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BOGIDIELLA VENERIS, A NEW SPECIES OF SUBTERRANEAN AMPHIPODA (BOGIDIELLIDAE) FROM AUSTRALIA, WITH REMARKS ON THE SYSTEMATICS AND BIOGEOGRAPHY

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ABSTRACT

A new species of subterranean amphipod, *Bogidiella veneris*, from Venus Bay, South Australia is described. The species was found in a groundwater observation well drilled in an aeolianite limestone formation only 500 m from the seashore. The discovery of the new bogidiellid amphipod is one of the outcomes of a three year stygofauna survey in South Australia. *Bogidiella veneris* is the fourth species of Bogidiellidae from the Australian region.

KEY WORDS: anchialine, Bogidiella veneris, DNA sequencing, groundwater fauna, stygobiont

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INTRODUCTION

Specimens of the new amphipod species were collected during two fieldtrips to the Eyre Peninsula, South Australia, December 2007 and June 2008, as part of a three-year project to study the biodiversity of groundwater in South Australia.

Bogidiella veneris is a small species, with typical facies of the subterranean family Bogidiellidae. It can be unambiguously distinguished from other bogidiellids by a propodus of gnathopod 2 that is distinctly larger than that of gnathopod 1, a prominent, very long pereiopod 7, and epimeral plates with truncated, slightly rounded, distoposterior corners.

With the description of Bogidiella veneris, Bogidiellidae presently encompasses 108 described species, assigned to 35 genera. Although the vast majority of bogidiellids occur in subterranean freshwaters, some species have been found in marine sediments. In Australia, Bogidomma australis Bradbury and Williams, 1996 occurs in a classical carbonate karst anchialine system where it is associated with a well recognised anchialine fauna (Humphreys, 2002). In addition, two marine species of the genus Xystriogidiella Stock, 1984 have been described from sandy, intertidal sediments. Therefore, the discovery of a new species from Southern Australia less than 500 from the shoreline certainly adds to our knowledge of the global distribution of Bogidiellidae. However, the assignment of the new species also reveals some serious short comings of the present taxonomy of the family. We found that most genera lack satisfactory diagnostics, and we urgently advise a taxonomic revision of the family. With the description of this species, which includes partial sequencing of the mitochondrial CO1 gene and the nuclear 28S gene, we hope to contribute to a future revision of the family. Our study would also assist in the management and conservation of the aquifer in which *B. veneris* occurs.

MATERIALS AND METHODS

Specimen Collection

The amphipods were collected using a 60 mm diameter, weighted plankton net by filtering the water column in the groundwater well repeatedly, making sure that material and fauna became dislodged from the bottom and walls of the well. We stored the collected fauna alive until sorting during the evening of the same day. Specimens were preserved in absolute ethanol.

Water Quality Parameters, and Bacteria and Virus-like Particle Enumeration

As part of the description of the ecology of the sample location, water quality parameters were recorded using a Hach Hydrolab® MS5 water quality probe, and virus like particles (VLP) and bacteria were counted. Thus, 1 ml water samples (triplicate) collected for virus-like particle (VLP) and bacterial enumeration were fixed in 1% glutaraldehyde (final concentration) at 4°C in the dark for 15 minutes, snap-frozen in liquid nitrogen, and stored at -80° C until flow cytometric analysis (Brussard 2004). Thawed samples were then stained with SYBR® Green solution (Sigma-Aldrich) and incubated at 80°C (Brussard 2004) prior to analysis using a FACSCanto flow cytometer (Becton-Dickson). 1 µm fluorescent beads (Molecular Probes, Eugene, Oregon) were added to the sample to normalize the flow cytometric parameters of fluorescence and particle concentration. Microbial populations were discriminated according to differences in cell side scatter and fluorescence (Brussaard 2004). Data were analyzed using Win Midi 2.8 software (© Joseph Trotter).

Morphological and Taxonomic Terms

In the following taxonomic description, we adopt the terminology that has traditionally been used in bogidiellid systematics. For example, the terms "spines" and "setae" are employed to distinguish between thin or fine and more robust setal structures. In our description, both terms refer to articulated cuticular outgrowths, arising from a socket (opposed to non-articulated cuticular extensions, i.e., "spines" sensu Watling, 1989).

