Review of the hydrothermal vent shrimp genus *Mirocaris*,
redescription of *M. fortunata*
and reassessment of the taxonomic status of the family
Alvinocarididae (Crustacea: Decapoda: Caridea)

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Abstract: The hydrothermal vent shrimp genus *Mirocaris* is reviewed. Morphological comparison between the two nominal species in the genus, *M. fortunata* and *M. keldyshi*, was made based on the re-examination of the holotype and paratypes of *Mirocaris fortunata* and the paratypes of *M. keldyshi*. Samples newly collected from various sites on the Mid-Atlantic Ridge were also examined. The validity of the genus *Mirocaris* has been confirmed. However, our study has revealed that the supposed morphological characters distinguishing *M. fortunata* and *M. keldyshi* do not provide significant taxonomic differences and further comparison failed to detect morphological differences between the two taxa. Thus *M. keldyshi* is synonymized with *M.fortunata*, and so there is only one single species in the genus *Mirocaris*. This supports the suggestion by Shank et al. (1999), based on a molecular study, that the two taxa might be conspecific. A redescription of *M. fortunata* is provided to better establish the morphology of the species. The clarification led us to improve the morphological descriptions of the caridean species associated with vent or seep environments and to reassess the relationships among *Mirocaris* and the other shrimp taxa in the superfamily Bresilioidea. The generic diagnosis of *Mirocaris* is emended. Because a number of presumably apomorphic characters are shared by *Mirocaris* and other alvinocaridid genera, the genus *Mirocaris* is now assigned to the family Alvinocarididae. The generic diagnosis of *Mirocaris* is synonymized with the Alvinocarididae and the diagnosis of this family is emended.

Résumé: Révision du genre *Mirocaris*, crevette des sources hydrothermales océaniques, redescription de *M. fortunata* et réexamen du statut de la famille des Alvinocarididae. Le genre *Mirocaris*, créé pour des crevettes hydrothermales, est révisé. Une étude morphologique comparative des deux espèces *Mirocaris fortunata* et *M. keldyshi*, basée sur le réexamen des holotypes et paratypes et sur l’étude de nombreux échantillons provenant de divers sites hydrothermaux de la dorsale médio-atlantique, a été effectuée. La validité du genre *Mirocaris* est confirmée. Il apparaît que les caractères qui distinguent *M. keldyshi* et *M. fortunata* ne sont pas des critères taxonomiques suffisants et une étude morphologique plus poussée n’a pas révélé de différences morphologiques entre les deux taxa. Ceci est en accord avec l’interprétation de Shank et al. (1999) qui, à la suite d’une étude moléculaire, suggèrent la synonymie des deux espèces. Une redescription détaillée de *M. fortunata* est donnée et les relations entre *Mirocaris* et les autres genres de la superfamille des Bresilioidea sont discutées. La diagnose générique de *Mirocaris* est modifiée. Comme plusieurs caractères apomorphes...
TAXONOMY OF MIROCARIS

The genus *Mirocaris* was established by Vereshchaka (1997) to accommodate *M. keldyshi* Vereshchaka, 1997 (type species of the genus), described as a new species from hydrothermal vent site in TAG (Trans-Atlantic Geotraverse) on the Mid-Atlantic Ridge, and *Chorocaris fortunata* Martin & Christiansen, 1995, described from specimens collected at several vent sites along the Mid-Atlantic Ridge near the Azores. Vereshchaka (1997) also established a new monotypic family Mirocarididae to accommodate *Mirocaris*, recognizing four families within the superfamily Bresilioidae Caiman, 1896, i.e. Bresiliidae Caiman, 1896, Disciadidae Rathbun, 1902, Alvinocarididae Christoffersen, 1986 and Mirocarididae. Later, Shank et al. (1999), using the mitochondrial cytochrome c oxydase subunit I (COI), analyzed the molecular phylogenetic relationships among the shrimp species associated with hydrothermal vents and cold brine or hydrocarbon seeps, including: - four species of *Alvinocaris* (*A. lusca* Williams & Chace, 1982, *A. markensis* Williams, 1988, *A. stactophila* Williams, 1988 and *A. sp.* from the Edison Sea Mount in the western Pacific), - two species of *Chorocaris* (*C. vandoverae* Martin & Hessler, 1990 and *C. chacei* (Williams & Rona, 1986)] - two nominal species of *Mirocaris*, [M. fortunata (Martin & Christiansen, 1995), and *M. keldyshi*], - *Opaepele loihi* Williams & Dobbs, 1995, - *Rimicaris exoculata* Williams & Rona, 1986 and - one unnamed species. This analysis indicated that (1) those species form a monophyletic assemblage; (2) a group including the two nominal species of *Mirocaris* and the unidentified species is sisterly related to a group containing the other taxa; and (3) *M. fortunata* and *M. keldyshi* might be conspecific.

In an attempt to reassess the specific status of *Mirocaris keldyshi*, we have re-examined the holotype and paratypes of *Mirocaris fortunata* and the paratypes of *M. keldyshi*. Supplemental samples from various sites of the Mid-Atlantic Ridge have also been examined. During this examination we found that several important morphological characters of *M. fortunata* were insufficiently reported in the original description of Martin & Christiansen (1995). The supposed differences used by Vereshchaka (1997) to distinguish *M. keldyshi* from *M. fortunata* have been critically examined and further comparison failed to detect any significant differences between the type materials of the two taxa. Based on our morphological data and on the molecular study of Shank et al. (1999), we thus conclude that *M. fortunata* and *M. keldyshi* are conspecific, the former name taking priority over the latter. The validity of the genus *Mirocaris* has been confirmed, as certain characters clearly distinguish *Mirocaris fortunata* not only from *Chorocaris*, but also from other related genera, such as *Alvinocaris, Opaeppele* and *Rimicaris*. Furthermore, it was found that the previous descriptions done by Martin & Christiansen (1995) and Vereshchaka (1997) omitted several important details possibly providing taxonomic or phylogenetic characters. Thus, we decided to provide a full redescription and illustration of *M. fortunata*, and to emend the generic diagnosis of *Mirocaris*. A comparison of our morphological information on *Mirocaris* with previous descriptions of other shrimp taxa associated with vent and seep environments, assigned to the Alvinocarididae by Vereshchaka (1997), has shown that the homology of particular structures of the mouthparts of those taxa had to be clarified. Lastly, the morphological redescription enables us to reassess the relationship between *Mirocaris* and the related genera more precisely. We recognize the Alvinocarididae as a distinct family. The genus *Mirocaris* is assigned to the Alvinocarididae, as *Mirocaris* shares a number of presumably apomorphic characters with the other alvinocarid genera. Thus the family Mirocarididae is synonymized with the family Alvinocarididae.

