The morphology of woody bamboos

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STAPLETON, C.M.A., 1997. Traditional classification of bamboos has been based almost entirely upon morphological characters. In order to move closer to underlying evolutionary processes, various non-morphological data sources have been explored. However, even if such new data is natural and informative, it will still be necessary to combine it with morphology if it is to be used to full effect. This requires a re-evaluation of many morphological characters. Advances in understanding of several parts of the bamboo plant are presented, and a critique of modern interpretations of the bamboo inflorescence is given. Some areas of conflict between morphological and non-morphological characters are mentioned, and the need for continued, but more critical and objective morphological research is stressed.

KEYWORDS:— Bamboo — morphology — rhizome — branching — inflorescence — synflorescence — prophyll.

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INTRODUCTION

The taxonomy of bamboos, like that of most higher plants, has traditionally been based upon a classification derived from variation in gross morphology. One major aim of modern taxonomy is to improve upon artificial classifications, moving towards a natural classification system reflecting past relationships and evolution. To this end several other sources of taxonomically useful information have been explored. These have included anatomy, cytology, palynology, and phytochemistry,

and more recently, variation in different categories of molecular markers including DNA nucleotide sequences.

The value of such sources of information has varied widely between different groups of plants. Sometimes traditional morphological classifications have been supported, and sometimes the new evidence has suggested that they are superficial and make too many assumptions, usually about common ancestry of plants with shared characteristics that actually evolved separately. On the whole however, we can expect molecular markers to give us a valuable picture of past relationships within the bamboos. Clark (1993) predicted that gene sequences will provide the framework for further refinement of generic concepts and an overall classification.

Nevertheless, however useful or natural new data sources may be, their application still requires correlation with, or translation into morphologically-interpretable groupings. This is necessary for most work with dried material in the herbarium leading to the assignation of names, and it is essential for the recognition and identification of taxa in the field. Concepts such as the species and the genus also rely heavily upon morphology.

Morphology, therefore has both analytical and interpretative functions, and will always be of great importance in the naming and identification of bamboos. However, it requires rather more careful study than it has been afforded in the past. Three criticisms can be levelled at old-fashioned approaches to morphology. Firstly they were often superficial. Similarities have often taken priority over differences, and this can lead to lumping of distantly related plants into artificial groupings. Secondly, with most taxonomic work taking place in the herbarium, morphological characters that are more easy to assess from a mounted specimen have often taken undue precedence. It has often been assumed that reproductive characters have more evolutionary significance, and less accessible organs such as rhizomes and branch complements have only recently received detailed investigation.

Thirdly, characters have often been considered in isolation, and it might be assumed that a more equitable, and presumably more natural system would result from analysis of variation in several morphological characters together. In a natural classification there is often a need for flexible interpretation of rules. Using an artificial system it is possible to group too rigidly and dogmatically according to the possession of a single character. However, the evolution of plants is by definition a random process. One result of this is that some plants that might be expected to have certain morphological characters will lack them. Such enigmas may arise from throwbacks to earlier forms, or the loss of a character in an advanced community, or from the incorporation of new genetic material through hybridisation. This may be the case more often in benign environments where novelty is not a liability (the 'morphological caprices' of van Steenis, 1969), or in recently colonised areas where competition is reduced. Therefore, as natural variation can obscure a single character, it may be better to compare groups of morphological characters together.

Thus the study of morphology is here to stay. It involves give and take with newer, often more powerful and revealing technologies, and it requires a flexible degree of interpretation. Even if technology provides a hand-held DNA extractor and sequencer and access to vast data banks of known sequences for the identification of plants, someone is still going to ask, "What do they look like?"

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CLARIFICATION OF MORPHOLOGICAL DETAIL

Rhizomes

Little appreciated until McClure (1966) re-emphasised the earlier distinction made by Rivière & Rivière (1878) between two major forms, the rhizome is a fundamental component of the bamboo plant. It has undoubted ecological and phylogenetic significance. Different authorities have placed different emphasis upon the taxonomic importance of the rhizome, but it is now widely accepted to be of great importance at generic and higher levels, at least in the Old World bamboos.

The terminology used to describe rhizomes has often been confused or imprecise. Stapleton (1996) has reviewed terminology and made some suggestions as to the adaptive significance of certain forms.

The rhizome is by definition the part of the plant bearing roots. Two major groups of rhizome prevail, although it is still far from clear which should be considered ancestral, and derived forms may have evolved at different times in different groups of bamboos. The terms pachymorph and leptomorph were favoured by McClure (1966), probably for several reasons. Their use seems more appropriate than the terms sympodial and monopodial, which relate more to branching patterns than actual morphological form. In addition, the terms sympodial and monopodial invoke too much overlap with clump form. They are often translated directly to feet together and single feet, as though they related to the culms rather than the rhizomes. Both systems will no doubt continue to be used. Monopodial and leptomorph can be taken as synonymous, as can the terms sympodial and pachymorph.
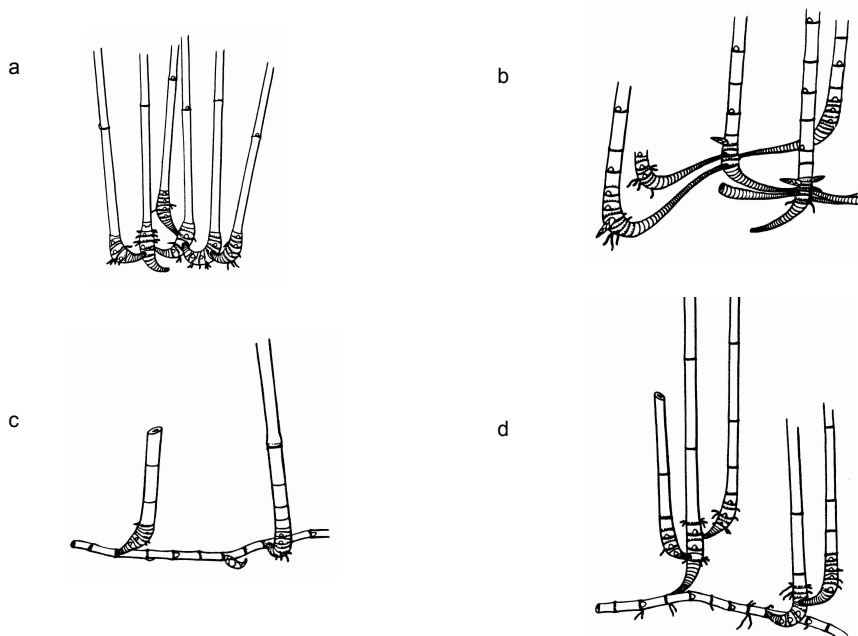

Figure 1. Four major forms of rhizome and culm growth (from But, Chia, Fung, & Hu, 1985, reproduced with permission from the artist Mr Ding Ying-feng): a, Pachymorph (short-necked); b, Pachymorph (long-necked); c, Leptomorph (culms single); d, Leptomorph (culms tillering).

