

## Molecular mechanisms of shell coiling in gastropods

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Various shapes of gastropod shells have evolved ever since the Cambrian. Although theoretical analyses of morphogenesis exist, the molecular basis of shell development remained unclear. We compared expression patterns of the decapentaplegic (dpp) gene in the mantle tissues at various developmental stages between coiled and non-coiled shell gastropods. In the two non-coiled shell limpets, *Patella vulgata* and *Nipponacmea fuscoviridis*, the dpp showed symmetric expression pattern at the mantle edge. On the other hand, in the dextral snail *Lymnaea stagnalis*, dpp is expressed at the right-hand side of the mantle. Moreover, we analyzed the functions of dpp using the Dpp signal inhibitor dorsomorphin in order to understand developmental mechanisms and evolution of shell formation in gastropods. When the embryos were treated with Dpp signal inhibitor at the trochophore and veliger stage after the shell gland formation, juvenile shells grew to show a cone-like form rather than a normal coiled form. These results suggest that the dpp gene plays important roles in the shell coiling in gastropods.

Keywords: Shell coiling, Left-right asymmetry, Shell, Gastropod

## Deposit-feeding strategy as an adaptation to substrate: comparison of Phymatoderma from shallow- and deep-sea deposits

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Phymatoderma is a branching burrow system consisting of tunnels filled with fecal pellets, and has been interpreted as a product of a surface deposit-feeding animal. Elemental analyses of Phymatoderma were conducted to reveal the feeding mode of its producer, using samples from the Lower Jurassic epicontinental shelf deposits in the Dotternhausen section, southern Germany and from the Upper Pliocene continental slope deposits in the Shioura section, central Japan. Elemental compositions of the pelletal infill of Phymatoderma and its overlying mudstone from the Dotternhausen section show no significant difference, suggesting that the tracemaker was a non-selective deposit feeder. In contrast, elemental compositions of the tuffaceous pellets of Phymatoderma from the Shioura section and its overlying volcanic ash show a difference: Ca is significantly concentrated in the pellets. Because microfossils such as foraminifera and coccoliths are occasionally found in the tuffaceous pellets, Ca accumulation in the pelletal infill indicates that the Phymatoderma-producer that lived in the Pliocene slope setting selectively ingested particles with higher biomass of such microorganisms (or ingested microorganisms themselves) when feeding the surface sediments. These two feeding modes of the producer were recognized in Phymatoderma of different bathymetrical settings, and each feeding mode seems to be an effective strategy to intake nutrients from the surface sediments, reflecting an adaptation of the tracemaker to the food-contents in the surrounding substrate. This study demonstrated for the first time that geochemical composition of fecal pellets of trace fossils can be a useful indicator of grain-selective/non-selective deposit-feeding strategies of ancient animals.

## Organic carbon cycling in deep-sea benthic ecosystem during the Paleocene-Eocene Thermal Maximum

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The Paleocene-Eocene Thermal Maximum (PETM) has been held up as a past analog to future warm environments and presents the opportunity to study climate impacts on marine communities. Today the deep-sea benthic ecosystem contributes substantially to carbon cycling in seafloor sediments. During the PETM, amount of carbon would have input into ocean and biosphere. The carbon could be taken up by organisms with higher metabolic rate under warm condition. However, the role of metabolic rates in benthic organisms has never been elucidated. Metabolic rates reflect respiration, that exchanges carbon between organic matter and carbon dioxide, thus respiration reflects both carbon cycling as well as metabolic rates in an organism. Here we evaluate respiration of ostracodes from DSDP Site 401, outer Bay of Biscay, North Atlantic through the onset of the PETM. Ostracode respiration can be calculated using body size and temperature. We measured ostracode body size and analyzed benthic foraminifer Mg/Ca thermometer. Body sizes of three species decreased through the onset of the PETM, while temperature of the bottom water increased. Estimates of the body size and temperature suggest a decline in lifetime respiration in ostracode individuals during the PETM interval. The reduced respiration might be related to decreases in metabolic rates and oxidation of organic matters. Dwarfed ostracodes during the PETM core interval would uptake less organic matters than ostracodes in the pre-PETM interval, since ecological studies show that modern ostracode grazing rates depend on their body-sizes. Hence we consider major changes in the energy and carbon balance of the benthic food-chains and the reduction of organic carbon flux between the ostracodes and sediments during the PETM. The decline in ostracode carbon flux contrasts with previous interpretations that benthic foraminifers switched their taxonomic composition that recycled more organic matters.

