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NEW SHRIMPS (FAMILIES PROCARIDIDAE AND ATYIDAE) FROM A SUBMERGED LAVA TUBE ON HAWAII

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ABSTRACT

A new genus and species of procaridid shrimp, *Vetericaris chaceorum,* and a new atyid species, *Halocaridina palahemo,* are described from the island of Hawaii. The new genus, regarded as more primitive than *Procaris,* is characterized by the possession of a larger number of gills than *Procaris,* including arthrobranchs and pleurobranchs on the third maxilliped and pereiopods 1–4, elongate pleopodal endopods, appendices internae on pleopods 3–5, and elongate dactyls on pereiopods 1–5. Reexamination of the two genera of procaridids would seem to indicate a greater affinity with the caridean shrimps than with the dendrobranchiate shrimps. The new *Halocaridina* differs from its only congener in several features, including a shorter rostrum, a more inflated carapace, and less inflated chelae. Reference to Pleistocene geological history, and present-day hydrological conditions strengthen the argument for relatively deep anchialine refugia from which dispersal took place, to explain the distribution of anchialine shrimps.

During a 1985 survey of anchialine and marine caves of the Pacific by Dr. Thomas M. Iliffe and the second author, several sites in the Hawaiian archipelago were investigated by diving with SCUBA. In the course of working in the cave called Lua o Palahemo on Hawaii Island, several crustaceans, including shrimps, isopods, and copepods were collected. These were passed on to the first author for evaluation. The discovery of an undescribed procaridid and atyid shrimp in this material revealed further problems in the relationships of the major taxa of decapod shrimps. These problems are explored in the present paper.

METHODS

Salinities were obtained with an American Optical Corporation temperature compensated refractometer, catalog number 10402.

Dissolved oxygen was measured in situ during the dives using test kits from Chemetrics Inc. Values above 1.0 ppm were obtained using their Model 0-12, K7512. Model 0.1, K7501, was used for values below 1.0 ppm.

Small animals (less than 10 mm) were collected in a Sket bottle (a squeeze bottle fitted with a one-way valve, allowing the collection of more than one animal at a time). Larger animals were collected with 30 × 30-cm plastic bags.

A plankton net, modified for hand-towing while diving, with a 72-μm filter, was used. After a dive the entire net was sealed in a plastic bag before being transported to the surface.

Description of Habitat

The lava tube cave known as Lua o Palahemo is situated on the extreme southern point of the island of Hawaii. It is less than one km east of the southwest rift zone of Mauna Loa volcano. The cave direction is parallel to this rift, which is one of the two areas of eruptive activity on Mauna Loa (Fornari *et al.,* 1979). The pond has previously been reported on by Holthuis (1973), and was surveyed by Maciolek and Brock (1974).

A minimum age of 11,780 years has been set by a radiocarbon date provided by charcoal fragments found under a surface layer of Pahala ash nine km to the northeast (Kelly *et al.,* 1979). The maximum age is uncertain; however, the lava tube must have formed during a time of lower sea level, since caves of this type usually form only subaerially (Jones and Nelson, 1970; Moore *et al.,* 1973). A maximum age of 25,000 years can be postulated if this lava tube formed during the sea-level lowering of the Wisconsin ice age (Milliman and Emery, 1968). It is unlikely that the formation of the tube took place during an earlier glaciation since the age of the southern part of the island is only 700,000 years.

The habitat on Lua o Palahemo is an anchialine pond under tidal influence, with deeper waters leading to a submerged lava tube. The surface opening is 150 m north of the shoreline at Ka Lae (South Point) (18°55′N, 155°40′42″E). The opening is 10 m in diameter, directly exposed to sunlight, with a surface temperature of about 24°C, surface salinity of 20 ppt, and a surface dissolved oxygen of 6.0 ppm. The rainfall is less than 0.5 m per year (County of Hawaii, 1972). The salinity of the ocean off the island of Hawaii at 10-m depth is 34 ppt (Barkley, 1968). The new procaridid shrimp was collected in total darkness at a depth of 33 m, 180 m from the opening. The salinity at this depth was 30 ppt, the dissolved oxygen 0.3 ppm.

The total explored length of the submerged lava tube is 305 m (see Fig. 1). From the area of collapse that formed the surface opening, the tube extends northwards towards the distant caldera for 86 m, terminating in breakdown. South from the opening the cave extends 219 m, terminating in a boulder choke 33 m below sea level. The diameter averages 4 m, and for much of its length there is a prominent lateral bench. All the cave surfaces are covered with a brown sediment, with floor deposits occasionally reaching 1.0 m in depth. Visibility was estimated at 20 m at the beginning of a dive. During the exit phase of a dive, visibility was reduced to a few centimeters as exhalation bubbles disturbed the ceiling sediment.

The area of the lava tube directly below the surface opening contained the highest density of animals. In addition to the new procaridid, four species of shrimps (*Halocaridina palahemo,* described below, *Procaris hawaiana* Holthuis, *Calliasmata pholidota* Holthuis, and an undetermined atyid), a species of sphaeromatid isopod, a harpacticoid copepod species of *Amphiascus,* and a cyclopoid halocyclopine copepod were collected. No attempt at an accurate assessment of populations was made, but it was estimated that *Procaris hawaiana* numbered in the thousands, and that the *Halocaridina* numbered in the tens of thousands. The *Calliasmata* were collected directly below the surface opening at a depth of 15 m, their population estimated at less than 100. The isopods and two species of green algae (*Valonia aegagrophila* Agardh and *Chaetomorpha antennina* (Bory) Kützing) were collected within the first meter from the surface. During the last dive two eels were found living in holes in the bottom sediment. They were about 20 cm long, pale in color, with small eyes. This section of the lava tube was in total darkness, and the dissolved oxygen less than 1.0 ppm.

Systematic Discussion

Family Procarididae

Vetericaris, new genus

Type-species.—*Vetericaris chaceorum,* new species.

Diagnosis.—Maxilliped 3 with 1 arthrobranch and 1 pleurobranch; pereiopods 1–3 each with epipod, 1 setobranch, 1 pleurobranch, 2 arthrobranchs; pereiopod 4 with epipod, 1 setobranch, 1 arthrobranch, 1 pleurobranch; pereiopod 5 lacking branchiae. Dactyls of all pereiopods moderately elongate-slender, armed with graded series of about 20 spines. Endopods of pleopods more than half length of exopods; appendices internae present on pleopods 3–5.

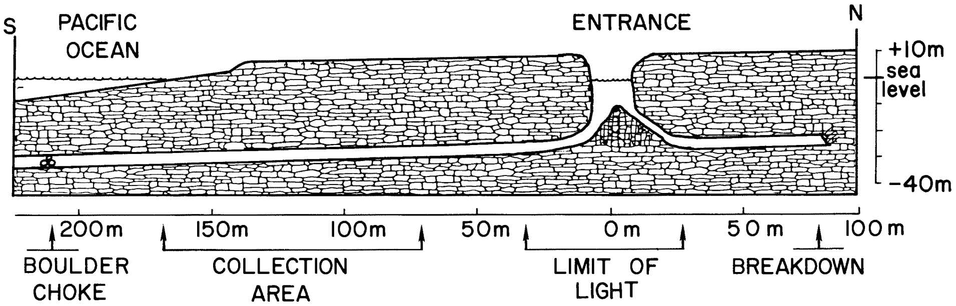

Fig. 1. Diagrammatic cross-section of Palahemo lava tube.

Etymology.—The generic name is derived from the Latin *vetus,* meaning old, and the stem word *caris,* a shrimp.

***Vetericaris chaceorum*, new species**
Figs. 2–7

Material.—Holotype ♀, USNM 211364, carapace length (cl) (including rostrum) 11.8 mm, total length (tl) 45 mm; paratype ♀, USNM 211365, dissected, cl 10.9 mm, tl 41 mm; lava tube, Lua o Palahemo, 150 m north of shoreline at Ka Lae (South Point), Hawaii Island, 18°55′N, 155°42′W, depth 33 m.

Description.—Integument thin, not particularly fragile. Rostrum (Fig. 3A) short, acutely triangular, unarmed, barely reaching midlength of eye. Carapace unarmed; anterior margin at antennal and antennular bases evenly convex, anteroventral margin with shallow sinus below hepatic region, remainder of ventral margin sloping posteroventrally; evenly inflated except for faint furrow running from near convex anterior margin to anterior branchial region. Abdomen having hinges between somites 1 and 2, 4 and 5, and 5 and 6; pleuron of somite 2 with ventral margin almost straight, posteroventrally broadly rounded; somite 3 lacking dorsal cap, pleuron posteroventrally evenly rounded; pleuron of somite 4 posteroventrally rounded, with slight indication of being produced; pleuron of somite 5 posteroventrally somewhat produced, subacute; somite 6 1.25 times length of somite 5 (measured at lateral articulation of pleuron and telson), with 2 rounded posterior lobes embracing telson; low acute tubercle in midventral line between each pair of pleopods; somite 6 with midventral tubercle on posterior margin (between uropodal bases) bearing strong posteriorly directed spine (Fig. 3E). Telson (Fig. 3B) about 1.5 times length of somite 6 (measured along middorsal line and excluding posterior spines), armed with 2 pairs of lateral spines, first pair situated just posterior to midlength; posterior margin with rounded apex extending very slightly beyond posterolateral corners, armed with 7 pairs of spines, median pair and next-to-outermost pair elongate, remainder short.

