

Descriptions of two new species of alpheid shrimps from Japan and Australia, with notes on taxonomy of *Automate* De Man, *Coronalpheus* Wicksten and *Bermudacaris* Anker and Iliffe (Crustacea: Decapoda: Caridea)

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Two new species of the caridean family Alpheidae are described from distant Indo-Pacific localities: *Automate hayashii* sp. nov. from Hakodate Bay, southern Hokkaido, Japan, and *Bermudacaris australiensis* sp. nov. from the North-West Shelf off Western Australia. *Automate hayashii* appears closest to the poorly known *A. salomoni* Coutière, 1908. *Bermudacaris australiensis* sp. nov., the second species of the genus, represents the first discovery of the genus in the Indo-Pacific. The type species of *Bermudacaris* Anker and Iliffe, 2000, *B. harti* Anker and Iliffe, 2000, was described from anchialine caves of Bermuda, while the unique specimen of *Bermudacaris australiensis* sp. nov. was collected from an apparently typical marine environment. Relationships among the species of *Automate* De Man, 1888, *Bermudacaris* and *Coronalpheus* Wicksten, 1999 are discussed. Characters separating these three closely related genera, including the development of the rostrum, the shape of the eye-stalks, the absence of the appendix masculina, and the features of the first pereopods, are reassessed. Three informal species groups are recognized in *Automate*, showing certain heterogeneity of this genus.

KEYWORDS: Crustacea, Decapoda, Caridea, Alpheidae, new species, Japan, Australia.

Introduction

The three most important general characteristics of the shrimp family Alpheidae are the robust first pereopods bearing usually an enlarged claw (with snapping mechanism in some genera), the posterior margin of the carapace having a well-developed cardiac notch, and the eye-stalks being dorsally at least partly, often

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completely covered by the anterior projections of the carapace (Coutière, 1899; Chace, 1988; Chace and Kensley, 1992). In many alpheid genera these projections form the so-called ‘orbital hoods’, which conceal the eye-stalks in dorsal, lateral and sometimes in frontal view. In some other genera, only the proximal half of the eye-stalks is covered, not by the distinct orbital hoods but rather by the latero-proximal section of the rostrum dorsally and the protruding extra-corneal teeth laterally or dorso-laterally. However, only three genera, *Automate* De Man, 1888, *Bermudacaris* Anker and Iliffe, 2000 and *Coronalpheus* Wicksten, 1999, are unique within the family in having the eye-stalks completely or almost completely exposed in dorsal view, without any trace of extra-orbital teeth.

In this paper, two new species, which appear to belong to *Automate* and *Bermudacaris*, respectively, are described from two geographically very distant localities in the Indo-West Pacific. A single female specimen collected intertidally in Hakodate Bay, southern Hokkaido, Japan, is assigned to a new species, *Automate hayashii* sp. nov. The new species represents the northern-most record of *Automate* in the world, as well as one of the most northern records of the Alpheidae in the western Pacific Ocean (Komai *et al.*, 1992; Hayashi, 2002). *Automate hayashii* sp. nov. appears closest to the poorly known *A. salomoni* Coutière, 1908 described from Chagos Islands, central Indian Ocean.

Another new species, *Bermudacaris australiensis* sp. nov., is described on the basis of a single specimen dredged at a depth of 38 m on the North-West Shelf situated in the Indian Ocean off Western Australia. This specimen, deposited in the collection of the Museum and Art Gallery of the Northern Territory, Darwin, was tentatively identified by the late D. M. Banner as *Automate dolichognatha* De Man, 1888, and later re-identified by Prof. Dr Y. Miya of Nagasaki University, Japan, as ‘*Automate truncata* n. sp.’. Surprisingly, close examination of this incomplete specimen revealed that the specimen was not referable to *Automate*, but showed strong affinity with *Bermudacaris harti* Anker and Iliffe, 2000, known only from anchialine caves of Bermuda in the western Atlantic Ocean. The new species is thus assigned to *Bermudacaris* with a minor emendation of the generic diagnosis provided by Anker and Iliffe (2000).

Anker (2001b) mentioned that three alpheid genera, *Automate*, *Bermudacaris* and *Coronalpheus* Wicksten, 1999 are closely related and form a clade characterized by dorsally exposed eye-stalks and several other features. In this study, we attempt a preliminary review of the relationships among these three genera, although a thorough revision of these genera, and particularly *Automate*, is beyond the scope of this paper. However, we propose to divide *Automate* in three informal species groups, here named and diagnosed as *A. dolichognatha* species group, *A. evermanni* species group and *A. hayashii* species group. *Automate hayashii* species group shares certain characteristics with *Coronalpheus*, suggesting a possible phylogenetic heterogeneity of *Automate*.

The holotype of *Automate hayashii* sp. nov. is deposited in the Natural History Museum and Institute, Chiba, Japan (CBM). The holotype of *Bermudacaris australiensis* sp. nov. remains deposited in the Museum and Art Gallery of the Northern Territory, Darwin, Australia (NTM). The comparative specimens used in this study are deposited in the Muséum National d’Histoire Naturelle, Paris, France (MNHN) and the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM). The size of specimens is indicated by carapace length (CL) measured in millimetres from the tip of the rostrum to the mid-point

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of the postero-dorsal margin of the carapace and/or total length (TL) measured in millimetres from the tip of the rostrum to the posterior end of the telson. The following species were examined for comparative purposes:

- Automate salomoni* Coutière, 1908: one ovigerous female, holotype (TL 17.5 mm), MNHN-Na 13749, Salomon Island, Chagos Archipelago, Percy Sladen Trust Expedition.
- Coronalpheus natator* Wicksten, 1999: one ovigerous female, paratype (CL 6.6 mm), USNM 287088, Devil's Crown, Isla Onslow, north of Isla Floreana, Galapagos, reef, 15 m, 18 August 1998, M. K. Wicksten coll.
- Bermudacaris harti* Anker and Iliffe, 2000: one ovigerous female (CL 4.5 mm), USNM 310840, Green Bay Cave, New Harrington Sound Passage, Bermuda, caught by hand while swimming in mid-water about 15 m deep, 27 August 1981, D. Williams coll. One female (CL 4.4 mm) and one juvenile, MNHN-Na 13696, Deep Blue Cave, Bermuda, 14 March 2003, T. Iliffe coll.

Taxonomic part

Family ALPHEIDAE Rafinesque, 1815

Genus *Automate* De Man, 1888

Automate hayashii sp. nov.

(figures 1–4)

Material examined. HOLOTYPE: non-ovigerous female (CL 8.5 mm, TL 26.0 mm), CBM-ZC 6559, tidal flat at Kamiiso, Hakodate Bay, southern Hokkaido, Japan, intertidal, 16 May 1991, S. Goshima coll.

Description. Carapace glabrous. Frontal region with very shallow orbital concavities on either side of very short, broad rostrum; rostrum distally rounded, reaching to level of antero-lateral margin of carapace, covering only medio-basal

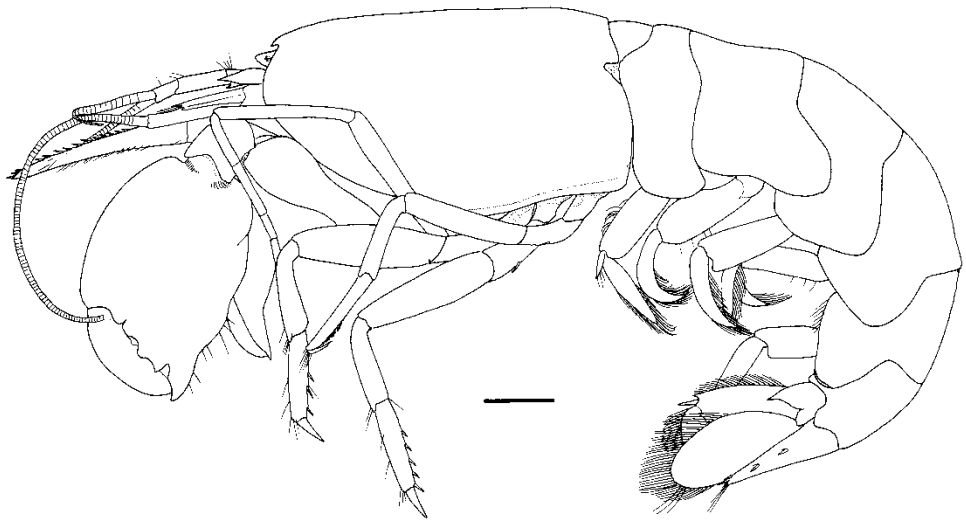


FIG. 1. *Automate hayashii* sp. nov. Holotype, female (CL 8.5 mm; CBM-ZC 6559), habitus. Scale: 2 mm.

