

PHYLOGENETIC ANALYSIS OF THE AMPHIPOD FAMILY
BOGIDIPELLIDAE S. LAT., AND REVISION OF TAXA ABOVE THE
SPECIES LEVEL

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ABSTRACT

The increasing number of world-wide discoveries of subterranean amphipods, especially during the last two decades, has led to additions of numerous new taxa in the stygobiont family Bogidiellidae s. lat. To date, the family is composed of 23 genera and 11 subgenera, and approximately 110 described species. However, given the uneven quality of generic and subgeneric diagnoses in the literature, there is considerable confusion regarding the status of some of the taxa at these levels. Even the family itself lacks a clear definition. In order to gain a better knowledge of the phylogeny of this group, a cladistic analysis, employing both PAUP 3.0s and MacClade, was performed on the genera and subgenera currently assigned to the Bogidiellidae s. lat. Supported by the results of this analysis, the taxonomic structure of this group is completely revised above the species level. The revision excludes 5 genera from the family, all remaining subgenera are elevated to generic level. Four taxa are split, resulting in 5 new genera. The family Bogidiellidae now consists of 33 genera.

ZUSAMMENFASSUNG

Die wachsende Zahl weltweiter Neuentdeckungen von Grundwasser-Amphipoden, insbesondere während der letzten zwei Jahrzehnte, erweiterte die Stygobiontenfamilie Bogidiellidae s. lat., um zahlreiche neue Taxa. Bis heute sind in der Familie etwa 110 beschriebene Arten in 23 Gattungen und 11 Untergattungen zusammengefasst. Aufgrund der unterschiedlichen Qualität diagnostischer Beschreibungen herrscht allerdings erhebliche Verwirrung hinsichtlich des taxonomischen Status einiger Gruppen. Sogar die Definition der Familie selbst ist relativ undeutlich. Um neue Einsichten in die Phylogenie der Bogidielliden s. lat., zu erhalten, führten wir eine kladistische Analyse der Gattungen und Untergattungen unter Verwendung der Computerprogramme PAUP 3.0s und MacClade durch. Die Resultate dieser Analyse dienten als hilfreiche Ergänzung bei der umfassenden taxonomischen Revision der Gattungen und Untergattungen. Fünf Gattungen wurden aus der Familie entfernt und alle Untergattungen zu Gattungen erhoben. Das Aufspalten von vier Taxa resultierte in 5 neuen Gattungen. Die Familie Bogidiellidae besteht somit aus 33 Gattungen.

INTRODUCTION

Close to 12% of the approximately 7,000 described species in the order Amphipoda inhabit subterranean groundwater environments. The vast majority of these species is distributed among 12 families, some of which are composed exclusively of hypogean species, whereas others comprise both epigean and hypogean representatives (see Holsinger, 1993, 1994). All known species of the family Bogidiellidae Hertzog, 1936, are true stygobionts. Bogidiellids are relatively small amphipods, with body lengths generally between 1 and 5 mm. They have a world-wide distribution pattern, occurring mostly in freshwater but also in brackish and marine environments. Bogidiellid habitats include caves, wells, cold mountain springs up to 2,500 m altitude, and the interstitial groundwater associated with river banks, lakes, and beaches.

The first comprehensive revision of the family was published by Ruffo (1973). Bousfield (1977), recognizing the morphological divergence within the family, introduced the concept of a superfamily Bogidielloidea, which he divided into two groups: the family Bogidiellidae and the family group of *Pseudocrangonyx-Paracrangonyx*, including the genera *Paracrangonyx*, *Procrangonyx*, *Pseudocrangonyx*, and *Sternophysinx*. Subsequent comprehensive revisions of Bogidiellidae s. lat., were made by Stock (1981) and Karaman (1981, 1982). Since then a substantial number of new, world-wide discoveries of bogidiellid amphipods has led to the introduction of taxa at both the generic and subgeneric levels. Naturally, the supplementary discoveries and records of bogidiellid amphipods help us to understand the evolutionary history of this enigmatic group. However, the addition of new taxa created some undesirable side effects, especially by increasing the uneven quality of generic diagnoses. Moreover, the familial diagnosis — which was never very solid anyway — gradually changed into a list of exceptions. For every diagnostic character there is at least one species that is an exception to the rule. Even the last diagnostic stronghold that defines bogidiellids as “exclusively blind stygobionts” had to be changed recently: *Bogidomma australis* Bradbury & Williams, 1996, from a cave in western Australia, despite being a perfectly typical bogidiellid, has large eyes!

Our basic criterion for a taxonomic reorganization of the Bogidiellidae s. lat. was the evaluation and comparison of significant morphological structures, hereafter referred to as diagnostic characters. In order to obtain a supplementary source of information for the taxonomic revision and also to clear up some of the unresolved questions about the evolutionary history of bogidiellid amphipods, a phylogenetic analysis was performed on the genera and subgenera of the family.

TAXONOMIC PART

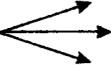
The present taxonomic composition of the family Bogidiellidae s. lat. is rather confusing. To date, the family is composed of 23 genera, 11 subgenera (all within the genus *Bogidiella*), and a total of 110 described species. In the following subsections, we will discuss several problematic aspects of bogidiellid taxonomy and propose our solution for each individual case (see Appendix A and fig. 1 for overview). We believe that our proposed revision results in the recognition of a monophyletic group, therefore, eliminating the need for a superfamily

► **Genera removed from the family:**

Bollegidia
Dussartiella
Kergueleniola
Paracrangonyx
Pseudingolfiella

► **Proposed changes to existing genera or subgenera:**

Subgenus *Antillogidiella*  Genus *Antillogidiella*
Bermudagidiella n. gen.

Subgenus *Medigidiella*  Genus *Medigidiella*
Arganogidiella n. gen.
Indogidiella n. gen.

Genus *Patagongidiella*  Genus *Patagongidiella*
Grossogidiella n. gen.

Subgenus *Stygogidiella*  Genus *Stygogidiella*
Argentinogidiella n. gen.

► **All remaining subgenera are elevated to generic level**

Fig. 1. Proposed changes to the family Bogidiellidae s. lat.

Bogidielloidea. The revised family Bogidiellidae can be differentiated from all other gammaridean amphipods by a refined familial diagnosis: uropods 1-3 with 1-segmented rami of equal or near equal length, reduced pleopodal rami, and a distinct carpal lobe of gnathopod 1 form a unique combination of diagnostic characters that distinguishes all bogidiellids known to science.

The taxonomic value of subgenera

The introduction of subgenera was made by Stock (1981) in his work on bogidiellid taxonomy and zoogeography. Stock established subgenera for several taxa that were defined by secondary sexually dimorphic characters only. He argued that "in cases in which only one of the sexes is known, the animals can at least be attributed to the 'mother genus', *Bogidiella*, without reference to a subgeneric name" (Stock, 1981: 348). In other words, as long as we have specimens of one sex only, we cannot be certain about the sexually dimorphic nature of the species, therefore, assign it to a separate subgenus within *Bogidiella*. Rather than being a helpful facilitation, this practice is disadvantageous for two reasons: (1) In case the missing sex is found, we may or may not have a sexually dimorphic species, but we unquestionably have a species with modified appendages. The genus *Bogidiella* s. str. has unmodified appendages, consequently, the designation of separate taxa for species with modifications is certainly justified. From this standpoint, a distinction between genus and subgenus becomes irrelevant. (2) The introduction of new taxa during the last two decades has obscured a clear, well-defined differentiation between genera and subgenera. The diagnostic character 'sexually dimorphic appendages' is not exclusively used for the subgenera but also became a principal feature for some of the genera, for example, *Aequigidiella* Botosaneanu & Stock, 1989, *Actogidiella* Stock, 1981, and *Mari-nobogidiella* Karaman, 1982. We propose to elevate all subgenera to generic level in order to rid the family of these inconsistencies.

Genus **Bogidiella** Hertzog, 1933

Type species. — *Bogidiella albertimagni* Hertzog, 1933, by monotypy.

The elevation of all subgenera to generic level entails several changes for the genus *Bogidiella*: (1) A subgenus *Bogidiella* is no longer consistent. All species in the subgenus *Bogidiella* remain in the genus *Bogidiella*. (2) The generic diagnosis of the subgenus *Bogidiella* becomes the valid diagnosis of the genus *Bogidiella* (i.e., pleopods and uropods without marked sexually dimorphic modifications).

We removed the following species from the genus *Stygogidiella* and assigned it to the genus *Bogidiella*, because the original description is apparently based on one immature female and, to our knowledge, there are no males reported or described:

***Bogidiella cerberus* Bou & Ruffo, 1979**

Bogidiella cerberus Bou & Ruffo, 1979: 303, figs. IV-VI; type locality: Alepotrypa Cave, Peloponnesus (Greece).

Bogidiella (Stygogidiella?) cerberus, Stock, 1981: 354.

Bogidiella (Bogidiella) cerberus, Karaman, 1981: 31.

Bogidiella (Stygogidiella) cerberus, Karaman, 1982: 49.

With 38 species, *Bogidiella* is by far the largest of the bogidiellid genera. Despite the relatively high morphological variation among these species, no successful attempts have been made to separate them taxonomically (see Karaman, 1982). Apparently, the morphological divergences are not distinct enough to justify the designation of new genera. In order to give a clearer profile of *Bogidiella*, we split the genus into 4 different groups (see Appendix A). We used the status of the inner rami of the pleopods to distinguish the *albertimagni* group (A) (rami absent) from the *skopljensis* group (B) (rami present). The great majority of both groups A and B are species from southern Europe. The *niphargoides* group (C) is composed of 4 species with one or several peculiar characters, e.g., telson much longer than wide, antenna 1 with 17 or more segments, mouthparts with conspicuous modifications, etc. In group C, the inner rami of the pleopods show different states of reduction (all reduced; all absent or vestigial on pleopods 1 and 2; absent on pleopod 3). We decided to place all species of which only one sex is reported or of which the sex is unknown in the *lindbergi* group (D). We separated these species mainly because their insecure taxonomic status would have biased the assessment of robust characters for the cladistic analysis (see Taxa).

