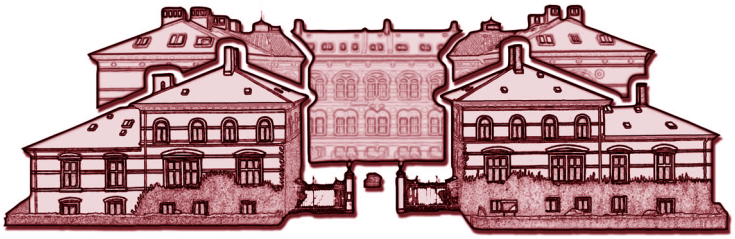

Fifth International Brachiopod Congress: Copenhagen 2005

Abstracts

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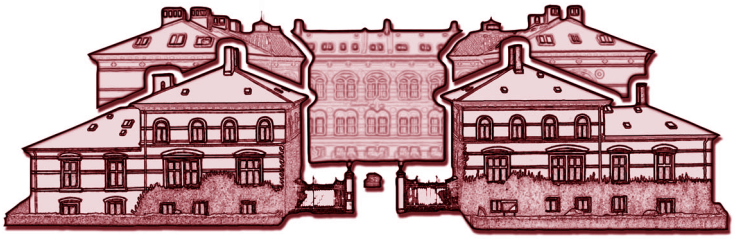

Geological Museum, Natural History Museum of Denmark, University of Copenhagen

Welcome to the 5th International Brachiopod Congress in Copenhagen. This is the first time that the congress has been held in Scandinavia. We hope you enjoy, not only the conference, but also the environs of the lively city of Copenhagen with its many attractions.

At the time of writing almost 120 delegates have registered for the conference and we expect more will register onsite. Delegates are from many parts of the world including Argentina, Australia, Bulgaria, Belgium, Brazil, Canada, China, Czech Republic, Denmark, Estonia, France, Germany, Great Britain, Hungary, Iran, Ireland, Italy, Japan, New Zealand, Netherlands, Norway, Poland, Russia, Serbia and Montenegro, Slovenia, Spain, Sweden and the USA.

During the four days of technical sessions much new data will be communicated in some 55 oral presentations and through over 50 posters, reflecting the diversity and healthy state of brachiopod research in 2005. Over 100 delegates will participate in the mid-conference excursion to the classic localities at Stevns Klint and Fakse Quarry, in the wake of the pre-conference excursion to Gotland and prior to the post-conference excursions to Estonia and Jutland.

Despite the large number of talks we have avoided parallel sessions. All the lectures will be held in the auditorium of the Geological Museum. Posters will be displayed in the ground-floor exhibition area of the west wing of the museum. We are very grateful to the following organizations for financial support: The Carlsberg Foundation, the Palaeontological Association, the Systematics Association, IGCP 503 and the Natural History Museum of Denmark (Geological Museum), University of Copenhagen. We are very grateful to the staff at the Geological Museum for their enthusiasm and generous help. In particular Annemarie Brantsen is thanked for her work with the abstract book and Anne Haastrup Hansen for the congress web pages and cover design. Students associated with both the museum and the Geological Institute are thanked for significant contributions to the organization of the conference.

We wish you an enjoyable and rewarding stay in Wonderful Copenhagen!

David Harper
Copenhagen, June 2005

TALKS

Brachiopod Faunas in the Permian Succession of the Alborz Mountains (North Iran)

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The Permian brachiopod faunas of the Alborz Mountains (North Iran) record biotic evolution during an interval of crucial geodynamic change, the rifting and drifting of the Iranian block from Gondwana to collide with the Asian margin at the beginning of the Late Triassic. Widespread and usually well preserved throughout the entire Permian succession, the North Iranian brachiopod faunas show some puzzling biostratigraphic anomalies, particularly in the Lower Permian. The lowest brachiopod assemblage from the Geirud Formation, Member D, comprises a *Juresaniini* close to *Bathymonia* and species of the genera *Cimmeriella* and *Trigonotreta*. Considered as Early Permian in age, according to Fantini Sestini (1966), this assemblage is associated with small Viséan foraminiferans.

Higher in the succession, the Dorud Formation comprises species of the genera *Neochonetes (Nongtaia)*, *Juresania*, *Linoproductus*, *Magniplicatina*, *Orthothetina*, *Kotlaia* and *Cartorhium,* suggesting Artinskian-Kungurian ages, in agreement with palynological data. Fusulinids however suggest older ages (Asselian - early Sakmarian).

Brachiopods are scattered in the overlying Ruteh Limestone and include species of the genera *Neochonetes* (*Nongtaia*), *Reticulatia*, *Marginifera*, *Spinomarginifera*, ?*Otariella*, *Paraplicatifera*, *Ogbinia*, *Haydenella*, *Linoproductus*, *Magniplicatina*, *Vediproductus*, *Orthothetina*, *Meekella*, *Kotlaia*, *Wellerella*, *Cleiothyridina*, *Callispirina*, *Whitspakia*, *Dielasma* and *Notothyris* which suggest a Wordian-Capitanian age, in agreement with foraminiferans occurring in the same beds.

The uppermost Permian faunas of the Nesen Formation are closely comparable to the Wuchiapingian-Changhsingian assemblages of the Djulfa region and South China, recording biotic events before the P/T mass extinction.

Fantini Sestini N. 1966. The geology of the Upper Djadjerud and Lar Valleys (North Iran). Brachiopods from Geirud Formation, Member D (Lower Permian). *Riv. It. Paleont. Strat.*, 72: 9-50.

Permian Chonetoidea and Spiriferoidea of Australasia: Gondwanan Relationships, Provincialism, Palaeobiogeography

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Members of the Spiriferoidea are dominant in the Permian marine invertebrate faunas of Australia. Genera can be endemic to a particular province, demonstrate a wider Gondwanan and peri-Gondwanan distribution and several indicate a bipolar distribution. Australasian spiriferoids are included within the families Spiriferidae, Neospiriferidae, Trigonotretidae and the Spiriferellidae. Several genera and species are the largest spirferoids ever recorded. Few genera are shared between the Westralian and Austrazean provinces but a higher proportion of genera are shared between the Westralian province and the Cimmerian Realm.

Representatives of the Chonetoidea are a less common but significant element of the faunas. They were used over 20 years ago to define the Westralian and Austrazean provinces of Australasia

– concepts that are in widespread use today. The Paratinan and Cimmerian provinces were also defined at that time despite difficulties in their definition. Through more recent studies the Cimmerian Province has been upgraded to a Realm while the Paratinan Province is more clearly defined for the earliest Permian, based on the chonetoids of Patagonia and western and eastern central Argentina.

Distribution of the various genera is best explained by an interplay of factors including surface and deeper oceanic currents, marine water temperatures and tectonic events such as the clockwise rotation of Gondwanan and the dispersal of the peri-Gondwanan Cimmerian terranes. Austrazean faunas developed in isolation under the influence of cooler and cold waters during the early Permian. Late Permian faunas demonstrated more widespread linkages.

The Micromorph Cave-Dwelling Rhynchonelloid *Tethyrhynchia mediterranea* Found in Bathyal Plio-Pleistocene Sediments of Rhodes, Greece

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Tethyrhynchia mediterranea was first described in 1994 from the nether reaches of long submarine caves in ca. 30 m. water depth near Marseilles, France. At the backs of the caves, environmental conditions resemble those of bathyal and deeper water, being dark, cool, still and oligotrophic. The brachiopods were found with a community of sponges so far only known from bathyal settings. Later, *T. mediterranea* has been found in caves in Croatia. It was therefore expected to find the species also in the deeper waters of the Mediterranean Sea. This has not happened so far.

T. mediterranea is not uncommon in the bathyal clay of the Plio-Pleistocene Lindos Bay Clay of Rhodes. Owing to the steep, tectonically controlled topography, much shallow-water fauna is found in the bathyal clay, having been transported out from nearshore environments. It is therefore a question as to whether *T. mediterranea* lived on bathyal mud floors, or was transported out from nearshore cave habitats, comparable to Recent material.

Micromorphic Brachiopods from the Early Carboniferous of South China

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Detrital limestone lenses within argillaceous limestones of the Muhua Formation (Middle–Upper Tournaisian) at the Muhua section, South China, yield numerous, typically silicified fossils. Chemical processing of hundreds of kilograms of detrital limestone samples revealed about 60 brachiopod species from the interval. This fauna is subsequent to biotic crises that occurred at the Devonian–Carboniferous boundary (Hangenberg Event). It provides insights into the process of community and taxonomic diversity recovery following such a crisis. Generally, rediversification is characterized by the appearance of specialized forms and the subsequent return of normally functioning biocoenoses. Typical examples of the process are micromorphic brachiopods from Muhua (four micro-articulates) which could inhabit distinct ecological niches, e.g. cryptic or crinoidal meadow habitats.

Productida are represented by the aulostegoid strophalosiidine *Muhuarina haeretica* Balinski & Sun, 2005. This species is characterized by a minute, slightly bilobed shell, spinose ventral valve, and a prominent subperiferal ridge internally. *M. haeretica* appears to be the oldest representative of the highly diverse, predominantly Permian, Cooperinidae.

Rhynchonellida are represented by *Lambdarina* sp. and a new genus. The strongly bilobed, minute shell of *Lambdarina* sp. possesses a very high, protruding ventral umbo. The yet undescribed genus exhibits identically shaped ventral umbo, but not a bilobed shell. Most probably the species

represents an unknown group of micro-rhynchonellidoids with a possible relationship to the Lambdarinidae.

Micromorphic Spiriferida are represented by the bizarre verneuliid *Changshunella yangi* Sun *et al*., 2004, which is distinguished by its minute shell reaching 2.6–4 mm in length, hemipyramidal ventral valve, and very prominent opposite radial plications.

Palaeoecological Responses of Benthic Associations to Relative Sea-Level Variations: Lower Devonian of the Massif Armoricain, France

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Sedimentological and palaeoecological analyses have been carried out to establish the impact of relative sea-level variations on fossil associations, in a platform depositional context. Three Lower Emsian sections have been selected in the Massif Armoricain. The approach consists of applying sequence stratigraphy and palaeontological studies simultaneously. Several sedimentary facies have been recognized in relation to the distance from the shoreline. The sedimentary succession consists of the stacking of genetic sequences related to sea level changes. Nine faunal associations, identified by means of multivariate analyses, are recurrent in similar facies along the sections. These are the *Adolfia*, *Stenorhynchia*, Chonetids, Crinoids-Brachiopods, Crinoids-Ostracods, Ostracods, Ostracods-Tentaculitids, Bryozoans and Dacryoconarids associations. Coupled palaeontological and sedimentological studies are efficient tools to understand association dynamics. The result of multivariate analyses, based on faunal content, is in good accordance with clustering based on the sequence analysis. Association replacements are closely related to relative sea level variations and are characterized by changes in their palaeoecological structures.

Sierra de Almeida Zorritas Formation, Northern Chile: Devonian Brachiopods

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Niemeyer's new collection from the Zorritas Formation is clearly of Eifelian-Givetian age based on the new evidence provided here. Palaeoecologically, a relatively nearshore, outer benthic assemblage 2, subtidal position is indicated. Biogeographically, the Zorritas fauna is extra-Malvinokaffric Realm in character, because of the abundant *Tropidoleptus* and a non-Malvinokaffric form of *Pacificocoelia*, although close to that realm as indicated by the Malvinokaffric Realm taxa *Pleurochonetes* cf. *P. sorucoi* and *Metaplasia* cf. *M. pseudoumbonata*.

A Review of Devonian Rhynchonellid and Spiriferid Brachiopods from Iran and Surrounding Areas, Useful for Biostratigraphy and Correlation

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The author reviews the Devonian rhynchonellid and spiriferid genera and species, from the Emsian to uppermost Famennian (Strunian), recognized on the northern border of Gondwanaland, mainly

in Iran and surrounding areas (Armenia, Turkey, Afghanistan, NW Pakistan...). The well described and illustrated selected taxa, useful for biostratigraphy and correlation, are analyzed. The selected genera are cited below in alphabetic order, followed by a number indicating their age *sensu lato*. Rhynchonellids: *Araratella* Abramian, Plodowski & Sartenaer (6)*, *Centrorhynchus* Sartenaer (5-6 ?), *Coeloterorhynchus S*artenaer (4), *Cupularostrum S*artenaer (3), *Cyphoterorhynchus S*artenaer (4), G*astrodetoechia* Sartenaer (5), *Kransia* Westbroek (3), *Ladogilina* Lyaschenko (4), *Leptocaryorhynchus* Sartenaer (5), *Megalopterorhynchus* Sartenaer (5), *Saurogastroderhynchus* Sartenaer (5), *Ripidiorhynchus* Sartenaer (4), *Trigonirhynchia* Cooper (1-2). Spiriferids**:** *Alatiformia* Struve (1-2), *Arduspirifer* Mittmeyer (1-2), *Cyrtospirifer* Nalivkin in Frederiks (4-5), *Diazoma* Dürkoop (4), *Dichospirifer* Brice (5), *Dmitria* Sidyachenko (5), *Eeleutherokomma* Crickmay (2-4), *Eobrachythyris* Brice (5-6), *Persianospirifer* Zaman (2-3), *Prospira* Maxwell (6), *Rigauxia* Brice (4-5), *Spinocyrtia* Frederiks (2-3), *Sulcatospirifer* Maxwell (5), *Subcuspidella* Mittmeyer (1), *Sphenospira* Cooper (6), *Syringospira* Kindle (6), *Uchtospirifer* Lyachenko (4).

* (1) = Emsian, (2) = Eifelian, (3) = Givetian, (4) = Frasnian, (5) = Famennian, (6) = Strunian.

Evolutionary and Biostratigraphic Significance of Early Cambrian Brachiopod Assemblages from South Australia

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Detailed sampling of key Lower Cambrian successions in eastern South Australia (Stuart Shelf, Flinders Ranges and Yorke Peninsula) combined with investigation of previously unstudied shelly fossil collections belonging to the late Brian Daily has revealed a plethora of exquisitely preserved, previously undocumented, organophosphatic and calciate brachiopods from this region. These new assemblages provide, 1.) new clues concerning the early evolution of the phylum and, 2.) new data for a preliminary biostratigraphic "biozonation" for the Lower Cambrian of South Australia based on brachiopods.

The accepted views on the early evolution of brachiopods are currently in a state of flux. Recent studies have shown that the Laurentian taxon *Mickwitzia* shares characters with both lingulate brachiopods and the problematic sclerites of the South Australian tannuolinid taxon *Micrina* (setigerous tubules). SEM examination of the ultrastructure of the cryptotretid genus *Askepasma* from the Wilkawillina Limestone shows the presence of similar setigerous tubules strongly suggesting that cryptotretids may also belong to the stem group lineage of the phylum Brachiopoda.

Whilst much work needs to be completed, four distinct brachiopod biozone assemblages can be recognized in the Lower Cambrian succession of South Australia. The oldest assemblage, dominated by the cryptotretid *Askepasma*, is broadly equivalent with the *Abadiella huoi* trilobite zone (upper Atdabanian) and best represented in the Flinders Ranges, but also occurs in the Stansbury Basin and on the Stuart Shelf. The succeeding assemblage, best defined in the Stansbury Basin, is early Botomian in age and characterized by *Eoobolus*, *Minlatonia*, *Eodicellomus* and *Kyrshabaktella*. This is followed by a mid-late Botomian assemblage with *Eoobolus*, *Karathele* and *Curdus*. The youngest (Toyonian) assemblage best represented in the Wirrealpa Limestone is characterized by the first acrotretid (*Vandalotreta*) in the South Australian sequence, along with *Karathele* and the calciate taxon "*Obolella" wirrialpensis*.

Podichnus centrifugalis Bromley & Surlyk, 1973 Revisited: Attachment Scars of Brachiopods

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The original description of the trace fossil *Podichnus centrifugalis* was based on Recent and Cretaceous material; it was previously unsuspected that the ability to etch carbonate substrates was widespread within the pedicle-bearing brachiopods. Subsequently, the trace fossil has been found back to the Silurian. Thus, through time, many different groups of brachiopods have produced this etching trace. The morphology of the trace fossil has remained remarkably constant throughout this time and the single ichnospecies adequately covers the structural range of the trace fossils. Nevertheless, it is hoped that minor variants may allow the work of different groups of brachiopods to be distinguished. Trace fossils produced by forms having a divided pedicle versus a massive one, and forms having a massive pedicle armed with short, as opposed to long, attachment papillae, are distinguishable. But fossilized pedicles are rare, and the precise identity of the different tracemakers remains unknown.

The reason for this complicated etching activity is not understood. Certainly it secures the attachment of the animal to its substrate very effectively. However, pediculate brachiopods are not restricted to carbonate substrates, and the etching activity is precluded on noncarbonate substrates. Nevertheless, brachiopods attach tenaciously to noncarbonate substrates by means that have not been investigated.

Influence of Brachiopod Taxonomy on Taphonomic Bias in the Fossil Record

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Silicification is the replacement of original shell material with silica, generally with biogenic opal and chalcedony precursors. Early diagenetic silicification is dependent on concurrent carbonate dissolution and silica precipitation in specific geochemical environments. It is well known that there are taxonomic differences in brachiopods in terms of mineralogy, shell ultrastructure, and presence, abundance, and location of organic material (particularly the presence of organic material in the caecae). Other factors also play a role in differential silicification, including environment of deposition, the general reactivity of sediment (carbonate vs. siliciclastic), the lifestyle of organisms, whether infaunal or epifaunal and attached or sessile, mineralogy, including variations in carbonate geochemistry, and secular variations in ocean geochemistry. Anecdotal evidence of preferential silicification by taxonomic group is common, but quantitative analyses are rare. The Yale Peabody Museum has material collected over the last two hundred years, which includes a geographically and taxonomically diverse collection of brachiopods, many of which are bulk rock specimens. Taphonomic analysis of silicified and non-silicified brachiopods, by observation, acid digestion, thin section analysis, and comparison with established diversity values, show that silicification is often mediated by taxonomic affinity as well as by other factors.

