

Description of *Bermudacaris harti*, a new genus, and species (Crustacea: Decapoda: Alpheidae) from anchialine caves of Bermuda

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Abstract.—A new genus is proposed for an unusual new species of alpheid shrimp, *Bermudacaris harti*, inhabiting subterranean anchialine caves on the Bermuda Islands. This unique cavernicolous new species, has been confused with *Automate dolichognatha*, de Man, 1888, a species widely distributed in tropical marine shallow waters. The new genus shows some affinities with *Automate* de Man, 1888 and can be distinguished from the latter genus by several important features, such as subsymmetrical first chelipeds with dactylus in ventral position, and presence of appendix masculina in males. This new species is unusual among the Alpheidae in the considerable reduction of corneal pigmentation, especially in female, most likely an adaptation to the cave environment. The presence of few large eggs in the female suggests that the new species has low fecundity and abbreviated larval development, which might result from its troglobitic lifestyle. The relationships of the new genus to *Automate* are discussed in some detail. Presumably marine ancestors of this troglobitic species entered anchialine caves from neighboring shallow, marine waters.

In an important contribution to the knowledge of the cavernicolous caridean fauna of Bermuda Islands in the Western Atlantic Ocean, Hart & Manning (1981: 453, figs. 56–77) reported *Automate dolichognatha* de Man, 1888 from an anchialine cave near Tucker's Town. Hart & Manning reported two specimens, and included short comments on spinulation of pereopods, branchial formula and color. Although a full description of these specimens was not provided, the figures alone were sufficient to raise suspicions concerning their identity. Possibly, the two specimens were misidentified because *A. dolichognatha* had been previously reported from coastal waters of Bermuda by Markham & McDermott (1980, as *A. gardineri* Coutière). Holthuis (1993) used Hart & Manning's (1981) figures in his recent catalogue of caridean genera.

Automate dolichognatha is presently considered a widely distributed, pantropical species found in shallow marine waters, mainly on soft substrates (Chace 1972, 1988; Banner & Banner 1973, Manning & Chace 1990). Hart & Manning (1981) is the first and only report of a member of the genus *Automate* de Man, 1888 from caves, and the authors suggested that the Bermudan caves could be an "unusual anchialine habitat" for this species.

During a visit to the Smithsonian Institution, Washington, D.C. in 1999, the first author was able to examine the two specimens from Bermuda. A third specimen identified as *Automate dolichognatha*, an ovigerous female, was collected in 1982 in Christie's Cave, Bermuda. After comparisons of these three specimens with those reported as *Automate dolichognatha* from Ascension Island by Manning & Chace

(1990), and with several other specimens reported by Chace (1972, as *A. gardineri*), we have concluded, that the Bermuda specimens are not *A. dolichognatha*, but a new undescribed species having several important features which do not agree with the generic diagnosis of *Automate* de Man, 1888, as given by de Man (1888), Banner & Banner (1973) and Chace (1988). These three specimens could not be assigned to any genus in the Alpheidae, although the presence of the distinct cardiac notch and the robust first chelipeds clearly indicate that they belong to this family. Therefore, a new monotypic alpheid genus is established herein for this new species.

Material and Methods

Specimens were examined and dissected with the aid of binocular microscope and all original illustrations were made using a camera lucida. The material used in this study remains deposited in the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM), and in the Muséum National d'Histoire Naturelle, Paris (MNHN).

Measurements of carapace length (CL) and total length (TL) are in millimeters. Other abbreviations used in the text: P = pereopod, Mxp = maxilliped.

The following specimens were used for comparison: *Automate dolichognatha* de Man, 1888, Ascension Island, Atlantic Ocean (USNM 256773), Caribbean Sea (USNM 136069, reported as *A. gardineri* Coutière by Chace 1972), Madagascar (MNHN 4567, 4571); *Automate evermanni* Rathbun, 1901, Principe Island, Gulf of Guinea (MNHN 3450).

Family Alpheidae Rafinesque, 1815

Bermudacaris, new genus

Diagnosis.—Carapace slightly compressed laterally, smooth; rostrum developed as broadly rounded median projection; orbital teeth lacking; pterygostomial region

rounded. Eystalks subconical, anterior portion visible in dorsal and lateral views, corneal pigmentation reduced or absent. Mandible with normally developed incisor and molar processes, and with 2-segmented palp. Ultimate segment of third maxilliped distally armed with slender spines. First pereopods subsymmetrical, equal in size, carried extended and elevated, with dactylus situated ventrally; chelae laterally compressed, without significant armature; adhesive discs and linea impressa absent. Second pereopods with 5-segmented carpus, second article longest. Third pereopods with dactylus simple, propodus armed with spines. Sixth abdominal segment without articulated plate. Second pleopods of male with appendix interna and appendix masculina. Telson distally truncated, with 2 pairs of spines on postero-lateral margin; anal tubercles absent. Branchial formula: pleurobranchs on P1-5, podobranch on Mxp2, arthrobranch on Mxp3, epipods on Mxp1-3 and P1-4, setobranchs on P1-5, exopods on Mxp1-3.

Type species.—*Bermudacaris harti*, new species.

Species included.—Only the type-species.

Etymology.—Generic name derived from the locality of collection, Bermuda Island, and the Greek *karis*, shrimp. Gender is feminine.

Bermudacaris harti, new species

Figs. 1-4

Automate dolichognatha—Hart & Manning, 1981:441, 453, figs. 56-77.—Holthuis, 1986:592; 1993:198, fig. 190 (in part.).—Manning & Hart, 1989:313.

Automate cf. dolichognatha—Iliffe, 1994:420.—Hobbs, 1994:98, 102 (not *Automate dolichognatha* de Man, 1888)

Material examined.—Holotype: ovigerous female (CL 3.9, TL 11.5), Bermuda Isl., Christie's Cave, 24 Oct 1982, coll. T. M. Iliffe, (specimen in excellent condition, not dissected, with both first pereopods at-

tached) (USNM 250781). Paratypes: male (CL 2.9, TL 10), Bermuda Isl., Tucker's Town, Tucker's Town Cave, 15 May 1980, coll. W. Sterrer and T. M. Iliffe, about 12 m deep (USNM 184014); male (CL 3.6, TL 11), Bermuda Isl., Tucker's Town, Tucker's Town Cave, 26 Aug 1980, coll. T. M. Iliffe & C. W. Hart, about 12 m deep (USNM 184015).

