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NEMATODES AND THEIR ROLE IN CAVES

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Little is known about the nematode fauna of caves. The number of works, discussing cavernicolous nematodes, is hardly half a dozen. In one of my works (Andrassy, 1959), I have summarized all known literature references, and it was found that there were shown about 100 species from caves. Sixteen of them have been described as new for science, - nor were they found in other habitats ever since. Although six years had passed since the publication of the above mentioned paper, there have been published but some few new nematological data even as a result of recent speleological investigations. Aside of the natural caves, there are scattered literature data concerning the nematode fauna of other subterranean habitats, but I have waived their discussion since they represent artificial sites (mines, shafts, artificial cavities). Let us restrict our discussion also in the followings to the nematode fauna of the natural caves.

Though, as I have mentioned above, there are but few data available, their prudent evaluation and comparison together with the results of my own investigations give a certain general picture of the nematodes inhabiting caves, the interrelations between the habitats, the physical features of the caves, and the animals populating them, as well as the role of the nematodes in these sites.

I have conducted my investigations, for a number of years up to these very days, in the Barradla Cave, Northern Hungary. The cave or cave-system, is in the Triassic limestone of the karst formation in North Hungary, formed by natural, subterranean waters. The length of the main branch is 6800 m, the complete length of the whole system 22000 m, being one of the biggest, and the most beautiful, dripstone cave of Europe. Today, it has no constant running water, save for two seasonal brooks. Its main annual temperature, fluctuating only by some tenths of degrees in the yearly seasons, is 11º C, the aerial humidity 95-100 per cent. Its soil consists of

sand, gravel, and clay. It is known since the XVIII century, hence the main pass shows certain human influences.

For years, our institution collected nematodes in the cave, that is, samples have been brought into the laboratory with the hope of finding nematodes in them. It goes without saying that the co - llectings were "blind", delimited to the taking of various samples, since the direct gathering of these extremely small animals - dis - cernible mostly by the microscope only - is wellnigh impossible. Furthermore, since conditions conductive to life are by far more restricted in caves than, in general, on surface localities, we have been obliged to transfer a great number of samples to the laboratory and to study them thoroughly, to find out empirically in which habitats, or rather micro-habitats, of the cave do nematodes live, in short: where nematodes are to be found at all. We took samples from almost all possible habitats, as well from the dry as from the aquatic ones, but we found, never the less, that the majority of the samples were entirely free of nematodes and only a comparatively small percentage yielded animals. All this, as I have mentioned and as it will yet be discussed, is a direct result of the adverse conditions of the caves.

The known and published nematode fauna of the Baradla Cave consists of 22 species. I hasten to add, however, that I have observed in some recent materials under examination some further species, and it is also quite sure that future collecting will yet yield still newer species for the fauna of the Cave. Three of the species published hitherto proved to be new for science, and the other species were as yet unknown from cave habitats. Consequently, I found nine nematode species only which were already known from caves of various other countries.

The habitats of the nematodes found in the Cave can, from a practical point of view, be relegated to two main types: "dry" and wet. The notion of the dry habitat is figurative in the present case, nor is it an air-dry locality. In sites like these nematodes do not occur at all in an active state, indeed, they cannot occur, since their cuticle acting as a semipermeable membrane could not, on the one hand, protect them against the evaporation of the corporeal fluids, and, on the other, their movements and feeding, and their entire life-activity at all, are always dependent on water. Hence also the so-called terrestrial species always reside in the capillary waters of the soil or other terrestrial substrates. But one cannot speak of air-dry habitats in the Baradla, or any other cave, by

the simple reason of their atmosphere being almost completely saturated by humidity.

After this preamble, we may state that the terrestrial habitats in which we found nematodes, of the cave under discussion, are the following: certain sites of the cave subsoil, decaying vegetable materials (mainly lying wooden planks, poles standing in water, scattered remnants of food left by visitors), living vegetable matters, (higher fungi and moulds) as well as their soil-substrates, and detritus of an animal origin (chiefly bat guano, dead bats, soil mixed with the excrement of isopods). Of the aquatic habitats, seasonal are the larger waters on the ground, infiltrating floods from above and their remaining pools, while constant are the dripping flows from above and their pools on the ground, the oozing waters constantly wetting the walls of the cave, and attainable groundwaters. These are the habitats in which nematodes have been found. Although the number of habitats seem to be great, only a small percent of the samples taken from them contained nematodes, and they, too, occurred only in rather few specimens. This phenomenon has manifold causes, all deducible to the special features and conditions of the cave. Of the factors determining the occurrence of the nematodes, let us discuss here only the most important one, namely the conditions of food.

