Phylogenetic evidence for the origin and diversification of whale-fall fauna

*Glover Adrian[1]
*Adrian Glover[1]

1. Natural History Museum, London
1. Natural History Museum, London

The first discovery of a chemosynthetic faunal assemblage on a whale-fall in 1987 was significant not just in advancing our understanding of deep-sea ecology and succession, but in also generating new hypotheses for the evolutionary origin of the deep-sea fauna. Could these remarkable habitats also provide avenues for dispersal and speciation over evolutionary time? The early phylogenetic studies provided some support for this controversial hypothesis. But more recent and comprehensive research has shown that the picture is more complicated. Here I review evidence for what I see as three possible hypotheses: the ‘evolutionary stepping-stone hypothesis’ where whale-falls have actually created a pathway for radiation into other chemosynthetic habitats, the ‘ecological stepping-stone hypothesis’ in which whale-falls play a role only in aiding dispersal in ecological time, and the ‘hotspots of adaptive radiation hypothesis’ in which whale -falls act as a biodiversity pump for fauna that originally evolved at hydrothermal vents or seeps.

ウミガメ遺骸の腐敗過程と遺骸に成立する生態系の解明
The deacay process of and the biological community on sea turtle-falls at the Tsukumo Bay, Noto Peninsula, Jpan

*鈴木 碧[1]、ジェンキンズ ロバート[2]、小木曽 正造[3]、又多 政博[3]、信雄 鈴木[3]
*Midori Suzuki[1], Robert Jenkins[2], Shouzo Ogiso[3], Masahiro Matada[3], Nobuo Suzuki[3]

1. 金沢大学院自然科学研究科自然システム学専攻、2. 金沢大学理工研究域自然システム学系、3. 金沢大学環日本海域環境研究センター
1. Division of Environmental Science and Engineering, Graduate School of Natural Science and Technology, Kanazawa University, 2. Kanazawa University, 3. Institute of Nature and Environmental Technology Kanazawa University

The whale-fall community is one of the unique biological community formed on decaying whale carcass on the sea floor. The community thought to be changed at least four stages of ecological successions, i.e. the mobile scavenger stage, the opportunist enrichment stage, the sulphophilic stage and the reef stage. Molecular studies on some organisms included in the community suggested that the origin of the vent- and/or seep-restricted animals have come from through environments formed around such organic-falls. In this point of view, the reptile-falls would be more important than the whale-falls because of its longer fossil record than the marine mammals. Although the ecosystem on the whale-fall has been studied well, the ecosystem on the reptile-fall hasn’t been studied in details. Thus, we examined the decaying process of four sea turtles deployed on shallow sea floor (11 to 14 m in depth) in Tsukumo Bay, Noto Peninsula, Japan. The carcasses were observed by scuba, and some bones of the carcasses were recovered time to time to examined organisms which lived on/in the bones.

5 days after deployment, the sea turtle carcasses were covered by white microbial mat (*Bggiatoa* spp., indicator of sulphophilic stage). 21 days after deployment, the carcass was eaten by fish (indicator of mobile scavenger stage). *Zoothamnium* sp. (indicator of sulphophilic stage) was observed on the carcass. 36 days after deployment, dorvilleid and nereidid polychaetes (indicator of opportunistic stage) lived in the bones and barnacles (Crustacea; indicator of the reef stage) were attached to the bone. Thus, all four stages of ecological succession observed on whale-falls have also been observed on the sea turtle falls within 36 days after deployment. It is noteworthy that the sea turtle-fall sustained chemosynthetic community as same as whale-falls.

To examine sustainability of opportunistic and sulphophilic stages, we compared faunal assemblages in/on the recovered bones of the sea turtle carcasses with different body size and deployment period. Organic matrix was still remained in the bones of 2016ST-1(green turtle, carapace length (CL) = 42 cm, 144 days after deployment) and 2013ST-L (loggerhead turtle, CL = 72 cm, 3 years after deployment). There were *Beggiatoa* microbial mats, *Zoomthamnium* sp. and dorvilleid polychaetes in/on the bones. In contrast, there is no organic matrix in the bones of 2013ST-S (green turtle, CL = 36 cm, 3years after deployment), and there were no *Zoothamnium* sp. and dorvilleids. Thus, the smaller sized carcass exhausted within 3 years, but the larger carcass sustained opportunistic and sulphophilic stages more than 3 years.