Keywords: DSDP Site 401, Ostracoda, Body size, Metabolic rate, Paleocene-Eocene Thermal Maximum, Organic carbon cycling

## Environmental changes spanning the end-Devonian extinction: Evidence from biomarkers

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Oceanic anoxia and marine extinction events occurred several times during the late Devonian marked by development of land vascular plant, which should have produced a lot of organic soils. One of the severe ocean anoxic and extinction events during the late Devonian occurred at the end of the Devonian ("Hangenberg Event" marked by "Hangenberg Black Shale"). However, the cause and processes of this event are still remained unknown. We investigated the strata, which were probably deposited on the continental slope, containing the D/C boundary of the Pho Han Formation located in the Cat Ba Island, eastern Vietnam to show the palaeoenvironment spanning the end-Devonian extinction using organic geochemical analyses.

The values of total organic carbon contents (TOC), total sulfur contents, and dibenzothiophene show a drastic increase from the base of the black shale to the D/C boundary in this section, which suggests anoxic condition extending in the sea at that time. Dibenzofuran and coronene, which are organic molecules indicative of the inputs of organic soils made by land vascular plants, have more detecting points in the beds between the base of the black shale and the D/C boundary than the other beds. Values of cadalene, which is derived from terrestrial higher plant, in the top Devonian beds are ten times of those in the other beds, which also showing an increase in inputs of terrestrial organic soils in the area at that time. Hopanes, which are derived from bacteria, and steranes, which come from eukaryote, are detected continually in the top Devonian beds show distinct increases compared with those in the other beds, and the values of  $C_{27}/(C_{27}+C_{29})$  sterane are more than 0.45 indicating the ratio of the organic matters from ocean primary production are more than that from terrestrial plants. These results indicate that bacteria and eukaryote kept on being active during the end of the Devonian, and thereby marine-derived organic matters are dominant compared with terrestrial-derived organic matters. It may have been resulted from the increases of the inputs of terrestrial nutrients. The increase in oceanic primary productivity may have caused consumption of seawater oxygen and reducing environment expanding in the sea resulting high TOC. Moreover, the values of 2-methyltetradecane and 3-methyltetradecane, which are derived from sulfate reducer, and aryl isoprenoids, which could come from green sulfur bacteria, show increases more continually in the top Devonian beds, implying that sulfate reducer kept on being active and reducing environment extended up to the photic zone in the sea at that time. Input of soils leading reducing environment in the sea may have caused the end-Devonian extinction.

## Leaking Earth: An ultimate trigger of the Cambrian explosion

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The Phanerozoic time began from the Cambrian explosion. Most of the ancestral life forms, more than at least 20 Phyla, appeared in a short time from 540-520Ma. Metazoans up to 35 Phyla appeared by the end of the Cambrian at 488Ma. Since then, animals and plants began to diversify extensively in association with environmental and geochemical diversifications. This is initiated by the global supply of nutrients. An abrupt increase of nutrient supply was caused by the emergence of huge landmass, because the amount of water in the mantle wedge must have increased from 1.0wt% to 6.5 wt%, if subduction zone geotherm began to cut the boundary of the stability field between clinoclone peridotite and antigorite peridotite during the cooling. This means the initiation of return-flow of seawater into mantle during the Neoproterozoic, so called Leaking Earth.

