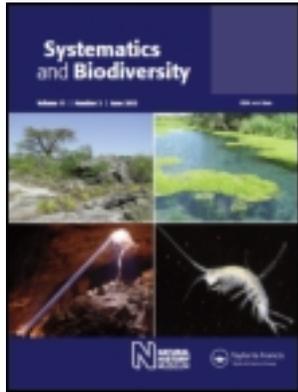


This article was downloaded by: [University of Ljubljana], [Cene Fišer]

On: 15 July 2013, At: 04:52

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



## Systematics and Biodiversity

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tsab20>

### Two new Amphipod families recorded in South America shed light on an old biogeographical enigma

Cene Fišer<sup>a</sup>, Maja Zgamajster<sup>a</sup> & Rodrigo L. Ferreira<sup>b</sup>

<sup>a</sup> SubBioLab, Department of Biology, Biotechnical Faculty, University of Ljubljana, Slovenia

<sup>b</sup> Departamento de Biologia Universidade Federal de Lavras, Lavras, Minas Gerais, Brasil

Published online: 21 Jun 2013.

To cite this article: Cene Fier, Maja Zgamajster & Rodrigo L. Ferreira (2013) Two new Amphipod families recorded in South America shed light on an old biogeographical enigma, *Systematics and Biodiversity*, 11:2, 117-139, DOI: [10.1080/14772000.2013.788579](https://doi.org/10.1080/14772000.2013.788579)

To link to this article: <http://dx.doi.org/10.1080/14772000.2013.788579>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <http://www.tandfonline.com/page/terms-and-conditions>

## Research Article

# Two new Amphipod families recorded in South America shed light on an old biogeographical enigma

CENE FIŠER<sup>1</sup>, MAJA ZAGMAJSTER<sup>1</sup> & RODRIGO L. FERREIRA<sup>2</sup>

<sup>1</sup>SubBioLab, Department of Biology, Biotechnical Faculty, University of Ljubljana, Slovenia

<sup>2</sup>Departamento de Biologia, Universidade Federal de Lavras, Lavras, Minas Gerais, Brasil

(Received 25 January 2013; revised 13 March 2013; accepted 14 March 2013; first published online 21 June 2013)

The known diversity of freshwater amphipods in South America is substantially lower than on other continents. This has puzzled biologists for decades. Two hypotheses have been proposed in attempts to explain this pattern. According to the first one, the majority of amphipod lineages never dispersed across South America. The alternative hypothesis is that the recently diversified hyallellids have outcompeted and depleted the ancestral amphipod fauna. The recently discovered freshwater amphipod species *Seborgia potiguar* sp. nov. (Seborgidae) and *Potiberaba porakuara* gen. nov., sp. nov. (Mesogammaridae) from Brazil reveals the existence of two additional families of amphipods in South America. In the light of these discoveries we have analysed the amphipod faunistic structure of South America to test the above two biogeographic hypotheses. First, the number of amphipod families in South America is not as low as was thought. Falklandellidae are limited to the Falkland Islands and Chile. All other families (Ingolfiellidae, Bogidiellidae, Phreatogammaridae, Paraleptamphopidae, Pseudoingolfiellidae, Paracorpohiinae, Mesogammaridae and Seborgidae) but one (Dogielinotidae) share two properties: (1) they have a transoceanic distribution and (2) they are from subterranean waters. Since the dispersal ability of amphipods is limited, trans-oceanic disjunctions are best explained by plate tectonics, which implies their early origin, negating the first biogeographical hypothesis. These ancient families, for unknown reasons, survived only in a stable subterranean environment which can be regarded as a refuge. The only recent colonizer of the continent might be Dogielinotidae with the species-rich genus *Hyalrella*. Although it cannot be determined whether hyallellids truly out-competed ancient amphipods, we suggest that the second hypothesis fits better to the data. Further findings of amphipods are expected in South America, especially from subterranean waters. This habitat is highly endangered in Brazil, and should be more rigorously protected.

<http://www.zoobank.org/urn:lsid:zoobank.org:pub:CBE21C1E-4748-4237-9EAD-FBD240A7D501>

**Key words:** Amphipoda, biogeography, Brazil caves, Mesogammaridae, plate tectonics, relict species, Seborgidae, South America, subterranean species

## Introduction

Understanding the origin of present-day faunas on a continental scale remains one of the challenges in biodiversity research. The central problem for such research is that it deals with events that occurred in the deep past. For this reason key determinants that shaped present-day distributions are difficult to identify. This paper is focused on the freshwater amphipod fauna of South America. Two hypotheses on their biogeography and origin were proposed 30 years ago. Since then, the inventory of South American amphipods has changed significantly and the theoretical framework of biogeography has been refined (Wiens & Donoghue, 2004; Wiens, 2011). In this study we (i) describe, for the first time, two species belonging to families

previously not recorded in South America, (ii) review the taxonomic structure and characterize ecologically the freshwater amphipods of South America, and (iii) reconsider existing proposed hypotheses in the light of new data.

Amphipod crustaceans comprise an important group of aquatic invertebrates with approximately 10 000 described species, a number that increases annually by approximately 100 new species (estimated from Amphipoda Newsletters 33–36). Freshwater species number fewer than 2000; however, they can be abundant and ecologically extremely important for local ecosystems (MacNeil *et al.*, 1997, 1999, 2000). The global distribution of amphipods is uneven. A recent review of freshwater amphipods is in agreement with earlier suggestions (Barnard & Barnard, 1983) that most of the diversity of species is seen in the northern hemisphere whereas that of genera is highest in the tropics

Correspondence to: Cene Fišer. E-mail: [cene.fiser@bf.uni-lj.si](mailto:cene.fiser@bf.uni-lj.si)

(Väinölä *et al.*, 2008). The proportionally low diversity (on species, genus and family levels) of freshwater amphipods in South America has been a puzzle for almost 30 years (Barnard & Barnard, 1983; Barnard & Karaman, 1983). So far, two hypotheses have been offered to explain this low amphipod diversity (Barnard & Barnard, 1983). The first suggests that the majority of amphipod lineages never dispersed across South America. The second postulates that the recently diversified genus *Hyaletta* (family Dogielinotidae) out-competed ancestral amphipod fauna in surface waters. Neither of these hypotheses has been explored in more detail over the past 30 years. The acquisition of further relevant data could help in their critical assessment.

Amphipods keep their offspring in a ventral pouch and lack a dispersal stage (Kristjánsson & Svavarsson, 2007; Myers & Lowry, 2009; Bauzá-Ribot *et al.*, 2012). Long-distance dispersal is therefore unlikely, and we are aware of only one genus (*Orchestia*) that could possibly exploit a natural means of long-distance transport, i.e. driftwood (see e.g. Wildish, 1982). Both hypotheses can suggest some predictions for consideration. If amphipods never dispersed across South America, we would expect the number of phyletic lineages (i.e. families) to be low compared with the numbers of phyletic lineages on other continents from the southern hemisphere. Most of the extant amphipods would therefore be expected to be recent arrivals, which means that their nearest extant relatives live in neighbouring seas. By contrast, if old lineages were out-competed, most extant lineages would be expected to be old, having survived mainly in habitats inaccessible to invasive Dogielinotidae. We therefore posed the simple question as to where, outside South America, relatives of extant South American amphipods live. This question includes both ecological (freshwater–marine, epigeal–hypogean) and geographical components, since we attempted to reconcile evolutionary and ecological processes at the species level (reviewed by Sexton *et al.*, 2009) with large-scale biogeographic events like plate tectonic or fauna interchange that might have happened in past times (e.g. Marshall, 1988; Vermeij, 2005). Data for this study have been derived from the literature and supplemented by new data on two amphipod species collected during recent caving expeditions. Our results support the second proposed hypothesis which is, in turn, reformulated.

## Materials and methods

### Data collection

Data on amphipods from South America were collected from the literature (references are listed in Appendix 1, see supplementary material, which is available on the Supplementary tab of the article's Taylor & Francis Online page at <http://dx.doi.org/10.1080/14772000.2013.788579>) and searched in four steps as follows:

1. **Species checklist of South America.** In the first step we relied on available checklists (Botosaneanu, 1986; Koenemann & Holsinger, 1995), including the web service of the World Register of Marine Taxa [<http://www.marinespecies.org/>]. For records of new species we relied on Amphipod Newsletters, a catalogue issued annually that summarizes newly discovered amphipod taxa ([http://www.oeb.harvard.edu/faculty/giribet/lab/docs\\_download/AN36.pdf](http://www.oeb.harvard.edu/faculty/giribet/lab/docs_download/AN36.pdf)). All the names were revised, using either taxonomic or phylogenetic revisions. We searched exclusively for amphipods living in South America; Central America was excluded (note the discrepancy in data with those of Väinölä *et al.*, 2008, in which the data for all Neotropics were merged).
2. **Monophyly.** Vicariance events can be inferred only from phylogenetic relationships, i.e. allopatric sister taxa imply vicariance of populations of common ancestor. Taxonomic ranks (genus, family) are not assigned in a unified way. For this reason, those in different groups cannot be considered either as surrogates for time or for detection of common vicariant events. To avoid this problem, we searched for monophyletic groups of species (at the rank of genus or family) that are distributed in fresh waters of South America and outside it (either in oceans or fresh water outside South America). The phylogenetic structure of amphipod groups from South America was obtained from available published sources (Table 1).
3. **Species checklists outside South America.** Using phylogenetic structure, we searched for sister clades outside South America. With the exception of Bogidiellidae and Ingolfiellidae, exhaustive checklists of entire families were not compiled; clades were limited to putative monophyletic groups that include South American species and their sister taxa.
4. **Ecological data.** All species in the final lists were assigned two parameters: the salinity of water where the species was found, and whether it lives in epigeal or hypogean waters. Wherever possible, we relied on information from revisions; in many cases we had to consult basic taxonomic works.

### Analysis of distributional data

The absence of molecular phylogenies does not allow rigorous biogeographic tests (see Bauzá-Ribot *et al.*, 2012; Botello *et al.*, 2013). The data are reviewed more descriptively (see Kristjánsson & Svavarsson, 2007). We employed chi-square tests in all issues raised, keeping in mind that this procedure requires the assumption that the same criteria were adhered to in field work and taxonomic evaluation and in data collection across all areas involved.

The assembled data were considered according to the following four assumptions:

**Table 1.** Zoogeographic comparison of South American amphipods.

Family	Number of genera/species (in South America)	Test of monophyly (quality)	Distribution of the group	Distribution in South America	Distribution outside South America <sup>c</sup>	Epi/hypogean (South American)	Salinity (South American)	Presumed original habitat
Bogidiellidae	38/116 (12/18) 9 genera endemic to continent, presumably representing early lineages of the family; 3 genera have relatives outside S. America	combination of cladistic analysis and diagnosis (Koenemann & Holsinger, 1999)	worldwide	Argentina, Brazil, Colombia, Ecuador, Venezuela	(i) Trans-Atlantic ( <i>Spyogidiella</i> , <i>Bogidiella</i> B) (ii) worldwide ( <i>Bogidiella</i> A) (iii) Caribbean Sea ( <i>Marigidiella</i> ) (iv) Trans Pacific ( <i>Bogidiella</i> C)	hypogean	marine-fresh water (fresh water)	not clear, last revision considers them of marine origin (Janilli <i>et al.</i> , 2006)
Ingoiffellidae	6/56 (1/5)	cladistic analysis (Vonk & Schram, 2003)	worldwide	Argentina; Brazil, Chile, Peru, Venezuela	at least three lineages, two of them with transatlantic sister species (57)	hypogean	marine-fresh water (fresh water)	presumably fresh water (Vonk & Schram, 2003)
Dogielinoitidae	1/61 <sup>a</sup> (1/43)	cladistic analysis (Serejo, 2004)	North and South America	continental	North America, Pacific, Atlantic	mainly epigean	marine-fresh water (fresh water)	marine (Serejo, 2004)
Mesogammaridae	6/7 (1/1)	diagnosis, defined on a basis of molecular phylogeny (Tomikawa <i>et al.</i> , 2007)	N Pacific rim distribution (Myers & Lowry, 2009)	Brazil	East India, South Korea, Japan, Alaska	hypogean	fresh water (fresh water)	fresh water (marine?) Tomikawa <i>et al.</i> , 2007
Pseudoingolfellidae	2/5 (1/1)	cladistic analysis (Grosso <i>et al.</i> , 2006)	Trans-Pacific (Myers & Lowry, 2009)	Chile	New Zealand, Kerguelen Island	hypogean	brackish to fresh water (brackish)	fresh water (Grosso <i>et al.</i> , 2006)
Paraleptamphopidae	3/4 (1/1)	cladistic analysis (Grosso & Petalita, 2009)	Trans-Pacific (Myers & Lowry, 2009)	Chile	New Zealand	hypogean	fresh water (fresh water)	fresh water
Phreatogammaridae	3/6 (1/1)	diagnosis, last revision by Bréhier <i>et al.</i> (2010)	Trans-Pacific (Myers & Lowry, 2009)	Chile	New Zealand, New Caledonia	mainly hypogean	fresh water (fresh water)	fresh water
Seborgiidae	1/7 (1/1)	diagnosis, based on non-fused body segments of urosoma (Jaume <i>et al.</i> , 2009)	Trans-Indo-Pacific-Caribbean (Myers & Lowry, 2009)	Brazil	Texas, Renell Islands, Loyalty Islands, Vanuatu, Vietnam	hypogean	brackish to fresh water (fresh water)	fresh water to brackish water
Corophriidae <sup>b</sup>	3/7 (1/1) <sup>d</sup>	cladistic analysis (Myers & Lowry, 2003)	Trans-Pacific (Myers & Lowry, 2009)	Chile	Australia, Philippines, New Zealand	epigean	marine-fresh water (brackish)	marine
Falklandellidae	2/2 (2/2)	diagnosis (Lowry & Myers, 2012, 2013)	Falklands, Chile (Pérez-Schultze 2013)	Falkland Islands, Chile	—	hypogean	fresh water	fresh water

<sup>a</sup>Number of species in North America is underestimated; there are at least 38 cryptic species (Witt *et al.*, 2006). <sup>b</sup>Only clade paracorphiini. <sup>c</sup>In Ingoiffellidae and Bogidiellidae we explored in detail putative sister relationships, based on the available phylogenies. <sup>d</sup>Species *Paracorphium chilensis* was synonymized with *P. harmannorum* (González, 1986).

