

Prebiotics in ancient diets

Jeff D. Leach

Paleobiotics Laboratory, 2401 Burgundy #7, New Orleans, LA 70117, USA

Abstract

While modern studies continue to expand our knowledge of the health benefits of prebiotics, virtually nothing is known of their use among ancient populations. Drawing on select ethnographical and archaeological data, examples of prebiotic use in ancient diet is presented. By utilizing the well-documented facilities used to cook inulin-bearing plants that are found throughout the archaeological records of North America as a proxy, prebiotic consumption is documented in Europe and the Mediterranean possibly as early as 40 000 years ago. Data is further provided to suggest that early members of the genus *Homo* had ample ecological opportunity to include prebiotic underground storage organs found throughout the arid African savannah into the diet as early as 2.5 million years ago. This cursory view into the nutritional past of our ancestors reveals that prebiotics were likely to have been consumed in higher quantities than is the case among modern humans.

Keywords: archaeology, cook-stone technology, evolution, nutrition, prebiotics

1. Introduction

Since the 1970s, there has been a renewed interest in the link between colonic function and human health (Jenkins *et al.* 1999), with much recent attention being given to prebiotic carbohydrates that are not available for the vertebrate digestive system in general and for the human digestive system in particular, and as such are available in their entirety for the abundant intestinal bacterial ecosystem. Prebiotics interact in a selective way with the intestinal ecosystem and tend to change its composition with potential positive health effects for the consumer (Gibson and Roberfroid 1995; Gibson *et al.* 2004; Van Loo 2005). The well-established $\beta(2-1)$ fructans inulin and oligofructose continue to drive much of the current research on the health benefits associated with prebiotics (Roberfroid 2002; Van Loo 2004a, 2004b). Although much current research is aimed at demonstrating health benefits for modern populations and the mechanisms for delivering prebiotics safely into the food supply (Franck 2002), very little is known about the consumption of inulin-type fructans throughout human history.

This paper briefly reviews archaeological evidence for prebiotic consumption in southern North America and select regions of the world. As a component of human health, it is useful to consider the evolutionary role of natural prebiotic foods from the perspective of nutritional

ecology (Leach *et al.* 2006a, 2006b). This is defined as the study of essential nutrient intake for the purpose of overall human health, growth and maintenance, and general trends towards population growth (Jenike 2001; Jenkins *et al.* 1999). In other words, a diverse and sufficiently nutritional human diet will result in sustained or improved human health patterns, as revealed by lower infant mortality and an extension of human life expectancy.

The time-depth afforded by archaeology is unique in that it provides a window into dietary and other environmental variables that have shaped our current genetic make-up and its nutritional parameters. Within the last 10 000 years, significant changes nutritionally (i.e. due to agricultural changes) and technologically (i.e. as a result of the industrial revolution) have occurred too recently on a genetic time-scale for our genome to adjust (Cordain *et al.* 2002; Eaton *et al.* 2002; Goldsmith 1993; Williams and Nesse 1991). Thus, modern populations are selected biologically and physiologically for an evolution-based diet that did not include many of the popular foods that currently dominate diets. As such, the nature and composition of the modern gut microflora is in discordance and is progressively divergent from the original, genetically determined composition.

2. Evolution-based nutrition and nutritional ecology

Humans require a diverse diet of nearly fifty essential nutrients for proper growth, metabolic function and cellular

repair (IOM 2002). Current nutrient requirements and physiology have been conditioned by selective pressure and adaptability played out on an ever-changing nutritional landscape spanning millions of years. Fossil evidence places the earliest members of our genus (*Homo*) at approximately 2 million years ago (Finlayson 2005; Wood 2002). Throughout much of our history (>99%), humans evolved on a diet that was void of dairy foods, margarine (separated fats), cultivated cereal grains, and refined sugars, all of which supply as much as 60–70% of the calories in many modern diets. Up until approximately 500 generations ago, all humans consumed plants and animals foraged from their environment, and consumed virtually no agricultural grains or processed foods. Our evolution-based hunter-gatherer diet was high in fibre (dietary and functional), lean animal protein, polyunsaturated fats (omega-3 [ω -3] fatty acids), monosaturated fats, vitamins, minerals, phytochemicals and antioxidants, and low in sodium (O’Keefe and Cordain 2004). Astonishingly, ‘semi-modern’ hunter-gatherers and less westernised groups that adhere more closely to this ancient diet and lifestyle than to more westernised diets are largely free from chronic degenerative diseases (Cordain *et al.* 2002; Shephard and Rode 1996) and biomarkers of illness such as rising blood pressure, increasing adiposity and insulin resistance (Blackburn and Poineas 1983; Glanville and Geerdink 1970; Joffe *et al.* 1971; Kuroshima *et al.* 1972; Merimee *et al.* 1972; Spielmann *et al.* 1982).

