Cryptic species of Archinome (Annelida: Amphinomida) from vents and seeps

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Since its description from the Galapagos Rift in the mid-1980s, Archinome rosacea has been recorded at hydrothermal vents in the Pacific, Atlantic and Indian Oceans. Only recently was a second species described from the Pacific Antarctic Ridge. We inferred the identities and evolutionary relationships of Archinome representatives sampled from across the hydrothermal vent range of the genus, which is now extended to cold methane seeps. Species delimitation using mitochondrial cytochrome c oxidase subunit I (COI) recovered up to six lineages, whereas concatenated datasets (COI, 16S, 28S and ITS1) supported only four or five of these as clades. Morphological approaches alone were inconclusive to verify the identities of species owing to the lack of discrete diagnostic characters. We recognize five Archinome species, with three that are new to science. The new species, designated based on molecular evidence alone, include: Archinome levinae n. sp., which occurs at both vents and seeps in the east Pacific, Archinome tethyana n. sp., which inhabits Atlantic vents and Archinome jasoni n. sp., also present in the Atlantic, and whose distribution extends to the Indian and southwest Pacific Oceans. Biogeographic connections between vents and seeps are highlighted, as are potential evolutionary links among populations from vent fields located in the east Pacific and Atlantic Oceans, and Atlantic and Indian Oceans; the latter presented for the first time.

1. Introduction

It has been more than three decades since the discovery of deep ocean chemosynthetic communities. Over 600 animal species have been described from these habitats, mainly from hydrothermal vents near active tectonic plate boundaries, as well as from hydrocarbon seeps along continental margins [1–3]. Biodiversity patterns among deep-sea chemosynthetic fauna have been discussed at length in the context of taxonomic and environmental affinities leading to the designation of various biogeographic ‘provinces’ [1,3–6]. The few rigorous studies that have inferred these patterns in a phylogenetic context and on a broad scale [7–11] have focused on Pacific Ocean taxa [8,12–15]. Deep ocean currents, plate tectonics, seafloor spreading rates, oxygen levels, bathymetry, larval dispersal capabilities and sulfide or methane-rich communities, such as sunken wood and whale falls, as potential evolutionary ‘stepping stones’, are just some of the extrinsic factors that have been posited to drive species distributions in deep ocean chemosynthetic habitats [1,15–17].
Significant effort has been put forth in characterizing the faunal communities of these dynamic ecosystems. Traditional taxonomy, which emphasizes the characterization of morphological diversity, cannot always account for other biological attributes, such as developmental [18] and ecological adaptations [7,19,20], leading to over or underestimates of diversity [17,21]. Molecular systematics has been a useful tool to provide a testable framework to infer evolutionary relationships of genetic lineages, independent of phenotypic, ontogenetic and ecological variation. The integration of molecular data has greatly improved our knowledge of species delimitations and distributions, however with the caveat that taxonomic, genetic and geographical diversity estimates are all sensitive to sampling [22].

Annelids account for approximately 20% (approx. 111 species) of the named hydrothermal vent animal species [2]. The East Pacific Rise (EPR) has among the best-studied vent annelids [23–30] and the incorporation of molecular data has shed light on cryptic diversity found along this system [12,14,21,31,32]. The giant vestimentiferan tubeworm, Riftia pachyptila [12,14,21,31,32], is a dominant feature of hydrothermal vent sites along the EPR and was shown to be genetically homogeneous [12,14,21,31,32]. The giant vestimentiferan tubeworm, Riftia pachyptila, is a dominant feature of hydrothermal vent sites along the EPR and was shown to be genetically homogeneous across a broad range (27° N–32° S), with a genetic break identified at the Easter microplate (approx. 26° S) [14]. The thermally tolerant Alvinella pompejana is known only from the EPR and although morphologically similar across a distance of approximately 5000 km (21° N–32° S), mitochondrial (mt) data revealed a north/south genetic break [14,33]. Species of Alvinella and Riftia are restricted to the east Pacific, whereas Panalvinella is amphi-Pacific, though so far not recorded outside of this ocean [2,34]. Major annelid clades are represented on a broad geographical scale throughout diverse chemosynthetic environments (e.g. Siboglinidae and Polynoidae), but among vent animals, only two ‘species’ have been recorded on a global scale: the ampharetid Amphisamytha galapagensis [8,35] and the amphinomid Archinome rosacea [36,37]; the latter being the focus of this study, while the former is now known to be a species complex [8].