The description amphipodial or amphimorph has often been applied, but it is also potentially rather misleading. It can obscure a clear-cut distinction between the two major groups of rhizome form. To improve upon all these single terms it is very helpful to separate terminology describing culm growth from that describing rhizome form. These characters are separate and can vary independently. Thus leptomorph with tillering culms is less liable to misinterpretation than amphipodial or amphimorph. The term monopodial has also often been misunderstood. Leptomorph with culms arising singly, or long-necked pachymorph with separated culms describe two superficially similar 'single-foot' forms with more clarity. Four major forms of rhizome and culm growth have been depicted in many publications. Appropriate terminology to describe them is given in Fig. 1.

Branch complements

Usui was the first to look in detail at buds and branching. He investigated the Japanese genera (1957), and McClure (1966: Fig. 28) reproduced his work, adding examples of more complex branching from New World bamboos. McClure did not have enough material to complete this work, however, and the terminology that he started to apply just before his death (1973) such as 'apsidate' and 'gremial' and 'insertion restricted' was a little incomplete and rather imprecisely defined. It has only been applied to the highly advanced branch complements found in the New World.

The mature bamboo branch complement is often rather complex and difficult to interpret accurately. McClure (1966) stressed the value of the prophyll in vegetative and floral branching patterns. The prophylls within a branch complement can show exactly where branching occurs and new axes commence. They provide reference points against which other sheaths can be mapped and named. Adaptation of the prophyll itself also provides very useful characters in its own right. In bud-scales it can become variously reduced or merged, and its margins can become fused together.

More recent studies (Hsiung et al, 1987; Usui, 1987; Stapleton, 1991) have added greater detail to show a wider range of distinctions and characters. A basic and presumably ancestral pattern of branching has been described for most tropical genera and a few temperate genera including *Arundinaria* and *Thamnocalamus* (Stapleton, 1994b), Fig 2a.

More complex branch complements are seen in genera such as *Fargesia*, *Yushania* and *Borinda* (Fig. 2b). A process of reduction can explain axes not subtended by sheaths, although some form of replication of axes at an early developmental stage would be an alternative explanation for ebracteate axes. Fusion can explain modification of the prophyll into a protective budscale. More substantial reduction of sheaths, including the prophyll, can explain the apparent insertion of multiple buds in S. American bamboos such as *Chusquea culeou*, in which vestigial remnants of such missing sheaths can be seen (Stapleton, 1991), Fig. 2c.

Characteristics of the buds and branch complements can serve to distinguish between species with superficially similar inflorescences. For example, *Himalayacalamus falconeri*, *Thamnocalamus spathiflorus*, and *Fargesia murieliae* all have dense inflorescences, and they have consequently all been placed in a broad interpretation of *Thamnocalamus* at one time or another. Radical differences between their buds and branch complements, however, suggest that they are not in
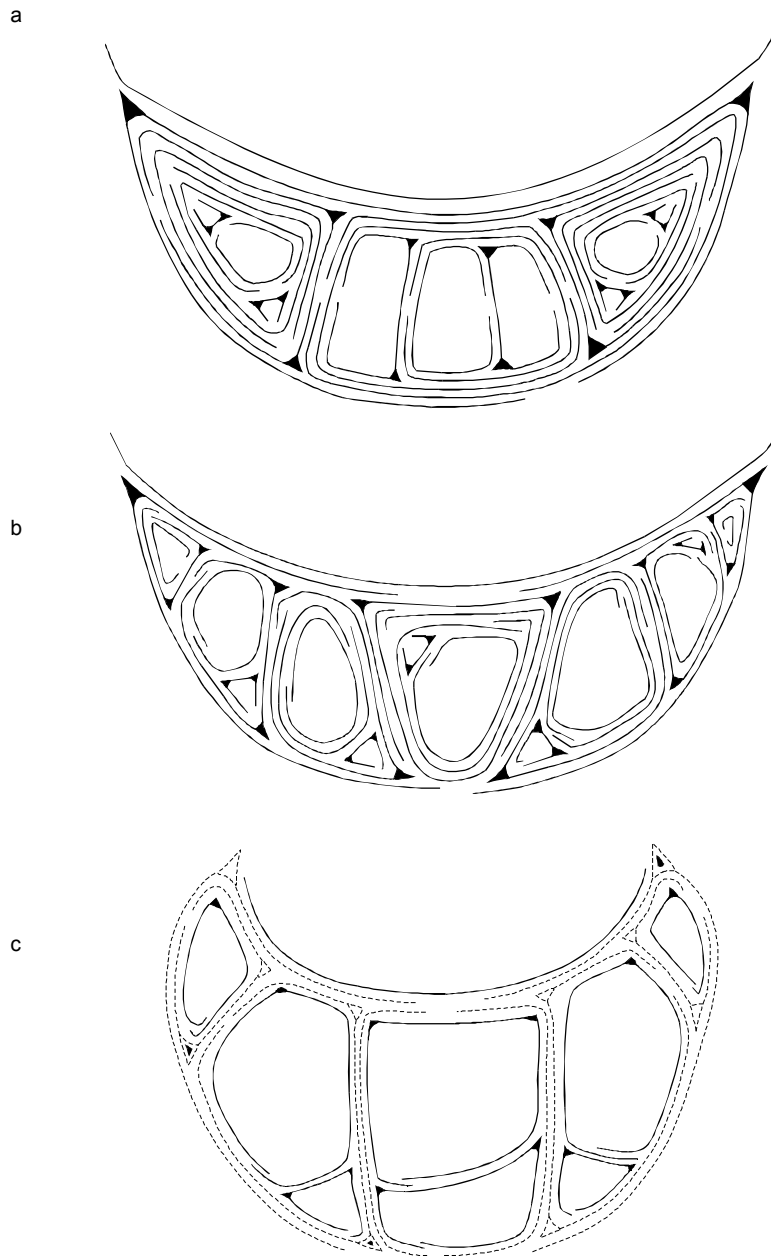
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Figure 2. Schematic cross-sections of mid-culm branching: a, Complete pattern in *Thamnocalamus spathiflorus*; b, Reduction of prophyll and sheaths in *Borinda grossa*; c, More substantial reduction in *Chusquea culeou* (solid lines—sheaths and keel remnants observed; dotted lines—hypothetical sheaths before reduction from pattern as seen in b).

