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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

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Abstract

The bogidiellid amphipod crustaceans *Stockigidiella aequimana* new genus and species and *Omangidiella parvidactyla* new genus and species are described from subterranean groundwater habitats in the Sultanate of Oman on the Arabian Peninsula. *Stockigidiella* is easily distinguished by a row of long, deeply bifid setae on pereopods 5 and 6, whereas *Omangidiella* is distinguished by a greatly reduced propodus of gnathopod 2 and elongate oostegites; it also possesses a third coxal lobe on the maxilliped, a unique character noted only in three other bogidiellid genera from northern and eastern Africa. At present, the family Bogidiellidae contains 35 genera and 105 species but a significant number of provisionally recognized new species and possibly several new genera await description. The geographic distribution of the family Bogidiellidae is nearly circumglobal, but species tend to be clustered in discontinuous regions. A number of important questions regarding the origin and biogeographic history of the family remains unanswered.

Key words: biogeography, Bogidiellidae, Oman, stygomorphic, subterranean waters

Riassunto

Nel presente lavoro vengono descritti due nuovi generi e specie di Crostacei Anfipodi Bogidiellidi, Stockigidiella aequimana e Omangidiella parvidactyla, provenienti da habitat di acque dolci

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sotterranee nel Sultanato dell'Oman (Penisola Arabica). *Stockigidiella* è facilmente distinguibile per una fila di lunghe setole, profondamente bifide, sui pereiopodi 5 e 6, mentre *Omangidiella* è riconoscibile per la notevole riduzione del propodite nello gnatopode 2 e per gli oostegiti allungati; è inoltre presente nel massillipede un terzo lobo coxale, carattere questo unico, evidenziabile solamente in altri tre generi di bogidiellidi dell'Africa nord orientale. Ad oggi, la famiglia dei Bogidiellidae comprende 35 generi e 105 specie, ma un numero significativo di nuove specie per ora solo riconosciute e forse di nuovi generi attendono di essere descritti. La distribuzione geografica della famiglia Bogidiellidae è approssimativamente circum-terrestre, ma le specie tendono a raggrupparsi in regioni discontinue. Numerose importanti questioni sull'origine e la storia biogeografica della famiglia rimangono irrisolte.

Parole chiave: biogeografia, Bogidiellidae, Oman, stigomorfi, acque sotterranee

Introduction

During a four-week expedition to the Sultanate of Oman in the spring of 1996 by the late Prof. Jan H. Stock and Jan J. Vermeulen of Amsterdam University (see Stock et al., 1997), 129 collections of invertebrate animals were made from a variety of subterranean groundwater habitats in several parts of the country. More than one-half of the samples is made with a Bou-Rouch groundwater pump (Bou, 1974) from coarse sediments in the bed of wadis (water courses that are dry except during the rainy season); the remainder were taken from water wells and springs with nets. Many of the samples contained amphipods as well as other crustaceans (e.g., ostracods, copepods, isopods, thermosbaenaceans), annelid worms, gastropods, insect larvae, and other aquatic organisms. A careful examination of the bogidiellid amphipods collected by Stock and his colleagues revealed two new genera, both of which are described below. In addition to the new taxa described in the present paper, the only amphipod species known to date from the subterranean waters of the central and southern Arabian Peninsula was *Indoweckelia stocki* Ruffo et al. (2003), which the 1996 Stock expedition also collected in Oman.

The specimens examined in the present study were preserved in glycerine drops on slides, probably because Stock proposed to study them himself. However, after his death the Zoological Museum of the University of Amsterdam made this material available to us for study. The material is now preserved in 70 % ethanol, except for the specimens dissected and mounted on slides in Faure's medium. This material also contains some additional specimens of Bogidiellidae that we could not determine because of their poor state of preservation. In addition to examination of specimens in the Stock collection, we also studied three specimens collected from Wadi Nakhl during an Austrian expedition in Oman.

Systematics

Stockigidiella new genus

Diagnosis

A stygomorphic bogidiellid amphipod distinguished by mandibles without molars, gnathopods 1 and 2 subsimilar in size, carpus and propodus of pereopods 5 and 6 with row of long, deeply bifid setae, pleopods without inner rami, and uropods 1 and 2 similar.

Type species

Stockigidiella aequimana new species, by monotypy. Gender is feminine.

Derivatio nominis

It is a distinct pleasure to name this new genus in honour of our late friend and eminent colleague, Prof. Dr. Jan H. Stock of the University of Amsterdam, whose expedition to the Sultanate of Oman and other parts of the world resulted in the collection of many new taxa of subterranean amphipods from biologically poorly known regions.

Remarks

The peculiar characters that collectively distinguish *Stockigidiella* from the other bogidiellid genera include the absence of a true mandibular molar, subequality of gnathopods 1–2 and the long, apically bifid setae on the carpus and propodus of pereopods 5 and 6. In all previously described bogidiellids the first pair of gnathopods differs from the second pair, especially in the shape of the propodus, which is typically piriform in the first and subtrapezoidal in the second. Whereas, in contrast the propods of both pairs of gnathopods in Stockigidiella are elongate and suboval. The carpal segment of gnathopod 1 in Stockigidiella is also different. In most other bogidiellids the carpal lobe of gnathopod 1 is typically more prominent, and in many it extends along the posterior margin of the propodus, sometimes nearly reaching the defining angle of the palmar margin. However, in *Stockigidiella* the posterior lobe of the carpus of gnathopod 1 is a relatively poorly developed prolongation not much extended along the posterior margin of the propodus. In comparison, the posterior lobe of the carpus of gnathopod 2 is rounded, not elongate, and similar to that in most other bogidiellids. We believe that the near equality of the gnathopods is a primitive or plesiomorphic character in bogidiellid amphipods, whereas the presence of the deeply bifid setae on the carpus and propodus of percopods 5 and 6 appears to be a novel or apomorphic character. The latter character was previously unknown, or at least un-recorded, in other genera of bogidiellids. Among all bogidiellids known to date, only the genus Hebraegidiella Karaman (1988) from the shore of the Dead Sea in Palestine shows a moderately close affinity with *Stockigidiella*. In this genus, the gnathopods are only weakly differentiated and the mandible lacks a triturative molar. However, several other important characters, including presence of inner rami on the ZOOTAXA