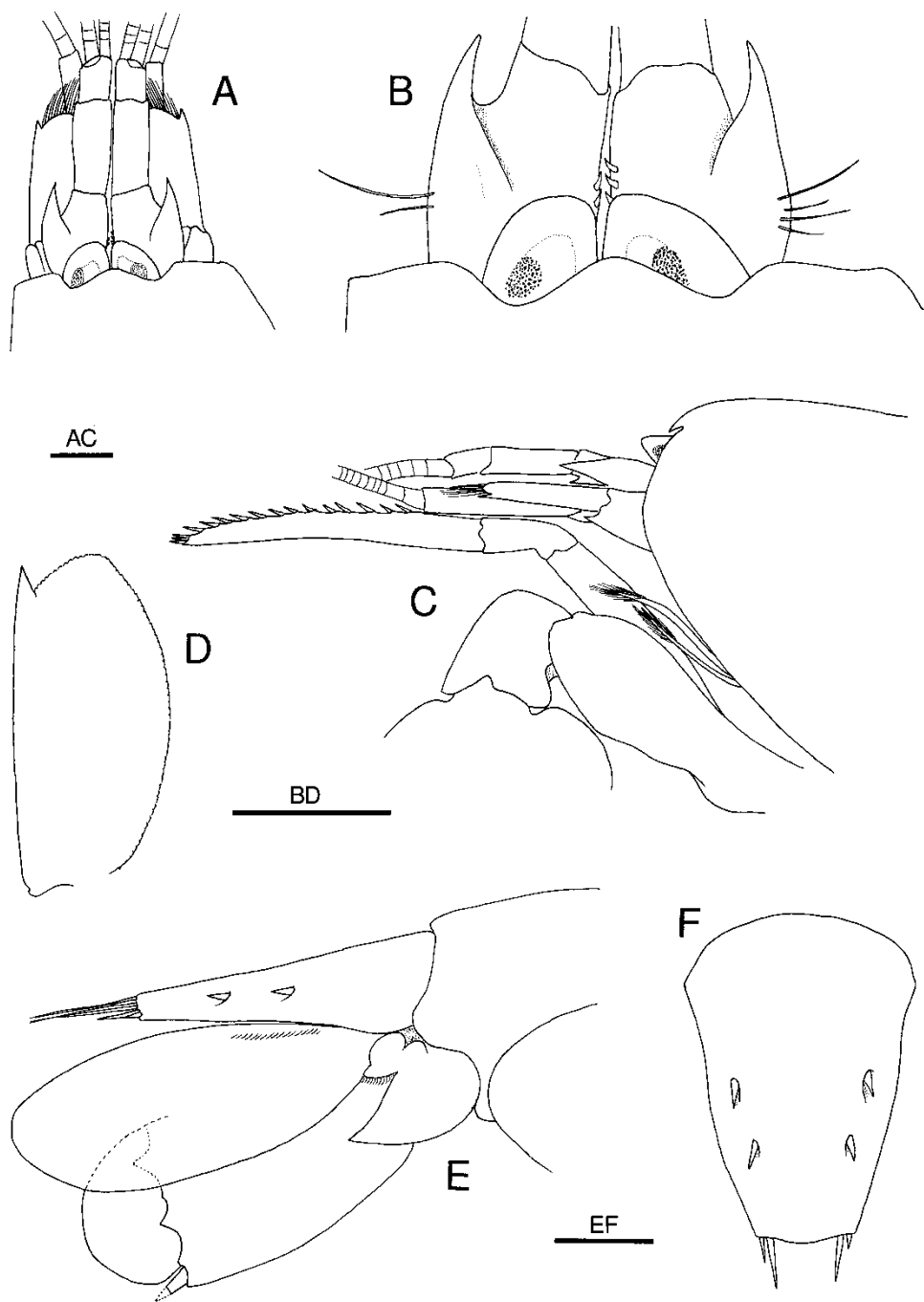


FIG. 2. *Automate hayashii* sp. nov. Holotype, female (CL 8.5 mm; CBM-ZC 6559). (A) Anterior part of carapace and cephalic appendages, dorsal view; (B) anterior part of carapace, eyes and basal segments of antennular peduncles, dorsal view; (C) anterior part of carapace, cephalic appendages and distal part of third maxilliped, lateral view; (D) right antennal scaphocerite, dorsal view (marginal setae omitted); (E) posterior part of sixth abdominal somite, telson and right uropods, lateral view (marginal setae on uropod omitted); (F) telson, dorsal view (setae omitted). Scales: 1 mm.

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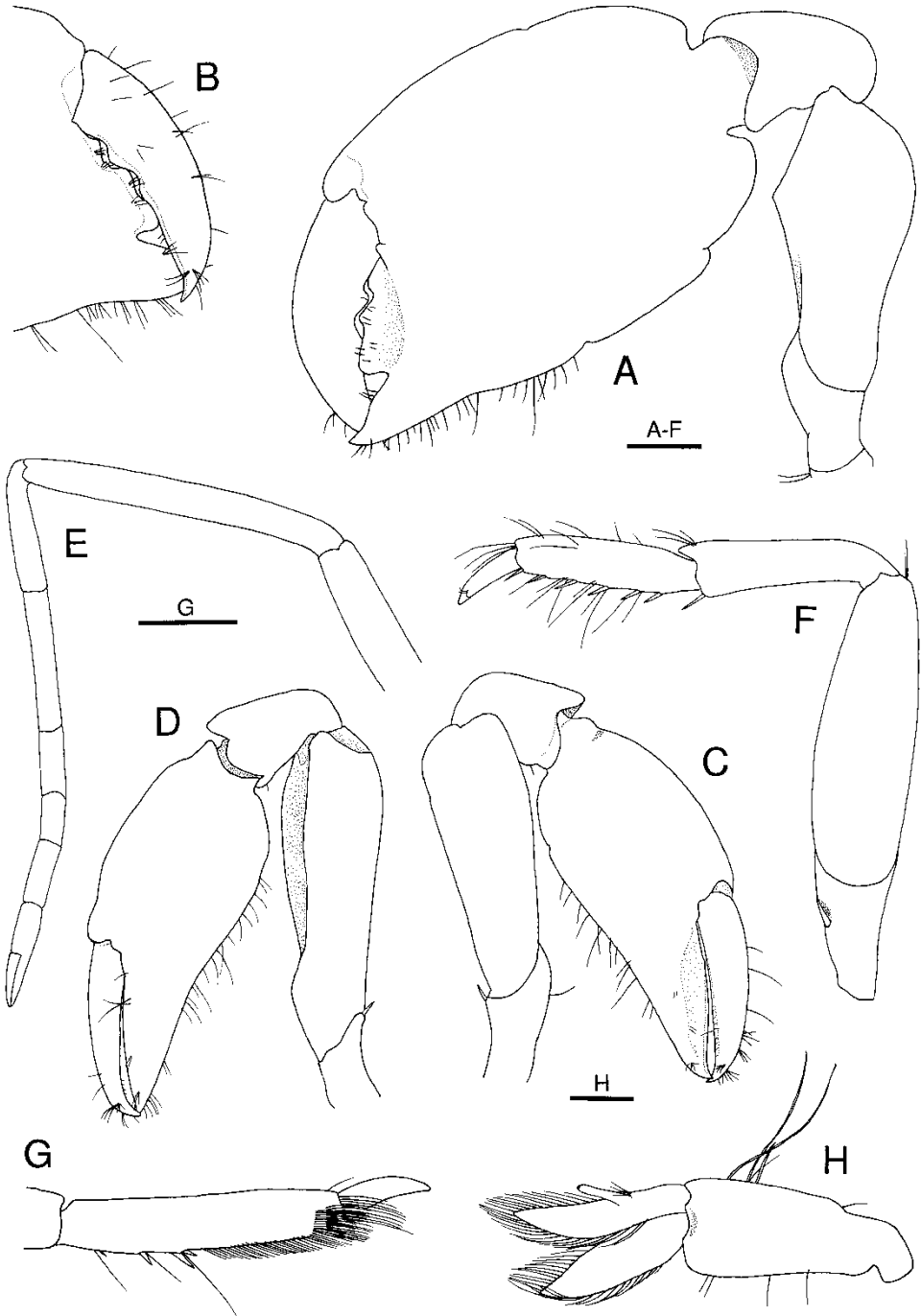


