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The genus *Maera* (Crustacea: Amphipoda: Melitidae) from Bermuda

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**The genus *Maera*
(Crustacea: Amphipoda: Melitidae)
from Bermuda**

Sandro Ruffo
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Michael F. Gable

(Received 18 December 1998; revised and accepted 2 August 1999)

Abstract

Traditionally, the Bermudian amphipod fauna has included three species of *Maera*. After examining collections that span more than 10 years, we retain one species, *M. tinkerensis*; report a second species, *M. quadrimana*, as a verified record for the Atlantic; and describe four new species: *M. ceres*, *M. miranda*, *M. ariel* and *M. caliban*. Discussion of *M. quadrimana* sensu lato, *M. pacifica* and *M. rathbunae* clarifies their taxonomic status and their relationship to the Bermudian fauna. *Maera tinkerensis* resides within the *grossimana* complex of species, and the other five species reside within the *quadrimana* complex. The zoogeographical implications of these morphological "complex" alignments are briefly considered. We provide data on habitat preferences and a key to the six species of *Maera* now recognized from Bermuda.

Key Words

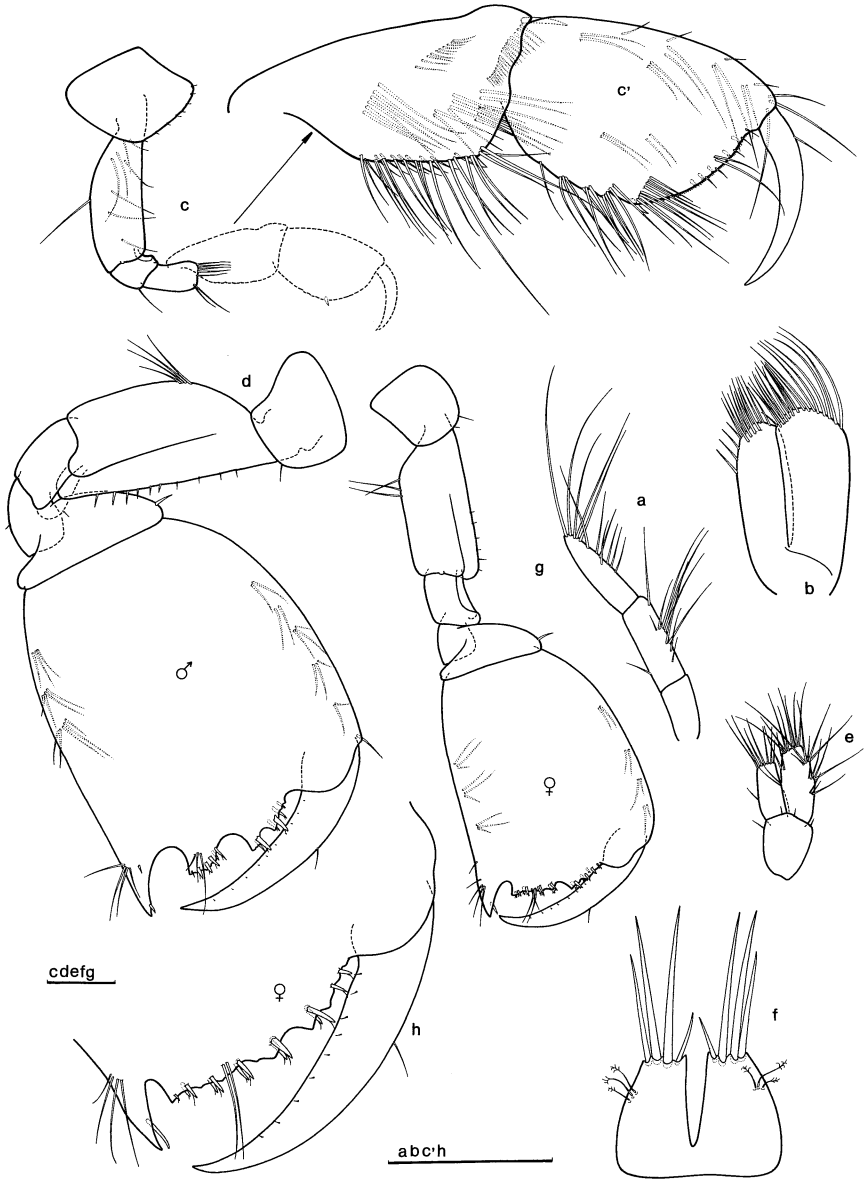
New species, *Maera quadrimana* complex, *Maera grossimana* complex, zoogeography, habitat preferences, taxonomic key.

Abbreviations

AI,2	antenna 1, 2
acc	accessory
art	article
Cx	coxa
Ep1-3	epimeral plate 1-3
Gn1,2	gnathopod 1,2
Md	mandible
Mx1,2	maxilla 1,2
ov	ovigerous
P3-7	peraeopod 3-7
T	telson
UI-3	uropod 1-3
BBSR	Bermuda Biological Station for Research
USNM	National Museum of Natural History
YPM	Peabody Museum of Natural History, Yale University

Introduction

In his work on the amphipods of Bermuda, Kunkel (1910) cited three species in the genus *Maera*. The first two, *Maera inaequipis* (A. Costa 1851) and *M. rathbunae* Pearse (1908), are of the *quadrimana* complex (sensu Barnard 1972, Krapp et al. 1996); the third species,

**Figure 1**

Maera quadrimana (Dana), Bermuda. YPM 21601, male: a, Md palp; b, Mx2; c, Gn1; d, Gn2; e, U3; f, T. YPM 21602, ovigerous female: g, Gn2. Unattributed immature female (3 mm): h, Gn2 palmar margin. Scale 0.2 mm.

Maera tinkerensis Kunkel (1910), was described as a new species. However, Kunkel's written descriptions and illustrations of these species lack sufficient detail for comparisons. Krapp et al. (1996) questioned the citation of *Maera inaequipes* from Bermuda and assumed the presence of a different taxon there. We had similar doubts concerning *M. rathbunae* Pearse (1908) because Kunkel's (1910) illustrations do not correspond with those of Pearse's (1908) description.

From 1985 through 1995, M. F. Gable (Eastern Connecticut State University), E. A. Lazo-Wasem (Peabody Museum of Natural History, Yale University), A. J. Baldinger (Museum of Comparative Zoology, Harvard University) and students from Eastern Connecticut State University collected amphipods in Bermuda. The authors have identified or described several species of *Maera* from these collections, all belonging to the *quadrimana* complex, except *M. tinkerensis*. One is an Indo-Pacific species, *M. quadrimana* (Dana 1853), already known from other regions; four species are new to science; and *M. tinkerensis* remains valid.

Materials and Methods

Specimens were collected in Bermuda over a decade from as many different habitats and microhabitats as possible. Some littoral and shallow infralittoral specimens were handpicked in the field with forceps either during low tide collections on shore or while snorkeling. Other specimens from the same habitats were screened from formalin washes of substrates in the field, or from formalin washes of substrates taken to the laboratory at the Bermuda Biological Station for Research (BBSR). Sublittoral samples were collected by SCUBA, and specimens

from these were picked out from formalin or 70% EtOH washes at the BBSR. All specimens were deposited at the Peabody Museum of Natural History, Yale University (YPM). Locality data (with YPM locality numbers) for those samples containing specimens of *Maera* are listed in the Appendix. YPM catalog numbers shown below are followed by YPM locality numbers.

Several lots collected from Bermuda and deposited in the National Museum of Natural History (USNM) were also examined for specimens of *Maera*. Amphipods in these lots were coincidentally collected from various expeditions in the 1870s, and in the 1970s to early 1980s.

Detailed investigation of entire specimens under light- and phase-contrast microscopes was made using alcohol/glycerin depression slides. Dissections were done in glycerine and permanent slides were made with Faure's medium.

Systematic Descriptions

MAERA QUADRIMANA (DANA 1853)
Figures 1 and 2.

Gammarus quadrimanus Dana
1853:955–956, pl. 65, fig. 9.

Maera quadrimanus Bate 1862:194–195,
pl. 35, fig. 5.

Maera quadrimana Schellenberg
1938:45–48, figs. 21–22.

Maera quadrimana J. L. Barnard
1965:511–512, fig. 17.

Maera quadrimana J. L. Barnard
1970:152–155, figs. 94–95.

Maera quadrimana J. L. Barnard 1971:84,
figs. 31, 38, 40.

Maera quadrimana Ledoyer
1982:542–544, fig. 206.

Maera quadrimana Berents 1983:128–129,
fig. 22.

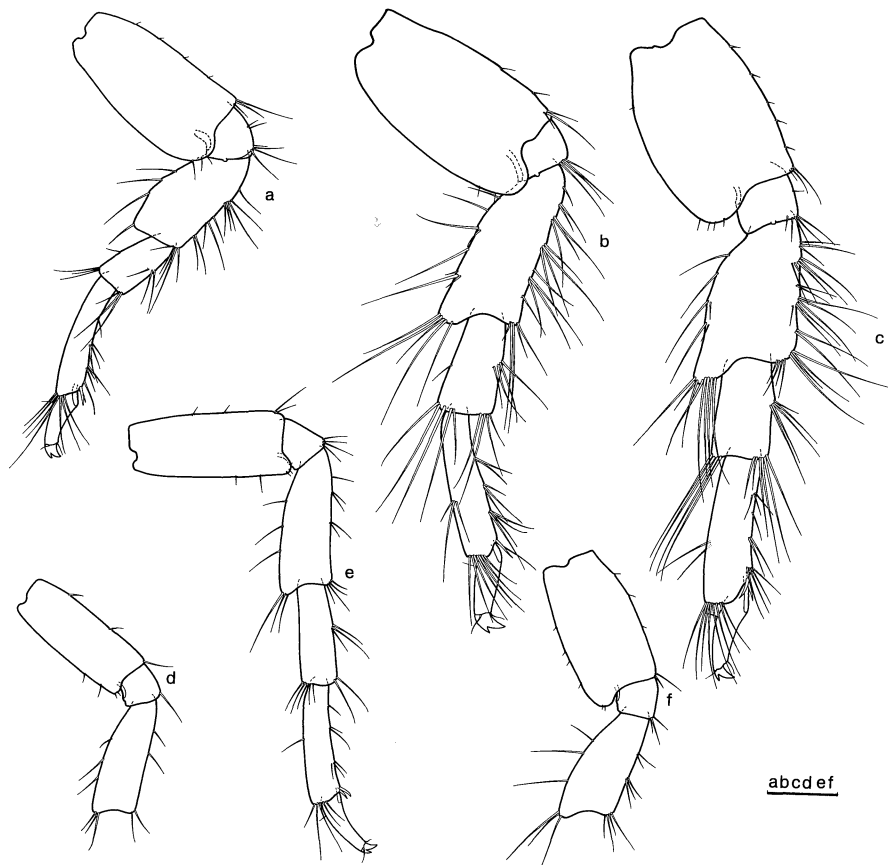


Figure 2

Maera quadrimana (Dana), Bermuda. YPM 21601, male: a-c, P5-7. YPM 21603, immature male (3 mm): d-f, P5-7. Scale 0.2 mm.

Maera quadrimana Myers 1985:116-117, fig. 91.
nec *Maera quadrimanus* Thomson 1882 (not Dana): 235-236, pl. XVII, fig. 4a (= *Maera tepuni* J. L. Barnard 1972).
nec *Maera quadrimana* Ledoyer 1986 (not Dana): 190, fig. 11 (= *Maera miranda nobis*).

Type locality. Fiji Islands.

