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Cover: Dr. Tarciso S. Filgueiras standing in a population of *Filgueirasia arenicola* just north of Parque Nacional das Emas in Central Brazil. Photo by G.F. Guala, 1990.

A New Genus of Bamboos from the Cerrados of Brazil

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Recent advancements in our knowledge of New World bamboos have shown that the genus *Apoclada*, as previously recognized, is clearly polyphyletic. A new genus, *Filgueirasia*, is described in honor of Dr. Tarciso S. Filgueiras. Two species, *F. arenicola* and *F. cannavieira*, are recognized. *Apoclada simplex* remains in the now monotypic genus.

The genus, *Apoclada* F.A. McClure (1967) has been a source of consternation since it was first published. The type species, *Apoclada simplex* F.A. McClure and L.B. Smith, is a beautiful tall and luxuriant bamboo of the mesic forests of southeastern Brazil but the other species published at that time, *A. diversa* F.A. McClure and L.B. Smith, turned out to be nothing more than a teratological specimen of the type species (Guala 1992, 1995). Five years later McClure (1973) described the cerrado species *A. arenicola* F.A. McClure and transferred another cerrado species, *Arundinaria cannavieira* Alvaro da Silveira, out of that, then very broadly defined, genus to become *Apoclada cannavieira* (Alvaro da Silveira) F.A. McClure.

Cerrado is a type of open savanna found in central Brazil. Fire is common on the cerrados and the two cerrado species are well adapted to it with compact knotty rhizomes with many buds, and a short and multi-stemmed habit as well as relatively course leaves. They are both good forage (Guala 1992, 2001) and are eaten by both domestic stock and wildlife.

When I began work on this group in 1988, there was relatively little known about the affinities of the genus and about the extent and interpretation of the important structures in determining affinities to other genera. The characteristics that held *Apoclada s.l.* together were having multiple separate equal primary branch buds at the nodes (hence the name *"Apoclada"*) and a lack of fusiod cells in the leaves. At the time, relatively few specimens had been examined for fusoid cells and what appeared to be a phylogenetically significant lack of these common bamboo leaf structures is now known to be not so unusual, in some species varying even with light conditions (March and Clark 2001). Part of the branch bud misinterpretation for *A. simplex* was due in large part to the single teratological specimen referred to as *A. diversa* that clearly shows two separate branch buds at a single node. The branches emerge from bud extremely early in this species as well and the difficulty of interpreting the ontogeny of branch buds in general also led to confusion. This in relation to the clearly multiple equal primary buds in the cerrado species along with ambiguity in the interpretation of the characteristic in *A. simplex* by myself and other workers was enough not to question McClure's judgement and consider them all to be in a single genus. Emmet Judziewicz (pers. comm.) even questioned how I knew that *Apoclada* was monophyletic in a prepublication review of the manuscript of Guala (1995). My explanation to the editor was that although the evidence was weak, we did not at the time have clear evidence showing that *Apoclada s.l.* was not monophyletic, so I chose to stick with the *status quo* until such evidence was discovered.

New and much more extensive work on the interpretation and extent and derivation of different branch bud complement configurations and a much better knowledge of New World bamboos in general (see Judziewicz *et al.* 1999 and references therin) has led to better interpretations of important characteristics and a better understanding of relationships. It is clear now from this new morphological work alone that the cerrado species probably show a

different tribal affinity than *A. simplex*. The cerrado species show the refractive papillae, intercostal sclerenchyma fibers, reduced foliage leaf midribs and an asymmetric leaf margin that are characteristic of the Arthrostylidiinae while *A. simplex* shows an overall general resemblence to *Otatea* in the Guaduinae but differs in leaf anatomy. *Apoclada simplex* also has adaxial papillae, the overarching papillae associated with its adaxial stomata and the absence of stomata on the abaxial leaf surface that is characteristic of the Guaduinae. Recent molecular analyses (Guala *et al.* 2000) have also supported this placement of the cerrado species in the Arthrostylidiinae and *A. simplex* in the Guaduinae conclusively.

Thus, the genus *Apoclada*, as previously recognized, must be split leaving the type species, and hence the name, with *A. simplex*. This is counterintuitive given that *"Apoclada"* means separate branches – a designation that applies much better to the cerrado species – but the rules of nomenclature are clear (Greuter *et al.* 2000) and a new genus must be published for the cerrado species.

It is with great pleasure that I am able to name the new genus in honor of Dr. Tarciso S. Filgueiras. He was the person who first showed me living populations of these bamboos (see the cover of this issue) and who knows more than anyone about them in their natural habitat. He has been a source of endless enthusiasm, expertise and encouragement to those of us who study grasses as well as a positive force for systematics and systematists in Brazil and globally. There is no one who deserves this honor more.

Filgueirasia G.F. Guala *gen. nov.* TYPE: *Filgueirasia cannavieira* (Alvaro da Silveira) G.F. Guala.

Valde caespitosae, culmis cavis, gemmis multis aequalibus ramorum primariorum ad nodos (raro 1), laminis foliorum stomatibus in utraque pagina et fibris sclerenchymatis inter-costalibus in mesophyllo instructis

Strongly caespitose bamboos, vegetative clumps 0.30-3.21 m in diameter. Rhizomes compact. Culms 0.45-1.75 m high (to 2.5 m in fertile condition), erect, green or glaucous, often short pubescent on new growth, straight, 1-9 mm in diameter, the walls 0.3-2 mm thick, the internodes rarely solid in fertile material, to 29.1 cm long. The vegetative midculm primary branch bud complement with 1-15 equal primary branch buds per node in both the vegetative and fertile culms. Culm leaves lanceolate, the sheath of those from the midculm 3.0-10.2 cm long, 0.4-2.7 cm wide at the base, glabrous on the abaxial and adaxial surfaces, adaxial ligule a short hyaline membrane to ca. 1 mm, the blades mostly erect to 39 mm long. Foliage leaf sheathes ciliolate to hispidulous or with copious white hairs and long flexuous white oral setae along the distal margin, the blade 3.3-31.4 cm long, 1.0-11.0 mm wide, stomata on both surfaces, the bulliform cells smooth on the surface and in fan-shaped groups of 3-12 cells in transverse section with one to several groups occurring between each pair of major vascular bundles, intercostal sclerenchyma fibers appressed to either side of the bulliform cell groups and often with up to 20 fiber strands above the bulliform cells near the abaxial surface, silica bodies rectangular to saddle or shield or double-axe shaped, bicellular micro-hairs 41-59 microns long with the basal cell longer than the distal cell and occurring only on the abaxial surface, the long cells of both epidermes papillate. Inflorescence branches secund, the spikelets 2.5-10.4 cm long, the florets 3-15 per spikelet, the lower lemmas 13-26 mm long, the upper lemmas 6-15 mm long, the palea subequal to the body of the lemma, 6-15 mm long, with two scabrous keels, scabrous to glabrous between the keels. Lodicules 1.3-2.5 mm long, ca. 0.6-1.6 mm wide, ovate to obovate, ciliate on the upper margins. Stamens 4.1-11.0 mm long. Style densely hispid, 0.3-0.6 mm long, the stigmas ca. 0.7-2 mm long. Caryopsis 8.3-9.9 mm long, 1.9-3.4 mm wide, with a beak ca. 0.4-0.7 mm long.

