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On the Anatomy of Asian Bamboos, with Special Reference to their Vascular Bundles

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Summary

A comparative histological investigation of 52 bamboo species from 14 genera, collected in seven Asian countries, was carried out; 1200 internodes from 250 culms were examined therein. The anatomical structure of the culms is characterized exclusively by the collateral vascular bundles embedded in parenchymatous ground tissue which exhibits four basic types. A classification system was devised for these vascular bundle types and their combinations within the culm; it was found to correlate well with the system of HOLTTUM based on the structure of the ovary. A comprehensive description of the marked variability of the vascular bundle structure within one culm and between culms of a single species is given. The implications of such a representative description of a singles pecies and the introduction of an identification key are discussed.

Introduction

Bamboos belonging to the Gramineae occur particularly in the tropics and subtropics but with some taxa also in the temperate climate of Japan, China, Chile and USA. They are natives of all continents except Europe. Altogether there are about 600 ... 700 species represented by about 60 genera. About 300 species grow in Asia, most of them within the Indo-Burmese region, which is also considered to be their area of origin.

Bamboo is one of the oldest organic raw-materials used for a large number of different purposes in the daily life of the people in the tropics. In several regions like East-Pakistan, Java and Taiwan bamboo is the most important building material. Besides its excellent properties for constructional purposes and its manifold uses as commodit, bamboo plays an important role as a basic material for pulp and paper. The increasing demand for paper in Asia is being met to a large extent by the use of bamboo [FAO 1962].

The properties of bamboo are mainly determined by the structure of the culm but in spite of its wide use knowledge of its anatomy is still rather limited. Although anatomical investigations have been carried out by SCHWENDENER [1874], STRASBURGER [1891], HABERLANDT [1924], TAKENOUCHI [1931a, b], OTA and SUGI [1953], GHOSH and NEGI [1959], only few detailed descriptions of its anatomical structure including comparative studies are available [VELASQUEZ and SANTOS 1931; SAMAPUDDHI 1959; METCALFE 1960; LI and CHIN 1960;

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LI, CHIN and YAO 1962; CHIANG 1968, 1969; LIN 1968; PATTANATH and RAMESH RAO 1969]. Little is therefore known about the possibility of differentiating bamboo species on the basis of their anatomical characters or about the structural variability within one culm as well as between different culms of one species. The aim of this investigation is to provide the basis for an authoritative description of the anatomical structure of certain species, to determine the variability and possible trends within and between culms of the same species and to evaluate characteristic features which could be used in an identification key.

Materials and Methods

The material for this investigation was collected by the second author between 1965 and 1969 in several Asian countries from the following locations[1]:

India (Dehra Dun, F. R. I., Botanical Garden)
Pakistan (Forests around Chittagong/East Bengal)
Thailand (Kanchanaburi Province)
Indonesia (Bogor, Botanical Garden)
Philippines (Laguna, Forestry Campus)
Taiwan (Experiment Forest of the National Taiwan University)
Japan (Forest near Kyoto)

The species were accurately identified. For the collection of the samples, in general the following procedure has been adopted: Starting with the second internode from the base every fourth internode was taken up to the top (Fig. 1). Also complete culms could be obtained from several species in Dehra Dun and Bogor. At each location the material was taken from at least two different clumps. Furthermore some authentic material collected between 1957 and 1960 in Dehra Dun/India and Bogor/Indonesia was used for additional investigations. Alto-

Fig. 1. Selected internodes from one bamboo culm

[1] The authors acknowledge sincerely the assistance given by their colleagues in collecting the material.

gether 1200 internodes from 250 culms of 52 species belonging to 14 genera were evaluated in this study.

In order to determine the structural variability within one internode samples of 1 cm length were cut out at 25, 50 and 75% relative to the length of the internode. The samples from the middle position (50%) were cut into four pieces, whereas from each of the other two samples only one piece was used. After having gained basic information from these samples, for the following investigations only two pieces from the middle position were taken. The number of internodes investigated depended on the height of the culm and the thickness of the wall. From smaller culms, every fourth internode was examined but from taller culms with more than forty internodes, only every eighth.

In order to soften the samples for sectioning they were pressure-steamed up to four hours in an autoclave at approximately 1 atm. and then kept in 70% alcohol for several weeks. After such a preparation, cross-sections of 20—50 µm thickness could be obtained from the entire wall. Safranin, chrysoidin/acridin-red and auramin proved to be most suitable for staining lignified cell-walls, and astra-blue, fastgreen, haematoxylin and azo-black for non-lignified parts. The sections were embedded in Entellan (E. Merck), which was found to be especially suitable for handling larger series of sections.

For the evaluation of the microscopical observations, photographs of the structure were enlarged 50 times and mounted together, so that the whole transverse area of the culm-wall from the epidermis to the central cavity was reproduced (for technical details GROSSER 1971). By this method the structural components, especially the size and arrangement of the vascular bundles, can be clearly evaluated for comparative studies.

Results

The Anatomical Structure of the Internodes

The structure of a bamboo culm in transverse-section is characterized by numerous vascular bundles embedded in the parenchymatous ground tissue. They are larger in the inner parts, but appear smaller and denser towards the periphery (Fig. 14). In the vicinity of the epidermis the hypodermis and primary cortex form a special layer whereas the inner part at the central cavity is often composed of tangentially oriented parenchyma cells which may be sclerotic. They are covered mostly by a thin paper-like layer of pith-cells.

The culm tissue consists of the following cell types: a) Parenchyma cells forming the ground tissue and b) the vascular bundles consisting of sclerenchyma cells, vessels and sieve tubes with companion cells.

Within the internode all cells are strictly axially arranged (Fig. 2). As a monocotyledonous plant, the bamboo does not possess any special cells for radial transport like the rays of dicotyledons and gymnosperms.

The parenchyma tissue

The parenchyma cells are mostly thin-walled and connected to each other by numerous simple pits. These are located predominantly on the longitudinal walls, whilst the horizontal walls are scarcely pitted at all. The parenchymatous tissue becomes lignified already during the sprouting of the culm and the cells may contain a considerable amount of starch. The parenchyma cells appear mainly elon-

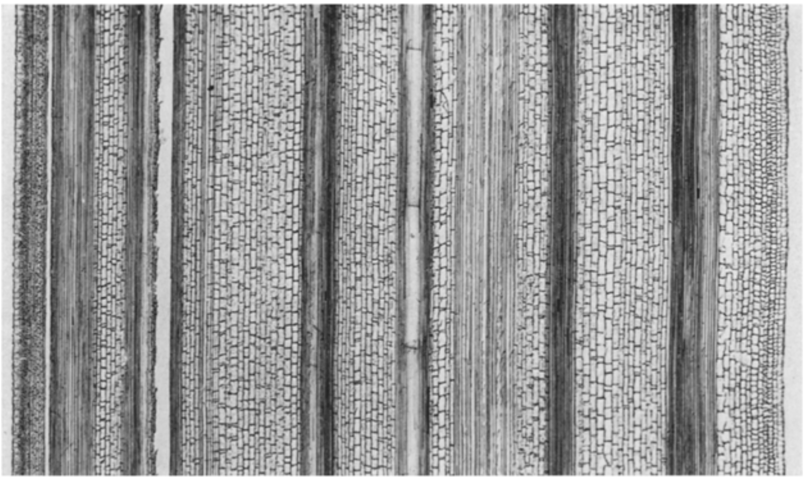


Fig. 2. Sector of culm wall — *Bambusa polymorpha* (25 x)

gated but small, almost cube-like cells are also present, interspersed between the long cells (Fig. 3). These short cells are characterized by denser cytoplasm and thin walls and exhibit no lignification even in mature culms. They exhibit a strong peroxidase reaction especially in young shoots, whereas the elongated cells have lignified walls without a peroxidase reaction in the cytoplasm.

Vascular bundles

A typical vascular bundle is shown in Fig. 4. The metaxylem consists of two large vessels between which an intercellular space exists which originates from the primary xylem. In monopodially growing taxa (rhizome system "leptomorph", McClure 1966) like *Arundinaria* and *Phyllostachys* the intercellular space often contains tyloses (Fig. 5). Li and Chin [1960] and Li, Chin and Yao [1962] also mentioned such protrusions in other leptomorph taxa like *Brachystachyum*, *Chimonobambusa*, *Indocalamus*, *Pleioblastus*, *Pseudosasa*, *Semiarundinaria*, *Shibataea* and *Sinobambusa*. However, in sympodially growing bamboo species (rhizome system "pachymorph", McClure 1966) tyloses have never been observed. Consequently the presence of tyloses could be used as a diagnostic feature.

