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THE CAVERNICOLOUS FAUNA OF HAWAIIAN LAVA TUBES

9. Amphipoda (Crustacea) from brackish lava ponds on Hawaii and Maui[1]

By J. Laurens Barnard[2]

Abstract: Ten species of amphipods have been discovered in lava ponds of Hawaii and Maui. The partially phreatic and brackish lava pond systems contain the following taxa: a new genus, *Rotomelita*, with 2 new species, bearing affinities to a 3rd species from Bismarck Archipelago; 3 new species of *Paramoera* with cold-temperate affinities; 2 new species of *Grandidierella;* a new species of *Hadzia* (=*Liagoceradocus*); and 1 species each of *Nuuanu* and *Parhyale.* The species of *Rotomelita* and *Hadzia* are blind and those of *Paramoera* and *Nuuanu* have reduced eyes, although several of these were captured in bright or shaded sunlight of inland pools.

Recent field explorations in lava ponds and a cave on the islands of Hawaii and Maui (Maciolek & Brock 1974, Howarth 1973) reveal a special fauna of aquatic amphipods. Holthuis (1973) has named this kind of environment "anchialine." For the sake of simplicity I use the term "open-sea" in this paper to describe nonanchialine marine environments when making various comparisons.

Three species of troglophilic amphipods occur near the lighted end of a lava tube cave on Maui. One of these is blind and belongs to a new genus, *Rotomelita,* with similarities to the marine genus *Melita.* The 2nd is a poorly oculate new species of cold-temperate *Paramoera* and the 3rd is an oculate species of the tropicopolitan genus *Grandidierella.* The remaining 7 species occur in sunlit or partially shaded open lava ponds on Maui and Hawaii. These ponds, like the cave on Maui, are terrestrial sinks in fissures and tubes of recent lava flows. They contain brackish water in a salinity range of 2.0 to about 14.0 0/00, the salt content coming from percolated seawater. The ponds are generally close to marine shorelines and have a strong faunistic connection with each other and between the 2 islands. This is evident because the remaining species comprise a 2nd blind member of *Rotomelita,* 2 more species of *Paramoera,* 1 of them blind, a blind species of the genus *Hadzia* (=*Liagoceradocus*) (heretofore Micronesian), a poorly oculate species of *Nuuanu* (heretofore marine on Oahu), an oculate tropicopolitan marine littoral species, *Parhyale hawaiensis,* and a 2nd species of *Grandidierella.*

All species, except *Parhyale hawaiensis* and *Nuuanu amikai,* are new and several appear to have evolved within the Hawaiian Archipelago from immediate marine ancestors; few of those ancestors have been recognized in the Hawaiian littoral, if, indeed, most of them are not extinct. Only *Grandidierella palama* can be tied to a known local open-sea ancestor. No *Hadzia* (=*Liagoceradocus*) has been found as yet, but exploration has been sparse. *Liagoceradocus* is a small-bodied and fragile subgenus and probably has some cryptic and dark open-sea habitat; the 2 known species of the subgenus are blind. *Liagoceradocus* and *Nuuanu* have been suggested as possible incipient members of interstitial habitats, perhaps in microcaverns of coral rubble (J. L. Barnard 1974).

The 3 species of *Paramoera* are of great interest. The genus, absent in the Atlantic Ocean, is ordinarily confined to cold-temperate waters of the southern hemisphere or the North Pacific Ocean. No open-sea Hawaiian species of the genus has been discovered but one

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must presume that a marine ancestor emigrated from cold-water shores of North America or Asia during some cool-water Hawaiian epoch and survived for time sufficient to spawn the descendents now living in lava ponds. The 3 Hawaiian species are unusual in the reduced ocular structure and oddities of the telson and may qualify together as a descendent subgenus of *Paramoera*. To erect such a subgenus now would be imprudent because of present taxonomic instability in genera related to *Paramoera* (see J. L. Barnard 1972) and various unknown characteristics of many species in the genus.

Nuuanu is a genus originally described from Hawaii, based on 1 male individual; a 2nd male is reported here from a lava pond on Maui but 2 other new species of the genus plus a companion genus have since been discovered in Australia (J. L. Barnard 1974). These genera have affinities with *Pherusana* (=*Gammarella*), a dominantly warm-temperate genus of the eastern Atlantic Ocean.

Rotomelita has affinities with *Melita latimerus* Bousfield, 1971, a species from anchialine waters of the Bismarck Archipelago. *Melita latimerus* should be removed from *Melita* but differs in several ways from *Rotomelita* and probably should have a genus of its own. *Rotomelita* and *Melita latimerus* are characterized by an unusual telson that suggests they have a strong affinity. No open-sea species of the complex has been discovered as yet, so that speculation on dispersal pathways over thousands of miles of sea is fruitless.

The 2 most widespread species are *Rotomelita lokoa* and *Paramoera paakai*. They occur in brackish lava ponds of Hawaii. The morphology of the few specimens from each pond of these 2 species is reasonably consistent from the point of view of an alpha taxonomist, suggesting a fairly continuous gene flow from one population to the other. How the blind species (*P. lokowai*) became evolutionarily isolated is unexplainable because no visible discontiguity between ponds has been found. The 2 species of *Paramoera* on Hawaii appear to be ecologically separated from each other and the blind species may be primarily phreatic. One is tempted to suggest that the 3rd species, from a cave on Maui, separated from Hawaii by more than 48 km (30 miles) of deep sea, is either a direct descendent or a direct ancestor of the oculate species on Hawaii, rather than a descendent of a common marine ancestor flourishing in the littoral of some earlier time. The 3 species are closely similar to each other but the cave species is much more similar to the blind species on Hawaii than to the contiguous oculate species. One must suppose coincidence alone is injustifiable as an explanation for this similarity. The coincidence would involve the presence of a littoral ancestor living on both Maui and Hawaii but spawning such similar species. However, these 2 species have vaguely similar habitats, more similar than does the 3rd species, which apparently lives in lighted pools. The cave and well species probably live in darkness, although the cave species retains its eyes whereas the well species has lost its eyes. Selection has therefore apparently played its role in producing 2 similar species in terms of telson and epimera.

One can scarcely conceive of the lava pond *Paramoera*, the logical ancestor, or that species closest to the ancestor, as a successful inhabitant of the open sea under the present environmental conditions of Hawaii. An organism with weak eyes and poor pigmentation would seem to be a poor competitor in the brightly lit Hawaiian littoral, but we now know of at least 4 such species living in the littoral of Hawaii and Micronesia in the genera *Nuuanu*, *Liagoceradocus*, and *Eriopisa*. They probably inhabit some cryptic habitat or have adaptations compensating for this apparent deficiency. In any event, these species make good evolutionary material preadapted to enter unusual habitats such as lava ponds, caves, or phreatic systems.

Amphipoda occur frequently in unusual habitats near the sea throughout the tropics, for example, in saline and freshwater ponds of Caribbean islands (Stephensen 1933a, b) and in Chilka Lake of India (Chilton 1921). The species are generally endemic locally unless they are tube-dwellers (e.g., *Corophium*, *Grandidierella*) which can be transported by ships and logs over long distances. Among many genera found in seashore ponds, lagoons and seeps, one may mention warm-water genera especially predilected to these habitats:

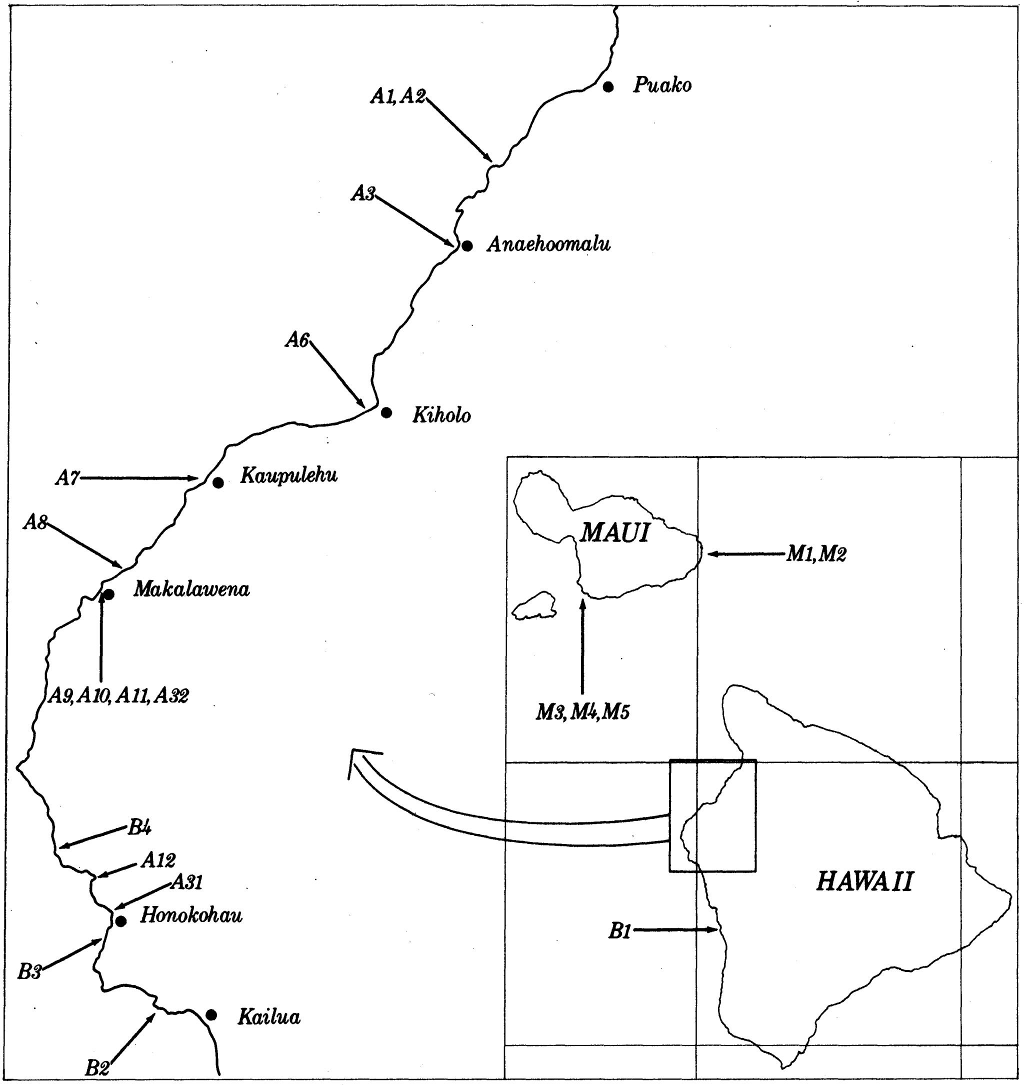

FIG. 1. Localities of aquatic amphipods. (See TABLE 1)

Grandidierella, Corophium, Quadrivisio, Eriopisa, Eriopisella and *Hadzia* (=*Metaniphargus*, =*Liagoceradocus*).

Members of dominant open-sea genera such as *Lysianassa* and *Parhyale* also penetrate into marginal habitats. Exploration of such habitats is rudimentary and many more genera than mentioned have been reported from these inland waters; many more are expected to be found. New Zealand and southern Australia have diverse endemic faunas in saline and freshwater aquifers. Nearctic and Palearctic provinces contain more than 500 species of freshwater amphipods, many of them phreatic.

Amphipods of inland ponds on islands and in fresh waters of the southern hemisphere are especially interesting because many of them can be traced directly to marine ancestors. In Palearctic environments this is difficult. Because of the immense diversity of the fauna in the Palearctic, one cannot determine easily whether or not certain amphipod groups have recently invaded fresh waters from the sea or are reinvading the sea from fresh water.

There have also been popular suggestions that amphipods originated in fresh waters of Palearctica and invaded the seas secondarily. Hence the study of evolutionary processes of amphipods on islands or in areas where a definite invasive direction is known should be valuable in attempting to determine the early history of amphipods, largely missing from the fossil record.

SYSTEMATICS

New names for species described herein are nouns placed in linguistic apposition to the names of genera and all new names, including a root for a generic name, come from various Polynesian and Hawaiian languages and refer to features such as ponds, lakes, wells, caves, warriors, gods and sacred enclosures.

Types are deposited in the Bishop Museum and duplicates are deposited in the Smithsonian Crustacea Division (USNM). Specimens collected by Dr E. L. Bousfield are deposited in the National Museum of Canada.

FIG. 1 shows the localities where specimens of amphipods were collected. TABLE 1 gives the station list for these localities.

Family COROPHIIDAE

GRANDIDIERELLA Coutière

Grandidierella Coutière, 1904: 3–11.

This genus now contains 19 species distributed throughout Indo-Pacific and Caribbean waters. Until 1970, *Neomicrodeutopus* Schellenberg could be separated from *Grandidierella* effectively by the shortness of article 1 on the mandibular palp and this character was confined to 2 species, *N. cabindae* Schellenberg, 1925, from West Africa, and *N. elongata* [Chevreux (1926) as *Grandidierella*], from the Sahara coast. For geographic reasons, *Neomicrodeutopus* could be retained as an eastern Atlantic genus or subgenus but Myers (1970) described a new marine species of *Grandidierella* from Hawaii with a similarly short article 1 on the mandibular palp, thus eliminating the geographic correlation for this character and demonstrating that such a character probably has no monophyletic descent. A companion species to Myers' *G. dentimera* from Hawaii is described herein; it bears an elongate article 1 on the mandibular palp but otherwise appears to have greater affinity to *G. dentimera* than to other species of the genus or to the 2 species of *Neomicrodeutopus. Neomicrodeutopus* therefore appears synonymous with *Grandidierella.* One additional point of evolutionary impact concerns the deep-sea eastern Atlantic genus *Chevreuxius* Bonnier, 1896, that appears to be a descendent of *Grandidierella* in which uropod 2 has lost 1 ramus; that monotypic genus also bears a short article 1 on mandibular palp and occurs in close proximity to the pair of species formerly placed in *Neomicrodeutopus. Chevreuxius* probably descended from an ancestor common to the species of *Neomicrodeutopus,* thus forming a line of descent from species already bearing the short palp article; however, the appearance of this short palp article on the other side of the earth at Hawaii suggests that the character alternative is nonconservative and should not be accorded genetic status.

A 2nd characteristic is common to the 2 species of *Neomicrodeutopus:* a thickened and slightly enlarged male gnathopod 2. This characteristic is found also in *G. grossimana* Ledoyer, 1967, from Madagascar. The mandibular palp is unknown in *G grossimana.* African seashores thus contain 3 species of *Grandidierella* with apparent affinities from which a deep-sea genus, *Chevreuxius,* may have descended. Until these species can be thoroughly reexamined and other characters of generic value assessed, one must retain *Neomicrodeutopus* at full generic level.

TABLE 1. Station list (See FIG. 1 for locations).

MAP DESIGNATOR	POND SURVEY IDENT.	DATE	TEMPERATURE °C	SALINITY 0/00
A-1	Tokyo-Land 5	17.VII.1972	26	4.0
A-2	Tokyo-Land 13	17.VII.1972	25	4.0
A-3	Anaehoomalu T-15	14.VII.1972	24.5–31.0	3.0
A-6	Kiholo 8	9.VIII.1972	27.0–29.5	2.0
A-7	Kona Village-7	16.VIII.1972	28	4.0
A-8	Makalawena North 3	20.VIII.1972	27	6.0
A-9	Makalawena T-2	21.VIII.1972	23–24	7.0
A-10	Makalawena BR-2	23.VIII.1972	24.5–25.5	8–12
A-11	Makalawena BR-3	23.VIII.1972	22–24	8–10
A-12	Kaloko 2	24.VIII.1972	25.0–27.5	12–14
A-31	Honokohau, JSL	14.I.1972		17
A-32	Makalawena, JSL	7.I.1972		
B-1	Honaunau Well 1	2.XII.1972		2.5
B-2	N. K. Air 1	3.XII.1972		7.0
B-3	N. K. Air 3	3.XII.1972		6–10
B-4	N of Pine Tree Pt. Series	1.XII.1972		11.5–13.0
M-1	Waianapanapa Cave [Hana, Maui]	16.VII.1972	[F. G. Howarth & S. Malecha]	
M-2	Waianapanapa Cave	19.II.1972	[J. S. Lenic]	1–2
M-2	Waianapanapa Cave, twilight pool	24.I.1973	[E. L. Bousfield & F. G. Howarth]	
M-2	Waianapanapa Cave, dark zone pool	24.I.1973	[F. G. Howarth & E. L. Bousfield]	
M-3	Cape Kinau, Maui, N. Pond	15.IV.1972	[J. S. Lenic]	10–34
M-4	Cape Kinau, Maui, Nukuele 1	5.I.1973	[J. S. Lenic]	10–34
M-4	Cape Kinau, Maui, Nukuele Pt., in brackish pond	22.I.1973	[J. Maciolek, E. L. Bousfield & F. G. Howarth]	
M-5	Kinau-w	11.I.1972	[J. S. Lenic]	10–34

Grandidierella palama Barnard, n. sp.