The vast majority of larger setae and spines of *Bogidiella veneris* have bifurcate (bifid) distal tips, with very fine hairs branching off subapically from the main stem. Because we could not unambiguously distinguish between bifid and simple ("naked") setae under the light microscope, we refrain from mentioning occurrences of bifid setae in the written description; however, bifid setae and spines are shown in the drawings of appendages in all instances where they could be detected.

In the following text, the term "bogidiellid" refers to any species currently assigned to Bogidiellidae.

Systematics

Bogidiella veneris n. sp. (Figs. 2-6)

Type Locality.—Groundwater observation well WRT011 in aeolianite limestone near Venus Bay, South Australia (134.68802E, 33.24583S).

Material Examined.-Five specimens, all females, were collected December 2007 and June 2008. Holotype, 3.6 mm (C6846); collected on 18 December 2007 by R. and P. Leijs; preserved in EtOH; some pereiopods used for DNA analysis. Four paratypes (C6847), collected by R. Leijs on 17 June 2008 from type locality. Paratype 1, 3.0 mm (C6846); dissected for description; pereiopods missing. Paratype 2, 3.2 mm (C6848); used for DNA analysis; antenna 1 broken, pereiopods 5-7 and third uropods missing. Paratype 3, 3.1 mm (C6849); dissected for description; pereiopods 5-7, third uropods and one gnathopod 2 missing. Paratype 4, 3.0 mm (C6850); pereiopods 5-7, third uropods and one gnathopod 2 missing. The collection samples contained a number of loose appendages that could not be assigned unambiguously to any of the type specimens. The holotype (C6846) and paratypes (C6847-C6850) are lodged in the South Australian Museum.

Etymology.—The new species is named after the Roman goddess Venus, referring to the type locality, Venus Bay, in South Australia.

Diagnosis.—Small amphipod of typical bogidiellid facies. Anterior (interantennal) head lobe distinctly rounded (Fig. 2A); all coxal plates wider (deeper) than long (Fig. 2C); posterior corners of epimeral plates 1 and 2 slightly angled, that of plate 3 subrectangular (Fig. 2B); antenna 1 slightly longer than antenna 2; accessory flagellum of antenna 1 with 2 articles; propodus of gnathopod 1 dinstinctly longer and more robust than that of gnathopod 2; coxal gills on pereiopods 4-6; paired brood plates on pereiopods 2-5. Male unknown.

Description (Based on Females).—Antenna 1 (Fig. 2D) slightly longer than antenna 2. Primary flagellum with 6 articles, with aesthetascs on most articles. Accessory flagellum composed of 2 articles, exceeding length of first article of main flagellum.

Antenna 2 (Fig. 2E) with 5 flagellar articles; flagellum much shorter than peduncular articles.

Mandibles (Fig. 3B, C1, C2) with asymmetrical, rather small laciniae mobiles; lacinia of left mandible apparently larger than right lacinia; both laciniae apparently with serrated apical margins accompanied by 1 larger lateral denticle, forming a semi-circular arc with adjacent row of 3-5 robust spines of varying length (but see Remarks below). Incisors prominent, with 4 denticles. Molars comparatively small. Palp composed of 3 articles, bearing only a few distal setae.

Lower lip (Fig. 3A) partly damaged. Outer lobes ovoid, without detectable setules.

Maxilla 1 (Fig. 2F, G): inner plate only seen in damaged condition, separated from maxilla. Outer plate with a row of 7 apical spines, including simple (naked) spines, and spines bearing 1, 2 or multiple denticles (see Fig. 2G). Palp with 2 articles.

Maxilla 2 (Fig. 2H): inner and outer plate about equally long. Apical margin of inner plate equipped with 3 slender spines and 3 setae; outer plate with 4 apical setae.

Maxilliped (Fig. 3D) with sparse setation. Palp composed of 4 articles; article 2 only weakly expanded, with a row of 5 setae on medial margin; article 3 robust, bearing rows of long setae and short spines apically and subapically; article 3 and dactylus with pubescent surfaces. Apical margin of inner plate equipped with 3 slender spines and 3 setae; outer plate bearing apically 1-2 undulated spines and 1 seta, accompanied by about 3 setae along medial margin.