Between the two large vessels some smaller xylem elements may be located (Fig. 6). All the vessels are surrounded by lignified parenchyma cells; however, the parenchyma of the protoxylem around the intercellular space remains often unlignified. The parenchyma cells of the vascular bundles are generally smaller than those of the ground tissue and possess more pits on their walls.

The phloem consists of large, thin-walled unlignified sieve tubes, always connected with several companion cells (Fig. 7). At the periphery there is a layer of compressed cells belonging to the primary phloem. The vessels and sieve tubes of mature culms partially become impermeable due to depositions of gum-like substances (Fig. 8). Sometimes a blocking of the sieve tubes by tylosoids—like outgrowths—occurs, whereas the companion cells become sclerified (Fig. 9). A similar obstruction of the metaphloem has been observed in the stem and leafstalk of palm species [Parthasarathy 1968].

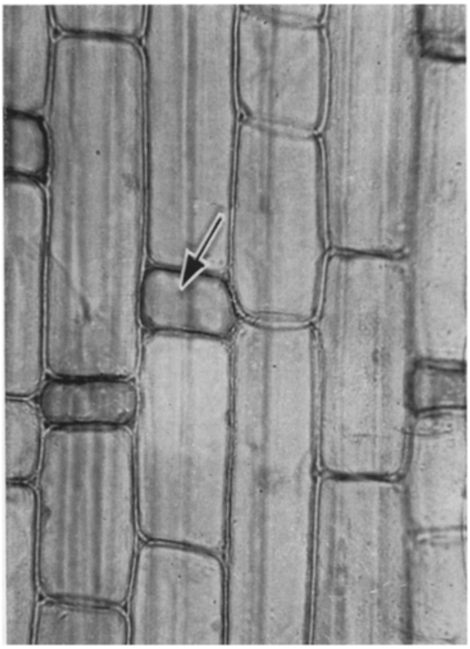


Fig. 3. Parenchyma tissue with elongated cells characteristically interspersed with short cells (arrowd) (370x)

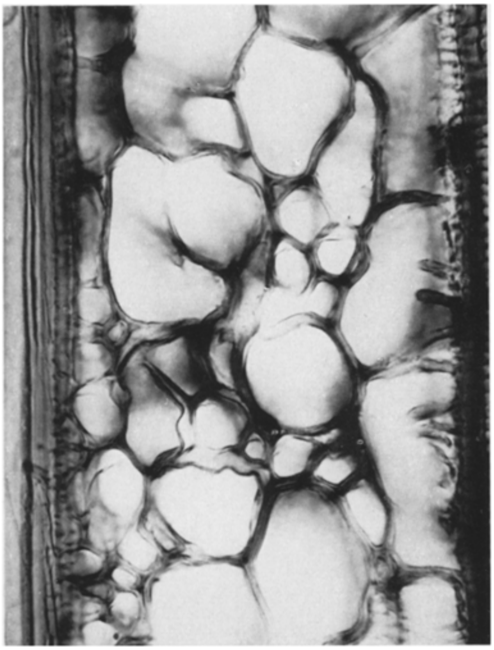


Fig. 5. Intercellular space with tyloses (500x)

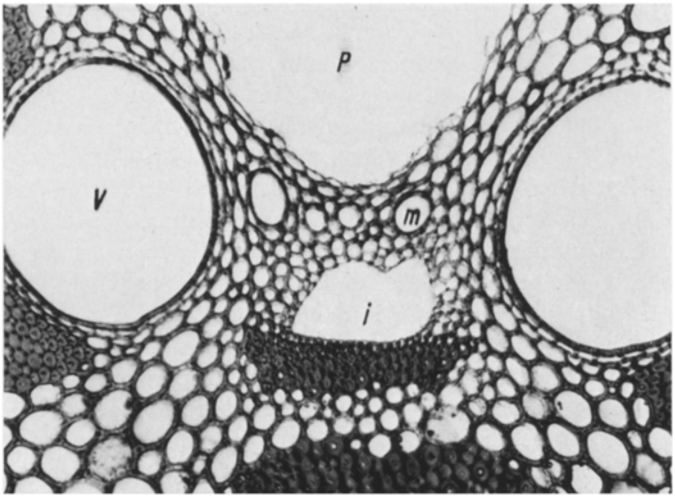


Fig. 6. Part of vascular bundle showing smaller metaxylem elements (m) between vessels (v), phloem (p) and intercellular space (i) (225x)

The phloem and xylem of a vascular bundle are each surrounded by sclerenchyma sheaths, differing in size and shape according to the bamboo species and their position within the culm. Vascular bundles of the middle and inner position of the culm have four sheaths, two lateral on either side of the vessels and two polar, one around the phloem and one around the intercellular space. Most of the

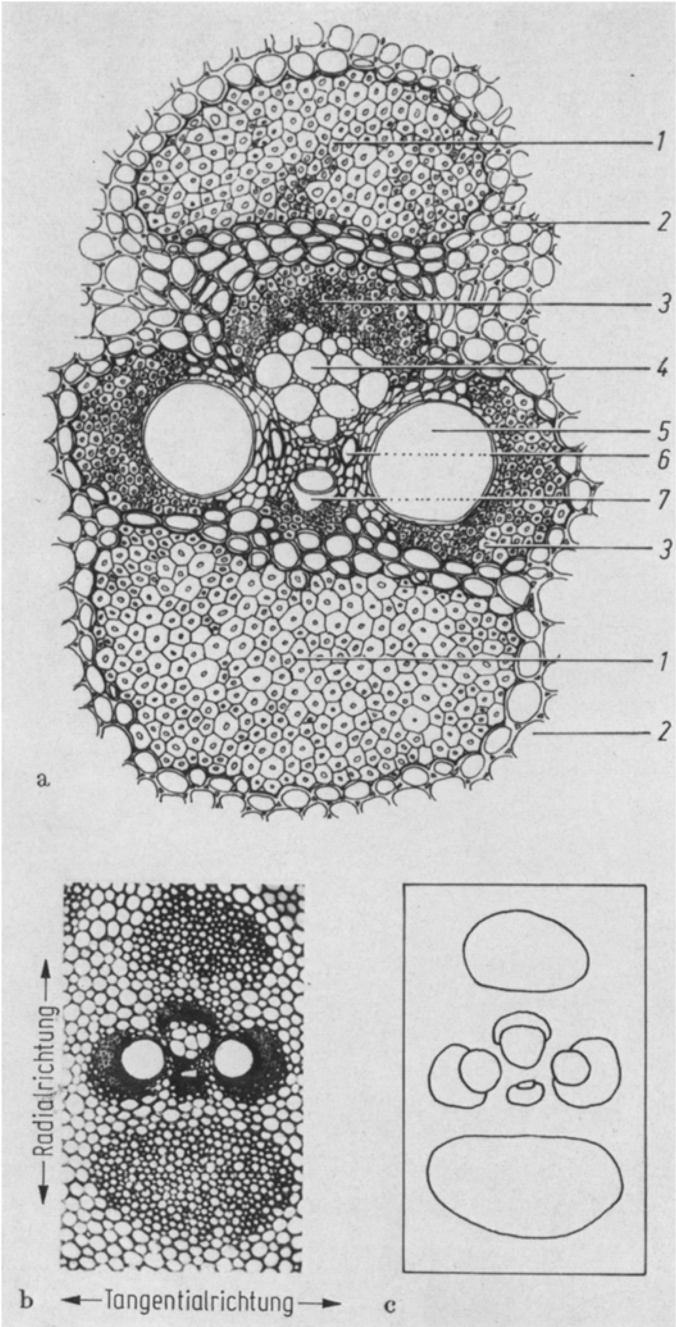


Fig. 4. a: Bamboo vascular bundle; (1) fibre strand; (2) parenchyma cells, (3) sclerenchyma sheath, (4) phloem, (5) metaxylem vessel, (6) small metaxylem elements, (7) intercellular space derived from protoxylem. b: Vascular bundle embedded in parenchymatous tissue and consisting of three parts (central vascular strand and two fibre strands); radial direction = radial diameter, respectively length of the vascular bundle, tangential direction = tangential diameter, respectively width of the vascular bundle. c: Simplified illustration of a vascular bundle as employed in the Plates I—IV

