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Adaptation in extreme underwater vent ecosystem: A case study on Pompeii worm (*Alvinella pompejana*)

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Abstract

The deep-sea habitats such as cold seeps and hydrothermal vents are very challenging environments displaying a high biomass compared to the adjacent environment at comparable depth. Because of the high pressure, the high temperature, massive concentrations of toxic compounds and the extreme physico-chemical gradients makes the lives very extreme in vent environment. Hypoxia is one of the challenges that these species face to live there. Therefore, most of the dwellers here lives in a highly integrated symbiosis with sulfide-oxidizing chemoautotrophic bacteria. Very few species belonging to annelids and crustaceans can survive in this ecosystem through developing specific adaptations of their respiratory system, the morphological, physiological and biochemical levels. Here, we review specific adaptations mechanisms of a prominent vent dweller Pompeii Worm (*Alvinella pompejana*) in order to know their morphological, physiological biochemical levels to cope with thrilling hypoxic vent environment. Most often Pompeii worm develop ventilation and branchial surfaces to assistance with oxygen extraction, and an increase in excellently tuned oxygen obligatory proteins to help with oxygen stowage and conveyance. Along with these respiratory adaptations have developed through augmentation of anaerobic capacities to contract with sulfide. The excellent thermo tolerance capacity and highly symbiotic activity makes this polychaete as one of the dominant inhabitants of the fragile vent condition.

Keywords: Adaptation, hypoxia, Pompeii worm, sulfide, hydrothermal vents

1. Introduction

Alvinella pompejana commonly known as Pompeii worm [12] is an annelid worm that exclusively dwells in deep-sea hydrothermal vent spot in the Pacific Ocean. They are used to live at depth of approximately 2500 meters therefore experience with extreme environmental conditions, including high temperature and pressure as well as high levels of sulfide and heavy metals [4, 19]. *Alvinella pompejana* is a small annelid about 10 cm lengths and diameter is less than 1 cm. [4]. This polychaete species is reflect on a pioneer in the colonisation of the hottest areas of vent chimneys [14, 33]. It is really interesting that only the young warms are suggested to observe at vents spots [11] however, larvae of *A. pompejana* were never identified at vent sites [33]. *A. pompejana* are said one of the most thermotolerant (about 80 °C) metazoans, making this animal a question of great interest for studies of eukaryotic thermo-adaptation [19, 33].

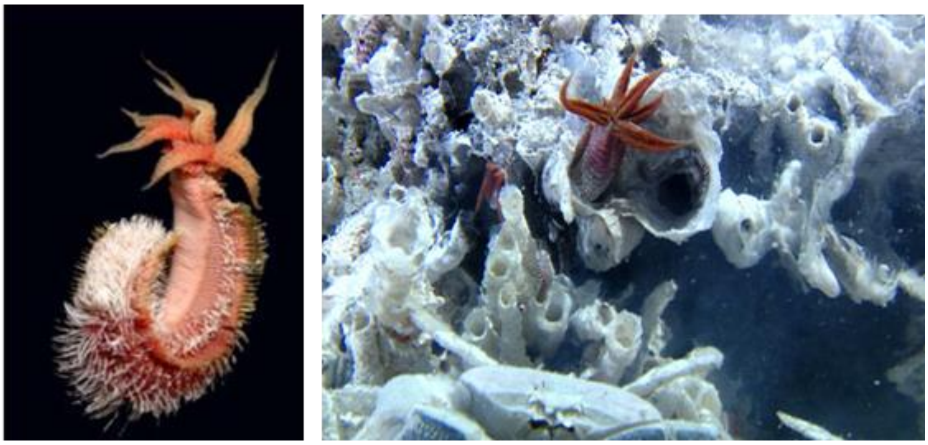

Fig 1: Species *Alvinella pompejana* (left) and the colony of the species (right). Figure modified from [4]

1.1 Taxonomic classification

Kingdom: Animalia
Phylum: Annelida
Class: Polychaeta
Order: Terebellida
Family: Alvinellidae
Genus: Alvinella
Species: *A. pompejana* [12]

