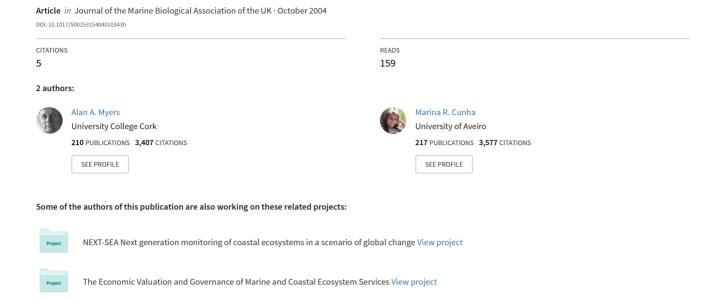
New and little known corophiidean amphipods from the 'Lucky Strike' hydrothermal vent, Mid-Atlantic Ridge



New and little known corophiidean amphipods from the 'Lucky Strike' hydrothermal vent, Mid-Atlantic Ridge

Alan A. Myers*[‡] and Marina R. Cunha[†]

*Department of Zoology, Ecology and Plant Science, National University of Ireland, Cork, Republic of Ireland.

†Departamento de Biologia, Universidade de Aveiro, 3810-193 Aveiro, Portugal. E-mail mcunha@bio.ua.pt

†Corresponding author, e-mail: alanmyers@crustacea.net

Two species of corophiid amphipods are described from the 'Lucky Strike' hydrothermal vent on the Mid-Atlantic Ridge near the Açores. One species, *Bonnierella compar* sp. nov. is new to science, the other, *Autonoe longicornis* has not been reported since the original description of a single female in 1909. Full descriptions are provided of the new species, and of the previously unknown male of *A. longicornis*.

INTRODUCTION

One decade after the discovery of the hydrothermal vent communities dominated by vestimentiferans and clams in the Pacific (Lonsdale, 1977; Corliss et al., 1979), the first observations of hydrothermal vents in the Atlantic revealed a faunal assemblage dominated by large beds of mussels and swarms of caridean shrimps (Rona et al., 1986; Van Dover, 1995; Desbruyères et al., 2001). Amphipods are often associated with hydrothermal vents and many new species have been described both from the Pacific (Shaw, 1989; Barnard & Ingram, 1990; Martin et al., 1993; Vinogradov, 1993) and from the Atlantic (Bellan-Santini & Thurston, 1996). Some species such as the lysianassoid Ventiella sulfuris (Barnard & Ingram, 1990), the pardaliscid Halice hesmonectes (Martin et al., 1993; Sheader et al., 2000) and the eusirid Bouvierella curtirama (Van Dover & Trask, 2000; Sheader et al., 2004) are known to occur at high population densities.

Although many differences in faunal composition and abundance have been revealed by studies on vent communities, the sampling effort has been focused in the most active areas of the fields. However, besides the variety of hydrothermal activity and the steep gradients of temperature and chemistry close to the vent openings and chimney walls, vent fields show a large diversity of geological settings that is seldom investigated. On the other hand, the sample collection is frequently directed to large-sized organisms that can be easily seen during submersible dives or remotely operated vehicle (ROV) operations. During geological surveys carried out in August 2000, and August 2002 by a joint programme of the Geological and Mining Institute of Portugal, Moscow State University and University of Aveiro, a TV-assisted grab was used to take a total of 27 samples mostly from inactive areas of the Lucky Strike vent field (Mid-Atlantic Ridge). Over 100 different taxa were retrieved and the fauna collected yielded not only the most typical vent species but also a variety of vagrant or background organisms (Cunha et al., 2001, 2003). Small crustaceans accounted for about 50% of the species richness and included 15 amphipod species that considerably increases

the number of taxa cited by Desbruyères & Segonzac (1997) for this location.

The recently collected specimens of corophiid amphipods from Lucky Strike are the first record of the families Aoridae and Ischyroceridae from hydrothermal vents in the Atlantic. Two species are described herein. One species, *Bonnierella compar* sp. nov. is new to science, the other, *Autonoe longicornis* (Chevreux) has not been reported since the original description of a single female (Chevreux, 1909)

Type material is deposited in the collections of the National Museum of Ireland (NMI).

