A new interstitial species of *Gammarella* (Amphipoda, Gammaridea) from the western Mediterranean Sea

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Abstract

A new species of *Gammarella* Bate, 1857 is described from shallow water, inhabiting the interstitial system in soft bottoms of the Chafarinas Archipelago (western Mediterranean, N. Africa). The relationships of *Gammarella* with the genera *Nuuanu* and *Cottesloe* are briefly discussed. Numerical taxonomic methods are utilized to differentiate between the morphologically related species and the intermediate species. In a table the principal differentiating characters of *Gammarella* species are presented. *Gammarella garciai* n. sp. is characterized by its intermediate position between *Gammarella*, *Nuuanu* and *Cottesloe*, showing an intergradation of characters. *Gammarella garciai* n. sp. and *G. merrigannee* show ecologically intermediate characters between the larger species, probably nestling, with preference for lightless environments, and the smaller species. The group of smaller species, with eyes poorly developed or absent, show interstitial preferences. A map of the world distribution and a key to the 11 known *Gammarella* species are presented.

Resumen

Se describe una nueva especie de *Gammarella* Bate, 1857 procedente del ambiente intersticial de los fondos de sustratos sueltos poco profundos del Archipiélago de Chafarinas (Mediterráneo occidental, N. Africa). Se discuten brevemente las relaciones de *Gammarella* con los géneros *Nuuanu* y *Cottesloe*. A partir de métodos de taxonomía numérica se distinguen las especies morfológicamente afines de las especies intermedias. En una tabla se presentan los principales caracteres disitintivos de las especies del género *Gammarella*. *Gammarella garciai* n. sp. se caracteriza por su posición intermedia entre *Gammarella*, *Nuuanu* y *Cottesloe*, mostrando una intergradación de caracteres. *Gammarella garciai* n. sp. y *G. merrigannee* presentan caracteres ecológicos intermedios entre las especies de mayor tamaño, probablemente anidadoras y con preferencia por ambientes poco iluminados, y las especies pequeñas. Estas últimas tienen los ojos poco desarrollados o ausentes y muestran hábitos intersticiales. Se presen-

tan una clave y un mapa con la distribución mundial de las 11 especies conocidas de *Gammarella*.

Introduction

The taxonomic position of the genus *Gammarella* Bate, 1857 within the gammaridean Amphipoda is difficult to establish. The family Gammaridae (sensu lato) was split into a number of superfamilies (Bousfield, 1973, 1977; Barnard, 1976) and the only species known for the genus, *Gammarella fucicola* (Leach, 1814), was included in the family Melitidae. When Karaman & Barnard (1979) started their revision, *Gammarella* was placed in "other Gammaridae". Later, Barnard & Barnard (1983: 141) established the term "Nuuanuids" to group the related genera *Gammarella* and *Tabatzius* McKinney & Barnard, 1977. In the same work (Barnard & Barnard, op.cit.: 636) both genera were also called "Gammarellids". Finally, Barnard & Karaman (1987) considered the "Nuuanuids" as a family group, but they delayed the family name because "there is already a family Gammarellidae Bousfield (1977), based on the unrelated genus *Gammarellus*" (op.cit.: 867).

The only species originally assigned to the genus was *Gammarella hybophora* Lowry & Fenwick, 1983. The rest of the species, including the type-species *G. fucicola*, have been described under actually synonymous genera, such as *Pherusana* J.L. Barnard, 1964; *Nuuanu* J.L. Barnard, 1970; *Cottesloe* J.L. Barnard, 1974; and *Valettiella* Griffiths,

Fig. 1. *Gammarella garciai* n. sp. ♀: lateral view of body.

1977 (see Karaman & Barnard, 1979; Barnard & Barnard, 1983; Barnard & Karaman, 1987).

Karaman & Barnard (1979) found a progression of morphological characters too broad to permit generic division. They concluded that “no discontinuity exists among *Gammarella*, *Nuuanu*, and *Cottesloe* (op.cit.: 157). Recently, Vonk (1988) considered the differences too large between *Nuuanu* and *Gammarella* “to make the use of such a genus workable”. Consequently, he retained the genus *Nuuanu*, describing a new species *Nuuanu curvata*.