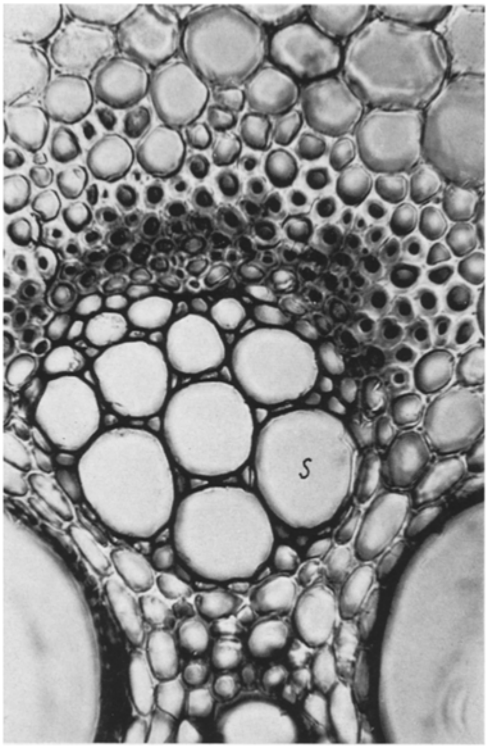


Fig. 7. Part of vascular bundle showing sieve tubes (s) with companion cells (350x)

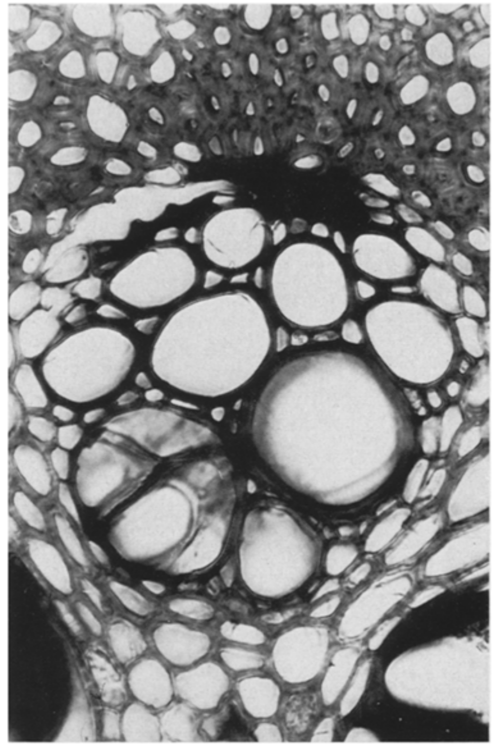


Fig. 9. Part of vascular bundle showing formation of tylosoids in sieve tubes (500x)

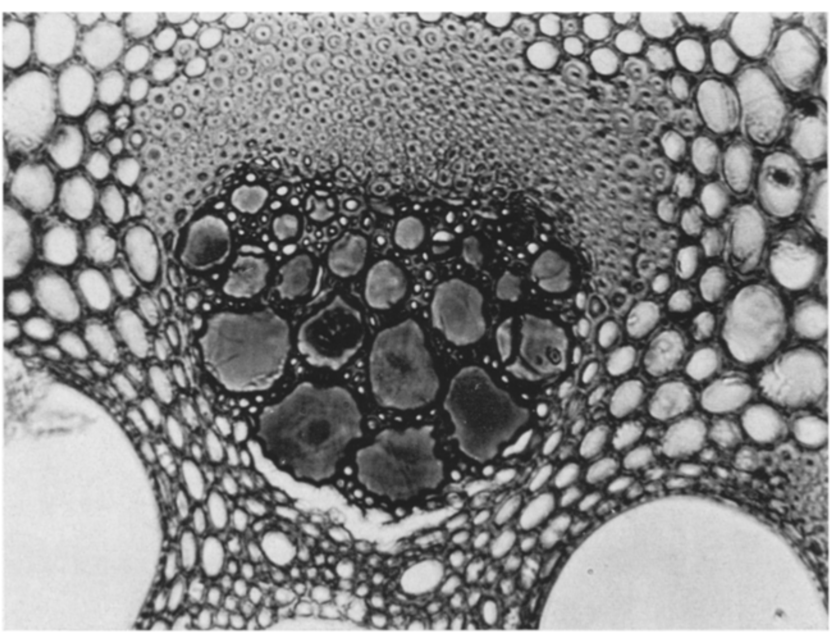


Fig. 8. Part of vascular bundle showing functionless phloem with deposition of gum-like substances and sclerified companion cells (260x)

species additionally have separate fibre strands on the inner side or inner and outer side of the vascular bundle (Fig. 4). According to the presence and location of these fibre strands one can distinguish different types of vascular bundles. In bamboo species which possess fibre strands, the complete vascular bundle may consist either of 2 or 3 parts: the central vascular strand and one or two separate fibre strands. In bamboo species in which there are only the sclerenchyma sheaths present as supporting tissue, the vascular bundle consists of only one part, namely the central vascular strand. In relation to these forms of vascular bundles four basic types can be differentiated which are explained in detail in Table 1 and illustrated in Figs. 10 to 13.

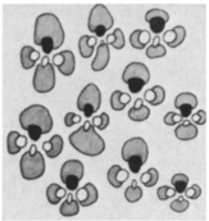
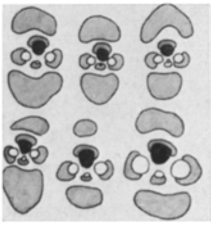
Variability of Vascular Bundles Across the Culm-wall

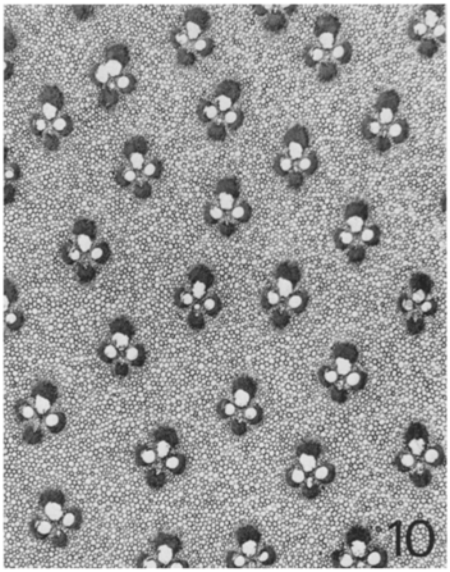
The distribution of the vascular bundles across the culm-wall is consistent with the typical monocotyledon anatomy. Form, size, number and concentration of the bundles change continuously from the periphery of the culm towards the centre (Fig. 14). Near the periphery the bundles are smaller and more numerous, so that there are only a few parenchyma cells between them. In this region the bundles are more simple with the 3 xylem-fibre sheaths amalgamated to give a half ellipsoid area; thus the xylem sheath is generally larger than the phloem sheath. In bamboo species with the vascular bundle types III and IV (Figs. 12, 13, 14, 15) the separate fibre strands too become smaller towards the outside and are united with the sclerenchyma sheaths (Fig. 14). In the outer part of the culm ($\frac{1}{3}$ of the width) the conducting tissue of the bundles is much reduced and generally consists only of 2 small vessels and a few sieve tubes with their companion cells. The intercellular space is rarely visible and may be absent altogether, as may be also the small xylem cells. The vascular bundles immediately below the primary cortex are circular in cross-section, sometimes only with small vessels and a few sclerenchyma cells or without conducting tissue at all. Towards the centre of the culm, the vascular bundles become bigger and more widely distributed. In most species they exhibit their maximum size and their characteristic form in the middle part of the culm-wall. In the inner part of many species the vascular bundles appear smaller again and are often inverted. Bamboo species with types III and IV have near the pith cavity often only vascular bundles with very small fibre strands or none at all.

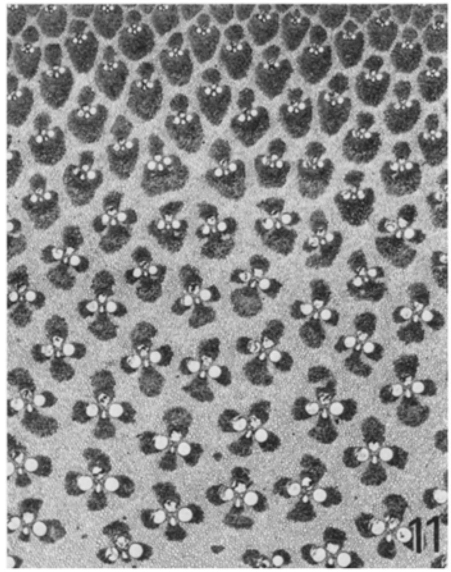
The sequence of vascular bundle types from the periphery towards the centre forms a distinct pattern which reflects the whole spectrum of variation across the culm-wall. Such arrangements of vascular bundles from different internodes of a single culm are given in Plates I to III.

