

Taxonomic status of the endemic South African bamboo, *Thamnocalamus tessellatus*

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ABSTRACT

Thamnocalamus tessellatus (Nees) Soderstrom & Ellis, comb. nov. [= *Arundinaria tessellata* (Nees) Munro] is the only endemic South African bamboo and occurs from the eastern districts of the Cape, through Lesotho and Natal, to the eastern Orange Free State at elevations of about 1 500-2 500 m. The Mountain Bamboo, or 'Bergbamboes' was first described by Nees in 1841 as a member of the genus *Nastus* because of the similarity, to him, of the spikelets between it and *N. borbonicus*, but was later transferred to the all-encompassing genus of the time, *Arundinaria*, the type species of which is endemic to the south-eastern United States of America. Based on our present knowledge of bamboo genera, this South African species may be excluded from *Nastus* because the inflorescence is not a panicle but bracteate racemiform, the vegetative branches do not arise in a verticillate manner but are a series of subequal branches that are borne in a row above the nodal line and *T. tessellatus* has an androecium of three stamens and not six as in *Nastus*. The Bergbamboes, with sympodial rhizomes and branch complement of several subequal branches, can also not be maintained in *Arundinaria*, for monopodial rhizomes and a single branch at the node are typical of this genus. The simple, ebracteate, and exserted inflorescence of *Arundinaria* is also quite distinct from that of the Bergbamboes.

In order to place the South African bamboo more precisely we have made comparative studies of its leaf anatomy and epidermis, gross morphology, and analyses of its inflorescence and spikelets. The results of all these studies reveal a striking resemblance to members of the Sino-Himalayan genus, *Thamnocalamus*, to which we have accordingly transferred the species. The results are presented, together with an interpretation of the phylogenetic position of the Bergbamboes and possible events that led to the disjunction of species in the genus.

INTRODUCTION

The Republic of South Africa has but a single endemic bamboo, commonly known as the 'Bergbamboes'. The crescent-shaped distribution range of this tree grass is marked in the south-west by the 'Bamboesberg', west of Tarkastad, and in the north-east by Van Reenen's Pass in the Drakensberg, the bamboo occurring in the mountains between both points as they pass from the Cape through Lesotho and into the Orange Free State and Natal. The Bergbamboes, whose smooth narrow culms may reach 5 metres, produces clusters of branches with stiff foliage from the upper nodes giving them the appearance of gigantic plumes. The plants prefer stream edges and produce roots with air canals that verify this adaptation for wet conditions. As is a common phenomenon in most bamboos, the plants remain vegetative for many years and spread by means of rhizomes, producing flowers and fruits only rarely.

The earliest collections were sterile gatherings, and Nees von Esenbeck named the bamboo as a species of *Nastus* in his grass treatment for the 'Florae Africae Australioris' (1841). His studies were made on collections of Ecklon and Drège from various mountains in the Cape and in these he noted a similarity to *Nastus borbonicus* J. E. Gmel., perhaps in the tessellate (?) foliage and clusters of subequal branches at the nodes, which are common to both. Munro (1868), in his treatment of bamboos of the world, transferred the species to the genus *Arundinaria*, remarking that he had no authority to

do so except for the great resemblance it bore in habit and general appearance to that genus, especially *A. macrosperma* Michx. (now considered a synonym of *A. gigantea* Michx., type of the genus).

The type species of *Arundinaria* is the only bamboo native to the United States and occurs principally in the south-eastern part of the country where it is called 'Canebrake'. Michaux (1903) described the bamboo as *Arundinaria gigantea* in his 'Flora Boreali-Americana', and since that time the genus has become a repository for innumerable kinds of bamboos from throughout the world. Munro's inclusion of the Bergbamboes in this genus was not at all unusual; his opinion was later supported by the agrostologist at Kew, Sir Otto Stapf, who wrote a detailed account of the bamboo in 1900. He pointed out the real need for flowering material.

Stapf's desire was soon fulfilled for in 1908 Mrs W. Putterill discovered flowering plants in the Drakensberg, near Harrismith, and sent specimens of these to Kew. Stapf (1909) immediately published a description of the flowering material, maintaining the species in *Arundinaria*, but noting its particular resemblance to the Himalayan species, *A. spathiflora* Trin. Stapf felt, however, that the 2-flowered spikelets (they are actually 4-flowered) and nature of the glumes (?) ruled out such an alliance.

The Bergbamboes has been maintained in *Arundinaria* since the time of Munro and its placement not questioned since Stapf. The late bamboo specialist, F. A. McClure, presented a detailed description and analysis of the type species of *Arundinaria* in his treatment of bamboo genera native to the New World (1973). For the New World alone, 53 species had been assigned to the genus and McClure allocated these among nine genera, showing how all-inclusive and heterogenous the

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genus had become. Although he did not treat the Old World species, McClure's unpublished notes indicate that he also did not regard the Bergbamboes as a member of *Arundinaria* but rather of *Thamnocalamus*, a Himalayan genus based on *Arundinaria spathiflora*.

In view of the different opinions concerning the taxonomic position of the Bergbamboes, we have made comparative studies of its leaf anatomy and epidermis and gross morphology, along with an analysis of the inflorescence and spikelets. Our studies confirm the suggestion by Stapf that a relationship does occur with '*Arundinaria*' *spathiflora*. We agree with McClure, who recognized Munro's genus *Thamnocalamus* (based on that species) and who felt that the Bergbamboes belonged there as well.

SYNOPSIS

***Thamnocalamus tessellatus* (Nees) Soderstrom & Ellis, comb. nov.** Lectotype: Cape, 'in monte Katberg, alt. 500' ', *Drège s.n.* (K; PRE, fragment ex K).

Nastus tessellatus Nees von Esenbeck. *Florae Africae Australioris*, 463 (1841). Syntypes: Cape, 'In monte Winterberg alt. VI. (Terrae Caffrorum), "*Ecklon s.n.*"; in praeruptis udis montium Witbergen alt. 5000–6500' vulgatissima, etiam in monte Los-Tafelberg 'in den Kränzen' eadem altitudine, in Bambusergen aliisque in locis editissimis circa fines Caffrorum, tum vero et in monte Katberg alt. 500', *Drège s.n.* (K; PRE fragment ex K).

Arundinaria tessellata (Nees) Munro. *Monograph of the Bambusaceae*, *Trans. Linn. Soc. Bot.* 26: 31. (1868); non Bean, *Gdnrs' Chron.* ser. 3, 15: 338 (1899).

In his original description of *Nastus tessellatus*, Nees listed specimens collected by Ecklon and Drège on various mountains in the Cape. We have chosen as the lectotype the collection of Drège on the Katberg, of which there is a fragment at PRE from the complete specimen at K.

MORPHOLOGICAL DESCRIPTION

Loosely tufted bamboo with hollow culms 1–5 m tall, 2 cm in diameter, erect or only slightly arching, dark maroon when young, becoming stramineous, waxy with age, the branches confined to the upper nodes and producing a plumelike effect. *Rhizomes* sympodial with necks 25–30 cm long and thick roots containing air canals. *Nodes* not thickened, containing a single bud. *Culm leaves* somewhat persistent: sheath pale maroon with fine pencil-thin stripes when young; blade persistent, at first ascending, becoming horizontal-concave. *Branching* intravaginal, occurring at the upper nodes of the culm, consisting of several (5–8) subequal branches above the nodal line, these rebranching and resulting in 10–12 branches that form dense tufts of foliage at the node, the branches 10–30 cm long. *Foliage leaves*: leaf complement of 3–5 closely overlapping leaves with blades up to 15 cm long and 1–1,5 cm wide on the primary branches, 5–6 cm long and up to 0,8 cm long on the branches of further orders, the blades stiff, narrowly lanceolate, gradually tapering below to a petiole 1–2 mm long and to an acuminate, navicular apex forming a hard point, the midrib prominent on the lower surface with 3 or 4

pairs of secondary nerves, the margins cartilaginous and antrorsely scabrous, both surfaces otherwise smooth, sometimes pubescent toward the base of the blade, especially on one side of the midnerve, the tessellation generally manifest on both surfaces; ligule a truncate membrane up to 1,5 mm long, glabrous except for a few cilia on the upper margin; sheath strongly ribbed, glabrous on the back, the upper margin consisting of a short-ciliolate collar and ciliate margins on either side of the petiole.

Inflorescence terminating the branches, the uppermost nodes of which bear long sheaths (their small blades caducous) that exceed the length of the inflorescence, these sheaths strongly overlapping, becoming stramineous and frayed with age; inflorescence consisting of 3–5 spikelets, the lowermost sessile and subtended by a bract, the succeeding spikelets preceding the terminal one each with a short pedicel, the whole unit (including the bracts) c. 4 cm long; subtending bracts glabrous, strongly ribbed, becoming incurved, truncate at the apex; axis of the inflorescence thick, angular, short-hispid with a few longer hairs at the nodes and on the angles; subtending bracts on the axis present below the lowest spikelet and sometimes at a higher node, white, many-nerved, glabrous, with an acute tip.

