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THE INFLUENCE OF A BAMBOO DIET ON THE EVOLUTIONARY ADAPTATIONS OF THE GIANT PANDA

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PROJECT TITLE: The Influence of a Bamboo Diet on the Evolutionary Adaptations of the Giant Panda

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The giant panda (*Ailuropoda melanoleuca*) of China is, anatomically, a carnivore trying to get by on an herbivorous diet (Dolnick, 1989). While it is a member of the order Carnivora, it is almost entirely herbivorous and lives "on bamboo to the exclusion of all other feedstuffs" (Dierenfeld, 1982). The giant panda has survived on a bamboo diet for millions of years and throughout its history has evolved numerous adaptations as a result of its unique diet. **This study examines these adaptations in an attempt to understand and uncover the influence diet has had on the evolution of the giant panda.**

ULTIMATE VS. PROXIMATE PERSPECTIVES

Biological phenomena can be approached from two basic perspectives: ultimate and proximate. They have also been called the "evolutionary" (why) and "functional" (how) explanations, respectively. Physiologists generally take the "proximate" position and answer questions concerning the *mechanism* by which behavior is influenced by *immediate environmental* factors. An evolutionist tends to answer questions with an "ultimate" perspective and in terms of what *strategy* is involved within a response to a *long-term* consistent pattern of environmental change (Pianka, 1988).

Neither completely tells the whole story and if a biological question is to be completely answered both must be considered. Often, however, only the "proximate" perspective can be examined by direct experiment and as a result, this investigation mainly looks at the evolutionary effects of a specified diet.

Evolution, in general, refers to any type of temporal change. These changes result from various mechanisms, the most prominent one being natural selection. This specific evolutionary process is so primary because it "results in conformity between organisms and their environments, or adaptations" (Pianka, 1988). The basic idea behind natural selection is that whenever one organism leaves more successful offspring than another, in time its genes will come to dominate the population gene pool. Thus, each time a panda produces offspring with characteristics beneficial to the processing of bamboo, the primary component of its specialized diet, the more likely these offspring are to survive and pass on these same beneficial characteristics.

The adaptations examined within this study can be broken down into the two categories: anatomical and behavioral. The anatomical adaptations can be further divided into various regions: head, forepaw and digestive tract. The adaptations of the head, forepaw and digestive tract are viewed from the ultimate perspective. A possible explanation for the known digestive (physiological) adaptations, however, will be examined proximately through the testing of the feedstuffs for a possible poison, cyanide. The numerous behavioral adaptations are considered only from the evolutionary perspective.

HISTORY

The panda's earliest ancestors can be traced back at least 60 million years to when the first carnivorous mammals appeared on the planet. These small creatures, called Miacids, branched out to produce the cats, dogs, bears, and other modern carnivores (Schaller, 1985) (**see Figure 1**). After much genetic research the ancestry of the giant panda was finally determined. In 1985, Stephen O'Brien and coworkers used the "technique of gel electrophoresis [using an electric field to separate different sized or different charged proteins] to compare 43 proteins from pandas, brown bears, spectacled bears, Asiatic black bears and racoons" (Catton, 1990). The results concluded that the giant panda actually split from the bears about twenty million years ago. Additionally, they determined that the red panda (a coinhabitant and fellow bamboo-feeder) split from the racoons "shortly after the bears and racoons separated" (Catton, 1990) (**see Figure 2**).

These results were confirmed by additional studies involving DNA-DNA hybridization and a comparison of chromosome number. DNA-DNA hybridization concerns the comparison of the finer details contained in the structure of DNA which takes into account different DNA sequences that result in the same protein and those sequences that do not even code for proteins (Catton, 1990). The chromosome comparison first seemed to reveal that the giant panda, having 42 chromosomes, was more similar to the red panda with 36 chromosomes than the average bear with 74 chromosomes. With further examination, however, it was determined that the giant panda's chromosomes were "bear chromosomes fused together" (Catton, 1990).

For many years taxonomists believed that the red panda and the giant panda were closely related because of the similarities found in their masticatory apparatus, their forepaws, their digestive tract and their behaviors. Both pandas have enlarged jaws containing broad, highly-cusped molars. They both show a lengthening in their radial sesamoid (wrist bone) and a short intestinal tract with no caecum. Additionally, the lesser and the giant panda share the unique feeding behavior of eating, almost exclusively, bamboo. This last shared characteristic is where the mix up in taxonomy occurs. The two pandas appear to be closely related because they have evolved convergently. These two animals have occupied similar habitats and been exposed to the same ecological pressures for so long, that they have evolved similar characteristics even though they are not that closely related (MacClintock, 1988).

Fossils of animals with the same anatomical structure of the modern giant panda have been found dating back two to three million years ago, during the Early Pleistocene. "These [animals] were about half the size of the present day pandas, and have been classified as a separate and now extinct species, *Ailuropoda microta*" (Catton, 1990). Little is known about the range or habits of this creature, but judging by tooth structure of these early fossils, these "pandas" had already specialized for subsisting on bamboo at the beginning of the Pleistocene (Catton, 1990).

By the mid-Pleistocene, "animals indistinguishable from modern giant pandas were widespread" (Catton, 1990). Fossil finds show that the panda used to range as far north as Hebei, as far south as Vietnam and from Anhui Province in the east to Burma in the west (Tyson, 1990) (**see Figure 3**). The population, undoubtedly, rose and fell throughout the Pleistocene, but the fossil records show the final decline began about 10,000-20,000 years ago. The drop in population has been most dramatic in the last 2,000 years, as the result of human disturbance and habitat destruction (Catton, 1990).

PRESENT SITUATION

"The giant panda survives only along the mountainous eastern edge of the Tibetan plateau, confined to an area totaling about 29,500 km^2 mainly in China's Sichuan province, but also southern Gansu and Shaanxi provinces" (Gittleman, 1989). Their habitat is made up of 14 natural preserves, the first one established in 1963 (Williams, 1990) (**see Figure 4**). Within each protected area, pandas are found only in suitable habitat. The pandas' altitude limit corresponds to the elevation limit of bamboo which is about 3200-3500 meters. On the lower end, pandas rarely go down below 1200-1300 meters for this area has been developed and cultivated by nearby human communities. The resulting 1000-2000 meter-wide strips of bamboo forest make up the habitat of isolated panda populations (Schaller, 1985).

The establishment of these reserves has been quite beneficial for the pandas, however, deforestation still occurs--mainly by farmers clearing land to make way for fields higher into the mountainside. It is because of the importance of producing large quantities of food and the inability to enforce laws on such an immense population that this deforestation has continued. As a result, the surviving panda population has become fragmented into panda "islands" (Schaller, 1985). These islands are patches of forest separated by cleared land. The populations within these islands, ranging from fewer than ten to more than 50 pandas, have become isolated because the animals are reluctant to cross open areas. Even creating just one road through panda habitat "may be enough to split a population in two" (Williams, 1990). The small populations have too few animals to be viable and will, inevitably, die out. The larger populations may be fine in the short term, but are quite vulnerable to genetic defects resulting from inbreeding (Williams, 1990).

"In evolution, as in television, it's not necessary to be good. You just have to be better than the competition.

And, until rather recently, the panda had none" (Dolnick, 1989). With the introduction of humankind, panda populations have been dramatically reduced leaving approximately 900-1000 pandas left in the wild (60% live within the natural reserves) and a few dozen can be found in various zoos around the world (Schaller, 1985).

Over ninety-nine percent of the giant panda's diet consists of bamboo (Schaller, 1985). Daily, it ingests about 20 kilograms of this plant diet. While it is not definitely known why the pandas feed on bamboo, proposed explanations generally involve bamboo's availability, as it provides an abundant year-round supply of food. Pandas can eat up to 28 different species of bamboo that grow in their natural habitat (**see Figure 5**), although, the most important are umbrella bamboo (*Fargesia robusta*) and arrow bamboo (*Sinarundinaria fangiana*) (Catton, 1990). *F. robusta* is also known as *Fargesia spathacea* and *S. fangiana* has also been called *Bashania fangiana*. The taxonomy of bamboo is quite difficult and is constantly under reconstruction (Thomas, 1992). In order to classify a bamboo species, some taxonomists have used such differences as the time intervals between flowering, distinct features of the flowers themselves, and the length and thickness of the sheaths covering the emerging shoots. Classification may even involve "close work with a hand-lens to recognize many of the finer points of differentiation" (Thomas, 1992).

ADAPTATIONS

Subsisting primarily on bamboo for some two million years, the panda has evolved numerous specializations for processing this plant efficiently. The anatomical description of bamboo and the different parts of the plant eaten by the panda will be considered followed by the anatomical adaptations for consumption efficiency. Second, the bamboo's cyanogenic capabilities will be examined and the possible influence this toxin may have had on the panda's digestive anatomy and physiology. Third, the reproductive cycle of the bamboo will be addressed and some consequential migration behavior. Finally, the nutritional aspects of bamboo and its abundance will be looked at, as well as the resulting reduction in behavior and conservation of energy.

BAMBOO DESCRIPTION AND ANATOMY

Bamboo belongs to the tribe *Bambusa* within the *Gramineae* (grass) family. The culms (stems) are hollow or rarely solid and are composed of distinctive nodes and internodes.

The upper segment of the plant is where most branching occurs. Underground stems, called rhizomes, develop and may spread horizontally for significant distances from the parent plant. The rhizomes, like the culms, contain nodes and internodes. Each node may bear a hard bud that is appressed to the side of the rhizome. At the beginning of the growing season, the buds on the rhizome begin to enlarge. The ensuing rapid growth and elongation is referred to as "shooting" (Austin, 1970) (**see Figure 6**). A coriaceous sheath covers the emerging shoot that attains maximum diameter soon after surfacing, and reaches full height in six to eight weeks. At a height of about 20 to 25 inches, the shoots are soft and edible. Rhizomes start from new culms when photosynthesized food reserves are sufficient (usually in May or June) to support growth (Schaller, 1985).

Because of its structure, bamboo is one of the strongest plants known to humans. The culms of this plant have, for centuries, been used as construction scaffolding, tools, walls of homes, fishing poles, baskets, etc. because of its incredible strength. Even the leaves are quite hardy and leathery making the consumption of this plant quite difficult.

ADAPTATIONS OF THE HEAD AND FOREPAW (INCLUDING ESOPHAGUS AND MUCUS PRODUCTION)

In general, leaves, branches, culms and shoots provide food for pandas, whereas rhizomes are not pulled or dug up. In order to take in adequate amounts of food efficiently and consuming as little energy as possible (this topic of conservation of energy will be thoroughly discussed later on within the paper), the panda has evolved both a modified masticatory apparatus and a sixth digit or opposable thumb. In order to protect itself from the rough, spiky bitten off chunks of bamboo the panda has evolved safeguarding features of the early organs of the digestive system (Davis, 1964).

The "breadth and depth of skull [and corresponding musculature] are increased in all herbivorous carnivores, and [they] reach a maximum" in the giant panda (Davis, 1964). The massive zygomatic arches are spread widely and the sagittal crest is prominent, serving as a place of attachment for powerful jaw muscles (**Figure 7**). These muscles show a "selective increase in mass, involving only those elements that produce the forces involved in pressure and grinding movements" (Davis, 1964). These enlargements of both muscle and bone, in addition to the increased density of the bone, "greatly improves efficiency for production of pressure at the level of the cheek teeth"

(Davis, 1964). With greater pressure, the panda is better able to crush the, sometimes, unyielding bamboo.

The typically carnivorous dentition has been greatly modified resulting in broad, flat molars with complex crown patterns. The posterior premolars are heavily cusped and superficially resemble that of ungulates (**see Figures 8 and 9**). The combination of a powerful bite and efficient crushing surfaces enables effective mastication even of such coarse material as bamboo (Schaller, 1985). Ironically, even with such helpful adaptations, the enlarged masticatory apparatus is used mostly for biting the culms off (sometimes 2 or 3 stems simultaneously), and not for thorough chewing. A panda chews each mouthful a relatively low average of 6.7 ± 2.3 times (Schaller, 1985).

The addition of the sixth digit or "thumb" is actually a result of the enlargement and elongation of the radial sesamoid (wrist bone) until it almost equals the metapodial bones of the true digits. The radial sesamoid underlies a pad on the panda's forepaw which is separate from the palmar, a second pad formed from the framework of the five other digits. A small furrow between the two pads "serves as a channel way for bamboo stalks" (Gould, 1980). The "thumb's" agility is maintained through an extensive rearrangement of musculature. The abductor of the radial sesamoid pulls the bone away from the true digits. Two shorter muscles run between the radial sesamoid and pollex and pull the "thumb" towards the true digits (**see Figures 10 and 11**). The end result is the remodeling of characteristic anatomy and, thus, the creation of a new, functional digit (Gould, 1980).

These specializations of the forepaw and the masticatory apparatus allow the giant panda to be a highly selective eater with particular behaviors for acquisition of various parts of the bamboo. When shoots and stems are eaten, they are selected, "hooked" with the forepaw, bent sideways and bitten off. The panda then manipulates the stem pushing it into the side of its mouth at right angles and takes a few quick bites from it. "While biting, the animal jerks the forepaw holding the stem up and down and lifts its head slightly" (Schaller, 1985). When eating the tough outside of a stem, the panda uses its incisors and premolars to "tear off strips by simultaneously twisting paw and head in opposite directions" (Schaller, 1985). Leaves are not arduously selected, like the shoots and stems, but are bitten off and eaten by the mouthful. Many times a panda will maneuver the bamboo stem through its mouth stripping the leaves so that they all gather in the corner of its mouth. The foliage can then be quickly chewed and swallowed (Schaller, 1985).

The esophagus of the giant panda, in order to cope with swallowing the rough and coarse pieces of bamboo, has a leathery and horny lining. This lining also shields the esophagus from the large, spiky chunks of bamboo that the panda fails to sufficiently chew (Davis, 1964).

