

PARAPSEUDONIPHARGUS BAETIS, NEW GENUS, NEW SPECIES, A STYGOBIONT AMPHIPOD CRUSTACEAN FROM THE GUADALQUIVIR RIVER BASIN (SOUTHERN SPAIN), WITH PHYLOGENETIC IMPLICATIONS

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ABSTRACT

Parapseudoniphargus baetis, representing a new monotypic genus closely related to *Pseudoniphargus* Chevreux, is described from hyporheic ground waters. The new taxon appears to be another endemic ground-water crustacean of the basin of the Guadalquivir River in the south of Spain. The morphological features of *Parapseudoniphargus baetis* suggest special adaptations to an interstitial life. The genus *Allomelita* Stock is hypothesized as the most plausible sister group of *Parapseudoniphargus* and *Pseudoniphargus*.

The Guadalquivir River Basin (Fig. 1) appears to harbor a rather large number of endemic stygobiont crustaceans. Up to now it seems to be the only Iberian region with records of Thermosbaenacea. Moreover, endemic species of widespread genera such as *Pseudoniphargus* and *Salentinella* (Amphipoda), *Proasellus* and *Stenasellus* (Isopoda), and *Parapseudoleptomesochra* (Harpacticoida) have been recorded. The distribution of hadziid Amphipoda in the Iberian Peninsula appears to be restricted to the Guadalquivir Basin and the Portuguese south coast. In Table 1 these records are listed. The new monotypic amphipod genus *Parapseudoniphargus*, described in the present paper, seems to be another indigenous element of this area.

Parapseudoniphargus was discovered first by Notenboom and Meijers (1985), cited as "Crangonyctidae," in the upper course of the Guadalquivir River in the Sierra de Cazorla (province of Jaén). During field work of fellow workers P. van den Hurk and R. Leys (unpublished) in the summer of 1986, additional localities of this species were found in tributaries of the lower course of the Guadalquivir River (the stations beginning with "A" in the descriptive part of this paper).

Parapseudoniphargus baetis was found in hyporheic habitats only. The accompanying amphipod fauna consisted frequently of members of the closely allied genus *Pseudoniphargus*, mostly *P. latipes* Notenboom, 1987a. However, at one locality both *P. latipes* and *P. illustris* Notenboom, 1987a,

were found together. Furthermore, the widespread Iberian genus *Haploginglymus* was found often co-occurring with *Parapseudoniphargus*. Other accompanying fauna is listed in the Material Examined section of this paper.

Through the compactness of the body, the deep coxal plates, the relatively short posterior pairs of pereopods, and the short third uropod, the habitus of *Parapseudoniphargus* looks, at first glance, like a species of *Crangonyx*. However, study of the dissected appendages demonstrates clearly the affinity of the new taxon to *Pseudoniphargus*. Similar modifications of the body and appendages are found also in other stygobiont amphipods, mainly inhabitants of hyporheic and phreatic waters, e.g., in *Parasalentinella*, *Metacrangonyx*, *Carinurella*, and *Niphargobates*. In *Carinurella* and *Parasalentinella* the morphology is related to its capacity for volvation (rolling into a ball) of the body (Karaman and Ruffo, 1986). In the collections studied of *Parapseudoniphargus* many individuals were strongly curved, but none of these preserved specimens was totally volvated. The characteristic morphology of *Parapseudoniphargus* and the fact that it is recorded only from hyporheic habitats suggest a special adaptation of the animal to ecological conditions related to interstitial life.

Parapseudoniphargus undoubtedly is closely related to *Pseudoniphargus*. The morphological differences between this genus and *Pseudoniphargus* are rather small but consistent. Through recent investiga-

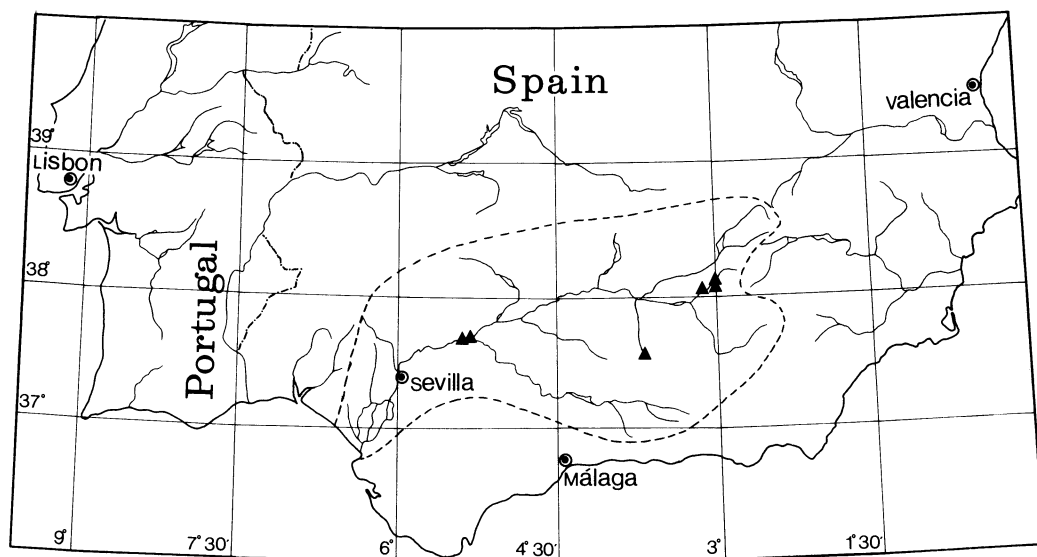


Fig. 1. Map of southern Spain with the watershed of the drainage system of the Guadalquivir River indicated by a broken line. The triangles indicate the localities where *Parapseudoniphargus baetis* was collected.

tions (Stock, 1980; Stock *et al.*, 1986; Notenboom, 1986, 1987a, b; Boutin and Coineau, in press) *Pseudoniphargus* has become a large and well-established genus with 38 described species. This genus has a peri-Mediterranean and amphi-Atlantic distribution. *Parapseudoniphargus* might be considered a "satellite" genus of *Pseudoniphargus*, which means a genus with few species and a limited distribution within the range of the "planet" genus to which it is phylogenetically closely allied. Other such "satellite" genera are, for example, *Carinurella* and *Niphargobates* of *Niphargus*, and *Parasalentinella* of *Salentinella*.

