Introductory Chapter: Half a Lifetime in Soda Lakes

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Soda Lakes and Biodiversity

My interest in soda lakes started more than 25 years ago from an encounter with a geologist colleague interested in astrobiology. At that time, the Mars exploration programme was underway and the chemical composition of the Mars regolith a matter for speculation. There are good reasons to believe that Mars and Earth may have experienced rather similar conditions after planet formation, with the development of extensive oceans. The chemical composition of the early oceans is a matter of debate – in particular, whether these were acid or alkaline (Kempe and Degens 1985; Kempe and Kazmierczak 1997). A consideration of weathering processes known to occur on Earth suggests that alkalinity is likely to arise as a consequence of an excess of Na^+ over Ca^{2+} in basaltic minerals, resulting in a carbonate-rich and therefore alkaline aqueous environment (Mills and Sims 1995). In view of the possibility of life on Mars, there was, and is, interest in examining possible terrestrial analogues of the alkaline environment in order to inform any life-detection experimentation.

The most stable highly alkaline environments on earth are the soda lakes and soda deserts (Table 1). These are widely distributed, but often in relatively inaccessible parts of the world. One of the most accessible areas is the East African Rift Valley, part of an enormous volcanic rift that stretches from the north of Africa with an eastern branch through Kenya and Tanzania (Fig. 1). My geologist colleagues in Leicester had been examining the geology and hydrology of the area for some time. The climate of the rift is semi-arid or arid with a geology dominated by Na^+ trachyte lavas as a consequence of vulcanism (still active in certain areas). The floor of the rift has a considerable number of highly alkaline soda lakes, ranging in salinity from around 5% (w/v) total salts, e.g. Lakes Bogoria, Elmenteita, to saturation with respect to NaCl and Na_2CO_3, e.g. Lakes Magadi, Natron, with pH values from 10.5–11 for the more dilute lakes to values in excess of 11.5 for the very hypersaline types like Lake Magadi. The alkalinity is a consequence of the high Na^+, low Mg^{2+} and Ca^{2+} geology (which may mimic early geology on Earth and Mars). Following

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Halophilic Microorganisms

Table 1. Alkaline environments

Continent	Country	Location
Africa	Libya	Lake Fezzan
	Egypt	Wadi Natrun
	Ethiopia	Lake Aranguadi, Lake Kilotes, Lake Abiata, Lake Shala, Lake Chilu, Lake Hertale, Lake Metahara
	Sudan	Dariba Lakes
	Kenya	Lake Bogoria, Lake Nakuru, Lake Elmenteita, Lake Magadi, Lake Simbi, Crater Lake (Lake Sonachi), Lake Oloidien
	Tanzania	Lake Natron, Lake Eyasi, Lake Magad, Lake Manyara, Lake Balangida, Bosotu Crater Lake, Lake Kusare, Lake Tulusia, El Kekhooito, Momela Lakes, Lake Lekandiro, Lake Reshitani, Lake Lgarya, Lake Ndutu
	Uganda	Lake Rukwa North, Lake Katwe, Lake Mahenga, Lake Kikorongo, Lake Nyamunuka, Lake Munyanyange, Lake Murumuli, Lake Nunyampaka
	Chad	Lake Bodu, Lake Rombou, Lake Dijikare, Lake Monboio, Lake Yoan
Asia	Siberia	Kulunda Steppe, Tanatar Lakes, Karakul, Chita, Barnaul, Slavgerod, Lake Baikal region, Lake Khatyn
	Armenia	Araxes Plain Lakes
	Turkey	Lake Van, Lake Salda
	India	Lake Looner, Lake Sambhar
	China	Outer Mongolia, various "nors"; Sui-Yuan, Cha-Han-Nor and Na-Lin-Nor; Heilungkiang, Hailar and Tsitsihar; Kirin, Fu-U-Hsein and Taboos-Nor; Liao-Ning, Tao-Nan Hsein; Jehol, various soda lakes; Tibet, alkaline deserts; Chahar, Lang-Chai; Shansi, U-Tsu-Hsein; Shensi, Shen-Hsia-Hsein; Kansu, Ning-Hsia-Hsein, Qinhgai Hu
Australia		Lake Corangamite, Red Rock Lake, Lake Werowrap, Lake Chidnup
Central America	Mexico	Lake Texcoco
Europe	Hungary	Lake Feher
	Former Yugoslavia	Pecena Slatina
North America	Canada	Manito
	USA	Alkali Valley, Albert Lake Lenore, Soap Lake, Big Soda Lake, Owens Lake, Borax Lake, Mono Lake, Searles Lake, Deep Springs, Rhodes Marsh, Harney Lake, Summer Lake, Surprise Valley, Pyramid Lake, Walker Lake, Union Pacific Lakes (Green River), Ragtown Soda Lakes
South America	Venezuela	Langunilla Valley
	Chile	Antofagasta