fact closely related after all. Similarly, species of *Pleioblastus* can be distinguished from N American and Asian *Arundinaria* species by the universal closure of the front of the buds. This is a characteristic the genus *Pleioblastus* shares with *Pseudosasa*, *Sasa*, and *Indocalamus*. McClure (1966) treated *Pleioblastus* as a synonym of *Arundinaria*, but that may be because he recorded this character incorrectly, repeating Takenouchi's incorrect illustration of *Pleioblastus simonii* with open prophylls (McClure, 1966: Fig. 42), even though he also reproduced Usui's more correct illustration (1957) of *Pleioblastus* with closed prophylls (McClure, 1966: Fig. 28).

INFLORESCENCE STRUCTURE

The bamboo inflorescence is an area of morphology with some serious problems of interpretation, homology and terminology. The similarity between vegetative structure and inflorescence components in many bamboos has often led to difficulty in delimitation of the inflorescence—where does it start? The sharp distinction between the inflorescence and the vegetative section of the normal grass plant is lacking in many bamboos.

A totally flowering bamboo clump was in the past sometimes called a single giant panicle. At the other extreme, the entire plant has also been considered in terms of a vegetative-style distichous branching system, with the trimerous nature of even the gynoecium being questioned. Clifford (1988) reviewed these and various intermediate interpretations. It would now seem safe to state that the lemma and palea cannot be derived from whorled perianth forbears and are essentially vegetative in origin, if only because they are borne on two different axes. Therefore the 'real flower', if anything in the grasses really is analogous to the two perianth whorls in other families, has to start after the palea at least. The conventional view, as portrayed by Arber (1934: Fig. 58) and repeated by McClure (1966: Fig. 54) interprets the lodicules as the inner perianth whorl, assuming from the topology relative to the prophyll that the outer whorl has become lost.

A modern interpretation

If we are to follow a modern approach to inflorescence structure (Weberling, 1989), we have to incorporate this definition of the real flower into our analysis and terminology. We ought to treat any bamboo 'inflorescence' as a modification of what seems best described as a simple polytelic synflorescence. Unfortunately the modern approach has been applied in different ways at different times. A more logical but possibly rather radical re-evaluation of the structures and terminology is long overdue in the grasses.

Following the simplest interpretation, each spikelet includes a fully bracteate florescence, as well as glumes or gemmiparous bracts. Soderstrom & Londoño (1988) used this homology in *Alvimia*, and this is much more satisfactory than the description of *Maclurolyra* given earlier (Calderón & Soderstrom, 1973), in which the whole spikelet was interpreted as a single flower. This type of synflorescence was depicted by Weberling (1979: Fig. 122). A hypothetical grass equivalent is portrayed in Fig. 3. The terminal spikelet of each synflorescence includes the main florescence. All the others, the lateral spikelets on the many different orders of branch (paraclades), include a coflorescence. As the grass spikelet is rather consistent, so is the 'florescence'. It is simple, sessile, and bracteate, and is always a spike.
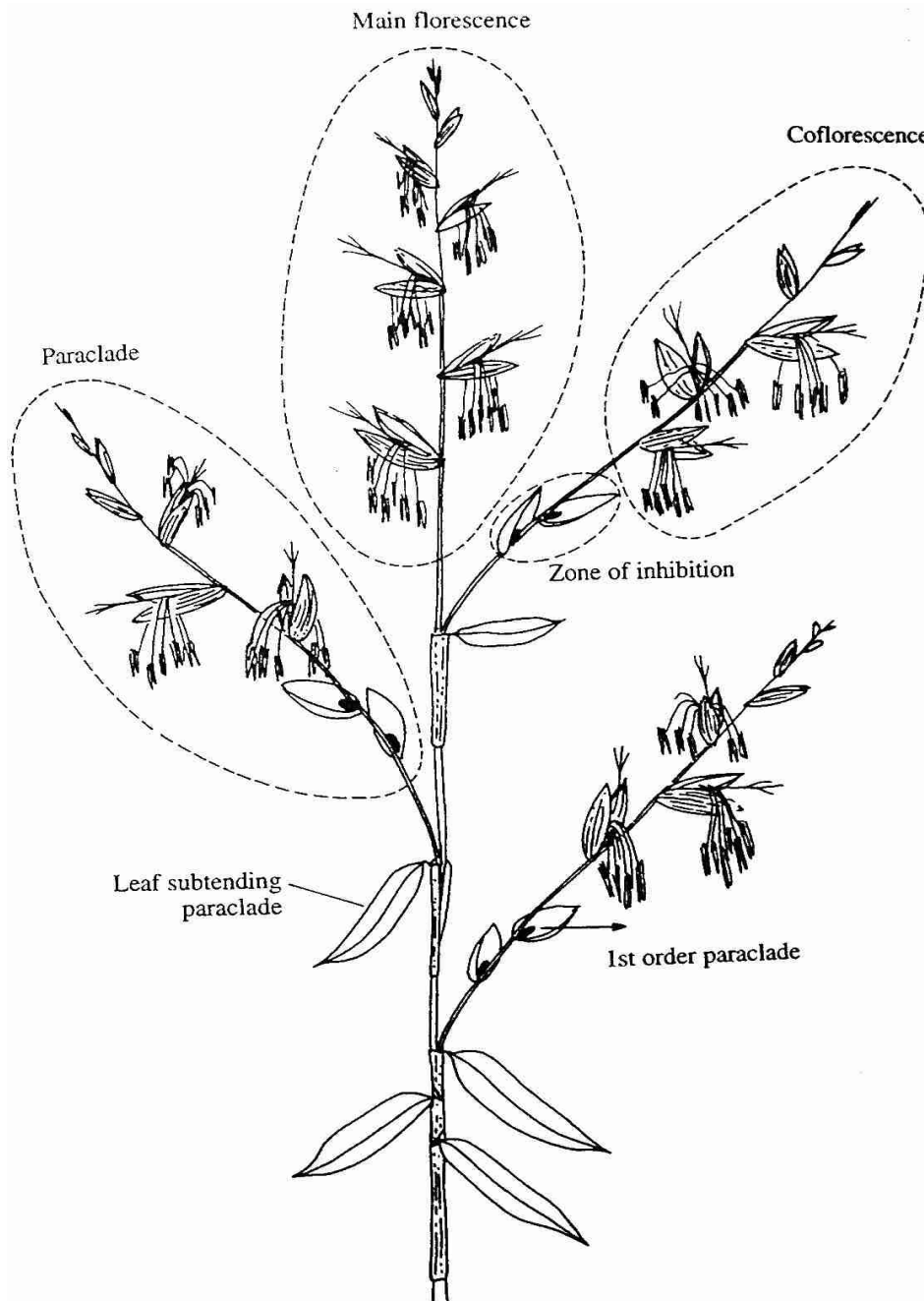
Figure 3. Hypothetical bamboo equivalent of the simple polytelic synflorescence portrayed in Weberling (1989: Fig. 122), with application of terminology for component parts.