To date, there has been no consensus about the phylogenetic position of *Pseudoniphargus* within the suborder Gammaridea. The discovery of a new genus very closely allied to *Pseudoniphargus* now allows us to develop a hypothesis about the phylogenetic relationships of the *Pseudoniphargus* group.

***Parapseudoniphargus*, new genus**

Diagnosis.—Similar to *Pseudoniphargus* Chevreux, 1901, but body compact and strongly bent; anterior head lobe prominent; coxal plates 1–4 deep, plate 1 ventrally wide, plate 4 with deep posterior excavation; posterior pairs of pereopods not elon-

gate, basis relatively long, pereopod 5 shorter than 4, pereopods 6 and 7 essentially similar; epimeral plates narrow, with oblique posterior margin and pointed pos-

Table 1. Ground-water crustaceans recorded only from the drainage area of the Guadalquivir River (southern Spain). Based on unpublished data, and Bou (1975, and personal communication), Henry (1983), Magniez (1983), Notenboom (1987a), Platvoet (in preparation), and Rouch (1986).

Amphipoda:

Metahadzia sp.

Pseudoniphargus latipes Notenboom.

P. illustris Notenboom

P. cazorlae Notenboom

P. vomeratus Notenboom

P. granadensis Notenboom

P. affinis Notenboom

Salentinella sp.

Parapseudoniphargus baetis, new species

Isopoda:

Stenasellus bragai Magniez

S. escolai Magniez

Proasellus escolai Henry and Magniez

P. espanoli Henry and Magniez

Thermosbaenacea:

Monodella sp.

Harpacticoidea:

Parapseudoleptomesochra almohadensis Rouch

P. almoravidensis Rouch

P. balnearia Rouch

teroverventral corner; basal segment of exopodite of pleopods slightly swollen but not sexually dimorphic; urosome segment 2 rather short; exopodite of uropod 3 short (1.5 times as long as peduncle); no secondary sexual differences.

Remarks.—*Parapseudoniphargus* is undoubtedly very similar to *Pseudoniphargus*. Differences, however, particularly those of the habitus, head, first coxal plate, posterior pereopods, and third uropod justify in my opinion recognition of this new taxon on the generic level.

Type Species.—*Parapseudoniphargus baetis*, new species, by monotypy.

Etymology.—The prefix “para” alludes to the close affinity between the new genus, *Parapseudoniphargus*, and *Pseudoniphargus*.

***Parapseudoniphargus baetis*, new species**

Material Examined.—Province of Jaén, Villacarillo, SBR Río Guadalquivir, near bridge S of Mogón, 03°02'W, 38°04'N, altitude 400 m; 24 January 1984 (Station 84-1/4), 4 ♂♂, 9 ♀♀, and 23 juveniles (paratypes), (ZMA Zoological Museum of Amsterdam collection number, Amph. 108.243); temperature 10.2°C, conductivity 746 μ S/cm, pH 7.37, chlorinity 22 mg/l. Accompanying fauna: *Pseudoniphargus latipes*, *Proasellus*, *Stenasellus*, Cyclopoidea, Ostracoda, Prosobranchia Hydrobioidea, insect larvae, and Oligochaeta.—Prov. Jaén, Villanueva del Arzobispo, SBR Río Guadalquivir, 10 km ENE of Villanueva del Arzobispo, 02°54'W, 38°11'N, alt. 520 m; 24 January 1984 (station 84-1/5), 4 ♂♂, 5 ♀♀, and 19 juveniles (paratypes), (ZMA coll. no. Amph. 108.242); 10.9°C, conductivity 428 μ S/cm, pH 8.30, chlorinity 6 mg/l. Accompanying fauna: *Pseudoniphargus latipes*, *Echinogammarus*, *Proasellus*, Cyclopoidea, Ostracoda, insect larvae, and Oligochaeta.—Prov. Jaén, Santiago de la Espada, Coto Nacional de Cazorla, SBR Río Guadalquivir, 2 km downstream of Cotorrios, 02°50'W, 38°04'N, alt. 650 m; 25 January 1984 (station 84-1/10), 3 ♂♂ and 2 juveniles (paratypes), (ZMA coll. no. Amph. 108.247); 9.6°C, conductivity 412 μ S/cm, pH 7.66, chlorinity 12 mg/l. Accompanying fauna: *Pseudoniphargus latipes*, *Haploginglymus*, *Proasellus*, Ostracoda, insect larvae, Oligochaeta, and Nematoda.—Prov. Sevilla, Peñaflor, SBR Río Retortillo, just downstream of Presa del Retortillo, 05°18'W, 37°45'N, alt. 55 m; 1 July 1985 (station A85-7/2), 1 ♂ holotype, 1 ♀ allotype, 3 ♂♂, 3 ♀♀, and 4 juveniles (paratypes), (ZMA coll. no. Amph. 108.244). Accompanying fauna: *Pseudoniphargus latipes*, *Haploginglymus*, *Proasellus*, *Copidiaptomus numidicus*, Cyclopoidea, Ostracoda, Cladocera, Prosobranchia Hydrobioidea, Diptera larvae, and Oligochaeta.—Prov. Sevilla, Lora del Río, SBR Río Guadalquivir, near bridge in the road C-431, 4.5 km NE of Lora del Río, 05°30'W, 37°41'N, alt. 35

m; 1 July 1985 (station A85-7/3), 1 ♂, 4 ♀♀, and 2 juveniles (paratypes), (ZMA coll. no. Amph. 108.245). Accompanying fauna: *Haploginglymus*, *Proasellus*, Cyclopoidea, Prosobranchia Hydrobioidea, Ephemeroptera, Tricladida, and Oligochaeta.—Prov. Jaén, Carchelejo, SBR Río Guadalquivir, near Ermita de Santa Lucia, 4.5 km SE of Carchelejo, 03°36'W, 37°36'N, alt. 840 m; 21 July 1985 (station A85-7/63), 15 paratypes (ZMA coll. no. Amph. 108.246). Accompanying fauna: *Pseudoniphargus latipes*, *P. illustris*, *Bogidiella*, *Echinogammarus*, *Proasellus*, Microparasellidae, Bathynellidea, Cyclopoidea, Ostracoda, Prosobranchia Hydrobioidea, Ephemeroptera, Diptera larvae, Hirudinea, Nematoda, and Oligochaeta.—Prov. Jaén, Santiago de la Espada, Coto Nacional de Cazorla, SBR Arroyo del Membrillo, 2.2 km SW of Cotorrios, 02°52'W, 38°03'N, alt. 650 m; 28 July 1985 (station A85-7/79), 4 juveniles. Accompanying fauna: *Pseudoniphargus latipes*, *Haploginglymus*, *Proasellus*, Prosobranchia Hydrobioidea, Plecoptera, Diptera larvae, and Oligochaeta.

