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REVISION OF THE GAMMARELLID GROUP, WITH A NEW SPECIES FROM THE ANDAMAN SEA (CRUSTACEA, AMPHIPODA, MELITIDAE)

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ABSTRACT

This paper reports the first record of the gammarellid group in the Andaman Sea. A new species (*Nuuanu kata*) is described and a phylogenetic hypothesis for the group is presented. This hypothesis suggests that there are two main lines of evolution in the gammarellid group. One line (represented by *Gammarella*) is made up of large animals with well developed eyes which live among algae, seagrasses and detrital deposits. In the other line (represented by *Nuuanu*) the animals are small, with poorly developed eyes. This line is more diverse in species and morphology. The species live in anchialine environments, interstitially in marine environments or they may be associated with other invertebrates. Based on this hypothesis, the genus *Nuuanu* is re-established, *Cottesloe* remains in synonymy with *Gammarella,* and *Tabatzius* is synonymised with *Nuuanu*. The gammarellid group is considered to be a sister taxon to the melitid group (*sensu stricto*). The hypothesis also suggests that the gammarellid group is probably a tethyan relict with its least derived species living in the eastern North Atlantic Ocean and the Mediterranean Sea; that the majority of species in the *Gammarella* clade are confined to the western Pacific Ocean; and that the *Nuuanu* clade is the most widespread and diverse part of the gammarellid group, occurring throughout the Indo West Pacific, and the Caribbean and Mediterranean Seas.

INTRODUCTION

Species in the gammarellid group are distinctive amphipods infrequently reported from disjunct localities in tropical and warm temperate parts of the world. The only areas where more than one species is known are Australia (J.L. Barnard, 1974), the Caribbean Sea (Ortiz, 1977; McKinney and Barnard, 1977; Vonk, 1989) and the Mediterranean Sea (Karaman, 1982; Marti and Villora-Moreno, 1995). Gammarellids have been considered by Barnard and Barnard (1983) to form their own group (the gammarellid group) within the Melitidae (*sensu lato*). The gammarellid group is currently known from the eastern North Atlantic, the Mediterranean Sea, Madagascar, southern Australia, southern New Zealand, southern Japan, Hawaii and the Caribbean Sea. This is the first record of the genus from the Andaman Sea and from the south-east Asian area. Species almost certainly await discovery in areas such as the Red Sea, eastern Africa, India, northern Australia, northern New Zealand, New Caledonia, the South China Sea and western Central America.

There have been as many as seven generic names proposed in the gammarellid group. At the moment two genera, *Gammarella* and *Tabatzius*, and 14 species are recognised. In this paper we redefine *Gammarella*, re-establish *Nuuanu*, synonymise *Tabatzius* with *Nuuanu*, describe one new species (*Nuuanu kata*), and present evidence which suggests that the amphipod reported from Madagascar as *N. amikai* by Ledoyer (1979) is probably an undescribed species.

The taxonomic description and the phylogenetic matrix presented in this paper was generated from a DELTA (Dallwitz *et al.*, 1993) database of world gammarellid species. Material used in this study is lodged in the Reference Collection of the Phuket Marine Biological Centre (PMBC), Thailand. The following abbreviations are used on the plates: **A**, antenna; **EP**, epimeron; **G**, gnathopod; **H**, head; **MD**, mandible; **MP**, maxilliped; **MX**, maxilla; **P**, pereopod; **T**, telson; **U**, uropod; **UR**, urosomite; **l**, left; **r**, right.

Melitidae Bousfield

Gammarellid group – New Generic Classification

The ceradocopsid group and the gammarellid group are the only melitids with short third uropods. But gammarellids have a different head shape and a different basis shape on peraeopods 5 to 7 from ceradocopsids, and gammarellids, unlike ceradocopsids, have small, dorsal robust setae on urosomite 2.

Within the gammarellids Vonk (1989) made a case to re-establish the genus *Nuuanu*. He argued that the differences between species such as *G. fucicola* and *G. amikai* were so great that the *Gammarella* concept had become unworkable. Marti and Villora-Moreno (1995) described *G. garciai*, a species they considered to show intermediate characters between *Gammarella*, *Cottesloe* and *Nuuanu*. They argued that this species made these generic divisions doubtful and that all species belonged in *Gammarella*. Based on the cladogram presented here *Gammarella* Bate, 1857, includes its type species plus the species in the *Cottesloe* J.L. Barnard, 1974, concept, but *Nuuanu* J.L. Barnard, 1970 forms a separate clade. In this case *Gammarella* is defined by the dorsal keel on urosomite 1 and contains four species. The more diverse and highly derived genus, *Nuuanu*, is defined by small body size, poorly developed eyes and a 3-4 articulate accessory flagellum, and contains ten species.

Gammarella Bate

Pherusa Leach, 1814: 432 (homonym, Polychaeta) (*Pherusa fucicola* Leach, 1814, monotypy).

Gammarella Bate, 1857: 143 (*Gammarella orchestiformis* Bate, 1857, monotypy, = *Pherusa fucicola* Leach, 1814).– Stebbing, 1906: 449.– Karaman and Barnard, 1979: 155 (in part).– Barnard and Barnard, 1983: 637 (in part).

Pherusana J.L. Barnard, 1964: 62, (new name for *Pherusa*, same type species).

Cottesloe J.L. Barnard, 1974: 27 (*Cottesloe berringar* J.L. Barnard, 1974, original designation).

Diagnosis

Body large, more than 9 mm long. *Head* with anteroventral margin notched; eyes well developed; ommatidia compacted. *Antenna 1*: accessory flagellum more than 4-articulate. *Antenna 2*: peduncular article 2 not dorsally produced. *Gnathopods 1 and 2* subchelate, dissimilar size and shape. *Gnathopod 1* with merus with subquadrate anteroventral corner. *Pereopod 7* longer than pereopod 5; basis expanded, plate-like with minutely crenulate posterior margin. Pleonites 1-2 with smooth or carinate dorsal margin. Epimeron 1 with rounded anteroventral corner or produced. *Urosomite 1* with dorsal keel. *Uropod 1* peduncle with or without basofacial seta. *Uropod 3* parviramous, with outer ramus short and inner ramus small to minute, always less than half length of outer ramus; outer ramus 2-articulate, article 2 short. *Telson* laminar, deeply cleft, broader than long.

Species Composition

Gammarella contains four species: *G. berringar* (J.L. Barnard, 1974); *G. cyclodactyla* (Hirayama, 1978); *G. fucicola* Bate, 1857; *G. hybophora* Lowry and Fenwick, 1983.

Remarks

Gammarella as defined here is a relatively unspecialised genus which differs from *Nuuanu* in its large body size, well-developed eyes and keel on urosomite 1. Aside from the apomorphic

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characters which define the gammarellid group, species of *Gammarella* have almost none of the apomorphies which occur in *Nuuanu*. Two species in each genus have elongate third mandibular palp articles and *N. curvata* has an acutely produced anteroventral corner on epimeron 1, an apomorphic character which occurs in three of the four species of *Gammarella*.