1.2 Habitat and Distribution

Alvinella pompejana is endemic of the East Pacific Rise from 21N to 32S [32] and exclusively associated with high temperature venting and inhabits the surface of active sulphide riches structures like chimneys and smokers [10]. Conversely, distinct alvinellid species are observed on the Juan de Fuca Ridge that was separated from the EPR by the migration of North America plate [4]. *A. pompejana* shares its habitat with several other species of polychaetes, including additional alvinellids, but also polynoids, nereidids, and hesionids. The main other taxa are amphipods and brachyuran crabs. Among alvinellids, the two additional species are *Alvinella caudata* and *Paralvinella grasslei* are found in same environment [4, 10]. A dense community of epibiotic bacteria is associated with hair-like projections from the worm's epithelium that provide a nutrient source for its host [1] or thermally insulate the host from its high-temperature environment [32]. As it is said to be the highest thermo-tolerant metazoans, our aim is to review the challenges and adaptation strategies of *A. Pompejana* to the extreme environmental conditions of its habitat.

2. Biology and physiology of *Alvinella pompejana*

Most of the function of *Alvinella* conducted by a U-shaped tube morphology these tubes upward during the apical growth of the sulphide edifice (Fig. 2A) [10, 11]. The anterior extremities of the tubes are oriented radially, giving a shaggy appearance to the smoker walls. The tube diameter increases anteriorly, reaching a maximum of ca. 2 cm. The external surface of the anterior end is often scaly (Fig. 2B), the tube opening being either cylindrical or funnel-shaped, sometimes with one transversal septum separating two coalescent tubes. The water stream direction within the Alvinella tube remains undetermined, depending on whether or not the intake of cold sea water is at the bottom of the tube. Outside the tube pH is ranged from 5.7-7.5 and sulphide concentrations are up to 300 µM [11, 25].

All alvinellids possess four pairs of gills located anteriorly, but Alvinella differs from Paralvinella in having lamellae inserted on the stem of each gill instead of filaments [10] *A. pompejana* has developed a large branchial surface area, up to 12 cm^2 per g wet weight, together with a short diffusion distance between water and blood, about 2-3 µM [27], probably enhancing oxygen extraction from a supposedly hypoxic medium [10]. *A. pompejana*, circulation of the blood to the gills is enhanced by mechanical movements of a rod-like heart-body, increasing the pumping efficiency of the heart.

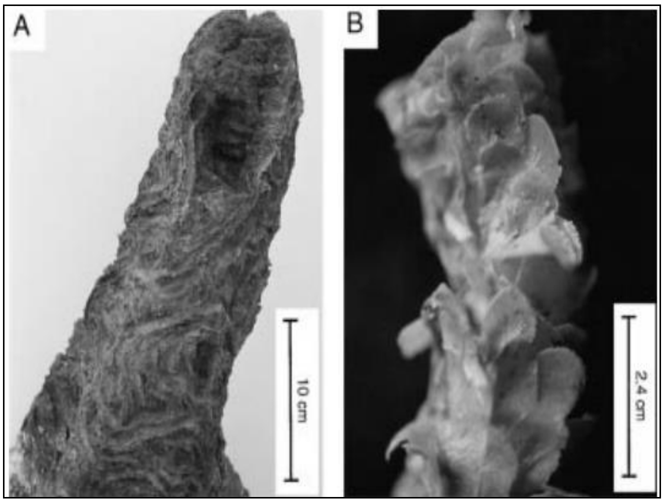

Fig 2: A) Tube of *Alvinella* spp. tubes on an inactive smoker; (B) scaly tube in anterior (Figure modified from [10])

The middle part of the heart is enclosed into a coelomic pouch that surrounds the oesophagus, the supra-oesophagal vessel, and a "red tissue" (space) made of a very large amount of coelomocytes, both granulocytes and erythrocytes, intermingled with a blood capillary plexus. (Fig.3) [10].