We envisage the following processes for the dawn of the Phanerozoic. (1) initiation of return-flow of seawater into mantle was caused by hydration of mantle wedge, (2) leading to the drop of sea-level. (3) Subsequently, the coast line moved oceanward to increase the size of landmass, (4) with the resultant birth of huge river systems to transport large volumes of sediments (5) which buried organic matter synthesized by photosynthesis by algae and cyanobacteria. (6) The burial of organic matter resulted in accumulating oxygen in atmosphere as back reaction to consume free oxygen in atmosphere is prevented. (7) High pO<sub>2</sub> began to be kept and finally diffused upwards to form the ozone layer. (8) Ozone layer shielded the ultraviolet radiation from Sun, thereby enabling plants and animals to invade the land. Firstly, cyanobacteria invaded in the swamp along the river to lake. It gradually evolved to algae, bryophytes and to Tracheophytes by late Devonian.

Initiation of return-flow of seawater into mantle began 4.0 b.y after the birth of planet with R (radius) = 6400km and only 3-5km thick ocean. It brought a golden era of life, accompanying global supply of nutrients continuously. The leaking Earth was the fate of cooling planet, Earth, covered by ocean. It is an ultimate trigger of the Cambrian explosion.

## Neoproterozoic thrombolite and spherical structures from Brazil: Expected images of the oldest multicellular animal

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Intensive researches on the Neoproterozoic sediments in the last two decades have demonstrated drastic climate changes and unveiled traces of biological evolution. We studied the Neoproterozoic Salitre Formation (Una Group) in central Bahia (Brazil) for seeking novel signature of early life. This formation contains cap carbonate on the base, and overlies diamictites corresponding to Marinoan or Sturtian glaciation.

Lithofacies of the Salitre Formation are various from shallow-water stromatolite to deep-water slumped bedded carbonate. Organic-rich carbonate unit partly appears an enigmatic feature consisting of digitate structures of 5 mm in width. This has been called thrombolite. The digitate structures are concentrated in a lentic body of ~5 m thick and ~20 m wide. In the silicified digitates, aggregation of clots or peloids was observed. The thrombolites could be microbial, as stromatolites, but this interpretation is inconsistent with homogenous outer forms and lack of internal lamination. This might be a structure originated from a lithified animal body. According to the historical background of the animal evolution, a most likely candidate was a sponge. The clots and peloids found in the silicified part resembles in appearance of structures formed in decayed body of sponge (Neuweiler et al., 2007).

The Salitre carbonate also contains spherical structures of ~4 mm in diameter. The spheroids have organic membrane and calcite filling. They are too large for acritarchs that are abundant in the Neoproterozoic strata. They are unlikely giant microbes, such as *Thiomargarita*. An animal egg was a possible origin, but they are again too large as an egg of the modern sponges. Digitate and spherical structures may bring novel material considering evolution of multicellular animals if they were originated from sponges.

Neuweiler et al. (2007) *Jour. Sediment. Res.*, 77, 552-563.

Sial et al. (2010) *Development in Precambrian Geology*, 16, 31-69.

Keywords: Neoproterozoic, animal evolution, carbonate, Brazil

## Chemostratigraphy of the Ediacaran Doushantuo Formation in central Guizhou province

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In the Ediacaran period (635 Ma ~ 542 Ma), the Marinoan and Gaskiers glaciations have been widely recognized as drastic climate changes. Because these changes were temporally associated with evolution of the metazoan, the crucial relationships has been discussed actively. The Ediacaran Yangtze platform in south China is a key locality for understanding the relationship due to well-preserved sedimentary rocks of various environments from shallow to deep ocean. Additionally there are many Ediacaran fossil records from this platform.

There are many sections that yield fossils, such as Miaohu biota and Wengan biota from the Ediacaran Yangtze platform. The Wenghui section in central Guizhou province is one of them, and exposes a basinal facies (Jiang et al., 2011). The fossils from this section include algae, sponges and annelids and are called the Wenghui biota (Jiang et al., 2011; Wang and Wang 2008, 2010). Despite the importance of this biota, geochemical analyses have never performed for the Wenghui section, and therefore the correlation with other Ediacaran sections is poorly understood.