Material examined. YPM 21539 (IZ.S00128),

14 specimens, 1 slide; YPM 21562 (IZ.S00196), 3 juveniles; YPM 21600 (IZ.S00128), 1 ovigerous female; YPM 21601 (IZ.S00128), 1 male on 7 slides; YPM 21602 (IZ.S00128), 1 female on 5 slides; YPM 21603 (IZ.S00128), 1 immature male on 3 slides; USNM 291165, 1 specimen, Bermuda, Hungry Bay Rocks, 16 August 1975, collector M. L. Jones.
Description of material from Bermuda.
Male: 4.5 mm. A1 slightly shorter than

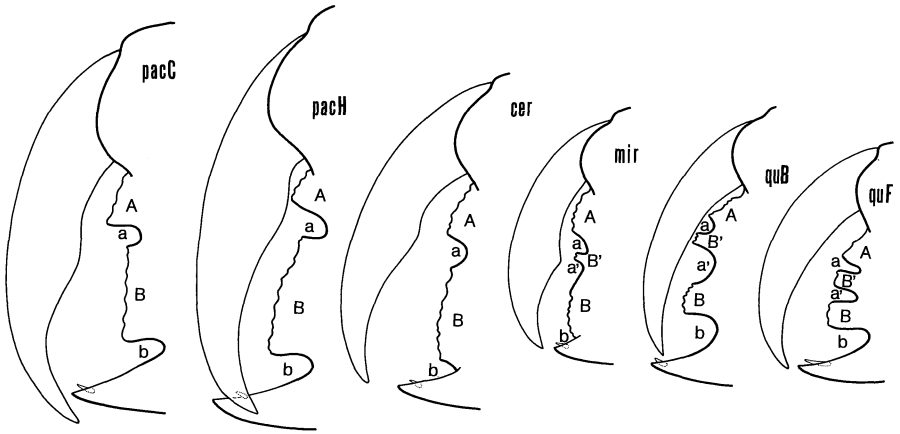
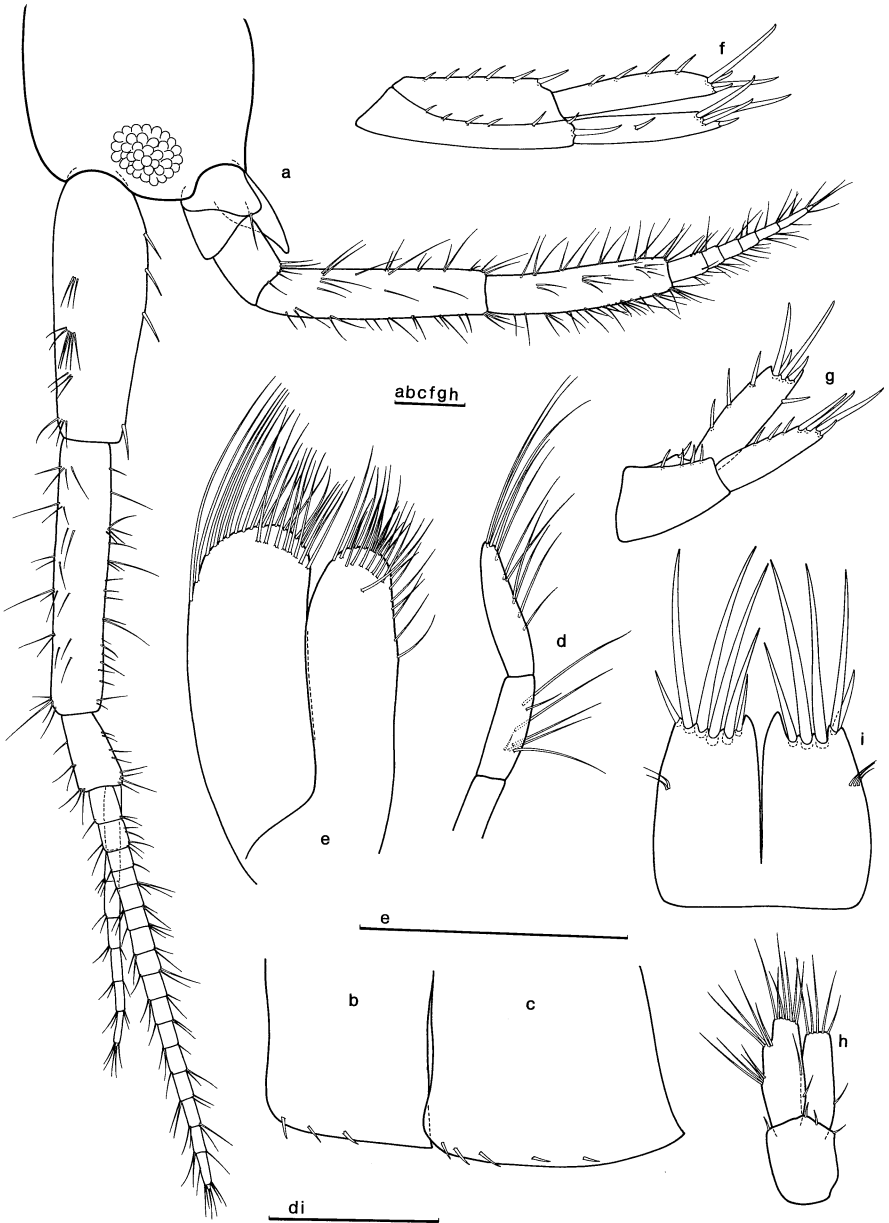


Figure 3

Schematic representation of Gn2 palmar margin: paC, *Maera pacifica* Schellenberg, Cuba; paH, *Maera pacifica* Schellenberg, Hawaii, syntype; cer, *Maera ceres* n. sp.; mir, *Maera miranda* n. sp.; quB, *Maera quadrimana* (Dana), Bermuda; quF, *Maera quadrimana* (Dana), Fiji, from Myers 1985.

one-half of body, ratio of arts 1:2:3 of peduncle equals 0.9:1:0.25, art1 with 4 elongate spines and long setae on ventral margin, flagellum with up to 17 articles, acc flagellum longer than one-half flagellum, with up to 6 articles. A2 is three-quarters of A1, peduncle robust, with numerous long setae, ratio of arts 4:5 equals 1.25:1, flagellum very setose with up to 10 articles. Md palp art1 distally smooth, art2 to art3 subequal in length, art2 with 8 setae on inner margin, art3 with 7 setae on inner margin and 5 long apical setae. Mx2 outer plate distinctly wider than inner one. Cx1 antero-ventrally rounded, not produced. Gn2 palmar margin of propodus with 2 excavations (Figure 3, a and a') defining 2 truncate, narrow processes (B' and B), delimited by a strongly acute prominent process, preceded by a wide semi-elliptical excavation (b); the acute process subdistally provided with 1 short spine on inner margin; dactylus inner margin smooth (rarely fee-

bly inflated medially); outer margin with 1 seta. P5 basis narrowly ovato-rectangular, with marked postero-distal rounded lobe, posterior margin feebly convex, nearly smooth, without setae. P6-7 basis similar in shape, size in $P5 < P6 < P7$, posterior margin markedly convex in P7, postero-distal rounded lobe much evident (particularly in P6); merus and carpus with numerous very long setae, postero-distal corner of merus with a group of setae exceeding carpal tip, propodus posterior margin with one medial tuft of 2 to 3 long setae. U3 stout, rami broad, flat, distally truncated, with long terminal spines, inner ramus slightly shorter than outer, art2 of outer ramus rudimentary, barely visible. T broader than long, lobes not distally incised, with short and acutely produced disto-interior corner and 3 long plus 1 medium distal spines, laterally with a group of 3 medio-distal plumose sensory setae. *Female*: Oviparous, 4 mm. Gn2 similar to

**Figure 4**

Maera ceres n. sp. YPM 21529, male, holotype, Bermuda: a, head with AI-2; b-c, Ep2-3; d, Md palp; e, Mx2; f-g, UI-2; h, U3; i, T. Scale 0.2 mm.

male but shorter and with palmar excavations less deep.

Remarks. Previously, no authors have definitively outlined the characters differentiating *M. quadrimana* and *Maera pacifica* Schellenberg (1938, cf. below). J.L. Barnard (1971) and Ledoyer (1982) stressed the possibly overlapping characters between the two species and discussed variability in *M. quadrimana*.

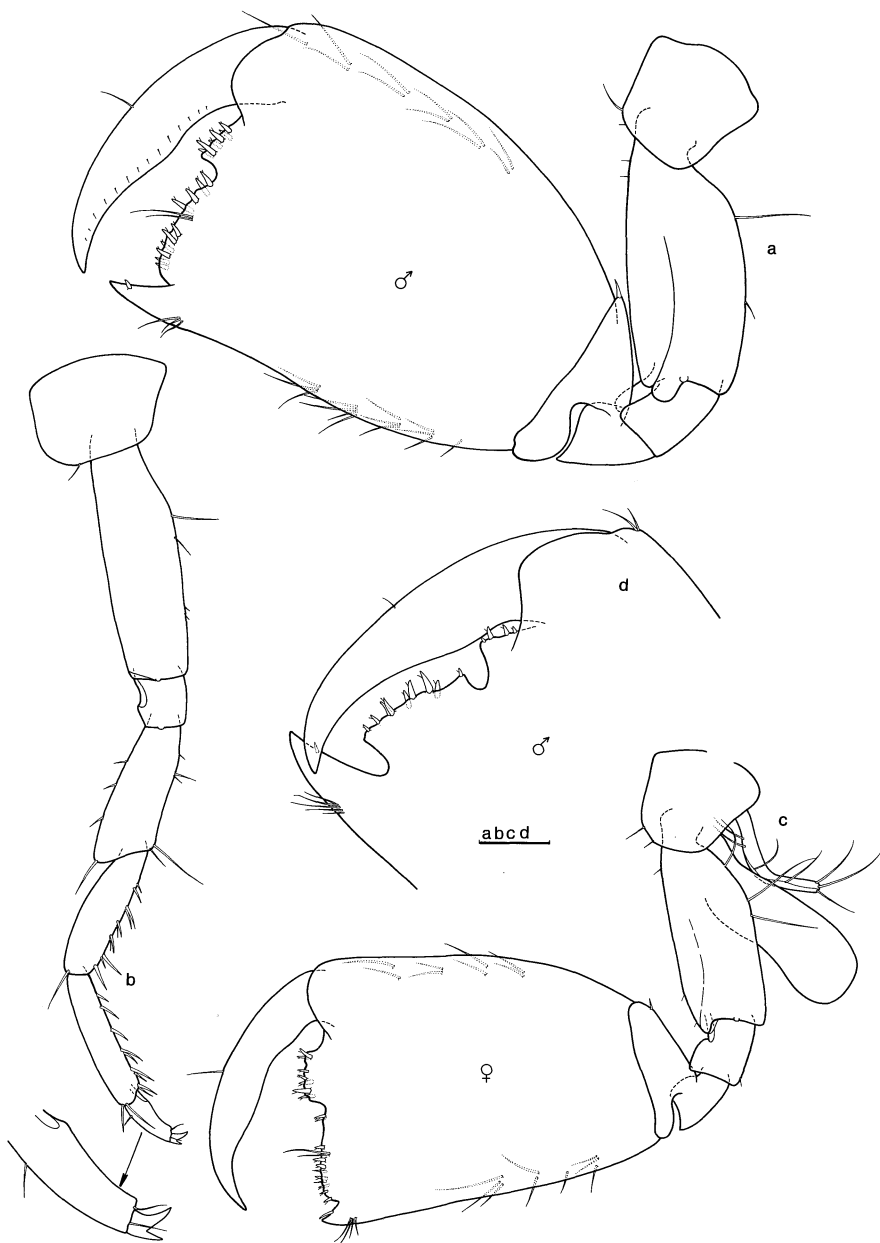
The Bermuda material is morphologically identical (especially in adults) to the original description from the Fiji Islands and the corresponding figures (Dana 1853, pl. 65, fig. 9a). In addition, the descriptions and figures of J.L. Barnard (1965, 1970, 1971) using material from Micronesia and Hawaii, of Ledoyer (1972, 1982) from Madagascar, of Berents (1983) from Lizard Island, Great Barrier Reef, Australia, and of Myers (1985) from the Fiji Islands seem to deal with the same species, although in Myers' material the excavation *a'* (Figure 3) is distinctly narrower than in the Bermuda material. The latter difference could be an indication that specimens from the Atlantic are not identical with Pacific material, but with the few adult specimens we examined this remains questionable.

Schellenberg (1938) redescribed and partly refigured *M. quadrimana* from the Gilbert Islands in the South Pacific, and added comparisons using one female from the Fiji Islands and one female from the Hawaiian Islands. He pointed out that many specimens had widened, rounded bases on P5–7, and that a few were narrow and linear. This same phenomenon was observed by Ruffo (1969) in a few specimens examined from the Red Sea, and by Myers (1985) in his Fiji Islands studies. In our Bermuda samples we observed immature and smaller specimens

with subrectangular P5–7 bases with a straight hind margin and a very small postero-distal lobe. Males, females and larger specimens have wider bases and varying degrees of posterior margin convexity. Immature and smaller specimens also have a smooth Gn2 palm without excavations. Because of the low number of specimens from Bermuda available for study, it is not possible to conclude whether the varying posterior convexities of the bases of P5–7 are species variations in adult morphology or the result of allometric growth, although the latter seems more probable.

Other mouthparts are not illustrated because no differences were observed in them among the species of *Maera* in Bermuda.