MATERIALS AND METHODS

Study site

The Lucky Strike segment is located at the Mid-Atlantic Ridge (MAR) south-west of the Acores (Fouquet et al., 1994). The hydrothermal field, centred at 37°17.5′N 32°16.5′W, is one of the largest currently known in the MAR and develops around a lava lake at approximately 1700 m in a depression surrounded by three volcanic cones. The lava lake, the first discovered in a slow spreading ridge (Fouquet et al., 1995) is characterized by typical lobated and draped lava, lava flows and lava pillars. The volcanoes are mostly composed of pillow lavas and volcanic breccia. Many chimneys and other edifices, most of which are inactive or only mildly active, surround the lava lake especially in the south-eastern and north-western areas. Near large chimneys, diffuse venting occurs through unconsolidated sediments. Further information on the geological setting and environmental conditions in the vent field can be found in Costa et al. (1995); Langmuir et al. (1997); Barriga (1999) and Khripounoff et al. (2000).

Collection of samples

Samples were collected during the cruises TTR-10 (August 2000) and TTR12 (August 2002) on-board the RV 'Professor Logachev' (Training Through Research

Table 1. Station data for the samples yielding corophiid amphipods. The active chimneys or vent sites closest to each sampling location are referred to in parentheses using the names given during French and American cruises (see Desbruyères et al., 2001).

Station	Taxa	Latitude	Longitude	Depth (m)	Lithology	Location
AT-252-Gr	aorid female	37°17.442′N	32°16.594′W	1673	Volcanic: high vesicularity lava	SE area (Y3) near active chimneys
AT-262-Gr	aorid female	37°17.509′N	32°16.925′W	1720	Volcanic: high vesicularity lava	NW area
AT-265-Gr	A. longicornis	37°17.438′N	32°16.599′W	1685	Volcanic: hyaloclastic rocks	SE area (Y3) near active chimneys
AT-268-Gr	aorid fragments	37°17.361′N	32°16.525′W	1700	Volcanic: hyaloclastic rocks	SE area (L'Aiguille)
AT-272-Gr	B. compar sp. n.	37°17.576′N	32°16.865′W	1710	Sulphide chimney: high temperature	NW area (Elisabeth) inactive chimney
AT-273-Gr	aorid fragments	37°17.446′N	32°16.611′W	1675	Sulphide rubble	SE area (Y3)
AT–279-Gr	A. longicornis	37°17.400′N	32°16.625′W	1703	Volcanic: high vesicularity lava	SE area (Y3)
AT-427-Gr	aorid female	37°17.502′N	32°16.808′W	1748	Volcanic glass	Central area, lava lake
AT-428-Gr	aorid female	37°17.289′N	32°16.522′W	1716	Hydrothermal slab	SE area (Chimiste) near active chimney
AT-436-Gr	B. compar sp. n.	37°17.300′N	32°16.563′W	1709	Hydrothermal slab	SE area (Chimiste) near active chimney

SE, south-eastern; NW, north-western; A. longicornis, Autonoe longicornis; B. compar, Bonnierella compar.

programme, IOC-UNESCO). The location of samples inside the vent field was predetermined and based on data (ROV 'Jason' images) obtained during the cruise LUSTRE-1996. A TV-assisted grab was used to locate different types of rocks allowing a minimally destructive sampling procedure. Macroinvertebrates were picked from the surface of the rocks or sorted from sieved sediments and rock washings. Samples were preserved in 70% ethanol. Data on the stations yielding corophiid amphipods are presented in Table 1.

SYSTEMATICS

Order AMPHIPODA Latreille, 1816
Suborder COROPHIIDEA Leach, 1814
Infraorder COROPHIIDEA Leach, 1814
Superfamily AOROIDEA Stebbing, 1899
Family AORIDAE Stebbing, 1899
Genus Autonoe Boeck, 1871
Autonoe longicornis comb. nov.
(Figures 1 & 2)

Hansenella longicornis Chevreux, 1909, 3-7, figure 3.

