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Distributional patterns in the Greek species of the terrestrial isopod genus *Armadillidium* Brandt, 1833

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ABSTRACT. The Mediterranean genus *Armadillidium* has radiation centres in Italy and Greece, with around 55 species in each of the two countries. Three of the Greek species are found in most parts of the Mediterranean region, and about 40 species are endemic to Greece. Island endemism is, however, low; five species are known from only a single island. Six species occur on several Ionian islands but not on the adjacent mainland. On the Aegean islands, with the exception of Crete, endemic species are lacking. The bulk of the Greek species have restricted distribution ranges on the mainland and the Peloponnese. A gradient of species density from west to east is correlated to climatic factors and a substitution by other conglobating genera in the east.

INTRODUCTION

The genus *Armadillidium* Brandt, 1833 comprises around 180 nominal species, and the question of its monophyly is still open to debate. Its autochthonous distribution covers Europe, the coasts of the Mediterranean and the Black Sea, and the Caucasus area (Fig. 1). The highest species numbers occur in Italy and Greece, with more than 50 species in each country. In the Aegean region there is an abrupt and rather enormous drop in the number of species numbers, with only five species known from the Turkish mainland, contrasting with around 55 species recorded from the Greek territory (compare ARCANGELI, 1914; STROUHAL, 1927; 1928 a; 1928 b; 1929 a; 1929 b; 1936; 1937 a; 1937 b; 1937 c; 1937 d; 1938; 1939; 1956; 1966; VANDEL, 1958, SCHMALFUSS, 1981, 1982, 1985 a, 1985 b; SFENTHOURAKIS, 1992; 1993; 1994; 1995; SFENTHOURAKIS & GIOKAS, 1998; around 8 undescribed species from Greece are in the Stuttgart collection).

Fig. 1. – Autochthonous distribution of the genus *Armadillidium*, with species numbers of selected regions.

DISTRIBUTION TYPES

The 55 Greek species exhibit a number of distribution types that can be ascribed to the following categories (listed in Table 1):

Holomediterranean

Armadillidium vulgare probably originated in the eastern mediterranean region and has today a rather cosmopolitan distribution, having been introduced by human activities to most parts of the world. But even these widely distributed species with obviously broad

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ecological tolerances have ecological limits beyond which they cannot exist. In the Aegean *A. vulgare* is missing on a number of larger islands, e. g. on Kárpathos and Ródhos (Fig. 2), where it should not have been overlooked. In a former paper I have interpreted this situation as competitive exclusion between *A. vulgare* and *Schizidium oertzeni* (Budde-Lund, 1896) (SCHMALFUSS, 1983: 15, 17). Since then, both species have been found sympatricly on several islands, e. g. Náxos, and I have dismissed the idea of direct competition that excludes *A. vulgare* from these islands. Probably climatic factors, e. g. very hot and dry summers, in combination with the lack of suitable biotopes, keep these islands free of *A. vulgare*.

