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Patterns of distribution and diversity in European mygalomorph spiders

ARTHUR E. DECAE

Terrestrial Ecology Unit, Department of Biology, University of Ghent, Ledeganckstraat 35, B–9000 Gent, Belgium.

Natuurhistorisch Museum Rotterdam, Postbus 23452, 3001 KL Rotterdam, The Netherlands.

Abstract

A coherent picture of the distribution and diversity of the European mygalomorph spider fauna is presented for the first time. The picture is based on geographical and taxonomical information, mainly obtained in recent collection work. The patterns reveal that (1) the current distribution of the Atypidae is the result of a Holocene dispersal event; that (2) Nemesiidae and Cyrtaucheniidae are building-up their diversity in situ as an effect of repeated fragmentation and isolation of local populations during successive Pleistocene glaciations; that (3) Ctenizidae, with three locally restricted and geographically isolated genera, are most probably remnants of a former geography of the Mediterranean region; that (4) the Theraphosidae seem to show both evidence of dispersal in *Chaetopelma* and of speciation in situ in *Ischnocolus*; that (5) the Hexathelidae are either very old remnants or recent man aided introductions into the European mygalomorph fauna.

INTRODUCTION

Thanks to collection efforts of mainly young arachnologists from southern Europe, a coherent picture of the European mygalomorph fauna is now emerging. The European mygalomorph spider fauna as discussed here includes species occurring in the northernmost parts of Africa (Fig. 1). Until recently, almost all the knowledge of European mygalomorphs was based on isolated taxonomic work mainly conducted in the late 19th and early 20th centuries. The problem was that nearly all this work was done as idiosyncratic descriptions of small haphazardly collected samples, from which it was very difficult to develop an overall view of the European mygalomorph fauna. Recently a number of larger and more systematically conducted collection programs have been carried out, mainly in relation to biodiver-

sity assessments and conservation studies. The here presented view on the European mygalomorph fauna was developed from the results of these studies. To make the emerging patterns visible, all available information on geographical locations from which identifiable mygalomorph spiders have been reported, are mapped (Fig. 1). The resulting patterns of diversity and distribution reflect important aspects of the evolutionary history of the different mygalomorph families, and contain basic information for developing prospective research programs studying the ecology, behaviour and evolution of these primitive spiders.