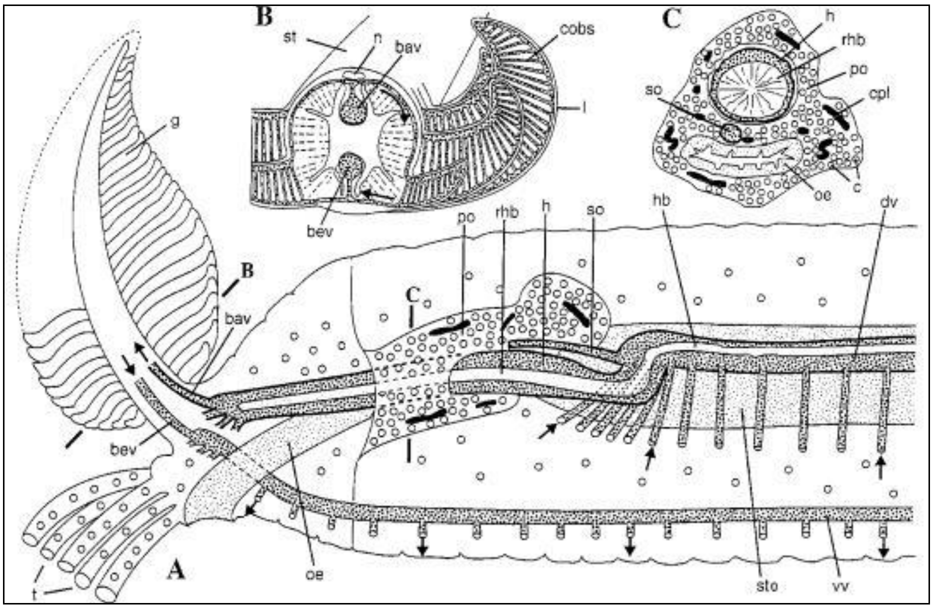

Fig 3. A): Circulatory and respiratory systems of *Alvinella pompejana*. (A) Diagrammatic lateral view of the anterior body region (B) Cross section of a gill (C) Cross-section of the perioesophageal pouch. (Figure adopted from [10])

3. Adaptation strategies in extreme environment

Deep-sea hydrothermal vents are a challenging habitat for metazoan life forms because of the high pressure, the high temperature, the high concentrations of toxic chemical compounds and the extreme physico-chemical gradients that occur over short spatial and temporal scales [31]. Strategies of adaptation to this extreme environment have been studied in a variety of vent organisms, but the polychaete worm *Alvinella pompejana* is considered as the most intriguing because of its ability to survive high temperatures (up to 80 °C) on active chimney walls. This animal was thus described as the most thermo tolerant marine metazoan [10, 33].

3.1 Physico-chemical features of the vent environment

Habitats associated to deep-sea hydrothermal vents have been described as some of the most challenging for animals on Earth. The high instability of their geological setting, subject to frequent volcanic and tectonic events, makes these habitats particularly ephemeral. The resulting chaotic change in fluid emission intensity and localization has been shown to induce dramatic changes in community composition over time [37]. Extreme physico-chemical characteristics, as compared to most oceanic environments, were also highlighted; e.g. temperatures exceeding 100^0C [8], hundreds of micromolar contents in sulfide [5], oxygen depletion [28], acidic pH [4], CO2-rich conditions [37], and several order of magnitude enrichments in various metals with respect to ocean waters [18].

3.2 Adaptation to Extreme Temperature

In hydrothermal vent external temperatures can fluctuate from 2-100 ˚C [10]. However, the temperature inside the tube is more stable (estimated at 30-35 ˚C as the worms cuticle will melt at 40 ˚C, although a temperature gradient may be present along the worms body) and enables the worm to survive in the extreme thermal conditions [6, 31]. Temperature variability can also be high, laterally on smoker walls, between the surface of worm colonies and bare mineral areas in their close vicinity where temperature as high as 105 °C [6]. High rate of temperature fluctuation associated to different microhabitats along the vents therefore *Alvinella pompejana* colonies differ within the microhabitat (Fig 4) [6]. The very high temperature at the surface of the smoker, however, undergoes a substantial decrease along the thickness of the colony. This fluctuation is in fact restricted to the shimmering plumes of discrete outflows that bathe nearby areas at the surface of the colony [6, 38].