**Material and methods**

This study was made with the holotype and 46 paratypes of *Mirocaris fortunata* deposited in the Los Angeles County Museum of Natural History (LACM), and two paratypes of *Mirocaris keldyshi* in the collection of the Muséum national d'Histoire naturelle, Paris (MNHN). The type material of *C. fortunata* was collected during a series of dives on the American Lucky Strike Cruise (see Martin & Christiansen, 1995). The type material of *M. keldyshi* was collected during the British-Russian Program BRAVEX-94 (see Vereshchaka, 1997). Supplemental specimens of *M. fortunata* accumulated from MAR by the junior author are deposited in MNHN and the Natural History Museum and Institute, Chiba (CBM). The newly obtained specimens were all collected by using slurp gun.

For comparative purpose, the following species were examined:
Alvinocaris markensis Williams, 1988: MICROSMOKE (DS Nautilie), dive 8, 21.11.1995, Mid-Atlantic Ridge, Snake Pit hydrothermal vent field, Les Ruches site (23°22.90′N; 44°57.13′W), 3480 m, baited trap, 1 female CL 16.3 mm (MNHN-Na).

Chorocaris chacei (Williams & Rona, 1986): NOAA VENTS Program, RV Researcher, Mid-Atlantic Ridge, TAG Hydrothermal Field (26°08.3′N; 44°49.6′W), 3620-3650 m, 03.08.1985, dredge, 1 female CL 17.3 mm (holotype: National Museum of Natural History, Smithsonian Institution, USNM 228452).

Chorocaris vandoverae Martin & Hessler, 1990: DS Alvin, dive 1843, Alice springs vent field (18°12.599′N; 144°42.431′E), Mariana Back-Arc Basin, 3640 m, nets manipulated by mechanical arm of submersible, 04.05.1987, 1 female CL 13.2 mm (holotype USNM 243946).

Opaepele lohii Williams & Dobbs, 1995: DSRV Pisces V, dive #213, Hawaii, Loihi Seamount (18°55′N; 155°16′W), 980 m, 28.08.1992, baited trap, 2 males 6.8, 8.9 mm, 2 females 9.2, 9.4 mm (paratypes USNM 251449).

Rimicaris exoculata Williams & Rona, 1986: PICO (DS Nautilie), dive PL 1264, Rainbow (36°13.40′N; 33°54.07′W), Mid-Atlantic Ridge, 2285 m, 30.06.1998, slurp gun, 1 male CL 18.6 mm, 1 female 18.6 mm (CBMZ-C 6446); MICROSMOKE, dive PL 01, Snake Pit, site Elan, (23°22.20′N, 44°57.08′W), 3500 m, 14.11.1995, 6 juv. 7.3-8.8 mm (MNHN-Na).

Bresiliatriloba Caiman, 1896: data unknown, 1 female CL 3.3 mm (MNHN-Na 3474). This specimen is in poor condition. Morphological information on this species was supplemented by literature examination (Kemp, 1910).

Bresiliacorsicana Forest & Cals, 1977: RV Calypso, station SME 17561, Corsica Channel, Mediterranean, 450 m, 26.06.1961, dredge, 1 female (?) CL 3.2 mm (holotype; MNHN-Na 2777). The condition of the holotype is very poor; the original description given by Forest & Cals, 1977 is also examined.

Disciascf. exul Kemp, 1920: Yonara Strait, Yuyama Group, Ryukyu Islands, 15 m, 23.14.1998, SCUBA, coll. K. Nomura, 1 female CL 1.6 mm (CBMZ-C 5016). Morphological information on this species, as well as the other disciadid genera, was supplemented by literature examination (Kensley, 1983).

The abbreviation ovig. indicates ovigerous female(s). One measurement, postorbital carapace length (CL, distance from the level of posterior margin of the orbit to midpoint of the posterodorsal margin of the carapace, provides an indication of specimen size). The drawings were made with the aid of a drawing tube mounted on a Leica MZ8 stereomicroscope.
Figure 1. *Mirocaris fortunata* (Martin & Christiansen, 1995). Holotype, ovigerous female (CL 8.7 mm; LACM 1993-045.1). A. carapace and cephalic appendages, lateral; B. carapace, dorsal (setae omitted); C. detail of surface structure of submedian region of carapace, dorsal; D. abdomen, lateral; E. anterior part of carapace and cephalic appendages, dorsal (setae partially omitted; right antenna removed).

Figure 1. *Mirocaris fortunata* (Martin & Christiansen, 1995). Holotype, femelle ovigère (CL 8.7 mm ; LACM 1993-045.1). A. vue latérale de la carapace et des appendices céphaliques ; B. carapace, vue dorsale (sans les soies) ; C. détail de la structure superficielle de la région sub-médiane de la carapace, vue dorsale ; D. abdomen, vue de profil ; E. partie antérieure de la carapace et premiers appendices céphaliques, vue dorsale (soies partiellement représentées; antenne droite non représentée).
ventral surfaces not dentate; dorsal surface weakly convex, without sharp carina.

