GROUNDWATER LIFE: SOME NEW BIOSPELEOLOGICAL VIEWS RESULTING FROM THE OPHEL PARADIGM

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Abstract. The functioning of the new chemoautotrophic biome Ophel (POR, 2007) is discussed based on its type locality, the Ayyalon groundwater pool, which is compared to the Movile cave and the Frasassi caves. The specific role of the thermosbaenaceans as first consumers in chemoautotrophic systems is emphasized. New views are presented concerning the zoogeography of the ophelic biome and a new theory is advanced about the origin of the ophelic fauna, which differs from the Tethyan stranding theory.

Key words: Ophel, groundwaters, Ayyalon, Thermosbaenacea, Chemolithotrophy.

1. INTRODUCTION

Five years ago, at the XVIIIth International Biospeleological Symposium in Cluj, I presented a last minute lecture on the new subterranean chemosynthetic ecosystem discovered that very year in Israel. The subject did not appear in the brochure of abstracts of the symposium and therefore, I feel that it is adequate to publish in the present journal a summing-up of my ideas, as they crystallized since then.

On the paradigm of this groundwater biome which I named Ophel, self-sustained by chemolithoautotrophy of a sulfide bacterial biomass, I published already several publications (POR, 2007, 2008, in press). This biome was mentioned and referred too, already in recent publications, among them, a critical review by NEGREA (2009) in the present journal.

The subterranean site at Ayyalon in Israel, in which the chemoautotrophic ecosystem was discovered, was further investigated during these years by the speleological team of Prof. AMOS FRUMKIN from the Hebrew University. Several species were identified and described: the blind prawn *Typhlocaris hyaline* Tsurnamal, 2008; the thermosbaenacean *Tethysbaena ophelicola* Wagner, 2011; the copepod *Metacyclops longimaxillis* Defaye et Por, 2010 and the pseudoscorpion *Ayyalonia dimentmani* Curcic, 2009, belonging to a new tribe. Outstanding was the thanatocoenosis of the scorpion *Akrav israchanani* Levy, 2007, belonging to a new family. A second copepod, *Metacyclops subdolus* Kiefer, 1938, a widespread species, was also reported (DEFAYE and POR, 2010). A collembolan, essential in the food chain, is not yet identified, as well as some protozoans. More important, the sulfur bacteria, preliminarily called *Beggiatoa*, are in need of a modern taxonomic treatment. It is important to mention that after all these years of survey of the Ayyalon cave pool no more taxa were added to this relatively short list. Dr. CHANAN DIMENTMAN and Mr. ISRAEL NAAMAN, the discoverer of the Ayyalon cave, surveyed the immediate

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surrounding areas of the aquifer, using also baited bore holes and failed to add other new taxa to the faunal list.

Since the discovery of the Ayyalon ecosystem, the most recent review publications by CULVER and PIPAN (2009) and PORTER (2009), have added no new chemolithoautotrophic ecosystem to the short list of the already known ones worldwide. Therefore, my presentation below, is the result my own in depth analysis of the Ayyalon zoological data and of their significance, based also on ample literature research, and more important on a stimulating convergence of ideas with two of my colleagues, Profs. DAN DANIELOPOL and BILL HUMPHREYS.

2. MOVILE, FRASASSI AND AYYALON

A first groundwater system based on sulfur-bacteria food was briefly mentioned by TSURNAMAL and POR (1968) and TSURNAMAL (1978). It is the important spring cave of En Nur in the Tabgha spring complex in Israel, from where the prawn *Typhlocaris galilea* Calman was discovered already in 1909. Even in preliminary investigations a diverse associated fauna was found, among it the crustaceans *Tethysbaena relicta* (Por), *Bogidiella hebraea* Ruffo and *Parabathynella calmani* Por. Unfortunately the studies at that spring complex were interrupted since then.

It was only after the wide publication of the findings at Movile (SÂRBU *et al.*, 1996), that it became generally accepted that subterranean ecosystems can subsist on chemoautotrophic bacterial food, independently of the exclusive allochthonous epigean food of photoautotrophic origin as it was believed before. The open question remained if this remarkable case of chemoautotrophy-based ecosystem and a few somewhat less dramatic but similar ones are special marginal cases, or indices for more basic and widespread biospeleological processes.

At this stage we can compare the rich Movile ecosystem as updated by SÂRBU (2000), the fairly well-investigated one of the Frasassi caves in Central Italy (SÂRBU *et al*., 2000), the biodiversity data summarized from other sulfidic karst habitats by ENGEL (2007) with our information from Ayyalon.

In Frasassi and Movile, as well as in the few other sulfurous caves, the karstic passages are dry and the groundwater is purely sulfidic and anaerobic. The fauna is therefore mainly composed of terrestrial taxa, chiefly arthropods. This terrestrial fauna feeds on the bacterial mats smeared on the rocky walls. It is in fact a wetland fauna concentrated around the pools and on the wet walls and the species are in fact amphibious, even if they are sometimes called aquatic in the literature. The very few really aquatic animals live in the uppermost oxygenated millimeter of the water surface like *Pontoniphargus* of Movile or in the sulfidic streams like the *Niphargus* of Frasassi (SÂRBU, 2000; SÂRBU *et al*., 2000).

What appears evident is the fact that sulfidic microbial mats, wherever accessible, served as a basis for establishing speleo-ecosystems. In the case of Frasassi, an extensive cave system of very recent origin, which furthermore is an open-access tourist site, yielded only a restricted fauna and only a few endemics. On the contrary, Movile, a Late Miocene karst system which lost its last epigean contact probably sometime in the Pleistocene, presents an amazingly diverse subterranean fauna, which till now counts already 30 described endemic species (SÂRBU, 2000). Some of these species present extremely abundant populations. Remarkable is the numerical abundance of the arachnid taxa among the endemics.

