

Review of oak gall wasps phylogeographic patterns in Turkey suggests a main role of the Anatolian diagonal

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Abstract: Distribution of genetic variation across a species range is shaped both by historical and contemporary factors such as topographical barriers, presence of diverse micro- and macrohabitats, complex geologic history and past climatic fluctuations. Signatures of the past events and the varied topography can be observed not only in plant taxa but also in the obligate parasites of plants such as oak gall wasps. The mountain barriers in Anatolia running from the southeastern towards the northern part of Turkey is accepted as a major faunistic and floristic belt, and is thought to underlie much of the genetic diversity in the region. Current findings show that complicated geologic history and a variety of mountainous areas have left imprints on the phylogenies and phylogeography of oak gall wasp taxa. Indeed, several oak gall wasp species studied across Turkey revealed the presence of this notorious pattern into west and east division of the genetic variation with respect to the location of the Turkish highlands. A number of published studies on the distribution and the allocation of the genetic diversity of several oak gall wasp species in Anatolia, which is located at the junction of several phytogeographic provinces, express the importance of an apparent genetic break in the examined oak gall wasp species.

Keywords: Anatolia, Anatolian diagonal, Oak gall wasps, Genetic break, Geographic barriers

Türkiye'deki mazi arılarının filocoğrafi örüntülerine dair inceleme, Anadolu çaprazının temel rolü

Özet: Bir türün sahip olduğu genetik varyasyonun yayılış alanı içindeki dağılımı mikro ve makrohabitatların çeşitliliği, topoğrafik bariyerler, alanın jeolojik tarihi ve geçmişteki iklimsel değişiklikler gibi hem tarihsel hem de bugünkü faktörler tarafından belirlenir. Topoğrafi ve tarihsel olayların etkileri sadece bitki taksonlarında değil aynı zamanda bitkilerin zorunlu parazitleri olarak kabul edilen gal arıları gibi taksonlarda da görülür. Ülkemizin güneydoğu kısmından başlayarak kuzeye doğru ilerleyen dağ sinsilelerinin Anadolu fauna ve florasını şekillendiren bariyerler arasında olduğu kabul edilmektedir ve bölgedeki genetik çeşitliliğin dağılımını da belirleyen önemli faktörlerden biri olduğu düşünülür. Elde edilen son bilgiler ülkemizin oldukça karmaşık jeolojik tarihi ve farklı dağlık alanların meşe gal arılarının filocoğrafik yapısının şekillenmesinde oldukça etkili olduğunu göstermiştir. Ülkemizdeki meşe gal arısı türlerinde genetik varyasyonun doğu ve batı şeklindeki dağılım ve yapılması dikkat çekicidir. Fitocoğrafik alanların çakışma noktasında yer alan Anadolu'dan çalışılan meşe gal arısı türlerindeki mevcut genetik farklılaşma gal arısı türlerinde popülasyon genetik yapısındaki kesintiye işaret etmektedir.

Anahtar kelimeler: Anadolu, Anadolu diagonalı, Meşe gal arıları, Genetik ayrım, Coğrafik bariyerler

1. Importance of Anatolia: A hotspot and refuge area

Current population genetic structure of a species is governed by historical and contemporary factors, and physical barriers such as mountain ranges are thought to be crucial for shaping the phylogeographic structure of many species (Avice, 2000). Turkey hosts more than 10000 plant and 80000 animal species (Demirsoy, 1999), which is much higher than the neighboring areas. Besides, recent studies have revealed that genetic diversity is also higher in Turkey compared to many of the European populations of the investigated taxa. Such high genetic diversity is thought to be due to the heterogeneous topography of Anatolia, complicated geologic history of the area, varied climates,

the presence of diverse phytogeographic regions, and unique geologic location of Turkey.