Many of the epithelial cells that line the stomach of all animals are specialized for the secretion of mucus. This mucus lubricates the stomach wall and facilitates the movement of food within the stomach and protects the stomach wall from serious abrasion by the food. Again, because of its diet's coarseness, the panda has evolved "plentiful mucous glands [and] thicker muscularis mucosae [lining of the stomach]" (Wang, 1989).

CYANOGENIC CAPABILITY OF BAMBOO

"Cyanogenesis, the ability...to release hydrogen cyanide (HCN)," can be found extensively throughout the plant kingdom (Poulton, 1988). While animals require small quantities of cyanide for primary metabolism, any significant increase could be fatal. With such a risk involved, why do plants produce this possible poison? Plausible explanations for this cyanogenic ability include: (1) elimination of waste products, (2) nitrogen store, and (3) defense (Montgomery, 1980). This study is looking solely at the defensive function of bamboo's cyanogenic capabilities.

In 1941, K.N. Bagchi and H.D. Ganguli discovered that "by simply soaking the mashed pulp of tips of bamboo shoots in plain water for about 2 hours and then acidifying and distilling it...varying amounts of HCN where obtained from bamboo shoots of different sizes and species." The quantity of HCN also differs between different parts of the bamboo plant. The tip of the growing point of the shoot was found to yield the maximum amount of HCN, while the base, culms, branches, and leaves yielded much less. The highest reported figures of cyanide yield in bamboo is 800 mg HCN per 100 gm of the tip of the immature shoot and 300 mg HCN per 100 gm of immature stem of bamboo (Bagchi and Ganguli, 1943). The shoot probably contains the highest cyanogenic ability for this location, when attacked by a herbivore, "would have the greatest effect on the plant's fitness" (McKey, 1974).

The source of cyanide is generally found to be cyanogenic glucosides. Free hydrocyanic acid can be liberated from the plant during the hydrolysis of a specific cyanogenic glucoside (Montgomery, 1980). Bagchi and Ganguli, in 1943, isolated bamboo's cyanogenic glucoside and found it to be (s)-dhurrin (**see Figure 12**). Dhurrin "is a β-glucoside, which is poorly soluble in water." As a result of this characteristic, this molecule is "well-suited for the storage of noxious substances such as cyanide" (Montgomery 1980). Over 75 cyanogenic glucosides have been discovered and documented, each one being a O-β-glucosidic derivative of α-hydroxynitriles (Bagchi and Ganguli, 1943).

The enzymatic hydrolysis of dhurrin begins with this cyanogenic glucoside coming into contact with the β-glucosidase(s). These enzymes show a great degree of specificity for the particular glucosidic compound with which they occur. "Catabolism of a cyanogenic glucoside is initiated by cleavage of the carbohydrate moiety by one or more β-glucosidases, yielding the corresponding α-hydroxynitrile" (Poulton, 1988) (**see Figure 13**). The next step will occur either spontaneously or requires the addition of a α-hydroxynitrile lyase to the α-hydroxynitrile intermediate to form HCN and an aldehyde or ketone. In general, unlike the β-glucosidase(s), the "substrate specificity of plant hydroxynitrile lyases has not been extensively studied" (Poulton, 1988). There seems to exist some specificity of the hydroxynitrile lyase with the hydroxynitrile, but more studies are needed.

In order for hydrolysis to occur the plant material must be physically damaged. The glucoside and its catabolic enzymes are thought to be compartmentalized within different tissues of the plant: dhurrin within the vacuoles of epidermal cells and the enzymes within the underlying mesophyll cells (Poulton, 1988). The β-glucosidase was found in the chloroplasts while the hydroxynitrile lyase was found in the cytosol. From these findings Poulton claims "that the large-scale hydrolysis of dhurrin, which probably provides a defense mechanism against herbivores by liberating HCN, occurs only after tissue disruption allows the mixing of contents of different tissues" (Poulton, 1988). This separation of reactants needed to form cyanide results from the fact that "defense chemicals must be inactive in the plant and yet exhibit chemical activity in the presence of herbivores (McKey, 1974).

For some time, cyanide has been quite well-known among other "metabolic poisons." Generally, hydrogen cyanide is very rapidly absorbed through the upper gastrointestinal tract but it can also be introduced into the body through the lungs and sometimes skin (Montgomery, 1980). The primary effect associated with chronic cyanide is the inhibition of respiration. Cyanide binds to and inactivates "cytochrome oxidase, the terminal component of the mitochondrial electron chain." This termination of cellular respiration causes cytotoxic anoxia (Solomonson, 1981). For a mouse, the oral lethal dose of HCN is 3.7 mg/kg body weight; dog, 4.0 mg/kg; cat, 2.0 mg/kg; rat, 10 mg/kg; sheep, 2.0 mg/kg (Seigler, 1989). Taking these numbers, an average lethal dosage would be 4.3 mg/kg body weight.

Generally, all the individual plants within a species are either cyanogenic or acyanogenic. Therefore, while some bamboo plants have been found to possess the ability to produce cyanide, that doesn't mean that all of them do. To determine if cyanide has had any possible evolutionary influence on the panda's digestive anatomy, the particular species of bamboo digested by the pandas must be tested for cyanide. This testing was done with two bamboo species known to be eaten by the giant panda, *Sinarundinaria fangiana* and *Fargesia denudata*. The samples obtained from the Chongqing Zoo and the Chengdu Zoo were divided into four categories: *Sinarundinaria* leaves, *Sinarundinaria* branches, *Fargesia* leaves and *Fargesia* branches. A description of the testing procedure followed can be found in Appendix A.

The results obtained confirmed the presence of cyanide in both the branches and leaves of both species, but in extremely low quantities. The leaves of both *Fargesia* and *Sinarundinaria* had higher CN concentrations than did the branches, while the leaves and branches of *Sinarundinaria* had higher concentrations than did their *Fargesia* counterparts. The highest amount of CN concentration was found in the leaves of *Sinarundinaria* and was 26 μg/g dry weight or .26 mg HCN per 100 g fresh weight. This measurement could be a low estimate, resulting from two possibilities. The first being that the bamboo samples obtained from the Chinese zoos were not very fresh. If the zookeepers had to bring the feed in from a far distance, the time it took to transport the plant could result in a decrease in the amount of CN released. Second, the method used to cleave the plant may not have been adequate enough to fully disrupt the plant's tissue, allowing the cyanogenic glucoside and the corresponding enzymes to mix.

As mentioned before, Bagchi and Ganguli obtained a concentration of 300 mg HCN per 100 g of immature stem of bamboo (1943). Even if this studies results were on the low side, a comparison of the two studies shows not all bamboo species possess similar cyanogenic capabilities.

DIGESTIVE SYSTEM ADAPTATIONS

While the panda has had ample time in which to evolve a more efficient gastro-intestinal tract for its bamboo diet, this animal, remarkably, still possesses a very simple, carnivore-like digestive system. The panda's digestive tract contains quite a few unique adaptations (resulting from its diet) concerning: esophagus, mucus secretions, stomach, caecum, microorganisms, retention time, short intestine and pH. Combined, these adaptations form the digestive system of a herbivorous carnivore.

Herbivores, those animals confined to a diet high in plant fiber and low in readily available nutrients, tend to possess a digestive tract capable of processing large volumes of food for long periods of time. These plant eaters, also, are well-known for the microorganisms they possess within their guts allowing for the conversion of "plant material [cell wall] of little direct nutritional value [quality] into readily utilizable nutrients" (Stevens, 1988). Most herbivores "assimilate about 80% of their food, including 40-60% or more of the cellulose and hemicelluloses" (Schaller, 1985). The panda, being a herbivorous carnivore, is confined to a high fiber, low nutrient diet and does process large volumes of food, however, it does not retain the food for very long, nor does it maintain any symbiotic relationship with gut microorganisms. As a result, the panda assimilates only about 17% of its total intake (Schaller, 1985).

This extremely low intake can easily be seen when examining panda droppings. The panda will eat bamboo until its stomach is full. At this point the animal rests or naps and when it arises, wanders off to start feeding again leaving behind up to 40 packages of dung. The dropping are "a mass of bamboo splinters, so poorly chewed that the length of splinters gives a good idea of the 'bite-size'" (Catton, 1990).

The amount of bamboo eaten by a giant panda in the wild varies, depending on what part of the plant is being eaten. When eating stems and leaves of *Sinarundinaria*, the panda consumes, on average, about 14.0 kg per day (Schaller, 1985). When feeding on new shoots of *Fargesia*, the panda can eat about 38.3 kg per day (Schaller, 1985). This large difference may be a result of the low retention time given to new shoots passing through the digestive tract.

When taking the cyanogenic capability of the two species found in my study, the amount of possible cyanide contained in the quantity of stems and leaves of *Sinarundinaria* consumed by the panda is approximately 36.4 mg. As mentioned before, an average lethal dosage of cyanide would be 4.3 mg/kg body weight. Since an average panda weighs about 100 kg (Schaller, 1985), the lethal dosage would be approximately 430 mg. Therefore, it appears that the leaves and branches of the bamboo I tested do not have lethal cyanogenic capabilities. Samples of the new shoots of *Fargesia* could not be obtained and therefore the concentration of cyanide within the new shoots is not known. If the results from Bagchi and Ganguli (1943) study on a different species of bamboo were used, the amount of possible cyanide contained in the quantity of new shoots of *Balcooa* consumed by the panda is approximately 364,800 mg.

While the panda most likely does not feed on this species of bamboo, it is likely that the cyanogenic ability of the new shoots of bamboo the panda does consume, also possesses high levels of cyanide.

"The digestive tract is one of the most readily accessible routes for substances to enter the body. Thus, it requires reasonably fail-safe mechanisms for the careful selection of the substances that will be allowed entry" (Stevens, 1988). In order to understand why the panda has failed to evolve the seemingly beneficial adaptations associated with herbivores, the cyanogenic capabilities of bamboo must be considered. Except for certain changes (esophagus and mucus production--mentioned earlier) that help in the consumption of such a course material, many of the alterations can be associated with bamboo's cyanide production.

In order to regulate or control the amount of a specific toxin in an animal's body, the animal can either develop a means of removal of the poison, or not allow it to form at all. For most animals, the primary mechanism of cyanide detoxification involves the conversion of cyanide to thiocyanate (Montgomery, 1980). "This process requires the enzyme rhodanese, which is present in most animal tissues, plus amino acids such as methionine or cysteine to convert cyanide to thiocyanate" (Seigler, 1989). Bamboo, however, contains very low levels of these sulfur-containing amino acids. In fact, methionine was found in the least quantities of all amino acids making it the limiting amino acid (Schaller, 1985). Thus, this detoxification method appears unlikely. Additionally, the physical location requirements of cyanide production (the intercellular separation of the reactants), make it seem likely that the panda evolved certain digestive adaptations that do not allow for the formation of cyanide within the body, as opposed to evolving methods to remove this poison.

The stomach of the giant panda is quite simple. There exists only one compartment; unlike that of a herbivore's stomach with compartmentalization of the foregut, modification of the hindgut, or even an enlarged caecum (as seen in the horse). **See Figures 14, 15 and 16.** This feature allows for a rapid movement of food through the digestive system. Without time to thoroughly digest the bamboo, the intercellular components will not have as ample an opportunity to come into contact (as they would in an herbivore-like digestive tract), thus the prevention of cyanide formation. Additionally, the section of the giant panda's gut immediately following the stomach has also been shorten, further enhancing the speed with which the food passes through the gut (Davis, 1964).

The giant panda possess no caecum; a feature which provides an additional site for digesta retention. Like the argument above, the less opportunity for fermentation, the lower the probability of cyanide production.

The digestive tract of the panda is not colonized by gastrointestinal microorganisms. Microbial fermentation is capable of breaking down the cell wall, obtaining nutrients from cellulose and hemicellulose, and synthesizing proteins--a very advantageous feature for a herbivore. While this ability would greatly enhance the panda's digestive capabilities (for mammalian enzymes do not affect cellulose), the panda has not evolved such a mechanism. This lack of adaptations makes sense, however, when considering the fact that "microbial action in the rumen can further release free cyanide" (Fraser, 1991). Without gut microorganisms there is a reduced amount of cellular disruption preventing the production of cyanide.

The small intestine of the panda is quite unique compared to a typical plant eater.

> The intestine is typically elongated in herbivorous mammals, but there are many exceptions to this rule. The exceptions can be only partly explained by large caeca, expanded intestinal diameter, [etc]...Secondary reduction of intestinal length in connection with secondary herbivory, such as must have taken place in *Ailuropoda*...is something else. (Davis, 1964)

The small intestine of the panda is a great deal shorter than the intestine of the average herbivore. "A deer's intestines...are 15 times longer than its body; a sheep's 25 time longer. But the panda, like the majority of carnivores, has intestines that are only 6 times its body length" (Dolnick, 1989). This is yet another feature of the giant panda's g.i. tract that reduces food retention time.

While a short retention time is advantageous for the panda because it allows for a greater intake of food, this increased rate of passage and degradation of substances can also prevent any toxins access to the more permeable intestinal tract. With a rate of passage averaging about 8 ± 3 hours (compared to 20 hours for an ungulate) it would appear that any toxin, including cyanide, would not have the time needed to significantly effect the giant panda (Dierenfeld, 1982). This argument is especially true for the new shoots of *Fargesia* which, seasonally, the panda eats as an exclusive food. These shoots can pass through the panda's digestive tract in as little as 5.1 hours (Schaller, 1985).

When Schaller (1985) examined digested bamboo microscopically he found that the bamboo had a "characteristic appearance: the tough, outer tissue of cellulose and lignin, though crushed and broken, remains relatively intact, whereas the parenchymal cells and other thin-walled cells have been digested, leaving gaps in the tissue." **See figure 17.** Parenchymal cells usually form a plant's ground tissue including the mesophyll of the leaf (Culter, 1978)--the location of the enzymes needed for cyanogenesis. The outer tissue of cellulose and lignin is made up of epidermal cells (Culter, 1978)--the location of dhurrin, the cyanogenic glucoside. Therefore, the enzymes are digested, while of the cyanogenic glucoside is trapped in the unused, undigested cellulose and lignin. The two reactants are not allowed to come in contact with each other preventing any possible cyanogenesis.