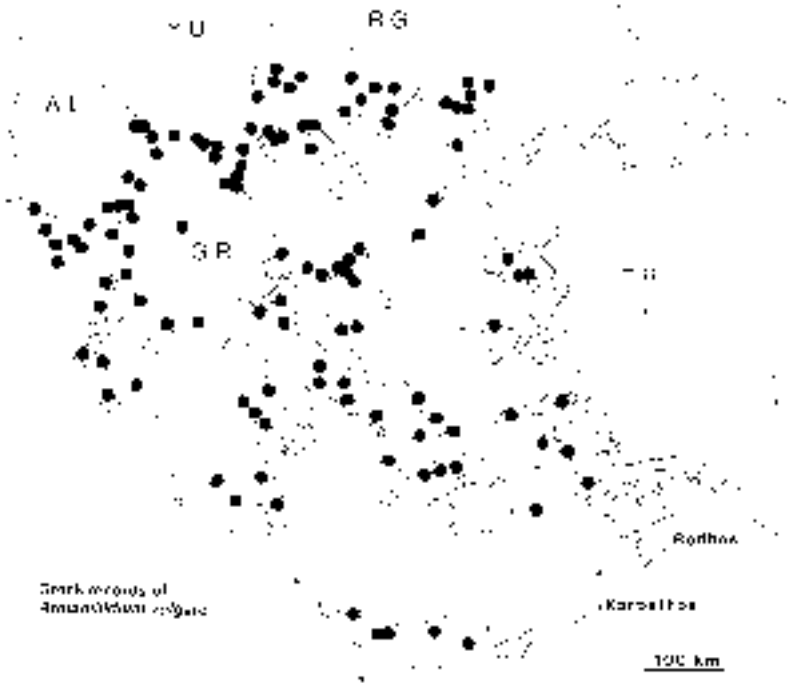

Fig. 2. – Greek records of *Armadillidium vulgare* (literature records and samples in the Stuttgart collection). Note the absence of the species on the islands Kárpathos and Ródhos.

Two more Greek species, both connected to litoral biotopes, exhibit an overall distribution throughout most of the Mediterranean and even along the Atlantic coast of Europe. *Armadillidium granulatum* occurs from the Atlantic coast of Portugal and France through the Mediterranean, also along the North African coast, to the Aegean and the southwestern Black Sea (Fig. 3). It is missing in the easternmost part of the Mediterranean, and it has not been found in the northwestern Aegean (Fig. 3). In the eastern Mediterranean it is substituted by a vicariant species, *Armadillidium fallax* (compare Schmalfuss 1989). Searching for an explanation for its absence in the northwestern Aegean I found a correlation with the 5 mm precipitation line for July (see PHILIPPSON, 1948). Since this correlation does not exist in the more western distribution area of the species it should not be a direct causal correlation, but a secondary regional phenomenon.

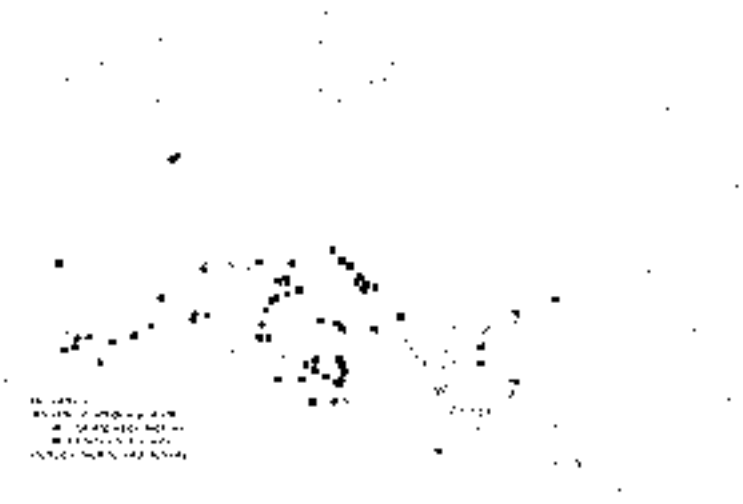

Fig. 3. – Recorded overall distribution od *Armadillidium granulatum*, including literature records and samples from the Stuttgart collection.

The second species of this distribution type is *Armadillidium album*, of which we have two new unpublished records from Greece. The species reaches up the Atlantic coast to the British Isles and the Netherlands. It is small and buries itself deep into the sand, so it is easily overlooked and may turn up in many other places of the Mediterranean.

Eastern Mediterranean

Armadillidium marmoratum is known from the coasts of the Aegean, reaching the Black Sea at the Bosporus, from Cyprus, Israel and Egypt (Fig. 4). It is still an open question whether it is conspecific with taxa described from Italy. In any case it is the only species distributed throughout the eastern Mediterranean.