The Ayyalon site is situated in an active aquifer, the fresh Ayyalon-Tanninim aquifer of Israel which has been locally impacted by thermo-saline deep confined groundwater (FRUMKIN and GWIRTZMAN, 2006). The collapsed bottom of a more than 100 m deep quarry and the access shafts left dry because the low water level in the aquifer, due to excessive water extraction and a series of dry years, permitted the approach by foot to a pool. In the pool of several tens of meters in diameter, the fresh ground water at 25°C overlays the sulfidic, mineral, 30°C warm anaerobic artesian upwelling ground water. The bacterial mats are floating in the pool and are stranded around it. The extremely abundant crustacean populations are found in the upper layer of the pool. The pseudoscorpions and collembolans are a wetland fauna around the pool.

The Ayyalon fauna is thus relatively poor compared to Movile. But Ayyalon gave us a chance to observe a site, with probably usual groundwater-ecosystem diversity, whereas Movile is a fortunate case with a terrestrial hot-spot diversity presently unrelated to circulating groundwater. Therefore, Ayyalon could serve as a model for a functioning chemolithotrophic Ophel groundwater biome. No doubt, the ecosystem of En Nur in the Tabgha spring complex, mentioned at the head of this chapter, will aware itself to be much more diverse, once it will be investigated again.

2. THE FUNCTIONING OF THE OPHEL BIOME

At Ayyalon we found *Typhlocaris,* the largest known subterranean invertebrate, in its most massive ever reported population, as well as *Tethysbaena,* in immense numbers, with its specimens gorged with bacterial food. As completely isolated as possible from the outside epigean world, there was no need to wait for isotopic analyses, in order to conclude that we came upon a routinely functioning autarchic chemosynthetic ecosystem, of the ophelic biome.

In this biome, with its own resources, the direction for the energy flow is opposed to that which is routinely supposed in speleobiology. It is not a diminishing trickle of photosynthetates reaching deeper inside, but a centrifugal nutrient flow outward, from deep situated chemo-producers. Much of the fauna and the organic material which emerges in the springs or appears in the caves is ultimately the product of primary consumers that feed on sulfide-oxidizing and other chemosynthesizing bacteria which grow in sites where fresh aquifers are contacted by deep confined anaerobic sulfidic groundwater (Fig. 1).

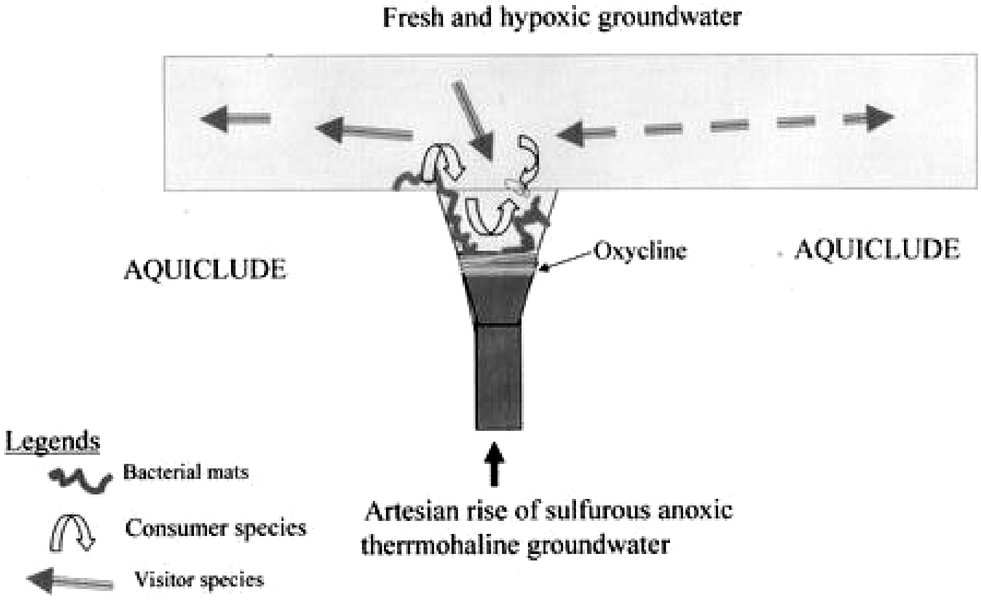

Fig. 1. Schematic presentation of the functioning of a chemoautotrophic sulfide bacterial pool in the ophelic groundwater biome.

The sites are most probably and generally, like in Ayyalon, pool-like water bodies, where the ascending anaerobic groundwater mixes with the oxygenated fresh groundwater. The bacterial populations develop in the thermo-chemocline between the two water masses, which at the same time is also an oxycline. The consumers of the bacterial biomass descend to the level of the oxycline, defying the adverse conditions of high temperature and dearth of oxygen.

Metacyclops longimaxillis and *Tethysbaena ophelicola* (Fig. 2) reproduce in the pool, despite the relatively high temperature, the aberrant salinity and the low DO values encountered there. Both species are found in the pool in very large populations and at all the stages of their reproductive cycle. *M. longimaxillis* (Fig. 3), as shown by its extremely developed maxillae is a swimming filtrator, probably of bacterial particles (DEFAYE and POR, 2010). *Tethysbaena ophelicola*, like all the members of its order, is an upside-down swimming bulk filtrator (Fig. 4). Both species are primary consumers of the ophelic biome, though, because of their difference in size (0.7 mm in *M. longimaxillis* and 4–5 mm in *T. ophelicola*), they might represent two steps in the food chain. Both species are typical standing water, lentic species.

Fig. 2. Ovigerous *Tethysbaema ophelicola* Wagner, specimens
from Ayyalon cave, in situ. Average lengths 4 mm.

