Chris Stapleton*: **Form and Function in the Bamboo Rhizome**

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Abstract

Bamboo rhizomes are taxonomically and horticulturally very important, but the terminology used to describe them has often been confused or imprecise. Two major forms of rhizome prevail. The terms pachymorph and leptomorph were favoured by McClure and their use is recommended, rather than the terms sympodial and monopodial. The separation of terminology describing culm growth from that describing rhizome form is considered beneficial, and the term amphipodial is considered to be potentially misleading and undesirable. The possible functions of two particular forms of rhizome are suggested. The long hollow necks of the pachymorph rhizomes in certain *Yushania* species may be an adaptation to seasonally waterlogged sites, and the metamorph II axis seen in *Vietnamosasa* species may be related to a high incidence of fires in their natural habitats. The distribution patterns of bamboos with several different rhizome forms in the Himalayas are described in relation to precipitation, and various functions of the two major rhizome forms are discussed.

Introduction

Although they are not the most accessible parts of the plant, rhizomes are particularly important in the bamboos, both ecologically and horticulturally. They control when the culms develop and how they spread, and they also dictate vegetative propagation techniques. Taxonomists have not always considered rhizome forms to be important in bamboo classification. They continue to this day to disagree upon their value, and whether they should be used to separate subtribes. However, it is now accepted that rhizome form, in conjunction with other characters, is very useful for the separation of bamboo genera. Nevertheless, there is a great deal of confusion at the present time as to which terminology is appropriate for bamboos with particular forms of rhizomes, and how the different terminologies relate. These misunderstandings can cause difficulties even at the highest levels of study. Watanabe et al (1994), in a cladistic analysis of chloroplast DNA from Asian bamboo genera related morphological variation to DNA restriction site mutations. They mistakenly thought they could not demonstrate a clear distinction between the DNA of genera with monopodial and sympodial rhizomes, as they did not apply the terms accurately, incorrectly attributing *Melocanna* Trin., *Thyrsostachys* Gamble, and *Yushania* Keng f. with possession of monopodial rhizomes. It is understandable that in this state of confusion many horticulturalists are happy to call them simply clumpers or runners.

McClure (1966) gave a very detailed and perceptive description of the bamboo rhizome. He separated two distinct forms, now most commonly known as the pachymorph (or sympodial) form, and the leptomorph (or monopodial) form. He generously attributed this distinction to the Rivières (1878), although they had been describing the clumping habit (caespitose or spreading) rather than the rhizome itself. McClure was in fact the first to describe the two different forms of rhizome, applying the terms sympodial and monopodial in his first publication (McClure, 1925).

This distinction is well understood by most of those who have any experience of handling bamboos. However, several terms have been coined for these two forms of rhizome, and this has caused confusion. The problem is compounded when ambiguous terminology is introduced, especially the term amphipodial, which blurs the distinction unnecessarily. McClure (1966) gave an illustration of *Chusquea fendleri* Munro, in which leptomorph rhizomes produce very swollen tillering culm bases, some having marked horizontal growth, and appearing very similar to pachymorph rhizomes. The rhizomes of such bamboos have been described as

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amphimorph or amphipodial. The use of these terms may be rather misleading, however. They clearly imply possession of both leptomorph and pachymorph rhizomes in a single plant, but so much depends upon how a rhizome is defined. In a segmented plant such as a bamboo, with all axes based simply upon nodes and internodes, it is difficult to produce a watertight definition of a rhizome or any other class of axis. When does a rooting culm base or branch base become a rhizome? In a plant such as *Chusquea fendleri* in which the mature leptomorph rhizome axes are so well differentiated from all other axes, it could be asked whether it is correct to describe any other part of the plant as rhizome as well.

I personally think that the principal cause of confusion in the description of bamboo rhizomes is the lack of separation of terminology that is applicable strictly to the rhizome from terminology designed to cover culm or clump habit. There has too often been an attempt to describe both with a single term. It is much more satisfactory if descriptions of bamboos include clear-cut simple terms for the rhizomes below the ground, and a further note of how the culms arise above the ground, in which case potentially misleading terms such as amphimorph and amphipodial are not necessary. McClure (1973) followed this practice in his precise descriptions of American bamboos.