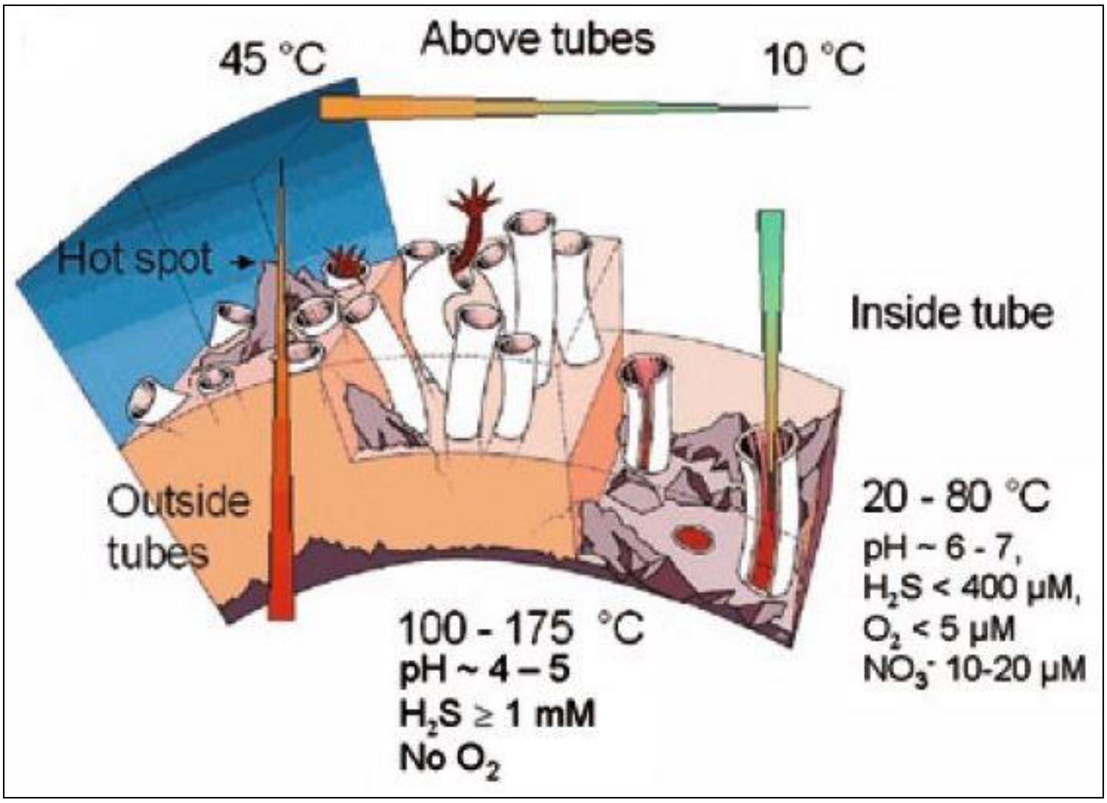

Fig 4: The Physico-chemical structure that characterizing a Pompeii worm colony. Ranges of temperature (mean values) reported for different microhabitats associated to *Alvinella pompejana* colonies. The blue layer is the vent fluid–seawater mixing zone bathing tube openings and orange layer show the embedded tubes and inner tube [3].

3.3 Mechanism to Adaptation at vent chimney

Vent water enters the tube through cracks in the chimney at around 120 ˚C [6], ambient seawater is drawn into the anterior end to cool it down (the outflow has been measured at 30-60 ˚C) [13]. The mixing of cool oxygenated sea water and hot sulphide-rich vent water inside the tube (Fig.5), provides an ideal habitat for oxidizing episymbionts on the worm's dorsal surface. Although micro-organisms growing in the tube are sulphide oxidisers, the methods by which the worm obtains organic carbon are still debated [10, 13].