Material examined

Mid-Atlantic Ridge: Lucky Strike, 37°17.438′N 32°16.599′W, 1685 m, RV 'Professor Logachev', TV-assisted grab, TTR-10 Station AT-265-GR, August 2000, 1 male (illustrated herein). Same locality, 37°17.442′N, 32°16.594′W, 1673 m, RV 'Professor Logachev', TV-assisted grab, TTR-10 Station AT-252-GR, August 2000, 1 incomplete female (lacking antennae and gnathopods).

$Diagnosis\ of\ male$

Antenna 1 and 2 subequal in length, less than half body length. Antenna 1 peduncle article 3, one-quarter length of

article 1; flagellum shorter than peduncle; accessory flagellum composed of one rudimentary article. Mandible palp article 3 longer than article 2, terminally falcate. Maxilla l inner plate with a single, long, pectinate seta. Labium mandibular processes acute. Gnathopod 1 coxa produced anterodistally, subacute; basis robust; carpus enlarged, longer than propodus, the posterodistal corner produced into a spine. Gnathopod 2 carpus and propodus elongate, subequal in length. Pereopods 5-7 basis only weakly expanded. Epimera 1-3 rounded. Uropod 1 peduncle with inter-ramal spine, about one-third length of peduncle; inner ramus longer than outer and subequal in length with peduncle. Uropod 2 peduncle with short inter-ramal spine about one-sixth length of peduncle; inner ramus longer than outer and subequal with peduncle. Uropod 3 peduncle longer than broad, rami subequal and only a little longer than peduncle, inner ramus with small second article. Telson with each dorsal crest bearing a fine seta.

Remarks

Hansenella longicornis was described by Chevreux (1909) from material collected near the Açores in 1360 metres depth. He had only female specimens available to him. He noted the similarity of his material with the genus Microdeutopus Costa, in which genus the males have an enlarged gnathopod 1 carpus which has a spine (or spines) at the posterodistal corner. In Microdeutopus this character state is not expressed in females. Chevreux (1909) therefore erected a new genus to accommodate Microdeutopus-like aorids in which the female had an enlarged gnathopod 1 carpus bearing a spine. Hansenella is not, however, closely related to Microdeutopus, since it lacks flanges on the maxilliped plates. It agrees with the diagnosis of the genus Autonoe (see Myers, 1988) some of

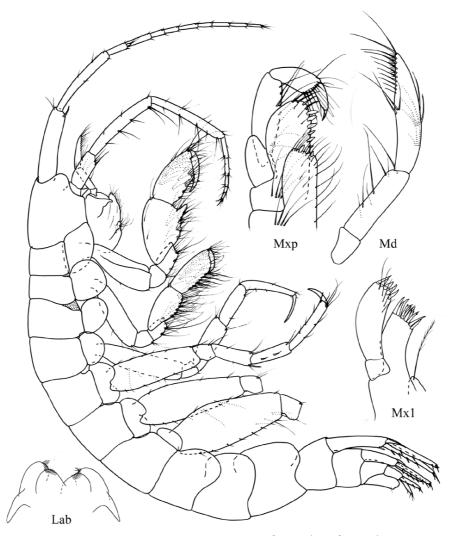


Figure 1. Autonoe longicornis (Chevreux) male, Station AT-265-GR, 37°17.438'N 32°16.599'W. Lab, labium; Md, mandible; Mxl, maxilla; Mxp, maxilliped.

which (A. denticarpus Myers & McGrath, A. catalaunica Ruffo, Cartes & Sorbe) also have a carpal spine on gnathopod 1.

Although Chevreux had only female specimens for description, and the current material consists only of one male and one very incomplete female, the similarity of the two materials leaves little doubt about their conspecificity.

The specimens of *A. longicornis* were retrieved from three samples of volcanic rocks (pillow lava and hyaloclastic rocks) all located in the south-west area around the vent site Y3. The proximity of active venting is inferred from the occurrence of some specimens of Bathymodiolus azoricus in the sample AT-265-GR and shell debris of the same species in the sample AT-252-GR. The specimens collected by Chevreux (1909) were retrieved from similar depths (1360 m) also in the Açores region (39°21′20"N $31^{\circ}05'45''W$).

