



# Are hydrothermal vent animals living fossils?

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**Since their discovery in 1977, hydrothermal vent communities have provided many surprises about life in the deep sea and in extreme environments. It has been suggested that vent communities contain many living fossils and that deep-sea chemosynthetic environments, such as vents and hydrocarbon seeps, are buffered from extinction events that affect the photic zone. This hypothesis is based on the dependence of these deep-sea communities on a geochemical energy source and the considerable levels of taxonomic novelty that they contain. Here, we review recent evidence from the fossil record of hydrothermal vents and hydrocarbon seeps, together with molecular phylogenies of several dominant hydrothermal vent and seep taxa. In spite of significant discrepancies between the fossil record and molecular divergence estimates for several important taxa, we show that most modern vent animal groups arose relatively recently and that the taxonomic composition of vent communities has changed considerably through time.**

Hydrothermal vents are found at mid-ocean spreading centers in the east Pacific, Atlantic, Arctic and Indian Oceans, and in back-arc basins in the west Pacific (reviewed in [1]). Hydrothermal fluid issuing onto the sea floor at these vent sites is hot (up to 390°C), anoxic, often very acidic, and enriched with hydrogen sulfide (H<sub>2</sub>S), methane (CH<sub>4</sub>), and various metals (especially iron, zinc, copper and manganese). One of the many surprises about vent sites is that these seemingly toxic hydrothermal fluids directly support exceptionally productive biological communities in the deep sea. These hydrothermal vent communities are characterized by their dependence on geochemical energy sources (mainly H<sub>2</sub>S). Many of the invertebrate animals that dominate vents (e.g. vestimentiferan tube worms, vesicomid and bathymodiolin bivalves, provannid gastropods and bresiliid shrimp) exploit these reduced compounds either directly, by way of symbiotic chemoautotrophic bacteria, or indirectly, by grazing and filtering free-living chemoautotrophs (reviewed in [1]) (Box 1). Vent communities contain remarkable taxonomic novelty at the specific and supra-specific level (e.g. new families, orders and classes), and 82% of vent species appear to be endemic [2]. Related taxa are found in hydrocarbon ('cold') seep communities [3].

Hydrocarbon seeps, which are also rich in geochemical energy sources (mainly CH<sub>4</sub> and H<sub>2</sub>S derived from CH<sub>4</sub>), differ from hydrothermal vents in that their seep fluids are cold, usually at ambient deep-sea temperatures [3]. This is because hydrocarbon seeps are usually found around continental margins and subduction zones (linear areas where ocean plates are being pushed beneath the continents or other ocean plates), and are not generally associated with spreading ridges and their heat sources [1,3]. Vents and seeps have several species in common, as well as many genera and families, which highlights the direct evolutionary links between these deep-sea chemosynthetic environments [2–6]. To understand the history of vent-endemic taxa, researchers must also consider evolutionary relationships with cognate taxa living in cold seeps and in other sulphide-rich environments, such as sunken wood and large decaying bones (e.g. those of whales) [7–9].

Given that several 'relic' species (living fossils) are found only at hydrothermal vents, it was suggested that these unusual communities provide us with a 'glimpse of antiquity' [10]. Combined with the exceptional level of endemism seen at higher taxonomic levels, it was postulated that hydrothermal vent taxa have experienced 'a long and continuing evolutionary history' [10], and that these unusual chemosynthetic environments might have served as refugia for relic faunas during major Phanerozoic extinction events that devastated organismic diversity in the photic zone [2]. The antiquity hypothesis derives principally from analyses of morphological characters in extant vent taxa [2,10,11]. By contrast, recent molecular studies of several ecologically dominant vent and seep taxa (vestimentiferans, bathymodiolins, vesicomids and bresiliids) suggest more recent diversifications during the past 100 million years, in the later Mesozoic and Cenozoic (reviewed in [12]). In spite of uncertainties regarding the calibration of the molecular clocks used to assess the evolutionary ages of these taxa, it is easy to reject the hypothesis that the dominant, modern vent taxa are Palaeozoic relics. Chevalloné *et al.* [13] recently suggested that late Mesozoic and Cenozoic estimated ages derived from molecular phylogenies might be linked to a hypothesis posited by Jacobs and Lindberg [14], that global, deep-water, anoxic/dysoxic events during the late Cretaceous (at the Cenomanian–Turonian boundary) and early Tertiary (end Palaeocene) would have wiped out contemporary vent communities. Accordingly, deep-sea vents were repopulated from shallower refugia, such as coastal vents and