Diagnosis.—Frontal margin lacking orbital teeth, with rounded, rostral projection; subconical eyestalks dorsally exposed, with reduced corneal pigmentation; first pereopods subequal in size and shape, with dactylus in inverted (ventral) position; articulated flap on sixth abdominal segment absent.

Description.—Holotype (Fig. 1a, b). Oviparous female carrying 3 large eggs (maximum size 1.3×1 mm). Carapace smooth, without setae or grooves. Anterior margin of carapace with short, broadly rounded, median rostral projection; orbital teeth lacking; infra-corneal angle only slightly protruding; pterygostomial angle rounded; ventral margin of carapace straight, without emarginations, not fringed with setae; posterior margin of carapace with well marked cardiac notch. Eyestalks subconical, enlarged at base, distal half visible in dorsal and lateral views; cornea reduced, without pigmentation (Fig. 1b). Ocellary beak not distinct.

Antennular peduncles somewhat flattened dorso-ventrally; second article slightly longer than first, and twice as long as third article; stylocerite distally acute, only slightly overreaching first antennular article, with statocyst well developed; ventral carina of first article represented by small acute tooth, situated on mesial margin proximal to second article; strong tooth protruding from base of first antennular article (only visible in ventro-lateral view); stylocerite and anterior margins of articles with conspicuous elongated setae; external flagellum not biramous, with fifth to tenth segments bearing 7 tufts of long aesthetascs. Carapocerite of antenna distinctly overreach-

ing antennular peduncle; scaphocerite broadly rounded anteriorly, with strong lateral spine reaching to about middle of carapocerite; basicerite with small ventral tooth.

Mouthparts not dissected (see paratype description). Third maxilliped reaching far beyond antennular peduncle when extended; exopod short (about 0.6 of length of antepenultimate segment); antepenultimate segment flattened proximally, slightly enlarged and thickened distally; ultimate segment triangular in cross-section, bearing approximately 12 semicircular rows of strong setae on mesio-ventral side, and several groups of spines on distal half of dorsal margin; coxa with blunt lateral plate, and slender strap-like epipod (mastigobranch); corresponding articulation surface of Mxp3 with small arthrobranch.

First pereopods subsymmetrical and almost equal in size, possibly carried elevated and slightly twisted mesially (Fig. 1a); superior margin of ischium with 3 distinct spinules curved anteriorly; merus triangular in section, not enlarged or excavated, with several small spinules on superior margin; distal margins of merus rounded, without acute teeth; carpus cup-shaped, with tiny spinules on dorsal margin; chela and carpus forming angle about 90° with merus and ischium; chela smooth, compressed laterally, palm as long as dactylus; dactylus situated in ventral position; both cutting edges unarmed, with exception of small irregular teeth proximal to dactylar articulation; fingers apically crossing when closed; superior margin of palm and fixed finger bearing conspicuous long setae.

Second pereopods very long and slender, reaching far beyond antennal peduncle when fully extended; merus and ischium elongated and slightly setose; carpus 5-segmented; second segment longest; proportions of carpal articles (from proximal to distal) approximately equal to 10:16:7:6:7; chelae slender, simple; dactylus slightly longer than palm; tufts of small setae present on both movable and fixed fingers.

Third to fifth pereopods slender, setose;

