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Prospects for life in the subglacial Lake Vostok

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Accretion ice, Antarctic ice sheet, chemolithoautotrophs, extreme environment, *Hydrogenophilus thermoluteolus*, life detection, subglacial aquatic environments.
Антарктический ледниковый покров, конжеляционный лёд, обнаружение жизни, подледниковые водные среды, хемолитоавтотрофы, экстремальная среда, *Hydrogenophilus thermoluteolus*.

The objective was to estimate the genuine microbial content of ice samples from refrozen water (accretion ice) from the subglacial Lake Vostok (Antarctica) buried beneath the 4-km thick East Antarctic ice sheet as well as surface snow nearby Vostok station. The lake ice samples were extracted by heavy deep ice drilling from 3764 m below the surface reaching the depth 3769.3 m by February 2012 (lake entering). High pressure, an ultra low carbon and chemical content, isolation, complete darkness and the probable excess of oxygen in water for millions of years characterize this extreme environment. A decontamination protocol was first applied to samples selected for the absence of cracks to remove the outer part contaminated by handling and drilling fluid. Preliminary indications showed the accretion ice samples to be almost gas free with the very low impurity content. Flow cytometry showed the very low unevenly distributed biomass in both accretion (0–19 cells per ml) and glacier (0–24 cells per ml) ice and surface snow (0–0.02 cells per ml) as well while repeated microscopic observations were unsuccessful meaning that the whole Central East Antarctic ice sheet seems to be microbial cell-free.

We used strategies of Ancient DNA research that include establishing contaminant databases and criteria to validate the amplification results. To date, positive results that passed the artifacts and contaminant databases have been obtained for a few bacterial phylotypes only in accretion ice samples featured by some bedrock sediments. Amongst them are the chemolithoautotrophic thermophile *Hydrogenophilus thermoluteolus* of *beta-Proteobacteria*, the actinobacterium rather related (95%) to *Ilumatobacter luminis* and one unclassified phylotype distantly related (92%) to soil-inhabiting uncultured bacteria. Combined with geochemical and geophysical considerations, our results suggest the presence of a deep biosphere, possibly thriving within some active faults of the bedrock encircling the subglacial lake, where the temperature can be as high as 50 °C and in situ hydrogen is probably present. Our approach indicates that the search for life in the subglacial Lake Vostok is constrained by a high probability of forward-contamination. Our strategy includes strict decontamination procedures, thorough tracking of contaminants at each step of the analysis and validation of the results along with geophysical and ecological considerations for the lake setting. This may serve to establish a guideline protocol for studying extraterrestrial ice samples.

The subglacial Lake Vostok is the largest, deepest, and most studied lake among 386 subglacial water features inventoried until now through airborne radio-echo sounding and satellite altimetry surveys [24]. It is located beneath the Russian Vostok Antarctic research station, and it was entered February 5, 2012 at the depth 3769.3 m but has not yet been sampled. The refrozen lake water, or accretion, ice collected by deep drilling and used as a proxy for the lake water has proved to be exceptionally clean, though much diluted, leading to controversial biological and chemical analyses. Nevertheless, the likely indigenous DNA fingerprint of a chemolithoautotrophic thermophile seems to fit with the lake's extreme environment.

Subglacial lakes are water bodies formed at the base of the 3–4 km thick Antarctic ice sheet due to the geothermal heat flux, which melts basal ice layers. The melt water accumulates in bedrock troughs with long residence times [5], and may be periodically discharged through a subglacial hydrologic network [26], depending on geological and bedrock relief settings.