Fourteen species of the genus Autonoe are now known. A dichotomous key is provided here to facilitate the identification of males of this Atlantic-Mediterranean genus. Females are difficult to identify, but those wishing to do so, are referred to the interactive keys available on www.amphipoda.com and www.crustacea.net.

Key to males of the genus Autonoe Boeck, 1871

1. Gnathopod 1 basis with brush of very long setae at

Gnathopod 1 basis lacking brush of very long setae at 2. Pereopods 3–4 merus with numerous very long setae, Pereopods 3-4 merus with only a few setae, much 3. Gnathopod 2 basis with convex flange on anterior Gnathopod 2 basis anterior margin without convex 4. Gnathopod 2 basis with brush of very long setae at posterodistal corner A. rubromaculatus (Ledoyer) Gnathopod 2 basis lacking brush of very long setae at 5. Gnathopod l ischium with brush of very long setae at

posterodistal corner A. viduarum (Myers)

Order AMPHIPODA Latreille, 1816
Suborder COROPHIIDEA Leach, 1814
Infraorder CAPRELLIIDA Leach, 1814
Superfamily PHOTOIDEA Boeck, 1871
Family ISCHYROCERIDAE Stebbing, 1899
Subfamily BONNIERELLINAE Myers & Lowry 2003
Genus Bonnierella Chevreux 1900
Bonnierella compar sp. nov.
(Figures 3 & 4)

Material examined

Holotype: Mid-Atlantic Ridge: Lucky Strike, 37°17.576′N 32°16.865′W, 1710 m, RV 'Professor Logachev', TV-assisted grab, TTR-10 Station AT-272-GR, August 2000, female, NMINH 2004.75-1 (illustrated herein).

Paratypes: same data: 4 males, 5 females, 9 immature, NMINH 2004.75-2.

Other material: same locality, 37°17.300′N 32°16.563′W, 1709 m, RV 'Professor Logachev', TV-assisted grab, TTR—12 Station AT—436—GR, August 2002, 3 males, 6 females, 34 immature and fragments.

Diagnosis

Head anteroventral margin strongly regressed. Eyes absent. Antenna 1 and 2 subequal in length, setose; accessory flagellum with one long and one rudimentary article. Maxilliped raptorial, with reduced plates and strong palp terminating in a dactyliform palp article 4. Gnathopod 1 small, unornamented. Gnathopod 2 similar in both sexes, massive, with palmar excavation and with defining spine on posterior margin.

Uropod 3 peduncle elongate, broad proximally, narrow distally, rami much less than half length of peduncle. Telson without cusps or spines.

Description of female holotype

Head lateral lobes triangular; anteroventral margin strongly regressed; eyes absent. Antenna 1 and 2 subequal in length. Antenna larticles 2 and 3 subequal in length and more than one and one-half times length of article 1, flagellum longer than peduncular article 3 with six articles; peduncular articles 2 and 3 and flagella articles with very long setae; accessory flagellum composed of one long and one rudimentary article. Antenna 2 peduncular articles 4 and 5 subequal, flagellum with four articles. Peduncular articles 4 and 5 and flagella articles with very long setae. Labrum with short blunt epistome, mandible palp article three shorter than article 2, spatulate with long distal setae. Maxilla l inner plate with one long distal seta. Maxilliped inner and outer plates small, outer plate reaching less than half way along palp article 2; palp well developed, article 4 dactyliform, elongate. Gnathopod 1 basis slender, anterior margin weakly concave; propodus only slightly longer than carpus, subovoid, palm evenly rounded; dactylus elongate and slender, closing over almost entire posterior margin of propodus. Gnathopod 2 basis stout, carpus short cup-shaped, propodus massive, more than twice length of carpus, posterior margin irregular with short, straight and crenulated weakly oblique palm, posterior to which is a deep round-bottomed excavation, followed by a very oblique crenulated portion leading to a blunt process about midway along the posterior margin; dactylus stout, opposable to spine on posterior margin of propodus. Pereopods 3 and 4 basis slender, dactylus about three quarters length of propodus. Pereopods 5-7 in the length ratios 6.0:7.5:8.0, basis moderately slender, weakly subovoid. Epimera 1-3 rounded. Uropod 1 peduncle with short inter-ramal spine about one-sixth length of peduncle, rami subequal, shorter than peduncle, lacking distal setae; inner ramus with a single medial seta. Uropod 2 peduncle one and one-half times length of subequal rami, lacking an inter-ramal spine; both rami without setae. Uropod 3 peduncle elongate, broad proximally, narrow distally with robust seta on inner margin and two robust setae distally; rami subequal in length, much less than half length of peduncle lacking setae. Telson triangular, with two marginal and two subdistal setae.