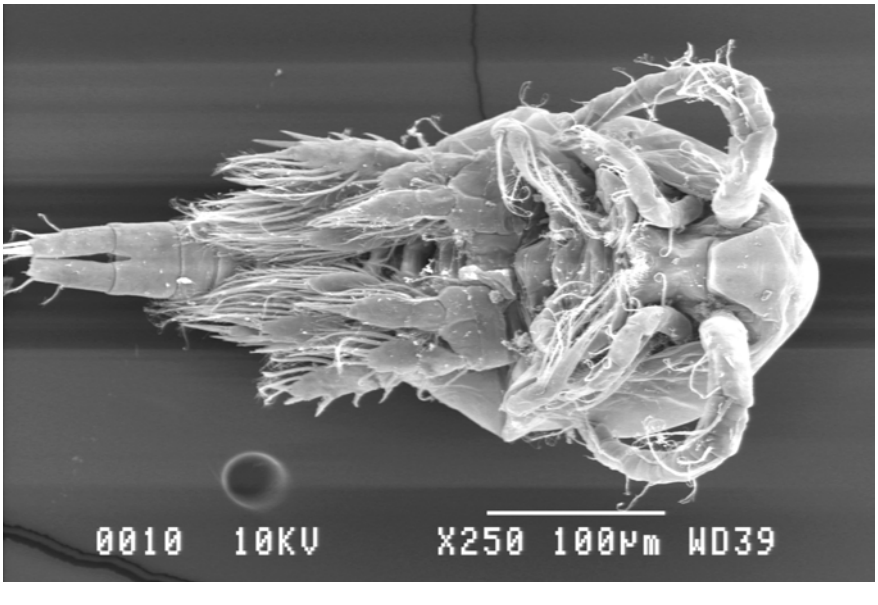

Fig. 3. *Metacyclops longimaxillis* Defaye et Por,from Ayyalon cave
in ventral view. The long filtrating maxillae are bent (photo D. Defaye).

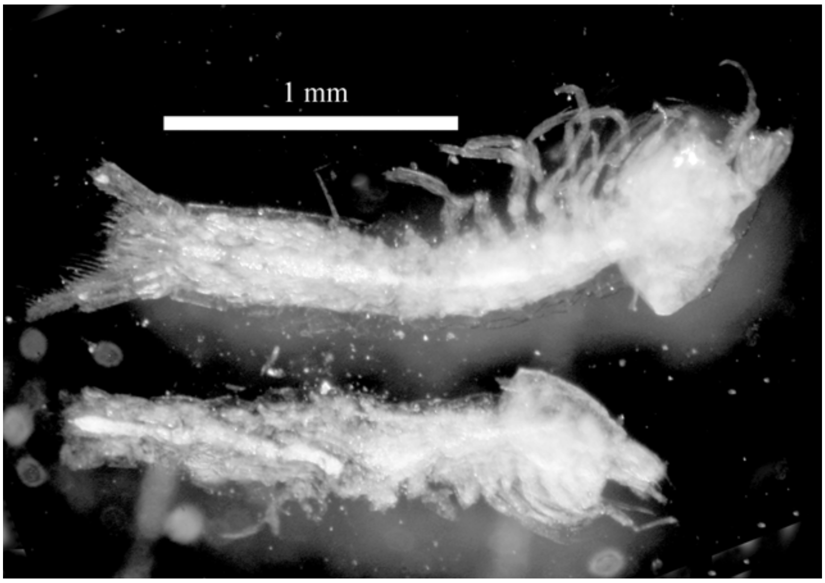

Fig. 4. Juvenile *Tethysbaena ophelicola* from Ayyalon cave,
with intestine filled with bacterial food (photo N. Ben Eliahu).

Typhlocaris ayyaloni (Fig. 5) and *Metacyclops subdolus* can be characterized as visitor species because they are not found in reproductive populations in the sulfidic pool of Ayyalon. The blind prawn was found in large numbers in the pool, but only as adults. It was found also in baited traps lowered in bore holes into the aquifer at some distance from the cave with the sulfidic pool (CH. DIMENTMAN personal communication). *M. subdolus* was rare in the pool itself but frequent in an epigean pond fed by the waters of the fresh aquifer (DEFAYE and POR, 2010). Both species feed in the warm and nutrient-rich cave pool but probably reproduce elsewhere in the cool and better aerated aquifer.

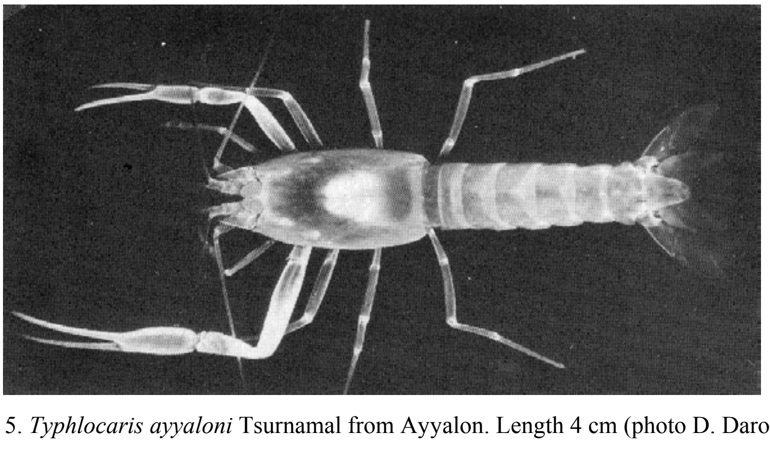

Fig. 5. *Typhlocaris ayyaloni* Tsurnamal from Ayyalon. Length 4 cm (photo D. Darom).

Eventually only a restricted number of species are able to live permanently and thrive in the extreme conditions of the sulfidic artesian pools which are the feeding centers of the ophelic biome. These are specialized lentic bacterial grazers and filtrators. Besides the two examples above, this central faunistic component of the ophelic biome contains probably several taxa of protozoans and other extremophilic crustaceans. Among the central primary consumer taxa we can probably count also the collembolan of Ayyalon which is the possible prey of the pseudoscorpions.

Typhlocaris in its turn is the best example for the faunal component of the visitors in the ophelic biome. These are omnivorous, more mobile crustaceans that feed in the bacteria-rich pools for short periods and move and reproduce elsewhere in the karstic systems. They distribute the bacterial chemolithoautotrophic production over the whole aquifer, between one sulfide pool and another. What is not done actively is the result of swept-off pieces of bacterial mat, of floating detritus of dead bodies, as this often appears in the spring heads. Several species of the lentic *Tethysbaena* have been described from damaged or fragmented specimens that appeared in springs (POR, 1962; WAGNER, 1994).