The present paper deals with a new species of the “nuuanuids”, *Gammarella garciai* n. sp., collected from shallow-water soft bottoms from the Chafarinas Archipelago (western Mediterranean, N. Africa). This species shows intermediate characters between *Gammarella*, *Cottesloe*, and *Nuuanu*, making doubtful the validity of any generic division, thus forcing us to propose *Gammarella curvata* (Vonk, 1988) as a new combination for Vonk’s species. Therefore, at present 11 species of *Gammarella* are recognized (cf. Barnard & Barnard, 1990): *G. fucicola* (Leach, 1814), *G. amikai* (J.L. Barnard, 1970), *G. berringar* (J.L. Barnard, 1974), *G. merri-gansee* (J.L. Barnard, 1974), *G. mokari* (J.L. Barnard, 1974), *G. numbadi* (J.L. Barnard, 1974), *G. castellana* (Griffiths, 1977), *G. cyclo-dactyla* (Hirayama, 1978), *G. hybophora* Lowry & Fenwick, 1983, *G. curvata* (Vonk, 1988), and *G. garciai* n. sp.

Materials and methods

Gammarella garciai n. sp. was collected during the CHAFARINAS’91 field survey in the Chafarinas Archipelago (south-western Mediterranean, North Africa). Meiobenthos samples were collected by means of scuba diving from a shallow sublittoral pool (3 m² area, –4.2 m depth) near a *Posidonia* meadow, located south of the island Isabel II. General environmental and biological (meiofauna) characteristics of the study area were described by Villora-Moreno (1993). The animals were extracted from the sediment samples using a decantation technique with 7.5% magnesium chloride in water. Material was fixed in buffered 10% formaldehyde in filtered seawater. Specimens were dissected in lactic acid and dissected parts were placed in glycerine mount. All drawings were prepared using a camera lucida on a Wild microscope. The type material has been deposited in the Museo Civico di Storia Naturale di Verona, Italy (MVR).

Taxonomic part

Gammarella garciai n. sp. (Figs. 1–4)

Material examined. – Holotype: (MVR Cr363, slides 3843–3846), male 2.5 mm. Allotype: (MVR Cr363, slides 3847–3849), female 2.5 mm. Paratypes: 3 specimens (MVR Cr363); 2 specimens (Museo nacional de Ciencias Naturales de Madrid, Spain). Type locality: southwestern Mediterranean, Chafarinas Archipelago, Isabel II island; collected by scuba diving east of “Titan” wharf (sta. IS11-CL1, 7 August 1991); well-sorted very coarse sand (mean diameter 1.56–1.77 mm) near *Posidonia* beds, depth 4.3 m; July 1991, coll. S. Villora-Moreno. Other material:

34 specimens from the type locality and 6 specimens from amphioxus gravel (sta. F6, 10 August 1991 and 22 February 1994), (Amphipoda coll., Marine Biology Laboratory of the University of Valencia, Spain).

Description of holotype. – Body (Fig. 1) length up to 2.5 mm. Lateral cephalic lobe quadratiform, anteroventral notch present. Eyes poorly developed, composed of about eight widely scattered ommatidia. Urosome segments 2 without pair of dorsolateral spines. Cuticle heavily villose.

Adult male: Antenna 1 (Fig. 2A) reaching 1/2 to 2/3 of body length, not geniculate; peduncle long, segment 1 stout, naked, segment 2 more slender and equal to length of 1, peduncle segment 3 nearly half length of segment 2. Flagellum as long as peduncle. Primary flagellum up to 11-articulate, poorly setose. Accessory flagellum 3-articulate, third segment short.

Antenna 2 (Fig. 2A) shorter than antenna 1: peduncle segment 3 short, segment 4 slightly longer than 5; flagellum 6–7-articulate and shorter than peduncle, poorly setose. Antennal gland cone short. Labrum (Fig. 2B) broader than long, with distal margin entirely fringed with fine hairs. Inner lobes of labium (Fig. 2I) very weak. Maxilla 1 (Figs. 2G–H): inner plate large with 6–7 marginal plumose setae, outer plate with 8–9 distal multidenticulate spines, palp asymmetric with 2 articles, bearing 4–5 (right–left) distal spines and 2 subdistal setae. Maxilla 2 (Fig. 2E): both plates moderately long, bearing numerous setae at distal margin, inner plate with oblique medial row of 5–6 setae.

Maxilliped (Fig. 2F): inner plate moderately long, with 3 stout distal spines; outer plate not reaching top of palp segment 2, with a row of 7 large spines at disto-internal margin; palp strong, with 4 segments, dactylus with distinct inner medial row of setules; nail short.