By maintaining a low pH, typical of a carnivorous digestive tract, the release of possible cyanide, from glucodises, would be inhibited. "For humans and other monogastric animals, acidic stomach conditions prevent the formation of cyanide" (Seigler, 1989). The panda must maintain an acidity that is low enough to prevent possible cyanide formation and high enough so as not to destroy the lining of the stomach. Mucus can protects the walls of the stomach from its own acidic gastric fluid [pH 1.5-3] (Teather, 1980). The action of the acidic fluid disintegrates the food into molecular fragments and thus is an essential prelude to digestion. The acid itself does not carry out any further digestive activity. It has a very limited ability.

BAMBOO REPRODUCTIVE CYCLE

A well-known aspect of bamboo is its lengthy reproductive cycle. For most of its life, bamboo produces new shoots asexually underground rhizomes (**see Figure 18**). There are two main types of growth: monopodial and sympodial. "In the monopodial type the rhizome travels very far...[sometimes] over a hundred yards underground," (Austin, 1970) resulting in single, free standing culms. This bamboo type continues to grow throughout the year, "periods of rhizome growth alternating with those in which new sprouts and culms develop" (Austin, 1970). The sympodial type, also known as clump bamboo, puts forth an underground shoot, but this is connected directly to the parent and the link is short (**see**

figure 19). Sympodial bamboo is more common for this type the rhizomes and culm have become one, so that the bamboo can accomplish all its growth during the rainy season of its tropical location (Austin, 1970).

After many years of either growth pattern, vast areas of land "may consequently be covered by genetically identical clones of a single plant" (Shipman, 1990). At a given time, depending on the species, almost all the plants of that variety enter into a sexual phase in which they mass-flower, produce seeds and die (Johnson, 1988). The interval between sexual phases within the life of a particular species remains constant, but varies among different species being as little as 12 months or as much as 120 years. Most species have an interval of 10-15 years (*Biotech Bamboozles Bamboo Blossoms,* 1990). With the sexual phase complete, all that is left to recolonize the forest is the sprouting seedlings (Shipman, 1990). "Seeds of the arrow bamboo [*S. fangiana*] remain dormant in the soil for at least two years" (Catton, 1990) while other seeds can remain in the soil for as long as five years. After germination, the new seedlings grow quite slowly "taking 15 years or more to reach maturity" (Catton, 1990).

This synchronized mass seeding may have evolved to permit the bamboo "to stay one step ahead" of its predators. Ideally, the bamboo grows in number asexually for numerous years allowing the panda to reproduce, however slowly, to build up their population. At this point, the bamboo abruptly flowers (which may continue for 4 or more years) and dies off leaving the large population to starve. While this process may have evolved for the purpose of ridding itself of predators, it never quite worked with the giant panda, until now (Shipman, 1990).

EFFECT ON PANDA MIGRATORY BEHAVIOR

Previously, the flowering and subsequent die-off of the bamboo wasn't a threat to giant pandas. Their populations were never large enough, in comparison to the amount of bamboo, to create a period of serious competition between individuals. There was simply always enough food to go around. When a bamboo die-off did occur, the panda merely moved on to a new location with more bamboo. In precisely this way, the panda has survived for millions of years. The resulting migration that occurred actually benefited the pandas by preventing inbreeding in otherwise sedentary populations; a prime example of coevolution between the panda and bamboo (Williams, 1990).

Presently, however, the panda populations within islands dominated by only a few bamboo species have nowhere to turn (Dolnick, 1989). One bamboo flowering could prove catastrophic because the panda populations are unable to emigrate (Williams, 1990). An example of this devastation occurred during the mid-1970's when at least three species of bamboo flowered and died in synchrony in China's Min Mountains; over 100 pandas perished (Johnson, 1988).

Inbreeding within giant panda groups already exist and its effects can be seen in the panda's vulnerability to various diseases. "Roundworms, intestinal obstructions, intestinal bleeding and liver illnesses are but a few most common ailments that threaten their lives" (Yi and Shuo, 1993) Inbreeding is considered the primary factor influencing the panda's "physical weaknesses and its slow adaptation to the changing environment" (Yi and Shuo, 1993).

BAMBOO NUTRITION AND ABUNDANCE

There exist two primary characteristics of bamboo which maintain the most influence on the behavior and evolution of the giant panda; its low nutritional quality and its high abundance. In general, like most plants, bamboo contains no cholesterol, is low in unsaturated fats and is high in fiber

(Whitney and Rolfes, 1993). These characteristics are exactly the opposite of those found in animal body products--the diet of giant panda's great carnivorous ancestors. The nutritive quality of different parts and species of bamboo makes it easy to understand: (1) why pandas select the food that they do--be it certain parts or certain species during certain times of the year and (2) how much energy the panda has for additional behaviors beyond basal metabolism.

No other food source in western China's mountains is more plentiful and available all year round, even in the snowy winters, than bamboo. Except after a die-off, bamboo is always close at hand for it is not only plentiful in areas but the groves are very dense, with up to 80 culms the thickness of a person's finger growing in a square meter of bamboo forest (Roots, 1989).

As for resource competitors, the giant panda has few. Only a small number of "wild mammals subsist on this locally abundant food source;" (Schaller, 1985) some of which include: an arboreal rodent (*Hapalomys longicaudatus*), the fossorial bamboo rat (*Rhizomys*), an African monkey (*Cercopithecus mitis kandti*), a lemur (*Hapalemur*) and the red panda (Schaller, 1985). If it wasn't for humankind's deforestation, the quantity of bamboo would be more than enough for these animals and more (Catton, 1990).

As for its nutritional quality, bamboo has always been known to be quite poor (Shipman, 1990). There exist many ways in which a plant can be assessed for nutrient quality. The primary factors considered include those elements that are beneficial to and digestible by the animal (protein, fat, carbohydrates, minerals, vitamins and water) and those that aren't (cellulose, lignin, and hemicellulose). Ellen S. Dierenfeld (1982) evaluated the nutritive quality of arrow and umbrella bamboo with two different methods: proximate analysis and the Van Soest method. While proximate analysis, which "provides information on ash [salts and minerals], ether extract (crude fat), crude fiber and nitrogen-free extract," is the more commonly used method, it remains somewhat imprecise for it "obscure[s] the actual contribution made by carbohydrates to the diet of animals" (Schaller, 1985). Thus, Dierenfeld focuses more on the findings from Van Soest's method, in which cell wall and cell content are considered separately. Specifically, she determined the nutritive quality of a plant by the relative proportions of cell wall to cell content and the availability of both to the animal. The proportions of cell material will be discussed in this section, while the availability will be examined with the digestive adaptations.

Bamboo does, surprisingly, contain enough organic and inorganic substances to sustain pandas. Like most plants, bamboo contains different levels of nutrients depending on the season, the altitude, and other environmental factors; as well as the part of the plant being considered. In general, however, the nutrient content of bamboo fluctuates little throughout the year, an unusual situation in the food supply of a large herbivore. This study will look at the nutrient quality of two common bamboo species fed on by the panda; *S. fangiana* (arrow bamboo), found at elevations of 3400 m, and *F. robusta* (umbrella bamboo), found at elevations of 1600 m (Schaller, 1985).

As for the organic constituents, bamboo contains protein, carbohydrates and vitamins (found in the cell content) and hemicellulose, cellulose and lignin (found within the cell wall). Bamboo's inorganic constituents include minerals, salts (found in cell content) and silica (found in cell wall and on leaf surfaces). Except for a small fraction of hemicellulose, it is generally found that the cell wall constituents are indigestible, while the cell contents (most of which are necessary for animal growth and maintenance) are quite rapidly digested. As a result, plant species and plant parts that have high levels of protein, carbohydrates, fats, vitamins, minerals and salts and low levels of hemicellulose, cellulose, lignin and silica are considered high in nutritive quality. To simplify this idea, Dierenfeld (1982) focused only on the ratio between protein and cellulose + lignin. Nutrient quality equals protein divided by cellulose + lignin. Therefore, an increase in protein means a higher nutrient quality, as does a decrease in cellulose and lignin (Schaller, 1985) (**Figure 20**). Throughout this study, this premise is termed the nutrient quality theory.

$$\text{Nutrient Quality} = \frac{\text{Protein}}{\text{Cellulose + Lignin}}$$

Figure 20: Definition of nutrient quality. (Schaller, 1985)

Overall protein levels, remarkably, remain constant throughout most of the year (**see Figure 21**), while levels of protein in different parts of the bamboo do vary. In percent of total dry matter, *Sinarundinaria* leaves have the highest levels of protein (15.5%), followed by new shoots (14.8%), branches (6.5%), old shoots (4.4%) and culms (2.4%) (Schaller, 1985). *Sinarundinaria* leaves, branches, old shoots and culms have significantly more protein than do the same parts of *Fargesia*, however, the new shoots of *Fargesia* have a higher protein level (17.6% dry matter). Unlike new shoots, however, the leaves of both species are available year-round having a protein content of 17-15% when green and 10% even when dead. In general, leaves contain higher protein levels and lower levels of cell wall constituents than do other plant parts (Schaller, 1985). Another potential protein source that cannot be overlooked is the underground rhizomes which do contain a protein content of 4.0-4.6%; a higher level than that of culms (Schaller, 1985).

Along with the amount of protein a plant or plant part contains, the quality of a protein must be considered. To evaluate protein quality, Dierenfeld used a method called chemical scoring. This method analyzes a food protein quality by determining "its amino acid composition in the laboratory and compar[ing] it with that of egg protein" (Whitney and Rolfes, 1993). In order for proteins to be synthesized, all necessary amino acids must be available. While an animal's body can synthesize more than half of the needed amino acids, there remain eight essential amino acids that must be supplied by the animal's diet--isoleucine,

leucine, lysine, phenylalanine, methionine, threonine, valine, and tryptophan. The last amino acid, tryptophan, was not tested. By knowing the "amino acid composition" of a protein, the scientist can then determine the quantity of any essential amino acids that make up the protein and compare this to a standard (an egg protein). Therefore, a protein with an adequate amount of all eight essential amino acids will have a high chemical score; a score close to 100 (Whitney and Rolfes, 1993).

Using chemical scoring, Dierenfeld (1982) obtained results similar to those found when analyzing different parts and species for quantity of protein. The new shoots of *Fargesia*, as well as the leaves of both *Fargesia* and *Sinarundinaria*, all contain high levels of the essential amino acids. **See Table 1.** When looking at each plant part's balanced amino acid content, however, it was found that the leaves (chemical score 31-40) and shoots (chemical score 43) of *Sinarundinaria* contain the best balance of seven of the eight essential amino acids, while the new shoots of *Fargesia* have a poor amino acid balance (chemical score 8.2). Of the seven amino acids tested, methionine was consistently "present in smaller amounts than the others" and therefore, probably "represents the limiting amino acid in the diet of pandas" (Schaller, 1985).

The carbohydrates, which make up most of the rest of the cell content, are found in the culms, branches, and leaves in similar average amounts. In *Sinarundinaria*, carbohydrates make up about 12-14% of bamboo dry matter, while in *Fargesia* the percent dry matter of carbohydrates is even lower. The new shoot of *Fargesia* has the lowest proportion of carbohydrates to total dry matter and is around 4% (Schaller, 1985).

Like most plants, bamboo contains little crude fat. Dierenfeld did find, like most other cell content constituents, that the leaves of both species of bamboo contain higher concentrations of fat than do old shoots.

These three organic elements--proteins, carbohydrates, and fats--are the only nutrients found in the body that are broken down to provide usable energy (Whitney and Rolfes, 1993). By combining the findings of the quantities of these nutrients, the available energy (measured in kCalories) can be determined. "[A] diet of 12.5 kg (fresh weight) of *Sinarundinaria* leaf and stem" contains 4,354 kcal of digestible energy per day in the spring, 5,488 kcal in summer-autumn and 5,542 kcal in the winter. A diet of new Fargesia shoots provides 6,741 kcal per day (Schaller, 1985). **See Table 2.**

Vitamins and minerals are the last of the cell content to be considered. The vitamin content of bamboo has not been significantly studied, except for vitamin C. Dierenfeld found that leaves contain much more vitamin C than do new or old shoots (Schaller, 1985). Mineral content is generally the same in both *Fargesia* and *Sinarundinaria*. Among different parts of the plant, the leaves are richer in minerals than stems. While "the mineral requirements of pandas are not known, bamboo has adequate levels of those elements the lack of which is most likely to cause a mineral deficiency in animals" (Schaller, 1985).

Of the cell wall constituents, hemicellulose--a complex polysaccharide associated with lignin and cellulose--is partly digestible. Similar to protein levels, the highest hemicellulose levels, expressed in percent dry matter, are found in leaves (35%), succeeded by culms (23%), branches (22%), and old shoots (18%). The cellulose and lignin are completely indigestible and are found in high concentrations in culms (52%), old shoots (48%), and branches (44%)

(Schaller, 1985).

Silica (SiO_2), also found in bamboo, is "a structural component of cell walls often complementing lignin" (Schaller, 1985). Occasionally, an accumulation of silica can be found of the surface of the leaves of plants. The highest content of silica is found in the leaves of *Sinarundinaria* and lowest is found in the old shoots and stems. The parts of *Fargesia* show similar values. Both bamboo species have the "highest silica levels during the coldest months and during spring" (Schaller, 1985).

Quite often ignored or forgotten, water is also an important part of nutrition. "Although the different bamboo parts contain roughly similar percentages of water, some seasonal fluctuations occur" (Schaller, 1985). Both species, in general, have significantly less water from January - June than from July - December and they seem to have the most water between August - October (Schaller, 1985).