Turkey is located in the Alpine-Himalayan Mountain belt between Eurasia, Africa and Arabia, with complex geological history which is a result of the collision of the Arabian and African plates with the European plate, promoting the closure of the Tethys Sea (Rögl, 1999). The mountain ranges presently seen in Anatolia formed during the Oligocene with a collision between Indian and Asian continental masses followed by Africa and Eurasia, the last collision ending up with the formation of the Taurus Mountains. In consequence, the most important upshot of Tertiary for Anatolia was the unfolding of the Anatolian highlands (Bozkurt, 2001) which was named as the Anatolian Diagonal by Davis in 1971. The Anatolian

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✓ **Received** (Geliş tarihi): 01.11.2014, **Accepted** (Kabul tarihi): 30.06.2015



Citation (Atıf): Mutun, S., 2016. Review of oak gall wasps phylogeographic patterns in Turkey suggests a main role of the Anatolian diagonal. Turkish Journal of Forestry, 17(Special Issue): 1-6.

DOI: [10.18182/tjf.65861](https://doi.org/10.18182/tjf.65861)

Diagonal is a line of mountain ranges that runs from the south of Gümüşhane- Bayburt in the north to southwest across Turkey to the Taurus Mountains (Davis, 1971; Ekim and Güner, 1986). This mountain belt has been proposed as a significant geographic barrier shaping current species composition distributed across Turkey and dividing species/lineage distribution into east and west (Davis, 1971; Ekim and Güner, 1986; Çıplak et al., 1993; Mutun, 2010). Turkey is located at the junction of three major phytogeographic regions as Mediterranean, Euro-Siberian, and Irano-Turanian (Avcı, 1993). It is also important to note that the Anatolian Diagonal divides the Irano-Turanian phytogeographic region in Turkey into eastern and western areas (Figure 1).

Anatolia not only acted as a corridor for the dispersal of African animals during the Early Miocene, but also played a significant role as refuge area during the climatic fluctuations of the Pleistocene. Indeed, Turkey acted as a large non-homogeneous refuge area playing important role for different taxa to help them to escape from the analogous effects of both glacial and interglacial cycles (Çıplak, 2008). Many plant and animal species are thought to expand their range after the glacial cycles from refugia to the present day-distribution (Hewitt, 2004). Moreover, in addition to the detection of great amount of genetic variation in diverse animal groups in Turkey, Anatolia has been proposed as the source of genetic diversity for many European species including oak gall wasps (Challis et al., 2007; Rokas et al., 2003).

Many western Palearctic species are thought to originate from eastern parts of their distribution range including Turkey, and those easterly located populations represent significant centers of genetic diversity (Rokas et al. 2003). Besides, recent studies have indicated that multiple oak gall wasp lineages diverged prior to the arrival of modern oaks in the western Palearctic and oak gall wasp lineages spread westwards from Anatolia (Stone et al., 2007).

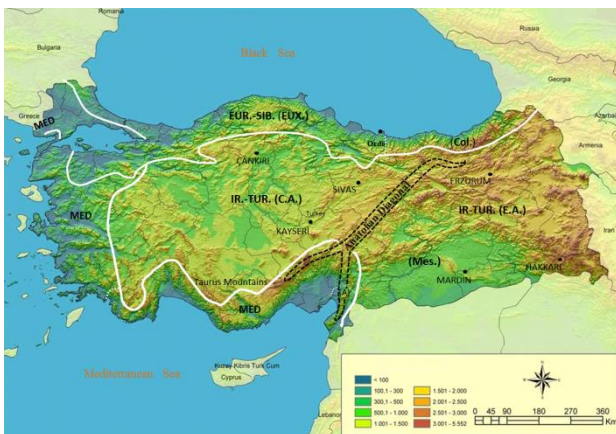


Figure 1. Representation of the Anatolian Diagonal and the approximate location of the phytogeographic regions in Turkey. Col.: Colchic, EUR.SIB.(EUX.) Euro-Siberian (Euxin), IR.TUR. (C.A.): Irano-Turanian (Central Anatolian), IR.TUR. (E.A.): Irano-Turanian (East Anatolian), Mes.: Mesopotamia, MED: Mediterranean. The location of the Diagonal is modified from Davis (1971).