One could try to understand this new way of looking at the groundwater world, which is the Ophel biome, by a somewhat far-fetched analogy with a tropical dry land ecosystem. Such ecosystems function only, because they contain life-giving central oases or watering places. The groundwaters are not deserts as once thought. They have their own food resources that can sustain abundant populations of large 4–6 cm prawns like *Typhlocaris*. However, the fauna of the newly encountered biome of Ophel has to face uncommon high water temperatures in the central sulfide pools and also constant to extreme hypoxia in the whole system.

THERMOSBAENACEA, THE SULFIDE SHRIMP

The Thermosbaenacea also called Pancarida, considered to have the rank of a suborder by WAGNER (1994) and a super-order by HOBBS (2000) are reported with a world-wide distribution excluding till now South America. The dorsal marsupium is their most remarkable synapomorphy. This exclusively subterranean taxon counts till now only 36 species with an extremely similar habitus and biology, but Wagner divides them into 4 families, with genus *Tethysbaena* alone, counting 24 species. What is remarkable about this homogenous taxon is the fact that in all the reported cases, the species have apparently the same feeding behavior of upside-down swimming-gathering of sulfur bacteria or bacterial mats of other bacterial origin. The dorsal marsupium is functionally correlated with this way of life. Moreover, when found *in situ* and not as marginal expatriate specimens, they are present in extremely numerous populations. *Tethysbaena halophila* (Karaman), known from several Dalmatian localities can have quite dense populations, especially under microaerobic conditions and in the presence of H_2S (SKET, 1986). L. BOTOŞANEANU (in letteris) speaking of *Tethysbaena haitiensis* Wagner, saw on Haiti “enormous populations literally pullulating in warm standing waters with minimal oxygen content and strong hydrogen sulfide smell". The case of the huge population of *T. ayyaloni* seem s to be therefore indicative for this whole group of sulfide shrimp, its remarkable specialization and strategy of local mass occurrence.

Several thermosbaenaceans live in anchialine cave environments, like for instance genus *Tulumella* of the Bahamas and of Mexico, where they are also feeding on the bacteria accumulating in the chemocline, although the chemoautotrophic bacteria there are not always exclusively sulfidic ones.

The ascending thermo-mineral sulfidic water of the ophelic pools is as a rule considerable warmer than the younger groundwater above. At Ayyalon, it is 30°C, some 5°C warmer than the fresh aquifer.

In tectonically active areas it could be even more than that. *Thermosbaena mirabilis* Monod, the species discovered in 1924, which lives in thermal waters in Tunisia which can reach the scorching temperatures of 47°C (BARKER, 1959) and gave its name to the whole subsequently discovered order, is probably the most heat-resistant known metazoan. *Tethysbaena relicta* (Por) near the Dead Sea, was found in a thermal bath at 31°C (POR, 1962), while the temperature inside the feeding groundwater is certainly higher. *T. somala* (Chelazzi & Messana) was reported from a thermal spring in Somalia at 31°C.

Sustained exposure at temperatures of a few degrees above 30°C is lethal to most metazoans, the tube worms and decapod crustaceans of the black smokers of the mid-oceanic ridges included. The thermosbaenaceans as a taxon seem to be adapted to the extremophilic conditions of high water temperatures.

By their specific adaptation to sulfide bacteria-feeding and their survival in microaerobic and hot environments makes the sulfide shrimp to be in a certain sense, the indicator organisms of the Ophel biome. They are the analogues of the vestimentiferan tube worms of the mid-oceanic ridges. The presence of thermosbaenaceans, of sulfide shrimp in the continental waters world-over, indicates indirectly, that the ophelic biome as sketched-out above has an equally wide world distribution.

OPHEL AND THE PROBLEM OF HYPOXIA

Groundwaters are poor in dissolved oxygen. DO values there, are usually around the hypoxic values of 1 ppm. As long as they were seen as uninhabited by animals and inhabited by saprobic bacteria only, this environmental parameter was neglected. Little need was seen for oxygen consumption. But if in the karst under our feet, the ophelic biome is throbbing with life and animals of the size of *Typhlocaris* are swarming around and sulfur bacteria mats are using up oxygen, the issue of respiration, of hypoxia turns to be a major environmental issue to count with. DO values of less than 0.2 ppm are considered to be anoxic or anaerobic, in fact technically difficult to measure in situ.

Since there are as yet no pertinent data from the biota of the continental groundwater, I shall use a few indications from the environment of the anchialine cave pools, where similar situations of stratification and oxycline develop. BISHOP *et al.* (2004) studied the biology of crustaceans, mainly of three species of Remipedia and two species of the thermosbaenacean *Tulumella*, and their adaptation to life in the hypoxic and anoxic zones in Bahamian anchialine caves.

I dealt with the problem of anaerobic adaptation elsewhere (POR, in press) and the conclusions can be resumed as follows, for the speleologist reader.

Evolution selected the class Crustacea to be the almost exclusive inhabitants of the subterranean waters. The main reason was probably the possession of their respiratory pigment, the arthropodan Hemocyanin. This copper-based protein is especially adapted to function under hypoxic conditions (HOCHACHKA and SOMERO, 2002). It can even have high affinity to O_2 under ambiental high temperature conditions, changing adequately its polymeric structure (HOURDEZ and LALLIER, 2007).

The possession of hemocyanin enable the crustaceans to extract even the smallest amounts of dissolved oxygen available in the groundwater spaces and still to lead a life of active movement, even if food is scarce or often temporarily lacking. The arachnids also possess hemocyanin as their respiratory pigment.

Crustaceans differ from the mollusks and some worms which can withstand periods of hardship by turning inactive and by switching completely to anaerobic respiration. The crustaceans employ an alternative capacity to make sustained long-term anaerobic activity possible. This is the Malate pathway, a modified Krebs cycle, known in parasitic nematodes, which uses Malate dismutase. Under conditions of prolonged anaerobiosis PEP is converted directly to Oxaloacetate, then to Malate and finally to Propionate. As much as 15 % of the aerobic ATP production per glucose mol can be obtained in this way and there is no accumulation of lactic acid. By the elevate values of Malate dehydrogenase measured in the anchialine crustaceans, BISHOP *et al.* (2004) concluded that this pathway is functioning in the Bahamian crustaceans.