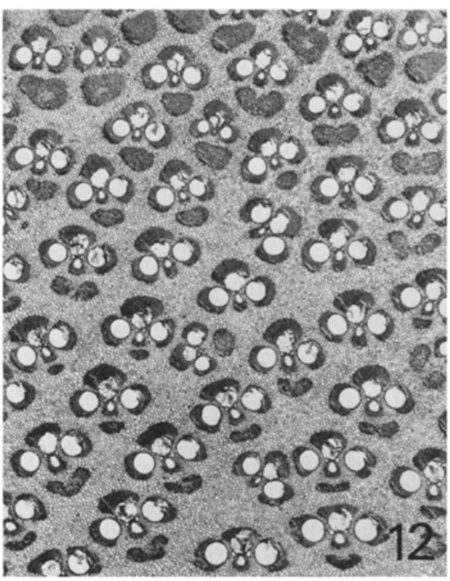
Across the culm-wall four zones of vascular bundles can be distinguished (Fig. 14). The first, the peripheral zone, is composed of vascular bundles immediately adjacent to the cortex, which are arranged generally in more or less tangentially orientated chains. In the second zone, the transitional zone, the sclerenchyma sheaths of the vascular bundles are more or less amalgamated with the fibre strands. Basic vascular bundle types are not formed in this zone. The third zone is the broadest, and the distribution of the vascular bundles determines the anatomical appearance of the cross section. In this central zone the bundles reach their highest stage of differentiation and in most bamboo species their largest size.

Table 1. *Basic vascular bundle types in bamboos*

Vascular bundle types	Characteristics	Occurrence
 I	Consisting of one part (central vascular strand); supporting tissue only as sclerenchyma sheaths; intercellular space with tyloses	In all species with leptomorph rhizomes throughout the culm as only type *(Arundinaria, Phyllostachys)* Fig. 10
 II	Consisting of one part (central vascular strand); supporting tissue only as sclerenchyma sheaths; sheath at the intercellular space (protoxylem) strikingly larger than the other ones; intercellular space without tyloses	In species with pachymorph rhizomes growing either in single-culm-formation *(Melocanna)* or in clumps *(Cephalostachyum, Schizostachyum, Teinostachyum)*. In *Cephalostachyum*, as only type throughout the culm; in *Melocanna Schizostachyum, Teinostachyum* in the base internodes often together with type III Fig. 11
 III	Consisting of two parts (central vascular strand and one fibre strand); fibre strand inside the central strand; sheath at the intercellular space (protoxylem) generally smaller than the other ones	In clump-forming species with pachymorph rhizomes *(Bambusa, Dendrocalamus, Gigantochloa, Thyrsostachys)*; at the base internodes combined mostly with type IV, in the middle and upper parts as only type. In *Melocanna, Schizostachyum, Teinostachyum* combined at the base internodes with type II. In some *Oxytenanthera spp.* as only type throughout the culm Fig. 12
 IV	Consisting of three parts (central vascular strand and two fibre strands); fibre strands outside and inside the central strand	In clump-forming species with pachymorph rhizomes *(Bambusa, Dendrocalamus, Gigantochloa, Thyrsostachys)*; mostly at the base internodes, seldom at the middle part; always combined with type III Fig. 13







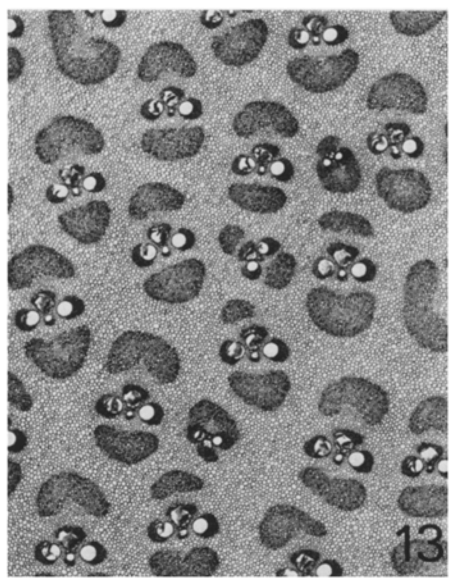


Fig. 10. Vascular bundle type I—e.g. *Phyllostachys edulis* (12x)
Fig. 11. Vascular bundle type II—e.g. *Cephalostachyum pergracile* (12x)
Fig. 12. Vascular bundle type III—e.g. *Oxytenanthera albociliata* (12x)
Fig. 13. Vascular bundle type IV—e.g. *Bambusa polymorpha* (12x)

One or two basic vascular bundle types are present according to the species and height in the culm. Towards the inner part a fourth zone can be distinguished, in which the vascular bundles are often small, simplified and disorientated. The width of this inner zone differs according to species and height in the culm, and it may even be absent in some bamboos.

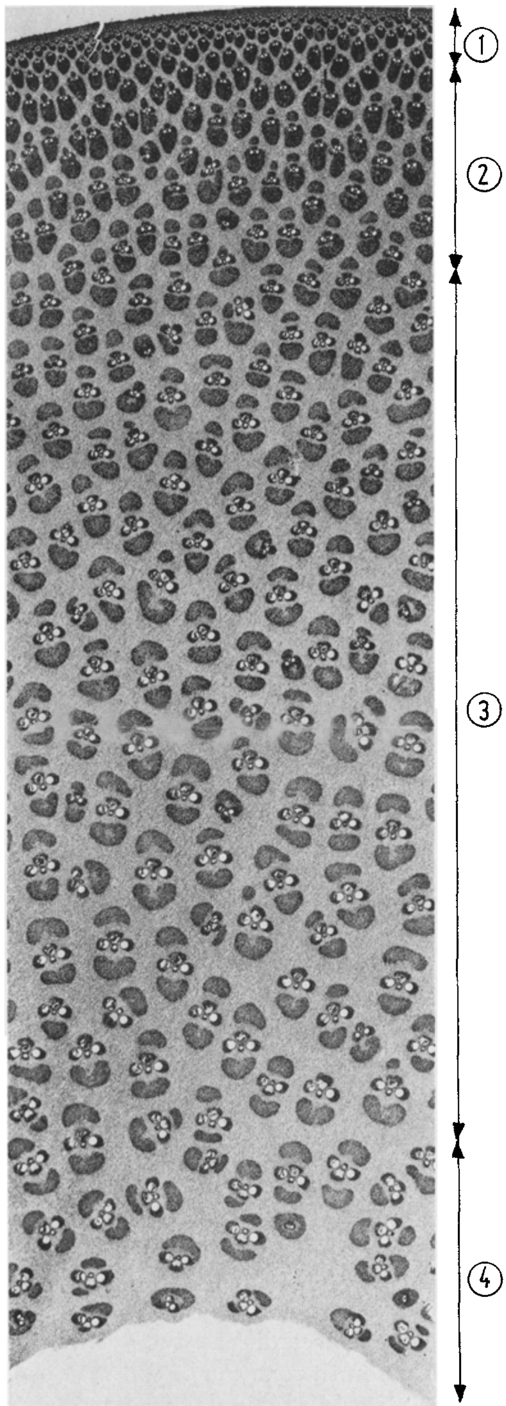


Fig. 14. Sector of culm wall at 2nd internode—*Bambusa polymorpha*—to show the peripheral (1), transitional (2), central (3) and inner (4) zones (6.5x)

Besides the central zone in which the vascular bundles govern the anatomical structure of the culm, each of the other three zones may have specific characteristics; these may be useful diagnostically in those species which have similar vascular bundles in the central zone. The width of the different zones varies according to species and thickness of the culm, but the outer third of the wall usually includes the peripheral and transitional zone.

The Orientation of Vascular Bundles Within one Internode

A more or less similar tissue pattern exists across each internode of the culm. The form, size and distribution of the vascular bundles is the same on all sides. This also applies to regions where branches originate. Similarly the tissue arrangement does not change within an internode in the longitudinal direction because the vascular bundles are strictly axially orientated (see Fig. 2). Since there is no branching or amalgamation of the vascular bundles, their arrangement is constant at any position along the internode. This is especially obvious with disorientated vascular bundles where the phloem may be on the inside rather than on the outside and which retain this orientation throughout. Form and size also do not change so that cross-sections at any level in an internode show the same anatomical appearance. Thus, in order to characterize an internode it is sufficient to obtain a sample from the middle. However, it is advisable to examine sections taken from diagonally opposite sides, in order to eliminate irregularities which occasionally occur due to differences in culm-wall thickness.

