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Remarks on Origin and Distribution of Troglobitic Spiders

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Abstract

Troglobitic animals are often considered - according to "Jeannelian" and "Vandelian" tradition - to be relicts of ancient hygrophilic faunas, extinct elsewhere. This view has been prompted by their peculiar morphology, which often differs markedly from epigean relatives, and by their patchy distribution, sometimes limited to a small area or a single locality.

In many areas cave spiders are better known than the spider fauna of cryptic habitats on the surface. Better knowledge of these faunas and a taxonomic regrouping based on phylogeny rather than adaptive characters lead to the viewpoint that at least some of the blind cave spiders may not be quite so old as was believed at first. Troglobitic characters, which are predominantly regressive, are an adaptation to a special environment, just like any other adaptation.

The author gives some examples of changed insights of relationships of South European troglobitic spiders which support this view.

Even so, it remains unexplained why troglobites are distributed so unevenly in the world. The author attempts to explain this by arguing that the crucial point is the enormous difference in ecological properties of subterranean environments in different parts of the world. Many factors contribute to the characteristic features of the environment as a habitat and this is reflected in the complexity of the life community it shelters. The more complex the subterranean community and the more isolated from that on the surface, the more chance that adaptational characters develop.

Résumé

Animaux troglobies sont souvent - après les idées de Jeannel et Vandel - considérées comme relictes d'anciennes lignées épigées hygrophiles, éteintes ailleurs. Ces idées sont basées sur leur morphologie souvent très différente de celle de leur parents épigés et sur leur distribution disjointe, souvent limitée même à une seule localité. Cependant, la faune hypogée en général a été mieux exploré que celle des milieux cryptiques superficiels. Une connaissance meillieure de cette dernière et un regroupement taxinomique basé plutôt sur la phylogénie que sur des caractères adaptifs, ont mené à croire qu'au moins quelques unes des araignées troglobies européennes ne soient pas si anciennes que l'on ne les croyait. Il va sans dire que les caractères troglobies (en grande partie regressives) ne sont rien d'autre que des adaptations à un milieu spécial, comme toute autre adaptation.

L'auteur donne quelques exemples d'un changement d'opinion pour ce qui est lesliens de parenté d' araignées cavernicoles européennes qui soutiennent cette idée.

Une autre question touche à la distribution très inégale de troglobies dans le monde. L'auteur présente l'opinion que ça s'explique par la nature écologique actuelle du milieu. L'ensemble de caractères écologiques de ce milieu est très diversifié selon sa situation sur terre, qui se traduit par une différente complexité et richesse de la biocénose. Une grande complexité de celle-ci en isolement avec celle de la surface favorise le développement de caractères troglobies.

In this communication I should like to discuss a few problems in Southeast European cave spiders in view of my own experiences and discoveries, mainly in Yugoslavia. They concern the phylogenetic relationships and age of some blind spiders and I shall make an attempt to relate ecology with the markedly uneven density of troglobites in different karst areas.

Troglobitic animals are often considered - according to Jeannelian and Vandelian traditions - to be relicts of hygrophilic faunas of the Tertiary tropical or subtropical forests, the only survivors of elsewhere extinct lines (Jeannel, 1943; Leleup, 1965; Gueorguiev, 1977; Deeleman-Reinhold, 1978; Deltshev, 1978; Kratochvil, 1978). This view has been prompted by the peculiar morphology, especially in Catopid and Carabid cave beetles, which are sometimes surprisingly different from their nearest relatives, by their patchy distribution, sometimes limited to a small area or a single locality, and by the absence of close relatives on the surface.

In many areas cave spiders are better known than the spider fauna of the surface. Better knowledge of these latter faunas and a taxonomic regrouping based on phylogenetic rather than adaptive characters lead to the viewpoint that at least some of the blind cave spiders may not be quite so old as was believed at first (Brignoli, 1979; Deeleman-Reinhold, 1980). Troglobitic characters, which are predominantly regressive, are an adaptation to a special environment, just like any other adaptation.

Considering cavernicolous spiders from an ecological point of view, they fall into a number of categories, filling various compartments within the hypogean environment. The following classification is based on my experience with Southeast European cave spiders.

1) Entrance spiders ("association pariétale, partim). The "wallé spiders are usually rather large, they are web-makers and find abundant prey among the numerous insects that migrate through cave entrances; examples are Meta menardi (Latreille), Meta merianae (Scopoli), Nesticus cellulanus (Clerck), various Tegenaria and Hoplopholcus species. They are also found in cellars, pits and superficial cavities.