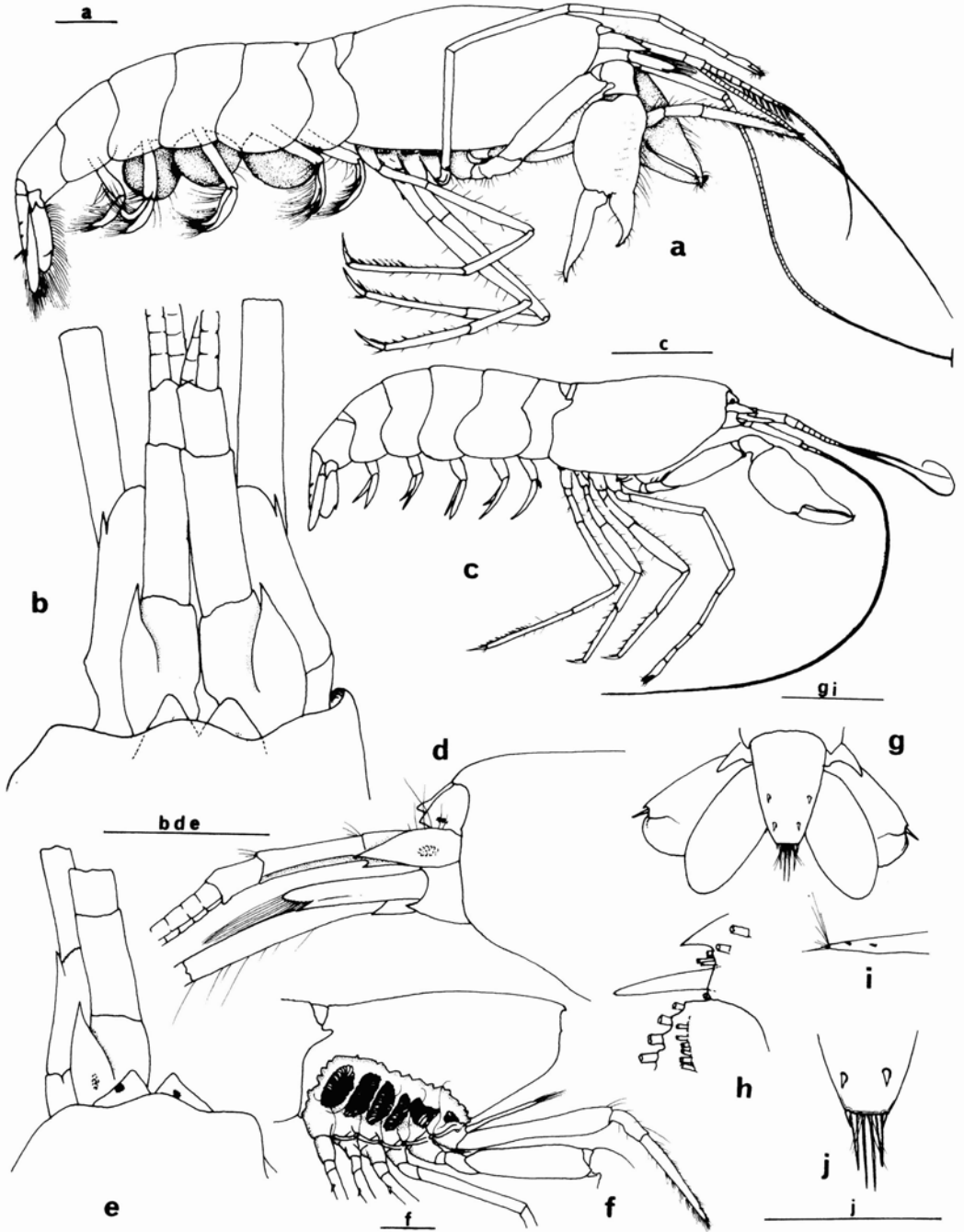


Fig. 1. *Bermudacaris harti*, new species, a, b, female holotype (USNM 250781). c-j, male paratype (USNM 184014). a, habitus with natural position of legs; b, frontal region in dorsal view; c, habitus; d, e, frontal region in lateral and dorsal views; f, gills; g, telson and uropods; h, detail of uropod diarsis and lateral spine; i, telson, lateral view; j, same, detail of posterior margin. Scales: 1 mm, except for c (2 mm); fig. h without scale. Figs. c, f-i after Hart & Manning, 1981.

ischium with spine on inferior margin; carpus and merus unarmed; propodus of P3 and P4 armed with 6–8 spines on inferior margin, including a pair of slender apical spines proximal to dactylar articulation; propodus of P5 more slender, (about 1.5 times longer than propodus of P3), bearing only few spines and well-developed grooming brush, composed of about 10–12 tufts of long setae; dactylus of P3–5 slender, slightly curved, without trace of secondary unguis; coxae of P1–4 with strap-like epipods.

Abdominal segments rounded ventrally; sixth pleosomite without articulated flap at postero-ventral angle; margin of preanal plate slightly convex, not protruding. First pleopod with reduced endopod. Second to fifth pleopod each bearing long appendix interna, reaching distal margin of endopod. Uropods distinctly exceeding posterior margin of telson; protopod with acute outer tooth; exopod with diarsis slightly curved, ending in acute lateral tooth; lateral spine well developed; endopod without specific structures. Telson relatively broad, tapering distally, with 2 pairs of dorsal spines situated in its distal half, at some distance from lateral margin; posterior margin short, about 0.2 of telson length, almost straight, with 2 spines at each angle, inner spines about 3 times longer than outer, 1 median pair of very long thickened setae overreaching inner spines, and numerous more slender setae directed upwards. Branchial formula as given in generic diagnosis.

Paratypes (Figs. 1c–j, 2, 3, 4). Differ from holotype in external margin of eye-stalks bearing subapically a small but distinct pigmented area (Fig. 1d, e); infra-corneal angle of frontal margin of carapace, above basicerite, apparently more protruding (incorrectly figured as a small tooth by Hart & Manning 1981, fig. 58). Endopod of second male pleopod bears slender appendix interna and much shorter, stout appendix masculina, distally bearing strong setae (Fig. 2k).

Mouthparts (Fig. 4a–h) typical for Al-

pheidae. Mandible complete, with 2-segmented palp, well developed molar process, and robust incisor process distally bearing 5 strong teeth. Maxillula with bilobed palp, each lobe bearing 1 long plumose seta; inferior lacinia with dense cover of setae on distal portion (Fig. 4d) Maxilla bearing narrow scaphognathite fringed with short setae, deeply incised upper lacinia, and small palp. First maxilliped with slender palp bearing short setae on lateral margin; lower endite with several long plumose setae; exopod with rather feebly developed caridean lobe, fringed with plumose setae (Fig. 4g); epipod large and rounded. Second maxilliped without distinguishing characters; exopod elongated; epipod small, mesially with small rounded podobranch (Fig. 4i).

Remarks.—The specimen dissected and illustrated by Hart & Manning (USNM 184014) is in quite poor condition having the frontal and anteroventral regions seriously damaged, and most legs detached. The maxilla and the second maxilliped appear to be missing. To verify Hart & Manning's figures, the mouthparts have been dissected and partly illustrated from another paratype (USNM 184015) in much better condition.

Two additional specimens collected in the caves of Bermuda Island belong to the new species (field notes by T. M. Iliffe), but could not be located in the collections of the USNM. These are not treated as paratypes: 1 ovigerous female, CL 4.5 (with 4 eggs, 1×1.7 mm), Green Bay Cave, New Harrington Sound Passage, 27 Aug 1981, coll D. Williams, caught by hand while swimming in mid-water about 15 m deep. 1 female, CL 4.4, Bat Cave, Government Quarry, 12 December 1981, silt substrate at 22.5 m., coll T. M. Iliffe., by hand, water anoxic between 1 and 10 m, together with *Typhlatya* sp. (not collected) at 10–20 m.

Color in life.—Uniformly whitish, lacking any other color (Hart & Manning 1981). Eggs yellow when collected but brownish after preservation in alcohol.