Phenology. The period between mass flow-erings is unknown although it is not less than eleven years and is probably more than twenty. Flowering may also be linked to burning.

Distribution and Habitat. Normally found in cerrado from ca. 44-55 deg. W. long. and 15-21 deg. S. lat. at elevations of 550-1075 m.

Filgueirasia cannavieira (Alvaro da Silveira) G.F. Guala., *comb. nov.,* BASIONYM: *Arundinaria cannavieira* Alvaro da Silveira 1919. Algumas especies novas da flora de Minas Gerais. Archiv. Museo Nacional Rio de Janeiro. 22: 101 figure 2. TYPE: Brazil, Minas Gerais: Serra do Cabral [Serra do Caparão in publication], November 1918, *Silveira 644* (holotype: R(6 + ca. 6 unmounted sheets)!; isotype: US!).

Filgueirasia arenicola (F.A. McClure) G.F. Guala., *comb. nov.,* BASIONYM: *Apoclada arenicola* F.A. McClure 1973. Genera of Bamboos Native to the New World Gramineae: Bambusoideae) Smithsonian Contributions to Botany 9; pp 9-12 + figures 1-2. TYPE: Brazil, Mato Grosso: Between Bonito and Rondonopolis, 8 March 1930, *Chase 11886* (holotype US(2)!).

Key to the species:

Foliage leaf blades 5.0-11.0 mm wide, one major vascular bundle between each pair of bulliform cell strands in the middle 2/3 of the lamina. Culm leaves persistent. Midculm branch complements with usually 1-3 primary branches in vegetative condition or 1-8 in fertile condition. Keels of the palea without perceptible wings – *Filgueirasia cannavieira.*

Foliage leaf blades 1-2.7 mm wide, two or more major vascular bundles between each pair of bulliform cell strands in the middle 2/3 of the lamina. Culm leaves quickly deciduous. Midculm branch complements with usually 5-15 primary branches in vegetative condition or 8-15 in fertile condition. Keels of the palea without perceptible wings – *Filgueirasia arenicola.*

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Some Commercial Edible Bamboo Species of North East India: Production, Indigenous Uses, Cost-Benefit and Management Strategies

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This paper reports on some commercially available edible bamboo species of Meghalaya, Mizoram and Sikkim states of North Eastern Himalayan (NEH) region. *Bambusa balcooa* Roxb., *Chimonobambusa hookeriana* (Munro) Nakai, *Dendrocalamus hamiltonii* Nees et. Arn and *Melocanna baccifera* (Roxb.) Kurz have been found commercial edible bamboo species in these tribal states. These edible species are also cultivated in home gardens besides their occurrence in forests. Edible shoots are harvested from first week of June to first week of September every year for consumption. However, market days for selling it varied from state to state and even from place to place within the state with an average value of 52.65, 80.71 and 31.50 days/yr, respectively, in Meghalaya, Mizoram and Sikkim. On average, 4,420.31, 4,326.34 and 266.39 quintal of bamboo shoots in general are harvested annually, respectively, in Meghalaya, Mizoram and Sikkim. Among the various species, tender edible shoots of *D. hamiltonii* are harvested and consumed most (4,838.10 q/ yr), followed by *M. baccifera* (3,610.61 q/ yr), *B. balcooa* (525.55 q/ yr) and *C. hookeriana* (36.99 q/ yr), respectively. The gross income was calculated to be Rs. 19.659 (US$ 41,872.5), 13.22 (US$ 28,157.6) and 8.197 lac/ yr (US$ 17,459), respectively, in Meghalaya, Mizoram and Sikkim. Thus, tribal communities could earn net revenue to the tune of Rs. 11.38 (US$ 24,250.4), 7.74 (US$ 16,485.6) and 7.01 lac/ yr (US$ 14,930.8), respectively, in Meghalaya, Mizoram and Sikkim by selling young edible bamboo shoots. On average, *D. hamiltonii, M. baccifera, B. balcooa* and *C. hookeriana* respectively, contributed 51.08, 35.14, 6.79 and 6.86% to total monetary benefits earned, irrespective of states. Besides food value, these species also have a very important role in the life of tribal folk, particularly for providing materials for various other quotidian needs, as well as for paper-pulp industries.

India is one of the leading countries of the world, second only to China, in bamboo production with 32.3 million ton/year (Pathak 1989). Bamboo species cover an area of around 10.03 million hectares, which contribute 12.8% of the total forest cover of the country. India ranks third, i.e., next to China (300 species) and Japan (237 species) in bamboo species diversity. Within India, North Eastern Hill (NEH) region possesses largest species diversity. Out of 126 plant species available in India, nearly half of the variability is available in this part of the country (Hore 1998). Among seven states of NEH, Mizoram occupy largest forest area (30.8%) under bamboo, followed by Meghalaya (26.0%) with total bamboo cover of 38,197 sq. km (Trivedi and Tripathi 1984; Anonymous 1999). Tribal communities of the region use this potential resource for food, shelter, furniture, handicraft, medicines and various ethno-religious purposes (Marden and Brandenburg 1980; Tewari 1992). This resource has also been considered valuable for agroforestry owing to its short gestation period and recurring return (Bhatt *et al.* 2001).

