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CLADISTIC ANALYSIS OF 37 MEDITERRANEAN BOGIDIELLIDAE (AMPHIPODA), INCLUDING *BOGIDIELLA ARISTA*, NEW SPECIES, FROM TURKEY

Stefan Koenemann, Ronald Vonk, and Frederick R. Schram

A B S T R A C T

A new subterranean amphipod species, *Bogidiella (Medigidiella) arista*, found in the mesopsammic ground waters of southern Anatolia, Turkey, is described, together with *Bogidiella (Bogidiella) calicali* Karaman, the latter being recorded for the first time in the eastern Mediterranean. A cladistic analysis of 37 Mediterranean species of the family Bogidiellidae is performed, using 4 species from the Canary Islands as an outgroup. Alternatively, 2 cladistic software packages, PAUP 3.1.1 and HENNIG86, are employed to calculate consensus trees of minimal length. The resulting trees show more or less identical robust clades, characterizing a central, a central-eastern, and an eastern Mediterranean group. Apart from this pattern of major geographical clusters, all species of the subgenus *Medigidiella* appear as a robust, monophyletic clade as well. This initial attempt to analyze the phylogeny of Mediterranean bogidiellids forms a useful basis for further, extended studies, using either different outgroup taxa or additional morphological data.

During the spring of 1987 a major biospeleological expedition of the Dutch speleological society "Speleo Nederland" was carried out along the coastal Taurus mountains in southwest Anatolia, Turkey. The expedition was focused on collecting the fauna of caves, wells, subterranean water flows, and the interstices of marine gravel beaches. The special yield of subterranean (or stygobiont) crustaceans, predominantly amphipods of the genus *Bogidiella* Hertzog, 1933, promised to serve as an interesting case study to the colonization of inland ground water by marine organisms. In July 1996, a second sampling program occurred along the southern Turkish coast between Antalya and Alanya. Its main objectives were, first, to visit one or two Speleo Nederland stations and enlarge the small original sample sizes (1-3 individuals), and, second, to collect a new series of samples east of where the 1987 expedition went, in order to obtain additional distribution data about stygobiont crustaceans.

Unfortunately, the first task could not be achieved. In contrast to Speleo Nederland, the 1996 sampling program took place in the dry season when the ground-water level was low and many minor streams and rivers had become partly or completely dry. This, combined with the fact that many bogidiellids seem to have extremely limited distribution ranges with low population sizes, may explain why the 1987 sampling sites appeared to be without bogidiellids in 1996. However, the 1996 trip led to the discovery of a new mesop-

sammic species, *Bogidiella (Medigidiella) arista*, as well as a new record of *B. calicali* G. Karaman, previously reported only from Rio di Quirra, Sardinia (Karaman, 1988b).

Taxonomy within the genus *Bogidiella* appears far from being resolved. Various criteria for a division into several subgenera are applied by different authors, so that in some cases it remains unclear as to which species can be grouped together, for example, membership in the subgenus *Medigidiella* Stock, 1981. An unstable taxonomy, however, is not especially restricted to the genus *Bogidiella*, but is rather a common problem among amphipods. The reasons for taxonomic problems in the amphipod genus *Niphargus*, given by Hovenkamp *et al.* (1984), characterize the situation of stygobiont amphipods in general. The overall interspecific similarity of their phenotypic appearance is relatively high, which, in combination with (often unknown) geographical and/or seasonal variability, complicates the classification of new species. The accuracy and completeness of species descriptions vary considerably. Many species descriptions are based on very few specimens, often with body parts missing or of one sex only.

Hertzog (1933) erected the genus *Bogidiella* with the discovery of his new species *B. albertimagni* from the subterranean fresh waters of the Rhine valley, Germany (see Karaman, 1979a). The discovery of new bogidiellids, however, has been increasing constantly over the last two decades, but their phylogeny is more or less unrevealed so far.

An attempt is made in this study to perform the initial step of a cladistic analysis of all Mediterranean bogidiellids. With the help of the published species descriptions and reviews, a data matrix of phenotypic characters was set up and analyzed by different computer programs using parsimony as a basic precept.

TAXONOMIC PART

Bogidiella (Medigidiella) arista, new species

Material Examined.—13 specimens (5 ♂♂, 7 ♀♀, and 1 individual of uncertain sex) were collected by means of a biophreatical pump, between 13 and 22 July 1996, at a sandy beach. The pump was driven 80–100 cm into the shingle sediment within the intertidal zone. Type location: 36°44'N, 31°34'E. Mainroad 400 from Manavgat to Antalya, dustroad to beach on the right ± 300 m east of the Karpuz river, beach at Meryem pavilion. Water temperature: 22°C.

Holotype ♂, 1.28 mm, allotype ♀, 1.6 mm, and 7 paratypes were dissected and mounted on microscope slides in Faure's medium. Four paratypes, some of which were partly dissected, were preserved in 70% ethanol. All specimens have been deposited in the collection of the Zoological Museum of Amsterdam (ZMA Amph. 202609).

Accompanying fauna: *Melita valesi* S. Karaman, *Bogidiella calicali*.

Description.—Head (Fig. 1a) as illustrated. Eyes absent, body unpigmented. Body length 0.8–1.6 mm (without antennae and uropods). Gnathopod 1 propodus larger than that of gnathopod 2. Pleopods unmodified. Sexual dimorphism in second uropods. No further secondary dimorphism in other characters.

Antenna 1 (Fig. 3b) about one-half body length. Peduncular article 1 and 2 of same length, first peduncular article with 2 thin ventral spines. Flagellum consisting of 7 articles, second article shorter than others. Accessory flagellum (Fig. 3c) 2-segmented, first article longer than or as long as first flagellum article, second article small. Aesthetascs on articles 4–7.

Antenna 2 (Fig. 3d) with subequal peduncular articles 4 and 5; gland cone short. Flagellum with 5 articles, slightly longer than third peduncular article.

Labrum (Fig. 1d) longer than broad, trapezoidal, with distally rounded corners.

Labium (Fig. 1f) with fine setules and 1 spine on each outer lobe. Outer lobe with distinctly shaped distal corners.

Maxilla 1 (Fig. 1b) with 2-segmented palp bearing 2 apical setae and 1 subapical seta. Two apical setae on inner lobe. Outer lobe

with 4 unidentate and 2 bifurcate apical spines (1 ♂ found with 1 tridentate spine, 2 bifurcate, and 3 unidentate spines (Fig. 1c)).

Maxilla 2 (Fig. 1e) bilobed, with 6 and 6–8 apical setae on inner and outer lobe, respectively.

Mandible (Fig. 1g–i) palp 3-segmented. Second and third articles subequal. Second article with 1 apical and 1 medioventral seta. Third article dilated, with 3 apical setae and 1 shorter subapical seta. With 2 or 3 blade-shaped spines between incisor and molar. Molar rounded, with 1 lateral seta. Incisor on left mandible with 5 rounded cusps, usually 2 or 3 being prominently shaped. Lacinia mobilis bearing 5 rounded cusps.

Maxilliped (Fig. 1j) bearing 2 prominent bifid spines on inner lobe and 3 blade-shaped apical spines on outer lobe. Subapical cilia on distal palp article and on lateral margin of dactylus.

Gnathopod 1 (Fig. 2a) with 2 long medial setae and 1 short distal seta on posterior margin of basis, anterior margin with 1 distal seta. Merus and pointed projection of carpus with ciliate posterior margin. Propodus ovoid. Palm oblique, with 2 long angular spines, 1 long subangular spine, 4 short bifid spines, and about 9 setae of various lengths. Palmar margin finely serrated at angle. Palmar index 0.49. Dactyl at inner margin with 2 fine short setae.

Gnathopod 2 (Fig. 2b) basis slender, with 1 long medial and 1 short distal seta on posterior margin of basis, anterior margin with 1 distal seta. Cilia on posterior margin of carpus. Propodus ovoid, with cilia on proximo-posterior and anterolateral margins. Palm oblique, with 2 long angular, 4 short bifid spines, and about 11 setae of various lengths. Palmar margin not serrated. Palmar index 0.51. Dactyl at inner margin with 2 fine short setae.

Pereiopods 3 and 4 (Fig. 4c, b) identical, about same size. Basis with 3 setae at posterior and 2 setae at anterior margin. Propodus with 1 midanterior seta. Dactyl ovoid, with short claw, reaching about one-third of propodus length. Lenticular organs about one-half of basis width, slightly ovate.

Pereiopods 5–7 (Fig. 3g–i) progressively longer. Lenticular organs circular to ovate in pereiopods 5 and 6, ovate in pereiopod 7. Basis with 4 spinelike setae at posterior and 2 spinelike setae at anterior margin. Dactylus elongate, almost half as long as propodus.