Longitudinal Variation of the Vascular Bundles Within the Whole Culm

An important characteristic of the bamboo culm, which has so far hardly been discussed in the literature, is the continuous change in the tissue pattern that occurs with increasing height. Thus the form, size and pattern of vascular bundles can vary so markedly, that an internode from the culm base exhibits a completely different structure from one taken at the middle, which in turn can differ considerably from one taken at the top [Figs. 15a—d, Plate IV).

Changes in the anatomical pattern coincide with the gradual reduction in wall thickness. This means that the more the wall thickness is reduced, the bigger the anatomical differences become, so that a close correlation exists between morphological and histological characteristics. The traditional methods of describing wood anatomy from three orientated sections cannot be applied to bamboo. Instead, for a representative characterization of a species it is necessary to describe the tissue pattern from several internodes at different positions in the culm as seen in Figs. 15a—d and Plate IV. However, the diagnostic description can be restricted to the cross-section, since radial and tangential sections do not exhibit any specific features. The height of the culm and the rate of reduction of wall thickness determine the number of internodes to be investigated. As a result of intensive study of more than 250 culms, it can be concluded that in general every fourth or eight internode is adequate, depending on the reduction of the culm-wall thickness (see Fig. 1).

In all bamboo species investigated, the size of the vascular bundles decreases steadily from the base to the top. This tendency is most pronounced in species which possess very large bundles at the base, whereas in species with smaller bundles at this point the reduction is less. Generally, the radial diameter of the vascular bundles decreases within the height of a culm much more than the tangential diameter. Thus the shape of the vascular bundles as seen in transverse section changes and near the top they appear roundish or oval, whereas further down they appear markedly elongated in the radial direction. Because the wall thickness is reduced faster in the lower part, the anatomical changes from internode to internode are more pronounced here. In the middle and top this reduction is slower, so that changes in the anatomy are less obvious.

The extent of variation in the vascular bundle form differs from species to species and is mainly determined by the basic types as defined in Table 1. In most species a combination of 2 types exists, and according to the position in the culm and the wall thickness either both types together or only one of them are present. The basic type I exists exclusively in leptomorph genera like *Arundinaria* and *Phyllostachys*, and never together with any other type. Because of its relatively simple construction the variation in this type is rather restricted. The basic type II as well as the types III and IV occur only in the culms of pachymorph genera. Basic type II exists either alone or in combination with type III. In the latter case, type III-bundles are restricted to the lower part of the culm, whereas type II largely occurs in the middle and upper parts but sometimes also at the base. Type III is present either alone or together with another type. Its combination with type II has just been mentioned, whereas in combination with type IV the type III occurs mainly in the middle and upper parts. The basic type IV, however, is almost entirely restricted to thick-walled basal internodes and is replaced further up by type III. Only rarely is type IV also present in middle or even higher internodes as found in *Dendrocalamus merrillianus* (Elm.) Elm. [GROSSER 1971; GROSSER and ZAMUCO 1971]. Bamboo species with combinations of types III and IV show the most obvious variation in the shape of vascular bundles. Table 1 outlines the occurrence of the different types among the genera investigated.

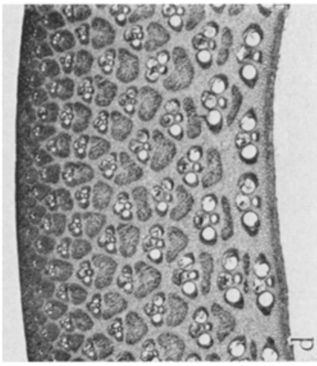
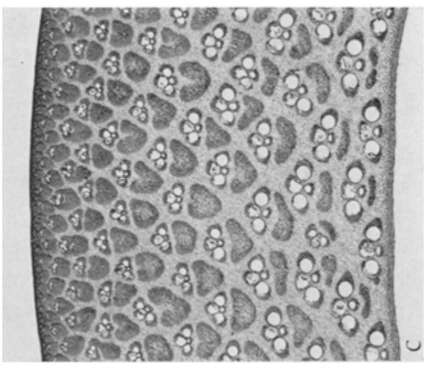
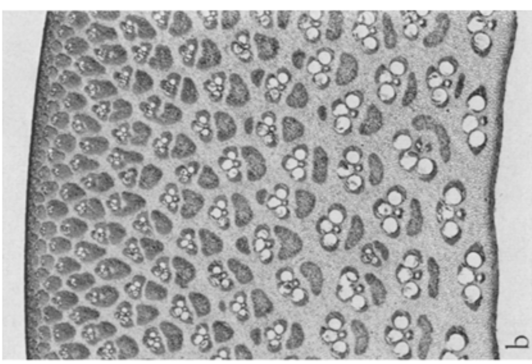
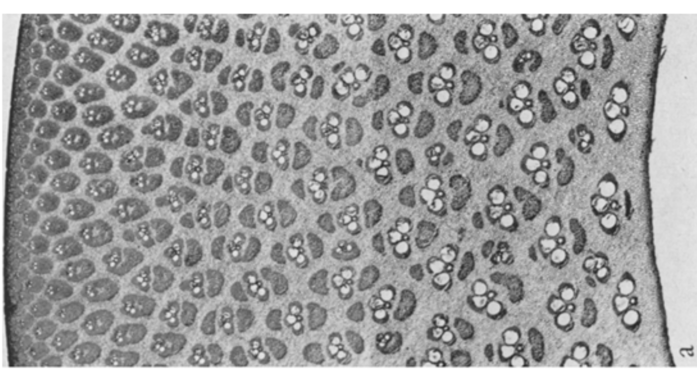





Fig. 15. Series of sectors through culm wall – *Oxytenanthera nigrociliata*; (a) 6th internode, (b) 10th internode, (c) 14th internode, (d) 18th internode (8 x)

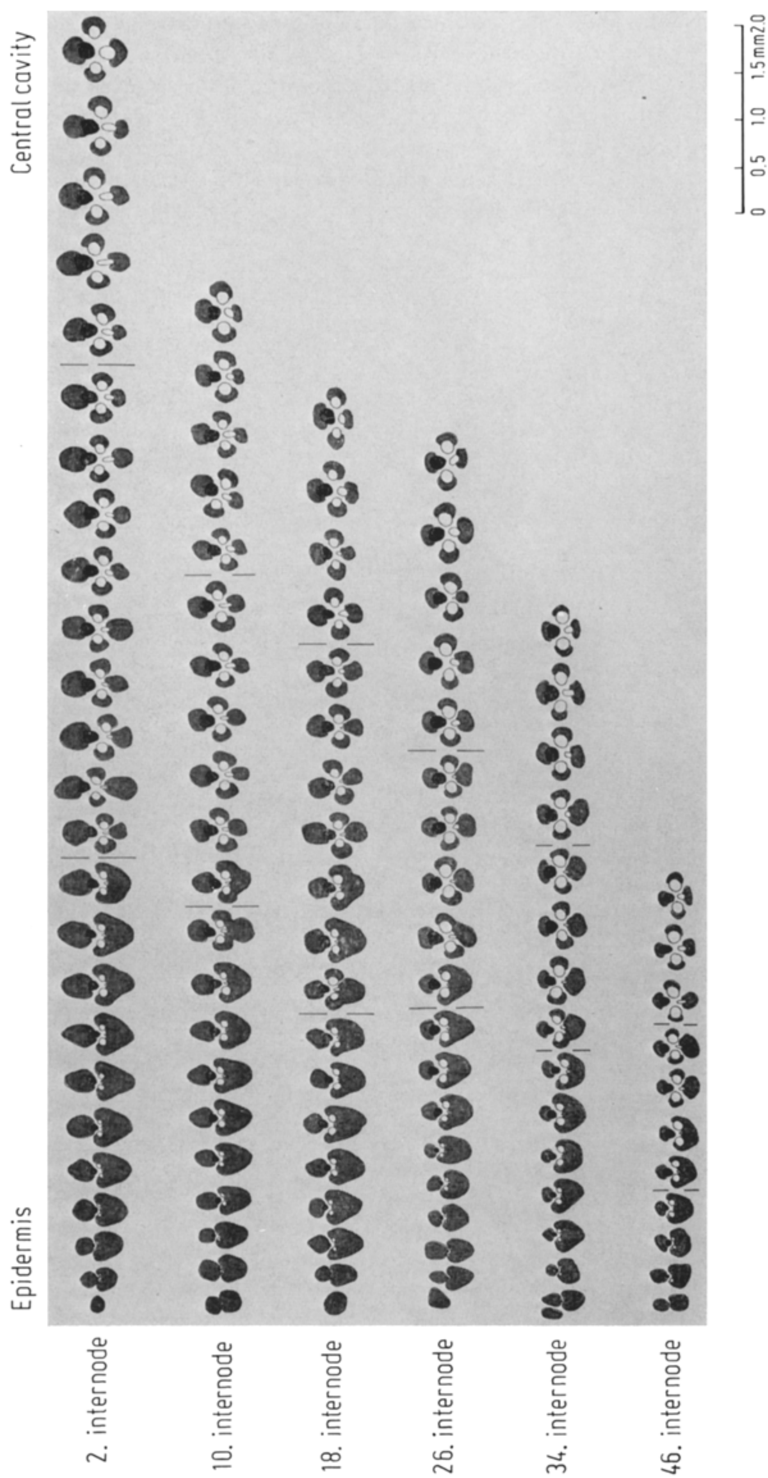


Plate I. Phyllostachys edulis Riv. *Variability of shape and size of vascular bundles in horizontal and vertical direction of the culm-wall*