zooTAXA pleopods and normal setation of pereopods 5 and 6, separate *Hebraegidiella* from (1208) *Stockigidiella*.

Stockigidiella aequimana new species Figs.1–3

Material examined (expedition station number in parentheses from Stock et al. 1997)

Sultanate of Oman. (96–22) open, shallow well at Dibab (23°04'31"N; 59°03'22"E), holotype specimen (probable male) collected 26 March 1996; dissected and mounted in Faure's medium on slides 4559–4562 and deposited in Museo Civico di Storia Naturale Verona (MVRCr 438)

Description

Male (?) (3.7 mm).—Antenna 1 (Fig. 1a) less than 1/2 the length of body; ratio of peduncular articles 1-3 = 1:0.9:0.5; article 1 of peduncle with distal spine accompanied by long seta, article 2 with few short setae, article 3 with distal group of 3 elongate aesthetascs; flagellum slightly shorter than peduncle, with 6 elongate articles, article 1 of flagellum. Antenna 2 (Fig. 1b) as long as antenna 1, gland cone not elongate, article 5 of peduncle slightly shorter than article 4, flagellum distinctly shorter than peduncle, composed of 4 elongate articles and 1 much shorter distal article.

Labrum (upper lip) not seen. Mandibles asymmetrical. Right mandible (Fig. 2b): incisor without evident teeth; lacinia mobilis 4-dentate, followed by 3 setulose rakers; molar not triturative, replaced by setulose area inferiorly provided with 2 short + 1 long spines; palp elongate, article 2 with 1 seta on inner margin, article 3 slightly shorter than article 2, outer margin bearing row of 6 B setae and a second row of very short setae distal to the B setae, apex with 4 long E setae. Left mandible (Fig 2a): incisor with 3 teeth, lacinia mobilis pluridenticulate followed by 3 spines; molar setulose area inferiorly provided with 4 short + 1 long spines; palp identical to the left one. Labium (lower lip) not seen. Maxilla 1: left and right (Fig. 2c) similar; palp reduced and bearing 3 distal setae on article 2; inner plate with 2 naked apical setae, outer plate with 6 spines, 5 bifid and 1 distally denticulate. Maxilla 2 (Fig. 2d) relatively short, inner lobe with 3 apical setae, outer lobe with 6 mostly long spines or coarse setae. Maxilliped (Fig. 2e): inner and outer lobes relatively short; inner lobe distally with 1 bifid spine, 1 simple spine and few subapical setae; outer lobe with 2 distal spines and row of few setae on inner margin.

Gnathopod 1 (Fig. 1c): coxa subrectangular, ratio length:height = 1:0.5, inferior margin weakly concave, with 2 setae on anterodistally rounded corner; basis wide, with 1 strong submedial spine on posterior margin, anterior margin with only 1 subdistal spine; merus with pubescent posterior margin; carpus with relatively small ventral lobe bearing 2 distal spines and light pubescence; propodus large, suboval and relatively elongate, palm

at least twice length of posterior margin, distal two-thirds of palmar margin with a row of about 10 small, weakly bifid spines, spaced by short simple spines, proximal third bearing 5 strong spines accompanied by inner row of 5 or 6 long setae; dactylus falcate and closing on defining angle spines; posterior margin short and lightly pubescent distally. Gnathopod 2 (Fig. 1d), subsimilar to gnathopod 1 but differing in several ways as follows: basis more elongate, posterior margin with 1 strong spine on proximal third, anterior margin with 3 spines; merus not pubescent; carpus with pubescent, convex ventral lobe bearing 2 long setae; palmar region of propodus generally similar to that of gnathopod 1 but posterior margin longer and strongly pubescent; dactylus slightly shorter than that of gnathopod 1.

Pereopods 3 and 4 generally similar (Fig. 2f, g): coxae subrectangular, ratio length:height = 1:0.5; ventral margins weakly concave and bearing 2 setae; dactylus not elongate, ratio propodus:dactylus = 1:0.37. Pereopod 5 (Fig. 2h) relatively short; coxa with short anterior lobe and with 1 long spine on posterior lobe; basis suboval; merus distinctly longer tha carpus; carpus with 1 curved posterodistal spine, anterior margin with spines and a row of long setae; posterior margin of propodus with row of long thin, deeply bifid setae, anterior margin with row of 5 spines; dactylus not elongate, ratio propodus:dactylus = 1:0.3. Pereopod 6 (Fig. 2i) similar to pereopod 5 but little longer; posterior margin of propodus with row of long, thin, deeply bifid setae; pereopod 7 (Fig. 2l) distinctly longer than pereopods 5 and 6; basis little broader than those of pereopods 5–6; merus as long as carpus, anterior and posterior margins with rows of long thin setae; dactylus elongate, ratio propodus:dactylus = 1:0.6, posterior margin with 3 setae, nail very short. Coxal gills subovate, on segments 3–5, elongate (Fig. 2h). Oostegites (brood plates) not observed.