FIG. 2–4

Diagnosis of ♂: Ocular lobes of short form for genus; antennae 1– 2 very long; length ratio of articles 1, 2, 3 of mandibular palp: 4:5:5; anterior coxae softly rectangular, lacking sharp points; gnathopod 1: article 2 slender, article 4 with apex free from article 5, bearing small tooth defined by sinus, article 5 with 3 teeth, 1 large, 1 medium, 1 small, smallest tooth distad, largest proximad, small and medium teeth forming distal pair and largest tooth separated from others by deep luna, bases of all teeth forming line oblique to long axis of article 5, article 6 very thin, weakly concave posteriorly, dactyl about as long as largest tooth on article 5; gnathopod 2 slender, article 5 elongate, article 6 about 2/3 as long as article 5, palm oblique, weaklv excavate; ramus of uropod 3 straight; sternal teeth absent.

♀: Articles 5–6 of gnathopod 1 of equal length, stout, palm oblique, defined by pair of spines in tandem, posterior margin of article 6 with additional spine similar to smaller defining spine; gnathopod 2 slender, article 5 about 1.4 x as long as article 6, palm nearly transverse.

Description: Article 2 of antenna 1 ca 1.4 x as long as article 1; article 3 of antenna 2 with pair of ventral spines subapically, spines apposed as forceps but bases not tangential; right mandibular molar with long plumose seta, left with seta vestigial, left mandible with 9 spines; epistome flat anteriorly; pereopods 1–2 with 1 locking seta, pereopods 3–5 with 1 long spine, 1 short spine at locking position; epimeron 2 with 1–2 facial setae; cuticle grossly smooth, ultra fine beading present.

Holotype ♂.(BISHOP S8410). 7.7 mm.

Type-locality: HAWAIIAN ISLANDS: Maui I, Waianapanapa, 19.II.1972, Lenic.

Material examined: 3 specimens from type-locality: holotype; ♂, 5.4 mm; ♀, 6.7 mm.

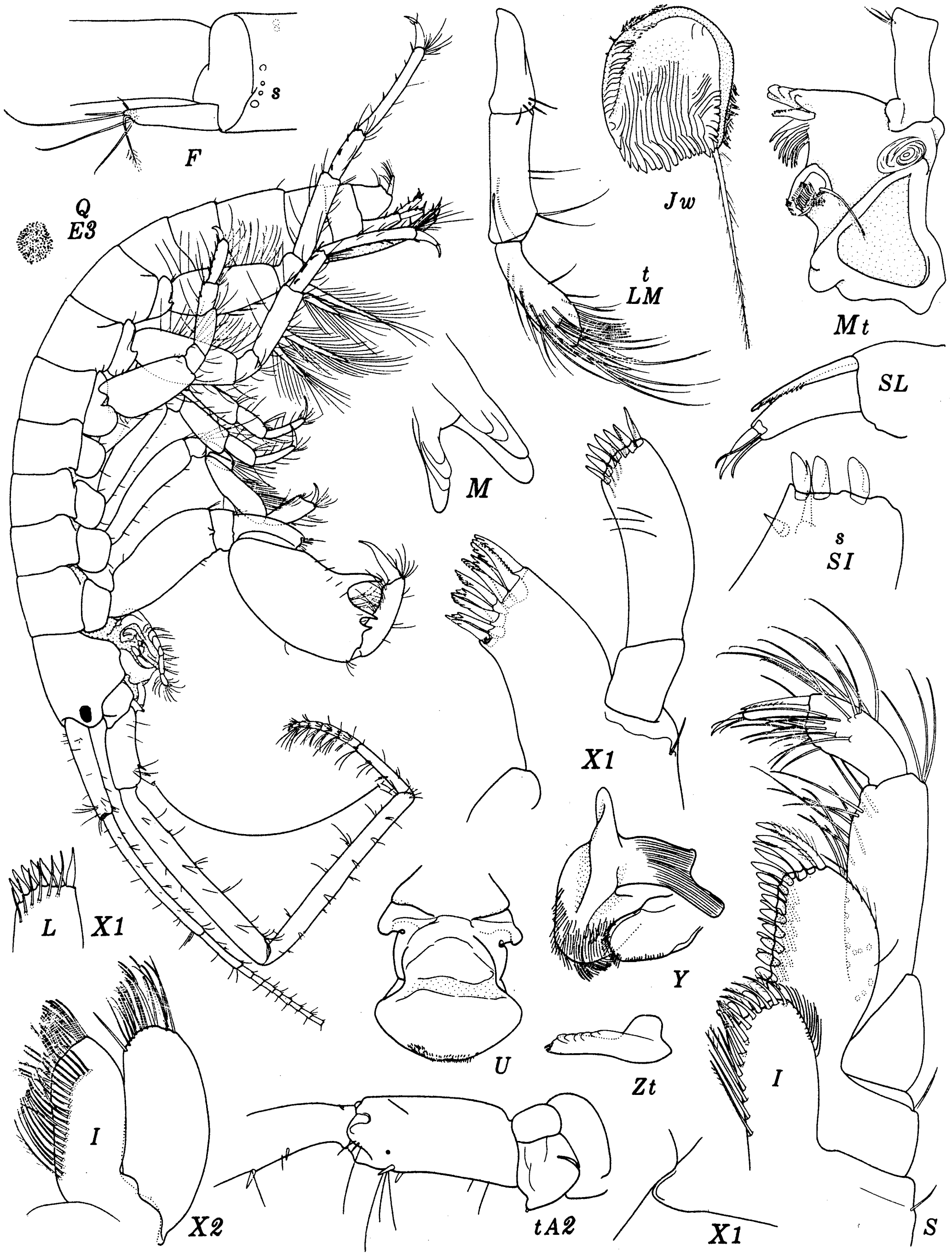

FIG. 2. *Grandidierella palama*, n. sp., holotype, ♂, 7.7 mm, Waianapanapa, 19.II.1972, Lenic; w = ♀, 6.7 mm; J = molar; Q = cuticle; scale near head on body is remainder of antenna 1.

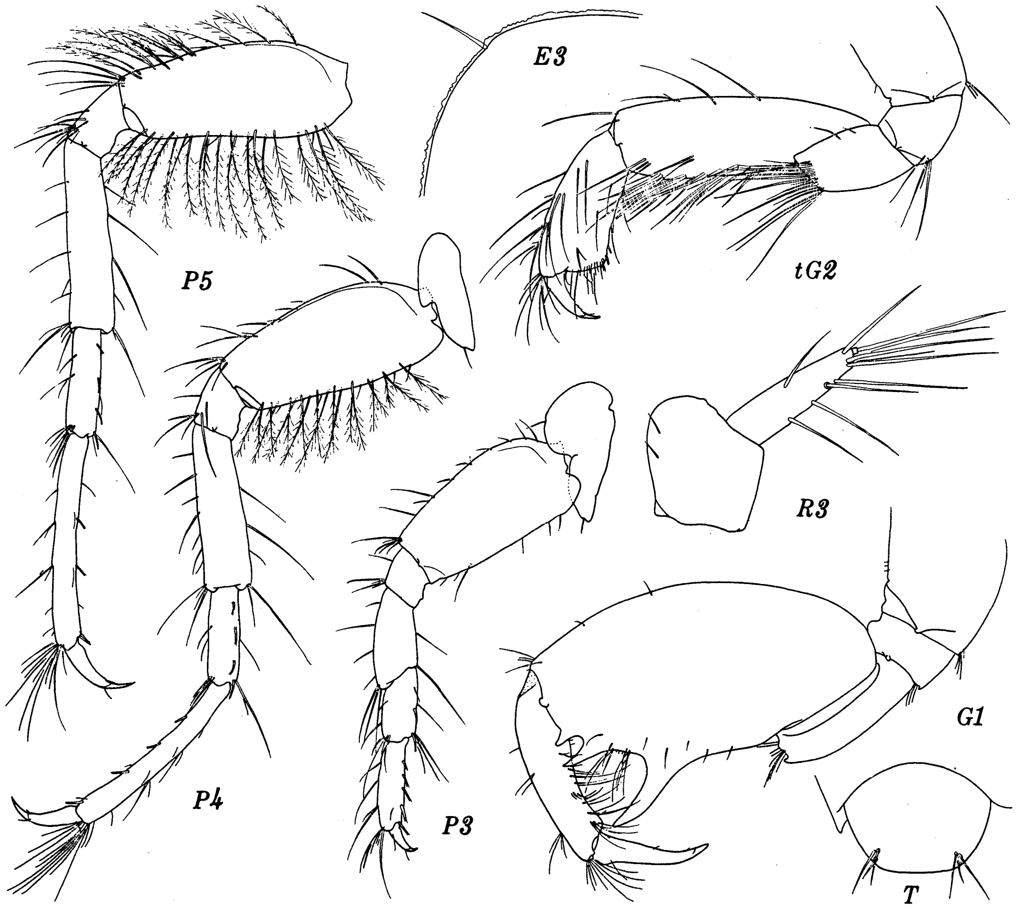

FIG. 3. *Grandidierella palama*, n. sp., holotype, ♂, 7.7 mm, Waianapanapa, 19.II.1972, Lenic.

Relationship: Because of the tooth on article 4 of male gnathopod 1, this species bears a weak affinity to *Neomicrodeutopus elongata* (Chevreux, 1926) and *N. cabindae* Schellenberg, 1925, but differs from both of those species in the presence of 3 (not 2) teeth on article 5 of male gnathopod 1. Of all the other species of *Grandidierella,* the new species appears closest to *G. dentimera* Myers, 1970, a Hawaiian open-sea species. The resemblance is strong because of the presence of 3 teeth on article 5 of male gnathopod 1 and the oblique arrangement of those teeth, and because of the presence on *G. dentimera* of a tooth on article 4. In the new species the teeth on article 5 are of 3 different sizes whereas in *G. dentimera* the 2 proximal teeth are of equal size. In *G. dentimera* article 2 and article 6 are stout and the tooth of article 4 is large and not marked by a sinus. The mandibular palp of *G. dentimera* has article 1 short, whereas in *G. palama* article 1 is about 80% as long as article 2.

Grandidierella palama also resembles *G. bonnieroides* Stephensen, 1933b, but differs in the free apex of and tooth on article 4 of male gnathopod 1 and in the obliquity of the tooth positions on article 5 of male gnathopod 1.

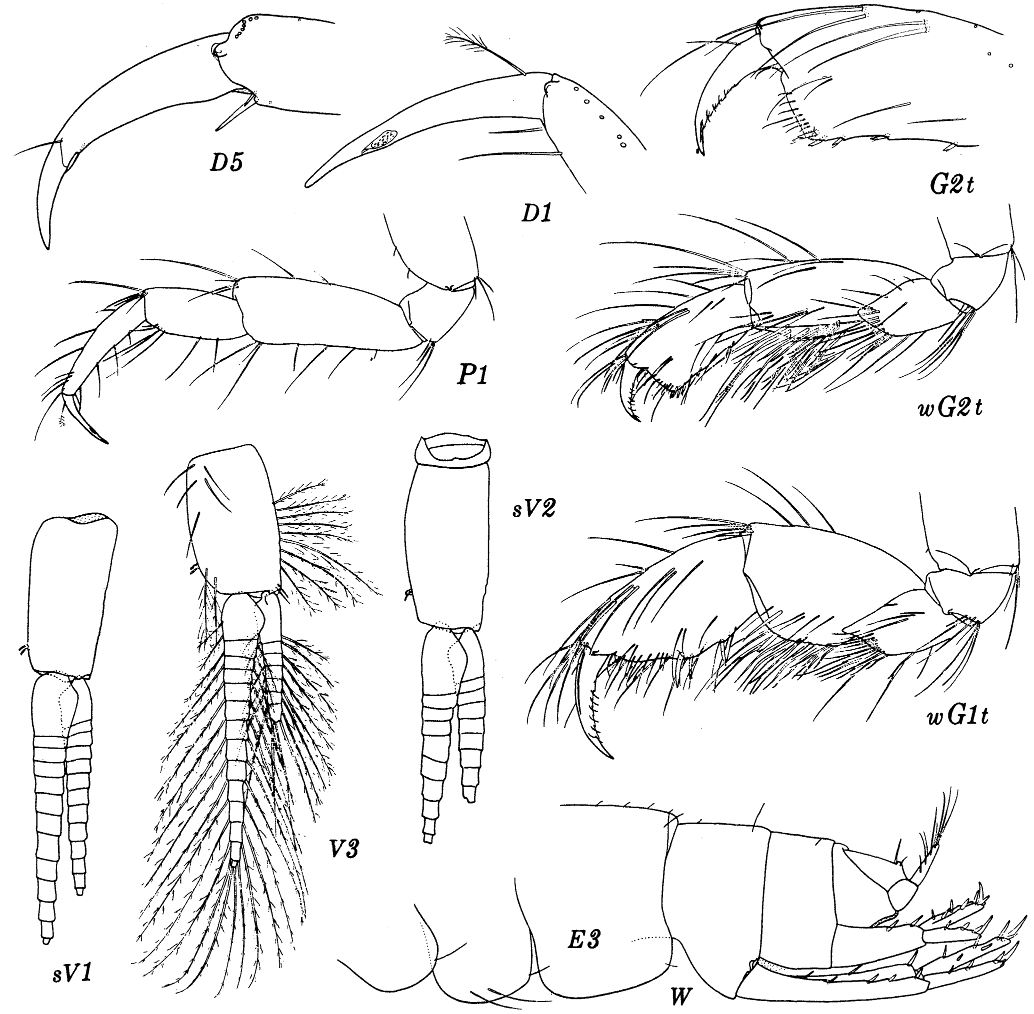

FIG. 4. *Grandidierella palama,* n. sp., holotype, ♂, 7.7 mm, Waianapanapa, 19.II.1972, Lenic; w = ♀, 6.7 mm.

Grandidierella koa Barnard, n. sp. FIG. 5–6

Diagnosis of ♂: Ocular lobes of short form for genus; antennae of medium length; length ratio of articles 1, 2, 3 of mandibular palp: 4:5:6; anterior coxae softly rectangular, lacking points; gnathopod 1: article 2 slender, article 4 with apex attached to article 5, lacking tooth; article 5 with 2 teeth set transversely, posterior tooth about 2x as long as anterior tooth, article 6 thin, posterior margin with excavation, then produced distally, dactyl slightly longer than longer tooth of article 5; gnathopod 2 slender, article 5 elongate, article 6 slightly more than 1/2 as long as article 5, palm almost transverse, straight; ramus of uropod 3 straight; sternal teeth absent.

♀: Articles 5–6 of gnathopod 1 of equal length, stout, palm oblique, defined by spine followed by 2 spines in tandem on posterior margin of article 6, article 5 with weak posterodistal tooth; gnathopod 2 slender, article 5 about 1.2 x as long as article 6, palm oblique.

Description: Article 2 of antenna 1 about 1.2 x as long as article 1, latter with 5 or 6 ventral spines; article 3 of antenna 2 with pair of ventral spines lying side by side, or in smaller ♂ situated in forceps fashion as in *Grandidierella palama;* both molars with long seta, left shorter than right; epistome flat anteriorly; gnathopod 1 of ♂ with nipple on anterior apex of article 2, apparently spine becoming enveloped in or fused with appendage as growth proceeds; uropod 1 with sharp and short interramal tooth, thick in ♂, thin in ♀; cuticle minutely punctate.

Illustrations: Following parts like those of *Grandidierella palama:* accessory flagellum; prebuccal; lower lip (evenly rounded below from anterior view); maxilla 1 (but palps with 6 apical spines and either 4 or 5 setae); maxilla 2 (but inner oblique row of inner plate with 26 setae); maxilliped; dactyls of pereopods. Density of setae on posterior margin of article 5 on ♀ gnathopod 2 reduced in illustration.

Holotype ♂(BISHOP S8414), 5.3 mm.

Type-locality: HAWAIIAN ISLANDS: Hawaii I, N. K. Air 3, 3.XII. 1972.