Amphinomids are best represented by the stinging fireworms (e.g. Eurythoe and Hermaphroditida), which are common inhabitants of tropical reef environments [38,39]. Archinome rosacea was the first amphinomid described from chemosynthetic habitats from the original 1979 collections from Rose Garden [8,36]. Since its description in 1985, Archinome has been recorded across major spreading centres in the Pacific, Atlantic and Indian Oceans (figure 1) [2,40]. Archinome specimens (figure 2 and electronic supplementary material, figure S1) are easily recognizable among vent fauna, with prominent calcareous, bifurcate (forked) chaetae, an elongate trilobed caruncle (figure 2c), a fusiform (spindle-like) body shape, prominent mid-ventral muscular scutes (figure 2g) and can range in size from just a few millimetres to several centimetres. In 2006, the distribution of A. rosacea was restricted to the GAR and the northeast Pacific Rise (NEPR) [2], in contrast to earlier accounts, which proposed a more widespread range including the Guaymas Basin (GB) sediments, Mid-Atlantic Ridge (MAR) and Central Indian Ridge (CIR) vent systems [41,42]. Referencing unpublished data (J. Kudenov 2006), Desbruyères et al. [2] suggested the presence of at least three additional species, yet until recently A. rosacea remained the only named species. In 2009, Archinome storchii [40] was described from the Pacific Antarctic Ridge (PAR, 37° S). Also until recently, Archinome...
had only been recorded from hydrothermal vents. In 2009 and 2010, specimens were collected from cold methane seeps located at the Costa Rica margin (CRM) [43]. Archinome has been collected from a broad range of vent localities (figure 1) and depths (1000–3500 m) [40], however it is now known to occur at depths greater than 4000 m, including Ashadze-1 (A1; 12°N, MAR; 4080 m) [44]. Given Archinome’s broad distribution and uncertainty as to the number of species within the genus, we used an integrative systematic approach to: (i) infer the identities of Archinome specimens from across the ‘cosmopolitan’ range among vent systems; (ii) infer the evolutionary relationships among vent and seep Archinome and (iii) explore the biogeographic links and diversification patterns across the Atlantic, Indian and Pacific Oceans.

2. Material and methods

(a) Sample collection

Archinome samples were collected using remotely operated vehicles including Woods Hole Oceanographic Institution’s (WHOI) Jason I (R/V Knorr) and Jason II (R/V Melville), Monterey Bay Aquarium Research Institute’s Tiburon (R/V Western Flyer) and Institut Français de Recherche pour l’Exploitation de la Mer’s (IFREMER) Victor 6000 (R/V Pourquoi Pas?), and human occupied vehicles Alvin (WHOI) and Nautile (IFREMER) during deep-sea expeditions between 1990 through 2010. Figure 1 shows known records and sampling localities from vent and seep communities included in this study. Specimens were sampled from among larger vent fauna such as Vestimentifera and mytilid bivalves, as well as from upper sediment layer samples obtained from suction samplers and mesh scoops.
Specimens were sorted aboard research vessels and when possible relaxed in a 50:50 (7% MgCl₂: seawater) MgCl₂ solution, followed by preservation in 10% formalin, then transferred to 70% ethanol for morphological evaluation and 80–95% ethanol or stored at −80 °C for molecular work. Molecular samples were kept cold at 4 °C or frozen at −80 °C or −20 °C. Collection and voucher information and details regarding evaluation of morphology can be found in the electronic supplementary material, text and tables S1, S4 and S5. Most specimens are lodged at the Scripps Institution of Oceanography Benthic Invertebrate Collection (SIO-BIC).