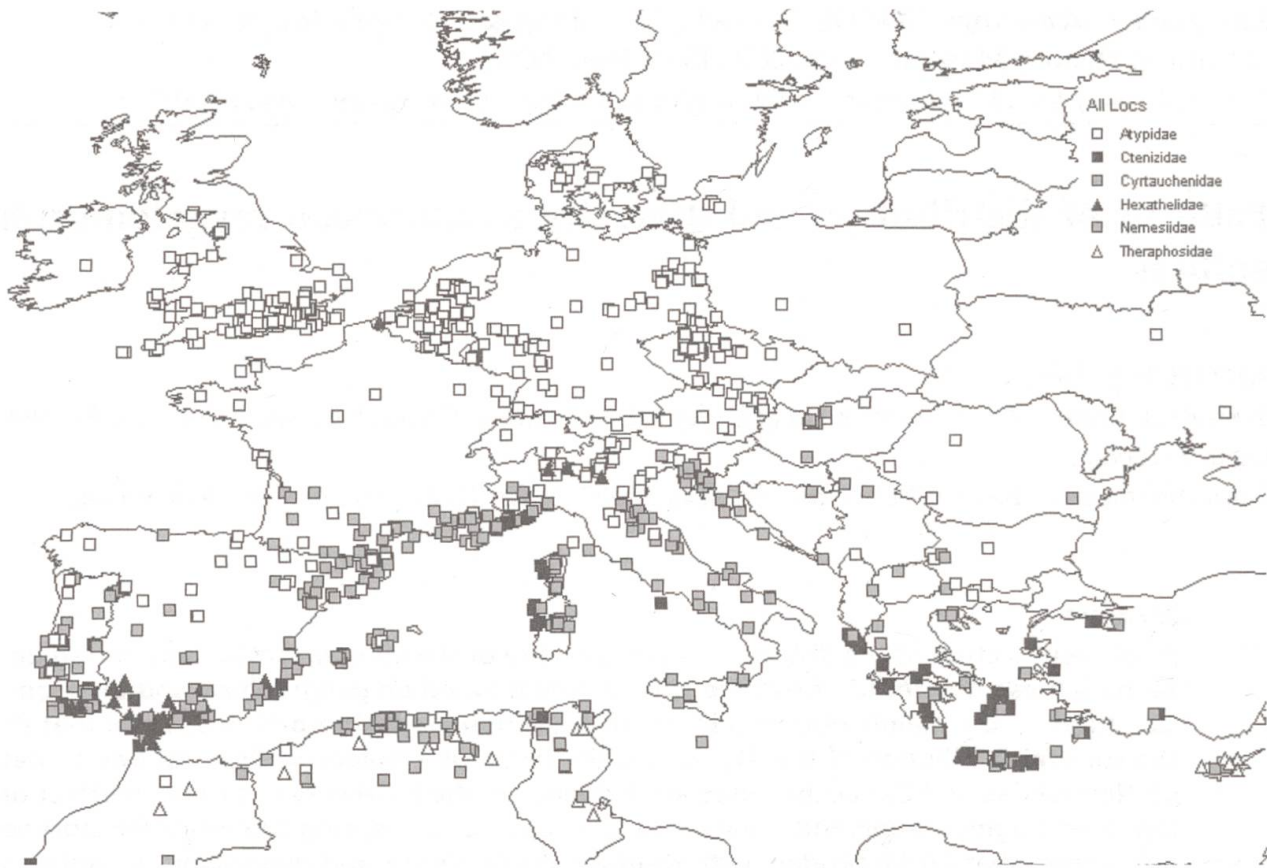


Fig 1. All locations from which identifiable mygalomorph spiders have been recorded in the course of this study.