1. **The number of phyletic lineages is low compared with that from other continents from the southern hemisphere.** This was tested using the family as surrogate for phyletic lineage (Table 1, column 1), the only category that made testing possible because of the limited availability of data from other continents. Data from other biogeographical regions were obtained from Väinölä *et al.* (2008) updated by Ianilli *et al.* (2011).
2. **Most phyletic lineages are of recent origin.** Given the poor migratory ability of amphipods this assumption would suggest recent origin from marine ancestors. The null hypothesis was that, in South America, lineages with nearest relatives in a marine environment prevail (Table 1, column 9).
3. **Most phyletic lineages are old.** In support of this prediction on a continental scale, we expected that nearest relatives would be found in disjunct, trans-oceanic areas. Such a distribution could best be explained by plate tectonics, consequently pointing to ancient origins of lineages (e.g. Myers & Lowry, 2009). To ensure robustness, we tested this prediction at the family level (Table 1, column 1). The families Falklandellidae and Paraleptamphopidae are presumably sister taxa (Lowry & Myers, 2013). The two families were considered as a single, biogeographically representative unit, in order to avoid inflating the number of South American taxa in the testing procedure.
4. **Most phyletic lineages survived in habitats inaccessible to invasive Dogielinotidae.** If Dogielinotidae were invasive and out-competed other amphipod groups in surface habitats, other groups would either have become extinct or would remain in environments inaccessible to the more recent colonizer. Ecologically harsh environments, i.e. those in which at least one of the environmental parameters reaches extreme values, might be difficult to colonize; this may be especially true if it already harbours species adapted to its habitat. Subterranean environments can be regarded as extreme, since they are determined with total darkness, reduced environmental fluctuations and mostly lower food supply (the last may be questionable in tropics (Culver & Pipan, 2009)). We postulate that the majority of extant phyletic lineages will live in subterranean environments (Table 1, column 7).

### Description of new species: collecting sites

The newly described specimens examined in this work came from collections conducted in two caves located in Rio Grande do Norte state in Brazil (Figs 1–3). The caves belong to a limestone formation called the Apodi group. Most of the area is covered by limestone outcrops locally called

‘lajedos’. Such formations contain hundreds of caves, with an extraordinary subterranean biodiversity that is just beginning to be revealed (Ferreira *et al.*, 2010). Specimens were collected manually in Três Lagos cave on 10 January 2006 and by baited traps installed in the lake in Caverna da Água cave on 3 June 2010. Detailed descriptions of caves are given in the descriptions of type localities.

### Description of new species: laboratory work

Specimens were cooked in KOH solution, washed in water, transferred into glycerol and finally dyed with chlorasol black. Specimens were partly dissected in glycerol, and mounted on slides in a glycerol–gelatine medium. Digital photos were taken with an Olympus DP10 camera mounted on an Olympus SZX9 stereomicroscope and a Euromex microscope. Measurements and counts were made using the computer program Olympus DP–soft. Finer details were examined using a Euromex microscope with magnifications 100 to 400×.

Specimens of one of the two species were also observed under an electronic scanning microscope. A specimen was placed with carbon tape, on aluminium support stubs, over a film of aluminium foil, sputter-covered with gold (Baltec SCD 050), and observed under a LEO EVO 40 XVP scanning electron microscope (Leo Electron Microscopy).

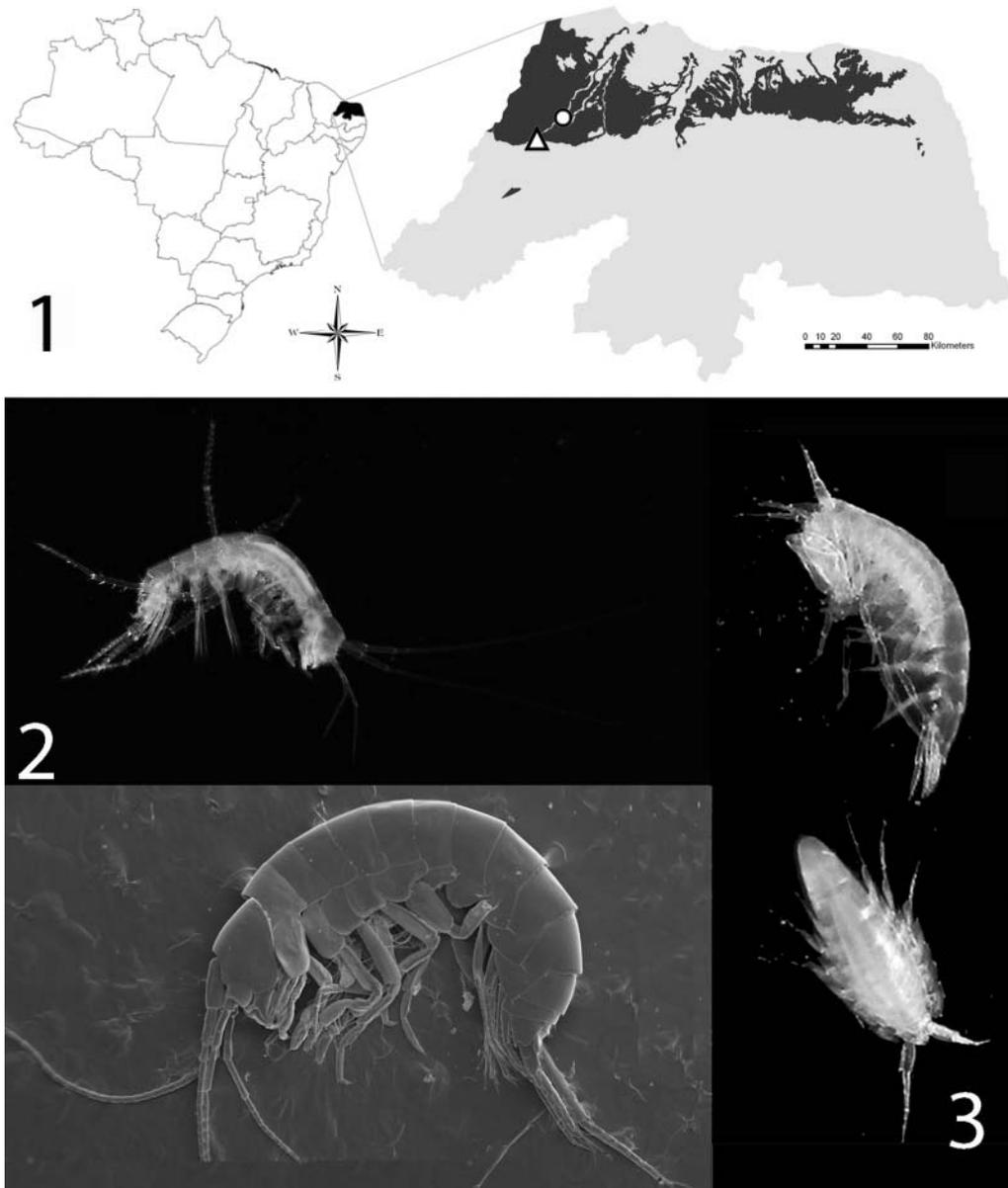
## Results

### Faunistic overview

The new discoveries and a detailed bibliographic overview jointly confirm the presence of ten amphipod families in South America (Table 1, Appendix 1, see supplementary material online). This revision has expanded the list of species in many cases; details are listed in supplementary material online. The data used in the main analyses are presented in Table 1.

The taxonomic rank that is biogeographically informative for the present purposes includes species present in and outside South America. This rank ranges from individual clades below genus level to family. The most critical element in the analysis, the monophyly of zoogeographically informative taxa, was tested in all but one case (family Seborgiidae, see Jaume *et al.*, 2009). The type of data (mainly morphology) and the quality of tests of monophyly vary and are summarized in Table 1 with references.

The number of currently established phyletic lineages in South America (10 families) is marginally higher than those in Africa (8 families,  $P = 0.64$ ; with Madagascar 9 families,  $P = 0.82$ ) and in Oriental (7 families,  $P = 0.47$ ; with Madagascar 8 families,  $P = 0.64$ ), and lower than in Australia (12 families,  $P = 0.67$ ); however, the data do not support the suggestion that the number of families

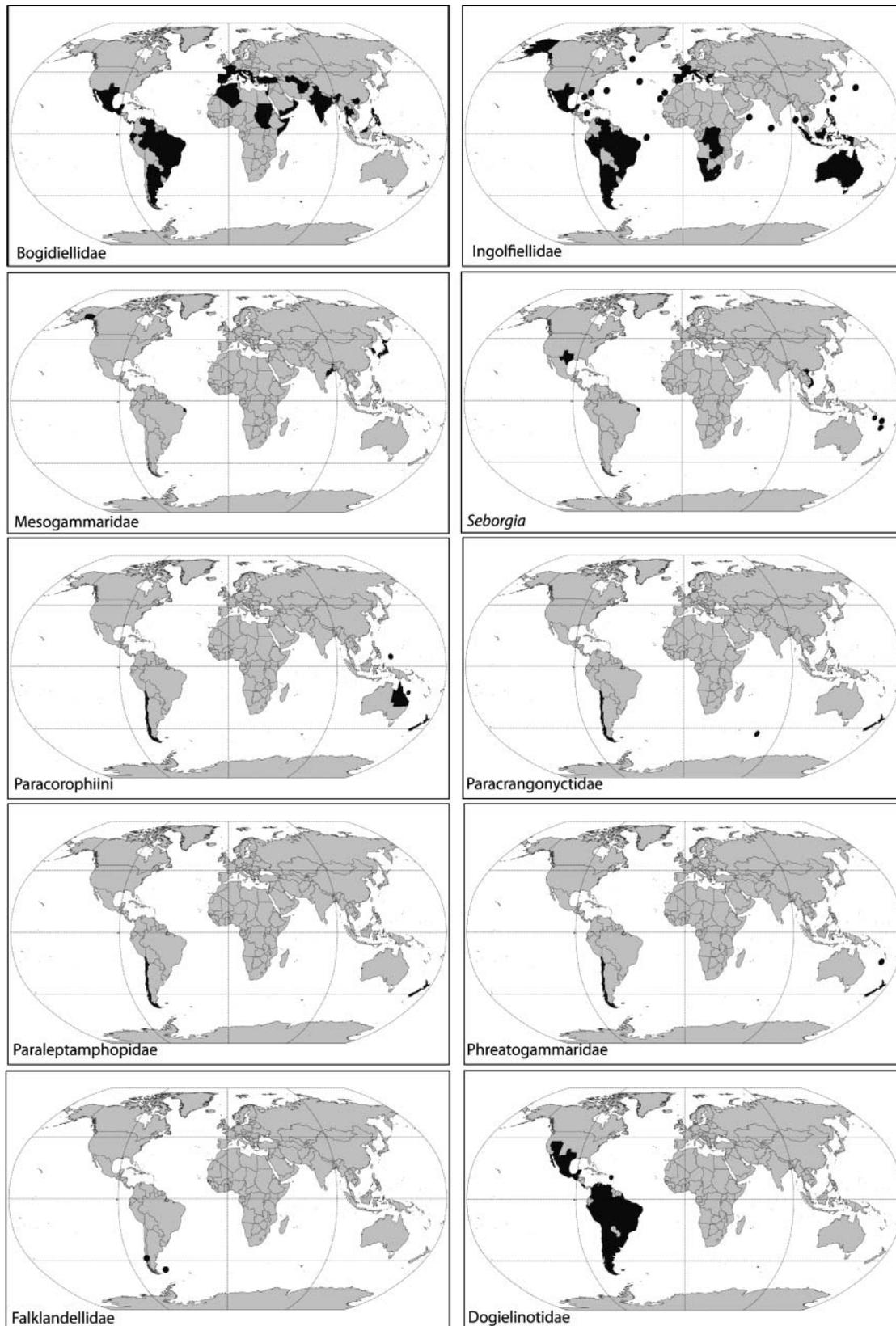


**Figs 1–3.** New findings of amphipods in Brazil, state Rio Grande do Norte. **1.** The localities where *Potiberaba porakuara* (triangle) and *Seborgia potiguar* (circle) were found. The black area represents the limestone outcrops from the Apodi Group. **2.** *Potiberaba porakuara* live and under scanning microscopy. **3.** *Seborgia potiguar* live; note the back-up position when crawling.

is considerably lower than in other southern hemisphere continents.

It is difficult to determine whether the taxa originate from marine or other environments. Many hypotheses have been proposed as to the origin of individual groups (see Table 1). The suggestion that recent taxa have close relatives in the sea cannot be rejected ( $P = 0.21$ ). On the other hand, if the global distribution of taxa that also have members in South America is considered (Fig. 4), it appears that most South American taxa exhibit a trans-

oceanic distribution ( $P = 0.02$ ). This is a robust estimation, since phylogenetic analyses indicate that the number of trans-oceanic lineages below genus level could be higher (Table 1, column 6,  $P > 0.001$ ). Comparison of hypogean and epigean fauna in South America indicates that hypogean lineages predominate (Dogielinotidae considered as epigean and included in the testing – marginal significance  $P = 0.057$ ; Dogielinotidae considered as ecologically ambiguous and excluded from testing  $P = 0.02$ ).



**Fig. 4.** Global distribution of amphipod taxa with representatives in South America. Dark shaded areas show areas where the members of taxa were found; the precision is adjusted to administrative units. Detailed data can be found in supplementary material online.

## Systematics

### SEBORGIIDAE

#### *Seborgia potiguar* sp. nov.

(Figs 3, 5–10)

**HOLOTYPE.** Female, partly dissected and mounted on slides; deposited in a collection of Department of Biology, Biotechnical Faculty Ljubljana, voucher number NB190.

**PARATYPE.** Female, partly dissected and mounted on slides; deposited in a collection of Department of Biology, Biotechnical Faculty Ljubljana, voucher number NB191.

**TYPE LOCALITY.** The Caverna da Água Cave (05°29'44.11"S, 37°32'42.24"W, Fig. 1) located in the municipality of Governor Dix-Sept Rosado (Rio Grande do Norte State) is the only known locality of this species. The small cave entrance (about 60 × 40 cm) connects to a vertical shaft 28 m deep, with a small (*c.* 5 m in diameter) lake at the bottom of the cave, fed from a phreatic (saturated) zone. According to reports from local residents, the water level in the lake varies by more than 15 m, depending on the season and rainfall in the region. Water parameters measured in January 2010 were pH = 7.3, conductivity = 0.14 μS-1, dissolved oxygen = 5.1 mg/L and temperature = 28.6°C. The organic components are bat guano and plant debris transported through the cave entrance. Although there are no visible submerged conduits, the phreatic level most probably connects to the nearest epigeal drainage of the Apodi River (located about 900 m linear distance from the cave entrance), as inferred from the presence of epigeal characid fishes *Astyanax* spp. in the lake. Due to the difficult access the cave is rarely visited, therefore direct human impacts on the system are low.

