Zootaxa 326: 1–16 (2003)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)
326

Haplomunnidae (Crustacea: Isopoda) reviewed, with a description of an intact specimen of *Thylakogaster* Wilson & Hessler, 1974

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Abstract

The distribution and ecology of the isopod family Haplomunnidae Wilson, 1976 are reviewed with new records given for *Thylakogaster* Wilson & Hessler, 1974, Mid-Atlantic Ridge and east Pacific Ocean, and for *Munella* Bonnier, 1896, Mid-Atlantic Ridge and the eastern Atlantic near the African coast. The specimens of these two genera, collected from Lucky Strike (Mid-Atlantic Ridge), are the first record of the family from hydrothermal vent habitats. The systematics of the Haplomunnidae is updated and the synonymy of *Aryballurops* Gamô, 1983 with *Haplomunna* Richardson, 1908 is proposed. *Thylakogaster lobotourus* Wilson & Hessler, 1974 is redrawn from the first known intact specimen and additional description of the appendages is provided.

Key words: Crustacea, Isopoda, Asellota, Haplomunnidae, *Haplomunna*, *Thylakogaster*, *Munella*, Mid-Atlantic Ridge, hydrothermal vents

Introduction

The isopod family Haplomunnidae Wilson, 1976 is a rare but widespread component of deep-sea communities. Unfortunately, long-limbed Haplomunnidae are rarely recovered undamaged, frequently appearing in deep-sea grab or dredge samples as badly damaged, appendage-free carcasses. Recent collections from the Lucky Strike vent field (Mid-Atlantic Ridge) yielded two nearly intact specimens of *Thylakogaster lobotourus* Wilson & Hessler, 1974, an incompletely described species. These specimens verify the original concept of the genus, as well as providing new records of these morphologically unusual deep-sea species. In this paper, we illustrate one intact specimen, provide new records for undescribed species, and review the taxonomy, distributions and ecological settings of the Haplomunnidae.

Accepted: 1 October 2003; published: 10 October 2003

The Haplomunnidae comprises four genera characterised by their axially compressed, deep body and long-legged ambulatory habit with an epibenthic life style (Wilson 1976). The first records of specimens (*Thylakogaster* Wilson & Hessler, 1974 and *Abyssaranea* Wilson & Hessler, 1974) from this family were mainly from abyssal equatorial and South Atlantic waters. Their similarities to *Munella* Bonnier, 1896, a genus previously known from the continental margins of France (Bay of Biscay) and Italy (Bay of Naples), were recognised at that time (Wilson & Hessler 1974). The family Haplomunnidae Wilson, 1976 was based on the genus *Haplomunna* Richardson, 1908 recorded from abyssal East Pacific waters. Collections from the Japan Trench (Gamô 1983) and from the epifauna of hexactinellid sponge stalks (Beaulieu 2001a, 2001b) have demonstrated that species of this family can be found in environments that span a wide range of available ecosystems in the deep-sea.

Although the Lucky Strike vent field has been the target of several oceanographic expeditions and experimental in situ studies, the sampling effort has been focused mainly in the most active areas of the field (Desbruyères *et al*. 1994, 2001; Van Dover *et al.* 1996; Colaço *et al*. 2002). Of the 473 species listed by Desbruyères & Ségonzac (1997), 159 are Crustacea, with a majority being copepod species (37.1%), followed by conspicuous decapods (28.3%). Other groups appear to have been understudied or overlooked (only two tanaid and eight amphipod species), and the isopod fauna remains almost unknown (six species). During a geological survey carried out in August 2000, a TV-assisted grab was used to take 24 samples mostly from inactive areas of the field. Over 4000 specimens were collected and ascribed to 92 different taxa, including 13 isopod species and 29 other crustacean species (Cunha *et al*. 2001). The recently collected specimens of Haplomunnidae from the Lucky Strike hydrothermal vent system are the first record of the family from this unusual habitat.

Abbreviations

AM, Australian Museum, Sydney; AMORES, Azores Mid-Atlantic Ridge Ecosystem Studies; CENTOB, Centre de tri d'océanographie biologique (Ifremer, Environnement Profond, Brest); DBUA, Departamento de Biologia da Universidade de Aveiro, Aveiro; Ifremer, Institut Français de Recherche pour l'Exploitation de la Mer, Brest; IOC, Intergovernmental Oceanographic Commission; MNHN, Muséum national d'Histoire naturelle, Paris; NOAA, US National Oceanographic and Atmosphere Administration; PRA, Preservational Reserve Area; SIO, Scripps Institution of Oceanography; TTR, Training Through Research Program; UNESCO, United Nations Educational, Scientific and Cultural Organization; USNM, United States National Museum of Natural History; WHOI, Woods Hole Oceanographic Institution; SMBA, Scottish Marine Biological Association; ZMUC, Zoologisk Museum, University of Copenhagen, Denmark.

TABLE 1. Localities of Haplomunnidae. Many samples are too poor a state for description, or have too few individuals, so are indicated by species undefined (sp.) or by a species number. Positions of samples with different beginning and ending latitudes or longitudes are given as midpoint positions. An asterisk (*) indicates the type locality for each species. W&H74 = Wilson & Hessler 1974