2) Versatile cave spiders; these species lack morphological adaptation like the first category, and they are ecologically rather flexible: they may be found anywhere, from the deepest cave parts to the surface in shaded, moist situations. Their stay in the cave is facultative, although they are perfectly capable of completing their life cycle and reproducing in the cave. Examples in Yugoslavia are Troglohyphantes excavatus Fage and other Troglohyphantes species, Lepthyphantes centromeroides Kulczynski and perhaps some Leptonetidae. These are all web-builders.

3) Endogean (edaphic) spiders, that live in the top meter or so in soil, clay- or rock-particles, only occasionally in caves; they do not appear on the surface and may show some morphological adaptations. They catch prey in various ways, with or without web; it is uncertain what kind of prey they live on. Examples are the Dysderid genera Minotauria and Rhode and certain Harpactea species, also some small spiders like Pseudanapis and certain Centromerus.

4) Obligate cave-dwellers, troglobites that are usually eyeless and live exclusively in the underground channel- and cave system. They hunt actively on the walls and the moist dripstones or build webs in the vicinity of the scarce organic debris. This group includes the majority of the blind Dysderids and Linyphiids (Troglohyphantes and Centromerus) and some Leptonetidae. They are as a rule unrelated to entrance spiders. Their adaptation consists of strongly reduced or absent eyes, pale colouring due to lack of melanin pigement and thinning of the teguments, elongated and thin appendages and hyperdeveloped sensory organs.

It is these last two categories with which the rest of this paper is dealing. Taking into account the fact that troglobites live most often in small populations, in which evolutionary changes can spread rapidly, the mere fact that they look different from epigean relatives does not involve necessarily that they have been separated from them a long time ago. Evidence that their phylogenetic characters are in a more primitive state than they are in their epigean counterparts is unconvincing or lacking, with a few exceptions (Deeleman-Reinhold, 1978, 1).

Does this mean that there are no relicts among troglobitic spiders in Europe? It has to be borne in mind that karst terrain is not one of the most stable environments, as exposed carbonate rock is continuously subject to corrosive destruction. But the very thickest deposits may last long enough to survive through some major climatic revolutions and the possibility should be visualized that the hypogean environment may have similar conservative qualities as for instance deep sea, or islands. Possibly the only witness of this as relicts are the South European troglobitic Telema tenella Simon (Telemidae) and the troglophilic Pseudanapis species

(Symphytognathidae) as representatives of typically tropical families.

An intriguing problem in European spiders is centered around a number of species, some of which with reduced eyes or even blind, that are habitually neither found in caves, neither in leaf litter. They have been found only under special conditions in cave entrances deep down underneath a layer of stones, between sheets of laminate rock, or in spring when wheather is cool and moist they could be obtained in very deep crevices, associated with decaying humus. Their habitat may correspond with what the Moulis workers call "milieu souterrain superficiel" (Juberthie, Delay & Bouillon, 1980). They are related to cave spiders but do not belong to the same species, they have been listed above under the category edaphic spiders; in theory they can also exist on non-carbonate bedrock. In this environment probably a large amount of spiders is still to be discovered, as it is difficult to collect them. Some of the rarer cave spider species probably have their main habitat here. From recent experience in spider collecting in Crete it appears that this habitat is particularly well developed and consists there of a mixture of crumbly, loose clay- and rock particles, and is relatively easily accessible around cave entrances.