Rhizome Terminology

The classification of bamboo rhizomes may appear to have become very complicated, but several terms are clearly synonymous. Essentially bamboo rhizomes vary only in how they branch, and in the appearance of their constituent internodes. There are two clear-cut forms of branching. Those rhizomes that branch rarely and can stay under the ground with indefinite apical growth have monopodial branching (Fig. 1). Those rhizomes that rise up to form a culm every year and cannot stay under the ground must branch repeatedly. They could form a structure known as a sympodium (Fig. 2), where an axis (the rhizome) is actually composed of many sections of separate axes that have branched repeatedly. This is why such rhizomes are said to have sympodial branching. In fact a single axis as portrayed in Fig. 2 is rarely produced, and a much more complex ramification is usual, without any clearly defined sympodium, so that the term sympodial is being applied rather loosely. The terms monopodial and sympodial can also cause confusion as they seem at first sight to be applicable to the culms rather than the rhizomes. Lin (1961) unfortunately misused them in this way, which may be why McClure decided not to continue using these terms himself.

The growth of the rhizome can also be described as determinate or indeterminate, and this distinction reflects an important difference in the longevity of their apical meristems, but these terms are now rarely used for the rhizome. Determinate is equivalent to sympodial, and indeterminate to monopodial.

There are also two forms of rhizome appearance. The internodes are usually either thickened somewhere along the rhizome (pachymorph) or uniformly thin (leptomorph), relative to the culm. Fortunately monopodial rhizomes are always leptomorph, and sympodial rhizomes are always pachymorph. Thus all these terms are synonymous: monopodial = leptomorph = indeterminate, and sympodial = pachymorph = determinate.

McClure in his final glossary (1973) used the terms pachymorph and leptomorph in preference to all other terminology, but in the Chinese taxonomic literature the terms monopodial, sympodial, and amphipodial reign supreme. In popular accounts a variety of terminologies are applied, and in one account (‘Bamboos of China’: Wang & Shen, 1987) their use seems difficult to understand at all unless the captions to the figures have become juxtaposed.

The term metamorph (changing form), introduced by McClure (1966; 1973), was never applied to the rhizome system as a whole, but was used to describe short sections of axes that

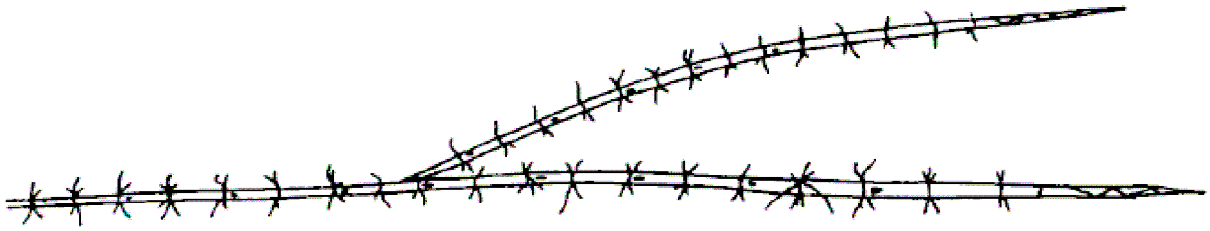

Figure 1. Rhizome branching pattern known as monopodial. The rhizome is leptomorph, with monopodial branching, and indeterminate growth. The culms may be diffuse or pluricaespitose, according to the degree of tillering at the culm base.