Distribution

North-eastern Atlantic Ocean; Mediterranean Sea; South-western Australia; southern New Zealand; southern Japan.

Nuuanu J.L. Barnard

Nuuanu J.L. Barnard, 1970: 166 (*Nuuanu amikai* J.L. Barnard, 1970, original designation).

Gammarella.– Karaman and Barnard, 1979: 155 (in part).– Barnard and Barnard, 1983: 637 (in part).

Tabatzius McKinney and Barnard, 1977 (*Tabatzius copillius* McKinney and Barnard, 1977, original designation, = *Nuuanu muelleri* Ortiz, 1976). – Barnard and Barnard, 1983: 639.

Valettiella Griffiths, 1977: 116 (*Valettiella castellana* Griffiths, 1977).

Diagnosis

Body small, less than 6 mm long. *Head* with anteroventral margin notched; eyes poorly developed, ommatidia separated. *Antenna 1*: accessory flagellum 3-articulate or less. *Antenna 2*: peduncular article 2 dorsally produced. *Gnathopods 1 and 2* subchelate, dissimilar size and shape. *Gnathopod 1* with merus with subacutely produced anteroventral corner. *Pereopod 7* longer than pereopod 5; basis expanded, plate-like with crenulate posterior margin. Pleonites 1-2 with dorsal spines. Epimeron 1 with rounded anteroventral corner. *Urosomite 1* without dorsal keel. *Uropod 1* peduncle with or without basofacial seta. *Uropod 3* parviramous, with outer ramus short and inner ramus small to minute, always less than half length of outer ramus; outer ramus 2-articulate, article 2 short. *Telson* deeply cleft, as long as broad.

Species Composition

Nuuanu contains ten species: *N. amikai* J.L. Barnard, 1970; *N. castellana* (Griffiths, 1977); *N. curvata* Vonk, 1989; *N. garciai* (Marti and Villora-Moreno, 1995); *N. kata* sp. nov.; *N. merringannee* J.L. Barnard, 1974; *N. mokari* J.L. Barnard, 1974; *N. muelleri* Ortiz, 1976; *N. numbadi* J.L. Barnard, 1974; *N. utwe* (Myers, 1995).

Remarks

Karaman and Barnard (1979) synonymised *Gammarella*, *Cottesloe* and *Nuuanu* because, despite the morphological diversity within these three genera, they concluded that 'no discontinuity exits' between them. At the same time they considered elevating *N. mokari* to generic status because of its peculiarly shortened coxa 3 and they retained *Tabatzius* 'without strong conviction as it may also be found to have intergradational relatives'.

More species have been described since Karaman and Barnard (1979) and the discontinuity that evaded them is now apparent. Even the intergradational relative they predicted for *Tabatzius*, has been described by Vonk (1989). Consequently *Nuuanu* is re-established and *Tabatzius* which was originally established on an autapomorphic character (styliform maxilla 1) is synonymised with *Nuuanu*.

J.L. Barnard (1970) described *N. amikai* from the Hawaiian Islands. Later Ledoyer (1979) reported *N. amikai* from Madagascar. There is no doubt that these populations are extremely similar. The only illustrated differences between them are: in the Hawaiian population the lateral cephalic lobe is more quadrate; the distoventral corner of peduncular article 1 of antenna 1 is subacute; on antenna 2 the dorsodistal corner of peduncular article 2 is not produced; and palp article 3 of the maxilliped is apparently much broader. The fact that J.L. Barnard (1970) had no females and Ledoyer (1979) had no males is unfortunate. A comparison of male second gnathopods would be helpful. Based on the apparent morphological differences between the Hawaiian and Madagascaran populations and the large distance separating them we think that the Madagascar population is most likely an undescribed species,

but until more material is available from both areas the problem must remain unresolved.

Distribution

Southern Australia; south-western Africa; Andaman Sea; Micronesia; Hawaii; Caribbean Sea.

Nuuanu kata sp. nov.
(Figs 1–3)

Material examined

Holotype: PMBC 14897, female, 3.8 mm, BIO-SHELF St. PB 7, 07º44´N 098º41´E, Ockelmann sledge, 32 m, coll. S. Bussarawit and C. Aungtonya, 02.02.1998.

Diagnosis

Antenna 1, peduncular article 1 subequal to article 2; article 2 not geniculate. *Pereopods 5-7*, basis with posterior margin strongly crenate. *Pleonites 1–2* each with small dorsodistal spine. Uropod 3 inner ramus minute.

Description

Based on holotype female, 3.8 mm. ***Head***: with obtuse lateral cephalic lobes, anteroventrally excavate and deeply notched; eyes apparently absent. *Antenna 1* longer than antenna 2; peduncular article 1 subequal in length to article 2, with 2 small setae along distoventral margin; article 2 not geniculate; accessory flagellum 3-articulate; primary flagellum 16-articulate. *Antenna 2* with gland cone well developed; peduncle longer than flagellum; flagellum 9-articulate. *Mandible* with well developed incisor, about 6 teeth; lacinia mobilis large, about 4 teeth; accessory seta row with about 7 long slender plumose setae; molar columnar, triturative; palp article 1 a little more than 2 x width; article 3 about 0.6 x length of article 2; distally falcate with about 12 slender setae distally. *Lower lip*. Outer plates with strong apical setae; inner plates apparently present, fleshy; mandibular processes short. *Maxilla 1*. Inner plate subtriangular with about 13 pappose setae along medial margin; outer plate with 10 setal-teeth; palp well developed, 2-articulate with 7 apical robust setae and 3 subapical slender setae. Maxilla 2. Medial

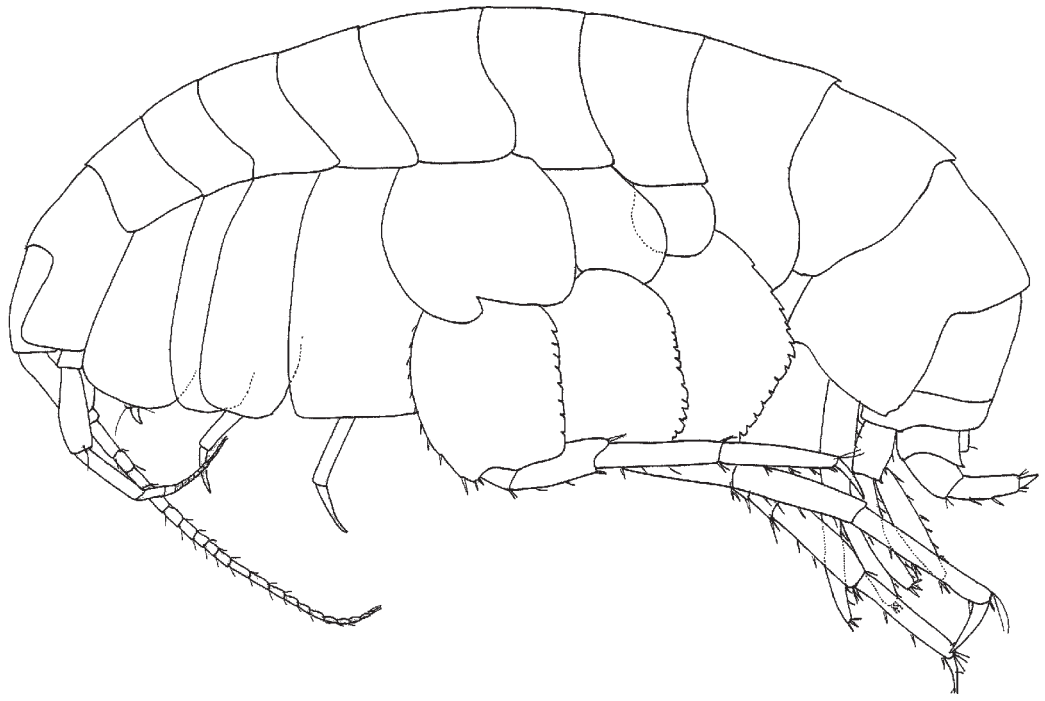

Figure 1 *Nuuanu kata* sp. nov. Female, 3.8 mm, PMBC 14897, Phuket Island, Andaman Sea.