(b) Gene data collection, phylogenetic methods and genetic structure

Protocols for whole genomic DNA extraction, amplification and sequencing procedures are as reported by Borda et al. [45], unless stated otherwise. Electronic supplementary material, text S2 lists primers and annealing temperature profiles used for amplification of mt cytochrome c oxidase subunit I (COI), and mt 16S rDNA (16S). Amplification protocols for the internal nuclear transcribed spacer 1 (ITS1) and 28S rDNA (28S) followed Nygren & Pleijel [46] and Borda et al. [45], respectively. All data were analysed using maximum-likelihood (ML) and Bayesian inference (BI) procedures following methods described in [45], as was the choice of outgroup to root the analyses (i.e. Chloria viridis). Notoptilus ornatus was included as an additional outgroup taxon based on hypothesized affinities associated with body shape and branchial morphology [37,45]. Phylogenetic trees (figure 3) are based on the BI topology, unless stated otherwise (see electronic supplementary material, figures S3 and S4), with support values (i.e. ML bootstrap (boot); posterior probabilities (pp)) indicated at nodes. Haplotype networks were generated for combined COI + 16S using TCS v. 1.21 [47], based on maximum parsimony and with a 95% probability (14-step connection limit) and fixed step connection limits ranging 10–50; gaps were treated as missing data. GenBank (16S, COI: JX027992–JX028115; 28S: JX028121–JX028141; ITS: KF288935–KF288959) and voucher accession numbers are provided in the electronic supplementary material, table S1. See also the electronic supplementary material, text for extended phylogenetic methods and sequence evaluation criteria.

3. Results

We inferred the phylogenetic relationships of Archinome specimens from COI (59 sequences; approx. 654 bp), 16S (65 sequences; approx. 472 bp), 28S (21 sequences; approx. 966 bp) and ITS1 (25 sequences; 572 bp). Table 1 provides mean intraclade and interclade TrN corrected and uncorrected pairwise distances for complete COI (dCOI) and ITS1 (dITS1). COI exhibited the highest genetic divergences among clade terminals with the majority of synonymous changes occurring in third codon positions. COI saturation plots (see electronic supplementary material, figure S2) indicated that third position transitions reached saturation after approximately 13% sequence divergence. First and second codon position transitions and first through third codon position transversions were not saturated (results not shown). Intraclade relationships and species identification were evaluated with the inclusion (COIincl) and exclusion (COIexcl) of COI third codon positions in combined analyses with 16S, 28S and ITS1 (figure 3). Results from individual and mt gene analyses can be found in the electronic supplementary material, figures S3 and S4. Mean COI intraclade-corrected genetic distances were 12.5%, ranging 2.7–18.3%, and mean intraclade-corrected genetic distances was 0.5%, ranging 0–1.1%. ITS1 exhibited low divergences in comparison to COI. The highest corrected genetic pairwise distance was 3.6%. Mean ITS1 interclade-corrected genetic distance was 1.8%, ranging 1.0–3.6%, and mean intraclade-corrected genetic distance was 0.1%, ranging 0–1.0% (see table 1 and electronic supplementary material, table S3). Refer to the electronic supplementary material text for results regarding morphological evaluation.

