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Origin, diversity and distribution of freshwater epigean amphipods in Maghreb

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Abstract – Northern Africa, although one of the world hotspots of biodiversity, is poorly studied and the freshwater fauna living in this part of the world remains partly unknown. This study focused on the diversity and distribution of the poorly known epigean freshwater amphipods. We performed an exhaustive analysis of the literature on this group of crustaceans and sampled 106 additional localities from the eastern part of Algeria and in Tunisia. Our results showed an important diversity with 25 species (including the presence of at least three new undescribed species) and a very high rate of endemism with 52% of species occurring at on only 1 or 2 sites. We also highlighted a very low diversity on each site with only 4.4% of sites harboring more than 1 species. The comparative distribution of certain species between Europe and Maghreb and also between the western and eastern part of Northern Africa allow us to discuss some hypotheses about the factors underlying this endemism and the biogeographical origin of species. However, our study revealed a general lack of knowledge in the region, especially in the South of Morocco and Algeria. Hence, more information would be needed to propose adapted conservation strategies of freshwater fauna in Maghreb.

Keywords: Amphipoda / biodiversity / biogeographical distribution / freshwater / Northern Africa

1 Introduction

The Mediterranean Basin is known as one of the world's biodiversity hotspots (Myers *et al.*, 2000). Its freshwater harbors 35% of Palearctic freshwater species and more than 6% of the world freshwater biodiversity with a very high rate of endemic species (Tierno de Figueroa *et al.*, 2013). This exceptional biodiversity is strongly threatened by anthropogenic pressure such as the destruction of habitat, biological invasions and climate change which may become the most important factor of the biodiversity decline (Sala *et al.*, 2000; Pereira *et al.*, 2010; Caro *et al.*, 2012). The biodiversity loss related to climate change may reach 39% to 43% of the world endemic species (Malcolm *et al.*, 2006).

Among Mediterranean countries, countries in Maghreb are very affected by anthropogenic impacts and have to deal with combined effects of both climate change and overexploitation of freshwater resources (Romagny and Cudennec, 2006). It is therefore very urgent to define conservation priorities using credible information on biodiversity which, unfortunately, remain acutely scarce in this part of the world. This is

especially true for aquatic invertebrates, even if they represent at least 80% of the world's freshwater species (Balian *et al.*, 2008). This group is much less studied than other groups such as fish or amphibians (Dudgeon, 2000). As a consequence, information concerning extinction rates or just species inventories remains lacking for most of freshwaters (Palmer *et al.*, 2000).

In this study, we worked with freshwater epigean amphipods. This group is much diversified in inland waters with more than 2400 known species over the world (WORMS, 2019). It also inhabits diverse kinds of freshwater environments (running waters, lakes, ground waters) in which they represent the leading invertebrate biomass (Navel *et al.*, 2010; Piscart *et al.*, 2009b, 2011). As their life cycle is entirely aquatic, they are also particularly threatened by climate change, contrary to insects which have a flying adult stage to avoid drought events (Aspin *et al.*, 2019).

In Maghreb, knowledge on freshwater amphipods is rather limited and consists mainly of few taxonomic works (Karaman and Pinkster, 1977; Kayo *et al.*, 2012; Pinkster, 1993; Rewicz *et al.*, 2014). We currently know 22 species able to colonize freshwaters (Ayati *et al.*, 2018; Rewicz *et al.*, 2014). All those species belong to the family Gammaridae, more precisely into four genera: *Echinogammarus* Stebbing, 1899 (13 species);

