

INTRODUCTION TO IBERIAN GROUNDWATER AMPHIPODS

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ABSTRACT

Zoogeographical data on Iberian ground water dwelling amphipods are given. The geographical ranges, habitats, and co-occurrences of the genera, are discussed. The Iberian peninsula is divided into zoogeographical districts based on these amphipods; some are correlated with geological units.

INTRODUCTION

Intensive sampling in continental Spain during the period 1983-1986 revealed many data about composition and distribution of ground water inhabiting fauna (stygo fauna), especially crustaceans. This paper will deal with the amphipods of this fauna mainly on the generic level. Data about other groups of crustaceans collected simultaneously have been published by HENRY & MAGNIEZ (1987, 1988), CAMACHO (1987), and PESCE & GALASSI (1988). A survey of localities sampled during our own investigation and on which most of the information provided in this paper is based is given in fig. 1.

First, a review is given of what has been published before 1983 about Iberian ground water dwelling amphipods. Rather few authors paid attention to this fauna and their findings were based on very scattered data. A first treatise on crustaceans from Iberian continental waters was published by MARGALEF (1953). It included the subterranean fauna as well and served as the starting point of this review. Stygobiont amphipods recorded by MARGALEF (op. cit.) are: *Pseudoniphargus* (as *P. africanus* Chevreux, 1901, from cave waters in the

Cantabrian Mountains), *Metacrangonyx* (from the Balearic islands only), and *Niphargus* (*N. ciliatus cismontanus* Margalef, 1952, from Guipuzcoa).

GINET published a short paper in 1977, including data from Portugal as well (reproduced in Spanish in 1980), in which he stressed the scarce knowledge about the distribution in Spain of the genera *Niphargus*, *Haploginglymus*, *Pseudoniphargus* and *Crangonyx*. However, he did not mention the genera *Bogidiella*, *Salentinella*, and *Hadzia*. RUFFO (1953) already reported an unnamed representative of *Bogidiella* near Sitges (S of Barcelona), while *B. hellenae* was described by MATEUS & DE LOURDES MACIEL (1967) from the mouth of the river Douro (Portugal). The genus *Salentinella* was recorded for the first time by MARGALEF (1970a) from a cave near Alcoy (Alicante). In the same paper Margalef mentioned the presence of *Pseudoniphargus* in southern Spain, in the central Pyrenees and in the Catalan hills. Other records of *Pseudoniphargus* in northern Spain were given by ORTIZ (1968), VILLOTA & GALAN (1970), MARGALEF (1970b), GOMARIN GUIRADO (1978), and ESCOLA (1980).

In 1972, MATEUS & MATEUS described *Hadzia tavaresi* from wells near the southern Portuguese coast (Algarve); STOCK (1977) established a new genus, *Metahadzia*, for this species and also men-

tioned some new localities. MATEUS & MATEUS (1978) provided up to date distributions of the genera *Bogidiella*, *Haploginglymus*, *Pseudoniphargus* and *Metahadzia* in Portugal. In 1980a STOCK described a second species of *Haploginglymus* from a hyporheic habitat in the Cantabrian Mountains (northern Spain) and published in the same year a revision of the genus *Pseudoniphargus*, in which five new species were recognized from the Iberian peninsula. In his revision STOCK (1980b), also incorporated new material from northern and southern Spain. Recently, KARAMAN (1986a,b) reported on *Niphargus* and *Haploginglymus* based on the study of the older collections of Ginet and of Mateus, and established the existence of a third *Haploginglymus* species in central Iberia. A fourth form of *Haploginglymus* coexisting with *Niphargus* was recently discovered a spring south of the Catalan Pyrenees (PRETUS & SABATER, in press.).

The area around Madrid has been investigated during the last years by colleagues of the Museo

Nacional de Ciencias Naturales. Their material contained only *Bogidiella* (STOCK & NOTENBOOM, 1988). In this paper, bogidiellids from eastern and southern Spain are recorded as well. Our own investigations have been concentrated on the Cantabrian Mts. and the western part of the Pyrenees, the central-eastern part of Spain, and Andalusia (see fig. 1). In all areas visited it was attempted to sample a range of biotopes, such as the underflow of rivers, springs, wells, and cave waters. Data on the localities investigated in 1983 and 1984 have been published by NOTENBOOM & MEIJERS (1985). Additional sampling has been executed in summer 1985 by Peter van den Hurk and Remko Leys in the western part of Andalusia, and by Ine Meijers and Jos Notenboom in southern Valencia and the eastern part of Andalusia, and also in summer 1986 by Remko Leys and Katja Hogedoorn in Galicia, and by Peter van den Hurk, Marc Koperdraat, and Jos Notenboom in Catalonia.

