A HISTORICAL VIEW OF TEA*

DEREK S. BENDALL**

The natural home of the tea plant, *Camellia sinensis*, is probably Yunnan in S.W. China, and the natural home for the scientific investigation of tea is Tocklai in N.E. India. Just as growth of the tea plant has spread around the world, far beyond its site of origin, so tea research has been taken up in many other countries, of which China and Japan are outstanding examples at the present time. Nevertheless, taking the historical point of view, we think of the pioneering work carried out in India. First, there was the establishment of the growth of tea on large scale plantations and the mechanisation of manufacture, both of which were necessary to satisfy the growing thirst for tea around the world. This was soon followed by recognition of the need for systematic study of the agronomic requirements of tea cultivation, optimum conditions for the manufacturing processes, and the fundamental chemistry that gives tea its desirable properties. The establishment of Tocklai Experimental Station in 1911 provided the nucleus around which earlier studies by men such as Kelway Bamber, George Watt and H.H. Mann could develop.

By the end of the first half century of its existence, despite the disruption caused by the Second World War, Tocklai Experimental Station had an established record of constructive advice to a flourishing Indian tea industry and an ongoing programme of research for the long-term improvement of all aspects of tea production. The influence of Tocklai was also felt in many other countries around the world where tea was being successfully produced commercially. In its early days Tocklai had largely been responding empirically in an *ad hoc* fashion to problems as they arose on the tea estates. The establishment of a long-term programme of research, coupled with an effective system for exchange of information between estates and research staff was, to a large extent, due to the insight of Sir Frank Engledow, Professor of Agriculture at Cambridge University, acting as chairman of Commissions of Inquiry in 1936 and 1953.

In the West at this time, that is around 1960, the overwhelming emphasis was on black tea and the most serious fundamental scientific problem for tea manufacture was regarded as the chemistry of fermentation. China was still largely closed to the world and had not yet emerged from its long series of political upheavals. This is the time when my own interest in tea was aroused as a result of Engledow's survey in 1957 of agriculture in the Central African Federation, a rather short-lived association between Northern and Southern Rhodesia and Nyasaland (eventually to become Zambia, Zimbabwe and Malawi, respectively). Tea was first planted in Nyasaland in 1896 and started to flourish as an industry in the 1930s. Nevertheless, the teas produced were plain rather than flavoury and regarded as poor quality by comparison with those produced in N.E. India. Recognizing this as a biochemical problem, the planters asked Sir Frank Engledow to seek out a biochemist to investigate it. Through his Cambridge contacts, Professor Sir Frank Young and the renowned plant biochemist Dr Robin Hill, the choice fell on me as a young, recently qualified biochemist with a special interest in plants. At that time (1958), research into the biochemistry of plants was still mostly concerned with the basic processes of metabolism such as photosynthesis, for which Robin Hill was best known. Nevertheless, Hill had a wide interest in plants, and as students in the laboratory, he had introduced us to the colourful variety of anthocyanins. However, secondary products of plant metabolism had not been a significant feature of our course.

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** University of Cambridge, Department of Biochemistry, Tennis Court Road, Cambridge CB2 1QW, U.K.

For me, it was not difficult to make the transition from the study of the biochemistry of plant respiration to that of the secondary products produced in tea leaves, partly because of a fascination with the variety of chemical structures and properties of flavonoids, and partly because it immediately put one in contact with the whole plant growing in a distinct environment. These two considerations have led me eventually to enquire into the history of the tea plant.

