PROCEEDINGS OF THE ROYAL SOCIETY B

rspb.royalsocietypublishing.org

Research

Cite this article: Borda E, Kudenov JD, Chevaldonné P, Blake JA, Desbruyères D, Fabri M-C, Hourdez S, Pleijel F, Shank TM, Wilson NG, Schulze A, Rouse GW. 2013 Cryptic species of *Archinome* (Annelida: Amphinomida) from vents and seeps. Proc R Soc B 280: 20131876. http://dx.doi.org/10.1098/rspb.2013.1876

Received: 18 July 2013
Accepted: 20 August 2013

Subject Areas:
taxonomy and systematics, evolution

Keywords:
deep sea, hydrothermal vents, cold methane seeps, cryptic species, polychaete

Authors for correspondence:
Elizabeth Borda
e-mail: lizborda@gmail.com
Greg W. Rouse
e-mail: grouse@ucsd.edu

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2013.1876 or via http://rspb.royalsocietypublishing.org.

Royal Society Publishing
Informing the science of the future

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

Elizabeth Borda[1,9], Jerry D. Kudenov[2], Pierre Chevaldonné[3], James A. Blake[4], Daniel Desbruyères[6], Marie-Claire Fabri[6], Stéphane Hourdez[7], Fredrik Pleijel[8], Timothy M. Shank[5], Nerida G. Wilson[1], Anja Schulze[9] and Greg W. Rouse[1]

[1]Scripps Institution of Oceanography, UC San Diego, La Jolla, CA 93093, USA
[2]Department of Biological Sciences, University of Alaska Anchorage, Anchorage, AK 99508, USA
[3]CNRS, UMR 7263 IMBE, Institut Méditerranéen de la Biodiversité et d'Ecologie Marine et Continentale, Aix-Marseille Université, Station Marine d'Endoume, Rue de la Batterie des Lions, 13007 Marseille, France
[4]AECOM Marine and Coastal Center, Woods Hole, MA 02543, USA
[5]Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA
[6]Département Etude des Ecosystèmes Profonds, Centre de Brest de l'IFREMER, 29280 Plouzané Cedex, France
[7]CNRS, UPMC UMR 7127, Station Biologique de Roscoff, 29682 Roscoff, France
[8]Department of Marine Ecology, University of Gothenburg, Tjärnö, Strömstad, Sweden
[9]Marine Biology Department, Texas A&M University at Galveston, Galveston, TX 77553, USA

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].