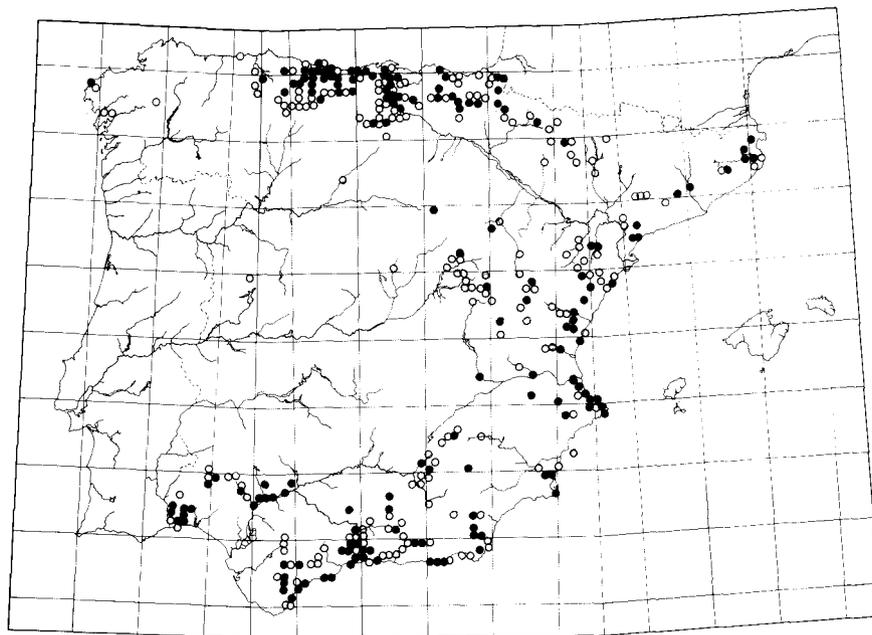


Figure 1.- Distribution of all groundwater samples taken during our campaigns of 1983-86. Squares indicate 100×100 km UTM-grid. Closed symbols indicate the situation of two or more samples taken within the same 10×10 km UTM-square. Distribución de las muestras de aguas subterráneas tomadas durante las campañas de muestreo realizadas entre 1983 y 1986. La cuadrícula corresponde a las coordenadas UTM de 100×100 km. Los símbolos negros indican la situación de dos o más muestras tomadas dentro del mismo cuadrado de 10×10 km.

THE IBERIAN GROUNDWATER AMPHIPOD GENERA

Niphargus Schiodte, 1849 (fig. 2)

This genus has an extended distribution; it stretches from western Europe into the Near East (KARAMAN & RUFFO, 1986). In Spain it reaches its southwestern distribution limit and occurs in two segregated areas on both edges of the Pyrenean mountain ridge only. In the eastern Catalan Pyrenees the genus is mentioned by GINET (1977) from La Mosquera cave near Beuda (prov. Gerona), identified by KARAMAN (1986b) as *N. delamarei* Ruffo, 1954. Our own investigations in Catalonia showed that *Niphargus* ranges from the Pyrenees into the province of Tarragona (about 150 km south of Pyrenees). In the area west of the Pyrenees (Basque Country and the northwestern part of the province of Burgos), the genus has been found frequently both in the past and during our own investigations. This is the classical Iberian

Niphargus region. Most likely the present distribution of *Niphargus* in Iberia is the result of dispersal from the area north of the Pyrenees, through the low altitude corridors west and east of the mountain ridge. This hypothesis is confirmed by the presence of trans-Pyrenean species, *N. delamarei* in the east, and *N. ciliatus* and *N. longicaudatus* in the west (MARGALEF, 1952, 1970a,b; KARAMAN, 1986b).

Niphargus is a widely distributed stygobiont amphipod genus with a high species diversity, including species with large ranges. Supposedly, one of the reasons for its wide range is a rather high dispersal ability related with its capacity to colonize not only the phreatic level but also the unsaturated zone and saturated layers situated above the regional water table, whereby lower mountain ridges can be crossed. In this context it is interesting to mention some biotopes from where *Niphargus* was recorded: in the Basque Country, for instance, in dripwater pools of a mine gallery, si-

