Pseudoniphargus (subterranean crustacean amphipod) from Morocco: systematics, phylogeny and ecological and biogeographic aspects

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Abstract

The interstitial groundwater amphipod *Pseudoniphargus* (Crustacea) is highly diversified in Morocco. Five species have been described from the northern part of the country. Recent surveys in the same region have resulted in the discovery of about ten species new for science. The phylogenetic relationships within the Moroccan species show three lineages. Freshwater species are derived from marine ancestors. Both the two-step model of colonization and evolution and the geological history of the region provide an understanding of their origin. During the Tortonian period, the marine ancestor lived in the coastal groundwater of the Tethyan South Rifian channel between the Rif and Africa. The establishment in continental groundwaters is due to the Tethys regressions in the late Tortonian and the early Messinian periods. Further diversification and speciation of extant endemic species result from the Rifian orogenesis as well as from the edification of recent hydrographic systems.

Introduction

The species of the genus *Pseudoniphargus* constitute a distinct group within the Hadzioida Superfamily (STOCK, 1980; NOTENBOOM, 1988). Species of this group are known from both continental freshwater and littoral brackish water. They are widely distributed in the central and western Mediterranean, as well as on Atlantic islands such as Bermuda and Canary islands (NOTENBOOM, 1988; SANCHEZ, 1991; STOCK *et al.*, 1986, COINEAU & BOUTIN, 1996; FAKHER *et al.*, 1999).

In Morocco, the genus *Pseudoniphargus* exhibits five known species (COINEAU & BOUTIN, 1996; FAKHER *et al.*, 1999).

Recent discoveries

Recent surveys in the northern areas of Morocco allowed to extend our knowledge on the biogeography of *Pseudoniphargus* species, and especially to discover about ten species unknown to Science (FAKHER, 1999).

In Morocco, *Pseudoniphargus* species occur only in the northern part of the country. It seems that they never lived beyond a line going from the Idrissid Land in the West, the Peri-Rifian corridor, to the coal-basin of Jerada in the east. Such a border line corresponds also to the northern limit of the amphipods *Metacrangonyx* distribution, where the two genera co-occur at several sites (MESSOULI, 1994)

Ecology, biology, evolution

The new species exhibit a high endemism degree and inhabit varied biotopes such as wells, springs and caves. Water conductivity is generally high and fluctuates from 116 to 17350 $\mu S.cm^2$. One species has been collected in a thermal spring with water temperature reaching 44°C.

Pseudoniphargus length varies from 3.5 to 11.5 mm in the Spanish species *P. incantatus* Notenboom, 1986 and *P. grandis* Notenboom, 1987 respectively. In Moroccan representatives, dwarfish species exist (1.7 to 2.2 mm). These latter species probably result from progenetic evolutionary processes. During the development, the ancestors reached a precocious sexual maturity and adults retain a number of characters which can be observed at the first post-embryonic developmental stages of large *Pseudoniphargus* species. Such evolutionary process may be viewed as an energy economy in an interstitial milieu provided with low energy allocation. Processes of heterochrony may result from one or a few molecular change in developmental genes and provide a better understanding of important discontinued morphological evolution within a crustacean group.

Phylogeny

A phylogenetic study of the Moroccan species results in three distinct lineages exhibiting both original characteristics and affinities with the species from the Canary islands and the Iberian Peninsula.

The first lineage, which is composed of only one species, is characterized by the coxal plates 1 to 4 clearly longer than wide, the flagellum of the antenna 2 shorter than the last peduncular segment, and epimeral plates without spines.

The second lineage comprises elongate species which have pereiopods 5 shorter thant pereipods 4, gnathopods with short carpus, pereiopods 7 longer than pereiopods 6, and uropods 3 with the peduncle armed with lateral spines.

Species of the third lineage can be easily recognized due to the epimeral plates exhibiting at least three ventral spines.

Historical biogeography

The present distribution of Moroccan *Pseudoniphargus* representatives shows that most of the species are located in regions which have been covered by the Tethys sea during the Tortonian period (BOUTIN & COINEAU, 1988; COINEAU & BOUTIN, 1996; FAKHER *et al.*, 1999). Furthermore, the location of different species within these latter areas in groundwater with a high content of chlorures (up to 1554 $mg.L^{-1}$) is an additional argument concerning the marine origin of these amphipods.