Distoposterior corners of pleonal plates (Fig. 3h) tiny and acute, posterior margin of 3 distally convex and bearing 2 setules. Pleopods (Fig.3a, b, c) without inner ramus, outer rami reduced in length and gradually stronger from pleopods 1 to 3, peduncles each with 2 coupling spines (retinacles). Uropods 1 and 2 (Fig. 3d, e) closely similar except peduncle of uropod 1 bearing strong basofacial spine. Peduncles of uropods 1 and 2 each with 2 distal spines; outer rami slightly shorter than inner and naked except for 3 apical spines. Uropod 3 (Fig. 3f): rami approximately equal in length; outer ramus with row of long setae on inner and outer margins; inner ramus bearing 3 to 4 strong spines on distal half of outer margin; both rami each bearing 5 or 6 strong spines apically. Telson (Fig. 3g) comparatively short, clearly broader than long; apical margin straight, with 1 long, robust spine inserted just below margin on either side.

Type locality

Open shallow well at Dibab (23°04'31"N; 59°03'22"E) in Sultanate of Oman (Fig. 6). According to Stock et al. (1997) the well water with the single specimen was filtered through a Cvetkov net. It was also pointed out that the bottom substrate of the well consisted of sand and gravel and the biota was composed of an amphipod, various

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zootaxamosquito larvae, and green filamentous algae. Water quality was rated moderate to(1208)suspect, with high salinity.

Derivatio nominis

The epithet *aequimana* is derived from the latin *aequus* (equal) and *manus* (hand), stressing the morphological similarity of the gnathopods.

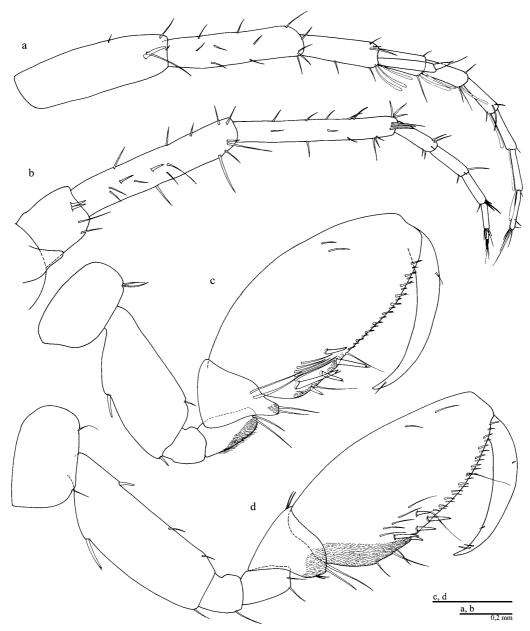


FIGURE 1. *Stockigidiella aequimana*, new species, male (?) holotype 3.7 mm, Dibab (Sultanate of Oman). a, b, antennae 1, 2; c, d, gnathopods 1, 2.

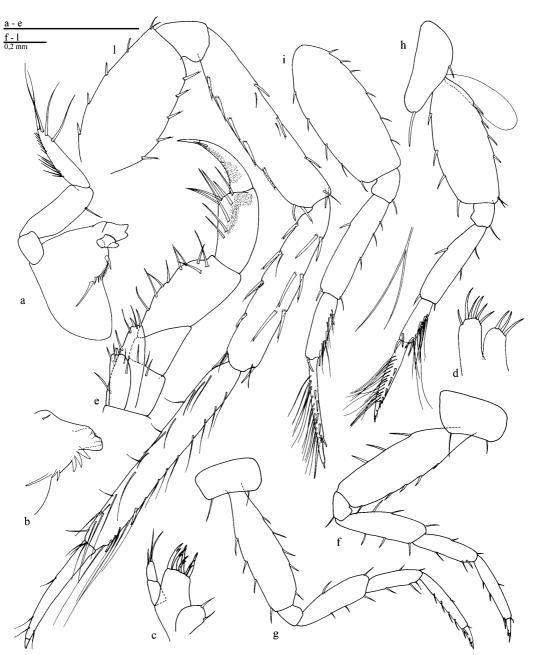


FIGURE 2. *Stockigidiella aequimana*, new species, male (?) holotype 3.7 mm, Dibab (Sultanate of Oman). a, left mandible; b, right mandible; c, d, maxillae 1, 2; e, maxilliped; f-l, pereopods 3–7.

Omangidiella new genus

Diagnosis

A highly aberrant stygomorphic bogidiellid distinguished from almost all other

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members of the family by the following combination of characters: mandibles with triturative molars; maxilliped with coxal endite partially fused with inner (basal) plate; accessory flagellum of antenna 1 uniarticulate; carpus of gnathopod 2 elongate and subequal in length to propodus; propodus of gnathopod 2 subrectangular and reduced in length, with very short dactylus and palm; large lenticular organs marginally present on bases of gnathopod 2 and pereopods 3–6; pleopods without inner rami; uropod 1 with 3 basofacial spines; telson with both lateral and distal spines; very long, narrow, linguiform oostegites on pereopods 2–5; and coxal gills on pereopods 4–6.