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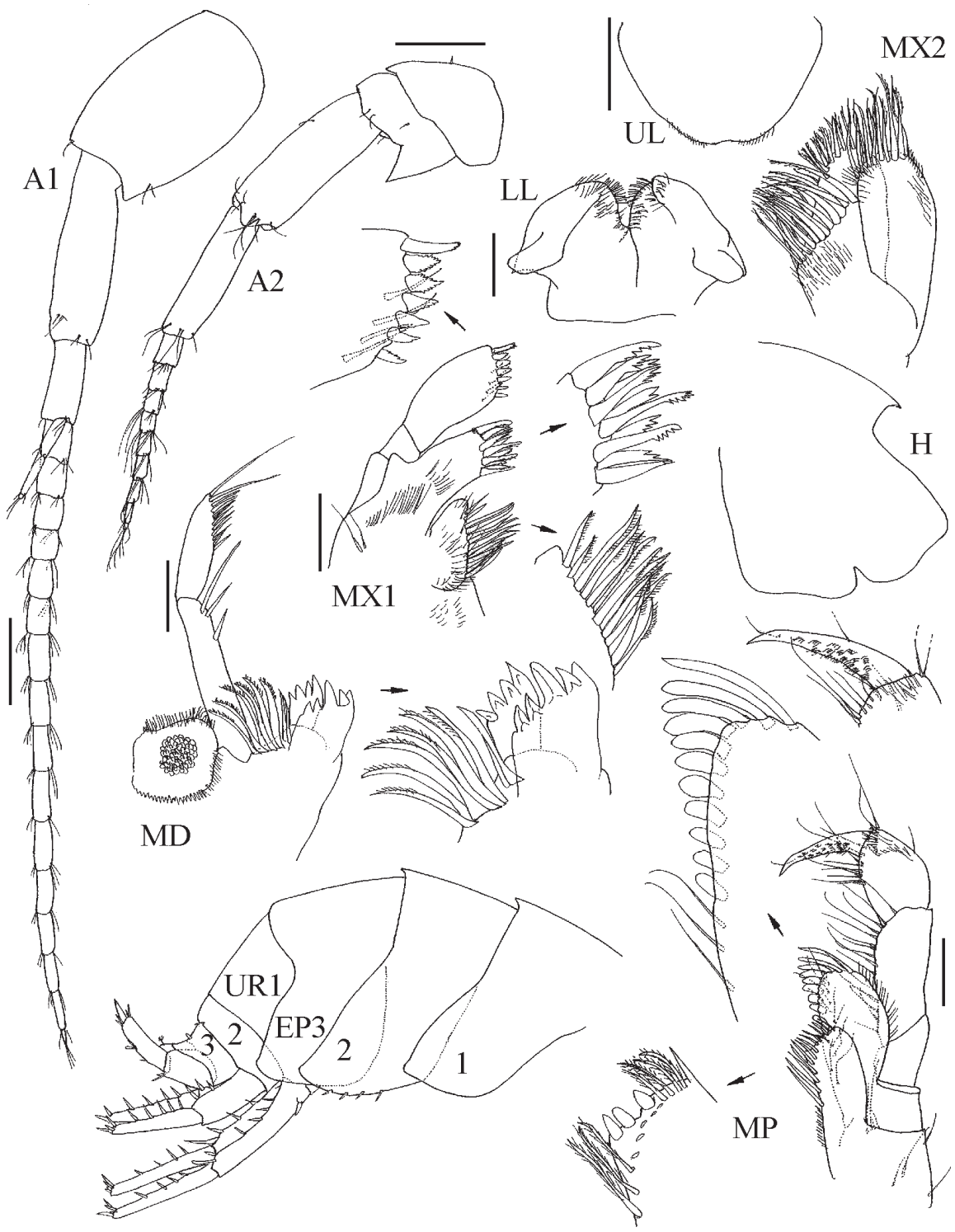

Figure 2 *Nuuanu kata* sp. nov. Female, 3.8 mm; PMBC 14897, Phuket Island, Andaman Sea. Scales represent 0.1 mm.