Pereiopod 6 (Fig. 3h) with 1 medial spine-

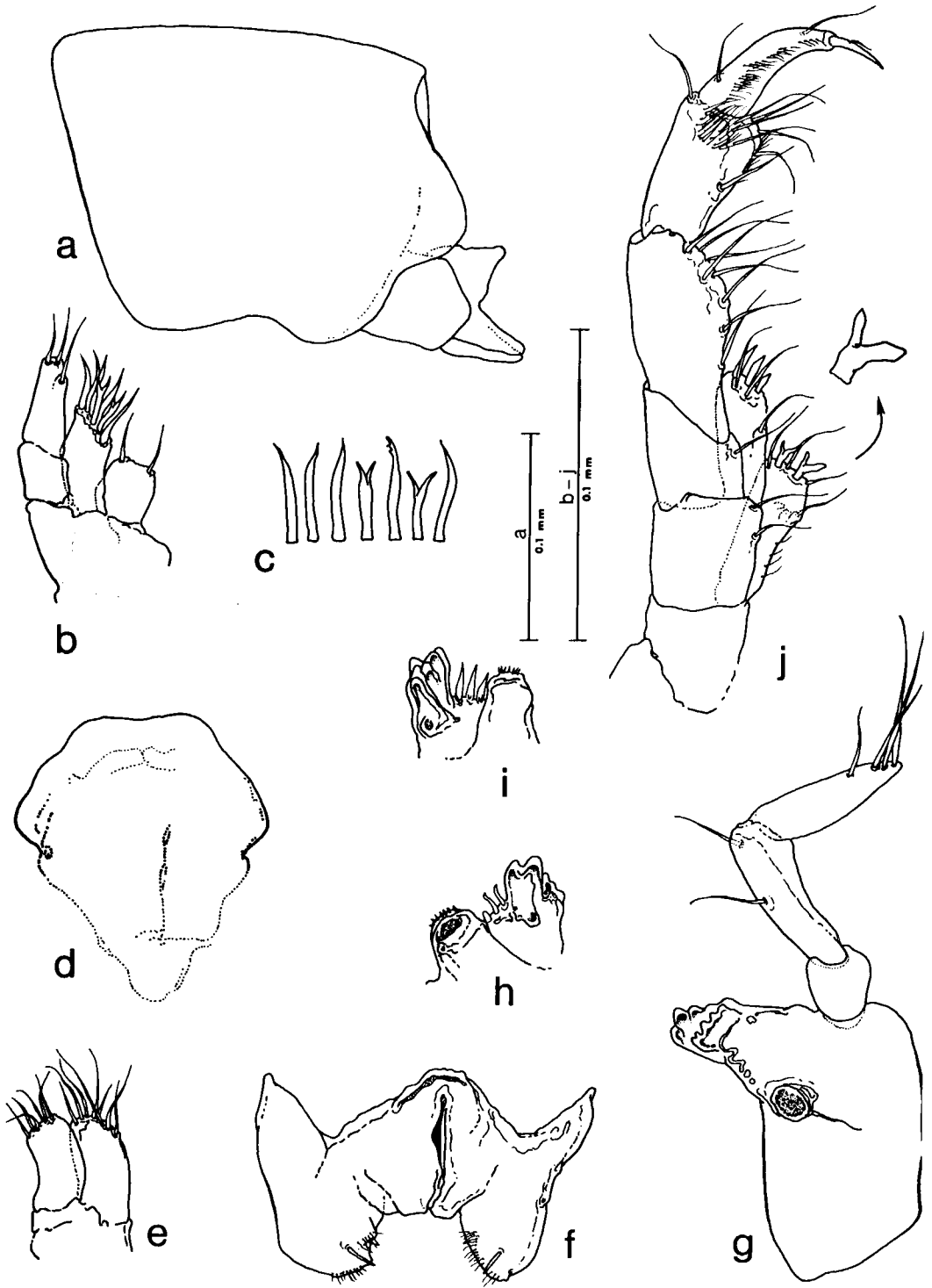


Fig. 1. *Bogidiella (Medigidiella) arista*, new species: a, cephalosome (♂); b, maxilla 1 (holotype, ♂); c, spines of outer lobe of maxilla 2 (allotype, ♀); d, labrum (allotype, ♀); e, maxilla 2 (♂); f, labium (holotype, ♂); g, left mandible (holotype, ♂); h, incisor and molar of right mandible (allotype, ♀); i, incisor and molar of left mandible (♂); j, maxilliped (holotype, ♂).

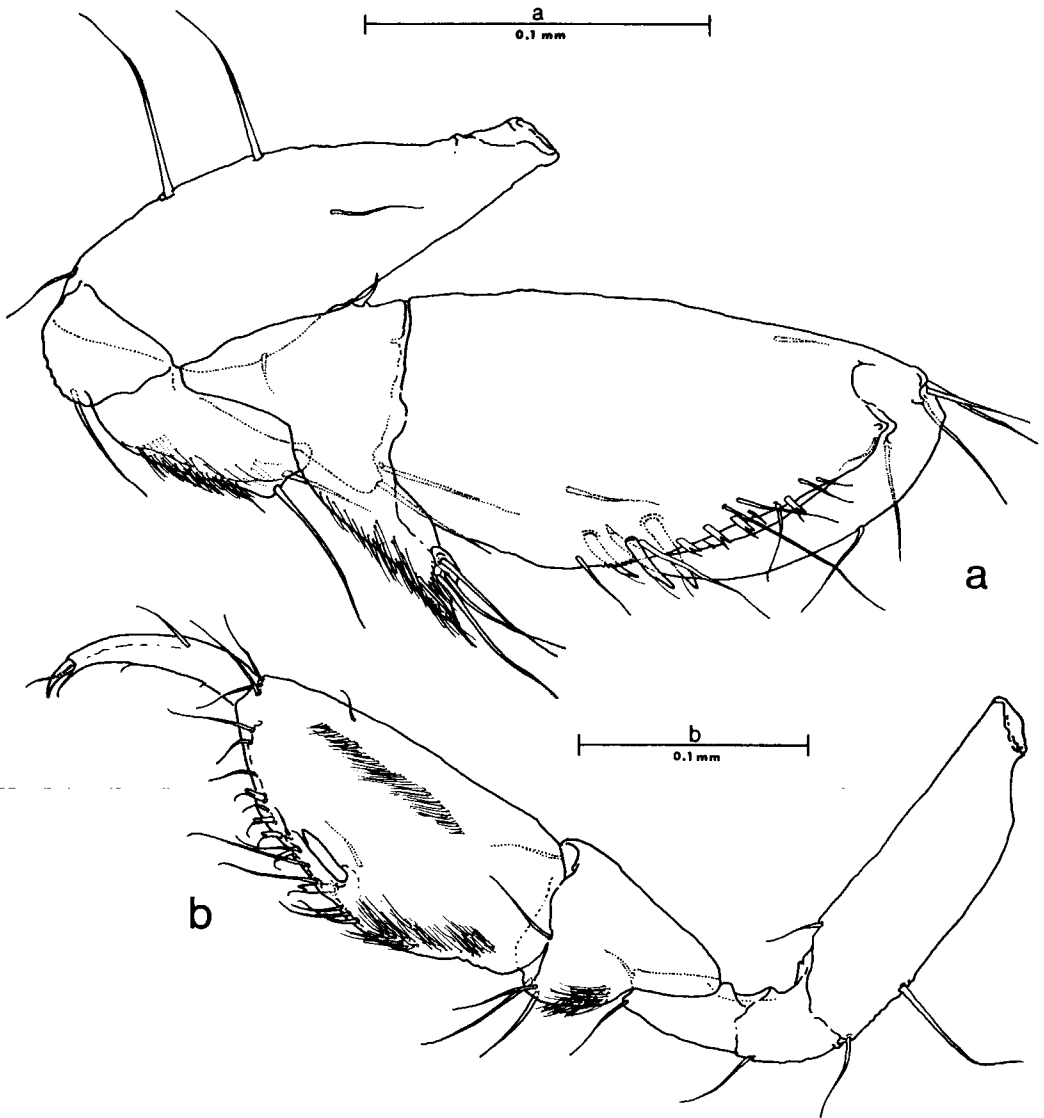


Fig. 2. *Bogidiella (Medigidiella) arista*, new species: a, gnathopod 1 (♂); b, gnathopod 2 (holotype, ♂).

like seta on anterior and posterior margin of merus, respectively. With midanterior spinelike seta on carpus.

Pereopod 7 (Fig. 3i) bearing 2 posterior spinelike setae and 1 midanterior spinelike seta on merus, 2 midanterior spinelike setae on carpus, 3 midanterior spinelike setae and several (usually 6) long thin posterior setae on propodus.

Pleopods 1–3 (Fig. 4d) identical, decreasing progressively in size. Endopods lacking. Peduncles with 2 retinacula. With 3-segmented exopods with 2 plumose setae on each segment.

Coxal plates (Fig. 3e) broader than long,

with 1–3 setae. Coxal plates 1–4 rectangular, with rounded corners, plates 5–7 triangular. Ventroposterior margin of plate 5 distinctly excavated and lobed.

Coxal gills (Fig. 3f) ovoid, occurring on pereionites 4–6.

Oostegites ovate, located on pereionites 3–5.

Epimeral plates 1–3 (Fig. 4a) with rounded points at ventroposterior corner. Posterior margins sinusoid, bearing 2 short setae, respectively.

Uropod 1 (Fig. 5a) with 2 subapical and 1 basifacial spine on peduncle. Exopod shorter than endopod. Both rami usually with 4 api-

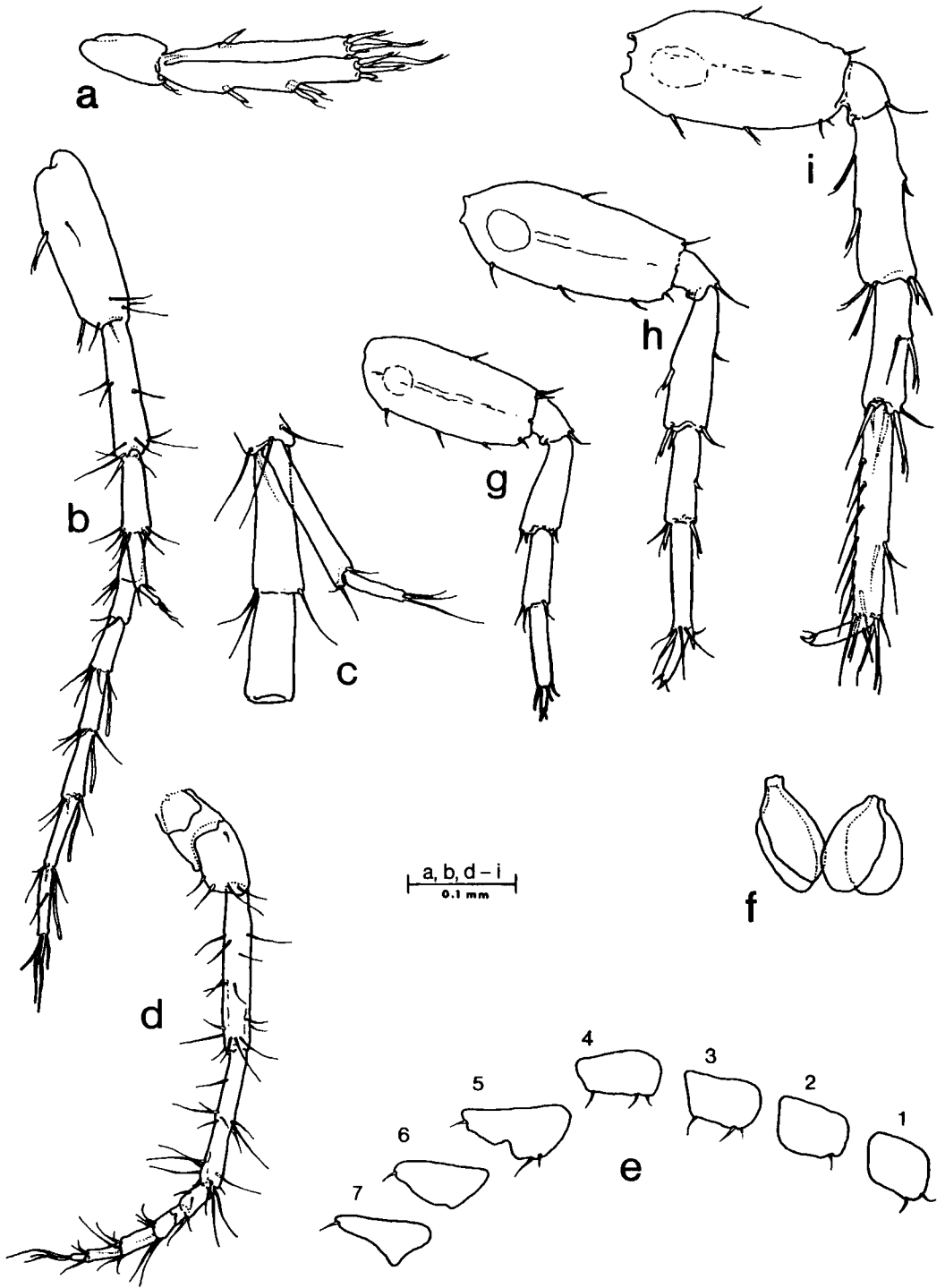


Fig. 3. *Bogidiella (Medigidiella) arista*, new species: a, uropod 3 (♀); b, antenna 1 (holotype, ♂); c, accessory flagellum of antenna 1 (♂); d, antenna 2 (holotype, ♂); e, coxal plates (♂); f, coxal gills (holotype, ♂); g, pereiopod 5 (♂); h, pereiopod 6 (♂); i, pereiopod 7 (♂).

