



The fossil record of hydrothermal vent communities

Crispin T. S. LITTLE

*School of Earth Sciences, University of Leeds, Leeds LS29 6HE, UK.
fax: (44) 113 233 5259. E-mail: c.little@earth.leeds.ac.uk*

An increasing number of hydrothermal vents with animal communities are being found in the Pacific, Atlantic and Indian Oceans. These communities are dominated in terms of biomass by animals harbouring symbiotic chemoautotrophic bacteria, including vestimentiferan tube worms, vesicomyid and bathymodiolid bivalves, provannid gastropods and bresiliid shrimp (Van Dover, 2000). Based on morphological characters it has been suggested that some of the obligate vent taxa (barnacles, neomphalid gastropods) are Mesozoic or even Palaeozoic relicts, and the vent environment has been an extinction resistant refuge (Newman, 1985; see McArthur & Tunnicliffe, 1998 for review). However recent molecular work has countered that other obligate vent taxa (vestimentiferans, vesicomyids and bresiliids) have a much younger origin, diverging less than 100 million years ago (Black et al., 1997; Peek et al., 1997; Halanych et al., 1998; Shank et al., 1999). The fossil record of hydrothermal vent animals has the potential to test these hypotheses. This paper gives an overview of the present state of knowledge of the fossil record of hydrothermal vent communities and discusses what this record can tell us about the origination of modern vent taxa.

Vent fossils are found in land-based deposits of sulphide minerals contained within volcanic rock sequences. These ancient sulphides are the direct analogue of the sulphide deposits forming at modern vent sites, and they share many gross morphological (e.g. black smoker chimneys), mineralogical and isotopic features (Little et al., 1999c). Fluid inclusion analyses from some of these ancient sulphide deposits shows they formed in deep water (>2000 m) and at high temperatures (up to 371°C) (Little et al., 1999c).

To date, 19 ancient sulphide deposits containing vent fossils have been found (Fig. 1), ranging in age from the Eocene to the Silurian (Little et al., 1997, 1998, 1999a,b,c). The temporal distribution of these deposits is not even, with most being concentrated in the Silurian and Devonian of the Urals, and the Cretaceous of Cyprus and Oman. There are large gaps in the record in the late Palaeozoic and most of the Tertiary. All of these vent deposits contain worm tubes *sensu lato*, but the Yaman Kasy, Sibay, Figueroa and Cypriot sulphides have more diverse faunas and are discussed here in more detail. Two fossil occurrences associated with sulphide deposits older than Silurian have been reported as representing vent communities

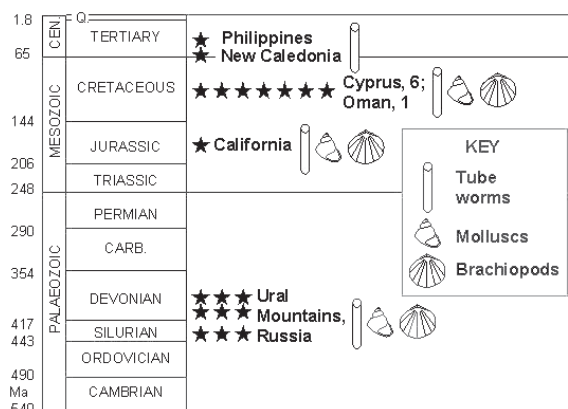


Figure 1. Temporal distribution of hydrothermal vent fossil assemblages. Cen. = Cenozoic; Q. = Quaternary.

(Rasmussen, 2000, Steiner et al., 2001), but the evidence that these are indeed vent related is equivocal at present.

All vent fossils are preserved as external and sometimes also internal moulds of pyrite; original shells and tubes are always missing (Little et al., 1998, 1999c). This preservation style makes some of the fossils hard to identify, and means that putative bacterial chemosymbiosis is impossible to prove. Preservation bias has almost certainly removed some of the biotic elements from the original communities, particularly those that are small, and/or mobile, and/or without hard parts.