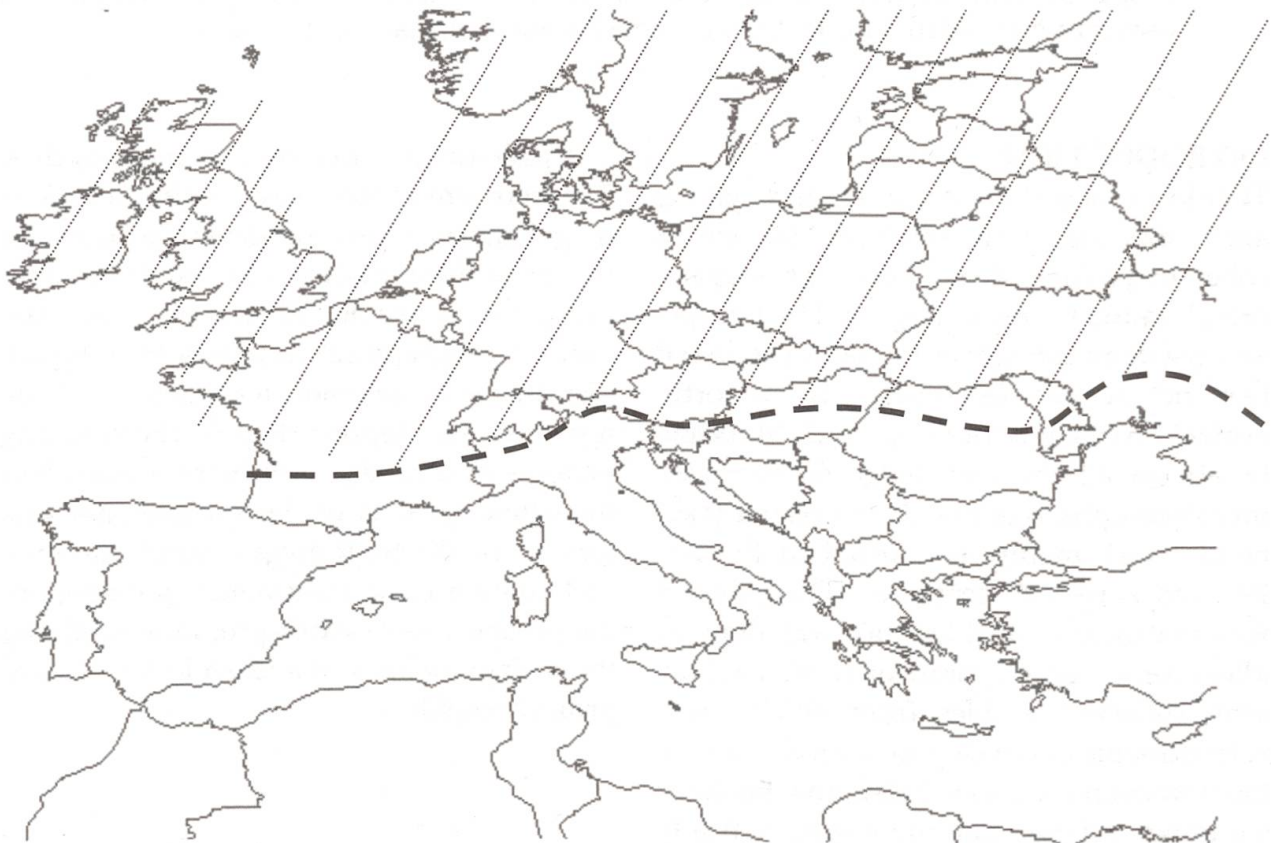


Fig. 2. Extent of permafrost at the end of the last ice age (hatched) and permafrost front (dashed line). After Hewitt (1999).

Family	Asia	Europe	Africa	N. America	S. America	Australia
Actinopodidae					+	+
Antrodiaetidae	+			+		
Atypidae	+	+	+	+		
Barychelidae	+		+		+	+
Ctenizidae	+	+	+	+	+	+
Cyrtoucheniidae	+	+	+	+	+	+
Dipluridae	+		+	+	+	+
Hexathelidae	+	+	+		+	+
Idiopidae	+		+		+	+
Mecicobothriidae				+	+	
Microstigmatidae			+		+	
Migidae			+		+	+
Nemesiidae	+	+	+	+	+	+
Paratropidae					+	
Theraphosidae	+	+	+	+	+	+
	10	6	11	8	13	10

Table 1. Occurrence of different mygalomorph spider families per continent showing the comparative poverty of the European mygalomorph fauna.

MATERIAL AND METHODS

Data on the distribution and diversity of European mygalomorph spiders were collected in an extensive survey of the extant literature, museum collections and large private and institutional collections from regions all over the area of interest. More than five hundred specimens, including representatives of all Western Palearctic genera, were morphologically studied with the aid of a Ceti-Medo 2 binocular microscope in order to assess the European mygalomorph diversity and to produce a determination key for European mygalomorph species now in preparation. These data were amassed in a Microsoft Access Data Base and analyzed for distribution and diversity with the aid of DIVA-GIS geographical computer program (Hijmans et al. 2005). The resulting distribution maps were reviewed in reference to current knowledge of the Pleistocene history of Europe (Fig. 2) and the repopulation of the central and northern parts of the continent after the last glaciation (for a comprehensive

review and general discussion see Hewitt, 1999).

RESULTS

With only six of the presently recognized fifteen families (Table 1), the European mygalomorph fauna is relatively poor. The mygalomorph distribution, when viewed at the family level appears as a pattern of curved lines running in an east-west direction that are separated with respect to their northern latitudes (Fig. 3). From this perspective mygalomorph families seem to have repopulated Europe from the south over a broad front after the melting of the last permafrost of the younger Dryas some 11.500 years ago. Focusing on the genus and species levels, however, the situation is more complex and more informative.