The broad outline of fermentation was already understood. Our aim was to gain sufficient understanding of the chemistry and biochemistry of fermentation to explain poor fermentation and suggest possible remedies. Africa was an entirely new experience and Nyasaland had a beauty of a kind not to be found in Europe, which was only enhanced by the broad expanse of tea fields shaded by Albizzia trees and lying on the slopes under the volcanic massif of Mlanje mountain. Simple qualitative tests soon revealed a large degree of variability in the fermentability of individual bushes. Initial testing was facilitated by Robin Hill's chloroform test, in which a tea shoot was placed in a boiling tube above a plug of cotton wool moistened with chloroform and checked for the development of brown colouration. More sophisticated analyses were greatly aided by the chromatographic methods for analysis of tea leaf polyphenols developed by Bradfield and Roberts in London[1]. It soon became apparent that a major cause of poor fermentation, however, was likely to be a deficiency of polyphenol oxidase, which was probably genetically determined. We set out to purify the oxidase, and this line of work culminated eventually in the experiments of Alistair Robertson on model reactions with purified catechins and oxidase[2]. He was finally able to define optimum conditions of pH, temperature and oxygen concentration, and the optimum catechin ratios, that gave the highest ratio of theaflavins to thearubigins during fermentation[3,4].

During the last 50 years the Western outlook on tea has been transformed. Greatly increased contact with China and its ancient traditions of tea drinking, with a strong preference for green tea, has reawakened the knowledge of the variety of teas to be found in China that used to exist when it was the only source of tea worldwide. Now we are aware and appreciate not only different types of tea, such as green, oolong, puer, white, even yellow, and Keemun black tea, but also of the more subtle differences that arise from the different tea growing areas of China. In Britain a nascent tea shop culture (which might be compared, for example, with Mariage Frères in Paris) was nipped in the bud by the recent recession. In the United States there has always been a greater interest in green tea, despite the Boston Tea Party, and American tour operators may now be found who organize specialized tours of Chinese tea gardens for tea devotees.

In the last few years great scientific interest has been aroused in the potential medicinal use of tea, harking back to the earliest Chinese legends of the discovery of tea by the emperor Shen Nong. A search of the scientific literature for papers referring to epigallocatechin gallate (EGCG) reveals well over 2,000 reports, very few of which are to do with tea itself. While there is little difficulty in accepting a stimulating effect of tea drinking, and a mildly beneficial effect on health, more specific effects on biochemical processes *in vivo* are complicated to establish and definite conclusions are premature. EGCG, of course, occurs in very few angiosperms, as far as we know, even though these are taxonomically widely distributed. The tea plant outclasses them all, except for its close relative *Camellia taliensis*[5].

We prize the tea plant for the unique chemistry of its young shoots. This is dominated by the catechins, especially a high concentration of EGCG, by caffeine, and by polyphenol (or catechol) oxidase. The unusual amino acid theanine is also a significant component, and largely responsible for the umami taste of tea[6]. Low molecular weight volatile compounds, such as linalool and geraniol, play an essential role in our appreciation of a cup of tea, but these are more elusive and less uniquely associated with the tea leaf. Polyphenol oxidase is a common plant enzyme but, as we have seen, EGCG is a tea speciality. It is known to occur in relatively small amounts in the persimmon (*Diospyros kaki*)[7] and *Vitellana paradoxa* (the Shea tree of Africa)[8], both of which, like *Camellia*, belong to the order Ericales, but also in more distantly related angiosperms such as some *Cistus* species[9], *Theobroma cacao*[10], the honeybush tea of South Africa (*Stryphnodendron adstringens*)[11] and *Salix aegyptiaca*[12]. Caffeine, too, seems to be widely but thinly scattered across the angiosperm clade. The few caffeine-rich plants have been well-known for centuries, if not millenia. Coffee is not tea's only rival, in South America there are *Ilex paraguariensis* (maté)[13], *Paullinia cupara* (guaraná)[14] and *Theobroma cacao*[15], and in Africa *Cola nitida*[13]. Caffeine has also been found recently in flowers of various *Citrus* species[16]. What makes the tea plant unique, of course, is not only the presence in the leaf of these unusual products of secondary metabolism, but the composition of the whole community of chemicals, their concentrations, both absolute and relative.