NAME	Remarks	Program	Station	Depth	Latitude			Longitude			ind.
*Abyssaranea rupis**	W&H74	WHOI	155	3757	00	03.0	N	27	48.0	W	2
Abyssaranea rupis	W&H74	WHOI	156	3459	00	46.2	N	29	25.8	W	14
Abyssaranea cf. *rupis*	coll. by R. Hessler	South Tow, leg 1	H84	4435–4438	03	01.9	N	125	00.8	W	1
Abyssaranea sp.	new	WHOI	334	4400	40	43.3	N	46	14.2	W	2
*Haplomunna caeca**	Richardson 1905	Albatross	4390	3998	33	02.2	N	120	42.0	W	1
Haplomunna hubbsi	Wilson 1976	SIO	70–92	3880–3950	31	32.9	N	120	13.4	W	1
*Haplomunna hubbsi**	Wilson 1976	SIO	70–94	3916–3950	31	25.2	N	120	08.5	W	2
*Haplomunna japonica**	Gamo 1983	R/V Hakuho-Maru	12 KH 81-4	6380–6450	38	34.4	N	144	15.4	E	10
Haplomunna n. sp.	Beaulieu 2001a,b	SIO	M, sponge stalks	4100	34	45.0	N	123	00.0	W	64
*Munella danteci**	Bonnier 1896	Caudan	13	950	44	17.0	N	04	38.0	W	1
Munella danteci (?)	Lo Bianco 1903	Puritan	25	200	40	33.0	N	14	05.0	E	1
Munella danteci (?)	Lo Bianco 1903	Puritan	29	100	40	38.0	N	14	22.0	E	1
Munella danteci		TTR-10	AT-272-Gr	1685	37	17.6	N	32	16.9	W	2
*Munella gayda**	W&H74	WHOI	118A	1144	32	19.2	N	64	34.8	W	6
Munella sp.	damaged	BALGIM (MNHN)	DW16	1283	36	45.8	N	09	29.4	W	1
Munella sp.	damaged	BALGIM (MNHN)	DW94	1175	34	24.9	N	07	28.5	W	1
Munella sp.		WHOI	299	2009	07	55.2	N	55	42.0	W	1
Munella sp.174		SIO, PRA	08	4797	12	54.6	N	128	20.7	W	1
Munella sp.533	Rowe 2003	DGOMB	S2	3732	23	29.4	N	92	0.4	W	1
*Thylakogaster lobotourus**	W&H74	WHOI	118A	1144	32	19.2	N	64	34.8	W	18
Thylakogaster lobotourus	W&H74	WHOI	119	2159	32	16.2	N	64	31.8	W	2
Thylakogaster lobotourus		TTR-10	AT-265-Gr	1710	37	17.4	N	32	16.6	W	1
Thylakogaster lobotourus	damaged	TTR-12	AT-436-Gr	1710	37	17.3	N	32	16.6	W	2
Thylakogaster lobotourus	illustrated herein	PICO AMORES	SMAC C6	1700	37	17.5	N	32	16.5	W	1
Thylakogaster majusculus	W&H74	WHOI	247A	5216	43	33.0	S	48	58.2	W	33
*Thylakogaster majusculus**	W&H74	WHOI	259A	3311	37	13.2	S	52	45.0	W	136
*Thylakogaster peterpauli**	W&H74	WHOI	155	3757	00	03.0	N	27	48.0	W	52

......continued on the next page

TABLE 1 (CONTINUED)

NAME	Remarks	Program	Station	Depth	Latitude	Longitude	ind.
Thylakogaster peterpauli	W&H74	WHOI	156	3459	00 46.2 N	29 25.8 W	82
Thylakogaster sp.1		WHOI	303	2848	08 28.8 N	56 04.5 W	2
Thylakogaster sp.1		WHOI	321	2879	50 12.0 N	13 36.0 W	2
Thylakogaster sp.1		WHOI	323	3347	50 07.8 N	13 52.2 W	8
Thylakogaster sp.1		WHOI	326	3859	50 05.4 N	14 26.4 W	29
Thylakogaster sp.1		WHOI	328	4431	50 05.4 N	15 45.0 W	14
Thylakogaster sp.1		WHOI	330	4632	50 48.0 N	17 57.6 W	3
Thylakogaster sp.1	Harrison 1988	SMBA	Perm.	2900	54 40.0 N	12 17.5 W	1
Thylakogaster sp.2	coll. by R. Hessler	SIO, South Tow, leg 1	H84	4435-4438	03 01.9 N	125 00.8 W	1

Material and methods

Study site: The Lucky Strike segment is located at the Mid-Atlantic Ridge (MAR) southwest of the Azores (Fouquet *et al*. 1994). The hydrothermal field, centred at 37º17.5’N, 32º16.5’W, is one of the largest currently known in the MAR and develops around a lava lake at approximately 1700 m in a depression surrounded by three volcanic cones. The lava lake, the first discovered in a slow spreading ridge (Fouquet *et al*. 1995) is characterised by typical lobated and draped lavas, lava flows and lava pillars. The volcanoes are mostly composed of pillow lavas and volcanic breccia. Many chimneys and other edifices, most of which are inactive or only mildly active, surround the lava lake. Near large chimneys, diffuse venting occurs through unconsolidated sediments. Further information on the geological setting and environmental conditions in the vent field can be found in Costa *et al*. (1995), Langmuir *et al*. (1997) and Barriga (1999).

Source of specimens: (Table 1). Specimens from Lucky Strike were collected during geological surveys of the vent field (2000 and 2002) by a joint program of the Geological and Mining Institute of Portugal, Moscow State University and University of Aveiro (TTR-10 and TTR-12, IOC-UNESCO). Michel Ségonzac (EP/CENTOB-Ifremer) provided a sample from Lucky Strike collected during the 1998 PICO expedition (AMORES program, EU MAST III; D. Desbruyères, chief scientist). This latter specimen was collected in colonisation trays (SMAC) deployed by submersible in the vicinity of a black smoker (Tour Eiffel) and recovered after a period of 321 days (D. Desbruyères, personal communication). A series of deep benthic sampling transects in basins of the Atlantic Ocean, conducted by WHOI under the direction of Howard Sanders, Robert Hessler and J. Frederick Grassle, provided most of the original specimens described by Wilson & Hessler (1974). Additional specimens came from the following oceanographic programs: 1984 BALGIM (MNHN; P. Bouchet, chief scientist) from the eastern Atlantic off Africa; South

Tow (SIO; R. Hessler, chief scientist) in the equatorial Pacific; ECHO1 (SIO; Wilson & Hessler 1987; Thistle & Wilson 1996) and PRA (SIO; Wilson 1990; Thistle & Wilson 1996) in the North Pacific between the Clipperton and Clarion Fracture Zones; Station M (SIO; Beaulieu 2001a, 2001b) at abyssal depths off the southern California Borderland of the USA; and the Sigsbee Abyssal Plain in the Gulf of Mexico (Rowe 2003).

Systematics

Suborder Asellota

Family Haplomunnidae Wilson, 1976

Haplomunnidae Wilson, 1976: 572; Kussakin, 1988: 355; Roman & Dalens, 1999: 250.
Dendrotionidae Wolff, 1962: 64 (part).
Munnidae Gamô 1983: 11 (part).

Type genus. *Haplomunna* Richardson, 1908.

Diagnosis (modified from Wilson 1976): Head without eyes, anteriorly rounded, dorsal surface sloping anteriorly, lacking anterior margin. Body with spines, dorsally vaulted, posterior pereonites axially compressed and reduced. Female spermathecal duct emerging anterodorsally near margin of pereonite 5. Anus covered by opercular pleopods. Antennula inserting dorsally on head, sexually dimorphic, with many flagellar articles and aesthetascs in male, and fewer and thinner articles in female. Antenna inserting anterodorsally, basal articles robust, article 3 without scale. Mandible palp (when present) elongate, longer than body of mandible, article 3 elongate with elongate setae only on distal tip. Pereopod I with major subchelate hinge between carpus and propodus; carpus palm (ventral margin) robust, with elongate robust setae. Pereopods II–VI and VII, if present, longer than body. Male pleopod II protopod strongly tapering and narrow distally; exopod lacking setose posterior projection. Pleopod III exopod biarticulate, narrower and longer than endopod, without plumose setae. Uropods emerging at pleotelson ventral margin; uniramous; tiny, not extending beyond terminal margin of pleotelson.