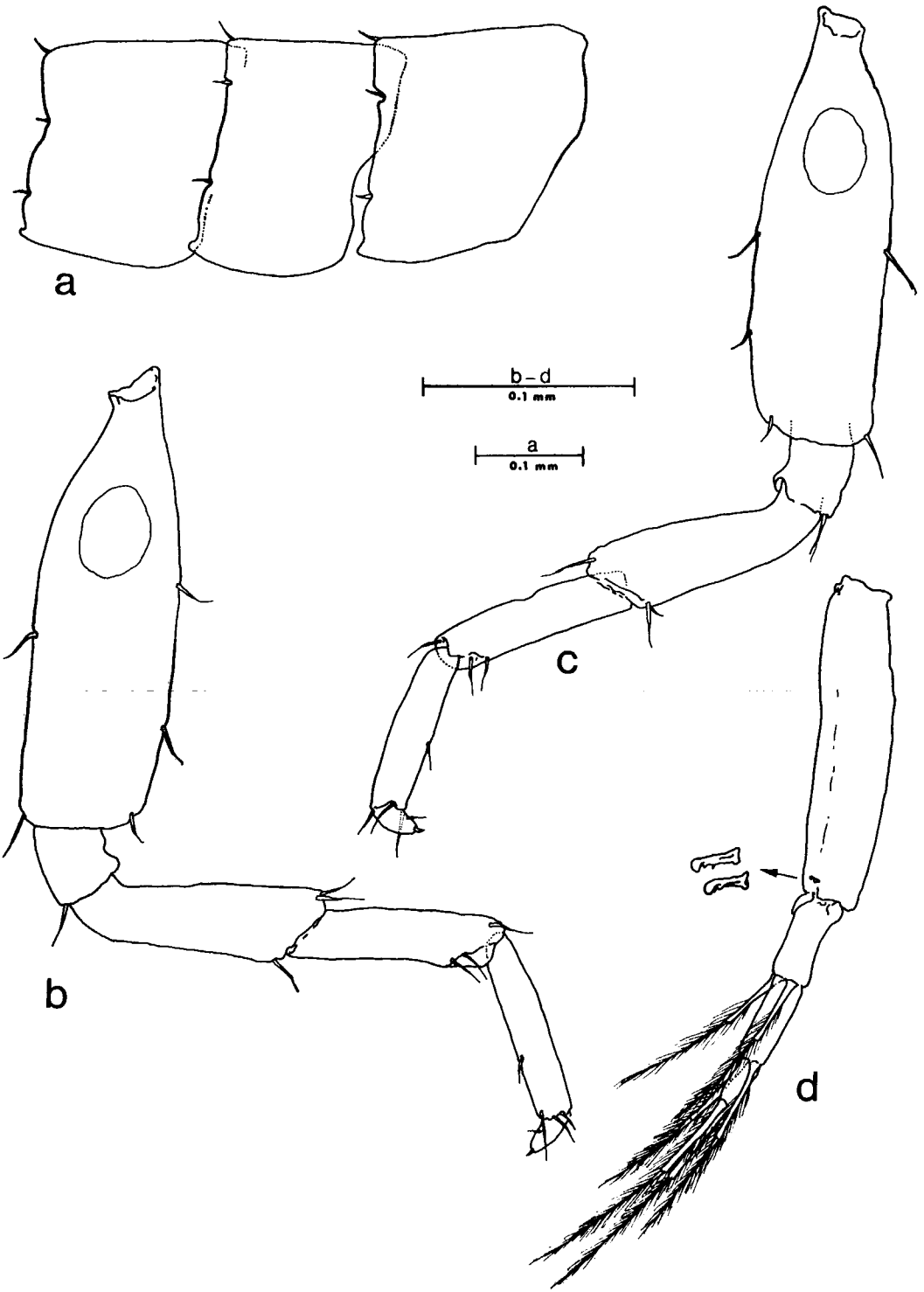


Fig. 4. *Bogidiella (Medigidiella) arista*, new species: a, epimeral plates (allotype, ♀); b, pereopod 4 (♂); c, pereopod 3 (holotype, ♂); d, pleopod 1 (♂).

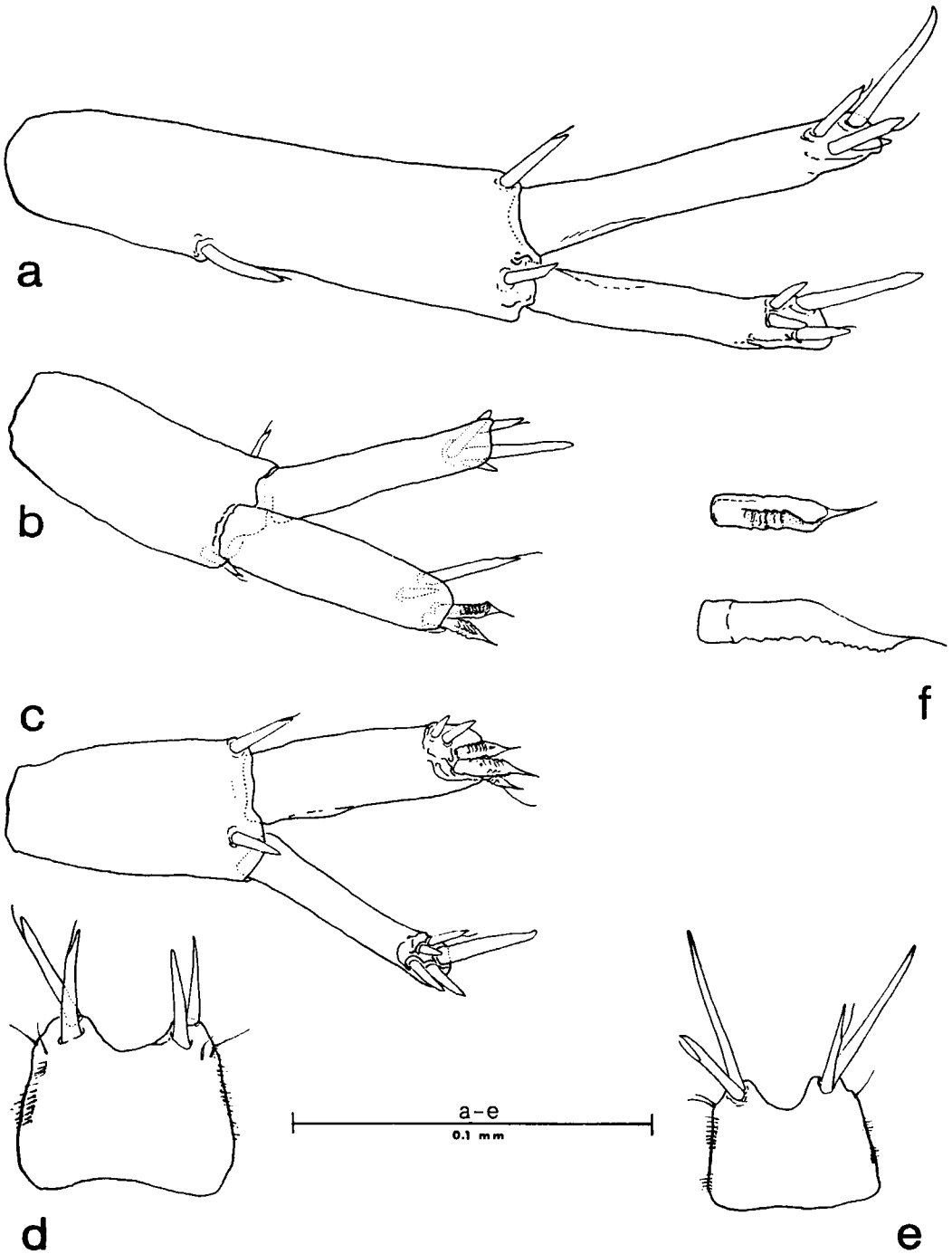


Fig. 5. *Bogidiella (Medigiella) arista*, new species: a, uropod 1 (holotype, ♂); b, uropod 2 (holotype, ♂); c, uropod 2 (♀); d, telson (allotype, ♀); e, telson (♂); f, modified spines of inner ramus of uropod 2 (♂).

cal spines, one of which distinctly exceeding length of others.

Uropod 2 (Fig. 5b, c) with 2 subapical spines on peduncle. Exopod thicker than en-

dopod. Both rami with 4 or 5 apical spines. Outer ramus usually with 1 long and 3 or 4 short apical spines. Inner ramus showing sexual dimorphism in shape of spines: ♂♂ bear-

ing 2 or 3 modified pointed spines (Fig. 5f), with slightly U- or V-shaped corpora being ribbed and toothed on dorsal side. In ♀♀, spines on inner ramus not differing from those of outer ramus.

Uropod 3 (Fig. 3a) peduncle shorter than one-half length of rami, with 2 subapical spines. Rami long, almost subequal, with 1 proximolateral spine, respectively, and 4 apical spines, of which 1 wavy spine twice as long as others. Inner ramus with 2 additional distolateral spines.

Telson (Fig. 5d, e) slightly wider than long, with 1 row of cilia on each lateral margin. Distal part with 2 subapical setae and 2 pairs of apical spines, one pair longer than or as long as telson and other pair as long as or shorter than telson. Mediodistal excavation U-shaped, less than one-third telson length.

Etymology.—The suffix *arista* alludes to the sexually dimorphic spines on the inner rami of the second uropods in ♂♂, which resemble an eared grain (*arista*, Latin: the beard of an ear of grain).

Remarks.—In some of the specimens examined, the distal spines on the basis of pereopods 3–7 were accompanied by one additional spine on either posterior or anterior or both margins. A minor degree of variability was also found in pereopod 7. The number of midanterior setae on the carpus and propodus (1–3), as well as posterior thin long setae on the propodus (2–6) varied, apparently depending on the age of the specimen.

The sexually dimorphic second uropods would seem to place *B. arista* in the subgenus *Medigiella*. Within the medigiellids, *B. arista* is morphologically closely related to *B. minotaurus* Ruffo and Schiecke, 1976, which appears next to *B. arista* in some of the consensus tree clades. *Bogidiella minotaurus* differs from the new Turkish species by: two multidentate spines on the outer lobe of maxilla 1 and two plumose setae on the inner lobe; inner lobe of maxilla 2 with one plumose seta; mandibular palp article 3 with cilia; gnathopod 1 basis bearing one seta at posterior margin, palmar margin of propodus with five bifid spines; modified A- and B-type spines on ♂ uropod 2 inner ramus (see Karaman, 1979a); uropod 3 outer ramus with six dorsolateral spines; and telson with shallow excavation (about one-sixth telson length).

Bogidiella arista shows also some morphological resemblance to *B. chappuisi*

Ruffo, 1952, but can be distinguished from that species by the following characters: 2-articulated accessory flagellum; labium with one spine on each outer lobe; gnathopod 1 basis with two long setae posteriorly, palmar margin of propodus crenulated only at corner, bearing four bifid spines; gnathopod 2 palmar margin not crenulated, bearing four bifid spines; inner ramus of ♂ uropod 2 bearing two or three modified pointed spines, which appear slightly U- or V-shaped, being ribbed and toothed on dorsal side; outer ramus of uropod 3 with three dorsolateral spines; and telson bearing one pair of apical spines that are longer than telson length.

