

Decapod crustaceans from hydrothermal vents and cold seeps: a review through 2005

JOEL W. MARTIN^{1*} and TODD A. HANEY^{1,2}

¹Research and Collections Branch, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA 90007, USA

²Ecology and Evolutionary Biology, University of California Los Angeles, 621 Charles E. Young Drive South, Los Angeles, CA 90095, USA

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The taxonomic status, biogeographical distributions and existing collections are reviewed for all species of decapod crustaceans known from the vicinity of hydrothermal vents and cold (hydrocarbon or brine) seeps. To date, more than 125 species representing 33 families of decapods have been reported. Represented families are, in alphabetical order within infraorder, the penaeoid families Benthescymidae and Sergestidae; the caridean families Alvinocarididae (all of which are vent or seep endemics), Crangonidae, Glyphocrangonidae, Hippolytidae, Nematocarcinidae, Oplophoridae, Palaemonidae, Pandalidae and Styliodactylidae; the anomuran families Chirostylidae, Galatheidae, Lithodidae and Parapaguridae; the brachyuran crab families Atelecyclidae, Bythograeidae (all of which are vent endemics), Cancridae, Epialtidae, Geryonidae, Goneplacidae, Homolidae, Majidae, Ocypodidae, Oregoniidae, Parthenopidae, Pisidae, Portunidae and Varunidae; the lobster (astacidean) family Nephropidae; and the thalassinidean families Axiidae, Callianassidae and Calocarididae. Some species appear to be vagrants, here defined as opportunistic species occasionally found in the vicinity of vent sites but not restricted to them. Other species, notably members of the shrimp family Alvinocarididae and the crab family Bythograeidae, are clearly endemics, known only from vent or seep sites and presumably restricted to them. All endemic vent shrimps, most of which were originally treated as members of the family Bresiliidae, are now treated as members of the family Alvinocarididae. The family Mirocarididae proposed earlier is no longer recognized following a recent review of the characters that define the genus *Mirocaris* and the family Alvinocarididae. Currently recognized vent-associated species of shrimp belong to six genera: *Alvinocaris*, *Chorocaris*, *Mirocaris*, *Nautilocaris*, *Opaepele* and *Rimicaris*; the genus *Iorania* is no longer recognized. Several more genera and species are in various stages of description (manuscripts in press or in review). Of the endemic shrimp genera, only *Alvinocaris* has been reported from both hydrothermal vents and cold seeps. Vagrant shrimp species include members of the families Crangonidae (one species), Hippolytidae (several species in the genus *Lebbeus*), Nematocarcinidae (genus *Nematocarcinus*, often seen but rarely collected), Oplophoridae (five genera), Palaemonidae (one species) and Pandalidae (one species of *Chlorotocus* questionably included). Within the Anomura, vent-associated species of the family Galatheidae (squat lobsters), most belonging to the genera *Munida* and *Munidopsis*, are probably vagrants rather than endemics, although some species are known only from vent sites to date and may prove to be true endemics. The galatheid genus *Munidopsis* is the most speciose and widespread of all vent-associated taxa and has been reported from both hot vents and cold seeps, although this probably reflects only the fact that it is a widespread and speciose deep-sea genus. Other galatheid genera reported from vent sites are *Alainius*, *Phylladorhynchus* and *Shinkaia*. Also in the Anomura, three chirostylids in two genera (*Eumunida* and *Uroptychus*) are known, and the family Lithodidae is represented at several sites (by species in five genera). All of these anomurans are assumed by us to be vagrants rather than endemics, although some species are known only from one or two sites and may prove to be true endemics. The anomuran hermit crab family Parapaguridae is represented by a single species described recently from an active hydrothermal vent; however, the family (or at least a hermit crab assumed to belong to this family) is also known from other locations where it has not been collected. Among the Brachyura, endemic crab species are all members of the family Bythograeidae, which currently consists of five genera (with the number of recognized species in parentheses): *Bythograea* (6), *Cyanograea* (1), *Segonzacia* (1), *Austinograea* (4) and *Allograea* (1). Vagrant crab species in the Atelecyclidae, Cancridae, Epialtidae, Geryonidae, Goneplacidae, Homolidae, Majidae, Ocypodidae, Oregoniidae, Parthenopidae, Pisidae and Portunidae reported from or near vents or seeps are assumed to be vagrants. One genus of Varunidae (Grapsoidae), *Xenograpsus*, is restricted

*Corresponding author. E-mail: jmartin@nhm.org

to shallow-water volcanic systems off Japan and Taiwan and is apparently endemic to shallow thermal sites. The lobster family Nephropidae (known from the Mid-Atlantic Ridge) is represented by one recently described species of the genus *Thymopides*, the only other species of which is known from Antarctic waters. The thalassinoid ('mud shrimp') families Axiidae, Callianassidae and Calocarididae (all reported from the Gulf of Mexico) are represented by species as yet undescribed, with the exception of one recently described axiid from the Gulf and one vagrant callianassid species reported from a shallow volcanic system in the Aegean Sea. Unresolved taxonomic problems, some of which are presently under study by traditional morphological methods and/or comparative studies employing allozymes as well as mtDNA data, are mentioned, and limited genetic information as it relates to biogeography is included where known. A discussion of vent biogeography as it pertains to information on the Decapoda is included. Biogeographical trends include the apparent overall similarity of the Indian Ocean sites to those of the Mid-Atlantic with respect to decapods. Both Indian Ocean and Mid-Atlantic systems exhibit a relatively low endemic crab diversity (one species each, though in different genera) and a relatively high diversity and density of shrimp, including the alvinocarid shrimp genera *Mirocaris* and *Rimicaris*, which are found nowhere else. Collection trends include the unfortunate tendency for oceanographic researchers to store vent and seep specimens in university or personal laboratory freezers and other non-recognized repositories, making access to specimens, as well as accurate assessment of their systematic and biogeographical status, difficult. © 2005 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2005, **145**, 445–522.

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INTRODUCTION

Following the exciting discovery of a new family of crabs and dense aggregations of bresilioid shrimps at hydrothermal vents in the eastern Pacific Ocean (Williams, 1980; Williams & Chace, 1982), there has been a steady stream of publications dealing with the taxonomy, ecology, physiology and distribution of decapod crustaceans from these sites in the deep sea. Soon after the discovery of hydrothermal vents, cold seeps, areas where chemically modified fluids emanate from non-heated hydrocarbon reservoirs, were discovered and found to host decapods and other invertebrates (reviewed by Sibuet & Olu, 1998; Van Dover *et al.*, 2002; Levin, 2005). Although hydrothermal vents and cold (hydrocarbon or brine) seeps differ significantly in many ways, communities at both types of sites are essentially chemosynthetically based and have ecological similarities, including, in some cases, shared higher-level taxa (Paull *et al.*, 1984; Van Dover *et al.*, 2002; Turnipseed *et al.*, 2003; Turnipseed, Jenkins & Van Dover, 2004). Decapod crustaceans often figure prominently in these communities. Shrimps of the family Alvinocarididae in particular are now known from a substantial number of vents and seeps in the Atlantic, Pacific and Indian oceans, where they are at times clearly the dominant macrofaunal invertebrates, especially at vents along the Mid-Atlantic Ridge (MAR) (e.g. Van Dover *et al.*, 1988; Tunnicliffe, 1991; Segonzac, 1992; Gebruk, Pimenov & Savvichev, 1993; Gebruk *et al.*, 1997, 2000a, b; Van Dover, 1995; Copley *et al.*, 1997, 1999; Desbruyères & Segonzac, 1997; Fowler & Tunnicliffe, 1997; Murton *et al.*, 1999) and in the Indian Ocean (Van Dover *et al.*, 2001a;

Watabe & Hashimoto, 2002). Because decapods are prominent members of the fauna at nearly all vent and seep environments, they have been included in a large number of general reviews of vent and seep faunas and vent ecology (e.g. see Grassle, 1985 and Tunnicliffe, 1988, eastern Pacific; MacDonald *et al.*, 1989, Gulf of Mexico seeps; Van Dover, 1990, 1995, and Gebruk *et al.*, 1997, MAR; Sibuet & Olu, 1998, cold seep ecology; Van Dover *et al.*, 2001a, Indian Ocean; Kojima, 2002, north-west Pacific); general overviews were provided by Tunnicliffe (1991), Chevaldonné (1997), Van Dover *et al.* (2002) and more recently by Wolfe (2005). However, the overall diversity of decapods at these sites remains underestimated. In the broad and often-cited review of the biology and ecology of hydrothermal vents by Tunnicliffe (1991), only 19 species of decapods were reported. With the exception of the compilation of anomuran species reported from vent and seep habitats by Chevaldonné & Olu (1996), and the inclusion of several decapods in a faunal handbook (Chevaldonné, 1997; Desbruyères & Segonzac, 1997) and at least one website (the *Vent Invertebrates Collections Database*, Field Museum of Natural History, <http://www.fieldmuseum.org>), decapods have not been the subject of a review specifically targeting their taxonomy, biogeography, natural history and physical collections.

Although some decapods from vents and seeps are clearly endemic species, found only at and presumably restricted to such habitats, the majority of species reported from vents and seeps are not endemic. Among the non-endemic species are those we refer to herein as vagrants, defined by us as opportunistic species found in the vicinity of vents and seeps but not

restricted to these habitats. Thus, this definition is similar to the use of 'penetrating' by Desbruyères *et al.* (2000) to describe non-endemic species that occasionally penetrate into vent communities. Other species might be accidentals – species that are found elsewhere in the deep sea and that might have been encountered in these same regions independent of the fact that there are vents or seeps here, a definition that differs only slightly from our definition of vagrants. An additional and confusing factor is the difficulty in determining where the influence of a vent or seep begins and ends. Crustaceans and other organisms collected tens of metres from an active hot vent in the deep sea may well have been influenced by it or attracted to it, whereas the same distance from a cold seep could mean that there is virtually no connection between the species and the site. Sites vary markedly as to their depth, temperature, emanating gases and fluids, and other physical and biological parameters, and the extent to which these factors might attract decapods is unknown. For these reasons, our list is perhaps longer than it should be, in that we have endeavoured to include all records of decapods collected at or near both hot and cold sites. Thus, among the species listed here are undoubtedly some for which a direct relationship to chemosynthetic communities has not been established.

Some of the crustaceans reported from vent and seep habitats have posed interesting taxonomic problems, and this is especially true of the vent shrimp fauna. Most workers placed these species in the caridean family Bresiliidae, while acknowledging that the family was an artificial assemblage. However, shrimp species endemic to chemosynthetic environments are morphologically distinct from bresiliids that are not restricted to these habitats. Recognition of Christoffersen's (1986, 1990) family Alvinocarididae (further diagnosed in a footnote in Segonzac, de Saint Laurent & Casanova, 1993, and more recently revised by Komai & Segonzac, 2003) has been increasing in acceptance (e.g. see Martin & Davis, 2001). The family Alvinocarididae is now considered a valid monophyletic family. Some of the taxonomic papers on vent shrimp (including one of our own) were developed without knowledge of other ongoing work in the field, leading to confusion and in some instances to multiple names being applied to the same species and/or to juveniles of previously described species. Indeed, the need to clarify the names of the vent-associated shrimp species is one of the primary incentives for the present work. To date, there are more than 50 shrimp species reported from hydrothermal vents or cold seeps (Table 1).

Anomuran decapods from vents and seeps are relatively well known as a result of the excellent compilation of Chevaldonné & Olu (1996). That paper summarized distributional data on approximately 22

species in three families (Galatheididae, Chirostylidae and Lithodidae) and mentioned the possibility of parapagurid hermit crabs at two locations (seen but not collected). The presence of parapagurids at vents has since been confirmed (Lemaitre, 2004). Several additional anomuran species have been described or reported from vent sites since the Chevaldonné & Olu (1996) publication appeared, such that there are now approximately 34 species in 13 genera known collectively from vents and seeps (Table 1).

Brachyuran crabs have not been as taxonomically difficult as have the shrimp and anomurans, in part because of the larger number of specialists working on crab systematics and in part because species of the Bythograeidae, all of which are restricted to hydrothermal vents, tend to be rather large and in some cases quite distinctive. Still, recent discoveries of new taxa in the eastern Pacific have revealed greater diversity than was previously thought to exist. Among the endemic bythograeids we now recognize 13 species in five genera (Table 1). Presumed vagrant crab species in the families Atelecyclidae, Cancridae, Epialtidae, Geryonidae, Goneplacidae, Homolidae, Majidae, Ocypodidae, Oregoniidae, Parthenopidae, Pisidae and Portunidae have been reported from (or near) vent or seep sites, and one genus of the Varunidae (formerly a subfamily of the Grapsidae) is restricted to shallow, volcanic vent systems off Taiwan and Japan. Other groups of decapods, including nephropid lobsters and at least three families of thalassinoids, have been reported and/or described recently (e.g. Felder & Kensley, 2004, for axiids). Because of their burrowing habits, thalassinoids are likely to be greatly undersampled and underreported in collections and reports to date.

In an attempt to summarize and perhaps add some stability to the growing list of species of vent- and seep-associated decapods, we have assembled the following list of species and their known occurrences. Descriptions of decapods in progress (i.e. undescribed species and higher taxa under study) are listed where known. The number of known hydrothermal sites alone exceeds 30 (see Van Dover *et al.*, 2002; Tyler *et al.*, 2003: table 1, for recent summaries), and the number of expeditions to these sites continues to increase. For example, during the 10-year period from 1992 to 2002, more than 300 expeditions were mounted to mid-oceanic ridges and back-arc basins (see the InterRidge website at: <http://www.interridge.org>). Additionally, the literature on the physical properties of vents and seeps is enormous, and occasionally in this body of literature associated organisms, including decapods, are mentioned. It has not been possible for us to survey all of the literature in related fields (e.g. the literature related to oil fields, geochemical surveys, sedimentology, stratigraphy and

Table 1. Known ranges of decapods associated with vent and seep sites. See Table 2 for coordinates of sites listed below. Localities in parentheses were provided by T. Wolff (pers. comm.) but are localities for which we have not been able to locate the original reports of the species from that locality. References are listed chronologically

Taxon	Known vent/seep site(s)	Primary references
PENAEOIDEA		
Family Benthescymidae		
<i>Benthescymus investigatoris</i>	KB: Omaezaki Spur, cold seep	Wood-Mason, 1891 Ohta <i>et al.</i> , 1995
Family Sergestidae		
<i>Sergia cf. robusta</i>	KEJ	Dana, 1852 Martin <i>et al.</i> , 2005
CARIDEA		
Family Alvinocarididae		
<i>Alvinocaris brevitelsonis</i> ¹ (see <i>A. dissimilis</i> below)	OT: Minami-Ensei Knoll	Christoffersen, 1986 Kikuchi & Hashimoto, 2000
<i>Alvinocaris dissimilis</i>	OT: Minami-Ensei Knoll	Komai & Segonzac, 2005a
<i>Alvinocaris leurokolos</i> ² (see <i>Shinkaicaris leurokolos</i> below)	OT: Minami-Ensei Knoll	Kikuchi & Hashimoto, 2000
<i>Alvinocaris longirostris</i>	OT: Iheya Ridge, Hatoma Knoll, Minami-Ensei Knoll; SB: Off Hatsuchima site; NZ: Kermadec Ridge	Fujikura <i>et al.</i> , 1995, 1996; Kikuchi & Ohta, 1995; Watabe & Miyake, 2000 Webber, 2004
<i>Alvinocaris cf. longirostris</i>	[PNG: Bismarck Back-Arc]	T. Wolff, pers. comm.
<i>Alvinocaris lusca</i>	GR: Rose Garden; EPR: 9N-13N	Williams & Chace, 1982; Shank, 1997, in Desbruyères & Segonzac, 1997; Shank <i>et al.</i> , 1999
<i>Alvinocaris markensis</i>	MAR: Snake Pit, TAG, Lucky Strike, Rainbow, Broken Spur, Logatchev	Williams, 1988; Segonzac <i>et al.</i> , 1993; Gebruk <i>et al.</i> , 1997; Shank, 1997, in Desbruyères & Segonzac, 1997; Shank <i>et al.</i> , 1999; T. Komai, pers. comm.
<i>Alvinocaris muricola</i>	GM: West Florida Escarpment; Barbados; GG: Blake Ridge Diapir	Williams, 1988; Olu <i>et al.</i> , 1996b; Komai & Segonzac, 2003; Van Dover <i>et al.</i> 2003; Komai & Segonzac, 2005a
<i>Alvinocaris methanopila</i>	Blake Ridge Diapir	Van Dover <i>et al.</i> , 2003; Komai <i>et al.</i> , 2005
<i>Alvinocaris niwa</i>	NZ: Kermadec Ridge	Webber, 2004
<i>Alvinocaris stactophila</i> ³	GM: Bush Hill site off Louisiana, West Florida Escarpment	Williams, 1988; Carney, 1994; S. Hourdez, pers. comm.
<i>Alvinocaris williamsi</i>	MAR: Menez Gwen	Shank & Martin, 2003
<i>Alvinocaris</i> sp. A	[NZ: Kermadec Ridge]	T. Wolff, pers. comm.
<i>Alvinocaris</i> sp. B	[MAR: Logatchev]	T. Wolff, pers. comm.
<i>Alvinocaris</i> sp. C	PNG: Edison Seamount	Shank <i>et al.</i> , 1999; Shank & Martin, 2003
<i>Alvinocaris</i> sp. D	NFB, LB	Desbruyères <i>et al.</i> , 1994.
<i>Alvinocaris</i> sp. E	OT: Minami-Ensei Knoll	T. Komai, pers. comm.
<i>Alvinocaris</i> sp. F	[MAR: Menez-Gwen]	T. Wolff, pers. comm.
<i>Alvinocaris</i> sp. G	Manus Back-Arc Basin: DESMOS site	Hashimoto & Ohta, 1999
<i>Chorocaris chacei</i>	MAR: Lucky Strike, TAG, Snake Pit, Logatchev, [Menez-Gwen]	Williams & Rona, 1986; Segonzac <i>et al.</i> , 1993; Martin <i>et al.</i> , 1998b
<i>Chorocaris paulexa</i>	EPR: 17S	Martin & Shank, 2005
<i>Chorocaris vandoverae</i>	MBA: Alice Springs, Burke [LB, NFB]	Martin & Hessler, 1990
<i>Chorocaris</i> sp. A	RTJ (see under <i>Mirocaris</i> sp. A)	Van Dover <i>et al.</i> , 2001
<i>Chorocaris</i> sp. B	NZ: Kermadec Ridge	N. Bruce, R. Webber, pers. comm.
<i>Mirocaris fortunata</i>	MAR: Menez Gwen, Lucky Strike, Rainbow, Broken Spur, TAG, Snake Pit, Logatchev	Martin & Christiansen, 1995; Vereshchaka, 1997b (as <i>M. keldyshii</i>); Komai & Segonzac, 2003; Turnipseed <i>et al.</i> , 2004
<i>Mirocaris</i> sp. A	RTJ: Kairei and Edmond fields	Van Dover <i>et al.</i> , 2001 ⁴ ; Komai <i>et al.</i> , in press
<i>Nautilocaris saintlaurentae</i>	NFB: White Lady; LB: Vai-Lili	Komai & Segonzac, 2004

Table 1. Continued

Taxon	Known vent/seep site(s)	Primary references
<i>Opaepele loihi</i>	Loihi Seamount (Hawaii)	Williams & Dobbs, 1995
<i>Rimicaris exoculata</i>	MAR: Rainbow, TAG, Snake Pit, Broken Spur, Logatchev	Williams & Rona, 1986; Van Dover <i>et al.</i> , 1988; Segonzac <i>et al.</i> , 1993; Martin <i>et al.</i> , 1997
<i>Rimicaris kairei</i>	RTJ: Kairei Field	Watabe & Hashimoto, 2002
<i>Shinkaicaris leurokolos</i>	OT: Minami-Ensei Knoll	Komai & Segonzac, 2005a
Family Crangonidae		Haworth, 1825
<i>Paracrangon</i> sp. A	SB	Fujikura <i>et al.</i> , 1995
<i>Paracrangon</i> sp. B	OT: Minami-Ensei Knoll	Fujikura <i>et al.</i> , 1995, 1996
Family Glyphocrangonidae		Smith, 1884
<i>Glyphocrangon</i> cf. <i>granulosus</i> ⁵	OT: Hatoma Knoll	Watabe & Miyake, 2000
Family Hippolytidae		Dana, 1852
<i>Lebbeus bidentatus</i> (?)	EPR: southern EPR	Shank & Martin, unpubl. data
<i>Lebbeus</i> 'carinatus' ⁶	EPR: 13N	de Saint Laurent, 1984
<i>Lebbeus washingtonianus</i> ⁷	OT: Hatoma Knoll, Iheya Ridge, Minami-Ensei Knoll	Ohta, 1990a; Fujikura <i>et al.</i> , 1995, 1996; Kikuchi & Ohta, 1995; Hashimoto, 1997, in Desbruyères & Segonzac, 1997; Watabe & Miyake, 2000
<i>Lebbeus</i> sp. A	LB	Desbruyères <i>et al.</i> , 1994
<i>Lebbeus</i> sp. B.	SB: off Hatsushima site	Fujikura <i>et al.</i> , 1995, 1996
Family Nematocarcinidae		Smith, 1884
<i>Nematocarcinus burukovskiyi</i>	southern EPR: 17S, 23S, 31S	Komai & Segonzac, 2005b
<i>Nematocarcinus ovalis</i>	EPR: 13N	Komai & Segonzac, 2005b
<i>Nematocarcinus ensifer</i> ⁸	EPR: 9N, 13N	Shank <i>et al.</i> , 1999; M. Segonzac, pers. comm.
<i>Nematocarcinus productus</i>	KB: Omaezaki Spur, cold seep	Ohta <i>et al.</i> , 1995
Family Oplophoridae		Dana, 1852
<i>Acanthephyra eximia</i>	KB: Omaezaki Spur, cold seep	Ohta <i>et al.</i> , 1995
<i>Acanthephyra purpurea</i>	MAR: Lucky Strike	Biscoito, 1997, in Desbruyères & Segonzac, 1997
<i>Hymenodora glacialis</i>	Gakkel Ridge, Arctic Ocean	Martin, 2003
<i>Janicella spinicauda</i>	KEJ	Martin <i>et al.</i> , 2005
<i>Oplophorus gracilirostris</i>	KEJ	Martin <i>et al.</i> , 2005
<i>Systellaspis braueri</i>	EPR: 13N	de Saint Laurent, 1984; Tunnicliffe, 1991
Family Palaemonidae		Rafinesque, 1815
<i>Periclimenes hydrothermophilus</i>	Vent fields in Kagoshima Bay, Japan	Hayashi & Ohtomi, 2001
<i>Periclimenes</i> sp.	GM: Bush Hill and GC234 sites	Bergquist <i>et al.</i> , 2003
Family Pandalidae		Haworth, 1825
<i>Chlorotocus novaezealandiae</i> ⁹	NZ: Whale Island	Clark & O'Shea, 2001; R. Webber, pers. comm.
Family Styrodactylidae		Bate, 1888
<i>Styrodactylus</i> sp.	OT: Hatoma Knoll	Watabe & Miyake, 2000
ANOMURA		
Family Chirostylidae		Ortmann, 1892
<i>Eumunida picta</i>	GM: Louisiana seeps	Carney, 1994
<i>Eumunida</i> sp.	NZ: Kermadec Ridge	Clark & O'Shea, 2001
<i>Uroptychus bicavus</i>	NFB: 'White Lady' chimney	Baba & de Saint Laurent, 1992
<i>Uroptychus edisonicus</i>	PNG: Edison Seamount	Baba & Williams, 1998
<i>Uroptychus thermalis</i>	NFB: 'White Lady' chimney	Baba & de Saint Laurent, 1992
<i>Uroptychus</i> sp.	NFB, LB (possibly = one of above species)	Tunnicliffe <i>et al.</i> , 1998
Family Galatheididae		Samouelle, 1819
<i>Alainius</i> sp.	NZ: Kermadec Ridge	Clark & O'Shea, 2001
<i>Munidopsis alvisca</i>	GB; ER; JDF	Williams, 1988

Table 1. Continued

Taxon	Known vent/seep site(s)	Primary references
<i>Munidopsis beringana</i>	Middle America Trench (questionable; see text)	Chevaldonné & Olu, 1996
<i>Munidopsis crassa</i>	MAR: Snake Pit; Peru Margin: cold seeps [LB plus seep]	Segonzac, 1992; Olu <i>et al.</i> , 1996a
<i>Munidopsis diomedea</i>	GB	Khodkina, 1991
<i>Munidopsis lauensis</i>	LB: Valu-Fa Ridge; NFB: 'White Lady' chimney; MBA: PACMANUS, DESMOS	Baba & de Saint Laurent, 1992; Hashimoto & Ohta, 1999
<i>Munidopsis lentigo</i>	EPR: 21N	Williams & Van Dover, 1983
<i>Munidopsis lignaria</i>	EPR: 11°52'N	Williams & Baba, 1989
<i>Munida magniantennulata</i>	LB: Valu-Fa Ridge	Baba & de Saint Laurent, 1992; Baba & Türkyay, 1992
<i>Munidopsis marianica</i>	MBA: Burke, Ilium	Williams & Baba, 1989
<i>Munida microphthalma</i>	BAP	Chevaldonné & Olu, 1996
<i>Munidopsis rostrata</i>	OT: Hatoma Knoll	Watabe & Miyake, 2000
<i>Munidopsis sonne</i>	NFB	Baba, 1995
<i>Munidopsis starmer</i>	NFB: 'White Lady' chimney	Baba & de Saint Laurent, 1992
<i>Munidopsis subsquamosa</i>	gr; EPR: 9N, 13N, 21N	Chevaldonné & Olu, 1996
<i>Munidopsis</i> sp.	MAR: Lucky Strike, TAG, Broken Spur; OT: Hatoma Knoll, Iheya Ridge; NZ: Kermadec Ridge; PAR: Foundation Seamount Chain	Ohta, 1990a; Fujikura <i>et al.</i> , 1995; Chevaldonné & Olu, 1996; Clark & O'Shea, 2001; Stecher <i>et al.</i> , 2002; Watabe & Miyake, 2000
<i>Phylladorhynchus pusillus</i>	NZ: Kermadec Ridge	Clark & O'Shea, 2001
<i>Shinkaiia crosnieri</i>	OT: Iheya Ridge, Hatoma Knoll; PNG: Edison Seamount; PAR: Foundation Seamount Chain (? , see text)	Baba & Williams, 1998; Tsuchida <i>et al.</i> , 2000; Watabe & Miyake, 2000; Stecher <i>et al.</i> , 2002
'Galatheans'	BT: Mount Manon and area	Olu <i>et al.</i> , 1997
Family Lithodidae		
<i>Lithodes manningi</i>	BAP	Samouelle, 1819 Macpherson, 1988
<i>Lopholithodes foraminatus</i>	OSZ: extinct vent sites only	Carey, 1987; Chevaldonné & Olu, 1996
<i>Neolithodes diomedea</i>	GB	Grassle, 1986; E. Escobar-Briones, pers. comm.
<i>Paralithodes</i> sp.	Bering Sea, Piip Volcano	Sagalevich <i>et al.</i> , 1992
<i>Paralomis arethusa</i>	BAP	Macpherson, 1994a
<i>Paralomis cubensis</i>	GM: Green Canyon seeps	Chevaldonné & Olu, 1996; Carney, 1994
<i>Paralomis hirtella</i>	LB: Valu-Fa Ridge; NFB: 'White Lady' chimney	de Saint Laurent & Macpherson, 1997
<i>Paralomis jamsteci</i>	OT: Minami-Ensei Knoll	Takeda & Hashimoto, 1990; Fujikura <i>et al.</i> , 1995, 1996
<i>Paralomis multispina</i>	SB: cold seeps	Hart, 1982; Horikoshi & Ishii, 1985; Ohta, 1990b
<i>Paralomis verrilli</i>	OT: Hatoma Knoll, Iheya Ridge	Kim & Ohta, 1991; Hashimoto <i>et al.</i> , 1995; Chevaldonné & Olu, 1996; Watabe & Miyake, 2000
<i>Paralomis</i> sp.	NZ: Kermadec Ridge; OT: Minami-Ensei Knoll; PAR: Foundation Seamount Chain	Fujikura <i>et al.</i> , 1995, 1996; Clark & O'Shea, 2001; Stecher <i>et al.</i> , 2002
Family Parapaguridae		
<i>Paragiopagurus ventillatus</i>	Tashi fishing grounds, Taiwan	Smith, 1882 Lemaitre, 2004
<i>Parapagurus</i> sp.	BAP	Chevaldonné & Olu, 1996, citing K. A. Olu, pers. observ.
Species not determined	CA: Monterey Canyon	Chevaldonné & Olu, 1996, citing J. Barry, pers. comm.

Table 1. Continued

Taxon	Known vent/seep site(s)	Primary references
BRACHYURA		
Family Atelecyclidae (species not reported)	GM: Bush Hill, off Louisiana	Ortmann, 1893 Bergquist <i>et al.</i> , 2003
Family Bythograeidae <i>Allograea tomentosa</i>	EPR: 31S	Williams, 1980 Guinot <i>et al.</i> , 2002; Guinot & Hurtado, 2003
<i>Austinograea alayseae</i>	LB: Valu-Fa Ridge (Vai-Lili); Manus Back-Arc Basin, PACMANUS	Guinot, 1990; Guinot, 1997, in Desbruyeres & Segonzac, 1997
<i>Austinograea rodriguezensis</i>	RTJ	Tsuchida & Fujikura, 2000; Tsuchida & Hashimoto, 2002
<i>Austinograea williamsi</i>	MBA: Alice Springs, Burke, Ilium, 13N (not 13N EPR)	Hessler & Martin, 1989; Tsuchida & Fujikura, 2000; Tsuchida & Hashimoto, 2002
<i>Austinograea yunohana</i>	EPSP: Myojin Knoll, Kaikata, Nikko and Suiyo seamounts	Takeda <i>et al.</i> , 2000; Tsuchida & Hashimoto, 2002
<i>Bythograea galapagensis</i>	GR: Rose Garden	Guinot & Hurtado, 2003
<i>Bythograea intermedia</i>	GR: Rose Garden	de Saint Laurent, 1988
<i>Bythograea laubieri</i>	EPR: 18S, 17S (Rehu and Stockwork sites)	Guinot & Segonzac, 1997; Guinot & Hurtado, 2003
<i>Bythograea microps</i>	EPR: 9N, 13N, 21N	de Saint Laurent, 1984
<i>Bythograea thermydron</i>	EPR: 18S to 21N; GR: Mussel Bed, Rose Garden	Williams, 1980; Guinot, 1988; Guinot & Segonzac, 1997; Guinot & Hurtado, 2003
<i>Bythograea vrijenhoeki</i>	EPR: 31S	Guinot & Hurtado, 2003
<i>Bythograea sp.</i>	NZ: Kermadec Ridge; PAR: Foundation Seamount Chain (?)	Clark & O'Shea, 2001; Stecher <i>et al.</i> , 2002
<i>Cyanagraea praedator</i>	EPR: 9N, 13N; possibly 18S; questionably 31S (see text)	de Saint Laurent, 1984; Guinot & Segonzac, 1997
<i>Cyanagraea sp.</i>	Southern EPR (17–19)	Guinot & Segonzac, 1997
<i>Segonzacia mesatlantica</i>	MAR: Menez Gwen, Lucky Strike, Snake Pit, Logatchev	Williams, 1988; Guinot, 1989; Gebruk <i>et al.</i> , 2000a
Family Cancridae <i>Cancer pagurus</i>	Denmark: off Kattegat	Latreille, 1802 Jensen <i>et al.</i> , 1992; Levin <i>et al.</i> , 2000
Family Geryonidae <i>Chaceon affinis</i>	MAR: Menez-Gwen	Colosi, 1923 Biscoito, 1997, in Desbruyeres & Segonzac, 1997; Biscoito & Saldanha, 2000
<i>Chaceon fenneri</i>	GM: off Louisiana	Carney, 1994
<i>Chaceon quinquedens</i>	GM: off Louisiana	Carney, 1994
<i>Geryon sp.</i>	GM: Bush Hill, off Louisiana	MacDonald <i>et al.</i> , 1989; MacAvoy <i>et al.</i> , 2002
Family Goneplacidae <i>Bathyplox typhla</i>	GM: Bush Hill, off Louisiana	MacLeay, 1838 MacDonald <i>et al.</i> , 1989
<i>Carcinoplax sp.</i>	NZ: Kermadec Ridge	Clark & O'Shea, 2001
<i>Pilumnoplax sp.</i>	NZ: Kermadec Ridge	Clark & O'Shea, 2001
Family Homolidae <i>Paromola cuvieri</i>	MAR: Menez-Gwen	de Haan, 1839 Biscoito, 1997, in Desbruyeres & Segonzac, 1997
Family Majidae <i>Dorhynchus thomsoni</i>	NZ: Kermadec Ridge	Samouelle, 1819 Clark & O'Shea, 2001
<i>Platymaia sp.</i>	NZ: Kermadec Ridge	Clark & O'Shea, 2001
Family Epialtidae <i>Sphenocarcinus sp.</i>	NZ: Kermadec Ridge	MacLeay, 1838 Clark & O'Shea, 2001
Family Parthenopidae <i>Tutankhamen sp.</i>	NZ: Kermadec Ridge	MacLeay, 1838 Clark & O'Shea, 2001

Table 1. Continued

Taxon	Known vent/seep site(s)	Primary references
Family Ocypodidae		
<i>Macrophthalmus hirtipes</i>	NZ: Whale Island	Rafinesque, 1815 Kamenev <i>et al.</i> , 1993; R. Webber, pers. comm.
Family Oregoniidae		
<i>Chionoecetes bairdi</i>	CA: Monterey Canyon	Garth, 1958 Barry <i>et al.</i> , 1996
<i>Hyas</i> sp.	JMR	Fricke <i>et al.</i> , 1989
<i>Macroregonia macrochira</i>	JDF	Tunncliffe <i>et al.</i> , 1985; Tunncliffe & Jensen, 1987; Tunncliffe, 1988; J. Voight, pers. comm.; our pers. observ.
Family Pisidae		
<i>Chorilia longipes</i>	CA: Monterey Canyon	Dana, 1851 Barry <i>et al.</i> , 1996
<i>Nibilia antilocarpa</i>	GM: off Louisiana	Carney, 1994
<i>Rochinia crassa</i>	GM: Bush Hill, off Louisiana	MacDonald <i>et al.</i> , 1989; Carney, 1994
Family Portunidae		
<i>Bathynectes maravigna</i>	MAR: Menez-Gwen	Rafinesque, 1815 Biscoito, 1997, in Desbruyeres & Segonzac, 1997
<i>Ovalipes ?molleri</i>	NZ: Kermadec Ridge	Clark & O'Shea, 2001
Family Varunidae ¹⁰		
<i>Xenograpsus noveainsularis</i>	Japan and Marianas, shallow volcanic arc region	Milne Edwards, 1853 Takeda & Kurata, 1977
<i>Xenograpsus testudinatus</i>	Taiwan, shallow volcanic arc	Ng <i>et al.</i> , 2000
ASTACIDEA		
Family Nephropidae		
<i>Acanthacaris cf. tenuimana</i>	OT: Hatoma Knoll	Dana, 1852 Watabe & Miyake, 2000
<i>Homarus gammarus</i>	Denmark: off Kattegat	Jensen <i>et al.</i> , 1992; Levin <i>et al.</i> , 2000
<i>Thymopides laurentae</i>	MAR: Snake Pit	Segonzac 1992; Segonzac & Macpherson, 2003
THALASSINIDEA		
Family Axiidae		
<i>Calaxius carneyi</i>	GM: Bush Hill, off Louisiana	Huxley, 1879 Felder & Kensley, 2004
Family Callianassidae		
<i>Callianassa truncata</i>	Aegean Sea: Milos	Dando <i>et al.</i> , 1995
Families Axiidae, Callianassidae, and Calocarididae	GM: various cold or methane seeps	D. Felder, pers. comm. (see text)

Abbreviations: BAP, Barbados Accretionary Prism; BT, Barbados Trench; CA, off California, United States; EPSP, eastern edge of Philippine Sea Plate; EPR, East Pacific Rise; ER, Explorer Ridge; GB, Guaymas Basin; GG, Gulf of Guinea; GM, Gulf of Mexico; GR, Galapagos Rift; HK, Hatoma Knoll, Japan; JDF, Juan de Fuca Ridge; JMR, Jan Mayen Ridge, Norwegian Sea; KB, Kanesu-no-se Bank, Enshu-nada, Japan; KEJ, Kick'em Jenny Volcano, Caribbean; LB, Lau Basin; MAR, Mid-Atlantic Ridge; MBA, Mariana Back-Arc Basin; NFB, North Fiji Basin; NZ, off New Zealand; OSZ, Oregon Subduction Zone; OT, Okinawa Trough; PAR, Pacific-Antarctic Ridge, Foundation Seamount Chain; PNG, Papua New Guinea, Edison Seamount of Bismarck Archipelago; RTJ, Rodriguez Triple Junction; SB, Sagami Bay.

¹Presumably, only the holotype in the type series is the true *A. brevitelsonis*. The paratype and non-type specimens belong to three other species, one of was recently described as *A. dissimilis* by Komai & Segonzac (2005a).

²This species was transferred from *Alvinocaris* to *Shinkaicaris* by Komai & Segonzac (2005a).

³The type series might include two species, as the status of the allotype is unclear (T. Komai, pers. comm.).

⁴Treated by Van Dover *et al.* (2001) as *Chorocaris* sp. (see text).

⁵Fujikura *et al.* (1995) reported *Glyphocrangon* from Sagami Bay, but the observation was made at a 'non-chemosynthetic' site.

⁶Species name previously occupied; this species will have to be renamed (see text).

⁷Reported also from the Guaymas Basin (Butler, 1980); see text.

⁸Questionable identification to species level; see text.

⁹Questionably included as a vent associate; see text.

¹⁰Although currently placed in the Varunidae by most workers, larval morphology and other evidence indicates that the genus *Xenograpsus* is probably deserving of separate familial status (P. Ng, pers. comm.).