Biology and distribution. Co-existing together with *M. ceres* n.sp. Ovigerous females observed in June. Originally described from the Fiji Islands (Dana 1853), this species apparently has a wide distribution within the Indo-Pacific Ocean, including: Red Sea (Ruffo 1969); Madagascar (Ledoyer 1972, 1982); possibly Mozambique (Griffiths 1976, sub *Maera pacifica*); India (Nayar 1959; Sivaprakasam 1968 [both needing confirmation]); Great Barrier Reef, Australia (Berents 1983); Gilbert Islands (Schellenberg 1938); Micronesia (J.L. Barnard 1965); and the Hawaiian Islands (J.L. Barnard 1970, 1971). In the Atlantic Ocean Ortiz (1978) cited *M. quadrimana* from Cuba. We had the opportunity to examine some of this material, and the specimens are clearly *M. pacifica*. Likewise, Wakabara et al. (1991) and Wakabara and Serejo (1998) cited *M. quadrimana* in the Atlantic Ocean from Brazil, but no figures were provided and the citations cannot be confirmed. Our citation of the Indo-Pacific species *M. quadrimana* from

**Figure 5**

Maera ceres n. sp. YPM 21529, male, holotype, Bermuda: a, Gn2; b, P3. YPM 21604, ovigerous female: c, Gn2. *Maera pacifica* Schellenberg, Hawaii, syntype: d, Gn2. Scale 0.2 mm.

Bermuda therefore is the first confirmed record for the Atlantic Ocean.

MAERA CERES RUFFO, KRAPP AND GABLE
N. SP.

Figures 4, 5 and 6.

?*Maera rathbunae* Kunkel 1910 (not
Pearse 1908):46–48, fig. 17

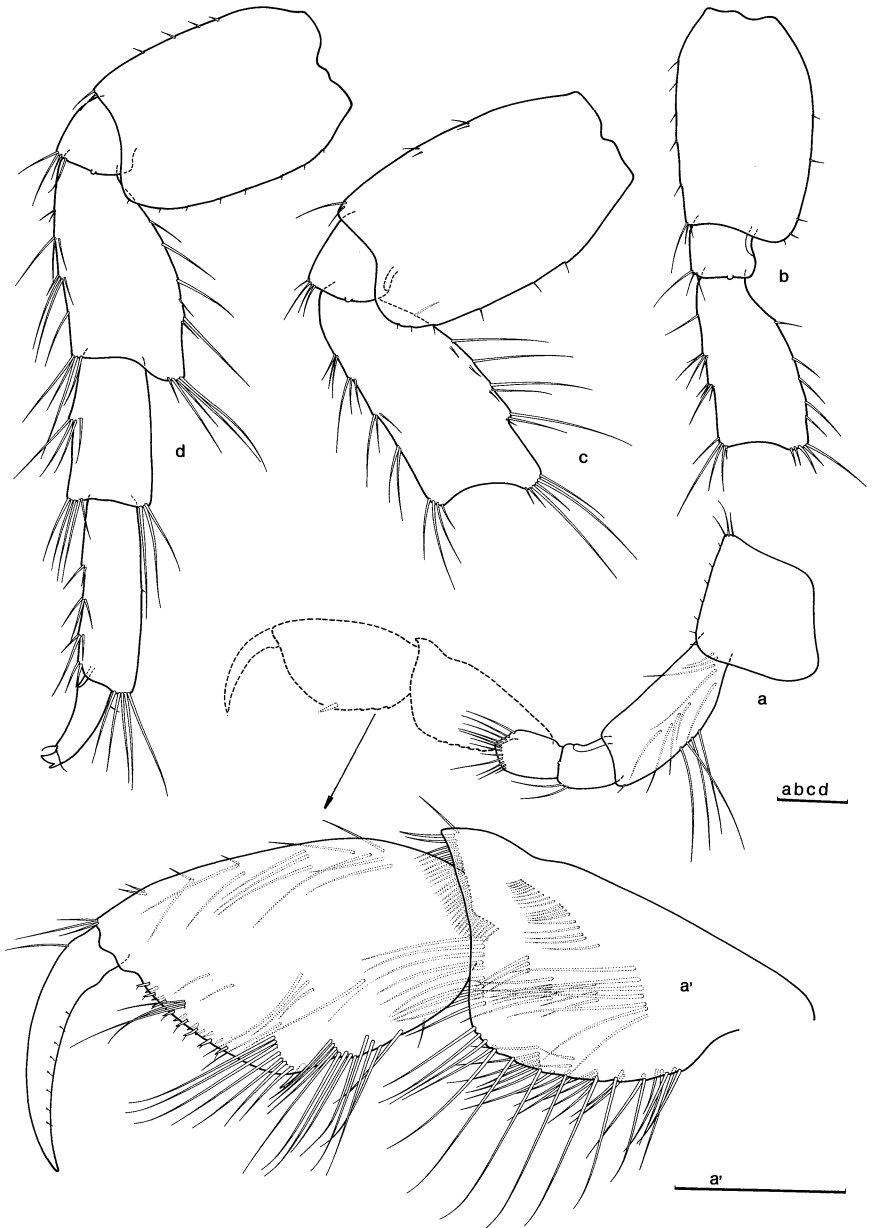
Type locality. Bermuda.

Material examined. *Male:* Holotype, YPM 21529 (IZ.S00048), on 5 slides.

All other specimens are paratypes, as follows: YPM 21537 (IZ.S00045), 1 ovigerous female; YPM 21542 (IZ.S00233), 15 juveniles; YPM 21546 (IZ.S00003), 3 juveniles; YPM 21547 (IZ.S00019), 4 juveniles; YPM 21548 (IZ.S00044), 1 female; YPM 21549 (IZ.S00020), 1 female, 3 juveniles; YPM 21555 (IZ.S00036), 1 male; YPM 21558 (IZ.S00021), 4 juveniles; YPM 21560 (IZ.S00027), 1 juvenile; YPM 21564 (IZ.S00196), 5 juveniles; YPM 21566 (IZ.S00048), 1 male, 1 ovigerous female, 2 juveniles; YPM 21570 (IZ.S00156), 1 ovigerous female; YPM 21604 (IZ.S00048), 1 female on 5 slides with carcass in alcohol; YPM 21605 (IZ.S00196), 3 males; YPM 21613 (IZ.S00196), 1 ovigerous female; 1 male and 1 female (IZ.S00019) deposited by YPM in the Museo Civico di Storia Naturale, Verona, Italy; 1 male (IZ.S00021) and 1 ovigerous female (IZ.S00003) deposited by YPM in the Bermuda Museum of Natural History.

Diagnosis. A *Maera* species of the *quadrimana* complex distinguished by Gn2 propodus palmar margin with 1 median shallow and short excavation, and defined by a shorter tooth, preceded by a shallow V-shaped excavation; dactylus inner margin smooth, sinuous, submedially inflated. P3–7 dactylus with bifid nail; P5–7 propodus posterior margin without tuft of setae.

Ovigerous female, Gn2 similar to male but shorter, with median palmar incision less deep than in male, sometimes lacking. Description. *Male:* 6 mm. A1 slightly longer than one-half of body, ratio of arts 1:2:3 peduncle equals 0.9:1:0.25, art1 with 4 elongate spines and short setae on ventral margin, flagellum with up to 18 articles, acc flagellum longer than one-half flagellum, with up to 8 articles. A2 is three-quarters of A1, ratio of peduncle arts 4:5 equals 1.25:1, flagellum not very setose, with up to 10 articles. Md palp art1 distally smooth, art2 three-quarters length of art3, with 7 setae on inner margin, art3 with 6 setae on inner margin and 5 long apical setae. Mx2 outer plate wider than inner. Cx1 antero-ventrally rounded, scarcely produced. Gn1 basis with 4 long setae on posterior margin and approximately 10 long setae on inner face; carpus elongate, dorsal margin grooved, distally minutely pointed, with 2 rows of relatively short facial setae and 5 rows of long facial setae on inner side, and with 7 groups of long setae on ventral margin; propodus ovate, palm oblique, slightly longer than hind margin, defined by 1 inner spine, with 4 ventral groups of long setae, dactylus slender. Gn2 propodus palmar margin divided into 2 parts by submedial, shallow, U-shaped excavation (a), distal part B distinctly longer than proximal part A, delimited by a sharp acute process, preceded by a narrow V-shaped excavation b (Figures 3 and 5); the acute process with a short subdistal spine on inner margin; dactylus robust, internal margin sinuous, submedially inflated, outer margin with one seta. P5 basis ovate, with weak postero-distal rounded lobe, posterior margin convex, minutely crenulate, with few short setules. P6–7 basis broader than in P5, posterior margin distinctly convex,

**Figure 6**

Maera cerea n. sp. YPM 21529, male, holotype, Bermuda: a–a', Gn I; b–d, P5–7. Scale 0.2 mm.

with postero-distal rounded lobe; merus and carpus with long setae, postero-distal corner of merus with a group of setae shorter than carpus, propodus posterior margin without a setal tuft. U3 relatively elongate, rami flat, distally truncated, with 2 groups of long setae on external margin of outer ramus, inner ramus slightly shorter than outer; art2 of outer ramus rudimentary, hardly visible, hidden between distal setae. T sub-quadrangle, lobes not distally incised, disto-interior corners markedly acute, with 3 to 4 distal spines as long as T and 2 shorter ones, outer margin with a group of 2 to 3 medio-distal setae.

Female: Ovigerous, 5 mm. Gn2 similar to male but shorter and with median palmar incision less deep than in male. Sometimes in females, and always in immatures, the median incision on Gn2 palm is lacking.

Remarks. *Maera ceres* is similar to *Maera pacifica* Schellenberg (1938). The principal difference is in the Gn2 male propodus: the medial excavation is less deep and excavation b (Figure 3) at the base of the palmar tooth is clearly less deep and V-shaped (vs. rounded, U-shaped in *M. pacifica* of Schellenberg [1938, fig. 19e], and in our Figure 3). This character is constant in all examined specimens from Bermuda. In addition, *M. pacifica* is "up to 7 mm," while *M. ceres* is not more than 6 mm in length.

Etymology. Local legend in Verona suggests that Shakespeare visited the city and stayed in the building that now houses the Museo Civico di Storia Naturale. Because much of the current laboratory analysis of *Maera* in Bermuda was carried out in this building, and because Shakespeare is said to have had the setting for his play *The Tempest* inspired by a 16th century shipwreck on Bermuda, we believe it appro-

priate to use specific epithets taken from characters in *The Tempest*.

Biology and distribution. Co-existing with *Maera quadrimana*, *M. tinkerenensis*, *M. ariel* n. sp. and *M. caliban* n. sp. Females ovigerous (up to 6 eggs) observed in May and June. Known only from Bermuda.