From the previous statistics, the nutrient quality of each part of the plant of both species can be quantified, thus, creating a list of plant parts with the highest nutritive quality to the lowest. The plant parts listed in order of decreasing food quality are: leaves of *Sinarundinaria* and *Fargesia*, branches of *Sinarundinaria* and *Fargesia*, old shoots of *Sinarundinaria* and *Fargesia*, and culms of *Sinarundinaria* and *Fargesia*. *Sinarundinaria* has a higher nutrient quality in each case than *Fargesia*, except for new shoots (**see Figures 22 and 23**). Both species' new shoots provide a food source for only a brief time during the year and have a nutrient quality close to that of leaves (Schaller, 1985).

CORRESPONDING PANDA BEHAVIOR

Every behavior and action done by a panda requires a certain amount of energy. From basal metabolism to active foraging, the total energy needed for all activities must be balanced out by the energy intake from the animal's diet. The existence and health of the animal, therefore, depends on whether the energy intake is below, equal to, or above the required amounts. In order to meet or exceed the energy requirements, an animal can (1) modify its diet, choosing resources that are high in energy-yielding nutrients, (2) alter its behavior, reducing the number of high-energy activities, lowering the required amount of energy or (3) modify its digestive tract to optimize digestibility. For the most part, the panda has chosen the second strategy.

The panda has modified its diet somewhat (this aspect will be examined in the food selection section), but its digestive tract has been changed only in minuscule ways.

The alteration of behavior has been greatly influenced by the nutritional quality and abundance of bamboo. "Bamboo obviously contains organic and inorganic substances in amounts and proportions adequate to sustain pandas, for, after all, the animals have depended on this plant" for millions of years (Schaller, 1985). To obtain these substances in adequate quantities, the panda must take in large amounts of bamboo. In doing so, the panda fills its digestive tract with indigestible cell wall material, therefore, limiting "the animal's food intake without contributing to maintenance" (Schaller, 1985). Because of this limited amount of energy available, the panda must be extremely conservative with how much time and energy it allocates to every behavior. The behaviors examined within this study include: feeding (Optimal Foraging Theory), reproduction, hibernation, social behaviors, and resting.

"**Feeding** is not a single behavior, but a large collection of functionally related behaviors" (Grier and Burk, 1992). All animals must locate, select, handle and ingest food in order to sustain life. In evolution, most animals have developed energy budgets by which benefits are maximized and costs are minimized. This biological process is known has the Optimal Foraging Theory (OFT) and states that "animals should forage to maximize the rate of caloric intake per time spent foraging," energy divided by time or E/t. Foraging time is divided into search time and handling time. Handling time includes both manipulation and ingestion (Grier and Burke, 1992).

In applying the Optimal Foraging Theory to the panda, many of its evolved feeding behaviors can be understood. The panda is, of course, a specialist. Within OFT, animals that are classified as specialists are characterized by having longer search times and shorter handling times. When specializing on one food source, it may be harder to find the foodstuff, but the animal will be able to manipulate it with greater skill and speed (Grier and Burk, 1992).

The reduction in handling time has mainly been accomplished as the giant panda has evolved various manipulation skills within its past ~2 million "specializing" years. The speed at which this creature can handle bamboo is extraordinary. As a panda eats leaves, culm or new shoots, one can easily observe the animal's great dexterity. Almost always, the panda sits or lays in order to free the forefeet for bamboo handling (Davis, 1964). These forepaws and mouth work together with great precision and superb economy of motion. The bamboo is grasped, plucked, peeled, stripped, bitten and otherwise prepared for being swallowed. "Forepaws often reach for more [bamboo] before the last bite has been swallowed." All the animals actions are smooth and rapid, as if the panda has little time and energy (Schaller, 1985). The panda's digestive efficiency is not as impressive, however, and is greatly overshadowed by its efficiency in gathering and consuming the bamboo.

As for the panda's search time, it is not characteristic of a specialist. The time needed for a panda to find its foodstuff is minimal; mainly because of a characteristic of the bamboo (abundance), not a characteristic of the panda. Pandas, while usually sitting when foraging, are "able to harvest stems all around" without so much as shifting (Schaller, 1985) (**see Figure 24**). Nevertheless, with an unlimited food source, efficient foragers still obtain the upper hand. The reduction in time needed for foraging allows the animal extra time for other important, non-foraging behaviors such as: reproduction, social behaviors, etc.

The Optimal Foraging Theory also predicts that "animals choose the most profitable food items among those available, be more selective when profitable items are more common, and ignore unprofitable food outside the optimal range no matter how common it is" (Grier and Burk, 1992). This aspect of the theory describes, precisely, the giant panda's **food selecting behavior**.

This behavior has been primarily patterned by the different nutrient levels found in particular species and specific parts of the plant. The optimal diet for the panda, based on the previous knowledge of bamboo nutrient quality, should consist of plant parts and species that are high in nutrients. Following the nutrient quality theory, this means plants high in nutrients (mostly found in cell content) and low in indigestible material (cell wall constituents).

In general, pandas readily eat many different species of bamboo, however, this study will be based on the two commonly eaten species, arrow and umbrella. George Schaller (1985), in his study of the pandas of the Wolong Nature

Reserve, found that 85% of the year the pandas fed on the species *Sinarundinaria fangiana* (arrow bamboo). During May and June, when the new shoots would begin to emerge, the pandas would move to lower elevations to feed on the shoots of *Fargesia robusta* (umbrella bamboo). When feeding on arrow bamboo, the pandas were highly selective. From July to October they fed almost exclusively on leaves; November to March, leaves and young stems; and April to June mainly old stems (Schaller, 1985).

Exactly why the panda selects different parts of different species of bamboo during different periods throughout the year is still not fully understood; however, certain possible explanations can make things somewhat more clear.

First, Schaller (1985) found that the pandas favored *Sinarundinaria* over *Fargesia* throughout most of the year. Most likely this favoring has resulted because the *Sinarundinaria* contains somewhat more protein and other nutrients and less cellulose and lignin, and additionally, the balance of essential amino acids is better than that of *Fargesia*. Altitude, itself, might also be influencing selection, as plants in higher elevations, such as *Sinarundinaria*, tend to be higher in nutrient quality than plants at lower elevations, such as *Fargesia* (Schaller, 1985).

Second, new shoots of *Fargesia* make up the greatest percentage of panda feed during May and June. The reasoning behind this selection, again, might follow the nutrient quality theory, as *Fargesia* new shoots have a higher protein, and, thus, a higher nutrient quality than those of *Sinarundinaria*. "Spring is nutritionally the poorest time of the year for the pandas that forage only on Sinarundinaria." At this time of the season, the leaves of both species are unpalatable (possibly because of excess silica) forcing the pandas to subsist mostly on stems. The new shoots of *Fargesia* provide "an important alternative" at this time (Schaller, 1985).

Third, the panda's choice of *Sinarundinaria* leaves during the long stretch from July to March is reasonable, for these leaves contain the greatest amount of nutrients and the least amount of indigestible bulk of all other bamboo parts. During the spring months of April to June, stems may be eaten because of the high levels of silica found in leaves at that time. Silica is both distasteful and difficult to digest. In fact, pandas eat, proportionally, the greatest amounts of leaves from July to October, when silica levels are lowest, and the least from April to June, when levels are highest (Schaller, 1985).

Fourth, the panda's selectivity of bamboo parts might also be a result of the low nutritional quality of bamboo on the metabolism of the animal. Because the panda must conserve all the energy it is capable of taking in, it selects those parts of bamboo that are easiest to eat. The rhizomes, while containing more protein than culms, are not eaten, mainly because the process of digging up these "underground stems" would take more energy than they can supply (Schaller, 1985). This reasoning also explains why pandas eat only portions of certain culms. Many times the panda will bite off a length of the stem, eat the softer portion of it and discard the harder excess (Schaller, 1985). Generally, the top part of the culm, where branching occurs is softer than the bottom section, closer to the ground. Additionally, the outside stem layer is quite tough to consume, so the panda "quickly and skillfully strip[s this layer] off with the incisors" (Davis, 1964).

Thus far, it appears as if the panda selects food based on the varying levels of protein found within different bamboo parts. Most likely, this is what they do; "however, [pandas] do not need to consume as much bamboo as they do to obtain the required amount of protein" (Schaller, 1985). The pandas appear to obtain more than adequate amounts of protein for maintenance and growth. The amount of bamboo that is eaten may be a result of the need for adequate amounts of "calories in the form of soluble carbohydrates and fats"--nutrients found in small amounts in leaves and stems of plants (Schaller, 1985).

Bamboo's poor nutrient quality and high amounts of fibrous material also has had a significant influence on the panda's **reproduction**. Little energy is allotted to non-foraging activities such as mating and reproduction. The female does not mature until she is 5.5 to 6.5 years old and at that time has a very short estrus period only once a year (Yi and Shuo, 1993). Courtship can last less than one day and there are only two or three days during the year when females can conceive (Schaller, 1985). Even when they do conceive, pandas conserve energy by giving birth to just one or two altricial cubs, unlike other bears, which have litters of as many as four. If a panda was to give birth to two cubs, which happens 60% of the time, the mother seldom tries to keep both cubs alive. The second cub is usually ignored and perishes so that the mother will only have to expend energy for the milk-production and care of one offspring (Dolnick, 1989).

Energy is also conserved with a short gestation period. The panda's gestation period usually lasts for five months. At birth the cubs are blind, helpless, and, at a weight of only 4 ounces. A panda mother still has to "forage for food while simultaneously carrying and caring for a helpless, rat-sized infant" (Dolnick, 1989). The mother nurses her cubs for three to five months and does not go into estrus right after she stops nursing. As a result, "she usually misses an entire year's breeding season" (Dolnick, 1989).

Again, the low nutritional quality of bamboo effects another aspect of panda behavior, **hibernation**. Even in the summer, when food supply is at its most nutritious, the chosen diet does not provide the fat resources need to sleep for five months, or even one month, for that matter. The panda must keep its stomach full at all times, alternating periods of sleep and forage. For most hibernators, hibernation results from the seasonal lack of food, not the inability to withstand cold. While the panda's food source is plentiful year round, the contents of bamboo do not allow for the retention of large amounts of energy/fat storage (Dolnick, 1989).

Social behaviors do exist, however, they are few and far between. For the most part, panda are essentially solitary creatures, spending days and weeks alone. Group living usually occurs when "an animal needs help getting food or warding off enemies" (Benyus, 1992). Its food supply not only encourages low-socializing levels because of its nutrition, but also through its even distribution and accessibility. And as for enemies, the large-sized panda has none--except for humans.

Direct contact is deterred between individual pandas because of its possible high costs in energy. In order to keep track of the activities of a neighbor, the panda uses low-energy olfactory signals. These signals are quite advantageous for they are long-lasting and serve several functions, including: delineating ranges, preventing or initiating encounters, and providing information about individual identity and reproductive condition. Scent posts of pandas are created with scratches, glandular secretions, and urine marks and serve many functions with minimal use of energy (**see Figure 25**). There exists two anal sacs on each side of the anus which secrete a substance for scent marking. The panda's tail, which is normally pressed close to the animal's body to protect this area also "serves as a brush painting the animal's scent" (Schaller, 1985). Additionally, territories are small and a panda can traverse its range in two hours or less (Schaller, 1985). Because the bamboo is so dense and abundant, it would be an energetic waste to defend a food supply.

Conservation of energy is at an optimum when **resting**. Life for the panda is a continual balancing act of activity and inactivity. During one twenty-four hour period, pandas are usually 59% active and 41% inactive. These figure remain relatively constant throughout the year, except for in the spring when the pandas are most active and rest less often. On average, a panda rests 9.8 hours a day. Occasionally it will simply sit or lie for only a few minutes, or it will sometimes remain still for an hour or two before returning to forage. Long rests may take place at any time of day or night and on some days it rests 1-4 times and others not at all, limiting itself to only brief inactive periods. While resting, the panda will continue to defecate, producing 5-10 droppings in less than a two hour period (Schaller, 1985).

Although a panda will sometimes just stop and rest wherever it happens to be, it more commonly will choose an area containing something with which it can lean against. Often, a panda will prop itself up against the base of a tree or simply within a bamboo thicket. No energy is used to construct a nest; however, a good resting site may be used repeatedly (Schaller, 1985).

A resting panda either remains relatively motionless for long periods of time or it may shift repeatedly, especially at the beginning or end of a long rest period. Pandas have been known to take different positions when resting including: lying on its back or side, reclined on its belly, forelegs or hindlegs tucked in, or even one hindleg in the air. Frequently, a panda merely sits hunched (Schaller, 1985).

CONCLUSION

The giant panda has evolved numerous adaptations in response to various aspects of its specialized bamboo diet. The evolutionary history has revealed various changes in anatomy (skull and forepaw)--to increase efficiency of foraging, various behavioral changes--to magnify nutrient intake and restrain energy usage and finally, the maintenance or lack of change, for the most part, in digestive anatomy--possibly to prevent the production of cyanide through bamboo degradation. We can really only view the panda as it is today and being that the study of any animal's evolutionary history will always be in retrospect, the best we can do is guess at possible explanations. George Schaller (1943), who has studied pandas for years, sums it up when he states, "we [the pandas and humans] shall always remain of two worlds. Humans can never know the truth about pandas. Therefore, enjoy the mystery--and help [them] endure."