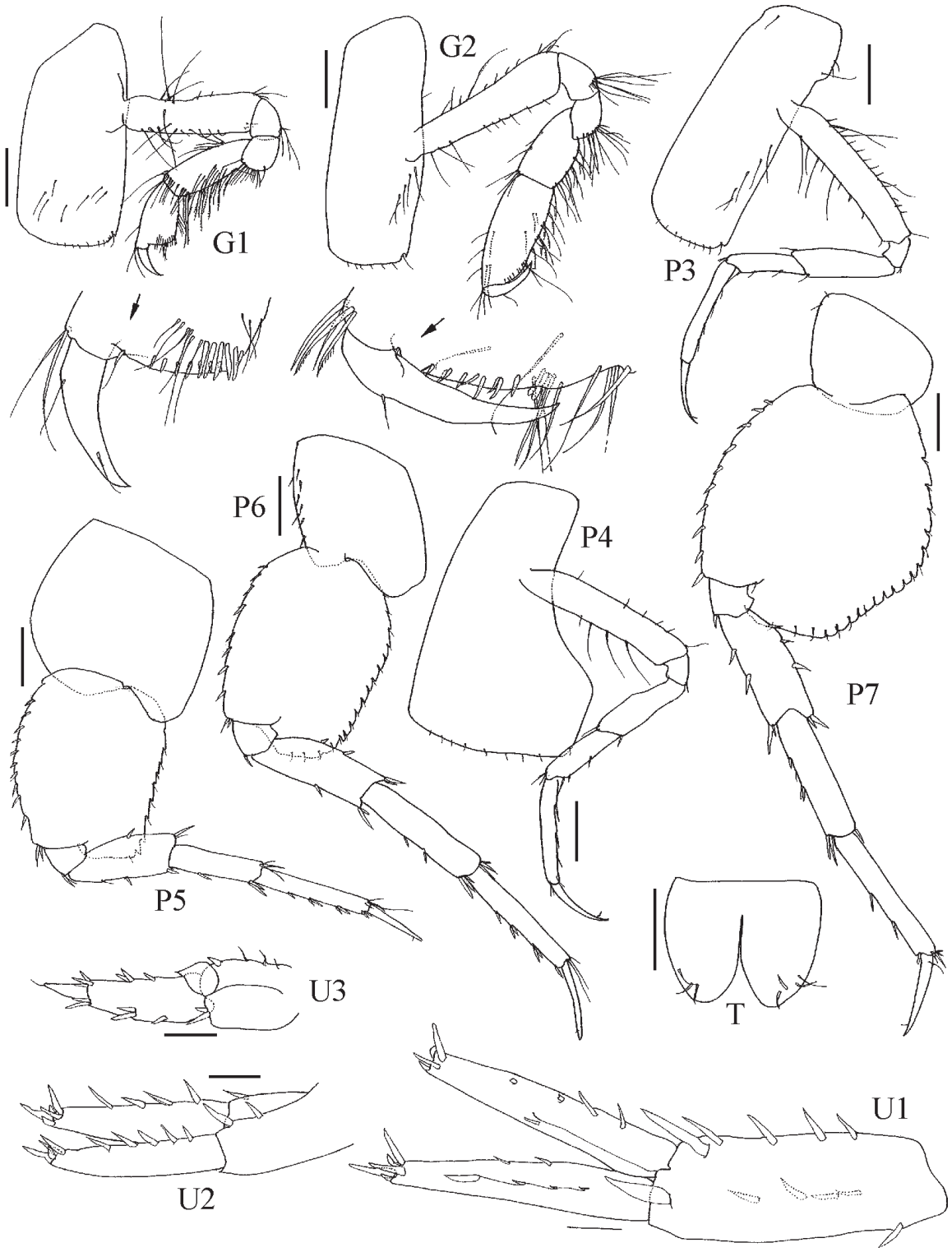

Figure 3 *Nuuanu kata* sp. nov. Female, 3.8 mm; PMBC 14897, Phuket Island, Andaman Sea. Scales for U1–3, T represent 0.1 mm, remainder represent 0.2 mm.

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margin of inner plate lined with setae; oblique setal row present. *Maxilliped*. Inner plate with 3 apical nodular setae and a row of about 15 long slender pappose setae; outer plate reaching about halfway along palp article 2, with about 11 strong medial and apical robust setae; palp with 4 articles, article 2 longest; dense short patch of setae covering distolateral third of article 3; dactylus long and slender.

Pereon: *Gnathopod 1* subchelate; coxa subrectangular, posteroventral corner with small notch; carpus long, length about 2.8 x width and about 1.5 x length of propodus, with pappose setae along posterior margin; propodus length about 2 x width, palm transverse with about 9 stout robust setae along margin; dactylus well developed, fitting palm. *Gnathopod 2* subchelate; slightly larger than gnathopod 1; coxa subrectangular with small posteroventral notch; basis long, slender; carpus without posterior lobe, length about 1.9 x width, about 0.75 x length of propodus; propodus subovate, long, length about 2.5 x width; palm acute, slightly convex with about 6 stout robust setae along margin and 2 robust setae defining palm, with about 5 long robust setae along posterior margin. *Pereopod 3* slender; coxa long, subrectangular with posteroventral notch; merus slightly shorter than propodus, margins subparallel; carpus about 0.6 x length of propodus; propodus slender with 4 slender setae along posterior margin; dactylus long, slender. Pereopod 4 slender; coxa with well developed posteroventral lobe; remainder of leg very similar to that of pereopod 3. *Pereopod 5* long slender; coxa equilobate ventrally; basis subrectangular with strong robust setae along anterior margin and a strongly crenate posterior margin; posteroventral corner narrowly rounded; merus slightly expanded posterodistally; carpus and propodus liners; dactylus long, slender. *Pereopod 6* long, slender; coxa with well developed posteroventral lobe; remainder of leg very similar to that of pereopod 5. *Pereopod 7* long, slender; anterior margin of basis with strong robust setae, posterior margin strongly crenate, rounded posterodorsally and slightly excavate posteroventrally; remainder of leg very similar to that of pereopod 6.

Pleon: *Pleonites 1 and 2* with small posterodorsal spines. *Epimeron 1* broadly rounded anteroventrally. *Epimeron 2* with 4 small setae along ventral margin and a slightly produced, rounded posteroventral corner. *Epimeron 3* without setae along ventral margin, posteroventral corner slightly produced and narrowly rounded. *Urosomite 1* length about 3.5 x that of urosomite 2. *Urosomites 2 and 3* each with a small slender setae on each side. *Uropod 1* peduncle slightly longer than rami with well developed basofacial seta, dorsal margins spinous. *Uropod 2* slightly shorter than uropod 1; peduncle and rami dorsally spinous. *Uropod 3* biramous; peduncle shorter than outer ramus; inner ramus scale-like, without distal setae; outer ramus about 4 x length of inner ramus and twice length of peduncle, 2-articulate, article 2 short. Telson deeply cleft, broader than long with a group of about 4 distal setae on each lobe.

Etymology

Named for Kata Beach, south-western Phuket Island.

Remarks

It is unfortunate that no male specimens of this species were discovered. This means that the sexually dimorphic characteristics of gnathopod 2 cannot be documented. Nonetheless the female can be adequately distinguished from other known species in the genus by a combination of characters. *Nuuanu kata* is most similar to *N. merringannee* from southern Australia, but is distinguished from that species by its slender pereopods with particularly long, slender dactyli and by the inner ramus of uropod 3, which is very short in relation to the outer ramus.

Key to Species of the Gammarellid Group

1. Urosomite 1 with keel *2*
— Urosomite 1 without keel 4
2. Urosomite 1 keel low and subrectangular.....*G. fucicola*
— Urosomite 1 keel a large recurved dorsal spine .....*G. hybophora*
— Urosomite 1 keel a rounded boss *3*
3. Antenna 1 much longer than antenna 2. Epimeron 1 with acutely produced anteroventral corner .....*G. cyclodactyla*
— Antenna 1 about as long as antenna 2. Epimeron 1 with a large anteroventrally produced spine .....*G. berringar*
4. Pleonites 1–2 each with a small dorsodistal spine 5
— Pleonites 1–2 dorsally smooth 9
5. Antenna 1 geniculate between peduncular articles 1 and 2….....6
— Antenna 1 not geniculate.....8
6. Antenna 1 much longer than antenna 2 ….....7
— Antenna 1 subequal in length to antenna 2 ….....*N. castellana*
7. Lateral cephalic lobe triangular ….....*N. numbadi*
— Lateral cephalic lobe subquadrate ventrally ….....*N. amikai*
8. Peraeopods 5-7 distal articles slender. Uropod 3, outer ramus longer than peduncle; inner ramus minute, about 0.25 x outer ramus .....*…N. kata*
— Peraeopods 5-7 distal articles broad. Uropod 3, outer ramus as long as peduncle; inner ramus short, about 0.5 x outer ramus .....*N. merringannee*
9. Peraeopods 5-7 basis minutely castellate.....10
— Peraeopods 5-7 basis castellate (at least partially) 12
10. Pereopod 4 coxa posteroventral lobe well developed 11
— Pereopod 4 coxa posteroventral lobe absent .....*N. garciai*
11. Epimeron 1 with a large anteroventrally produced spine .....*N. curvata*
— Epimeron 1 with an anteroventrally rounded corner .....*N. utwe*
12. Head lateral cephalic lobe triangular. Peraeopods 5-6 basis crenulate posteroproximally .....*N. mokari*
— Head lateral cephalic lobe rounded. Peraeopods 5-6 basis crenulate along entire margin .....*…N. muelleri*