REMARKS ON *MAERA PACIFICA*
SCHELLENBERG 1938

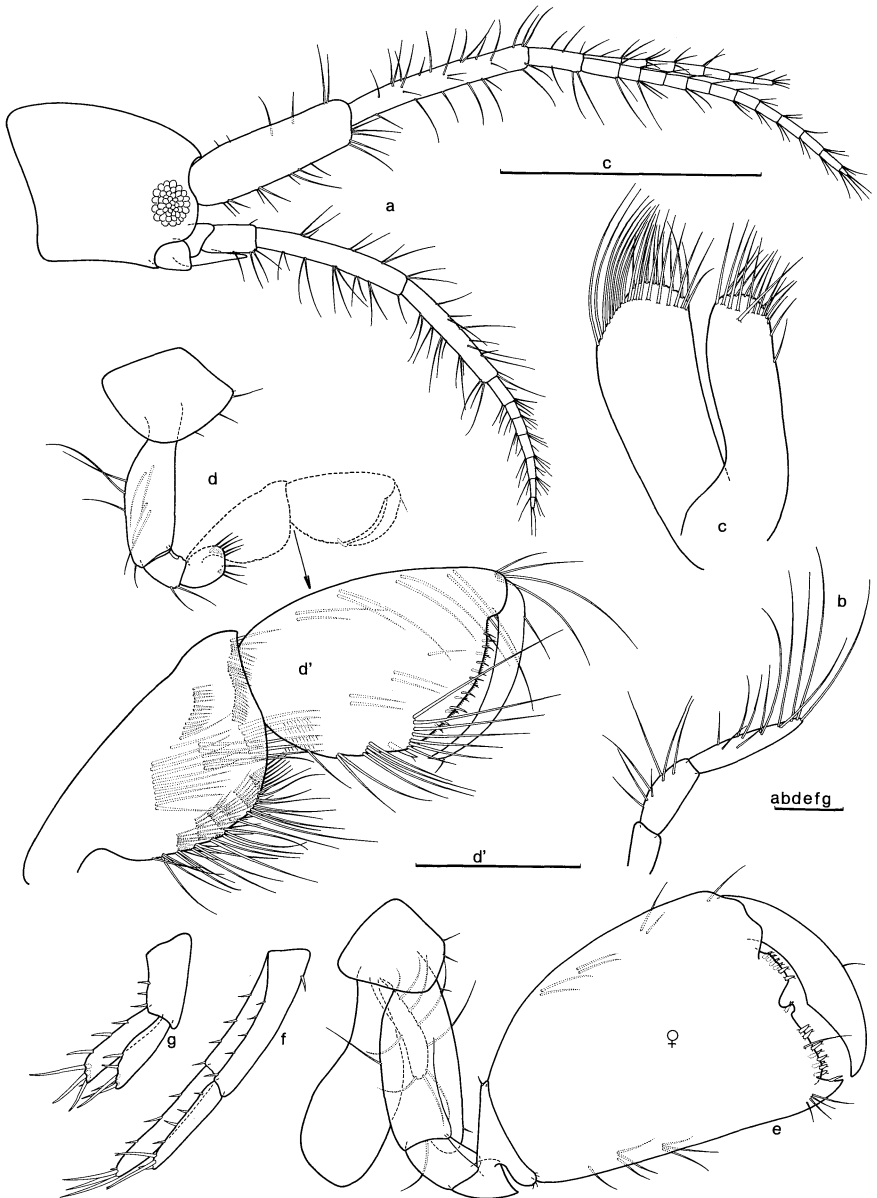
Maera pacifica has a wide distribution (Pacific and Caribbean) and taxonomically is still not clearly defined. The male dactylus (Schellenberg 1938, fig. 19e) has on the inner margin a small median triangular tooth ("während den Innenrand des Dactylus ein Zahn schmueckt"). In our Bermuda material the inner margin of the male dactylus is always smooth, and sinuous and swollen only in the middle, as in the female Gn2 (Schellenberg 1938, fig. 20a). We examined only one male (7 mm) from the syntype lot labeled "Hawaii Pearl Hermes Riff Pietschmann leg. 1928" (coll. Naturhistorisches Museum, Wien), presumably examined by Schellenberg. The dactylus of Gn2 of this male is morphologically similar to the males from Bermuda, both lacking the tooth on the inner margin. Also, all other authors who figured *M. pacifica* never reported a tooth on the inner side male dactylus of Gn2; it is therefore necessary to see topotypical specimens to evaluate this important character.

Maera pacifica Schellenberg 1938:42–45, figs. 19–20.

Maera pacifica J.L. Barnard 1970:150–152, figs. 92–93.

Maera pacifica J.L. Barnard 1971:84, figs. 31, 38, 40, 41.

Maera pacifica forme A Ledoyer 1972:227, fig. 43.

**Figure 7**

Maera miranda n. sp. YPM 21568, female, holotype, Bermuda: a, head with A1-2; b, Md palp; c, Mx2; d-d', Gn1; e, Gn2; f-g, U1-2. Scale 0.2 mm.

- Maera pacifica* forme A Ledoyer 1982:534–536, figs. 201–202.
nec *Maera pacifica* Nayar 1959:23–24, figs. 16–17 (= *Maera* sp.?) from Krusadai Islands, India.
nec *Maera pacifica* Ruffo 1969:26–27 (= ?*M. schellenbergi* Ruffo) from Red Sea.
nec *Maera pacifica* Griffiths 1970:25–26, fig. 8 (= ?*M. quadrimana* Dana) from Mozambique.
nec *Maera pacifica* forme B Ledoyer 1972:227, fig. 43 (= ?*M. quadrimana* Dana, partim) from Madagascar.
nec *Maera pacifica* forme B Ledoyer 1982:202, fig. 203 (= ?*M. quadrimana* Dana, partim) from Madagascar.
nec *Maera pacifica* Myers 1985:112–116, figs. 89–90 (= ?*M. quadrimana* Dana, as P6–7 has on the posterior margin a group of setae) from Fiji.

The often underlined variability of *Maera pacifica* (e.g., U3 male and female [J.L. Barnard 1970]; telson spination [J.L. Barnard 1970; Ledoyer 1972, 1982]) can be reconfirmed only after examining a large series of animals. Also, the geographical distribution of *M. pacifica* should be determined; *M. pacifica* has not been recorded from the Atlantic Ocean, although the *M. quadrimana* from Cuba (Ortiz 1978) is probably *M. pacifica*. We examined 5 specimens from Cuba (among them 3 adult males) and they are morphologically identical to the original description of Schellenberg (Figure 3). *Maera pacifica* is widely distributed in the Indo-Pacific, from Madagascar to the Hawaiian Islands.

Despite the seemingly close correlation between the Bermuda specimens and *M. pacifica*, the consistency of several diagnostic features argues that the Bermuda specimens indeed constitute a separate and new species, *Maera ceres*.

MAERA MIRANDA RUFFO, KRAPP AND GABLE N. SP.
Figures 7 and 8.

Maera quadrimana Ledoyer 1986 (not Dana 1853):190–191, fig. 11.

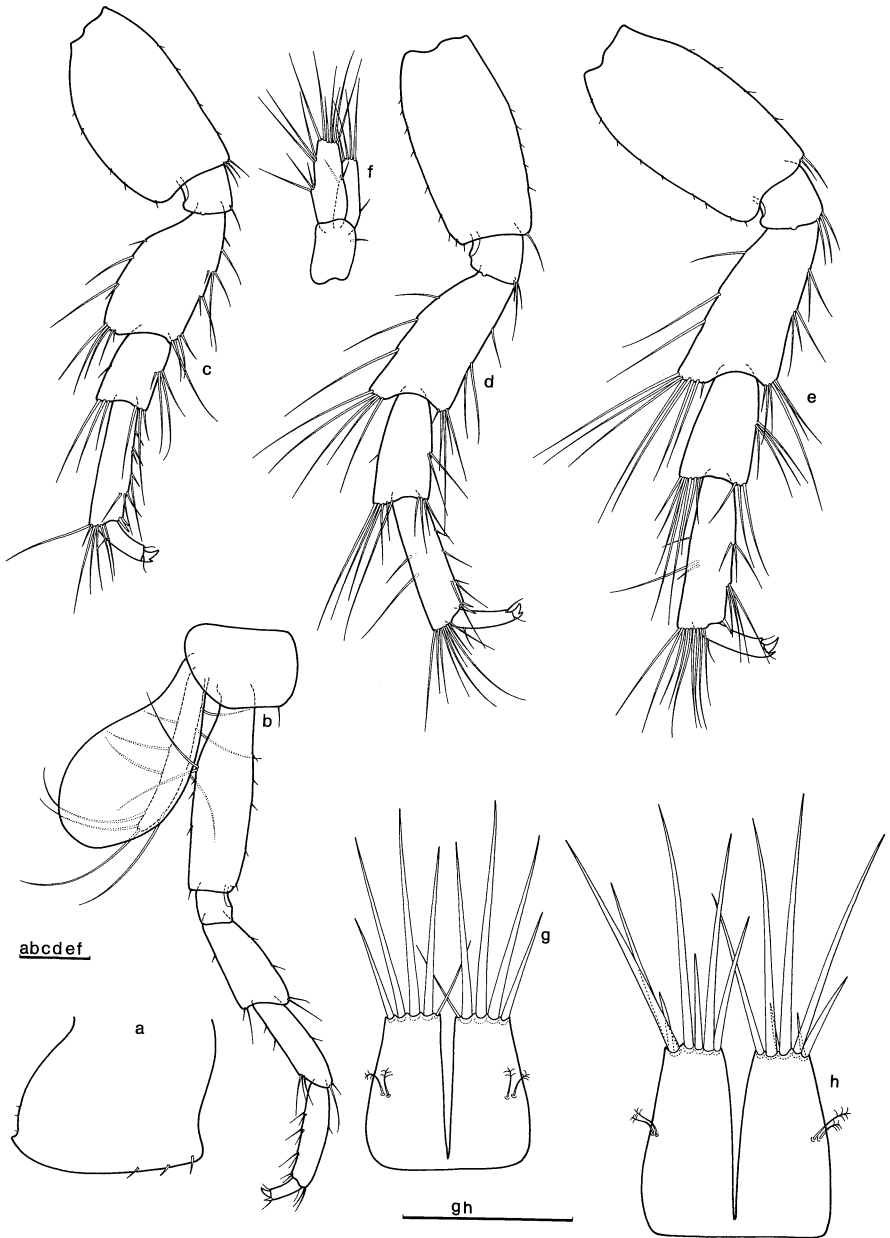
Type locality. Bermuda.

Material examined. *Female:* Holotype, ovigerous, YPM 21568 (IZ.S00158), on 8 slides with carcass in alcohol.

All other specimens are paratypes, as follows: YPM 21528 (IZ.S00163), 1 ovigerous female; YPM 21606 (IZ.S00158), 1 male on 5 slides with carcass in alcohol; YPM 21607 (IZ.S00158), 1 juvenile; YPM 21612 (IZ.S00196), 1 male; 1 ovigerous female (IZ.S00272) deposited by YPM in the Museo Civico di Storia Naturale, Verona, Italy.

Diagnosis. A *Maera* species of the *quadrimana* complex, distinguished by Md palp art2 shorter than art3; Cx1 antero-distally rounded, not produced; Gn1 carpus dorsal margin feebly grooved, distally minutely pointed, propodus palmar margin delimited by 1 inner spine; Gn2 palmar margin with 2 excavations delimiting a short median truncate process and defined by a strong and short tooth with 1 submedial spine, preceded by low V-shaped excavation; dactylus inner margin inflated, with a minute median point; P3–7 dactylus with bifid nail; P5–7 basis ovato-elongate, P6–7 propodus posterior margin with long setae; T lobes distally truncate, not incised, with 5 to 7 very long spines.

Description. *Female:* Ovigerous, 5 mm. Ep3 postero-ventral corner produced into a small acute tooth, ventral margin with 3 spines. A1 equals one-half of body, peduncle long, article ratio 1:2:3 equals 0.9:1:0.3; art1 moderately inflated, with 4 elongate spines and setae on ventral margin; art2 elongate with numerous long

**Figure 8**

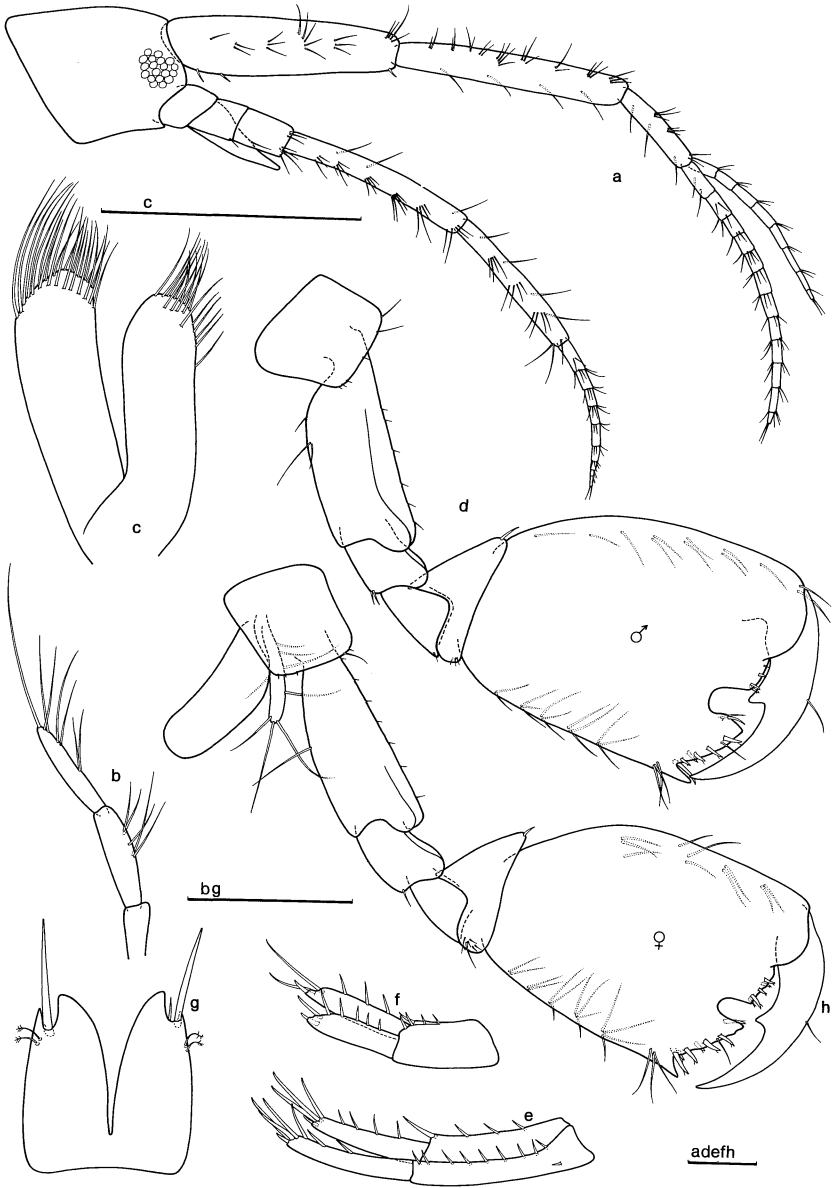
Maera miranda n. sp. YPM 21568, female, holotype, Bermuda: a, Ep3; b, P3; c-e, P5-7; f, U3; g, T. YPM 21606, male, paratype: h, T. Scale 0.2 mm.