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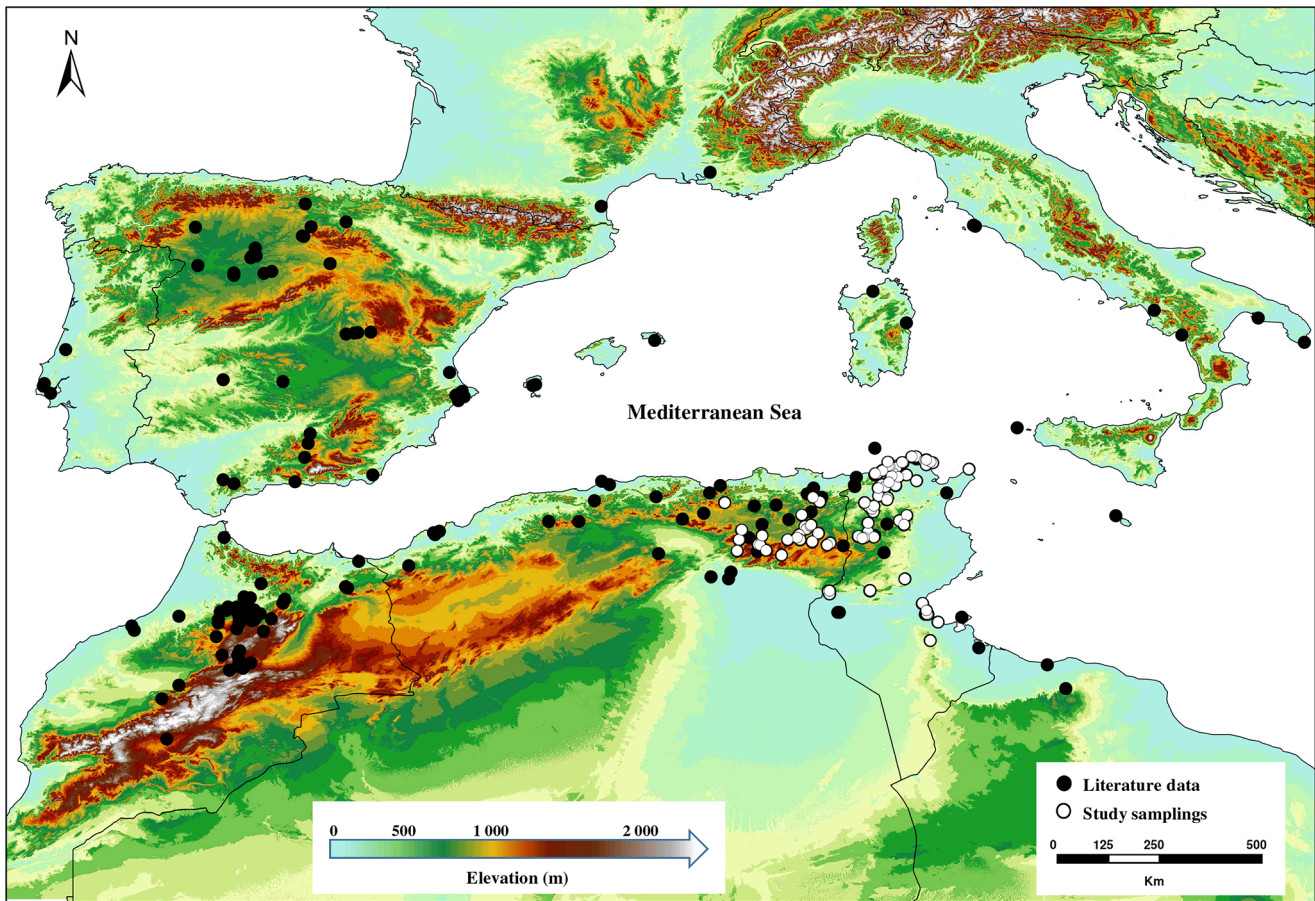


Fig. 1. Location of our sites and sites from literature.

Gammarus Fabricius, 1775 (7 species); *Chaetogammarus* Martynov, 1924 (1 species); *Rhipidogammarus* Stock, 1971 (1 species). The genus *Echinogammarus* is the most diversified and divided into three groups of species (*Echinogammarus-berilloni*, *-pungens*, and *-simoni* groups). Recently, the taxonomic position of species from these groups has been a subject of debate (Hou and Sket, 2016; Sket and Hou, 2018). From their molecular studies, these authors proposed the genus *Homoeogammarus* (Schellenberg, 1937) as a valid name and to consider species of the *Echinogammarus simoni* group as members of this genus (Hou and Sket, 2016). However, the diagnosis of the genus provided did not match the morphological description of the species recently described (Ayati *et al.*, 2018). The lack of clear morphological diagnosis of the genus *Homoeogammarus*, acknowledged by the authors themselves (Sket and Hou, 2018) and the few number of species from Northern Africa taken into account in these studies are not sufficient to clearly solve this issue. We hence decided to keep the *Echinogammarus* groups in our study.

In this context, the goal of our study is to complete the existing knowledge on the diversity and the distribution of epigeal freshwater amphipods in Maghreb. To do this, we summarized all the published literature and made additional samplings in Algeria and Tunisia. The comparison of old/recent information with our new dataset allows us to better understand the present biogeographical distribution of species in this part of the world.

2 Material and methods

2.1 Study area

Our study focusses on Maghreb (Morocco, Algeria, and Tunisia) representing around 3,000,000 km² of total area. These countries belong to the Mediterranean area of the Palearctic and are characterized by hot climates ranging from the hot desert climate in the South to the hot Mediterranean Climate in the North (Peel *et al.*, 2007). The three countries are also linked by the Atlas Mountains, which occupy a large part of Morocco, Northern Algeria and Tunisia with Djebel Toubkal (4167 m) in Morocco as the highest peak. Most rivers and streams flow on the North face of the Atlas Mountains and are also characterized by a high rate of intermittence (Schneider *et al.*, 2017).

