Two new species of *Pseudoniphargus* (Amphipoda), in Bermudian groundwaters*

JAN H. STOCK, JOHN R. HOLSINGER, BORIS SKET and THOMAS M. ILIFFE

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The amphipod genus *Pseudoniphargus* Chevreux, 1900 has a curious distribution (Schellenberg 1939; Stock 1980): in inland groundwaters around the Mediterranean basin, in Atlantic drainage systems of Portugal and Spain, and on the islands of Madeira and Faial (Azores); a single Mediterranean species is anchialine to marine. It has been postulated that the insular areas now inhabited by *Pseudoniphargus* were populated when no sea barrier was present (Schellenberg 1939), but it is more likely that they have been populated from marine ancestors stranded during the lowering of sea level during the Tertiary (Stock 1980).

The occurrence of this genus on Bermuda (Sket 1979; Sket & Iliffe 1980) is therefore of great biogeographical interest, since it represents another case of amphi-Atlantic distribution of stygofaunal elements (Iliffe et al. 1983, 1984).

No species of *Pseudoniphargus* has formally been described from Bermuda until now, because of the small number of adult specimens available. The occurrence of the genus in Bermuda is documented by Sket & Iliffe (1980), who cited it as “*Pseudoniphargus* cf. Adriaticus S. Karaman”, since at the time their paper was written only two taxa had been described, of which *Adriaticus* was the only salty water taxon. This original material consists mostly of small, juvenile specimens, originating from Admiral's, Shop and Bat (Government Quarry) Caves in the Walsingham area of Bermuda, and belongs entirely to the first of the two species described hereafter.

The genus *Pseudoniphargus* comprises a number of stygobiont Amphipoda, distributed on both sides of the Atlantic. In Bermuda, groundwaters are inhabited by two species, *P. grandianus* and *P. carpalis*, both new. They occur throughout the entire salinity spectrum, from infrahaline to euhaline, but are most abundant in oligohaline waters. Large adults, but no ovigerous specimens, are found at greater distance from the sea coast than juveniles, which may indicate that *Pseudoniphargus* needs anchialinemarine waters for its reproduction and that juveniles migrate inland to grow up.

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Introduction

The amphipod genus *Pseudoniphargus* Chevreux, 1900 has a curious distribution (Schellenberg 1939; Stock 1980): in inland groundwaters around the Mediterranean basin, in Atlantic drainage systems of Portugal and Spain, and on the islands of Madeira and Faial (Azores); a single Mediterranean species is anchialine to marine. It has been postulated that the insular areas now inhabited by *Pseudoniphargus* were populated when no sea barrier was present (Schellenberg 1939), but it is more likely that they have been populated from marine ancestors stranded during the lowering of sea level during the Tertiary (Stock 1980).

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Material

A more or less systematic groundwater survey was undertaken in October 1984, during and after the International Symposium on the Biology of Marine Caves in Bermuda. This material complements collections made earlier by Iliffe et al. in the island's anchialine cave waters. The freshwater lenses of Bermuda, and—to a lesser extent—its caves, revealed an abundant material of *Pseudoniphargus* (c. 500 specimens, from infrahaline (1 sample), oligohaline (13 samples), ß-mesohaline (1 sample), Ô-mesohaline (4 samples) and euhaline (1 sample) groundwaters, mostly from wells. The total number of samples taken was 80, of which 20 contained *Pseudoniphargus*. Some additional samples were also examined (collection T. Iliffe, preserved in the U.S. National Museum of Natural History, through the courtesy of Dr. J. L. Barnard; collection B. Sket, Ljubljana, collected by Sket and Iliffe). Fifty-five per cent of the samples, comprising more than 80% of the specimens, originated from oligohaline waters, which appear to be the preferred habitat for members of this genus in Bermuda.

List of stations yielding *Pseudoniphargus* (see also Fig. 1)

The number of specimens of each species collected at each station is shown in Table I.

