures from Δ47 and $\delta^{18}O$ values in brachiopods.

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A diverse Early Frasnian brachiopod fauna from central Poland and its palaeoecological characteristics

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The recent monographic description of Early Frasnian (*transitans* Zone) brachiopods from Józefka Hill in southern region of the Holy Cross Mountains, Poland, made by the present authors (Baliński et al., 2016), revealed a rich, parautochthonous and unusual fauna (24 species, out of which 6 new). On the basis of geological data, the fauna is interpreted as having lived in relatively cool and nutrient-poor waters on a local palaeoelevation within the basin, before the global *punctata* Event. The importance of this brachiopod fauna is threefold. First of all, it records a fauna from a deeper-water setting, otherwise poorly documented for this Devonian interval. Secondly, the relatively complete fossil record of Early Frasnian brachiopods from the Holy Cross Mountains (both deep- and shallow-water communities) coupled with good biostratigraphic resolution of the Frasnian epoch allows a detailed palaeobiogeographic and palaeoecological analysis within a relatively short time interval (Halamski 2018). Last, a relatively good record of Eifelian and Givetian faunas from the Holy Cross Mountains (e.g., Biernat, 1959, 1964, 1966; Baliński, 1973, 1995; Racki, 1993; Halamski, 2008) allows assessment of the relative importance of appearances of new brachiopod taxa through either evolution in place or immigration (Halamski 2018).

The high-diversity brachiopod-dominated fauna from sets XXI–XXII at Józefka section consists of 24 species. These beds represent a deeper-water setting, seldom represented in the fossil record for this interval. However, a detailed analysis of brachiopod and other faunas clearly shows that they are derived from more than one benthic assemblage. The brachiopod fauna appears rather as a mixture of a low-diversity assemblage of nearer-shore, rough-water species with a diverse, more offshore, quiet-water assemblage. Majority of species from sets XXI–XXII lived in relatively quiet-water environments as indicated by the common occurrence of well-preserved, articulated shells. This high-diversity brachiopod fauna represents the *Biernatella lentiformis* Assemblage.

One of the most notable characteristics of this *Biernatella lentiformis* Assemblage is the small size of the shells of all important species. No brachiopod order is dominant in terms of taxa (Orthida and Rhynchonellida, 5 species each; Atrypida and Spiriferida, 4 species each). Representatives of *Biernatella* (67% of the assemblage) and *Teichertina* (2%) exceptionally reach more than 6–7 mm in length whereas adults of *Monelasmina* (8%), *Echinocoelia* (6%), *Komiella* (4%), *Skenidioides* (4%), and *Biernatium* (3%) do not exceed 5 mm in length. All these small-sized forms constitute 94% of the brachiopod fauna from sets XXI–XXII and they presumably lived in a quiet-water environment.

Besides generally small-sized brachiopods characteristic for the offshore, quite-water, high diversity *Biernatella lentiformis* Assemblage there occur also forms strongly suggesting a nearer-shore, rough-water setting. The latter represents a fauna that has probably undergone extensive transport from nearby topographically higher sources, like reef or reef-related structures, and finally deposited in a more quiet-water location. A notable example is the pentameride *Physemella* sp. the shell of which is characterized by medium to large size with heavy deposits of shell material in the umbonal regions. Other reef-related brachiopods include atrypides *Spinatrypa (Exatrypa) explanata* and *Davidsonia enmerkaris*. Besides brachiopods, other redeposited reefal organisms are represented by stromatoporoids, tabulates, dendroid rugosans and receptaculitids.

The rich brachiopod fauna from sets XXI–XXII of Józefka is quite dissimilar to coeval brachiopod faunas from other regions of the Holy Cross. It consists of the ecologically coherent, diversified *Biernatella lentiformis* Assemblage representing intra-basin shoal setting and numerically minor allochthonous dwellers of the shallower reefal habitats.

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The origin of the Middle–Late Devonian brachiopod shell concentration within intrashelf basinal carbonates in the Holy Cross Mountains (central Poland)

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A huge isolated lens of densely packed brachiopod shells has been found in Józefka quarry (southern region of the Holy Cross Mountains, central Poland) within Middle to Late Devonian carbonates deposited in relatively deep environment of intrashelf basin. The unit directly underlying the lens is composed of thin-bedded, strongly bituminous, fine-grained bioclastic wackestones, while the layers above the interval with brachiopod coquina are more diversified, but dominated by medium-bedded wackestones and mudstones. The brachiopod coquina forms a massive, lens-shaped body laterally cut by two faults. The lens exceeds 10 m horizontally while the greatest thickness reaches about 3 m. The lower boundary of the lens is convex downwards and clearly marked although not erosional.

The brachiopod low-diversity assemblage constituting the shell accumulation is strongly dominated by the atrypide *Desquamatia globosa* subsp. nov. and, to a lesser degree, by the rhynchonellide *Coeloterorhynchus dillanus* which constitute, respectively, 72.8% and 22.1% of the fauna. These two species constitute together nearly 95% of the assemblage. Both dominant species possessed very efficient, spirally coiled lophophore (spirolophe) which provided a large surface to capture food particles and to maximize respiration. The efficiency of the lophophore was probably further enhanced by the deflection of the anterior commissure (uniplication) which enabled these brachiopods to separate inhalant and exhalant water currents. The remaining three species: *Schizophoria schnuri prohibita, Phlogoiderhynchus polonicus* and *Hypothyridina* sp. are very infrequent and definitely less important. The brachiopod shells within the lens are mostly not crushed or disarticulated. Thus, it seems that the assemblage inhabited rather deeper water settings on the submarine sea-mount. The associated fauna includes numerous crinoids, and less frequent bryozoans, receptaculitids, sponges and solitary corals. According to conodonts found within the coquina, the stratigraphic position of the shell accumulation is close to the Givetian–Frasnian boundary.

Isotopic composition of shells, matrix and cements unequivocally exclude the coquina as seep induced assemblage. On the other hand, the position of the brachiopod coquina in the succession of deep-marine anoxic facies, their lateral thinning-out, the lens-shaped geometry, high diversification of internal sediment within shells and preferred orientation of shells strongly suggest that the coquina represent an allochthonous accumulation. It appears that the brachiopods mixed with crinoidal debris were redeposited to deep intrashelf basin by low velocity, high-density gravity-induced debris flows. The triggering mechanism of this redeposition was rather an earthquake than storm activity. The great thickness of brachiopod lens is probably caused by a sinkage of bioclastic material in the soft, muddy bottom.

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Micrornamentation and other external features as distinctive criteria for the Coniacian (Upper Cretaceous) terebratulides from Northern Spain

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Fossil brachiopods are poorly known in the Upper Cretaceous of Western Europe. The first detailed study of the Coniacian (Upper Cretaceous) brachiopods from the North Castilian Platform (Northern Spain) is currently being carried out. This work is being performed in several sections, displaying a detailed biostratigraphy and a precise interregional correlation based mainly upon the study of fossil cephalopods and other invertebrates (Barroso-Barcenilla et al., 2011; Berrocal-Casero et al., 2017). The terebratulides of the study area show some common features and they can be easily confused. Most of them exhibit oval to almond shape, ventral and dorsal valves of about equal convexity, oblique lateral commissure, uniplicate to sulciplicate anterior commissure, and permesothyrid foramen. Nevertheless, these forms can be differentiated by their microornamentation and other external features. In this way, three different morphotypes of terebratulides have been recognized in the Coniacian of Northern Spain.

Morphotype 1 (Fig. 1.A1-A6) appears in the lower Coniacian of the study area. The shell of this morphotype shows radial ornamentation that is not capillation, but rather takes the form of narrow and very shallow grooves in the smooth shell surface (graphillate ornament, *sensu* Middlemiss, 1970). The ornamentation of this morphotype is very weak and more defined close to the commissure (Fig. 1.A6). Morphotype 2 (Fig. 1.B-C) is restricted to the middle Coniacian. These terebratulides show a characteristic ornamentation with fine radiating lines (or very fine radial ridges) on the outer surface of shell (capillae). The capillation of the umbo is covered by small regular granules (Fig. 1.B4-B5). These granules are present in the umbo, but pass to continuous lines towards the commissure. In some specimens, the capillation shows zig-zag waviness close to the commissure (Fig. 1.C1-C2). Morphotype 3 (Fig. 1.D1-D7) is middle-upper Coniacian, and shows strong, continuous capillate ornament. The capillation of these terebratulides is much stronger than the capillation of the specimens previously mentioned. The characteristic ornamentation of the shell is especially marked in the umbos, where the capillate ornament is composed of small and continuous granules upon the radial lines (Fig. 1.D4-D5). These granules are present in the umbo, but pass to lines without granules towards the commissure, forming continuous strong capillation (Fig. 1.D7). On both sides of the dorsal valve, two lateral expansions with auricular shape can be well distinguished (Fig. 1.D1, 1.D4). In the articulate area, between two lines, very weak lines with micro-granules can be differentiated (Fig. 1.D6). This type of capillation and the presence of auricles are only present in some levels of the studied sections, where these features are present in all of the terebratulids so far recorded. The presence of auricles supposedly is a diagnostic feature of *Platythyris cristobali* (Middlemiss, 1978). However, the auriculate shell is a feature present in the holotype of *P. cristobali*, but it is not present in the topotypes examined in the Natural History Museum of London (U.K.), which show microornamental features corresponding to Morphotype 2, which appears stratigraphically below in the studied sections.

The study of the internal structures of these three morphotypes throughout serial sections and acetate peels also reveals certain morphological differences with probable systematic value. In order to advance with these preliminary results and to provide a correct systematic classification, numerous Upper Cretaceous terebratulide specimens (some of them original types) are currently being revised in different institutions around Europe, and future work will allow the first detailed classification, distribution, and palaeoecological implications of these brachiopods.

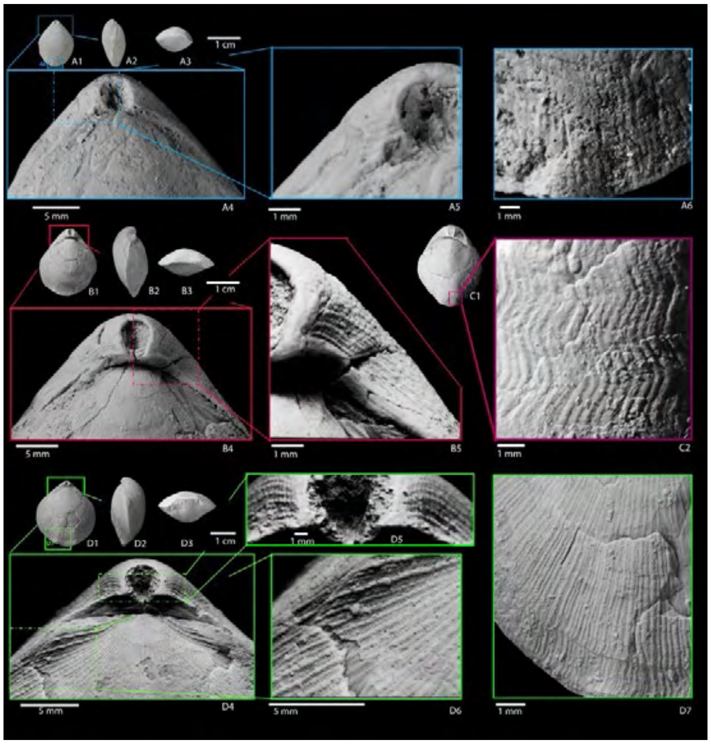

Fig. 1. A. Morphotype 1, from the lower Coniacian of Northern Spain, specimen Tu1923. A1: Dorsal view, A2: Lateral view, A3: Frontal view. A4-A5: Zoom of the umbo without ornamentation. A6: Enlargement of the shell surface showing graphillate ornament close to the commissure. B-C: Morphotype 2, from the middle Coniacian of Northern Spain, specimens Tu4306 and Tu4303. B1: Dorsal view, B2: Lateral view, B3: Frontal view. B4: Detail of the umbo. B5: Detail of the capillation with small granules. C1: Dorsal view. C2: Ornamentation with zig-zag waviness close to the commissure. D: Morphotype 3, from the middle Coniacian of Northern Spain, specimen Tu6202. D1: Dorsal view, D2: Lateral view, D3: Frontal view. D4: Detail of the umbo. Two lateral expansions with auricular shape can be distinguished in the dorsal valve. D5: Detail of the ornamentation with continuous granules upon the radial lines. D6: Ornamentation of the dorsal valve in the auricle area. D7: Ornamentation close to the commissure with strong, continuous capillate ornament, without granules.

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The first Recent record of the genus *Neobouchardia* (Brachiopoda: Bouchardiidae) from the Coral Sea, SW Pacific

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Bouchardiid brachiopods constitute a significant element of the fossil record in the Southern Hemisphere, being known since the Lower Cretaceous. In Recent waters, however, only one representative, *Bouchardia rosea* (Mawe, 1823) living on the outer shelf off Brazil (Logan, 2007), has been recorded. Here the first Recent record of the genus *Neobouchardia* Thomson, 1927 is reported. This genus was erected by Thomson (1927) for *Bouchardia minima* Thomson, 1918 from the Miocene. It is characterized by a high dorsal median septum not connected to the cardinalia and no brachidial lamellae. So far *Neobouchardia* has been reported from the Oligocene to early Pliocene from New Zealand, Chatham Islands and Australia (MacKinnon & Lee, 2006).

The material presented here was collected during the French cruise EBISCO in 2005 to the southern Coral Sea, west of New Caledonia. This part of the Coral Sea is separated from Australia and from New Caledonia by deep-water zones and is characterized by a very endemic molluscan fauna (Bouchet et al., 2008). However, only two brachiopod species can be considered as endemic to the Coral Sea, *Gyrothyris williamsi* Bitner et al., 2008 and a newly discovered species of *Neobouchardia*.

The family Bouchardiidae Allan, 1940 contains 5 genera among which the stratigraphically oldest genus is *Australiarcula* Elliott, 1960 known only from the Lower Cretaceous of South Australia. It can be treated as an ancestral form for *Bouchardiella* Doello-Jurado, 1922 known since the Upper Cretaceous of Australia and South America. In *Bouchardiella* the brachial lamellae are strongly reduced, constituting only two short flanges. Perhaps *Bouchardiella* represents a common ancestor of *Bouchardia* Davidson, 1850, *Malleia* Thomson, 1927 and *Neobouchardia*.

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Recent brachiopods from the Tonga Islands, SW Pacific: taxonomy and biogeography

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Since 1976 the South-West Pacific region has been intensively surveyed within the program Tropical Deep-Sea Benthos (formerly MUSORSTOM) established by the Muséum National d'Histoire Naturelle (Paris, France) and the Institut de Recherche pour le Developpement (Nouméa, New Caledonia). The present report focuses on the Tonga island group, explored during the cruise BORDAU 2 in 2000. Twenty brachiopod species belonging to the genera *Novocrania* Lee & Brunton, *Basiliola* Dall, *Basiliolella* d'Hondt, *Dyscolia* Fischer & Oehlert, *Xenobrochus* Cooper, *Terebratulina* d'Orbigny, *Septicollarina* Zezina, *Frenulina* Dall, *Fallax* Atkins, *Amphithyris* Thomson, *Annuloplatidia* Zezina, *Leptothyrella* Muir-Wood, *Dallina* Beecher, *Campages* Hedley, *Nipponithyris* Yabe & Hatai, *Thecidellina* Thomson, and *Minutella* Hoffmann & Lüter have been identified among the dredged samples. Apart from *Novocrania turbinata* (Poli) and *Frenulina sanguinolenta* (Gmelin) (Logan, 2007, Robinson, 2017), all species represent the first records for Tonga. As may be expected, the fauna shows the greatest affinity to that from the Fiji region (Bitner, 2008, Hoffmann & Lüter, 2010), with 17 species in common. Three of these species, *Leptothyrella fijiensis* Bitner, *Campages ovalis* Bitner and *Nipponithyris lauensis* Bitner seem to be restricted to those two regions. Strong similarity is also observed with the brachiopod fauna around New Caledonia, with 12 species in common. Although there is less similarity between the Tonga and New Zealand regions, two species, *Terebratulina australis* Bitner and *Amphithyris buckmani* Thomson are so far known only from Fiji, Tonga and New Zealand areas.

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Recent brachiopods from the South China Sea, NW Pacific

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Although Recent brachiopods from the West Pacific have been intensively studied, those from the South China Sea are still poorly known. The South China Sea is a marginal sea encompassing the area from Taiwan to Malaysia and Indonesia. Recently two oceanographic expeditions DongSha 2014 and ZhongSha 2015 have been organized to the northern part of the South China Sea by the Muséum National d'Histoire Naturelle, Paris and the National Taiwan University, Taiwan, within the program Tropical Deep-Sea Benthos. Sixteen brachiopod species have been identified in the dredged samples. Among them four species, namely *Acanthobasiliola doederleini* (Davidson), *Terebratulina photina* Dall, *Frenulina sanguinolenta* (Gmelin), and *Campages mariae* (Adams), were previously recorded from the South China Sea (Hatai, 1940, Richardson et al., 1989, Logan, 2007). The remaining species are new records for the South China Sea, however, eight of them, *Novocrania lecointei* (Joubin), *Basiliola pompholyx* Dall, *Gryphus tokionis* Dall, *Zygonaria davidsoni* (Adams), *Terebratulina japonica* (Sowerby), *Eucalathis rugosa* Cooper, *Laqueus* sp., and *Dallina triangularis* Yabe & Hatai are known from the adjacent waters (Logan, 2007, Robinson, 2017). Three species, *Annuloplatidia curiosa* Bitner, *Phaneropora galatheae* Zezina, and *Nipponithyris afra* Cooper, although widely distributed in the Indo-SW Pacific Province (Logan, 2007, Bitner, 2014, Bitner & Logan, 2016), were found for the first time in the Northern Hemisphere, extending significantly their geographical range. The genus *Macandrevia* is widely distributed in modern waters, being known from the North Atlantic, off the west coast of Africa, the Indian Ocean, the Pacific coast of both Americas, and around Antarctica (Logan, 2007, Bitner & Logan, 2016) but this is its first record from the West Pacific.

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Plenary lecture

Modern and fossil brachiopods: superheroes of archives

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Geoscientists depend on rocks, minerals and fossils to record and provide information about their genesis as well as the changes they endured during their travel through geologic time. The fidelity of this information becomes increasingly compromised with the passage of time. Over the decades, we have learned to glean more and more information from archives employing a multitude of sophisticated tools and proxies. Our tools now encompass everything from simple visual inspection to highly technical atomic forcing microscopy, from wet chemical determinations to the characterization of exotic elements and isotopes by the most advanced mass spectrometers and other instruments.

Tracing the low-temperature geology, biology and chemistry of the Earth requires the most intricate information from a multitude of archives and as many proxies as possible. The most obvious archive is whole rock formed in a sedimentary environment, which is supplemented in the Phanerozoic by biogenic archives such as brachiopods, molluscs, conodonts, rugose corals, trilobites and foraminifera, just to name the most important ones. However, several critical questions need to be asked of any archive, among them, 1) what is the geologic range of the archive? 2) Does it occur only in a single or a multitude of environments? 3) What is its life style? 4) Is its test, shell, skeleton suitable for geochemical investigation? 5) Will the archive represent strictly limited local conditions or will it be a recorder of broader regional/global conditions? 6) Has evolutionary change placed limitations/restrictions on the archive's geochemistry? 7) does the archive record geochemical information in equilibrium with ambient oceanographic conditions? And 8) ultimately, was the archival material able to resist alteration in the post-depositional diagenetic and/or metamorphic environment?

The first step in answering all those questions is a detailed investigation of the biologic parameters of the archive, once this is satisfactorily concluded, we may move to the next step of extracting the geologic history from the archive. The extraction process starts with the cleaning of specimens of all extraneous contaminants covering the external as well internal surfaces (Zaky et al., 2015). Morphometric investigation at the micro- and nanostructural levels also demand specialized preparations to optimize features and thus evaluations (Griesshaber et al., 2007; Crippa et al., 2016; Gaspard and Nouet, 2016; Ye et al., 2018), since there is a potential impact of them, by and on the original geochemical signal (Garbelli et al., 2012). Some of the latest technology has produced stunning results about preservation and alteration potentials at the 'most' detailed (micro- to nanostructural) level, such as features within fibres of the secondary and columns of the tertiary layers of brachiopods. This detailed investigation of morphometric features must apply equally to all archives, including whole rock, to assure the fidelity of the proxy-based results. Examination of shell, skeleton or fragment may also involve cathodoluminescence to highlight infilling by diagenetic cement of pores, punctae and fractures as well enhanced alteration of the primary layer as well as the outer inner layer of shells.

Other means of extracting information from archives may depend on trace element analysis, of REEs, of stable isotopes (d^{13}C, d^{18}O), radiogenic (^{87}Sr/^{86}Sr), clumped (Δ47) and exotic isotopes (d^{17}O, d^{24}Mg, d^{44}Ca, d^{11}B) using state-of-the-art instrumentation. Each of these proxy results offer up information about the depositional environment that may be complicated by post-depositional impacts (Brand and Veizer, 1980). Thus, screening for diagenetic alteration is of paramount importance to obtaining a chemical signature with high fidelity of the depositional oceanographic conditions and parameters (such as water temperature, pH, salinity, etc.). Alteration of carbonates can be a complicated issue, everything from a complete change of the original mineralogy, microstructures, and geochemistry to partial alteration limited to the outer surfaces, to partial alteration of inner areas near punctae and/or fractures, or limited alteration to select areas.

Trilobites and rugose corals are rarely used because their geologic range is limited, and in addition, they lack modern representatives critical for a most robust evaluation. Molluscs, foraminifera, conodonts, brachiopods and whole rock are the remaining archives under consideration. Any of these have weaknesses and strengths that need to be critically assessed before considering deep-time reconstructions, with the latter three currently favoured by geoscientists. Whole rock is evaluated with just a few screening tests among them cathodoluminescence and the Mn/Sr ratio (Brand and Veizer, 1980; Kaufman and Knoll, 1994), while being cognizant of their potentially confounding multi-mineralogical content. Molluscs may be infaunal to epifaunal to free-swimming, may be either calcite, aragonite or bimineralic that complicates preservation and evaluation of their original mineralogy and proxies. Conodonts, the exception in this group, are free-swimming organisms with no modern counterparts, and this lack of information is critical to the assessment of their robustness. Brachiopods with their sessile lifestyle consist strictly of calcite with mostly two- or three-layer shells, which makes them quite resistant to diagenetic alteration, and their continued presence since the Cambrian and modern representatives makes them a premier archival candidate.

A survey of the carbon, oxygen and strontium isotope compositions of coeval brachiopods, conodonts and whole rock from the Pennsylvanian Bird Spring Formation of southern Nevada (Brand et al., 2012), suggest the comparison of d^{13}C values in screened brachiopods and whole rock shows that the former retained values that may be considered representative of the ambient seawater DIC.

A vital effect for the most part can be discounted because it would lead to more negative d^{13}C values and not positive ones. The comparison of Mn/Sr values in coeval brachiopods and whole rock follows a distinct pattern highlighting the delicate nuance of alteration in the 'best' of the whole rock material. The strontium isotope content, which is highly susceptible to alteration as well as represents no or little concern with local oceanographic influences, is a most robust screening tool for identifying original, thus primary compositions of the global ocean. The comparison of ^{87}Sr/^{86}Sr between brachiopods and whole rock shows that brachiopods retained ratios that are most compatible with an original composition, similarly the same assumptions hold true in the comparison between the coeval brachiopod and conodont based results. In both instances, the isotope geochemistry of the screened brachiopods reflects more closely the chemistry of their ambient and original seawater than any other archive.

The issue of the clumped isotope proxy is complicated by the fact that multiple calibrations exist in the literature. Aside from extreme susceptibility to diagenetic resetting of the clumped isotope composition, the calibrations tend to diverge and the deep-time reconstruction specialist is cautioned against cherry-picking a calibration that 'gives' satisfactory paleo-temperatures and consequently reasonable seawater-^{18}O values. A review of clumped isotopes of modern tropical and polar brachiopods clearly demonstrates the conundrum with results generated with the different calibrations. The calibrations of Kelson et al. (2017) and Bajnai et al. (2018) provide the most satisfactory temperature results comparable to ambient seawater conditions.

In summary, we conclude that brachiopods with their sessile lifestyle, long geologic history, modern representatives, ease of analysis of many geochemical parameters, clear identification of macro- to micro- and nanostructural morphometric features makes them ideal candidates for an integrated geologic and geochemical screening process that is second to none (Brand et al., 2011; Ullmann and Korte, 2015). They may be subject to no or minor vital effects, except in specialized areas such as the primary layer, etc. (e.g., Carpenter and Lohmann, 1995; Bajnai et al., 2018), and thus well-preserved material should represent the oceanography of modern to deep-time ambient seas or oceans (e.g., Angiolini et al., 2012; Ye et al., 2018). Without reservation, but with proper screening, articulated brachiopods and their shells are the optimal archive that should serve the geoscience community well in unravelling the evolution and history of the Earth's hydrosphere.

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Chromium isotopes in brachiopods as a redox proxy

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The chromium isotope system is increasingly used as a proxy for redox changes in the Earth's ocean and atmosphere. As Cr fractionation is redox-sensitive, the Cr isotope compositions (δ^{53}Cr) of carbonates are thought to capture the changing redox state of their precipitating fluid, making them a potential archive of environmental changes through time. We assess the capacity for modern brachiopods from the Huinay Fjord in Chile to record the δ^{53}Cr composition of their ambient seawater and thus to test their potential as a paleo-redox proxy.

Preliminary results show Cr concentrations between 108 and ^{53}2 ppb, with the dorsal valves containing approximately 100 ppb more Cr than ventral valves. The δ^{53}Cr values range from -0.44 ± 0.14 ‰ (2SD) to -0.08 ± 0.10 ‰.

The δ^{53}Cr compositions of these modern brachiopods are lower than typical δ^{53}Cr values found in other modern biogenic carbonates (usually ≥ 0 ‰). Assuming normal seawater δ^{53}Cr values between 0.5 and 1.5 ‰ (Holmden et al., 2016), this suggests a strong negative fractionation of between 0.6 and 1.9 ‰ between brachiopod samples and precipitating seawater. Alternatively, an exceptionally low δ^{53}Cr value of the seawater in the Huinay Fjord due to unique prevailing chemical conditions could lead to the observed low δ^{53}Cr values of the brachiopods. Cr isotope analyses of the ambient seawater will provide further insight into the use of brachiopods to trace seawater changes.

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Famous Brachiopods, part 1: Brachiopods in lapidary stones

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The use of lapidary rocks for decorative purposes has a very long history: started in pre-history, noticeably increased during ancient Roman times, and thrived again from the Renaissance until today. Of course, a lot of those rocks contain fossils, sometimes brachiopods. Also, it often happened that "marbles" containing fossils were particularly valued because of their aesthetic effects, and sometime because of their rarity also (see Table 1 and 2).

Additionally, some of those were used as base for paintings, becoming part of true artwork. One of these masterpieces is painted on a "astracane veronese giallo" slab: "The Idolatry of King Solomon" (Florentine school, early 17th century, private collection; Di Castro and Kugel, 2017) (see Table 2, M).

A consequence of the interest in lapidary rocks during the 19th century has been the building of numerous rock slab collections, as the well-known "Corsi's collection" hosted at the Oxford University Museum of Natural History (Price et al., 2012).

Looking at the description of those collections, I noticed several errors related to the location of the caves, their geological and paleontological features, and so on. As a consequence, the purpose of this study is to list "marbles" in which brachiopods are reported, and give them the correct geographical, geological, and paleontological description. Preliminary results are shown in Table 1 and illustrated in Table 2.

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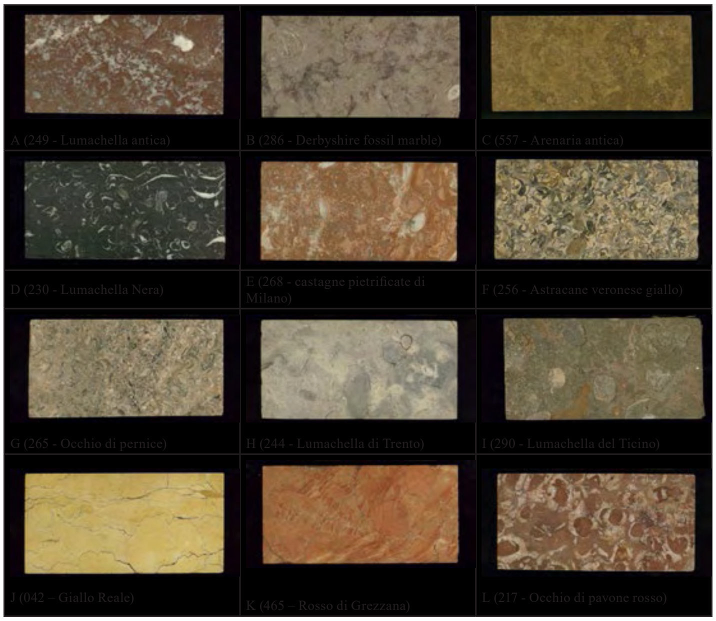
Marble type	Corsi n° 1	**Geology and Geography**		**Brachiopods** presence, typicity, main taxa
Lumachella antica	249 A	? Belgian red marble: Neuville Fm., possibly Petit-Mont mb., Devonian (Frasnian), Belgium		Yes – typical various
Derbyshire fossil marble (Hopton Wood Stone)	286 B	Bee Low Limestones Fm., Carboniferous, Visean pp. (Asbian) Great Britain, Derbyshire, next Middleton		Yes – typical various
Arenaria antica	557,C	? Dont Fm., Anisian, Southern Alps, NE Italy		Yes – typical *Coenothyris*, spiriferinids
Lumachella Nera	230,D	? Calcare di Recoaro Fm. Anisian, Southern Alps, NE Italy		
Marmo castagne pietrificate di Milano	268 E	Broccatello d'Arzo Fm., Sinemurian Switzerland, Canton Ticino (Arzo, Bisaccio)		Yes – typical various
Lumachella di San Vitale (fig.12 in Lazzarini, 2014)		Calcari Grigi di Noriglio group, Rotzo Fm. Pliensbachian p.p. Veneto Prealps, NE Italy	*Lithiotis* facies, with pterioid bivalves in longitudinal section	Yes – Subordinate *Hesperithyris renierii* and *Lychnothyris rotzoana*
Astracane veronese nero (fig.21-23 in Lazzarini, 2014)			*Lithiotis* facies, with mainly *Cochlearites* sp. in transversal section	
Astracane veronese giallo (fig.19-20 in Lazzarini, 2014)	7 sp. F		lumachella facies, with preponderance of bivalves and brachiopods	Yes – Locally typical *Hesperithyris renierii* and *Lychnothyris rotzoana*
Occhio di pernice (fig.15 in Lazzarini, 2014)	265 G			
Lumachella di Trento	244,H		Facies eteropic to the Lithiotis banks	
Lumachella del Ticino	290 I	Calcare di Morbio Fm., Jurassic (Domerian – Toarcian p.p.) Prealpi lombarde, N Italy		Yes – typical
Bronzetto (with many local varieties)	many J	Oolite di S.Vigilio Fm., Jurassic (Toarcian p.p. – Aalenian) Prealpi veronesi, NE Italy		Yes – typical *Soaresirhynchia clesiana*
Rosso ammonitico veronese (many varieties)	many K	Rosso ammonitico veronese Fm., Jurassic (Bajocian, upper - Tithonian) - Prealpi veronesi, NE Italy		Yes – occasional and subordinate Mostly Nucleatidae
Occhio di pavone rosso, Occhio di pavone pavonazzo (*triponticum*, *pneumonusium*)	217 L	Kutluca limestones Fm., Cretaceous (Campanian) Kutluca, near Izmit (ancient Nicomedia), NW Turkey		Very doubtful, (probably Corsi's "*Anomia ampulla*" = rudists molluscs)

Table 1 – Lapidary stones reported in literature containing brachiopods, and relative geological and paleontological description. 1-Corsi n° is relative to slabs in Corsi collection figured in tab. 2 (see also Price et al., 2012).


A (249 - Lumachella antica)
B (286 - Derbyshire fossil marble)
C (557 - Arenaria antica)
D (230 - Lumachella Nera)
E (268 - castagne pietrificate di Milano)
F (256 - Astracane veronese giallo)
G (265 - Occhio di pernice)
H (244 - Lumachella di Trento)
I (290 - Lumachella del Ticino)
J (042 – Giallo Reale)
K (465 – Rosso di Grezzana)
L (217 - Occhio di pavone rosso)


M - "The Idolatry of King Solomon"

Table 2 – A-L see description in Table 1, slabs size approx. 145 x 73 x 40 mm; M: "The Idolatry of King Solomon" (private collection).

Famous Brachiopods, part 2 – Brachiopods on archeological remains

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Here we present the first occurrences of brachiopods on archaeological remains. They refer to some specimens of *Novocrania anomala* (O. F. Müller, 1776) found in Blue Grotto of Capri (Naples, Italy) and in the Roman city of Baiae (Pozzuoli, Naples).

The archaeological remains of Blue Grotto were part of a nymphaeum, a sacred building in honour of the Roman divinities nymphs, generally located next to water springs or, as in our case, inside natural caves on the sea. It was built by ancient Romans probably during reign of the emperor Tiberium (1st sec. AD), and it represented a Tritons parade leaded by the god Neptune/Poseidon arising from the water.

Baiae was a famous seaside town much praised in the Antiquity for its temperate climate, beautiful setting and the properties of its mineral and thermal waters. It was the most popular resort among the Roman aristocracy and the Imperial family up until the end of the fourth century A.D., when a bradyseism caused the submersion of the city. Today the remains of the luxurious villas and other structures of the city lie underwater at a distance of up to 400 - 500 metres from the coast at a depth of 5-7 metres.

The archeological remains investigated for bioerosion comprise six statues (Poseidon, 3 tritons, 1 female statue with peplophoros, 1 fragment) and one column. Encrusting and endolithic organisms were found, beyond grasping traces. The endolithic organisms were represented by Bivalvia and Porifera. Encrusters were more various being represented by Foraminifera, Porifera, Bryozoa, Cnidaria, Anellida and Brachiopoda. More common organisms were endolithic clionaid sponges (7 artefacts) and encrusting serpulid worms (5). The brachiopod *N. anomala* was found only on 2 artefacts: the Poseidon statue (in association with other 8 taxa) and one of the Triton statues (with other 5 taxa) (more details in tab. 1 and 2; see also Davidde and Ricci 2015, Ricci et al., 2013, 2014). The occurrence of *N. anomala* is congruent with the known habitat of this species (and of most of the actual brachiopod species) in shallow sea, i.e. in cryptic environments.

Under an ecological point of view, more significant is the occurrence of several specimens of *N. anomala* on a basal column fragment found in the underwater archeological site of Baiae. At least in a very shallow water of the Mediterranean Sea, *N. anomala* occurrences are in fact condensed in cryptic environments.

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Species (or other taxa)	Phylum	Class	Order	Archeological remains	Poseidon statue	Triton statue	Triton (bearded) statue	Triton (young) statue	Peplophoros statue	Head fragment statue	Column fragment	tot.
				life style								
Serpulidae undet.	Anellida	Polychaeta	Sabellida	encruster	1		1	1	1	1		5
Novocrania anomala	Brachiopoda	Craniata	Craniida	encruster	1	1						2
Bryozoa spp.	Bryozoa			encruster	1		1		1	1		4
Reteporella grimaldii	Bryozoa	Gymnolaemata	Cheilostomatida	encruster				1				1
Anthozoa undet.	Cnidaria	Anthozoa		encruster	1			1				2
Miniacina miniacea	Foraminifera	Polythalamea	Rotaliida	encruster	1			1	1	1		4
Lithophaga lithophaga	Mollusca	Bivalvia	Mytiloida	endolithic		1	1	1		1		4
Chama sp.	Mollusca	Bivalvia	Veneroida	encruster		1		1				2
*Coralliophaga lithophagell*a	Mollusca	Bivalvia	Veneroida	endolithic	1	1			1			3
Petricola lithophaga	Mollusca	Bivalvia	Veneroida	endolithic			1					1
Clionidae undet.	Porifera	Demospongiae	Hadromerida	endolithic	1	1	1	1	1	1	1	7
Petrobiona massiliana	Porifera	Calcarea	Lithonida	encruster	1		1	1				3

Table 1 – List of bioeroding organism on the examined archeological relics from Grotta Azzurra (Capri, Napoli, southern Italy).

Ricci S., Davidde Petriaggi B., Sacco Perasso C. 2014. Marine bioerosion of lapideous archaeological artifacts found in the Grotta Azzurra - Capri island and in the Underwater Archaeological Park of Baiae (Naples, Italy): role of microflorabiota, boring Porifera and Bivalvia. In Eds. Dávid A. and Fodor R., Abstract Book and Exhibition Guide of the 8th International Bioerosion Workshop.

Table 2 - A: Sites location. Europe, Campania region in Italy, Gulf of Naples. Satellite map by NASA; B: Statues found in Grotta Azzurra, (Capri, Naples, Italy); B.1: the statues hosted in the Casa Rossa museum (Capri), with Poseidon in front, and three tritons behind; B.2: Poseidon statue in lateral view (photo by Marco Amitrano).

Famous Brachiopods, part 3 – Brachiopods in philately

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Following the report about brachiopod on stamps of the last International Brachiopod Congress in Nanjing (China) 2015 (Buono, 2015a, b), here I update that study.

In spite of a relatively good number of issues relating fossils and prehistoric animals on stamps in the last three years (see Kogan 2018), not one of those has involved brachiopods, with the exception of an issue from Spain.

During 2015, the postal bureau in Spain released an interesting issue entitled "Dinosaurs" during the 47º Expo National stamp fair in Madrid. Moreover, the main theme of the fair was linked to these prehistoric animals, with the intention of attracting children and young people in addition to those interested in philately.

This stamp set contained four stamps, each one printed with a different technique: scales texture, augmented reality, phosphorescence, 3D and special glasses. In spite of these interesting printing novelties, reactions among collectors have been quite critical because of bad reconstructions, childish graphics, and several incongruences (as example, figured dinosaurs that have not been found in Spain). The stamp set illustrates four dinosaurs, one for each stamp: *Ankylosaurus*, *Triceratops*, *Tyrannosaurus*, and *Diplodocus*, each with a value of 2 euros. For each of them, a "First Day Cover" has also been issued and two different "commemorative postmarks." In addition, for the *Tyrannosaurus* stamp, a "Postcard" and a "Mini-sheet" have also been issued (see Kogan, 2017a).

This last one is a "Mini-sheet" composed of 12 stamps with *Tyrannosaurus*, framed with a label figuring a slab with some common fossils: an ornithomimid dinosaur skull, the pachypleurosaur marine reptile *Keichousaurus hui* (typical of the Chinese Triassic), an ammonite, and a brachiopod on the top right corner. Unfortunately, it is not reported which kind of brachiopod it is, however, in spite of a very low-resolution picture, it can be referred to as a spiriferid (Table 1). The text comes from the "Discours sur les révolutions de la surface du globe et sur les changements qu'elles ont produits dans le règne animal" of the famous French naturalist and zoologist Georges Cuvier (1825).

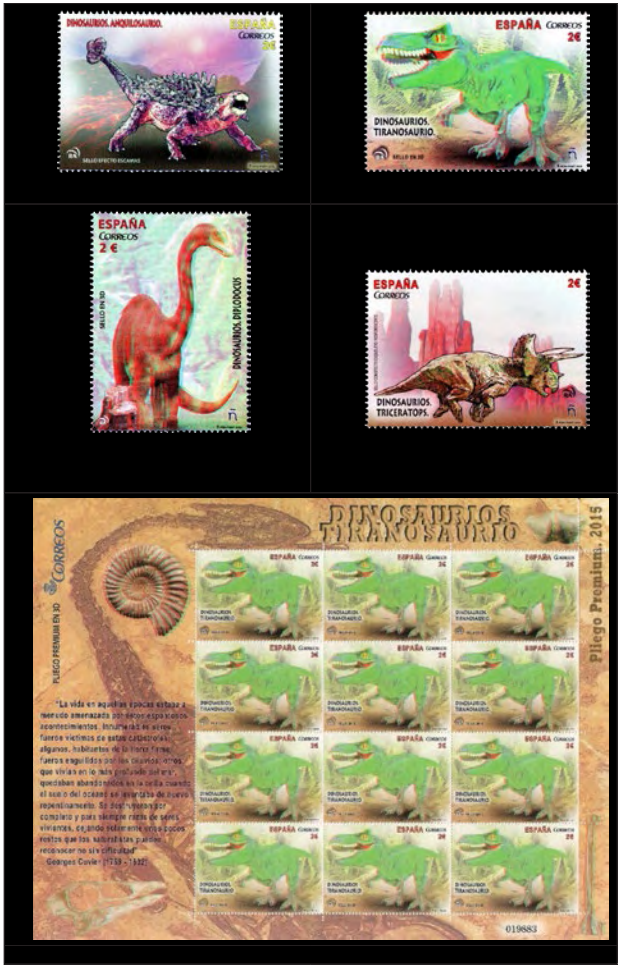

Table 1 – "Dinosaurs" issued by the postal bureau in Spain in 2015. A-D: stamps. A) *Ankylosaurus*; B) *Tyrannosaurus*; C) *Diplodocus*; D) *Triceratops*. Stamp size: 57.6 x 40.9 mm; E) "Minisheet", note the spiriferid brachiopod in the upper right corner.

In addition, during 2016, Spain has also released the second issue of the series about dinosaurs (Kogan, 2017b).

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Kogan M., 2017b. www.paleophilatelie.eu/description/stamps/spain_2016.html.

Kogan M., 2018. www.paleophilatelie.eu/index.html.

Brachiopods in Italy: a very long record and a new database

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Italy has an extraordinary brachiopod record lasting from the Cambrian until today (see table 1; Buono, 2018a). This is due primarily to the complex geological history of the "Italian Area" which, as consequence of tectonic plate interactions, for example the Alpine and Apennine orogenesis, resulted in: a) the partitioning (with habitat differentiation), and stacking of strata in the mountain chains, which favoured the exhumation and fragmentation of the original carbonate platforms; b) the amalgamation of different palaeogeographic units: Italy is the union of the main Adria block (itself previously part of Africa), with pieces of Europe (Sardinia, Calabro-Peloritan area) and Africa (most of Sicily) (e.g. Gaetani, 2010). This has favoured faunal differentiations with the development of: a) endemism, b) transitional faunas between different palaeobiogeographical units, c) colonization of different palaeoenvironments, sometimes with unusual adaptations (e.g. conical shapes in the Permian of Palazzo Adriano, Sicily).

Italian brachiopod faunas are recorded from the Cambrian of Sardinia (lingulids and acrotretids), and younger faunas have been recognized in the Palaeozoic in spite of very few outcrops (Sardinia, Carnic Alps, Tuscan Apennines and Sicily). During Mesozoic, following the first Triassic faunas with NW European affinities (*Coenothyris*, diplospirellid athyridids) (Southern Alps, Southern Apennines, Sardinia), the fragmentation of the Liassic carbonate platforms enabled high degrees of differentiation in palaeoenvironments, and consequently in faunas too, see for example the development of basinal, seamount and slope "smooth brachiopods" faunas (cf. Vörös, 2005). Meanwhile the Sardinian and "Calabrian" faunas continued to have a NW European affinity based on their palaeogeographic position. The Cretaceous is instead characterized by scattered occurrences of basiliolids and dimerellids (*Orbirhynchia*, *Erymnaria, Costerimnaria, Peregrinella*), which continued also during the Cenozoic (*Aphelesia*, *Cryptopora*). Cenozoic faunas were also characterized by both large brachiopods (terebratulids and the same *Aphelesia*) indicting optimum habitats, and micromorphic faunas (e.g. Nebelsick et al., 2011). The latter live today in the Mediterranean, even if mostly confined to cryptical environments (e.g. Logan et al., 2004).

In addition, there are faunas in peculiar ecological niches such as those linked to hydrothermal environments (Dimerellidae), or to mass extinctions (Toarcian *Soaresirhynchia*) and/or to OAEs events (Cretaceous faunas) (see Graziano and Ruggiero Taddei, 2008); these are often also characterized by micromorphism (P/T boundary Carnic Alps faunas, Liassic *Nannirhynchia* and/or koninckinid faunas, "Danian fauna" of Sardinia (e.g. Baeza-Carratalá et al., 2017)). Noticeably such an abundance of associations has also increased the occurrence of good pristine shell preservation in some, suitable for geochemical analyses (e.g. Price et al., 2013).

Since the first articles regarding Italian brachiopods were written by Soldani and Brocchi between 18th and 19th centuries, most have been described in following 100 years (*i.e.* before 1920), often by researchers considered the fathers of the Italian geology and palaeontology: Canavari, Capellini, Dal Piaz, De Gregorio, Di Stefano, Fucini, Gemmellaro, Gortani, Greco, Meneghini, Parona, Seguenza, Stoppani and Vinassa De Regny. More recently additional articles with new faunas and revisions have been mostly published by Benigni, Dieni, Gaetani, Posenato, Ruggiero Taddei, Vörös and their collaborators.

However, between the 482 articles related to Italian brachiopod faunas listed in the Doescher bibliographic database, 50% were published before 1920, 70% before 1950, 84% before 1974, only 16,4% between 1974 and 1994, and the trend has decreased in the last 15 years (Buono, 2018b). This, of course, is a consequence of the progressive depletion of new assemblages to study, but probably it is also due to a progressive lack of interest in the study of palaeontology, and also of brachiopods, in Italy.

In any case, as an outcome of the lack of new articles regarding brachiopods in Italy, there are consequences: a) lack of systematic updates, so that we still today read in museums, or even worse in articles, specimens classified as *Anomia*, *Leptaena*, *Rhynchonella* or *Terebratula*; b) sparse citations, often even without references, in the description of the new official sheets of the Italian Geological cartography units (from the palaeontological point of view definitely worse than the equivalent sheets of decades before); c) faunas are not updated, or completely forgotten, in the more recent articles about the brachiopods palaeogeography. In trying to reverse this trend I'm working on the construction of an "Italian brachiopod database". Ideally it will include all the available information about systematic palaeontology (eventually updated), geography, palaeogeography, palaeobiogeography, lithology, palaeoecology and a bibliography, for all Italian brachiopod occurrences.

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#	**Brachiopods associations**	**Geography**	**Chronostratigraphy**
1	Lingulid and Acrotretid fauna	Sardinia	Cambrian (Early-Middle p.p.)
2	*Svobodaina* fauna	Sardinia, Carnic Alps	Ordovician – Katian
3	*Nicolella* community	Sardinia	Ordovician – Katian
4	*Foliomena* fauna	Sardinia	Ordovician – Katian
5	*Hirnantia* fauna	Sardinia, Carnic Alps	Ordovician – Hirnantian
6	“*Megaera*” fauna	Carnic Alps	Silurian – upp.Ludlow-Pridoli
7	“*Karpinskia*” fauna	Carnic Alps	Devonian (Lower p.p.)
8	“*Pentamerus*” fauna	Carnic Alps	Devonian – Eifelian
9	“*Stringocephalus*” fauna	Carnic Alps	Devonian – Givetian
10	Brachiopods limestones (various horizons)	Carnic Alps	Devonian – Frasnian-Famennian
11	Metamorphosed faunas (various horizons)	Tuscany	Carbonif. upp. – Permian, early
12	“*Martinia*” faunas (various horizons)	Carnic Alps	Permian, early
13	*Permophricodothyris* spp. + conical brachiopods	Sicily	Permian – Wordian
14	Lingulids, *Comelicania*	Carnic Alps	P/T Boundary
15	NW European faunas (*Coenothyris*, spiriferinids)	S. Alps, Basilicata, Sardinia	Trias. – Anisian-Carnian
16	NW European faunas (various horizons)	Sardinia	Juras. – Sinemurian-Bathonian
17	Dimerellidae faunas (*Rhvnchonellina, Sulcirostra*)	Abruzzo, Sicily	Juras. – Sinemurian
18	“Calabrian” fauna	Calabria, Sicily	Juras. – Sinemur.-Pliensbach.
19	“Strati a *Terebratula aspasia*”	S. Alps, C. Apennines, Sicily	Juras. – Pliensbachian
20	Spiriferid Fauna (*Cingolospiriferina*, *Tauromenia*)	Marche	Juras. – Pliensbachian
21	Koninckinids & *Nannirhynchia* fauna	C. Apennines, Sicily	Juras. – Toarcian (early)
22	Jurassic Basiliolid fauna (*Soaresirhynchia*)	Abruzzo, Lazio, Campania	Juras. – Toarcian (early)
23	Jurassic Basiliolid associations (*Stolmorhynchia*)	Veneto, Sardinia	Juras. – Toarcian p.p. - Aalenian
24	Nucleatidae faunas (various horizons)	S. Alps, C. Apennines, Sicily	Juras., middle – Cret., lower
25	*Peregrinella* fauna	Apulia	Cret. – Valanginian (early)
26	Cretaceous Basiliolid fauna 1 (*Orbirhynchia*)	Apulia	Cret. – Early Aptian p.p.
27	Cretaceous Basiliolid fauna 2 (*Orbirhynchia*)	Sardinia	Cret. – Albian (uppermost)
28	Erymnaridae fauna A (*Costerymnaria italica*)	Molise	Cret. – Cenomanian (earliest)
29	Erymnaridae fauna B (*Costerymnaria apula*)	Apulia	Cret. – Campanian (uppermost)
30	Danian microfauna (*Meonia semiglobularis*)	Sardinia	Cret. – Maastrichtian
31	Microfauna, Large Terebratulids, Basiliolidae	NE Italy	Paleogene
32	Microfauna, Large Terebratulids, Basiliolidae	All Italy, Sicily, Sardinia	Neogene
33	Microfauna	Campania, Sicily, Med. Sea	Recent

Tab.1 – Selected significant brachiopod associations found in Italy, illustrating the long record since Cambrian to nowadays. A more complete version of the table with bibliography, and eventual updating, is available on: www.researchgate.net/project/Brachiopods-of-Italy (Buono, G. 2018a).

Keynote lecture

Phylogenomic analysis of Brachiopoda: revealing the evolutionary history of biomineralization with an integrated palaeontological and molecular approach

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Within Lophotrochozoa, brachiopods and allied clades are among the first biomineralized Cambrian metazoans to appear and represent a major component of the oldest known fossil record of animals. While the brachiopod fossil record is ultimately the key to determining character homology and polarity during the evolution of the brachiopod body plan, reading this record has been clouded by disagreement about relationships among the crown clades. Specifically, the monophyly of brachiopods with respect to phoronids, and the relationships of the calcitic to phosphatic-shelled brachiopods. Much of this phylogenetic uncertainty stems from difficulties in rooting the brachiopods and their sister groups within Lophotrochozoa. Phylogenomics—the analysis of hundreds to thousands of orthologous genes in concatenated supermatrices—has been instrumental in resolving difficult phylogenetic relationships in diverse metazoan clades. We have conducted the first such extensive phylogenomic investigation of Brachiopoda/Phoronida with analyses that combine novel sequence data with all publicly available brachiopod and phoronid transcriptomes and a broad range of protostome outgroups. Analyses were run under best fitting evolutionary models utilizing a published 106-gene lophotrochozoan ortholog set. Preliminary results strongly (99% bootstrap) support a monophyletic Brachiopoda with Phoronida as sister group within Lophotrochozoa. Weak bootstrap support (~50%) is found for Inarticulata.

Continued original morphological and systematic investigations remain critical in the molecular era. In tandem with the new molecular efforts we are also developing a comprehensive collaborative morphological database through the MorphoBank platform for living and fossil brachiopods. In addition, we are also generating a set of best-practice molecular clock calibration points. This encompasses *a priori* evaluation of relevant paleontological, phylogenetic, stratigraphic, and geochronological data, all of which are critical to establishing effective and well supported time calibration points.

This combined dataset will allow us to test, under a Bayesian analytical framework, the hypothesis that the Cambrian explosion was a synchronous period of rapid molecular evolution, in addition to the rapid appearance of high-level morphological disparity (Erwin et al., 2011). Testing the relationship between molecular and morphological evolution in the Cambrian has important implications for arbitrating between potential driving mechanisms including ecological opportunism, body size evolution, and changes to gene regulation (Lee et al., 2013) and for understanding how evolutionary rates vary across geologic and clade history (e.g. (Hopkins and Smith, 2015). Combining fossil and molecular data in this integrated framework provides novel insights into brachiopod biomineralization and evolutionary patterns during the Cambrian radiation.

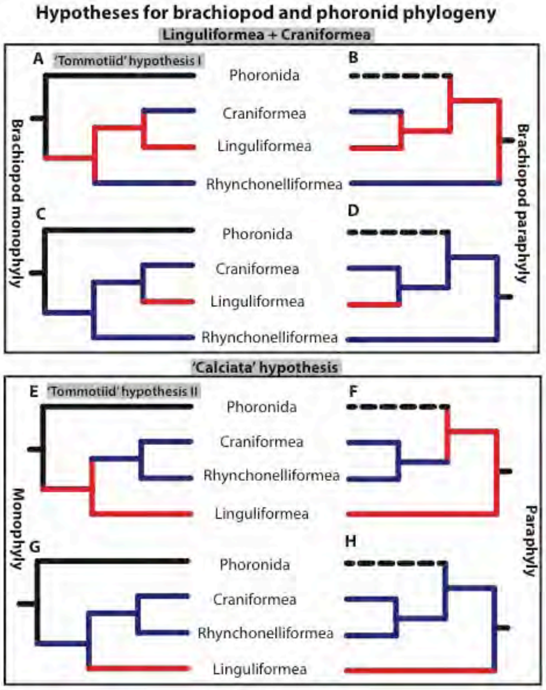

Fig. 1: Implications for the evolution of brachiopods. Brachiopods may be monophyletic (A,C,E,G) or paraphyletic (B,D,F,H) with respect to phoronids. Shifting the root position implies different evolutionary gain/loss events (e.g. secondary loss of shell in phoronids). Within brachiopods, the Craniiformea may be more closely related to Linguliformea or Rhynchonelliformea. Colors depict evolution of biomineralization assuming a single origin of mineral secretion. Blue = calcitic, Red = phosphatic, Dashed line = secondary loss. The 'tommotiid ancestry' hypothesis would correspond to A and E, with a phosphatic ancestral state for brachiopods.

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Early Ordovician (late Tremadocian – early Floian) brachiopods from the Fezouata Shale, Anti-Atlas, SE Morocco

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The Fezouata Biota, located 20 km north of Zagora, in the Anti-Atlas of Morocco, was discovered less than 20 years ago, although shelly fossils were known and have been collected from the area since the 1950s. Within a few years of collecting, an incredibly diverse and exceptionally preserved fauna of soft-bodied specimens has been assembled and described. Until now it is unfortunate that little attention has been devoted to the brachiopod fauna by contrast to Cambrian-like taxa or those exhibiting soft-tissue preservation.

The brachiopod fauna as a whole shows high γ-diversity, whereas at a local scale, α-diversity is somewhat low, which may be interpreted as a rapid turn-over of short-lived populations of opportunistic taxa. The taxonomic composition and taphonomy of the fauna indicate a relatively shallow-water environmental setting, nevertheless above the storm-wave base.

