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Alvinellidae Desbruyères & Laubier 1986

Didier Jollivet & Stéphane Hourdez

Introduction

The family Alvinellidae Desbruyères & Laubier 1986 comprises only 12 currently described species and is only found at deep-sea hydrothermal vents in the Pacific Ocean. The Pompeii worm *Alvinella pompejana* Desbruyères & Laubier, 1980 was the first species described from deep-sea hydrothermal vents, only three years after the discovery of diffuse vent emissions and associated communities on the Galapagos Rift (Lonsdale et al. 1977, Corliss et al. 1979), and only one year after they were first collected on the 21°N East Pacific Rise chimneys called 'black smokers' in 1979 (Rise Project Group 1980). The genus is named after the manned submersible Alvin which was the first submersible to collect the species and the species names refers to its environment, on chimney walls, where it is permanently exposed to a rain of polymetallic particles associated with the abrupt cooling of the very hot (300-350°C) and sulfidic hydrothermal vent fluid. In their initial description, Desbruyères and Laubier (1980) indicated that the species represents an 'aberrant' Ampharetidae, with a very well developed reddish branchial crown. Two years later, the first species in the genus *Paralvinella* was described (Desbruyères and Laubier, 1982) in what was then considered a subfamily of Ampharetidae (Alvinellinae). With the description of new species, Desbruyères and Laubier (1986) eventually erected the family Alvinellidae, that comprises two genera, *Alvinella* and *Paralvinella*. Species from this family correspond to Terrebellomorpha with a relatively high number (55-180) of short setigerous segments, and a body that is not sub-divided into distinct regions.

The extreme environment in which these species are found prompted a series of studies on their taxonomy, biology, reproduction, physiology, and evolution. This chapter provides an overview of what is known on species belonging to this family. An extensive review on the very emblematic species *Alvinella pompejana* was published in 1998 (Desbruyères et al., 1998) but much progress has been made since, not only on this species but also on other species of the family.

Morphology

According to Desbruyères and Laubier (1986), diagnosis of the family Alvinellidae relies on several specific morphological features, which are: (1) a reduced prostomium with a retractable buccal apparatus positioned ventrally that comprises grooved ciliated tentacles and a dorsal organ, (1) four pairs of hypertrophied gills made of lamellae (*Alvinella*) or simple unbranched filaments (*Paralvinella*) with the first pairs of branchiae inserted on the first asetigerous segment and others on the fused second and third ones, (3) parapodia are biramous with a capillary setae on the notopodia, and a single row of breviavicular uncini on the neuropodia, and (4) fourth and fifth (*Alvinella*) or seventh (*Paralvinella*) anterior parapodia highly modified with capillary setae replaced by two (*Alvinella*) or one (*Paralvinella*) pair(s) of hooks. The Alvinellidae belongs to the order Terebellida sharing several morphological traits such as the retractable buccal tentacles with a ciliated groove directely inserted on the ventral lobe of the pharyngeal cavity similarly to ampharetid worms, the avicular shape of uncini and the long-shafted neuropodia similarly to Trichobranchid worms and, the plesiomorphic distribution of notopodia over the whole body like some other sub-families of terebellid worms. Alvinellids differ however from species belonging to the Terebellida order by the lack of a clear separation between the thorax and the body of the worm and, this trait may be considered as plesiomorphic.The dorsal organ of alvinellid worms, which is a glandular and ciliated evagination of the pharyngeal cavity dorsally, is also specific and not shared with other families of the Terebellida order. The genital pore located at the basis of the branchial crown is also a characteristic typifing alvinellid worms and, together with the sexual tentacles plays a crucial role in their reproduction. They can be used to discriminate males and females as, unlike other terebellomorph species, all alvinellid species display a clear sexual dimorphism that might represent a secondary adaptation of the worm to secure egg fertilization in the highly fragmented and instable hydrothermal vent environment (Faure et al. 2007).

History of species discovery

The epibiotic Pompeii worm *Alvinella pompejana* and its sister species *Alvinella caudata* were first described as two successive ontogenetic forms of the same species by Desbruyères and Laubier in 1980 from the top of vent chimneys at the site 21°N/EPR. Because of the presence of an elongated and flattened tail supporting filamenteous proteobacteria, *A. caudata* was indeed first considered as a possible juvenile form of the worm able to swim for dispersal. The genetic analysis of the two forms by Autem et al. (1985) using allozymes demonstrated then without any doubt that they represent ‘old’ and distinct morphological species with no allele sharing. Recent comparative analyses of the transcriptomes of the two worms confirmed this latter hypothesis with reciprocal monophilies at nearly all loci and an average gene divergence of *c.a.* 0.3 fixed substitutions per site (Fontanillas et al. 2017, Thomas-Bulle et al. submitted).

