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Article in *Bijdragen tot de Dierkunde* · January 1997

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***Parastenocaris hispanica* n. sp. (Copepoda: Harpacticoida: Parastenocarididae) from hyporheic groundwaters in Spain and its phylogenetic position within the *fontinalis*-group of species**

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Keywords: Harpacticoida, *Parastenocaris hispanica*, new species, *fontinalis*-group, *Fontinalicaris*, taxonomy, phylogeny, zoogeography

Abstract

Parastenocaris hispanica n. sp. is described from hyporheic groundwaters in Spain. The phylogenetic position of the new species within the *fontinalis*-group Lang is discussed. As a result *P. fontinalis meridionalis* Rouch is elevated to species rank. The *fontinalis*-group is characterized by six autapomorphic characters.

Resumen

Se describe una nueva especie, *Parastenocaris hispanica* sp. n., de aguas subterráneas de España y se discute su posición filogenética dentro del grupo-*fontinalis* Lang. Como resultado, *P. fontinalis meridionalis* Rouch debe ser elevado a categoría de especie. El grupo-*fontinalis* está caracterizado por seis autapomorfias.

Introduction

Very little is known about the Parastenocarididae inhabiting the groundwaters of the Iberian Peninsula. Three papers have been published previously: Chappuis (1937) described two new species from caves in Santander (northern Spain), Enckell (1965) found two new species in the river Fuen-girola (Andalucía, southern Spain) and Noodt & Galhano (1969) studied the groundwater fauna of northern Portugal and described five new *Paraste-nocaris* species. During an intensive study of the freshwater harpacticoid fauna of the Iberian Peninsula, eight additional Parastenocarididae have been found, four of them new to science. One of these new species belongs to the *fontinalis*-

group (Lang, 1948) and is described here in the first of a series of contributions to the systematics of Iberian Parastenocarididae.

The phylogenetic relationships within the Parastenocarididae are still uncertain. The genus *Parastenocaris* is without doubt polyphyletic (Schminke, 1993). Discussions about affinities of the known species are based on the assignment of these species to different “phyletic” groups (Lang, 1948). In order to elucidate the phylogenetic position of the newly discovered species, the *fontinalis*-group is characterized and phylogenetically analysed applying the methods of phylogenetic systematics as defined by Hennig (1982).

Methods

Groundwater samples were taken by the Karaman-Chappuis method (Chappuis, 1942) in Spanish rivers, filtered through a nylon net of 100 µm mesh and preserved in 5% formaldehyde. Additional samples were kindly made available by Dr. Rouch (Saint-Girons, France). These samples were taken in Spanish rivers by Dr. R. Rouch, Dr. F. Lescher-Moutoué and Dr. N. Goubault in the years 1976 and 1978. The specimens were transferred to a medium consisting of a mixture of lactic acid and glycerine gelatine and dissected for slide preparation. The figures have been prepared with a Leitz Dialux phase contrast microscope using a camera lucida.

Abbreviations used in the text and figures are: A1 = antennule, A2 = antenna, ap = apomorphy, Ae = aesthetasc, Md = mandible, Mx1 = maxillule, Mx2 = maxilla, Mxp = maxillipede, P1–P6 = legs 1 to 6, pl = plesiomorphy.

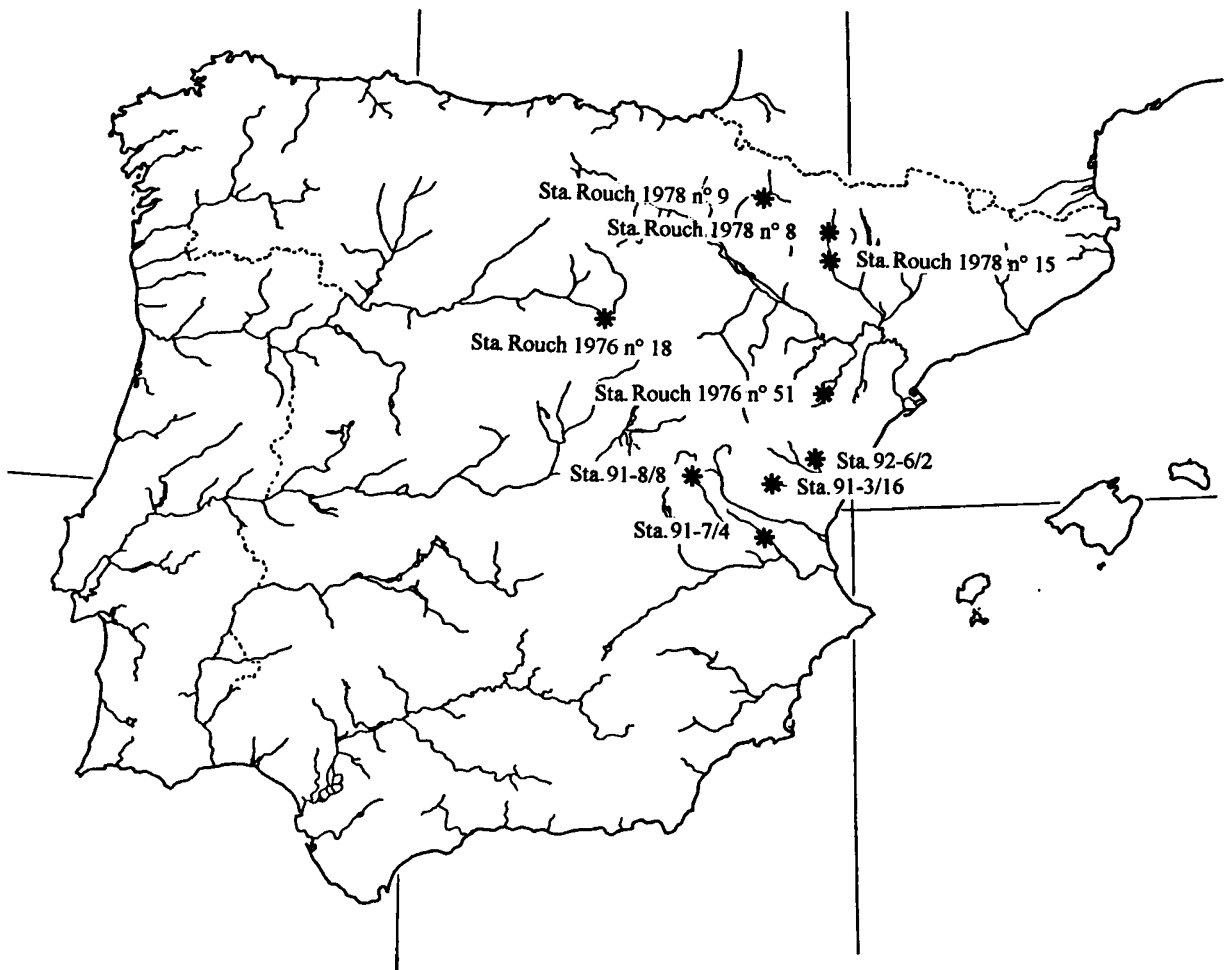


Fig. 1. Map of the Iberian Peninsula with stations where *P. hispanica* n. sp. has been found indicated by an asterisk.