Mandible (Figs. 2C–D): molar and incisor well developed, rakers row with 5–6 denticulate strong setae. Left lacinia mobilis with 4 teeth, right lacinia mobilis with 2 teeth (inner denticulate). Palp short with 3 articles, articles 1 and 3 subequal and shorter than 2, article 1–2 smooth, article 3 not falciform, without D-setae and only 2 unequal E-setae.

Coxal plates 1–4 (Figs. 3A–B, 4A–B) large,

longer than broad, coxal plates 1–2 with posterodistal notch with a small tooth, coxal plate 1 weakly dilated distally, coxal plate 4 not lobed, coxal plate 5 (Fig. 1) shorter than 4, bilobed distally.

Gnathopod 1 (Fig. 3A): basis with 2 long plumose setae medially on posterior margin; carpus not elongate, with pectinate setae; propodus slightly shorter than carpus, palm transverse and slightly convex, defined by apically bifid stout spines; dactylus stout, with one dorsal seta and 4–5 ventral setae.

Gnathopod 2 (Figs. 3B–C) much larger than gnathopod 1. Merus without distal tooth. Carpus triangular; propodus large and elongate, ovoid, palm short, convex, inclined, crenulate, provided with a row of short bifid palmar spines, separated from posterior margin by a tooth and two bifid spines.

Pereiopods 3–4 (Figs. 4A–B) with poorly spinose propodus, dactylus shorter than half of propodus, nail short. Dactylus with 2 setae, 1 posterior seta and the other at base of nail. Pereiopods 5–7 (Figs. 4C–E) short, base large, weakly serrate, with moderate posterodistal lobe; base of P5–6 weakly excavate posteriorly, tapering distally; base of P7 broadly expanded, shield-like. Dactylus short, stout, as on pereiopods 3–4.

Epimeral plates 2–3 unextended, with small posterodistal tooth, almost smooth. Uropods 1–2 (Figs. 4G–H) rami short and subequal, with stout distal spines. Uropod 1: peduncle with one lateroproximal (basofacial) spine, one dorsal spine, and two strong distal spines at base of each ramus; rami with one dorsal spine. Uropod 2 shorter than 1, nearly reaching end of uropod 1; peduncle with one distal spine, dorsal margin of outer ramus naked and inner ramus with 1 spine. Uropod 3 (Fig. 4I) very short, not reaching end of uropods 1–2; peduncle with distal spine. Outer ramus nearly half length of peduncle, article 1 with two unequal spines, article 2 small; inner ramus 1-articulate, scale-like, as long as article 1 of outer ramus. Telson (Fig. 4F) broader than long, fully cleft, each lobe with 4 distal setae.

Allotype: Female 2.5 mm. Similar to holotype except gnathopod 2 (Fig. 3D) slender and elongate,

Fig. 2. *Gammarella garciai* n. sp. ♂: A, head; B, labrum; C, left mandible; D, right mandible; E, maxilla 2; F, maxilliped; G, left maxilla 1; H, palp of right maxilla 1; I, labium.

Fig. 3. *Gammarella garciai* n. sp.: A, gnathopod 1 ♂; B, gnathopod 2 ♂ (½ reduced); C, detail of palm of gnathopod 2 ♂; D, gnathopod 2 ♀; E, oostegite of pereopod 5 ♀ (2 × increased).

Fig. 4. *Gammarella garciai* n. sp. ♂: A, pereopod 3; B, pereopod 4; C, pereopod 5; D, pereopod 6; E, pereopod 7; F, telson; G, uropod 1; H, uropod 2; I, uropod 3.

carpus subtriangular, larger than wide, propodus elongate with oblique palm defined by two large bifid spines.

Oostegites (Fig. 3E) on second to fifth pereopods, narrow, armed with 3 long setae and 1 short seta.