FIG. 3. *Automate hayashii* sp. nov. Holotype, female (CL 8.5 mm; CBM-ZC 6559). (A) Major left cheliped, lateral view; (B) same, dactylus and pollex, mesial view; (C) minor right cheliped, lateral view; (D) same, mesial view; (E) chela, carpus, merus and distal part of ischium of left second pereopod, lateral view; (F) left third pereopod, lateral view; (G) dactylus and propodus of left fifth pereopod, mesial view; (H) second pleopod, ventro-mesial view. Scales: 1 mm.

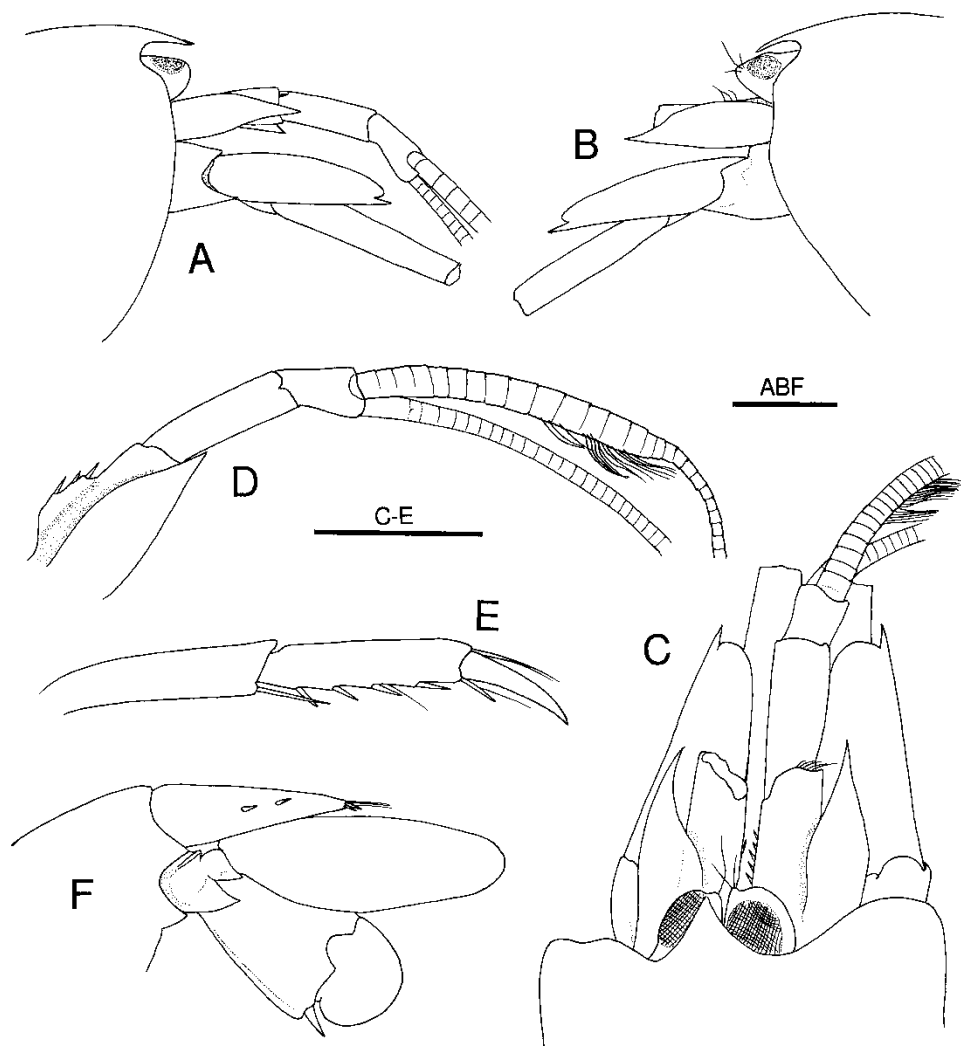


FIG. 4. *Automate salomoni* Coutière, 1908. Holotype, sex undeterminable. (A) Anterior part of carapace and cephalic appendages, right lateral view; (B) same, left lateral view (left antennular peduncle broken off); (C) same, dorsal view; (D) right antennule, lateral view; (E) dactylus, propodus and carpus of right third pereopod, lateral view; (F) sixth abdominal somite, telson and left uropod, lateral view. Scales: 1 mm.

portion of eye-stalks (figure 2A); rostral carina and orbital teeth absent. Eye-stalks exposed dorsally and laterally (figure 2B, C), mesial margins nearly parallel and mesially almost touching; cornea moderately developed, lateral (figure 2B). Pterygostomial angle rounded, continuous with branchiostegal margin (figures 1, 2C); cardiac notch conspicuous (figure 1).

Antennular peduncle with second segment somewhat longer than visible portion of first segment; dorso-mesial margin of first segment with a row of two or three small, somewhat anteriorly curved spines (figure 2B); stylocerite acute, short, not appressed, exceeding distal margin of first segment (figure 2A); ventro-mesial carina

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on first segment terminating anteriorly in acute tooth (shown under stylocerite in figure 2C); outer flagellum not subdivided, aesthetasc-bearing portion moderately thickened. Antenna with basicerite bearing strong ventro-lateral tooth; carpuccerite slender, reaching far beyond scaphocerite and exceeding distal margin of antennular peduncle (figure 2C); scaphocerite oval (figure 2D), slightly falling short of distal end of second segment of antennular peduncle, lateral margin nearly straight, disto-lateral tooth strong, not reaching bluntly angular anterior margin of blade.

Mouthparts not dissected (except second maxilliped), nevertheless appearing to be quite typical for Alpheidae. Second maxilliped without podobranch. Third maxilliped slender, over-reaching distal end of scaphocerite by full length of ultimate segment; ultimate segment armed with row of strong spines along superior margin (figure 2C); lateral plate on coxa inconspicuous; strap-like epipod and single arthrobranch present.

First pereopods (chelipeds) robust and strongly asymmetrical (figures 1, 3A–D). Major cheliped (figure 3A) with ischium unarmed; merus very stout, somewhat thickened in central portion, margins not rugose; carpus robust, cup-shaped, slightly elongated; chela somewhat compressed laterally; palm oval-shaped, slightly constricted at base; fingers in strongly oblique position to main palm axis; pollex short, robust, with one basal, triangular tooth followed by a large truncated central molar-shaped tooth and subdistal hiatus on cutting edge (figure 3B); dactylus robust, much shorter than full palm length, slightly curved, cutting edge armed with one low tooth fitting into space between basal and central tubercles of pollex (figure 3B); tips of fingers crossing. Minor cheliped (figure 3C, D) also stout, but merus and carpus more slender compared to major cheliped; superior margin of ischium distally armed with one spine (figure 3C); chela much less inflated, more slender than chela of major cheliped, constricted at base; fingers slightly shorter than palm, only slightly curved, sub-parallel to main palm axis, unarmed on cutting edge, tips crossing.