Paralvinella grasslei was then described from the washing of the chitinous tubes of the siboglinid worm *Riftia pachyptila* from samples collected at 13°N/EPR by the French submersible Cyana in 1982 (the Biocyatherm expedition). Since, a number of nine additional *Paralvinella* species were described from a series of expeditions at deep-sea vent hydrothermal sites all over the globe, indicating that the family Alvinellidae is only endemic to the Pacific Ocean. Although several species are associated with the tubes of Siboglinid worms such as *Riftia pachyptila*, *Tevnia jerichonana* or *Ridgeia piscesae* or cracks in the basaltic crust where diffuse hydrothermal venting occurs, some species also live on the walls of vent chimneys and could represent ecological homologs to the *Alvinella* spp. on either the Northeastern Pacific ridges (Tunnicliffe et al. 1993) or the ridges of western back-arc basins (Desbruyères et al. 1994). Description of additional material sampled from the East Pacific Rise and the Northeastern Pacific Juan de Fuca Ridge led to the concept that deep-sea hydrothermal organisms may form sibling species according to the geography and the plate movement history (also see Tunnicliffe 1988). Two pairs of sibling species have been proposed by Desbruyères and Laubier (1986):
Paralvinella palmiformis, usually present on Juan de Fuca, Explorer and Gorda ridges of the northeast Pacific, is morphologically similar to *P. grasslei* with only few minor differences, which only occurs along the northern East Pacific Rise. Similarly, *Paralvinella pandorae pandorae* sampled at the same localities along the northeastern Pacific is almost identical to *Paralvinella pandorae irlandei* also collected from the East Pacific Rise. Genetic analyses of these pairs of species also showed that they have similar levels of divergence (about 7.5% of divergence), which allowed Chevaldonné et al. (2002) to propose a new substitution rate on the Cytochrome oxidase 1 gene for the vent annelids
In 1988, Detinova described a new *Paralvinella* species found in association with *P. pandorae pandorae* in the deep-sea vent communities of Axial Seamount. *This species previously* called ‘megaplume worm’ was named *Paralvinella dela* in honor of D. Desbruyères (de) and L. Laubier (la). This new species also represents a sibling species

to *Paralvinella bactericola* described one year later from specimens collected in hydrothermal vent sediments of the Guaymas basin (Desbruyères and Laubier 1989).
Finally, a series of three additional species were also described from the western Pacific back-arc basins following the first American expedition on the Marianas trench (Hessler & Lonsdale 1991) and French-Japanese expeditions STARMER/Biolau/BioAccess (Desbruyères et al. 1994, Auzende et al. 1997) in this part of the globe. These type species are *Paralvinella hessleri* from Marianas trench and *Paralvinella fijiensis* and *Paralvinella unidentata* from both the Lau and North Fiji basins (Desbruyères and Laubier 1989, Desbruyères and Laubier 1993). A fourth species from the North Pacific ridge was also secondarily identified thank to diagnostic alleles of several enzyme loci when compared to *P. palmiformis* (Tunnicliffe et al. 1993). *P. sulfincola*, while shorter and thicker than *P. grasslei* and *P. palmiformis*, is morphologically and genetically more similar to *P. fijiensis*, and pointed out the possibility of a geographic expansion of several distinct ancestral lineages at the scale of the Pacific Ocean (Jollivet et al. 1995).

Biology and ecology

Ecology

Most species of Alvinellidae build tubes or cocoons either on the wall of vent chimneys, in basaltic cracks with venting, or at the base of vestimentiferan (Siboglinidae) tubes (see Figure 1-3). The inner part of the tube and/or the mucus threat of cocoons are covered by either filamentous epsilon proteobacteria or rod bacteria (Desbruyères & Laubier 1986, Tunnicliffe et al. 1993, Le Bris et al., 2005, Le Bris and Gaill 2010). The mucus secreted by the worm is made of polysaccharides and glycoproteins often used to trap metallic compounds in order to detoxify their immediate surroundings (Taghon et al. 1988).