Tree Balance, Clade Size Distribution, and Extinction Selectivity in Palaeozoic Terebratulide Brachiopods

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How does extinction affect our understanding of relationships among extant taxa? What is the best method to use to evaluate the impact of extinction on phylogenetic patterns? Neontologists, utilizing

information on character distribution among extant taxa, investigate patterns of tree balance, under particular models of diversification, to estimate the "hidden" effects of extinction. Palaeontologists can test these hypothesized effects directly, with character-state and temporal information from the fossil record. Because the Terebratulida survived (and thrived following) a series of mass extinction episodes over its 400-million-year history, it serves as an informative empirical example for exploring the use of phylogenetic hypotheses in investigating extinction dynamics. I assembled a list of 84 morphological characters, examined 24 Palaeozoic and Triassic terebratulide genera (as familial exemplars, using the classification in Lee *et al*., in press), and investigated their relationships in a series of time-stratified phylogenetic analyses, using PAUP 4.0b10. Thirteen atrypide, athyridide, and rhynchonellide genera were used as outgroups; retzioid athyridides appear to be most closely related to terebratulides. Tree balance indices increase following extinction episodes, confirming the prediction that topologies become more imbalanced (pectinate). However, these indices alone cannot adequately capture different patterns of extinction that result in identical post-extinction topologies, therefore I devised a simple measure of clade size distribution to evaluate the phylogenetic signature of extinction. Together with patterns of specific character loss from extinction, the evaluation of tree balance and clade size distribution appears to provide a promising, multi-pronged approach to the study of extinction dynamics.

Brachiopod Faunas across the Palaeozoic-Mesozoic Transition: The Lost World

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The end-Permian mass extinction not only caused the largest crash in brachiopod biodiversity since their origin in the Early Cambrian, but also redirected dramatically the course of brachiopod evolution. As a consequence of the event, Brachiopoda lost their dominance in Mesozoic and later marine benthic communities. A total of 420 species in 143 genera within 50 families and 102 species in 43 genera of 27 families have been reported, respectively, from the strata below and above the end-Permian mass extinction horizon worldwide. The surviving brachiopods were mainly Productida, followed by Spiriferida. Widespread, broadly adapted and small-sized taxa preferentially survived. Frequent intrageneric speciation of widely adapted generalists enabled surviviors to occupy rapidly and efficiently vacant ecospace after the disaster. The true Mesozoic-type brachiopods (32 species from 20 genera and 12 families) have been reported in eight regions worldwide. The Early Triassic recovery of brachiopods is characterized by widespread brachiopod dispersal, multiprovincialism and the presence of rare Lazarus genera at that time. Taxonomic selectivity of the recovery brachiopod faunas favoured the rhynchonellides. The re-population of post-extinction brachiopods varies geographically: there is a preference for regions either previously barren of latest Permian taxa and/or with rare latest Permian and surviving brachiopods. A dramatic reduction in brachiopod diversity at the end-Permian extinction is followed by several stepwise declines in diversity in the survival interval, which was followed by a slow re-population of new lineages dominated by progenitor taxa.

Intense Biotic Interactions during the Permian-Triassic Transition: A Link between Predation/Parasitism and Mass Extinction

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Brachiopod faunas were dominant constituents of benthic communities in Palaeozoic oceans; they

underwent, however, a rapid decline in diversity during the Permian-Triassic (P/T) transition and since then lost their dominance in the Mesozoic and later marine communities. The ultimate cause for the demise of most major groups of the Brachiopoda remains controversial. This study evaluates the roles predation and parasitism in the evolution and extinction of brachiopods during the P/T transition in South China. We have extracted abundant silicified fossils from the pre-extinction Changhsingian strata in South China. Of these, possible polychaete worms are extremely abundant and attach onto shells of brachiopods (for example, *Orthothetina*, *Spinomarginifera*, and *Permophricodothyris*) and various sponge species. These were drilling predators because some specimens record the driller "in the act". Many additional drillholes are also found on various brachiopod taxa, and they are produced by a small, snail-like, predatory gastropods based on the co-occurrences of gastropods and the bored taxa, together with the superficial similarity between brachiopod borings and holes generated by modern gastropods. Predation is an important agent in natural selection and has been regarded as an important driving force of biotic evolution. Accordingly, the predatory evidence indicates that intense interactions between predators (worms and gastropods) and prey (brachiopods) may have played an important role triggering the end-Permian mass extinction. Similarly the predatory or parasitic behavior of snail-like gastropods has been also documented from the Early Triassic bivalves (*Pteria* and *Claraia*) suggesting this factor was partly accountable for the long-delayed recovery of biota following the end-Permian mass extinction.

Living Craniids: Molecular Evidence for Their Inter-Relationships

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The evolutionary relationships and morpho-taxonomy of extant craniids are uncertain because of a paucity of clear-cut morphological characters. We will report phylogenetic reconstructions based on both slow- and fast-evolving, mitochondrial and nuclear gene sequences from a wide geographic sample of craniids including *Novocrania*-like forms from the N. Atlantic, E. and W. Mediterranean, Caribbean, NE. Pacific, Japan, Taiwan, SE. Pacific, New Zealand and Antarctica, as well as *Neoancistrocrania*-like forms from Japan and the Norfolk Ridge (S.W. Pacific). The results shed new light on craniid taxonomy, inter-relationships, and biogeography.

Morphological and shell-structural comparisons of the same specimens are also being made, and will be reported separately (Long, Saito & Cohen, work in progress).

Strong Molecular Evidence for the Monophyly of Phoronids and Brachiopods

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We have determined about 2,000 bp of sequence from the nuclear-encoded large ribosomal RNA subunit gene (23S-rDNA or LSU) of two phoronids and two members of each of the principal brachiopod lineages, excluding only thecideidines. When added to existing SSU rDNA gene sequences, the data give very strongly supported phylogenetic reconstructions (Cohen & Weydmann, *Organisms, Diversity & Evolution*, in press) in which:

1. (phoronids + brachiopods) are monophyletic,

2. (phoronids (craniids (discinids + lingulids))) are monophyletic,
3. rhynchonellates are monophyletic,
4. (phoronids (craniids (discinids + lingulids))) and rhynchonellates are sister-groups
5. (discinids + lingulids) are monophyletic,
6. craniids and (discinids + lingulids) are sister-groups,
7. (terebratulidines + terebratellidines) are monophyletic,
8. rhynchonellides and (terebratulidines + terebratellidines) are sister-groups,
9. craniids and discinids are relatively slow-evolving,
10. regression analysis of rate-smoothed branch-lengths against palaeontological divergence-time estimates gives a linear correlation ($r^2 = 0.92$) and, by extrapolation, puts the ancestral divergence between (brachiopods + phoronids) and chitons at ~680 Ma and the divergence between Rhynchonelliformea and Linguliformea (including phoronids) at ~570 Ma.

Palaeoenvironmental Reconstructions Based on Oxygen Isotope Ratios from Brachiopod Shells

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The shells of fossil brachiopods have been extensively used for stable oxygen isotope ratio determinations to provide oceanic palaeotemperature proxies. However, it is only comparatively recently that the extent to which the oxygen isotope ratios of brachiopod shells accurately reflect that of the surrounding seawater has been investigated in a comprehensive range of extant taxa. The results of these studies (for example Parkinson *et al*., *Chemical Geology*, in press) revealed that certain parts of the brachiopod shell do indeed provide an accurate reflection of oxygen isotope ratios in the surrounding seawater, but that other areas of the shells displayed pronounced disequilibrium or 'vital effects' that would distort any palaeotemperature interpretation. Following on from this work, this project investigated the oxygen isotope ratios from the brachiopod *Moutonithyris* from the Lower Cretaceous Carstone Formation, a shallow-water, transgressional horizon that is widely distributed in southern England. Oxygen isotope determinations from the Carstone brachiopods, and from co-occurring nektonic belemnites, contribute towards our understanding of oceanic conditions during the Cretaceous 'Greenhouse World'. The implications, and constraints, of transforming oxygen isotope ratios into absolute temperatures will also be discussed.

Oxygen Isotope Composition, Magnesium Distribution and Crystallography of *Terebratulina retusa*

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Brachiopods have long been considered excellent environmental indicators since the assertion (Lowenstam, 1961) that their shells of low Mg-calcite are precipitated in isotopic equilibrium with seawater. The influence of biological processes (vital effects) on the recording of environmental information has caused some concern (Popp *et al*., 1986). However, studies reveal that, in general, the brachiopod secondary layer is in isotopic equilibrium with seawater and accurately records seawater temperature while the primary layer does not (e.g. Carpenter & Lohmann, 1995, Auclair *et al*., 2003, Parkinson *et al*., in press). Mg-Ca ratio as a temperature proxy has not been applied to any significant extent in brachiopods. This study presents a comparison of the oxygen isotope

composition with the Mg distribution in *T. retusa*. This work is presented in the context of detailed crystallography obtained from electron backscatter diffraction (EBSD) in order to understand the relationship between Mg-Ca ratios, ^{18}O and crystal growth.

Auclair, A-C., Joachimski, M.M., & Lécuyer, C. 2003. *Chemical Geology* **202,** 59-78.
Carpenter, S.J. & Lohmann, K.C. 1995. *Geochimica et Cosmochimica Acta*, **59**, 3749-3764.
Lowenstam, H.A. 1961. *The Journal of Geology* **69**, 241-260.
Parkinson, D., Curry, G.B., Cusack, M. and Fallick, A.E. (in press, *Chemical Geology*).
Popp, B.N., Anderson, T.F., & Sandberg, P.A. 1986. *Journal of Sedimentary Petrology* **56**, 715-727.

Taxonomic Versus Phylogenetic Estimates of Extinction Severity in Palaeozoic Terebratulide Brachiopod Genera

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What can phylogenetic analysis contribute to studies of extinction dynamics that taxon counting alone cannot? At the end-Permian, terebratulide brachiopod genera suffer 100% generic extinction, yet some lineages clearly survived because this clade is extant. Taxonomic ranges alone provide little information concerning lineage survival. Phylogenetic analysis can provide estimates of lineage survivorship by identifying post-boundary taxa that form sister-taxon relationships to pre-boundary taxa. I demonstrate this by performing phylogenetic analyses on all 35 Early Devonian terebratulide genera, and comparing extinction severity in terebratulide lineages to extinction severity measured by generic LAD's at Early Devonian stage boundaries.

Using a list of 55 morphological characters, phylogenetic analyses were performed using PAUP 4.0b10. Twenty atrypide, athyridide, and rhynchonellide genera were used as outgroups. Taxonomically, three of 10 Lochkovian terebratulide genera (30%) survive into the Pragian stage, and six of 11 Pragian terebratulide genera (55%) survive into the Emsian stage. However, phylogenetic analysis suggests that in addition to the three surviving Lochkovian genera, two additional lineages may have given rise to Pragian genera, (50 % lineage survival). In addition to the six surviving Pragian genera, 10 lineages may have given rise to Emsian genera (85% lineage survival). At both stage boundaries, taxon counting methods substantially overestimate extinction severity. Phylogenetic analyses involving the remaining Devonian terebratulide genera will compare taxonomic and lineage extinction estimates for the remaining Devonian stage boundaries to test the generality of this phenomenon.

The Transition from Planktotrophy to Lecithotrophy in Larvae of Lower Palaeozoic Brachiopods

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Extant brachiopods have a life cycle with larval (pelagic) and juvenile-adult (benthic) stages. These larvae are either planktotrophic or lecithotrophic. Planktotrophic larvae grow prior to settlement, generating a relatively large mantle that the protegulum forms on following settlement. This is the basis for using protegular size for inferring larval feeding in fossil brachiopods. Larvae are an important stage that has to be considered in thinking about the life history of brachiopods because this is the dispersal mechanism for these sessile animals. At the time that the revised edition of the treatise began to appear (2000), it was recognized that during the Lower Palaeozoic all of the classes in the Linguliformea had planktotrophic larvae, and it was thought that none of the genera in the Cranii-

formea and Rhynchonelliformea had planktotrophic larvae. Subsequent work (Freeman and Lundelius, 1999, Lethaia 32:197) has shown that members of the Craniopsida and Craniida had planktotrophic larvae during the Lower Palaeozoic and that the transition from planktotrophy to lecithotrophy began in different lineages of the Craniida during the Jurassic. Our recent work has shown that planktotrophic larvae were a feature of the Obolellata, Strophomenata and the Protorthida and Orthida in the Rhynchonellata during the Lower Palaeozoic. Lecithotrophy is first detected in the Rhynchonellida, Atrypida and Athyrida near the Ordovician-Silurian boundary. A planktotrophic larva was clearly an integral part of the ancestral brachiopod life cycle.

Preliminary Analysis of Soluble Organic Matrix in Some Recent Terebratulid Brachiopoda

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To build up their shell, brachiopods secrete a mixture of proteins and polysaccharides, collectively called the shell organic matrix. This matrix mediates the calcification process by allowing crystal nucleation and elongation and by finally stopping crystal growth. This matrix also controls the different shell microstructures found in brachiopods. This work represents a first attempt to characterize some matrices extracted from different terebratulid brachiopods in two combined manners: a) using the scanning electron microscopy to localize the matrices within the shell; b) at the molecular level, for evidencing their biochemical properties.

Terebratulid shells are observed according to a standard procedure highlighting the microstructural details. For the second aspect, the acetic acid-soluble shell matrices are extracted and analyzed by SDS-PAGE. Gels are subsequently stained with silver, PAS, Alcian Blue and with carbocyanine. In addition, the shell matrices are tested for their ability to bind ^{45}Ca. Finally, functional *in vitro* tests are performed to check the effect of some of the shell matrices on the precipitation of calcite. Preliminary results show that all the tested matrices are extremely minor components of the shell and that different genera exhibit similar electrophoretical patterns. Furthermore, some matrices modify the morphology of calcite *in vitro.* Putative similarities between brachiopod and molluscan shell matrices are discussed, as well as the "early diagenesis effect" that may affect brachiopod matrices.

Old World Middle Devonian Brachiopod Palaeobiogeography

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Two investigations were carried out. The first was to analyze the affinities of the Middle Devonian fauna of the Łysogóry Region (Northern Holy Cross Mountains, Poland; 119 taxa) together with coeval assemblages was executed at the species level. The aim of the second was to study the palaeobiogeography of Old World Middle Devonian brachiopods; relationships between pairs of eleven coeval faunas were therefore investigated at the genus level.

The palaeobiogeographical analysis of the studied fauna is based on 77 species (42 described under open nomenclature are excluded). Of these, 34 could not be proven to occur outside the studied region; they may therefore represent endemic taxa. The strongest faunal affinities of the Łysogóry region are with those of the Eifel Mountains (32 species in common, 9 of them occurring only in those two regions) and with Moravia (respectively 10, 2). The studied region shows also notable affinities

with the Rhenish Slate Mountains (east side of the Rhein; 9, 0), Spain (7, 1) and Burma (7, 0).

The analysis of the distribution of 237 genera of Middle Devonian Brachiopods within 11 regions of the Old World Province (Łysogóry, Kielce, Eifel, Rhenish Slate Mountains, Ardennes, Spain, Moravia, Bohemia, Urals, Siberia, Burma) indicates the existence of a strongly-linked cluster Łysogóry-Eifel (Moravia), the very strong isolation of Bohemia (Hercynian-type faunas) and a well-defined Siberia (cold climatic zone). The position of six other regions is not so clear, in particular the loosely-linked cluster of Ardennes-Burma and of Spain that appears in different places in different analyses. The distribution of Middle Devonian Brachiopods was controlled by facies and climate; migrations within the equatorial zone were rather extensive (Burma), though impeded by facies (Kielce).

Brachiopod Fauna in the Lower Part of the Ordovician (Caradoc) Arnestad Formation in the Oslo Region, Norway

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Brachiopods from two sections representing the lower part of the Caradoc Arnestad Formation in the Oslo-Asker district, southeastern Norway, have been sampled in order to document the changes prior to the immigration of Scoto-Appalachian taxa into the Oslo Region.

Based on the occurrence of the species *Onniella bancrofti* and the presence of thin K-bentonite beds referred to the Idaverian Grefsen K-bentonite complex, this part of the formation appears to correlate with the Idavere Substage, Lower Haljala Stage. Apparently the main immigration took place during the deposition of the Upper Haljala Stage and the succeeding Keila Stage.

With the facies change from the limestone dominated Vollen Formation to the shaly Arnestad Formation, the *Onniella-Chonetoidea / Sericoidea* association, here represented by *Onniella bancrofti* and *Chonetoidea alpha*, became established for the first time in the Oslo Region. This marked the first step towards a less endemic brachiopod fauna and took place at about the same time as in the Swedish part of the Baltoscandian Sea. The association succeeded one including the subgenus *Leangella* (*Leptestiina*). The outer shelf environment suggested by both associations is supported by sedimentological and fossil evidence.

The Otta Brachiopod Fauna: Palaeogeography of Early Palaeozoic Terranes and Biotas across Baltoscandia

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The diverse, early Ordovician shelly fauna from Otta, in the central Scandinavian Caledonides, has prompted much debate regarding the development and palaeogeography of key parts of the Scandinavian Caledonides. During the last 35 years, the Scandinavian Caledonides have yielded a further range of variably-preserved fossils from platform, margin and oceanic environments: for example, early Ordovician brachiopod faunas from the Lower Allochthon in Valdres, with Baltic affinities, contrast with the Celtic and Toquima Head biotas from parts of the Upper Allochthon. The early Ordovician faunas thus demonstrate a range of provincial signatures and the relationship between these and the coeval faunas of the parautochthon and autochthon provide an alternative palaeogeographic model for the developing orogen. New data from Otta and multivariate statistical analyses of the Iapetus brachiopod assemblages confirm the intraoceanic position of the Otta archipelago. Shelly faunas from the allochthons have little in common with coeval assemblages from Siberia; the

latter are of low diversity and dominated by plectorthoid and porambonitoid brachiopods, within carbonate facies, similar to those of continental Laurentia. Rather the faunas of the higher Upper Allochthon may be accommodated within the Laurentian marginal Toquima-Table Head province. These, together with the Otta fauna, demonstrate that the provincial signatures of the Upper Allochthon assemblages are consistent with settings within the Iapetus Ocean associated with one or more microcontinents, seaward of Baltica.

Hirnantian Brachiopod Faunas in Baltoscandia

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The latest Ordovician *Hirnantia* fauna was widely distributed in the pericratonic Baltic Basin of the Baltic palaeocontinent. It is preserved in separate areas of Norway and Sweden and characterizes the carbonate rocks across the East Baltic (western Latvia and Lithuania, southern Estonia and northern Poland) exposed in numerous drill core sections. In the East Baltic, the first characteristic brachiopods appear within the chitinozoan *Spinachitina taugourdeaui* Zone correlated with the lower half of the graptolite *Normalograptus extraordinarius* Zone (the lowermost Porkuni Stage). This new fauna replaces the low diversity fauna in the red and grey coloured rocks of the central East Baltic. At the same time, patch stromatoporoid-coral reefs developed in onshore environments. A fall in sea level during the chitinozoan *Conochitina scabra* Zone (= upper *extraordinarius* Zone) restricted the extent of the basin and the earlier onshore belts became land. The shallow-water environmental conditions in the central part of the basin now favoured the distribution of the *Hirnantia* fauna in the East Baltic. The most diverse *Hirnantia* brachiopod fauna characterizes the lower *scabra* Zone. This interval also displays the maximum excursions in isotopic data.