Relationships: The family Haplomunnidae was argued by Wilson (1976) to be the sister group of the Dendrotiidae, and not closely related to Munnidae, Santiidae or Paramunnidae. The primary similarities between the former two families include general body spinosity, vaulted thoracic region, compact anteriorly-sloping emarginate head capsule with antennae and antennulae placed on anterodorsal surface, and elongate pereopods II–VII that exceed the body length. While not fully consistent among species in both families, the ischium and merus of the walking legs are often subequal and shorter than the basis. Notably, the opposite situation occurs among the Munnidae, where the basis is often shorter than the ischium. Although *Acanthomunna* Beddard, 1884 is somewhat similar in body form to *Haplomunna*, male dendrotiids have a setose posteriorly-directed appendage on exopod of pleopod II, an apomorphy of the family. Tiny marginal uropods are an apomorphy of the Haplomunnidae, although reductions of the uropods are common among other deep-sea isopod taxa. Some, but not all, members of both families share the heterochronic non-expression of the last pereonite. This oddity also occurs among other deep-sea families (e.g., Munnopsidae, Ischnomesidae), so its phylogenetic significance is limited to those clades that reach adulthood without the last pereonite.

Regarding higher-level relationships, Wägele (1989), partially following Wolff (1962), suggested that the asellotan families Munnidae, Santiidae (as Pleurocopidae), Dendrotiidae and Haplomunnidae were related in a group referred to as ‘munnoiden’, or as having a ‘munnoid habitus’. The sister group relationship between the Dendrotiidae and the Haplomunnidae, as discussed above, was not in dispute, but the principal difficulty with Wägele’s (1989) hypothesis lies in the underlying assumption of similarity of body form (Wilson 1996). In Wägele’s (1989: 67) concept, the munnoid habitus includes the following features: an approximately oval body outline, in which the middle pereonites are somewhat broader than the anterior or posterior segments, head broader than long, eyes laterally projecting and often clearly stalked, pereonites 5 to 7 not only narrower but also shorter than the anterior pereonites, pleotelson dorsally convex, and at its origin somewhat narrower, distally rounded and often spindle-like. Other than the stalked eyes, most of these features are seen throughout the Janiroidea, especially among the deep-sea families. *Acanthomunna* is the only genus with eyes among the Dendrotiidae or the Haplomunnidae, but only has rounded lateral projections, somewhat similar to those seen among some Janiridae and clearly unlike the stalked eyes of the presumptive ‘munnoiden’ clade. Although not fully relevant here, the form of the stalked eyes (where present) varies consistently between the eyed families: short, thick and generally with many ocelli among the Munnidae and Santiidae, elongate and often with few ocelli among the Paramunnidae and extremely elongate and thin, with few ocelli in *Pleurocope*, which belongs to its own separate family, Pleurocopidae. The ‘munnoiden’ are unlikely to be a cohesive phylogenetic group because different taxa have different positions for the spermathecal duct and configurations of pereopod I (Wilson 1987; personal observation). Additionally, antennae in Paramunnidae, Munnidae and Santiidae, and Pleurocopidae all insert anteroventrally, but with differing positions among the three groups; Haplomunnidae and Dendrotiidae have antennae inserting anterodorsally, often on projections of varying sizes. Other features, such as the above-mentioned comparative lengths of the pereopodal podomeres, also differ considerably among these families. Clarification of the haplomunnid classification will require detailed morphological study and phylogenetic analysis of all families of Janiroidea.

Distribution: Although Kussakin (1988), in his useful compendium of the isopods of the Northern Hemisphere, characterised the Haplomunnidae as an equatorial and Southern Hemisphere group and only listed the equatorial Atlantic species *Thylakogaster peterpauli* Wilson & Hessler (1974), recent records (Table 1, Figure 1) indicate that this family is much more widespread than previously suspected, and clearly not limited to equatorial regions. Species of *Haplomunna* are known from abyssal and hadal waters of the North Pacific, off southern and Baja California (Wilson 1976; Beaulieu 2001a, 2001b) and the Japan Trench (Gamô 1983) from depths of 3880 to 6450 m. *Thylakogaster* has the broadest distribution from depths of 1135 m to 5223 m, including the equatorial Atlantic, Argentine Basin, north of Surinam, Bermuda slope, off Ireland, in the Rockall Trough (Harrison 1988) and in the east Pacific (Thistle & Wilson 1987). New records include the Lucky Strike vent field on the Mid-Atlantic Ridge, and the east Pacific Ocean. *Abyssaranea* has been found at depths from 3459 to 4438 m in the equatorial Atlantic and East Pacific, as well as a new record from a Woods Hole Oceanographic Institution deep-benthic station in the northwestern Atlantic. This latter record is the first non-equatorial record for this genus. *Munella* has most records in the bathyal deep sea (950–2076 m) including the Bay of Biscay, the Bermuda Slope and north of Surinam in the Atlantic. Unconfirmed records of *Munella* in the central Mediterranean are from depths of 100–200 m (Bay of Napoli; Lo Bianco 1903). *Munella* also occurs at abyssal depths in the east Pacific (4797 m, Thistle & Wilson 1996). New records of *Munella* include Lucky Strike vent field on the Mid-Atlantic Ridge (1685m, TTR-10), the eastern Atlantic near the African coast (1175–1283 m, BALGIM stations), and the Gulf of Mexico (3732 m., Rowe 2003). A new species and new genus of Haplomunnidae collected by Poore *et al*. (1994) occurs in southeastern Australia at bathyal depths (J. Just, personal communication).