Indeed, several western Palearctic oak gall wasps currently ranging from Iberia to Iran pointed out an eastern origin (Challis et al., 2007). From the phylogeographic point of view, glacial refugia are assumed to harbor high diversity of genotypes and major lineages within a species (Hewitt, 2000). In fact, researches have shown that Turkish genetic variation was greatest among all examined Palearctic populations and had several otherwise rare alleles, and represented the source for pre-Pleistocene colonization of European gall wasps (Rokas et al., 2003).

2. Review of phylogeographic patterns for oak gall wasps in Anatolia

Oak gall wasps with nearly 1300 species constitute the primary group of insects that induce galls mainly in the members of *Quercus*, and are accepted as obligatory parasites of their hosts being highly specialized for different plant parts, tissues and organs (Stone and Cook, 1998). Turkey constitutes one of the oak-rich regions with 20 defined species and hybrids between these oak taxa from three sections of the genus *Quercus* (Kasaplıgil, 1992).

Members of the different oak sections host a variety of gall wasp species with high species diversity in Turkey (Mutun et al., 2014). Since oak gall wasps are obligate parasites of their plant hosts, their distribution is directly correlated with the range of their specific oak host. They may be good candidates for studying both the effects of geographical barriers and of oak gall wasp distributions. In recent years, there is growing number of studies in Turkey to search for if a general pattern is observed in gall wasps to distinguish the factors responsible for creating the current genetic structure. Thus, the main objective of this study is to make a brief evaluation through using the up to date published data currently present on oak gall wasp species from Turkey to see if i) a general phylogeographic pattern is observed, and ii) the major mountain lines shaped the oak gall wasp population structure.

In recent years, several studies concerning oak gall wasps revealed the amount of genetic diversity present in the Turkish populations, the allocation the genetic variation across the species range, and the phylogeographic structure within species (Dinç and Mutun, 2011; Mutun, 2011; Mutun et al., 2013). Previous studies on oak gall wasps in the Palearctic region showed that the highest genetic variation is observed in the Turkish populations. In a study conducted on *A. coriarius* using mitochondrial DNA cytochrome b gene, nucleotide diversity was revealed as 0.005 and 0.006 in Iranian and Lebanese populations, respectively; however nucleotide diversity was 0.015 in Turkey (Challis et al., 2007). Other similar investigations on the Anatolian oak gall wasps showed that the genetic diversity across the Turkish populations was quite high (Table 1). Average haplotype and nucleotide diversity in *A. lucidus* was 0.808 and 0.115, respectively (Mutun, 2011). Likewise, in *A. caputmedusae* haplotype and nucleotide diversity was 0.463 and 0.101 (Mutun, 2010), and in *A. quercustozae* haplotype and nucleotide diversity was 0.450 and 0.050, respectively (Dinç and Mutun, 2011).

Table 1. Genetic diversity estimates for different oak gall wasp taxa from Turkey

Species	Genetic diversity		Marker	Reference
	Haplotype div.	Nucleotide div.		
<i>Andricus caputmedusae</i>	0.4631 ± 0.00447	0.101214 ± 0.00027	PCR-RFLP, mtDNA	Mutun, 2010
<i>A. lucidus</i>	0.8089 ± 0.00041	0.115542 ± 0.00016	PCR-RFLP, mtDNA	Mutun, 2011
<i>A. quercustozae</i>	0.4573 ± 0.00856	0.054948 ± 0.00017	PCR-RFLP, mtDNA	Dirç & Mutun, 2011
<i>A. lignicola</i>	0.3251 ± 0.00109	0.008795 ± 0.00516	mtDNA sequencing	Karagözoglu, 2013
<i>A. gallaetinctoriae</i>	0.3415 ± 0.01289	0.025720 ± 0.00009	PCR-RFLP, mtDNA	Mutun et al., 2013
<i>Cynips quercusfolii</i>	0.7285 ± 0.11431	0.009240 ± 0.00611	mtDNA & nDNA seq	Dirç & Mutun, 2014
<i>Trigonaspis synapsis</i>	0.8554 ± 0.00002	0.013461 ± 0.00121	mtDNA & nDNA seq	Atay, 2014