Spikelets more or less ovoid, 15,4–17,4 mm long, 4-flowered, the lower two florets most fully developed with the second slightly elevated above the first but a little smaller in size, the third depauperate and consisting of a small lemma enclosing a tiny rudimentary palea and flower, the fourth quite rudimentary; glumes 2, glabrous, the lower a little shorter than the upper, broad at the base and narrowing to an acute tip; glume 1 lanceolate from the side, 9,9–11,5 mm long, 8- or 9-nerved with a few transverse veinlets, glabrous; glume 2 lanceolate from the side, pointed, 14,0–15,0 mm long, 9–13 nerved with transverse veinlets, glabrous; lemma oblong-lanceolate from the side, 11,1–15,0 mm long, 10- or 11-nerved with transverse veinlets, minutely ciliolate on the upper margins, otherwise glabrous; palea broadly lanceolate in side view, 10,0–12,5 mm long, 2-keeled with a sulcus between the keels and shortly bifid at the summit between them, with 2 broad wings, faintly 2- or 3-nerved between the keels on the upper part and with a few transverse veinlets, 3-nerved in each wing with transverse veinlets, glabrous except for the ciliate keels and truncate upper margin between them; lodicules 3, rhomboid above with a broad base, 1,8–2,4 mm long, thickened on the lower half and thin above with densely ciliate margins, the single posterior lodicule similar in all ways to the anterior pair except a little smaller; stamens 3, the anthers orange, 7,2–8,5 mm long, with the filament attached to the connective on the lower 1/4-1/5; ovary with 3 short stigmas (plumose ?); fruit not seen.

Specimens examined:

O.F.S.—Without precise locality: Drakensberg range, *Putterill s.n. sub Medley Wood 11336* (=Galpin 8576) (PRE; US fragment ex NH). 2828 (Bethlehem); SE of Visierskerf, ± 15 km W of Fouriesburg (–CA), *Scheepers 1863* (PRE), Franshoek



FIG. 1.—Vegetative features of *Thamnocalamus tessellatus*: a, rhizomes, somewhat diagrammatic (from photograph); b, new culm showing erect blades, $\times 0,5$; c, leaf complement, $\times 0,5$; d, summit of culm leaf showing reflexed blade, $\times 0,5$; e, branches with foliage, $\times 0,5$; f, section of leaf blade showing cartilaginous margin and tessellate venation, $\times 12,5$; g, new culm leaf, inside view, $\times 1,5$; h, branch bud covered by prophyllum, $\times 1$; i, bud emerging through prophyllum as primary branching, $\times 1$; j, young primary and secondary branches, $\times 1$; k, branch complement, $\times 1$; l, under part of foliage leaf showing outer and inner ligules, $\times 4,5$; m, upper part of foliage leaf showing outer and inner ligules, $\times 4,5$. (All figures from Soderstrom & Du Toit 2610 except c from Van Zinderen Bakker 13 and e, f, l and m from Codd & Dyer 2778. Illustration by Alice R. Tangerini).

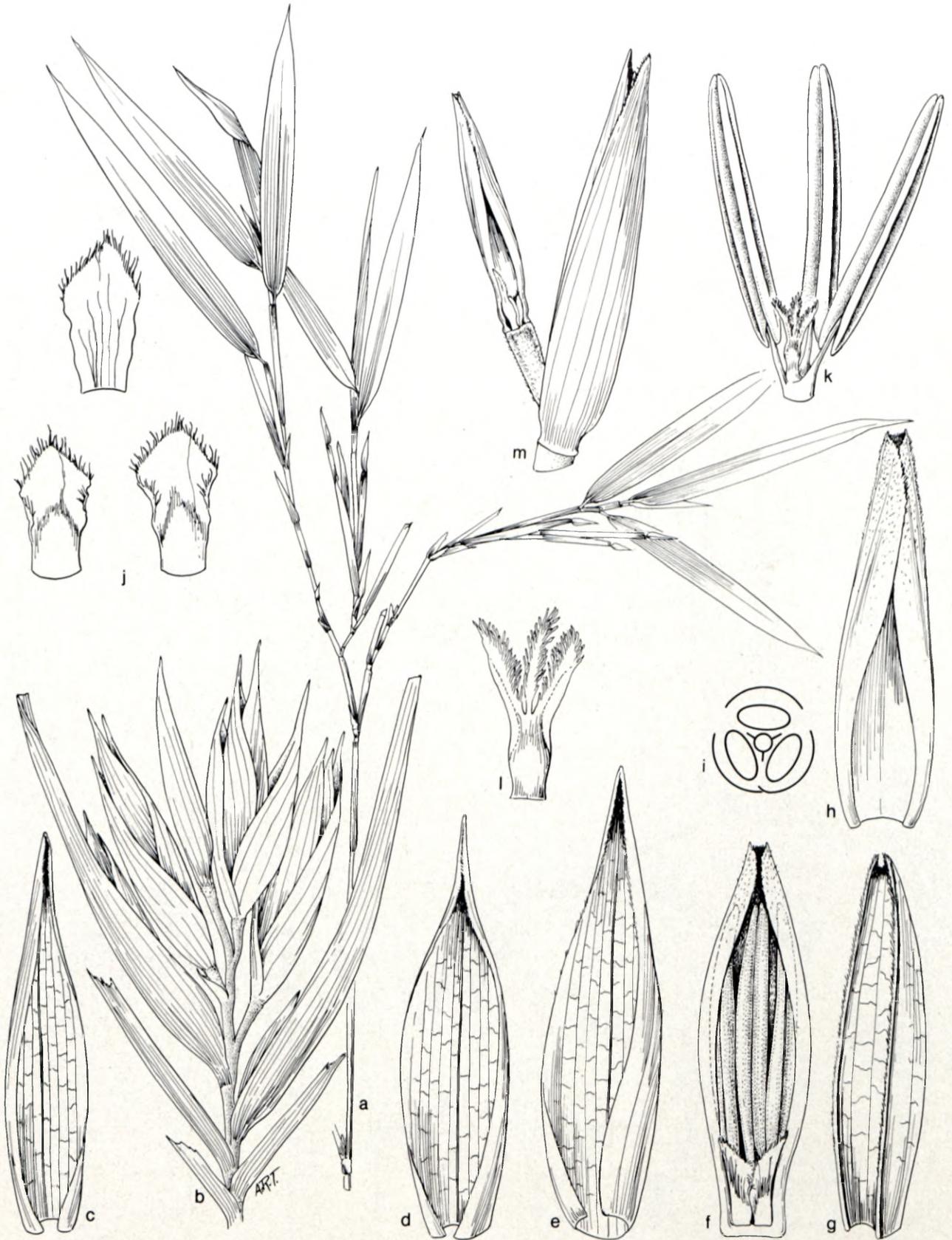


FIG. 2.—Flowering features of *Thamnocalamus tessellatus*: a, branch at commencement of flowering with small leaf blades that precede spikelet formation, $\times 0,5$; b, spikelet, $\times 3$; c, glume 1, $\times 6$; d, glume 2, $\times 6$; e, lemma, $\times 6$; f, palea, front view, showing the anterior pair of lodicules with overlapping margins and enclosed anthers, $\times 6$; g, palea, back view, showing the two strong keels, $\times 6$; h, palea, front view, $\times 6$; i, schematic of flower in cross section showing 3 lodicules, 3 stamens and ovary with 3 stigmas; j, lodicules, $\times 12,5$; k, stamens and pistil, $\times 6$; l, gynoecium, showing the 3 stigmas, $\times 15$; m, upper part of spikelet with 2nd, 3rd and 4th florets, the 4th a rudimentary flap of tissue enclosed within the small lemma of the 3rd floret, $\times 6$. (Fig. 2a based on Killick 1863, b–m on Medley Wood 11336 (= Galpin 8576). All drawings rendered by Alice R. Tangerini).

Farm, Ficksburg, *Loxton & Ellis 990* (PRE). 2829 (Harrismith): Platberg, Harrismith (-AC), *Putterill (?)* (PRE); Maweni Heights (-BD), *Van Zinderen Bakker 13* (PRE).

NATAL.—2828 (Bethlehem): Royal Natal National Park (-DB), *Codd & Dyer 2778* (PRE); Mont aux Sources (-DD), *Mogg 422* (PRE), *Hutchinson, Forbes & Verdoorn 54* (PRE). 2829 (Harrismith): Cathedral Peak Forestry Reserve (-CC), *Killick 1893* (PRE), *Soderstrom & Du Toit 2610* (PRE, US). 2929 (Underberg): Giants Castle Game Reserve (-AB), *Symons 150* (PRE), *Sim 20517* (PRE); Highmoor Forest Station (-BC), *Ellis 3161* (PRE); Bushman's Nek (-CC), *Killick & Vahrmeijer 3976*, (PRE); Underberg Dist. (-CD), *McClellan 739* (PRE).