Bogidiella (Bogidiella) calicali
G. Karaman, 1988

Bogidiella vandeli Coineau, 1969: 199–207; figs. 26B, D, F; 27A, C, F, G, H; 28D, F–H [In part].

Bogidiella (Bogidiella) vandeli.—G. Karaman, 1981: 31 [In part]; 1982: 46 [In part].

Bogidiella (Bogidiella) calicali G. Karaman, 1988b: 30–36; figs. 1–4.

Material examined.—1 ♂ and 1 ♀ were collected by the same means at the same location as *Bogidiella arista*, new species. Both specimens were dissected and mounted on microscope slides in Faure's medium. They have been deposited in the collection of the Zoological Museum of Amsterdam (ZMA Amph. 202639).

Accompanying fauna: *Melita valesi*, *Bogidiella arista*.

Description.—♀ 1.8 mm, with oostegites; ♂ 1.8 mm. Pleopods with inner rami unmodified. No secondary sexual dimorphism.

Female: Matches exactly Karaman's description from 1988b except for the following supplemental or different characters: Antenna 1: flagellum with 9 articles. Antenna 2: fourth article with 1 ventral spine (found by Karaman in 1 ♂ only). Mandible: second palp article on left mandible with 3 setae (right mandible with 2 setae on same palp segment). Maxilla 1: with 5 unidentate and 2 bidentate apical spines on outer lobe (Karaman described 7 spines with 0 or 1 lateral tooth on each, which is by definition not a contradicting diagnosis). Maxilla 2: outer and inner lobe with 6 or 7 and 6 apical setae, respectively. Maxilliped: inner lobe with 2 Y-shaped apical spines (instead of 2 or 3 simple, pointed spines, according to drawing).

Gnathopod 1: posterior margin of basis with 3 or 4 long setae and 1 short distal seta (instead of 3 long setae and 1 short distal seta). Palm of propodus bearing 3 strong angular spines, 1 strong subangular spine, and 6 or 7

short bifid spines. Palmar margin proximally serrated. Gnathopod 2: palm of propodus with 2 strong angular and 5–8 short bifid spines.

Uropod 1: peduncle with 2 distal spines, 1 proximolateral and 1 mediolateral spine. Uropod 2: peduncle with 2 distal spines and 1 proximolateral spine (instead of 2 distal spines). Uropod 3 peduncle slightly shorter than one-half length of rami, bearing 3 distal spines. Inner and outer ramus with 3 and 4 lateral spines and 4 or 5 apical spines, respectively.

Male: Matches exactly Coineau's description of ♂ of *B. vandeli* from 1969 and Karaman's description from 1988b except for the following supplemental or different characters: Antenna 1: flagellum with 8 articles.

Mandible: third palp article with 3 or 4 distal setae (instead of 4). Maxilla: 1 and 2 identical with ♀. Maxilliped identical with ♀.

Gnathopod 1: posterior margin of basis with 2 or 3 long setae and 1 short distal seta (instead of 3 long setae and 1 short distal seta). Palm of propodus bearing 2 or 3 strong angular spines, 1 strong subangular spine, and 4 or 5 short bifid spines. Gnathopod 2: posterior margin of basis with 2 or 3 long setae and 1 short distal seta. Palm of propodus with 2 strong angular and 3–5 short bifid spines.

Pereiopods without trace of lenticular organs (corresponding with Karaman, but contradicting Coineau who found lenticular organs with sinusoid margins on pereiopods 3–6).

Uropod 1: identical with ♀ (corresponding with Coineau). Uropod 2: peduncle with 2 distal spines only (corresponding with Coineau). Uropod 3: peduncle slightly smaller than one-half length of rami, bearing 2 distal spines. Inner and outer ramus with 2 and 4 lateral spines and 4 or 5 apical spines, respectively (instead of 6 and 2 lateral spines found on outer and inner ramus by Coineau).

Telson bearing 2 apical spines and 1 subapical spine (instead of 2 apical and 2 subapical spines found by Coineau and Karaman).

Remarks.—*Bogidiella calicali* was described as a new species by Karaman (1988b), who noticed that ♂♂ and ♀♀ of *B. vandeli* Coineau, 1969, from Rio di Quirra (Sardinia), belonged to two different species. Karaman left the original species name (*B. vandeli*) for the ♀♀ and described the ♂♂ together with one additional ♀ as the new species *B. calicali*.

Although there are differences with the descriptions of both Karaman and Coineau, the

combination of several distinct characters leaves no doubt about the identification of the Turkish specimens as *B. calicali*. The existence of unmodified inner rami on all 3 pleopods with 3-segmented outer rami and, in addition, apical and subapical spines on the telson, are found only in three Mediterranean species: *B. silverii* Pesce, 1981, *B. stocki* Karaman, 1990b, and *B. calicali*. Antenna 1 flagellum with eight or nine articles, gnathopods with three (three or four) long spines on their bases, three apical setae on the inner lobe of maxilla 1, and, especially, the armature of uropods 1 and 2 point to *B. calicali*. The morphological deviations of the Turkish individuals from the descriptions by Karaman and Coineau, of which the armature of uropod 3 and the Y-shaped spines on the inner lobe of the maxilliped appeared constant in both sexes, do not justify the establishment of a new species and shall, therefore, be interpreted as geographic variation in a mesopammic population.

PHYLOGENETIC ANALYSIS Cladistic Methods

The cladistic analysis was performed alternatively on two different computer platforms. A Macintosh IIvx (system 7) was used to run the phylogenetic software programs PAUP 3.1.1 (Swofford, 1993) and MacClade 3.0 (Maddison and Maddison, 1993). The software packages HENNIG86 1.5 (Farris, 1988) and COMPONENT 2.0 (Page, 1993) were employed on an Intel 80486 DX 33 with DOS 6.2 as operating system and Windows 3.1 as user interface.

In HENNIG86, the most parsimonious search algorithm, effected with the commands "ie*" (implicit enumeration; retaining up to 100 trees) and "ie-" (retaining 1 tree), was intolerably time-consuming. These algorithms were replaced by the command combination "mhennig*;bb." This applies branch swapping to each of the initial trees, retaining one tree for each initial tree, on which "bb" subsequently performs extended branch swapping, producing a new tree file and retaining all shortest trees it can find. The tree files generated by the "mhennig*;bb" command were imported into the program COMPONENT and used as input files for the calculation of different types of consensus trees (Strict, Semi Strict, Majority Rule, Nelson, and Adams consensus).

In PAUP, the Heuristic Search option was exercised on the same matrix. For the initial run, a random Stepwise Addition was chosen, the Branch Swapping option MULPARS (saving all minimal trees) was deactivated. All trees obtained by this choice of options were loaded into memory, so that they could serve as input trees for subsequent Heuristic Search runs, this time with the MULPARS option selected. From the resulting trees, four different types of consensus trees were calculated (Strict, Semi Strict, Majority Rule, and Adams consensus). One Strict consensus tree was transferred to MacClade for a detailed investigation. Finally, COMPONENT was used to edit the PAUP consensus trees.

Both in PAUP and HENNIG86, each analysis was based on an identical data matrix (Table 1), which was left at first unordered and unweighted. In this case, characters were treated as randomly reversible states, assuming that, for example, in character 27/28 any observed number of short spines on the gnathopods could evolve directly. Subsequently, a second analysis was performed with partly ordered and weighted characters. In these second runs, most multistate characters were ordered, under the assumption that they have evolved in linear transformation series, moving progressively from one character state to the next. Furthermore, some characters were weighted according to their possibly complex evolution and/or their functional significance for the individual. In the following text, these two alternative analyses will be referred to as the "default run" and the "second run." Additionally, HENNIG86 was used to produce a tree with unordered character states employing the Successive Weighting method: character weights from 0–10 were set according to the best fits in consecutive runs until a stable tree was found. Furthermore, in HENNIG86, four bogidiellid taxa from the Canary Islands, which served as an outgroup, were excluded from the matrix in order to perform an ingroup analysis.

Taxa

The family Bogidiellidae Hertzog, 1936, comprises 86 described subterranean species in 16 genera (Holsinger, 1993). Although stygobiont bogidiellids are widely distributed and can be found on all continents, excluding Antarctica, their distribution in central and

southern Europe, especially the Mediterranean (Fig. 6), forms a distinct pattern (Stock, 1981; Barnard and Barnard, 1983; Holsinger, 1986, 1993). The Mediterranean "bogidiellid cluster" has characteristic qualities: (1) With 38 species (at present) the diversity is relatively high; (2) 35 of those 38 species of the family Bogidiellidae belong to the genus *Bogidiella*; and (3) Their contemporary known distribution range extends from the Sinai Peninsula to the Atlantic coast of Portugal, from southern France to Rumania. The *Bogidiella* "cluster" seems to be sharply demarcated, except for a few external "spots" (e.g., Canary Islands, Madeira Island). Both high diversity and distinct demarcation, however, could to a certain extent be the result of the relatively intensive research on the Mediterranean fauna (Stock, 1981; Holsinger, 1993).

Two species that do not belong to the genus *Bogidiella* have been included in the list of operational taxonomic units (OTUs): *Marinobogidiella thyrrhenica* Schiecke, 1978, and the monotypic *Aurobogidiella italica* Karaman, 1988c. These species occur at the center of the Mediterranean "distribution cluster," in the Bay of Naples, and their phylogenetic relation to one another, as well as to the "surrounding" bogidiellids, promised to be worth an investigation. Furthermore, all subspecies of the subgenus *Medigidiella*, e.g., *B. (Med.) chappuisi chappuisi*, *B. (Med.) chappuisi pescei* Karaman, 1988d, and *B. (B.) ichnusae africana* Karaman and Pesce, 1980, have been excluded from the cladistic analysis, inasmuch as they are considered to be geographic variations, and thus there is no need to analyze their phylogeny in this context. Their recorded locations, however, have been included in the distribution map in Fig. 6.