The coquinas of brachiopods, commonly of monospecific taxa (e.g. *Dalmanella testudinaria*, *Plectothyrella*, strophomenids), dominate benthic associations in carbonate rocks with organodetrital and marl interlayers. *D. testudinaria* is a common species occurring in deep-water onshore facies and the lingulate *Trematis norvegica* represents the youngest brachiopod of the *Hirnantia* fauna. The faunal succession suggests a continuous lowering of sea level, which resulted in the extinction of the *Hirnantia* fauna in the Baltoscandia region before the *persculptus* Zone.

Palaeobiology of Silurian Leptaenine Brachiopods (Strophomenida) of Gotland, Sweden

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Leptaenine brachiopods are widespread from the late Ordovician to the early Carboniferous. On Gotland they are very common throughout the late Llandovery-Ludlow succession. Five species are recognized, one of which is new. *Lepidoleptaena poulseni* and *Leptaena rhomboidalis* retained a large, functional apical pedicle throughout ontogeny and both had strong adductor muscles and robust ornamentation, allowing them to occupy an ecological niche uncommon for leptaenines (shallow-water, high energy environments). A muscle scar after a pedicle-shortening muscle is present within the pedicle tube of *Leptaena rhomboidalis*. *Leptaena sperion*, *L. depressa visbyensis* and *L. depressa lata* lived in low energy environments, but retained a very slender pedicle, while *L. depressa depressa* and *L. parvorugata* atrophied the pedicle in very early ontogeny and then lived ambitopically in deeper water. The presence or absence of a functional apical pedicle strongly influenced the morphology

of the cardinal process lobes. All leptaenines had a small angle of gape, and the lophophore was probably simple, similar to those in productides and *Leptaenoidea*. The inner epithelium on the trail of leptaenines remained directly exposed to the sea when the valves were closed and probably was important in gas exchange. The life position of pedically attached species was generally with the disc vertical, and some ambitopic specimens may have retained a similar attitude. Shells of *Leptaena depressa depressa* and *Lepidoleptaena poulseni* are commonly heavily encrusted by epibionts. Repaired shell damage to the disc is rare, but is often evident along the commissure.

Organophosphatic Stem Group Brachiopods – Implications for the Phylogeny of the Subphylum Linguliformea

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The recognition of organophosphatic stem group brachiopods has important implications for the understanding of brachiopod phylogeny. These stem groups fall outside any of the formal taxonomic units within the two currently recognized classes of the Subphylum Linguliformea - the Lingulata and Paterinata. However, their organophosphatic shell, evidence of penetrative setae, and the exceptional preservation of a lophophore demonstrates that they are linked phylogenetically with the linguliforms. The proposed Early Cambrian stem-group brachiopods include the vermiform, organophosphatic, sclerite-bearing tannuolinids and the more brachiopod-like *Mickwitzia* and *Heliomedusa*. A "columnar fabric" (*sensu lato*), which was previously considered as a derived feature of acrotretides, is known also from the tannuolinid *Micrina* and from *Mickwitzia*, thus indicating that this type of shell structure may be a plesiomorphic character; it was retained in acrotretides and some lingulids, like the Lingulellotretidae and the Curticiidae. The shells of *Mickwitzia* and *Heliomedusa* also have thicker cylindrical tubes, which were clearly open to the exterior surface and can be inferred to have contained setal structures penetrating the shell. Similar perforations are present in the tannuolinid *Micrina*. A similar function can be inferred both for shell perforations in some recently discovered paterinids as well as in early siphonotretides. However, the siphonotretides lack columnar shell structure. A columnar shell structure has also been identified in the enigmatic Ordovician linguliform brachiopod *Bistramia*.

Constraint in the Evolution of Development in the History of the Thecideide Brachiopod Clade

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Combining morphological phylogenetic analysis with stable isotope sclerochronology and morphometrics in the analysis of fossil and recent thecideide brachiopod species reveals contrasting morphologies with similar constraints in different thecideide subclades. Phylogenetic analysis in this case is sensitive to taxon sampling density; including more than one species per genus increased the resolution of the two major sub-clades that include living species (one that includes *Thecidellina*, the other *Lacazella*). Oxygen stable isotopic analysis of serially-sampled fossil and recent thecidede individuals demonstrates that thecideides grow for one to five years only. Placed into a phylogenetic context, these data support the hypothesis that thecideides owe their small (<15mm) size to a single evolutionary event early in or prior to their origin. Adult thecideide lophophores are configured as trocholophes, schizolophes, or ptycholophes. Ptycholophes, which are multi-lobed, occur in phylo-

genetically basal (and stratigraphically early) thecideides as well as within the *Lacazella* clade, and ptycholophes are constructed using three distinct developmental modes. Despite phylogenetic and developmental differences among thecideide species, morphometric analysis of the brachidial outline of >500 individuals shows that there is a consistent, linear relationship between lobe number and lophophore length. Further, there is a maximum lophophore size of approximately 20 mm for schizolophe individuals, which constrains the body size of monoseptate species, including all members of the *Thecidellina* clade.

Although relationships within the thecideide clade are well resolved, the question of thecideide origins remains. This nagging question may be addressed by additional morphological and shell microstructural analyses of possible ancestors, and by using supertrees.

A Brachiopod Biozonation in the Lower Devonian of the Rhenish Slate Mountains

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The Ardenno-Rhenish Mountains are the type region of the traditional Lower Devonian stages "Gedinnian", "Siegenian", and "Emsian" developed in "Rhenish" siliciclastic facies. A further subdivision into regional substages is also present. The stage and substage subdivisions follow litho- and biostratigraphic criteria. Due to the lack of pelagic index fossils, biostratigraphy is predominantly based on brachiopods, but up to now no formal brachiopod biozonation has been established.

As a result of extensive taxonomic revisions, a new brachiopod biozonation beginning in the Pridolian and ending in the Eifelian is proposed. This biozonation consists of 21 total-range zones with spiriferid species and subspecies as zonal fossils. Corresponding to these spiriferid zones, "faunal intervals" with typical brachiopod assemblages are defined.

Materials from museum collections have been studied supplemented by personal collections. Almost 100 taxa are presently revised, some new genera and species have been recognized, and the stratigraphic ranges of relevant index fossils have been clarified.

With some restrictions, the biozonation or parts of it may also be recognized in other regions, e.g., in the Harz Mts. (Germany), the Holy Cross Mts. (Poland), the Ardennes (Belgium), S England, the Armorican Massif (NW France), the Cantabrian Mts. (N Spain), the Celtiberian Chains (NE Spain), the Anti-Atlas Mts. (S Morocco), and the Ougarta Chains (Algeria).

Brachiopod Community Evolution during the Multiple Late Ordovician Mass Extinction Events on Anticosti Island, Eastern Canada

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Multivariate analyses of the rich, diverse brachiopod fauna of the Hirnantian (Late Ordovician) Ellis Bay Formation reveal four shelly associations. The *Onniella* Association represents a stable brachiopod community that commonly recurs throughout the Anticosti Hirnantian carbonate succession. The dominants, *Onniella* and *Hebertella*, were holdover cosmopolitans perhaps tolerant to fluctuating water depth and/or temperature. The other three associations with short stratigraphic ranges were marked by opportunistic benthic invaders. The *Plaesiomys* Association (basal Grindstone Member) shows rapidly evolving species of typical late Caradoc to mid-Ashgill genera, e.g. *Barbarorthis* and *Vellamo*. The dominance of large, thick- shelled *Plaesiomys* suggests a warmer, early Hirnantian interglacial episode. In the overlying Velleda Member, the *Parastrophinella* Association shows species

whose genera either made their first appearance, or first became abundant, in the early Hirnantian (e.g. *Mendacella uberis*, *Parastrophinella reversa*, *Hindella umbonata*); most experienced declines during the late Hirnantian with some, except *Hindella*, surviving into the Early Silurian. The *Orthorhynchyllion-Gnamptorhynchos* Association in the sandy Prinsta Member is dominated by exotic species (e.g. *Hirnantia* sp.), associated with aulacerid biostromes. Early to mid-Hirnantian high diversity was maintained by frequent invading opportunists. Declining immigrations led to a drop in shelly diversity in the higher Lousy Cove and uppermost reefal Laframboise members (late Hirnantian).

An Agglutinated Brachiopod-Like Fossil from the Lower Cambrian of China

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Fossil and living brachiopods are known as having either phosphatic or calcareous shells. Their origin has been a great puzzle, but phoronid-like "worms" and slug-like halkieriids have been suggested as possible ancestors. Here we introduce a new agglutinated brachiopod-like fossil from the Chengjiang Lagerstätte of the Early Cambrian in Yunnan, South China. The animal consists of a lingulid-type pedicle, conical tube and cuppy aperture of ventral valve, and cap-shaped dorsal valve. Internally, it contains a horseshoe-shaped lophophore, median rod-shaped projection and pinnate mantle canal systems. The shell of the ventral conical part is composed of calcareous lamina filled with coarse silt grains while the ventral apertural part and the dorsal valve are constructed with calcareous agglutinated silt grains. Phylogenetic analysis indicates that it may represent a stem group of brachiopods related to the hypothetic phoronid-like ancestor. It is further supported by the phoronids and relevant fossils from the Chengjiang Lagerstätte. This find suggests that early steps in the brachiopod lineage may have been more morphologically diverse than previously assumed.

Life Style of Early Cambrian Brachiopods on Mud Substrate

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Brachiopods were the most abundant benthic macrofauna of the Palaeozoic, thus the Early Cambrian substrate colonization by brachiopods marked a major breakthrough. However, the origin and adaptation of early brachiopods have remained matters for speculation because of the lack of critical ecological features in the fossil record. Here we report a diverse array of lifestyles demonstrated by exceptionally well-preserved brachiopods from the Lower Cambrian in Yunnan, China. Lingulids bore a long pedicle similar to their extended counterpart and probably burrowed into the substrate. The newly discovered agglutinated brachiopod, *Wangyuina*, lived with conical umbo implanted on the soft bottom coupled with lingulid-type pedicle anchorage. The earliest craniiform, *Heliomedusa*, is interpreted as free-lying. A paterinid genus is characterized by a very robust pedicle that could be able to adjust the animal's position to changing levels of sediment. The acrotheloid *Diandongia* was anchored by a long thread-like pedicle in the muddy substrate. With a thick pedicle, the obolellid *Longtancunella* was capable of attaching to shell debris and the anterior shell margin of living *Diandongia* and remained suspended through its life or clustered together on dermal sclerites of active *Microdictyon* or lobopodians. These brachiopods illustrate that the fundamental ecological strategies of attachment and suspension-feeding around the sediment-water interface had been already well established by brachiopods. They also indicate that major stocks of Early Cambrian brachiopods were characterized by distinct attachment models.

Famennian Brachiopoda of the Geirud Formation from Damghan (Eastern Alborz - Iran)

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The Geirud Formation is widely developed in the Damghan region. Lithologically it is mostly composed of limestone, marly limestone, shale and quartzitic sandstone and its thickness ranges from 30- 70 meters. The Famennian Brachiopoda of Geirud Formation in the northeast and north of Damghan region (Deh- Molla and Simeh-Kuh sections) were studied and the following taxa are recognized:
Schellwienella sp., *Mesoplica* sp., *Buxtonia* sp., *Schizophoria impressa*, *Leptaena* sp., *Aulacella interlineata*, *Zaigunrostrum iranicum*, *Araratella dichotomians assimulata*, *Araratella* sp., *Centrorhynchus charakensis*, *Megalopterorhynchus chanakchiensis*, *Paurogastroderhynchus nalivkini*, *Paurogastroderhynchus bikniensis*, *Cleiothyridina coloradensis*, *Athyris tau*, *Composita* cf. *globosa*, *Lamellosathyris* sp., *Cyrtospirifer sergunkovae*, *Cyrtospirifer* sp., *Cyrtiopsis graciosa chakhaensis*, *Cyrtiopsis lapparenti*, *Prospira struniana*, *Prospira lapparenti*, *Rigauxia cyrtinaeformis*, *Rigauxia crassiplicatus*, *Dichospirifer thylakistoides*, *Eobrachythyris* sp., *Toryniferella echinulata*, *Cryptonella* sp.

Based on the above mentioned Brachiopoda, an age of Late Famennian- Strunian can be determined for the Geirud Formation in these sections. Also, the Geirud Formation in these sections is equivalent to the upper part of Geirud Formation in the type section (central Alborz).

Holocene Terebratulid Brachiopods from the Southern Brazilian Shelf (South Atlantic): Ecology, Taphonomy, and Time-Averaging

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Terebratulid brachiopods are widely but patchily distributed across open habitats of the Southeast Brazilian Bight; a present-day, upwelling-influenced tropical shelf. Extensive sampling revealed dense brachiopod populations between 24° and 26°S. However, the brachiopod diversity is low: only four species representing four genera (*Bouchardia*, *Terebratulina*, *Argyrotheca*, and *Platidia*) were identified among >16,000 specimens. The most abundant occurrences coincide with shelf-break upwelling zones, where the colder, nutrient-rich South Atlantic Central Water is brought upward by cyclonic meanders of the South Brazil Current, a western boundary current. This is consistent with previous studies suggesting that upwelling may play a role in sustaining brachiopod-rich associations.

The brachiopod assemblages are dominated by empty shells with variable taphonomic signatures suggestive of age mixing. Time-averaging was assessed by amino acid dating calibrated against radiocarbon (r-square=0.933). Individually dated shells of *Bouchardia rosea* (n=90) varied in age from modern to 7725 years (standard deviation=2178yrs). Young shells dominated and older shells were increasingly less common. The dated shells vary in the quality of preservation, but there is no significant correlation between taphonomic condition and age. These results imply that fossil brachiopod shells may show considerable time-averaging, but their taphonomic condition need not be a reliable indicator of pre-burial history of individual shells or the scale of temporal mixing within the entire assemblage. The results are strikingly similar to those previously documented for molluscs and incongruent with the rapid destruction of brachiopod shells observed in taphonomic experiments,

suggesting that shells remain protected below (but perhaps near) the surface through their early taphonomic history.

A Pickled Biodiversity Hotspot – the Recent Brachiopod Collection of the Museum für Naturkunde, Berlin

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After more than 60 years since publication of Helmcke's catalogue of the brachiopod collection of the Zoological Museum in Berlin, recent funding allowed a databasing and profiling campaign resulting in a complete revision of the collection. The total number of accessible lots was increased from 1290 (Helmcke, 1939) to 2051 (dry and wet material). The collection houses primary types of 30 species, possibly including the syntypes of the enigmatic *Terebratula seminulum* Philippi. The history of the collection dates back to the 'Gesellschaft Naturforschender Freunde zu Berlin' (GNF), which was founded in 1773. Both the GNF and Humboldt University collections built the initial stock for the brachiopod collection of the Museum für Naturkunde. Several private collections of e.g. Philippi, Dunker, Monterosato and others where integrated over time, the most important of which being the collection (specimens, documentation and correspondence) of Friedrich Blochmann presented to the Museum in 1938. Integration of Blochmann's material made Berlin one of the biggest collections of Recent brachiopods at that time. During WWII, the scientific collections of the Museum were evacuated and survived. In 1948 the brachiopod collection was re-installed in the Museum, which then happened to be in the Soviet sector. Erection of the wall made it impossible for Helmcke to continue with his studies and the brachiopod collection remained untouched until its integration into the collection of marine invertebrates in 2001. The new research activity resulted in a first paper, an annotated type catalogue soon to be published in one of the Museum's journals.

New Observations on Species Referred to the Problematic Recent Platidiid Brachiopod Genus *Amphithyris* Thomson

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During our study of a new amphithyrid platidiid from Doubtful Sound, Fiordland, New Zealand, we found that existing descriptions of all three previously described species of *Amphithyris* were deficient because they lacked illustrations of dorsal valve internal morphology, which is crucial in platidiid taxonomy. The genus *Amphithyris* (type species, *A. buckmani*) was erected by Thomson (1918), based on a single specimen dredged from Cook Strait, New Zealand. Subsequently, two further species were referred to the genus, namely *A. hallettensis* Foster, 1974 from the Ross Sea, Antarctica and *A. richardsonae* Campbell and Fleming, 1981 from Long Sound, Fiordland. At the times of erecting the latter two species, the holotype of *A. buckmani* was missing and both morphological comparisons with the type species were made using "topotypic material" that had been collected and referred to *A. buckmani* at some later date. Although the authors of all three species made reference in their written descriptions to internal dorsal valve morphology, no illustrations were presented for either *A. hallettensis* or *A. richardsonae*, and the dorsal valve interior of *A. buckmani* (embedded in Canada balsam) was obscured by mantle and lophophore tissue. Attempts to separate the valves of the unique holotype of *A. richardsonae* proved unsuccessful but new SEM illustrations obtained by us of

the dorsal valve interiors of the holotype of *A. buckmani*, topotype *"A. buckmani"* and a previously unfigured paratype of *A. hallettensis* have prompted a revision of their taxonomic relationships with each other and with several previously undescribed platidiids from New Zealand and elsewhere.

New Observations on Loop Morphology and Systematic Revision of the Antarctic Eocene Brachiopods *"Laqueus" cockburnensis* and *Laquethiris curiosa*

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Although not as diverse as Australian and New Zealand faunas, the Cenozoic brachiopod faunas of the Antarctic Peninsula are important elements of the fossil marine biota of higher southern latitudes. Reinvestigation of the type collection of *"Laqueus" cockburnensis* from beds of Eocene age on Cockburn Island, Antarctic Peninsula, has revealed the existence of remnants of both lateral and mediovertical connecting bands on the dorsal median septum of the holotype which provide new evidence of an adult bilacunar loop, typical of representatives of the Family Kingenidae. Attention is drawn to the strong similarity of the reconstructed loop of *"Laqueus" cockburnensis* to the penultimate loop phase in the only known modern-day kingenid brachiopod *Ecnomiosa* Cooper. Comparison of the newly discovered septal structure in *"Laqueus" cockburnensis* with the published illustrations of *Laquethiris curiosa* Bitner, from the Eocene La Meseta Formation, Seymour Island, confirms a virtually identical septal complexity (and bilacunar loop) in the latter species, prompting the synonymizing of *"Laqueus" cockburnensis* with *Laquethiris curiosa* and the reassignment of the genus *Laquethiris* to the Subfamily Kingeninae Elliott, 1948.