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### Box 1. Modern hydrothermal vent animals

Figure 1 illustrates some of the key species in hydrothermal vent communities on the East Pacific Rise [(a), 21°N latitude; (b), Clam Acres site, 21°N latitude; (c), 9°N latitude] and the Mid-Atlantic Ridge [(d), Lucky Strike site, 37°N latitude]. Although most of the species diversity at hydrothermal vents can be attributed to taxonomic groups that comprise small, inconspicuous individuals (e.g. polychaete worms, gastropods, copepod crustaceans and nematodes [1,45]), most of the biomass is formed by a few large and visually striking species (Figure 1). These include vestimentiferan tube worms (Siboglinidae, Figure 1a,b), vent clams (Vesicomyidae, Figure 1a), vent mussels (Bathymodiolinae, Figure 1c) and the blind vent shrimp (*Rimicaris exoculata*, Figure 1d), all of which harbour chemoautotrophic bacterial symbionts [1].

The giant vestimentiferan tube worm *Riftia pachyptila* (Figure 1a–c) builds a durable chitin-rich tube and lacks a gut as an adult, relying nutritionally on endosymbiotic bacteria [1]. They supply their chemoautotrophic endosymbionts with reduced sulfur compounds from vent fluids plus oxygen and carbon dioxide from seawater via haemoglobin in their blood, which can be seen through their bright red gills projecting from the tubes in Figure 1b. Vestimentiferans are common at eastern and western Pacific vent localities, but, for as yet unknown reasons, are absent from Indian Ocean and Atlantic vents, although they are found in Atlantic cold seeps [12,45,46].

The giant vent clam *Calyptogena magnifica* (white shells in Figure 1a), similar to other vesicomyids, houses sulfide-oxidizing (thiotrophic) endosymbionts in its gill tissues and has an extremely reduced gut [1]. A great diversity of vesicomyid species occurs at cold seeps throughout the world [3], but, although several species are found at Pacific hydrothermal vents, they are rare at Atlantic and Indian Ocean vents [12,45–47].

The vent mussel *Bathymodiolus thermophilus* (yellow shells in Figure 1c) also harbours thiotrophic endosymbionts in its gill tissues, but, unlike vesicomyids, it has a functional filter-feeding apparatus and gut [1]. Bathymodiolin species from Mid-Atlantic Ridge vents simultaneously harbour thiotrophic and methanotrophic symbionts in their gill tissue, enabling them to use dual geochemical energy sources [1]. The capacity for feeding and dual symbiosis enables vent mussels to be far more versatile in their habitat preferences than are vestimentiferans and vesicomyids. Thus, bathymodiolins are abundant at most known vent sites, except for those on the northeastern Pacific Ridges [12,45–47], and are also abundant at most Atlantic cold seeps [3].

Vent sites in the Atlantic and Indian Oceans are dominated by the

bresiliid shrimp *Rimicaris exoculata* (Figure 1d), which lives in close proximity to high temperature hydrothermal discharge [1,46,47]. A proportion of the energy of the shrimp is gained from feeding on 'exosymbiotic' bacteria growing on its body surfaces [1]. Other, nonsymbiont-bearing bresiliid species are found at most vent sites [37,46].

In addition to the large symbiont-bearing taxa, Figure 1 also shows a range of other vent animals. These include the squat lobster *Munidopsis subsquamosa* (Figure 1a, scattered throughout; Figure 1c, left corner), a scavenger, and the vent crabs *Bythograea thermydron* (Figure 1a, centre; Figure 1c, centre and right) and *Segonzacia mesatlantica* (Figure 1d, centre left), which are scavengers and predators. Clusters of coiled gastropods (possibly *Protolira thorvaldssonii*) are attached to vent chimneys in Figure 1d (top and right). Other gastropods include the grazing vent limpet *Lepetodrilus elevatus* on worm tubes in Figure 1b, and the clear limpet *Eulepetopsis vitrea* on the large mussel near the lower middle of Figure 1c. *Eulepetopsis vitrea* belongs to a group that is considered a Mesozoic relic [2,40].

Figure 1c courtesy of Richard Lutz and Steven Low Productions.