Incompatible taxa

A thorough comparison of bogidiellid genera and subgenera reveals several taxa with highly reduced or modified morphological structures, indicating a distinct departure from the familial diagnosis. In our opinion, sternal gills, uniramous uropods, 2-segmented rami of the third uropods, absent or multi-segmented outer rami on pleopods 1-3, and a deeply cleft telson are examples of characters that are incompatible with our refined familial diagnosis. The development of these characters most likely followed an extensive pattern of progressive evolutionary steps, forming a sharp contrast to the overall conservative morphological

evolution of bogidiellid amphipods. If bogidiellids are indeed an ancient group as some workers have suggested (see Stock, 1981), their conservative morphology, which is reflected by the absence of complex modifications, particularly implies their monophyly. We do not regard these characters as apomorphies for the bogidiellids because it is more probable that unrelated groups developed similar troglomorphic structures as a result of their adaptation to subterranean environments, for example, vermiform bodies and reduced coxal plates. Substantial morphological differences can be found in five genera only, some of which are formed by a combination of two or more atypical characters. In an attempt to establish the bogidiellids as a bona fide monophyletic group, we propose to remove the following genera from the family. Clarification of their taxonomic status and familial assignment is open for future study.

Genus **Bollegidia** Ruffo, 1974

Bollegidia Ruffo, 1974a: 405.

Type species. — *Bollegidia capensis* Ruffo, 1974.

Bollegidia capensis Ruffo, 1974a: 405, figs. III-V; type locality: Blaauwberg Beach, Table Bay, Cape Town (South Africa); known only from type locality.

Second species: *Bollegidia sootai* (Coineau & Rao, 1972).

Bogidiella sootai Coineau & Rao, 1972: 85-92, figs. 11-14; type locality: Andaman Islands, Gulf of Bengal (India).

Bollegidia sootai, Ruffo, 1974a: 411; 1994: 365, fig. 4j; locality: Sabang Beach, eastern Mindoro (Philippines); also reported from Malaysia (Ruffo, 1985).

Remarks. — The unusual combination of a uniramous uropod 1 and extremely reduced rami of pleopods 1-3 is not diagnostic for bogidiellids according to our concept. Excluding *Bollegidia*, bogidiellids have a biramous uropod 1. The only bogidiellids with a reduced inner ramus of uropod 1 occur in the subgenus *Guagidiella* Stock, 1981. However, this modified ramus (shortened and fused with the peduncle, 1 apical spine extremely modified) is a sexually dimorphic character. It presumably is a male modification that facilitates sperm transfer. In *Bollegidia*, uniramous rami are reported for both sexes and, therefore, cannot be related to the reduction in *Guagidiella*.

Similarly, the extremely reduced pleopods of the *Bollegidia* are a peculiar phenomenon, even for the family Bogidiellidae that is characterized by a trend towards a decreased number of segments of the pleopodal rami. This reduction is sexually dimorphic for the genus *Bollegidia*: the female outer rami of pleopods 1 and 2 are completely absent, and on pleopod 3 the outer ramus is reduced to a 1-segmented bud, whereas the male has a 2-segmented outer ramus on pleopod 1,

a 1- or 2-segmented outer ramus on pleopod 2, and a 1-segmented outer ramus on pleopod 3. A comparable reduction of pleopodal rami segments can only be found in the genera *Pseudingolfiella* Noodt, 1965, and *Kergueleniola* Ruffo, 1974 (cf. Ruffo, 1974b), both of which we also consider incompatible with the familial diagnosis.

There are two additional, but minor morphological divergences of *Bollegidia* that do not occur in any other bogidiellid: brood plates attached to pereopods 3-4 (usually on pereopods 2-5) and a weakly lobed carpus on gnathopod 1, bearing one strong spine with several short marginal setules.

Genus **Dussartiella** Ruffo, 1979

Dussartiella Ruffo, 1979: 429.

Type species. — *Dussartiella madegassa* Ruffo, 1979.

Dussartiella madegassa Ruffo, 1979: 431, figs. VI-VII; type locality: spring near artificial lake Mantasoa, Manjakandriana (Madagascar); known only from type locality.

Remarks. — A greatly reduced, scale-like inner ramus next to a 2-segmented outer ramus on uropod 3 and outer rami of pleopods 1-3 with 11, 8, and 5 segments, respectively, clearly mark *Dussartiella* as an atypical bogidiellid. Both characters are not unique for the family. Remarkably, however, they both occur in one of the other incompatible taxa: *Paracrangonyx* Stebbing, 1899, has an identically structured uropod 3, also combined with a set of 11-, 6-, and 3-segmented outer rami on pleopods 1-3. Pleopodal outer rami with more than (usually) 3 segments are very uncommon for bogidiellids. They are found in three taxa only: 6-segmented outer rami in *Artesia* Holsinger, 1980, and 3- to 5-segmented outer rami in both *Aurobogidiella* Karaman, 1988 (cf. Karaman, 1988c) and *Patagongidiella* Grosso & Fernández, 1993.

Minor incompatible characters are a 2-segmented, naked mandibular palp; maxilla 1 with an extremely asymmetrical palp (vestigial, 1-segmented on left and strong, 2-segmented palp on right maxilla 1) and an outer plate with 9 apical spines (usually 7 in other bogidiellids); and the absence of a carpal lobe on gnathopod 1.

Genus **Kergueleniola** Ruffo, 1970

Kerguelenella Ruffo, 1970b: 45.

Kergueleniola, Ruffo, 1974b: 507 (emend.).

Kerguelenicola, Stock, 1981: 355 (lapsus calami).

Type species. — *Kergueleniola macra* (Ruffo, 1970).

Kerguelenella macra Ruffo, 1970b: 45, figs. I-III; type locality: Kerguelen Island; known only from type locality.

Kergueleniola macra Ruffo, 1974b: 507 (emend.).

Remarks. — Sex unknown; only known specimen found in the stomach of a freshwater trout (*Salvelinus fontinalis* Mitchell, 1814). *Kergueleniola* departs significantly from the bogidiellid familial diagnosis by the following unique characters: deeply cleft telson without spines; 1-segmented outer rami and aequiramus, 1-segmented inner rami on pleopods 1-3; carpus of gnathopod 1 without distal lobe; segment 3 of mandibular palp with row of subapical setae (C-setae).

Furthermore, there are several minor incompatible characters, for example, the unusually shaped palp of the maxilliped, the long, rounded epimeral plates, and the armature and shape of the mandibles and uropods.

Genus **Paracrangonyx** Stebbing, 1899

Paracrangonyx Stebbing, 1899: 422.

Type species. — *Paracrangonyx compactus* (Chilton, 1882).

Crangonyx compactus Chilton, 1882: 177, pl. 10 figs. 13-19; type locality: well at Eyreton, North Canterbury (New Zealand); also reported from several other localities in New Zealand (Chilton, 1894; Karaman, 1981).

Paracrangonyx compactus Stebbing, 1899: 422.

Material examined: 1 female (broken) and 1 male (USNM 21283), both from type locality; 1 female (USNM 22810), partly dissolved, head missing, also from type locality.

Remarks. — *Paracrangonyx* can be unmistakably distinguished from all bogidiellids by the following characters: head with rudimentary eye, consisting of ± 3 unpigmented cells; carpus of gnathopod 1 without lobe; mediosternal gills on pereonites 2-7; outer rami on pleopods 1-3 with 11, 6, and 3 segments, respectively (compare with *Dussartiella*); peduncles of pleopods 2-3 with several marginal spines; epimeral plates with row of strong spines along ventral margins; uropod 3 with vestigial inner ramus and 2-segmented outer ramus (compare with *Dussartiella*).

Additional, lesser divergence from the bogidiellid diagnosis includes a very long mandibular palp with an unusually high number of setae and an exceptionally asymmetrical lacinia mobilis.

Genus **Pseudingolfiella** Noodt, 1965

Pseudingolfiella Noodt, 1965: 27, fig. 1B.

Type species. — *Pseudingolfiella chilensis* (Noodt, 1959).

Ingolfiella chilensis Noodt, 1959: 200, figs. 1-18; type locality: Quebrada de Córdoba, El Tabo, near San Antonio (Chile); also reported from several other localities in Chile (Noodt, 1965; Karaman, 1981).

Pseudingolfiella chilensis, Noodt, 1965: 28, fig. 1B.

Second species: *Pseudingolfiella soyeri* Coineau, 1977.

Pseudingolfiella soyeri Coineau, 1977: 288, figs. 1-4; type locality: Kerguelen Island.

Remarks. — The following characters are the most striking morphological differences in *Pseudingolfiella*: uniramous uropod 3, with 2-segmented (or bipartite) outer ramus; uropods 1 and 2 sexually dimorphic, with distinctly modified rami in both sexes, inner ramus of uropod 2 vestigial in female (unknown in *P. chilensis*); pleopods 1-3 uniramous, eminently reduced, consisting of a single, naked stump (plp. 1-2) or an additional, vestigial segment, bearing a single seta (plp. 3), pleopod 3 sexually dimorphic (unknown in *P. chilensis*); carpus of gnathopod 1 without distal lobe.

New taxa

Another taxonomic problem of the family Bogidiellidae are taxa that contain morphologically incompatible species or species groups. This is especially the case with several of the subgenera. As pointed out above, the primary designation of these taxa is based on sexual dimorphism only. The subgenus *Medigidiella* Stock, 1981, for example, is defined by sexually dimorphic modifications of uropod 1 and/or 2, without a necessary discrimination between the two (see also Karaman, 1982 and Ruffo, 1994: 364). Furthermore, the occurrence of additional diagnostic characters has been more or less neglected (e.g., different states of reduction in pleopodal rami). With the addition of new species, the diagnostic definition of some of these taxa became increasingly unclear and blurry. We, therefore, propose to split the following subgenera and genera into more clearly defined taxa and, in doing so, elevate all subgenera concerned to generic level (see fig. 1 for overview):

Proposed split of the subgenus *Antillogidiella* Stock, 1981

Genus **Antillogidiella** Stock, 1981, new status

Bogidiella (*Antillogidiella*) Stock, 1981: 354.

Type species by monotypy. — *Bogidiella martini* Stock, 1978.