Though traditional hunter-gatherer diet and lifestyle vanished in its ‘purest’ form in the early 20th century (Murray *et al.* 2001), ongoing studies of diet and lifestyle among less-westernised groups that remain throughout the world are demonstrating that models of optimal nutrition (therapeutic diets) may be developed from these extant evolution-based diets. Within the medical community (Eaton 2007; Eaton *et al.* 2002), there is a slow but significant movement towards acknowledging that a conceptual framework for preventing diseases of affluence may be built upon a foundation constructed within evolutionary theory. At the core of this theoretical movement, often referred to as Darwinian medicine (Stearns 1999; Trevathan *et al.* 1999), is the idea that our current genetic pool was shaped by millions of years of natural selection in environments very different than the ones we live in today, and that much of our genetic make-up is based on a nutritional landscape that did not include the foods that currently dominate our westernised diet. The discordance between the rapid pace of our recent (last 10 000 years) cultural adaptations (agriculture, food processing technology) is far outstripping our biological (genetic) ability to keep pace.

While some single-gene mutations (e.g. against malaria) are examples of the speed at which natural selection can occur, the pathophysiology of many chronic diseases

involves many more genes and much greater periods of time to evolve (Sing *et al.* 1996). While we are culturally and socially modern, driving around in hybrid cars for example, we are literally and biologically ancient hunter-gatherers.

Our modern requirements for a great number of essential nutrients to sustain health and well-being suggest this pattern developed early in our ancestral history. Humans, along with other extant hominoids (apes), evolved from a common plant-eating ancestor some 5 to 10 million years ago (Milton 1999). While orangutans, gorillas and chimpanzees have evolved on a diet of mainly fruits, leaves, flowers and bark, humans have developed a dietary path based on a mixture of plant and animal foods that has allowed for cerebral growth, gut anatomy and digestive kinetics. It is this diverse diet, and our ability to optimise it through intensification and technology, that makes us unique among all mammals.

Due to poor preservation of food remains in the archaeological record, it is difficult to derive exact macronutrient levels for food intake in a given diet for a specific region. However, field studies of the few remaining hunter-gatherer and foraging groups carried out during the early and mid-20th century provide some insight into the likely range and variability of our ancestral, evolution-based diet. In a comprehensive review of the ethnographical data on 229 hunter-gatherer and forager groups from all over the world, Cordain *et al.* (2000) suggested that the typical hunter-gatherer diet derived as much as 45–65% of total energy from animal food whenever and wherever possible, but that plant to animal ratios ranged from 35:65 to 65:35, depending on environment, season and latitude.

Clearly no single diet characterises the ‘typical or best’ hunter-gatherer and, by extension, ancestral, diet. Humans can, and do, thrive on a variety of diets. For example, the Australian aborigines are known to have eaten some 300 different species of fruit and 150 varieties of roots and tubers (Brand-Miller and Holt 1998; Gould 1980), while Alaskan Artic Eskimos are famous for a diet consisting almost exclusively of raw fat and protein from marine mammals (Ho *et al.* 1972).

In the 5–7 million years since bipedal primates appeared, nearly 20 species within the taxonomic tribe *hominin* have been identified in the fossil record, with only modern *Homo sapiens sapiens* still standing (Finlayson 2005; Wood 2002). At six billion strong, modern humans are clearly well-adapted and successful. Within nutritional ecology, the physical and biological success of our species, coupled with our genetically predetermined nutrient requirements and digestive physiology, indicate that a diverse diet of essential nutrients has characterised much of our history. As a cornerstone of modern health and nutrition, diverse diets are known to result in lower rates of infant mortality and an increased life expectancy (IOM

2002; Shuman 1996), both of which have a significant impact on population demographics.

Support for our diverse diet is found in the ethnographical and historical accounts among the 'relic' hunter-gatherer and foraging societies discussed above. The nutritional ecology approach suggests, due to their wide-spread occurrence among the world's flora and the direct evidence in archaeological records, that inulin-type fructans played an important role within a suite of essential nutrients in long-term health and the ultimate demographic success of our species.

3. Prebiotics in ancient diets

The discovery that the storage carbohydrate, fructan, occurs in a significant portion (>36 000 species) of the world's flora (Hendry 1987) all but guarantees that the now well-studied prebiotics, inulin and oligofructose, were consumed by our Pliocene and Pleistocene ancestors millions of years ago. As our early ancestors moved from the rainforest to the parched savanna woodlands of subtropical Africa, subsurface tubers, rhizomes, corms and perennial bulbs, many rich in prebiotics, would have been a ready and important source of energy (Hatley and Kappelman 1980; Laden and Wrangham 2005). Today, many of these same resources serve as staples for the modern foragers and farming groups that inhabit the same subtropical environs (Murray *et al.* 2001; Vincent 1985). However, digestion-inhibiting compounds and plant toxins present in many below-ground food sources would have limited their role as staples in the early diet of *Homo* until technological adaptations, such as fire, were introduced (Ragir 2000; Stahl 1984). Nevertheless, as early members of the genus *Homo* began their evolutionary march to mammalian dominance, the inclusion of prebiotics within a diverse and mixed diet would have no doubt conferred a selective advantage for the consuming population. As the archaeological evidence reveals, prebiotics have long been a part of the human diet and, in some areas and time periods, in quantities that far exceed those currently consumed by modern populations (Van Loo 1995).