Material examined: 8 specimens from the type-locality.

Remarks: This species is very close to *G. lutosa* K. H. Barnard, 1952 from South Africa, but differs from that species in the thin article 6 on male gnathopod 1 and in the very stout female gnathopod 1. Numerous minute details of *G. lutosa* require illustration or description so that further distinctions cannot be determined at present.

Grandidierella koa appears close to *G. bispinosa* Schellenberg, 1938, from Bismarck Archipelago, but differs from that species in the simple (not bifid) dactyl of male gnathopod 1 and in the thin article 5 of male gnathopod 2. However, young male *G. bispinosa* is like the largest available specimen of *G. koa,* while the juvenile of *G. bispinosa* has article 6 of gnathopod 1 stout. Otherwise male *G. bispinosa* is poorly described and other features of distinction are unknown. Bousfield (1971) described a female attributed to *G. bispinosa* in which the gnathopods are thinner than in *G. koa,* the ramus of uropod 3 is more elongate and the shape and placement of the seta on epimeron 3 differ.

Grandidierella koa differs from *G. palama,* its sympatriot, in numerous features and would appear to be in a species cluster quite distinct from *G. palama.* These features include the interramal tooth of uropod 1 and the transverse tooth arrangement of gnathopod 1.

Grandidierella koa differs from the type-species *G. mahafalensis* Coutière, 1904, from Madagascar, in the more elongate article 5 of male gnathopod 2, the stouter article 5 and larger teeth of male gnathopod 1, and the enlarged and heavily spined female gnathopod 1. *G. koa* differs from *G. grossimana* Ledoyer, 1967 (Madagascar), because as far as is known, male gnathopod 2 article 5 remains slender in adults and female article 6 is stout.

Grandidierella gilesi Chilton, 1921, from India, has a merochelate gnathopod 2 in the male similar to that of *Xenocheira* or *Paracorophium* and has heavily setose gnathopods in both sexes, the male gnathopod 1 article 6 bearing a midposterior conical process.

Family EUSIRIDAE

Genus PARAMOERA Miers

Three apparent species of this genus comprise a geminate triad, 1 species from a cave on Maui, 1 from a well on Hawaii, and the other from open lava ponds of Hawaii. Their eyes are partially reduced in complexity and they differ from other species of *Paramoera* in the conspicuous apical denticulation of the telsonic lobes seen faintly in 2 species from British Columbia (Bousfield 1958). The latter character might be useful for subgeneric segregation of the Hawaiian species but other complications in the taxonomy of *Paramoera* suggest that such a designation is unwise at present. Ordinary members of *Paramoera* are confined to temperate waters of the southern hemisphere and the North Pacific Ocean, well outside the thermal ranges found in shallow waters of Hawaii. They are absent in the North Atlantic basins. Species of *Paramoera* are generally confined to the shallowest marine waters, scarcely penetrating below lowest tidal levels. Of the 29 known species, 10

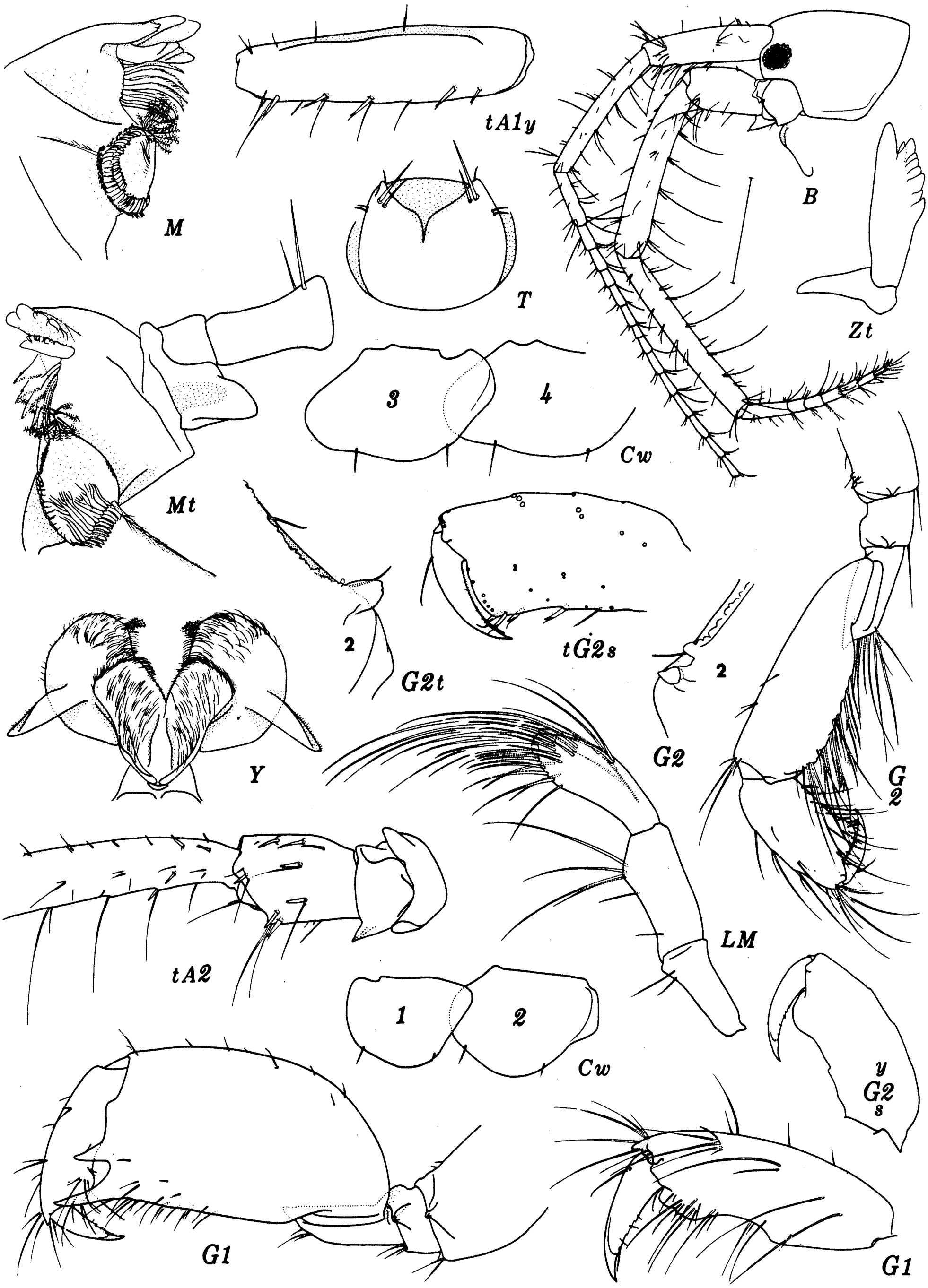

FIG. 5. *Grandidierella koa*, n. sp., holotype, ♂, 5.3 mm, N. K. Air 1; y = ♂, 5.6 mm; w = ♀, 6.5 mm; scale near head is remainder of antenna 1.

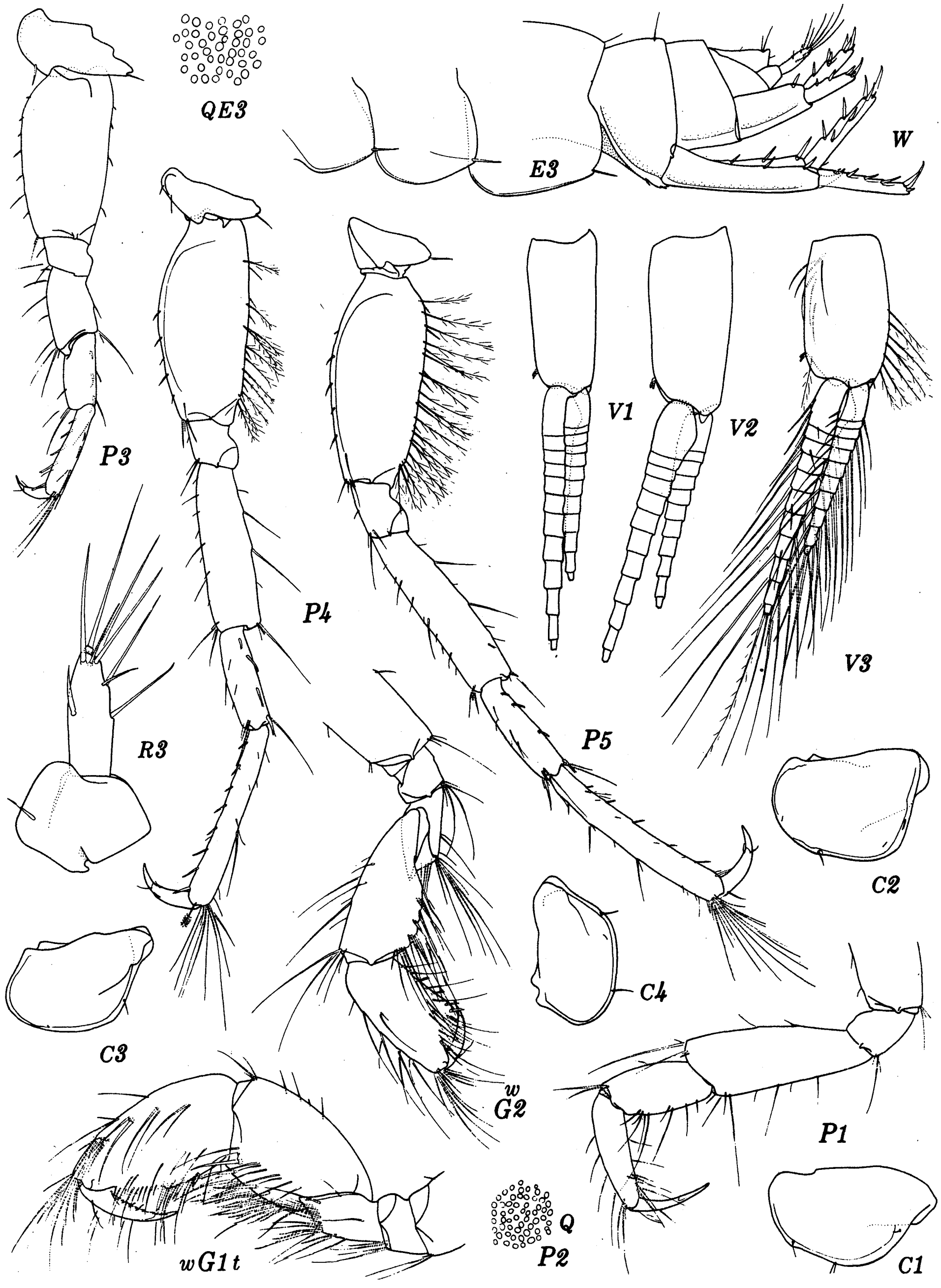

FIG. 6. *Grandidierella koa,* n. sp., holotype, ♂, 5.3 mm, N. K. Air 1; w = ♀, 6.5 mm; Q = cuticle.

are found in North Pacific waters, as follows: *P. carlottensis* Bousfield, *P. columbiana* Bousfield, *P. koreana* Stephensen, *P. mohri* Barnard, *P. hayamenensis* Stephensen, *P. japonica* (Tattersall), *P. udehe* (Derzhavin), *P. yezoensis* Ueno, *P. relicta* Ueno and *P. tsushimana* Ueno. The latter 6 are found in fresh water, and at least 2 of those have sternal gills, a condition not found in other species of the genus. The Hawaiian species lack those gills, so, presumably, are not derived from those fresh water species; in any respect one might hypothesize that the Hawaiian species descended from a marine species swept in from marine waters of the Asian or American continents. *Paramoera* has not been found in the open sea of the Hawaiian Islands and would not be expected to be in that situation; the discovery of these species in Hawaii is extraordinary because of the strict and cold thermal limits of the known open-sea species. Unusual occurrences of amphipods do, however, occur in the open seas of Hawaii (Barnard 1970) as about 20% of the known species come from cool (but not cold) parts of adjacent continents; these are the only marine animals in Hawaii that have been shown to have their origins from other than tropical waters. Because of the absence of sternal gills and the weakly subchelate and sublinear gnathopods with weak dactylar dentition, the ancestor of these species of *Paramoera* may have been in the species group formed by *P. koreana* Stephensen, 1944, *P. columbiana* Bousfield, 1958, and *P. mohri* J. L. Barnard, 1952, from Asia and America. The 3 Hawaiian species differ from those continental species in the poorly developed eyes. The cave species, *P. rua*, is unusual because of the deep telsonic cleft, whereas the other 2 Hawaiian species have a specially elongate telson distinct from the kind in continental species. *Paramoera columbiana* differs from Hawaiian species in the numerous denticulations of the epimera and the presence of coxal gills on pereonite 7; *P. mohri* differs in the shortness of article 5 and the subtransverse palms on the gnathopods; *P. koreana* differs in the shortness of article 5 on the gnathopods.

Two species of *Paramoera*, recently described by Ueno (1971a, b) from the island groups of Tsushima and Gôto, off Japan, in lava caves apparently similar to the cave on Maui, appear to bear little relationship to the Hawaiian species even though Ueno finds they probably had their ancestry in *P. koreana* Stephensen. These 2 species, *P. relicta* and *P. tsushimana*, differ conspicuously from the Hawaiian species and most other species of *Paramoera* in the odd anterolateral cephalic margin on which a notch occurs just anterior to the ocular region, below which the margin is convex, whereas the ordinary ocular lobe and anteroventral recess are absent. The 2 subterranean Japanese species also have an elongate antenna 1. One has vestigial eyes, the other is blind. *Paramoera relicta* has a slightly elongate accessory flagellum and *P. tsushimana* has excavate palms on the gnathopods. Spination patterns on the gnathopodal palms are also unusual in the Japanese species.

Paramoera relicta and *P. tsushimana* thus appear to be more remote from the Asian and American marine ancestry than do the Hawaiian species and deserve generic recognition.

The ommatidia of the eyes in the Hawaiian species are usually spaced apart so that they fail to touch, but occasional specimens apparently have a preservational defect with the ommatidia coagulated together.

The species from the fresh-water well (*P. lokowai*) has 1 large male with calceoli. The calceoli of antenna 1 are very small and infrequent, suggesting that the specimen is a young male.

No males with calceoli have been found in the other 2 species.

In the keys and diagnoses to species the word "form" is a substitute for words to describe conditions better seen in the figures.

KEY TO HAWAIIAN SPECIES OF *Paramoera*

1. Eyes present, antennae of short and thin form (see figures) 2

Eyes absent, antennae of long and thick form (epimeron 2 partly extended, telson cleft 3/4, apices narrow, elongate) .... **lokowai, n. sp.**

2. Epimera 1–3 with thin setule(s) posteriorly, telson short, apices broad, cleft almost fully, epimeron 2 with posteroventral corner nearly quadrate .... **rua, n. sp.**
   Epimera 1–3 each with 1 thick seta or spine posteriorly, telson elongate, apices narrow, cleft only 3/4, epimeron 2 with posteroventral corner extended sharply .... **paakai, n. sp.**

Paramoera rua Barnard, n. sp.

FIG. 7, 8, 9 (part)

Diagnosis: Eyes present but poorly developed; antennae 1–2 of short and thin form; article 3 of mandibular palp lacking outer seta; pereopods 3–5 with broad form of article 2; rami of uropod 3 of short form; telson of short form, almost fully cleft, apices broad; epimera 1–3 with tiny posterior setule(s); epimeron 2 with nearly quadrate posteroventral corner.