2.2 Data on amphipods

An exhaustive survey of literature on freshwater epigeal amphipods (species descriptions, identification keys, monography, PhD theses, books, and papers) has been done for all species known in Maghreb. For species known from both Europe and Maghreb, European localities were also taken into account (Fig. 1), except for *Echinogammarus pungens* inhabiting a great number of localities from Catalonia to Greece and for which we

Table 1. Faunal list of epigeal amphipods known in Maghreb. Literature used to determine the distribution area are: 1 = Ayati *et al.* (2018); 2 = Chevreux (1894); 3 = Chevreux and Fage (1925); 4 = Fadil and Dakki (2001); 5 = Fadil and Dakki (2003); 6 = Fadil and Dakki (2006); 7 = Fadil *et al.* (2009); 8 = Gauthier (1928); 9 = Karaman (1993); 10 = Karaman (1935); 11 = Karaman and Pinkster (1977); 12 = Pinkster (1971); 13 = Pinkster (1993); 14 = Piscart *et al.* (2013); 15 = Rewicz *et al.* (2014); 16 = Hou and Sket (2016).

Genus	Species	References
<i>Echinogammarus</i> Stebbing, 1899	<i>E. afer</i> Stock, 1974	13
	<i>E. annandalei</i> (Monod, 1924)	8, 13
	<i>E. carthaginiensis</i> Ayati, Dhaouadi, Mahmoudi, Piscart, 2018	1
	<i>E. dactylus</i> G. Karaman, 1987	13
	<i>E. haraktis</i> Piscart, Merzoug, Hafid, 2013	14
	<i>E. klaptoczi</i> Schäferna, 1908	13
	<i>E. oujdae</i> Fadil and Dakki, 2003	5, 7
	<i>E. pungens</i> (H. Milne Edwards, 1840)	13, 15
	<i>E. reductus</i> Pinkster, 1993	13
	<i>E. simoni</i> (Chevreux, 1894)	2, 8, 13, 16
	<i>E. tacapensis</i> (Chevreux and Gauthier, 1924)	13
	<i>E. tunetanus</i> Ayati, Dhaouadi, Mahmoudi, Piscart, 2018	1
	<i>E. valedictus</i> Pinkster and Platvoet, 1990	13
	<i>Echinogammarus</i> sp1	–
	<i>Echinogammarus</i> sp2	–
	<i>Echinogammarus</i> sp3	–
<i>Gammarus</i> Fabricius, 1775	<i>G. acalceolatus</i> Pinkster, 1971	11
	<i>G. gauthieri</i> (S. Karaman, 1935)	7, 8, 10, 11, 12
	<i>G. marmouchensis</i> Fadil and Dakki, 2006	6
	<i>G. maroccanus</i> Fadil and Dakki, 2001	4
	<i>G. microps</i> Pinkster and Goedmakers, 1975	11
	<i>G. riftalensis</i> Fadil and Dakki, 2006	6
	<i>G. rouxi</i> Pinkster and Goedmakers, 1975	7, 11
<i>Chaetogammarus</i> Martynov, 1924	<i>C. saisensis</i> Fadil <i>et al.</i> , 2009	7
<i>Rhipidogammarus</i> Stock, 1971	<i>R. rhipidiophorus</i> (Catta, 1878)	3, 8, 9

indicated the whole distribution area in Europe (Piscart and Bollache, 2012; Rewicz *et al.*, 2014). For *Gammarus gauthieri*, localities provided by Karaman and Pinkster (1977) in Algeria and Tunisia could not be confirmed neither in the literature cited by the authors nor with our own samplings in the same areas. So, these localities have been removed from our maps.

In order to complete existing knowledge, freshwater amphipods were collected in the East of Algeria (30 sites) and in Tunisia (76 sites) from 2016 to 2019 (Fig. 1). Amphipods were sampled using a hand net sampler (Ø 500 µm mesh size) in all kinds of freshwater environment (sources, streams, lakes, reservoirs, and ponds). On each site, all habitats were prospected (stones, roots, macrophytes) to collect at least 10 amphipods (but generally, more than 30 animals were sampled).

Samples were preserved in 96% alcohol on the field. All amphipods were identified at the species level using a stereomicroscope Olympus SZX16 (Olympus™) and adapted identification keys (Karaman and Pinkster, 1977; Pinkster, 1993), updated with new descriptions (Ayati *et al.*, 2018; Fadil and Dakki, 2003, 2006, 2001; Piscart *et al.*, 2013). For some animals, microscopic slides were used to confirm the identification (see Ayati *et al.*, 2018 for details on microscopic preparation).

2.3 Data analysis

All maps were realized with ArcGis Desktop 10.4 software (Esri™) and using GIS data available on DIVA website (<http://www.diva-gis.org>) or provided by (Schneider *et al.*, 2017) and WGS 84 projection.