The terms “pars incisiva”, “pars molaris”, and “lacina mobilis” are omitted from the description of the mandible (Mielke, 1984); the terms “furca” and “telson” are used according to Schminke (1976a); terms of the phylogenetic analysis are used sensu Hennig (1982). The cladogram was made by hand using the so-called “Hennigian principle” (cf. Meier, 1992).

Descriptive part

Family Parastenocarididae Chappuis, 1933

Parastenocaris hispanica n. sp.

Material. – Sta. 91-3/16: River Maimona, near bridge at road CS-V-2002, Mas del Molino at Villanueva de Viver (CS), Prov. Teruel, Spain; 4 m from shore, water temp. 11°C, 8 ♂♂ and 11 ♀♀, 28.3.'91.

Sta. 91-7/4: River Magro, between Macastre and Casas de Millas, Prov. Valencia, Spain; 4 m from shore, water temp. 22°C, > 50 individuals, 10.7.'91.

Sta. 91-8/8: River Cabriel at Las Hondonadas, between El Cañigral and Salvacañete, Prov. Cuenca, Spain (type locality), spring at shore, water temp. 16°C, 15 ♂♂, 26 ♀♀ and 2 copepodids, 24.8.'91.

Sta. 92-6/2: River Argelita at Fuente de los Ignacios, Argelita, Prov. Castellón, Spain; 1 m from shore; > 20 individuals, 15.6.'92.

Sta. Rouch 1976, n° 18: Well between Velamazán and Barca, road Soria-C116, Prov. Soria, Spain; 1 ♂ and 1 ♀, leg. R. Rouch, 13.9.'76.

Sta. Rouch 1976, n° 51: River Guadalupe at Mas de las Matas, Prov. Teruel, Spain; 2 ♂♂ and 1 ♀, leg. R. Rouch, 21.9.'76.

Sta. Rouch 1978, n° 9: River Guarga, road C136 at Sabiñánigo, Pito de Momepos, Prov. Huesca, Spain; 2 ♂♂ and 3 ♀♀, leg. R. Rouch, 14.09.'78.

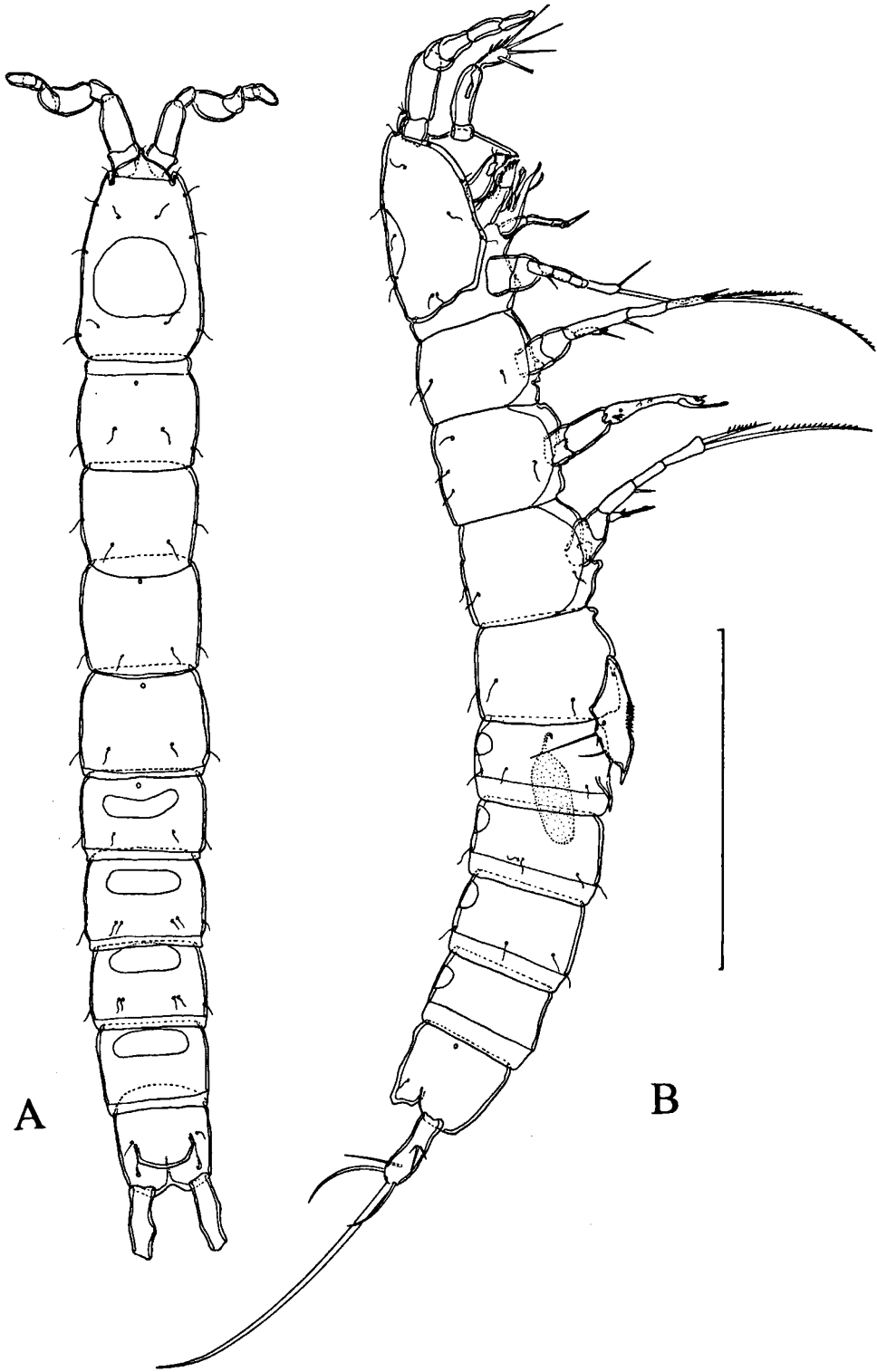


Fig. 2. *Parastenocaris hispanica* n. sp., male habitus: A, dorsal view; B, lateral view. Scale bar 100 μ m.