Description (♂ and ♀ alike): Rostrum small, lateral cephalic lobe prominent, mammilliform, quadrate anteroventral part of head separated from lobe by right angular incision, anteroventral corner rounded; eyes weak, formed of turgid ovate capsule bearing circular or bigeminate ommatidia sparsely plastered to outer shell of capsule, pigment absent in alcohol, presumably no pigmented core present, retinal tails of ommatidia absent or invisible and not forming normal ocular core; antennae extending equally, short, thin, poorly setose, about 45% as long as body, accessory flagellum typical, scale-like, bearing fan of 4 setae, gland cone with 2–3 stiff setae; prebuccal mass unproduced anteriorly, upper lip and epistome fused together but their parts regionally distinct; mandibles ordinary, each molar with long seta, right lacinia mobilis with 3 projections, right mandible with 6 spines, left with 9, palp article 2 swollen, with 1 subbasal seta and group of diverse subdistal setae, article 3 with 2 subbasal setae on 1 face, article scarcely falcate but heavily setose on distal 3/4 of inner margin and apex; lower lip with truncate mandibular lobes, inner lobes, if present, visible as 2 oblique creases; inner plate of maxilla 1 fully setose medially; inner plate of maxilla 2 with submarginal oblique row of 5 large setae becoming stouter distad; apical setal nail of maxillipedal palp article 4 about 1/3 as long as remainder of article; coxae 1–4 ordinary, each with posterolateral ridge line; gnathopods 1–2 very thin, small, palms oblique, defined by fan of 3 lateral and 2 medial spines, palm weakly crenulate, article 5 on gnathopod 1 triangular, rectangular on gnathopod 2, articles 5–6 longer on gnathopod 2 than on gnathopod 1; defining spines on pereopods 1–2 composed of 1 short spine and 2 setae, on pereopods 3–5 composed of 1 short spine and 2 long spines, dactyls with subapicad constriction and slit bearing facial setule, margin proximal to slit bearing long free seta; article 2 of pereopods 3–5 broad, suborbicular, remaining articles thin; uropods 1–2 ordinary, dorsally spinose, outer ramus of uropod 1 nearly as long as inner, outer of uropod 2 much shorter than inner; rami of uropod 3 thin, outer uniarticulate; telson cleft nearly to base, lobes slightly thinner than in ordinary species of genus, apices subtruncate but weakly toothed, with 2–3 such protrusions and 1 long apical seta each and other shorter setae; epimeron 1 with weak posteroventral tooth and setule-notch and one midposterior setule notch, epimeron 2 almost evenly quadrate posteroventrally, with 2–3 posterior notches bearing setules, epimeron 3 almost evenly quadrate and bearing 3 posterior setule notches, epimeron 1 with naked ventral margin, epimeron 2 with 0 or 1 ventral spine, epimeron 3 with 1 or 2 ventral spines, epimera 1–2 with lateral ridges; cuticle covered with long setules, subcuticular matrix polygonal, each polygon with nucleus, scattered here and there small granulated tubules (possible excretory or lubricant ducts with granules precipitated by preservative).

Variant: Specimens collected by E. L. Bousfield & F. G. Howarth also from type-locality: Eyes reduced to 2–4 elements, antenna 1 article 1 with distolateral patch of 4–5 setae, 2 or 3 of these long; epimera 1–2 and occasional epimeron 3 with corners slightly more produced but epimeron 2 lacking ventral spine on 1 specimen; article 2 of mandibular palp with groups of 5 stout and 4 thin setae or group of 2–3 stout with 2–3 thin plus 5 thin setae, article 3 often with 3 basofacial setae; specimens otherwise typical in telson, antennae, uropod 3, and article 2 of pereopods 3–5; possibly representing a new species distinct from that diagnosed and figured.

Illustrations: View of body with rami of uropod 1 and most of epimeron 3 added by extrapolation from other specimens; rami of uropod 3 unflattened in view presented; upper lips of ♂ and ♀ from different aspects.

Holotype ♀. (BISHOP S8415), 5.2 mm.

Type-locality: HAWAIIAN ISLANDS. Maui I, Waianapanapa Cave, Hana, 16.VII.1972,F.G. Howarth & S. Malecha.

Material examined: 5 specimens from type-locality; 11 specimens from Waianapanapa, 19.II.1972, J. S. Lenic; 21 specimens from Waianapanapa, twilight pool, 24.I.1973, E. L. Bousfield & F. G. Howarth; 2 specimens from Waianapanapa, dark zone pool, 24.I.1973, F. G. Howarth & E. L. Bousfield.

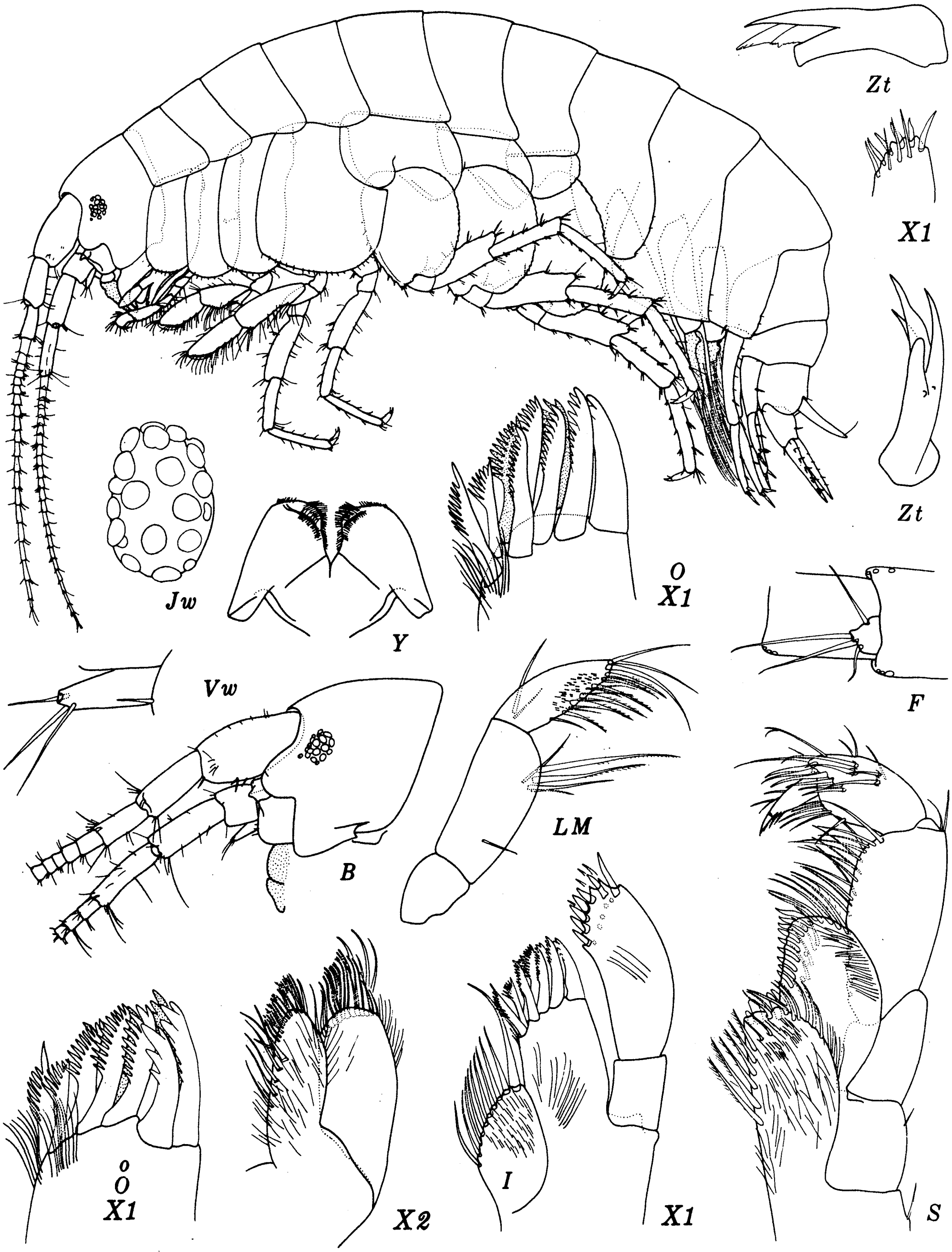

FIG. 7. *Paramoera rua*, n. sp., holotype, ♀, 5.2 mm, Waianapanapa, 16.VII.1972; w = ♀, 4.1 mm, 19.II.1972; J = eye, V = gland cone.

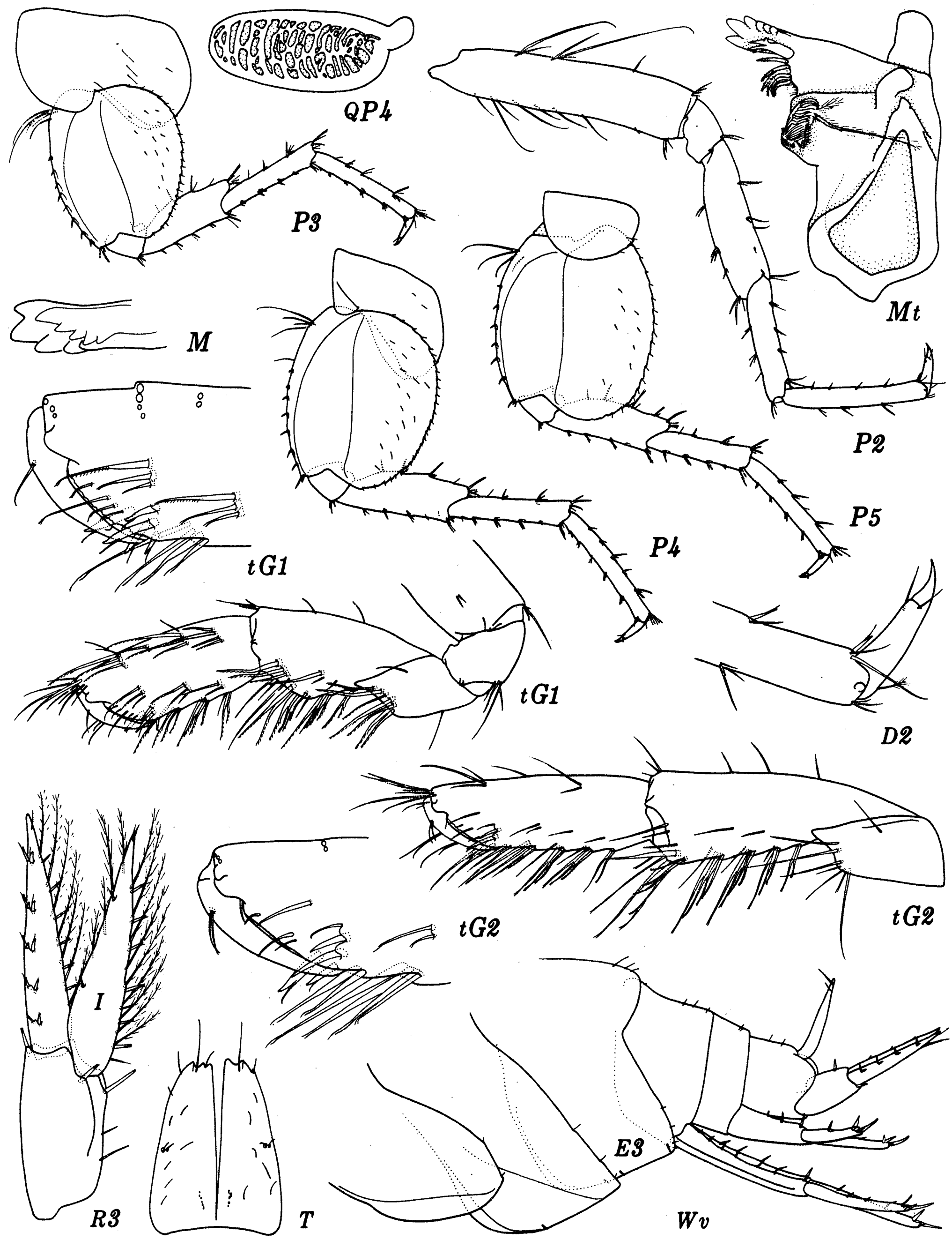

FIG. 8. *Paramoera rua*, n. sp., holotype, ♀, 5.2 mm, Waianapanapa, 16.VII.1972; v = ♂, 4.5 mm.

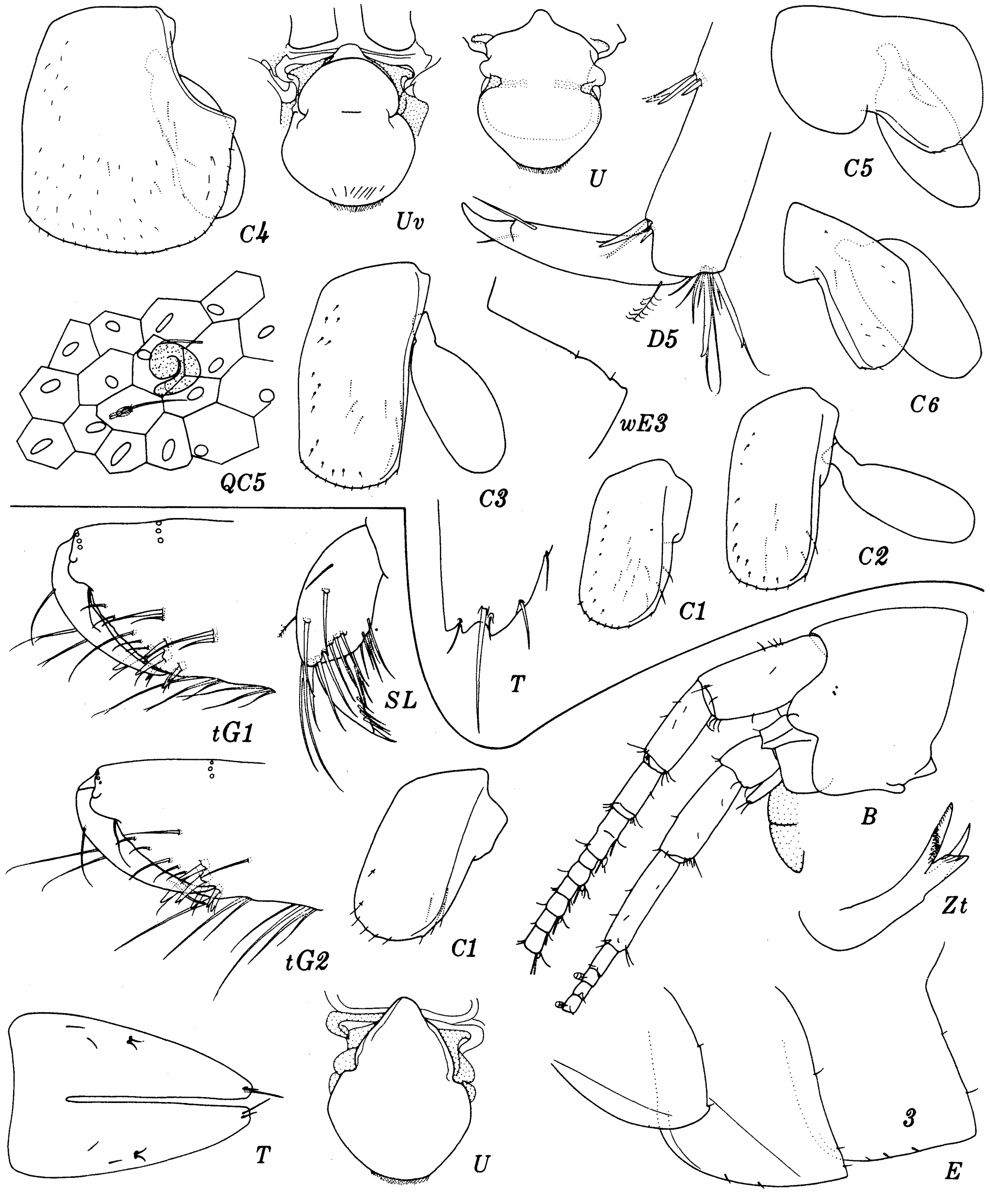

FIG. 9. Upper, *Paramoera rua*, n. sp., holotype, ♀, 5.2 mm, Waianapanapa, 16.VII.1972; v = ♂, 4.5 mm; w = ♀, 4.1 mm, 19.II.1972; Q = cuticle. Lower, *Paramoera lokowai*, n. sp., holotype, ♂, 3.6 mm, Honauau Well 1.

Paramoera paakai Barnard, n. sp. FIG. 10 (part)

Diagnosis: Eyes present but poorly developed; antennae 1–2 of short and thin form; article 3 of mandibular palp bearing outer seta; pereopods 3–5 with narrow form of article 2; rami of uropod 3 of short form; telson of elongate form, apices narrow, cleft only 3/4 its length; epimera 1–3 with 1 large midposterior spine; epimeron 2 with extended and attenuate posteroventral corner.