Eyestalk (Fig. 3A) distally bilobed, both lobes rounded, mesial lobe longer than lateral; faint scattered pigment visible in sinus between lobes.

Antennular peduncle (Fig. 3A) reaching distal margin of scaphocerite; stylocerite basally convex, embracing outer base of antennule, lanceolate-tapering, distally acute, reaching to proximal part of peduncle article 3; 3 peduncle articles subequal in length, article 1 with basally lobed rib on mesioventral margin; lateral flagellum reaching posteriorly to second abdominal somite, basal portion of about 10 swollen articles, bearing clusters of ventrally directed elongate setae; mesial flagellum reaching posteriorly to first abdominal somite.

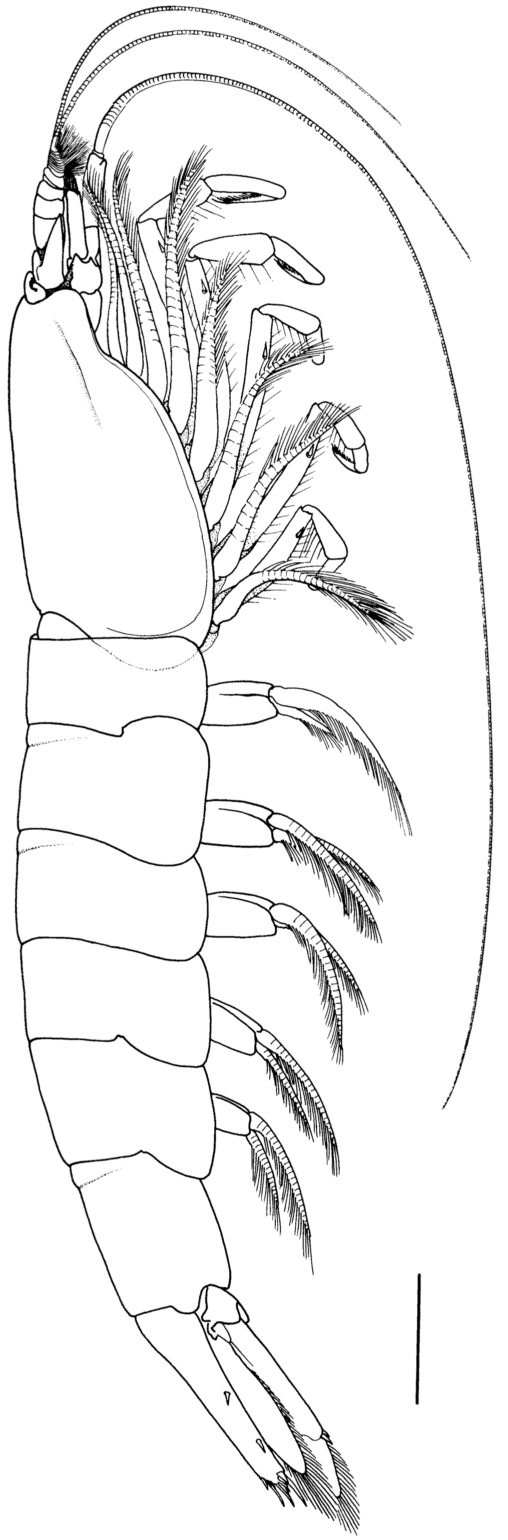

Fig. 2. *Vetericaris chaceorum*, holotype in lateral view. Scale = 5.0 mm.

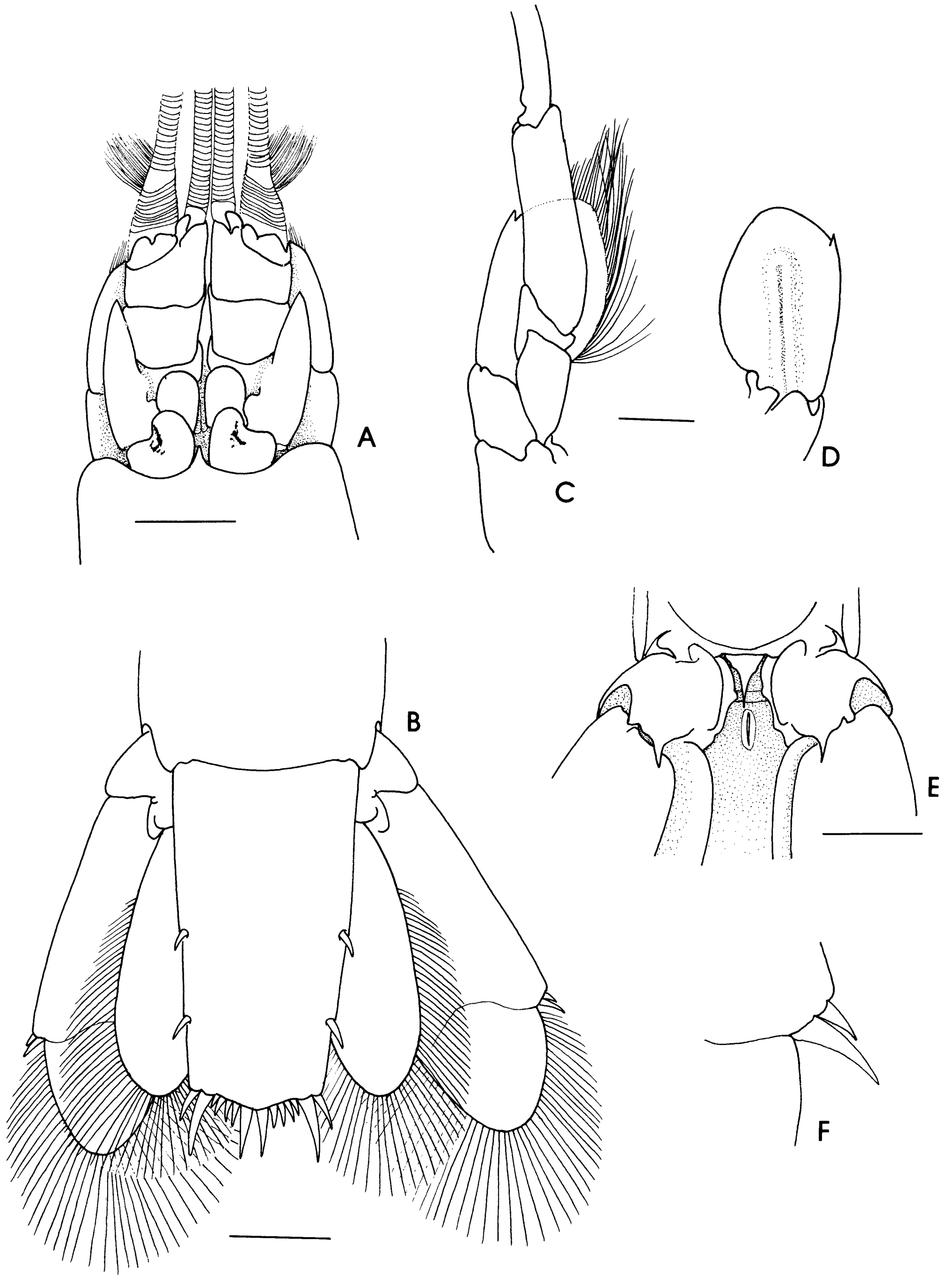

Fig. 3. *Vetericaris chaceorum*: A, anterior carapace, eyestalks, and antennae in dorsal view; B, telson and uropods in dorsal view; C, antenna; D, antennal scaphocerite; E, uropodal bases in ventral view; F, spines of outer margin of outer uropodal ramus enlarged. Scales: A, B, E = 2.0 mm; C, D = 1.0 mm.

Distal article of antennal peduncle reaching beyond scaphocerite apex by half its length (Fig. 3C, D); scaphocerite about 1.25 times longer than wide, almost subcircular in outline, lateral margin faintly convex, ending in acute tooth situated well short of rounded apex of blade, with well-defined longitudinal groove; flagellum slightly longer than total body length.