3 Results

Among the 22 species known in Maghreb (Tab. 1), only five species are also present in Europe. *Echinogammarus simoni* and *Gammarus gauthieri* are found in the Iberian Peninsula, *Echinogammarus klaptoczi* inhabits Balearic and Malta Islands, while *Echinogammarus pungens* and *Rhipidogammarus rhipidiophorus* are only known from localities very close to the Mediterranean Sea, from Catalonia to Greece and from Southeastern France to Sicily respectively. All other 17 species are native to Maghreb among which 10 are restricted to only one or two localities (Fig. 2). All these rare species are located on the Northern Face of the Atlas Mountains, except in few localities near Chottes Melhrir and El Djerid between Algeria and Tunisia. Another characteristic of amphipods in Maghreb is the very few number of species per site. Indeed, among the 274 locality recorded, only 12

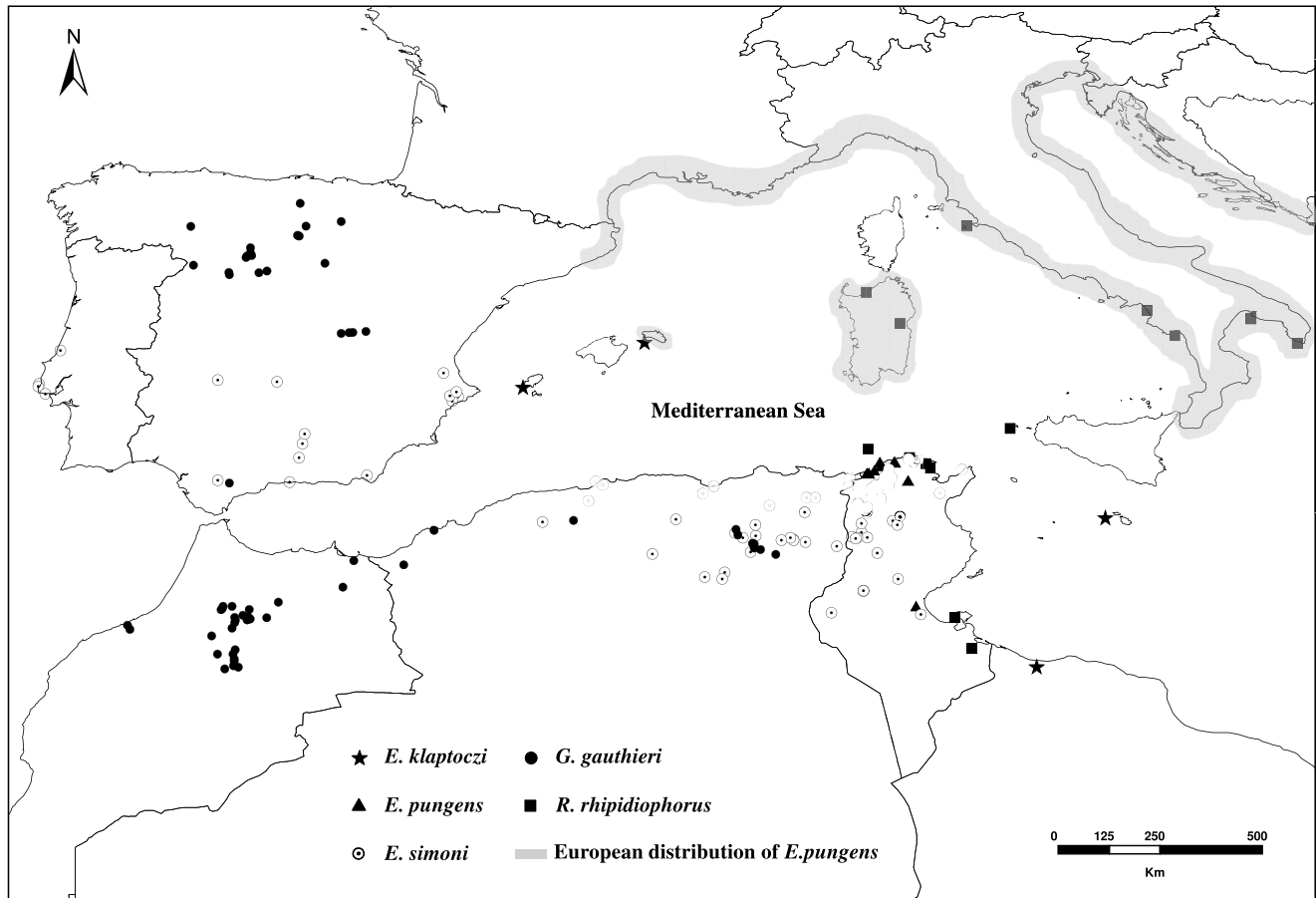


Fig. 2. Distribution of species present in Europe and Maghreb.

sites (4.4%) harbored two species whereas all other sites are monospecific.

From a diversity point of view, the genus *Echinogammarus* is the most diversified with 13 known species and likely three new species from Algeria were discovered in our study (ongoing description). Among these species, 8 (50% of the total richness of the genus) belong to the *Echinogammarus simoni*-group (Tab. 1). For this group, only *E. simoni* is widely distributed from Tunisia to Iberian Peninsula, all others having restricted distribution areas in Eastern Algeria and Tunisia (Fig. 3).