キーワード：ウミガメ、遺骸、鯨骨群集
Keywords: sea turtle, carcass, whale-fall

メタン酸化古細菌のバイオマーカー炭素同位体比による古冷湧水メタンの起源推定

Origin of methane at ancient seeps inferred from carbon isotopic signatures of biomarkers of methane-oxidizing archaea

*宮嶋 佑典[1,3]、渡邊 裕美子[1]、井尻 暁[2]、後藤（桜井） 晶子[3]、ジェンキンズ ロバート[3]、長谷川 卓[3]、坂井 三郎[4]、松本 良[5]

*Yusuke Miyajima[1,3], Yumiko Watanabe[1], Akira Ijiri[2], Akiko S Goto[3], Robert Jenkins[3], Takashi Hasegawa[3], Saburo Sakai[4], Ryo Matsumoto[5]

1. 京都大学大学院理学研究科地球惑星科学専攻地質学鉱物学分野、2. 海洋研究開発機構高知コア研究所、3. 金沢大学理工研究域自然システム学系、4. 海洋研究開発機構生物地球化学研究分野、5. 明治大学ガスハイドレート研究所

1. Department of Geology and Mineralogy, Division of Earth and Planetary Sciences, Graduate school of Science, Kyoto University, 2. Kochi Institute for Core Sample Research, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 3. School of Natural System, College of Science and Engineering, Kanazawa University, 4. Department of Biogeochemistry, JAMSTEC, 5. Gas Hydrate Laboratory, Organization for the Strategic Coordination of Research and Intellectual Properties, Meiji University

メタンは有機物の微生物分解または熱分解により生成し，その起源はメタンの炭素安定同位体比などから推定できる．海洋へのメタンの主要な放出場であるメタン湧水では，湧出するメタンの起源を知ることで海底下の生物地球化学プロセスや水循環について知ることができる．地質時代の古メタン湧水は，微生物が起こす嫌気的メタン酸化によって形成されたメタン起源炭酸塩岩として地層中に保存される．メタン起源炭酸塩岩はメタン由来の炭素を引き継いでいるが，形成時に海水中の溶存無機炭素などメタン以外の炭素も取り込むため，炭酸塩岩の炭素同位体比から過去に湧出していたメタンの同位体比を推定することは難しい．本研究では，メタンの同位体組成をより直接反映していると考えられるメタン酸化古細菌の脂質バイオマーカーの炭素同位体比をもとに，古メタン湧水のメタンの起源推定を試みた．分析には日本海側陸域11か所の下部中新統～中部更新統より採集した古メタン湧水炭酸塩岩と，上越沖海底の熱分解メタンの湧出域で採取された現世の炭酸塩ノジュールを用いた．すべての炭酸塩の初生的な組織は−64.7～−4.7‰（vs. VPDB）の幅広いδ^{13}C値を示し，微生物または熱分解メタンの両方が起源として考えられる．古メタン湧水炭酸塩岩より抽出したバイオマーカーであるペンタメチルイコサン（PMI）はほとんどが−100‰より低いδ^{13}C値を示したのに対し，上越沖の現世炭酸塩ノジュールから抽出したPMIは−80‰というより高いδ^{13}C値を示した．上越沖で湧出するメタン（−36‰）と炭酸塩中のPMIとの炭素同位体分別は−44‰であり，この分別が過去も同じであったと仮定すると，対象とした日本海側地域の古メタン湧水ではδ^{13}C値が−50‰より低い微生物起源のメタンが湧出していたと推定できる．このことは，対象とした古メタン湧水では海底下浅部で生成したメタンが供給されており，断層などの経路を通じた深部起源の熱分解ガスの海底への湧出はなかった可能性を示唆する．過去の湧水中のメタンの同位体組成をより制約するため，炭酸塩中に残留しているメタンを抽出する試みも進行中である．今後は炭酸塩の微量元素組成などの流体の起源指標と合わせて，古メタン湧水のメタンの起源を推定する必要がある．

キーワード：メタン、冷湧水、バイオマーカー、新生代、日本海

Keywords: Methane, Cold seep, Biomarker, Cenozoic, Japan Sea

Mussel genomes provide insights into adaptation to deep-sea chemosynthetic environments