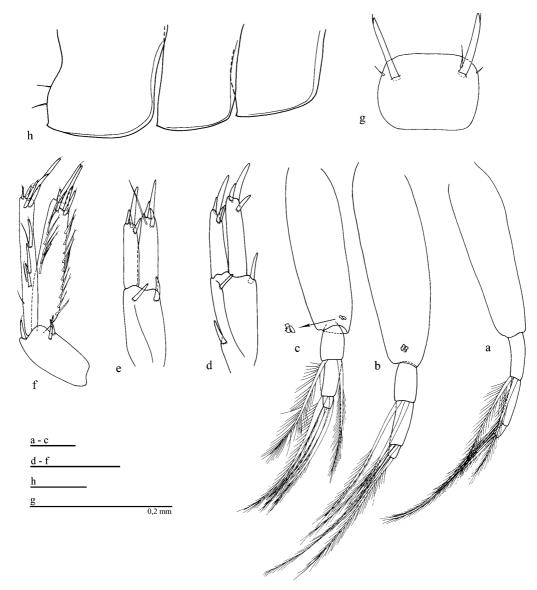


FIGURE 3. *Stockigidiella aequimana*, new species, male (?) holotype 3.7 mm, Dibab (Sultanate of Oman). a–c, pleopods 1–3; d–f, uropods 1–3; g, telson; h, pleonal plates.

Type species

Omangidiella parvidactyla new species, by monotypy. Gender is feminine.

Derivatio nominis

The name of the new genus is derived from a fusion of Oman and *Bogidiella*, the nominate genus of the family.

Remarks

The genus *Omangidiella* is clearly distinguished from all other genera of bogidiellids by the remarkably different structure of gnathopod 2 and development of prominent oostegites, which suggest existence of a strong marsupium to hold and protect developing eggs. It should be noted that female bogidiellids have never been observed to brood eggs, although a number of them possess very small oostegites, which probably allow eggs to be given out freely in the environment. The exceptional development of oostegites in Omangidiella parvidactyla described below suggests that it has a different behavior than most other bogidiellids. However, this must be confirmed by future studies. The oostegites development could also be linked to tegumental respiration, because the gills are very small. The lenticular organs, which are very wide in Omangidiella, are in a marginal position on gnathopod 2 and percopods 3-6, which is an unusual position for these organs in the bogidiellids. There is no existing hypothesis about the exact function of these "organs," except that they could play a role in tegumental respiration. The fact that they are not always present in the bogidiellids, argues against a phylogenetic significance, and instead suggests only a functional importance. In support of this suggestion is the presence of analogous structures in several other subterranean amphipod families, such as the ingolfiellids and paracrangonyctids.

Perhaps of greater phylogenetic importance is the highly unusual presence of a third coxal lobe on the maxilliped, which is in addition to the basal and ischial endites and appears to be similar to that observed in *Nubigidiella* and discussed in a recent paper by Iannilli et al. (2005). This unusual structure is present in addition to these two endites, which are typically present in amphipods and often called, respectively, inner and outer plates or lobes. In *Omangidiella* the coxal lobe is partially fused with the basal lobe. A third coxal lobe or endite is also present in other African bogidiellids besides *Nubigidiella*, including *Maghrebidiella* and *Afridiella*. In *Maghrebidiella* the coxal endite is totally fused with the basal endite, whereas in *Afridiella*, a recent re-examination revealed a slender structure, largely fused with the basal endite. This unique structure appears to characterize a group of genera from Africa and Arabia. The presence of the coxal endite is clear in *Nubigidiella*, partially fused in *Maghrebidiella*. The degree of fusion of the coxal endite appears to follow a graduated trend or pattern, leading us to regard the presence of this structure in the Afro-Arabian group as a plesiomorphic character state, with the more

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fused condition representing increasing reduction phases that tend toward an apomorphic state. Whether or not this actually represents a trend from primitive to advanced for this character is questionable for the moment and will remain unclear until the maxillipeds of specimens in the other bogidiellid genera are carefully re-examined.

Omangidiella parvidactyla new species Figs. 4, 5

Material examined (expedition station number in parentheses is from Stock et al. 1997)

Sultanate of Oman. (96–67) border of wadi Taww at Halban (23°34'N; 58°01' E), 3 paratype specimens, 1 April 1996, with thermosbaenaceans, cyclopid copepods, oligochaetes, diverse insect larvae; (96–75) Wadi Bani Henay (26°30'35"N; 57°19'34"E), pump in gravel at 50 cm below sediment surface, 10 paratype specimens, 1 April 1996, with thermosbaenaceans, stenasellid isopods, oligochaetes, chironomids; (96–76) same place and date as (96–75), probe; at 1.20 cm, 10 paratype specimens (very damaged), with thermosbaenaceans, stenasellid isopods, cyclopid copepods; (96–77) Wadi Bani Henay (26°30'35"N; 57°19'34"E) pump in gravel probe at 90 cm, 1 female paratype, 1 April 1996, with thermosbaenaceans, stenasellids, chironomids. Wadi Nakhl (ca. 23° 26' N 57° 52' E), Oesterreich Expedition, female holotype (collection date unknown) dissected and mounted in Faure's medium on slides 4577–4581, 2 paratypes (slides 4582–4591) deposited in Museo Civico di Storia Naturale Verona (MVRCr 444), and 5 paratypes in ethanol deposited in Zoological Museum Amsterdam.

Description

The description is based on the holotype female from Wadi Nakhl, with exception of the mouthparts, which are based on a paratype female from Wadi Bani Henay (see above).