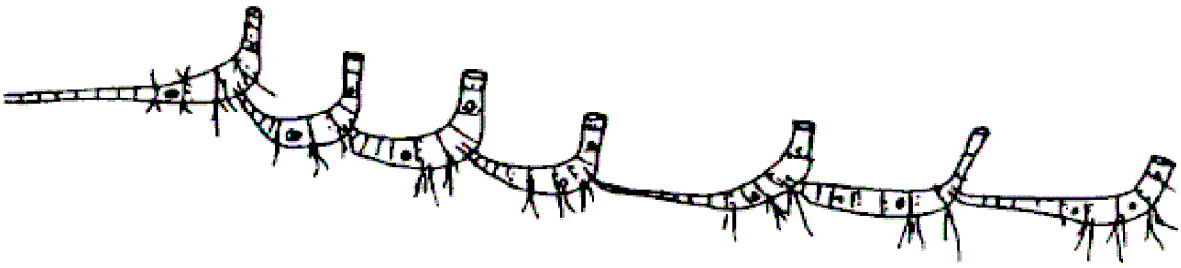

Figure 2. Rhizome branching pattern known as sympodial. The rhizome is pachymorph, with sympodial branching, and determinate growth. The culms may be unicaespitose, pluricaespitose, or diffuse according to the neck length and variability.

Figure 3. Rhizome leptomorph with monopodial branching and indeterminate growth, with tillering culms giving a pluricaespitose habit. This is often known as an amphipodial rhizome.

came between the rhizome and the culm, in effect culm bases. I do not believe that McClure would ever have applied the term to the entire rhizome system of the plant as applied by Lin (1978) or in the book 'Chinese Bamboos' (Chen & Chia, 1988), and it should be considered an optional accessory refinement rather than a fundamental category. The metamorph I axis of McClure (1966) encompasses tillering of culm bases in both leptomorph and pachymorph rhizomes. The metamorph II axis is apparently peculiar to the pachymorph rhizomes of the genus *Vietnamosasa* T.Q. Nguyen, and I suggest below that this may reflect an unusual adaptation of the rhizome to a particular habitat.

The term amphipodial is widely used for bamboos that tiller from the base of culms arising from leptomorph rhizomes (Fig.3). As stated before, the term amphipodial implies possession of both monopodial and sympodial rhizomes. However, the tillering culm bases are not usually as thickened as a normal pachymorph rhizome, and they do not usually have a pronounced horizontal growth habit (diageotropic growth). Given the disparity between culm and leptomorph rhizome in such plants it is hard to consider these culm bases to be rhizome at all. Are all swollen branch bases with aerial roots from the mid-culm region of bamboos also to be classed as rhizomes?

Pachymorph rhizomes are thickened at some point, but they may have long thin necks (long-necked pachymorph), which usually bear no roots. These long necks have also been termed pseudowhips (Keng, 1982) and rhizoids (Wen, 1985). In some bamboos with long-necked pachymorph rhizomes, such as *Melocanna baccifera* Kurz and *Guadua angustifolia* Kunth, the neck length is fairly uniform. In others, such as *Yushania* species, the length of the neck varies greatly. The thickened portion of the rhizome has several buds, from which new rhizomes can grow. In *Yushania* new rhizomes that arise from buds at nodes lower down and closer to the neck of the parent rhizome will themselves have long necks. New rhizomes that arise from buds at nodes higher up the parent rhizome and closer to the culm have progressively shorter necks, the highest nodes giving the shortest rhizomes. In this way each rhizome gives birth to an array of daughter rhizomes with different neck lengths (see Fig. 4).

Culm and Clump Terminology

How the culms arise from the rhizome is also very important. In many cases the actual rhizomes of a bamboo are not investigated and a description of a bamboo is based upon what can be seen above the ground. In many cases it is not possible to deduce what the rhizome is like from the above-ground appearance. Similarly it may not be possible to predict how a bamboo will appear above the ground from the form of rhizome alone. Therefore a separate description is very useful for the culm or clumping habit, and fortunately the terminology for this is not as complicated as rhizome terminology.