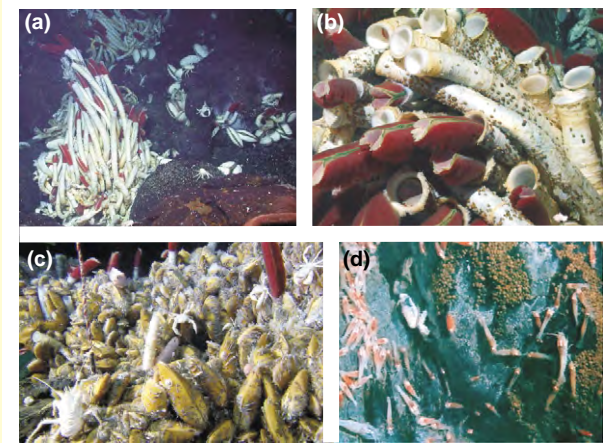


Figure 1.

seeps. In contrast with the antiquity hypothesis [10], the extinction/repopulation hypothesis appears to be consistent with an onshore–offshore pattern of evolutionary diversification seen in marine organisms [15].

The fossil record provides alternative means for investigating the origins and ages of vent taxa. Fossil vent communities contain both taxa that are present at modern vents and numerous representatives of extinct taxa [16–18]. Based on discrepancies between evolutionary ages inferred from molecular divergence versus fossil evidence for several vent taxa, doubts have been raised about the correct identification of some vent fossils [12,18,19]. Here, we review recent evidence from the fossil record of hydrothermal vent and hydrocarbon seep groups (Box 2) and molecular phylogenetic analyses of some common vent and seep taxa (Box 3), and discuss the implications of these data for the antiquity hypothesis. Factors affecting the quality of these fossil and molecular phylogenetic data are discussed in Box 4. In spite of significant discrepancies between the fossil record and molecular divergence estimates for several important taxa, we show that most modern vent animal groups arose relatively recently and that the taxonomic composition of

vent communities has changed considerably through time, indicating that deep-sea chemosynthetic environments might not be immune from global extinction events that affect diversity in the photic zone.

### Stratigraphic ranges of vent taxa based on fossil occurrences

#### Palaeozoic vent taxa

Of three taxa found in ancient vent communities, two belong to extinct families (ambonychiid and modiomorphid bivalves) and one belongs to a group that is not found at modern vent sites (lingulate brachiopods) (Figure 1). The exclusively Palaeozoic ambonychiids had a vent representative in the Silurian [18]. Modiomorphids became extinct during the late Cretaceous, but they had a vent representative in the Devonian [18], and seep representatives in the Devonian [20,21] and Cretaceous [22]. Lingulates do not occur at modern vents, but they were common at a Silurian vent site [18] and, although they closely resemble other Devonian and Carboniferous congeners, they are unrelated to modern lingulates [18]. Two other modern vent taxa have Palaeozoic vent representatives:

## Box 2. Hydrothermal vent and hydrocarbon seep fossils

### Vent fossils

Hydrothermal vent fossils are found in sulphide deposits within volcanic rock sequences in accreted volcanic arc terranes and ophiolites (fragments of old ocean crust thrust onto continental margins) [18]. Nineteen vent fossil occurrences are known, ranging in age from the Eocene to the Silurian [18] (~500–~430 Mya). Their temporal distribution is uneven, with most being concentrated in Silurian and Devonian arc-related rocks of the Ural Mountains of Russia, and in the Cretaceous ophiolites of Cyprus and Oman; large gaps exist in the late Palaeozoic and Tertiary. Fossil vent taxa include vestimentiferan-like tube worms, brachiopods and molluscs. All fossils are preserved as external and sometimes internal moulds of pyrite, but the original shells and tubes are always missing [18,35]. This preservation style makes some of the vent fossils hard to identify and associations with microbial chemoautotrophs impossible to demonstrate.