The *Echinogammarus pungens*-group is the second most diverse group with five species (Fig. 4). *Echinogammarus pungens*-group has only one species, *E. pungens*, widely distributed between Tunisia and the southern European coast (Fig. 2). However this species is always restricted to coastal streams and sources and was never found at more than 50 km from the Mediterranean Coast. The other species of this group are distributed throughout Maghreb but always on small distribution areas (Fig. 4). This group also harbors the only one *Echinogammarus* species from Morocco, *Echinogammarus oujdae*. *Echinogammarus berilloni*-group is the least diverse with only three species and in contrast to other groups of *Echinogammarus*, does not have common species between continental Europe and Maghreb because *E. klaptoczi* is

known only in Libya and some Mediterranean Islands (Fig. 2). This group is distributed from East Algeria to Libya (Fig. 4).

There are two other genera present in Maghreb with only one species each (Fig. 4). The genus *Chaetogammarus* with *C. saisensis* distributed only in the Saïss Vallée and Rift Mountains in the North of Morocco and the genus *Rhipidogammarus* with the species *R. rhipidiophorus* which is observed only in coastal sources very close (few meters) from the Mediterranean Sea in Tunisia and European coast from France to Italy.

Finally, the genus *Gammarus* is also well represented in Maghreb with 7 species known (Fig. 5), among which only *G. gauthieri* is widely distributed from Algeria to Spain (Fig. 2). All other species are only restricted to few localities on the North Face of Atlas Mountains in Morocco.

4 Discussion

Our study of the distribution of epigeic freshwater amphipods in Maghreb confirms the important richness according to the scarcity of surface waters and a high rate of endemism in this part of the world (Tierno de Figueroa *et al.*, 2013). With 13 rare species (considering the three potential new species) inhabiting in less than three localities among the

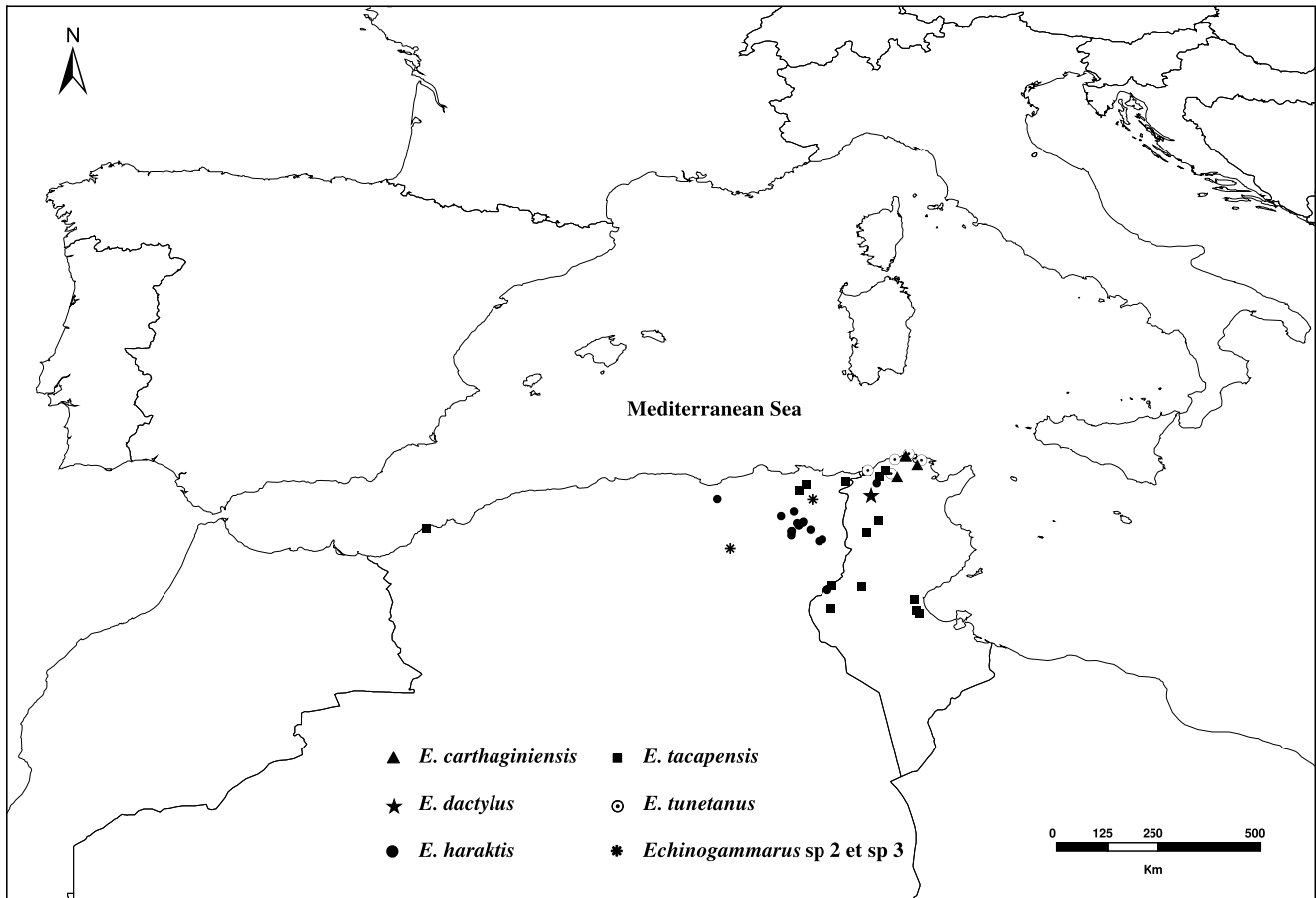


Fig. 3. Distribution of *Echinogammarus simoni*-group in Maghreb.