Bogidiella martini Stock, 1978: 104, figs. 1-30; type locality: Saint-Martin, Lesser Antilles.

Bogidiella (*Antillogidiella*) *martini*, Stock, 1981: 354.

Bogidiella (*Bogidiella*) *martini* (group A), Karaman, 1981: 31.

Bogidiella (*Antillogidiella*) *martini*, Karaman, 1982: 43.

Diagnosis. — Sexual dimorphism in pleopod 2 and uropod 1: male with reduced, 1-segmented inner ramus on pleopods 1-3, segment 2 of male pleopod 2 bearing one modified spine; female pleopods without inner rami; female with dagger-shaped rami on uropod 1 (male uropod 1 normal); pars molaris strongly reduced to several small denticles, bearing one long seta; telson with 2 apical spines.

Bermudagidiella new genus

Type species by monotypy. — *Bogidiella* (*Antillogidiella*) *bermudensis* Stock, Sket & Iliffe, 1987.

Bogidiella martini ssp. Sket & Iliffe, 1980: 876; type locality: anchialine caves, Bermuda.

Bogidiella (*Antillogidiella*) *martini* ssp. Stock, 1981: 354.

Bogidiella (*Antillogidiella*) *bermudensis* Stock, Sket & Iliffe, 1987: 55, figs. 1-16.

Diagnosis. — Sexual dimorphism in pleopod 2: male with shortened segment 2 on outer ramus, bearing one modified spine; pleopods without inner rami in both sexes; female with dagger-shaped rami on uropod 1 (male uropods lacking); pars molaris strongly reduced to wide lobe with 4 spinules; telson with 2 apical and 2 subapical spines.

Etymology. — The new generic name is a combination of the geographic locality and part of the generic name *Bogidiella*, the gender is feminine.

Remarks. — Several similar morphological reductions and modifications suggest a close relationship of *Antillogidiella* and *Bermudagidiella*. The designation of 2 distinct genera, however, is in general accordance with the diagnostic generic concept in the family. Moreover, the differentiation of 2 separate phylogenetic lines is strongly supported by the cladistic analysis.

Proposed split of the subgenus *Medigidiella* Stock, 1981

When Stock (1981) established the subgenus *Medigidiella*, he placed 5 named species into the new taxon and listed another 4 species as possibly belonging to *Medigidiella* as well. The only diagnostic character he used to define *Medigidiella* were sexually dimorphic uropods 1 and/or 2. In the last two decades, the number of medigidiellids has trebled. Accordingly, the quality of modifications in male uropods 1 and 2 has become more diverse and complex. Likewise did the occurrence of other potentially diagnostic characters. We propose to split the subgenus *Medigidiella* into the following genera:

Genus **Medigidiella** Stock, 1981, new status

Medigidiella Stock, 1981: 353.

Type species. — *Bogidiella (Medigidiella) chappuisi* Ruffo, 1952.

Bogidiella chappuisi Ruffo, 1952 (in Ruffo & Delamare Deboutteville, 1952); type locality: Argelès, Pyrenees (France); reported from several localities in Southern Europe, Turkey, and North Africa.

Bogidiella (Medigidiella) chappuisi, Stock, 1981: 353.

Species included. — *Bogidiella (Medigidiella) antennata* Stock & Notenboom, 1988; *Bogidiella (Medigidiella) aquatica* Karaman, 1990 (cf. Karaman, 1990a); *Bogidiella (Medigidiella) arista* Koenemann, Vonk & Schram, 1998; *Bogidiella (Medigidiella) dalmatina* (S. Karaman, 1953); *Bogidiella (Medigidiella) hebraea* (Ruffo, 1963); *Bogidiella (Medigidiella) minotaurus* (Ruffo & Schiecke, 1976); *Bogidiella (Medigidiella) paolii* Hovenkamp, Hovenkamp & Van der Heide, 1983; *Bogidiella (Medigidiella) paraichnusae* (Karaman, 1979); *Bogidiella (Medigidiella) uncinata* Stock & Notenboom, 1988.

Diagnosis. — Sexual dimorphism in uropod 2: some male spines on uropod 2 ramus/rami modified; inner rami of pleopods 1-3 absent.

Arganogidiella new genus

Type species. — *Bogidiella arganoi* Ruffo & Vigna Taglianti, 1973.

Bogidiella arganoi Ruffo & Vigna Taglianti, 1973: 115, figs. 8-9; type locality: well near Paraje Nuevo, Cordoba (Mexico).

Bogidiella (Medigidiella) arganoi, Stock, 1981: 354.

Bogidiella (Bogidiella) arganoi (group C), Karaman, 1981: 28.

Bogidiella (Guagidiella) arganoi, Karaman, 1982: 44.

Second species: *Arganogidiella arganoides* Karaman, 1982.

Bogidiella cfr. *arganoi*, Ruffo & Vigna Taglianti, 1977: 153, fig. 13; type locality: Etna, Oaxaca (Mexico).

Bogidiella (Guagidiella) arganoides Karaman, 1982: 44.

Diagnosis. — Sexual dimorphism in uropod 1: some male spines on uropod 1 rami modified; inner rami on pleopods 1-3 absent.

Etymology. — *Arganogidiella* is named in honor of Prof. Roberto Argano; the gender of the name is feminine.

Remarks. — Karaman (1982) placed both *Arganogidiella arganoi* and *A. arganoides* in the subgenus *Guagidiella*. However, the modification of the male uropod 1 in both guagidiellid species is highly apomorphic as compared to the modified spines in *Arganogidiella* (see Incompatible taxa, genus *Bollegidia*). Moreover, *Guagidiella* can be distinguished from *Arganogidiella* by vestigial inner rami on pleopods 1 and 2 (absent in *Arganogidiella*), differently shaped, sexually dimorphic gnathopods, and a 3-segmented accessory flagellum on antenna 1 (2-segmented in *Guagidiella*).

Indogidiella new genus

Type species. — *Bogidiella (Medigidiella) sarawacensis* Stock, 1983.

Bogidiella (Medigidiella) sarawacensis Stock, 1983: 198, figs. 1-26; type locality: Niah Great Cave in Batu Niah National Park, Sarawak (Borneo).

Second species: *Indogidiella dacordii* (Ruffo, 1994).

Bogidiella dacordii Ruffo, 1994: 361, figs. 3-4; type locality: pump water St. Paul, Palawan (Philippine Islands).

Diagnosis. — Sexual dimorphism in uropods 1 and 2: some male spines on uropods 1 and 2 rami modified; pleopods 1-3 with 1-segmented, reduced inner rami.

Etymology. — The new name combines the geographic distribution of the type species (East Indies) and part of the generic name *Bogidiella*, its gender is feminine.

Proposed split of the subgenus *Stygogidiella* Stock, 1981

Genus **Stygogidiella** Stock, 1981, new status

Stygogidiella Stock, 1981: 354.

Type species. — *Bogidiella bredini* Shoemaker, 1959.

Bogidiella bredini Shoemaker, 1959: 273, fig. 1; type locality: Dark Cave, Barbuda.

Bogidiella (Stygogidiella) bredini, Stock, 1981: 354, fig. 3.

Species included. — *Bogidiella (Stygogidiella) atlantica* Sánchez, 1991; *Bogidiella (Stygogidiella) cypria* (Karaman, 1989) (cf. 1989b); *Bogidiella (Stygogidiella) perla* Stock, 1981; *Bogidiella (Stygogidiella) purpuriae* Stock, 1988; *Bogidiella (Stygogidiella) uniramosa* Stock & Rondé-Broekhuizen, 1987; *Bogidiella (Stygogidiella) virginalis* Stock, 1981.

Diagnosis. — Sexual dimorphism in pleopod 2: male with modified spine on 2nd segment of pleopod 2; telson wider than long or as wide as long.

Argentinogidiella new genus

Type species. — *Bogidiella (Stygogidiella) hormocollensis* Grosso & Fernández, 1988.

Bogidiella (Stygogidiella) hormocollensis Grosso & Fernández, 1988: 65, figs. on pls. 1-2; type locality: Sierra de Medina, Tucumán (Argentina).

Second species: *Argentinogidiella lavillai* (Grosso & Claps, 1984).

Bogidiella (Stygogidiella) lavillai Grosso & Claps, 1984: 224, figs. 1-32; type locality: Rio Grande near Jujuy (Argentina).

Diagnosis. — Sexual dimorphism in pleopods 1 and 2 and uropod 2: male pleopod 2 bearing modified spine on 2nd segment; male pleopod 1 with initial stage of sexual dimorphism; male uropod 2 with reduced spines and reduced inner ramus; telson much longer than wide.

Etymology. — *Argentinogidiella* refers to the geographic distribution of both species, combined with part of the generic name *Bogidiella*; the gender of the name is feminine.

Remarks. — Apparently, *A. hormocollensis* shows sexually dimorphic pleopods 1 and 3: the male has shortened setae on the 1st segment of pleopod 1 (normal in female) and a relatively stronger pleopod 3. The drawings of *A. lavillai* seem to indicate almost identical reductions. It would be interesting to re-examine the pleopods of *A. lavillai* in both sexes for similar structures.

Proposed split of the genus *Patagongidiella* Grosso & Fernández, 1993

Genus **Patagongidiella** Grosso & Fernández, 1993

Patagongidiella Grosso & Fernández, 1993: 340.

Type species by subsequent designation herein. — *Patagongidiella danieli* Grosso & Fernández, 1993.

Patagongidiella danieli Grosso & Fernández, 1993: 366, figs. on pl. IV; type locality: Del Arenal Cave, Nequén (Argentina); sympatric with *Grossogidiella mauryi*.

Diagnosis. — Peduncle of male uropod 1 with highly modified spine; 2nd segment of male pleopod 2 with modified spine; large mediosternal processes on pereonites 2-5.

Grossogidiella new genus

Type species by monotypy. — *Patagongidiella mauryi* Grosso & Fernández, 1993.

Patagongidiella mauryi Grosso & Fernández, 1993: 362, figs. on pls. II-III; type locality: Del Arenal Cave, Nequén (Argentina).

Diagnosis. — Appendages without sexual dimorphism; large mediosternal processes on pereonites 2-5.