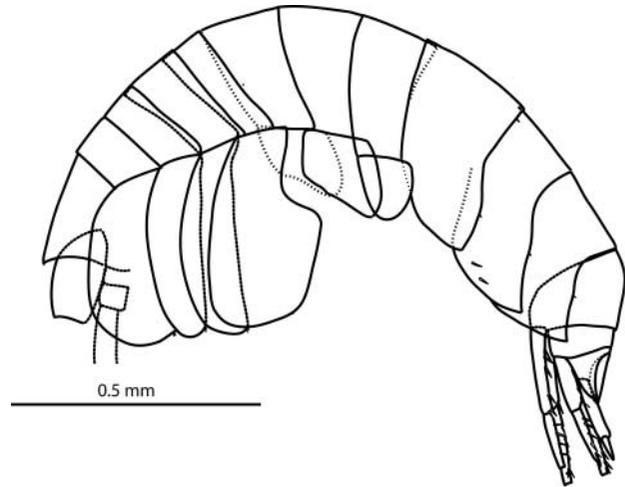
All amphipod individuals were collected by traps using goat liver as bait. No specimens were observed in the lake by visual inspection, implying either that the population density of *Seborgia* is low, or that we did not sample their primary habitat.

**ETYMOLOGY.** The new species is named *potiguar*, which is a local name for residents born in the Rio Grande do Norte State, Brazil. The name is to be treated as a noun in apposition.

**DIAGNOSIS.** *Seborgia* defined with exclusive combination of strongly setose distal segment of mandibular palp (three D and four E-setae); maxilla II bilobed; gnathopods I–II parachelate; basis of uropod I with several mid-lateral spiniform seta.

**DESCRIPTION OF FEMALE (MALE UNKNOWN).** **BODY** (Figs 3, 5, 10). Compact, stout; colourless and eyeless, approximately 1.5 mm in length. When alive, crawls on the sediment oriented upright. Head without rostrum; head lobe undeveloped; antennary sinus broad. Posterodorsal margin of pleonites smooth, each with one tiny seta.

Epimeral plates I–III with posterodistal angle produced; ventral margins concave; posterior margins convex in plate



**Fig. 5.** Body shape of *Seborgia potiguar* sp. nov. Appendages were removed and are not shown.

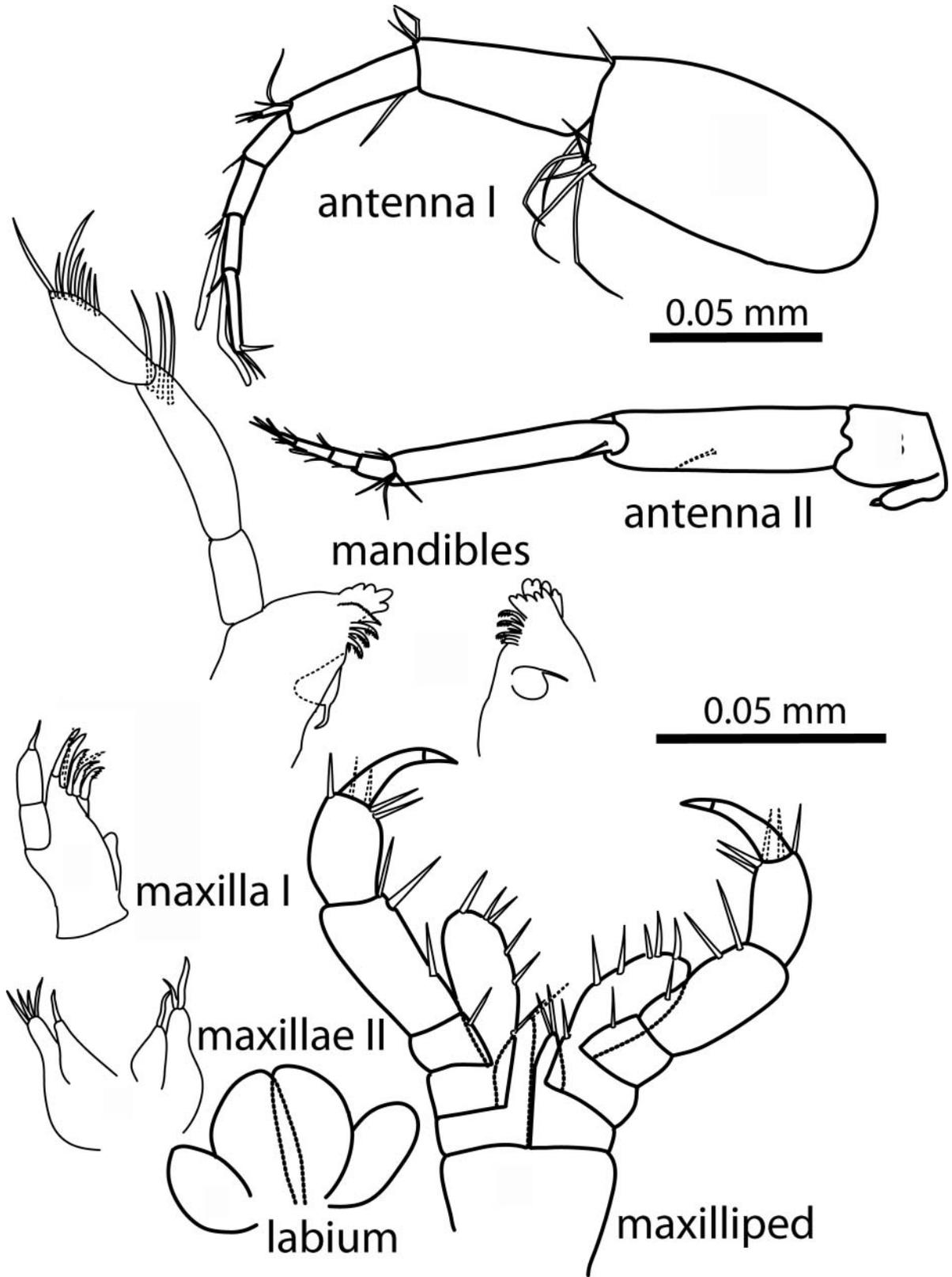
I and slightly sinusoid in plates II–III. Posterior margins of epimeral plates with 1 tiny seta, ventral margins of plate I and III without armature, plate II with two spiniform setae submarginally.

Urosomites I–III free, the third somite posteriorly strongly produced and almost reaches the tip of the telson. No armature was detected on uronites. Telson entire, approximately twice as long as wide, narrowed apically, with two single and one pair of tiny setae close to lateral margins.

**ANTENNAE I–II** (Fig. 6). Antenna I short, approximately 1/3 of body length. Peduncle segments in proportion 1 : 0.6 : 0.45; each peduncular article with 2–7 distal setae. Accessory flagellum uniaarticulate, approximately 1/2 of the length of the first flagellum, apically with 3 setae. Main flagellum 4 articulated, as long as the first peduncular article. Each of the distal-most articles with 1 long aesthetasc.

Lengths of antenna I and II in ratio 1 : 0.6. Antenna II peduncle with long gland cone, directed anteriorly. Peduncle segments 4 and 5 of approximately equal length, both articles with one facial and 1 and 7 distal setae. Flagellum with four articles, approximately 1/2 of the length of the first flagellum; each article with up to 5 setae, the distal two articles with one aesthetasc.

**MOUTHPARTS** (Fig. 6). Incisor and lacinia of the right mandible both with 5 teeth, spine row comprising four elements with brush-like setules between. Molar process weak, distal seta slender. Left mandible as right counterpart except for fine-denticulated lacinia, and three elements in spine row. Palp segments length ratio 1 : 2.2: 1.7; second segment with cluster of 3 setae on distomedial margin. Distal segment with three D-setae and four E-setae.



**Fig. 6.** Antennae I–II and mouthparts of *Seborgia potiguar* sp. nov. Upper scale bar refers to antennae, lower to the rest of appendages.

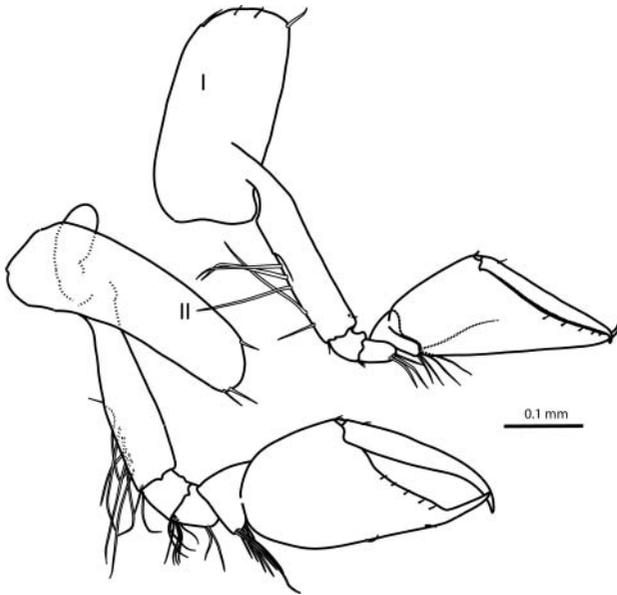


Fig. 7. Gnathopods of *Seborgia potiguar* sp. nov. The number corresponds to the order of appendage.

Maxilla I with conical inner plate bearing no setae. Outer lobe with seven strong and spiniform setae, the inner 3 apically finely denticulated. Maxillar palp biarticulated, both articles approximately equally long, with a single apical seta. Maxilla II bilobed, inner lobe of approximately 2/3 of outer lobe; inner lobes with 1 apical seta, outer lobes with up to 4 setae.

Maxilliped inner lobes small and narrow, with 1–2 apical seta; outer lobes broad, reaching middle of carpal article in palpus, with 5 mesial-subapical setae. Palpus four articulated, articles in ratio 1 : 2.7 : 1.8 : 2; each article with 1–5 setae. Basal articles if maxilliped not fused. Labium inner lobes remarkably larger than outer lobes, fully separate.

COXAL PLATES (Figs 5, 7, 8). Coxal plates I–IV dorsoventrally elongated, the respective widths (anteroposterior lengths) are 0.5, 0.4, 0.35 and 0.55 of their depths (dorsoventral distances). Coxal plate I partially covers the head. Coxal plate IV with deep incision, measuring 0.2 of its depth and 0.37 of its width; anterior and posterior margins subparallel. Along distal margins 1–4 setae. Gills II–V small, ovoid or narrow. Coxal plates V–VI approximately bilobed, posterior lobe much larger. Coxa VII roughly triangular.

GNATHOPODS I–II (Fig. 7). Articles 2–5 similar in both pairs, in gnathopod II slightly more densely setose. Article 5 produced anteriorly and supports remarkably enlarged propodus. Both gnathopods distally chelate, the second gnathopod somewhat longer and bulkier. Gnathopod I with triangular propodus, postero-distal processus hooked, palm concave, finely crenulate with 5 submarginal setae; at joint with dactylus two tiny setae. Dactylus slender, distally

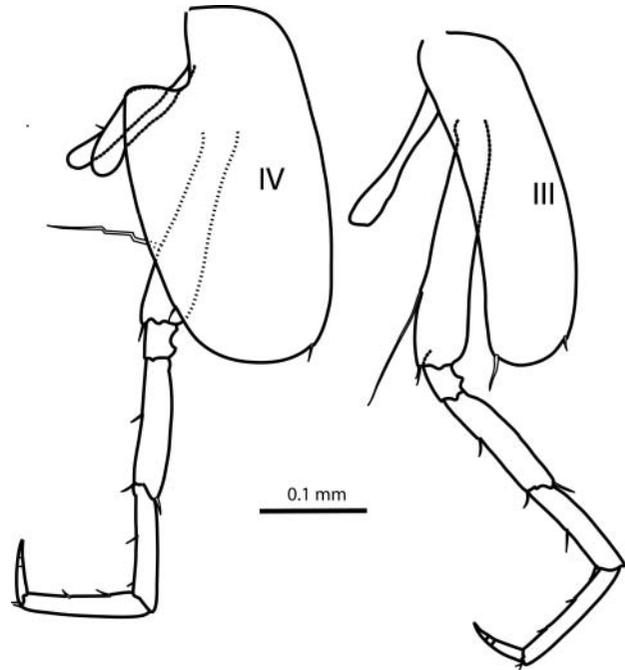


Fig. 8. Pereopods III–IV of *Seborgia potiguar* sp. nov. The number corresponds to the order of appendage.

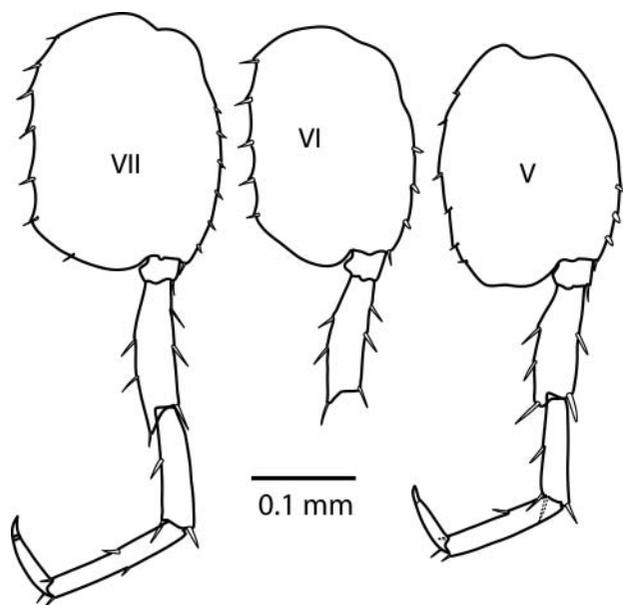
hooked, with single dorsal seta in proximal part. Gnathopod II with 2 tiny posterior setae; blade-like posterodistal processus; palm concave with 5 submarginal setae; at joint with dactylus two tiny setae. Dactylus slender, distally hooked, with single dorsal seta in proximal part.