The nematodes, found in the Baradla and in all other caves discussed in literature, represent three main types of life. The majority of the species are those feeding on composed organic matter. A part of them live on bacilli, another is fungivorous or lichenophagous, and still, another feed on minute vegetable or animal detritus. The other type is constituted by the fluid-sucking - we might say fluid-eating - forms. These suck the fluids of vegetable cells and tissues, rarely those of other small animals (eventually other nematodes). The third type is represented by the predators which consume unicellular beings, tardigrades and small worms (rotatorians small annelids, but mainly nematodes). It is now quite manifest that with respect to the rather reduced food conditions of caves, the first type is the one which can yet best procure its food. If not everywhere and not in any great amount, composed organic matter is still the easiest to find. There occur, at least seasonally in every cave with running waters some driftwood, vegetable parts, and, in caves which draw tourists, organic refuse left behind intentionally or unintentionally. But a significant role in submitting food is played in most caves by diverse bat species (guano, dead animals),

and in decomposing materials, there are always to be found bacteria or microscopic fungi for nematode species which live on them. It is readily understandable therefore that it is the members of the first type which occur in the greatest numbers in caves, thus also in the Baradla whose fauna consists in 80 percent of these species.

Considerably more adverse conditions are met with by the animals sucking fluids. Their sole food is more or less the cellular liquids of higher and lower fungi. Finally, the food-sources of the raptors are also severely delimited. Microscopic animals are by far not as plentifully available here as in supraterrestrial habitats, and my own investigations as well as all relevant literature data insist that predatory nematodes are to be found in greater numbers only in habitats which abound in other nematodes, protozoa, etc. This is but natural, since the acquiring of food necessitates the greatest amount of work, if only for the fact that the locomotive ability of the nematodes is very slight and extremely restricted. And in fact, there was found only a single predatory nematode species in the Baradla Cave up to now.

Active nematodes in caves can therefore be found only in or near "heaps of food". And yet, recently introduced organic materials entirely removed from already existing sites of food, will sooner or later be populated by nematodes. The active, foodsearching locomotion of the animals hardly counts for much, since, as we have seen it, their arbility in this respect is very slight. On the other hand we may safely assume that there must occur, as well, in aquatic as in dry habitats, that is, in the very lifeless soil of the cave, the so called inactive (passive) species, too scattered and distributed everywhere. Inactive nematodes are forms which do not show any discernible life-activity, resting in an anabiotic state as eggs or permanent larvae, activizing only when the necessary environmental conditions, thus available food, are given. Forms like these can be found or bred usually in great numbers also from surface soils or other habitats, but a part of also the active species might convert themselves into inactive forms if the environmental conditions tend to become adverse or inimical, precluding active life.

This is emphatically so in the case of caves. The occurences within the cave of the nematodes, their foci evolved in the vicinity of the foodstuffs, and their active populations, can be explained only by the presence of the presumed inactive forms. Due to their minute size alone, the locomotion of the nematodes is slow and insignificant. They cannot bridge over greater, foodless distances by

merely their movements, because they will either starve or go into an inactive state. Of course, there are some means even in caves which assist animals in finding their food. Such, first of all, is water, which might carry the animals, even within the cave, far away and to diverse sites, and such might be the passive transference by other animals and man. However, they are all eventual or chance factors, emphasizing still more the importance of the inactive forms. In the last analysis, it is only explainable by the presence of the inactive groups that the nematodes can largely utilize casual food sources - and a significant part of the food available in caves is invariably of an incidental character. The inactive forms were therefore the ones which, evenly distributed in the greater part of the cave, would, as it were, wait for the occurrence of food. If this occurs, they will become activized, proliferate, and thus perpetuate their species to tide over future unfavourable circumstances.

These are not mere suppositions. In the Baradla Cave, I conducted a series of experiments to find out what inactive nematodes lie latent, and what dispersion they show, in the clayey and rocky soil nearly completely free of organic matter, of the cave. Although the experiments are not closed yet, we have already obtained some interesting partial results. The samples, taken from diverse localities, were inoculated in sterile conditions with various kinds of food - tuffs and kept for weeks and months in the cave laboratory - where the climatic conditions were identical with those in the free parts of the cave. Control examinations were also made on the soil samples and it was found that they have been completely free of nematodes prior to the inoculations. Despite this fact, I found, in one or two weeks, or in a few days in some samples, that there appeared smaller or greater numbers of nematodes in the cultures. Let me emphasize again that the samples contained no active animals prior to the inoculation, and that the foodstuffs used for the culture were carefully sterilized. The nematodes had evidently appeared in the culture from the soil sample itself, having been lying in an undemonstrable, inactive state in the soil and appearing in an active and for us demonstrable form only by the effects of the presence of available food. It could also be shown that the inactive nematodes are evently distributed in the soil substrate. In all inoculated soil samples, regardless of their place of origin from within the cave, the active nematodes appeared sooner or later.