Table 2. Hydrothermal vent and cold seep decapods grouped by locality. See Kojima (2002) for more detailed coordinates and descriptions of north-western Pacific sites, Tunnicliffe (1991) and Van Dover (2000) for physical descriptions of individual hydrothermal vent sites, and Sibuet & Olu (1998) for cold seep sites. Localities in square brackets were provided by T. Wolff (pers. comm.) but are localities for which we have not been able to locate the original reports of the species from that locality

Vent or seep site	Decapod taxa recorded	Primary references
ARCTIC OCEAN		
Gakkel Ridge 85°15'N, 12°20'E to 83°55'N, 01°17'W	<i>Hymenodora glacialis</i>	Martin, 2003
Jan-Mayen Ridge	<i>Hyas</i> sp.	Fricke <i>et al.</i> , 1989
NORTH ATLANTIC		
Menez Gwen 37°50'N, 31°31'W	<i>Alvinocaris williamsi</i> , <i>Alvinocaris</i> sp. G, <i>Bathynectes maravigna</i> , <i>Chaceon affinis</i> , [<i>Chorocaris chacei</i>], <i>Mirocaris fortunata</i> , <i>Paromola cuvieri</i> (off site), <i>Segonzacia</i> <i>mesatlantica</i>	Williams, 1988; Guinot, 1990; Biscoito, 1997, in Desbruyères & Segonzac, 1997; Komai & Segonzac, 2003; Shank & Martin, 2003
Lucky Strike 37°17'N, 32°16'W	<i>Acanthephyra purpurea</i> , <i>Alvinocaris</i> <i>markensis</i> , <i>Chorocaris chacei</i> , <i>Mirocaris</i> <i>fortunata</i> , <i>Munidopsis</i> sp., <i>Segonzacia</i> <i>mesatlantica</i>	Williams, 1988; Guinot, 1990; Martin & Christiansen, 1995; Chevaldonné & Olu, 1996; Biscoito, 1997, in Desbruyères & Segonzac, 1997; Shank, 1997, in Desbruyères & Segonzac, 1997; Martin <i>et al.</i> , 1998b; Komai & Segonzac, 2003
Rainbow 36°13'N, 33°54'W	<i>Alvinocaris markensis</i> , <i>Mirocaris fortunata</i> , <i>Rimicaris exoculata</i>	Shank, 1997, in Desbruyères & Segonzac, 1997; Komai & Segonzac, 2003
Broken Spur 29°10'N, 43°10'W	<i>Alvinocaris markensis</i> (video only), <i>Mirocaris fortunata</i> , <i>Munidopsis</i> sp., <i>Rimicaris exoculata</i>	Martin & Christiansen, 1995; Chevaldonné & Olu, 1996; Shank, 1997, in Desbruyères & Segonzac, 1997
TAG 26°09'N, 44°50'W	<i>Alvinocaris markensis</i> , <i>Chorocaris chacei</i> , <i>Mirocaris fortunata</i> , <i>Munidopsis</i> sp., <i>Rimicaris exoculata</i>	Williams & Rona, 1986; Chevaldonné & Olu, 1996; Vereshchaka, 1996a, 1997b
Snake Pit (MARK) 23°22'N, 44°57'W	<i>Alvinocaris markensis</i> , <i>Chorocaris chacei</i> , <i>Munidopsis crassa</i> , <i>Mirocaris fortunata</i> , <i>Rimicaris exoculata</i> , <i>Segonzacia</i> <i>mesatlantica</i> , <i>Thymopides laurentae</i>	Guinot, 1989; Segonzac, 1992; Segonzac <i>et al.</i> , 1993; Martin <i>et al.</i> , 1997; Shank, 1997, in Desbruyères & Segonzac, 1997; Komai & Segonzac, 2003; Segonzac & Macpherson, 2003
Logatchev (14–45) 14°45'N, 44°58'W	<i>Alvinocaris markensis</i> , [Alvinocaris sp. B], [<i>Chorocaris chacei</i>], <i>Mirocaris fortunata</i> , <i>Rimicaris exoculata</i>	Komai & Segonzac, 2003
Blake Ridge Diapir 32°30'N, 76°11'W	<i>Alvinocaris muricola</i> , <i>Alvinocaris</i> cf. <i>muricola</i>	Van Dover <i>et al.</i> , 2003; Komai & Segonzac, 2005a
Kick'em Jenny Volcano, eastern Caribbean 12.3°N, 61.6°W	<i>Janicella spinicauda</i> ; <i>Oplophorus</i> <i>gracilrostris</i> ; <i>Sergia</i> cf. <i>robusta</i>	Martin <i>et al.</i> , 2005; Wishner <i>et al.</i> , 2005
Barbados Accretionary Prism ~14–16°N, 58–59°W	<i>Lithodes manningi</i> , <i>Munida</i> <i>microphthalma</i> , <i>Paralomis arethusa</i> , Parapaguridae (?)	Macpherson, 1988, 1994a; Chevaldonné & Olu, 1996
Barbados Trench 13°49'N, 57°38'W to 13°51'N, 57°45'W	'Galatheans,' 'rarely observed shrimps'	Olu <i>et al.</i> , 1997
South Barbados 10°20'N, 58°53'W	<i>Alvinocaris muricola</i>	T. Komai, pers. comm.
Gulf of Guinea Régab site ~05°47–48'S, 09°41–43'E	<i>Alvinocaris muricola</i>	T. Komai, pers. comm.; Komai & Segonzac, 2005a

Table 2. Continued

Vent or seep site	Decapod taxa recorded	Primary references
GULF OF MEXICO		
West Florida Escarpment 26°01'N, 84°54'W	<i>Alvinocaris muricola</i>	Williams, 1988
Green Canyon, Bush Hill site and other seeps off Louisiana Bush Hill ~27°47'N, 91°30'W	<i>Alvinocaris stactophila</i> , <i>Bathyplox typhla</i> , <i>Eumunida picta</i> , <i>Munidopsis</i> sp., <i>Chaceon fenneri</i> , <i>C. quinquegens</i> , <i>Geryon</i> sp., <i>Periclimenes</i> sp., atelecyclid crab (undetermined), <i>Rochinia crassa</i> , <i>Nibilia antilocarpa</i> , <i>Calaxius carneyi</i>	Williams, 1988; MacDonald <i>et al.</i> , 1989; Carney, 1994; Bergquist <i>et al.</i> , 2003; Felder & Kensley, 2004
Green Canyon ~27 to 28 N, ~91 to 92 W		
Green Canyon (site not specified; possibly including Bush Hill above)	<i>Paralomis cubensis</i> , Atelecyclidae	Carney, 1994; Chevaldonné & Olu, 1996; Bergquist <i>et al.</i> , 2003
Campeche Knolls ~21°54'N, 93°26'W	<i>Munidopsis</i> sp., 'shrimp resembling <i>Alvinocaris</i> sp.'	MacDonald <i>et al.</i> , 2004
INDIAN OCEAN		
Rodriguez Triple Junction, Edmond and Kairei Fields ~25°19'S, 70°02'E	<i>Austinograea rodriguezensis</i> , <i>Rimicaris kairei</i> , <i>Mirocaris</i> sp. A	Van Dover <i>et al.</i> , 2001; Tsuchida & Hashimoto, 2002; Watabe & Hashimoto, 2002; Komai <i>et al.</i> , in press
INDO-WEST PACIFIC		
New Zealand, Kermadec Ridge 37–35°S	<i>Alvinocaris longirostris</i> , <i>A. niwa</i> , <i>Alvinocaris</i> sp. A, <i>Chorocaris</i> sp. B; <i>Alainius</i> sp., <i>Eumunida</i> sp., <i>Munida</i> sp., <i>Munidopsis</i> sp., <i>Paralomis</i> sp., <i>Phylladiorhynchus pusillus</i> , <i>Carcinoplax</i> sp., <i>Pilumnoplax</i> sp., <i>Bythograea</i> sp., Majidae (unspecified), <i>Sphenocarcinus</i> sp., <i>Dorhynchus thomsoni</i> , <i>Platymaia</i> sp.(?), <i>Tutankhamen</i> sp., <i>Ovalipes ?molleri</i> ,	Clark & O'Shea, 2001; Webber, 2004; R. Webber, pers. comm.
New Zealand, Whale Island 37.52°S, 177.18°E	<i>Chlorotocus novaezealandiae</i> , <i>Macrophthalmus hirtipes</i>	Webber, 2004; R. Webber, pers. comm.
Lau Basin, Valu-Fa Ridge, Vai-Lili site 22°13'S, 176°38'E	<i>Alvinocaris</i> sp. D, <i>Nautilocaris saintlaurentae</i> , <i>Chorocaris vandoverae</i> , <i>Austinograea alayseae</i> , <i>Lebbeus</i> sp., <i>Munida magniantennulata</i> , <i>Munidopsis lauensis</i> , <i>Paralomis hirtella</i> , <i>Uroptychus</i> sp. nov.	Guinot, 1990; Baba & Türkay, 1992; Baba & de Saint Laurent, 1992; Desbruyères <i>et al.</i> , 1994; de Saint Laurent & Macpherson, 1997; Tunnicliffe <i>et al.</i> , 1998; Shank & Martin, 2003; Komai & Segonzac, 2004
North Fiji Basin ~16°50'–18°S, 173°50'–55°E	<i>Alvinocaris</i> sp. D, <i>Nautilocaris saintlaurentae</i> , <i>Chorocaris vandoverae</i> , <i>Austinograea alayseae</i> , <i>Munidopsis lauensis</i> , <i>Munidopsis sonne</i> , <i>Munidopsis starmar</i> , <i>Paralomis hirtella</i> , <i>Uroptychus bicavus</i> , <i>Uroptychus thermalis</i>	Guinot, 1990; Baba & de Saint Laurent, 1992; Desbruyères <i>et al.</i> , 1994; Baba, 1995; de Saint Laurent & Macpherson, 1997; Shank <i>et al.</i> , 1999; Komai & Segonzac, 2004
Papua New Guinea, Edison Seamount 03°19'S, 152°34'E	<i>Alvinocaris</i> sp. C, <i>Shinkaia crosnieri</i> , <i>Uroptychus edisonicus</i>	Baba & Williams, 1998; Shank & Martin, 2003
Papua New Guinea, Rabaul Caldera 4°14'S, 152°12'E	<i>Hippa</i> sp., <i>Macrophthalmus</i> sp., <i>Actaea</i> sp., <i>Pilumnus</i> sp., <i>Dardanus</i> sp., <i>Pagurus</i> sp.	Tarasov <i>et al.</i> , 1999
Manus Back-Arc Basin, PACMANUS ~03°44'–64'S, 151°40'–55'E	<i>Austinograea alayseae</i> , <i>Munidopsis lauensis</i>	Guinot, 1990; Hashimoto & Ohta, 1999

Table 2. Continued

Vent or seep site	Decapod taxa recorded	Primary references
Manus Back-Arc Basin, DESMOS ~03°40–42'S, 151°52'E	<i>Alvinocaris</i> sp., <i>Nematocarcinus</i> sp., <i>Munidopsis lauensis</i> , <i>Munidopsis</i> sp.	Hashimoto & Ohta, 1999
Mariana Back-Arc 18°11'N, 144°43'E	<i>Austinograea williamsi</i> , <i>Chorocaris</i> <i>vandoverae</i> , <i>Munidopsis marianica</i>	Hessler & Martin, 1989; Williams & Baba, 1989; Martin & Hessler, 1990; Tsuchida & Hashimoto, 2002
Taiwan, off I-Lan County (incl. Tashi Fishing Grounds)	<i>Xenograpsus testudinatus</i> , <i>Paragiopagurus</i> <i>ventilatus</i>	Ng <i>et al.</i> , 2000; Lemaitre, 2004
Japan, 27°14.6 N, 140°52.6'E, and Mariannas, shallow volcanic arc region	<i>Xenograpsus noveainsularis</i>	Takeda & Kurata, 1977; Türkay & Sakai, 1995
Okinawa Trough, Iheya Ridge 27°32'N, 126°58'E	<i>Alvinocaris longirostris</i> , <i>Lebbeus</i> <i>washingtonianus</i> , <i>Munidopsis</i> sp., <i>Paralomis verrilli</i> , <i>Shinkaia crosnieri</i>	Ohta, 1990a; Kim & Ohta, 1991; Hashimoto <i>et al.</i> , 1995; Kikuchi & Ohta, 1995; Chevaldonné & Olu, 1996; Baba & Williams, 1998
Okinawa Trough, Minami-Ensei Knoll 28°23'N, 127°38'E	<i>Alvinocaris brevitelsonis</i> , <i>A. dissimilis</i> , <i>A. longirostris</i> , <i>Alvinocaris</i> sp. E, <i>Shinkaicarisleurokolos</i> , <i>Munidopsis</i> sp., <i>Paracrangon</i> sp., <i>Paralomis jamsteci</i>	Ohta, 1990a; Takeda & Hashimoto, 1990; Fujikura <i>et al.</i> , 1995, 1996; Kikuchi & Hashimoto, 2000; T. Komai, pers. comm., Komai & Segonzac, 2005a
Okinawa Trough, Hatoma Knoll 24°51'N, 123°50'E	<i>Paralomis verrilli</i> , <i>Munidopsis rostrata</i> , <i>Munidopsis</i> sp., <i>Shinkaia crosnieri</i> , <i>Acanthacaris cf. tenuimana</i> , <i>Alvinocaris</i> <i>longirostris</i> , <i>Bresiliidae</i> gen. sp., <i>Stylodactylus</i> sp., <i>Glyphocrangon</i> cf. <i>granulosis</i> , <i>Lebbeus washingtonianus</i>	Tsuchida <i>et al.</i> , 2000; Watabe & Miyake, 2000
Philippine Sea Plate, Nikko Seamount 23°04.7'N, 142°19.9'E	<i>Austinograea yunohana</i>	Takeda <i>et al.</i> , 2000
Philippine Sea Plate, Kaikata Seamount 26°42.6'N, 141°04.6'E	<i>Austinograea yunohana</i>	Takeda <i>et al.</i> , 2000; Tsuchida & Hashimoto, 2002
Philippine Sea Plate, Suiyo Seamount 28°34.5'N, 140°38.5'E	<i>Austinograea yunohana</i>	Takeda <i>et al.</i> , 2000
Philippine Sea Plate, Myojin Knoll 32°06.19'N, 139°52.04'E	<i>Austinograea yunohana</i>	Takeda <i>et al.</i> , 2000
Kanesu-no-se Bank 34°15'N, 138°02'E	<i>Acanthephyra eximia</i> , <i>Benthesicymus</i> <i>investigatoris</i> , <i>Nematocarcinus</i> <i>productus</i>	Ohta <i>et al.</i> , 1995
Sagami Bay, including off Hatsushima site 35°00'N, 139°14'E	<i>Alvinocaris longirostris</i> , <i>Lebbeus</i> sp., <i>Paralomis multispina</i>	Hart, 1982; Horikoshi & Ishii, 1985; Ohta 1990b; Fujikura <i>et al.</i> , 1995, 1996
EAST PACIFIC		
PAR: Foundation Seamount Chain 37°30'S, 110°30'W	Bythograeid crabs (undetermined), <i>Munidopsis</i> sp., <i>Paralomis</i> sp., Shinkaiinae (galatheid crabs)	Stecher <i>et al.</i> , 2002
EPR 31S 31°09–51'S, 111°56'W	<i>Allograea tomentosa</i> , <i>Bythograea laubieri</i> , <i>B. vrijenhoeki</i> , <i>Cyanograea praedator</i> (questionable; see text), <i>Nematocarcinus</i> <i>burukovskyi</i>	Guinot <i>et al.</i> , 2002; Guinot & Hurtado, 2003; Komai & Segonzac, 2005b

Table 2. Continued

Vent or seep site	Decapod taxa recorded	Primary references
EPR 18S 18°25–36'N, 113°23'W	<i>Bythograea laubieri</i> , <i>B. thermydron</i>	Guinot & Segonzac, 1997; Guinot & Hurtado, 2003
EPR 17S 17°24'–17°37'S, 113°12'–113°15'W	<i>Bythograea laubieri</i> , <i>Chorocaris paulexa</i> , <i>Lebbeus bidentatus</i> (?), <i>Nematocarcinus</i> <i>burukovskyi</i>	Guinot & Segonzac, 1997; Martin & Shank, 2005; Shank & Martin, unpubl. data; Komai & Segonzac, 2005b
Peru Margin 05–06°S, –81–82°W	<i>Munidopsis crassa</i>	Olu <i>et al.</i> , 1996a
Galapagos Rift 0°48'N, 86°09–13'W	<i>Alvinocaris lusca</i> , <i>Bythograea</i> <i>galapagensis</i> , <i>B. intermedia</i> (doubtful), <i>B. thermydron</i> , <i>Munidopsis subsquamosa</i>	Williams, 1980; Williams & Chace, 1982; de Saint Laurent, 1988; Guinot & Hurtado, 2003
Middle America Trench EPR 9N 09°50'N, 104°17'W	<i>Munidopsis beringana</i> <i>Alvinocaris lusca</i> , <i>Nemataocarcinus ensifer</i> (questionable), <i>Bythograea microps</i> , <i>B. thermydron</i> , <i>Cyanagraea praedator</i> , <i>Munidopsis subsquamosa</i>	Chevaldonné & Olu, 1996 Guinot & Segonzac, 1997; Shank <i>et al.</i> , 1999
EPR 11°52'N	<i>Munidopsis lignaria</i>	Williams & Baba, 1989
EPR 13N 12°48'N, 103°56'W	<i>Alvinocaris lusca</i> , <i>Bythograea microps</i> , <i>B. thermydron</i> , <i>Cyanagraea praedator</i> , <i>Lebbeus carinatus</i> , <i>Munidopsis lignaria</i> (off site), <i>M. subsquamosa</i> , <i>Nematocarcinus ensifer</i> (tentatively), <i>Nematocarcinus ovalis</i> , <i>Systellaspis</i> <i>braueri</i>	de Saint Laurent, 1984; Guinot, 1988; Williams & Baba, 1989; Guinot & Segonzac, 1997; M. Segonzac, pers. comm.; Shank <i>et al.</i> , 1999; Komai & Segonzac, 2005b
EPR 21N 20°49'N, 109°06'W	<i>Bythograea thermydron</i> , <i>B. microps</i> , <i>Munidopsis lentigo</i> , <i>M. subsquamosa</i>	Williams & Van Dover, 1983 Grassle, 1986; Williams, 1988; Khodkina, 1991
Guaymas Basin 27°00'N, 111°25'W	<i>Munidopsis alvisca</i> , <i>M. diomedea</i> , <i>Neolithodes diomedea</i>	
Loihi Seamount 18°55'N, 155°16'W	<i>Opaepele loihi</i>	Williams & Dobbs, 1995
Juan de Fuca Ridge (Endeavor and Axial) 45°55'N, 130°03'W to 47°57'N, 129°06'W	<i>Macroregonia macrochira</i> , <i>Munidopsis</i> <i>alvisca</i>	Tunnicliffe <i>et al.</i> , 1985; Tunnicliffe & Jensen, 1987; Williams, 1988; Martin & Pettit, 1998; J. Voight, pers. comm.
Explorer Ridge 49°45'N, 130°16'W	<i>Munidopsis alvisca</i>	Tunnicliffe, 1988; Williams, 1988
Gorda Ridge 40°20'N to 43°00'N	<i>Munidopsis</i> sp., <i>Macroregonia macrochira</i>	J. Voight, pers. comm.
Oregon Subduction Zone*	<i>Lopholithodes foraminatus</i>	Carey, 1987; Chevaldonné & Olu, 1996
Bering Sea, Piip Volcano 55°25'N, 167°16'E	<i>Paralithodes</i> sp.	Sagalevich <i>et al.</i> , 1992
MEDITERRANEAN		
Aegean Sea, Milos 36°40'N, 24°32'W	<i>Callianassa truncata</i>	Dando <i>et al.</i> , 1995

*See Kulm *et al.* (1986) for location and map of the Oregon Subduction Zone.

physical oceanography in general). Thus, it is clear that our list is a preliminary assessment of the diversity of decapods that will ultimately be known from hydrothermal vents and cold hydrocarbon seeps. Additionally, we have not clearly defined the term 'vicinity', such that for the non-endemic species, it is

unclear as to how much, if any, association really exists between a species and the vent or seep where it was observed. Although the boundaries are relatively clear for endemic vent or seep fauna, they are not clear, and are indeed somewhat artificial, for the vagrant species.

MATERIAL AND METHODS

Our primary source of information for this compilation has been the primary taxonomic literature on decapod crustaceans from hydrothermal vents and cold seeps. Our primary interest is with taxonomy, systematics and distribution. Additionally, we have attempted to survey much of the secondary literature (publications on the ecology, physiology, behaviour, distributions, etc.) on these decapods to gather anecdotal (and in some cases new) information on the distribution or natural history of these species. Although we have consulted many of these non-taxonomic works where vent or seep decapods are mentioned or studied, this work is not intended to be exhaustive from that point of view. Apart from the literature, we searched collections at the Natural History Museum of Los Angeles County and the National Museum of Natural History (Washington, DC) and queried many of our colleagues who work on deep-sea crustaceans. Unpublished records of decapods from vents and seeps have been provided by some of these colleagues (see Acknowledgements). Information on the holdings of decapods at several museums was obtained by contacting collection staff at those institutions. Abbreviations for repositories for the species are: ASIZ, Academia Sinica, Nankang, Tapei; BMNH, Natural History Museum, London; CBM, Natural History Museum and Institute, Chiba; FMNH, Field Museum of Natural History, Chicago; JMSTC, Japanese Marine Science and Technology Center, Yokosuka; LACM, Natural History Museum of Los Angeles County, Los Angeles (including AHF, the former Allan Hancock Crustacea collection); MCZ, Museum of Comparative Zoology, Harvard University; MNHN, Muséum National d'Histoire Naturelle, Paris; MNZ, Museum of New Zealand Te Papa Tongarewa, Wellington; NFU, National Fisheries University, Japan; NIWA, National Institute for Water and Atmosphere, Wellington; NSMT, National Science Museum, Tokyo; NTOU, National Taiwan Ocean University, Keelung; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden; SMF, Forschungsinstitut Senckenberg, Frankfurt; TMCD, Taiwan Museum, Tapei; USNM, National Museum of Natural History, Washington, DC; WHOI, Woods Hole Oceanographic Institution, Woods Hole; ZMUC, Zoologisk Museum, Copenhagen; ZRC, Zoological Reference Collection, Raffles Museum, National University of Singapore. Taxa are listed in the following order, with families, genera and species listed alphabetically within these groups: Dendrobranchiata, Caridea, Anomura, Brachyura, Astacidea and Thalassinidea. Our classification and recognition of decapod families within these infraorders follows the recent classification of all crustacean families by Martin and Davis (2001), which in turn has been followed by McLaughlin *et al.* (2005) with slight modifications.

Physical descriptions of individual sites are not given here; we refer readers to the reviews of Tunnicliffe (1991) and Van Dover (2000) for hydrothermal vents and of Sibuet & Olu (1998) for cold seeps.

RESULTS

ORDER DECAPODA LATREILLE, 1802

SUBORDER DENDROBRANCHIATA BATE, 1888

FAMILY BENTHESICYMIDAE WOOD-MASON, 1891

GENUS *BENTHESICYMUS* BATE, 1881

Remarks: As currently understood, the genus *Benthescycymus* includes 17 species, collectively occurring throughout the world ocean (Pérez Farfante & Kensley, 1997). Pérez Farfante & Kensley (1997) summarized the known distributions of these species. Roberts & Pequegnat (1970) presented a review and key for species of *Benthescycymus* found in the Gulf of Mexico. Kickuchi & Nemoto (1991) described collections of *Benthescycymus* from the western North Pacific, commented on the vertical distribution of these shrimps and presented a taxonomic key to 15 species. Only one species from this genus has been noted from seep environments.

BENTHESICYMUS INVESTIGATORIS (ALCOCK & ANDERSON, 1899)

Type locality: Indian Ocean, Andaman Islands; 13°7'–14°13'N, 93°14'30"–94°44'15"E; 677–741 m.

Known range: This species inhabits tropical and subtropical waters from the westernmost Indian Ocean to the Pacific Ocean; records include the Gulf of Aden and Madagascar, through Indonesia and Philippines, to New South Wales, Japan, Hawaii and the islands of Salas-y-Gomez in the south-eastern Pacific Ocean (Pérez Farfante & Kensley, 1997).

Occurrence at vents or seeps: North Pacific Ocean, Japan, Enshu-nada, south-western flank of Kanesuno-se Bank; *Shinkai 2000* dive 771; 1000 to 1220 m (from Ohta *et al.*, 1995).

Material: No known material from vent or seep habitats.

Remarks: This is a fairly widely distributed deep-sea species throughout much of the western Pacific. Ohta *et al.* (1995) reported this species from the Enshu-nada cold seeps off Japan.

FAMILY SERGESTIDAE DANA, 1852

GENUS *SERGIA* STIMPSON, 1860

SERGIA CF. *ROBUSTA* (SMITH, 1882)

Type locality: western North Atlantic Ocean, United States, Massachusetts, off Martha's Vineyard.

Known range: 'Gulf of Mexico, Caribbean Sea, Surinam, North Sea, Faroe Islands, off Bermuda, Mediterranean, Cape Verde Islands to Congo and Angola' (Pérez Farfante & Kensley, 1997: 200) (but see discussion in Frogliia & Gramitto, 2000, and Martin, Wishner & Graff, 2005).

Occurrence at vents or seeps: See below.

Material: Vent material restricted to: eastern Caribbean Sea, Kick'em Jenny Volcano; 12°18.076'N 61°88.25'W; Ronald H. Brown cruise RB-03-03, Eastern Oceanics Remotely Operated Vehicle, Dive 3; 261 m; 16 March 2003; LACM CR 2003-010.3 (1 damaged individual); additional material in the private collection of K. Wishner.

Remarks: The identification of the single specimen from the Kick'em Jenny Volcano reported by Martin *et al.* (2005) was tentative, and there is some controversy over the accepted number of species and their biogeographical ranges in this genus (see Discussion in Martin *et al.*, 2005). Martin *et al.* (2005) noted that if the species from the Kick'em Jenny submarine volcano is indeed *S. robusta*, then this would be well within the range of that species as given by Pérez Farfante & Kensley (1997) but not as given by Vereshchaka (1994).

This species, the first reported penaeoid from a hydrothermal (as opposed to cold seep) locality, was found with two other caridean species on the floor of the submerged volcano's caldera. It is believed that all three species may be trapped there by toxic gases issuing from the sediment of the caldera during their diel migrations (Martin *et al.*, 2005; Wishner *et al.*, 2005).

SUBORDER PLEOCYEMATA

INFRAORDER CARIDEA DANA, 1852

FAMILY ALVINOCARIDIDAE CHRISTOFFERSEN, 1986

Remarks: Many shrimp species now treated as members of the Alvinocarididae (see Martin & Davis, 2001; Komai & Segonzac, 2003) were initially treated as members of the family Bresiliidae. However, the caridean family Bresiliidae Calman, 1896, in which *Rimicaris*, *Alvinocaris* and *Chorocaris* were originally placed, has now been restricted to the comparatively shallow-water genera *Encantada*, *Bresilia*, *Agostocaris* (sometimes treated as a member of its own family, the Agostocarididae), *Pseudocheles*, *Kirnasia*, *Lucaya*, *Tridiscias* and *Discias*, with *Discias* sometimes treated under the family Disciadidae (e.g. see Martin & Hessler, 1990; Holthuis, 1993; Martin & Davis, 2001; Calado, Chevaldonné & dos Santos, 2004), and with the vent-endemic genera now transferred to the Alvinocarididae (see above and also Christoffersen, 1986; Segonzac *et al.*, 1993, footnote;

Martin & Davis, 2001; Komai & Segonzac, 2003). The family Bresiliidae is therefore not currently represented at any hydrothermal vent or seep site.

The family Mirocarididae Vereshchaka, 1997, created by Vereshchaka (1997b) to accommodate the genus *Mirocaris* and two species, *M. fortunata* and *M. keldyshi* (which have since been synonymized; see under *M. keldyshi*), was synonymized with the Alvinocarididae by Komai & Segonzac (2003).

The family Alvinocarididae, initially established by Christoffersen (1986) and later modified (see Komai & Segonzac, 2003), currently includes the genera *Alvinocaris*, *Rimicaris*, *Chorocaris*, *Mirocaris*, *Nautilocaris* and *Opaepele*. We are aware of ongoing (unpublished) descriptions of additional species of *Alvinocaris*, *Chorocaris* and *Mirocaris* as of this writing (see below). Additionally, one of the currently described species of *Alvinocaris* from the Okinawa Trough was recently transferred to a newly recognized genus, *Shinkaicaris*, by Komai & Segonzac (2005a).

GENUS ALVINOCARIS WILLIAMS & CHACE, 1982

Remarks: *Alvinocaris* is the most widespread of the vent- and seep-associated shrimp genera and is the only genus known from both hot vents and cold seeps. Kikuchi & Ohta (1995) presented the most recent diagnosis of the genus. However, a complete review of the genus has just been completed (T. Komai & M. Segonzac, pers. comm.; Komai & Segonzac, 2005a). Several studies report only the presence of, or photographs of, *Alvinocaris* sp. without naming the species (which in some cases was undescribed at the time of publication). Examples of such works include an apparently new species shown in photographs from the Blake Ridge Diapir (methane seeps off South Carolina) by Van Dover *et al.* (2003), Kim & Ohta (1991, figs 7, 9), Ohta (1990a, fig. 6, described later as *A. longirostris* by Kikuchi & Ohta 1995), an undescribed species of *Alvinocaris* from newly discovered vents at seamounts off New Zealand (Webber & Bruce, 2002, on the NIWA website at <http://www.niwa.co.nz/pubs/bu/05/blind>), and other reports (see Table 1). The genus occurs in relatively shallow water (200 m) in the Gulf of Mexico (Escobar-Briones & Villalobos-Hiriart, 2003, and unpublished video sequences of what is probably *A. muricola*; M. Segonzac, pers. comm.). Shrimp probably belonging to this genus were also reported recently from a region of asphalt volcanism in the Campeche Knolls, Gulf of Mexico (MacDonald *et al.*, 2004). Specimens of the genus (identified only as *Alvinocaris* sp.) have also been collected from Alvin dive 3936 at an area of new lava flow in the East Pacific Rise (EPR); these are housed at the Field Museum as FMNH 11401 (J. Voight, pers. comm.). Because there is only one species of *Alvinocaris* known from the EPR

(*Alvinocaris lusca*; see Table 1), it is likely that this specimen belongs to that species.

In addition to the nine named species listed below and in Table 1, the ubiquity of this genus at vents and seeps has resulted in numerous recent discoveries, and we are aware of several undescribed species that have been reported or are currently being described. These are listed in Table 1 as *Alvinocaris* sp. A–G, the details of which are as below.

Alvinocaris sp. A: According to T. Wolff (pers. comm.), R. Webber has reported 'four small specimens representing a further one or two species' of *Alvinocaris* (in addition to Webber's recently described species, *A. niwa*) collected from the Kermadec Ridge.

Alvinocaris sp. B: T. Wolff (pers. comm.) informs us that yet another undescribed species of *Alvinocaris* is known from the Logatchev site, MAR.

Alvinocaris sp. C: Shrimp that apparently belong to *Alvinocaris* also have been reported from the Edison Seamount of the Bismark Archipelago north of Papua New Guinea (Shank *et al.*, 1999; Shank & Martin, 2003). According to T. Komai (pers. comm.), Drs K. Baba and M. Türkay are currently studying specimens.

Alvinocaris sp. D: Desbruyères *et al.* (1994) reported a species of *Alvinocaris* from the North Fiji and Lau Basins.

Alvinocaris sp. E: The paratypes of *A. brevitelsonis* are considered to represent a different, undescribed species of *Alvinocaris* (T. Komai, pers. comm.) that has just been described as *A. dissimilis* (Komai & Segonzac, 2005a) (see below).

Alvinocaris sp. F: T. Wolff (pers. comm.) informs us that there is another undescribed species of *Alvinocaris* at the Menez Gwen site of the MAR.

Alvinocaris sp. G: Hashimoto & Ohta (1999) reported an undescribed species of *Alvinocaris* has been reported from the DESMOS site of the Manus Back-Arc Basin.

ALVINOCARIS BREVITELSONIS KIKUCHI &
HASHIMOTO, 2000

Type locality: western Pacific Ocean, Mid-Okinawa Trough, 140 km W of Amami-Ohshima Island, Minami-Ensei Knoll, Depression C; 28°23.35'N, 127°38.38'E; 705 m.

Known range: limited to the type locality.

Material: type locality; Marine Ecosystems Research Department, JMSTC, *Shinkai 2000* dive 547; 3 June 1991; hydraulically driven suction sampler; NSMT-Cr 12454 (holotype, female), NSMT-Cr 12455 (allotype,

male), NSMT-Cr 12456 (paratypes, 1 male, 1 female), (non-types, 6 males) (Kikuchi & Hashimoto, 2000).

Remarks: Some of the specimens upon which this species description was based (paratypes registered as NSMT-Cr 12456) apparently differ sufficiently from the type specimen to warrant their recognition as a new species of *Alvinocaris* (see *A. dissimilis* below).

ALVINOCARIS DISSIMILIS KOMAI & SEGONZAC, 2005A

Type locality: western Pacific Ocean, Minami-Ensei Knoll, Mid-Okinawa Trough, 705 m (Komai & Segonzac, 2005a).

Known range: limited to type locality.

Material: western Pacific Ocean, Mid-Okinawa Trough, 140 km W of Amami-Ohshima Island, Minami-Ensei Knoll, Depression C; 28°23.35'N, 127°38.38'E, *Shinkai 2000* dive 547; 705 m; 3 June 1991; Holotype female, NSMT-Cr 12456A; Paratypes, 1 male, 1 female (ovigerous), NSMT-Cr 12456B; all originally reported as paratypes of *Alvinocaris brevitelsonis* by Kikuchi & Hashimoto, 2000, under NSMT-Cr 12456. No locality data; non-type, 4 males, T. Kikuchi's personal collection (T. Komai, pers. comm.).

Remarks: This new species was recognized among the paratypes of *A. brevitelsonis* by Komai & Segonzac (2005a).

ALVINOCARIS METHANOPHILA KOMAI, SHANK &
VAN DOVER, 2005

Type locality: Northwestern Atlantic Ocean, Blake Ridge Diapir, 32°29.623'N, 76°11.467'W, 2155 m.

Known range: limited to the type locality.

Material: Komai *et al.* (2005) reported 33 adult specimens, most of which came from mussel beds at ODP site 996, Alvin dives 3709–3712, September 2001; two additional specimens came from just outside the mussel beds, Alvin dive 3910, July 2003. Specimens are housed at LACM, MNHN, CBM, USNM, and SMF (numbers not given).

Remarks: This new species is morphologically very similar to *A. muricola* and was listed as *Alvinocaris cf. muricola* by Van Dover *et al.* (2003).

ALVINOCARIS LEUROKOLOS KIKUCHI &
HASHIMOTO, 2000

Type locality: western Pacific Ocean, Mid-Okinawa Trough, 140 km W of Amami-Ohshima Island, Minami-Ensei Knoll, Depression C; 28°23.35'N, 127°38.38'E; 705 m.

Known range: limited to the type locality.

Material: type locality; Marine Ecosystems Research Department, JMSTC, *Shinkai 2000* dive 549; 5 June 1991; hydraulically driven suction sampler; NSMT-Cr 12457 (holotype, female), NSMT-Cr 12458 (allotype, male), NSMT-Cr 12459 (paratypes, 2 males and 2 females), non-types, 5 males, 39 females, 12 juveniles (Kikuchi & Hashimoto, 2000).

Remarks: T. Komai (pers. comm.) has indicated to us that *A. leurokolos* differs from other species of *Alvinocaris* to the extent that it warrants placement in its own genus (*Shinkaicaris*); this transfer was recently published by Komai & Segonzac, (2005a).

ALVINOCARIS LONGIROSTRIS KIKUCHI & OHTA, 1995

Type locality: western Pacific Ocean, Okinawa Trough, Iheya Ridge, north-eastern slope; Clam Site; 27°32.70'N, 126°58.20'E; 1360 m.

Known range: Okinawa Trough, Iheya Ridge, Clam and Pyramid sites (Kikuchi & Ohta, 1995; Hashimoto, 1997, in Desbruyères & Segonzac, 1997), Sagami Bay seeps (P. Chevaldonné, pers. comm.; Fujikura *et al.*, 1999), and seamounts of the Kermadec Ridge off New Zealand (Webber, 2004).

Material: type locality; *Shinkai 2000* dive 409; 10 June 1989; hand net attached to manipulator; NMST-Cr 11439 (holotype, non-ovigerous female), non-types (2 ovigerous females).

–type locality; *Shinkai 2000* dive 480; 16 May 90; baited trap; NSMT-Cr 11440 (paratypes, 3 female specimens), no registration number provided (non-types, 4 female specimens) (Kikuchi & Ohta, 1995).

–western Pacific Ocean, Okinawa Trough, Iheya Ridge, north-eastern slope, Pyramid site; 27°32.70'N, 126°58.20'E; *Shinkai 2000* dive 481; 1410 m; 17 May 90; baited trap; no registration number provided, non-types, 11 female specimens (Kikuchi & Ohta, 1995).

–western Pacific Ocean, Okinawa Trough, Iheya Ridge, north-eastern slope; 27°47.179'N, 126°54.091'E; 1053 m; JMSTC, *Shinkai 2000* dive 1094; 8 May 99; coll. S. Tsuchida; non-type, 7 females.

–Sagami Bay, Hatsushina site, cold seeps (Fujikura *et al.*, 1995, 1996)

–South Pacific Ocean, off New Zealand, southern Kermadec Ridge, Brothers Caldera, sta. X553; 34°52.77–53.25'S, 179°4.33–4.59'E; 1335–1490 m; 2 February 1996; rock dredge; 1 male, NIWA 3274; 1 female, NIWA 3275. –sta. TAN0107/131; 34°52.58–52.28'S, 179°3.80–3.64'E; 1370–1200 m; 21 May 2001; benthic sled; 3 specimens (131, D–F), NIWA 3263; 52 specimens, NIWA 3269; 1 specimen (A), MNZ CR. 9978; 5 specimens, MNZ CR. 9988. –sta. TAN0107/134; 34°52.87–52.76'S, 179°4.17–4.60'E; 1518–1210 m; 21

May 2001; epibenthic sled; 1 female, NIWA 3264; 6 specimens, NIWA 3270; 2 specimens, MNZ CR. 9985. –sta. TAN0107/135; 34°52.89–52.87'S, 179°3.76–3.21'E; 1346–1196 m; 21 May 2001; benthic sled; 2 specimens (A, C), NIWA 3265; 94 specimens, NIWA 3271; 1 specimen (B), MNZ CR. 9979; 5 specimens, MNZ CR. 9987. –sta. TAN0107/136; 34°53.12–53.35'S, 179°4.49–5.09'E; 1526–1197 m; 21 May 2001; benthic sled; 2 specimens (A, B), NIWA 3266; 80 specimens, NIWA 3272; 1 specimen (A), MNZ CR. 9980; 5 specimens, MNZ CR. 9986. –sta. TAN0107/140; 34°51.69–51.46'S, 179°3.35–3.11'E; 1850–1460 m; 22 May 2001; benthic sled; 1 female, NIWA 3267. –sta. TAN0107/141; 34°52.96–52.69'S, 179°4.02–4.93'E; 1538–1197 m; 22 May 2001; benthic sled; 1 female, NIWA 3262 (Webber, 2004: fig. 5); 23 specimens (141vou, B–U, Y, Z); 73 specimens, NIWA 3273; 1 specimen (V), MNZ CR. 9981; 1 specimen (X), MNZ CR. 9982; 1 specimen (W), MNZ CR. 9983; 10 specimens, MNZ CR. 9984.