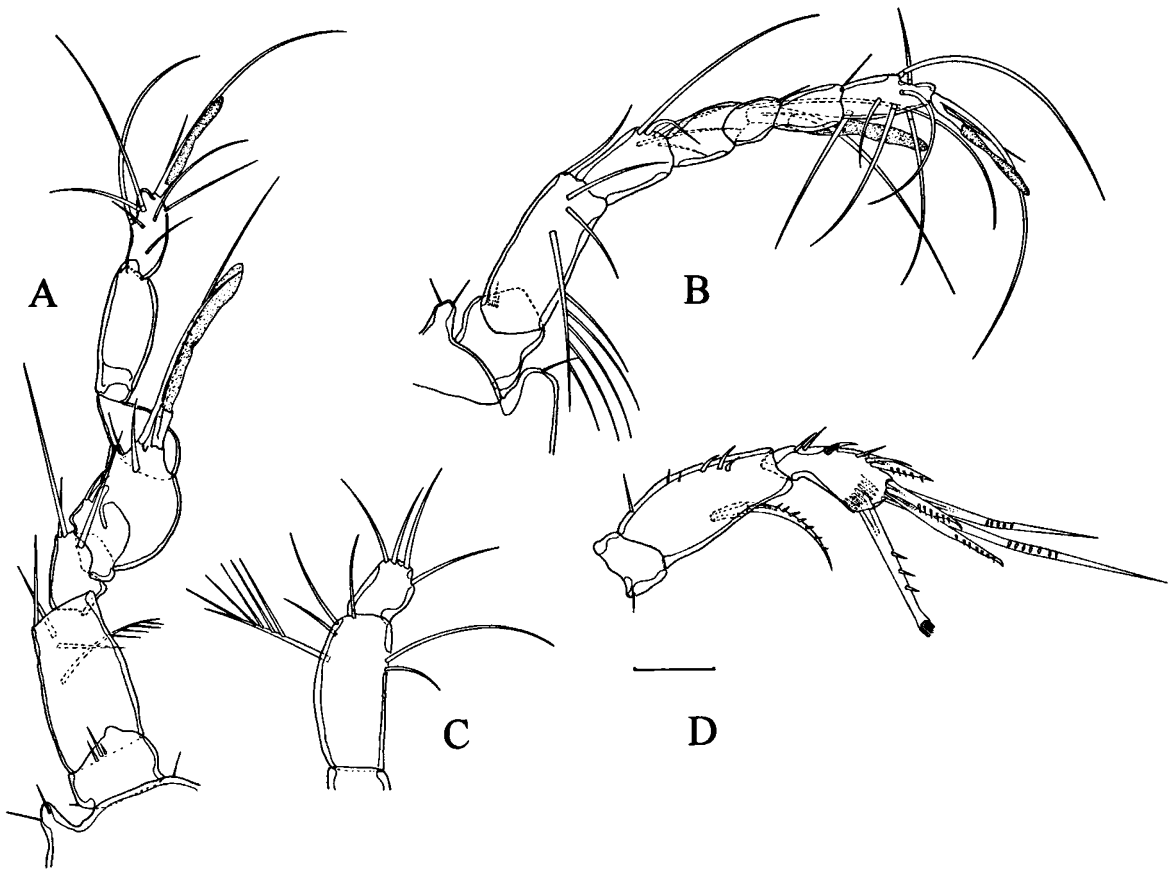


Fig. 3. *Parastenocaris hispanica* n. sp.: A, male antennule; B, female antennule; C, proximal segments of left male antennule; D, antenna. Scale bar 10 μ m.

Sta. Rouch 1978, n° 15: River Alcanadre, road M240 between Angües and Ponzano, Prov. Huesca, Spain; 8 σ and 8 \varnothing , leg. R. Rouch, 14.9.'78.

Sta. Rouch 1978, n° 8: River Alcanadre at Bierge, Prov. Huesca, Spain; 1 σ , 2 \varnothing and 2 copepodids, leg. R. Rouch, 13.9.'78.

Sta. Rouch 1978, n° 8bis: River Alcanadre at Bierge, Prov. Huesca, Spain; 1 σ , leg. R. Rouch, 13.9.'78.

The material is stored at the Copepod collection of the Arbeitsgruppe Zoomorphologie, University of Oldenburg, Germany. The type material examined for the description below (from Sta. 91-8/8) consists of 1 dissected σ (holotype, Coll. No. 1996.22/1–1996.22/4) and 1 dissected \varnothing (allotype, Coll. No. 1996.23/1–1996.23/4), each mounted on 4 slides.

Distribution. – Northeastern Spain, from the Pyrenees to Valencia, in the river systems of Ebro, Mijares and Júcar. Also at the river Duero on the Iberian Plateau (Meseta). This river flows into the Atlantic in north Portugal, so that the species may have a wider westerly distribution. Fig. 1 shows

the localities where *Parastenocaris hispanica* n. sp. has been found. The type locality is Sta. 91-8/8, river Cabriel at Salvacañete, Prov. Cuenca, Spain.

Description of holotype and allotype. – Length 380 μ m (from rostrum to operculum). Rostrum with large base and two sensillae on tip. Cephalothorax and abdominal segments 1–4 with dorsal “windows” (Fig. 2A). For sensillae on tergites see Fig. 2A–B. Operculum convex (Fig. 6C). Furca (Fig. 7A) with 7 setae, all 3 anterolateral setae located in first third of ramus.

Male: A1 (Fig. 3A, C) 8-segmented, prehensile, number of setae starting at proximal segment: 0/6/4/2/4+Ae/0/0/9+Ae. A2 with allobasis and 1-segmented exopod carrying 1 pinnate seta (Fig. 3D). Distal endopod segment with 7 setae (2 of them