The physical evidence for plant consumption by our early ancestors is virtually nonexistent, owing to poor preservation of organic plant parts in archaeological records; although stable isotope analysis of skeletal remains of early hominids is providing some insight into the quality and diversity of early diet (Lee-Thorp *et al.* 1994; Richards *et al.* 2001). For adequate preservation of prebiotic food evidence in the early human diet we must travel millions of years forward to the Upper Paleolithic (approximately 40 000 to 12 000 years ago) of Western Europe and the Mediterranean Basin, and to the early Holocene (approximately 10 000 years ago) of North America,

before significant direct and indirect evidence of prebiotic food consumption becomes evident.

Decades of large-scale archaeological research in North America have documented extensive exploitation of prebiotic-rich plants such as agave (*Agave* spp.), sotol (*Dasyilirion* spp), camas (e.g. *Camassia quamash*, *C. leichtlinii*) and wild onion (*Allium* spp.). While a great number of inulin-bearing plants were known as food sources among the prehistoric and historic groups of North America (Wandsnider 1997), these particular plants provide by far the oldest evidence of prebiotic consumption in North America, dating back over 9000 years (see Table 1).

In the Lower Pecos region of the Chihuahuan Desert in west Texas along the US-Mexican border, deeply stratified cave deposits document the uses of agave, sotol and onion that date back nearly 9500 years. Kept dry and preserved by the large overhangs that characterise many of the caves and shelters of the region, an extraordinary collection of human coprolites and preserved macro-botanical plant remains suggest that pit-baked prebiotic foods (e.g. agave, sotol, onion) were a mainstay of this desert economy (Sobolik 1990).

East of the Lower Pecos on the western edge of the Edwards Plateau in central Texas, the deeply buried Wilson-Leonard site has produced a 2 m-diameter rock-lined earth oven that would have been used to cook the nutritious onion-like bulbs of camas (*Camassia* spp.). Charred camas bulbs recovered during excavation of the oven produced a date of approximately 8200 years ago (Bousman *et al.* 2002). However, although no charred camas bulbs were recovered from deeper excavations, 'stone-lined hearths' underlying the camas oven were dated to approximately 9410–9990 years ago, suggesting possible earlier use of prebiotics.

At the Stigewalt site in southeastern Kansas, remains of large (>2 m diameter), rock-filled earth ovens with charred onion (*Allium* spp.) bulbs were dated to approximately 8810–7910 years ago (Thies 1990). As with the large oven at the Wilson-Leonard site in central Texas, the occurrence of hand-excavated pits lined with preheated stones seem to be consistently associated with the cooking of prebiotic foods. This same pattern continues throughout the American Southwest, where thousands of agave-roasting pits (also known as *mescal* pits) are scattered about the landscape (Leach 2005). Similarly, in the American Northwest, large, rock-lined ovens were used to cook as much as 1500 kg of inulin-rich camas bulbs in a single firing event (Thoms 2003).

The reoccurring use of large, rock-lined earth ovens, which are often associated with cooking of inulin-rich plants (Wandsnider 1997), is well-documented in the historical and ethnographical records for North America and northern Mexico. For example, Castetter *et al.* (1938) describe cooking agave in pits among the Mescalero and Chiricahua Apache of the American Southwest:

Table 1. A sample of inulin-containing plants identified as food among indigenous populations (adapted from Wandsnider 1997)

Plant	Common name	Edible part	Reference
Liliaceae			
<i>Allium ampeloprasum</i>	Leek, great-headed garlic	Leaf, bulb	Incoll and Bonnett 1993
<i>Allium cepa</i>	Onion, shallot	Bulb	Darbyshire and Henry 1981
<i>Allium porrum</i>	Leek	Bulb	Darbyshire and Henry 1981
<i>Allium sativum</i>	Garlic	Bulb	Darbyshire and Henry 1981
<i>Asparagus racemosus</i>	-	Tuber	Incoll <i>et al.</i> 1989
<i>Arthropodium milleflorum</i>	-	Tuberous root	Incoll <i>et al.</i> 1989
<i>Asphodelus aestivus</i>	Asphodel	Tuberous root	Incoll <i>et al.</i> 1989
<i>Bulbine bulbosa</i>	-	Corm	Incoll <i>et al.</i> 1989
<i>Caesia calliantha</i>	-	Tuberous root	Incoll <i>et al.</i> 1989
<i>Camassia</i>	Camas	Bulb	Yanovsky and Kingsbury 1938
<i>Dichopogon strictus</i>	-	-	Incoll <i>et al.</i> 1989
<i>Erythronium gradiflorum</i>	Glacier lily	Corm	Turner <i>et al.</i> 1990
Agavaceae			
<i>Agave vera cruz</i>	Agave*	Meristem	Meier and Reid 1982
<i>Cordyline terminalis</i>	Palm lily	Tuber	Meier and Reid 1982
<i>Dracaena australis</i>	-	Tuber	Meier and Reid 1982
<i>Yucca filamentosa</i>	-	Stem	Meier and Reid 1982
Asteraceae			
<i>Arctium lappa</i>	Edible burdock	Tap root	Incoll and Bonnett 1993
<i>Cichorium intybus</i>	Chicory	Tap root	Vukov <i>et al.</i> 1993
<i>Cirsium oleraceum</i>	Meadow cabbage	Tap root	Vukov <i>et al.</i> 1993
<i>Helianthus tuberosus</i>	Jerusalem artichoke	Tuber	Vukov <i>et al.</i> 1993
<i>Inula helenium</i>	Elecampane	Root	Incoll and Bonnett 1993
<i>Microseris lanceolata</i>	Murnong	Tuberous root	Incoll <i>et al.</i> 1989
<i>Polymnia sonchifolia</i>	Yacon	Tuber	Ohyama <i>et al.</i> 1990
<i>Scorzonera hispanica</i>	Black salsify	Tap root	Incoll and Bonnett 1993
<i>Taraxacum officinale</i>	Dandelion	Tap root	Yanovsky and Kingsbury 1938
Campanulaceae			
<i>Campanula rapunculus</i>	Rampion	Tap root	Incoll and Bonnett 1993
Boraginaceae			
<i>Symphytum officinale</i>	Comfrey	Leaf	Incoll and Bonnett 1993