Inferring Feeding Currents of Spire-Bearing Brachiopods: A Reappraisal

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Spire-bearers are a peculiar group of articulated brachiopods, which have suffered the effects of several mass extinction crises and have long attracted the attention of palaeontologists. Strictly speaking, they are currently classed into different rhynchonelliform orders from a phylogenetic / taxonomic viewpoint, yet they do share a number of special characteristics nonetheless. Relevant among those shared features stand out the possession of a spiral calcified brachidium, which has obviously supported a spirolophe when in life, and the development of a complementary median system of opposite fold and sulcus, that presumably may have served to efficiently separate currents carrying food in suspension from those evacuating filtered water. In contrast to living beings amenable to direct observation, dealing with extinct marine animals and making inferences about their vital functions pose a special challenge. A controversy (dating back to the early sixties) involves a couple of alternative models that sought to explain the most likely position of inhalant and exhalant currents, which may be somewhat simplistically called the Ager-Williams and the Rudwick-Schumann models, respectively. The question is considered afresh, broadly discussing available actualistic arguments and contributing a functional analysis resorting to the plankton net as a suitable paradigm for microorganism-collecting apparatus. Insight gained from such analysis leads to conclusions, with an original solution, which accounts for the prevailing conditions in each of the main orders considered, and is also compatible with evidence yielded by hydrodynamic experiments in flume-channels, and by studies of the spatial distribution of epizoic and/or parasitic organisms recognized in the palaeontological record.

Brachiopods in the Steep Slope of a Pennsylvanian Carbonate Platform (Sierra Del Cuera, Asturias, N Spain)

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The Sierra del Cuera outcrops (Cantabrian Mountains, N Spain) represent a cross-section of a Pennsylvanian carbonate platform characterized by a steep (up to 40º) depositional slope. The vertical orientation of bedding allows recognition of different stratal domains of the platform and estimation of the palaeowater depth along the slope. The brachiopods derive from the red-coloured, highly-cemented intervals (bryozoan-brachiopod biocementstones), which alternate with massive microbial boundstone units in the upper slope.

The studied brachiopod fauna was collected at a palaeodepth of 150-200 m and consists of at least 74 taxa, although open nomenclature was used for many identifications. Productida (really Productidina, 29 taxa) and Spiriferida (23 taxa) are the most abundant orders. Some productids have various morphological adaptations interpreted as allowing them to be attached to hard surfaces: trail reversed to form flanges or gutters (Institiferini n. gen. et n. sp., n. gen. close to *Limbifera, Admoskovia* sp.), trail extended anteriorly (*Kutorginella* cf. s*tepanovi, Alitaria*? sp., *Kozlowskia* sp. 1); moreover, among the productids there are 3 representatives (Dasyalosiinae gen. et sp. indet., *Plicatiferina* cf. *sinecosta, Rugicostella*? sp.) of the Strophalosiidina suborder, having their ventral valve attached to the substrate by cementation or creeping spines; the assemblages also contain one cemented Orthotetida (Areostrophiidae gen. et sp. indet.). These morphological characteristics are typical of reef brachiopods, especially those of British and Belgian Mississippian and of the Permian of Texas. The closest affinity of the Spanish fauna is with the coeval faunas of the Ellesmere Island (lower Hare Fiord Formation), with 24 genera in common.

Diversity, Origin and Affinity of the Tremadoc-Arenig Brachiopod Fauna of the Mediterranean Realm

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A compilation of new and existing brachiopod data from the Mediterranean Realm indicates that among rhynchonelliform brachiopods are both endemic genera (*Poramborthis, Jivinella, Kvania, Robertorthis, Apheoorthina, Protambonites)* and genera with more extensive occurrences (*Ranorthis, Nereidella, Nocturnellia, Orthambonites*). In general, the rhynchonelliform brachiopods show higher endemism and very local occurrence of particular species; a few evolutionary lineages of successive species may be recognized. Lingulate brachiopods indicate much lower endemism, with numerous genera common outside the Mediterranean Realm. This is evident from common occurrences of genera such as *Thysanotos, Mamatia, Dactylotreta, Numericoma, Elkania, Orbithele* etc. in other palaeocontinents and adjacent territories (Baltica, Kazakhstan). This remarkable disproportion of the brachiopod distribution can be explained by different reproductive strategies of both groups. Lecithotrophic rhynchonelliform larvae with short pelagic phase were unable to cross the oceanic barriers while planktotrophic larvae of lingulate brachiopods with long pelagic phases easily crossed the oceanic barriers.

Shell Mineralogy of Cambrian Linguloids from the *Obolus* Sandstone of Estonia and NW Russia

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Whole-pattern fitting of XRD patterns was applied in a study of shell mineralogy of the linguloid genera *Obolus, Ungula* and *Schmidtites* from 13 localities of Cambrian *Obolus* Sandstone in Estonia and NW Russia, with Recent *Lingula*, as comparative material. This study confirmed that apatite lattice parameters of Recent *Lingula* are within the range of *a*~9.38-9.40 Å and c~6.87-6.88 Å and revealed its crystallite dimensions: ~200×400 Å. Most of the Cambrian lingulate valves consist of apatite with lattice parameters a<9.37 Å and c~6.88 Å, with crystallite dimensions ~400×700 Å, close to those of sedimentary apatite. Two distinct series of apatite varieties can be distinguished in some valves: the first with lattice parameters a>9.37 Å (9.38 Å in average) and c~6.89 and crystallite dimensions 250×500 Å and the second with lattice parameters a<9.37 Å (often about 9.33 Å) and c~6.88Å and crystallite dimensions 850×1500 Å. We relate these two series to original shell biomineralization and early diagenetic precipitation, respectively. It is likely that both series have altered, but preserved their distinction through time. Parallel SEM-EDS studies (Puura and Uibopuu, this volume) revealing the *post-mortem* apatite and pyrite precipitation into the shell pore space corroborate this conclusion.

Statistical Study of the Devonian Cyrtospiriferid *Cyrtospirifer syringothyriformis* Paeckelmann, 1942, from the Highest Givetian?-Lower Frasnian of Northern France

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In this paper, *Cyrtospirifer syringothyriformis* Paeckelmann, 1942 from the highest Givetian? – Lower Frasnian of Boulonnais (North of France) has been studied in detail and re-defined based on very abundant material (several hundreds of specimens) collected in the type area. Many aspects have been examined:
€main external features of *C. syringothyriformis* have been treated by multivariate statistic analysis. This study reveals a great specific variability and allows separation of this species into four distinct morphological groups. Is it due to the variation of lithology and more generally environment or can it be attributed to the strong genetic potential of the species?
€internal characteristics of *C. syringothyriformis*, studied through transversal serial sections of about 30 specimens, are much more constant. Besides the typical characters of the genus (well-developed delthyrial plate and dental plates in the ventral valve, lamellar cardinal process in the dorsal valve), other main characteristics are remains of deltidial plates preserved in some specimens, cardinal process showing a concavity in its central part, presence of crural basis and absence of pseudoseptum (character given by Ma & Day, 2003 for some species of *Cyrtospirifer*),
€phylogenetic relationships between *C. syringothyriformis* and some other species of *Cyrtospirifer* from coeval strata and for which there are sufficient data have been examined by cladistic methods,
€other cladistic analysis have been made in order to check the homogeneity of genera placed by Carter *et al*. (1994) in the subfamily Cyrtospiriferinae.

Originations and Extinctions of Pennsylvanian Brachiopods from the Great Basin (USA): Response to Late Palaeozoic Palaeogeographic and Climatic Changes

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Originations and extinctions of brachiopod faunas have been reported within the Pennsylvanian, most likely in response to palaeogeographic and climatic changes during the Late Palaeozoic. Previous studies were mainly based on analyses of global databases and, therefore, little is known about how the palaeoenvironmental changes affect the faunas regionally. Using a newly compiled 30 Myr record of Pennsylvanian brachiopods species from the Great Basin (USA) the following matters are addressed: 1) examination of species-level origination and extinction patterns; 2) the importance of changing palaeogeography in brachiopod origination events; 3) causes of long-term extinction of brachiopod faunas.

The results show an extinction event at the Desmoinesian-Missourian boundary and three origination events: at the Mid-Carboniferous boundary, the Missourian-Virgilian boundary, and in the Desmoinesian. The extinction event at the end of the Desmoinesian is related to a warming episode. The appearance of new brachiopod faunas is most likely related to migration in response to new oceanic currents. The oceanic currents developed during the Pennsylvanian as a result of palaeogeographic changes that accompanied the formation of Pangea toward the end of the Palaeozoic. These extinctions and originations represent long-term biotic responses to climatic and palaeogeographic changes during the Pennsylvanian.

Taphonomy of Cambrian Linguloids: Implications for Geochemical Studies

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Chemico-structural studies of linguloid brachiopods by A. Williams *et al*. have revealed three structural types of the secondary layer of linguloid shell: columnar (e.g., acrotretoids and siphonotretoids), botryoidal (e.g., *Lingula*) and baculate (e.g., *Glottidia*, *Discinisca* and *Discina*).

The baculate structure of the Cambrian linguloids is characterized by alternation of compact and baculate laminae. Our SEM-EDS study of the genera *Obolus, Ungula* and *Schmidtites* from the uppermost Cambrian *Obolus* beds of Estonia and NW Russia revealed a large variety of chemico-structural situations resulting from different *post-mortem* geochemical scenarios. We conclude that compact laminae consisting of densely packed apatite crystals have been comparatively resistant to the *post-mortem* changes, although they can dissolve and recrystallize. In contrast, baculate laminae, consisting of needle-like crystals (*baculi*) and high levels of organic matter in protein and chitin fibres, are less resistant. Thus, the pore space available after the decay of organic tissues was filled by precipitated minerals. The presence of decaying organic matter could enhance the precipitation of apatite or pyrite.

The fossilization environments and available pore space, depending on initial shell structure of a particular taxon, appear to be the main factors that influence the composition of a fossil valve. Therefore, it would be essential for geochemical studies to consider the properties related to the shell structure of the analyzed taxa and the geochemical situations influencing the composition of fossil valves.

Brachiopod Pedicle Traces: Redefinition of *Podichnus centrifugalis* to Differentiate Three Types of Trace

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The rootlets or papillae of brachiopod pedicles attach the animal to the substrate, often dissolving calcareous substrates and, after death of the animal, leaving a pedicle trace or 'footprint'. This distinctive trace or trace fossil has been formally named *Podichnus centrifugalis*. There are at least three distinct types of footprint, which are related to the brachiopod pedicle type and which appear to be correlated with separate orders or suborders. These three types can be recognized at least as far back as the Cretaceous. The ichnogenus *Podichnus* and the ichnospecies *P. centrifugalis* are redefined and two new footprint ichnospecies are proposed. New terms 'colonist' and 'host' are proposed for an attaching brachiopod and its animal substrate respectively. Long term colonist – host relationships may occur in the New Zealand fossil record, from the Eocene and Miocene to the Recent, based on the evidence of footprints. In three examples one or both animals evolve into new species while maintaining the colonist – host relationship.

Implications of the Earliest Silurian Brachiopods from Southeast China

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Relatively little attention has been paid to the survivors in the immediate aftermath of the mass extinction, compared with surge of interest in the extinction event itself. Study of the survival phase following the extinction is informative. Earliest Rhuddanian (Llandovery, Silurian) brachiopods after the end-Ordovician mass extinction are recorded from the basal part of the Llandovery Shiyang and Anji formations in western Zhejiang and northeastern Jiangxi, eastern China. Associated graptolites including *Normalograptus jerini* and *N. nanjingensis* indicate an assignment to the *Akidograptus ascensus* Biozone, lowest Silurian. Brachiopods, the richest components of the shelly fossils include 22 species and genera that can be attributed to 20 families, dominated by orthids and strophomenids. Three associations are present: the *Levenea qianbeiensis* Association, *Levenea-Katastrophomena* Association, and *Glyptorthis-Levenea-Epitomyonia* Association are recognized and assigned to BA (Benthic Assemblage) 2, BA3, and close to the BA3-4 boundary respectively. Both families and superfamilies are represented by one or rarely by two genera, a distinctive feature of the survival phase. Rare pentamerid, atrypid and spiriferid genera in the collections are either unknown or extremely rare in the cool/cold Hirnantian faunas. The great majority of the genera investigated are widely distributed and extended upwards from the Ordovician. None of them are Lazarus taxa that temporarily "disappeared" in the Hirnantian fossil record and reappeared in the Llandovery. Only a single new genus first appeared in our collections from the Lower Llandovery, suggesting a much lower origination rate in the survival interval than in the survival-recovery (Hirnantian) and recovery (late Rhuddanian-early Aeronian) intervals.

Cardiarinidae Cooper, 1956, Order Uncertain

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The genus *Cardiarina*, described by Cooper (1956) from the Upper Pennsylvanian of New Mexico, is characterized by its small size, bilobed outline, parathyridia, and long symphytium. Although

assigned to the Rhynchonellida by Cooper, he considered the ordinal affinities uncertain. *Lambdarina*, and *Hampsia* from the Carboniferous Limestone, resemble *Cardiarina* in outline, symphytium, and other features but lack the parathyridia. *Minysphenia* is coeval with *Cardiarina* but lacks both parathyridia and symphytium. *Loborina* from the Upper Devonian of Poland has a similar outline but also lacks both parathyridia and symphytium. Richard Hoare (personal communication, 1995) examined Dickerson Shale brachiopods (Pennsylvanian, Desmoinesian, Texas) that included specimens he assigned to *Cardiarina*. He observed a partial loop during serial sectioning and concluded *Cardiarina* was possibly a terebratulid. Hoare and Mapes (1997) described the Texas material as ?*Cardiarina cordata* and illustrated sections and a reconstructed dorsal valve interior. Although no punctae were observed and evidence of the loop was not recorded in the sections, I decided during preparation of the Rhynchonellida for the Treatise to transfer *Cardiarina* to the Terebratululida where it might be loosely associated with *Disphenia*, a small bilobed genus that possesses punctae but no known loop and was tentatively assigned to the Terebratulida by Grant (1988). Punctae are not unknown in the Rhynchonellida, however.

It now appears that the Cardiarinidae has slipped through the cracks and is not included with the rhynchonellids or terebratulids in the revised Treatise. It seems desirable to include the Cardiarinidae somewhere in the Treatise, possibly in the Supplement under Order Uncertain.

Middle and Upper Devonian Brachiopods from the Western Sahara (Morocco)

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Devonian reefs near Smara at the SE flank of the Tindouf Synclinorium (Western Sahara, Morocco) are studied in a cooperation programme of the Forschungsinstitut Senckenberg and Moroccan institutions. The investigated brachiopods come from sedimentary successions close to the reefs and from the reefs themselves and indicate a late Givetian to Frasnian age.

The majority of the taxa shows close affinities to European forms from France, Spain and the Eifel region of Germany, e. g., *Dagnachonetes* cf. *supragibbosus* (Sobolev, 1909), *Douvillina dutertrei* (Murchison, 1840), *Devonaria* sp., *minuta* ? (Buch, 1837), *Xystostrophia* cf. *umbraculum* (von Schlotheim, 1820), and "*Kransia parallelepipeda*" (Bronn, 1837). Certain taxa from the Western Sahara, such as *Cyrtina* cf. *hamiltonensis* (Hall, 1857), *Devonochonetes* cf. *scitulites* (Cooper, 1945) and *Rhipidomella* cf. *vanuxemi* (Hall, 1857), are similar to forms from eastern North America, especially from the Middle Devonian Hamilton Group. Very interesting is the occurrence of representatives of the enigmatic genus *Paracrothyris* Wu, 1974 that has hitherto only been known from Nevada and South China. *Nalivkinaria issoumourensis* (Drot, 1971) and *Tropidoleptus carinatus freuloni* Boucot, Massa & Perry, 1983 have been described from other localities in Morocco, Algeria and Libya. Finally, a new species of *Schizophoria* is identified.

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Intraspecies Variation between Two Extant Populations of *Laqueus californianus* as Modeled by Elliptical Fourier Analysis

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The range of morphological variability within and among populations and species of living brachiopods is surprisingly poorly known. In order to evaluate the boundaries of morphological species in the fossil record, our knowledge of recent variation must be improved. We used Elliptical Fourier Analysis (EFA) to study intraspecific variation among dorsal valve commissural outlines of

90 *Laqueus californianus* specimens collected from Catalina Island, California and 19 specimens from Puget Sound, Washington. EFA uses outline data points to find harmonic coefficients which complete a series of sine and cosine curves which, when summed together, can reproduce the original outline, simplifying the outline into fewer shape variables.

Principal Component Analysis (PCA) of the harmonic coefficients reveals that both populations can be clearly differentiated in morphometric shape space. Moreover, size and shape variation along the PC axes reveal that while Puget Sound individuals are smaller overall, some individuals have shell shapes most closely comparable to the larger Catalina Island specimens, suggesting that growth rates and growth directions in these two populations of *L. californianus* vary considerably along a latitudinal gradient. Further analysis of *L. californianus* specimens from five other localities along the western coast of North America verifies this trend: smaller adult body size at higher latitudes, while the range of ontogenetic shape change remains constant across all latitudes. With age and longevity information, determined from oxygen isotope analysis, these differences in size and shape have the potential to suggest intriguing hypotheses about the role of heterochrony in the evolution of this lineage.

Palaeozoogeography of the Late Permian Terebratulids (Brachiopoda)

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Evaluation of the taxonomic composition of Late Permian terebratulid faunas permits the definition of the Palaeo-Equatorial and Boreal realms. The Palaeo-Equatorial Realm includes the superfamilies Centronelloidea, Terebratuloidea, Loboidothyroidea, Angustothyrididoidea, Gilledioidea, and the families Notothyrididae, Heterelasminidae, Angustothyrididae, Pseudodielasmatidae, and Gilledidae. The brachiopods of the Palaeo-Equatorial Realm are the more abundant and diverse characterized by terebratulids preferring warm water. There are about 140 species, 18 genera, 5 families and 5 superfamilies. It exceeds 5 times the species quantity and has twice the number of higher taxa than those in the Boreal Realm, where there are 24 species, 8 genera, 3 families, 2 superfamilies. The Boreal Realm is defined by the superfamilies Dielasmatoidea, Compositelasmatoidea and the families Dielasmatidae, Beecheriidae, Compositelasmatidae. The generic associations define regions and subregions. The presence of common genera such as *Heterelasmina*, *Levenolasma*, and *Rostranteris* in Sicily, SW Darvaz, and North China indicate a connection between the basins of the Mediterranean Region in the Late Permian. The genera *Notothyris*, *Gefonia* and *Labaia* are distributed in Mediterranean and Cimmerian regions. Moreover the presence of the common genera *Heterelasmina*, *Gundarolasmina* and *Hemiptychina* in the basins of the Mediterranean, Cimmerian and Cathaysian Region demonstrates a wide mobility of taxa within the Palaeo-Equatorial Realm. The presence of *Dielasma* and *Beecheria* in the Texas Province, in the East-European and West-European subregions prove the possible connections of Texas basin and the basins of the Central and North Europe through the seas of the Canadian Arctic and North Europe. We confirm the appearance of the ancestors of the general branches of Mesozoic terebratulids in the Upper Permian of Tethys and the absence of their direct ancestors in the Late Permian of the Boreal seas.