Female (3.0 mm) with oostegites.— Antenna 1: (Fig. 4a) ratio of articles 1-3 of peduncle = 1:0.8:0.5, articles without spines, with only few short setae; flagellum little longer than peduncle, with 13 articles increasing in length distally, bearing only fine setae, and without aesthetascs; accessory flagellum uniarticulate, shorter than article 1 of flagellum. Antenna 2 (Fig. 4b) shorter than antenna 1, with few short setae; gland-cone not elongate; articles 4 and 5 of peduncle subequal in length; flagellum less than half length of peduncle, with 5 articles, the distal one very short.

Mouthparts: labrum (upper lip) rounded distally (Fig. 4c). Left mandible (Fig. 4d): incisor 5-dentate; lacinia mobilis also 5-dentate and followed by 4 setulose rakers; molar triturative and articulated on short conical base, bearing 1 long plumose seta; mandibular palp reduced in length, article 2 longer than article 3; article 3 bearing only single apical seta; right mandible (Fig. 4e) similar to left but lacinia mobilis pluridenticulate; labium (lower lip) (Fig. 4f) with well developed inner lobes and rather short, blunt lateral processes. Maxilla 1 (Fig. 4g); palp reduced in length and bearing only 2 apical setae;

outer plate with 7 serrate spines (3 external ones 4-toothed and 4 internal ones pectinate); inner plate with 3 naked apical setae. Maxilla 2 (Fig. 4h): inner plate little shorter than outer, with many fine setae along inner margin distally, apically with 6 distal spines, the 2 inner ones plumose. Maxilliped (Fig. 4i): coxal endite partially fused with inner lobe and similar to those of *Nubigidiella*, bearing fine setae distally and 1 spine apically; inner lobe bearing 2 short, stout bifid spines apically; outer lobe scarcely expanded, bearing 3 blade spines subapically on inner margin; palp article 2 expanded; dactylus as long as preceding article, with fine pubescence on inner face.

Gnathopod 1 (Fig. 41): coxa subrectangular, ratio length:height = 1:0.7, with 2 setules on anterodistally rounded corner; basis relatively broad, with 3 long setae on posterior margin; merus with pubescent posterior margin; carpus produced into narrowly rounded ventral lobe, partly pubescent and bearing 2 long distal and 2 long subdistal setae; propodus (Fig. 41') subtrapezoidal, palm rather short, only about 40 percent as long as the posterior margin, margin uneven and bearing only few setae and 1 or 2 spines near defining angle; posterior margin nearly straight, without spines or setae; dactylus falcate and closing on defining angle. Gnathopod 2 (Fig. 4m, n) strikingly different from gnathopod 1: coxa similar to coxa 1 but ventral margin weakly rounded; basis with 2 long setae on posterior margin; carpus elongate, as long as basis and longer than propodus, posterior margin pubescent and bearing 2–4 groups of 2 long setae each; propodus (Fig. 4n') elongate and weakly suboval but little shorter than carpus, medial and lateral faces with inferior and superior rows of numerous short, fine setae; palmar margin very short, without defining spines; posterior margin with approximately 9 long setae; dactylus reduced to small, curved, toothlike process.

Percopods 3 and 4 similar (Fig. 5a): ratio $\cos a \operatorname{length:height} = 1:0.6$, ventral margin with 2 anterodistal setules each; basis broad, anterior margin convex and bearing large lenticular organ; merus, carpus and propodus subequal in length, with few short marginal setae; dactylus rather short, ratio propodus: dactylus = 1:0.4. Posterior and inferior margins of coxal plates 1–4 thinly sclerotized. Pereopod 5 (Fig. 5b): coxa anteriorly lobed, with posterodistal spine; basis suboval, anterior and posterior margins with 4 or 5 short spines, distal half with a large lenticular organ; merus, carpus, and propodus subequal in length, with few short marginal spines; ratio propodus:dactylus = 1:0.4. Pereopod 6 (Fig. 5c) similar to pereopod 5 but distinctly longer; coxa with anterior lobe of coxa reduced; basis with a large lenticular organ on distal half of posterior margin; ratio propodus:dactylus = 1:0.4. Pereopod 7 the longest (Fig. 5d); basis little wider than those of percopods 5 and 6, without lenticular organ, anterior margin with 4 short spines, posterior margin with 6 short spines; merus, carpus and propodus subequal in length but much stronger than those of pereopods 5 and 6; propodus little longer and more robust than two preceding articles, anterior margin with row of 5 or 6 short spines accompanied by long setae; dactylus comparatively long, ratio propodus:dactylus = 1:0.37. Anterior and inferior margins of coxal plates 5–7 thinly sclerotized. Oostegites on percopods 2-5, elongate, with long marginal and distal setae.

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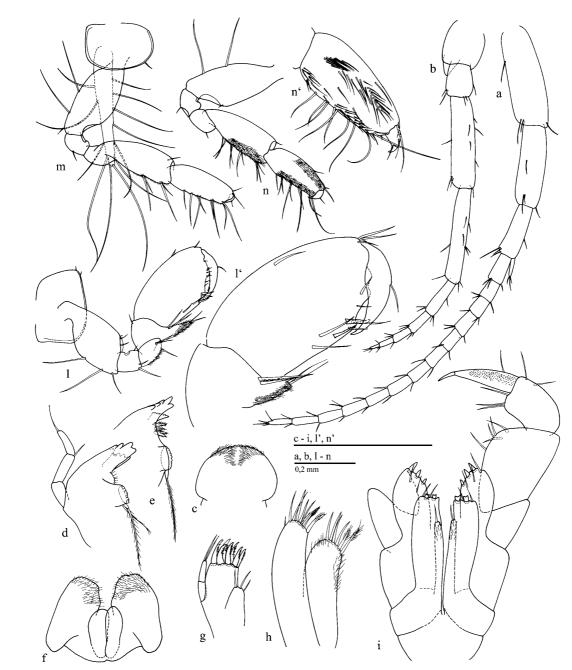


FIGURE 4. *Omangidiella parvidactyla*, new species, female holotype 3 mm, Wadi Nakhl and paratype, Wadi Bani Henay (Sultanate of Oman) (mouthparts). a, b, antennae 1, 2; c, labrum; d, left mandible; e, right mandible; f, labium; g, h, maxillae 1, 2; i, maxilliped; l, gnathopod l; l'carpus, propodus and dactylus of gnathopod 1; m, gnathopod 2, outer side; n, gnathopod 2, inner side; n', carpus, propodus and dactylus of gnathopod 2.