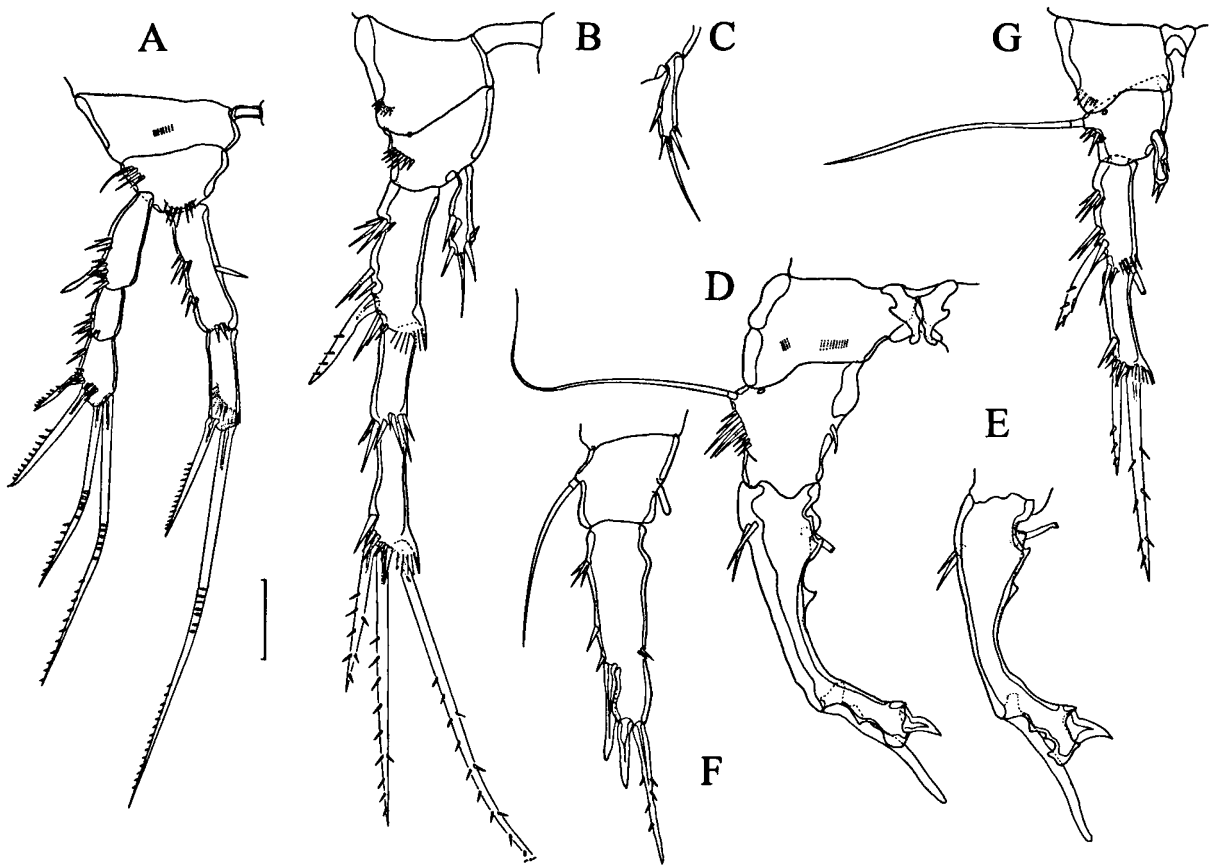


Fig. 4. *Parastenocaris hispanica* n. sp.: A, male pereopod 1; B, male pereopod 2; C, female endopod 2; D, male pereopod 3; E, male pereopod 3 from sta. Rouch 1978 n° 8; F, male pereopod 3 copepodid V; G, female pereopod 3. Scale bar 10 µm.

geniculate) and hyaline frill. Md with 1-segmented palp (Fig. 6D) carrying 2 setae. Mx1 (Fig. 7D), precoxal arthrite with 5 setae (1 dorsal surface seta, 3 claw-like pinnate setae and 1 slender seta), coxa with 1 seta, basis with 3 setae. Mx2 (Fig. 7C) syncoxa with 2 endites, proximal endite with 1, distal one with 3 setae, basis with strong apical pinnate claw, endopod represented by 2 setae, exopod absent. Mxp 3-segmented (Fig. 6E), distal segment with 1 seta.

P1 (Fig. 4A) with 3-segmented exopod, segment 2 without setae, segment 3 with 4 setae, endopod of 2 segments, segment 1 with 1 strong inner spine in middle of segment, segment 2 with 2 setae and hyaline frill. P2 (Fig. 4B) with 3-segmented exopod, segments 1 and 3 with hyaline frill, segment 1 without seta, segment 2 without setae, segment 3 with 3 setae, endopod 1-segmented with 1

seta and 6 spinules, outer seta of basis absent. P3 (Fig. 4D) with both exopod segments fused, portion of proximal segment ending in a large seta ("thumb") reaching beyond end of whole exopod, inner margin with protuberances and tube pore reaching beyond inner margin of segment; portion of distal segment ("apophysis") terminally with strong spine (seta), on outer margin with protuberance giving "apophysis" look like a bird finger; endopod represented by 1 seta. P4 (Fig. 5A) with 3-segmented exopod, segment 1 subterminally with row of 8 large and slender spinules on inner margin, segment 2 without setae, segment 3 with 2 apical setae and inner hyaline frill, endopod 1-segmented with terminal seta fused to it and 3 spinules, seta subterminally with 3–4 subordinate spinules fused to its outer margin, basis with hyaline spinule between exopod and endopod,