25 species, the rate of endemism in Maghreb (52%) is much higher than the endemism in Europe ($\approx 20\%$) for epigean amphipods (Karaman and Pinkster, 1987, 1977; Karaman, 1993; Pinkster, 1993; Piscart and Bollache, 2012). Indeed, Maghreb was a refuge area during the last glacial periods (Husemann *et al.*, 2014) and the high topographic heterogeneity due to the presence of Atlas Mountains impose geographical orographic barriers that limit the existence of wide distribution areas (Pleguezuelos *et al.*, 2010). Another important factor to consider in studying the diversity of aquatic fauna in Maghreb is the limitation of the water resources during the last 6000 years (Schneider *et al.*, 2017). This factor, in combination with interspecific interactions, may explain the very low species richness per site. Indeed, we know that interspecific interaction in amphipods may lead to the displacement or the disappearance of species locally (Piscart *et al.*, 2007, 2009a, 2010). The scarcity of water could reduce the presence of refuge areas for species with low competitive abilities and the low species richness recorded could be the results of disappearance of the less competitive species in the very harsh environmental conditions in Maghreb. However, it is very difficult to confirm this hypothesis because amphipods do not leave fossil traces, contrary to Ostracods or Mollusks.

Another explanation for the endemism may be the lack of knowledge on the distribution of amphipods in Maghreb.

Indeed, Africa remains largely unknown for aquatic fauna, especially for crustaceans (Kayo *et al.*, 2012) and the Amphipoda is itself one of the least known taxonomic group for which the rate of discovery increase regularly with 20% of the total number of known species described during the last 10 years (Arfianti *et al.*, 2018). The lack of knowledge on the species distribution is also one of main justification of our study. However, our study, based on both extensive literature survey and complementary field samplings confirmed the high rate of endemism and the restricted distribution area of species, except for two species previously known only from the type locality. For *E. valedictus*, previously known from Djurdjura Mountains near Tizi Ouzou (Algeria), we found another locality near Batna at 270 km of Djurdjura Mountains and for *Echinogammarus haraktis* described near Oum El Bouaghi (Algeria), we found several new localities in Algeria and also in Tunisia at 300 km from the type locality. On the contrary, recent works in this region (Ayati *et al.*, 2018; Piscart *et al.*, 2014) showed that species with wide distribution areas such as *E. simoni* consist of several morphologically closely related species. In our study, the discovery of likely three new species during our samplings in Algeria, with two of these species (*Echinogammarus* sp2 and *Echinogammarus* sp3) belonging to the *Echinogammarus simoni*-group tend to validate the previous results.