The studied specimens were collected from horizons, in the lower part of the Fezouata Shale, ranging from the *Araneograptus murrayi* to the lower *Hunnegraptus copiosus* biozones (upper Tremadocian), and in the upper part of the Fezouata Shale, mainly from the ?*Baltograptus jacksoni* Biozone (lower Floian).

Overall the fauna is dominated by orthide and lingulide taxa, and the Tremadocian horizons have yielded a more diverse and abundant fauna than the Floian horizons. The fauna represents a mix of Cambrian-early Ordovician taxa originating, on the one hand, on the western margins of Gondwana (Bohemia, Morocco, Avalonia), with about half of the taxa restricted to western Gondwana. On the other hand, the remaining fauna is represented by cosmopolitan taxa originating in the tropics of the southern hemisphere (Laurentia in the middle-late Cambrian and Baltica in the early Ordovician).

In addition, the lower part of the Fezouata Shale has yielded a number of taxa that are the oldest on record, bridging the gap between the Cambrian and Ordovician radiation events.

Extant Terebratellidina phylogeny and homology of the long loop

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Terebratellidina is the most diverse clade of extant brachiopods (Lee et al., 2006; Carlson, 2016), yet we have not determined two important, interrelated aspects of terebratellidine evolutionary history: the time of origin of either the crown or total clade (Devonian or Triassic), and the purported homology of the "long loop" among species in which it occurs. Early discussion and debate about these two issues (Beecher, 1897; Elliott, 1953; Stehli, 1956; Williams, 1956; Cooper, 1957; Williams & Wright, 1961) resulted in an apparent consensus view that long loops present in Paleozoic and later terebratulides are homologous and can be interpreted as having originated from Devonian mutationellids, from which cryptonellids and then Triassic zeilleriids evolved (Stehli, 1965). Later evaluation of terebratellidine evolution and loop ontogeny (MacKinnon et al., 2006; MacKinnon & Lee, 2006), placed the origin of the extant long loops in the Triassic, with the superfamilies Zeillerioidea, Kingenoidea, and Laqueoidea all originating in an undetermined pattern from Permian-Triassic angustothyridids. This interpretation renders the early Paleozoic long loops as analogues, rather than homologues, to extant long loops, and is in conflict with molecular clock analyses (Sperling et al., 2011) that place the divergence of *Terebratalia* and *Terebratulina* in the Devonian. In addition, heterochrony (both paedomorphosis and peramorphosis) has been raised as a potential mechanism driving the evolution of the loop in all Terebratulida (Stehli, 1956, 1965; Boucot, & Wilson, 1994), but this hypothesis has never been tested. Given the functional significance of the long mineralized loop in supporting and positioning the lophophore in the mantle cavity, it will be informative to determine if the long loop evolved once or twice within this clade, through which morphological transformations, and by what combination of evolutionary mechanisms.

We are investigating the morphological phylogenetic relationships among extant terebratellidine genera, using both parsimony and Bayesian methods of analysis. We are analyzing these taxa in three temporal groups: including only those genera named (initially) prior to 1900 (15); adding those named prior to 1965 (+17); adding those named prior to 2018 (+23). This stepped process reveals something of the history of thought about homology and phylogeny as new fossils are discovered and reinterpreted over the past century. With this final, most complete morphological matrix, we are completing two additional combined analyses: adding data from 18S and 28S rDNA (Bitner & Cohen, 2015); and adding recently acquired transcriptomic sequence data from a much larger suite of orthologous genes, as they are expressed in selected terebratellidine species. These "total evidence" analyses will allow us to produce ancestral state reconstructions of characters of the loop, and begin to test hypotheses of heterochrony in loop evolution. Utilizing a broad suite of both morphological and molecular sequence data combined, we will obtain a more thoroughly documented pattern of phylogenetic relationships among these extant terebratellidines, as well as a more complete understanding of loop homology among all Terebratulida. In the process, the timing of origin of the crown clade will be better constrained, using a combination of dated fossils and estimates of evolutionary rate from genomic data. With this study as a foundation for comparison, extinct taxa can then be added to the combined analysis to further broaden our understanding of the phylogeny of the most diverse clade of extant articulated brachiopods.

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The linguliform and craniiform brachiopods from the latest Ordovician *Hirnantia* fauna of South China and Myanmar

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The cool/cold-water *Hirnantia* brachiopod fauna lived in a short period between the double-pulsed end Ordovician extinctions. Investigation of this fauna was systematically carried out for more than half a century since Temple (1965). Works on this fauna of South China and Myanmar were mostly on the rhynchonelliforms (e.g. Rong, 1984; Cocks and Fortey, 2002). But the linguliforms and craniiforms with their low diversity and rarity of fossils were briefly recorded and were usually left in an open taxonomic nomenclature. This study contains more than 1000 specimens of the linguliforms and craniiforms represented by craniides and craniopsides from Kuanyinchiao beds (lower-middle Hirnantian) of Changning and Gongxian, southern Sichuan, Xiushan, southeastern Chongqing, Renhuai and Meitan, northern Guizhou, and Yichang, western Hubei (South China Palaeoplate) and the Hwe Mawng Purple Shale Member (middle Hirnantian), Mandalay Division, Myanmar (Sibumasu Palaeoplate).

Based on new materials from South China and Myanmar, seven genera of the linguliforms and craniiforms are recognized. They include *Pseudolingula*, *Trematis*, and *Orbiculoidea* of the lingulides, *Pseudopholidops* and *Paracraniops* of the craniopsides, and *Petrocrania* and *?Philhedra* of the craniides. They are minor but distinctive components of the *Hirnantia* fauna.

Among the taxa, *Pseudopholidops partibilis* (Rong) accounts for more than half of the total number of the specimens collected from the two main regions. Both ventral and dorsal molds show clear concentric laminae and exquisite muscle scars (Figure 1A–E). *Pseudopholidops* has a mixoperipheral growth, different from *Paracraniops* with a holoperipheral growth. The latter has been rarely known from the Kuanyinchiao beds of South China.

The second most common and distinctive taxon is *Philhedra ?haimei* (Reed) in the *Hirnantia* fauna of South China and Myanmar, containing a little more than 300 individuals. It was originally recorded as a coral *Palaeocyclus* from the basal Panghsa-pye Formation (=Hwe Mawng Purple Shale Member) in Northern Shan State, Myanmar (Reed, 1915) and then assigned to *?Orthisocrania* (Cocks and Fortey, 2002). Based on new materials, the present authors verify the craniide brachiopod nature of *P. ?haimei*. Population analysis indicates that it is characterized by a tremendously variable ornamentation of fine ribs and/or tubular, hollow spines, different from *Philhedra*, *Orthisocrania* and *Acanthocrania*. The number of ribs and/or spines is also highly considerably variable, from less than 20 up to more than 230 (Figure 1 F–I).

In addition to *P. ?haimei*, the following species, *Philhedra ?stawyenesis* (Temple, 1965, p. 382, pl. 2, figs 3–7, the *Dalmanitina*

Beds, Holy Cross Mountain, southern Poland, and the Ashgill Shales at Hol Beck, Westmorland, England), *Acanthocrania* sp. nov. morph A (Temple, 1968, p. 18, pl. 2, figs 11, 12, 15–18, the Hirnantian limestone and shales just above the Keisley Limestone Formation of Keisley, Cumbria, England), and *Philhedra* sp. (Havlíček, 1994, p. 64, pl. 2, fig 9, the Kosov Formation, Czech Republic) are similar to *P. ?haimei* revised herein, if not conspecific. It is presumed that they may represent an opportunistic, especially plastic stock in the craniides that generated considerable phenotypic pleiotropy (exemplified by a highly variable ornament) within sympatric or allopatric populations to confront with a severe ecological stress and to survive the end Ordovician crisis. However, they are provisionally assigned to ?*Philhedra* in this abstract and future investigation is necessary.

Additionally, *Petrocrania* occurs rarely in many localities of South China and Myanmar. The linguliforms *Pseudolingula, Trematis* and *Orbiculoidea* rarely occur in Guizhou and Sichuan, South China, and Mandalay Division, Myanmar.

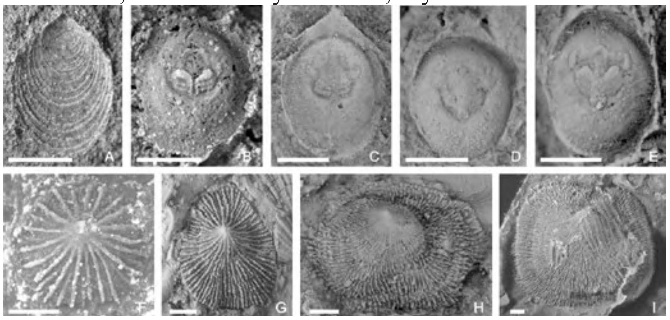

Figure 1. A–E. *Pseudopholidops partibilis* (Rong, 1979), A, external mold (SGT0004); B, C, two ventral internal molds (SGT0051, MD0040); D, E, two dorsal internal molds (MD0029, SGH0030). F–I. *Philhedra ?haimei* (Reed, 1915), latex casts of four dorsal external molds (MD0005, SCS3006, SCS3004, HYC0002). Localities: 1) Chaqi, Yichang of western Hubei Province (HYC); 2) Shuanghe, Changning (SCS), Huangtian, Gongxian (SGH) and Tianbatou, Gongxian (SGT) of southern Sichuan Province; 3) Mandalay Division, Myanmar (MD). Scale bars represent 1mm.

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First report on Guanshan Biota (Cambrian Stage 4) at the stratotype area of Wulongqing Formation in Malong County, eastern Yunnan

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Exceptionally preserved fossils, such as those from Cambrian Burgess Shale-Type fossil-Lagerstätten are critical because of their unique contributions to knowledge of the phylogenetic radiation and palaeoecological expansion of metazoans during the Cambrian explosion (Zhao et al., 2005; Luo et al., 2008; Erwin and Valentine, 2013; Shu et al., 2014; Lan et al., 2018). Critically, these deposits provide information that is usually unobtainable from shelly and skeletonized fossils alone. The Guanshan Biota (Cambrian Series 2, Stage 4) in the Yunnan Province of South China has produced abundant and diverse, exquisitely preserved fossils that often retain soft tissues and organs. To date, most fossils from the Guanshan Biota have been collected from localities such as Gaoloufang and Gangtoucun, close to or surrounding Kunming (Liu et al., 2012; Hu et al., 2013). Regrettably, these classic sections have been destroyed by urban landscaping and are now covered by new roads and residential buildings, making further collection impossible. Here we present the first report of soft-bodied fossils from a new section at Luoshuidong, close to the village of Wulongqing in Malong County, approximately 3 km east of the Wulongqing Formation stratotype section. Fossils recovered retain soft morphology, and include brachiopods with delicate marginal setae (Fig. 1), priapulids with well-preserved sclerites and vetulicolians. In addition, this fauna includes rare occurrences of brachiopods encrusted by tubeworms, as well as trilobites and hyoliths preserved with soft tissues. This discovery represents an important palaeogeographical extension of soft-bodied fossils of the Guanshan fauna to the east of the Xiaojiang Fault (related to Tsinning tectonic movements ca. 700Ma). The fauna from the new Luoshuidong section is similar to that reported from the Wulongqing Formation west of the Xiaojiang Fault, and thus has significant implications for Early Cambrian palaeogeography and palaeoenvironments of eastern Yunnan.

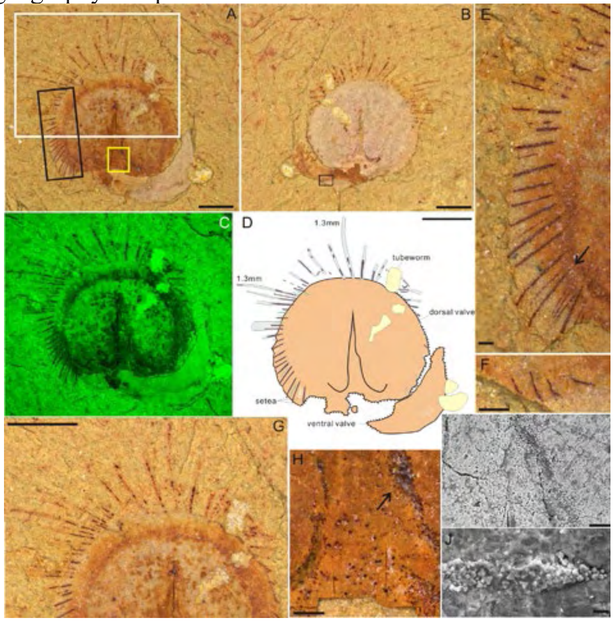

Fig. 1. *Neobolus* sp. collected from the lower part of the Wulongqing Formation at Luoshuidong section, Malong (ELI-LSD-B-189AB). A and B, part and counterpart of *Neobolus* sp. with setal fringes. C, fluorescence imaging showing the different composition between shells, setal fringes and sediments in A (dark colour indicates higher Fe content). D, interpretative drawings of A, showing the ventral and dorsal valves with setae, and tubeworms encrusting the shell. E, enlargement of setae in A (black box). F, enlargement of setae from ventral valve in B (black box) showing the setae on the ventral valve. G, enlargement of setae in A (white box), showing frontal setae replaced as reddish-brown stains. H, enlargement of yellow box in A, showing reddish spherulites. I, SEM image showing the euhedral pyrite crystals from H (black arrow). J, SEM image showing euhedral pyrite crystals on setae in E (black arrow). Scale bars: A, B, D, G, 1 mm; E, F, H, 100 um; I, 50um; J, 10 um.

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Size evolution of brachiopods from the Late Permian through the Middle Triassic in South China

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Body size is a key character that affects most aspects of an organism on its biology, behavior and ecology, and is also affected by its living environment. Based on the analysis of size data for 3310 brachiopod specimens from South China, this study investigates the size evolution of brachiopods spanning the Late Permian through the Early to Middle Triassic. The results show that the maximum and median size among species decreased dramatically from the latest Permian (Changhsingian) to the earliest Triassic (Griesbachian), and then increased during Olenekian and Anisian time. Our data support the Lilliput effect on brachiopods in the Permian-Triassic mass extinction and its immediate aftermath. Size plots at species, genus and family levels suggest that the earliest Triassic size reduction resulted from two factors, one is preferential extinction of large brachiopod taxa (size-selective extinction); the other is size reduction in the survivors. The essential cause of the earliest Triassic size reduction might to be the environmental pressures such as warming, anoxia, and hypercapnia. Size reduction did not last through the entire Early Triassic: small size distributions in the earliest Triassic (Griesbachian) are followed by size recovery in the Dienerian and succeeding intervals. Persistent increase of brachiopod's size in the Olenekian and Anisian are likely the result of the extinction of small survivors, the appearance of large sized species and the Cope's rule that the new lineages tended to increase in body size in the early evolutionary time.

Geometric morphometric analysis reveals the ontogeny of Early Cambrian (Series 2) brachiopods *Eohadrotreta zhenbaensis* from Zigui, Hubei Province, South China

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The ontogenetic series of several brachiopods has been documented in detail in the last two decades (e.g., Popov et al., 2007, 2012; Zhang et al., 2017, 2018a, b), however it has been rarely revealed statistically. Here, we use geometric morphometric methods for the first time in the study of the ontogeny of the Early Cambrian acrotretoid *Eohadrotreta zhenbaensis*. In total, 158 well preserved specimens were randomly picked for SEM photos and subsequently digitized using the software TpsDig2 v. 2.16 (Rohlf, 2010a). Thirty-eight landmarks including 35 semi-landmarks were defined for the outline of the ventral valve and the pedicle opening. A principal component (PC) analysis using TpsRelw v. 1.49 (Rohlf 2010b) resulted in 72 components with PC1, PC2 and PC3 explaining 76.06%, 14.03% and 2.75% of the total shape variation, respectively. Thin-plate splines suggest that PC1 is mainly related to the distance between the poster margin of the valve and the pedicle opening, while PC2 is mainly related to the size of the pedicle opening relative to the size of the valve (Figure 1). A regression of shape on length indicates a strong relationship between size and morphology of *E. zhenbaensis* and indicates subsequent allometry in Early Cambrian acrotretoids. Viewed from the exterior of the ventral valve, the relative distance from the posterior margin to the pedicle foramen increases in brachiopods of length 0.3 mm to 1.3 mm, while it decreases in those from 1.3 mm to 2.4 mm in length (Figure 2A). The relative diameter of the pedicle opening increases during the whole ontogenetic process (Figure 2B). The allometric growth confirms previous empirical observations (e.g., Zhang et al., 2018a) and both non-linear and linear relationships between size and components of the shape of *E. zhenbaensis* have been revealed for the first time.

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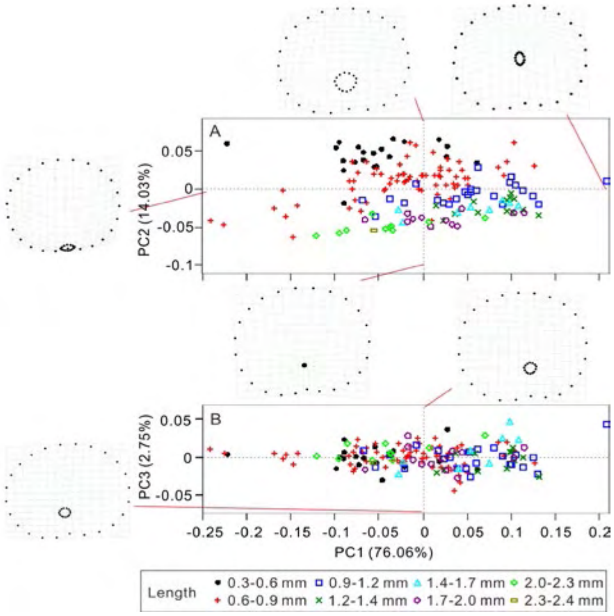

Figure 1. Plots for PC 1–2 (A) and PC 1–3 (B) of the relative warp analysis of the shape of the ventral valve with indication of characteristic thin-plate splines.

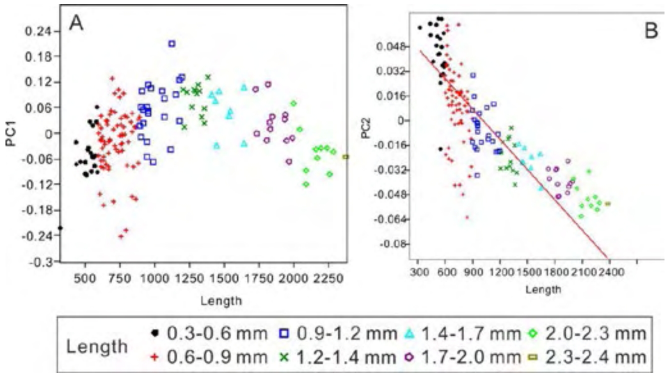

Figure 2. The X-Y plot of PC1 and PC2 with the length of the studied Early Cambrian brachiopods showing the nonlinear (PC1-Length) and linear (PC2-Length) relationships between shape and size.

Carboniferous-Permian glacial-deglacial events and their effects on the brachiopod faunas from Argentina and Australia

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Late Palaeozoic sequences from Argentina and Australia provide a complete record of the glacial-deglacial events and their effects on marine benthic faunas can be evaluated in several key sections.

In Argentina, two different scenarios for the postglacial transgressions are possible to identify according to the glacial episodes suggested in the early Late Carboniferous-Early Permian interval (López-Gamundí, 1997): to the west, the Late Carboniferous paleopacific transgression, related to the Glacial Episode II represented in the Andean basins, is characterized by a well diversified brachiopod fauna developed in arc-related and retroarc basins; to the east, the Late Carboniferous-Early Permian transgression associated with the Glacial Episode III, the most widespread, is documented in the Sauce Grande Basin. This transgression can be distinguished by fossil assemblages dominated by bivalves (*Eurydesma* Fauna) with a low-diversity brachiopod fauna, which inhabited epeiric seas generated by flooding over an intraplate basin.

Carboniferous postglacial faunas of late Serpukhovian-early Bashkirian age (*Levipustula* and *Aseptella-Tuberculatella/Rhipidomella Micraphelia* faunas) from western Argentina have been widely studied in their type sections of the Calingasta-Uspallata Basin (Cisterna & Sterren, 2016; Cisterna et al., 2017). In this basin, postglacial mudstones with marine invertebrate faunas can be present in fjords systems and in open shelf. The marine flooding over different coast configurations and the availability of sediments would have favoured the development of coeval faunas with differences in their taxonomic composition and paleoecological structure. Our study is now focused on brachiopods of the postglacial *Eurydesma* Fauna from East and West Gondwana, particularly those from the Sauce Grande basin and southern Sydney Basin in Australia.

Fossil assemblages of the *Eurydesma* Fauna from the Sauce Grande basin are identified in the lower part of the Bonete Formation (Pillahuincó Group, Sierras Australes, Buenos Aires province), which records the transgression related to the retreat of the South African glaciers and would have been deposited at low slope platform (Andreis & Ribeiro, 2003). This fauna is composed of more than 80% of bivalves, many of them species of the key genus *Eurydesma*, accompanied by the brachiopods *Tivertonia* and *Tomiopsis.* This last genus has often been recognized in the *Eurydesma* Fauna of several Gondwana basins. In particular, the postglacial brachiopod faunas of the Wasp Head Formation, a shallow marine sandstone dominated unit in the southern Sydney basin, is characterized by the abundant occurrences of the spiriferids *Tomiopsis* and *Trigonotreta*, and bivalves are more than 60%. This succession encloses records of the first Permian glacial interval suggested for eastern Australia (Fielding et al., 2008), and its brachiopod assemblages are characterized by a group of diagnostic species whose diversity and stratigraphic occurrences in relation to sedimentary facies reflect the transition from an intraglacial interval to post-glacial conditions (Cisterna & Shi, 2014). The predominance of bivalves in relation to brachiopods has also been observed in the postglacial faunas of the Itararé Group in the Parana Basin, Brazil (Neves et al., 2014; Taboada et al., 2016). Further analytic studies will be necessary to understand the paleoenvironmental conditions (i.e. substrate stability, turbidity, nutrient availability, variation in oxygen levels, poor circulation and salinity variations in the water column), directly related to glacial retreat dynamics that would have controlled the composition and distribution patterns of the postglacial *Eurydesma* fauna.

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Useful and useless – brachiopods and palaeogeogeography

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Brachiopods have often been prominent in Phanerozoic benthic communities, particularly during the Palaeozoic. Their associations are usually varied, with diversity increasing with depth, so that Benthic Associations can be identified, often as many as five progressively deepening on clastic substrates and sometimes many more in niche environments such as often occur with carbonate deposits. As with most faunas, diversity is usually highest around the Equator and progressively lessening in higher latitudes. However, even though they often dominate their associations, their usefulness in deciphering palaeogeography varies; for example, in the Palaeozoic it peaked during the earlier Ordovician, earlier Devonian, and the Permian, whilst in contrast provinciality was poorly developed during the Cambrian, Silurian, and Carboniferous. Those differences were caused by several factors such as the width of the oceans which separated large continents, the continuity or breakdown of major ocean current systems, and the availability or lack of mid-oceanic islands to act as stepping-stones for the successful migration of the larvae of the different genera. In particular, the larva of inarticulated brachiopods have a longer life than 'articulates', which explains why the Cambrian faunas (in contrast to trilobites) do not reflect the palaeogeography and are thus useless in understanding it. The Permian extinctions destroyed many brachiopods, so that the distributions of Mesozoic and later faunas are less distinctive, but, since from then onwards there was much more reliable geophysical data than before, including the 'fossil' magnetic stripes on the preserved ocean floors, the value of the faunas in establishing the positions of ancient continents and other terranes became very much less important. Less fundamental scientific background factors are the decreasing availability of specialist palaeontologists to study the different rocks and faunas, as well as the occurrence of accessible outcrops for collecting the specimens needed prior to assessment.

Examples from the later Ordovician and Permian are discussed in more detail. During the Darriwilian, Sandbian, and Katian, several oceans, such as the formerly extensive Iapetus, were closing, whilst others, like the Rheic, were widening. Recent work by Liljeroth et al. (2017) has documented how faunas from isolated mid-oceanic islands, such as the Leinster Terrane in Ireland, can reveal when larvae from the various brachiopod genera managed to get across the Iapetus and thus how the assemblages changed on the edges of both oceans. Comparably, Popov & Cocks (2017) statistically analysed over 80 brachiopod faunas from six different Kazakh terranes, and established how those faunas were different from or related to relatively nearly continents in South China and north-western Gondwana (Australia). Thus, Ordovician reconstructions have been much helped by the plotting of the differing faunal assemblages, in those times both trilobites and brachiopods.

In the Late Palaeozoic, we discussed the Early Devonian provinces and their useful distribution in the previous brachiopod congress in Nanjing, and commented then how that usefulness peaked in the Emsian before the continents became close enough together for those differences progressively dwindled, so that during the later Devonian and Carboniferous little can be learnt about palaeogeography from brachiopods. However, the situation had improved again by the Early Permian. Shen et al. (2009) plotted distributions of the brachiopod provinces during the Middle Permian, some of which are shown on the figure here (from Torsvik & Cocks 2017). Those brachiopod provinces have been integrated with much other data derived from sedimentology, igneous activity, and plate tectonics to generate maps in a kinematically progressive sequence throughout the period. Thus, in this case the brachiopods have been useful.

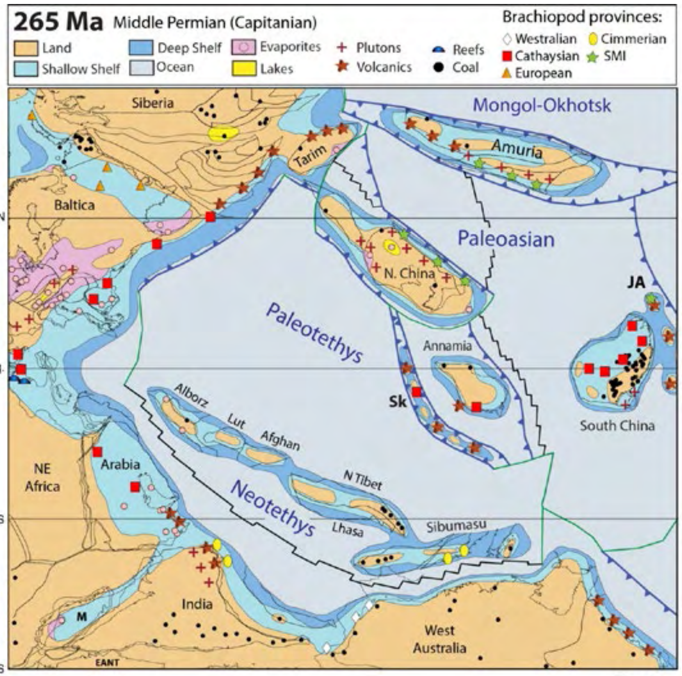

Fig. 10.2

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Eocene brachiopods of the Thrace Basin (NW Turkey)

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Eocene brachiopods are relatively well-known from Western and Central Europe; however, we have very limited data from Eastern Europe and Turkey. The only detailed description was published by Zelinskaya (1975), who - after several smaller papers - published a small monograph on the Paleogene brachiopods of Ukraine. Recently a new paper was published also from Ukraine by Bitner & Müller (2017). The Eocene brachiopod records from Turkey are generally very rare (e.g., d'Archiac, 1866) while the fauna of the Thrace Basin is almost unknown.

This study focuses on the brachiopod fauna from the Eocene shallow marine units, cropping out widely in the Thrace Basin in NW Turkey. A significant part of the studied fauna is from the samples collected by Ercan Özcan (Istanbul, Turkey) and György Less (Miskolc, Hungary), who studied the larger foraminifers and also established a biostratigraphic framework for these units (e.g., Özcan et al., 2010; Less et al., 2011). Later, some of the most important sections (e.g. Şamlar near Istanbul, and Gizliliman and Dereköy in Gökçeada Island) were sampled bed-by-bed for brachiopods. Some of the studied sections are located at the northern part (Şamlar, Akören, Kirklareli, Çatalca, Karabarun, Hacimaşli) while others are located at the southern part (Tayfur, Beşyol, Mürefte, Gizliliman, Dereköy) of the Thrace Basin.

The studied micromorphic brachiopods are derived from Ypresian, upper Lutetian and lower Bartonian samples at the southern part, while micromorphics are from upper Bartonian to upper Priabonian layers in the northern area. In this way, we have coverage of nearly the whole Eocene of the Thrace Basin, although the sample sizes are rather uneven. Most samples (and therefore most brachiopods) are from the Bartonian sediments, upper Lutetian and upper Priabonian material is less numerous, while Ypresian is minimal.

Altogether 2,200 specimens were separated, which represent 22 brachiopod species. Most common species are *Lacazella mediterranea*, *Terebratulina tenuistriata* and *Orthothyris pectinoides*, but the most diverse is the genus *Argyrotheca*, which is represented by 7 different species. Several other genera occur less abundantly (*Discinisca*?, *Novocrania*, *Rugia*, *Bronnothyris*, *Joania*, *Platidia*, and *Minutella*?). The studied brachiopod material has yielded some new species (*Rugia* n. sp., *Minutella*? n. sp.). The upper Lutetian and lower Bartonian layers of the Gizliliman section (Gökçeada Island) contain relatively numerous representatives of two new species of a new genus, which belong to the Family Megathyrididae, on the basis of the external and internal morphological characters. In spite of the several studied localities and many checked samples, no rhynchonellids or large terebratulids were found.

Stratigraphically, *Lacazella*, *Argyrotheca* and Megathyrididae n. gen. are equally important in the upper Lutetian. The lower Bartonian samples are dominated by cementing *Lacazella*, but *Argyrotheca* and *Orthothyris* are also common. *Lacazella* is much less significant in upper Bartonian and the dominant brachiopod is *Terebratulina*, which was nearly absent in the older layers. *Argyrotheca* and *Joania* are also significant in upper Bartonian. *Lacazella*, *Orthothyris* and *Terebratulina* are equally important in the limited Priabonian samples.

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A new locality of a living platidiid in northern Japan observed by a remotely operated vehicle

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Platidiids are relatively uncommon terebratulides known from Cretaceous to Recent. In the seas around Japan, *Platidia japonica* Dall, 1920 was reported from Yokohama, central Japan, at 65 fathoms adhering to the shell of the terebratulide *Terebratulina crossei* Davidson, 1882. However, not a single specimen was found in the large collection of the living brachiopods procured by the Steamship Soyo-maru from the shelf seas bordering Japan (Hatai, 1940). Here we report the discovery of a new locality of a platidiid (tentatively identified as *Platidia*? *Japonica*, Fig. 1) at a depth of about 80 meters off Otsuchi, in the mouth of Otsuchi Bay, northern Japan. The specimens were collected by dredge operations first, and were found adhering to the shells of *Terebratulina crossei*, which is a common and well known species from this locality. The terebratulide *Laqueus blanfordi* (Dunker, 1882) and the rhynchonellide *Hemithiris psittacea* (Gmelin, 1790) are also common in this locality, and were found in the same dredge haul. In order to observe the mode of life of those brachiopods, we surveyed this locality using a remotely operated vehicle (ROV) equipped with a video camera. The observations revealed that the locality is a rocky mound covered with sub-rounded to sub-angular boulders, some of which being massive with several square-meters of flat-surfaces. Remarkably, the rock surfaces are dominated by *L. blanfordi* and *T. crossei*, forming "a bunch of brachiopods". *H. psittacea* is less common, but forms patches of clusters sporadically. Associated fauna include sponges, sea pens, bryozoans and brittle stars. Abundance and flows of marine snow indicate that ample nutrients are supplied to the suspension-feeders in this locality. *L. blanfordi* and *T. crossei* are often attached to the substrate side-by-side, but since *T. crossei* directly attach their shells to the substrate with a short pedicle, while *L. blanfordi* support their shells 1-2 cm above the substrate with a long pedicle, they occupy effectively two different tiering levels above the sea floor. The platidiid is yet to be found in the video record taken by the ROV, and further studies are needed to make clear the nature of the commensal relationship between the platidiid and *T. crossei*. The newly found locality of the platidiid provides an ideal field to study ecology and other aspects of biology of living brachiopods.

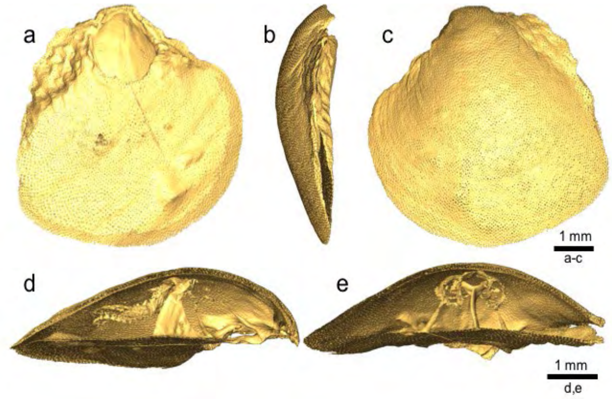

Figure 1. CT scanned images of *Platidia*? *japonica* collected from off Otsuchi, northern Japan. a: dorsal, b: left lateral, and c: ventral views of the valves. d: left lateral, and e: anterior views of the brachidium and the spicules contained in the lophophore.

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Reconstructing $^{87}Sr/^{86}Sr$ and $\delta^{88/86}Sr$ in Pliocene-Pleistocene seawater by fossil brachiopods, bivalves, gastropods and foraminifera

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The isotopic composition of the stable isotopes of Sr (expressed by the $\delta^{88/86}Sr$ notation) in fossils and carbonate rocks provide a new tool for constraining the marine Sr budget throughout the geologic history that complements the commonly used $^{87}Sr/^{86}Sr$ ratios. This is because the fractionation of the stable Sr isotopes provides additional information regarding geochemical processes occurring in the sea that are not revealed by the $^{87}Sr/^{86}Sr$ ratios. Fossils of brachiopods have been commonly used for the reconstruction of the Sr isotope in ancient seawater and paleoenvironmental studies, because this group of fossils appears in the geological record since the Early Cambrian and it is generally resistant to diagenetic alterations. So far, determination of $\delta^{88}/^{86}Sr$ in ancient seawater was conducted only on brachiopods (Vollstaedt et al., 2014). Brachiopods however, are quite infrequent in Cenozoic geological sections, hence, obtaining a high temporal resolution record of marine $\delta^{88}/^{86}Sr$ values from young deposits requires measurements on alternative groups of more common marine fossils (bivalves, gastropods, foraminifera). The potential use of the other types of marine fossils is examined here applying the trace element approach to discriminate fossil that underwent diagenesis. We collected recent and fossil mollusks and brachiopods from: 1. A single fossil-rich stratigraphic bed in the section exposed at the banks of Stirone River (northern Apennines, Italy); 2. Recent *Glycymeris insubrica* shells from Ashkelon Beach (Israel); 3. *Aequipecten opercularis* and *Pecten jacobeus* from the offshore of Ashkelon/Ashdod (Israel); and 4. Gastropods from the northern Red Sea, Eilat (Israel). Fossil skeleton can be altered by contamination with sediment or secondary calcite (chalky fabric in *Ostrea edulis*, filling of brachiopod endopunctae). The Sr isotopic composition of the recent fossils were determined to obtain the fractionation factor between the specific organism and seawater ($\Delta^{88}/^{86}Sr_{skeleton-seawater}= \delta^{88}/^{86}{}_{Srskeleton}$- $\delta^{88}/^{86}Sr_{seawater}$), which is still unknown for many species. Finally, the well-preserved fossils were used to determine the $^{87}Sr/^{86}Sr$ ratios and $\delta^{88}/^{86}Sr$ values in seawater of the late Pliocene-early Pleistocene time interval - the onset of the Ice Ages in the northern hemisphere. The $^{87}Sr/^{86}Sr$ ratios of this time interval followed well the marine $^{87}Sr/^{86}Sr$ curve, while the $\delta^{88}/^{86}Sr$ was relatively invariant with an average value of 0.39±0.02 ‰. The results demonstrate that it is possible to use alternative fossil groups to reconstruct the secular variation in the marine $\delta^{88}/^{86}Sr$ after evaluating the respective $\Delta^{88}/^{86}$Srskeleton-seawater value.

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Quantitative study of geochemically diagenetic impact on fossil brachiopod shells from northeastern Japan

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Stable carbon and oxygen isotope composition ($\delta^{13}C$ and $\delta^{18}O$) of fossil brachiopod shells is used as proxies for $\delta^{13}C$ of dissolved inorganic carbon (DIC) and seawater $\delta^{18}O$/temperature, respectively, for the Phanerozoic. To reliably reconstruct paleoenvironment, it is essential to quantitatively estimate to what extent the initial isotope composition of the shells (= isotopic composition when shells formed) has been modified by diagenetic processes. To select well-preserved shells, three qualitative criteria have been commonly used: (i) well-preserved shell microstructure, (ii) non-luminescent shell with "cold cathode", and (iii) high strontium (Sr) and low manganese (Mn) contents in the shell. However, the diagenetic alteration of shells detected by these criteria has been only qualitatively considered. A few attempts have been made to establish quantitative relationship among modification of isotopic composition and minor/trace element concentrations, degradation of shell microstructure, and luminescence/non-luminescence with "cold cathode".

The objectives of this study are to (1) show the inter-shell and intra-shell variations in carbon and oxygen isotope composition, minor/trace element (Mn, Fe, Sr) concentration, luminescence/non-luminescence in CL images and preservation state derived from shell microstructure analysis with SEM of fossil brachiopod shells (*Terebratalia coreanica* and *Laqueus rubellus*) from upper Pliocene sandy conglomerate (Tentokuji Formation, Minehama, northeastern Japan), (2) compare these fossil data with those from modern shells (*T. coreanica* from Otsuchi Bay, northeastern Japan and *L. rubellus* from Sagami bay, central Japan), and (3) evaluate the extent to which the original isotopic composition has been modified by the process of meteoric diagenesis. The analyzed fossil brachiopod shells were collected from a land outcrop and have been subject to meteoric diagenesis. Ventral valves of brachiopod shells were cut along the maximum growth axis. Following Takizawa et al. (2017), powder samples for isotope and minor/trace element analysis were extracted from spot locations on the inner surfaces of the shells (ventral valves), from vertical sections along the maximum growth (longitudinal) axis. CL and SEM observations were conducted at the portion adjacent to the spot locations from which the samples for the isotopic and chemical analyses were extracted.

Modern shells: The $\delta^{13}C$ and $\delta^{18}O$ values varied in relatively wide ranges (<2‰) near the posterior shell edge. On the other hand, those values from the central convex portion to the anterior shell edge fell in narrow ranges (<0.8‰). Therefore, the latter shell portion is suitable to evaluate diagenetic impact on the initial isotope composition of the two brachiopod species. Mn and Sr concentrations were 2–29ppm and 798–1139ppm, respectively, with no systematic trend, whereas the profiles of Fe concentration (mostly 27–571ppm) were associated with some outlier spots with anomalously high Fe concentration (>660ppm). Modern shells were non-luminescent or showed weakly luminescent banding in CL images and the outline of calcite fibers was well defined in SEM images.

Fossil shells: The $\delta^{13}C$ and $\delta^{18}O$ values of the shell portion from the central convex portion to the anterior shell edge exhibited large variations (up to 5.4 and 2.3‰, respectively) compared with the modern shells, showing a positive correlation. The $\delta^{13}C$ and $\delta^{18}O$ values of cement were plotted on the linear regression line between those values of brachiopod shells. Mn concentration was much higher (mostly >200ppm) than that of the modern shells. Fe concentration (177–1413ppm) was higher or similar to that of the modern shells. Some of spots with anomalously high Fe concentration (>1500ppm) corresponded to those of high Mn concentration. In contrast, Sr (732–1086ppm) concentration of the fossil shells was similar to that of the modern shells. Bright orange luminescence was observed at some shell portions. We defined Mean CL Intensity (MCLI) as a mean value of red component per unit area of a shell in RGB color space (0–255). The MCLI ranged from 12 to 216. SEM images showed diagenetic degradation of shell microstructure in most shells. The altered fiber ratio (AFR; defined as the ratio (%) of the total area of altered fibers per unit area) varied from 1 to 95%.

The $\delta^{13}C$ and $\delta^{18}O$ values are negatively correlated with Mn concentration, MCLI, and AFR with correlation coefficients (*r* values) ranging from –0.76 to –0.53. These indicate that Mn concentration, MCLI and AFR can be useful to detect diagenetically altered portions of brachiopod shells, which is confirmed by factor analysis.

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The effect of pH and precipitation rate on $\Delta^7\mathrm{Li}_{\mathrm{solid\text{-}fluid}}$ during the growth of calcite - An experimental approach

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The isotopic signals of trace elements in carbonates are routinely used as geochemical tools to unravel the environmental conditions occurred throughout the geological past. Amongst them, the Li isotope system has received large attention mainly due to the large isotope fractionation effects observed during continental weathering providing information e.g. about the intensity of silicate weathering and secondary mineral formation at the seafloor and therefore about the controlling forces climate and tectonics (Misra and Froelich, 2012). Another important archive for paleoenvironmental conditions is carbonates, as for example brachiopods. To date the mechanisms controlling the fractionation of Li isotopes during the incorporation in the crystal lattice of carbonates remains unclear as Li is strongly hydrophilic with a small ionic radius and the substitution of Li^+ for Ca^{2+} in $CaCO_3$ crystal lattice demands electrical balance. In order to contribute to a better knowledge of the mechanisms controlling Li isotope fractionation during its incorporation into calcite, we conducted inorganic precipitation experiments at well controlled physicochemical conditions.

In the present study calcite precipitation was induced by simultaneous pumping of two solutions ($CaCl_2$ + LiCl; Na_2CO_3) into a reaction vessel containing calcite seeds using a peristaltic pump at 25 °C. The pH was adjusted by distinct pCO2 of the introduced gas phases or by NaOH titration. In particular, the influence of precipitation rate ($10^{-8.2} < \log(rp) < 10^{-7.1}$) and pH ($6.3 < pH < 9.6$) on the incorporation behavior of lithium is investigated.

The obtained $\Delta^7Li_{solid\text{-}fluid}$, defined as the difference between δ^7Li_{solid} and δ^7Li_{fluid} shows a larger fractionation (-2.6 ‰ < $\Delta^7Li_{solid\text{-}fluid}$ < -5.3 ‰) with increasing precipitation rate at constant pH = 8.5.

At a constant precipitation rate, the $\Delta^7Li_{solid\text{-}fluid}$ indicates with increasing pH a smaller fractionation (from -5.3 ‰ to -2.3 ‰) until pH 8.5 is reached, whereas at pH > 8.5 the $\Delta^7Li_{solid\text{-}fluid}$ shows again a larger fractionation (from -2.3 ‰ to -4 ‰). These changes in $\Delta^7Li_{solid\text{-}fluid}$ positively correlate with the dominance of HCO3- species in solution.

This isotope fractionation behaviour might be related to the increasing affinity for complexation of Li+ with HCO_3^- as the heavier Li isotope is stronger bounded to $LiHCO_3$ in solution than the lighter isotope, with increasing supersaturation the adsorption of the lighter Li isotope onto the calcite surface is preferred.

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Modelling the shape of brachiopod valves

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Brachiopod valves present an unfathomable variation of shapes and the study of their morphology provides both an occasion and a challenge for paleobiologists, since the external phenotype is often the unique preserved part of the organism. To explore their morphological evolution and variability, the employment of morphospaces is increasing among paleo- and neontologists, which often involves the application of empirical morphospaces (e.g. Laurin & García-Joral, 1990; Lee et al., 2018), but rarely delineates theoretical spaces (e.g. McGhee, 1980). A metric Euclidean structure of the morphospace is always required to measure the morphological distances in a proper manner and, thus, to make coherent inferences about the evolutionary processes under investigation (Mitteroecker & Huttegger, 2009). On the other hand, maintaining a Euclidean structure while analysing different shapes is hard to achieve, mostly due to the difficulties in finding analogous points of reference between valves of different taxa. An alternative approach lies in the generation of theoretical morphologies using geometric parameters, which can be exploitable to compare shapes bearing differences, which are otherwise immeasurable (Pappas & Miller, 2013).

Here, models of brachiopod valves have been produced using a series of parametric equations and the resulting empirical morphospaces provide powerful examples of the benefit given by this approach. This method has the undeniable advantage of making possible the comparison of morphologies at different evolutionary scales, thus analyzing problems ranging from large-scale macroevolution to small intrapopulation variation. The simulation of morphological patterns can be useful to study questions related to allometry, ontogenesis, and morphological disparity. Biological issues such as the body volume/surface ratio against shape variation can be investigated through computer-based simulations. Moreover, since the definition of species and genera, and consequently the study of biodiversity among brachiopods have been based almost entirely on morphology, the proposed approach should help to delineate the evolutionary boundaries among several species and genera, if their shapes are correctly modelled. In addition, studies related to applied functional morphology, such as those implying experiments on fluid dynamics (i.e. Shiino and Suzuki, 2015), can gain benefits from this method since, through reverse engineering, it is easy to produce replicates of fossil shells.

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Cyclicity of *Terebratula* pavements in a mixed carbonate-siliciclastic prograding wedge: Early Pliocene of SE Spain

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During the early Pliocene, subaqueous delta-scale clinoforms developed in the Águilas Basin (SE Spain), then a small coastal embayment, in a warm-temperate, mixed carbonate-siliciclastic sedimentary system. Stratal architecture and sedimentary facies are consistent with the Infralittoral Prograding Wedge model. The high rank sequence developed during highstand and falling sea-level stages. Over twenty-three prograding clinothems crop out along a distance of ≥ 1 km. Biostratigraphic marker indicate a time span shorter than 700 kyr for the whole unit (MPl3 biozone of the Mediterranean Pliocene), indicating that the clinothems represent high-frequency (low rank) sequences. Cyclic pavements and occasional biostromes of suspension feeders (terebratulid brachiopods, modiolid bivalves and adeoniform bryozoan colonies), glauconite and occasionally *Glossifungites* ichnofacies formed during stages of low rank relative sea-level rise, marking the clinoform surfaces, which bound the clinothems. This is in contrast with other examples from the literature, where shellbeds formed under comparable eco-sedimentary conditions occur in transgressive units located at the base and the top of the clinobedded units, but not in the clinoforms as in this case study. We interpret these features as the result of increased accommodation space in the topset of the clinoforms during relative sea-level rise and concomitant strong reduction of terrigenous input into the foreset and bottomset areas, which provided favorable conditions for the suspension feeder palaeocommunities. During stillstand stages, however, reduced accommodation space in the topsets led to progradation in the foresets, where high abundance of *Ditrupa* tubes is consistent with frequent storm-driven siltation events, which led to the demise of terebratulid populations in the toeset and bottomset subenvironments. The occurrence of shellbeds between clinothems suggests that our case study represents lower progradation rates than other examples where shellbeds bound the clinobedded units at their base and top only. Most importantly, the distribution of biofacies and ichnoassemblage associations contribute significantly to the understanding of the effects of high-frequency relative sea level fluctuations on the evolution of subaqueous delta-scale clinoform systems.

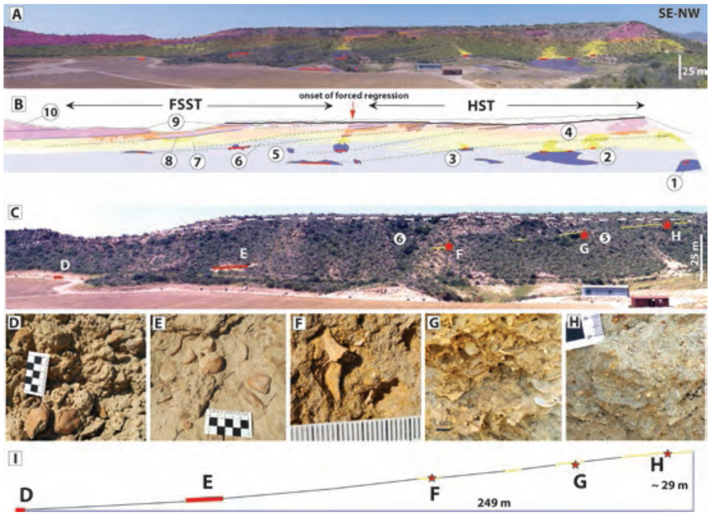

Fig.1.- A) Photomosaic of the basal interval of the early Pliocene prograding wedge from the Águilas Basin (SE Spain). B) Bedding planes visible in the field are marked in blue, interpreted ones are dashed lines, and bold red are *Terebratula* pavements. Main facies types indicated by colour codes: from proximal to distal, hybrid siliciclastic-rhodolith floatstone (pink), hybrid packstone with bryozoans and red algae (orange); hybrid packstone and fine-grained sands with *Ditrupa* (yellow) and hybrid packstone and fine-grained sands with *Costellamussiopecten* (blue). Numbering of the clinothems identified in the Cabezo Alto area is indicated within circles. C) Example of the clinoform separating clinothems 5 and 6, with features across a proximal-distal gradient. Asteriks indicate the spots where the photographs were taken. D) and E) are details of the same pavement at the toeset and inner bottomset of the clinoform. F) foreset *Ditrupa* facies with loosely-packed fragments of adeoniform bryozoan colonies (*Schizoretepora* sp.). G) Detail of the rollover zone with densely-packed concentration of the same bryozoan taxon. H) Outer topset facies with loosely-packed fragments of the same bryozoans, and small fragments of rhodoliths. I) Dimensions of the clinoform from bottomset to topset.

Disorder introduced in the hierarchical architecture of selected fossil rhynchonelliform brachiopod shells

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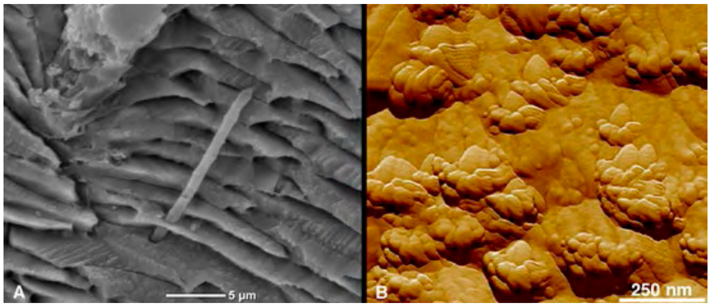
Attempts to understand the hierarchical organization of the inners layers of the calcite shell during the process of biomineralization have been made on selected modern rhynchonelliform brachiopods, using the Atomic force microscopy (AFM) to complement the observations from the Scanning electron microscopy (SEM) thus reaching a nanometric level (Gaspard, 2006, Griesshaber et al., 2007, Gaspard & Nouet, 2016) to illustrate the result of the biomineralization process by the way of crystallization since an amorphous transient phase controlled at the epithelial cell level. During this process and the life span, the shell growths in equilibrium with the environment (sea water). After the death of the organisms, the exoskeleton (the low-Mg calcite shell) is subject to various aggressions on the sea floor and/or by weathering when exposed.

Drawing our attention to biomaterials from the fossil record (cf. *Sellithyris cenomanensis* Gaspard from the upper Middle Cenomanian, and *Moutonithyris dutempleana* (d'Orbigny) from the Late Albian-Early Cenomanian) allow to reveal chemical/physical alterations occurring in the shell components (organic and inorganic fractions) in the course of fossilization.

Using SEM and AFM observations as for modern shells reveal an alteration of the original information and emphasize the disorder introduced in the patterns of the hierarchical architecture during the process of fossilization. Element contents can be approached as for modern shells with elemental maps and microprobe analysis (Gaspard et al., 2018). Among alterations observed are: silicification due to bacterial activity and, more often, the disappearance of a great part of the organic matrices (more evident is that of the peri-crystalline organic matrix, hardly noticeable is that of the intracrystalline fraction). In such situation, boundaries of the calcite fibrous elements of the secondary layer are p. pr. or completely merged and the nanoparticles or elementary granules previously highlighted are progressively amalgamate leading to shape secondary blocky calcite as it was also the case when microboring organisms are present. Thus, the hierarchical organization observed at the sub-micrometric level, for the two-layered shells (cf. *S. cenomanensis*) as for the three-layered shells (*M. dutempleana*), can be rubbed out partly or completely with, as results of diagenetic impacts, the presence of either recrystallized calcite or silica nodules in the shell thickness.



A SEM view of altered fibres of *Sellithyris cenomanensis* in the shell thickness (A). Close-up AFM view in the fibres revealing the heterogeneous arrangement of the nanoparticles (B).

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Recent brachiopods of the French Insular Caribbean Region

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Although brachiopods first appeared in the Early Cambrian, their occurrence in the Caribbean is much more recent. Brachiopods, with a bivalved calcite shell, live at various depths in the Caribbean, and may have a wide depth tolerance. They are sensitive to modifications of the environment and, as attached benthic marine invertebrates, they are witnesses of their immediate environment, recording environmental change.

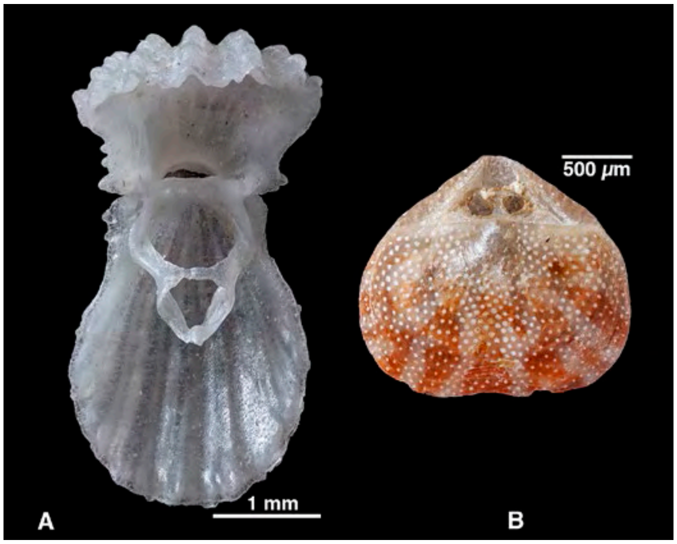
Two oceanographic expeditions, with the N/O "l'Antea", aimed to improve the knowledge of the marine fauna in the littoral and deep-sea benthos of the French Caribbean area in order to protect and value the natural heritage. Representatives of the phylum, sampled during the Expeditions Karubenthos 2 (around Guadeloupe, 2015) and Madibenthos (around Martinique, 2016), reveal an impressive diversity with a rich fauna of twenty or so species belonging to the Rhynchonelliformea (one of the three subphyla of the phylum Brachiopoda), uncommon Linguliformea and a few Craniiformea. Among the rhynchonelliform: *Terebratulina cailleti* is an endemic Cancellothyrididae of the Caribbean Sea and Gulf of Mexico, first reported by Crosse (1865) around La Guadeloupe, a fairly common and widespread species. The sampled fauna is dominated by several species of the genus *Tichosina* (Terebratulidae) along with a few *Erymnia muralifera* Cooper, uncommon *Stenosarina* Cooper, and *Dallina floridana* (Pourtalès) with their large shells.

The small shell size of the species from several genera is striking and include *Discradisca antillarum* (d'Orbigny) (Discinidae), *Cryptopora* Jeffreys, *Eucalathis* (Chlidonophoridae), *Terebratulina cailleti* and some others belonging to several families of the Terebratellidina: *Argyrotheca* species, *Platidia* and *Amphithyris* sp., with a similarity with late Cretaceous micromorphic species from NW Europe. *Cryptopora* Jeffreys is the only rhynchonellide found in the Recent fauna of the Caribbean, in other respects world-wide in occurrence.