Of course, when food is abundant, like in the case of the bacterial mats of the Ophel biome, even at the relatively low energy yield of this improved anaerobic respiration pathway, massive populations of active crustaceans can flourish.

Anaerobic conditions go hand in hand with accumulation of free H_2S. In the case of the ophelic biome, hydrogen sulfide is a permanent presence in the oxycline and below it. This gas is toxic to all animals and its detoxification to thiosulfate requires oxygen (HOCHACHKA and SOMERO, 2002). Moving in and out of the strictly anoxic layer is no problem for swift swimmers like *Typhlocaris*, but is certainly one for the small and less active *Tethysbaena* and *Metacyclops* of Ayyalon.

In general, the lowermost limits of hypoxia a metazoan animal can tolerate are being questioned here, since for the animals living in the sulfidic pools there is no seasonal relief, neither does their offspring spread out into more aerated waters.

3. A ZOOGEOGRAPHY OF ITS OWN

There are two parallel continental worlds: the photosynthesis-based epigean world and the chemosynthesis-based hypogean one. Each has its own zoogeographic patterns.

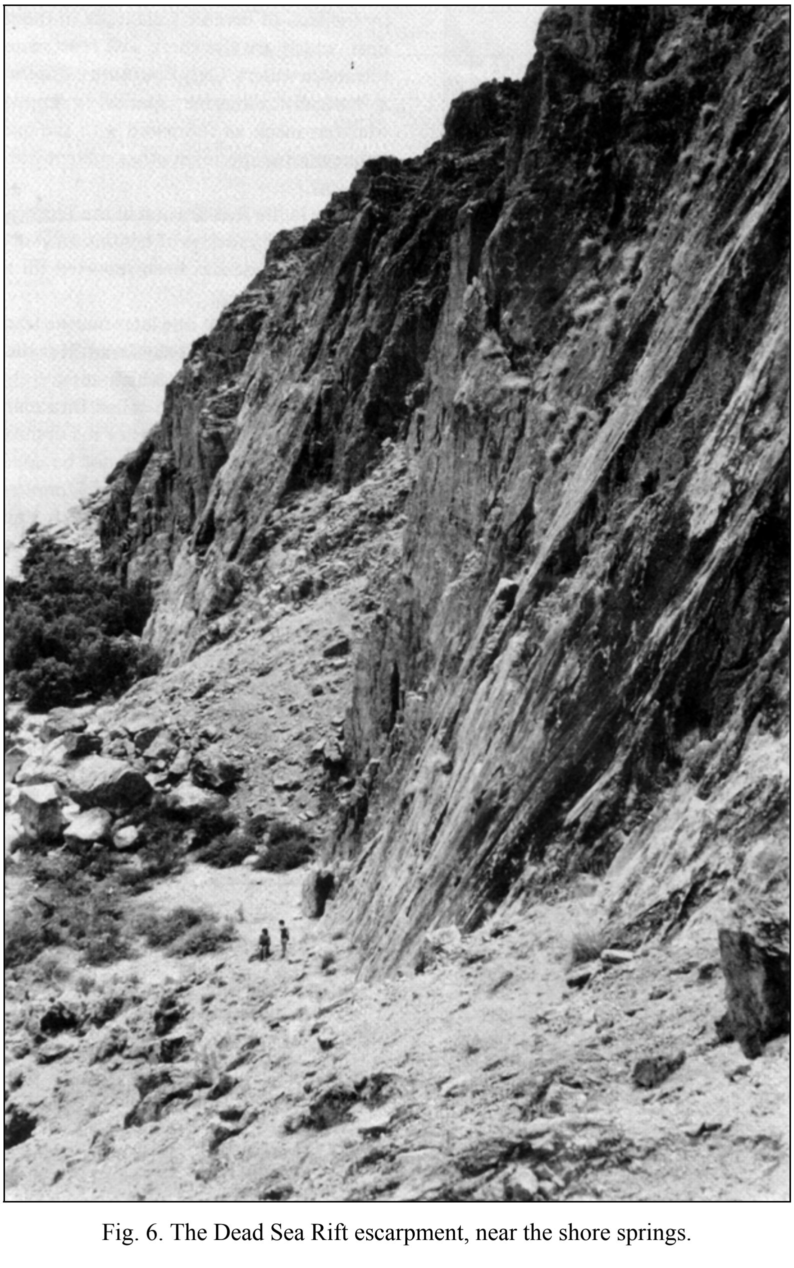

Fig. 6. The Dead Sea Rift escarpment, near the shore springs.