Etymology. — *Grossogidiella* is named in honor of Dr. Luis E. Grosso; the gender of the name is feminine.

PHYLOGENETIC ANALYSIS

Cladistic methods

We used PAUP, version 3.0s, to perform a cladistic analysis on the bogidiellid genera and subgenera. Because our matrix contained a relatively high number of Operational Taxonomic Units (OTUs), each series of runs was started with the Heuristic Search option. For the initial run, only minimal trees were kept by random Stepwise Addition, the ancestral OTU included, TBR branch swapping, and the MULPARS option deactivated. For subsequent runs, we generally used all trees in memory from the preceding run, activating the MULPARS option and keeping all trees that were as short as or one step shorter than those loaded into memory. These steps were repeated until no shorter trees could be found. As a double-check, a second, complete Heuristic Search was performed on all shortest trees obtained from the previous Heuristic Search series. This search procedure was conducted for numerous runs with modified character sets, i.e., unweighted and unordered versus partially weighted and ordered character sets (for unordered and unweighted runs, the ancestral OTU was excluded from the search; see also Character assessment and choice of out-group). From the resulting, most parsimonious trees, we calculated Strict Consensus trees. All consensus trees were finally evaluated and edited in MacClade ver. 3.0. The exclusion of doubtful or weak characters during test runs generally led to less resolved trees. For this analysis, the best results were obviously obtained using as many data available as possible.

References to taxa in the phylogenetic subsections, including Appendix B, are based on the unrevised family Bogidiellidae s. lat., and were used as follows: subgenus *Medigidiella* A = genus *Medigidiella*; subgenus *Medigidiella* B = new genus *Arganogidiella*; subgenus *Medigidiella* C = new genus *Indogidiella*; subgenus *Stygogidiella* A = genus *Stygogidiella*; subgenus *Stygogidiella* B = new genus *Argentinogidiella*. See New taxa for additional information on *Antillogidiella* and *Patangogidiella*.

Taxa

The cladistic analysis was performed on 23 genera and 10 subgenera assigned to the unrevised family Bogidiellidae s. lat. That way, we were able to directly compare the bogidiellid phylogeny with the taxonomic revision we propose for the family. Because we decided to split some of the genera, we ended up with 40 OTUs instead of 33 (table I). Basically, these splittings helped us to code characters for large, polytypic taxa like the subgenera *Bogidiella*, *Medigidiella*, and *Stygogidiella*, which contain morphologically diverse species. We also wanted

to test the coherence of some of the genera and subgenera. For this reason in particular, we split the genera *Antillogidiella* and *Patagongidiella*. We arranged the species of the subgenus *Bogidiella* s. str. in 4 separate groups, of which we designated groups A-C as OTUs. We did not use group D for the analysis because of the uncertain taxonomic status of its species (see The genus *Bogidiella*).

Character assessment and choice of out-group

With the exception of the genera *Megagidiella*, *Paracrangonyx*, and *Spelaeogammarus*, the choice of characters employed in the analyses is based on descriptions and drawings from the literature (see Appendix B and table I). Unfortunately, the uneven quality of both species and generic descriptions obstructed or even prevented the use of several potentially contributive characters, for example, secondary sexual dimorphism in gnathopods and pereopods. The manifestation of secondary sexual dimorphism can be very subtle, with continuous interspecific changes. In several instances, assumptions about these traits could not be obtained, neither from drawings nor descriptions and, therefore, have been excluded from this analysis.

The same matrix was employed for two alternative analyses (table I): in the first run, we left all characters unweighted and unordered, so that a character has randomly reversible states (e.g., in character 24, state 5 (spines absent) can evolve directly from state 0 (4 or more spines)). For the second analysis, we ordered and weighted some of the characters differently, assuming a relatively complex evolution as opposed to more simple structures (e.g., the modification of spines and/or inner rami on male uropods have most likely evolved progressively, in linear transformation series from one state to the next, whereas the reduction of telsonic spines might occur as a spontaneous mutation within one generation). Analyses with partially weighted and ordered character sets will hereafter be referred to as ‘alternative run’, the unweighted and unordered run as ‘default run’.

Autapomorphies, although undoubtedly important for the taxonomy of bogidiellid genera and subgenera, have also been excluded from the analyses because they are uninformative for the cladograms shown in fig. 2. Distinct autapomorphies occurred as follows: sexually dimorphic pereopod 7 and uropod 3 in the subgenus *Orchestigidiella* Stock, 1981; heavily modified inner rami on pleopods 1 and 2 in the genus *Marinobogidiella* Karaman, 1982; mediosternal processes (gills?) on pereonites 2-7 in the genus *Paracrangonyx*; mandibular palp absent in the genus *Megagidiella* (cf. Koenemann & Holsinger, in MS); outer ramus of male pleopod 2 with lamellar expansions on segments 1 and/or 2

TABLE I

Character matrix. Ancestor = out-group. Genera are capitalized to facilitate the discrimination between genera and subgenera. Shaded character states were subjected to different coding methods. See subsection Characters and Appendix B for a description of characters. Characters are numbered according to the list in Appendix B

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>ACTOGIDIELLA</i>	0	1	1	5	1	0	1	0	1	0	0	0	2	0	2	2	0	2	2	0	1	1	1	4	6	0	2
<i>AEQUIGIDIELLA</i>	0	0	0	0	0	2	0	0	0	0	0	1	2	1	2	0	4	2	0	0	1	0	2	2	0	2	0
<i>AFRIDIELLA</i>	0	0	1	3	0	0	0	0	0	0	0	0	2	0	0	1	0	2	2	0	1	0	2	4	3	0	2
<i>ARTESIA</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	3	2	5	2	1	1	0	1	0	6	0	2
<i>AUROBOGIDIELLA</i>	? ?	0	3	? ?	1	1	? ?	0	0	0	0	1	0	1	2	0	0	2	0	0	1	2	4	6	0	2	0
<i>Bogidiella A</i>	0	0	1	5	0	0	0	0	0	0	0	0	2	1	1	1	0	1	1	0	0	1	2	3	5	0	2
<i>Bogidiella B</i>	0	0	1	3	0	0	0	0	0	0	0	0	2	0	1	1	0	1	2	0	0	1	1	4	5	0	2
<i>Bogidiella C</i>	0	0	1	4	0	0	0	0	0	0	0	0	2	0	1	2	0	0	2	0	0	1	2	4	4	0	2
<i>Antillogidiella bermudensis</i>	0	0	1	5	? ?	1	0	? ?	0	0	0	0	2	0	1	2	0	2	2	0	1	2	4	4	0	2	0
<i>Antillogidiella martini</i>	0	1	1	3	0	0	1	0	0	0	0	0	2	0	1	2	0	2	2	0	1	2	4	6	0	2	0
<i>Dycticogidiella</i>	0	1	1	3	0	2	0	0	0	0	0	0	2	?	1	2	1	0	2	0	1	2	4	4	0	2	0
<i>Guagidiella</i>	0	0	1	3	2	0	0	0	0	0	0	0	2	0	2	2	0	2	2	0	1	1	2	4	4	0	2
<i>Hagidiella</i>	0	1	1	5	1	0	0	0	0	0	0	0	2	0	1	2	0	2	2	0	1	1	2	5	4	0	2
<i>Medigidiella A</i>	0	0	1	5	0	1	0	0	0	0	0	0	2	0	2	1	0	2	2	0	0	1	2	3	6	0	2
<i>Medigidiella B</i>	0	0	1	5	1	0	0	0	0	0	0	0	2	?	1	0	0	2	2	0	0	1	2	4	4	0	2
<i>Medigidiella C</i>	0	0	1	3	1	1	0	0	0	0	0	0	2	0	0	0	0	2	2	0	0	1	2	3	6	0	2
<i>Mesochthongidiella</i>	1	1	1	3	0	2	0	0	0	0	0	0	2	0	1	2	0	0	2	0	0	1	0	4	2	0	2
<i>Mexigidiella</i>	1	1	1	4	0	0	0	0	0	0	0	0	2	1	1	2	0	1	3	0	1	1	1	4	4	0	2
<i>Orchestigidiella</i>	0	0	1	4	1	0	0	0	0	0	0	0	2	0	2	2	0	2	2	0	0	1	2	3	4	0	2
<i>Syngogidiella A</i>	0	0	1	5	0	0	0	0	0	0	0	0	2	0	1	1	0	1	2	0	0	1	2	3	5	0	2
<i>Syngogidiella B</i>	1	1	1	3	0	1	0	0	0	0	0	0	2	?	1	2	1	2	2	0	0	1	0	4	3	0	2
<i>Xystrogidiella</i>	0	1	1	3	0	1	0	0	0	0	0	0	2	0	1	0	0	0	2	0	0	1	2	3	3	0	2