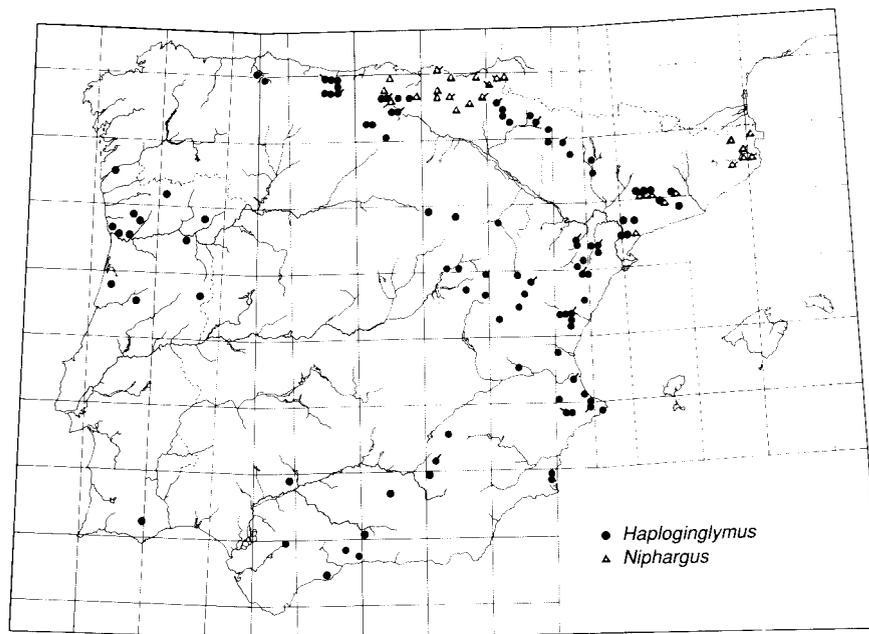


Figure 2.- The distribution of *Haploginglymus* and *Niphargus* in the Iberian peninsula. Squares indicate 100×100 km UTM-gnd. Symbols with stack-bars indicate the situation of two or more localities of the genus within the same 10×10 km UTM-square. Distribución de *Haploginglymus* y *Niphargus* en la península Ibérica. La cuadrícula corresponde a las coordenadas UTM de 100×100 km. Los símbolos marcados con una línea indican la situación de dos o más localidades del género dentro del mismo cuadrado de coordenadas UTM de 10×10 km.

tuated in non-carbonate rocks at 600 m altitude, without contact with the local groundwater table, and in a spring from red sandstone, situated high up a hill at 320 m altitude and with a pH of the water of 4.0. This spring is being fed most likely by a perched groundwater aquifer. In Catalonia most *Niphargus* records are from wells and hyporheic habitats, but it was found also in seeps of a railway tunnel.

In Basque Country *Niphargus* has been found in caves, springs, and wells, frequently together with *Pseudoniphargus*, very few times with *Salentinella*, and only once with *Haploginglymus*. In Catalonia the only amphipod co-occurring with *Niphargus* was *Haploginglymus*, in particular along the border of the range.

Haploginglymus Mateus & Mateus, 1958 (fig. 2)

This genus, strictly endemic of the Iberian peninsula, is the most widely distributed Iberian

stygobiont amphipod. It is uncertain if *Haploginglymus* occurs in the central part of Iberia, since few investigations have been done there. Until now four species are recognized (KARAMAN, 1986a; PRETUS & SABATER, in press), but since more material awaits identification, it is to be expected that more forms will be recognized.

The genus inhabits particular wells and underflows of rivers, but it has been found in springs as well. Only in the mid-eastern part of the peninsula are cave-dwellers recorded, possibly because of the absence of *Pseudoniphargus* in this region.

Haploginglymus is closely related to *Niphargus* (cf. MATEUS & MATEUS, 1958; BARNARD & BARNARD, 1983; KARAMAN, 1986a; KARAMAN & RUFFO, 1986). The observation that these two genera occur together only along the borders of their distribution areas would suggest that there is some kind competition between them. The genus is frequently found together with other amphipod genera.