Male gnathopod 2 scarcely different from that of female, but carpus even shorter; process on posterior margin of propodus subacute.

Etymology

From the latin *compar*=shared, referring to the minimal sexual dimorphism of this species.

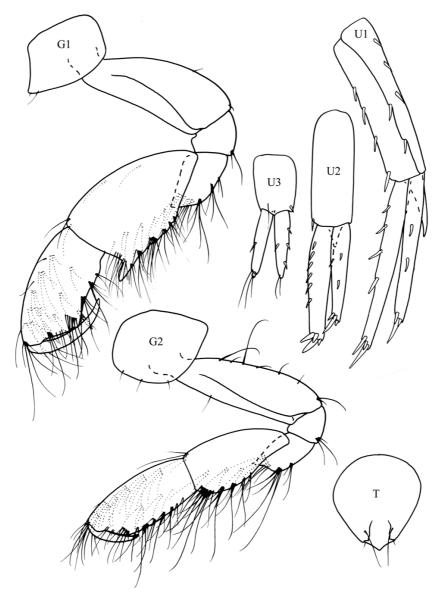


Figure 2. Autonoe longicornis (Chevreux) male, Station AT-265-GR, 37°17.438'N 32°N.599'W. G1, gnathopod 1; G2, gnathopod 2; T, telson; U1, U2, U3, uropods 1-3.

Remarks

Bonnierella compar shows similarities with members of the genus Gammaropsis Liljeborg, but differs in the elongated and distally narrow peduncle and short rami of uropod 3. This is a diagnostic character state for the Ischyroceridae. The reduced inner and outer plates of the maxilliped are characteristic of the genus Bonnierella Chevreux. Bonnierella compar differs from B. abyssi Chevreux and B. abyssorum (Bonnier), both from the north-eastern Atlantic, and from B. angolae Barnard from West Africa, in having an un-enlarged gnathopod 1 with an unornamented palm to the propodus. It shows some similarities with B. lapisi (Barnard) from the Cape Basin, but differs from that species in its more setose antennae, non sexually-dimorphic gnathopod 2, as well as in differences in the shape of both gnathopoda.

A previous record of the genus in hydrothermal vents is given by Shaw (1989) who collected a single specimen of B. linearis from a station in the Pacific (Juan de Fuca, 46°46′N 130°18′W, 1797 m).

The specimens of B. compar were retrieved from two samples, one in the north-west area and the other in the south-west area. Both samples were collected in the vicinity of active venting sites and in both samples filterfeeding organisms (small sponges, hydrozoans and cirripeds) were present. According to Colaço et al. (2002) faunal assemblages are distributed in three concentric rings around the vent openings: the chimney walls, the area of diffuse mild venting and an external ring where the filter feeding organisms settle. Of the amphipod species collected in the vent field, B. compar was second only to Bouvierella curtirana in abundance but apparently they occupy different areas in the vent zonation scheme and they also have different life styles. Some of the specimens of Bonnierella compar were found inside their tubes of fine pelagic sediments cemented with mucous,

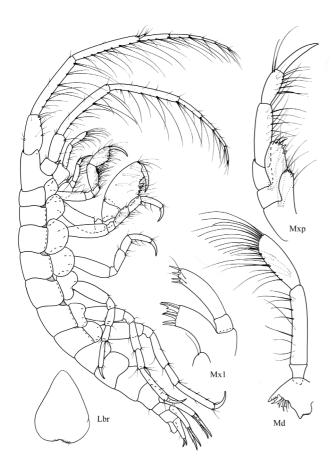


Figure 3. Bonnierella compar sp. nov. holotype female, Station AT-272-GR, 37°17.576′N 32°16.865′W. Lbr, labrum; Md, mandible; Mxl, maxilla; Mxp, maxilliped.

in some cases (AT-272-GR) built around hydrozoan stalks.