Gnathopod 1 (Fig. 4A) with expanded basis. Lateral margin of merus pubescent. Carpus with pubescent, tapered distolateral lobe. Propodus twice as long as wide, about 20% larger than propodus of gnathopod 2; palmar margin not angled, more or less even, slightly longer than pubescent posterior (proximolateral) margin; palmar margin with about 6 short spines and a few setae of variable length; proximal end of palmar margin (closure of dactylus with propodus) marked by 2 medial and 3 lateral, robust spines (extending on proximolateral margin). Dactylus reaching about 60% length of propodus.

Gnathopod 2 (Fig. 4B) about as long as gnathopod 1, but more slender. Basis not expanded, longer than that of gnathopod 2. Merus shorter than that of gnathopod 2, without pubescence. Carpus expanded, but without tapered projection, distolateral margin pubescent. Propodus twice as long as wide, with row of very fine pubescent hairs on medial surface; palmar margin oblique, even, subequal in length to posterior margin, bearing row of 4-6 short spines and several setae of variable length; proximal end of palmar margin with 2 parallel rows of narrowly inserted robust spines (defining closure of dactylus); posterior margin with a few long setae, and a row of apparently soft, very fine hairs (see Remarks below). Dactylus about half as long than propodus.

Pereiopods 3-7 with sparse setation, including setae of variable length and slender spines; number and length of straight, posterodistal setae on propodi increasing in pereiopods 3-7. Pereiopods 3 and 4 similar (Fig. 5A, B); bases with slightly expanded posterior margins; dactyli

(compared to propodi) shorter than those of pereiopods 5-7. Pereiopod 5 (Fig. 5C) as long as pereiopods 3 and 4; basis narrow; propodus slightly shorter than that of pereiopods 3 and 4. Pereiopod 6 (Fig. 5D) about 25% longer than pereiopods 3-5, but bearing a few more setae and spines; posterior margin of basis nearly straight. Pereiopod 7 (Fig. 5E) prominent, more than 50% longer and much more robust than pereiopod 6; basis comparatively short, not expanded; carpus as long as merus; propodus with a cluster of long, posterodistal setae.

Coxal plates 1-7 small (Fig. 2C), longer than wide (deep); coxal gills on pereiopods 4-6; brood plates on pereiopods 2-5.

Epimeral plates (Fig. 2B) each with a single seta on posterior margin; posterior corners of plates 1 and 2 truncated (slanted anteriorad), slightly rounded; that of plate 3 more rectangular.

Pleopods 1-3 (Fig. 5F) similar, but slightly decreasing in length from anterior to posterior; inner ramus absent; outer ramus composed of long, narrow peduncle, and 3 distal articles. Each pleopod with 2 retinaculae on distal margin of peduncle.

Uropods 1-3 (Fig. 4C-E), sparsely setose, with outer rami slightly shorter than inner rami. Peduncles of uropods 1 and 2 somewhat longer than distal articles. Uropod 3 (Fig. 4E) distinctly different from uropods 1 and 2; peduncle comparatively shorter and expanded; rami conspicuously longer than peduncle.

Telson (Fig. 4F) small, as long as wide, with straight distal margin, equipped with two spines.

Remarks.—Light-microscopic examination of the posterior propodal margin of gnathopod 2 revealed a row of apparently soft, very fine hairs that differed from the pubescence on carpus and/or merus of both gnathopods. Unlike the fine, pubescent setules on merus and carpus, the hairs on the propodus appeared as broader, but very thin and soft setal structures. Further investigation is required to determine whether these leaf-like setae represent an autapomorphic character of *Bogidiellla veneris*.

Similarly, the light-microscopic resolution was not sufficient to unambiguously identify the mandibular spine rows and lacinia mobiles. For example, one mandible of paratype 1 seemed to lack a lacinia mobilis (see Fig. 3C1). For this reason, a clear distinction between left and right mandible was not possible.

Bogidiella veneris lacks any conspicuous morphological characters that warrant a separate generic status. Since males of the new species are still unknown, we assign it to the *lindbergi* group (group D) within the genus *Bogidiella*. The *lindbergi* group encompasses all species for which sexually dimorphic characters are not known because one of the two sexes has not yet been described (Koenemann and Holsinger, 1999; see also Discussion).