The species compositions of the Yaman Kasy, Sibay, Figueroa and Cypriot vent fossil assemblages (Little et al. 1999a,b,c) are shown in Figs 2-5. The Yaman Kasy (~430 Ma.) and Sibay (~385 Ma.) deposits formed in arc-related settings in the Uralian Ocean, a major water mass that had disappeared by the early Carboniferous. The Figueroa deposit formed on a mid-ocean ridge or close to an oceanic island somewhere in the equatorial Pacific about 190 million years ago. The Cypriot deposits are hosted by the 91 million year old Troodos Ophiolite, a fragment of ocean crust that formed at a spreading ridge close to a subduction zone in the Neotethyan Ocean, a precursor to the present day Mediterranean.

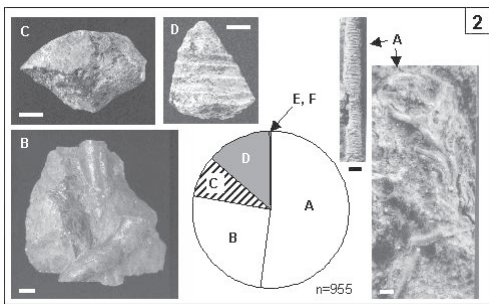


Figure 2. Abundance pie chart of fossils comprising the Silurian Yaman Kasy vent assemblage. White sectors = tube worms; hatched sectors = brachiopods; grey sectors = molluscs. A: ?polychaete tube *Eoalvinellodes annulatus* Little et al., 1999; B: vestimentiferan *Yamankasia rifeia* Shpanskaya, Maslennikov & Little 1999; C: lingulate brachiopod *Pyrodiscus lorrainae* Little et al., 1999 (articulated specimen); D: *Thermoconus shadlunae* Little et al., 1999; E = indeterminate vetigastropod; F = ambonychiid bivalve *Mytilarca* sp. Scale: A = 1mm; B-D = 10mm.

All these fossil vent assemblages are dominated by annelid tube worms (Little et al., 1998); some of which have been classified as vestimentiferans (Shpanskaya et al., 1999). There is some controversy about the identification of the Palaeozoic tube worm fossils as vestimentiferans, as they lack diagnostic soft parts and tubes have few characters (Halanych et al., 1998). However, I am confident that the Mesozoic tube worm fossils from Figueroa and Cyprus (which have yet to be formally described) are vestimentiferans, because they share with the modern vestimentiferan species (including both vent and seep representatives) distinctive longitudinal ridges on the tube walls. I have not found these ridges on the tubes of other

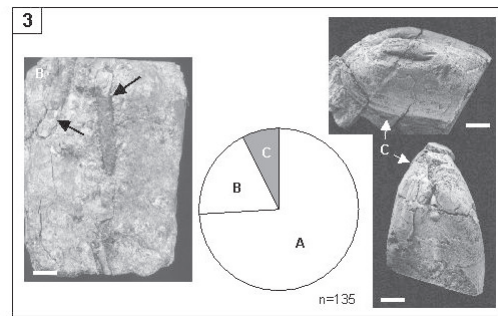


Figure 3. Abundance pie chart of fossils comprising the Devonian Sibay vent assemblage. A: indeterminate ?annelid tubes; B: vestimentiferan *Tevidestus serriformis* Shpanskaya, Maslennikov & Little, 1999, black arrows point to two specimens in a sulphide block; C: modiomorphid bivalve *Sibaya ivanovi* Little et al., 1999, two views of articulated specimen. Scale: B-C = 10 mm.

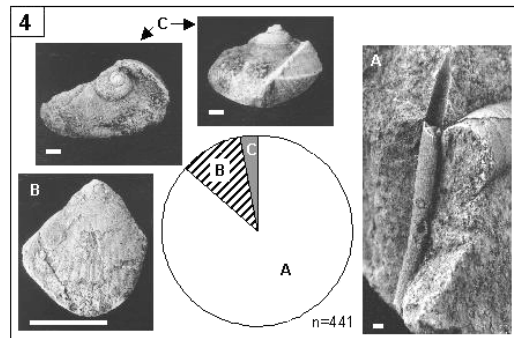


Figure 4. Abundance pie chart of fossils comprising the Jurassic Figueroa vent assemblage. A: vestimentiferan tubes; B: rhynchonellid brachiopod *Anarhynchia* cf. *gabbi* Ager, 1968; C: trochid gastropod, two views. Scale: B = 10 mm; A, C = 1 mm.