As the flowers are sessile and borne in a spike, there is never any true pedicel. This would have to come somewhere between the lemma and the lodicules if it existed. In addition the palea never subtends buds or additional axes. Therefore there is no way the florescence can become a multi-axial or compound panicle in the sense in which this term is used in other plant groups. Each pherophyll (the lemma) subtends an unbranched axis bearing a single addorsed prophyll (the palea) and a single flower (lodicules, androecium and gynoecium). Thus there is technically no such thing as a real panicle in the grasses. If there were, it would imply more than one set of lodicules, stamens and carpels within a single palea. True panicles as described by Weberling (1989) are very different, having terminal flowers and branching pedicels. As each florescence is simple there cannot be any partial florescence, and the different term partial inflorescence as referred to by Soderstrom & Londoño (1988), and Gielis & Goetghebeur, (1996) would not seem to be required either.

The closest compound florescence would be the heterothetic compound spike, but the grass glumes and certainly the gemmiparous bracts of some bamboos seem to have no counterpart in such florescences, and the similarity is probably superficial. If we were to interpret bamboo inflorescences with gemmiparous bracts as simple florescences, and those without as compound ones, then we might be creating a wholly artificial division, and it is best to assume homology in the first instance.

Applying this terminology we only need the terms florescence, paraclade and synflorescence. In addition to this, development of axes basal to the florescence becomes variously refined in the bamboos and grasses, and to understand this we need the terms enrichment zone and inhibition zone.

Below the florescence of fertile lemmas we have various empty or bud-bearing (gemmiparous) bracts. Weberling (1989) illustrated the occurrence of zones in which paraclades developed (the enrichment zone) or were inhibited (inhibition zone). Following this terminology the bamboo spikelet could be interpreted as a florescence and a proximal inhibition zone (empty glumes and gemmiparous bracts). Developed paraclades form the enrichment zone (sometimes called the supplementing zone). A third category of zone, called the innovation zone, found at the base of the main axis is responsible for annual vegetative regrowth of perennial plants. In the bamboos this would only occur in the rhizomes or from the very base of tillering culms in erect bamboos, and also from re-iterative central branches in climbing bamboos.

Such an interpretation levels grass inflorescences with those of other families, but it radically alters our concepts and terminology. It is useful for comparison of grasses to other families, but at first sight it seems to take away most of the traditional terminology that has been applied within the grasses. No wonder that it has not been widely adopted, and when applied has been used somewhat selectively and perhaps rather inconsistently.

However, if we re-apply the old terminology to the new synflorescence rather than the old 'inflorescence', we need not lose information, and we don't actually need to change many terms. A new system of terminology would accord the same distinctions used in the past, but would apply them to typology of the synflorescence, not the redefined inflorescence itself. Instead of a panicle we now have a synflorescence with paniculate branching. It may be bracteate or ebracteate, involving a certain number of orders of paraclade. As there was considerable overlap in the old terminology with one person's racemose panicle being someone else's

paniculate raceme, this could be an opportunity to become more precise and objective. Fasciculation of paraclades is another area where a better consideration of the real branching involved would also be helpful. Arber (1934) suggested that different orders of branch often coalesce at their bases, but others have treated them as whorls of primary branches instead. Some terms would have to be changed, however. Pedicels, peduncles, the rhachis, and the rhachilla would all have to be interpreted differently. We now have a rhachis in the spikelet, a peduncle below it, and paraclade internodes at all the higher orders of branching.

Although the new system of terminology may seem an unnecessary complication, some advantages may become apparent when we use it to compare the different forms of synflorescence within the bamboos. It remains to be seen whether the advantages of the new terminology increase or diminish when applied to other grasses as well.

Application to bamboo groupings

McClure (1966) introduced a major distinction between two groups of bamboos. He coined the terms iterauctant (repeatedly growing) and semelauctant (once growing) to describe two forms of the old-fashioned 'inflorescence'. The criterion he used to distinguish between the two groups was the presence of buds at the base of the spikelet. He also mentioned several other characteristics often associated with the presence of buds, and thus described two broad syndromes, acknowledging that there was considerable variation within each syndrome.

Looking carefully at his descriptions of the two syndromes and comparing these to synflorescences of a wide range of Asian genera it is possible to refine his important distinction somewhat. Three characters are associated with the syndromes, each having several character states. These are 1) the bracts subtending paraclades, 2) the prophylls on the paraclades, and 3) the buds at the base of the spikelet .