setae; flagellum distinctly shorter than peduncle, with up to 12 articles, acc flagellum longer than one-half flagellum, with up to 7 articles. A2 is three-quarters the length of A1, peduncle article ratio 4:5 equals 1:0.8, with marginal tufts of long setae, flagellum as long as peduncle art5, with up to 7 articles; gland cone reaching tip of art3 of peduncle. Md palp art1 distally smooth, art2 distinctly shorter than art3 (ratio = 0.6:1) with 7 setae on inner margin, art3 with 9 setae on inner margin and with 3 long apical setae. Mx2 outer plate distinctly wider than inner one. Cx1 antero-distally rounded, not produced. Gn1 basis with 3 long setae on posterior margin and with 4 long setae on inner face; carpus elongate, anterior margin feebly impressed, distally minutely pointed, with 2 rows of facial short setae and 3 rows of facial long setae on inner side, and with 7 groups of long setae on posterior margin; propodus ovate, palm oblique, slightly longer than hind margin, defined by 1 inner spine, with 4 groups of long setae, dactylus slender. Gn2 basis and ischium antero-distally enlarged into 2 unequal lobes defining, in the basis, an elongate groove, posterior margin of the basis with 1 long seta, merus postero-distally acute, carpus short, cup-like, propodus broadly rectangular, slightly expanded distally, palmar margin divided into parts A and B (Figure 3) by submedial low excavation (a), part B proximally elevated into a short truncate process, delimited between excavation (a) and a low, wide excavation (a'); palmar margin delimited by a strong and short triangular process, with a subdistal inner spine, preceded by very low V-shaped excavation b; dactylus strong, inner margin medially inflated and elevated into a minute obtuse point. P3-4 slender, similar in shape, but P4 somewhat longer than P3, both with

few short setae, dactylus with bifid nail. P5 basis ovate, with postero-distal rounded lobe hardly evident, posterior margin distinctly convex, feebly serrulate with very short spines, merus broad, with long marginal setae, carpus short and strong, propodus posterior margin naked, distally with long setae, dactylus nail bifid. P6-7 similar; basis ovato-elongate with postero-distal lobe hardly evident (particularly in P6), posterior margin not very convex, feebly serrulate, with short spines; merus elongate, postero-distal corner with row of long setae markedly exceeding tip of carpus; propodus strong (particularly in P7), posterior margin with 2 single setae (in P7 one additional, but in 2 different groups); dactylus with bifid nail. U1-2 outer ramus distinctly shorter than inner. U3 rami flat, truncate distally, inner ramus shorter than outer, art2 of outer ramus vestigial, barely visible between long distal setae. T subquadrate, deeply incised, lobes distally truncate, armed with 5 to 7 very long spines, some as long as 1.5 times T, with 2 medial submarginal setae. Oostegites very narrow, short, tongue-shaped, with long marginal setae.

Male: Very similar to female.

Remarks. This species corresponds to the descriptions and the figures given by Ledoyer (1986) as sub *Maera quadrimana* from Punta Gorda, Gulf of Mexico. There seems also to be some similarity to *Melita setipes* var. *superba*, described by Lejeune de Oliveira (1953) from Rio de Janeiro, Brazil. The description of de Oliveira (1953), however, is incomplete and the figures are not detailed enough to allow us to include his *Melita setipes* in the synonymy of *Maera miranda*. If further topotypical material should confirm a congruence between the species, the name *superba* would become a junior synonym of *miranda*. For the moment we

**Figure 9**

Maera ariel n. sp. YPM 21557, male, holotype, Bermuda: a, head with AI-2; b, Md palp; c, Mx2; d, Gn2; e-f, U1-2; g, T. YPM 21608, female, paratype: h, Gn2. Scale 0.2 mm.

believe it judicious to describe the Bermuda material as a new species.

Maera miranda is morphologically close to *M. quadrimana*, *M. pacifica* and *M. ceres* n. sp. In fact, Ledoyer (1986) treated his material as an intermediary between *M. quadrimana* and *M. pacifica*. The dactylus and palm of Gn2, however, are good differentiating characters between *M. quadrimana* and *M. miranda*. Also, the distal spines of the telson are much more numerous and longer in *M. miranda*. In addition, art2 Md palp is clearly shorter in length than art3 in *M. miranda*. Compared with *M. pacifica* and *M. ceres*, the new species is different in the narrower and longer bases of the peraeopods and in the long setae on the posterior margin of the P6–7 propodus.

Maera quadrimana, *M. pacifica*, *M. ceres* and *M. miranda* constitute a morphologically similar group or complex with differentiating characters not easily recognized. Mature individuals are needed in samples for identification, as in juveniles and in many non-ovigerous females the species differentiating characters are scarcely evident or totally lacking. The characters that differentiate these four species are the palm and dactyls of the male Gn2, the shape of the basis, and the presence of setae on the hind margin of P5–7. The shape and disposition of the excavations of the palm of male Gn2 (Figure 3) are critical for identification. An overview of the most salient differentiating characters for the species that occur in Bermuda appears in Table 1.

Etymology. See *Maera ceres*.

Biology and distribution. In Bermuda, occurring with *Maera ariel* n. sp.; females ovigerous in May and June. This species is known from the type locality Bermuda and from the Gulf of Mexico (sub *Maera quadrimana* Ledoyer 1986).

MAERA ARIEL RUFFO, KRAPP AND GABLE
N. SP.

Figures 9 and 10.

?*Maera inaequipes* Kunkel 1910 (not A.
Costa 1851): 44–46, fig. 16.

Type locality. Bermuda.

Material examined. *Male:* Holotype, YPM 21557 (IZ.S00021), on 7 slides.

All other specimens are paratypes, as follows: YPM 21530 (IZ.S00076), 1 male; YPM 21531 (IZ.S00045), 1 ovigerous female; YPM 21532 (IZ.S00045), 2 males; YPM 21534 (IZ.S00124), 1 juvenile; YPM 21535 (IZ.S00162), 1 ovigerous female; YPM 21544 (IZ.S00045), 1 ovigerous female; YPM 21545 (IZ.S00019), 1 juvenile; YPM 21550 (IZ.S00036), 1 male; YPM 21552 (IZ.S00272), 1 female; YPM 21553 (IZ.S00281), 1 male; YPM 21559 (IZ.S00027), 1 male, 1 ovigerous female, 1 juvenile; YPM 21561 (IZ.S00196), 1 male, 1 ovigerous female; YPM 21563 (IZ.S00196), 12 specimens; YPM 21567 (IZ.S00158), 1 male; YPM 21608 (IZ.S00021), 1 ovigerous female on 5 slides with carcass in alcohol; YPM 21609 (IZ.S00021), 13 specimens, mixed sexes and stages; USNM 291166, Bermuda, collector G. B. Goode, 1876–1877, 1 specimen; USNM 291167, Bermuda, collector G. B. Goode 1876–1877, 15 specimens, including 1 ovigerous female; 1 male and 2 ovigerous females (IZ.S00223) deposited by YPM in the Museo Civico di Storia Naturale, Verona, Italy; 1 male (IZ.S00196), 1 ovigerous female and 1 juvenile (IZ.S00036) deposited by YPM in the Bermuda Museum of Natural History.

Diagnosis. A *Maera* species of the *quadrimana* complex, with an elongate art3 of the peduncle of A1, Cx1 antero-ventrally acutely produced; Gn1 carpus anterior margin with slight subapical depression;

Table 1

Characters used to distinguish three closely related species of *Maera* from Bermuda.

Characters	<i>M. quadrimana</i>	<i>M. ceres</i>	<i>M. miranda</i>
Gn2 palm excavation a (Figure 3)	2 (a, a')	1	2 (a, a')
Gn2 palm part B (Figure 3)	divided into 2 similar narrow processes (B, B')	not divided	divided into 2 processes: 1 proximal (B) very wide, 1 distal (B') very narrow
Gn2 palm excavation b (Figure 3)	deep and wide	low, V-shaped	very low, V-shaped
Gn2 dactylus inner margin	smooth	medially inflated	medially inflated with median minute point
P5 basis	narrowly ovato-rectangular, posterior margin feebly convex to straight	ovate, posterior margin clearly convex	ovate, posterior margin clearly convex
P6, 7 basis	ovate-elongate, (particularly P6) posterior margin moderately convex	broad, posterior margin strongly convex	ovate-elongate, posterior margin moderately convex
P7 merus postero-distal corner	with tuft of long setae exceeding tip of carpus	with tuft of setae not exceeding tip of carpus	with tuft of long setae exceeding tip of carpus
P6, 7 propodus posterior margin	with medial tuft of 2 to 3 long setae	naked, without tuft of long setae	with 2 long setae

Gn2 palmar margin in both sexes with deep median excavation, dactylus with triangular tooth opposite to palmar excavation; dactylus of P3–7 each with a bifid nail; posterior margin of propodus of P6–7 with 1 tuft of long setae; U3 rami stout, distally truncate, T lobes deeply incised, with one long distal spine in each lobe.

Description. *Male:* 5.3 mm. Ep2 postero-

ventral corner minutely pointed, ventral margin with 2 spines; Ep3 postero-ventral corner subrounded, with minute upturned tooth, ventral margin with 6 spines. Al slightly longer than one-half of body, peduncular ratio of arts 1:2:3 equals 1:1:0.43, art1 elongate with 2 short proximal spines and 1 short distal spine on ventral margin, art2 with groups of short marginal setae,

art3 elongate, flagellum shorter than peduncle, with up to 17 articles, acc flagellum longer than half the flagellum, with up to 7 articles. A2 equal in length to A1, peduncular ratio of arts 4:5 equals 1.25:1, with marginal short setae, flagellum as long as peduncle art5, with up to 7 articles, gland cone reaching tip of peduncle art3. Md palp art1 distally smooth, art2 and art3 elongate, art2 equals art3 in length, art2 with 5 setae on inner margin, art3 with 6 setae on inner margin and 1 long apical seta. Mx2 outer lobe slightly wider than inner. Cx1 antero-ventrally acutely produced. Gn1 carpus elongate, with 5 facial rows of setae on internal side and 7 groups of long setae on ventral margin, dorsal margin with slight subapical depression, distally acutely produced; propodus palm delimited by 1 inner spine, with 7 groups of long setae on ventral margin. Gn2 basis and ischium antero-distally enlarged into 2 lobes, that of the basis defining an elongate groove, posterior margin of basis with only 1 group of long setae; merus ventro-distally acute, carpus cup-like with a short ventral lobe; propodus broadly rectangular, palmar margin divided into 2 parts by median deep U-shaped excavation, distal part (Figure 3, part B) forming an obtuse angle with ventral margin, and delimited by a sharp tooth with a strong spine located on the inner edge; dactylus with a median triangular tooth on inner margin, fitting median palmar excavation. P3–4 slender, similar in shape but P4 slightly longer than P3, basis with a few short setae on posterior margin, dactylus with bifid nail. P5–7 robust, basis broadened, especially in P6–7, posterior margin distinctly convex, minutely crenulate with very short setae, merus and carpus wide, with numerous long setae, propodus of P6–7 strong, particularly in P7, with a median tuft of long setae on posterior mar-

gin, dactylus nail short, bifid, posteriorly smooth. U1 peduncle with 1 short ventrofacial spine, not easily visible. U3 relatively stout, inner ramus shorter than outer; rami flat, truncate distally, outer ramus unarticulate, with distal spines two-thirds length of ramus. T slightly longer than broad; lobes distally incised with 1 spine three-quarters length of lobes, sometimes accompanied by 1 short spine.

Female: 5.3 mm with oostegites, morphologically similar to male. Palmar incision and dactylus of Gn2 with median tooth as in male. Oostegites very short and narrow, with long marginal setae.