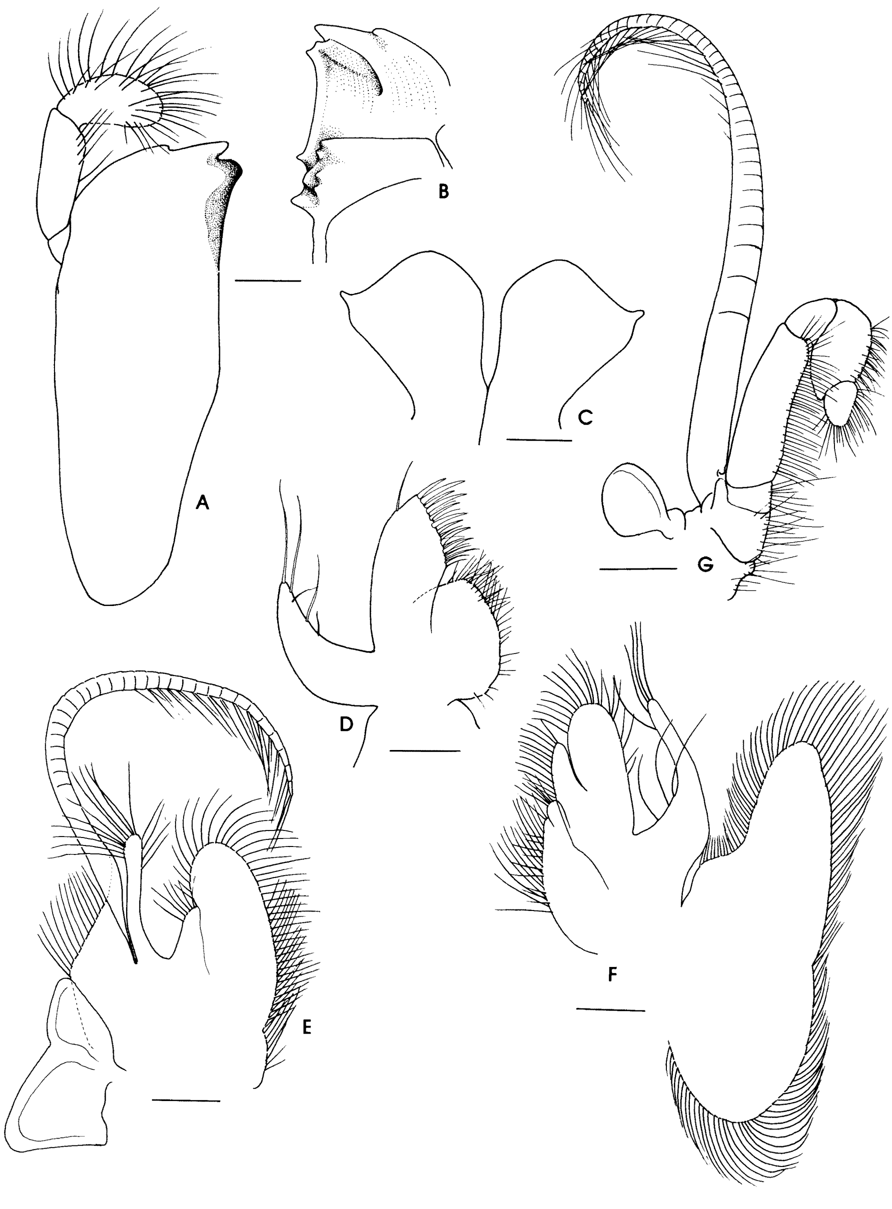

Fig. 4. *Vetericaris chaceorum*: A, mandible in outer view; B, mandible, incisor and molar area; C, paragnaths; D, maxilla 1; E, maxilliped 1; F, maxilla 2; G, maxilliped 2. Scales: A, B, C = 0.5 mm; D, E, F, G = 1.0 mm.

Mandible (Fig. 4A, B) massive; palp of 3 articles, with basal article short, article 2 about 1.25 times length of distal article; latter ovate, bearing numerous lateral and distal elongate setae; incisor and molar fused; incisor apically subacute-conical, with tricuspid sclerotized process on ventral surface; molar connected to incisor by concave bladelike ridge; molar well sclerotized, with grinding surface having 7 subconical cusps.

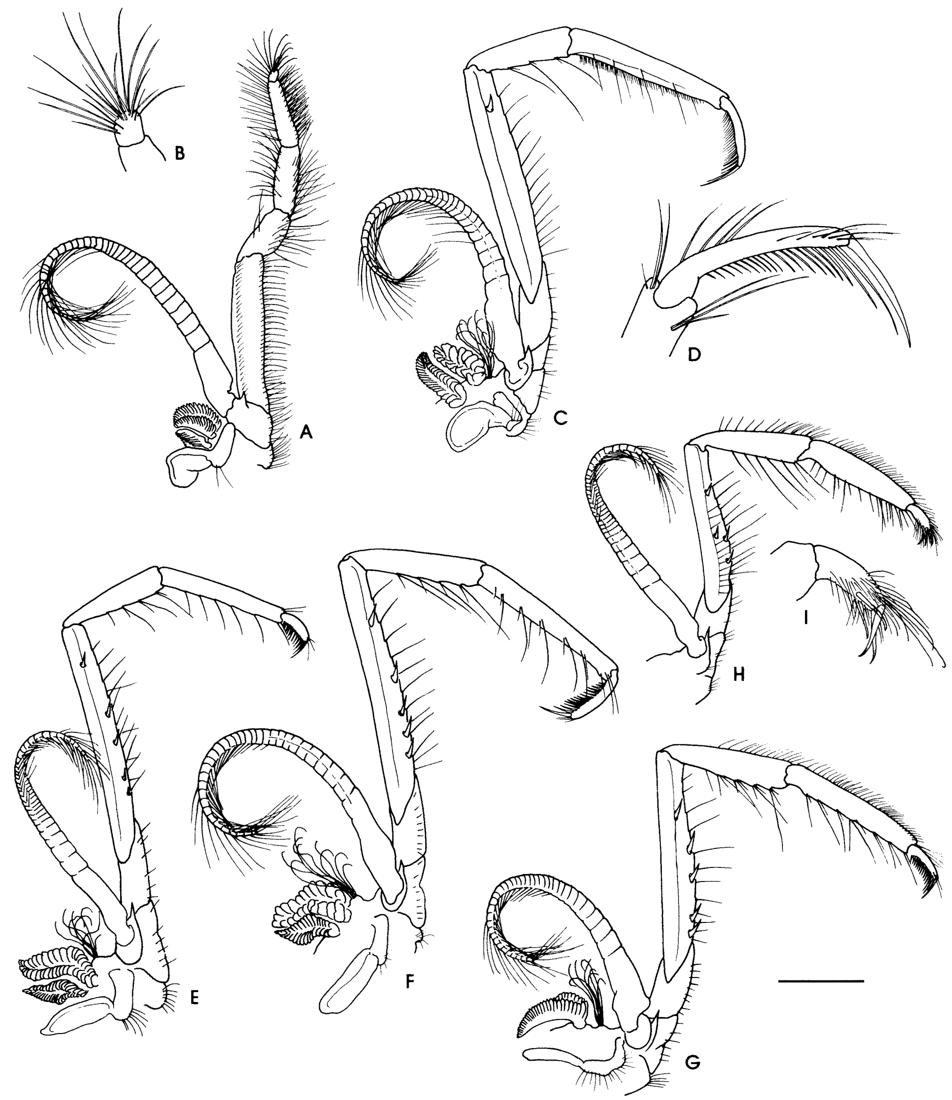

Fig. 5. *Vetericaris chaceorum*: A, maxilliped 3; B, dactyl of maxilliped 3 enlarged; C, pereiopod 1; D, dactyl of pereiopod 1 enlarged; E, pereiopod 2; F, pereiopod 3; G, pereiopod 4; H, pereiopod 5; I, dactyl of pereiopod 5 enlarged. Scale = 2.0 mm (except B, D, I).

Paragnaths broad, mesiodistally rounded, with digitiform process distolaterally (Fig. 4C).

Maxilla 1 (Fig. 4D), palp with 2 elongate distal setae and few shorter setae on anterior margin; endites broad.

Maxilla 2 (Fig. 4F), with 2 unequally cleft setose endites; palp slender, with 4 elongate distal setae; scaphognathite broad proximally.

Maxilliped 1 (Fig 4E) with ovate endite; short digitiform endopod; slight indication of caridean lobe at base of exopod; epipod broadly bilobed.