Although scattered information is available on bamboo resources of the region (Singh 2002; Sarkar and Sundriyal 2002; Sharma 1980; Soderstrom and Calderon 1979; Sharma et al 1992), no attempts have been made so far to evaluate the consumption pattern of young bamboo shoots as food and its production potential. Keeping this fact in view, attempts have been made to survey the three tribal states

of the region for identification of bamboo rich localities, bamboo shoot consumption and the monetary benefits. This information could be used to understand the rate of harvesting of young tender shoots for domestic consumption from the natural habitats and home gardens along with cost-benefit analysis and market potential of commercial bamboo species. The other objective was to understand the export possibilities of potential edible species to generate revenue by creating employment opportunities and to frame a comprehensive policy for mass afforestation of commercially available edible bamboo species.

Arunachal Pradesh, Assam, Manipur, Meghalaya, Mizoram, Nagaland and Tripura including Sikkim are localized in NEH region of India. Being rich in biodiversity, it is recognized as one of the 18 'hot spots' of the world. The region is inhabited by diverse ethnic groups, which have their unique lifestyle and are dependent on forests to a great extent for their subsistence. Our study was conducted in Meghalaya, Mizoram and Sikkim states of the region. Meghalaya has a geographical area of 2.24 million ha with forest cover of 0.95 million ha (Anonymous 1999). It is located between 25°02' to 26°7' N latitude and 89°49' to 92°50' E longitude, and 150 m to 1950 m asl altitude. Khasi, Garo and Jaintia are the major tribes of the state. Mizoram is located at the extreme southern part of NEH, in between 21°5' to 24°30' N latitude and 92°15' to 93°29' E longitude. It has the geographical area of 2.11 million ha, out of which 1.59 million is classified as forest cover. The terrain is hilly and mostly undulating with the elevation range of 500- 2,157 m asl. Mizo and Mara are the major tribal inhabitants of the state. Sikkim has a geographical area of 0.71 million ha with 37.34% forest area. It is located between 27°46' to 28°7'48" N latitude and 88°0'5" to 88°55'25" E longitude, and 1300 m to 6,000 m asl altitude. Nepali and Tibetans are the major tribal inhabitants of the state.

Shifting cultivation is the mainstay of subsistence in the region excluding Sikkim. Until three decades ago, jhum cultivation was not problematic, as its cycle was 20-30 years, but of late it has been reduced to 3 to 5 years, partly due to the population explosion and partly to loss of fertile soil due to over exploitation of forest resources (Ramakrishnan 1992). Even today, about 52,990 and 50,000 families, respectively, in Meghalaya and Mizoram are practicing shifting cultivation (Anonymous 2000a). Large-scale deforestation has brought 36.64% of the total geographical area of NEH region under degraded lands, which is 1.82-fold higher than the national average of 20.17% (Anonymous 2000b).

MATERIALS AND METHODS

Meghalaya, Mizoram and Sikkim are comprised, respectively, of 7, 4 and 8 districts. Overall 250 localities with 45 market places of all the 19 districts of the three states have been covered to undertake the study. The methods employed in this study were designed with the purpose of producing baseline information for the use of bamboo shoots in the local systems. A preliminary survey was conducted to identify the important edible bamboo species at different places in each district of Meghalaya, Mizoram and Sikkim. As production of young shoots of all the bamboo species in NEH region begins at the onset of the rainy season, i.e., May-June of the calendar, a continuous survey of randomly selected market places of all the districts of the entire three states were made to find out the commercial edible bamboo species. The entire primary as well as secondary vendors available in each market place explored were interviewed through pre-prepared questionnaires to understand the annual rate of bamboo shoot consumption and its commercial value. All the possible information on merchandizing edible bamboo shoots like, monetary input/output, physical efforts made for collection and selling, mode of utilization and ecological status (distribution, frequency and availability in the forest/home garden etc.) were collected from all the market places. On the basis of the information and primary data recorded, other secondary data sheets were prepared and represented in the present communication. Rich pockets of edible bamboo species were identified following quadrate method (Mueller Dombios and Ellenberg 1974).

The food energy value of young edible shoots was established after burning the over dried samples in a bomb calorimeter. The protein content was estimated by multiplying the percent nitrogen (estimated by Kjeldhal method of Allen *et al.* 1974) by a factor of 6.25. Fat content was determined by extraction in a soxhlet apparatus.

The time and labor spent in bamboo shoot collection was measured in hrs and than converted to MJ. Energy expenditure/hr was taken to be 0.418, 0.488 and 0.679 MJ, respectively, for sedentary, moderate and heavy work for an adult male; and 0.331, 0.383 and 0.523 MJ for an adult female, accordingly. For heavy work of child of the age category of 9-12 years, the energy value was used as 0.412 MJ. These values were used to calculate the total energy input in young bamboo shoot collection, cleaning, transportation through head load and selling etc following Gopalan et al (1978).

RESULTS AND DISCUSSION

On average, area under bamboo cover is 6047 and 5863 sq km, respectively, in Mizoram and Meghalaya, which constitute 30.81 and 26.0% to total forest cover in these two states. For Sikkim, the actual area under bamboo species is yet to be worked out. In all, 29, 32 and 20 places were randomly explored, respectively in Mizoram, Meghalaya and Sikkim (Figure 1a-d).

The rich pockets of edible species were identified. *Bambusa balcooa*, *Melocanna baccifera* and *Dendrocalamus hamiltonii* were found the main commercial edible bamboo species in Meghalaya. While *M. baccifera* and *B. balcooa* has been confined mainly in Garo hill districts of Meghalaya, it was *D. hamiltonii,* which had wide range of distribution throughout the state. M. baccifera was the commercially available edible species in Mizoram and its distribution was homogeneous in all the districts surveyed. In Sikkim, *Chimonobambusa hookeriana* and *D. hamiltonii* has been recorded the main commercial edible species. All the above-mentioned species have been cultivated frequently in home gardens in all the states, besides their occurrence in forests.

Of 102 total market places, 45 markets covering 289 vendors have been surveyed randomly in different states. Per day consumption of edible shoots was highest (ca. 95.60 q) in Meghalaya and lowest (ca. 12.54 q) in Sikkim. Whereas, annual consumption of bamboo shoots from all the markets was highest in Meghalaya (ca. 4,420.31 q), followed by Mizoram (ca. 4,326.34 q). No. of market days for sell of young tender bamboo shoots varied from state to state and even place -to- place within a state, however, it was highest (80.71 days/ yr) in Mizoram, followed by Meghalaya (52.65 days/ yr) and Sikkim (31.5 days/ yr), respectively (Table 1).