Second pereopod (figure 3E) slender, elongated, reaching to or even beyond the tip of the third maxilliped when fully extended; carpus five-articulated, second article longer than first, ratio of articles from proximal to distal approximately equal to 1:1.3:0.6:0.4:0.6. Third pereopod (figure 3F) robust, laterally compressed; ischium armed with one ventral spine; merus unarmed; carpus armed with one slender disto-ventral spine; propodus armed with five or six spines; dactylus robust, somewhat compressed laterally, slightly curved, tip subacute (figure 3F). Fourth pereopod similar to third pereopod (cf. figure 1). Fifth pereopod much more slender than third and fourth, but otherwise similar (cf. figure 1); propodus armed with two spines; propodal grooming brush well developed (figure 3G).

Abdomen with pleura of first to fifth somites rounded ventrally and covering only most basal portions of coxae of pleopods (figure 1); sixth segment without distinct articulated flap, postero-lateral projection rounded (figure 2E); preanal plate posteriorly rounded. Telson (figure 2F) broad at base, slightly tapering distally, with two pairs of dorso-lateral spines, first and second pair situated at about half and posterior three-quarters of telson length, respectively (figure 2F); posterior margin slightly convex, with two pairs of slender spines at lateral corner (inner spine about three times longer than outer spine) and numerous (dozen) setae between spines; anal tubercles absent.

Second pleopod bearing only appendix interna and a few elongated setae (figure 3H). Uropod distinctly exceeding telson (figure 2E); endopod somewhat

longer than exopod; exopod with two posterior projections bordering a shallow cleft on diaeresis (figure 2E), postero-lateral corner only weakly produced and subacute, accompanied with rather stout spine arising just mesial to it.

Gill formula typical for Alpheidae: pleurobranchs on fourth to eighth thoracic somites (above third to fifth pereopod); one arthrobranch above third maxilliped; strap-like epipods (mastigobranchs) on first maxilliped to fourth pereopods; setobranchs on first to fifth pereopod.

Colour in life. Uniform light orange.

Size. Fairly large *Automate* species, attaining 8.5 mm in CL, 25.0 mm in TL.

Distribution and habitat. Presently known only from Hakodate Bay, Hokkaido, Japan, where the holotype was collected intertidally. The new species is the northern-most species of *Automate*, and one of the northern-most alpheid shrimps in the Pacific Ocean. In Japan, it is the only species of *Automate* reported from Hokkaido. Another species known from Japan, *A. dolichognatha*, is known only from warm temperate to subtropical waters from Sagami Bay southward to the Ryukyu Islands (Miyake and Miya, 1966; Hayashi, 1995; Nomura *et al.*, 1998; Nomura and Asakura, 1998).

Etymology. This new species is named in honour of our dear colleague Dr Ken-Ichi Hayashi (National Fisheries University, Shimonoseki, Japan), who contributed so much to the taxonomic and biological knowledge of shrimps in Japan and elsewhere in the world.

Discussion. The genus *Automate* was established by De Man (1888) for *A. dolichognatha* De Man, 1888, described from Pulau Tuguan, Indonesia. Although 12 species have been described in the genus, four nominal species were reduced to synonyms of *A. dolichognatha*, which is presently considered to be a highly variable, almost pantropical species (Chace, 1972, 1988; Banner and Banner, 1973). These are: *A. gardineri* Coutière, 1902 (type-locality: Maldive atolls, Gilbert Islands, Masqat and Djibouti); *A. kingsleyi* Hay, 1917 (type-locality: Beaufort, North Carolina); *A. haightae* Boone, 1931 (type-locality: Taboguilla, Gulf of Panama) and *A. johnsoni* Chace, 1955 (type-locality: Bikini Atoll, Marshall Islands). At present, the following seven species are recognized as valid other than the type species, *A. dolichognatha* (pantropical, cf. Chace, 1988): *A. evermanni* Rathbun, 1901 (western Atlantic: from North Carolina to southern Brazil; eastern Atlantic: Gulf of Guinea); *A. talismani* Coutière, 1902 (known only from Cape Verde Islands); *A. rugosa* Coutière, 1902 (Pacific coast of Mexico south to Panama), *A. salomoni* Coutière, 1908 (known only from the type-locality, Salomon Island, Chagos Archipelago); *A. anacanthopus* De Man, 1910 (Indo-West Pacific: Hong Kong, Vietnam, Indonesia, Papua New Guinea and Madagascar); *A. branchialis* Holthuis and Gottlieb, 1958 (Mediterranean Sea: France, Croatia, Israel); and *A. rectifrons* Chace, 1972 (Caribbean Sea: Quintana Roo, Mexico, and possibly Antigua Island) (e.g. Rathbun, 1901; Coutière, 1902, 1908; De Man, 1911; Holthuis, 1951; Holthuis and Gottlieb, 1958; Ledoyer, 1970; Chace, 1972, 1888; Banner and Banner, 1973; Wicksten, 1981; Dworschak and Coelho, 1999). Chace (1988) remarked that the true identity of *A. talismani* remains unclear, but in the absence of more data he preferred to treat it as a distinct species, as did Banner and Banner (1973).

We are not fully convinced by the synonymies proposed by the previous authors, as recent studies have revealed the existence of many sibling or cryptic species in Alpheidae (e.g. Knowlton and Keller, 1983, 1985; Knowlton and Mills,

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1992; Williams *et al.*, 1999; Anker, 2000, 2001a). Although a thorough review of the genus *Automate* is beyond the scope of this paper, we would like to suggest that at least *A. gardineri* and *A. johnsoni* might be valid and would need to be resurrected. The generic assignment of *A. salomoni* and *A. talismani* remains not fully confirmed, as these two species are represented by one damaged holotype of unknown sex and two apparently lost syntypes, respectively. Wicksten (1999) recommended a comparison between *Coronalpheus natator* Wicksten, 1999 and the above-mentioned two species of *Automate*.

The present new species is assigned to *Automate* on account of the following features (De Man, 1888; Chace, 1988; Holthuis, 1993): the sixth abdominal somite lacks an articulated plate at the postero-lateral angle; the eye-stalks are juxtaposed and fully exposed in the dorsal view; at least the anterior two pairs of pereopods bear a strap-like epipod. Within *Automate*, *A. hayashii* sp. nov. appears to be closest to the poorly known *A. salomoni*. Coutière's (1908) original description of *A. salomoni* was not accompanied by illustrations, but subsequently he (Coutière, 1921) published somewhat diagrammatic figures of this species. To ascertain the affinities and differences between the two species, the holotype of *A. salomoni* deposited in the MNHN has been re-examined. The holotype is lacking most of its thoracic appendages, including chelipeds. Beside the lack of the appendages, however, the specimen was in reasonably good condition (figure 4). The similarities between the two species are confirmed: they share indeed several important characters, such as the clearly formed, broad rostrum, the uropodal endopod being longer than the exopod, and the ventro-mesial carina on the basal segment of the antennular peduncle produced anteriorly in a small acute tooth. Nevertheless, *Automate hayashii* sp. nov. is specifically distinct from *A. salomoni*, differing in the broadly rounded and shorter rostrum (compare figures 2A and 4C) and the more robust third pereopod (compare figures 3F and 4E). Further, the disto-lateral spine of the scaphocerite does not exceed the anterior margin of the blade in *A. hayashii* sp. nov. (figure 2D), rather than distinctly over-reaching it, as is the case in *A. salomoni* (figure 4C).