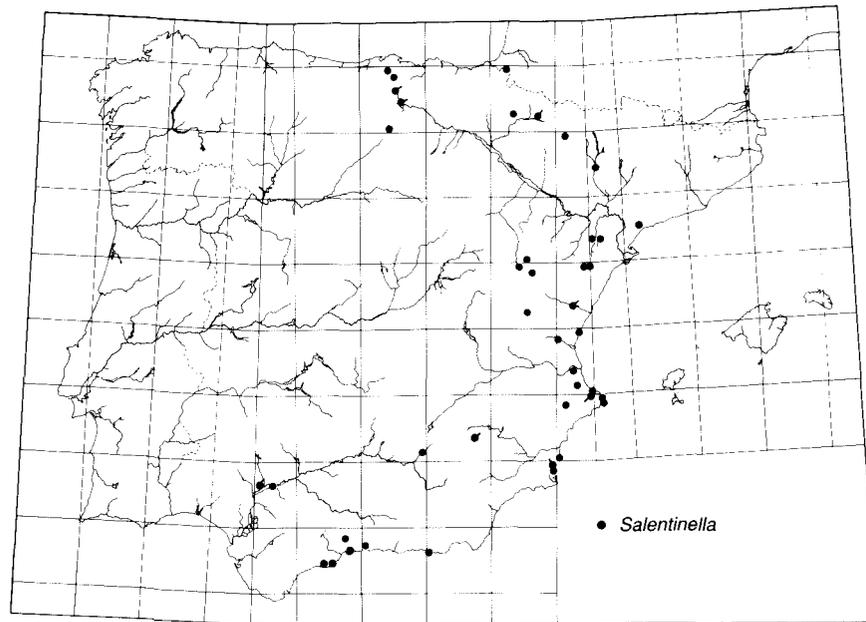


Figure 3.- The distribution of *Salentinella* in the Iberian peninsula. See also legend of fig. 2. Distribución de *Salentinella* en la península Ibérica. Véase también la leyenda de la figura 2

Salentinella Ruffo, 1947 (fig. 3)

The genus is confined to fresh or slightly brackish habitats of the western peri-Mediterranean region (RUFFO, 1986). In Spain *Salentinella* occurs in all regions prospected by us, not only close to the Mediterranean sea board, but also in inland ground waters and even in the vicinity of the Bay of Biscay. They are principally inhabitants of wells and underflows, although MARGALEF (1970a) recorded them also from a cave. Frequently *Salentinella* was found together with other stygobiont amphipods, especially with *Haploginglymus*.

PLATVOET (1987) studied the Spanish material and recognized nine different forms, belonging to eight different (sub)species and one *incertae sedis*. The most widely distributed species is *S. angelieri*, whose distribution coincides with that of the entire genus, and it occurs in various habitats near the Mediterranean coast, including insular habitats. In Spain it has been found up to some 100 km from the coast. The remaining Spanish

species have restricted distributions often confined to a single hydrographic basin, including the uppermost parts of Atlantic drainage systems.

Bogidiella Hertzog, 1933 (fig. 4)

Species of *Bogidiella* were found in coastal ground waters, but also in continental ground waters. A part of the material available was studied by STOCK & NOTENBOOM (1988). They recognized five different species all endemic to Iberia belonging to the subgenera *Bogidiella* s.s. and *Medigidiella*. Cases of sympatry within *Bogidiella*, and between *Bogidiella* and *Medigidiella* are found in Iberian inland water (STOCK & NOTENBOOM, op. cit.). In spite of intensive investigations, *Bogidiella* has not been found in the northern part of the central plateau (Meseta), the Cantabrian Mountains, the western Pyrenees, and inland waters of Catalonia.

Above all *Bogidiella* species are inhabitants of hyporheic habitats, although occasionally also

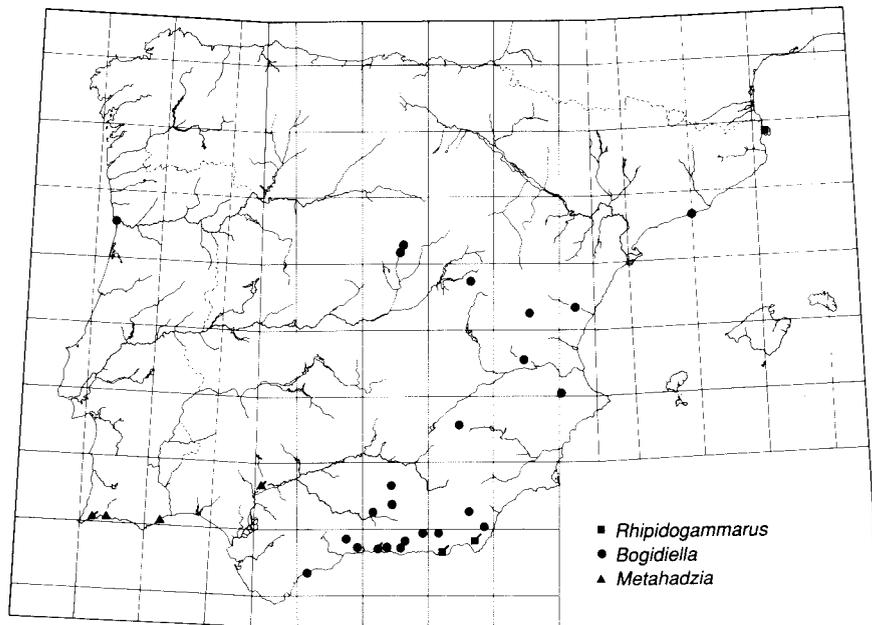


Figure 4.- The distribution of *Rhipidogammarus*, *Bogidiella* and *Metahadzia* in the Iberian peninsula. See also legend of fig. 2. Distribución de *Rhipidogammarus*, *Bogidiella* y *Metahadzia* en la península Ibérica. Véase también la leyenda de la figura 2.

found in wells. Frequently other stygobiont amphipods occurred in the same habitats, viz., *Pseudoniphargus*, *Haploginglymus*, and *Salentinella*.