The culms of a bamboo may arise in a consistently well-separated fashion from vigorous leptomorph rhizomes. In such a pattern of growth we can simply call the culms diffuse, arising singly, or isolated. The culms of bamboos with pachymorph rhizomes without long necks arise in a clump and are caespitose (strictly unicaespitose, alternative spellings cespitose, unicespitose, etc.), and always arise together in a clump. In bamboos with consistently long-necked pachymorph rhizomes, the culms may also arise singly in an isolated fashion, as in *Melocanna baccifera*. In bamboos in which the neck length varies, such as species of *Yushania*, a series of small separate clumps is produced. Such culms are pluricaespitose (also sometimes called multicaespitose or compound-caespitose). The culms of many bamboos with leptomorph rhizomes will often tiller at the base giving small separated clumps of culms. These are indistinguishable from the small separated clumps of culms arising from bamboos with long-necked pachymorph rhizomes, and their culms can also be called pluricaespitose. It is felt that 'rhizomes leptomorph; culms pluricaespitose' is a better way to describe these bamboos than

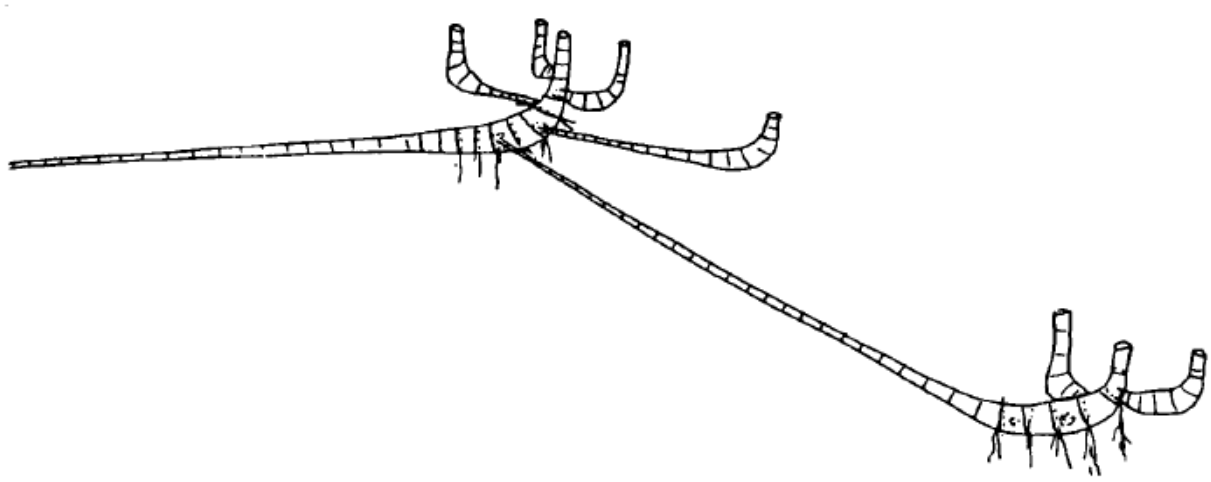

Fig. 4. Pachymorph rhizome of *Yushania* with variable neck length, giving a pluricaespitose culm arrangement.