### Seep fossils

Hydrocarbon seep fossils are found in discrete carbonate lenses hosted by deep-water sedimentary rock sequences in a variety of tectonic settings. These seep carbonates have very distinctive negative carbon isotope values and complex internal structures [25,31,33]. At least 50, possibly as many as 200 fossil cold seep communities are known from the early Devonian to the Pleistocene. Most of these are in Tertiary rocks of the western USA [31,33], Japan [48,49] and Italy [32]. A good record also exists from the Mesozoic of the western USA ([25], K.A. Campbell, unpublished), Japan [26,50] and France [51], and a few Palaeozoic occurrences are found in Germany [28] and Morocco [20,21]. Fossil seep taxa are much more diverse than are fossil vent taxa and include sponges, tube worms, brachiopods (dominant in Palaeozoic and some Mesozoic seeps), molluscs (dominant in Tertiary and some Mesozoic seeps) and crustaceans. Seep fossils are generally better preserved than are those at vents (which might also explain their greater diversity); mollusc shells often show original mineralogy, although complete dissolution is common in some seep deposits. For the complete seep fossil data base, please contact the corresponding author.

monoplacophoran molluscs and vestimentiferan-like tube worms (Figure 1). The Silurian vent monoplacophoran belongs to an extinct early Palaeozoic family [18] and is therefore not related to the modern vent species [23]. Identification of the Silurian and Devonian vent tube worm fossils as vestimentiferans is, however, controversial. Tube-worm fossils that might have a vestimentiferan affinity have also been found in a Devonian seep site [20].

### Mesozoic vent taxa

All but one Mesozoic vent taxa have representatives at modern vent sites (Figure 1). Three gastropod groups, trochoideans (Jurassic), cerithioideans (Cretaceous) and, although their identification is uncertain, provannids (Cretaceous) also occurred in Jurassic seeps [18]. Vestimentiferan-like tube-worm fossils have been found at Jurassic and Cretaceous vent sites [18] and seep sites [24–26]. Serpulids have been found in Cretaceous and younger seep sites [27] and possibly also in a Cretaceous vent site [18]. Peregrinellid brachiopods occurred at Jurassic vents and Devonian, Carboniferous, Jurassic and Cretaceous seeps [16,28,29]. Members of this family, which became extinct during the early Cretaceous, were abnormally large among contemporary rhynchonellids, and seem to have been endemic to chemosynthetic environments [29,30]. This could mean that the peregrin-

## Box 3. Molecular evidence

### Vestimentiferan tube worms

Recent attempts to estimate the evolutionary age of vestimentiferan tube worms are based on mitochondrial cytochrome oxidase subunit I (COI) sequences and a vicariant event that intersected an eastern Pacific ridge system [13]. Subduction of the Farallon-Pacific Ridge beneath a portion of the North American Plate 28.5–35 million years ago (Mya) [52], separated the present-day East Pacific Rise (EPR) from the Gorda/Juan de Fuca/Explorer (GFE) ridge systems. Using a nucleotide substitution rate of 0.46% My<sup>-1</sup>, obtained from the splits between sister species that presently occupy the EPR and GFE, separation of vestimentiferans from their pogonophoran relatives would have occurred <60 Mya [13]. Work in progress reveals that a slower clock calibration should also be considered for COI. It yields a maximum age estimate of ~126 Mya for vestimentiferans (L.A. Hurtado, PhD thesis, Rutgers University, 2002). Nevertheless, the <60 Mya age encompasses the 50 Mya estimate based on borrowed substitution rates for rRNA [34] (Box 4). In spite of the liberal range of estimates obtained with various calibration methods (50–126 Mya), molecular evidence places the origin of vestimentiferans in the mid-Mesozoic to early Cenozoic, rather than in the Palaeozoic.

### Vesicomylid clams

Mitochondrial COI divergence suggests that vent- and seep-endemic vesicomylids arose during the early Cenozoic [43]. COI substitution rates were calibrated from the veneroid fossil record, assuming that vesicomylids and dreissenids separated during the early Triassic (245 Mya) or, alternatively, that these taxa diverged shortly after the appearance of heterodonts during the Ordovician (500 Mya). This uncertainty notwithstanding, the range of COI amino-acid substitution rates (0.1–0.2% My<sup>-1</sup>) suggests that the common ancestor of vesicomylids lived only 22–44 Mya, during the Cenozoic.

### Bathymodiolin mussels

Limited 18S rRNA divergence among vent and seep bathymodiolins suggests a relatively recent origin from ancestors that occupied wood and bone [8]. Significant rate heterogeneity among bathymodiolin lineages complicated attempts to estimate their age, but the common ancestor of modern vent and seep species might have lived as recently as 22 Mya (D. Distel, pers. commun.). We re-analyzed these data by removing the long-branches associated with a few lineages in the subfamily to eliminate rate heterogeneity. Using borrowed rRNA substitution rates ranging from 0.6–1.0% 50 My<sup>-1</sup> [53], we estimate that the subfamily Bathymodiolinae could have split from other mytilids 56–94 Mya, placing their origins in the mid-Mesozoic to early Cenozoic.