Metahadzia Stock, 1977 (fig. 4)

The genus *Metahadzia* has mainly a Mediterranean distribution. In the Iberian peninsula it was formerly known by a single species, *M. tavaresi*, from wells of the Algarve. Our own investigations revealed the existence of a second species, *M. uncispina*, in wells in the basin of the Guadalquivir river near Sevilla (NOTENBOOM, 1988b). Probably the distribution in Spain of *Metahadzia* is limited to this river basin. The co-occurring amphipod fauna existed of *Salentinella*.

Rhipidogammarus Stock, 1971 (fig. 4)

A small number of localities with representatives of this genus are known from continental Spain, restricted to regions close to the Mediterranean sea board in fresh to brackish waters. STOCK

(1971) mentioned *R. rhipidiophorus* from an epigeal pool in a riverbed at Gerona. Our own investigations yielded a new species, *R. triumvir*, from wells in Almería (NOTENBOOM, 1985, 1988a).

Sensonator Notenboom, 1986 (fig. 5)

This monotypic endemic genus was discovered in the southern part of the province of Valencia. It is a rather large amphipod with remarkable characteristics for a stygobiont, such as many calceoli on both antennae in both sexes, and a subfoliaceous, natatory third uropod. The phylogenetic position of the genus is uncertain (NOTENBOOM, 1986a).

S. valentiensis was found in a phreatic cave lake (near Corbira de Alcira), but also in wells (near Corbera and Gandía) and in an hyporheic habitat of the Río Turia; all these localities are situated within 30 km from the sea shore in a rather restricted area. It has been found together with *Haploginglymus*, *Salentinella*, and *Bogidiella*. *S. valentiensis* is a bottom dweller but also free-swim-

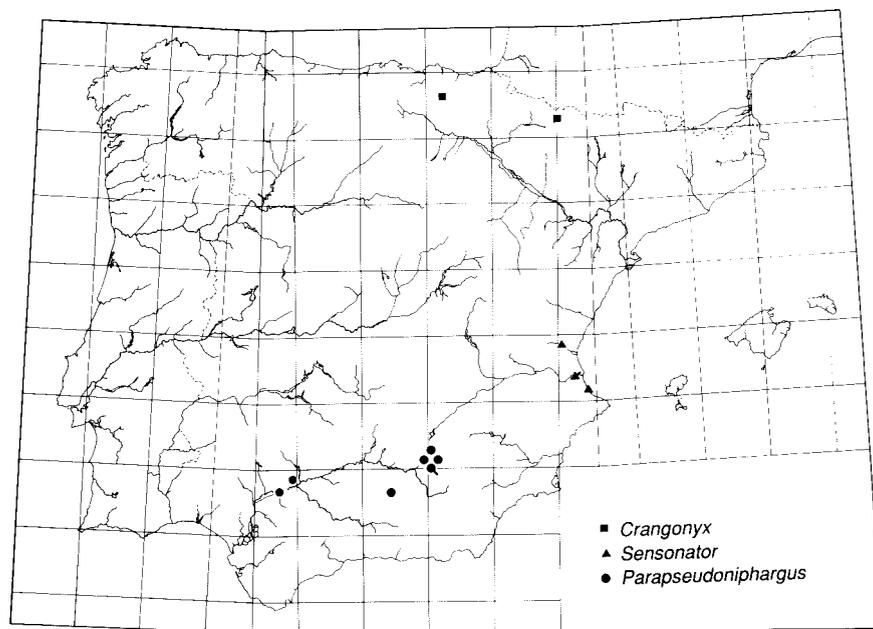


Figure 5.- The distribution of *Crangonyx*, *Sensonator* and *Parapseudoniphargus* in the Iberian peninsula. See also legend of fig. 2. Distribución de *Crangonyx*, *Sensonator* y *Parapseudoniphargus* en la península Ibérica. Véase también la leyenda de la figura 2.

ming, and is supposed to be very sensitive to water-borne pressure waves, whether produced by animal vibrations or other disturbances in the water. Probably it is a predator which has its most favourable habitat in large waterfilled fissures of the saturated karst.

Crangonyx Bate, 1859 (fig. 5)

During our investigations species of this genus have not been discovered. Previously the genus was mentioned by GINET (1977) from two caves in the north of Spain (Basque Country and Navarra). In spite of intensive sampling, also in one of the caves mentioned by Ginet (Cueva de Mairuelego-retta), it was not found again.