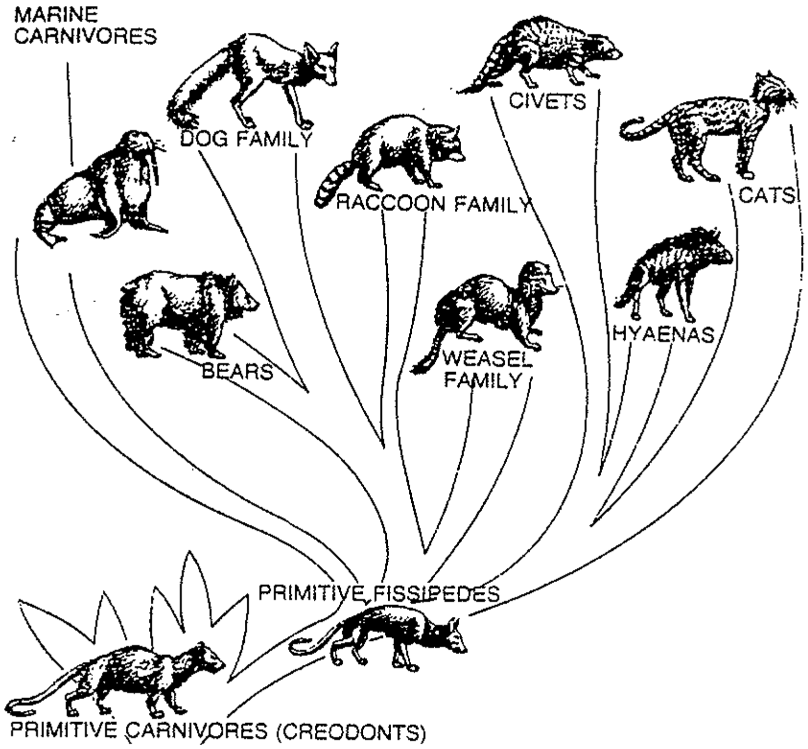


Figure 1: Simplified family tree of carnivores (Romer & Parsons, 1986).

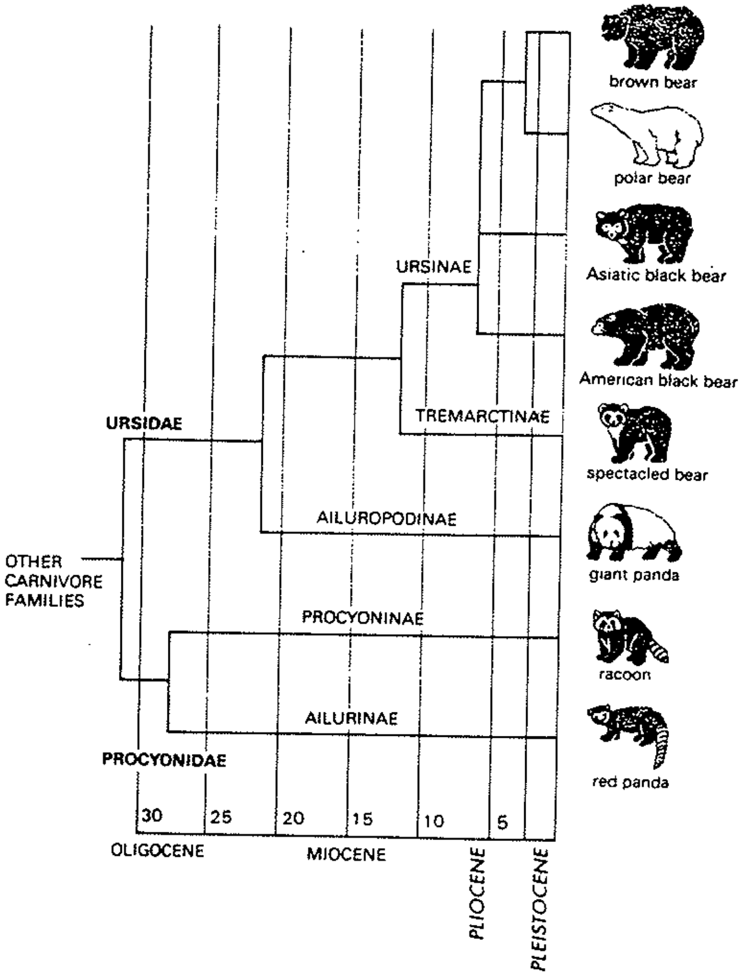


Figure 2: Ancestry of pandas and relatives as determined by DNA-hybridization studies. Numbers indicate millions of years before the present (Catton, 1990).

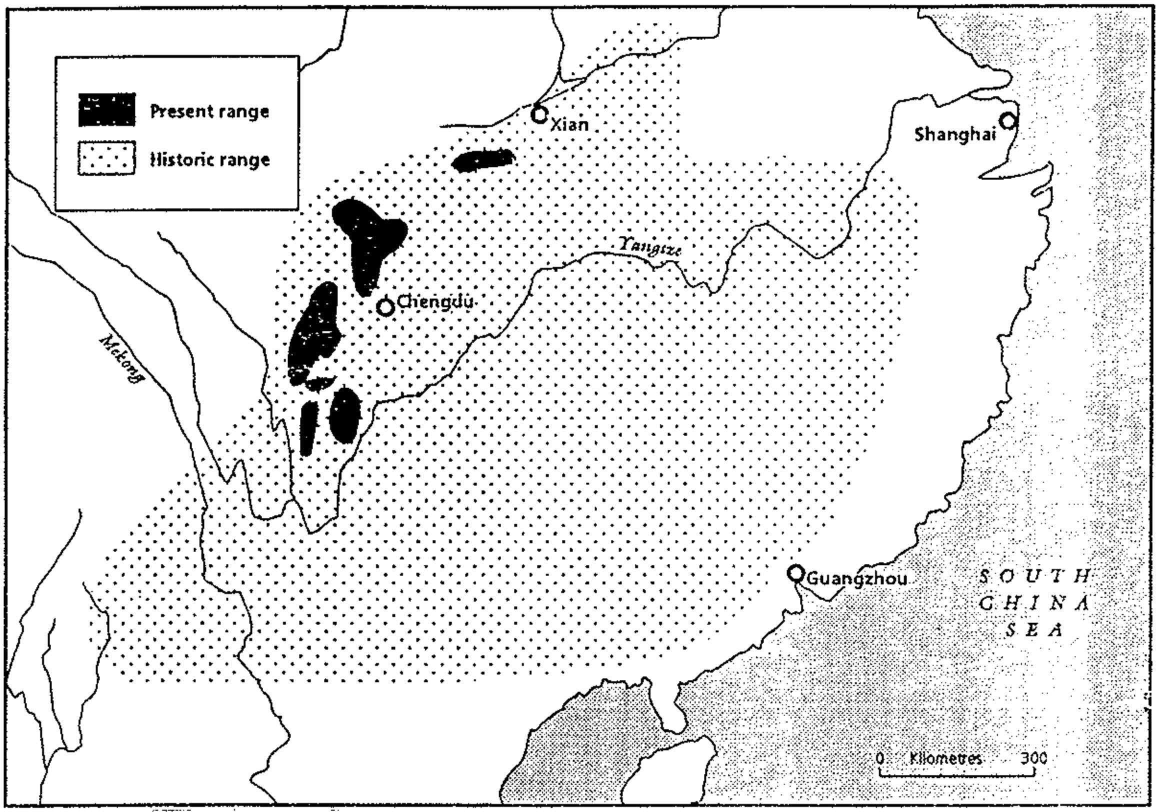
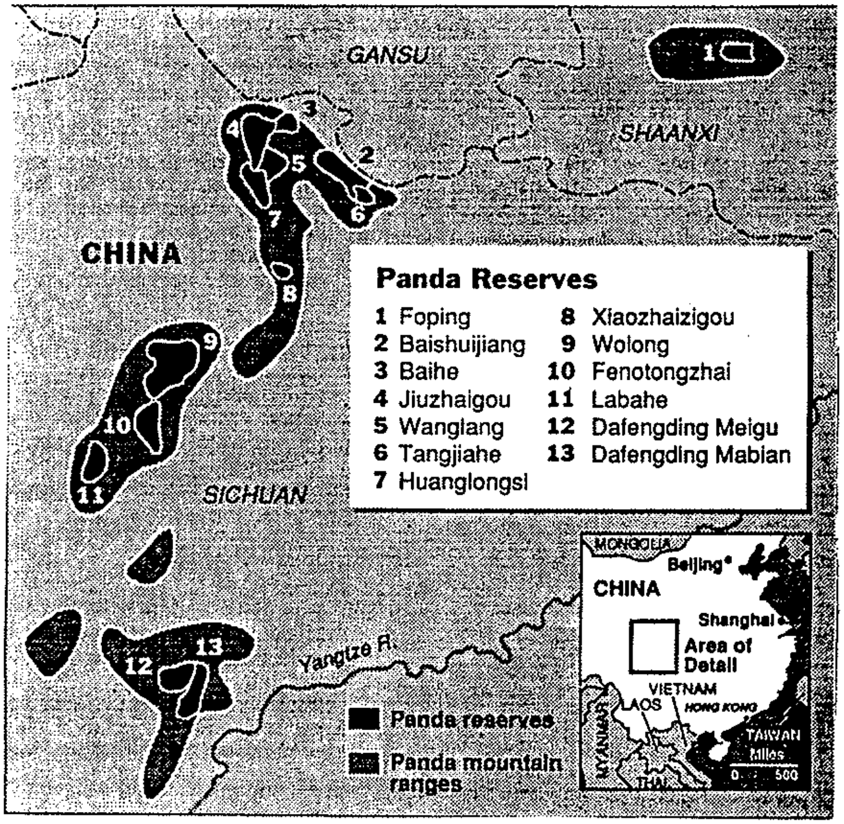
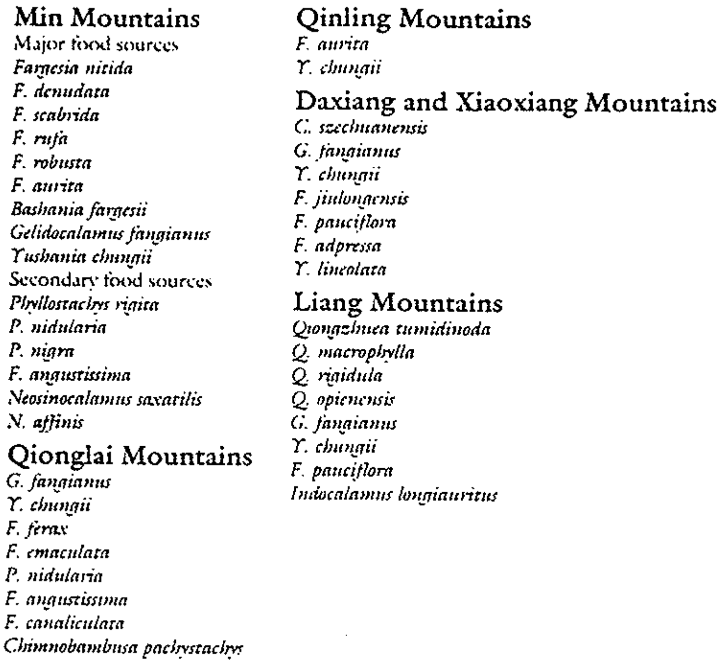


Figure 3: Past and present range of the giant panda (Catton, 1990).

Figure 4: 13 of the 14 Panda Natural Reserves (Map by New York Times)





Min Mountains
Major food sources
Fargesia nitida
F. denudata
F. scabrida
F. rufa
F. robusta
F. aurita
Bashania fargesii
Gelidocalamus fangianus
Yushania chungii
Secondary food sources
Phyllostachys rigida
P. nidularia
P. nigra
F. angustissima
Neosinocalamus saxatilis
N. affinis

Qionglai Mountains
G. fangianus
Y. chungii
F. ferax
F. emaculata
P. nidularia
F. angustissima
F. canaliculata
Chimnobambusa pachystachys

Qinling Mountains
F. aurita
Y. chungii

Daxiang and Xiaoxiang Mountains
C. szechuanensis
G. fangianus
Y. chungii
F. jiulongensis
F. pauciflora
F. adpressa
Y. lineolata

Liang Mountains
Qiongzhuea tumidinoda
Q. macrophylla
Q. rigidula
Q. opienensis
G. fangianus
Y. chungii
F. pauciflora
Indocalamus longiauritus

Figure 5: Bamboo species known to be eaten by pandas in their native habitat (Catton, 1990).

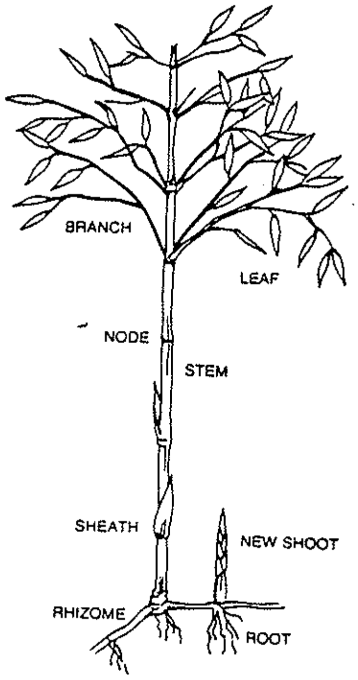


Figure 6: Structure of bamboo culm and connected rhizome system (Schaller, 1985).

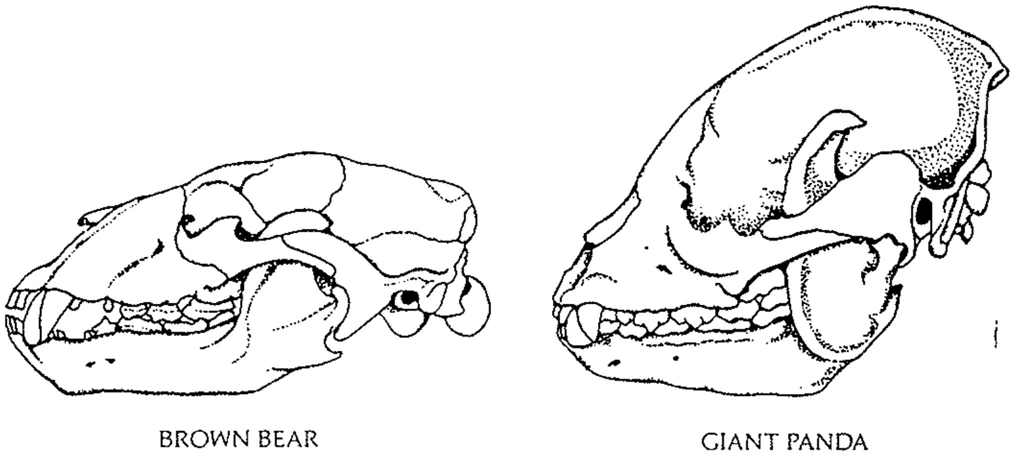


Figure 7: Skulls of the giant panda and the brown bear showing the tremendous enlargement of the panda's cranium and sagittal crest and its massive teeth, which evolved to provide the grinding power to eat the bamboo's tough stems and fibrous leaves (Roots, 1989).