Habitat and Ecology: All Haplomunnidae have long-legged ambulatory morphologies, and are unlikely to be burrowers. Because they are primarily epibenthic and exposed to erosion, they are not likely to be found at high energy sites. This family has not been recorded from the HEBBLE (high energy benthic boundary layer experiment) sites (Thistle & Wilson 1987, 1996), and haplomunnid species are a reasonably consistent member of benthic assemblages at quiescent sites. In the Clipperton-Clarion Fracture Zone region of the East Pacific, a region characterised by low abyssal hills, pelagic clay and manganese nodules, *Thylakogaster* has been found at the ECHO 1 site (Thistle & Wilson 1987) and *Munella* at the PRA site (Wilson 1990; Thistle & Wilson 1996). The recorded substrates for haplomunnids range from typical deep-sea sediments to rocky outcrops, manganese nodules and carbonate crusts. Several Atlantic records are from continental margins in muddy sediments (Bonnier 1896), sand and volcanic gravel (Lo Bianco 1903), mixed *Globigerina* and pteropod oozes (Bermuda slope; Wilson & Hessler 1974). We now report them from hydrothermal vents (Lucky Strike) including a high temperature, diffuse venting area. In this case, the *Thylakogaster* specimens were collected on volcanic rocks (hyaloclastic breccia and pillow lavas) in the vicinity of active venting areas and in colonisation trays deployed near black smokers in the SE part of the field, while *Munella* specimens were collected on fragments of inactive chimneys in the NW part of the field. Biogenic structures appear to be favoured, because *Haplomunna* sp. was found highly aggregated on *Hyalonema* sponge stalks (Beaulieu 2001a, 2001b).

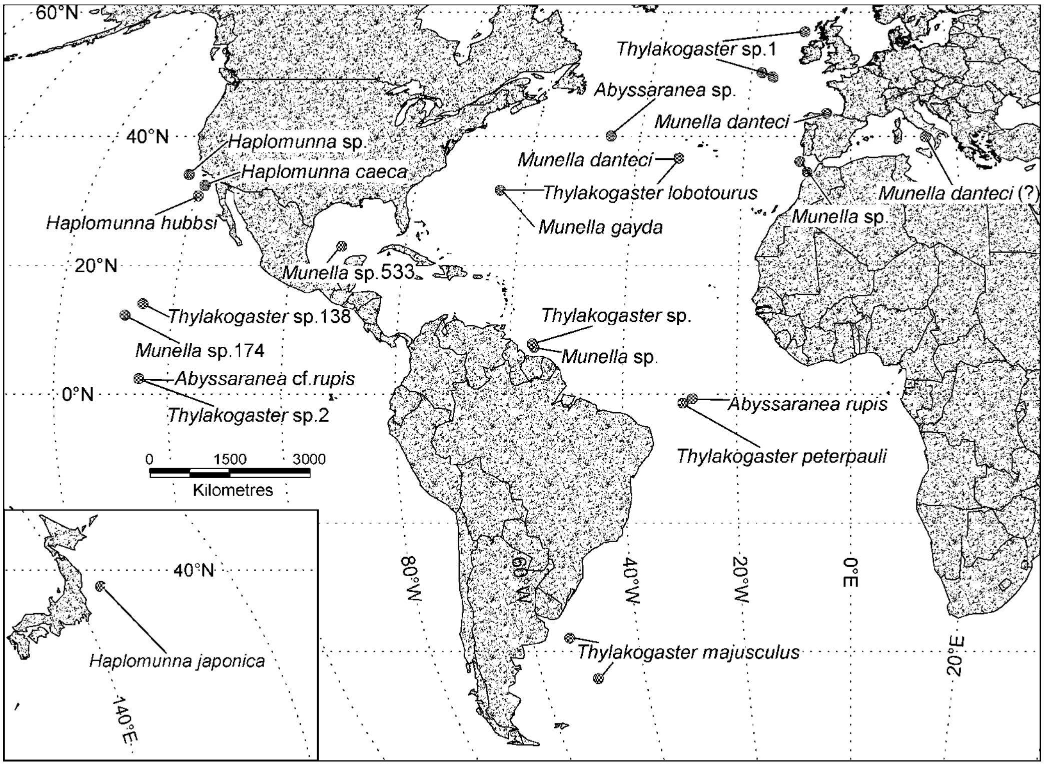

FIGURE 1. Distribution of known Haplomunnidae species.

Like most deep-sea isopods, the trophic habit of Haplomunnidae species appears to be mostly detritivory. *Haplomunna* sp., found on the basal and middle portions of hexactinellid sponge stalks, may be feeding upon particles accumulating in pockets (Beaulieu 2001a). *Thylakogaster* species have elongate and setose pereopods II–III that may be used to search food in the sediments or catching suspended particles. These legs on preserved specimens are generally held with the carpus and propodus curving under the mouth field and the first pereopods, like a basket.

Genus *Haplomunna* Richardson, 1908

Munna Richardson, 1905: 483 (part).
Haplomunna Richardson, 1908: 79; Menzies, 1962: 32; Wilson, 1976: 574.
Aryballurops Gamô, 1983: 13–16, figs 8 and 9; Saito, Itani & Nunomura, 2000: 25.

Type species. *Munna caeca* Richardson, 1905, by monotypy.

Species included: *Haplomunna caeca* (Richardson, 1905); *Haplomunna hubbsi* Wilson & Hessler, 1976; *Haplomunna japonica* (Gamô, 1983).

Diagnosis (modified from Wilson 1976): Head rounded in dorsal view; depth and width less than pereonite 1, with distinct frons-clypeal ridge, antennae on low projection. Body ovate in dorsal view, vaulted in lateral view; surfaces and margins spinose, with two distinctly different sizes of spines: large robust spines, often on raised portions of the cuticle, and small thin spines ('stiff hairs' in Richardson 1905), pereonites 5–7 with spines only on lateral edges, dorsal surfaces smooth. Pereonites 1–4 sculptured, dorsal surfaces often with parallel transverse ridges arching across dorsum; lengths subequal. Female coxal developing oostegites external to sternal surface. Pereonites 5–7 dorsomedial axis compressed; lateral portions extending posteriorly beneath elevated pleotelson. Preparatory female with external developing oostegites. Pleotelson longitudinal axis nearly perpendicular to pereonal axis; inflated, width subequal to pereonite 5 width, somewhat bilobed anterodorsally, heart shaped in dorsal view; distal tip smooth, produced ventroposteriorly. Mandible molar process truncate with two distal ridges: distal ridge finely denticulate; proximal ridge with inner row of stout spines, and outer row of long sharp, minutely serrate spines; palp elongate, longer than body of mandible, article 1 longer than articles 2–3, article 3 subequal to article 2, with elongate setae in group at distal tip. Maxillipedal palp with segment 2 distinctly broader, segment 3 only slightly broader than segment 1. Pereopod I strong, subchelate; carpus somewhat elongate; distinct rows of many stiff unequally bifid setae on occlusive margins of both carpus and propodus. Pereopods II–VII similar to each other. All pereopods with two dactylar claws. Opercular pleopods with strong spines. Uropod tiny, uniarticulate, directed ventroposteriorly.