Parapseudoniphargus Notenboom, 1988 (fig. 5)

Our investigations revealed the existence of this monotypic genus closely related to *Pseudoniphargus* and probably endemic to the Guadalquivir river basin. The body of this amphipod is rather

compact with deep coxal plates and relatively short posterior pereopods and uropods, suggesting special adaptation to interstitial life (NOTENBOOM, 1988c). *Parapseudoniphargus* is distributed in hyporheic habitats of tributaries and upper courses of the Guadalquivir river, and occurred together with *Pseudoniphargus*, *Haploginglymus*, and *Salentinella*.

Pseudoniphargus Chevreux, 1901 (fig. 6)

The genus has a western Mediterranean-amphi-Atlantic distributional range and the Iberian peninsula occupies a central position in it. In Iberia *Pseudoniphargus* has a disjunct distribution, with three ranges: northern Spain, southern Spain, and Lusitania. All these three ranges have their own assemblages of endemic species. Striking is the absence of *Pseudoniphargus* in the mid-eastern part of the peninsula. An ecological cause of this pattern seems unlikely because many other stygobiont crustaceans such as *Haploginglymus*, *Salentinella*, *Proasellus*, *Stenasellus*, and *Ibero-*

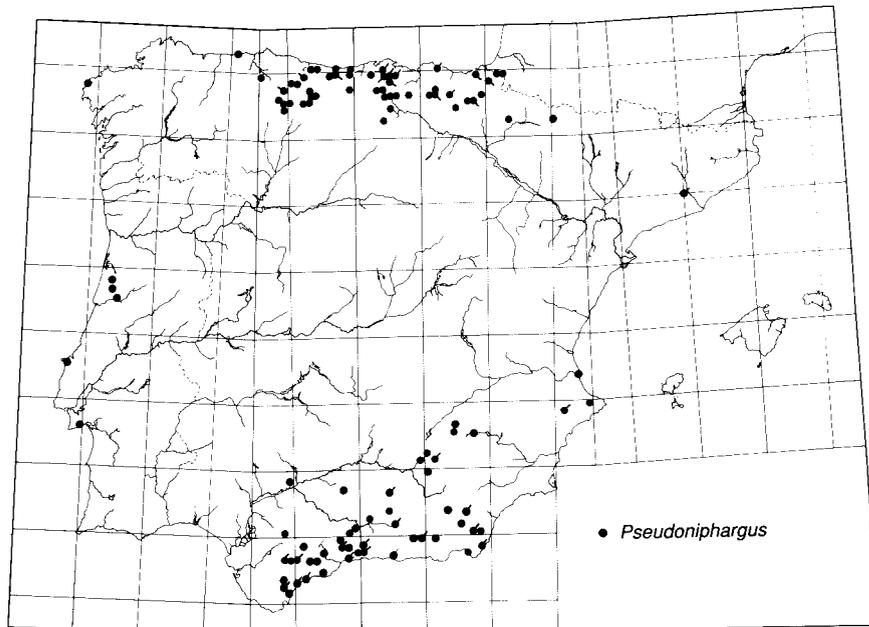


Figure 6.- The distribution of *Pseudoniphargus* in the Iberian peninsula. See also legend of fig. 2.
Distribución de *Pseudoniphargus* en la península Ibérica. Véase también la leyenda de la figura 2.

bathynella are abundant in this mid-eastern region, especially in hyporheic habitats, while *Pseudoniphargus* in the other areas investigated often co-occurred with these elements.

Karst waters provide important habitats for *Pseudoniphargus* in northern Spain, in addition, representatives are found in hyporheic waters, springs, and a few wells. Altogether 13 species have been recognized in the area, most of them with rather small allopatric ranges, limited to a single drainage basin or a karst area. In the Basque Country *Pseudoniphargus* frequently co-occurred with *Niphargus*. In hyporheic habitats, in particularly of the area around the Picos de Europa, *Haploginglymus* was often found together with *Pseudoniphargus* (NOTENBOOM, 1986b). The presence of *Pseudoniphargus* in the Catalan hills (MARGALEF, 1970b) remains enigmatic, our own investigations in that area in 1986 did not reveal its presence.

Subterranean waters of southern Spain apparently support an important diversity of *Pseudoniphargus* species. In the 15 species recognized

morphological divergence is larger than in northern Spain. Most of the southern species are allopatric with quite point shaped distributions. In the Guadalquivir basin, however, the widely distributed *P. latipes* co-occurred with the very localized species, *P. illustris*. Other amphipods frequently found together with *Pseudoniphargus* were *Haploginglymus* and *Bogidiella*, both mainly in hyporheic habitats, and *Salentinella*, only in wells (NOTENBOOM, 1987a).