*Over 300 species of agave have been reported throughout the American Southwest and northern Mexico (Gentry 1982), all of which are thought to contain inulin.

“Pits in which the crowns [*agave*] were baked were about ten to twelve feet in diameter and three or four feet deep, lined with large flat rocks... Upon this, oak and juniper wood was placed, and before the sun came up was set on fire. By noon the fire had died down, and on these hot stones was laid moist grass, such as bunch grass... The largest mescal crown was selected... they threw it in and threw the other crowns after it... After, the mescal [*agave*] had been covered with the long leaves of bear grass and the whole with earth to a depth sufficient to prevent steam from escaping.”

In the American Southwest, ideal surface conditions and slow rates of soil accumulation, accompanied by repeated use of oven facilities and subsequent accumulation of oven debris (discarded cooking stones) over multiple seasons, has made it possible to map thousands of cooking facilities, which often reach over 1 m in height and cover areas tens of meters in diameter (Leach *et al.* 2005). The synthesis of hundreds of radiocarbon dates from cook-stone

facilities across extensive areas of southern North America (Leach 2005) has revealed a steady increase in prebiotic food consumption beginning over 9000 years ago, culminating in substantial intensification around 1250 years ago. The intensification of prebiotic foods in southern North America (specifically the American Southwest) coincides with an increased reliance on cultivated crops such as corn (*Zea mays*), squash (*Cucurbita* sp.) and beans (*Phaseolus* sp.), and a large-scale growth in the human population. Therefore, while populations were making the transition to a diet heavily dependent on starchy cultivars, prebiotic foods played an important and often increasing regional role in this subsistence economy.

As we see in North America, the occurrence of cook-stone technology in the absence of recoverable plant remains may be used as a proxy indicator of the exploitation of prebiotic foods in the archaeological record. While a great number of foods are known to have been processed with a cook-stone, the occurrence of large (>1 m

diameter), ovens are consistently associated with many prebiotic foods (Leach 2005; Wandsnider 1997).

Throughout Western Europe, similar remains of massive cooking facilities are known to occur in Wales, England, Scotland, Ireland and Scandinavia. Referred to locally as *fulacht fiadh*, recent urban development has led to the excavation of a number of these mounds, which can reach over a meter in height and several meters in diameter, representing dozens, if not hundreds, of individual oven events. While moist ground conditions have all but destroyed any evidence of the plants that may have been processed in these features, radiocarbon dates on small amounts of carbonised wood charcoal from the initial heating of cook-stones indicates that the majority of mounds were constructed within the last 6000 years. Similar cook-stone mounds of varying sizes, dating roughly within the same time period, are known in southern parts of Australia (Holdaway *et al.* 2002). As seen for North America, historical and ethnographical accounts of using large, hand-excavated pits and heated cook-stones is noted throughout Australia. In one example, between 1884 and 1850 British explorers observed the following among the people at Menindee on the Darling River:

“The oven is a hole dug into which are placed stones; a fire is then made and when the stones are become sufficiently hot, whatever fibrous things they eat, or animal, is put into this oven and covered over and a fire made over it, when it soon gets cooked (Brock 1988).”

Among the 800-plus plant foods known to have been eaten for tens of thousands of years by Aborigines in Australia (Brand-Miller and Holt 1998), many were tuberous roots and corms that contained prebiotic inulin (Van Loo 1995) and required prolonged cooking in rock-lined pits (Gott 1982; Gould 1980; Incoll *et al.* 1989).

By far the oldest known evidence of cook-stone technology (ovens) in Europe comes from the cave site of Abri Pataud in the Dordogne region of southern France. In excavations by a joint American-French team between 1958 to 1964, a series of cook-stone features, some greater than 1 m in diameter, were dated to approximately 33 000–18 000 years ago (Movius 1963). While it is impossible to know if prebiotic plant tissue was processed in these ancient features, as no direct evidence in the form of plant material was reported, their use in cooking ~~vegetal~~ material is inferred from the overwhelming evidence of similar features recorded throughout the world.

In one final example, ancient cook-stone features were recently excavated on the southern Japanese island of Tanegashima (Dogome 2000). The oldest two features are buried 10 cm below a layer of Tane-4 volcanic ash, which is radiocarbon dated to about 30 500 years ago. One is a sandstone lens of about 0.75 m in diameter and the other is a sandstone-filled basin about 1.15 × 0.75 m in diameter that is underlain by carbon-stained sediment.