Remarks: Kikuchi & Ohta (1995) made 'biological and ecological surveys of deep-sea benthic macrobiota and planktonic organisms in hydrothermal vent fields in the Okinawa Trough.' It is assumed that this species is the undescribed *Alvinocaris* reported by Ohta (1990a: 148) from this region. Although all 21 specimens reported by Kikuchi & Ohta (1995) were females, there were no ovigerous females and no other mention of the reproductive status of the specimens. The original description (Kikuchi & Ohta, 1995) was also the basis for the summary by Hashimoto (1997, in Desbruyères & Segonzac, 1997). Watabe & Miyake (2000) reported this species from Hatoma Knoll, south of the Okinawa Trough. Fujikura *et al.* (1995, 1999) reported its presence in chemosynthetic communities of Sagami Bay. Webber (2004: 18) reported the collection of 374 specimens of *A. longirostris* from the Brothers Caldera of the Kermadec Ridge; the specimens were collected almost entirely by benthic sled during a survey of the volcanic seamount using the R/V *Tangaroa*. Webber (2004) examined 41 of the 374 specimens collected from Brothers Caldera and found their morphology to be consistent with that reported by Kikuchi & Ohta (1995) for *A. longirostris*. However, Webber (2004) reported several differences between the collection from Brothers Caldera and those from the type locality; these included the ratio of rostrum length to carapace length, and the presence of a plumose seta on the proximal article of the mandibular palp, third maxilla and first maxilliped. *Alvinocaris longirostris* has not been reported from closely associated systems such as those of the Lau and North Fiji basins. Hence, with Brothers Caldera at 34°S and Iheya Ridge at 27°N, the geographical distribution alone appears to warrant comparison of specimens from Brothers Caldera with the type series.

T. Wolff (pers. comm.) has indicated that this species, or a very similar one, occurs at Papua New Guinea vent sites.

ALVINOCARIS LUSCA WILLIAMS & CHACE, 1982

Type locality: eastern Pacific Ocean, Galapagos Rift, Rose Garden area; 0°48.25'N, 86°13.48'W; 2450 m.

Known range: Known from the Galapagos Rift and the 9°N and 13°N vent fields of the EPR, at depths of 2450–2600 m (Shank, 1997, in Desbruyères & Segonzac, 1997).

Material: type locality; *Alvin* dive 990; 9 December 1979; USNM 184534 (holotype, male), USNM 184535 (allotype, female), USNM 184537 (paratype male), USNM 184536 (paratypes, 11 females), USNM 184538 (1 juvenile) (Williams & Chace, 1982).

–Galapagos Rift, 00°48.2'N, 86°13.4'W; *Alvin* dive 2224; 2461 m; 29 May 1990. Non-type: 2 specimens, sex not listed (Shank *et al.*, 1999).

–EPR, 9°N site, 09°50.3'N, 104°17.4'W; *Alvin* dive 2692; 2520 m; 26 December 1993; non-type, 2 specimens, sex not listed (Shank *et al.*, 1999).

Williams & Chace (1982) noted that 1 paratype female would be transferred to each of the following collections: MCZ, AHF/LACM, BMNH, RMNH, MNHN.

Remarks: This is the only species of *Alvinocaris* reported from the eastern Pacific to date. Hessler & Smithey (1983) provided brief observations on ecology and behaviour of the species at the Rose Garden site. Van Dover (1986) examined stable isotope ratios and compared them with another vent decapod (the galatheid *Munidopsis subsquamosa*). Van Dover *et al.* (1985) described planktotrophic larval development. Shank (1997, in Desbruyères & Segonzac, 1997) provides limited ecological observations on its ecology and feeding. Fustec, Desbruyères & Juniper (1987) noted the species from the 13°N site on the EPR, but the specimens that they observed might have been *Lebbeus* (T. Komai, pers. comm.). Shank *et al.* (1999: 251) listed *A. lusca* from the site at 13°N but did not provide any information on that record.

ALVINOCARIS MARKENSIS WILLIAMS, 1988

Type locality: North Atlantic Ocean, MAR, Snake Pit hydrothermal vent field, 70 km S of Kane Fracture Zone; 23°22.09'N, 44°57.12'W; 3437 m.

Known range: Known from the Snake Pit (23°N, 3480 m), TAG (26°N, 3734 m), Logatchev and Broken Spur vent fields of the MAR (Williams, 1988; Segonzac *et al.*, 1993; Gebruk *et al.*, 1997, 2000a; Shank, 1997,

in Desbruyères & Segonzac, 1997: 192; Turnipseed *et al.*, 2004).

Material: type locality; NSF Ocean Drilling Program Leg 106, *Alvin* dive 1683; 3437 m; 30 May 1986; USNM 234286 (holotype, female), USNM 234287 (paratypes, 2 females, both damaged) (Williams, 1988).

North Atlantic Ocean, MAR:

–Snake Pit hydrothermal vent field, Elan site; HYDROSNAKE, *Nautila* HS 03; 3515 m; 21 June 88; MNHN-Na 14279 (non-types, 4 males). –Les Ruches site; 23°22.13'N, 44°57.13'W; HYDROSNAKE, *Nautila* HS 10; 3482 m; 28 June 1988; slurp gun; MNHN-Na (non-types, 1 female, 1 juvenile, damaged). –Les Ruches site; 23°22.13'N, 44°57.13'W; *Alvin* dive 2619; 3482 m; 20 June 1993; MNHN-Na 14280 (non-type, 1 male, 2 females), MNHN-Na 14281 (non-type, 1 female). –Moose Mound, 23°22.1'N, 44°57.1'W; *Alvin* dive 2621; 3398 m; 22 June 1993; 2 specimens? (Wharton *et al.*, 1997). –Moose Mound, *Alvin* dive 2623; June 1993; 3 specimens? (Wharton *et al.*, 1997). –Les Ruches site; 23°22.90'N, 44°57.13'W; MICROSMOKE, *Nautila* dive MS 16; 3500 m; 15 November 95; MNHN-Na 14283 (non-type, 1 female). –Les Ruches site; 23°22.90'N, 44°57.13'W; *Nautila* dive 08; 3480 m; 21 November 95; baited trap; MNHN-Na 14282 (non-types, 1 male, 13 females), MNHN-Na (non-types, 2 females, 5 undetermined (Komai & Segonzac, 2003; T. Komai, pers. comm.). –Les Ruches site; 23°22.90'N, 44°57.13'W; *Nautila* dive 16; 3500 m; 29 November 95; MNHN-Na (non-types, 4 females). –Les Ruches site; 23°22'N, 44°56'W; HYDROSNAKE, *Nautila* dives 03, 08 and 10 (Segonzac, de Saint Laurent & Casanova, 1993).

–Lucky Strike field, Tour Eiffel, 37°13.48'N, 32°19.42'W; ROV *Victor* dive 119-17; 1693 m; 16 July 2001; MNHN-Na 14284 (non-type, 1 ovigerous female).

–Rainbow site, 36°13.759'N, 33°54.169'W; ROV *Victor* dive 104-02; 25 June 2001; MNHN-Na 14285 (non-type, 1 male). –same locality; IFREMER, ROV *Victor* dive 107-05; 30 June 2001; slurp gun; non-types, 1 female, 1 juvenile. –Rainbow site, 36°13.759'N, 33°54.169'W; ROV *Victor* dive 119-17; 2292 m; 8 August 2002; slurp gun; CBM-ZC 7041 (non-type, 1 female).

Remarks: *Alvinocaris markensis* has been reported at least twice (Segonzac *et al.*, 1993; Komai & Segonzac, 2003) from the Snake Pit vent field since its original description (see above), but in some cases the numbers of specimens and where (or if) they were deposited in a museum was not given. Shank (1997, in Desbruyères & Segonzac, 1997) noted that this species is the least abundant of the three alvinocaridids at the TAG and Snake Pit sites, and that it is 'typically found several

meters from edifices venting high temperature fluids.' Shank *et al.* (1999: 246) reported the distribution of *A. markensis* as one that includes the Broken Spur, TAG, Snake Pit and Logatchev sites along the MAR. However, they noted that the record from the Broken Spur site was based solely on video footage, and they provided collection data only for two specimens from Snake Pit (from DSMV *Alvin* dive 2621, listed above). Shank *et al.* (1999: 247) did not provide collection-related data upon which their report of *A. markensis* from the TAG and Logatchev sites was based, but they did report collections of *Chorocaris chacei*, *Mirocaris keldyshii* and *Rimicaris exoculata* from the TAG site and *M. keldyshii* from Logatchev, all collected during a cruise in 1997. Desbruyères *et al.* (2000: table 4) listed the species as rare at the TAG site. Feeding morphology and behaviour were studied by Casanova, Brunet & Segonzac (1993) and Segonzac *et al.* (1993), carotenoid pigments were analysed by Nègre-Sadargues, Castillo & Segonzac (2000), lipid fatty-acid composition was studied by Pond *et al.* (1997a, b, c) and eye morphology was described by Wharton *et al.* (1997). Because the holotype and paratypes of *A. markensis* are juvenile specimens, the species currently is being rediagnosed (T. Komai, pers. comm.).

ALVINOCARIS MURICOLA WILLIAMS, 1988

Type locality: Gulf of Mexico, West Florida Escarpment, from cold brine seep; 26°01'N, 84°54.61'W; 3277 m.

Known range: type locality, Gulf of Guinea, and possibly Blake Ridge seeps (Van Dover *et al.*, 2003; see below), as well as the Barbados Accretionary Prism (Olu *et al.*, 1996b, 1997).

Material: type locality, *Alvin* dive 1754; 3277 m; 15 October 1986. Holotype: male, USNM 234288. Allotype: type locality, *Alvin* dive 1753; 3277 m; female, USNM 234289; 14 October 1986; Paratype: 1 female, USNM 234290 (Williams, 1988).

–*Alvin* dive 3636; 29 October 2000; C. Van Dover's personal collection (non-types, 2 males, 12 females, 1 juvenile) (T. Komai, pers. comm.; see also Turnipseed *et al.*, 2004).

–South Barbados, Orénoque A site, 10°19.64'N, 58°53.33'W; DIAPISUB, *Nautile* dive DS 04; 1697 m; 27 December 1992; MNHN-Na (non-type, 1 female).

–Gulf of Guinea, west equatorial African margin, Régab site; ZAÏROV, ROV *Victor* dive 74-14; 3200 m; 27 December 2000; 'claw jaw'; MNHN-Na 14277 (non-type, 1 female), CBM-ZC 7042 (non-type, 1 female).

–Gulf of Guinea, west equatorial African margin, Régab site; BIOZAÏRE 1, ROV *Victor* dive 81-5; 3200 m; 10 January 2001; slurp gun; MNHN-Na 14278 (non-types, 1 male, 2 females, 4 juveniles).

–Gulf of Guinea, west equatorial African margin, Régab site; BIOZAÏRE 2, ROV *Victor* dive 146-9; 3200 m; 28 November 2001; slurp gun 1; IFREMER (non-types, 3 females); same dive, slurp gun 2-1; IFREMER [non-types, 7 males, 14 females (2 ovigerous), 9 juveniles]; same dive, slurp gun 2-2; IFREMER (non-types, 7 males, 18 females, 12 juveniles).

–Gulf of Guinea, west equatorial African margin, Régab site; BIOZAÏRE 2, ROV *Victor* dive 146-9, slurp gun 3; IFREMER (non-types, 20 males, 1 juvenile).

–Gulf of Guinea, west equatorial African margin, Régab site; BIOZAÏRE 2, ROV *Victor* dive 147-10; 1 December 2001; slurp gun 1-1; IFREMER (non-type, 1 male); same dive, slurp gun 1-2; IFREMER (non-types, 2 females); same dive, slurp gun 3; IFREMER (non-types, 2 males, 18 females, 3 juveniles); same dive; slurp gun 5-1; IFREMER (non-types, 4 males, 10 females, 2 juveniles); same dive; slurp gun 5-2; IFREMER (non-type, 4 males, 1 female).

–Gulf of Guinea, west equatorial African margin, 2 km from Régab site; BIOZ-RECUP using R/V *Suroit*, MAC (module autonome de colonisation); 3150 m; January 2003; MAC 10-147; IFREMER (non-types, 3 juveniles). –same site; MAC 10-151; IFREMER (non-types, 2 juveniles). –same site; MAC 10-159; IFREMER (non-types, 2 juveniles).

Remarks: This species is the only *Alvinocaris* known from any cold seep (although a second species is being described from the Blake Ridge Diapir; T. Komai, pers. comm.). Until recently, this species was known only from its type locality in the Gulf of Mexico. It is now known from South Barbados and from extensive collections made in the Gulf of Guinea (Olu *et al.*, 1996a; T. Komai, pers. comm.) and from the Blake Ridge Diapir (T. Komai, pers. comm.).

A morphologically very similar shrimp (referred to as *Alvinocaris* cf. *muricola*) was reported from the Blake Ridge seeps by Van Dover *et al.* (2003); that species is being described as new by Komai *et al.* (in press).

ALVINOCARIS NIWA WEBBER, 2004

Type locality: South Pacific Ocean, off New Zealand, southern Kermadec Ridge (midway between the Kermadec Islands and Bay of Plenty, New Zealand), Brothers Caldera, 34°52.89'–52.87'S, 179°3.76'–3.21'E, R/V *Tangaroa* sta. TAN0107/135, 1346–1196 m, benthic sled (Webber, 2004).

Known range: Known only from the Brothers Caldera and Rumble V Seamount, southern Kermadec Ridge (midway between the Kermadec Islands and Bay of Plenty, New Zealand) (Webber, 2004).

Material: type locality, Brothers Caldera, sta. TAN0107/135; 34°52.89'–52.87'S, 179°3.76'–3.21'E; R/

V. Tangaroa; 1346–1196 m; benthic sled; 1 female (specimen C), NIWA P1388; 3 females (specimens A, D, E), NIWA 3255; 1 female (specimen B), MNZ CR. 9977. –Brothers Caldera, sta. TAN0107/141; 34°52.96–52.69'S, 179°4.02–4.93'E; 1538–1197 m; benthic sled; 3 specimens (141, 141A, 141C), NIWA 3256; 1 specimen (C), MNZ CR. 9967. Kermadec Ridge, Rumble V, sta. TAN0107/228; 36°8.63–8.57'S, 178°11.77–11.50'E; R/V *Tangaroa*; 877–655 m; benthic sled; holotype, female, NIWA H837; 18 specimens (A–D, F–Q, S–T), NIWA 3257; 1 specimen (E), MNZ CR. 9969; 1 specimen (R), MNZ CR. 9970. –Rumble V, sta. TAN0107/230; 36°8.48'–8.79'S, 178°11.70'–11.53'E; 755–360 m; benthic sled; 4 specimens (A, B, D, E), NIWA 3258; 1 specimen (C), MNZ CR. 9971. –Rumble V, sta. TAN0107/233; 36°8.35'–8.70'S, 178°11.74–11.58'E; 520–367 m; benthic sled; 3 specimens (A–C), NIWA 3259. –Rumble V, sta. TAN0107/235; 36°8.36'–8.08'S, 178°11.76'–11.96'E; benthic sled; 4 specimens (B–E), NIWA 3260; 1 specimen (A), MNZ CR. 9972. –Rumble V, sta. TAN0107/325; 36°8.27'–7.96'S, 178°11.74–11.70'E; benthic sled; 42 specimens (A, C, E-AC, AE-AS), NIWA 3261; 1 specimen (D), MNZ CR. 9973; 1 specimen (B), MNZ CR. 9974; 1 specimen (AD), MNZ CR. 9975; 1 specimen (AT), MNZ CR. 9976 (Webber, 2004).

In addition to the ovigerous female holotype (H-837, NIWA 3253), Webber (2004) listed 87 specimens collected on voyage TAN0107 by the R/V *Tangaroa*, all from hydrothermal vents at the Brothers Caldera and Rumble V Seamount on the southern Kermadec Ridge. All specimens are deposited at the National Institute of Water and Atmospheric Research (NIWA), Wellington, New Zealand, with the exception of some paratypes deposited at the Museum of New Zealand Te Papa Tongarewa, Wellington.

Remarks: *Alvinocaris niwa* is the species mentioned earlier (as *Alvinocaris* sp. A) by Webber & Bruce (2002: 6). Webber (2004) described additional specimens of *Alvinocaris longirostris* found on the same voyage to the Kermadec Ridge, extending the known range of that species. Clark & O'Shea (2001) listed other species collected during this voyage. See Webber (2004) for thorough coverage of morphological variability in both species. Webber (2004) also noted that 'four small specimens' from this same expedition represent 'a further one or two species.'

ALVINOCARIS STACTOPHILA WILLIAMS, 1988

Type locality: Gulf of Mexico, 129 km S of Louisiana, from Bush Hill hydrocarbon seep; 27°46.94'N, 91°30.34'W; 534 m.

Known range: limited to type locality.

Material: type locality; Minerals Management Service Northern Gulf of Mexico Outer Continental Slope (MMS/NGOMCS) Regional Office Project, *Johnson-Sea-Link* dive 1879; 534 m; 28 September 1986; USNM 234291 (holotype, male). USNM 234292 (allotype, female), USNM 234293 (paratypes, 5 males, 2 females) (Williams, 1988).

Remarks: This species was reported also by Bergquist *et al.* (2003) from the upper continental slope off Louisiana and has been seen on the Florida Escarpment and Alaminos Canyon in the Gulf of Mexico (S. Hourdez, pers. comm.). The allotype of *A. stactophila* apparently is a separate, undescribed species (T. Komai, pers. comm.).

ALVINOCARIS WILLIAMSII SHANK & MARTIN, 2003

Type locality: North Atlantic Ocean, MAR, Menez Gwen hydrothermal vent field; 37°50.5'N, 31°31.3'W; 850 m.

Known range: limited to the type locality.

Material: type locality; *Alvin* dive 3117; 850 m; 7 July 1997; 30 × 30 cm square black net operated with the manipulator arm; USNM 1009651 [holotype, female (ovigerous, specimen ID: BN 70)], USNM 1009652 [paratypes, 2 females (specimen ID: BN 68 and BN 51), abdomen torn from body], USNM 1009653 (non-types, 11 females; not named) (Shank & Martin, 2003).

–Menez Gwen hydrothermal vent field, 37°51.60'N, 33°31.35'W; SALDANHA, *Nautila* dive 1274; 865 m; 15 July 1998; SMAC tray; MNHN-Na (non-type, 1 female).

–Menez Gwen hydrothermal vent field, 37°50.46'N, 31°31.35'W; DIVA 1, dive 14; 845 m; 22 May 1994; MNHN-Na (non-types, 1 female, 1 male).

–Menez Gwen, 37°50.54'N, 31°31.30'W; DIVA 2, dive 12; 866 m; 14 June 1994; slurp gun; MNHN-Na (non-type, 1 juvenile). –same site, dive 13; 19 June 1994; MNHN-Na (non-type, 1 male). –same site, dive 16; 22 June 1994; MNHN-Na [non-types, 3 females (1 ovigerous)]. –same site, dive 26; 2 July 1994; MNHN-Na (non-type, 1 male).

Remarks: To our knowledge there has been no other mention in the literature following the original description (Shank & Martin, 2003).

GENUS CHOROCARIS MARTIN & HESSLER, 1990

Remarks: The genus *Chorocaris* was established by Martin & Hessler (1990) to accommodate *C. vandoverae* from the Mariana Back-Arc Basin, western Pacific, and the former *Rimicaris chacei* Wil-

Williams & Rona, 1986, from the mid-Atlantic Ridge. A third species was recently described from the southern part of the EPR (Martin & Shank, 2005). There is also a shrimp species reported as *Chorocaris* sp. from the Kairei Field in the Indian Ocean (Van Dover *et al.*, 2001), although that species now appears to be a member of the genus *Mirocaris* (T. Komai, pers. comm., and Komai *et al.*, in press; see under *Mirocaris*). Another species of *Chorocaris* (as yet undescribed) has been found at vents on seamounts off New Zealand (Webber & Bruce, 2002, on the NIWA website at <http://www.niwa.co.nz/pubs/bu/05/blind>, and N. Bruce, pers. comm.), and Desbruyères *et al.* (1994) noted the possibility of the genus in samples from the Lau and Fiji basins; this needs confirmation. Shank *et al.* (1999) suggested, based on molecular evidence, that the genus (known at that time only from *C. chacei* in the Atlantic and *C. vandoverae* in the western Pacific) might be paraphyletic. We have listed the possibly erroneous report of an Indian Ocean species as *Chorocaris* sp. A and the Kermadec Ridge report as *Chorocaris* sp. B in our tables, with the following information.

Chorocaris sp. A. Van Dover *et al.* (2001: 820, fig. E) reported '*Chorocaris* sp.' from the Indian Ocean, Central Indian Ridge, Kairei Field. The species appears to be a member of *Mirocaris* rather than *Chorocaris* (see under *Mirocaris* sp. A. for materials and additional information). Thus, the *Chorocaris* sp. A in Table 1 is probably the same species as listed below (and in Table 1) under *Mirocaris* sp. A, although it is also possible that there is a species of *Chorocaris* in the Indian Ocean that was not collected.

Chorocaris sp. B. A few specimens of a shrimp species that appears to belong to *Chorocaris* have been found recently on seamounts of the Kermadec Ridge off New Zealand (R. Webber, pers. comm.; see also Clark & O'Shea, 2001; Webber, 2004).

CHOROCARIS CHACEI (WILLIAMS & RONA, 1986)

Type locality: North Atlantic Ocean, MAR, TAG vent field; 26°08.3'N, 44°49.6'W; 3620–3650 m.

Known range: North Atlantic Ocean, MAR, Snake Pit (23°N), TAG (26°N), Lucky Strike (37°17'N) and Logatchev vent fields (Williams & Rona, 1986; Martin & Hessler, 1990; Segonzac *et al.*, 1993; Shank, 1997, in Desbruyères & Segonzac, 1997: 193; Gebruk *et al.*, 2000a; Turnipseed *et al.*, 2004).

Material: type locality; NOAA VENTS Program, R/V *Researcher*; 3 August 1985; dredge haul; USNM 228452 (holotype, female), USNM 228453 (paratypes, 1 female), USNM 228524 (6 juveniles) (Williams & Rona, 1986).

–Snake Pit hydrothermal vent field, Les Ruches site; 23°22'N, 44°56'W; HYDROSLAKE, *Nautile* dives 08 and 10, cruise (Segonzac, de Saint Laurent & Casanova, 1993).

–North Atlantic Ocean; JOIDES, DV *Resolution*, leg 106, site 649, Hole 649H; 23°22.160'N, 44°57.072'W; 3522 m; 17 December 1985; USNM 228526 (19 juvenile females) (Williams, 1987, as *Rimicaris chacei*).

–North Atlantic Ocean, MAR, Lucky Strike hydrothermal vent site; *Alvin* dive 2607; non-type, 1 specimen (Martin, Signorovitch & Patel, 1998b).

Remarks: Originally described as *Rimicaris chacei* by Williams & Rona (1986), this species was transferred to the genus *Chorocaris* by Martin & Hessler (1990). Williams & Rona (1986) indicated that one juvenile specimen would be sent to each of the following institutions: LACM, MCZ, BMNH, RMNH, MNHN. Shank (1997, in Desbruyères & Segonzac, 1997) commented on the ecology of this species as compared with the sympatric and numerically dominant *Rimicaris exoculata*. Casanova *et al.* (1993) and Segonzac *et al.* (1993) described feeding morphology and behaviour in this species, and Lakin *et al.* (1997) described the morphology of the eye. Carotenoid pigments were analysed by Nègre-Sadargues *et al.* (2000). The organ of Bellonci and sinus gland were described by Charman-tier-Daures & Segonzac (1998). Vereshchaka *et al.* (2000) studied carbon and nitrogen composition. Martin *et al.* (1998b) examined the carpal cleaning brush of this species in comparison with that of other vent shrimp species. The species was listed by Desbruyères *et al.* (2000: table 4) as rare/patchy but at the same time a dominant species on chimneys and walls at Lucky Strike and on chimney bases at Snake Pit, TAG, Rainbow and Menez Gwen.

CHOROCARIS PAULEXA MARTIN & SHANK, 2005

Type locality: South Pacific Ocean, southern EPR, Rapa Nui Homer Vent Site; 17°37.220'S, 113°15.123'W (Martin & Shank, 2005).

Known range: limited to type locality and other nearby vents in the Rapa Nui (Easter Microplate) area.

Material: type locality; *Alvin* dive 3296; 2596 m; 27 October 1998; LACM CR 1998–151.1 (holotype, ovigerous female), LACM CR 1998–151.2 (paratype, non-ovigerous female, slightly abnormal) (Martin & Shank, 2005). Seven other specimens, not designated as paratypes, from nearby vents are also housed at the LACM as LACM CR 1998–152.1 (2 females, 1 of which is ovigerous, *Alvin* dive 3283), LACM CR 1998–153.1 (1 male, 1 female, *Alvin* dive 3292) and LACM CR 1998–154.1 (3 small damaged specimens, *Alvin* dive 3294).

Remarks: This recent find extends the range of the genus *Chorocaris* virtually across the entire Pacific Basin, from the Mariana Back-Arc Basin where *C. vandoverae* is found (Martin & Shank, 2005). This species is almost certainly what Segonzac *et al.* (1997) described from the 17–19°S and Easter Microplate region as ‘alvinocaridid shrimp *Chorocaris*-like . . . rarely observed on previously described 17–19°S sites . . . present on the Pito seamount’ (see also Naar *et al.*, 2004). The species occurs in large numbers on black smokers (Martin & Shank, 2005).

CHOROCARIS VANDOVERAE MARTIN & HESSLER, 1990

Type locality: Western Pacific Ocean, Mariana Back-Arc Spreading Center, Alice Springs vent field; 18°12.599'N, 144°42.431'E; 3640 m.

Known range: Pacific Ocean, Mariana Back-Arc Basin, Burke and Alice Springs vent fields, 3640 – 3660 m (Martin & Hessler, 1990; Shank, 1997, in Desbruyères & Segonzac, 1997: 194).

Material: type locality; *Alvin* dive 1843; 3640 m; 4 May 1987; hand nets attached to manipulator; USNM 243946 (holotype, female). USNM 243947 (paratypes, 10 specimens), LACM 87-274.1 (paratypes, 7 specimens), MNHN-NA 11924 (paratypes, 10 specimens), SIO (La Jolla) (non-types, 2 specimens) (Martin & Hessler, 1990).

–Burke vent field; Snail Pits and Anemone Heaven; 18°10.917–18°10.948'N, 144°43.210–144°43.204'E; *Alvin* dive 1836; 3660 m; 27 April 1987; hand nets attached to manipulator; LACM 87-273.1 (paratypes, 7 female specimens), SIO (non-types, 35 specimens) (Martin & Hessler, 1990). –Burke vent field; Snail Pits; 18°10.948'N, 144°43.204'E; *Alvin* dive 1835; 3660 m; 26 April 1987; hand nets attached to manipulator; LACM 87-272.1 (non-types, 12 specimens, examined also in Martin *et al.*, 1998b), SIO [non-types, 25 specimens (4 missing)] (Martin & Hessler, 1990).

–Alice Springs vent field; 18°10.0'N, 144°43.2'E; *Alvin* dive 1837; 3660 m; 28 April 1987; hand nets attached to manipulator; SIO (non-types, 10 specimens, all frozen) (Martin & Hessler, 1990).

Remarks: This species is typically found alongside mussels and snails of the genus *Alviniconcha* (Shank, 1997, in Desbruyères & Segonzac, 1997). Martin & Hessler (1990) noted the existence of additional specimens probably belonging to this species in the collections of R. Hessler, C. L. Van Dover, S. Ohta and the Emperor of Japan. Martin *et al.* (1998b) examined the carpal cleaning brush of this species in comparison with that of other vent shrimp species. The feeding biology of this species has been discussed in several papers (Casanova *et al.*, 1993; Segonzac *et al.*, 1993; Gebruk *et al.*, 2000b).

GENUS *MIROCARIS* VERESHCHAKA, 1996

The genus *Mirocaris*, originally established by Vereshchaka (1996b) to accommodate *M. keldyshi*, was rediagnosed by Komai & Segonzac (2003). At the same time, those authors synonymized *M. keldyshii* with *M.* (formerly *Chorocaris*) *fortunata* described by Martin & Christiansen (1995), such that the genus currently contains one species. We are aware of a second species: the shrimp tentatively identified as *Chorocaris* sp. by Van Dover *et al.* (2001) from the Indian Ocean vents is apparently a species of *Mirocaris* (T. Komai, pers. comm.), which we have listed in the tables as *Mirocaris* sp. A.

Mirocaris sp. A. Van Dover *et al.* (2001) reported *Chorocaris* sp. from Indian Ocean hydrothermal vents (Kaarei & Edmonds sites). Although we cannot rule out the possibility of a species of *Chorocaris* at those sites, the most common ‘*Chorocaris*-like’ shrimp collected from those sites is actually an undescribed species of *Mirocaris* that will soon be described (Komai *et al.*, in press). It is most probable that this is the same species referred to by Van Dover *et al.* (2001) as *Chorocaris* sp. Material of the new species of *Mirocaris* is currently in the JAMSTEC collections and at the Natural History Museum of Los Angeles County, on loan to J. Martin from T. Shank. Material upon which the description is being based will be deposited at the National Science Museum, Tokyo, and the Natural History Museum of Los Angeles County.

MIROCARIS FORTUNATA (MARTIN & CHRISTIANSEN, 1995)

Type locality: North Atlantic Ocean, MAR, Azores, Lucky Strike hydrothermal vent, vent site 3 (Sintra site); 37°17'N, 32°16'W; 1624 m.

As *Mirocaris keldyshi* Vereshchaka, 1997b: Atlantic Ocean, MAR, TAG vent field, 30 m SW of Point ‘0’, set at sta. 3369, retrieved at sta. 3394; 26°09'N, 44°50'W; 3650 m.

Known range: North Atlantic Ocean, MAR, at Logatchev, TAG, Broken Spur, Rainbow, Snake Pit, Lucky Strike and Menez Gwen hydrothermal vent fields, 14°45.19'N to 37°50'N [Colaço *et al.*, 1998; Martin & Christiansen, 1995 (as *Chorocaris fortunata*); Segonzac, 1997, in Desbruyères & Segonzac, 1997; Vereshchaka, 1997b (as *Mirocaris keldyshi*); Turnipseed *et al.*, 2004].

Material: type locality; American Lucky Strike Cruise, *Alvin* dive 2607, 1624 m; 4 June 1993. LACM 93-45.1 (holotype, ovigerous female), LACM 93-45.2 (paratypes, 21 specimens), LACM 93-45.3 (paratypes, 39 specimens), MNHN (paratypes, 5 specimens), ULP

(paratypes, 5 specimens) (Martin & Christiansen, 1995).

North Atlantic Ocean, MAR:

–Menez Gwen hydrothermal vent field; 37°50'N, 31°31'W; DIVA2; dive 13/924; 850 m; 15 June 1994; slurp gun; MNHN-Na 14139 [non-types, 3 males, 23 females (2 ovigerous)] (Komai & Segonzac, 2003).

–Lucky Strike hydrothermal vent field; 14 September 1992; paratype(?), 1 specimen (Martin & Christiansen, 1995). –Lucky Strike hydrothermal vent field, Eiffel Tower site; 37°17.20'N, 32°16.20'W; ATOS dive 119-17; 1689 m; 16 July 2001; slurp gun; MNHN-Na 14142 [non-types, 33 females (7 ovigerous)] (Komai & Segonzac, 2003).

–Rainbow; 36°13.44'N, 33°54.20'W; ATOS dive 107-05; 2285 m; 1 July 2001; slurp gun; MNHN-Na 14140 (non-types, 6 males, 5 females, 2 juveniles), MNHN-Na 14141 (non-types, 5 females) (Komai & Segonzac, 2003).

–Broken Spur vent site; 29°10'N, 43°10'W; *Alvin* dive 2624; 3044 m; 26 June 1993; non-types, 10 specimens (2 ovigerous) (Martin & Christiansen, 1995: 221, citing pers. comm. with Dr. E. Southward, Plymouth).

–Snake Pit vent site (Turnipseed *et al.*, 2004); location of specimens not known.

–Logatchev, Irina 2 site; 14°45.19'N, 44°58.76'W; MICROSMOKE, *Nautila* dive 20; 3008 m; slurp gun; MNHN-Na 14143 (non-types, 2 males, 5 females) (Komai & Segonzac, 2003). –Logatchev, Irina 2 site; 14°45.19'N, 44°58.76'W; DIVERSExpedition, *Alvin* dive 3668; 3008 m; 7 July 2001; slurp gun; MNHN-Na 14144 [non-types, 5 males, 19 females (2 ovigerous)], CBM-ZC 6445 (non-types, 1 male, 2 females) (Komai & Segonzac, 2003).

–(As *M. keldyshi*) Atlantic Ocean, MAR, TAG vent field, 30 m SW of Point 'O', set at sta. 3369, retrieved at sta. 3394; 26°09'N, 44°50'W; 34th cruise of R/V *Akademik Mstislav Keldysh* for British–Russian Programme BRAVEX-94, *Mir-1*, *Mir-2*; 3650 m; 22 September 1994; baited traps, 5-day exposure; Oceanology Institute (Moscow) (holotype, female), Oceanology Institute (Moscow) (paratypes, 17 females), Oceanology Institute (Moscow) (paratypes, 7 males) (Vereshchaka, 1997b).

Remarks: This species, originally described as *Chorocaris fortunata* by Martin & Christiansen (1995), was transferred to the genus *Mirocaris* by Vereshchaka (1997b) along with a second species (*M. keldyshi*) that has since been found to be a junior synonym of *M. fortunata* (see Shank *et al.*, 1999; Komai & Segonzac, 2003; and below). *Mirocaris fortunata* appears to have the broadest range of any alvinocaridid shrimp, occurring at seven vent sites along the MAR. Desbruyères *et al.* (2000: table 4) listed it as a common

to rare/patchy species that is ecologically dominant on chimney walls or chimney bases at Broken Spur, Rainbow, Lucky Strike and Menez Gwen. Because it occurs to the south [e.g. at Logatchev, Gebruk *et al.*, 2000a, where Desbruyères *et al.*, 2000, listed it (as *M. keldyshi*) as a 'dominant accompanying species'] and to the north of the Snake Pit (MARK) site, the relative scarcity of reports of this species at Snake Pit (e.g. Turnipseed *et al.*, 2004) is curious, especially given substantial faunal overlap between the Snake Pit and TAG sites (see Van Dover, 1995: 264). Three other shrimp species are known from the Snake Pit site: *Alvinocaris markensis* Williams, 1988, *Chorocaris chacei* (Williams & Rona, 1986) and *Rimicaris exoculata* Williams & Rona, 1986. This 'gap' (few reports and few numbers) in the distribution of *M. fortunata* – and the general similarity of shrimps from the genera *Chorocaris* and *Mirocaris* – might indicate that a detailed comparison between the specimens of *C. chacei* collected from Snake Pit (see Segonzac *et al.*, 1993) and the type series of *M. fortunata* is warranted. Colaço *et al.* (1998) noted the occurrence of this species at Menez-Gwen. Kuenzler *et al.* (1996) described eye morphology in this species (which, at the time, was still known as *Chorocaris fortunata*). Martin *et al.* (1998b) described the carpal cleaning brush and compared it with those of other vent shrimp genera and species. Dixon *et al.* (2001) studied rates of cell division. Tyler & Dixon (2000) studied the tolerance of larvae to pressure and temperature. Ramirez-Llodra, Tyler & Copley (2000) discussed its reproductive biology, in a study that also included *Chorocaris vandoverae*. Komai & Segonzac (2003) found *Mirocaris keldyshi* to be a junior synonym of *M. fortunata*; the authors noted that the slight morphological differences between the two mentioned by Shank *et al.* (1999) and Gebruk *et al.* (2000a) probably were not valid (i.e. were attributable to intraspecific variation). Thus, all records and information concerning *M. keldyshi* have been combined with those of *M. fortunata* under the latter name. Vereshchaka (1997b) indicated that 1 female and 1 male paratype of the material originally described as *M. keldyshi* would be transferred to each of the following collections: ZMUC, MNHN, RMNH. Evidently, such specimens have not yet been deposited at the RMNH in Leiden (reviewer citing C. H. J. M. Fransen, pers. comm.).

GENUS NAUTILOCARIS KOMAI & SEGONZAC, 2004
NAUTILOCARIS SAINTLAURENTAE KOMAI & SEGONZAC,
2004

Type locality: North Fiji Basin, White Lady site, 16°59.50'S, 173°55.47'E, STARMER II, dive 10, 2000 m.

Known range: Known only from the type locality and from the Lau Basin's Vai-Lili site (Komai & Segonzac, 2004).

Material: type locality; 5 July 1989; slurp gun; MNHN-Na 15261 (holotype female). –same data; MNHN-Na 15262 (paratypes, 3 males and 4 females). –Lau Basin, Vai-Lili site; 22°13'S, 176°38'W; BIOLAU BL 06; 1750 m; 18 May 1999; baited trap; MNHN-Na 15263 (paratypes, 1 male, 2 females). –Vai-Lili site; BIOLAU BL 10; 22 May 1989; slurp gun; MNHN-Na 15264 (paratypes, 2 males, 3 females). –same data; CBM-ZC 7976 (paratypes, 1 male and 1 female).