Lusitania harbours a few species from Portugal and a single one from the northwesternmost part of Spain. The three species of Portugal are limited to the central-western part of the country (NOTENBOOM, 1987b).

Zoogeographical districts

Based on the known distributional data of stygobiont amphipods an attempt is made to divide to Iberian peninsula into areas characterized

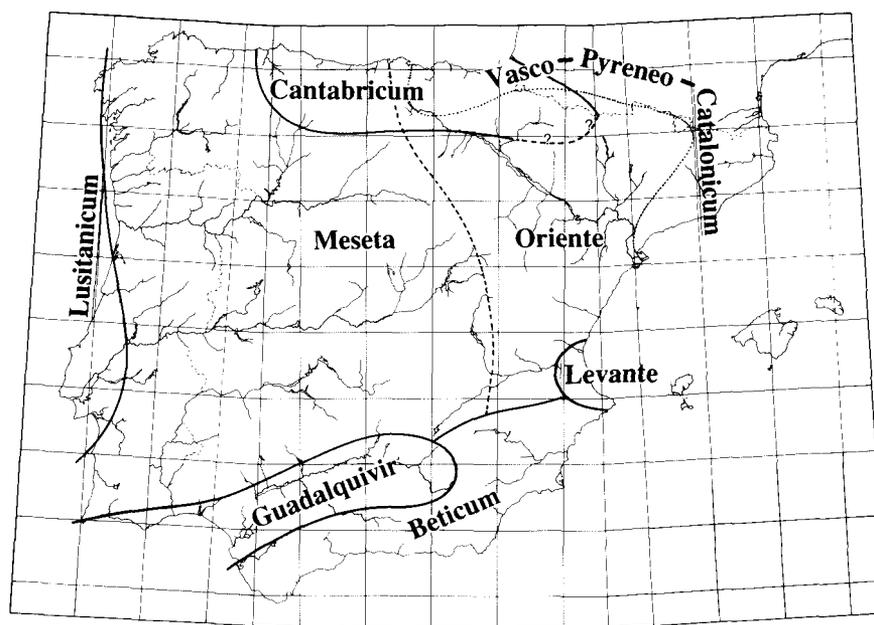


Figure 7.- Zoogeographic districts of the Iberian peninsula based on presence or absence of stygobiont amphipods. Distritos zoogeográficos de la península Ibérica según la presencia o ausencia de anfípodos estigobiontes.

by presence or absence of certain taxa. This approach is presented in fig. 7, but it needs emphasize that not all Iberian regions are equally thoroughly investigated (see fig. 1).

The stygobiont amphipod districts tend to be situated at the periphery of the Iberian Meseta. The Meseta district apparently has the lowest diversity with *Bogidiella* and *Haploginglymus* only. The latter genus is not particularly bound to any district, but an endemic for the entire peninsula. Regions with particular cases of endemism are the Guadalquivir and Levante with the endemic genera, *Parapseudoniphargus* and *Sensonator*, respectively. The unnamed taxon close to *Salentinella*, mentioned by PLATVOET (1987), might be an endemic of Levante, too. Moreover, the Guadalquivir district has endemic species of *Pseudoniphargus* and *Salentinella*, and is the only Iberian region with representatives of *Metahadzia*. Cantabricum, Lusitanicum, and Beticum are districts distinguished

by the presence of various species of *Pseudoniphargus*, each with its own assemblage of endemnic species. The eastern border of Cantabricum could not be established with certainty since it remains uncertain if *Pseudoniphargus* occurs in inland waters of the region southeast of the Pyrenees. The border between Oriente and Meseta is the western limit of the range of *Salentinella*. A Vasco-Pyreneo-Catalonicum district is distinguished due to the penetration of *Niphargus* in Iberian ground waters. In northern Spain the ranges of the genera *Pseudoniphargus*, *Niphargus* and *Salentinella* are partially overlapping, the eastern zone of Cantabricum is inhabited by *Salentinella*, and the northern part of that zone by *Niphargus*.

In Iberia predominantly Mediterranean elements like *Metahadzia* and *Salentinella* are found in Atlantic drainage basins of Guadalquivir, Oriente and Cantabricum. The latter genus is recorded as well from the adjacent Aquitanian area