Carapace (Figs 1A, B, 5A, B) somewhat compressed laterally, with short transverse (vertical) rows of short setae on lateral parts, and scattered short setae particularly anteriorly (including rostrum) along midline; dorsal surface rounded in males and non-ovigerous females, broadly carinate in ovigerous females; general outline in lateral view faintly simious to weakly convex; in ovigerous females, submedian areas very shallowly depressed and ornamented with numerous longitudinal striae (Fig. 1B, C); orbital margin evenly rounded; antennal spine slightly directed mesially; pterygostomian angle not exceeding antennal spine; anterolateral margin between antennal spine and pterygostomian angle weakly concave; posterior submarginal groove shallow, rather inconspicuous.

Thoracic sternite with pair of slender submedian spines on seventh somite (reduced in ovigerous females); median spur on eighth thoracic somite (Fig. 4A) terminating in acute spine in males and non-spawning females, subacute or blunt spine in spawning females.

Abdomen (Fig. 1D) rounded dorsally in all somites. Pleura of anterior four somites all broadly rounded; on fifth somite, acute or subacute posteroventral tooth. Sixth somite 1.74-1.83 times longer than fifth somite, 1.40-1.43 times longer than proximal depth; posterolateral process short, terminating in small acute tooth; posteroventral corner produced, terminating in subacute point. First abdominal sternite with pair of rudimentary, slender submedian spines, similar spines better developed and more strongly curved mesially on second and third sternites, again less developed spines on fourth sternite (those submedian spines greatly reduced in spawning females); fifth sternite with distinct median keel terminating posteriorly in acute spine; sixth sternite flattened, thin, transparent, with small preanal spine.

Telson (Figs ID, 2C) 1.25-1.36 times longer than sixth abdominal somite, slightly tapering posteriorly, width between posterolateral corners 0.75-0.80 of greatest anterior width; dorsal surface with very slight trace of median longitudinal concavity in posterior 0.75-0.80, bearing row of 7-9 spines (excluding spines at posterolateral corner) on either side along posterior 0.80 length; posterior margin (Fig. 2D) broadly convex, occasionally with shallow median emargination, bearing 12-19 spines in total; 1-3 spines at posterolateral corner shorter than mesial spines, simple, while remaining mesial spines elongate, bearing minute marginal setules.

Eye-stalks (Fig. 1E) rather large but degenerated, broadly fused mesially without trace of median separation (in holotype left eye abnormally smaller than right eye); cornea unfaceted, poorly organized retinal pigment discernible inside, through cuticle; no distinct spine or tubercle on anterior surface of eye.

Antennular peduncles (Fig. 1A, E) stout, slightly flattened dorsoventrally. Basal segment with distal width nearly half of its length; dorsal surface fairly inflated in distal part, but remaining proximal part depressed below, continuous with deep groove separating basal segment and stylocerite; distal margin slightly oblique in dorsal view; distotolateral tooth well developed, acute, overlapped by stylocerite, exceeding midlength of penultimate segment, distomesial tooth much shorter than distotolateral tooth, usually blunt; stylocerite strong, tapering to slender point reaching or overreaching level of midlength of penultimate peduncular segment. Penultimate segment with scattered short setae on dorsal surface; distomesial tooth as large as corresponding tooth on basal segment, terminating acutely. Ultimate segment slightly longer than wide. Flagella rather stout, unequal, inserted side by side on oblique terminal margin of distal segment; flagellum shorter than mesial, aesthetasc-bearing portion occupying 0.80-0.85 of total length of flagellum, article each with tufts of aesthetasc on mesial face; mesial flagellum with annuli much denser than those on lateral flagellum.

Antenna (Figs 1A, E, 2B) with basiscerite stout, bearing blunt distolateral dorsal projection and acute distolateral ventral tooth exceeding former projection. Carapocerite (fifth segment of antennal peduncle) very stout, cylindrical, exceeding midlength of scaphocerite. Scaphocerite broadly oval with greatest width across level of midlength; lateral margin very slightly convex to simious, terminating in short, stout tooth separated by narrow incision and considerably exceeded by rounded blade; mesial margin noticeably convex; dorsal surface with distinct median ridge accompanied by deep groove. Flagellum stouter than antennular flagella, slightly longer than body, annuli dense.

Mandible (Fig. 2E, F) with incisor process broad, somewhat tapering distally, bearing 6-8 unequal, acute or subacute teeth on mesial margin (distalmost tooth distinctly separated from remaining teeth); molar process slender, unarmed, extending as far as incisor process; basal article of palp with deep notch on mesial surface proximal to midlength, distal article stout, shorter than basal article, bearing scattered plumose setae with variable length.

Maxillule (Fig. 2G) with coxal endite slightly tapering distomesially, with dense setae on mesial margin; basal endite broad, mesial margin with 2 rows of small spines (spines more numerous and denser in internal row than in external row); external surface of basal endite with submarginal row of setae and few small spines adjacent to mesial margin; palp (Figs 2G, 4B) somewhat curved, slightly bilobed distally, bearing 2 setae; outer setae short, simple, arising subterminally from ventral surface slightly proximal to base of somewhat produced outer lobule (in holotype, outer lobule broken off); inner lobule small, bearing a long plumose seta.
Maxilla (Fig. 4C) with coxal endite composed of single lobe separated from basial endite by deep incision and following suture; basial endite consisting of 2 lobes, proximal lobe with rounded mesial margin, distal lobe subtriangular, with submarginal row of setae on external surface; palp slender, sinuously curved, slightly exceeding distal lobe in length. Scaphognathite greatly expanded, anterior lobe subovate, with densely setose margin bearing longest setae along distomesial sector, posterior lobe (broken off in holotype) elongate subtriangular, fringed on mesial margin with very long setae becoming further longer posteriorly.

First maxilliped (Fig. 2H) with coxal endite somewhat thickened, with short setae on external surface and longer setae on mesial face; basial endite moderately broad, strongly convex and densely setose on external surface, mesial margin convex to concave, densely fringed with setae; palp (not visible in ventral view) slender, weakly curved mesially, bearing short apical bristles; exopod greatly expanded, 1.40-2.10 times as long as broad, broadly longer than propodus, slightly curved, tapering to rounded apex, bearing numerous short setae on mesial to distal margins; exopod absent; epipod subtriangular, with slender rudiment of podobranch reaching midlength to distal margin of basis-ischium fused segment and occasionally bearing 1 or 2 small papillae possibly representing rudimentary filaments.