PHYLOGENETICS

The gammarellid group is a small generic complex which belongs with those taxa that have a basofacial seta on the peduncle of uropod. These include the bogidielloid, crangonyctoid , hadzioid and some corophioid amphipods. Within this group, gammarellids fit into the broad concept of Melitidae, proposed but not defined, by Bousfield (1973). Later Bousfield (1977) defined the family in very general terms and split it into two 'subfamily units' which he referred to as the *Maera-Elasmopus* complex and the *Melita–Eriopisa* complex. The one character he gave to define these groups was uropod 3 with subequal rami (*Maera–Elasmopus* complex) or uropod 3 with unequal rami (*Melita–Eriopisa* complex). In Table 5 Bousfield (1977) listed the genera included in the Melitidae and in each melitid subgroup. According to this list *Cottesloe* and *Nuuanu* was part of the *Maera-Elasmopus* complex and *Gammarella* was part of the *Melita–Eriopisa* complex. It is unclear in his paper how the Hadziidae and the Melitidae differ.

The gammarellid group was originally proposed (as the *Nuuanu* group) and defined by McKinney and Barnard (1977) to include the genera *Cottesloe* J.L. Barnard, 1974, *Gammarella* Bate, 1857, *Nuuanu* J.L. Barnard, 1970 and *Tabatzius* McKinney and Barnard, 1977. They indicated how

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similar the genera *Gammarella* and *Cottesloe* were and later Karaman and Barnard (1979) synonymised *Gammarella*, *Cottesloe* and *Nuuanu*, leaving only two genera in the group, *Gammarella* and *Tabatzius*.

In Barnard and Barnard (1983) only informal groups within the hadzioid amphipods were recognised. Several groups relevant to this study were distinguished in a key (Barnard and Barnard, 1983: 612). Melitids (*sensu stricto*) and hadziids were separated by the inner lobes of the lower lip which are apparently well developed in melitids and vestigial or absent in hadziids. In the Barnard and Barnard (1983) concept there are more groups within the Melitidae (*sensu lato*). They recognised a ceradocid group, a ceradocopsid group, an eriopisellid group, a gammarellid group, a melitid group and a parapherusid group.

According to Barnard and Barnard (1983) the gammarellid group is most closely related to the ceradocopsid group, the ceradocid group and the Melitid group. Gammarellids differ from all of these groups in the plate-like basis of peraeopods 5 to 7. Neither ceradocopsids nor ceradocids have small, dorsal robust setae on urosomite 2, a character which apparently only gammarellids and melitids (sensu stricto) share. Gammarellids and ceradcopsids both have small third uropods in which the outer ramus is not, or only slightly, longer than the peduncle. Gammarellids are least similar to ceradocids and most similar to melitids (sensu stricto). Gammarellids and melitids both have an anteroventral notch on the side of the head, antenna 1 is longer than antenna 2, gnathopod 1 has a long carpus, gnathopod 2 has a short carpus and large propodus in the male, urosomite 2 has two small, dorsal setae and uropod 3 has a significantly reduced inner lobe. The main difference between them is that melitids always have an elongate outer ramus on uropod 3 and in gammarellids it is relatively short.

Outgroup

McKinney and Barnard (1977) thought that *Ceradocopsis* was a good candidate to share a common ancestor with *Gammarella*. There are many morphological similarities, but ceradocopsids do not have an anteroventral cheek notch. *Elasmopus* also shares many morphological similarities including the cheek notch and a falcate mandibular palp, but the third uropods are different. Neither of these taxa (*Ceradocopsis* or *Elasmopus*) have the twin dorsal robust setae on urosomite 2 shared by gammarellids and melitids (*sensu stricto*). Melitids such as *Desdimelita* or *Megamoera* have many morphological similarities to gammarellids, but all melitids (*sensu stricto*) have a minute inner ramus on uropod 3, an apomorphic character state derived independently of the minute inner ramus found in some gammarellids. This makes them an equivocal outgroup candidate. *Ceradocopsis* appears to be the nearest sister group to the gammarellids and is used here as the outgroup. The only conflicting character is coxa 4 which has no posteroventral lobe in *Ceradocopsis*, a state considered to be apomorphic in the gammarellid group.

Character Description

Thirty-two characters were originally used to describe the morphological diversity of *Gammarella*. All of these characters were used in the original PAUP analyses, but through attrition, caused by high homoplasy values and autapomorphy, the final analyses contained only 17 characters. All 17 characters are described here.

1. Body size
    1. large
    2. small

Marti and Villora-Moreno (1995: Table 2) showed that there are two distinct body sizes among gammarellids, large species with a body length of more than 8 mm and small species, less than 6 mm in length.

2. Head, lateral cephalic lobe (Fig. 4a, 2.1–2.4)
    1. rounded without anteroventral notch
    2. ventrally subquadrate with anteroventral notch
    3. triangular with anteroventral notch
    4. rounded with anteroventral notch

Ceradocopsis has a rounded lateral cephalic lobe, but without a notch. Some ingroup species have a rounded cephalic lobe with a notch. After a number of preliminary analyses where *N. muelleri*

and *N. numbadi* continued to appear as sister taxa within the tree, it became apparent that the rounded lobe with a notch of the ingroup species was derived independently of the outgroup and it was scored as an independently derived state. Species such as *N. castellana* and *N. mokari* have a distinctive triangular cephalic lobe. The most common type of cephalic lobe is the distinctive ventrally subquadrate lobe, such as that of *C. berringar*.