*Pei-Yuan Qian[1], Jin Sun[1], Jian-Wen Qiu[2]

1. Hong Kong University of Science and Technology, 2. Hong Kong Baptist University

The environment of deep-sea hydrothermal vents and methane seeps is characterised by darkness, lack of photosynthesis-derived nutrients, high hydrostatic pressure, variable temperatures and high concentrations of heavy metals and other toxic substances. Despite this, these ecosystems support dense populations of specialised macrobenthos such as giant tubeworms, mussels, limpets, clams and shrimps. Lack of genome information hinders understanding of the adaptation of these animals to such inhospitable environment. Here we report the genomes of a deep-sea vent/seep mussel *Bathymodiolus platifrons* Hashimoto & Okutani, 1994 and a shallow-water mussel *Modiolus philippinarum* (Hanley, 1843). Phylogenetic analysis shows that these mussel species diverged approximately 110.4 million years ago (MYA). Many gene families, especially those for stabilising protein structures and removing toxic substances from the cell, are greatly expanded in *B. platifrons*, indicating adaptation to extreme environmental conditions. The *B. platifrons* innate immune system is considerably more complex than that of other lophotrochozoan species including *M. philippinarum*, with significant expansion and high expression of gene families related to immune recognition, endocytosis and caspase-mediated apoptosis in the gill, revealing presumed genetic adaptation of the deep-sea mussel to the presence of its chemoautotrophic endosymbionts. A follow-up metaproteomic analysis of the gill of *B. platifrons* found methanotrophy, assimilatory sulfate reduction, and ammonia metabolic pathways in the symbiont, providing energy and nutrients to allow the host to thrive without dependent on photosynthesis derived food. Our study of the genomic composition allowing symbiosis in extremophile molluscs gives wider insights into the mechanisms of symbiosis in other organisms such as deep-sea tubeworms and shallow-water corals.

In addition, we would also like to take this opportunity to introduce a large-scale program on “U-Shape” area that targets at the vents along the Mid-Ocean Ridge of both South Atlantic and Western Indian Ocean, to be launched by China Ocean Mineral Resource Research and Development Association, for which we call for international collaboration in next 15 years.

Keywords: Genome sequencing, Bathymodiolus, Symbiosis

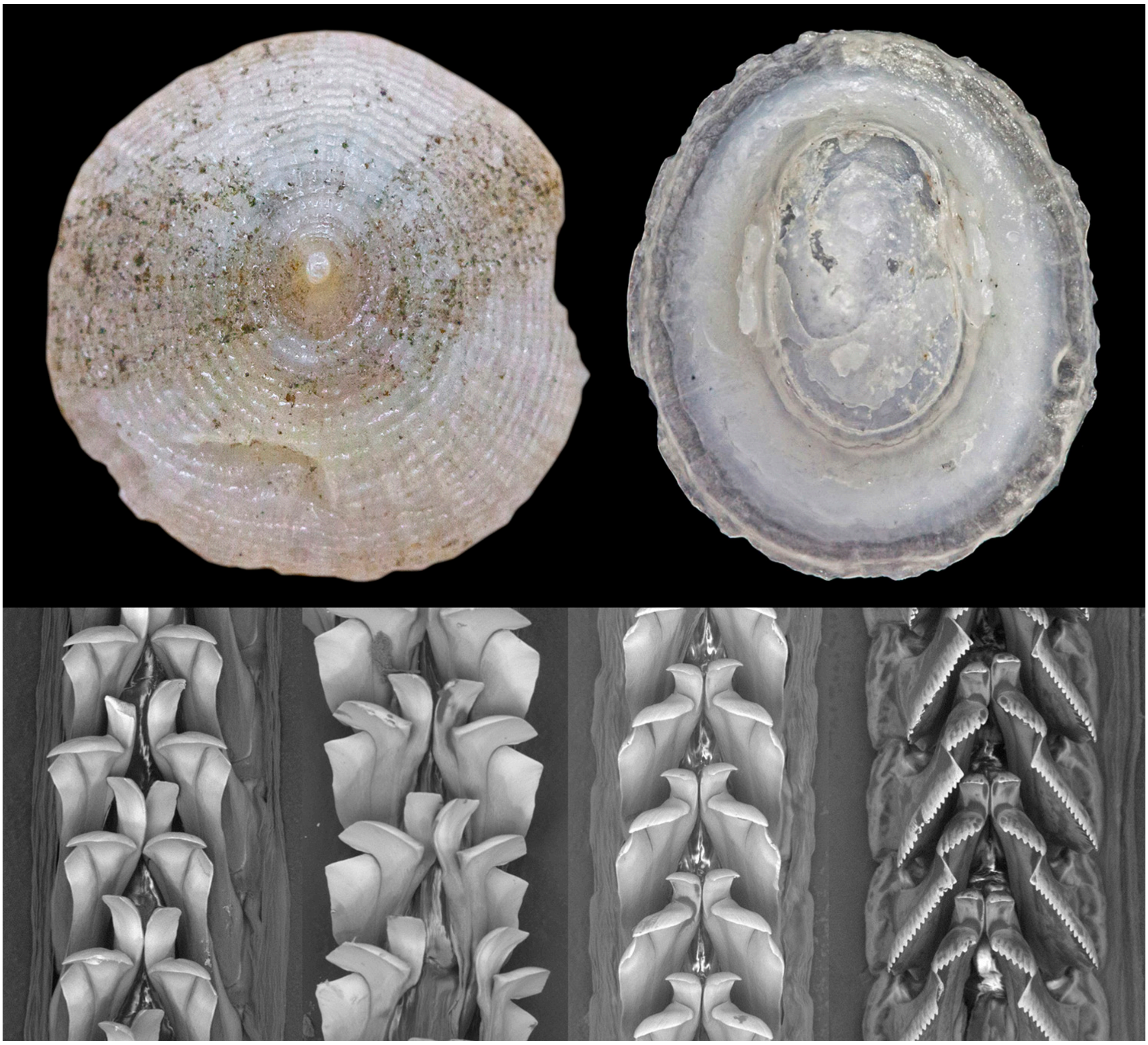
One, two, or many species? Morphological and genetic analyses of vent and seep pectinodontid limpets reveal extreme morphological plasticity