We observed that *M. baccifera* is sold in the market from first week of June to second week of September every year with a maximum of 85 days in Saiha and Serchip District of Mizoram. In Meghalaya, young tender bamboo shoots are sold for a period of maximum 71 days/ yr in West Khasi Hill District, followed by East Khasi Hill District (66 days/yr) and Jaintia Hills (55 days/ yr). But in Garo Hill Districts, these are sold only for a period of 41 days/yr. In Sikkim, the market days for bamboo shoot consumption was, however, very low, i.e., 31.5 days/yr compared to other two states.

On average, *M. baccifera* contributed 53.69% to the total annual bamboo shoot consumption, followed by *D. hamiltonii* (40.06%) and *B. balcooa (5.83%)*, respectively, irrespective of the states explored. *C. hookeriana* contributed only 0.40% to the total consumption because of its occurrence only in Sikkim. In Meghalaya, *D. hamiltonii* contributed 76.52% to the total shoot consumption, followed by *B. balcooa* (11.89%) and *M. baccifera* (11.58%), respectively. Similarly, *D. hamiltonii* made up 86.12% of the total requirement of edible bamboo shoots in Sikkim with the rest being *C. hookeriana*. So far as weight of young bamboo shoot was concerned, it was highest (2.624 kg/ shoot) in *B. balcooa,* followed by *D. hamiltonii* (0.850 kg/ shoot) and *M. baccifera* (0.592 kg/shoot), respectively. Whereas, lowest (0.334 kg/ shoot) weight was recorded in *C. hookeriana* (Table 2).
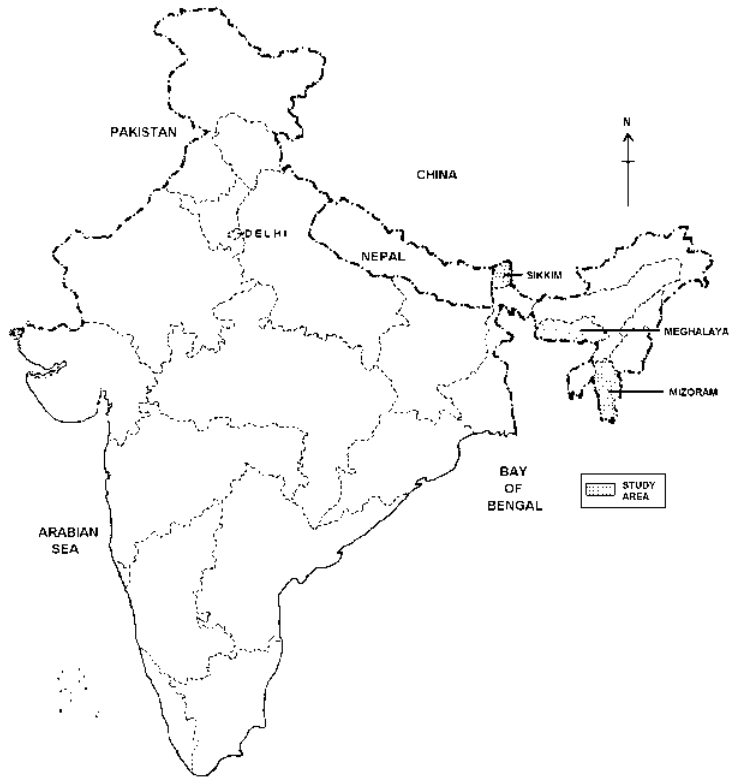
Figure 1(a): Location of the three states in India

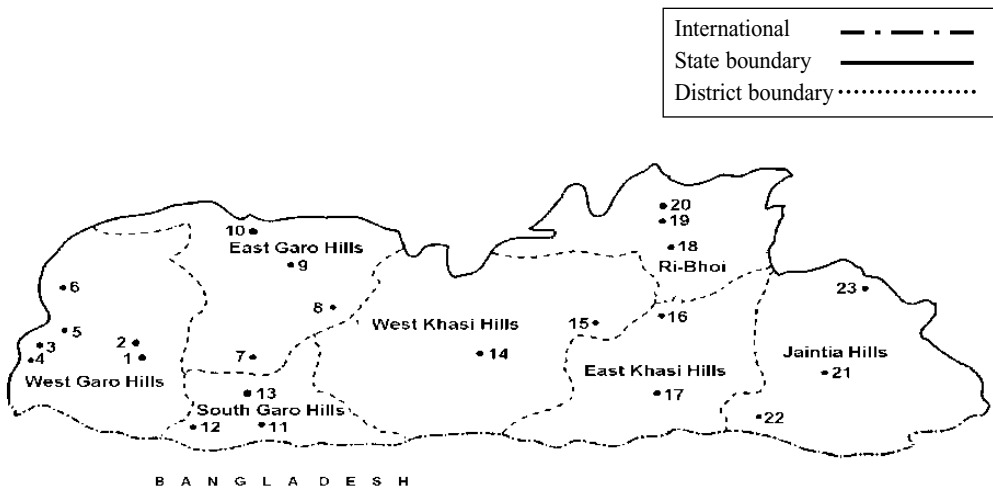| International | — · — · — |
| State boundary | ———— |
| District boundary | ················· |

Figure 1(b): Market places explored for young edible bamboo shoots from Meghalaya, India: 1- Tura;
2- Modinagar; 3- Ampati; 4- Salampara; 5- Garobodha; 6- Manchor; 7- Williumnagar; 8- Rangung;
9- Songsah; 10- Bajingodha; 11- Baghmara; 12- Barangapara; 13- Siju; 14- Nongstoin; 15- Mairang;
16- Shillong; 17- Sohra; 18- Umsning; 19- Karbalu; 20- Nongpoh; 21- Jowai; 22- Dawki; 23- Sailsana
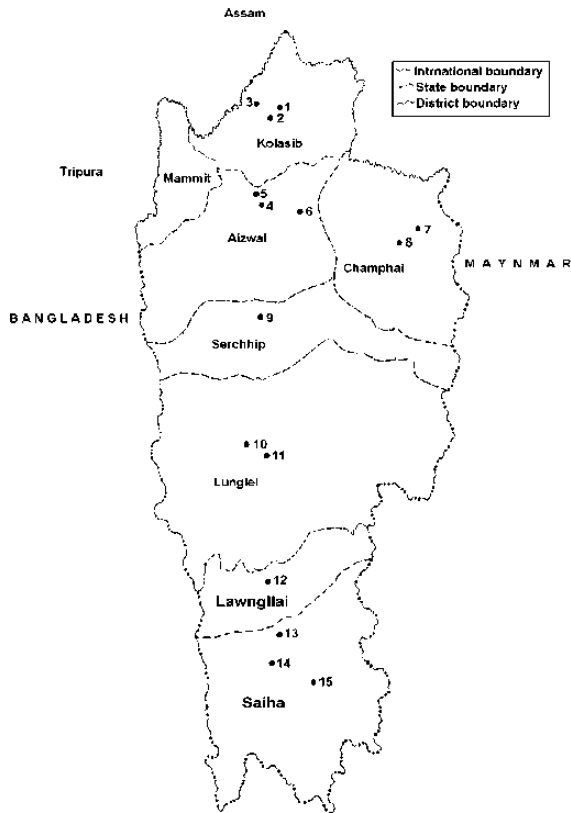
Figure 1(c): Market places explored for young edible bamboo shoots from Mizoram, India: 1- Kolasib; 2- Banglakawn; 3- Serkhan; 4- Aizwal; 5- Sairang; 6- Seling; 7- Champhai; 8- Kawlkuhl; 9- Serchhip; 10- Lunglei; 11- Zobawk; 12- Lawngllai; 13- Saiha; 14- Mawbawk; 15- Tuipang