Etymology.—After Charles Willard Hart

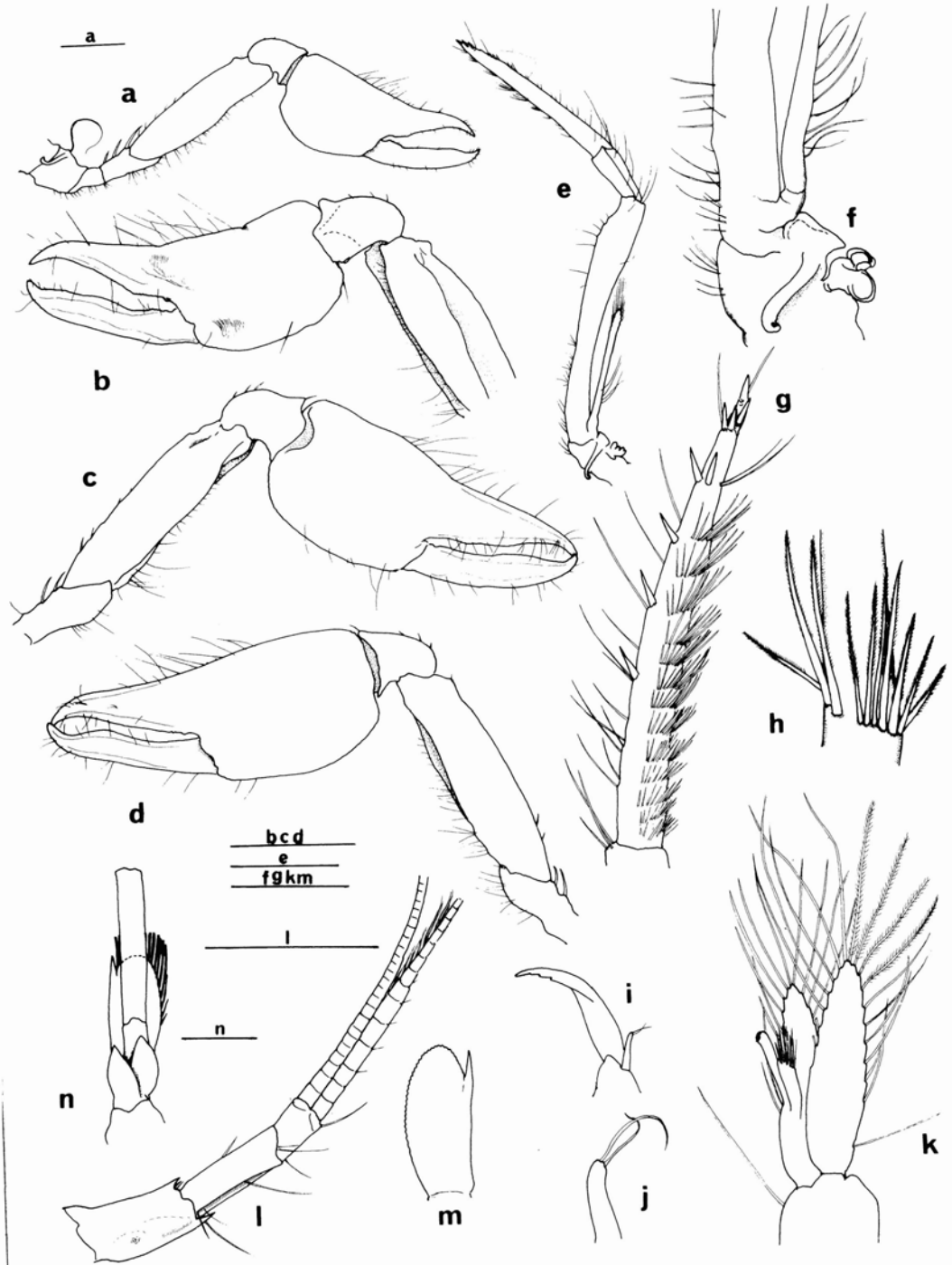


Fig. 2. *Bermudacaris harti*, new species, a–e, h–j, l–n, paratype (USNM 184014); f, g, k, paratype (USNM 184015). a, right first pereiopod, external view; b, same, detail of right chela and carpus, mesial view; c, d, left first pereiopod, inner and outer views; e, third maxilliped; f, same, detail of proximal region; g, h, same, details of ultimate segment; i, first pleopod; j, same, detail of endopod; k, second pleopod; l, antennule, ventral view; m, scaphocerite; n, antennal peduncle, ventral view. Scales: 1 mm, except figs. f, g, k, m (0.5 mm); figs h–j without scale. (Figs. a, h–j after Hart & Manning, 1981).