Genus *Bermudacaris* Anker and Iliffe, 2000

***Bermudacaris australiensis* sp. nov.**

(figures 5–7)

Material examined. HOLOTYPE: ovigerous female (CL 2.7 mm, TL *ca* 9 mm), NTM Cr-000476, north-west shelf, Western Australia, 19°54.0'S, 117°52.2'E, depth 38 m, 7 April 1983, FRV 'Soela', P. Blyth, coll.

Description. Carapace smooth; rostrum very short, broad, distally rounded, reaching level of antero-lateral margin of carapace (figure 5A); rostral carina and orbital teeth absent; orbital concavity very shallow; antero-lateral margin continuous with ventro-lateral margin without formation of pterygostomial angle; cardiac notch conspicuous (figure 5C). Eye-stalks exposed dorsally and laterally (figure 5A, B), mesial margins not parallel and separated from each other by median space; cornea well pigmented, occupying most of distal third of eye-stalk (figure 5A).

Antennular peduncle with second segment as long as visible portion of first segment; stylocerite short, not appressed, not reaching distal margin of first segment, tip acute (figure 5A); ventro-mesial carina on first segment low,

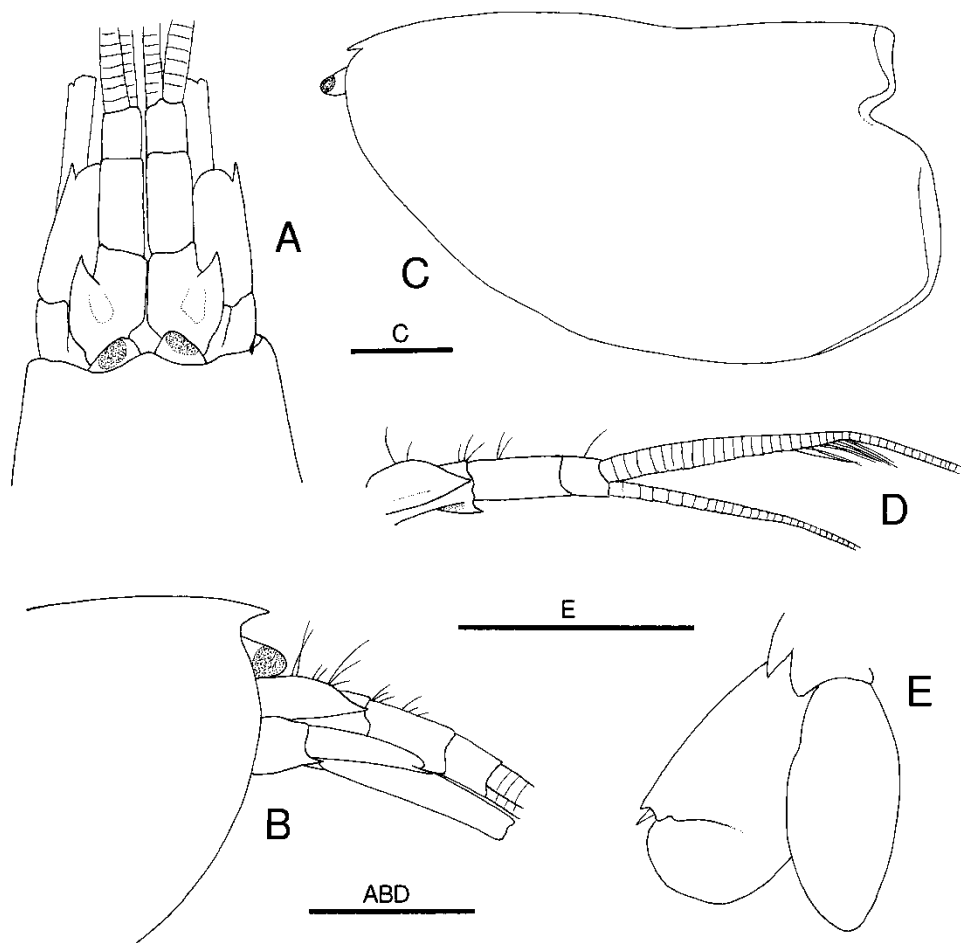


FIG. 5. *Bermudacaris australiensis* sp. nov. Holotype, ovigerous female (CL 2.7 mm; NTM-Cr 000476). (A) Anterior part of carapace and cephalic appendages, dorsal view; (B) same, lateral view; (C) carapace and eye, lateral view; (D) right antennule, lateral view; (E) left uropod, dorsal view. Scales: 1 mm.

terminating anteriorly in acute tooth (figure 5D); outer flagellum not subdivided. Antenna with basicerite bearing ventro-lateral tooth; carpopocrite slender, twice as long as scaphocerite and exceeding distal margin of antennular peduncle (figure 5B); scaphocerite rectangular-oval in general outline, with nearly straight lateral margin, nearly reaching distal margin of second segment of antennular peduncle, with strong disto-lateral tooth slightly over-reaching distal margin of rounded blade (figure 5A).

Mouthparts typical for Alpheidae (figure 6A–E). Second maxilliped with bilobed podobranch (figure 6E). Third maxilliped (figure 6F) elongated, reaching far beyond distal end of antennal peduncle; antepenultimate segment robust; ultimate segment armed with strong spines on distal half of superior margin; lateral plate on coxa conspicuous, rounded oval in shape (figure 6G, H); exopod short, not reaching

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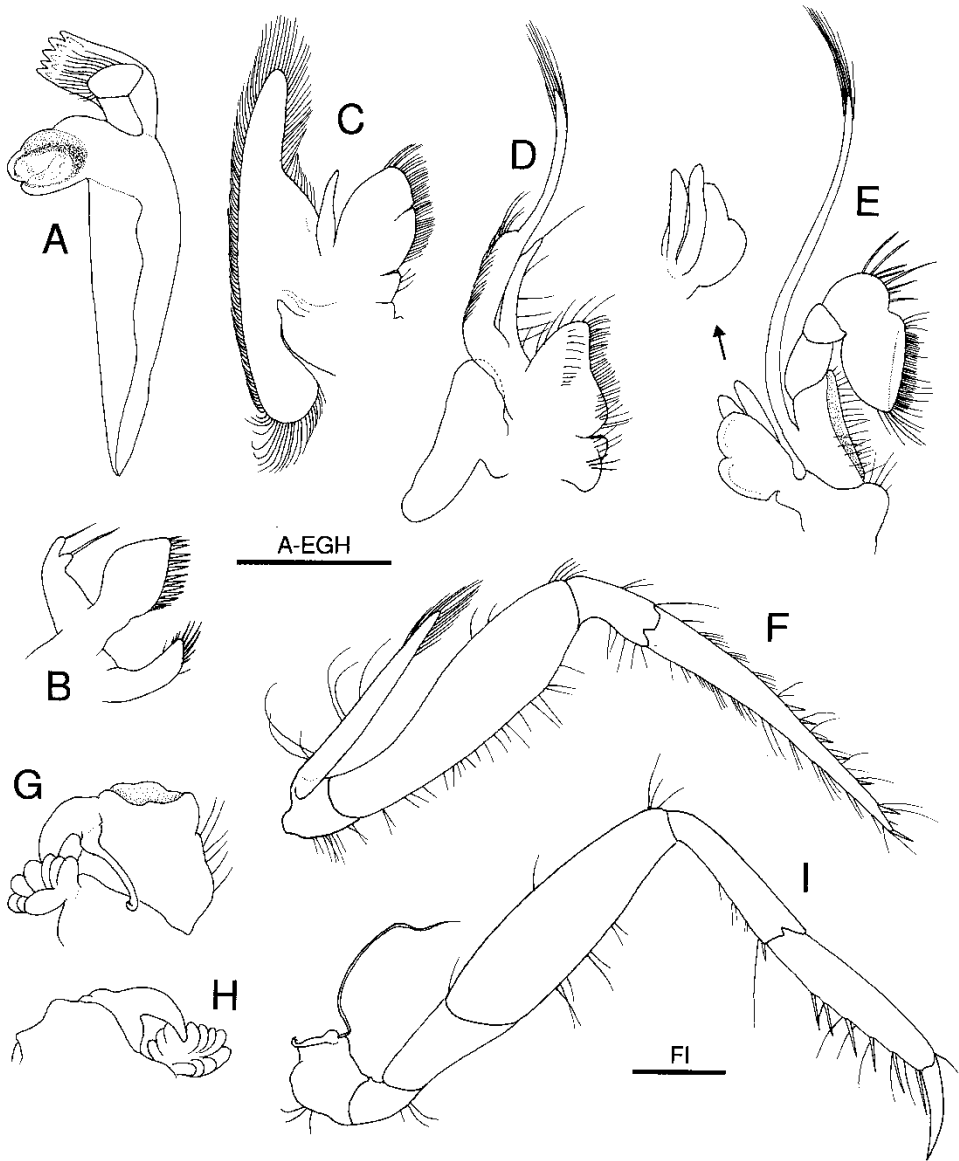


