When Did Decapods Invade Hydrothermal Vents? Clues from the Western Pacific and Indian Oceans

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Abstract

Hydrothermal vents are typically located in midocean ridges and back-arc basins and are usually generated by the movement of tectonic plates. Life thrives in these environments despite the extreme conditions. In addition to chemoautotrophic bacteria, decapod crustaceans are dominant in many of the hydrothermal vents discovered to date. Contrary to the hypothesis that these species are remnants of relic fauna, increasing evidence supports the notion that hydrothermal vent decapods have diversified in more recent times with previous research attributing the origin of alvinocarid shrimps to the Miocene. This study investigated seven representative decapod species from four hydrothermal vents throughout the Western Pacific and Indian Oceans. A partitioned mix-model phylogenomic analysis of mitochondrial DNA produced a consistent phylogenetic topology of these vent-endemic species. Additionally, molecular dating analysis calibrated using multiple fossils suggested that both bythograeid crabs and alvinocarid shrimps originated in the late Mesozoic and early Cenozoic. Although of limited sampling, our estimates support the extinction/repopulation hypothesis, which postulates recent diversification times for most hydrothermal vent species due to their mass extinction by global deep-water anoxic/dysoxic events during the Late Cretaceous and Early Tertiary. The continental-derived property of the West Pacific province is compatible with the possibility that vent decapods diversified from ancestors from shallow-water regions such as cold seeps. Our results move us a step closer toward understanding the evolutionary origin of hydrothermal vent species and their distribution in the Western Pacific–Indian Ocean Region.

Key words: hydrothermal vent, decapod, mitogenome, molecular estimation, West Pacific–Indian Ocean.

Hydrothermal vents, well known for their unusual chemistry, are home to unique life forms. Despite the presence of extremely high temperatures, low oxygen levels, and high levels of toxins, invertebrates thrive in these extreme environments (Van Dover 2000). Concerning the origin and distribution of vent fauna, the argument between the antiquity and extinction/repopulation hypotheses has been going on almost since the discovery of the hydrothermal vent (Little and Vrijenhoek 2003). Molecular divergence estimates of vent taxa may provide powerful evidence to help uncover the real story.

Decapods represent approximately 10% of all taxa identified from hydrothermal vents (Desbruyères et al. 2006) and are dominant in many of these sites (Martin and Haney 2005). Current opinions on decapod evolutionary histories are based mainly on morphology and fossils. Although many research groups have devoted considerable effort to this area since the last century (reviewed by Bracken et al. 2009), results from molecular dating of Decapoda remain sparse in comparison with that of vertebrates such as mammals and amphibians. The growing number of sequenced mitochondrial genomes may provide sufficient sequence data from organisms with relatively comparable evolutionary rates. In addition, in spite of the relative richness of decapod fossils (Schweitzer et al. 2010), validity of using these fossils as molecular constraints needs strict tests. In this study, we performed mitochondrial phylogenomics and divergence time estimation using multiple fossils to reconstruct the systematic relationships, evolutionary origins, and possible history of the distribution of decapods from hydrothermal vents in the Western Pacific and Indian Oceans.

In addition to the mitogenome sequences of Shinkaiia croesierei and Candalus yunohana (Yang et al. 2008, 2010), we sequenced the mitogenomes of five other vent decapods (supplementary tables S1 and S3, Supplementary Material online). We applied a multilocus phylogeny that proved more apt to recover true relationships (Thorne and Kishino 2002). First, we separated mitogenomic sequences according to the codon positions of protein-coding genes (PCGs) and the stem/loop structures of RNA genes. Saturation analysis discarded every third codon. Five representative partitioning
strategies were compared using both harmonic mean (HM) and generalized stepping-stone (SS) algorithms in Phyca (Fan et al. 2011), where all 32 nucleotide partitions (p32; all partitions treated separately; supplementary table S4, Supplementary Material online) were always assigned the highest scores (supplementary table S6, Supplementary Material online) and were therefore sustained throughout our phylogenetic and molecular dating analyses.