The brightly coloured patterns of *Argyrotheca* shells are unmatched elsewhere other than the Mediterranean. There are also representatives of Craniidae with coloured patterns. The significance of this colouration is unknown but could provide protection against UV radiation or help prevent predation. Apart from external morphological features, internal characters, and micro and nano details have been observed using SEM. Pigments involved in colouration were tentatively analysed using Raman spectroscopy.

The brachiopod shell is punctate, with the exception of that of the rhynchonellides. Mainly specimens of the genus *Tichosina* (common) reveal brown traces that could result from oil pollution. While the caeca, outgrowths of the external mantle epithelium housing the punctae, have a nutrient storage capacity and allow chemical components to circulate within the mantle (Owen & Williams, 1969), they could be sealed by the oil product, what may lead to the death of the organisms, followed by the disappearance of part of the fauna in some places.

To conclude, the location of the coloured patterns on the shell is a challenge to include in identification of *Argyrotheca* species since the colouration may disappear and/or only first stages are observed. In other respects, the micromorphic brachiopod species sampled around the French Lesser Antilles, as well as those in the vicinity of other Caribbean islands, off Columbia, Gulf of Mexico (Cooper, 1977), Venezuela (Logan, 1990), Guyana and Brazilian coasts (Simões et al. 2004), compared to those from the Mediterranean Sea and from the Late Cretaceous in NW Europe, were for most part already established since the Late Cretaceous or derived from Cretaceous ancestors at the time of the Central and North Atlantic opening.



A. Specimen of *Terebratulina cailleti* Crosse from W. Marie Galante, revealing internal details. B. *Argyrotheca bermudana* Dall, a littoral species sampled off E. Martinique.

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Lithium in brachiopods – proxy for seawater evolution?

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In order to compile information about past weathering processes, Li has been found to have the potential to serve as a proxy for weathering processes (i.e. Pogge von Strandmann & Henderson, 2015). Some important characteristics for this purpose of Li are its uniform spatial distribution throughout the oceans, the long residence time of ~1.5–3 Myr (Stoffyn-Egli & Mackenzie, 1984; Huh et al., 1998) and its global occurrence in abundant marine carbonates. So far various biogenic carbonates have been studied and tested as possible archives for Li in seawater, such as scleractinian corals, belemnites or foraminifera. However, only a foraminifera-based record appears to accurately reflect the Li isotope composition of ocean water. At present, this record is available for the Cenozoic with implications for major events during this period of time, including the K/T event (Misra & Froelich, 2012). A record for the entire Phanerozoic has not yet been obtained since reliable archives/proxies have not been identified. To extend the existing record into the more distant past, brachiopods were chosen to serve as an archive. These organisms were already present in the Early Cambrian oceans, are abundant in the fossil record and less sensitive to diagenesis-induced modifications due to their shell mineralogy (low-Mg calcite). The preliminary data indicates a species-, temperature- and salinity-independent behaviour of Li isotopes in modern brachiopod shells. Also, no vital effects have been observed for different shell parts. The consistent offset of ~−4‰ relative to modern seawater is in accordance with experimental data (Marriott et al., 2004). This indicates that a Li record relying on brachiopods can faithfully reflect large-scale continental events tied to weathering, i.e. as a consequence of land colonization by plants. However, fossil brachiopods show very different Li data and a wider range than modern ones. In order to further understand these differences and to exclude other factors than changes in weathering regimes and ocean chemistry, culturing experiments with brachiopods were set up for different conditions (pCO_2, T, Mg/Ca) which should cover the overall range of life conditions of brachiopods. The Li elemental/isotope data from these experiments is now being collected.

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Facies control on the Lower Emsian (Lower Devonian) brachiopod faunas in South China

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Following the Caledonian orogeny in the Early Palaeozoic, an extensive northward transgression occurred in the Early Devonian of South China. Divergent sedimentary facies and biofacies developed in different areas of South China during the transgression, and the Lower Emsian brachiopod faunal replacement shows a close relationship with the environmental changes.

In the early Emsian (Early Devonian), during the incipient phase of the transgression, epicontinental sea spread widely in South China. The first widespread Lower Emsian brachiopod fauna in South China and adjacent regions was called the "*Spirifer tonkinensis* Fauna", which has been reported in Guangxi Province (Wang, 1956; Wang & Rong, 1986; Xian et al., 1980), southeastern Yunnan Province (Yin, 1938; Jin et al., 2005), northern Sichuan Province (Wan, 1980; Hou et al., 1988; Chen, 1990), China, and also northern Vietnam (Mansuy, 1908). According to recent conodont biostratigraphic work (Lu & Chen, 2016; Guo, 2017), the occurrence of *Rostrospirifer* and *Dicoelostrophia*, the index taxa of the "*Spirifer tonkinensis* Fauna", had an obvious chronological trend from south to north, ranging from Upper Pragian to the upper *Polygnathus* *excavatus* conodont Zone, which coincided with the transgression. Faunal composition, taphonomic and sedimentary features all suggest that the "*Spirifer tonkinensis* Fauna" lived in a shallow-water marine environment and preferred an argillaceous substrate. The disappearance of the "*Spirifer tonkinensis* Fauna" was also diachronous across different areas. Palaeoecological study indicates that the disappearance of the "*Spirifer tonkinensis* Fauna" had two probable causes: in some areas (e.g. Nandan and Liujing, Guangxi Province) it was associated with a deepening, while in other areas driven by the development of carbonate sediments and disappearance of argillaceous substrates (Guo, 2017). Both factors were related to the Early Devonian transgression.

After the "*Spirifer tonkinensis* Fauna" disappeared, divergent patterns of brachiopod faunal replacement in different facies were recorded in Devonian of South China.

In Nandan area, where basinal facies developed from the late Early Emsian, the succeeding "*Sinathyris* Fauna" preserved in dark mudstone within the *P. nothoperbonus* Zone is of rather low diversity and dominated by the small-sized, double-spiral bearing *Sinathyris* Guo, Sun & Baliński, 2015 and accompanied by very rare orthids, atrypids and athyrids that together constitute 1% of the brachiopod fauna. Besides brachiopods, sporadic rugose corals, trilobites, nautiloids, and gastropods also occur. Composition of the "*Sinathyris* Fauna" and the abundant accompanying thin-shelled tentaculitids suggests a quiet, relatively deep-water marine environment.

While in central Guangxi Province, where carbonate platform facies developed from the late Early Emsian, the "*Spirifer tonkinensis* Fauna" was succeeded by the "*Howellella fecunda–Reticulariopsis ertangensis* assemblage", preserved in calcareous mudstone and marl and mainly comprised of spiriferids, athyrids, rhynchonellids, etc. (Chen, 1983). Accompanying taxon include tabulate corals, rugose corals, gastropods, bivalves, and also the conodont *P. perbonus* (Yu & Yin, 1978). This brachiopod fauna is approximately contemporary with the "*Sinathyris* Fauna" in Nandan, but is of a much higher diversity and lived in a relatively shallow-water environment.

After the Emsian, divergent patterns of brachiopod faunal replacement were associated with differentiation of the basinal facies and carbonate platform facies in South China, which continued through the rest of Devonian.

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Palaeobiogeography and evolutionary affinities of the Early Frasnian brachiopod fauna from Central Poland

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The Early Frasnian (*transitans* Zone) brachiopod fauna from the Holy Cross Mountains, central Poland consists of 41 species representing a shallow-water community (*e.g.*, Wietrznia; Baliński, 2006) and a deeper-water community, taxonomically unique on a global scale (*Biernatella lentiformis*

Assemblage, Józefka; Baliński et al. 2016). The palaeoecology of the latter is presented in detail by Baliński *et al.* (2018). The object of the present communication is the palaeobiogeography and historical analysis of the brachiopod fauna as a whole.

The aim of the palaeobiogeographical analysis was twofold: first, the elucidation of the biogeographic pattern for the given time slice within the Late Devonian; secondly, methodological questions, like the choice of the initial database (genera vs. species), of the time interval, and of mathematical methodology (see below for details). Two of these three problems were listed by Halamski (2008) in a palaeobiogeographical analysis of Middle Devonian brachiopods, but a consensus approach has not yet been agreed.

Primary data consist of a binary (presence-absence) matrix of 298 brachiopod species from eight regions (Poland, southern Laurussia, eastern Laurussia, western Laurussia, Gondwana excl. Australia, Australia, South China) and a genus-level matrix (117 genera) derived from it. The analysis has been carried out using three co-occurrence matrices (species, genera, reduced genera), similarity measures (three 'classical', Jaccard, Dice-Sorensen and Ochiai, and one probabilistic, Raup-Crick), and five linkage methods (single, average between groups, average within groups, complete, and centroid). In total, 108 dendrograms were obtained. Similarities between dendrograms are correlated first with the matrix used for their construction, to a lesser extent to the linkage method, whereas the similarity measure used has very little influence on the shape of the dendrograms. Best (biologically and/or historically interpretable) results were obtained with a genus-level co-occurrence matrix insofar as the species-level matrix turned out to be largely unreliable due to taxonomic bias (an improbable value of 91% of endemic species). The genus-level matrix is biased due to the impossibility of taxonomic standardisation. The genus-level matrix without cosmopolitan taxa (reduced; recommended by a few previous workers) proved to introduce a major bias. Using and comparing both species- and genus-based similarity analyses is thus recommended as a standard procedure in palaeobiogeography.

Early Frasnian brachiopod faunas cluster into two distinctly separated groups corresponding to the New and Old World, distinctly to previously reported brachiopod-based patterns and similarly to foraminifer-based patterns (Aretz *et al.*, 2014). Palaeobiogeographic units were explained above by palaeogeographic proximity.

A diachronic analysis of Middle to earliest Late Devonian brachiopod faunas from central Poland is based on four rich assemblages belonging to a generally similar deeper-slope fore-reef biofacies (*brachiopodetum*): lower Skały beds at Skały (late Eifelian; 44 species, Biernat, 1966; Halamski and Zapalski, 2006 and refs therein); upper Skały beds at Świętomarz (early Givetian; 30 species, Halamski, 2004); late Givetian at Laskowa (Racki *et al.*, 1985; revision in progress); Early Frasnian (46 species – 29 at Józefka, 20 at Wietrznia, and 5 at Dębnik). The question is: in each fauna, which lineages have evolved in place and which result from immigration events? The methodology is a modification of that by Brett *et al.* (2009) for eastern North America.

26 species out of 46 apparently represent lineages evolving in place, 5 represent lineages having migrated from the west, 1 probably from the south, and 15 from an unknown direction. Given the high ratio of lineages evolving in place (57%), the area of the present Holy Cross Mountains may be considered an important centre of brachiopod evolution during the Devonian.

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Keynote lecture

The rise of the rhynchonelliform brachiopods: the role of the Great Ordovician Biodiversification Event

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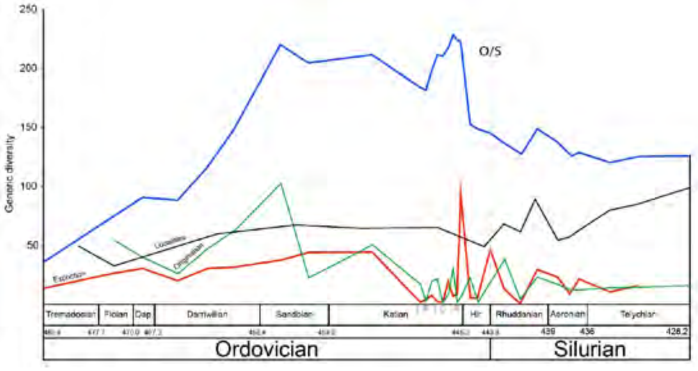
Most of the key Early Palaeozoic rhynchonelliform groups (Harper et al. 2017) and their lifestyles (Topper et al. 2018) were already established during the Cambrian, though the subphylum lacked visibility during the late Cambrian (Furongian) gap. Associations dominated by billingsellides, protorthides and syntrophides were dominant in later Cambrian faunas, particularly around the tropical parts of Gondwana. The Great Ordovician Biodiversification, however, confirmed the rhynchonelliforms as the dominant benthos for the rest of the Palaeozoic. The GOBE was complex, involving a series of sequential changes, rooted in the diversification of the plankton that had implications for the benthos and nekton together with reef building organisms and structures (Harper & Servais 2018). Three pulses of diversification have been identified within the Brachiopoda, the most marked (Figure), during the Middle Ordovician (Darriwilian), was associated with global cooling associated with the initiation of an ice-house world (Rasmussen et al. 2016). Within the rhynchonelliforms, articulatory systems together with their adductor and diductor muscle sets were fine-tuned and platforms in both ventral and dorsal valves appeared across the subphylum; taxa with sophisticated lophophore supports arose later in the period, to diversify following the Late Ordovician Mass Extinction (Finnegan et al. 2017).



Ordovician generic brachiopod diversity, illustrating changing diversity through the seven Ordovician time-slice together with three for the Silurian, indicated by maximum number of genera (blue) and maximum number of localities together with extinction and origination curves, modified after Harper et al. (2013).

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Plenary lecture

Living Brachiopods: hanging on or fit for a modern world?

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It is very easy to portray living brachiopods as examples of ‘Nature’s losers’. Certainly they are a shadow of their former successes in both Palaeozoic and Mesozoic shallow seas. But are they just hanging on? How have they been impacted by increasing biotic interactions of the Mesozoic Marine Revolution? How will they cope with rapidly changing climate and ocean chemistry?

Much of what is known about the biology of modern brachiopods has been acquired piecemeal, often by palaeontologists seeking to breathe life into their fossils. Relatively few taxa and geographic regions have been studied in any detail and there are notable holes in what we know. Much (though not all) of the really detailed biology we have is focussed on the Antarctic species *Liothyrella uva*. The Antarctic fauna is dominated by long-lived, slow growing organisms with exceptionally low metabolic rates and which are used to living in highly seasonal environments. How generally can the *L.uva* data be applied to other living brachiopods? In this talk I will try to collect together key life history/morphological traits from a range of living brachiopods to attempt to identify patterns and to discuss their capacity to adapt to environmental and biotic stressors (e.g. shell repair – Harper & Peck (2016)) both in the last 100 million years during the ‘Mesozoic Marine Revolution’ and in the future. Does the current distribution reflect a group driven into refuges? And if so what happens if those refuges disappear? In doing so I will highlight prominent gaps in our knowledge and hope to suggest fruitful avenues for research on living brachiopods which may further address these questions.

The world's oceans are changing. IPCC (2013) predictions suggest that by the end of the current century our seas will be warmer and their pH significantly lower. Although this will be a challenge to all organisms, how will it impact brachiopods? Given that they have a higher proportion of mineralised tissue than virtually any other invertebrate group what will be the threat to them either in terms of growing their shells in the first instance or repairing and maintaining that shell once it is made? In this talk I will review a series of experiments and historical studies undertaken with Emma Cross and Lloyd Peck (Cross et al., 2015, 2016, 2018) that seek to explore the answers to these questions.

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Plenary lecture

Brachiopod Phylogeny in the Cambrian

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Brachiopods are richly represented in the rock record and as early as the Cambrian, where they show an impressive diversity of form and in shell morphology (e.g., Harper et al., 2017). Presently, the group is firmly rooted within the lophotrochozoan branch of the bilaterian tree based on molecular data. Our research has identified some members of the enigmatic Early Cambrian organophosphatic tommotiids as belonging to the brachiopod stem (e.g., Holmer et al., 2002). Subsequent discoveries of the first-ever articulated scleritomes of *Eccentrotheca*, *Paterimitra*, and the inferred bivalved scleritome of *Micrina* from the lower Cambrian of South Australia reveals these three tommotiid taxa as likely lophophorate sessile filter feeders, which in the *Paterimitra* includes a preserved pedicle tube (Skovsted et al., 2008, 2009; Holmer et al., 2008, 2011). It is likely that the Brachiopoda may have evolved, by sclerite reduction and modification, from a sessile, scleritome tube-dwelling *Eccentrotheca*. *Micrina* and *Paterimitra* also preserve traces of their earliest ontogeny, including bivalved larval shells with evidence of the earliest larval attachment. The conjoined bivalved shell of adult living brachiopods most likely represents a plesiomorphic character retained from planktic tommotiid larvae; the crown group body plan probably evolved independently in living linguliform and rhynchonelliforms (Holmer et al., 2011; see also Zhang et al., 2018a,b). Studies of new records of exceptionally preserved soft-bodied fossil assemblages (Konservat-Lagerstätten) are also critical. For example, we have now been able to reassess highly problematic Chengjiang fossils such as the *Cotyledion* as a sclerite-covered sessile tube-shaped probable stem "lophophorate" (Zhang et al., 2013). We have also recognized *Yuganotheca* from the Chengjiang as a tubular, agglutinated stem lophophorate (Zhang et al., 2013). This observation adds to our understanding of more derived brachiopods, such as linguliforms, obolellates and rhynchonelliforms (e.g., Zhang et al., 2009, 2014, 2015; Holmer et al., 2018a). Exceptionally preserved pedunculated Cambrian rhynchonelliforms from both the Chengjiang and Utah also indicate that early members of this most important group of living brachiopods had two widely different types of pedicles (Holmer et al., 2018a, b). Despite these new findings, many aspects of the phylogeny and radiation of the Brachiopoda in the Cambrian remain problematic and controversial issues. Presently only two of the three major brachiopod clades, the Linguliformea and the Rhynchonelliformea, have known Cambrian representatives. The origin and phylogeny of the Craniiformea remains problematic, but it is possible that Cambrian rhynchonelliform chileate-like brachiopods are involved in the processes.

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Diversification patterns of brachiopods after the end Ordovician mass extinction and its palaeobiogeographic significance

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The Late Ordovician biotic crisis was associated with a brief but intense glaciation episode in earth history. Post-glacial marine transgression created vast habits in epicontinental seas, in which benthic faunas established and diversified, with brachiopods being one of the most abundant and diverse fossil groups. Based on detailed data of brachiopod occurrences after the end-Ordovician mass extinction, together with newly published data, we analyzed the diversification patterns of brachiopods from the Rhuddanian to the Aeronian (early Silurian) by Network Analysis (Fig. 1) and Frequency Distribution Analysis. Rhuddanian brachiopod faunas were characterized by low diversity and localized high abundance, except for a relatively high-diversity early Rhuddanian fauna in Avalonia-Baltica and South China. Invariably, these faunas were predominated by re-established holdover and once-cosmopolitan taxa from the Late Ordovician, primarily orthides and strophomenides. By the Aeronian, global brachiopod diversity nearly doubled in comparison with the Rhuddanian, owing to a major diversification of Silurian-type brachiopods in both the paleotropics and high-latitude Gondwana, as well as the concomitant proliferation of endemic and cosmopolitan taxa, in association with a global expansion of epicontinental seas and heterogeneity of specialized local habitats. A drastic turnover of brachiopods from the Ordovician to the Silurian type significantly affected the Paleozoic evolutionary fauna. With the ordinal data of brachiopods in major palaeoplates, we discussed the turnover process. Compared with Ordovician orthides and strophomenides, which globally increased their diversity after the extinction, atrypides and pentamerides of Silurian group displayed a drastic diversification from Rhuddanian to Aeronian only in lower latitude continents, demonstrating the two new orders preferred more warm water environments than the Ordovician groups. Atrypides recovered from the early Rhuddanian, whereas diversification of pentamerides delayed until to Aeronian, and this is typically demonstrated by the record of many endemic taxa from South China. The Silurian-type atrypide and pentameride communities thrived mainly in relatively shallow environments (BA2–3) during the Rhuddanian, but expanded and dominated in deeper, mid-shelf and outer-shelf settings (BA3–5) by the Aeronian (Huang et al., 2018).

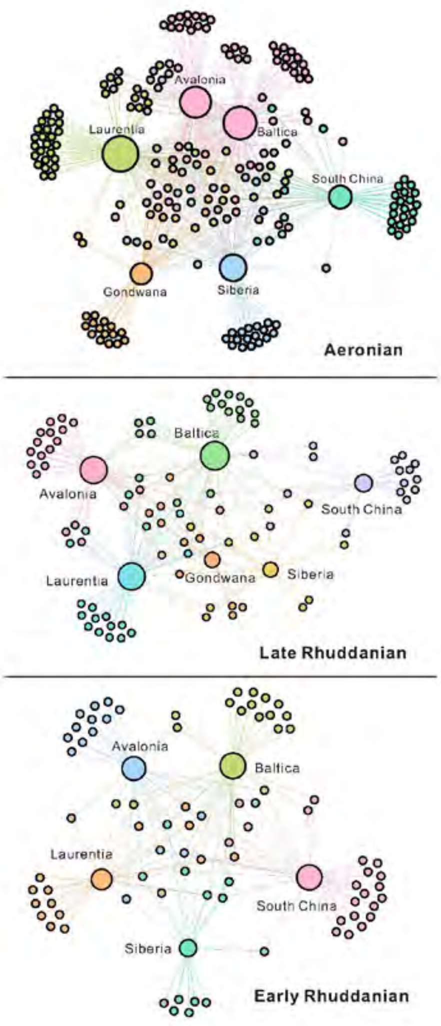

Fig. 1 Network diagram showing the diversified process through three time interval. The diversity of both cosmopolitan and endemic taxa among major palaeoplates is increasing, and the palaeoplates are more closing connected.

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Brachiomatic: Utilising new museum collections digitisation protocols to examine brachiopod size across extinction boundaries cases

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Brachiopods are useful for understanding how biota have responded to environmental changes in deep time. Museums are increasingly digitising collections, using high-throughput workflows based on rapidly imaging material. We are interested in whether these images can be used to collect standardised morphological data more efficiently to document changes in size across intervals of past environmental change. Using a collection of fossil brachiopods spanning the Early Toarcian hyperthermal event, we aim to test whether body size measurements generated automatically from images of specimens are more accurate, more precise and quicker to generate than measurements made by hand of the physical specimens. We completed a pilot study of a collection of 1200 brachiopods from the Jurassic of Spain. The results show that image quality and specimen orientation are important for the automated extraction of size data. Precision varies between taxa: automated measurements from those which are harder to orientate (smaller specimens) or which are harder to balance (lateral and anterior) are less precise. Precision of measurements using callipers also varies between individual researchers. Overall, length and width are more precise than depth using both methods. An additional benefit of the automated approach is better reproducibility compared to manual measurements.

Stage one in the process: Digitisation.

An immunological study of the shell matrix protein ICP-1 in brachiopods

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Brachiopod shells contain matrix proteins, which are considered to have crucial roles for shell formation. Recently, proteomic identifications of skeletal proteins have been performed across a wide range of animal phyla, and the amount of sequence information of skeletal proteins is explosively increasing. In brachiopods, *de novo* sequencing by tandem mass spectrometry (MS/MS) was performed on the three rhynchonelliforms *Gryphus vitreus*, *Terebratella sanguinea* and *Aerothyris kerguelenensis*, and MS/MS proteomic analysis assisted by transcriptome and/or genome data was carried out on the two rhynchonelliforms (*Magellania venosa* and *Laqueus rubellus*) and on the linguliform *Lingula anatina* (Immel et al., 2015; Isowa et al., 2015; Jackson et al., 2015; Luo et al., 2015). In the previous study of *L. rubellus*, we identified a complete sequence of ICP-1, which is originally identified from the three rhynchonelliform brachiopods *Neothyris lenticularis*, *Calloria inconspicua*, and *Terebratella sanguinea* by Edman degradation and predicted to be the most abundant protein in the shell (Cusack et al. 1992). In this study, we prepared a specific antibody against a synthetic peptide designed from the ICP-1 sequence of *Laqueus rubellus* (*Lr*ICP-1), and verified the binding specificity of the antibody using the shell extracts from *L. rubellus*. Dot blotting indicated that antigenic determinants exist in the shell extracts. Western blotting showed a single band at approximately 60 kDa, which is substantially higher than the molecular mass expected from the theoretical amino acid sequence of ICP-1 (17.5 kDa). One possibility is that *Lr*ICP-1 undergoes post-translational modifications. Searches using NetNGlyc 1.0 Server (http://www.cbs.dtu.dk/services/NetNGlyc) indicated that *Lr*ICP-1 has one potential glycosylation site. To confirm this, three major bands in the SDS-PAGE for total shell extracts including a band of approximately 60 kDa were cut out from the gel, and in-gel digestions were carried out with trypsin. We shall report the sequences of those digested peptides at the conference.

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Evolution, stratigraphy and palaeobiogeography of late Pridolian–early Eifelian brachiopods from the Rhenish Massif (Germany)

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The present revision of late Pridolian–early Eifelian brachiopods from the Rhenish Massif provides a steady flow of new implications for brachiopod taxonomy, biostratigraphy, evolutionary dynamics, palaeoenvironments and palaeobiogeography; the main results have recently been summarized (Jansen, 2016). Classic taxa are revised and partly subdivided into stratigraphically significant new species and subspecies. Evolutionary change is discernible in genera of different orders, for example in *Arduspirifer*, *Euryspirifer*, *Paraspirifer*, *Plicostropheodonta*, *Rhenostropheodonta*, *Iridistrophia*, *Platyorthis*, *Sartenaerirhynchus* and *Cryptonella*. Spiriferide brachiopods are most suitable for biostratigraphic subdivision: 22 taxon range zones from the upper Pridolian to lower Eifelian are proposed. Vertical distribution patterns of numerous brachiopod taxa show the presence of succeeding 'faunas' named after characteristic spiriferide species (Fig. 1). Faunal turnovers separating these are attributed to regional faunal events or crises in the context of short or more extended phases of palaeoenvironmental change, possibly triggered by rapid eustatic sea-level fluctuations in combination with varying crustal subsidence and sedimentation rates. Relationships to global events are possible but not easy to substantiate. The 'Variscan succession' in the Ardenno-Rhenish area starts with an extensive transgression referred to the 'Köbbinghausen Event' (new) in the late Pridoli which leads to immigration of the *Quadrifarius dumontianus* Fauna. The stratigraphic range of this fauna corresponds to the 'lowermost

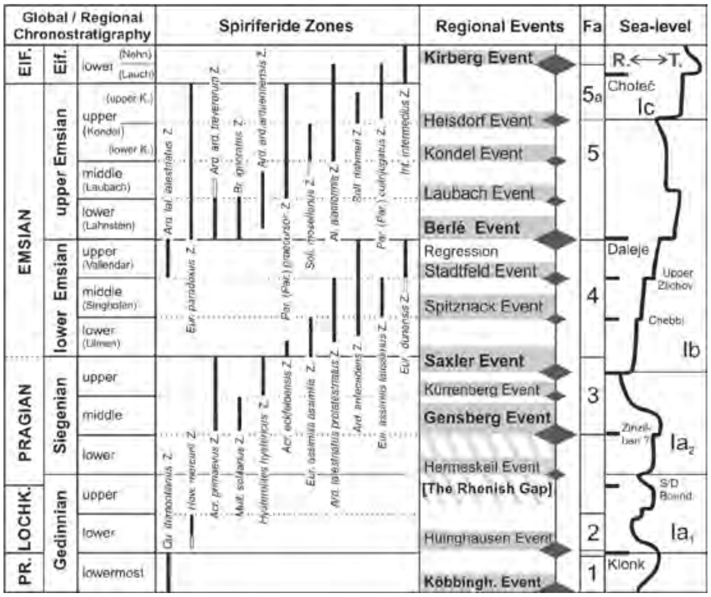

Fig. 1: Spiriferide zones, regional events, faunas (Fa) and sea-level fluctuations with the suggested position of global events documented in the upper Pridolian to lower Eifelian successions of the Rhenish Massif (from Jansen 2016, emended; more explanations and references in that work). Diamonds symbolize the regional events, the size of the diamonds the suggested importance of these. The extent of the 'Rhenish Gap' *sensu stricto* is indicated. Lochk., Lochkovian; K., Kondel; Köbbingh., Köbbinghausen; R., Regression; S/D Bound., Silurian/Devonian Boundary; T., Transgression; Z., Zone. Faunas: 1, *Quadrifarius dumontianus* Fauna; 2, *Howellella mercurii* Fauna; 3, *Acrospirifer primaevus* Fauna; 4, *Arduspirifer antecedens* Fauna; 5, *Euryspirifer paradoxus* Fauna; 5a, *Paraspirifer cultrijugatus* Fauna.

Gedinnian'. The succeeding regional events resulted in shelf-wide or more regional extinction or emigration of substantial parts of a brachiopod fauna and subsequent replacement by a largely new one. New species dispersed across the Rhenish Shelf after they had either evolved by allopatric speciation in small isolated populations with reduced gene pool or immigrated from outside. The 'Rhenish Gap' in the upper Lochkovian–lower Pragian represents an interval of 6–8 myr with deltaic to terrestrial conditions and therefore a lack of brachiopod faunas with the exception of local pararhenotypic assemblages. The significance of this gap was underestimated for a long time resulting in incorrect stratigraphic and palaeobiogeographic conclusions. The 'Heisdorf Event' (new) corresponds to the onset of the '*Paraspirifer cultrijugatus* Fauna'. This fauna went extinct with the 'Kirberg Event' (reintroduced term, = previous "OCA Extinction Event") in the earliest Eifelian.

The Rheic Ocean represented a 'soft' barrier to migration resulting in restricted faunal exchange between the Rhenish and North Gondwanan shelves in the Lochkovian. Faunal relationships increased with its narrowing during the Pragian–Emsian. The width of this ocean was probably only some hundreds or near 1,000 km wide whereas values of 4,000–6,000 km as suggested in some recent reconstructions for the Emsian are highly improbable. A number of Rhenish species appearing, for example, with the 'Gensberg Event' at the beginning of the mid-Siegenian (~ mid-Pragian in the original sense) migrated from North Gondwana. Based on large material and side-by-side comparisons of specimens it is concluded that the studied brachiopod faunas from the Rhenish Massif belonged to a discrete 'Rhenish Province' (including, e. g., Ardennes, Rhenish Massif, SW England, Artois, Poland). Palaeobiogeographic affinities to a 'North Gondwana Province' (including, e. g., Ibero-Armorica, Central Bohemia, North Africa) existed at the genus and species levels; the ensemble of both provinces represented a 'Maghrebo-European Realm'.

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Morphological plasticity in the early diversification of the post-extinction Silurian Pentameride fauna

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During the first pulse of the Late Ordovician mass extinction event, brachiopods were among the heavy casualties, with the pentameridine suborder reduced to a thin hanging thread in the Hirnantian Stage worldwide. By the early Silurian, however, the shallow marine shelly fauna became rapidly dominated globally by the usually large-shelled pentameridine brachiopods in terms of diversity and substrate space occupancy. Their origin and early evolution, therefore, was a striking case of near total extinction during the latest Ordovician, represented by a single genus *Brevilamnulella* during the Hirnantian. The rapid diversification and rise to dominance of the pentamerides, in contrast, demonstrated extremely rapid radiation at the ordinal level, analogous to the collapse-and-boom evolution of ammonoids from the end-Devonian, end-Permian, and end-Triassic near-extinctions.

Pentameride brachiopods originated during the middle Cambrian and became extinct near the end of the Devonian. Its early evolution in the Cambrian and Ordovician was mostly confined to the suborder Syntrophiidina. By the Late Ordovician, syntrophiidine diversity had declined substantially, with a concomitant rise of the suborder Pentameridina, especially manifest in the large-shelled family Virgianidae throughout the paleotropical carbonate depositional environments during the late Katian. This thriving marine shelly fauna, however, was punctuated by the Hirnantian glaciation and mass extinctions. During the Hirnantian, a generally small and thin-shelled genus, *Brevilamnulella*, was the only survivor of the Pentameridina, known from Laurentia, Kolyma, Siberia, Baltica, Kazakhstan, and South China. Its wide distribution during the major biotic crisis suggests that *Brevilamnulella* was a generalist or opportunist that could survive in a wide range of paleoecological conditions.

From the late Hirnantian to earliest Silurian (early Rhuddanian), *Brevilamnulella* went through rapid morphological transformations to adapt to a wide range of water depth and substrate conditions, and gave rise to three major pentameridine groups (the virgianids, stricklandiids, and clorindids), which in turn went through several pulses of radiations within their own clades in post-Rhuddanian times (notably the rise of pentamerids from virgianids) to become the dominant shallow marine shelly fauna, especially in tropical environments. From a small, subcircular, moderately biconvex, weakly ribbed shell of *Brevilamnulella*, the large, strongly ventribiconvex and variously ribbed virgianids evolved to dominate the inner- to mid-shelves by the late Rhuddanian, and the smooth virgianid *Borealis* gave rise to *Pentamerus* and pentameroid desendents that went through major diversifications from the mid Llandovery to Ludlow. During the Rhuddanian, both *Stricklandia* and *Clorinda* can be traced to the ancestral stock of *Brevilamnulella*, with the stricklandioids evolving towards a large, often flattened, strophic shell with distinct interareas and a relatively wide hingeline to adapt to relatively deep-water, soft muddy substrate in mid- to outer-shelf environment. The clorindioids retained a relatively small shell, but evolved towards a globular, tumid ventral umbo, to specialize in living in low-energy, deep water, on muddy substrates in the outer-shelf environment. The early Silurian diversification of pentamerides from *Brevilamnulella* was the result of rapid exploration and establishment in a wide range of ecological niches from shallow, high-energy settings to deep and quiet outer-shelf environments, left largely "empty" by the Late Ordovician mass extinction event.

Major marine carbon cycle perturbations during the Permian-Triassic mass extinction

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The Permian-Triassic boundary-interval (PTB) witnessed the most severe environmental crisis in Earth's history, which dictated the course for evolution of life until today. Current lines of evidence on causation point towards massive flood-basalt magmatism from Siberian Traps, inducing a combination of global warming by ~6°C, substantial input of relatively light carbon to the atmosphere, sporadic to widespread anoxia or euxinia, and ocean acidification, however, the trigger mechanism and its feedbacks are yet to be fully understood. In order to reconstruct the potential changes in seawater chemistry during this time interval, we examined the boron isotope composition ($\delta^{11}B$) of brachiopod shells. Although to-date hardly applied in Paleozoic settings, the $\delta^{11}B$ of marine biogenic carbonates is considered to be one of the most reliable paleo-pH proxies (e.g., Gutjahr et al., 2017). Brachiopods present an advantageous and largely underutilised archive for Phanerozoic reconstructions considering their high abundance in the geological record and its origin dating back to the Early Cambrian.

Moreover, their low-magnesium calcite shell renders them more resilient to post-depositional diagenetic alteration of primary chemical signals. Using carefully chosen pre-screened (Brand et al., 2012) pristine specimens (class Rhynchonellata and Strophomenata), selected $\delta^{11}B$ to pH relationships, and bulk seawater $\delta^{11}B$ scenarios we present a high-resolution seawater pH record for the Tethys Ocean. This interval covers the negative carbon isotope excursion in excess of 4 ‰ and is associated with major climate and environmental changes that led to the mass extinction event. Our results show a significant decline in $\delta^{11}B$ values succeeding the $\delta^{13}C$ excursion, suggesting substantial and lasting suppression of seawater pH at the onset of the extinction event in the Late Permian related to carbon cycle perturbations. Combining our pH record with paired $\delta^{13}C$ data and a quantitative modelling approach, we delineate unfolding carbon cycle dynamics that may have been responsible for initiating the catastrophic extinction. Using a new redox-resolving ocean model we determine the series of changes in the ocean chemistry that may have lead to the gradual collapse of marine ecosystems terminating in the Early Triassic, which enables us to assemble the first congruent reconstruction of events throughout and post PTB mass extinction.

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Major and trace element composition and microstructure of cultured brachiopods – New proxies?

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Reconstructing past seawater composition is fundamental for understanding the long-term geochemical processes and the functioning of Earth's systems. While brachiopods present an advantageous archive for Phanerozoic paleo-reconstructions owing to their good preservation and abundance in the geological record, their proxy relationships have been hardly examined under controlled laboratory conditions. In contrast to other marine calcifiers only little is known regarding the mechanisms that control the incorporation of various key elements into brachiopod calcite. To evaluate the feasibility and robustness of multiple calcium-to-element ratios proxies we cultured *Magellania venosa*, *Terebratella dorsata* and *Pajaudina atlantica* under controlled experimental settings over a period of more than one year with closely monitored ambient conditions, carbonate system parameters and elemental composition of the culture seawater. The experimental setup used in this study includes control aquariums and treatments where the temperature, pH, and Mg/Ca composition of the seawater were manipulated. Using a solution-based ICP-MS mini-bulk approach as well as high spatial resolution electron microbe maps we investigated the incorporation of several major and trace elements (Li, B, Na, Mg, Al, Ca, Mn, Fe, Zn, Sr, Cd, Ba, Nd, and U) into brachiopod calcite. To assess the effects of prolonged severe warming, acidification and chemical change of the seawater on the brachiopods and examine their potential links to the shell structure, we investigated the variations in shell density and punctae occurrence using micro-computed tomography (micro-CT). Combining the two approaches, we aim to provide new constraints for paleo-proxy applications. Emphasise will be also placed on the effect of extreme ambient condition on brachiopod survival and growth and their mechanisms to cope with such environmental changes – a key ability to withstand the increasing anthropogenic pressures.

Geochemical and physiological responses of brachiopods to ocean acidification – New insights from boron isotopes

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CO_2-induced ocean acidification and associated decrease of seawater carbonate saturation state contributed to multiple environmental crises in the past and presently poses a major threat for marine calcifying organisms. The boron isotope ($\delta^{11}B$) composition of marine calcifiers is considered to be one of the most reliable pH proxies, permitting us to reconstruct past ocean pH as well as studying calcification processes and organism internal pH-regulatory capacities. To investigate the geochemical and physiological responses of brachiopods to prolonged low-pH conditions we cultured *Magellania venosa*, *Terebratella dorsata* and *Pajaudina atlantica* under controlled experimental settings over a period of more than one year. Our experimental setup includes a control ($pH_0 = 8.15$, $\Omega_{cal} = 10$) and two low-pH treatments ($pH_1 = 7.60$, $\Omega_{cal} > 1$; $pH_2 = 7.35$, $\Omega_{cal} < 1$), with closely monitored carbonate system parameters and elemental and isotopic composition of the culture seawater. Our experiments demonstrate that brachiopods form their calcite shells under strong biological control, which enables them to survive and grow under acidic conditions and even in seawater undersaturated with respect to calcite. Using boron isotope ($\delta^{11}B$) systematics including MC-ICP-MS as well as SIMS analyses, validated against in vivo microelectrode measurements, we show that this is achieved by strict biological regulation of the calcifying fluid pH between the epithelial mantle and the shell. We provide a culture-based $\delta^{11}B$–pH calibration, which as a result of the internal pH regulatory mechanisms deviates from the borate ion to pH relationship, but confirms a clear yet subtle pH dependency for brachiopods and thus their potential for application as an archive in paleo-pH and paleo-pCO_2 reconstructions. At a micro-scale level, the incorporation of $\delta^{11}B$ appears to be principally driven by a physiological gradient across the shell, where the $\delta^{11}B$ of the innermost calcite records the internal calcifying fluid pH, while the composition of the outermost layers is influenced by seawater pH, rather than the different biomineralization processes between the primary and the secondary layer. These findings have implications for past climate studies, as well as research on calcification processes and physiological adaptations to environmental change (e.g. current global ocean acidification).

The ecology of brachiopods in ancient methane-seep environments

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Brachiopods were thought to have dominated deep-sea hydrothermal vents and hydrocarbon seeps for most of the Paleozoic and Mesozoic, and were believed to have been outcompeted and replaced by chemosymbiotic bivalves during the late Cretaceous. But recent discoveries of bivalve-rich seep deposits of Paleozoic and Mesozoic age have questioned this paradigm. By tabulating the generic diversity of the dominant brachiopod and bivalve clades from hydrocarbon seeps through the Phanerozoic, we show that their evolutionary trajectories are largely unrelated to one another, indicating that they have not been competing for the same resources. Whereas chemosymbiotic bivalves mostly rely on sulfide-oxidizing symbionts for nutrition, for the brachiopods bacterial aerobic oxidation of methane likely played a more prominent role. The availability of hydrogen sulfide and methane at seeps is governed by geochemical gradients and marine sulfate concentrations. Low sulfate concentrations result in low rates of sulfate-driven anaerobic oxidation of methane and consequently more methane is available to aerobic oxidation. Assuming lower marine sulfate concentrations during the Mesozoic compared to the Cenozoic, and consequently higher methane concentrations above the sediment surface at seeps, Mesozoic seeps facilitated colonization by epifaunal brachiopods. Thus, rather than competition, geochemical gradients and ocean chemistry are considered to have controlled the distribution and diversity of brachiopods and bivalves at hydrocarbon seeps throughout the Phanerozoic.

Geochemical study of *Megathiris detruncata*, a brachiopod species known since the Eocene in Europe

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The *Megathiris* genus belongs to the Family Megathyrididae in the Order Terebratulida. Their ventral and dorsal valves contain low-Mg calcite. *M. detruncata* can have variable external morphology but based on internal structures it is easily recognizable. The species is one of the most common micromorphic brachiopod in shallow water marine environments of the Mediterranean and the eastern North Atlantic (Logan, 2007). It commonly occurs at depths between 15 and 200 metres, but have been observed as deep as about 900 metres as well. It is a sessile form and generally fixes itself with a short pedicle to hard substrates. The species is known since the late Eocene and, with this long fossil occurrence, it represents a valuable record to see whether and how it was affected by the Cenozoic climatic and environmental changes, and whether it could be used as a paleo-archive for the past.

Here, we present stable isotope composition ($\delta^{13}C$, $\delta^{18}O$) and trace element ratios (e.g., Mg/Ca, Sr/Ca) of modern and fossil specimens derived from 46 locations of 13 countries (Eocene: Italy, Austria; Oligocene: Hungary, France; lower Miocene: Germany; middle Miocene: Hungary, Poland, Romania, Austria; middle and upper Miocene: Malta; lower Pliocene: Italy, Spain; upper Pliocene: Greece, Spain; Pleistocene: Italy; Recent: Turkey, Italy, Spain, Morocco). The study is divided into two parts, one regarding the recent forms that come from the Mediterranean Sea (southern Italy, west coast of Turkey) and the Atlantic Ocean (Madeira, Canary Islands, Morocco), and the second focusing on the fossil brachiopods covering a time range of late Eocene - Pleistocene. Results from the modern samples are used as a base line when interpreting data from the fossils. The modern samples yielded similar stable isotope ranges indicating similar ecological conditions for the living brachiopods. The slightly lower average $\delta^{18}O$ value in the Atlantic specimens could reflect lower $\delta^{18}O$seawater composition and in few cases a deeper habitat. Generally, all the data agree well with the range of environmental temperature reported from the region (Schmidt et al., 1999).

The fossil samples yielded more scattered geochemical data. Most of the Miocene localities from the Paratethys (Austria, Hungary and Romania) yielded stable isotope results that overlap with the modern dataset of positive $\delta^{18}O$ and $\delta^{13}C$ values. On the other hand, for some Pliocene and Miocene Mediterranean coastal fossil localities (Malta, Spain), much lower isotopic compositions were obtained where both isotope systems show negative values with some as low as -5‰. Interestingly, for the older Oligocene and Eocene samples (Austria, France, and Italy), only $\delta^{18}O$ reach such negative values, but the δ13C data range is in similar to modern samples. These offsets from the modern base line could be explained by three factors (1) changing habitat, (2) environmental differences such as different temperature and/or $\delta^{18}O$seawater at the time, and (3) alteration of shells during diagenesis. Scanning electron microscope images with well-preserved internal structure versus recrystallized shells together with trace element composition would help further assessing among these factors.

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Support of the "brachiopod fold hypothesis" in recent rhynchonelliformeans: a new view on the evolution of brachiopod life cycles

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The brachiopods are invertebrates with a pelago-benthic life cycle. All adult brachiopods are similar in body plan, but the organization and life style of planktonic stages strongly vary among all three brachiopod subphyla. Though the monophyly of brachiopods is generally accepted, the evolution of their life cycles remains unclear.

Investigation of the structure and metamorphosis of larvae of the craniiformean *Novocrania anomala* allowed the "brachiopod fold hypothesis" to be proposed, which purports to explain the formation of the body plan of recent brachiopods (Nielsen, 1991; Cohen et al., 2003). The lecithotrophic larva of *N. anomala* consists of anterior and posterior lobes. The larva of *N. anomala* has a pair of coelomic pouches in the anterior lobe and three pairs of coelomic sacs in the posterior lobe arranged one after another along the anterior-posterior axis (Nielsen, 1991). The posterior lobe bears three pairs of setal bundles. At settlement, the third pair of setae is shed and the larva curls ventrally and, therefore, both valves seem to be secreted by the dorsal epithelium of the larva. The metamorphosis of recent craniids is supposed to be a recapitulation of the origin of the brachiopod body plan by the folding of a creeping ancestor to evade attack by predators.

The "brachiopod fold hypothesis" has been subjected to criticism based on the re-investigation of *N. anomala* larval metamorphosis and developmental gene expression data (Altenburger et al., 2013; Martín-Durán et al., 2016; Altenburger et al., 2017). The secretion of both valves on the dorsal side of the larva was not confirmed, though they definitely described the ventral curvature of larvae at settlement: "The anterior lobe and the posterior end of the posterior lobe are bent ventrally, thus exposing the dorsal posterior lobe to the environment" (Altenburger et al., 2013, page 381). According to Altenburger et al. (2013), only the dorsal mantle forms during metamorphosis, whereas the ventral mantle develops 17 days after metamorphosis. The expression patterns of developmental genes in larvae of *N. anomala* show that "anterior" genes are expressed in the anterior lobe and "posterior" genes are expressed in the posterior domain of the posterior lobe (Martín-Durán et al., 2016; Altenburger et al., 2017). However, as these data are relevant to the unbent larva they cannot be considered to be convincing in an argument against the "brachiopod-fold hypothesis."

We assume that the primary ancestral brachiopod life cycle included true planktotrophic larvae with ciliary bands that are typical of benthic invertebrates. During metamorphosis the larvae bend on the ventral side. The life cycle of recent craniids evolved from this ancestral life cycle with the difference that the larvae lost primary planktotrophy and became lecithotrophic. How could other types of brachiopod life cycles evolve?

The purpose of the present research is to study in detail the development of rhynchonelliformean *Coptothyris grayi* (Terebratulida) using scanning electron microscopy and confocal laser scanning microscopy, to analyze data on the ontogeny of recent brachiopods, and to propose a hypothesis of the evolution of brachiopod life cycles.

The larvae of *C. grayi* were studied in the laboratory using the method of artificial insemination. The early ontogenetic stages of *C. grayi* are similar to those of many rhynchonelliformean brachiopods. All floating stages of recent rhynchonelliformeans are lecithotrophic. Young larvae consist of apical and posterior lobes separated by the first constriction. The rudiment of the mantle lobe forms obliquely: its dorsal side is displaced anteriorly and its ventral side is displaced posteriorly. Cytochemistry revealed a pair of coelomic pouches in the apical lobe and two pairs of pouches in the rudiment of the mantle lobe. The last two pairs are obliquely arranged (the first dorsal pair is shifted anteriorly, the second lateral pair is shifted posteriorly). The mesoderm of coelomic pouches participates in the formation of setal sac musculature as was shown for craniids (Nielsen, 1991). Unlike the craniids, whose coelomic pouches and setal bundles are successively arranged along the anterior-posterior axis, the coelomic pouches and setal bundles of *C. grayi* larva are obliquely arranged on the dorsal and lateral sides. Hence it may be assumed that the young larva of *C. grayi* with an oblique rudiment of the mantle lobe corresponds to the larva of *N. anomala* in a semi-folded condition. The mantle lobe of a fully developed larva of *C. grayi* increases in size by growth of its dorsal sector; this stage corresponds to the folding juvenile of *N. anomala*. Therefore, the folding of recent rhynchonelliformeans occurs at the floating stage. It should be emphasized that the larva of *N. anomala* sheds the third pair of setal bundles at settlement, and thus the settled larva of *N. anomala* and floating larva of *C. grayi* have an equal number of setal bundles. The mantle reversal after larval settlement is a synapomorphy of recent rhynchonelliformeans and is not connected to the folding. Hence, the data on the development of recent rhynchonelliformeans conform to the "brachiopod fold hypothesis." As to gene expression patterns, the so-called "posterior" genes are expressed in the posterior lobe of young two-lobed rhynchonelliformean larvae (Martín-Durán et al., 2016). In young three-lobed larvae, the cdx-expression disappears, while the mesodermal genes are obliquely expressed according to the arrangement of setal sacs that conform to the "brachiopod fold hypothesis." The recent rhynchonelliformean life cycle could evolve from the primary life cycle with true planktotrophic larvae by a transition to lecithotrophy and prolongation of the floating stage of the "folded juvenile."

In recent discinids, a two-lobed lecithotrophic larva with a closed blastopore hatches out from the egg envelope. The larva consists of anterior and posterior lobes and bears three long larval setae on each side (Chuang, 1977; Lüter, 2000). We suppose that this larva, which continues to float, corresponds to the folded, settled stage of recent craniids. Later, the two-valved shell is formed. The two-valved swimming stage of recent discinids corresponds to the attached juvenile of recent craniids with the shell. In recent lingulids, all stages mentioned above (with the exception of the two-valved juvenile) are compressed within embryogenesis and the planktotrophic juvenile already has the shell and rudiment of the lophophore at hatching. Thus the life cycle of recent linguliformeans is considered to be the most evolutionarily advanced of all recent brachiopods.

Therefore, we suppose that the ancestral brachiopod had a life cycle with a ciliary planktotrophic larva (not to be confused with the shelled planktotrophic juvenile of recent lingulids), that folded during metamorphosis. The next evolutionary stage was the transition from planktotrophy to lecithotrophy, but the lecithotrophic larvae of recent brachiopods are not homologous. Recent craniiformeans retain true unfolded lecithotrophic larvae. The full-grown lecithotrophic larva of recent rhynchonelliformeans corresponds to the folded juvenile elevated to the plankton. The pelagic stage of the recent discinid life cycle comprises a folded lecithotrophic larva and two-valved planktotrophic juvenile. As to the recent lingulids, their life cycle may be considered as the most apomorphic and characterized by the embryonization of all developmental stages except for the shelled planktotrophic juvenile.

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Microbrachiopods from the Las Aguaditas and Las Chacritas formations (Middle Ordovician), Precordillera terrane of western Argentina: a preliminary taxonomic analysis

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Linguliform brachiopods from Ordovician strata of the Argentine Precordillera have received little attention in past years. Recently, however, there has been growing interest in the knowledge of their taxonomy and stratigraphic ranges. Benedetto (2015) described a Middle Ordovician lingulate brachiopod assemblage from the black shales and marls of the Los Azules Formation. Lavié and Benedetto (2016 a, b) described the linguliforms and craniiforms from the Darriwilian *Athiella argentina* brachiopod Zone of the San Juan Formation, and Lavié et al. (2017) listed two assemblages of microbrachiopods from the top of the San Juan Formation at Cerro La Chilca. On the other hand, Holmer et al. (2016) described a fauna composed of lingulids, siphonotretids, and acrotretids from the San Rafael Block (Lindero and Ponón Trehué Formations). Here we describe for the first time assemblages of lingulate microbrachiopods recovered from the Las Aguaditas and Las Chacritas Formations cropping out in the Jáchal area of the San Juan Province.

The Las Aguaditas Formation crops out on the eastern flank of the Los Blanquitos Range, in the Central Precordillera where it rests conformably on the San Juan Formation limestones. This unit includes shales, marls, limestones, and reef limestones deposited in varied deep-water environments (Astini, 1995). It consists of a 43 m-thick lower member characterized by mixed calcareous-pelitic deposits of early to middle Darriwilian age (Feltes et al. 2016), reflecting a deepening of the platform caused by a flooding event (Keller et al., 1993; Carrera and Astini, 1998). Recently, Feltes (2017) recognized in the Las Aguaditas Formation a 138 m-thick middle member and a120 m-thick upper member of Sandbian age. In the northern part of the La Trampa Range at the Las Chacritas River section, the middle Darriwilian Las Chacritas Formation is paraconformably overlain by the lower Sandbian Las Aguaditas Formation (Carrera and Astini, 1998). The Las Chacritas Formation is a 60 m-thick succession made up of fine-grained siliciclastic and carbonate sediments deposited on a continental shelf setting. According to Astini (1995), it was deposited on structural highs within the basin, which served as a reservoir of carbonate remnants. The overlying Las Aguaditas Formation represents further drowning and cessation of carbonate deposition on the platform. From a biostratigraphic viewpoint, the *Yangtzeplacognathus crassus* Zone was recognized in the base of the Las Aguaditas and the Las Chacritas formations in their respective type sections, the *Eoplacognathus pseudoplanus* Zone in the upper part of the lower member of the Las Aguaditas Formation (Las Aguaditas Creek section) and in the middle part of the Las Chacritas Formation (Las Chacritas river section), the *Eoplacognathus suecicus* Zone in the upper part of the latter unit, and the *Pygodus anserinus* and *Nemagraptus gracilis* zones in the upper part of the Las Aguaditas Formation in both study areas (Serra et al., 2015; Feltes et al., 2016).

This preliminary taxonomic study allows us to group the specimens in two high-diversity associations of Darriwilian age; however, few valves were recovered in the upper member of the Las Aguaditas Formation (Sandbian age). The two Darriwilian associations have five taxa in common, mainly dominated by a new species of the genus *Conotreta* Walcott, and include the obolid *Elliptoglossa* Cooper and the acrotretids *Eocunulus* Cooper, *Numericoma* Popov and *Scaphelasma* Cooper. Fragments of *Orbiculoidea* D'Orbigny and valves of *Opsiconidion* Ludvigsen appear only in the Las Chacritas Formation, and *Myotreta* Gorjansky, *Paterula* Barrande and *Spondylotreta* Cooper are confined to the Las Aguaditas Formation. Both associations are closely comparable to the contemporaneous faunas from Ponon Trehué and Lindero Formations (Holmer et al., 2016), and also show affinities with the Antelope Valley Limestone in Laurentia as well as the assemblages from the Kunda and Azeri Regional Stages in Baltica. The specimens recovered from the Sandbian Las Aguaditas Formation consist of rare valves assigned with doubts to *Lingulops* Hall and *Mendozotreta* Holmer et al., which do not allow us to set out their biogeographic affinities.

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Shelled archives: using brachiopods to reconstruct the seawater δ^{11}B record across the Late Paleozoic climate shift

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The Late Paleozoic was a time of climate transformation, going from a very wet Carboniferous to a very dry Early Permian. This occurred as the supercontinent Pangaea began to fully assemble, leading to extreme aridity, major changes in ocean circulation, and the demise of Paleozoic glaciation.