Habitat and geographic range

In the East Pacific, both *A. pompejana* and *A. caudata* live syntopically on the wall of hydrothermal vent chimneys along the East Pacific Rise and the Pacific-Antarctic ridge from 21°N to 38°S (Hurtado et al. 2004) and. *A. pompejana* is also present on active chimneys of the Guaymas basin. The two species have also been recently sampled from newly formed chimneys on the Galapagos Rift near the Rose Garden vent field. *P. grasslei* is typically found at the base of the Siboglinidae *Riftia pachyptila* and has a geographic range very similar to that of the two *Alvinella* species but seems to be quite rare on the Southern EPR and absent further South. Finally, *P. pandorae irlandei* has been found in association with the Siboglinidae *Tevnia jerichonana* on most of the sites of the East Pacific Rise and the Pacific-Antarctic ridge but is not present at sites of the Guaymas basin and the Galapagos Rift. In the Northeast Pacific, the three species *P. palmiformis*, *P. sulfincola* and *P. pandorae pandorae* are present over all the vent fields of the Northern Pacific Ridge segments from Gorda Ridge to the Explorer Ridge but inhabit different niches. *P. sulfincola* inhabits chimney walls, while *P. pandorae pandorae* and *P. palmiformis* is found with the Siboglinidae *Ridgeia piscesae* (Tunnicliffe et al. 1993). *P. dela* is mostly restricted to Axial Seamount but can also be observed although rare at Middle Valley, Cleft and Endeavour (Detinova, 1988). Its geographic counterpart, *P. bactericola* is endemic to diffuse venting of the Guaymas basin in hydrothermal sediments. Other species are only present along the fragmented ridges of back-arc basins of the western Pacific. *P. hessleri*, originally described from the Marianas trench is mostly found on the chimney walls of the north western part of the Pacific from the Okinawa trough to the Manus basin. *P. unidentata* and *P. fijiensis* are more likely present in the eastern part of the western Pacific on the base and top of vent chimneys of the Lau, and North Fiji basins but have also been observed on hydrothermal vents from active seamounts of the Vanuatu subduction arc. Some of the main alvinellid species are pictured in Figure 4.

Thermal adaptation

One of the main adaptations investigated in Alvinellidae is their ability to cope with high temperature and rapid temperature variations. Tubes represent a very efficient mean to insulate the worm from high temperatures (Gaill and Bouligand 1987) and from the chaotic variations of temperature over short time intervals (<1 min). Alvinellidae are well-adapted to live in severe hypoxic conditions (see the respiration section) and have high activities of anaerobic and oxidative stress enzymes (Dilly et al. 2012, Genard et al. 2013). These activities are even more pronounced for species that live in colder but diffuse venting conditions, where H_2S concentrations can be higher than on the chimney walls (Rinke and Lee 2009). Temperature tolerance and preference has been investigated in a few species. The chimney-dwelling *Alvinella pompejana* was observed near a temperature probe that indicated 105˚C during a dive (Chevaldonné et al., 1992), and a study reports temperature values consistently close to 80˚C (Cary et al., 1998). Chevaldonné et al. (2000) however question this consistently high temperature based on the available biochemical and physiological data that suggest that the worm probably cannot withstand temperatures greater than 50˚C over long periods of time. This was confirmed by controlled lab experiments that indicated that an exposure to temperature of 50-55˚C for 2 hours was lethal (Ravaux et al., 2013). Temperature preference investigations revealed that another chimney-dwelling species, *Paralvinella sulfincola*, preferred temperatures between 40 and 50˚C (some individuals remaining at the upper temperatures for 7 hours, the duration of the experiment), and some specimens spend at least 15 minutes at 55˚C (Girguis and Lee, 2006). The same experiments carried out on the species *P. palmiformis*, usually encountered mixed with the tubeworm *Ridgeia piscesae* (Siboglinidae), preferred temperatures ranging from 25 to 35˚C, consistently avoiding higher temperatures. A series of specific adaptations at the molecular level to cope with high temperatures has been reported, including a protective tube/cocoon made of positively and negatively twisted polymers layers of unusually stable glycoprotein matrix and elemental sulfur (Gaill and Hunt 1986, Taghon 1988), a very efficient arsenal of heat shock proteins and stress oxidative enzymes (Dilly et al. 2012), enzymes able to remain stable and still active at temperatures greater than 50°C after 15 minutes (Rinke and Lee 2009) or up to one hour (Jollivet et al. 1995) of incubation, a thermally stable collagen (Sicot et al., 2000), … Overall, the proteome comprises proteins with specific enrichments in charged, aromatic and alanine residues in a way similar to the protein composition of thermophilic/ultrathermophilic prokaryotes (Jollivet *et al.* 2012, Fontanillas *et al.* 2016). In *A. pompejana*, exposure to 55˚C, although lethal, induced a heat shock response, while exposure to 42˚C did not (Ravaux *et al*. 2013). A similar response was observed in *P. palmiformis* when transferred from 12 to 38˚C but no response was observed in the chimney dwelling *P. sulfincola* when transferred from 10 to 45˚C, suggesting this species constantly expressed heat shock proteins (Dilly et al. 2012).