Remarks. *Maera ariel* is similar to *Maera aurora* Krapp et al. (1996) from the Mediterranean Sea, but distinguished by the median triangular tooth on inner margin Gn2 dactylus in both sexes (only in male of *M. aurora*) and by the 1 long distal spine on each lobe of the telson.

The spination of the telson in *M. ariel* is similar to *Maera vigota* J. L. Barnard (1969) from along the coast of California, but the morphology of Gn2 of *M. vigota* is significantly different. In addition, the dactyls of P3–7 are simple and not bifid. *Maera ariel* seems to be closely allied to *Maera trisinuata* Mateus and Mateus (1986), known from the Principe Islands, Gulf of Guinea. Although incompletely described and figured, *M. trisinuata* differs from *M. ariel* in the lack of a tooth on the inner margin of Gn2 dactylus and in the possession of a telson with 3 long spines on each lobe.

The inner tooth of the Gn2 dactylus in immature specimens from Bermuda is not always visible and the median excavation of the palmar margin is shallow or absent. This species, however, is easily distinguished by the telson lobes, which are incised and have 1 long spine. In addition, art3 of A1 is clearly longer than in all

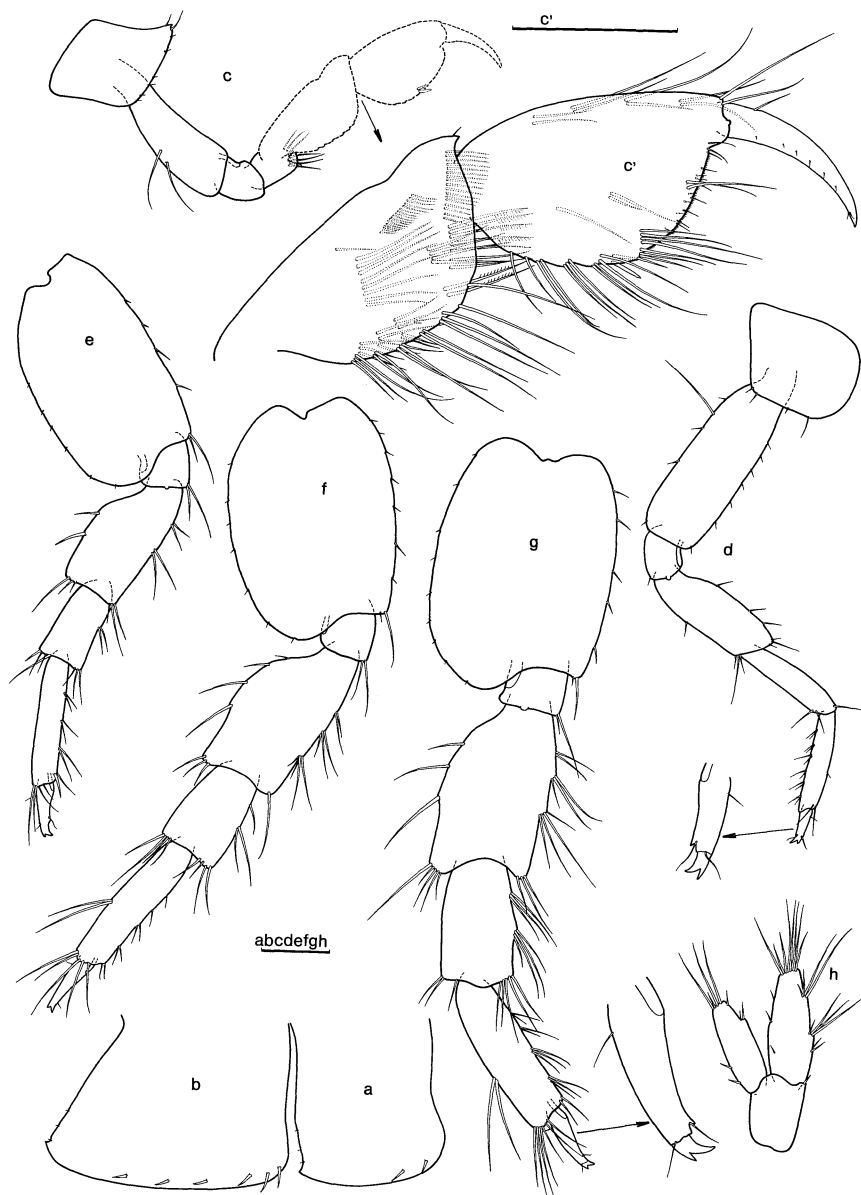


Figure 10

Maera ariel n. sp. YPM 21557, male, holotype, Bermuda: a-b, Ep2-3; c-c', Gn1; d, P3; e-g, P5-7; h, U3. Scale 0.2 mm.

other *Maera* species from Bermuda.

Those animals described by Kunkel (1910) as *Maera inaequipes* (A. Costa 1851) are surely not the named species; the description seems more similar to *M. ariel* than that of any other species, but a synonymy must remain in question.

Etymology. See *Maera ceres*.

Biology and distribution. Sometimes collected with *Maera ceres*, *M. quadrimana*, *M. miranda* and *M. tinkerensis*. Ovigerous females with 4 to 6 eggs in May and June. Known only from Bermuda.

MAERA CALIBAN RUFFO, KRAPP AND GABLE
N. SP.

Figures 11 and 12.

Type locality. Bermuda.

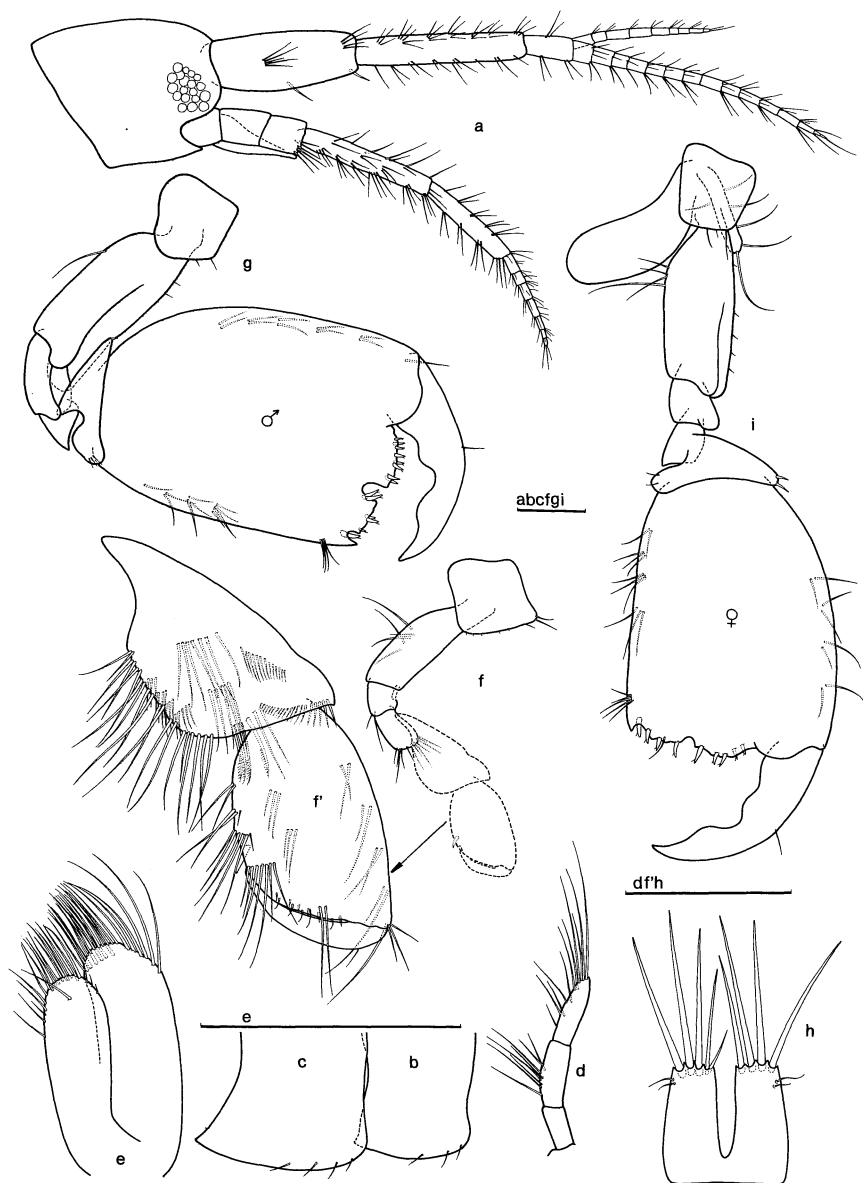
Material examined. *Male:* Holotype, YPM 21572 (IZ.S00196), on 8 slides.

All other specimens are paratypes, as follows: YPM 21558 (IZ.S00021), 2 females; YPM 21610 (IZ.S00196), 1 ovigerous female on 5 slides with carcass in alcohol; YPM 21611 (IZ.S00196), 7 specimens; YPM 21614 (IZ.S00196), 1 specimen; 1 male and 1 ovigerous female (IZ.S00196) deposited by YPM in the Museo Civico di Storia Naturale, Verona, Italy; 1 male and 1 ovigerous female deposited by YPM in the Bermuda Museum of Natural History.

Diagnosis. A *Maera* species of the *quadrimana* complex with Cx1 anteroventrally rounded, not produced; Gn1 carpus dorsal margin with slight subapical depression; Gn2 palmar margin in both sexes with median semicircular excavation, delimited by a short triangular tooth, dactylus inner margin sinuous, with two humps delimiting a medial wide excavation, dactylus of P3–7 each with a bifid nail; posterior margin of propodus of P6–7 with 2 to 3 tufts of

long setae; U3 with stout rami, distally truncate; T lobes distally truncate, with 4 to 5 very long spines.

Description. *Male:* 5 mm. Ep2–3 posteroventral corner acutely pointed, ventral margins with 3 and 4 spines respectively. A1 slightly shorter than one-half of body, peduncle long, arts 1:2:3 ratio equals 0.85:1:0.25, art1 inflated with 2 long spines on ventral margin, art2 elongate with approximately 7 tufts of relatively short setae on dorsal and ventral margins, flagellum distinctly shorter than peduncle with up to 14 articles, acc flagellum with up to 7 articles, slightly longer than half the flagellum. A2 flagellum as long as peduncle art5, with up to 7 articles; gland cone reaching tip of peduncular art3. Md palp art1 distally smooth, art2 as long as art3, with 8 setae on interior margin, art3 with 7 setae on interior margin and with 4 long apical setae. Mx2 outer lobe slightly wider than inner. Cx1 subquadrate, anteroventrally rounded, not produced. Gn1 carpus elongate, with 2 rows of short facial setae and 3 rows of long facial setae on inner side, and 7 groups of long setae on ventral margin, dorsal margin with slight subapical depression and distally acutely produced; propodus palm delimited by 1 inner spine, ventral margin with 4 groups of long setae. Gn2 basis and ischium antero-distally enlarged into 2 lobes, that of the basis defining an elongate groove, posterior margin of the basis with 1 to 2 long setae, merus ventro-distally acute, carpus cup-like with a short ventral lobe; propodus broadly subrectangular, palmar margin divided into 2 parts by a median semicircular excavation, distal margin (Figure 3, part B) distinctly shorter than proximal part A, forming a right angle with the ventral margin, and delimited by a short triangular tooth, with a basal strong spine located on the inner edge, excavation b very

**Figure 11**

Maera caliban n. sp. YPM 21572, male, holotype, Bermuda: a, head with AI-2; b-c, Ep2-3; d, Md palp; e, Mx2; f-f', Gn1; g, Gn2; h, T. YPM 21610, female, paratype: i, Gn2. Scale 0.2 mm.