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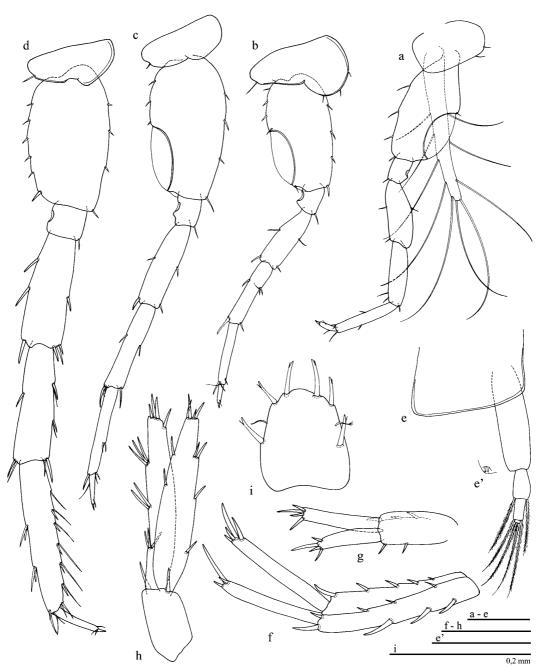


FIGURE 5. *Omangidiella parvidactyla*, new species, female holotype 3 mm, Wadi Nakhl (Sultanate of Oman). a, pereopod 3 with oostegites; b–d, pereopods 5–7; e, pleonal plate and pleopod; e' retinacula; f–h, uropods 1–3; i, telson.

Pleonal plates: posteroventral corners rounded and not produced (Fig. 5e). Pleopods (Fig. 5e) greatly reduced; inner rami absent; outer rami reduced to 3 articles, the terminal one very short; peduncles nearly twice length of rami, each with 2 coupling spines (Fig.

zootaxa (1208) zootaxa (1208) 5e'). Uropod 1 (Fig. 5f): inner and outer rami subequal in length, armed with only 3 apical spines on outer and 4 on inner; peduncle longer than either rami, armed with 9 or 10 spines on upper margin and 3 basofacial spines. Uropod 2 shorter than uropod 1 (Fig. 5g): outer ramus shorter than inner ramus, armed with 4 apical spines; inner ramus as long as peduncle, armed with 4 apical spines; peduncle with 5 spines. Uropod 3 (Fig. 5h): rami approximately equal in length (aequiramus), each bearing several sets of lateral spines in groups of 1, 2, or 3; apex with 3 or 4 spines. Telson (Fig. 5i) about as broad as long at base but slightly tapered distally; each side with 1 mediolateral spine and 1 penicillate seta; apical margin convex and armed with 2 + 2 distolateral spines.

Male unknown.

Type-locality

Wadi Nakhl, located at approximately 23° 26' N; 57° 52' E (Fig. 6). There are no other details available on the date of collection or the physical/chemical characteristics of this locality.

Derivatio nominis

The epithet *parvidactyla* is derived from the latin *parvus* (small) and *dactylus* (finger), denoting the very small dactylus of gnathopod 2.

Biogeographic considerations of bogidiellid amphipods

Including the new taxa described in this paper, the family Bogidiellidae (sensu Koenemann & Holsinger, 1999; see also Stock, 1981) contains 35 genera and 105 species. Despite the relatively large number of taxa, questions regarding the biogeography of bogidiellid amphipods are becoming more numerous and complex with the addition of new species. With the exception of Bogidomma australis Bradbury & Williams (1996) from a cave on Barrow Island in Western Australia, which is eyed but otherwise stygobitic, all species described to date are stygomorphic (i.e., absence of eyes and pigment) and restricted to a subterranean waters. The family is widespread and nearly circum-global in distribution (Ruffo, 1973; Stock 1981; Koenemann & Holsinger, 1999), but unlike a number of other subterranean crustacean groups (e.g., hadziid amphipods, cirolanid isopods, thermosbaenaceans), the distribution of bogidiellid amphipods does not fit a classic "Tethyan" pattern (see also Stock, 1981). Although more than one-half of the species is recorded at present from subterranean freshwater habitats, a significant number inhabits anchialine waters in coastal areas and the interstices of marine sands. Their overall distribution is discontinuous, with the largest concentrations of species in southern North America (Texas, Mexico and the West Indies), South America (especially Brazil and Argentina) and southern Europe (primarily the Mediterranean region). However, a significant number of species occurs outside these regions in parts of Asia Minor, eastern Africa, Arabian Peninsula, Asia, and Australia, but to date none is recorded from central and southern Africa, Madagascar, southern Australia, New Zealand and islands in the central or eastern Pacific. In order to present a clearer picture of the distribution of the family, brief summaries of its representation in different regions of the world are given below.