*チェン チョン[1]、渡部 裕美[1]、長井 裕季子[1]、豊福 高志[1]、徐 婷[2]、孫 進[2,3]、邱 建文[2]、小島 茂明[4]、山本 啓之[1]、矢吹 彬憲[1]、川口 慎介[1]、高井 研[1]、佐々木 猛智[5]
*CHEN CHONG[1], Hiromi Kayama Watanabe[1], Yukiko Nagai[1], Takashi Toyofuku[1], Ting Xu[2], Jin Sun[2,3], Jian-Wen Qiu[2], Shigeaki Kojima[4], Hiroyuki Yamamoto[1], Akinori Yabuki[1], Shinsuke Kawagucci[1], Ken Takai[1], Takenori Sasaki[5]

1. 国立研究開発法人　海洋研究開発機構、2. 香港浸会大学、3. 香港科技大学、4. 東京大学大気海洋研究所、5. 東京大学総合研究博物館
1. Japan Agency for Marine-Earth Science and Technology, 2. Hong Kong Baptist University, 3. Hong Kong University of Science and Technology, 4. Atmosphere and Ocean Research Institute, The University of Tokyo, 5. The University Museum, The University of Tokyo

Chemosynthetic ecosystems harbour rich megafauna communities, of which gastropod molluscs comprise a major component and have received considerable taxonomic efforts. Pectinodontid limpets, characterised by a white shell with cancellate sculpture and a radula with a single trifurcating lateral teeth on each side, are a common constituent of vents and seeps in the western Pacific. Thus far, two genera (*Bathyacmaea* and *Serradonta*) totalling eight species have been described based on shell and radula characteristics. However, no data on their intraspecific variation or genetic characterisation have been published. In the present study, numerous pectinodontid specimens from Sagami Bay and Okinawa Trough were investigated morphologically, revealing great disparity in both shell and radula in each locality, rendering existing species and even genera boundaries questionable. Changes in shell form according to substrate shape was confirmed through live-rearing in a controlled aquarium. Furthermore, phylogenetic and population genetic analyses of *Bathyacmaea* and *Serradona* specimens from Sagami Bay to the South China Sea clearly demonstrated that most specimens belonged to one single molecular operational taxonomic unit regardless of their morphological affinity. Although a number of individuals from Minami-Ensei and Hatoma Knoll fields in Okinawa Trough were found to be genetically divergent, these did not exhibit obviously morphological differences and are likely cryptic. Altogether, these results strongly suggest that most (if not all) currently described vent and seep pectinodontids are actually mere forms of a single extremely morphologically plastic species. As a case study, the present study serves to raise awareness against splitting and describing species solely based on hard part morphology without carefully assessing the reliability of characteristics used.