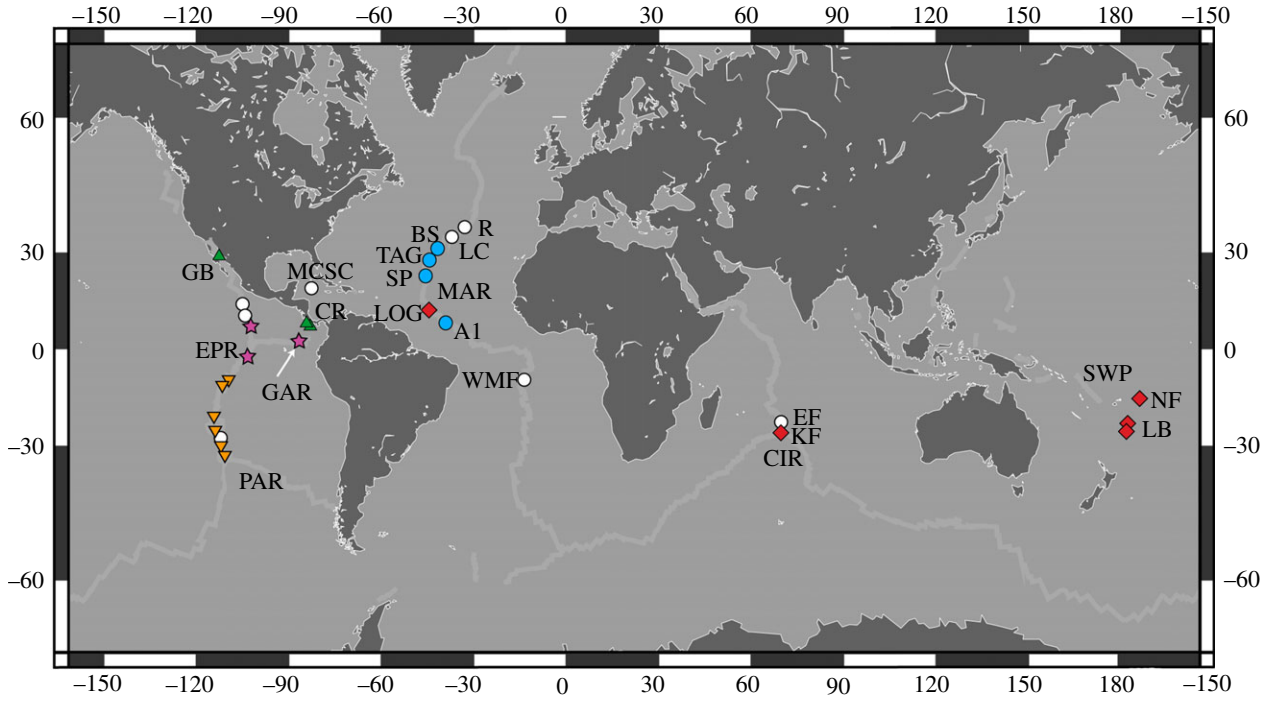

Figure 1. Distribution map of *Archinome* species. Symbols indicate all known records, with sites sampled for this study denoted by triangles (*A. levinae* n. sp.), stars (*A. rosacea*), inverted triangles (*A. storchi*), circles (*A. tethyana* n. sp.), diamonds (*A. jasoni* n. sp.) and open circles (unsampled records). A1, Ashadze-1; BS, Broken Spur; CIR, Central Indian Ridge; CRM, Costa Rica Margin; EF, Edmund Field; EPR, East Pacific Rise; GAR, Galapagos Rift; GB, Guaymas Basin; KF, Kairei Field; LOG, Logatchev; LB, Lau Basins (KLM and TML); LC, Lost City; MAR, Mid-Atlantic Ridge; MCSC, Mid-Cayman Spreading Center; PAR, Pacific Antarctic Ridge; R, Rainbow; SP, Snake Pit; SWP, southwest Pacific basins; TAG, TAG; WMF, Wideawake Mussel Field. (Online version in colour.)

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*, 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 *Paralvinella* 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 *Hermodice*), 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*, located at the Galapagos Rift (GAR; 0° N; 2400 m) in the eastern Pacific [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 2*b*,*c*), a fusiform (spindle-like) body shape, prominent mid-ventral muscular scutes (figure 2*g*) 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) sedimented vents, 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 storchi* [40] was described from the Pacific Antarctic Ridge (PAR, 37° S). Also until recently, *Archinome*