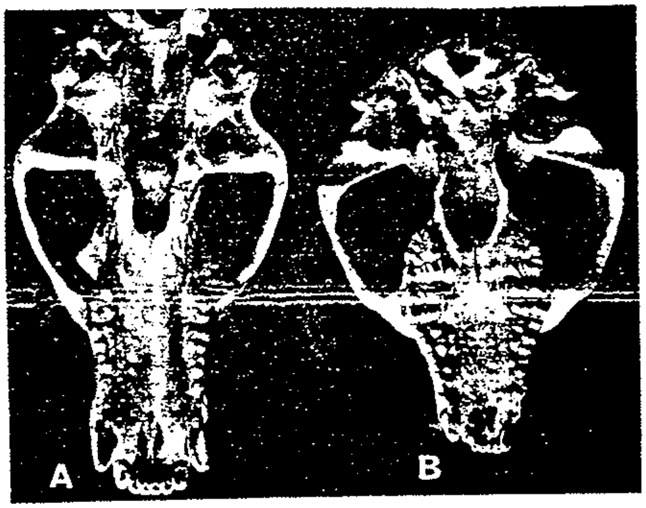


Figure 8: Teeth of the (A) polar bear and (B) giant panda, showing the modification of carnivorous dentition (Catton, 1990).

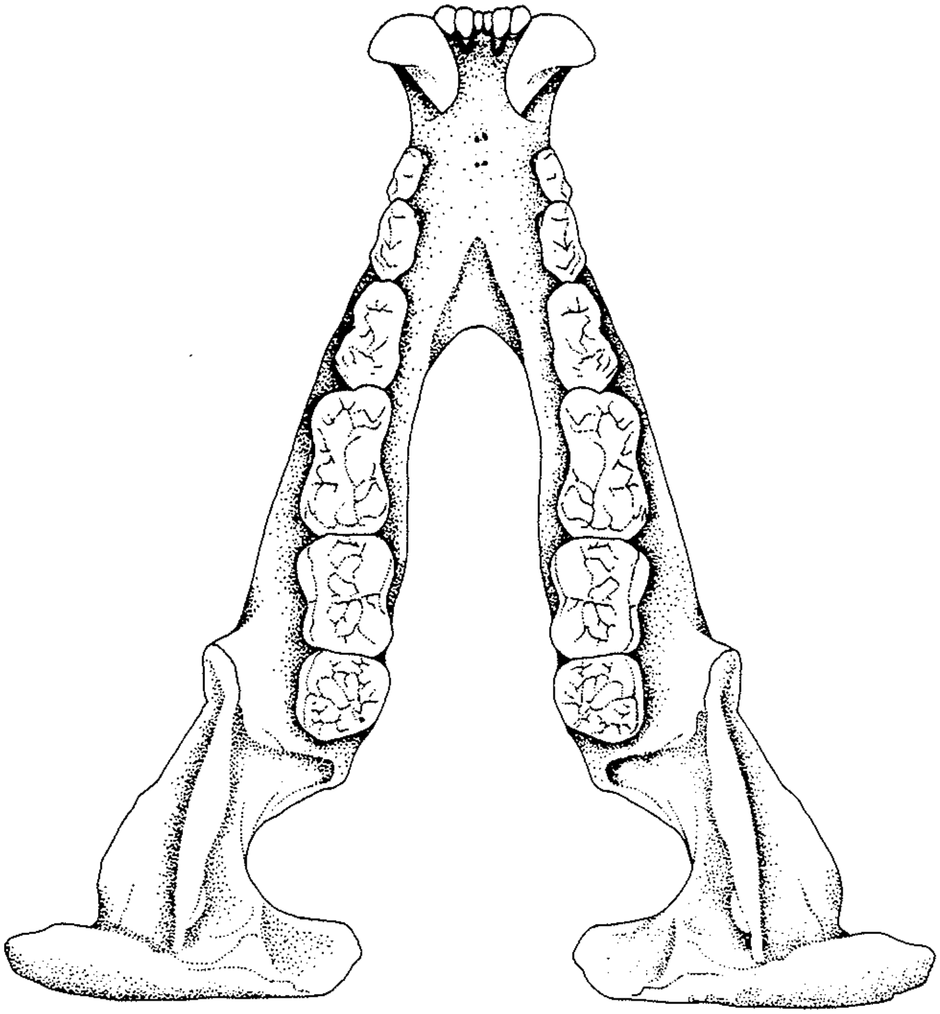


Figure 9: Dentition of the giant panda. The canines of a carnivore dentition remain, while the molars are greatly modified for crushing bamboo (Catton, 1990).

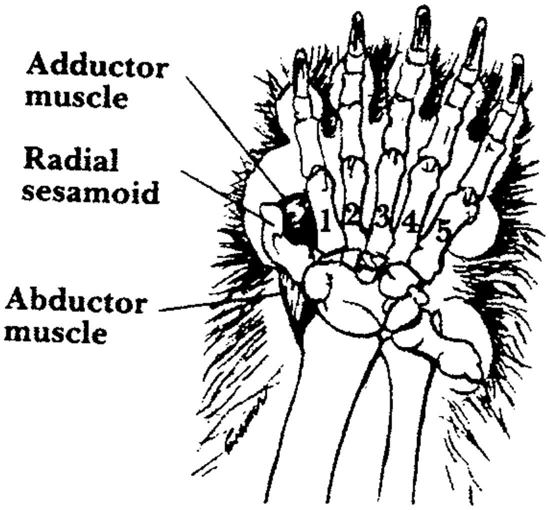
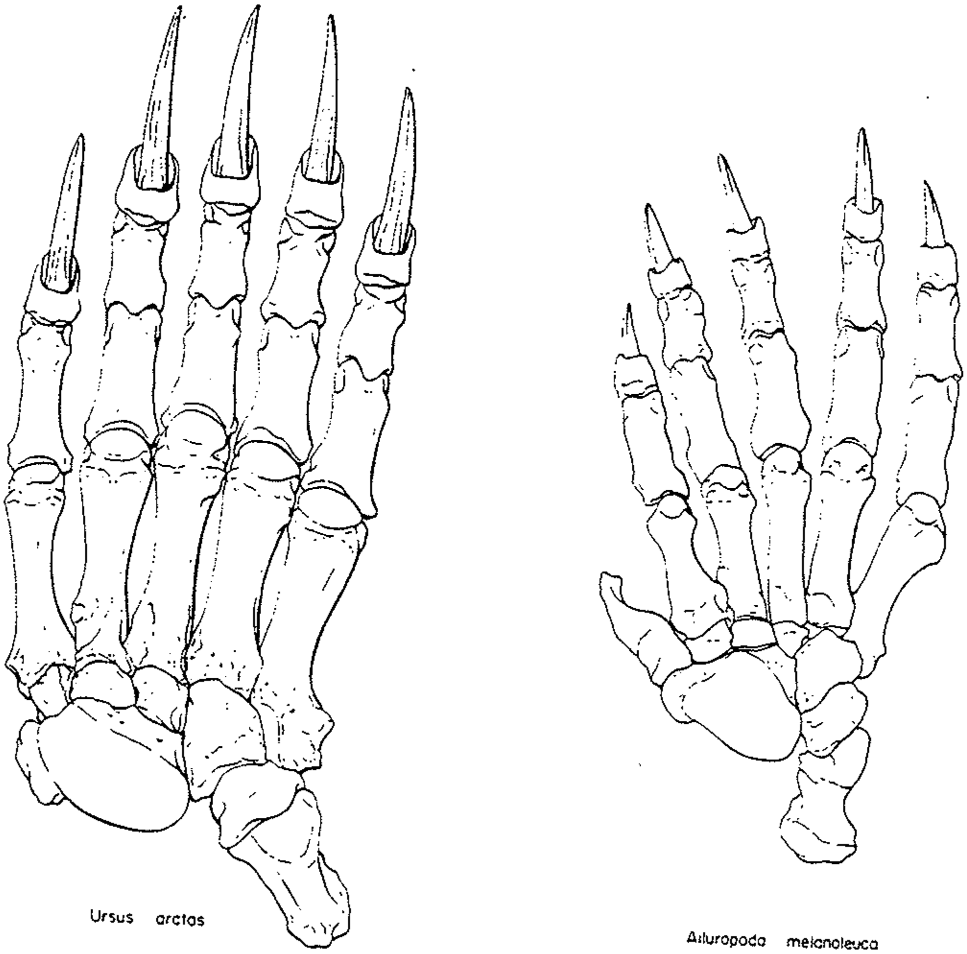


Figure 10: Enlargement and elongation of the radial sesamoid and corresponding musculature to create a "pseudothumb" (Gould, 1980).



Ursus arctos

Ailuropoda melanoleuca

Figure 11: Right manus of a typical bear (*Ursus*) and the giant panda (*Ailuropoda*) (Davis, 1964).

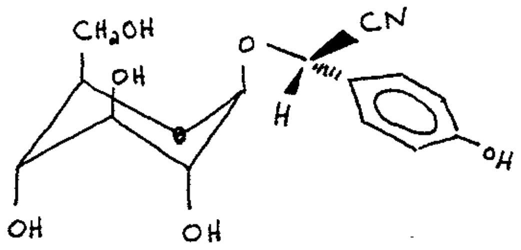


Figure 12: Chemical structure of (s)-dhurrin, the cyanogenic glucoside of bamboo (Bagchi and Ganguli, 1943).

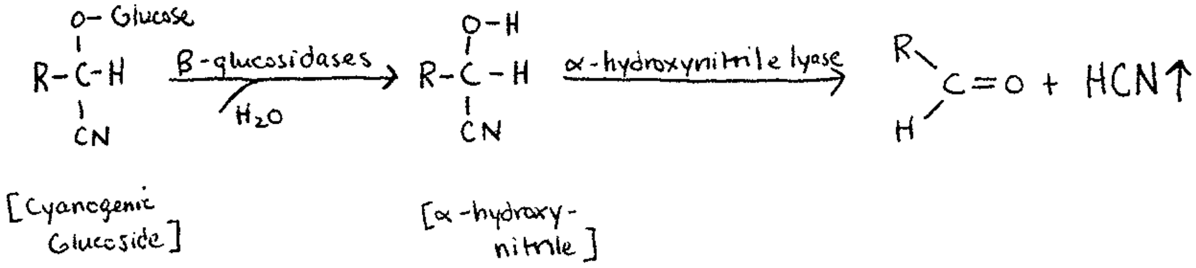


Figure 13: Chemical reaction of the production of HCN from cyanogenic glucoside and corresponding enzymes (Poulton, 1988).

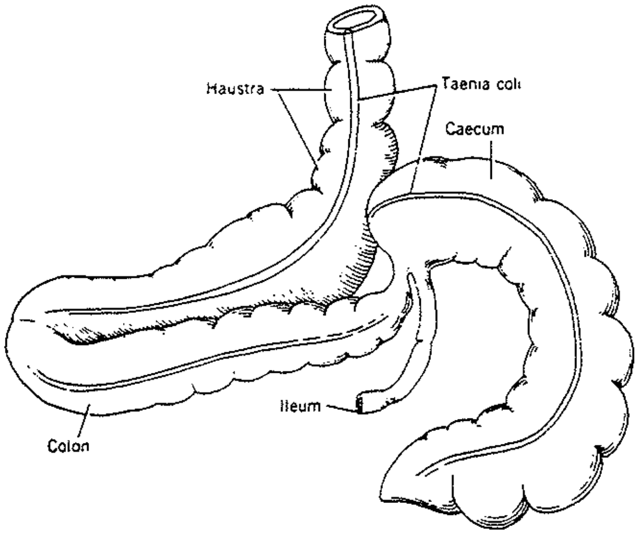


Figure 14: The caecum and colon of the horse (Montagna, 1959).

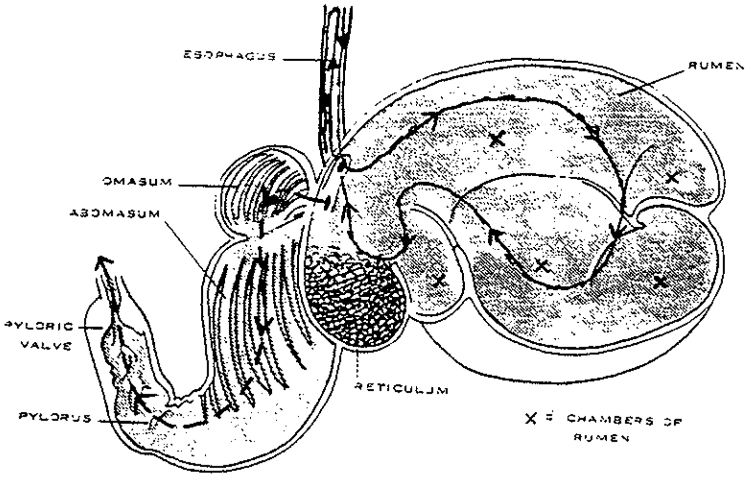


Figure 15: Typical stomach of a ruminant, with lines showing the course of the food (Ballard, 1964).