Description.—Largest male 5.0 mm from Peñaflor, largest female (nonovigerous) 5.1 mm from Villacarillo. Only ovigerous female in the material studied from Peñaflor 5.0 mm, carrying 5 eggs.

Male.—Antenna 1 (Fig. 2c) about half of body length; peduncle poorly setose, segment 1 slightly longer than segment 2; accessory flagellum 2-segmented (terminal segment minute) almost as long as flagellum segment 1; flagellum about 11-segmented, aesthetascs lacking on proximal segments, appearing on distal segments 0.5–0.75 of length of corresponding segments, that on penultimate segment as long as terminal segment. Antenna 2 (Fig. 2d) peduncle slightly longer than that of A1, poorly setose, segments 4 and 5 subequal; flagellum short, 5-segmented, slightly longer than peduncle segment 5.

Head shown in Fig. 2a. Upper lip (Fig. 2e) with rounded apical margin. Mandible (Fig. 2f) lacinia mobilis asymmetrical, left 4-dentate, right lacinia figured in Fig. 2g; palp segment 2 poorly setose, segment 3 very short with 1 or 2 A-setae, 1 or 2 B-setae, about 8 D-setae, and 3 E-setae. Maxilla 1 (Fig. 2h) inner lobe with 2 naked setae, outer lobe with 7 strong spines, 3 inner spines unidenticated, remaining spines smooth, palp reaching slightly beyond the outer lobe, with several simple distal elements, asymmetrical. Both lobes of maxilla 2 (Fig. 2i) with distal armature only, outer lobe widest with 2 separate groups of distal setae, lateral group with longer setae than medial group. Lower lip (Fig. 2b) with well-developed in-

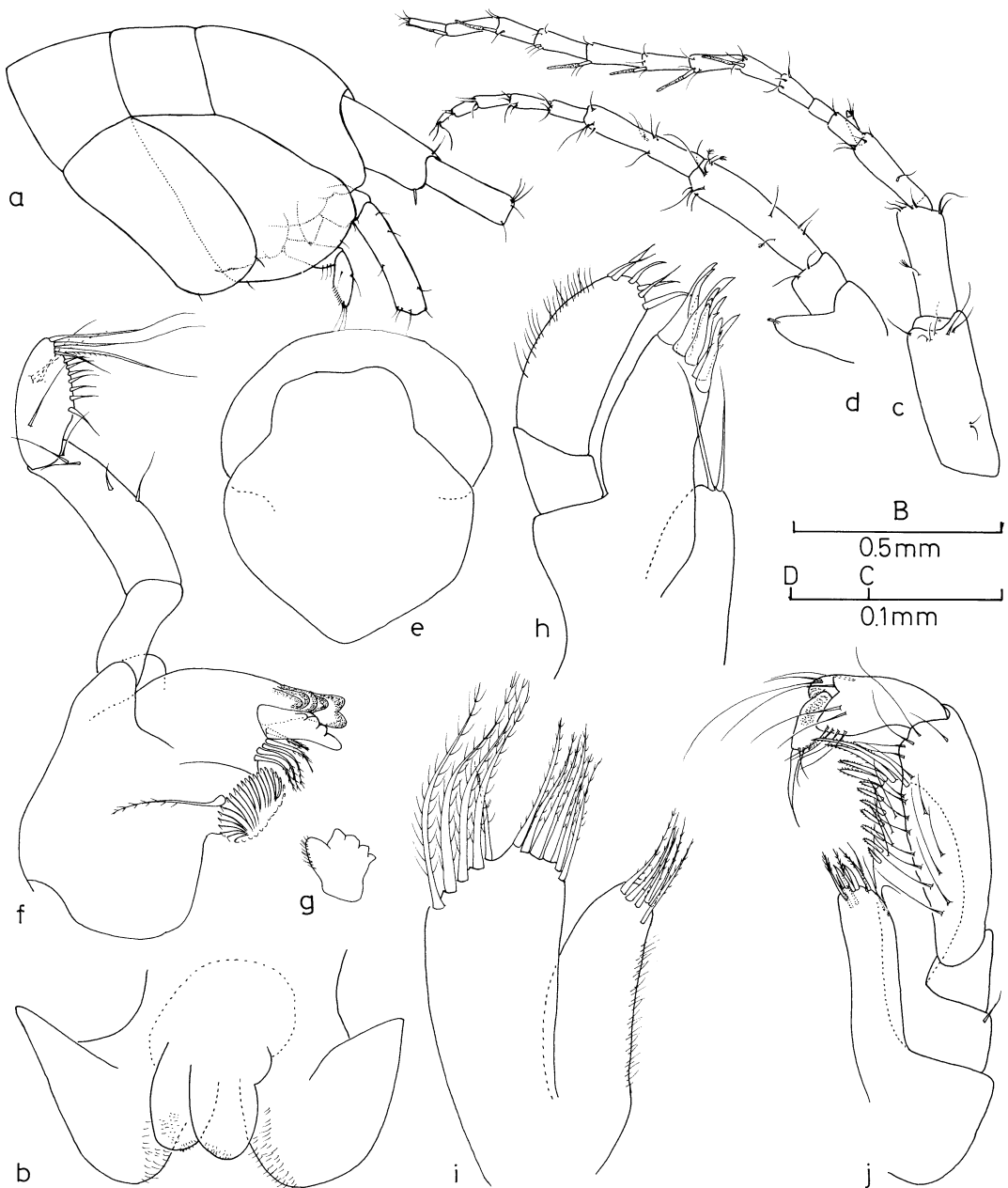


Fig. 2. *Parapseudoniphargus baetis*. Male 4.5 mm from Lora del Río: a, head and anterior pereionites (scale B). Male 5.0 mm from Retortillo: b, lower lip (C). Ovigerous female 5.0 mm same locality: c, first antenna (A, on Fig. 3); d, second antenna (A, on Fig. 3); e, upper lip (C); f, left mandible (C); g, lacinia of right mandible (D); h, maxilla 1 (D); i, maxilla 2 (D); j, maxilliped (C).

ner lobes, outer lobe broad with lateral process tapering. Maxilliped (Fig. 2j) inner lobe slender with distally 2 smooth spines and 3 short plumose setae, 1 distolateral slender simple seta, and 2 subapical simple setae; outer lobe reaching up to 0.8 of length

of palp segment 2, with along medial margin row of blunt spines and submarginally row of setae; palp with slender claw.