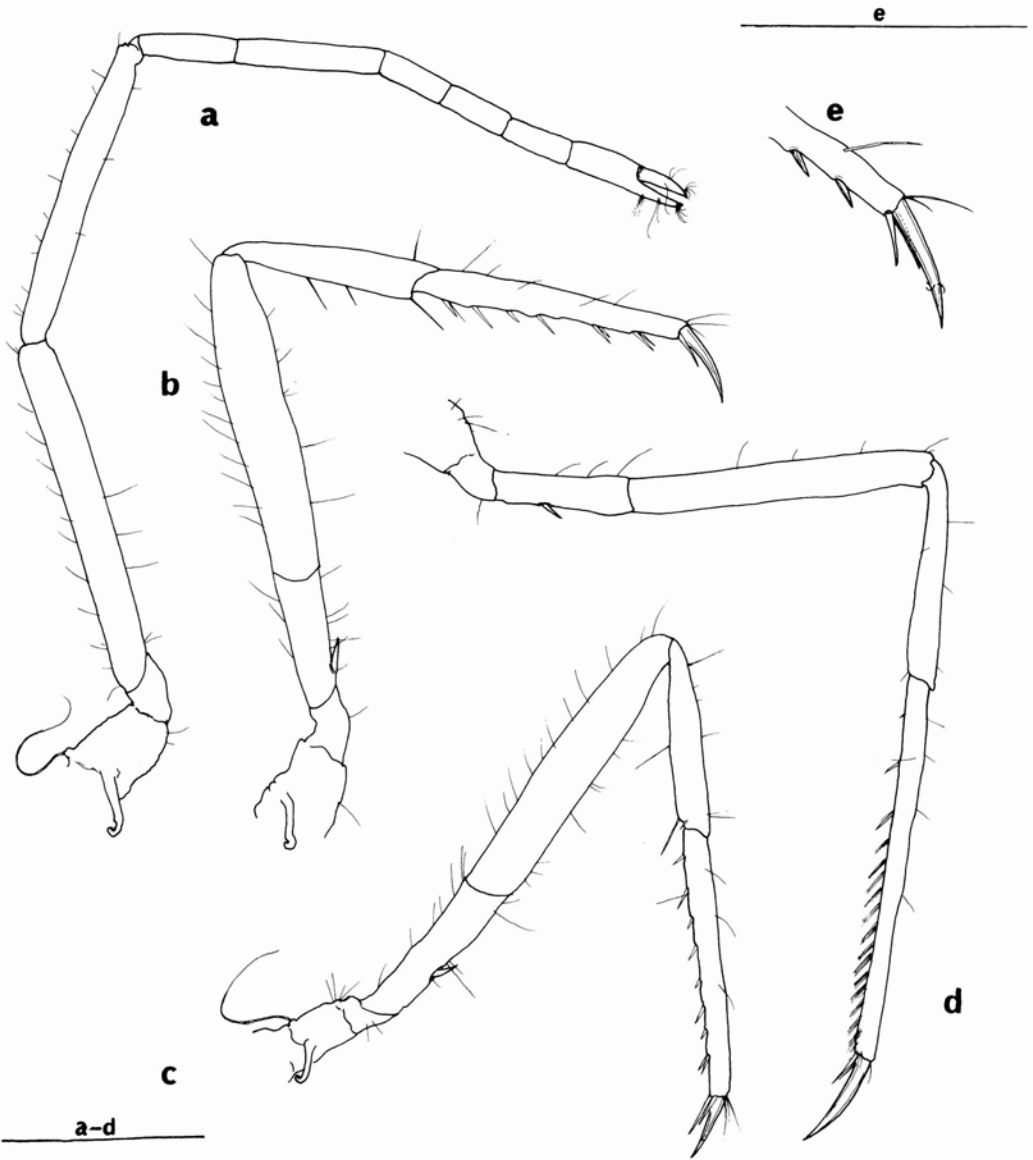


Fig. 3. *Bermudacaris harti*, new species, paratype (USNM 184014). a, second pereiopod; b, third pereiopod; c, fourth pereiopod; d, fifth pereiopod; e, detail of apical part of propodus and dactylus of third pereiopod. Scales: 1 mm.

Jr., retired USNM curator, in recognition of his research on the decapod fauna of Bermudan caves, and who also collected the holotype.

Habitat.—More than 90 anchialine caves are known from Bermuda, most of which are clustered in the area between Castle Harbour and Harrington Sound. They con-

sist primarily of inland limestone caves that extend down to sea level and contain tidally influenced brackish pools. More or less extensive networks of underwater cave passages often interconnect these otherwise seemingly isolated cave pools. An exceedingly rich and diverse troglobitic fauna inhabits these caves, including more than 50

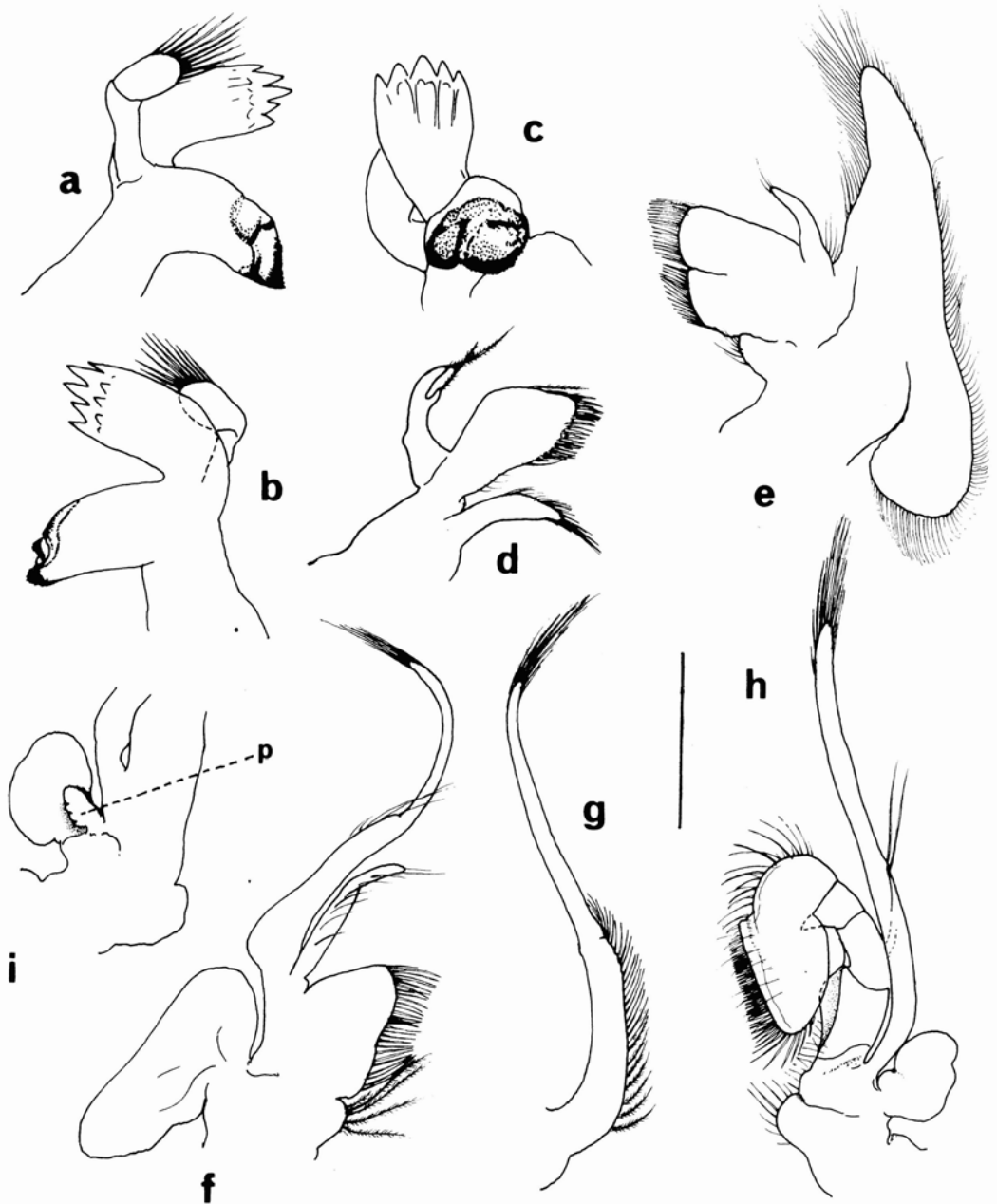


Fig. 4. *Bermudacaris harti*, new species, a–d, f, paratype (USNM 184014); e, g–i, paratype (USNM 184015). a–c, mandible, d, maxillula; e, maxilla; f, first maxilliped; g, same, detail of exopod; h, second maxilliped; i, same in mesial view, detail of podobranch. Scales: 0.5 mm.

endemic species (Sket & Iliffe 1980, Iliffe et al. 1983, Iliffe 1994).

Bermudacaris harti has been found in four caves, all located in the northeastern part of the main island of Bermuda (Fig. 6).