Thermally-altered sandstone ranges in size from a few centimetres to a maximum of 25 cm. Similar cook-stone features and fire-cracked rock scatters were found in overlying deposits dated as late as 6500 years ago, including several features associated with 12 000-year-old Incipient Jomon pottery. Investigators concluded the Late Paleolithic cook-stone features and heavy stone tools were indicative of a plant-based diet (Dogome 2000). These cook-stone features, especially the basin-shaped forms, closely resemble remains of earth ovens found throughout western North America that were used to cook inulin-rich plant tissue (Leach 2005).

Although it is evident that our ancestors consumed large amounts of inulin-containing crops, it could be questioned whether the heat generated by means of cook-stone ovens or other cooking methods would destroy the inulin present in these plants. Direct tests in conditions mimicking cook-stone ovens have not been performed to date. In Louisiana and Northern Europe, inulin-containing chicory roots are roasted. The roots are spread on grids that are stacked in a particular building. Hot air that is generated by burning wood or coal is led through the roots, thereby heating them up to a temperature of 180°C (356°F). It was observed that under these conditions, between 10 and 20% inulin was degraded (Pazola and Cieslak 1979; Van Loo 1995). In cooking or frying experiments with inulin-containing food plants such as onions, it was shown that the losses of inulin were limited to 10% or less. From these observations it can reasonably be concluded that the heat treatment in the cook-stone ovens (<100°C, products not immersed in water) preserved the inulin content of the food plants very well, with expected losses of less than 10%.

4. Discussion

From the current discussion it is clear that our distant ancestors consumed, in varying quantities, plants containing prebiotic carbohydrates. These by definition are not digested in the upper intestinal tract, but rather interact in a specific way with the bacterial ecosystem that is abundantly present in the lower intestinal tract. Consumption of prebiotic carbohydrates such as inulin selectively promotes the growth of bacteria that are associated with a healthy condition (e.g. *Lactobacilli*, *Bifidobacteria*) and suppresses bacteria that are associated with disease (e.g. *Clostridia*). At the same time the metabolic activity of the bacteria is stimulated, which results in the production of metabolites that are absorbed into the blood and exert beneficial effects in the rest of the body with, as a direct consequence: improved resistance to infection, better skeletal bone quality and a reduced risk of chronic diseases such as cancer, cardiovascular disease etc. (Van Loo 2004a, 2004b, 2005).

The interesting association between cook-stone technology and prebiotics offers some proxy of initial intensification, in the absence of the direct recovery of prebiotic plant tissue. Further, the durability of many of these cook-stone features makes their identification and possible utility in recognizing large-scale patterns of prebiotic use across space and time feasible through inductive principles of investigation. We suspect that while our ancestors have always included amounts of prebiotic plants in their diet through daily foraging activities and some evidence for the use of cook-stones is present during the Middle Paleolithic (Mellars 1996), it was not until the onset of the Upper Paleolithic (approximately 40 000 years ago) with its ornaments, decorated tools, deliberate storage facilities, crudely tailored clothing, art and clear demographical pulses (Steiner 2002), that prebiotic plant foods began to play an increasing role in the dietary evolution of our species.

Increased demographical pressure resulted in shrinking territories, making access to preferred plants and high-return animal and aquatic resources less reliable. It is possibly as a result of this cultural pressure that the initial intensification (increased diet breadth) of under-utilised below-ground resources (tubers, bulbs), many rich in prebiotics, took place. This form of land-use intensification (Holly 2005; Thoms 2003) was the beginning of a long-term—albeit punctuated—prebiotic revolution, made possible by the adaptation of cook-stone technology. The evolutionary implications of prebiotic consumption on the development and relative success of our species is unknown, and requires further research. However, advances in processing technology brought about during the industrial revolution in the late 19th century, in conjunction with the increase in 'Westernised diets' and accompanying medical maladies, have forever altered the delicate evolutionary-induced balance between food and human health, thereby resetting our metabolic and genetic clocks.

The concept of prebiotic food ingredients is an important development in nutritional research. Beyond local effects, the idea that prebiotics can selectively modulate gastrointestinal microbial fermentation to influence physiological processes that are known biomarkers of potential illness and human health is profound. However, in the case of even the best-designed human nutrition intervention trial, optimal controls may never be achieved, as the diet and lifestyle of—most likely all—members will differ significantly from their evolutionary-based and thus genetically determined optimal diet.

The future of prebiotic research may benefit from a better understanding of the essential nutrient profiles for humans that have evolved over millions of years of selective pressure and how these relate to intestinal health, as our evolutionary trajectory has arguably been towards maximizing our adaptability—both physically and physio-

logically (Schlicting and Pigliucci 1998). In other words, the biological and physiological parameters of essential nutrients and their conditioning of human health are, for the most part, predetermined and grounded in our ancient past. The recent genome sequencing of *Bifidobacterium longum* (Schell *et al.* 2002) further points to a symbiotic and ancient relationship between our genus and the prebiotic plants on the landscape.