Description (♂ and ♀ alike): Rostrum small, lateral cephalic lobe prominent, mammilliform, quadrate anteroventral part of head separated from lobe by right angular incision, anteroventral corner rounded; eyes weak, formed of turgid ovate capsule bearing circular or bigeminate ommatidia sparsely plastered to outer shell of capsule, pigment absent in alcohol, presumably no pigmented core present, retinal tails of ommatidia absent or invisible and not forming normal ocular core; antennae extending equally, short, thin, poorly setose, about 45% as long as body, accessory flagellum typical, scale-like, bearing fan of 4 setae, gland cone with 2–3 stiff setae; prebuccal mass unproduced anteriorly, upper lip and epistome fused together but their parts regionally distinct; mandibles ordinary, right molar with long seta, left with very short seta, right lacina mobilis with 3 projections, right mandible with 5 spines plus rudimentary 6th, left with 4, palp article 2 slightly swollen, with 1 subbasal seta and group of diverse subdistal setae, article 3 with 4 subbasal setae on 1 face and outer marginal seta, article scarcely falcate but heavily setose on distal 3/4 of inner margin and apex; lower lip with truncate mandibular lobes, inner lobes if present visible as 2 oblique creases only; inner plate of maxilla 1 fully setose medially (7 setae only); inner plate of maxilla 2 with submarginal oblique row of 5 large setae becoming stouter distad; apical setal nail of maxillipedal palp article 4 about 1/3 as long as remainder of article; coxae ordinary, coxae 1–4 each with posterolateral ridge line; gnathopods 1–2 very thin, small, palms oblique, defined by fan of 2 lateral and 2 medial spines, palms weakly crenulate, article 5 on gnathopod 1 softly triangular, rectangular on gnathopod 2, articles 5–6 longer on gnathopod 2 than on gnathopod 1; defining spines on pereopods 1–2 composed of 1 short spine, 1 long seta, 1 rudimentary seta, on pereopods 3–5 composed of 1 short spine and 2 long spines, dactyls with subapical constriction and slit bearing facial setule, margin proximal to slit bearing long free seta; article 2 of pereopods 3–5 narrower and relatively longer than in *P. rua,* remaining articles thin; uropods 1–2 ordinary, dorsally spinose, outer ramus of uropod 1 nearly as long as inner, outer ramus of uropod 2 much shorter than inner; rami of uropod 3 thin, outer uniarticulate; telson cleft only 3/4, elongate in comparison to *P. rua,* lobes apically thinner, poorly denticulate, obliquely truncate, each apex bearing 1 long, 1 short seta; epimeron 1 with weak posteroventral tooth and setule notch and 1 midposterior notch bearing spine (or stiff seta), epimeron 2 extended and sharply attenuate posteroventrally, with 1 midposterior spine in notch, epimeron 3 with unevenly quadrate posteroventral corner and 1 midposterior spine in notch, epimeron 1 with naked ventral margin, epimeron 2 with 2 ventral spines in tandem or only 1 spine, or 1 spine position bearing 2 spines for total of 3 ventral spines, epimeron 3 with 0, 1 or 2 ventral spines, spines occasionally absent when epimeron 2 bearing 2 spines (in larger juveniles); cuticle covered with long setules, subcuticular matrix polygonal, each polygon with nucleus, scattered here and there small granulated tubules.

Illustrations: Most parts resemble those of *P. rua* so closely that duplicate illustrations have been omitted; additional minor differences are illustrated in coxae 1–2 and the apex of the maxillipedal palp; coxae 3–4 are unillustrated but differ from *P. rua:* coxa 3 bears 2–3 medial and posterior setae only, coxa 4 lacks medial setae; gills of this species are poorly preserved but external shapes are generally similar to those of *P. rua.*

Variations: One adult of the Honokohau sample lacks a dorsal spine on the outer ramus of uropod 2 but a companion juvenile bears this spine; epimeron 1 occasionally lacks a midposterior spine or setule in adults but this spine or setule is present in juveniles; the doubling of spines in 1 position on epimeron 2 appears to be rare but may be characteristic of terminal adults.

Holotype ♀ (BISHOP S8408), 3.84 mm.

Type-locality: HAWAIIAN ISLANDS: Hawaii I, Tokyo-Land lava pond sample 5, 17.VII.1972.

Material examined: The type-locality (5); following lava ponds on Hawaii: Makalawena-BR 3 (12), Tokyo-Land 13 (4, in fragments); Anaehoomalu T-15 (1 chewed specimen probably dead before collection), Kona Village-7 (3), Makalawena T-2 (1 juvenile), Kaloko 2 (9), Makalawena 7.I.1972 JSL (2), Honokohau 14.I.1972 JSL (2).

Relationship: Although this species lives in open lava ponds rather than in a cave pond as does *P. rua,* it seems more advanced or "descendent" in its characters than does the cave species of Maui. The heavy spines of the epimera and the elongate telson are advanced characters, not those of an ancestral species. So many cold-temperate species of *Paramoera* have a poorly cleft telson as in *P. paakai* that one might suggest the fully cleft telson of the cave species, *P. rua*, is an advancement. No species of *Paramoera* discussed in this paper is the living ancestor of the species pool because the ancestor probably had a poorly cleft telson of the short form, normal epimera (no posterior spines), and, of course, had normal eyes.

Paramoera lokowai Barnard, n. sp. FIG. 9 (part), 10 (part)

Diagnosis: Eyes absent; antennae 1–2 of long and stout form; article 3 of mandibular palp lacking outer seta; pereopods 3–5 of long form, article 2 of narrow form; rami of uropod 3 of elongate form; telson of elongate form, cleft only 3/4, apices narrow; epimera 1–3 with tiny posterior setule(s); epimeron 2 with nearly quadrate posteroventral corner but very weakly extended.

Description: Rostrum small, lateral cephalic lobe prominent, mammilliform, quadrate anteroventral part of head separated from lobe by right angular incision, anteroventral corner rounded; eyes absent; antennae stout and elongate (apically broken but at least 2/3 as long as body), poorly setose, accessory flagellum typical, scale-like, bearing fan of 4 setae, gland cone with 2 stiff setae, ♂ with small calceoli on antennae 1–2, much smaller on antenna 1, 1 each on articles 2–10 + 12 on flagellum of antenna 1, alternating zigzag because alternate even articles swollen, 1 large calceolus on articles 2, 3, 4, 5, 6, 9 of antenna 2 flagellum (possibly broken off on articles 7–8); prebuccal mass unproduced anteriorly, upper lip and epistome fused together but their parts regionally distinct; mandibles ordinary, each molar with long seta, right lacinia mobilis with 3 projections, each mandible with 6 spines, palp article 2 slightly swollen, with 1 subbasal seta and group of diverse subdistal setae, article 3 with 2 subbasal setae on 1 face, article scarcely falcate but heavily setose on distal 3/4 of inner margin and apex; lower lip with truncate mandibular lobes, inner lobes if present visible as 2 oblique creases; inner plate of maxilla 1 fully setose medially; inner plate of maxilla 2 with submarginal oblique row of 4 large setae becoming stouter distad; apical setal nail of maxillipedal palp article 4 about 1/3 as long as remainder of article; coxae 1–4 ordinary, each with posterolateral ridge line; gnathopods 1–2 very thin, small, palms oblique, defined by fan of 3 lateral and 3 medial spines, palms weakly crenulate, article 5 on gnathopod 1 softly triangular, rectangular on gnathopod 2, articles 5–6 longer on gnathopod 2 than on gnathopod 1; defining spines on pereopods 1–2 composed of 1 short, thin spine and 2 setae, on pereopods 3–5 composed of 1 short spine and 2 long spines, dactyls with apicad constriction and slit bearing facial setule, margin proximal to slit bearing long free seta; article 2 of pereopods 3–5 narrower than in *P. rua* and pereopods longer than in *P. rua* and *P. paakai;* uropods 1–2 ordinary, dorsally spinose, outer ramus of uropod 1 nearly as long as inner, outer ramus of uropod 2 much shorter than inner; rami of uropod 3 thin and longer than in *P. rua* or *P. paakai;* telson cleft 3/4, lobes slightly to strongly thinner than in ordinary species of genus and much longer and apically narrower than in *P. rua,* apices softly truncate, almost smooth, bearing 1 long, 1 short setae; epimeron 1 with weak posteroventral tooth and setule notch and 1 midposterior setule notch; epimeron 2 subquadrate, weakly extended posteroventrally, with 2–3 posterior setule notches, epimeron 3 almost evenly quadrate posteriorly and bearing 2 setule notches, epimeron 1 naked ventrally, epimeron 2 with 2 spines, epimeron 3 with 2 spines and setule, epimera 1–2 with lateral ridges; cuticle covered sparsely with long setules, subcuticular matrix polygonal, each polygon with nucleus, scattered here and there small granulated tubules.

Illustrations: Most characters resemble those of *P. rua* and illustrations of similar parts have been omitted; minor deviations as follows: palps of maxillae 1 with 8 spines and 4 setae or 7 spines and 2 setae (opposite sides of adult ♂); shapes of coxae 3–4 like those of *P. rua* but coxa 4 lacking medial setae and coxa 3 with only 1 medial posterior seta (see illustrations of coxae 1–2 for differences from *P. rua*); prebuccal mass from anterior view and maxillipedal palp articles 3–4 are illustrated to show minor distinctions.

♀: Fully adult ovigerous ♀ not present, ♀♀ bearing rudimentary buds of brood plates, antennal bases generally like those of ♂ and flagella probably similar to that of ♂ in length and size of articles but apices broken; articles of antenna 1 not differentially swollen.

Holotype ♂. (BISHOP S8413), 3.6 mm.

Type-locality: HAWAIIAN ISLANDS: Hawaii I, Honaunau Well No. 1, 2.XII.1972.

Material examined: The type-locality (4).

Relationship: Because of the elongate and poorly cleft telson and the slightly extended epimeron 2, this species appears closer to *P. paakai* from lava ponds than to *P. rua* from a cave on Maui. *Paramoera lokowai* differs from *P. paakai* in the small epimeral setules, absence of eyes and long thick antennae. One could not determine at present which, *P. lokowai*

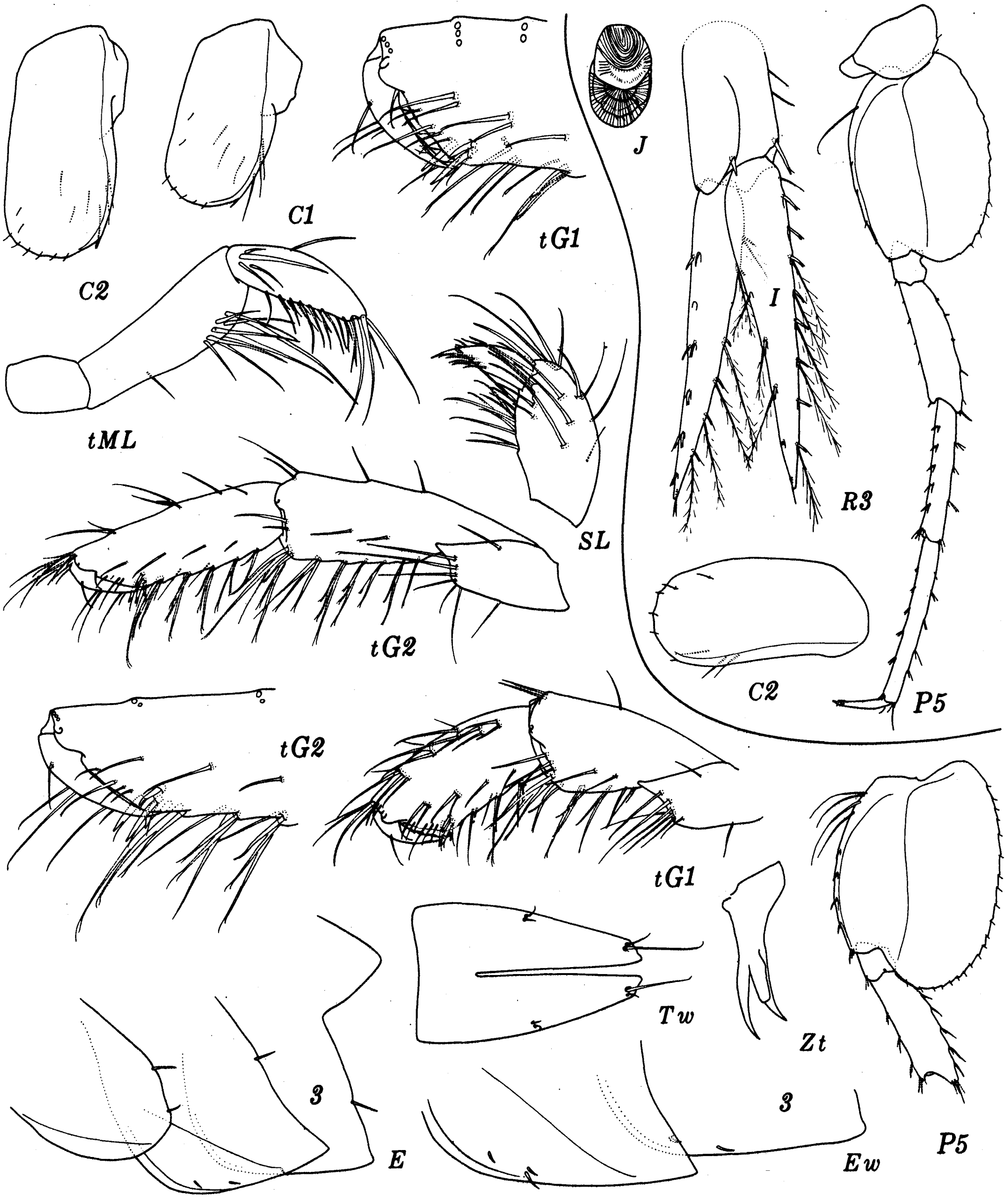

FIG. 10. Upper right, *Paramoera lokowai,* n. sp., holotype, ♂, 3.6 mm, Honaunau Well 1; J = calceolus. Lower and left, *Paramoera paakai,* n. sp., holotype, ♀, 3.84 mm, Tokyo-Land 5; w = ♀, 4.00 mm, Makalawena BR-3.

or *P. paakai*, might have been ancestral to the other, whereas it is possible to hypothesize that either species could be descendent from the Maui cave species *P. rua*. This begs ecological logic. Probably more species remain to be discovered in the Hawaiian Islands and a better approximation of ancestry may be forthcoming when more species have been described.

Family GAMMARIDAE

Genus HADZIA Karaman

Hadzia S. Karaman, 1932: 214.

Metaniphargus Stephensen, 1933a: 426, **new synonymy** (valid subgenus)

Liagoceradocus J. L. Barnard, 1965: 504–05, **new synonymy** (valid subgenus)

Diagnosis: Accessory flagellum 2-articulate; antenna 1 much longer than antenna 2; mandibular palp ordinary, 3-articulate; lower lip lacking inner lobes; inner plate of maxilla 1 fully setose medially; inner plate of maxilla 2 with fully developed oblique row of submarginal setae on medial margin; gnathopods small, slender, gnathopod 1 with article 5 tumid, article 6 subtumid, weakly shorter than article 5, palm transverse or subtransverse, gnathopod 2 with article 5 strongly tumid posteriorly, fuzzy, article 5 thus wider but shorter than article 6, latter slender, palm very oblique, imperceptibly merged with posterior margin of hand, palm near folded apex of dactyl armed with medial and lateral rows of medium-sized spines bearing subapical trigger setule, palm defined by brush of long setae and occasional enlarged spine; coxa 4 subquadrate, not expanded, unexcavate posteriorly; epimera 2–3 with ventral spines; uropod 3 bearing small article 2 on outer ramus; telson cleft to base, each lobe with 3 or more spines near apex, often with spines on apposing medial margins; some coxal gills with basal pedicles (as far as known); urosomites 1–2 often with 1 or 2 spines each on dorsolateral faces.

Type-species: *Hadzia fragilis* S. Karaman, 1932 [cave in Yugoslavia].

Remarks: Stock & Nijssen (1965) suggested that the Caribbean phreatic genus *Metaniphargus* is synonymous with the Mediterranean phreatic genus *Hadzia* although the lower lip and gills of *Hadzia* are unknown. One conspicuous distinction may be seen, the inner ramus of uropod 3 on species of *Hadzia* is almost as long as the outer ramus whereas the inner ramus on species of *Metaniphargus* is 1/2 as long as the outer ramus. Palp article 4 of the maxilliped in *Metaniphargus* bears a strong nail-spine but *Hadzia* bears only 2 or more thin flexible setae on that article. G. S. Karaman (1969) also noted that species of *Metaniphargus* bear lateral spines on the telsonic lobes, absent in *Hadzia*, but, like Stock & Nijssen (1965), he synonymized *Metaniphargus* with *Hadzia*.