A) North and Central America (Texas and Mexico south to Panama): 18 species in 7 genera are recorded from this region. The greatest density of species occurs in caves and wells of southern Mexico and Guatemala, where 13 species in five genera are recorded; all are regional endemics. The northern part of the region in Texas is inhabited by *Artesia*, which is probably the most primitive (plesiomorphic) genus in the family, and *Parabogidiella*, which is also one of the more primitive genera in the family (Holsinger & Longley, 1980). In addition to the freshwater species, a marine interstitial species in the genus *Bogidiella* (*s. lat.*) was described recently from Isla de Coiba off the southern coast of Panama (Ortiz et al., 2001).

B) South America: 17 species in 10 genera are recorded from this region, and all are regional endemics restricted to freshwater habitats on the continent except one species in the marine genus *Marigidiella*. *Spelaeogammarus*, which along with *Artesia* is one of the most primitive genera in the family, contains four species that are recorded from caves in karst areas of northeastern Brazil (Koenemann & Holsinger, 2000). Of added interest is *Megagidiella* from a cave in southwestern Brazil, which is the largest bogidiellid amphipod recorded to date. Also of interest is the concentration of six genera (*Argentinobogidiella, Dycticogidiella, Eobogidiella, Grossogidiella, Mesochthongidiella, Patagongidiella*) east of the Andes in central and northern Argentina, all but two of which are monotypic.

C) Western Atlantic Islands (West Indies and Bermuda): 9 species in 7 genera are recorded from this region. Four of the genera are monotypic (*Actogidiella, Antillogidiella, Bermudagidiella, and Hagidiella*) and are regional endemics. The other genera are also represented by species outside the region, including the marine genus *Marigidiella*, which is also known from the Brazilian coast, and the genus *Stygogidiella*, which is represented by species in the Canary Islands and Mediterranean area.

D) Eastern Atlantic Islands (Canary Islands, Cape Verde Islands, and Madeira): 6 species in 4 genera are recorded from this region. Four species in two genera (one in *Xystriogidiella* and three in *Stygobogidiella*) are endemic to the Canary Islands, whereas single species are recorded from the CapoVerde Islands (*Cabogidiella littoralis*) and Madeira (*Bogidiella madeirae*). Most of the records for these species are from either anchialine or marine interstitial habitats.

E) Southern Europe/Mediterranean Region: 39 species in 7 genera are recorded from this region. Two of these genera, including *Bogidiella* (groups A, B & D of Koenemann & Holsinger, 1999) with 23 species and the regionally endemic genus *Medigidiella* with 10 species, contain the majority of species. Four monotypic genera (*Aurobogidiella*,

Hebraegidiella, Marinobogidiella and Maghrebidiella) are endemic to the Mediterranean region, whereas the genus Stygogidiella, which is represented in the Mediterranean area by one species, is also known from Canary Islands and Barbuda in the West Indies. The first published description of a bogidiellid amphipod was that of Bogidiella albertimagni Hertzog (1933) from an interstitial groundwater habitat in the flood plain of the Rhein River near Strasbourg in northeastern France. It has since been recorded from a number of sites in central and southern Europe, including interstitial waters in northern Italy.

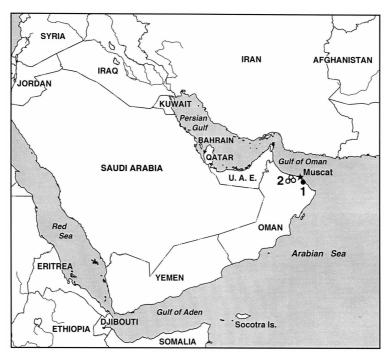


FIGURE 6. Geographic distribution of *Stockigidiella* and *Omangidiella* in the Sultanate of Oman. 1, *S. aequimana* (solid circle). 2, *O. parvidactyla* (open circles).

F) Sudan, eastern Africa and southern Arabia: 7 species in 4 genera are recorded from this region. These four genera, all of which are structurally unique in one or more ways, include *Nubigidiella* (one species from the Sudan and one from Abd al Kuri Island in the Arabian Sea), *Afridiella* (three species from Somalia), and the two monotypic genera *Omangidiella* and *Stockigidiella* described in this paper. Three of these genera (*Nubigidiella*, *Afridiella* and *Omangidiella*) are characterized by the presence of a unique third coxal endite on the maxilliped that was recently described by Iannilli et al. (2005) and is discussed above in Remarks under the genus *Omangidiella*. Other than for the species from Morocco, Sudan, and Somalia, bogidiellids are so far unrecorded from elsewhere on the African continent or on Madagascar.

G) Central Asia: 2 species in 1 genus are recorded. Only two regional endemics in the genus *Bogidiella* (group D) are recorded to date, including one from Afghanistan and the

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other from Turkmenistan.

H) Southeastern Asia: 7 species in 3 genera are recorded from this region. The species known to date are widely scattered and recorded largely from caves in southern Japan (Ryukyu Islands), the Philippines, Sarawak (on the island of Borneo), Indonesia (Halmahera Island), Thailand, and southern China. Both the monotypic genus *Aequigidiella* and a species of *Bogidiella* (group C) are recorded from Thailand, whereas the genus *Indogidiella* is represented by single species in Sarawak and on the western Philippine island of Palawan. The species from Japan and China are assigned respectively to groups A and D in the genus *Bogidiella*. Perhaps the most unique genus in this region is *Aequigidiella* Botosaneanu & Stock (1989) from interior Thailand, which along with several genera in North and South America is one of the most primitive in the family.