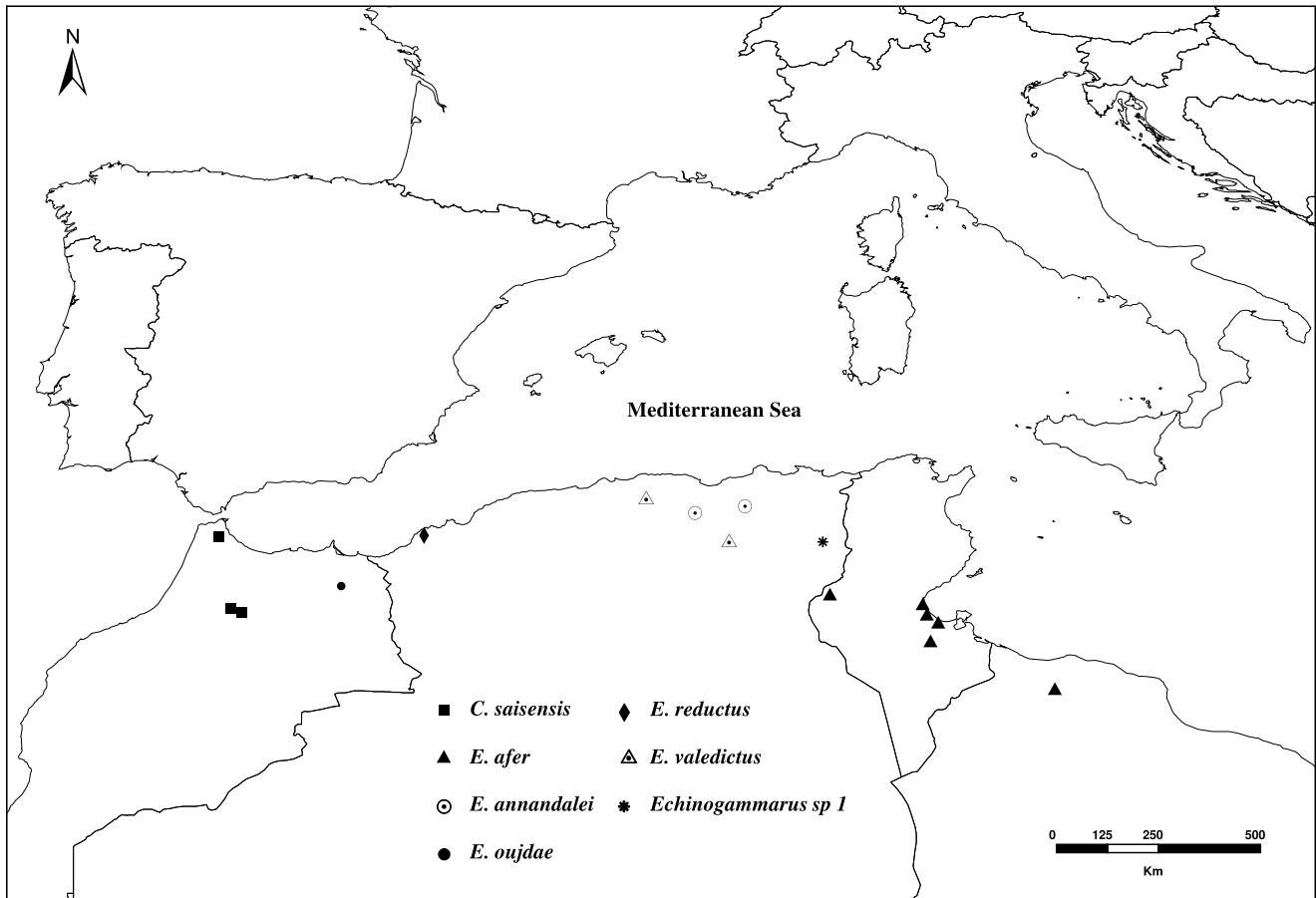


Fig. 4. Distribution of *Echinogammarus berilloni*- and *Echinogammarus pungens*-groups in Maghreb.

The origin of species in Maghreb is likely very old as suggested by the common species known in Europe and in Maghreb. The presence of the genus *Gammarus*, and especially *G. gauthieri* in Morocco and in Iberian Peninsula testifies an old exchange between these two regions. Indeed, Europe and Maghreb are separated by the Mediterranean Sea which represents a strong geographical barriers for most of non-flying animals. However, we know that the Mediterranean Sea was dry 5.5 million years ago during the messinian crisis (Hsü *et al.*, 1977; Krijgsman *et al.*, 1999) and several examples of exchanges between European and Maghrebian fauna during this period have been documented (Carranza *et al.*, 2006; Guy-Haim *et al.*, 2018; Stöck *et al.*, 2012). In addition, some exchanges could be older. Indeed, phylogeographical analyses suggested the presence of the genus *Gammarus* in European freshwaters since at least 40 million years during the Eocene (Hou *et al.*, 2011). The presence of the genus and the low depth of the Mediterranean Sea between Iberian Peninsula and Maghreb at the end of the Eocene (Meulenkamp and Sissingh, 2003) may have promoted the presence of *G. gauthieri* on both sides of the Mediterranean Sea. The distribution of *E. simoni* in Iberian Peninsula, East Algeria and Tunisia is more complex. The Messinian crisis may also promote the range expansion of the species in Maghreb but its absence in Morocco and, more generally, the under representation of the genus *Echinogammarus* in this country are not congruent with this hypothesis.

It is also unlikely that the establishment of the *Echinogammarus simoni* started from Sicily because this species is not present in Italy. The most plausible explanation is that the colonization of Maghreb by species of the genus *Echinogammarus* resulted from another geological event and could have possibly been from successive colonizations from Mediterranean marine species along Algerian or Tunisian coasts where the genus is the most diversified. Indeed, this genus is only known in freshwaters of Mediterranean Basin (Pinkster, 1993), that is congruent with a diversification from the Mediterranean Sea instead of a colonization during Messinian crisis (Barnard and Barnard, 1983; Hou and Sket, 2016).

For some species of Maghreb, the colonization from European Coasts is very recent and gene flow is still present (unpublished data). We suppose that it is the case for species living closed to the coast and on islands (*E. klaptoczi*, *E. pungens*, and *R. rhipidiophorus*). These three species colonized only a small stretch of freshwater close to the Mediterranean Sea and are mainly distributed in the eastern part of our study area. In addition, these species are known to have a high tolerance to salinity which explains their presence in the estuarine environment (Pinkster, 1993). The decrease of the sea level during the last glacial period (–25,000 years) may have reduced the distance between Europe and North Africa and fostered the exchange between salt tolerant populations.