A full and accurate inventory of all these fundamental characters is necessary to compare different genera effectively, and to produce the character states required for any critical quantitative analysis. If we look at these characters in depth we may learn far more about the relationships between different forms. One of the best ways to investigate a bamboo synflorescence thoroughly is to map the sheaths as they are dissected away to give a branching pattern. This can be undertaken in the same manner as for the vegetative branch complement. As an example, a *Thamnocalamus spathiflorus* inflorescence, illustrated in Fig. 4a, is depicted in Fig 4b. Once the components are mapped it is much easier to describe the four characters listed above, and then to compare synflorescences of different bamboos. The method of numbering the axes and sheaths is given in Stapleton (1991), with several examples.

SUBTENDING BRACTS

There has been a little disagreement as to how the various sheaths or bracts subtending bamboo synflorescence paraclades and spikelets have evolved. As in vegetative branching the most primitive pattern ought to consist of all axes being subtended by a proper sheath, and all sheaths subtending an axis. Whether such a truly primitive structure has really persisted in bamboos is hard to tell, but it is almost exactly what is seen in many iterauctant tropical bamboos and in the Shibataeinae.

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b

AXIS 0

(MAIN AXIS)

KEY

AXES OF SYNFLORESCENCE

2-KEELED PROPHYLL

ONE-KEELED PROPHYLL

UNKEELED BRACT

FLORET

0,(10) TO 0,(15)

FLOWERING GLUMES
IN TERMINAL SPIKELET
(MAIN FLORESCENCE)

0,(9)

UPPER EMPTY GLUME

0,8,(1)

0,(8)
(HAIRS)

0,7,(1)

AXIS 0,7

(PARACLADE)

0,(7)

AXIS 0,6

(PARACLADE)

0,(6)

0,4,(1)

0,(5)

AXIS 0,5,2

0,3,(1)

(1ST ORDER PARACLADE)

0,4,(4)
(HAIRS)

0,(4)
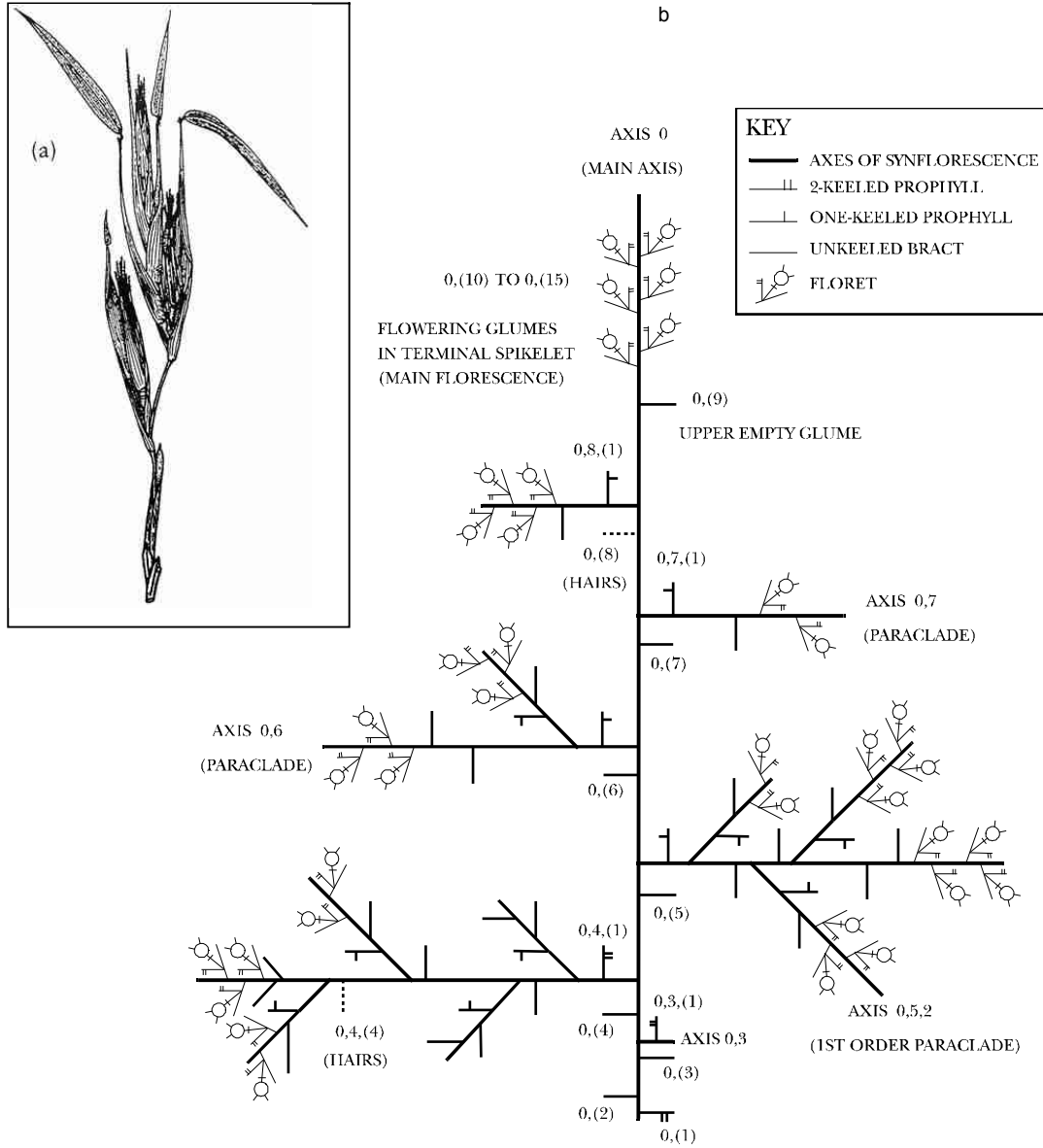
AXIS 0,3

0,(3)

0,(2)

0,(1)

Figure 4. Synflorescence of *Thamnocalamus spathiflorus*: a, Illustration; b, Map of branching and sheaths. Axes are numbered sequentially in each order of branching, e.g. AXIS 0,5,2 is the 2nd potential branch from the fifth potential branch from the main axis, AXIS 0. Sheaths are numbered sequentially on each axis and given in brackets, 0,5,(2) being the 2nd sheath on AXIS 0,5.