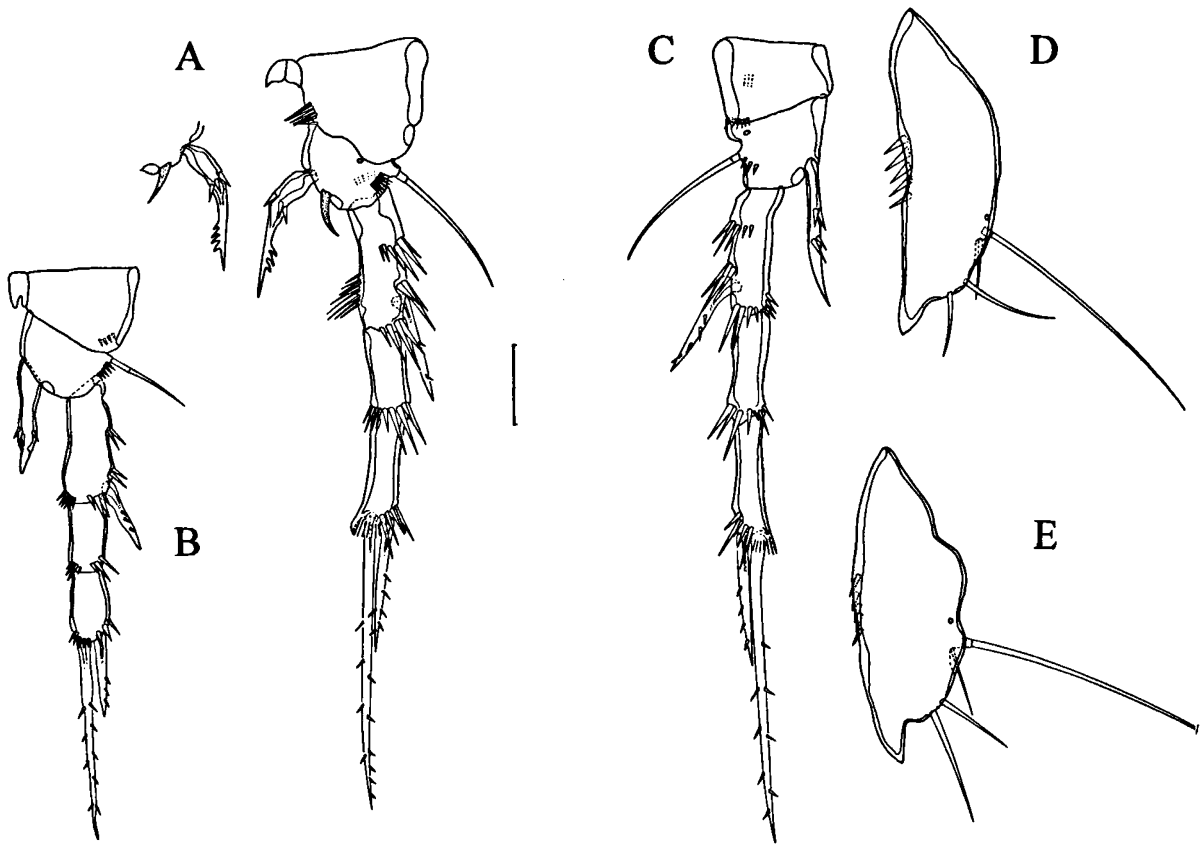


Fig. 5. *Parastenocaris hispanica* n. sp.: A, male P4 and opposite endopod; B, male pereopod 4 copepodid V; C, female pereopod 4; D, male pereopod 5 ventral view; E, male pereopod 5 lateral view. Scale bar 10 μ m.

coxa with 6 slender spinules on inner margin. P5 (Fig. 5 D–E) with convex outer margin bearing 4 setae and inner thorn, and with row of spinules along inner margin.

Female: Sexual dimorphism in A1, P1, P2, P3, P4, P5, and genital field. A1 (Fig. 3B) 7-segmented, not prehensile, number of setae starting at proximal segment: 0/4/5/2+Ae/1/1/9+Ae.

P1 endopod segment 1 with 2 small spinules at inner margin instead of 1 thick spinule. P2 endopod (Fig. 4C) with 1 seta and only 4 spinules. P3 (Fig. 4G) exopod 2-segmented, segment 1 with outer seta, segment 2 with 2 apical setae and inner frill, proximally with tube pore at inner margin, endopod 1-segmented with 4 spinules, without setae. P4 (Fig. 5C) exopod 1 apically with spinules, endopod 1-segmented, with terminal seta

without subordinate spinules fused to it, and 4 spinules, basis without hyaline spinule between exopod and endopod, coxa without spinules on inner margin. P5 (Fig. 6A) with only 3 spinules at inner margin. Genital field as illustrated in Fig. 6A, seminal receptacles dotted.

Derivatio nominis. – The specific name *hispanica* refers to Spain.

Variability. – Material from Sta. Rouch 1978 n° 8 and Sta. Rouch 1978 n° 8bis differs from the holotype and allotype in the following characters:

Male: P3 exp (Fig. 4E) “apophysis” with stronger outer protuberance, tube pore orientated upwards. Telson (Fig. 7B) ventrally with 2 strong spinules at base of each furcal ramus.

Female: Furca (Fig. 6B) modified as “bulbifera type” (Noodt, 1963; Schminke, 1991).

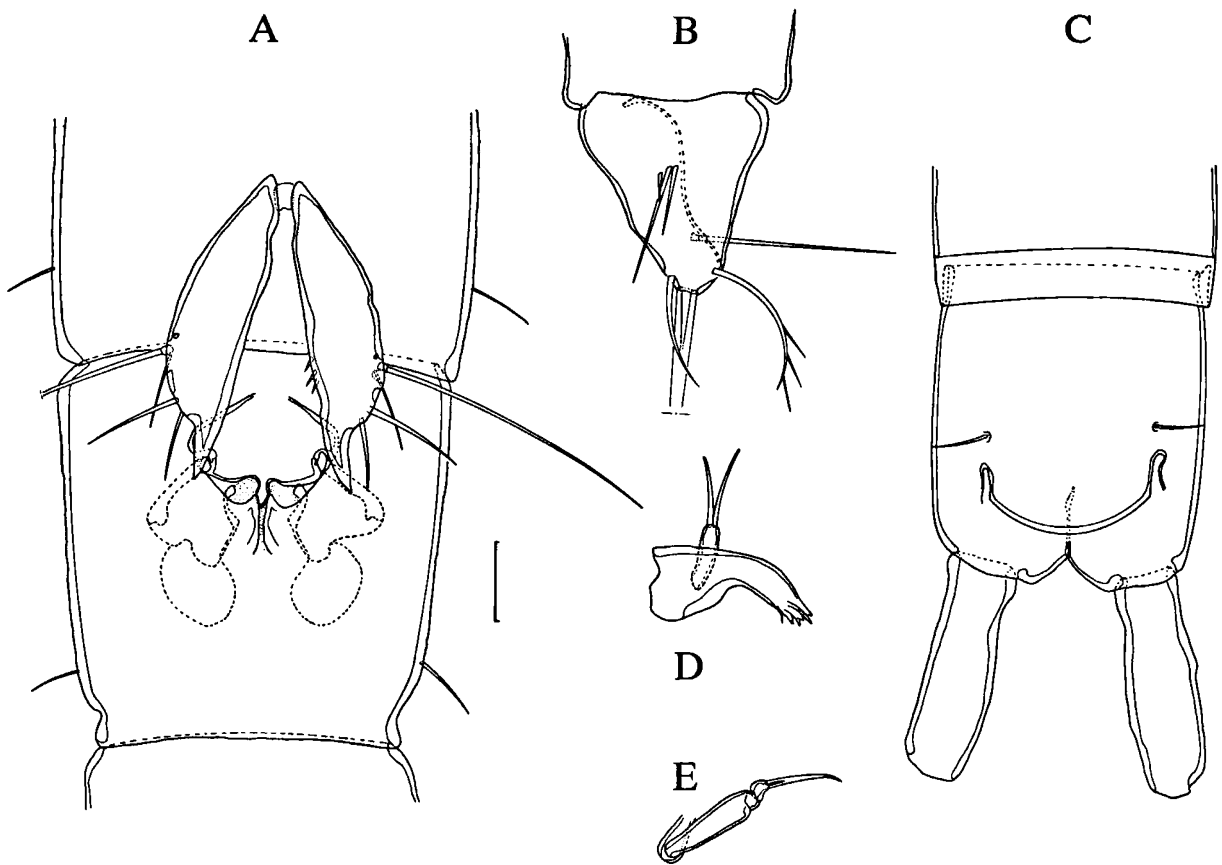


Fig. 6. *Parastenocaris hispanica* n. sp.: A, female pereopod 5 and genital field; B, female furca from Sta. Rouch 1978 n° 8; C, male telson dorsal view; D, mandible; E, maxillipede. Scale bar 10 μ m.