Wenghui section is about 65 m thick and divided into the Nantuo Formation, the Doushantuo Formation and the Liuchapo Formation in ascending order. The Nantuo Formation is extensively distributed as post-Marinoan diamictite in the Ediacaran Yangtze platform. The Doushantuo Formation consists of carbonate-shale sequence, and the occurrences of pyrite throughout this formation indicate a reductive environment. This formation includes the Wenghui biota in black shale of the upper part (Wang and Wang 2008, 2010). Additionally, we found a new fossil horizon of carbonate rock in lower part, which yields algae and sponge spicules from. These fossils are mainly preserved as apatite. The overlying Liuchapo Formation exposed in the upper section consists of the alteration of black chert and black shale. This Formation is correlated with the Dengying Formation distributed in shallow facies of the Ediacaran Yangtze Platform.

We are analyzing inorganic carbon and oxygen isotopes in order to consider paleoenvironment of Wenghui section and provide chemostratigraphic correlation, and will represent the results.

Keywords: Ediacaran, chemostratigraphy, China



## Repeated anoxia-extinction episodes progressing from slope to shelf during the latest Cenomanian

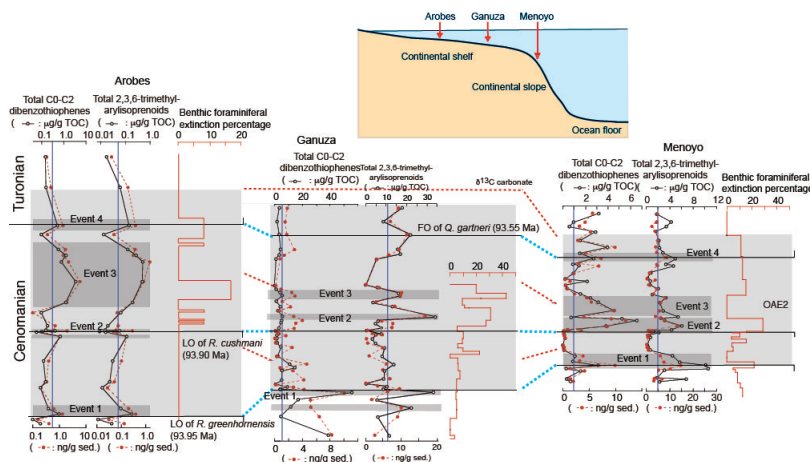
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Oceanic Anoxic Event 2 (OAE 2) during the Cenomanian-Turonian (C/T) transition caused stepwise marine extinctions. Using organic compounds, stable carbon and oxygen isotopes, and foraminifera from three depth-transect sections in northern Spain, this study revealed repeated anoxic/euxinic events coinciding with warming and stepwise extinctions of planktonic and/or benthic foraminifera within intermediate to surface waters in the proto-North Atlantic during the C/T transition. Those short-duration euxinic events occurred four times: at 93.95 Ma, marked by the extinction of *Rotalipora greenhornensis*; at 93.90 Ma, marked by the extinction of *Rotalipora cushmani*; at the mid-time maximum of the plateau of the  $\delta^{13}C$  of carbonates (93.70 Ma); and at the time of the C/T boundary (93.55 Ma). Furthermore, the main benthic foraminiferal extinctions occurred during the first and second euxinic events in the upper slope, during the second and third euxinic events in the outer to middle shelf, and during the third and fourth events in the middle shelf. The main euxinic events in each section also showed a progression to the shallow shelf. The main anoxia-extinction events occurred in the upper slope and outer shelf then moved to the middle shelf. The shallowest section had relatively weak anoxia and a proportionally low extinction rate. These new findings indicate that foraminiferal extinctions started from the intermediate water and the continental slope and then moved to the continental shelf. This was the result of the repeated progression of euxinic-anoxic water from the upper slope to the middle shelf on the eastern continental margin of the proto-North Atlantic four times during a 400 kyr period, to the end of the Cenomanian.