Phylogeny was reconstructed under both the likelihood and Bayesian frameworks. Three data sets were used: p32, PCG nucleotides (26 partitions), and PCG amino acids (13 partitions). Partitioned mix-model phylogenies were conducted by RAxML and MrBayes and by PhylolBayes, which introduced the CAT mixture model. Six topologies were observed (supplementary fig. S1, Supplementary Material online), where conflicting points may have resulted from short branches of shallow relationships (Wiens et al. 2008) or phylogenetic bias by amino acids (Yang et al. 2008). A Shimodaira-Hasegawa test assigned the highest score to tree3; the other topologies showed no significant differences (P > 0.05). Thus, we used tree3 for divergence time estimates.

Although sample sizes were limited, the relationships within the endemic vent crabs and shrimps provided some clues to their origin and distribution. Compared with Austinograea alayasee (1,600–2,500 m) and A. rodriguezensis (2,447–3,300 m), G. yunohana was associated with relatively shallow waters (400–1,600 m) (Fujikura et al. 2008). Interestingly, this shallow-to-deep pattern was also observed for Bathymodilinae mussels (Jones et al. 2006), which may indicate a universal mechanism for vent taxa distribution. Also, Alvinocaris longirostris lies at the basal location of Bresilioida (Alvinocarididae). Considering A. longirostris is the only decapod that occurs in both hydrothermal vents and cold seeps (Kikuchi and Ohta 1995; Fujikura et al. 1999) and this species (and younger vent shrimp species) may have emerged in regions other than hydrothermal vents (e.g., cold seeps).

Multiple-fossil calibration can effectively reduce the inaccuracy introduced by a single calibration. We selected eight decapod fossil calibrations (table 1), some previously validated (nodes 51, 59, 76, and 78; Porter et al. 2005) and the rest unclear. However, we did not include the fossil record of a hydrocarbon-seep decapod (S. katapsyxis; Schweitzer and Feldmann 2008) as its date of ~40 Ma was obviously too young to calibrate the divergence between S. crozieri and Pagurus longicarpus. In the fossil-based cross-validation test (Near et al. 2005), sequential fossil removals from greater to smaller SS values did not effectively improve the estimation (F < FSS; supplementary fig. S2, Supplementary Material online). No fossils showed a significant discrepancy and could safely be used for the minimum constraints. In addition, using Marshall’s method (2008), node 78 (“Reptantia”) proved the calibration lineage with 529.3 and 396.9 Ma being assessed with 95% and 50% confidence intervals (CIs), respectively (supplementary calculation, Supplementary Material online). Both constraints were used for molecular dating, but no essential difference was identified (supplementary table S7, Supplementary Material online). Therefore, a narrower calibration interval (354.0–396.9 Ma) was assigned to node 78 for the final estimations. The Kolmogorov–Smirnov test showed that these fossils were uniformly distributed, and none could be excluded as outliers.

Both the relative rate test of all taxon pairs (supplementary table S8, Supplementary Material online) and the molecular clock test of the whole data set rejected the null hypothesis of global equal rates. This favored the relaxed molecular clock model. To compare the impact of hard versus soft bounds on the partitioned data set, we chose both multidivtime and mcmctree for estimation. Multidivtime only supports hard bounds, whereas mcmctree also implements soft bounds, which can correct poor calibrations to help provide more accurate estimates (Yang and Rannala 2005). Final results were obtained from multidivtime analysis with eight minimum and two maximum hard constraints and from mcmctree analysis with eight hard minimum and two soft maximum constraints. Thirty-five out of 40 node intervals overlapped on the two chronograms (fig. 1 and table 2). The intersections of two 95% CI estimates on the Bythograeoida and Bresilioida nodes are located at 48.4–55.9 and 51.5–69.7 Ma, respectively, which refers to the Early Tertiary origin of bythograeid crabs and the Late Cretaceous/Early Tertiary divergence of alvinocarid shrimps. Similar results were obtained from molecular dating of five other topologies with the exception of an underestimation from tree2

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Table 1. Calibrations Used to Constraint the Divergence Time Estimates.