Affinities of *Parastenocaris hispanica* sp. n.

The greatest similarities are with those species of the genus belonging to the *fontinalis*-group (Lang, 1948). Unfortunately, both of Lang's discriminating characters for the *fontinalis*-group, i.e., "endopod P4 male as female" and "endopod P2 1-segmented", are useless. The endopod P4 of males is different from that of females (see Fig. 5 A, C; Zinzenco, 1971; Songeur, 1961; Rouch, 1990) even in the species *Parastenocaris fontinalis* Schnitter & Chappuis, 1915 (cf. Herzog, 1938). Furthermore, the endopod P2 is 1-segmented in all known Parastenocarididae, this being a symplesiomorphy within the family (cf. Martínez Arbizu & Moura, 1994).

Lang grouped 5 species together in the *fontinalis*-group, of which *P. entzi* Török, 1935, *P.*

similis Török, 1935, and *P. aedes* Hertzog, 1938 are not closely related to the nominal species *P. fontinalis*. These three species belong to what Schminke (1993) calls "Parastenocaridinae" in which all three anterolateral setae of the furca insert on its distal third. On the other hand, *P. fontinalis* belongs to what Schminke (1993) calls "Fontinalicaridinae". The *fontinalis*-group contains *P. fontinalis fontinalis*, *P. fontinalis borea* Kiefer, 1960, *P. fontinalis meridionalis* Rouch, 1990, *P. aquaeductus* Chappuis, 1925, *P. psammica* Songeur, 1961, and *P. hispanica* n. sp. (*P. bohemica* Sterba, 1968, is a junior synonym of *P. fontinalis*).

All these taxa share the same construction of the male endopod P4 as described above. However, *P. aquaeductus* differs from the other taxa in some important characters: (1) Male P4 endopod fused

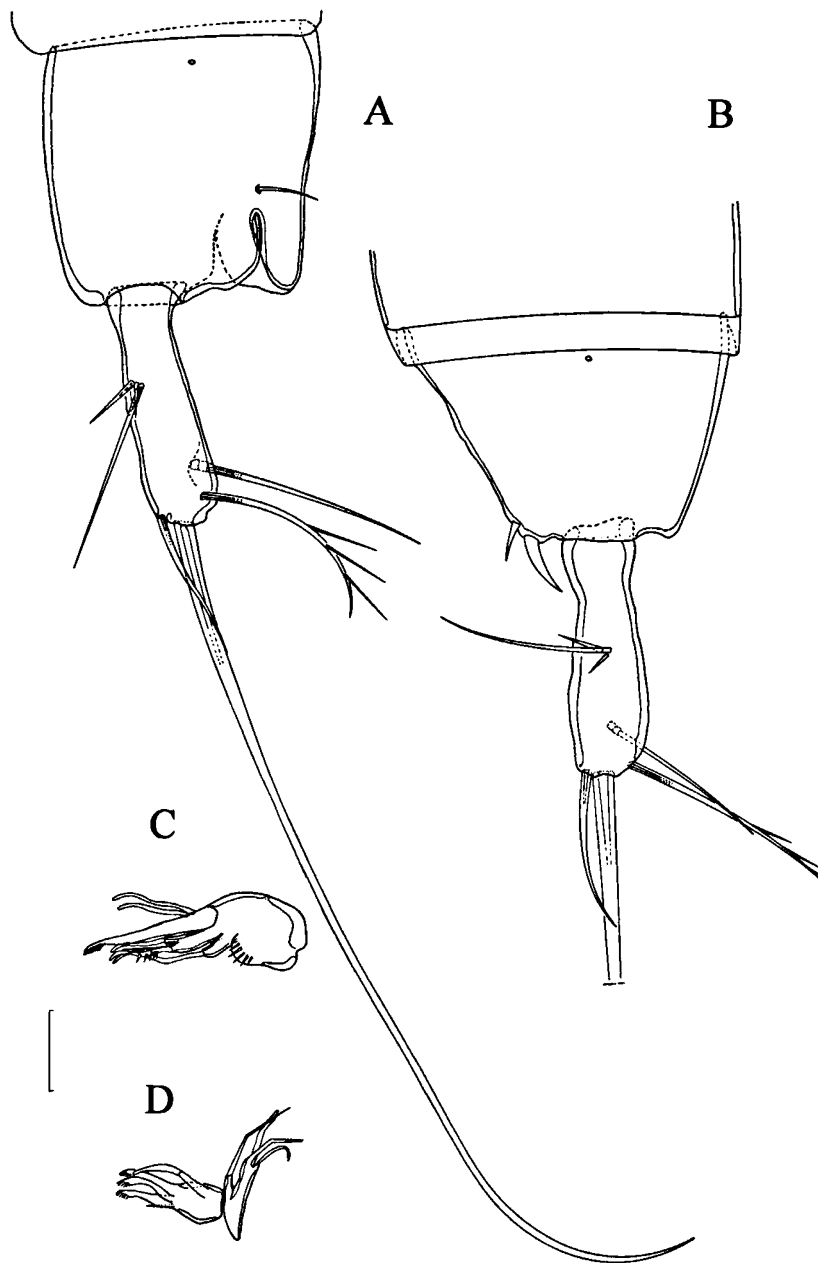


Fig. 7. *Parastenocaris hispanica* n. sp.: A, male telson lateral view; B, male telson from Sta. Rouch 1978 n° 8 lateral view; C, maxilla; D, maxillule. Scale bar 10 μ m.

seta with subordinate spinules on both margins, not only on the outer margin. (2) Male P3 basis with a row of spinules on inner margin. (3) Male P3 exopodal portion of segment 1 ends distally on inner margin with 2 little spinules. (4) Male P4 exopodal segment 1 ends distally in a row of spinules on inner margin. (5) Male P3 exopodal

“apophysis” as long as wide. (6) Female P4 basis with a row of spinules between exopod and endopod.

Characters 1–6 represent the plesiomorphic state within the *fontinalis*-group. This allows us to define a well-founded monophyletic group for the remaining species. However, this does not exclude

Table I. Character matrix.