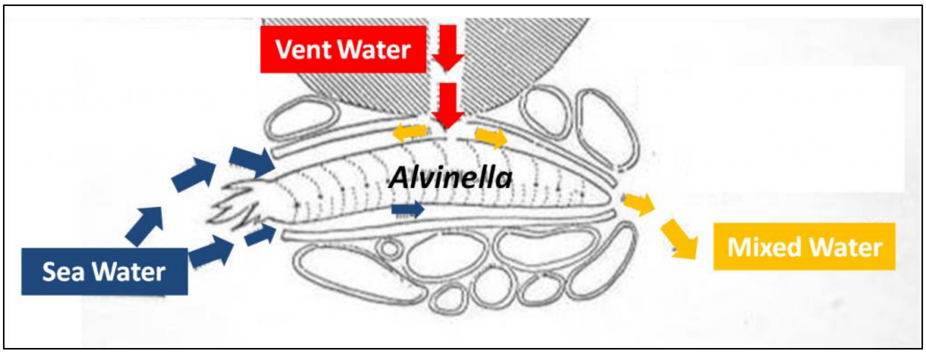

Fig 5: Tube of *Alvinella pompejana*. The movement of water through the tube is indicated by arrows and shows cold oxygenated sea water (blue) and hot sulphide rich vent water (red) producing mixed water (yellow) used by the symbionts (Figure adapted from [6])

Due to great variability in both special and time scales, it is very difficult to assess in situ temperature precisely in the habitat of *Alvinella* species. Adaptation to high temperature environments have been investigated (Table 1) at various levels in *A. pompejana* including the molecular characteristics of extracellular matrices (ECMs) and behavioral characteristics of adult warms. ECMc are the first barrier for the protection from the external condition that is depends on temperature variation in colonies [36]. It is obvious that a diversity of mechanisms involved in regulatory processes occur in living organisms and most of them adapted in animals during evolution. Some structural proteins whose stability mostly depends on physical parameters. Collagen, for instance, is one of the most well-known extracellular proteins of the animal kingdom and is a relevant marker of thermal adaptation. Its stability is critical to the survival of the animal in controlling the deformation of the body wall by hydrostatic pressure. This molecule in *Alvinella pompejana* has been well characterized in the last decade and shown that this species has the most thermostable protein ever known and that pressure is not involved in such a characteristic [17]. The temperature at which the collagen molecule is denatured (Tm) is 46 ºC for the cuticular collagen covering the animal epidermis and 45 ºC for the interstitial one which is found in the worm tissue.

The level of thermal stability of *Alvinella pompejana* cuticular interstitial collagen is significantly higher than that of other vent annelids. In comparison, Riftia pachyptila molecular collagen stability only reaches 29oC [29]. The origin of the thermal stability of this molecule has been characterized by [39]. These authors have shown that this property is not as new as previously expected but rather that this species has amplified all the molecular characteristics which are known to be involved in the stability of vertebrates or synthetic collagens.

Table 1: Temperatures variation in the close surrounding of *A. pompejana* colonies

Origin of Data	Among Tubes (Mean)	Inside Tube (Mean)
[Desbruyeres *et al*. (1998)]	-100 °C	nd
[Chevaldonne *et al*. (1992)]	40-80 °C	nd
[Cary *et al*. (1998)]	nd	68±6 °C
[Le Bris *et al*. (2003)]	60±10 °C	nd
[Di Meo-Savoie *et al*. (2004)]	nd	29-84 °C
[Le Bris *et al*. (2005)]	61±38 °C	59±6 °C

nd=nondetermined
Source: Adapted from [2,36]

3.4 Adaptation to Toxic Sulfides

Concentrations of several hundreds of micromoles to millimoles per liter have been listed for *A. pompejana* colonies (Table 2). These concentrations are the highest reported in various hydrothermal vent habitats. Although they are sometimes distant by less than one meter, the mixing zone surrounding *A. pompejana* appears several times richer in sulfide than the habitats of tubeworms, for a given temperature range [4]. Micromolar levels of sulfide are lethal to most aerobic organisms. [28] proposed that sulfide might be naturally detoxified in the environment of *A. pompejana*. A voltammetric study of sulfide speciation within an *A. pompejana* colony revealed that free sulfide forms, H_2S and HS–, were undetectable while aqueous iron sulfide complexes were dominant. Since large differences in the iron to sulfide ratio were highlighted in the environment of *A. pompejana* colonies, even within a kilometer apart (Table 2). More generally, a large range of sulfide speciation patterns should be expected among sites, the iron to sulfide ratio in endmembers being largely modulated by subsurface processes [9] (According to chemical calculations, the predominance of the toxic H2S form at nearly millimolar concentration was predicted for iron-depleted sites (e.g. Genesis EPR 13oN), while sulfide toxicity would be effectively attenuated at sites where iron concentration equal or exceed that of sulfide in fluids (e.g. Elsa EPR 13oN) [5]. Exposure to toxic sulfide in the environment of *Alvinella pompajana* might thus reach some of the highest levels experienced in the marine world [3].

