ISSN 0738-9388

Molluscs found in hydrothermal vents of Okinawa Trough: extreme species living in a poisonous paradise

Chong Chen
Department of Zoology, University of Oxford, OX1 3PS, United Kingdom
chong.chen@zoo.ox.ac.uk

Hydrothermal vents are essentially hot springs in the sea and collectively they may form vent fields. Vents develop when cold seawater seeps down through the ocean's crust, and becomes super heated by hot rocks deep inside the crust. Super heated water becomes less dense, loses oxygen, and becomes rich in hydrogen sulphide and other metals. The less dense heated water rushes up back to the surface of the undersea crust and is violently expelled into cold seawater (Van Dover, 2000). The temperature of exiting water can exceed 350 ℃ (Van Dover, 2000; Rogers *et al.*, 2012), but are quickly mixed with surrounding cold water. The temperature where animals live is typically around 4~20 ℃ (although some exceptional species such as alvinellid worms can tolerate more than 50 ℃ ; Fujikura, Okutani & Maruyama, 2012). An amazing array of invertebrates have adapted to these high temperature, mineral rich waters. First discovered at the Galapagos Rift in 1977 (Grassle *et al.*, 1979), vent associated organisms rely on energy not from the sun, but from chemicals. Symbiotic microbes are capable of creating energy by the process of chemosynthesis (Cavanaugh *et al.*, 1981; Felbeck, 1981). Chemosynthetic ecosystems do not rely on the sinking of plant or animal material from surface waters into the abyss as a source of energy. The discovery of this unique biological process is often quoted as one of the greatest biological discoveries of the 20^{th} Century (Kiel, 2010; Smith 2012). Molluscs are a prominent and dominant feature of the vent communities. Many mollusc groups such as the giant clam *Calyptogena* and the giant mussel *Bathymodiolus*, have been discovered at numerous vent fields around the world (Warén, Bouchet & Cosel, 2006).

The author was fortunate to be able to study and view, via remote monitoring, the hydrothermal vent fields in the Okinawa Trough, off Japan in early 2014, and collect molluscs for research from these extreme environments ranging from -1000~1700m in depth. Collection was done using the deep-diving Remotely Operated Vehicle *Hyper-Dolphin* (Japan Agency for Marine-Earth Science and Technology, JAMSTEC, Figure 1). Five interesting species endemic to these vents are discussed and illustrated in this paper. Ocean depths are most commonly discussed in relation to five

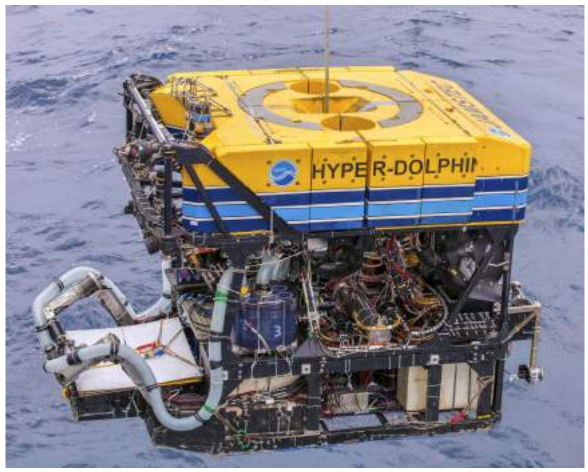

Figure 1. Image of Remotely Operated Vehicle ("ROV") the *Hyper-Dolphin*

depth zones; Epipelagic near the surface, mesopelagic, bathypelagic, abyssopelagic, and the deepest hadopelagic/trench zone. The molluscs discussed in this paper were collected from the bathypelagic zone, although some of their congeners have been collected in the deepest zones by other researchers (e.g., *Calyptogena phaseoliformis* Métivier, Okutani & Ohta, 1986, from Japan Trench).

SPECIES ACCOUNT

***Calyptogena okutanii* Kojima & Ohta, 1997** Figure 2, Family VESICOMYIDAE
Location: -1080m, Iheya North Knoll Hydrothermal Vent Field, Okinawa Trough.