<table>
<thead>
<tr>
<th>Node</th>
<th>Taxonomy</th>
<th>Species</th>
<th>Geological Age (Ma)</th>
</tr>
</thead>
<tbody>
<tr>
<td>63</td>
<td>Eriocheir japonica</td>
<td>Eriocheir japonica</td>
<td>Early Pliocene (Zanclean) (3.6–5.3)</td>
</tr>
<tr>
<td>71</td>
<td>Scylla (genus)</td>
<td>Scylla costata</td>
<td>Late Oligocene (Chattian) (23.0–28.4)</td>
</tr>
<tr>
<td>51</td>
<td>Palaemonoidea (superfamily)</td>
<td>Palaemon antonellae</td>
<td>Early Cretaceous (Albian) (99.6–112)</td>
</tr>
<tr>
<td>53</td>
<td>Atyoidea (superfamily)</td>
<td>Delciolla roselii</td>
<td>Late Jurassic (145.5–161)</td>
</tr>
<tr>
<td>74</td>
<td>Xanthoidae (superfamily)</td>
<td>Ereocrinus xestos</td>
<td>Late Cretaceous (Campanian-Maastrichtian) (65.5–83.5)</td>
</tr>
<tr>
<td>76</td>
<td>Brachyura (infraorder)</td>
<td>Eocarcinus praecursor</td>
<td>Early Jurassic (Pliensbachian) (190–195)</td>
</tr>
<tr>
<td>59</td>
<td>Astacidea (infraorder)</td>
<td>Chimaeraatustus pacificulus</td>
<td>Middle Triassic (Upper Ladinian) (227–234)</td>
</tr>
<tr>
<td>78</td>
<td>“Reptantia”</td>
<td>Palaeopalaeamon newberryi</td>
<td>Late Devonian (Famennian) (354–364)</td>
</tr>
<tr>
<td>58</td>
<td>Split of the Astacoidea and Parastacoidea</td>
<td></td>
<td>Splitting of Pangea (~185)</td>
</tr>
</tbody>
</table>

Node numbers correspond to those in figure 1 and table 2.

A maximum constraint of 396.9 Ma was calculated and used for the divergence time estimates (supplementary methods, Supplementary Material online).
Although only three species were involved, our result on vent shrimp origin contrasts with a previous Miocene estimate (Shank et al. 1999), where the evolutionary rate of the mitochondrial \textit{cox1} gene was inferred from the geological age of the closure of the Isthmus of Panama. However, this rate may have been underestimated if the gene flow between the Pacific and Atlantic vents did not occur directly through the Isthmus of Panama but rather indirectly through the Indian Ocean (Tunnicliffe et al. 1996). The present preliminary hypothesis on the intermediate role of the Indian Ocean should be supported with more extensive sampling, especially from Atlantic species.

The Late Cretaceous/Early Tertiary, an active period in both biological and geological terms, was marked by the continuing separation of continents (fig. 1; Parker and Gealey 1985). During this period, the back-arc systems of Southeast Asia and northeast Australia were opened and subsequently formed the main back-arc basins of the Western Pacific. A new spreading center, the present Rodriguez Triple Junction, also emerged in the southern Indian Ocean. This period was also marked by global deep-water anoxic/dysoxic events, which are thought to underlie the extinction of nearly all contemporary vent
species (Jacobs and Lindberg 1998). The vent areas of these continental-derived back-arc basins may have been recolonized by surrounding shallow-water species after this mass extinction, for example, via stepping stones from cold seeps (as in the case of A. longirostris). Evidence for the recent diversification of many vent invertebrate species (<100 Ma) also supports the extinction/repopulation hypothesis (Van Dover et al. 2002; Little and Vrijenhoek 2003).

Future investigations of deep-sea hydrothermal fields should help clarify the evolutionary history and historical distribution events associated with vent taxa. Our findings shed some light on these processes.

### Materials and Methods

See supplementary methods, Supplementary Material online.

#### Supplementary Material

Supplementary tables S1–S8, figures S1–S3, methods, and calculation are available at Molecular Biology and Evolution online (http://www.mbe.oxfordjournals.org/).

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### References


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