Second maxilliped (Fig. 2I) somewhat pediform, 6-segmented; coxa somewhat expanded mesially, with numerous setae on mesial face; basis and ischium completely fused, this fused segment longest and broadest, with row of setae on mesial and lateral margins; merus about half length of basis-ischium fused segment, with long setae on lateral face; carpus short, with long plumose setae on distal surface, proximomesial margin weakly to somewhat produced on external surface, partially covering basal part of propodus; propodus obliquely articulated to dactylus, with row of setae on mesial margin; dactylus longer than propodus, slightly curved, tapering to rounded apex, bearing numerous short setae on mesial to distal margins; exopod absent; epipod subtriangular, with slender rudiment of podobranch reaching midlength to distal margin of basis-ischium fused segment and occasionally bearing 1 or 2 small papillae possibly representing rudimentary filaments.

Third maxilliped (Fig. 4D, E) 4-segmented (broken in holotype), slightly overreaching anterior margin of scaphocerite. Coxa stout; lateral surface (Fig. 4E) with prominent slender process directed laterally; epipod (Fig. 4F) with 3-5 curved bristles distally. Antepenultimate segment (basis-ischium-merus fused segment) somewhat flattened dorsoventrally, strongly sinuously curved in dorsal view, setose, with slender spine at distolateral ventral corner. Penultimate segment (= carpus) weakly curved ventrally, with dense setae on mesial face. Ultimate segment slightly curved, gradually tapering distally and terminating in small corneous spine, with scattered long setae on lateral surface and obliquely transverse tracts of short stiff setae; 2-4 spinules adjacent to base of terminal spine.

First pereopod (Figs 3A, 4G, H) short, stout, slightly overreaching (when extended) distal margin of scaphocerite at most, with chela and carpus oriented toward midline. Articulation between ischium and merus strongly oblique. Ischium and merus with scattered plumose setae on lateral and ventral surfaces. Merus somewhat compressed laterally and slightly tapering distally, ventral surface slightly concave for reception of flexed carpus. Carpus (Figs 3A, 4I) shorter than merus, somewhat inflated, irregularly funnel-shaped, dorsal surface bent at right angle near tapered proximal end articulating with merus; distolateral margin slightly produced medially; distomesial margin more strongly produced, forming broadly triangular lobe; mesial face as in generic diagnosis. Palm short, strongly inflated, with patch of minute setae on mesial surface ventrally. Fingers curved and closing without hiatus; internal surfaces deeply concave; external surface of each finger convex; cutting edges uniformly offset, each armed with row of uniform, minute, erect, closely set tooth; cutting edge of fixed finger bordered with narrow, thin corneous plate including tip; internal surface with submarginal row of sparse short setae along cutting edge; external surface of fixed finger with some submarginal rows of longer setae. Dactylus 1.20-2.80 times longer than palm, uniformly narrowed distally, considerably flattened in distal 0.50-0.75; internal surface with submarginal row of short, sparse setae along cutting edge; external surface with some submarginal rows of longer setae along cutting edge in distal half.

Second pereopod (Fig. 3B) slightly slender than other pereopods, reaching distal margin of scaphocerite at most. Articulation between ischium and merus oblique. Ischium

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**Figure 2. Mirocaris fortunata.** Holotype. A. anterior part of carapace and eye, right side (setae omitted); B. part of right antenna, dorsal (setae omitted); C. telson and left uropod, dorsal (setae omitted); D. posterior margin of telson, dorsal; E. right mandible, internal; F. same, external; G. right maxillule, external (outer distal lobe of palp broken off); H. right first maxilliped, external; inset, palp, internal; I. right second maxilliped, external; upper inset, dactylus and propodus, mesial; lower inset, epipod and podobranch, internal.

**Figure 2. Mirocaris fortunata.** Holotype. A. partie antérieure droite de la carapace et œil (soies non représentées). B. une partie de l’antenne droite, vue dorsale (soies non représentées) ; C. telson et uropode gauche, vue dorsale (soies non représentées) ; D. bord postérieur du telson, vue dorsale ; E. mandibule droite, face interne ; F. idem, face externe ; G. maxillule droite, face externe (lobe distal du palpe absent) ; H. premier maxillipède droit, face externe ; en haut à droite, palpe, face interne ; I. deuxième maxillipède droit, face externe ; en haut à droite, dactyle et propodus, vue méritale ; en bas à gauche, épipodite et podobranchie, vue interne.
Figure 3. Mirocaris fortunata. Holotype. A. right first pereopod, lateral; B. right second pereopod, lateral; C. chela of right second pereopod, external; D. same, tips of dactylus and fixed finger (setae partially omitted); E. left third pereopod, lateral; F. dactylus of left third pereopod, lateral; G. left fourth pereopod, lateral; H. left fifth pereopod, lateral.

Figure 3. Mirocaris fortunata. Holotype. A. premier péréiopode droit, vue latérale ; B. deuxième péréiopode droit, vue latérale ; C. pince du deuxième péréiopode droit, vue externe ; D. idem, extrémités du dactyle et du doigt fixe (soies partiellement représentées) ; E. troisième péréiopode gauche, vue latérale ; F. dactyle du troisième péréiopode gauche, vue latérale ; G. quatrième péréiopode gauche, vue latérale ; H. cinquième péréiopode gauche, vue latérale.
usually with one movable spine strongly pressed on lateral surface. Merus 5.10-5.30 times as long as maximal height, with sparse long setae on dorsal surface and row of shorter setae, present also on ischium on ventral surface. Carpus with sparse setae on dorsal and lateral surfaces. Chela (Fig. 3C) 1.10-1.20 times longer than carpus, slightly broadened distally, 3.30-3.70 times longer than greatest width; fingers longer than palm, each terminating in small conoform spine (Fig. 3D), crossing at tip; external surfaces slightly depressed toward cutting edges, with scattered minute setae and longer setae on distal part of fingers; cutting edges each with row of minute conoform spines at least in distal half.