Figure 2. *Calyptogena okutanii* Kojima & Ohta, 1997

It is amazing that giant molluscs like *Calyptogena* that measure 155.5 mm are found at great depths, and some species of this genus such as *Calyptogena phaseoliformis* Métivier, Okutani & Ohta, 1986, live in the hadal zone at depths exceeding -6000m and is one of the most well-known species from Japanese waters, along with its sister species *C. soyoae* Okutani, 1957. *Calyptogena okutanii* host endosymbiotic chemosynthetic bacteria in its giant gills and relies on these bacteria for nutrition by supplying them with hydrogen sulphide (Arp, Childress & Fisher, 1984; Fujikura, Okutani & Maruyama, 2012); thus the clam is endemic to the chemosynthetic environment. The soft parts of the clam are blood-red, as it uses haemoglobin for oxygen carriers, just like humans (Kawano, Iwasaki & Suzuki, 2003). This species is known from many chemosynthetic sites in Sagami Bay, Nankai Trough, and Okinawa Trough ranging from -750 to 2100m in water depth; and is often the dominant species especially in areas rich in mixed organic/inorganic sediment (Fujikura, Okutani & Maruyama, 2012). The shell is very thick and covered by a thick, brown periostracum which is mostly eroded in adult shells. The typical shell length ranges from 100mm to 120mm, and the specimen shown here is quite large. Specimens from vent sites are usually larger than those from other chemosynthetic environments (Fujikura, Okutani & Maruyama, 2012).

***Bathymodiolus japonicus* Hashimoto & Okutani, 1994** Figure 3 Family MYTILIDAE
Location: -1083m, Iheya North Knoll Hydrothermal Vent Field, Okinawa Trough, 90.5mm. The genus *Bathymodiolus* contains large to very large mussels specialized for living in chemosynthetic environments, they also host endosymbiotic bacteria which enable the molluscs to perform of chemosynthesis in their gills (Warén,

ISSN 0738-9388

Figure 3. *Bathymodiolus japonicus* Hashimoto & Okutani, 1994

Bouchet & Cosel, 2006). However, like other mytilids, they are also filter feeders to a certain degree, depending on the species and the environment. Some species such as *B. boomerang* Cosel & Olu, 1998 may exceed 350 mm in shell length. *Bathymodiolus japonicus* is a species endemic to chemosynthetic environments around Japan, including seep sites in Sagami Bay and vent sites in Okinawa Trough ranging from -705~1170m deep. Its endosymbiont is the methane-oxidising type that uses methane as an energy source (Fujiwara *et al*., 2000). Typical shell length is around 90mm. Very large specimens may reach 110mm. It often occurs sympatrically in the same habitat with another similar species, *Bathymodiolus platifrons*, which has more anterior umbones and lighter colored periostracum (Fujikura, Okutani & Maruyama, 2012). Both species form extensive mussel beds in the vent field, and consequently their shells provide habitat for many smaller species.

***Cantrainea jamsteci* (Okutani & Fujikura, 1990)** Figure 4. Family COLLONIIDAE
Location: -1016m, Iheya North Knoll Hydrothermal Vent Field, Okinawa Trough, 15.7mm.

Figure 4. *Cantrainea jamsteci* (Okutani & Fujikura, 1990)

Cantrainea jamsteci is a medium-sized colloniid gastropod endemic to chemosynthetic ecosystems around Japan, named after JAMSTEC (Okutani & Fujikura, 1990). It is known from hydrothermal vents in Okinawa Trough and a cold seep site, the Kuroshima Knoll in the Ryukyu Trench; ranging from -600~1000m in water depth (Fujikura, Okutani & Maruyama, 2012). It is apparently an omnivorous detritus layer grazer mainly found associated with *Bathymodiolus* mussel beds and tubeworm bushes. Very large specimens may approach 20mm in diameter, the average diameter being

ISSN 0738-9388

15mm. Specimens found close to vent effluents usually are covered in black deposits and the apex is often heavily corroded. The family Colloniidae, which share a similar thick, calcareous operculum are closely related to Phasianellidae.

Lepetodrilus nux **(Okutani, Fujikura & Sasaki, 1993)** Figure 5 Family LEPETODRILIDAE

Figure 5. *Lepetodrilus nux* (Okutani, Fujikura & Sasaki, 1993)