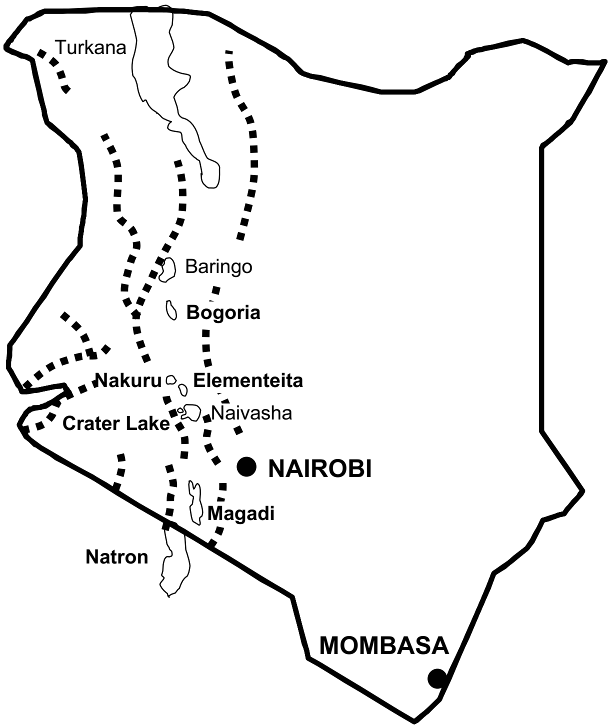

Fig. 1. Outline map of Kenya showing the major rift systems and the location of soda lakes (names in *bold*)

evaporative concentration in the absence of significant amounts of Ca^{2+} and Mg^{2+}, which normally buffer the aquatic environment by the precipitation of insoluble carbonates, an alkaline sodium carbonate brine develops, typically presented by the East African soda lakes (Fig. 2). Present-day aqueous environments are usually particularly rich in Ca^{2+} deposits as a consequence of mobilisation and deposition by microbial activity in the past – environments prior to the origins of life would not have had these localised concentrated deposits. Neutral salt lakes develop in the presence of high Ca^{2+} levels, and slightly acid types like the Dead Sea develop in the presence of high Ca^{2+} and high Mg^{2+} levels (Fig. 2). Typical ionic compositions for East African lakes are shown in Table 2.

Soda lakes, particularly the more dilute soda lakes, are the most productive aquatic environments in the world, with productivities, on average, an order of magnitude greater than the average for terrestrial aquatic environments (Grant et al. 1990). The ecosystem is, unusually, driven by cyanobacterial primary productivity, usually the cyanobacterium *Arthrospira platensis*, sometimes almost a cyanobacterial monoculture with more than 10^4 filaments/ml, occasionally together with other cyanobacteria such as *Cyanospira* and *Synechocystis* spp. Dense populations of alkaliphilic and organotrophic bacteria are supported by the primary productivity, and there are active sulphur and

Table 2. Typical ionic compositions for east African lakes

Lake	Na^+	K^+	Ca^{2+}	Mg^{2+}	SiO_2	PO_4^{3-}	Cl^-	SO_4^{2-}	CO_3^{2-}	pH
Elmenteita	195.7	3.6	0.07	<0.004	2.9	0.03	65.1	2.0	68.0	10.5
Nakuru	326.1	5.6	0.15	<0.004	3.3	0.15	57.5	0.5	198.3	10.5
Bogoria (north)	734.8	5.5	0.21	0.008	2.2	0.09	100.9	1.0	476.7	11.0
Bogoria (south)	795.7	6.8	0.19	0.008	2.0	0.17	115.5	1.1	516.7	11.0
Sonachi	140.4	9.0	0.05	0.008	2.1	0.04	12.4	0.8	90.0	10.0
Oloidien	8.7	1.8	0.28	0.65	1.0	0.003	4.8	0.5	<10.0	9.0
Magadi (lake brines)	7000.0	57.0	<0.01	<0.01	14.9	1.82	3154.9	17.5	3900.0	>11.5
Magadi (lagoon brines)	2826.1	26.1	0.03	<0.01	7.1	0.23	1123.9	12.8	1816.7	>11.5
Little Magadi	4626.1	61.1	0.02	0.03	7.5	0.31	1856.3	13.1	2433.3	>11.5
Natron	4521.7	43.7	0.04	0.03	3.1	4.21	1464.8	1.7	2666.7	>11.5