PEREPODS III–IV (Fig. 8). Slender, similarly long, sparsely setose, with unguis not incorporated into dactylus, i.e. articulating basally with it; dactylus with tiny dorsal seta proximally.

PEREPODS V–VII (Fig. 9). Pereopod V broken distally, pereopods VI : VII as 1 : 1.15. Bases broad, dilated posteriorly; the respective bases widths are 0.81, 0.88 and 0.88 of their lengths. Posterior margins convex, with 5, 6, 7 setae, respectively; anterior margins with 4, 4 and 7 stout setae respectively. Dactylus slender, approximately 1/2 of propodus length, unguis visible, single dorsal seta in proximal part.

PLEOPODS with protopod smooth, with two retinacles each.

UROPODS (Figs 5, 10) progressively shorter towards posterior. Uropod I protopod as long as inner ramus, with 5–6 lateral spiniform setae and 1 mesio-distal seta. Uropod I rami pointed; outer ramus approximately 2/3 of inner ramus; outer ramus with 6 single dorsal spiniform setae; inner ramus with 4 dorsal spiniform setae. Uropod II rami pointed; outer ramus approximately 1/2 of inner ramus; outer ramus with 5 pairs and 1 single dorsal spiniform setae; inner ramus with 3 dorsal spiniform setae. Uropod III



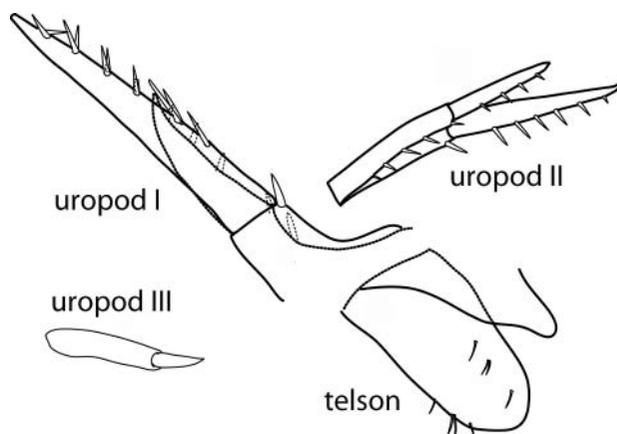
**Fig. 9.** Pereopods V–VII of *Seborgia potiguar* sp. nov. The number corresponds to the order of appendage.

biarticulated, distal article approximately 1/2 of the proximal article; no setae have been seen.

**REMARKS AND AFFINITIES.** The newly described species matches with a revised diagnosis of genus *Seborgia* in all characters (see Jaume *et al.*, 2009). Using the framework of characters important in species delimitation, the newly described species most closely matches *S. relictata*, *S. hershleri* (both from USA) and *S. minima* (from Rennell Island). Our comparison is restricted to three readily observed traits that distinguish newly described species from all other species in the genus. First, the shape and size of both gnathopods differ from those of all other species described. While the shape of gnathopod I resembles the shapes of those observed in *S. relictata* and *S. kanaka* (Loyalty island, Melanesia), the shape of the second gnathopod in males is yet to be observed. Perhaps most closely resembling the one in *S. kanaka* the latter species, however, has a propodus of the second gnathopod smaller than that of the first. The second important character is the setal pattern of uropod I. With the exception of *S. vietnamica* (Vietnam), the protopod of uropod I has only one spiniform seta in each of the described species. Finally, the ramus of uropod III is shorter than the peduncle, a somewhat similar trait to that in *S. kanaka*, *S. sanctensis* (Vanuatu) and *S. schieckei* (Andaman Islands). For the sake of completeness, we present the comparative analysis of Jaume *et al.* (2009) completed with new data in Table 2.

**Mesogammaridae**  
***Potiberaba* gen. nov.**

**TYPE SPECIES.** *Potiberaba porakuara* sp. nov.



**Fig. 10.** Uropods and telson of *Seborgia potiguar* sp. nov.

**TYPE LOCALITY.** The Três Lagos Cave (05° 35' 32.44''S; 37° 41' 10.26''W, Fig. 1) located in the municipality of Felipe Guerra (Rio Grande do Norte State) is the only known locality of this species. The cave has four entrances, three of which are vertical and located at the bottom of three separate sinkholes. The fourth entrance is submerged and connected to an external lake. The cave has a phreatic level which fills most of the cave floor, forming three interconnected lakes after which the cave was named. Organic debris falls into the cave via the three vertical entrances, and there is input of bat guano (mainly insectivorous bats *Lonchorhina aurita* and haematophagous *Desmodus rotundus*) as well as via water connection to the outside lake. Water parameters in one of the subterranean lakes measured in January 2010 were: pH: 6.6, conductivity: 0.18  $\mu$ S, dissolved oxygen: 3.6 mg/L and temperature: 31.2°C. Fish and turtles enter the cave via this entrance when they seek shelter. Other troglobitic fauna found in the cave include undescribed cirrolanid isopods and flatworms.

At sampling sites we observed hundreds of individuals in the submerged guano deposits and also on submerged rocks. Most of the specimens were found in the lake with the submerged haematophagous bat guano pile; however it is uncertain whether this is their preferred source of food.

The cave is located near Felipe Guerra city and is visited regularly by local residents, who use the cave for swimming. Candles, bottles and cans are frequently left inside the cave. The fauna is probably affected by physical stepping, and by waste input that alters the physico-chemical properties of the water.

**ETYMOLOGY.** *Potiberaba* means 'transparent shrimp' in Tupi-Guarani language (Brazilian Indian language). The *poti* means shrimp and *beraba* means transparent or shiny. The name is to be treated as a noun in apposition.

**DIAGNOSIS.** Mesogammarid with three unique features: pars incisiva in left mandible with 7 denticles, remarkably

**Table 2.** Main diagnostic differences between *Seborgia* species. Completed with new species, after Jaume *et al.* (2009)

	<i>S. sanctensis</i>	<i>S. vietnamica</i>	<i>S. kanaka</i>	<i>S. relictata</i> + <i>S. hershleri</i>	<i>S. minima</i>	<i>S. schieckekei</i>	<i>S. potiguar</i>
Eyes: either vestigial or fully developed (+) vs. absent (-)	+	-	+	-	-	+	-
Rostrum: well developed (+) vs. reduced (-)	+	+	-	+	-	+	-
Pleonites, posterodorsal margin: serrate (+) vs. smooth (-)	+	-	-	-	-	+	-
AI flagellum: longer than peduncle (+) vs. shorter (-)	+	-	-	-	-	-	-
All peduncle segment 5: elongate (+) vs. ordinary (-)	+	-	-	-	-	-	+/-
Md palp segment 3 outline: rhomboidal (+) vs. slender subrectangular (-)	+	-	-	-	-	-	-
Md palp segment 3: number of E-setae	4	4	3	3	4	4	3
Md palp segment 3: number of D-setae	3	0	0	0	0	1	4
Labium, inner lobes: separate (+) vs. partially fused (-)	+	+	-	-	-	?	+
Maxilla II: bilobed (+) vs. unilobed (-)	+	-	-	-	-	-	+
Maxilliped: basis of left and right sides fused (+) vs. separate (-)	-	-	+	-	-	-	-
GI propodus form: subchelate (+) vs. parachelate (-)	+	+	+	-	+	+	-
GI female propodus proportions: longer than broad (+) vs. broader than long (-)	+	+	(-)	-	?	+	+
GI propodus palm angle: number of robust setae	2	2	2	0*	0*	1	0
GI unguis: elongate (+) vs. short (-)	+	-	-	-	?	-	-
GI–GII, relative size of propodus: strongly unequal (+) vs. equal (-)	-	-	-	+	-	-	-
GII female, propodus proportions: longer than broad (+) vs. equal or broader than long (-)	+	-	(-)	-	?	+	-
GII female, propodus palm angle: strongly protruded (+) vs. not protruded (-)	-	-	(+)	+	-	-	+
Coxa IV, posterior margin: strongly oblique (+) vs. subparallel to anterior margin (-)	-	+	(-)	-	-	-	-
PV, anterior lobe of coxa: present (+) vs. absent (-)	+	+	-	+	?	?	-
PV–PVII, posterodistal margin of basis: profusely serrate (+) vs. hardly serrate or smooth (-)	-	-	-	+	-	-	-
PV–PVII, posterior margin of basis: convex (+) vs. angled (-)	+	+	-	+	+	+	+
UI, length of rami: subequal (+) vs. distinctly unequal (-)	+	+	-	-	-	+	-
UI protopod mid-lateral armature: several robust setae (+) vs. 1 robust seta at most (-)	-	+	-	-	-	-	+
UIII condition: biramous (+) vs. uniramous (-)	+	-	-	-	-	-	-
UIII rami: longer than peduncle (+) vs. shorter (-)	-	+	-	+	+	-	-

Abbreviations: AI, II – antenna I, II; Md – mandible; GI, II – gnathopods I, II; PV–VII – pereopods V–VII; UI, III – uropods I, III. \*Denotes changed character states from original source, for we found them inappropriately labelled.

reduced dactylus of gnathopod II and peduncle of uropod III as long as peduncle of uropod I.

**DESCRIPTION.** Colourless and eyeless, without rostrum; posterodorsal margin of pleonites without seta. Urosomites I–III free, with up to five tiny setae along dorsoposterior margins. Telson clefted to the base, each lobe rectangular and approximately as wide as long, apically two setae with few tiny setae. Antenna I long, peduncle segments in proportion 1 : 0.75 : 0.45; accessory flagellum uniaarticulate, slightly longer of the first flagellar article, apically and subapically with 3 setae. Lengths of antenna I and II in ratio 1 : 0.45. Neither aesthetascs nor calceoli were observed. Incisors of the right and left mandibles with 7 and 6 teeth, laciniae with 6 teeth (right) and multidentulate (left mandibles); both molars well developed, tritritative. Mandibular palpus proximal segment with 2 distal setae, middle segment with cluster of 2 distomedial setae and distal segment with 11 D and 2 E setae; surface covered with carpet of setulae. Left and right maxilla I similar to each other; inner plate roughly triangular, with oblique row of rather long and well-developed setae; outer plate broad, with 9 and 10 pectinate spines, which are from medial towards lateral progressively more curved, medio-subapically, two tiny setae; maxillar palpus biarticulated; proximal article short, distal distally dilated with 6 and 7 spiniform marginal setae apically-subapically and 1 submarginal seta subapically. Maxilla II bilobed, inner lobe slightly shorter than outer; long, hairy hairs medio-distally and tiny setae medially and facially; outer lobe with long curved setae apically and tiny setae laterally. Maxilliped palpus 4-articulated. Labium with poorly developed inner lobes; inner and outer lobes hairy. Coxal plates I–IV dorsoventrally elongated or subquadrate, coxal plate IV without incision. Gills II–V pedicellate and ovoid, progressively larger until gill IV which extends beyond basis, gill V short. Coxal plates V–VII without distinct lobes. Oostegites on pereopods II–VI, narrow, with sparse, long setae. Gnathopod I carpus approximately triangular and propodus of gammaroid shape; palmar corner defined with spiniform setae; palm with numerous densely packed submarginal bifid spiniform setae. Gnathopod II slenderer than gnathopod I, with elongated carpus and with narrow propodus tapering distally; posterodistally produced into distal lobe bearing 2 bifid spiniform setae; dactylus largely reduced. Pereopods V : VI : VII as 1 : 1.17 : 1.28; bases ovoid, without distal lobes; propodi V–VII with bunches of posterior long setae; dactyli slender, with several spiniform ventral setae. Uropod I protopod : inner : outer ramus as 1 : 0.73 : 64; no basofacial spine on protopod was seen. Uropod III with elongated basis and equally long rod-shaped rami, outer ramus of 2 articles.

**REMARKS AND AFFINITIES.** We consider *Potiberaba* as a member of Mesogammaridae as its morphology agrees completely with the diagnosis justified by molecular analy-

sis (Tomikawa *et al.*, 2007). *Potiberaba* shows several similarities with *Octopupilla felix*, like fully cleft, albeit differently shaped, telson; shape of distal article of mandibular palp, shape of carpal articles of gnathopods I–II, the weaker propodus of gnathopods II than I, stalked gills, narrow oostegites, the elongated cylindrical endopod of uropod III and biarticulated exopod of uropod III. Diagnostic combination of *Potiberaba* is summarized comparatively in Table 3.

Despite the fact that *Potiberaba* fully matches the diagnosis, some additional comparative notes should be added. Tomikawa *et al.* (2007) redefined Mesogammaridae using a posteriori mapping of diagnostic characters onto a tree, suggesting that the revised diagnosis was based on synapomorphies. Comparison with previous diagnoses (Bousfield, 1977; Barnard & Barnard, 1983) shows that Mesogammaridae are much more diverse than traditionally perceived. Individual traits of *Potiberaba* can be assigned to several families, but classification of the genus to any of them would require modification of the concept of family.

*Potiberaba* shows some similarities with Phreatogammaridae, a family distributed in New Zealand, New Caledonia and recently found in Chile (Chapman, 2003, 2004; Ianilli & Ruffo, 2007; Bréhier *et al.*, 2010). Similarities include densely packed palmar spines, rod-shaped uropods III with elongated basis, and shape of telson (Barnard & Barnard, 1983). *Potiberaba* has no sternal gills (crangonyctid features), however, these gills are not developed in all phreatogammarids and are not a key property of the group (Bréhier *et al.*, 2010). Assigning *Potiberaba* to Phreatogammaridae would require significant redefinition of the latter. A new diagnosis should accommodate the presence of weakly developed inner lobes on labrum, absence of an oblique row of setae on inner lobe of maxilla II, pedicellate gills, narrow oostegites, the shape of gnathopod II, and well-developed distal article of exopodite on uropod III.

Another family, Liljeborgiidae shares the densely packed palmar spines on gnathopods I–II, cleft telson, narrow oostegites, equiramous uropods III with slightly elongated basis and two-articulated exopodite. However, in Liljeborgiids, antennae I are shorter than antennae II, mandibular molar is not developed, gnathopod II has a different shape, gills are not pedicellate, and rami of uropod III are not lanceolate and are less armed.