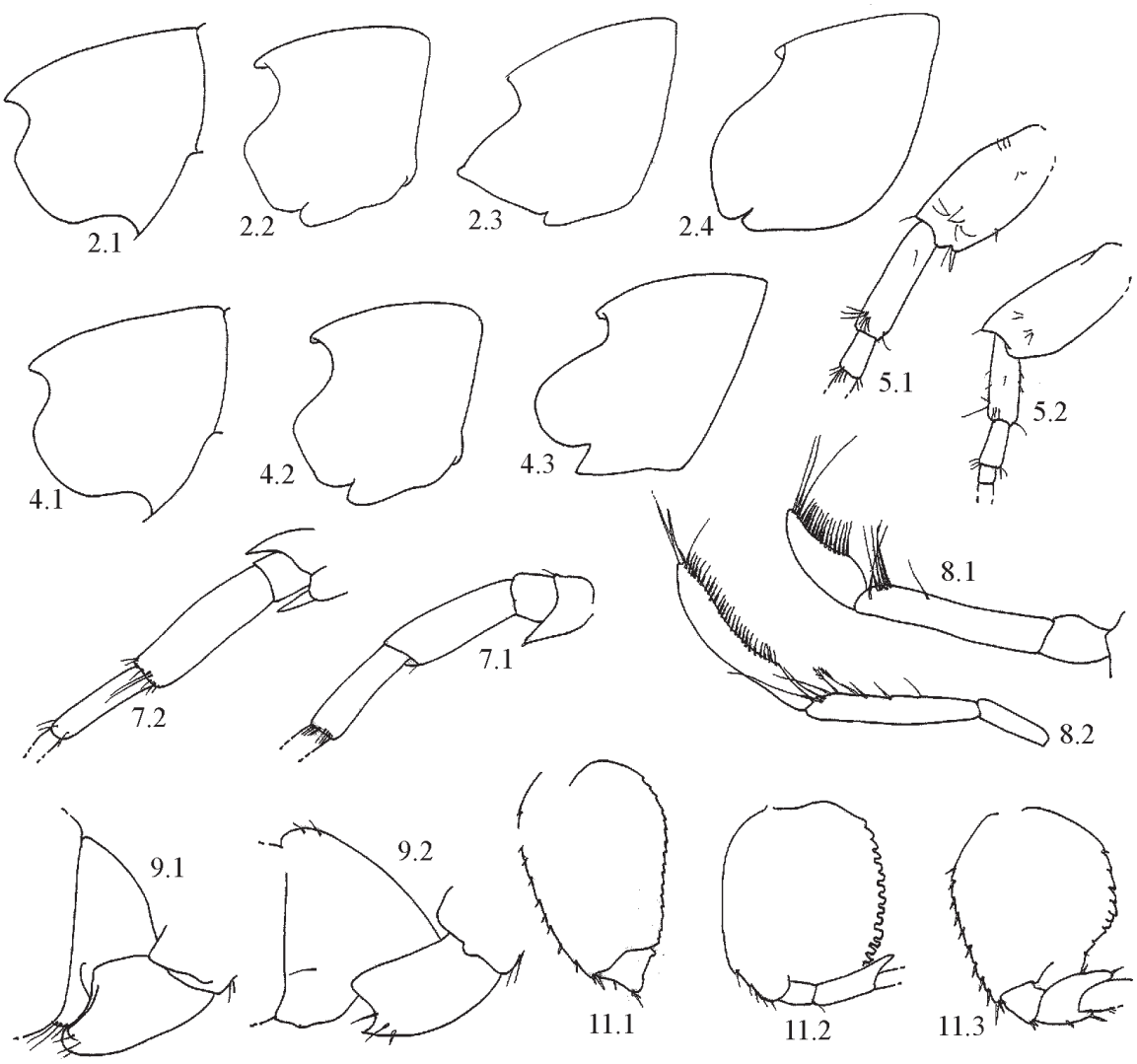

Figure 4a Character states. Head, lateral cephalic lobe: rounded without an anteroventral slit (2.1); triangular with anteroventral slit (2.2); ventrally subquadrate with anteroventral slit (2.3); rounded with an anteroventral slit (2.4). Head, lateral cephalic lobe: without anteroventral notch or slit (4.1); with anteroventral notch and slit (4.2); with anteroventral notch (4.3). Antenna 1, peduncular article 2: not geniculate (5.1); geniculate with article 1 (5.2). Antenna 2, peduncular article 2: not produced dorsodistally (7.1); produced dorsodistally (7.2). Mandible palp article 3: shorter than article 2 (8.1); subequal in length to article 2 (8.2). Gnathopod 2 merus: subquadrate to rounded distoventrally (9.1); acutely produced distoventrally (9.2). Pereopods 5–6, basis: posterior margin minutely crenulate (11.1); posterior margin crenulate (11.2); posterior margin partially crenulate (11.3).

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3. Head with eyes
   1. well developed
   2. ovate, ommatidia compacted or eyes poorly developed
   3. ommatidia separate or eyes absent

All large species have well developed eyes with compacted ommatidia, except possibly *G. hybophora*. All small species (except *N. utwe*) have poorly developed eyes with separated ommatidia.

4. Head, lateral cephalic lobe (Fig. 4a, 4.1–4.3)
   1. without anteroventral notch or slit
   2. with anteroventral notch and slit
   3. with anteroventral notch

5. Antenna 1, peduncular article 2 (Fig. 4a, 5.1–5.2)
   1. not geniculate
   2. geniculate with article 1

In *Ceradocopsis* and many gammarellids antenna 1 is not geniculate. In some species of *Nuuanu* antenna 1 is distinctly geniculate. It is possible that in some preserved material one cannot determine whether geniculation occurs. These species have been scored as not geniculate.

6. Antenna 1, accessory flagellum
   1. more than 4 articles
   2. less than 4 articles

Marti and Villora-Moreno (1995: Table 2) showed that large-sized gammarellids have an accessory flagellum of more than 4 articles and small-sized species always have 4 articles or less.

7. Antenna 2, peduncular article 2 (Fig. 4a, 7.1–7.2)
   1. not produced dorsodistally
   2. produced dorsodistally

In *Ceradocopsis* there is usually no dorsal development on article 2 of antenna 2. In some species of the gammarellid group a dorsodistal projection occurs on article 2 of antenna 2. This projection is usually distinctive, but occasionally it is weakly developed such as in *N. merringannee*.

8. Mandible palp article 3 (Fig. 4a, 8.1–8.2)
   1. shorter than article 2
   2. subequal in length to article 2

The third article of the mandibular palp is shorter than article 2 in *Ceradocopsis* and in most species of the gammarellid group, but in two species from Australia, *C. berringar* and *N. merringannee*, the third article is as long as the second.

9. Gnathopod 2 merus (Fig. 4a, 9.1-9.2)
   1. subquadrate to rounded distoventrally
   2. acutely produced distoventrally

In *Ceradocopsis* and most species of the gammarellid group the distoventral corner of the gnathopod 2 merus is rounded or subquadrate. In some highly derived species of the gammarellid group it forms an acutely produced spine, well developed in *N. numbadi* and weakly developed in *N. muelleri*.

10. Pereopod 4 coxa posteroventral lobe
   1. well developed, subquadrate or rounded
   2. slightly developed, acute
   3. absent

In *Ceradocopsis* the posteroventral lobe is absent, but this is considered to be a derived condition in the outgroup. In most species the posteroventral lobe is well developed. In three of the four species of *Gammarella* the lobe is distinctly pointed.

11. Pereopods 5–6, basis (Fig. 4a, 11.1–11.3)
   1. posterior margin minutely crenulate
   2. posterior margin crenulate
   3. posterior margin partially crenulate

In *Ceradocopsis* and some species within the gammarellid group the posterior margin of the basis of peraeopods 5 and 6 are minutely crenulate. In other species the margin is distinctly crenulate and in one species (*N. mokari*) it is only crenulate along the distal part of the margin. Because this state is autapomorphic it was combined with crenulate margins for this analysis.