LESOTHO.—2828 (Bethlehem): Matalane River, Leribe Dist. (-CC), *Dieterlen 279, 279a* (PRE). 2928 (Marakabei): Pitseng, Leribe Dist. (-AA), *Dieterlen 1010* (PRE). Meniaming Stream, *Jacot Guillarmod 2207* (PRE). 3027 (Lady Grey): upper Outhing River gorge, Makoae (-BD), *Schmitz 8315*. 3028 (Matatiele): tributary of Likhaibaning River (-AC), *Archibald 2750* (PRE); mountain side above Buffalo River waterfall (-CA), *Galpin 6931* (PRE).

CAPE.—3027 (Lady Grey): Wittebergen (-CA), *Drège s.n.* (US fragment ex W); Haskally below Mt Newton, Barkley East (-DC), *Acocks 23872* (PRE). 3126 (Queenstown): Bamboesberg (-AC), *Archibald 2810* (PRE); Shepstone Berg near Andriesberg (-DA), *Galpin 2616* (PRE). 3226 (Fort Beaufort): Katberg, Stockenstrom Div. (-DA), *Drège s.n.* (PRE fragment ex K); top of Gaika's Kop, Hogsback (-DB) *Archibald 01* (PRE); Victoria (-DD), *Morton s.n.* (PRE). 3227 (Stutterheim): Gxulu Kop, Keiskammahoeck (-CA), *Story 3515* (PRE).

Hubbard and Vaughan (1940) listed a specimen (*Vaughan A.139*) as occurring on Mauritius but we have not seen this specimen.

MORPHOLOGICAL DISCUSSION

The Bergbamboes grows in loose tufts with the culms separated by the short necks of the rhizomes, which may be 25–30 cm long. The habit of growth is sympodial with each new rhizome eventually turning up into a culm, the intervening short and solid internodes without roots or buds except where they are enlarged in the transition zone to culm. In *Soderstrom & Du Toit 2610*, which was collected next to a stream, the thick roots terminated in a mass of fine roots (Fig. 1a) and the main part of the root itself was found to have air canals (Fig. 5). The senior author has also observed thick roots with air canals on another bamboo, '*Arundinaria densifolia*' Munro, which occurs in marshes in the highlands of Sri Lanka.

The new culms are maroon and smooth, covered by culm leaves in which the blade is at first ascending (Fig. 1a), then becoming horizontal to reflexed (Fig. 1d). The culm leaf, a pale maroon when fresh, soon dries and becomes stramineous, eventually falling off. The culm leaf, especially the sheath and foliage leaf-blades are strongly marked by cross veins. This tessellate venation, which also occurs in the glumes, lemma, and palea, is the basis of the specific epithet. Branching occurs on the upper part of the culm with a cluster of stiff subequal branches at each of the nodes (Fig. 1e). The naked culms, each with a panache of foliage above, contributes to the highly ornamental appearance of this bamboo.

The mature branch complement (Fig. 1k) consists of several stiff subequal branches that emanate from the culm at about a 45 degree angle. The bases of the major 5 or 6 branches form a line just above the nodal line itself. A study of the developmental stages reveals that a single bud at the node (Fig. 1h)

produces a primary axis (Fig. 1i) and soon thereafter two secondary axes (Fig. 1j). The primary axis pushes through the apex of the flaps of the prophyllum that have covered and protected the bud. The two secondary axes split the prophyllum during their growth and these ultimately remain as flaps of tissue on either side of the branch complement. The secondary branches arise in succession from the lower nodes of the primary axis and each bears a prophyllum. The prophyllum is the modified sheath of the first node of the axis and in our bamboo it subtends a bud capable of producing another branch. Tertiary axes develop from buds subtended by prophylla. Tertiary axes (Fig. 3b & d) develop at the nodes above the prophyllum and are subtended by a sheath.

The growth of all axes occurs rapidly and almost simultaneously and in the early stages the new branches are mixed with prophylla and subtending sheaths.

In the accompanying diagram (Fig. 4) the branching system is shown in 2 dimensions. Some subtending sheaths are either lacking or were not located in the dissection: we have indicated these by dotted lines. The lower nodes of the major axes run close together in reality and are not clearly marked as in this diagram. An occasional bract was found without a bud: either it was lacking or not well developed.

The pattern appears to be that the first (prophyllate) and the second nodes of the single primary axis and two secondary axes bear buds that develop into axes (those of the primary giving rise to the two secondaries and the secondaries giving rise to four tertiaries). In the diagram (Fig. 4) one branch of 4th order has begun to develop and another is beginning to develop at the prophyllate node of the third. If a 4th order branch develops at the prophyllate node of each tertiary branch the total number of developed axes in the branch will be 11. Theoretically a greater or lesser number can develop but this number seems to be average in this bamboo, probably because of space limitations.

The stiff foliage is quite resistant to wilting; even an hour and a half after severing the branches and exposure to full sun the leaves do not begin to curl. In most bamboos wilting occurs immediately or very shortly after cutting. The leaf blades have a scabrous cartilaginous margin and grill-like appearance due to the numerous and strong transverse veinlets (Fig. 1f).

The first signs of flowering come with the diminution of the leaf blades, as shown in Fig. 2a. The ultimate nodes of the branch bear spikelets, the lower ones of which may be subtended by a leaf sheath and the upper ones by a bract, or reduced leaf sheath. The uppermost spikelets are not subtended by a bract. The whole cluster of spikelets (Fig. 2b) is covered by long leaf sheaths from the lower nodes: these at first bear tiny blades that are deciduous, leaving the summit of the sheath truncate.

Ultimately all branches bear spikelets and few leaves, these falling away with the development of

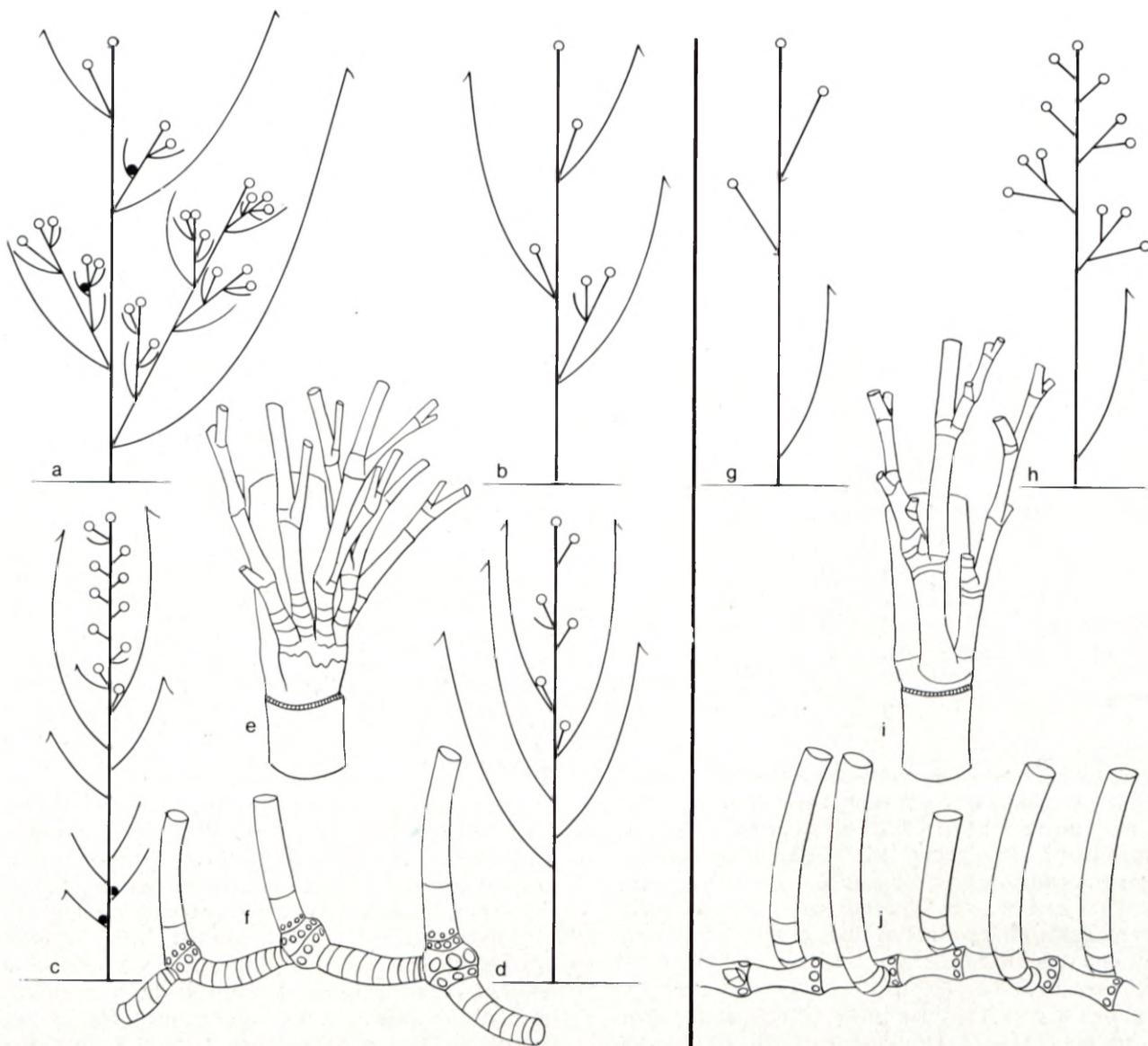


FIG. 3.—Schematic of the inflorescence, rhizome and branching patterns of *Thamnocalamus tessellatus* and related taxa compared with *Arundinaria gigantea*: a & b, inflorescence of *Thamnocalamus spathiflorus*; c, inflorescence of *Thamnocalamus spathaceus*; d, inflorescence of *Thamnocalamus tessellatus*; e, branch complement of *Thamnocalamus*; f, sympodial rhizome system of *Thamnocalamus* showing the short internodes of the neck and absence of buds or roots except in the transition zone; g, inflorescence of *Arundinaria gigantea*; h, inflorescence of *Sasa paniculata*; i, branch complement of *Arundinaria* (the *Sasa* type is not shown); j, monopodial rhizome system of *Arundinaria* showing that each node has a bud and roots. Open circles represent a spikelet and closed circles a bud, curved lines with hooks a sheath with blade and curved lines only a reduced sheath (bract).