Remarks: We propose a synonymy of *Haplomunna* Richardson, 1908 and *Aryballurops* Gamô, 1983. The species *H. japonica* differs from the East Pacific species *H. caeca* and *H. hubbsi* in having a much more inflated pleotelson, but in all other respects, the three species are similar. Gamô (1983) provides the first description of a male in the *Haplomunna* clade, details of which we can confirm from specimens of an undescribed species provided by S. Beaulieu (SIO). In particular, the tip of the male pleopod I is rounded and not laterally produced (i.e., not saggitate) as in *Thylakogaster*, thus having a form more like that of *Abyssaranea* or *Munella*. An elongate mandibular palp, another similarity with the latter two genera, and the less modified form of pereopods II–VII clearly separates *Haplomunna* from *Thylakogaster.* Nevertheless, *Thylakogaster* and *Haplomunna* are similar in several respects, the most conspicuous being the reflexed and inflated pleotelson.

Genus *Thylakogaster* Wilson & Hessler, 1974

Thylakogaster Wilson & Hessler, 1974: 48; Kussakin, 1988: 355.

Type species. *Thylakogaster peterpauli* Wilson & Hessler, 1974, by original designation.

Species included: *Thylakogaster peterpauli* Wilson & Hessler, 1974; *Thylakogaster majusculus* Wilson & Hessler, 1974; *Thylakogaster lobotourus* Wilson & Hessler, 1974.

Diagnosis (modified from Wilson & Hessler 1974): Head laterally angular or curved in dorsal view; with transverse ridge and frons-clypeal furrow; depth subequal or greater than pereonite 1. Body with many thin-walled spines or spinules, including cuticle of dorsolateral sides of head, lateral and posterior sides of pleon, and external surfaces of pleopods 1and 2; spines also on coxae, lateral margins of pereonites 1 and 2; dorsum of pleon devoid of such spines. Female developing oostegites on coxae internal to sternal surface. Pleotelson strongly inflated, hollow, expanded dorsally and laterally into somewhat bilobed form, reflected anteriorly, lying above pereonites. Mandible without palp; molar process tapering distally into tuft of thin, curved spines. Maxilliped epipodite triangular, small, width less than basis width, length less than half basis length. Pereopods II and III elongate, distinctly longer than head–pereon length; carpus and propodus curving medially, strongly opposing each other, combined lengths exceeding two-thirds total pereopod length, with large curved setae; dactylus short, covered with fine cuticular hairs, with single claw. Pereopods IV–VII longer than pereopods II and III, more slender and straight, with smaller setae and with long, slender claw and second vestigial claw on dactylus. First pleopod copulatory male posterior margin sagittate. Uropods uniarticulate, positioned ventroposteriorly close to tip of pleon.

Thylakogaster lobotourus **Wilson & Hessler, 1974 (Figs. 2–3)**

Thylakogaster lobotourus Wilson & Hessler, 1974: 56–58, fig. 4.

Type material.— NW Atlantic: Bermuda Slope, southeast of northern tip of the Bermuda Islands, 32º19’N, 64º32’W, 1135–1153 m, stn WHOI 118a, holotype 1 copulatory male (USNM 141471), paratypes 1 immature female (USNM 141472) and 2 copulatory males (ZMUC).

Material examined.— **Mid-Atlantic Ridge**: Lucky Strike, 37º17.36’N, 32º16.49’W, 1695 m, Submersible *Nautile,* colonisation tray, stn PICO SMAC C6, 6.VII.1998, D. Desbruyères, 1 female (illustrated herein) head–pereon length 1.46 mm (CENTOB). Same locality, 37º17.44’N, 32º16.60’W, 1685 m, RV *Prof. Logachev*, TV-assisted grab, stn TTR-10 AT-265-Gr, 10.VIII.2000, M.R. Cunha, 1 manca IV–V head–pereon length 1.24 mm (DBUA). Same locality, 37º17.30’N, 32º16.56’W, 1709 m, RV *Prof. Logachev*, TV-assisted grab, stn TTR-12 AT-436-Gr, 29.VIII.2002, M.R. Cunha, 1 female head–pereon length 3.07 mm, and 1 anterior fragment. **NW Atlantic:** Bermuda Slope, southeast of northern tip of the Bermuda Islands, stn WHOI 118a (type locality), 14 individuals or fragments, most in poor condition (AM P64368); 32º16’N, 64º32’W, 2095–2223 m, stn WHOI 119, 1 individual, pleotelson only (AM P64369).