Third to fifth pereopods similar in structure, but increasing in length from anterior pair to posterior pair. Third pereopod (Figs 3E, 5C) at most overreaching distal margin of scaphocerite by length of dactylus and full length of propodus, somewhat compressed laterally; ischium with 1 or 2 spines on lateral surface ventrally; merus 4.50-5.70 times longer than greatest height, with sparse setae; carpus-propodus combined slightly shorter than merus-ischium combined; carpus 0.75-0.80 times as long as propodus; propodus (Fig. 4I) increasing slightly in depth toward distal end, with 2 rows of spinules on ventral surface (spinules of mesial row fewer than those of lateral row); dactylus (Fig. 3F) stout, 0.22-0.37 times as long as propodus, unguis rather clearly demarcated, sometimes elongate, ventral margin with 3-4 accessory spinules becoming larger distally. Fourth pereopod (Fig. 3G) at most overreaching distal margin of scaphocerite by length of dactylus and half of propodus; ischium with 0-1 spine; carpus-propodus combined subequal in length to merus-ischium combined. Fifth pereopod (Fig. 3H) at most overreaching distal margin of scaphocerite by length of dactylus and half of propodus; ischium unarmed; carpus-propodus combined longer than merus-ischium combined; ventral surface of propodus (Fig. 4K) with double or triple row of setulose spines on lateral side and single row of simple spines on mesial side.

Branchial formula summarized in Table 1. Pleurobranchs on fourth to eighth thoracic somites asymmetrically Y-branched, noticeably increasing in length posteriorly, apices directed forward. Arthrobranchs on third to seventh thoracic somites moderately developed, nearly symmetrically U-branched, but last one on seventh somite distinctly smaller than preceding ones. Epipods on first to fourth pereopods strap-like, similar to that on third maxilliped in shape. Setobranchs on first to fifth pereopods corresponding to epipods on third maxilliped to fourth pereopod respectively.

Endopod of first pleopod in males (Fig. 5E) with row of sparse plumose setae on both margins, terminating distomesially in subtriangular lobe bearing 1 apical and 2-3 subdistal bristles, all bristles essentially directed to midline of body; in female, endopod (Fig. 5D) uniformly tapering with margins fringed sparsely with plumose setae.

In males, second to fourth pleopods bearing greatly reduced, rudimentary appendix interna (cf. Fig. 5F, G) and fifth pleopods bearing normally developed appendix interna bearing terminal cluster of cincinnuli; in females, appendix interna absent on second to fourth pleopods; fifth pleopod with normally developed appendix interna. Appendix masculina on second pleopod (Fig. 5F, G) arising from proximal 0.30 of mesial margin of endopod, exceeding midlength of endopod, bearing 8-10 long bristles distally.

Uropod (Fig. 2C) with both rami elongate oval, exceeding posterior margin of telson; endopod shorter and narrower than exopod; exopod with straight lateral margin terminating in tiny acuminate tooth; long movable spine arising just mesial to distolateral tooth; suture distinct, sinuous.

**Variation**

In the ovigerous females, the submedian regions of the carapace are very shallowly depressed, and the surface of the integument of this area is ornamented with irregular pattern of thin longitudinal striae; the midline of the carapace forms a broad, rounded carina (Figs 1B, 5B). In the males and non-ovigerous females such a modification is not found (Fig. 5A). The reason of this peculiar modification remains unknown.

There seem to be two forms of ambulatory legs in the specimens examined, but careful observation of abundant samples has revealed the presence of intermediate forms between the two extremes as shown in Figs 3E and 5C. Moreover, we have been unable to associate the difference with any other morphological characters, and the occurrence of various forms of ambulatory legs, even in the same samples, dissuaded us from considering this feature.

The holotype of *Chorocaris fortunata* is an aberrant specimen. The carapace is somewhat deformed, and thus the submedian depressed areas on the carapace are asymmetrically formed, and the posterodorsal margin of the carapace is also asymmetrical (Fig. 1B), as illustrated by Martin & Christiansen (1995). The eyes are dissimilar with the left distinctly smaller than the right. This asymmetry is presumably due to injury and regeneration of the left eye.

**Distribution**

Known from hydrothermal vent sites along the Mid-Atlantic Ridge between 38°N and 14°N: Menez Gwen, 37°50'N-31°31'W, 850 m; Lucky Strike, 37°17'N-32°16'W, 1700 m (Martin & Christiansen, 1995; Shank et al., 1999; present study); Rainbow, 36°13'N-33°54'W, 2289 m, (present study); Broken Spur, 29°10'N-43°10'W, 3000 m, (Martin & Christiansen, 1995; Shank et al., 1999); TAG, 26°08'N-44°49'W, 3650 m (Vereshchaka, 1997; Shank et al., 1999); Snake Pit, 23°22'N-44°57'W, 3480 m (unpublished data: the junior author observed once a juvenile of *M. fortunata*); Logatchev, 14°45'N-44°58'W, 3008 m (Shank et al., 1999; present study).
Discussion

Specific status of Mirocaris keldyshi

Vereshchaka (1997) cited the following seven characters in distinguishing *M. keldyshi* from *M. fortunata,* although he did not examine the type specimens of the latter taxon: (1) structure of two distal setae on palpal of maxillule (setae simple in *M. fortunata*, plumose in *M. keldyshi*); (2) proportion of exopod of first maxilliped (3 times as long as broad in *M. fortunata*, 2 times in *M. keldyshi*); (3) on second maxilliped, relative length of podobranch (attributed to an exopod by Vereshchaka, see below) and epipod (podobranch 1.0 times as long as epipod in *M. fortunata*, 1.5-2.0 times in *M. keldyshi*); (4) carpus and merus of second maxilliped fused in *M. fortunata,* but separated in *M. keldyshi*; (5) patch of setae on ventral surface of palm of first pereopod (absent in *M. fortunata,* present in *M. keldyshi*); (6) armature of ischium of second pereopod (a movable spine absent in *M. fortunata,* present in *M. keldyshi*); (7) number of setulose spines on posterior margin of telson (10 spines in *M. fortunata* vs. 12-18 in *M. keldyshi*).