<table>
<thead>
<tr>
<th>Station</th>
<th>Location</th>
<th>Coordinates</th>
<th>Water depth</th>
<th>Chlorinity</th>
<th>Salinity</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stn. 251</td>
<td>Roadside Cave, Hamilton Parish</td>
<td>38°37'17.2&quot;N, 69°19'42.4&quot;W</td>
<td>0.5 m</td>
<td>0.0%</td>
<td>0.1%</td>
<td>Closed well, marked &quot;July 1951&quot;, with broken pump; Cvetkov net; water level at 1.8 m, water depth 1.8 m; slight smell of H2S; 7 Oct. 1984; chlorinity 0.10%</td>
</tr>
<tr>
<td>Stn. 252</td>
<td>Wonderland Cave, Hamilton Parish</td>
<td>38°37'17.2&quot;N, 69°19'42.4&quot;W</td>
<td>0.5 m</td>
<td>0.0%</td>
<td>0.1%</td>
<td>Closed well, marked &quot;July 1951&quot;, with broken pump; Cvetkov net; water level at 1.8 m, water depth 1.8 m; slight smell of H2S; 7 Oct. 1984; chlorinity 0.10%</td>
</tr>
</tbody>
</table>

* Bermuda Biological Station for Research, Contribution No. 1049.
Fig. 1. Distribution of *Pseudomphargus* in Bermuda, based on the 1984 sampling (arrows). The approximate boundaries of the island's five freshwater lenses (after Vacher 1974) are dotted (*D* Devonshire lens; *G* St. George's lens; *S* Somerset lens; *SH* Southampton lens; *W* Warwick lens).
Pseudoniphargus in Bermudian groundwaters


Material. 1♂ (holotype, body length 8 mm), Stn. 315; 1♀ (allotype, 7 mm), Stn. 310; paratypes from Stns. 251, 252, 255, 259, 269, 271, 301, 3021, 305, 306, 309, 310, 316, 317 and 320 (all in Zoologisch Museum Amsterdam, ZMA), from Church and Wonderland Caves (U.S. National Museum of Natural History, USNM), and from Admirals’s and Shop and Bat (Government Quarry) Caves (collection Sket), as listed in Table 1.

Description. Colourless, eyeless. Adult female (with setose oostegites) 7 mm, adult (‘senile’) males 6.5–8 mm. Subadult females (without setose oostegites) 4–6 mm, subadult males (with genital papillae) 4–6 mm. Identifiable juveniles 2–4 mm.

Cephalosome (Fig. 4a) without rostrum; antennal sinus shallow. No teeth on body somites in either sex. Small setules at dorsoposterior margin of all peraeon and pleon somites, and on urosomites 1 and 2.

First antenna (Fig. 3a): Pedunculus segment 3 rather short (50–60% of length of segment 2, both in adults and subadults). Accessory flagellum 2-segmented (adult and subadult), not very slender (Fig. 3b), 55–63% of the length of peduncle segment 3. Flagellum 15–21-segmented (adult); flagellum 6–7-segmented (subadult); not very slender (Fig. 4b), 55–63% of the corresponding flagellum segments; proximal flagellar segments not slender.

Second antenna (Fig. 3c) short; gland cone robust; several strong spines on peduncle segment 4; flagellum 6–7-segmented (adult); no calceoli.

Upper lip broadly rounded (Fig. 4b). Lower lip with large inner lobes (Fig. 4e).

Mandible palp 3-segmented (Fig. 3d); segment 1 unarmed, segment 2 with several ventral setae (less setose than in segment 3).

Table 1. Distribution of Pseudoniphargus in Bermudian caves and wells

<table>
<thead>
<tr>
<th>Localities/station no.</th>
<th>P. grandimanus</th>
<th>P. carpalis</th>
<th>Unidentifiable juveniles (&lt;2 mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1984 sampling (Stock/liffe/Holsinger) (material in ZMA):</td>
<td></td>
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<td></td>
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<tr>
<td>251</td>
<td>1</td>
<td></td>
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<tr>
<td>252</td>
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<td>305</td>
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<td>3</td>
<td></td>
</tr>
<tr>
<td>316</td>
<td></td>
<td>1</td>
<td></td>
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<tr>
<td>317</td>
<td></td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>320</td>
<td></td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