Figure 1(d): Market places explored for young edible bamboo shoots from Sikkim, India: 1- Mangan; 2- Namchi; 3- Melli bazar; 4- Gangtok; 5- Pakyong; 6- Singtam; 7- Geyzing

Table 1. Consumption of bamboo shoots (± S.D.), irrespective of species

Sl. No.	State	No. of markets	Markets surveyed	No. of vendors surveyed	Young shoot consumption per market (q/ day)	Young shoot consumption all the markets (q/ day)	Availability in the market* (days/ yr)	Total** consumption (q/ yr)
1	Meghalaya	50	23	113	1.90±0.29	95.60±4.63	52.65±12.45	4,420.31±297.13
2	Mizoram	30	15	86	1.87±0.64	66.16±4.47	80.71±2.92	4,326.34±353.69
3	Sikkim***	22	07	90	0.57±0.12	12.54±1.74	31.50±15.06	266.39±23.89
	Total	102	45	289	1.45±0.23	58.10±9.74	–	9,013.04±1,171.39

*Remains available for sell w.e.f. 1st week of June to 1st week of September every year and market days varies from place to place
**Total consumption has been recorded after deducting the losses occurred during the selling.
***Bamboo shoots of both the species are sold in boiled form in Sikkim

Table 2. Species wise consumption (± S.D.) of edible bamboo species

Sl No.	State	Total availability of bamboo shoots (q/ day)				Total consumption of bamboo shoots (q/ yr)			
		1	2	3	4	1	2	3	4
1	Meghalaya	9.72±0.83	64.22±4.77	10.02±0.18	N.A	511.76±30.53	3,381.18±324.79	525.55±9.40	N.A
2	Mizoram	53.58±4.47	N.A	N.A	N.A	4,326.34±353.69	N.A	N.A	N.A
3	Sikkim	N.A	16.75±1.17	N.A	6.66±0.65	N.A	229.43±20.11	N.A	36.99±4.16
	Total	63.30±14.35	80.97±15.74	10.02±0.18	6.66±0.65	4,838.10±1200.25	3,610.61±955.23	525.55±9.40	36.99±4.16

1. *Melocanna baccifera* (average weight per shoot = 0.592 kg, n=20 for each market)
2. *Dendrocalamus hamiltonii* (average weight per shoot = 0.850 kg, n=20 for each market)
3. *Bambusa balcooa* (average weight per shoot = 2.624 kg, n=20 for each market)
4. *Chimonobambusa hookeriana* (average weight per shoot = 0.334 kg, n=20 for each market)
N.A.=Not available

Table 3. Cost-benefit analysis (± S.D.) of edible bamboo shoots, irrespective of species

Sl. No.	State	Gross output/market (Rs/ day)	Gross output from all the markets (Rs/ day)	Gross output (Rs/ yr)	Net input* excluding physical efforts made for collection and selling (Rs/ yr)	Gross income** (Rs/ yr)	Wages for man days required (Rs/ yr)***	Net income (Rs/ yr)
1	Meghalaya	784.66±303.73	39,238.02 ±1,676.89	22,63600.00 ±1,15,127.67	2,97,671.73 ±13348.24	19,65,915.20 ±1,03,003.96	8,27,358.65 ± 33,953.00	11,38,554.30 ± 77,734.00
2	Mizoram	340.40±281.48	11,591.00 ±1900.52	18,61195.90 ±1,49,917.00	5,48,907.99 ±1,01,689.91	13,12,287.90 ±58,583.32\	5,37,460.00 ± 44,151.02	7,74,827.90 ± 31241.99
3	Sikkim	1,001.00±483.50	23,025.14 ±3,118.80	8,58,782.56 ±1,05963.50	38,984.00 ±000.00	8,19,798.56 ±99,772.9	1,18,281.42 ± 10,419.40	7,01,517.12 ± 89,206.20
		2,126.30±933.51	73,854.42 ±3,301.77	49,83,578.40 ±4,15,166.05	8,85,563.72 ±1,31,078.73	40,98,001.60 ±2,24,529.01 (US$ 87,284)	14,83,100.00 ± 2,55,619.99	26,14,899.30 ± 2,10,280.07 (US$ 55,695)

*Gross input includes transportation cost, purchase cost and various other miscellaneous expenditures excluding man-days required for collection and selling.
**Gross income was calculated including the wages of man-days besides other inputs
***Wages for man-days varied from place to place, i.e., Rs. 61.78±10.41, 70.66±10.32 and 50.00±12.45/day/person, respectively, in Meghalaya, Mizoram and Sikkim.
1 US$ = Rs. 46.95 in Indian currency

The selling price for bamboo shoots varied from place to place within a district of a state, and between the states as well. In Meghalaya, the average price (Rs/ kg) was highest (5.16 ± 2.53) for *D. hamiltonii,* followed by *M. baccifera* (4.95 ± 0.41) and *B. balcooa* (4.82 ± 0.51). The rate of *D. hamiltonii* was highest (7.66 ± 2.09) in Jaintia hills and lowest (4.23 ± 0.72) in West Garo hills. Similarly price of *M. baccifera* was highest (5.31 ± 1.21) in South Garo Hills and lowest (5.01 ± 0.98) in West Garo Hills. Likewise the rate of *B. balcooa* was highest (5.39 ± 0.75) in West Garo Hills and lowest (4.41 ± 0.33) in South Garo Hills of Meghalaya. In Mizoram, the rate of tender shoots of *M. baccifera* was highest (7.50 ± 3.53) in Lunglei and lowest (3.79 ± 0.65) in Saiha District with an average of 5.27 ± 3.53 for the state. But in Sikkim, the market rates were reasonably high for bamboo shoots, compared to other states. Rate of *D. hamiltonii* was highest (20.00 ± 0.00) in North District and lowest (15.00 ± 0.00) in West District with average value of 17.34 ± 2.26 Rs/ kg. For *C. hookeriana* the rate was highest in South and East Districts (30.00±14.44) and lowest (20.00±0.00) in North District of Sikkim.