Gnathopod 1 (Fig. 3a) coxal plate deep and ventrally widened (Fig. 2a), with few setules on ventral margin; carpus as long as

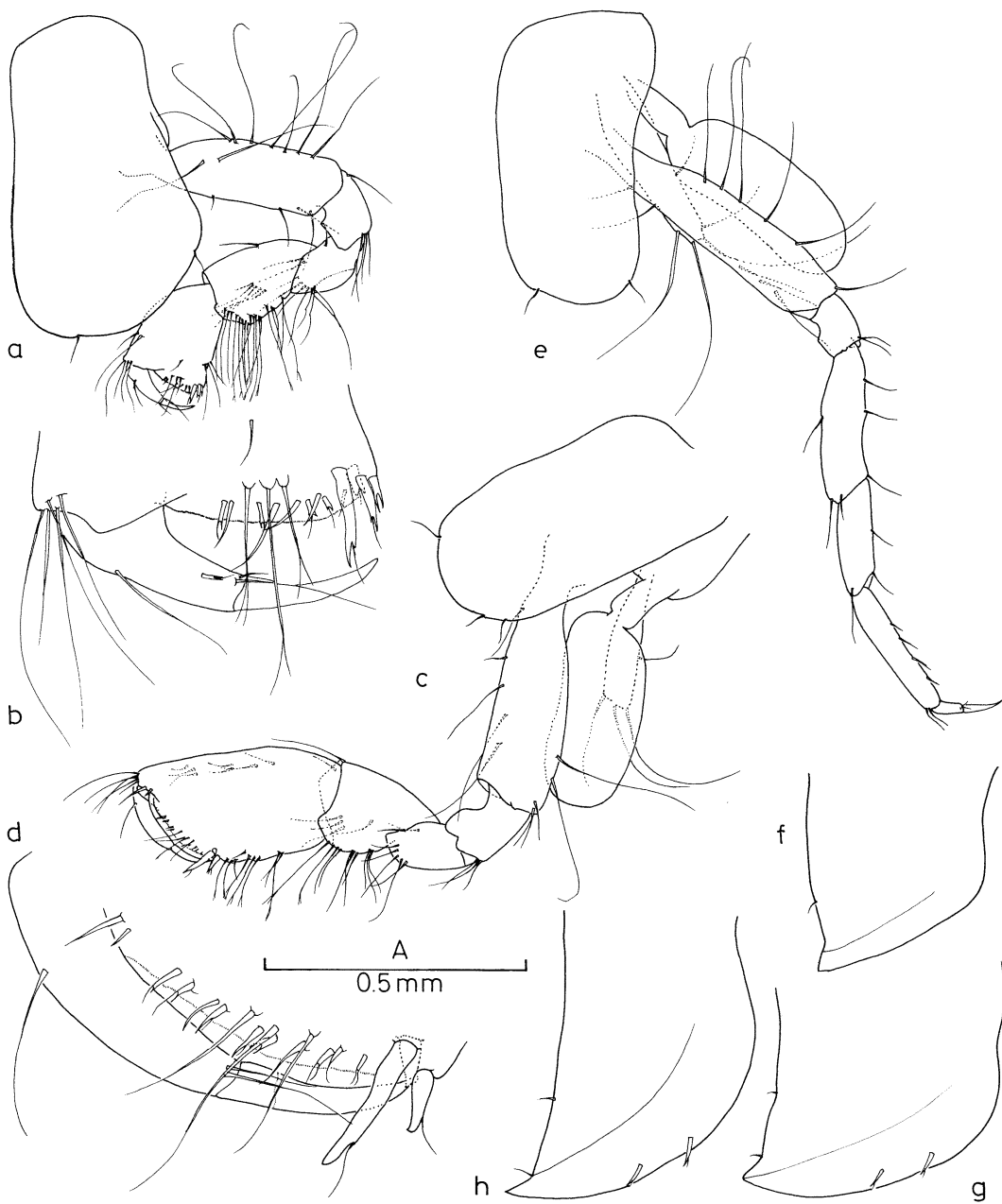


Fig. 3. *Parapseudoniphargus baetis*. Ovigerous female 5.0 mm from Retortillo: a, gnathopod 1 (scale A); b, detail of palmar margin of gnathopod 1 (D); c, gnathopod 2 (A); d, detail of palmar margin of gnathopod 2 (D); e, pereopod 3 (A). Male 5.0 mm, same locality: f, epimer 1 (A); g, epimer 2 (A); h, epimer 3 (A).

propodus, with 4 rows of posterior setae; propodus slightly longer than wide, posterior margin with 1 small group of setae; palm (Fig. 3b) slightly convex, defining angle with 4 unequal bifid spines; ungulus as long as dactylus. Gnathopod 2 (Fig. 3c) coxal plate narrow, twice as deep as wide, ventral mar-

gin with 3 setae; carpus shorter than in Gn1, with 3 posterior groups of setae, propodus subrectangular, palm short, slightly oblique, defining angle (Fig. 3d) with 3 setule-tipped spines (1 longer); ungulus slightly longer than half of dactylus.