In order to perform an outgroup comparison, the bogidiellid fauna of the Canary Islands seemed an appropriate choice. Their distribution range is geographically restricted to a group of small islands, and, belonging to the subgenera *Stygogidiella* Stock, 1981, and *Xystriogidiella* Stock, 1984, they apparently show a closer relation to some Antillian and Australian bogidiellids than to most of the Mediterranean species (Stock, 1981). The following Canarian species have been chosen to serve as an outgroup: *B. (Stygogidiella) atlantica* Sánchez, 1991, *B. (Stygogidiella) purpuriae* Stock, 1988, *B. (Stygogidiella) uniramosa* Stock and Rondé-Broekhuizen, 1987,

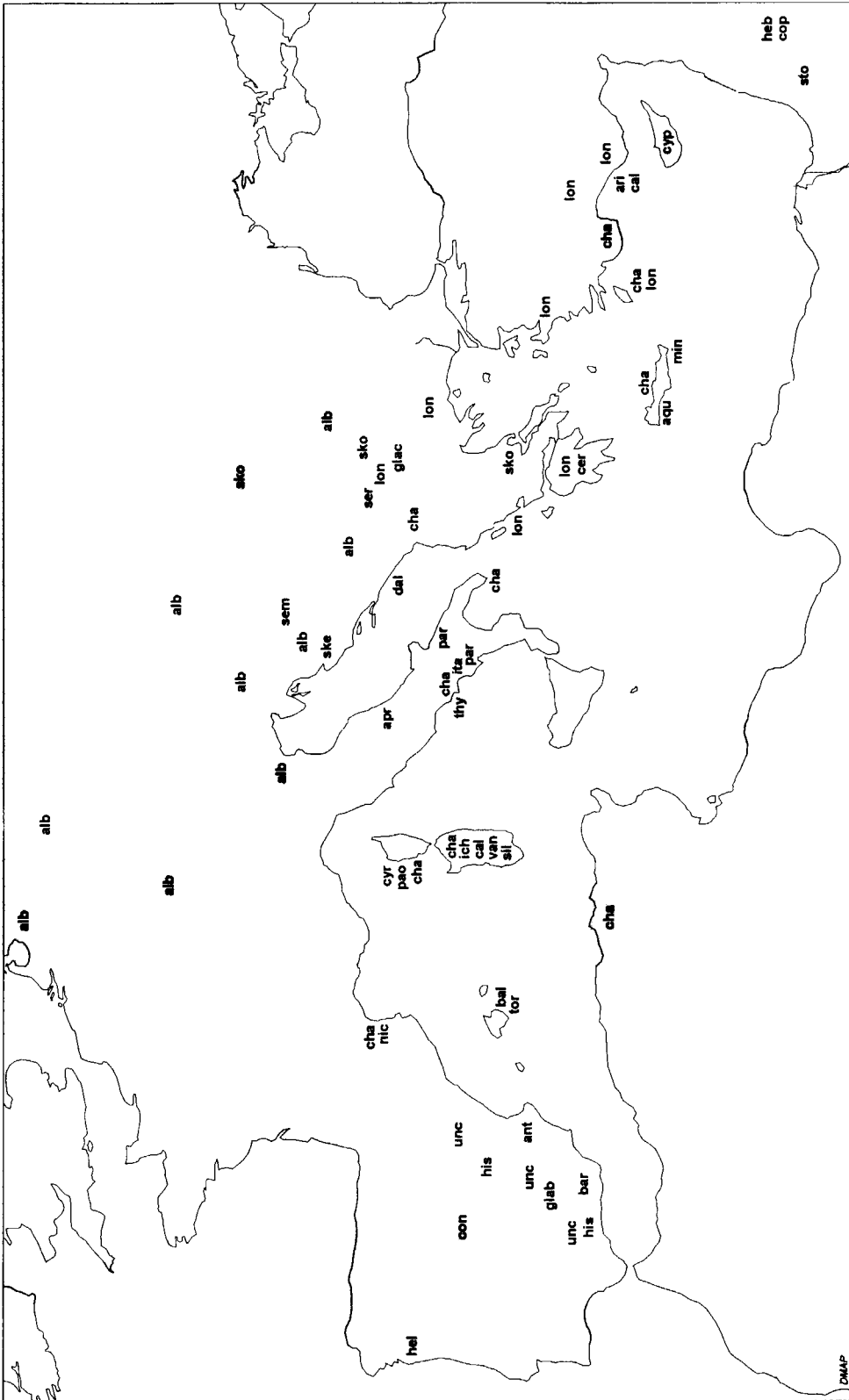


Fig. 6. Distribution map of analyzed taxa (outgroup taxa excluded). The record of *B. albertinagni* in The Netherlands given by Barnard and Barnard (1983: part 1, map 21) could not be found elsewhere in the literature. It should, therefore, be regarded as questionable. For identification of abbreviated suffixes see Table 1.

and *B. (Xystriogidiella) spathulata* Stock and Rondé-Broekhuizen, 1987.

Characters

The selection of characters depended on the literature. Since the quality of descriptions varies considerably, our choice of useful characters had to be reduced to a common denominator. Therefore, some potential characters could not be employed, because their descriptions were incomplete, for example, incisors and molar processes of mandibles or teeth/setae on the inner margin of the dactyli of gnathopods.

Polymorphic traits, for example, varying numbers of setae on the third palp article of the mandible, were coded according to the Scaled method (Wiens, 1995), so that the presence of four or five setae becomes the intermediate state between four and five setae. In some cases, it would have been more satisfactory to have been able to code polymorphic characters in relation to their frequencies. If the majority of the specimens with four or five setae have four setae, four becomes the coded state (Frequency or Majority method). However, most species descriptions do not supply this information (or are merely based on an inadequate number of specimens). The problems of deriving a consistent and effective morphological data set from the literature illustrates yet again how often existing taxonomic descriptions impede rather than facilitate the execution of robust cladistic analyses.

Adaptation to life in ground-water habitats is typically directed at the reduction of morphological structures that would obstruct mobility in an interstitial network of narrow channels. Furthermore, the reduction of functional structures for swimming and water circulation, important for respiration in epigeal amphipods, can be generally observed in stygobionts. These modifications can comprise pleopodal and uropodal appendages, gills, ventral groove, anterior pereopods, and coxal plates. Morphological structures can either display different stages of reduction or evolve into organs or instruments with new, specialized functions, as may be the case with modified pleopodal and uropodal rami (Notenboom, 1991). For the coding of those characters, the basic functional model of an epigeal amphipod was regarded as the common ancestor of stygobiont bogidiellids.

Character states nearest to this morphological prototype were scored as plesiomorphies (state 0). The loss or acquisition of small structures, however, are very likely to occur as homoplasies within a lineage. For this reason, the reduction of spines and setae was not strictly considered apomorphic and their coding remains hypothetical at this initial phase of a cladistic analysis (see also, Stock, 1981; Lindeman, 1991; Notenboom, 1991).

The appended list contains several characters with one of two possible states expressed in one taxon only. These characters are uninformative for the cladistic analysis and have, therefore, been ignored in PAUP (where this option was available). They are, nevertheless, listed because of their taxonomic importance for bogidiellids as a whole. If not explicitly stated differently, a character is by default unordered and/or unweighted (that is weight 1 for the second run).

PHYLOGENETIC RESULTS

The use of alternative software programs and analytical methods resulted in a relatively large number of cladograms. In order to facilitate the discussion of these phylogenetic results, a representative choice of consensus trees, depicted in Figs. 7–10, is sorted by method or program employed and divided into three groups: (1) Outgroup comparison, (2) Ingroup analysis, and (3) Successive Weighting. Trees of the first group are further subdivided between two categories, either obtained by alternative programs (PAUP versus HENNIG86 trees, Figs. 7, 8) or methods (default run versus second run, Figs. 7–9).

Outgroup Comparison

In the default runs, the analysis failed to keep all four Canarian taxa as a monophyletic sister group of the ingroup. Therefore, *B. purpuriae* and *B. spathulata* were chosen for a corresponding outgroup rooting in HENNIG86 and PAUP consensus trees of both runs (Figs. 7, 8). Although the parsimony algorithms in both software programs were not identical and produced trees with different lengths, there are surprisingly many topologic similarities. Accordingly, congruent topologic patterns can be found in trees resulting from the initial, default, as well as the second runs. To a considerable extent, differences in lengths were caused by the fact that several uninformative characters were automatically ignored

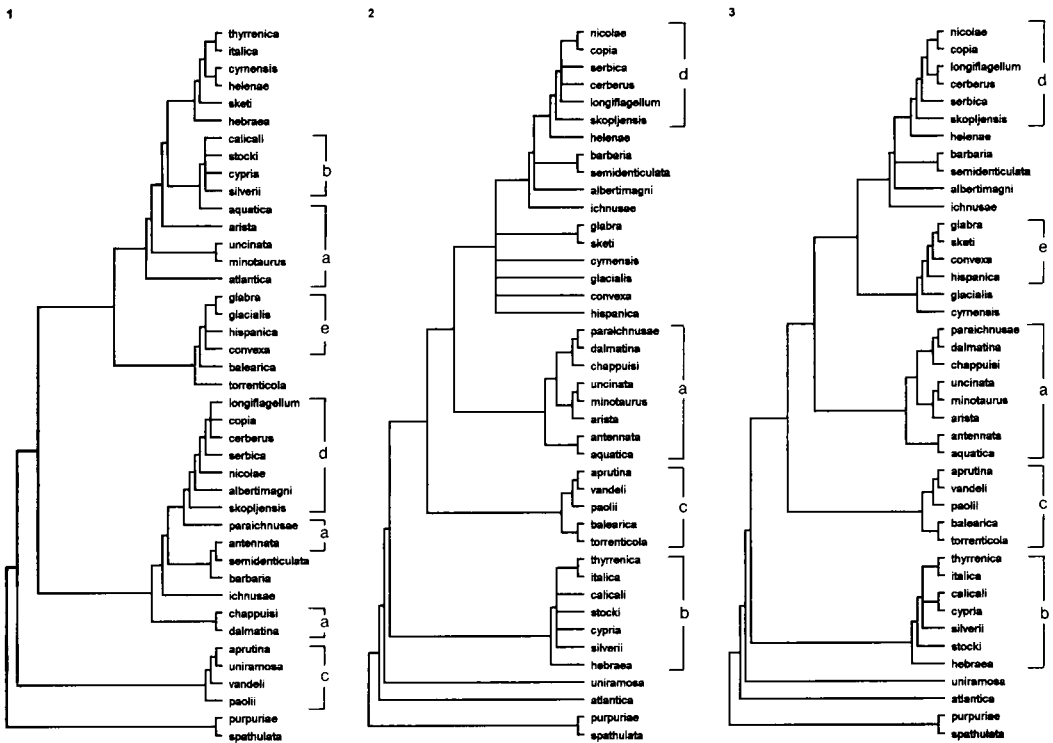


Fig. 7. PAUP consensus trees of outgroup analysis. Trees rooted with outgroup (*purpuriae*, *spathulata*). Letters a–e show robust clades (see Phylogenetic Results). 1, Strict consensus tree from 8 trees of the default run (unordered and unweighted characters). This tree is identical with the Semi Strict Majority Rule, and Adams default consensus trees. Length: 411. Rohlfs' CI: 0.97. 2 and 3, consensus trees from 33 trees of the second run (partly weighted and ordered characters). Length: 652. 2, Strict consensus tree. Rohlfs' CI: 0.71. 3, Majority Rule consensus tree. Rohlfs' CI: 0.95.

in PAUP, where this option was available, but not in HENNIG86. These characters lead to additional steps in HENNIG86 trees.

In each category (program or method), there is at least one consensus tree that presents the species of the subgenus *Medigidiella* (*B. chappuisi*, *B. dalmatina* S. Karaman, 1953, *B. paraichnusae* Karaman, 1979b, *B. aquatica* Karaman, 1990a, *B. antennata* Stock and Notenboom, 1988, *B. uncinata* Stock and Notenboom, 1988, *B. minotaurus*, and *B. arista*) as a monophyletic group (Figs. 7.2a, 7.3a, 8.2a, 8.3a). Two trees of the default run do not support a monophyletic medigidiellan clade: the extremely unresolved HENNIG86 Strict consensus tree (Fig. 8.1) and the PAUP Strict consensus tree, where in each case the medigidiellans are split in smaller subunits (Fig. 7.1a). The robustness of this clade in each category is remarkable insofar as the distribution of its taxa is widely spread over the whole Mediterranean (Fig. 6). *Bogidiella chappuisi*, the only species of this cluster with

a more or less wide distributional range, which might suggest a possible ancestral position within the *Medigidiella* subclade, appears only as a branch at a lower level in the category "default trees" (Figs. 7.1a, 8.2a).

