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Are there any Tertiary relict species in the modern Bulgarian spider fauna (Arachnida: Araneae)?

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Abstract. The species classified by various authors as Tertiary relicts in the Bulgarian spider fauna are reviewed. The classification criteria used by previous authors are evaluated and discussed, and an attempt is made to identify the zoogeographical status of these species. Based upon the arguments presented below, it can be concluded that the existence of spider species with Tertiary origin in the modern Bulgarian spider fauna is highly doubtful.

Keywords: faunistic elements, neoendemics, palaeoendemics, zoogeography

Zusammenfassung. Gibt es Tertiär-Relikte in der heutigen Spinnenfauna Bulgariens (Arachnida: Araneae)? Die Klassifizierungen von Arten als Tertiär-Relikte verschiedener Autoren werden überprüft. Die Kriterien dieser Autoren werden bewertet und diskutiert und der zoogeografische Status dieser Arten wird versucht zu ermitteln. Gemäß den gelieferten Argumenten kann gefolgert werden, dass die Existenz von Arten tertiären Ursprungs in der heutigen Spinnenfauna Bulgariens höchst fraglich ist.

In the zoogeographical literature concerning the Balkan Peninsula and, in particular, the Bulgarian spider fauna, the endemic species are often divided into palaeoendemics and neoendemics. The palaeoendemics are considered to be extant species with a Tertiary origin that have survived the glaciations during the Pleistocene and lasted until the present day (Drensky 1946, Gruev & Kuzmanov 1994, Deltshv 1996). Although the existence of Tertiary relicts in the sense of species phyletic lines is generally acknowledged, it is quite controversial whether there are any contemporary spider species that originated during the Tertiary and remained unchanged until now, as stated by the above-mentioned authors. No such species is known from fossil material (Dunlop et al. 2020) and molecular phylogenetics does not support such a hypothesis either. Therefore, most of the spider species previously recorded from Bulgaria as palaeoendemics (Tertiary relicts), as well as the criteria used by the authors to classify them as such, are reviewed and discussed in the present paper. An alternative view of the zoogeographical status of each species is given.

An overview of the zoogeographical classification system of the Bulgarian fauna

An attempt is made to classify species according to the classification of Gruev & Kuzmanov (1994) with some changes and additions (Gruev 2000). This classification is based on De Lattin (1967) and is more focused on the centres of origin and dispersal of the species, rather than on their present distribution areas. Besides, it is specifically adapted to the Bulgarian fauna, which is the main reason to follow it. However, since it is published only in Bulgarian and deals mainly with the faunistic elements forming the Bulgarian fauna, it is almost unknown to foreign readers. For this reason, it is described and illustrated in brief below.

The species are grouped into complexes, elements and sub-elements, based on their origin and phylogeny (Fig. 1).

The recent Bulgarian fauna belongs to six complexes: Northern Holarctic, Siberian, European, Euroasiatic Steppic (Pontic), Southwestern Asiatic and Mediterranean, plus endemics and cosmopolitan species. For completeness, the scheme is supplemented by the category Neobiota (species introduced by human impact).

The **Northern Holarctic complex** comprises species whose origin is connected to the formation of the tundra and the boreal forests in Eurasia and North America during the Neogene. They are now characterized by European, Euro-Asian and Holarctic distributions. The complex includes the Arctic and the Boreal elements.

The **Siberian complex** comprises species with Siberian (Angaridan) origin that have spread mainly during the Quaternary, colonizing the whole Palaearctic and parts of the Nearctic. It includes the Euroasiatic Palaearctic element and the Holarctic element. The Euroasiatic Palaearctic element is divided into four sub-elements, according to the distribution of their species: Eurosiberian, Subsiberian (South Siberian), Transpalaearctic and Holopalaearctic. The Holarctic element is compact and does not have any sub-elements.