TABLE I
(Continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
<i>BOGIDOMMA</i>	?	?	1	5	?	?	0	0	?	?	0	0	2	0	1	2	0	5	2	1	1	1	0	2	6	0	0
<i>BOLLEGIDIA</i>	0	0	3	5	0	0	1	1	1	1	0	0	1	3	1	2	2	5	1	0	0	1	1	4	6	0	2
<i>CABOGIDIELLA</i>	0	0	1	5	0	0	1	0	1	0	0	0	0	0	1	2	0	2	2	0	1	1	2	3	4	0	2
<i>DUSSARTIELLA</i>	0	0	0	3	0	0	?	?	1	1	1	1	0	?	0	2	1	3	0	0	1	0	4	6	0	2	
<i>EOBOGIDIELLA</i>	?	?	1	3	?	?	0	0	?	?	0	?	?	?	1	2	2	0	2	0	0	1	2	4	1	0	2
<i>HEBRAEGIDIELLA</i>	0	0	1	3	0	0	?	?	0	0	?	?	2	?	1	0	0	2	2	0	0	1	2	4	6	0	2
<i>KERGUELENIOLA</i>	?	?	3	1	?	?	?	?	?	?	0	0	1	?	0	3	0	4	4	0	0	1	2	5	6	0	2
<i>MAGHREBIDIELLA</i>	?	?	1	4	?	?	0	0	?	?	0	0	2	0	1	2	0	5	2	0	1	1	2	2	2	0	2
<i>MARIGIDIELLA</i>	0	0	2	2	0	0	1	1	1	1	0	0	2	0	1	2	2	2	2	1	1	1	0	4	6	0	2
<i>MARINOBOGIDIELLA</i>	0	0	1	2	0	0	?	?	1	1	0	0	1	?	1	2	2	0	2	1	0	1	2	4	6	0	2
<i>MEGAGIDIELLA</i>	0	0	1	3	0	0	0	0	0	0	0	0	2	0	1	3	0	0	2	0	0	1	1	1	0	0	2
<i>NUBIGIDIELLA</i>	?	?	1	5	?	?	0	0	?	?	0	0	1	0	1	2	0	5	2	0	1	1	2	4	6	0	2
<i>PATAGONGIDIELLA DANIELI</i>	0	1	0	2	2	0	0	0	0	0	0	0	2	?	0	0	0	0	2	0	0	1	0	2	4	1	2
<i>PATAGONGIDIELLA MAURYI</i>	0	0	0	2	0	0	0	0	0	0	0	0	2	?	0	0	0	0	2	0	0	1	0	2	4	1	2
<i>PARABOGIDIELLA</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	?	1	3	2	5	2	1	1	1	0	2	4	0	2
<i>PARACRANGONYX</i>	0	0	0	5	0	0	0	0	0	0	1	1	0	0	2	2	0	2	2	0	1	1	0	4	6	0	1
<i>PSEUDINGOLFIELLA</i>	0	0	3	5	0	0	1	1	1	1	2	1	0	4	2	2	0	5	2	1	1	1	0	4	6	0	2
<i>SPELAEOGAMMARUS</i>	0	0	1	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0	3	1	0	2

in the subgenus *Xystrigidiella* Stock, 1981; different, minor sexually dimorphic reductions in pleopods 1-3 in the genera *Bollegidia* and *Pseudingolfiella*, and in the subgenus *Antillogidiella*.

In some of the genera and subgenera, the occurrence of a character showed a variable or transitional state, for example, the number of apical and subapical spines on the telson (characters 24 and 25). These variations were treated as separate morphological conditions, so that the varying occurrence of 2 to 3 telsonic spines is assumed to be the transitional evolutionary state between 2 and 3 spines in the alternative runs. Another problem we encountered was the pronounced degree of interspecific variation among polytypic taxa, for example, inner rami of pleopods 1-3 absent in species A, reduced in species B, and vestigial in species C and D. We used two different approaches for polytypic OTUs. For the first method, variable characters were coded as question marks. Alternatively, we coded the same characters according to the majority of their occurrences in all species of an affected taxon (see also Wiens, 1995, 1998). Because the basic difference of the resulting trees was the degree of polytomy, we chose the better resolved trees of the Majority Coding method as representative. A third solution to this problem may be obtained by an inferred groundplan character state (Exemplary Method). In this approach, the ancestral state of a polytypic OTU is determined by a partial cladistic analysis of some exemplary species (or higher taxa), investigating the variable character only (Yeates, 1995).

Assumptions about morphological adaptations of amphipods to life in subterranean environments seem to have achieved a level of well-founded, broad consensus in the literature (Stock, 1981; Notenboom, 1991; Holsinger, 1993, 1994; Koenemann et al., 1998; see also Barnard & Barnard, 1983). Hence, we decided to treat morphological reductions attributed to hypogean adaptation as apomorphies. Accordingly, each corresponding plesiomorphic condition was coded as state 0. We think that the relatively frequent occurrences of homoplasies in stygobiont amphipods tend to impede the choice of effective out-groups and will most likely fail to produce a probable phylogenetic reconstruction of the family Bogidiellidae (see Koenemann et al., 1998). For this reason, we considered a hypothetical, 'allzero' ancestor the optimal choice for an out-group.

Results

Because the great majority of the resulting consensus trees had the same basic structure, two exemplary trees are chosen to represent the outcome of default and alternative analyses (fig. 2).

There is a distinct pattern that could be observed in all of the better resolved Strict Consensus trees obtained from partially weighted and ordered charactersets

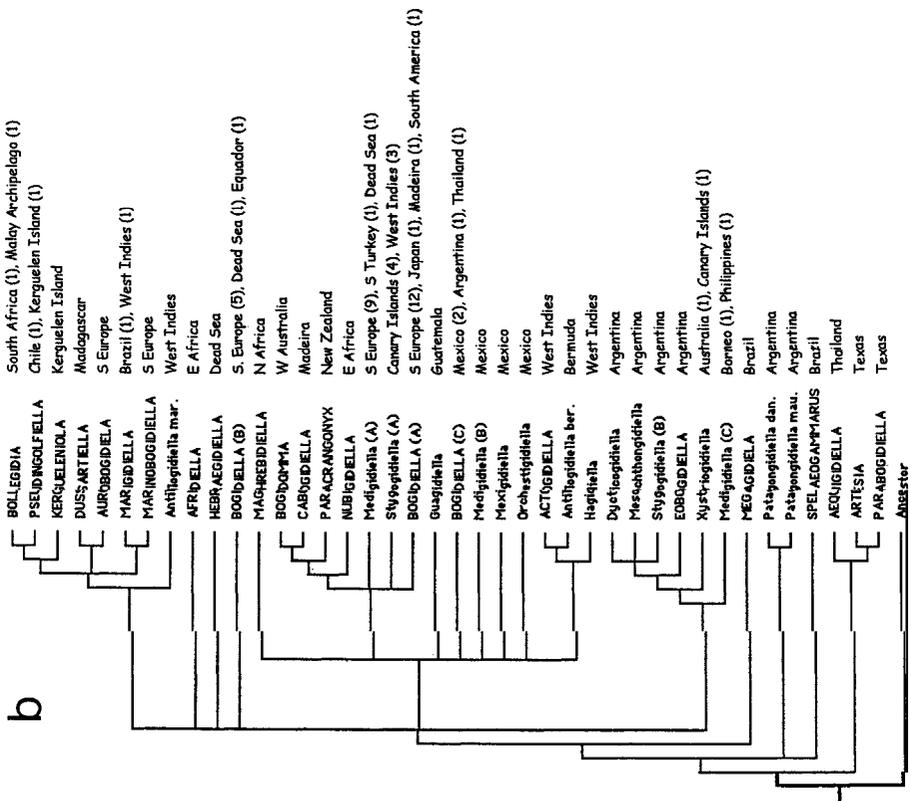
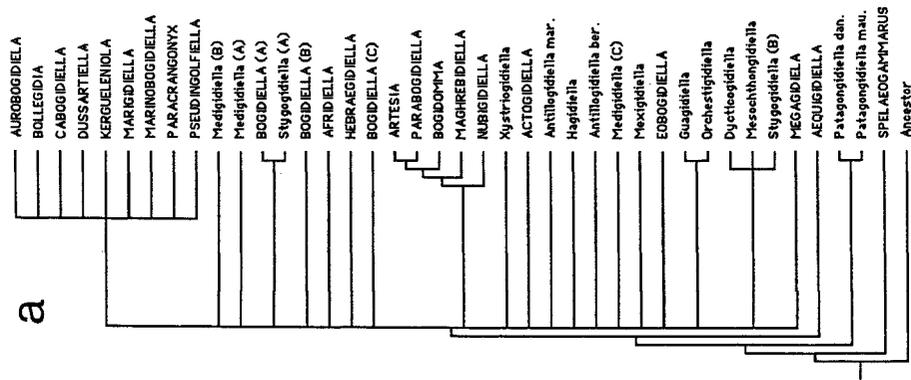
(fig. 2b): (1) Several stable clades can be related to geographic regions, for example: *Artesia* and *Parabogidiella* Holsinger, 1980 (in Holsinger & Longley, 1980) from Texas and a relatively large group with mostly Argentinean taxa. (2) There is another very robust clade that cannot be related to a specific geographic range but contains all or almost all of the genera we propose to remove from the family: the incompatible taxa *Bollegidia*, *Pseudingolfella*, *Kergueleniola*, and *Dussartiella* are accompanied by *Aurobogidiella*, *Marinobogidiella*, and *Marigidiella* Stock, 1981. Like the genera to be removed from the family, these three taxa either inhabit coastal interstitial habitats and/or also show distinct morphological modifications. (3) The clades closest to the hypothetical ancestor contain almost exclusively taxa of the New World (*Artesia*, *Parabogidiella*, *Patagongidiella*, *Spelaogammarus*, and *Megagidiella*). (4) The New World taxa, as opposed to the Mediterranean and African groups, also show a greater tendency to form robust clades and to maintain basal topographic positions close to the hypothetical ancestor. (5) The split taxa *Medigidiella*, *Stygogidiella*, *Patagongidiella*, and *Antillogidiella* occupy clearly separate topological positions in all better resolved consensus trees.

Strict Consensus trees of unordered and equally weighted charactersets were generally poorly resolved (fig. 2a). In spite of that, some of the clades from alternative runs still appeared in these more polytomous trees, e.g., a small Argentinean cluster and again the “non-geographic” clade with mostly marine, distinctly modified taxa. Also, the basal positions are again predominantly occupied by New World taxa. Interestingly, the split genus *Patagongidiella* remains separated, but still on the same clade in this equally weighted analysis.

DISCUSSION

A look at the distribution map of bogidiellid amphipods (fig. 3) reveals several particularities:

(1) Bogidiellids occur world-wide, except for boreal, arctic, and Antarctic regions. (2) There are several major concentrations of species, the largest of which is in the Mediterranean region, and smaller ones in Central America, South America, and the West Indies. (3) Species richness is highest in the Mediterranean region (33 species in 4 genera), whereas generic diversity is greater in the New World (South America: 10 genera, 18 spp.; Central America: 5 genera, 12 spp.; West Indies: 7 genera, 10 spp.). (4) The majority of bogidiellids are located no further than ± 160 km from coastlines. In several instances, however, they live



in inland, continental habitats, especially in South America but also in Europe and the Middle and Far East.