Bogidiella veneris can be distinguished from other bogidiellids by the following characters.

1) The propodus of gnathopod 1 is distinctly larger than that of gnathopod 2. In many bogidiellids, the gnathopodal propodi are approximately of the same length; typically, the propodus of gnathopod 1 is more robust (broader), than that of gnathopod 2. A relatively larger propodus on gnathopod 1 has also been found in *Xystriogidiella juliani* Coleman, 2009 from Lizard island (northeastern Australia), *B. cerberus* Bou and Ruffo, 1979 from Greece and *B. convexa* Stock and Notenboom, 1988 from Spain.

- 2) The prominent seventh pereiopod 7 in *B. veneris* is more than 50% longer than pereiopod 6, which, to our knowledge is unparalleld among bogidiellids. A tendency towards elongated seventh pereiopods has been described for a number of European bogidiellids, including, inter alia, *B. cerberus*, *B. convexa*, and *B. skopljensis*.
- 3) The maxillipedal palp bears 3-4 short, robust spines on the distal margin of article 3. To our knowledge, this feature is unique among bogidiellids; a similar spine row has only been described for *Xystriogidiella capricornea* Stock, 1984 from Heron Island, eastern Australia. However, *X. capricornea* can easily be differentiated from *B. veneris* by a number of characters, including an antennal accessory flagellum with 3 articles, differently shaped coxal plates, and pereiopod 7 being only about 15% longer than pereiopod 6.
- 4) The flagellum of antenna 1 in *B. veneris* is composed of only 6 articles; the majority of bogidiellids are equipped with 7 or 8 flagellar articles, a few taxa have more than 8 articles.
- 5) The epimeral plates of *B. veneris* have truncated, slightly rounded distoposterior corners, opposed to acuminate or pointed corners that are typical of many bogidiellid species.

The general habitus of *B. veneris* (Fig. 6) shows some resemblances to that of *X. juliani*. The latter species can be distinguished from *B. veneris* by the following characters.

- 1) Flagellum of antenna 1 with 7 articles (6 in *B. veneris*);
- 2) Plates and palp of maxilliped with different setal types and patterns;
- 3) Propodus of gnathopod 1 only about 12% longer than that of gnathopod 2 (20% longer in *B. veneris*);
- 4) Defining angles of dactyli in gnathopods 1 and 2 with only 2-3 spines (3 and 5 spines in *B. veneris*);
- 5) Dactylus of gnathopod 2 clearly shorter than half the length of propodus (about half as long in *B. veneris*);
- 6) Basis of pereiopod 7 with expanded posterior margin (not expanded in *B. veneris*);
- 7) Telson with 2 apical and 2 subapical spines on each lobe (1 apical spine in *B. veneris*).

Molecular Analyses.—From two specimens of *B. veneris*, the holotype (C6846) and one paratype (C6848), tissue from pereiopods was used for DNA extraction and partial sequencing of the CO1 and 28S genes as well as partial sequencing of CO1 of some specimens of *albertimagni* and *B. indica* (GeneBank Accession numbers JF278082-JF278090). At the moment there is insufficient molecular data available from bogidiellid amphipods to make phylogenetic analyses worthwhile. However, the pairwise uncorrected sequence divergences, calculated using PAUP* (Swofford, 2001), of the three species of which CO1

	Taxon	Species group	1	2	3	4	5	6	7
1	B.albertimagni OffbgF2	А							
2	B.albertimagni Offbg34 2	А	0.000						
3	B.albertimagni OffbgF1	Α	0.000	0.000					
4	B.albertimagni EimsE1	А	0.006	0.006	0.006				
5	B.albertimagni HamlnH1	А	0.007	0.007	0.007	0.003			
6	B.veneris	D	0.229	0.229	0.229	0.231	0.232		
7	B.indica RR1 COI	Е	0.242	0.242	0.242	0.245	0.247	0.233	
8	B.indica RR2 COI	Е	0.239	0.239	0.239	0.242	0.244	0.238	0.015

Table 1. Uncorrected pairwise sequence divergences of three species of Bogidiella based on CO1 sequences.

sequence data is available, show remarkably deep inter specific divergences (Table 1). *Bogidiella albertimagni* and *B. indica*, respectively from Germany and India, have sequence divergences ranging 23.9-24.7%, while these northern hemisphere taxa differ 22.9-23.8% when compared to *B. veneris*.