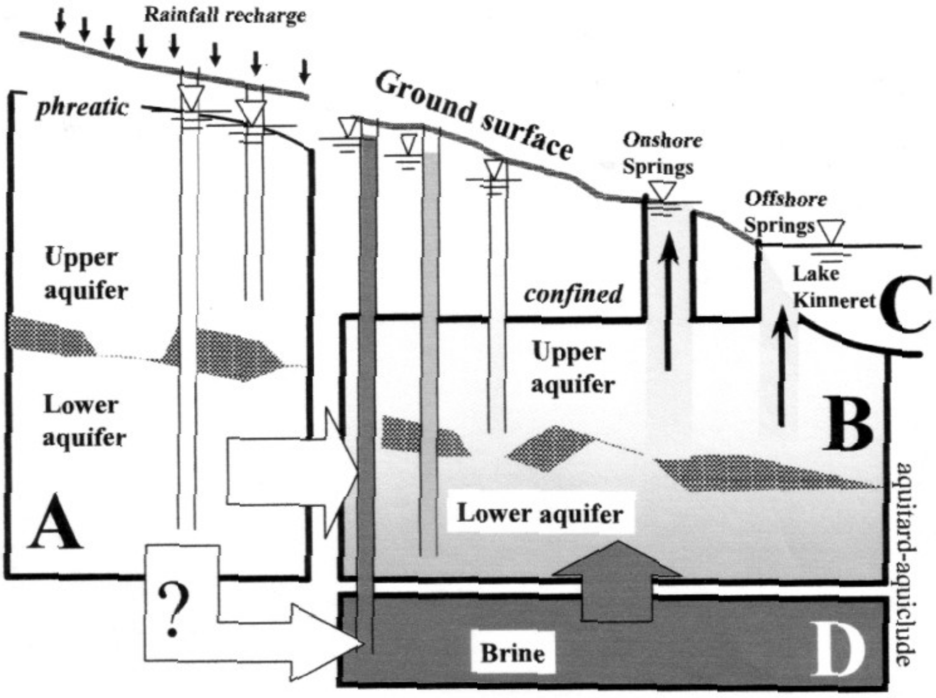

Fig. 7. A scheme of the aquifers of Lake Kinneret slope, by Rimer (2008).
The springs of Tabgha appear as "Onshore springs".

The subterranean ophelic world is that of simple food chains and of relatively slow-moving animals, chiefly crustaceans, but also a variety of arachnids and apterygotes. Insects and vertebrate predators are probably lacking. Local endemism is very high. Areas are delimited by aquifers and barrier can be tectonic faults, aquicludes, basaltic outpours, simply argilose colmatation, etc. Aquifers on the other hand can continue undisturbed also below the bottom of lakes and shallow seas, connecting ophelic faunas of islands that today are far distant from the shore.

Although the dominant environments are the very slow-streaming groundwaters, there are local lotic, fast-flowing environments and even cataracts as well as the artesian ascending nearly stagnant pools of sulfidic thermo-haline waters which feed the whole ophelic biome. Important are the humid and wet areas in the so-called air-bells, around and above the pools, where bacterial mats sustain a terrestrial and amphibious arthropodan fauna (Fig. 1). The whole biome has a pronounced tri-dimensional character.

The hotspots of the ophelic fauna are to be expected in areas, where complicated tectonic histories led to a mixing of the different fossil confined groundwaters with the recent aerated aquifer. For instance, one of the main factors which explain the extremely rich subterranean fauna of the Dinaric hotspot is the complicated tectonic history of the hydroscape of the region (SKET, 1999). The different layers of the paleo-Mediterranean, the Messinian, the Ponto-Caspian influx and the various Pleistocenic phases, left their aquatic imprints there, in a diversity of tectonically mingled-up recent and fossil confined aquifers.

In the Dead Sea-Jordan Rift Valley, the subterranean crustacean fauna which appears in the thermohaline springs is also especially rich. The tectonic escarpment which abruptly falls to the deepest chasm in the Earth's continental surface (Fig. 6) led to the mixing of at least three known types of groundwater and to the exposure of a diverse ophelic fauna. Only the springs of the Israeli side have been investigated in the Dead Sea-Jordan Rift Valley, but already 16 species of subterranean crustaceans have been found there. The springs of the Jordanian side, which are much stronger, have so far not been investigated in this respect. The well known spring cave of Tabgha, near Lake Kinneret (Sea of Galilee), with saline waters and temperatures up to 29°C (see above) (Fig. 7), yielded till now five species of subterranean crustaceans. The spring of Enot Samar on the shores of the Dead Sea brought to light six species of crustaceans (DIMENTMAN and POR, 1991).

AN ALTERNATIVE TO TETHYS STRANDING

In accordance with the dominant paradigm of biospeleology, I first considered the subterranean crustaceans of the Dead Sea valley to be relics of a Pliocene marine transgression (POR, 1963). Later, as it became clear that the Piacenzian transgression into the Dead Sea Rift Valley was only a short-lived estuary and that the Piacenzian Mediterranean itself was not a restored tropical sea anymore, I reconsidered them as stranded from the closing Miocene Tethys (POR, 1986). The meaning of this would have been that parent species from the orders Syncarida, Thermosbaenacea and the families Bogidiellidae and Typhlocarididae found in the Rift Valley were last living in the open tropical sea that covered the Middle East in the Mid Miocene, only some 10 million years ago. As I showed recently (POR, 2010), the pre-Messinian fauna of the fossiliferous taxa of the foraminiferans, the mollusks and the teleost fishes was not different from the recent Red Sea fauna or different only at the species level. There is no indication that major crustacean taxa became selectively extinct during the Tertiary and no justification that subterranean crustaceans are often seen collectively as "living fossils".

The Ophel paradigm falsified first of all my own, previously held views.

The other horn of the dilemma was, however, a real one. It was always difficult to explain how tens of exclusively subterranean taxa at the rank of orders and families could evolve in ecosystems that supposedly subsisted only on minimal and rhapsodic nutrient supply from above ground. How could this ample zoological panorama evolve under conditions of permanent hunger and uncertainty?

But once we admit that there are multiple sources of ample bacterial chemoautotrophic food in the karst underground, the ophelic biome reveals to have a history of its own, possibly at least as old as the Cambrian, which had such a diverse aquatic crustacean and arthropodan palaeofauna.

Chemoautotrophy was older than photoautotrophy and the Ophel biome could have been in existence in the sediments even before a full marine life developed. It could have been settled, most probably much before the Silurian and later Paleozoic expansion of the epigean terrestrial environments which required a potent ozone screen and a well developed land flora. The two environments had a parallel development and the ophelic, subterranean one could have been easily the much older one.

The presence of the three species of the Spelaeogriphaceae on the three Precambrian cratons and the Pangean distribution of the Bogidiellaceae, of the Syncarida and others, speak of the very old origin of several major crustacean taxa that inhabit the ophelic biome.