The extensive descriptions of the caves of Bermuda may be found in Kornicker & Iliffe (1989), and Iliffe (1993). Tuckers Town Cave is an isolated cave located on the Tuckers Town peninsula between Castle

Harbour and the South Shore of Bermuda. The cave is entered by way of a 13 m deep vertical shaft that opens into a dimly illuminated, sea level pool measuring 12 by 18 m. The sand-bottom pool slopes steeply down to a large, completely submerged cavern in total darkness with depths to 21 m. This cavern is about 80 m long by 20 m wide, and 10 m high. In October 1981, salinity in the pool was 22.7‰ at the surface, 27.5‰ at 1 m, 34.3‰ at 10 m and 35.5‰ at 21 m. Temperature increased with depth, from 17.8°C at the surface to 21.5°C at 21 m, while dissolved oxygen decreased from 6.11 ml/l at the surface to 2.97 at 21 m. Tides in the cave occur 58 minutes later than tides in the open ocean, and with an amplitude 62% that of open ocean tides. Specimens of *Bermudacaris harti* were collected at about 15 m depth. Other notable troglobitic species in this cave include the shrimps *Typhlatya iliffei* Hart & Manning, 1981, *Barbouria cubensis* (Von Martens, 1872) and *Parhippolyte sterreri* (Hart & Manning, 1981), the mictacean *Mictocaris halope* Bowman & Iliffe, 1985, the halocyprid ostracods *Spelaeoecia bermudensis* Angel & Iliffe, 1987, *Micropolycope styx* Kornicker & Iliffe, 1989 and *Polycopissa anax* Kornicker & Iliffe, 1989, and the calanoid copepod *Enantiosis* sp.

Christie's Cave is located just 30 m from the edge of Castle Harbour. The cave contains a clear 8 m-deep pool just inside a collapsed entrance. No cave passages were found extending away from the pool. In October 1983, surface salinity in the pool was 6.9‰, increasing to 19.5‰ at 1 m. Surface water temperature was 18.2°C, increasing to 20.4°C at 1 m. A *Bermudacaris harti* specimen was collected from the bottom in 8 m depth. Other troglobitic species from this cave include the archannelid polychaete *Nerilla* sp.; the calanoid copepods *Erebonectes nesioticus* Fosshagen & Iliffe, 1985 and *Exumella* sp., and the halocyprid ostracods *Spelaeoecia bermudensis* and *Polycopissa anax*.

Bat Cave (Government Quarry Cave) is

also located along the shoreline of Castle Harbour. The cave was uncovered during quarrying operations in the 1960's. It contained two pools reaching depths of at least 23 m. In December 1981, salinity in the pool was 6.5‰ at the surface, 23.0‰ at 1 m, 35.2‰ at 10 m and 35.7‰ at 19 m. Surface water temperature was 19.1°C, increasing to 21.2°C at 19 m. A specimen of *Bermudacaris harti* was collected in 15–20 m depths, below a layer of polluted, anoxic water. Other troglobitic species from this cave include the shrimp *Typhlatya iliffei*. In 1980, rubbish was bulldozed into one of the cave pools, grossly polluting the water (Iliffe et al. 1984). The cave was completely destroyed by quarrying in the mid 1980's.

Green Bay Cave is the longest cave in Bermuda with more than 2 km of explorer underwater passageways. The cave is located on the peninsula separating Harrington Sound from the North Lagoon. It has two entrances, one at the end of Green Bay on Harrington Sound, and another, an inland sinkhole, known as Cliff Pool. Average depth in the cave is 18 m. In March 1982, salinity in the Cliff Pool entrance was 21.3‰ at the surface, 27.3‰ at 1 m, 36.2‰ at 10 m and 36.3‰ at 18 m. Surface water temperature was 20.0°C, decreasing to 18.7°C at 18 m. A specimen of *Bermudacaris harti* was collected at mid water in 15 m depth from a more hydrologically isolated section of the cave. Other troglobitic species from this cave include the unique shrimp *Procaris chacei* Hart & Manning, 1986; the halocyprid ostracod *Spelaeoecia bermudensis*; and the mictacean *Mictocaris halope*.

Interestingly, two other alpheids have been found in the Green Bay Cave system, but to our knowledge this data has never been published. These are: *Synalpheus* cf. *sanctithomae* Coutière, 1909 (juvenile specimen, CL 3.0, in "yellow sponge"), and *Alpheus* cf. *normanni* Kingsley, 1878 (small male, CL 3.5).

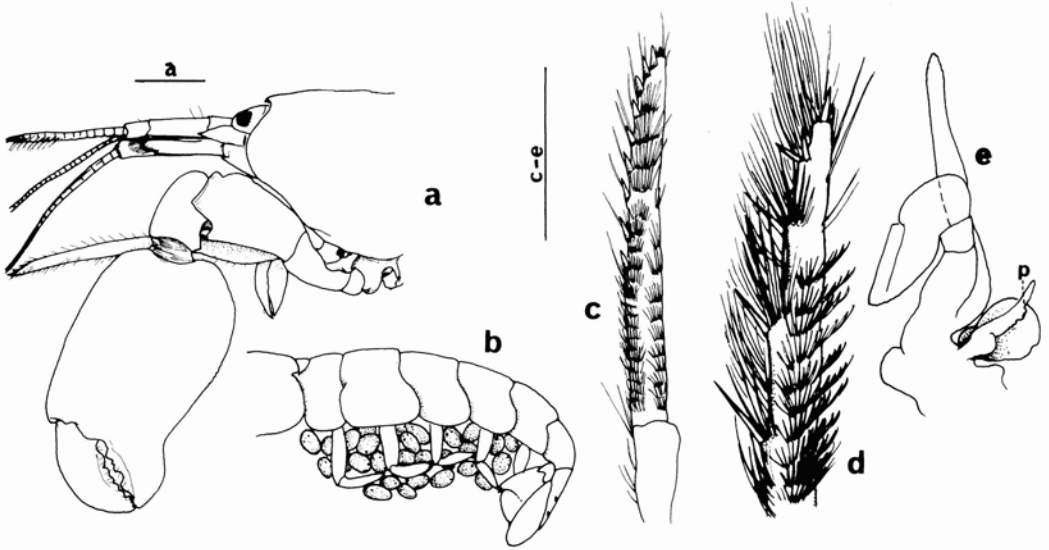


Fig. 5. *Automate dolichognatha* de Man, 1888 (a-c) and *A. evermanni* Rathbun, 1901 (d, e). a, anterior region of *A. dolichognatha* from Ascension Isl. (female, USNM 256773); b, abdomen of ovigerous female of *A. dolichognatha*, probably from Djibouti (after Coutière, 1899, without scale); c, d, details of ultimate segment of third maxilliped of *A. dolichognatha* from Madagascar (MNHN 4571) and *A. evermanni* from Gulf of Guinea (MNHN 3450); e, second maxilliped of *A. evermanni* in mesial view, detail of podobranch (MNHN 3450). Scales: 1 mm.