We have examined these differences critically, and found that none provides any taxonomic significance as discussed below. The morphological variation of the mouthparts was checked using the seven specimens from Logatchev collected during MICROSMOKE Cruise (see “Material examined”).

First character. As described above, the apical seta on the inner lobe of the maxillule palp is actually plumose in the holotype of *M. fortunata,* as well as in the holotype of *M. keldyshi* (see Vereshchaka, 1997, fig. 2B) and in other specimens we examined. However, the subterminal seta on the outer lobe of the maxillule palp is simple in our specimens. Vereshchaka’s description of *M. keldyshi* is not consistent with the illustration which is exact (Vereshchaka, 1997, fig. 2B), because the outer seta illustrated as simple is considered as plumose in the text.

Second character. According to the illustration of the first maxilliped by Vereshchaka (1997, fig. 3A), the length and width of the exopod represent the distance between anterior margin and base of the endopod, and the greatest width, respectively. However, according to the figure by Martin & Christiansen (1995, fig. 2g), the ratio should be 1.5 for *M. fortunata,* a value conformable to the holotype of *M. keldyshi*.

Further examination of other specimens (including the paratypes of *M. keldyshi*) has shown that the proportional ratio of the exopod is quite variable, ranging from 1.40 to 2.10, and that the shape of the entire exopod is easily affected by the preservation conditions.

Third character. According to the illustrations by Vereshchaka (1997, fig. 3B) and Martin & Christiansen (1995, fig. 2i, j), the length of the podobranch (exopod, according to Vereshchaka) is similar in the holotypes of *M. keldyshi* and *M. fortunata,* although the epipod appears smaller in the holotype of *M. keldyshi* than in the holotype of *M. fortunata.* The difference in the ratio given by Vereshchaka (1997) does not reflect the length of the podobranch, but actually the size of the epipod. The epipod is soft and fragile, and thus easily affected by preservation in ethanol. In fact, we have found that the size of the epipod in the examined specimens varies individually and thus this character does not provide any taxonomic significance.

Fourth character. Interpretation on the segmentation of the second maxilliped by Vereshchaka (1997) is confusing: the second maxilliped is described as five-segmented, in the familial description, but the illustration (Vereshchaka, 1997, fig. 3B) shows a second maxilliped composed of at least six segments. In all the specimens examined, we observed that the second maxilliped is six-segmented with carpus and merus clearly separated. The pattern of segmentation is not consistent with Vereshchaka’s figure where the coxa is not illustrated and the carpus appears subdivided, although Vereshchaka confirmed it is not (personal communication). In the specimens we examined (Fig. 21), the carpus is not subdivided and the six-segmented condition of this appendage is due to a complete fusion of the ischium and basis.

Fifth character. It has been found that there is actually an oval patch of short setae on the ventromesial face of the palm of the first pereopod in the type specimens of *M. fortunata* and other examined specimens. This patch of...
Figure 5. Mirocaris fortunata. A. female from Lucky Strike (as in Fig. 4); B. paratype, ovigerous female (CL 8.1 mm; LACM 1993.045.3); C. paratype, ovigerous female (CL 5.7 mm; LACM 1993.045.3); E-G, male from Logatchev (DIVERSE Expedition, PL 3668) (CL 5.4 mm; MNHN-Na 14144). A, B. carapace, dorsal (setae omitted in both); limits of submedian regions indicated in B, but striae omitted; C. left third pereopod, lateral; D, E. endopod of left first pleopod, ventral; F. endopod of left second pleopod, ventral; G. appendix masculina on left second pleopod, mesial.

Figure 5. *Mirocaris fortunata*. A.-D. femelle de Lucky Strike (comme Fig. 4) ; B. paratype, femelle ovigère (CL 8.1 mm ; LACM 1993.045.3) ; C. paratype, femelle ovigère (CL 5.7 mm ; LACM 1993.045.3) ; E.-G. mâle de Logatchev (DIVERSE Expedition, PL 3668) (CL 5.4 mm ; MNHN-Na). A, B. carapace, vue dorsale (soies non représentées) ; limites des zones sub-médianes indiquées en B, mais stries non représentées ; C. troisième péréiopode gauche, vue latérale ; D, E. vue ventrale des endopodites du premier pléopode droit, vue ventrale ; F. endopodite du deuxième pléopode gauche, vue ventrale ; G. appendix masculina du deuxième pléopode gauche, vue mésiale.
setae probably represents a grooming apparatus together with the setal assemblage on the carpus. This structure may be easily overlooked without a careful observation.

Sixth character. Our examination has shown that the ischium of the second pereopod is armed with a movable spine ventrolaterally in the type specimens of *M. fortunata* which was not mentioned or illustrated in the original description by Martin & Christiansen (1995). This spine may be easily overlooked, as it is usually pressed into a shallow cavity on the ischium.

Seventh character. Martin & Christiansen (1995) illustrated 10 spines on the posterior margin of telson of *M. fortunata* holotype, although the authors did not specify the number of spines in the descriptive text. Our examination has shown that there are 13 spines in the holotype of *M. fortunata*, and 12-19 spines in the paratypes. Martin & Christiansen failed to illustrate the shorter spines at the postero-lateral corners of the telson (one on the left and two on the right). Thus there is no difference in this character between *M. fortunata* and *M. keldyshi*.

Our morphological examination of the two taxa reveals that the differences cited by Vereshchaka (1997) separating *M. fortunata* and *M. keldyshi* do not provide any taxonomic significance. We could not find any other significant differences during our examination of the type and other materials. Our morphological analysis strongly indicates that *M. fortunata* and *M. keldyshi* are conspecific. Therefore, *M. keldyshi* is considered to be a junior synonym of *M. fortunata*. Our conclusion supports the results of the phylogenetic analysis using the mitochondrial COI gene (Shank et al., 1999).