Atypidae (Fig. 4)

The Atypidae, probably thanks to their capacity to balloon, have the broadest extent in Europe being distributed all over the con-

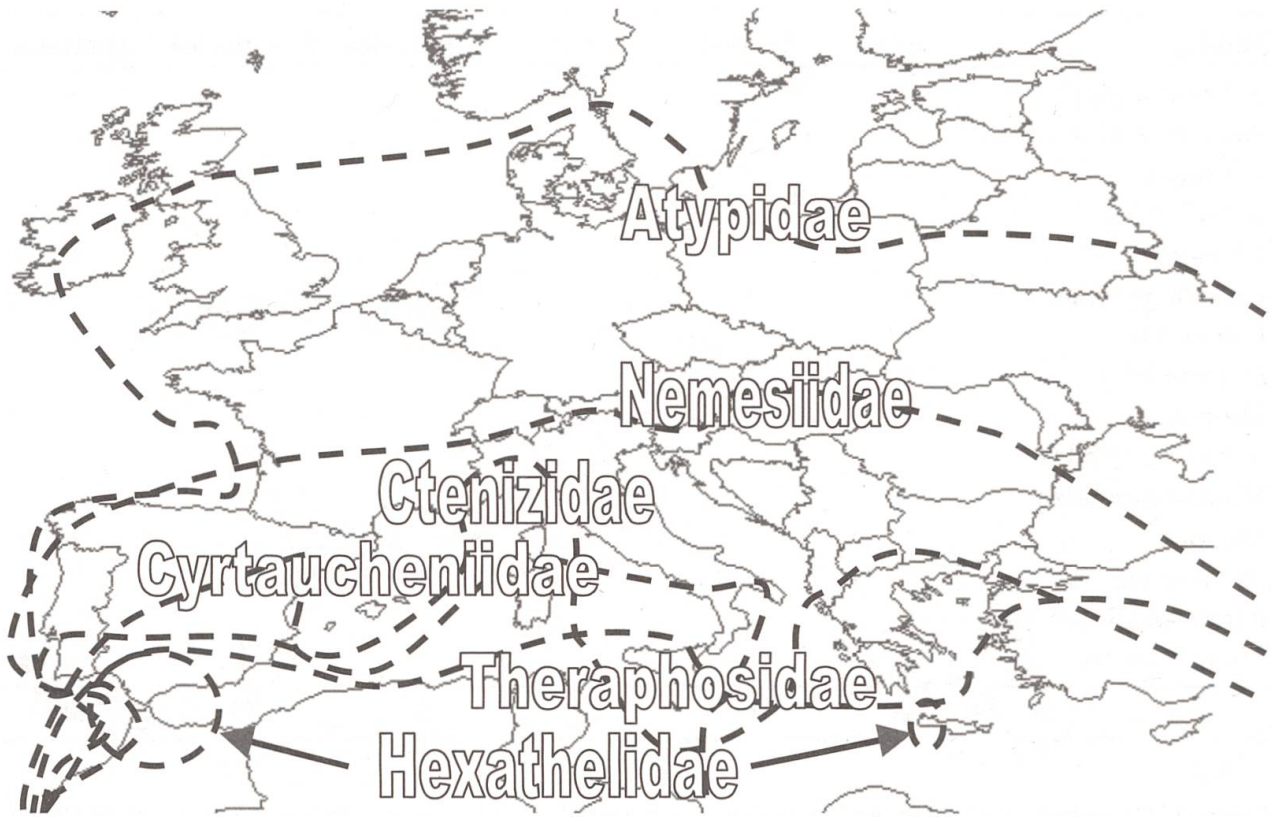


Fig. 3. Broadly east-west running curved dashed lines indicate the northern limits of the distributions of the six mygalomorph spider families occurring in Europe.