Pereopod 3 (Fig. 3e) coxal plate twice as

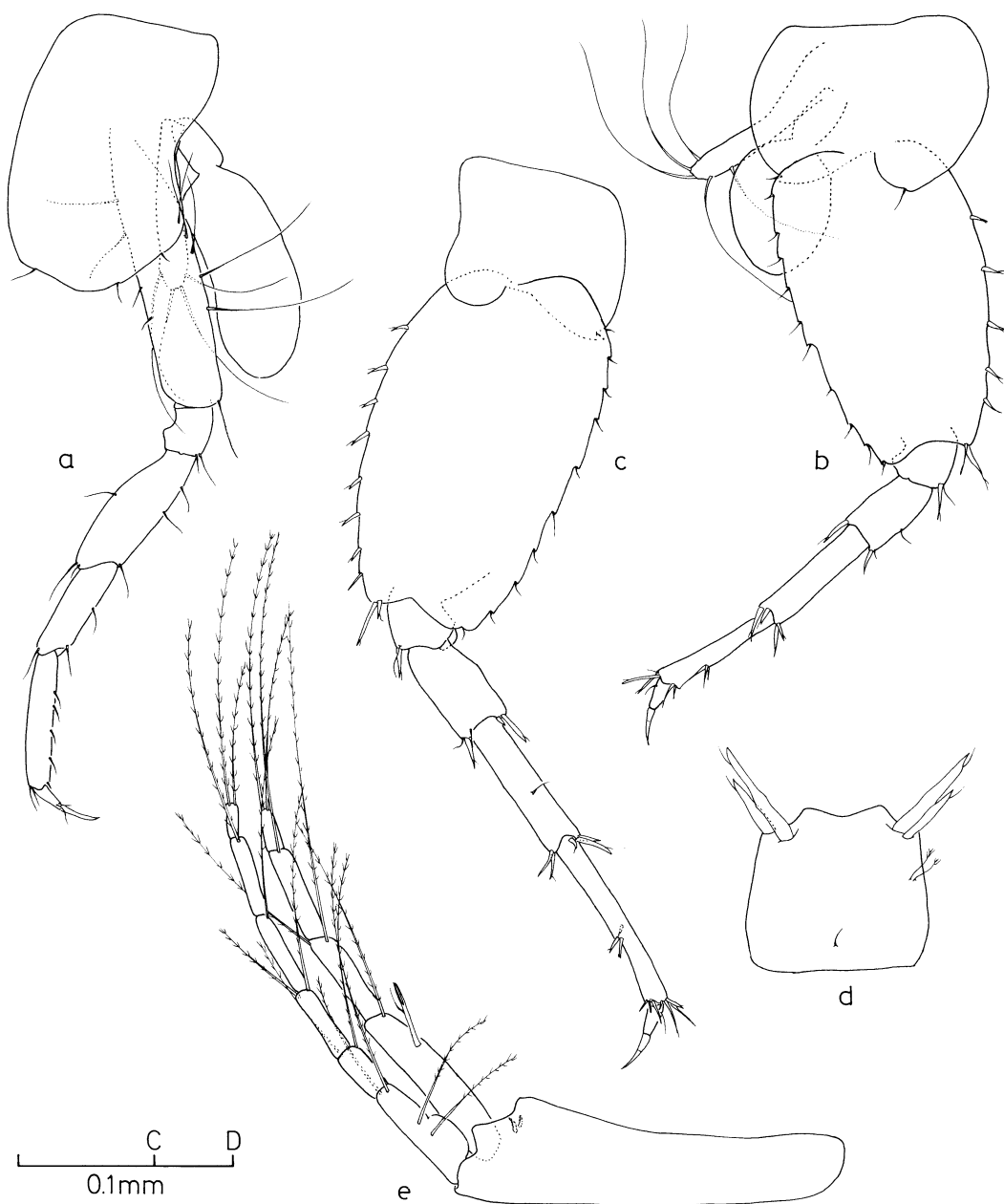


Fig. 4. *Parapseudoniphargus baetis*. Ovigerous female 5.0 mm from Retortillo: a, pereiopod 4 (scale A); b, pereiopod 5 (A); c, pereiopod 6 (A); d, telson (C). Male 5.0 mm, same locality: e, pleopod 3 (D).

deep as wide, with an antero- and postero-ventral seta. Pereiopod 4 (Fig. 4a) coxal plate deep, with well-developed posterior excavation and 3 separate setae on lower margin. Pereiopods 3 and 4 otherwise similar, with slender distal segments, posterior margin of propodus with 4 setules, and ungulus as long as dactylus. Pereiopod 5 (Fig. 4b) shorter

than P4, coxal plate bilobed, slightly wider than deep, with anterior lobe slightly deeper than posterior lobe, latter with small posteroventral tooth; basis ovoid, narrowing distally, anterior margin with 5 spinules, posterior lobe well developed and slightly overhanging; posterior margin crenulated, with approximately 10 setules; merus short,