The **European complex** comprises species originating in the forests of Central and Eastern Europe (from the Atlantic Ocean to the Ural Mountains). It is split into four elements: Central European, European Mountainous, Submediterranean and Atlantic. The Central European element is compact. The European Mountainous element consists of two sub-elements: Central European Mountainous and South European Mountainous. The Submediterranean element is probably the most complex one and consists of four subelements: Holosubmediterranean, East Submediterranean, West Submediterranean (missing in Bulgaria) and Euxinic (species distributed around the Black Sea). The Atlantic element includes the Subatlantic and Atlanto-Mediterranean subelements.

The **Euroasiatic Steppic complex** is represented in Bulgaria by a single element – the Steppic one. The centre of dispersal of its species lies in the Eastern European steppes, mainly north of the Black Sea and the Caspian Sea.

The **Southwestern Asiatic complex** consists of species that originated in the northern parts of South-west Asia. It is also represented in Bulgaria by a single element – the Irano-

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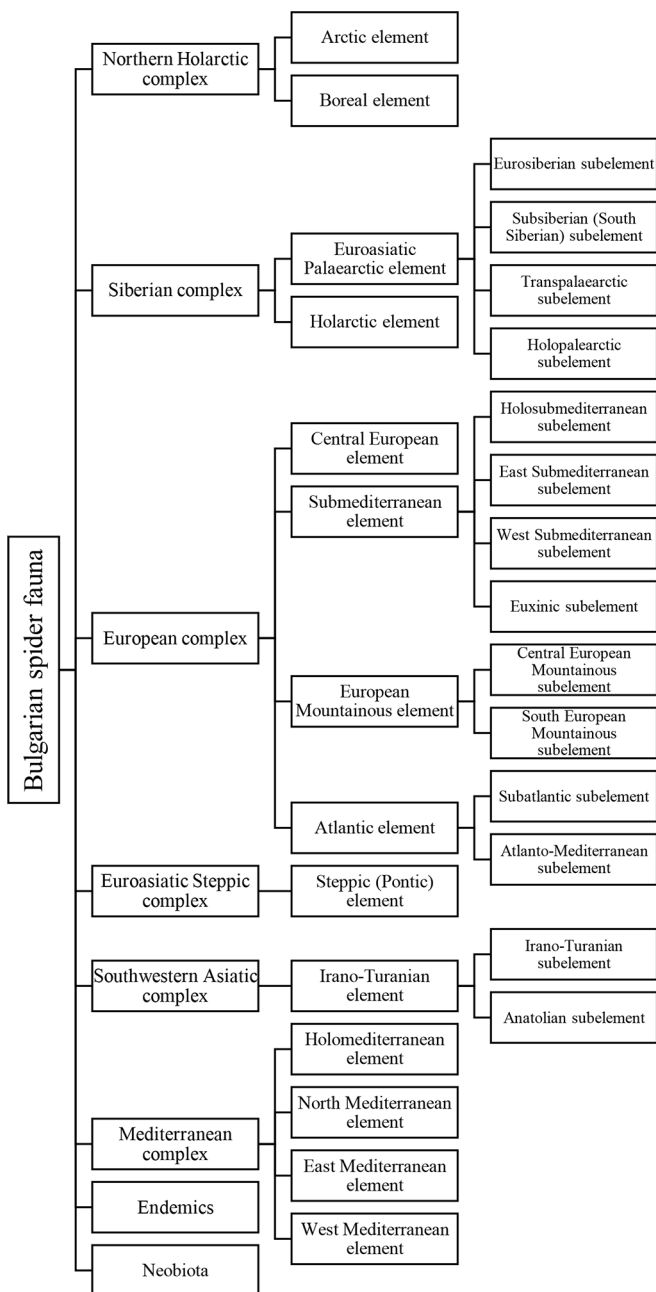


Fig. 1: Faunistic complexes, elements and subelements, forming the Bulgarian spider fauna (based on Gruev & Kuzmanov 1994, Gruev 2000)

Turanian one. It is divided into two subelements – typical Irano-Turanian and Anatolian.