Liagoceradocus is based on a marine species from Micronesia with a body size of about 1.5 mm, as contrasted to lengths up to 10 mm for *Hadzia*. The type-species of *Liagoceradocus* was poorly analyzed because of this small size, extreme fragility of the 2 known specimens and mediocre microscopy. The excellent specimens found in Hawaiian lava ponds, however, fit the picture of Micronesian *Liagoceradocus* sufficiently well to suggest affinity. *Liagoceradocus* cannot be distinguished from *Hadzia* except by the presence of dorsal spinules on the urosome, the presence of a comb of spines on the medial apex of the peduncle on uropod 2 and lateral spines on the telson. The Hawaiian specimens of *Liagoceradocus* bear a nail on maxillipedal palp article 4 like *Metaniphargus* but unlike *Hadzia* and apparently unlike the Micronesian *Liagoceradocus;* however, the latter illustration or observation may be defective because of the lack of oil immersion lenses to study that appendage. This appendage is now missing from both known specimens of the type-species of *Liagoceradocus* despite a protracted search in early 1973.

Several purely phreatic and troglobitic genera are closely similar to *Hadzia*. These are *Alloweckelia* Holsinger & Peck, 1968, *Mexiweckelia* Holsinger & Minckley, 1971, and

Weckelia Shoemaker, 1942. They resemble *Hadzia* in the reduction or absence of inner lobes on the lower lip, the presence of setular fuzz on article 5 of gnathopod 2 (common on gnathopod 1 in many more distant genera), and generally small gnathopod 2 with elongate wrist. *Eriopisa laakona* J. L. Barnard, 1970, from the Hawaiian intertidal, also bears setular fuzz on gnathopod 2 and must be reexamined to determine whether it might have affinities with the *Hadzia* group. *Paraweckelia* Shoemaker, 1959 is removed from this group because of its strong gnathopod 2 lacking fuzz and reasonably strong inner lobes on the lower lip and is aligned more closely with the *Melita-Eriopisa-Paraniphargus* group. *Eriopisella* Chevreux bears setular fuzz on gnathopod 2 but is clearly distinctive in its neotenic gnathopod 2 and joins *Netamelita* J. L. Barnard, *Microniphargus* Schellenberg, and *Indoniphargus* Straskraba. *Quadrivisio* Stebbing is also removed from the *Hadzia* group because of its cephalic notch, inner lobes on the lower lip, flabellate rami of uropod 3 and powerful gnathopod 2. It joins *Paraceradocus* in these characters. *Psammoniphargus* Ruffo, 1956, from Reunion, lacks inner lobes on the lower lip but also apparently lacks fuzz on gnathopod 2 and is therefore removed from the *Hadzia* group. *Paraniphargus lelouparum* Monod, from the Galapagos Islands, lacks setular fuzz on gnathopod 2 and bears poorly developed inner lobes on the lower lip but differs in so many other ways from *Paraniphargus* that it should be removed from the *Melita-Eriopisa* group to a genus and section of its own.

The Caribbean genera *Alloweckelia*, *Mexiweckelia* and *Weckelia* differ from *Hadzia* in various morphological losses such as absence of article 2 on the outer ramus of uropod 3 and reduction or loss of mandibular palp, and in gains such as the broad expansion of coxa 4. The Caribbean genera have an elongate inner ramus on uropod 3, suggesting that the hypothetical ancestor of the Caribbean genera was similar to European or Indo-Pacific *Hadzia* (*Liagoceradocus*) and not the Caribbean *Hadzia* (*Metaniphargus*).

KEY TO THE SUBGENERA OF *Hadzia*

1. Inner ramus of uropod 3 half or less as long as outer ramus .... **Metaniphargus**
   Inner ramus of uropod 3 more than 3/4 as long as outer ramus, generally reaching to base of article 2 on outer ramus 2
2. Telson bearing 1 or more lateral spines on each lobe .... **Liagoceradocus**
   Telson lacking lateral spines .... **Hadzia**

Hadzia (Liagoceradocus) lonomaka Barnard, n. sp. FIG. 11, 12

Diagnosis: Maxillipedal palp article 4 with well-defined nail-spine; outer ramus of uropod 2 dorsally spinose; palm of gnathopod 1 perfectly transverse.

Description: Lateral cephalic lobe evenly rounded, broad, separated from anteroventral quadrate cephalic extension; eyes absent; rostrum obsolete; antenna 1 about 80% as long as body, antenna 2 about 40%, accessory flagellum 2-articulate; prebuccal mass pyriform from lateral view, broadly pyriform from anterior view; seta on left molar 1/2 as long as on right; article 3 of maxillipedal palp very broad, spinose, minutely setulose, article 4 unguiform, apical nail well developed; ♂ and ♀ gnathopods 1–2 similar to each other; uropod 2 with apicomedial comb of peduncular spines; lobes of telson separated basally; cuticle bearing sparse numbers of bulbar setules, subcuticle with scattered granular bodies.

Illustrations: Upper lip shown for holotype is a view of dissected and mounted part, for ♀ 2.85 mm, view is in situ; apices of palp and outer plate of maxilla 1 much enlarged from inner plate; 1st maxillary palp not illustrated, bearing 5 spines and 2 setae; pereopod 4 article 2 breadth similar to pereopod 5.

Variations: Largest ♂, 3.08 mm, with 2 spines on epimeron 2, 3 spines on epimeron 3, and 3 dorsal spines on outer ramus of uropod 2; smallest juvenile, 2.25 mm, with 1 spine on epimeron 2, 2 spines on epimeron 3, rami of uropods 1–2 each with 1 dorsal spine.

Holotype ♂ (BISHOP S8412), 2.54 mm.

Type-locality: HAWAIIAN ISLANDS: Maui I, Cape Kinau, Nukuele No. 1, 5.I.1973.

Material examined: 7 specimens from type-locality.

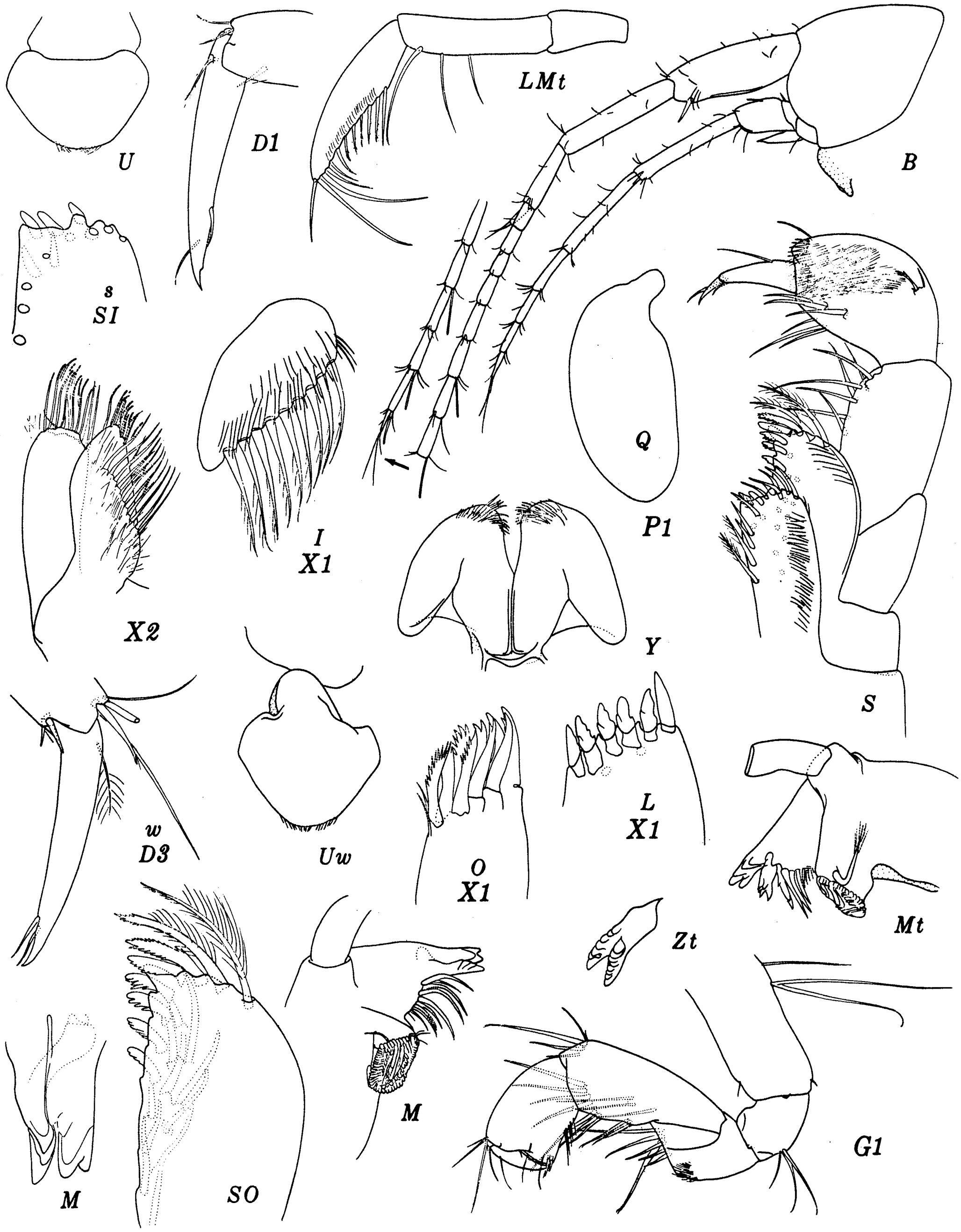

FIG. 11. *Hadzia lonomaka*, n. sp., holotype, ♂, 2.54 mm, Cape Kinau, Maui; w = ♀, 2.85 mm.

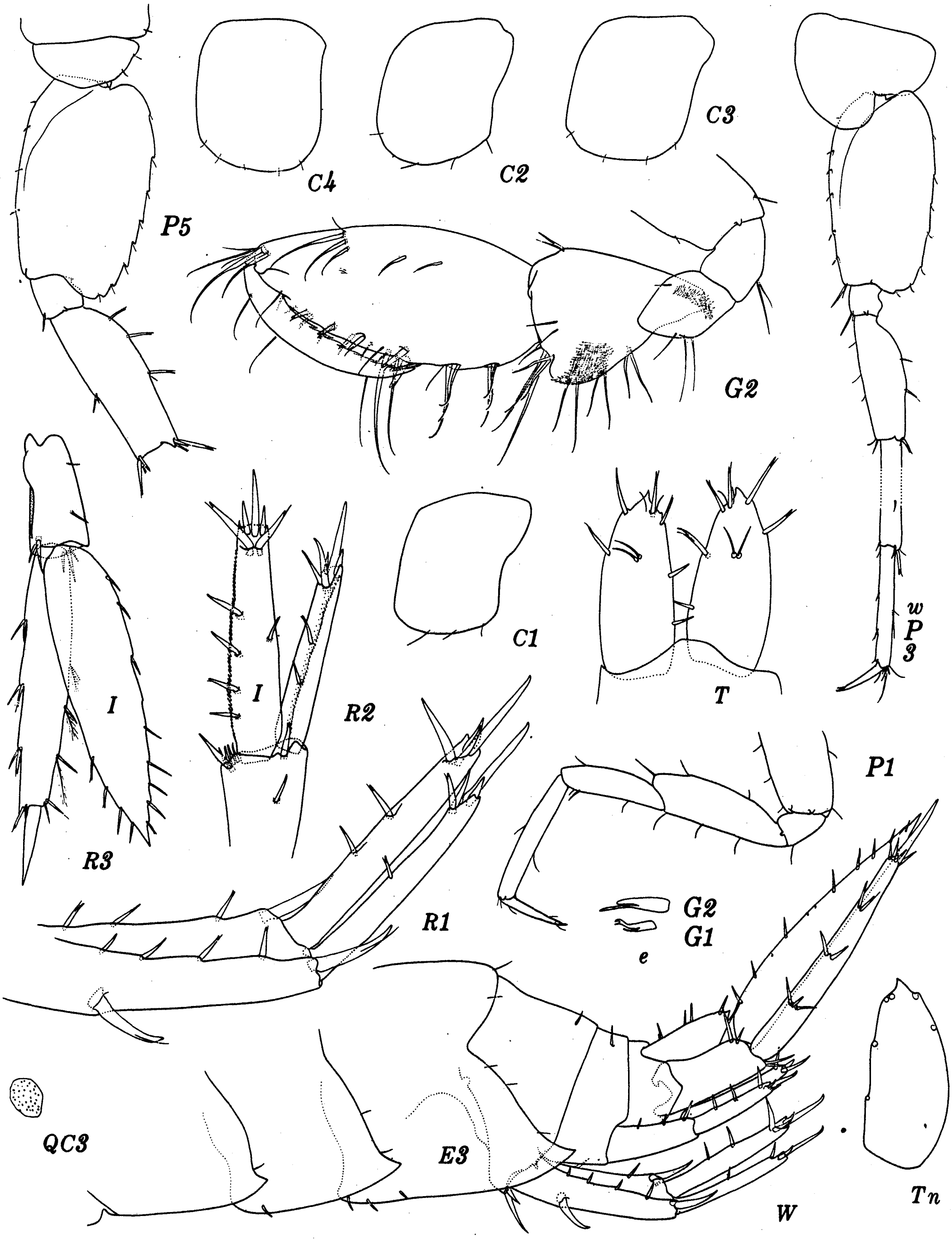

FIG. 12. *Hadzia lonomaka*, n. sp., holotype, ♂, 2.54 mm, Cape Kinau, Maui; w = ♀, 2.85 mm; Q = cuticle.

Remarks: Uropod 3 is missing from all specimens but the holotype. The female, 2.85 mm long, bears 1 egg sufficiently filling brood pouch to suggest that only 1 egg is carried by females this size; the other females in the collection bear rudimentary brood plates and no eggs.

I have reexamined the holotype and 2nd specimen of *L. pusillus* J. L. Barnard, 1965, but, unfortunately, the maxillipeds of both specimens are missing from the vials enclosing the dissected parts. I therefore cannot reconcile the distinctive articles 3–4 of the maxilliped as illustrated herein and in the 1965 report. Despite conformity of almost all other characters, these 2 maxillipeds, from Hawaii and Micronesia, are highly distinct and suggest that the Hawaiian specimens must be accorded a distinct name. In *L. pusillus* article 3 is slender and apically produced, while article 4 is short, apically truncate and apically setose.

Additional observations on *L. pusillus:* uropod 1 similar to that of *L. lonomaka,* bearing large facial spine on peduncle, large spine on each apical margin of peduncle; uropod 2 with large apicolateral spine on peduncle and 1 spine on dorsal margin of outer ramus; pleonites 4–5 each with dorsolateral spine on each side as in *L. lonomaka;* pleonite 4 with 2 large spines at base of uropod 1 as in *L. lonomaka.*

Maera sp. C

Material examined: 4 specimens from Cape Kinau, Maui, Nukuele Pt., in brackish pond, 22.I.1973, J. Maciolek, E. L. Bousfield & F. G. Howarth; largest a ♀, 4.3 mm long.

Remarks: This species is designated *Maera* sp. C because J. L. Barnard (1970) already designated 2 other species of the genus by the letters A and B. This species, represented by 4 imperfect specimens, is similar to *M. othonides* Walker and may be identical with that species; it differs from *Maera* sp. A in the more complex palm of gnathopod 2.

Genus NUUANU J. L. Barnard

Nuuanu amikai J. L. Barnard FIG. 13
Nuuanu amikai J. L. Barnard, 1970: 166, fig. 105, 106.

The specimen in hand differs from the holotype and only other known specimen of the species in the presence of distinct lateral ridges on epimera 1–2; the holotype has been reexamined and is interpreted to be a specimen near ecdysis just prior to death, the ridges having disappeared prior to molting.

Additional illustrations are presented here to clarify the locking spines of the pereopods, the inner and outer plates of the maxillipeds and the cuticle. These have been compared between holotype and the lava pond specimen and found to correspond, the holotype bearing 3 cones instead of 2 on the outer lobe of the maxilliped. Antenna 1 in both specimens has a midventral spine on article 1 overlooked in the original description. The holotype has 2 ventral spines on epimeron 1 and 2 on epimeron 2.

The cuticle is peculiar and corresponds on both specimens; it is covered with tiny thin spicules and punctations, the spicules disconnected from the punctations but perhaps attached to them during life; however, no attachment remains in death.

The left mandibular molar bears 1 seta as long as the breadth of the molar, but the right molar lacks this seta as far as can be determined.