There is no doubt that the majority of the intermediate markers of disease risk and health that are currently being addressed using prebiotics and the modulation of intestinal flora have, at their source, multifactorial causes (Leach 2007). Evolution has the consequence that successful living organisms do best in those environments in which they were selected. As a consequence, an informed research agenda that includes an evolutionary perspective on 'ancestral' parameters of diet and microflora composition may advance the realisation and potential of future prebiotic research, with the aim being to achieve optimal health and nutrition. Through this research agenda, it may be possible to characterise the differences between modern and ancient intestinal health in relation to microflora composition in order to integrate microbiological, nutritional and epidemiological studies and data into an overarching paradigm that can serve to establish formulations resulting in effective recommendations for consumers.

5. References

- Blackburn, H. and Poineas, R. 1983. Diet and hypertension: anthropology, epidemiology, and public health implications. *Progress in Biochemical Pharmacology* **19**: 31-79.
- Bousman, C.B., Collins, M.B., Golberg, P., Stafford, T., Guy, J., Baker, B.W., Steele, D.G., Kay, M., Kerr, A., Fredlund, G., Dering, P., Holliday, V., Wilson, D., Gose, W., Dial, S., Takac, P., Balinsky, R., Masson, M. and Powell, J.F. 2002. The Paleoindian – archaic transition in North America: new evidence from Texas. *Antiquaries* **76**: 980-990.
- Brand-Miller, J.C. and Holt, S.H.A. 1998. Australian Aboriginal plant foods: a consideration of their nutritional compositional and health implications. *Nutrition Research Reviews* **11**: 5-23.
- Brock, D.G. 1988 [1844–6]. *To the desert with Sturt*, Royal Geographical Society of Australasia, Adelaide, Australia.
- Castetter, E.F., Bell, W.H. and Grove, A.R. 1938. The early utilization and the distribution of Agave in the American Southwest. *University of New Mexico Bulletin, Biological Series* **5**(4). The University of New Mexico, Albuquerque, USA.
- Cordain, L., Brand Miller, J., Boyd Eaton, S., Mann, N., Holt, S.H.A. and Speth, J.D. 2000. Plant-animal subsistence ratios and macronutrient estimations in worldwide hunter-gatherer diets. *American Journal of Clinical Nutrition* **71**: 682-92.
- Cordain, L., Eaton, S.B., Miller, J.B., Mann, N. and Hill, K. 2002. The paradoxical nature of hunter-gatherer diets: meat-based, yet non-atherogenic. *European Journal of Clinical Nutrition* **56**: S42-S52.
- Darbyshire, B. and Henry, R.J. 1981. Differences in fructan content and synthesis in some *Allium* species. *New Phytologist* **87**: 249-256.