12. Pleonites 1–2 (Fig. 4b, 12.1–12.3)
   1. smooth
   2. each carinate
   3. each with small dorsodistal spine

In *Ceradocopsis* pleonites 1 and 2 are dorsally smooth. In some species of the gammarellid group

distinctive dorsodistal spines develop and in at least two species (*C. berringar* and *C. hybophora*) a weak carina develops.

13. Epimeron 1 (Fig. 4b, 13.1–13.3)
    1. with rounded anteroventral corner
    2. with acutely produced anteroventral corner
    3. with large anteroventral spine

In *Ceradocopsis* and most species of the gammarellid group the anteroventral corner of epimeron 1 is rounded. In *Gamarella* the corner is produced.

14. Urosomite 1 (Fig. 4b, 14.1–14.3)
    1.without dorsal keel
    2.with dorsal keel

In *Ceradocopsis* and most species of the gammarellid group the dorsum of urosomite 1 is smooth, but in species of *Gammarella* a keel is present.

15. Uropod 3, inner ramus (Fig. 4b, 15.1–15.2)
    1. short, half to nearly as long as outer ramus
    2. minute, less than 1/3 length of outer ramus

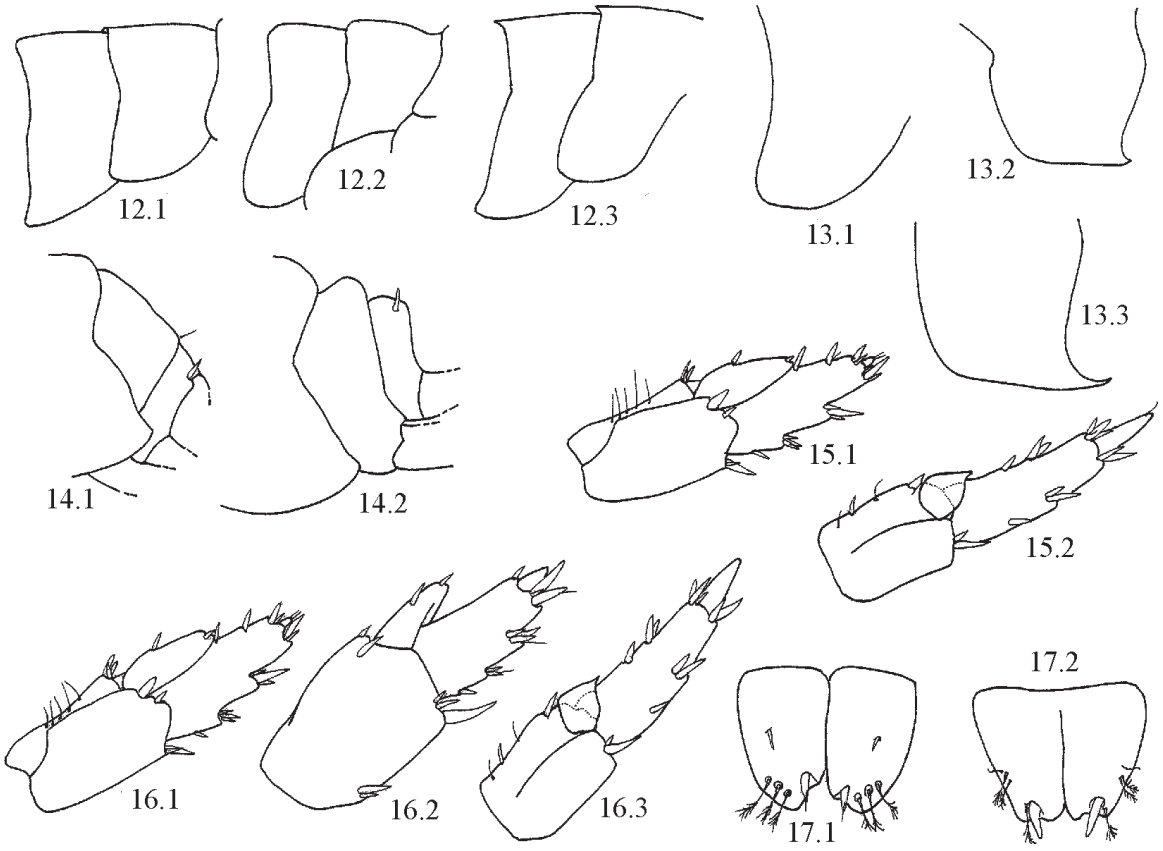

Figure 4b Character states. Pleonites 1–2: dorsally smooth (12.1); each carinate dorsally(12.2); each with small dorsodistal spine (12.3). Epimeron 1: with rounded anteroventral corner (13.1); with acutely produced anteroventral corner (13.2); with large anteroventral spine (13.3). Urosomite 1: without dorsal keel (14.1); with dorsal keel (14.2). Uropod 3 biramous, inner ramus: long (length 4 to 2 x breadth) (15.1); short (length 1.75 to 1 x breadth) (15.2). Uropod 3, outer ramus: subequal in length to peduncle (16.1); shorter than (up to 0.9 x) peduncle (16.2); longer than (more than 1.1 x) peduncle (16.3). Telson cleft: as long as broad (17.1); broader than long (17.2).

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16. Uropod 3, outer ramus
    1.subequal in length to peduncle
    2.shorter <0.9 x> than peduncle
    3.longer <1.1 x> than peduncle

In *Ceradocopsis* and a number of species in the gammarellid group the outer ramus of uropod 3 is subequal in length to the peduncle. Several species have the outer ramus shorter than the peduncle and several species have it longer.

17. Telson length to breadth (Fig. 4b, 17.1–17.2)
    1. as long as broad
    2. broader than long

In the outgroup the telson is broader than long and this is the case for many species of the gammarellid group, but among some taxa the telson is lengthened and becomes at least as long as broad.

RESULTS AND DISCUSSION

The analyses were performed using DELTA (Dallwitz *et al.*, 1993), PAUP (Swofford, 1998) and MacClade (Maddison and Maddison, 1999). All species currently considered in the gammarellid group were used in the analyses. Only females were analysed. Where only males are known the species was used in the analysis, but the sexually dimorphic characters were considered to be unknown. Using *Ceradocopsis* as an outgroup, a heuristic search with the branch and bound option, nine trees were produced (tree length 36, consistency index 0.63). One tree (figure 5) is presented here.