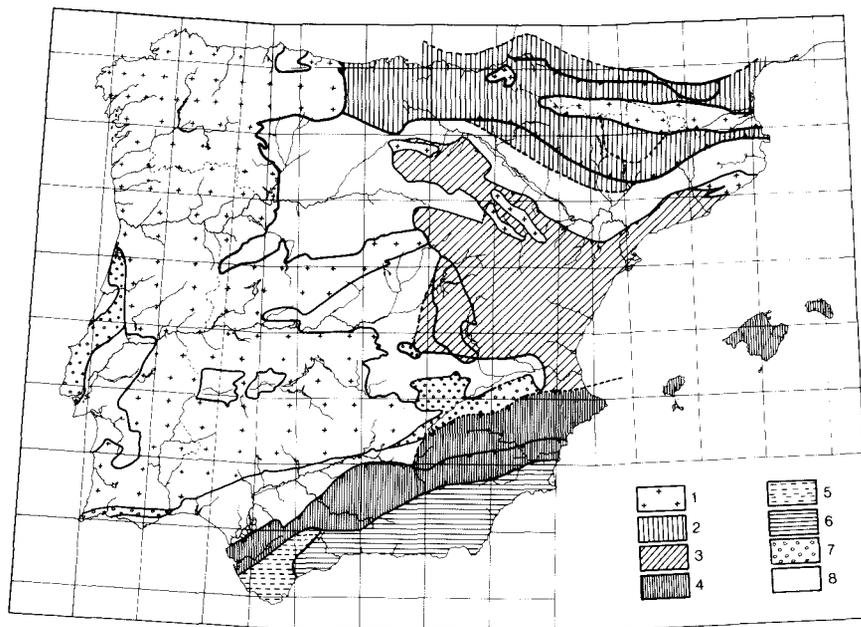


Figure 8.- Major geotectonic units of the Iberian peninsula. 1) Hercynian basement; 2) deformed Mesozoic cover of the Pyrenean realm; 3) Mesozoic aulocogenic area; 4) Mesozoic external units of the Betic realm; 5) intermediate Flysch units of the Gibraltar arc; 6) internal units (Mesozoic and Paleozoic) of the Betic-Rif realm; 7) undeformed Mesozoic cover; 8) continental and marine. Principales unidades geotectónicas de la península Ibérica. 1) Zócalo hercínico; 2) cubierta mesozoica deformada del dominio pirenaico; 3) área ulocogénica mesozoica; 4) unidades mesozoicas externas del dominio bético; 5) unidades intermedias del Flysch del arco de Gibraltar; 6) unidades internas (Mesozoico y Paleozoico) del dominio Bético-Rif; 7) cubierta mesozoica indeformada; 8) continental y marino.

in France. Another Mediterranean element is *Rhipidogammarus* which is restricted to coastal areas. *Niphargus* is a western paleartic element in Iberian ground waters. If the presence of *Crangonyx* could be confirmed this would be a holarctic element in the Iberian fauna. *Pseudoniphargus*, *Parapseudoniphargus*, and *Metahadzia* are hadzioid amphipods restricted to Tethyan areas. The Iberian range of *Metahadzia* apparently falls together with that of the thermosbaenacean *Monodella* with an amphi-Atlantic Tethyan distributional pattern as well. It is a remarkable fact that members of the *Metacrangonyx* group have not been found in Iberian ground waters; their presence in ground waters of the peninsula would be expected owing to their distribution in the Maghreb of North Africa and the Balearic islands.

DISCUSSION

The major geotectonic units of the Iberian peninsula are given in fig. 8. The Hercynian massif has remained uncovered by Mesozoic seas. Along the margins of this massif areas are situated which are strongly deformed during Alpine orogeny or which consist of Tertiary sedimentation basins. By comparing figs. 7 and 8 it is quite obvious that a certain correspondence exist between the amphipod districts and geological structures. The Hercy-

nian massif roughly corresponds with the Meseta district and is poor in stygobiont amphipods. In contrast, the ranges of especially the hadzioid amphipods *Pseudoniphargus*, *Parapseudoniphargus*, and *Metahadzia* are limited to Mesozoic and Tertiary units. These genera are considered of direct marine origin and of low dispersal ability. These observations may indicate that the origin of hadzioid amphipods in continental ground waters demands mainly a vicariant explanation. The observation that the distribution of *Pseudoniphargus* and other hadzioid amphipods outside Iberia is limited to areas influenced by Late Cretaceous and Tertiary seas supports this idea. The distribution of the remaining genera shows no clear correlation with geotectonic units. In the explanation of the origin in Iberian ground waters of widespread genera, like *Haploginglymus*, *Niphargus*, *Bogidie-lla*, and *Salentinella*, apparently greater importance must be attached to dispersal and probably ecological determinism.

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RESUMEN

INTRODUCCIÓN AL ESTUDIO DE LOS ANFÍPODOS SUBTERRÁNEOS IBÉRICOS

Se incluyen datos zoogeográficos de anfípodos de aguas subterráneas. Se discuten los rangos geográficos, los hábitats y la distribución de los géneros. La Península Ibérica se divide en distritos zoogeográficos basados en la distribución de los anfípodos, algunos de los cuales se correlacionan con unidades geológicas.

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