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>P. hispanica</i>	1	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0
<i>P. meridionalis</i>	1	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0
<i>P. psammica</i>	1	1	1	1	1	1	1	1	0	0	1	1	0	0	1	0
<i>P. f. fontinalis</i>	1	1	1	1	1	1	1	1	0	0	1	1	0	1	0	0
<i>P. f. borea</i>	1	1	1	1	1	1	1	1	0	0	1	1	0	1	0	1

the possibility that another group of species of Parastenocarididae, characterized by an advanced transformation of endopod P4 male, e.g., the group around *P. kabyloides* Enckell, 1969 (Martínez Arbizu, in prep.), may be the sister group of the *fontinalis*-group excluding *P. aquaeductus*. This species would then be the sister group of a taxon including the *fontinalis*-group and the group around *P. kabyloides*. For this reason *P. aquaeductus* is excluded from the following phylogenetic discussion, although it is considered an appropriate outgroup to polarize the characters within the *fontinalis*-group.

Phylogenetic relationships within the *fontinalis*-group

Fig. 8 shows the phylogenetic relationships within the *fontinalis*-group. The different subspecies are treated for this analysis as separate taxa. A character matrix is given in Table I. The characters are listed and polarized as follows:

- (1) Male P4 endopod fused seta with subordinate spinules only on outer margin (ap); *P. aquaeductus* and other "Fontinalicaridinae" such as *P. kabyloides* have subordinate spinules on both margins (pl).
- (2) Male P3 basis without row of spinules (ap); *P. aquaeductus*, *P. kabyloides*, and most Parastenocarididae have a row of spinules on inner margin of basis of P3 (pl), this being a symplesiomorphy of the family.
- (3) Male P3 exopod portion of segment 1 without spinules on inner margin (ap); 2 spinules are present in adult *P. aquaeductus* (pl) and also in the fifth copepodid stage of *P. hispanica* (Fig. 4F), while these spinules get lost with the moult to the adult.
- (4) Male P4 exopod 1 row of spinules on inner margin inserting subterminally (ap); these spinules insert terminally (pl) in *P. aquaeductus* and in the fifth copepodid stage of *P. hispanica* (Fig. 5B), being relocated to subterminal position with the adult moult.

(5) Male P3 exopod "apophysis" twice as long as wide (ap); the "apophysis" is as long as wide (pl) in *P. aquaeductus* and in the fifth copepodid stage of *P. hispanica* (Fig. 4F).

(6) Female P4 basis without any spinules between exopod and endopod (ap); *P. aquaeductus* has a row of spinules at this position (pl).

(7) Male P4 exopod 1 subterminally on inner margin with 4–5 strong spinules (ap); *P. hispanica* has 8 slender spinules (pl).

(8) Male P4 coxa with 2–3 strong spinules (ap); *P. aquaeductus* has 5, *P. hispanica* has 6 slender spinules (pl).

(9) Male P3 exopod, "apophysis" with a protuberance on outer margin (ap); this protuberance is absent (pl) in *P. aquaeductus*, *P. psammica*, *P. f. fontinalis*, *P. f. borea*, and *P. f. meridionalis*. (10) Male P3 exopod "apophysis" curved inwardly at an angle of 60° (ap); *P. aquaeductus*, *P. psammica*, *P. f. fontinalis*, *P. f. borea*, and *P. f. meridionalis* have an angle of 45° (pl).

(11) Male P5 slender (ap); *P. aquaeductus*, *P. f. meridionalis*, and *P. hispanica* have a broad P5 with convex outer margin (pl).

(12) Male P3 "thumb" shorter than "apophysis" (ap); *P. aquaeductus*, *P. f. meridionalis*, and *P. hispanica* have a "thumb" longer than "apophysis" (pl).

(13) Female P5 without spinules at inner margin (ap); *P. aquaeductus*, *P. psammica*, *P. f. fontinalis*, *P. f. borea*, and *P. hispanica* have spinules at inner margin (pl).

(14) Operculum triangular (ap); *P. aquaeductus*, *P. psammica*, *P. f. meridionalis*, and *P. hispanica* have a round operculum (pl).

(15) Male P5 inner distal corner with two setae (ap); *P. aquaeductus*, *P. f. fontinalis*, *P. f. borea*, *P. f. meridionalis*, and *P. hispanica* have no setae at this position (pl). No setae are present in the ground pattern of Parastenocarididae (Martínez Arbizu & Moura, 1994). The acquisition of these 2 setae in *P. psammica* is considered an autapomorphy of this species, this being the most parsimonious assumption.

(16) Male P5 with a strong and large spinule at inner margin (ap); *P. aquaeductus*, *P. psammica*, *P. f. fontinalis*, *P. f. meridionalis*, and *P. hispanica* have a row of small spinules at this position (pl).

Biogeography

The new species has its known distribution in eastern Spain, the Pyrenees being its northern boundary (Fig. 1). On the French (north) side of the Pyr-

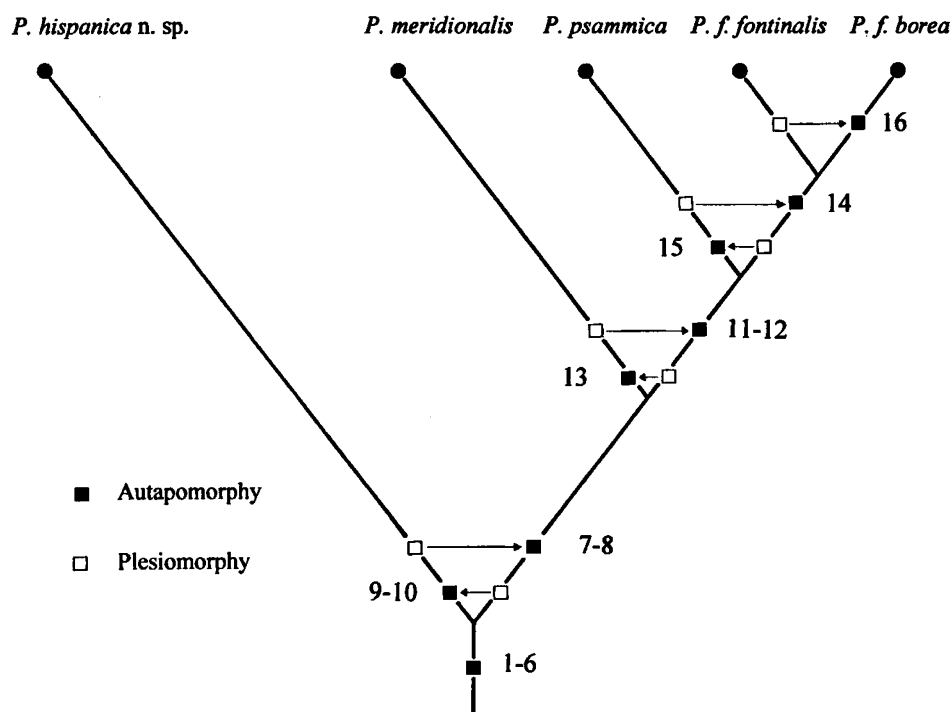


Fig. 8. Phylogenetic position of *P. hispanica* n. sp. Explanation of characters in text.