Kaiho, K., Katabuchi, M., Oba, M., Lamolda, M. (2013) Repeated anoxia-extinction episodes progressing from slope to shelf during the latest Cenomanian. *Gondwana Research*, in press.

Keywords: biomarker, Oceanic Anoxic Event 2, extinction, anoxia, surface temperature





## Kerogen analysis of sedimentary rocks deposited during the Cretaceous OAEs

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Some of the formations deposited during the mid-Cretaceous, which is extremely warm period, are characterized by organic-rich laminated black shale which was thought to be deposited as a result of repeated expansion of ocean anoxia, called 'the oceanic anoxic events (OAEs)'. Organic matter in the black shales from the levels of the OAEs is well preserved and abundantly contains organic microfossil (palynomorph). Palynomorph analysis under transmitted light microscope has been performed in the sedimentary rocks from the levels of the OAEs (e.g., Heimhofer et al., 2006), although most of the analyses were focused on only a few specific organic microfossils such as spore, pollen and marine algal cyst. In the present study, we analyze palynofacies and palynomorph including very-small size palynomorph such as acritarch of kerogens in sedimentary rocks from the levels of the OAEs in the Vocontian Basin.

Black shales were collected from the outcrops of the Goguel (OAE1a), Jacob, Kilian, Paquier, Leenhardt (OAE1b), unnamed (OAE1c), Breistroffer (OAE1d) and Thomel (OAE2) levels in SE France. These crushed samples were extracted with ultrasonication and their residues were sequentially treated by HCl and HF in a water bath shaker (Sawada et al., 2012).

From results of palynofacies analyses, it is found that amorphous organic matter (AOM) account for more than 80 % in whole kerogen. The relative abundances of weakly-fluorescent AOM (WFA), which is thought to be marine origin, were higher at the Goguel, Breistroffer and Thomel levels, while non-fluorescent AOM (NFA), which may be terrigenous origin was abundant at the Paquier and unnamed OAE1c levels. Moreover, the Thomel level is characterized by abundant fluorescent AOM (FA), which is thought to be fragment of terrestrial phytotissue, and phytoclasts (particle of cuticle and wood) were abundant at the Paquier, OAE1c and Thomel levels. We suppose that terrestrial input was enhanced during the OAE1b, 1c and 2. Above the Paquier level, trilete and monolete-type spores (spore of bryophyte or pteridophyte) were dominant in spore/pollen assemblage. These results imply that eutrophic condition at sea surface water in the Vocontian Basin after the OAE1b, because they favored wetter environment and their spore might be efficiently transported by fluvial system. The Paquier and more upper levels were predominated by dinocyst and related small acritarch, whereas Sphaeromorph-type acritarch that is related to Chlorophyta was mainly identified at the Goguel level. These cysts were thought to be originated from marine autotroph algae. Hence, it indicated that marine producer was different between these OAEs.

Keywords: oceanic anoxic events (OAEs), kerogen, dinoflagellate, acritarch, palynomorph, palynofacies

## Analysis of shell beds from Yabu Formation in Semata, Ichihara City, Chiba Prefecture, Japan.

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This is study of shell beds in the Middle Plesitocene Yabu Formation of the Shimousa Group. Many studies have been done for the Yabu Formation(e.g. Aoki and Baba, 1970 ; Nishikawa et al. , 2000). However, these literatures didn't focus on detailed scale of shell beds in the Yabu Formation. So, we studied detailed analysis of the shell beds using oriented block sample.

In Semata, Ichihara City, Chiba Prefecture, a part of Yabu Formation(ca, 3m thick) has been exposed. The Yabu Formation is composed of sandstone. The exposed strata can be classified into lower and upper parts. Boundary between upper and lower parts are 1.3m above the bottom of outcrop. There are HCS and SCS in the lower part,shells parallel to their bedding planes. Shell beds are frequently intercalated in the upper part. We took oriented block sample (40cm\*40cm\*30cm) from the outcrop. The Yabu Formation is not enough to consolidate for block sampling. Thus, we made wooden frame(called " GOSSON " ) to prevent collapsing of the strata. Base of the sample is same as boundary of upper and lower units.