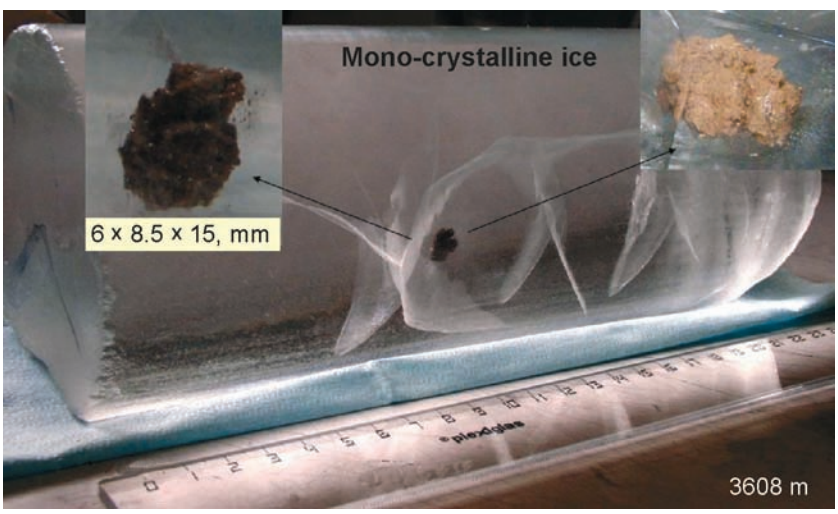
The subglacial Lake Vostok was discovered by radioechosounding in the late 1960s [18]. It was mapped in detail by radar-altimetry in the 1990s [23] and defined as a lake after seismic ground studies in 1996 [12]. It is the largest and deepest subglacial lake located beneath Vostok station (78 S, 106 E, elev. 3488 m, ~1,300 km from the coast, mean surface annual temperature –55.1 °C) under the ~3,750–4,200 m thick and rather ancient [19] central East Antarctic ice sheet. The subglacial Lake Vostok is the best-studied water feature in Antarctica [20]. It is crescent shaped and extends northward from Vostok station for more than 275 km in a deep trough and has a surface area of ~15,000 km^2, similar to that of Lake Ontario in North America. It is 65 km wide and ~400 m deep on average with a volume of ~6,100 km^3 [1]. There are two rather separate basins, one with a trough as deep as 1,650 m in the southern region [2, 15, 25]. Lake Vostok is a tectonically controlled subglacial lake with minor recently recorded tectonic activity [25]. The lake has likely been isolated from the surface for about 14 million years, the time of the major East Antarctica glaciation [6].

The overlaying glacier flows at ~2 m/year across the lake. From South (Vostok region) to North, the ice thickness increases from 3,750 to 4,200 m because of the deepening bedrock trough. This imposes a tilted interface between the lacustrine water and the overlying ice. As the melting point changes with pressure, the base of the glacier melts on the thick side (Northern region) supplying the lake. Water also refreezes in the upper layers of the lake in the Southern region, and the so-called accretion ice is exported by the glacier's movement out of the lake. This leads to replacement of the lake water every ~40–80 ka [5, 20]. The subglacial lake environment is characterized by high pressure (~400 bars) and in-situ temperatures close to the freezing point of water (−2.6 °C). Energy resources are seriously limited as there is complete darkness and an ultra-low dissolved organic carbon content (DOC < 13 mkg C/L [21], S. Preunkert, pers. comm.). The lake water is likely highly saturated with air, particularly molecular oxygen, released over long periods of time from the continuous ice melting (~800 mg/L [1]) (upper limit 700 and 1300 mg/L for dissolved O_2 concentration) [14, 17, respectively]. The accretion ice is also enriched in radiogenic ^4He originating from the bedrock and degassed through deep faults [20].

The accretion ice is composed of two distinct layers: the uppermost ice (from 3,539 to 3,608 m) containing millimeter size mica-clay inclusions (accretion ice I) (Fig.) and the deeper ice (below 3,608 m), which is transparent and very clean (accretion ice II). Various groups have studied the biological content of accretion ice samples. The nature of the samples, the integrity of microbes, the possibility of contamination from the drilling and recovery process, introduction of non-indigenous materials, and the sparse microbial populations all suggest that caution should be taken when interpreting the results. Not unexpectedly, these limitations have led to differing opinions and, in some cases, contradictory results [7, 9, 22]. For example, measured microbial populations in ice range from thousands of cells per ml (up to 36000 [3, 9, 22]) to only a few (1–10) cells/mL [7, 8]. Such a large variation (three orders of magnitude) may be caused by differences in methodology used to decontaminate, retrieve, and process the samples, and some microbes may originate from external contamination during ice coring with drilling fluids [4].

From the most recent studies, for which chemical and biological contamination is better documented and controlled, the Lake Vostok ice appears very clean and much diluted with respect to chemical and biological content and the lake water (at least the upper layer which seems to be enriched with glacier melt water due to insufficient mixing [1]) appears almost entirely lifeless. Only a few bacterial phylotypes were identified in accretion ice, which were not related to contamination [7]. The confidently recorded DNA fingerprint of the chemolithoautotrophic thermophile *Hydrogenophilus thermoluteolus* suggests the presence of a deep biosphere within the bedrock [25], while the expected high oxygen stress of the water may be very restrictive for biology [7].