The extremely arid conditions of the Early Permian would have reduced delivery of continental weathering materials to the ocean. This hypothesis is supported by the dramatic decline in the seawater ^{87}Sr/^{86}Sr curve beginning just before the Carboniferous-Permian boundary and decreasing monotonically to the Late Permian (Bruckschen et al., 1999; Korte et al., 2006). The change in ^{87}Sr/^{86}Sr – particularly if it resulted from a reduction in silicate weathering – provides an important backdrop from which we can better understand controls on the δ^{11}B of seawater. As riverine discharge controlled by continental weathering is the most important source of boron to the oceans today (59% of total boron input to modern oceans) with a much lighter δ^{11}B than the ocean reservoir (average δ^{11}B of modern rivers is approximately 10‰; average δ^{11}B of modern seawater is 39.6‰; Lemarchand et al., 2002), a significant decrease in continental weathering should drive the δ^{11}B of Early Permian seawater higher as a major source of light boron isotopes is removed. However, the δ^{11}B of brachiopods across the Carboniferous-Permian transition decreases instead. In this study, we combine δ^{11}B, ^{87}Sr/^{86}Sr, and δ$^{44/40}$Ca from well-preserved brachiopods to explore the possible reason(s) for this change.

The brachiopods used in this study were collected from Carboniferous and Permian strata in the United States Midcontinent (USM), Ural Mountains (UM), and Moscow Basin (MB; Fig. 1). All three sites were low-latitude locations during the Carboniferous-Permian transition. USM brachiopods represent North American Carboniferous-Permian epicontinental seas and interior basin environments. UM and MB brachiopods are predominantly Carboniferous from the Carboniferous type localities in the Ural Mountains (Mid-Serpukhovian through Early Permian) and Moscow Basin (Mid-Visean through Gzhelian with a break in the Serpukhovian). All brachiopods were screened for diagenesis using the TAMU method described by Grossman et al. (2008). Only those brachiopods with no evidence of diagenesis were used in this study.

Throughout the Pennsylvanian, brachiopod δ^{11}B averages around 15‰ with fluctuations of ±2‰, which are likely responses to pCO$_2$ changes that would have accompanied the waxing and waning of glaciers expressed by the cyclothems across the interval. By the Early Permian, brachiopod δ^{11}B declines rapidly to ~10-11‰ where it again stabilizes through the Roadian. This trend in brachiopod δ^{11}B is nearly identical to the trend in brachiopod ^{87}Sr/^{86}Sr for the same time interval (Bruckschen et al., 1999; Korte et al., 2006; Fig. 2). Our preliminary δ$^{44/40}$Ca measurements suggest a coincident change to lighter values going across the Carboniferous-Permian boundary. Because the trends in these isotope systems are so similar, they are likely controlled by and/or responding to the same environmental changes.

The major controlling factors for both the δ^{11}B and ^{87}Sr/^{86}Sr of seawater are continental weathering and hydrothermal systems. During the Carboniferous-Permian transition, oceanic crust production was at a Phanerozoic minimum (Gaffin, 1987), so hydrothermal activity was likely reduced. Continental weathering was also reduced based on multiple lines of evidence for continental aridity. We scaled hydrothermal fluxes based on Carboniferous and Permian seafloor spreading rates and modelled changes in the continental weathering flux to the ocean using brachiopod $^{87}Sr/^{86}Sr$ and Sr concentration data (Popp et al., 1986; Veizer et al., 1999; Steuber and Veizer, 2002). We then applied those results to a box model of the oceanic B isotope budget based on Lemarchand et al. (2002). The results of our first models using Sr data show that continental weathering reaches a minimum of 53.5% of today's weathering flux at 276 Ma, similar to the calculations of Martin and Macdougal (1995). Using these results to create a scaling factor for continental weathering, we modelled the secular variation in the B isotopic composition and concentration of seawater across the transition. The hydrothermal flux is isotopically lighter than the continental flux, and the decrease in weathering does produce the observed drop in $\delta^{11}B$. Future work will attempt to understand how B appears to go from one steady state to the next with rapid drops and long-term stability.

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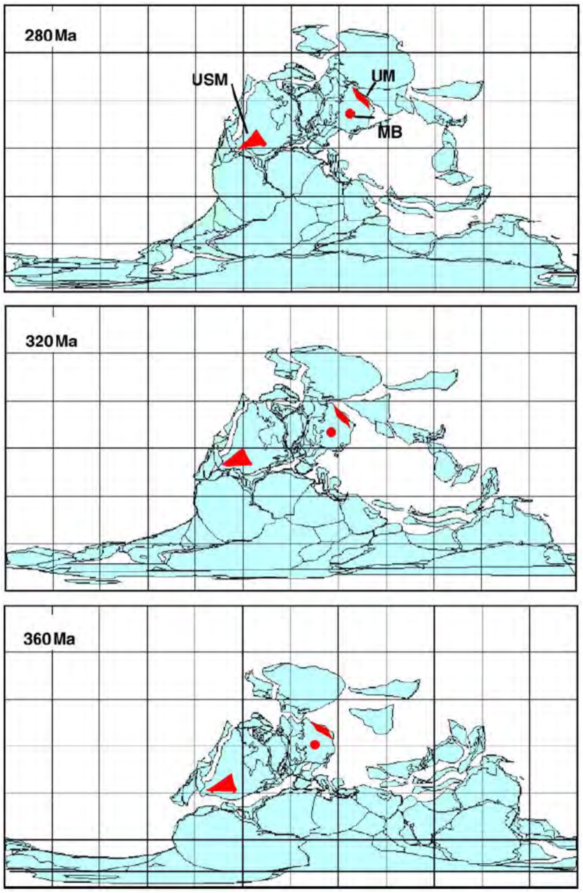

Figure 1. Carboniferous and Permian locations of brachiopod samples used in this study (from Grossman et al., 2008).

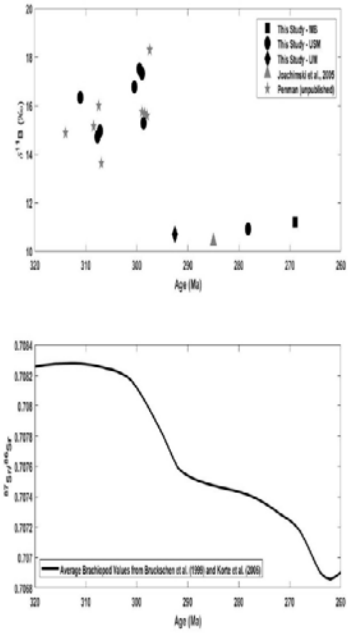

Figure 2. Brachiopod $\delta^{11}B$ and $^{87}Sr/^{86}Sr$ across the Carboniferous-Permian boundary.

Gigantoproductid and allied brachiopods from "L'Ardoisiere" (Visean), northern Massif Central, France

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The « L'Ardoisière » locality, near Vichy city, northern Massif Central, produced Carboniferous brachiopods described by A. Julien (1896), and later examined by G. Delépine (in Jung et al., 1939). Their age, provided by associated trilobites, is Asbian (Hahn & Hahn, 1993). The brachiopod shells, preserved in greywacke beds, are often folded and compressed.

(1) The bigger shells, formerly described as *Productus giganteus*, and later *P. cora*, are attributable to the genus *Globosoproductus* Litvinovich & Vorontsova, 1983: type species, *G. magnificus* Shimansky, 1940, middle Viséan in the Urals. Characters of that genus are: large dimensions, shell substance very thin especially on anterior part of the shell; ornamentation of rather thin radial ribs, rugae prominent on dorsal valves, spine bases conspicuous on the ventral valve anterior part.

(2) Other productid brachiopods collected at l'Ardoisière, smaller in size, are attribuable to the genus *Linoprotonia* Fredericks, 1971: type species: *Productus hemisphaericus* Sowerby, 1822, Asbian of England.

These L'Ardoisière faunas are quite different from the Montagne Noire (Southern Massif Central) gigantoproductids, which are late Viséan and Serpukhovian in age (Aretz et al., in press).

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Phylogenetic relationships of the Silurian Afro-South American Realm rhynchonellide brachiopods *Anabaia*, *Harringtonina* and *Clarkeia*: new insights from their ontogeny

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In recent years the crucial role that changes occurring during ontogeny play in generating intrinsic phenotypic variation within a species, and hence in originating micro- and macroevolutionary trends, has been widely accepted (McNamara and McKinney, 2005 and references therein). Processes involving heterochrony, defined as changes over time in the rate and timing of development, are ubiquitous in several taxonomic groups. In the last years, significant advances have been made in detecting heterochronic processes in early Paleozoic orthoidean and plectorthoidean brachiopods (Benedetto, 2007, 2008; Benedetto and Muñoz, 2017).

Kozlowski (1923), in his original description of the rhynchonellide *Clarkeia antisiensis*, had already noticed the strong morphological differences between small and large specimens of this species, and Benedetto (1988) described the substantial ontogenetic changes experienced by the related genus *Harringtonina* affecting even morphologically 'stable' features (e.g. cardinal process, hinge plates) which are considered as having generic and familial diagnostic value (Savage et al., 2000). Interestingly, knowledge of ontogenetic development not only provides additional criteria for taxonomic placement at suprageneric level but also for unraveling evolutionary lineages. This study is based on hundreds of specimens of *Clarkeia antisiensis* (d'Orbigny) recovered from the Upper Silurian Tarabuco Formation of Bolivia, which form a complete series of growth stages providing a good opportunity for reconstructing its ontogenetic development. On the basis of the ontogeny of *Clarkeia antisiensis* the case for a close phylogenetic relationship between *Harringtonina* and *Clarkeia* is compelling. The fact that juvenile specimens of *C. antisiensis* are nearly indistinguishable from adult individuals of *Harringtonina australis* Boucot strongly suggests that *Clarkeia* evolved from *Harringtonina* by the heterochronic process of peramorphosis. On the other hand, adult specimens of both the Brazilian *Anabaia paraia* Clarke and the Precordilleran *Anabaia* sp. never exceed the youngest ontogenetic stage of *Harringtonina australis* to which share small hinge plates supported by a septalium-like structure and absence of cardinal process. The overlap of adult morphology of *Anabaia* sp. with juvenile shells of *Harringtonina australis* allows interpreting this succession as an evolutionary lineage showing increasingly peramorphic characters. This hypothesis is supported by the close correlation between the stratigraphic record of the studied taxa and the inferred developmental sequence, being *Anabaia* the oldest member (Early Silurian), *Harringtonina australis* intermediate (Wenlock-Ludlow), and *Clarkeia antisiensis* the youngest (Pridoli). Although this hypothesis may give more integrative insight into the phylogenetic relationships of these genera it raises an intricate systematic problem because the leptocoelids *Anabaia* and *Harringtonina* are currently classified within the superfamily Rhynchotrematoidea whereas *Clarkeia* is placed among the Uncinuloidea. If the hypothesis is proven these superfamilies, as presently constituted, would be polyphyletic groups and should be redefined considering the ontogenetic evidence whose importance has been emphasized by some authors (cf. Manceñido and Walley, 1979) but has been mostly neglected in the current classification of the Order Rhynchonellida.

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New data on shell structure in *Heliomedusa orienta*: taxonomic and phylogenetic implications

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Heliomedusa orienta Sun and Hou,1987 from the lower Cambrian Chengjiang *Konservat*-Lagerstätte (Yu'anshan formation) of Yunnan province, southwestern China, is one of the most problematic Early Cambrian brachiopods. They were originally identified as a jellyfish-like organism (Sun and Hou, 1987), and later re-interpreted as discinids (Chen et al., 2007). In recent studies, detailed documentation of well-preserved soft parts, revealed the unique architecture of the lophophore of this taxon (Zhang et al., 2009). Almost nothing is known about the shell structure of this enigmatic taxon. However, new exceptionally preserved specimens from Chengjiang imaged using scanning electron microscopy, micro-XRF and high resolution optical z-stacked (Zeiss Smartzoom 5) analysis revealed the general shell outline and pustulose ornamentation in both larval and adult shells. The closely spaced costellae form at the intersection between fine concentric and radial ridges that radiate from the apex of valves. Moreover, at the anterior margin of valves, there are tiny openings filled with pyritized matter, potentially representing replaced chaetae. In addition, in some well-recrystallized specimens, four to five broad concentric growth bands can be seen from the shell surface. All these characters closely resemble structures previously noted in *Mickwitzia* (Holmer and Popov, 2007; Holmer et al., 2008) which indicates that *H. orienta* is probably closely related to *Mickwitzia* within the stem of the organophosphatic brachiopods.

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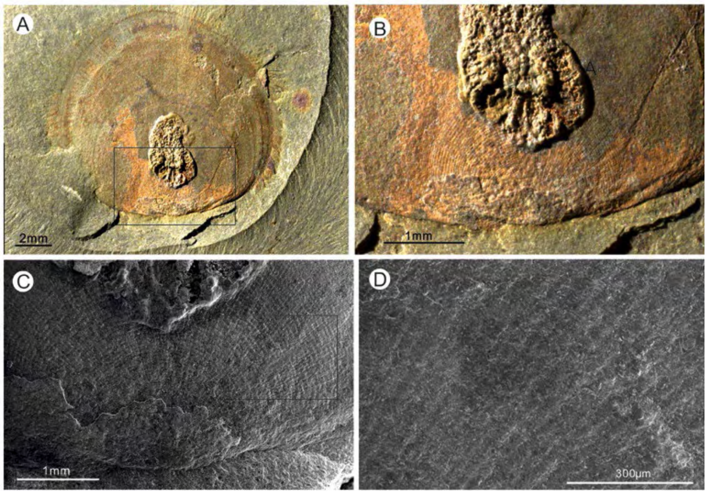

Figure 1. *Heliomedusa orienta,* Lower Cambrian, Yuanshan Formation, Yunnan, China. Specimen 2337. A, Light photograph of the ventral valve. B. Detail of the apex. C. SEM image of the ventral valve. D. Detail of closely spaced costellae.

A diverse fossil assemblage from a new section through the Shipai Formation (Cambrian Series 2, Stage 4) in western Hubei Province, South China

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Previous studies on the Shipai Formation in the Three Gorges area focused on chemostratigraphy (Ishikawa et al., 2014) and documenting crack out fossils present in the muddy siltstone facies (Zhang and Hua, 2005; Zhang et al., 2015; Liu et al., 2017). Non-mineralized Burgess Shale-type fossils from the Shipai Formation (Cambrian Series 2, Stage 4) were discovered by Zhang and Hua (2005) for the first time near Wangjiaping Village on the northern bank of the Yangtze River in the Sandouping Town, Yichang, Hubei province. Ten years later, brachiopods preserved with non-mineralized soft tissues were also reported from the Shipai Formation in the Three Gorges area (Zhang et al., 2015). This fossil locality, however, is poorly exposed and is now covered by vegetation and buildings, making further collection difficult. Here, we present a new section, named Xiachazhuang (Liu et al., 2017), where the 208 m thick Shipai Formation is well exposed and characterized by siltstone layers that are interbedded with thin calcareous mudstone layers that produce abundant Small Shelly Fossils (SSFs). This is the first report of SSFs from this locality where the Shipai Formation is mostly composed of siltstones and calcareous mudstones.

Fossils documented from this new locality include brachiopods, hyoliths, arthropods, palaeoscolecids (Cycloneuralia), sponges, chancelloriids and other problematic organisms. The fauna occurs most abundantly at three stratigraphic horizons: (1) a green-yellowish silty mudstone (*Palaeolenus lantenoisi* trilobite Zone) ca.120 meters from the base of the Shipai Formation. This level yields a rich fossil assemblage including brachiopods such as *Eohadrotreta* sp., abundant hyoliths, a wide variety of arthropods, palaeoscolecids and sponge and chancelloriid sclerites. Between the green-yellowish silty mudstone there are two calcareous mudstone layers, with each layer approximately 10 cm thick, that preserve a variety of SSFs including hyoliths, brachiopods, molluscs and arthropods; (2) a green-greyish siltstone, ca. 30 m above horizon 1, where the brachiopod *Eoobolus* sp. is particularly abundant; (3) the top of the Shipai Formation at this locality is characterized by a black-reddish to greyish silty shale (roughly corresponding to the *Redilichia meitanensis* trilobite Zone), that occurs ca. 50 m above horizon 2, that yields brachiopods such as *Kutorgina* sp. and *Nisusia* sp. Based on the presence of these fossils, the Shipai Fauna shows strong similarities with the Guanshan Fauna from eastern Yunnan. The SSFs and crack-out fossils from the Shipai Formation are of great importance in reconstructing the Cambrian seafloor on the South China Block. The preliminary fossil collections from the Shipai Fauna in the Xiachazhuang section demonstrate that the section has high potential to yield additional well-preserved fossils, either hosted in the siltstones or in the calcareous mudstone beds, that will be critical for understanding the Cambrian Explosion in South China.

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Quantifying variability and understanding species delimitation: a case study integrating morphological and genetic datasets in terebratulide brachiopods

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Species conceptualization and delimitation have always been controversial and highly debated topics in biology. From an operational standpoint, setting species boundaries requires multiple sources of information (e.g. morphology, genetics, ecology, biogeography, etc.). Paleontologists, however, are limited to fewer lines of evidence when delimiting species and rely heavily on morphology. Considering the fundamental role morphology plays in species recognition in the fossil record, analyzing morphology in a quantitative manner and examining phenotypic variability in both fossils and extant close relatives is fundamental. Furthermore, we can take advantage of living specimens to incorporate additional sources of data, such as genetics and biogeography, in order to characterize species in a more accurate manner. Therefore, the objective of our research is to understand how extant terebratulide brachiopod species are delimited, both morphologically and genetically, and compare observed ranges of phenotypical variability to the fossil record to make better informed decisions when recognizing extinct species.

In order to quantify variability in extant terebratulide brachiopods, we chose to analyze long loops—the calcareous structures that support the lophophore. We CT scanned a total of 59 individuals (41 specimens of *Laqueus,* 13 of *Terebratalia,* and 5 of *Dallinella*). The 3D isosurface models generated were then analyzed using 3D geometric morphometrics, which uses landmark coordinates to examine changes in the geometry of morphologic structures using statistical analyses. To simplify patterns of variation, exploratory methods, such as Principal Component Analysis (PCA) and Canonical Variate Analysis (CVA), were implemented. To test if shape is dependent on species designation and size, Procrustes ANOVA analyses testing landmark coordinates against species identification and against size, respectively, were performed. Based only on loop morphology, our results show that all of the species analyzed were statistically different from one another, including those with a contentious taxonomic history. Our results suggest that even when external characters are not considered (e.g. shell ornamentation and folding), the loop offers sufficient resolution to discriminate among named species.

To translate these results to the fossil record, we integrated our 3D dataset with 2D images of the outlines of their respective dorsal valves to test for correspondence between loops and overall shell shape. This is particularly important since long loops are rarely preserved in the fossil record. If we can find a correlation between long loop shape and outline shape, we can then make assumptions of species delimitation using only outline data. We digitized the outlines and analyzed them using Elliptical Fourier Analysis (EFA) to quantify variation of the shell shape. In this method, shape is described by harmonics, each representing a closed contour. Once Fourier coefficients are obtained, they were used as input for PCAs, as well as statistical analyses to assess if there is significant difference between the outline shapes from different named species. Based on preliminary results, shell outlines do not appear to offer enough resolution to discriminate among different named species.

Finally, to add another source of information that will help us test our morphological predictions on species boundaries, we propose analyzing genetic data of living brachiopods. The species *Terebratalia transversa* (Sowerby), *T. coreanica* (Adams & Reeve), *Laqueus erythraeus* Dall, *L. vancouveriensis* Davidson, and *L. rubellus* (Sowerby) will be examined using a RADSeq protocol. The resulting DNA sequences will be analyzed under the multispecies coalescent model to estimate species delimitation and population genetic parameters, such as heterozygosity and population differentiation [*FST*]. Comparing genetic and morphologic species delimitation results will help us determine if species can be successfully discriminated using only morphology, which is the main source of information in the fossil record. Studying variability in extinct and living specimens will help clarify how extant species are delimited based on genetic, and morphological characteristics, as well as test and improve our understanding of morphologically defined fossil species as evolutionary biological entities. This comparison of fossil and extant species delimitation in brachiopods is essential to evaluate the common assumption in paleontology that morphology alone proxies for biological species.

Small-sized brachiopods from the Upper Frasnian (Devonian) of central Hunan, China

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Abundant small-sized brachiopods of the uppermost Frasnian (probably the *Palmatolepis linguiformis* Conodont Zone) from South China were recently reported (Lü and Ma, 2017a). These brachiopods range in size from less than 1 mm to approx. 7 mm and are composed of, in order of abundance, the spiriferides (*Thomasaria*? *baii*, *Thomasaria*? *liangi*, *Xiangia liaoi*, and Spiriferida gen. and sp. indet., the terebratulide *Qidongia tani*, the athyridide *Athyris supervittata* and *Athyris*? sp., the rhynchonellide *Levipugnax*? *liui*, the spiriferinide *Cyrtinaella*? *houi*, the pentameride *Gypidula xui*, and the orthide *Aulacella*? sp., associated with abundant atrypid juveniles (mostly *Iowatrypa pseudobodini*), *Productella* sp., and *Hypothyridina* sp. This fauna represents the last significant episode in which brachiopods flourished in the Frasnian before the Frasnian–Famennian extinction event in South China.

The small-sized brachiopods (mostly 1–5 mm in size) in the C1 bulk sample are composed of two groups of specimens. One is composed of the juveniles of a larger or normal-sized species; the other consists of taxa that are themselves very small as adults. The latter group is not considered to be juveniles of other larger-sized existing species since those species of similar morphology are neither present in the same bulk sample nor in the Frasnian of South China. The C1 fauna consists of 16 species, of which 12 have been found in the C1 bulk sample. This doubles the previously known diversity (seven species) of the same fauna. Eleven species were described and/or illustrated in Lü and Ma (2017a) for the first time, including two new genera and seven new species. Spiriferide and atrypide brachiopods (both three species) are the most abundant and diverse groups, accounting for 38.8% and 37.2% of the total faunal abundance, respectively. The only species of the Terebratulida is also abundant and accounts for 10.8% of the brachiopod population. The other orders comprise nine species, but account for only 13.2% of the total abundance. Brachiopods of the C1 fauna disappeared upwards in the Jiangjiaqiao section. This further demonstrates that the Mass Extinction of Benthic Faunas-1 of Ma et al. (2016) represents a level of the most significant brachiopod diversity decline before the Frasnian–Famennian Event in South China.

Survivorship curves and size-frequency distributions of 10 fossil species populations have been depicted based on abundant small-sized brachiopod specimens of various growth stages from two samples (C1-0 of Jiangjiaqiao and S-Y-4 of Shetianqiao sections) from Hunan Province of southern China (Lü and Ma, 2017b). None of the size-frequency distributions of the C1-0 fauna have a normal bell-shaped distribution; only those of *Thomasaria*? *baii*, *Thomasaria*? *liangi*, *Xiangia liaoi*, *Cyrtinaella*? *houi* and *Gypidula xui* somewhat resemble a bell-shaped distribution, whereas *Qidongia tani*, *Athyris supervittata* and *Levipugnax*? *liui* display a distinct right-skewed pattern.

The survivorship curves of various populations are of a concave type of various degrees, which is probably related to their living on a muddy substrate. The survivorship curve of *Thomasaria*? *baii* is slightly concave, whereas those of other species are either of a moderately concave type, e.g., *Levipugnax*? *liui*, *Xiangia liaoi*, *Gypidula xui*, *Qidongia tani* and *Cyrtinaella*? *houi*, or a strongly concave type, e.g., *Athyris supervittata* and *Thomasaria*? *liangi*, suggesting a high mortality rate during the juvenile stage and decreasing mortality rate towards the gerontic stage.

The above differences in size-frequency distributions and survivorship curves of various species are probably a result of their adaptational differences to the muddy environments. For example, differences in shell shape might be related with their adaptational differences to muddy substrates and feeding efficiency. Study of *Iowatrypa pseudobodini* and *Hunanotoechia tieni* shows that size-frequency distributions and survivorship curves of brachiopod populations can be affected by sampling methods to various degrees in case of fewer specimens by hand-picking. Bulk sampling is recommended for population analysis, in combination with hand-picking in some cases for more actual survivorship curves.

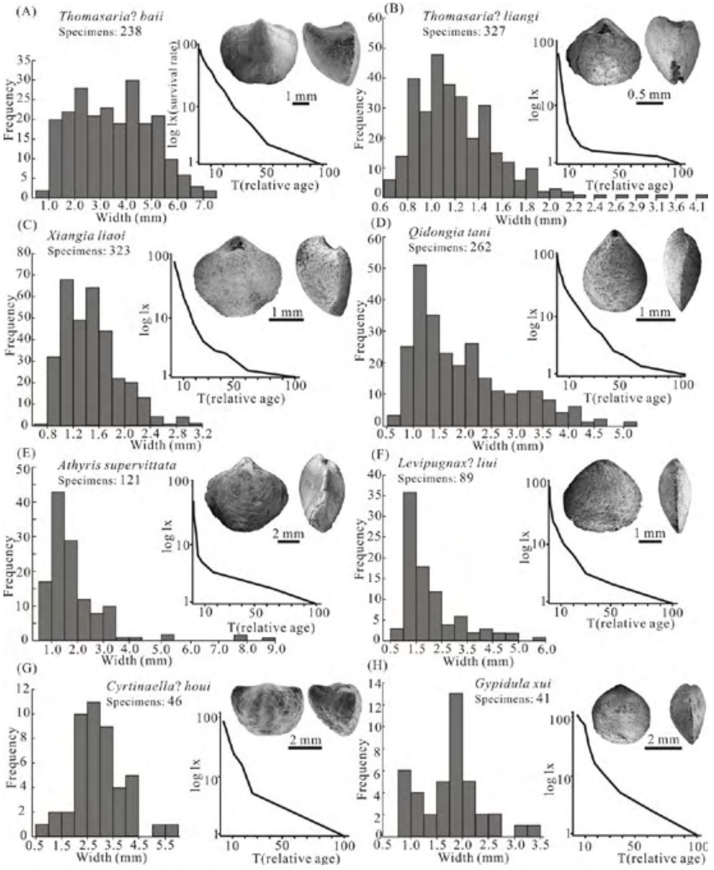

Fig. 1 Size-frequency distribution and survivorship curves of the C1-0 brachiopod fauna, adapted from Lü and Ma (2017b)

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Light sensation in adult brachiopods

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Adult brachiopods have been observed to be light sensitive. Retraction into the sediment (linguliforms), fast closure of the valves, and jerking movements of the animal (rhynchonelliforms) are behavioral responses to changing light conditions. However, in contrast to lecithotrophic larvae of some rhynchonelliform taxa, adult animals throughout the phylum have never been reported to have visible light sensitive organs such as eyes, pigment spots or similar structures. Using taylormade antibodies against ciliary opsin based on transcriptomic data from the laqueoid brachiopod *Terebratalia transversa*, we were able to detect a regular distribution of copsin expressing epidermal cells along the mantle margin in adult *T. transversa*. This is in line with the occurrence of ciliary photoreceptors in the apical lobe of the larvae of this species and enables the sessile adult to detect changes in light intensity over the whole length of its shell commissure. As adult rhynchonelliforms are firmly attached to the substrate and, therefore, are unable to move away from their attachment site, this marginal epidermal light sense may preferably be used to detect shadowing events caused by approaching predators and accordingly trigger protective behavior. The detection of light intensity

changes could even be possible when the valves are firmly closed, because hundreds of setae ("bristles") fringing the shell margin may serve as optical fibres guiding the light stimulus towards the photoreceptive epidermal cells protected inside the shell.

Early Jurassic terebratulide brachiopods from Zealandia

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Terebratulides, which are a minor group in New Zealand and New Caledonian Triassic faunas, become second in prominence only to rhynchonellides in the Jurassic. They have received little attention from palaeontologists, with only two species described to date. This study, which is based on collections held by GNS Science and the Universities of Auckland and Otago, has recognised a total of seven genera and twelve species.

The key sections for this study are in the Southland Syncline (Otapiri Valley, Hokonui Hills, in Southland, South Island; Hettangian to Pliensbachian or early Toarcian) and in the Kawhia Syncline (the open Tasman Sea coast of Te Maika Peninsula, Kawhia Harbour area, west coast of North Island; Late Hettangian to Toarcian). A few localities elsewhere in the Kawhia and Southland synclines and in the Baie de St. Vincent in New Caledonia have also yielded terebratulides.

Genera identified in this study include the cosmopolitan *Lobothyris*, with one species present throughout the Sinemurian to middle Toarcian. Another cosmopolitan genus, *Loboidothyris*, has one species common in the late Sinemurian to Pliensbachian of the Hokonui Hills, and as a few specimens from scattered Pliensbachian-Toarcian localities elsewhere, including one from New Caledonia. Further species of *Loboidothyris* are present in the middle and late Jurassic of Zealandia. The other major genus is *Zeilleria*, which first appears with *Zeilleria spiculata* in a narrow zone along the Triassic-Jurassic boundary in the Hokonui Hills. A further species is found throughout the later part of the Early Jurassic, and is numerically the most abundant species in this study. Two more species with restricted stratigraphic and geographic ranges are also recognised. *Zeilleria* is also a significant member of Middle and Late Jurassic brachiopod faunas. The sulcate genus *Aulacothyris* is represented by one Sinemurian form, known from Ben Bolt in the Hokonui Hills, and the coast north of Marokopa (south of Kawhia Harbour). A few specimens from near the Triassic-Jurassic boundary appear to belong to a second species, and two small specimens from later in the Early Jurassic to a third. *Aulacothyris* is also present in the Middle and Late Jurassic.

Linguithyris agerorum was described from a single specimen from near Port Waikato (north of Kawhia Harbour). Three further specimens from New Caledonia have now been found. Two genera are recorded for the first time in Zealandia. *Tegulithyris* is known from the Sinemurian to Toarcian of Kawhia, and *Rugithyris* from two localities in the Awakino area (south of Kawhia Harbour).

Lobothyris, *Aulacothyris* and *Zeilleria* are cosmopolitan and widely distributed. *Loboidothyris* is also cosmopolitan, but has a Tethyan aspect. *Tegulithyris* and *Rugithyris* are Tethyan, but less widely distributed. *Linguithyris* is also known from southern Europe, North Africa and western Asia, with one specimen known from the Late Jurassic of Indonesia.

The faunas described here span the interval between the end-Triassic extinction event, and the Toarcian event. *Zeilleria spiculata* straddles the Triassic/Jurassic boundary. The highest Early Jurassic brachiopod faunas are from at or just above the *Dactylioceras* band exposed on the Te Maika coast near Kawhia, which is correlated with the top of the early Toarcian and lies somewhat above the Toarcian event in Western Europe. The overlying Middle Jurassic terebratulide and rhynchonellide faunas are entirely different at the species level, and the spiriferides become extinct. The terebratulides remain a major group of brachiopods in the Late Jurassic, and by the Cenozoic are much the larger group.

Terebratulides are less common in the Early Jurassic of New Caledonia than in New Zealand, but the species appear to be the same.

Fossil records of the evolution of brachiopod life cycles

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Recent brachiopods have four different types of ontogeny that are variously reflected in posterior regions of their juvenile shells. Recently Kuzmina et al. (present abstract volume) suggested a hypothesis of the evolution of life cycles. However, this hypothesis is based only on data on recent brachiopods; data on fossil brachiopods were not considered. Here we will try to correlate data on the structure of protegula and life cycles of recent and fossil brachiopods and reconstruct life cycles of extinct brachiopods. The following terms are used:

The larva is the stage from hatching and up to metamorphosis. Brachiopod larvae lack the shell; the shell may be developed only in juveniles. The larvae possess larval structures such as apical cilia, ciliary bands, eyespots, and larval setae.

The secondary larva is the stage from metamorphosis and up to the beginning of shell secretion; it preserves some larval organs such as larval setae, which are shed during formation of the protegulum. Here we support the "brachiopod fold hypothesis" (Nielsen, 1991; Cohen et al., 2003). We assume that metamorphosis in brachiopods is the folding of larva on the ventral side as it was observed in recent craniids, whose true larva folds on the ventral side after settlement (Nielsen, 1991). Recent rhynchonelliform brachiopods fold on the ventral side at the floating stage (Kuzmina et al., present abstract volume) and therefore their three-lobed planktonic stages are the secondary larvae. The secondary larva is also known in recent discinids.

The juvenile stage starts at the formation of the protegulum and lasts up to sexual maturity. It is characterized by the disappearance of larval structures and the formation of the adult body plan.

The protegulum is the first-formed shell, which is simultaneously secreted by the whole mantle surface and may increase in size before the shedding of larval setae. The protegulum does not bear growth lines, i.e. it lacks marks of accretionary growth that correspond to the initial determination of the protegulum by Beecher (1891) and determination of the protegulum by Chuang (1977) and Zhang et al. (2018). In all subphyla, the protegulum forms at the beginning of the juvenile stage. We suppose the protegula of all brachiopods to be homologues irrespectively of the time of their formation: after settlement (recent calcitic brachiopods), at the floating stage (recent discinids) or in the egg envelopes (recent lingulids).

The brephic shell forms immediately after the secretion of the protegulum. It corresponds to the adult type of secretion, may be separated from the protegulum by halo rings, and bears growth lines. The adult shell differs from the brephic shell in the presence of adult radial ornamentation and, in some cases, the presence of nick points, which testify to the development of adult setae (Biernat & Williams, 1970; Stricker & Reed, 1985; Zhang et al., 2018). The border between the brephic and adult shells is often sharply pronounced in phosphatic brachiopods as it usually also corresponds to the change of life mode, while in calcitic brachiopods the brephic shell gradually transforms into the adult shell or may be absent.

According to the cited biologists, the first brachiopods had a pelago-benthic life cycle with true planktotrophic larvae. At settlement, the larva folded ventrally and shell secretion began. This life cycle gave rise to all other life cycles of brachiopods. The planktotrophic larvae became lecithotrophic. Recent craniids retain true lecithotrophic larvae that fold at settlement. Another type of life cycle evolution involves a prolongation of the pelagic lecithotrophic stage by transformation of the folding stage into the secondary larva, as had happened in Rhynchonelliformea. The development of recent Linguliformea is strongly compressed within embryogenesis: the embryo folds on the ventral side in the egg envelope. In recent discinids, the floating stage includes the secondary larva, which transforms into the juvenile with a protegulum after a few days. In recent lingulids, the juvenile hatches with the protegulum.

All these stages may be reconstructed in fossil brachiopods. Cambrian brachiopods often preserve molds of larval setal sacs shaped as paired lobes along the anterolateral margins of the dorsal protegulum; the ventral protegulum lacks these lobes (Balthasar, 2009). We suggest that the presence of setal sac molds on the dorsal protegulum identifies the larval stage; the protegulum formed immediately after settlement and hence it preserved the imprints of larval setal sacs. We support the opinion of Freeman and Lundelius (2005) that the planktotrophic and lecithotrophic types of larvae may be recognized by the size of the protegulum; protegula larger than 400–500 μm probably indicate brachiopods with planktotrophic larvae. Small protegula testify to lecithotrophy and large protegula testify to planktotrophy but the true larva lacks the shell even in the case of planktotrophy.

Most of the studied Cambrian phosphatic brachiopods have typical 600–800 μm wide dorsal protegula with paired anterolateral lobes and a central posterior lobe (Zhang et al., 2018). These protegula lack growth lines, and their relief indicates the presence of larval setal sacs; therefore, this region may be considered only as a protegulum, but not as a brephic shell. The same type of dorsal protegulum is known in the Ordovician orthids and clitambonitidines (Madison, 2009; Popov et al., 2007). The protegula of recent craniids and terebratulids show similar lobes soon after settlement (Stricker & Reed, 1985; Nielsen, 1995). As the setal sacs indicate the larva and their size indicates planktotrophy, we postulate the presence of planktotrophic larva (but not juvenile swimming stage with a shell!) in all groups of Early Paleozoic brachiopods.

Two types of protegula are known in the Ordovician orthids (Madison, 2009). While the first type is the large protegulum with paired lobes typical for the Cambrian phosphatic brachiopods, the second type is about 200 μm wide, a small, smooth, and uniformly convex protegulum. Its small size indicates lecithotrophic larva. Another important characteristic feature is the microstructure of 1–2 µm spherules while the rest of the shell is composed of well-preserved fibers; the primary layer was not observed. We suggest that the transition from planktotrophic to lecithotrophic larva occurred in the order Orthida; both types of larvae lacked the shell at the floating stage.

One of the first brachiopods with a floating juvenile stage were possibly the strophomenids. Our material (Madison and Kuzmina, present abstract volume) possibly testifies to a swimming planktotrophic juvenile, which floated with a protegulum. The brephic shell formed after settlement.

Of all the abundance of phosphatic brachiopods, only discinids and lingulids survived up to recently. The secondary larva of recent discinids forms a smooth protegulum in a few days after hatching; its brephic shell grows at the floating stage, bears frequent growth lines, and strongly differs from the adult shell, which appears after settlement, in the absence of radial ornamentation and with a different plane of growth (Williams et al., 2001). The protegula and brephic shells of extinct and extant discinids are generally similar, which testifies to the similarity of their life cycles. In the order Lingulida, there was probably a gradual transition during the Paleozoic and Mesozoic from a true planktotrophic larva typical for Cambrian brachiopods through a discinid-like life cycle to the complete absence of the larval stage (Zhang et al., 2018).

For the craniids, the cited biologists suggest that primitive larvae are preserved with the transition from lecithotrophy to planktotrophy. The first-formed shells of the extinct craniids were repeatedly described; sometimes they are very well preserved, but their interpretation is controversial. The most striking example is the Ordovician *Orthisocrania*, which has a large (up to 1 mm) probably brephic shell covered with frequent growth lines and with a smooth umbo at the apex, possibly representing the protegulum. It differs from the adult shell in the plane of growth and the absence of radial ornamentation; besides, it strikingly resembles the brephic shells of discinids. Thus the life cycle of *Orthisocrania* probably was considerably more derived than that of recent craniids and was more similar to the discinid life cycle.

Conclusions:

1. All Early Cambrian brachiopods had true planktotrophic larva lacking the shell. This type of life cycle is not preserved in recent brachiopods but it was present initially for the phylum.

2. The life cycle with lecithotrophic larvae appeared by the Late Ordovician and became the base for the life cycles of the recent Craniiformea and Rhynchonelliformea. Fossil craniiformean brachiopods had a planktotrophic juvenile stage in ontogeny; their life cycles probably were similar to the discinid life cycle.

4. Of recent brachiopods, the life cycle with a planktotrophic juvenile stage is preserved only in phosphatic brachiopods.

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The intermediate stages of diagenetic overprint deduced from hydrothermally altered and fossil brachiopod shells

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Biogenic carbonate skeletons form the basis of studies on past climate dynamics and environmental change. The greatest challenge that all proxies face is their capacity to retain original signatures, as alteration of the hard tissue starts with the death of the organism, with the decay of biopolymers within them as well as the precipitation of abiogenic minerals within and at the two surfaces of the shell. Understanding how diagenetic overprinting influences microstructural and geochemical archival data is of fundamental importance, as with progressive alteration pristine biogenic characteristics are replaced by diagenetic microstructural features and chemistries.

Recrystallization of the original organism-specific skeletal microstructure is a clear indicator for diagenetic overprint (Casella et al., 2016, 2018a-c). Thus, microstructural data are of great value for the assessment of the reliability of geochemical proxies on environmental conditions derived from fossil material. So far very few quantitative studies exist that relate recrystallization of carbonate hard tissues to temperature, pressure, and pore fluid composition. In the study presented here we investigate fossil brachiopod shells from various sedimentary basins, that are well studied with respect to their thermal history and the quantification of the impact of heat flow on skeletal mineralogies and geochemistries. Our hypothesis is that there is a correlation between the microstructural and nanostructural state of carbonate fossils and the diagenetic heat flow to which the fossil material was subjected to, as well as to the pressure and the chemical composition of the overprinting pore fluid. We investigate fossil brachiopods from the following sedimentary basins and report microstructural data: (A.) The Palaeo-Adriatic Basin in northern Italy (thermal heat flow: < 50 °C), (B.) The Peak District, Pennine Basin, central England (thermal heat flow: 100-120 °C), (C) The Southern Alps, northern Italy (thermal heat flow: 150-200 °C) and the Central Australpine Nappe, northern Italy, (thermal heat flow: up to 350 °C) and (D.) The Karakorum Basin, northern Pakistan (thermal heat flow: 300-350°C). For a more precise interpretation of observed fossil microstructures we supplement the above described approach with laboratory based alteration experiments, where we obtain time-temperature series data on the evolution of microstructure, texture and material properties signals in modern analogue taxa. With this approach we gain more than just a descriptive understanding of shell microstructure patterns and crystal orientation distributions. We gain knowledge of the different intermediate stages of overprinting and alteration. This is especially important for moderate overprint that is often difficult to detect and highlight.

So far we observed that hydrothermal alteration fluid chemistry influences the degree of destruction of fibres. In comparison to meteoric water (Mg-free), burial water (Mg-rich) etches the calcite to a higher degree and causes an increased distortion of the fibre morphology (Figure 1b). Alteration at 175°C for 28 days in Mg-rich burial fluid evokes the coagulation of nano-sized calcite particles and amalgamation of fibres (Casella et al., 2018a,b). New calcite formation takes place between neighbouring fibres and calcite ingrowth occurs from one fibre into the other (Figure 1b). However, fibre distortion and amalgamation does not take place homogenously. Within a relatively small area, we find highly distorted shell portions as well as little distorted shell portions next to each other (Casella et al., 2018a). Even though laboratory-based hydrothermal alteration experiments last only for short time spans, they mimic natural diagenetic overprint processes to some extent. Figures 1b and 1c, highlight the similarity in fibre distortion between hydrothermally altered and markedly overprinted fossil brachiopod fibres. With an increasing temperature during hydrothermal alteration and correspondingly an increasing heat flow in the sedimentary basin, the fibre morphology becomes almost fully destroyed and abiotic calcite unit formation starts at many places within the hard tissue (Figure 1d).

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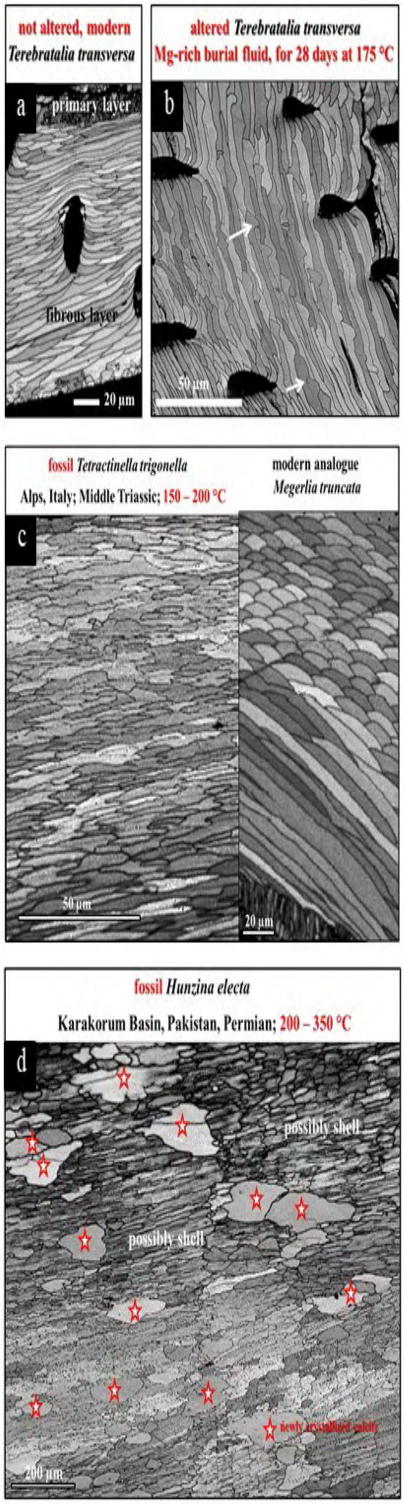

EBSD band contrast measurement image showing the difference in shell microstructure between modern and hydrothermally altered *Terebratalia transversa* (for further details see Casella et al. 2018a, 2018b), the markedly overprinted fossil brachiopod *Tetractinella trigonella* and the highly overprinted and recrystallized *Hunzina electa*.

Fossil brachiopod shell calcite: How well is the oxygen isotope composition and minor element ratios preserved within the shell microstructure?

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Fossil brachiopod shells are potential archives due to their extensive record and shells made of stable low-Mg calcite, the diagenetically most stable polymorph of calcium carbonate. For these reasons, oxygen isotopic and trace element compositions of fossil brachiopod shells have been used to reconstruct physicochemical conditions of past oceans (e.g. Lowenstam, 1961; Veizer et al., 1986), assuming that brachiopod calcite is in equilibrium with ambient seawater and the original calcite has not been altered. Here, our aims are to assess the preservation of the oxygen isotopic and trace element signals in the brachiopod calcite through time. We compared the oxygen isotopic composition and trace element ratios (i.e. Li/Ca, Na/Ca, Mg/Ca, Mn/Ca and Sr/Ca) of three modern species (*Terebratalia transversa, Magellania venosa* and *Gryphus vitreus*) and three well-preserved fossil brachiopods (*Pliothyrina perforata*, and Terebratulinae gen et sp. ind., both from the Miocene and collected in Loué-la-Fontaine and Noellet, respectively, Maine et Loire, France and *Oxycopella oxycolpos,* from the Late Triassic, collected in Hybe, Western Carpatians, Slovakia). Their shells are constituted of a primary layer, a secondary fibrous layer and for some species a columnar tertiary layer (*G. vitreus* and

O. oxycolpos). Oxygen isotopic composition was measured at the micrometer scale with high-resolution ion microprobe and trace element ratios were determined by laser ablation coupled to an ICP-MS. In modern and fossil brachiopods, there is an equivalent O isotope trend between the different shell layers. O isotope values in the secondary layers show a progression towards more positive values from the outer primary layer to the inner secondary layer. The columnar tertiary shell layer, in agreement with Angiolini et al. (2012), has the lower oxygen isotopic variability and moreover, displays the highest isotopic O values. In modern brachiopod shells, the innermost secondary layer is near oxygen isotopic equilibrium with ambient seawater, while the tertiary layer is in oxygen isotopic equilibrium. The elemental ratio profiles of the secondary shell layers in modern species show a decreasing trend towards the innermost regions of the shell, eventually reaching equilibrium with seawater. However, in fossil brachiopods, the decreasing trend is only recorded in the innermost regions of the shell, indicating a possible modification in the outermost parts. Values of both, modern and fossil two-layered shell brachiopods, are in good agreement with previous studies (e.g. Delaney et al., 1989; Perez-Huerta et al., 2008). In modern and fossil three-layered shells, there is a depletion of all the trace elements measured relative to the secondary layer, as observed by Grossmann et al. (1996), indicating different biomineralization mechanisms. The results of this study suggest that the oxygen isotopic and trace element content is well preserved in the tertiary and innermost secondary layer and therefore, these parts are the best targets to focus on for paleoenvironmental studies.

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Evolution of the brachiopod assemblages at the Devonian–Carboniferous boundary (Hangenberg Crisis) in basinal facies from SE Thuringia (Germany)

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Worldwide, the mostly rare Famennian and basal Tournaisian (Hastarian) brachiopods of aphotic zones (cephalopod limestones, entomozoid ostracod shales) are not well known and often remained even uncollected. Primary studies started in Germany with the monograph of Münster (1840) in which he described the brachiopod faunas of the Upper Devonian Limestones of Upper Franconia. Immediately after Münster, similar palaeontological studies of the now classical Bohlen section near Saalfeld (Fig. 1) in Thuringia were published by Richter (1848, 1856). In this area, the Famennian and Hastarian succession (Gleitsch Formation) outcrops in some sections located in the Saale valley to the southeast of Saalfeld (Schwarzburg Anticlinorium) (Bartzsch et al., 2008).

The Gleitsch Formation (Fig. 1) corresponds to shales with levels of nodular limestones which yielded, besides brachiopods, a rich pelagic and benthic fauna (e.g., bivalves, cephalopods, trilobites). The environment was generally quiet with some periods of agitation and bottom currents, reflected notably by the presence of millimetric silty and sandy layers, crinoidal lenses and accumulations of dissociated valves of posidoniid bivalves (*Guerichia*) and fragments of trilobites (Weyer, 1979). At least ten brachiopod species are recognized within the Breternitz Member (late and latest Famennian) (Fig. 1) (Mottequin et al., submitted). The smooth or poorly ornamented rhynchonellides (e.g., *Hadyrhyncha*, *Novaplatirostrum*, *Rozmanaria*) are clearly predominant (40 % of the whole assemblage) as is the case elsewhere in similar and contemporaneous facies from the southern margin of Laurussia and the northern margin of Gondwana. In contrast, spire-bearers (Athyridida, Spiriferida) are scarce and the presence of terebratulides within the Breternitz Member is noteworthy. The onset of the Hangenberg Crisis is marked by an anoxic black shale horizon at the top of the Breternitz Member (equivalent to the Hangenberg Black Shale) followed by the Obernitz Member mostly consisting of turbiditic sandstones (equivalent to the Hangenberg Shale and the Hangenberg Sandstone); both horizons did not yield brachiopods. The Hastarian Pfaffenberg Member yielded at least 15 species of brachiopods which are of smaller size (width rarely exceeding 10 mm) than those from the Breternitz Member (Mottequin et al., submitted). Productides and spiriferides represent almost 50 % of the whole assemblage whereas the rhynchonellides are scarce. In Thuringia, a probable complete turnover is recorded among the rhynchonelliform brachiopods at the base of the Hastarian with a rapid post-Hangenberg recovery including species belonging to pre-existing genera and to new ones. Based on Pérez-Huerta and Sheldon (2006)'s discussion, the nutrient availability, the water oxygenation, and the depth are most probably the biotic and physicochemical factors that played the most important roles in controlling the size of brachiopods in the Thuringian deep-water environments. The small size of the Tournaisian species reflects environmental conditions that were as stressful as previously during the first steps of the post-Hangenberg Crisis and could result from heterochronic processes. Nevertheless these aphotic environments are colonized from now on by a more diverse brachiopod panel as a result of the dramatic decline of the rhynchonellides which were so abundant during the Late Devonian.

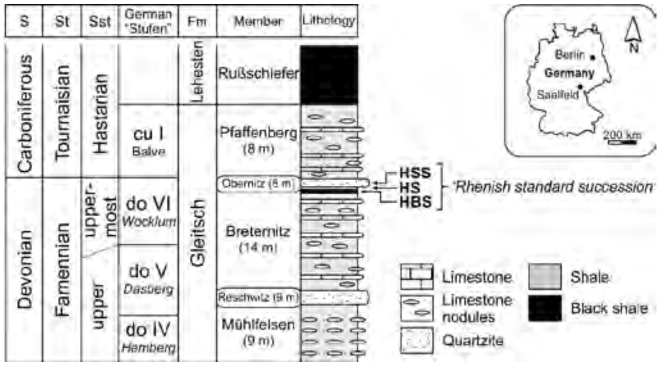

Figure 1. Lithostratigraphy (with indication of thickness for each member) at the Devonian–Carboniferous boundary in the basinal facies developed on the southeastern flank of the Schwarzburg Anticlinorium in Thuringia (Saalfeld area) (Bartzsch *et al.*, 2008) and correlation with the 'Rhenish standard succession' (Kaiser *et al.*, 2016). Abbreviations: Fm, Formation; HBS, Hangenberg Black Shale; HS, Hangenberg Shale; HSS, Hangenberg Sandstone; S, System; St, Stage; Sst, Substage.

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A review of the brachiopod subfamily Septosyringothyridinae (Spiriferinida) from the Carboniferous of Laurussia and Gondwana

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The Syringothyridoidea is one of the most important lineages of spire-bearer brachiopods that survived the global Hangenberg Crisis and flourished in many parts of the world during the Carboniferous–Permian interval (Carter & Gourvennec, 2006; Mottequin et al., 2014). Only three genera of this superfamily are distinguished by the presence of a syrinx, namely the Syringothyridinae *Syringothyris* Winchell, 1863 and the Septosyringothyridinae *Septosyringothyris* Vandercammen, 1955 and *Histosyrinx* Termier & Termier (in Massa et al., 1974), which are both characterized by a syrinx supported by a median septum.

Septosyringothyris is defined as a syringothyridid with the syrinx suspended between the delthyrial plate and the floor of the valve by a median septum (Carter, 2006). The poorly preserved type material of its type species (*S. demaneti* Vandercammen, 1955) from the lower part of the Tournaisian Yvoir Formation (southern Belgium) has been herein studied using for the first time computed tomography (CT scan), allowing us to discriminate specimens without a median septum that were initially considered in the definition of the genus by Vandercammen (1955). Although these specimens are externally similar to *S. demaneti*, they are markedly different internally as their syrinx is attached to the ventral valve floor by a septal pillow, resulting from the thickening of the internal faces of the dental plates. This feature has been described in *Syringothyris* species and is sometimes mistakenly interpreted as a median septum (e.g., Abramov & Grigorjewa, 1986). They are thus assigned to a new species of Winchell's (1863) genus.

Unlike *Septosyringothyris,* there is no delthyrial plate in the genus *Histosyrinx* and the syrinx is inserted at the junction of two partly joined plates. Dental adminicula thickened by callus deposits converge to simulate a delthyrial plate and the syrinx is supported by a stout median septum (Legrand-Blain, 1974; Carter, 2006). The type species of *Histosyrinx* (*H. vautrini* Termier & Termier in Massa et al., 1974) is from the Tournaisian (Ivorian) Marar Formation (Serdeles area in the Murzuq Basin, Western Libya) and the type material consists of internal moulds and worn limonitic moulds, as is the case of the holotype. The ventral interior of *H. vautrini* is strongly variable (syrinx size, development of the septum) as suggested by Legrand-Blain (1974) and our recent observations of the material collected by Delépine (Legrand-Blain, 1974) and Massa (Termier & Termier in Massa et al., 1974; Mergl & Massa, 1992).

The genus *Septosyringothyris* has a particular palaeogeographic pattern of distribution with occurrences in tropical latitudes of Laurussia (Belgium), and in higher latitudes of Gondwana, in western basins of South America (Argentina and Chile). In Argentina, *Septosyringothyris* shows a temporal diversification that appears to increase from the Carboniferous glacial sequences (late Palaeozoic ice age) to those associated with the climatic amelioration interval that took place during the latest Carboniferous–earliest Permian. Argentinean species of this latter interval have been referred to the subgenus *Septosyringothyris* (*Precosyringothyris*) (Cisterna, 2011), to characterize species with a large syrinx partially enclosed by the delthyrial plate, with a median septum that becomes more conspicuous in mature specimens. Occurrences of Carboniferous *Septosyringothyris* species in South America, as is the case with other Carboniferous genera (Cisterna & Simanauskas, 1999; Taboada & Shi, 2009), could be reflecting a faunal interchange with the Northern Hemisphere regions. However, many of Argentinean species must be reviewed in the light of the new results of the study of the *Septosyringothyris* type material.