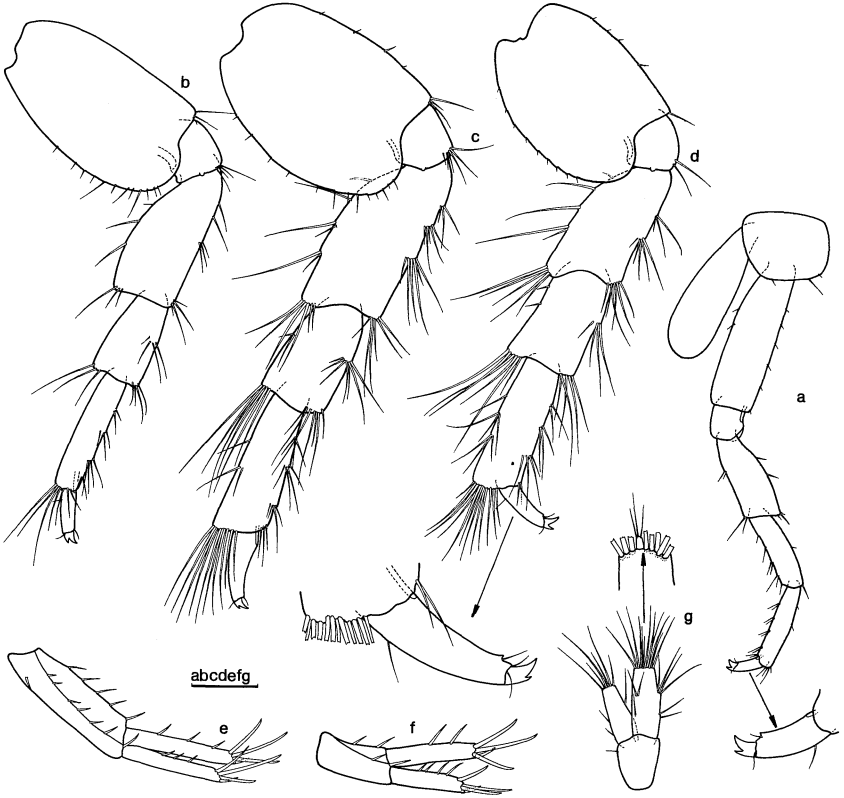


Figure 12

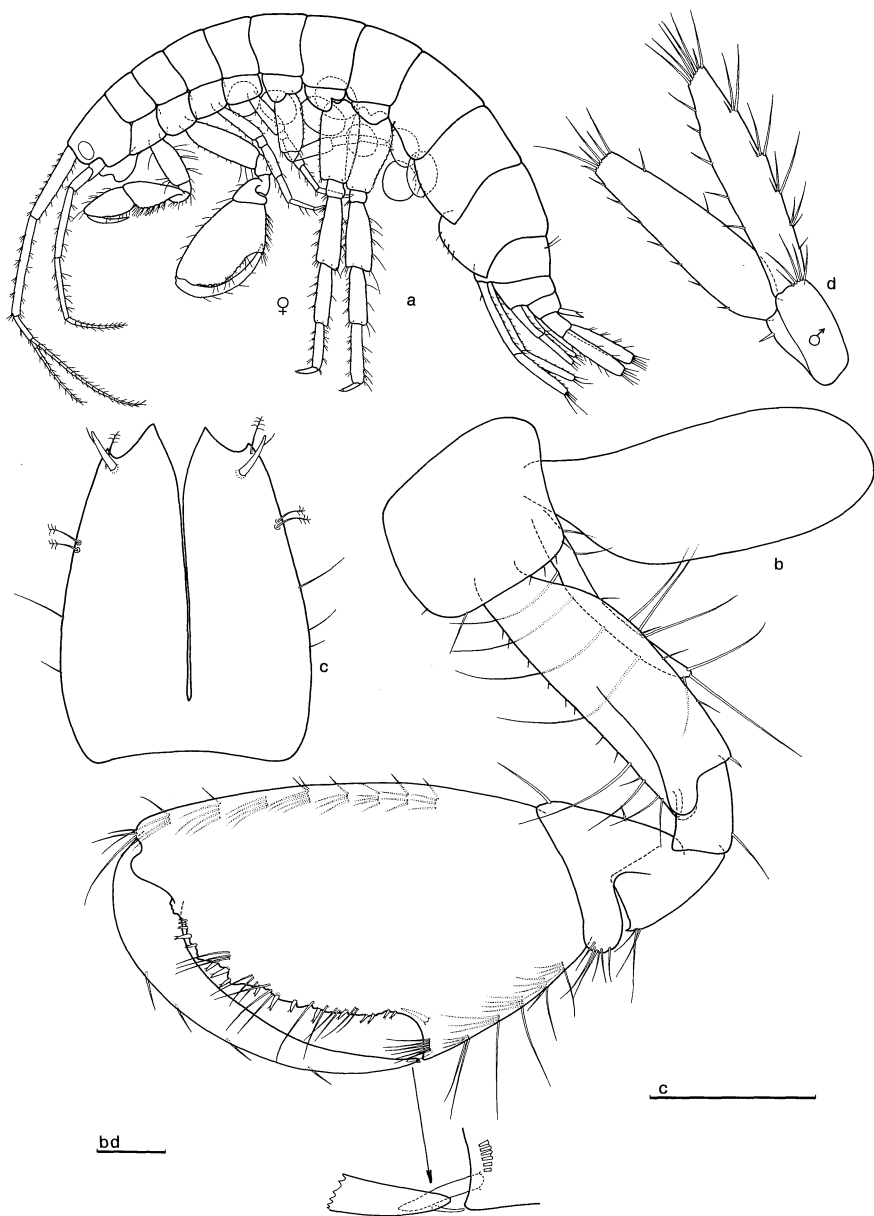
Maera caliban n. sp. YPM 21572, male, holotype, Bermuda: a, P3; b-d, P5-7; e-g, UI-3. Scale 0.2 mm.

low, dactylus inner margin sinuous with 2 humps delimiting a wide medial sinus. P3-4 slender, similar in shape but P4 somewhat longer than P3, basis with few short setae on posterior margin, dactylus with bifid nail. P5-7 robust, basis broadened, especially in P6-7, posterior margin distinctly convex, finely crenulate, with short spines, merus and carpus wide with numerous very long setae, propodus of P6-7 strong, particularly in P7, with 2 to 3 tufts of long setae on posterior margin, dactylus nail short, bifid, posteriorly smooth. UI peduncle with 1 short ventro-facial spine, not

easily visible. U3 relatively stout, inner ramus shorter than outer, rami flat, truncated distally, outer ramus with art2 very reduced and scarcely visible among the numerous long distal spines. T subquadrate, lobes distally truncate, not incised, with 4 to 5 very long spines on each lobe, some 1.5 times the T length.

Female: Ovigerous, 3.5-4 mm, very similar to male, only with less deep median palmar incision of Gn2. Oostegites short, narrow, with long marginal setae.

Remarks. *Maera caliban* is easily distinguished from other species in the *quadri-*

**Figure 13**

Maera tinkerenis Kunkel. YPM 8326, female, Bermuda: a, body, lateral view; b, Gn2; c, T. YPM 8330, male; d, U3. Scale 0.2 mm.

mana complex, in particular by the sinuous inner margin of the dactylus of Gn2, by the short triangular tooth delimiting the palmar margin of Gn2 (preceded by a very low excavation) and by the shape and spination of the distally truncated lobes of the telson. In the small series of specimens examined the characters remain constant. In juveniles the sinuosity of the inner margin of Gn2 dactylus is barely evident. The species, however, is always easily discernible by the shape of the telson and the presence of 2 to 3 tufts of long setae on the posterior margin of P6–7 propodus.

Etymology. See *Maera ceres*.

Biology and distribution. Co-existing with *Maera ariel* and *M. ceres*. Females with 4 to 6 eggs in May. Known only from Bermuda.

MAERA TINKERENSIS KUNKEL 1910
Figure 13.

Maera tinkerensis Kunkel 1910:49–51, fig. 18.

Maera tinkerensis Lazo-Wasem and Gable 1987:322–323, figs. 1–2.

Material examined. YPM 8326 (IZ.S00171), 1 ovigerous female on 2 slides with carcass in alcohol; YPM 8330 (IZ.S00171), 1 male on 5 slides; YPM 8361 (IZ.S00033), 1 male on 4 slides; YPM 21533 (IZ.S00171), 1 male; YPM 21538 (IZ.S00171), 2 juveniles; YPM 21543 (IZ.S00045), 1 male, 1 juvenile; YPM 21571 (IZ.S00091), 5 juveniles; YPM 21575 (IZ.S00091), 1 juvenile; YPM 21616 (IZ.S00171), 3 specimens; USNM 291168, Rocky Hill Park, Bermuda on Mullet Bay about 0.75 mi towards St. George's from BBSR, collected 3 September 1981, 1000 hrs, 27°C, 3 ppt, M. L. Jones, sieving, coarse sand under algae, 1.2 m, 2 males.

Additional material available: Large series of specimens in YPM.

Remarks. This species was described by Kunkel (1910) and redescribed by Lazo-Wasem and Gable (1987) with clear illustrations of a male syntype (YPM 8220). As this syntype was without U3, we now describe and illustrate it (Figure 13). U3 has elongate, flat, apically truncate rami with not particularly long spines; outer ramus lacks a rudimentary art.2.

Females (10mm, 8 eggs), not previously figured, are similar to males, including the shape of Gn2 and the telson (Figure 13). Oostegites are very narrow, elongate, and have long marginal setae.

Maera tinkerensis is distinguished from other *Maera* by art 1 of the Md palp having a sharp distal tooth, the series of setae on the outer margin of Gn2 dactylus (always 1 in the *quadrimana* complex), the simple nail dactyls on peraeopods with denticulate outer margin of the nail (cf. Lazo-Wasem and Gable 1987, fig. 1), and the elongate U3. This species belongs to the group similar to *Maera grossimana* Montagu (1808), which, unlike the essentially Indo-Pacific *quadrimana* complex, contains mostly Atlantic and Mediterranean species (e.g., *M. grossimana* Montagu [1808]; *M. danae* Stimpson [1853]; *M. loveni* Bruzelius [1859]; *M. hironellei* Chevreux [1900]; *M. schieckei* G. Karaman and Ruffo [1971]; *M. sodalis* G. Karaman and Ruffo [1971]).

Biology and distribution. Co-existing with *M. ceres* and *M. ariel*. Ovigerous females found in May. Known only from Bermuda.

REMARKS ON *MAERA RATHBUNAE* PEARSE

Pearse (1908) described *Maera rathbunae* (Figure 14) based on a 13 mm specimen, while the single male cited by Kunkel (1910), described and partially illustrated,

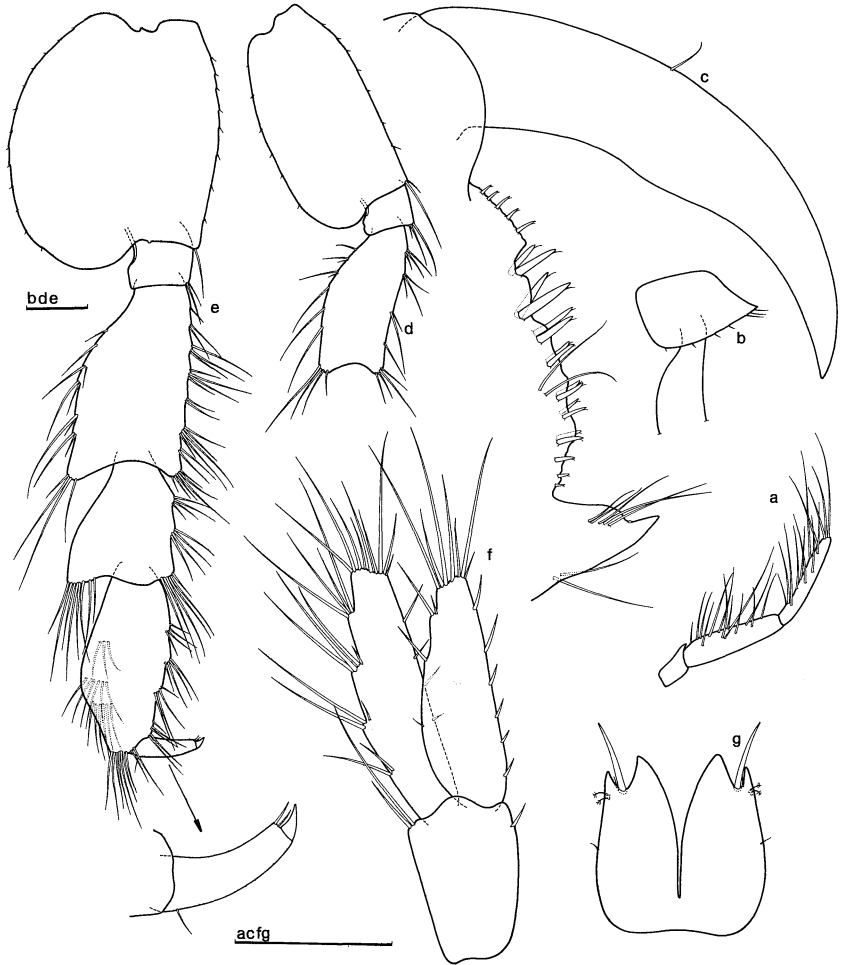


Figure 14

Maera rathbunae Pearse. USNM 38341, male, syntype, off Key West, Florida: a, Md palp; b, coxa I; c, Gn2 palmar margin; d, P5; e, P7; f, U3; g, T. Scale 0.5 mm.

was only 5 mm. The difference between *M. rathbunae* and Kunkel's Bermuda specimen is still more evident in the telson. In *M. rathbunae*, the telson is incised with 1 long distal spine. However, the illustration shown by Kunkel (1910) has the telson with truncate lobes, each with 5 long setae. Kunkel's collection is deposited at

the YPM (Lazo-Wasem and Gable 1987). He apparently did not allocate a type series for this species and we could not determine which of the now known *Maera* species Kunkel used to describe *M. rathbunae*. However, we believe it was probably *M. ceres* n. sp., based mainly on the shape and spination of the telson.