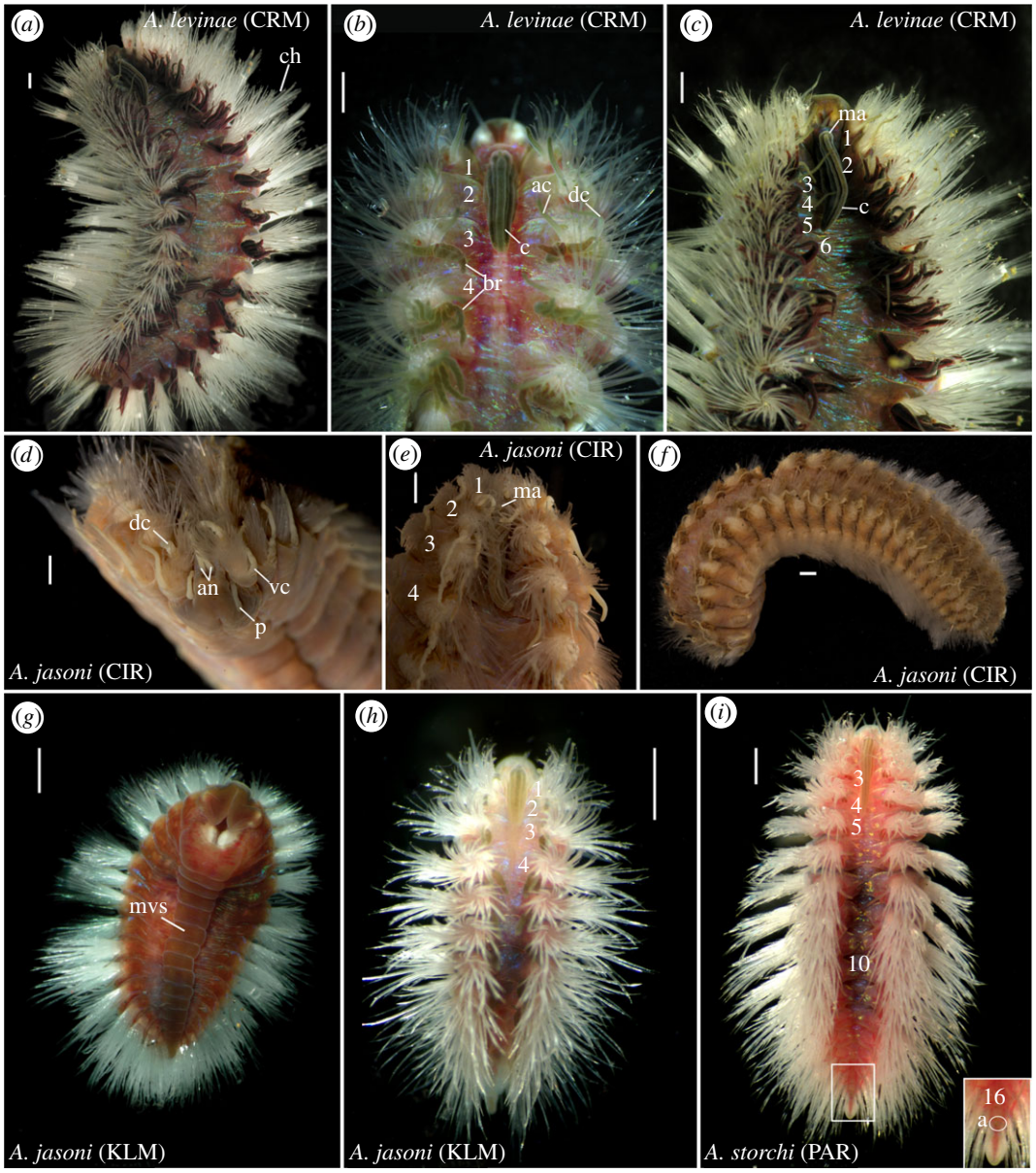

Figure 2. *Archinome* species. (*a*) (Live) whole body, dorsal view of *A. levinae* n. sp. (SIO-BIC A1316); (*b*) (live) dorsal view of anterior body segments of *A. levinae* n. sp. (SIO-BIC A1398; CRM, 9° N); (*c*) (live) dorsal view of anterior body segments of *A. levinae* n. sp. (SIO-BIC A1316); (*d*) (preserved) frontal view of *A. jasoni* n. sp. (SIO-BIC A2313; CIR); (*e*) (preserved) dorsal view of anterior body segments of *A. jasoni* n. sp. (SIO-BIC A2313); (*f*) (preserved) whole body, dorso-lateral view of *A. jasoni* n. sp. (SIO-BIC A2313); (*g*) (live) whole body, ventral view of *A. jasoni* n. sp. (KML); (*h*) (live) whole body, dorsal view of *A. jasoni* n. sp. (KML); (*i*) (live) dorsal view of *A. storchi* (PAR). Note within species variation in caruncle length and size for *A. levinae* n. sp. and *A. jasoni* n. sp. Scale bars, 1 mm. a, Anus; an, antennae; ac, accessory dorsal cirrus; br, branchia; c, caruncle; ch, chaetae; dc, dorsal cirrus; ma, median antenna; mvs, mid-ventral scutes; vc, ventral cirrus; numbers denote segments. (Online version in colour.)

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% $MgCl_2$: seawater) $MgCl_2$ 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, table 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 nuclear internal 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. *Chloeia viridis*). *Notopygos ornata* 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 (d_{COI}) and ITS1 (d_{ITS}). 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). Interclade relationships and species identification were evaluated with the inclusion (COI_{ALL}) and exclusion (COI_{no3rd}) 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 interclade-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 $COI_{no3rd} + 16S + 28S + ITS$ (figure 3*a*). 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 $COI_{ALL} + 16S + 28S + ITS1$ (figure 3*b*; see also the electronic supplementary material, figure S3A). Clade I (boot/pp = 82/0.94; $d_{COI} = 1.7\%$), hereafter *Archinome jasoni* n. sp., included the southwest (SW) Pacific vent specimens (clade 3; boot/pp = 94/1.0; $d_{COI} = 0.5\%$) 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; $d_{COI} = 0.3\%$), 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. d_{COI} was 3.6% between specimens from NF/KML and LOG. The lowest interclade d_{COI} 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 for A1 (MAR) specimens; only three representative 16S sequences (see electronic supplementary material, figure S3B) 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 $d_{COI} = 0.4\%$), 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 d_{COI} was 14.0% (with Clade IV). *Archinome levinae* n. sp. was sister to Clade IV (boot/pp = 98/1.0; $d_{COI} = 2.7\%$), representing *A. rosacea* and *A. storchi* (Clade V) from the GAR, EPR and PAR (clades 5 and 6; figure 3*b*). Clade 5 ($d_{COI} = 0.6\%$) included *A. rosacea* from GAR, as well as specimens from EPR 9° N (2500 m) and 7° S (2700 m). Clade 6 ($d_{COI} = 0.3\%$; 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 d_{COI} was 5.0%, between representatives from the GAR (*A. rosacea*) and 17° S (*A. storchi*). The lowest interclade d_{COI} was 12.4%, between *A. tethyana* n. sp. and *A. rosacea*. The positions of *A. tethyana* n. sp. and *A. levinae* n. sp. received low (boot/pp = 52/0.78) to moderate support (boot/pp = 74/1.0), respectively.

Evaluation of concatenated $COI_{ALL} + 16S + 28S + ITS1$ (figure 3*b*) supported that *Archinome* comprised five clades showing minimal geographical overlap. The resulting topology was similar to that of COI_{ALL} (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 3*a*). The topology deviated from that observed in figure 3*a*, in that vent/seep