The **Mediterranean complex** comprises species originating in the region of the present Mediterranean. It is split into four elements: Holomediterranean, North Mediterranean, East Mediterranean and West Mediterranean.

An additional category of **Neobiota** is added to the classification in the present paper. This category groups different introduced spider species that do not belong to any of the complexes naturally forming the Bulgarian fauna. Such as, for example, species introduced from South America, East Asia, etc.

The **Cosmopolitan** category, used by Gruev & Kuzmanov (1994) is excluded here, because the origin of most of the cosmopolitan spider species discussed by them is already known.

History, examples and arguments

Drensky (1946: 116) introduced the concept of “ancient autochthonous species” for species that, according to him, have survived from the early or middle Tertiary to the present day. He described them as “widely distributed not only in Europe, but also in North America, not ubiquitously, but only in localities, where there are certain conditions: altitude, temperature, humidity, etc.”. He split them into three types:

- Species distributed in Europe and North America. Here he placed *Aculepeira carbonaria* (L. Koch, 1869), *Callobius claustrarius* (Hahn, 1833), *Amaurobius ferox* (Walckenaer, 1830), *Parasteatoda lunata* (Olivier, 1789), *Steatoda bipunctata* (Linnaeus, 1758), *Cyclosa conica* (Pallas, 1772), *Ara-neus angulatus* Clerck, 1757, *Zygiella atrica* (C. L. Koch, 1845), etc.
- Species distributed only in the Palaearctic. He pointed to Europe as a centre of dispersal of these species. In this group he included *Amaurobius fenestralis* (Ström, 1768), *Hyptiotes paradoxus* (C. L. Koch, 1834), *Dysdera erythrina* (Walckenaer, 1802), *Harpactea bombergi* (Scopoli, 1763), *Dictyna uncinata* Thorell, 1856, *Nigma flavescens* (Walckenaer, 1830), etc.
- Ancient autochthonous species with limited distribution. He split them into “old Tertiary relics” and “glacial relics”. He described the first group as remains from the preglacial period. He emphasized that it is difficult to identify which are the Tertiary relics among the modern spiders and it can be done only using indirect criteria, without clarifying what these criteria are. As examples of such species he pointed to *Euxinella strandi* Drensky, 1938 (now a synonym of *Nurscia albosignata* Simon, 1874), *Brachythele denieri* (Simon, 1916) and *Scytodes thoracica* (Latreille, 1802).

Gruev & Kuzmanov (1994) also accepted the existence of Tertiary remains in the present-day terrestrial invertebrate fauna. They formulated more clearly the indirect criteria to identify them: species in monotypic genera; small, disjunctive or local distribution areas; taxonomic rift. They described the Tertiary relics as species that have survived the glaciations during the Pleistocene in refugia with suitable conditions. All the examples of spider species with Tertiary origin they provided are taken from Drensky (1946). Also, they gave caves as an example of such refugia and classified the troglobitic species as Tertiary relics.

Deltshev (1978), based on Gueorguiev (1977), divided the Balkan troglobitic spiders into the following categories:

- descendants from Gondwanan phyletic lines
- descendants from Laurasian phyletic lines
- descendants from Mesoegeidan phyletic lines
- Palaeoegeidan relics
- North Egeidan relics
- South Egeidan relics