Location: -1638m, Irabu Knoll Hydrothermal Vent Field, Okinawa Trough, Japan, 10.1mm. *Lepetodrilus* is one of the most widely distributed endemic vent gastropod genera around the world, and although small these limpets often dominate by their sheer abundance (Warén, Bouchet & Cosel, 2006). *Lepetodrilus nux* is abundantly found in Okinawa Trough vents and is widely distributed across the vent field attached to rocks or other organisms. *Lepetodrilus* limpets are generally considered to be substrate and detritus grazers; but they may also filter-feed using specialized gill lamellae or host chemoautotrophic bacteria associated with the gills (de Burgh & Singla, 1984; Fox, Juniper & Vali, 2002; Bates 2007a & b). The feeding strategy of *L. fucensis* McLean, 1988 is particularly well documented by Bates (2007a & b). By utilizing all three feeding mechanisms these limpets are capable of surviving in habitats varying in a wide variety of food sources and availability. The shape and height of individuals vary greatly depending on the substrate, and are therefore not reliable features for identification. Typical shell length is 5~8mm, while very large specimens may reach 12mm. A very similar species, *L. japonicus* Okutani, Fujikura & Sasaki, 1993 is also known from Okinawa Trough and can only be reliably differentiated by investigating the radula (Fujikura, Okutani & Maruyama, 2012).

Thermosipho desbruyeresi **(Okutani & Ohta, 1993)** Figure 6. Family BUCCINIDAE

Figure 6. *Thermosipho desbruyeresi* (Okutani & Ohta, 1993)

Location: -1002m, Iheya North Knoll Hydrothermal Vent Field, Okinawa Trough, 80.2mm. *Thermosipho desbruyeresi* is a large buccinid endemic to hydrothermal vent fields. It has a wide distribution across Japanese vent sites in the Okinawa Trough and Izu-Ogasawara Arc (depth range - 600~1400m). Its range extends more than 8000km to Mariana, North Fiji and Lau Basins (depth range -1750~2750m) (Fujikura, Okutani & Maruyama, 2012). The Japanese population was described as a separate subspecies, *T. d. nipponensis* (Okutani & Fujiwara, 2000), but was recently synonymised with *T. d. desbruyeresi* (Kantor *et al*., 2013). A carnivorous/scavenging species, it has rather low population density and only rarely encountered especially in the Okinawa Trough. It is usually found on rock surfaces and also in association with *Bathymodiolus* mussels. This is by far the largest gastropod endemic to Okinawa Trough vents. The average shell length is 70~80mm, but large specimens may reach 100mm. The spire is always heavily corroded in adult specimens, this is common among vent gastropods, because vent fluids are usually very acidic (may be pH 3 or lower; Van Dover, 2000) and calcium more readily dissolves in deep-sea environments (Sasaki *et al*., 2010). Like many species of vent gastropods, *T. desbruyeresi* develop a heavy periostracum which is not easily corroded, but eventually the periostracum is breached on early whorls and since it cannot be repaired the exposed shell begins to quickly dissolve.

This is only a small selection of molluscan diversity found at hydrothermal vents – there are many other species with a wide range of strange adaptations allowing them to survive in this 'poisonous paradise'. Unfortunately, as vents are only visited by research submersibles, these species are extremely rare on the market and thus virtually unobtainable for shell collectors. This also has led most shell books and guides to overlook or ignore species from hydrothermal vents. Nevertheless, vent molluscs contain some of the most biologically interesting species. It is important for both biologists and shell collectors to recognize the extraordinary nature and adaptations of these species in order to understand the true diversity of phylum Mollusca.

ACKNOWLEDGEMENTS

The author would like to thank scientists on-board research cruise KY14-01 led by the principal investigator Dr Ken Takai (JAMSTEC), captain and crews of R/V *KAIYO*, as well as pilots and technical team of ROV *Hyper-Dolphin* for their tremendous support and great work during the cruise.

REFERENCES

Arp, A. J., J.J. Childress, & C.R. Fisher Jr.
1984. Metabolic and blood gas transport characteristics of the hydrothermal vent bivalve Calyptogena magnifica. *Physiological Zoology*, 57(6) 648-662.

Bates, A. E.
2007a. Persistence, morphology and nutritional state of a gastropod hosted bacterial symbiosis in different levels of hydrothermal vent flux. *Marine Biology, 152*(3), 557-568.
2007b. Feeding strategy, morphological specialisation and presence of bacterial episymbionts in lepetodrilid gastropods from hydrothermal vents. *Marine Ecology Progress Series*, 347: 87-99.

Cavanaugh, C. M., S.L. Gardiner, M.L. Jones, H.W. Jannasch, & J.B. Waterbury.
1981. Prokaryotic cells in the hydrothermal vent tube worm Riftia pachyptila Jones: possible chemoautotrophic symbionts. *Science,* 213: 340-342.