Discussion

The new genus *Bermudacaris* shares several characters with *Automate* de Man, 1888. In both, the frontal region is similar, with partly exposed parallel eyestalks; the exopod of Mxp3 is short (only slightly overreaching distal half of penultimate segment); the spines on superior margin of ultimate segment of Mxp3 are present; the second pereopod is elongated and has similar proportions of carpal articles; and there is no deep bifurcation on the external flagellum of the antennule. Other features common to these two genera are also shared by numerous other, not closely related alpheid genera.

Using the most recent key of alpheid genera (Holthuis 1993), *Bermudacaris* would key out to *Automate*, but the new genus differs from *Automate* in several important points, notably those concerning first chelipeds and appendix masculina. The first chelipeds of *Bermudacaris* are unique within Alpheidae. In both sexes they are not

especially enlarged, carried extended, elevated, and are almost symmetrical. The merus is slender, the chela rather slim, the cutting edges of both fingers unarmed, and the dactylus is situated clearly in ventral position (Figs. 1c, 2b-d). In contrast to *Bermudacaris*, all species of *Automate* possess asymmetrical and unequal first chelipeds (Fig. 5a), with major cheliped bearing enlarged, rounded or rectangular palm, dactylus always situated in dorsal position, cutting edges of fingers usually armed with large teeth (Fig. 5a), and stout, ventrally excavated merus.

The presence of appendix masculina in male specimens of *Bermudacaris harti* and its absence in all males of species of *Automate* (Coutière 1899, D. M. & A. H. Banner 1973, pers. obs.) is another feature useful for the separation of the two genera. Assuming that the presence of an appendix masculina is a plesiomorphic state for Alpheidae, and for all Caridea, its absence in *Automate* can be explained by a secondary loss.

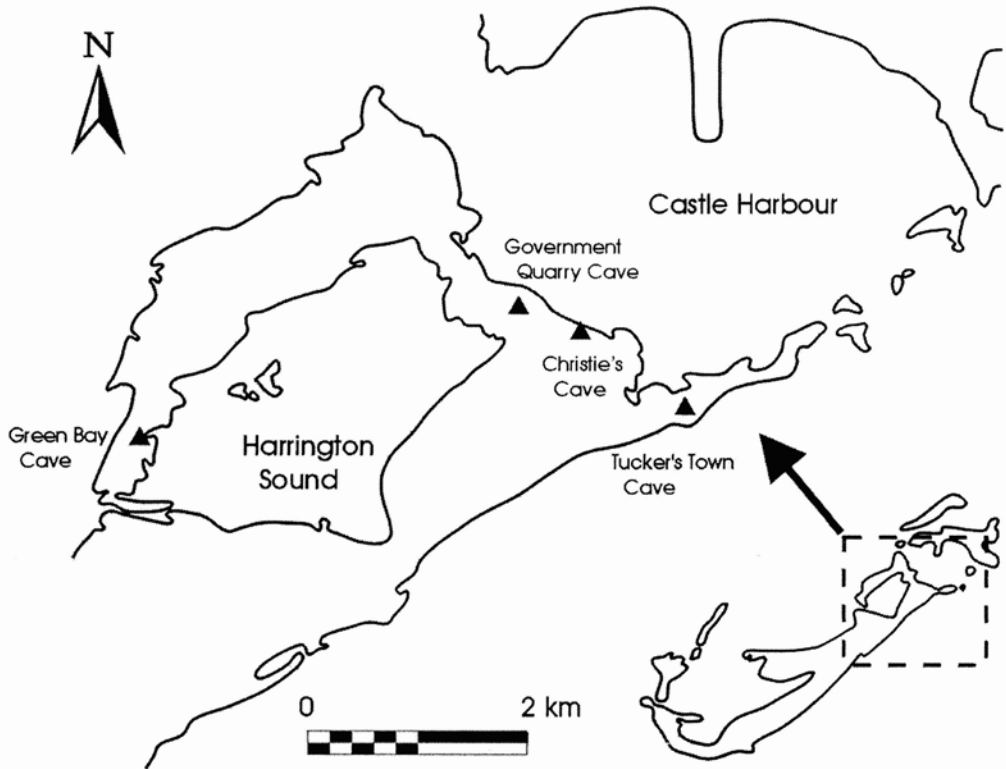


Fig. 6. Map of Bermuda Island showing the locations of caves: Tucker's Town, Christie's, Government Quarry and Green Bay Caves.

Other, less striking points of difference between the new genus and *Automate* are: shape of frontal margin not emarginate in *Bermudacaris* vs. broadly emarginate in *Automate*; shape of eyestalks subconical, not juxtaposed in *Bermudacaris* vs. more or less cylindrical, parallel and juxtaposed medially in *Automate*; eyes depigmented or with reduced pigmentation in *Bermudacaris* vs. well-pigmented in *Automate* (Fig. 5a); small acute antennular carina present in *Bermudacaris* vs. absent in all species of *Automate*; third to fifth pereopods slender in *Bermudacaris* vs. robust in *Automate*; ischium of fifth leg with small spine in *Bermudacaris* vs. unarmed in *Automate*; few (3 or 4), very large eggs in female of *Bermudacaris* vs. numerous, small eggs (0.3×0.5 mm, Bhuti et al. 1977, Coutière 1899, see fig. 5b, pers. obs.) in females of *Auto-*

mate dolichognatha; pleosomites relatively well developed and more rounded, partially covering large eggs in female of *Bermudacaris* vs. pleosomites weakly developed in females of *Automate* (Figs. 1a, c, 5b). For all the reasons cited above, the new species could not be assigned to *Automate* without significant changes in the diagnosis of this genus.

The observed difference between the female and the males in the pigmentation of eyes is highly unusual for alpheids and possibly for all caridean shrimps. In the holotypic female of *Bermudacaris* almost no pigmented area is apparent on the eyestalks (Fig. 1b), while both paratypic males present a small, but distinct black spot proximal to the anterior margin (Fig. 1e). With only one female specimen, it would be speculative to suggest a sexual dimorphism

in pigmentation of cornea, and more specimens of both sexes are needed to investigate further this interesting feature.