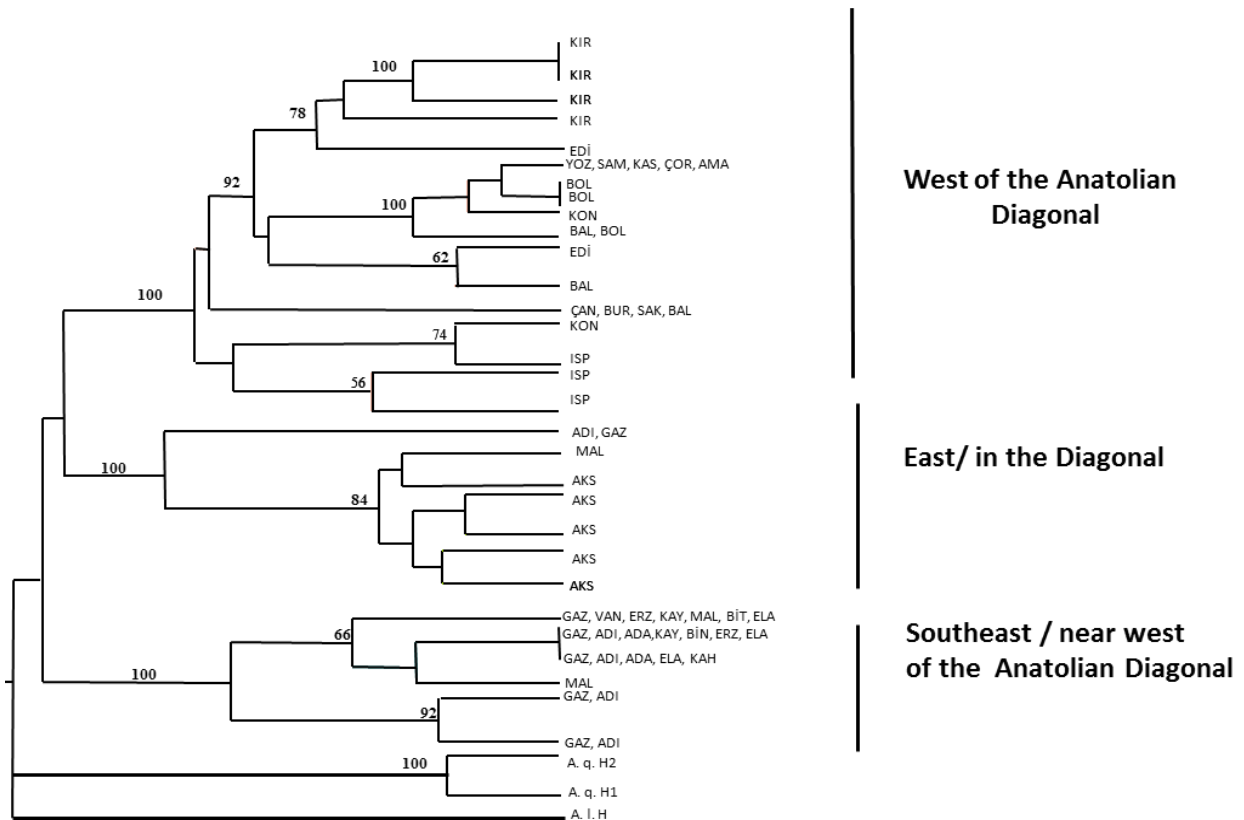


Figure 2. Dendrogram showing three major clades in *A. caputmedusae* (from Mutun, 2010)