Stringent decontamination procedures have to be applied in order to remove the outer part of the ice core contaminated by heavy drilling operations with a kerosene-based drilling fluid. The protocol consists of scraping off the outer surface, washing off the kerosene with special solutions followed by ozone treatment, and a series of washes with ultrapure low-DOC content water in certified clean room conditions. The chemical composition of the ice has to first meet the reference profiles imposed by clean working condi-



3608 m deep Vostok mono-crystalline accretion ice segment containing the biggest mineral inclusion called «Big Kamina». Magnified images of the inclusion are given as inserts to the left (with size denoted in mm) as well as to the right on a picture. Artificial (due to temperature change during ice transportation) cracks can be seen inside the ice crystal

Сегмент монокристаллического льда керна Восток с глубины 3608 м, содержащий наибольшее из известных минеральных включений и получившее наименование «Большая Камина». Увеличенное изображение включения для разных режимов съёмки приведено на вставках слева (с указанием размера в мм) и справа. В сегменте льда видны трещины искусственного происхождения (неправильная транспортировка) tions. Microscopic observations, flow cytofluorometry assays, and culturing trials were implemented to assay the biomass. Finally, DNA-based techniques including very sensitive DNA amplifications were applied. To validate the DNA results, a contaminant library was established [7].

Referring to Bulat et al.'s 2009 data [8], cell concentrations would not exceed 19–24 cells/mL in both accretion and glacial ice, respectively, values comparable to those found in other works [11]. The chemical content is very low in accretion ice II (less than 100 mg/L for total ions) suggesting the lake is poorly saline (< 0.1‰ taking into account ion partitioning during freezing) while sulfate salts (gypsum) and carbonates are likely present (up to 1 mg/mL) within the mineral inclusions in accretion ice I [10]. Dissolved organic carbon (DOC) is present in less than 10 mkg C/L (S. Preunkert, pers. comm.) imposing ultraoligotrophic conditions. The accretion ice has the total gas volume content two to three orders of magnitude lower than the glacier ice [1], imposing anaerobic conditions. No light is available for photosynthesis. The overall environmental conditions in the lake and accreted ice would restrict any possible biota to chemoautotrophs. Possible redox couples seem to be limited to hydrogen and/or sulfides as electron donors and sulfates and oxygen (in sediment inclusions) as electron acceptors. The carbon dioxide or carbonate from sediments could serve as a carbon source. Therefore, if life is present, one may expect to discover anaerobic chemoautotrophic piezophilic psychrophiles in accretion ice as a special habitat and the same forms, but with high oxygen tolerance in the lake water which is likely supersaturated with oxygen.

In particular, sequencing of 16s rRNA genes, constrained by numerous contaminant controls and criteria, showed that the accretion ice is essentially free of microbial DNA. The only ice containing mica-clay inclusions (accretion type I) (see Fig.) allowed the detection of few bacterial phylotypes all passing contaminant controls but not fitting groups expecting to discover. These phylotypes included the well-known chemolithoautotrophic thermophile *Hydrogenophilus thermoluteolus* (β-*Proteobacteria*) [7, 13] along with unclassified uncultured bacterium of OP11 Candidate Division (91% similarity with closest relative) and unknown bacterium related (95% similarity) to lake-river sediment-inhabiting *Ilumatobacter fluminis* (*Actinobacteria*) [16] (Table). The niche for the thermophile was suggested to be within deep faults of the bedrock encircling the lake (Fig. 3 in [7]), where the environmental conditions of warm, anoxic, CO_2–rich sediments along with probable hydrogen emission due to water radiolysis would support this type of organism. Sporadic seismotectonic activity [25] might have flushed out some material from the veins into the lake and the accretion ice I [7, 20]. The lake water as a liquid has not yet been sampled for study but the results could be surprising, i.e. it could be sterile or contain unusual «oxygenophilic» life forms.

Microbial cell concentrations and bacterial phylotypes (v2-v3-v4-v5 region of 16S rRNA genes) detected at high confidence in Vostok ice core

Ice type	Sample, m	Cells per ml	Similarity with closest sequence in GenBank, phylotype (amplicon length in bp, GenBank acc. no.), %
Snow	4.0–4.3	0–0.02*	Contaminants [7]
Glacier	122	1.9	No PCR signal
	2005	2.4	
	2054	3–24*	
	3471	1–4*	
	3489	0	
	3504	1–5*	
	3519	0–1*	Contaminants [7]
Accretion I	3547	0	
	3548	1	
	3561	4–9[2*]	99%, *Hydrogenophilus thermoluteolus* (504 bp, DQ422863)
	3607	ND[2*]	100%, *Hydrogenophilus thermoluteolus* (430 bp, AF532060)
	3607-re	1	No PCR signal
	3608	0–19*	92%, Uncultured bacterium[3*] (410 bp, AF532061)
	3608BK-re (see Figure)	ND[2*]	95% *Ilumatobacter fluminis* (526 bp, NR_041633)
	5G2-3608	0	Contaminants [7]
Accretion II	3613	3	No PCR signal
	3621	2	
	3622	0.6	
	3635	4.7	
	5G2-3646	0	Contaminants [7]
	3650	3.1	No PCR signal
	3650	4777[4*]	Not analyzed
	3659	12	No PCR signal
	5G2-3714	0	
	5G2-3764	0	

Range values for several segments; [2]ND – not determined; [3*]Unclassified phylotype; [4*]Untreated ice surface.