FIG. 6. *Bermudacaris australiensis* sp. nov. Holotype, ovigerous female (CL 2.7 mm; NTM-Cr 000476). Right appendages. (A) Mandible, mesio-ventral view; (B) maxillule, ventral view; (C) maxilla, ventral view; (D) first maxilliped, ventral view; (E) second maxilliped, ventral view; inset, epipod and podobranch, dorsal view; (F) third maxilliped, lateral view; (G) basal part of third maxilliped, showing epipod, coxal lateral process and arthrobranch, ventro-lateral view; (H) same, dorsal view; (I) third pereopod, lateral. Scales: 0.5 mm.

distal third of antepenultimate segment; strap-like epipod and single arthrobranch present.

First pereopods (chelipeds) robust, symmetrical, carried extended, elevated; ischium with two curved spines on superior margin (figure 7A, B); merus stout,

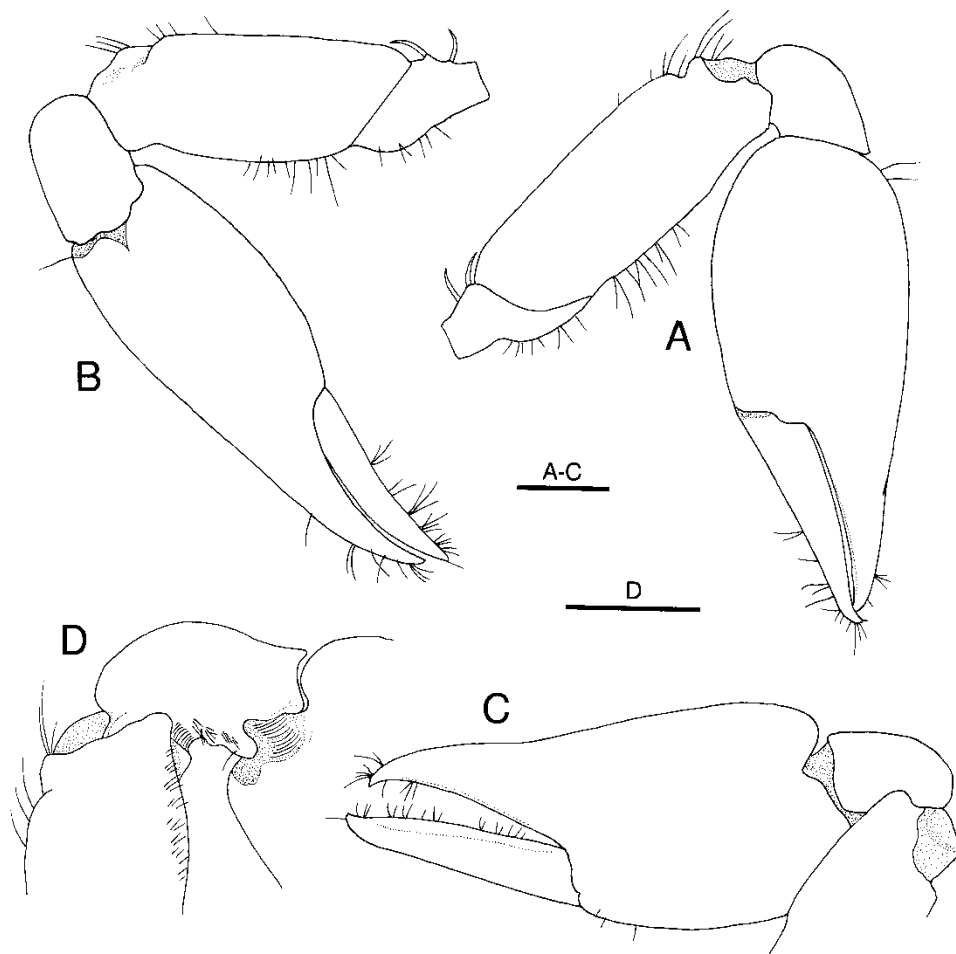


FIG. 7. *Bermudacaris australiensis* sp. nov. Holotype, ovigerous female (CL 2.7 mm; NTM-Cr 000476). (A) Right cheliped, lateral view; (B) same, mesial view; (C) same, chela, mesial view; (D) proximal part of chela, carpus and distal part of merus of left cheliped, mesial view. Scale: 0.5 mm.

margins straight, ventral margin distally with rows of setae (figure 7D); carpus robust, relatively large, cup-shaped (figure 7D); chela laterally compressed; palm oval-shaped, depressed proximal to carpo-propodal articulation, otherwise without sculpture; fingers as long as palm, dactylus in ventral to ventro-lateral position (figure 7A, C), slightly longer than pollex, cutting edges unarmed (figure 7C).

Second pereopods missing. Third pereopod (figure 6I) robust, compressed laterally; ischium unarmed; merus unarmed; carpus armed with small disto-ventral spine; propodus armed with four or five slender spines; dactylus subconical, slightly curved, slightly less than half as long as propodus, tip acute. Fourth and fifth pereopods missing.

First to fifth abdominal somites with pleura rounded ventrally and covering only most basal portions of pleopod coxae. Sixth somite without articulated flap,

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postero-lateral projection rounded; preanal plate rounded. Telson obviously dissected (detached at basis), but missing.

Uropod with endopod nearly as long as exopod; exopod with weak postero-lateral tooth and small movable spine arising just mesial to postero-lateral tooth, diaeresis weakly developed, laterally sinuous (figure 5E).

Gill formula as given for genus by Anker and Iliffe (2000): pleurobranchs on first to fifth pereopods; single arthrobranch above third maxilliped; podobranch on second maxilliped; exopods on all three maxillipeds; strap-like epipods (mastigobranchs) on first maxillipeds to fourth pereopods; setobranchs on first to fifth pereopods.

Colour in life. Unknown.

Size. Small species, ovigerous female 2.7 mm in CL, about 9 mm in TL.

Distribution and habitat. Presently known only from North-West Shelf off Western Australia, where the unique specimen was dredged from the depth of 38 m.

Etymology. The specific name of the species refers to the collection locality in a broader geographic sense, the continent of Australia.

Discussion. The holotype of this new species is somewhat damaged. The second, fourth and fifth pereopods and the telson are missing; most of the preserved pereopods were removed at the basis-ischium articulation; the palm of the left cheliped is damaged, too. Nevertheless, most body parts and the appendages that are important to make a definite identification of the generic and specific status are present. The new species is assigned with little doubt to *Bermudacaris*, based on the following features: (1) rostrum short, rounded; (2) podobranch present on the second maxilliped; (3) chelipeds symmetrical, with dactyli situated in ventral position; (4) ventro-mesial carina of the first antennular segment armed with an acute tooth distally; (5) ventral margin of the propodus of the third pereopod bearing a row of spines; (6) dactylus of the third pereopod conical, simple; and (7) mesial margins of eye-stalks not parallel and not juxtaposed. The combination of these features would not allow the new species to be placed in either *Automate* or *Coronalpheus*.