He wrote that the origin of most ancient troglobitic spiders (genera and species), which persist in the recent fauna of the Balkans, dates back to the time before the final division of the ancient supercontinents Gondwana and Laurasia, i.e. approximately 160 million years ago (Deltshev 1978). He gave *Zanagherella relictica* (Kratohvil, 1935) as an example of

a Gondwanan descendant, with the argument that the family Symphytognathidae, where the species was placed at that time, also occurs in the Neotropical and Australian regions. As Laurasian descendants he identified *Typhlonesticus absoloni* (Kratochvíl, 1933) and *Carpathonesticus parvus* (Kulczyński, 1914), both in the genus *Nesticus* Thorell, 1869 at that time. According to him, the proof for this is the existence of the genus *Nesticus* in the USA, Mexico and Japan. As Mesoegeidan descendants, he pointed out the genera *Rhode* Simon, 1882, *Typhlorhode* Kratochvíl, 1935 (now a synonym of *Rhode*) and *Paraleptoneta* Fage, 1913, without discussing any particular species. It is worth mentioning the discrepancy with Gueorguiev (1977: 41) who listed the same three genera as North Egeidan relics. Deltshv (1978) did not provide any explanation about what the word “Mesoegeidan” means. It looks to be mistaken, since Gueorguiev (1977) call this phyletic line Mesoegeidan. According to him the descendants from Mesoegeidan lines originated in Mesogeida – a territory that existed in the Palaeocene until the Early Eocene between the Cantabrian Mountains and the Caucasus. For this statement the author refers to Jeannel (1944: 169, 293). Deltshv (1978: 146) explicitly said that he cannot indicate palaeoegeidan species among the troglobitic spiders on the Balkan Peninsula and did not provide an explanation of the name “Palaeoegeidan” either.

Later, in his work about the Bulgarian endemic spiders, Deltshv (1996) divided the endemics into two groups according to their origin: palaeoendemics and neoendemics. He described the palaeoendemics as possible remains of the ancient Mediterranean mountain fauna. Here, he placed *Antrohyphantes rhodopensis* (Drensky, 1931), known only from high mountain caves. He claimed that its restricted distribution area could be explained by the fact that the species is a remainder of such a fauna. He also identified *Zodarion pirini* Drensky, 1921 as a palaeoendemic because of its morphological similarities to *Z. turcicum* Wunderlich, 1980, *Z. korgei* Wunderlich, 1980 and *Z. abantense* Wunderlich, 1980, all known from the north-eastern Mediterranean, according to him. He considered this similarity as an indication of a possible Mediterranean origin. He also classified as palaeoendemics all the Balkan endemic species of the agelenid genera *Inermocoelotes* Ovtchinnikov, 1999 and *Tegenaria* Latreille, 1804, despite their close relationships with some Central European ones, like *Inermocoelotes inermis* (L. Koch, 1855) and *Tegenaria campestris* (C. L. Koch, 1834). He explained these relationships with the possible expansion of these genera to the north in recent times. Later, citing the above mentioned paper, Deltshv (2000: 63) again classified the species of the genus *Antrohyphantes* Dumitrescu, 1971 as palaeoendemics, although he claimed that “...due to the lack of knowledge, it is difficult to determine with certainty which cave spider endemics of the Balkans are Tertiary and which are Quaternary elements”.

Results and discussion

It remains unclear whether Drensky (1946) considered all three types to be Tertiary relics or only the last one (type c). The first assumption is more likely, bearing in mind that in the introduction he claimed that “the evolution of all insects and arachnids happened in the Tertiary, while later only some insignificant changes have taken place” (Drensky

1946: 113). In both cases, however, it is clear that Drensky accepted the existence of species with Tertiary origin in the recent fauna. Obviously, in type a he spoke about the Holarctic species, although the examples he gave are not correct in most cases. Among the discussed species, only *Cyclosa conica* has a typical Holarctic distribution. *Amaurobius ferox*, *Steatoda bipunctata* and *Zygiella atrica* were introduced to America (World Spider Catalog 2020) and the others are known only from the Palaeartic. In type b he described species with different distributions in the Palaeartic. According to the zoogeographical classification accepted here (Fig. 1), the species with a Holarctic distribution belong to the Siberian complex, Holarctic element. The Palaeartic species with a distribution range from the Atlantic to the Pacific, listed as type b, belong to the Transpalaeartic subelement of the Euroasiatic Palaeartic element, Siberian complex. Such a species in type b is *Dictyna uncinata*. The species with a typical European distribution, such as *Dysdera erythrina* and *Amaurobius fenestralis*, belong to the European complex. Neither the Siberian nor the European species can be qualified as ancient. According to Gruev & Kouzmanov (1994) the Holarctic species penetrated North America across the Bering Land Bridge during the Pleistocene. This means they cannot be remnants from the time before the separation of Europe and North America as Drensky (1946) obviously meant. Although he did not define explicitly the criteria for the ancient autochthonous species (type c), he implied that these are species with small distribution areas and primitive morphology. None of the species that he listed in type c, however, meets these criteria. *Scytodes thoracica*, for instance, is a common and widespread species all over the world.