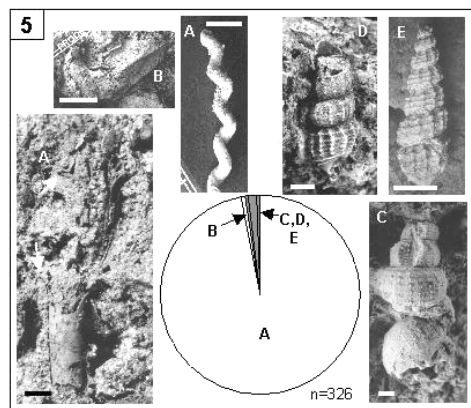


Figure 5. Abundance pie chart of fossils comprising the Cretaceous Cypriot vent assemblages. A: vestimentiferan tubes, white arrows point to flanges; B: ?serpulid tube; C: epitioid or provannid gastropod; D: cerithioid or provannid gastropod sp.; E: cerithioid or provannid gastropod sp. A. Scale: A-E = 1 mm.

vent polychaetes belonging to the frenulate siboglinids, chaetopterids or serpulids. The implications of this identification are discussed below.

Brachiopods are important constituents in the Yaman Kasy and Figueroa fossil assemblages. The Yaman Kasy representatives are lingulates (= inarticulates) and are extremely large for this group. The Figueroa species *Anarhynchia* cf. *gabbi* Ager, 1968 belongs to the extinct family Peregrinellidae. Members of this family were abnormally large among contemporary rhynchonellids, and appear to have lived exclusively at vent and cold seep sites in the late Palaeozoic and Mesozoic.

Unlike modern vent communities, molluscs are not abundant in fossil vent assemblages, although overall they form the most species-rich group. The Yaman Kasy assemblage contains the cone-shaped monoplacophoran *Thermoconus shadlunae* Little et al., 1999, two small indeterminate vetigastropod specimens and a single valve of the bivalve *Mytilarca* sp. It is notable that *T. shadlunae* is the youngest and by far the largest member of the extinct family Kirengellidae. Other kirengellids were common in Cambrian and Ordovician non-reducing shelf environments. *Mytilarca* belongs to the extinct Palaeozoic family Ambonychiidae and is the first member of that taxon to be found at vent sites. The Sibay mollusc representative, *Sibaya ivanovi* Little et al., 1999, is a homeomorph of modern vesicomyids and was originally described being a member of that family. However, it actually belongs to another extinct Palaeozoic family called the Modiomorphidae (Little et al., 1999c).

Bivalves are absent from the Mesozoic vent assemblages, but gastropods make up a small proportion of these faunas. Figueroa contains a species of trochid, while the Cypriot assemblages contain a single epitoniid specimen and two species of small cerithioids. All these gastropods are at present undescribed, and it is possible that all the Cypriot gastropods belong instead to the extant family Provannidae (C. Little, personal observation).

The species data from these ancient vent sites, in terms of the temporal distribution of selected vent higher taxa (families and orders), are shown in Fig. 6. In addition, there are molecular divergence estimates from Peek et al. (1997) and Halanych et al. (1998) and data from the fossil record of cold seep sites. The graph has several major features, the first of which is that there are serious discrepancies between molecular estimates of the origin of the vestimentiferans and vesicomyids, and their fossil records. According to molecular estimates the vestimentiferans arose no earlier than 100 (Black et al., 1997) or 65 (Halanych et al., 1998) million years ago, yet the earliest fossils are more than 330 million years older than this estimate. Even the Mesozoic fossil vestimentiferans are 90 million years older than these estimates. This discrepancy between the molecular and fossil dates means that either 1) the Palaeozoic and possibly Mesozoic vestimentiferans represent an earlier lineage that is not ancestral to the extant taxa, or 2) the rate of evolutionary change in the genes analysed by Black et al. (1997) and Halanych et al. (1998) have slowed substantially, and the divergence date is a serious underestimate. According to Peek et al. (1997) the origin of