Remarks: Komai & Segonzac (2004) described the genus *Nautilocaris* as being morphologically intermediate between the monotypic genus *Mirocaris* (*M. fortunata*) and the genus *Alvinocaris*. The White Lady site of the North Fiji Basin was described by them as consisting of 'chimneys of anhydrite from one to three metres height, emitting vigorous transparent hydrothermal fluids at 296 °C'; the Lau Basin site where the species is found is similar but contains 'tall black and white smokers venting fluids up to 400 °C' (Komai & Segonzac, 2004: 1187).

GENUS *OPAPELE* WILLIAMS & DOBBS, 1995

OPAPELE LOIHI WILLIAMS & DOBBS, 1995

Type locality: Pacific Ocean, Hawaii, Loihi Seamount; 18°55'N, 155°16'W; 980 m.

Known range: limited to the type locality.

Material: type locality; *Pisces V*, dive 213; 980 m; 28 August 1992; baited traps, baited with exocetid fish; USNM 251447 (holotype, female), USNM 251448 (allotype, male), USNM 251449 (paratypes, 6 males, 7 females) (Williams & Dobbs, 1995).

–*Pisces V*, dive 242; 980 m; 7 September 1993; baited traps, baited with exocetid fish; USNM 251450 (paratypes, 26 females) (Williams & Dobbs, 1995).

Remarks: Shank *et al.* (1999) mentioned two specimens collected by the US Navy submersible *Turtle* (DSV-3) in 1993. An eruption of the Loihi volcano in 1996 might have eliminated or severely decreased the population size of this species.

GENUS *RIMICARIS* WILLIAMS & RONA, 1986

Since the original erection of this distinctive genus by Williams & Rona (1986) to accommodate *Rimicaris exoculata*, the genus description has been slightly modified twice. Martin & Hessler (1990) restricted the diagnosis (by removing *Rimicaris chacei* to their newly created genus *Chorocaris*), and Watabe & Hashimoto (2002) expanded it slightly to accommodate

R. kairei (see below). At least two described species (*R. aurantiaca* and *Iorantia concordia*; see below) were later determined to be based on the juvenile form of *R. exoculata*. The report of *Rimicaris* from the PAC-MANUS site in the Manus Basin (Hashimoto & Ohta, 1999) was apparently in error, as the genus has not been recorded to date from any of the western Pacific sites.

RIMICARIS EXOCULATA WILLIAMS & RONA, 1986

Type locality: North Atlantic Ocean, MAR, TAG vent field; 26°08.3'N, 44°49.6'W; 3620–3650 m.

Known range: North Atlantic Ocean, MAR, from hydrothermal vent fields at the Snake Pit, TAG, Broken Spur, Lucky Strike, Logatchev and Rainbow sites, 1700–3650 m (Williams & Rona, 1986; Van Dover *et al.*, 1988; Galkin & Moskalev, 1990a; Segonzac, 1992; Segonzac, 1997, in Desbruyères & Segonzac, 1997; Segonzac *et al.*, 1993; Vereshchaka, 1997a; Gebruk *et al.*, 2000a; Turnipseed *et al.*, 2004).

Material: type locality, NOAA VENTS Program, R/V *Researcher*; 3 August 1985; dredge haul. USNM 228443 (holotype male), USNM 228444 (allotype female), USNM 228445 (paratypes, 5 males, 6 females), USNM 228446 (paratypes, 69 males), USNM 228447 [paratypes, 64 females, (1 ovigerous)], USNM 228448 (paratypes, 14 juveniles), USNM 228449 (non-type, 1 male, fragmented), USNM 228450 (non-type, 1 female, fragmented), USNM 228451 (unsexed fragments) (Williams & Rona, 1986).

–Rainbow hydrothermal vent field; 36°13.40'N, 33°54.07'W; 2285 m; PICO, *Nautilite* dive 1264; 30 June 1998; slurp gun; CBM-ZC 6446 (1 male, 1 female) (Komai & Segonzac, 2003).

–TAG hydrothermal vent field, 26°8'N, 44°49'W; 3630 m (Van Dover *et al.*, 1988, specimen data not provided).

–Snake Pit hydrothermal vent field, Elan site, site 649, Hole 649H; 23°22.160'N, 44°57.072'W; 3522 m; JOIDES, D/V *Resolution*, leg 106; 17 December 1985, USNM 228525 (2 males, 2 females) (Williams, 1987). –Elan site; 23°22.20'N, 44°57.08'W; 3500 m; MICRO-SMOKE; dive 01; 14 November 1995; MNHN-Na, registration number not provided (6 juveniles) (Komai & Segonzac, 2003). –Les Ruches site; 23°22'N, 44°56'W; HYDRO-SNAKE, *Nautilite* dives 03, 08 and 10 (Segonzac *et al.*, 1993).

Williams & Rona (1986) indicated that 2 males and 2 females would be sent to each of the following: LACM, MCZ, BMNH, RMNH, MNHN. At least two paratypes were deposited at MNHN, as noted by Watabe & Hashimoto (2002). Nuckley *et al.* (1996) mentioned additional material from *Alvin* dives 2613, 2618 and 2623.

–As *Rimicaris aurantiaca*: North Atlantic Ocean, MAR, Snake Pit hydrothermal vent field, Moose vent (Elan) site; 23°22.1'N, 44°57.0'W; 3520 m (type locality for *Rimicaris aurantiaca*); R/V *Atlantis II* cruise 129-7, *Alvin* dive 2618; 3520 m; 19 June 1993; LACM 93-46.3 (holotype: female), LACM 93-46.2 (paratypes, 17 adults) (Martin, Signorovitch & Patel, 1997; mentioned also by Martin *et al.*, 1998b).

–As *Iorania concordia*: North Atlantic Ocean, MAR, TAG vent field, point 'D', sta. 3415; 26°09'N, 44°50'W; 3650 m (type locality for *Iorania concordia*).

34th cruise of R/V *Akademik Mstislav Keldysh* for British–Russian Programme BRAVEX-94, *Mir-2*; 3650 m; 24 September 1994; slurp gun; Oceanology Institute (Moscow) (holotype, female), Oceanology Institute (Moscow) (paratypes, 30 females) (Vereshchaka, 1996b). Vereshchaka (1996b) additionally indicated that one female paratype (of *I. concordia*) would be transferred to each of the following collections: ZMUC, MNHN, RMNH.

Remarks: *Rimicaris exoculata* is perhaps the most extensively studied vent decapod to date. It is known only from sites along the MAR, where it occurs in active swarms that may be as dense as 2500 individuals per square metre and on chimney walls where temperatures range from 15 to 30 °C. The density and unusual eye morphology and function have resulted in photographs and brief articles on the species appearing in a large number of popular as well as scientific articles (e.g. Monastersky, 1989; Tunnicliffe, 1991: 337, fig. 4B, 1992b; Van Dover, 1995: 262, fig. 3a, d; Copley *et al.*, 1997, 1999; Herring, Gatén & Shelton, 1999). Renninger *et al.* (1995) studied sulphide as a chemical stimulus in this species, Vereshchaka *et al.* (2000) reported on carbon and nitrogen composition, and general physiology was reviewed by Childress & Fisher (1992). Feeding biology and ecology were studied by Van Dover *et al.* (1988) and Rieley *et al.* (1999); feeding morphology and behaviour were further investigated by Gebruk *et al.* (1993, 2000b), Casanova *et al.* (1993), Segonzac *et al.* (1993) and Polz *et al.* (1998). In part because bacteria are involved with feeding in this species, the associated bacteria have been examined by many workers (e.g. see Raguénès *et al.*, 2003). Lipid fatty-acid composition was studied in a series of papers by Pond, Dixon & Sargent (1997b), Pond *et al.* (1997a, c, 2000a, b), Allen Copley, Tyler & Varney (1998), Allen Copley, Copley & Tyler (2001) and Rieley *et al.* (1999). Carotenoid pigments were analysed by Nègre-Sadargues *et al.* (2000). The morphology and function of the novel eye structure in this species, consisting of rhodopsin-containing organs beneath the transparent dorsal cuticle of the carapace, and the question of what these organs might be perceiving, have been the subject of several studies, including

those of Pelli & Chamberlain (1989), Van Dover *et al.* (1989), Chamberlain (2000), Chamberlain *et al.* (1994a, b), Johnson *et al.* (1995), O'Neil *et al.* (1995), Curra *et al.* (1996), Nuckley *et al.* (1996, as *Rimicaris* sp.), Kuenzler *et al.* (1996, as ?*Chorocaris* [juveniles]), Jinks *et al.* (1998), Gatén *et al.* (1998a, b), Herring *et al.* (1999) and others (see also Meyer-Rochow, 2001). Dixon *et al.* (2001) studied rates of cell division, Compere *et al.* (2002) studied sulphide detoxification, Galchenko *et al.* (1989) studied CO₂ assimilation, Lallier & Truchot (1997) examined haemocyanin properties, and Geret *et al.* (2002), Larsen *et al.* (1997; arsenic) and Martins *et al.* (2001; mercury) investigated the bioaccumulation or presence of metals. Studies of allozyme data from populations at TAG and Broken Spur sites showed no significant genetic differentiation, suggesting gene flow among these sites is not restricted (Creasey, Rogers & Tyler, 1996). Ramirez-Llodra *et al.* (2000) addressed aspects of reproductive biology. The organ of Bellonci and sinus gland were described by Charmantier-Daures & Segonzac (1998). Larvae and postlarvae of alvinocaridids, some of which undoubtedly belong to this species, have been collected at a distance from MAR vents (Herring, 1998; Herring & Dixon, 1998; see also Dixon *et al.* 1998). Martin *et al.* (1998b) examined the carpal cleaning brush of this species in comparison with that of other vent shrimp species (see also comments above under *R. aurantiaca* concerning this brush).

The very different coloration (usually bright orange, in large part due to the four-fold increase in carotenoids; see Nègre-Sadargues *et al.*, 2000) and morphology of juveniles of *R. exoculata* have led to taxonomic confusion (e.g. see comments and discussion in Murton, Van Dover & Southward, 1995; Creasey *et al.*, 1996; Polz *et al.*, 1998; Vereshchaka, 1996a, b, 1997a). Several authors were convinced early on that the small orange shrimp found at many MAR sites was a distinct species until it was shown (mostly by Shank, Lutz & Vrijenhoek, 1998b; Shank *et al.* 1999) that some of these were simply juveniles of *R. exoculata*. Indeed, juveniles of *R. exoculata* were given at least two different names, *Rimicaris aurantiaca* (by Martin *et al.*, 1997) and *Iorania concordia* (by Vereshchaka, 1996b).

The genus *Iorania* and the species *Iorania concordia*, both described by Vereshchaka (1996b), were based on juveniles of *Rimicaris exoculata*, according to genetic studies by Shank *et al.* (1998b, 1999). Thus, all distributional and collection records of *Iorania* can be combined with those of *R. exoculata*. This finding of course brings up questions about the morphological differences noted by Vereshchaka (1996b), especially those larger differences (such as the extended 'lash' on the first maxilliped) that he attributed to generic significance. Ontogenetic studies of this species are needed to resolve this issue.

The species described as *Rimicaris aurantiaca* by Martin *et al.* (1997) was, like *Iorania concordia*, also based on juveniles of *R. exoculata*, which, as noted above, differ from adults dramatically in coloration and to a lesser extent in morphology. Thus, there are three names in the literature that all refer to one species (*Rimicaris exoculata*): *R. exoculata*, *R. aurantiaca* and *Iorania concordia*, only the first of these is still a valid name. Interestingly, characters of the carpal brush cleaning setae on the cheliped of '*Rimicaris aurantiaca*' (the juvenile of *R. exoculata*) were intermediate between what is found in *Chorocaris* (with a well-developed carpal brush) and what is found in adult *Rimicaris exoculata* (which lacks a carpal cleaning brush) (Martin *et al.*, 1998b). The original conclusion of Martin *et al.* (1998b) – that characters of '*R. aurantiaca*' were morphologically intermediate between those of *Chorocaris* species and *Rimicaris exoculata* – must now be reinterpreted as an ontogenetic progression; *Rimicaris exoculata* has a poorly developed carpal brush as a juvenile but loses it by the adult stage.

T. Komai and M. Segonzac (pers. comm.) inform us that indeed the postlarval stages of *R. exoculata* can be roughly divided into three ontogenetic stages based on morphology, thus explaining to some degree the previous confusion.

RIMICARIS KAIREI WATABE & HASHIMOTO, 2002

Type locality: Indian Ocean, Central Indian Ridge, Kairei Field; 25°19.16'S, 70°02.40'E; 2454 m.

Known range: limited to the type locality (Kairei vent field) and the Edmonds vent field (approximately 160 km NNW of the Kairei field), Indian Ocean, 2415–3320 m (Van Dover *et al.*, 2001; Watabe & Hashimoto, 2002).

Material: type locality; KR00-05 Indian Ocean Cruise (JMSTC), ROV *Kaiko*, dive 10K#168; 26 August 2000; suction sampler, hydraulically driven; NSMT-Cr-14112 (holotype male), JMSTC 032688 (paratypes, 1 male, 1 female); MNHN-Na 13797 (paratypes, 1 male, 1 female); NSMT-Cr 14113 (paratypes, 1 male, 1 female), USNM 2026541 (paratypes, 1 male, 1 female), ZRC 2001.1053 (paratypes, 1 male, 1 female) (Watabe & Hashimoto, 2002).

Remarks: This species, first mentioned by Hashimoto *et al.* (2001) and reported as *Rimicaris* aff. *exoculata* by Van Dover *et al.* (2001: 820–822, fig. 2A, B, G), is morphologically extremely similar to *R. exoculata* from the MAR systems (T. Komai, pers. comm.). Indeed, some of the morphological characters proposed by Watabe & Hashimoto (2002) for separating the two species – length of the antennal flagella and stoutness of the third to fifth pereopods – now appear

to be unreliable because of overlap of morphological variation, although other slight differences (e.g. the higher number of tufts of dense setae on the carapace of *R. exoculata*) do exist (T. Komai, pers. comm.). Van Dover *et al.* (2001) compared *mtCOI* gene sequences from specimens collected at the Kairei and Edmonds vents and found essentially no differences; only slight differences were detected between *R. kairei* and *R. exoculata* from the MAR sites. Trophic relationships among Kairei vent invertebrates including this species were addressed by Van Dover (2002a).

GENUS *SHINKAICARIS* KOMAI & SEGONZAC, 2005A
SHINKAICARIS LEUROKOLOS (KIKUCHI & HASHIMOTO, 2000)

The genus *Shinkaicaris* was erected by Komai & Segonzac (2005a) to accommodate the former *Alvinocaris leurokolos* (see above under *A. leurokolos*).

FAMILY CRANGONIDAE HAWORTH, 1825
GENUS *PARACRANGON* DANA, 1852

Fujikura *et al.* (1995) reported the presence of an unidentified species of *Paracrangon* from the Hatsushima site in Sagami Bay (35°00.2'N, 139°13.5'E) (listed as *Paracrangon* sp. A in Table 1) and in the Okinawa Trough at Minami-Ensei Knoll (28°24.4'N, 127°37.9'E) (*Paracrangon* sp. B). The latter record from the Minami-Ensei Knoll (*Paracrangon* sp. B) was also noted by Fujikura *et al.* (1996).

FAMILY GLYPHOCRANGONIDAE SMITH, 1884

GENUS *GLYPHOCRANGON* A. MILNE-EDWARDS, 1881

The genus *Glyphocrangon* is represented by some 39 species. These shrimp are predominately deep-water species, known from depths of 258–6364 m, and, collectively, they occur in every major ocean basin (Chace, 1984). Only one species has been noted from an area adjacent to active hydrothermal vents. Watabe & Miyake (2000) reported the presence of the genus at Hatoma Knoll in the Okinawa Trough.

GLYPHOCRANGON CF. *GRANULOSIS* BATE, 1888

Type locality: western Bismarck Sea; 02°33'S, 144°04'E; 1957 m.

Known range: tropical western Pacific Ocean from Bismarck Sea to Indonesia and the Philippines, with the record of Watabe & Miyake (2000), if correct, extending the range northward to the Okinawa Trough.

Occurrence at vents or seeps: Hatoma Knoll, Okinawa Trough (see below).

Material: As far as we are aware, no material has been collected.

Remarks: Watabe & Miyake (2000: 32) reported this species from the Hatoma Knoll in the Okinawa Trough. However, the authors indicated that the shrimp were observed in areas of the site not directly influenced by hydrothermal activity. A recent study by Komai has restricted *Glyphocrangon granulosis* to only the female holotype (from off New Guinea); subsequent records of '*G. granulosis*' (e.g. Chace, 1984) have been referred to a separate and newly identified species, *Glyphocrangon major* Komai, 2004 (Komai, 2004, and T. Komai, pers. comm.). Thus, the Hatoma Knoll species is in all likelihood not true *G. granulosis*, and its true identity is not known.

FAMILY HIPPOLYTIDAE DANA, 1852

GENUS *LEBBEUS* WHITE, 1847

Although species have been reported from several hydrothermal vent sites, members of the genus *Lebbeus* are almost certainly vagrants rather than endemics, as they occur in other areas of the deep sea; indeed, *Lebbeus* is one of the more widely occurring genera of deep sea hippolytid shrimp (M. Wicksten, pers. comm., see also Wicksten, 1978, 1982; Wicksten & Méndez, 1982; Hayashi, 1992; Fransen, 1997; Komai, 2001). Most of the known species are found in the northern Pacific Ocean (Wicksten, 1982; Hayashi, 1992). Species of *Lebbeus* have been observed along with *Alvinocaris* shrimps and have been attracted to baited traps on the Iheya Ridge of the Mid-Okinawa Trough (Kim & Ohta, 1991: fig. 7, 2); shrimps of the genus *Lebbeus* also have been collected from baited traps near vents in the eastern Pacific (T. Shank, unpubl. data; see below under *L. bidentatus*). Two described species of *Lebbeus* have been reported from vents in the Pacific (Desbruyères & Segonzac, 1997: 197–198). The species reported as *Lebbeus* sp. by Ohta (1990a: fig. 7) from the Iheya Ridge was later identified as *Lebbeus washingtonianus* by Kikuchi & Ohta (1995) (see below). Fujikura *et al.* (1999, table) listed *Lebbeus* sp. at Sagami Bay seeps. Fransen (1997) redescribed in detail all three species described originally by Zarenkov – *L. bidentatus*, *L. carinatus* and *L. curvirostris* – based on the original type material. There is also a catalogued specimen of *Lebbeus* (though currently unnamed) at the Field Museum (FMNH 11289) that was collected on DSMV *Alvin* dive 3940 at Caldera, an off-axis site (approximately 1.5 km off axis) in the EPR where there is considerable hydrothermal activity (J. Voight, pers. comm.).

Lebbeus sp. A. The unidentified species of *Lebbeus* reported from the Lau Basin by Desbruyères *et al.* (1994) is referred to in Table 1 as *Lebbeus* sp. A.

Lebbeus sp. B. The species of *Lebbeus* from Sagami Bay reported by Fujikura *et al.* (1999) is listed in Table 1 as *Lebbeus* sp. B.

LEBBEUS BIDENTATUS ZARENKOV, 1976

Type locality: R/V *Academik Kurchatov*, sta. 276, off Chile, 1680 m (Fransen, 1997, after Zarenkov, 1976).

Known range: Known only from the type locality (but see below). The species has not been collected or reported since its original description (Fransen, 1997). The only possible vent occurrence consists of the specimens noted below.

Material: The single holotype was the only specimen known to Fransen (1997) at the time of his redescription of the species. Fransen referred to the male holotype as having a carapace length of 15.3 mm and being registered as Ma 4046 (Zoological Museum of the Moscow Lomonossov State University). Unpublished collections of shrimp of the genus *Lebbeus* that 'key' to this species (based mostly on the length of the rostrum and number of epipods) were collected from traps near a vent field in the southern portion of the EPR (T. Shank & J. Martin, unpubl. data). We are aware of 4 specimens possibly belonging to this species (see below) that were collected in a baited trap from a vent field on the southern EPR. The specimens were collected by Tim Shank and donated to the Natural History Museum of Los Angeles County (LACM CR 1999-050.1-3; LACM CR 1999-051.1).

Remarks: Zarenkov's (1976) description of *Lebbeus bidentatus* is woefully inadequate by today's standards, with incomplete illustrations, and apparently some of the illustrations do not match the holotype (Fransen, 1997). Fransen's (1997) redescription is far more detailed, and will eventually allow us to identify the EPR shrimp. Zarenkov (1976) gave no information on the substrate. Tentative identification (because of the uncertainties noted above concerning Zarenkov's descriptions and specimens) was provided for us by M. K. Wicksten, Texas A&M University.

LEBBEUS 'CARINATUS' DE SAINT LAURENT, 1984

Type locality: Pacific Ocean, EPR, 12°49'N, 103°56.3'W; 2620 m.

Known range: Known only from the type locality (de Saint Laurent, 1984: 355, de Saint Laurent, 1997, in Desbruyères & Segonzac, 1997).

Material: type locality; BIOCYATHERM; dive 35; 12 March 1982; MNHN-B 5617 (holotype female) (de Saint Laurent, 1984).

Remarks: De Saint Laurent (1997, in Desbruyères & Segonzac, 1997: 197) noted that the species named by her in 1984 will have to be renamed, as another species of *Lebbeus* was named *L. carinatus* eight years earlier by Zarenkov (1976). The information given here thus refers to de Saint Laurent's species, and not to the 'true' *L. carinatus* named earlier by Zarenkov (1976). De Saint Laurent's species differs markedly from Zarenkov's (1976) species of the same name (as well as from *Lebbeus washingtonianus*) in lacking an epipod on the third pereopod (T. Komai, pers. comm.). However, there are also problems with Zarenkov's (1976) original *Lebbeus carinatus* description. It is based on a single damaged specimen that is 'apparently very close, if not identical to *L. washingtonianus*' (Hashimoto, 1997, in Desbruyères & Segonzac, 1997). Fransen (1997) redescribed in detail all three species described originally by Zarenkov (*L. bidentatus*, *L. carinatus* and *L. curvirostris*) based on the original type material.

LEBBEUS WASHINGTONIANUS (RATHBUN, 1902)

Type locality: North Pacific Ocean, United States, Washington, off Sea Lion Rock; 1253 m (as *Spirontocaris washingtoniana* Rathbun, 1902: 895, 1904: 76).

Known range: Eastern Pacific Ocean, west coast of North America, between Washington and Santa Rosa Island; Guaymas Basin (Butler, 1980).

Occurrence at vents or seeps: Western Pacific Ocean, Iheya Ridge and Minami-Ensei Knoll in the Mid-Okinawa Trough, at depths of 690–1808 m (Hashimoto, 1997, in Desbruyères & Segonzac, 1997).

Material: western Pacific Ocean, Okinawa Trough, Iheya Ridge, north-eastern slope; Clam Site; 27°32.70'N, 126°58.20'E; biological and ecological surveys of deep-sea benthic macrobiota and planktonic organisms in hydrothermal vent fields in the Okinawa Trough, *Shinkai 2000* dive 409; 1360 m; 10 June 1989; either hand net attached to manipulator, or baited trap (ambiguous); non-type, 1 female (Kikuchi & Ohta, 1995). –Clam Site; 27°32.70'N, 126°58.20'E; biological and ecological surveys of deep-sea benthic macrobiota and planktonic organisms in hydrothermal vent fields in the Okinawa Trough *Shinkai 2000* dive 480; 1360 m; 16 May 1990; either hand net attached to manipulator, or baited trap (ambiguous); non-type, 1 female (Kikuchi & Ohta, 1995). –Pyramid Site; 27°32.70'N, 126°58.20'E; biological and ecological surveys of deep-sea benthic macrobiota and planktonic organisms in hydrothermal vent fields in the Okinawa Trough *Shinkai 2000* dive 481; 1410 m; 17 May 1990; either hand net attached to manipulator, or baited trap (ambiguous); non-types, 3 females (Kikuchi & Ohta, 1995).

Remarks: If the species of *Lebbeus* reported from the Mid-Okinawa Trough is indeed *L. washingtonianus*, then this is a geographically very widespread and clearly non-endemic shrimp (although its density around hydrothermal vents can be 'extremely high'; Hashimoto, 1997, in Desbruyères & Segonzac 1997). However, there is reason to doubt the identity of the Mid-Okinawa Trough specimens. Although the genus is very widespread, species tend to be geographically narrowly distributed, and no species other than *L. washingtonianus* is known to range from the north-eastern Pacific to the subtropical western Pacific; thus, the range itself is suspect. Additionally, Kikuchi & Ohta's (1995) identification was based on comparison with other descriptions in the literature only (T. Komai, pers. comm.). Direct comparison of the Okinawan and eastern Pacific populations is needed to resolve this question. See Hashimoto (1997, in Desbruyères & Segonzac 1997), Butler (1980) and Fransen (1997) for additional references to non-vent literature (e.g. Rathbun, 1902; Schmitt, 1921; Holthuis, 1947; Wicksten, 1978). Vent literature includes Hashimoto *et al.* (1995) and Kikuchi & Ohta (1995). Butler (1980) reported the species from the Guaymas Basin, where there is hydrothermal activity, but it is not known if the species is found in association with such systems in the Guaymas Basin. See Kikuchi & Ohta (1995) for a redescription of the species based on specimens from the Okinawa Trough as well as vent and non-vent distributional records.

In addition to the above records, specimens attributed to '*Lebbeus* sp. aff. *washingtonianus*' (based on preliminary identifications by the late M. de Saint Laurent) were reported from the North Fiji and Lau basins by Komai & Segonzac (2004). For the same reasons noted above for the Okinawa Trough specimens, we are doubtful that the North Fiji Basin and Lau Basin specimens are true *L. washingtonianus*.

FAMILY OPLOPHORIDAE DANA, 1852

The family Oplophoridae contains approximately 61 species of caridean shrimp partitioned among 10 genera (see Chace, 1986, for a taxonomic review). Nearly all known species are mesopelagic, with many species known from the deep sea. Their reported presence at hydrothermal vent or seep areas is almost certainly facultative (see below).

GENUS ACANTHEPHYRA A. MILNE-EDWARDS, 1881
ACANTHEPHYRA PURPUREA A. MILNE-EDWARDS, 1881

Type locality: North Atlantic Ocean, off Portugal, Ilhas Berlengas; 39°25'N, 9°30'W; 2590 m.

Known range: North-eastern Atlantic Ocean, between 20° and 53°N, 600–1800 m (Chace, 1940, 1986; Zariquiey-Álvarez, 1968; Noël, 1992).

Occurrence at vents or seeps: limited to the Lucky Strike vent field of the MAR, 37°17'N, c. 1700 m (Bischoito, 1997, in Desbruyères & Segonzac, 1997: 189).

Material: Although specimens have been collected from the Lucky Strike vent field, we have not been able to locate them (see below). Non-vent specimens are mentioned in the reviews of Chace (1940, 1986), Zariquiey-Álvarez (1968) and Noël (1992).

Remarks: Bischoito (1997, in Desbruyères & Segonzac, 1997) described this species as bathypelagic to benthic on continental slopes and locally abundant. He also noted that at Lucky Strike, one specimen had been caught at a baited fish trap 'near the hydrothermal vent field'. We do not know the location of that specimen or any specimens from vent areas. M. Segonzac (pers. comm.) notes that the baited trap was 'clearly out of vent influence'; thus, the species is questionably included here and will probably be deleted from the next version of the handbook of vent fauna.

ACANTHEPHYRA EXIMIA SMITH, 1884

Type locality: North Atlantic Ocean, off United States; 35°09'50"N, 74°57'40"W; 1715 m.

Known range: widely distributed, found throughout the Indo-West Pacific and Atlantic oceans, and throughout basins of the Mediterranean Sea; from depths of 200–4700 m (see Pohle, 1992; Poupin, 1996).

Occurrence at vents or seeps: reported from cold seep off Japan (below).

Material: Although reported as observed from a cold seep at 1000–1220 m (bathyal zone of the Kanesu-nose Bank, Enshu-nada, Japan) by Ohta *et al.* (1995), we are aware of no collections of seep or vent material.

GENUS HYMENODORA SARS, 1877

HYMENODORA GLACIALIS (BUCHHOLZ, 1874)

Type locality: Arctic Ocean, off Greenland, north of Jan Mayen Island; ~74°N, 7°W.

Known range: Reported from the Sea of Okhotsk and the Bering Sea south to the Gulf of Panama in the Pacific, and from the Arctic Ocean and North Atlantic in the Atlantic; recorded depths range from near the surface in polar seas to 5610 m in the Pacific and to approximately 3900 m in the Atlantic (Havens & Rork, 1969; Butler, 1980; Hendrickx & Estrada Navarrete, 1996; Wicksten, 2002). Rathbun (1904) reported records further south, including off Ecuador in the

Pacific, but it is unclear if these reports were discounted by Butler (1980), who noted that this species has been confused often in the past with *H. gracilis* (see Wasmer, 1972; Butler, 1980). Wicksten (2002) additionally lists the western South Atlantic, Chile, the subantarctic Pacific and the south-western Indian Ocean (see Martin, 2003).

Occurrence at vents or seeps: limited to a single report from a slow spreading centre (the Gakkel Ridge) in the Arctic Ocean (Martin, 2003).

Material: Arctic Ocean, Gakkel Ridge; 4365–4456 m; joint US–German expedition, U. S. C. G. C. *Healy*; 24 August 2001; dredging; LACM CR 2001-027.1, vial 1F, sample HLY 01-02-D36, 'Moss Landing sample' (1 male). –same site; 3132–3282 m; U. S. C. G. C. *Healy*; 17 August 2001; dredge; LACM CR 2002-028.1, vial 2F, sample HLY 01-02-D22, 'Moss Landing sample' (1 male) (Edmonds *et al.*, 2003; Martin, 2003).

Remarks: Martin (2003) reported this species from Arctic hydrothermal vents (Gakkel Ridge), though he noted that in light of the method of collection, association with actual vent sites was open to question. The record of *Hymenodora frontalis* Rathbun, 1902, from the Gorda Ridge axial valley (Carey *et al.*, 1987), may represent an additional vent-associated species of the genus, though specific ecological information is unknown; as with *H. glacialis*, there is no firm indication that the species is associated with active venting.

GENUS JANICELLA CHACE, 1986

JANICELLA SPINICAUDA (A. MILNE-EDWARDS, 1883)

Type locality: Off Casablanca, Morocco: *Travailleur* sta. 65; 34°13'30"N, 7°43'W, 636 m.

Known range: 'Widespread mesopelagically in the tropical seas of the world, except in the eastern Pacific off the Americas' (Chace, 1986).

Occurrence at vents or seeps: limited to the Kick'em Jenny underwater volcano, eastern Caribbean (see below).

Material: Vent material restricted to: eastern Caribbean, Kick'em Jenny Volcano; 12°18.076'N 61°88.25'W; *Ronald H. Brown* cruise RB-03-03, Eastern Oceanics Remotely Operated Vehicle, dive 3; 261 m; 16 March 2003; LACM CR 2003-010.1 [2 individuals (one ovigerous)]; additional material in the private collection of K. Wishner.

Remarks: Clearly a non-endemic species, *Janicella spinicauda* (transferred from the genus *Oplophorus* by Chace, 1986) is believed to have been trapped in the toxic plume of gases issuing from the underwater Kick'em Jenny volcano during the diel migrations of

this species. Dead or at least moribund specimens were found on the crater floor (Martin *et al.*, 2005; Wishner *et al.*, 2005).

GENUS *OPLOPHORUS* A. MILNE-EDWARDS, 1881
OPLOPHORUS GRACILIROSTRIS A. MILNE-EDWARDS,
 1881

Type locality: Caribbean Sea, off Dominica, Lesser Antilles; 216 m.

Known range: 'Off southeastern Africa, Indian Ocean, Indonesia, Philippines, southern Japan, Fiji Islands, Hawaii, Gulf of Mexico, Bahamas, Caribbean Sea; mesopelagic' (Chace, 1986).

Occurrence at vents or seeps: limited to the Kick'em Jenny underwater volcano, eastern Caribbean (see below).

Material: Vent material restricted to: eastern Caribbean, Kick'em Jenny Volcano; 12°18.076'N 61°88.25'W; Ronald H. Brown cruise RB-03-03, Eastern Oceanics Remotely Operated Vehicle, Dive 3; 261 m; 16 March 2003; LACM CR 2003-010.3 (1 male); additional material in the private collection of K. Wishner.

Remarks: This species was collected along with *Janicella spinicauda* (see above) and the sergestid *Sergia* cf. *robusta* from the caldera of the Kick'em Jenny Volcano, eastern Caribbean (Martin *et al.*, 2005; Wishner *et al.*, 2005). Like *Janicella spinicauda*, the species was found on the floor of the submarine volcano and was probably trapped by toxic gases issuing from the sediment within the caldera.

GENUS *SYSTELLASPIS* BATE, 1888

Systellaspis is a relatively small genus, including only five named species (Chace, 1986). The genus has been collected from depths ranging between 291 and 3292 m in temperate and tropical seas (Chace, 1986). Poore (2004: 68) noted that at least one species of *Systellaspis* can be easily confused with species of *Acanthephyra*. However, the vent-related records for the *Acanthephyra* are so far restricted to the MAR, whereas the sole sighting of *Systellaspis* from a vent field has been the record from the EPR.

SYSTELLASPIS BRAUERI (BALSS, 1914)

Type locality: Atlantic Ocean, off Africa, Gulf of Guinea, from two different stations (*Valdivia*): 0°26'N, 6°32'W and 0°56'N, 4°34'W; 0–4000 m (Chace, 1940).

Known range: Bay of Bengal; eastern Pacific off Oregon, California and Mexico; western North Atlantic

from south-east of Newfoundland to Bahamas; eastern Atlantic from south-west of Ireland to off Congo; mesopelagic (Chace, 1940: 64).

Occurrence at vents or seeps: limited to vents on the EPR (de Saint Laurent, 1984: 355; Tunnicliffe, 1991).

Material: Presumably, no physical collections of this species were made at the 13°N site where it was noted on the EPR.

Remarks: Reported by de Saint Laurent (1984) from the 13°N site of the EPR (de Saint Laurent, 1984: 355). Although the type locality for this species is the Gulf of Guinea, the original collection was made well north of the known methane seep sites off Zaire. To date, only *Alvinocaris muricola* has been collected from the chemosynthetic communities in the southern Gulf of Guinea (T. Komai, pers. comm.).

FAMILY NEMATOCARCINIDAE SMITH, 1884

GENUS *NEMATOCARCINUS* SMITH, 1884

The family Nematocarcinidae contains only three genera and approximately 39 species (Burukovsky, 2003; Komai & Segonzac, 2005b). Most of the species are in the genus *Nematocarcinus*, reviewed by Chace (1986) and more recently in a series of papers in Russian by Burukovsky (e.g. 1988, 1991, 2000a, b, 2002a, b, c, 2003, 2004a, b, c; *Zoologicheskoy Zhurnal*). Members of this genus are characterized by highly elongate third, fourth and fifth pereopods. Although shrimp that resemble (and probably are) species of *Nematocarcinus* have been observed at several sites, including the Galapagos (Hessler & Smithey, 1983), collections from vent or seep sites are surprisingly rare. Ohta *et al.* (1995) reported *Nematocarcinus productus* from the Enshu-nada cold seeps off Japan, but it is unclear as to whether they collected any specimens. Hashimoto & Ohta (1999) listed the genus in their table of collected and observed specimens from the DESMOS site of the Manus Basin. Specimens of the genus *Nematocarcinus* were included in the collections of deep-sea shrimps made by beam trawl sampling in the Antarctic by the Japanese Antarctic Research Expedition (see Komai, Takeuchi & Takeda, 1996); however, none of the material was collected from known vent sites (although the possibility exists that vents are there). One of the authors (T. Haney) observed shrimp of this genus to be the most abundant decapod species adjacent to areas of diffuse hydrothermal venting on the Eastern Pacific Rise from 08°47'N to 12°48'N during the FIELD cruise of November 2003; one specimen was collected and is housed at the Field Museum (Chicago) as FMNH 11367, collected on DSMV *Alvin* dive 3935 at a site of new lava flow. Shank *et al.* (1998a) reported *Nematocarcinus ensifer* (Smith, 1882) from

vents at 09°50'N. Although most records of *N. ensifer* are from the North Atlantic Ocean, it has been reported from the Gulf of Mexico at and below 1646 m (Pequegnat, 1970) and from the eastern Pacific Ocean (Faxon, 1895; Shank *et al.*, 1998a). We include the two aforementioned species, *N. ensifer* and *N. productus*, in our review. However, these identifications are tentative and should be verified by first-hand study of material. Two new species have been described by Komai & Segonzac (2005b) from the EPR and are listed here as *Nematocarcinus burukovskyi* and *N. ovalis* (below).

Nematocarcinus burukovskyi. This new species was described by Komai & Segonzac (2005b) based on three specimens from sites along the southern EPR: 17°S (subadult male holotype, MNHN-Na 15768, 2595 m), 23°S (young paratype, CBM-ZC 8360, 2612 m) and 31°S (female paratype, USNM unspecified, 2330 m).

Nematocarcinus ovalis. This new species was described by Komai & Segonzac (2005b) based on a single ovigerous specimen (MNHN-Na 15765) collected from waters above hydrothermal vents at the 13°N site on the EPR at a depth of 2558–2619 m.

NEMATOCARCINUS ENSIFER (SMITH, 1882)

Type locality: North Atlantic Ocean, United States, collected from six Steamer *Blake* stations, including sta. 340; 31–41°N, 65–74°W; 1481–2549 m.

Known range: North Atlantic Ocean, Gulf of Mexico, north-eastern Pacific Ocean.

Occurrence at vents or seeps: Reported from near MAR sites and from sites on the EPR (questionably; see below).

Material: EPR, 13°N site (12°48'N, 103°56.54'W, 2647 m); one ovigerous female, HOT 96 cruise, PL 11, 21 February 1996, slurp gun, housed at the MNHN (M. Segonzac, pers. comm.). Another specimen was collected during the HOPE 99 cruise (M. Segonzac, pers. comm.). According to P. Chevaldonné (pers. comm.), three specimens were collected during the French HOT 96 cruise noted above; one was retained for the IFREMER collections in Brest and may be the above-mentioned MNHN specimen, and the other two were given to T. Shank for genetic work. Shank *et al.* (1999) mentioned another two specimens, tentatively assigned to *N. ensifer*, from the 9°50'N site on the EPR (*Alvin* dive 2688, 22 December 1993) (but see below).