The assumption of Deltshv (1978) that some currently existing species originated approximately 160 million years ago (in the early Jurassic) is, in my opinion, not acceptable. In fact, the ancient origin of many extant cave spiders was rejected by various authors long ago (Brignoli 1978, Deeleman-Reinhold & Deeleman 1980). The examples *Zangherella relicta*, as well as the whole genus *Zangherella* Caporiacco, 1949, are known only from Europe, while the genus *Pseudanapis* Simon, 1905, where the species was placed at that time, is missing in Europe. Such conclusions are unacceptable on a species level.

The existence of the genus *Nesticus* in the USA, Mexico and Japan cannot serve as a proof for an ancient origin of *Typhlonesticus absoloni* and *Carpathonesticus parvus* too. In fact, *Nesticus* is an even more widespread genus, but such a conclusion cannot be made for a particular species. Moreover, today none of the two species belong to *Nesticus*, while both *Typhlonesticus* Kulczyński, 1914 and *Carpathonesticus* Lehtinen & Saaristo, 1980 where they are placed at the moment are known only from the western Palaeartic.

Since here I focus only on the **species** recorded as Tertiary relics, I prefer not to discuss the origin of the higher taxa. Therefore, I exclude the genera *Typhlorhode*, *Rhode* and *Paraleptoneta* classified by Deltshv (1978) as Mesoegeidan descendants.

From the zoogeographical point of view, accepted in this paper (Fig. 1), the origin and zoogeographical status of the species classified as palaeoendemics by Deltshv (1996) look quite different:

It is more likely that *Antrohyphantes rhodopensis* belongs to the European complex, European Mountainous element, South European Mountainous subelement. According to Gruev (2002) the species of this subelement are derivatives of the Central European Mountainous species that have migrated to the south and populated the Balkan's mountains. These species originated in the mountains of the Balkan peninsula (in geographical isolation) as glacial neoendemics.

The other example, *Zodarion pirini*, does not meet the indirect criteria for an ancient origin either. It belongs to the European complex, Submediterranean element, East Submediterranean subelement. The whole group of *Z. germanicum* (C. L. Koch, 1837), where it is placed (Bosmans 1997, 2009), is rather homogenous and rich with closely related species, so we cannot speak of a taxonomic rift as well. Besides, all the three related *Zodarion* species mentioned by Deltshv (1996) are incorrectly classified as Mediterranean. They are all described from Bolu Mountain (Turkey) and have typical Euxinic distribution (South Black Sea coasts), so they are more likely to belong to the European complex, Submediterranean element, Euxinic subelement. The distribution areas of the *Z. germanicum*-related species illustrate very well not only the connection between the East Submediterranean and Euxinic species within the Submediterranean element, but also between the Submediterranean and Central European element within the European complex. The transition from Central European (*Z. germanicum*), through East Submediterranean (*Z. pirini*) to Euxinic (*Z. turcicum*, *Z. abantense*, *Z. korgei*) distribution areas of the discussed species is one more proof that the Submediterranean species are more likely to belong to the European, rather than to the Mediterranean complex, as already stated by Gruev & Kuzmanov (1994). It is well known that during the Pleistocene the European species were forced to migrate either southeast or southwest, avoiding the high mountains (Gruev 2000: 83).