The lava pond specimen is much smaller than the holotype (3.4 mm as compared with 4.2 mm), is also a male but lacks the medial fuzz on the hand of gnathopod 2. The lava pond specimen has 3 dorsal spines on each ramus of uropod 1 and 4 spines on each ramus of uropod 2. Except for the absence of gnathopodal fuzz, the lava pond specimen appears better developed morphologically than the holotype.

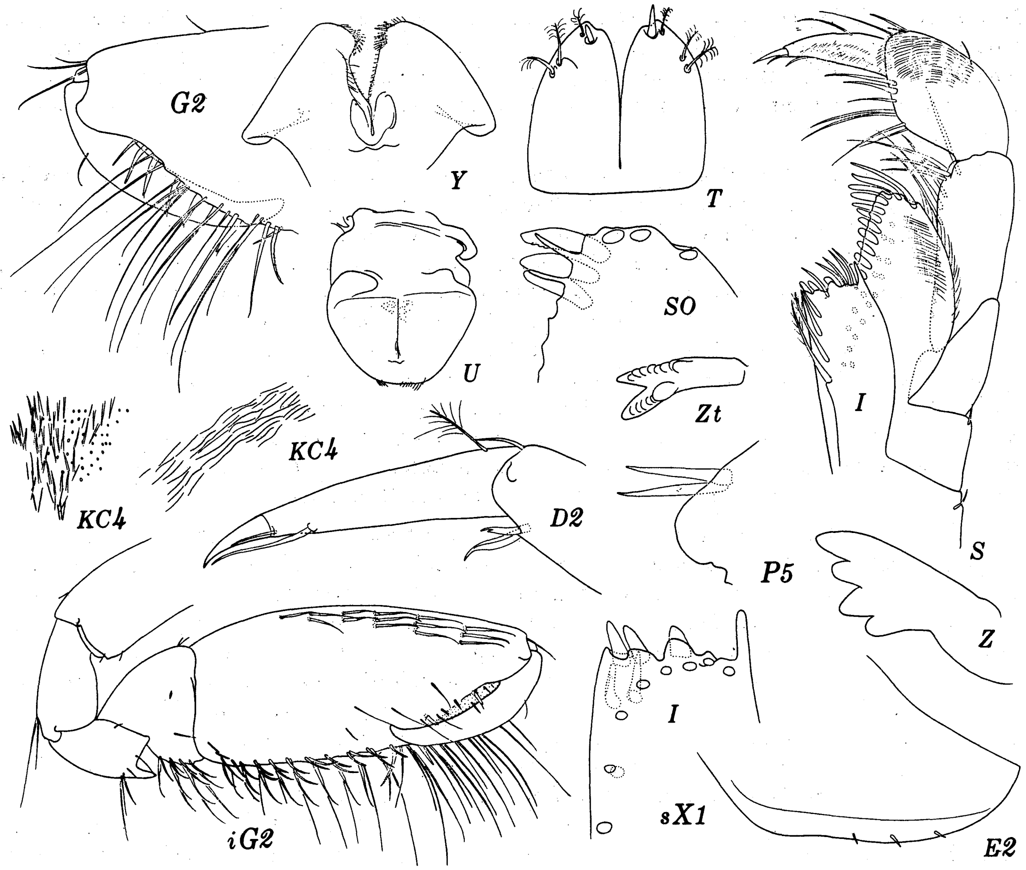

FIG. 13. *Nuuanu amikai* J. L. Barnard, ♂, 3.4 mm, Cape Kinau, Maui.

Material examined: ♂, 3.4 mm, Cape Kinau, Maui, Nukuele No. 1.

Distribution: Oahu, open sea, 18 m; lava pond on Maui.

Genus **ROTOMELITA** Barnard, **n. genus**

Diagnosis: Accessory flagellum 3+ articulate; mandibular palp thin, weak, articles linear, article 3 bearing few apical setae only; lower lip with small but fully discrete inner lobes; inner plate of maxilla 1 with only terminal setae; inner plate of maxilla 2 lacking medial setae; maxillipedal palp 4-articulate, article 4 unguiform; gnathopods ordinary, gnathopod 2 larger than gnathopod 1, lacking fuzz on article 5; uropod 3 greatly overreaching uropod 1, inner ramus small and scale-like, outer ramus immensely elongate, bearing short article 2; telson short, cleft, lobes very broad and apically truncate; urosomite 1 bearing 1 subdorsal spine on each side, otherwise pleonites dorsally smooth; anterior coxae (1–4) longer than posterior coxae (5–7); some gills pediculate.

Type-species: *Rotomelita lokoa,* n. sp.

Relationship: This genus has strong affinities with the *Melita* group of genera, composed of *Melita* Leach, *Melitoides* Gurjanova, *Eriopisa* Stebbing and *Paraniphargus* Tattersall, in which the inner lobes on the lower lip are strong to moderately developed, and male gnathopod 2 is enlarged but lacks setular fuzz on article 5. *Psammoniphargus* Ruffo, 1956 and a probable new genus represented by *Melita seticornis* Bousfield, 1970 also form a satellite to the

Melita group, being characterized by somewhat reduced male gnathopod 2 and loss of palp articles on the mandible. See *Hadzia* for placement of *Eriopisella* and the hadzia-like genera. *Dulzura* J. L. Barnard forms a group of its own and the genera *Pherusana, Cottesloe* and *Nuuanu* represent yet another group characterized by miniaturized uropod 3 among other things.

The broadened lobes of the telson with truncate or weakly excavate apices, somewhat reduced gnathopod 2, and fully pedunculate gills on several coxae differentiate *Rotomelita* from other members of the *Melita* group, except for *Melita latimerus* Bousfield, 1971. The latter species, from anchialine environments in the Bismarck Archipelago, differs from *Rotomelita* in the presence of eyes, a large ocular lobe, much more strongly developed gnathopod 2 with short wrist, generally shorter pereopods 3–5 with smaller diversity in size and with broader and strongly lobate article 2, absence of a dorsal spine on the outer ramus of uropod 1 and relatively shorter and more sparsely spinose article 1 on the outer ramus of uropod 3. *Melita latimerus* therefore appears to belong in a genus distinct from *Rotomelita*. Establishment of such a genus might await further exploration of anchialine environments in the Indo-Pacific region so as to determine the degree of intergradation between *Rotomelita* and the morphology characterizing *M. latimerus*.

Two species of *Rotomelita* have been found in the Hawaiian Islands, the so-called typical species, selected as the type-species, from lava ponds on the island of Hawaii, the 2nd, perhaps derived species, from a cave on the island of Maui. Despite the fact that the species in lava ponds lives in sunlight, both species are blind. As preserved in alcohol the pond species has a faint cast of brownish purple pigment, whereas the cave dweller lacks any visible pigment. Presumably the genus does not inhabit the open sea and so its pathway from one island to another is enigmatic. One might hypothesize that Polynesians could have carried the genus from one island to another during transferrals of fishes from one royal fish pond to another, but the Polynesians have lived in Hawaii for perhaps only a thousand years and few evolutionists would accept the thesis that a cave species could have evolved from a lava pond species in that short span. Actually, the cave species may be a case of simple genetic drift or a phenotype fully fertile with the lava pond species of the nearby island. The paucity of localities of the cave species and the absence of lava pond material from islands other than Hawaii prevents further speculation; other islands and other caves must now be explored to solve this riddle.

The 2 species are diagnosed, but, to conserve space, a joint description of characters common to both species is provided. Illustrations are based mainly on the cave species as numerous attributes of both species are fully congruent.

Description of the species complex: Blind; head with submammilliform lateral lobe, weakly excavate below lobe; antenna 1 nearly 2X as long as antenna 2, article 2 as long as or longer than article 1, article 3 varying between 40% and 70% as long as article 1, accessory flagellum with 3 or more articles; article 1 of antenna 2 bulbous, gland lobe large and stubby, article 3 very short; epistome and upper lip visibly distinct but more heavily articulate in lava pond species; mandibular incisors 4–5 toothed, right lacinia mobilis with 4 radiating teeth, left with 4 teeth in tandem, 3 raker spines on right, 4 on left, molars triturative, each bearing long seta, palp slender, linear, article 3 highly variable, slightly shorter to slightly longer than article 2, bearing only 3 setae apically; discrete inner lobes of lower lip forming 2 peaks above basal plaque; inner plate of maxilla 1 broad, bearing 3 widely spaced apical setae, outer plate narrow, with 9 apical spines, palp apex of 2 versions, right and left (see figures); inner plate of maxilla 1 with 3 distinctive subterminal and slightly mediad setae, otherwise medial margin naked; inner and outer plates of maxilliped broad, inner with 3 stout spines and 4th smaller mediad locking spine, outer plate with numerous apicolateral spines, palp article 3 slightly falciform but not strongly produced anywhere, article 4 unguiform, bearing stout apical nail and accessory setules lining inner edge; anterior coxae longer than posterior coxae, poorly setose, anterior 4 pairs with posterolateral ridge; gnathopod 1 ordinary, subchelate, palm transverse, dactyl fitting palm, article 5 much longer than article 6; gnathopod 2 ordinary, subchelate, palm oblique, article 6 much longer than 5; pereopods 1–2 ordinary, bearing 2 small locking spines, dactyl with apicad notch and slight constriction, 1 inner and 1 facial setule; pereopods 3–5 increasingly elongate, 5 immensely elongate, article 2 subpyriform, posteriorly with weak teeth or notches, dactyls like those of pereopods 1–2 except on cave species from Maui, dactyl of pereopod 4 with 1 additional marginal seta, of pereopod 5 with 2 additional setae; uropod 1 with basofacial spine, large apicolateral spine on peduncle and several dorsal spines, outer ramus with 1 small spine-seta attached to medial face and largely hidden from lateral view, inner ramus with 2–3 spines; uropod 2 with 1 apicolateral spine and usually 1 dorsal spine, inner ramus with 1–2 spines, outer ramus variable (see diagnoses); uropod 3 with basofacial ridge on peduncle, inner ramus short, scale-like, bearing 1 apicomedial spine, apicolateral margin scalloped or crenulate; epimeron 1 with lateral ridge, naked, posteroventral tooth small, with 1 or more weak posterior protrusions above main tooth, or with notches bearing setules, epimeron 2 with facial ridge, epimera otherwise variable (see diagnoses); pleonite 4 bearing 1 large subdorsal spine on each side, body otherwise lacking teeth and spines; cuticle bearing minute surficial granules, especially dense on gnathopods, subcuticular pattern of polygons highly visible especially on epimera and bases of pereopods 3–5; gills suborbicular, capillaries discrete, gills flat, unlobed, attached by short peduncles, projecting well below ventral coxal line, illustrated herein as attached to their respective coxae; broodplates ordinary, bearing a few marginal setae bent subapically.

Rotomelita lokoa Barnard, n. sp. FIG. 14 (part), 15 (part)

Diagnosis: Outer ramus of uropod 2 with 2 large dorsomarginal spines in adult, 1 spine in juveniles; epimeron 3 with small ventral notch just anterior to posteroventral tooth of main angle; posteroventral tooth of epimeron 2 small or medium in size, often obsolescent; posteroventral tooth of epimeron 3 of medium size; telson lacking proximal spine in middle of each lobe; dactyls of pereopods 4–5 lacking any accessory marginal setules in addition to normal complement; article 3 of antenna 1/2 or less than 1/2 as long as article 1; article 1 of antenna 1 with 2 spines in tandem on ventroproximal margin, in juveniles often with 1 spine; apex of article 1 on antenna 1 with ventral spine in about 20% of specimens, absent in 80%; epimeron 2 with 2 facial spines in adults, 1 in juveniles, occasionally juveniles with 2; accessory flagellum 4-articulate (3 long and 1 tiny).

Variations: The largest adult bears 2 spines on the outer ramus of uropod 2, juveniles down to 3.2 mm bear 1 spine and the 2.5–mm juvenile lacks such spines. The ventral notch on epimeron 3 is lacking only in the 4.4–mm juvenile of Tokyo-Land 5. The tooth on epimeron 2 is either obsolescent or medium in size; apparently it becomes relatively smaller in adults as the 7.7 – and 5.6–mm individuals have the tooth relatively the smallest in comparison to smaller individuals. Article 3 of antenna 1 varies in length from about 40% to 50% of the length of article 1; article 2 varies between 100% and 125% of the length of article 1. The ventroproximal spines of article 1 on antenna 1 vary between 1 and 2 without any growth trend apparent in the material; the distal spine on that article is absent in all specimens except for the 4.4–mm juvenile from KV-7 and on the left antenna of the smaller juvenile from Makalawena BR-3. Only the largest adult has 2 spines on epimeron 3; all others have 1. The spines on epimeron 3 vary between 1 and 2, with the 2nd spine small in 1 case; no growth trend is apparent, as the 7.7–mm specimen has 2, the 5.6–mm specimen has 1 but several smaller individuals have 2. All specimens have only 1 ventral notch on epimeron 2 except for the Tokyo-Land 5 specimen which has 2 of these notches on both epimera 2 and 3. Only the specimen from Tokyo-Land 5 has article 3 of antenna 1 significantly longer than 1/2 of article 1.

Holotype ♀ (BISHOP S8407), 7.17 mm.

Type-locality: HAWAIIAN ISLANDS: Hawaii I, Makalawena BR–3, 23.VIII.1972.

Material examined: The holotype; Makalawena BR-2 (juveniles, 3.2 and 2.5 mm); Makalawena BR-3 (♀, 7.7 mm, juveniles, 4.8 and 4.5 mm); Makalawena N-3 (juvenile, 4.4 mm); Kona Village-7 (juveniles, 5.6 and 4.4 mm); Tokyo-Land 5 (juvenile 4.7 mm); N.K. Air 1 (juveniles, 3.50, 3.31, 3.28 and 2.90 mm); Kiholo 8 (1 fragment).

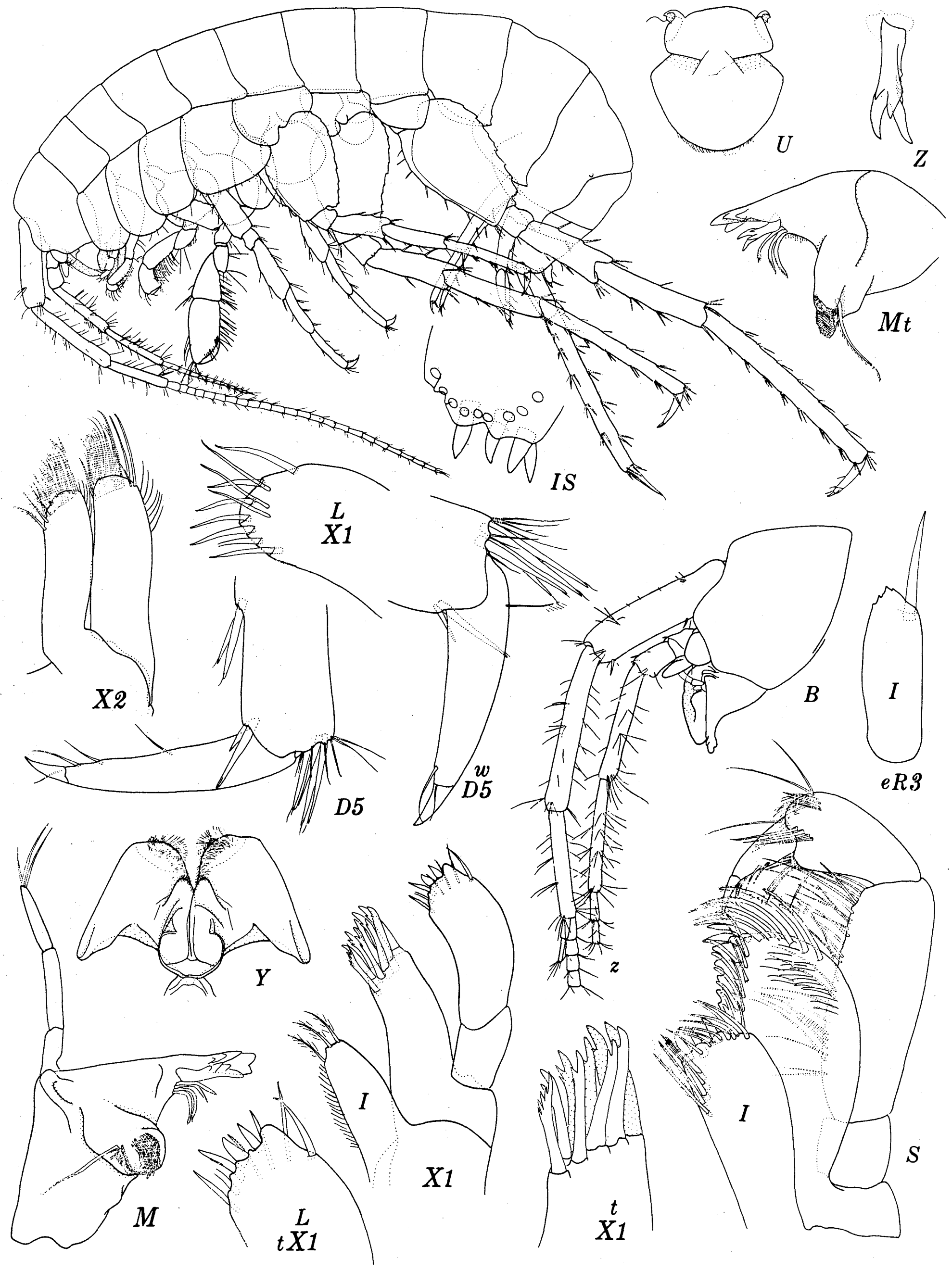

FIG. 14. *Rotomelita ana,* n. sp., holotype, ♀, 7.8 mm, Waianapanapa, 16.VII.1972. w = *Rotomelita lokoa,* n. sp., holotype, ♀, 7.7 mm, Makalawena BR-3; z = broken; e = lateral.