Table 2: Comparative references of maximum sulfide content and iron to sulfide ratio at tube openings levels of hydrothermal vent

Reference	Vent field/location/year		Maximum sulfide (µM)	Fe: S
[Sarradin *et al*. (1998)]	EPR 13oN	Genesis/1996	300	nd
[Luther *et al*. (2001) and Di Meo-Savoie *et al*. (2004)]	EPR 9oN	Alvinella stump/1999	360	2.0
[Le Bris *et al*. (2003)]	EPR 13oN	Genesis PP12/1999	1520	0.4
		Elsa PP50/1999	563	1
[Le Bris *et al*. (2006)]	EPR 9oN	M-Vent/2002	916	1.0

3.4 Adaptations for oxygen extraction

3.4.1 Ventilation

Oxygen is considered as limiting factor in vent habitats. The prime way to advance oxygen extraction is to renew the diffusion layer at the surface of the gas exchange organs. Convective circulation of water and blood at the gill level contributes to increase oxygen extraction in an integrative process. This maintains an optimal difference of partial pressure between the two sides of the diffusion barrier [22]. The gills of Alvinellas are external therefore they have little control over the ventilation of the gill surface by water, except through movements of cilia which are abundant in vent species [20, 22, 26]. Perfusion of the gills by body fluids may also increase but this parameter is difficult to measure in polychaetes.

3.4.2 Increasing Gill surfaces

Oxygen depletion is a general feature of sulfidic environments, resulting of abiotic or microbial sulfide oxidation [2]. Oxygen extraction by gills can thereby be increased by increasing the total surface area or by decreasing the diffusion distance through the epithelium, or both. Different studies have been stated about increased specific gill surface area in numerous hydrothermal vent polychaetes (Table 3).

An increase in gill surface area reduces diffusion distance that can help gas exchange across the gills. Most of the vent species studied to date show very short diffusion distances. Most of the time in hypoxic condition *Alvinella* perfused by the coelomic fluid inside their gills to reduce diffusion distance [21].

Table 3: Gill surface areas and diffusion distances for annelids from hydrothermal vent (HTV), Table modified from [22].

Species	Environment	Specific gill surface area (cm^2/g)	Diffusion distance (µm)
Alvinella pompejana	HTV	12	1-3
Paralvinella grasslei	HTV	47	4
Riftia pachyptila	HTV	12	1-3
Branchipolynoe symmytilida	HTV	14.2	10
Branchipolynoe seepensis	HTV	10.3	9
Branchipolynoe pettiboneae	HTV	7.7	10

3.4 Adaptations for oxygen transport

Oxygen availability in the *Alvinella pompejana* environment is still undetectable inside tubes, despite a high content of other seawater oxidizing compounds like nitrate and sulfate [32]. Therefore, Alvinellids possess specific adaptations that allow them to extract oxygen even with its low levels in the environment and they most likely often rely on anaerobic metabolism. Sometime anaerobic metabolism may be happening even when oxygen is not completely absent. According to [24] it have shown that, in the tubeworm habitats, oxygen can coexist with sulfide until temperature is over 11 °C. In order to improve oxygen delivery to the organs, many organisms used to increase capacitance of the blood as well the blood flow [22]. There is a general trend for a high oxygen affinity, which would facilitate uptake at the level of the gills, and a strong Bohr effect that would allow the release of this oxygen at the level of metabolically active tissues. In case of *Alvinellas* possess hemoglobinin at high concentrations, with a high affinity for oxygen. In addition, Alvinellidae possess typical extracellular hexagonal bilayer (HBL) hemoglobin and circulating intracellular hemoglobin contained in coelomocytes in their vascular system [26]. Most of the cases oxygen transfer is unidirectional, but in only bi-directional oxygen transfer found in *Alvinella pompejana*. This property allows the buffering of environmental oxygen variations using the coelomic compartment as an oxygen store. Again alvinellid, developed a capillary network by extending gular membrane posteriorly and enveloping the esophagus and also the peri-esophageal pouch thus formed contains very numerous erythrocytes (Fig 6). This complex association with a high density of capillaries and coelomocytes, forms an internal gas exchange system [26] thus allowing bidirectional transfer in the gas exchange system [23].