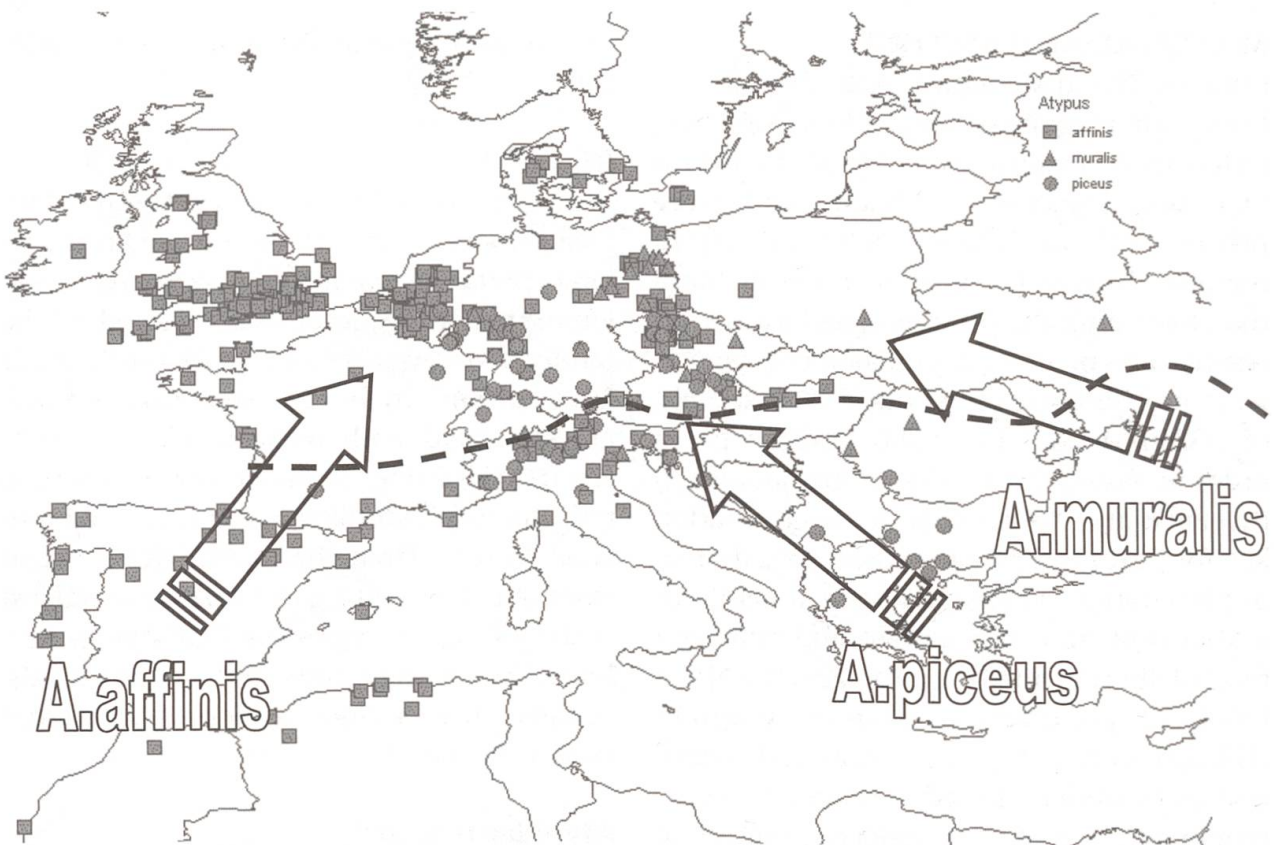


Fig. 4. Distribution of the genus *Atypus* in Europe (as based on the currently included data points). Dashed line indicates latest permafrost front (see Fig 2). Block arrows indicate supposed Holocene dispersal routes of three *Atypus* species into formerly frozen territory.

continent with exception of the most northern parts. Their distribution reaches far into the latest permafrost coverage of the continent and can therefore best be explained as the result of a relatively recent Holocene dispersal event. This hypothesis gains further support from the low diversity observed within the Atypidae with just one genus, *Atypus* Latreille, 1804, and three species broadly distributed in eastern, central and western ranges. It has been suggested that the *Atypus* species have survived the last ice-age in three isolated southern refuge populations in the Iberian Peninsula, the Southern Balkans and a region near the Caspian Sea respectively (e.g. Schwendinger 1990).