Maxilliped 2 (Fig. 4G) of 7 articles, large exopod, subcircular epipod, dactyl

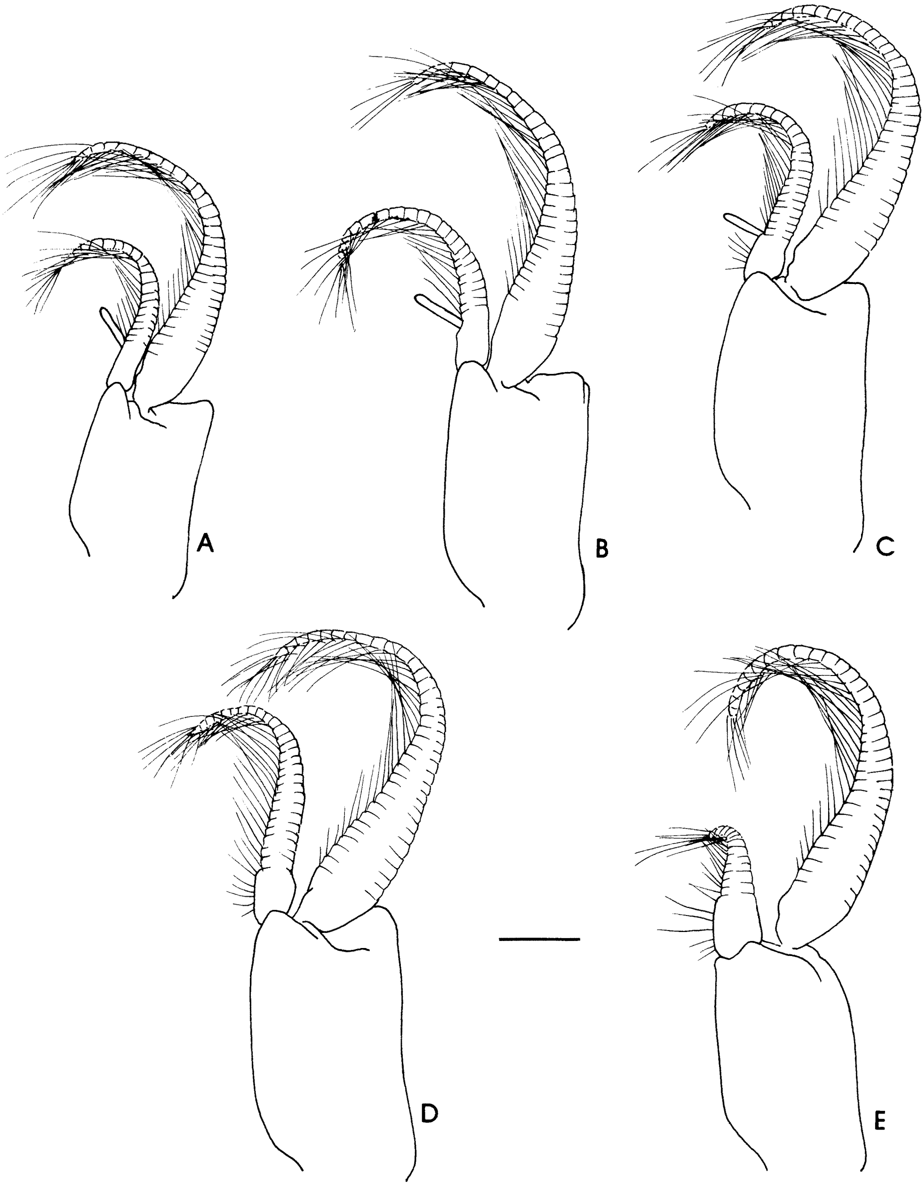

Fig. 6. *Vetericaris chaceorum*: A, pleopod 5; B, pleopod 4; C, pleopod 3; D, pleopod 2; E, pleopod 1. Scale = 1.0 mm.

barely obliquely attached, with 2 strong distal spines and numerous marginal setae.

Maxilliped 3 (Fig. 5A, B) overreaching scaphocerite by dactyl and most of propodus; of 7 articles; exopod almost as long as endopod; dactyl short, between 0.2 and 0.16 times length of propodus, setose; propodus bearing several ranks of setae over entire length; epipod subcircular, stalked; 2 well-developed arthrobranchs present.

Pereiopods similar, each with large exopod. Pereiopod 1 (Fig. 5C, D) overreaching scaphocerite by dactyl, propodus, and most of carpus; dactyl slightly less than half length of propodus (excluding terminal spines), armed with row of spines increasing in length distally, with strong elongate terminal spine; propodus with dense band of stiff setae on ventral margin; carpus slightly more than half length of propodus; merus more than twice length of dactylus, with single articulated distolateral spine; basis with short mediodistal tooth; large stalked epipod, setobranch, and 2 arthrobranchs present.

Pereiopod 2 (Fig. 5E), dactylus almost 0.25 times length of propodus, with row of spines increasing in length distally, with strong elongate terminal spine; propodus with sparse setae on mesioventral surface; carpus slightly shorter than propodus; merus about twice length of carpus, armed with 1 distolateral and 4 ventromesial articulated spines; basis with mesiodistal tooth; elongate exopod, large pedunculate epipod, 2 arthrobranchs, and 1 setobranch present.

Pereiopod 3 (Fig. 5F) with dactyl almost 0.34 times length of propodus, with row of spines increasing in length distally, with elongate terminal spine; propodus 1.4 times length of carpus, with dense ventral band of setae; merus twice length of carpus, armed with 1 distolateral and 4 ventromesial articulated spines; basis with short mesiodistal tooth; elongate exopod, larger pedunculate epipod, 2 arthrobranchs, and 1 setobranch present. In dissected paratype, genital aperture clearly visible on posterior surface of coxa.

Pereiopod 4 (Fig. 5G), dactyl slightly less than 0.34 times length of propodus, with row of spines on posterior margin becoming distally longer, with elongate terminal spine; propodus with dense band of setae ventrally; carpus about 0.85 times length of propodus; merus armed with 1 distolateral and 4 ventromesial articulated spines; basis with short mesiodistal tooth; elongate exopod, slender pedunculate epipod, 1 arthrobranch, and 1 setobranch present.

Pereiopod 5 (Fig. 5H, I), dactylus 0.28 times length of propodus, distally bluntly rounded, bearing numerous setae and 4 distal spines; propodus with dense lateral band of setae, equal in length to carpus; merus with 2 mesiolateral and 2 ventral articulated spines, about 1.34 times length of carpus; basis with short mesiodistal spine; strong exopod present; epipod and branchiae absent.

Pleopod 1 (Fig. 6E), endopod about 0.34 times length of exopod; pleopod 2 (Fig. 6D) endopod 0.75 times length of exopod. Pleopods 3–5 (Fig. 6A–C) similar, each with appendix interna, endopod 0.75 times length of exopod.

Uropod, inner ramus parallel-sided, distally evenly rounded, barely reaching telsonic apex, bearing numerous marginal plumose setae; outer ramus reaching beyond telsonic apex, with lateral notch at distal 0.6 of length, notch having 2 articulated spines, inner longer.

The branchial formula is as follows (see Fig. 7):

Maxilliped 1	epipod	—	—	—
Maxilliped 2	epipod	—	—	—
Maxilliped 3	epipod	1 arthrobranch	1 pleurobranch	—
Pereiopod 1	epipod	2 arthrobranchs	1 pleurobranch	1 setobranch
Pereiopod 2	epipod	2 arthrobranchs	1 pleurobranch	1 setobranch
Pereiopod 3	epipod	2 arthrobranchs	1 pleurobranch	1 setobranch
Pereiopod 4	epipod	1 arthrobranch	1 pleurobranch	1 setobranch
Pereiopod 5	—	—	—	—

Foregut with lateral teeth consisting of regular row of small spinelike structures; median tooth strong, as in *Procaris*.

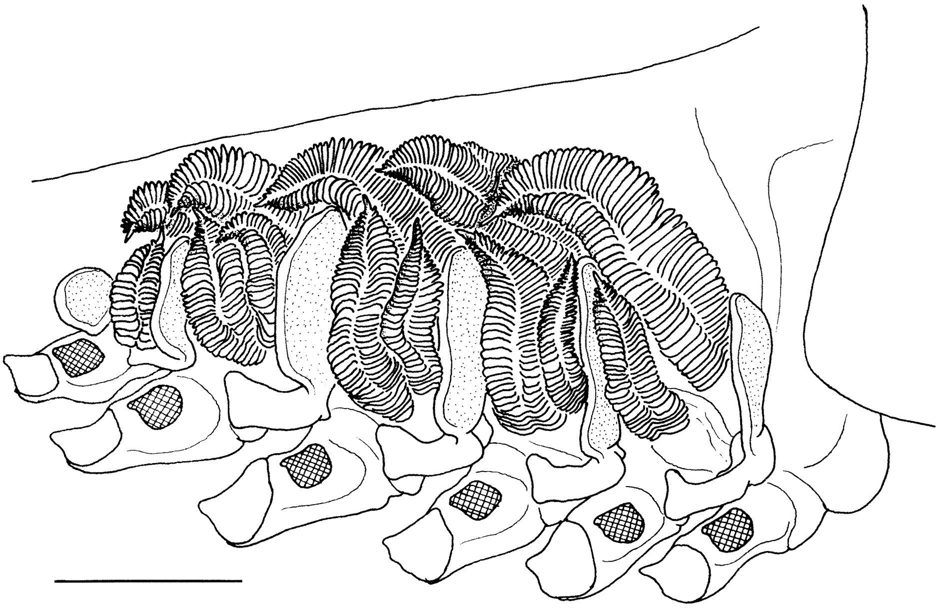

Fig. 7. *Vetericaris chaceorum*: Left branchial chamber showing gill arrangement. Scale = 2.0 mm.