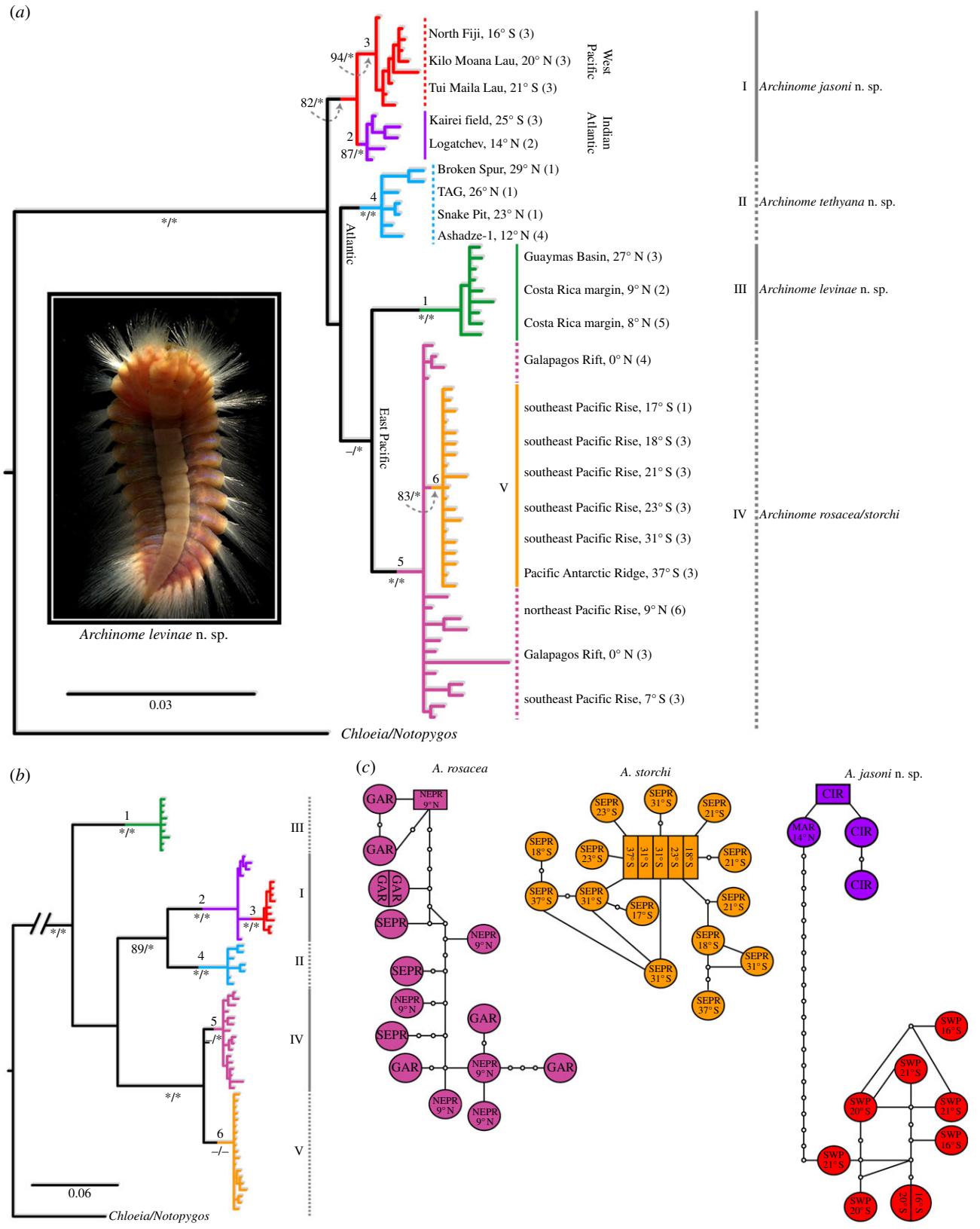

Figure 3. Phylogeny (BI topology shown) and genetic diversity of *Archinome* species. (*a*) COI_{no3rd} + 16S + 28S + ITS1; (*b*) COI_{ALL} + 16S + 28S + ITS1. Roman numerals specify species clades; numerals 1–6 (above nodes) correspond to clades recovered in (*b*); ML bootstrap and BI posterior probabilities (boot/pp) shown below nodes; asterisk (*) denotes boot > 90% and pp > 0.95; values below 80% denoted by a dash '–'. (*c*) COI_{ALL} + 16S statistical parsimony haplotype networks (fixed 21-step connection limit) for *A. rosacea*, *A. storchi* and *A. jasoni* n. sp. Shaded circles and rectangles are scaled to size according to number of individuals per haplotype. Two or more names indicate shared haplotypes. Small open circles represent unsampled haplotypes. (Online version in colour.)

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 3*c*).

Table 1. *Archinome* pairwise distances. Mean Tamura Nei (TrN; below diagonal) and uncorrected (above diagonal) interclade and intraclade (TrN; italics along diagonal) pairwise distances for COI and ITS1 (bold).

	I	II	III	IV	V
I. *Archinome jasoni* n. sp.	*0.017* ***0.001***	0.106 **0.013**	0.133 **0.020**	0.144 **0.013**	0.139 **0.013**
II. *Archinome tethyana* n. sp.	0.118 **0.014**	*0.009* ***0.000***	0.130 **0.032**	0.112 **0.025**	0.112 **0.025**
III. *Archinome levinae* n. sp.	0.150 **0.020**	0.145 **0.033**	*0.004* ***0.000***	0.125 **0.031**	0.130 **0.032**
IV. *Archinome rosacea*	0.168 **0.013**	0.124 **0.025**	0.140 **0.032**	*0.006* ***0.004***	0.047 **0.004**
V. *Archinome storchi*	0.161 **0.014**	0.125 **0.026**	0.147 **0.033**	0.049 **0.004**	*0.003* ***0.000***

No haplotypes were shared among *A. rosacea* (7° S) and *A. storchi* (17° S) individuals found approximately 1200 km apart. A single network (figure 3*c*; 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 3*a*) required the exclusion of COI third codon position (owing to saturation), resulting in a conflicting topology when the third position was considered (figure 3*b*). 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 3*a*). 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 3*b*). Furthermore, these two clades were disparate enough not to form a single haplotype network (figure 3*c*) 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*i*; 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 3*a–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 2*d–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]. Zelnio & Hourdez [64] found west Pacific *Chorocaris vandoverae* as sister to *Rimicaris exoculata* + *Chorocaris chacei* (MAR); however, the phylogenetic placement of CIR *Rimicaris kairei* has not yet been inferred. The gastropod, *Alviniconcha hessleri*, reportedly 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 divergences were also observed among CIR and SW Pacific *A. jasoni* n. sp., and the inclusion of MAR samples now corroborates previously 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 representatives 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 formerly 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 distribution 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 *Amphisamytha*, *Branchipolynoe*, *Hesiolyra*, *Riftia* and *Tevnia* 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 distribution 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 representatives 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 diversification and evolution among deep-sea invertebrate species from chemosynthetic environments.