Nemesiidae (Fig. 5)

The Nemesiidae do not occur north of the Alpine mountain ranges. Apparently they did not colonize the former permafrost regions of central and northern Europe as *Atypus* did. Also in contrast to the Atypidae the European Nemesiidae are very diverse with three genera and over sixty species known (Platnick 2008). The limited species ranges and great species diversity in the Nemesiidae are believed to indicate a very limited capacity for dispersal combined with a very strong potential for surviving adverse conditions. The idea is that Nemesiidae in Europe have been repeatedly 'pushed back' into small fragmented and isolated refuge populations in a series of Pleistocene glaciations that have hit the continent in the past 1.5 million years, and that these ongoing cycles of fragmentation and isolation have lasted sufficiently long for extensive diversification and speciation to have occurred. Their apparent strong capacity for survival might explain the current presence of *Nemesia* species at high altitudes, approaching 2000 m, in the Alps and the Pyrenees. Prospective research programs into the evolutionary backgrounds of nemesiid ecology and behaviour could be developed, for instance to study the apparent character displacement in sympatric *Nemesia* species as for example the re-

peated close coexistence of cork- and wafer-door strategies in many *Nemesia* populations (Moggridge 1873, Dcaea 1996).

Cyrtaucheniidae (Fig. 6)

Although more restricted to the south-west, the European Cyrtaucheniidae appear to have a somewhat similar evolutionary history as the Nemesiidae. Here also we see restricted species ranges and high species diversity (Platnick 2008). However, too little is currently known about cyrtaucheniid taxonomy, occurrence and behaviour to draw further conclusions about survival capacity, ecological or behavioral versatility or to suggest prospective research programs for this group.

Ctenizidae (Fig. 7)

The focus of diversity in the European Ctenizidae is on the genus, rather than on the species level. This might indicate an older evolutionary history, not so much influenced by Pleistocene glaciations, as by tectonic events that shaped the present day geography of the Mediterranean region. This hypothesis gains support from the observation that the three European ctenizid genera, *Ummidia* Thorell, 1875, *Cteniza* Latreille, 1829 and *Cyrtocarenum* Ausserer, 1871, are all locally restricted and widely separated in space. Each genus occurs solely in one specific geological and geographical region. *Ummidia* is restricted to the south of the Iberian Peninsula and adjacent geologically related (Ager 1980) areas of North Africa. *Cteniza* inhabits the Tyrrhenian islands and a narrow strip of continent along the northern shores of the Tyrrhenian Sea. *Cyrtocarenum* is centered in the Aegean region and has as yet not been found outside Greece and Western Anatolia. These areas all correspond to geologically recognized 'microplates' (Ager 1980) and the present distributions of European ctenizids are probably best explained in terms of vicariance biogeography (Platnick 1976). The European ctenizids therefore seem to offer good opportunities for studies in bio-



Fig. 5. Distribution of the Nemesiidae in Europe (as based on the currently included data points). Dashed line indicates latest permafrost front (see Fig. 2). Numbers of recognized species in the three genera are: *Iberesia* (squares) three, *Nemesia* (circles) approx. sixty, *Brachythele* (triangles) four.