Cost-benefit analysis of edible bamboo shoots has shown the total gross income (excluding physical efforts made for collection and selling, but including the transportation charges and various miscellaneous expenditures incurred during harvesting to selling) of ca. 40.98 lac rupees/ yr (or US$ 87,284.33) for all the three states with highest (ca. Rs. 19.659 lac/ yr, US$ 41,872.53) for Meghalaya and lowest (ca. Rs. 8.197 lac/ yr, US$ 17,461.1) for Sikkim. The net income (calculated after deducting the cost of man-days and various expenditures) was highest (ca. Rs. 11.38 lac/ yr; US$ 24,540.4) for Meghalaya and lowest (ca. Rs. 7.01 lac/ yr; US$ 14,941.8) for Sikkim. On average, Meghalaya state earned maximum (ca. 43.65%) income, followed by Mizoram (ca. 29.63%) and Sikkim (ca. 26.82%) of the total gross income, respectively, irrespective of bamboo species (Table 3).

Comparing the cost-benefit analysis of various species, net income was highest with *D. hamiltonii* (ca. 13.35 lac rupees/ yr, US$ 28,447.1), followed by *M. baccifera* (ca. 9.19 lac rupees/ yr, US$ 19,587.6) and *C. hookeriana* (ca. 1.82 lac rupees/ yr, US$3,876.5), respectively, irrespective of states. On average, *M. baccifera, D. hamiltonii, B. balcooa* and *C. hookeriana* contributed, respectively, 35.17, 51.08, 6.79 and 6.96% to total income, irrespective of states surveyed. Within state, *M. baccifera, D. hamiltonii* and *B. balcooa* partitioned, respectively, 12.7, 71.7 and 15.6% to total income in Meghalaya. Similarly in Sikkim *D. hamiltonii* and *C. hookeriana,* respectively, contributed 74.06 and 25.94% to total income (Table 4).

Physical efforts made for collection and selling of tender shoots were also recorded. On average, tribal communities of Sikkim travel comparatively longer distances in search of bamboo collection than those of Meghalaya and Mizoram. The edible shoots in Sikkim are sold in boiled form, whereas, in the rest of the states it is sold as fresh. Average shoot weight was recorded highest (2.624 kg/ shoot) in *B. balcooa* and lowest (0.334 kg/ shoot) in *C. hookeriana.* Each vendor in Meghalaya carries an average 31.33 kg bamboo shoots for selling, followed by Mizoram (27.64 kg/seller) and Sikkim (7.78 kg/seller). In all the states, primary vendors are more numerous than the secondary sellers, and females contribute the most physical efforts to harvesting and selling of bamboo shoots (Table 5).

The data on energy (MJ) expenditure required for bamboo shoot harvesting, transportation, cleaning, boiling and selling has also been estimated. On average, there was highest (2.34 MJ/ kg of bamboo shoots) energy consumption in Sikkim as compared to 0.24 and 0.23 MJ/ kg of bamboo shoots in Mizoram and Meghalaya, respectively. Females contributed maximum energy (≥60%) for bamboo shoot collection, followed by male (≥30%) and child (≥10%), respectively, irrespective of states. On average, highest energy is consumed for selling (≥40%), followed by cleaning of bamboo shoots (≥22%), harvesting (≥20%) and transportation (≥10%), respectively. Based on annual consumption of young edible shoots, the total energy consumption was highest (47,810.63 MJ) for Mizoram and lowest (284.25 MJ) for Sikkim (Table 6).

Table 4. Species wise cost-benefit analysis of edible bamboo species

Sl No.	State	Gross income including wages for man days required (Rs/ yr)				Net income excluding wages for man days required (Rs/ yr)			
		1	2	3	4	1	2	3	4
1	Meghalaya	2,11,654.34 ±22,334.00	15,06,726.00 ±1,21,800.00	2,47,534.78 ±20,965.90	N.A	1,44,810.86 ±16,533.39	8,16,069.55 ±87,319.37	1,77,673.91 ±15,780.00	N.A
2	Mizoram	13,12,287.90 ±58,583.32	N.A	N.A	N.A	7,74,827.90 ±31,241.99	N.A	N.A	N.A
3	Sikkim	N.A	6,17,892.00 ±73,005.50	N.A	2,01,906.57 ±30,208.15	N.A	5,19,520.56 ±64,288.00	N.A	1,82,002.85 ±28,778.64
	Total	15,23,942.20 ±3,54,081.57 (US$ 32,459)	21,24,618.00 ±3,57,196.48 (US$ 45,253)	2,47,534.78 ±20,965.90 (US$ 5,272)	2,01,906.57 ±30,208.15 (US$ 4,300)	9,19,638.76 ±59,490.29 (US$ 19,588)	13,35,590.10 ±1,88,140.78 (US$ 28,447)	1,77,673.91 ±15,780.00 (US$ 3,784)	1,82,002.85 ±28,778.64 (US$ 3,876)

1. *Melocanna baccifera*
2. *Dendrocalamus hamiltonii*
3. *Bambusa balcooa*
4. *Chimonobambusa hookeriana*
N.A.= Not available

Table 5. Physical efforts made for collection and selling of young edible bamboo shoots,
irrespective of districts