Important similarities can be identified with a broader group treated as a group of Hadziids–Melitids (Bousfield, 1977; Barnard & Barnard, 1983). Traits found within the broader context of this group include weakly developed lobes of lower lip, narrow oostegites, pedicellate gills, well-developed rami of uropods III and cleft telson, acknowledging that any of the traits may differ in one or the other genus. In any case, uropod III is rod-shaped, on an elongated basis, and uropod I has no basofacial spine. Interestingly, gnathopods of *Potiberaba* are a kind of ‘reversed melitid’

**Table 3.** Main diagnostic differences between genera of Mesogammaridae.<sup>a</sup>

	<i>Mesogammarus</i>	<i>Paramesogammarus</i>	<i>Eoniphargus</i>	<i>Octopupilla</i>	<i>Potiberaba</i>	<i>Indoniphargus</i>
Eyes present or at least vestigial (+) vs. absent (-)	+	+	-	+	-	-
Calceoli present (+) vs. absent (-)	-	+	+	-	-	+
AI accessory flagellum – number of articles	4	3–4	3–4	4	2	2
Md-left incisive (number of denticles)	5	5	5	5	7	?
Md-right incisive (number of denticles)	4	5	6	4	6	?
Md-palpus basal article setose (+) vs. not (-)	+	+	-	-	+	-
Md – distal article with setae	DE	ADE	ADE	ADE	DE	DE
Md-palpus distinctly falciform (+) vs. indist. falciform (-)	-	-	-	+	+	+
Maxilla II – oblique row of setae present (+) vs. absent (-)	-	-	+	+	-	-
Labium inner lobes vestigial (+) vs. absent (-)	-	+	-	+	+	-
Gills stalked (+) vs. non-stalked (-)	-	-	+	+	+	+
GI-propus length : width	1.6 : 1	2.5 : 1	1.8 : 1	1.8 : 1	1.6 : 1	1 : 0.83
GII carpus length : propus length	1 : 0.9	1 : 1.25	1 : 0.88	1 : 0.85	1 : 1.4	
GII propus length : width	2.2 : 1	1.6 : 1	2.3 : 1	2.5 : 1	2.6 : 1	
GII dactylus well developed (+) vs. strongly reduced (-)	+	+	+	+	-	+
PIII–VII dactyli with more than one seta (+) vs. one seta the most (-)	-	-	-	-	+	-
PV–PVII propods long post.dist setae present (+) vs. absent (-)	-	-	-	-	+	-
UI peduncle basofacial spines present (+) vs. absent (-)	-	+	+	+	-	+
UIII peduncle, elongated, as in UI (+) vs. short (-)	-	-	-	-	+	-
UIII rami of equal length (+) vs. unequal (-)	+	+	-	+	+	-
UIII exopodite distal article developed (+) vs. rudimentary (-)	+	+	+	+	+	-
Pleon segments spiny (+) vs. smooth (-)	+	-	-	-	-	-
Uronite III with rough setae (+) vs. no setae (-)	+	+	-	+	+	-
Telson longer than broad (+) vs. broader than long (-)	-	-	+	+	-	?
Telson lobes tapering distally (+) vs. lobes broadly rounded (-)	+	+	+	+	-	-

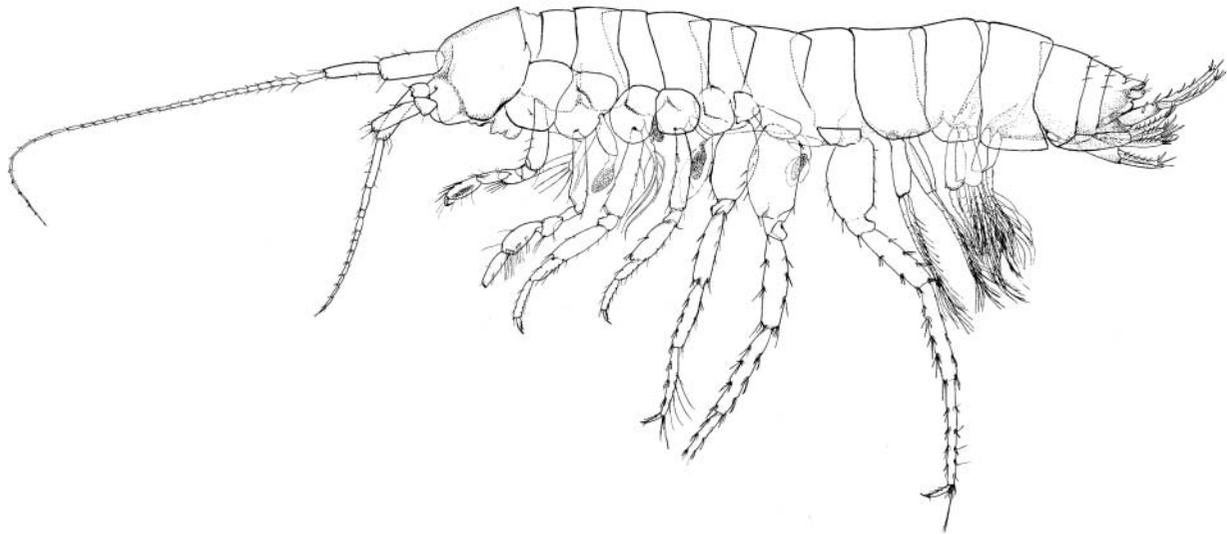
<sup>a</sup>Sources: Cvetkova, 1975; Barnard & Barnard, 1983; Tomikawa *et al.*, 2007; Lowry & Myers, 2012.

gnathopod. In the melitid type of gnathopod, females have the first gnathopod feeble, with elongated carpus and propus and short dactyli, which suit the short palm. The second gnathopod is larger, with an approximately triangular carpus, supporting a less elongated propodus with oblique palm (e.g. Ruffo, 1982). *Potiberaba* shows extreme phenotypes of this kind of gnathopod, although the functions and shapes of the first and the second pair appear to be reversed.

***Potiberaba porakuara* sp. nov.**

HOLOTYPE. Intact female, and mounted on slides; deposited in a collection of Department of Biology, Biotechnical Faculty Ljubljana, voucher number NB192.

PARATYPES. Five females, one of them partly dissected and mounted on slides; deposited in a collection of Department of Biology, Biotechnical Faculty Ljubljana, voucher numbers NB193–NB197.



**Fig. 11.** Body shape of *Potiberaba porakuara* sp. nov.

**DIAGNOSIS AND TYPE LOCALITY.** Diagnosis and type locality are the same as diagnosis of the genus, see also Fig. 1.

**ETYMOLOGY.** The species epithet is derived from the Tupi-Guarani (Brazilian Indian language), in which *pora* means inhabitant and *kûara* means burrow (referring to the subterranean habitat). The name is to be treated as a noun in apposition.

**DESCRIPTION OF FEMALE (MALE UNKNOWN).**  
**BODY** (Figs 2, 11, 18, 19). Slender; colourless and eyeless, approximately 3.5 mm. Head without rostrum; head lobe poorly developed; antennary sinus shallow. Posterodorsal margin of each pleonite without seta.

Epimeral plates I–III posterodistally angulate; ventral margins straight to concave; posterior margins slightly sinusoid in plates I–II and straight in plate III. Posterior and ventral margins of epimeral plates with single seta in postero-distal corner.

Urosomites I–III free, each with up to five tiny setae along dorsoposterior margins. Telson clefted to the base, each lobe rectangular and approximately as wide as long, apically two setae with few tiny setae (only inserta have been visible).

**ANTENNAE I–II** (Fig. 12). Antenna I long, as long as body or longer. Peduncle segments in proportion 1 : 0.75 : 0.45; each peduncular article with up to 6 facial and up to 8 distal setae. Accessory flagellum uniaarticulate, slightly longer of the first flagellar article, apically and subapically with 3 setae. Main flagellum with 20 articles, approximately twice as long as the peduncle. Neither aesthetascs nor calceoli were observed.

Lengths of antenna I and II in ratio 1 : 0.45. Antenna II peduncle with short gland cone. Peduncle segments 4

and 5 of approximately equal length, both articles with up to 4 facial and up to 6 distal setae. Flagellum with 10 articles, approximately 1.3 times longer than peduncle articles 4 and 5 together. Neither aesthetascs nor calceoli were observed.

**MOUTHPARTS** (Figs 12–13). Incisor of the right mandible with 7 teeth, lacinia with 6 teeth and plumose seta; spine row comprising of 2 long plumose setae; molar well developed, triturative. Incisor of the right mandible with 6 teeth, lacinia with two multidenticated plates, spine row comprising 2 long plumose setae; molar process well developed, triturative with long seta.

Palp segments length ratio 1 : 2.3 : 1.7; proximal segment with 2 distal setae, middle segment with cluster of 2 distomedial setae and distal segment with 11 D and 2 E setae; surface covered with carpet of setulae. Left and right maxilla I similar to each other; inner plate roughly triangular, with oblique row of rather long and well-developed setae; outer plate broad, with 9 and 10 pectinate spines, which are from medial towards lateral progressively more curved, medio-subapically, two tiny setae; maxillar palpus biarticulated; proximal article short, distal apically dilated with 6 and 7 spiniform apical-subapical marginal setae and 1 submarginal seta. Maxilla II bilobed, inner lobe slightly shorter than outer; long, hairy hairs medio-distally and tiny setae medially and facially; outer lobe with long curved setae apically and tiny setae laterally. Maxilliped inner lobes well developed and broad, with two strong, spiniform setae medio-distally, 6 apical setae, 6 medio-facial setae and several facial tiny setae; outer lobes with 6 medio-apical spiniform spines, apical seta, 5 mesio-submarginal setae and 4 latero-marginal setae. Palpus 4-articulated in ratio 1 : 2.2 : 1.9 : 0.72, proximal-most article without

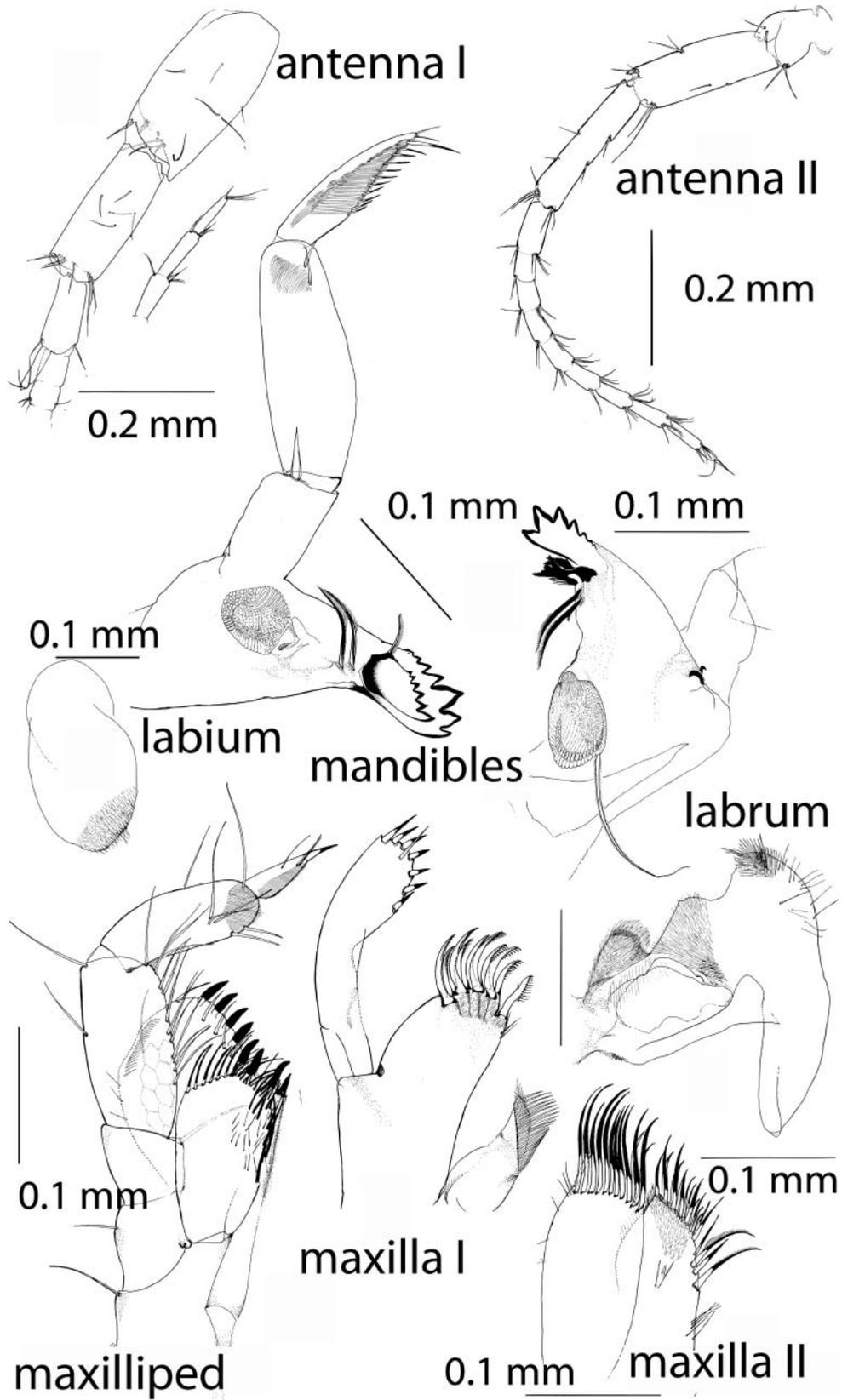


Fig. 12. Antennae I–II and mouthparts of *Potiberaba porakuara* sp. nov.