Cosel, R. V., & K.Olu.
1998. Gigantism in Mytilidae. A new *Bathymodiolus* from cold seep areas on the Barbados accretionary Prism.*Comptes Rendus de l'Académie des Sciences-Series III-Sciences de la Vie*,321(8) 655-663.
de Burgh, M. E., & C.L. Singla.
1984. Bacterial colonization and endocytosis on the gill of a new limpet species from a hydrothermal vent. *Marine Biology*, 84: 1-6.
Grassle, J. F., G.P. Patil, W.K. Smith, & C. Taille.
1979. Galapagos '79: Initial findings of a biology quest. *Oceanus* 22(2) 2-10.
Felbeck, H.
1981. Chemoautotrophic potential of the hydrothermal vent tube worm, *Riftia pachyptila* Jones (Vestimentifera). *Science* 213: 336-338.
Fox, M., S.K. Juniper, & H. Vali.
2002. Chemoautotrophy as a possible nutritional source in the hydrothermal vent limpet *Lepetodrilus fucensis*. *Cahiers de Biologie Marine,* 43: 371-376.
Fujikura, K., T. Okutani, & T. Maruyama.
2012. Deep-sea life–biological observations using research submersibles. 2nd Edition. *Kanagawa, Japan: Tokai University Press (in Japanese).*
Fujiwara, Y., K.Takai, K. Uematsu, S. Tsuchida, J.C. Hunt, & J. Hashimoto.
2000. Phylogenetic characterization of endosymbionts in three hydrothermal vent mussels: influence on host distributions. *Marine Ecology Progress Series*, 208: 147-155.
Kantor, Y. I., N. Puillandre, K. Fraussen, A.E. Fedosov, & P. Bouchet.
2013. Deep-water Buccinidae (Gastropoda: Neogastropoda) from sunken wood, vents and seeps: molecular phylogeny and taxonomy. *Journal of the Marine Biological Association of the United Kingdom*, 93(8) 2177-2195.
Kawano, K., N.Iwasaki, & T. Suzuki.
2003. Notable diversity in hemoglobin expression patterns among species of the deep-sea clam, Calyptogena.*Cellular and Molecular Life Sciences CMLS*, 60(9) 1952-1956.
Kiel, S.
2010. The Vent and Seep Biota: Aspects from Microbes to Ecosystems. Heidelberg: Springer. 350pp.
Okutani, T., & K. Fujikura.
1990. A new turbinid gastropod collected from the warm seep site in the Minami-Ensei Knoll, west of the Amami-Oshima Island, Japan. *Venus*, 49: 83-92.
Okutani, T., & Y. Fujiwara
2000.
Gastropod fauna of a thermal vent site on the North Knoll of Iheya Ridge, Okinawa Trough [Japan]. *Venus*, 59(2) 123-128

Rogers, A. D., P. A. Tyler, D. P. Connelly, J. T. Copley, R. James, R. D. Larter, K. Linse, R. A. Mills, A. N. Garabato, R. D. Pancost, D. A. Pearce, N. V. C. Polunin, C. R. German, T. Shank, P. H. Boersch-Supan, B. J. Alker, A. Aquilina, S. A. Bennett, A. Clarke, R. J. J. Dinley, A. G. C. Graham, D. R. H. Green, J. A. Hawkes, L. Hepburn, A. Hilario, V. A. I. Huvenne, L. Marsh, E. Ramirez-Llodra, W. D. K. Reid, C. N. Roterman, C. J. Sweeting, S. Thatje and K. Zwirglmaier 2012.
The Discovery of New Deep-Sea Hydrothermal Vent Communities in the Southern Ocean and Implications for Biogeography. *PLoS Biol,* 10(1), e1001234.
Sasaki, T., A.Warén, Y. Kano, T. Okutani, K Fujikura, & S. Kiel.
2010. Gastropods from Recent Hot Vents and Cold Seeps: Systematics, Diversity and Life Strategies. In S. Kiel (Ed.), *The Vent and Seep Biota* (pp. 169-254). Heidelberg: Springer.

ISSN 0738-9388

Smith, C.
2012. Chemosynthesis in the deep-sea: life without the sun. *Biogeosciences Discussions,* 9: 17037-17052.

Warén, A., P. Bouchet, & R.V. Cosel. 2006. Mollusca, Gastropoda (Handbook of Deep-Sea Hydrothermal Vent Fauna). *Denisia,* 18: 82-137.

Van Dover, C.
2000. *The ecology of deep-sea hydrothermal vents*. Princeton: Princeton University Press. 352pp.