Table I. Matrix of values for 18 taxonomic characters used in the cluster analysis of *Gammarella* species (1 = presence, 0 = absence): A, size < 6 mm; B, sparse eyes; C, antenna 1 geniculate; D, accessory flagellum with 3 articles; E, mandible palp, article 2 without setae; F, mandible palp, article 3 with only E-setae; G, mandible palp not falciform; H, Gn1 carpus < 2 × propodus; I, Gn2 (♂), merus without distal tooth; J, Gn2 (♂), carpus very short; K, Gn2 (♂), palm short, defined from posterior margin; L, P3–4 propodus poorly spinose; M, P7 base serrate (not castellated); N, epimeral plate 1 with an anteroventral curved tooth; O, metasomites 1–2 with a dorsal tooth each; P, uropod 3, inner ramus > 1/2 outer ramus; Q, telson without spines; R, telson fully cleft.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
<i>fucicola</i>	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	0
<i>berringar</i>	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0
<i>cyclodactyla</i>	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1	0	1
<i>hybophora</i>	0	0	0	0	0	0	0	1	1	0	1	0	1	1	0	1	1	0
<i>merringannee</i>	1	1	0	1	0	0	0	1	1	1	0	0	0	0	1	0	1	0
<i>mokari</i>	1	1	1	1	0	0	1	1	0	0	1	1	0	0	0	1	1	1
<i>numbadi</i>	1	1	1	1	0	0	1	1	0	0	1	1	0	0	1	1	1	0
<i>amikai</i>	1	1	1	1	0	0	1	0	0	0	0	1	0	0	1	1	1	0
<i>castellana</i>	1	1	1	1	1	1	1	0	0	0	1	1	0	0	1	1	1	0
<i>curvata</i>	1	1	1	1	0	1	1	0	0	1	1	1	1	1	0	1	1	0
<i>garciai</i>	1	1	0	1	1	1	1	1	1	0	1	1	1	0	0	0	0	1

Diagnosis. – Cuticle heavily villose. Urosomite 2 lacking dorsolateral spines. Antenna 1 not geniculate, accessory flagellum 3-articulate. Mandibular palp, articles 1–2 smooth, article 3 not falciform with only 2 unequal E-setae. Male gnathopod 2, merus without distal tooth, palm short, separated from posterior margin by a tooth. Pereiopods 3–4 propodus poorly spinose, coxae of P4 not lobate. Pereiopods 5 to 7, base weakly toothed posteriorly. Uropod 3, peduncle almost twice as long as outer ramus, inner ramus as long as article 1 of outer ramus. Telson without spines.

Etymology. – This species is dedicated to our colleague and friend Dr. A.M. García-Carrascosa, who directed the CHAFARINAS'91 benthic survey.

Discussion

Morphology and affinities

As the discovery of new species progresses, the identity of the genus *Gammarella* becomes better understood, and character intergradation, suggested previously by other authors (Barnard, 1974; McKinney & Barnard, 1977; Karaman & Barnard, 1979), is more evident. Nevertheless, differences

between the two extremes are so large that Vonk (1988) proposed to retain the genus *Nuuanu*, including the smaller species.

In an attempt to group all known species of *Gammarella*, a cluster analysis was performed using 18 morphological characters (see Table I). Each character was defined as 0 for absence and 1 for presence. Numerical taxonomic methods were utilized to enhance the objectivity of the results, helping us to elucidate which are the morphologically related species and which the intermediate species. A dissimilarity matrix was generated using the Manhattan distance index and the UPGMA cluster method (Sneath & Sokal, 1973; Norusis, 1992). The phenogram (Fig. 5) shows two major groups, A and B, in accordance with the two genera of Vonk's hypothesis. However, within each group we can see one intermediate species with dissimilarity lower than 50%, labeled as A2 and B2. These species, *Gammarella merringannee* from cluster A and *G. garciai* from cluster B, share morphological characteristics with species from B and A clusters, respectively.

Gammarella merringannee was already identified by Barnard (1974) as an intermediate species, and an evolutionary sequence from *G. berringar* through *G. merringannee* to *G. mokari* was proposed. *Gammarella numbadi* and *G. amikai* were considered very "advanced" species (with many apomorphic characters). If *G. merringannee* ap-

Fig. 5. Phenogram showing morphological similarity of species of *Gammarella*.

proaches the species from cluster A to species of cluster B, *G. garciai* does it from cluster B to A. However, it should be kept in mind that the relationships shown in the phenogram reflect only the morphological resemblance of the species. So, inference of phyletic relationships should be made with great caution.

Gammarella garciai is generally similar to the species of cluster B but does not appear to be closely related to any particular species of this cluster. *G. garciai* differs from these species by A1 not geniculate, cuticle heavily villose, no tooth on merus of Gn2, and base of P5–7 not castellated. On the other hand, this species shows characters in common with the species of cluster A (*G. fucicola*, *G. berringar*, *G. merringannee*, *G. cyclodactyla*, and *G. hybophora*), but differs in its size, in having reduced eyes, propodus of pereopods 3–4 poorly spinose, accessory flagellum with 3 articles, article 3 of mandible palp not falcate, telson deeply cleft, and distinct palm of Gn2 (male). These characteristics explain the situation of *G. garciai* in the phenogram and confirm the idea proposed in the above paragraph, allowing us to consider *G. garciai* as an intermediate species between cluster B and A.