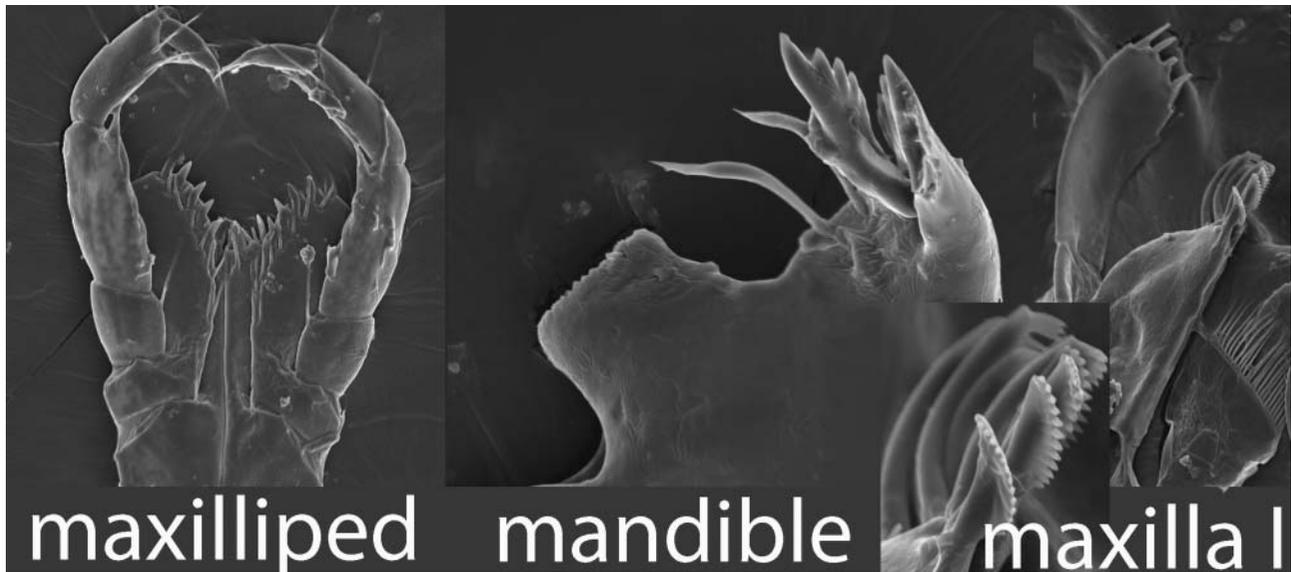


Fig. 13. Mouthparts of *Potiberaba porakuara* sp. nov. Details under SEM.

seta; second article with lateral setae in the mid-of article and apically and 13 mesio-mariginal setae; propodus with distal setae mesially, laterally and facially in poorly defined groups, dactylus with three mesial setae. Labium with poorly developed inner lobes; inner and outer lobes hairy.

**COXAL PLATES** (Figs 2, 11, 14, 16). Coxal plates I–IV respective widths (anteroposterior lengths) are 0.74, 0.73, 0.84 and 0.96 of their depths (dorsoventral distances). Coxal plates I–II sub-quadrated, plates III–IV ventrally irregularly shaped with slightly concave margin; coxal plate IV without proxi-posterior incision. Along antero-distal margins 3–6 setae, in coxa I also few facial setae present. Gills II–V pedicellate and ovoid, progressively larger until gill IV which extends beyond basis, gill V short. Coxal plates V–VII without distinct lobes, V with 4 setae along anterior margin and 1 posteroventral seta, VI with one anterior and 1 posteroventral seta; VII with single posteroventral seta. Oostegites on pereopods II–VI, narrow, approaching mid-of basis, with sparse, long setae.

**GNATHOPODS I–II** (Figs 14–15). Basis I elongate, with 2 anterior and 2 posterior marginal setae; ischium with posterofacial and posterodistal seta; merus with mid-posterofacial group of setae and 4 sparse setae distally; carpus approximately triangular, with anterodistal seta, 2 latero-facial setae and postero-marginal row of 8 plumose setae; propodus of gammaroid shape, anterior and posterior margins subparallel, width : length as 1 : 1.4; palm slightly oblique; anterior margin with 3 submarginal and 3 antero-apical setae, posterior margin with a row of 6 submarginal setae and 2 long facial setae along inner side; palmar corner defined with 2 spiniform setae; palm with numerous densely packed submarginal bifid spiniform setae. Dacty-

lus well developed, slightly longer than a palm, with single seta. Unguis distinguishable.

Basis II more elongated than basis I, with 1 anterior and 3 posterior setae; ischium with 1 postero-distal facial

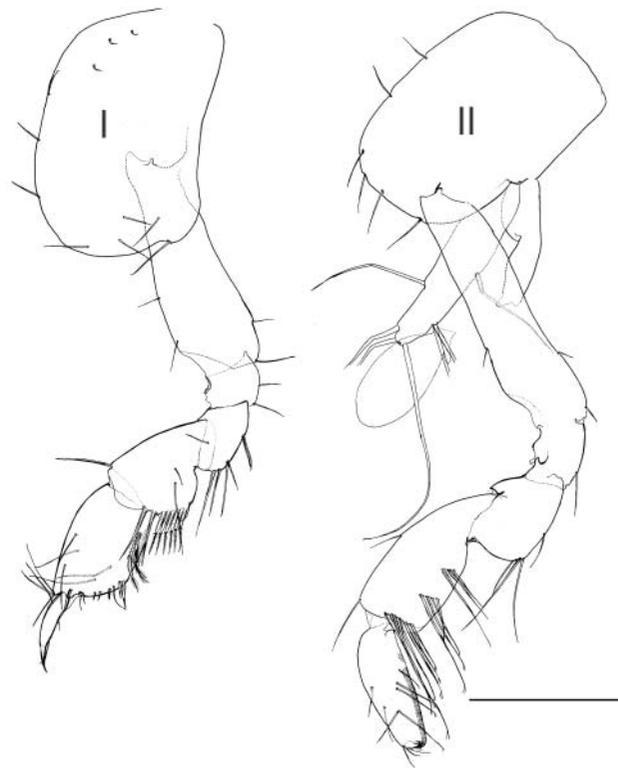


Fig. 14. Gnathopods of *Potiberaba porakuara* sp. nov. The number corresponds to appendage. All scale bars indicate 0.2 mm.

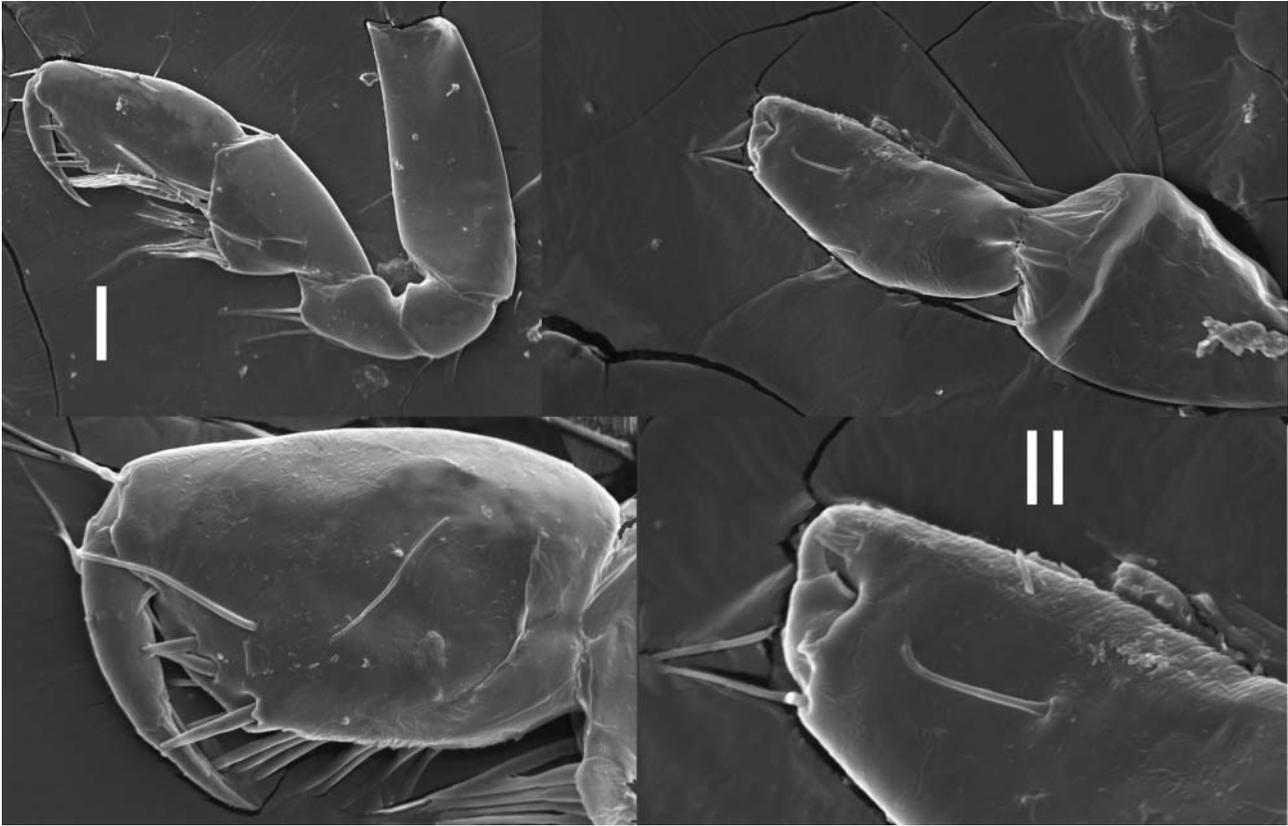


Fig. 15. Gnathopods of *Potiberaba porakuara* sp. nov. Details under SEM. The number corresponds to appendage.

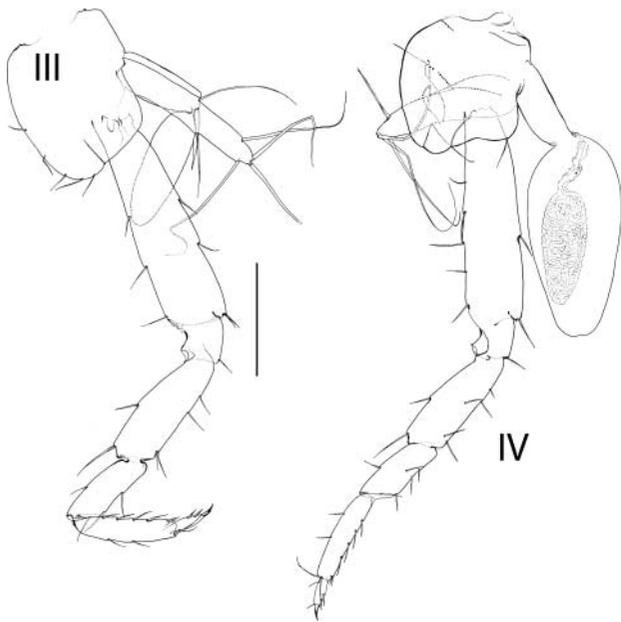
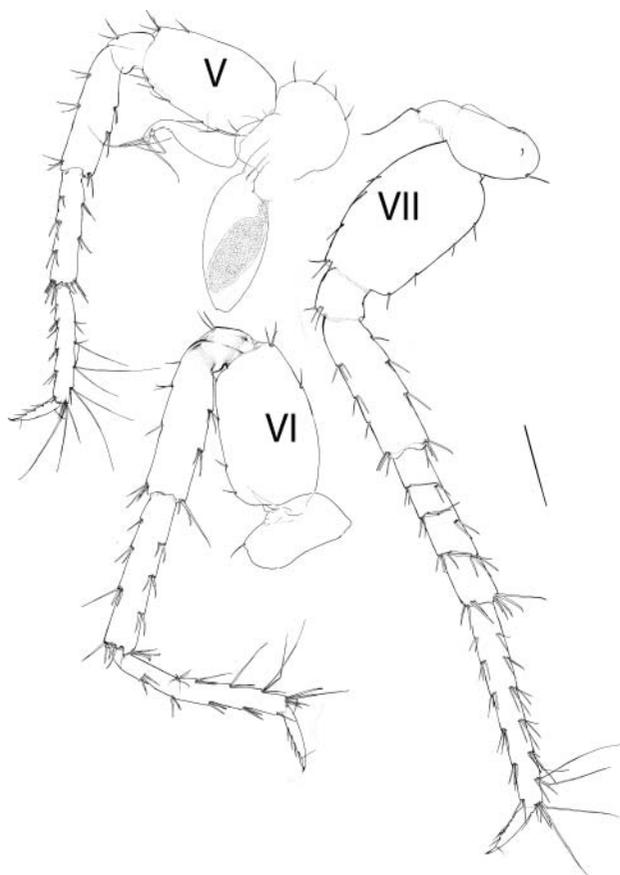


Fig. 16. Pereopods III–IV of *Potiberaba porakuara* sp. nov. The number corresponds to appendage. All scale bars indicate 0.2 mm.

seta, merus with 1 mid-postero facial seta and posterodistal seta; carpus elongated, long as  $1/2$  of the basis and twice longer than propodus II; with 1 mid- and 1 distal anterior seta, and with 3 oblique rows of posterior setae. Propodus narrow, tapering distally, anterior margin convex, posterior margin straight, posterodistally produced into distal lobe bearing 2 bifid spiniform setae; anterior margin with 2 mid-submarginal setae and 3 distal setae, posterior margin with 3 submarginal setae and tiny posterior setae; a pair of facial setae on lateral side; dactylus largely reduced, attached to the palm and hardly seen under light microscope.

PEREOPODS III–IV (Fig. 16). Slender, similarly long, sparsely setose with setae along anterior and posterior margins of all articles, dactylus with well-defined unguis, with 2 tiny dorsal seta and 2 ventral spiniform setae.

PEREOPODS V–VII (Fig. 17). Pereopods V : VI : VII as 1 : 1.17 : 1.28. Bases ovoid, without distal lobes, anterior and posterior margins slightly convex, with 5, 4, 4 posterior single setae respectively; anterior margins with 1, 1, 3 respective single setae in addition to distal setal group. All articles between ischium-propodus with groups of spiniform setae anteriorly and posteriorly; propodi V–VII with 4, 3, 2 respective bunches of posterior long setae. Dactyli slender, with dorso-proximal and dorso-distal (at junction with unguis) seta; each dactylus with 3, 4, 5 spiniform



**Fig. 17.** Pereopods V–VII of *Potiberaba porakuara* sp. nov. The number corresponds to appendage. All scale bars indicate 0.2 mm.

ventral setae, respectively. Unguis well defined, dactylus of pereopod VII measures approximately 0.15 of propodus length.

PLEOPODS (Fig. 18) with protopod smooth, with two retinacles each.

UROPODS (Fig. 18). Uropod I protopod : inner : outer ramus as 1 : 0.73 : 64; protopod with 4 lateral spiniform setae and 1 mesio-distal seta. No basofacial spine was seen. Uropod I rami distally rounded; outer ramus approximately 0.88 of inner ramus; outer ramus with 4 single dorsal spiniform setae and 4 apical spines; inner ramus with 4 dorsal spiniform setae. Uropod II rami pointed and do not exceed length of uropod I. Uropod III with rod-shaped rami, outer ramus of 2 articles. Protopodit with 4 facial spiniform setae, 1 facial plumose seta and 1 distal spiniform and 1 spiniform seta. Inner ramus with 5 lateral groups mixed of plumose and spiniform setae, and with 6 apical spiniform setae; outer ramus proximal article with 5 lateral groups of spiniform setae and at least 2 mesial single spines (partially damaged); distal article with mid-mesial slender seta and 5 apical spines. Outer : inner ramus as 1 : 0.95, distal article measures 0.39 of proximal article.