We brought oriented specimen in the laboratory, and carefully removed sediments parallel to the bedding plane from upper side of the sample. On this occasion, we defined section as that a layer including shells, i.e. boundary between each section is a layer with no fossils. We described following information; a convex-up/down of bivalve, horizontal position, species, apex orientation, maximum shell length(=L),articulation. In addition we calculatate convex-up rate, number of individuals, area density of fossil (=the area that a fossil accounts for / whole area in each section), size distribution(three demarcation:  $L \geq 40\text{mm}$ ,  $40\text{mm} > L > 20\text{mm}$ ,  $20\text{mm} \geq L$ ) in each section.

Totally 60 section were recognized in the sample. The thickness of each section was 3 ? 12mm. 427 specimens( 425 specimens with 13 species for bivalve, 2 specimens with 2 species for gastropod and 2 specimens with 1 species for scaphopod) have been identified from the sample. All the bivalves were disarticulated. Thus, the all shells were transported from their original living place. The convex-up rate was more than 80% in 48 sections. The results suggest that the shells were deposited not under influence of turbulent flow, but unidirectional flow. In contrast, the convex-up rate in section 10, 58, 59 was less than 50%. It indicates that shells didn't deposit by unidirectional flow in this horizons. The number of individuals and area density of fossil increased from section 01 to section 44. It tends to decrease above section 44. The results indicate that conditions of transportations and sea floor were changed several times during the shell accumulated beds were forming. According to shell size distribution, i.e. the large ( $L \geq 40\text{mm}$ ) shells are rare when the small ones ( $20\text{mm} \geq L$ ) are abundant in the section, the shells are well sorted during transportations.

It is concluded that 1) by using the abovementioned method, it is possible to take oriented block samples even from the unlithified sandstone. 2) as a careful and detailed analyses within a shell bed revealed that the shell bed was formed by a multiple sedimentation event.

Keywords: oriented block sampling, shell beds, Yabu Formation, taphonomy

## Measuring morphological richness in morphospace: another look at disparity

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Detecting patterns of change in biodiversity has been at the center of paleontological studies during the past quarter-century. Recently, there has been much interest in relationship between taxonomic diversity and morphological disparity. Studies on diversity change need an appropriate measure of diversity as well as removal of sampling overprints. The taxonomic diversity is assessed through compilations of the number of taxa, i.e., taxonomic richness. Meanwhile, the morphological disparity is commonly based on measurements of morphological distance between objects, e.g., sum of variance, mean pairwise distance, range of variation etc. Richness and distance (or dissimilarity) are different properties of diversity and cannot be compared on an equal plane. Comparison between taxonomic diversity and disparity needs to develop measures of morphological richness such as number of pairwise character-state combinations and participation ratio. Counting the number of pairwise characters requires the division of the morphospace up into discrete bins. However, measures of morphological richness hitherto been available highly depends on how to bin the morphospace as well as on sample size.

Here, I would propose a method to assess morphological richness and morphological evenness that are robust with respect both to option for analysis and sampling effort. At the first step, the probability density of data in a morphospace is estimated using multi-dimensional kernel density estimation instead of depicting a histogram. In the next step, randomized subsampling of data is designed to remove sampling intensity biases using the probability densities at the positions where the sampled data occupy in the morphospace. Subsampling is carried out until the data that have been sampled have a summed total of the probability densities which equals a fixed proportion. This approach is closely related to the shareholder quorum sampling rather than classical rarefaction. A morphological richness is assessed by an extent of the Bayesian highest posterior density region of the probability density of the subsample in the morphospace. Conventional participation ratio based on discrete criteria is extended to a case of continuous variables so as to define a new measure of morphological evenness.

Keywords: disparity, richness, evenness, morphospace