Remarks: P. Herring (pers. comm.) has collected *Nematocarcinus ensifer* near MAR sites, although he correctly notes that his collections could have come from several kilometres away from any actual vent. A nem-

atocardinid shrimp tentatively identified as this species was shown to be a very rapid colonizer of new vent areas (documented presence within 11 months of new venting) and very abundant (with densities of up to 0.5 m⁻²) in the peripheral area (approximately 4 to 40 m from vent openings) by Shank *et al.* (1998a: 483) at the 9°50'N EPR vents. However, given the range of *N. ensifer* (most confirmed records are from the Atlantic) and the taxonomic difficulties with this genus, it would seem wise to question the identity of the EPR species at least for now.

NEMATOCARCINUS PRODUCTUS BATE, 1888

Type locality: Philippines, off Luzon, H. M. S. *Challenger*, sta. 205; 16°42'N, 119°22'E; 1920 m (1050 fathoms); from blue mud. –off Banda Island, sta. 195; 04°21'S, 129°07'E; 2602 m (1425 fathoms), blue mud. –Japan, near Yokohama, sta. 237; 34°37'N, 140°32'E; 3429 m (1875 fathoms). –off the New Hebrides, sta. 176; 18°30'S, 173°52'E; 2652 m (1450 fathoms).

Known range: Chace (1986), because of taxonomic uncertainty concerning the known populations of *Nematocarcinus productus* and the similarity of the species to *N. ensifer* in the Atlantic, noted that 'until...populations from different parts of the world, particularly the eastern Pacific, are carefully compared, the distributional limits of *N. productus* must remain indeterminate.'

Occurrence at vents or seeps: Kanesu-no-se Bank, Japan (see below).

Material: The report of Ohta *et al.* (1995) does not mention collections.

Remarks: Ohta *et al.* (1995) reported observations of this species from the south-western flank of Kanesu-no-se Bank at 1000 to 1220 m during *Shinkai 2000* dive 771. See our comments on the genus *Nematocarcinus*.

FAMILY PALAEMONIDAE RAFINESQUE, 1815

GENUS *PERICLIMENES* COSTA, 1844

Remarks: *Periclimenes* is a speciose genus; Okuno & Mitsuhashi (2003) considered the genus to include 174 valid nominal species, most of which are commensal with scleractinian corals or their associated invertebrates, and a few of which are now known from deep (more than 100 m) waters (Hayashi & Ohtomi, 2001). The genus is largely circumtropical, and, although most records are for specimens collected in relatively shallow waters, the genus has been found as deep as 1285 m (see Chace & Bruce, 1993; Poore, 2004: 95).

Bergquist *et al.* (2003) listed, in an appendix, several decapod taxa from the Bush Hill and GC234 sites (cold seeps) in the northern Gulf of Mexico, and included '*Periclimenes* sp.' among the taxa observed. No specimens were collected. To date, only one nominal species of this genus is known from hydrothermal vents off Japan (see below).

PERICLIMENES THERMOHYDROPHILUS HAYASHI
& OHTOMI, 2001

Type locality: Pacific Ocean, southern Japan, Kagoshima Bay, hydrothermal vent fields, associated with *Lamellibrachia satsuma*, 90–100 m.

Known range: known only from hydrothermal springs at the eastern end of Kagoshima Bay, Japan, from 90–115 m (Hayashi & Ohtomi, 2001).

Material: type locality, *Shinkai 2000* dive 980, 30 September 1997, NFU 530-2-2367 (holotype, ovigerous female), NFU 530-2-2368 (paratypes; 11 ovigerous females, 1 male).

–Kagoshima Bay, *Dolphin 3K* dive 340, 1 September 1997, 31 39.5'N, 130 48.2'E, 97 m; NFU 530-2-2369 (paratypes, 2 ovigerous females).

–Kagoshima Bay, northern part, 105 m, 20 April 2001, NFU 530-2-2370 (paratypes, 4 males, 1 female).

Remarks: Hayashi & Ohtomi (2001: 160) reported 'considerable numbers of unusual shrimps . . . found in the tube worm [*Lamellibrachia satsuma*] colonies at depths of about 100 m', all of which belonged to their new species, *Periclimenes thermohydrophilus*, the first palaeomonid shrimp reported from a hydrothermal vent field. The species was always found in or around colonies of *L. satsuma* and other unidentified polychaetes (K. Hayashi, pers. comm.). The relatively large number of specimens allowed them to make notes on fecundity and natural history; colour photographs of the species were also provided.

FAMILY PANDALIDAE HAWORTH, 1825

GENUS *CHLOROTOCUS* A. MILNE-EDWARDS, 1882

Remarks: This small genus containing only 3 species (Chace, 1985; Poore, 2004) is known from the Mediterranean Sea and eastern Atlantic Ocean, from Spain to central Africa, and from the Andaman Sea, Indonesia, Philippines, Japan, New Zealand and eastern Australia (see Chace, 1985). The only report from a vent site is somewhat questionable (see below).

CHLOROTOCUS NOVAEZEALANDIAE
(BORRADAILE, 1916)

Type locality: South Pacific Ocean, New Zealand, North Island, 7 miles east of North Cape; 128 m.

Known range: New Zealand, eastern Australia (Poore, 2004).

Occurrence at vents or seeps: possibly at or near a hydrothermal site off Whale Island, New Zealand (see below).

Remarks: This species is only questionably included by us. Russian divers collected specimens of the species off Whale Island, New Zealand, but it is unclear as to whether they were near the active vent areas known in that region (see Clark & O'Shea, 2001, and also under Ocypodidae, *Macrophthalmus hirtipes*). R. Weber (pers. comm.) tells us that the species is otherwise distributed along the northern and central New Zealand shelf and the upper continental slope on both coasts of South Island (NZ) as well as off eastern Australia, but there are apparently no data that would confirm its presence at hot vents.

FAMILY STYLODACTYLIDAE BATE, 1888

GENUS *STYLODACTYLUS* A. MILNE-EDWARDS, 1881

Remarks: Shrimp of the family Stylodactylidae, recognizable by their peculiar first and second pereopods, are widely distributed from tropical to temperate regions (e.g. Cleva, 1990), although most of the species described to date have come from the tropical Indo-Pacific (Chace, 1983; Cleva, 1994, 1997; Wicksten & Martin, 2004). Chace (1983) and Cleva (1994) reviewed the members of the family, described new species and provided keys. The single report from a vent or seep site is that of Watabe & Miyake (2000) who reported '*Styloactylus* sp.' adjacent to active sites on the Hatoma Knoll (Okinawa Trough). They noted that the species was observed on a coarse sand to mud bottom at the base of the knoll bearing the vents and was unaffected by the vents. Apparently no specimens were collected. This is listed in Table 1 as *Styloactylus* sp.

INFRAORDER ANOMURA

Remarks: Chevaldonné & Olu (1996) reviewed the anomurans known from vent and seep sites. In addition to the species noted below, they noted that at least two hermit crabs had been observed, one 'from cold seeps of the Barbados accretionary prism, at depths of 1000–2000 m' and another from Monterey Bay seeps at depths of 600–1000 m. For both of these observations they cited personal observations (K. Olu and J. Barry, respectively). The Barbados hermit 'seems to belong to the genus *Parapagurus*' (Chevaldonné & Olu, 1996: 287), whereas the Monterey hermit had not been identified as of that writing (listed as Paguridae unknown sp. in Barry *et al.*, 1996). Chevaldonné

& Olu (1996) mentioned the possibility that the Monterey specimen might be a parapagurid, as these crabs are common at those depths. We are not aware of the location of either specimen. To our knowledge this information has not been published other than that reference. One species of parapagurid from vents off Taiwan has since been described (Lemaitre, 2004). A study of a very shallow volcanic site off Papua New Guinea (Tarasov *et al.*, 1999) includes several other anomuran genera not listed here (*Hippa*, *Dardanus* and *Pagurus*) that most likely were not affected by the volcanism; we have not included those records here.

FAMILY GALATHEIDAE SAMOUELLE, 1819

Remarks: Galatheids, considered as a group to be ubiquitous members of the deep-sea fauna, have been reported from vents and seeps since the discovery of these habitats in the late 1970s (see Chevaldonné & Olu, 1996). As pointed out by Chevaldonné & Olu (1996), the great morphological similarity among genera and species of galatheids has led to some rather vague general references to these decapods at vents and seeps, such that identification even to genus is not always possible from the literature or from photographs. Although several species have been described and are to date known only from vent areas, all species are assumed by us to be vagrants rather than endemics. See Chevaldonné & Olu (1996: 293) for an in-depth discussion of sightings of various galatheids (some of which might be chirostylids) that are as yet unidentified. These reports include Kim & Ohta (1991: fig. 10, 'galatheid crabs with broad rostrum') and other unconfirmed sightings.

GENUS *ALAINIUS* BABA, 1991

Remarks: This genus, created by Baba (1991) for a species of galatheid from New Caledonia (*Alainius crosnieri* Baba, 1991), is, as far as we can determine, known only from that region. Clark & O'Shea (2001) reported a species of this genus (as *Alainius* sp.) from the vent system of the Kermadec Ridge, New Zealand. To our knowledge, no specimens were collected.

GENUS *MUNIDA* LEACH, 1820

Remarks: The high diversity and biogeographical range of the genus *Munida* (more than 56 species are known from waters around New Caledonia alone; see Macpherson, 1994b) would seem to support the idea that the two species known from vents are vagrants rather than endemics. Taxonomic reviews of *Munida* include those of Pequegnat & Pequegnat (1970, Gulf of Mexico), Macpherson & de Saint Laurent (1991,

French Polynesia; 2002, Indian Ocean), Macpherson (1993, Indo-Pacific; 1994b, New Caledonia), Baba (1988, Philippines), and Macpherson & Baba (1993, Indo-Pacific).

MUNIDA MAGNIANTENNULATA BABA & TÜRKAY, 1992

Type locality: south-western Pacific Ocean, Lau Basin, Valu-Fa Ridge.

Known range: Vent records are restricted to the Lau Basin (type locality). Non-vent records include off Australia (Baba, 1994). It is also included (albeit only in the key) by Macpherson (1994b) in his review of species of the genus from New Caledonia and adjacent waters.

Material: type locality; SONNE; (holotype male).

—Lau Basin, north of Hine Hina, Vaï-Lili; 23°13'S, 176°38'W; 1750 m; BIOLAU 89 sta. 2, *Nautila* dive BL08; 20 May 1989; MNHN Ga 2352 (non-type, 1 male) (Baba & de Saint Laurent, 1992; Baba & Türkay, 1992; Baba, 1994; Chevaldonné & Olu, 1996).

Remarks: The original collection consisted of two specimens from hydrothermal vents in the Lau Back-Arc Basin (Baba & Türkay, 1992). Baba & de Saint Laurent (1992) added a third specimen from the same general area. Baba (1994) later reported the species from a non-vent region off Australia (see also Chevaldonné & Olu, 1996).

MUNIDA MICROPHTHALMA A. MILNE-EDWARDS, 1880

Type locality: United States Coast Survey, Steamer *Blake*, Caribbean Sea, Phare Morro, sta. 2, 1472 m (805 fathoms). —23°52'N, 88°58'W, sta. 35, 1470 m (804 fathoms). —Martinique, sta. 196, 1884 m (1030 fathoms). —St. Vincent, sta. 227, 1048 m (573 fathoms).

Known range: Atlantic Ocean, south of Iceland to Ascension Island, in the Gulf of Mexico, the Caribbean and the Bay of Biscaye, from 194 to 2129 m (Pequegnat & Pequegnat, 1970; Wenner, 1982; Chevaldonné & Olu, 1996).

Occurrence at vents or seeps: cold seeps of the Barbados Accretionary Prism (see below).

Material: Chevaldonné & Olu (1996) noted that only one of the Barbados Accretionary Prism galatheid species has been collected and identified (as *M. microphtalma* see below) but gave no details as to where the specimens are housed.

Remarks: Chevaldonné & Olu (1996: 290) cited a personal communication from M. de Saint Laurent to the effect that *Munida microphtalma* occurs in the seep areas of the Barbados Accretionary Prism. A second,

larger species observed in that region might belong instead to the genus *Munidopsis* (Chevaldonné & Olu, 1996: 290). Henderson (1885: 127) reported this species from 713, 777 and 1097 m (as 390, 425, and 600 fathoms); Chace (1942) noted specimens from off the northern coast of Cuba obtained during an expedition of the R/V *Atlantis* in 1938 and 1939; it was recovered from depths of 677–1216 m. Chace (1942) suggested the species was more widely distributed throughout the Gulf of Mexico and North Atlantic Ocean, and south to Ascension Island, at depths ranging from 627 to 2163 m. Wenner (1982) cited collections from 750 to 1698 m.

GENUS *MUNIDOPSIS* WHITEAVES, 1874

Remarks: The galatheid genus *Munidopsis* is one of the most speciose and widely distributed of all decapod genera. It is also the most commonly encountered galatheid genus at vent and seep sites (e.g. see Chevaldonné & Olu, 1996). A large number of publications mention the presence of this genus in the vicinity of vent or seep sites without further information or without identifying the taxa to species level [e.g. Van Dover *et al.*, 2001 (Indian Ocean); Bergquist *et al.*, 2003; MacDonald *et al.*, 2004 (Gulf of Mexico seeps); see also Chevaldonné & Olu, 1996]. Unpublished records from vent fields include specimens from dive T-452 (*Tiburron*) in the Escanaba Trough, south Gorda Ridge (J. Voight, pers. comm.). Baba & Poore (2002) reviewed the species of *Munidopsis* known from Australia. Species off Oregon and adjacent waters were reviewed by Ambler (1980). We assume, despite the fact that several species have been described from vents, that the species of *Munidopsis* are vagrants rather than endemics. The species *Munidopsis granosicorium* was described by Williams & Baba (1989), based on a specimen collected off the coast of Oregon. Although the species was described along with other species from vents, *M. granosicorium* itself is not known from vent or seep sites. Carey (1987) reviewed the distribution and ecology of 11 species in the abyssal plains adjacent to the Gorda Ridge; some of those species may be vagrants at vent fields.

Munidopsis sp. Because galatheids are so often encountered at vents and seeps, a large number of papers report the presence of '*Munidopsis* sp.'. These include the following reports, some of which mention collected specimens but without further identification or comment: Hecker (1985), Laubier, Ohta & Sibuet (1986), Mayer *et al.* (1988), MacDonald *et al.*, (1989), Embley *et al.* (1990), Galkin & Moskalev (1990a), Hashimoto, Fujikura & Hotta (1990), Hashimoto *et al.* (1995), Jollivet *et al.* (1990), Ohta (1990a), Van Dover & Hessler (1990), Kim & Ohta (1991), Galkin (1992),

Sagalevich *et al.* (1992), Carney (1994), Hashimoto *et al.* (1995), Murton *et al.* (1995), Ohta *et al.* (1995), and probably many others. The genus is also known from observations and specimens from the Escanaba Trough, south Gorda Ridge, from dive T-452 (J. Voight, pers. comm.). Additionally, Barry *et al.* (1996) reported a species of the genus from the Monterey Canyon, and Hashimoto & Ohta (1999) report an unidentified species of *Munidopsis* from the DESMOS site of the Manus Basin. We have noted below those reports that can be reconciled with a known species; in most cases this is not possible.

MUNIDOPSIS ALVISCA WILLIAMS, 1988

Type locality: eastern Pacific Ocean, Gulf of California, Guaymas Basin; 27°00'N, 111°25'W; 2008 m.

Known range: Known only from the periphery of hydrothermal vent fields on the Explorer and Juan de Fuca ridges at 1545–1800 m in the North Pacific (Williams, 1988) and in the Guaymas Basin (Gulf of California) at 2000 m (Williams, 1988; Khodkina, 1991; Chevaldonné & Olu, 1996; Van Dover, 1997, in Desbruyères & Segonzac, 1997).

Material: eastern Pacific Ocean, Gulf of California, Guaymas Basin; 27°00'N, 111°25'W; 2008 m; *Alvin* dive 1616; 8 August 1985; USNM 234294 (holotype female), USNM 234301 (paratype, 1 female) (Williams, 1988).

–Magic Mountain, Explorer Ridge, Gulati Gusher-base; 49°45.6'N, 130°16.16'W; 1818 m; Canadian American Seamount Expedition(?), *Pisces IV* dive P-1494; 1 July 1984; USNM 234295 (paratype male) (Williams, 1988).

–Upper Magic Mountain, Explorer Ridge, Lunch Hour Vent; 49°45.5'N, 130°16.1'W; 1812 m; Canadian American Seamount Expedition(?), *Pisces IV* dive P-1497; 4 July 1984; USNM 234296 (paratype, 1 ovigerous female) (Williams, 1988).

–Upper Magic Mountain, Explorer Ridge, Crab Vent; 49°45.5'N, 130°16.1'W; 1812 m; Canadian American Seamount Expedition(?), *Pisces IV* dive P-1497; 4 July 1984; USNM 234297 (paratype, 1 ovigerous female), USNM 234298 (paratype, 1 ovigerous female) (Williams, 1988).

–north-eastern Pacific Ocean, Juan de Fuca Ridge, Limbo Vent, 3 m from Holland's Hillock Axial Seamount; 45°55'N, 130°03'W; 1545 m; ASHES Expedition, *Pisces IV* dive P-1732; 2 August 1986; USNM 234299 (paratypes, 2 ovigerous females) (Williams, 1988).

–Gulf of California, Guaymas Basin; 27°02'79"N, 111°22'80"W; 1987 m; Expedition 12, R/V *Academician Mstislav Keldysh*, *Pisces IV* sta. 1534; non-types, 1 male, 1 ovigerous female. –27°02'70"N, 111°24'50"W;

1967 m; Expedition 12, R/V *Academician Mstislav Keldysh*; *Pisces IV* sta. 1575; non-type, 1 ovigerous female (Khodkina, 1991).

Remarks: Collections of this species from the Guaymas Basin include the holotype and a paratype female, as well as three specimens noted by Khodkina (1991) found on the slope of a smoker among colonies of *Riftia*. The species, or a similar one, has been observed but not collected at several other vent sites along the Juan de Fuca ridge apart from sites listed above. Chevaldonné & Olu (1996) noted the possibility that the galatheid reported by Van Dover, Grassle & Boudrias (1990) from vents of the Escanaba Trough on the Gorda Ridge might also be *M. alvisca*. Van Dover (1997: 201, in Desbruyères & Segonzac, 1997) gives anatomical characters that distinguish the species from the morphologically similar *Munidopsis subsquamosa* (which is possibly a species complex; see below under *Munidopsis subsquamosa*).

MUNIDOPSIS BERINGANA BENEDICT, 1902

Type locality: North Pacific Ocean, Bering Sea, Steamer *Albatross* sta. 3603; 3373 m.

Known range: Bering Sea to Oregon at 2800–3276 m (Ambler 1980, non-vent areas).

Occurrence at vents or seeps: questionably in the Middle America Trench at 3700–4000 m and at shallower seep communities in the same region (Chevaldonné & Olu, 1996) (see below).

Material: type locality; 3 specimens; USNM 20557 (holotype).

Remarks: Because *M. beringana* is usually found from the Bering Sea to Oregon at 2800–3276 m (Ambler, 1980), the presence of this species at a vent site that is out of this range and depth (3700–4000 m depth, west of Mexico in the Middle America Trench) is questionable (Chevaldonné & Olu, 1996: 290). The collected specimens apparently have slight morphological variations that also suggest the possibility that they are not conspecific with true *M. beringana* (Chevaldonné & Olu, 1996: 290); the authors cited personal communication with E. Macpherson in connection with samples but did not provide the details of such collections.

MUNIDOPSIS CRASSA SMITH, 1885

Type locality: North Atlantic Ocean, off East Coast of United States, Steamer *Albatross*, sta. 2224; 36°16'30"N, 68°21'W; 4902 m, from globigerina ooze.

Known range: Non-vent records are restricted to the Atlantic (Pequegnat & Pequegnat, 1970; Wenner, 1982).

Occurrence at vents or seeps: Vent and seep records include the Snake Pit hydrothermal field on the MAR (3480 m) (Segonzac, 1992) and cold seeps off Peru (Olu *et al.*, 1996a) at 3000–3600 m; unidentified galatheids at 5040 m off Peru might also belong to this species (Chevaldonné & Olu, 1996: 291).

Material: Wenner (1982) reported the collection of a single specimen at 2679 m from 36°59.2'N, 73°43.4'W. Non-vent record: type locality; 8 September 1884; USNM 8563 (holotype female).

Remarks: As noted by Chevaldonné & Olu (1996), the Peruvian record is in need of confirmation, as the previous known range for the species was restricted to the Atlantic at depths of 2679–5315 m (Wenner, 1982).

MUNIDOPSIS DIOMEDEAE (FAXON, 1893)

Type locality: Steamer *Albatross*, sta. 3357, 782 fathoms. –sta. 3363, 978 fathoms. –sta. 3364, 902 fathoms. –sta. 3366, 1067 fathoms. –sta. 3371, 770 fathoms. –sta. 3373, 1877 fathoms. –sta. 3393, 1020 fathoms. –sta. 3407, 885 fathoms. –sta. 3429, 919 fathoms. –sta. 3418, 660 fathoms. –sta. 3419, 772 fathoms. –sta. 3424, 676 fathoms. –sta. 3429, 919 fathoms. –sta. 3435, 859 fathoms. –sta. 3436, 905 fathoms.

Known range: California south to Chile, at depths of 768–3790 m, and common in the Gulf of California (Haig & Wicksten, 1975). Chevaldonné & Olu (1996) note the possibility that the unidentified galatheid observed by Lutz (1992) at cold seeps in this area may also be *M. diomedae*.

Occurrence at vents or seeps: restricted to the Guaymas Basin (Gulf of California), 2000 m (Khodkina, 1991).

Material: Gulf of California, Guaymas Basin, 27°02'48"N, 111°22'90"W; 1994–2006 m; Expedition 12, R/V *Academician Mstislav Keldysh*; *Pisces IV* sta. 1522; non-type, 1 male. –26°59'82"N, 111°25'31"W; 2023–2026 m; Expedition 12, R/V *Academician Mstislav Keldysh*; *Pisces IV* sta. 1551; non-types, 1 male, 2 ovigerous females, 1 immature male, 1 immature female. –27°00'55"N, 111°24'6"W; 2026 m; Expedition 12, R/V *Academician Mstislav Keldysh*; *Pisces IV* sta. 1572; non-types, 2 females (Khodkina, 1991).

Remarks: This species was originally described as *Galacantha diomedae* (Bull. Mus. Comp. Zool. 1893: 180). Khodkina (1991) reported the collection of eight specimens from hydrothermal vents in the Guaymas Basin.

MUNIDOPSIS LAUENSIS BABA & DE SAINT LAURENT, 1992

Type locality: south-western Pacific Ocean, Lau Basin, Hine Hina, Valu-Fa Ridge; 22°32'S, 176°43'W; 1750 m.

Known range: type locality and North Fiji Basin, 1750 m and 2000 m, respectively (Baba & de Saint Laurent, 1992), and probably the Manus Basin (Hashimoto & Ohta, 1999).

Material: type locality; BIOLAU, *Nautile* dive BL03; 15 May 1989; MNHN Ga 1924 (holotype male). NSMT (paratype, 1 female), MNHN Ga 2355 (paratypes, 1 male, 1 female). –same locality; *Nautile* dive BL01, 13 May 1989; MNHN Ga 2353 [paratypes, 1 male, 3 females (2 ovigerous)]. –same locality; *Nautile* dive BL02, 14 May 1989; MNHN Ga 2354 (paratypes, 3 ovigerous females). –Lau Basin, south of Hine Hina, dive BL05, 17 May 1989. MNHN Ga 2356 (paratype, 1 male).

–North Fiji Basin, active chimney ‘White Lady’; 16°59.50’S, 173°55.47’W; 2000 m; STARMER II sta. 4, *Nautile* dive 20; 15 July 1989; MNHN Ga 1925 [paratypes, 1 male, 2 females (1 ovigerous)] (Baba & de Saint Laurent, 1992; Chevaldonné & Olu, 1996).

Remarks: This species is known only from hydrothermal vents to date. Chevaldonné & Olu (1996) noted that it co-occurs with *Munida magniantennulata* at vents in the Lau Back-Arc Basin. Hashimoto & Ohta (1999) reported it from all three vent sites in the Manus Basin.

MUNIDOPSIS LENTIGO WILLIAMS & VAN DOVER, 1983

Type locality: north-eastern Pacific Ocean, EPR; 21°N; 2600 m.

Known range: Known only from the type locality (Williams & Van Dover, 1983; Van Dover, 1997, in Desbruyères & Segonzac, 1997).

Material: EPR, vent sites at 21°N; 2600 m; OASIS Expedition, R/V *Melville*, *Alvin* dives 1211 and 1221, 12 April–8 May, 1982; USNM 191160 (holotype male), USNM 191163 (paratype male), USNM 191163 [*sic*], 191162 and 191161 (paratype females) (Williams & Van Dover, 1983).

Remarks: This species is considered a ‘high-temperature’ species because of its occurrence near high-temperature fluid venting (Williams & Van Dover, 1983; Chevaldonné & Olu, 1996) and black smokers (Van Dover, 1997: 202, in Desbruyères & Segonzac, 1997). Treated as an endemic by Van Dover *et al.* (1985) and by Chevaldonné & Olu (1996), which it may truly be, although it is considered a vagrant here (see earlier discussion under family Galatheidae). Van Dover *et al.* (1985) reported lecithotrophic larvae for the species. The species is characterized by having unusual oval-shaped organs of unknown function on the chelipedal propodus and flattened eyes.

MUNIDOPSIS LIGNARIA WILLIAMS & BABA, 1989

Type locality: north-eastern Pacific Ocean, off Oregon, Cascadia Basin; 44°39.8’N, 125°36.4’W; 2875 m (for holotype); paratype material includes material from Cascadia Basin and the EPR off central Mexico.

Known range: Cascadia Basin south to the EPR off central Mexico (Williams & Baba, 1989).

Occurrence at vents or seeps: possibly not at all; see below.

Material: north-eastern Pacific Ocean, off Oregon, Cascadia Basin, sta. CP-1-E; 44°39.8’N, 125°36.4’W; 2875 m; R/V *Yaquina*; 16 March 1970; Y 7001 B; 3-m Beam Trawl, BMT 184; USNM 240202 (holotype male). –sta. CP-2-C; 45°18.6’N, 126°31.5’W; 2750 m; R/V *Yaquina*; 18 February 1971; Y 7001 B; 3-m Beam Trawl, BMT 265; USNM 240203 (allotype female). –sta. CP-2-D; 44°53.7’N, 126°33.4’W; 2774 m; R/V *Yaquina*; 19 January 1970; Y 7001 B; 3-m Beam Trawl, BMT 162; OSUBI 00189 (paratypes, 19 males, 13 females). –sta. CP-1-A; 45°55.3’N, 125°36.1’W; 2030 m; R/V *Yaquina*; 20 March 1970; Y 7003 B; 3-m Beam Trawl, BMT 194; USNM 171342 (paratype, 1 female). –sta. CP-2-A; 45°52.5’N, 126°40.8’W; depth not provided; R/V *Yaquina*; 16 January 1970; Y 7001 B; 3-m Beam Trawl, BMT 154; USNM 171343 (nontypes, 6 males, 7 females) (Williams & Baba, 1989).

–eastern Pacific Ocean, EPR, off south-central Mexico; 11°52’N, 103°51’W; 2750 m; *Alvin* dive 2000; 22 March 1988; from piece of wood; USNM 240204 (paratypes, 8 males, 12 females) (Williams & Baba, 1989).

Remarks: Inclusion of this species in our list is questionable (it was not included in the list of vent and seep anomurans compiled by Chevaldonné & Olu, 1996). As the name implies, this species, and several other species of *Munidopsis*, are found associated with wood in the deep sea. According to Williams & Baba (1989), specimens of this species came from ‘among samples of biological specimens collected from both vent and non-vent environments’. Thus, its ‘presence’ near vent or seep sites is probably coincidental and has little or nothing to do with chemosynthetic environments per se. According to Williams & Baba (1989), this is also the species referred to as *Munidopsis* sp. by Van Dover (1988, unnumbered figure). To our knowledge the species has not been mentioned in the literature since its original description.

MUNIDOPSIS MARIANICA WILLIAMS & BABA, 1989

Type locality: western Pacific Ocean, hydrothermal vents of the Mariana back-arc basin; 3600–3700 m.

Known range: Known only from the type locality (Williams & Baba, 1989; Van Dover, 1997, in Desbruyères & Segonzac, 1997).

Material: Western Pacific Ocean, Mariana Back-Arc Basin, Burke Field; 18°11'N, 144°43'E; 3680 m; *Alvin* dive 1837; 28 April 1987; USNM 240198 [holotype female (ovigerous)], USNM 240199 (paratypes, 2 ovigerous females, 1 male) (Williams & Baba, 1989).

–Ilium Vent Field; 18°15'N, 144°42'E; 3620 m; *Alvin* dive 1829; 14 April 1987; USNM 240200 (paratype, 1 ovigerous female) (Williams & Baba, 1989).

–Burke Field; 18°11'N, 144°43'E; 3727 m; *Alvin* dive 1847; 8 May 1987; USNM 240201 (paratype, 1 ovigerous female) (Williams & Baba, 1989).

Remarks: Because this species is known only from vent sites to date, Chevaldonné & Olu (1996) considered it an endemic. For reasons given earlier we are treating it as a probable vagrant. This large species (up to 52 mm carapace length; Van Dover, 1997, in Desbruyères & Segonzac, 1997) is found among dense carpets of actinians (Williams & Baba, 1989; Hessler & Lonsdale, 1991; Chevaldonné & Olu, 1996). Williams & Baba (1989) mentioned video sequences taken during *Alvin* dive 1845 (18°13'N, 144°42'E, 3716 m, 6 May 1987) that might be of this species.

MUNIDOPSIS SONNE BABA, 1995

Type locality: south-western Pacific Ocean, North Fiji Basin; 16°59.49'S, 173°54.83'E; 1992 m.

Known range: Known only from the type locality (Baba, 1995; Chevaldonné & Olu, 1996).

Material: Known from 2 specimens, the whereabouts of which are not known to us.

MUNIDOPSIS STARMER BABA & DE SAINT LAURENT, 1992

Type locality: south-western Pacific Ocean, North Fiji Basin, active chimney 'White Lady'; 18°50'S, 173°29'W; 2750 m.

Known range: Known only from the type locality.

Material: type locality; *Nautila* dive 18; 2750 m; 13 July 1989; MNHN Ga 1926 (holotype female), MNHN Ga 2362 [paratypes, 1 male, 4 females (3 ovigerous)], NSMT Cr 11267 (1 male). –same site; *Nautila* dive 19. MNHN Ga 2357 (paratype, 1 female). –same site; *Nautila* dive 20; MNHN Ga 2358 (paratypes, 2 females) (Baba & de Saint Laurent, 1992; Chevaldonné & Olu, 1996).

Remarks: *Munidopsis starmer* occurs in the same general area in the North Fiji Basin where *M. lauensis*,

M. sonne, and the chirostylids *Uroptychus bicavus* and *U. thermalis* are found (Baba & de Saint Laurent, 1992; Chevaldonné & Olu, 1996).

MUNIDOPSIS SUBSQUAMOSA HENDERSON, 1885

Type locality: North Pacific Ocean, south of Japan, off Yokohama; H. M. S. *Challenger* sta. 237; 34°37'N, 140°32'E; 1875 fathoms (3571 m), 'bottom, blue mud'.

Known range: Caribbean and Gulf of Mexico (Van Dover, 1997, in Desbruyères & Segonzac, 1997) and 'widely distributed in the Pacific and Indian Oceans' (Khodkina, 1991: 76, English summary), though some of the previous records may be of different species (see Remarks below and also Ambler, 1980).

Occurrence at vents or seeps: records from hydrothermal vents include nearly every known vent site in the eastern Pacific, including 21°N, 13°N, 10–12°N, 9°50'N, Galapagos Rift (e.g. see Khodkina, 1991; Chevaldonné & Olu, 1996; Van Dover, 1997: 204, in Desbruyères & Segonzac, 1997; Lutz *et al.*, 1998).

Material: Material of this widespread and locally abundant species, if indeed all of the material represents a single species (see below), is mentioned by numerous workers (e.g. de Saint Laurent, 1984; Hessler, Smithey & Keller, 1985; Van Dover *et al.*, 1985; Van Dover, 1986; Van Dover & Hessler, 1990; Kaartvedt *et al.*, 1994; and see also Lutz, 1992, as cited by Chevaldonné & Olu, 1996).

Remarks: This species, which can be found 'in great abundance in peripheral areas of vent fields on the East Pacific Rise' (Van Dover, 1997: 204, in Desbruyères & Segonzac, 1997; see also Shank *et al.*, 1998a, for rapid colonization of new vents) may represent a species complex. Indeed, in a paper by K. Baba that is currently in review, the material reported as *M. subsquamosa* from the eastern Pacific (Galapagos Rift and 13° and 21°N sites) will be treated as distinct from 'true' *M. subsquamosa* (anonymous information from confidential reviewer). Separate species within this complex would in part explain the apparent geographical range (see above) currently attributed to *M. subsquamosa*. Lutz (1992) suggested that at the 9°50'N (EPR) location two different species of the genus might be present. Van Dover (1986) compared stable isotope ratios within the species and also noted slight differences in temperature preferences between males and ovigerous females. Lutz *et al.* (1998) reported it from an EPR site dominated by Stauromedusae. Hessler & Smithey (1983) provided brief observations on ecology and behaviour of the species at the Rose Garden site. Chevaldonné & Olu (1996) noted that a complete taxonomic re-examination of the species is needed. Van Dover *et al.* (1985) reported

lecithotrophic larvae for the species (based on observations or collections made at three sites in the EPR). Creasey *et al.* (2000: 111) discussed the genetic difference between this species and *M. crassa*, which some previous authors had considered conspecific.

GENUS *PHYLLADIORHYNCHUS* BABA, 1969

PHYLLADIORHYNCHUS PUSILLUS (HENDERSON, 1885)

Type locality: South Pacific Ocean, off New South Wales, *Challenger* Expedition sta. 163; 220 m (120 fathoms).

Known range: Eastern Indian Ocean, Japan, New Caledonia, New Zealand and Australia, intertidal to 310 m (Poore, 2004); possibly eastern Pacific (Baba, 1991; see below).

Occurrence at vents or seeps: Kermadec Ridge (Clark & O'Shea, 2001).

Material: See Baba (1991: 486) for material and additional references to western Pacific localities.

Remarks: The genus *Phylladorhynchus* currently includes four species, all from the Indian Ocean and/or Indo-West Pacific, and possibly one eastern Pacific species, although the latter might be synonymous with *P. pusillus*. If so, it would extend the range of *P. pusillus* significantly (Baba, 1991). *Phylladorhynchus pusillus*, originally described by Henderson (1885: 407) as *Galathea pusilla*, was transferred to *Phylladorhynchus* by Baba (1969; see also Baba, 1991), and the species has been the source of some taxonomic confusion (discussed in Baba, 1991). The only record associated with vents or seeps is the listing by Clark & O'Shea (2001) from the Kermadec Ridge system.

GENUS *SHINKAIA* BABA & WILLIAMS, 1998

SHINKAIA CROSNIERI BABA & WILLIAMS, 1998

Type locality: West Pacific Ocean, Bismarck Archipelago, Edison Seamount; 03°18.85'S, 152°34.92'E; 1483 m. –Okinawa Trough, Iheya Seamount; 27°32.7'N, 126°58.2'E; 1394 m.

Known range: active hydrothermal vents in the Bismarck Archipelago and Okinawa (Baba & Williams, 1998; Ohta & Kim, 2001 for Iheya Ridge) and off Taiwan (Chan, Lee & Lee, 2000).

Material: West Pacific Ocean, Bismarck Archipelago, Edison Seamount, north-eastern crater rim near Lihir Island; 03°18.85'S, 152°34.92'E; 1483 m; R/V *Sonne*, S29-1531; 20 March 1994; holotype male, USNM 251480; 2 paratype females (1 ovigerous), USNM 251481).

–Okinawa Trough; 27°32.7'N, 126°58.2'E; 1394 m; *Shinkai 2000*, 2K#479; 13 May 1990; 1 male paratype, USNM 251482; 1 male paratype, JMSTC Ano-0001-90. –27°16.2'N, 127°04.9'E; 1330 m; *Shinkai 2000*; 10 September 1988; 1 female and 1 male paratype, MNHN-Ga 4239. –27°33.0'N, 126°58.0'E; 1390 m; *Shinkai 2000*, 2K#672; 14 May 1993; 1 male and 2 female paratypes, JMSTC Ano-0006-93.

–Additional material was apparently collected by Chan *et al.* (2000), as measurements were given; we have not seen that publication. .

Remarks: Both Tsuchida *et al.* (2000) and Watabe & Miyake (2000) considered *S. crosnieri* to be the dominant member of the fauna at Hatoma Knoll, as did Watanabe *et al.* (2005). The species was also mentioned by Chan *et al.* (2000) as the first known hydrothermal crustacean reported from Taiwan. Ohta & Kim (2001: photograph 4) noted the presence of *Beggiatoa*-like filamentous bacteria on the abdomen of specimens from the Iheya Ridge.

FAMILY CHIROSTYLIDAE ORTMANN, 1892

Remarks: Chirostylids, morphologically similar to galatheids but usually more delicate, are typically found associated with gorgonian corals in deep reef areas. To date, three species of *Uroptychus* have been described from vents in the North Fiji Basin. Additionally, one species of the genus *Eumunida* is known from cold seeps in the northern Gulf of Mexico.

GENUS *EUMUNIDA* SMITH, 1883

EUMUNIDA PICTA SMITH, 1883

Type locality: north-eastern coast of the United States; 38°39'N to 39°58'N; 115–159 fathoms (219–303 m); Steamer *Albatross* sta. 1043 (see de Saint Laurent & Macpherson, 1990b: 650).

Known range: Amphi-Atlantic, in the western Atlantic from off Massachusetts to Florida, the Gulf of Mexico and the Caribbean, from depths of 200 to 600 m (de Saint Laurent & Macpherson, 1990b: 650). Wenner (1982) reported the previously known depth range as 234–522 m but collected this species at 248–613 m between 36°40.4'N, 74°40.0'W and 37°05.0'N, 74°39.5'W.

Occurrence at vents or seeps: reported from cold seeps off the continental slope off Louisiana at depths of 400–1000 m (Carney, 1994).