Another stable congruent pattern of clades in both Hennig86 and PAUP trees is represented by taxa that form the following geographic clusters:

(1) An eastern Mediterranean group with *B. calicali*, *B. cypria* Karaman, 1989, and *B. stocki* as a stable core (Figs. 7b, 8b). In second run consensus trees, *B. hebraea* Ruffo, 1963, as well as the mid-Italian doublet *M. thyrenica* and *A. italica* appear firmly integrated into the eastern Mediterranean cluster (Figs. 7.2b, 7.3b, 8.3b). The appearance of *B. hebraea* as one of four known bogidiellids from the Sinai Peninsula in this group is not as self-evident as it seems, because its original description is relatively vague, resulting in a character code with 18 question marks (38%) and an unclear subgeneric sta-

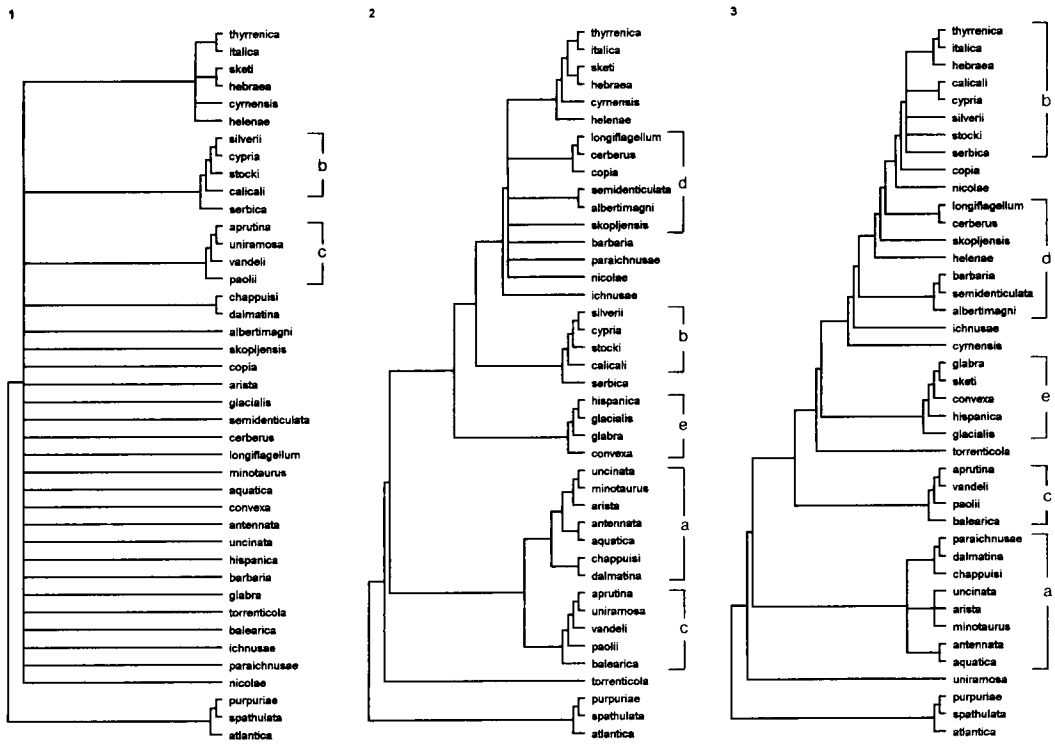


Fig. 8. HENNIG86 consensus trees of outgroup analysis. Trees rooted with outgroup (*purpuriae*, *spatulata*, *atlantica*). Letters a–e show robust clades (see Phylogenetic Results). 1 and 2, consensus trees from 100 trees of the default run (unordered and unweighted characters). Length: 548. 1, Strict consensus tree. CI: 25. 2, Majority Rule consensus tree. 3, Strict consensus trees from 4 trees of the second run (partly weighted and ordered characters). Length: 678. CI: 24.

tus. The eastern group is accompanied by *B. silverii* in each category. Like *B. calicali*, *B. silverii* has a Sardinian-type location.

(2) A central-western Mediterranean group consisting of *B. aprutina* Pesce, 1980, *B. paolii* Hovenkamp, Hovenkamp, and van der Heide, 1983, and *B. vandeli* group (Figs. 7c, 8c). In most trees, this cluster was increased by the Mallorcan species, *B. balearica* Dancau, 1973, and *B. torrenticola* Pretus and Stock, 1990 (Figs. 7.2c, 7.3c, 8.2c, 8.3c).

(3) A central-eastern Mediterranean group, less homogeneous than the small central-western group and not always monophyletic, but nonetheless closely grouped in each category. This group comprises *B. longiflagellum* S. Karaman, 1959, *B. cerberus* Bou and Ruffo, 1979, *B. semidenticulata* Meštrov, 1961, *B. skopljensis* (S. Karaman, 1933), *B. semidenticulata*, and *B. serbica* Karaman, 1987 (PAUP only), constantly joined by *B. copia* Karaman, 1988a, and *B. nicolae* Karaman, 1988b (Figs. 7d, 8.2d, 8.3d).

Apart from these three major, more or less constant clusters, a pattern of related taxa can be traced in each category, either arranged as doublets or triplets within alternating larger clades with incongruous geographic distribution ranges. *Aurobogidiella italica* and *M. thyrenica* form such a robust subclade, often pairing to the eastern Mediterranean cluster (Figs. 7.2b, 7.3b, 8.3b). A stable triplet of Spanish species (*B. hispanica* Stock and Notenboom, 1988, *B. glabra* Stock and Notenboom, 1988, and *B. convexa* Stock and Notenboom, 1988) appears, polytomous or in separate clades, intermingled with taxa from different geographic settings (Figs. 7.1e, 7.3e, 8.2e, 8.3e).

Ingroup Analysis

After the exclusion of the four Canarian taxa, the same matrix was employed for an ingroup comparison, this time in HENNIG86 exclusively. The analysis was again exercised in a default (unordered and unweighted) and

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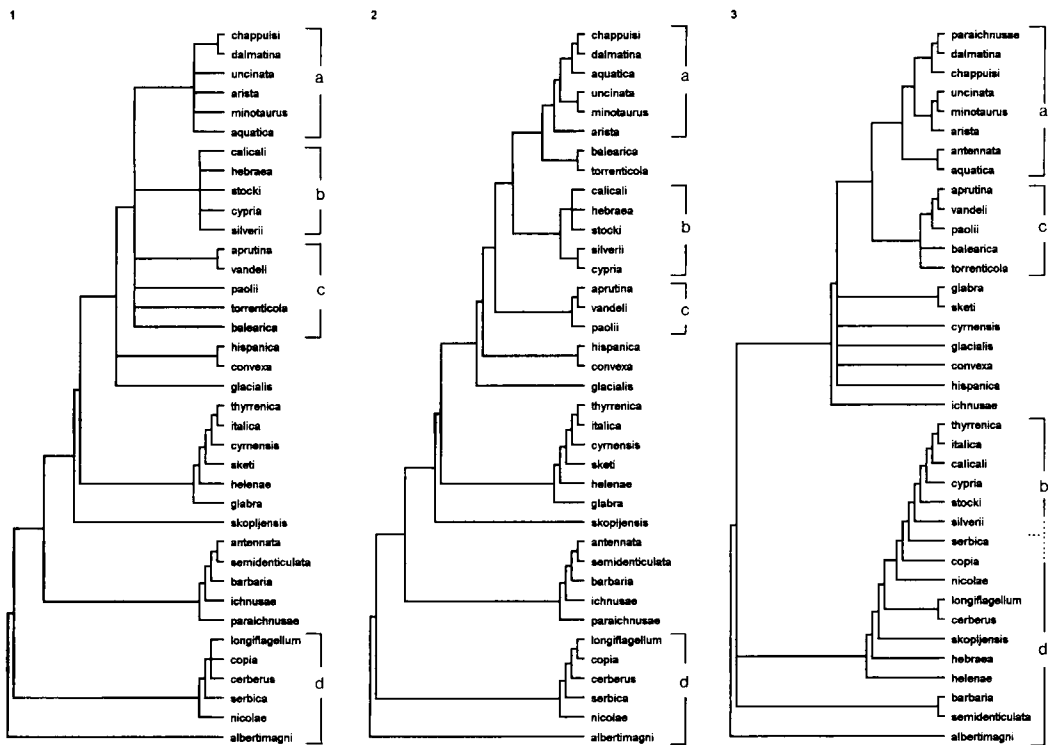


Fig. 9. HENNIG86 consensus trees of ingroup analysis. Letters a–d show robust clades (see Phylogenetic Results). 1 and 2, consensus trees from 100 trees of the default run (unordered and unweighted characters). Length: 398. 1, Strict consensus tree. CI: 32. 2, Majority Rule consensus tree. 3, Strict consensus tree from 12 trees of the second run (partly weighted and ordered characters). Length: 606. CI: 25.

a second, partly ordered and weighted run.

As compared to the outgroup analysis, the topology of the three consensus trees in Fig. 9 reveal the same major clusters: a medigidiellian clade (Fig. 9a; without *B. antennata* and *B. paraichnusae* in the default run), the central-western Mediterranean group (Fig. 9c), and the eastern Mediterranean cluster (united with the central-eastern group in one large clade in the second run, Fig. 9.3b, d). In the default run, the eastern Mediterranean clade (including *B. hebraea*, *B. calicali*, and *B. silverii*) shares character state 9/0 (apical + subapical telson spines) as an apomorphy.

As with the analyses including outgroups, the ingroup analyses show smaller geographic units in each tree: *A. italica*-*M. thyrrhenica*, *B. convexa*-*B. hispanica*, and *B. torrenticola*-*B. balearica*. Both ingroup runs result in trees with the medigidiellian clade maintaining a position at the highest level within each tree. This seems to indicate that the medigidiellids evolved from an unspecialized common ancestor.

Successive Weighting in HENNIG86

The Successive Weighting (SW) method yielded a tree that shows the least topologic congruence with any previously discussed cladograms (Fig. 10). This may not be too surprising, since the setting of weights according to best fits leads to different weights for pairs of characters with presumably identical taxonomic value (characters 23/24 and 27/28). Furthermore, characters with a high functional value and a probable complex evolution (e.g., character 1) seem to be under-rated as compared to numerical variations of spines and setae (e.g., character 13). However, some elements of the aforementioned stable clades can also be recognized in the SW consensus tree. Both the eastern Mediterranean clade (Fig. 10b) and some of the geographically related doublets (*A. italica*-*M. thyrrhenica* and *B. convexa*-*B. hispanica*) are almost unchanged. The *Medigidiella* group, reduced to six (of eight possible) taxa, forms an intermingled clade with three central-west-

ern Mediterranean species (Fig. 10f). Also less homogeneous, though still grouped closely together, the taxa of the central-eastern cluster now form a large, predominantly polytomous clade, accompanied by several taxa that belonged to "own" distinct clusters in trees of previous methods (Fig. 10g).

DISCUSSION OF PHYLOGENETIC RESULTS AND CONCLUSIONS

The resulting trees of the different analyses performed in this study show a surprisingly congruent topology. These congruencies are characterized by: (1) a stable pattern of geographically related taxa; (2) the constant appearance of the same "foreign" taxa in some of the geographic clusters; and (3) a major monophyletic group of taxa without geographic relation, all belonging to the subgenus *Medigidiella*.