Weird, Weirder, *Mickwitzia* – the Odd Features of a Stem-Group Brachiopod and Their Implications for Brachiopod Phylogeny

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Intensive study of shell fragments of the stem-group brachiopod *Mickwitzia* Schmidt found in acid

resistant residues revealed several previously unknown features of the shell of this still poorly understood genus. The shell fragments, which are tentatively assigned to *Mickwitzia occidens* Walcott, all show a typical multilamellar shell fabric and conical structures on the internal surface of the shell which are associated with shell penetrating canals visible as distinct pores on the outer surface of the shell. However, besides these characteristic features, various fragments show peculiar structures, whose interpretation results in the reconstruction of a bivalved animal that is characterized by a conical 'ventral' valve with a subcentral apex, and a planar 'dorsal' valve with a minute pseudointerarea-like structure at its beak and an apex close to the posterior margin. Two types of setae were present that distinctly differ in size: a small type penetrated the shell via the conical structures and a large type represents marginal mantel setae that were occasionally enclosed by the shell. The assumed mode of growth of *Mickwitzia*, which distinctly differs from the incremental growth of the crown group, and the presence of sealed pores imply that at least parts of the external shell surface were covered by soft tissue during life. The results also indicate that the multilamellar shell fabric of *Mickwitzia* may be homologous to the baculate shell of lingulids. Also, structures reminiscent of the columnar fabric observed within the apical parts indicate the columnar fabric to be an ancestral state within the Class Lingulata. This may explain the presence of columnar fabrics within both the Lingulida and Acrotretida.

Origin of Brachiopod Shell Beds: Positive Feedback between Sedimentation and Hardpart-Input Rates (Lower Jurassic of Morocco)

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A 150 cm thick, densely packed shell bed with brachiopods in growth position from the Lower Jurassic of Morocco gives new insights into the dynamics of autochthonous shell bed formation. First, the brachiopod shell bed shows a decrease in post-mortem alteration, in contrast to shell-poor beds. This negative correlation between shelliness and alteration indicates that an increase in net rate of hardpart-input was the primary factor which governed its formation, in accord with the R-hardpart model. Second, the micro-fabric and lateral replacement of the shell bed by shell-poor beds indicate that the shell bed did not form positive relief above a sediment-water interface in the surrounding areas, indicating relatively continuous sedimentation on a scale exceeding the life span of several generations. Third, based on actualistic data from modern bivalve shell beds, the suspension-feeding of a high-density population leads to high biodeposition rates through production of faeces and pseudofaeces. Extrapolating this into the fossil record, the brachiopod shell bed, with about 4000 individuals/m^2, probably also induced a higher rate of biodeposition, in contrast to shell-poor beds. Both biodeposition and sediment trapping inevitably decreased the rate of shell destruction, led to stabilization of, and protected the brachiopod shell concentration. This resulted in a positive feedback between the increased hardpart-input rate and increased biogenic sedimentation rate, enhancing the preservation potential of the shell bed. This positive feedback thus provides one possible answer for the long-standing question of how well preserved shell concentrations can form by gradual accumulation on the sea-floor.

A Thorny Problem Revisited: A Systematic Review of the Siphonotretid Brachiopods

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The Siphonotretida is a small, monophyletic order of linguliformean brachiopods united by the presence of hollow spines. The affinities and origins of the siphonotretids have long remained problematic as evidenced by their association with a number of groups, including the obolides, discinides, acrotretids, dysoristides and lingulellotretides. To resolve these problems, and to determine the affinities of recently discovered post-Ordovician siphonotretids, a cladistic analysis utilizing all accepted siphonotretid genera (excluding the poorly known *Mesotreta* and ?*Quasithambonia*) was performed using 34 unweighted, unordered morphological and ultrastructural shell features. Six taxa representing other major linguliformean groups (*Obolus*, *Lingulellotreta*, *Schizotreta*, *Dysoristus*, *Eothele* and *Acotreta*) were selected as outgroups, as was the stem group brachiopod, *Mickwitzia*. Two trees, 131 steps long, were generated using PAUP 4.0 beta 10. The resulting strict concensus tree supports previous cladistic analyses in showing that the siphonotretids form a monophyletic group, but indicates that the siphonotretids form a sister group to the rest of the linguliformeans. Unlike previous cladistic analyses, a sharper resolution of the relationships between siphonotretid genera was achieved providing some support for previously proposed subfamilies. Based on these results, the siphonotretids would appear, at present, to have a "hidden" ancestry.

Brachiopod Ornamentation and the Mesozoic Marine Revolution: A Temporal Predation Gradient?

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Four ornament categories were defined among Mesozoic brachiopods: 1. smooth or capillate; 2. costate; 3. strongly costate (amplitude of ribs in the mid-portion exceeds 5% of shell length); 4. spinose, rugose, crenulate. Strongly costate taxonomic groups (Spiriferinida) became extinct in the Early Jurassic. Among the usually smooth Terebratulida, strongly costate genera appeared in the Late Triassic, became abundant in the Early Jurassic and flourished no longer than the Middle Jurassic. Temporal change in ornamentation of Mesozoic Rhynchonellida was examined in detail at the genus level. The number of rhynchonellid genera (generic diversity) increases during the Triassic from 7 to 46 (Norian); then, after a minor decrease around the Triassic/Jurassic boundary, rises to 57 in the Bajocian. The Late Jurassic decline and Cretaceous diversity minimum fits to the Mesozoic marine revolution model. The strength of ornamentation (expressed as a mean ornamentation index) shows an even more marked temporal change: steady increase through the Triassic and Jurassic and a gradual decrease during the latest Jurassic and Early Cretaceous. Representatives of the most strongly ornamented category (No. 4), e. g. the spinose Acanthothirididdae, appeared in the second half of the Jurassic. These trends and phenomena are interpreted as late efforts of adaptation to the threat of durophagous and boring predation gradually increasing through the Mesozoic. In the Cretaceous, brachiopods mostly gave up their strongholds in the level-bottom communities and survived in the less vulnerable deep-sea environments.

Synecological Diversification of Early-Mid Ordovician Brachiopods of Southwest China

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The coeval Daguanshan Formation at Shuanghe, Changning, Sichuan Province, the Meitan Formation at Honghuayuan of Tongzi and Shatuo of Yanhe, Guizhou Province, and the Yingpan Formation at Houping, Chengkou, Chongqing City contain diverse brachiopod faunas. A species-level dataset, based on more than 30, 000 brachiopod specimens from 207 collections made at four Lower to Middle Ordovician sections of the Upper Yangtze Platform, South China palaeoplate, has been completed for the Early to Mid Ordovician (*Acrograptus filiformis* Biozone to *Exigraptus clavus* Biozone) brachiopods of Upper Yangtze Platform and forms the basis for quantitative synecological analyses. A series of brachiopod-dominated benthic communities and associations have been recognized within each graptolitic biozone (altogether six biozones) with the help of Principal Component Analysis and Cluster Analysis, and detailed synecological analysis has been made for all those communities and associations recognized and the synecological diversification has been discussed zone by zone. The first evolutionary radiation of the Early to Mid Ordovician brachiopods of the Upper Yangtze Platform was a gradual process marked by the macroevolutionary history of the *Sinorthis* Fauna, a regional brachiopod fauna developed during the Early to Mid Ordovician transition. The *Desmorthis* Community, *Paralenorthis* Community, *Sinorthis* Community and *Euorthisina* Community of the *Sinorthis* Fauna developed on the Upper Yangtze Platform simultaneously or consecutively or intercalated at different sections. The first acme of the brachiopod radiation was manifested by the origination and strong diversification of the *Sinorthis* Community which flourished mainly in the normal marine shallow-water benthic regimes (lower BA2 to BA3). The *Sinorthis* Fauna first occurred and developed in shallow or shallower benthic regimes corresponding to the lower part of BA2 to the upper part of BA3, and then moved gradually both upward to nearshore (BA1) and downward to offshore (lower part of BA3 and BA4) to greatly enlarge its spatial distribution. The macroevolution of brachiopod taxonomic diversity (α-diversity) (Zhan and Rong, 2003; Zhan *et al*., 2004) and synecological diversity (β-diversity) are apparently heterogeneous.

A Species-Level Brachiopod Database – Building a Digital Knowledge Base for Brachiopod Studies

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Currently available palaeontological databases are inadequate for many types of in-depth studies in brachiopod biology and palaeobiology. We propose to construct, with extensive help from the broader brachiopod community, a comprehensive species-level brachiopod database containing such diverse data as systematics, stratigraphic and geographic occurrences, ecological and depositional attributes, and taxon-character (morphological, molecular, embryological) matrices. Detailed information compiled, critiqued, edited, and evaluated by brachiopod workers, will serve as an invaluable knowledge base for brachiopod studies, and will provide a collaborative platform for information exchange and problem solving. Once populated, the taxon-character matrix will provide a common dataset for constructing and testing a wide variety of macroevolutionary and phylogenetic hypotheses. The matrix will also be useful in developing computer-aided taxonomic identification systems.

To fill the database with useful content is a daunting task. Software tools will be developed to import structured data such as taxonomic descriptions, but more importantly, the database will be designed as a collaborative web application consisting of a public account and customizable private accounts. Users will be able to register individual accounts and thus have a ready made database tool for their own projects. The account owners have the option of keeping sensitive data private and can choose when to publish what to the public site. To credit data contributions, the database will keep track of who entered what as well as a running count of data usage by source. Through these built-in incentives, we hope to attract contributions from the brachiopod research community towards this database endeavor.

POSTERS

Megathyrididae Loop: A Simple Complication

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The growth dynamics of the dorsal interior of Recent megathyridid brachiopods from the western Mediterranean were studied using scanning electron microscopy. Early results indicate that loop ultrastructure and development is similar to that previously described for the terebratellidine *Calloria inconspicua* (Sowerby), which seems to be the typical ultrastructural pattern for the terebratulidine loop. The megathyridid loop consists of two long, slender, descending blade-like branches that may continue in a narrow, semicircular pattern, that commonly unite on a narrow and high dorsal median septum. These descending branches are variably "fused" to the floor of the dorsal valve, leaving a trace of their position on the dorsal valve interior. In adult *Megathiris,* these blades may be folded ventrally onto the tops of their crested and serrated lateral septa. This simple, and quite dorsally placed, megathyridid loop is unknown in other present-day long-looped terebratulids. In many of the adult specimens of *A. cuneata*, a pair of postero-ventrolaterally directed prongs or wings in different states of growth were observed on the dorsal median septum. These could be interpreted as abortive ascending branches, such as seen in long-looped terebratulides. These new data on the morphology, development and structure of the megathyridid loop helps to establish the affinity between the Megathyrididae and other terebratellidine families.

Secondary Shell Layer of *Novocrania*, Its Fabric and Canal System

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Recent brachiopods have been recovered from the Finisterre coasts of Galicia (NW Spain), just before and a year after the oil-carrier "Prestige" sank. Of these materials, well preserved dorsal valves of *Novocrania anomala* were studied under the SEM. The shell structure of the dorsal valve of this "inarticulate", although a calcitic-shelled brachiopod, typically consists of a thin primary layer succeeded by a thicker and laminar secondary layer. Inner surfaces of dorsal valves display holes (punctae) with densities of from 180 to 260 per mm^2; their diameters vary and "dumb-bell" shaped paired punctae within slots on the inner surface indicate positions where division has taken place. On fracture surfaces, more or less perpendicular to inner surfaces, the laminae are wrapped around the punctae in a distinctive fashion. Each lamina is strongly deflected outwards and around the punctal cavity throughout the secondary layer. The punctae originate from fine tubes converging towards the primary to secondary junction. Here the laminae are already deflected outwards into cavities in the primary layer. As the secondary layer thickened, the laminar deflections increased in amplitude forming highly developed cone in cone structures, resembling a stack of closely fitting egg-boxes, but with hollow centres, in life filled by soft tissues. The deflections became so long as to resemble tubes of laminae lining the punctae. An ultrastructural comparison of this fabric with the endopunctae and standard shell structure of rhynchonellate brachiopods, as typified by living terebratulides, emphasize the peculiarities of the shell structure and canal system of *Novocrania*.

Brachiopod Biostratigraphy in the Late Permian Nesen Formation of the Alborz Mountains (N Iran)

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Upper Permian brachiopods have been collected from the Nesen Formation of the Alborz Mountain (North Iran) along five sections and have been analysed by means of the Unitary Associations method, a deterministic mathematic model to construct biozones.

Based on the quantitative biostratigraphic analysis of the brachiopod assemblages, seven biozones have been detected. This biozonation has been then compared with the brachiopod biozones already established in the Djulfa area, both at Dorasham (Ruzhentsev & Sarytcheva, 1965) and at Kuh-e-Ali Bashi (Stepanov *et al*., 1969).

Biozones 1 to 5 of Central Alborz fit with the *Araxilevis*, *Oldhamina* and *Haydenella* biozones of Djulfa, which are Wuchiapingian in age. Biozones 6 and 7 of the Alborz Mountains do not easily correlate with the Changhsingian *Comelicania* Biozone of Djulfa, which is poorly diversified. However, the occurrence of *Comelicothyris* in Biozone 6 indicates a Changhsingian age. This is also supported by the similarity of biozones 6 and 7 to the lower Changhsingian assemblage of South China and by the dwarfism of the fauna in these beds. The genus *Ombonia* which characterizes Biozone 7 is a characteristic component of the low diversity brachiopod faunas of latest Permian age.

Two independent pieces of evidence support the brachiopod-based age assignment: 1) the occurrence of the Wuchiapingian-lower Changhsingian conodont *Hindeodus julfensis* below Biozone 4; 2) the $\delta^{18}O$ and $\delta^{13}C$ isotope curves through the Permo-Triassic succession of the Elikah section.

Ruzhentsev V.E. & Sarycheva T.G. 1965. Evolution and succession of marine organisms at the Permo-Triassic boundary. *Akad. Nauk SSSR, Trudy Paleont. Inst*., 108, 430 pp.
Stepanov D.L., Golshani F. & Stocklin J. 1969. Upper Permian and Permian-Triassic boundary in North Iran. *Geol. Surv. Iran Rep*., 12, 72 pp.

A New Late Ordovician Brachiopod Assemblage from Kazakhstan

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The main Palaeozoic region of central Kazakhstan comprises a complex of accreted terranes whose current juxtaposition does not necessarily reflect their original geographical position. The Upper Ordovician (Caradoc) section near Lidievka in northern Central Kazakhstan demonstrates a transition from a basinal environment to the middle parts of an accretionary fan. This complex formed along a prograding slope of a narrow shelf of an early Palaeozoic terrane known as the Stepniak-Betpakdala volcanic arc. Some sandstone units derived from mass flow deposits contain a taxonomically diverse brachiopod fauna, possibly derived from the shallow shelf. This allochthonous assemblage contains *Acculina, Anoptambonites, Christiania, Dolerorthis, Dulankarella, Kajnaria, Limbimurina, Mabella, Phragmorthis, Shlyginia, Sortanella and Sowerbyella* as main components. The fauna closely resembles the *Acculina-Dulankarella* Association previously reported from the early to mid Caradoc Anderken Formation of the Chu-Ili terrane, where it is associated with carbonate build-ups. Among these taxa, *Acculina, Kajnaria, Shlyginia* and *Sortanella* are currently considered as endemic for Kazakhstan, whereas *Dulankarella* and *Mabella* are otherwise known also from the Australian sector of Gondwana. A low diversity brachiopod assemblage from hemipelagic background deposits preserved as fine clastics is dominated by the minute plectambonitoids *Durranella* and *Kassinella*, which occur in association with the trilobites *Taklamakania, Telephina* and agnostides suggesting BA 5-6. Despite the different tectonic setting, possibly representing a separate volcanic arc in the Late Ordovician,

the brachiopod assemblage shows distinct affinity with the contemporaneous fauna of the Chu-Ili terrane. Overall, the two brachiopod assemblages and associated trilobites indicate close links with contemporaneous faunas of the low latitude Australian part of Gondwana and related terranes (e.g. Tarim and South China).

Spatial and Stratigraphic Distribution of the Rhynchonelliformean Brachiopod *Productorthis* Kozlowski: Fast Migrations or Parallel Evolution?

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Productorthis angulensis Benedetto, the oldest presently known species of *Productorthis*, is a conspicuous element of the volcano-sedimentary Molles Formation (Arenig, *Oepikodus evae* Zone) of the Famatina Range, western Argentina. Its origin by heterochrony from *Panderina ambigua* Benedetto – which comes from the underlying Suri Formation – is well supported by ontogenetic data, suggesting that *Productorthis* may have originated in the volcanic-arc settings developed along the proto-Andean margin of Gondwana. Outside of Famatina, its lowest occurrence is in the Volkhov Stage (*B. navis* Zone) of Baltica. There, as in Famatina Range, the first appearance of *Productorthis* almost immediately postdates the occurrence of *Panderina*. Two different explanations can be proposed to account for such stratigraphic and palaeogeographic distribution: (1) the Baltic species of *Productorthis* evolved from the Famatinian *P. angulensis* and subsequently migrated rapidly to Baltica, (2) the Baltic species of *Productorthis* evolved from the local species *Panderina abscissus* (Pander), lacking direct phylogenetic relationships with the Famatinian lineage. The second hypothesis implies that *Productorthis* originated independently in Gondwana and Baltica. The parallel evolution of Baltic and Famatinian lineages may have been the result of heterochronic processes operating on morphologically close, but geographically segregated, species of *Panderina*. By the late Arenig-early Llanvirn, *Productorthis* dispersed into volcanic islands and microcontinents within the Iapetus Ocean, and by the Caradoc, it becomes largely confined to Laurentia. The parsimony analysis of 14 species of *Panderina* and *Productorthis* supports the existence of different subclades, and shows that *Productorthis cienagaensis* Herrera and Benedetto, from the Precordillera terrane of western Argentina, is closer to the 'Baltic' than the 'Celtic' subclade.