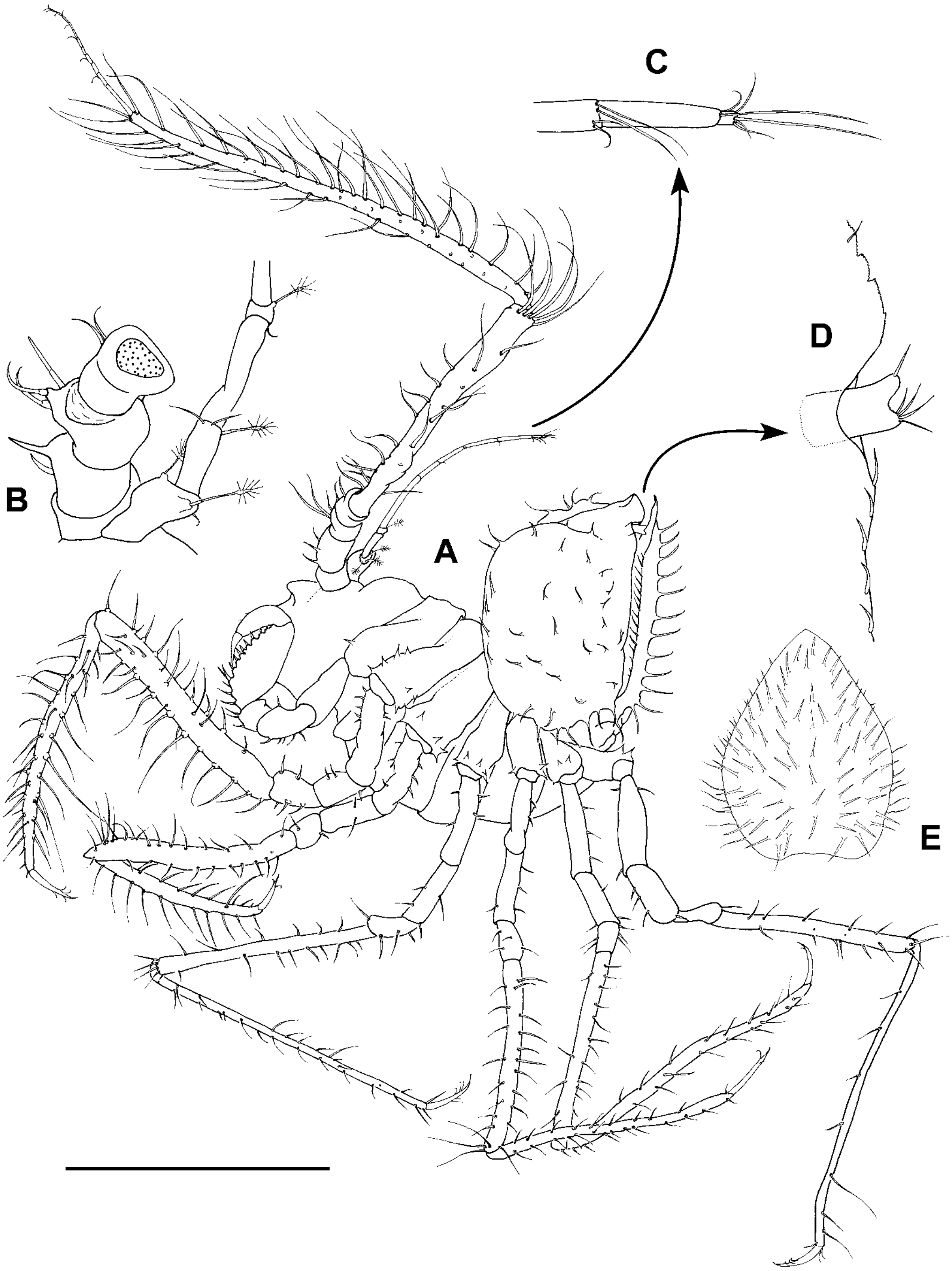

FIGURE 2. *Thylakogaster lobotourus* Wilson, 1974, female; **A**, habitus, lateral view (scale bar 1 mm); **B**, base of antennula and antenna, dorsal view; **C**, tip of antennula; **D**, left uropod, lateral view; **E**, pleopod II, ventral view.

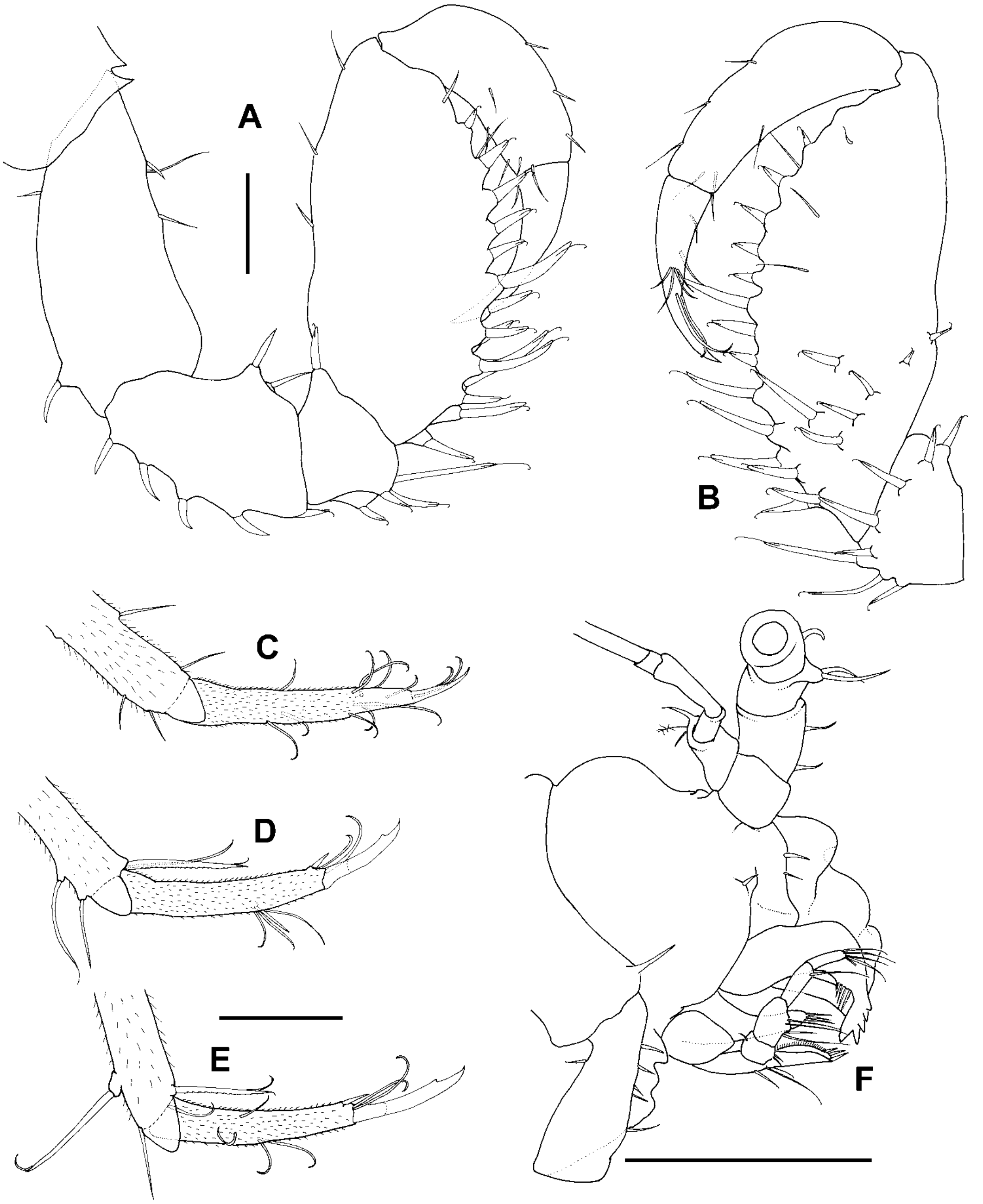

FIGURE 3. *Thylakogaster lobotourus* Wilson, 1974, female; **A**, pereopod I, lateral view; **B** pereopod I, mesial view; **C**, dactylus, pereopod II; **D**, dactylus, pereopod IV; **E**, dactylus, pereopod V; **F**, head, lateral view (scale bars: A–B, 0.1 mm; C–E, 0.1 mm; F, 0.5 mm).