The scattered distribution of caffeine and EGCG may be partly explained by the fact that both are synthesised by offshoots of primary metabolism which involve enzymes closely related to those already occurring in primary metabolism. Thus caffeine is a byproduct of purine metabolism and derives from xanthosine (a precursor of guanine) by loss of the ribose and by a series of methylations involving *S*-adenosyl methionine. These reactions are catalysed by enzymes that evolved by small modifications of essential enzymes of primary metabolism. Biosynthesis of catechins and other flavonoids is more complicated. They are derived from *p*-coumaroyl CoA, which is an essential intermediate in the metabolism of all vascular plants by virtue of the fact that it is the precursor of lignin. An alternative fate for *p*-coumaroyl CoA is to undergo condensation with three molecules of malonyl CoA (an intermediate of fatty acid metabolism) under the influence of chalcone synthase to produce a series of flavonoids by specific hydroxylations and reductions. *p*-Coumaroyl CoA is derived from phenylalanine by a three-step process in which the first, and crucial, one is deamination by phenylalanine ammonia lyase (PAL). So here we have two novel enzymes, PAL and chalcone synthase, that are essential for flavonoid biosynthesis. Flavonoids occur in virtually all angiosperms and the acquisition of PAL was a crucial step in the evolution of vascular plants. The current view is that PAL is likely to have originated in a primitive land plant by lateral gene transfer from either a bacterium or a fungus[17]. It is worth mentioning here that the enzyme catalysing the final step in the biosynthesis of EGCG, which is the esterification of the 3-hydroxyl group of epigallocatechin, has not been purified.

There are many different ways of using tea leaves, or occasionally tea seeds, such as making various kinds of soup, or boiling the leaves to eat as a vegetable, and eating pickled leaf. These methods are still to be found in Yunnan, Tibet, Burma or Thailand, and may be compared with methods used by various indigenous peoples in South America for consuming other caffeine-rich plant material such as maté, guayusa or guaraná. These customs may give a clue as to how the beneficial effects of such plants were first discovered. Modern methods of making an infusion of dried leaves for use as a beverage have developed over a long period of hundreds of years. Tradition has it that tea was originally used as a medicine in China, and those who remember their childish responses to medicine would find this plausible. For fresh young tea shoots have various properties. They are succulent and might be treated as a food. They are rich in caffeine, the effects of which are usually beneficial. But they are also bitter, which generally imparts an unpleasant taste, both to animals and humans, although to varying degrees. Techniques for preparing tea as a drink are partly designed to minimize the bitter aspects but to enhance the flavour so that the stimulating effect of caffeine can be obtained in an enjoyable way.

Many plants have a bitter taste, but clearly there was something special about the tea plant growing amongst the lush vegetation of sub-tropical Yunnan. To understand this situation we must step back and take a broad view of the whole of the plant world. To illustrate the point we might start by asking how it was that the human inhabitants of Easter Island, isolated in the Pacific Ocean, eventually completely destroyed the native population of trees. One half of the answer lies in the fact that the trees were defenceless against the axes of humans. Taking the world as a whole, however, the plant kingdom is prolific, despite the constant depradations of animal herbivores on which, in fact, life for the whole of the animal kingdom depends. For this situation to persist, plants must have developed effective defences against herbivore attack, even if not against humans.

So let us cast our minds back to the origin of the land flora. The first, very simple plants are thought to have invaded land about 450 million years ago in the Ordovician period. We must use our imaginations, guided by such scientific evidence as we can muster, to get a picture of what the earth was like at that time. Even the continents would have had a totally unfamiliar disposition. The largest land mass was Gondwana, spreading from the equator to the South pole, and several small areas of dry land were scattered over the rest of the globe. As the earth's flora evolved over geological time towards the present, the continental plates would have moved to form one large supercontinent of Pangaea spread more evenly over the two hemispheres, which would have encouraged the distribution of new species around the globe, and then slowly drifted apart into the continents as we now know them. The global climate would initially have been considerably warmer than it is today, but soon it would have been followed by marked cooling in an ice age, only to be succeeded by another warm period in the Silurian. Further swings in average temperature followed, although relatively warm periods predominated. Sea levels affecting the continental margins fell and rose over a few hundred meters as the oceans froze and thawed.