Recent Brachiopods from the Fiji and Marquesas Islands, Southern Pacific, collected during the French Cruises Musorstom 9, 10 and Bordau 1

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Although Recent brachiopods were intensively investigated in the Pacific Ocean, especially around Japan, Australia and New Zealand, they are rather poorly known from off the archipelago islands. Recently the region of the Pacific islands has been studied by the three French oceanographic expeditions carried out on board the R.V. "*Alis*": Musorstom 9 to the Marquesas Islands in 1997, and Musorstom 10 and Bordau 1 to the Fiji Islands in 1998 and 1999, respectively. Among the brachiopods collected around the Marquesas, two species belonging to two genera, *Eucalathis* and *Frenulina,* have been recognized. The brachiopod fauna collected during the two cruises to the Fiji region includes representatives of four orders and comprises 17 species, including new forms, belonging to 14 genera, *Novocrania*, *Cryptopora*, *Basiliola*, *Abyssothyris*, *Dallithyris*, *Xenobrochus*, *Terebratulina*, *Fallax*, *Nipponithyris*, *Frenulina*, *Argyrotheca*, *Amphithyris*, *Phaneropora* and *Thecidellina*. The pattern of decreasing species number from the western to central Pacific, observed also among other groups of inver-

tebrates, is clearly visible in the brachiopod assemblages. The brachiopods from Fiji, being much more diversified than those from the Marquesas Islands, display low diversity when compared to 26 species in the New Caledonia region. The Fiji brachiopods show a close affinity to the brachiopods from New Caledonia as well as to the New Zealand fauna, having nine and eight genera in common, respectively.

Revision of Middle Miocene Brachiopods in the Meznerics Collection (Hungary)

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Meznerics (1943) summarized the Hungarian Tertiary brachiopod fauna in a small monograph based on the large Hungarian collections. The significant part of her Miocene material is kept separately in the Hungarian Natural History Museum as the "Meznerics brachiopod collection". There are also additional brachiopod specimens in the Miocene collection, arranged according to locality. We have examined 277 specimens of the Karpatian (Middle Miocene) age, coming from 10 localities and containing nine species. From the Badenian (Middle Miocene) 309 specimens were studied from 17 localities; thirteen species were recognized in the Badenian material. Inarticulated brachiopods are represented by *Ancistrocrania abnormis* while rhynchonellids belong to two species of *Aphelesia* (*A. bipartita* and *A. acuta*). All the other species belong to terebratulids. Large species of *Terebratula* were classified into six species/subspecies (*T. hoernesi*, *T. macrescens, T. styriaca*, *T. sinuosa*, *T. sinuosa pedemontana*, *T. kemenczeiensis*) by Meznerics but unfortunately the poor preservation of the material prevents any real revision of these species. The genus *Megerlia* is represented mainly by *M. truncata*, while the second species *M. margaritata* is known only from one specimen. Among micromorphic species, *Gryphus miocaenicus* is the most frequent, while *Terebratulina retusa* is very rare. The species *Platidia anomioides* is mostly associated with the Bryozoa-rich sandstone of Mátraverebély. The family Megathyrididae is well-represented by two species of *Argyrotheca* (*A. cordata*, *A. cuneata*) and *Megathiris detruncata*. The species *A. cuneata* is reported for the first time from the Miocene of Hungary.

Carboniferous Brachiopods from the "*Levipustula* Fauna" in Central-Western Argentina: Biostratigraphic, Palaeoclimatic and Palaeobiogeographic Implications

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The "*Levipustula* fauna" is a relatively diverse fossil assemblage composed of brachiopods, bivalves, bryozoans, gastropods and crinoids that appears in glaciomarine sequences related to the Carboniferous glacial event that affected the central-western Argentinean basins. Brachiopods that characterize this fauna have been studied in some of the classical localities of the Argentine Precordillera in San Juan province.

In the Hoyada Verde Formation, the "*Levipustula* fauna" is usually located immediately above the glacial diamictite horizons and appears to be associated with the mudstones facies of the postglacial transgression. From a palaeoecological study, three brachiopod subfaunas are distinguished in this formation: the lower *"Neospirifer"* ("*Trigonotretidae*" gen. nov.) subfauna, above which the more diversified *Kitakamithyris* subfauna occurs, and the upper *Levipustula* subfauna, with the dominant

species being attributed to *Levipustula levis* Maxwell. The Hoyada Verde fauna, as well those identified in the La Capilla Formation (Cerro El Morado locality), have been proposed as the typical "*Levipustula* fauna". However, in the Leoncito Formation, the "*Levipustula* fauna" occurs in sandstones horizons located below the glacial diamictite beds. This fauna is poorly diversified and the brachiopods are characterized by "*Neospirifer*" ("*Trigonotretidae*" gen. nov.)-*Septosyringothyris* assemblage and *Levipustula* is not abundant. This fauna has been considered a colder "pre-interglacial fauna".

The significant taxonomic, palaeoecologic and taphonomic variations of the "Levipustula fauna", as well as its position in the glacial sequences, suggest an important palaeoenvironmental control related to Carboniferous glacial dynamics. From the palaeobiogeographic viewpoint, this fauna shows the highest affinity with the Eastern Australian basins from where it was previously described.

Rhynchonellate Relationships Inferred by Bayesian and Maximum Likelihood Reconstruction from SSU rDNA Gene Sequences, Taking Account of rRNA Secondary Structure

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As additional specimens and SSU rDNA gene sequences continue to come to hand they are added to an alignment than now contains data from ~80 different phoronids and brachiopods (over 50 rhynchonellates, including thecideidines).

Previous analyses explored this growing database using maximum and weighted parsimony, distance, and maximum likelihood (ML) approaches (Cohen & Gawthrop 1996, 1997, Cohen *et al.*, 1998). Recent developments make it possible to apply different ML models of evolution to stem (paired, slow-evolving)) and loop (unpaired, faster-evolving) rRNA secondary structural regions, and to use these models in a Bayesian phylogenetic inference framework, potentially maximizing evolutionary inference from these data.

Trees showing the rhynchonellate relationships inferred from the current SSU rDNA alignment will be presented and discussed.

Some Issues for Discussion

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We highlight some issues that need discussion:

1. Does the "brachiopod fold" hypothesis (Nielsen 1991, Cohen *et al.*, 2003) adequately interpret the evolution of ontogenetic changes in body axis? If so, "dorsal" and "ventral" are misleading terms. Should we revert to "brachial" and "pedicle" (even for forms with no pedicle)? Are there better terms?
2. Gene trees recover (phoronid (craniid (discinid + lingulid))) and (rhynchonellate) sister-clades. This conflicts with the current classification (Williams *et al.*, 2000). A revision has been proposed, including phoronids as a Class within the subphylum Linguliformea (Cohen and Weydmann, *Organisms, Diversity & Evolution*, in press).
3. But how best should this inclusion of phoronids within Brachiopoda (*s.l.*) be handled (assuming it survives more molecular tests)? Is a new name for the phylum justified?

4. Phoronids apart, clades do correspond to the former categories "articulate" and "inarticulate". Should these terms be revived for informal descriptions? If so, should phoronids be treated as "honorary inarticulates" that never developed (or later lost) shell mineralization?
5. Must the subphylum Linguliformea be renamed to reflect the inclusion of phoronids?

SSU rDNA and Cox1 Gene Sequences of Terebratellidines: Do They Tell the Same Story?

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We will present new separate and combined analyses of nuclear-encoded SSU rDNA and mitochondrial *cox1* gene sequences, mainly of terebratellidines, for which independent analyses have hitherto resulted in some disagreements. The results should be relevant to:
1. the monophyly and sister-group relations of the New Zealand endemic taxa and of laqueoids,
2. the relationships of *Ecnomiosa* to megathyridids,
3. the nature of and reasons for disagreements between the SSU and *cox1* gene trees.

Palaeocene Monospecific Rhynchonellid (Brachiopoda) Assemblage from Kambühel (Austria)

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Brachiopods suffered strongly from the end-Cretaceous mass extinction and only a few taxa and a limited number of localities with brachiopods are known from the Palaeocene. Most of the European Palaeocene brachiopods are known from chalk facies. A new locality of Palaeocene brachiopods, probably Danian in age, was found at Kambühel (Austria) and about 200 specimens were collected. The lithology of the brachiopod-bearing rocks is rather peculiar, not only for the Palaeocene, but also for the whole Cenozoic: it is a massive, brownish red limestone. The monospecific assemblage is definitely autochthonous, practically all the specimens have articulated valves and we were unable to find any signs of transportation and/or resedimentation. In our opinion the sedimentation depth must have been under the storm wave-base. The relatively deep-water setting is confirmed by the absence of any trace of epibenthic sessile organisms or predator drillholes in the brachiopod valves. The medium-sized, dorsibiconvex specimens are uniplicate, sometimes slightly asymmetrical. They have conjunct deltidial plates and a small foramen. The numerous (9-19), rounded ribs are generally stronger at the anterior margin. The internal characters are diagnostic, with the dental plates roof-shaped in transverse section, horizontal hinge plates, no cardinal process and falciform crura. All these suggest that the investigated brachiopods represent a new genus and species attributable to the family Basiliolidae. The shell ultrastructure is of coarse-fibrous basiliolidine type *sensu* Kamyshan (1977) with the secondary layer fibres of a rhomboidal shape, and confirms the above attribution to the Basiliolidae.

East Baltic Rhynchonelliformean Brachiopods from the Billingen and Volkhov Stages

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A presentation of rhynchonelliformean brachiopods found in material from nine localities along the Baltic-Ladoga Klint, from the Tallinn and St. Petersburg regions.

The brachiopods were sampled from limestone as well as from unconsolidated clay horizons and mud mounds. Detailed sampling and excellent preservation, especially in the soft sediments, have yielded a great collection of brachiopods including several new taxa.

Bed by bed sampling in the Putilovo quarry shows, with few exceptions, no difference in species distribution between consolidated and unconsolidated horizons in the standard succession. Likewise, there is no obvious difference between juveniles and adults in material from clay and limestone, except for the mud mound material, which shows an overrepresentation in juveniles, indicating a rapid sedimentation rate in those buildups resulting in burial of small specimens.

The rhynchonelliformean brachiopods in the region show a marked shift at the sequence boundary between the Billingen and Volkhov stages, and a distinct turnover pattern may be distinguished also within the Volkhov Stage as well as at the transition to the overlying Kunda Stage. This turnover pattern seems to correspond quite well with the suggested sea level curve for the region, in the sense that several disappearances occur at major sea level drops and migration of new taxa seems to coincide with peaks of high sea level.

Linguliform and Craniiform Brachiopods from the Ordovician Tvären Crater, Sweden

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During the Ordovician, several bolides hit the Baltoscandian Epicontinental Sea. One of the impacts occurred at a water depth of 300 m and resulted in the 2 km wide Tvären crater, now situated in the Stockholm Archipelago, Sweden. The pre-impact sedimentary sequence at Tvären consisted of Ordovician carbonates resting on non-lithified sands of Early to earliest Middle Cambrian age. Following the impact event, deposition of carbonates continued (Dalby Limestone). The crater acted like a sheltering rim for the deposition of sediments, also displaying pure new settings for the fauna still living in the surrounding sea.

The studied material from Tvären consists of glacial erratics from the area immediately southeast of the bay of Tvären on the coast of Södermanland. The limestone boulders are all fairly fossiliferous and have yielded numerous ostracods and brachiopods, the brachiopods being the next most common group; however the brachiopod fauna has never been previously studied in detail. The linguliform brachiopod fauna recorded from the erratic boulders include a large new lingulid genus and species, as well as new species of *Schizotreta* and *Paterula*. *Eoconulus robustus* Holmer is the only linguliform species previously recorded from the Dalby Limestone in Sweden.

Lost Brachiopods – Found in Dublin

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The National brachiopod collection of Ireland has been almost completely inaccessible for more than

40 years due to collection moves and chronic under-staffing. Now, for the first time, we present a survey of fossil and Recent material held in the National Museum of Ireland (Natural History Division; NMINH). The central purpose of this assessment was to make details of the material—including a substantial number of type specimens of Ordovician and Carboniferous brachiopods—available to researchers worldwide. Our assessment covered the diversity and representation of groups through geological time, including Recent specimens in the NMIMH zoological collections. Various historical collections contribute to the NMINH holdings, including Sir R. Griffith and more recently J.C. Harper. New analysis of the geographical distribution of samples in Ireland and Great Britain illuminates patterns in historical collecting and palaeofaunal diversity. This poster portrays the localities and ages of the specimens in the collections. The information provided will help potential researchers by better informing them of the collections available for research in the NMINH. Survey results have also enabled Museum staff to develop a comprehensive strategy for improving collection housing and future development.

Brachiopod Biodiversity Changes during the Late Silurian Lau Event, Gotland, Sweden

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The Late Silurian Lau Event is associated with a prominent stable carbon isotope excursion, significant ecological changes in shallow seas (microbial resurgence), and extensive conodont extinctions. Brachiopod diversity did not drop, but there was a major re-organization. There have been 64 brachiopod species recorded in this study. However, of the 42 that existed before the event, only 18 are found in the immediate pre-event fauna. During the early part of the event, five taxa disappeared (e.g. *Jonesea grayi*, *Atrypa* (*A.*) *sowerbyi*, cf. *Kirkidium knighti*) and five new replaced them (e.g. *Ptychopleurella bouchardi*, *Atrypa* (*A.*) *alata*, *Navispira pusilla*). Several Lazarus taxa also reappeared. The intermediate part of the event records the greatest diversity, with 31 pre-event taxa and six taxa appearing during the event. No extinction is proven during the later part of the event. Five taxa disappeared at the end of the event. Since this is associated with a major lithological change, it is not yet established whether they disappeared due to the lithological or the oceanic change. At least 25 of the pre-event taxa survived the event. Among taxa that first appeared during the event, at least two survived. After the event, the atrypids, especially, radiated quickly. Among the nine or ten taxa with continuous ranges through the event, several suffered from adverse conditions. Lilliput effects are recorded within at least three species (*Isorthis canaliculata*, *Microsphaeridiorhynchus*? *nucula*, *Protochonetes striatellus*) and possibly also among pentamerids.

Early Cretaceous Brachiopods from North-East Greenland: Biofacies and Biogeography

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Augmentation and revision of the relatively diverse Valanginian brachiopod faunas from North-East Greenland confirm the existence of two mutually exclusive but broadly coeval assemblages,

associated with two contrasting facies types. A Boreal, relatively shallow-water assemblage dominated by large terebratulids and ribbed rhynchonellids, including *Cyrtothyris*, *Lamellaerhynchia* and *Praelongithyris* characterizes the Falskebugt fauna. By contrast the Albrechts Bugt and Rødryggen fauna contains Tethyan elements, more typical of deeper water, including *Lacunosella*, *Placothyris*, *Pygope* and *Rugitela*. This early Cretaceous Out-of-Tethys migration confirms the early and persistent northward track of a proto Gulf Stream current. A new species of *Placothyris* is reported from the Albrechts Bugt and Rødryggen members of the Palnatokes Bjerg Formation.

Furcitellinine Brachiopods (Strophomenida) from the Silurian of Gotland, Sweden

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Brachiopods of the Subfamily Furcitellinae are moderately common and diverse components of the late Llandovery and early Wenlock succession on Gotland. Six species belonging to three genera are represented on Gotland; *Bellimurina wisgoriensis* (lower Visby-Högklint), *Pentlandina tartana* (lower Visby), *P. loveni* (Högklint), *P. lewisii* (middle Slite), *Katastrophomena penkillensis* (lower Visby-middle Slite) and *K. antiquata scabrosa* (upper Slite-middle Hemse). Most of the species are confined to low energy environments, exhibiting subdued shell sculpture, but the strongly sculptured *P. loveni* was evidently specialized for the high energy reef environments of the Högklint Formation, even retaining an open pedicle foramen. Specimens of this species often have highly irregular shell shape, suggesting crowded growth in crevices and other more sheltered locations within the reefs. Specimens of *B. wisgoriensis* occurring in the Högklint Formation also have much stronger shell sculpture than those found in the low-energy Visby Formation, showing frilly growth lamellae similar to that seen in many atrypides .

Rhynchonelliform Brachiopods of the Merishkor Regional Stage (Silurian, Wenlock), North Nuratau Range, Uzbekistan and their Biogeographical Affinities

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Silurian brachiopods from Uzbekistan are known mainly from a pioneering paper by O. I. Nikiforova (1938), but there has been little progress on faunas from the region since that time. Preliminary results of current studies based on new collections from the Urtakul Formation, and the Abratkan Aidynsai and Galvabet beds (all upper Wenlock) reveal a moderately diverse fauna comprising up to 30 taxa dominated by pentamerides, rhynchonellides, atrypides, athyrididdes and spiriferides. Early occurrence of *Retziella* in shallow-water assemblages (BA2) of the Andysai and Gavalbet beds is important for understanding the origin of the so-called '*Retziella*-fauna', which is characteristic elsewhere in the late Silurian of North and South China, Anamia, the Australian sector of Gondwana, Iran and terranes of Central Asia. There is also an important link with contemporaneous brachiopod faunas of Perunica (Bohemia) as emphasized by the occurrence of such taxa as *Pleurocornu amissum* (Barrande), *Sufetirhyncha* sp., *Gracianella umbra* (Barrande) and *Araspirifer araneus* Havliček. The spiriferide *Nurataella* (=*Baterospirifer*) has generally been considered as endemic to the Karakum-Tajik microcontinent and associated island arcs, but is now known also to make a later appearance in the Ludlow of North China.

Linguliformean Brachiopods from the Ordovician-Silurian Boundary Beds, Osmundsberget, Dalarna, Sweden

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Late Ordovician (Harju Regional Series) to Middle Llandovery (*sedgwickii* Zone) linguliformean brachiopods from the top Boda Limestone and lower Kallholn Shale are documented from the Osmundsberget quarry, Dalarna, Sweden. The Late Ordovician linguliform fauna includes a new species of the enigmatic lingulid *Litoperata* as well as the acrotretid *Scaphelasma*. The unconformably overlying Middle Llandovery beds yielded a somewhat more diverse linguliformean fauna comprising the cosmopolitan acrotretids *Acrotretella* and *Opsiconidion*, the discinid *Acrosaccus* as well as a new species of the siphonotretid *Orbaspina*, which is otherwise only known from the Silurian of Australia and Bohemia.