Observations on Live Animals.—On three dives, *Vetericaris* was sighted five times, but only two animals were collected. The shrimp is a strong swimmer in midwater, and was never observed sitting still or walking on the cave walls. If, while swimming, the shrimp made contact with the cave wall, it changed direction and swam away. The animals swim upright, holding the legs steady in a basket formation beneath the body. Propulsion is provided by both pereiopodal exopods and pleopods. These appendages move together in a metachronous rhythm that travels from the first exopod to the last pleopod. There was no observable response to light being shone on the animal. No tail flick was seen while collecting the shrimps, and all escape responses involved forward swimming.

Examination of the gut-contents of the paratype showed a large quantity of orange-colored oil, and numerous crustacean fragments, some of which proved to be from *Procaris hawaiana*.

Etymology.—The species is named for Fenner and Janice Chace, the former a most renowned carcinologist and valued colleague, the latter a delightful friend.

Remarks.—The family Procarididae to date contains the single genus, *Procaris* Chace and Manning, 1972, represented by two species, namely, *P. ascensionis* Chace and Manning, 1972, from Ascension Island, and *P. hawaiana* Holthuis, 1973, from Hawaii. The finding of the present new genus, *Vetericaris,* demands a comparison with *Procaris,* as well as a reexamination of the suprafamilial and familial diagnoses of the group.

While *Vetericaris* has several features in common with those given in the diagnosis of *Procaris,* such as the presence of exopods on all the pereiopods, large epipods on the maxillipeds and pereiopods, and the lack of chelae on any of the pereiopods, several features immediately separate it from *Procaris.* These are summarized in the following comparison:

	Procaris	*Vetericaris*
Pleon somite 3	with dorsal cap	lacking dorsal cap
Posterior telsonic margin	with 4 pairs spines	with 7 pairs spines
Scaphocerite	reaching well beyond antennular peduncle	reaching to end of antennular peduncle
Maxilliped 2, dactylar attachment	strongly oblique	moderately oblique
Maxilliped 3, gills	1 epipod	1 epipod 1 arthrobranch 1 pleurobranch
Pereiopods 1–3, gills	1 epipod 1 pleurobranch 1 setobranch	1 epipod 1 pleurobranch 1 setobranch 2 arthrobranchs
Pereiopod 4, gills	1 epipod 1 pleurobranch 1 setobranch	1 epipod 1 pleurobranch 1 setobranch 1 arthrobranch
Pereiopodal dactyls	short, stumpy	relatively elongate
Pleopodal endopods	less than half length of exopod	more than half length of exopod
Appendices internae	absent	present on pleopods 3–5
Foregut	2 strong lateral teeth*	row of small lateral teeth

* See Felgenhauer and Abele, 1983, fig. 10.

Given the features of *Vetericaris* above, the diagnoses of the Procaridoidea and Procarididae are revised as follows:

Superfamily Procaridoidea

Diagnosis.—Phyllobranchiate gills consisting of axis and pairs of lateral lamellae. All maxillipeds and pereiopods with strong exopods. Third maxilliped pediform, of 7 articles. None of pereiopods chelate or subchelate. Epipods of anterior 4 pairs of pereiopods large, right-angled, extending into branchial chamber. Pereiopod 1 not stouter than pereiopod 2. Carpus of pereiopod 2 undivided. Pleopodal endopods poorly (*Procaris*) or well developed (*Vetericaris*); appendices internae absent (*Procaris*) or present, at least on posterior 3 pairs (*Vetericaris*). Gastric mill well developed, with strong median teeth, and several weak (*Vetericaris*) or few strong (*Procaris*) lateral teeth. Pleuron of abdominal somite 2 overlapping pleura of first and third somites.

Family Procarididae

Diagnosis.—In addition to the features mentioned in the diagnosis of the superfamily, the following: Rostrum small, unarmed. Mandible with fused molar and incisor processes, palp large, of 3 articles.

Genus *Procaris*

Diagnosis.—Anterior 4 pereiopods each with pleurobranch, setobranch, and massive simple epipod; dactyls short and stout, armed with 8 or 9 long curved spines. Pleopods with short endopods, lacking appendices internae or masculinae. Abdominal somite 3 with dorsal cap.

Relationships

The question of the position of the procaridids in the higher classification of the decapod shrimps is a vexing one, with several interpretations having been offered.

Chace and Manning (1972) placed the Procarididae in a superfamily of the infraorder Caridea. These authors indicated a similarity to penaeideans and stenopodideans in the 7-articulate maxilliped 3, the subterminally attached pleurobranchs, massive epipods, and the lack of appendices internae on the pleopods. They also indicated the similarity to the Caridea in the overlapping pleuron of the second abdominal somite, the form of the telson and uropods, mandible, and other mouthparts, and especially in the phyllobranchiate gills. Because of the features in common with both the penaeoids and the Caridea, Chace and Manning (1972) suggested that the concept of the Natantia as a "natural group" again be examined. Bowman and Abele (1982) repeated the classification put forward by Chace and Manning (1972).

Felgenhauer and Abele (1983) divided the Natantia into four groups, the Dendrobranchiata Bate, 1888, Procarididea Chace and Manning, 1972 (although, in fact, Chace and Manning proposed the superfamily Procaridoidea and not Procarididea), Stenopodidea Bate, 1888, and the Caridea Dana, 1852. These authors stated their belief that the former three groups are "natural taxa," and that the Caridea may require further revision. Felgenhauer and Abele (1983) did not indicate the status of these four taxa, nor did they indicate if they are to be regarded as equivalent. The use of the -idea suffix, however, would seem to suggest that they regarded them as infraorders.

Felgenhauer and Abele (1985), commenting on the infraorder Caridea, suggested that foregut structure may contribute to an understanding of phylogenetic relationships. Examination of the foregut of *Procaris* shows a strong resemblance to the Dendrobranchiata (as does that of *Vetericaris*). Based on foregut structure, Felgenhauer and Abele (1985) also placed the caridean family Atyidae close to the base of the caridean line.

The role of gill formulae in providing insight into phylogeny is difficult to assess. Burkenroad (1984: 277) stated that "the slightly richer formula found in other Eukyphida is more primitive than the *Procaris* formula . . . ." Just how conservative or labile are gill arrangements is not known, and while, in general, a full complement of single pleurobranchs and paired arthrobranchs may be considered to be a basic primitive pattern, there are at least grounds for suspicion that number of gills may be correlated with habitat, e.g., the present case of *Vetericaris* which inhabits waters of very low oxygen concentration.

The new genus *Vetericaris* has several features which color these earlier considerations. Four features in particular would suggest a condition more primitive than *Procaris*: (1) the elongate pleopodal endopod, (2) the appendices internae on the posterior three pairs of pleopods, (3) the elongate and spinose dactyls of the pereiopods, and (4) the lack of a dorsal cap on abdominal somite 3.

We could consider the shortened pleopodal endopods and the lack of appendices internae in *Procaris* as advanced characters associated with a benthic habit and the lack of necessity for prolonged or sustained swimming. The dorsal cap, associated with enlarged flexing muscles of the abdomen for backward flicks, can be considered an advancement over an abdomen used purely for forward swimming.

Other features of *Vetericaris* which may or may not be primitive compared to the condition in *Procaris* include the row of several lateral teeth in the foregut, and the larger number of spines on the posterior telsonic margin. Since little is known about these characters in terms of degree of advancement, an evaluation based on them should be tentative.

The presence of appendices internae in *Vetericaris* would seem to indicate some affinity with the heterogeneous Caridea, along with the overlapping second pleuron and the phyllobranch gills. Both *Procaris* and *Vetericaris* show some indication of a caridean lobe at the base of the exopod of the first maxilliped, another feature indicating affinity with the Caridea.

The presence of large epipods on the pereiopods, and the pediform 7-articulate maxilliped 3, which would seem to ally the procaridids and the dendrobranchiates, should be regarded as primitive characters and therefore not indicative of affinity.

One character which would be of value in indicating possible affinity is the disposition of eggs, i.e., whether released into the surrounding water (presumably a primitive condition as in the dendrobranchiates), or retained under the female abdomen and attached to the pleopods (as in the carideans). Unfortunately, this character in the procaridids is still an unknown, although the overlapping second pleuron might hint at retention of eggs. The relative importance of this character can be demonstrated in the two cladograms in Fig. 8. Should the procaridids retain eggs, they would be linked with the Caridea at a fairly high level, with the stenopodideans and dendrobranchiates being ranked progressively more primitive (Fig. 8A). Should eggs not be retained in the procaridids, they would still be linked to the carideans, but the relationship of this group to the dendrobranchiates and stenopodideans becomes less clear (Fig. 8B). (We would emphasize that these dendrograms, and the characters used in their construction, are preliminary, relatively simplistic, and not at all exhaustive.) Both dendrograms imply a loss of chelae on pereiopods 1 and 2 in the procaridids, a condition difficult to accept given the unspecialized dactyls on all five pairs of pereiopods in *Vetericaris.*

Given that the overlapping second pleuron, the phyllobranch gills (derived from the dendrobranchiate type), the appendices internae, the dorsal cap, and possibly the caridean lobe are all advanced characters present in the procaridids, it would seem wisest to accept this apparent affinity with the Caridea. This is best achieved by retaining the Procaridea as a superfamily of the infraorder Caridea, as proposed by Chace and Manning (1972).