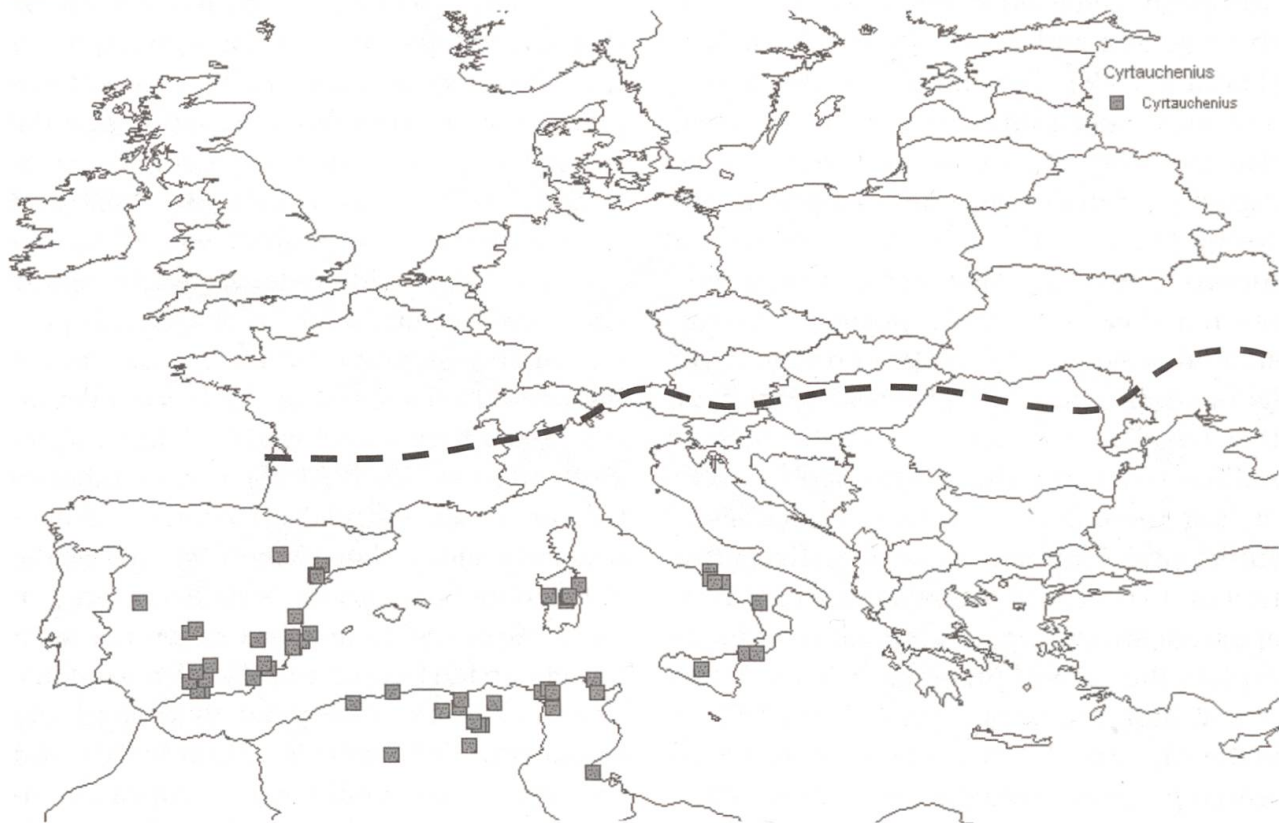


Fig. 6. Distribution of the genus *Cyртаuchenius* in Europe (as based on the currently included data points). Dashed line indicates latest permafrost front (see Fig. 2). Number of recognized species in *Cyртаuchenius* currently is sixteen (Platnick 2008).



Fig. 7. Distribution of Ctenizidae in Europe (as based on the currently included data points). Dashed line indicates latest permafrost front (see Fig 2). Three genera are separated in space; *Ummidia* (squares) NW Africa + southern Iberia, *Cteniza* (circles) Tyrrhenian region, *Cyrtocarenum* (triangles) Aegean region.

and phylogeography. Their localized occurrence may furthermore indicate that it here concerns remnant populations that deserve attention from a conservation point of view.