All concentrations given in mM

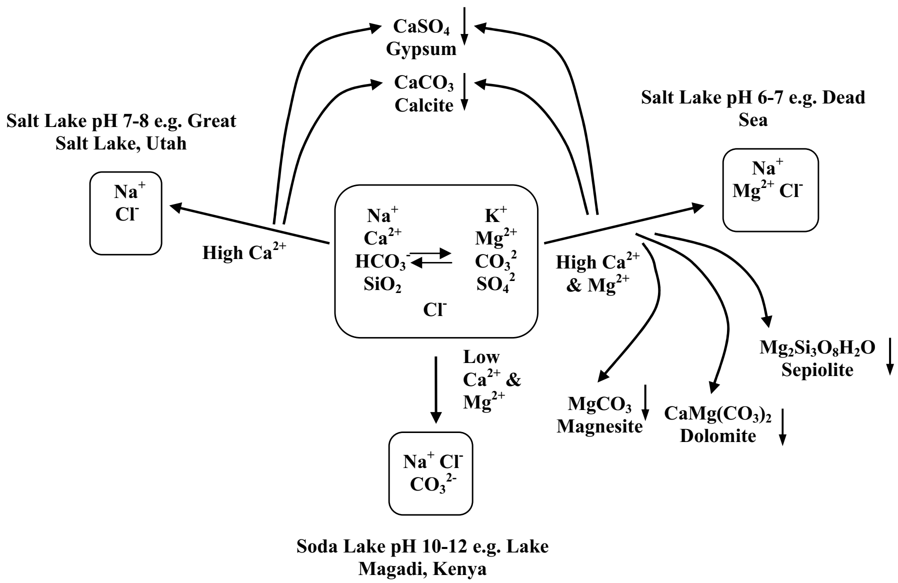

Fig. 2. Schematic representation of the genesis of saline and alkaline lakes. In all aquatic systems, CO_2-charged water leaches minerals (*central square* shows typical ions). Soda lake formation is dependent on low levels of Mg^{2+} and Ca^{2+}. Salt lake formation depends on high levels of Ca^{2+} and for Mg^{2+} where alkaline carbonate is precipitated out of solution. High Mg^{2+} salt lakes are more acid due to reactions involving sepiolite precipitation

nitrogen cycles in the lakes (Grant and Jones 2000). Table 3 lists some of the prokaryotes that have been cultured from soda lakes. The reviews of Zavarzin and colleagues (Zavarzin 1993; Zhilina and Zavarzin 1994; Zavarzin et al. 1999) and Grant and colleagues (Grant et al. 1990; Jones et al. 1994, 1998; Grant and Jones 2000) should be consulted for specific details of aerobic and anaerobic processes, and references to particular isolates.

Since the microorganisms in the lakes are mostly alkaliphilic (alkaline-loving, with pH optima for growth usually around pH 10–10.5), it is to be expected that extracellular enzymes produced by these microorganisms would be active under alkaline conditions, moreover, active in the virtual absence of significant levels of Mg^{2+} and Ca^{2+} (which are removed as insoluble carbonates by precipitation; see Table 2). This is indeed the case, and such enzymes are of biotechnological interest, particularly as detergent additives, since detergents used in domestic and industrial washing processes are alkaline and contain sequestering agents to remove Ca^{2+} (which adversely affects the water hardness and foam characteristics). Two enzymes derived from soda lake organisms have been marketed as detergent additives. The first of these, Puradax, marketed by Genencor, is a cellulase incorporated in domestic detergents used for washing clothes. This particular enzyme was the first enzyme from an extreme environment to be produced for the mass market