The first true land plants, or embryophytes, are thought to have been multicellular green algae related to the present-day genera *Chara* and *Nitella*, which grow in fresh water. They were unlikely to have found themselves alone, however. There is evidence from the rate of weathering of rocks that living organisms, capable of raising the local concentration of CO_2 in water, were present up to 1.2 billion years ago in the late Precambian. The essential component of such a primitive biota would have been photoautotrophs, especially cyanobacteria which had already learnt the trick of handling visible light most effectively at least 2.5 billion years ago, and possibly some unicellular eukaryotic algae; other bacteria could then have lived on the organic material so produced. $^{13}C/^{12}C$ isotope ratios of Precambrian carbonate rocks support this interpretation[18]. The distinctive feature of the Characean algae that gave them the edge over the early colonisers, in addition to their eukaryotic nature, was that they were multicellular with cells containing a large central vacuole. This gave them the advantages of size, a large surface to cytoplasm ratio giving improved access to nutrients, and the potential for cellular differentiation.

All the early colonisers of land would have faced two serious environmental problems that would have been very much weaker challenges in their previous marine habitat. The most obvious of these was the danger of dessication, so primitive embryophytes would have needed to remain in contact with ground water, ponds, streams or rivers and the aerial parts would have developed a water-repellent cuticle coated with wax. Much of the subsequent development of embryophytes was driven by the need to keep cells fully hydrated.

The second problem was the greatly increased exposure to sunlight. Light is both blessing and misfortune. The sun is the source of almost all the energy that allows life to flourish. Sunlight, however, needs to be handled carefully because random light absorption by coloured molecules and those absorbing in the ultraviolet, as do many of the chemicals of life including nucleic acids and proteins, causes destructive photochemical reactions. Cyanobacteria and other prokaryotic invaders of land would probably have synthesized mycosporine-like amino acids which filter out UVA and UVB[19]. To protect against the most damaging short wave UVC they would have needed to find special aqueous habitats until the atmospheric O_2 concentration had risen sufficiently to generate enough ozone to act as an efficient filter. Plants, on the other hand, lack mycosporine-like amino acids, but very soon after first arrival on land, they developed an ability to use for this purpose phenylpropanoid compounds, the metabolic products of phenylalanine and *p*-coumaroyl CoA, and the presence of a large, central vacuole in each cell would also have been an advantage. Topologically, vacuole contents are extracellular, making it possible to accumulate large quantities of substances such as flavonoids and organic acids which are of value to the plant but could interfere with primary metabolic processes in the cytoplasm. This development signals the striking and characteristic ability of present day plants to synthesize a wide variety of secondary chemical products, many more in total than the number of distinct species. These substances function in the adaptation of the plant to its environment, and so are frequently referred to as specialized metabolites, which either act as attractants for other organisms or have a role in defence against pathogens or herbivores.

The competitive search for the basic nutritional requirements of a plant, light, minerals, water and atmospheric CO_2, led to structural differentiation and growth of the plant. Those that had mastered the problems of transporting water upwards against gravity and into the air and light were able to dominate the canopy. By the Jurassic period (200 – 145 million years ago) there were giant ferns, cycads, and above all gymnosperms. The evolution of these plants was a slow process, taking tens or hundreds of millions of years. It occurred in response not only to the changing physical conditions of climate and geography, but also to the corresponding development of their animal predators, notoriously the dinosaurs but also insects. A large dinosaur could consume enormous quantities of leaf material so that the earth's flora might have become seriously endangered. One can imagine that a dynamic equilibrium might have been established between the size of the population of herbivorous animals and the supply of plant food, although this is questionable. Plants are unable to run away from their predators, so there was strong evolutionary pressure for them to develop ways of defending themselves from these attacks, whether by large animals, insects or microorganisms. Defence mechanisms took a variety of forms. They could be structural modifications to render the plant unpalatable, such as leaf hairs, spines or tough, woody tissue, but the most general kind of defence would have been chemical.