Sampling by T. M. Liffe (material in USNM): Church Cave 4
Watlington Wells 1
Wonderland Caves 2
Collection B. Sket, I.,ubljana: Admirals’ Cave 3 Shop and Bat (Government Quarry) Caves 5

Genus Pseudoniphargus Chevreux, 1900

In the sequel we will describe two new species from Bermuda. There can be no doubt that these species belong to the genus Pseudoniphargus, in spite of the ocean-wide gap that separates them from European and East Atlantic insular populations, inasmuch as all characters are in perfect agreement with the diagnosis of the genus (cf. Stock 1980). The Bermudian P. grandimanus sp.n. is the first species of the genus with a marked sexual dimorphism in the propod of gnathopods 1 and 2 of fully differentiated specimens (‘senile’ specimens in the terminology of Schellenberg). Both Bermudian species differ from their congeners by the presence of a hyaline lobe on the posterior margin of the merus of gnathopod 1, the slender rami of uropods 1 and 2, and the larger number of spines on the ventral margin of the epimeral plates in adults, and the unarmed tip of the telson lobes.
numerous in subadult than in adult); segment 3 with angularly bent ventral margin, distal part of margin with row of 11 D-setae (fewer in subadult), all barbed; 2 A-setae, 1 or 2 B-setae, 2 C-setae, 3 E-setae (most proximal barbed in basal part). Left lacina mobilis with 3 proximal + 1 distal teeth (Fig. 3d); right lacinia bicuspidate, both cusps finely toothed, proximal cusp moreover ciliated (Fig. 3f). Four (left) or 3 (right) setae between incisor and molar. Molar flake small, only observed in right mandible. Molar small; molar seta present on both sides.

First maxilla (Fig. 3g) contralaterally symmetrical. Palp 2-segmented, segment 2 sausage-shaped, with 8 + 2 distal spines (fewer in subadult). Outer lobe with 7 distal spines; medial margin of these spines, from lateral to medial, with 3-1-2-5-4-3-6 denticles; lateral margin of spines with 0–3 denticles. Inner lobe short, with 2 or 3 distal setae.
Fig. 3. *Pseudoniphargus grandimanus* sp. n.—a. First antenna, $\delta$, Stn. 316 (scale AB).—b. Accessory flagellum of same (AD).—c. Second antenna, $\delta$, Stn. 316 (AB).—d. Left mandible, $\delta$, Stn. 316 (AC).—e. Right mandible, palp omitted, $\delta$, Stn. 316 (AC).—f. Lacinia mobilis of right mandible, $\delta$, Stn. 316 (freehand sketch).—g. Left first maxilla, $\delta$, Stn. 316 (AC).—h. Second maxilla, $\delta$, Stn. 316 (AC).—i. Epimeral plates, from the left, $\delta$, Stn. 316 (PO).—j. Third uropod, $\delta$, Stn. 316 (AB).—k. Third uropod, $\delta$ juv., Stn. 301 (AB).—l. Endopodite of third uropod, $\delta$, Stn. 316 (AE).

Scales as on Fig. 7.
Fig. 4. *Pseudoniphargus grundimanus* sp.n.—a. Cephalosome, from the left, ♂, Stn. 316 (scale PQ).—b. Upper lip, ♂, Stn. 316 (PR).—c. Lower lip, ♂, Stn. 316 (AC).—d. Maxilliped, ♂, Stn. 316 (AC).—e. First gnathopod, ♂, Stn. 316 (AB).—f. Distal segments of first gnathopod, ♂, Stn. 302 (AB).—g. Palma of first gnathopod, ♂, Stn. 316 (AD).—h. Basal part of third pereiopod, ♂, Stn. 316 (PQ).—i. Fourth coxal plate, ♀ juv., Stn. 317 (AB).

Scales as on Fig. 7.
Fig. 5. Pseudoniphargus grandimanus, sp.n.—a. Second gnathopod, ♂, Stn. 316 (scale AB).—b. Distal segments of second gnathopod, ♀, Stn. 310 (AB).—c. Fourth pereiopod, ♂, Stn. 316 (PQ).—d. Oostegite of fourth pereiopod, ♀, Stn. 310 (AB).—e. Fifth pereiopod, ♂, Stn. 316 (AF).—f. Retinaculum of third pleopod, ♂, Stn. 316 (AF).—g. Clothes-peg spines of endopodite of third pleopod, ♂, Stn. 316 (top second spine; bottom first spine) (freehand sketch).