Because shape and size of the vascular bundles also differ considerably across the wall, the extent of variation within the culm is strongly two-dimensional. In order to characterize a bamboo species it is therefore not only necessary to identify the existing vascular bundle types but also their vertical variation within the whole culm. Such a characterization can be achieved by producing vascular bundle diagrams (Plates I to III) in which vascular bundle sequences for the second and every subsequent fourth or eighth internode are given in horizontal rows. Within

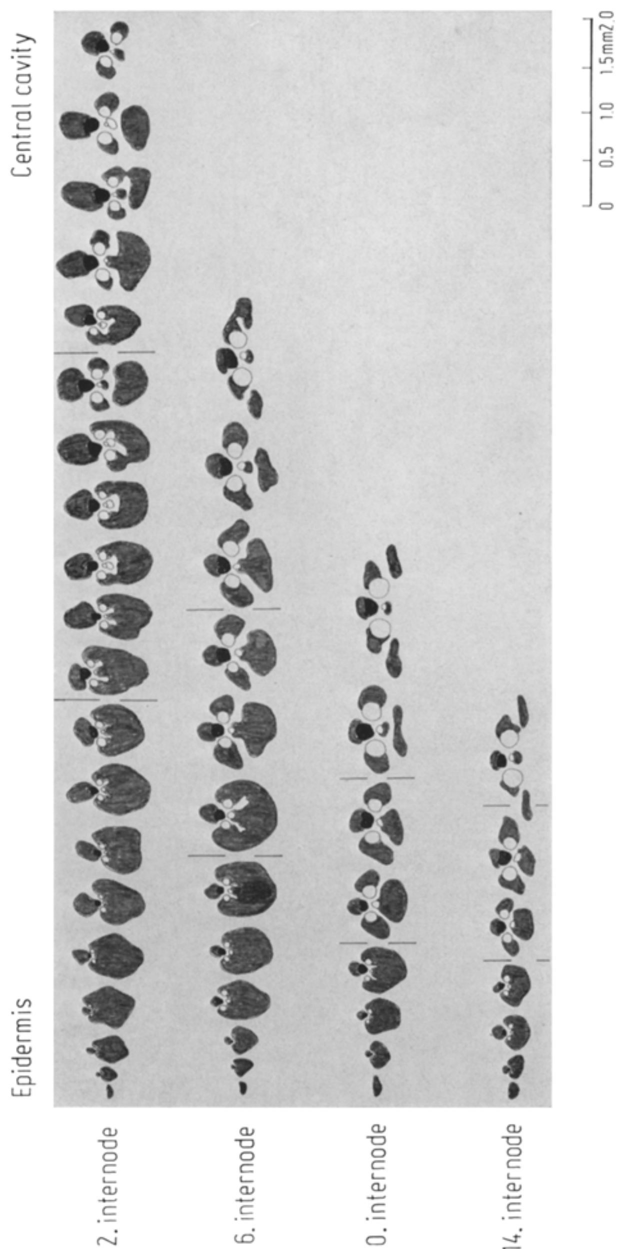


Plate II. Teinostachyum dullooa Gamble. Variability of shape and size of vascular bundles in horizontal and vertical direction of the culm-wall these rows the bundles of the outer, middle and inner zones have been marked off by vertical lines. Altogether 25 bamboo species have been investigated by using this system. The three selected examples given in these plates are *Phyllostachys edulis* Riv. (characterized by bundle type I), *Teinostachyum dullooa* Gamble

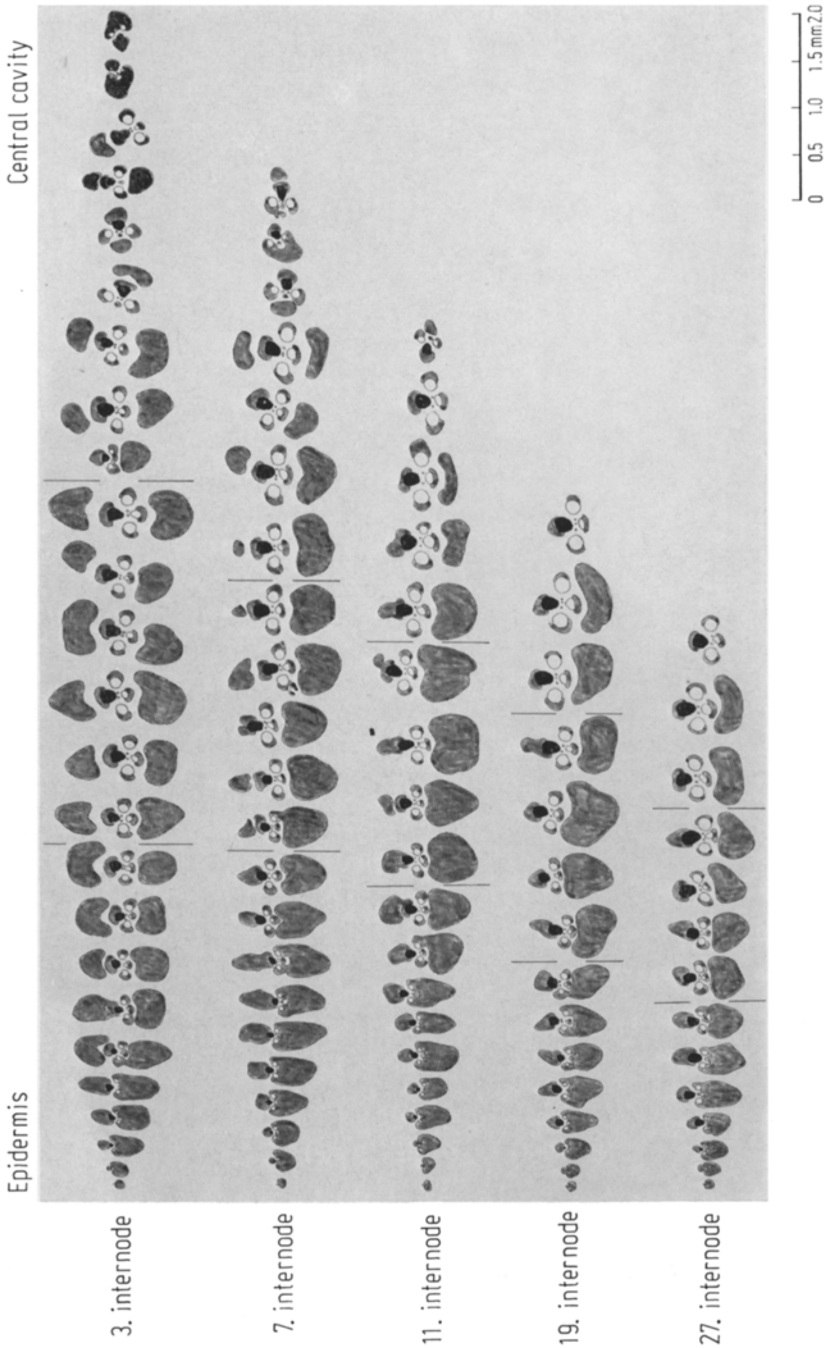


Plate III. Thyrsostachys siamensis Gamble. Variability of shape and size of vascular bundles in horizontal and vertical direction of the culm-wall (types II and III) and *Thyrsostachys siamensis* Gamble (types III and IV). In combination with illustrations of the cross-sections at different heights in the culm (as given for *Thyrsostachys siamensis* in Plate IV) a complete anatomical characterization of a bamboo species can be obtained.