There are different points of view about the biogeographic history of bogidiellid stygobionts. Because it is assumed that some of their isolated freshwater habitats have been separated from marine waters since the break-up of Pangaea, 180-200 million years ago, and have remained isolated ever since, bogidiellids might have a very old freshwater origin. On the other hand, we also see a distribution in geographically much younger regions like the West Indian islands, most of which emerged from the sea during tectonic uplifts and sea level regressions in the early to middle Tertiary, between 20 and 50 million years ago.

According to these two vicariant scenarios, alternative hypotheses are generally used to explain the evolution of bogidiellid amphipods. The first theory postulates an ancient freshwater origin, suggesting that bogidiellids were already adapted to freshwater habitats before (!) the break-up of Pangaea and adapted progressively to brackish and marine environments as continents drifted apart. The second model renders bogidiellids as primarily a marine group, which massively invaded continental freshwaters and subsequently adapted to subterranean inland habitats (see: Stock, 1981; Notenboom, 1991).

However, we have to be careful with final conclusions about the origin of bogidiellids. The growing number of new discoveries seems to increase the complexity of their evolutionary history and many questions still remain unanswered. There are apparently no obvious vicariant events that offer an explanation for the abundant occurrences in continental South America as opposed to an almost 'bogidiellid-free' African continent. Similarly enigmatic is the high specific radiation in the Mediterranean coastal regions. Land masses in southern Europe emerged in a complex pattern during the Miocene (Adams, 1981) and must have been subsequently inhabited by precursors of modern bogidiellids. This strongly implies that Mediterranean bogidiellids either evolved from a relatively young marine ancestor or that Bogidiellidae are generally able to re-adapt from freshwater to saline waters (and vice versa) more quickly than previously envisioned. Recent discoveries and reports of bogidiellids from marine interstitial habitats in

Fig. 2. Cladistic analysis of the family Bogidiellidae s. lat. (see Cladistic Methods for details). With the exception of *Bogidiella* and *Patagongiella*, genera are capitalized to facilitate the discrimination between genera and subgenera. Several taxa are split as indicated by capital letters in parentheses. Numbers in parentheses refer to number of species known from each region, respectively. a, PAUP Strict Consensus tree of default run; characters unordered and equally weighted (CI: 0.29; RI: 0.29; length: 426, min. length: 124, max. length: 549); b, PAUP Strict Consensus tree of alternative run with areas related to OTUs; characters partially weighted and ordered (CI: 0.36; RI: 0.48; length: 346).

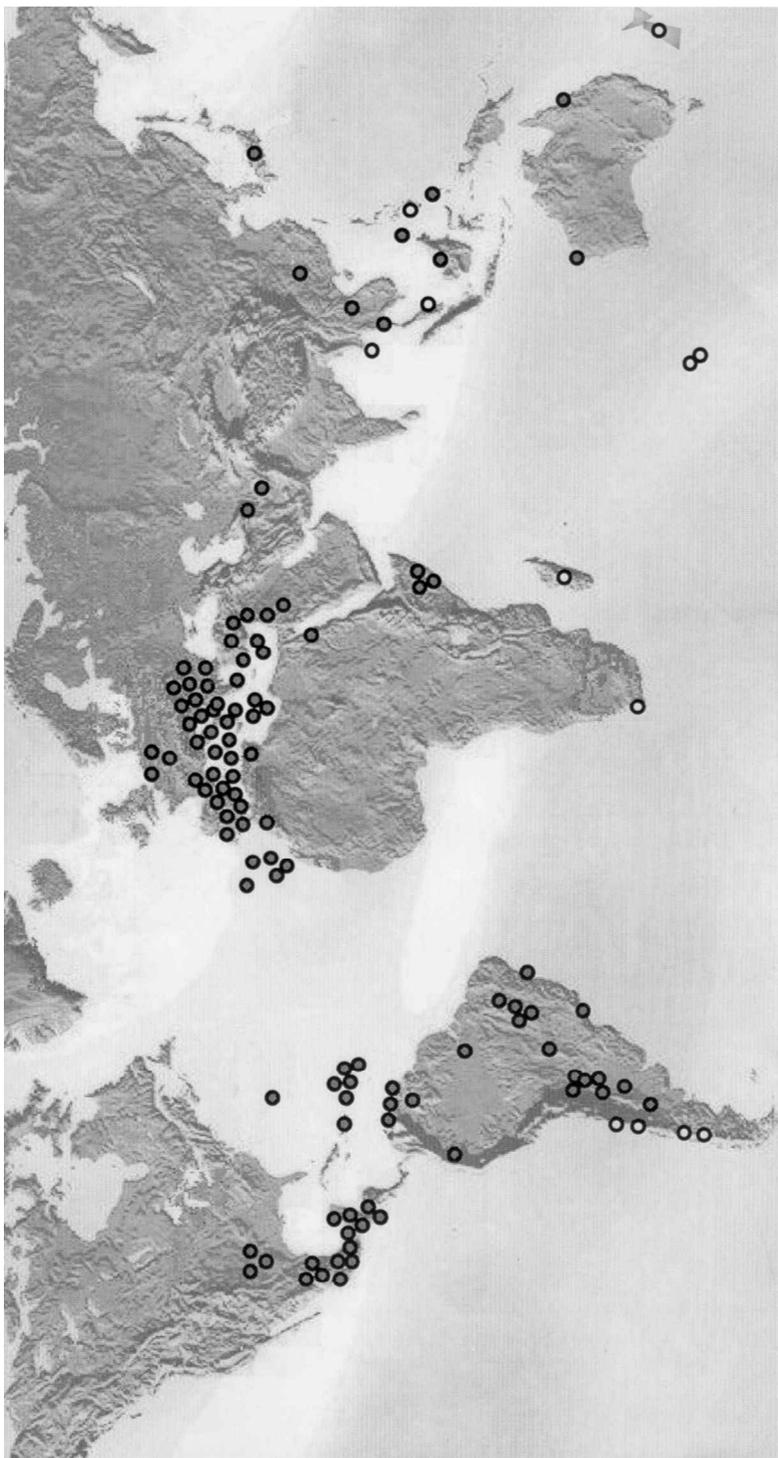


Fig. 3. Geographic distribution of bogidiellid amphipods. The shaded circles represent the approximate number of records of described species (the number of records in southern Europe is actually slightly higher than shown on the map). The white circles represent genera which we propose to remove from the family.

Turkey seem to support this view (Koenemann, 1998; Koenemann et al., 1998; see also Notenboom, 1991). If bogidiellids do have an ancient freshwater origin, we would also expect to find generally more primitive taxa in isolated continental habitats and more apomorphic ones on the Caribbean islands and in the Mediterranean coastal regions. At present, the geographic distribution of known taxa does not convincingly support this idea.

The results of the phylogenetic analysis characterize bogidiellids from the Western Hemisphere as the more plesiomorphic taxa. For some genera, e.g., *Spelaeogammarus* and *Artesia*, these results are not unexpected and are in general accordance with the literature (Stock, 1981; Barnard & Barnard, 1983). In other cases, however, the basal appearance of OTUs, close to the hypothetical ancestor, is less apparent. The new genus *Megagidiella* from a cave in central-western Brazil does not exhibit a particular plesiomorphic morphology after a first or even second examination. This large-sized bogidiellid, reaching a body length up to 16 mm, features short, non-overlapping coxal plates, pleopods with 3-segmented outer rami and reduced inner rami, and absence of a mandibular palp. A comparative morphological examination would not necessarily reveal a relationship with the obviously primitive *Spelaeogammarus* from caves in eastern Brazil. In the cladistic analysis, however, *Megagidiella* tends to appear close to *Spelaeogammarus* and *Patagongidiella*, indicating a possible relationship of species that inhabit disjunct caves between 1300 and 2200 km apart on the same continent. Similarly surprising is the basal position of the sympatric genera *Patagongidiella* and *Grossogidiella* n. gen. Both taxa are from the same cave system in western Argentina and show distinct apomorphic modifications (see New taxa). These results allow us to draw several hypothetical conclusions with regard to bogidiellid phylogeny:

(1) The appearance of primitive and advanced structures seems to be more complex than assumed, exhibiting various transitional, intermingled states. A conspicuous apomorphic character might not necessarily indicate an apomorphic species or genus. It may occur in primitive as well as in advanced taxa and the arbitrary use of a few discriminating characters for phylogenetic assumptions must be considered highly doubtful.

(2) Despite the extraordinary generic diversity of bogidiellids from the New World, especially South America, an explicit tendency to form robust clades could be observed for these taxa. This trend probably indicates a close relationship of taxa from several disjunct localities. The analysis also renders South American groups as the more plesiomorphic bogidiellids. Both tendencies might be correlated with the highest frequency of isolated inland habitats on the South

American continent, strongly pointing towards an ancient freshwater origin of bogidiellid amphipods.

The results of the phylogenetic analysis also suggest the removal of five genera from the family Bogidiellidae (see Incompatible taxa). At least four of the five taxa removed formed a remarkably solid clade in all of the obtained consensus trees. Notably, most of these genera have two additional particularities in common: they inhabit marine interstitial habitats in coastal areas either outside of or marginal to the bogidiellid distribution range.

In a future project, it would be interesting to further investigate relationships within the family Bogidiellidae with molecular techniques, employing DNA sequencing or protein analyses. A conceivable objective of such an investigation could, for example, focus on the comparison of morphologically similar taxa or taxa endemic to distinct geographic regions.

ACKNOWLEDGEMENTS

We thank the Graphics Office at Old Dominion University for assistance with the preparation of the figures and the National Museum of Natural History (Smithsonian Institution) for lending us the topotypes of *Paracrangonyx compactus*. We would also wish to thank Drs Kent Carpenter and L. B. Holthuis, who read drafts of the manuscript and offered helpful suggestions for improvement. This study was supported by a PEET grant from the National Science Foundation to JRH (DEB-9521752).

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APPENDIX A

List of all described genera and species of the revised family Bogidiellidae (102 species).