Scales as on Fig. 7.
Second maxilla (Fig. 3h): outer lobe slightly bilobed, as indicated by 2 separate groups of setae; inner lobe with 2 distal rows of setae.

Maxilliped (Fig. 4d) with 4-segmented palp; claw long and very slender. Outer lobe with 13 medial spines and 7 distal setae (fewer spines and setae in subadult). Inner lobe narrow, with 4–5 distal spines and 6–7 distal setae.

First gnathopod (Fig. 4e, f) sexually dimorphous in large specimens: propodus of ? larger in size than that of ? though similar in shape and armature (compare the figures, which are drawn to the same scale). Number of setae on basis larger in adults than in subadults. Merus with semi-hyaline triangular lobe on posterior margin. Carpus with 5 rows of marginal setae and 2 rows of lateral setae. Propodus much longer than carpus, with 3 or 4 groups of setae on posterior margin. Palmar margin with 2 rows of small, bicuspidate spines (about 12 per row in adult); palmar angle with 6 bicuspidate spines (Fig. 4g).

Second gnathopod sexually dimorphous in the propodus (Fig. 5a, b) at a body length of about 6 mm and above. Basis with fewer setae in subadults than in adults. Merus non-lobate. Carpus triangular, with rounded, posterior lobe, armed with 2 groups of setae. Male propodus (Fig. 5a) much larger than that of ?, and with longer palmar margin and shorter posterior margin. Posterior margin (?–?) with 5 groups of setae. Subadult propodi of feminine shape. Palmar margin with 2 rows of simple spinules, 20–30 spinules per row; palmar angle with 3 or 4 setule-tipped spines (1 long, others short).

Coxal gills ovate, with a short, non-articulated basal stalk (stalk in ? a trifle longer than in ?), on P2 through P6. Oostegites (Fig. 5d) linear, armed with long setae in adults, on P2–P5.

Pereiopods 3 (Fig. 4b) and 4 (Figs. 4i, 5c) similar, except for coxal plate, which is shallowly emarginate over almost its entire length in P4. Ventral margin of plates 3 and 4 with few (4–7) setules. Propodus with up to 9 spines in row on posterior margin (about 5 in subadults).

Fifth pereiopod (Fig. 5e) with aequilobate coxal plate. Basis elongate-ovate, posterior margin with about 12 small setules; postero-ventral corner (Fig. 6f) slightly lobate and overhanging in both sexes (l/l ratio, measured as shown in Fig. 6e, close to 0.5 in adult, about 0.35 in subadults).

Sixth pereiopod (Fig. 6a) longer than fifth; seventh pereiopod (Fig. 6b) with longer distal segments than sixth. Basis elongate, with 12–15 setules at posterior margin) postero-ventral lobe slightly overhanging (l/l ratio 0.2 in adult, almost 0.7 in subadult, cf. Figs. 6c–e). Basis less elongate and with fewer setules and spinules in subadults. Coxal plate of P6 equilobate, of P7 non-lobate.

Epimeral plates (Fig. 3i) with 1–5 ventral spines (fewer in subadults); postero-ventral corner produced into a minute tooth; posterior margin ciliated (more cilia in adult than in subadult).

Pleopods biramous; exopodites of pleopods 1, 2 and 3 of 15, 12 and 11 segments, respectively; endopodites of 11, 10 and 10 segments. Medial margin of endopodite proximally with 1 clothes-peg spine on pleopod 1, and 2 such spines (Fig. 5g) on pleopods 2 and 3. Two retinacula on each pleopod, with 2 or 3 pairs of marginal teeth (Fig. 5f).

Uropod 1 (Fig. 6h) with ventro-proximal peduncular spine; rami relatively slender and elongate, with distal armature only.

Uropod 2 (Fig. 6i) with slender rami. Endopodite slightly longer than exopodite.