Northeastern Mediterranean

Armadillidium pallasii lives along the shores of the Adriatic, the northeastern Aegen and the Black Sea (Fig. 5). If we suppose the southern distribution boundary to be formed by temperature and/or precipitation factors we can imagine a continuous distribution along the coasts

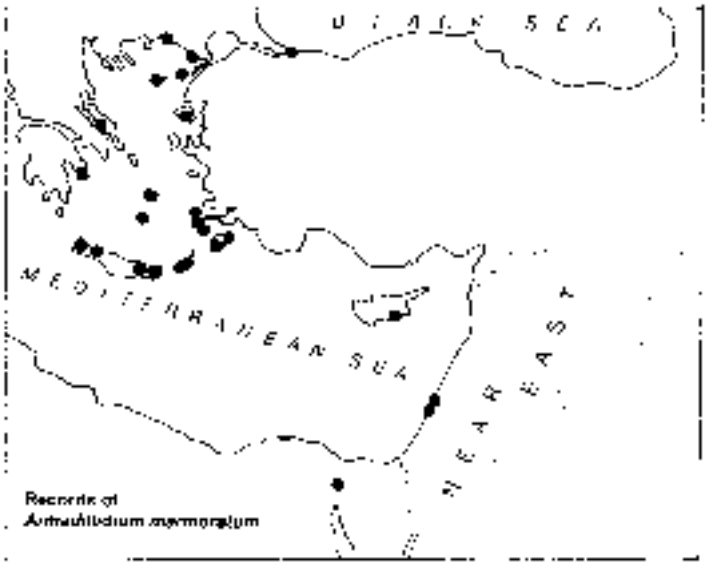

Fig. 4. – Recorded overall distribution of *Armadillidium marmoratum* (literature records and samples in the Stuttgart collection). Some species described from Italy may be synonyms of *A. marmoratum*.

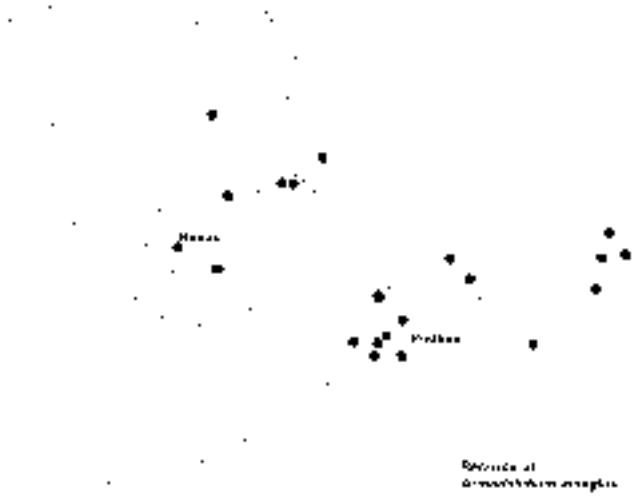

Fig. 5. – Safe records of *Armadillidium pallasii* (literature records and samples in the Stuttgart collection; the type locality Crimea is mentioned with a question mark). The subspecific classification of this species group has yet to be clarified.

of the Greek mainland during colder and wetter periods of the Ice Age.

Southwestern Balkans

Five species of *Armadillidium* are known from Albania and western Greece. One of these is *Armadillidium bicurvatum*, whose eastern distribution limit seems to coincide with the 100 mm precipitation line for December (after Philippson 1948) (Fig. 6).

Aegean

Armadillidium insulanum populates the northern Aegaean islands (compare SCHMALFUSS, 1985 b: 298, fig. 13) and the adjacent mainland coasts to the north and the east. *Armadillidium ameglioi* is recorded from the southeastern Aegean islands and the adjacent coasts of Asia Minor (Fig. 7).

Greek endemics

The bulk of the Greek species of *Armadillidium*, around 40, have been found only in Greece. Some of them have a rather wide distribution inside Greece, as e.g. *Armadillidium peloponnesiacum* (Fig. 8), most of them are however restricted to a limited region as e.g. *Armadillidium janinense* (see SCHMALFUSS, 1985 b: 298, fig. 13) or are even known only from the type localities.

Ionian island endemics

Six species are known from several Ionian islands but not from the adjacent mainland (*A. beieri, frontemarginatum, humile, jonicum, justi, werneri*), each species inhabiting several islands. This phenomenon should have been caused by an increased predation or/and competition pressure that extinguished these species on the mainland. A speciation *in situ* can be excluded because the islands were isolated earlier from each other than from the mainland.