In agreement with Barnard & Barnard (1983), the presence of intermediate species with evident intergradation of characters justifies the existence of a single, unique genus, making doubtful the validity of any generic division.

Key to all known species of *Gammarella* (cf. Table II)

1. Base of P7, posterior margin castellated 2
- Base of P7, posterior margin serrate 7
2. Length over 8 mm; eyes well developed; urosomite 1 with large reverted dorsal tooth ... *G. berringar* (Barnard, 1974)
- Length less than 6 mm; eyes weakly developed; urosomite 1 without dorsal tooth 3
3. Coxa 3 shortened; metasome segments 1–2 untoothed ... *G. mokari* (Barnard, 1974)
- Coxa 3 as long as coxa 4; metasome segments 1–2 each bearing a single middorsal tooth 4
4. Cephalic slit gaping; articles 1–3 of antenna 2 processiferous *G. numbadi* (Barnard, 1974)
- Cephalic slit not gaping; articles 1–3 of antenna 2 not processiferous 5
5. Lateral cephalic lobes acute; urosomite 1 with a simple mediodorsal tooth *G. castellana* (Griffiths, 1977)
- Lateral cephalic lobes quadratiform; urosomite 1 without mediodorsal tooth 6
6. Antenna 1 geniculate; palm of Gn2 male distinct from posterior margin; U3 inner ramus < 1/2 outer ramus ... *G. amikai* (Barnard, 1970)
- Antenna 1 not geniculate; palm of Gn2 male occupying all the posterior margin; U3 inner ramus > 1/2 outer ramus *G. merringannee* (Barnard, 1974)
7. Large size, longer than 9 mm; eyes well developed; mandibular palp falciform, article 3 with D–E setae; urosomite 1 carinate 8
- Small size, less than 3 mm; eyes little developed; mandibular palp not falciform, article 3 with only E-setae; urosomite 1 not carinate 10
8. Epimeral plate 1 with a large anteroventral curved tooth (hook) *G. hybophora* Lowry & Fenwick, 1983
- Epimeral plate 1 with small or without anteroventral tooth 9
9. Telson fully cleft, lacking spines and setae; palm of Gn2 male with four protuberances and defined from posterior margin *G. cyclodactyla* (Hirayama, 1978)
- Telson cleft almost to base, with spines and setae; palm of Gn2 male not separated from posterior margin *G. fucicola* (Leach, 1814)
10. Antenna 1 geniculate between articles 1–2; epimeral plate 1 with a large anteroventral curved tooth (hook); telson with two spines *G. curvata* (Vonk, 1988)
- Antenna 1 not geniculate; telson without spines; epimeral plate 1 without anteroventral tooth *G. garciai* n. sp.

Ecology and distribution

Available ecological data on *Gammarella* species are difficult to interpret because no data are usually offered with species descriptions. On the other

Table II. The main differentiating characters of *Gammarella* species.

	<i>fucicola</i>	<i>mokari</i>	<i>numbadi</i>	<i>amikai</i>	<i>castellana</i>	<i>berringar</i>	<i>hybophora</i>	<i>merringannee</i>	<i>cyclodactyla</i>	<i>curvata</i>	<i>garciai</i>
Size (mm)	10–12	3.2–3.9	5.8	3.4–4.5	4	8.2–13.3	9.3	4.4–5.2	9.3	2.8	1.5–2.5
Eyes well developed	+	–	–	–	–	+	+	–	+	–	–
Accessory flagellum n° arts.	3–5	3	3	3	1	6–7	3–6	3	5	3	3
A1 geniculate	–	+	+	+	+	–	–	–	–	–	–
Md. palp	{ art. 2 with setae art. 3 with D–E setae	+	+	+	+	–	+	+	+	+	–
		+	+	+	+	+	+	+	+	– (4-E)	– (2-E)
Gn.1 carpus : 2 × propodus	=	<	<	=	=	>	<	<	=	=	<
♂ Gn.2	{ Merus tooth Carpus very short palm distinct	–	+	?	+	?	–	–	–	+	–
		+	–	?	–	?	+	–	+	+	–
		–	+	?	+	?	–	+	–	+	+
Propodus P3–4 very spinose	+	–	–	–	–	+	+	+	+	–	–
Base P7 castellate	–	+	+	+	+	+	–	+	–	–	–
Ep1 antero-ventral tooth	–	–	–	–	–	+	+	–	–	+	–
Urosomite 1 dorsal margin	carina	flush	flush	frilled	a tooth	large reverted tooth	dorsal boss	flush	dorsal boss	flush	flush
Ramus U3 inner : ½ outer	<	=	<	<	=	=	=	>	=	<	>
Telson	spines + setae	spines + setae	spines + setae	spines + setae	spines + setae	spines + setae	spines + setae	spines + setae	bare	spines + setae	setae
Metasomites 1–2 with dorsal teeth	–	–	+	+	+	–	– (carinate)	+	– (carinate)	–	–