enees *Parastenocaris f. meridionalis* has been collected at the River Nert (Rouch, 1990), this being the only record of this taxon. *Parastenocaris psammica* is described from different locations in Lorraine, northern France (Songeur, 1961). The widest distribution has been recorded for *Parastenocaris fontinalis*, which is present all over Germany, The Netherlands, northern France, Switzerland, and Czechoslovakia (Janetzky et al., 1996), its subspecies *P. fontinalis borea* being distributed in northern Germany and The Netherlands.

A projection of the cladogram on a map showing the approximate distributions of the species of the *fontinalis*-group shows a high amount of concordance between phylogeny and distribution. The higher the latitude, the relatively more derived the species (Fig. 9). This condition suggests an origin of the *fontinalis*-group in southwestern Europe and a slow colonization northwards. The first vicariant event is the origin of the Pyrenees isolating the groundwater basins south and north of it. Other vicariant events cannot be explained satisfactorily at the present state of knowledge of the distribu-

tion of the French species *P. f. meridionalis* and *P. psammica*. The subspecies *P. f. borea* is distributed in groundwaters that were covered with ice during the last glaciation. Assuming the extinction of most groundwater organisms due to the formation of permafrost in the soil during glacial times, we may conclude a colonization of these areas after glaciation by a sub-population of *P. fontinalis* that was better adapted to cold conditions.

Discussion

The polarization of the characters was done following Hennig's criteria (Hennig, 1982: 98–116) and by outgroup comparison, not only with *Parastenocaris aquaeductus*, but with all known Parastenocarididae. Only some relevant examples from other taxa were considered in the text to explain the polarization of the characters chosen. In addition, the Hennigian "criterion of ontogenetic character precedence" has been successfully applied to polarize characters 3, 4, and 5. Some structures

present in *P. aquaeductus* appear in *P. hispanica* n. sp. during ontogenetic development and are secondarily lost with the final moult to the adult. The polarization of the characters as presented above is also in concordance with the Hennigian “criterion of the correlation of series of transformations” and the “criterion of biogeographic progression”. As a result of this analysis, *Parastenocaris meridionalis* Rouch (syn. *P. fontinalis meridionalis* Rouch), cannot be considered a subspecies of *P. fontinalis* anymore. It is the sister group of a taxon consisting of *P. psammica* and *P. fontinalis*, that are separate biological species as they are sympatric, having been found together in the same sample (Songeur, 1961). *P. meridionalis* must therefore be considered a separate species, of which the Pyrenees are the southern distribution limit. *P. fontinalis borea* is further considered a subspecies of *P. fontinalis*.

The phylogenetic relationships of the different species-groups of *Parastenocaris* are unknown. Jakobi (1972) proposed a new system for the family Parastenocarididae by splitting it into 26 new genera. This artificial system has been strongly criticized by Schminke (1976b) and has not been adopted by Dussart & Defaye (1990).

One of Jakobi's new genera was *Fontinalicaris*, having as type species *P. fontinalis*. In this genus, Jakobi included a second species, *P. phyllophora* Noodt, 1954, that is quite unrelated to *P. fontinalis*. A revision of *Parastenocaris* will result in the recognition of a number of monophyletic groups, one of which will be the genus *Fontinalicaris* including the species *P. fontinalis*, *P. psammica*, *P. meridionalis*, and *P. hispanica* as is discussed here. *Fontinalicaris* with its type species *Fontinalicaris fontinalis* will be the type genus of the subfamily Fontinalicaridinae as advanced by Schminke (1993). Waiting upon this revision, I prefer to use the concept of species-group (in this case *fontinalis*-group) rather than the genus *Fontinalicaris*.

Acknowledgements

I am especially indebted to Dr. Raymond Rouch (C.N.R.S., Saint-Girons, France), who kindly loaned me abundant material for this work. I wish to thank Prof. Dr. H.K. Schminke for his

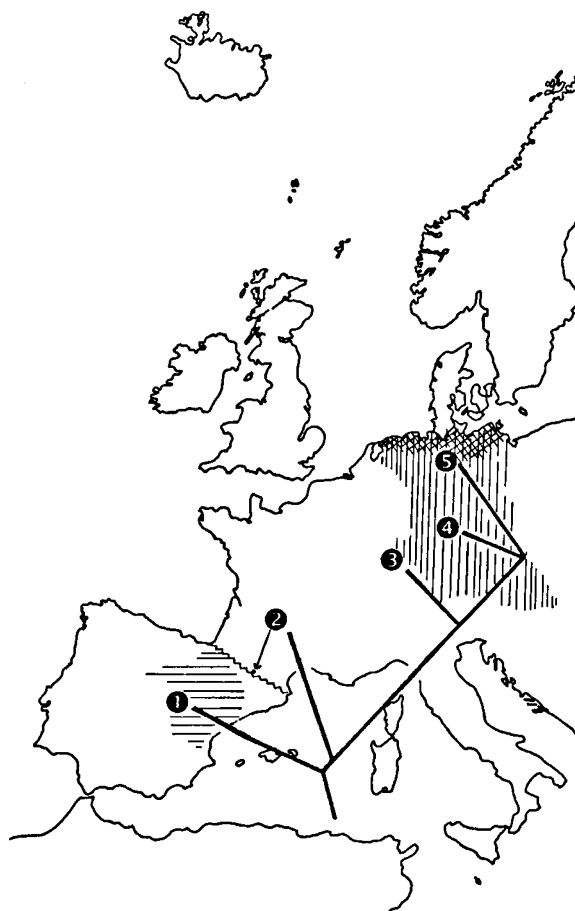


Fig. 9. Projection of the cladogram (Fig. 8) on a map of the western of middle part of Europe showing the distribution of the species belonging to the *fontinalis*-group. 1, *Parastenocaris hispanica* n. sp.; 2, *P. meridionalis*; 3, *P. psammica*; 4, *P. fontinalis*; 5, *P. f. borea*.

unconditional support and continuous discussions especially on parastenocaridid phylogeny. This work has been supported partially by a grant of the Deutscher Akademischer Austauschdienst (D.A.A.D.).

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Accepted: 6 September 1996