Material: Non-seep material mentioned by de Saint Laurent & Macpherson (1990b, as cited by Chevaldonné & Olu, 1996). We are not aware of any collections of this species from the Louisiana seeps.

Remarks: For a taxonomic review of the genus, see de Saint Laurent & Macpherson (1990a, b).

GENUS *UROPTYCHUS* HENDERSON, 1888

Remarks: *Uroptychus* is a deep-sea genus of chirostylids now known to be widely distributed in Atlantic and Pacific deep reef areas. The original report (Henderson, 1888) was based on specimens collected during the *Challenger Expedition*, with specimens collected from 15–734 fathoms (up to 1398 m). Shortly afterwards, Benedict (1902) reported material from slightly greater depths of 163–805 fathoms (310–1533 m). The genus was reported from hydrothermal vents for the first time by Baba & de Saint Laurent (1992), who described two new species from the North Fiji basin. Baba & Williams (1998) added a third vent species. The relatively recent descriptions of these three vent-associated species have extended the depth range to 2750 m.

Uroptychus sp. Tunnicliffe, McArthur & McHugh (1998) noted a species of *Uroptychus* from the North Fiji and Lau basins. It is not yet clear whether these represent records of an undescribed species or additional sightings of one of the known species listed below.

UROPTYCHUS BICAVUS BABA & DE SAINT LAURENT, 1992

Type locality: south-western Pacific Ocean, North Fiji Basin, active chimney 'Mussel Valley'; 18°50'S, 173°29'W; 2750 m.

Known range: Known only from the type locality.

Material: type locality; STARMER II sta. 14, *Nautila* dive 18; 13 July 1989. MNHN Ga 2350 (holotype male) (Baba & de Saint Laurent, 1992; Chevalloné & Olu, 1996).

UROPTYCHUS EDISONICUS BABA & WILLIAMS, 1998

Type locality: Western Pacific Ocean, Papua New Guinea, Bismarck Archipelago, Edison Seamount, near Lihir Island; 03°19.07'S, 152°34.92'E; 1492 m.

Known range: Known only from the type locality.

Material: Type locality, R/V *Sonne*, EDISON cruise, Sbb-1535; 29 March 1994; holotype female, USNM 251479.

Remarks: Baba & Williams (1998) noted that this species was morphologically more similar to other (non-vent) species of *Uroptychus* in the Banda Sea and central North Pacific Ocean than it is to the other two

vent-associated species. The description of this species, named for the Edison Seamount, was based on the single specimen collected there.

UROPTYCHUS THERMALIS BABA & DE SAINT LAURENT, 1992

Type locality: south-western Pacific Ocean, North Fiji Basin, active chimney 'Mussel Valley'; 16°59.50'S, 173°55.47'W; 2000 m.

Known range: Known only from the type locality.

Material: Type locality; STARMER II, sta. 4; dive PL 04, 15 June 1989; MNHN Ga 2351 (holotype male) (Baba & de Saint Laurent, 1992).

FAMILY LITHODIDAE SAMOUELLE, 1819

Remarks: Chevalloné & Olu (1996), in their review of anomurans from vents and seeps and citing Suess *et al.* (1985) and Kulm *et al.* (1986), noted that the first record of any lithodid from such habitats was an illustration of what was clearly a lithodid in a sketch of the cold-seep community along the lower Oregonian Subduction Zone (Suess *et al.*, 1985: fig. 1; see Kulm *et al.*, 1986, for map). From this same area but at slightly shallower depths, Carey *et al.* (1988) later reported *Lopholithodes foraminatus*, but it is not known if the earlier observations were of this same species. Tunnicliffe & Jensen (1987) noted that the earlier illustration might have been based on a species of *Paralomis* found by them at vents in the Juan de Fuca Ridge system (see below). Chevalloné & Olu (1996) listed 'two species and six occurrences not yet clearly assigned to species'. The situation has not changed appreciably since then (see below), and the review by Chevalloné & Olu (1996) remains a well-written and succinct introduction to the literature on vent- and seep-associated lithodids. According to those authors, cold-seep lithodids are known from 250 to 2037 m depths, with one personal observation (M. Sibuet) of a depth of 3800 m in the Nankai Trough of the Japan subduction zone, whereas hydrothermal vent-associated lithodids are known from 350–2000 m. Many reports exist of unidentified lithodids at vent or seep sites (in some cases, such as the paper by Sassen *et al.*, 1993, the species was later identified). Interestingly, despite their wide depth and geographical range, lithodids have not been reported from any of the EPR, Galapagos Rift (with the possible exception of a report by Guinot & Macpherson, 1987) or MAR systems (Chevalloné & Olu, 1996).

Species belonging to this large and widespread family are assumed to be vagrants as opposed to vent- or seep-endemics, even though some are known only

from such sites (see below and also Chevaldonné & Olu (1996). Macpherson (1988) provided an in-depth revision and review of all known Atlantic species of this family; see Macpherson (2001) for a brief overview of the family in the Indo-Pacific.

GENUS *LITHODES* LATREILLE, 1806
LITHODES MANNINGI MACPHERSON, 1988

Type locality: Caribbean Sea, R/V *Oregon II*, sta. 10829, 640 m (holotype) and 10611, 777 m (allotype) (see Macpherson, 1988: 62).

Known range: Caribbean Sea: Barbados, Dominican Republic and French Guiana, from 640 to 777 m (at non-vent, non-seep sites).

Occurrence at vents or seeps: cold seep site of the Barbados Accretionary Prism, south of Barbados (Macpherson, 1988: 64, 1994a).

Material: Barbados Accretionary Prism, Caribbean Sea, south of Barbados; 11°13'82"N, 59°21'82"W; 1236 m; DIAPISUB Expedition sta. DS16/7; 8 January 1993; MNHN (non-type, 1 male) (Macpherson, 1994a; Chevaldonné & Olu 1996). For additional (non-vent, non-seep) material, see Macpherson (1988: 62–64).

Remarks: Chevaldonné & Olu (1996) noted that the two species of lithodids found at seeps in Monterey Bay were tentatively assigned to this genus by J. Barry; these were referred to later by Barry *et al.* (1996) as *L. aequispina?* and *L. couesi?*, obviously somewhat tentatively.

GENUS *LOPHOLITHODES* BRANDT, 1848
LOPHOLITHODES FORAMINATUS (STIMPSON, 1859)

Type locality: eastern Pacific Ocean, United States, off California, near San Francisco; depth not provided.

Known range: North of Banks Island, British Columbia, to San Diego, California, and from the intertidal to 547 m (Hart, 1982).

Occurrence at vents or seeps: not known at any active vent or seep sites (but see below).

Material: type locality; type material presumably deposited at CAS and destroyed in 1906 earthquake and fire; no known material has been collected from vents or seeps. For occurrences (some only tentatively suggested), see Suess *et al.* (1985), Carey *et al.* (1988) and Chevaldonné & Olu (1996).

Remarks: Stimpson (1859) described this species as *Echidnocerus foraminatus* and noted that several specimens had been collected off the coast of Califor-

nia, near San Francisco; there was no mention of the depth from which the original specimens had been collected. Carey *et al.* (1988) noted large aggregations of this species at extinct seep areas in the upper Oregon subduction zone at approximately 250 m depth. According to Chevaldonné & Olu (1996), there is a possibility that this is the species observed and illustrated by Suess *et al.* (1985) at far greater depths (2037 m) at active (extant) cold seeps, which is why we have included it here.

GENUS *NEOLITHODES* A. MILNE-EDWARDS & BOUVIER, 1894
NEOLITHODES DIOMEDEAE (BENEDICT, 1894)

Type locality: Eastern Pacific Ocean, southern Chile, west of Isle de Chiloe; 42°36'S, 75°28'W, Steamer *Albatross* sta. 2789; 2454 m (lectotype and paralectotypes). –Archipelago de Los Chonos, off Bahia Anna Pink; 45°35'S, 75°55'W, Steamer *Albatross* sta. 2788; 1920 m (paralectotypes).

Known range: from waters off Peru and off the coast of Chile in the eastern Pacific north to the Sea of Cortez (see below), and in waters around South Georgia Island in the south-eastern Atlantic, 640–2450 m (Macpherson, 1988: 32 and fig. 11).

Occurrence at vents or seeps: Guaymas Basin (see below).

Material: type locality; USNM 018526 (lectotype). – same locality; USNM 134421 (4 male and 1 female paralectotypes). –Archipelago de Los Chonos, off Bahia Anna Pink; USNM 18527 (34 juvenile paralectotypes, 1 male paralectotype). According to the USNM records, single paralectotype specimens were given to each of the following institutions or persons: BMNH, MNHN, RMNH, ZMUC and E. Macpherson. The cards from the USNM catalogue refer to 'Yaldwin (1970)' as the publication in which the lectotype was designated. However, no such designation has been published (J. Yaldwin, pers. comm.), and therefore the aforementioned specimens, if indeed those of the original collection, should be considered syntypes. Specimens from vent localities have been collected by IFREMER and *Alvin* cruises in the Guaymas Basin (E. Escobar-Briones, pers. comm.), and some of these specimens formed the basis of studies on the natural history of the species at this site (Soto, Escobar & Cifuentes, 1996; Romero Jarero *et al.*, 1996; Escobar-Briones *et al.*, 2002; Gonzalez Ocampo, 2002). Specimens used for isotopic and elemental analysis were destroyed during those processes, and unfortunately the location of additional specimens from the Guaymas Basin, although some exist, is not known (E.

Escobar-Briones, pers. comm.). Abundant non-vent material is cited by Macpherson (1988).

Remarks: This species was originally described as *Lithodes diomedae* by Benedict (1894). *Neolithodes diomedae* was the first lithodid crab reported from hydrothermal vents (as opposed to seeps) (Chevaldonné & Olu, 1996). The species was reported by Grassle (1986) as the most commonly encountered crab at hydrothermal vents at 2000 m in the Guaymas Basin, Sea of Cortez. The species appears to feed mainly on organic matter of photoautotrophic origin near bacterial mats and hydrothermal vents in the Guaymas Basin (Chevaldonné & Olu, 1996; Escobar-Briones *et al.*, 2002; Soto *et al.*, 1996).

GENUS *PARALITHODES* BRANDT, 1848

Remarks: The genus *Paralithodes* is a fairly widespread and commonly encountered deep-sea genus of lithodids. According to Chevaldonné & Olu (1996), Sagalevich *et al.* (1992) reported *Paralithodes* sp. from 350–400 m 'on the periphery of active hydrothermal vents on the summit of Piip Volcano, in the Bering Sea, on dense populations of actinians' (Chevaldonné & Olu, 1996: 287). The observations were made using a submersible, and to our knowledge no specimens were collected. This is the basis for our listing of *Paralithodes* sp. in Table 1.

GENUS *PARALOMIS* WHITE, 1856

Remarks: *Paralomis*, a diverse and widespread lithodid genus with approximately 47 described species (Macpherson, 1994a), is the best-represented lithodid genus at vents and seeps.

Paralomis sp. In addition to the species noted below, Chevaldonné & Olu (1996: 288–289) cited several earlier works where currently unidentified species assumed to belong to *Paralomis* (the generic placement is questionable in some cases) have been reported or collected from vent or seep sites. These reports include Hashimoto *et al.* (1990: fig. 2, and 1995, Minami-Ensei Knoll vents, Mid-Okinawa Trough), possibly Jollivet *et al.* (1989, 'white coloured lithodid crabs' from the North Fiji back-arc basin), Desbruyères *et al.* (1994, Lau back-arc basin), Tunnicliffe & Jensen (1987, Axial Seamount vents co-occurring with the majid crab *Macroregonia macrochira*), Galkin & Moskalev (1990b, Juan de Fuca Ridge) and Suess *et al.* (1985, Oregon subduction zone cold seeps). To that list we could also add Ohta & Kim (2001: photograph 1) and Kim & Ohta (1991: fig. 11, *Paralomis* sp. from a baited trap on the Iheya Ridge). See Chevaldonné & Olu (1996) for a more detailed discussion of

species of *Paralomis* reported from vent and seep sites, and Macpherson (2003) for a key to all western and central Pacific Ocean species. It is likely (based on the number of reports of *Paralomis* sp. in the literature) that many more species will be reported and/or described as exploration of these habitats continues (Chevaldonné & Olu, 1996). Tunnicliffe & Jensen (1987) noted the presence of pieces of vestimentiferan worm tubes in stomachs of '*Paralomis* sp.' from the Axial Seamount vents.

PARALOMIS ARETHUSA MACPHERSON, 1994

Type locality: Caribbean Sea, Barbados Accretionary Prism; 10°19'64"N, 58°53'2"W; 1691 m; from cold seep.

Known range: Known only from the type locality (above).

Material: Barbados Accretionary Prism, Caribbean Sea, south of Barbados, 10°19'64"N, 58°53'42"W; 1691 m; DIAPISUB Expedition, sta. DS01/2, from cold seep; 24 December 1992; MNHN (holotype female) (Macpherson, 1994a).

Remarks: To date this species is known only from the single specimen noted above.

PARALOMIS CUBENSIS CHACE, 1939

Type locality: Off north-western Cuba, Harvard-Havanna Expedition, R/V *Atlantis* sta. 3003, 23°12.3'N, 82°12'W, 439–550 m (from Macpherson, 1988: 97).

Known range: Cuba, east of Florida, Gulf of Mexico, and off northern Brazil, 329–730 m (Macpherson, 1988: 99).

Occurrence at vents or seeps: Gulf of Mexico, Green Canyon (see below).

Material: We are not aware of any existing material from vents or seeps. Sassen *et al.* (1993) included a photograph of a lithodid from cold seeps within the Green Canyon area (a large offshore drilling area) off Louisiana that is probably this species (see below).

Remarks: According to Chevaldonné & Olu (1996), the photograph of a lithodid from the Green Canyon methane seeps on the upper continental slope of the Gulf of Mexico (off Louisiana) provided by Sassen *et al.* (1993: fig 5) was subsequently identified as belonging to this species. The crabs were recorded from 620 m among tubeworms and mussels, but material was presumably not collected. Carney (1994) noted that this species is a vagrant (i.e. not usually found associated with vents or seeps).

PARALOMIS HIRTELLA DE SAINT LAURENT & MACPHERSON, 1997

Type locality: Indo-West Pacific Ocean, Lau Basin, Valu-Fa Ridge, Hine Hina site; 22°13'S, 176°38'W; 1750m. –North Fiji Basin, White Lady hydrothermal vent site; 16°59'S, 173°55.4'W; 2000 m.

Known range: hydrothermal vent sites in the Lau Basin and North Fiji Basin (de Saint Laurent & Macpherson, 1997).

Material: Indo-West Pacific Ocean, Lau Basin, Valu-Fa Ridge, Hine Hina site, 22°13'S, 176°38'E; 1750 m; BIOLAU Expedition; sta. BL08; 14–18 May 1989; MNHN Pg 4658 (holotype male). –sta. BL03; 14–18 May 1989; MNHN Pg 4659 (paratype male); –sta. BL02; 14–18 May 1989; MNHN Pg 4662 (paratypes, 2 ovigerous females). –North Fiji Basin, White Lady hydrothermal vent site; 16°59'S, 173°55.4'E; 2000 m; STARMER II Expedition, dive 16; 13 Jul 1989; MNHN Pg 4661 (paratype female). –dive 20; MNHN Pg 4660 [1 paratype male, 2 paratype females (1 ovigerous, 1 immature)]. –16°59.65'S, 173°54.73'E; 2003m; HYFIFLUX Expedition, R/V *Sonne*, Croisière 99; sta. SO-115; SMF, registration number not provided (paratype juvenile).

Remarks: The species is known from only 9 specimens, and the original description remains the only report of this species to date.

PARALOMIS JAMSTECI TAKEDA & HASHIMOTO, 1990

Type locality: North Pacific Ocean, Okinawa Trough, hydrothermal vents of the Minami-Ensei Knoll; 28°23.4'N, 127°38.4'E; 710 m.

Known range: Known only from the type locality (above).

Material: North Pacific Ocean, Okinawa Trough, Minami-Ensei Knoll, 28°23.4'N, 127°38.4'E; 710 m; *Shinkai 2000* dive 428; 26 July 1989; NSMT-Cr 10172 [holotype female (ovigerous)], NSMT-Cr 10173 (paratype, 1 male), USNM and MNHN (2 ovigerous females) (Takeda & Hashimoto, 1990; also see Hashimoto *et al.*, 1990, 1995; Hashimoto, 1997, in Desbruyeres & Segonzac, 1997).

Remarks: *Paralomis jamsteci* was described as living among beds of mytilid mussels near vent openings (Takeda & Hashimoto, 1990; Hashimoto *et al.*, 1995). Hashimoto (1997, in Desbruyeres & Segonzac, 1997: 199) described the ecology of the species as 'crawling around bacterial mats close to hydrothermal vents' with vent temperatures reaching 269 °C. Hashimoto *et al.* (1995) also mentioned two other unidentified species of *Paralomis* living at the Minami-Ensei vent

fields (Hashimoto *et al.*, 1995; Chevaldonné & Olu, 1996). To date the species is known only from that site and from the specimens noted above. See Chevaldonné & Olu (1996: 289) for reports of this species feeding on vesicomid and mytilid bivalves.

PARALOMIS MULTISPINA (BENEDICT, 1894)

Type locality: North Pacific Ocean, Canada, British Columbia, off Queen Charlotte Islands; Steamer *Albatross* sta. 2860; 1602 m (originally as 876 fathoms).

Known range: North Pacific Ocean, from Shumagin Bank, Alaska, to southern California at depths of 500–1665 m (Hart, 1982).

Occurrence at vents or seeps: Sagami Bay, Japan, from cold seeps at 900–1200 m (Chevaldonné & Olu 1996).

Material: Benedict (1894) listed the type specimens under the registration number USNM 18535. We are not aware of any collections from vents or seeps, although the species is known to occur at cold seeps in Sagami Bay, 35°00.1'N, 139°13.7'E; *Shinkai 2000* dive 177; 1210 m (Hart, 1982; Horikoshi & Ishii, 1985; Ohta, 1990b; Chevaldonné & Olu, 1996).

Remarks: This species is found at cold seep communities in Sagami Bay, Japan, described by Horikoshi & Ishii (1985), Hashimoto *et al.* (1987, 1989) and Ohta (1990b). *Paralomis multispina* is common at these communities and, along with the clam *Calyptogena soyoae*, is the dominant macrofaunal species (Chevaldonné & Olu, 1996: 288). Horikoshi & Ishii (1985) reported seeing *P. multispina* feeding on black sediment adjacent to a colony of these giant clams but did not report the collection of specimens. See Chevaldonné & Olu (1996: 289) for reports of this species feeding on vesicomid and mytilid bivalves.

PARALOMIS VERRILLI (BENEDICT, 1894)

Type locality: North Pacific Ocean, Bering Sea, off Pribilof Islands, Steamer *Albatross* sta. 3501; 1258 m (originally as 688 fathoms).

Known range: North-eastern Pacific, Bering Sea and Sea of Okhotsk to Cortez Bank, California; 1238–2379 m (Hart, 1982; Chevaldonné & Olu, 1996: 288).

Occurrence at vents or seeps: vents in the Mid-Okinawa Trough (see below).

Material: The type specimens are housed at the National Museum of Natural History (Washington, DC) under the registration number USNM D-5685, according to Macpherson (2001: 802). Benedict (1894)

listed the types under the catalogue number USNM 18537.

Remarks: Although *Paralomis verrilli* has been observed often at hydrothermal vent sites in the Mid-Okinawa Trough (e.g. photograph 1 of Ohta & Kim, 2001), we are not aware of any collections from these sites. This is supported by Chevaldonné & Olu's (1996) observation that identification of the species observed at these sites is 'still to be confirmed' (suggesting specimens are not in hand). Chevaldonné & Olu (1996: 288) noted that its occurrence at such sites would not be surprising given its non-vent range and reported depths ('1500–3500 m around Japan and from the Bering Sea to California') (Hart, 1982; Ohta, 1990a; Kim & Ohta, 1991; Hashimoto *et al.*, 1995). However, the coloration of the species seen at the Mid-Okinawa Trough vent sites differs from the coloration seen at non-vent (cool water) populations (T. Komai, pers. comm.), such that close examination of specimens from the Mid-Okinawa Trough vent site is needed before confirming this identity.

Remarks: According to Chevaldonné & Olu (1996), *Paralomis verrilli* is 'believed to be the species found at hydrothermal vents of the Iheya Ridge, at 1400 m, in the Mid-Okinawa Trough' (citing pers. comm. with S. Ohta as well as Ohta, 1990a; Kim & Ohta, 1991; Hashimoto *et al.*, 1995).

FAMILY PARAPAGURIDAE SMITH, 1882

Remarks: Chevaldonné & Olu (1996: 287) mentioned the possibility of parapagurid hermit crabs at two locations: cold seeps of the Barbados Accretionary Prism (BAP) (probably the genus *Parapagurus*) and a cold seep of Monterey Bay (not identified). The latter record was listed by Barry *et al.* (1996) as Paguridae, rather than Parapaguridae. The animals were apparently seen but not collected. These observations constituted the only known records of hermit crabs associated with hydrothermal vents until Lemaitre (2004) described a new species of the genus *Paragiopagurus* from the Tashi fishing grounds off north-eastern Taiwan (see below).

GENUS PARAGIOPAGURUS LEMAITRE, 1996

PARAGIOPAGURUS VENTILATUS LEMAITRE, 2004

Type locality: North-eastern coast of Taiwan, Tashi fishing grounds, sta. CP 113; 24°50.8'N, 121°59.9'E; 281 m.

Known range: limited to the type locality.

Material: A total of eight specimens are known, from depths of 128–281 m, all collected by beam trawl

('chalut à perches', explaining the abbreviation CP), as follows: type locality, sta. NTOU A00438 (holotype male). –same data, MNHN-Pg 6736 [2 paratype males, 1 paratype female (ovigerous)]. –same data, USNM 1068936 (1 male, 2 ovigerous female paratypes). –same data; NTOU A00439 [6 paratype males, 1 paratype female (ovigerous)]. –24°50.5'N, 121°59.9'E; 205 m; sta. CP 81; MNHN-Pg 6735 (paratype male). –24°51.0'N, 121°51.3'E; 128–250 m; sta. CP 114; MNHN-Pg 6737 (1 paratype male).

Remarks: Lemaitre's (2004) report is the first description of a hermit crab from any hydrothermal vent system (though some were seen earlier; see above), which is somewhat surprising in light of the ubiquity of hermits in so many marine environments. The Tashi fishing grounds off the north-eastern coast of Taiwan and their hydrothermal vents were the subject of a joint expedition by Taiwanese and French scientists. Lemaitre (2004) cites a paper in press by Richer de Forges *et al.*, which we have not seen, for a full description of the expedition and all station data. Lemaitre uses the term 'bacteriophage setae', coined originally by Segonzac *et al.* (1993:50) in their discussion of the shrimp *Rimicaris exoculata*, to describe the 'specialized plumose setae that facilitate the growth of bacterial strands' in this species.

INFRAORDER BRACHYURA LATREILLE, 1802

Remarks: Because true (brachyuran) crabs are among the most diverse and geographically widespread crustaceans, it is not surprising that members of several families have been found at vents or seeps. In addition to the brachyuran species noted below, one of us (J.W.M.) has seen an illustration (K. Jacobsen, artist) of a small crab collected on *Alvin* dive 3633 in the eastern Gulf of Mexico. Based only on the illustration (the specimen was not kept or tracked and its whereabouts are unknown; I. Macdonald, pers. comm.), this was either a juvenile of the portunid *Raymanninus schmitti*, which is abundant at these depths (D. Felder, pers. comm.), or, as seems more likely based on features in the illustration, an undescribed species.

FAMILY ATELECYCLIDAE ORTMANN, 1893

Remarks: Bergquist *et al.* (2003) listed, in an appendix, crabs of this family from the Bush Hill and GC234 sites (cold seeps) in the northern Gulf of Mexico (within the large Green Canyon offshore drilling area), where it is apparently fairly common and is found buried in the mud at the base of tubeworm colonies (S. Hourdez, pers. comm.). This record and the observations of MacAvoy *et al.* (2002) constitute the only reports of any atelecyclid crabs from vent or seep

sites. Although the species has apparently been collected (18 specimens in 4 collections; see Bergquist *et al.*, 2003), we are not aware that the genus or species is known as of this writing.

FAMILY BYTHOGRAEIDAE WILLIAMS, 1980

Remarks: The family Bythograeidae, first described by Williams (1980) to accommodate *Bythograea thermydron* from vents in the eastern Pacific, remains the only family of crabs truly endemic to deep-sea hydrothermal vents. To date, the family is represented by five genera: *Allograea* Guinot, Hurtado & Vrijenhoek, 2002, *Austinograea* Hessler & Martin, 1989, *Bythograea* Williams, 1980, *Cyanagraea* de Saint Laurent, 1984 and *Segonzacia* Guinot, 1989. All species are assumed to be predators rather than bacterial feeders or grazers (e.g. Gorodezky & Childress, 1994); indeed, they are probably top predators at vent sites (see Jollivet, 1993; Voight, 2000; Micheli *et al.*, 2002). The southern extent of the family, as is currently known, appears to be at approximately 40°S, as indicated by observations of unnamed bythograeids by Stecher, Türkay & Borowski (2002) from the Foundation Seamount Chain of the Pacific-Antarctic Ridge and by Clark & O'Shea (2001) from the Kermadec Ridge off New Zealand, slightly further north.

GENUS ALLOGRAEA GUINOT, HURTADO & VRIJENHOEK, 2002

ALLOGRAEA TOMENTOSA GUINOT, HURTADO & VRIJENHOEK, 2002

Type locality: south-eastern Pacific Ocean, EPR, south of Easter Microplate; 31°09'S, 111°56'W; 2335 m.

Known range: Known only from vents south of the Easter Microplate (31–32°S) on the southern EPR (Guinot, Hurtado & Vrijenhoek, 2002; Guinot & Hurtado, 2003).

Material: type locality; *Alvin* dive 3337; 13 January 1999; MNHN-B28619 (holotype female), MNHN-B28620 (paratypes, 2 females). –same site; *Alvin* dive 3338; 2335 m; 14 January 1999; MNHN-B28621 (paratypes, 1 female and 1 specimen with broken carapace) (Guinot *et al.*, 2002).

Remarks: Guinot *et al.* (2002) presented preliminary data, some based on limited DNA sequences, suggesting that *Allograea* may be more closely related to *Cyanagraea*. Guinot & Hurtado (2003) noted that this species has been collected on the same dives as has *Bythograea vrijenhoeki* (see below) from vents on the southern EPR, implying that the two species are at least broadly sympatric.

GENUS AUSTINOGRAEA HESSLER & MARTIN, 1989

This genus, described initially to accommodate *A. williamsi* from the Marianas Back-Arc Basin (Hessler & Martin, 1989), is now, with the relatively recent description of *A. rodriguezensis* from the Indian Ocean (see below), the most widespread of the known bythograeid genera.

AUSTINOGRAEA ALAYSEAE GUINOT, 1990

Type locality: south-western Pacific Ocean, Tonga archipelago, Lau Basin, Vai-Lili hydrothermal vent site; 22°13'S, 176°38'W; 1900 m.

Known range: Western Pacific, from the Lau Back-Arc Basin, Valu-Fa Ridge, at 1750 m, and from the Manus Back-Arc Basin at 2190–2630 m (Guinot, 1997: 208, in Desbruyères & Segonzac, 1997).

Material: type locality; BIOLAU 1989, *Nautila* dive 09; 21 May 1989; MNHN-B 24021 (holotype male), MNHN-B 24022 (allotype female) (Guinot, 1990).

–Manus Basin, PACMANUS site; *Shinkai 2000*; 2K#1071; depth not provided; December 1998; non-types, number of specimens not noted (Tsuchida & Hashimoto, 2002).

Remarks: Guinot (1997, in Desbruyères & Segonzac, 1997) describes this species as actively moving in the vicinity of 'mollusk beds' (possibly a mixture of mussels and the large gastropods common at these sites).

AUSTINOGRAEA RODRIGUEZENSIS TSUCHIDA & HASHIMOTO, 2002

Type locality: Indian Ocean, 22 km N of Rodriguez Triple Junction, Kairei Field; 25°19.2'S, 70°02.4'E; 2420–2454 m.

Known range: Known to date only from the type locality.

Material: type locality; KR00-05 Indian Ocean Cruise (JMSTC), ROV *Kaiko*; 10K#167, 10K#168, 10K#169, 10K#170; 26 August 2000. NSMT-Cr 14228 (holotype male), JMSTC 037445 (allotype female), JMSTC 037446 (paratype, juvenile) (Tsuchida & Hashimoto, 2002).

Remarks: To our knowledge only the three specimens reported by Tsuchida & Hashimoto (2002) have been collected; all were collected by the ROV *Kaiko* (exact dates and dive numbers corresponding to the three specimens not known). Tsuchida & Hashimoto (2002: 642) also referred to earlier video sequences in which bythograeid crabs, presumably belonging to this species, were recorded at this site (Hashimoto *et al.*, 2001). This is also likely the species referred to as

'*Austinograea* n. sp.' by Van Dover *et al.* (2001: 820–822). Watabe & Hashimoto (2002) did not mention vent-associated crabs in their description of a new shrimp, *Rimicaris kairei*, from the same locality.

AUSTINOGRAEA WILLIAMSII HESSLER & MARTIN, 1989

Type locality: western Pacific, Mariana Back-Arc Basin, Burke Vent Field, 18°10.917–10.948'N, 144°43.210–43.204'E; 3660 m.

Known range: Known only from the Mariana Back-Arc Basin (Hessler & Martin, 1989; Tsuchida & Fujikura, 2000; Tsuchida & Hashimoto, 2002).

Material: type locality; *Alvin* dive 1836; USNM 243241 (holotype male); *Alvin* dive 1836; 27 April 1987; USNM 234242 (allotype female).

Pacific Ocean, West of Mariana Island Arc, Mariana Back-Arc Basin:

–Ilium vent field; 18°12.805'N, 144°42.425'E; 3595 m; *Alvin* dive 1825; 10 April 1987; SIO (paratype, 1 female) (Hessler & Martin, 1989).

–exact locality unknown; *Alvin* dive 182?; depth not known, between 3620 and 3799 m; ? April 1987, between 7 and 14 April; baited traps; SIO (paratype, 1 female) (Hessler & Martin, 1989).

–Burke vent field, Snail Pits; 18°10.948'N, 144°43.204'E; 3660 m; *Alvin* dive 1835; 26 April 1987; baited traps; SIO (paratypes, 10 males, 3 females) (Hessler & Martin, 1989).

–Burke vent field, Snail Pits and Anemone Heaven; 18°10.917–18°10.948'N, 144°43.210–144°43.204'E; 3660 m; *Alvin* dive 1836; 27 April 1987; baited traps; USNM 243241 (holotype male), USNM 243242 (allotype female), USNM 243243 (paratypes, 3 males, 3 females); LACM (paratypes, 4 males, 1 female); RMNH D37730 (paratypes, 1 male, 1 female), ZMM (paratypes, 1 male, 1 female), NSMT (paratypes, 1 male, 1 female), SIO (paratypes, 29 males, 4 females) (Hessler & Martin, 1989).

–Ilium vent field; 18°12.805'N, 144°42.425'E; 3595 m; *Alvin* dive 1838; 29 April 1987; baited traps; SIO (paratypes, 2 females) (Hessler & Martin, 1989).

–Alice Springs hydrothermal vent field; 18°12.599'N, 144°42.431'E; *Alvin* dive 1843; 3640 m; 4 May 1987; baited traps; SIO (paratypes, 4 males, 3 females) (Hessler & Martin, 1989). –same data; *Alvin* dive 1845; 3640 m; 6 May 1987; baited traps; ANSP (paratypes, 1 male, 4 females), MNHN-B 20910 (paratypes, 1 male, 1 female), ZMUC (paratypes, 1 male, 1 female), SIO (paratypes, 14 males, 42 females) (Hessler & Martin, 1989). –18°12.9'N, 144°42.5'E, *Shinkai* 6500; dives 6K#355–357, 3600 m (83 specimens total from all 5 dives) (Tsuchida & Fujikura, 2000). –18°N Vent Site; *Shinkai* 6500; 6K#357; depth

not provided; December 1996; non-types, number of specimens not noted (Tsuchida & Hashimoto, 2002).

–Marianas Back-Arc Basin; 13°23.7'N, 143°55.2'E; *Shinkai* 6500, dives 6K#353 and 6K#354; 1450 m (Tsuchida & Fujikura, 2000).

Remarks: This species is very abundant at active vent sites in the Mariana Back-Arc Basin (see photographs in Hessler, Lonsdale & Hawkins, 1988). Tsuchida & Fujikura (2000) described heterochely, relative growth and gonopod morphology in this species.

AUSTINOGRAEA YUNOHANA TAKEDA, HASHIMOTO & OHTA, 2000

Type locality: north-western Pacific Ocean, hydrothermal vents, Myojin Knoll; 32°06.19'N, 139°52.04'E; 1263 m. –eastern edge of Philippine Sea Plate, off central Japan. –Suiyo Seamount; 28°34.50'N, 140°38.50'E; 1380 m. –Kaikata Seamount; 26°42.60'N, 141°04.60'E; 420–450 m. –Nikko Seamount; 23°04.70'N, 142°19.90'E; 433–762 m.

Known range: Known from the type locality (above) and from vents on the Suiyo Seamount, Kaikata Seamount, Nikko Seamount, all off central Japan (Takeda, Hashimoto & Ohta, 2000; see below).

Material: north-western Pacific Ocean, Myojin Knoll; 32°06.19'N, 139°52.04'E; 1263 m; *Shinkai* 2000 dive 1007; 5 May 1998; NSMT-Cr1665 (holotype), MNHN (paratypes, 2 males).

–Suiyo Seamount; 28°34.50'N, 140°38.50'E; 1380 m; *Shinkai* 2000 dive 626; 11 July 1992; NSMT-Cr 13656 (allotype), JMSTC, no number given (paratypes, 2 females).

–Kaikata Seamount, 26°42.60'N, 141°04.60'E; 420–450 m; *Kaiyo* cruise DK88-3-IZU; 31 August 1988; small dredge on deep-tow TV system; NSMT-Cr 13657 (paratypes, 2 males), NSMT-Cr 13658 (paratypes, 2 females). –26°42.35'N, 141°04.67'E; 448 m; *Shinkai* 2000 dive 1014; 18 May 1998; USNM, number not given (paratypes, 2 males). Additional (non-type) material: 11 males, 1 female, same data as for *Kaiyo* cruise DK88-3-IZU.

–Nikko Seamount; 23°04.70'N, 142°19.90'E; 433–762 m; *Shinkai* 6500 dive 144; 19 September 1992; NMFS, number not given (paratype, 1 male), NSMT-Cr 13660 (paratypes, 2 females).

–Kaikata Seamount; *Shinkai* 2000, 2K#1014; depth not provided; December 1998; (non-types, number of specimens not noted) (Tsuchida & Hashimoto, 2002).

Holotype, allotype, and selected paratypes and young are in NSMT. One paratype female was retained at JMSTC. Takeda *et al.* (2000) indicated that 'some paratypes' were to be sent to NHML, NMFS and USNM.

Remarks: This species occurs in great abundance at some sites, especially on the Kaikata (= Kaikēi) Seamount (see Takeda *et al.*, 2000: fig. 7). A study of locomotor activity in 'eyeless crabs' under different lighting conditions by Kabasawa (1991) presumably used this species, as the specimens in that study came from the Kaikata Seamount and were collected by the *Shinkai* 2000 at 470 m (Kabasawa, 1991: 21).

GENUS *BYTHOGRAEA* WILLIAMS, 1980

By far the most diverse of the bythograeid genera, *Bythograea* contains at least six and possibly more species, all of which are endemic to hydrothermal vents in the eastern Pacific (see below). It is probable that the bythograeid crabs encountered (but not collected) by Stecher *et al.* (2002) from the Foundation Seamount Chain of the Pacific-Antarctic Ridge also belong to this genus, as it is due south of known sites where crabs of the genus *Bythograea* have been documented and collected. Clark & O'Shea (2001) reported an undescribed species of *Bythograea* from the Kermadec Ridge, New Zealand; we are not aware of that species having been described.

BYTHOGRAEA GALAPAGENSIS GUINOT & HURTADO, 2003

Type locality: Eastern Pacific Ocean, Galapagos Rift, Rose Garden vent; 00°48.2'N, 86°13.9'W; 2461 m.

Known range: limited to type locality.

Material: type locality; *Alvin* dive 2224; 29 May 1990; MNHN-B 28725 (holotype male), MNHN-B 28744 (allotype female), MNHN-B 28745 (paratype, 1 female juvenile) (Guinot & Hurtado, 2003).

Remarks: This species, based on two adults and one juvenile, is morphologically extremely similar to *B. thermydron*, which occurs at the same site. The possibility exists that these two are conspecific, although Guinot & Hurtado (2003) pointed out some morphological differences between the species as well as differences in a fragment of the mitochondrial cytochrome oxidase c subunit I gene (COI). More confusing still is the relationship between *B. galapagensis* and *B. intermedia* (see below), a species based on larval and juvenile material and for which the type material was not clearly marked and is still of questionable provenance (see Guinot & Hurtado, 2003: 431–432).

BYTHOGRAEA INTERMEDIA DE SAINT LAURENT, 1988

Type locality: East Pacific Ocean, EPR, Galapagos Rift, Rose Garden vent; 00°48.25'N, 86°13.30'W; 2460 m.

Known range: Known only from the type locality.

Material: type locality; *Alvin* dive 983; 30 November 1979; USNM 180065 (holotype 1 megalopa) (de Saint Laurent, 1988). See Guinot & Hurtado (2003) and below for additional material and for clarification of type materials and USNM catalogue numbers.

Remarks: Hessler & Martin (1989: 645) lamented the fact that this species was erected 'on the basis of a single megalopa larva and on the assumption that some of the smaller juveniles described by Williams (1980) were of this previously described species' (see also Guinot, 1997, in Desbruyères & Segonzac, 1997). Guinot & Hurtado (2003) clarified this by noting that de Saint Laurent (1988) actually never saw the juvenile she selected as the holotype of *B. intermedia*, which came from a lot of juveniles identified by Williams as *B. thermydron*. About this lot, Guinot & Hurtado (2003: 432) stated: 'The exact locality of the juvenile material of Williams, which perhaps contains *B. thermydron* mixed with *B. intermedia*, is unknown.' Furthermore, the holotype is actually a juvenile (now USNM 268862), and the megalopa noted above is a paratype (now USNM 180065), according to Guinot & Hurtado (2003). The similarity between de Saint Laurent's description and specimen and the description of *B. galapagensis* by Guinot & Hurtado is such that comparisons 'do not allow us to establish whether they correspond to the same species' (Guinot & Hurtado, 2003: 432). Because the species description 'was based on a total of six early crab stages and a megalopa, all mixed with *B. thermydron* specimens from the original collection of the Galapagos Rift studied by Williams (1980),' Guinot & Hurtado (2003) felt that this is 'a poorly known species'. We agree with that assessment and believe that *B. intermedia* is of questionable status and in need of re-evaluation.