The allocation of genetic diversity among the Turkish oak gall wasp populations has been also studied across the distribution range of the examined taxa (Dinç and Mutun, 2011; Mutun, 2010; Karagözoglu, 2013; Atay, 2014). The geographic distribution of the genetic variation within *A. caputmedusae* in Turkey was divided into mainly East/in the Diagonal, Southeast/nearwest of the Diagonal, and West of the Diagonal (Figure 2) (Mutun, 2010). A conspicuous break in the partitioning of the genetic variation was proposed to be associated with the mountain belts in Anatolia (Figure 3).

Likewise, in *A. quercustozae* samples collected from 16 populations scattered both sides of the Anatolian Diagonal produced three major clades as ‘Eastern and Western Clade’, ‘Western Clade’, and ‘Eastern Clade’ supporting further the existence of a genetic break in the Anatolian oak gall wasp taxa (Figure 4 and 5) (Dinç and Mutun, 2011).

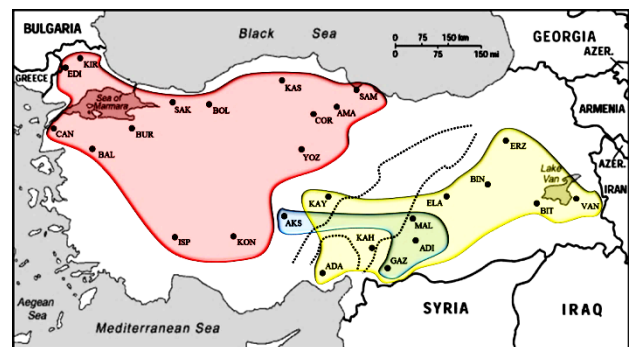


Figure 3. Representation of the major clades of *A. caputmedusae*. Dotted lines indicate the Anatolian Diagonal.

- : West of the Anatolian Diagonal,
- : East/In the Diagonal,
- : Southeast/near West of the Anatolian Diagonal.

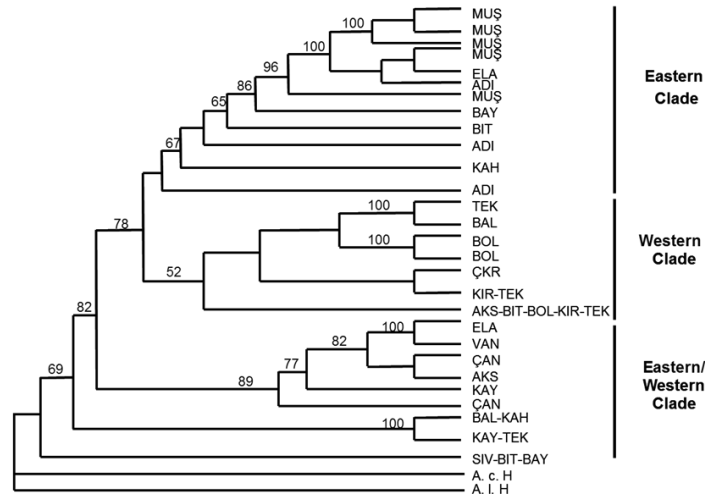


Figure 4. Dendrogram of the 28 haplotypes of *A. quercustozae* presenting three clade structure in the Turkish populations (from Dinç and Mutun, 2011)

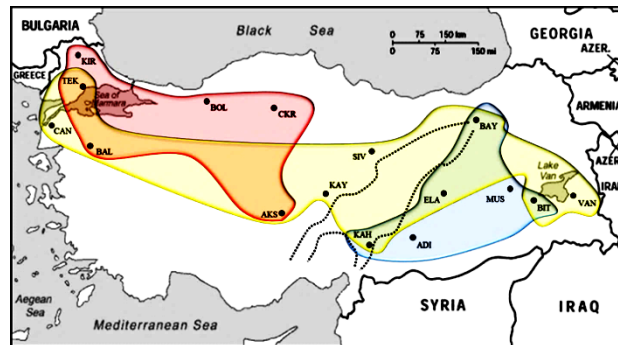


Figure 5. Representation of the major clades of *A. quercustozae*. Dotted lines indicate the Anatolian Diagonal. ●: Western Clade, ●: Eastern Clade, ●: Eastern/Western Clade.