Bermudacaris harti has a small podobranch inserted near the base of the epipod of the second maxilliped. This podobranch was not illustrated by Hart & Manning (1981: 454, fig. 66), but its existence has been noted in the branchial formula. It is generally absent in all members of the family Alpheidae, but its presence has been shown in many Hippolytidae (Coutière 1899). Within Alpheidae a podobranch has been observed in *Automate branchialis* Holthuis & Gottlieb, 1958, *A. rugosa* Coutière, 1902 (see Wicksten 1981), *A. anacanthopus* de Man, 1910, *A. rectifrons* Chace, 1972, and *A. evermanni* Rathbun, 1901 (Fig. 5e), in which it is particularly well developed and acutely produced; the podobranch has not been observed in *A. dolichognatha* and is also lacking in *A. salomoni* Coutière, 1908. The presence of this podobranch could indicate a closer relationship of the new genus to species showing this structure, or in general to the genus *Automate*.

The ultimate segment of the third maxilliped of *Bermudacaris harti*, new species, bears numerous rows of thick setae on its ventral side (Fig. 2h), and strong spines along its superior margin (Fig. 2g). Similar spines are found in *Automate dolichognatha* (Fig. 5c), *A. evermanni* (Fig. 5d), *A. branchialis* (Holthuis & Gottlieb 1958), *A. anacanthopus* and also in other species of *Automate*. To our knowledge, this type of armature has never been observed in other alpheid genera; when strong spines are present on the ultimate segment, they are always situated on its distal part or on the apex itself.

Thus, *Bermudacaris harti* could either derive from the ancestors common to both *B.* and *Automate* or could represent a "highly modified species" of *Automate*, adapted to the unique anchialine cave environment, which is radically different from the usual habitat of recent species of *Automate*. Almost depigmented eyes, and few

very large eggs suggesting highly abbreviated development and low fecundity of *B. harti*, are features certainly related with the evolution in an environment characterized by deficiency of light and fluctuation of salinity.

It is probable that the Bermudan caves were colonized by a marine ancestor of *B. harti*, which could also be those of the modern species of *Automate*. Indeed, all anchialine caves in Bermuda still have an underground connection with the sea as is evidenced by their tidal fluctuations and fully marine salinities at depth (Hart & Manning 1981). Generally, these caves comprise crevicular habitats in rock extending potentially from the sea surface to the deep sea, therefore these habitats could have been entered anywhere in the water column (Manning et al. 1986). This would explain the presence of both deep-sea and shallow water (epigeal), or both old and recent forms in caves.

Bermuda originated on the Mid-Atlantic Ridge and was formed about 100 million years ago (Manning et al. 1986). Hart et al. (1985) stated that there are significant ties between marine cave fauna and the fauna of deep sea, that caves can contain very old elements ("Mesozoic relicts"), and that they could serve as refuges over long periods of time, especially during periods of glaciation (Iliffe et al. 1983). These statements, though partially explaining the distribution patterns of many cave inhabitants, can not explain the origin of *Bermudacaris*. All modern species of *Automate* (and generally all Alpheidae) are found in shallow waters, excluding the hypothesis of an ancestral form coming from the deep sea. Also *Bermudacaris* cannot be considered a relict form, since it shares many characters of modern Alpheidae (such as those shared with *Automate*). A more probable explanation would be the relatively late colonization of Bermudan caves by a marine, probably shallow-water ancestor. This ancestor frequented crevicular habitats (marine caves), from which it could progressively

penetrate into limestone anchialine caves, situated at considerable distance from the sea.

A similar hypothesis has been put forward by Manning et al. (1986: 160–161), to explain the distribution of two closely related species of *Typhlatya*. The salt-water precursors of modern *Typhlatya* species could frequent crevicular habitats along the Mid-Atlantic Ridge while the continents were approximated. Also, Manning et al. (1986) briefly mentioned that a similar scenario could explain the puzzling distribution of the two populations of *Procaris* in the Atlantic.

More recently a common littoral crab, *Panopeus lacustris* Schramm, was reported to be relatively abundant in several Bermudan caves (Manning & Hart 1989). Crabs found in caves differed from those living on the open shore in their colour pattern (being much lighter), and in having little wear on the fingers of the chelae, possibly the initial changes induced by life in a cave environment.

Bermudacaris harti is a seventh alpheid reported from crevicular habitats (marine, anchialine or freshwater), and it seems to be the most adapted to life in caves. Recent cave investigations show that Alpheidae seem to be relatively well represented in this particular environment. Other cavernicolous alpheid species are *Potamalpheops stygicola* (Hobbs, 1973) from freshwater caves in Oaxaca, Mexico (Hobbs 1973, 1983); *Potamalpheops pininsulae* Bruce & Iliffe 1992 from freshwater limestone caves in Ile des Pins, New Caledonia; *Salmoneus sketi* Fransen, 1992 from marine caves in the northern Adriatic Sea; *Yagerocaris cozumel* Kensley, 1988 from marine caves off Cozumel, western Mexico [transferred from Hippolytidae to Alpheidae by Chace & Kensley (1992)], and an undescribed species of *Potamalpheops* from a freshwater cave system in northern Palawan, Philippines (Anker, pers. obs.). Two other stygophilic alpheids have been reported from anchialine lava pools and tubes

in the Pacific Ocean; these are *Metabetaeus Iohena* Banner & Banner, 1960 from Hawaii (Holthuis 1973), and *Hamalpheus acanthops* Bruce & Iliffe, 1991 from Samoa.

In addition to *Bermudacaris harti*, four other species of troglobitic caridean shrimps from three families inhabit anchialine caves of Bermuda: *Parhippolyte sterreri*, *Barbouria cubensis*, *Typhlatya iliffei* and *Procaris chacei* (Hart & Manning, 1981, 1986), illustrating the relatively high level of diversity of this habitat: *Procaris chacei*, and *Bermudacaris harti* seem to be very uncommon, in contrast to relatively abundant *Barbouria cubensis* and *Typhlatya iliffei*. Only four individuals of *Bermudacaris harti* were collected in 11 years of cave diving in Bermuda by the junior author. Unfortunately, the anchialine caves of Bermuda are more and more exposed to the anthropogenic activities (Iliffe et al. 1984), but we hope that the unique, endemic cave fauna of this island group can be preserved for the future generations.

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