The number of spider species or species groups without apparent epigean, "normal" relatives, used as an argument in favour of the theory of troglobites as relicts, has been overestimated as a result of insufficient knowledge of epigean faunas and their phylogenetic relationship with them. In the course of my taxonomic studies on Yugoslav cave spiders I have come across quite a few of such cases. Thus, the apparently isolated taxonomic position of the Dysderid genera of exclusively blind species: Folkia, Stalagtia and Typhlorhode, the troglobitic Roeweriana dibens, dubius and myops (Agelenidae) the Troglohyphantes species of group salax and the singular blind Nesticus absoloni Kratochvil have all been refuted by recent finds by Brignoli, Wunderlich and myself, or by newly established relationships. Still remain to be resolved the relationships of a.o. the blind Yugoslave cave spiders Typhlonyphia reimoseri Kratodhvil, Nesticus parvus Kulczynski, the enigmatic Agelenid Hadites tegenarioides Keyserling, the male of which is still unknown, after 120 years in spite of intensive searching in the few accessible caves of the island of Hvar to which it is endemic, and the Linyphiid genus Icariella (Brignoli, 1979, 1). The distribution patterns of a number of the above mentioned groups are shown in Figures 1-6. (Data a.o. from Brignoli, 1972, 1975, 1976 1 and 1; Deeleman-Reinhold, 1978, 1 and 2; Kratochvil, 1938, 1970.) Troglohyphantes group salax was believed to include at least 13 blind or semiblind species with a remarkable distribution (Figure 6). Recently a new species, epigean and with normal eyes, yet unnamed, was discovered in Turkey. In each of the mentioned cases the bline species were found to be closely associated taxonomically to normally-eyed species, but never from the same area. From these distribution patterns a fascinating trend is distilled: the blind members of each of these units are all centred in approximately the same area in Yugoslavia. Indeed, the absolute number of troglobitic spiders (and also other invertebrates) is exceptionally high in this area. Compared to other well investigated karst areas in the world the ratio blind:nonblind cavernicolous spiders is unique: very roughly 1 blind to 2 nonblind in Yugoslavia, 1:9 in the Pyrenees, 1:18 in Japan (see also Deeleman-Reinhold, 1980).

What could be rhe reason of this extraordinarily high density of blind spiders in southwestern Yugoslavia?

Two basic causes can be proposed: a) the geological and climatological history of the area, and b) the present conformation of the area and its implications on its quality as a habitat. Explanation a) does not account for the poorness of troglobites in adjacent karst areas (eastern Serbia, northern Greece, Bulgaria, Italy) as these areas have good karst terrain and similar climatical histories as western Yugoslavia. As regards b), Yugoslavia is distinguished from the surrounding areas today by the much greater extent of the karst surface, the larger scale, more dynamically, of the karstification processes. It is my suggestion that b) is of much more importance than a) in the development of the terrestrial troglobites. In Yugoslavia, in my opinion the major agent in their evolution is the physical properties of the subterranean environment, and the climate. Factors playing a part in this specific conformation are the high rainfall, the great, uninterrupted mass of uncovered carbonate rock, the enormous depth of them (up to 5000 m) and the specific structure of the rock, offering optimal conditions to support a diversified community of microflora and fauna which is relatively independent from that of the surface and in which loss of eyes and other adaptational transformations are selectively advantageous.

Elsewhere in the world, i.e. one of the Hawaiian Islands, a rich troglobitic spider fauna has been found in the lava caves which apparently are not older than 10,000 years (Gertsch, 1973). This fauna includes the first two blind Lycosidae and a blind erigonid Linyphiidae. It suggests, that, if only the proper environmental conditions are realized, troglobitic forms may develop almost in any family, in any place and rather rapidly. It certainly opposes the idea that troglobites are among the oldest elements of the fauna.

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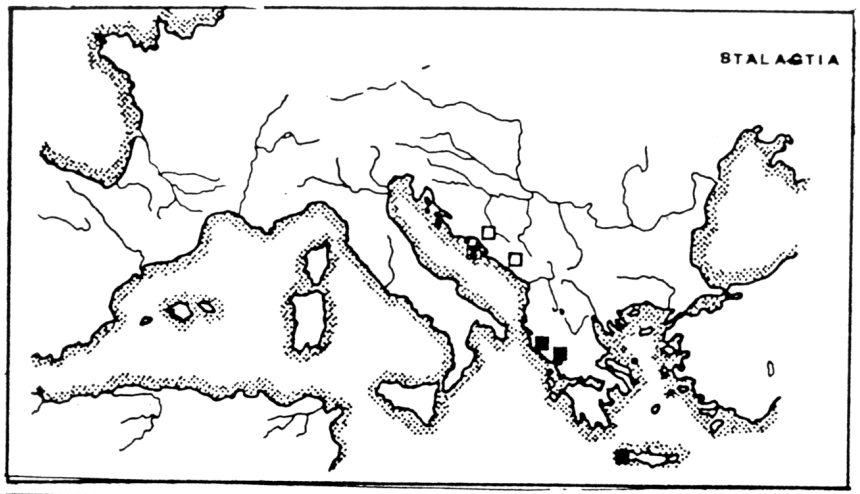

Figure 1. Distribution of species of Stalagtia (Dysderidae). White squares, blind species: S. hercegovinensis (Nosek), S. inermis (Absolon & Kratochvil), S. monospina (Absolon & Kratochvil) and others. Black squares, species with normal eyes: S. kratochvili Brignoli, S. argus Brignoli, S. spec.