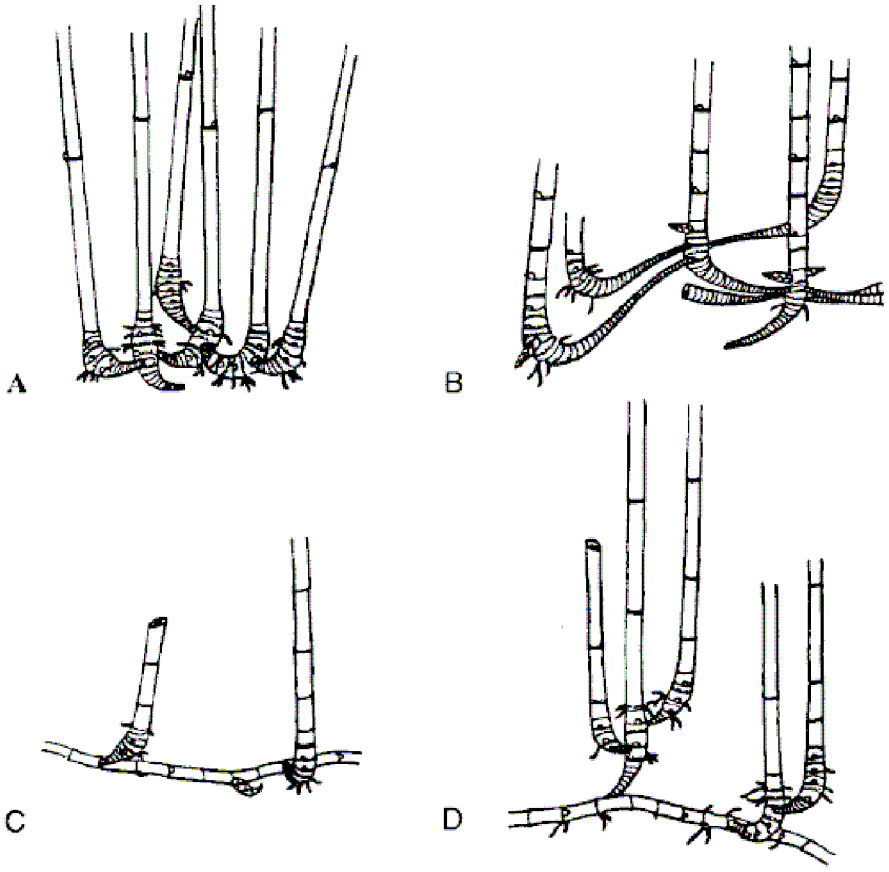

Fig. 5. Suggested terminology for four classic forms of rhizome and culm development. (Illustration from But et al., 1985, with permission of artist Mr. Deng Ying-feng)

A – Rhizome pachymorph with short necks, culms unicaespitose.
B – Rhizome pachymorph with consistently long necks, culms diffuse.
C – Rhizome leptomorph, culms diffuse.
D – Rhizome leptomorph, culms pluricaespitose.

referring to their rhizomes as amphipodial.

The rhizomes and culms of some bamboos are well known for their different behaviour under different environmental conditions, and in juvenile and mature stages of growth. This usually applies to those bamboos that have leptomorph rhizomes when they are mature and growing vigorously. They can at times produce tillering clumps of culms with no real rhizome development. This can easily cause confusion in young plants or in plants growing away from their natural habitat. This variation in habit is one argument against the use of the term amphipodial. It leads to great overlap between the terms monopodial and amphipodial in the bamboos with leptomorph rhizomes at maturity, making the terms very difficult to define accurately or consistently.

Thus it seems accurate and quite adequate in presently known bamboos to describe the rhizome and culm habit of a bamboo according to whether the mature rhizomes are thickened (pachymorph) or uniformly thin (leptomorph); if thickened then either short or long (with or without elongated necks); and whether the culms arise singly (diffuse), in one large clump (unicaespitose), or in many small clumps (pluricaespitose). Combinations of these characteristics can be used in cases where they are variable. Leptomorph and pachymorph seem more appropriate than monopodial and sympodial, and amphipodial or amphimorph seem to be rather ambiguous and potentially misleading. As it is now becoming customary in definitions of bamboo rhizome terminology to give one's own preferred names for the four classic illustrations (But et al., 1984; Wen, 1985; Chen & Chia, 1988), I give my own interpretations of these in Fig. 5. This terminology will be followed in Kew's World Grasses Database, and in morphological and cladistic analyses undertaken at Kew.

Function of Different Rhizome and Clump Forms

The rhizome is obviously a crucial component of the bamboo plant, and it clearly has several different functions. The balance between these functions can be related to different habitats under which bamboos with different classes of rhizome grow, and a few interesting forms of rhizome development can probably be attributed to adaptation to particular environments.

In *Yushania microphylla* (Munro) R.B. Majumdar the elongated rhizomes necks are completely hollow, even at the nodes, forming long uninterrupted tubes, and this may be related to the seasonally waterlogged sites in which this species is usually found. Hollow rhizomes may have developed from solid rhizomes, as an adaptation allowing transport of air to culms growing in wetter locations, or just to allow the rhizomes to grow further through soft soil. On the other hand, it may be that solid rhizomes have evolved from weaker, hollow rhizomes, in order to break through drier soil. McClure (1973) described small hollow rhizome canals in *Arundinaria gigantea* (Walter) Muhlenberg, which also often grows in seasonally waterlogged conditions.