Family Atyidae de Haan, 1849

Halocaridina Holthuis, 1963

Halocaridina palahemo, new species

Figs. 9–11

Material.—Holotype ♂, USNM 211366, station H-5, cl 2.3 mm; paratypes, 3 ♀♀, USNM 211367, station H-4, cl 1.9–2.1 mm; station H-5, 1 ♂, cl 2.3 mm, 14 ♀♀, cl 2.0–2.8 mm; station H-11, 1 ♂, cl 2.3 mm, 5 ♀♀, cl 2.2–2.9 mm; lava tube pool, Lua o Palahemo, Ka Lae, Hawaii Island, 18°55′N, 155°42′W.

Description.—Carapace (Fig. 9A) relatively inflated; rostrum (Fig. 9B) short, triangular, unarmed, dorsally depressed, reaching anteriorly as far as eyes, directed

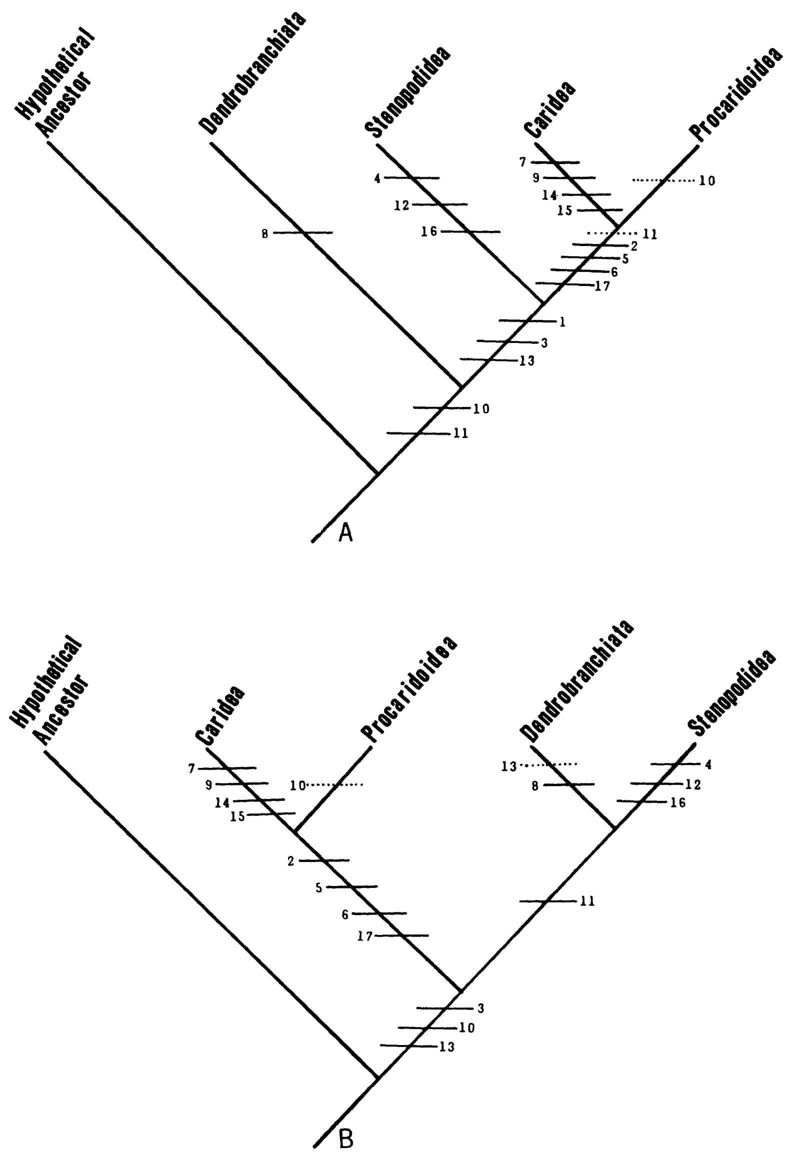

Fig. 8. Dendrograms generated with Wagner 78 program, illustrating hypothetical relationships of four major shrimp groups and hypothetical ancestor. A, with character 1 (eggs retained); B, without character 1. Summary of characters 1–17 used in dendrograms. (Apomorphic state only.) 1, eggs retained under female abdomen; 2, phyllobranchiate gills present; 3, dendrobranchiate gills absent; 4, trichobranchiate gills present; 5, abdominal pleuron 2 overlapping pleura 1 and 3; 6, appendix interna present; 7, appendix masculina present; 8, petasma present; 9, maxilliped 3 showing fusion of articles; 10, pereiopods 1 and 2 chelate; 11, pereiopod 3 chelate; 12, pereiopodal exopods absent; 13, dorsal cap on abdominal somite 3 present; 14, foregut showing reduced complexity; 15, carpus of pereiopod 2 multiarticulate; 16, carpi of pereiopods 4 and 5 multiarticulate; 17, caridean lobe present.

somewhat anteroventrally; lower orbital angle rounded; pterygostomian region broadly rounded.

Abdominal somites 4 and 5 with pleura somewhat posteroventrally produced and narrowly rounded; somite 6 one-fifth longer than somite 5, subequal to telson

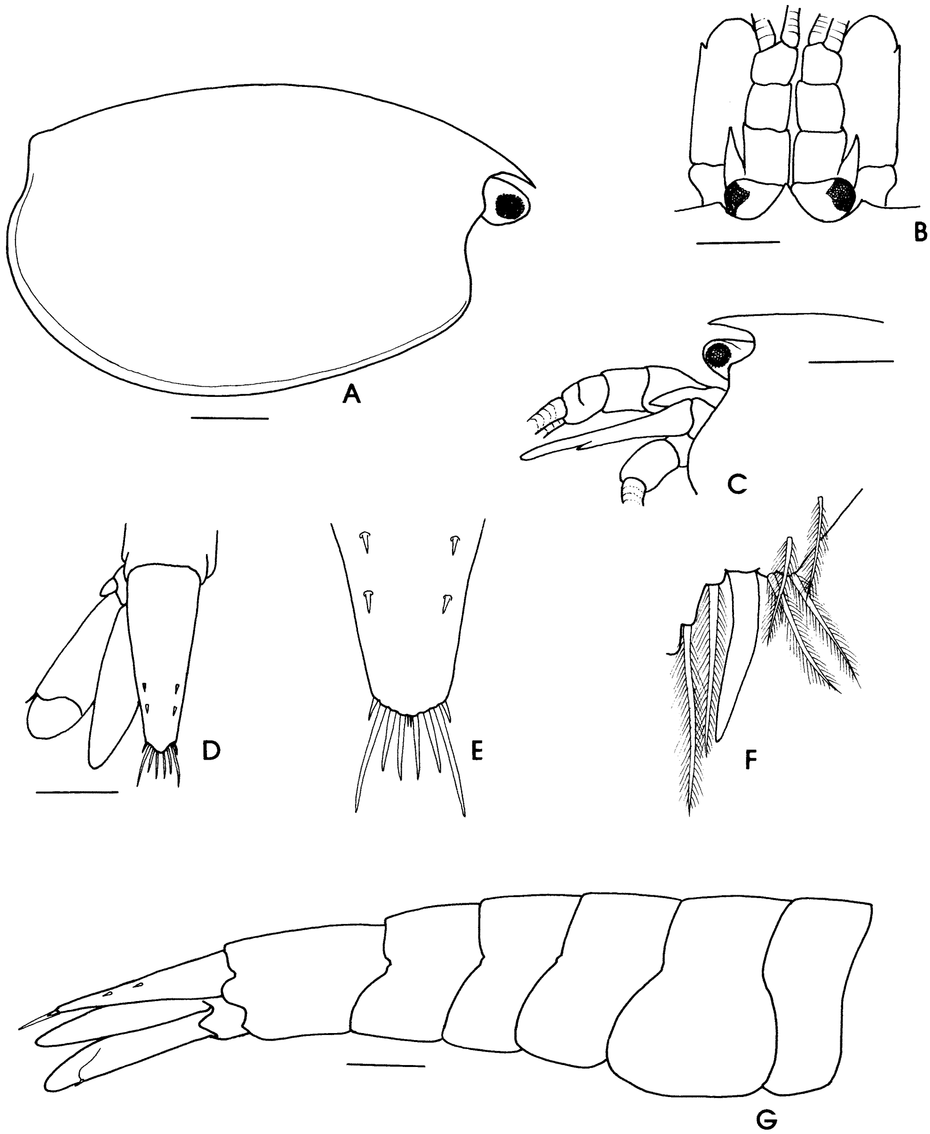

Fig. 9. *Halocaridina palahemo*: A, carapace in lateral view; B, anterior carapace, eyestalks, and antennae in dorsal view; C, anterior carapace, eyestalks, and antennae in lateral view; D, telson and left uropod in dorsal view; E, distal half of telson enlarged; F, spine on lateral margin of outer uropodal ramus; G, abdomen in lateral view. Scales = 0.5 mm (except E, F, both enlargements from D).

in length (Fig. 9G). Telson (Fig. 9D, E) with 2 pairs of dorsolateral spines in posterior half; posterior margin armed with 4 pairs of spines, outermost pair shortest, next pair longest, 2 inner pairs subequal in length.