BYTHOGRAEA LAUBIERI GUINOT & SEGONZAC, 1997

Type locality: south-eastern Pacific Ocean, EPR, Rehu hydrothermal site; 17°24.85'S, 113°12.15'W; 2580 m.

Known range: East Eastern Pacific Ocean, southern EPR, from hydrothermal vents between 11°S and 21°S; absent from northern EPR vent sites (Guinot, 1997, in Desbruyères & Segonzac, 1997; Guinot & Segonzac, 1997; Guinot *et al.*, 2002; Guinot & Hurtado, 2003).

Material: type locality; Naudur, *Nautila* dive ND18-5-8B; 23 December 1993; MNHN-B 24897 (holotype male), MNHN-B 24900 (allotype female) (Guinot & Segonzac, 1997).

–Rehu hydrothermal site; 17°24.85'S, 113°12.15'W; 2580 m; NAUDUR, *Nautila* dive ND6-2-6B; 11 Decem-

ber 1993; MNHN-B 24893 (paratype, 1 male) (Guinot & Segonzac, 1997).

–Rehu hydrothermal site; 17°24.85'S, 113°12.15'W; 2578 m; NAUDUR, *Nautila* dive ND18–0-1B; 23 December 1993; MNHN-B 24895 (paratype 1 male) (Guinot & Segonzac, 1997).

–Rehu hydrothermal site; 17°24.85'S, 113°12.15'W; depth not provided; NAUDUR, *Nautila* dive ND18-4-7B; date not provided; MNHN-B 24896 at USNM (paratypes, 1 male juvenile, 4 females) (Guinot & Segonzac, 1997).

–Rehu hydrothermal site; 17°24.85'S, 113°12.15'W; 2578 m; NAUDUR, *Nautila* dive ND19-1-1B; 24 December 1993; ex-MNHN-B 24898 (paratype, 1 female) (Guinot & Segonzac, 1997).

–Stockwork hydrothermal site; 18°25.82'S, 113°23.60'W; 2623 m; NAUDUR, *Nautila* dive ND8-4-4B; 13 December 93. MNHN-B 25392 (non-type, 1 male juvenile) (Guinot & Segonzac, 1997).

Remarks: Guinot (1997, in Desbruyères & Segonzac, 1997) noted that this species occurs near black smokers at high temperatures and that it is 'probably associated with *B. thermydron*'. Guinot & Hurtado (2003) extended the known range of the species south to 32°S in their description of *B. vrijenhoeki*, with which *B. laubieri* co-occurs (Guinot & Hurtado, 2003: 430).

BYTHOGRAEA MICROPS DE SAINT LAURENT, 1984

Type locality: north-eastern Pacific Ocean, EPR; 21°N; 2615 m.

Known range: EPR, from vents at 9°50'N (2535 m) and 13°N (2620 m) and from the Galapagos Rift at 2450 m (Guinot, 1997, in Desbruyères & Segonzac, 1997) to 21°N. Guinot & Hurtado (2003: 437).

Material: type locality; Oasis, *Alvin* dive 1211; 17 April 1982; USNM 195002 (holotype female) (de Saint Laurent, 1984). –EPR; 12°48.85'N, 103°56.60'W; 2620 m; BIOCYPHERM, *Nautila*, dive 33; 8 March 1982; MNHN B107108 (allotype male) (de Saint Laurent, 1984).

–Totem hydrothermal site; 12°48.80'N, 103°56.45'W; 2640 m; MISSION HOT 96, *Nautila*, dive 29; 18 March 1996; MNHN-B 25393 (non-types, 1 male, 1 male juvenile, 2 female juveniles) (Guinot & Segonzac, 1997).

–Parigo hydrothermal site; 12°48.57'N, 103°56.41'W; 2648 m; MISSION HOT 96, *Nautila*, dive 26; 15 March 1996; MNHN-B 25394 (non-type, 1 juvenile) (Guinot & Segonzac, 1997).

–M-Vent hydrothermal site; 09°50.83'N, 104°17.57'W; 2535 m; MISSION HOT 96, *Nautila*, dive 22; 10 March 1996; MNHN-B 25395 (non-type, 1 juvenile male) (Guinot & Segonzac, 1997).

–EPR, 12–13°N, Pogonord and Parigo vent sites, 10 small specimens from dives 32, 38 and 41 (MP-B12826, MP-B12828 and MP-B13000 (Guinot, 1988).

Remarks: This is a small species (13 × 24 mm), and most of the known specimens are juveniles. De Saint Laurent (1988) briefly illustrated the megalopa and young crab stages. Guinot (1997, in Desbruyères & Segonzac, 1997) noted that the species came from *Riftia* and clam washings. Guinot & Hurtado (2003) compared the morphology of this species with others in the genus.

BYTHOGRAEA THERMYDRON WILLIAMS, 1980

Type locality: East Pacific Ocean, EPR, Galapagos Rift, Mussel Bed; 0°48.89'N, 86°09.12'W; 2488 m.

Known range: Eastern Pacific Ocean, found associated with (and the most dominant crab species at) most hydrothermal vent sites in the EPR between 21°N and 18°38'S and on the Galapagos Rift, but not known to date from vents south of the Easter Microplate (31–32°S) on the southern EPR (Guinot & Segonzac, 1997; Guinot & Hurtado, 2003).

Material: type locality; *Alvin* dive 887; 12 February 1979; USNM 172830 (holotype male), USNM 172832 (paratypes, 4 males, 1 female), MCZ (paratype, 1 male), AHF/LACM (paratype, 1 male), BMNH (paratype, 1 male), MNHN (paratype, 1 male), WHOI (paratype, 10 males, 3 females), (Williams, 1980). –type locality; 2493 m; *Alvin* dive 880; 21 January 1979; WHOI (paratype, 1 male) (Williams, 1980).

–Galapagos Rift, Mussel Bed; 0°48.89'N, 86°09.12'W; 2483 m; *Alvin* dive 888; 13 February 1979; Paratypes: 1 male, RMNH; 11 males, 29 females, WHOI (Williams, 1980).

–Galapagos Rift, Rose Garden area; 0°48.25'N, 86°13.48'W; 2447 m; *Alvin* dive 890; 15 February 1979; MCZ (paratype, 1 female), AHF/LACM (paratypes, 2 females), BMNH (paratypes, 2 females), RMNH (paratypes, 2 females), MNHN (paratype, 1 female), WHOI (paratypes, 16 females) (Williams, 1980). –0°48.25'N, 86°13.48'W; 2457 m; *Alvin* dive 894; 19 February 1979; WHOI (paratypes, 6 females) (Williams, 1980). –0°48.25'N, 86°13.48'W; 2482 m; *Alvin* dive 895; 20 February 1979; WHOI (paratype, 1 male) (Williams, 1980). –0°48.25'N, 86°13.48'W; 2460 m; *Alvin* dive 896; 21 February 1979; USNM 172831 (allotype female), USNM 172833 (paratypes, 2 males, 4 females), WHOI (paratypes, 1 male, 31 females) (Williams, 1980).

–Locality not recorded; depth unknown; *Alvin* dive unknown; date unknown; WHOI (paratype, 1 female) (Williams, 1980).

–southern EPR, Fromveur hydrothermal vent site; 18°25.96'S, 113°23.35'W; 2622 m; NAUDUR, *Nautila* dive ND9-1-2B; 14 December 1993; MNHN-B 24916 (non-type, 1 juvenile) (Guinot & Segonzac, 1997). –Animal Farm hydrothermal vent site; 18°36.50'S, 113°23.98'W; 2673 m; NAUDUR, *Nautila* dive ND12-7-3B; 17 December 1993; MNHN-B 24899 (non-types, 2 males, 2 females) (Guinot & Segonzac, 1997). –Animal Farm hydrothermal vent site; 18°36.50'S, 113°23.98'W; 2673 m; NAUDUR, *Nautila* dive ND12-7-6B; 17 December 1993. MNHN-B 25391 (non-type, 1 juvenile) (Guinot & Segonzac, 1997).

–Galapagos Rift, Rose Garden vent site; 2500 m; February, November and December 1979; 215 crabs collected from traps (DeBevoise, Childress & Withers, 1990).

–EPR, Riftia-Field hydrothermal vent site; 09°50.72'N, 104°17.56'W; 2532 m; MISSION HOT 96, *Nautila*, dive 23; 11 March 1996; non-types, 32 males, depository not named, likely MNHN (Guinot & Segonzac, 1997).

–EPR, 12–13°N, Actinoir, Pogonord and Parigo sites; 2430 to 2610 m; BIOCARYSE 1984 cruise; 38 total specimens (see Guinot, 1988). –EPR; 12°48'N, 103°57'W; *Nautila*; November and December 1987; number of specimens not given (Sanders & Childress, 1992). –EPR; 12°48.675'N, 103°56.386'W; 2640 m; Hydrothermal Ecosystem Research Observatory (HERO) expedition, *Nautila*; October–November, 1991; number of specimens not given (Boetius & Felbeck, 1995). –same general area, HERO 1991 and 1992 cruises and DSV *Alvin* dives, from the following vent sites: Elsa, Genesis, Julie, Parigo (numbers of crabs not given) (Gorodezky & Childress, 1994). –EPR, Totem hydrothermal site; 12°48.80'N, 103°56.45'W; 2640 m; MISSION HOT 96, *Nautila*, dive 28; 17 March 1996; non-types, 3 females, depository not named, likely MNHN (Guinot & Segonzac, 1997). –EPR, Genesis site; PHARE'02 expedition to 13°N vent sites; 2600 m; May 2002, number and fate of specimens not given (Sanglier *et al.*, 2003).

–EPR, collapse pit site; 20°50'N, 109°00'W; 2600 m; May 1982; from traps; 19 specimens (DeBevoise *et al.*, 1990).

Remarks: As the first species of true (brachyuran) crab reported from hydrothermal vents as well as the species for which the family Bythograeidae was erected, *B. thermydrion* understandably has been the subject of a large number of studies, not all of which are listed here. Hessler & Smithey (1983) provided comments on its habitat and ecology, some of which are also summarized by Guinot (1997, in Desbruyères & Segonzac, 1997). Van Dover *et al.* (1985) described planktotrophic larval development and included a photograph of an ovigerous female (p. 224, fig. 1B). Van

Dover, Franks & Ballard (1987) used crab densities to predict vent locations, and although they mentioned only the genus name we assume, based on the locality, that the species was *B. thermydrion*. Other studies on this species include investigations of its digestive enzyme activities (Boetius & Felbeck, 1995), oxygen consumption and regulation (Gorodezky & Childress, 1994), effects of temperature and pressure on oxygen consumption (Mickel & Childress, 1980, 1982a; reviewed by Somero, 1992) and on heart rate (Mickel & Childress 1982b; Airriess & Childress, 1994), foregut morphology (Martin, Jourharzadeh & Fitterer, 1998a), general physiology (Childress & Fisher, 1992), mouthpart morphology (Factor, Van Dover & Williams, 1982), ability to detoxify sulphide (Powell & Somero, 1986; Vetter *et al.*, 1987), oxygen consumption rates and their regulation (Childress & Mickel, 1985), haemocyanin structure and function (Terwilliger & Terwilliger, 1985; Lallier *et al.*, 1998; Zal *et al.*, 2002), hyperglycemic hormones (Toullec *et al.*, 2002), haemocyanin activity and oxygen affinity (Arp & Childress, 1981; Sanders, Art & Childress, 1988; Sanders & Childress, 1992), dietary carotenoids (DeBevoise *et al.*, 1990), predation on other vent organisms (Voight, 2000, citing Jollivet 1993 (see also Micheli *et al.*, 2002, and Childress, Felbeck & Somero, 1987)), enzyme activities (Hand & Somero, 1983), haemocyanin protein structure (Sanglier *et al.*, 2003), larval development (Van Dover, Williams & Factor, 1984; Van Dover *et al.*, 1985), colonization of new vents (Shank *et al.*, 1998a), occurrence in a Stauromedusae-dominated region (Lutz *et al.*, 1998), ontogeny of vision and visual metamorphosis (Jinks *et al.*, 2002), radiometric ages (Bennett & Turekian, 1984), osmotic and hydromineral regulation (Martinez *et al.*, 2000, 2001), temporal patterns in egg development (Perovich *et al.*, 2003) and development and swimming behaviour of megalopal stages (e.g. Epifanio *et al.*, 1999). Epifanio *et al.* (1999) successfully reared the species from late larval (megalopal) stages through metamorphosis and the first several juvenile stages. Megalopal and early crab stages were also briefly described by de Saint Laurent (1988), and food sources of megalopae and early juveniles were studied using stable isotopes by Dittel, Epifanio & Perovich (2005).

BYTHOGRAEA VRIJENHOEKI GUINOT & HURTADO, 2003

Type locality: south-eastern Pacific Ocean, EPR, south of the Easter Microplate; 31°51'S, 112°02'W; 2334 m.

Known range: Known only from the type locality and immediate vicinity (Guinot & Hurtado, 2003: 427).

Material: type locality; *Alvin* dive 3340; 16 January 1999; –dive 3341; 17 January 1999; MNHN-B28751

(holotype male), MNHN-B28752 (allotype female). –2335 m; *Alvin* dive 3337; 13 January 1999; MNHN-B28753 (paratypes, 1 male, 2 females, paratypes), USNM 1009516 (paratypes, 1 male, 1 female). –2334 m; *Alvin* dive 3338; 14 January 1999; MNHN-B28754 (paratypes, 1 male, 4 females). –2338 m; *Alvin* dive 3339; 15 January 1999; MNHN-B28755 (paratypes, 2 males). –2334 m; *Alvin* dive 3340; 16 January 1999; MNHN-B28756 (paratypes, 2 males, 2 females). –2333 m; *Alvin* dive 3341; 17 January 1999; MNHN-B28757 (paratype, 1 male). –2338 m; *Alvin* dive 3342; 18 January 1999; MNHN-B28758 (1 male, 1 female) (Guinot & Hurtado, 2003).

Remarks: Guinot & Hurtado (2003) commented on the close similarity between this species and *B. laubieri*, with which it is sometimes collected. *Bythograea vrijenhoeki* also occurs sympatrically with, and has been collected on the same dives (*Alvin* dives 3337 and 3338) as, *Allograea tomentosa* (see Guinot & Hurtado, 2003: 430).

GENUS *CYANAGRAEA* DE SAINT LAURENT, 1984
CYANAGRAEA PRAEDATOR DE SAINT LAURENT, 1984

Type locality: north-eastern Pacific Ocean, EPR; 12°48.85'N, 103°56.60'W; 2620 m.

Known range: Eastern Pacific Ocean, hydrothermal vents between 9°N and 18°S on the EPR (Guinot 1988, 1990, 1997, in Desbruyères & Segonzac, 1997; de Saint Laurent, 1984; Guinot & Hurtado, 2003).

Material: type locality; BIOCYATHERM, dive 33; 8 March 1982; MNHN-B 10709 (holotype female) (de Saint Laurent, 1984). –type locality; dive 34; 2620 m (?); date not provided; MNHN-B 10710 (paratype, 1 female) (de Saint Laurent, 1984).

–M-Vent hydrothermal site; 09°50.83'N, 104°17.57'W; 2535 m; MISSION HOT 96, *Nautile* PL 1081/22; 10 March 1996; MNHN-B 25398 (non-type, 1 male) (Guinot & Segonzac, 1997). –same locality; 2535 m; PL 1083/24; 12 March 1996; MNHN-B (non-type, 1 female) (Guinot & Segonzac, 1997).

–Elsa hydrothermal site; 12°48.85'N, 103°56.30'W; 2630 m; HERO 91, *Nautile* dive 14; 18 October 1991; depository not named, likely MNHN (non-type, 1 female) (Guinot & Segonzac, 1997). –Elsa hydrothermal site; 12°48.13'N, 103°56.30'W; *Nautile* PL 1089/30; 2630 m; 19 March 1996. Non-type: 1 female, depository not named; Mission Hot 96 (Guinot & Segonzac, 1997). –Elsa hydrothermal site; 12°48.13'N, 103°56.30'W; *Nautile* PL 1091/32; 2630 m; 21 March 1996. Non-type: 1 female, MNHN-B 25399; Mission Hot 96 (Guinot & Segonzac, 1997).

–EPR, 12–13°N, Pogonord site, 2600 m, Biocyarise 1984 expedition, dive 34, 2 large females (MP-B12822) (Guinot, 1988).

–Totem site (12°48.816'N, 103°56.433'W), from sides of smokers, 4 specimens (Gorodezky & Childress, 1994).

Additionally, Hessler & Martin (1989) mentioned 3 specimens of *Cyanagraea praedator* collected by SIO researchers on the French HYDRONAUT Expedition to the EPR; it is not clear if any of those specimens are the same as those mentioned above.

Remarks: Despite the impressive size of this species (females may reach 123 mm in carapace width), it is not often encountered or collected. Guinot & Segonzac (1997) reported seeing (but not collecting) large crabs possibly belonging to this species on the southern East Pacific Rise (17–19°S), extending the known range to the south; however, the uncertainty (because they could not examine any specimens) led them to refer to the southern EPR species as *Cyanagraea* sp. (Guinot & Segonzac, 1997: 121). Knowledge of the biology of *C. praedator* includes studies on oxygen consumption and regulation by Gorodezky & Childress (1994) and on haemocyanin functional properties by Chausson *et al.* (2001). Guinot (1997: 213, in Desbruyères & Segonzac, 1997) summarized what little is known of the species' ecology. The species, which is almost invariably found near black smoker vents, is associated with alvinellid polychaetes, which also make up part of its diet, along with other worms and young *Bythograea* crabs (Guinot, 1997, in Desbruyères & Segonzac, 1997). Secretan & Guinot (1988) described the endophragmal skeleton. The male of the species was described by Hessler & Martin (1989) in their description of *Austinograea williamsi*. Guinot & Segonzac (1997) mentioned seeing (but not collecting) a large crab at the 31°S site of the EPR that might have been *Cyanagraea*, but, because of the large range extension this would be, and the lack of specimens, we are somewhat doubtful of that record.

GENUS *SEGONZACIA* GUINOT, 1989

Remarks: To date, this genus and its sole species, *S. mesatlantica* (originally described by Williams, 1988, as *Bythograea mesatlantica*), is the only genus of bythograeid crab known from the Atlantic. Reports of '*Segonzacia* sp.' (e.g. Desbruyères *et al.*, 2000, 2001) are assumed by us to be *S. mesatlantica* (below).

SEGONZACIA MESATLANTICA (WILLIAMS, 1988)

Type locality (as *Bythograea mesatlantica*): North Atlantic Ocean, MAR, 70 km south of Kane Fracture Zone, MARK vent, sta. 1; 23°22.09'N, 44°57.12'W; 3437 m.

Known range: North Atlantic, hydrothermal vent fields of the MAR, including Snake Pit (3480 m) and Lucky Strike (1700 m) (Guinot, 1989; Guinot, 1997, in Desbruyères & Segonzac, 1997; Turnipseed *et al.*, 2004), Logatchev (Gebruk *et al.*, 2000a) and, tentatively, at Menez Gwen (Colaço *et al.*, 1998; Sanglier *et al.*, 2003).

Material: type locality; NSF Ocean Drilling Program Leg 106, Alvin dive 1683; 30 May 86; scoop; USNM 234300 (holotype female) (Williams, 1988).

–Snake Pit hydrothermal site; 23°22.094'N, 44°56.946'W; 3478 m; HYDROSNAKE cruise 1988, *Nautila* dive HS 03; 21 June 1988; MNHN-B 20612 (non-type, 1 male). –same locality; *Nautila* dive HS 08; 26 June 1988; MNHN-B 20613 (non-types: 2 females, 1 juvenile). –same locality; *Nautila* dive HS 10; 28 June 1988; MNHN-B 20614 (non-type, 1 female). –same locality; *Nautila* dive HS 10, 28 June 1988; MNHN-B 20615 (non-types, 2 females) (Guinot, 1989).

–Menez Gwen hydrothermal field; 850 m; ATOS'01 cruise; number and fate of specimens not given (Sanglier *et al.*, 2003).

Remarks: This species was reported in the literature as *Bythograea* sp. by Grassle *et al.* (1986) and observed by Rona *et al.* (1986). It was originally described as *Bythograea mesatlantica* by Williams (1988) and was later transferred to the genus *Segonzacia* by Guinot (1989), who also provided a thorough treatment of its morphology and ecology. The species was described by Guinot (1997, in Desbruyères & Segonzac, 1997) as being 'necrophagous, feeding on dead shrimps and exuviae'. *Segonzacia mesatlantica* has been observed at many Mid-Atlantic vent sites (see above) and remains the sole vent-endemic crab from the MAR sites. Desbruyères *et al.* (2000: table 4) listed the species as being rare or patchy but 'dominant carnivorous' at Logatchev, Snake Pit, TAG, Broken Spur, Rainbow, Lucky Strike and Menez Gwen (see also Colaço *et al.*, 2002); however, Gebruk *et al.* (2000a) did not mention it in their study of the Logatchev fauna. Haemocyanin protein structure was studied by Sanglier *et al.* (2003), and respiratory adaptations were investigated by Chausson *et al.* (2004). The organ of Bellonci and sinus gland were described by Charman-tier-Daures & Segonzac (1998). Tudge *et al.* (1998) described the ultrastructural morphology of the sperm and compared it with that of other vent crab genera.

FAMILY CANCRIDAE LATREILLE, 1802

GENUS *CANCER* LINNAEUS, 1758

CANCER PAGURUS LINNAEUS, 1758

Type locality: 'in Oceano Europaeo, Asiatico', Marstrand, north of Goteborg, west coast of Sweden (Nations, 1975).

Known range: north-west coast of Norway south to Portugal; Mediterranean (Nations, 1975).

Occurrence at vents or seeps: reported from methane seeps off Denmark.

Material: No material from vent or seep sites is known.

Remarks: Levin *et al.* (2000: 23) reported *Cancer pagurus* from methane seeps off Kattegat, Denmark, citing Jensen *et al.* (1992) as the original source of the record.

FAMILY EPIALTIIDAE MACLEAY, 1838

GENUS *SPHENOCARCINUS* A. MILNE-EDWARDS, 1878

Remarks: Tavares (1991) reviewed and redefined the genus *Sphenocarcinus*, which he described as 'an endemic amphi-American genus, with just one species on each side of the continent.' Clark & O'Shea (2001) reported the genus from vent sites on the Kermadec Ridge off New Zealand, listing their observation as *Sphenocarcinus* sp. However, in light of the restriction of *Sphenocarcinus* to the Americas and the confusion (in the past) of species of *Rochinia* and *Sphenocarcinus* (according to Tavares, 1991), it is quite possible that the species reported by Clark & O'Shea as *Sphenocarcinus* sp. was instead a member of the more widely distributed genus *Rochinia*, now considered a member of the family Pisidae (see below and also Richer de Forges, 1995, and Webber & Richer de Forges, 1995: 514, for a comparison of Pacific species of *Sphenocarcinus*, *Rochinia* and *Oxypleurodon*). Apparently no specimens of *Sphenocarcinus* sp. were collected from vents sites on the Kermadec Ridge, so we cannot rule out the possibility of *Sphenocarcinus* occurring here, although it would appear unlikely.

The family Epialtidae, a former subfamily of the Majidae, is now recognized as a distinct family by many workers (Martin & Davis, 2001; McLaughlin *et al.*, 2005), although often *Sphenocarcinus* is treated as a member of the Majidae (e.g. Tavares, 1991; Richer de Forges, 1995).

FAMILY GERYONIDAE COLOSI, 1923

GENUS *CHACEON* MANNING & HOLTHUIS, 1989

CHACEON AFFINIS (MILNE-EDWARDS & BOUVIER, 1894)

Type locality: Atlantic Ocean, Azores, east of Corvo; 844 m (from Manning & Holthuis, 1981: 111).

Known range: North-eastern Atlantic Ocean, from Iceland to Cape Verde, including the Azores, Madeira, Canary Islands and Cape Verde Islands, at depths of 130–2047 m (Manning & Holthuis, 1981 [as *Geryon affinis*], 1989).

Occurrence at vents or seeps: restricted to the Menez Gwen site of the MAR (Biscoito, 1997, in Desbruyères & Segonzac, 1997; Colaço *et al.*, 1998; Desbruyères *et al.*, 2000; Colaço, Dehairs & Desbruyères, 2002).

Material: M. Segonzac (pers. comm.) informs us that some specimens were collected but were eaten on board; Colaço *et al.* (2002) mentioned three specimens.

Remarks: Biscoito (1997, in Desbruyères & Segonzac, 1997) noted that this species usually occurs on hard and soft substrates of the upper continental slope (see also Pinho *et al.*, 2001). At Menez Gwen, 'several specimens were observed over pillow lavas, near active vent sites. At least one specimen was observed eating dead mussels.' Perhaps for this reason Biscoito described the species as necrophagous. Desbruyères *et al.* (2000: table 4) listed the species as rare/patchy at Menez Gwen. Biscoito & Saldanha (2000) observed the species 'on the fringe of a hydrothermal vent site', though M. Segonzac (pers. comm.) reports that specimens were seen among mussels. Colaço *et al.* (1998) also noted this species at the periphery of the Menez Gwen site. Weinberg *et al.* (2003) examined genetics of several species of *Chaceon*, including *C. affinis*. P. Chevaldonné (pers. comm.) informs us that MacAvoy *et al.*'s (2002) report of *Chaceon quinquedens* may refer instead to a species of *Geryon* (see below); the crab in question was reported as a vagrant but had a depleted $\delta^{13}\text{C}$ value, more indicative of primary feeding at seeps.

CHACEON FENNERI (MANNING & HOLTHUIS, 1984)

Type locality: North Atlantic Ocean, United States, off eastern Florida, Key West and Dry Tortugas, and the Gulf of Mexico; 247–732 m.

Known range: Gulf of Mexico.

Occurrence at vents or seeps: methane seeps off Louisiana.

Material: United States, eastern Florida, off Fernandina; 31°47'30"N, 79°49'W; *Albatross* sta. 2666; 494 m; 5 May 1886; USNM 14376 (holotype male). A substantial amount of paratypic material is also housed in the USNM collections; the reader is referred to Manning & Holthuis (1984) for collection-related data for the paratype specimens. Although Carney (1994) reported observations of this species from methane seeps off Louisiana, there is no mention of the collection of any specimens (see Carney, 1994: 151).

Remarks: This species, originally assigned by Manning & Holthuis (1984) to the genus *Geryon*, was reported by Carney (1994) from methane seeps off Louisiana in the Gulf of Mexico.

CHACEON QUINQUEDENS (SMITH, 1879)

Type locality: Gulf of Mexico; *Albatross* collections (Pequegnat, 1970).

Known range: western Atlantic from Nova Scotia to Brazil and throughout the Gulf of Mexico with the exception of the south-western quadrant, from 366 to 1463 m (200–800 fathoms) (Pequegnat, 1970).

Occurrence at vents or seeps: methane seeps off Louisiana.

Material: No material is known from the methane seep site where the species was reported (Carney, 1994; MacAvoy *et al.*, 2002).

Remarks: This species, originally described as *Geryon quinquedens*, was transferred to the genus *Chaceon* by Manning & Holthuis (1989). It was reported by Carney (1994) and MacAvoy *et al.* (2002) from methane seeps off Louisiana in the Gulf of Mexico. Pequegnat (1970) noted that this species (as *Geryon quinquedens*) was one of only three brachyurans in the Gulf of Mexico that live in excess of 500 fathoms (914 m).

GENUS *GERYON* KRØYER, 1837

Remarks: MacDonald *et al.* (1989: 241) mentioned crabs that they attributed to this genus from still photographs and video footage taken of 'common slope fauna' in the vicinity of a hydrocarbon seep (Bush Hill site) off Louisiana in the northern Gulf of Mexico. We are not aware of any other mention of the genus in connection with vents or seeps. P. Chevaldonné (pers. comm.) informs us that this might be the same species reported by MacAvoy *et al.* (2002) as *Chaceon quinquedens*. *Geryon* is a common deep-sea crab genus, and it is often confused with *Chaceon* and other geryonid genera.

FAMILY GONEPLACIDAE MACLEAY, 1838

GENUS *BATHYPLAX* A. MILNE-EDWARDS, 1880

BATHYPLAX TYPHPLUS A. MILNE-EDWARDS, 1880

Type locality: off Frederickstadt, St Croix Island, 825 m (451 fathoms) (Rathbun, 1918: 19).

Known range: North Carolina to Brazil and throughout the Gulf of Mexico, 402–878 m (as 220–480 fathoms) (Rathbun, 1918; Pequegnat, 1970).

Occurrence at vents or seeps: Bush Hill site, off Louisiana.

Material: Abundant non-vent material was listed by Rathbun (1918) and Pequegnat (1970). Although no specimens appear to have been collected from the Bush Hill site, Pequegnat (1970) listed abundant

material from *Alaminos* deep-sea collections, some of which may have come from oil-seep areas (see below).

Remarks: The spelling of the species name was corrected from *B. typhla* to *B. typhlus* by Tavares (1996: 414); the older name is unfortunately more prevalent in the literature. MacDonald *et al.* (1989: 241) identified this species from still photographs and video tapes taken of 'common slope fauna' in the vicinity of a hydrocarbon seep (Bush Hill site) off Louisiana in the northern Gulf of Mexico. We are not aware of any other mention of the species or genus in connection with vents or seeps. Interestingly, however, Pequegnat (1970: 192), who described the species as 'very likely the most abundant deep-sea brachyuran in the Gulf of Mexico', also noted that 'blackened specimens are common and are probably befouled from natural oil seeps'. Goneplacids are common members of the deep-sea fauna, and it is somewhat surprising that there are so few other published reports of goneplacids in connection with vents or seeps.

GENUS *CARCINOPLAX* H. MILNE EDWARDS, 1852

Remarks: Although the only record of *Carcinoplax* from areas of hydrothermal venting is that of Clark & O'Shea (2001) from the Kermadec Ridge (as *Carcinoplax* sp.), the genus is known from other regions where hydrothermal activity occurs in relatively shallow waters. For instance, Hseuh & Huang (2002) presented a taxonomic key to seven species of *Carcinoplax* and 12 other species of goneplacids found off Taiwan. Most of these species were found off the same region of Taiwan (Ilan County) described for vent-associated taxa (i.e. *Paragiopagurus ventilatus* Lemaitre, 2004, and *Xenograpsus testudinatus* Ng, Huang & Ho, 2000).

GENUS *PILUMNOPLAX* STIMPSON, 1858

Remarks: The only report of this genus (as *Pilumno-plax* sp.) from vents is the report from the Kermadec Ridge system by Clark & O'Shea (2001). The genus is not mentioned in the list of New Zealand crab species compiled by McLay (1988) and apparently does not occur in southern Australia (Poore, 2004).

FAMILY HOMOLIDAE DE HAAN, 1839

GENUS *PAROMOLA* WOOD-MASON IN WOOD-MASON & ALCOCK, 1891

PAROMOLA CUVIERI (RISSO, 1816)

Type locality: Mediterranean Sea, France, Nice, 'des grandes profondeurs'.

Known range: Known from the North Atlantic and eastern Atlantic Ocean, from the Hebrides and south-

ern Scandinavia south to Angola, including the Azores, Madeira and the Canary Islands, the Tripp Seamount, and the Mediterranean, from 10 to 1000 m depth (although usually from 80 to 300 m) (Manning & Holthuis, 1981; Guinot & Richer de Forges, 1995; Biscoito, 1997, in Desbruyères & Segonzac, 1997).

Occurrence at vents and seeps: limited to the Menez Gwen site of the MAR (Biscoito, 1997: 205, in Desbruyères & Segonzac, 1997).

Material: No material known from hydrothermal vents or cold seeps (see below).

Remarks: We are aware of only one mention of this species in association with hydrothermal vents or cold seeps. Biscoito (1997: 205, in Desbruyères & Segonzac, 1997) included this species in a handbook of hydrothermal vent fauna, noting 'one specimen was observed over an arborescent coral, off the active site' (Menez Gwen) (see photograph in Biscoito, 1997: 205, in Desbruyères & Segonzac, 1997). Biscoito also noted its coloration (bright orange) and propensity for carrying a sponge with the prehensile back (5th) pereopods. See Guinot & Richer de Forges (1995) for the taxonomic history, distribution and behaviour of this species.

FAMILY MAJIDAE SAMOUELLE, 1819

GENUS *DORHYNCHUS* THOMSON, 1873

DORHYNCHUS THOMSONI THOMSON, 1873

Type locality: North Atlantic Ocean, between the Faroe Islands and Scotland.

Known range: eastern Atlantic, west and south of Iceland and the Faroes southward to the Cape Verde Islands, 100–2100 m (Manning & Holthuis, 1981); western and eastern Atlantic and Indian oceans (Davie, 2002).

Occurrence at vents and seeps: Kermadec Ridge (see below).

Material: The holotype is housed in the BMNH collection. No material was collected from the vent sites of the Kermadec Ridge.

Remarks: Clark & O'Shea (2001) reported this species as *Archaeopsis* [= *Achaeopsis*] *thomsoni* from the Kermadec Ridge off New Zealand. Poore (2004) noted that species of the genus *Dorhynchus* often have been incorrectly assigned to *Archaeopsis*, a junior synonym (according to Davie, 2002).

GENUS *PLATYMAIA* MIERS, 1886

Remarks: Poore (2004) noted that the genus *Platymaia* comprises at least seven Indo-West Pacific species. Of these, Poore (2004) reported the occurrence of

three species in southern Australia but notes also that 'identity of southern Australian species remains in doubt'. Clark & O'Shea (2001) reported the presence of this genus (as *Platymaia* sp.) at vent sites of the Kermadec Ridge off New Zealand.

FAMILY OCYPODIDAE RAFINESQUE, 1815
GENUS *MACROPHTHALMUS* DESMAREST, 1823
MACROPHTHALMUS HIRTIPES (HELLER, 1862)

Type locality: South Pacific Ocean, New Zealand, Auckland Harbour (from McLay, 1988).

Known range: Endemic to New Zealand: North, South and Stewart Islands, and possibly Campbell Island (McLay, 1988: 336).

Occurrence at vents or seeps: Whale Island, New Zealand.

Remarks: Specimens of this species were collected by Russian divers at relatively shallow (30–40 m) hydrothermal seeps off Whale Island, a volcanic island at the southern end of the Kermadec Arc (R. Webber, pers. comm.; see also Kamenev *et al.*, 1993; Clark & O'Shea, 2001). The species is a New Zealand endemic that is normally found in the lower intertidal zone to a depth of only 13 m (although records from the stomach of a snapper may indicate depths to 40 m or more; R. Webber, pers. comm.; and see McLay, 1988). It is almost certainly a vagrant at this hydrothermal site. The species is known to burrow deeply into black (presumably anoxic) sediments, and so it may to some degree be pre-adapted for taking advantage of an environment rich in sulphide-eating bacteria. Kamenev *et al.* (1993) reported it at a range of temperatures (17–81°C) within a 'volcanic depression' near Whale Island, suggesting the species is fairly heat-tolerant.

Crabs collected at deeper sites (to 42 m) were taken with a 0.25-m² grab device; when collected they buried themselves in the sediment within the grab, which under normal circumstances would be a logical escape response but which, because of the hydrothermally heated sands off Whale Island, resulted in their death by cooking (R. Webber, pers. comm.).

FAMILY OREGONIIDAE GARTH, 1958

Remarks: The family Oregoniidae was formerly a subfamily (Oregoniinae) of the family Majidae; it is now treated as a family following Hendrickx (1995) and McLaughlin *et al.* (2005).

GENUS *CHIONOECETES* KRÖYER, 1838
CHIONOECETES BAIRDI RATHBUN, 1924

Type locality: North Pacific Ocean, Canada, British Columbia, head of Kingcombe Inlet.

Known range: south-eastern Bering Sea and Aleutian Islands, eastward and southward to British Columbia (Rathbun, 1924) and Oregon, and the coasts of Hokkaido, Japan and west coast of Kamchatka peninsula, from 6 to 474 m, usually on soft mud or sand.

Occurrence at vents or seeps: Seeps in Monterey Canyon (see below).

Material: Type locality: USNM 5862 (holotype, male). We know of no material collected from vent or seep localities.

Remarks: Barry *et al.* (1996) reported two 'majid' crabs from seeps in the vicinity of Monterey Canyon, California; one was *Chionoecetes bairdi* Rathbun, 1924 (now considered a member of the family Oregoniidae), the well-known and commercially fished 'tanner' crab more common to the north, and the other was *Chorilia longipes* Dana, 1851 (now treated as a member of the Pisidae following Martin & Davis, 2001).

GENUS *HYAS* LEACH, 1814

Remarks: The genus *Hyas* has been mentioned in only one vent-related study, a report of shallow-water subpolar North Atlantic hot vent communities at Kolbeinsey Island, Jan-Mayen Ridge, off northern Iceland (Fricke *et al.*, 1989: 428, table 1, as *Hyas* sp.). Crabs were described by Fricke *et al.* as being 'extremely rare . . . and probably of minor importance for the local food web' at this site. To our knowledge, no collections were made of these crabs.

GENUS *MACROREGONIA* SAKAI, 1978
MACROREGONIA MACROCHIRA SAKAI, 1978

Type locality: North of and on Nintoku Seamount; 42°20'N–41°11'N, 170°50'E–170°36'E; 800–1100 m.

Known range: North Pacific, from the Emperor Seamount Chain off Japan (Sakai 1978) eastward to British Columbia and south to California.

Occurrence at vents or seeps: restricted to the vicinity of the Juan de Fuca and Explorer vents off British Columbia (e.g. Tunnicliffe, Juniper & de Burgh, 1985; Tunnicliffe & Jensen, 1987; Van Dover, Grassle & Boudrias, 1990; Tunnicliffe, 1988) and the Patten-Murray Seamount (J. Voight, pers. comm.).

Material: North-eastern Pacific Ocean, Juan de Fuca Ridge (Tunnicliffe *et al.*, 1985: fig. 1; Tunnicliffe, 1988: 360).