The phylogenetic relationships among Archinome species accepted here are based on COIexcl + 16S + 28S + ITS1 (figure 3a). The data supported four Archinome clades, I–IV, of which three are regarded as new species and described in the electronic supplementary material, text. Numerical clades 1–6 above nodes correspond to those recovered in the analyses of concatenated COIexcl + 16S + 28S + ITS1 (figure 3b; see also the electronic supplementary material, figure S3A). Clade I (boot/pp = 82/0.94; dCOI = 1.7%) was the sister clade to Clade III (boot/pp = 94/1.0; dCOI = 0.5%) from North Fiji (NF; 16 °S; 1985 m), Kilo Moana Lau (KML; 20 °S; 2650 m) and Tui Malila Lau (TML; 21 °S; 1900 m) and clade 2 (boot/pp = 87/1.0; dCOI = 0.3%), which included specimens from Logatchev (LOG; 14 °N, MAR, 3038 m) and Kairei field (25 °S, CIR, 2432 m). Archinome jasoni n. sp. was supported as sister to the remaining Archinome species (boot/pp = 100/0.98). The highest A. jasoni n. sp. dCOI = 3.6% was supported as being from specimens from NF/KML and LOG. The lowest interclade dCOI was 11.8% (CIR, clade 2) with Clade II (boot/pp = 100/1.0); hereafter, Archinome tethyana n. sp. The A. tethyana n. sp. clade included the northern MAR specimens (clade 4; boot/pp = 99/1.0). Sequence data for all four genes were available from Broken Spur (29 °N; 3056 m), TAG (26 °N; 3655 m) and Snake Pit (23 °N; 3660 m). Clade III (clade 1; boot/pp = 98/1.0; mean dCOI = 0.4%), hereafter, Archinome levinae n. sp., included specimens from GB vents (27 °N; approx. 2400 m) and CRM seeps (8–9 °N; 1000–1800 m). The lowest interclade dCOI was 14.0% (with Clade IV). Archinome levinae n. sp. was sister to Clade IV (boot/pp = 98/1.0; dCOI = 2.7%), representing A. rosacea and A. storchii (Clade V) from the GAR, EPR and PAR (clades 5 and 6; figure 3b). Clade 5 (dCOI = 0.6%) included A. rosacea from GAR, as well as specimens from EPR 9 °N (2500 m) and 7 °S (2700 m). Clade 6 (dCOI = 0.3%; boot/pp = 83/1.0) comprised PAR specimens and those sampled northward along the southeast Pacific Rise (SEPR) from 31 °S to 17 °S (2200–2500 m). Clade 6 was a subclade nested among unresolved A. rosacea representatives (see also the electronic supplementary material, figures S3B and S4A). The highest dCOI was 5.0%, between representatives from the GAR (A. rosacea) and 17 °S (A. storchii). The lowest interclade dCOI was 12.4%, between A. tethyana n. sp. and A. rosacea. The positions of A. tethyana n. sp. and A. levinae n. sp. were fixed with moderate support (boot/pp = 74/1.0), respectively.

Evaluation of concatenated COIexcl + 16S + 28S + ITS1 (figure 3b) supported that Archinome comprised five clades showing minimal geographical overlap. The resulting topology was similar to that of COIexcl (see electronic supplementary material, figures S3A and S2B), with the exception that A. jasoni n. sp. clade 3 was nested within clade 2, instead of showing reciprocal monophyly (figure 3a). The topology deviated from that observed in figure 3a, in that vent/
A. levinae n. sp. was the sister group to the remaining Archinome species and reciprocally monophyletic (boot/pp = 95/1.0) A. rosacea (boot/pp = 77/0.66) and A. storchi (boot/pp = 75/1.0) clades were recovered; each clade with low support, however. Combined COI_all + 16S data (n = 35) supported distinct networks (even with a fixed 50 step connection limit) for A. rosacea (n = 16) and A. storchi (n = 19), each containing 15 haplotypes. A single haplotype was shared between two A. rosacea individuals (GAR), while one haplotype was shared among five A. storchi individuals from the SEPR (figure 3c).
No haplotypes were shared among *A. rosacea* (7°S) and *A. storchi* (17°S) individuals found approximately 1200 km apart. A single network (figure 3c; fixed 21-step limit connection), covering approximately 25 000 km distance, was recovered for *A. jasoni* (n = 13), with 12 haplotypes, of which one was shared between two individuals from SW Pacific basin (16°S, 20°S).

4. Discussion

(a) Delineation of cryptic species in the deep sea

Accounts of cryptic species in the marine realm are no longer new phenomena. Molecular phylogenies often deviate from those relying on traditional taxonomic tools and continue to reveal cryptic diversity [7,21,38,48]. In the deep sea, morphological stasis may not coincide with speciation events owing to stabilizing selection driven by extreme abiotic factors (e.g. low dissolved oxygen, low temperatures and darkness), in turn, introducing challenges in biodiversity estimates [21,49]. In recent years, mtDNA has been a primary tool for the detection of cryptic species [7,50], although the approach remains controversial [51–54], and can be sensitive to sampling [55]. As such, integrative taxonomic approaches (e.g. multi-locus datasets) are recommended [21,56,57]. Morphological taxonomic approaches (e.g. light microscopy, SEM) alone did not allow conclusive identification of new species, as sampling comprised individuals varying in size and exhibiting variable and/or overlapping morphologies, within and among clades (figure 2 and electronic supplementary material, table S5). Future work based on larger sample sizes and consideration of size-related variation, may reveal species-specific characters. Based on the currently available material, we designate new *Archinome* species on the basis of molecular evidence alone (see also [58]).