### Bresiliid shrimp

Bresiliids left no fossil record, but COI nucleotide substitution rates borrowed from Trans-Panamanian carideans suggest that they diversified <20 Mya [37]. All DNA sequences used for the preceding age estimates are available from GenBank (<http://www.ncbi.nlm.nih.gov/GenBank/index.html>) with accession numbers in the associated publications.

nellids, unlike modern brachiopods, had chemosymbionts [29,30], or, similar to modern brachiopods, were ecological generalists in low oxygen settings [29].

### Cenozoic vent taxa

Poorly preserved worm tubes, which might have vestimentiferan affinities, are the only Cenozoic vent fossils (Figure 1) [18]. The lack of Cenozoic vent fossil diversity is a function of the lack of data from this period (Box 2). By contrast, tube-worm fossils, which also might have vestimentiferan affinities, were common in Eocene–Pliocene seep deposits [31–33].

#### Box 4. Factors affecting the quality of fossil and molecular data

Molecular clock methods are useful for estimating the evolutionary ages of taxa that exhibit considerable morphological homoplasy, and they are the only methods for estimating the ages of taxa with no fossil record. The molecular clock hypothesis assumes that the rate of change of a gene is nearly constant across evolutionary lineages [54]. Although evolutionary rates can vary greatly, both through time and among taxa, methods do exist to accommodate such rate heterogeneity [55]. Molecular clocks have been calibrated in several ways. Some molecules, such as the small subunit rDNA, are assumed to have 'universal clocks' that appear to be relatively constant [53], and other molecules behave more erratically [56], yielding 'local clocks' with limited timescales. Ideally, molecular clocks should be calibrated with independent data, such as fossil evidence [57]. Calibrations have also been based on the dates of vicariant events, such as closure of the Isthmus of Panama [58]. Because molecular substitution rates vary over time, it is unwise to extrapolate to distant times from 'local clocks' calibrated with recent events, and vice versa. Also, substitution rates calibrated for particular genes in one taxon are often applied to unrelated taxa ('borrowed'). Such borrowed clocks are also risky, because substitution rates might not be constant across taxa. Although molecular clocks are imperfect chronometers, they have been used to estimate approximate timescales for the evolutionary divergence of many organisms with poor fossil records [59] including vent- and seep-endemic taxa (Box 3).

Fossil data have a great potential advantage over hypotheses of origination derived from morphological and molecular analysis of modern species, because stratigraphic records can provide direct observation of the first appearance of a taxon [38]. However, two problems are common to all fossil data. First, the initial appearance of a taxon in the fossil record will undoubtedly be younger than its true origin because of the random processes affecting the likelihood of fossilization and the intensity of collection efforts. Second, the quality of the record and fossil preservation is highly variable [38,60]. Unfortunate features of the fossil record of hydrothermal vents are the limited number of known localities, their temporal unevenness and, particularly, a lack of Cenozoic sites (Figure 1, main text). In addition, vent fossils are not always well preserved, leading to problems with taxonomic identification and homoplasy masking true evolutionary patterns. The seep record is better, particularly during the Tertiary, and seep fossils are often well preserved (Box 2).