Thus a classification grouping can be achieved wich is based on the presence of the four vascular bundle types, together with their different combination within one culm. The anatomical classification system introduced comprises four main groups and two sub-groups:

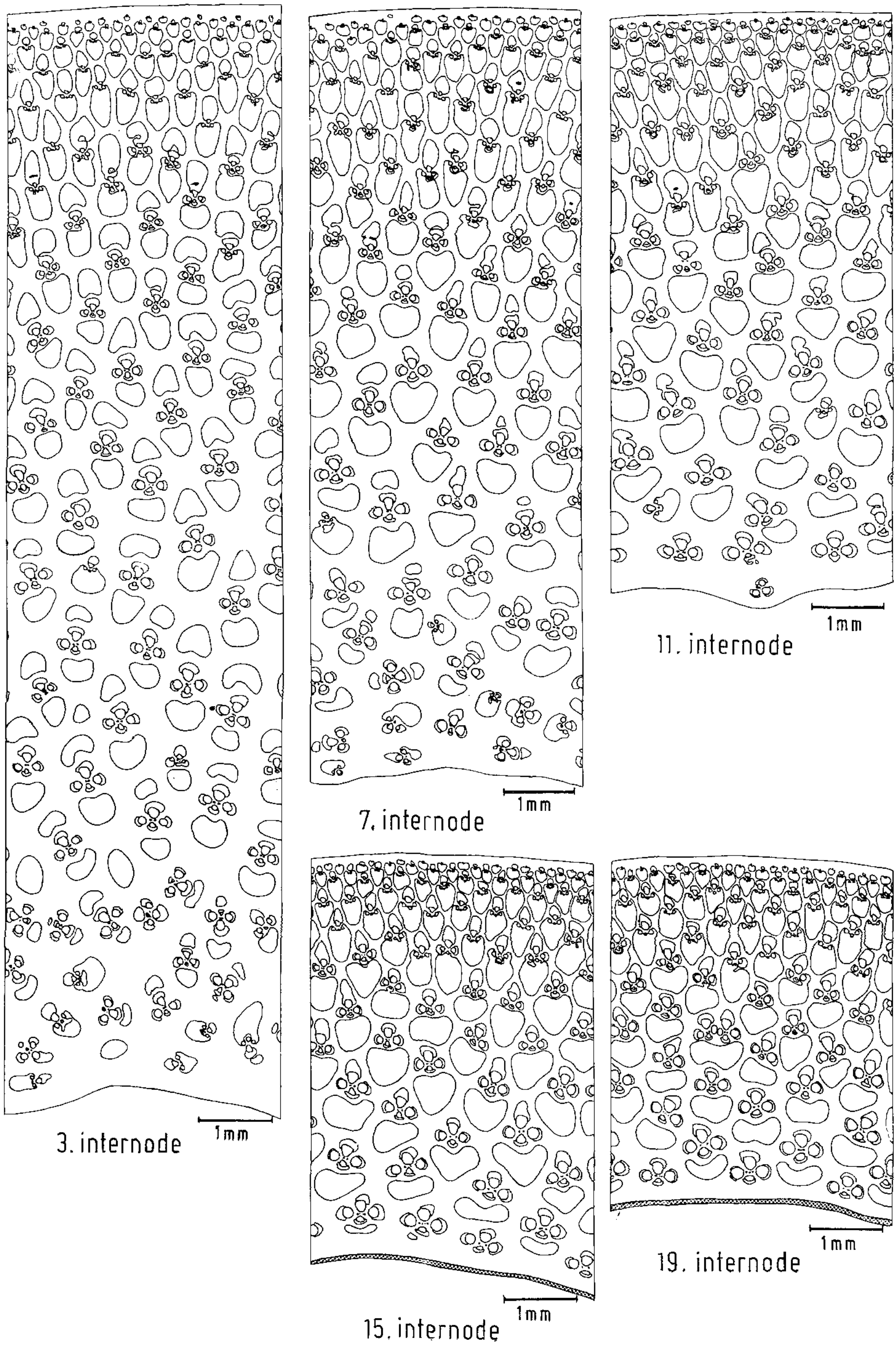
Group A		Genera having type I alone e.g.: *Arundinaria*, *Phyllostachys*, *Tetragonocalamus*
Group B		All genera having type II
	B 1	Genera having type II alone e.g.: *Cephalostachyum*
	B 2	Genera having type II and type III e.g.: *Melocanna*, *Schizostachyum*, *Teinostachyum*
Group C		Genera having type III alone e.g.: *Oxytenanthera*
Group D		Genera having type III and type IV e.g.: *Bambusa*, *Dendrocalamus*, *Gigantochloa*, *Thyrsostachys*.

Group A with vascular bundle type I comprises the leptomorph genera, whereas the pachymorph genera are classified in groups B, C and D with types II, III and IV, respectively. Therefore, considerable anatomical differences exist between these two morphologically different bamboo groups.

Together with the shape and size of vascular bundles also their number changes with the height in such a way that the number of bundles decreases steadily. In order to determine the variability of the number of vascular bundles wall-sectors described by one cm circumference were employed as basis for comparison. The size of this area is dependent on the wall thickness in such a way that it becomes smaller with the height due to the decrease in wall thickness. But since this decrease compensates the gradual decrease in the actual number and size of the vascular bundles, they get closer together in the thinner walls towards the top, i.e. the density of the vascular bundles is in contrast to their number, increasing with the height of a culm. The vascular bundle density is defined therefore by the number of vascular bundles per cm^2 culm-wall area composed of equal parts of the outer, middle and inner zones.

In general the number and density of vascular bundles are characteristic for a species. In thin-walled species the actual number of bundles is of course smaller than in species with thick walls. However, to determine the number and the density of the vascular bundles their average size is an important factor. The bigger the vascular bundles of the species, the smaller is the number present within a given area. On the contrary species with smaller bundles—but with a similar distribution of the bundles like in a species with bigger ones—possess much more vascular bundles within a corresponding area. For example,

Plate IV. Thyrsostachys siamensis Gamble. Cross-sections representing different internodes of a culm



Phyllostachys edulis Riv. with small bundles exhibits 25 bundles in a given area (Fig. 10), whereas in *Bambusa polymorpha* Munro with large bundles only 17 are present (Fig. 13). However, the 25 bundles in *Phyllostachys* appear in fact to be even wider spaced than the 17 bundles in *Bambusa.* Consequently data on the vascular bundle density must be carefully interpreted when characterizing a species. Thus the vascular bundle density expressed numerically only is insufficient and should rather be judged from the overall view of the cross-section.

Variability of Vascular Bundles Between Different Culms of a Single Species

In the same way as a correlation exists between morphological and histological characteristics within one culm, there is also a correlation between different culms of the same species. The greater the morphological differences between two culms of a single species are, the greater also their histological differences. In order to compare culms of a single species, their length and in particular their wall thickness must be taken into account. In a comparative investigation of internodes of different culms it is more important to choose internodes with the same wall thickness than homologous ones. Homologous internodes of two culms possess the same structure only when they have approximately identical wall thickness.

Species having usually two vascular bundle types only show the simple one in smaller culms. Different sites do not seem to influence the structure significantly as long as culms of similar dimensions are produced. However, when the site conditions differ so much that culms in one area are much bigger than those in another, their anatomical structure may also be different.

Terminal Layers

The parenchymatous ground tissue containing the vascular bundles is lined on the outer and inner sides by special terminal layers. Both the outer epidermis as well as the inner cell-layers exhibit specific diagnostic characteristics to some extent. These have been described by GHOSH and NEGI [1960], PATTANATH and RAMESH RAO [1969], GROSSER [1971]. In an identification key characteristics of the terminal layers such as the presence of sclereids in the innermost layer should therefore be considered.

The Anatomical Structure of the Nodes

Since this study is concerned mainly with the structure of the internodes, only an outline of the nodal anatomy will be given in the following, and some general features will be described. Whereas the anatomical structure remains almost constant within the internodes, it becomes highly modified in the nodes due to the presence of connections between the isolated bundles [HAYASHI and SUGIYAMA 1969].