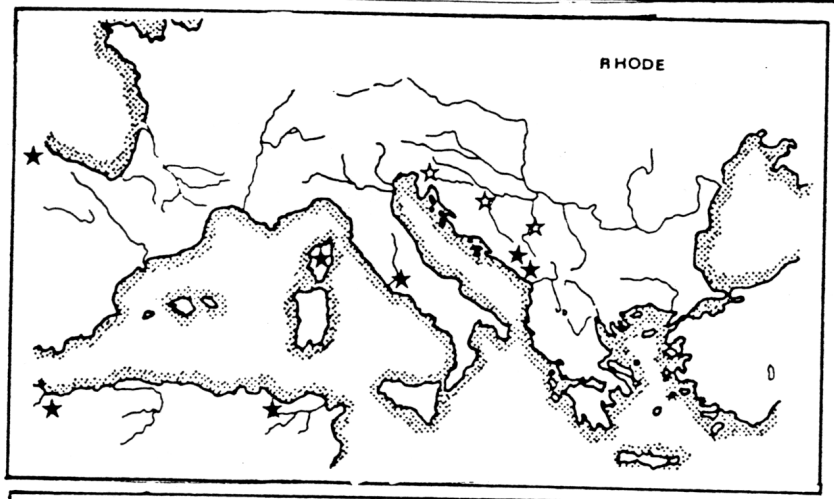

Figure 2. Distribution of species of Rhode (Dysderidae). White asterisks, blind species: R. aspinifera Nikolić, R. stalitoides Deeleman-Reinhold, R. subterranea (Absolon & Kratochvil). Black asterisks, species with normal eyes: R. biscutata Simon, R. scutiventris Simon, R. tenuipes (Simon), R. maginifica Deeleman-Reinhold, R. spec.

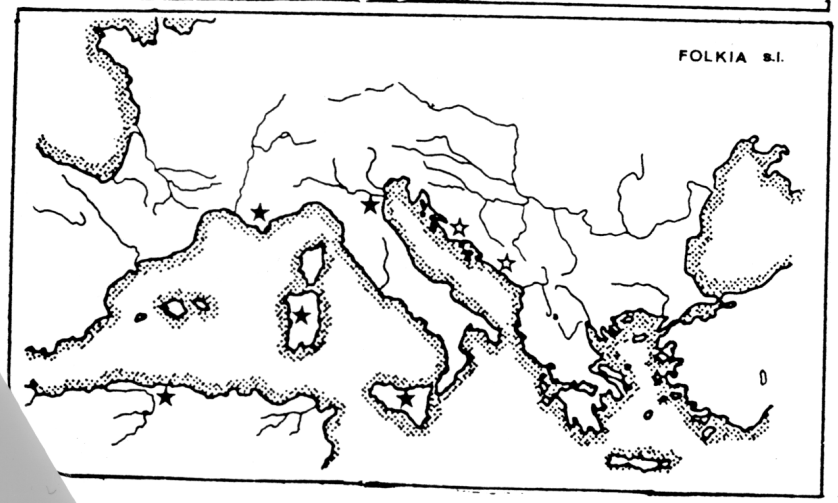

Figure 3. Distribution of species of Folkia s.l. (Dysderidae). White asterisks, blind species: Folkia haasi (Reimoser), F. mrazeki (Nosek) and others. Black asterisks, species with normal eyes: Harpactea arguta Simon, H. muscicola Simon, H. sardoa Alicata.