- Dogome, H. 2000. Summary (English). In: *The Yokomine C Site* (in Japanese): 1–2. Town Board of Education, Minami Tane, Kagoshima. Torai, Kagoshima, Japan.
- Eaton, S.B. 2007. Preagricultural diets in evolutionary health promotion. In: Ungar, P.S., editor. *Evolution of the Human Diet: The Known, the Unknown and the Unknowable*: 384-394. Oxford University Press, UK.
- Eaton, S.B., Strassman, B.I., Nesse, R.M., Neel, J.V., Ewald, P.W., Willaims, G.C., Weder, A.B., Eaton II, S.B., Lindeberg, S., Konner, M.J., Mysterud, I. and Cordain, L. 2002. Evolutionary health promotion. *Preventive Medicine* **34**: 109-188.
- Finlayson, C. 2005. Biogeography and evolution of the genus *Homo*. *Trends in Ecology and Evolution* **20**: 457-463.
- Franck, A. 2002. Technological functionality of inulin and oligofructose. *British Journal of Nutrition* **87**: S287-S291.
- Gentry, H.S. 1982. *Agaves of continental North America*. University of Arizona Press, Tucson, USA.
- Gibson, G.R. and Roberfroid, M.B. 1995. Dietary modulation of the human colonic microbiota: introducing the concept of prebiotics. *Journal of Nutrition* **125**: 1401-1412.
- Gibson, G.R., Probert, H.M., Van Loo, J.A.E., Rastall, R.A. and Roberfroid, M.B. 2004. Dietary modulation of the human colonic microbiota: Updating the concept of prebiotics. *Nutrition Research Reviews* **17**: 259-275.
- Glanville, E.V. and Geerdink, R.A. 1970. Skinfold thickness, body measurements and age changes in Trio and Wajana Indians of Surinam. *American Journal of Physical Anthropology* **32**: 455-462.
- Goldsmith, M.F. 1993. Ancestors may provide clinical answers, say 'Darwinian' medical evolutionists. *Journal of the American Medical Association* **269**: 1477-1480.
- Gott, B. 1982. Ecology of root use by the aborigines of southern Australia. *Archaeology in Oceania* **17**: 59-67.
- Gould, R.A. 1980. *Living archaeology*, Cambridge University Press, UK.
- Hatley, T. and Kappelman, J. 1980. Bears, pigs, and Plio-Pleistocene Hominids: A case for the exploitation of belowground food resources. *Human Ecology* **8**: 371-387.
- Hendry, G. 1987. The ecological significance of fructan in a contemporary flora. *New Phytology* **106**: 201-216.
- Ho, K.-J., Mikkelsen, B., Lewis, L.A., Feldman, S.A. and Taylor, C.B. 1972. Alaskan arctic Eskimos: response to a customary high fat diet. *American Journal of Clinical Nutrition* **25**: 737-745.
- Hockett, B. and Haws, J. 2003. Nutritional ecology and diachronic trends in Paleolithic diet and health. *Evolutionary Anthropology* **12**: 211-216.
- Holdaway, S.J., Fanning, P.C., Jones, M., Shiner, J., Witter, D. and Nicholls, G. 2002. Variability in the chronology of late holocene aboriginal occupation on the arid margin of Southeastern Australia. *Journal of Archaeological Science* **29**: 351-363.
- Holly, D.H., Jr. 2005. The place of "others" in hunter-gatherer intensification. *American Anthropology* **107**: 207-220.
- Incoll, L.D. and Bonnett, G.D. 1993. The occurrence of fructan in food plants. In: Fuchs, A., editor. *Inulin and inulin-containing crops*: 309-322. Elsevier, Amsterdam, Netherlands.
- Incoll, L.D., Bonnett, G.D. and Gott, B. 1989. Fructans in the underground storage organs of some Australian plants used for food by aborigines. *Journal of Plant Physiology* **134**: 196-202.
- IOM (Institute of Medicine). 2002. *Dietary reference intakes of energy, carbohydrate, fiber, fat, fatty acids, cholesterol, protein, and amino acids*. National Academy Press, Washington, DC, USA.
- Jenike, M.R. 2001. Nutritional ecology: diet, physical activity and body size. In: Panter-Brick, C., Layton, R.H. and Rowley-Conway, P., editors. *Hunter-gatherers: an interdisciplinary perspective*: 205-238. Cambridge University Press, UK.
- Jenkins, J.A., Kendall, C.W.C. and Vuksan, V. 1999. Inulin, oligofructose and intestinal function. *Journal of Nutrition* **129**: 1431S-1433S.
- Joffe, B.I., Jackson, W.P.U., Thomas, M.E., Toyer, M.G., Keller, P. and Pimstone, B.L. 1971. Metabolic response to oral glucose in the Kalahari bushmen. *British Medical Journal* **4**: 206-208.
- Kuroshima, A., Itoh, S., Azuma, T. and Agishi, Y. 1972. Glucose tolerance test in the Ainu. *International Journal of Biometeorology* **16**: 193-197.
- Laden, G. and Wrangham, R. 2005. The rise of the hominids as an adaptive shift in fallback foods: Plant underground storage organs (USOs) and australpith origins. *Journal of Human Evolution* **49**: 482-498.
- Leach, J.D. 2005. Sharp increase in cook-stone use in the Chihuahuan Desert during periods of agricultural intensification. *Antiquaries* **79**. Available at: <http://antiquity.ac.uk/ProjGall/leach05/>.
- Leach, J.D., Bousman, C.B. and Nickels, D. 2005. Comments on assigning a primary context to artifacts recovered from burned rock middens. *Journal of Field Archaeology* **30**: 201-203.
- Leach, J.D., Gibson, G.R. and Van Loo, J. 2006a. Human evolution, nutritional ecology and prebiotics in ancient diet. *Bioscience and Microflora* **25**(1): 1-8.
- Leach, J.D., Rastall, R.A. and Gibson, G.R. 2006b. Prebiotics: past, present and future. In: Gibson, G.R. and Rastall, R.A., editors. *Prebiotics: development and application*: 237-248. John Wiley and Sons Ltd., UK.
- Leach, J.D. 2007. Evolutionary perspective on dietary intake of fibre and colorectal cancer. *European Journal of Clinical Nutrition* **61**: 140-142.
- Lee-Thorp, J.A., van der Merwe, N.J. and Brain, C.K. 1994. Diet of *Australopithecus robustus* at Swartkrans from stable carbon isotope analysis. *Journal of Human Evolution* **27**: 361-372.
- Lee, R.B. and Daly, R., editors. 1999. *The Cambridge encyclopedia of hunters and gatherers*. Cambridge University Press, UK.
- Mellars, P. 1996. *The Neanderthal legacy: an Archeological perspective from Western Europe*. Princeton University Press, New Jersey, USA.
- Meier, H. and Reid, J.S.G. 1982. Reserve polysaccharides other than starch in higher plants. In: Loewus, F.A. and Tanner, W., editors. *Encyclopedia of plant physiology, vol 13A*: 418-471. Springer, Berlin, Germany.
- Merimee, T.J., Romoin, D.L. and Cavalli-Sforza, L.L. 1972. Metabolic studies in the African pygmy. *Journal of Clinical Investigation* **51**: 395-401.
- Milton, K. 1999. A hypothesis to explain the role of meat-eating in human evolution. *Evolutionary Anthropology* **12**: 11-21.
- Movius, H.L. 1963. The hearths of the Upper Périgordian and Aurignacian horizons at the Abri Pataud, Les Eyzies (Dordogne), and their possible significance. *American Anthropology* **68**: 296-325.
- Murray, S.S., Schoeninger, M.J., Bunn, H.T., Pickering, T.R. and Marlett, J.A. 2001. Nutritional composition of some wild plant foods and honey used by the Hadza foragers of Tanzania. *Journal of Food Composition and Analysis* **13**: 1-11.
- O'Keefe, J.H., Jr and Cordain, L. 2004. Cardiovascular disease resulting from a diet and lifestyle at odds with our Paleolithic genome: how to become a 21st-century hunter-gatherer. *Mayo Clinic proceedings* **79**: 101-108.
- Pazola, Z. and Cieslak, J. 1979. Changes in carbohydrates during the production of coffee substitute extracts especially in the roasting process. *Food Chemistry* **4**: 41-47.