Acknowledgements. We thank the captains and crews of the R/V *Atlantis*, R/V *Western Flyer*, R/V *Knorr*, R/V *Melville*, R/V *L'Atalante*, R/V *Pourquoi-Pas*? and the pilots of ROVs *Tiburon*, ROVs *Jason I* and *Jason II*, and *Victor 6000* and the pilots and crews of HOVs *Alvin* and *Nautile* for their technical support. Special thanks to Bob Vrijenhoek, chief scientist of the cruises to the SEPR (2005) and SWP (2005), for inviting G.W.R., F.P. and N.G.W. aboard. We are grateful to Didier Jollivet, chief scientist of the *BioSpeedo* 2004 cruise (R/V *L'Atalante*, HOV *Nautile*), Yves Fouquet, chief scientist of the *Serpentine* 2007 cruise (R/V *Pourquoi Pas?* ROV Victor 6000) and to Lisa Levin, chief scientist of the CRROCKS cruises (2009; 2010). Thanks also to Bob Vrijenhoek, Rich Lutz, Didier Jollivet and Cindy Van Dover for providing specimens from GB, MAR and CIR. We also thank Dieter Fiege and Gordon Bock for initial discussions on the morphology of *Archinome*. Harim Cha kindly accessioned the material into the SIO-BIC.

Funding statement. Financial support for this study was provided by NSF DBI-0706856, Census of Marine Life TAWNI, SSB Mini-PEET and EOL Rubenstein Fellowship (E.B.), with additional support from DBI-1036186 (A.S.) and OCE-1029160 (G.W.R.).