The production of products of so-called secondary metabolism is a common feature of living organisms. Any one substance has a limited distribution, is not essential for normal growth and reproduction, but in general has a function related to the ecology of the organism, most commonly either defence or allelopathy. Plants have developed an especially rich variety of secondary products, which mirrors the numbers of animals and microorganisms that depend on them. The importance of such substances to the welfare of a plant species is shown by the large proportion of available resources they commit to their synthesis. In the Jurassic period gymnosperms were major components of the climax vegetation. Judging by the properties of contemporary species the main secondary products of the Jurassic would have been terpenes accumulated in resins and also flavonoids. Both groups of substance possess toxins, although they are probably effective against different groups of organism. The full development of secondary metabolism, however, was a characteristic of the angiosperms. Generally speaking, for example, gymnosperms do not produce alkaloids, the group which has the largest number of specific toxins. All known caffeine plants are angiosperms.

The origin of angiosperms has been a mystery since the time of Darwin. Although the mist is gradually clearing, there is still considerable uncertainty. Phylogenetic evidence suggests an earlier origin than do fossils, but one can be reasonably confident that genuine angiosperms existed by 150 million years ago, towards the end of the Jurassic[20], and it is generally agreed that a rapid development of angiosperm variety took place during the Cretaceous. Angiosperms were rapidly replacing gymnosperms as the major component of climax vegetation in many parts of the earth, and their diversification was matched by that of the insects at the same time. Darwin wrote about the coevolution of insects and flowering plants based on cross-pollination by insects and the consequential development of a rich variety of flowers. There is a cryptic aspect, however, to the coevolution of angiosperms and insects, which has taken much longer even to begin to unravel. This mostly concerns parts of the plant other than the flowers, especially the leaves, as the vacuoles of leaf cells are a major site for the accumulation of the secondary products of metabolism. These substances include toxins and those that reduce palatability or digestibility of the tissue which will discourage both insects and larger foraging animals. In response to such feeding inhibition some insects may move over to alternative host plants, but others will be under pressure to develop ways of minimising the effects of the plant's chemical weapons. The plant then comes under evolutionary pressure to develop new, more lethal weapons. One strategy is for the plant to signal that it is under attack by a herbivorous insect by producing a specific volatile chemical. This will encourage another class of insects, such as the ladybirds (coccinellids), which feed on the herbivores. These reciprocal effects are coevolution in action, and can help to explain the enormous diversity of both angiosperms and insects, as well as that of secondary plant products.

The Cretaceous came to a catastrophic end about 65 million years ago with the impact of a large asteroid on the tip of the Yucatan peninsula in what is now Mexico. Evidence points to the devastation caused by the impact having been worldwide[21]. In the short term there would have been a vast dust cloud which obliterated the sun, thereby reducing light available for photosynthesis and causing serious cooling. Much of the earth's forests disappeared in huge fires. Such an overwhelming environmental change, which for animals included much of their food supply, exceeded the adaptability of many organisms, especially the very large, such as some dinosaurs, and the specialised (many phytophagous insects). This led to major extinction of species, both animals and plants. Amongst the angiosperms, although many species disappeared the major groupings persisted so that over the course of time new species became established in old families, or possibly minor pre-catastrophe species were now able to flourish[22]. Phylogenetic evidence indicates that several genera of flowering plants appeared at about this time[23], often it would seem as a result of whole genome duplication[24]. *Camellia* is a genus that can be dated to approximately the end of the Cretaceous, although it has not been examined for the possibility of genome duplication.