VARIABILITY. Several samples have been collected. We reviewed approximately 20 specimens, however, inter-individual variability is low. We found no male with well-developed penile papillae, and it remains unclear whether samples include any males at all.

## Discussion

### Amphipods and their origin in South America

The results of our analysis are striking. Species diversity is higher in epigean habitats, whereas generic and family diversity are higher in hypogean habitats. The analyses thus better support the second hypothesis, i.e. that recently diversified Dogielinotidae out-competed ancestral amphipod fauna. In this discussion we overview three key elements of this hypothesis: age of origin, ecology of species and role of competition.

The majority of lineages found in South America have nearest relatives on other continents, which indicates that vicariance mediated by plate tectonics played a major role in the faunistic structure of South American amphipods (e.g. Myers & Lowry, 2009; Chakrabarty *et al.*, 2012; Lowry & Myers, 2013). We postulate that all amphipod taxa, with the possible exception of Dogielinotidae, had been present on the South American continent before the break up of Gondwana. The origin of Dogielinotidae might be an exception, which is in line with the central hypothesis. *Hyalella* is nested within a clade with worldwide distribution; however its nearest relatives are distributed along the coasts of both Americas (cf. Serejo, 2004). This means that the genus might have invaded the fresh waters of South America when the continent was already fully separated from other landmasses. However, dated molecular phylogenies are needed for more rigorous testing.

Niche evolution, from marine to fresh water and vice versa, might have occurred many times, as in other groups of animals (Hou *et al.*, 2011; Vega & Wiens, 2012). Such niche evolution can explain how present freshwater species from New Caledonia survived the episodes of submergence (Espeland & Muriene, 2011). Even though the salinity barrier might be less impermeable than it appears, recent trans-oceanic invasions seem highly unlikely. Amphipods are poor dispersers and this is particularly true for the hypogean taxa (e.g. Trontelj *et al.*, 2009) that dominate in South America.

Most amphipod lineages from South America live in hypogean waters. Even more, many South American hypogean amphipods also have exclusively hypogean relatives outside South America; the only exception is *Phreatogammarus* (Phreatogammaridae, New Zealand) in which three out of four species also occur, but not exclusively, in surface habitats (see supplementary material online). Does this

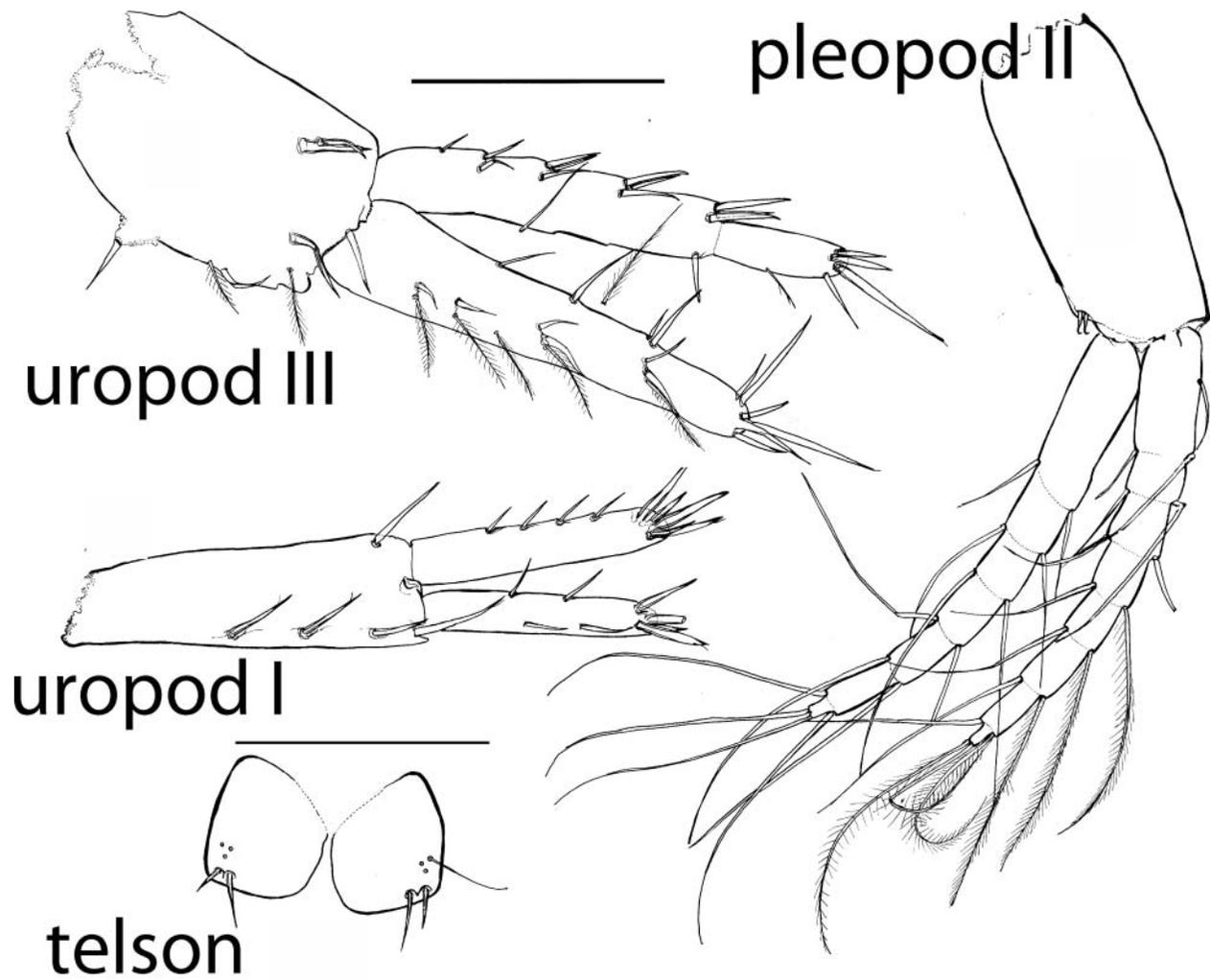


Fig. 18. Uropods and telson of *Potiberaba porakuara* sp. nov. All scale bars indicate 0.2 mm.



Fig. 19. Urosoma of *Potiberaba porakuara* sp. nov. Details under SEM.

mean that affiliation to subterranean habitats persisted from the Mesozoic onwards and can be regarded as niche conservatism? At the moment, it is not possible to give any definite answers, as such a pattern can also emerge as a result of mass extinctions of surface relatives (for example in extinction at the end of Mesozoic). But whether abiotic or biotic distractions are considered, the subterranean environment can present a refuge (e.g. Humphreys, 2000; Kristjánsson & Svavarsson, 2007).

The role of competition in species richness and distribution on a continental scale is difficult to assess. Competition affects species distribution (Sexton *et al.*, 2009), but there are no data that support competition alone being the cause for mass extinctions (Marshall, 1988; Stachowicz & Tilman, 2005; Wiens, 2011). We therefore suggest rather that ancestors of the present amphipods in South America had become extinct in surface habitats prior to the colonization of *Hyaletta*. Such colonization would, in a way, be similar to the colonization of *Gammarus* in the northern hemisphere. This genus diversified remarkably in surface freshwater habitats after habitat shift in the Eocene (Hou *et al.*, 2011). *Hyaletta* could have, in a similar way, successfully colonized surface freshwaters (e.g. ecological opportunity, Parent & Crespi, 2009) and could have undergone a remarkable diversification that is still not fully described. All other South American amphipods appear to be relicts that had managed to successfully colonize ecologically demanding and remote subterranean environments. In such environments, with environmental fluctuations buffered relative to the surface, colonizing potential can be modified. That is, successful colonizers of surface waters are not necessarily successful colonizers of subterranean waters, especially if these habitats are already occupied. This might be the reason why diversification of *Hyaletta* dominates only in surface waters. Recently, new troglobiotic species of this genus are being discovered in Brazil (see Supplement), but their distribution does not overlap with the distribution of any other subterranean families. Further insight into this theme will be possible only with the advent of strongly supporting molecular phylogenies that would enable the inclusion of timescale.

### **The great potential of discoveries in subterranean habitats – a call for further faunistic research and a conservation appeal**

In the past six years the number of known higher amphipod taxa in South America has doubled in number. All new discoveries are from subterranean habitats, where issues of incomplete sampling are evident, even in well-studied karst areas (Culver & Pipan, 2009). Even though this problem is applicable to all South America, we here draw attention

to the particularly problematic situation in Brazil, which harbours the main carbonatic areas in South America.

Ferreira (2005) suggested that inventories of Brazilian cave animals have been seriously incomplete. Recent research in previously unstudied areas is revealing dozens of new subterranean taxa, some of them described only in the last three years (Volkmer-Ribeiro *et al.*, 2010; Souza & Ferreira 2010, 2011a, 2011b, 2012; Cardoso *et al.*, 2011; Hernandez *et al.*, 2011; Machado *et al.*, 2011; Pellegrini & Ferreira, 2011a, 2011b; Rizzato *et al.*, 2011; Bernardi *et al.*, 2012; Dantas-Torres *et al.*, 2012; Prevorčnik *et al.* 2012). More than 11 000 caves are officially registered in Brazil, yet it has been estimated that 150 000 caves could be present in both karstic and non-karstic areas of the country (Auler *et al.*, 2001). Considering all the biological inventories currently available, probably less than 20% of the officially registered Brazilian caves have been sampled by biologists. Some no-karst lithologies (e.g. iron ore) reveal remarkable subterranean diversity (Souza-Silva *et al.*, 2012). The fauna in such environments is, however, currently endangered more than ever due to increased mining activities allied to changed cave protection legislation in Brazil in 2008. Even though the law protects at least part of the obligate cave fauna, the conservation acts cannot come into effect if species remain unregistered. Therefore, any delay in taxonomic research may yield permanent loss of species even before they are discovered and described. Brazil harbours two of the leading world's biodiversity hotspots in the surface ecosystem (Myers *et al.*, 2000) and it has the potential to become one of the hotspots in the subterranean counterpart. Large regions with carbonate rocks and potentially high densities of caves could support high regional diversity of subterranean species (Culver *et al.*, 2006). This is even more important, for this would be the sole case of a global hotspot in the southern hemisphere, and would make testing the generality of hypotheses developed in the northern hemisphere feasible. Apart from this, the destruction of subterranean fauna, even prior its discovery, will permanently delete the tracks that may guide the reconstruction of patterns of fauna formation in history. The importance of such discoveries is demonstrated by our study, in which knowledge of subterranean biodiversity of South America is expanded, contributing to a deeper understanding of the global diversity patterns. These arguments should be convincing enough and hopefully will be used for protection of subterranean habitats, not only in Brazil but also globally.

### **Acknowledgements**

We cordially thank John R. Holsinger, Stefan Koenemann, Traudl Krapp, Ed Bousfield and Oliver Coleman, who generously shared their taxonomic opinions on newly discovered taxa and helped us with bibliography. Ronald Vonk and Valentina Ianilli helped compile the checklist of

Ingolfiellidae. Peter Trontelj and two anonymous reviewers offered many helpful comments on an early draft of the manuscript. Professor Roger Pain improved the language. We thank Jocy Cruz, Diego Bento, Iatagan, Uilson and Darci (from CECAV- Rio Grande do Norte) for all their invaluable help during our expeditions into Rio Grande do Norte caves. We also thank Geilson Goes and Maria Gorete Goes and their family for all their hospitality in Felipe Guerra. We thank the entire staff of the Laboratory of Underground Ecology of the Section of Zoologia of the Federal University of Lavras (UFLA) for their efforts in the collections and Eduardo Alves (Laboratório de Microscopia – Departamento de Fitopatologia – UFLA) for enabling us to use the scanning microscope. RLF is grateful to the National Council of Technological and Scientific Development (CNPq) (process N° 477712/2006-1 and CNPq grant 301061/2011-4) and to Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG) for financial support (Process N°: PEE-00570-10). CF and MZ were funded by Slovenian Research Agency (program P1-0184(D)). This research is also part of a bi-lateral cooperation project between Brazil and Slovenia (CNPq process N° 490537/2010-3 and Slovenia Agency, BI-BR/11-13-006).