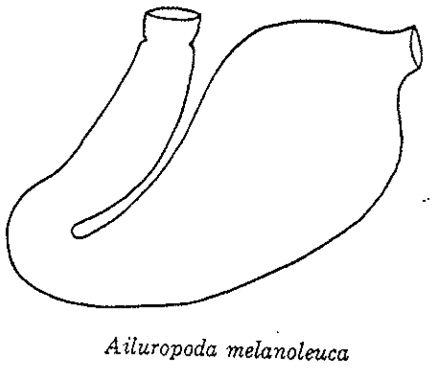


Figure 16: Simple stomach of the giant panda (*Ailuropoda melanoleuca*) (Davis, 1964).

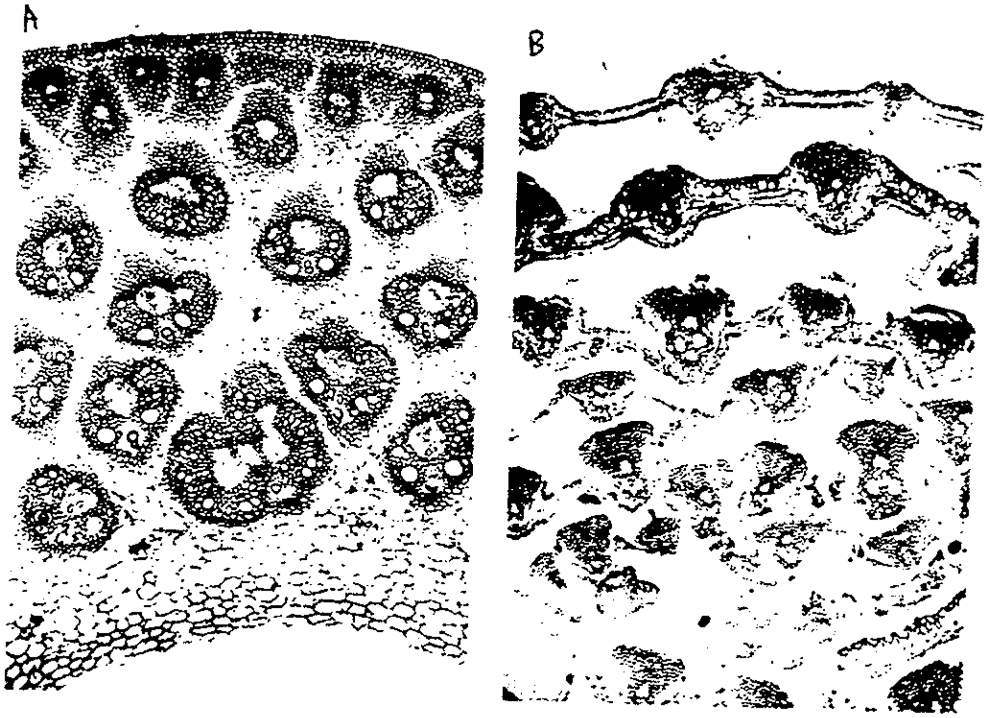


Figure 17: A. A cross section through the middle of a new *Fargesia* shoot reveals the normal arrangement of cells. B. A shoot section from a dropping indicates that many vascular bundles were little affected by digestion during the rapid passage through the alimentary tract (Schaller, 1985).

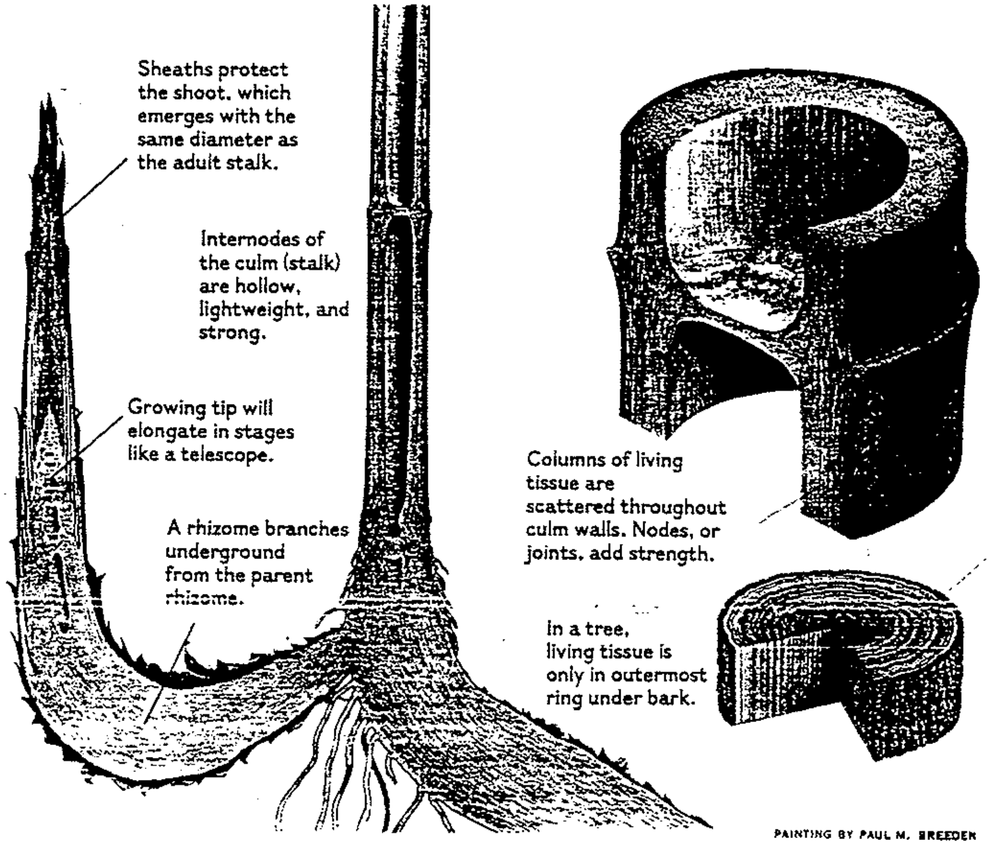


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Figure 18: Bamboo growth and structure (Marden, 1980).

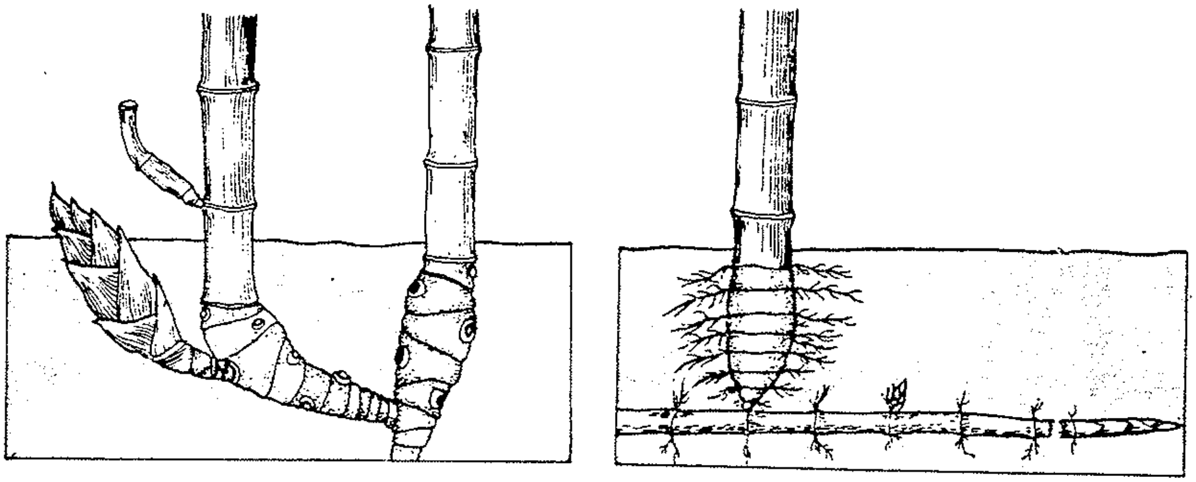


Figure 19: Bamboo growth patterns: sympodial (left) and monopodial (right) (Austin, 1970).

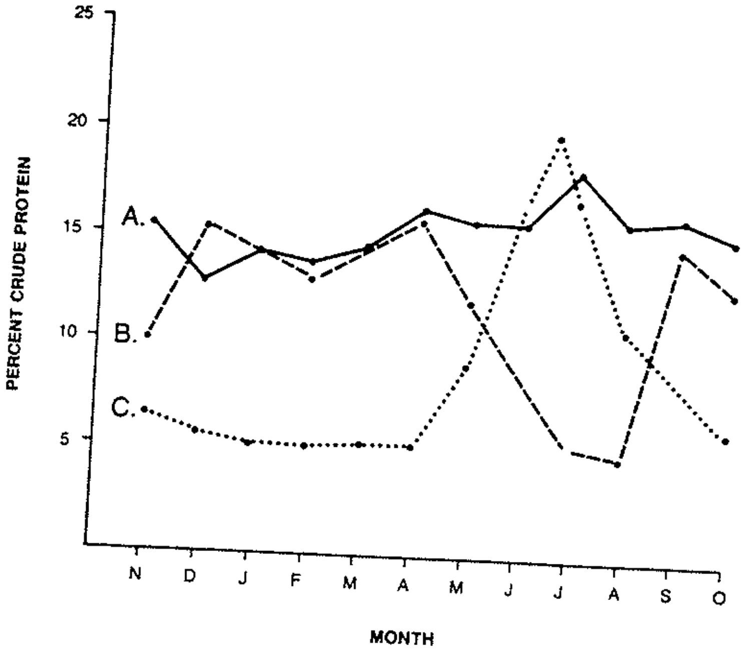


Figure 21: Consistancy of protein levels in giant panda's feedstuff. The percentage of crude protein available in principle food of three herbivores throughout the year.
A--*Sinarundinaria* leaves--giant panda
B--Grass--Wildebeests in the Serengeti
C--Browse foraged by mule deer in Colorado
(Schaller, 1985).

Food	Plant part	Isoleucine	Leucine	Lysine	Phenyl-alanine	Methionine	Threonine	Valine	Amino acid score[b]
Egg	—	.428	.565	.396	.368	.342	.310	.460	100.0
Beef	—	.332	.515	.540	.256	.237	.275	.345	69.3
Maize	—	.351	.834	.178	.420	.205	.223	.381	44.9
Fargesia	new shoot	.360	.739	.412	.357	.028	.362	.397	8.2
	old shoot-middle	.122	.246	.240	.014	.057	.175	.213	3.8
	leaf	.310	.613	.238	.377	.056	.495	.596	16.3
Sinarundinaria	old shoot-middle	.529	.874	.350	.462	.146	.532	.788	42.6
	leaf	.113	.221	.149	.100	.032	.184	.202	9.3
Fargesia	old shoot-middle	.086	.162	.255	.053	.054	.153	.189	15.9
	leaf	.345	.658	.362	.389	.056	.397	.528	16.4
Sinarundinaria	old shoot-middle	.207	.310	.172	.088	.030	.148	.137	8.8
	leaf	.393	.729	.512	.410	.105	.478	.607	30.7
Fargesia	old shoot-middle	.146	.213	.101	.063	.035	.050	.107	10.2
	leaf	.363	.847	.459	.516	.024	.595	.632	7.0
Sinarundinaria	old shoot-middle	.166	.302	.220	.075	.044	.145	.156	12.8
	leaf	.411	.835	.454	.469	.138	.564	.728	40.4

Table 1: Content of essential amino acids in various bamboo parts and in selected other foods (in mg/100g) (Schaller, 1985).

	Dry matter intake (kg)[a]	Diet ratio, Leaf:stem	Gross energy (kcal)[b]	Dry matter digestibility (%)	Digestible energy (kcal/day)
Spring					
Leaf and stem	7.56	9:91	34,912	12.47	4,354
New *Fargesia* shoot	3.83	—	16,852	40.00	6,741
Summer-autumn	4.95	89:11	23,604	23.25	5,488
Winter	6.63	30:70	29,638	18.70	5,542

[a] Based on 12.5 kg (fresh weight) intake except for 38.3 kg new *Fargesia* shoot.

[b] Based on 4,800 kcal/kg leaf, 4,600 stem, 4,400 new shoot (Dierenfeld 1981).

Table 2: Estimated total digestible energy (in kcal/day) obtained by free-living pandas (Schaller, 1985).

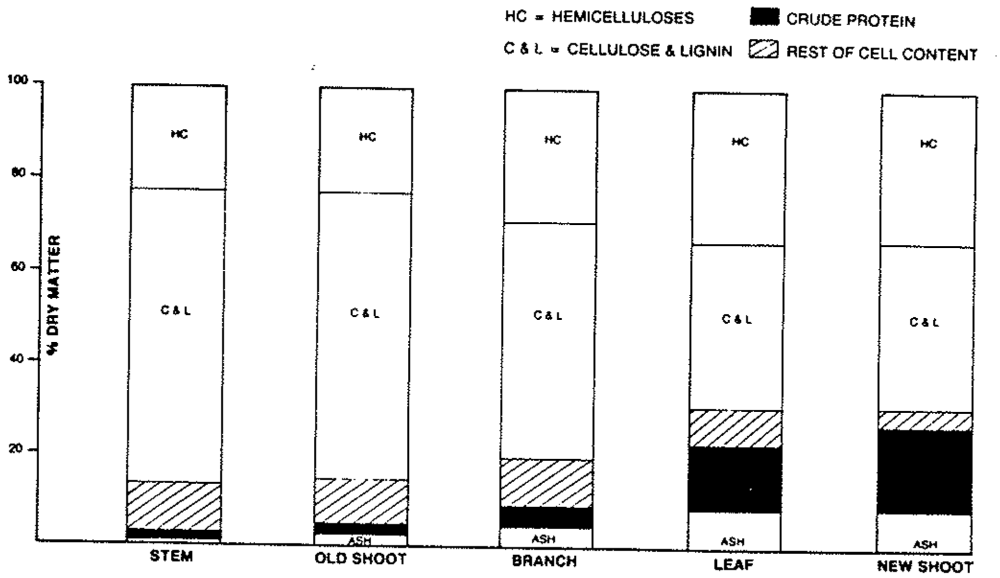


Figure 22: Nutrient content of different *F. robusta* parts, expressed as percent dry matter (Schaller, 1985).