Eyestalks (Fig. 9B) broader than long, with pigmented corneal areas directed laterally.

Stylocerite of antennule (Figs. 9B, 10G) reaching to outer distal margin of basal peduncular article, outer margin gently convex, apically acute, basally notched. Two distal articles of peduncle together equal to basal article in length.

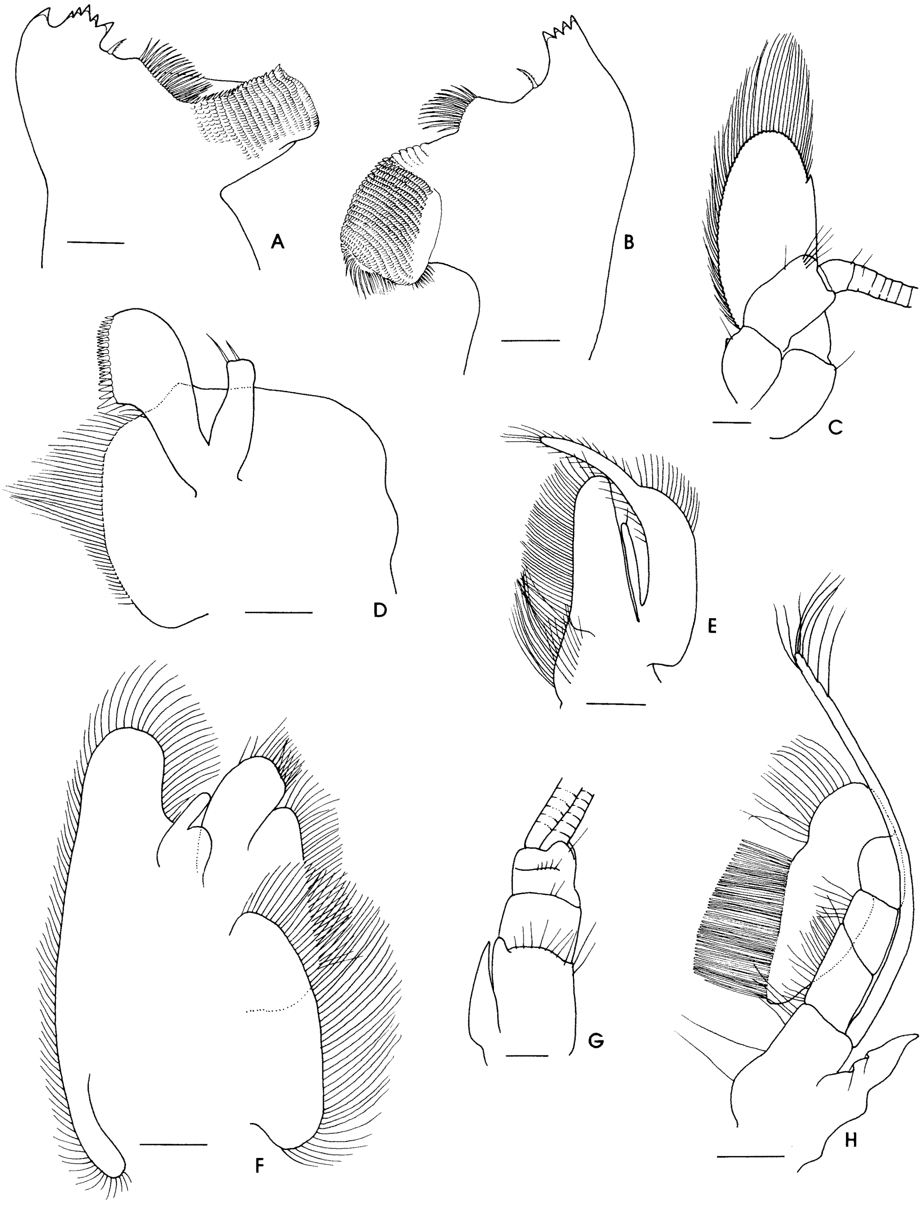

Fig. 10. *Halocaridina palahemo*: A, left mandible; B, right mandible; C, antenna; D, maxilla 1; E, maxilliped 1; F, maxilla 2; G, antennule; H, maxilliped 2. Scales: A, B, E = 0.1 mm; C, D, F, G, H = 0.2 mm.

Scaphocerite (Figs. 9B, 10C) reaching anteriorly by about one-fourth of its length beyond antennular peduncle, tooth on outer margin at distal three-fourths of length, distal margin broadly rounded; mesial and distal margin to tooth bearing setae. Small blunt tubercle on distomesial margin of basal peduncular article.

Mandible (Fig. 10A, B) lacking palp; left incisor of 1 large tooth separated by distinct gap from 5 smaller teeth; right incisor of 4 small teeth; single fringed

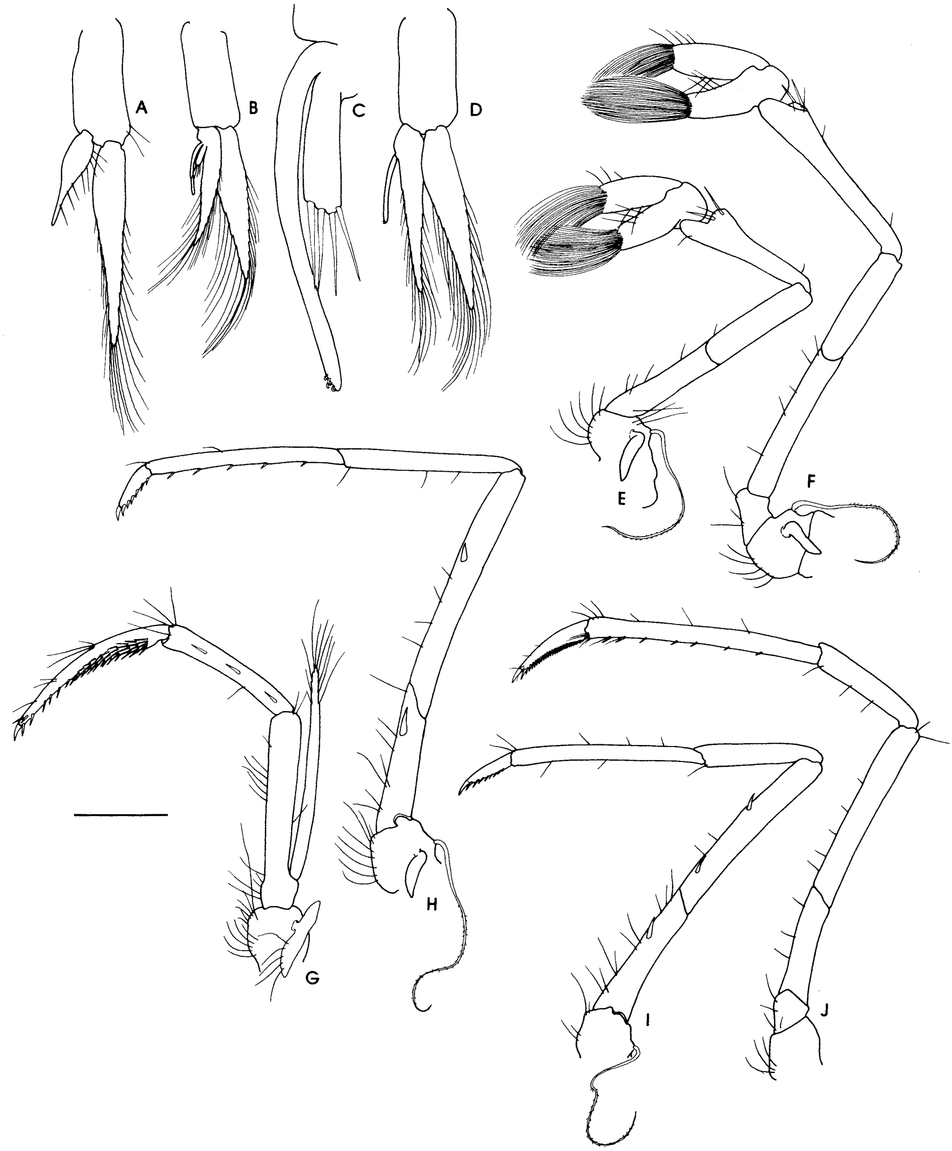

Fig. 11. *Halocaridina palahemo*: A, pleopod 1 ♂; B, pleopod 2 ♂; C, appendix interna and appendix masculina of pleopod 2, enlarged; D, pleopod 3; E, pereiopod 1; F, pereiopod 2; G, maxilliped 3; H, pereiopod 3; I, pereiopod 4; J, pereiopod 5. Scale = 0.5 mm (except C, an enlargement from B).

spinule between incisor and row of closely set spinules; molar broadly quadrate, set with rows of denticles.