Holttum (1958) suggested that the ebracteate grass panicle developed from a fully bracteate inflorescence such as that of *Bambusa* by loss of bracts. However, it has also been suggested (Clayton & Renvoize, 1986) that such bracts are vegetative sheaths incorporated into a compound inflorescence of '1-spikelet racemes', each reduced from a larger synflorescence that already had lost its bracts and developed ebracteate paniculate branching of paraclades. It seems impossible to tell which is correct, as the end result is the same, but whichever evolutionary history we favour there is certainly great variation in the development of bracts subtending paraclades and spikelets.

For the sake of description, we may as well assume that the presence of large sheaths is actually primitive, so that loss of sheaths would become a matter of reduction. This is common in sheaths subtending paraclades in many flowering plants, with all the intermediate stages expected in such a process visible in different species or even within a single inflorescence. Leaves subtending paraclades (frondulose) are progressively reduced to sheaths or bracts (bracteose) and smaller bracts often eventually become just a ring or tuft of hairs at the expected locus of insertion of the bract, on the mother axis around the base of each paraclade, Fig. 5a.

PROPHYLLS

While a gradual reduction process is extremely common in sheaths subtending paraclades or spikelets, it is most interesting that it is never seen in the prophyll, at least not in its normal axillary position. It is described as being either present or completely absent. Conventional comparisons of the iterauctant and semelauctant inflorescence patterns (Holttum, 1958; McClure, 1966; Clayton, 1992) have assumed that the prophyll has simply become lost from the axil of the branch in the same manner as the bracts subtending paraclades. This sudden absence has often been taken as the major morphological distinction between iterauctant and semelauctant inflorescences. Not only is it considered that the prophyll has become lost throughout the synflorescence, several sheaths and internodes are also assumed to have disappeared to give the 'pedicel' of the normal grass spikelet.

In the absence of intermediate stages in this postulated reduction process, I have applied an interpretation of the lower glume of the lateral bamboo spikelet in the semelauctant synflorescence as a prophyll inserted on a greatly elongated promontory of the mother axis (Stapleton, 1994). The term promontory was used by McClure (1973) in the vegetative branching of South American bamboos. Calderón & Soderstrom (1973) interpreted such a portion of the branching system as the first internode of the branch, rather than the mother axis. Various compositions for the fundamental units or phytomers of grass morphology have been discussed without any clear conclusions (Clark & Fisher, 1988), but it seems more reasonable to consider such a region as an extended part of the parent axis, rather than a branch internode.

This postulated glume origin would substantially reduce the apparently dramatic difference between the two forms of inflorescence in the bamboos. Morphological evidence supporting the hypothesis is the gradual extension of successive vegetative, paracladial, and spikelet promontories in *Thamnocalamus spathiflorus*, Fig. 5b. This process would represent a form of metatopic displacement, or the displacement of fused organs. This is similar to the recaulescence of bracts seen in many other plants and illustrated by Weberling (1989). Caulescence might be a better term for this

(a)

sheath 0,(8) reduced
to ring of hairs

base of entire sheath 0.(7)

(b)

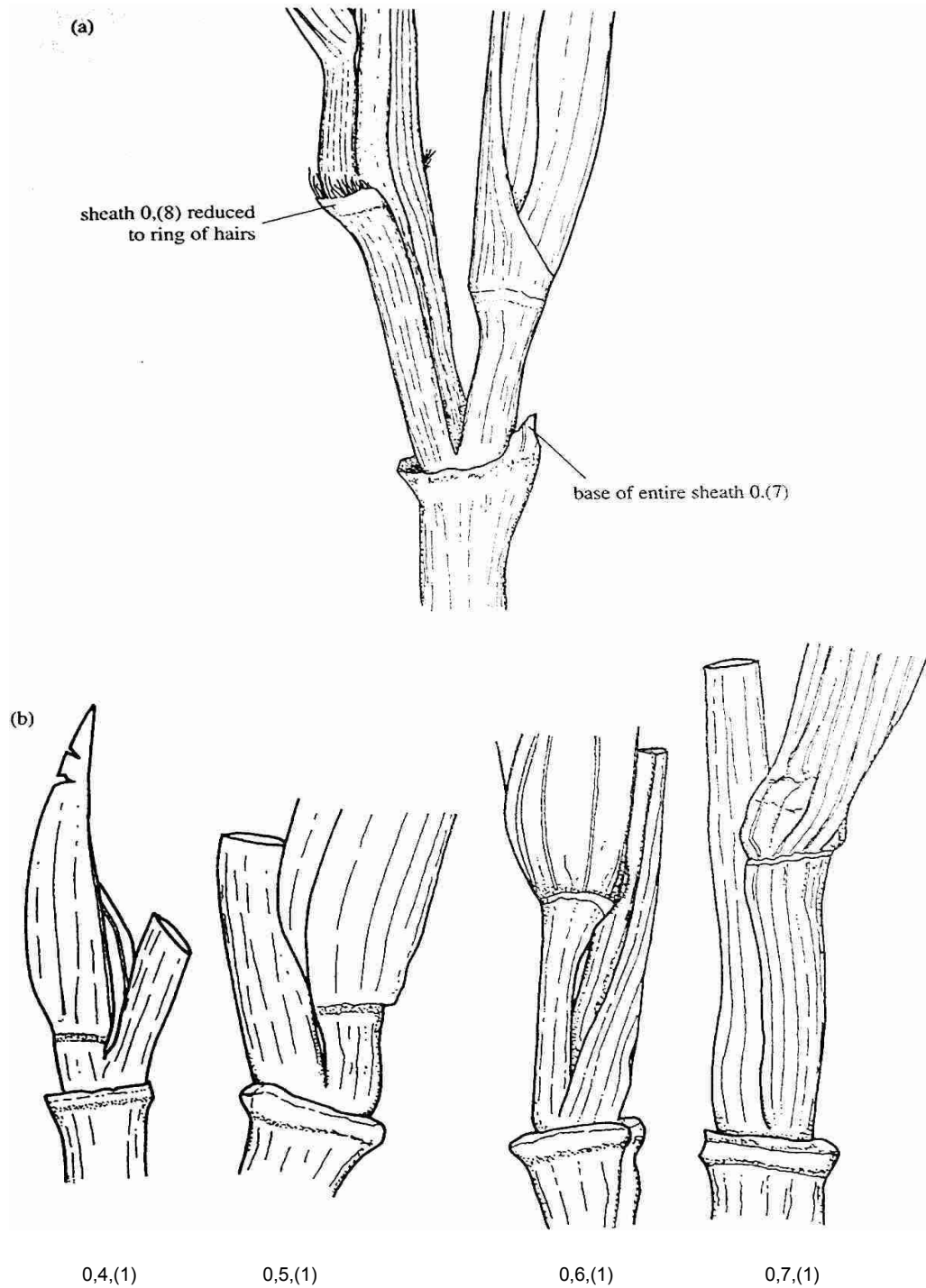| 0,4,(1) | 0,5,(1) | 0,6,(1) | 0,7,(1) |