- Actogidiella* Stock, 1981
A. cultrifera Stock, 1981
- Aequigidiella* Botosaneanu & Stock, 1989
A. aquilifera Botosaneanu & Stock, 1989
- Afridiella* Karaman & Barnard, 1979
A. messanai Diviacco & Ruffo, 1985
A. pectinicauda Ruffo, 1982
A. somala Ruffo, 1970 (cf. Ruffo, 1970a)
- Antillogidiella* Stock, 1981
A. martini (Stock, 1978)
- Arganogidiella* n. gen.
A. arganoi (Ruffo & Vigna Taglianti, 1973)
A. arganoides (Ruffo & Vigna Taglianti, 1977)
- Argentinogidiella* n. gen.
A. horcomollensis (Grosso & Fernández, 1988)
A. lavillai (Grosso & Claps, 1984)
- Artesia* Holsinger, 1980
A. subterranea Holsinger, 1980 (in Holsinger & Longley, 1980)
A. welbourni Holsinger, 1992
- Aurobogidiella* Karaman, 1988 (cf. Karaman, 1988c)
A. italica (Karaman, 1979)
- Bermudagidiella* n. gen.
B. bermudensis (Stock, Sket & Iliffe, 1987)
- Bogidiella* Hertzog, 1933 — **albertimagni group (A)** (inner rami of pleopods absent)
B. albertimagni Hertzog, 1933
B. aprutina Pesce, 1980
B. balearica Dancau, 1973
B. broodbakkeri Stock, 1992
B. convexa Stock & Notenboom, 1988
B. cyrnensis Hovenkamp, Hovenkamp & Van der Heide, 1983
B. glabra Stock & Notenboom, 1988
B. glacialis S. Karaman, 1959
B. helenae Mateus & Maciel, 1967
B. hispanica Stock & Notenboom, 1988
B. ichnusae Ruffo & Vigna Taglianti, 1975

- B. madeirae* Stock, 1994
B. neotropica Ruffo, 1952
B. semidenticulata Mestrov, 1961
B. torrenticola Pretus & Stock, 1990
- Bogidiella* — **skopljensis group (B)** (inner rami of pleopods 1-segmented, reduced)
B. calicali Karaman, 1988 (cf. Karaman, 1988b)
B. copia Karaman, 1988 (cf. Karaman, 1988a)
B. gammariformis Sket, 1985
B. longiflagellum S. Karaman, 1959
B. nicolae Karaman, 1988 (cf. Karaman, 1988b)
B. serbica Karaman, 1987
B. skopljensis S. Karaman, 1933
- Bogidiella* — **niphargoides group (C)** (one or more characters distinctly modified; inner rami of pleopods reduced, vestigial, or absent)
B. cooki Grosso & Ringuelet, 1979
B. niphargoides Ruffo & Vigna Taglianti, 1977
B. thai Botosaneanu & Notenboom, 1988
B. vomeroi Ruffo & Vigna Taglianti, 1977
- Bogidiella* — **lindbergi group (D)** (only one sex described)
B. barbaria Karaman, 1990 (cf. Karaman, 1990c)
B. cerberus Bou & Ruffo, 1979
B. deharvengi Stock & Botosaneanu, 1988
B. lindbergi Ruffo, 1958
B. michaelae Ruffo & Vigna Taglianti, 1977
— *B. paolii* Hovenkamp, Hovenkamp & Van der Heide, 1983
B. ruffoi Birstein & Ljovuschkin, 1968
B. sinica Karaman & Sket, 1990
B. silverii Pesce, 1981
B. sketi Karaman, 1989 (cf. Karaman, 1989a)
B. stocki Karaman, 1990 (cf. Karaman, 1990b)
B. vandeli Coineau, 1969
- Bogidonma* Bradbury & Williams, 1996
B. australis Bradbury & Williams, 1996
- Cabogidiella* Stock & Vonk, 1992
C. littoralis Stock & Vonk, 1992
- Dycticogidiella* Grosso & Claps, 1985
D. talampayensis Grosso & Claps, 1985
D. ringueleti Grosso & Fernández, 1988
- Eobogidiella* Karaman, 1982
E. purmamarcensis (Grosso & Ringuelet, 1969)
- Grossogidiella* n. gen.
G. mauryi (Grosso & Fernandez, 1990)
- Guagidiella* Stock, 1981
G. holsingeri (Ruffo & Vigna Taglianti, 1973)
G. pasquinii (Ruffo & Vigna Taglianti, 1977)
- Hagidiella* Stock, 1985
H. prionura Stock, 1985
- Hebraegidiella* Karaman, 1988 (cf. Karaman, 1988a)
H. bromleyana Karaman, 1988 (cf. Karaman, 1988a)
- Indogidiella* n. gen.

- I. sarawacensis* (Stock, 1983)
I. daccordii (Ruffo, 1994)
Maghrebidiella Diviacco & Ruffo, 1985
M. maroccana Diviacco & Ruffo, 1985
Marigidiella Stock, 1981
M. brasiliensis (Siewing, 1953)
M. crassipes Stock, 1981
Marinobogidiella Karaman, 1982
M. thyrrhenica (Schiecke, 1978)
Medigidiella Stock, 1981
M. antennata Stock & Notenboom, 1988
M. aquatica Karaman, 1990 (cf. Karaman, 1990a)
M. arista Koenemann, Vonk & Schram, 1998
M. chappuisi (Ruffo, 1952) (in Ruffo & Delamare Deboutteville, 1952)
M. dalmatina (S. Karaman, 1953)
M. hebraea (Ruffo, 1963)
M. minotaurus (Ruffo & Schiecke, 1976)
M. paolii Hovenkamp, Hovenkamp & Van der Heide, 1983
M. paraichnusae (Karaman, 1979)
M. uncinata Stock & Notenboom, 1988
Megagidiella Koenemann & Holsinger, 1999*)
M. azul Koenemann & Holsinger, 1999*)
Mesochthongidiella Grosso & Fernández, 1985
M. tucumanensis Grosso & Fernández, 1985
Mexigidiella Stock, 1981
M. chitalensis Karaman, 1982
M. hamatula Stock, 1985
M. mexicana Karaman, 1982
M. sbordonii (Ruffo & Vigna Taglianti, 1973)
M. tabascensis (Villalobos, 1961)
Nubigidiella Karaman, 1988a
N. nubica (Ruffo, 1984)
Orchestigidiella Stock, 1981
O. orchestipes (Ruffo & Vigna Taglianti, 1977)
Parabogidiella Holsinger, 1980
P. americana Holsinger, 1980 (in Holsinger & Longley, 1980)
Patagongidiella Grosso & Fernández, 1990
P. danieli Grosso & Fernández, 1990
Spelaeogammarus Da Silva Brum, 1973
S. bahiensis Da Silva Brum, 1973
S. sp. A Koenemann & Holsinger (in MS)
S. sp. B Koenemann & Holsinger (in MS)
S. sp. C Koenemann & Holsinger (in MS)
Stygogidiella Stock, 1981
S. atlantica Sánchez, 1991
S. bredini (Shoemaker, 1959)
S. cypria Stock, 1990

*) In: Proc. biol. Soc. Washington, **112** (3): 572-580.

- S. perla* Stock, 1981
S. purpuriae Stock, 1988
S. uniramosa Stock & Rondé-Broekhuizen, 1987
S. virginalis Stock, 1981
Xystriogidiella Stock, 1984
X. capricornea Stock, 1984
X. spathulata Stock & Rondé-Broekhuizen, 1987

APPENDIX B

List of characters and character states employed in the cladistic analysis. References to taxa are based on the unrevised family Bogidiellidae s. lat. (see Taxa)

(1) Modifications of the outer ramus in male pleopod 1

State 0 = absent; state 1 = present.

Alternative run: weight factor: 6; ordered. Modified outer rami on pleopod 1 occur in three taxa only. *Mesochtongidiella* bears 1 modified spine on segment 2, whereas *Mexigidiella* has 1 modified spine on segment 2 and 3, respectively. The modifications of *Stygogidiella* B are less pronounced but still distinguishable (see New taxa).

(2) Modifications of the outer ramus in male pleopod 2

State 0 = absent; state 1 = present.

Alternative run: weight factor: 6; ordered. Modifications in the male pleopod 2 occurred more frequently than in pleopod 1. The majority of affected taxa had 1 modified spine on segment 2. A few taxa showed additionally slightly modified segments or differently reduced segments (see Characters and Incompatible taxa).

(3) Number of outer ramus segments in pleopods 1-3

State 0 = 3 or more segments; state 1 = 3 segments; state 2 = 2 or 3 segments; state 3 = 2 or less segments.

Alternative run: weight factor: 6; ordered. State 0 comprises genera with more than 3 outer rami segments in pleopods 1-3 (*Artesia* and *Dussartiella*), genera with 3 segments in the outer rami of 1 pleopod and more than 3 segments in the outer rami of the other 2 pleopods (*Aurobogidiella* and *Paracrangonyx*), and genera with a varying number of outer rami segments (*Aequigidiella* with 3 or 4 segments and *Patagongidiella* with 3-5 segments). In *Marigidiella*, the specimens had 3-segmented outer rami in pleopods 1 and 2 and a 2-segmented outer ramus in pleopod 3 (state 2). State 3 refers to a differently varying number of segments in both sexes (*Bollegidia*: 0-2 segments) and also to a 1-segmented outer ramus (*Bollegidia* and *Pseudingolfella*) (see also Characters).

(4) Inner rami of pleopods 1-3

State 0 = multiarticulate, aequiramous; state 1 = uniarticulate, aequiramous; state 2 = uniarticulate, small; state 3 = uniarticulate, reduced; state 4 = vestigial; state 5 = absent.

Alternative run: weight factor: 6; ordered. State 2 includes inner rami that are shorter than the outer ramus but distinctly longer than segment 1 of the outer ramus. A uniarticulate, reduced inner ramus that is shorter than segment 1 of the outer ramus is coded as state 3. Vestigial inner rami (state 4) are small, bud-like structures without setae. Majority Coding was applied to the following OTUs: *Bogidiella* C (1 species with absent inner rami, 1 species with reduced inner

rami, 2 species with vestigial inner rami on pleopods 1 and 2 and absent inner ramus on pleopod 3: state 4); *Stygogidiella* A (3 species with absent inner rami, 2 species with reduced inner rami: state 5); *Antillogidiella martini* (male with reduced inner rami, female inner rami are lacking: state 3); *Guagidiella* (2 species with vestigial inner rami on pleopods 1 and 2 and inner ramus absent on pleopod 3: state 4).