the inflorescence and doubtless leading to death of the plant after flowering and seed-set. As in many bamboos flowering is rare in this species and probably occurs at long intervals. The only flowering specimens I have seen are those of Mrs Putterill collected in 1908 (appearing variously as *Medley Wood* 11336 or as *Galpin* 8576) and of Killick, collected in 1953.

The spikelets are 4-flowered, with the lower two florets best developed and reduction occurring in the 3rd and 4th (Fig. 2m). Stapf (1908) erred in referring to the spikelets as 2-flowered. The spikelet contains 2 glumes (Fig. 2c & d) and the floret a lemma (Fig. 2e) and palea (Fig. 2f–h). All of these organs are many-nerved and with numerous transverse veinlets.

The flower consists of 3 lodicules (Fig. 2j), of the

type that is most common in bamboos — apex pointed, margins ciliate, and numerous vascular bundles. The posterior lodicule is similar to the anterior pair and little reduced as is so often the case in bamboos.

The androecium consists of three basifixed anthers (Fig. 2k) and gynoecium of an ovary with 3 stigmas (Fig. 2k & 1). These are small in the few spikelets available for dissection but are bristly and are apparently of the plumose type, which condition would become more apparent after elongation.

ANATOMICAL DESCRIPTION

The root in transverse section

Epidermis: uniseriate; epidermal cells thin walled

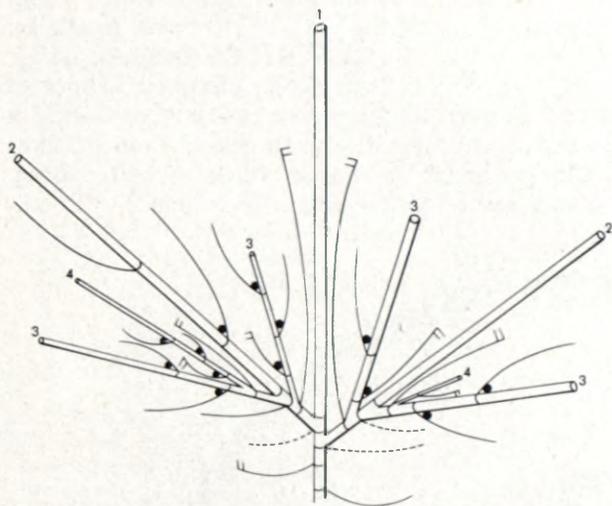


FIG. 4.—Schematic of branch complement in *Thamnocalamus tessellatus*.

and lacking cuticle. Root hairs absent. *Exodermis*: cells of outer subepidermal layers of cortex suberized and slightly thickened to form exodermis (Fig. 5a). Intergrades into cortex. *Cortex*: consists of inflated parenchyma cells of uniform size but becoming smaller externally and intergrading into exodermis (Fig. 5a & b); lack chloroplasts but few crystals present. Elongated radially orientated AIR CANALS located adjacent to the central cylinder; occupy about $\frac{2}{3}$ the width of the cortex; conspicuous, numerous and regularly arranged (Figs. 5a & b). *Endodermis*: well-developed uniseriate cylinder of conspicuous cells with considerably thickened and lignified inner tangential and radial walls (Fig. 5b). No passage cells seen. *Vascular cylinder*: single layered sclerified pericycle surrounds primary vascular tissue; phloem strands located on periphery of vascular cylinder external to the circle of protoxylem and metaxylem vessel members; metaxylem vessels very wide, circular and thin walled. Centre of cylinder occupied by a pith containing a single large air canal (Fig. 5a).

The leaf blade in transverse section

Leaf outline: expanded; flattened to loosely inrolled from one margin only. *Ribs and furrows*: slight adaxial undulations with no regular pattern associated with the vascular bundles. Definite but slight abaxial ribs and furrows present; may be better developed than on adaxial surface; rib development opposite first order vascular bundles usually greater and composed of sclerenchyma girder. *Midrib*: SINGLE FIRST ORDER VASCULAR BUNDLE ONLY; projects abaxially; no adaxial development of amphivasal bundles (Fig. 6a). *Vascular bundle arrangement*: 7, 9, 11 or 13 first order vascular bundles in section (including median vascular bundle). 5 THIRD ORDER VASCULAR BUNDLES BETWEEN CONSECUTIVE FIRST ORDER VASCULAR BUNDLES; no second order vascular bundles; first order vascular bundles located in centre of blade; third order vascular bundles located closer to the abaxial surface (especially noticeable in freshly fixed material).

Vascular bundle description: third order vascular bundles elliptical in shape; xylem and phloem distinguishable; first order vascular bundles rounded in outline; lysigenous cavity protoxylem vessel present; metaxylem vessels circular; diameter greater than width of parenchyma sheath cells. *Vascular bundle sheaths*: first order vascular bundle sheaths double (Fig. 6c); outer sheath horse-shoe-shaped with wide abaxial interruption; slight adaxial interruption. No extensions present; cells elliptical, often irregular in size; considerably smaller, but with thicker walls, than the mesophyll cells; chloroplasts absent or considerably fewer than in mesophyll cells. Inner sheath complete; cells with uniformly and heavily thickened walls. 3 SHEATH-LIKE LAYERS PRESENT IMMEDIATELY OUTSIDE THE METAXYLEM VESSELS in all specimens examined (Fig. 6b & c). *Sclerenchyma*: adaxial and abaxial girders associated with all vascular bundles; narrow towards bundle (particularly the adaxial girders) and especially well developed in association with the first order vascular bundles. All fibres with very thick walls; lumens almost excluded. No sclerenchyma between bundles. Small rounded sclerenchyma cap at margin. *Chlorenchyma*: comprised of ARM CELLS; INVAGINATIONS OF EQUAL LENGTH and from all directions in abaxially located cells but tend to be vertically arranged in uppermost adaxial layer (this distinction not very conspicuous) (Fig. 6c). FUSOID CELLS (cavities) present on either side of all vascular bundles; narrow, tapering gently, horizontal or downward projecting (Fig. 6b & c). Successive fusoid cells separated by 1 or 2 arm cells. *Colourless cells*: absent. *Adaxial epidermis*: bulliform cell groups fan-shaped with central cell equal in size to $\frac{1}{2}$ leaf thickness; central cell inflated, fan-shaped. Located between all vascular bundles. Epidermal cell outer walls covered by a continuous, thick cuticle. NO PRICKLES, hooks, macro hairs or PAPILLAE. *Abaxial epidermis*: no bulliform cells occur; each epidermal cell covered by individually thickened cuticle projecting into thickened, narrow papillae; more than 1 papilla per cell (Fig. 6c). No macro-hairs. Large prickles common opposite the vascular bundles as well as between them (Fig. 6c).