#### Modern vent taxa with fossil record at seeps, but not vents

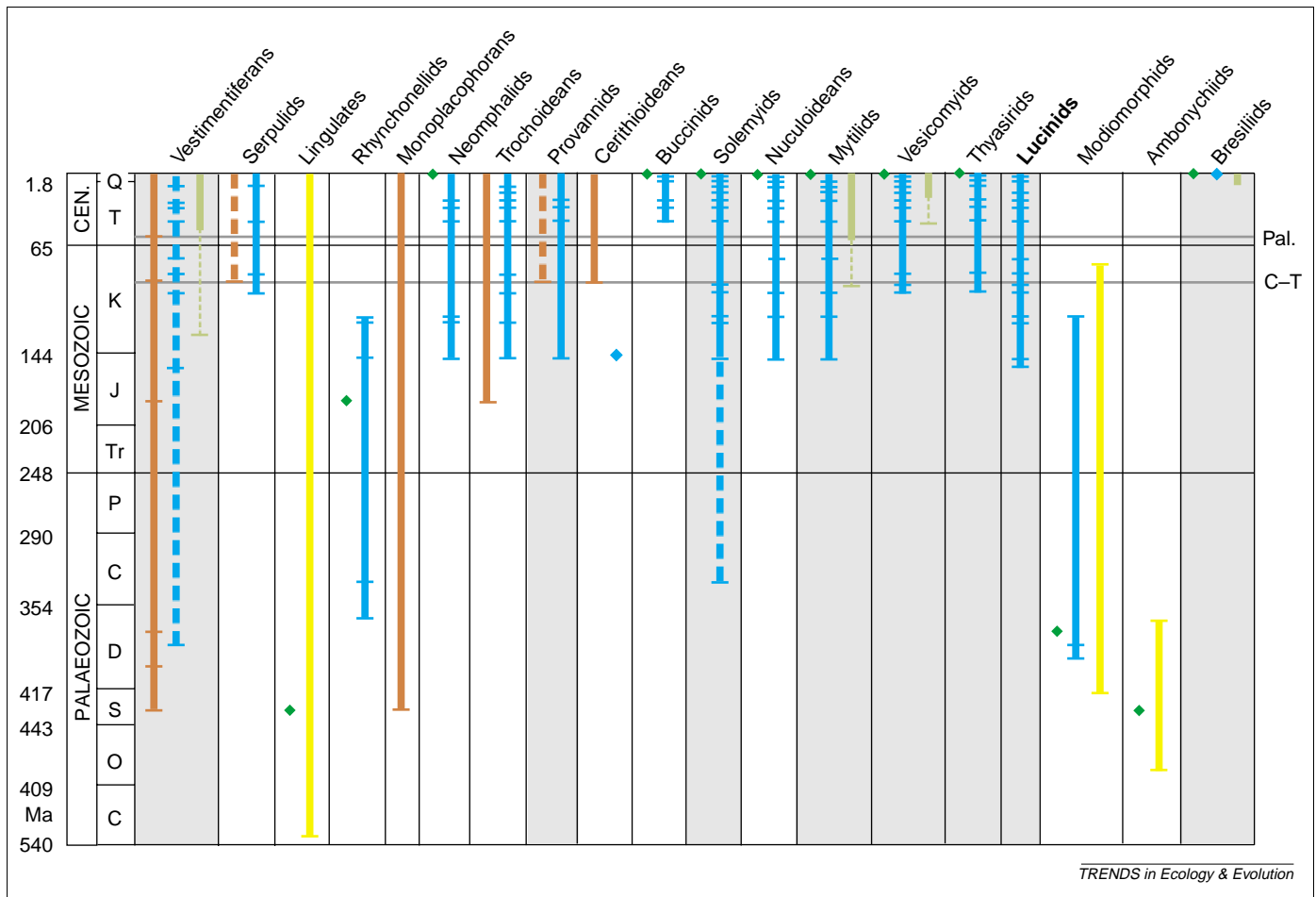
Most modern vent taxa, including several groups with chemosymbionts (thyasirid, solemyid, vesicomid and bathymodiolin bivalves, and bresiliid shrimp), have not been found in fossil vent deposits [18] (Figure 1). However, a subset of modern vent taxa do have a fossil record at seeps: buccinid gastropods from the late Eocene, vesicomid and thyasirid bivalves from the Cretaceous, neomphalid gastropods, mytilid and nuculoidean bivalves from the Jurassic, and solemyid bivalves from the Jurassic (and possibly Carboniferous) (Figure 1). Lucinid bivalves, another group with chemosymbionts, are very common in fossil seep communities from the Jurassic onwards [22,24,25,32], but, unlike the closely related thyasirids, have yet to be discovered at modern vent sites.

#### Molecular versus fossil data

Significant discrepancies exist between molecular estimates of the origin of several vent taxa and their first fossil appearance at vents and seeps (Figure 1) [12,18]. For three out of four taxa (bathymodiolins, vesicomids and