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Variation of Mg/Ca in brachiopod shell: expression of growth rate rather than temperature seasonality

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Determining secular changes in seawater temperature and Mg/Ca is of high importance in paleooceanographic, paleoenvironmental and paleoecological studies. Brachiopod shells tend to show major ontogenetic variation in Mg/Ca, and this variation was used in inferences about past seasonality, assuming that Mg/Ca variation can be used as a paleothermometer. However, intrashell variation based on high-resolution transects showed high variance in Mg/Ca rather than regular fluctuations, and was rarely mapped to growth increments. Mg/Ca minima should correspond to growth during colder seasons, but several studies suggested that enrichment in Mg/Ca occurs at growth lines when growth is slowest or interrupted. Here, using extant brachiopods from cool-temperate latitudes in the NE Pacific (San Juan Islands) and the SW Pacific (New Zealand) and fossil upper Triassic brachiopods (Western Carpathians), we measure intrashell variation in Mg/Ca with laser ablation and electron microprobe, we map this variation to growth increments, and we assess the generality of the relation between Mg/Ca and growth increments. We find that, first, zones of Mg/Ca enrichment, visible as major maxima forming single bands or cluster of bands in high-resolution LA-ICP-MA or EMPA transects, consistently correspond to major external growth breaks that tend to be regularly spaced. The magnitude of Mg/Ca observed in the secondary layer in some specimens becomes comparable to values in the primary layers, with range in Mg/Ca exceeding 10 mmol/mol in the NE Pacific and 5 mmol/mol in the SW Pacific. Second, Mg enrichment closely correlates also with an increase in S concentrations and a decrease in Ca concentrations whereas it does not co-vary with changes in Mn or Sr concentrations. Biological information on growth rates shows that extant brachiopods analyzed here (*Terebratalia transversa, Magasella sanguinea, Notosaria nigricans*) slow down their growth and form growth lines during cold seasons when food supply is limited, indicating that Mg enrichment temporally does not coincide with warmer seasons. During the mantle retraction at times of the formation of the growth increments, an organic membrane is deposited by the mantle on the inner side of the primary or secondary layer in living brachiopods. Mg enrichment associated with S enrichment can thus trace these zones enriched in organics. Therefore, intrashell variation in Mg/Ca of brachiopods is primarily determined by changes in growth rate, not by seasonal changes in temperature. However, given that some studies found negative inter-shell relation between Mg/Ca and d18O, it is possible that Mg/Ca in shell portions not affected by increments can be used to apply Mg/Ca as a thermometer.

Variations in trace element concentrations of modern brachiopod shells

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Carbon- ($\delta^{13}C$) and oxygen- ($\delta^{18}O$) isotope composition and trace element/calcium ratio (Me/Ca; e.g., Mg/Ca and Sr/Ca) in skeletal carbonates are powerful tools for reconstructing various paleoenvironmental conditions. Of many marine invertebrates, $\delta^{13}C$ and $\delta^{18}O$ values of Rhynchonelliformea brachiopods have been preferentially used as a reliable recorder of $\delta^{13}C$ of dissolved inorganic carbon and temperature and $\delta^{18}O$ of seawater in the past because: (1) their dense, low-magnesium calcite shells are less susceptible to diagenetic alteration, (2) their calcitic secondary shell layer is assumed to have been precipitated in or near isotopic equilibrium with ambient seawater, and (3) they have extensive geographic distributions throughout the Phanerozoic. As a consequence, Paleozoic and Mesozoic oceanographic conditions have mostly been reconstructed with $\delta^{13}C$ and $\delta^{18}O$ values of fossil brachiopod shells. Trace element concentrations of brachiopod shells are commonly used in a screening technique of diagenetic alterations. However, trace element/calcium ratio of brachiopod shells are not well established as recorders of paleoceanographic conditions in contrast with Mg/Ca and Sr/Ca in skeletal carbonates of foraminifers, molluscs, and corals, which are commonly used as paleothermometers.

Previous studies focused on ontogenetic variations of trace element/calcium ratios in modern brachiopod shells to understand environmental controls on uptake, partition, and distribution of those elements (Buening and Carlson, 1992; Ullmann et al., 2017). However, it is still uncertain what factors are critical for trace element incorporation. One of the main reasons for this is that the time-series variations of trace element concentrations in brachiopod shells are not compared directly with those of oceanographic properties (temperature, salinity) and chemistry at their growth sites. Some previous studies showed the presence of biological controls on trace element incorporation into brachiopod shells (Buening and Carlson, 1992; England et al., 2007; Cusack et al., 2008). In order to solve these problems, high-resolution ontogenetic profiles of trace element concentrations in conjunction with those of $\delta^{13}C$ and $\delta^{18}O$ values needs to be delineated from a single brachiopod shell.

We conducted high-resolution analyses of trace element/calcium ratios (Mg/Ca, Mn/Ca, Fe/Ca, Sr/Ca) and $\delta^{13}C$ and $\delta^{18}O$ values of ontogenetic samples from modern brachiopod shells collected in Otsuchi Bay, Iwate prefecture, Japan. We show within-shell, intraspecific, and interspecific variations in the trace element/calcium ratios, compare the time-series trace element/calcium ratios with those of ambient seawater and temperature and salinity measured at/near the brachiopod growth site, and assess biological and physicochemical factors controlling the trace element/calcium ratios in the shells. A new method is proposed to convert the distance domain profile of trace element/calcium ratios in the ontogenetic-series samples to the time-series profile. The factors controlling the ontogenetic time-series variations in Mg/Ca are discussed.

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Preservation of brachiopod soft tissues outside the lagerstätte conditions

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As a rule, soft tissues after the death of an organism decay. In rare cases they may be preserved. One of the reasons is the stability of natural polymers. For example, sporopollenin in spores and pollen does not undergo complete decomposition. Collagen can remain in the vertebrate bones. Organic polymers can be destroyed, but their monomers, for example, amino acids from proteins, can be preserved. A unique location where not only organic molecules are stored, but also whole bodies of organisms or their parts, is the permafrost. However, more often organic substances and soft tissues are transformed or replaced by minerals. Such lagerstätten are well known. Brachiopods with fossilized soft tissues are found in lagerstätten; for example, Chengjiang Lagerstätte, Guanshan Lagerstätte, Burgess Shale, Herefordshire Lagerstätte. Special conditions occur here, such as rapid burial, lack of bioturbation, oxygen deficiency and few decomposers. When this happens, brachiopod lophophores with tentacles, pedicles, part of mantle, setae, digestive system can be preserved. Fossilization occurred by converting organic substances or replacing them with minerals. In the latter case, pyritization, chloritization, substitution by clay minerals, calcification, phosphatization are observed.

However, the process of preserving soft structures in brachiopods is more common. It can occur outside the lagerstätten. This was demonstrated by Rachebaeuf and Copper (1990) in the chonetid brachiopod *Archeochonetes primigenius* (Twenhofel, 1914), in the shell of which a pyritized lophophore was found.

The process of soft tissue phosphatization, which occurs at cell level, is well known. As a result, structures or imprints of soft tissues are preserved. This process is known on brachiopods from different locations (Ushatinskaya & Parkhaev, 2005). The internal moulds of the rhynchonellid *Rhynchonella loxiae* Fischer von Waldheim 1809 from Upper Jurassic deposits (Tithonian stage) of the Kuntsevo-Filevsky Park in Moscow are studied. The deposits are represented by sandstones and clays rich in phosphorites. The imprints of the cells of the mantle epithelium on the internal moulds are clearly visible (Fig. 1). Cells had various shapes in different parts of the mantle.

After the death of an animal, within an enclosed shell anoxic conditions may develop which are favorable for the fast replacement of soft tissues with minerals. Probably, the bacteria played an important role in this process. Fragments of the lophophores substituted by minerals were found in two of the 454 shells of Devonian and Lower Carboniferous rhynchonellids (Transcaucasia) by using X-ray microtomography. Paired contrast structures were identified in several shells. They may also belong to lophophores or crus. An incomplete spiral of the lophophore was found in the shell of the holotype of the rhynchonellid brachiopod *Sharovaella mirabilis* Pakhnevich, 2012 (Lower Famennian). In these cases there was soft tissue pyritization. So it was revealed that rhynchonellids already had a spirolophe lophophore in the lower Famennian (Pakhnevich, 2017). The identification of these structures would have been impossible without using X-ray microtomography.

Thus, the replacement of soft tissues by minerals can occur not only in lagerstätte, but in any brachiopod shell, if there are the conditions for fast mineralization.

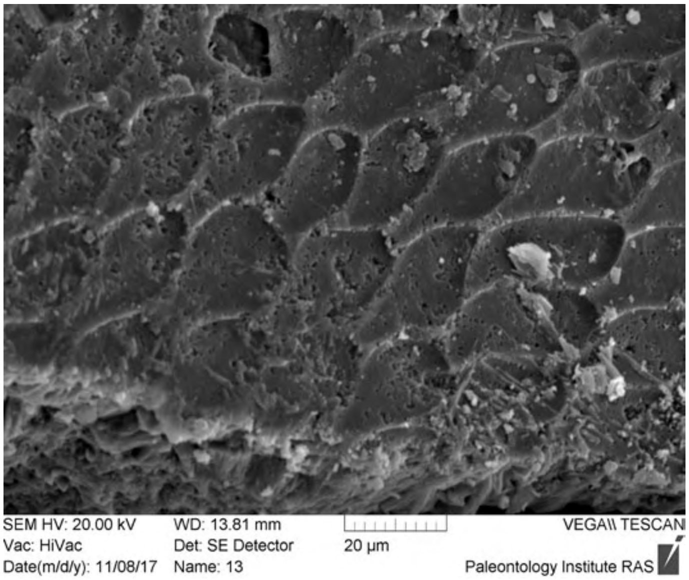

Fig. 1. Cell imprints on a surface of the umbo of *Rhynchonella loxiae* (Upper Jurassic, Tithonian, Moscow).

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New data on brachiopods at the underwater Piip Volcano (Bering Sea)

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The Piip Volcano is located in the southwestern part of the Bering Sea. It is the peak of the Vulkanologov massif. Here, manifestations of hydrothermal activity (hot vents and seeps) were previously detected (Galkin and Sagalevich, 2012). This is one of the shallowest hydrothermal vent regions worldwide. Bacterial mats are associated with seeps, with the predominant bacterium *Beggiatoa* sp. At various distances from the hot vent, a diverse fauna is observed, including brachiopods. Zezina (2008) has published the first data on the brachiopod fauna of the Piip Volcano. It consists of four species: *Frieleia halli* Dall, 1895, *Terebratulina kiiensis* (Dall and Pilsbry, 1891), *Laqueus vancouveriensis* Davidson, 1887 and *Laqueus blanfordi* (Dunker, 1882). Brachiopods were collected from the eastern slope of the southern peak of the volcano from a depth of 480-660 m, from a northern slope of the southern peak from a depth of 602-750 m, from a northeast slope of the southern peak from the depth of 607 m and from the western rising of a northern peak from a depth of 358 m. The density of *T. kiiensis* at the last site was estimated to be 30-40 specimens per m^2.

The new data were obtained as a result of photo, video recording and sampling using a remotely operated vehicle (ROV) “Comanche-18”. Brachiopods occur at depths starting from 2920 m, but are most numerous in shallower communities at a depth of 380-400 m. Three specimens of *T.* cf. *kiiensis* are in the collection, on photos and video materials. The ornamentation differs from that characteristic of the species: the ribs clearly stand out, they are the same in height. According to the ornamentation, these specimens are similar to the closely related species *T. austroamericana* Zezina, 1981 and *T. unguicula rotunda* Cooper, 1973. However, Zezina (2008) referred brachiopods found on the slopes of the Piip Volcano, to the species *T. kiiensis*.

The largest settlement of *T.* cf. *kiiensis* belongs to a community dominated by Cnidaria (sea anemones, alcyonarians). Also starfishes, chitons, bivalves, rockfishes, holothurians, crabs and nudibranchs are common. *Laqueus* sp. does not form aggregations, but it is represented by single individuals.

Previously (Zezina & Pakhnevich, 2000; Zezina, 2008) it was noted that brachiopods are rarely observed near the vents but inhabit the periphery of vent fields. In the present case, both species are found directly near the diffuse flows, but not near the hot vents. For the first time it was noted that the shells of the brachiopods of both species were inhabited by bacteria, *Beggiatoa* sp., forming sometimes dense accumulations. Bacterial filaments are already observed on the shells of juvenile animals 2-3 mm in length. For the first time it was found that the bacteria also live on a lophophore of *T.* cf. *kiiensis*. But it is difficult to assess the role of bacteria in the nutrition of brachiopods.

Fig. 1. Brachiopods *Terebratulina* cf. *kiiensis* near the hydrothermal seeps of the Piip Volcano.

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Cold seep-related occurrence of the Early Jurassic rhynchonellid brachiopod *Anarhynchia* from the Canadian Cordillera

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Cold seeps, where seepage of methane and/or other hydrocarbon-rich fluids and hydrogen-sulfide occurs in the sea floor, are sites which harbor highly specialized ecosystems associated with distinctive carbonate sediments. Although their Mesozoic record is scarce and patchy, it commonly includes rhynchonellid brachiopods, often of large size. Each new occurrence is valuable in filling gaps and providing additional insight into these peculiar ecosystems. Here, we report a monospecific assemblage of *Anarhynchia* from a boulder-sized limestone clast of Early Pliensbachian (Early Jurassic) age in the Inklin Formation of the Whitehorse Trough in Stikine terrane, recovered from a locality at Copper Island in Atlin Lake, northern British Columbia, Canada. Specimens are of unusually large size, up to 9 cm in length, and their external and internal morphology allows assignment to *Anarhynchia,* but warrants introduction of a new species. Although d^{13}C and d^{18}O values of the shells are close to equilibrium with ancient seawater, early precipitated carbonate cement phases of the enclosing limestone are characterised by highly depleted carbon isotopic composition, indicative of the influence of microbial oxidation of methane derived from a cold seep. Carbonate petrography of the isopachous, banded-fibrous cement supports its origin in a cold seep environment. Volcanogenic detrital grains in the micritic matrix of the limestone clast are indistinguishable from those in the sandstone layers of the siliciclastic sequence, suggesting that the seep carbonate is broadly coeval with the enclosing conglomerate. Previously, *Anarhynchia* has been known from the Lower Jurassic of California and Oregon, from both cold seep and hydrothermal vent deposits. Our new record extends the geographic range and species-level diversity of the genus, but supports its endemism to the East Pacific and membership in chemosynthesis-based ecosystems.

The Cambrian Epoch 2 brachiopod fauna from the Xinji Formation, Shuiyu section of North China

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Cambrian Series 2 strata have a wide distribution along the western, southern and eastern margin of the North China Plate (NPC). In the past several decades, many metazoan skeletal fossils had been published from these rocks, the Xinji and Houjiashan formations, along the western and southern margin of NPC. Some brachiopods have also been reported together with these fossils. However, only one brachiopod, *Kutorgina sinensis* Rong in Lu 1979, has been illustrated (but without description) in one Chinese publication. All other taxa have only been briefly mentioned in stratigraphic descriptions without detailed taxonomic nomenclature. Hitherto, many investigations of coeval Cambrian brachiopods from many other areas, including Australia, Antarctica, South China, Siberia, Greenland, Canada and the United States etc. have been published. Thus, systematic research on the brachiopods from North China will be important in our understanding of the global distribution and evolution of brachiopods as well as stratigraphic correlation of Cambrian Series 2. Here, we report an abundant brachiopod fauna from the Xinji Formation at Shuiyu section, Ruicheng County, Shanxi Province. The brachiopods include *Askepasma toddense*, *Eohadrotreta* cf. *zhenbaensis*, *Eodicellomus elkaniiformis*, *Spinobolus popovi*, *Palaeobolus*? *liantuoensis*, *Eoobolus* sp., *Karathele yorkensis* and a new species of *Curdus*. In addition, the fauna includes a mickwitziid (i.e. stem brachiopod) that likely represents a new genus that combines distinctive characters of other mickwitziid genera (morphology and structure of the shell) and some new characters (protruding ventral apex, well-developed ventral pseudointerarea and groove) and may be important for elucidating the earliest evolution of the Linguliformea. The fauna shows strong similarities to the coeval (Cambrian Epoch 2) brachiopod faunas of east Gondwana, especially those from South Australia (6 genera and 4 species in common) and South China (5 genera and 3 species in common). Furthermore, most of the brachiopods common to North China, South Australia and South China are endemic to these three areas which may suggest their adjacent palaeogeographic position in the Early Cambrian. Compared with the stratigraphic ranges of the brachiopods in South Australia and South China, this brachiopod assemblage indicates a late Age 3 to early Age 4 age for the Xinji Formation.

Disparity and diversity in Early Jurassic first colonizing brachiopods of the Lusitanian Basin (Portugal)

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In the Lusitanian Basin (west of Iberian Peninsula), a protected and shallow-water basin related to the North Atlantic opening, records its first marine sedimentation during the Sinemurian (Early Jurassic) (Azerêdo et al., 2010). In this sedimentary context, the Upper Sinemurian stratigraphic succession evidences the first brachiopod records which are restricted to the Oxynotum Chronozone interval. These records are of "*Terebratula*" *riberoi* Choffat 1901, supposedly endemic to the basin (Choffat, 1948, Mouterde et al., 1981, Paredes et al., 2013 and 2016). Putative genus name assignations were attempted such as *Plectoidothyris* (Colo, 1953, Almerás et al., 2014), *Hesperithyris* (Ager and Walley, 1977), *Plectothyris* (Paredes et al., 2012) or *Merophricus* (Paredes et al., 2013). In fact it is recognized as a high polymorphic terebratulid species. "*T.*" *ribeiroi* is the earliest brachiopod occurrence in the Jurassic record of the basin. It is abundant in the lowermost Oxynotum Chronozone and became extinct during the Oxynotum Subchronozone in the transition from Coimbra to Água de Madeiros formations in S. Pedro de Moel area (species type locality). New detailed stratigraphic observations showed that the occurrence of "*T.*" *riberoi* is related to the beginning of transgressive influxes marked by thin marly sedimentation. This overlaps bioturbated hardgrounds with sub-aerial exposures and with *Liostrea* spp. pavements. The succession is interpreted as a 2nd-order transgressive phase (Duarte et al., 2014).

The commonly observed geopetal infilling of the shell or geode features gives the perspective of sudden burial with no evidence of transportation or other taphonomic process.

The performed biometrical analysis reveals that the first appearing individuals of "*T.*" *ribeiroi* show more variability, including plicate and globose forms, and that plication and globosity decreases over time. Although there is a preference of larger forms to develop ribs (plicae), ribbing as a purely ontogenetic process is discarded. Also, the hypothesis that ribbed and smooth specimens could correspond to different morphospecies is put aside by the high correlation as evidenced in length-width and width-high variograms.

It is plausible to relate the modern south-hemisphere *Magellania venosa* (Solander, 1789) to those terebratulid assemblages as analogues. In both cases they can be regarded as opportunistic species because they are dominant benthic macrofaunal assemblages exhibiting all morphologies, even aberrant forms. *M. venosa* is a successful competitor and a pioneer with low juvenile mortality, as indicated by settling dynamics (Baumgarten et al., 2014). Possibly *"T." ribeiroi* had a similar ecological status. Furthermore, regarding the observed population density it might have had a high growth rate, a difficult fact to prove but the analogue *M. venosa* has the highest growth rate among modern brachiopods (Baumgarten et al., 2014). With a coastal Antarctic to Sub-antarctic distribution (Chile and south Argentina), it is usually found from sub-tidal (or even inter-tidal) to 1900 m-deep bathyal zones (McCammon, 1973), pedicle-attached to bioclasts, pebbles or even clustering each other's. "*T.*" *ribeiroi* and also the recent *Magellania* species exhibit apparently random shell ribbing. Cohen et al. (2011) underwent studies to better understand ribbing development in those modern shells and its morphogenesis and achieved scarce evidences. Cold and nutrient-rich waters are the main ecologic limitation factors governing the *M. venosa* distribution, more than bathymetry (McCommon, 1973). This author pointed out that this species apparently lives directly in muddy substrate. In the case of "*T.*" *ribeiroi* the presence of frontal plication in the first stages of colonization could be related to the grain size of the sediments, according to the classic scheme of Rudwick (1964) that relates the plication of the commissure to the necessity to avoid the entry of sand particles into the shell. Nevertheless, high density occurrence was observed in the maximum flooding interval associated to 3rd-order phase evolution (Duarte et al., 2014), related with more marly sedimentation. Then the plication tends to disappear and the shell becomes flatter. This can be an adaptive function to more laminar hydrodynamic flux as a selective advantage compared to ribbed shells (Cohen et al., 2011).

In summary, during the occurrence as an opportunistic species, "*T.*" *ribeiroi* colonized the platforms and displayed disparate morphologies, including adaptions to high energy shallow environments. That corresponds to the dominance time when there was no competition for space. Thereafter, the stability and increasing diversity in the platform forced those populations to keep a stable morphology. So when species diversity increases, a decrease in "*T.*" *ribeiroi* disparity is observed.

It is plausible to admit a brachiopod larval dispersal flux from the Tethys at deep water context to shallow water epi-continental basins. Accepting that, an epi-oceanic to epi-continental colonization process is a likely hypothesis to explain how "*T.*" *ribeiroi* was established in the Lusitanian Basin during the Oxynotum Chronozone. That species is regarded as opportunistic, developing large forms and a high disparity in morphologies. A dominance mechanism is interpreted as a result of vacant niche occupancy in the platforms. Thereafter, the progressive stabilization of substrate and the increase of brachiopod species diversity led to species disparity decrease and a stable morphology predominated. Smaller and smooth individuals were the last representatives of that endemic terebratulid species. Ribbed shells were no longer present prior to the taxon extinction during the middle-late Oxynotum Subchronozone.

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Selectivity of temperature-related stresses towards brachiopods across the early Toarcian (Early Jurassic) extinction event in Neo-Tethys

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Global warming and temperature-related stresses (TRS), in particular deoxygenation and ocean acidification, are important drivers of past and present biotic crises. Amongst their observed consequences are changes in the body size of organisms and in biodiversity. Here, we tested whether population- and community-level body size distribution of benthic marine bivalves and brachiopods changed in relation to TRS associated with the Early Toarcian event.

We performed a detailed bed-by-bed study of faunal assemblages at the stratigraphically complete sections of Fonte Coberta/Rabaçal in the Lusitanian Basin of Portugal and Barranco de la Cañada in the Celtiberian Chain of Spain. In contrast to most other localities globally, both sections represent fully oxygenated environments and are composed of an alternation of marlstones and micritic carbonates. The time span sampled ranges from the Pliensbachian–Toarcian boundary to the middle of the Levisoni Zone in Portugal and to the lower Bifrons Zone in Spain. Body size analyses were performed for the pre-extinction interval using the log geometric mean of shell width and length. Standardized sample-level diversity (Alroy's Quorum Subsampling) was used as a measure of species richness.

The linear regression of shell size against sampling level shows that the mean body size of faunal samples from Portugal decreased significantly across the pre-extinction interval (Fig. 1A), driven by larger-sized brachiopod species becoming smaller (Fig. 1B) and less abundant. By contrast, the Spanish fauna reveals an overall body size increase in the pre-extinction interval (Fig. 1C), again evident only in the larger-sized brachiopod species (Fig. 1D). No significant body size change is observed in bivalves in both sections, suggesting a decoupling of the faunal response of brachiopods and bivalves to TRS.

Diversity patterns also differ at both localities. In Portugal, species richness is moderately high in the pre-extinction interval before the lowest values are reached ~1.5 m below the crisis interval, driven by brachiopods becoming less diverse. The crisis interval preserves virtually no shelly fossils in its lower half, and the sporadic occurrence of survivors and occurrences of potential disaster taxa such as the rhynchonellid *Soaresirhynchia bouchardi* and the bivalve *Parvamussium* in the upper half. The post-extinction interval starts with the first new taxa in low-diversity assemblages before species richness recovers to pre-extinction values in the uppermost part of the studied section. In Spain, species richness is markedly higher, especially that of bivalves. The brachiopod taxa *Pseudokingena deslongchampsi* and *Nannirhynchia pygmaea*, both prominent in Portugal, are absent and *Liospiriferina* species are rare. No change in species richness is observed before the crisis, as the observed diversity decrease in brachiopods is compensated by bivalves becoming more diverse. A steady increase in biodiversity takes place immediately after the extinction level. Unlike in Portugal, *S. bouchardi* appears immediately at the onset of the crisis interval, in which bivalves are highly diverse but not abundant. Such increase in biodiversity, more prominent overall for brachiopods, is halted around the boundary between the Levisoni and the Bifrons zones.

In both sections, scenarios invoking ocean acidification and deoxygenation seem incompatible with the observed selective trends in shell size and diversity, and can be preliminarily excluded as potential main drivers. Hypoxic conditions are an unlikely driver of faunal change because the sedimentary rocks of the crisis interval at both locations are heavily bioturbated and experimental work on modern brachiopods suggests that they are hardly affected by ocean acidification, unlike bivalves. We tentatively suggest a strong role of heat stress, although a secondary role of acidification is not excluded. The opposite directions of changes in body size suggest that size reductions in marine invertebrates are not a general response to environmental stress before the Toarcian extinction event, and differential patterns may reflect variable strengths of TRS and/or differences in the adaptation of local faunas against environmental change.

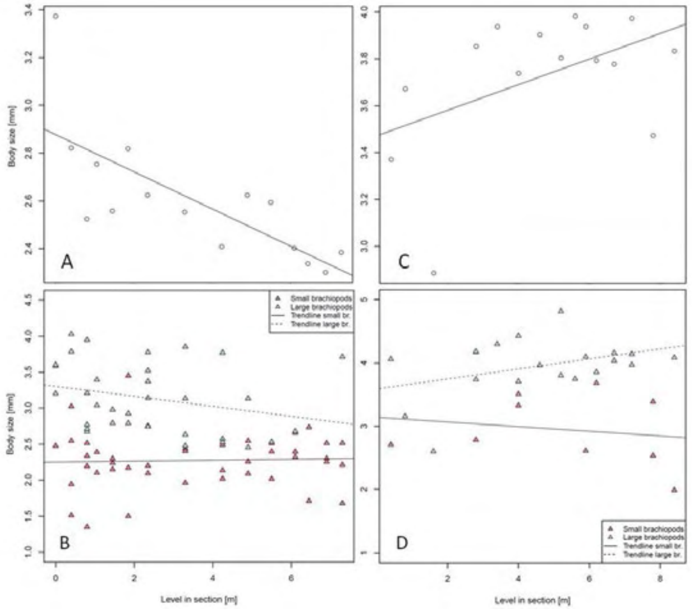

Fig. 1 Body size variation in the pre-extinction interval at Fonte Coberta (A-B) and Barranco de la Cañada (C-D). Body size is represented by the mean of the log geometric mean of all individuals of respective samples. Figs. 1A, C show the mean body size of the community for each sample. The specific trends for larger- and smaller-sized brachiopods for the same interval are shown in Figs. 1B, D.

A cancelled field excursion: Upper Permian to Middle Triassic brachiopod beds of the Dolomites (Italy)

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The Upper Permian marine succession of the Dolomites is represented by the Bellerophon Fm, an overall transgressive sequence, punctuated by some transgressive-regressive cycles. It consists of a lower sulphate-evaporite unit, deposited in a barren basin, and an upper shallow-marine carbonate unit, deposited along a low-energy ramp setting. The older brachiopod occurrence is represented by large sized lingulid shells of *Trentingula prinothi* Posenato, which has been found in a clayey fine-grained sandstone bed from the upper part of the Val Gardena Sandstone tongue (lower part the Lo 4 sequence; Posenato et al., 2014; Posenato, 2016).

The older rhynchonelliform brachiopod-bearing beds (lower *Comelicania* beds) of the Bellerophon Fm, about 1.5 m thick, contain only the athyridid *Comelicania*. They are located at about 50 m (maximum flooding surface of the sequence Lo 4) below the top of the Bellerophon Fm and have been correlated to the Changhsingian *Clarkina changxingensis* Zone. In the Gardena Valley, the lower *Comelicania* beds contain a rich nautiloid fauna characterized by *Tirolonautilus crux* (Stache). *Comelicania* is represented by *C. doriphora* Merla and *C. haueri* (Stache), characterized by mid sized shells (about 50 mm wide; Posenato and Prinoth, 2004; Posenato, 2010).

The middle *Comelicania* beds (about 2 m thick) occur at about 15 m below the top of the Bellerophon Fm (maximum flooding surface of Lo 5 sequence). The brachiopods (*C. haueri*, about 10-12 cm in width) are contained in black bioclastic wackestone with abundant calcareous algae and diversified foraminifer assemblage, which suggest more stable and fully marine conditions with respect to the lower *Comelicania* beds.

The upper *Comelicania* beds (from 0.4 cm to 1.5 m thick) are contained within the black bioclastic wackestone/grainstone of the Bulla Member (upper Bellerophon Fm), which contains the most diversified foraminifer assemblage of the Upper Permian marine succession. The brachiopod fauna is again dominated by the athyridid *Comelicania*, which is represented by very large sized shells (up to 15 cm in width) of *C. haueri* (Stache), *C. megalotis* (Stache), and *C. merlai* (Posenato). The latter species, characterized by short wings, is frequent in the uppermost packstone/grainstone (max 10-15 cm thick) of the Bulla Member, where many other brachiopod species first appear (*Janiceps peracuta* (Stache), *J. cadorica* (Stache), *J. papilio* (Stache), *J. bipartita* (Stache), *Comelicothyris recticardinis* (Merla), *C. laterosulcata* Posenato, *Ombonia tirolensis* (Stache) and *Orthothetina ladina* (Stache) (Broglio Loriga et al., 1988; Posenato, 1988, 2001, 2010, 2011). The upper *Comelicania* beds have been referred to the lower *H. praeparvus* Zone (Farabegoli et al., 2007).

The Bulla Mb (Bellerophon Fm) is overlain by the Tesero Mb of Werfen Fm, a thick mixed siliciclastic-carbonate succession, predominantly Lower Triassic in age (approximately 200 - 600 m thick), which records the survival and early recovery phases connected with the end-Permian mass extinction. The Bulla and Tesero members are separated by a barely perceptible erosional surface, which occurrence and interpretation have been deeply discussed in the literature (subaerial erosion and microkastification, leaching by acid rain or acid marine water; Farabegoli et al., 2007; Posenato, 2009; Farabegoli and Perri, 2012). The basal beds, 5 – 20 cm thick, of the Tesero Mb consist of crystalline ooid grainstones, which record the end Permian mass extinction and thermal peaks in the Dolomites (e.g., Farabegoli et al., 2007; Posenato, 2010, Brand et al., 2012). This unit (*Ombonia* and *Orthothetina* beds) contains a brachiopod assemblage dominated by the orthotetid *Ombonia* and *Orthothetina*. The athyridid *Janiceps* and *Comelicothyris* (reworked?) are still present, while *Comelicania* seems to be disappear (Posenato 2010, 2011).

The last occurrence of the rhynchonelliform brachiopods is recorded within marlstone lenses occurring between microbial limestone and stromatolitic beds of the Tesero Mb (*H. changhsingensis* Zone and lower *H. parvus* Zone). The brachiopods are common only in the Tesero section, where they disappear at about 2.5 m above the formational base. The brachiopod assemblage is dominated by the ambocoelid *Orbicoelia dolomitensis* Chen followed, in order of abundance, by the orthotetid *Teserina nerii* (Posenato) and *Ombonia tirolensis* (Stache). The athyridids are represented by mm-sized individuals of ?*Spirigerella teseroi* Chen. *Spinomarginifera* and *Prelissorhynchia* are also present, but very rare (e.g., Broglio Loriga et al., 1988; Chen et al., 2006; Posenato 2009, 2010).

The brachiopods occurring in the overlying members of Werfen Fm are only represented by lingulids, a disaster taxon recording the early Triassic aftermath of the end-Permian mass extinction. They appear in the Mazzin Mb, few meters above the base of Werfen Fm (8 m at Tesero section, *H. parvus* Zone). These lingulids (*Trentingula mazzinensis* Posenato) are characterized by small-sized shells (4-5 mm in length) and occur in great abundance, generally as storm accumulations, throughout the Mazzin Mb. These brachiopods record the Lilliput effect, a survival strategy of skeletal miniaturization related to the end-Permian environmental crisis (e.g., Twitchett, 2007; Posenato et al., 2014, Posenato, 2016). Lingulids are also occasionally present in the overlying members, where they are characterized by larger shells (*Trentingula lorigae* Posenato), generally double in size with respect to those of the Mazzin Member.

The Triassic recovery of the rhynchonelliform brachiopods occurs in the Pelsonian (Anisian) Recoaro / Dont Fms. The most common brachiopod species belong to the following genera: *Angustothyris, Coenothyris, Decurtella, Koeveskallina, Mentzelia, Punctospiriferella*, and *Tetractinella* (e.g., Posenato, 2008).

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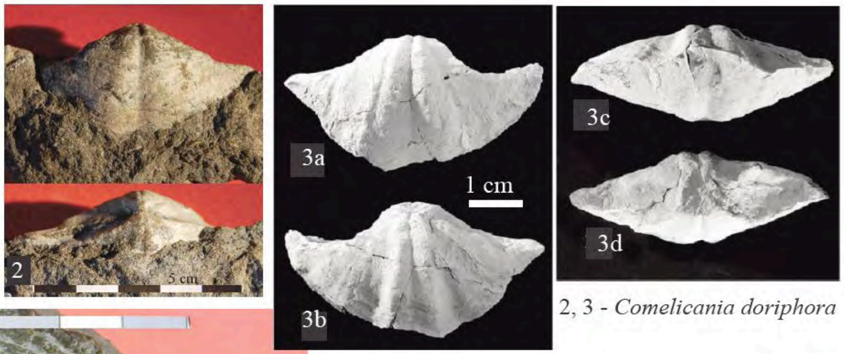
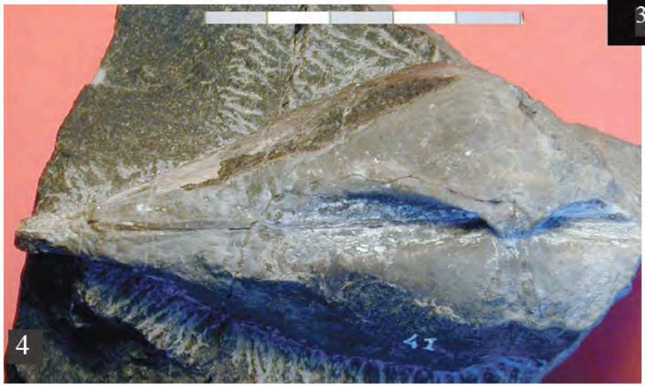
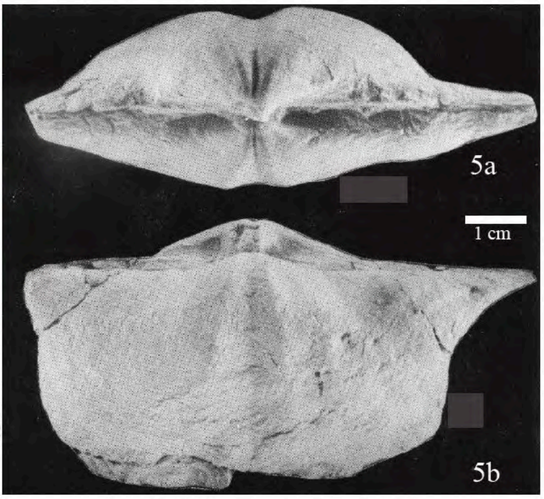
1 - *Trentingula prinothi*



2, 3 - *Comelicania doriphora*



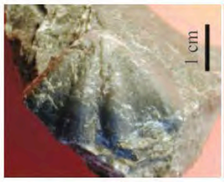
4 - *Comelicania haueri*



5 - *Comelicania megalotis*

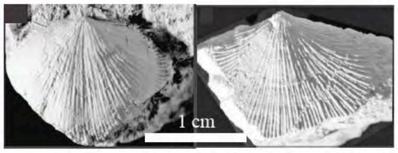
6 - *Comelicania merlai*

7 - *Comelicothyris laterosulcata*

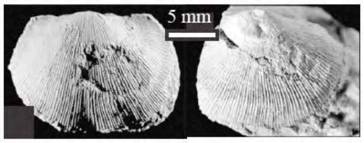


8 - *Janiceps peracuta*

9 - *Janiceps cadorica*

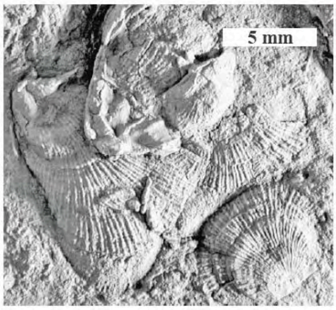


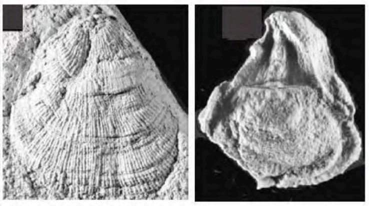
10 - *Orthothetina ladina*



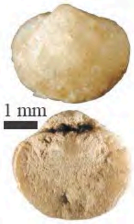
11 - *Ombonia tirolensis*

14 - *?Spirigerella teseroi*

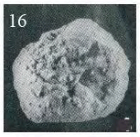




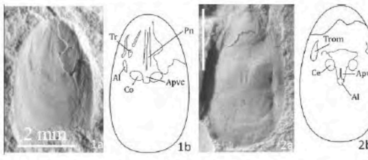
12 - *Teserina nerii*



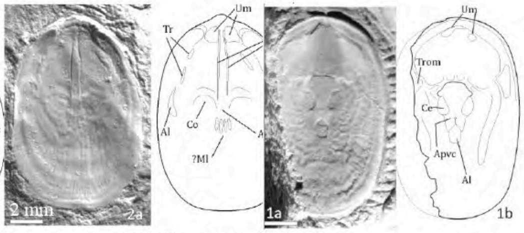
13 - *Orbicoelia dolomitensis*



15 - ? *Prelissorhynchia* sp.
16 - *Spinomarginifera* sp.



17 - *Trentingula mazzinensis*



18 - *Trentingula lorigae*

12 - *Teserina nerii*

Devonian brachiopod fauna from the Baoshan Block in western Yunnan, China

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The Devonian succession of the Shidian area in Baoshan Block, western Yunnan, China begins with alternating sandstones, shales and, in the upper part, limestones and marls. The limestones of the upper part which were named as the Hoyuanchai = (Heyuanzhai) Formation (Sun and Szetu, 1947) contain diverse macrofossils, including brachiopods, corals, bryozoans, echinoderms, stromatoporoids, etc. Fang and Zhu (1974) and Jiang (1996) illustrated some of the most frequent forms of brachiopods (e.g., *Levenea*, *Gypidula*, *Atrypa*, *Spinatrypa*, *Cyrtina*, *Pyramidalia*), and considered them to be Middle Devonian in age. This conclusion, however, is inconsistent with the coral fauna from the same horizons in the Heyuanzhai Formation of Shidian area (Wang, 1994). Wang (1994) described and attributed the rugose coral fauna of the Heyuanzhai Formation to the Givetian-Frasnian, and first indicated the dissimilarity of coral faunas between the Baoshan and Yangtze blocks.

Here we report the brachiopod fauna from the Heyuanzhai Formation with twice the diversity of previous studies, based on our new collections and investigations in the Shidian area during 2017-2018. Brachiopods come from three outcrops, Heyuanzhai, Douyashan, and Baiyazi. A preliminary study reveals 25 species belonging to 19 genera. Our new material (with special notes on occurrences of cyrtospiriferoids and pugnacoids) considerably enriches the Heyuanzhai brachiopod fauna, and more importantly suggests a potential age determination from Givetian to Frasnian. The brachiopod fauna from the Heyuanzhai Formation of the Baoshan Block is distinctive in light of the high level of endemic species. It seems that the Baoshan brachiopod fauna maintains closer palaeobiogeographical similarities to those of the Eastern North American Realm than to those of the Yangtze Block, with about 80% of the genera in common during the Givetian-Frasnian.

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Drill-hole repair in Cenozoic and Recent Brachiopods

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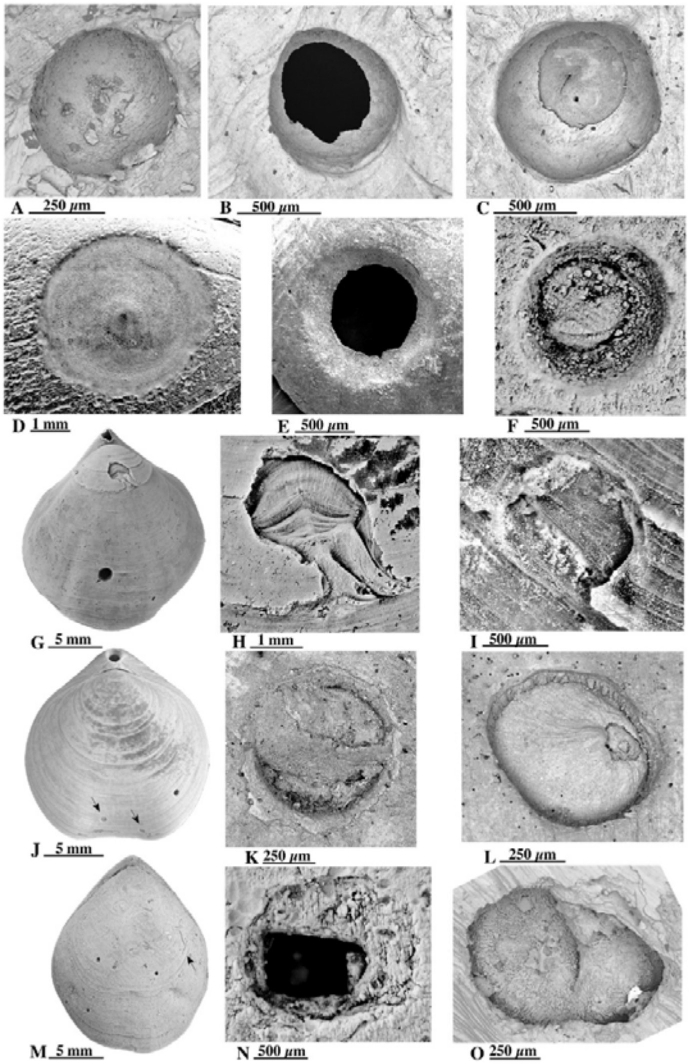
Several extant invertebrate groups are known to repair shell damage inflicted by predators, including molluscs (bivalves, gastropods, nautiloids), echinoderms and brachiopods. Repair traces on the shells of living and fossil brachiopods reveals they are attacked by a range of predators. There has been considerable discussion in the literature as to whether gastropods drill brachiopods intentionally. Tyler et al. (2012, p. 724) stated that "although brachiopods may be unwanted prey in the presence of energetically more desirable targets, they do appear to be edible and subject to intense predator-prey interactions under certain conditions."

Repaired drill-holes in brachiopods are known from the Paleozoic but I am aware of only two publications that described drill-hole repair in extant brachiopods (Alexander, 1992; Robinson, 2013) and none for Cenozoic brachiopods. Over the last 6 years I have examined thousands of individual brachiopods from New Zealand and elsewhere for a variety of research projects and during curating of collections. All specimens were investigated for repaired drill-holes which were found in thirteen Cenozoic and Recent brachiopod species including discinids, rhynchonellids, terebratulids and terebratellids. Where repaired drill-holes were present the number of specimens with repaired drill-holes in a population ranged from 0.9% to 27% (the latter from a population of 49 specimens).

Four types of hole were repaired. These included drill-holes made by muricid gastropods (Fig. 1A-C) and drill-holes that appear to be made by naticid gastropods (Fig. 1D-F); however, species in other groups of gastropod can produce a similar drill-hole (Harper et al., 2011). A small number of holes in two fossil species from one locality were elongate and irregular with rough edges but appeared to be consistent and may be drill-holes (Fig. 1N-O), perhaps produced by ranellid gastropods. Two repaired holes were irregular and their provenance is unknown.

Surprisingly, there were six types of drill-hole repair. It appears that brachiopods may regrow the mantle beneath the drill-hole and then produce a new layer of shell or they may regrow the mantle and new shell at the same time, incrementally, as occurs at the commissure during normal growth. Each of these methods produces variations of drill-hole repair (see Figure). Also, surprisingly, several populations included specimens with multiple drill-holes and multiple repaired drill-holes. One specimen of *Abyssothyris* had eight drill-holes, four of which had been repaired. The placement on the shell of all drill-holes (incomplete, complete and repaired) was plotted for seven populations (not shown). In two cases the gastropods appeared to be preferentially attacking the brachiopods in a particular area; the posterior half of the ventral valve in *Abyssothyris* and the shell anterior in *Basiliola*.



A. Incomplete muricid drill-hole on fossil *Aetheia*. **B**. Complete muricid drill-hole on living *Notosaria*. **C**. Repaired muricid drill-hole on living *Notosaria*. **D**. Incomplete naticid drill-hole with central boss on bivalve (image previously published in Kong et al. 2017). **E**. Complete naticid-like drill-hole on bivalve. **F**. Repaired naticid-like drill-hole on fossil *Aetheia*. **G-H**. Living *Basiliola* with two drill-holes, one repaired. **H**. Close-up of repaired drill-hole. **I**. Repaired drill-hole on living *Grammetaria*. **J**. Living *Abyssothyris* with three drill-holes, two repaired (arrowed). **K**. Close-up of repaired drill-hole on *Abyssothyris*. **L**. Close-up of repaired drill-hole on *Abyssothyris*. **M**. Fossil *Aetheia* with 5 drillholes, one repaired (arrowed). **N**. Elongate possible drill-hole on *Aetheia*. **M**. Repaired elongate possible drill-hole on fossil *Aetheia*.

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Keynote lecture

What can geochemical proxies tell about the biomineralization processes of brachiopods?

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Biocarbonates are used as recorder of environmental conditions through their isotopic and elemental compositions. But these compositions are often offset from the equilibrium field determined for inorganic calcite. This offset, the so-called vital effect, is likely due to the impact of the biology of the organisms on the carbonate precipitation. Among biocarbonates, brachiopods were extensively used to reconstruct past environmental conditions because of their shell composed of low-magnesium calcite and their fossil record extending from the Cambrian to the present. Whereas vital effects are considered as a problem for paleo-environmental reconstructions, they are of great interest to have some clues of the biomineralization processes. To better understand how the different shell microstructures (primary, secondary and tertiary layers) are precipitated, we investigated various modern species for their boron, oxygen and magnesium isotopic compositions, as well as their elemental contents (Li, B, Mg, Na, Sr). Combining all these geochemical systems with literature data, we propose that the primary layer results from the precipitation via amorphous calcium carbonate precursors, as it was observed in the brachiopod *Megerlia truncata* by Griesshaber et al (2009). The secondary layer seems to reflect some kinetic effects linked to the growth rate of the brachiopod shells during its lifetime. The tertiary layer presents the most stable geochemical signal, and so it is likely that the precipitation of this layer is not affected by any kinetic effects. This layer has also very low content of Li, B, Mg, Na and Sr, as it was observed in fossil three-layered brachiopod (e.g. Grossman et al., 1996; Angiolini et al., 2012). This depletion in trace element relative to the secondary and primary layers could be the result of the precipitation via a fluid depleted itself, i.e. a differentiated seawater.

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Cement-filled fossil brachiopod punctae and potential analytical bias in paleoenvironmental reconstructions

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Fossil brachiopods have been extensively used as archives in paleoenvironmental studies due to their shell resistance to diagenesis. The majority of analyses on fossil brachiopods focus on carbon and oxygen stable isotopes, minor and trace elements, and the larger part of the analyses is still done on the bulk of the shell low-Mg calcite (LMC). A lot of work has been recently done concerning sample preparation and cleaning procedures in order to avoid unwanted contaminations, but no investigation has yet looked into the possible analytical bias caused by the brachiopod punctae, which may be filled with diagenetic carbonate cement. In this preliminary study, we compared the chemical compositions of the biogenic shell-calcite and the cement-filled punctae. Fossil specimens of *Megerlia truncata*, *Gryphus kickxi* and *Terebratula sinuosa* from different locations and outcrops were studied. Electron microprobe analysis, in wavelength dispersive mode, was done in order to measure the Ca, Mg, Sr, Mn, Fe, Ba, Al, P and Si contents in a valve thin section, targeting both biogenic calcite of the shell and the calcite cement in the punctae. Results show a clear offset only in *G. kickxi*, with all the targeted punctae having much higher Fe and Mg contents. *M. truncata* and *T. sinuosa* specimens are more homogeneous and with less distinct chemical differences between punctae calcite and shell calcite. Such differences might be easily explained by different diagenetic stages: e.g. similar in *M. truncata* and *T. sinuosa*, and basically different in *G. kickxi*. The case of *G. kickxi* points a possible analytical bias that punctae might cause even in well preserved specimens. The differences in chemical composition that we observed are not species-specific, but rather related to the depositional environment and geological history of the depositional basin. We believe that a large-scale survey is needed to more accurately understand the influence of calcite-infilled punctae across a large variety of geological settings. This will ultimately lead to a better calibration of geochemical proxies when using brachiopod shell geochemistry as environmental archive.

Trace elements, stable isotope composition and shell microstructure, defining the optimal sampling shell segment for geochemical analyses in five modern brachiopod species

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Recent and fossil brachiopod shells are excellent biomineral archives for (palaeo)climatic and (palaeo)environmental reconstructions, as they precipitate their calcite shells in isotopic equilibrium with ambient seawater mostly with no or limited vital effect; also, their low-magnesium calcite shell is generally quite resistant to diagenetic alteration. Despite this, only few studies address the issue of identifying the best part of the shell to sample for geochemical analyses. Here, we examined the link between shell ontogeny, microstructure and geochemical signatures recorded in different parts of the brachiopod shell. To reach this aim, we analyzed Mg, Sr, Na concentrations and oxygen and carbon stable isotope compositions of five different recent brachiopod species (*Magellania venosa, Liothyrella uva, Aerothyris kerguelensis, Liothyrella neozelanica* and *Gryphus vitreus*), collected from different latitudes and different environments (Chile, Antarctica, Indian Ocean, New Zealand and Italy) and having different shell layer successions (two-layer and three-layer shells). Different trends are shown by the two- and three-layer shells in their trace element and stable isotope records, but similar patterns have been observed in the ventral and dorsal valves of these two groups, suggesting the use of both valves for geochemical and isotope analyses. This study on recent brachiopods leads us to conclude that the best region to sample is the middle part of the mid-section of the shell, and that the primary layer, the posterior and anterior parts as well as the outermost part of the secondary layer should be avoided. Likewise, the outermost and innermost rims in fossil specimens should also be discarded as they may be the first parts to be diagenetically altered. Finally, among all proxies, $\delta^{18}O$ values seem to be least affected by different microstructures and shell ontogeny, thus, making it a most powerful and important recorder of (palaeo)climatic and (palaeo)environmental changes.

The brachiopod record around the Devonian–Carboniferous boundary: insights from the sedimentary sequences of Armenia

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Enclosed in the Caucasian mountains, Armenia offers exceptional outcrops of Upper Palaeozoic sedimentary sequences. They are encountered mainly in the southern part of Central Armenia within the South-Armenian block of Gondwanan origin. These shallow marine series consist of mixed carbonate–siliciclastic deposits including sequences of limestones, shales and quartzites. They are particularly rich in brachiopods, which are helpful for their dating, especially for the Upper Devonian–Lower Carboniferous succession. The last comprehensive contributions dedicated to the brachiopods date back to Abrahamian (1957, 1974a, 1974b); no modern study was carried for the last 40 years, especially to explore the fluctuations of brachiopod diversity and their biotic response to the Hangenberg Crisis. A synthesis of Abrahamian's papers and our own data establish the occurrence of 46 brachiopod species throughout the Famennian–Tournaisian interval, assigned to seven different orders. The lower Famennian Ertych and Noravank Formations, composed mainly of alternations of sandy limestones and shales, contain a relatively impoverished brachiopod fauna composed essentially of a few rhynchonellide and spiriferide species (seven in total). In contrast, the uppermost Famennian Arshakiaghbyur Formation, composed mainly of limestones, contains an extremely abundant and highly diverse fauna, composed of 27 species assigned to 23 genera such as the productides *Hamlingella*, *Mesoplica* and *Spinocarinifera*, the rhynchonellides *Araratella*, *Ptychomaletoechia*, *Sinotectirostrum* and *Tchanakhtchirostrum*, the athyridide *Gruntathyris*, and the spiriferide *Sphenospira*. The overlying lower Tournaisian Gerankalasy Formation, composed chiefly of sandy limestones, includes a much less diverse brachiopod fauna. A drop in diversity is recorded at the transition between the Arshakiaghbyur and Gerankalasy Formations and it is regarded as the record of the Hangenberg Crisis in Armenia. In this country, the biotic response of the seven brachiopod orders to this crisis is different from the specific viewpoint. At first view, the athyridides seem to have been poorly affected contrary to the rhynchonellides and the orthotetides. For instance, only one rhynchonellide species out of ten crossed the boundary. A major turnover is observed among the orthides, productides and spiriferides as none of the uppermost Famennian species crossed the Devonian–Carboniferous boundary. The post-crisis diversification of the productides and spiriferides at the base of the Tournaisian appears to be quite low in the Armenian sections.

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Keynote lecture

A sudden end-Permian mass extinction in South China

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Previous studies of the end-Permian mass extinction have established that it was geologically rapid, but condensed sections have made it difficult to establish the exact timing of the extinction relative to fluctuations in the ocean carbon cycle, oxygen levels, and temperature. Integrated high-precision U-Pb geochronology, biostratigraphy, and chemostratigraphy from a highly expanded section at Penglaitan, Guangxi, South China reveal a sudden end-Permian mass extinction that occurred at 251.939 ± 0.031 Ma, which is temporally coincident with the extinction recorded in Bed 25 of the Meishan section. Despite the significantly expanded nature of the section and extensive collecting of more than ten major marine fossil groups, there is no evidence of a decline of biotic diversity prior to the extinction interval and no Permian-type species survive the extinction at this location. Fossil range data suggest a nearly instantaneous extinction at the top of a narrow stratigraphic interval limited to 31 ± 31 kyr. The extinction was preceded by and/or accompanied by fluctuations in δ^{13}Ccarb and δ^{13}Corg of 2-3‰, and 3-5 ºC in seawater temperature. A larger, more rapid seawater temperature rise of 6-8 ºC immediately followed the extinction level at Penglaitan. The extinction is spatially associated with a thick unit of tuff and tuffaceous sandstones (Bed 141) indicating massive pyroclastic input. It is correlative with an ash layer (Bed 25) in the deeper water setting at Meishan, where some Permian-type organisms survived the extinction. Our study reveals that the survivability of Permian taxa after the major extinction pulse is variable and dependent upon the severity of environmental perturbation in different sedimentary settings. The sudden extinction may fit a scenario in which the onset of Siberian Traps and South China intensive volcanism *ca.* 420 kyr before the extinction may have diminished the ecological resilience of communities and reduced ecological functions with little change in diversity. In such an environmentally stressed condition, a single environmental disturbance could trigger the sudden collapse of global ecosystems.

Keynote lecture

Form and function of fossil brachiopods: insights into evolutionary morphology

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Since macroevolution involves change in adaptive strategies, an understanding of autecology for extinct animals may lead to deeper insight into the evolutionary process. However, there is no reliable way to test the biological features of fossils, almost all of which preserve only hard, skeletal parts without soft tissues. One way to find a better conclusion is to study functional morphology, which enables understanding of the autecology of fossil organisms within each body organization.