The richness of the subterranean fauna which accompanies the extent of the Cretaceous-Tertiary Tethys Ocean can be explained through an extrapolation of the Rouch-Danielopol (1987) concept of active migration of the subterranean fauna. The retreating Tethys was perhaps a nadir for the tropical open sea marine fauna, but much more a golden opportunity of expansion for the ophelic biome. The subterranean fauna which evolved in the Paleozoic and early Mesozoic paleokarsts expanded into the massive neo-karst of the major calcareous deposits left behind on the globe by the regressive high Cretaceous seas (Fig. 8).

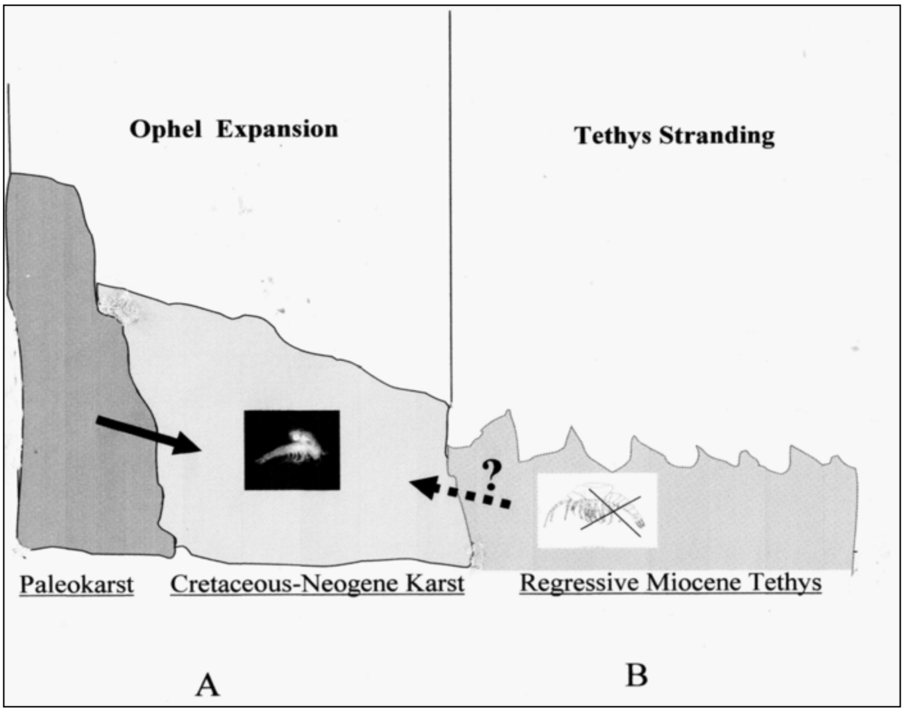

Fig. 8. **A**. The proposed concept of the expansion of the Ophel fauna from the Paleokarst into the Neokarst. **B.** The rejected concept of the stranding on the regressive Tethyan shores and the subsequent extinction of the parental forms in the free marine waters.

The old Tethys bottom was massively colonized by the ophelic fauna. It becomes however visible, first of all in areas of tectonic unconformities, especially at the boundaries of the Tethyan deposits, where the aquifers are disturbed and exposed.

The Paleo-karsts of South-west Brazil and of South Africa remained isolated.

While colonizing newly formed karst areas, the ophelic biome is also still being settled by taxa newly adapting to subterranean life. Likewise, out in the world of light, aquatic animals are still adapting here and there to terrestrial life. The Typhlocarididae could have joined Ophel not earlier than the Triassic, whence the first fossil caridid prawns are known. Much younger still are the Niphargidae which are the opportunists in Movile and Frasassi. Yet, there is impossible to suppose that the precursors of *Thermosbaena mirabilis* Monod were still free living in the Pliocene Mediterranean sea, a mere 4–5 million years ago before being stranded (JAUME, 2008). The sulfur shrimp are without doubt ancestral companions of the chemoautotrophic ecosystems and sulfur bacteria-rich subterranean artesian groundwater pools of the Ayyalon type, their typical environment, must have been primordial continental features.

POSTSCRIPT: The ideas presented above are resulted from the discovery of the Ayyalon ecosystem. The Ophel paradigm is a fundamentally new way of interpreting groundwater life. It proposes the reformulation of several previously accepted ideas in speleobiology, Some wider aspects, such as the extremely dynamic interphase between the continental ophelic biome and the marine anchialine cave ecosystems (Por, in press) and the place of the ophelic biome in the global primary chemolithoautotrophic biosphere, the deuterobiosphere (Por, 2008), have not been discussed here.

I am curious to know how the readers of this article will react to the ideas exposed here and I am only sorry that I met the opportunity to formulate them late in my life.

REFERENCES

BARKER, D., *The distribution and systematic position of the Thermosbaenacea*. Hydrobiologia, **13**, p. 209–235, 1959.

BISHOP, R.E., KAKUK, B., TORRES, J.J., *Life in the hypoxic and anoxic zones: Metabolism and proximate composition of Caribbean troglobitic crustaceans, with observations on the water chemistry of anchialine caves.* Journal of Crustacean Biology, **24**(3), p. 379–393, 2004.

CULVER, D.C., and PIPAN, T., *The Biology of Caves and Other Subterranean Habitats*. Oxford University Press, 2009.

ČURČIĆ, B.P.M., *Ayyalonia dimentmani n. g., n. sp. (Ayyaloniini, n. trib., Chthoniidae, Pseudoscorpiones) from a cave in Israel.* Archives of Biological Sciences Belgrade**,** **60**(1), p. 331–339, 2008.

DEFAYE, D., and POR, F.D., *Metacyclops (Copepoda, Cyclopidae) from Ayyalon Cave, Israel.* Crustaceana, **83**(4), p. 399–423, 2010.

DIMENTMAN, CH., and POR, F.D., *The origin of the subterranean fauna of the Jordan-Dead Sea Rift Valley: new data*. Stygologia, **6(3)**, p. 155–164, 1991.

ENGEL, A.S. *Observations on the Biodiversity of Sulfidic Karst Habitats*. Journal of Cave and Karst Studies, **69**(1), p. 187–206, 2007.

FRUMKIN, A., and GVIRTZMAN, H., *Cross-formational rising groundwater at an artesian karstic basin: thje Ayalon Saline Anomaly, Israel*. Journal of Hydrology, **318**, p. 316–333, 2006.