—Juan de Fuca Ridge, Endeavour site; 47°56.9'N, 129°06.1'W; 2201 m; *Alvin* dive 2065, 16 July 1988; (from Martin & Pettit, 1998; mouthparts only). Specimens also exist at the FMNH, and video images exist

from the High Rise Field of the Endeavour segment (J. Voight, pers. comm.).

Remarks: Tunncliffe *et al.* (1985: 454; see also their fig. 11) noted that these large spider crabs, although not considered part of the vent fauna, were found in higher numbers in the vicinity of vents at Axial Seamount of the Juan de Fuca Ridge (off Washington and Oregon); Tunncliffe (1988: 360) suggested that they occupy the same ecological niche at Juan de Fuca as crabs of the genus *Bythograea* do in the EPR sites. Tunncliffe & Jensen (1987) commented further on the distribution and behaviour of the species at these same sites. Martin & Pettit (1998) described a new species of caprellid amphipod from the mouthparts of this species; specimens of these caprellids are housed at the LACM; the Field Museum (Chicago) additionally houses caprellids taken from the legs of these crabs (J. Voight, pers. comm.).

FAMILY PARTHENOPIDAE
GENUS *TUTANKHAMEN* RATHBUN, 1925

Remarks: Rathbun (1925) erected this genus for the species *Mesorhoea cristatipes* A. Milne-Edwards, 1880. The holotype is presumably housed in the MNHN collections in Paris; Rathbun (1925) noted that an additional specimen had been deposited in the Museum of the State University of Iowa. Clark & O'Shea (2001) reported an undetermined species of *Tutankhamen* from vents at the Kermadec Ridge. Records of this genus are lacking from the accounts of Australian Crustacea by Davie (2002) and Poore (2004).

FAMILY PISIDAE DANA, 1851

Remarks: The family Pisidae was formerly a subfamily (Pisinae) of the Majidae (see Martin & Davis, 2001; McLaughlin *et al.*, 2005). Several former 'majid' genera, a few of which (e.g. *Chorilia*, *Nibilia* and *Rochinia*) contain species that have been reported from vent or seep sites, are now treated under the family Pisidae.

GENUS *CHORILIA* DANA, 1851
CHORILIA LONGIPES DANA, 1851

Type locality: 'ad oras Oregonenses' (Oregon; type not extant) (Rathbun, 1925).

Known range: Western coast of North America, from the Alaskan Peninsula to San Diego, and east to Japan (though possibly a subspecies), 33–119 m (as 18–650 fathoms) (Rathbun, 1925).

Occurrence at vents and seeps: Reported from seeps in Monterey Canyon (see below).

Material: None known from vents or seeps; see Rathbun (1925) for USNM holdings from other areas.

Remarks: Rathbun (1925) commented on the subspecies that had been described as occurring from Monterey south to San Diego (*C. longipes turgida*) and from Japan (*C. longipes japonica*); not all subsequent workers have recognized the southern California subspecies as distinct (see McLaughlin *et al.*, 2005). The species was reported from seeps in Monterey Canyon, California (Barry *et al.*, 1996), which is the intermediate point between northern and southern subspecies (Rathbun, 1925).

GENUS *NIBILIA* A. MILNE-EDWARDS, 1878
NIBILIA ANTILOCARPA (STIMPSON, 1871)

Type locality: Florida, off Carysfort Reef, 95 and 109.7 m; and off Alligator Reef, 25.1 m (Williams, 1984).

Known range: Off Cape Hatteras, North Carolina, to Gulf of Mexico just east of Mississippi River Delta and Gulf of Campeche; Windward Islands, West Indies, off Guayana (Williams, 1984).

Occurrence at vents and seeps: Methane seeps off Louisiana.

Material: See below.

Remarks: Carney (1994) reported this species from methane seeps off Louisiana in the Gulf of Mexico, but apparently no specimens were collected.

GENUS *ROCHINIA* A. MILNE-EDWARDS, 1875

Remarks: *Rochinia* is a worldwide genus of mostly deep-sea crabs that currently contains some 30 described species (Tavares, 1991). Only one species, *Rochinia crassa* (A. Milne-Edwards, 1879), has been reported from vents or seeps.

ROCHINIA CRASSA (A. MILNE-EDWARDS, 1879)

Type locality: Between Cuba and Florida, 24°15'N, 82°13'W (Williams, 1984).

Known range: Nantucket Shoals, Massachusetts, to Gulf of Mexico off southern Texas; northern Cuba; west of Cabo de la Vela, Colombia; off French Guiana (Williams, 1984), north to Nova Scotia, Canada (Moriyasu *et al.*, 2001).

Material: Abundant non-vent specimens of this relatively common species are housed at the USNM (e.g. see Williams, 1984) and presumably at other institutions. No known specimens have been collected at or near vent or seep sites.

Remarks: *Rochinia crassa* (A. Milne-Edwards), the 'inflated spider crab' (McLaughlin *et al.*, 2005), is a relatively deep-water majid found on soft bottoms in the western Atlantic at depths of 66–1216 m from Canada (Nova Scotia) to Cuba, including the Gulf of Mexico (Williams, 1984; Moriyasu *et al.*, 2001). MacDonald *et al.* (1989: 241) identified this species from still photographs and video tapes taken of 'common slope fauna' in the vicinity of a hydrocarbon seep (the Bush Hill site) off Louisiana in the northern Gulf of Mexico, where it was also reported by MacAvoy *et al.* (2002) and Bergquist *et al.* (2003). Carney (1994) reported this species from the same area.

FAMILY PORTUNIDAE RAFINESQUE, 1815

GENUS *BATHYNECTES* STIMPSON, 1871

BATHYNECTES MARAVIGNA (PRESTANDREA, 1839)

Type locality: Mediterranean Sea, Italy, Sicily, near Messina.

Known range: General distribution includes eastern Atlantic Ocean from Norway and the Faroes south to north-western Morocco, Madeira, the Canaries and throughout the Mediterranean at depths of 100–1000 m, and the western North Atlantic from Massachusetts to Florida (Manning & Holthuis, 1981; Fariña, Freire & González-Gurriarán, 1997; Abello *et al.*, 2001).

Occurrence at vents or seeps: Restricted to the vicinity of the Menez Gwen hydrothermal site of the MAR, 37°50'N, 850 m (Biscoito, 1997, in Desbruyeres & Segonzac, 1997: 207).

Material: We are aware of no material collected from the Menez Gwen site (see above). A photograph of this species appears in Biscoito (1997, in Desbruyeres & Segonzac, 1997), a compilation of hydrothermal vent fauna, but it is unclear whether the photograph is of a vent-collected specimen. M. Segonzac (pers. comm.) confirms that no specimen was collected from Menez Gwen, the record being based instead on a video observation in the local bathyal community probably beyond the influence of the vents.

Remarks: This species, a relatively common deep-sea portunid known throughout the eastern north Atlantic, is clearly a vagrant. The only report from vents or seeps is the listing by Biscoito (1997, in Desbruyeres & Segonzac, 1997) close to Menez Gwen, as noted above. M. Segonzac (pers. comm.) has expressed doubts as to the identification based on the above video sequence and may delete the record from his next version of the 'Desbruyeres and Segonzac' handbook of vent fauna.

GENUS *OVALIPES* RATHBUN, 1898

OVALIPES ?MOLLERI (WARD, 1933)

Type locality: South of Montague Island, New South Wales (Davie, 2002).

Known range: New Zealand, southern Australia, 150–270 m (Poore, 2004); New South Wales, Queensland, Bass Strait, New Zealand (Davie, 2002).

Occurrence at vents or seeps: Kermadec Ridge (see below).

Material: We are aware of no material from vents or seeps.

Remarks: This species was reported (tentatively, as *Ovalipes ?molleri*) from the Kermadec Ridge (New Zealand) vent sites by Clark & O'Shea (2001).

FAMILY VARUNIDAE H. MILNE EDWARDS, 1853

Remarks: The varunids were formerly treated as a subfamily of the Grapsidae, most of which are commonly called 'shore crabs' (Williams *et al.*, 1989; McLaughlin *et al.*, 2005). Recognition of the Varunidae as a separate family follows the classification of Martin & Davis (2001) and papers cited therein. The only genus of the family Varunidae known from vents, *Xenograpsus* (see below), is probably deserving of its own family (P. Ng, pers. comm.) based on larval morphology and other characters; if so this would leave the varunids without known vent representatives.

XENOGRAPSUS TAKEDA & KURATA, 1977

Remarks: Although referred to occasionally as 'hydrothermal vent crabs', crabs of the genus *Xenograpsus* are clearly related to and derived from nearby grapsoid shore crabs and are thus quite different from the 'true' vent crabs of the family Bythograeidae. To our knowledge they are restricted to the shallow volcanic vent habitat and are thus endemic (rather than vagrant) species. To date these two species are the only known obligate shallow-water hydrothermal vent crabs (Jeng, Clark & Ng, 2004a; Jeng, Ng & Ng, 2004b). Larvae have been described for one species (see below). The two described species are known from Japan and Taiwan (below), although a crab of this genus also has been observed (though apparently not yet reported) from off New Zealand (P. Ng, pers. comm.).

XENOGRAPSUS NOVEAINSULARIS TAKEDA & KURATA, 1977

Type locality: North Pacific Ocean, Ogasawara Islands, Nishino-shima-shinto; from inlet (Takeda & Kurata, 1977).

Range: Shallow-water hydrothermal vents (volcanic arc) in Japan (Takeda & Kurata, 1977) and the Marianas (Türkay & Sakai, 1995).

Material: type locality; under volcanic debris; 25 July 1975; NSMT-Cr. 5472 (holotype male), NMST-Cr. 5473 (allotype), NMST-Cr. 5474 (paratypes, 1 male, 1 ovigerous female).

Remarks: This species was described from shallow volcanic vents off Japan.

XENOGRAPSUS TESTUDINATUS NG, HUANG
& HO, 2000

Type locality: Taiwan, Ilan County, Peikuan, Gengxin fish port, rocky reef; 15 m.

Range: Known from the type locality (Ng *et al.*, 2000) and additional sites off north-eastern Taiwan (Jeng *et al.*, 2004a).

Material: Taiwan, Han County, Peikuan, Gengxin fish port, rocky reef; 15 m; 3 October 1991; coll. P.-H. Ho; TMCD (holotype male), TMCD (paratype, 1 male), NTOU (paratype, 1 male), USNM (paratype, 1 male), ZRC (paratypes, 3 males, 4 females). –Taiwan, Ilan County, Kueishan (= Turtle) Island; 16 m; near thermal vent; 18 April 1999; ASIZ 72116-2 (paratypes, 5 males, 7 females).

Remarks: In addition to material mentioned in the original description (Ng *et al.*, 2000), specimens (number not given) were collected from a shallow-water hydrothermal vent off Kueishan Island (Turtle Mountain), coast of Peikuan, Ilan County, north-eastern Taiwan, August 2001 (Jeng *et al.* 2004a). Jeng *et al.* (2004a), who described the larvae of this species, also mention large numbers of individuals observed by scuba divers in this area; the novel feeding behaviour of the species (the crabs are opportunistic feeders that eat dead zooplankton killed by sulphurous vent plumes) was described by Jeng *et al.* (2004b). An ovigerous female from which larvae were obtained was deposited in the Institute of Zoology, Academia Sinica, Nankang, Taipei, Taiwan (Jeng *et al.*, 2004a).

INFRAORDER ASTACIDEA LATREILLE, 1802
FAMILY NEPHROPIDAE DANA, 1852
GENUS *ACANTHACARIS* BATE, 1888

Remarks: According to Holthuis (1991), the genus *Acanthacaris* currently contains only two known species, both from the deep sea. Watabe & Miyake (2000) mentioned the presence of '*Acanthacaris* cf. *tenuimana*' at the Hatama Knoll (Okinawa Trough). If verified as true *A. tenuimana* Bate, 1888, the find would be well within the known range of this species,

which was given by Holthuis (1991) as 'Indo-West Pacific area (Natal, Mozambique, Madagascar, Laccadive Islands, Japan, Philippines, South China Sea, Indonesia, New Caledonia).' The other species of the genus, *Acanthacaris caeca* A. Milne-Edwards, 1881, is restricted to the western Atlantic (Caribbean, Gulf of Mexico and Straits of Florida; Holthuis, 1991). The report by Watabe & Miyake (2000) is the only record of the genus from any vent or seep site.

GENUS *HOMARUS* WEBER, 1795
HOMARUS GAMMARUS (LINNAEUS, 1758)

Type locality: Marstrand, west coast of Sweden, approximately 57°53'N, 11°32'E (Holthuis, 1991).

Known range: eastern Atlantic from north-western Norway south to the Azores and the Atlantic coast of Morocco; also along the north-west coast of Black Sea and in the Mediterranean (Holthuis, 1991: 60).

Occurrence at vents or seeps: off Kattegat, Denmark (see below).

Remarks: Levin *et al.* (2000: 23) listed the occurrence of *Homarus vulgaris* on 'bubbling reefs' off Kattegat, Denmark, citing Jensen *et al.* (1992) as the original source of the record. Apparently no specimens were collected from this site. The species *H. vulgaris* Milne-Edwards is considered a junior synonym of *H. gammarus* (Linnaeus), known as the European lobster.

GENUS *THYMOPIDES* BURUKOVSKY & AVERIN, 1977

Remarks: Prior to 2003, the genus *Thymopides* contained a single species, *Thymopides grobovi*, known from relatively deep (525–1220 m) waters in the southern Indian Ocean and Kerguelen Islands and Heard Island near Antarctica (Holthuis, 1991). The second known species of the genus was described from near a North Atlantic hydrothermal vent site (below).

THYMOPIDES LAURENTAE SEGONZAC &
MACPHERSON, 2003

Type locality: North Atlantic Ocean, MAR, near Snake Pit hydrothermal vent field, Les Ruches site; 23°22.15'N, 44°57.15'W; 3505 m; base of black smokers.

Known range: Known only from the type locality (above).

Material: Type locality; HYDROSNAKE cruise, *Nautilus*, dive HS 08; 26 June 1988; baited trap (PT 01); MNHN-As-547 (holotype female).

Remarks: This second known species of the nephropid lobster genus *Thymopides* was first observed and collected from sulphide deposit areas of the Snake Pit vent site on the MAR in 1988 (Segonzac, 1992: 596 [as *Thimopides*]; Desbruyères & Segonzac, 1997: 266), but the species was not described until 2003 (Segonzac & Macpherson, 2003). According to M. Segonzac (pers. comm.), the species was collected at a distance of approximately 20–30 m from 'Les Ruches' on the slope of the Snake Pit vent site. There is some question as to the exact locality, as the trap was collected at 3480 m, lost and found later at a slightly greater depth some 100 m away from where the trap was originally placed (Segonzac & Macpherson, 2003). The only other species of the genus is known from subantarctic waters at depths of 525–1220 m (Holthuis, 1991; Segonzac & Macpherson, 2003).

INFRAORDER THALASSINIDEA LATREILLE, 1831

At least three different thalassinidean species are known from cold brine or methane seeps in the northern Gulf of Mexico, all from sites off Louisiana (D. L. Felder, pers. comm.). To date, there is at least one member of the Callianassidae (an undescribed genus), one member of the Axiidae (a species of the genus *Calaxius* recently described by Felder & Kensley, 2004) and one member of the Calocarididae (an undescribed species) (D. Felder, pers. comm.). Bergquist *et al.* (2003) also listed a species of *Calaxius* from a collection at Bush Hill (northern Gulf of Mexico). Dando, Huges & Thiermann (1995) reported *Callianassa truncata* from shallow vents in the Aegean Sea. Because of the comparative difficulty in collecting burrowing organisms in the deep sea, it is not surprising that few have been collected or seen to date, and it is highly likely that more thalassinideans will be found eventually at other seep and vent sites.

FAMILY AXIIDAE HUXLEY, 1879

GENUS *CALAXIUS* SAKAI & DE SAINT LAURENT, 1989
CALAXIUS CARNEYI FELDER & KENSLEY, 2004

Type locality: Northern Gulf of Mexico, Louisiana continental slope, Bush Hill site; *Johnson Sea-Link* submersible sta. 3269; 27°46.904'N, 91°30.286'W, approximately 2 m from chemosynthetic mussel community; 544 m.

Known range: limited to the type locality.

Material: type locality; *Johnson Sea-Link* sta. 3269; 11 August 1992; box core; USNM 1009165 (holotype male). –same locality; *Pisces II* sta. 880031 (8831); August 1988; USNM 1009166 (paratype; male exuvium).

Remarks: The locality (Bush Hill site) is a cold methane seep. The two specimens (one of which is an exuvium) were collected by manned submersibles (the *Johnson Sea-Link* and the *Pisces II*) from the same locality and microhabitat (adjacent to clam beds) but several years apart (1988, 1992). Felder & Kensley (2004) noted that both specimens were collected adjacent to communities of clams and commented on the fact that many thalassinoids may be pre-adapted to such environments. The find is only the second species of the genus *Calaxius* (reviewed recently by Kensley & Hickman, 2001) in the Atlantic Ocean. This may be the same species noted by Bergquist *et al.* (2003) from the Bush Hill site.

FAMILY CALLIANASSIDAE DANA, 1852

GENUS *CALLIANASSA* LEACH, 1814

CALLIANASSA TRUNCATA GIARD & BONNIER, 1890

Type locality: Gulf of Naples, Italy.

Known range: Atlantic coasts of France south to Atlantic coast of Morocco, and widespread throughout the Mediterranean including Greece, Italy, Adriatic Sea, Ionian Sea, Aegean Sea and south-east of Black Sea (Ngoc-Ho, 2003).

Occurrence at vents or seeps: shallow-water vents in the Aegean Sea.

Material: See below under Remarks.

Remarks: Dando *et al.* (1995) reported *Callianassa truncata* as one of several species collected from shallow water (intertidal to approximately 115 m) vents around the islands of Milos and Santorini in the Hellenic Volcanic Arc of the Aegean Sea. None of the species collected by them, including *C. truncata*, was considered endemic to hydrothermal vents. The specimens of *C. truncata* came from core samples taken around a single vent at 12 m in the centre of Paleohori Bay. Dando *et al.* (1995) noted that 'burrows of *C. truncata* were confined to the lower temperature region of the transect, <40°C at 10 cm sediment depth.' Although eight specimens are listed in their table 3, it is not clear if any of the specimens were retained. The Aegean is an area of great volcanic activity; Dando *et al.* (1995) listed several other shallow volcanic regions yet to be fully explored.

This species was transferred to the genus *Necallianassa* by Heard & Manning (1998) and then back to *Callianassa* by Ngoc-Ho (2003), who reviewed all Mediterranean and European species of the genus. *Callianassa truncata* is a widespread opportunistic species throughout much of the eastern Atlantic and the Mediterranean (Abed-Navandi & Dworschak, 1997; Ngoc-Ho, 2003; D. Felder, pers. comm.) and clearly is not endemic to vent or seep habitats.

DISCUSSION

Although hydrothermal vents and cold seeps have been studied for nearly 30 years (Corliss & Ballard, 1977; Lonsdale, 1977; Corliss *et al.*, 1979), it is clear that our understanding of the ecology and fauna of these systems is still in its infancy. Manned and unmanned vehicles (e.g. Bachmayer *et al.*, 1998) are used to discover new vent and seep sites every year (e.g. see Tyler *et al.*, 2003, table 1, for hydrothermal vents; Coleman & Ballard, 2001, for cold seeps), and with these discoveries, almost without exception, come discoveries of new and interesting associated taxa. As of this writing, we are aware of several vent fields for which complete data on the decapods have not been published. These include the Kick'em Jenny Volcano and its associated shrimp in the Caribbean (K. Wishner & J. Graff, pers. comm., and Martin *et al.*, 2005), the bythograeid crabs reported from the Pacific-Antarctic Ridge by Stecher *et al.* (2002), a wide variety of decapods reported from the Kermadec Ridge by Clark & O'Shea (2001), several brachyuran crabs from the recent (2004) 'Ring of Fire' expedition to the Marianas Arc (V. Tunnicliffe & J. Rose, pers. comm.; J. Martin, unpubl. data), the decapods associated with the slow-spreading Gakkel Ridge in the Arctic Ocean (Martin, 2003), and the galatheids associated with asphalt flows in the Campeche Knolls off Mexico (MacDonald *et al.*, 2004; see also Tyler *et al.*, 2003). New hydrothermal vents also have been discovered recently off Chile (L. Levin, pers. comm.). Thermal plumes have been identified recently along the south-west and south-east Indian Ocean Ridge and along the southern portion of the MAR (German *et al.*, 1998, 2000; Scheirer, Baker & Johnson, 1998; Tyler & Young, 2003), and it is only a matter of time before the vents responsible for those plumes are discovered and investigated. It is understood that additional species, as well as higher taxa, will continue to be discovered as vents and seeps are explored in the years to come. The fact that approximately 71–82% of vent-associated species found to date appear to be endemic (MacArthur & Tunnicliffe, 1998; Little & Vrijenhoek, 2003; Wolfe, 2005) virtually guarantees that novel taxa will be found. For the taxa that have been described, we know precious little about their natural history (for a review of experimental ecology see Van Dover & Lutz, 2004). Additionally, it is in many cases quite difficult to ascertain the 'association' of a given species with a vent or seep system. Many of the species reported herein are facultative or 'vagrant' species (or 'penetrating' species in the sense of Desbruyères *et al.*, 2000) that would have been found in the vicinity whether or not a vent or seep was present. Finally, we have been somewhat arbitrary with our selection of 'hydrothermal' sites. We have endeavoured to include all 'deep-sea' sites and

most shallow-water volcanic sites known to us, but we have excluded some other shallow-water thermal areas, some of which are clearly also of volcanic origin, such as Tarasov *et al.*'s (1999) study on shallow-water venting in Papua New Guinea, where the decapod genera *Hippa*, *Macrophthalmus*, *Actaea*, *Pilumnus*, *Dardanus* and *Pagurus* were recorded, all but one of which are unknown from other vents or seeps (see Tarasov *et al.*, 1999, for a review of shallow-water hydrothermal systems). Thus, with these caveats in mind our current compilation is presented as a starting point in our understanding of the diversity and biogeography of decapod crustaceans from vents and seeps. Even with such preliminary data, some comments on apparent biogeographical distributions are warranted.

Based only on the distribution of the decapods, it is possible to recognize the six biogeographical provinces previously described for the deep-sea vent fauna (see Van Dover *et al.*, 2002; Tyler & Young, 2003). But the evidence is not strong, as there is a considerable amount of faunal overlap or at least faunal connections between and among many of the vent regions.

In the Atlantic, all known endemic shrimp genera are represented except for *Opaepele*, known to date only from the Hawaiian Loihi seamount, and *Nautilocaris* from the western Pacific. Thus, Atlantic endemic shrimp diversity at the generic level is quite high. Shrimp abundance at the MAR sites is also extremely high, as the Mid-Atlantic is one of only two regions in the world where some alvinocaridid shrimps (in the genus *Rimicaris*) are known to swarm in amazingly dense aggregations (the other region is the vicinity of the Rodriguez Triple Junction in the Indian Ocean; see Van Dover *et al.*, 2001). By contrast, the diversity as well as the abundance of endemic crabs (bythograeids) at the Mid-Atlantic vent fields is comparably low, with only the genus *Segonzacia*, and its single species *S. mesatlantica*, reported to date.

Eastern Pacific sites exhibit an almost completely different pattern, with a high number and diversity of bythograeid crabs (including members of the genera *Bythograea*, *Cyanograea* and *Allograea*) but with relatively few shrimp species (e.g. Martin & Shank, 2005). The western Pacific also contains a large number of crab species, though currently the 'deep vent' species (that is, excluding the shallow volcanic system varunids off Japan and Taiwan) all are treated within one genus (*Austinograea*). In part because of difficulties with shrimp taxonomy, the picture is less clear for western Pacific alvinocaridids. However it is becoming apparent that at least *Alvinocaris* is relatively widespread, and *Chorocaris* is known from at least two widely separated western Pacific sites (the Marianas Back-Arc Basin and off New Zealand). Webber's (2004) description of *Alvinocaris niwa* from off New Zealand also included records of *A. longirostris* in numbers

that indicate that this species may be swarming, in addition to the significant range extension of *A. longirostris* from Japan. Apart from that report, swarming has been documented to date only for *Rimicaris* and to a lesser degree for the EPR species of *Chorocaris* (*C. paulexa*). The latter is one of the more interesting recent finds, as *Chorocaris paulexa*, from the southern portion of the EPR, is morphologically very similar to the western Pacific *C. vandoverae*. This suggests that there exists, at least concerning the southern portion of the EPR, some sort of faunal connection between western and eastern Pacific sites that is stronger than previously imagined. Also in support of a faunal connection between the western and eastern Pacific sites is the occurrence of closely related species of the limpet genus *Lepetodrilus* at each area (see Vrijenhoek *et al.*, 1997) and the report of a similarly distributed gastropod genus (*Eosipho*) by Van Dover (2002b).

The Indian Ocean vents, although still incompletely known, appear with respect to the decapods most similar to those of the MAR. Here, there is only one genus and species of crab (*Austinograea rodriguezensis*) described to date, similar to the situation with the single species of *Segonzacia* in the Atlantic. Concerning the alvinocaridid shrimp, the two genera *Rimicaris* and *Mirocaris*, both of which were known previously only from the Mid-Atlantic sites, are found also in the Indian Ocean. Yet Hashimoto *et al.* (2001) and Van Dover *et al.* (2001), after considering all of the diversity at the Indian Ocean hydrothermal sites (in contrast to just the Decapoda), suggested a closer faunal affinity to the Pacific.

Martin & Hessler (1990), in establishing the genus *Chorocaris* for a western Pacific and Mid-Atlantic species, hinted at a faunal connection between the western Pacific and the Atlantic. Such a faunal corridor would necessarily include vent systems in the Indian Ocean as an intermediate. In support of this faunal connection they mentioned, in addition to the MAR and Marianas distribution of *Chorocaris*, the very similar distribution of a genus of vent snails (*Pseudorimula* McLean) found only at vents of the Marianas and the MAR. The same distribution was noted for an undescribed (at that time) mussel (see Martin & Hessler, 1990: 10). The gastropod genus *Shinkailepas* apparently exhibits the same distribution pattern, with species known only from the Kaikata Seamount off Japan and the Manus Back-Arc Basin in the western Pacific and from the Lucky Strike and Menez Gwen sites in the Atlantic (Bouchet & Warén, 1997, in Desbruyeres & Segonzac, 1997: 132). More recent finds in the Indian Ocean (see Van Dover *et al.*, 2001), especially in light of the species of *Rimicaris* found there (*R. kairei*) and its extreme morphological similarity to *R. exoculata* in the Mid-Atlantic, would seem

to support a faunal connection between the Indian Ocean and Atlantic Ocean vent sites as well. The finding of a second species of the genus *Mirocaris* (Komai *et al.*, in press), a genus also known previously only from the MAR, from the Indian Ocean would seem to support further a connection between the Atlantic and Indian oceans. Yet the only crab genus present in the Indian Ocean, *Austinograea*, is known only from western Pacific vent sites. Further exploration of both the south-east and the south-west segments of the Indian Ridge, as listed by Tyler *et al.* (2003) among their recommendations for future vent work, should shed light on the extent of these faunal corridors and the evolutionary origin(s) of the Indian Ocean fauna.

Direct evolutionary connections between hydrothermal vents and cold seeps, perhaps not surprising in light of the fact that both are deep-sea chemosynthetic environments, have been suggested by a number of workers (e.g. Hecker, 1985; Sibuet & Olu, 1998; Van Dover, 2000; see Little & Vrijenhoek, 2003). Sibuet & Olu (1998) gave reasons to expect that overall species diversity might be higher at cold vents, with their somewhat longer and more stable association with continental margins, than at the presumably more ephemeral hydrothermal vents. To some degree, this higher overall macrofaunal diversity in seep communities was supported in a direct comparison made by Turnipseed *et al.* (2004). With regard only to the decapods, however, no such pattern is apparent to date, in part because most species fall into the secondary consumer category (see Desbruyères *et al.*, 2000, 2001; Turnipseed *et al.*, 2004). Only one genus of shrimp (*Alvinocaris*) and none of the crab genera found at hot vents have been reported from cold seeps, and overall the hydrothermal vents are more species- and genera-rich in decapods than are seeps.

If vent-associated faunal elements 'represent a relict fauna that has remained distinct from other marine faunas for tens to hundreds of millions of years' (Tunnicliffe, 1992a) and/or are providing us with a 'glimpse of antiquity' (Newman, 1985; see also MacArthur & Tunnicliffe, 1998), it is not obvious to us from examination of the decapods. Based on only the decapods, it appears to us that Van Dover *et al.*'s (2002) suggestion of a more recent origin of the vent fauna (considerably less than 100 million years) is more accurate for this group, and molecular evidence at least for the shrimp (Shank *et al.*, 1999) seems to confirm this, as does the recent review by Little & Vrijenhoek (2003) based on fossil and molecular data. Most vent decapod species appear similar to other extant members of their clade (where known), and there are very few morphological features that would indicate an unusual habitat or exceptional time spent in isolation. Exceptions might include the dorsal 'eye' beneath the carapace in the shrimp genus *Rimicaris*,

and the absence of eyes or eyestalks in some members of the crab genus *Austinograea*. On the other hand, some common members of the deep-sea decapod community are notably absent from vents or seeps, such that there may indeed be some 'physiological barrier to the colonization of the habitat' as Tunnicliffe (1992a: 338) proposed. For example, members of the crab families Geryonidae, Homolidae and Homolodromiidae have been found only rarely (or not at all in the case of the homolodromiids), yet they are relatively common and widespread throughout deep basins in all oceans.

It is somewhat surprising that we still know so little about the dispersal and settlement of larvae of vent organisms (Vrijenhoek, Shank & Lutz, 1998; Tyler & Young, 1999, 2003; Marsh *et al.*, 2001; Van Dover, Jenkins & Turnipseed, 2001b; Van Dover & Lutz, 2004), including the decapod Crustacea. Some of the work on larval and juvenile bythograeid crabs (e.g. see Epifanio *et al.*, 1999; Dittel *et al.*, 2005) suggests that entrainment of larvae in hydrothermal plumes and subsequent vertical transport by the 'buoyant plume', followed by horizontal transport via the 'effluent layer' (terminology after Tyler & Young, 2003), is not only possible but is occurring. Anecdotal evidence, mostly concerning the types of visual receptors found in larvae vs. adults, would seem to indicate that the larvae can survive as part of the plankton in mesopelagic waters, in some cases as much as 1000 m above active vent sites (Jinks *et al.*, 2002). Megalopa larvae of bythograeids also survive at surface pressures and temperatures, whereas adult crabs do not, supporting the idea that larvae of these crabs might reach upper (mesopelagic) waters (e.g. see Epifanio *et al.*, 1999; Jinks *et al.*, 2003; Dittel *et al.*, 2005). If so, this would be in contrast to the 'along-ridge' dispersal at depth that appears responsible for larval transport in some other vent invertebrates (e.g. Marsh *et al.*, 2001). Dittel *et al.* (2005) found that prey items of vent crab megalopae were more similar to those of non-vent species, supporting the idea that development occurs away from vents. Other work on shrimp larvae and postlarvae suggests that horizontal transport in the deep sea is occurring (see review of vent and seep invertebrate distributions and the discussion of deep-ocean dispersal, gene flow and circulation in Van Dover *et al.*, 2002), as apparently occurs with at least some vent-inhabiting polychaetes (Marsh *et al.*, 2001). Near the MAR's Broken Spur and TAG fields, Herring (1998) and Herring & Dixon (1998) reported postlarvae and juveniles of bresilioid vent shrimp, tentatively identified as belonging to *Chorocaris* and *Alvinocaris*, at distances of up to 100 km from any known active vent, a distance that would allow them to colonize new vent fields. Additionally, decapods have been reported from the 'off-axis' Lost City vent fields (Kelley *et al.*, 2001)

and other off-axis sites, and postlarval (megalopal) stages of bythograeid crabs have been collected from considerable distances from vents (T. Shank, pers. comm.; T. Shank & J. W. Martin, unpubl. data). Also supporting the relative ease of gene flow among vent sites is the work of Creasey *et al.* (1996) using allozyme data, in which populations of *Rimicaris exoculata* appeared relatively homogeneous among all MAR sites, and various other studies on vent-associated invertebrates (e.g. Miyazaki *et al.*, 2004, on mussels) indicating few barriers to genetic exchange among vent sites. It is interesting to note that even though larval stages of some alvinocarid shrimp appear to feed on phytoplankton from surface waters (Allen Copley, Tyler & Varney, 1998), the reduced pressure (1 atm) at the surface is fatal at least to larvae of the shrimp *Mirocaris fortunata* (based on laboratory experiments by Tyler & Dixon, 2000). Thus, evidence for vertical transport seems somewhat contradictory. Conclusive evidence for the mode of dispersal in vent crabs, in the form of identifiable larvae collected from surface or mesopelagic waters, remains elusive. It is clear that the physical surroundings of vents and seeps affect water flow and therefore larval dispersal such that the overall picture can be extraordinarily complex and may differ greatly among ocean basins (see reviews by Van Dover, 1990 and Tyler & Young, 2003). Whatever the mechanism, long-range dispersal must certainly be occurring at least occasionally, as otherwise we would be at a complete loss to explain the tremendous morphological similarity of the two species of *Rimicaris* in the Atlantic (*R. exoculata*) and Indian (*R. kairei*) oceans, and the great similarity of the shrimp species *Chorocaris vandoverae* and *C. paulexa* on either side of the Pacific (Martin & Shank, 2005). The relative ease of gene flow among active vent sites is also supported by the observation by Shank *et al.* (1999: 244) that 'evolutionary relationships of vent-endemic shrimp species [do] not appear to be correlated either with their extant biogeographical distribution or with the history of sea floor spreading.'

There is some obvious bias in terms of the numbers and types of decapods that have been collected to date. Bythograeid crabs respond well to baited traps, and as a result some species are known from relatively large numbers of specimens [e.g. the more than 80 specimens forming the basis of Hessler & Martin's (1989) description of *Austinograea williamsi*, and the more than 200 specimens of *Bythograea thermydron* noted by DeBevoise *et al.* (1990)]. In comparison, when crabs are collected using the manipulator arms of submersibles, it is common to have only one or two specimens upon which to base the description (e.g. Guinot & Segonzac, 1997, for *Bythograea laubieri*). Alvinocarids have also been collected with baited traps, as have

species of the hippolytid genus *Lebbeus*. By contrast, some shrimp species are not attracted to baited traps and are more mobile, making them far more difficult for manned or unmanned submersibles to capture. Shrimp of the genus *Nematocarcinus* are a good example, as they are widely reported but only rarely collected. Thalassinideans are also likely to be greatly underrepresented in existing collections from vents and seeps because of their tendency to burrow. Collecting decapods at great depths depends on far more than encountering the species; often the success or failure depends on what pieces of equipment are currently mounted on the submersible or ROV as well as on the time that can be devoted to collection activities.

Another obvious and somewhat disturbing pattern that is apparent from our compilation is the relative scarceness of specimens of most of the vent and seep taxa. Several species are known in the literature from one or very few specimens. However, from informal discussions with several workers in the field of deep-sea biology, we know that this trend is in some ways artificial; the actual number of known specimens is in some cases quite high. Discussions with deep-sea biologists in the US and other countries has convinced us that many specimens are stored in freezers or in unrecognized (unpublished) personal or university collections of deep-sea biologists whose primary research interests may be ecological, physiological, behavioural or biogeographical rather than taxonomic or systematic. Thus, although the taxonomic literature usually includes reports of the first occurrence and a few type specimens, additional specimens, and especially the details of their collection (number, locality, depository, etc.), often are not mentioned in subsequent publications. Two websites created partially to address this problem are the Hydrothermal Fauna Database of the InterRidge website hosted by the University of Tokyo (<http://triton.ori.u-tokyo.ac.jp/~intridge/index.html>) and the *Vent Invertebrates Collection Database* hosted by the Field Museum of Natural History (<http://fm1.fieldmuseum.org/collections/search.cgi?dest=vent>). At both sites, scientists are encouraged to post collection information on materials collected from vents and seeps. However, as of this writing the former site has only 47 records of decapods, and the latter has only eight records. One additional database, the ChEss database of vent fauna (<http://www.soc.soton.ac.uk/chess/home.html>), also lists data on a variety of vent-associated decapods. Many of those data were borrowed from a copy of the current manuscript.

An additional problem is that some specimens collected during non-biological cruises often are not reported, and in some cases are deliberately thrown overboard or are otherwise lost. As an example, a small undescribed species of deep-water crab from the Gulf of Mexico came to our attention by way of a beau-

tiful colour painting of the species; a professional artist, funded as part of the expedition, rendered the illustration. However, the specimen was not recorded or sent to a specialist for identification and has apparently been lost (I. Macdonald, pers. comm.). Clearly, there is a distinct need for a centralized archival repository or at least a detailed and accessible electronic database for tracking these specimens, all of which have been collected at enormous expense. Such a database, and its potential integration with OBIS (the Ocean Biogeographic Information System), is precisely what Tyler *et al.* (2003) proposed as one of the goals of the ChEss (Biogeography of Deep-Water Chemosynthetic Ecosystems) programme of the Census of Marine Life (see Tyler *et al.*, 2003), and indeed what has been attempted to varying degrees of success with the InterRidge and Field Museum websites noted above. Finally, it is all too clear that a primary reason for the relatively rare mention in the literature of vent and seep decapods, as well as for the description of these species occurring in some cases many years after their discovery, is the deplorably low number of taxonomists actively working on these groups. It is clear that a major focus of initiatives such as the Census of Marine Life should be the training of additional morphology-based systematists. The use of molecular evidence will help greatly, but it is equally clear that the molecular systematists remain heavily dependent upon students of decapod morphology and taxonomy for positive identifications and, in most cases, to help frame the pertinent questions that can be addressed using molecular techniques. A perusal of the 100+ species listed in this paper and of the relatively few people responsible for having described them [e.g. K. Baba, T. Komai, A. Williams (deceased), D. Guinot, M. de Saint Laurent (deceased)] underlines how few workers have described the number of species known to date from hydrothermal vents and cold seeps. An increase in the number of molecular biologists will not, by itself, solve the problem of how to increase our understanding of the systematics of vent species. There is an acute need to train a new generation of decapod crustacean systematists and morphologists. Unfortunately, the same could be said for nearly every other taxon of marine invertebrates.

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