The existence of relatively robust clades in each category of consensus trees implies phylogenetic relationships that are associated with certain regions. These regions comprise large parts of the Mediterranean rather than naturally compartmented (smaller) areas like islands and peninsulas. If speciation events happen at a high rate in bogidiellids, one might expect distinct phylogenetic patterns of species from small isolated areas with a marked diversity (e.g., Sardinia). The Spanish triplet, as well as the mid-Italian and Mallorcan doublets, seems to indicate such sympatric or peripatric speciation events, typically resulting from dispersal of individuals or populations (see Notenboom, 1991). *Aurobogidiella italica* and *M. thyrrhenica*, the doublet from the Bay of Naples, share three character states (7/1-2, 8/0, and 16/3) as apomorphies and are thus apparently closely related.

A pattern of descent that encircles large regions, for example, the eastern Mediterranean, is, however, more obvious and conspicuous than speciation on a small scale.

The three major geographic clusters have two features in common: first, they do not include all species found in that specific area, and, second, they are accompanied by "foreign" species. A phylogenetic pattern of this kind resembles a mosaic with complete parts and missing pieces. The record of *B. calicali* in South Anatolia particularly illustrates the evolutionary mosaic of bogidiellids; *B. calicali* until now was known only from its Sardinian type location. In the consensus trees of these analyses, *B. calicali* steadily appears in

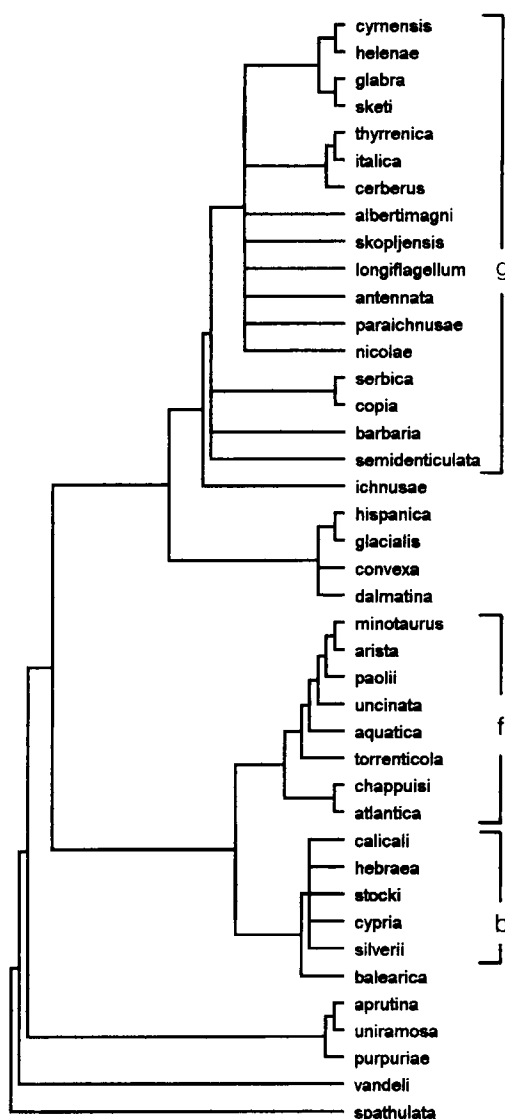


Fig. 10. HENNIG86 Strict consensus tree from 100 trees of Successive Weighting method (outgroup analysis). Tree rooted with outgroup (*spathulata*). Letters b, f, and g show robust clades (see Phylogenetic Results). Length: 436. CI: 61.

the eastern Mediterranean clade and would have been considered a "foreign" element in the eastern Mediterranean if it had not been found in southern Turkey. Accordingly, other constant taxa in marked geographic clusters (e.g., *B. silverii*, *B. copia*, *B. nicolae*) might also be misinterpreted as foreign because of missing distributional data.

The concept of a mosaic evolution in bogidiellids, with an assumed ancient, Mesozoic origin (Stock, 1981; Barnard and Barnard,

1983; Notenboom, 1991), is supported by the steady appearance of the *Medigiella* cluster in each category of consensus trees. The species of this cluster cannot be related to a specific region; their males have modified second uropod rami spines in common, a morphological adaptation that is believed to play a functional role during sperm transfer (Stock, 1981; Karaman, 1979a). Provided that (1) the evolution of this character from a normal, straight spine into a serrated, spoon-shaped instrument proceeded over a considerable period of time with intermediate states, and that (2) it did not evolve in a parallel way in different species, the medigiellans share sexual dimorphic uropods as a synapomorphy. In this case, this character would seem to possess a high taxonomic as well as phylogenetic value.

However, the assumption of an ancient origin, whose present-day phylogenetic pattern is clouded by missing information, should not be overvalued. Various conceivable scenarios may have led to the present distribution of stygobiont amphipods, including major and minor ancient vicariant events, dispersal by rivers and currents, and the transportation of sand or shingle (plus adhering stygobionts) during the last 10,000 years of human history.

The cladistic analysis here of all Mediterranean species of the genus *Bogidiella* should be considered as an initial, comparative study rather than as a definitive, complete phylogenetic reconstruction. A subsequent step in the direction of the latter could consist in the employment of added information obtained by, for example, electron microscopy for additional morphological characters or molecular sequencing. The choice of Canarian taxa as an outgroup failed to achieve its most prominent goal. It could not be held together as a monophyletic sister group of the ingroup (except for the second run) and was thus incapable of indicating an evolutionary direction of character development in the ingroup. Another, more promising approach could be attempted by an extended outgroup comparison using North African, Caribbean, and Asian taxa as several major sister groups or different amphipod families (e.g., Niphargidae or Ingolfiellidae).

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Appendix.

The characters listed below appear in a random order, reflecting the stepwise development of the matrix in numerous prunings. The following characters describe corresponding body parts or morphological traits: antennae: 11, 44–50; labium: 15; mandible: 20, 21, 22; maxillae: 2, 13, 14, 51; maxilliped: 16, 17, 19; gnathopods: 23–33; pereopods: 39–43; pleopods: 1, 4, 5, 6; uropods: 2, 3, 7, 34, 35; telson: 9, 10, 36–38; gills: 8; and sexual dimorphism: 18.

(1) Sexual dimorphism in second pleopod rami setae. State 0 = absent; State 1 = present.

Excluded as an alternative to character 18. A modified seta on the second pleopod outer ramus in males defines the subgenus *Stygogidiella* Stock, 1981.

(2) Modifications in second uropod rami spines.

State 0 = spines straight, unmodified; State 1 = spines straight, but not serrate; State 2 = spines straight, serrate; State 3 = spines spoon-shaped, serrate; State 4 = spines spade-shaped, not serrate.

Second run: ordered; weighted with 2. Successive weighting: 1. Modified rami spines occur in males only. State 1 comprises the single recurved, wavy spine found in *B. aquatica* as well as the single hook-shaped spines of two Spanish species, *B. antennata* and *B. uncinata* (see also character 18).

(3) Sexual dimorphism in third uropod peduncle spines.

State 0 = absent; State 1 = present.

Excluded as an alternative to character 18; uninformative. Sexual dimorphism in third uropod peduncle spines was found in *B. (Stygogidiella) uniramosa* only: males have 2 mediolateral spines, females have 3 mediolateral spines.

(4) Inner rami on pleopods.

State 0 = present on pleopods 1–3; State 1 = reduced; State 2 = vestigial; State 3 = absent.

Second run: ordered in HENNIG86, ordered as Dollo-up (forward transformation) in PAUP; weighted with 4. Successive weighting: 3. The reduction of articulated pleopodal endopods is considered to be an apomorphy within the family Bogidiellidae (Stock, 1981). In the taxa examined, several phases of reduction were noted: the reduced state refers to *B. (Medigidiella?) hebraea* with normal (one-articulated) inner rami on the first pleopod, vestigial rami on the second pleopod, and none on the third. The Dollo-up option was chosen because an exact reversion from stage 3 to stage 0 seems very unlikely.

(5) Number of articles of pleopod outer rami.

State 0 = 3–5 articles; State 1 = 3 articles.

Both runs: ignored in PAUP as an uninformative character. Successive weighting: 10.

(6) Modifications in pleopod inner rami.

State 0 = absent; State 1 = present.

Both runs: ignored in PAUP as an uninformative character. Successive weighting: 10.

(7) Modification in first and second uropod rami.

State 0 = absent; State 1 = uropod 2 modified; State 2 = uropod 1 and 2 modified.

Second run: ordered in Hennig86, ordered as Dollo-up (forward transformation) in PAUP; weighted with 4. Successive weighting: 10. State 1 refers to the reduction of rami spines and the serrated, recurved rami tips of the second uropod in *Aurobogidiella italica*. In *Marinobogidiella thyrenica* this reduction has obviously reached an advanced stage; the rami of the first and second uropods are clawlike, each with only 1 apical spine. The weight has been applied because these distinct modifications are considered as having evolved in several consecutive steps. As in the case of the modified pleopodal rami, an exact reversion to the ancestral condition seems very unlikely.

(8) Gills.

State 0 = occurring on pereonites 3–6; State 1 = occurring on pereonites 4–6; State 2 = occurring on pereonites 3–5.

Second run: weighted with 3. Successive weighting: 10. The loss of gills, a common evolutionary trend in stygobiont interstitial amphipods, comprises morphological as well as physiological aspects, and is therefore weighted with 3. It is, however, hypothetical whether an initial posterior or anterior reduction should be preferred as a first evolutionary step; character states 1 and 2 are interchangeable and thus this character was not ordered.

(9) Topography of telson spines.

State 0 = apical + subapical spines; State 1 = apical spines only.

Successive weighting: 4. The existence of subapical telson spines obviously represents an intermediate stage between the ancestral amphipod telson with rows of lateral spines and the reduced, typical bogidiellid telson with apical spines only. It is considered a distinct evolutionary feature and weighted with 4.

(10) Number of telson spines.

State 0 = 2; State 1 = 2–4; State 2 = 2, 4; State 3 = 4; State 4 = 4–6; State 5 = 6.

Second run: ordered. Successive weighting: 3. Unlike the spines in character 9, these spines always appear at the apical part of the telson. Although the majority of the bogidiellids examined have constant numbers of apical telson spines (2 or 4 spines), some descriptions report polymorphism in this character. If the type material of the latter comprises 4 or fewer specimens, the diagnosis lacks a sound backup. There are, however, descriptions with sufficient sample material that effectively establish polymorphism in telson spines (e.g., *B. (B.) torrenticola* with mostly 2, occasionally 4 telson spines; type material: 41 specimens). For the obviously consecutive loss (or acquisition) of single spines or pairs of spines, character 10 has been ordered in the second run. In this case, the ancestral state is assumed to consist of 2 terminal spines.

(11) Number of first antenna flagellum articles.

State 0 = 7; State 1 = ≤ 8 ; State 2 = ≤ 9 ; State 3 = ≤ 10 ; State 4 = ≤ 11 ; State 5 = ≤ 15 .

Second run: ordered. Successive weighting: 1. In most papers, a varying number of flagellum articles is described by the term "flagellum with up to x articles," which is meant to be represented by the symbol \leq .

(12) Number of palp articles on first maxilla.

State 0 = 2; State 1 = 1.

Both runs: ignored in PAUP as an uninformative character. Successive weighting: 10.