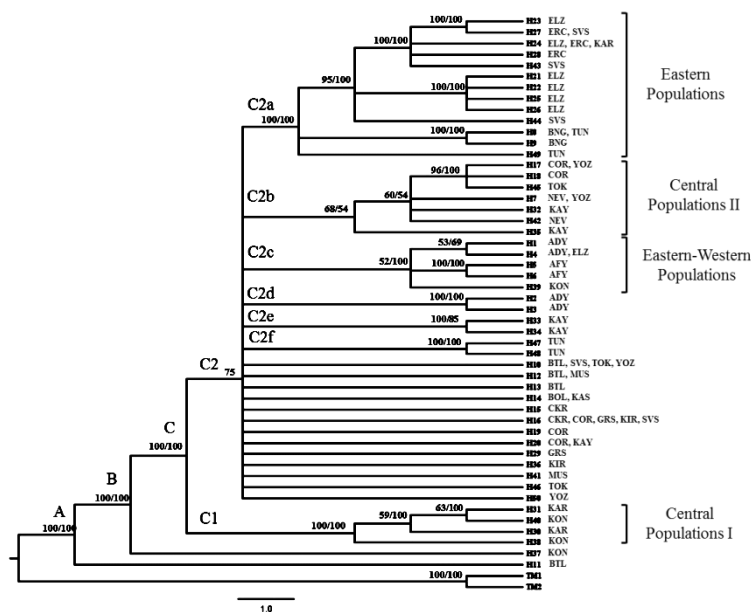


Figure 6. The consensus tree of maximum parsimony and maximum likelihood of mitochondrial cytochrome b gene of *T. synapsis* (from Atay, 2014)

A latest study on *Trigonaspis synapsis* from Anatolia (Atay 2014) showed a much more complex distribution pattern of haplotypes indicating though shallow but supporting evidence with an eastern haplotype being the most basal one in the maximum parsimony, maximum likelihood and Bayesian phylogenetic trees (Figure 6). Furthermore, the placement of a ‘Central Populations I’ haplogroup in the tree was remarkable. In a large polytomic part of the three the grouping of four haplogroup structure produced ‘Eastern Populations’, Central Populaton II’, and a clade referred to a mix of populations covering ‘Eastern-Western Populations’ (Figure 7). The formation of the major haplogroups was shown to be closely correlated with the effect of the Pleistocene climatic fluctuations together with the topographic barriers in Anatolia.

The similarity of a genetic break in some degree in the Anatolian oak gall wasp taxa have been also reported for *A. gallaetinctoriae* producing three major haplogroups within the sampled range of the species from Turkey (Figure 8 and 9) (Mutun et al., 2013). The distribution pattern of *A. gallaetinctoriae* haplotypes reflect also the partitioning of some shared haplotypes between some westerly and easterly located populations with respect to the location of the Anatolian Diagonal.