Abaxial epidermis

Intercostal long cells: elongated; anticlinal horizontal walls parallel; end walls vertical; unthickened; moderately to deeply undulating with undulations U-shaped. Cell shape constant throughout intercostal zones. Hooks or micro-hairs present between successive long cells. No bulliform cells present. *Stomata*: low dome-shaped to parallel-sided; 6 rows of stomata in each intercostal zone restricted to 3 adjacent files adjoining the costal zones. SUNKEN IN PITS OVERARCHED BY PAPILLAE (Fig. 7a). *Intercostal short cells*: unsilicified with crenate outline; between virtually all long cells; bases for hooks and micro-hairs. *Papillae*: small, thickened cuticular papillae on all intercostal cells; many per cell; IRREGULARLY ARRANGED (not in rows); all similar in size and shape. OCCUR ON BASES OF HOOKS, intercos-

tal short cells and overarch the stomata. Mainly intercostal but sometimes present on costal long cells of narrow costal zones overlying third order vascular bundles. *Prickles*: bases large (twice as long as stomata); short barbs all oriented in same direction (distal?). Costal, frequent especially on narrow costal zones; in same files as silica bodies. *Hooks*: circular bases about same diameter as stomata; short

barbs pointing in all directions; common throughout intercostal zones (Fig. 7a). *Micro-hairs*: bicellular; **BASAL CELL 3× LENGTH OF DISTAL CELL** (Fig. 7a); both cells markedly elongated; about 4x length of stomatal complexes; base not constricted at point of attachment; emerge straight out of short cell; restricted to centre of intercostal zones. *Macro-hairs*: none seen. *Silica bodies*: TALL,

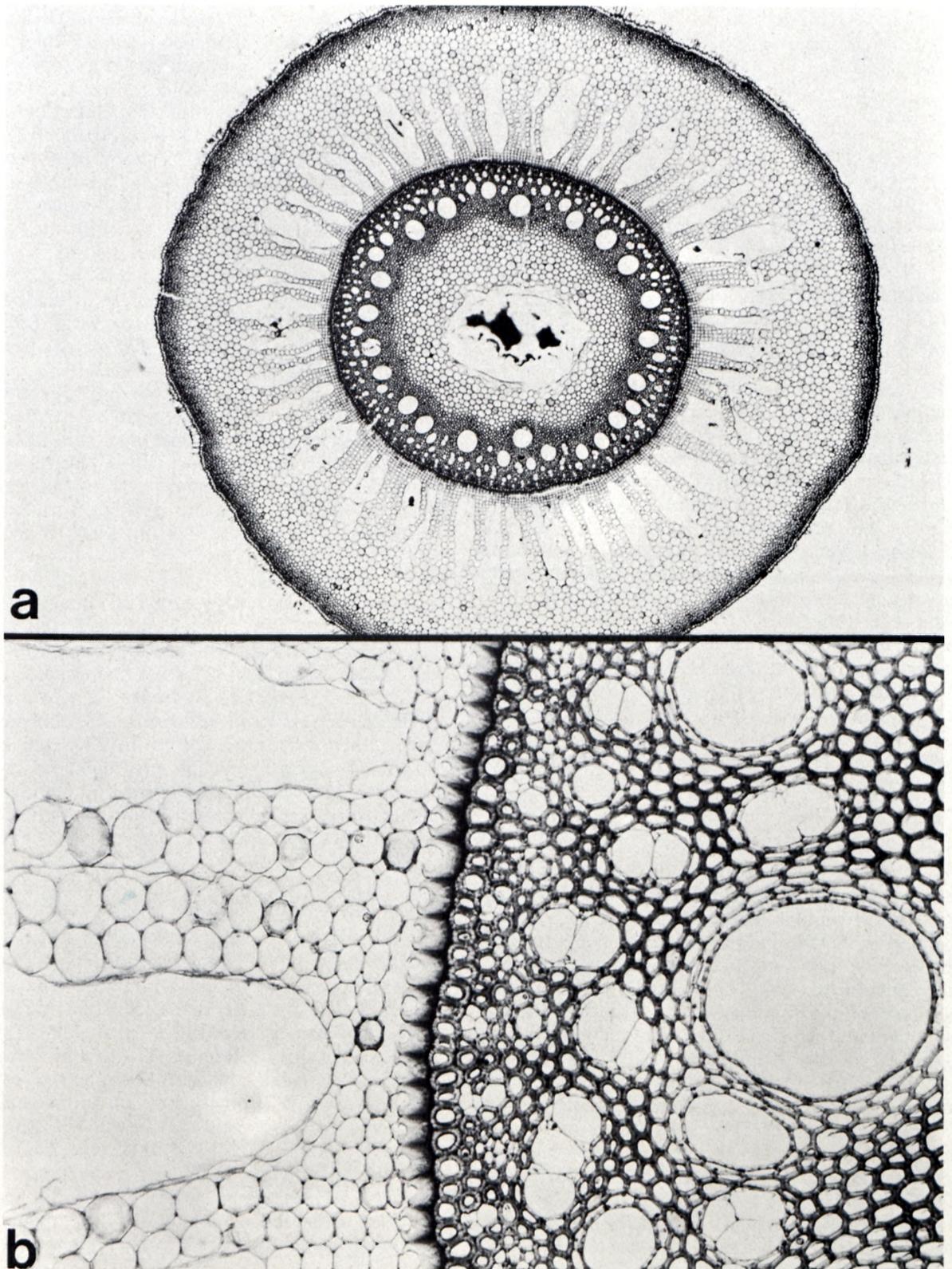


FIG. 5.—Transverse sections of the root of *Thamnocalamus tessellatus*: Soderstrom & Du Toit 2610; a, $\times 40$; b, $\times 400$.

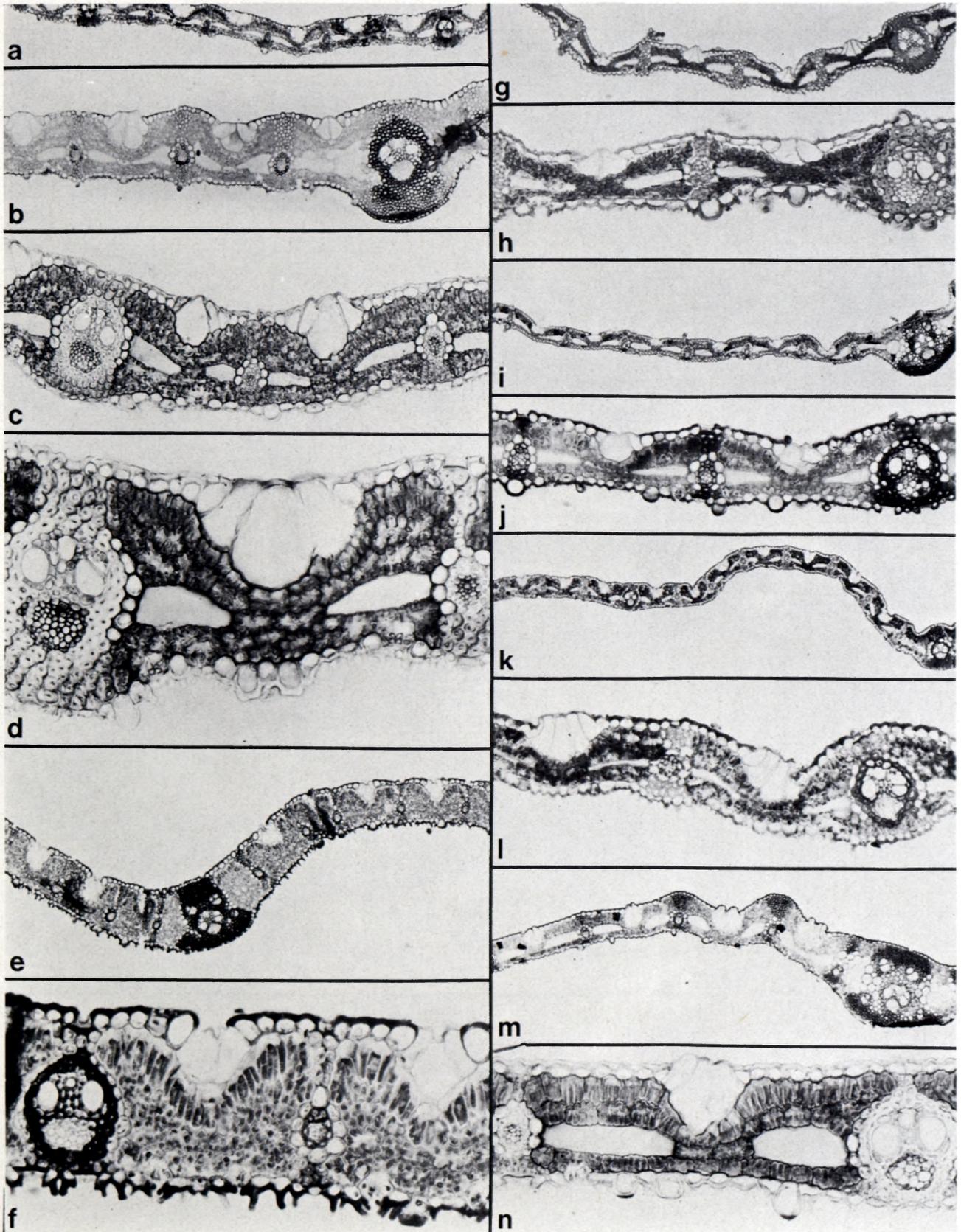


FIG. 6.—A comparison between the leaf blade anatomy of *Thamnocalamus tessellatus* and various other bamboos: a–d, *T. tessellatus*; a, *Soderstrom & Du Toit* 2610, $\times 100$, note five small vascular bundles between consecutive first order bundles; b, *Ellis* 3161, $\times 160$, simple midrib containing single vascular bundle; c, *Soderstrom & Du Toit* 2610, $\times 400$; d, *Soderstrom & Du Toit* 2610, $\times 640$, invaginations of arm cells not vertically orientated. Papillae absent on adaxial surface; e–f, *Phyllostachys aurea*, *Ellis* 3511; e, $\times 100$, midrib with first order bundle and two small vascular strands; f, $\times 400$, fusoid cells absent and note vertical orientation of adaxial mesophyll cells and well developed abaxial cuticular papillae and prickles; g–h, *Thamnocalamus spathiflorus*, *McClure* 22006; g, $\times 160$, midrib with single vascular bundle; h, $\times 400$, mesophyll poorly preserved but note minute adaxial papillae; i–j, *Arundinaria gigantea*; i, *Soderstrom* 2530, $\times 100$, midrib with complex vasculature and 7 bundles between larger bundles; j, *Soderstrom & Calderon* 2047, $\times 400$, leaf much narrower than that of *T. tessellatus* (Fig. 6c); k–l, *Arundinaria alpina*, *Greenway & Kanuri* 13638; k, $\times 100$, midrib of single vascular bundle only but 7 smaller bundles between consecutive larger bundles; l, $\times 400$; m–n, *Bambusa balcooa*, *Smook & Soderstrom* 1982; m, $\times 160$, complex midrib vasculature; n, $\times 400$, arm cell invaginations vertically orientated.