References

1. Tunnicliffe V, McArthur AG, McHugh D. 1998 A biogeographical perspective of the deep-sea hydrothermal vent fauna. *Adv. Mar. Biol.* **34**, 353–442. (doi:10.1016/S0065-2881(08)60213-8)
2. Desbruyères D, Segonzac M, Bright M. 2006 *Handbook of deep-sea hydrothermal vent fauna*. Linz, Austria: Denisia 18.
3. Van Dover CL, German CR, Speer KG, Parson LM, Vrijenhoek RC. 2002 Evolution and biogeography of deep-sea vent and seep invertebrates. *Science* **295**, 1253–1257. (doi:10.1126/science.1067361)
4. Rogers AD *et al*. 2012 The discovery of new deep-sea hydrothermal vent communities in the southern ocean and implications for biogeography. *PLoS Biol.* **10**, e1001234. (doi:10.1371/journal.pbio.1001234)
5. Moalic Y, Desbruyères D, Duarte CM, Rozenfeld AF, Bachraty C, Arnaud-Haond S. 2011 Biogeography revisited with network theory: retracing the history of hydrothermal vent communities. *Syst. Biol.* **61**, 127–137. (doi:10.1093/sysbio/syr088)
6. Bachraty C, Legendre P, Desbruyères D. 2008 Biogeographic relationships among deep-sea hydrothermal vent faunas at global scale. *Deep-Sea Res.* **56**, 1371–1378. (doi:10.1016/j.dsr.2009.01.009)
7. Johnson SB, Waren A, Vrijenhoek RC. 2008 DNA barcoding of *Lepetodrilus* limpets reveals cryptic species. *J. Shellfish Res.* **27**, 43–51. (doi:10.2983/0730-8000)
8. Stiller J, Rousset V, Pleijel F, Chevaldonné P, Vrijenhoek RC, Rouse GW. 2013 Phylogeny, biogeography and systematics of hydrothermal vent and methane seep *Amphsamytha* (Ampharetidae, Annelida), with descriptions of three new species. *Syst. Biodivers.* **11**, 35–65. (doi:10.1080/14772000.2013.772925)
9. Gollner S, Fontaneto D, Martinez Arbizu P. 2011 Molecular taxonomy confirms morphological classification of deep-sea hydrothermal vent copepods (Dirivultidae) and suggests broad physiological tolerance of species and frequent dispersal along ridges. *Mar. Biol.* **158**, 221–231. (doi:10.1007/s00227-010-1553-y)
10. Kyuno A, Shintaku M, Fujita Y, Matsumoto H, Utsumi M, Watanabe H, Fujiwara Y, Miyazaki J. 2009 Dispersal and differentiation of deep-sea mussels of the genus *Bathymodiolus* (Mytilidae, Bathymodiolinae). *J. Mar. Biol.* **2009**, 625672. (doi:10.1155/2009/625672)
11. Miyazaki J, de Oliveira ML, Fujita Y, Matsumoto H, Fujiwara Y. 2010 Evolutionary process of deep-sea *Bathymodiolus* mussels. *PLoS ONE* **5**, e10363. (doi:10.1371/journal.pone.0010363)
12. Chevaldonné P, Jollivet D, Desbruyères D, Lutz RA, Vrijenhoek RC. 2002 Sister-species of eastern Pacific hydrothermal vent worms (Ampharetidae, Alvinellidae, Vestimentifera) provide new mitochondrial COI clock calibration. *Cah. Biol. Mar.* **43**, 367–370.
13. Tyler PA, German CR, Ramirez-Llodra E, Van Dover CL. 2002 Understanding the biogeography of chemosynthetic ecosystems. *Oceanol. Acta* **25**, 227–241. (doi:10.1016/S0399-1784(02)01202-1)
14. Hurtado LA, Lutz RA, Vrijenhoek RC. 2004 Distinct patterns of genetic differentiation among annelids of eastern Pacific hydrothermal vents. *Mol. Ecol.* **13**, 2603–2615. (doi:10.1111/j.1365-294X.2004.02287.x)
15. Plouviez S, Shank TM, Faure B, Daguin-Thiebaut C, Viard F, Lallier FH, Jollivet D. 2009 Comparative phylogeography among hydrothermal vent species along the East Pacific Rise reveals vicariant processes and population expansion in the South. *Mol. Ecol.* **18**, 3903–3917. (doi:10.1111/j.1365-294X.2009.04325.x)
16. Tyler PA, Young CM. 1999 Reproduction and dispersal at vents and cold seeps. *J. Mar. Biol. Assoc. UK* **79**, 193–208. (doi:10.1017/S0025315499000235)
17. Vrijenhoek RC. 2010 Genetic diversity and connectivity of deep-sea hydrothermal vent metapopulations. *Mol. Ecol.* **19**, 4391–4411. (doi:10.1111/j.1365-294X.2010.04789.x)
18. Shank TM, Lutz RA, Vrijenhoek RC. 1998 Molecular systematics of shrimp (Decapoda: Bresiliidae) from deep-sea hydrothermal vents, I: enigmatic 'small orange' shrimp from the Mid-Atlantic Ridge are juvenile *Rimicaris exoculata*. *Mol. Mar. Biol. Biotechnol.* **7**, 88–96.