(5) Modifications in male uropod 1

State 0 = absent; state 1 = spines modified; state 2 = rami/peduncle and spines modified.

Alternative run: weight factor: 6; ordered. State 2 could be observed in two taxa. In *Patagongidiella danieli*, a process of the uropod 1 peduncle was apparently fused with a suspiciously modified spine. Similarly, *Guagidiella* had 1 strongly modified spine on a distinctly reduced inner ramus that was partly fused with the peduncle.

(6) Modifications in male uropod 2

State 0 = absent; state 1 = spines modified; state 2 = rami and spines modified.

Alternative run: weight factor: 6; ordered. As with state 2 of character 5, a strongly reduced inner ramus, bearing 1 modified spine, appears to be in different states of fusion with the peduncle in *Mesochthongiella* and *Dycticogidiella* (state 2). A reduced inner ramus plus modified spine without any signs of fusion occurs in *Aequigidiella* (state 2).

(7) Dagger-shaped rami in female uropod 1

State 0 = absent; state 1 = present.

Alternative run: weight factor: 6; ordered. “Dagger-shaped rami” was the most commonly used term in the literature for advanced reductions in uropods 1 and 2 (characters 7-10). It covers a variety of different reduction states from distinctly pointed rami tips without apical spines to slightly pointed tips with 1 or 2 apical spines. In all cases, however, the term “dagger-shaped” seemed to be appropriate. The only exceptions were *Bollegidia* and *Pseudingolfella*, showing pointed, dagger-shaped reductions as well as sack-like rami (in some instances, differently reduced on outer and inner ramus of the same uropod). Because dagger-shaped rami occurred randomly in either sex on both uropods 1 and 2, this reduction was split into 4 independent characters.

(8) Dagger-shaped rami in female uropod 2

State 0 = absent; state 1 = present.

Alternative run: weight factor: 6; ordered.

(9) Dagger-shaped rami in male uropod 1

State 0 = absent; state 1 = present.

Alternative run: weight factor: 6; ordered.

(10) Dagger-shaped rami in male uropod 2

State 0 = absent; state 1 = present.

Alternative run: weight factor: 6; ordered.

(11) Rami of uropod 3

State 0 = biramous, aequiramous; state 1 = biramous with inner ramus greatly in size reduced; state 2 = uniramous.

Alternative run: weight factor: 6; ordered. A greatly reduced, almost scale-like inner ramus on uropod 3 is exceptional for bogidiellids. It occurs in *Dussartiella* and *Paracrangonyx*. *Pseudingolfiella* is the only bogidiellid genus with a uniramous uropod 3 (see Incompatible taxa).

(12) Outer ramus of uropod 3

State 0 = 1-segmented; state 1 = 2-segmented.

Alternative run: weight factor: 6; ordered. A 2-segmented outer ramus occurs in *Dussartiella*, *Paracrangonyx*, and *Pseudingolfiella* only (see Incompatible taxa). Because only some species in a few amphipod families have 2-segmented outer rami, a 1-segmented outer ramus was considered the plesiomorphic state.

(13) Gills

State 0 = on pereonites 2-6; state 1 = on pereonites 3-6; state 2 = on pereonites 4-6.

Alternative run: weight factor: 3; ordered. Majority Coding has been applied to *Stygogidiella* A (state 2). According to Sánchez (1991), *Bogidiella* (*Stygogidiella*) *atlantica* has gills on pereonites 3-5, which makes it the only species in the family with this character.

(14) Oostegites

State 0 = on pereopods 2-5; state 1 = on pereopods 2-5 or 3-5; state 2 = on pereopods 3-5; state 3 = on pereopods 3-4; state 4 = "absent".

Alternative run: weight factor: 3; ordered. Oftentimes, this character is poorly or not at all described in the literature. Consequently, some states are adapted from drawings. State 1 occurred in the polytypic taxa *Artesia*, *Bogidiella* A, and *Mexigidiella*. States 3 and 4 are autapomorphic modifications of *Bollegidia* and *Pseudingolfiella*. The term "absent" is adopted from the literature. Apparently, brood plates were lacking in all females of both *Pseudingolfiella* sp.

(15) Number of segments in flagellum of antenna 2

State 0 = 5 or more segments; state 1 = 5 segments; state 2 = 5 or less segments.

Alternative run: unweighted; ordered. The number of segments in the flagellum of antenna 2 is a relatively constant character. In some instances, a varying number of segments occurred intraspecific as well as interspecific. Examples for intraspecific variation are *Aequigidiella* (5-7 segments = state 0) and *Orchestigidiella* (4-5 segments = state 2). Interspecific variation could be observed in the polytypic taxa *Medigidiella* A (4-5 or 5 segments = state 2), *Medigidiella* C (5 or 6 segments = state 0), and *Guagidiella* (4 or 5 segments = state 2).

(16) Number of segments in accessory flagellum

State 0 = 3 or more segments; state 1 = 2 or 3 segments; state 2 = 2 segments; state 3 = 1 segment.

Alternative run: unweighted; ordered. Corresponding to character (15), state 1 was assigned to the polytypic OTUs *Afridiella*, *Bogidiella* A and B, *Medigidiella* A, and *Stygogidiella* A.

(17) Number of palp segments in maxilla 1

State 0 = 2 segments; state 1 = 1-2 segments; state 2 = 1 segment.

Alternative run: weight factor: 3; ordered. Three taxa showed an interesting case of variable numbers of palp segments in maxilla 1, coded as state 1: *Stygogidiella horcomollensis* (*Stygogidiella* B) obviously bears a 1-segmented palp. In some individuals, however, a weakly developed articulation, separating palp segments 1 and 2, could be perceived visually. *S. lavillai*, the other species of *Stygogidiella* B had a 2-segmented palp. Almost identical with the situation in *Stygogidiella* B, both species of *Dycticogidiella* had 2-segmented and 1-segmented, weakly articulated palp segments and state 1 was applied, too. The third OTU with state 1 was the only described specimen of *Dussartiella madegassa* which had a long 2-segmented palp on the right, and a 1-segmented, reduced palp on the left maxilla 1.

(18) Number of setae on inner lobe of maxilla 1

State 0 = 3 setae; state 1 = 2 or 3 setae; state 2 = 2 setae; state 3 = 1 or 2 setae; state 4 = 1 seta; state 5 = setae absent.

Alternative run: unweighted; ordered. Characters 18 and 19 were left unweighted because of their assumed minor phylogenetic significance. See Characters for an explanation of transitional states in characters 18 and 19.

(19) Number of spines on outer lobe of maxilla 1

State 0 = 9 spines; state 1 = 7 or 8 spines; state 2 = 7 spines; state 3 = 6 or 7 spines; state 4 = 6 spines.

Alternative run: unweighted; ordered.

(20) Maxilla 2

State 0 = normal; state 1 = reduced.

Alternative run: unweighted; ordered. In the literature, the choice of descriptive terms for the inner plates on maxilla 2 varies considerably. State 1 comprises inner plates that are usually described as "small", "reduced", or "weak".

(21) Mandibular molar

State 0 = triturrative; state 1 = non-triturrative.

Alternative run: unweighted; ordered. Like in character 20, state 1 refers to molars that are described as "small", "weak", etc.

(22) Coxal plates

State 0 = longer than wide; state 1 = wider than long.

Alternative run: unweighted; ordered. In *Artesia*, coxal plates 1 and 2 were wider than long or as wide as long, whereas coxae 3-7 were distinctly longer than wide. We chose state 0 as apt coding for *Artesia*.

(23) Telson shape

State 0 = longer than wide; state 1 = approximately as long as wide; state 2 = wider than long.

Alternative run: unweighted; ordered. The majority of bogidiellid amphipods have a telson that is wider than long. State 0 seems to be typical for non-European taxa. The Majority Coding method has been applied to *Bogidiella* A and C, and *Medigidiella* A (all state 2).

(24) Apical spines of telson

State 0 = 4 or more spines; state 1 = 2 or 3 spines; state 2 = 2 spines; state 3 = 1 or 2 spines; state 4 = 1 spine; state 5 = spines absent.

Alternative run: unweighted; ordered. See Characters for an explanation of variable or transitional states 1 and 3 of characters 24 and 25. The Majority Coding method has been applied to *Stygogidiella* A (state 3).

(25) Subapical spines of telson

State 0 = 3-5 spines; state 1 = 2-4 spines; state 2 = 2 spines; state 3 = 1 or 2 spines; state 4 = 1 spine; state 5 = 0 or 1 spine; state 6 = spines absent.

Alternative run: unweighted; ordered. State 0 and 1 occurred as highly variable, autapomorphic characters in *Megagidiella* and *Spelaeogammarus*, respectively. The 3 subapical spines in *Hebraegidiella* were coded as transitional condition of state 1. We applied the Majority Coding method to *Bogidiella* C (state 4).

(26) Mediosternal processes

State 0 = absent; state 1 = present.

Alternative run: weight factor: 6; ordered. Mediosternal processes were present in *Patagongidiella mauryi* and *Patagongidiella danieli* only. We are of the opinion that these structures are both morphologically and physiologically different from the mediosternal gills in *Paracrangonyx*. Therefore, the gills in *Paracrangonyx* have been treated as true autapomorphies and excluded from the analysis.

(27) Eyes

State 0 = eyes present; state 1 = 2-3 unpigmented lens cells; state 2 = eyes absent.

Alternative run: weight factor: 6; ordered. As mentioned above, we performed a phylogenetic analysis on the (unrevised) family Bogidiellidae s. lat., attempting to code all different states of homologue structures as independent characters. Since *Paracrangonyx* is removed from the family, however, the phylogenetic relationship of reduced eye structures in *Paracrangonyx* (state 1) and large, fully developed eyes observed in *Bogidomma* (state 2) becomes irrelevant. In the revised family, *Bogidomma australis* remains the only bogidiellid with eyes, a fact that certainly raises attention because of its uniqueness. The biology of this species from Barrow Island, Western Australia, may be worth further study. All the more, because it is reported from a cave (!) at the outer margin of the bogidiellid distribution range, with a possible connection to marine waters.