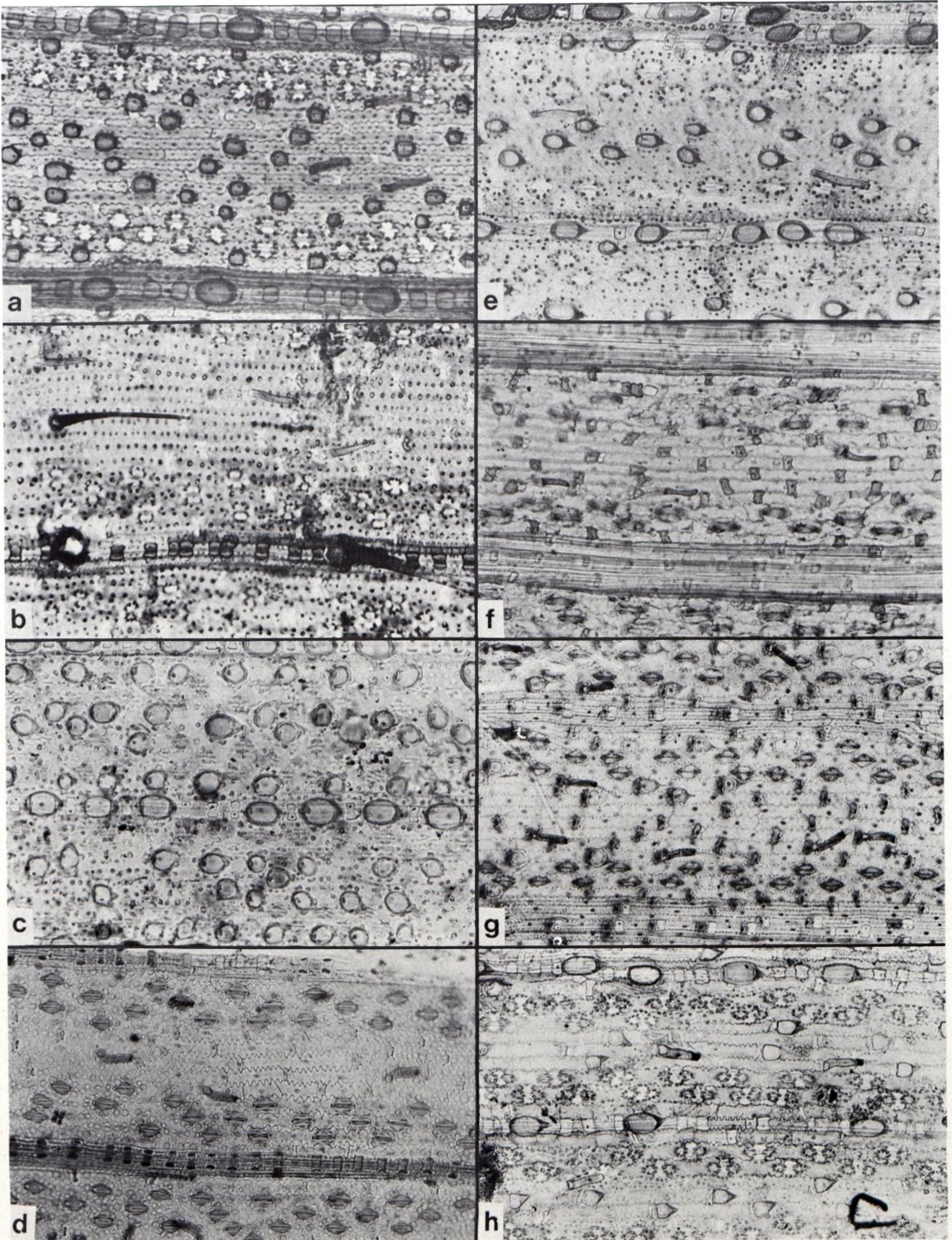


FIG. 7.—Abaxial epidermal structure of *Thamnocalamus tessellatus* compared with various other bamboos. All $\times 400$: a, *Thamnocalamus tessellatus*, Soderstrom & Du Toit 2610, note saddle shaped silica bodies, prickles and hooks, papillate intercostal long cells with papillae overarchng stomata and elongated basal cells of microhairs; b, *Arundinaria gigantea*, Soderstrom 2530, costal and intercostal macro-hairs present; c, *Phyllostachys aurea*, Ellis 3511, hooks abundant and micro-hairs very small; d, *Oxytenanthera abyssinica*, Smook & Soderstrom 1983, hooks and prickles absent and intercostal long cells with undulating cell walls; e, *Thamnocalamus spathiflorus*, McClure 22006, very similar to *T. tessellatus* except that some silica bodies are dumb-bell shaped; f, *Arundinaria alpina*, Greenway & Kanuri 13638, papillae absent on this part of the leaf blade; g, *Bambusa balcooa*, Smook & Soderstrom 1982, undulate intercostal long cell walls; h, *Chimonobambusa marmorea*, Makino s.n., cells of micro-hair of equal length.

SADDLE-SHAPED to square with angular outlines. Granules present. Same width as adjacent long cells. *Costal cells*: files of costal long cells alternate with files of alternating silica cells and costal short cells (and prickles). About 7 files comprise first order vascular bundle costal zones and 3-5 files third order vascular bundle costal zones.

Compiled from the following material:

Loxton & Ellis 990: 2828 (Bethlehem): Ficksburg (-CA). Soderstrom & Du Toit 2610: 2829 (Harrismith): Cathedral Peak (-CC). Ellis 3161: 2929 (Underberg): Highmoor (-BC). De Wet 1124: collection locality unknown but doubtless S. Africa.

ANATOMICAL DISCUSSION

To enable an assessment of the relationships of *T. tessellatus* to be made, the leaf anatomy of the Bergbamboes has been compared with various other bamboo species. The results of this comparative study are presented graphically in Table 1. Anatomical characteristics of the leaf in transverse section and of the abaxial epidermis, which in

combination appear to be diagnostic of *T. tessellatus*, have been used for this comparison and have been printed in block capitals in the preceding anatomical description.

It is immediately evident from Table 1 that no single character distinguishes *T. tessellatus* from all the other bamboo species in the sample studied. In fact there appear to be no diagnostic characters separating any of the genera or species examined and combinations of different characters are the only effective means of distinguishing any of the taxa examined. Even the presence of fusoid cells, which is generally considered to be characteristic of the bambusoid grasses (Brandis, 1907; Chih-Ying Wu, 1958; Metcalfe, 1960; Calderon & Soderstrom, 1973) is not consistent throughout the sample studied and *Phyllostachys aurea* A. & C. Riv. (Fig. 6f), *Chimonobambusa marmorea* (Mitf.) Makino and *C. falcata* (Nees) Nakai lack fusoid cells completely. Arm cells are present in all taxa studied but these structures are not exclusive to these woody bambusoid grasses but also occur in the herbaceous bambusoid (Calderon & Soderstrom, 1973), oryzoid