The whole genus *Camellia* seems to have evolved in southern China. By this time the continents had taken on a disposition easily recognizable from today's viewpoint, except that the Atlantic ocean had only just started to open up, separating America from Europe and Africa. Southern China occupied much the same latitude as today, so that at first sight one might think of *Camellia* developing in a fairly stable environment. However, a process of enormous significance for the whole of Asia, the collision with India, did not begin until about 50 million years ago. The Indian plate had been slowly moving northwards for many millions of years after its separation from Gondwanaland and is still continuing today at the rate of about 5 cm per year. The collision between two continental land masses led to the development of enormous pressures which were relieved by a crumpling up of the continental crust (the alternative of subduction does not occur with two masses of similar density). Thus the Himalayas were born. In a few million years they reached a height of 9 km, and are still growing at about 1 cm a year. The snow fields and glaciers of the Himalayas may not have spread more widely, but they have had a marked influence on the climate and its seasonal variations over a large part of eastern and southern Asia, including Yunnan. The mountains of Yunnan run in north-south ridges representing the final eastwards extension of the Himalayas, as the collisional pressure was partially satisfied by extrusion of landmass to the East and South. Much of the change occurred during the last 10 million years, the period during which *Camellia sinensis* evolved from its camellian ancestors. Yunnan had developed a varied series of habitats differentiated both by altitude and latitude, and the north-south orientation of the mountains meant that plants were not trapped in a narrow range of latitude when the climate changed.

Two further environmental variables, which contribute to the rich variety of the flora of Yunnan, are rainfall and soil, and these are of crucial importance for *Camellia*. Yunnan is exposed to the Southwest monsoon coming from the Bay of Bengal, which leads to warm, wet summers, cooler, dry winters and a gradient of rainfall and mean annual temperature from Southwest to Northeast. The geological structure of Yunnan leads to marked variations in soil pH. *Camellia sinensis*, at least as it grows under cultivation, requires a rainfall of at least 120 cm per year and an acidic soil, and these conditions are best met in restricted locations in southwestern Yunnan, often running in north-south strips where the underlying rock is granite. The long dry season is not ideal for tea, but can be tolerated on a deep soil and with winter fog. In view of the fact that tea is cultivated successfully in many different parts of the world (including much of China itself), it is surprising that the tea plant seems not to have broken out of a restricted area of Southwest China (Yunnan, Sichuan and Guizhou), and an indeterminate surrounding area in Burma, Laos, Vietnam and India, until propagated artificially by man.

Any attempt to understand the natural environment in which the tea plant evolved, and in particular the biological hazards to which it was exposed, is hampered by the fact that it is very doubtful whether any truly wild tea still exists. In Yunnan there are patches of tea still to be found which appear to be wild, with the occasional large tree which is several hundred years old. It is difficult to decide whether these plants are truly wild or might better be described as feral, that is the residue of earlier cultivation by native peoples. Charles Bruce explored much of Northeast of Assam in the 1840s and discovered a large number of tracts of apparently wild tea amongst the Singpho people[25]. However, both he and, a century later, Frank Kingdon-Ward[26] noted how the tea plant had been spread by the Shan tribes migrating through Burma and Manipur as far as Assam. An ancient route connecting Yunnan to Assam through Burma is known to have been in use at least as early as the second century BC, and possibly much earlier[27]. A few years later than his exploration of Manipur, Kingdon-Ward found one or two isolated tea plants growing in the jungle of the Mishmi hills in Arunachal Pradesh, and thought that these could not have been relics of former cultivation[28]. A further puzzle is the origins of the two main varieties of *Camellia sinensis*, var. *assamica* and var. *sinensis*. Did one derive from the other or are they both descended separately from the same precursor? Did they evolve naturally, or is one (probably var. *sinensis*) the result of human selection from the other? It is the var. *sinensis* that spread most easily eastwards and northwards across much of China, and eventually to Korea and Japan. In Yunnan itself latitude 25ºN provides a very rough demarcation between the two varieties, *assamica* to the South and *sinensis* to the North. The crucial difference is that the China variety is more hardy, which could have resulted from slow but deliberate human selection for hardiness.