Fig. 6. – Greek records of *Armadillidium becurvatum*. the eastern distributional border seems to be formed by the 100 mm December precipitation line. From SCHMALFUSS 1985 b.

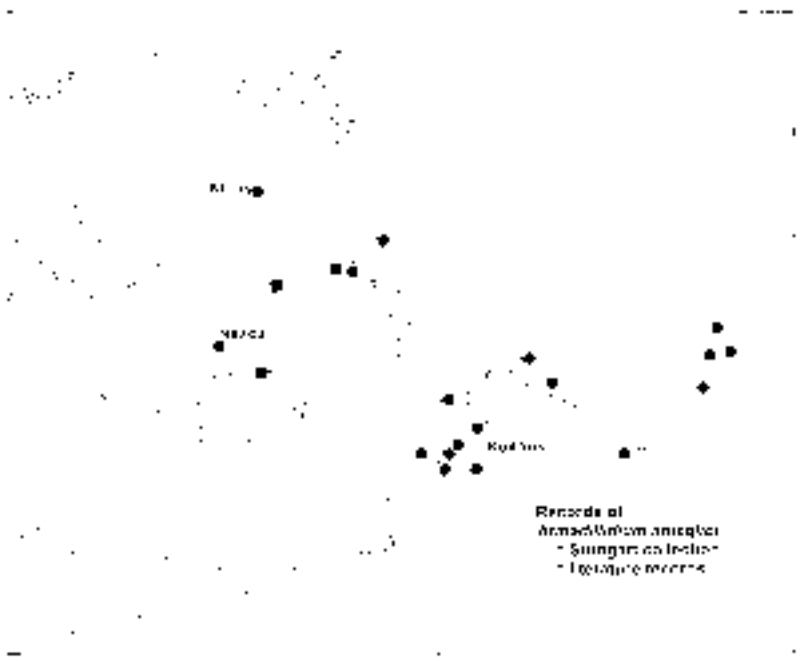

Fig. 7. – Distributional records of *Armadillidium ameglioi* (literature records including the synonyms *A. ephesiacum* Strouhal, 1927 and *A. samium* Strouhal, 1929, and samples from the Stuttgart collection).

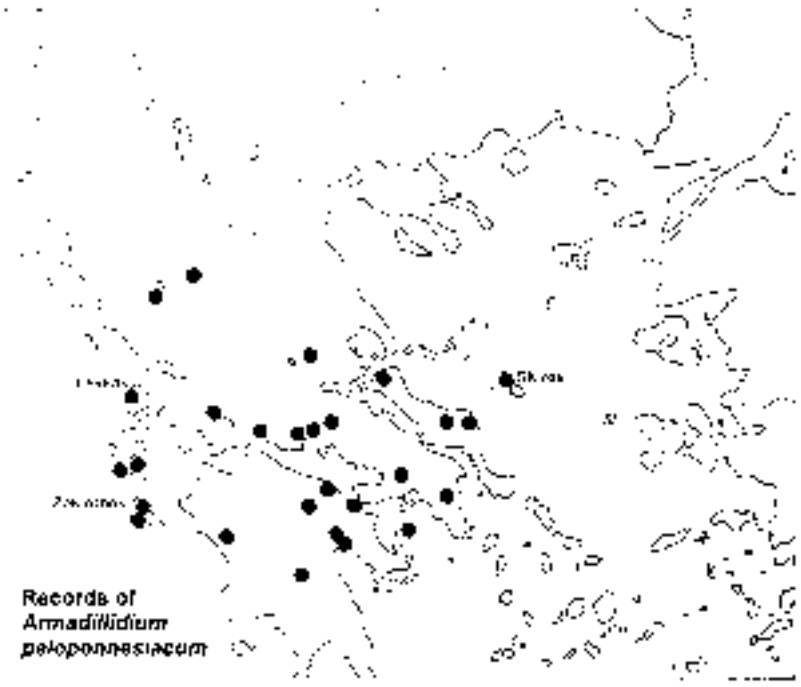

Fig. 8. – Records of *Armadillidium peloponnesiacum*. From SCHMALFUSS 1985 b.