Fig. 6. Map of world distribution of *Gammarella* species: 1, *G. merringanee*; 2, *G. berringar*; 3, *G. mokari*; 4, *G. numbadi* (Australia); 5, *G. hybophora* (Campbell Island); 6, *G. cyclodactyla* (Japan); 7, *G. amikai* (Madagascar and Hawaii); 8, *G. castellana* (South Africa); 9, *G. fucicola* (Mediterranean Sea including Black Sea, and N.E. Atlantic); 10, *G. curvata* (Caribbean Sea, Curaçao); 11, *G. garciai* (Mediterranean Sea, Chafarinas Archipelago).

hand, most descriptions are very recent and species are often known from a single locality (Fig. 6). *Gammarella fucicola* is the only exception, since it has been frequently recorded from both the Atlantic and Mediterranean. This species is intertidal and sublittoral and found in algae and seagrass. Lowry & Fenwick (1978) described *G. hybophora* from intertidal (including shallow pool) to sublittoral (0–50 m depth) substrata, mainly in deposits of detritus (terrestrial plants), also under boulders (on coarse shelly sand) or with bryozoans. Another species collected from midlittoral (lava) ponds to sublittoral (–18 m depth, among bryozoans) is *G. amikai*, identified by Barnard (1970, 1977).

Gammarella mokari, *G. numbadi*, *G. berringar*, and *G. merringanee* were found by Barnard (1974) in shallow water, without any additional indication about soft or hard substrata. In the same way, poor

ecological data are available for *G. castellana*, even when station data of cruises (Louw, 1977) are consulted. This species represents the deepest record for the genus, –550 m depth in soft bottom.

Two species are known exclusively from the intertidal zone: *Gammarella cyclodactyla* in boulder beaches, and *G. curvata* in coarse sand beaches or rockpools. The latter inhabits the macroporous interstitial stygohabitat.

Gammarella garciai n. sp. was recorded from shallow water, –4.2 m depth, inhabiting the interstitial system in a sublittoral pool near *Posidonia oceanica* meadows. The sole species of *Gammarella* identified from the midlittoral level in the Chafarinas Archipelago was *G. fucicola* (midlittoral rockpools).

The discovery of the last two species of *Gammarella*, *G. curvata* and *G. garciai*, allows us to take

into account the hypothesis of Barnard (1974) on the existence of two extremes (evolutionary and ecological) within *Gammarella* (this hypothesis was referred to the genera *Cottesloe* and *Nuuanu*, now synonymized with *Gammarella*).

In our opinion, the two clusters found using morphological characters may be also considered as representing the two extremes proposed by Barnard (1974). Cluster A groups the larger species, probably nesting ones, with preference for lightless environments (under stones, in boulder beaches, within deposits of plant detritus, within bryozoans, etc.). On the other hand, cluster B groups the smaller species, with eyes poorly developed or absent, showing interstitial preferences. In this way we consider *Gammarella amikai*, *G. curvata*, and *G. garciai* as true stygobionts that have colonized substrata from dimly lighted anchialine waters (lava pond, Barnard, 1977), macroporous interstitia (Vonk, 1988) to a sublittoral interstitial environment.

The genus *Gammarella* is widely distributed in the world's seas, showing a circumglobal distribution. Species of the genus *Gammarella* have been mainly identified from Australia, where four are known (Fig. 6). *Gammarella fucicola* and *G. amikai* are the only species known from distant geographic areas. The former species has an eastern Atlantic-Mediterranean distribution (including the Black Sea). *Gammarella amikai* has been reported from Hawaii (Pacific Ocean) and Madagascar (Indian Ocean). Although *Gammarella* may be considered as a genus of tropical affinity and Tethyan origin (Barnard & Barnard, 1983), most of the species are known from a single locality, so biogeographical relationships are difficult to establish.

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