Shank et al. (1999) used three of the seven characters cited by Vereshchaka (1997) for making preliminary distinction between *M. fortunata* and *M. keldyshi*: number of telson spines, presence or absence of movable spines on ischium of second pereopod and presence or absence of an oval patch on palm of first pereopod. As discussed above, however, there are no real differences in these characters in the specimens examined by us. The specimens used by Shank et al. (1999) have not been available for study. It is necessary to reexamine those specimens in order to make clear whether the differences are true.

Gebruk et al. (2000) also suggested that *M. fortunata* and *M. keldyshi* were distinguishable by morphology and color in life, but they did not comment any further.

**Homology of particular structures of mouthparts in alvinocaridid shrimps**

The homology of the following morphological structures of shrimp species from vent and seep environments, assigned to the Bresiliidae or Alvinocarididae, is here clarified.

The presence of an exopod on the second maxilliped in the species of *Alvinocaris*, *Opaepele*, *Mirocaris* and *Rimicaris*, for example, was reported by several authors (Williams & Chace, 1982; Williams, 1988; Kikuchi & Ohta, 1995; Williams & Dobbs, 1995; Vereshchaka, 1996, 1997; Kikuchi & Hashimoto, 2000). However, Segonzac et al. (1993) pointed out that this "exopod" is not a true exopod, but a rudimentary podobranch, since it arises in fact from the basal part of the epipod, not from the basis.

The coxal (or proximal) endite of the maxilla was described as divided into two lobes in different species by several authors (Williams & Chace, 1982; Williams & Rona, 1986; Williams, 1988; Martin & Hessler, 1990; Williams & Dobbs, 1995; Kikuchi & Ohta, 1995; Vereshchaka, 1996, 1997; Kikuchi & Hashimoto, 2000). However, our study demonstrated that the proximal lobe and the two distal lobes are primarily separated from each other by a deep notch followed by a suture in *Alvinocaris markensis*, *Chorocaris chacei*, *C. vandoverae*, *Mirocaris fortunata* and *Rimicaris exoculata*. Therefore, we consider the proximal lobe as a one-lobed coxal endite, and the two distal lobes as basial endite, a usual structure in caridean species (Komai, 1994).

The third maxilliped has been reported as bearing an exopod in the species of *Alvinocaris*, *Chorocaris*, *Mirocaris* and *Rimicaris* (Williams & Chace, 1982; Williams & Rona, 1986; Williams, 1988; Martin & Hessler, 1990; Kikuchi & Ohta, 1995; Vereshchaka, 1996, 1997; Kikuchi & Hashimoto, 2000). However, our study demonstrated that the short projection arising from the coxo-basal endite in *Alvinocaris, Chorocaris, Mirocaris* and *Rimicaris* was not a true exopod, but a rudimentary podobranch. This projection may be homologous to the coxal lateral process reported in other caridean taxa (Komai, 1994). In taxa

**Table 1. Mirocaris fortunata** (Martin & Christiansen, 1995). Branchial formula; epipods and corresponding setobranchs, as well as exopods, are also indicated (r: rudimentary).

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associated to vent and seep environments, the projection is slender and laterally or ventrally directed (Fig. 4E), while in other carideans, the coxal lateral process, if present, is often semi-oval in shape and flattened dorsoventrally (Komai, 1994).

Invalidity of the family Mirocarididae and status of the genus Mirocaris

The recognition of the Bresiliidae and Disciadidae as separate families have been long accepted (e.g. Holthuis, 1955; Forest, 1977). Following the discovery of the bizarre polychelate shrimp *Pseudocheles* Chace & Brown, 1978, the family Disciadidae was synonymized with the Bresiliidae by Chace & Brown (1978) rather than establishing a new monotypic family for the genus *Pseudocheles*, characterized by the chelate third to fifth pereopods, a character of uncertain significance at family level. Subsequently, the Bresiliidae *sensu* Chace & Brown (1978) was accepted by many carcinologists (e.g. Williams & Chace, 1982; Williams & Rona, 1986; Williams, 1988; Burukovsky, 1988; Wicksten, 1989; Martin & Hessler, 1990; Williams & Dobbs, 1995). On the other hand, according to a morphological phylogenetic analysis, the Bresiliidae *sensu lato* were divided into three families, Bresiliidae *s. s.*, Disciadidae and Alvinocarididae (Christoffersen, 1986, 1990). Subsequently, Vereshchaka (1997) established a new monotypic family Mirocarididae to accommodate the genus *Mirocaris*. He distinguished four families on the basis of the development of pereopodal exopods and epipods: Alvinocarididae and Mirocarididae were distinguished from Bresiliidae and Disciadidae by the absence of pereopodal exopods; further the Mirocarididae was separated from the Alvinocarididae by the presence of pereopodal exopods and the absence of appendices internae on the second to fourth pleopods in the females. Gebruk et al. (2000) cited opinion of some taxonomic experts (A. B. Williams, J. W. Martin, F. A. Chace, Jr. and A. L. Vereshchaka) who agreed in placing vent or seep shrimps in the families Alvinocarididae and Mirocarididae, separating them from non-vent or seep genera which remain in the family Bresiliidae.

A phylogenetic analysis is necessary to establish apomorphies, and to identify homoplasy and reversals. However, a comprehensive treatment of the phylogenetic relationships among the bresilioid taxa is beyond the scope of this paper. We follow Christoffersen (1986, 1990), Segonzac et al. (1993) and Vereshchaka (1997) in recognizing Bresiliidae, Disciadidae and Alvinocarididae as separate families, because several distinct characters of Alvinocarididae *sensu* Vereshchaka (1997) have been found during our study.