Activities	States		
	Mieghalaya	Mizoram	Sikkium
Distance traveled from forest to			
Village (km)	1.12 (0.40-2.33)	0.63 (0.05-2.00)	2.15 (1.50-3.33)
Market (km)	2.67 (1.00-5.00)	1.70 (1.25-3.00)	4.38 (2.00-10.00)
Average weight (kg/shoot)			
Bambusa balcooa	2.87 (2.25-3.28)	N.A.	N.A.
Chimonobambusa hookeriana	N.A.	N.A.	0.15 (0.14-0.165)
Dendrocalamus hamiltonii	0.585 (0.33-0.82)	N.A.	0.70 (0.60-0.83)
Melocanna baccifera	0.35 (0.29-0.41)	0.18 (0.13-0.22)	N.A.
Average weight of young shoot (kg/seller/day) carried to market	31.33 (12.66-46.66)	27.64 (11.54-33.53)	7.78 (7.0-9.04)
Total time (hr/seller) consumed for harvesting, carrying, cleaning, selling etc.	3.05 (1.50-4.50)	4.78 (1.74-8.57)	5.80 (5.4-6.07)
No. of vendors surveyed			
Primary	12.14 (8.0-17.0)	8.14 (6.0-15.0)	14.75 (8.0-28.0)
Secondary	5.60 (1.0-12.0)	4.0 (2.0-6.0)	21.0 (-)
Labour contribution (%)			
Male	31.43 (10.0-50.0)	31.14 (15.0-45.0)	37.63 (23.07-52.11)
Female	61.43 (50.0-75.0)	60.71 (50.0-80.0)	50.40 (33.56-71.22)
Child	10.00 (5.0-15.0)	8.86 (5.0-12.0)	11.47 (5.71-18.31)

N.A. – Not applicable   Figure in parenthesis represents the range of the data

The food energy was highest (16.40 MJ/ kg) for *D. hamiltonii* and lowest (15.64 MJ/ kg) for *B. balcooa.* The protein content was also highest (3.90% DM basis) in *D. hamiltonii.* However, the fat and carbohydrate content was comparatively higher in *C. hookeriana* and *M. baccifera,* respectively. Average calorie and protein values range between 16.8 MJ/ kg and 148.0 g/ kg for cereals and grains; between 15.8 MJ/ kg and 42.0 g/ kg for leafy and fruit vegetables and for tuber and rhizome crops between 15.3 MJ/ kg and 17.0 g/kg (dry weight basis). These values are considerably higher than those of food value of edible shoots. However, keeping in view the delicacy and availability of young bamboo shoots, these are important supplements to the nutritious diets of tribal communities for a period of almost three months per year in the study area (Table 7).

Indigenous technical ingenuity of tribal people since time immemorial is revealed in the preparation of food items from bamboo shoots. It is worth mentioning here that no preservative is used for a storage life of 6 months to 2 years in fermented products of bamboo shoots. The various indigenous methods of reducing acidity/bitterness from fresh bamboo shoots has also been recorded and some of them include chopping of tender shoots into small pieces, partial drying of fresh shoots, boiling in water/saltwater and draining or keeping the tender shoots in hot water for 10 to 15 minutes or in water for a week at ambient temperature, etc. Table 8 depicts the data on various traditional dishes/recipe of bamboo shoots prepared by the tribal folk of the region.

Besides the consumption of young edible shoots, the mature culm and branches are used for various purposes. Housing is the main activity, which needs extensive bamboo consumption for foundation, frames, floors, walls, partitioning, ceiling, door, windows, roof etc, followed by agricultural tools and implements and kitchen wares, traditional handicrafts, fencing, etc. A major share of bamboo biomass is also used as firewood. This resource is harvested almost every day for various purposes and details of the uses of each species have been shown in table 9.

Table 6. Energy (MJ) expenditure for bamboo shoot collection, irrespective of species

Activities	Meghalaya			Mizoram			Sikkim		
	Male	Female	Child	Male	Female	Child	Male	Female	Child
Harvesting	5,433.95	1,770.67	341.92	3,965.46	4,695.26	945.31	60.53	11.21	8.56
Transportation	2,957.80	929.04	1,676.54	2,969.47	3,102.69	1,004.26	14.74	14.69	4.92
Cleaning/ boiling	3,942.50	5,092.34	321.54	5,291.45	4,245.38	1,836.54	20.12	30.92	10.23
Selling	480.50	15,650.60	1,866.72	3,321.64	15,782.46	650.71	17.514	80.56	10.26
Sub-total	12,834.75	23,442.65	4,206.72	1,5548.02	27,825.79	4,436.82	112.90	137.38	33.97
Total		40,484.12			47,810.63			284.25	

Table 7. Nutritive value of commercial edible bamboo shoots

Species	Food energy (MJ/kg)	Moisture (%)	Protein (% DM)	Fat (% DM)	Carbohy-drates (% DM)
Bambusa balcoa	15.64	84.0	3.87	0.60	5.23
Chimonobambusa hookeriana	15.96	79.0	3.56	0.62	5.94
Dendrocalamus hamiltonii	16.40	87.0	3.90	0.50	5.70
Melocanna baccifera	15.80	75.5	3.62	0.57	6.12s

Tribal folk of the region rely heavily on traditional practices of forest exploitation. For nearly seven months per year tribal communities depend on forest resources particularly on minor forest produce for their subsistence as agricultural produce meet their food require-ments only for a period of 4-5 months. Bamboo is one of the important minor forest products that assists in subsistence of tribal folk to a greater extent (Bhatt *et al.* 2001; Haridashan et al 1987; Sundriyal *et al.* 2002; Singh 1989). According to the legal classification of forests, the percentage of reserve forests, protected forests and unclassed forests varies from state to state in the study area and the bamboo is mainly harvested from unclassed forests (Bhatt and Sachan 2003). All the species are also cultivated in home gardens. In Meghalaya and Sikkim, the home gardens are comparatively more than the Mizoram. On average, 10-15 year jhum fallow allows luxuriant growth of bamboo species but as the jhum cycle has reduced to 3-5 years in the recent past and is adversely affecting production of young bamboo shoots in these states.

Bamboo is harvested almost every day either for marketing (in any form) or household consumption. The major share of young edible shoot goes to immediately consumed food and the rest to making pickle and other fermented products. Since bamboo is a potential resource of the region, it is important to develop strategies for its *in situ, ex situ* and village or community based conservation. Monospecific stands are most common in the region and are stretched over large areas. Such areas may be conserved and declared as bamboo gene sanctuaries for conservation of a particular species. For example, a large hill track of Blue mountain of Mizoram is dominated by *M. baccifera,* although there is disturbance, because there is less population pressure, this area can be saved through *in situ* conservation. Similarly a large natural area of *D. hamiltonii* of Mikir Hills and Khasi Hills of Meghalaya is subjected to destruction for jhum cultivation. Excessive felling of bamboo for paper and pulp mills also cause damage to young shoot production and the annual harvest for different uses has been estimated to be 3.2

million tons for India, one third of the world's harvest of 10 million tons (Khoshoo 1992).