(13) Number of setae on second palp article of first maxilla.

State 0 = 4 setae; State 1 = 3 or 4 setae; State 2 = 3 setae.

Both runs: ignored in PAUP as an uninformative character. Successive weighting: 10.

(14) Number of setae on inner lobe of first maxilla.

State 0 = 3 setae; State 1 = 2 setae.

Successive weighting: 0.

(15) Spines on outer lobe labium.

State 0 = absent; State 1 = present.

Successive weighting: 4. The presence of one relatively strong spine on each outer lobe of the labium obviously forms a distinct character. Most written descriptions, however, fail to mention it (although, in some instances, the spines are depicted in the drawings). The character has been weighted because the existence or absence of this structure in the mouthparts is assumed to play a considerable functional role.

(16) Number of spines on outer lobe maxilliped.

State 0 = 3 spines; State 1 = 2 or 3 spines; State 2 = 2 spines; State 3 = 1 spine.

Second run: ordered. Successive weighting: 2. Like the labium spines in character 15, these spines probably play a functional role in the cooperation of mouthparts and are weighted with 2.

(17) Form of spines on outer lobe maxilliped.

State 0 = simple spines; State 1 = mixed spines (1 simple, 1 bifid); State 2 = bifid spines; State 3 = crooked, finger-shaped spines.

Successive weighting: 10. The tendency to crooked, finger-shaped spines was observed in several species with character state 0 (simple spines), but was in no instance developed as strongly as in *B. (Styg.) uniramosa*, the only OTU with state 3.

(18) Sexual dimorphism in uropods or pleopods.

State 0 = absent; State 1 = present.

Second run: weighted with 3. Successive weighting: 0. Modifications in second uropod rami spines and second pleopod outer rami setae occur in males only and are believed to play a functional role during the sperm transfer (Stock, 1981; Karaman, 1982). These characters define the subgenera *Medigidiella* and *Stygogidiella*, respectively. Their evolution has very likely taken place in several consecutive steps and is, therefore, weighted with 3.

(19) Number of spines on inner lobe maxilliped.

State 0 = 3 spines; State 1 = 2 spines.

Successive weighting: 0.

(20) Number of setae on third palp article mandible.

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

Second run: ordered. Successive weighting: 0. Scoring character 20 (and 21) as ordered implies that the acquisition of one additional seta is generally preceded by a polymorphic trait; in this case, the evolution from, for example, 3 to 4 setae cannot have occurred directly, but has to pass the intermediate state with "3 or 4" setae. Here it would have been more satisfactory to apply the Frequency or Majority method (see Characters).

(21) Number of setae on second palp article mandible.

State 0 = 1 seta; State 1 = 1 or 2 setae; State 2 = 2 setae; State 3 = 2 or 3 setae.

Second run: ordered. Successive weighting: 2.

(22) Cilia on third palp article mandible.

State 0 = absent; State 1 = present.

Successive weighting: 0. The presence of cilia on the third palp segment is only exceptionally mentioned in descriptions. The scoring of these character states has been derived from the drawings.

(23) Number of long (sub) angular spines on propodus gnathopod 1.

State 0 = 2 spines; State 1 = 3 spines; State 2 = 4 spines; State 3 = 5 spines.

Second run: ordered. Successive weighting: 1. Generally, these long propodal spines on both gnathopods serve as corner spines for the dactyl tip. If their number increases, additional spines are always inserted on the proximal (subangular) side of the corner.

(24) Number of long (sub) angular spines on propodus gnathopod 2.

State 0 = 1 spine; State 1 = 2 spines; State 2 = 3 spines; State 3 = 4 spines.

Second run: ordered. Successive weighting: 0.

(25) Short spines on propodus gnathopod 1.

State 0 = absent; State 1 = simple spines; State 2 = bifid spines.

Second run: ordered. Successive weighting: 1. Unlike the long (sub) corner spines (characters 23 and 24), which appear on the proximal part of the palmar margin, short spines are inserted along the whole palm. As counterparts of the dactyl, they might increase the ability to grip objects.

(26) Short spines on propodus gnathopod 1.

State 0 = absent; State 1 = simple spines; State 2 = bifid spines.

Second run: ordered. Successive weighting: 1.

(27) Number of short spines on propodus first gnathopod.

State 0 = absent; State 1 = 1 spine; State 2 = 2 spines; State 3 = 3 spines; State 4 = 4 spines; State 5 = 5 spines; State 6 = 6 spines; State 7 = 7 spines; State 8 = 9 spines.

Second run: ordered. Successive weighting: 2. Unfortunately, not all descriptions explicitly state the number of short spines. Therefore, the coding of these character states often depend on the quality of the drawings.

(28) Number of short spines on propodus gnathopod 2.

State 0 = absent; State 1 = 1 spine; State 2 = 2 spines; State 3 = 3 spines; State 4 = 4 spines; State 5 = 5 spines; State 6 = 6 spines; State 7 = 7 spines; State 8 = 8 spines.

Second run: ordered. Successive weighting: 1.

(29) Shape of palmar margin of propodus gnathopods.

State 0 = both margins sinusoid; State 1 = both margins uneven; State 2 = margins mixed (even/uneven or uneven/sinusoid); State 3 = both margins even.

Second run: ordered. Successive weighting: 0. The term "mixed margins" means that one of a pair of gnathopods has a different state than its opponent.

(30) Serration of palmar margin of propodus gnathopods.

State 0 = absent; State 1 = serration proximal or distal; State 2 = serration proximal and distal; State 3 = mixed serration (wholly/absent or wholly/proximal and distal); State 4 = wholly (serration on whole margin).

Second run: ordered. Successive weighting: 0. Similar to character 29, the term "mixed serration" means that one of a pair of gnathopods has a different state than its opponent.

(31) Number of long posterior setae on basis first gnathopod.

State 0 = 3 or 4 setae; State 1 = 3 setae; State 2 = 2 or 3 setae; State 3 = 2 setae; State 4 = 1 or 2 setae; State 5 = 1 seta; State 6 = setae absent.

Second run: ordered. Successive weighting: 0.

(32) Number of long posterior setae on basis gnathopod 2.

State 0 = 2–4 setae; State 1 = 3 setae; State 2 = 2 or 3 setae; State 3 = 2 setae; State 4 = 1 or 2 setae; State 5 = 1 seta; State 6 = setae absent.

Second run: ordered. Successive weighting: 0.

(33) Plumose posterior setae on basis gnathopod 2.

State 0 = absent; State 1 = present.

Successive weighting: 0.

(34) Number of lateral spines on peduncle first uropod.

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

Second run: ordered. Successive weighting: 4. The term lateral spines in characters 34 and 35 refers to all medial and/or proximal spines on the peduncle, excluding the apical spines.

(35) Number of lateral spines on rami third uropod.

State 0 = 12–17 spines; State 1 = 7–11 spines; State 2 = 3–6 spines.

Second run: ordered. Successive weighting: 0.

(36) Length of telson spines.

State 0 = all spines < telson length; State 1 = all spines ~ telson length; State 2 = 2 spines ≤ telson length and 2 spines ≥ telson length; State 3 = all spines > telson length; State 4 = all spines >> telson length.

Second run: ordered. Successive weighting: 0. State 2 comprises all species with 4 spines in which the following combinations were found: 2 spines shorter than telson length—2 spines longer than or as long as telson length; 2 spines longer than telson length—2 spines shorter than or as long as telson length.

(37) Number of plumose setae on telson.

State 0 = 2 setae; State 1 = 4 setae; State 2 = 4–6 setae; State 3 = ≥6 setae.

Second run: ordered. Successive weighting: 1.

(38) Cleft telson.

State 0 = cleft > one-third of telson length; State 1 = cleft = one-third–one-fourth of telson length; State 2 = cleft = one-fifth–one-eighth of telson length; State 3 = no cleft (telson with straight apical margin); State 4 = telson with concave apical margin.

Second run: ordered. Successive weighting: 0.

(39) Size of lenticular organs on pereopods.

State 0 = absent; State 1 = lenticular organ small (about one-third of basis width); State 2 = lenticular organ large (about one-half of basis width); State 3 = lenticular organ maximum (about basis width).

Excluded as an alternative to character 40.

(40) Shape of lenticular organs on pereopods.

State 0 = not visible; State 1 = simple ring; State 2 = double ring; State 3 = double ring with sinusoid inner margin.

Second run: ordered. Successive weighting: 0. Due to the fact that little is known about the function and structure of lenticular organs, the descriptive terminology is unclear about this issue. Pereopods without visible lenticular organs are described with terms such as “absent,”

“not visible,” or “without any trace of lenticular organs.” In characters 39 and 40, the state “absent” is identical with the state “not visible.”

(41) Lenticular organ on pereopods.

State 0 = present or absent on pereopods 3–7; State 1 = present on pereopods 3–6, absent on pereopod 7.

Excluded as an alternative to character 40.

(42) Length of dactylus pereopod 7. State 0 = dactylus < one-half of propodus length; State 1 = dactylus ≤ one-half of propodus length; State 2 = dactylus ≥ one-half of propodus length; State 3 = dactylus > one-half of propodus length; State 4 = dactylus >> one-half of propodus length.

Second run: ordered. Successive weighting: 0.

(43) Number of anterolateral setae on propodus pereopod 7.

State 0 = 1–3 setae; State 1 = 4–6 setae; State 2 = 7–9 setae; State 3 = > 9 setae.

Second run: ordered. Successive weighting: 0. This character comprises all anterior setae on the propodus, which are usually thinner and longer than the posterior and apical armature of the same article.

(44) Spines on peduncles antenna 2.

State 0 = absent; State 1 = present.

Successive weighting: 0.

(45) Number of accessory flagellum articles.

State 0 = 2; State 1 = 2 or 3; State 2 = 3.

Successive weighting: 0.

(46) Length of accessory flagellum.

State 0 = ≤1 flagellum article; State 1 = ≤2 flagellum articles; State 2 = > 2 flagellum articles; State 3 = ≥3 flagellum articles; State 4 = > 4 flagellum articles.

Second run: ordered. Successive weighting: 5. The length of the whole accessory flagellum is measured relative to the number of antennal flagellum articles.

(47) Number of spines on peduncles first antenna.

State 0 = no spines; State 1 = 1 spine; State 2 = 1 or 2 spines; State 3 = 2 spines; State 4 = 2 or 3 spines.

Second run: ordered. Successive weighting: 0.

(48) Aesthetascs on antenna 2.

State 0 = absent; State 1 = present.

Successive weighting: 0.

(49) Setose organ or setules on first peduncular article of antenna 1.

State 0 = both absent; State 1 = setose organ present; State 2 = bunch of setules present.

Second run: ordered. Successive weighting: 10. Both setose organ and bunch of plumose setules occur ventrodistally on the first antennal peduncular article.

(50) Bunch or row of setae on peduncles antenna 2.

State 0 = absent; State 1 = 1 bunch of setae present; State 2 = several rows of setae present.

Second run: ordered. Successive weighting: 0. These setae appear narrowly inserted and can be easily distinguished from the normal armature.

(51) Armature of maxilla 2.

State 0 = normal setae; State 1 = at least 1 plumose seta; State 2 = at least 1 spine.

Successive weighting: 0. Similar to character 50, both plumose setae and spines occur in addition to the normal armature.