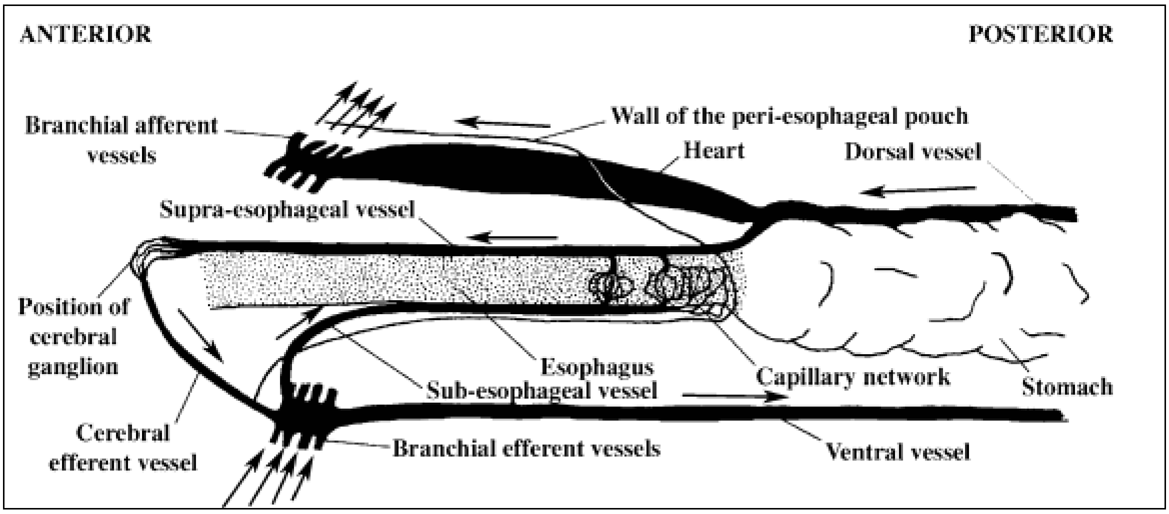

Fig 6: Anterior circulatory system in *Alvinella pompejana* showing the periesophageal pouch containing the capillary network. (Modified from [4])

4. Symbiosis with microorganism

Symbiosis is a close ecological relationship between the individuals of two or more different species. Sometimes a symbiotic relationship benefits both species, sometimes one species benefits at the other's expense, and in other cases neither species benefits. *A. pompejana* not the harbor of endosymbionts like other vent organism, *R. pachyptila*, but abundant of microbial communities have been described that cover the inner part of its tube and attach to posterior appendages as well of the animal [15]. The contribution of the associated microflora to the mechanisms that protect those warms from environmental threats [36]; for example, its role in buffering temperature at the surface of the animals and also in forming dense sulfur filamentous mats and protects grazing from other surrounding microflora [16]. So, the worms stay near the sulfur-rich vent fluids to encourage chemosynthetic bacteria to grow on them. The worms use their own bodies like “farms” to grow bacteria that they “harvest” and eat [15, 36].

Again, those microorganism uses to reduce chemicals such as hydrogen sulfide, methane and sometime in carbon fixing [36]. Bacteria associated with the dorsal epidermis of *A. pompejana* are morphologically and metabolically diverse [15, 34]. Approximately 80% of these epibiotic communities are epsilon protoebeteria [36] and those epibiotic bacteria use inorganic compound from vent fluids as well as organic compounds secreted by the warms. In return, the worm gets dissolved organic compounds produced by the associated bacteria.