Biology

Symbiosis/epibiosis

Amongst Alvinellidae, only the two *Alvinella* species have developed a complex epibiotic relationship with filamentous epsilon proteobacteria, located either on the dorsal part of the animal (*A. pompejana;* Haddad et al., 1995, Cary et al., 1997) or the modified parapodia of the worms' tail (*A. caudata*). Other *Paralvinella* species that live on the wall of vent chimneys such as *P. hessleri*, *P. fijiensis* and *P. sulfincola* also inhabit tubes covered by rod and filamentous bacteria on their inner surface but are not epibiotic although they harbor rod bacteria attached to uncini. Nearly all studies on the trophic relationship between the worm and its epibiotic bacteria have been performed on *A. pompejana* (Gaill et al. 1988, Gulik & Gaill 1988, Desbruyères et al. 1998, Campbell et al. 2001, Lee et al. 2008). The gain of epibiotic bacteria led to specific adaptations of the worm such as dorsal or tail expansions with modified geniculate setae (Desbruyères et al. 1998) and, the evolution of its antibacterial peptide arsenal by duplication and positive selection (Papot et al. 2017), some of which appear to be used for the control of the epibiosis. The epibiotic bacteria consortium is made of a few dominant filamentous bacteria that are eurythermal and involved in a unilateral non-obligatory symbiotic relationship possibly leading to nutritional (but see below) and detoxifying processes that can be beneficial for the worm.

Feeding

The digestive system is linear, and subdivided into an oesophagus, followed by a stomach and an intestine that ends in a terminal anus (Saulnier-Michel et al. 1990)(Figure 5). As in all Terebellomorpha, Alvinellidae have buccal tentacles and, as in most Ampharetidae, they are attached to a dorsal organ on the roof of the mouth (Desbruyères and Laubier, 1986). Their number is moderate, they are grooved and ciliated, and they are shorter than those of Terebellidae (Rouse & Pleijel, 2001). They can be fully retracted into the mouth, and, on *in situ* videos of live specimens, are rarely seen. The tentacles are used to deposit feed, including on the bacterial residents of the worm tubes (Desbruyères and Laubier 1982). Attached, filamentous bacteria on the posterior dorsal surface of *Alvinella,* however, do not appear to be directly involved in their nutrition (Alayse-Danet et al. 1986). In addition, male Alvinellidae also have a pair of larger tentacles attached to the ventral surface of the buccal cavity that are used in sperm transfer (Desbruyères and Laubier, 1986). The ventral pharynx is muscular and thought to be eversible (Saulnier-Michel et al. 1990) (Figure 5). Unusual structures in this part of the worm resemble racks of teeth that could be used for sorting or shredding particles that were collected by the tentacles (Saulnier-Michel et al. 1990). In *Alvinella pompejana*, the oesophageal gland seems to be the origin of the proteolytic activity detected in the lumen. The stomach lining is the siege of intracellular enzymatic activities and contains numerous iron concretions and polyphagosomes (Saulnier-Michel et al. 1990). Finally, the intestinal wall is composed of cells consistent with an absorbing function (enterocytes, myocytes, and cells that contain zymogenic granules). In the hindgut, the feces are mostly composed of elemental sulfur (Saulnier-Michel et al. 1990).

Authors have suggested that some *Paralvinella* species could supplement their deposit feeding diet by collecting particles suspended in the water (Desbruyères & Laubier 1991), essentially filtering water with their gills. This feeding strategy has been observed in *Flabelliderma commensalis* (Flabelligeridae) (see Jumars et al., 2015 and references therein). Desbruyères & Laubier (1991) also suggested that the two large tentacles in *P. bactericola* could be used to feed on larger suspended particles while the smaller tentacles are used in deposit feeding.

Stable isotope analyses show a consistent reliance on chemoautotrophic bacteria (Levesque et al. 2003, Bergquist et al. 2007, Lelièvre et al. 2018, Desbruyères et al., 1998) Interestingly, that sympatric species of *Paralvinella* often exhibit significantly different stable isotope values, suggesting differences in diet between species (Levesque et al. 2003, Bergquist et al. 2007, Lelièvre et al. 2018). Sites also affect the stable isotope values, and evidence indicates a change in diet with size in *P. palmiformis* (Levesque et al. 2003).

Vascular system

All Alvinellidae possess a closed vascular system (Figure 5). As in other Terebellida, the dorsal vessel separates from the gut anteriorly at the stomach-esophagus junction. In *Alvinella pompejana*, a supra-esophageal vessel separates from the main dorsal branch, adheres to esophagus, and runs forward (Jouin-Toulmond et al., 1996, Hourdez and Lallier, 2007, Figure 6). As in other Terebellida, the main dorsal branch corresponds to a contractile heart and contains a heart body that is responsible for vascular hemoglobin synthesis (Figures 5-6). In *A. pompejana*, both the supra-esophageal and the heart penetrate the wall of a dissepiment that separates the coelomic cavity between segments 1 and 2 and extends far back on the esophagus (Figure 6). In other Terebellida, this dissepiment exists but does not extend far around the esophagus. *In A. pompejana* and other Alvinellidae, the peri-esophageal pouch thus formed contains large numbers of coelomocytes that contain intracellular hemoglobin (Hourdez et al., 2000, pers. obs.). Anteriorly, the heart splits into 4 pairs of branchial afferent vessels (Figure 6). The branchial efferent vessels merge ventrally with the ventral vessel that runs to the end of the body. From the region where the 4 pairs of efferent branchial vessels merge, the sub-esophageal vessel originates and carried oxygenated blood to the back of the pouch. In the pouch, the supra-esophageal vessel is further connected to the sub-esophageal vessel through a dense capillary network that allows exchange with the densely packed coelomocytes. Metameric blood vessels encircle the stomach and intestine, connecting the dorsal and the ventral vessels.