SPECIES	VOUCHER SPECIMEN COLLECTORS NUMBERS	MIDRIB		NO. OF 30VBS BETWEEN CONSECUTIVE 10VBS		FUSOID CELLS		ARM CELL INVAGINATIONS		ADAXIAL EPIDERMAL PAPILLAE		ADAXIAL APIDERMAL PRICKLES		ABAXIAL STOMATA		ABAXIAL PAPILLAE		ABAXIAL PAPILLAE ARRANGEMENT		MICRO-HAIR BASAL CELL LENGTH		SILICA BODIES				
		COMPLEX OF VBS	SINGLE VB ONLY	MORE THAN 5	5-30 VBS	ABSENT	NOT NEAR MARGIN	PRESENT	VERTICAL FROM LOWER WALL	RADIAL FROM ALL WALLS	PRESENT	ABSENT	PRESENT	ABSENT	NOT OVERARCHED BY PAPILLAE	OVERARCHED BY PAPILLAE	HOOKS WITHOUT PAPILLAE	ON BASES OF HOOKS	SINGLE ROW	IRREGULAR	LESS THAN 3X DISTAL CELL	3X LENGTH OF DISTAL CELL	DUMB-BELL SHAPED	SADDLE SHAPED TALL	SADDLE SHAPED	
<i>Thamnocalamus tessellatus</i>	Loxton & Ellis 990																									
	Ellis 3161																									
	Soderstrom & Du Toit 2610																									
	De Wet 1124																									
<i>Thamnocalamus spathiflorus</i>	McClure 22006																									
<i>Thamnocalamus aristatus</i>	Emery 133																									
<i>Arundinaria alpina</i>	Greenway & Kanuri 13638																									
<i>Arundinaria amabilis</i>	Soderstrom 2526																									
<i>Arundinaria auricoma</i>	Kew slide 1953																									
<i>Arundinaria gigantea</i>	Soderstrom 2530																									
	Soderstrom & Calderon 2047																									
<i>Arundinaria japonica</i>	Kew slide 1953																									
<i>Arundinaria maling</i>	Emery 146																									
<i>Arundinaria</i> sp	Soderstrom 2500																									
<i>Sinarundinaria nitida</i>	McClure 21148																									
<i>Chimonobambusa falcata</i>	Soderstrom 2255																									
<i>Chimonobambusa khasiana</i>	Soderstrom 2599																									
<i>Chimonobambusa marmorea</i>	Makino s.n.																									
<i>Oxytenanthera abyssinica</i>	Smook & Soderstrom 1983																									
<i>Bambusa balcooa</i>	Smook & Soderstrom 1982																									
<i>Phyllostachys aurea</i>	R. Ellis 3511																									

TABLE 1.—Comparison of the leaf anatomy and epidermal structure of *Thamnocalamus tessellatus* and the other bamboo species examined in this study

(Tateoka, 1963) and some arundinoid grasses (Gordon Gray & Ward, 1971; Clifford & Watson, 1977).

The possession of a conspicuous midrib, containing a complex vascular system, is another anatomical feature which is considered to be characteristic of the bambusoid type of leaf anatomy (Metcalf, 1960; Calderon & Soderstrom, 1973). Exceptions to this condition have been observed in this study and Table 1 shows that the Bergbamboes has a simple midrib (Fig. 6b) as has *Thamnocalamus spathiflorus* (Trin.) Munro (Fig. 6g), *Arundinaria alpina* K. Schum. (Fig. 6k) and *Sinarundinaria nitida* (Mittf.) Nakai. *T. tessellatus*, therefore, shares this significant characteristic with *T. spathiflorus*, a fact which supports their placement in the same genus. *Thamnocalamus* is not homogenous for this character, however, as *T. aristatus* (Gamble) E. G. Camus has a complex vasculature of the midrib. The simple midrib condition is consequently not diagnostic of the genus and, in addition, also occurs in *Arundinaria* and *Sinarundinaria*.

The character which comes closest to being diagnostic of *T. tessellatus* is the number of third order vascular bundles between successive lateral first order bundles. There are 5 of these smaller bundles between consecutive larger bundles in *T. tessellatus* (Fig. 6a) and *T. spathiflorus* whereas the other species studied have 7 or more. An exception is an undescribed *Arundinaria* sp. (Table 1) which also only has 5 smaller bundles. Once again this characteristic is not exclusive to *Thamnocalamus* and within the genus, *T. aristatus* differs from the other two species studied with respect to this character. Furthermore, this attribute is not completely reliable and is dependent on the position along the width of the leaf blade at which it is determined and tends to be somewhat variable, particularly towards the margin.

Anatomically the Bergbamboes resembles *T. spathiflorus* most closely (Table 1), the only difference being the presence of minute papillae (Fig. 6h) and dumb-bell shaped silica bodies (Fig. 7e) on *T. spathiflorus*. Neither of these differences is absolutely consistent, however, and, consequently little taxonomic emphasis has been placed on them. Thus *T. spathiflorus* also has saddle-shaped silica bodies (Fig. 7e) in addition to the dumb-bell shaped bodies and in this respect resembles *T. tessellatus*. The possession of papillae appears to be inconsistent and sometimes only one half of the lamina is papillate (either adaxially or abaxially) and the other not or papillae may be absent laterally but present in the region of the midrib. This variable condition is clearly illustrated by the example of *Arundinaria alpina* where the abaxial epidermal preparation is clearly without papillae (Fig. 7f) whereas, they are present on the abaxial epidermal cells of the transverse section (Fig. 6l) prepared from a different leaf from the same plant. This character is, therefore dependent on the part of the leaf blade studied and differences in the number and distribution of these intercostal papillae are consequently of limited taxonomic significance and not of specific diagnostic value as has been reported (Ghorai & Sharma,

1980). For these reasons it is concluded that the Bergbamboes shows closer anatomical relationships with *T. spathiflorus* than with any of the other bamboos studied and these slight differences are considered to be of little consequence.

The lack of anatomical conformity in the genus *Thamnocalamus*, after the inclusion of the Bergbamboes, appears most unsatisfactory and possibly implies that taxonomic adjustment may be required. *T. tessellatus* and *T. spathiflorus* show close anatomical agreement but *T. aristatus* differs significantly. However, it must be realized that generic characters of the woody bamboos are not well defined and species within the same genus can show greater differences than with species belonging to different genera. The decision to transfer the Bergbamboes to *Thamnocalamus* was based on our combined comparative anatomical and morphological studies and although the inference may be drawn from Table 1 that anatomically *T. tessellatus* closely resembles *Arundinaria alpina* these species differ substantially in gross morphology, spikelet and inflorescence structure. The anatomy of the Bergbamboes and *A. gigantea* (Walt.) Muhl., the type species of the genus, shows many significant differences such as the midrib structure (Fig. 6i), leaf thickness (Fig. 6j) and epidermal macro-hairs (Fig. 7b). On these grounds the removal of the Bergbamboes from *Arundinaria* is obviously justified but the placement of *A. alpina* warrants review in light of the anatomical similarities with *T. tessellatus* and the fact that they are both African species.

An observation, which has not been incorporated in Table 1, but which is of considerable interest and contrary to published information is the presence of three sheath layers surrounding the first order bundles of *T. tessellatus*. Double bundle sheaths have been reported for the Bambuseae (Brown, 1958; Metcalfe, 1960; Calderón & Soderstrom, 1973) but Fig. 6d clearly illustrates that three sheath-like layers are present externally to the metaxylum vessels — two mestome-like layers and the parenchyma sheath. These three sheath-like layers were also observed in *T. spathiflorus* (Fig. 6h), *Arundinaria gigantea* (Fig. 6j) and *Bambusa balcooa* Roxb. (Fig. 6n) and appear to be a common feature of these woody bamboos.

CONCLUSIONS

Our quest to establish the relationships of the Bergbamboes has led to a comparative study of its leaf anatomy, gross morphology, spikelet and inflorescence. The results indicate that this bamboo was originally misplaced in *Nastus* and subsequently so in *Arundinaria*.

The leaf anatomy of the Bergbamboes is bambusoid and specifically of the type found in the woody bamboos (Calderón & Soderstrom, 1973). Our studies have been made on many widely divergent genera and the results have corroborated the statement of Metcalfe (1960: 540), that '... the bamboos form a remarkably homogeneous group so far as the structure of their leaves is concerned'. It is

immediately evident that there are no mutually exclusive characters separating any of the genera studied and generic anatomical characters appear to be difficult to find or not to exist. Even the presence or absence of what would appear to be a significant character, such as fusoid cells, seems to be meaningful only at the specific level, as in *Chimonobambusa*, for example. We were unable to find any character that is diagnostic of any species to the exclusion of all others. The dumb-bell-shaped silicabodies of *Thamnocalamus* seem to come closest; however, these bodies are rather irregular in shape and not distinct. In fact, *Thamnocalamus spathiflorus* seems to match our Bergbamboes more closely than any other species examined, differing only in the presence of adaxial papillae. The adaxial epidermises of these two species therefore look considerably different but show similarities in all other respects, including silica body shape.

A great deal of attention has been given to the use of vegetative characters in bamboo classification due to the rarity of flowering in this group of grasses and lack of spikelets and inflorescences for study. Significant at the generic level are the type of rhizome system and branching pattern. For example, the Bergbamboes and *Nastus* have sympodial rhizomes while *Arundinaria* possesses a monopodial one. The branching of all three is distinct: *Nastus*, as exemplified in the type, *N. borbonicus*, produces a large cluster of subequal branches at the nodal line (perhaps derived from more than one bud as in the putatively related *Chusquea*?); *Arundinaria*, as exemplified in the type, *A. gigantea*, produces a single branch at the node with each node in turn giving rise to a single branch; while the Bergbamboes produces a primary branch that gives rise almost immediately to secondary and tertiary axes that result in a row of sub-equal branches above the nodal line. The combination of rhizome and branching types, different in all three, implies that we are dealing with distinct genera.