The population by nematodes of the caves can occur by several means: by water, introduction by animals or man, or by other, less

important channels. The most important factor is undoubtedly water. It is superfluous to emphasize its role, and I would merely point out that, of all multicellular animals, it is the nematodes which can most thank water for their presence in caves. Their small size, their organism constituted for a passive distribution, and their considerable adaptive abilities are the very factors which make possible that even the most insignificant seepages of water can convey nematodes into caves, where they remain capable of life either in an active or an inactive state. I found numerous nematodes in the Baradla in the slowly dripping water, collected in a suitable container, though this water seeped through an entire mountain until it appeared on the ceiling of the cave. In the same way, the capillary waters oozing through the walls of the cave might also carry nematodes. But the introduction of nematodes by water into caves happened not only in the present but surely also in the past. An excellent proof of this statement is the three nematode species which have been discovered in 1936 by Stammer and in 1940 by Schneider in the karst caves of Yugoslavia. They belong to genera, indeed, to families whose recent living representatives are exclusively maritime and have no terrestrial allies. The three species -Desmoscolex aquaedulcis Stammer. Thalassoalaimus aquaedulcis Stammer, and Halalaimus stammeri Schneider - are manifestly relict species of the Tertiary seas. No similar species were as yet found in the Baradla Cave, but their occurrence would not be surprising and the more so as the famous and also a maritime relict species of the Polychaeta, namely Troglochaetus beranecki Delachaux, was also successfully demonstrated from the Baradla.

Finally, I should like to touch on an interesting problem. Namely whether there can be found in caves nematode species which might be regarded as true eutroglobiont organisms, that is, which live exclusively in caves. I have already mentioned that, among the nematodes found in diverse caves, about a dozen and a half new species had been described. They are all known only from caves, never found in other subsurface localities. I have also stated that I found three new nematode species in the Baradla. Whether they are really true eutroglobiont organisms is, however, not so easy to decide. The three Yugoslavian relict species are without doubt eutroglobionts, since they have survived entirely isolated from their relatives, in cave-conditions hardly affected by the external environmental factors and their changes on the continent. The origin of the other cavernicolous nematodes cannot be clarified so unequivocally. And besides, it is very difficult or almost impossible to

point out morphologically any adaptation to cave conditions in nematodes. These animals are, from the very first, colourless, transparent organisms, without eyes (a primitive pigment spot, sensitive to light, can be observed only in some aquatic species). Hence the loss of coloration and the abortion of the eyes can, from the outset, not be interpreted as adaptive phenomena. The cavernicolous species examined by me have in all respects the same organisation as their other allies occuring in other habitats, and a great part of the nematodes live also on the "surface" in the soil, hance to a certain degree in identical conditions. (Of course, up to a certain degree only, since the non-cavernicolous are much more exposed to climatic changes, food-conditions are more favourable, etc.) Some species found in the Baradla are also known from other caves, but they cannot be interpreted as eutroglobionts since they are the very species which can be met with in the most diverse habitats, and are thus true euryoic animals.

There was found in the Baradla Cave, however, a nematode species which was described by Schneider in 1940. The Baradla Cave is its second known place of occurrence. Though this species, too, has a rather extensive supraterranean alliance, it is not impossible that it can be regarded as the sole true eutroglobiont nematode of the cave. I refer to that very predator of which I spoke earlier. I have also stated that one cannot expect much in the way of predacious nematodes in caves, due to the scarcity of their exclusive foodstuffs. That this species, known hitherto solely from caves, belongs to this very rapacious type allows the assumption that there still occur predatory nematodes which can, from the point of view of procuring quarries, adapt itself to the considerably less favourable cave conditions, indeed, that, perhaps for the maintenance of the biological equilibrium, it had specialized itself to these very conditions.

It remains to be pointed out, by the way, that the majority of the nematode species possess an almost unique ability of adaptation in the animal kingdom, and this is the reason why a part of the species known as "supraterranean" can, if not in abundance in the rather adverse cave-conditions, still be found in most cases also in caves, constituting and indispensable link in the chain of living beings in the cavernicolous fauna.

All these observations have been but single chapters, some more interesting themes, of the nematode world of the natural caves.