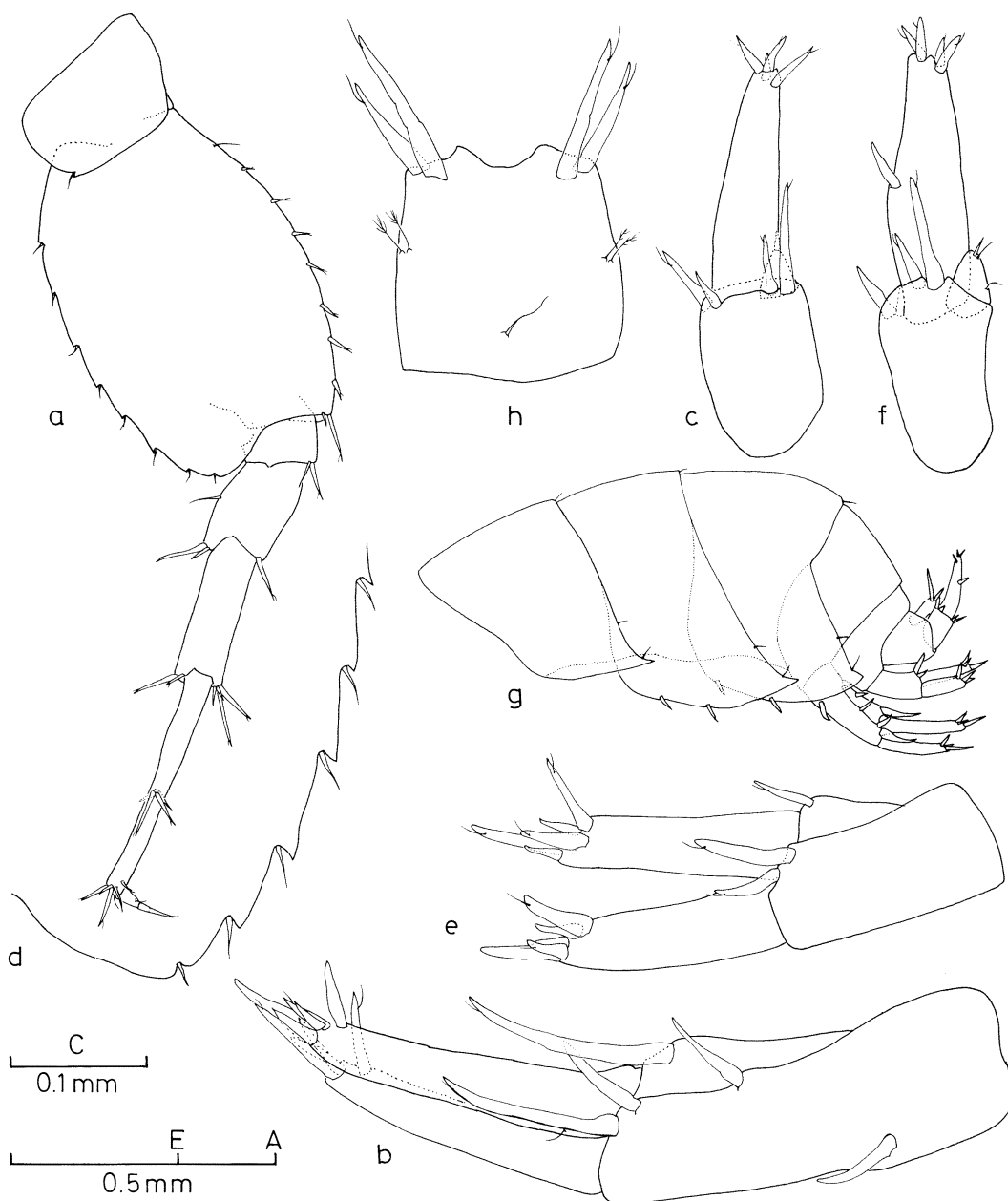


Fig. 5. *Parapseudoniphargus baetis*. Ovigerous female 5.0 mm from Retortillo: a, pereiopod 7 (scale A); b, uropod 1 (C); c, uropod 3 (C). Male 5.0 mm, same locality: d, detail of posterodistal margin of basis of pereiopod 7 (C); e, uropod 2 (C); f, uropod 3 (C). Male 4.5 mm from Lora del Río: g, posterior part of body (E). Female 4.9 mm from Carchelejo: h, telson (C).

carpus and propodus subequal, with few distal spines, propodus with 1 group of small anterior spines and few longer distal spines; ungulus as long as dactylus. Pereiopod 6 (Fig. 4c) slightly longer than P5, coxal plate bilobed, anterior lobe as deep as posterior lobe, latter with small tooth; basis ovoid,

longer than that of P5 and P7, anterior margin with 8 spinules, posterior lobe well developed and overhanging, posterior margin crenulated with about 10 setules; propodus longest segment, armature of distal segments similar to P5. Pereiopod 7 (Fig. 5a) about as long as P6, coxal plate shallow,

nonlobate, with small posteroventral tooth; basis wider than in P5 and P6, anterior margin with 7 spinules and 1 proximal setule, posterior lobe strongly developed and overhanging, posterior margin (Fig. 5d) more clearly crenulated than in P5 and P6; propodus longest segment, armature similar to previous pereopods. Coxal gills present on P2–P6, sacklike and pedunculated.

Epimera (Figs. 3f–h; 5g) plate 2 wider than plates 1 and 3; ventral margin of plate 1 rather straight and unarmed, that of plates 2 and 3 convex with 2 spines; posteroventral corner slightly produced; posterior margin straight and oblique with 2 setules. Pleopods (Fig. 4e) peduncle slender with 2 pinetree-shaped (conical with small barbs along margins) retinacula, other armature lacking; rami with 4–6 segments, slender, elongate, segment 1 of endopodite with 1 distally split seta, remaining setae of rami plumose, basal segment of exopodite medially slightly swollen.

Uropod 1 (Figs. 5b, g) peduncle slightly longer than endopodite with strong basoventral spine, 1 strong dorsal spine, long mediodistal spine, reaching up to half length of endopodite, and 2 laterodistal spines, longest exceeding half length of exopodite; exopodite shorter than endopodite, both with unarmed margins. Uropod 2 (Figs. 5e, g) peduncle with 1 + 2 distal spines only; margins of rami unarmed. Uropod 3 (Figs. 5c, f, g) peduncle with 1 rather long, and 3 or 4 shorter distal spines; endopodite scalelike with 1 or 2 short terminal spinules; 1-segmented exopodite short, about 1.5 times as long as peduncle, slightly tapering, marginal armature lacking or restricted to 1 group of 2 spines on either side.

Telson (Figs. 4d, 5h) subquadrate or slightly longer than wide; 2 subterminal spines on either side (medial one slightly longer); distal emargination hardly developed or shallow or wide.

Female.—Oostegites on P2–P5, linear with up to 7 setae in P3. Peduncle of coxal gills slightly longer than in male. Remaining characters as in male.

Etymology.—The name *baetis* was used in ancient times for the Guadalquivir River, and alludes to the geographic distribution of the new species.

PHYLOGENETIC CONSIDERATIONS

The phyletic classification of gammaridean amphipods is a subject of much controversy (see, e.g., Bousfield, 1978; Barnard and Karaman, 1980). The genus *Pseudoniphargus*, sister group of *Parapseudoniphargus*, might serve as an example of an amphipod genus of which the taxonomic position at higher levels is problematical. Table 2 shows the gammaridean groupings to which it is considered to be most closely related according to different authors. From this table it can be concluded that there is no consensus about a family or superfamily grouping to which *Pseudoniphargus* belongs. Such difficulties are rather common, in particular among the genera and families of stygobiont amphipods that do not have obviously related marine or fresh-water groupings (see, e.g., Karaman and Ruffo [1986] on the *Niphargus* group; Ruffo [1986a] on the *Metacrangonyx* group; and Ruffo (1986b) on the Salentinellidae.)

In this paper relationships (see Table 2) of *Pseudoniphargus* with *Allocrangonyx*, Niphargidae, *Allomelita*, and the Hadzioidea will be discussed, suggesting that the most plausible phylogenetic position of the *Pseudoniphargus* group is as sister group of *Allomelita* within the Hadzioidea.

The alleged, but superficial, similarity between *Allocrangonyx* and *Pseudoniphargus* strongly influenced Bousfield's opinion about the phyletic classification of *Pseudoniphargus*. Important similarities between those two genera are: (1) weakly armed inner lobe of maxilla 1; (2) outer lobe of maxilla 2 with 2 separate distal groups of setae and no facial armature; (3) propodus of gnathopod 1 subrectangular and smaller than propodus of gnathopod 2; and (4) presence of distally notched spines on palmar margins of both gnathopods.