Respiration and oxygen transport

Alvinellidae are endemic of deep-sea hydrothermal vents and are therefore exposed to chronic hypoxia (Hourdez and Lallier, 2007). They all possess 4 pairs of well-developed gills anteriorly (on segments 2-5; see Jouin-Toulmond and Hourdez, 2006). These gills represent a very large specific surface area, reaching 12 $cm^2\ g^{-1}$ wet weight in *Alvinella pompejana* and 47 $cm^2\ g^{-1}$ wet weight for *Paralvinella grasslei* (Jouin and Gaill, 1990). In comparison, that surface only reaches 6 $cm^2\ g^{-1}$ in the Trichobranchidae *Terebellides stroemii* (Jouin-Toulmond and Hourdez, 2006). This enlarged gill surface area favors gas exchange across the gills, a key feature in a chronically hypoxic habitat (Hourdez and Lallier, 2007). Gas exchange is further facilitated by a reduced diffusion distance in *A. pompejana* and *P. grasslei* (1-4 µm) compared to that measured in *T. stroemii* (7-10 µm; Jouin-Toulmond and Hourdez, 2006). This reduced diffusion distance is made possible by the presence of intraepidermal loops forming a shallower blood network (Jouin and Gaill, 1990).

All Alvinellidae studied to date possess an extracellular hexagonal-bilayer hemoglobin (HBL-Hb) in their well-developed closed vascular system and, at least for *A. pompejana*, *A. caudata* and *P. grasslei* a globin contained in erythrocytes in the coelomic fluid (Toulmond et al. 1990, Hourdez et al 2000, pers. obs.). The presence of a HBL-Hb in the vascular system and intracellular hemoglobin in the coelomic fluid is typical among Terebellomorpha. In Alvinellidae however, these hemoglobins exhibit very high affinities for oxygen, another characteristic that bears an adaptive value in a chronically hypoxic habitat (Hourdez and Lallier, 2007). This high affinity is counterbalanced by a pronounced Bohr effect that allows an enhanced release of oxygen when pH decreases (*e.g.* near metabolically active tissues; Terwilliger and Terwilliger, 1984, Toulmond et al., 1990, Hourdez et al., 2000, Hourdez and Weber, 2005).

In the peri-esophageal pouch, the very close proximity of the dense capillary network and the numerous erythrocytes allows gas exchange between the vascular and coelomic compartment. This gas transfer system has been described in other Terebellomorpha, although the peri-esophageal pouch is specific of Alvinellidae. Compared to other Terebellomorpha, the exchange can be bidirectional in *Alvinella pompejana*, while it is unidirectional in Terebellidae (Hourdez et al., 2000). This likely buffers the changes in environmental oxygen concentrations, especially for the cerebral area that is directly perfused by the supra-esophageal vessel after the capillary network in the peri-esophageal pouch (Hourdez and Lallier, 2007).

Reproduction and larval development

Alvinellidae are all gonochoristic with a marked sexual differentiation on the dorsal organ with a well-developed genital pore in females and a pair of modified buccal tentacles in males on the first setigerous segment (Zal et al. 1994, Zhadan et al. 2000, Pradillon et al. 2003). Females possess a widely open genital pore located dorsally at the base of the branchial crown on the first asetigerous segment. Depending on the species, females also have one or two pairs of gonoducts that connect to the pore with a spermatheca on the path. Males also have a less developed genital pore which is connected to pair of spermiducts and seminal vesicles (Zal et al., 1994; Zhadan et al., 2000). The sperm is usually transferred as bundles (spermatozeugmata) to the female genital opening by the modified sexual tentacles (Zal et al., 1994; Desbruyères et al., 1998). *Paralvinella pandorae pandorae* and *P. pandorae irlandei* may be exceptions to this reproductive strategy. In both *Alvinella* species and *P. grasslei*, a specific sexual behavior has been observed from close-up videos of individuals located on the wall of vent chimneys showing neighboring individuals entering the tube of other congeners and/or mating head to head (Chevaldonné and Jollivet 1993, Faure et al. 2007). Such a behavior has also been described in several intertidal Terebellidae such as *Ramex californiensis* and *Nicolea zostericola* (Herpin 1925, Eckelbarger 1975, Rouse & McHugh 1994). In *P. pandorae irlandei*, large cocoons of white mucus have also been found containing males and females and small juveniles, suggesting that mating could still occur but in a slightly different way (D. Jollivet, pers. obs.). Because the two sub-species of *P. pandorae* are lacking sexual appendages, cocoons may be a way to maximize internal reproduction without sperm transfer.