General discussion

Sexual dimorphism is the normal state in corophiideans. In showing almost no sexual dimorphism, *A. longicornis* is unique amongst described species of the genus *Autonoe* and likewise, *B. compar* is unique amongst described species of the genus *Bonnierella*. It is perhaps coincidental, that both are from hydrothermal vents.

Thanks are due to the chief-scientists Hipólito Monteiro (Geological and Mining Institute of Portugal) and Michael Ivanov (Moscow State University) for the invitation to participate in the TTR cruises (Training Through Research Programme, IOC-UNESCO).

REFERENCES

Barnard, J.L. & Ingram, C., 1990. Lysianassoid Amphipoda (Crustacea) from deep-sea thermal vents. Smithsonian Contributions to Zoology, 499, 1–80.

Barriga, F.J.A.S., 1999. Actividade hidrotermal no fundo do mar dos Açores: estado da arte. *Colóquio Ciências*, 23, 44–59.

Bellan-Santini, D. & Thurston, M.H., 1996. Amphipoda of the hydrothermal vents along the mid-Atlantic Ridge. *Journal of Natural History*, **30**, 685–702.

Boeck, A., 1871. Crustacea Amphipoda borealia et arctica. Forhandlinger i Videnskabs-Selskabet i Christiania, 1870, 81–280.

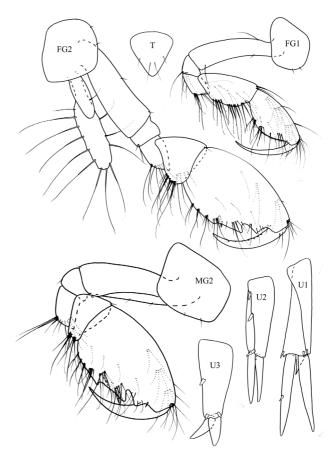


Figure 4. Bonnierella compar sp. nov. holotype female (FG 1–2, U1–3, T), paratype male (MG2), Station AT-272-GR, 37°17.576′N 32°16.865′. FG1, FG2, female gnathopods 1 and 2; MG2, male gnathopod 2; T, telson; U1, U2, U3, uropods 1–3.

Chevreux, E., 1900. Amphipodes provenant des campagnes de l'Hirondelle (1885–1888). Résultats des Campagnes Scientifiques Accomplies sur son Yacht par Albert Ier Prince Souverain de Monaco, 16 1–195

Chevreux, E., 1909. Diagnoses d'amphipodes nouveaux provenant des campagnes de la Princesse-Alice dans l'Atlantique nord (suite). Lysianassidae. Bulletin de l'Institut Océanographique, Monaco, 150, 1–7.

Colaço, A., Dehairs, F. & Desbruyères, D., 2002. Nutritional relations of deep-sea hydrothermal fields at the Mid-Atlantic Ridge: a stable isotope approach. *Deep-Sea Research I*, **49**, 395–412.

Corliss, J.B. et al., 1979. Submarine springs on the Galapagos Rift. *Science, New York*, **203**, 1073–1083.

Costa, I., Barriga, F.J.A.S. & Fouquet, Y., 1995. Alteration processes associated with active hydrothermal sites—the Lucky Strike and Menez Gwen examples (37°20'N and 37°50'N, Mid-Atlantic Ridge). Memórias do Museu e Laboratório Mineralógico e Geológico da Faculdade de Ciências da Universidade do Porto, 4, 979–983.

Cunha, M.R., Hilário, A.M. & Teixeira, I.G., 2001. The faunal community from the Lucky Strike hydrothermal vent field. *IOC Workshop Report*, **175**, 73–74. [Abstract.]

Cunha, M.R., Peralta, N., Amaral, M.J., Blinova, V. & Ravara, A., 2003. Biological surveys of the Lucky Strike segment (MAR) and the Atlantis Seamount. Preliminary results of TTR-12 cruise in the Azores area (Leg 5). *IOC Workshop Report*, 187, 22–23. [Abstract.]