Figure 5. Sheathing at paraclade branching in *Thamnocalamus spathiflorus*. a, Reduction from sheath to ring of hairs at successive nodes; b, Prophylls at successive nodes showing progressive displacement of prophyll on paraclades and spikelet 'pedicels', suggesting homology between prophylls and lower glumes.

process than recaulescence in the grasses, as the stem seems to be splitting rather than fusing.

Following this interpretation the prophyll is always present on racemose branches, and the important variation is in its locus of insertion, whether close to the point of branching or more distant. Presumably the same interpretation could also be made for the lower glume of the 'pedicellate' lateral spikelet in non-bambusoid members of the grass family. In more paniculate synflorescences prophylls subtending further paraclades abound, and these become reduced, so that the homology between them, vegetative prophylls, and lower glumes is less apparent.

Thus the old pedicel, which now should be known as a peduncle instead, would be interpreted as part of the axis from which the spikelet branches, rather than part of the spikelet itself. Whether this displacement happened in the bamboos as bracteate synflorescences developed from ebracteate ones, or whether it happened as an ancestral ebracteate synflorescence developed before the time of bamboos is impossible to tell. The term promontory is preferable to podium, as the latter could cause confusion with the hypopodium and epipodium, which are extensions of the axis below and above the flower prophyll (palea) rather than the florescence, and thus are not seen in the grasses, which have sessile flowers.

BUD PRESENCE

Presence of buds at the base of the spikelet is a fairly straightforward character, although in younger material it is sometimes difficult to say whether such buds will develop into further axes or whether they are merely vestigial. These buds can be interpreted as constituting a zone of paraclade inhibition below the florescence. McClure (1966) gave instances of vestigial buds in the iterauctant inflorescence. This seems to be a contradiction, and it might be more logical to define an iterauctant synflorescence as one in which buds are not only present, but capable of development. Again, if we leave the difficulty of defining the boundary between the two syndromes behind by progressing to the description of three separate characters, this is no longer important. The three character states would be viable buds present, vestigial buds present, and buds absent. In *Phyllostachys* and related genera presence of such buds is highly variable, as it is in vegetative growth. This makes it almost impossible to define the genus and also the subtribe as either semelauctant or iterauctant.

Interestingly, McClure (1966) reported the presence of vestigial buds in *Arundinaria* (*Neomicrocalamus*) *prainii*, a bamboo with the primitive number of 6 stamens in an otherwise advanced paniculate synflorescence. I cannot find any such buds in that species myself, but I have seen them in *Thamnocalamus spathiflorus*, a species with the most primitive branch complement structure found in 3-stamened bamboos. They are also seen in the S American genus *Criciuma* (Soderstrom & Londoño, 1987).

Attempts to divide the whole woody bamboo subfamily according to McClure's two categories have been made, and nomenclatural status has been given to two groups, formalized as Bambusodae Keng & Keng f. ex L.Liou (Bambusateae Keng & Keng f.) and Arundinarodae Keng & Keng f. ex L.Liou (Arundinariateae Keng & Keng f.). However, the characters adopted for this distinction have varied, and the two groupings have not been supported by molecular data. This should not be

surprising as McClure (1966) stated that he was describing only two extremes of inflorescence structure.

DETERMINATE AND INDETERMINATE SYNFLORESCENCES

McClure would not have been surprised himself at how his distinction was adopted in a simplified manner. He stated (1966):
"The results of determinateness and indeterminateness that appear in the bamboo inflorescence are commonly interpreted by the taxonomist only in terms that will most simply describe the superficial aspect of the resulting growth forms."

McClure used the terms determinate and indeterminate rather loosely at first, and he later refined them into his semelauctant/ iterauctant distinction instead. The terms definite, indefinite, determinate and indeterminate relate more properly to the real terminus, not to lateral growth substantially further down the axis. Termination is now a very important character in angiosperm inflorescences. Two categories occur, determinate (monotelic) inflorescences, and indeterminate (polytelic) synflorescences. If we define the spikelet as the inflorescence, then all bamboos have strictly indeterminate inflorescences. The terminal floret of the bamboo spikelet is always clearly lateral, having a subtending leaf or pherophyll (the lemma) and an addorsed prophyll (the palea), so that even if it does effectively terminate the spikelet it is technically subterminal, not truly terminal. That is why the bamboo synflorescence is polytelic.

Thus there is no connection between McClure's distinction between the determinate (semelauctant) and the indeterminate (semelauctant) bamboo inflorescences, and Troll's distinction between the determinate (monotelic) inflorescence and indeterminate (polytelic) florescences.

This has to be clarified as Weberling (1989) considered the monotelic state to be primitive and mentioned that there might be isolated cases of monotelic inflorescences in the bamboos. Indeed Calderón & Soderstrom (1973) suggested that the solitary floret in *Maclurolyra* could represent a primitive monotelic inflorescence. However, as long as we interpret the grass floret as the florescence rather than the whole spikelet, the florescences are always lateral, and can never form a monotelic inflorescence. In addition, although molecular studies have not included *Maclurolyra* itself, other members of the subtribe Olyreae do not have a basal position (Clark et al., 1995) relative to the bamboos or the grasses as a whole.