The axes of *Vietnamosasa* species described as metamorph II by McClure (1966) are also quite distinctive. At first sight it seems as though the elongated neck has been placed at the wrong end of the rhizome. I suspect that the metamorph II axis between the rhizome and the shoots may be an adaptation to fire. All the collections that I have seen have suffered from fire-damage, coming from seasonally dry areas in Vietnam and Thailand, such as the area through which McClure travelled in 1953. It may seem surprising for a plant which is generally considered to require abundant water to be adapted to a fire-climax environment, but one form of bamboo fire-adaptation has already been described (Soderstrom, 1981), in the South American genus *Actinocladum* Soderstrom. In *Vietnamosasa* the metamorph II axis would ensure that the real rhizome remains deeply buried during fires, while still allowing rapid new growth of shoots, despite the variation in intensity and depth of soil-penetration of the

fire. The axis slants through the soil and bears many buds. It can produce new tillering culms and rhizomes from its new apex when all above-ground parts of the plant are burnt away. It will always have new buds just below the level of penetration of the fire, so that new shoots can compete well with other vegetation immediately. Slanting of the metamorph axis would reduce apical dominance and allow several shoots to grow at once.

It is not quite so easy to postulate why leptomorph and pachymorph rhizomes have developed, but their distribution is certainly interesting. In the Himalayas there are only two species with leptomorph rhizomes, *Arundinaria racemosa* Munro and *Chimonobambusa callosa* (Munro) Nakai. These species are restricted to the eastern end of the mountain chain, where rainfall is highest. The endemic species with long-necked pachymorph rhizomes, such as *Yushania maling* (Gamble) R.B. Majumdar, extend further west to areas where the rainfall is only moderate. They are also found at the western end of the Himalayas, where although the rainfall is lower, it is more evenly distributed, with more winter rain. In the central Himalayas, where spring rainfall is lowest, there are only unicaespitose bamboos.

This variation in distribution could be related to the ability of long rhizomes to penetrate through very dry soil during a spring drought. To reach up to several metres underground as well as producing tall culms, spreading bamboo rhizomes require a longer period during which growth is possible. Thus the unicaespitose habit as seen in most Himalayan genera such as *Bambusa* Schreb. and *Drepanostachyum* Keng f. could be an adaptation to the driest conditions under which bamboos can grow. The pluricaespitose habit in pachymorph bamboos, as exemplified by *Yushania*, could reflect a combination of the ability to consolidate in one location when spreading is not possible, with the ability to spread when conditions are more suitable. The pluricaespitose habit in leptomorph bamboos, as seen in *Chimonobambusa* Makino and *Arundinaria* Michx., leads to an emphasis on spreading rather than consolidation, but is possible only when spring rainfall is more reliable. The true diffuse monopodial habit, as exemplified by the leptomorph rhizomes of many species of *Phyllostachys* Sieb. & Zucc. in their natural environments, is not indigenous to the monsoonal Himalayas, and may only occur where conditions are most favourable, in areas with ample rainfall more evenly distributed throughout the year, allowing sustained growth through spring, summer, and autumn.

The advantages of spreading bamboos over non-spreading types in suitable locations are apparent. Quick colonisation of new sites is possible, and the sharp rhizomes can also penetrate the rooting systems of existing vegetation, with vigorous shoots benefiting from photosynthesis occurring elsewhere while they grow up to overshadow the vegetation at a different site. Such an effective vegetative dispersal mechanism may have implications for aspects of reproductive biology, for example length of flowering cycles, and the ability to survive flowering. Longer flowering cycles might be expected in spreading bamboos, with a reduced tendency for the plant to exhaust all reserves and die after producing too much seed. In addition, spacing of the culms may reduce parental competition and the benefits to seedlings of parental death, further encouraging polycarpy.