Spermatozoa are greatly modified in *A. pompejana*, *A. caudata* (Jouin-Toulmond et al., 2002) and *P. grasslei* and *P. palmiformis*, with a very reduced flagellum in the former species, and no flagellum at all in the two latter species (Zal et al., 1994, Jouin-Toulmond et al., 2002)(Figure 7). This contrasts with the spermotozoa ultrastructure of *P. pandorae pandorae* and *P. pandorae irlandei*, which are also modified but with a longer flagellum (McHugh, 1995, Jouin-Toulmond et al., 2002). The small length of the flagella clearly indicates a lack of sperm motility in *Alvinella* and absence in *P. grasslei* and *P. palmiformis* that fits well with the occurrence of specific sexual assemblages and the head-to-head sperm transfer behavior (Figure 7). By contrast, the presence of a more elongated spermatazoa with a longer flagellum in the two *P. pandorae* sub-species may represent a more plesiomorphic reproductive strategy, closer to Ampharetidae (Giangrande 1997). Although quite diverse, all spermatozoa morphologies belong to the introsperm category because of modified structures (see Jamieson & Rouse, 1989): although they can have flagella, they have no acrosome and an atypical or absent midpiece.

The presence of spermathecae in all species is a characteristic not found in any other Terebellomorpha to date (Jouin-Toulmond et al., 2002). This morphological character could be a way of maximizing reproductive success with a slightly male-biased sex ratio (Faure et al. 2007). Female fecundities vary widely, from a maximum of 978 000 oocytes per female in *A. pompejana* (Faure et al. 2007), down to 3900 oocytes per female in *P. grasslei* (Zal et al. 1995). A ventral gonad in the anterior part of the worm releases immature oocytes in the coelomic cavity, and, in *A. pompejana*, from 0 to 5 oocyte size cohorts (ranging from 80 to 275 µm in diameter) can be found. As a result, reproductive females have high but unequal coelomic fecundities, ranging between 67 000 to 978 000 oocytes (all maturation stages combined) but the number of mature oocytes recruited into gonoducts was always small (hundreds of eggs) and very similar between individuals (with exception of females having spawn all their mature oocytes (empty gonoducts)). The same type of observation was made for *P. pandorae* (McHugh, 1989), *P. grasslei* (Zal et al. 1995) and *P. palmiformis* (Copley et al. 2003), this suggestings that Alvinellidae exhibit a continuous to semi-continuous gametogenesis with a great accumulation of oocytes in the coelom but are likely to produce discontinuous and synchronized spawnings throughout the year. Alvinellidae seem to have a very rapid growth phase, followed by an intensive effort of reproduction during which size cohorts are mixing. Such a dynamics in reproduction is probably advantageous in a highly variable and patchy environment with periodic cohorts of settlers in populations throughout the year for nearly all species (McHugh 1989, Zal et al. 1995, Copley et al. 2003, Pradillon et al. 2005, Faure et al. 2007).

Very little information has been reported on the larval development of Alvinellidae but a 7-chaetiger erpochaet larva of *P. grasslei* has been sampled and described by Desbruyères & Laubier (1986), suggesting that this species may have restricted capabilities of dispersal and/or a direct development (Figure 8). The size of fertilized eggs is quite large (greater than 250 µm) in *Paralvinella* spp. and a little bit less but negatively buoyant in *Alvinella* spp. (Faure et al. 2007). This suggests that Alvinellidae likely have lecithotrophic embryos and may represent poor dispersers. This is reminiscent of a great number of Ampharetidae, which usually settle a week after spawning at a 3 or 4-chaetiger stage (Grehan et al. 1991, Giangrande 1997), or some Terebellidae, which brood their progeny in tubes or inside cocoons (Rouse & McHugh 1994). Brooding seems to likely occur in the two subspecies of *P. pandorae*, for which cocoons containing juveniles have been found among faunal samples. However, because of cold and oligotrophic conditions of the deep-sea waters outside areas of venting, larval development may be stopped or slowed down and the vitellus storage of the egg may be sufficient to delay settlement and metamorphosis for a long period of time, until environmental conditions are appropriate (Pradillon et al. 2000).