Supplementary description: Female (Figs. 2–3): Head–pereon length 1.46 mm measured laterally. Antennula with 11 articles, article 1 with 2 penicillate setae, article 2 with 1 penicillate seta, article 4 with 1 penicillate seta, all located distally; article 3 length 1.6 article 2 length; article 4 length 0.28 article 2 length (proportions similar to *T. peterpauli* and *T. majusculus*). Antenna length 2.6 head–pereon length; article 5 length 2.5 articles 1–4 length altogether; article 6 length 1.7 article 5 length, both articles bearing numerous long setae; flagellum length 0.30 article 6 length, with 10 articles. Pereopod I basis length 2.3 width; ischium with 5 ventral setae, 2 dorsal setae; merus with 3 ventral setae, 1 dorsal seta, 4 medial setae; carpus length approximately 2 width, slightly longer than basis, with 11–12 setae on ventral margin, with 5–6 short stout setae distal to large central seta, proximal medial surface with 10 setae in two rows; dactylus length approximately 0.85 propodus length. Pereopod II long, length 2 head–pereon length; basis length approximately 3 width; propodus slender and curved, length approximately 15 width; both carpus and propodus with numerous setae arising from short cuticular protuberances, setae largest on occlusive margin on carpus and lateral and medial side of propodus; dactylus length 0.2 propodus length, with 1 claw. Pereopod III shorter than but similar to pereopod II. Pereopods IV–VII less robust and longer than pereopod II, length approximately 1.1 pereopod II length; basis width approximately 0.8 pereopod II width; propodus and carpus approximately two-thirds total pereopod length; propodus slender, length 1.4 carpus length (somewhat longer in pereopod VII); propodus with long robust mediodistal seta at dactylar insertion.

Remarks: Although the Lucky Strike specimens are distant from the original Bermuda Slope type locality of *T. lobotourus*, we found no differences that require the establishment of a new species. These new specimens suffered some bending and twisting of their thin legs, so the whole body illustration (Fig. 2A) was made by merging several views of the limbs to obtain an approximation of the ‘natural’ condition.

Males and juvenile specimens (mancas or females) of *Thylakogaster* species have usually one or two pairs of setae on the distal margin of pleotelson (between the uropods), and indentations of the margin; mature females lack these setae or indentations. Our observations on *Thylakogaster* specimens held at the Australian Museum show the following patterns: *T. lobotourus* WHOI 118a (AM P.64368), female no setae, male two pairs of setae; *T. lobotourus* Lucky Strike female, one pair of setae and indentations (Fig. 2D); *T. majusculus* WHOI 242a (AM P.64371), juvenile female no setae, male two pairs of setae and indentations; *T. peterpauli* WHOI 155 (AM P.64372), small male several small setae, female no setae, both with abundant cuticular hairs and no indentations; *T.* n. sp.1 WHOI 303 (AM P.64373), manca two pairs of setae. The cuticle of *T. peterpauli* has fine spinules, especially on the pleotelson, that are missing in *T. lobotourus*.

We have observed several differences between species of *Thylakogaster*:

i) The pereopod I carpus setae distal to large central seta on ventral margin differ: 5 or 6 in *T. lobotourus*, 7 in *T. peterpauli*; 7–9 in *T. majusculus*.

ii) The antenna of *T. lobotourus* is longer, with a longer flagellum and smaller setae than in *T. peterpauli* (antenna ~3.1 and 2.5 head–pereon length for *T. lobotourus* and *T. peterpauli*, respectively).

iii) The antennula of an adult male is slender with fewer aesthetascs in *T. peterpauli* and more robust in *T. lobotourus* and *T. majusculus*.

iv) Spines on body and pleotelson differ among the species. Relative to each other, number of spines varies as follows: *T. majusculus* > *T. peterpauli* > *T. lobotourus*. The length of the spines shows a different trend: *T. lobotourus* > *T. majusculus* > *T. peterpauli*. The pleotelson in *T. lobotourus* has fewer spines (10–15% less for the same area) but longer spines (1.1 times) than in *T. peterpauli*.

Acknowledgements

We are grateful to Michel Ségonzac (EP/ CENTOB–Ifremer), who has provided the specimen herein illustrated. Thanks are due to Hipólito Monteiro (Geologic and Mining Institute of Portugal) and Michael Ivanov (Moscow State University) for the invitation to participate in the TTR cruises (Training Through Research Programme, IOC–UNESCO). The authors gratefully acknowledge the attention to detail by several colleagues (including Jean Just and Niel Bruce) whose efforts improved our manuscript.

References

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

Beaulieu, S.E. (2001a) Life on glass houses: sponge stalk communities in the deep sea. *Marine Biology*, 138, 803–817.

Beaulieu, S.E. (2001b) Colonization of habitat islands in the deep sea: recruitment to glass sponge stalks. *Deep–Sea Research I*, 48, 1121–1137.

Bonnier, J. (1896) Résultats scientifiques de la Campagne du Caudan dans le Golfe de Gascogne. Edriophthalmes. *Annales de l'Université de Lyon*, 1895, 527–689.

Costa, I., Barriga, F.J.A.S. & Fouquet, Y. (1995) Alteration processes associated with active hydrothermal sites – The Lucky Strike and Menez Gwen examples (37º20'N and 37º50'N, Mid-Atlantic Ridge). *Memórias do Museu e Laboratório Mineralógico e Geológico da Faculdade de Ciências da Universidade do Porto*, 4, 979–983.

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

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

Desbruyères, D., Alayse, A.M., Antoine, E., Barbier, G., Barriga, F., Biscoito, M., Briand, P., Brulport, J.-P., Comtet, T., Cornec, L., Crassous, P., Dando, P., Fabri, M.C., Felbeck, H., Lallier, F., Fiala-Médioni, A., Gonçalves, J., Menard, F., Kerdoncuff, J., Patching, J., Saldanha, L. & Sarradin, P.M. (1994) New information on the ecology of deep-sea vent communities in the Azores Triple Junction Area: preliminary results of the Diva 2 cruise (May 31–July 4, 1994.

InterRidge News, 3 (2), 18–19.

Desbruyères, D., Biscoito, M., Caprais, J.C., Comtet, T., Colaço, A., Crassous, P., Fouquet, Y., Khripounoff, A., Le Bris, N., Olu, K., Riso, R., Sarradin, P.M. & Vangriesheim, A. (2001) Variations in deep-sea hydrothermal vent communities on the Mid-Atlantic Ridge when approaching the Azores plateau. *Deep-Sea Research I*, 48, 1325–1346.

Desbruyères, D. & Ségonzac, M. (1997) *Handbook of deep-sea hydrothermal vent fauna.* Éditions Ifremer, 280 pp.

Fouquet, Y., Charlou, J.L., Costa, I., Donval, J.P., Radford-Knoery, J., Pellé, H., Ondréas, H., Lourenço, N., Ségonzac, M. & Tivey, M.K. (1994) A detailed study of the Lucky Strike hydrothermal vent site and discovery of a new hydrothermal site: Menez Gwen; Preliminary results of the Diva 1 cruise (2–29 May). *InterRidge News*, 3 (2), 14–17.

Fouquet, Y., Ondréas, H., Charlou, J.L., Donval, J.P., Radford-Knoery, J., Costa, I Lourenço, N., & Tivey, M.K. (1995) Atlantic lava lakes and hot vents. *Nature*, 377, 201.