Ecological Profile of the Type Locality.—The specimens were collected in a groundwater observation well associated with a small water extraction field in calcareous sand dunes near the township of Venus Bay, South Australia. The well, drilled into Pleistocene limestone (0-6 m) (Bridgewater formation) overlaying clay and quartz deposits (6-11 m), was 11 m deep, cased with an 80 mm PVC pipe, with 2 mm slots at 4.5-6.5 m. The water level in the well was 3.9 m below ground level during sampling (June 2008). The following water quality values were measured: temperature 20.05°C; pH 7.54; EC (electrical conductivity) 8.76 mS/cm; salinity 4.93 ppt; dissolved oxygen 6.16 mg/L; TDS (total dissolved solids) 5.61 g/L; NH₄⁺ 0.54 mg/L; NO₃⁻ 0.30 mg/L; PO₄³⁻ 0.30 mg/L. These values indicate moderately saline, but well-oxygenated water. It is of interest to mention that since the construction of the observation well in August 1982, the salinity of the water has increased significantly: EC 3.44 mS/cm and TDS 1.92 g/L. The latest measurements (November 2009) were EC 18.29 mS/cm and TDS 10.76 g/ L (data from South Australian Drillhole Enquiry System, https://des.pir.sa.gov.au/new/des, accessed 11 January 2010). These highly increased salinity values, which were first found in the mid-nineties, were the consequence of overextraction of this small aquifer in combination with insufficient recharge. Although, as yet it is unclear whether the increased salinity is coming from natural underlying



Fig. 1. Geographic distribution of bogidiellid amphipods. Large map: type localities of: 1, *Bogidiella veneris* n. sp.; 2, *Bogidomma australis*; 3, *Xystriogidiella capricornea*; and 4, *Xystriogidiella juliani* on the Australian continent (with kind permission of demis.nl). Insert map: global distribution of Bogidiellidae and several, possibly closely related taxa (modified after Koenemann and Holsinger, 1999).



Fig. 2. Bogidiella veneris n. sp. from Venus Bay, South Australia. A-C, holotype (3.6 mm female); E, H, paratype 1 (3.0 mm female); D, F, G, paratype 3 (3.1 mm female). A, head; B, epimera 1-3; C, coxal plates 1-7 (from left to right), with brood plates exemplarily shown on coxa 4, and gills on coxae 4 and 5; D, antenna 1, with arrows pointing at enlarged accessory flagellum (above) and aesthetasc (below); E, antenna 2; F, maxilla 1; G, enlarged serrate setae from outer plate of maxilla 1; H, maxilla 2. Scale bars: A-E = 0.1 mm; F, H = 0.1 mm.



Fig. 3. *Bogidiella veneris* n. sp. from Venus Bay, South Australia. A, B, C2, F, paratype 3 (3.1 mm female); C1, D, E, paratype 1 (3.0 mm female). A. lower lip; B, right mandible (with palp from paratype 1); scale bar = 0.1 mm; C1, enlarged view of mandible from paratype 1; C2, enlarged incisor and lacinia mobilis from left mandible; D, maxilliped; E, dactylus of maxilliped; F, inner plate of maxilliped. Scale bar A, C, D = 0.1 mm.

saline groundwater or from intrusion of sea water, which would be possible since the locality of the bore is less than 500 m from the seashore. Because *B. veneris* was only discovered for the first time in December 2007, we do not have evidence that this species is adapted to fluctuating salinity levels or that it migrated to the bore site under influence of seawater intrusion.

The groundwater observation well with the *B. veneris* also contained large numbers of an undescribed stygobiontic chiltoniid amphipod, as well as some cyclopoid Copepoda. Flow cytometric enumeration of microbes in water samples from the well showed 1.83×10^4 cells/ml (std. dev. 1.41×10^3) for bacteria and 5.43×10^4 cells/ml (std. dev. 1.01×10^4) for virus-like particles. These numbers are within the normal range for microbes detected in South Australian groundwater observation bores (unpublished data).