The diagnoses of the 2 species are arranged so that the 1st characters mentioned are absolutely diagnostic, the later characters becoming more subject to variation and thus unreliable except in a population context. Undoubtedly analysis of more specimens will reveal modifications of these diagnoses.

Rotomelita ana Barnard, n. sp. FIG. 14 (part), 15 (part), 16

Diagnosis: Outer ramus of uropod 2 dorsally naked or bearing 1 spine; epimeron 3 usually lacking ventral notch anterior to posteroventral tooth; posteroventral teeth of epimera 2 and 3 usually large; telson bearing or lacking proximal spine in middle of each lobe; dactyls of pereopods 4–5 with or without 1–2 marginal setules in addition to normal complement; article 3 of antenna 1 more than 1/2 as long as article 1; article 1 of antenna 1 with 1–2 spines on ventroproximal margin; apex of article 1 on antenna 1 with ventral spine; epimeron 2 with 0–1 facial spine in adult; accessory flagellum 3-articulate (2 long + 1 tiny); article 2 of pereopod 5 weakly narrower than in lava pond species.

Variations: The only gross variation between the 2 specimens in the type collection, the holotype and a ♀, 5.3 mm, is the presence on the smaller ♀ of an extra facial spine, small and seta-like, on epimeron 3; the 5.3–mm ♀ also has only 1 accessory setule on the dactyl of pereopod 5. Specimens in the 2 collections made by E. L. Bousfield & F. G. Howarth, also in the type-locality, differ from the holotype in the absence of the midproximal spine on each lobe of the telson and demonstrate a wide variability in attributes of the diagnosis, therefore approaching the conditions diagnostic of *R. lokoa.* Absolute distinctions between the 2 species concern the accessory dactylar setae on the pereopods and elongate article 3 of antenna 1 as seen in *R. ana.* There appears to be no correlation to size in the following attributes: presence or absence of a dorsal spine on the outer ramus of uropod 2; presence of 1 or 2 spines on the ventroproximal margin of article 1 on antenna 1, 1 of these spines occasionally occurring as a seta; presence or absence of a facial spine on epimeron 2, though this spine is usually present; presence or absence of a ventroposterior notch on epimeron 3, though this notch is usually absent. Two of the 20 specimens in the Bousfield-Howarth collection have the tooth on epimeron 2 reduced almost to the small size of that seen in *R. lokoa* and 1 other specimen also has the tooth of epimeron 3 reduced in size. These specimens therefore merge strongly with *R. lokoa* but are distinguished by dactylar setae and elongate article 3 of antenna 1.

♂: Twilight pool; gnathopod 2 enlarged, palm slightly elongate, with 2–3 enlarged palmer spines (♀ with only 2), article 5 somewhat shortened, terminal ♂ with slightly enlarged serrations on article 2 of pereopods 3–5; 3 ♂♂ present, 5.80, 7.50 and 7.87 mm long, largest with 1 posteroventral notch below main tooth of epimeron 3, 7.5–mm ♂ with 2 notches, smallest ♂ without notch; uropod 3 missing on all ♂♂.

Holotype ♀. (BISHOP S8409), 7.8 mm.

Type-locality: HAWAIIAN ISLANDS: Maui I, Waianapanapa Cave, 16.VII.1972, F. G. Howarth & S. Malecha.

Material examined: The holotype and a ♀, 5.3 mm, from the type-locality; 8 specimens from Waianapanapa Cave, dark zone pool, 24.I.1973, F. G. Howarth & E. L. Bousfield, largest specimen 7.96 mm long, smallest 4.79 mm; 12 specimens from Waianapanapa Cave, twilight pool, 24.I.1973, E. L. Bousfield & F. G. Howarth, largest 7.87 mm long.

Family HYALIDAE

Parhyale hawaiensis (Dana)

Parhyale hawaiensis: Shoemaker, 1956: 351–57, fig. 3, 4 (with references). – J. L. Barnard, 1965: 521–23, fig. 24.

Parhyale inyacka (K. H. Barnard): J. L. Barnard, 1955: 23, fig. 12 (not K. H. Barnard). – Sivaprakasam, 1970: 562–64, fig. 6. – ?Ledoyer, 1972: 275, pl. 80.

not *Parhyale hawaiensis:* Sivaprakasam, 1970: 560–62, fig. 5.

Material examined: Cape Kinau, Maui, 15.IV.1972, N. pond (5); Kinau-w, 11.I.1972, J. S. Lenic (2); Pine Tree Pt. Series, Hawaii, 1.6 km (1 mile) N of Kaloko Pond, 1.XII.1972

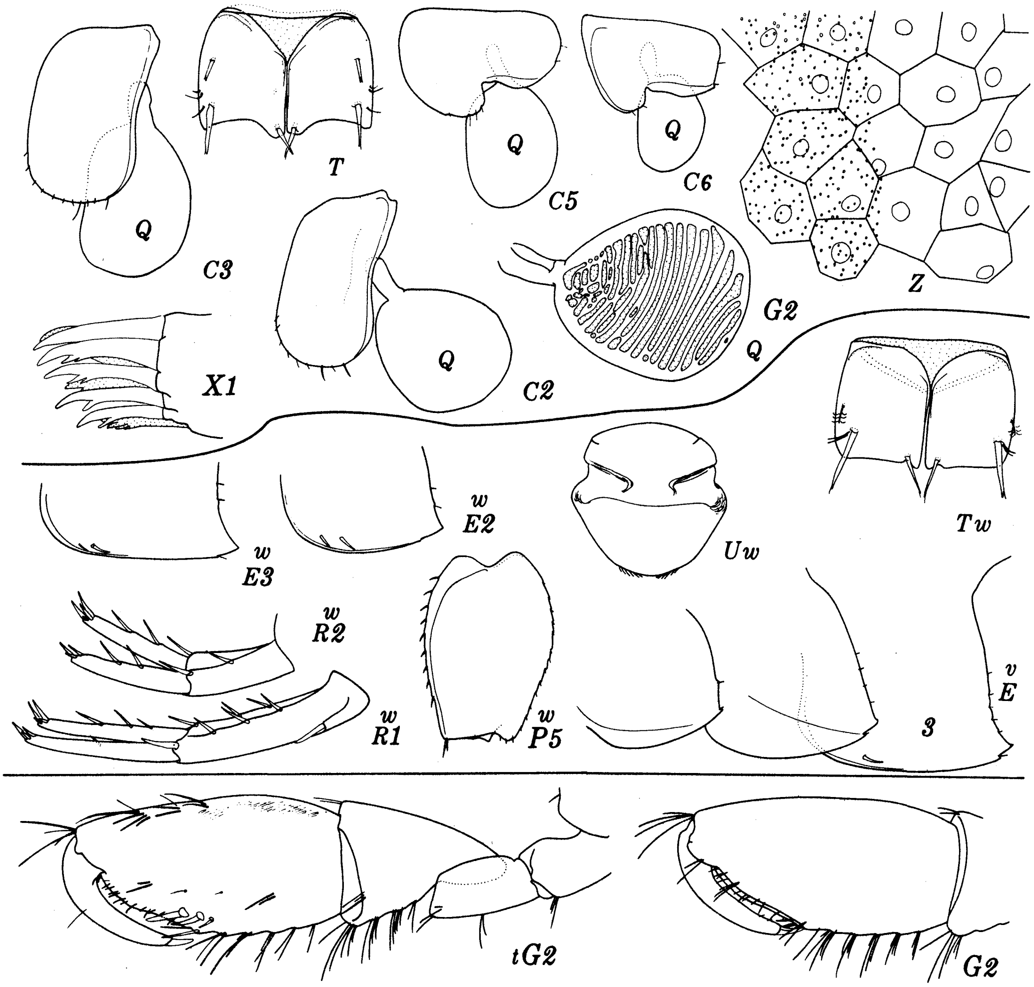

FIG. 15. Upper, *Rotomelita ana*, n. sp., holotype, ♀, 7.8 mm, Waianapanapa, 16.VII.1972; Z = cuticle. Middle, *Rotomelita lokoa*, n. sp., w = holotype, ♀, 7.7 mm, Makalawena BR-3, v = juvenile, 5.6 mm, Kona Village-7. Lower, *Rotomelita ana*, ♂, 7.87 mm, twilight pool.

(5); Cape Kinau, Nukuele Pt., in brackish pond, 22.I.1973, J. Maciolek, E. L. Bousfield & F. G. Howarth (3).

This tropicopolitan species appears euryhaline as it is found in the Pine Tree Pt. ponds with a salinity of 11.5—13.0 0/00; it is the only truly open-sea amphipod found so far in the Hawaiian lava ponds, except perhaps for *Nuuanu amikai*, which see.

The literature on this species remains confused despite Shoemaker's (1956) extensive analysis and synonymy; references to *Parhyale inyacka* (K. H. Barnard) continue to appear in the literature, some of them perhaps owing to my error (J. L. Barnard 1955) in identifying that species from Hawaii, which at the time of the work was the only name available for this species. Shoemaker (1956) demonstrated that the previously obscure *Hyale hawaiensis* Dana was a senior synonym of *P. inyacka* and that this species differs from the type-species, *P. fascigera* Stebbing, in the presence of posterior marginal spines on article 6 of pereopods 4—5 and in the ordinary defining spine distribution on male gnathopod 1.

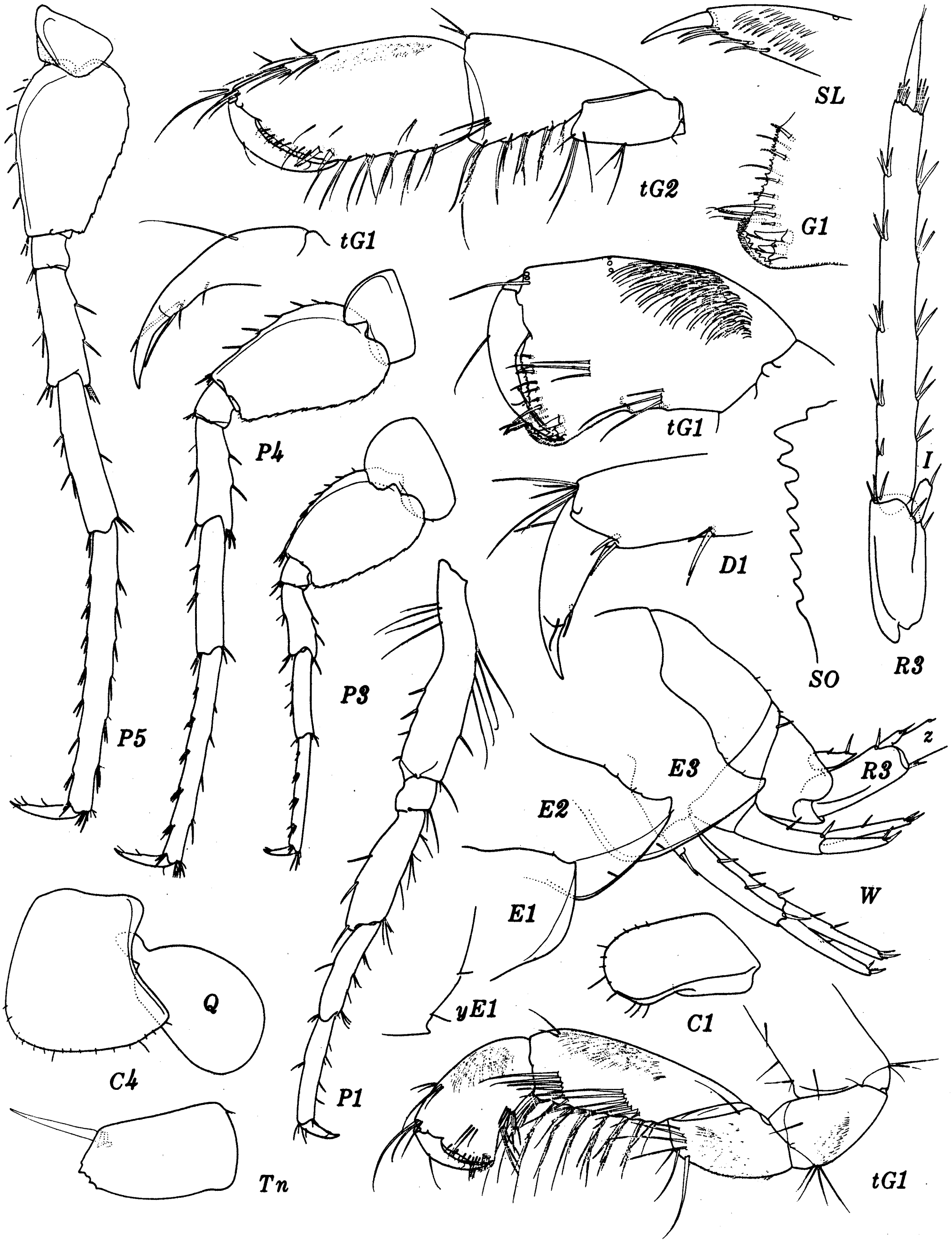

FIG. 16. *Rotomelita ana,* n. sp., holotype, ♀, 7.8 mm, Waianapanapa, 16.VII.1972; y = ♀, 5.3 mm, Maui; Q = gill, z = broken.

The apicolateral spine on the peduncle of uropod 1 is enlarged in both *P. hawaiensis* and *P. fascigera* Stebbing and antenna 2 is very long.

The reference to *P. hawaiensis* by Sivaprakasam (1970) appears to be a distinct species characterized by setose telson (are these green algal tufts?), the short antenna 2 and the very broad male gnathopod 2 with palm defined by exceptionally enlarged hump. Ledoyer's (1972) identification of *P. inyacka* appears to concern a young male but antenna 2, pereopods 4–5 and uropod 1 appear normal for *P. hawaiensis.*

Parhyale hawaiensis from Hawaii and Micronesia bears a distinct acclivity on the posterodorsal margin of coxa 1, whereas this acclivity is obsolete or obsolescent on specimens from the Caribbean Sea. This character difference suggests that specimens from the 2 oceans, Pacific and Atlantic, are, at the least, racially distinct. The name "*inyacka*" may therefore have to be revived at subspecific level to designate the Atlantic race. According to the literature this race apparently also occurs in the western Indian Ocean at Madagascar and possibly in India; careful analysis of specimens from the eastern Indian Ocean and western Pacific Ocean must be undertaken to determine if and where these 2 races meet. I have reexamined my specimens (Barnard 1955) from Hawaii and find my illustration of coxa 1 erroneous; the strong coxal acclivity typical of Hawaiian *P. hawaiensis* is present.

Distribution: Tropicopolitan.

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LEGEND

A, antenna; B, head; C, coxa; D, dactyl of pereopod; E, epimeron(a); F, accessory flagellum; G, gnathopod; I, inner plate or ramus; K, cuticle; L, palp; M, mandible; O, outer plate or ramus; P, pereopod; Q, gill or cuticle, see figure captions; R, uropod; S, maxilliped; T, telson; U, upper lip; V, pleopod or gland cone, see figure captions; W, pleon; X, maxilla; Y, lower lip; Z, lacinia mobilis or cuticle, see figure captions; e, spine; i, inside; n, half; o, opposite; s, seta removed; t, right; v, w, y, various specimens.