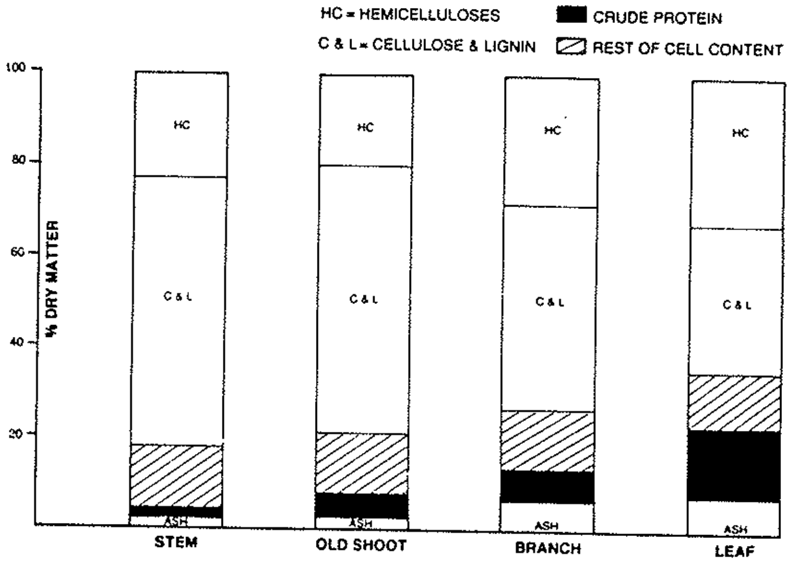


Figure 23: Nutrient content of different *S. fangiana* parts, expressed as percent dry matter (Schaller, 1985).

Figure 24: By sitting down to feed, the giant panda saves precious energy (Catton, 1990).

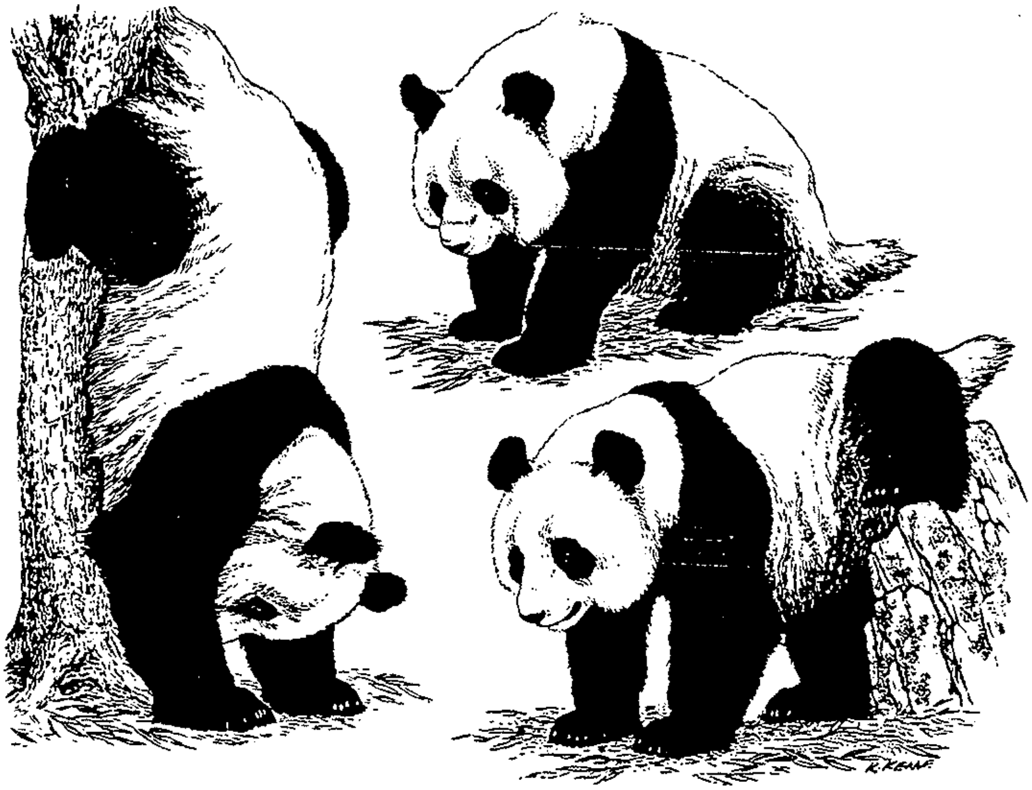


Figure 25: Postures of giant panda when scent marking the ground, a stump, and a tree while in a handstand (Schaller, 1985).

Appendix A

Determination of Cyanide

The determination of HCN produced by the two different bamboo species was attained through the following outlined steps. NOTE: the two species of bamboo, *Sinarundinaria fangiana* and *Fargesia denudata*, were obtained through the generosity of the Chongqing Zoo in Chongqing, Sichuan, China and the Chengdu Zoo in Chengdu, Sichuan, China. All samples of bamboo leaves and branches were dried (until brittle) by placing them between two pieces of hardware cloth and newspapers situated above a 60 Watt bulb. The samples were then placed into coin envelopes and transported back to the United States under proper Customs' regulations.

PREPARATION:

Step 1. The plant material was separated in four groups: *Sinarundinaria* leaves, *Sinarundinaria* branches, *Fargesia* leaves, and *Fargesia* branches. Five samples from each group were tested. Each sample weighed approximately 0.1 grams.

Mass of Bamboo Samples (in grams--dry weight)					
	1	2	3	4	5
Sinarundinaria Leaves	.100	.104	.105	.099	.100
Sinarundinaria Branches	.108	.098	.104	.099	.098
Fargesia Leaves	.101	.102	.103	.101	.099
Fargesia Branches	.100	.103	.099	.097	.103

Step 2. The reaction mixture components used included: phosphate buffer, and emulsin. The phosphate buffer (pH 6) was made by adding **.2M NaH_2PO_4** (87.7ml) to **.2M Na_2HPO_4** (12.3ml). This mixture was diluted in half with 100ml deionized water. The emulsin was made to a concentration of 3.3 mg/mL by adding **.165 grams β-Glucosidase** (almond emulsion) to **50 mL of Pi buffer**.

Step 3. The cyanide reagents needed included: acetic acid, succinimide reagent and barbituric acid and pyridine. A 1.0 N solution of acetic acid was made with **57.4 mL acetic acid** added to 1 liter of deionized water. The succinimide reagent was made by adding **2.5 g succinimide, .25g chlorosuccinimide** and 1 liter of deionized water. The barbituric acid/pyridine solution was made by adding **7.5 g barbituric acid** to **75 ml of pyridine** and 250 ml of deionized water.

Step 4. 1.0 N and 0.1 N solutions of NaOH were made. The 1.0 N solution was made by combining **4 g NaOH** with 100 ml of deionized water. The 0.1 N solution was made by combining **2 g NaOH** with 500 ml of deionized water.

REACTION MIXTURE MADE

Step 5. **0.1 g bamboo sample** was placed into a test tube. **4.9 ml phosphate buffer** was added to the test tube. The mixture was homogenized in a Polytron machine at a setting of 4 for 5-10 minutes. Usually, the branches took a lot longer than the leaves. Each sample was homogenized until all large pieces were shreaded. The mixture was transferred to a capped container. **0.1 ml emulsin** was added and the time was recorded for each sample to ensure consistent reaction time. As soon as each mixture was made, the capped container was refrigerated.

The Polytron was rinsed and cleaned with distilled water after each sample was homogenized.

Step 6. The reaction mixture, in the capped container, was incubated with shaking for 1 hour at 35° Celsius.

Step 7. An aliquot (0.1 mL) of reaction mixture was removed and placed into a test tube. This step was repeated again so that there were two samples from each reaction mixture. Forty total samples were created.

Step 8. **0.9 ml of NaOH (.1M)** was added to each reaction mixture. All samples were then refrigerated over the weekend. This addition of NaOH had three functions: (1) to stop the enzymic reaction, (2) to ensure complete hydrolysis of p-hydroxymandelonitrile into p-phydroxybenzaldehyde and cyanide and (3) to trap free HCN from the gas phase.

CN ASSAY

Step 9. The assay was completed using the Lambert precedure [Lambert et al 1975] (see page 81). **0.5 mL of acetic acid** (1.0 N) was added to the reaction mixture, along with **5 mL of succinimide reagent** and **1 mL of**

barbituric acid/pyridine.

Step 10. A standard curve was created by making six different solutions with varying concentrations of CN. 0.0650 g of KCN was dissolved in 100 mL of 0.1 N NaOH (260 μg CN/mL). The stock was diluted 1:20 by adding 0.5 mL of cyanide stock to 9.5 mL of 0.1 N NaOH (13 μg/mL). The samples were prepared according to following table:

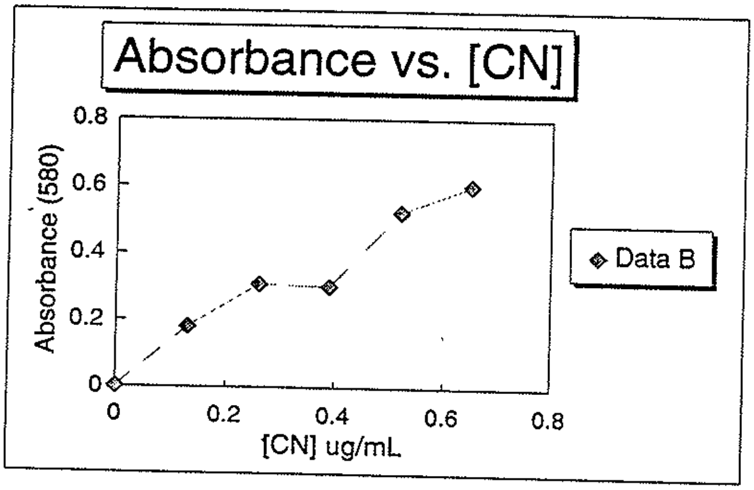
[CN] μg/mL	**0.1 N NaOH (mL)**	**Dilute CN stock (μL)**	**Total Volume (mL)**
0	1.0	0	1.0
.13	1.0	10	1.01
.26	1.0	20	1.02
.39	1.0	30	1.03
.52	1.0	40	1.04
.65	1.0	50	1.05

**based on Colorimetric determination of cyanide (Halkier 1988) and Lambert Cyanide Assay

Step 11. Each samples was transferred into a smaller test tube that was wiped with tissue to make sure fingerprints were eliminated. The smaller test tube was then placed in the spectrophotometer and the absorbance was read and recorded. The aborbances obtained follows.

Results from Standard Curve and Regression:

Standard	**Absorbance (580)**	**Predicted Absorbance**	**[CN] μg/mL**
0	0	0	0
1	.18	.171	.13
2	.307	.292	.26
3	.3	.285	.39
4	.522	.494	.52
5	.602	.572	.65



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                    Regression Output:
Constant                                          0
Std Err of Y Est                            0.05057
R Squared                                  0.947354
No. of Observations                               6
Degrees of Freedom                                5

X Coefficient(s)            0.94993
Std Err of Coef.           0.052453
```

***Sinarundinaria fangiana* Leaves**				
Sample #	Absorbance (580)	Average Absorbance	[CN] μg/mL	[CN] μg/g dry weight
1A	.022	.0265	0.028	14
1B	.031			
2A	.012	.011	0.012	6
2B	.010			
3A	.013	.0135	0.014	7
3B	.014			
4A	.051	.0495	0.052	26
4B	.048			
5A	.018	.018	0.019	9.5
5B	.018			

***Sinarundinaria fangiana* Branches**				
Sample #	Absorbance (580)	Average Absorbance	[CN] μg/mL	[CN] μg/g dry weight
1A	.013	.0115	0.012	6
1B	.010			
2A	0	.004	0.004	2
2B	.008			
3A	.020	.017	0.018	9
3B	.014			
4A	.005	.007	0.007	3.5
4B	.009			
5A	.010	.010	0.011	5.5
5B	.010			

***Fargesia denudata* Leaves**				
Sample #	Absorbance (580)	Average Absorbance	[CN] μg/mL	[CN] μg/g dry weight
1A	0	0	0	0
1B	0			
2A	.005	.004	0.004	2
2B	.003			
3A	.011	.0095	0.010	5
3B	.008			
4A	.005	.0055	0.006	3
4B	.006			
5A	.015	.0125	0.013	6.5
5B	.010			

***Fargesia denudata* Branches**				
Sample #	Absorbance (580)	Average Absorbance	[CN] μg/mL	[CN] μg/g dry weight
1A	0	0	0	0
1B	0			
2A	.010	.0125	0.013	6.5
2B	.015			
3A	.005	.004	0.004	2
3B	.003			
4A	.011	.009	0.009	4.5
4B	.007			
5A	.003	.0035	0.0035	1.75
5B	.004			

Sample Calculations:

$$\text{Average Absorbance:}\quad \frac{\text{Absorbance 1A + Absorbance 1B}}{2}$$

$$\frac{.022 + .031}{2} = .0265$$

$$[\text{CN}]\ \mu\text{g/mL:}\quad \frac{\text{Average Absorbance}}{\text{Slope from Regression}} = \frac{0.0265}{0.94993} = 0.028$$

$$[\text{CN}]\ \mu\text{g/g:}\quad \frac{\frac{\mu\text{g [CN]}}{\text{mL}}}{\frac{0.002\ \text{g}}{\text{mL}}} = \frac{0.028}{0.002} = 14$$

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