If we are still far from being able to relate much of this world, the results of the investigations conducted in caves have already demonstrated that nematodes can be found, similarly to so many other areas and habitats in nature, also in the communities of the caves, where they fill a primary role in the decomposition and humifica - tion of organic refuse.

R E S U M E N

Nemátodos y su papel en las cavernas

Alrededor de 100 diferentes especies de nemátodos son conocidos en las diferentes grutas del mundo. De ellos, 16 especies han sido descritas como nuevas para la ciencia.

Aunque poseemos pocos datos sobre estos nemátodos, las investigaciones del autor nos dan cierta imagen general de los nemátodos de las cavernas.

El autor hizo sus investigaciones en la gruta Baradla en Hungría, la cual mide 22.000 metros de largo y es una de las más grandes y más hermosas grutas con estalactitas de Europa. El autor, durante varios años, ha coleccionado muestras de esta gruta, por supuesto, como las condiciones de vida en la caverna son mucho más reducidas que en la superficie, la mayoría de las muestras carecían de nemátodos.

A pesar de esto, la fauna de nemátodos de la gruta de Baradla contiene 22 especies conocidas y este número crecerá con futuros ensayos.

El habitat de los nemátodos de cavernas puede dividirse en 2 grandes grupos: secos y húmedos. Los secos, o biotipos terrestres, son los siguientes: el subsuelo de la gruta, material vegetal en descomposición, plantas (algas y hongos) y detritus de origen animal (guano de murciélagos, murciélagos muertos, excrementos de insectos). Los biotopos húmedos son: aguas temporáneas sobre el suelo, agua de infiltración, pequeños charcos, y las aguas del suelo. Los nemátodos de la gruta de Baradla, y de todas las cavernas conocidas, pertenecen a los siguientes tipos de vida: 1. Especies que se nutren con restos orgánicos (bacteriófagos, fungífagos y detrítofagos). 2. especies chupadoras de sustancias vegetales y animales; y 3. predatores, los cuales consumen protozoarios, tardígrados y pequeños vermes. Teniendo en cuenta que en las grutas las condiciones de vida

son restringidas, es el tipo primero el que puede encontrar mejor su nutrición. Si bien no en gran cantidad, y tampoco en todos los lugares, la materia orgánica es lo que será lo más fácil de encontrar para ellos.

Los nemátodos activos en las cavernas pueden ser encontrados únicamente en o sobre depósitos orgánicos. La movilidad de estos animales es muy reducida, así que no cuenta en la búsqueda de su alimento. Pero en el suelo de las cavernas encontramos otro tipo de nemátodos, los llamados inactivos. Nemátodos inactivos o pasivos son aquellos que no demuestran ningún signo de vida y están presentes en forma anabiótica, como huevos o larvas permanentes, y que se activizan únicamente en cuando el ambiente les permite. El papel de estos nemátodos inactivos, en especial de las grutas, tiene un valor muy importante.

Son los nemátodos inactivos, los que, esperando condiciones adecuadas de nutrición para su activización, mantienen la especie. Esto no es meramente una suposición. El autor hizo ensayos sobre qué nemátodos inactivos están presentes en los suelos de las cavernas y también ensayó su dispersión.

Encontró que prácticamente en todos los suelos de las grutas existen estas formas inactivas, mediante la técnica de agregar nutrientes esterilizados a muestras de suelo, y manteniendo éstas dentro de la misma caverna.

La población de las cavernas por los nemátodos se realiza de varias maneras. Por el agua, traídos por el hombre o animalles mediante otros factores de menor importancia. El factor más importante, sin duda alguna, es el agua. Esto es lo que ha pasado anteriormente también . Muy bien ejemplo nos dieron 3 especies de nemátodos en las grutas de Yugoeslavia. Estos: Desmoscolex, aquaedulcis, Halalimus stammeri y Thalassoalaimus aquaedulcis, pertenecen a géneros y familias que están hoy representados exclusivamente en el mar, siendo así especies relictas. No es fácil de determinar si existen formas eutroglobiontes, quiere decir formas que viven únicamente en grutas. Los nemátodos no muestran sensible adaptación al ambiente de las grutas. Ellos son ya en su origen incoloros, sin ojos, etc. y en su mayor parte viven también en suelos de la superficie, en condiciones ya similarea a la gruta. Las tres especies Yugoeslavas mencionadas son, sin duda alguna, eutroglobiones.

La mayor parte de los nemátodos posee una gran capacidad de a-

daptación y esta es la razón por la cual una parte de los nemátodos supraterraneos también se encuentra en las cavernas, constituyendo un papel muy importante en la cadena alimenticia de la fauna cavernícola. Así, ellos tienen un papel principal en la descomposición y humificación de la materia orgánica.