I) Australia: 2 species in 2 genera are presently recorded from this region, including a marine species in the genus *Xystriogidiella* from the Great Barrier Reef and the monotypic, eyed *Bogidomma*, which is known only from subterranean freshwater on Barrow Island just off the coast of Western Australia.

J) In addition to the described taxa reviewed above, a number of undescribed new bogidiellids (both genera and species) reside in various research collections, including those of the authors. Included in this material, some of which has not been described because of poor preservation or lack of mature individuals, are specimens from subterranean waters in western Australia (John Bradbury, pers. comm.), Fuerteventura in the Canary Islands (wells), the English Channel (Spooner, 1959), south-central France (cave), Galapagos (marine littoral) (Coineau & Stock, 1986), French Guyana (cave), northeastern Greece (wells/hyporheic) (Coineau & Stock, 1986), southeastern India (wells), southern Mexico (wells) (Ruffo & Vigna Taglianti, 1977), Texas (wells) (Holsinger & Longley, 1980), Tunisia (interstitial/hyporheic), Yucatan Peninsula (caves), and elsewhere.

Whereas most of these undescribed taxa are potentially interesting biogeographically, further clarification of their taxonomic affinities and phylogenetic relationships is neccessary relative to their importance. Clearly, however, two of the most important undescribed taxa include a provisionally recognized new genus and species from a cave in the Department of Tarn in France, which was discovered by Claude Bou (pers. comm.) some years ago, and a new species tentatively assigned to the genus *Bogidiella* s.lat. from wells in southeastern India, which was recently discovered by Prof. Y. Ranga Reddy of Acharya Nagarjuna University and sent to one of us (JRH) for determination and description. The new genus from France is especially interesting because the propodus and carpus of gnathopod 2 is morphologically convergent on that of a hadzioid amphipod, even though the remainder of its *Gestalt* is typically bogidiellid. Moreover, there is a remarkable resemblance of the propodus of gnathopod 2 of the undescribed French taxon to that of the new genus *Omangidiella* described above. However, the carpus of gnathopod 2 in *Omangidiella* is narrow (subrectangular), whereas that of the new French genus bears

zootaxa (1208) a distinct distoposterior lobe closely similar to that of many hadzioids.

The specimens from India were collected with phreatoicidean isopods of the family Nichollsidae from the vicinity of Guntur about 50 km from the east coast. A description of this new Indian taxon is in preparation by Holsinger and Reddy and is especially significant because it represents the first collection of fully intact specimens of bodigiellid amphipods from the entire subcontinent of India. Their association with stygobitic phreatoicid isopods is also of interest. To our knowledge, the only other sample of a bogidiellid from India is a poorly preserved broken specimen in the U. S. National Museum of Natural History (USNM 262176) that was collected in 1965 by S. Swaminathan with a suction pump from groundwater near Chidambaram, approximately 550 km south of Guntur near the coast.

Also of biogeographic interest is the high generic diversity among the bogidiellids on the continents of North and South America, combined with the occurrence in this part of the world of all but one of the most primitive genera in the family. Does this combination of high generic diversity and primitive taxa based on perceived plesiomorphies suggest that bogidiellids originated in this part of the world, or is this theory contradicted by the presence of the equally primitive (plesiomorpic) *Aequigidiella* half way around the globe in southeastern Asia? Yet another biogeographically interesting but somewhat paradoxical bogidiellid is *Bogidomma* from Western Australia, which aside from the presence of eyes, is not a plesiomorphic genus. However, the development of eyes in a single species of bogidiellid may be a character reversal and not the relict of an ancestral character. Thus, the occurrence of primitive genera in two widely separate parts of the world and the presence of an eyed taxon on yet another continent prevent us from drawing any firm conclusions from these data about the early biogeographic history of the family.

Speculation on the origin of the bogidiellids and attempts to explain their biogeography are found in papers by Ruffo (1973), Stock (1981), Notenboom (1991), and Koenemann & Holsinger (1999). Alternative hypotheses are discussed that focus on whether this exclusively subterranean group originated in marine waters, with subsequent invasion of freshwaters during marine embayments, or whether the family originated in freshwaters on Pangaea II, with subsequent dispersal into anchialine and marine waters over a long period of geological history in concert with continental spreading in the Mesozoic. Despite the discovery and description of new bogidiellid taxa since publication of these papers, nothing really new has been revealed about bogidiellid biogeography except that new taxa continue to be discovered in widely scattered parts of the world in both marine/brackish and freshwater habitats. However, given our current knowledge of the global distribution of the Bogidiellidae, we believe a marine origin for the family is the more likely scenario. In support of this hypothesis is the fact that the majority of species either inhabit areas that were previously covered by Cretaceous or Tertiary marine embayments, or are presently in direct contact with marine or brackish waters. Only species living in the interior of South America (Brazil and northern Argentina) and southcentral China are exceptions inasmuch as they occur in areas that have probably not been directly exposed to marine waters since the Paleozoic. There is also a complex mixture of primitive and advanced character states among many of the bogidiellid taxa, which at the moment cannot be fully reconciled with distributional patterns. Thus, considerably more data on the global distributional of component taxa, combined with a careful evaluation of character states among the species from different parts of the globe as well as from different subterranean habitats, are clearly needed before we can construct a complete picture of phylogenetic and biogeographic history. However, cladistic analyses that combine morphological and molecular data will be helpful in teasing out lineages that should provide further insight into the evolutionary history of this large, significant subterranean amphipod family.

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