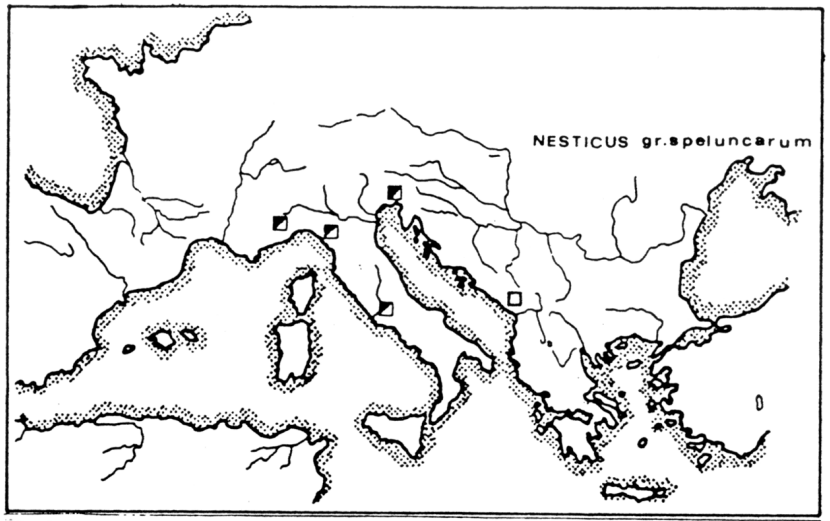

Figure 4. Distribution of Nesticus species group speluncarum. Black/white squares, species with depigmented eyes: N. speluncarum Pavesi, N. menozzii Di Caporiacco, N. morisii Brignoli, N. sbordonii Brignoli, N. idriacus Roewer. White squares, species without any eyes: N. absoloni Kratochvil.

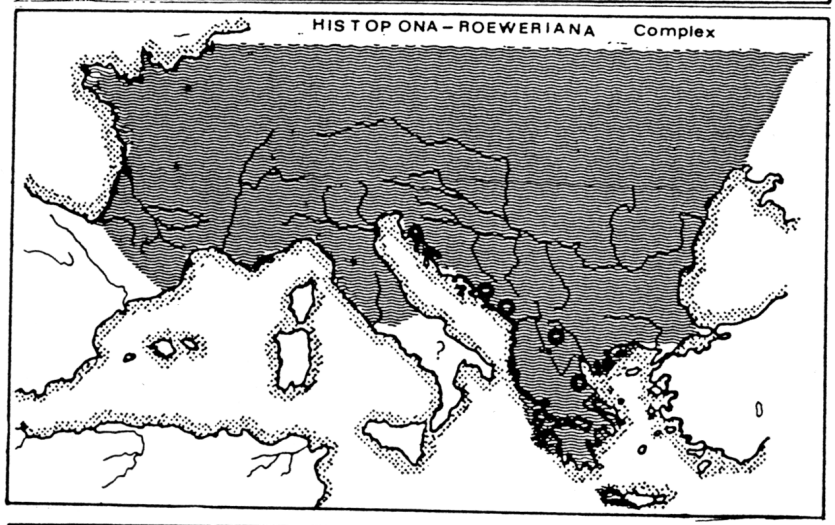

Figure 5. Distribution of the species of the Histopona-Roeweriana complex (Agelenidae). Hatched area: species with normal eyes: H. torpida (C.L. Koch), H. conveniens (Kulczynski), H. luxurians (Kulczynski), H. sinuata (Kulczynski), H. italica Brignoli, H. palaeolithica (Brignoli), H. tranteevi Deltshev, H. vignai Brignoli, Roeweriana hauseri Brignoli, R. strinatii. Asterisks, species with reduced eyes: Roeweriana dubius (Absolon & Kratochvil), R. bidens (Absolon & Kratochvil), R. myops (Simon).

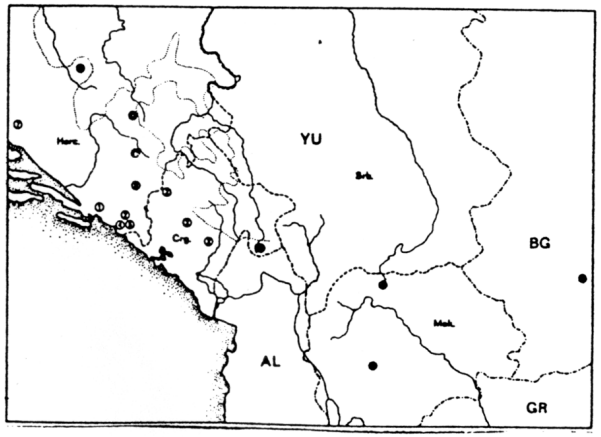

Figure 6. Distribution of the species of Troglohyphantes group salax (Linyphiidae). White circles: blind species, black circles: species with reduced eyes. Not shown: one epigean species with normal eyes in Turkey.