vestmentiferans), the first fossil appearances in vent and seep sites pre-date the corresponding molecular estimate of their age. Mytilid bivalves have a good fossil record at seeps from the late Jurassic, 150 million years ago (Mya). However, molecular evidence suggests that modern seep and vent bathymodiolins (a subfamily within the Mytilidae) arose more recently, during the late Cretaceous–early Cenozoic (56–94 Mya; Box 3). Whether the Jurassic seep mytilids are closely related to the modern bathymodiolins is equivocal, however, because the mytilids are a morphologically conservative group and are difficult to classify. Morphological misidentification is less of a problem in the vesicomid bivalves (at least at the family level), because these clams have distinctive shell characters that are obvious in fossils. Vesicomids first appear at seeps in the mid Cretaceous (~100 Mya), much earlier than the Cenozoic dates suggested by molecular estimates (22–44 Mya) based on modern vent and seep species (Box 3). The greatest discrepancy between molecular and fossil ages exists for the vestimentiferan tube worms, which has led to some controversy about the identification of these fossils [12,18,34]. Sulphide-replaced worm-tube fossils from Silurian and Devonian vent sites have been formally described as vestimentiferan tubes, although they have few characters and lack diagnostic internal soft parts [35,36]. The Silurian worm tube fossils are ~290 million years older than the most liberal molecular estimate for the origin of the vestimentiferans (L.A. Hurtado, PhD thesis, Rutgers University, 2002) (Box 3). This is also the case for worm-tube fossils in a Devonian seep deposit [20]. Occurrences of vestimentiferan-like worm tubes from early Jurassic and late Cretaceous vent sites [18] fit better with the molecular estimates. Molecular evidence also indicates that vent and seep-endemic bresiliid shrimp diversified very recently, perhaps <20 Mya [37] (Box 3). Unfortunately, this molecular estimate cannot be corroborated using fossil evidence, because bresiliids do not yet have a fossil record, possibly because, being mobile organisms with easily scavenged chitinous exoskeletons, they have low preservation potential.

Several hypotheses must be considered to explain discrepancies between the fossil and molecular age estimates. First, the fossils might have been misidentified and might actually belong to different, homeomorphic groups [12,19,34]. As discussed above, misidentification is a distinct possibility for the Silurian and Devonian vestimentiferan-like tube-worm fossils, but is less likely for the mytilids and unlikely for the vesicomids, because these mollusc fossils preserve more morphological characters for taxonomic analysis. Second, molecular studies might have underestimated the divergence dates because of inaccurate calibrations (Box 4). Based on recent attempts to calibrate molecular clocks for mitochondrial cytochrome oxidase subunit I (COI) (Box 3), substitution rates for vent and seep taxa appear to be at the low end of the range of rates seen in other animals [13]. Nevertheless, for the Silurian and Devonian tube-worm fossils to be directly related to modern vestimentiferans, COI substitution rates in this group would have to be three times lower than any rate seen in animals to date (L.A. Hurtado, PhD thesis, Rutgers University, 2002). Third, vent and



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**Figure 1.** Stratigraphic ranges of modern hydrothermal vent higher taxa that have a fossil record at vents, and/or a fossil record at hydrocarbon seeps, and/or molecular divergence estimates. Also shown are four vent taxa that are found at fossil vent sites but do not have modern vent representatives (lingulate and rhynchonellid brachiopods, and modiomorphid and ambonychiid bivalves) and the lucinid bivalves (in bold), which are only known from seeps. Fossil data derived from references in Box 2. Key: diamonds, single stratigraphic taxon occurrences; solid red lines, taxon ranges at vents; solid blue lines, taxon ranges at seeps; dashed lines, uncertain taxon ranges; horizontal ticks, occurrence data; solid yellow lines, total taxon ranges; green lines, molecular divergence estimates; thin lines show estimate ranges from Box 3; taxa with grey shading are those in which either all or some vent and seep representative species have chemosymbionts. Abbreviations: Cen., Cenozoic; C–T, Cenomanian–Turonian oceanic anoxic/dysoxic event; Pal., end Palaeocene oceanic anoxic/dysoxic event.

seep fossils might represent earlier stem-group lineages that are not ancestral to the crown-group taxa [38]. Thus, extant vent taxa might comprise parallel or convergent radiations from common stem ancestors [2]. This hypothesis is particularly likely for the bathymodiolins and vestimentiferans, because they both belong to families containing older sister groups.