Predation

Alvinellidae are often predated upon by Bythograeidae crabs such as *Cyanagraea praedator* or Lithodidae crabs such as *Macroregonia macrochira* (Desbruyères et al. 1982, Tunnicliffe and Jensen 1987). They do not seem to fall prey to zoarcid fishes (Sancho et al. 2005), which are also endemic of deep-sea hydrothermal vents. Fragments of body and cirri have been recovered in large numbers in the stomach of the crabs *Bythograea thermydron* and *Cyanagraea praedator* along with limpet shells on the East Pacific Rise (Jollivet 1993). Young recruits and juveniles could also be a prey for other errant polychaetes such as *Nereis sandersi* or some Polynoidae such as *Lepinotopodium fimbriatium*.

Phylogeny and Taxonomy

Taxonomy

The family Alvinellidae only comprises two genera: the genus *Alvinella* with 2 morphological species already described from the Eastern Pacific and the genus *Paralvinella* with 10 described species. The genus *Paralvinella* was initially erected by Desbruyères and Laubier (1982) based on the discovery of a first species, *Paralvinella grasslei* in the washing of the chitinous tubes of the siboglinid worm *Riftia pachyptila*.

All Alvinellidae have 4 pairs of gills located on segments 2 through 5 (Figures 6, 9). In *Paralvinella*, the first setigerous segment is segment 3, and in *Alvinella*, the first setigerous segment is segment 6. In *Alvinella*, the gills correspond to stacked lamellae attached to the stems, while in *Paralvinella*, they are simple filaments attached to the stems. The two genera also differ by the presence of modified hooks on segment 9 only for *Paralvinella* (setiger 7) and on segments 9 and 10 for *Alvinella* (setigers 4 and 5). Other differences have been reported. The prostomium is also sometimes bilobate in *Paralvinella*. The capillary notosetae are smooth for *Paralvinella* and geniculate with two rows of teeth for *Alvinella*. The presence of a conspicuous ventral shield in the anterior part of the worm involved in the mucus secretion in *Alvinella.* Epibiotic bacteria have only been reported in that latter genus, on either the dorsal part (*A. pompejana*) or the tail (*A. caudata*) of the worm where the notopodia are modified.

Important morphological characters

Essential morphological features in identifying the species of Alvinellidae are (Figure 9):

- the structure of the gills (lamellae in *Alvinella* vs. filaments in *Paralvinella*)
- presence of hooks on segment 9 (*Paralvinella*) or segments 9 and 10 (*Alvinella*)
- the position of the first setiger (segment 3 in *Paralvinella* and 6 in *Alvinella*)
- whether the tip of each gill is a free filament or undistinguishable among the other filaments for species of *Paralvinella*
- number of rows of branchial filaments on each stem
- the position of the first segment with ventral uncini
- the shape and number of teeth on the uncini
- the presence of a digitiform lobe on the notopodia.

Desbruyères and Laubier proposed (1993) proposed to subdivide the genus *Paralvinella* into 3 subgenera (*Paralvinella*, *Miralvinella* and *Nautalvinella*). They used the shape and disposition of the gill filaments on the stem of the branchiae, the shape of the modified buccal paired tentacles associated with the dorsal organ, the presence of lobes on the notopodia of the worm and the position of the uncinigerous tori (see Figure 10 for the species diagnostic keys initially proposed by Desbruyères and Laubier 1991).

A diagnosis of the genera and subgenera follows.

Family Alvinellidae Desbruyères & Laubier 1986

Type genus: *Alvinella* Desbruyères & Laubier, 1980

Diagnosis: Large specimens with a large number of setigers (>100) with epibiotic bacteria covering either the dorsal part of the worm or the notopodia of the posterior part of the worm. Anterior part of the worm exhibiting a ventral shield used to secrete a parchment-like tube. Numerous buccal grooved tentacles inserted on a semi-circular buccal membrane, a pair of thick buccal tentacles in males. Stalked gills with lamellar filaments inserted along the stem. Two pairs of hooks inserted on setigerous segments 7 and 8 (i.e. setigers 4 and 5).

Genus *Paralvinella* Desbruyères & Laubier, 1982

Subgenus *Paralvinella* Desbruyères & Laubier 1993

Type species: *Paralvinella grasslei* Desbruyères & Laubier, 1982

Other species: *Paralvinella palmiformis* Desbruyères & Laubier 1986, *Paralvinella fijiensis* Desbruyères & Laubier 1993, *Paralvinella sulfincola* Tunnicliffe et al. 1993
Diagnosis: Large specimens with a number of setigers varying from 55 to 180. Numerous buccal grooved tentacles inserted on a semi-circular buccal membrane, large pair of trilobate appendages in males, with a globular eversible ventral organ. Stalked bipennate gills with two rows of cylindrical filaments inserted on opposite sides along the stem. Digitiform or rounded notopodial lobes mostly present on the anterior part of the worm. One pair of hooks inserted on setiger 7. First uncini appear inserted well after the 7th modified setiger (setigers 13-32).