HOBBS, H.H. III., *Crustacea*. In: Wilkens, H., Culver, D.C. & Humphreys, W.F. (eds.): *Subterranean Ecosystems*. Ecosystems of the World 30, Elsevier, 95–107, 2000

HOCHACHKA, P.W. and SOMERO, G.N., *Biochemical Adaptation. Mechanism and Process in Physiological Evolution.* Oxford University Press, 2002.

HOURDEZ, S., and LALLIER, F.H., *Adaptations to hypoxia in hydrothermal vent and cold-seep invertebrates*. Revue of Environmental Sciences and Biotechnology, **6**, p. 143–159, 2007.

JAUME, D., *Global diversity of speleogripgaceans & thermosbaenaceans (Crustacea; Speleogriphacea & Thermosbaenacea) in freshwater*. Hydrobiologia 595: 519–524, 2008.

LEVY, G., *The first troglobite scorpion from Israel and a new chaetoid family (Arachnida: Scorpiones)*. Zoology in the Middle East, **40**, p. 91–96, 2007.

NEGREA, S., *A remarkable finding that suggests the existence of a new groundwater biome based on chemoautotrophic resources, named "Ophel" by F.D. Por.* Travaux de l'Institut Spéologie «Émile Racovitza», **48**, p. 83–91, 2009

POR, F.D., *Un nouveau thermosbenacé, Monodella relicta n.sp. dans la depression de la Mer Morte*. *CRUSTACEANA* **3**(4), p. 304–310, 1962.

POR, F.D., *The relic fauna of the Jordan Rift Valley, new contributions and a review*. Israel Journal of Zoology, **12(**1–4), p. 47–58, 1963.

POR, F.D., *Crustacean biogeography of the late Upper Miocene Middle Eastern Landbridge*. In Gore, R.H, and Heck, K.L. (eds.): *Crustacean Biogeography*. (Crustacean Issues 2), Balkema Rotterdam, pp. 69–84, 1986.

POR, F.D., *Ophel: a groundwater biome based on chemoautotrophic resources. The global significance of the Ayyalon cave finds*. Hydrobiologia **592**, p. 1–10, 2007.

POR, F.D., *Deuterobiosphere the Chemosynthetic Second Biosphere of the Globe. A First Review.* Integrative Zoology **3**, p. 101–114, 2008.

POR, F.D. (in press). *The Anchialine cave- Ophel continuum as substantiated in the Eastern Mediterranean area*. Hydrobiologia.

POR, F.D. *The Anchialine cave- Ophel continuum as substantiated in the Eastern Mediterranean area*. Abstract. Symposium on Anchialine ecosystems: Reflections and prospects. Palma de Mallorca November 2009

POR, F.D. *Ophel, the newly discovered hypoxic chemolithoautotrophic groundwater biome – a window to ancient animal life*. In: Altenbach, A.V., Seckbach, J., and Bernhard, J. (eds.): Anoxia: Paleontological Strategies and Evidence for Eukaryotic Survival**.** Springer Verlag**.** (*in press*).

PORTER, M.L., ENGEL, A.S., KANE, T.C. & KANE, B.K., *Productivity-Diversity Relationship from Chemolithoautotrophically Based Sulfidic Karst Systems*. International Journal of Speleology, **38**(1), p. 27–40, 2009.

RIMER, A., *The influence of water extraction from the Eastern Galilee aquifer on the salinity regime in the prawn's spring of Tabgha* (Report in Hebrew to the Nature Reserves Authority), 2008.

ROUCH, R., and DANIELOPOL, D. L., *L'origine de la fauna aquatique souterraine, entre le paradigme du refuge et le modèle de la colonization active*. Stygologia, **3,** p. 345–372, 1987.

SÂRBU, S. M., *Movile Cave a chemoautotrophically based groundwater ecosystem*. In: Wilkens, H., Culver, D.C. & Humphreys, W.F. (eds.): *Subterranean Ecosystems*. Ecosystems of the World 30. Elsevier p. 319–343, 2000.

SÂRBU, S.M., KANE, T.C., KINKLE, B.K., *A chemoautotrophically based groundwater*. Science, **272**, p. 1953–1955, 1996.

SÂRBU, S.M., GALDENZI, S., MENICHETTI, M., GENTILE, G., *Geology and Biology of the Frasassi caves in Central Italy: An Ecological Multi-Disciplinary Study of a Hypogenic Underground Karst System*. In: Wilkens, H., Culver, D.C. & Humphreys, W.F. (eds.): *Subterranean Ecosystems*. Ecosystems of the World 30. Elsevier, pp. 359–378, 2000.

SKET, B., *Ecology of the mixohaline hypogean fauna along the Yugoslav coasts*. Stygologia **2**(4), p. 317–338, 1986.

SKET, B., *The nature of biodiversity in the hypogean waters and how it is endangered.* Biodiversity and Conservation, **8**, p. 1319–1338, 1999.

TSURNAMAL, M., *The biology and ecology of the blind prawn Typhlocaris galilea Calman (Decapoda, Caridea)*. Crustaceana **34**(3), p. 195–213, 1978.

TSURNAMAL, M., *A new species of the stygobitic blind prawn* Typhlocaris *Calman 1906 (Decapoda, Palaemonidae,Typhlocaridinae) from Israel*. Crustaceana, **81**(4), p. 487–501, 2008.

TSURNAMAL, M., and POR, F.D., *The subterranean fauna associated with the blind palaemonid prawn* Typhlocaris galilea *Calman*. International Journal of Speleology, **3**, p. 219–223, 1968.

WAGNER, H.P, *A monographic review of the Thermosbaenacea (Crustacea: Peracarida).* Zoologische Verhandelingen, **291**, p. 1–338, 1994.

WAGNER, H.P. (in press.), Tethysbaena ophelicola *(Crustacea, Thermosbaenacea), a new prime consumer of the Ophel biota, Ayyalon Cave, Israel.* Crustaceana.

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