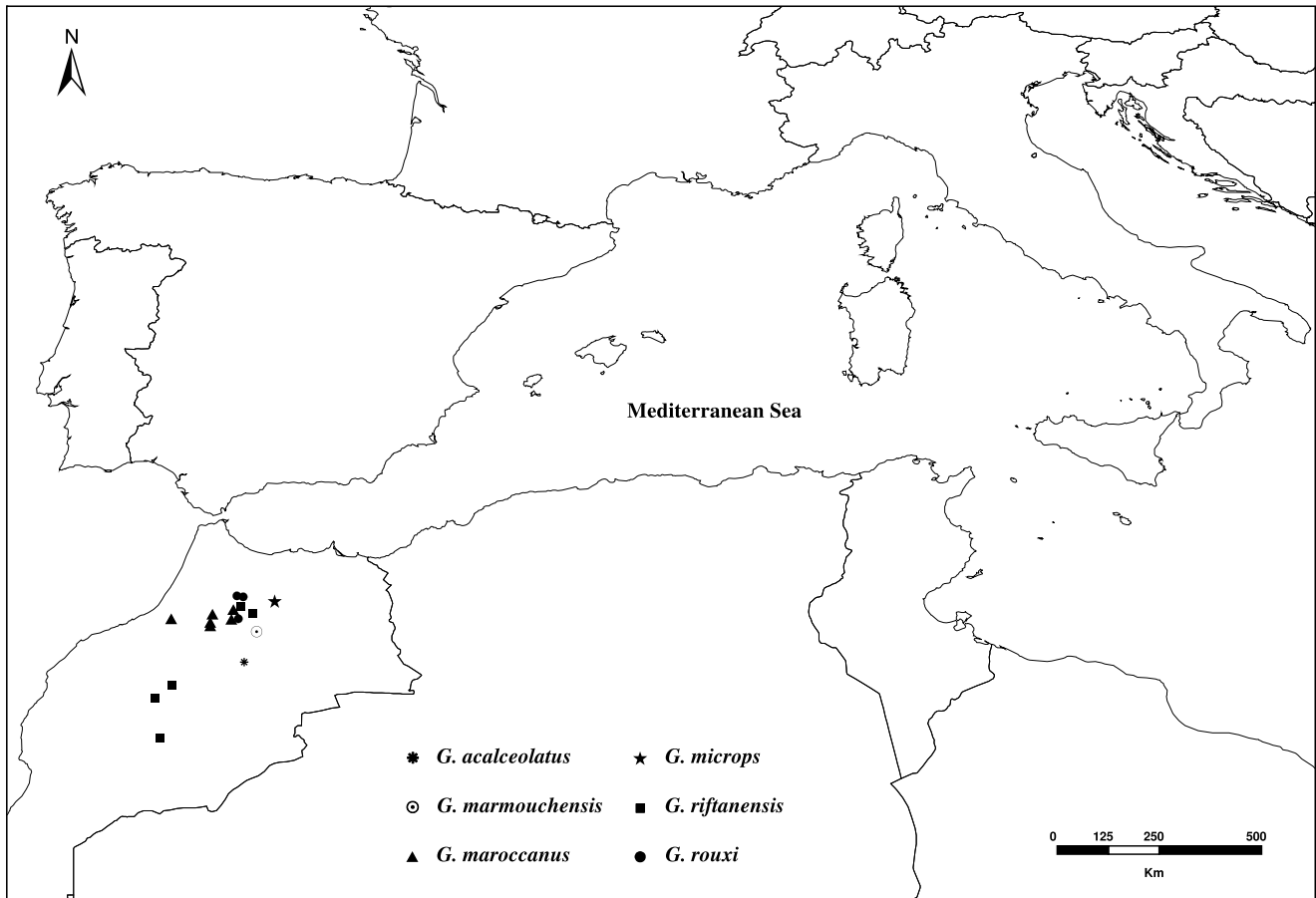


Fig. 5. Distribution of *Gammarus* species in Maghreb.

The distribution of these species in the Eastern Part of Maghreb suggests the use of the Sicily strait which is already known for the exchange of fauna between Europe and Maghreb before glacial period (Husemann *et al.*, 2014) but also more recently during the glacial period (Habel *et al.*, 2009, 2010; Stöck *et al.*, 2008). Rewicz *et al.* (2014) proposed that the colonization of Tunisia by *E. pungens* might be the result of a recent invasion by this species from Europe. This hypothesis was based on the belief that this species is present in only one locality in Tunisia. However, our study clearly showed that the distribution of *E. pungens* is much more widespread in Tunisia and confirms that *E. pungens* must be considered as native form this country.

Our study proved the important biodiversity of epigean amphipods in Maghreb and clarified the origin of the 22 known species. Our results also highlighted the lack of knowledge in this part of the world with the discovery of several new species, even in the most well-known part of Maghreb. In regions where the threats on biodiversity are numerous, additional studies are recommended to define new and adapted conservation plans for freshwater fauna, especially in the South parts of Algeria and Morocco.

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