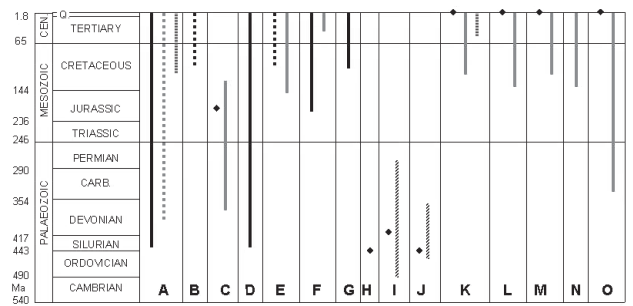


Figure 6. Stratigraphic ranges of selected fossil and recent vent and seep higher taxa. Codes: **A**: vestimentiferans; **B**: serpulids; **C**: rhynchonellid brachiopods; **D**: monoplacophorans; **E**: provannid gastropods; **F**: trochid gastropods; **G**: cerithioid gastropods; **H**: indeterminate vetigastropod; **I**: modiomorphid bivalves; **J**: ambonychiid bivalves; **K**: vesicomyid bivalves; **L**: mytilid bivalves; **M**: thyasirid bivalves; **N**: lucinid bivalves; **O**: solemyid bivalves. Key: diamonds = single stratigraphic taxon occurrences; solid black lines = taxon ranges at vents; solid grey lines = taxon ranges at seeps; dashed lines = uncertain taxon ranges; cross hatched lines = taxon ranges in non-reducing habitats; horizontal hatched lines = molecular divergence estimates.

the modern vesicomyid bivalves was no more than 43.8 million years ago, and yet, like the vestimentiferans, they have a substantially longer fossil record. The oldest described fossil vesicomyid is from a late Cretaceous (~95 Ma.) seep site in Japan (Kanie & Nishida, 2000), almost double the molecular estimate. Again, as Peek et al. (1997) suggest, the gene change rate may have slowed down in this group.

The second feature of Fig. 6 is that there are a significant number of taxa missing from fossil vent sites that are important constituents of modern vent communities. These include vesicomyid and bathymodiolid bivalves, many gastropod families and all arthropods. Interestingly some of these missing taxa have fossil representatives at seep sites (e.g. vesicomyid, mytilid, thyasirid, lucinid and solemyid bivalves). Amongst the taxa not present at fossil vent sites are a number that have been considered Mesozoic or possibly Palaeozoic 'relics', these include neomphalid gastropods and barnacles (McArthur & Tunnicliffe, 1998). There are several possible explanations for the absence of these various groups from fossil vent sites. First, these groups were present at ancient vents but have yet to be discovered, because either the fossil record is too sparse, or representative specimens did not get preserved (a distinct possibility for the mobile taxa like decapods). Second, the missing taxonomic groups invaded vent sites from other environments only in the past 40 million years or so. This may be corroborated for bresiliid shrimp, which Shank et al. (1999) suggest originated in the Miocene (~24 Ma.), and a study by Craddock et al. (1995) that indicated modern vent bathymodiolids are derived from the group of bathymodiolids living at seep sites.

The third feature of the fossil record of vent communities is that in addition to the groups that have both modern and fossil vent representatives, there are a small number of taxa

in ancient communities that belong to either extinct families or groups no longer present at vent sites. *Sibaya ivanovi* Little et al., 1999 and *Mytilarca* sp. belong to families that had exclusively Palaeozoic ranges and were diverse in non-reducing shallow marine environments. Rhynchonellid brachiopods like *Anarhynchia* cf. *gabbi* Ager, 1968, were present in vents and seeps from the late Devonian but disappeared from these environments by the early Cretaceous. This shows that the modern vent environment is not a refuge for some taxa that have previously been present at ancient vent (and seep) sites and that major taxonomic groups have moved in and out of the vent environment through geological time.

A final point is that the fossil record also has the potential to test hypotheses about the biogeographic origins of extant obligate vent and seep groups. For example, the presence of vestimentiferans at vent sites in the Neotethys at 91 Ma. and in the Western Pacific at 190 Ma. shows that this group cannot have derived from Pacific cold seep progenitors in the Cenozoic, as has been suggested using cladistic or molecular analyses of extant species (Black et al., 1997, Schulze, 2001).

In conclusion then the oldest well-proven hydrothermal vent fossil assemblage is Silurian (~430 Ma.) in age and comprises annelid tube worms, molluscs and brachiopods. All fossil vent communities contain 'tube worms' *sensu lato*, some of which belong to the Vestimentifera (part of the Siboglinidae). A number of common extant vent groups are presently without a fossil record at vents, including vesicomid and bathymodiolid bivalves, many gastropod families, all arthropods, and a number of taxa considered to be Mesozoic or even Palaeozoic 'relics'.

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