19. Goffredi SK, Hurtado LA, Hallam S, Vrijenhoek RC. 2003 Evolutionary relationships of deep-sea vent and cold seep clams (Mollusca: Vesicomyidae) of the '*pacifica/lepta*' species complex. *Mar. Biol.* **142**, 311–320. (doi:10.1007/s00227-002-0941-3)
20. Johnson SB, Young CR, Jones WJ, Waren A, Vrijenhoek RC. 2006 Migration, isolation, and speciation of hydrothermal vent limpets (Gastropoda; Lepetodrilidae) across the Blanco Transform Fault. *Biol. Bull.* **210**, 140–157. (doi:10.2307/4134603)
21. Vrijenhoek RC. 2009 Cryptic species, phenotypic plasticity, and complex life history: assessing deep-sea fauna diversity with molecular markers. *Deep-Sea Res.* **56**, 1713–1723. (doi:10.1016/j.dsr2.2009.05.016)
22. Audzijonyte A, Vrijenhoek RC. 2010 When gaps really are gaps: statistical phylogeography of hydrothermal vent invertebrates. *Evolution* **64**, 2369–2384. (doi:10.1111/j.1558-5646.2010.00987.x)
23. Cavanaugh CM, Gardiner SL, Jones ML, Jannasch HW, Waterbury JB. 1981 Prokaryotic cells in the hydrothermal vent tube worm *Riftia pachyptila* Jones: possible chemoautotrophic symbionts. *Science* **213**, 340–342. (doi:10.1126/science.213.4505.340)
24. Marsh AG, Mullineaux LS, Young CM, Manahan DT. 2001 Larval dispersal potential of the tubeworm *Riftia pachyptila* at deep-sea hydrothermal vents. *Nature* **411**, 77–80. (doi:10.1038/35075063)
25. Fisher CR *et al*. 1988 Physiology, morphology, and biochemical composition of *Riftia pachyptila* at Rose Garden in 1985. *Deep-Sea Res.* **35**, 1745–1758. (doi:10.1016/0198-0149(88)90047-7)
26. Fisher CR, Childress JJ, Sanders NK. 1988 The role of vestimentiferan hemoglobin in providing an environment suitable for chemoautotrophic sulfide-oxidizing endosymbionts. *Symbiosis* **5**, 229–246.
27. Grzymski JJ *et al*. 2008 Metagenome analysis of an extreme microbial symbiosis reveals eurythermal adaptation and metabolic flexibility. *Proc. Natl Acad. Sci. USA* **105**, 17 516–17 521. (doi:10.1073/pnas.0802782105)
28. Le Bris N. 2007 How does the annelid *Alvinella pompejana* deal with an extreme hydrothermal environment? *Rev. Environ. Sci. Biotech.* **6**, 197–221. (doi:10.1007/s11157-006-9112-1)
29. Pradillon F, Gaill F. 2007 Adaptation to deep-sea hydrothermal vents: some molecular and developmental aspects. *J. Mar. Sci. Technol.* **15**, 37–53.
30. Gagnière N *et al*. 2010 Insights into metazoan evolution from *Alvinella pompejana* cDNAs. *BMC Genomics* **11**, 634. (doi:10.1186/1471-2164-11-634)
31. Jollivet D, Desbruyeres D, Bonhomme F, Moraga D. 1995 Genetic differentiation of deep-sea hydrothermal vent alvinellid populations (Annelida: Polychaeta) along the East Pacific Rise. *Heredity* **74**, 376–391. (doi:10.1038/hdy.1995.56)
32. Young CR, Fujio S, Vrijenhoek RC. 2008 Directional dispersal between mid-ocean ridges: deep-ocean circulation and gene flow in *Ridgeia piscesae*. *Mol. Ecol.* **17**, 1718–1731. (doi:10.1111/j.1365-294X.2008.03609.x)
33. Plouviez S, Le Guen D, Lecompte O, Lallier FH, Jollivet D. 2010 Determining gene flow and the influence of selection across the equatorial barrier of the East Pacific Rise in the tube-dwelling polychaete *Alvinella pompejana*. *BMC Evol. Biol.* **10**, 220. (doi:10.1186/1471-2148-10-220)
34. Rousset V, Rouse GW, Feral J-P, Desbruyeres D, Pleijel F. 2003 Molecular and morphological evidence of Alvinellidae relationships (Terebelliformia, Polychaeta, Annelida). *Zool. Scr.* **32**, 185–197. (doi:10.1046/j.1463-6409.2003.00110.x)
35. Zottoli RA. 1983 *Amphisamytha galapagensis*, a new species of ampharetid polychaete from the vicinity of abyssal hydrothermal vents in the Galapagos Rift, and the role of this species in rift ecosystems. *Proc. Biol. Soc. Wash.* **96**, 379–391.
36. Blake JA. 1985 Polychaeta from the vicinity of deep-sea geothermal vents in the eastern Pacific. 1. Euphrosinidae, Phyllodocidae, Hesionidae, Nereidae, Glyceridae, Dorvilleidae, Orbiniidae, and Maldanidae. *Bull. Biol. Soc. Wash.* **6**, 67–101.
37. Kudenov JD. 1991 A new family and genus of the order Amphinomida (Polychaeta) from the