Recent Brachiopods from the Red Sea and Gulf of Aden

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Recent brachiopods are rare in the Red Sea and Gulf of Aden, with four species: *Argyrotheca cuneata* (Risso), *Argyrotheca jacksoni* Cooper, *Megerlia echinata* (Fischer & Oehlert) and *Leptothyrella ignota* (Muir-Wood) previously identified from a total of only six specimens. Here we report on the discovery of almost 1000 specimens from neritic and bathyal zone sediments obtained mainly by *Meteor* cruises to the region in 1987 and 1995, from *Calypso* in 1951-2 and from specimens in Israeli museum collections. Preliminary identifications are: *Discinisca* sp. indet., *Novocrania* cf. *anomala* (Müller), *Cryptopora curiosa* Cooper, *Thecidellina* cf. *blochmanni* Dall, *Frenulina* sp. indet., *Argyrotheca cuneata*, *Argyrotheca cordata* (Risso), *Argyrotheca* spp. indet., *Platidia anomioides* (Scacchi & Philippi) and *Megerlia echinata* from the Red Sea and *Cryptopora curiosa* and *Leptothyrella ignota* from the Gulf of Aden. Cluster analysis reveals four associations that occupy different depth habitats and substrate types, with non-reefal shallow sediments virtually brachiopod-free. Low abundance, moderate diversity and small shell sizes appear to characterize modern Red Sea brachiopods, although this may change with more sampling. The affinities of Red Sea brachiopods are with those of the Indian Ocean and Mediterranean, the Gulf of Aden species with the Indian Ocean.

Davidson and King (1872) Establish the Trimerellids: Unlikely Collaborators on a Remarkable Nonarticulated Brachiopod Group

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During the middle to latter part of the 19th Century individual genera of what were to become known as the trimerellids were being described by Gustaf Lindström (the Keeper of Geology at the Riksmuseum in Stockholm), Elkanah Billings (of the Geological Survey Canada), Fielding Meek (Geologist at the Smithsonian) and James Hall (of the New York State Museum). However, it was Thomas Davidson and William King who first recognized them as a distinct group and attempted to interpret the musculature and the functional morphology of the shells. Their ideas were developed in discussion

with and using specimens lent by Lindström, Billings Meek and Hall. How their thoughts developed are recorded in their correspondence and through the exchange of drawings and reconstructions held in the Department of Palaeontology as part of the Davidson archive. This presentation looks at Davidson and King's somewhat fragile relationship, how they came to be working together, how they synthesized their ideas and how those ideas have stood the test of time.

Brachiopods of the Deep-Sea Expedition SO 168 – Diversity and Biogeography

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Seven species of Recent brachiopods belonging to the genera *Kakanuiella, Liothyrella, Neothyris, Gyrothyris, Dallina, Ecnomiosa,* and *Amphithyris* have been identified from dredging samples collected during the deep-sea expedition SO 168 with the German research vessel FS SONNE on Mt. Spong in the Tasman Sea, the Hikurangi Plateau and the Chatham Rise in the SW Pacific east of New Zealand. The brachiopods partly represent a typical combination of New Zealand shelf-inhabiting forms. The remaining brachiopods were unusual: two species (*Dallina raphaelis*, *Ecnomiosa inexpectata*) are first records for the New Zealand area, the occurrence of *Amphithyris buckmani* in the deep sea is recorded for the first time and the thecideid *Kakanuiella chathamensis* was recently described as a new species representing the first thecideid brachiopod discovered in deep water. Other yet unidentified species found in the samples belong to the genera *Novocrania*, *Eucalathis*, and (possibly) *Gwynia*, the latter unfortunately represented only by a single specimen.

The absence of typical deep-sea forms like *Pelagodiscus* and *Platidia* in the samples is briefly discussed. In comparison to deep-sea samples from the E Pacific (Galápagos region) obtained with the same collecting methods and crew, the species diversity in New Zealand deep waters seems to be rather low.

A Diverse Brachiopod Fauna from the Lower Silurian (Telychian) Purple Shales of Shropshire, England

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A large, temporary exposure of the Purple [Hughley] Shales was excavated in 1967 at Devil's Dingle in Shropshire, to dispose of ash from a new power station (Cocks & Walton 1968). P.D. Lane (Curtis & Lane 1998) collected extensively from the section while it was accessible during the late 1960s and early 1970s. On the basis of the presence of the brachiopods *Eocoelia curtisi* and *Costricklandia lirata*, Ziegler (1966) dated the sequence within the C_5 substage of the shelly Llandovery facies. It is the most diverse Llandovery brachiopod fauna recorded in the U.K.

Most abundant is *Jonesea grayii*. Otherwise, the fauna is dominated by the plectambonitid *Eoplectodonta penkillensis*, strophomenides (*Mesopholidostrophia salopiensis salopiensis*, *Amphistrophia whittardii*), atrypides (*Glassia*, *Gotatrypa*, *Atrypina*) and the protorthide *Skenidioides lewisii.* These are consistent with the assignment of the assemblage to the *Clorinda* Community by Cocks & Walton (1968), who noted that the top of the section contained a mixture of elements from *Clorinda* and *Costricklandia* Communities. *Clorinda* is common in Lane's collection, and other genera typical of this community are also present: *Coolinia*, *Leptaena*, *Dicoelosia*, *Cyrtia*, *Craniops*, *Streptis*, *Resserella* and *Visbyella.* Elements of the *Costricklandia* Community are present at low relative abundances (*Costricklandia lirata lirata*, *Eocoelia curtisi* and *Eospirifer* sp.), suggesting an intermediate community. The fauna is typical of low energy, relatively offshore shelf environments (Benthic Assemblages 4-5). Most small taxa are attached (including the craniid *Deliella*), but larger taxa are ambitopic.

Brachiopods of Malvinokaffric Realm Affinity in Central Sahara and Their Implications

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The Malvinokaffric Realm has been defined as the South Hemisphere cold-water marine province in Emsian to early Eifelian ages. It is characterized by generally low-diversity brachiopod communities, generally with *Tropidoleptus*, terebratulids, chonetoids and a few spiriferids in coarse clastic sediments. Corals, bryozoans and stromatoporoids are rare or absent.

The eastward limit of the Malvinokaffric Realm has been proved in South Africa, Ghana and Guinea-Bissau. New brachiopod data from the late Pragian, Emsian and Eifelian of the Tamesna Basin (Algeria-Niger boundary area) indicate that eastward extension of some typical Malvinokaffric brachiopod genera as far as the Central Saharan area. A terebratulid *Pleurothyrella* previously known from Argentina, Bolivia, Antarctica, South Africa and Guinea-Bissau is recognized in a transgressive Lower Devonian sequence in the Tamesna Basin together with very large discinoid *Gigadiscina* of Malvinokaffric Realm affinity. An ambocoeliid *Pustulatia*, considered as typical Eifelian-Givetian North American taxon, appeared in several successive species in the late Pragian to Eifelian sequence in the Tamesna Basin. A chonetid *Lomaella* has similar range there. *Pustulatia* and *Lomaella* are present in the upper Pragian and Emsian of Bolivia.

In summary, the brachiopods with Malvinokaffric Realm affinity can be traced much farther eastwards than suggested formerly.

Microstructure and Microhardness in Inarticulate Brachiopods

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The microstructure of the lingulid brachiopods *Discradisca*, *Discinisca* and *Lingula* were examined with SEM, TEM, Vickers microhardness indentation and EDX-analysis. The shell can be described as an organic/inorganic composite structure with varying organic content. The inorganic material is a hexagonal or at least pseudohexagonal calcium phosphate, most likely a carbonate substituted Apatite with an average size of 10nm in diameter. A texture can be seen which corresponds to the growth direction of the shell. Microhardness indentations show large variations in microhardness throughout the shell, but no anisotropic behavior occurs. As the shell structure is still under investigation, preliminary results will be presented.

The Need of Using Complex Techniques When Investigating the Internal Morphology of Some Post Palaeozoic Rhynchonellides

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Most Cretaceous rhynchonellide authors in the past have used only serial sectioning techniques for discerning the internal morphology of the shell. Some common methodological difficulties are related to applying dissimilar techniques of this method, e.g. differing orientations. Dissected car-

dinalia of some representatives of the genera *Cyclothyris* McCoy and *Cretirhynchia* Pettitt have been observed under low vacuum SEM. Both genera are members of the superfamily Hemithyridoidea, characterized by raduliform crura. Surprisingly, two different kinds of crura were revealed in different representatives of the genus *Cretirhynchia*. The type species *Cr*. (*Cretirhynchia*) *plicatilis* (J. Sowerby) has typical thick-shelled cardinalia and raduliform crura. While in *Cr*. (*Harmignirhynchia*) *intermedia* Pettit finer falciform crura were observed, which according to traditional systematics should place them in another superfamily. The differences between the two groups of species were confirmed by shell ultrastructure investigations. The preliminary results call for a new revision of the genus *Cretirhynchia*

Conversely, the authors of Tertiary and Recent genera have mainly used observations of dissected cardinalia. We studied the internal morphology of the Pliocene species *Sphenarina sicula* (Davidson) using both serial sections and prepared cardinalia under SEM. Our serial sections revealed a septalium, which was overlooked by the author of the genus Cooper (1959) when examining only prepared cardinalia, which calls for revision of the genus.

This research proves the importance of extensive morphological studies applying a comprehensive combination of new and classical methods to investigate the shell interior wherever possible. No single method can give a clear unbiased image of the internal morphology in brachiopods.

Types of Size-Age Distribution in Recent Brachiopod Populations

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On the basis of the study of 40 mass samples of the Recent brachiopods: *Lingula anatina*, *Hemithyris psittacea*, *Terebratulina retusa s.l.*, *Terebratulina unguicula*, *Macandrevia cranium*, *Laqueus californianus*, *Diestothyris frontalis*, *Terebratella enzenspergeri* and literature reviews, eight types of size-age populations distribution have been defined. The following criteria have been used: the presence of animals of different size classes and their domination in populations; the presence or absence of recruitment, the type of age distribution, the asymmetry of size distribution.

Type 1. The population consists of several juvenile size classes; average size and adult individuals absent. This type corresponds to the young population.

Type 2. Juvenile individuals dominate, but they do not belong to the last recruitment.

Type 3. One or several size groups of adult individuals dominate. Juvenile brachiopods and individuals of the average sizes are present in smaller amounts.

Type 4. Two size groups dominate in populations: juvenile and adult.

Type 5. Juvenile, adult and average size individuals dominate populations.

Type 6. One or several size groups of the average size or adult individuals dominate. Juvenile individuals absent.

Type 7. The individuals of the average size dominate. Adult and juvenile individuals are not numerous.

Type 8. As a result of the death of older brachiopods, juvenile individuals appeared directly after recruitment, supplementing the basic part of populations.

New Locality of the Holocene Brachiopods from the Ancient Aleutian Midden

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The Recent brachiopod fauna of the Aleutian Islands is still not well recognized. In this area, eight species of brachiopods are known: *Hemithyris psittacea*, *Frieleia halli*, *Terebratulina unguicula*, *Terebratulina kiiensis*, *Laqueus californianus*, *Terebratalia tisimana*, *Terebratalia transversa*, and *Diestothyris frontalis*.

So any new information about the island's fauna and its origin is very important.

Brachiopods have been found in shell-middens of the ancient Aleutian site on the shore of the Sweeper Cove, Adak Island (ADK-009). The occupation layer formed 1880-750 ^{14}C years BP. Brachiopods have been found on all five levels of the this layer, except level III. They are represented by one species - Hemithyris psittacea, which was noted earlier on the Aleutian Islands` littoral. Two full shells, three ventral valves, eight dorsal valves, and fragments of the shells have been found. The length of the largest shell with nine growth-rings is 24 mm. Such rates of growth are typical for *H. psittacea* from the harbour area of the Norwegian, Barents, south-west part Kara, Chukchi, Bering, and Okhotsk seas.

It seems, the brachiopods have not been gathered specially. On the internal surfaces of some valves there are epibiotic animals. The valves were found already empty, probably, on the byssus of the mussels *Mitylus trossulus*. The material has been kindly given to me by A.B. Savinetsky (A.N. Severtsov, Institute of Ecology and Evolution, RAS).

Thysanotos siluricus and Associated Lingulate Brachiopods from the Lower Ordovician of the Alborz Mountains, Iran and Their Biogeographical Significance

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The lingulide brachiopod *Thysanotos* is widespread in late Tremadoc and early Arenig successions of Baltica (Estonia, Poland, South Urals) and some peri-Gondwanan terranes (Perunica). In Iran, a low diversity *Thysanotos* association has been discovered recently in the middle part of the Lashkarak Formation exposed at the Simeh-Kuh, north-west of Damghan. Below the first occurrence of *Thysanotos siluricus*, there are conodonts of the lower *Paroistodus proteus* Biozone together with the distinctive trilobites *Taihungshania miqueli*, known previously from the lower Arenig of Southern France and the lingulide brachiopods *Hyperobolus*, *Rowellella* and *Wahwahlingula* The conodont *Trapezognathus diprion* appears in the lower part of the overlying carbonate unit suggesting the upper *Oepikodus evae* Biozone. These carbonates also contain a medium diversity lingulate microbrachiopod assemblage, including *Acanthambonia*, *Acrotreta*, *Biernatia*, *Orbithele*, *Paterula*, *Pomeraniotreta* and *Rowellella*, among others. As in Baltoscandia, the first appearance of *Thysanotos* in the eastern Alborz Mountains is associated with the immediate onset of storm generated carbonate sedimentation in a period of significant environmental and faunal changes, resulting in the proliferation of rhynchonelliform brachiopod, bryozoan and ostracode dominated benthic assemblages typical of the early Palaeozoic evolutionary Fauna. Affinity with the early Ordovician (Billingenian to Volkhovian) linguliformean microbrachiopod assemblages of Baltica is accentuated by the presence of *Acrotreta*, *Alichovia* and the early appearance of *Biernatia*. By contrast, the Early Ordovician trilobite faunas from the Eastern Alborz retain strong affinities with contemporaneous faunas of South China and there is no sign of a close link to Baltica.

A New Rhynchonellid Brachiopod Genus from the Late Barremian of Eastern Serbia: Type Species *Rhynchonella panicici* Antula, 1903

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A new genus is erected based on examination of the internal morphology and shell ultrastructure of

Rhynchonella pancici Antula, 1903, a common species in the Upper Barremian shallow-water limestones of Carpatho-Balkanides of eastern Serbia. The shell of the new genus is small in size, spherical to transversely oval, fully costate, with hypothyrid rimmed foramen. The dorsal median septum is very much reduced. Dental plates are thin, ventrally convergent to subparallel, hinge plates straight to ventrally convex. Crura are canalifer, sometimes with widened distal ends, which fit well the diagnosis of Cretaceous Cyclothyridinae. The shell is composed of two calcitic layers. The primary layer is microgranular, 20µm thick in the sulci and 30 µm in the ribs. The secondary layer is built up of more anisometric and finer fibres close to the exterior (W = 15-25 µm; T = 3-5 µm) and larger and more isometric towards the internal margin of the shell (W = 35-45 µm; T = 8-12 µm).

'*Rhynchonella*' *pancici* occurs in association with other brachiopods showing strong Tethyan affinity and having close similarity to the Subtethyan (Jura) fauna: *Cyclothyris desori* (de Loriol), *C. gillieroni* (Pictet), *C. renauxiana* (d'Orbigny), *C. rostriformis* (Roemer), *Loriolithyris russillensis* (de Loriol), *L. valdensis* (de Loriol), *Musculina sanctaecrucis* (Catzigras), *Sellithyris carteroniana* (d'Orbigny), *S. essertensis* (Pictet), *Timacella timacensis* (Antula), *Dzirulina pseudojurensis* (Leymerie) and *Oblongarcula*? *equisita* (Pictet & Loriol). Only few brachiopods from the assemblage, such as *C. rostriformis* (Roemer), *Musculina sanctaecrucis* (Catzigras) and *Sellithyris carteroniana* (d'Orbigny) are typical Boreal forms.

A New Pliensbachian Rhynchonellid Brachiopod from Livari (Rumija Mountain, Montenegro)

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Using transverse serial sections and shell ultrastructure, a new rhynchonellid genus and new species is described. The new species is from brachiopod and crinoidal limestones of the periplatform facies (Dinaric Carbonate Platform) of the Rumija Mountain, Montenegro. It appears in association with *Cuneirhynchia lubrica* (Uhlig, 1880), *Prionirhynchia fraasi* (Oppel, 1861) and representatives of the genus *Rhapidothyris*, which indicate a Pliensbachian age of this fossiliferous limestone. Other rhynchonellids also occur in the assemblage.

Gemmellaro (1874) designated this rhynchonellid species from the Pliensbachian (zone with *Terebratula aspasia*) of Sicily as *Rhynchonella serrata* Sow. Referring to the external characters, such as medium size shell, roundly triangular outline, strong and subangular ribs, the new taxon shows a close similarity to *Prionorhynchia serrata* (J. de C. Sowerby), from which it differs in its slightly asymmetric rounded uniplication. Internally, it is different in having very short dental plates, hamiform crura and in the absence of a dorsal umbonal cavity. All these features allow the erection of a new genus.

SEM reveals a microgranular primary layer 20 µm thick and undifferentiated secondary layer built of a coarse-fibrous basiliolidine type. The fibres have a square to rhombic cross-sections, 40-55 µm wide and 30-35 µm thick.

The external and internal characters as well as shell ultrastructure of this new species list it among the family Basiliolidae Cooper, 1959, subfamily Pamirorhynchiinae Ovcharenco, 1983.

Mitochondrial Gene Order Comparisons in Long-Looped Brachiopods

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The complete mitochondrial gene arrangement has been determined, to date, for four brachiopod

species (*Lingula anatina, Terebratulina retusa*, *Laqueus rubellus* and *Terebratalia transversa*). Two of them are of the long-looped Laqueoidea (*L. rubellus* and *T. transversa*), but even within this superfamily their gene maps differ radically. Morphological and molecular inferences suggest that they are closely related; therefore, the differences must be due to rapid evolutionary changes of gene arrangements, and this in turn suggests that the mitochondrial gene order can be used as a convenient phylogenetic marker for the long-looped brachiopods. To gain detailed insight into this, however, a larger sampling of long-looped taxa within and outside the Laqueoidea is needed. We report here partial mitochondrial genome arrangements, determined by means of long-PCR, of long-looped taxa including several laqueoids (*Coptothyris grayi*, *Pictothyris picta*, *Jolonica nipponica* and *Shimodaia pterygiota*), dallinids (*Dallina raphaelis* and *Campages* sp.) and an ecnomiosid (*Ecnomiosa* sp.) collected from seas around Japan. The partial sequences of all examined laqueoids indicated a gene arrangement similar to *T. transversa*, as expected from the cytochrome *c* oxidase subunit I (*cox1*) phylogenetic tree. The results of long-PCR performed for the dallinids and ecnomiosid showed a pattern different from that of laqueoids and previously reported brachiopods, suggesting that they have a still different gene arrangement.