The North American stygobiont genus *Allocrangonyx* itself is an enigmatic genus with some elements of its morphology resembling both *Crangonyx* and *Niphargus* (Holsinger, 1971). The genus exhibits a number of characters by which it strongly deviates from *Pseudoniphargus*: (1) strongly setose mandible palp segments 2 and 3; (2) bilobed coxal gill 2; (3) dactylus of posterior pereopods with spine groups on ventral and dorsal margins; (4) serial spines on rami of

uropods 1 and 2; and (5) 2-segmented exopodite of uropod 3 provided with plumose setae, and secondarily segmented in mature males. Similarities between *Pseudoniphargus* and *Allocrangonyx* are presumed to be the result of convergence due to colonization of subterranean waters and acquisition of adaptive characters. Weak relationships between *Allocrangonyx* and *Pseudoniphargus* were previously alluded to by Stock (1980) and Barnard and Karaman (1980), although hardly discussed.

Another suggested affinity of *Pseudoniphargus* is with the large European genus *Niphargus* and related genera. However, although the name *Pseudoniphargus* might indicate such a relationship, the two genera are essentially different, above all in gnathopods, urosome, and uropods. In contrast to *Pseudoniphargus*, *Niphargus* exhibits: (1) terminal segment of mandible palp well provided with setae (often in rows); (2) no distinct groups of setae on distal margin of outer lobe of maxilla 2; (3) gnathopods 1 and 2 subsimilar in shape and ornamentation; (4) absence of pubescent lobe on merus of gnathopod 1 (as other pubescent surfaces on gnathopods); (5) ventral margin of dactylus of posterior pereopods sometimes with spinules; (6) urosome segments 1 and 2 with dorsal spines; (7) presence of ecdysial spine on prepeduncle of uropod 1; and (8) plumose setae sometimes present on exopodite of uropod 3.

Stock (1984) erected a monotypic genus, *Allomelita*, to encompass the species *Melita pellucida* Sars, 1882. In his opinion, separate generic status of this species was justified by a number of characters in which it resembles *Pseudoniphargus* more than *Melita*. According to Stock (1984) and my personal observations, similarities between *Pseudoniphargus* and *Allomelita* are seen in: (1) relative lengths of peduncle and flagellum articles in and between both antennae; (2) shallow antennal sinus; (3) all mouthparts, but in particular arrangement of setae on maxilla 2; (4) pubescent posterior lobe on merus of gnathopod 1; (5) shape of propodus of gnathopods 1 and 2, and armature on palm of gnathopod 1; (6) pedunculated, sacklike coxal gills; (7) shape and ornamentation of uropods 1 and 2; (8) sexual differences in length of exopodite of uropod 3; and (9) fused telson lobes.

However, despite some striking similarities, *Allomelita* possesses a number of features not found within the *Pseudoniphargus* group, such as (1) pigmented ommatidia, (2) strong sexual differences in armature of palmar margin of gnathopod 2, (3) inner margin of dactylus of gnathopod 2 toothed, (4) peduncle of pleopods with row of lateral setae, and (5) both setae and spines on rami of uropod 3. *Allomelita pellucida* occurs along the east Atlantic coast from Norway to Portugal; it is a benthic, epibenthic, and interstitial species of brackish waters of estuaries. Stock (1984) described the occurrence of the species in intertidal sediments, 0.5–1.0 m below the beach surface, at a place where a fresh spring rises. This habitat is characterized by brutal changes in salinity depending on the tides.

The similarities between the *Pseudoniphargus* group and *Allomelita*, which are for the most part based on mouthparts, gnathopods, and urosome, are considered to be rather strong indications of their close phylogenetic relationship. These genera are characterized by: (1) slender mandible palp; (2) reduced setation of maxillae; (3) well-developed inner lobe of lower lip; (4) gnathopod 2 larger, and of different form and armature than gnathopod 1, and with slight tendency to be enlarged in the male of some species; (5) gnathopods with well-demarcated palmar angle with obvious group of bifid spines on gnathopod 1; (6) merus of gnathopod 1 with pubescent posterior lobe; (7) exopodite of uropod 3 linear and with reduced setation; and (8) coxal gills on pereopods 2–6 sacklike and pedunculated. These diagnostic features fit rather well within the concept of the Hadzioidea (=synonym of Melitoidea), a superfamily established by Bousfield (1977) but formerly considered part of the Gammaridae sensu lato. Moreover, placement of the *Pseudoniphargus* group within the Gammaridae sensu stricto is less convincing because the genus *Gammarus* and allied genera differ considerably from *Allomelita* and the *Pseudoniphargus* group (see diagnosis of the Gammaroidea in Bousfield, 1982).

The superfamily Hadzioidea is composed of two important families: the Hadziidae S. Karaman, 1932, and Melitidae Bousfield, 1973. The monophyly of the superfamily has not yet been clearly demonstrated and

Table 2. Affinity and systematic position of the genus *Pseudoniphargus* as proposed by different authors.

Barnard, 1976, p. 425	Hadzioidea, Pseudoniphargidae (containing <i>Pseudoniphargus</i> only)
Bousfield, 1977, p. 304	Niphargoidea, family group 2 (containing <i>Pseudoniphargus</i> and <i>Allocrangonyx</i> Schellenberg, 1938)
Karaman, 1978a	Gammaridae
Bousfield, 1978, p. 361	Niphargoidea, <i>Pseudoniphargus</i> - <i>Allocrangonyx</i> complex?
Barnard and Karaman, 1980, p. 13	Melitidae
Stock, 1980, p. 115	Gammaridae (sensu lato)
Bousfield, 1982, p. 263	Crangonyctoidea, <i>Allocrangonyx</i> group (containing <i>Allocrangonyx</i> and <i>Pseudoniphargus</i>)
Karaman, 1982, p. 354	Gammaridae (sensu lato)
Barnard and Barnard,* 1983, p. 685	Hadzioids, pseudoniphargids
Stock, 1984, p. 97	Gammaridae (sensu lato), closely allied to <i>Allomelita pellucida</i> (Sars, 1882)
Stock, 1986, p. 510	Melitid grouping (Melitidae sensu Bousfield, 1973, emend.)

* The diagnosis of *Pseudoniphargus* by these authors is based on a wrong interpretation of uropod 3.

intergrading genera with the superfamily Gammaroidea are described. The Melitidae are global in distribution and exclusively marine and brackish, epigean, epifaunal, or epibenthic. The family Hadziidae occurs in the Caribbean (including Texas and Central America), Mediterranean, and Indo-Pacific regions; its members are hypogean, occurring in phreatic and karstic ground waters, brackish wells, and coastal marine seeps (Bousfield, 1982). A para- or polyphyletic origin of the Hadziidae cannot be excluded because their monophyly is not proved. Some authors consider the Hadziidae to be of melitid facies which invaded continental ground waters (Barnard and Barnard, 1983; Stock, personal communication). Owing to these difficulties, the affinity of the Hadziidae with the *Pseudoniphargus* group will not be discussed further. Of greater importance is that the *Pseudoniphargus* group appears to be more closely related to the Hadzioidea than to the other superfamily groupings of the Gammaridae.