Latest studies expose the presence of high genetic diversity in the Turkish populations of oak gall wasps and underlie the importance of Anatolia as a source of genetic diversity for European taxa (Rokas et al. 2003, Challis et al., 2007). Similar results have also been reported from other species including plants (Ansell et al., 2011) and various animal groups such as bicolored shrew (Dubey et al., 2007), yellow-necked field mouse (Michaux et al., 2004), Anatolian mountain frog (Veith et al., 2003), fishes (Hrbek et al., 2002), ground squirrels (Gündüz et al., 2007) and grasshoppers (Korkmaz et al., 2010). In addition to the studies searching for the amount of genetic variation in the Turkish populations, the distribution of this diversity across Turkey and the factors shaping the contemporary pattern are also the subject of recent studies. Among these, studies of species distribution and regional composition have suggested that, together with the Tertiary history of Turkey, the Anatolian Diagonal is responsible for breaks in distributions at both specific and generic levels (Çıplak, 2004). In addition to the Diagonal, several other altitudinal belts in Anatolia have been proposed either to fragment species/lineage distributions or provide limits for east-west or north-south distributions (Çıplak, 2008). Thus, defining range distributions of lineages or genetic structuring of individual species including oak gall wasps has particular importance in understanding the biogeography of Anatolia. In the Turkish oak gall wasp taxa it seems that either deep or shallow there is a genetic break in the allocation of the genetic variation. Further and more detailed studies on oak gall wasps are still necessary for revealing a general pattern to be drawn for the genetic break shown by the investigated species from Anatolia.

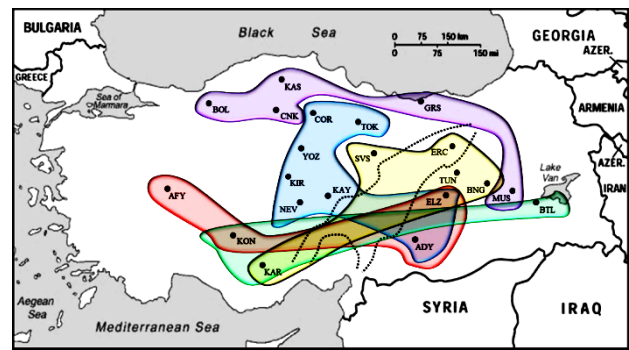


Figure 7. Location of the major haplogroups of *T. synapsis*. ●: Eastern-Western Populations, ●: Central Populations II, ●: Eastern Populations, ●: Central Populations I, ●: Mixed haplogroup.

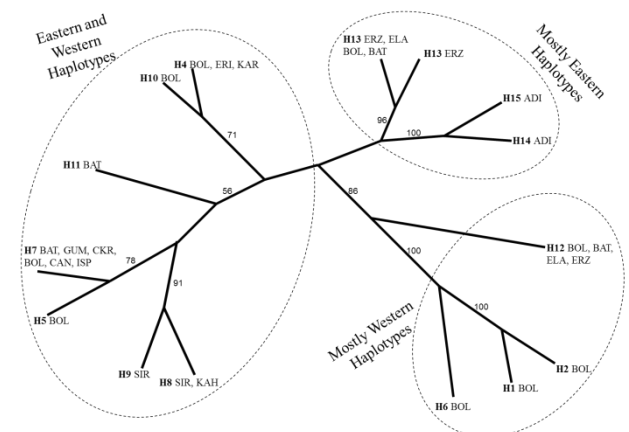


Figure 8. Unrooted Dollo parsimony majority-rule consensus tree of *A. gallaetinctoriae* haplotypes (modified from Mutun et al., 2013)

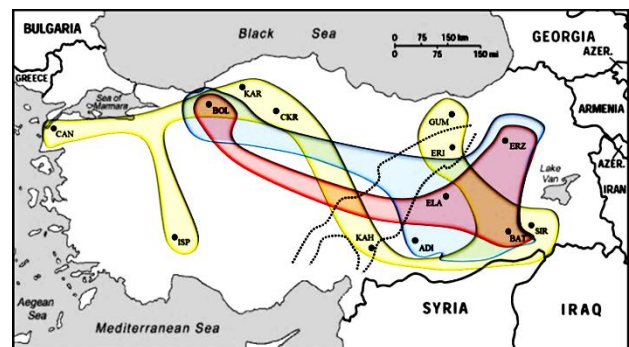


Figure 9. Distribution of main haplogroups of *A. gallaetinctoriae*. ●: Mostly Western Haplotypes, ●: Mostly Eastern Haplotypes, ●: Eastern and Western Haplotypes

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