Theraphosidae (Fig. 8)

Theraphosidae, with two genera *Ischnocolus* Ausserer, 1871 and *Chaetopelma* Ausserer, 1871, occur over a wide front in the southernmost parts of Europe and directly adjacent regions. A recent revision of *Chaetopelma* (Guadanucci & Galton 2008) shows that the species diversity in this genus is low (three or four species) and the distribution range, extending all over the Middle East and as far south as the Sudan, is comparatively large. As in *Atypus*, these two factors combined (low diversity and wide distribution) may argue for dispersal as the main factor shaping the present day distribution. The

fact that *Chaetopelma* has recently been reported from Greece (personal observation) seems to support this idea, although it cannot be ruled out that here it concerns a man mediated introduction. The genus *Ischnocolus* differs from *Chaetopelma* in exhibiting a considerable localized species diversity in the Mediterranean region (Platnick 2008) that might indicate a Pleistocene isolation and fragmentation of refuge populations as described above for Nemesiidae and Cyrtaucheniidae. However, *Ischnocolus* is at present insufficiently studied and a revision of the genus might provide more clarity.

Hexathelidae (Fig. 9)

The Hexathelidae are represented in Europe with one genus, *Macrothele* Ausserer, 1871 and just two species. The world distribution of *Macrothele* shows some peculiar disjunc-



Fig. 8. Distribution of Theraphosidae in Europe (as based on the currently included data points). Dashed line indicates latest permafrost front (see Fig 2). Two genera are separated in space; *Ischnocolus* (squares) twelve regional species (Platnick 2008) western Mediterranean, *Chaetopelma* (triangles) three species (Guadanucci & Galton 2008) eastern Mediterranean.

tions. The centre of diversity for this genus, with 20 recognized species, is in South-East Asia. A second area of distribution with four recorded species exists in West Africa. The third area of distribution is in South Europe where two isolated species occur; one on the Iberian Peninsula and one on Western Crete. It is very difficult to explain this distribution in terms of geological, geographical, historical or biological arguments as used above. A recent molecular study of *Macrothele calpeiana* (Arnedo & Ferrández 2006) has indicated that this particular species is a very old Iberian endemic. The peculiar distribution of two isolated *Macrothele* species in Mediterranean coastal areas, however, rather seems to suggest a recent man aided import of the genus into the European fauna. This idea is further supported by recent findings of *M. calpeiana* far away from the Iberian

Peninsula in northern Italy (Pantini & Isaia in press) and in Belgium (personal observation). These findings show the likelihood of *M. calpeiana* to be transported by man, possibly as an unintentional 'stowaway' with the export of garden materials or plants such as ornamental olive trees (as is reported for the Italian records, Pantini pers. comm.). Another fact that might explain recent outlying records of *M. calpeiana* is that the species has attracted some general publicity as the only formally protected spider species in Europe. This might have encouraged intentional transport by collectors of illegal animal species. In general, however, the question of *Macrothele* being an old endemic element in the European mygalorph fauna or a recent man aided introduction awaits further research.



Fig. 9. Distribution of the genus *Macrothele* in Europe (as based on the currently included data points). Dashed line indicates latest permafrost front (see Fig 2). Two species are separated in space; *M. calpeiana* (squares), southern Iberia with probably man aided transports into northern Italy and Belgium, *M. cretica* (triangles) restricted to western Crete.

CONCLUSIONS

From reading their present distributions the Atypidae in Europe seem to be a clear case of Holocene dispersal. The Nemesiidae and Cyrtaucheniidae appear to be responding to glacial cycles with building up diversity in situ through repeated fragmentation, isolation and speciation. The Ctenizidae appear to be old relict populations confined to distinct tectonic regions. The Theraphosidae seem to show evidence of dispersal in *Chaetopelma* and of building diversity in response to glacial cycles in *Ischnocolus*. The Hexathelidae could be very old endemics of small, isolated regions in southern Europe, or recent man mediated imports. All these conclusions offer exciting opportunities for future research into the evolutionary backgrounds of the ecology and behaviour of European mygalomorph spiders.

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