キーワード：熱水噴出孔、冷水湧出域、軟体動物、表現型可塑性、分類学、集団遺伝学
Keywords: Hydrothermal vent, Cold seep, Mollusca, Morphological plasticity, Taxonomy, Population genetics



Locomotion and move tracking of "*Calytogena*" clams *in situ* and in patented H_2S controlling tanks

*太田 未来[1]、延原 尊美[1]、土井 佑太[1]、早瀬 磨菜[1]、杉村 誠[2]、長井 裕季子[3,4]、豊福 高志[3]、岩瀬 良一[3]

*Miku Ohta[1], Takami Nobuhara[1], Yuta Doi[1], Mana Hayase[1], Makoto Sugimura[2], Yukiko Nagai[3,4], Takashi Toyofuku[3], Ryoichi Iwase[3]

1. 静岡大学教育学部、2. 新江ノ島水族館、3. 独立行政法人海洋研究開発機構、4. 横浜国立大学
1. Faculty of education, Shizuoka University, 2. Enoshima Aquarium, 3. Japan Agency for Marine-Earth Science and Technology, 4. Yokohama National University

Vesicomyid clams are one of the representative chemosynthetic animals, which have flourished in seep and vent sites during the Cenozoic. We report locomotion and behavior patterns of “*Calytogena*” clams to examine their adaptability to fluctuation of seep activity and disturbance of rapid burial. We analyzed time-lapse image data of *in situ* Real-time Deep Seafloor Observatory off Hatsushima Island in Sagami Bay, 1174 m in depth (3 min. interval) and patented H_2S controlling tanks in JAMSTEC (30 sec. interval) and Enoshima Aquarium (3 min. interval).

The “*Calytogena*” clams usually show semi-infaunal standing position with anterior side down and foot penetrating into underground sulfide layer, but sometimes crawl laying their shells with ventral side down. In standing position, the clams rearrange their postures swaying and obliquely rotating shells with foot as an axis. The clams sometimes push one another maybe quarreling over their favorite seep spots.

In crawling mode, they move forward by repeating the following steps: 1) laying shell down, 2) extending and penetrating foot in anterior direction, 3) maybe forming an anchor by foot expansion, and 4) pulling shell forward by foot contraction. In cases, the clams gathered into one spot and stranded one another, but could restore their postures into normal semi-infaunal position by extending and bending foot, which has wide movable range and high flexibility. During foot re-penetrating into the sediment, we observed that mass of sediment particles travels on whole surface of foot from its tip to root. Our SEM observation confirmed that the foot surface is densely covered by mucous cilia. The ciliary movement maybe enables the sediment conveying backward, which helps foot penetration.

In patented H_2S controlling tanks of Enoshima Aquarium, the “*Calytogena*” clams migrated keeping their track along the outer margin of bacteria mat. The average time and distance of one move action is about 15 min and 3.22 cm, so the average speed is about 0.38 cm/min. “*Calyptogena*” clams have been reported to form a ring colony surrounding bacteria mat, and this ring colony is a result guided by best condition of chemical subbottom profile. The positions and areas of bacteria mats in the Enoshima Aquarium tank have been rather stable but the margin fluctuated. The Enoshima clam tracks seem to be a result of tracing the best spot for getting subbottom hydrogen sulfide. In contrast, the “*Calyptogena*” clams of *in situ* the Hatsushima observation seem to move breaking bacteria mats, which were newly formed just after turbiditic rapid burial. In emergency where they lost their favorite seep spots just after such physical disturbance, the clams also repeated round trips from one position, back and forth in various directions, with maximum speed about 12 to 14 cm/min.

“*Calytogena*” clams have high ability of moving and restoring of their postures, as noted above. This ability is one of the keys of their adaptability to fluctuation of seep activity and disturbance of rapid burial, leading to their flourishing since the Cenozoic.

キーワード：化学合成、メタン湧水、オトヒメハマグリ科、ロコモーション

Keywords: chemosynthesis, methane seep, Vesicomyclae, locomotion