Genus *Paralvinella* Desbruyères & Laubier, 1982
Subgenus *Miralvinella* Desbruyères & Laubier 1993
Type species: *Miralvinella dela* Detinova, 1988
Other species: *Miralvinella hessleri* Desbruyères & Laubier 1989, *Miralvinella bactericola* Desbruyères & Laubier 1991
Diagnosis: Small specimens with a number of setigers varying from 50 to 75. Complex buccal apparatus with grooved tentacles inserted on the buccal membrane dorsally above a pair of pointed and coiled tapering tentacles in males and the globular eversible ventral organ. Stalked bipennate gills with two rows of cylindrical filaments inserted on opposite directions along the stem. Digitiform notopodial lobes mostly present on the anterior part of the worm. One pair of hooks inserted on setiger 7. First uncini appear inserted well after the 7th modified setiger (setigers 18-20).

Genus *Paralvinella* Desbruyères & Laubier, 1982
Subgenus *Nautalvinella* Desbruyères & Laubier 1993
Type species: *Nautalvinella pandorae* Desbruyères & Laubier, 1986
Other species: *Nautalvinella pandorae irlandei* Desbruyères & Laubier 1986, *Nautalvinella unidentata* Desbruyères & Laubier 1993
Diagnosis: Small specimens with a number of setigers varying from 50 to 75. Unpaired pointed buccal apparatus with a longitudinal slit surrounded by numerous grooved tentacles with or without an eversible globular organ. No pair of large tentacles in males. Stalked bipinnate gills with leaf-shaped filaments inserted on two adjacent rows along the stem as a comb. No gill filaments at the tip of the branchiae. No digitiform notopodial lobes. One pair of hooks inserted on setiger 7. First uncini appear inserted well after the 7th modified setiger (setigers 5-6) for the two *pandorae* subspecies but not *unidentata* (first insertion on setiger 28-29).

Phylogeny

Although the initial description qualified Alvinellidae as aberrant Ampharetidae, their position among Terebellomorpha remains unclear. Rousset et al. (2003), based on morphological and molecular (28S rRNA) characters, did not support the view that Ampharetidae are a sister taxon to Alvinellidae, although the obtained trees were poorly resolved. The tree solely based on the morphology placed the Alvinellidae close to the Ampharetidae, in agreement with Rouse and Fauchald (1997) but support for this relationship is weak. The combined data yielded four equally parcimonious trees that only differed by relationships among Ampharetidae. In this tree, Alvinellidae is sister group to Terebellides (Trichobranchidae), the next sister group being Pectinaria (Pectinariidae).
Within the family, some studies have used molecular data to produce phylogenies. Using a fragment of mitochondrial marker COI, a phylogenetic tree of Alvinellidae (without species of the subgenus *Miralvinella*) proposed that the genus *Paralvinella* could be polyphyletic as *P. pandorae pandorae* was basal to the clades grouping the two *Alvinella* species on one hand, and a clade comprising the remaining *Paralvinella* species on the other hand

(Vrijenhoek et al. 2013). New phylogenomic analyses using 423 orthologous genes obtained from the comparison of the transcriptome assemblies of 9 Alvinellidae, including species of the three *Paralvinella* subgenera and the two *Alvinella* species, clearly indicates that the family Alvinellidae and the two genera *Paralvinella* and *Alvinella* are monophyletic (unpublished data; see Figure 11). However, the phylogenetic signal does not totally agree with the taxonomic arrangement of Avinellidae proposed by Desbruyères and Laubier (1993) suggesting that *P. unidentata* and *P. pandorae* are clearly basal to the *Paralvinella* lineage and not sister species. The four other *Paralvinella* species (*P. grasslei, P. palmiformis, P. fijiensis* and *P. sulfincola*) cluster together and clearly form pairs of sibling geographic species. *P. hessleri* has a basal position to this *Paralvinella* clade, which may validate its placement into another clade. To clarify this point, acquiring transcriptomes of *P. dela* and *P. bactericola* is still needed to validate this potential clade as corresponding to the subgenus *Miralvinella*.

Molecular dating using the Farallon plate subduction date around 28 Mya to calibrate the molecular clock indicates that both the speciation events leading to *A. pompejana* and *A. caudata* on one hand, and *P. fijiensis* and *P.sulfincola* on the other hand occurred before this geological event. It also suggests that radiation in Alvinellidae predates the series of anoxic episodes in the deep sea at the end of the Cretaceous about 60 Mya (Jacobs & Lindberg 1998).

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