What we can do is relate the ecology of tea as it is grown today, mostly in large areas of monoculture, to the chemical make-up of the plant. Until now, at least, the tea plant has been remarkably successful in resisting large-scale epidemics caused by insects, fungi or microorganisms, even though they would be favoured by the growth conditions. The outstanding illustration of this is the highly successful development of tea estates in Ceylon after the devastation of the original coffee plantations in the 1870s caused by the coffee rust fungus.

The chemical defences offered by the tea plant fall mainly, but not entirely, into the two categories of polyphenols and purine alkaloids, which is an unusual combination. The polyphenols are present in tea shoots in rich variety and high total concentration, representing about 30% of the dry weight. This reflects a massive investment of synthetic energy, but it is notable that they are synthesised entirely from carbon dioxide and water, which are abundant and do not require scarcer nutrients such as nitrogen. The variety of substances is not readily explained. Some might be regarded simply as biosynthetic intermediates which remain in the tissue at low concentration. The best general explanation for secondary products is probably the so-called screening hypothesis of Firn and Jones[29]. The basic idea behind the screening hypothesis is that potent biological activity is a rare property for any one molecule. The plant cannot predict, of course, the nature of a substance which would be toxic for a new predator, so that from an evolutionary point of view it becomes economical for the plant to maintain a variety of substances which might be ‘screened’ for a new specific activity. This is not an entirely adequate explanation with regard to the polyphenols, however, especially in the case of the tea plant.

The two general properties of polyphenols which are relevant is that they tend to be astringent and bitter rather than specifically toxic, and both properties may reduce the palatability and digestibility, and hence nutritional value, of the plant material. Astringency is a property of plant tannins, and is the result of the combination in the same molecule of hydrophobicity from the aromatic rings, and multiple hydrogen bonding sites from the hydroxyl groups. The effect in the mouth is particularly associated with the cross-linking of proline-rich proteins in the saliva[30]. For tannins to be effective as protein precipitants they need to be present at high concentration, as is true for tea leaves, and to be of appropriate molecular size. Thus, although plant tannins are generally polyphenols, not all polyphenols are effective tannins. The best tannins have molecular weights in the range 500 to 3000. Catechins are the major components of tea polyphenols, and only the two gallate esters come close to the 500 mark. There is a significant concentration of proanthocyanidins, however, which are essentially catechin dimers or oligomers[31]. The role of these compounds in tea chemistry has not received as much attention as it should. It may also be significant that chewing of a tea leaf destroys cell structure and allows the polyphenol oxidase to act on the catechins. This is exactly what happens during the manufacture of black tea, so the same products would be formed, predominantly theaflavins and thearubigins. Furthermore, the intermediates of enzymic oxidation are quinones, which are highly reactive in a fairly non-specific manner. Theaflavins, being formed from two catechin molecules, are particularly good tannins. Black tea manufacture is thus taking advantage of a natural defence mechanism of the tea plant.

Curiously, the most potent compounds present in the tea leaf that affect astringency, or perhaps what a tea taster would describe as pungency, are a series of flavonol glycosides, especially quercitin rhamnoglucoside, rather than the catechins[32]. However, these two groups of compound affect the mouthfeel of a liquor in different ways. The flavonol glycosides have a velvety mouthdrying effect whereas the catechins cause a puckering, rough tasting type of astringency. Possibly this is an indication that only the catechins interact with the oral mucosa, whereas the flavonol glycosides interact predominantly with the salivary proteins. An important function in leaves of high concentrations of polyphenols is often suggested to be screening against UVB, in which case they are expected to occur predominantly in the epidermal cells. In tea leaves, however, they are concentrated in the vacuoles of mesophyll cells with little or none in the epidermis[33]. On the other hand, one would expect young tea shoots to be an attractive source of food for herbivores if it were not for the fact that they would find it difficult to avoid ingesting a rich batch of catechins, proanthocyanidins and other flavonoids. Nevertheless, the effects of these substances are not absolute and tea plants are subject to attack by a number of insects and arachnoids which have presumably developed some degree of tolerance, the most successful probably being the red spider mite.