Since the subglacial Lake Vostok may be viewed as the only extremely clean giant aquatic system on the Earth, it provides a unique test area for searching for life on icy worlds such as Jupiter's moon Europa or Saturn's moon Enceladus. Confirmation of life living in Lake Vostok would strengthen the prospect for the possible presence of life on icy moons and planets. Exploration of Antarctic subglacial lakes is entering an active phase. Three major Subglacial Antarctic Environments (SAE) programs are now funded and scheduled: Subglacial Lake Vostok (Russia), Subglacial Lake Ellsworth (UK), and the Whillans Ice Stream Subglacial Access

Research Drilling (WISSARD, USA). Drilling operations at the Vostok station reached the depth of 3769 m (5G-2 borehole) at which the entering the lake have been occurred at the first time February 05, 2012. The lake water rose several hundred meters up into the borehole, got frozen and this 'fast' frozen lake water ice remains to be drilled within 2 years before to enter the lake 2nd time.

Regarding abundance and diversity of living forms in individual lakes, because these lakes have differing origins and geological histories, the limnological conditions, the age, the source of founder microbes, the time of isolation, the populations of extant microbes, if they exist, may vary from location to location. Thus, the findings in Lake Vostok will not necessarily be typical of other lakes and ice stream sediments. The subglacial Lake Vostok could be a unique reservoir of genetic material evolving in cold darkness under high oxygen stress isolated from other biota for the last 14 million years, and might contain organisms with distinctive adaptations. However, it is worth to notice that preliminary results of flow cytofluorometry and DNA studies of the lake water frozen on a drill bit (along with the drill fluid) during (at the period of) the Lake Vostok entering have revealed 167 cells per ml coming up with 4 bacterial phylotypes. Amongst them 3 phylotypes were encountered in our contaminant library [7] while remaining one minor actinobacterial phylotype of *Microbacterium sp* successfully passing the contaminant library is nevertheless proved to be originating from the drill fluid (aliphatic hydrocarbons) source. Does it mean the upper lake water horizon is lifeless (no ingenious cell populations) the farther investigations will show.

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Перспективы поиска жизни в подледниковом озере Восток

Цель исследования – обнаружить по отпечаткам ДНК микроорганизмы в замёрзшей воде (конжеляционном льду) подледникового озера Восток, погребённого под 4-километровым ледниковым щитом в Центральной Антарктиде. Образцы озёрного льда получены в результате глубокого бурения во льду (глубина 3769,3 м). Высокое давление, низкое содержание химических ионов и органического углерода, изоляция, полная темнота и вероятный избыток кислорода на протяжении миллионов лет характеризуют это экстремальное по свойствам озеро. Специальный деконтаминационный протокол был применён к образцам озёрного льда без каких-либо трещин для удаления внешней части керна льда, загрязнённого как людьми, так и промывочной жидкостью. При предварительных исследованиях данного льда установлено почти полное отсутствие какого-либо загрязнения. Проточная цитофлуорометрия показала очень низкую неравномерно распределённую биомассу, тогда как микроскопические наблюдения оказались безуспешными. В своей работы мы следовали правилам работы с Древней ДНК, которые включают в себя создание собственных баз контаминантов и выработку критериев для верификации результатов амплификации ДНК. До настоящего времени находки, которые преодолели все артефакты и прошли тест на сравнение с библиотекой контаминантов, относятся к трём филотипам (видам) бактерий, выявленных лишь в образцах озёрного льда с минеральными включениями (тип I). Это – хемолитоавтотрофный термофил *Hydrogenophilus thermoluteolus* и два неидентифицированных филотипа. В совокупности с геохимическими и геофизическими предположениями полученные результаты указывают на существование биосферы, выживающей в глубоких активных разломах в окружении подледникового озера, где температура может быть 50 °C и водород, вероятно, присутствует.

В целом наш подход свидетельствует, что поиск жизни в подледниковом озере Восток осложнён высокой вероятностью загрязнения чужеродной микрофлорой. Стратегия поиска предусматривает строгие деконтаминационные процедуры и тщательное «отслеживание» контаминантов на каждой ступени исследования с учётом геофизических и экологических особенностей озера. Это может помочь в выработке направлений при последующем биологическом изучении образцов воды как подледникового озера Восток, так и других подледных водоёмов, вероятно существующих на ледяных планетах и лунах нашей Солнечной системы.