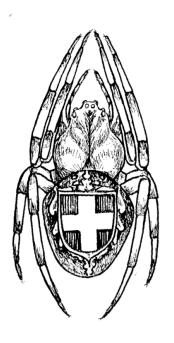
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SEPARATUM

REMARKS ON TROGLOBITISM IN SPIDERS

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In discussing the evolution of troglobitic arthropods of southern Europe, most authors have emphasized the impact of the geological and climatological history of the area; most forms are assumed to be relics without any close relatives on the surface (6,8,17,24,25). The point I want to make here is, that in my view the qualities of the actual habitat have not sufficiently been taken into account.

Since their discovery, blind cave animals have always intrigued zoologists, perhaps mostly by the incongruity of their abundance and the apparent absence of food. Indeed, troglobites are highly specialized cave animals, considered to be unable to live and to reproduce outside caves. They are characterized by the loss of eyes (and wings) and pigmentation and by the elongation of appendages and they present also various physiological modifications. Troglobites occur in most orders of arthropods (and in several more aquatic phyla as well); in spiders they occur predominantly in haplogynes and mygalomorphs, but there are also many species in the Nesticidae, Linyphiidae and Agelenidae. Increasing numbers of blind spiders are being found in other habitats, like deep leaf litter and termite nests.

A fascinating aspect of the cave fauna is the uneven distribution of troglobites in the world.When comparing some reasonably well surveyed cave areas in various continents, we find that the number and ratio of troglobitic spiders vary enormously. In table I very rough approximations are given for a number of cave areas. Data are taken for Mexico from GERTSCH(11,12,14) and BRIGNOLI(1,2), for Japan from YAGINUMA(28,29,30 a.o.), for Hawaii from GERTSCH(13), for the Pyrenees from FAGE(9) a.o. and for Yugoslavia from KRATOCHVIL(18,19,20,21,22,23,24)

	tota l karst surface in km ²	total no.of species	no.of troglo- bites (blind	-	ra	tio
Mexico Prov.San Luis Potoci(subtrop.) Prov.Tamaulipas(subtrop.) Prov. Chiapas (trop.)	? 60,000 75,000 70,000	137 25 28 9	25 3 6	5½ 8 5		1
Japan, total Akiyoshi Plateau	350 , 000 200	25 123 19	6	18 19		
Hawaii Island (lava caves)	9,000	18	6	3	:	1
Pyrenees and adjacent provinces	45,000	47	5	9	:	1
Yugoslavia West and Middle Slowenia Southwest Yugoslavia	12,000	30 65	9 33	3 2		1 1

Table I. Total karst surface, total number of cave spiders (including troglobites and troglophiles, excluding trogloxenes) and ratio of troglobites for a number of cave areas.

and myself(3,4,5,6 and unpublished). Some not mentioned, but well investigated cave areas offering suitable conditions are very poor in cave animals. Obviously, the presence of apparently suitable caves alone is not sufficient for the existence of a specialized fauna.

Why then, are troglobites numerous in some, rare or absent in other areas which nevertheless abound in caves offering the required conditions? Is it determined just by historical events or are there other agents playing a role?

Since JEANNEL in a.o."les fossiles vivants des cavernes" launched (17) his sometimes audacious ideas, it has become more or less universally accepted that most South European troglobites are remnants of Tertiary tropical or subtropical forests. Any hypothesis however, bearing on the relative age of a troglobitic animal should be tested by finding answers to the following questions:

1) are relatives with normal eyes found in the same area?

2)does the cave form differ much from its nearest epigean relative?
3)has the cave form more characters in a primitive state than have its epigean relatives?

In fact, these answers may be very different for different spider species within a given area. Let us look at some examples. At least in haplogyne spiders, eyes apparently can get lost easily: in the Mexican Tetrablemmid Matta sbordonii (BRIGNOLI) there are eyeless cave populations side by side with epigean, eyed forms with reduced lateral eyes (27). On the other hand, some South European eyeless species appear at present to be without near relatives at all: the Pyrenese Telema tenella SIMON is the only European representative of a tropical family. No close relatives have yet been found for the blind Yugoslav Linyphiid Typhlonyphia reimoseri KRATOCHVIL, the blind Nesticid Typhlonesticus parvus KULCZYNSKI and the blind Agelenid Hadites tegenarioides KEYSERLING. Until the last decade, it looked as if many more Yugoslav blind spiders were without relatives on the surface, but in more than one case this has been refuted by recent finds. I may refer to the 13 blind or halfblind Troglohyphantes species of group salax in southern Yugoslavia and Bulgaria that I published two years ago (6); at that time the group included only troglobitic species(fig 1)

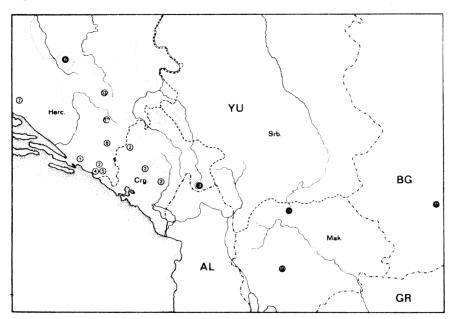


Fig.l.Distribution of the the species of Troglohyphantes group salax; open circles: blind species, black circles: semiblind species

Recently an epigean species of this group with normal eyes was discovered in Turkey byWUNDERLICH(personal correspondence). In southern Yugoslavia also lives the pale eyeless Nesticus absoloni KULCZYNSKI apparently without any close relatives. The finding of the hitherto unknown male of N.idriacus ROEWER(unpublished) in northwestern Yugoslavia reveals that this troglophilic species with nearly normal eyes is a close relative of N.absoloni. The Dysderid genus Folkia KRATOCHVIL till now only comprised a number of blind species, all in southern Yugoslavia When comparing Folkia with the Harpactea species of group corticalis SIMON(fig.2) and group arguta SIMON(fig.3), it is evident that they are closely related, much closer than are these groups with other species within the genus Harpactea.