The phylum Brachiopoda is one of the most interesting subjects for the study of form and function because the external morphology of brachiopods is closely related to ecophenotypic variations in adaptation to benthic conditions and generation of feeding flows (e.g., Alexander, 1999). Maintaining attachment to the substrate is a primary requirement, and secondarily, brachiopods need to generate flows for feeding and respiration (Shiino and Angiolini, 2014). Extant species can generate feeding flows via ciliary motion and in a passive manner as if "cast adrift" on the sea bottom (LaBarbera, 1977, 1981, 1984). When an animal relies heavily on passive flows, a precise relationship between the shell form and ambient flows is required.

In contrast to the modern decline in taxonomical diversity, rhynchonelliformean brachiopods were the most successful invertebrate group in the Palaeozoic sea, as revealed by the presence of a large number of species with peculiar forms that have never been seen in modern times. There were two major morphotypes in the Palaeozoic: spiriferid and productid brachiopods. The former, spiriferid brachiopods, were the main group underlying the "brachiopod golden age" in the Devonian sea (Droser et al., 2000), and they are characterized by a wing-like outline and a major depression along the midline so-called sulcus. Spiriferids have a conical coil- or spring-shaped lophophore with a right-and-left directional axis. The latter, productid brachiopods, have a concavo-convex shell, and they thrived in the Permian sea and had the largest number of genera among the orders of Brachiopoda (Carlson and Leighton, 2001). The two morphotypes differ in the tempo and pattern of biodiversity, possibly due to differences in autecological properties.

Hydrodynamic, biomechanical approaches to spiriferid and productid brachiopods revealed functionality of the shell in generating passive flows, whereby the shell, when combined with ambient flows, provides a unique pressure gradient along the gape (e.g., Shiino and Kuwazuru, 2010; Shiino and Suzuki, 2011). In spiriferids, the sulcus, a major depression of brachiopod shell, is subjected to higher pressure, resulting in inflows through the sulcus gape (median inhalant and lateral exhalant flows). By contrast, the productid shell functions to generate inflows through the ear gape and outflows through the anterior gape (lateral inhalant and medial exhalant flows). Although the relationships of inflows and outflows were completely opposite to each other, the generated passive flows of both morphotypes exhibited a gyrating movement to produce alignment on the spiral lophophore (Fig. 1). Such a relationship between flows and the lophophore is beneficial for food filtration of brachiopods.

Spiriferids with sulcus-bearing shells and a spiral lophophore appeared in the Ordovician age (Zhan et al., 2012), but these features may not have been functionalized. Following the increase in food matter in the Devonian sea, both morphological features developed and thus became functionalized to generate spiral flows for effective feeding. Productids gradually increased in taxonomic diversity through the middle Palaeozoic, and they thrived spectacularly during the middle Permian. Productid diversification remains unclear, although one may imagine that the lower rate of metabolism and thus lower requirements for food and oxygen (Pérez-Huerta and Sheldon, 2006) fulfilled a unique autecological niche, resulting in adaptations to a wide range of environmental conditions.

Much remains unknown regarding fossil brachiopods and their dramatic history of biodiversity (Fig. 2). Fossil biomechanics may lead to likely scenarios of how brachiopods have achieved biodiversity as a compromise based on intrinsic and extrinsic constraints, and these are topics of long-term evolutionary morphology.

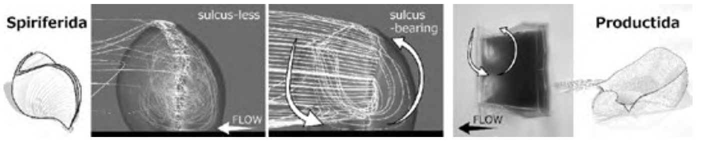

Fig. 1. Passive feeding flows of spiriferid and productid brachiopods. The sulcus-bearing model of spiriferid generated spiral vortex flows aligning the spiral lophophore, unlike the case in the sulcus-less model (Shiino and Kuwazuru, 2010). Passive feeding flows of productids were also demonstrated using flume experiments. Visualized flows suggest gyrating flows were beneficial for supposed lophophore (Shiino and Suzuki, 2011).

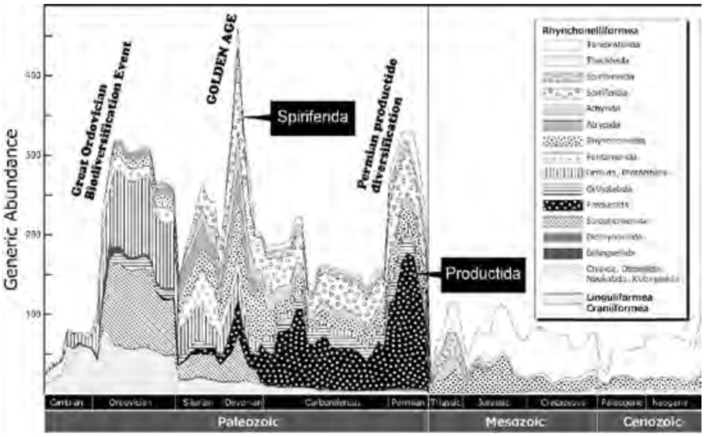

Fig. 2. Generic abundance of brachiopods throughout the Phanerozoic. Modified from Curry and Brunton (2007).

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A hydrodynamic approach to orthid brachiopod *Vinlandostrophia ponderosa*: reevaluation of zig-zag function

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Orthid brachiopods diversified taxonomically and morphologically through the Ordovician as the dominant players in the Great Ordovician Biodiversification Event (Harper, 2006; Harper et al., 2013). Platystrophiids have peculiar morphology among the orthids, being characterized by a strophic biconvex shell with angular ribbing producing a zig-zag commissure line. Because of this wing-like appearance, platystrophiids are traditionally compared to spiriferid brachiopods as the ‘spiriferoid’ or ‘spirifer’ form (see McEwan, 1919).

The ‘spirifer’ form of brachiopods is one of the key morphological innovations that may have permitted a new biological activity within a benthic mode of life. With the possession of spiralia, the spiriferid shell form has a hydrodynamic function to efficiently capture suspended food matter, thereby generating spiral flows inside the shell under fluidic conditions (e.g., Shiino, 2010). In light of these facts, the ‘spirifer’ form of platystrophiid brachiopods may reflect a morpho-functional convergence that enables the generation of spiral feeding flows as seen in spiriferids.

Using a flow tank and a hollow model with a zig-zag commissure (zig-zag model), we performed water flow experiments to examine the hydrodynamic function of a platystrophiid shell. We reconstructed an artificial model without the zig-zag commissure (smooth model) and analysed its hydrodynamic function in terms of passive flow generation.

Regardless of the presence or absence of the zig-zag commissure, the experimental models generated weak gyrating flows inside the models, with the inflows through the sulcus gape and the outflows through the lateral gape, highly similar to those of spiriferids (Shiino, 2010). Hydrodynamically, the flow pattern can be explained by the pressure gradient along the gape: the higher pressure around the sulcus gape usually causes inflows (Shiino et al., 2009). The velocity of gyrating flows in the zig-zag model was slower than that in the smooth model. Because the intensity of passive flows inside the shell was closely related to the extent of valve opening (e.g., Shiino and Angiolini, 2014), zig-zag commissure is beneficial for maintaining a narrower gape as suggested from the morphologic viewpoint (Rudwick, 1964).

These results indicate that platystrophiids had a similar mode of life to that of spiriferids, as the case of morpho-functional convergence. If so, platystrophiids may have a spiral lophophore, which guarantees effortless feeding under the fluidic environment. However, platystrophiids lack a brachidium inside the lophophore, which seems to confer risk of feeding dysfunction via deflection of the lophophore. To reduce the risk of functional failure, the zig-zag commissure played a role in maintaining stable and moderate passive flows inside the shell as these organisms adapted to the shallower sea bottom (Holland, 1997; Stigall, 2011).

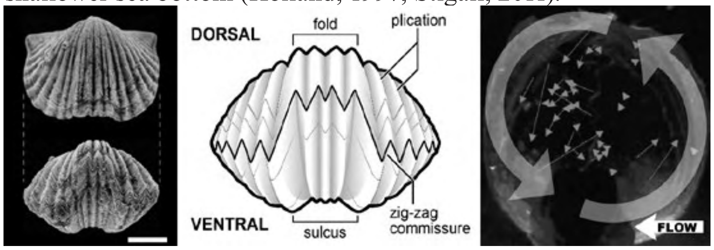

Fig. 1. Morphology and experimental results of platystrophiid brachiopod *Vinlandstrophia ponderosa*. Vector representations of flow behaviours inside the experimental model suggest the morpho-functional convergence to generate spiral flows for effective feeding.

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Diving into the morphology and ontogeny of the micromorphic rhynchonellide genus *Tethyrhynchia* Logan, 1994 in an attempt to elucidate a conflict between morphological and molecular phylogenies

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A population of 232 specimens of the rhynchonellide brachiopod *Tethyrhynchia mediterranea* Logan *in* Logan & Zibrowius, 1994 (Fig. 1) was collected by diving in a submarine cave at Lošinj Island, off Croatia coast. This is an exceptional micromorphic rhynchonellide (100 µm to 1.2 mm shell width) with a trocholophous lophophore. Logan *in* Logan & Zibrowius (1994) placed the peculiar crura of the new taxon in a new type called *lunifer* pointing to their unusual morphology. Manceñido & Motchurova-Dekova (2010) placed this type of crura in the arcual group, naming it *flared subtype of the arcuiform type*. Today the extant rhynchonellide group is drastically reduced to only nineteen known genera. This represents a first difficulty for establishing taxonomical hierarchy, because the very few living species are placed in different superfamilies, and it is often difficult to propose reliable phylogenetic relationships between them. When phylogenetic studies on *T. mediterranea* were carried out, Schreiber et al. (2013) placed this species in the superfamily Norelloidea as already proposed by Manceñido et al. (2002). However, phylogenetic studies on *T. mediterranea* using morphological (Schreiber et al., 2013) and molecular approaches (rDNA analyses by Cohen & Bitner, 2013) strongly disagree. They place *Tethyrhynchia* in totally different clades on different phylogenetic trees.

In order to provide a more detailed description of *Tethyrhynchia* and to attempt to understand the mismatch of morphological and molecular approaches to phylogeny for this genus, we reappraised several morphological characters of *T. mediterranea* using multiple techniques (observation under SEM, serial sections and shell microstructure study).

Detailed observations of the shell of multiple individuals led to the documentation of several new features and details, as for instance the incipient capillate shell in the early shell growth of the smooth shell. An ontogenetic study of the crural development was done for the first time in order to understand more precisely the type of crura hidden under the term “luniform” and why this type was later classified within the arcual group. We observed that in the early ontogeny the incipient crura are of raduliform type, and later during growth ventral budding expansions appear and increase, while the flared final structure of the typical luniform type reveals itself at about mid-shell growth corresponding to the young adult stage. We thus concluded that the crura of *Tethyrhynchia* are better accommodated in the radical group of crura. We propose the term *luniform* to be conserved as one of the types in the radical group. The radical character excludes the accommodation of the genus *Tethyrhynchia* in the superfamily Norelloidea which is known for its arcual crural type.

The shell microstructure was further analysed and its importance for taxonomical purpose is discussed. The secondary shell layer in *Tethyrhynchia* appears very thin and homogeneous, built up of fibres that are predominantly anisometric in cross section. Having in mind the anisomery of the cross section and the size of the fibres, the shell microstructure can be determined as fine fibrous (or leptinoid). This result excludes also the superfamily Norelloidea as a possible host for *Tethyrhynchia*.

T. mediterranea lives today in refugia in cryptic habitats in submarine caves. It appears to be a relict species from the Tethyan bathyal fauna. *Tethyrhynchia* (or its ancestral form) was possibly confronted by very strong modifications of its living environment after the Messinian crisis, so it occupied the rare spots in submarine caves where some conditions similar to those prevailing in bathyal environments have been more or less preserved.

We suggest that the adaptation of *Tethyrhynchia* was partly heterochronic as its paedomorphic aspect has been presumably acquired by elimination of a number of morphological characters typical of the adult stage. In the adult shell of *Tethyrhynchia* there is no cardinal process, no clear inner and outer hinge plates, no dental plates, no anterior fold and no ventral or dorsal septum. The secondary smooth shell is also a simplification of the shell structure which was probably capillate or costate in an ancestral form. The rectimarginate anterior commissure is usually considered as a juvenile character preserved into the adult stage. The trocholophous lophophore is neotenous as already suggested by Logan *in* Logan & Zibrowius (1994) because it is representative of the early juvenile stage of all extant brachiopods. All these simplifications in morphological development possibly allowed *Tethyrhynchia* to reach the adult stage for reproduction much more rapidly. Like all micromorphic brachiopods, this rhynchonellide developed a brooding system producing very few larvae but increasing their chance of settlement when released in the open environment. This way of reproduction offers an appreciable gain of energy in the development process which is the aim of a heterochronic evolution.

However, some characters of *Tethyrhynchia* could be seen as indicating complexity of the developmental process. The trocholophous lophophore for instance is not a simple primitive trocholophe model made by a small crown with a reduced number of tentacles. A more developed bell-shaped trocholophous lophophore is observed and it occupies a quite large part of the volume of the body chamber (Logan *in* Logan & Zibrowius, 1994). This bell-shaped lophophore needed to be effectively supported by the crura. Presumably for this reason the raduliform crura developed ventrally a wide flaring structure. In fact this luniform type of crura does not seem to be paedomorphic but, on the contrary, it looks like a new more elaborate structure (i.e. peramorphic).

Thus, the general aspect of the development of *Tethyrhynchia* appears to be partly paedomorphic and partly a result of the production of new characters. This mixed situation highlights that the process of evolution for this taxon is often more subtle than previously thought, known in the literature as “mosaic evolution”. Hence, the heterochronic development of this taxon may be one of the reasons for the discordance between molecular and morphologic phylogenies. The unusual aspect of the luniform crura has possibly misled taxonomists so far. This shows that an analysis that applies multiple methods is a more reliable approach for accurately describing rhynchonellides and other brachiopods. We suggest that many of the mismatches between morphological and molecular classification systems are additionally due to the subjectivity of describing morphological characters using different single techniques for different taxa by different authors. Our study opens new possibilities for understanding the correct hierarchical place of the crura as a taxonomic criterion. This one could be considered as a character submitted to evolution allowing a response through time to the environmental pressures. The phylogenetic results of Cohen & Bitner (2013) may serve as a molecular reference. However, new morphological detailed investigations on other extant rhynchonellides are strongly encouraged. Ontogenetic studies are unfortunately missing for most of them.

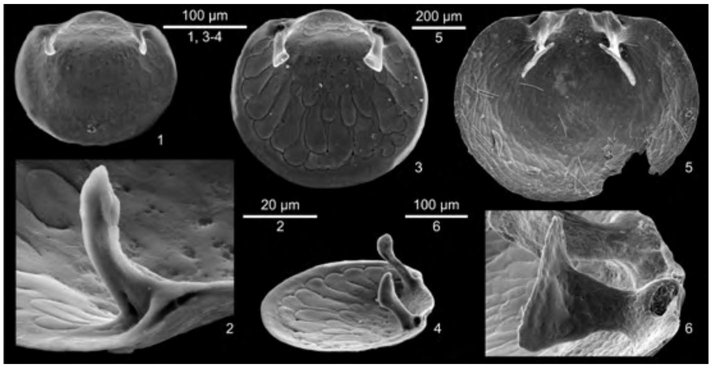

Figure 1. *Tethyrhynchia mediterranea* Logan, 1994 collected in a submarine cave at 40 m depth, Lošinj Island, Croatia. Width of dorsal valves: 1-2 (early juvenile), 190 µm; 3-4 (juvenile), 240 µm; 5-6 (adult), 880 µm.

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Microstructure formation in the shell of the Antarctic brachiopod *Liothyrella uva* (Broderip 1833): transition from larval to juvenile stages

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Rhynchonelliformean brachiopods acquire mineralized shells during very early stages of ontogeny (Chuang, 1977, 1994, 1996; Peck & Robinson, 1996). In contrast to many studies on biomineralization of adult shells (Williams, 1966, 1968; Ziegler et al., 2008) only very few studies deal with mechanisms of mineralization in larval shells (Chuang, 1996; Peck & Robinson, 1994). With the exception of Chuang (1996) none of these studies investigate mineral nucleation, shell development and growth during the different ontogenetic stages. In particular, there is no information on shell microstructure formation and variation for the different larval, postlarval and early metamorphosis stages.

In the present contribution we investigate for the terebratulid brachiopod *Liothyrella uva* carbonate mineral nucleation in late larval stages and trace phases of shell formation from larval to early postlarval and late postlarval developments (Figs. 1 to 3). We studied wedge-shaped larvae (Fig. 1a), three-lobed larvae forming a mantle fold prior to settlement (Figs. 1b to 1e), larvae that settled on a substrate, postlarvae stages (Figs. 1f, 1g), small metamorphosed individuals (Figs. 2b, 2c) firmly attached to the substrate and minute juveniles (Fig. 3a). All larva and shell samples were imbedded in EPON in order to stabilize them. For investigation in SEM the samples were microtome cut and microtome polished. Ca and Mg contents were investigated with EDS, mineral microstructure and texture analyzed with EBSD (electron backscattered diffraction).

As EDS measurements show, mineral nucleation starts in lobed larvae, prior to settlement onto a substrate (see yellow circle in Fig. 2a). Subsequent to permanent settlement and in the postlarval stage a first pair of valves is formed (Figs. 2b, 2c), these within a mantle lobe (the white dashed line in Fig. 2b) indicates the still preserved extent of the mantle lobe. These first formed valves are non-hinged (white stars in Figs. 2b, 2c) and impunctate. The valves are composed of a thick outer layer (yellow stars in Fig. 2b) and two or three rows of inward positioned, calcite laths (yellow arrows in Fig. 2B). Are these laths sectioned in 2D a fibrous appearance results, however, not at all comparable to the typical outer morphology of calcite fibres in modern adult brachiopod shells (Ye et al., 2018). At this stage of shell development the mineral units that comprise the shells have highly irregular shape and size (e.g. Fig. 2d); the typical fibre morphologies of modern adult brachiopod shells (e.g. Ye et al., 2018) are absent. The strength of calcite co-orientation is low within the first formed shells (Figs. 2c, 3a), contrasting to what we find for the shells of adult animals (Fig. 3b). With further development, when the juvenile reaches sizes of about 3mm x 1mm, the primary and the fibrous shell layers become well developed, fibrous shell portions contain a sequence of about 10 rows of fibres; these arranged to stacks and with the latter being oriented to each other to about 90°, such that, when sectioned in 2D, longitudinally and transversely cut fibres result. In conclusion: (a) We see distinct differences in microstructure and texture between settled larval/postlarval stages and the shells of young animals. Thus, with progressive growth, there is an evolution in microstructure. (b) The microstructure and texture of the shells of adult *Liothyrella uva* is already fully developed from very early, however, postlarval growth stages.

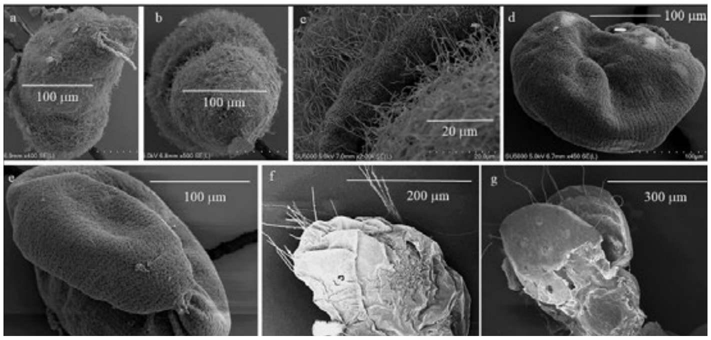

Figure 1. Stages of larval development: from wedged larvae (a to e) to settlement and metamorphosis (f, g).

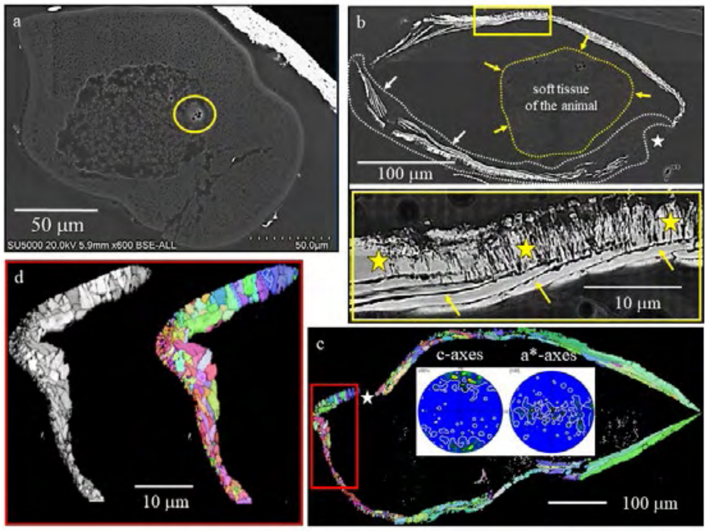

Figure 2. Ca carbonate nucleation (yellow circle in a), shell formation in settled larval/postlarval stages (b, c, d).

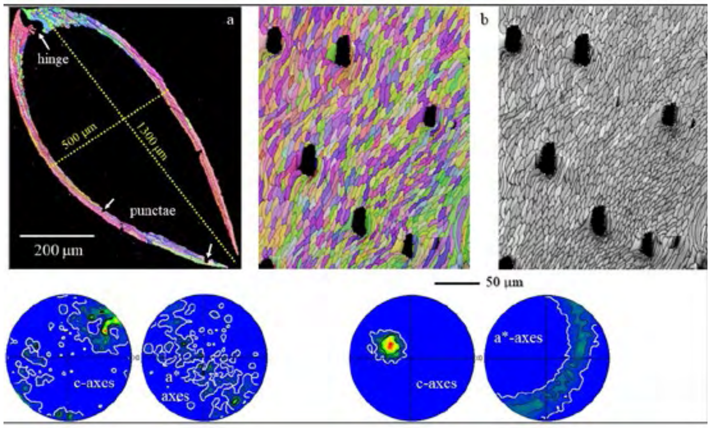

Figure 3. Shell microstructure in settled postlarval (a) and adult stages (b).

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The evolution of thecideide brachiopod shell microstructure from Triassic to modern times

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The investigation of thecideidine shell morphology and structure, histological characteristics of the mantle and metabolism in general has been the subject of research for several decades and revealed the distinctiveness of this group of brachiopods relative to species of other extinct and modern brachiopod genera (e.g. Pajaud, 1970, Grant, 1972, Williams, 1972 and references herein). The comparison of stable isotope results (Figure 1) between the terebratulide brachiopod *Magellania venosa* and the thecideide brachiopod *Pajaudina atlantica* illustrates well the distinctness of thecideide brachiopods in relation to species of other brachiopod families. In the fibrous shell layer of *Magellania venosa* ventral valve the overall variability in $d^{18}O$ in an external-internal transect is 4.5‰, with a clear trend towards heavier $d^{18}O$ values. In the dorsal valve of *Pajaudina atlantica* $d^{18}O$ variability scatters between -0.25 and +1.0 ‰, with the values being in or close to the zone of d18O calcite equilibrium with seawater. The outermost shell portion of the ventral valve of *Pajaudina atlantica* is depleted in $d^{18}O$ relative to equilibrium, while its innermost portion is in equilibrium. Between the outermost and the innermost shell sections of *Pajaudina atlantica* there is a variability in $d^{18}O$ of 2.3‰. The comparison of shell microstructure and texture between modern rhynchonellide, terebratulide and thecideide brachiopod shells shows that mineral unit organization in modern thecideide brachiopod shells is entirely different (Goetz et al. 2009). Instead of the clear distinction between an outer primary and an inward fibrous shell layer and the presence of stacks of fibres, as it is the case in modern rhynchonellide and terebratulide brachiopod shells, we do not find any obvious mineral unit organization in the shell of modern thecideides.

The objective of this study is to trace the formation and evolution of thecideide microstructure and fabric from the Triassic to modern times. In four species of the order Thecideida, we investigate the relationship between fibrous and granular, acicular fabrics, and thus, the progressive disappearance of fibres and the emergence of granules. We imaged and measured the shell microstructure and fabric of selected taxa: the Triassic species *Thecospira tenuistriata*, *Thecospira tyrolensis*, *Bactrynium bicarenatum*, the Jurassic species *Neothecidella ulmensis*, the Cretaceous species *Thecidiopsis digitatum*, *Thecidea papillata*, the Paleogene species *Thecidea papillata*, *Lacazella mediterranea*, the Pleistocene species *Thecidellina* sp. and the modern species *Pajaudina atlantica* and *Kakanuiella chathamensis* with FE-SEM and electron backscattered diffraction (EBSD). EBSD is an automated microdiffraction method which provides space-resolved information on the phase state of the samples and crystallite orientation of the constituting mineral. Figure 2 highlights with EBSD band contrast measurement images the (measured) shell microstructure of selected thecideide species. The presence of fibres is clearly visible for the Triassic and Jurassic specimens. It disappears subsequently, and from the Cretaceous to modern times granular microstructures prevail. The latter consist of highly irregularly shaped mineral units with calcite being assembled with a low degree of co-orientation. Larger calcite granules are embedded in a matrix of small crystallites. From the modern species *Pajaudina atlantica* and *Kakanuiella chathamensis* we know that an extracellular matrix is present in the shells of these two thecideide species, however, this biopolymer matrix does not have a regular structure such as that of organic sheaths encasing the fibres. We consider the granular microstructure of thecideide shells as a recently evolved feature, highlight its development with time, and discuss its interlinkage with the fibrous fabric from a microstructural point of view.

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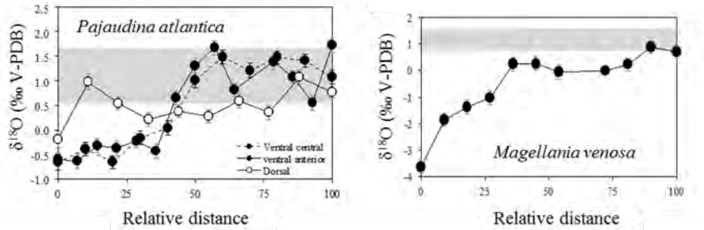

Figure 1. Difference in oxygen isotope composition between the thecideide brachiopod *Pajaudina atlantica* and the terebratulide brachiopod *Magellania venosa*. Grey fields indicate the region of inorganic calcite equilibrium δ^{18}O values for each brachiopod locality. The relative distance is calculated with 0% corresponding to the outermost part of the shell and 100% the innermost part.

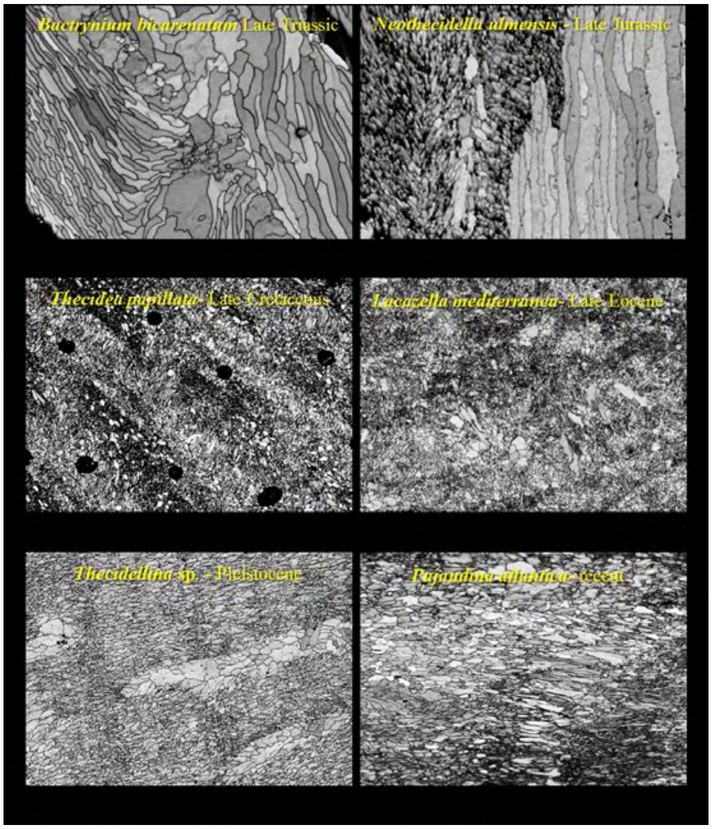

Figure 2. EBSD band contrast measurement images of the microstructure of fossil and modern thecideide brachiopods.

Brachiopods of the late Turonian hemipelagic strata of the Saxo-Bohemian Cretaceous Basin (Central Europe)

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The north-western portion of the Saxo-Bohemian Cretaceous basin shows typical hemipelagic siliciclastic-input oscillation. Even if the area was relatively close to the land, the siliciclastic influx was restricted for a long time interval (hundreds of kyr) resulting in the formation of a carbonate platform in a part of the basin. This has been interpreted as the result of tectonically induced isolation from the sediment supply (Western Sudetic Island; Uličný et al., 2009). The oscillations in siliciclastic supply as well as eutrophic/oligotrophic conditions (Wiese et al., 2004) have been reflected within the benthic taphocenoses.

Hemipelagic strata and their macrofaunal assemblages of the late Turonian of the area have been object of research since the first half of the nineteenth century (Reuss, 1845-1846, Geinitz, 1871-1875, Frič, 1889). Rhynchonellid brachiopods as well as rare Linguliformea were studied in detail by Nekvasilová (1974, 1977) and the cancellothyrid *Gyrosoria* by Sklenář and Simon (2009).

Comprehensive studies on upper Turonian brachiopods involving the rest of Terebratulida and Craniiformea as well as the palaeoecological interpretation of the structure of the taphocenoses have been hitherto missing. The purpose of the poster is to present the hemipelagic brachiopod fauna in general, with special emphasis on the hitherto neglected taxa, as the hemipelagic facies restricted Gibbithyrididae, the free-lying Craniidae and the opportunistic Cancellothyrididae of the area.

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Are hyoliths brachiopods?

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Hyoliths have long been recognized as Palaeozoic invertebrates and as one of the main components of the Cambrian evolutionary fauna. The two main orders of hyoliths, orthothecids and hyolithids, have a calcareous skeleton composed of a cone-shaped conch and a lid-like operculum but hyolithids also have two projecting spine-shaped helens inserted between conch and operculum (Marti Mus & Bergström, 2005). Although hyoliths have sometimes been regarded as a unique "extinct phylum," most authors have until recently regarded them as either closely related to molluscs or sipunculans (Malinky & Yochelson, 2007). However, the recent discovery of tentaculate feeding organs in hyolithids from the Burgess and Spence Shale lagerstätten led to the suggestion that hyoliths are lophophorates (Moysuik et al., 2017) or even nest within the Brachiopoda, as derived lingulids (Zhao et al., 2017). Newly discovered hyolith specimens from the Chengjiang biota of Yunnan, South China reveal that the stratigraphically older hyolithid order, the Orthothecida, also had tentaculate feeding organs (Fig. 1). However, the orientation and morphology of the feeding organs show that the orthothecid animal was a deposit feeder, as previously indicated by sediment-filled guts (Devaere et al., 2014). The new discovery, together with a detailed comparison of the tentaculate feeding organs to lophophores of fossil and living lophophorates clearly show that hyoliths were not brachiopods. While hyolithids seem to be filter feeders, relying on their helens to lift the conch aperture and the feeding organs above the sea floor, our study shows that the older orthothecids which lack helens, were likely to be reclining on the sea floor and used their tentacles to feed from particles on or in the sediment (Fig. 2). Filter feeding in hyoliths was a secondary adaptation derived from deposit feeding. However, the gross morphology of the hyolith feeding apparatus, with two main arms with projecting tentacles, is broadly comparable to lophophores, particularly to the lophophores of problematic Cambrian stem group brachiopods such as Yuganotheca (Zhang et al., 2014). This observation, in combination with the lack of compelling molluscan or sipunculan apomorphies, means that morphological evidence from hyoliths is more consistent with the group occupying a basal position in the lophotrochozoa, on the stem of the Lophophorata.

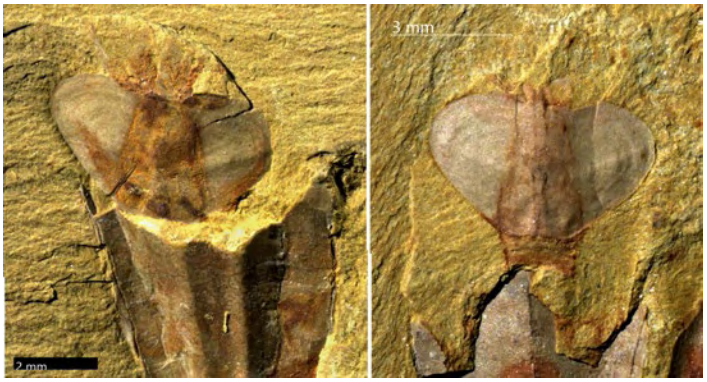

Fig. 1. Two specimens of the orthothecid hyolith *Triplicatella optimus* from the Chengjiang Lagerstätte of Yunnan, South China. The left picture shows part of the conch and the operculum with preserved soft parts, including tuft-like arrangement of tentacles in front of the operculum. The right picture shows a similar specimen with a neck-like projection of the soft parts connecting the conch and operculum and partially preserved tentacles.

Figure 2. Artistic reconstruction of *Triplicatella optimus* from the Chengjiang Lagerstätte.

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New approach in stable isotope analysis of carbonates: isotope ratio infrared spectrometry

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Stable carbon and oxygen isotopic composition ($\delta^{13}C$ and $\delta^{18}O$) of carbonates has been widely used for the reconstruction of paleo-environments. The isotopic signature of carbon, $\delta^{13}C$, is significant as a tracer for the origin of carbon, metabolic processes and perturbations of the global carbon cycle, while variations of $\delta^{18}O$ in biogenic carbonates are used as a proxy indicator for paleotemperature and paleosalinity. Well established, and most commonly used technique for measurements of stable isotopic compositions is isotope ratio mass spectrometry (IRMS), which offers high throughput and high precision of the measurements. It is employed in different applications for environmental and geochemical studies, and one example is paleo-environmental reconstruction based on fossil carbonates.

Here we present a new approach in carbonate measurements using laser based spectrometry. The Thermo Scientific™ Delta Ray™ Isotope Ratio Infrared Spectrometer (IRIS) with the Universal Reference Interface (URI) Connect is based on direct absorption spectrometry, and because of its size and robustness it is a field-deployable instrument.

Main goal of our study is to demonstrate the method and precision of $\delta^{13}C$ and $\delta^{18}O$ measurements using the Delta Ray Connect. The sample preparation is based on reaction of H_3PO_4 with solid carbonate: carbonate samples are placed into the vials and after removing the residual air from the headspace, phosphoric acid is added. The resulting reaction releases CO_2 gas, which is then introduced into the analyzer.

We present the results from measurements of three international standards of carbonate material (NBS18, NBS19 and IAEA-CO-1). To confirm the high accuracy and precision, NBS 18 and NBS 19 were used as reference materials for calibration, while IAEA-CO-1 was treated as the unknown sample. The Principle of Identical Treatment was applied in sample and standard preparation, in measurement procedure, as well as in the evaluation of the results. With this workflow, approximately 100 samples can be analysed per day with a $\delta^{13}C$ and $\delta^{18}O$ precision better than 0.1‰, which is comparable to IRMS method for carbonates (Table 1 and Figure 1).

Using the knowledge from mass spectrometry technique, and adjusting the sample preparation and the analytical method to the IRIS system, we can provide high accuracy and precision data of the isotopic composition of carbonates for both $\delta^{13}C$ and $\delta^{18}O$. This method offers new possibilities for studying and reconstructing paleo-environments and past climate changes.

IAEA-CO-1	Measured	1SD	Certified*
$\delta^{13}C$ (‰VPDB)	2.44	0.03	2.49 ± 0.03
$\delta^{18}O$ (‰VPDB-CO_2)	-2.37	0.05	-2.4 ± 0.1

*Recommendation only for $\delta^{18}O$

Table 1. Resulting $\delta^{13}C$ and $\delta^{18}O$ values for the IAEA-CO-1 standard samples based on the calibration data.

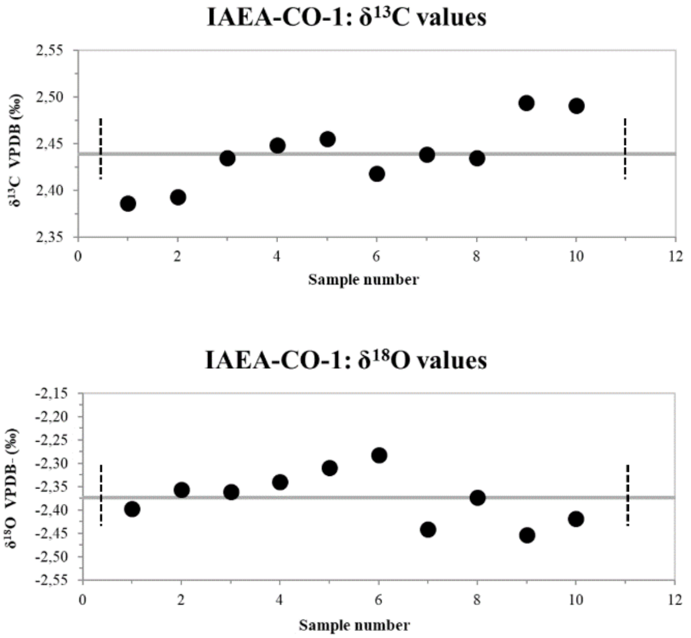

Figure 1. $\delta^{13}C$ and $\delta^{18}C$ values of ten IAEA-CO-1 standard samples. The vertical dotted lines indicate the position of NBS 18 and NBS 19 standards used for scale calibration.

A late Katian (Late Ordovician) low diversity and high dominance brachiopod fauna from the Tarim Basin in northwest China

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This is the first report of a late Katian brachiopod fauna from a remote region on the edge of the Tarim Basin in Northwest China. The fossils were collected from the upper Katian Hadabulaktag Formation at a locality in the northern part of the Kuruktag region, southern Xinjiang.

The Hadulaktag Formations consists of thin- to medium-bedded argillaceous limestone interbedded with bioclastic limestone and micrite. Brachiopods, corals, bryozoans, bivalves, and gastropods are common in the formation, with less common trilobites and crinoids. The sedimentology and fossil assemblage are indicative of a normal marine tropical shallow marine carbonate shelf. There are no significant disconformities in the section.

The brachiopod fauna is dominated by two genera: the rhynchonellide *Altaethyrella* and an undescribed atrypide (Figure 1).

Altaethyrella tarimensis, a newly established species of the genus, has already been systematically documented by Sproat and Zhan (in press), and the atrypide will be addressed in an upcoming paper. Aside from these species, orthides (most notably *Mimella*), strophomenides (including *Sowerbyella, Strophomena,* and *Rafinesquina*), and other groups are present but are much fewer in number than either *Altaethyrella* or the atrypide.

Although there are numerous shells from the study area, the preservation of individual shells is often poor. Commonly most, if not all, of the original shell material has been stripped from the shell surface. Shell features such as the interarea and umbonal areas are often damaged or missing. The mantle cavity is commonly filled with coarse calcite crystals that obscure delicate internal shell features such as the spiralia in the atrypides.

Although the Tarim paleoplate was likely located near the paleoequator during the Late Ordovician (e.g Popov et al. 2017, fig. 13; Torsvik and Cocks 2017, fig. 6.4), its precise location remains uncertain largely due to limited paleomagnetic data. These brachiopods from Tarim are similar to those reported from parts of Kazakhstan (e.g. Popov et al. 2000; Popov and Cocks 2006) and the Zhejiang-Jiangxi border region in South China (Zhan and Cocks 1998). These similarities indicate close proximity of these paleoplates and terranes during the Late Ordovician, or at least an arrangement of these plates that would allow dispersal of the brachiopod fauna via ocean currents.

This brachiopod fauna in this region shares a number of superficial similarities with that of paleoquatorial North America (on the opposite side of the earth during the Late Ordovician—see Torsvik and Cocks 2017), but significant differences are apparent upon careful examination. For example, although large rhynchonellides evolved in both regions, the ancistrorhynchoide *Altaethyrella* became dominant in the shallow marine settings of the Kazakh terranes and North and South China paleoplates while the rhynchotrematoides *Rhynchotrema* and *Hiscobeccus* dominated similar environments in Laurentia. Additionally, larger atrypides such as *Ovalospira/Schachriomonia* were abundant on the Asian plates while only small atrypides such as *Zygospira* and *Anazyga* became established in coeval shallow marine settings of Laurentia. The evolution of different forms on these paleoplates despite similar paleolatitudes may reflect paleoenvironmental and ecological differences between these regions, or the isolation of brachiopod faunas in each region as sea levels rose in the early Late Ordovician and the continents became separated by anoxic seafloor in the open ocean.

The underlying factors that led to the establishment of this high dominance, low diversity fossil assemblage are unclear. There is neither evidence of storm activity regularly disrupting the benthic ecosystem that would have favoured groups that could quickly colonize the seafloor following a storm event, nor any evidence of adverse environmental conditions such as hypersalinity or low oxygen that may have selected for specialized forms adapted to adverse living conditions. Rather, this biodiversity pattern may reflect other, less evident factors such as limited inorganic nutrient supply due to lack of any major orogenic events in this region during this time, for example. Relatively low diversity coeval faunas existed elsewhere near the equator (e.g. in the epicontinental seas of North America—see Jin and Zhan 2001), so this diversity pattern may be a result of a global phenomenon rather than regional environmental and ecological factors.

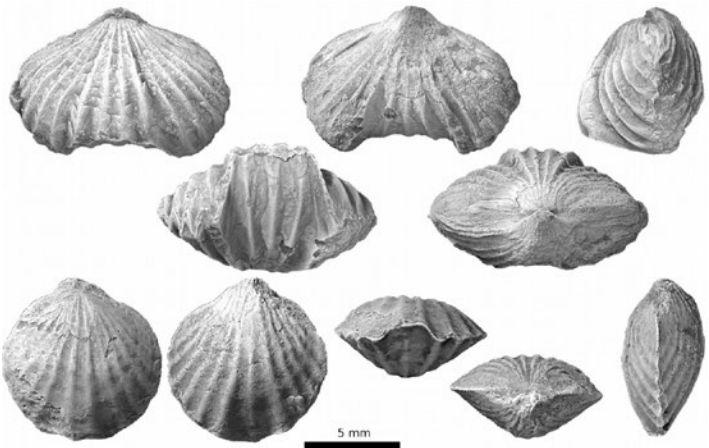

Figure 1. *Altaethyrella tarimensis* (top) and an undescribed atrypide (bottom) from the late Katian Hadabulaktag Formation in Xinjiang, Northwest China.

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Skeletal ultrastructure, ecology, and functional morphology of the permian lyttoniid brachiopod *Pirgulia*

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The Yale Peabody Museum (YPM) has several specimens of *Pirgulia* sp. from the Upper Permian Sosio Limestone of Sicily, collected by G. Bonafede of Palermo and given to Charles Schuchert in 1936. They were collected from within the Sosio megablocks that outcrop three km from the Palazzo Adriano ("Pietra di Salomone" megablock of Flugel et al., 1991). The assemblage includes ammonoids, fusulinids, crinoid fragments, sponges, corals, and other brachiopods (orthid, orthotetid, productid, rhynchonellid, spiriferid, spiriferinid, and terebratulid). The collection was free from matrix, so microfossil and lithological analyses were not possible. Several examples were cataloged as *Leptodus fasciculata* and *Leptodus princeps*. Based on the conical wrapping of the ventral valve and similarity with those described by Verna et al. (2010) from Tunisia, we place these in the genus *Pirgula* species undet.

Lyttoniid brachiopods have a unique morphology characterized by a lobate dorsal valve with rib-like processes resembling a ptycholophe support that interdigitate with ridges, or septa, in the ventral valve. *Pirgulia* is morphologically similar to other lyttoniids in being inequivalve with a lobate dorsal valve. However, it also bears morphological similarity, and possibly therefore functional similiarity, to the richthofenioids in its conical shell, but differs in the orientation of the dorsal valve relative to the ventral valve. The goal of this study was to use various techniques to examine the functional morphology of the modified dorsal valve and infer the lifestyle of the *Pirgulia* at YPM. Serial sections and acetate peels were used to examine shell structure and infer the relationship to substrate and feeding methods.

The ventral valve of *Pirgulia* forms a rugate cone which completely encloses and obscures the dorsal valve from the exterior (Fig. 1A). Specimens in which part of the ventral valve is exofoliated show a lobate infilling pattern indicative of the septa (Fig. 1B). In section, the dorsal valve has a concave curve to fit snugly into the ventral valve (Fig. 1C). Throughout growth of the organism, the shell grew with irregular torsion around the longitudinal axis. We find no evidence of a cicatrix of attachment, even on specimens where the hinge is well-preserved, and no specimens are found cemented to other *Pirgulia* (although specimens were not observed *in situ*). We therefore reconstruct *Pirgulia* as sticking in sediment, rather than affixed to rock or reef like related taxa.

It has been argued that the homology of the lyttoniid lobate dorsal valve is actually to a brachidium, extending from a reduced true dorsal valve that articulates posteriorly at the hinge (Termier and Termier, 1949). While the lyttoniids appear to be functionally bivalved, this interpretation makes them anatomically essentially univalved. Williams (1953) identifies the vestigal remnant of the true dorsal valve as the triangular structure at the posterior tip where the interarea would be in other brachiopods, based on the observation that unlike the rest of the structure it does have a lamellar primary shell layer, and includes remnants of a cardinal process and denticular sockets.

We attempted to test this hypothesis with *Pirgulia* by studying valve ultrastructure. Specimens were CT scanned at Harvard University, but results were insufficient to reveal the ultrastructure and disposition of the two valves. Instead, serial sections and acetate peels were used to evaluate the ultrastructure. The dorsal valve exhibits organocalcitic deformations of shell material (pseudopunctae) that give the surface a pustular texture (Williams et al. 2000:310). Connected to the pseudopunctae appear to be taleolae, rods of calcite permeated by networks of organic material, a condition found to have evolved independently in some groups of strophomenids (Williams and Brunton, 1993). More pseudopunctae appear to emerge from the dorsal side of the dorsal valve than its ventral side, which has been used as a proxy for presence of mantle tissue (Williams, 1953). Primary shell is observed in the posterior region of the dorsal valve; it is otherwise secondary shell. Thin sections reveal lobes in the dorsal valve that are gently arched toward corresponding callused shell on the ventral valve.

The lifestyle of *Pirgulia* was inferred based on morphology and analogy to other organisms. Most lyttoniids are thought to have been affixed to substrates by cementation, but these *Pirgulia* exhibit no cicatrix or other signs of attachment. Thin sections do not reveal any thickening or ballasting (as in Seilacher, 2005) of the ventral valve, nor keel (Seilacher et al., 2008) which would support a theory of secondary soft bottom reclining. These characters suggest an organism which inhabited low energy waters characterized by deposition of mud or fine sediment, in which the organism grew upwards to keep up with sedimentation, a lifestyle facilitated by the presence of a conical shell. Although apical attachment to the substrate probably occurred in the juvenile to support initial growth, the surrounding sediment was likely the primary support system for the organism, as suggested by the thinness of the ventral valve. This could be confirmed through analysis of this genus *in situ*.

Our findings for *Pirgulia* morphology are consistent with the "flapping valves" functional morphology proposed for richthofenids (Rudwick, 1961) and modified for lyttoniids (Rudwick and Cowen, 1967). This model proposes that the unique dorsal valve served in filter feeding by rhythmic movement, and that active filtration was necessary due to the shallow angle of the aperture. The dynamics of water flow to the lophophore via flapping are potentially complicated by the fact that *Pirgulia* exhibits complete ventral valve enclosure.

We infer that the conical shape of *Pirgulia* is derived with respect to other lyttoniids like *Leptodus* and *Poikilosakos* that were open scoops. The fully conical ventral valve is not widespread among productids, occurring only in *Pirgulia,* although there may be a general trend towards wrapping around of the ventral valve, as subconical morphology appears to have evolved multiple times within lyttoniids, in both the Lyttoniinae (*e.g. Eolyttonia, Keyserlingia, Loxophragmus*) as well as in their sister clade the Poikilosakinae (*Pseudoleptodus*, *Choanodus*) (Williams et al*.,* 2000:635-637). The conical shell may have been beneficial for protection from predation, as a secondary reacquisition of protective dorsal covering after this feature from the ancestral brachiopod body plan was lost by modification of the dorsal valve into the lobate structure. It also enabled a potential novel feeding mechanism, the "flapping valve," in which the circulation of water is modified by the presence of a fully enclosing ventral valve. If *Pirgulia* indeed lived stuck in soft sediment, this morphology would have played an important role in preventing fouling, and the dorsal valve could have been used to flush the cavity free of sediment. Understanding the morphological evolution of the highly modified lineage *Pirgulia* helps contextualize wider lyttoniid evolution and convergent patterns in other biomineralizing species.

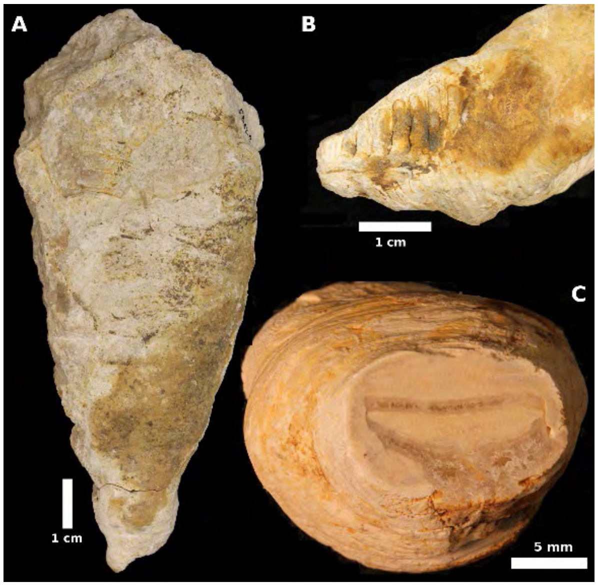

Figure 1 *Pirgulia* from the YPM Schuchert Collection A. complete specimen of *Pirgulia* sp. (YPM IP.238675), B. Partially exfoliated ventral valve of *Pirgulia* (YPM IP.S-2295), and C. cross section of same specimen, showing pseudopunctate dorsal valve.

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Keynote lecture

Brachiopods as key to evolutionary theory: from foundational systematics and phylogenetics to speciation and biogeography

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The outstanding quality and quantity of the brachiopod fossil record provides tremendous opportunity for studying the evolution of life and the relationships between biotic evolution and the Earth system. The utility of the brachiopod fossil record has shifted through time from foundational systematic work to developing phylogenetic hypotheses and addressing evolutionary patterns and processes.

Brachiopods have been central to resolving questions about evolution of life through time. Indeed, a detailed understanding of the relative distribution of brachiopod forms among sedimentary layers was pivotal to developing early stratigraphic systems, particularly in Paleozoic strata. Intensive research that produced copious volumes dedicated to delineating and describing brachiopod species were central to deciphering the geologic history of regions, which is exemplified by the monographic works which circumscribed taxa in the Paleozoic strata of North America. Primary systematic work remains central today for continuously improving our understanding of the evolution of brachiopods through time. Newly described faunas have exciting potential to fill in gaps in the record and provide new insights into intervals of Earth history and constrain paleogeographic reconstructions.

As the field of evolutionary biology has progressed, so too has brachiopod research. The combination of stable skeletal mineralogy and high initial population abundance provide a dense fossil record, from which many types of specimen-based analyses ranging from paleoecology, biogeography, and macroevolutionary studies can be facilitated.

In this presentation, I will focus on two case studies in which the fossil record of articulated brachiopods is leveraged to tackle broad questions about the co-evolution of Earth and life. The first case study explores the causes of biodiversity decline during the Late Devonian Mass Extinction by combining phylogenetic analyses and biographic analysis of Laurentian brachiopod assemblages. The second case study contrasts the role of species dispersal in facilitating speciation during the Great Ordovician Biodiversification Event at a global scale with regional-scale impacts during the Late Ordovician Richmondian Invasion in eastern North America. Both examples underscore the importance of systematic and evolutionary analysis for identifying processes and patterns in speciation and biogeography that combine to produce a complex understanding of Earth system events.

Dzieduszyckia in southern China: morphological variation and population dynamics

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Dzieduszyckia is one of the largest Paleozoic rhynchonelloids, characterized by bisulcate, strongly costate shell. It is normally found in low-diversity, but high-abundance faunas, and has a world-wide distribution. Recent investigation reveals that this brachiopod is widely distributed in the lower Famennian offshore carbonate platforms in southern China, forming a unique low-diversity fauna in offshore settings, in sharp contrast to the near shore *Yunnanella-Yunnanellina* faunas with high diversity. Brachiopods samples were collected from three fossiliferous layers in the Dazhai, Dalong, and Longmi sections in Guizhou and Guangxi provinces of southern China. The brachiopod-rich beds are 2.5 m thick and within the conodont Middle *crepida* Zone at Dazhai Section; 1.5 m thick and within the Lower *crepida* Zone at Dalong Section; and ca. 2.0 m thick and within the Lower *marginifera* Zone at Longmi Section. Brachiopods in these layers are mostly articulated, and show high fractions of growth malformation and shell asymmetry, probably due to growth in a crowded environment, suggesting they were autochthonous-buried brachiopod assemblages without transportation or reworking. Thin section observation indicates that the brachiopods lived in a lower energy subtidal environment. Over 500, 250 and 400 specimens were collected from the Dazhai, Dalong and Longmi sections, respectively. Because few constant morphological characters can be used to discriminate them from different populations due to the strong morphological variation in shell outline, shape, and costation of the brachiopods, a statistical analysis was carried on these brachiopods for comparison of the morphological variation and population dynamic among the three faunas.

The shell width ranges from 5.6 to 34 mm (mean=17 mm, n=540), 12.3 to 43 mm (mean=26.5 mm, n=226) and 11 to 37.5 mm (mean=24.3 mm, n=375) for the Dazhai, Dalong, and Longmi sections, respectively. The shell outlines vary from subtriangular or quadrate to transverse oval, while the lateral profile ranges from flat lenticular to strong globular. Over 97-99% specimens have larger shell-width than the apparent shell-length (LA), and there are overlapping ranges of W/L and T/L ratios (ranging from 0.8 to 1.9 and from 0.4 to 1.1, respectively). However, the proportion of individuals with the real shell-length (LR) equal to or greater than the shell width is quite different among the three samples, i.e., >53% in Dalong, ~20% in Longmi, and ~38% in Dazhai. Such difference can be partially explained by the fact that the Dalong samples have relatively more convex shell shape (mean T/L ratio 0.66) than the other two (mean T/L ratio 0.58-0.59). The variation of W/L ratio does not show clear correlation with shell length, instead, has a crude correlation with shell width, probably reflecting allometric growth.

The ribs are generally simple, but sometimes sparsely dichotomous, highly variable in shape and density. The rib number of the brachiopods varies from a few to over 30, but there is no clear correlation with the shell width. The Longmi samples have the lowest rib number (mean=17.7), while the rib numbers are normally distributed in a frequency histogram. In contrast, both the Dalong and Dazhai samples have higher mean rib numbers (mean=20.3and 18.1, respectively); the rib number is evenly distributed in the histogram, suggesting strong variations of the rib numbers among individuals of the two samples.