A possible historical biogeographic scenario for the Moroccan species of *Pseudoniphargus* is discussed. This scenario is based on the "Two-step Model of Colonization and Evolution" (BOUTIN & COINEAU, 1990; NOTENBOOM, 1991; HOLSINGER, 1994) on the one hand, the palaegeography and the geological history of the areas populated by *Pseudoniphargus* species on the other hand (MICHARD, 1976; DERCOURT *et al.*, 1985; ALVINERIE *et al.*, 1992; Cartes E.S.G. Maroc, 1992; DERCOURT *et al.*, 1993).

During the Tortonian period (10 Ma), Tethian marine south Rifian corridor separated the new allochtonous Rifian area from the northern African continent. The Tethyan Mediterranean domain communicated with the Atlantic ocean through this Rifian corridor. The common ancestor of all species of the Moroccan *Pseudoniphargus* lived in the interstitial sands of the littoral area of this south Rifian channel during the Tortonian period. This ancestor settled in continental freshwater due to the regressions of the western and the eastern parts of the south Rifian channel in the Late Tortonian (ALVINERIE *et al.*, 1992; COINEAU & BOUTIN, 1996; FAKHER *et al.*, 1999). Thereafter, further diversification, speciation and vicariance resulted from the Rifian orogenesis and the subsequent erosion: the edification of new important hydrographic systems contributed to evolution through vicariance and endemism in isolated valleys. Furthermore, passive dispersal of groundwater populations downstream of present rivers, extended their distribution to locations not covered by the former Tethys corridor. Such latter species are therefore secondary established; it is corroborated by sympatric and sometimes syntopic species, by the site proximity of different species, as well as by the overlap of the distribution areas of different lineages of *Pseudoniphargus.*

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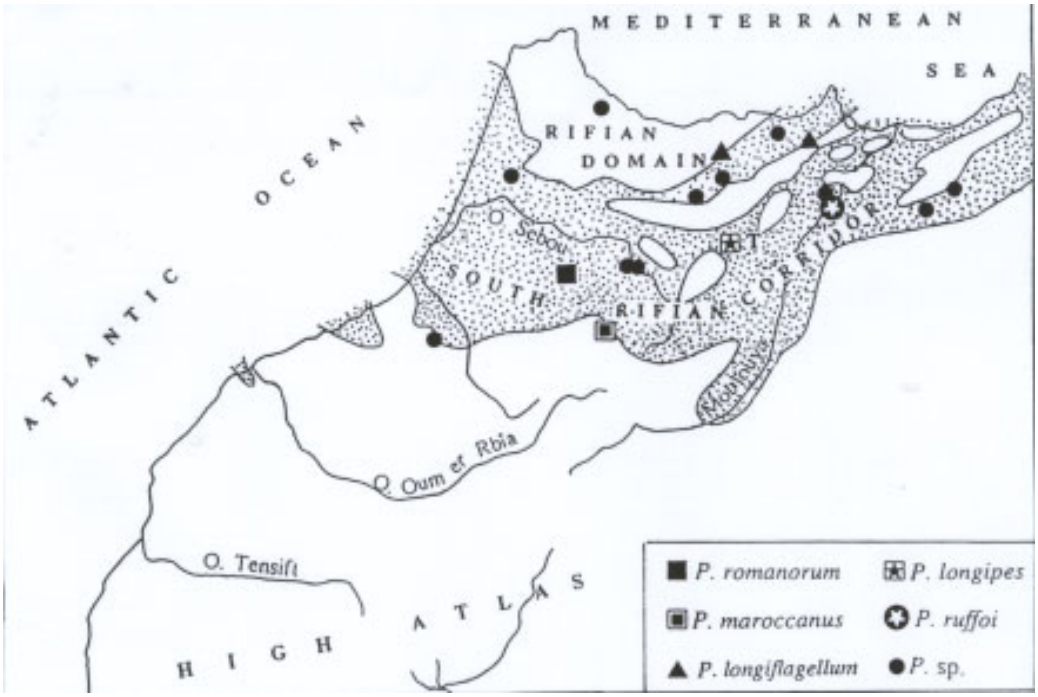

Figure 1 - Distribution of the species of Pseudoniphargus in the northern region of Morocco and extension of the Tethyan south-Rifian channel in the Tortonian period (dotted area). Small solid circles: species to be described. After the maps of the Edition du Service Géologique du Maroc, Rabat and ALVINERIE et al. (1992)

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