The distribution of the genus *Inermocoelotes* follows a similar pattern. The only difference is that there is no typical Euxinic representative in this genus, but *I. karlinskii* (Kulczyński, 1906) is a common species near the Black Sea coast. Therefore, all these species are more likely to belong to the European complex, Submediterranean element, East Submediterranean subelement. The hypothesis of their Mediterranean origin followed by expansion to the north, suggested by Deltshv (1996), appears implausible because, as a rule, Mediterranean species are rather stenobiotic.

The above argumentation shows that all the species recorded by Deltshv (1996) as palaeoendemics belong to the Central European Mountainous element or to the Submediterranean element of the European complex and thus cannot be classified as palaeoendemics. This raises the question whether any Tertiary remnants really exist in the modern Bulgarian spider fauna at species level.

Opatova & Arnedo (2014) disputed the ancient Mediterranean origin of the Canarian endemics with the argument that modern molecular phylogenetics reveals a large amount of in situ diversification. The fact that the Mediterranean fauna is not as ancient as was previously widely accepted supports the opinion expressed by Gruev & Kuzmanov (1994) that the Mediterranean should be interpreted in a strict sense, not as the ancient Mediterranean.

A checklist of fossil spiders (Dunlop et al. 2020) shows that the earliest fossil records of modern spider species come from the late Pleistocene and Holocene. While discussing this problem with Jason Dunlop (pers. comm.), he expressed the opinion that it is highly unlikely that Tertiary species could remain unchanged until present day.

Deeleman-Reinhold & Deeleman (1980), in their study on troglobitism in spiders, proved that eye reduction in cave spiders takes place rather rapidly – in less than 10000 years. They gave as an example the blind Lycosidae found in lava caves in Hawaii not older than 10000 years in age. In this study, they disputed the widespread opinion that cave species, and especially troglobitic ones, are remnants from an ancient Tertiary fauna that survived the glaciations in caves. According to these authors, troglobitic forms may develop in any place, in any spider family, and rather rapidly, as long as the proper environmental conditions are realized, which contradicts the view that troglobites are among the oldest elements in the fauna. Their estimation fully corresponds with the view of some authors like Stewart & Lister (2001) proving that the contemporary animal and plant communities have a remarkably short history from a geological perspective – approximately 10000 years. Of course, it is still possible that some of the recent cave species are **derivatives** of Tertiary species that developed during the Pleistocene.

Conclusions

Based upon the above-mentioned arguments, it can be concluded that the existence of spider species with a Tertiary origin in the Recent Bulgarian spider fauna is very unlikely bearing in mind the following:

1. There is no fossil material of recent species from the Tertiary, and only indirect criteria were used by past authors to classify species as Tertiary relics.
2. The hypothesis for comparatively fast development of troglobitic forms suggested by Deeleman-Reinhold & Deeleman (1980) disputes the opinion that troglobitic spiders have ancient origins.
3. Results from molecular phylogenetics show that the extraordinary biological richness of the Mediterranean endemics is a result of a recent local diversification (Opatova & Arnedo 2014), rather than a remnant of Tertiary Mediterranean diversity.
4. Several extinctions caused by drastic climatic changes and followed by replacement of the plant communities and the fauna, the last of which took place at the Pleistocene–Holocene boundary (Stuart 2014), should have affected the invertebrate fauna too.
5. The remarkably short history from a geological perspective (approximately 10000 years) of recent animal and plant communities (Stewart & Lister 2001).

The concept of Tertiary relics is in use in molecular phylogenetics as well, but in a different sense. It is not used in relation to particular species that have originated in the Tertiary and survived unchanged until the present days, but rather refers to species whose phyletic line can be traced back to an ancestor that lived in a particular region during this period of time (Arnedo pers. comm.). There are no such phylogenetic studies on any of the discussed species and therefore, none of the latter can be classified as Tertiary relics in the phylogenetic sense either.

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