Bermudacaris australiensis sp. nov. is the second species described in this genus, and can be easily distinguished from the type species *B. harti* by the much more robust chelipeds (especially the more stout merus); more robust third to fifth pereopods, lacking ischial spine; the shorter stylocerite; and the darkly pigmented cornea of the eye. Because of the presence of the corneal pigmentation and the absence of an ischial spine on the third pereopod in *B. australiensis* sp. nov., the original diagnosis of *Bermudacaris* is slightly modified (see below).

The habitat of *B. australiensis* sp. nov. remains unknown, all we know is that the specimen was dredged from 38 m deep and that it is apparently a marine benthic species. The discovery of *B. australiensis* sp. nov. and the recent finding of what appears to be a third, possibly yet undescribed species of *Bermudacaris* in an anchialine sinkhole on Mallorca Island in the Mediterranean Sea (T. M. Iliffe and D. Jaume, personal communication) indicates that the genus is more widely distributed in the world oceans.

Relationships among *Automate*, *Coronalpheus* and *Bermudacaris*

As already mentioned, the taxonomy of the genus *Automate* is not satisfying, and the morphological diversity indicates that *Automate* is a quite heterogeneous

Table 1. Summary of the characters distinguishing the three informal species groups in the genus *Automate*.

Features	<i>A. dolichognatha</i> group	<i>A. evermanni</i> group	<i>A. hayashii</i> group
1. Rostrum	Small, triangular	Small, triangular or absent	Broadly rounded or triangular
2. Eye-stalks	Parallel, without tubercle	Parallel, without tubercle	Subparallel, with antero-mesial tubercle in <i>A. salomoni</i>
3. Ventro-mesial carina of first antennular segment	Unarmed	Unarmed	Armed with tooth
4. Stylocerite relative to first antennular segment	Not exceeding first segment	Not exceeding first segment	Exceeding first segment
5. Scaphocerite	Somewhat reduced	Somewhat reduced	Relatively well developed
6. Second maxilliped	Without podobranch	With podobranch	Without podobranch
7. Major chela	Oval or sub-rectangular	Variable (more or less rounded)	Rounded in <i>A. hayashii</i>
8. Propodus of third pereopod	With row of spines	With long, stiff setae	With row of spines
9. Dactyli of third to fifth pereopods	Subconical	Subspatulate	Subconical
10. Uropodal endopod relative to exopod	Slightly exceeding exopod	Slightly exceeding exopod	Clearly exceeding exopod
11. Diaeresis of uropodal exopod	With two blunt teeth	Smooth	With two blunt teeth

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assemblage. The genus can be divided into three informal species groups by a number of morphological characters (summarized in table 1):

Automate dolichognatha species group, with two species, *A. dolichognatha* s. l. and *A. talismani*. The species group is characterized by: (1) rostrum not concealing eye-stalks, very short, triangular, not reaching to level of antero-lateral margin of carapace; (2) eye-stalks parallel and mesially juxtaposed; (3) ventro-mesial carina on first segment of antennular peduncle unarmed; (4) stylocerite usually not reaching distal margin of first segment of antennular peduncle; (5) scaphocerite somewhat reduced, not reaching distal margin of second segment of antennular peduncle; (6) second maxilliped without podobranch; (7) major chela oval or sub-rectangular in general outline; (8) propodus of third pereopod armed with spines; (9) dactyli of third to fifth pereopods simple, subconical; (10) uropodal endopod only slightly exceeding exopod; (11) diaeresis on uropodal exopod bearing dorsally two blunt teeth.

Automate evermanni species group, with five species, *A. evermanni*, *A. rectifrons*, *A. rugosa*, *A. branchialis* and *A. anacanthopus*. This species group is characterized by: (1) rostrum not concealing eye-stalks, very short, triangular, not reaching to level of lateral margins of frontal concavity, completely reduced in *A. rectifrons*; (2) eye-stalks parallel and mesially juxtaposed; (3) ventro-mesial carina on first segment of antennular peduncle unarmed; (4) stylocerite not reaching distal margin of first segment of antennular peduncle; (5) scaphocerite somewhat reduced, not reaching distal margin of second segment of antennular peduncle; (6) second maxilliped with podobranch; (7) major chela variable in shape, more or less rounded in general outline, sometimes with inferior margin constricted, mesial face usually densely covered with anteriorly directed setae, fingers sometimes largely gaping; (8) propodus of third pereopod without spines, instead with long stiff setae; (9) dactyli of third to fifth pereopods subspatulate; (10) uropodal endopod only slightly exceeding exopod; (11) diaeresis on uropodal exopod devoid of teeth.

Automate hayashii species group, with presently two species included, *A. salomoni* and *A. hayashii* sp. nov. The inclusion of *A. salomoni* in the *A. hayashii* species group is tentative because of the incompleteness of the unique type specimen of *A. salomoni*. This species group can be defined by: (1) rostrum concealing at least most basal mesial portion of eye-stalks, broadly triangular (*A. hayashii* sp. nov.) or triangular (*A. salomoni*), reaching or slightly overarching level of antero-lateral margin of carapace; (2) eye-stalks subparallel, with small antero-mesial tubercle in *A. salomoni*; (3) ventro-mesial carina on first segment of antennular peduncle terminating anteriorly in acute tooth; (4) stylocerite overreaching distal margin of first segment of antennular peduncle; (5) antennal scaphocerite relatively well developed, reaching or nearly reaching distal margin of second segment of antennular peduncle; (6) second maxilliped without podobranch; (7) major chela more or less rounded in general outline (in *A. hayashii* sp. nov., unknown in *A. salomoni*); (8) propodus of third pereopod armed with spines; (9) dactyli of third to fifth pereopods subconical; (10) uropodal endopod reaching far beyond exopod; (11) diaeresis on uropodal exopod with two blunt teeth.

Notably, *Coronalpheus natator* Wicksten, 1999, the type species of the monotypic genus *Coronalpheus* Wicksten, 1999, shares several characters with the *A. hayashii* species group (cf. figure 8). These characters include: triangular rostrum; ventro-mesial carina on basal segment of antennular peduncle terminating anteriorly in sharp tooth; scaphocerite not markedly reduced, reaching distal margin of second segment of antennular peduncle; uropodal endopod distinctly