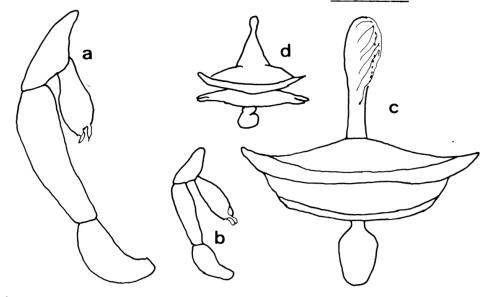


Fig. 2. Folkia mrazeki(NOSEK):a)male palp,c)vulva. Harpactea corticalis SIMON:b)male palp,d)vulva.

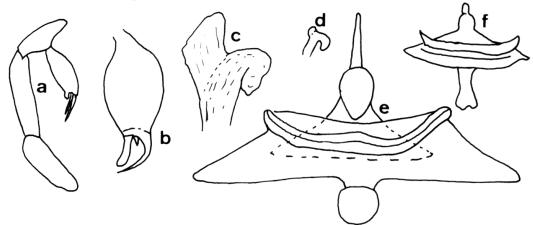


Fig. 3. Male palp of:a) Folkia purhrabeki KRAT., b) Harpactea muscicola SIMON. Female spermathecae in lateral view of:c) Folkia haasi (REIMOSER) d) H. muscicola. Vulva of:e) F. haasi, f) H. muscicola. (a, after FAGE, b and f after ALICATA.

Each time we are concerned with a group with mediterranean distribution, in which only the south Yugoslav species are blind (fig. 4)

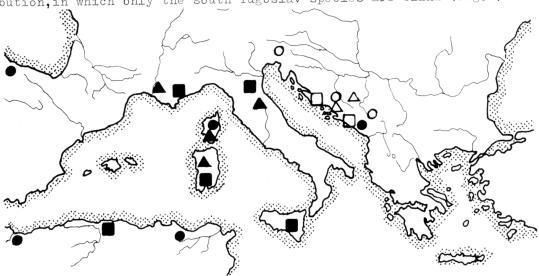


Fig. 4. Distribution of the <u>Harpactea</u> species group <u>corticalis(black</u> squares), <u>Folkia mrazeki</u> and related species(open squares), <u>Harpactea</u> species group <u>arguta(black triangles)</u>, <u>Folkia haasi</u> and related species(open triangles), the normal-eyed species of <u>Rhode</u> (black circles) and blind <u>Rhode</u>-species(open circles).

This leads to the main objective of this communication , namely to present a possible explanation of the much higher incidence of blind spiders in West Yugoslav caves than in caves of other areas.

Caves in fact constitute only a small part of the total hypogean environment and this may be the key to the answers of the questions put above. The primary habitat of terrestrial troglobites, in contrast to that of troglophilic animals is what the french call"réseau de fentes": the underground network system of faults, solution channels, etc. This system is distracted from our observation, we see a glimpse when a rock face is exposed after explosions for road works etc. We meet the troglobite only in the largest of the cavities, the caves, which may be for them only a marginal habitat. The quality of this domicile in its capacity of supporting a specific fauna is determined by a number of factors, such as extension and depth of the (carbonate) rock, climate and rainfall and the chemical composition of the rock and its history and their effect on the conformation of the inner spaces and their microflora and -fauna. The subterranean habitat should be large and varied enough to support a population (in which having eyes is selectively a disadvantage), that should be clearly separated from the populations of adjacent habitats in which possession of eyes plays a positive rôle in survival.

Ecological experiments with blind cave beetles (7,26) have shown that there are considerable seasonal fluctuations in density within a cave. The species studied were abundant in summer, scarce in winter. This could not be correlated with reproduction peaks. The results lead the authors to draw up a theory of migration to and from other parts of the habitat, inaccessible to Man in response to a.o. fluctuations of temperature, humidity and food supply. This would also explain the occasional finding of blind animals in deep surface layers during cool and wet seasons in the Mediterranean region.

Our own experience concerns mostly Yugoslavia, whose karst holds the world's record for abundance of troglobites; we have been able to compare it with other karst areas in the world. Our observation is that indeed it is distinguished from other such areas by: 1) the enormous extent in horizontal and vertical dimension of uninterrupted and uncovered carbonate rocks, and 2) the intensity and dynamic character of its karst processes. GEZE and GINET(15) (see also 10) are greatly impressed by the Yugoslav karst: "...ou la spéléogénèse et morphologie karstique paraîssent bien poursuivre aujourd'hui leur développement et leur évolution sans aucune restriction..." and "...les facteurs topographiques, géologiques et climatiques rarement réunis d'une façon favorable à la karstification."

The baffling discovery of troglobites in mines in non-carbonate rock in Japan (30) and the existence of a rich troglobite fauna in lava caves in Hawaii, not more than 10,000 years of age (15), including the first two blind Lycosids, suggest that if only the proper environmental conditions are realized, troglobitic forms may develop almost in any family, in any place and rather rapidly. It is at variance with the view that troglobites are among the oldest elements of faunas.

*) Folkia lugens BRIGNOLI from Greece is of uncertain relationship: the male is unknown, the vulva suggests that it is not close to Folkia.

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