Caffeine, the major purine alkaloid of tea, has a bitter taste, which is enhanced by the presence of catechins and flavonol glycosides, so one can expect it to be a feeding deterrent. It readily crosses the blood-brain barrier and has various effects on the central nervous system. The modest amounts found in a cup of tea have a pleasant stimulating effect for most humans, as long as they want to stay awake, although a few people find it makes them hyperactive and it can have other unpleasant physiological effects. A massive dose (say 10 g) would probably be fatal. For insects and some other invertebrates, however, it is an effective neurotoxin at the concentrations found in tea leaves[34]. Spiders lose the ability to spin a proper web[35], and it is lethal for slugs and snails[36]. It has also been shown to be toxic for fungi. In Ceylon, for example, the shot-hole-borer beetle is a pest which seriously weakens tea bushes; the beetle depends on a symbiotic, wood-rotting fungus which provides the food (‘ambrosia’) for the developing larvae, and caffeine in the stems provides an important means by which the plant attempts to control growth of the fungus[37]. Among the multifarious effects of caffeine one should also include allelopathy and autotoxicity, as it inhibits the growth of seedlings, whether or not of the same species[38]. Thus leaf litter around a tea bush tends to restrict growth of competing plants in its immediate vicinity. Similarly caffeine in the coats of tea seeds is released into the soil and inhibits germination of other seeds[39]. The mechanism of this inhibition has not been established.

The genus *Camellia* is the largest in the family Theaceae. This is consistent with the very varied ecological conditions in S.W. China. The final question we would like to be able to answer regarding the evolutionary history of the tea plant is what were the selective pressures that led to its distinctive chemical features. We have looked for clues from the responses to present-day pests and diseases of tea, which have partially overcome the defences of the plant. Primitive forms of these organisms, perhaps, provided the driving force for the success of certain mutant forms of a near ancestor of the tea plant. We have seen that the distinctive features of *Camellia sinensis* are a high concentration of catechins and proanthocyanidins, the presence of gallocatechins and catechin gallates, which are necessary for the oxidative formation of theaflavins, and of caffeine. One should also mention theanine as the dominant free amino acid, but although it affects the taste of tea infusions, it is not known to play any significant role in defence. Of other members of the genus, very few come near to the constitution of *C. sinensis*, and all of them occur in section Thea along with *C. sinensis*[5]. The geographical distributions are also similar. Flexibility in defence may be enhanced by the fact that the gene for caffeine synthase is found more widely than caffeine itself[40]. Whether this is true for catechins is not known. This battery of defences seems to have acted as a significant deterrent to all but a few potential herbivores and pathogens. The organism that perhaps comes closest to overcoming these defences is probably the blister blight fungus (*Exobasidium vexans*). This is highly successful in attacking younger leaves of the tea plant, and a Ceylon-type disaster is only avoided because it seems incapable of attacking mature leaves. It would be of considerable interest to know how the fungus is able to feed successfully on the contents of leaf cells without ill effect.

The final chapter in the history of the tea plant is cultural rather than evolutionary. Written records cover approximately the last two millenia and the earliest reference to what is indubitably tea is dated 59 BC. There was probably a gradual process in which tea was used first as a medicine, then more as a tonic, and eventually became the beverage as we now know it. This occurred first in Sichuan, and from there tea drinking and tea cultivation spread to the East and North. Tea as a beverage was resisted for several centuries in the North, except within the Imperial court and amongst Buddhist and Taoist monks, but by the time of Lu Yu, who published his famous Tea Classic in 760 AD it had become a more widely popular drink. It was not until about that time that the word cha, and its associated character, became firmly established. The outline of the story taking us up to the present day, is well known. The earliest human use of tea, however, is legendary, and takes us back into prehistory which for now is largely speculative. Humans are likely to have been interacting with the tea plant in one way or another for millenia before the time of Shen Nong. What role have they played in selecting the properties of the tea plants we now cultivate?

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