5. Reproduction and development

Alvinella pompejana is a gonochoric species that exhibits a sexual dimorphism [10, 41]. Their male to female sex ratio is approximately 1. The males have a pair of well-developed peribuccal tentacles, which are lacking in the females (Fig. 7A and B). The female reproductive system of *Alvinella pompejana* composed of oviducts and coelomic cavity [41]. Oocytes are free in the coelomic cavity of the females and are also often found densely packed in the oviducts. Oviducts are somewhat U-shaped and usually smaller than the spermiducts. Oocytes are flattened spheres bearing what seems to be a micropyle in their centre [10]. The maximum oocyte diameter, measured at the largest dimension, could reach 200 µm at most, and the total numbers of oocytes yield highly variable values averaging 80,000 with a maximum of 230,000 per female [10]. The fecundity of *A. pompejana* is higher than that of the other alvinellids [30, 42]. The maximum oocyte size is often correlated to the developmental mode in polychaetes.

Different study reported that *A. pompejana* individuals do not reproduce synchronously at the patch scale in contrast to what was previously suggested at the vent scale [10]. Such an asynchrony could be a strategy of adaptation of the Pompeii worm to respond very quickly to the disturbance of the fluctuating environment.

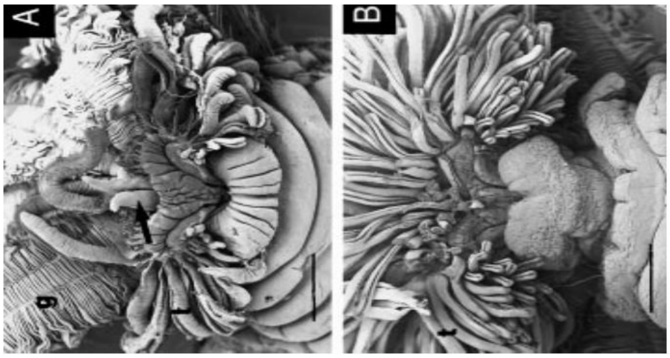

Fig 7: *A. pompejana*. (A) Male reproductive specimen, ventral view (B) Female Reproductive specimen, ventral view. Modified from [10]

6. Colonization

Usually for *Alvinella pompejana*, embryonic development occurs at low temperature (2 °C) because embryos cannot survive at high temperature. Therefore Low-temperature areas at the surface of adult’s colonies provide suitable habitats for embryos development. This characteristic of *Alvinella pompejana* colonies is clearly emphasized by the synthesis of temperature surveys could lead to refine the assumption that early stages are excluded from the adult habitats. After development the settlement of the first individuals within a few days on colonization devices deployed over a smoker wall, following the formation of filamentous microbial mats [40]. From different study observed that newly opened substrates are colonized mostly by post-larvae stages whereas juveniles or adults, migrating from the adjacent colony. The Migration of adult individual from the colonies is occurred by means of tube secretion along the substrates or existing tubes

[16, 33]. Within less than 50 days, non-reproductive post-larvae individuals exclusively composed these pioneer populations. The percentage of reproductive female subsequently increased to reach almost that of native colonies in 150 days. The temperature is strongly influence early colonization and migration of adult individuals from the colony. The formation of several centimeter-thick assemblages of tubes can be possible within 2 months due to rapid production of newly available substrates [43].

7. Conclusion

The strongly chaotic, steeply changing and ephemeral environment of the *A. pompejana* environment is undoubtedly some of the most challenging encountered on Earth. The exceptional thermal characteristics of its collagen is the best example of the adaptation of these organisms to this hot environment on evolutionary timescales. The formation of tube is an excellent characteristic to adapt in the high temperature and toxic sulfides. *Alvinella pompejana* could thus stand at the limits authorized for its biological machinery in a highly dynamic environment where temperature can exceed lethal limits, but where micro-habitat thermal regulation by the animal would prevent exposure to deleterious temperature spikes. The ability of *Alvinella pompejana* to colonize these substrates is because of the exceptional properties of the tube and the behavior of the worm. Ecologically, the dynamic system associating this pioneer species and the associated microflora might be viewed as a key to the subsequent colonization of these environments by less tolerant species, highlighting *A. pompejana* as a new type of ecosystem bioengineer. Only part of the puzzle is now solved. Much remains to be known concerning the molecular adaptation of this organism to the combination of multiple thermal and chemical stresses that make this habitat one of the most extreme marine environments.

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