The size frequency histograms of the three faunas display similar bell-shaped distribution, suggesting low juvenile mortality. Furthermore, the similar pattern shared by three faunas indicates that a cluster life style of brachiopod fauna might promote the survivorship of young individuals and enable most grow to adults. Finally, our study suggests that organisms could enhance their survivorship by actively modifying life style and environment.

The old, misnamed, misunderstood *Terebratula sinuosa*

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In 1616 Fabio Colonna first described two brachiopod specimens as "*concha anomia vertice rostrato.*" On page 22, he figured the specimens and referred to the individual to the upper-right as n. 1. Such specimen comes from the "Calcareniti di Gravina" Formation (near Andria, Apulia, Southern Italy) aged Pliocene-Pleistocene. The specimen to the upper-left, indicated as n. 4, refers to a sulciplicate specimen coming from the private collection of Ferrante Imperato. Its provenance is unknown.

Linnaeus (1758) applied the formal nomenclature scheme to Colonna's drawings. Unfortunately, he misinterpreted captions to illustrations in Colonna. While the description clearly refers to Colonna's specimen n. 4, he reported it as n.1. Consequently, Linnaeus' reference to the formal name *Anomia terebratula* did not match the numbering scheme used by Colonna.

In 1814, Brocchi named the species *Anomia sinuosa*, in reference to the same figure as Linnaeus. He further described *A. ampulla* referring to an individual brachiopod figured in Agostino Scilla's Vana speculazione (1670, tab. 14, figs. 1, 2).

In 1998, Lee & Brunton designated the specimen BM(NH) BG152 from the Pliocene of Andria as the neotype of *A. terebratula* considering Colonna's two specimens as conspecifics, following the numbering scheme of Linnaeus.

Lee and colleagues (2001) revised *T. terebratula*. Their synonymy list included *T. sinuosa* (Brocchi), *T. calabra* Seguenza and *T. costae* Seguenza. The validity of *T. ampulla* (Brocchi) and *T. scillae* Seguenza was confirmed.

However, many scholars have later used the species name "*Terebratula sinuosa*" in reference to heavily sulciplicate *Terebratula* brachiopods which are morphologically (Taddei Ruggiero et al. 2008a) and ontogenetically different from *T. terebratula* (Taddei Ruggiero et al. 2008b).

The key to understand whether *T. sinuosa* deserves the species status stands in its stratigraphic distribution. Somewhat typical *T. sinuosa* shells are not just sulciplicate. The most distinctive character is a long, massive and well-distinct fold running longitudinally along the ventral valve from the umbonal zone. Specimens of this kind are just known in Miocene deposits in Italy, Spain, and Malta.

Here we aim to fix the nomenclatural problems regarding the *Terebratula* genus. In particular, we find it timely to propose an emendment of the current definition of *T. terebratula*. Given the designation of BM(NH) BG152 from Andria as the neotype of *Terebratula terebratula* (Linnaeus), we suggest the species *T. ampulla* (Brocchi) has to be recognized as junior synonym. However, the sulciplicate specimen originally figured in Colonna and there indicated as n. 4 refers to a Miocene *Terebratula*, which is quite distinctive and deserves species recognition. It could be safely indicated as *T. sinuosa*, given the long tradition of the name in the literature.

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The original drawings by Fabio Colonna.

A generalized monthly growth curve of modern brachiopod shells

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Geochemistry of brachiopod shells has been considered as an excellent archive for reconstructing paleoceanographic conditions throughout the Phanerozoic since Lowenstam (1961) reported that modern brachiopods precipitate their shell calcite in oxygen isotope equilibrium with ambient seawater. Recent studies, however, indicated that carbon and oxygen isotope values ($\delta^{13}C$ and $\delta^{18}O$ values) of modern brachiopod shells are often not identical to those of calcite precipitated in isotopic equilibrium with ambient seawater (called "equilibrium calcite"). Furthermore, it was shown that the isotopic composition and minor element concentrations of brachiopod shell calcite are highly variable even in a single shell. These observed difference and variability are resulted from kinetic, metabolic, and other effects during shell secretion, which limit the use of brachiopod shell geochemistry as a reliable tool for paleoenvironmental reconstruction. Therefore, we need to find clear relationships among shell geochemistry, calcification site chemistry, and ecology and physiology of modern brachiopods to consider the effects of calcification site chemistry and biological controls on geochemical composition, such as $\delta^{13}C$ and $\delta^{18}O$ composition, clumped isotope, and trace element concentrations, of brachiopod shells.

Growth rates of brachiopod shells are one of essential physiological factors to understand kinetic, metabolic, and other effects on isotope composition and minor element concentrations during shell formation. Previous research established growth curves of modern brachiopod shells by biological observation (e.g., Peck et al., 1997; Peck, 2007; Baumgarten et al., 2013), growth-line analysis (e.g., Brey et al., 1995), and variations in high-resolution oxygen isotope records along the maximum growth axis of shells (e.g., Auclair et al., 2003; Yamamoto et al., 2010a, b, 2013, Takayanagi et al., 2015). However, in previous studies, the growth curves are species-specific and the growth lines on the brachiopod shell surface do not necessarily represent annual growth bands. Minor growth lines may be formed by temporary cessation of shell growth (Hiller, 1988). This indicates that the number of such bands cannot be used to estimate the ages of specimens. Such inappropriate measurements of "annual" bands likely cause under- and overestimation of shell ages and growth rates, resulting in inaccurate assessments of kinetic, metabolic, and other biological/physicochemical effects on chemical composition of brachiopod shells. Therefore, we should establish a new protocol to establish monthly shell growth curves, which are applicable to all modern brachiopod species and enable us to estimate ages and growth rates of brachiopod shells.

In this study, we compare growth lines on the shell surface with high-resolution oxygen isotope profiles along the maximum growth axis to detect visual differences between annual growth bands and the other minor ones and establish a generalized growth curve on monthly time resolution applicable to majority of modern brachiopod shells. This new method is expected to improve our understandings regarding the relationship of chemical and isotopic composition at the calcification site with those in the shells. The biological controls on brachiopod calcification are also expected to be better formulated.

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Keynote lecture

Organization of the lophophore in linguliform *Pelagodiscus atlanticus* (King) and the evolution of the lophophore in brachiopods

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The lophophore is a specific tentacular apparatus, in which tentacles surround the mouth but not the anus (Emig, 1976). Based on their possession of a lophophore, three phyla of invertebrates have been traditionally regarded as lophophorates: phoronids, brachiopods, and bryozoans. Although the monophyly of the lophophorates is actively discussed (Temereva, 2017) and is not supported by recent molecular results, the organization of the lophophore in all three groups exhibits tremendous morphological similarity.

In brachiopods, the lophophore consists of brachial axis, which bears two rows of tentacles (inner and outer) and the brachial fold. On the distal ends of brachial axis, the zone, where new tentacles arise, is located. Two coelomic canals (large and small) extend at the base of the brachial axis. A small canal gives rise to the coelomic protrusion into each tentacle. Among brachiopods, brachial axis can transform in different ways (twist, bend, coil, etc) forming complex structures. In brachiopods, there is a tendency to complication of the lophophore morphology from the simplest trocholophe lophophore to schizolophe lophophore, which gave rise to three stems of the lophophore organization: spirolophe, ptycholophe, and zygolophe that led to plectolophe (Kuzmina and Malakhov, 2007) (Fig. 1).

According to our new results, which are obtained by µCT and histology, the deep sea linguliform *Pelagodiscus atlanticus* has a specific organization of the lophophore. The lophophore consists of two arms, each of which is formed by a bended brachial axis. In each brachial arm, the large canals of two halves of the brachial axis do not fuse with each other and do not form a united cavity at the base of the arm as it is typical for zygolophe lophophores. In contrast to all other brachiopods, the brachial arms of *P. atlanticus* are extended backward. This type of organization may be regarded as a modification of a zygolophe lophophore, whose morphology is similar because of the bending of the distal ends of the brachial axis, but whose brachial arms are extended forward. Apparently, *P. atlanticus* demonstrates a particular way of the evolution of the lophophore in brachiopods.

Investigation of the lophophore in recent brachiopods will help to understand evolution of the brachiopods as a whole including the abundance of extinct brachiopods. At the same time, the study of the lophophore, which is the most prominent peculiarity of all lophophorates, may help to clarify the status of the

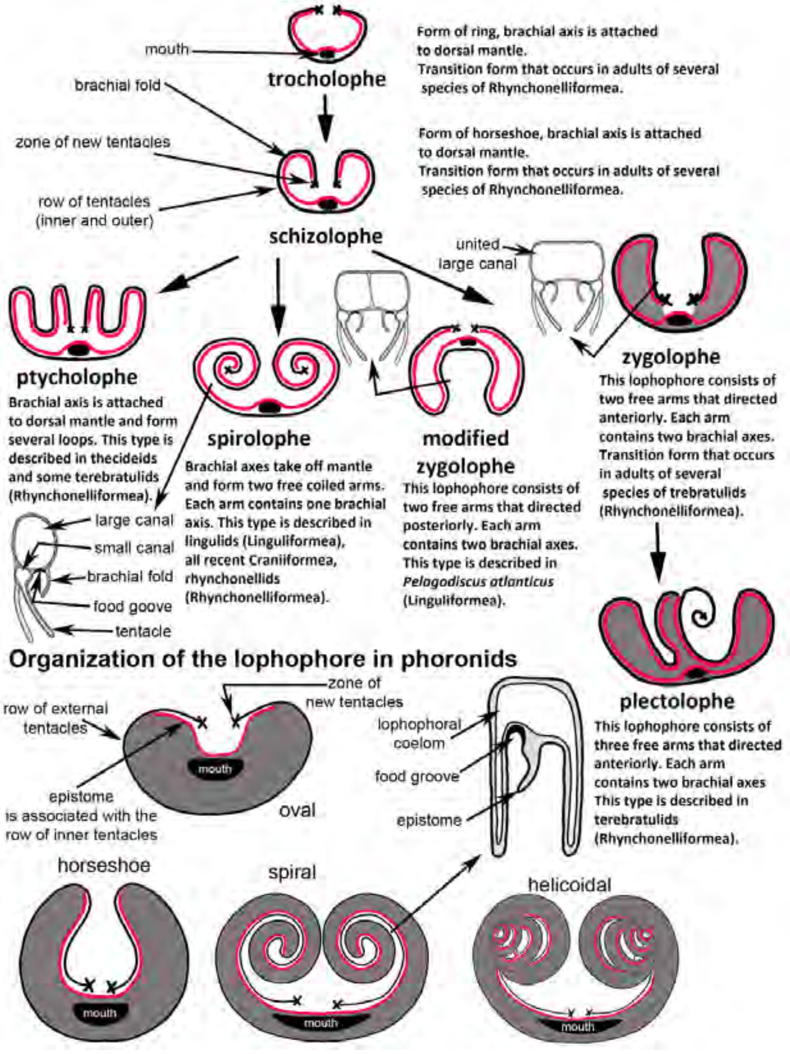

Figure 1. Scenario of evolution of the lophophore in brachiopods and organization of some types of lophophores in phoronids (Kuzmina and Malakhov, 2007; Temereva and Malakhov, 2009). The grey color indicates the presence of a united coelom.

clade Lophophorata. According to all recent molecular results, brachiopods and phoronids form a united clade, which is called Brachiozoa. Although phoronids and bryozoans have a very similar morphology of the lophophore and body plan in general, Bryozoa is regarded as a separated clade, not related to Brachiozoa.

The organization of the lophophores of phoronids and brachiopods show several main differences. First, in most brachiopods the tentacles are arranged in two rows – inner and outer; tentacles of the inner and outer rows are alternated. In phoronids, there is a single row of tentacles. Interestingly, trocholophe lophophores of brachiopods bear a single row of tentacles. Moreover, in all brachiopods, there is a single row of tentacles (outer tentacles) near the mouth. Probably the presence of one row of tentacles is an ancestral state of the brachiopod lophophore organization. Second, in brachiopods the brachial fold always conducts tentacles, whereas in phoronids, the epistome closely contacts the only tentacles of the anal side. It looks as if the space between tentacles and epistome is much wider in phoronids than in brachiopods. Thus, each arm of the phoronid lophophore bears two rows of tentacles (internal and external), the epistome, and the food groove between inner tentacles and epistome. Third, in most brachiopods there are two lophophoral coeloms: large and small canals, whereas in phoronids, there is only a single lophophoral coelom, which gives rise to canals into the tentacles. The lophophoral coelom of phoronids is similar to the small canal of brachiopods, which also gives rise to the coelom extentions into the tentacles. The large canal is probably a novelty of brachiopods with large lophophores: it works as a skeleton of long and large lophophoral arms. The small trocholophe lophophore lacks the large canal. In case of zygolophe lophophores, the large canal undergoes changes: there is a fusion of the large canals of two halves of each arm (Fig. 1). *P. atlanticus* exhibits an unusual organization of the lophophore, which looks like a modified zygolophe, but contains two large canals in each arm. This type may be regarded as a transitional state between schizolophe and true zygolophe lophophores.

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Spermatogenesis in the deep-sea brachiopod *Pelagodiscus atlanticus* (Brachiopoda: Linguliformea)

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Peculiarities of spermatogenesis and organization of spermatozoa are usually useful for the reconstruction of phylogeny in closely related groups of invertebrates. It is especially important for reconstruction of phylogeny of such an enigmatic group as brachiopods. In addition, the organization of mature spermatozoa may help to understand the reproductive biology of deep sea animals.

The spermatogenesis and ultrastructure of sperm are studied in the deep water discinid brachiopod *Pelagodiscus atlanticus*. Testes of *P. atlanticus* are voluminous sacs, which are located along the lateral sides of the body. Each testis has a complex shape with a large external portion and a folded inner portion. Spermatogonia develop around the blood capillaries and contain germ plasm, numerous mitochondria of small diameter, a Golgi apparatus, and lipid droplets. Spermatocytes form clusters of four cells, which connect via cytoplasmic bridges. In secondary spermatocytes, the Golgi apparatus produces several proacrosomal vesicles, which are located at the posterior pole of each cell which then fuse and migrate to the anterior pole. The orthogonal distal and proximal centrioles are visible in secondary spermatocytes. In early spermatids, the nucleus undergoes changes including a condensation of the chromatin. Their acrosomal vesicles are large and consist of peripheral electron dense material and a central portion of medium electron density. Mitochondria are less numerous than they had been in spermatogonia; mitochondria become bigger and their matrix becomes denser. Early spermatids still contain a Golgi apparatus, which is located near the centrioles. Late spermatids look like spermatozoa (see below), but have a larger amount of cytoplasm, which is then eliminated as residual body.

Each spermatozoon has a barrel-shaped head. The acrosome vesicle looks like a hat with a central small invagination on its basal surface. A margin of the acrosome vesicle narrows forming a small projection that resembles a brim of the hat. The inner space of the acrosome vesicle is heterogeneous. About 20 bundles of electron-dense material occur around the brim and each of them gives rise to the narrow bands running to the top of the acrosome vesicle. The central part of the acrosomal vesicle, in front of the invagination, contains electron-dense homogeneous material. Subacrosomal material consists of fibrils. The round nucleus has an anterior broad depression with a deep central invagination that is filled with subacrosomal material. The posterior part of the nucleus has a fossa that partially contains the proximal centriole. The lateral sides of the nucleus are indented laterally to accommodate the mitochondria. The nucleus contains electron-dense chromatin with several small electron-lucent lacunas. The predominant part of the nucleus is surrounded by 8 mitochondria arranged into two rows. The proximal and distal centrioles are orthogonal in their arrangement and located in the center of the mitochondrial ring. Nine satellite projections arise from the distal centriole. Each of them bifurcates twice and has striated structure. The flagellum has a typical 9+2 pattern of microtubules.

The organization of mature spermatozoa is studied in several brachiopod species from all three clades: *Discinisca* and *Lingula* (Linguliformea), *Novocrania* (Craniiformea), *Calloria*, *Kraussina*, *Terebratulina*, and *Coptothyris* (Rhynchonelliformea) (Sawada, 1973; Chuang, 1983; Afzelius and Ferraguti, 1978; Hodgson and Reunov, 1994; Drozdov et al., 2012). Spermatozoa of all brachiopods studied to date, may be considered as spermatozoa of the primitive type with some modifications. The presence of such type of mature spermatozoa shows that deep water *P. atlanticus* has external fertilization with its mature oocytes lacking of any kind of thick envelopes.

The organization of mature spermatozoa is similar in *P. atlanticus* and *Discinisca tenius* (Hodgson and Reunov, 1994). In both species, all organelles of spermatozoon are represented in their ancestral condition as it is described in literature (Reunov, 2005). Comparative analysis of all data on organization of brachiopod spermatozoa allows to insist that discinids maintained the most primitive type of the spermatozoon. We suppose that the last common brachiopod ancestor had spermatozoon, which looked like spermatozoon of discinids. This primitive spermatozoon has trapeziform acrosome, small compact nucleus, eight mitochondria around the nucleus, and two orthogonal centrioles (Fig. 1).

In comparison with this primitive type, spermatozoa of all other brachiopods underwent some changes. Thus, in lingulids, acrosoma little changes in shape and the number of mitochondria reduces to six (Sawada, 1973; Chuang, 1983). In craniid *Novocrania anomala*, the acrosome drastically changes in shape and number of mitochondria reduces to four (Afzelius and Ferraguti, 1978). In Rhynchonelliformea, acrosoma is very small, there is a single circular mitochondria, and centrioles are located parallel to each other.

There are three main ways of evolution of mature spermatozoon in brachiopods. This conclusion supports the brachiopod phylogeny, which is based on data of morphological and molecular analysis and suggests the presence of three main stems within brachiopods: Linguliformea, Craniiformea, and Rhynchonelliformea. At the same time, our results do not corroborate the idea about presence of "articulate" and "inarticulate" brachiopods as taxonomically valid clades.

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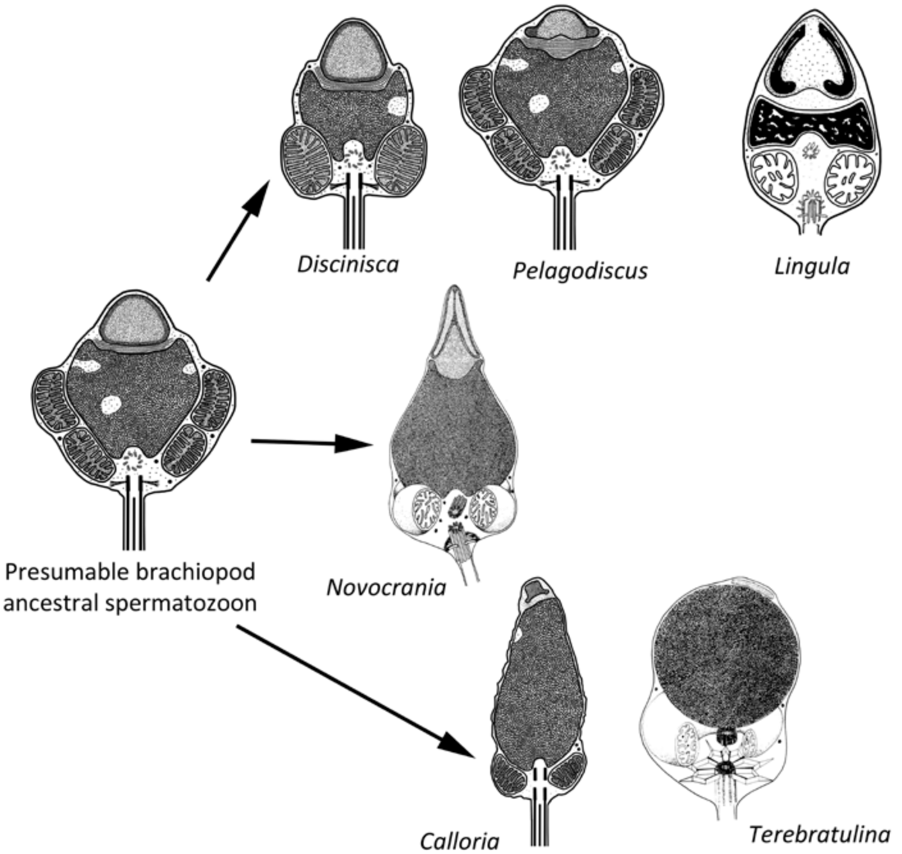

Figure 1. Scenario of evolution of spermatozoon in brachiopods. Pictures of all spermatozoa except *Pelagodiscus* and ancestral type are done on the base of literature data (Sawada, 1973; Chuang, 1983; Afzelius, Ferraguti, 1978; Hodgson, Reunov, 1994).

Time averaging of brachiopods in the southern California bight: implications for paleoecology, taphonomy, and conservation paleobiology

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Temporal resolution of brachiopod assemblages depends on sedimentological conditions (net sedimentation rate and bioturbation), on shell disintegration rate, and on the duration and magnitude of shell production, and is thus of high importance in paleoecological and taphonomic inferences. Previous studies indicate that brachiopods in tropical habitats are averaged to centuries or millennia, but quantitative estimates of brachiopods in warm-temperate environments remain limited. Here, we estimate time averaging of two brachiopods (*Dallinella* and *Laqueus*) on mainland and island shelves in the Southern California Bight. Age dating of 190 shells of *Laqueus* from the mainland shelf, collected at depths between 50 and 100 m at four sites, showed that no shells of this species have been produced on the mainland shelf during the 20th century, shell production declined steeply during the 19th century, and *Laqueus* had formerly been present continuously in the Southern California Bight for at least 4 kyr. These analyses showed that benthic communities on the now-muddy mainland continental shelf of southern California were affected by extirpation of an extensive offshore shell-gravel ecosystem, most likely driven by anthropogenic siltation. Living populations of *Laqueus* are limited today to rocky seafloor along the shelf edge and to the sandier shelves of offshore islands. Interquartile age range of *Laqueus* at four mainland sites is 50-150 years at sites with moderate sedimentation rates and 600-1000 years at sites with very low sedimentation rates. New dating of 46 shells of *Dallinella* and 57 shells of *Laqueus* from island shelves shows similar scales time averaging (interquartile age range is ~500-1000 years in *Dallinella* and ~800 years in *Laqueus* on island shelves). These scales are comparable to those observed in tropical brachiopods. To assess stability in seawater temperature of shelf habitats off the Southern California Bight over these scales of time averaging, we analyzed $\delta^{18}O$ and Mg/Ca ratio of *Laqueus*. Mg/Ca ratios show centennial-scale fluctuations but generally remain remarkably constant, and $\delta^{18}O$ values over the past 2,500 years also tend to remain within bounds of values in shells collected in the late 20th century.

Back to the beginning: the life and times of Cambrian brachiopods

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Brachiopods possess one of the most enviable fossil records of any marine animal phylum. The group were one of the first metazoan organisms to secrete a shell (Ushatinskaya, 2008; Topper et al., 2013; Skovsted et al., 2015; Harper et al., 2017) and wasted little time establishing themselves as a significant and widespread component of the Cambrian Evolutionary Fauna (Brock et al., 2000; Ushatinskaya, 2008). Cambrian brachiopod communities were dominated by the organophosphatic linguliforms, with the earliest forms (the curious paterinates) first appearing in the marine shallows of Siberia and Gondwana in Cambrian Stage 2 (Topper et al., 2013; Skovsted et al., 2015). The linguliforms were soon joined by groups of disparate rhynchonelliform taxa, such as the chileates, obolellates, kutorginates and the strophomenates as the phyla underwent a dramatic diversification in Cambrian Stage 3 (Fig. 1). Rhynchonelliforms at this time only constituted a small percentage of the total Cambrian brachiopod biodiversity, however within the space of 20 million years, 13 out of the 19 brachiopod orders had already appeared and spread around the globe. The first brachiopod communities predominantly formed on low-latitude carbonate platforms, notably on the margins of Gondwana, Siberia and Laurentia, however the group was present on all major palaeocontinents within Stage 3. Brachiopods witnessed a drop in diversity heading into Stage 4, a loss that may correspond with what has been recognized as the Botomian extinction (Zhuravlev and Wood, 1996). This decrease, however, pales in comparison to the succeeding drop in brachiopod diversity heading into the later half of Series 3 (Fig. 1). Despite this interval witnessing the extinction of several short-lived rhynchonelliformean groups, such as the obolellates and kutorginates, the loss of diversity reflects more of a drop in origination rather than an increase in extinction. This decline in brachiopod diversity is somewhat alleviated by the rapid rise and expansion of the Acrotretida, a group of tiny phosphatic brachiopods that spread like wildfire over the palaeocontinents in the latter half of the Cambrian. The later part of the Cambrian has been recognized as one of low marine diversity (Servais and Harper, 2018) and this is also reflected in the brachiopods, which retain a relatively low, yet stable diversity throughout the Furongian. Despite their relatively low diversity, brachiopods became widespread across the shallow clastic shelves in the Furongian, developing adaptations that permitted colonization of sandy substrates. These assemblages display a clear partition from those in shallow-water carbonate environments and are typically characterized by a higher proportion of rhynchonelliforms, as strophomenates become more prominent. Compared to the Ordovician (Harper et al., 2013, Topper et al., 2018), Cambrian brachiopod assemblages were almost invariably of low taxonomic diversity, generally comprising few species or even dominated by a single species, typically characterizing near shelf and carbonate platform environments. Despite this, the Cambrian record shows that brachiopods had already achieved considerable evolutionary success during the initial Cambrian radiation setting the stage for the striking diversification in the Ordovician that was to follow.

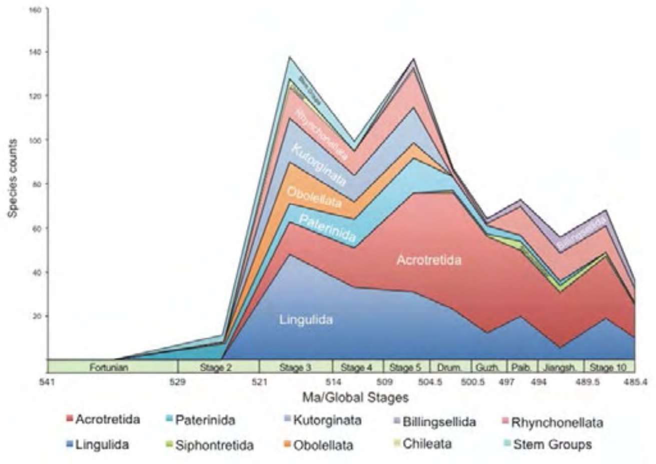

Fig. 1. Raw species-level diversity curve for the Brachiopoda through the Cambrian.

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Keynote lecture

Brachiopods in post-Permian hothouse worlds

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Since November 2015 – a few months after the last brachiopod congress! – atmospheric CO_2 concentrations on Earth have not dropped below 400ppm. There is more CO_2 in the atmosphere today than at any time in the past 2 million years. This is the first time such levels have been experienced in the evolutionary history of our species, and probably of our genus. Understanding the consequences of current climate change for the biosphere, and in particular how marine ecosystems will respond to changing ocean biogeochemistry in a warming world, is a major scientific concern (Harnik et al., 2012; Mora et al., 2013).

The fossil record is a critical source of information to address these concerns. It can be viewed as a time series of ‘natural experiments’ on the effects of global warming on life on Earth (Jablonski 2004). Responses of past marine ecosystems can be assessed, and hypotheses tested, at spatial and temporal scales that are beyond those of modern experiments. Each event has a different set of starting conditions, different species, different rates and magnitudes of warming. Although no single event can ever be a direct analogue for the future, taken together they become a powerful predictive tool: if we see the same responses to global warming repeated time and time again, *despite* the differences in starting conditions, then it is very likely that those same responses will occur again in the future.

Although brachiopods are currently a minor component of most marine ecosystems, this was not always the case. Most of the major extinction events to have affected life on Earth during the Phanerozoic are associated with evidence of global warming (e.g. Harnik et al., 2012), and during their evolutionary history brachiopods have experienced all of these. Although the late Permian and late Triassic mass extinctions selected against epifaunal, non-motile suspension feeders, including brachiopods (e.g. Foster and Twitchett, 2014; Dunhill et al., 2018), during the peak hothouse times in their immediate aftermaths, and after other warming events such as the Early Toarcian extinction, there are examples of marine ecosystems dominated by brachiopods. In addition, brachiopods have one of the lowest mean extinction rates of marine animals through the warming episodes of the past 60 million years (Harnik et al., 2012), and are often abundant in shallow marine deposits of the Pliocene, which is widely considered to be one possible future analogue interval (Williams et al., 2009). As brachiopods are also key palaeoenvironmental archives (e.g. Price et al., 2013), they have a major role to play in debates concerning the rates and magnitudes of past changes.

This presentation provides a comparative palaeoecological study of brachiopod response to selected global warming episodes through the past 250 million years, from the earliest Triassic to the Pliocene. The study will document ecosystem-scale responses and will demonstrate how brachiopods are also critical model organisms for testing hypotheses of future change.

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Giants in the hot tub? Sclerochronology of Pliocene brachiopods of southeast UK

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Body size is a key trait with implications for many aspects of an animal's biology, ecology and behaviour, and is correlated with many ecosystem functions such as productivity and nutrient cycling (Woodward et al., 2005). Body size is known to respond to environmental conditions, such as temperature, and one key hypothesis for future change is that marine animals will become smaller in size over the next few decades due to current global warming with important consequences for food resources, productivity and ecosystem function at local, regional and global scales (Sheridan and Bickford, 2011; Mora et al., 2013). The Pliocene (2.58-5.33 Ma) represents the most recent time in Earth's history when atmospheric CO_2 levels last exceeded 400ppm, and is widely considered to be a potential analogue for future change (Williams et al., 2009). Pliocene rocks of southeast UK, (i.e. the Coralline Crag Formation), were deposited in a shallow marine setting and their most common fossils include brachiopods of unexpectedly gigantic size. Originally described as '*Terebratula maxima*', these giants may exceed 10 cm in length, which is far larger than any living brachiopods inhabiting temperate latitudes today. Apart from a single predation study (Harper, 2005), little is known of their ecology. In order to reach gigantic size they presumably grew unusually rapidly or lived an unusually long time. Given the known relationship between body size and temperature, the expectation is that they were living in cold waters. Previous studies have, however, provided contradictory evidence: some analyses have indeed concluded that the Coralline Crag sea was a lot cooler than the present-day southern North Sea, whereas other data suggest much warmer conditions (Williams et al., 2009). If these giant brachiopods were really living under much warmer conditions then there are significant implications for our understanding of the general relationship between body size and temperature.

We undertook morphometric and geochemical analyses of selected individual brachiopods from the Coralline Crag Formation, housed in the Natural History Museum (NHM-UK) collections, in order to address the following key questions: (1) what was their growth rate and lifespan, and (2) what was the temperature of the seawater in which they lived?

Complete and well-preserved specimens from two species were studied: *Pliothyrina maxima* and *Pliothyrina orfordi*. Laser-ablation ICP-MS was used to determine the trace element chemistry of their shells, following the methodology and approach of Butler et al. (2015). Concentrations of Al, Fe and Mn were used to screen individual data points for potential diagenesis or contamination; particularly important given the number of punctae within the shells. Individual data points were rejected from further analysis if concentrations of those key elements exceeded acceptable, published thresholds (e.g. Butler et al., 2015; Kearsey et al., 2009, and refs therein). Palaeotemperatures were estimated from Mg/Ca ratios. Recent data from southern North Sea locations close to the study sites show that near-surface seawater temperatures presently range from approximately 5-6°C in winter to 18-19°C in summer. Results from the fossil brachiopods show some variability, probably due to the different stratigraphic horizons of the specimens, but preliminary results suggest that both winter temperatures and summer temperatures were several degrees warmer than present day. Our results contrast with 'cool' temperature estimates derived from isotopic studies of fossil molluscs, but support the warmer estimates derived from microfossils such as ostracods (cf. Williams et al. 2009). Growth increments were measured from well-preserved specimens and were coupled with Mg/Ca data to assess each animal's longevity. Again, considerable variations were recorded between individuals, with some of the larger individuals living for multiple decades.

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Lower to Middle Permian brachiopods from the Qarari Unit, Oman

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The Qarari Unit is the oldest interval of the allochthonous Batain Group, with an age ranging from the Early to the Middle Permian, deposited in a southern failed rift arm of the Neo-Tethys. This newly-formed marine environment hosted a number of niches that were occupied by rich and diversified brachiopods, crinoids, blastoids, trilobites, corals, bryozoans, conodonts and fusulines, found in outcrops at Wadi Khawr al Jaramah, Shiya and Jebel Qarari in northeastern Oman.

The brachiopod fauna comprises 244 specimens belonging to 68 different species of the following genera: *Neochonetes*, *Costispinifera*, *Echinauris*, *Neoplicatifera*, *Nudauris*, *Retimarginifera*, *Transennatia*, *Kozlowskia*, *Callytharrella*, *Calliprotonia*, *Juresania*, *Bilotina*, *Waagenoconcha*, *Magniplicatina*, *Edriosteges*, *Derbyia*, *Perigeyerella*, *Goniarina*, *Rhipidomella*, *Parenteletes*, *Acosarina*, *Orthotichia*, *Stenoscisma*, *Goleomixa*, *Cleiothyridina*, *Posicomta*, *Hustedia*, *Martinia*, *Purdonella*, *Spiriferella*, *Arcullina*, *Tipispirifer*, *Squamularia*, *Permophricodothyris*, *Paraspiriferina*, *Callispirina*, *Spiriferellina*, *Hunzina*. There are also two undetermined genera from the tribe Costispiniferini and the subfamily Auriculispininae.

Among these taxa, 12 are potentially new species of the genera *Costispinifera*, *Neoplicatifera*, *Nudauris*, *Retimarginifera*, *Callytharrella*, *Calliprotonia*, *Stenoscisma*, *Cleiothyridina*, *Spiriferella*, and *Arcullina*.

Following the systematic study, a palaeoecological analysis was made based on the taphonomical features of the brachiopods, such as fractures, deformation, degree of corrasion, bio-encrustation and bio-erosion, their dimensions and their life-habits, derived from their morphology. The analysed assemblages are life to neighbourhood assemblages. Most shells are corraded and some show traces of biotic interactions - mainly fouling by bryozoans and cnidarians– and rare praedichnia by gastropods.

The morphology and lifestyles of the brachiopod shells reflects the heterogeneity of the environment: there are seminfaunal concave-convex shells adapted to soft muddy substrates, and epifaunal biconvex pediculate shells, thriving on firm substrates, like crinoid shoals or hardgrounds. The percentage of different morphologies and life-styles shows that the soft fine-grained substrates predominated and the bioclastic shoals were localised to certain localities (WKJ2 and WKJ3), where semi-infaunal brachiopods nearly represent 100% of the specimens.

The width of the specimens ranges from 10 to 50 mm, with some specimens exceeding 70 mm; considering the average size of each taxon, they reached different sizes based on the effectiveness of the lophophore filtration process and on variations in nutrient supply.

We conclude that the Qarari palaeocommunities were adapted to carbonate shelf settings below the normal wave base, with soft and hard substrates and variations in nutrient supply.

Keynote lecture

Mass extinctions and fatal extinctions in the history of brachiopods: review and post-Paleozoic cases

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The changes in generic abundance of brachiopods (Curry and Brunton, 2007) clearly show the traces of crises in the ancient marine ecosystems. The "Big Five" mass extinctions definitely appear, but with significantly different amplitudes, and further two mass extinctions can be recognized (Late Silurian, Early Carboniferous). In the following, the focus will be on the history of the subphylum Rhynchonelliformea (Articulata), which chiefly accounts for the dramatic changes in diversity, much more than the other subphyla. On the range chart of the orders (Carlson, 2007) the difference between "mass extinctions" and "fatal extinctions" can well be demonstrated. The latter term is applied to the events when orders of Rhynchonelliformea became extinct. Only three of the "Big Five" mass extinctions coincide with fatal extinctions: the end-Ordovician, the Late Devonian and, most drastically, the end-Permian. No fatal extinctions appear at the time of the end-Triassic and end-Cretaceous mass extinctions. On the other hand, two, very significant fatal extinctions are seen in the Late Cambrian and in the Early Jurassic (Toarcian) which left no trace in the diversity (generic abundance) graph. In the Paleozoic history of the Rhynchonelliformea the mass and fatal extinctions were followed by usually rapid recoveries accompanied by significant morphological innovations. This system completely changed after the end-Permian catastrophe. The remaining four orders Rhynchonellida, Terebratulida, Athyridida, Spiriferinida (and the additional Thecideida) show limited recoveries and minor diversity peaks in the Triassic and Jurassic, but almost without morphological innovations. Nevertheless, even this post-Paleozoic history offers remarkable examples of fatal extinctions, recoveries, Lazarus extinctions and turnovers.

After the devastating end-Permian extinction, the last fatal extinction in the history of brachiopods happened in the Jurassic, in the Early Toarcian, when the orders Athyridida and Spiriferinida vanished. These spire-bearing orders reached their maximum Triassic diversity in the Carnian, and were only slightly surpassed by terebratulids and rhynchonellids in the Norian. Athyridida and Spiriferinida were severely affected by the end-Triassic crisis, and had a short and limited recovery before their extinction in the Early Jurassic (Vörös et al., 2016). The Early Jurassic recovery of spire-bearers was similar in taxonomic diversity but very different in development of adaptive morphologies. During the recovery, spiriferinides retained their morphological diversity (biconvex, alate, cyrtiniform), while athyridides lost the adaptive flexibility, what may be considered as a herald of incoming extinction of the latter clade. Yet, not only the Athyridida but both spire-bearing clades were eradicated at the early Toarcian Jenkyns Event. The morphologically diverse spire-bearers represent specialized adaptation, which further increased their extinction vulnerability compared to the other clades (Rhynchonellida, Terebratulida) with conservative biconvex shell morphology. Another key difference is the physiological disadvantage of fixed lophophore and passive feeding of spire-bearers, which became critical at times of increased environmental stress. The end-Triassic and Toarcian bottlenecks in the taxonomic diversity of spire-bearer brachiopods are mirrored by their spatial distribution. In the Late Triassic all four articulate orders had worldwide distribution. For the Hettangian, the scatter of the spire-bearer occurrences became strongly reduced, with a focus in the western Tethys, and a similar spatial contraction is seen in the Toarcian.

The last survivors of the spire-bearers were confined to the European shelf and epicontinental seas, most notably to Iberia. Here an extremely short extinction phase was recorded, simultaneously with the sudden warming in the Early Toarcian Jenkyns-event (around the Tenuicostatum–Serpentinum zonal boundary) (Garcia Joral et al., 2011). The taxonomical impact of this extinction was the disappearance of the Spiriferinida and Athyridida, together with the disappearance of around 70 % of the genera of the order Rhynchonellida. At the same time, an important recovery and turnover was recorded in the order Terebratulida.

Some post-Paleozoic groups of Rhynchonelliformea (Norelloidea, Basiliolidae, Dyscolioidea) give examples of Lazarus extinctions at high taxonomic level. Their, mostly smooth, genera are abundant in the Triassic, Jurassic and Early Cretaceous, apparently absent in the Late Cretaceous and earliest Cenozoic, re-appear in the Paleogene and profusely occur in the Recent deep-seas (Vörös, 2005). The history of these "thalassobathyal" brachiopod groups is connected to the low-latitude, west-oceanic segments of the bathyal zone. These stocks originated in the Early Mesozoic western Tethys and their Cenozoic and Recent proliferation is related to the western closures of low-latitude oceans (western Pacific, western Indian Ocean, Caribbean Sea). The Late Cretaceous- earliest Cenozoic pseudo-extinction (Lazarus extinction) of these groups can be explained by two major circumstances: (1) The formation of a circum-equatorial Tethys ocean in the Cretaceous resulted in a circum-equatorial oceanic current system and, with the demise of the western closure of the Tethys Ocean, the thalassobathyal environments disappeared; (2) The Cenomanian/Turonian and the Late Paleocene anoxic/dysoxic events (and partly the end-Cretaceous extinction) punctuated the sparse Late Cretaceous to Paleogene record in most lineages of these groups of brachiopods. They did not become extinct, but only disappeared from the shallow marine settings and their lineages survived in the deep-sea.

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Brachiopods and the Early Cretaceous Weissert event (Bakony Mountains, Hungary)

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The studied brachiopod material was collected from 10 well-dated sections and 11 other localities in the Bakony Mountains, Hungary. The sections straddle the stratigraphic interval from the Kimmeridgian to the Barremian. The brachiopod material is extremely diverse and abundant in international standard: the 1364 identified specimens represent 34 species of 14 genera. The overwhelming part belongs to the Pygopidae (1048 specimens); the most abundant genera of the family are: *Antinomia* (423), *Triangope* (378), *Pygope* (226) and *Pygites* (132). Nucleatidae are represented by 183 specimens; rhynchonellids appear subordinately (87 specimens).

The brachiopod fauna, collected bed-by-bed, together with ammonoids from 10 sections, offers exceptional possibility to determine the stratigraphic ranges of the brachiopod species at a level of substage or even ammonoid zone. Our present database is substantially unique; similar results were published only from the Polish Carpathians, though with much less supporting data (Barczyk, 1991, Krobicki, 1994, 1996).

The stratigraphic ranges recorded in the Bakony sections show that the five most abundant brachiopod species occurred from the late Kimmeridgian to the Berriasian (partly even to the early Valanginian). Further six species appeared in the early Tithonian, some of them occurred also in the early Valanginian. A less diverse assemblage was restricted to the late Berriasian to early Valanginian interval. None of the above mentioned species crosses the base of the late Valanginian; most of them disappeared abruptly at this level. A fundamental faunal change appeared in the lowermost ammonoid zone of the late Valanginian. In the Hárskút sections (HK-12, Édesvíz) a poorly preserved, almost monospecific brachiopod fauna (*Fortunella praemoutoniana, Lingularia* sp.) was collected in the Verrucosum Zone. Lingulides are regarded as typical "disaster taxa"; on the other hand, the minute *F. praemoutoniana* was found exclusively in this horizon, what may point to special adaptation to harsh environment. Considering all above pieces of information, we postulate a biotic crisis in the marine biota at the time of the Verrucosum Zone in the studied area. Afterwards, an abundant and diverse brachiopod fauna appeared in the late Valanginian, but with a complete turnover of species within the genera *Nucleata* and *Triangope*. *Pygope* and *Antinomia* disappeared ultimately. The species *Pygites diphyoides*, which was not recorded in lower stratigraphic levels, abounds in masses in the Hauterivian. This abundant assemblage of low diversity persisted to the Barremian.

The complete turnover of brachiopod species at the Verrucosum Zone and the appearance of disaster forms, restricted to the same horizon, are synchronous and are apparently in causal relationship with the Weissert oceanic anoxic event, proved by isotope geochemical study in the section HK-12 by Főzy et al. (2010).

The effect of the Valanginian Weissert event on the change of brachiopod faunas can be recognized in other parts of Europe. The brachiopod ranges, published from the Polish Carpathians (Krobicki, 1996), are interrupted in the Valanginian Verrucosum Zone; on the other hand, no turnover was recorded after this hiatus. In the sections of the Gargano peninsula (southern Italy), platform drowning, nannoconid crisis and mass accumulation of brachiopods were recorded synchronously with the Weissert event (Graziano & Ruggiero Taddei, 2008). The monospecific mass occurrence of *Peregrinella* brachiopods was interpreted as a chemosynthesising community fostered by methane-bearing cold seeps brought by local fracture system. This local phenomenon could hardly be in causal relationship with the global anoxia, but the synchroneity is remarkable. The common triggering factor might be a peak of activity of the Paranà Large Igneous Province (Erba et al., 2004).

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Brachiopod paleobiogeography in the western Tethys during the Early Jurassic taxonomic diversity maximum: identification of a new Pontic province

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The peculiarity of Jurassic brachiopod distributions in the western Tethys was recognized long ago (Ager, 1967). Recently Vörös (2016) discussed this subject in detail, and gave a re-evaluation of the Early Jurassic Euro-Boreal and Mediterranean brachiopod provinces by quantitative assessments. The existence of further Pliensbachian brachiopod biochores in the western Tethyan region was also indicated, in line with the global taxonomic diversity trajectory of brachiopods, driving the significant diversification of biochores in the Early Jurassic (Vörös et al., 2016).

Here we further investigate the structuring of Pliensbachian brachiopod biogeography in western Tethys. We build on the five-step quantitative biogeography analytical protocol described in Brayard et al. (2015), involving: (*i*) Metric (Principal Coordinate analysis; PCoA) and Non-Metric (NMDS) ordination analyses with Minimal Spanning Tree (MST) overlay; (*ii*) Ultrametric (UPGMA) and additive (Neighbour-Joining; NJ) cluster analyses; (*iii*) Bootstrapped Spanning Network (BSN) analysis; (*iv*) One-way Analysis of Similarity (ANOSIM); and (*v*) Similarity Percentage (SIMPER) analysis. The four first steps are based on the Dice and Simpson taxonomical dissimilarity coefficients, the latter being the taxonomic richness-free, compositional turnover part of the former (Baselga 2012); SIMPER analysis involves only the Dice index. All analyses were achieved on brachiopod occurrence datasets involving 24 assemblages homogenized taxonomically at the species level, with (403 taxa) or without (210 taxa) unique occurrences (i.e., species found in only one assemblage, representing 0-35% of the species per assemblage). No major differences emerged from the analyses with or without unique occurrences using either the Dice or Simpson indices – which give dissimilarity matrices showing very high ($R > 0.9$; $p < 10\text{-}5$) Mantel correlations in both cases.

The cross-comparison of results from the three first steps points toward a highly consistent biogeographical picture involving three main clusters: The Euro-Boreal, Mediterranean and Pontic biochores (Fig. 1), confirmed *a posteriori* by ANOSIM (overall $p < 10\text{-}5$ and pairwise contrasts with $p < 10\text{-}3$ in all cases). The three assemblages from the Atlas, which first appear as members of the Euro-Boreal biochore, can alternatively be interpreted as a fourth biochore, compositionally intermediate between the Euro-Boreal and Mediterranean ones (4-group ANOSIM $p < 10\text{-}5$ and pairwise contrasts with $p < 10\text{-}2$ in all cases but Atlas *vs.* euro-Boreal, where $p = 0.012$). In addition, the Mediterranean biochore can be divided into an intra- and a peri-Mediterranean group showing a statistically significant compositional difference (2-group ANOSIM $p = 0.029$). Overall, the resulting 4-group biogeographical structure shows a palaeogeographically highly consistent organization. Finally, based on this four-group structure, the SIMPER analyses allow the identification of the species most contributing to the compositional differences between the biochores, including endemics – for the newly defined biochores, ten Pontic and 18 Atlas species. The Pliensbachian brachiopod biochores show high degree of endemicity (Euro-Boreal: 57%; Intra-Mediterranean: 55%; Peri-Mediterranean: 31%; Pontic: 28%; Atlas: 22%). After a reasonable cutback of the customary scale of ranks, and considering our new results, the following palaeobiogeographical categories and names are suggested for the western Tethyan Pliensbachian brachiopod biochores: Euro-Boreal Province, Mediterranean Province (including Intra-Mediterranean Subprovince and Peri-Mediterranean Subprovince), Pontic Province, and Atlas Subprovince. Besides these five biochores, a poorly documented brachiopod faunal region appears on the Gondwana margin (Levantinian and Arabian regions), as a possible precursor of the extensive Middle to Late Jurassic Ethiopian province.

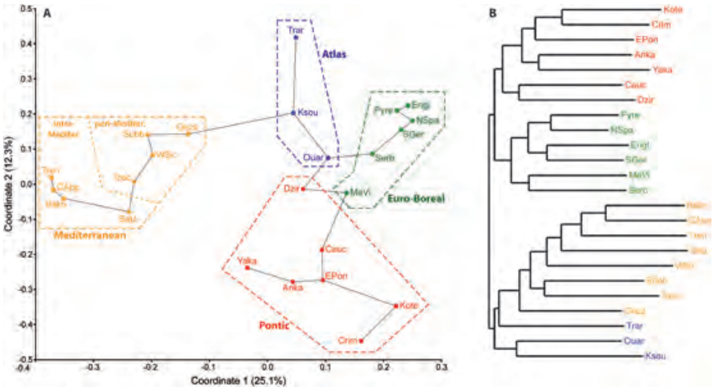

Fig. 1. Examples of PCoA+MST (A) and NJ (B) analysis results based on the Dice dissimilarity matrix computed for the dataset without unique occurrences.

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A new Induan (Early Triassic) brachiopod fauna from South China and implications for biotic recovery after the Permian-Triassic extinction

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The Permian-Triassic mass extinction caused the greatest loss of biodiversity in the Earth history (Erwin, 2004). It killed more than 90% of the marine species. Biotic recovery from the Permian-Triassic mass extinction witnessed the great shift in marine ecological structure from Paleozoic- to Mesozoic-type (or Modern-type). Many studies show that the final biotic recovery occurred in the early Middle Triassic, which was documented by several fossil groups including gastropods, echinoderms, and reef-building organisms. However, recent studies show that some marine organisms began to diversify in the Early Triassic (e.g., conodonts, ammonoids, foraminifers, and brachiopods). And thus the recovery time and pattern from the Permian-Triassic mass extinction seem to be still quite variable.

As one of the key organisms in the Paleozoic oceans, brachiopods suffered severe extinction during the Permian-Triassic crisis. Brachiopod diversity was extremely low in the Early Triassic, making it difficult to uncover the evolution process of brachiopods. Here, we found a new brachiopod fauna (306 specimens) in the Induan of Lichuan, South China. This fauna consists of three species in three genera, including one new genus and one new species, i.e. *Lichuanorelloide lichuanensis* gen. et sp. nov., *Lissorhynchia* sp. and *Crurithyris* sp. The brachiopod fauna co-occurred with ammonoids *Ussuridiscus*, *Jieshaniceras*, *Hubeitoceras* and *Vishnuites*, suggesting a late Griesbachian-early Dienerian age. The relatively diverse and abundant brachiopod fauna represents one pulse of brachiopod recovery in the early Dienerian, supporting a fitful recovery pattern after the Permian-Triassic mass extinction. Geographic distributions of brachiopods in family Norellidae during the Early Triassic show a high-latitude-toward migration which may be caused by the extreme warming climate that happened during the Early Triassic (Sun et al., 2012).

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Permian strontium isotope stratigraphy based on brachiopod shells from south China

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Strontium isotopes ($^{87}Sr/^{86}Sr$) ratios are widely used to correlate strata, reveal environmental changes and estimate the ages of marine sedimentary rock. Among different mineralogical components used to obtain the strontium isotopic composition of the seawater, the brachiopod low-Mg calcite shell (bLMCs) is most resistant to diagenesis and it is thus the best archive to record the original $^{87}Sr/^{86}Sr$ of marine environment.

To reconstruct an overall $^{87}Sr/^{86}Sr$ curve based on bLMCs for the entire Permian, thousands of brachiopod specimens were collected from three different stratigraphic sections in South China. They are the Xikou section in Shaanxi Province; the Bianping section in Guizhou Province and the Shangsi section in Sichuan Province. Three hundred and twenty specimens were selected for multiple screening tests in order to evaluate the preservational quality of their shells. Shell preservation was initially evaluated using scanning electron microscope (SEM) to assess the quality of shell microstructure, and cathodoluminescence microscope with cold cathode luminoscope (CL) to evaluate the degree of permeation by diagenetic fluids (i.e. Garbelli et al., 2012). A subset of samples (N=170), deemed to bear good preservation of the microstructure and non-luminescent, and their enclosed matrix have been analysed for trace elements (Mg, Sr, Fe, Mn), carbon and oxygen stable isotopes, to assess preservation level through comparative chemistry (Brand et al, 2012). Brachiopod samples with pristine elemental, carbon and oxygen isotopic composition (141 specimens, 200 samples) were subsequently analysed for Sr isotopic composition.

Comparisons of trace element, carbon and oxygen isotopes between the calcitic shells and the rock matrix showed that brachiopod shells are more resistant to diagenesis and more likely to hold the original signal of the seawater. The $^{87}Sr/^{86}Sr$ ratios of different taxa from the same stratigraphic horizon were compared, and results showed that no taxonomic effect is observed for the $^{87}Sr/^{86}Sr$ ratios. Comparison of $^{87}Sr/^{86}Sr$ from the anterior and posterior parts showed evident differences in a single shell.

A new $^{87}Sr/^{86}Sr$ curves was built based on these well-preserved brachiopod shells which are constrained by high-resolution conodont and fusulinid biostratigraphic schemes. The $^{87}Sr/^{86}Sr$ ratio decreased from 0.708115 around the Carboniferous-Permian boundary to the lowest value of 0.706838 in the late Capitanian, then increased to 0.707137 around the Permian-Triassic boundary. The $^{87}Sr/^{86}Sr$ curve from South China provides an important reference for temporal correlation of the Permian. The changing continental weathering rate during the formation and dispersal of Pangea and the associated mid-ocean ridge spreading are considered to be the dominant factors causing the changes of the seawater Sr isotope ratios during the Permian Period.

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Investigating the ecology and environmental tolerance to sedimentation of the brachiopod *Calloria inconspicua* in Otago Harbour, New Zealand

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With over 50 species living in seas around New Zealand, brachiopods form an important component of the marine biodiversity in this region (MacFarlan et al., 2009). Brachiopods comprise a small but integral part of the marine biodiversity and ecology of Otago Harbour, southern New Zealand where the present study was undertaken. While not being commercially exploited, brachiopods can provide an indication of the water quality and health of the coastal environment.

The smooth, red, long-looped *Calloria inconspicua* (Sowerby 1846) (Terebratellidae) is a common brachiopod endemic to intertidal and shallow subtidal seas around New Zealand (Fig. 1A). It can be locally abundant in harbour environments, where it may be exposed to a range of turbidity and sedimentation levels. Populations exist in the Otago Harbour where the local port company is undertaking a program of dredging and channel widening within the harbour, potentially increasing sedimentation rates and turbidity (as much as 20-times the natural turbidity present in the harbour (Berthelsen, 2016)). This may have negative impacts on the harbour's ecosystem (Rogers, 1990; Johansen & Jones, 2013). The aim of this study was to determine how *Calloria inconspicua* responds to increased levels of turbidity in the harbour, and more broadly, to understand how brachiopods are affected by turbidity and sedimentation. The effect of turbidity on brachiopods in the Otago harbour has been of concern, given the dramatic decline over the past several decades in the once abundant populations of a sympatric species, *Pumilus antiquatus.*

Over one hundred *C. inconspicua* individuals, still attached to rocks, were collected from Pudding Island, Otago Harbour, and transported to the Portobello Marine Laboratory and the width of each brachiopod measured.

Experiments were then carried out in a controlled temperature room set at 10 °C with individual responses to turbidity and sediment levels examined. For this the 'snap' rate of brachiopods was measured in response to turbidity and sediment build-up, with one 'snap' being defined as a rapid closure of the valves. The treatment levels chosen were 0, 2, 4, 20, 40 and 100 nephelometric turbidity units (NTU, a measure of the suspended sediment in the water column), to mirror the levels that have been recorded in the harbour previously. To determine the response of individuals to sediment exposure, time lapse videography of individuals was made over a 1-hour period, with 4 individuals filmed for each sediment treatment level. Each replicate experiment was conducted for one week with sampling on day 1, 3, and 5. Later, video footage of brachiopod behaviour (Fig. 1B-C) was analysed for 'snap' occurrence, and the rate of snapping per hour as a function of turbidity was statistically analysed by a generalised linear mixed effects model. When planning the experiment, we predicted that *C. inconspicua* specimens would close their valves at the higher NTU treatment levels and cease feeding. However, all experimental subjects continued to feed throughout the experiment, but those exposed to the higher treatment levels increased their snap rate.