Galapagos hydrothermal vents. In *Proceedings of the 2nd International Polychaeta Conference* (eds ME Petersen, JB Kirkegaard), *Copenhagen*, *1986*. Systematics, Biology and Morphology of World Polychaeta. *Ophelia* (*Supplement*) 5, 111–120.

38. Barroso R, Klautau M, Sole-Cava AM, Paiva PC. 2010 *Eurythoe complanata* (Polychaeta: Amphinomidae), the 'cosmopolitan' fireworm, consists of at least three cryptic species. *Mar. Biol.* **157**, 69–80. (doi:10.1007/s00227-009-1296-9)
39. Arhens J, Borda E, Barroso R, Campbell AM, Wolf A, Nugues M, Paiva P, Rouse GW, Schulze A. 2013 The curious case of *Hermodice carunculata* (Annelida: Amphinomidae): genetic homogeneity throughout the Atlantic Ocean and adjacent basins. *Mol. Ecol.* **22**, 2280–2291. (doi:10.1111/mec.12263)
40. Fiege D, Bock G. 2009 A new species of *Archinome* (Polychaeta: Archinomidae) from hydrothermal vents on the Pacific Antarctic Ridge 37° S. *J. Mar. Biol. Assoc. UK* **89**, 689–696. (doi:10.1017/S0025315409000174)
41. Desbruyères D, Segonzac M. (eds) 1997 *Handbook of deep-sea hydrothermal vent fauna*. Brest, France: IFREMER.
42. Van Dover CL *et al*. 2001 Biogeography and ecological setting of Indian Ocean hydrothermal vents. *Science* **294**, 818–823. (doi:10.1126/science.1064574)
43. Levin LA *et al*. 2012 A hydrothermal seep on the Costa Rica margin: middle ground in a continuum of reducing ecosystems. *Proc. R. Soc. B* **279**, 2580–2588. (doi:10.1098/rspb.2012.0205)
44. Fabri MC, Bargain A, Briand P, Gebruk A, Fouquet Y, Morineaux M, Desbruyères D. 2011 Hydrothermal vent community of a new deep-sea field Ashadze-1, 12° 58′ N on the Mid-Atlantic Ridge and a comparison of all northern Atlantic chemosynthetic ecosystems. *J. Mar. Biol. Assoc. UK* **91**, 1–13. (doi:10.1017/S0025315410000731)
45. Borda E, Kudenov JD, Beinhold C, Rouse GW. 2012 Towards a revised Amphinomidae (Annelida: Amphinomida): description and affinities of a new genus and species from the Nile Deep-sea Fan, Mediterranean Sea. *Zool. Scr.* **41**, 307–325. (doi:10.1111/j.1463-6409.2012.00529.x)
46. Nygren A, Pleijel F. 2011 From one to ten in a single stroke: resolving the European *Eumida sanguinea* (Phyllodocidae, Annelida) species complex. *Mol. Phylogenet. Evol.* **58**, 132–141. (doi:10.1016/j.ympev.2010.10.010)
47. Clement M, Posada D, Crandall KA. 2000 TCS: a computer program to estimate gene genealogies. *Mol. Ecol.* **4**, 331–346.
48. Knowlton N. 2000 Molecular genetic analyses of species boundaries in the sea. *Hydrobiologia* **420**, 73–90. (doi:10.1023/A:1003933603879)
49. Bickford D, Lohman DJ, Sodhi NS, Ng PKL, Meier R, Winker K, Ingram KK, Das I. 2007 Cryptic species as a window on diversity and conservation. *Trends Ecol. Evol.* **22**, 148–155. (doi:10.1016/j.tree.2006.11.004)
50. Hebert PD, Penton EH, Burns JM, Janzen DH, Hallwachs W. 2004 Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. *Proc. Natl Acad. Sci. USA* **101**, 14 812–14 817. (doi:10.1073/pnas.0406166101)
51. Meyer CP, Paulay G. 2005 DNA barcoding: error rates based on comprehensive sampling. *PLoS Biol.* **3**, e422. (doi:10.1371/journal.pbio.0030422)
52. Cameron S, Rubinoff D, Will K. 2006 Who will actually use DNA barcoding and what will it cost? *Syst. Biol.* **55**, 844–847. (doi:10.1080/10635150 600960079)
53. Rubinoff D, Cameron S, Will K. 2006 A genomic perspective on the shortcomings of mitochondrial DNA for 'barcoding' identification. *J. Hered.* **97**, 581–594. (doi:10.1093/jhered/esl036)
54. Moritz C, Cicero C. 2004 DNA barcoding: promise and pitfalls. *PLoS Biol.* **2**, e354. (doi:10.1371/journal.pbio.0020354)
55. Wiemers M, Fiedler K. 2007 Does the DNA barcoding gap exist? A case study in blue butterflies (Lepidoptera: Lycaenidae). *Front. Zool.* **4**, 8. (doi:10.1186/1742-9994-4-8)
56. Will KW, Mishler BD, Wheeler QD. 2005 The perils of DNA barcoding and the need for integrative taxonomy. *Syst. Biol.* **54**, 844–851. (doi:10.1080/10635150500354878)
57. Dasmahapatra KK, Elias M, Hill RI, Hoffman JI, Mallet J. 2010 Mitochondrial DNA barcoding detects some species that are real, and some that are not. *Mol. Ecol. Resour.* **10**, 264–273. (doi:10.1111/j.1755-0998.2009.02763.x)
58. Cook LG, Edwards RD, Crisp MD, Hardy NB. 2010 Need morphology always be required for new species descriptions? *Invert. Syst.* **24**, 322–326. (doi:10.1071/IS10011)
59. Connelly DP *et al*. 2012 Hydrothermal vent fields and chemosynthetic biota on the world's deepest seafloor spreading centre. *Nat. Commun.* **3**, 620. (doi:10.1038/ncomms1636)
60. Williams AB, Rona PA. 1986 Two new caridean shrimps (Bresiliidae) from a hydrothermal field on the Mid-Atlantic Ridge. *J. Crus. Biol.* **6**, 446–462. (doi:10.2307/1548184)
61. Shank TM, Black MB, Halanych KM, Lutz RA, Vrijenhoek RC. 1999 Miocene radiation of deep-sea hydrothermal vent shrimp (Caridea: Bresiliidae): evidence from mitochondrial cytochrome oxidase subunit I. *Mol. Phylogenet. Evol.* **13**, 244–254. (doi:10.1006/mpev.1999.0642)
62. Teixeira S, Serrão EA, Arnaud-Haond S. 2012 Panmixia in a fragmented and unstable environment: the hydrothermal shrimp *Rimicaris exoculata* disperses extensively along the Mid-Atlantic Ridge. *PLoS ONE* **7**, e38521. (doi:10.1371/journal.pone.0038521)
63. Teixeira S. 2010 Recent population expansion and connectivity in the hydrothermal shrimp *Rimicaris exoculata* along the Mid-Atlantic Ridge. *J. Biogeogr.* **38**, 564–574. (doi:10.1111/j.1365-2699.2010.02408.x)
64. Zelnio KA, Hourdez S. 2009 A new species of *Alvinocaris* (Crustacea: Decapoda: Caridea: Alvinocarididae) from hydrothermal vents at the Lau Basin, southwest Pacific, and a key to the species of Alvinocarididae. *Proc. Biol. Soc. Wash.* **122**, 52–71. (doi:10.2988/07-28.1)
65. Kojima S, Fujikura K, Okutani T, Hashimoto J. 2004 Phylogenetic relationship of *Alviniconcha* gastropods from the Indian Ocean to those from the Pacific Ocean (Mollusca: Provannidae) revealed by nucleotide sequences of mitochondrial DNA. *Venus* **63**, 65–68.
66. Suzuki Y *et al*. 2006 Host–symbiont relationships in hydrothermal vent gastropods of the genus *Alviniconcha* from the southwest Pacific. *Appl. Environ. Microb.* **72**, 1388–1393. (doi:10.1128/AEM.72.2.1388-1393.2006)
67. Black MB, Halanych KM, Maas PAY, Hoeh WR, Hashimoto J, Desbruyères D, Lutz RA, Vrijenhoek RC. 1997 Molecular systematics of vestimentiferan tubeworms from hydrothermal vents and cold-water seeps. *Mar. Biol.* **130**, 141–149. (doi:10.1007/s002270050233)
68. Burton KW, Ling H-F, O'Nions RK. 1997 Closure of the Central American Isthmus and its effect on deep-water formation in the North Atlantic. *Nature* **386**, 382–385. (doi:10.1038/386382a0)
69. Nye V, Copley J, Plouviez S. 2011 A new species of *Rimicaris* (Crustacea: Decapoda: Caridea: Alvinocarididae) from hydrothermal vent fields on the Mid-Cayman Spreading Centre, Caribbean. *J. Mar. Biol. Assoc. UK* **92**, 1057–1072. (doi:10.1017/S0025315411002001)
70. Helenes J, Carreno AL, Carrillo RM. 2009 Middle to Late Miocene chronostratigraphy and development of the northern Gulf of California. *Mar. Micropaleontol.* **72**, 10–25. (doi:10.1016/j.marmicro.2009.02.003)
71. Fisher RL. 1961 Middle America trench; topography and structure. *Geol. Soc. Am. Bull.* **72**, 703–719. (doi:10.1130/0016-7606(1961)72[703:MATTAS]2.0.CO;2)
72. Simoneit BRT, Lonsdale PF, Edmond JM, Shanks III WC. 1990 Deep-water hydrocarbon seeps in Guaymas Basin, Gulf of California. *Appl. Geochem.* **5**, 41–49. (doi:10.1016/0883-2927(90)90034-3)
73. Lonsdale P, Becker K. 1985 Hydrothermal plumes, hot springs, and conductive heat flow in the Southern Trough of Guaymas basin. *Earth Planet. Sci. Lett.* **73**, 211–225. (doi:10.1016/0012-821X(85)90070-6)
74. Eakins BW, Lonsdale PF. 2003 Structural patterns and tectonic history of the Bauer microplate, eastern tropical Pacific. *Mar. Geophys. Res.* **24**, 171–205. (doi:10.1007/s11001-004-5882-4)