Uropod 3 (Fig. 3j): Pedunculus not elongated. Exopodite in adults slightly elongated, with 4 groups of spines on both inner and outer margin; distal spines short. Endopodite elongate-triangular (Fig. 3l), with 1 distal spine and 1 subbasal, medial setule. No sexual dimorphism in adults. In subadults, the exopodite is less elongate (Fig. 3k) and bears only 2 groups of spines on the lateral and medial margins.

Telson (Fig. 6j) with broad, rounded, medial cleft. Two or 3 spines on each lobe, distal part of lobe unarmed. One to 3 setules in the centro-basal part of dorsal surface of telson.

Male genital papillae small, rounded, on pereionite 7.

Intersexes. We have found two specimens that have a propodus of gnathopod 2 intermediate in size between ? adult and ? adult, and of male morphology, but at the same time, these specimens have non-setiferous oostegites. The two specimens are 6 mm long. We are inclined to call these specimens intersexes.

Etymology. The specific name, granulimanus (= with large hands) refers to the allometrically enlarged propodus of the second gnathopod in ‘senile’ males.

Ecology. Known from wells, waterworks and cave waters in Bermuda, throughout the entire salinity range, but mostly from oligohaline waters.

Figures. Unless otherwise stated in the legends, illustrations (Figs. 2–6) have been made from large (old) specimens of 7 mm body length.

*Pseudoniphargus carpalis* sp.n. (Figs. 7–8)

Material. 1 ? (holotype, body length 4 mm), Stn. 266; 1 ? (allotype, 4 mm), Stn. 230; paratypes from Stns. 301, 302, 310, and 320, as listed in Table I (all Zoologisch Museum Amsterdam, ZMA).

Description. Female with spiniferous oostegites 4 mm; male with genital papillae 4 mm. Characters differentiating this species from the previous one are enumerated (characters not mentioned are similar in both species).

First antenna (Fig. 7a) with elongate third peduncle segment (61–78% of length of segment 2). Accessory flagellum with very slender basal segment (Fig. 7b). Flagellar segments slender, up to 14 in number.

Second antenna (Fig. 7h) with slender peduncle, flagellum 6-segmented.

First maxilla (Fig. 8c): second palp segment slightly more slender. Outer lobe with 7 spines, each spine with 8 or 9 fine denticles on medial margin, lateral margin with 0–4 fine denticles.

Maxilliped: outer lobe with 1 distal seta only.

First gnathopod (Fig. 8a): carpus elongate–rectangular, posterior margin with 6 groups of setae. Propodus as long as carpus, posterior margin with 2 groups of setae.

Second gnathopod (Fig. 8b): coxal plate very narrow. Carpus non-lobate, elongate–triangular, posterior margin with 4 groups of setae. Propodus slender, with 3 groups of setae on posterior margin; palmar angle spines short; palmar margin with about 7 pairs of small spinules.
Fig. 6. *Pseudoniphargus grandimanus* sp.n.—a. Sixth pereiopod, ♂, Stn. 316 (scale PQ).—b. Seventh pereiopod, ♂, Stn. 316 (PQ).—c. Postero-ventral lobe of basis on seventh pereiopod, ♀ juv., Stn. 317 (AC).—d. Same of ♀ juv., Stn. 301 (AC).—e. Same of ♂ ad., Stn. 316 (AC) (i and l indicating ischial and lobal length, respectively).—f. Postero-ventral lobe of basis of fifth pereiopod, ♂ ad., Stn. 301 (AC).—g. Same of ♀ juv., Stn. 317 (AC).—h. First uropod, ♂, Stn. 316 (AB).—i. Second uropod, ♂, Stn. 316 (AB).—j. Telson, ♂, Stn. 316 (AC).

Scales as on Fig. 7.
Coxal plate of 3rd and 4th pereiopods (Figs. 8c–d) with 11 or 12 ventral setules. Posterior emargination of 4th plate occupying about half the margin. Propodus with 6 spines on posterior margin.

Pereiopods 5–7 (Fig. 7c–d) with ovate basal segment; posterior margin of basis with 11–12 setules; postero-ventral lobe well-developed (\( \delta \)i ratio 0.76 in P5, 0.91 in P7, cf. Figs. 7e–f).