In the unicaespitose bamboos with pachymorph rhizomes dispersal is more reliant upon successful seed production. Short rhizomes cannot transport the plant very far. Dispersal can sometimes be effected above the ground by the rooting of branch bases when older culms fall down or arch across a stream. This may be one reason why the unicaespitose bamboos have retained relatively primitive, heavy branch architectures, while spreading genera such as *Phyllostachys* have developed more sophisticated and more efficient arrangements of their branches and foliage. The thickening of the pachymorph rhizome definitely allows greater storage potential, however, especially in those tropical bamboos that lose most of their leaves in an annual drought, and in these bamboos this is certainly a more important function of the rhizome than dispersal. Overall, as a broad generalisation, pachymorph rhizomes clearly

represent a better adaptation to relatively dry conditions, with hard soils and periodic droughts.

The preponderance of primitive, iterauctant 6-stamened inflorescences in bamboos with pachymorph rhizomes has been taken to suggest that other characteristics of such bamboos are closer to the most primitive ancestors of today's bamboos, and therefore it has been conventional to treat pachymorph rhizomes as more primitive and ancestral, consequently considering leptomorph rhizomes to be relatively derived. Selection pressures upon the inflorescence and the rhizome are rather different, however, and there are pachymorph-rhizomed bamboos with 3-stamened semelauctant inflorescences, as well as leptomorph-rhizomed bamboos with 6 stamens or iterauctant inflorescences. It seems likely that all different rhizome forms would have evolved from ancestors with much less differentiation between culms and rhizomes, possibly with a more irregular scrambling or stoloniferous growth habit, rooting from most nodes. This might be closer to a leptomorph rather than a pachymorph rhizome system. It is very difficult to draw any conclusions as to which of these two rhizome forms would be more primitive. Today's leptomorph and pachymorph rhizomes may both be sophisticated modifications of ancestral rhizome forms. Moreover, bamboos with pachymorph rhizomes may have evolved independently from those with leptomorph rhizomes and/or vice-versa at different times in different subtribes, and there seems no reason why such developments would not be reversible. Comprehensive morphological and molecular phylogenetic analyses are required before any firm conclusions could be drawn.

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References

But, P.P.H., Chia, L.C., Fung, H.L., 1985. *Hong Kong Bamboos*. Urban Council, Hong Kong.

Chen, S.L. & Chia, L.C., 1988. *Chinese Bamboos*. Science Press, Beijing, & Dioscorides Press Inc.

Dajun, D. & Shen, S.J., 1987. *Bamboos of China*. Christopher Helm, London.

Keng, P.C., 1982. A Revision of the Bamboo Genera of the World. *Journal of Bamboo Research 1(1):* 1-19.

Lin, W.C. 1961. Study on the Classification of Bambusaceae in Taiwan. *Bulletin of Taiwan Forestry Research Institute 69:* 1-144.

Lin, W.C. 1978. *Flora of Taiwan 5:* 706-783.

McClure, F.A., 1925. Some Observations on the Bamboos of Kwangtung. *Lingnan Agr. Rev. 3:* 40-47.

McClure, F.A., 1966. *The Bamboos: a Fresh Perspective.* Harvard University Press.

McClure, F.A., 1973. Genera of Bamboos Native to the New World. *Smithsonian Contributions to Botany 9:* 1-148.

Rivière, A. & C., 1878. *Les bambous*. Société d'Acclimatation. Paris.

Soderstrom, T.R., 1981. Observations on a Fire-adapted Bamboo of the Brazilian Cerrado, *Actinocladum verticillatum* (Poaceae: Bambusoideae). *American Journal of Botany 68(9):* 1200-1211.

Watanabe, M., Ito, M., & Kurita, S., 1994. Chloroplast DNA Phylogeny of Asian Bamboos (Bambusoideae, Poaceae) and its Systematic Implication. *Journal of Plant Research 107:* 253-261.

Wen, T.H., 1985. Some Ideas about the Origin of Bamboos. *Journal of the American Bamboo Society* 6:104-113.