## References

- AULER, A., RUBBIOLI, E. & BRANDI, R. 2001. *As grandes cavernas do Brasil*. Grupo Bambuí de Pesquisas Espeleológica.
- BARNARD, J.L. & BARNARD, C.M. 1983. *Freshwater Amphipoda of the World (Volume I–II)*. Hayfield Associates, Mt. Vernon, Virginia, USA.
- BARNARD, J.L. & KARAMAN, G.S. 1983. Australia as a major evolutionary centre for Amphipoda (Crustacea). *Australian Museum Memoir* **18**, 45–61.
- BAUZÀ-RIBOT, M., JUAN, C., NARDI, F., OROMI, P., PONS, J. & DAMIÀ, J. 2012. Mitogenomic phylogenetic analysis supports continental-scale vicariance in subterranean thalassoid crustaceans. *Current Biology* **22**, 2069–2074.
- BERNARDI, L.F.O., PELLEGRINI, T.G. & FERREIRA, R.L. 2012. New species of *Neoteneriffiella* (Acari: Trombidiformes: Teneriffiidae) from Brazilian caves: geographical distribution and ecological traits. *International Journal of Acarology* **38**, 410–419.
- BOTELLO, A., ILIFFE, T.M., ALVAREZ, F., JUAN, C., PONS, J., & DAMIÀ, J. 2013. Historical biogeography and phylogeny of *Typhlatya* cave shrimps (Decapoda: Atyidae) based on mitochondrial and nuclear data. *Journal of Biogeography* **40**, 594–607.
- BOUSFIELD, E.L. 1977. A new look at the systematics of Gammaroidean amphipods of the world. *Crustaceana Supplement* **4**, 282–316.
- BRÉHIER, F., VONK, R. & JAUME, D. 2010. First South American phreatogammarid, with comments on the arrangement of coxal and sternal gills, and on the biramous condition of the seventh pereopod in amphipods. *Journal of Crustacean Biology* **30**, 503–520.
- CARDOSO, G.M., BUENO, A.A.P. & FERREIRA, R.L. 2011. A new troglobitic species of *Hyaella* (Crustacea, Amphipoda, Dogielinotidae) from Southeastern Brazil. *Nauplius* **19**, 17–26.
- CHAPMAN, M.A. 2003. A revision of the freshwater amphipod genus *Phreatogammarus* in New Zealand. Part 1: A re-description of *P. helmsii* Chilton, 1918 and a new species from Northland. *Journal of the Royal Society of New Zealand* **33**, 633–661.
- CHAPMAN, M.A. 2004. A revision of the Phreatogammaridae (Crustacea, Amphipoda) of New Zealand. Part 2: *Phreatogammarus fragilis* and *P. propinquus*. *Journal of the Royal Society of New Zealand* **34**, 59–79.
- CHAKRABARTY, P., DAVIS, M.P. & SPARKS, J.S. 2012. The first record of a trans-oceanic sister-group relationship between obligate vertebrate troglobites. *Public Library of Science ONE* **7**, e44083. doi:10.1371/journal.pone.0044083.
- CULVER, D.C. & PIPAN, T. 2009. *The Biology of Caves and other Subterranean Habitats*. Oxford University Press, Oxford, UK.
- CULVER, D.C., DEHARVENG, L., BEDOS, A., LEWIS, J.J., MADEN, M., RADDELL, J.R., SKET, B., TRONTELI, P. & WHITE, D.J. 2006. The mid-latitude biodiversity ridge in terrestrial cave fauna. *Ecography* **29**, 120–128.
- CVETKOVA, N.L. 1975. Pribrežnye Gammaridy Severnyh i Dal'nevostočnyh Morei SSSR i Sopredel'nyh vod (Coastal Gammarids of Northern and far Eastern Seas of USSR and Nearby Waters). "Nauka", Leningrad, Russia.
- DANTAS-TORRES, F., VENZAL, J.F., BERNARDI, L.F.O., FERREIRA, R.L., ONOFRIO, V.C., MARCILI, A., BERMÚDEZ, S.E., RIBEIRO, A.F., BARROS-BATTESTI, D.M. & LABRUNA, M.B. 2012. Description of a new species of bat-associated Argasid tick (Acari: Argasidae) from Brazil. *Journal of Parasitology* **98**, 36–45.
- ESPELAND, M. & MURIENNE, J. 2011. Diversity dynamics in New Caledonia: towards the end of the museum model? *BioMed Central Evolutionary Biology* **11**, 13. (<http://www.biomedcentral.com/1471-2148/11/254/abstract/>, accessed 18 March 2013)
- FERREIRA, R.L. 2005. A vida subterrânea nos campos ferruginosos. *O Carste* **3**, 106–115.
- FERREIRA, R.L., XAVIER, P., BERNARDI, L.F.O. & SOUZA-SILVA, M. 2010. Fauna subterrânea do Estado do Rio Grande do Norte: Caracterização e impactos. *Revista Brasileira de Espeleologia* **1**, 25–51.
- GONZÁLES, E. 1986. A new record of *Paracorophium hartmannorum* Andres, 1975, from the Chilean coast, with a description of the adult (Amphipoda: Corophiidae). *Proceedings of Biological Society Washington* **99**, 21–28.
- GROSSO, L.E. & PERALTA, M. 2009. A new Paraleptamphopidae (Crustacea Amphipoda) in the burrow of *Virilastacus rucapihuelensis* (Parastacidae) and surrounding peat bogs. *Rudolphia macrodactylus* n. gen., n. sp. from southern South America. *Zootaxa* **2243**, 40–52.
- GROSSO, L.E., PERALTA, M. & RUFFO, S. 2006. Description of *Pseudoingolfiella morimotoi*, sp. nov. (Crustacea, Amphipoda) from New Zealand and transantarctic distribution of the genus. *Subterranean Biology* **4**, 67–77.
- HERNANDES, F.A., BERNARDI, L.F.O. & FERREIRA, R.L. 2011. Snout mites from caves in Brazil, with description of a new species. *Journal of Natural History* **45**, 799–812.
- HOU, Z., SKET, B., FIŠER, C. & SHUQIANG, L. 2011. Eocene habitat shift from saline to freshwater promoted Tethyan amphipod diversification. *Proceedings of the National Academy of Science USA* **108**: 14533–14538.
- HUMPHREYS, W.F. 2000. Relict faunas and their derivation. In: WILKENS, H., CULVER, D.C. & HUMPHREYS, W.F., Eds., *Ecosystems of the World 30: Subterranean Ecosystems*. Elsevier, Amsterdam, The Netherlands, pp. 417–432.
- IANILLI, V. & RUFFO, S. 2007. A new genus and species of Phreatogammaridae (Caledonietta maryae n. gen. n. sp.)

- from New Caledonia (Crustacea, Amphipoda). *Bollettino del Museo Civico di Storia Naturale di Verona* **31**, 23–29.
- IANILLI, V., HOLSINGER, J.R., RUFFO, S. & VONK, R. 2006. Two new genera and two new species of the subterranean family Bogidiellidae (Crustacea, Amphipoda) from groundwaters in northern Oman, with notes on the geographic distribution of the family. *Zootaxa* **1208**, 37–56.
- IANILLI, V., KRAPP, T. & RUFFO, S. 2011. Freshwater amphipods from Madagascar with description of a new family, three new genera and six new species (Crustacea, Amphipoda). *Bollettino del Museo Civico di Storia Naturale di Verona* **35**, 93–137.
- JAUME, D., SKET, B. & BOXSHALL, G.A. 2009. New subterranean Sebidae (Crustacea, Amphipoda, Gammaridea) from Vietnam and SW Pacific. *Zoosystema* **31**, 249–277.
- KOENEMANN, S. & HOLSINGER, J.R. 1999. Phylogenetic analysis of the amphipod family Bogidiellidae s. lat., and revision of taxa above the species level. *Crustaceana* **72**, 781–816.
- KRISTJÁNSSON, B.K. & SVAVARSSON, J. 2007. Subglacial refugia in Iceland enabled groundwater amphipods to survive glaciations. *American Naturalist* **170**, 292–296.
- LOWRY, J.K. & MYERS, A.A. 2012. New, mainly southern hemisphere, freshwater families of Amphipoda (Crustacea), together with a description of the first freshwater calliopiid, *Lutriwita bradburyi* gen. nov. et sp. nov. *Zootaxa* **3499**, 27–45.
- LOWRY, J.K. & MYERS, A.A. 2013. A phylogeny and classification of the Senticaudata subord. nov. (Crustacea: Amphipoda). *Zootaxa* **3610**, 1–80.
- MACHADO, E.O., FERREIRA, R.L. & BRESCOVIT, A.D. 2011. A new troglomorphic *Metagonia* Simon 1893 (Araneae, Pholcidae) from Brazil. *Zootaxa* **3135**, 59–62.
- MACNEIL, C., DICK, J.T.A. & ELWOOD, R.W. 1997. The trophic ecology of freshwater *Gammarus* (Crustacea: Amphipoda); problems and perspectives concerning the functional feeding group concept. *Biological Reviews of the Cambridge Philosophical Society* **72**, 349–364.
- MACNEIL, C., DICK, J.T.A. & ELWOOD, R.W. 1999. The dynamics of predation on *Gammarus* spp. (Crustacea: Amphipoda). *Biological Reviews of the Cambridge Philosophical Society* **74**, 375–395.
- MACNEIL, C., ELWOOD, R.W. & DICK, J.T.A. 2000. Factors influencing the importance of *Gammarus* spp. (Crustacea: Amphipoda) in riverine salmonid diets. *Archiv für Hydrobiologie* **149**, 87–107.
- MARSHALL, L.G. 1988. Land mammals and the great American interchange. *American Scientist* **76**, 380–388.
- MYERS, N., MITTERMEIER, R.A., MITTERMEIER, C.G., DA FONSECA, G.A.B. & KENT, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858.
- MYERS, A.A. & LOWRY, J.K. 2003. A phylogeny and a new classification of the Corophiidea Leach, 1814 (Amphipoda). *Journal of Crustacean Biology* **23**, 443–485.
- MYERS, A.A. & LOWRY, J.K. 2009. The biogeography of Indo-West Pacific tropical amphipods with particular reference to Australia. *Zootaxa* **2260**, 109–127.
- PARENT, C.E. & CRESPI, B.J. 2009. Ecological opportunity in adaptive radiation of Galapagos endemic land snails. *American Naturalist* **174**, 898–905.
- PELLEGRINI, T.G. & FERREIRA, R.L. 2011a. Ultrastructural analysis of *Coarazuphium formoso* (Coleoptera: Carabidae, Zuphiini), a new Brazilian troglitic beetle. *Zootaxa* **2866**, 39–49.
- PELLEGRINI, T.G. & FERREIRA, R.L. 2011b. *Coarazuphium tapiaguassu* (Coleoptera: Carabidae, Zuphiini), a new Brazilian troglitic beetle, with ultrastructural analysis and ecological considerations. *Zootaxa* **3116**, 47–58.
- PERÈZ-SCHULTEISS, J. 2013. *Osornodella gabriellae*, n. gen. and n. sp., a new falklandellid (Amphipoda: Gammaridea) from freshwaters of the Chilean Coastal Range. *Zootaxa* **3599**, 446–456.
- PREVORČNIK, S., FERREIRA, R.L. & SKET, B. 2012. Brasileiriniidae, a new isopod family (Crustacea: Isopoda) from the cave in Bahia (Brazil) with a discussion on its taxonomic position. *Zootaxa* **3452**, 47–65.
- RIZZATO, P.P., COSTA, E.P. JR., TRAJANO, E. & BICHUETTE, M.E. 2011. *Trichomycterus dali*: a new highly troglomorphic catfish (Siluriformes: Trichomycteridae), from Serra da Bodoquena, Mato Grosso do Sul State, Central Brazil. *Neotropical Ichthyology* **9**, 477–491.
- RUFFO, S. 1982. The Amphipoda of Mediterranean, Part 1. *Memoires de l'Institut ocnographique* **13**, 1–364.
- SEREJO, C.S. 2004. Cladistic revision of talitroidean amphipods (Crustacea, Gammarida), with a proposal of new classification. *Zoologica Scripta* **33**, 552–586.
- SEXTON, J.P., MCINTYRE, P.J., ANGERT, A.L. & RICE, K.J. 2009. Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution and Systematics* **40**, 415–436.
- SOUZA, M.F.V.R. & FERREIRA, R.L. 2010. *Eukoenia* (Palpigradi: Eukoeniidae) in Brazilian caves with the first troglitic palpigrade from South America. *Journal of Arachnology* **38**, 415–424.
- SOUZA, M.F.V.R. & FERREIRA, R.L. 2011a. A new species of *Eukoenia* (Palpigradi: Eukoeniidae) from Brazilian iron caves. *Zootaxa* **2886**, 31–38.
- SOUZA, M.F.V.R. & FERREIRA, R.L. 2011b. A new troglitic *Eukoenia* (Palpigradi: Eukoeniidae) from Brazil. *Journal of Arachnology* **39**, 185–188.
- SOUZA, M.F.V.R. & FERREIRA, R.L. 2012. *Eukoenia virgemdalapa* (Palpigradi: Eukoeniidae): a new troglitic palpigrade from Brazil. *Zootaxa* **3295**, 59–64.
- SOUZA-SILVA, M., PARENTONI MARTINS, R. & FERREIRA, R.L. 2012. Cave lithology determining the structure of the invertebrate communities in the Brazilian Atlantic Rain Forest. *Biodiversity and Conservation* **20**, 1713–1729.
- STACHOWICZ, J.J. & TILMAN, D. 2005. Species invasions and the relationships between species diversity, community saturation, and ecosystem functioning. In: SAX, D.F., STACHOWICZ, J.J. & GAINES, S.D., Eds., *Species Invasions: Insight into Ecology, Evolution and Biogeography*. Sinauer Associates, Sunderland, MA, USA, pp. 41–64.
- TOMIKAWA, K., KOBAYASHI, N., MORINO, N. & MAWATARI, S.F. 2007. New gammaroid family, genera and species from subterranean waters of Japan, and their phylogenetic relationships (Crustacea: Amphipoda). *Zoological Journal of the Linnean Society London* **149**, 643–670.
- TRONTELI, P., DOUADY, C., FIŠER, C., GIBERT, J., GORIČKI, Š., LEFÉBURE, T., SKET, B. & ZAKŠEK, V. 2009. A molecular test for hidden biodiversity in groundwater: how large are the ranges of macro-stygobionts? *Freshwater Biology* **54**, 727–744.
- VÄINÖLÄ, R., WITT, J.D.S., GRABOWSKI, M., BRADBURY, J.H., JAŽDZEWSKI, K. & SKET, B. 2008. Global diversity of amphipods (Amphipoda; Crustacea) in freshwater. *Hydrobiologia* **595**, 241–255.
- VEGA, C.G. & WIENS, J.J. 2012. Why are there so few fish in the sea? *Proceedings of the Royal Society B* **279**, 2323–2329.
- VERMEIJ, G.J. 2005. From Europe to America: Pliocene to Recent trans-Atlantic expansion of cold-water North Atlantic molluscs. *Proceedings of the Royal Society B* **272**, 2545–2550.

- VOLKMER-RIBEIRO, C., MACHADO, V. & BICHUETTE, M.E. 2010. *Racekiela cavernicola* (Porifera: Demospongiae) new species and the first record of cave freshwater sponge from Brazil. *Neotropical Biology and Conservation* **5**, 53–58.
- VONK, R. & SCHRAM, F.R. 2003. Ingolifiellida (Crustacea, Malacostraca, Amphipoda): a phylogenetic and biogeographic analysis. *Contributions to Zoology* **72**, 39–72.
- WIENS, J.J. 2011. The niche, biogeography and species interactions. *Philosophical Transactions of the Royal Society B* **366**, 2336–2350.
- WIENS, J.J. & DONOGHUE, M.J. 2004. Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution* **19**, 639–644.
- WILDISH, D. 1982. Talitroidea (Crustacea, Amphipoda) and the driftwood ecological niche. *Canadian Journal of Zoology* **60**, 3071–3074.
- WITT, J.D.S., THRELEOFF, D.L. & HEBERT, P.D.N. 2006. DNA barcoding reveals extraordinary cryptic diversity in an amphipod genus: implications for desert spring conservation. *Molecular Ecology* **15**, 3073–3082.

**Associate Editor: Elliot Shubert**