Our third avenue of inquiry, the spikelet and inflorescence, confirms this implication. The spikelet of *Nastus* consists of a series of glumes, as many as five, that precede two fertile florets, these each containing a flower with three lodicules, six stamens, and three stigmas. On the contrary, the spikelets of the Bergbamboes and *Arundinaria* contain two glumes, which is common in most grasses, and several florets, the lowermost developed and uppermost reduced. The flower itself contains, in each case, a similar complement—three lodicules, three stamens, and an ovary with three stigmas.

The combination of sympodial rhizome, branching type, and spikelet type that is found in the Bergbamboes also occurs in the Sino-Himalayan genera, *Sinarundinaria* and *Thamnocalamus*. The inflorescence pattern, however, is quite different in these two, with that of the former an open panicle and that of the latter a bracteate racemiform structure as found in the Bergbamboes.

As shown diagrammatically in Fig. 3, the inflorescence of the Bergbamboes (Fig. 3d) consists of several short-pedicellate spikelets covered by the

elongated sheaths of subtending leaves. The lower leaves of the series contain no buds in their axils, while the upper ones (lower two of the inflorescence) contain a spikelet, somewhat aborted. The uppermost spikelets are without a bract or may bear a rudimentary one.

The same basic inflorescence pattern is found in the genus *Thamnocalamus*. As shown in the diagram of an inflorescence of the type species, *T. spathiflorus* (Fig. 3a), each spikelet is subtended by a bract. In the case of Fig. 3a, the terminal part of an inflorescence is shown and here the buds have developed into branches that have rebranched, each primary branch subtended by a leaf with a well-developed sheath and each secondary branch by a bract. In another part of the same inflorescence (Fig. 3b), the leaves with expanded sheaths subtend a single spikelet or branch. The degree of branching and development of buds varies at different nodes.

In *T. spathaceus* (Franchet) Soderstrom (Fig. 3c), the several leaves with well-developed sheaths develop close together, the lower ones subtending a bud, the upper ones empty. In the flowering stage, each branch terminates in an inflorescence, which consists of several leaves with expanded sheaths increasingly longer upwards, covering the inflorescence. The lowermost spikelet is subtended by a leaf with expanded sheath and the following spikelets (in the case shown, two) by bracts. Several succeeding spikelets are ebracteate except the penultimate.

All of these taxa are similar in having at least some bracteate spikelets and the tendency for them to be covered by leaves with well-developed sheaths. The most complex inflorescence shown is that of *T. spathiflorus*: variations in the extent of development of the buds could theoretically lead to the type we are observing in *T. spathaceus* and the Bergbamboes. All of these taxa possess a similar branching habit as depicted in Fig. 3e and sympodial rhizome system as depicted in Fig. 3f.

In contrast to these taxa is *Arundinaria gigantea*, type of the genus, whose monopodial rhizome system is depicted in Fig. 3j and branching pattern in Fig. 3i. The inflorescence is a raceme that is long-exserted and not covered by overtopping sheaths. Generally the lowermost spikelet is bracteate and the upper one(s) usually ebracteate or with tiny bracts as depicted in Fig. 3g. A related genus is *Sasa* in which the spikelets are arranged in a long-exserted panicle, shown in Fig. 3h. It also has monopodial rhizomes but a pattern of branching different from *Arundinaria* and not shown here. The inflorescence of *Sinarundinaria* is of the type represented by Fig. 3h, which is seen to be totally distinct from that of *Thamnocalamus*.

Based on present knowledge, we are assigning the Bergbamboes to the Sino-Himalayan genus, *Thamnocalamus*, in which the following five species are currently recognized: *T. spathiflorus* (Trin.) Munro, common in fir forests of north-west Himalayas above 7 000 ft; *T. aristatus* (Gamble) E. G. Camus, north-eastern Himalayas in eastern Nepal, Assam, Sikkim, and Bhutan, above 8 000 ft in temperate broadleaf forests; *T. spathaceus* (Franchet) Soderstrom, above 7 500 ft in fir forests of southern

Gansu, eastern Sichuan and western Hupeh provinces of China; *T. sparsiflorus* (Rendle) Keng f., above 8 000 ft in conifer woods in Hupeh Province of China; and *T. cuspidatus* (Keng) Keng f., from Kwangsi Province of China in woods at about 5 000 ft elevation.

The isolated occurrence of the South African member of *Thamnocalamus* is intriguing and raises the interesting question of how this came about. The nature of the bamboo plant, especially the infrequent flowering and production of seeds not adapted for long-distance dispersal, favours the assumption that the present-day distribution of these species reflects past land connections and overland migration. A few possibilities come to mind: 1) the genus evolved in west Gondwanaland and was present in Africa and on the Indian subcontinent prior to the latter's movement northward and abutment with the Asiatic landmass, speciation occurring in the newly forming Himalayas, leaving the South African element as a relict; 2) species of the genus migrated from the eastern Himalayas during the Miocene followed by deterioration in the climate and isolation in favourable mesophytic sites of the coastal and mountain belt that extends from the Cape to Natal; 3) migration occurred from the south in the Miocene reaching the Himalayas with subsequent extinction of taxa between there and South Africa.

Although there are no known bamboos of the *Thamnocalamus* alliance that occur between South Africa and the Himalayas, bamboos of the *Sinarundinaria* alliance do occur in Madagascar and in east Africa (under the name *Arundinaria*) and from the western Himalayas to the Phillipines (under the names *Arundinaria*, *Sinarundinaria*, and *Yushania*), indicating that such a distribution is not out of the question.

The isolated position in the United States of the canebrake, whose sibling species occur in eastern Asia, is reminiscent of the far-flung dominions of the Bergbamboes and its sibling species. While the South African-Himalayan disjunction may not be so clear, that of eastern United States and eastern Asia is well understood and documented. During warmer periods of the Tertiary, a continuous forest extended across the Northern Hemisphere from Asia to eastern North America. Ensuing cooler climatic conditions with the advance and retreat of glaciers, eliminated much of the forest, except in parts of Asia and eastern North America. Many genera today are common to both regions and reflect an Arcto-Tertiary distribution: *Celtis*, *Liriodendron*, *Magnolia*, and *Ulmus* are a few. Species of *Arundinaria* were doubtless understory plants in this forest, represented today by a single species in North America and many in eastern Asia. Such phytogeographical evidence for *Arundinaria* corroborates the viewpoint that the relationships of South Africa's endemic Bergbamboes are not to be found with this genus but elsewhere.

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UITTREKSEL

Thamnocalamus tessellatus (Nees) Soderstrom & Ellis, comb. nov. [= *Arundinaria tessellata* (Nees) Munro] is die enigste inheemse Suid-Afrikaanse bamboessoort en kom in die oostelike distrikte van die Kaapprovinsie, deur Lesotho en Natal, tot in die oostelike Oranje-Vrystaat op hoogtes van omtrent 1 500–2 000 m voor. Die Bergbamboes is eers deur Nees in 1841 beskryf as 'n verteenwoordiger van die genus *Nastus* weens die ooreenkoms van die blompakkies met dié van *N. borbonicus*. Die Bergbamboes is later oorgeplaas na die omvattende genus van daardie tyd, *Arundinaria*, waarvan die tipe spesie endemies in die suidoostelike dele van die Verenigde State van Amerika is. Ons huidige kennis van die bamboesgenera dui aan dat die Suid-Afrikaanse spesie van *Nastus* uitgesonder kan word omdat die bloeiwyse nie 'n pluim is nie maar 'n tros met skudblare is, die vegetatiewe stingels word nie kransgewys gedra nie maar is 'n reeks halfgelyke stingels wat in 'n ry bokant die knoop gedra word en *T. tessellatus* het 'n meeldraadkrans van drie meeldrade en nie ses soos in *Nastus* nie. Die bergbamboes, wat simpodiale wortelstokke en verskeie halfgelyke stingels het, kan ook nie in *Arundinaria* gehou word nie, omdat monopodiale wortelstokke en 'n enkele stingel by die knoop kenmerkend van hierdie genus is. Die eenvoudige, uitgestote bloeiwyse, sonder skutblare, van *Arundinaria* is ook heeltemal kenmerkend van dié van die Bergbamboes.

Om die Suid-Afrikaanse bamboes meer spesifiek te plaas het ons vergelykende studies van die blaaranatomie, epidermis en morfologie onderneem en die bloeiwyse en blompakkies ontleed. Die resultate van hierdie studie toon 'n opvallende ooreenkoms met verteenwoordigers van die Sino-Himalaja genus, *Thamnocalamus*. Gevolglik is die Bergbamboes oorgeplaas na hierdie genus. Die resultate word saam met 'n interpretasie van die filogenetiese status van die Bergbamboes voorgelê en moontlike gebeurtenisse wat tot die skeiding van die spesies in die genus gelei het, word bespreek.

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