Our approach for estimating *Archinome* species diversity was to include broad geographical sampling and to use a multi-locus framework (figure 3). We recognize that our sampling exhibits large geographical gaps (figure 1) leaving an incomplete picture of species distributions. Our phylogenetic hypothesis for *Archinome* as a whole (figure 3a) required the exclusion of COI third codon position (owing to saturation), resulting in a conflicting topology when the third position was considered (figure 3b). The designation of *A. levinae* n. sp. and *A. tethyana* n. sp. was unambiguous, however, this was less so for the remaining species. In particular, *A. rosacea* appeared to be paraphyletic with respect to *A. storchi* (figure 3a). However, COI was not saturated at more restricted levels, and when the third codon position was included, it became clear that both species were reciprocally monophyletic (figure 3b). Furthermore, these two clades were disparate enough not to form a single haplotype network (figure 3c) and showed a nearly 5% COI divergence. Although we did not find clear morphological differences between *A. rosacea* and *A. storchi* in terms of the argued diagnostic features [40] (figure 2; for further discussion, see the electronic supplementary material, table S5), we accept both as distinct species. On the same criteria, *A. jasoni* n. sp. was best left as a broadly distributed species (figure 3a–c), despite vast distances separating LOG, CIR and SW Pacific vent populations. COI sequence divergences were less than 4%, with no shared haplotypes. Given this low genetic divergence, the absence of clear morphological distinction and variable size classes among *A. jasoni* n. sp. populations (figure 2d–f), we do not have sufficient evidence to designate them as separate species at this time. We recognize the presence of two, possibly three lineages, as *A. jasoni* n. sp., which only further sampling will be able to resolve.

(b) Distribution and diversification of *Archinome* across chemosynthetic systems

The diversification of *Archinome* appears to align (in part) with Moalic et al.’s [5] hypothesis, which proposed west Pacific vent fauna as ‘ancestral’ and ‘central’ to those found elsewhere. Our phylogenetic hypothesis deviated with respect to identifying potential links between the Atlantic and eastern Pacific seep/vent communities. However, the biogeographic roles of cold seeps and the Mid-Cayman Spreading Center (MCSC) [59], for example, were not considered in their study. *Archinome jasoni* n. sp. was the sister taxon to the remaining species and included one clade that...
was exclusive to the SW Pacific basins. Although taxonomic
affinities between the CIR and west Pacific have previously
been reported [6,42], only a handful of phylogenetic studies
have included CIR fauna, and none have evaluated annelids
prior to this study. Archinome jasoni n. sp. also included a
CIR–LOG clade. Van Dover et al. [42] proposed CIR as a
mid-point for faunal exchange between the Atlantic and west
Pacific along the southwest and southeast Indian Ridges,
respectively. This scenario appears to be consistent with the
presence of A. jasoni n. sp. in both regions.

High rates of gene flow and low genetic variation have been
reported for Rimicaris vent shrimp from 36°N to 4°S [60–64].
Zelnhio & Hourde [64] found west Pacific Chorocaris vadovae
dasister to Rimicaris exoculata + Chorocaris chacei (MAR); how-
ever, the phylogenetic placement of CIR Rimicaris kairei has not
yet been inferred. The gastropod, Alviniconcha hessleri, report-
edly occurs in the west Pacific and Indian Oceans [42],
however A. aff. hessleri (CIR) was genetically distinct from its
west Pacific counterpart, yet clustered among west Pacific
Alviniconcha sp. Type 2 [65,66]. A CIR + SW Pacific clade has also
been reported for Bathymodiolus mussels, showing little
sequence divergences among them [10,11]. Low genetic diver-
gences were also observed among CIR and SW Pacific A. jasoni
n. sp., and the inclusion of MAR samples now corroborates pre-
viously reported affinities among Atlantic, Indian and western
Pacific Ocean fauna [5,42]. Unlike widespread R. exoculata, we
recovered two species in the MAR. However, our limited
sampling could have missed the co-occurrence of A. jasoni
n. sp. and A. tethyana n. sp. Alternatively, their colonizing
routes leading to A1 and LOG might be significantly separate,
and they may never be found in sympatry. Only more
extensive sampling will be able to clarify this.