Desbruyères, D. et al., 2001. Variations in deep-sea hydrothermal vent communities on the Mid-Atlantic Ridge when approaching the Azores plateau. *Deep-Sea Research I*, **48**, 1325–1346.

- Desbruyères, D. & Ségonzac, M., 1997. Handbook of deep-sea hydrothermal vent fauna. Éditions Ifremer.
- Fouquet, Y. et al., 1994. A detailed study of the Lucky Strike hydrothermal vent site and discovery of a new hydrothermal site: Menez Gwen; preliminary results of the Diva 1 cruise (2-29 May). InterRidge News, 3, 14-17.
- Fouquet, Y., Ondréas, H., Charlou, J.L., Donval, J.P., Radford-Knoery, J., Costa, I., Lourenço, N. & Tivey M.K., 1995. Atlantic lava lakes and hot vents. Nature, London, 377, 201.
- Khripounoff, A., Comtet, T., Vangriesheim, A. & Crassous, P., 2000. Near-bottom biological and mineral particle flux in the Lucky Strike hydrothermal vent area (Mid-Atlantic Ridge). Journal of Marine Systems, 25, 101–118.
- Langmuir, C. et al., 1997. Hydrothermal vents near a mantle hot spot: the Lucky Strike vent field at 37°N on the Mid-Atlantic Ridge. Earth and Planetary Science Letters, 148, 69-91.
- Latreille, P.A., 1806. Genera crustaceorum et insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata. Amand Koenig, Parisiis et Argentorati.
- Leach, W.E., 1814. Crustaceology. The Edinburgh Encyclopaedia, 7,
- Lonsdale, P.F., 1977. Clustering of suspension-feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centres. Deep-Sea Research, 24, 857-863.
- Martin, J.W., France, S.C. & Van Dover, C.L., 1993. Halice hesmonectes, a new species of pardaliscid amphipod (Crustacea, Peracarida) from hydrothermal vents in the eastern Pacific. Canadian Journal of Zoology, 71, 1724–1732.
- Myers, A.A., 1988. A cladistic and biogeographic analysis of the Aorinae subfamily nov. Crustaceana, Supplement 13, 167 - 192.
- Myers, A.A. & Lowry, J.K., 2003. A phylogeny and a new classification of the Corophiidea Leach, 1814 (Amphipoda). Journal of Crustacean Biology, 23, 443-485.

- Rona, P.A., Klinkhammer, G., Nelsen, T.A., Trefry, J.H. & Elderfield, H., 1986. Black smokers, massive sulphides and vent biota at the Mid-Atlantic Ridge. Nature, London, 321, 33-
- Shaw, P., 1989. New amphipods from geothermal vent sites off the west coast of Vancouver Island, British Columbia, with a reappraisal of the amhipod family Sebidae. Canadian Journal of Zoology, **67**, 1882–1890.
- Sheader, M., Van Dover, C.L. & Shank, T.M., 2000. Structure and function of Halice hesmonectes (Amphipoda: Pardaliscidae) swarms from hydrothermal vents in the eastern Pacific. Marine Biology, 136, 901-911.
- Sheader, M., Van Dover, C.L. & Thurston, M.H., 2004. Reproductive ecology of Bouvierella curtirama (Amohipoda: Eusiridae) from chemically distinct vents in the Lucky Strike vent field, Mid-Atlantic Ridge. Marine Biology, 144, 503-514.
- Stebbing, T.R.R., 1899. Revision of Amphipoda. Annals and Magazine of Natural History, Series 7, 3, 350.
- Van Dover, C.L., 1995. Ecology of Mid-Atlantic Ridge hydrothermal vents. In Hydrothermal vents and processes (ed. L.M. Parson et al.). The Geological Society of London Special Publication, **87**, 257–294.
- Van Dover, C.L. & Trask, J.L., 2000. Diversity at deep-sea hydrothermal vent and intertidal mussel beds. Marine Ecology Progress Series, 195, 169-178.
- Vinogradov, G.M., 1993. Amphipods (Crustacea) from the 'black smokers' from hydrothermal vent areas of the eastern Pacific. Zoologicheskii Zhurnal, 72, 40-53.

Submitted 14 May 2004. Accepted 16 July 2004.