We examined 3 syntypes (USNM 38341) of *M. rathbunae* and are therefore able to provide a more complete diagnosis than that of Pearse (1908). Our study of these syntypes allowed us to compare *M. rathbunae* with other species of the *quadrimana* complex, to which this species undoubtedly belongs.

Diagnosis. Large body size (male 12 mm, female with oostegites 10 mm); Md palp art I with acute distal tooth; Cx I acutely produced antero-distally; Gn I carpus anterior margin with slight subapical depression, distally acutely produced; Gn 2 palmar margin crenulate, without excavations in both sexes, delimited by a relatively short and strong triangular tooth, subdistally with slight depression, without spines but with a tuft of short setae, dactylus inner margin feebly inflated medially; dactylus of P3–7 simple, not bifid; P5–6 with 1 to 2 tufts of long setae on posterior margin; P6–7 basis broad, posterior margin very convex, minutely serrulate; P7 propodus strong, inflated with 3 groups of long setae on posterior margin; U3 rami relatively elongate, flat, subequal with long distal spines; T distinctly longer than wide, lobes deeply incised distally, with 1 relatively long spine inserted at the base of the incision on each lobe.

Maera rathbunae is known only from the type locality of the Gulf Stream, off Key West, Florida, from a depth of 32 to 40 m.

Ecology of *Maera* species in Bermuda

Species of the genus *Maera* in Bermuda were sometimes found in the rocky littoral zone, usually under or in rocks, but most often were collected as sublittoral inhabitants of various substrates down to

a depth of 8 m. The sublittoral substrates were practically bare rock, algal holdfasts and thalli, debris in sandy sediments, and rocks or pilings with macroencrusting flora and/or fauna. In Bermuda, *Maera* is notable in its absence from any sheltered coastal habitat and from all inland marine pools, mangrove stands (with huge encrusting colonies of both algae and invertebrates), and the shallow sublittoral of all bays and coves within the islands' arch.

In fact, we have collected five of the six species of *Maera* in Bermuda from high energy environments. *Maera quadrimana*, *M. ceres*, *M. ariel* and even *M. tinikerensis*, the species most likely to be found littorally, were all found in debris near reef areas where surges make the bottom sediments unstable. *Maera ariel* inhabits macroencrusting communities of pilings that lie between the open ocean and an entrance to Castle Harbour; maximum tidal flow in these areas makes them unsafe for snorkelers or divers. The honeycombed, sheet rock coves of Smith's and Devonshire Parishes create an environment that is precarious for balance with even small wave action at low tide. One to several free-lying rocks can be found within the hollowed out depressions on these sheet rocks, and the mini-whirlpools created within the depressions with each passing wave have enough force to move these rocks about. Indeed, the rocks have a polished appearance and are devoid of any macroalgae. Nonetheless, both *M. ceres* and *M. ariel* exist clinging to the rocks in these depressions. Perhaps even more remarkable is the macroalgal habitat for some populations of *M. ceres* and *M. caliban* on the outer walls of the Bermuda boilers. Thomas and Stevens (1991) listed the amphipod *M. inaequipes* for the same habitat. Any snorkeler who has at-

Table 2Key to species of *Maera* in Bermuda (adult specimens).

1.	Gn2 with numerous setae on outer margin of dactylus	<i>M. tinkerensis</i>
	Gn2 with only 1 seta on outer margin of dactylus	2
2.	T lobes deeply incised distally, with only 1 spine (not particularly long)	<i>M. ariel</i>
	T lobes truncate distally, not incised, with 4 to 7 long spines	3
3.	P6–7 propodus without tufts of long setae on posterior margin	<i>M. ceres</i>
	P6–7 propodus with 1 to 3 tufts of long setae on posterior margin	4
4.	Gn2 dactylus inner margin smooth or feebly inflated; palmar margin delimited by long triangular tooth preceded by a deep U-shaped sinus	<i>M. quadrimana</i>
	Gn2 dactylus inner margin markedly inflated or sinuous; palmar margin delimited by short triangular tooth preceded by low V-shaped sinus	5
5.	Gn2 dactylus sinuous with 2 humps on inner margin; P7 propodus with 2 to 3 tufts of long setae on posterior margin	<i>M. caliban</i>
	Gn2 dactylus inner margin medially inflated with a median minute point; P7 propodus with 1 tuft of long setae	<i>M. miranda</i>

tempted to swim near these boiler reefs has appreciated the impossibility of maintaining one's position in the heavily swirling waters created by even moderate wave action.

Summary

For nearly a century the literature has viewed the Bermudian amphipod fauna as including three species of *Maera*: two species reported by Kunkel (1910), *M. rathbunae* and *M. inaequipes*, and a new species described by him, *M. tinkerensis*. We maintain there are six species of *Maera* in Bermuda, with only *M. tinkerensis* retained as one of them. In developing our conclusion, we have attempted to re-

define and clarify the status of three species: *M. quadrimana* sensu lato, *M. pacifica* and *M. rathbunae*.

Reporting of *M. quadrimana* from Bermuda is significant, as this is the first valid record for the species outside the Indo-Pacific and Pacific regions. Our four new species are all aligned with the *quadrimana* complex through characteristic morphological features such as the mandibular palp, Gn2 and P5–7. The characters separating these four species are seemingly minute, yet they are consistent. The alignment of these species with the *quadrimana* complex is also significant zoogeographically. Until now the *quadrimana* complex has had prevalently an Indo-Pacific distribution. With five species

of *Maera* from Bermuda in this complex and with the paucity of current knowledge on the Caribbean amphipod fauna allowing for a strong possibility of even more Atlantic *Maera* species in this complex, we may well have to reevaluate the traditional zoogeography of the entire *quadrimana* complex.

The morphological alignment of *M. tinkerensis* with the *grossimana* complex, consisting primarily of Atlantic species, raises an additional zoogeographical question: Why would evolution in Bermuda have occurred to a greater extent in the *quadrimana* complex than in the *grossimana* complex, given our current knowledge of the distribution of the species within the two complexes? Finally, the discovery of such diversity within one genus in such a small island group suggests a potentially greater diversity in the Caribbean amphipod fauna.

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Appendix

List of YPM locality numbers for samples from Bermuda with specimens of *Maera*. YPM locality numbers use the prefix IZ.S and are not the same as YPM catalog numbers.

- IZ.S00003. Bermuda, St. George's Parish, Tobacco Bay. Semi-protected cove on small island. Collector: Gable, M.F., 2 June 1985. [MFG 85-12]
- IZ.S00019. Bermuda, St. George's Parish. Near Parry and Grenadier Roads. In algal clumps near pipes. Depth: 10 ft. Collector: Gable, M.F., 2 June 1985. [MFG 85-56]
- IZ.S00020. Bermuda, Hamilton Parish, Shelly Bay. Among mixed subtidal algae. Collector: Gable, M.F., 3 June 1985. [MFG 85-57]
- IZ.S00021. Bermuda, Devonshire Parish, Devonshire Bay. Under rocks, at low water, subtidal. Collector: Gable, M.F., 29 May 1985. [MFG 85-58]
- IZ.S00027. Bermuda, Smith's Parish, Gravelly Bay. Subtidal honeycombs. Collector: Gable, M.F., 31 May 1985. [MFG 85-66]
- IZ.S00033. Bermuda, St. George's Parish, Whalebone Bay. Intertidal, under rock and in algae. Collector: Gable, M.F. and students, 22 May 1985. [MFG 85-89]
- IZ.S00036. Bermuda, Devonshire Parish, Devonshire Bay. Honeycomb cove W of other Devonshire Bay locality [MFG 85-58], subtidal. Collector: Gable, M.F., 31 May 1985. [MFG 85-94]
- IZ.S00044. Bermuda, St. George's Parish. Just N of Long Bird Bridge. From *Padina* on rock tops, high subtidal. Collector: Gable, M.F., 29 May 1985. [MFG 85-124]
- IZ.S00045. Bermuda, St. George's Parish, Whalebone Bay. Rocky intertidal. Collector: Gable, M.F. and students, 24 May 1987. [ELW/MFG 87-1-11]
- IZ.S00048. Bermuda, Hamilton Parish, Shelly Bay. N side of Shelly Bay. Shallow subtidal; scrapings of coralline algae. Collector: Lazo-Wasem, E.A., 28 May 1987. [ELW/MFG 87-14]
- IZ.S00076. Bermuda, St. George's Parish, Whalebone Bay. Picked from submerged rocks. Collector: Lazo-Wasem, E.A., 31 May 1987. [ELW/MFG 87-42]
- IZ.S00091. Bermuda, St. George's Parish. Off Natural Arches Beach, boiler reefs. Small chunks of debris. SCUBA. Depth: 5 m. Collector: Lazo-Wasem, E.A., 1 June 1987. [ELW/MFG 87-57]
- IZ.S00099. Bermuda, Hamilton Parish, Harrington Sound, Shark Hole. 2 subtidal encrusted rocks. SCUBA. Collector: Lazo-Wasem, E.A., 1 June 1987. [ELW/MFG 87-65]
- IZ.S00108. Bermuda, St. George's Parish. Underneath Long Bird Causeway (NW end). From large brown sponge. Collector: Lazo-Wasem, E.A., 31 May 1987. [ELW/MFG 87-75]

- IZ.S00124. Bermuda, St. George's Parish. Off Natural Arches Beach. Algae covered rock and sediment. SCUBA. Depth: 8 m. Collector: Baldinger, A.J. and Lazo-Wasem, E.A., 1 June 1987. [ELW/MFG 87-93]
- IZ.S00128. Bermuda, St. George's Parish. Off Natural Arches Beach. From debris on bottom sediment. SCUBA. Depth: 8-10 m. Collector: Baldinger, A.J. and Lazo-Wasem, E.A., 1 June 1987. [ELW/MFG 87-97]
- IZ.S00156. Bermuda, St. George's Parish, Tobacco Bay. High to mid-tidal range. Collector: Denette, R., 25 May 1987. [ELW/MFG 87-131]
- IZ.S00158. Bermuda, St. George's Parish, Tobacco Bay. Low intertidal. Collector: Mennone, J., 25 May 1987. [ELW/MFG 87-133]
- IZ.S00162. Bermuda, St. George's Parish, Tobacco Bay. Lower intertidal. Collector: Churchill, L., 25 May 1987. [ELW/MFG 87-137-138]
- IZ.S00163. Bermuda, St. George's Parish, Tobacco Bay. Low rocky intertidal. Collector: Damon, J., 25 May 1987. [ELW/MFG 87-139]
- IZ.S00171. Bermuda, St. George's Parish, Tobacco Bay. Lower tidal zone, under rocks in sand. Collector: Baldinger, A.J., 25 May 1987. [ELW/MFG 87-150-151]
- IZ.S00196. Bermuda, Devonshire Parish, Devonshire Bay. Cove W of Devonshire Bay. Washings of rocks, mean low water. Depth: 0.3 m. Collector: Lazo-Wasem, E.A., 15 June 1988.
- IZ.S00223. Bermuda, St. George's Parish. Underneath Long Bird Causeway. S side and under. Washings of rocks. Collector: Lazo-Wasem, E.A., 20 June 1988.
- IZ.S00232. Bermuda, St. George's Parish. Ferry Reach, cove W of BBSR. In *Halimeda* holdfast. Depth: 1 m. Collector: Patnode, A.H., 28 May 1989.
- IZ.S00233. Bermuda, St. George's Parish. Off Natural Arches Beach. Boiler reefs. Algae on boilers. Low water and calm seas. Collector: Gable, M.F., 30 May 1989.
- IZ.S00272. Bermuda, Sandys Parish, Fort Scaur. Great Sound at Fort Scaur. Snorkeling. Algae and invertebrate washings. Depth: variable to 15 ft. Collector: Rose III, W., 2 June 1991. [MFG 91-30]
- IZ.S00281. Bermuda, St. George's Parish, Whalebone Bay. Railroad pilings between Whalebone Bay and Coney Island. SCUBA. Algal and invertebrate scrapings from a piling and a few coral heads. Depth: 10 ft. Collector: Elston, A.L. and Rose III, W., 3 June 1991. [MFG 91-39]

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