Within the group of hadzioid genera the *Pseudoniphargus* group closely resembles the *Eriopisa*-*Eriopisella* group and some species of *Melita*, e.g., *M. bulla* G. Karaman, 1978, and *M. valesi* S. Karaman, 1955 (see Karaman, 1978b). These taxa exhibit: (1) a tendency towards reduction of setation of the maxillae; (2) a well-developed inner lobe of the lower lip; (3) a pubescent posterior lobe on the merus of gnathopod 1; (4) gnathopod 2 slightly stronger in male than in female; (5) uropod 3 unequally biramous; and (6) telson lobes variously fused.

The hypothetical phylogenetic relation-

ships among the genera under consideration are presented in the cladogram of Fig. 6. The character state polarities are assigned through comparison with the outgroups x and y. Rules for uncertain outgroup relationships as established by Maddison *et al.* (1984) are used for assessment on the outgroup node (see Fig. 6). The dashed lines of the lower branches of the cladogram indicate unresolved clusters of terminal taxa.

Allomelita is considered to be a phylogenetically (and ecologically) intermediate form between marine benthic and continental ground-water taxa. The ancestor of the *Pseudoniphargus* group is presumed to have adapted to interstitial conditions along the coast, from where *Parapseudoniphargus* colonized interstitial waters related to river alluvia, and *Pseudoniphargus* colonized a wider range of ground-water habitats, including phreatic and karst aquifers.

DISCUSSION

The proposed hypothesis about the phyletic position of the *Pseudoniphargus* group presented here needs further evidence. The synapomorphic characters (numbers 4–7 in Fig. 6) of the *Allomelita*-*Pseudoniphargus* group are based on the fusion of telson lobes, and reductions in the setation of the maxillae and of the terminal exopodite segment of uropod 3. None of these character states is unique for this group because they are found in other amphipod taxa as well. Another weakness in the analysis is the uncertain outgroup relationships. In a wider context the monophyly of the Hadzioidea,

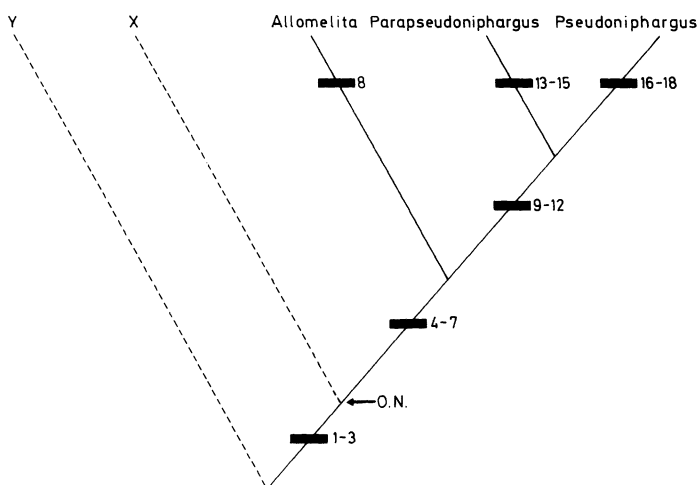


Fig. 6. Cladogram of hypothesized phylogenetic relationships of the new genus *Parapseudoniphargus*. X is an unresolved cluster of the *Eriopisa-Eriopisella* group, and Y of *Melita* sensu stricto and related genera, respectively. Dashed lines indicate uncertain outgroup relationships. The outgroup node (O.N.) of the *Allomelita-Pseudoniphargus* ingroup is indicated by an arrow. Characters used (apomorphic states only): 1, tendency to reduction of setae on maxillae; 2, pubescent posterior lobe on merus of gnathopod 1; 3, weakly developed sexual dimorphism in gnathopod 2; 4, medial setae on inner lobe of maxilla 1 totally lacking; 5, medial and facial setae lacking on inner lobe of maxilla 2; 6, 1-segmented exopodite of uropod 3; 7, basal part of telson lobes fused; 8, accessory flagellum 1-segmented; 9, maxilla 2 with 7 distal spines; 10, armature of palmar margin of gnathopod 2 similar in both sexes; 11, posterior pereopods and uropod 3 without setae; 12, telson lobes more than three-fourths fused; 13, body compressed and strongly curved; 14, posterior pereopods short; 15, exopodite of uropod 3 pygidized; 16, anterior head lobe weakly developed; 17, coxal plate 1 with subparallel margins; and 18, tendency to (strong) elongation of peduncle and exopodite of uropod 3.

to which the group under study is proposed to belong, has not been satisfactorily proved and their multiple origin cannot be excluded. Furthermore, there is insufficient knowledge about the phylogenetic relationships of generic groupings within the Hadzioidea.

A general tendency in stygobiont amphipods is that they show structural reductions and troglomorphic characters (Culver and Fong, 1986). These modifications are linked with the life in energy-poor, hypogean habitats, and are seen in many other stygobiont and troglobiont animals as well. Well-known structural reductions are the reduced or absent eyes and pigment. Perhaps the reductions, especially in armature of mouthparts, in coxal plates, and in pleopods, which many stygobiont amphipods show, should be seen in the same light. Lengthening of the posterior pereopods, of the peduncle and exopodite of the third uropod, and the general appearance of fragility might be considered as a set of troglomorphic characters, and there are likely more of them. According to Culver and Fong (1986) "cave" dependent characters, which evolved independently in the hypogean members of different groups,

cannot be considered as synapomorphies. Only within monophyletic groups clearly defined on "cave" independent characters can structural reductions and troglomorphic characters be autapomorphies. This implies that such "cave" dependent, homoplastic characters may have only a restricted use in phylogenetic studies and that the morphology of the animal must be well understood in order to recognize homologies.

Amphipods, particularly stygobiont species, are not a group of animals in which phylogenetic relationships are easily resolved. An important reason for proceeding, despite these problems, is that they appear to be good candidates for zoogeographic studies (Holsinger, 1986). Amphipods are one of the most successful groups of animals in the colonization of subterranean waters. They show interesting patterns of distribution in which historical geological events probably had great influence.

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