- Ragir, S. 2000. Diet and food preparation: rethinking early hominid behavior. *Evolutionary Anthropology* **9**: 153-155.
- Richards, M.P., Pettitt, P.B., Stiner, M.C. and Trinkaus, E. 2001. Stable isotope evidence for increasing diet breadth in the European mid-Upper Paleolithic. *Proceedings of the National Academy of Science USA* **98**: 6528-6532.
- Roberfroid, M. 2002. Functional food concept and its application to prebiotics. *Digestion and Liver Disease* **34**: S105-S110.
- Schell, M.A., Karmirantzou, M., Snel, B., Vilanova, D., Berger, B., Pessi, G., Zwahlen, M.C., Desiere, F., Bork, P., Delley, M., Pridmore, R.D. and Arigoni, F. 2002. The genome sequence of *Bifidobacterium longum* reflects its adaptation to the human gastrointestinal tract. *Proceedings of the National Academy of Science USA* **99**: 14422-14427.
- Schlichting, C.D. and Pigliucci, M. 1998. Phenotypic evolution. A reactive norm perspective. Sinauer, Sunderland, Massachusetts, USA.
- Shephard, R.J. and Rode, A. 1996. *The health consequences of modernization: evidence from circumpolar peoples*: 101-108. Cambridge University Press, UK.
- Shuman, J.M. 1996. Nutrition in aging. In: Mahan, L.K. and Escott-Stump, S., editors. *Food, nutrition, and diet therapy*: 287-308. W.B. Saunders, Philadelphia, USA.
- Sing, C.F., Haviland, M.B. and Reilly, S.L. 1996. Genetic architecture of common multifactorial diseases. In: Chadwick, D. and Cardew, G., editors. *Variation in the human genome*. Ciba Foundation Symposium **197**: 211-232. Wiley, Chichester, UK.
- Sobolik, K.D. 1990. A nutritional analysis of diet as revealed in prehistoric human coprolites. *Texas Journal of Science* **42**: 23-36.
- Spielmann, R.S., Fajans, S.S., Neel, J.V., Pek, S., Floyd, J.C. and Oliver, W.J. 1982. Glucose tolerance in two unacculturated Indian tribes of Brazil. *Diabetologia* **23**: 90-93.
- Stahl, A.B. 1984. Hominid dietary selection before fire. *Current Anthropology* **25**: 151-157.
- Stearns, S.C., editor. 1999. *Evolution in health and disease*. Oxford University Press, UK.
- Steiner, M.C. 2002. Carnivory, coevolution, and the geographic spread of the genus *Homo*. *Journal of Archaeological Research* **10**: 1-63.
- Thies, R.M. 1990. *The Archeology of the Stigewalt Site, 14LT351*. Kansas State Historical Society, Contract Archeology Series, Publication 7. Kansas State Historical Society, Lawrence.
- Thoms, A.V. 2003. Cook-stone technology in North America: Evolutionary changes in domestic fire structures during the Holocene. In: Frere-Sautot, M.-C., editor. *Colloque et experimentation: le feu domestique et ses structures au Neolithique aux Auges des Metaux*: 87-96 Collection Prehistories No. 9, Editions Monique, Mergoil, France.
- Trevathan, W.R., Smith, E.O. and McKenna, J.J., editors. 1999. *Evolutionary medicine*. Oxford University Press, UK.
- Van Loo, J., Coussement, P., De Leenheer, L., Huybregts, H. and Smits, G. 1995. On the presence of inulin and oligofructose as natural ingredients in the Western diet. *Critical Reviews of Food Science and Nutrition* **35**: 525-552.
- Van Loo, J. 2004a. Prebiotics promote good health. The basis, the potential and the emerging evidence. *Journal of Clinical Gastroenterology* **38**: S70-S75.
- Van Loo, J. 2004b. The specificity of the interaction with intestinal bacterial fermentation by prebiotics determines their physiological efficacy. *Nutrition Research Reviews* **17**: 89-98.
- Van Loo, J. 2005. Prebiotics: a nutritional concept gaining momentum in modern nutrition. *Food Science and Technology Bulletin: Functional Foods* **2**(8): 83-100.
- Vincent, A.S. 1985. Plant foods in savanna environments: a preliminary report of tubers eaten by the Hadza of northern Tanzania. *World Archaeology* **17**: 131-148.
- Wandsnider, L. 1997. The roasted and boiled: food composition and heat treatment with special emphasis on pit-hearth cooking. *Journal of Anthropological Archaeology* **16**: 1-48.
- Williams, G.C. and Nesse, R.M. 1991. The dawn of Darwinian medicine. *Quarterly Review of Biology* **66**: 1-22.
- Wood, B. 2002. Palaeoanthropology: hominid revelations from Chad. *Nature* **418**: 133-135.
- Yanovsky, E. and Kingsbury, R.M. 1938. Analyses of some Indian food plants. *Journal of the Association of Official Agricultural Chemists* **21**: 648-665.