Single island endemics

Five species have been, up to now, found only on one island. Two of them live on Crete (*A. cavernarum* and an undescribed species), three are known from single Ionian islands (*A. simile* from Kérkira, *A. hauseni* from Paxí, *A. kalamium* from Kálamos). So single island endemism is low, and in the Aegean it is completely lacking, if we exclude Crete which by its size is not comparable to the other Aegean islands. An explanation would be that the islands are very similar and comparably young so speciation processes have not yet been working.

SPECIES NUMBERS

The species numbers of single islands reflect the general gradient in the region, a decline of numbers from west to east. The Ionian islands house a much higher number than Aegean islands of corresponding size (Fig. 9). On a greater scale the drop from west of the Aegean to east of the Aegean is rather drastic. Looking for an explanation of this phenomenon the following observations can be helpful. The considered region is characterized by rather severe changes from mesic to xeric conditions. The summers become very dry, with practically no precipitation. Under these conditions the plant cover of the ground is greatly reduced, which leads to a reduced number of micro-habitats and thus generally to reduced species numbers. Additionally, the predator spectrum changes, with an increased number of forms with pincer-like gripping appendages, and the attack possibilities increase on open ground. This leads to a substitution of *Armadillidium* by genera with more optimized conglobation facilities, such as *Schizidium* Verhoeff, 1901 and *Armadillo* Duméril, 1816 (compare SCHMALFUSS, 1988 and 1996). These genera have developed structures that protect the rolled-up animal against shearing forces, such as e.g. grooves on the margin of the first tergite in which the edges of subsequent tergites are locked. The outside of the rolled up animal is completely closed, so it leaves no possibility for predators to open it and to reach the vulnerable ventral parts. The distribution of the genera *Schizidium* and *Armadillo* complies with these contentions. They populate xeric environments in western Asia, reaching their western limit in the southern Aegean, as demonstrated in the map for the genus *Schizidium* (Fig. 10).

CONCLUSIONS

The genus *Armadillidium* is a *sensu latu* mediterranean taxon with radiation centres in Italy and Greece. The fact of more than 40 out of 55 species being Greek endemics reflects the restricted mobility of these animals. Only 12

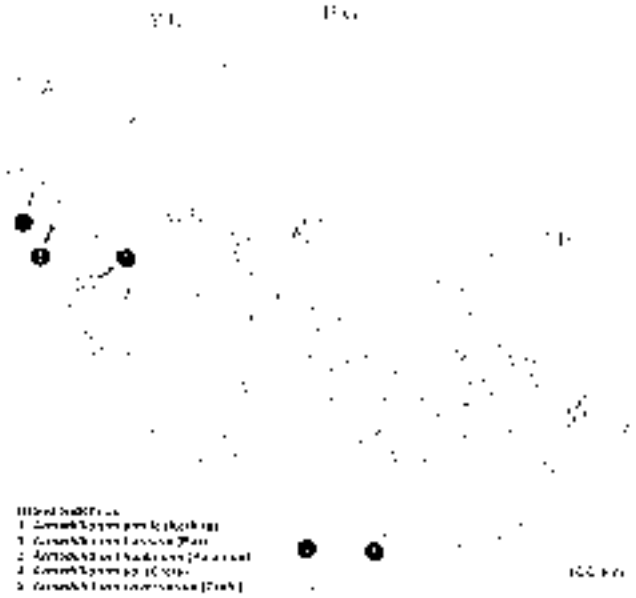

Fig. 9. – Numbers of *Armadillidium* species on selected Greek islands.