The Palaeoenvironmental and Palaeogeographical Implications of Late Palaeozoic Brachiopods from the Taebaeksan Basin in Korea

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The Upper Palaeozoic strata in the Taebaek area are mainly composed of a thick siliciclastic sequence containing diverse marine invertebrate fossils. In particular, the Geumcheon-Jangseong Formation (Moscovian-Artinskian), formed in a lagoonal environment, and yields abundant brachiopods.

They can be divided into several assemblages based on local and lithological differences as well as on the faunas themselves. It indicates that the palaeoenvironment was locally heterogenous and complex. Each assemblage reflects the ecology and environment on a small scale.

The brachiopod fauna has some important implications for the palaeogeographical relationships within and between the blocks of the Palaeo-Tethys Sea and Gondwananland.

Phylogeny of *Arduspirifer* (Brachiopoda, Delthyridoidea, Early Devonian)

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A phylogenetic tree of the Early Devonian brachiopod genus *Arduspirifer* Mittmeyer, 1972 is presented including figures of characteristic representatives of each species and subspecies. The reconstruction is based on data published by Solle (1953), Jansen (2001), and recent observations (Schemm-Gregory, 2004).

Fourteen taxa from Central and Western Europe and from North Africa have been identified, three of which are new: *A. arduennensis* n. subsp. A from the lowermost Upper Emsian (with reference to the regional chronostratigraphy) represents the phylogenetic link between *A. arduennensis arduennensis* (Schnur, 1853) and *A. extensus* (Solle, 1953). The derivation of *A. extensus* from *A. arduennensis prolatestriatus* Mittmeyer, 1973 as assumed by Jansen (2001) turned out to be improbable. The Upper Siegenian *A.* n. sp. B is considered as an early ancestor and the upper Lower Emsian *A. arduennensis* n. subsp. C as a late descendant of *A. arduennensis antecedens* (Frank, 1898).

The new results confirm the high biostratigraphic value of *Arduspirifer* in the neritic Lower Devonian of Europe and North Africa.

Jansen, U. (2001): Morphologie, Taxonomie und Phylogenie unter-devonischer Brachiopoden aus der Dra-Ebene (Marokko, Prä-Sahara) und dem Rheinischen Schiefergebirge (Deutschland). – Abh. Senckenb. naturforsch. Ges., **554**, 389 p.; Frankfurt a. M.
Schemm-Gregory, M.-D. (2004, unpubl.): Die Spiriferen-Fauna des Emsquarzits (Unter-Devon, Rheinisches Schiefergebirge). – diploma thesis, 127 p.; Marburg.
Solle, G. (1953): Die Spiriferiden der Gruppe *arduennensis-intermedius* im rheinischen Devon. – Abh. hess. L.-Amt Bodenforsch., **5**, 156 p.; Wiesbaden.

Brachiopods from the Upper Triassic Reef Habitats of the Northern Calcareous Alps (Dachstein Limestone, Hochschwab, Austria)

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The Hochschwab massif (Mürzalpen Nappe, upper Styria, Austria) is an extended, intensively karstified plateau. Its Upper Triassic (Norian-Rhaetian) is represented by the Dachstein platform, where a transition of facies zones from lagoonal to reef and forereef Dachstein Limestone is well developed. Brachiopod-bearing rocks were discovered during recent geological mapping at two places. Both localities - Karlhochkogel (2096 m) and Fölzalm are situated within the central reef facies. They yielded more than 900 variably preserved specimens belonging to 28 species. This collection represents the most taxonomically diverse brachiopod fauna known from the Dachstein Limestone. The brachiopod fauna is dominated by *Aulacothyropsis* ex gr. *reflexa* (Bittner), *Sinucosta emmrichi* (Suess) and *Oxycolpella eurycolpos* (Bittner). Seven species are known from the Kössen Formation. Some of them like *Laballa suessi* (Zugm.), *Zugmayerella koessenensis* (Zugm.), *Schwagerispira fastosa* (Bittner) and *Zeilleria austriaca* (Zugm.) are very similar to the same taxa from the Kössen Formation. Several other species differ in various details from their average Kössen namesakes (*Fissirhynchia fissicostata*, *Rhaetina pyriformis* and *Sinucosta emmrichi)*. All these different features are understood as intraspecific variability. There might be both stratigraphical and environmental significance in these variations. *Adygella biplicata* (Dagys) and Ladinian *Hungarispira loretzi* (Bittner) are newcomers in the Alpine Dachstein Limestone. The accompanying macrofauna consisted of poorly preserved bivalves. Very rare conodonts found at Karlhochkogel were identified as *Epigondolella triangularis* (Budurov, 1972) confirming a Lower Norian (Lacian 2) age (det. L. Krystyn, Vienna).

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Very Different Adult Specimens of *Terebratulina chrysalis* from the Upper Maastrichtian in Maastricht and from the Lower Maastrichtian from Rügen: Probably a Case of Ecotypical Adaptation

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The cancellothyrid brachiopod *Terebratulina chrysalis* (VON SCHLOTHEIM, 1813) is a species originally illustrated by FAUJAS DE SAINT-FOND (?1803, pl. 26, fig. 9).

FAUJAS certainly collected his material in Maastricht from the Meerssen Formation which was, during the period 1795-1803, the lowest Maastrichtian level accessible in this area. This Chalk of Meerssen is of latest Maastrichtian age. However, STEINICH (1965) revised *T. chrysalis* considering it as a common brachiopod from the Lower Maastrichtian white Chalk. Adult specimens from Rügen

(Germany) presented here exhibit distinctive characters: a relatively wide oval shell with a high number of fine costae and with a strong convexity of the posterior part of the dorsal valve.

Specimens of *T. chrysalis*, collected from Maastricht, appear much more regularly biconvex and are more elongate. The number of costae is variable but sometimes relatively lower. The "type" specimen of FAUJAS is a young specimen and juveniles from Rügen and from Maastricht are rather similar. Upper Maastrichtian juveniles from Maastricht are sometimes more elongate and with a lower number of costae, but these characters are rather variable. Moreover, the ring-like loops of the two *Terebratulina* are nearly identical. Adults from both places appear as distinct species while juveniles are very similar, as are the brachidia.

Numerous observations of large growth series suggest that strong differences between adults could represent ecotypical adaptations because white chalk in northern Europe (great depth, quiet water) and rough calcarenite in Maastricht (low depth, agitated water) are two very distinct ecological situations. This interpretation seems to be the most plausible.

Assemblages of *Terebratulina lata* Etheridge at the Locality Úpohlavy Quarry (Upper Turonian, Bohemian Cretaceous Basin, Czech Republic)

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The working quarry Úpohlavy near Lovosice (Czech Republic) lets us study a relatively large section through the Upper Turonian deposits. Two main maxima of *Terebratulina lata* Etheridge abundance in marls of the Teplice Formation have been observed in its outcrops. The origin, possible biostratigraphical correlation with the British Chalk and even some palaeoecological and taphonomical aspects of these two high abundance bands are discussed. To accomplish these intentions an accurate taxonomical determination is needed. Therefore the solution of the question of taxonomical position and/or determination of these so-called "minute terebratulinas" in the hemipelagic sediments of the Bohemian Cretaceous Basin is also given.

Faroese Articulate Brachiopods as Biogene Habitats, in a North Atlantic Fauna Perspective

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Six brachiopod species were recorded in Faroese waters before and during the recent inter-Nordic BIOFAR investigation. *Macandrevia cranium* (Müller, 1776), *Terebratulina retusa* (Linné, 1758) and *Dallina septigera* (Lovén, 1846) are the most often recorded, occurring in highest abundance between 200 and 500 m depth. While *Terebratulina* and *Macandrevia* are mostly confined to Atlantic Water (temperature above 7°C), *Dallina* is common also in slightly colder water, a mixture of Atlantic Water and Arctic Intermediate Water (temperature above 6°C). *Terebratulina* lives mostly on stones, dead corals (*Lophelia*), shell debris and other brachiopods, while *Macandrevia* prefers stones, but is also found regularly on shell debris and in monospecific clusters. *Dallina* is almost always attached to stones. The three species are substrate for an epifauna comprising foraminiferans, poriferans, hydrozoans, serpulids, cirripedians, bivalves, bryozoans and other brachiopods, dominated by thinly encrusting poriferans and bryozoans. Comparison to other North Atlantic areas allows the conclusion that all

over the northern boreal region, these brachiopods offer a biogenic substrate in localities with good water movement. Although there may be some competition for food particles between the brachiopod and its epiphytes, even heavy overgrowth seems normally not to be of inconvenience to the brachiopod, neither in its movements, nor in its growth and reproduction.

Morphological Variation within the Genus *Terebratula* Müller, 1776 from Italy

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We have analysed samples of brachiopods belonging to the genus *Terebratula* Müller. Two samples are of the species *T. terebratula* (Linnæus): the first is a Piacenzian (Pliocene) population from calcarenites of the Gravina Formation, near Canne della Battaglia (Apulia). The formation is the same as that containing the neotype of *T. terebratula*. The locality is very close to Andria, the type locality. The second "population" is a Miocene collection of *T. terebratula* from southern Italian localities.

Another population is from Upper Pliocene sands cropping out at Valle Botto (Asti, Piemonte). It contains *T. ampulla* (Brocchi). Finally, we included a population of *T. scillae* Seguenza. It is early Pleistocene in age (Emilian), and is from brachiopod-bearing sands nearby Lecce (Apulia). *T. scillae* was a very large brachiopod (up to 9.5 cm in length). It is the youngest known species of the genus *Terebratula*, and went extinct during the Sicilian (early Pleistocene).

Overall, our samples include hundreds of individuals. In order to recognize evolutionary trends and variability within the genus, we have analysed *Terebratula* specimens for their shape dissimilarity with the aid of geometric morphometrics.

Reorientation Ability in *Terebratalia transversa*: Ontogeny of Dorsal Pedicle Muscle Scars

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Dorsal pedicle muscles are ecologically important as they are responsible for active reorientation of rhynchonelliformean brachiopods. This project is focused on exploration of ontogeny of dorsal pedicle muscle scars in order to better understand life habits and distribution patterns of brachiopods. Two predictions were made by LaBarbera and Richardson. First, the increase in between-scar distance of dorsal adjustors with growth would imply a decrease in reorientation ability. Second, the decrease in size of dorsal adjustors with growth can correlate with a decrease in reorientation ability. A modern terebratulid *Terebratalia transversa* reorients in the juvenile stage only, with reorientation angle observed in the laboratory gradually decreasing up to zero at the stage of about 5-8 mm. Larger individuals have never been observed to reorient. It was tested if the two predictions accord with the observed behavior in *Terebratalia*. Both between-scar distance and size of scars show significant allometry, thus supporting the predictions. However, although an angle alpha (theoretical measure of reorientation) decreases gradually with growth, it attains about 30^{O} in adult *Terebratalia.* This means that no movement in the adult stage indicates a presence of some other morphologic or behavioural constraint which inhibits reorientation. In addition, it is shown that alpha is delimited not only by the position of scars with respect to the pedicle bulb, but also by the diductor muscle and its attachment site. Two predictions are thus supported, but the relationship between the theoretical and actual rotation angle is very complex.

Neospiriferin Brachiopods (Spiriferida, Trigonotretidae) from Ixtaltepec Formation, Pennsylvanian of Oaxaca State, Southern Mexico

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The brachiopods of the Subfamily Neospiriferinae (Order Spiriferida) *Neospirifer dunbari* King, *Neospirifer* sp. 1, *Neospirifer* sp. 2, *Septospirifer* sp. 1 and ?*Septospirifer* sp. are described for Pennsylvanian rocks of southern Mexico. The material was recovered from the type section of the Ixtaltepec Formation, near Santiago Ixtaltepec town, Nochixtlán Municipality, in Oaxaca State. Mexican *Neospirifer* species are associated with the *Neospirifer cameratus-dunbari* lineage, a typical North American group, and their presence in Oaxaca confirms the Morrowan-Desmoinesian age for the Ixtaltepec Formation and the faunistic similarity that exists between Carboniferous faunas from southern Mexico and those from the Midcontinent Palaeoprovince of North America. *Septospirifer* species represent the first record of the genus for Mexico and the third occurrence worldwide.

Several stratigraphic levels of the Ixtaltepec Formation contain abundant invertebrate faunas in which brachiopods referred to herein are a common component. In those faunas, bivalves are the most diverse group, although the number of specimens of brachiopods is higher. It is also possible to find abundant bryozoans and crinoids, some trilobites, rugose corals, and cephalopods in this association. The Ixtaltepec Formation, according to its sedimentological characters and the stratigraphic distribution of the fossils associations, is thought to represent deposition in a wide range of sedimentological settings, from prodelta, through reef and peri-reef lagoon, to offshore neritic environments with a high percentage of fine terrigenous sediments.

Stratigraphical Distribution of Jurassic Brachiopods in the Bakony Mountains (Hungary)

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The Jurassic brachiopod fauna of the Bakony Mountains (Transdanubian Central Range) is well-known: several thousand specimens were collected from the different stages. The collecting work encompassed the whole Jurassic sequence except the Callovian and Oxfordian, which are mainly represented by radiolarites. Brachiopods were collected together with ammonites and this offered an exceptional possibility to record their stratigraphic distribution. The ooidal-oncoidal, shallow-water Hettangian Kardosrét Limestone yielded 10 species. The Lower Sinemurian Pisznice Limestone and the cherty, crinoidal Isztimér Formation yielded 46 species. The Upper Sinemurian Hierlatz Limestone is extremely rich in brachiopods and 66 species were found at three localities. The Pliensbachian is the best studied stage (101 species); more than a dozen sections were collected in four different lithologies: red, condensed, manganiferous limestone; Hierlatz Limestone; crinoidal cherty limestone; ammonitico rosso-type limestone. The red limestone facies following the Early Toarcian anoxic event yielded only very few specimens of each species. The Aalenian ammonitico rosso-type limestone and greyish siliceous limestone are totally devoid of brachiopods. The same lithologies in the Early Bajocian yielded only a few brachiopods. The Middle and Upper Bajocian shows more diverse lithology (pelagic limestone; red, manganiferous limestone; Hierlatz-like limestone; radiolarite) with the bloom of brachiopods from the Humpriesianum Zone until the end of the Bajocian. Red, ammonitico rosso-type limestones are widespread in the Kimmeridgian but brachio-

pods are extremely rare. This limestone is predominant in the Tithonian but Hierlatz-like limestone and white micritic limestone also occur. Brachiopods are especially abundant and diverse in the Hierlatz-like limestones.

Upper Permian Brachiopods from Greenland: Preliminary Results of a Revision of Collections in the Geological Museum of Copenhagen

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Taxonomic revision of the collections of Permian brachiopods from Greenland housed at the Geological Museum in Copenhagen is in progress. Among the collections available is material from Frebold's 1931-1950 publications, material collected by W. Maync (listed in Maync, 1942), and material collected by Lars Stemmerik and his colleagues as part of a research project on Permian-Triassic boundary sections in East Greenland (Stemmerik *et al*., 2001).

The stratigraphic and palaeogeographic relationships of these brachiopod faunas will be analyzed. This study confirms the identity of a distinct biogeographic group, including the Permian faunas of Ellesmere Island, East Greenland, Spitzbergen and Novaya Zemlaya, with some similarities to those from the Zechstein basin but quite different from the better-known Tethyan assemblages.

Frebold, H., 1931. Fauna, stratigraphische und palaeogeographische Verhältnisse des Ostgrönländische Zechsteins. *Meddelelser om Grønland*, **84** (1): 1-55, 5 pls.
Frebold, H., 1931. Weitere Beiträge zur Kenntnis des Oberen Paläozoikums Ostgrönlands. *Meddelelser om Grønland*, **84** (7): 1-61, 6 pls.
Frebold, H., 1937. Das Festungsprofil auf Spitzbergen, IV: Die Brachiopoden- und Lamellibranchiatenfauna und die Stratigraphie des Oberkarbons und Unterperms. *Norges Svalbard- og Ishavs-Undersøkelser, Skrifter om Svalbard og Ishavet*, **69**: 1-85, 11 pls.
Frebold, H., 1950. Stratigraphie und Brachiopodenfauna des marinen Jungpalaeozoikums von Holms und Amdrups Land (Nordostgrönland). *Meddelelser om Grønland*, **126** (3): 1-97, 6 pls.
Maync, W., 1942. Stratigraphie und Faziesverhaltnisse der Ober-Permischen Ablagerungen Ostgronlands. *Meddelelser om Grønland*, **115** (2): 1-128, 6 pls.
Stemmerik, L., Bendix-Almgren, S.E. & Piasecki, S., 2001. The Permian-Triassic boundary in central East Greenland: past and present views. *Bulletin of the Geological Society of Denmark*, **48**: 159-167.

Porambonites and Related Taxa of the Family Porambonitidae from the Lower to Middle Ordovician of Baltoscandia

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Porambonites is presently considered the most important syntrophiidine taxon of the Baltic Ordovician fauna; the genus contains numerous species ranging from the Billingenian to Pirgu regional stages. The type species of the genus is *Porambonites intermedius*, designated by Hall and Clarke (1894). It was previously known only from the original publication of Pander (1830) but unfortunately Pander's original material has been lost. However, a number of brachiopods including several species of *Porambonites* collected and identified by Pander are still preserved in the St. Petersburg Mining Institute, Russia. This collection represents a potential source of neotypes for some forgotten brachiopod

taxa originally described by Pander. Rediscovery of specimens of *Porambonites intermedius* in the Billingenian of the East Baltic shows that the existing concept of the genus must be reconsidered and the generic name *Porambonites* (*sensu strictum*) can be applied only to the Early to Mid Ordovician porambonitid species with a smooth shell; the genus itself is endemic to Baltoscandia. Most of other Baltic species traditionally referred to the genus, including *Porambonites reticulatus* and *Porambonites intercedens*, are in a fact not congeneric with the type species, neither are all the taxa assigned to *Porambonites* from outside Baltica. The taxonomic position of *Porambonites* and related genera within the suborder Syntrophiidina also requires re-evaluation. Existing reasons for their attribution to the order Pentamerida are relatively weak and include mostly a presence of the astrophic shell and characteristic, long brachiophore plates. However, the absence of spondylial structures, long subparallel dental plates, characters of dorsal and ventral muscle fields and cardinalia in the early species of the group is quite different from typical syntrophiidines.