Biogeographic links between the Atlantic and east Pacific
were proposed by Van Dover et al. [3] and were also observed
here in the sister group relationship between the Atlantic
A. tethyana n. sp. and the eastern Pacific species. Atlantic/east
Pacific affinities have been shown for several annelid
taxa [1,8,67] pointing towards a former connection between
both oceans via a deep ocean passage [68] prior to the closure
of the Isthmus of Panama. Recent discoveries of MCSC vent
fauna suggest affinities with MAR fauna [59,69], including a
new Rimicaris species [69] and Archinome spp. (A. Glover
2013, personal communication). Although A. tethyana n. sp.
was sister to the east Pacific clades, its position was not
highly supported. This could be attributed to missing data
for northern MAR specimens and/or unsampled representa-
tives from intermediate geographical regions (e.g. MCSC; to
be evaluated elsewhere).

The diversification of A. rosacea, A. storchi and A. levinae
n. sp. is likely attributed to vicariant events involving a for-
merly widespread ancestor that became isolated from the
Atlantic; the latter possibly coincident with the rise of the
Central American (CA) Isthmus (approx. 15 Ma; [68]) and
subsequent tectonic shifts and subduction events of the
Pacific, Cocos and Nazca Plates. The continental margin dis-
tribution of A. levinae n. sp. may be associated with vicariance
coincident with the rise of the CA Isthmus and the formation
of the Gulf of California in the Late Miocene (less than 8 Ma;
[70,71]). Although records are few, species shared between
GB and CRM have previously been reported [7,8], and now
include A. levinae n. sp. Archinome samples from cold seeps
at the GB (27°34′N, 111°27′W) were not available for this
study, though we suspect A. levinae n. sp. may be found
there given comparable depths (approx. 1700 m) and being
located a mere 50 km north from the GB vent communities
[72]. Hydrothermal vents at GB are particular with seeping
fluids that circulate through thick sediment layers [73]. The
presence of A. levinae n. sp. nearly 4000 km south at methane
seeps of the CRM suggests either long distance dispersal
capacity of larvae or perhaps the presence of overlooked
chemosynthetic environments along the CA margin. Genetic
isolation between A. levinae n. sp. and A. rosacea/A. storchi
may have been caused by the formation of the deep Middle
American Trench [70] having served as a dispersal barrier
to vent populations at GAR (approx. 1000 km south) and the
EPR. The genetic break between 7°S and 17°S (SEPR), as
seen between A. rosacea and A. storchi, may be due to the
sampling gap [22] or the result of vicariance associated
with the formation and rotation of the Bauer microplate
(between 10° and 15° S) in the Miocene [74]. This event has
been proposed to have disrupted vent communities and
flow of ocean currents along the SEPR, potentially restricting
gene flow from more northerly populations (e.g. 7°S; [15]).
Compared to other EPR taxa, Bathymodiolus, Lepetodrilus
and Alvinella, appear to conform to this trend, whereas species
distributions of Amphisamphyta, Branchipolyne, Hesiolyra, Riftia
and Tecnia appear to be less constrained across this presumed
dispersal barrier [8,14,15].

5. Conclusion
We evaluated the phylogeny of Archinome from chemosynthetic
environments on a global scale to redefine the geographical dis-
tribution of A. rosacea and A. storchi, the former of which had
been unclear, and revealed the presence of three previously
undescribed cryptic species. Among these, A. levinae n. sp.,
inhabiting both vent and methane seep sites found 4000 km
apart and A. jasoni n. sp., which for the first time potentially
supports biogeographic links among Atlantic, Indian and
Pacific Ocean vent systems. With the inclusion of representa-
tives from poorly sampled chemosynthetic sites, in particular
CIR and cold seep communities, we hope this study will
provide a framework for continued elucidation of the diversifi-
cation and evolution among deep-sea invertebrate species from
chemosynthetic environments.

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