#### A relic fauna at vents?

Examination of the fossil record provides limited support for the suggestion that modern vent fauna provide a ‘glimpse of antiquity’ [10]. Certainly, the fossil record does not support suggestions that vent fauna are Palaeozoic relics, because the Palaeozoic vent fauna are either extinct (modiomorphid and ambonychiid bivalves) or are not represented at modern vents (lingulate brachiopods) (Figure 1). Palaeozoic vent monoplacophorans are not closely related to their modern counterparts, and the identity of the vestimentiferan-like tubes has been seriously challenged. Nevertheless, of the six extant vent bivalve families (vesicomyids, nuculanids, thyasirids, solemyids, pectinids and mytilids), the latter three (50%) have Palaeozoic origins in other environments, a particularly

high percentage when compared with 19% (six out of 32) of extant principle bivalve families with Palaeozoic origins present across the entire marine realm [39]. Fossil evidence supports the hypothesis that some of the modern vent taxa arose in the Mesozoic: trochoideans, cerithioideans and, possibly, vestimentiferans, provannids and serpulids (Figure 1). However, several modern vent taxa that are considered to be Mesozoic (or possibly Palaeozoic) relics have not been found at fossil vent sites (neomphalid and neolepetopsid gastropods [2,40] and barnacles [41]). Several hypotheses might explain the absence of these groups and other common modern taxa (vesicomyid and bathymodiolin bivalves, and bresiliid shrimp) from fossil vents [18]. First, they were present at ancient vents but have yet to be discovered, either because the fossil record is too sparse (Box 2) or representative specimens did not get preserved. Second, the record can be taken at face value, and the missing taxonomic groups invaded vent sites from other environments during the past 40 million years. The fossil record from seeps is informative, however, because some of the modern vent taxa without vent fossil records have representatives in fossil seeps (Figure 1). Apart from the putative vestimentiferans and the solemyids, which

the are difficult to identify, none of the modern seep taxa has a Palaeozoic fossil record. Some appeared in the Cenozoic, but most appeared in the Mesozoic (Figure 1). This Mesozoic group includes the neomphalids, which supports McArthur and Koop's [42] hypothesis about the timing of origination of the neomphalines. Finally, several taxa appear earlier at seep sites than they do at vents (serpulids and provannids). Although this pattern is probably an artefact stemming from the paucity of fossil vent faunas compared with fossil seep faunas, it is intriguing that a seep-vent pattern has been identified in the molecular phylogenies of modern bathymodiols, vestimentiferans and vesicomysids [5,43,44]. Perhaps some of the modern vent taxa invaded vents repeatedly during the Cenozoic, having derived from seep ancestors that persisted from the Mesozoic. However, it remains unclear whether this re-invasion hypothesis can be linked to oceanic anoxic/dysoxic events at the Cenomanian-Turonian boundary or the end Palaeocene [14], because all of the seep taxa appearing in the Mesozoic passed through both of these events, as did the vent trochoideans and vestimentiferans (Figure 1).

In spite of uncertainties about the true age of vent and seep taxa, the fossil data generally confirm the molecular evidence that the ecologically dominant modern vent and seep taxa (e.g. vesicomysids, bathymodiols and bresiliids) are not living fossils from the Palaeozoic. The molecular evidence for relatively recent radiations (or re-radiations) of vent and seep taxa also does not support the hypothesis that these deep-sea chemosynthetic environments are immune from global extinction events affecting diversity in the photic zone.

### Future research

Future research is needed to provide further information about the origin and evolution of vent and seep taxa. This includes finding more fossiliferous vent sites, particularly from the late Palaeozoic, early Mesozoic and Cenozoic (Box 2), data from which will help to test molecular hypotheses and to assess whether the 'relic' hypothesis has been falsely rejected. For example, the ~120 million year gap in fossil data between the early Jurassic and early Carboniferous might hide novel vent taxa, or might connect taxa from earlier (Palaeozoic) and later Mesozoic or Cenozoic periods. More detailed systematic analyses of the vent and seep fossils are also needed. The level of analysis (families, orders and classes) is fairly crude at present and probably masks patterns of extinction and origination at vent and seep sites that are only apparent at sub-family level (e.g. bathymodiols). Molecular analyses of vent and seep taxa with reasonable fossil records (e.g. provannid gastropods) might prove useful for investigating fossil versus molecular origination estimates and might help to generate more-accurately calibrated molecular clocks (Box 3). Molecular analysis of several modern vent taxa that seem morphologically primitive such as the stalked barnacles [2,10,41], but lack a corroborating vent and seep fossil record could provide data that could be used to assess the antiquity of these groups in comparison to other vent taxa. In a wider context, it will be interesting to compare evolutionary rates and trends displayed by vent

and seep animals to those of other marine taxa to see what evolutionary advantages or disadvantages are associated with living at sites where geochemical energy sources are abundant.

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