Gamô, S. (1983) Some species of abyssal asellote isopods (Crustacea) from east of the Japan Trench, with the descriptions of *Janirella* (*Janirella*) *aculeata* sp. nov., *J.* (*Parajanirella*) *sedecimtuberculata* sp. nov., and *Aryballurops japonica* gen. et sp. nov. *Science Reports of the Yokohama National University II*, 30, 1–18.

Harrison, K. (1988) Deep-sea Asellota (Crustacea: Isopoda) of the Rockall Trough: preliminary faunal analysis. *Ophelia*, 28, 169–182.

Kussakin, O.G. (1988) *Marine and brackishwater likefooted Crustacea (Isopoda) from the Cold and Temperate Waters of the Northern Hemisphere. Suborder Asellota*. Part 1. Families Janiridae, Santidae, Dendrotionidae, Munnidae, Paramunnidae, Haplomunnidae, Mesosignidae, Haploniscidae, Mictosomatidae, Ischnomesidae. Vol. 3. In Series *`Opredeliteli po Faune SSSR, Izdavaemye Zoologicheskim Institutom Academii Nauk SSSR'*, 152,. Izdatel'stvo Nauka: Leningrad, 500 pp. [In Russian.]

Langmuir, C., Humphris, S., Forniari, D., Van Dover, C., Von Damm, K., Tivey, M.K., Colodner, D., Charlou, J.-L., Desonie, D., Wilson, C., Fouquet, Y., Klinkhammer, G. & Bougault, H. (1997) Hydrothermal vents near a mantle hot spot: the Lucky Strike vent field at 37ª N on the Mid-Atlantic Ridge. *Earth and Planetary Science Letters*, 148, 69–91.

Lo Bianco, S. (1903) Le pesche abissali eseguite da F. A. Krupp col Yatch Puritan nelle adiacenze di Capri ed in altre località del Mediterraneo. *Mettheilungen aus der Zoologischen Station zu Neapal zugleich ein Repertorium fur Mittelmeerkunde*, 16, 109–279.

Menzies, R.J. (1962) *Reports of the Lund University Chile Expedition 1948–49, 42. The Zoogeography, Ecology, and Systematics of the Chilean Marine Isopods*. (Lunds Universitets Årsskrifter 57 (11), Kungliga Fysiografiska Sällskapets Handlingar 72 (11)) C.E.K. Gleerup, Lund. 162 pp.

Poore, G.C.B., Just, J. & Cohen, B.F. (1994) Composition and diversity of Crustacea Isopoda of the southeastern Australian continental slope. *Deep-Sea Research*, 41(4), 677–693.

Richardson, H. (1905) A monograph on the isopods of North America. *Bulletin of the United States National Museum*, 54, 1–717.

Richardson, H. (1908) Some new Isopoda of the superfamily Aselloidea from the Atlantic Coast of North America. *Proceedings of the United States National Museum*, 35, 71–86.

Roman, M.-L. & Dalens, H. (1999) Ordre des isopodes (Épicarides exclus) (Isopoda Latreille, 1817). *In*: Forest J. (Ed.) *Crustacés Péracarides* [Grassé P.-P. (Series Ed), *Traité de Zoologie*, Tome VII. Fascicule IIIA, Mémoires de l'Institut Océanographique, Monaco, 19], Chapt. 7, pp. 177–278.

Rowe, G.T. (2003) Deepwater Program: Northern Gulf of Mexico continental slope habitats and benthic ecology (DGoMB), U. S. Dept. of the Interior, Minerals Management Service Contract No. 1435-01-99-CT-30991. Texas A&M University, Galveston, Texas. Available from http://www.gerg.tamu.edu/menu_fieldProgram/DGoMB/dgomb.htm (accessed 26 September 2003).

Saito, N., Itani, G. & Nunomura, N. (2000) A preliminary check list of isopod crustaceans in Japan. *Bulletin of the Toyama Science Museum*, 23, 11–107.

Thistle, D. & Wilson, G.D.F. (1987) A hydrodynamically modified, abyssal isopod fauna. *Deep-Sea Research*, 34, 73–87.

Thistle, D. & Wilson, G.D.F. (1996) Is the HEBBLE isopod fauna hydrodynamically modified? A second test. *Deep-Sea Research I*, 43 (4), 545–554.

Van Dover, C. L., Desbruyères, D., Ségonzac, M., Comtet, T., Saldanha, L., Fiala-Médioni, A. & Langmuir, C. (1996) Biology of the Lucky Strike hydrothermal field. *Deep-Sea Research*, 43 (9), 1509–1529.

Wägele, J.-W. (1989) Evolution und phylogenetisches System der Isopoda. Stand der Forschung und neue Erkenntnisse. *Zoologica*, 140, 1–262.

Wilson, G. (1976) The systematics and evolution of *Haplomunna* and its relatives (Isopoda, Haplomunnidae, new family). *Journal of Natural History*, 10, 569–580.

Wilson G.D.F. (1987) The road to the Janiroidea: the comparative morphology and evolution of the asellote isopods. *Zeitschrift für zoologische Systematik und Evolutionsforschung*, 25, 257–280.

Wilson, G. (1990) *Biological evaluation of a preservational reserve area ("BEPRA I"): Cruise report and interim report on laboratory analysis.* Cruise Report prepared under National Oceanic and Atmospheric Administration contract number 50-DSNC-9-00108. La Jolla, California. Scripps Institution of Oceanography, Reference 90–37, 34 pp.

Wilson, G.D.F. (1996) Of uropods and isopod crustacean trees: a comparison of 'groundpattern' and cladistic methods. *Vie et Milieu*, 46 (2), 139–153.

Wilson, G. & Hessler, R. (1974) Some unusual Paraselloidea (Isopoda, Asellota) from the deep benthos of the Atlantic. *Crustaceana*, 27 (1), 47–67.

Wilson, G., & Hessler, R. (1987) The effects of manganese nodule test mining on the benthic fauna in the North Equatorial Pacific. *In*: Spiess, F.N., Hessler, R.R., Wilson, G. & Weydert, M. (Eds.) *Environmental Effects of Deep-Sea Dredging*, Final Report to the National Oceanic and Atmospheric Administration on contract NA83-SAC-00659. La Jolla, California, Scripps Institution of Oceanography Reference 87(5), pp. 24–86.

Wolff, T. (1962) The systematics and biology of bathyal and abyssal Isopoda Asellota. *Galathea Report (Scientific Results of The Danish Deep-Sea Expedition Round the World 1950–52)*, 6, 1–320.