It was observed that between the control treatment (0 NTU) and 20 NTU treatment there were low snapping rates (i.e. <4 snaps h-1), but above 20 NTU the 'snap' rate (thought to be an indirect estimate of the rate of clearing inedible particles from within the mantle (Rudwick, 1962)) almost doubled, to 6-7 snaps h-1 (Figure 2).

This is in agreement with the expected behaviour of brachiopods given that the harbour data shows intense turbidity spikes (above 40 NTU) lasting from a few days to a few weeks. A median of 1.37 NTU was reported by Port Otago Ltd. for 2014 at Pudding Island, with large spikes of turbidity readings rising to 100 NTU from October through the end of March (Berthelsen, 2015). It is apparent that above 20 NTU *C. inconspicua* are potentially required to exert more energy to physiologically respond to sedimentation and turbidity. We also observed the production of mucous in brachiopods subjected to elevated turbidity

Overall, these results suggest that brachiopods expend more energy (via snapping and mucous production) to maintain normal function when exposed to higher levels of turbidity, such as those produced during dredging.

The extra energy needed to cope with high levels of turbidity and sedimentation may increase the risk of mortality, especially in juvenile brachiopods, thus leading to a reduction in population size, and a loss of biodiversity within the Otago Harbour. These results provide a foundation for future studies into understanding the impacts of anthropogenic activities on the Otago Harbour ecosystem and on brachiopods in general.

Future work includes an expansion of this initial study to several brachiopod species (*Liothyrella neozelanica*, *Notosaria nigricans*, and *Calloria inconspicua*) from Doubtful Sound, Fiordland, measuring the effects of turbidity on growth, respiration/excretion, feeding rates and survival. We will also explore the potential for local adaption to sedimentation by contrasting populations of *C. inconspicua* from high sediment (Otago Harbour) and low sediment environments (Doubtful Sound, Fiordland).

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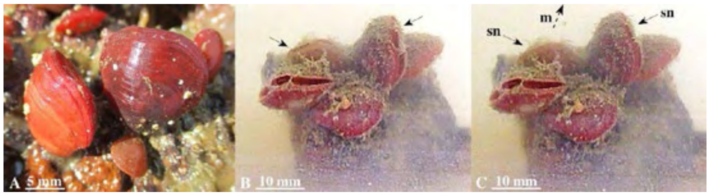

Figure 1. A. *Calloria inconspicua* found on the underside of rocks, Pudding Island, Otago Harbour. B-C. Screenshots from footage taken during high turbidity experiment of brachiopods attached to rock. The images taken ~ 10 seconds apart, shows two specimens snapping their valves (sn) and some ejected mucous (m).

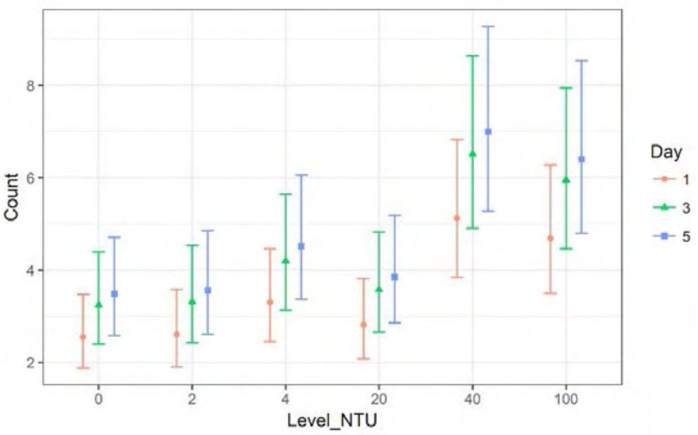

Figure 2. *Calloria inconspicua* snap rate (count = snaps per hour ± 95% CI) for each NTU treatment level. The measurements of snapping are given for day 1, 3, and 5 of the sediment treatment.

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A quantitative taxonomic review of *Fusichonetes* and *Tethyochonetes* (Chonetidina, Brachiopoda)

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Two Middle Permian (Capitanian) to Early Triassic (Griesbachian) rugosochonetid brachiopod genera, *Fusichonetes* Liao in Zhao et al. 1981 and *Tethyochonetes* Chen et al. 2000, have been regarded as two distinct taxa and used as such for a wide range of discussions including biostratigraphy, paleoecology, paleobiogeography, and the Permian-Triassic boundary mass extinction. However, the supposed morphological distinctions between the two taxa are subtle at best and appear to represent two end members of a continuum of morphological variations. Herein, we applied a range of quantitative and analytical procedures (bivariate plots, Kolmogorov-Smirnov test, categorical principal component analysis, and cladistic analysis) to a dataset of 15 quantified morphological variables, integrating both key external and internal characters, measured from 141 specimens of all well-known *Fusichonetes* and *Tethyochonetes* in order to test whether or not these two genera could be distinguished in view of the chosen characters. The results indicate that these two genera are morphologically indistinguishable and that the species classification previously applied to these two genera appears to represent polyphyletic groupings within the genus *Fusichonetes*. Consequently, *Tethyochonetes* is concluded to be a junior synonym of *Fusichonetes*. The diagnosis and key characteristics of *Fusichonetes* are clarified and refined based on a new suite of well-preserved specimens from the Permian − Triassic Xinmin section in South China.

A new Changhsingian (Late Permian) brachiopod fauna from the Xiala Formation at Coqen in the central Lhasa Block and its palaeogeographical implications

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Lopingian brachiopods have been rarely reported from the Lhasa Block except for a small brachiopod assemblage from the Lielonggou Formation near the Lhasa (Sun et al., 1981). However, a new brachiopod fauna with 20 species belonging to 17 genera is described from the uppermost part of the Xiala Formation at the Aduogabu section in the central Lhasa Block. The age of this fauna can be confidently assigned to the Changhsingian as indicated by the *Spinomarginifera chengyaoyenensis*, *Haydenella wenganensis*, *Neochonetes* (*Zhongyingia*) *zhongyingensis*, *Araxathyris* cf. *dilatatus* and so on. This age assignment is also supported by the associated foraminifer *Colaniella parva* derived from the same horizons as those with brachiopods. Palaeobiogeographically, this fauna is dominated by *Spinomarginifera* and other Cathaysian genera such as *Haydenella*, *Acosarina* and some endemic elements, but lacking typical cold-water elements. However, at about the same interval, the brachiopod faunas from the Himalaya Tethys Zone are dominated by typical Gondwanan cold-water taxa (e.g., *Costiferina indica*, *Retimarginfera xizangensis*, *Neospirifer* (*Quadrospina*) *tibetensis*) (e.g., Shen et al., 2000, 2003; Xu et al., 2018). Thus, it is clear that the Lhasa Block had drifted into a relative warm-water region and was far away from the cold northern peri-Gondwanan margin where the Himalaya Tethys Zone was situated during the Changhsingian. The discovery of this brachiopod fauna also implies that the rifting time of the Lhasa Block was no later than the Late Permian.

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Variation in brachiopod microstructure and isotope geochemistry under low PH - ocean acidification - conditions

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Throughout the last decades and in the near future, there is a growing concern about ocean acidification and a need to assess the impact of ocean acidification on calcite-shelled animals (e.g., brachiopods, bivalves and gastropods). Despite the great number of studies focusing on the effects of acidification on shell growth, metabolism, shell dissolution and shell repair, the consequences on biomineral formation remain poorly understood, as few studies addressed the impact of acidification on shell microstructure and geochemistry.

A detailed microstructure and stable isotope geochemistry investigation was performed on nine adult brachiopod specimens of *Magellania venosa* (Dixon, 1789), grown in the natural environment as well as in controlled culturing experiments at different pH conditions (7.35 to 8.15 ±0.05). Several shell microstructural features such as thickness of the primary layer, density of endopunctae and morphology of the basic structural unit in the secondary layer were analysed using scanning electron microscopy (SEM). Secondary shell layer increments along an ontogenetic direction in both dorsal and ventral valves were sampled and analysed for carbon and oxygen stable isotope geochemistry. Based on our data, we concluded that: 1) when exposed to low pH conditions, *M. venosa* produced a more organic-rich shell with a thicker primary layer, higher density of endopunctae and smaller secondary layer fibres, when subjected to a longer interval of about one year of culturing, 2) increasingly negative values of $\delta^{13}C$ and $\delta^{18}O$ are recorded by the shell produced during culturing; they are mostly related to the C-source in the culture setup, and 3) both the microstructural change and the stable isotope results are similar to observations from the fossil record and strongly support the value of brachiopods as robust archives of proxies for studying ocean acidification events in the geologic past.

Evolution and fabric differentiation of Palaeozoic Rhynchonelliformean brachiopod shells

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Due to the unique features of their biominerals, their high biodiversity and their dominant ecological role in Palaeozoic oceans, brachiopods are considered very robust archives to understand the evolution of marine calcifiers in changing climates and environments in the geological past. However, after the seminal works of (Williams, 1968, 1970, 1997; Brunton, 1972; Mackinnon and Williams, 1974; Williams and Cusack, 2007), few researches have been devoted to unravel brachiopod shell microstructure evolutionary changes and fabric differentiation, in particular for what concerns the classes Rhynchonellata and Strophomenata.

Here, a detailed study of the microstructure of Cambrian to Permian fossil brachiopod shells from Iran and China is presented. The shell microstructure of 37 brachiopod species, representatives of 22 families and 10 orders, was analysed using Scanning Electron Microscope (SEM) on 125 shell sections (Figure 1). A comprehensive database of their shell structure was built, considering several features from the macro-scale to the micro-scale (e.g. size and shape of the shell, shell layers organization, morphological statistics of the basic units forming the shell layers, shell perforations type and other unusual microstructural features). In all the investigated shells, primary layer and tertiary layer are not always present, the two main microstructural variants being the fabrics of the secondary layer: fibrous fabrics vs. laminar fabrics.

The results show that biomineralization strategies are different in Rhynchonellata and Strophomenata and species-specific, but the general patterns are still comparable to the processes observed in recent brachiopods. An attempt to reconstruct evolutionary changes for the two main shell fabrics may provide important information to understand how brachiopod microstructure responds to different environmental conditions and climate change in the long term.

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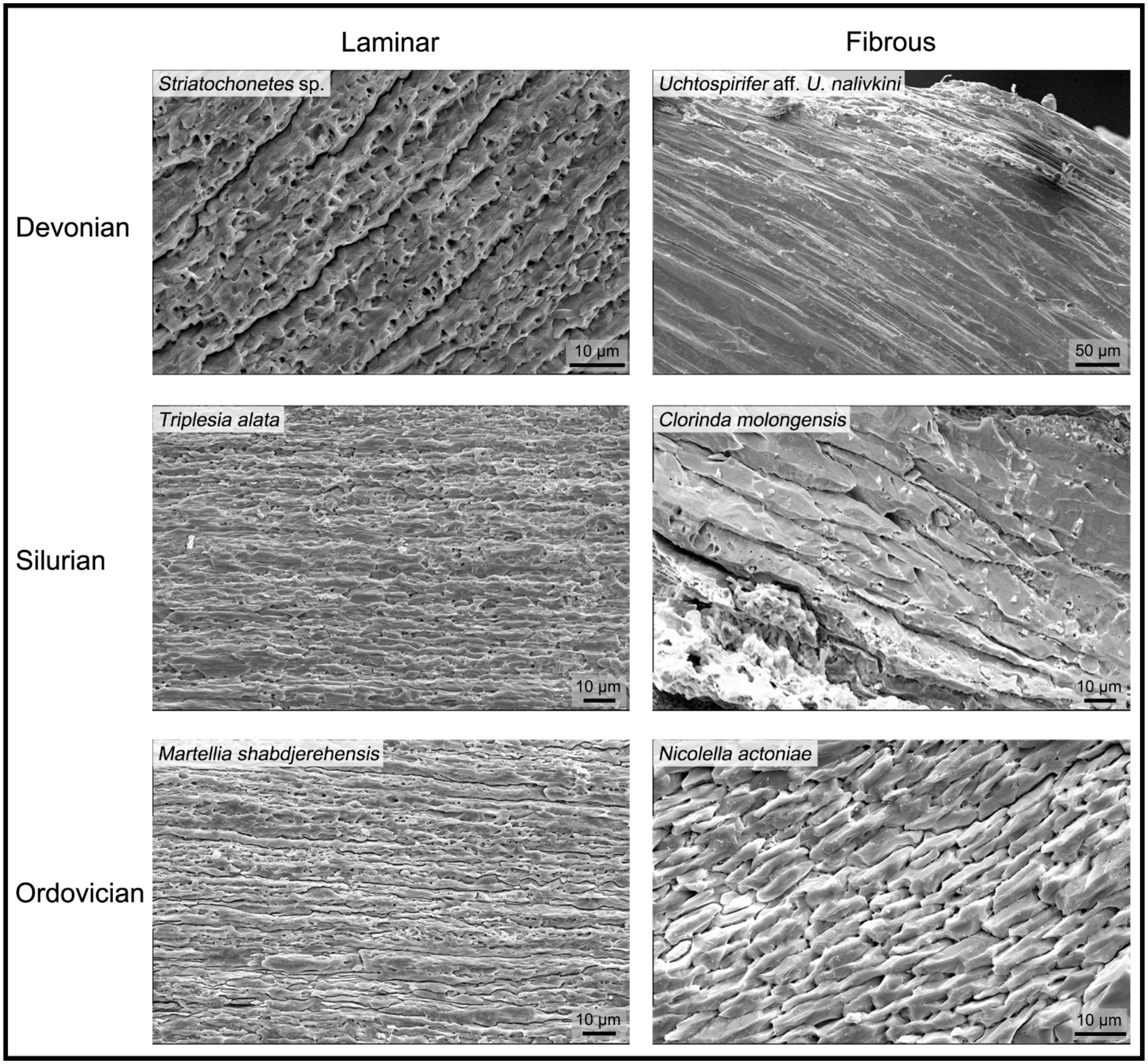

Shell microstructure: laminar fabrics vs. fibrous fabrics.

An in situ preserved Late Early Carboniferous brachiopod fauna in southern Guizhou, China

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Lower Carboniferous marine deposits are widely distributed and exposed in southern Guizhou, China. Here we report an autochthonous brachiopod fauna from the Baizuo Formation (Serpuhovian, Lower Carboniferous) exposed along a road-cut near Zongdi, Ziyun County, Guizhou, China. The brachiopods are preserved in a bioclastic packstone bed, 0.3 to 0.4 m-thick, locally highly concentrated to form some 0.3 to 0.4 m-high and 1.5 m to several meter-long bioherms, intermittently distributed along the strike. Most brachiopods are well preserved in their original life-position without any sign of transport by current, strongly suggesting an *in situ* buried benthic community. To investigate the faunal composition and the community structure, two bulk samples (each ca. 0.2×0.3×3 m3 in volume) were collected from one bioherm and its nearby non-bioherm assemblage, respectively.

Thin-section observation reveals that the packstone in the non-bioherm sample contains more bioclasts than that in the bioherm one, indicating weak current transport in the non-bioherm assemblage.

Based on the two samples, eight species of 8 genera have been recognized, including *Megachonetes zimmermanni* (Paekelmann), *Striatifera striatus* (Fischer de Waldheim), *Echinoconchella elegans* (M'Coy), *Gigantoproductus schajenwanensis* (Ozaki), *Fluctuaria undatus* (Defrance), *Productus* sp., *Cleiothyridina submabranacea* (Grabau), and a new martiniid spiriferid.

The bioherm sample yields 278 specimens, including 194 martiniid spiriferid, 81 *Striatifera striatus*, 1 *Productus* sp., and 2 *Cleithyridina submabranacea. Striatifera, Productus* and *Cleithyridina* are restricted to basal part of the sample, suggesting that the bioherm is formed by the martiniid spiriferid. The specimens of *Striatifera striatus* are generally preserved with their ventral valves downward in the sediment or lying on the dorsal valve of other individuals; they play an important role as biogenic hard substrates for the martiniid spiriferid and *Cleithyridina* to attach. Some specimens of *Striatifera striatus* colonized by the martiniid spiriferid displayed a sudden change of shell-growth direction from horizontal to upward to make the anterior portion perpendicular to the posterior portion of the shell, suggesting that the martiniid spiriferid attached on alive *Striatifera striatus* shell. More than 70% specimens of the martiniid spiriferid are articulate shells, with size ranging from 6-55 mm wide, preserved in life-position tightly against each other, using their ventral beaks to attach on the dorsal valves of *Striatifera striatus* in the lower part of the sample and to attach on conspecifc shells in the upper part of the sample. Some shells show evident growth malformation resulting from their crowded life style. The single specimen of *Productus* sp. is preserved with its ventral valve downward. Although some shells of other species are distributed around it, none is in direct contact with it.

The non-bioherm sample yields 148 specimens, including 121 *Striatifera striatus,* 10 martiniid spiriferid and 6 *Cleithyridina submabranacea*, 2 *Megachonetes zimmermanni*, 5 *Productus* sp., 2 *Echinoconchella elegans*, 1 *Gigantoproductus schajenwanensis*, and 1 *Fluctuaria undatus*. All the specimens are randomly distributed in the sample. Most *Striatifera striatus* shells them are roughly parallel to bedding plane with the ventral valve downward and a few are almost vertically oriented with the ventral beak downward or upward, probably resulting from current disturb. *Cleithyridina submabranacea* is preserved in the same way as in the martiniid spiriferid-rich sample. *Megachonetes zimmermanni* and other four productoid species are well preserved with their ventral valves downward, suggesting they were free-lying or spine-supporting dwellers on sea floor. Almost all specimens of the martiniid spiriferid found in this sample are disarticulated valves, suggesting that they were dead shells falling down from the nearby bioherms.

Based on field observation and results from the two samples, we can conclude that this brachiopod fauna represents an *in situ* preserved benthic community, dominated by the new martiniid spiriferid and *Striatifera striatus.* The presence of many free-lying or spine-supported productoid species suggested the community was thriving on a soft carbonate mud sea floor, where the new martiniid spiriferid attached on shells of *Striatifera striatus* and locally crowded together to form shelly bioherms. *Megachonetes zimmermanni* and productoid species were scattered on the area between the shelly bioherm.

Foliomena fauna: macroevolution of deep water benthic communities with the environmental changes

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Foliomena Havlíček, 1952 is a strophomenoid brachiopod characterized by a small and smooth shell with a ventral apical spine, and a bilobate cardinal process and a pair of short side septa in dorsal interior. It first occurred in a small depression on the Upper Yangtze Platform (South China palaeoplate) at Jieling of northern Yichang, western Hubei Province during the latest Darriwilian (Middle Ordovician), i.e. the lower part of the Miaopo Formation (Liang et al., 2014). The formation of such depression might be related to the commence of the Kwanghsian Orogeny, a regional tectonic movement corresponding to the European Caledonian movement and the North American Taconian movement. The *Foliomena* fauna (Harper, 1979) represents a group of benthic marine animals characterized by small or even tiny shells of Late Ordovician age. It has some common constituents like *Foliomena, Dedzetina, Cyclospira, Epitomyonia, Kassinella*, etc. Besides brachiopods, graptolites, ostracods, trilobites, and some individuals of bryozoans, gastropods and bivalves are also found in the rocks.

Since its origination in the offshore locality of the Upper Yangtze Platform, the *Foliomena* fauna expanded to the entire Yangtze Platform during the Sandbian (i.e. in the Pagoda Formation stretching for about 3000 km from east to west and 800 km from south to north), eventually migrated to North China, Sibumasu and several other palaeoplates or terranes in the early Katian, and got its widest distribution around the world during the middle-late Katian (Rong et al., 1999; Zhan and Jin, 2005; Zhan et al., 2014). Palaeoecological analysis shows that most of its representatives are from deeper water benthic settings (i.e. the typical *Foliomena* fauna) with only a few exceptions where it occurs in a relatively shallower benthic environment (corresponding to upper BA4 or even BA3) (i.e. the atypical *Foliomena* fauna). Its macroevolutionary acme occurred during the eustatic Buda event (a global warming event, Fortey and Cocks, 2005) when the Ordovician radiation got its last and the biggest diversity acme globally during the late Katian. But its extinction at each particular palaeoplate or terrane was controlled by both global (end-Ordovician glaciation) and regional (tectonic movements like the Kwanghsian orogeny in South China) factors. So the last appearance datum (LAD) of the *Foliomena* fauna is diachronous at different places, all constituting part of the first episode of the end-Ordovician mass extinction (EOME) at each region or even a particular locality.

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Early warning signals of marine benthic ecosystem prior to the Permian–Triassic boundary mass extinction event in South China

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The Permian–Triassic boundary mass extinction (PTBME), the biggest biological crisis event during the whole Phanerozoic eon, caused the most severe biodiversity decline in both marine and terrestrial ecosystems, and the transition from the Palaeozoic-type marine ecosystem to the Mesozoic and Cenozoic-type marine ecosystem (Jin et al., 2000; Shen et al., 2011; Chen and Benton, 2012). In the past decades, masses of high-quality papers published on this mass extinction itself and the possible causes; however, there is few research focusing on the changes of marine ecosystem prior to the PTBME. According to the secondary negative shift of organic carbon $\delta^{13}C$ and global warming event occurring in or below conodont *Clarkina changxingensis* Zone, the marine environment began to deteriorate just before the major crisis (between the top of conodont *C. yini–C. zhangi* Zone and *Isarcicella staeschei* Zone) (Shen et al., 2011; Sun et al., 2012). To investigate the possible changes of marine ecosystem before the PTBME, the quantitative work on the Permian–Triassic boundary brachiopods fauna had been undertaken in the shallow-water clastic-shelf facies, carbonate facies and deep-water siliceous rock facies of South China. It is demonstrated that, the community structure of brachiopods fauna already changed (e.g., dominance shift, body-size reduction, biodiversity indices change) just before the PTBME occurrence, which indicates the early warning signals of the major biotic crisis in South China (Zhang et al., 2017; Wu et al., 2018).

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Late Ordovician brachiopods from Xichuan, southwestern Henan, central China and their implications

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Xichuan County lies in southwestern Henan Province, central China, and paleogeographically belongs to the northern part of South China paleoplate and was close to the Qinling Orogenic belt, which is the boundary between South and North China paleoplates. The Shiyanhe Formation (Katian, Upper Ordovician) is well developed and widely exposed in Xichuan and its neighbor counties. It has a carbonate-dominated succession yielding different kinds of fossils including brachiopods, corals, trilobites, bryozoans, stromatoporoids, etc.

Some brachiopods have been collected from the middle and upper Shiyanhe Formation, such as *Pionorthis, Dinorthis, Mimella, Skenidioides, Sowerbyella, Altaethyrella, Rongatrypa* and *Zygospria?*. The genus *Rongatrypa* is an early representative of the subfamily Clintonellinae and could be distinguished from Silurian representatives of this subfamily (such as *Clitonella, Anabaria* and *Nalivkinia*). It has been formerly found in Kazakh terranes and indicates a tropical shallow water environment during the Late Ordovician (Zhang *et al.*, 2017). *Altaethyrella* is another typical shallow water genus in the Late Ordovician and it has been found in South China, North China, Tarim, Siberia and the Altai Mountains. Other constituents of the fauna were commonly reported from the shallow water environmental settings elsewhere in the world, such as *Mimella, Sowerbyella* and *Dinorthis*.

Consistent with the last diversity acme of the Great Ordovician Biodiversification Event (GOBE) that occurred during the late Katian, the brachiopod fauna found in southwestern Henan, central China is now interpreted to have been living in a shallow water environment (BA 2-3) on the northern margin of South China, representing the manifestation of GOBE in this particular area. The Shiyanhe Formation could be correlated with the Xianzhen or the Sanqushan or the Changwu formations in the Zhejiang-Jiangxi border region, eastern China. These are the only two regions yielding the shallow water *Altaethyrella* fauna in South China while the majority of the plate was overwhelmingly occupied by black shales (i.e. the Wufeng Formation) during the middle to late Katian. Numerical analysis on the fauna studied in this paper and its equivalents around the world supports the close relationship between Kazakh terranes, Tarim, North and South China, and indicates the existence of close faunal exchanges between these paleoplates or terranes during the Late Ordovician.

Further study on the systematics of this fauna is ongoing, which will not only solve some important systematic problems but also deepen our understanding on the paleobiogeography and regional geology of this particular realm during the late Katian (Late Ordovician).

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Keynote lecture

Paleoecological complexities during Cambrian explosion: evidence from brachiopods

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Although tiering history can be traced back to the Proterozoic (Ausich and Bottjer 1982), the Ediacaran biota represents the initial establishment of soft-substrata benthos that are only limited to vertically differentiated epifaunal primary tierers (Clapham and Narbonne, 2002). Analysis of Cambrian (Series 2) brachiopods from eastern Yunnan of China demonstrates that brachiopods were the first benthic metazoan that achieved their success in ecological stratification and tiering complexity by Stage 3 (equivalent to Atdabanian) (Figure 1) (Zhang and Holmer 2013; Topper et al., 2018). They were either cemented by a ventral valve or attached by variable types of pedicles to establish complex community encompassing primary tierers and variable secondary tierers (>60 mm in heights) (Zhang et al., 2010; Wang et al., 2012). During this time, the Cambrian Stage 3 brachiopods exhibited at least five types of lifestyles: pedicle attachment, pedicle anchoring, cemented, free-lying and semi-infaunal. By Cambrian Stage 4, linguloid brachiopods became progressively abundant, and for the first time aggregated as dense concentrations of in vivo shells. The bedded monotaxic shells, in some cases preserved with pedicles and marginal setae, were commonly overgrown by populous encrusting serpulid-like tubeworms with annulations on the tubes, distributed in wide areas of eastern Yunnan. Thus, the fossils represent the earliest evidence on the brachiopod-supported Paleozoic benthic communities on Cambrian soft substrates. In younger communities, the lingulate brachiopods are commonly utilized as basibionts (biological exoskeletons) to support the upright lifestyles of eocrinoid echinoderm community, as seen in the Kaili Biota (Stage 5) of southern China (Lin et al., 2008). In addition, the calcareous-shelled brachiopods derived from the Epoch 3 Cambrian Chengjiang fauna exhibited remarkably similar pedicle attachments to those found from the early Paleozoic (Ordovician and Silurian) brachiopods (Holmer et al., 2018a, b). Thus, the Cambrian Stage 4-5 interval may represent a transition from trilobite to brachiopod-dominated Paleozoic communities on soft substrates. The Cambrian Explosion and the GOBE (Great Ordovician Biodiversification Event) might be postulated to represent different phases of the same ecological dynamics of diversification.

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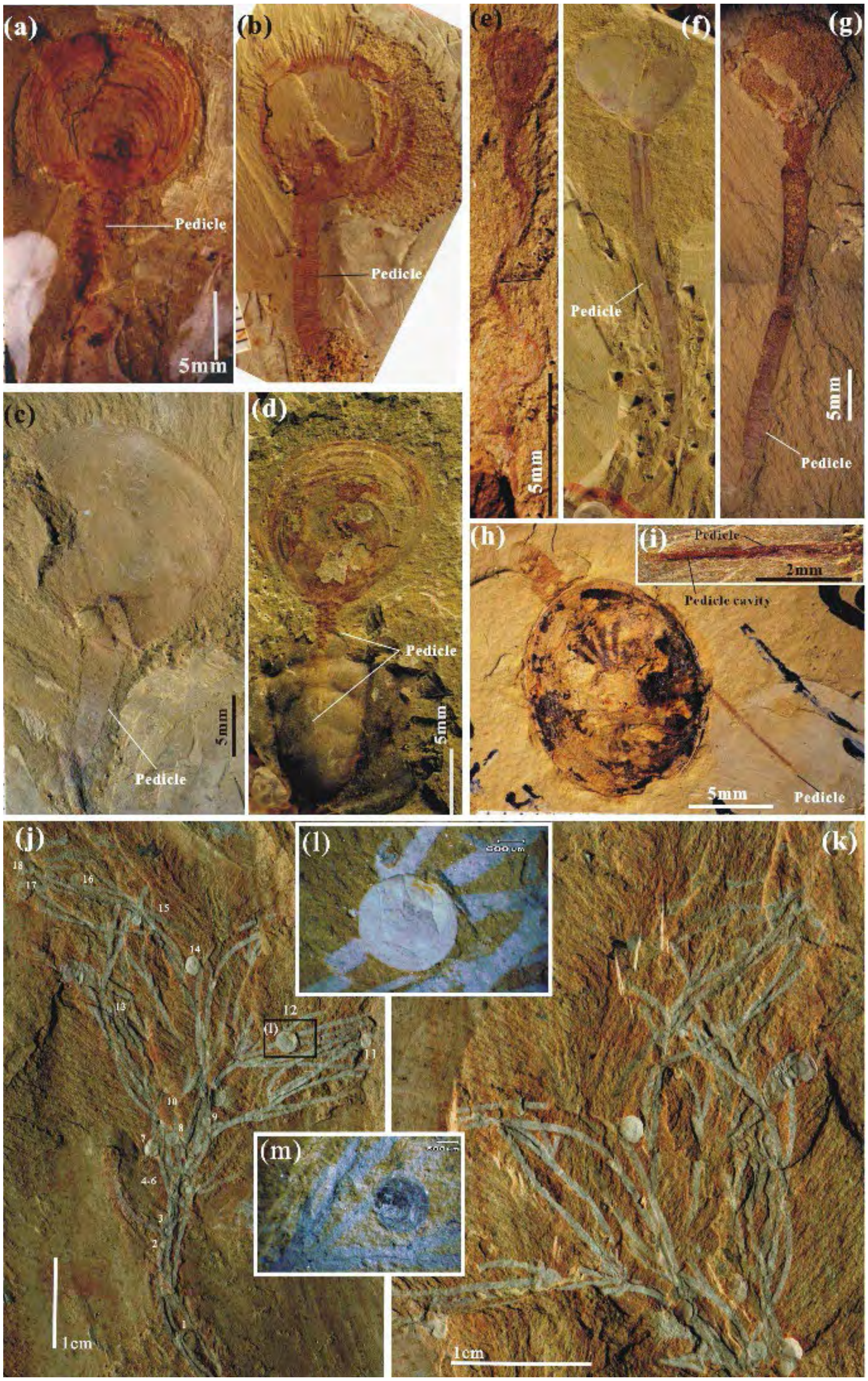

Figure 1. Different morphology of the pedicle attachment structures in the Cambrian brachiopods from the Chengjiang fauna (Cambrian Stage 3) of eastern Yunnan, China. (a-d) Secondary tiering brachiopods bearing massive pedicle with their end attached onto biotic exoskeletons. (a) *Kutorgina chengjiangensis*. (b) *Xianshanella haikouensis*. (c) *Longtancunella chengjiangensi*s. (d) *Alisin*a sp. (e-h) primary tiering brachiopods bearing slim pedicles ended by a bulb-like structure buried into soft sediments. (e) *Lingulellotreta malongensis*. (f) *Eoglossa chengjiangensis*. (g) unpublished material of *Yuganotheca elegans*. (h) *Diandongia pista* preserved with thin pedicle (lower right) and attached by a pedicle of *Longtancunella* (upper left). (i) Detailed view of the pedicle of h to show the pedicle lumen in *Diandongia pista*. (j-m) Median-high tiering pediculate attached acrotretoid *Kuangshanotreta mulongensis*, attached onto graplite-like pterobranch brachches. (j-k) part and counterpart, general views of *Malongitubus kuangshanensis* attached by acrotretid brachiopods from the upper part of the Yu'anshan Formation. (l-m) details of the attached brachiopods. (modified from Zhang and Holmer, 2013).

Brachiopods with soft parts from the Early Cambrian Wulongqing Formation (Series 2, Stage 4) of Yunnan, Southern China

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Similar to brachiopods from the Chengjiang biota (Zhang et al., 2008; Zhang & Holmer. 20,3), the brachiopods with soft tissue preservation from the Wulongqing Formation are strongly crushed and compressed parallel to the bedding plane (Hu et al., 2013; Zhang et al., 2011). The fine preservation of soft parts in the brachiopods comprises setal fringes, variable imprints of the lophophore, mantle canals and pedicles (Hu et al., 2010, 2013). These younger records from the Wulongqing Formation have the ability to give us a much more complete picture of brachiopod evolution and functional morphology and ecology during the Early Cambrian.

Despite great similarities to the Chengjiang fauna, in terms of preservation, the Guanshan biota exhibits a dramatic change in faunal composition, with taxa at the genus and species level distinct from their precursor representatives of the Chengjiang fauna (Zhang & Holmer, 2013). The Chengjiang brachiopod assemblage consists of ten documented species, tentatively assigned to ten families within seven superfamilies and seven orders (Zhang & Holmer, 2013); it is dominated numerically by the fossils of *Lingulellotreta* (Lingulellotretidae), *Heliomedusa* (Mickwitziidae) and *Diandongia* (Botsfordiidae). By contrast, the brachiopod assemblage in the Epoch 4 Guanshan fauna is composed of at least eight identifiable species, unambiguously assigned to nine genera (Table 1). The Guanshan fauna and Chengjiang biota share no common taxa at species level. The Guanshan (Stage 4) brachiopods are numerically dominated by abundant eobolids (rather than the lingulellotretid *Lingulellotreta malongensis*), Neobolids, and some small-sized acrotheloid and acrotretoid brachiopods. The occurrence of *Nisusia* sp. in Stage 4 represents the FAD of the superfamily Nisusioidea in the Cambrian of eastern Yunnan. *Diandongia pista*, the most

Subphylum	Class	Order	Superfamily	Family	Genera/species
LINGULIFORMEA	LINGULATA	Lingulida	Linguloidea	Obolidae	*Palaeobolus liantuoensis*
				Eoobolidae	*Eoobolus malongensis*
			Acrotheloidea	Acrothelidae	*Shijiangjunthele gubaiensis*
				Neobolidae	*Neoobolus wulongqingensis*
				Botsfordiidae	*Karathele wulongqingensis*
		?Siphonotretida	Siphonotretoidea	?Siphonotretidae	*Acanthotretella decaius*
		Acrotretida	Acrotretoidea	Acrotretidae	*Eohadrotreta* cf. *zhenbaensis*
RHYNCHONELLIFORMEA	KUTORGINATA	Kutorginida	Kutorginoidea	Kutorginidae	*Kutorgina sinensis*
				Nisusiidae	*Nisusia* sp.

Table 1 Taxonomy and diversity of brachiopods from the Guanshan Fauna (Cambrian, Stage 4) in the eastern Yunnan of South China, with dominant fossils in numbers of taxa marked by yellowish grids.

common component of the brachiopod assemblages in Stage 3, have disappeared and have been suddenly replaced by abundant Neobolids (*Neoobolus wulongqingensis* sp. nov.) and acrothelids (*Shijiangjunthele gubaiensis*) in the Guanshan biota (Stage 4) of eastern Yunnan, China.

In conclusion, the brachiopod assemblage from the Guanshan biota represents a complete genus- and species- level turnover of the Chengjiang brachiopods in the soft muddy-substrate seafloor during the temporal interval of Cambrian Epoch 3-4 transition. This turnover coincides with the trilobite (*Palaeolenus-Megapalaeolenus*) assemblage replacement events (Luo et al., 2008), suggesting that the brachiopod faunal assemblages were affected by the same factors that affected mobile trilobites.

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Earliest ontogeny of Early Cambrian acrotretoid brachiopods — first evidence for metamorphosis and its implications

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Well-preserved juvenile shells of the earliest Cambrian acrotretoid brachiopods *Eohadrotreta zhenbaensis* and *Eohadrotreta*? *zhujiahensis* (Cambrian Series 2, Shuijingtuo Formation, Three Gorges area, South China), give new insights into early acrotretoid ontogeny with implications for elucidating the poorly understood early phylogeny of linguliform brachiopods. The acrotretoid larval body plan included a bivalved shell secreted at the beginning of the pelagic stage, as well as two pairs of dorsal setal sacs and a straight anterior–posterior gut alignment (Zhang et al., 2018a). These characters are also shared with both Early Cambrian mickwitziids (Balthasar, 2004), paterinates (Williams et al., 1988) and lingulates (Ushatinskaya, 2016) as well as some later rhynchonelliforms (orthoideans and gonambonitoideans) (Popov et al., 2007; Bassett & Popov, 2017). This suggests that the acrotretoid type of ontogeny most likely is plesiomorphic for the Brachiopoda and probably was a character of stem group brachiopods. The acrotretoids were characterised by an indirect development, quite unlike recent lingulates, and heterochronic modifications clearly played an important role in the evolution of linguliform brachiopods (Fig. 1).

A more comprehensive understanding of the applied terminology based on new observation, especially in the definition of the major growth stages (embryo, planktotrophic larva, post-metamorphically sessile juvenile and adult), is established. The so-called acrotretoid "larval shell" of both valves of *Eohadrotreta* demonstrates evidence for metamorphosis (shedding of the larval setae and transitions of shell secretion), during the planktotrophic stage. Therefore, it is here termed the metamorphic shell (Bassett & Popov, 2017; Zhang et al., 2017, 2018a, b). The inferred early acrotretoid larval body plan included a bivalved protegulum, secreted at the beginning of the pelagic stage, which later developed two pairs of larval dorsal setal sacs and anterior–posterior alignment of the gut during metamorphosis.

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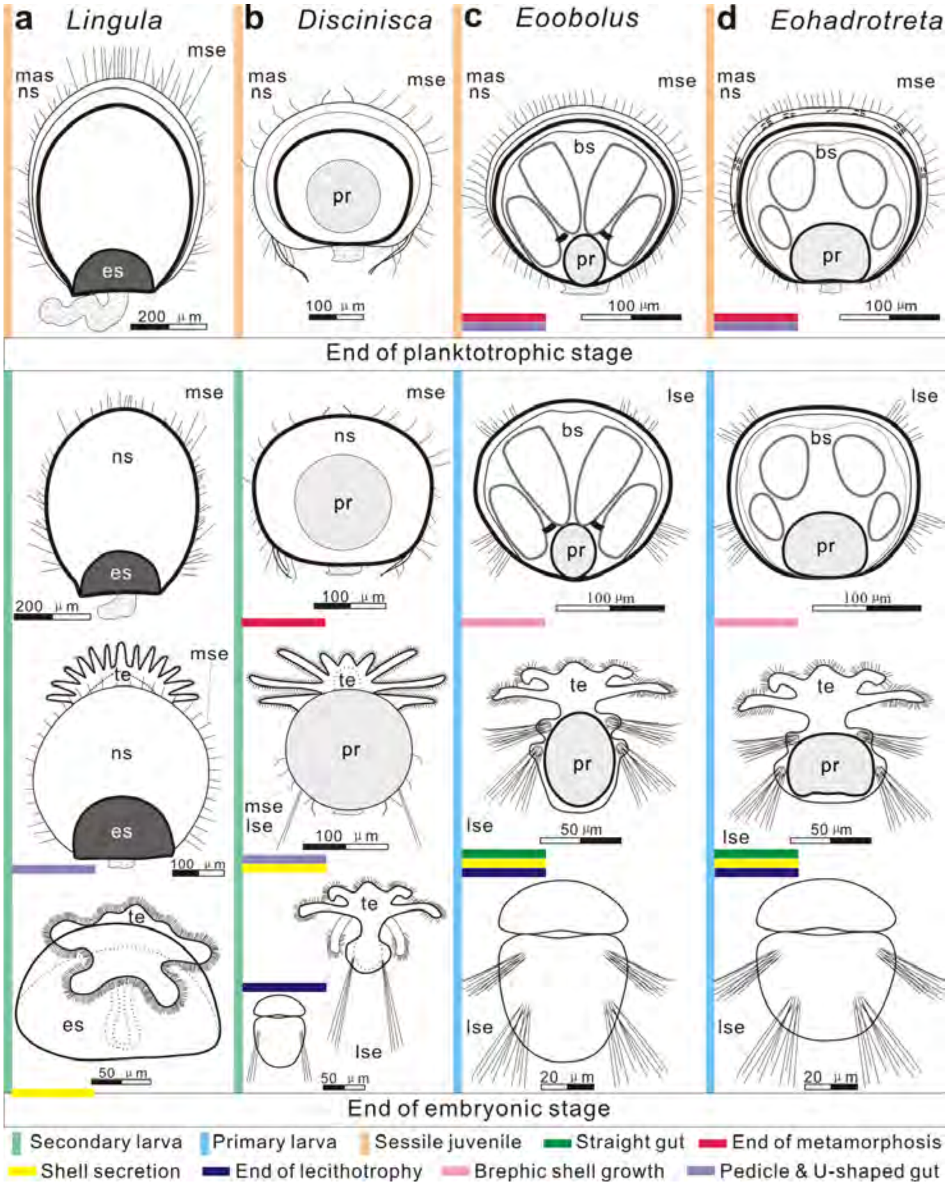

Fig. 1. Life cycles, including earliest ontogenetic development stages, in different lingulate brachiopods. a extant *Lingula*, showing life cycle of secondary larva. b extant *Discinisca*, showing life cycle of secondary larva. c Early Cambrian *Eoobolus*, showing life cycle of primary larva with the completion of metamorphosis after settlement. d Early Cambrian *Eohadrotreta*, showing life cycle of primary larva with the completion of metamorphosis after settlement (modified from Yatsu, 1902; Chuang, 1977; Nielsen, 1991; Williams et al., 1998; Balthasar 2009). Abbreviations: bs, brephic shell; lse, larval setae; mas, mature shell; mse, marginal mantle setae; ns, neanic shell; pr, protegulum; te, tentacle

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Population analysis of the Silurian brachiopod *Atrypoidea foxi* Jones from Qujing, Yunnan Province

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For the same species, a group of fossil specimens confined within a certain geographical and lithological condition is considered as a population (Rong, 1986; Li, 1996). Structure and variation of the population can reveal some traits of environmental changes, and contains rich ecological information (Li, 1996).

In this study, a population analysis is conducted on a Silurian brachiopod species, *Atrypoidea foxi* Jones, to detect the ecological conditions of the population and to reveal variation in the species. The specimens were collected from the lower Kuanti Formation of Longwangmiao Village of Qujing city, Yunnan province, South China. The Kuanti Formation bears brachiopods with high abundance but low diversity, which is dominated by *Atrypoidea foxi* Jones. There are 381 conjoined valves of *Atrypoidea foxi* Jones that were collected from the same fossil bed and identified by a series of transverse sections for six specimens (Fig. 1). Most of the specimens are relatively intact with a thin shell wall. The good state of preservation suggests that the structure and ecological environment of the population of *Atrypoidea foxi* Jones can be evaluated.

There are several methods to analyze population structure, such as life tables, size-frequency histograms, survivorship analysis and regression analyses. In this study, we performed all methods except the life tables, which could be replaced by the survivorship analysis.

The changes in population mortality can be reflected in the size-frequency histogram. By curve fitting, three types of results can be recognized: 1) Positively skewed, which indicates that the population was dominated by small specimens or juveniles; 2) Bell-shaped, in which the population was dominated by medium-sized specimens, 3) Negatively skewed, in which the population was dominated by large-sized specimens. The size - frequency curve in this study fits a normal distribution and is slightly negatively skewed, which suggests that adult individuals are predominant in this population (Fig. 2A).

The survival curve can be used for detecting the mortality rate of all stages of the population, as the steeper the curve, the higher the death rate. Meanwhile, the flatter the curve, the lower the death rate. To understand the structure of the population of the *Atrypoidea foxi* further, we constructed a survival curve, showing that the curve is convex from small (young) to adult individuals and concave from adult to old age (Fig. 2B), which reveals that most individuals can develop to adults and even older, suggesting a suitable living environment.

The ontogeny of *Atrypoidea foxi* can be illustrated by regression analysis on body size. We performed the analysis, and the results show that some larger individuals tend to be wider, which indicates that the thickness of shell is not stable for them. Furthermore, we also found that when an individual becomes more convex rather than longer and wider (Fig. 2C), its sulcus grows deeper.

Considering the size of brachiopods as calculated by length, width, and thickness, the cubic root of body volume is suggested as an index to represent body size rather than traditional length or width alone. Based on a published study(Novack-Gottshall, 2008) and "density method," a new empirical formula $V=3/25*ATD*\pi$ is given to calculate body volume for atrypides (Fig. 2D).

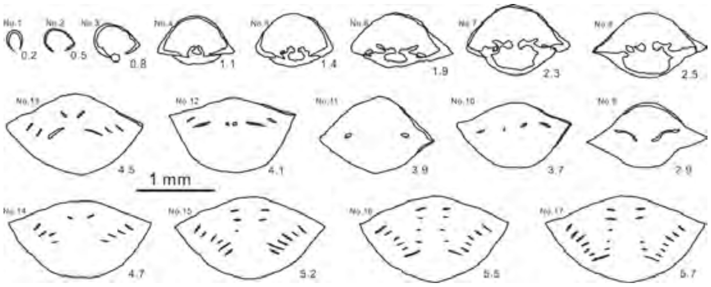

Fig. 1. Series of transverse sections of *Atrypoidea foxi* Jones. Numbers at bottom right of each section indicate distance (mm) from shell apex.

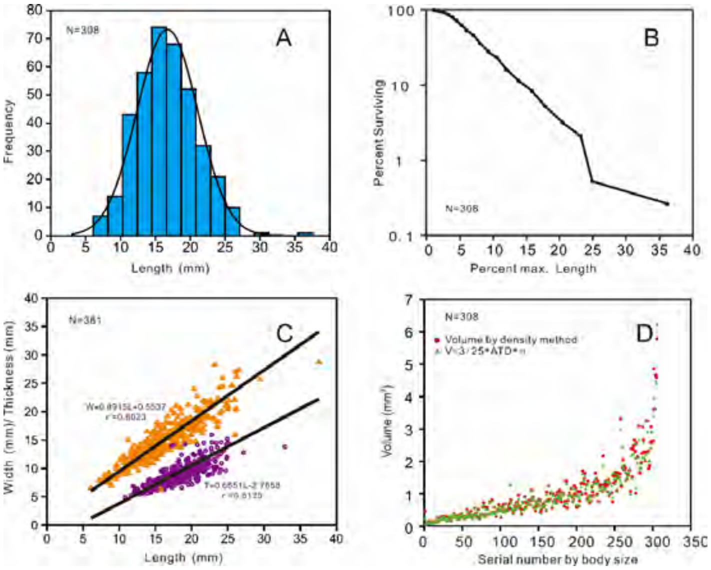

Fig. 2. A. Size-frequency distributions by length; B. Survivorship curves by length; C. Results of simple linear regression analysis of length/width and length/thickness(L-Length, W-Width, T-Thickness); D. Scatter plot of body volume by density method and the fitted function established by this study.

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Keynote lecture

Mechanisms of calcite fibre formation in *Magellania venosa*

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Modern rhynchonellide and terrebratulide brachiopods consist of up to three calcite layers, the seaward primary and the inner fibrous and columnar layers. These layers and the outermost entirely organic periostracum are secreted by the outer mantle epithelium (OME) of the animal. The fibrous layer is of particular interest as it forms a space filling three dimensional tessellate of calcite fibres separated from each other by organic membrane (e.g. Williams, 1966, 1968, Griesshaber, et al. 2007, Griesshaber et al. 2009). Nevertheless, despite several decades of research it is still unknown how OME cells transport the mineral from the body cavity to the site of fibre formation and how the characteristic shape of modern brachiopod fibres is accomplished. Understanding these mechanisms, is of major interest, as fossil brachiopod shells are major archives for geochemical proxies for the reconstruction of paleo-environment development. Transport of mineral across the OME may cause isotope and element fractionation, thus modifying the original environment related signature.

In order to trace calcite fibre shape formation, and to better understand mineral deposition and cellular transport pathways, we investigated the ultrastructure of the OME cells and their spatial relation to the growing calcite fibres in the recent rhynchonelliform brachiopod *Magellania venosa*. Transmission electron microscopy of chemically fixed and simultaneously decalcified samples were used to investigate ultrastructural characteristics within the outer mantle epithelium. A morphometric approach was used to obtain quantitative data on organelle volume fractions in various regions of the OME and, as a control, from regions of epithelial cells within the punctae, which do not secrete mineral. Of particular value were preparations where we first fixed the specimens with the mineral shell intact, either chemically or by high-pressure freezing and freeze-substitution. After block staining with OsO_4 and uranyl acetate and embedding the samples in resin, polished faces of mineral and epithelium were examined with field emission scanning electron microscopy (FESEM). This approach allows to visualize the spatial relation of epithelial cells with the proximal side of the shell that is subject to mineralisation.

Near the commissure, the OME consists of several cell layers (Figure 1A). The cells form long oblique extensions to the shell in direction to the commissure. These extensions are roundish in cross section, however, become thin and flat just before they touch the calcite fibres (Figure 1A). Some distance apart from the commissure of the shell, OME cells are present in a single layer (Figure 1B). Apical hemidesmosomes attach the OME to the organic membrane of the calcite fibres. At the single-celled region of the OME, large tonofilaments connect the apical hemidesmosomes with large basal ones that attach the cells to the basal lamina of the extracellular matrix (Figure 1B). We found that at least 50% of the interface between the OME and the shell is covered by organic membrane. At these sites, no mineral is secreted to the shell. Mineral deposition takes place only at sites where cells are not attached to an organic membrane. At these sites, we observe no strict one-by-one relation between calcite fibres and epithelial cells, revealing that more than one cell contributes to the formation of a calcite fibre at a given time, in contrast to studies of Williams and co-workers. On some occasions, we observed that in the single layered region cell thickness decreases tremendously at the sites of mineral secretion (Figure 1B).

Comparison of volume fractions of membrane bound cell organelles revealed differences for some but not all regions of the OME: 1) Near the commissure the volume fraction of vesicles, multi vesicular bodies and mitochondria are significantly higher than in the single layered regions. 2) When organelle-volume is normalised to epithelium area instead of cytoplasm-volume the value for lysosomes is significantly higher at the commissure as well. 3) Between secreting and non-secreting regions of the single layered OME and the epithelium of the punctae, values are not significantly different, except for the rough endoplasmic reticulum that is higher in non-secreting than in secreting regions, and for lysosomes that are significantly higher in the epithelium of the punctae.

FESEM analysis of the polished samples revealed that there is virtually no space between the OME and the calcite fibres (Figure 2). Etching of the sample at pH 8 gave no indication for an amorphous precursor phase.

Our results suggest that calcite fibre formation is under tight cellular control requiring communication and cooperation of neighbouring OME cells. The shape of the calcite fibres is generated by a sequence of spatially and temporally changing processes at the apical cell surface. This sequence involves local detachment from the organic membrane, secretion of mineral at the detached sites, local secretion of new organic membranes, attachment of cells to the newly formed membrane and intermission of mineral secretion at the attached sites.

The analysis of the ultrastructure of the OME and volume fractions of organelles do not give a clear indication for mineral transport by organelles. The very narrow space between the epithelium and the calcite fibres and the reduction in cell thickness at sites of mineral secretion suggests that cells secrete calcium and carbonate ions via transport mechanisms in the cell membrane rather than secretion of a mineral phase by organelles.

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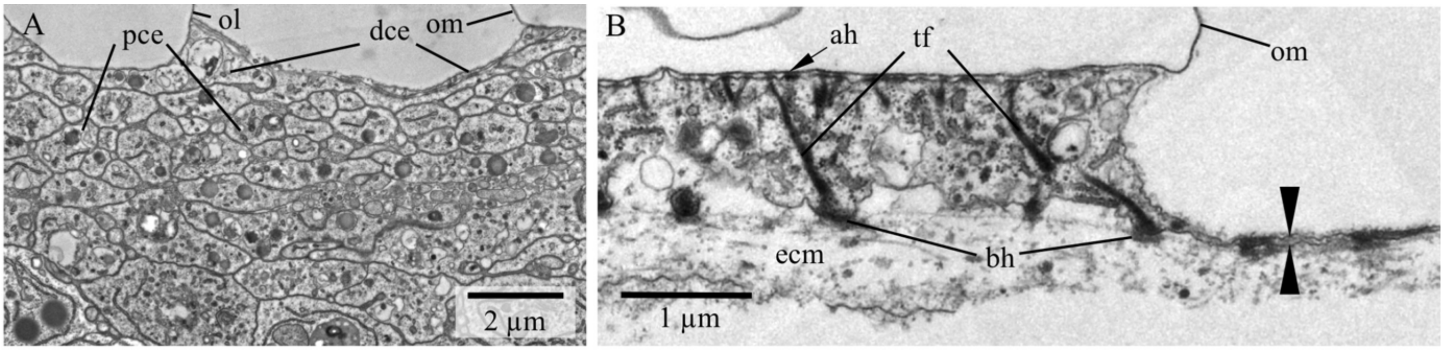

Figure 1. TEM micrographs of chemically fixed and decalcified shell samples. (A) Structure of the outer mantle epithelium near the commissure showing flat distal (dce) and roundish proximal cell extensions (pce) in cross section; ol, organic membrane of calcite fibre. (B) Outer mantle epithelium at some distance of the commissure. The apical cell membrane attach to the organic membrane of the calcite fibres by apical hemidesmosomes (ah) connected to basal ones (bh) by tonofilaments (tf). Regions without an organic membrane contain no tonofilaments and the cells are sometimes very thin; ecm, extracellular matrix.

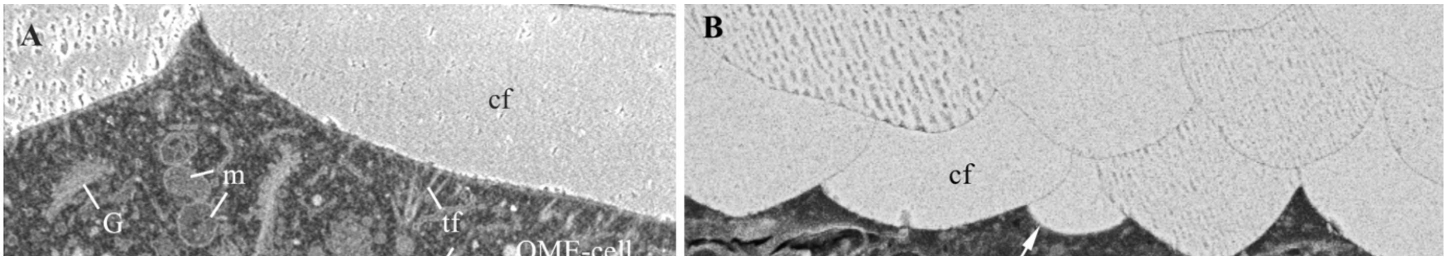

Figure 2. FE-SEM micrographs of polished faces of a chemically fixed (A) and a high-pressure frozen and freeze-substituted shell (B). A) Calcite fibres (cf) are closely attached to the outer mantle epithelium (OME). At their basal side the cells are connected to the basal lamina of the extracellular matrix (emc). Golgi stacks (G) mitochondria (m) and tonofilaments (tf) are visible. B) at sites of mineral secretion (arrow) the OME is in immediate vicinity to the calcite fibre as well.

Index

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