The characters of Alvinocarididae include:

1. Telson relatively broad, bearing numerous setae or spines on broadly rounded posterior margin (vs. telson relatively slender, bearing 2 or 3 pairs of spines on pointed posterior margin in Bresiliidae and Disciadidae);
2. Eyes greatly reduced, lacking faceted structure on corneal surface in adults vs. eyes normally developed in adults in Bresiliidae and Disciadidae (except for the cave dwelling shrimp *Agostocaris williamsi* Hart & Manning, 1986);
3. Basal segment of antennular peduncle with distolateral spine and rounded projection on dorsal surface proximal to base of styllocerite (vs structures secondarily reduced in adults of *Rimicaris exoculata*), and with a deep groove separating styllocerite and main part of basal segment (vs none of these structures present in Bresiliidae and Disciadidae);
4. Penultimate segment of antennular peduncle armed with small but distinct distomesial spine (vs spine absent in Bresiliidae and Disciadidae);
5. Exopod of first maxilliped greatly expanded, subovate in outline, and fringed with single or double row of long plumose setae (vs exopod narrow, fringed with single row of sparse setae in Bresiliidae and Disciadidae);
6. Basis and ischium of second maxilliped completely fused, with fine row of numerous setae on mesial margin of coxa and basis-ischium segment (vs second maxilliped 7-segmented in Bresiliidae, and 6-segmented with merus-ischium fused in the Disciadidae; no fringe of setae on mesial margin of basal segments in both families); exopod absent (vs exopod present in Bresiliidae and Disciadidae); podobranch rudimentary, simple or sparsely papillate (vs podobranch absent in Bresiliidae and Disciadidae);
7. Coxae of third maxilliped with cluster of fine long setae on mesial face and a prominent slender projection directed laterally or ventrally on lateral face (vs no cluster of fine long setae on coxa of third maxilliped in Bresiliidae and Disciadidae, but normal coxal lateral projection on lateral face); distal two segments of third maxilliped arched (vs not arched in Bresiliidae and Disciadidae);
8. First pereopod with chela highly specialized, “bird-head with bent beak” shaped (flamingo-like), at least in young stages, ventral face of closed fingers forming deep excavation (vs morphology variable, but quite different in Bresiliidae and Disciadidae); carpus with shallow concavity filled with cluster of fine stiff setae in ventral part and one to three small movable spines arising at posterior border of concavity (vs no concavity or spines but sparse setae on mesial face of carpus in Bresiliidae and Disciadidae).

It is remarkable that these characters are all present in *Mirocaris*. Particularly, the similarity in the structure of the first and second pereopods is striking, as it has been effectively used in diagnosing caridean families (see
Holthuis, 1993). Vereshchaka (1997) considered the possession of pereopodal epipods and the greatly reduced appendices internae on the second to fourth pleopods as significant characters defining the family Mirocarididae. Indeed, the presence of pereopodal epipods represents a clear-cut difference separating *Mirocaris* from other alvinocaridid, bresiliid and disciadid genera (cf. Chace, 1992). However, in other caridean taxa, it is known that the development and number of pereopodal epipods are variable even in the same genus, for example the hippolytid *Eualus, Heptacarps* and *Lebbeus*, having a row of submarginal setae along cutting edge on the dactylus and fixed finger of the first pereopod. Also, Vereshchaka (1997) himself noted, a tendency toward reduction of appendices internae, although in lesser degree, is also found in *Alvinocaris, Chorocaris, Opaepele* and *Rimicaris*. Appendices internae on the second to fourth pleopods are slender and simple, lacking cincinni in *Alvinocaris, Chorocaris* and *Opaepele*; they are slender and simple in second and third pleopods in *Rimicaris*. In *Mirocaris*, the development of the appendices internae on the second to fourth pleopods is different between male and female: in males the second to fourth pleopods bear rudimentary appendices internae, and in females the pleopods are devoid of appendices internae. Thus a trend towards the reduction of appendices internae can be recognized in a group including alvinocaridids and *Mirocaris*. Considering the morphological similarity between *Mirocaris* and other alvinocaridid genera and the uncertain significance of this character at family level is questionable. The validity of the genus *Mirocaris* has been confirmed. Besides the presence of pereopodal epipods and corresponding setobranchs and the greatly reduced appendices internae on the second to fourth pleopods, *Mirocaris* differs from all other alvinocaridid genera in having, in ovoiderous females, the peculiar longitudinal depression on either side of the midline of the carapace, ornamented with microscopic longitudinal striae, and having a row of submarginal setae along cutting edge on the external surface of the dactylus and fixed finger of the first chela. *Mirocaris* is distinguishable from *Alvinocaris* and *Opaepele* by the completely toothless rostrum and the blunt pterygostomian angle of the carapace. From *Chorocaris, Opaepele* and *Rimicaris*, it differs in the presence of only a single row, rather than two to four rows, of accessory spines on the dactyli of the third to fifth pleopods.

As a result of the above comparisons, emended diagnoses the family Alvinocarididae and the genus *Mirocaris* are given below.
Genus Mirocaris Verscheshchaka, 1997


Emended diagnosis
Rostrum flattened dorsoventrally, triangular in dorsal view, not distinctly carinate or dentate dorsally, not reaching distal margin of basal segment of antennular peduncle; ventral surface without tooth. Carapace somewhat compressed laterally, with shallow hepatic groove; no distinct median carina, but in ovigerous females, shallow longitudinal depression ornamented with minute longitudinal striae on either side of midline; antennal spine acuminate; pterygotomian angle weakly produced anteriorly, rounded. Telson with dorsolateral spines forming sinuous row. Eyes rather large but degenerate, broadly fused mesially. Antennal scaphocerite broadly oval, with distinct dorsolateral tooth. Third maxilliped to fourth pereopods with hooked epipods and first to fifth pereopods with corresponding setobranchs. Dactyli of third to fifth pereopods compressed laterally, each with single row of accessory spinules on ventral margin. Second to fourth pleopods lacking appendices internae in females; in males rudimentary appendix interna present on second pleopod, but no appendices internae on third and fourth pleopods; appendix interna of fifth pleopod normally developed, bearing distal cluster of cincinni.

Composition
Mirocaris fortunata (Martin & Christiansen, 1995).

Acknowledgements
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