Maxilla 1 (Fig. 10D) with distally truncate palp bearing 2 setae; distal endite bearing row of short spines on mesial margin; proximal endite broadly convex and setose on mesial margin, expanded into broad subcircular lamella laterally.

Maxilla 2 (Fig. 10F) typical of genus, with broad proximal endite, short, broad palp having digitiform process, basally narrowed scaphognathite.

Maxilliped 1 (Fig. 10E) with distinct caridean lobe at base of exopod; palp narrow-slender, not extending distally as far as distal endite.

Maxilliped 2 (Fig. 10H) with 2 distal articles fused, distomesial margin bearing dense band of fringed spines; exopod slender-elongate; epipod triangular-tapering.

Maxilliped 3 (Fig. 11G) reaching beyond scaphocerite by most of distal article; latter with numerous short spines proximally on posterior margin, becoming fewer distally, ending in single stronger spine; penultimate article about three-fourths length of distal article, bearing 3 evenly spaced spines on lateral surface; exopod reaching to proximal part of penultimate article; epipod bilobed.

Pereiopod 1 (Fig. 11E) barely reaching apex of scaphocerite; fingers of chela twice longer than palm, not inflated, slight constriction near base of fixed finger; carpus slightly longer than chela, anteriorly excavate; merus slightly shorter than carpus, subequal to ischium in length; epipod of single lobe; single whiplike setobranch present.

Pereiopod 2 (Fig. 11F) reaching beyond scaphocerite by most of chela, longer than pereiopod 1; chela as in pereiopod 1; carpus twice length of chela, distally excavate; merus two-thirds length of carpus, three-fourths length of ischium; single-lobed epipod and single whiplike setobranch present.

Pereiopod 3 (Fig. 11H) overreaching scaphocerite by length of dactyl; latter with 6 short spines on posterior margin, single stronger spine terminally; propodus with 5 small spines on posterior margin; carpus slightly shorter than propodus, two-thirds length of merus; latter with single spine just distal of midlength, on lateral surface; ischium slightly more than half length of merus, with single strong distal spine; single-lobed epipod and single whiplike setobranch present.

Pereiopod 4 (Fig. 11I) barely reaching distal margin of scaphocerite; essentially similar to pereiopod 3 but with 2 spines on merus, and lacking spines on propodus; single setobranch present, epipod absent.

Pereiopod 5 (Fig. 11J) barely reaching apex of scaphocerite; dactyl bearing 30 spines on posterior margin, increasing in length distally; propodus with 7 spines on posterior margin; carpus half length of propodus, three-fifths length of merus; setobranch and epipod absent.

Pleopod 1 of male (Fig. 11A), endopod half length of exopod, basally broad, then tapering over half its length to narrow apex.

Pleopod 2 of male (Fig. 11B, C), endopod having elongate slender appendix interna tipped with 4 retinacula; appendix masculina half length of appendix interna, distally truncate with 4 stout setae.

Outer ramus of uropod having single articulated spine at diaeresis (Fig. 9F); outer ramus distally broader than inner ramus.

The branchial formula is as follows:

Maxilliped 1	—	—	—
Maxilliped 2	epipod	—	—
Maxilliped 3	epipod	—	—
Pereiopod 1	epipod	1 pleurobranch	1 setobranch
Pereiopod 2	epipod	1 pleurobranch	1 setobranch
Pereiopod 3	epipod	1 pleurobranch	1 setobranch
Pereiopod 4	—	1 pleurobranch	1 setobranch
Pereiopod 5	—	—	—

Remarks.—The type and until now the only species of *Halocaridina* is *H. rubra* Holthuis, 1963, described from fresh-water or slightly brackish pools on the island of Hawaii. Holthuis (1973) and Maciolek (1983) recorded the species from the islands of Maui, Oahu, and also from Hawaii at Lua o Palahemo, the source of the material of this report.

The present species differs markedly from *H. rubra* in a number of easily seen features summarized below:

	H. rubra	*H. palahemo*
Rostrum	reaching well beyond eyestalks to antennular peduncle article 2	just reaching to end of eyestalks
Carapace	moderately inflated	strongly inflated
Maxilla 1	endite not expanded	endite expanded into lateral lamella
Chelae	strongly inflated	barely inflated
Carpus, pereiopods 1 and 2	shorter or subequal to chela	equal to or longer than chelae
Dactyl, pereiopod 5	with 25 spines	with 30 spines
Outer uropodal ramus	2 spines at diaeresis	1 spine at diaeresis

The apparently anomalous situation of two species of *Halocaridina* occurring in the same lava tube may be explained in the following way: Holthuis (1973) recorded *H. rubra* from Cape Kinau, Maui Island, as well as from Lua o Palahemo on Hawaii Island. For the latter record, Holthuis referred to Maciolek (in correspondence, 5 March 1973) who described *H. rubra* as being ". . . very abundant, especially in midwater (at a depth of about 1 meter), presumably grazing on phytoplankton" (Holthuis, 1973: 11). While *H. rubra* undoubtedly occurs in some pools in Hawaii, the superficially similar *H. palahemo,* which Holthuis did not see (Holthuis, in correspondence, 1985), was probably mistaken for the earlier species.

The absence of *Antecaridina lauensis* from the present collection is unexplained. This atyid was recorded by Holthuis (1973), as well as by Maciolek and Brock (1974) and Maciolek (1983) from the lava tube under discussion. Potentially even more confusing is the presence in the present collection of a single atyid (unfortunately lacking most of its legs) that is neither the new *Halocaridina* nor *A. lauensis.*

Etymology.—The specific name is the Hawaiian name for the pool from which the shrimps were taken. This *Pala-hemo* was believed to be connected underground to the sea and haunted by a spirit of the same name; in times of rain it was taboo to bathe there.

General Discussion

It is probable that neither temperature nor salinity imposed barriers to the dispersal of these shrimps in the deep crevicular habitat during the Pleistocene. Mink (1964) stated that the basalt beneath the Oahu aquifer is extremely permeable. The ground-water temperature from the surface to as deep as 400 m below sea level is a fairly constant 22°C. The present-day Hawaiian sea surface temperature of about 25°C is close to that estimated for 18,000 years ago (CLIMAP project members, 1976). Further, Mink (1964) found that the salinity increased from 4 ppt directly beneath the fresh-water lens at 100 m below sea level, to 30 ppt at 400 m. Similar aquifers with large volumes of ground water have been found on the islands of Hawaii and Maui (Stearns, 1966). Thus, in spite of Pleistocene sea-level fluctuations, a suitable habitat for these shrimps probably was present in these deep crevicular habitats, and it is not necessary to invoke contiguous surface populations to explain the distribution of procarid shrimps. The colonization by *Procaris hawaiana* of shallow anchialine pools formed during the 1790 lava flow on Maui (Oostdam, 1965) provides further evidence for this method of dispersal.

Given the relative youth of the Lua o Palahemo lava tube, the above-mentioned and unexplained absences and occurrences, and the presence of some of these shrimps in modern wells and quarries, Maciolek's postulate (1983: 615) that these habitats are colonized from long-existing subterranean populations, must be strengthened.

An interesting correlation appears to exist in the co-occurrence of procarid and atyid shrimps: *Procaris ascensionis* with *Typhlatya rogersi* on Ascension Island, *Procaris hawaiana* and *Vetericaris chaceorum* with *Antecaridina lauensis, Halocaridina rubra,* and *H. palahemo* in the Hawaiian archipelago, and an undescribed species of *Procaris* with *Typhlatya iliffei* on Bermuda. These co-occurrences of two primitive and presumably ancient caridean families also support the contention of Hart *et al.* (1985) that crevicular habitats have served as faunal refuges for long periods of time.

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ANNOUNCEMENT

The following opinion (1369) has been published by the International Commission on Zoological Nomenclature in the Bulletin of Zoological Nomenclature, volume 43, part 1 (9 April 1986):

Astacilla Cordiner, 1793 (Crustacea, Isopoda): conserved.

The Commission also gives six months notice of the possible use of its plenary powers in the following case (2357):

Atyidae De Haan [1849] (Crustacea, Decapoda) and Atyidae Thiele, 1926 (Mollusca, Gastropoda): proposals to remove the homonymy.