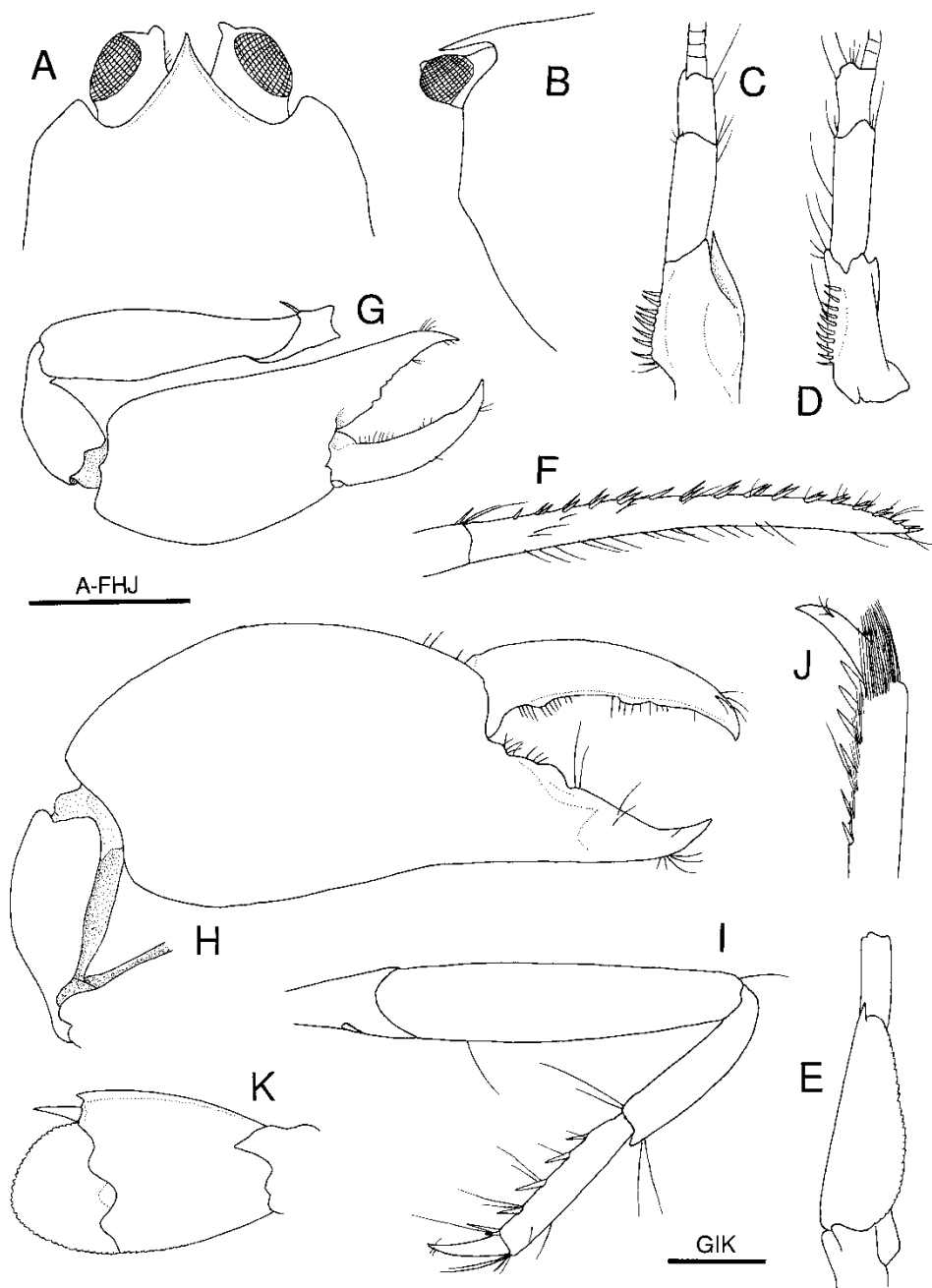


FIG. 8. *Coronalpheus natator* Wicksten, 1999. Paratype, ovigerous female (CL 6.6 mm; USNM 287088). (A) Anterior part of carapace and eyes, dorsal view; (B) same, lateral view; (C) left antennular peduncle, ventro-mesial view; (D) same, dorso-mesial view; (E) left antenna, dorsal view; (F) ultimate segment of right third maxilliped, lateral view; (G) major left cheliped, lateral view; (H) same, carpus and chela, mesial view; (I) right third pereopod, lateral view; (J) dactylus and distal part of propodus of fifth pereopod, mesial view; (K) exopod of left uropod, dorsal or ventral view. Scales: 1 mm.

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over-reaching exopod. Nevertheless, *Coronalpheus natator* differs from all *Automate* species in having the rostrum much more elongated (figure 8A); the eye-stalks clearly separated and divergent (not parallel and not mesially touching) (figure 8A); the antero-mesial angle of the eye-stalk bearing a conspicuous tubercle (figure 8A, B) (there is a similar, although much smaller tubercle at the same position in *A. salomoni*); more slender chelipeds, with the carpi being more elongated, ventrally slightly excavated, fingers more slender, and the pollex of the major chela armed with a single, large tooth in adult males (figure 8G, H). These differences seem to warrant a full generic status for *Coronalpheus*. Furthermore, future phylogenetic study may eventually reveal that *Automate* is a non-monophyletic group; in this case the three informal species groups recognized herein could be considered as distinct genera.

At an earlier stage of this study, the presence of a row of small spines on the dorso-mesial margin of the first segment of the antennular peduncle in *A. salomoni* and *A. hayashii* sp. nov. appeared to be significant in suggesting a close relationship between *A. hayashii* species group and *Coronalpheus*. However, examination of several *Automate* specimens in the MNHN collections has shown that one to three homologous spines are present on the dorso-mesial margin of the first segment of the antennular peduncle in *A. branchialis*, *A. anacanthopus*, *A. dolichognatha* s. l., and also in *Bermudacaris harti*. Although in *Coronalpheus natator* these spines are much more developed and more numerous than in *Automate* (forming a peculiar row, cf. figure 8C, D), this character should be not considered anymore as unique to *Coronalpheus*, as suggested by Wicksten (1999).

The absence of the appendix masculina in males in *Automate* is a feature generally believed to be of generic significance (Chace, 1988; Wicksten, 1999). However, the absence of the appendix masculina in males has not been confirmed in *A. salomoni* and *A. talismani*. Although the holotype of *A. hayashii* sp. nov. lacks an appendix masculina, the presence of several flexible elongated setae typical of ovigerous females suggest that this specimen is a pre- or post-ovigerous female. Wicksten (1999) stated clearly that the appendix masculina is present in the males of *C. natator*. When the absence of the appendix masculina is confirmed for all species of *Automate*, this character will further support the generic separation between *Automate* and *Coronalpheus*.

Bermudacaris can be easily separated from *Automate* and *Coronalpheus* by the symmetrical chelipeds with the dactyli situated in the ventral position (=inverted). *Bermudacaris harti*, the type species, is a troglobitic species characterized by the reduced pigmentation of corneas, a feature that was included in the diagnosis of the genus (Anker and Iliffe, 2000). Since *B. australiensis* sp. nov. has relatively well-pigmented corneas, the generic diagnosis given by Anker and Iliffe (2000) is slightly modified. The statement 'corneal pigmentation reduced or absent' is changed to 'corneal pigmentation normal or reduced to small spot'. Anker and Iliffe (2000) noted that while the two paratype males had at least a small pigmented spot, the corneas of the holotype female were almost devoid of pigment. This raised the possibility of sexual dimorphism. Recently, two more specimens of *B. harti* mentioned as 'not traced' in the original description (cf. Anker and Iliffe, 2000: 765) were finally located in the USNM collections and examined by one of us (A.A.). One is an ovigerous female carrying four large eggs, and having a clear small pigment spot in the eye-stalks. A series of 11 specimens of *B. harti* was recently collected by T. Iliffe in the Deep Blue Cave, Bermuda (T. Iliffe, personal

communication). Two of them, an adult non-ovigerous female and a juvenile specimen, both deposited in the collections of the MNHN, also have a small pigmented spot on each eye-stalk. This clearly rejects the sexual dimorphism in the eye-stalk pigmentation in *B. harti*; the quasi-absence of pigmentation in the female holotype is simply due to more advanced destruction of the pigments in ethanol.

A single specimen, collected at low tide on the Grand Récif de Tuléar (now Toliara) in the south-western part of Madagascar, referred to *Automate dolichognatha* by Ledoyer (1970), is very unusual for *Automate*. The first pereopods of Ledoyer's specimen are equal or subequal in size (cf. Ledoyer, 1970: pl. 24B), with dactyli situated clearly in ventral position (cf. Ledoyer, 1970: pl. 18, the two figures depicting the cheliped are actually upside down), which is one of the characteristics of *Bermudacaris*. However, in all other respects (frontal region, third maxilliped, second pereopod, etc.) the specimen exhibits features typical of *Automate*. Unfortunately, our efforts to locate Ledoyer's specimen in the collections of MNHN, the University of Marseilles and the Endoume Marine Station, France, were fruitless. Future collections of small alpheid shrimps in the Toliara region, south-western Madagascar, may result in a discovery of a new taxon, which appears to be intermediate between *Automate* and *Bermudacaris*.

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