The gammarellid group is defined by the distinctive subquadrate cephalic lobes, an

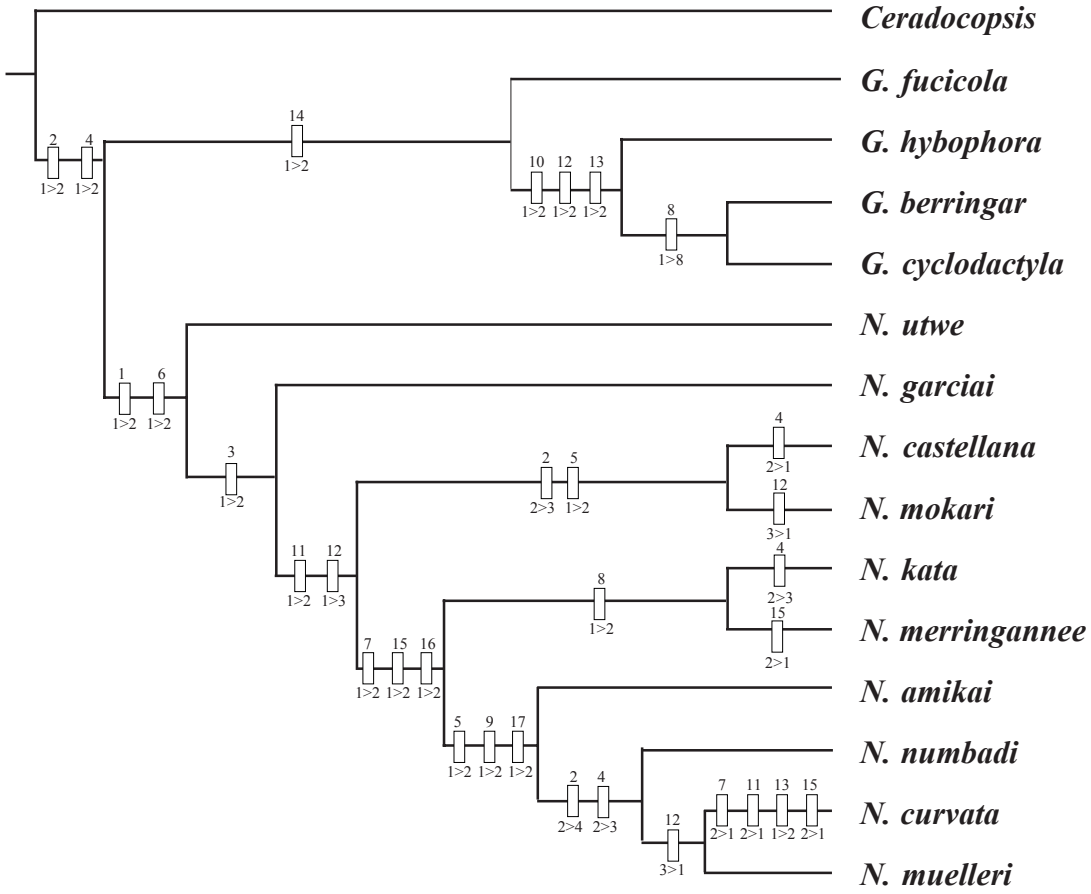

Figure 5 Cladogram for *Gammarella* group.

anteroventral notch and slit and by the plate-like basis on peraeopods 5 to 7. The base of the cladogram presents a dilemma because, without changing the tree length, *G. fucicola* will align with the '*Cottesloe*' clade or align with the '*Nuuanu'* clade. If it sits in the '*Cottesloe*' clade then two genera (*Gammarella* and *Nuuanu*) occur. If it sits in the '*Nuuanu*' clade then a different set of genera (*Gammarella* and *Cottesloe*) occur. If *G. fucicola* sits with the '*Cottesloe'* clade then the keel on urosomite 1 becomes the defining character for *Gammarella*. If *G. fucicola* sits with the '*Nuuanu*' clade then the keel becomes an independently derived character in both clades and the '*Nuuanu*' clade has one species that is too large and retains well developed eyes. If *G. fucicola* sat as a paraphyletic taxon outside both clades, then '*Cottesloe*' and *Nuuanu* would be more strongly defined, but this does not happen because of the keel on urosomite 1. In this case *G. fucicola* is placed in the '*Cottesloe*' clade in order to maintain the keel as a true synapomorphy.

There are then two distinct clades in the gammarellid group. One clade contains the large-bodied gammarellids with well developed eyes and carinate pleonites (*Gammarella*) and the other clade contains small species with poorly developed eyes and smooth or spinose pleonites (*Nuuanu*). Marti and Villora-Moreno (1995) argued that *N. garciai* was an intermediate species between *Gammarella* and *Nuuanu*. In our analysis *N. garciai* and *N. utwe* are distinct, although unspecialised members of the *Nuuanu* clade. *Nuuanu utwe* is confusing because it has the plesiomorphic, well developed eyes of a *Gammarella*, but it has a small body and reduced accessory flagellum, which aligns it with the *Nuuanu* clade. *Nuuanu garciai* has a small body, poorly developed eyes and reduced accessory flagellum, all of the synapomorphies which define the *Nuuanu* clade, but these are the only synapomophies which it shares with the remaining species in the clade.

The *Gammarella* clade is defined by a keel on urosomite 1. This is the only apomorphy which *G. fucicola* shares with the group. The western Pacific species have developed a number of synapomorphies. All three species have: a triangular posteroventral lobe on coxa 4; the anteroventral corner of epimeron 1 modified into an acute spine; and a dorsal carina on each pleonite. *Gammarella berringar* and *G. cyclodactyla* both have an elongate third article on the mandibular palp, a homoplastic character which also occurs in the *Nuuanu* clade.

The *Nuuanu* clade is defined by small body size, poorly developed eyes (except for *N. utwe*) and four or less articles (usually three) in the accessory flagellum. It could be argued that if an animal is going to become anchialine, marine interstitial, or an invertebrate associate it is likely to develop the above characters and therefore such characters are likely to be homoplastic. However, at this stage, the evidence does not support this conclusion. *Nuuanu utwe* and *N. garciai* are the least specialised members of the clade. More specialised members of the clade develop geniculate first antennae, dorsally produced second articles on antennae 2, strongly crenulate basis on peraeopods 5 to 7 and dorsal spines on pleonites 1 and 2. *Nuuanu castellata* and *N. mokari* have distinctive triangular cephalic lobes and *Nuuanu numbadi*, *N. curvata* and *N. muelleri* have distinctive rounded cephalic lobes. These three species plus *N. amikai* share a geniculate antenna 1 and acutely produced anteroventral corner on the merus of gnathopod 2.

The closest living relatives to the gammarellids appear to be cool-water ceradocopsids. The original gammarellids may have been temperate-water benthic species, probably unspecialised deposit-feeders. Among extant representatives there is a group of well defined large-bodied species (*Gammarella* clade) with the least specialised member living in the western North Atlantic and the Mediterranean Sea and more specialised species living in the temperate western Pacific (Japan, New Zealand and Australia), possibly as surface deposit feeders. A second group of well defined small-bodied species (*Nuuanu* clade) has a wider distribution and appears to live in a variety of habitats (anchialine, marine interstitial, invertebrate associates). The least specialised members of this group occur in the Mediterranean and in the tropical western Pacific. Moderately derived species occur in south-western Africa and southern Australia and

the most highly derived species occur in Madagascar, Australia and the Caribbean Sea. The temperate-water Australian species therfore appear in each part of the clade: *N. mokari* appears as a sister species to the temperate southern Africa species *N. castellana*; *N. merrigannee* appears as a sister species to the tropical Andaman Sea species *N. kata* and *N. numbadi* sits between the tropical Hawaiian species, *N. amikai* and the two tropical Caribbean species *N. curvata* and *N. muelleri*.

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