SUMMARY

Thus the two major groups formalized to reflect McClure's iterauctant and semelauctant syndromes are not likely to be as clearly separated as their authors might have hoped. Weberling (1965) pointed out that systematics must be based on a comparison of homologous structures. Applying a modern interpretation, artificial differences between the two syndromes are seen to be substantially reduced, and homologous structures can be identified. Different characters are involved in the two syndromes, and they are likely to have evolved independently on different occasions, especially in the Old and New World bamboos. Early molecular results (Watanabe et al., 1994; Clark et al., 1995) are support this contention. No division based upon the semelauctant/ iterauctant distinction has been demonstrated. They do suggest two major well-supported monophyletic clades within the woody bamboos, but it seems unlikely that there will be any single globally consistent

morphological inflorescence character that separates them. Change in stamen number may accompany the major division, but it has also changed at other times within the subfamily. It would appear that a system of subtribes is more likely to be useful to those who wish to establish morphologically-interpretable concepts of groups of woody bamboos above the generic level. Within the bamboo synflorescence a description of the three characters associated with McClure's two syndromes, along with other characters, is clearly much more useful than merely assigning the labels iterauctant or semelauctant.

Evidently there is still considerable scope for considering various interpretations of the bamboo inflorescence. It is still not clear which character states are ancestral and which are derived. However, it is clear that a more analytical approach to the different components of floral and vegetative morphology is required. Referral to syndromes is not likely to satisfy the need for clarity and objectivity. A critical analysis of all the different components of the major organs, including the rhizome, the vegetative branching system, and the synflorescence is required. It is probably not worth undertaking a cladistic analysis of morphological variation within the bamboos until the various character states in these organs are properly understood and a wider range of genera have been more thoroughly investigated.

CORRELATION BETWEEN DIFFERENT MORPHOLOGICAL & OTHER DATA SOURCES

Because of the unit-based pattern of grass morphology and the apparent paucity of characters, different sources of taxonomically informative data have long been sought, with varying degrees of success. To assess the importance of any taxonomic data it is important to understand the level at which the characters are informative. Looking at morphological variation, characters such as waxiness or pubescence of a petiole are not of great significance. They can come and go without affecting success. Their significance, if any, will be at the community or species level. Other characters such as branch number or rhizome form will have more fundamental impact, often involving several characters together. They should be inherited for much longer, and such conservative characters have significance at higher taxonomic levels. However, characters that are highly adaptive tend to evolve quickly and independently.

Comparing other sources of data to morphological data, it is important to compare variation that is likely to have impact at the same sort of taxonomic level. Conflict can arise because of a mismatch here. Moving to higher taxonomic levels it becomes increasingly difficult to relate morphological data to other sources. Each taxon becomes so large and variable that consistent morphological characters are harder to find, as has been seen with the supposedly major division within the woody bamboos based on semelauctant and iterauctant syndromes.

Non-molecular data

Leaf anatomy has been studied in depth in the hope of addressing certain problems such as the relationships between bamboos of Africa and Asia (Soderstrom & Ellis, 1982), and to investigate bamboos of Sri Lanka (Soderstrom & Ellis, 1988). In the former case *Arundinaria tessellata* Nees was compared to Asian species of *Thamnocalamus* and *Fargesia*. It was found that *A. tessellata* shared 10 out of 11 characters of leaf anatomy with *Thamnocalamus spathiflorus*. Therefore the new

combination *Thamnocalamus tessellatus* was made, on the assumption that the characters were useful at the generic level. Unfortunately their own data shows that *A. tessellata* shared only 5 out of 11 characters with *Thamnocalamus aristatus*, while sharing 7 out of 11 characters with *Fargesia nitida*. Moreover, *T. spathiflorus* and *T. aristatus*, now considered conspecific, themselves only shared 6 out of 11 characters. Similarly, when looking at leaf anatomy of Sri Lankan bamboos they found that *Bambusa bambos* had more in common with species of the Arundinariinae than it had with other species of the Bambusinae, including *Bambusa vulgaris*.

It would seem that there is little correlation between traditional morphologically-based groupings and generic groupings based upon the characters of leaf anatomy they investigated. However, this is probably because the anatomical characters are of relevance at a different, much lower level, rather than because of any more fundamental conflict between the data sets. Leaf anatomy may be so adaptive that variation in the characters is too rapid for consistency at higher levels. After all, bamboos are plants that exploit small differences in light conditions to succeed. However, there may well be certain characters of leaf anatomy that are more conservative than others.

Culm anatomy is another area where data has not been quite as informative as had at first been hoped. It seems that the variation between different patterns of vascular bundle may be of significance at the subtribe level, although there are apparently also characteristics that allow those with experience to distinguish species as well. Further clarification of the taxonomic value of culm anatomy is required.

Molecular data

Experience of the difficulties in comparing data from different non-molecular sources can be applied directly to combination of different molecular data sets, and mixed data sets. The differences here are the sheer volumes of molecular data available once sequencing is undertaken, and the total reliance upon objective mathematical (cladistic) analysis.

In some groups of plants it has been possible to obtain a hierarchy of relationships from molecular data, grouping species into units that bear some similarity to generic concepts, and also showing up more deeply-rooted divisions (e.g. Oxelman & Lidén, 1995). In the bamboos resolution has not yet been obtained at the all-important generic level, but investigations are still in their early stages. Other tools such as the assessment of total nuclear DNA content are still being developed.

It is difficult to say at this point whether morphological concepts of either species or genera in the bamboos will be supported or rejected by molecular characters. What seems certain is that considerable modification of our morphological knowledge may be required. Not only has much of it been rather selective and superficial so far, our very concepts of species and genera may prove to be highly artificial. If that is so, there is bound to be some discussion of the different objectives of taxonomy. Despite all the scientific advances, it seems there will always be people who expect us to give a binomial system of names to their plants, applying names at generic and species level on the basis of visible morphological characters. If such concepts are rather artificial however, we may have a difficult task balancing high-tech scientific knowledge with morphological pragmatism.

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