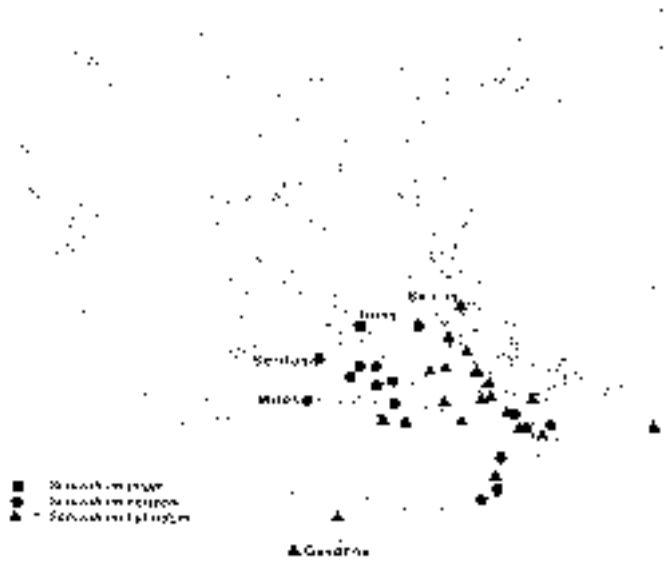

Fig. 10. – Greek records of epigean species of the genus *Schizidium* which is supposed to partly substitute *Armadillidium* east of the Greek mainland.

TABLE 1

Distributional categories to which the Greek species of *Armadillidium* can be ascribed.

HOLOMEDITERRANEAN
A. album Dollfus, 1887
A. granulatum Brandt, 1833
A. vulgare (Latreille, 1804)
EASTERN MEDITERRANEAN
A. marmoratum Strouhal, 1929
NORTHEASTERN MEDITERRANEAN
A. pallasii Brandt, 1833
SOUTHWESTERN BALKANS
A. albanicum Verhoeff, 1901
A. bicurvatum Verhoeff, 1901
A. frontetriangulum Verhoeff, 1901
A. humectum Strouhal, 1937
A. laminigerum Verhoeff, 1907
AEGEAN
A. ameglioi Arcangeli, 1913
A. insulanum Verhoeff, 1907
GREEK ENDEMICS
A. aegaeum Strouhal, 1929
A. arcadicum Verhoeff, 1902
A. argolicum Verhoeff, 1907
A. artense Strouhal, 1956
A. atticum Strouhal, 1929
A. cephalonicum Strouhal, 1929
A. corcyraeum Verhoeff, 1907
A. cythereium Strouhal, 1937
A. epiroticum Strouhal, 1956
A. fossuligerum Verhoeff, 1902
A. inflatum Verhoeff, 1907
A. irmengardae Strouhal, 1956
A. janinense Verhoeff, 1902
A. kalamatense Verhoeff, 1907
A. lobocurvum Verhoeff, 1902
A. messenicum Verhoeff, 1902
A. parvum Strouhal, 1938
A. pelionense Strouhal, 1928
A. peloponnesiacum Verhoeff, 1901
A. pseudovulgare Verhoeff, 1902
A. stolikanum Verhoeff, 1907
A. tripolitzense Verhoeff, 1902
A. versluysi Strouhal, 1937
A. xerovunense Strouhal, 1956
A. zuellichi Strouhal, 1937
plus the two following categories
plus ± 8 undescribed species
IONIAN ISLAND ENDEMICS
A. beieri Strouhal, 1937
A. frontemarginatum Strouhal, 1927
A. humile Strouhal, 1936
A. jonicum Strouhal, 1927
A. justi Strouhal, 1937
A. werneri Strouhal, 1927
SINGLE ISLAND ENDEMICS
A. sp. (Crete)
A. cavernarum Vandel, 1958 (Crete)
A. hauseni Schmalfuss, 1985 (Paxí)
A. kalamium Strouhal, 1956 (Kálamos)
A. simile Strouhal, 1937 (Kérkira)

species surpass the boundaries of Greece, half of which are ecologically connected to litoral biotopes. The distributional categories to which the Greek species can be ascribed are somewhat arbitrary, since every species has a distribution range different from all others. The most obvious result of this analysis is the gradient of species density from west to east of the Greek territory, with a drastic decline on the Turkish mainland. This gradient is correlated to a decrease of precipitation and an increase of seasonality from west to east. This leads to a reduction of niches and of biodiversity, i. e. species density. The gradient is enhanced by the fact that the genus is replaced in the east by morphologically related genera with more opitmized conglobation abilities.

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