Most of the bundles inside the diaphragm originate from the inner part of the culm but some bundles from the periphery bend also radially and pass into the diaphragm (Fig. 16). This consists of a ground tissue of shorter and longer parenchyma cells and is lined with rows of heavily sclerified cells. The small and mostly round vascular bundles in the diaphragm consist mainly of conducting cells surrounded by supporting tissue (Fig. 17). All the bundles together form an irregular interwoven texture so that even in a longitudinal section, cross-sections of bundles

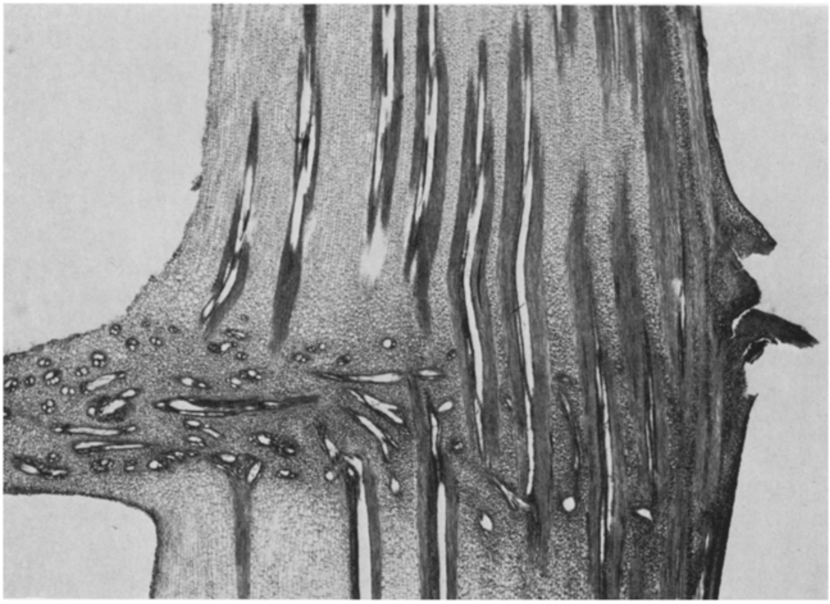


Fig. 16. Nodal region and diaphragm (7.5 x)

can also be seen. Within the diaphragm an intensive fusion and re-separation of conducting cells occur.

In the culm-wall of the nodes the fibre strands and lateral sclerenchyma sheaths of the metaxylem vessels are almost completely lost, whilst the size of the two polar sclerenchyma sheaths increases considerably. The sclerenchyma sheath of the phloem is generally larger than that of the protoxylem. The ring vessels of the

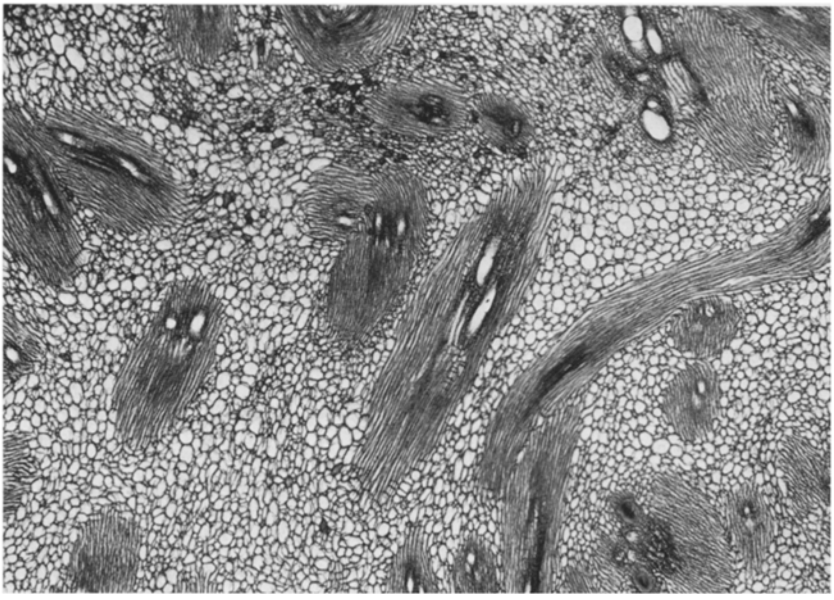


Fig. 17. Diaphragm region showing interwoven, complex vascular bundle arrangement (22 x)

primary xylem are retained and become extensively branched and re-united; each vascular bundle may possess a number of such ring vessels. Between the two metaxylem vessels several other xylem elements are usually located having considerably larger diameters than those in the internodes. The phloem also exhibits an extensive branching, and an increase in the number of cell elements. All conducting elements become extensively interconnected by repeated anastomoses.

Bundles originating in the leaf sheaths and side branches bend near the cortex and amalgamate with the peripheral bundles of the culm. After amalgamating they continue downwards. Only a few of the bundles pass right through the ground tissue to the inner parts where they may either join with other bundles there or pass on into the diaphragm.

Discussion

Differences in form, size and arrangement of the vascular bundles have already been observed by KRATZSCH [1933] who investigated the structure of *Bambusa vulgaris* and *Phyllostachys aurea* as well as other species from these two genera. He therefore indicated the possibility of distinguishing between different genera by microscopic characteristics. SAMAPUDDHI [1959] and METCALFE [1960] established that significant differences actually existed between a larger number of genera and species, and that these could be used for diagnosis. SAMAPUDDHI observed different tissue structures in 7 species and although he concluded that for each species a specific form of the vascular bundles exists, he did not give details. METCALFE described the microscopic differences between species from several genera and came to the same conclusion. Both authors however restricted their investigation to one internode of each species; SAMAPUDDHI took his samples only from the middle part of the culm and METCALFE gave no details of his sample selection. In a similar way VELASQUEZ and SANTOS [1931] in their not widely known description of five Philippine bamboo species neglected the real extent of the distinct structural differences within the culm. Indeed, because the main diagnostic character is the anatomical variability within the culm the true structure is not adequately represented by any of the studies mentioned above.

Only GHOSH and NEGI [1959] and in particular LI and CHIN [1960] as well as LI, CHIN and YAO [1962] have pointed out the structural variability that exists between the internodes of different culm parts. The observations of the Chinese authors were based on a comparative investigation of 25 Chinese bamboo species. However, the differences have not been given sufficient weight in their identification key—considered more fully below. Changes in form, size and arrangement of vascular bundles within the culm have also been observed by GROSSER [1965] as well as PATTANATH and RAMESH RAO [1969]. It is imperative for a representative species description that complete culms are to be investigated from the base to the top as has been done for the first time at the Institut für Holzbiologie und Holzschutz der Bundesforschungsanstalt für Forst- und Holzwirtschaft, Hamburg-Lohbrügge [GROSSER 1971]. Consequently, the pattern of variation in the proportions of cell types in various parts of the culm as observed by LIESE and GROVER [1961], YU and CHANG [1964] as well as LIESE and MENDE [1969] can be explained by this variation along the culm.

A first classification key based on anatomical characteristics was given by LI and CHIN [1960] and LI, CHIN and YAO [1962]. However, their observations were made mainly on internodes from the middle part of the culm which they regarded as representative for the whole plant. In contrast another identification key by PATTANATH and RAMESH RAO [1969] refers only to the internodes from the base. Because no generalization for the total culm can be made from any part alone, the internodes of all parts have to be given the same weight. With this in mind an identification key has been worked out by GROSSER [1971] which includes until now about 30 Asian bamboo species.

It has been shown for the pachymorph bamboo genera that a grouping into four culm types is possible, consisting of 3 anatomical groups, one of which is further divided into 2. All leptomorph genera, on the other hand, exhibit a similar vascular bundle structure which is characterized by the simple type I. Thus, vascular bundles of the type I found in the particular species of the leptomorph genera investigated in this paper (*Arundinaria*, *Phyllostachys* and *Tetragonocalamus*) were also described in other leptomorph species of the genera *Brachystachyum*, *Chimonobambusa*, *Indocalamus*, *Phyllostachys*, *Pleioblastus*, *Pseudosasa*, *Semiarundinaria*, *Sinobambusa* and *Shibataea* by LI and CHIN [1960], LI, CHIN and YAO [1962]. These authors have divided 24 bamboo species from 14 genera into 15 different culm types based on anatomical characters. For their classification they have selected the radial order of vascular bundles from the periphery to the inner zone of internodes taken from the middle part of the culm. As a result, because each species possesses more or less characteristic vascular bundles rows, a rather complex and insufficiently defined system arises. Genera related anatomically and morphologically are not turned out well enough as related ones by this system which consequently is inadequate as a practical identification key. Furthermore, since the system refers only to internodes from the middle part of the culm it does not typify the anatomical composition of the whole culm or of a single species.

The anatomical classification system presented in this paper, based on the presence of four vascular bundle types and their combinations, shows a remarkable coincidence with that of HOLTTUM [1956] which has been proposed on grounds of the morphological structure of the ovary of the *Bambusoideae*. Thus genera which are characterized by HOLTTUM as being related because of the similarity in their reproductive structures also seem to possess a similar anatomical structure. This implies that anatomical characteristics beside morphological features can be used successfully for the differentiation of bamboo genera into natural systematic units and for the development of a modern classification system [GROSSER and LIESE, in press].

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