DISCUSSION

The taxonomy of the species-rich Bogidiellidae has long been an irksome issue. Koenemann and Holsinger (1999) suggested a rigorous revision of the family based on a phylogenetic analysis of all then known species. Although their attempt provided a more stringent taxonomic structure, a number of urgent problems still remain to be solved. For example, Koenemann and Holsinger elevated all subgenera to the generic level. However, the erection of subgenera, first introduced by Stock (1981), was primarily defined by sexually dimorphic spines or setae on the



Fig. 4. Bogidiella veneris n. sp. from Venus Bay, South Australia. A, B, E, paratype 1 (3.0 mm female); C, D, F, paratype 3 (3.1 mm female). A, gnathopod 1; B, gnathopod 2; C, uropod 1; D, uropod 2; E, uropod 3; F, telson. Scale bar A-F = 0.1 mm.



Fig. 5. *Bogidiella veneris* n. sp. from Venus Bay, South Australia. A, B, F, paratype 3 (3.1 mm female); C-E, holotype (3.6 mm female). A, pereiopod 3; B, enlarged dactylus of pereiopod 4; C, pereiopod 5; D, pereiopod 6; E, pereiopod 7; F, pleopod 1. arrow pointing at enlarged retinaculae. Scale bar A, C-F = 0.1 mm.



Fig. 6. *Bogidiella veneris* n. sp. from Venus Bay, South Australia. Photo showing habitus of female holotype (3.6 mm).

pleopods and/or uropods. Koenemann and Holsinger only used these sexually dimorphic characters to define their new genera. To date, the majority of genera still lacks comprehensive diagnoses that include detailed intergeneric comparisons.

With the addition of B. veneris, Bogidiellidae now contains 108 described species that are distributed among 35 genera. Many of these genera are monotypic or composed of a limited number of species that occur within the same region or area, and as just noted their generic definitions are mostly limited to sexually dimorphic modifications or reductions of the urosomal appendages. Bogidiella Hertzog, 1933 is the historically oldest and also the largest genus of the family, embracing 39 species assigned to four groups by Koenemann and Holsinger (1999). Species assigned to group A are defined by the absence (complete reduction) of the inner pleopodal rami, while in groups B and C, the inner rami are present, but largely reduced (with the sole exception of B. thai Botosaneanu and Notenboom, 1988, a species with absent inner rami in group C). Group D contains species, of which only one sex is known, which prevented an ambiguous assignment to one of the groups defined by sexual dimorphism. Holsinger et al. (2006) erected a fifth group (E) based on the discovery of B. indica, a species characterized by absent inner pleopodal rami and a morphologically conspicuous pereiopod 5.

Bogidiella is distinguished by the absence of marked morphological modifications rather than the presence of synapomorphies. A clear-cut distinction between morphologically similar genera such as *Bogidiella*, *Medigidiella*, and *Stygogidiella* is not available. Thus, our assignment of the new species from Venus Bay to the genus *Bogidiella* is mainly based on: 1) shared plesiomorphies, and tempered by 2) the fact that morphological characters of males are still unknown. As such, our assignment is in accordance with the present taxonomic framework. However, the present taxonomy is far from satisfactory. The deep sequence divergences that were found between taxa belonging to three species groups in *Bogidiella* (Table 1) indicate ancient separation of these taxa and ordinarily would warrant separate generic status. To assign new taxa, a thorough taxonomic revision based on morphology as well as DNA sequence data is much-needed.

Together with *Xystriogidiella capricornea*, *X. juliani* and *Bogidomma australis* Bradbury and Williams, 1996, *Bogidiella veneris* is the forth described species of Bogidiellidae from the Australian continent. The recent discoveries of new bogidiellids, including of *B. indica* (Holsinger et al., 2006) and species from Oman (Iannilli et al., 2006) fill several gaps in the global distribution pattern of the family (see Fig. 1).

Moreover, the presence of the new species in shallow calcareous Pleistocene dune formations (Bridgewater formation) near the coast might suggest that the species evolved relatively recently from a marine ancestor, probably during one of the marine transgressions that took place during interglacials in the Pleistocene. This observation, as well as the occurrence of other Australian species in anchialine systems of small islands in the Great Barrier Reef (Coleman, 2009) and Barrow Island (Humphreys, 2002), could add to the growing support for the hypothesis that freshwater bogidiellids evolved from marine ancestors.

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