Epimeral plate 1 without ventral spines, plate 2 with about 4–5 spines, plate 3 with 2–4 spines. Posterior margin of all plates devoid of setules (Fig. 7g).

Exopodite of uropod 3 (Fig. 8g) not elongated, armed with 3–4 groups or marginal spines.

Male: except for the absence of oostegites and the presence of genital papillae, no sexual differences. Propodi of P1 and P2 exactly the same size as in \( \delta \). It is not impossible, however, that ‘senile’ males (unknown for this species) will show differences in the gnathopods.
Fig. 8. Pseudoniphargus carpalis, sp.n., Stn. 266.—a. First gnathopod (scale AC).—b. Second gnathopod (PR).—c. Third coxal plate (AB).—d. Fourth coxal plate (AB).—e. First maxilla (AD).—f. Oostegite of fourth pereiopod (AC).—g. Third uropod (PR).
Scales as on Fig. 7.
Remarks. A number of characters mentioned above are influenced by age (shape of basis of P5-P7, length of exopodite of uropod 3, number of ventral spines on propodus of P3-P4, number of flagellar segments in A1 and A2). Other characters, however, appear to be more stable, and serve for a clear-cut distinction of the new species (which has not only been compared with ‘senile’ adults of *P. grandimanus*, but also with young specimens of identical size as the present species): (1) posterior margin of epimeral plates without setules; (2) third peduncle segment of A1 more slender; (3) first segment of accessory flagellum more slender; (4) higher number of denticles on the spines of the outer lobe of Mx 1; (5) longer carpus in P1 and P2, and more numerous groups of setae on the posterior carpal margin; (6) higher number of setules on ventral margin of coxal plates 3 and 4; (7) shorter posterior emargination of coxal plate 4; (8) larger posterior-ventral emargination on basis of P5-7.

Etymology. The specific name *carpalis* alludes to the elongate carpus in P1 and P2.

Ecology. Known from wells in the oligohaline and β-mesohaline zone of Bermuda, usually together with *P. grandimanus*.

Discussion

Specimens of *Pseudoniphargus* have been found in or near three of the freshwater lenses of Bermuda (Fig. 1), viz. the Warwick lens (1 sample), the Devonshire lens (13 samples), and the St. George’s lens (3 samples); moreover, it was found in 4 caves in the Walsingham area, outside the range of the freshwater lenses. So far, no *Pseudoniphargus* has been found in the Somerset and Southampton lenses, in the western part of Bermuda.

Two samples originate from groundwaters in the oldest limestone unit of Bermuda, the Walsingham formation (and of course the four cave samples also come from the Walsingham area): most samples (12) come from the younger Belmont formation, whereas 6 samples come from the youngest unit, the Paget formation (Vacher 1974, fig. 2.5). There is no apparent relationship between the age of the limestone unit and the distribution of *Pseudoniphargus*, especially when one considers that the unit with the lowest number of samples occupies the smallest area of the island.

Juveniles occur throughout the salinity range, but, significantly, the samples containing only juveniles are all taken close to the sea (11-180 m), whereas samples containing larger specimens (>3 mm body length) in addition to juveniles, are found at greater distances from the sea (147-853 m). The significance level is better than 0.1% (Table II). This seems to indicate that reproduction takes place in anchialaline/marine conditions and that juveniles produced near the margin of the sea migrate inland to grow up. This supposition is supported by the fact that not a single ovigerous female was found in our samples (over 500 specimens examined) or in any previously collected sample (collection Sket and in the U.S. National Museum of Natural History) from inland cave and groundwaters of Bermuda.

This hypothesis requires also that ovigerous females be in or near salt water, since amphipods brood their young and lack free-living larval stages.

Since ovigerous females are unknown (not found in inland, but neither in salty waters), one of us (B.S.) thinks that an alternative explanation is equally convincing: reproduction takes place inland, where the adults are living, whereas juveniles spread in all directions avoiding population pressure.

The greatest surprise is no doubt that the island of Bermuda, small as it is, harbours at least two different species of *Pseudoniphargus* which are not geographically isolated (several samples contain both species). In terms of speciation or evolution, this remains an enigma for the moment, although the rise and fall of the sea level during the Pleistocene might have been a mechanism that explains successive invasions from the marine environment. The morphology of the two Bermudian species is so similar in many respects that a common ancestor is not excluded.

The taxonomic interpretation of the material, notwithstanding its abundance, proved to be difficult for a number of reasons: (1) none of the specimens is ovigerous; (2) juvenile specimens (<3 m in body length) form the majority of the material; (3) both males and females show allometric growth in the appendages, in particular in the propodus of the second gnathopod; (4) old, fully differentiated males ("senile Männchen", as Schellenberg called them in the thirties) are very rare; (5) several intersexes have been found; (6) sexual dimorphism is well-developed in old specimens (body length 6-8 mm), but in juveniles (<2 mm) and in (sub)adult specimens (3-6 mm) it is absent or restricted to the presence of oostegites in the female and penial lobes in the male, both visible after dissection only.

### Table II. Distribution of *Pseudoniphargus* in Bermuda

<table>
<thead>
<tr>
<th>Stn. no.</th>
<th>Chlorinity (%)</th>
<th>Distance to sea (m)</th>
<th>Species present in sample</th>
</tr>
</thead>
<tbody>
<tr>
<td>Large-sized specimens (&gt;3 mm)</td>
<td>Small-sized specimens only (&lt;3 mm)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>310-g,c</td>
<td>1.10</td>
<td>147</td>
<td>306-g,?</td>
</tr>
<tr>
<td>255-g</td>
<td>8.80</td>
<td>242</td>
<td>307-?</td>
</tr>
<tr>
<td>269-g</td>
<td>9.22</td>
<td>242</td>
<td>305-?</td>
</tr>
<tr>
<td>316-g</td>
<td>0.22</td>
<td>258</td>
<td>259-?</td>
</tr>
<tr>
<td>315-g</td>
<td>0.15</td>
<td>263</td>
<td>273-g,?</td>
</tr>
<tr>
<td>271-g</td>
<td>0.45</td>
<td>326</td>
<td>251-g</td>
</tr>
<tr>
<td>317-g</td>
<td>0.62</td>
<td>347</td>
<td>300-?</td>
</tr>
<tr>
<td>252-g</td>
<td>0.65</td>
<td>411</td>
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</tr>
<tr>
<td>266-c</td>
<td>0.44</td>
<td>437</td>
<td></td>
</tr>
<tr>
<td>320-g,c</td>
<td>0.40</td>
<td>621</td>
<td></td>
</tr>
<tr>
<td>309-g</td>
<td>0.13</td>
<td>679</td>
<td></td>
</tr>
<tr>
<td>302-g,c</td>
<td>0.16</td>
<td>774</td>
<td></td>
</tr>
<tr>
<td>301-g,c</td>
<td>0.62</td>
<td>853</td>
<td></td>
</tr>
</tbody>
</table>

$g = P. grandimanus; c = P. carpalis$. Small-sized specimens have not always been identified to species level, indicated by a question-mark.

The large-sized specimens live significantly at greater distance from the sea than the small-sized specimens (Mann-Whitney test, significance level better than 0.1%, one-tail). The chlorinities at which large-sized and small-sized specimens are found do not differ significantly, however, at the 5% level.
Pseudoniphargus in Bermudian groundwaters

Ecology

_Pseudoniphargus grandimanus_ is common in groundwater lenses of Bermuda, most frequently in the oligohaline parts. Caves containing this species are isolated from more direct connection with the open sea and contain only small populations of this and other trogloditic species. Cave waters in general (in Bermuda) contain several other amphipods, mostly of marine affinities (Ingolfiella, EriopisalPsammogammarus, Bogidiella, Idunella, Coco- 

_harpinia, Gitanopsis_, cf. Sket & Iliffe 1980), none of which is found in the fresher groundwater lenses. The only amphipods observed in these lenses are juvenile Talitridae (sandhoppers) and oculate members of the genus _Melita_ (so far unidentified).

_P. carpalis_ is known only from the freshwater lenses, and has not been observed so far in the anchihaline caves.

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References