Mass flowering of a few dominant com-mercial bamboo species are also the natural threats for the drastic change in their population structure, productivity and young shoot pro-duction. Gregarious flowering is expected in *M. baccifera* between the years 2005-2007. An indication of this is that sporadic flowering of this species has already begun in parts of Mizoram and Meghalaya (Singha *et al.* 2003). It is expected that bamboo flowering will occur in approximately 18,000 sq km area of Mizoram, Tripura, Manipur and parts of Assam and Meghalaya. The epicenter of flowering will be Mizoram, where 0.92 million ha of forest is occupied by *M. baccifera* with production potential of 12.2 ton/ha. This huge natural resource will rot and go waste if not utilized in time and may result in many environmental problems including epidemic, fire and ecological imbalance besides famine due to sudden increase in rodent population. The last such gregarious flowering of bamboo was recorded in Mizoram, Tripura and Barak valley of Assam in 1959. This was followed by a severe famine in those areas (Trivedi and Tripathi 1980; Pathak and Kumar 2000). Keeping this fact in view, mass afforestation of *M. baccifera* is required in the region, particularly in Mizoram and Manipur so that by the time of flowering, the new plantlets could come up and sustain the subsistence of tribal folk of the region.

Being a versatile and renewable resource, bamboo has been over-exploited so much that concerns are being expressed over erosion of this gene pool (Renuka 1996). Some of the research involves bamboo based agroforestry systems highlighting the capacity of bamboo in increasing the soil moisture, nutrients, and reducing water run off and soil erosion (Ramakrishnan and Toky 1981). Unfortunately, the edible characteristics have not been given due importance perhaps because consumption of tender shoots of bamboo is witnessed only in northeast India (Bhatt *et al.* 2001). Moreover, there is no systematic documentation on edible bamboo and its utilization pattern in NEH region. Hence planning priorities should be

Table 8. Traditional dishes prepared from bamboo shoots

Sl. No.	States	Tribal communities accessing the resource	English name	Local dialect/ community	Preparation procedure/ recipe
1	Meghalaya	Khasi, Garo and Jaintia	Boiled vegetable	Jhur/Khasi	• Plain boil with salt or with meat/ fish, etc.
			Fried vegetable	Jingtah/Khasi	• Fried with vegetables/ non-veg. components, dry fish, black pepper, and other spices.
			Pickle	Achar lung/Khasi	• Sliced/ chopped young shoots with mustard oil, pickle powder, chili, and other local spices.
			Fermented product	Syrwa/Khasi	• Sliced/ chopped bamboo shoots moistened with plain water and fermenting them for 5-10 days in a heap - container.
2	Mizoram	Mizo and Mara	Boiled vegetable	Chum/Mizo	• Small pieces of edible shoots boiled with only salt in plain water.
			Fried vegetable	Kang/Mizo	• Bamboo shoots fried in oil and spices along with other vegetables.
			Fried curry/ soup	Vaipaden/Mizo	• Young shoots cooked with vegetable or non-vegetable components along with spices.
			Pickle	Um/Mizo	• Small pieces of bamboo shoots are put into vinegar, mustard oil, spices, chili etc.
			Fermented product	Rep/Mizo	• Bamboo shoots are boiled, squeezed and stored for fermentation for several months. They are used as vegetable throughout the year.
3	Sikkim	Nepali and Tibetan	Boiled/fried vegetable	Sabji/Nepali	• Small pieces of young shoots are boiled with salt or with dry fishes. They are also cooked with fish or meat along with spices and used as curry.
			Fermented food	Mesu/Nepali	• It is a boiled-fermented tender bamboo shoot prepared by packing and fermenting them in tightly packed bamboo chuunga (internode) for 7-15 days.
			Pickle	Achar/Nepali	• Small pieces of bamboo shoots are treated in vinegar, mustard oil, other pickle powder, raw chili, ginger, and spices.

Table 9. Other uses of edible bamboo species in northeast India

Species	Uses of branch, leaf, culm, rhizome and seeds	
Bambusa balcooa	• Agricultural implements • House roofing and partition wall • Winnowing tray • Rice carrying baskets • Carrying and storing baskets • Mat • Hen coop and chicken baskets • Food container for long term preservation and use • Musical instruments • Incense sticks, broom, tooth brush and tooth pick. • Paper and pulp industry	• For making *Nal* to feed aqueous feed/solutions to livestock. • Bait station for keeping poison in rodent management. • Levelling stocks. • For making drip irrigation. • Firewood • Branches are used for making brooms • Leaves are used as fodder for cattle and goat. Leaves are also used to produce smoke as insect repellent in the cattle farms.
Chimonobambusa hookeriana	• Fishing rod • Handloom and handicraft • Musical instruments • Stand for mosquito net • Walking stick • Winnowing tray • Decorated baskets • Seeds cooked and used as substitute of rice; also used for brewing and other fermentation products. • Rice plate, cup and plates	• Chick baskets and feeder • Branches are used for making brooms • For making *Nal* to feed aqueous feed/solutions to livestock. • Levelling stocks. • Firewood • Leaves are used as fodder for cattle and goat. Leaves are also used to produce smoke as insect repellent in the cattle farms.
Melocanna baccifera	• Winnowing tray • Rice carrying baskets • Betelvine and betelnut baskets • Vegetable containers • Carrying and storing baskets • Mat • Weeding implements • Stool • Hen coop and chicken baskets • House pole ceiling, partition wall, fencing, water pipe, etc. • Bridge and supporting materials for concrete building and bridge construction. • Implements for handloom craft • Handicraft, animal cage and farm house, etc. • Food container for long term preservation and use. • Musical instruments • Paper and pulp industry • Tool handles and agricultural implements • Traditional hockey stick and ball • Firewood • Rodent traps • Fishing rod • Rain shield	• Chick baskets and feeder • Bridge • Cattle trough • Piglet carry baskets • Duckling carry baskets • Used for making pegs for hanging crabs to trap gundhibug (*Leptocorisa oratorius*) of rice crop. • For making *Nal* to feed aqueous feed/solutions to livestock. • Bait station for keeping poison in rodent management. • Levelling stocks. • For making drip irrigation. • For making *Machan* used as shelter to protect crops in jhum fields. • For making coat. • Branches are used to provide support to climbers and twiners and also to make brooms, map pointers and firewood. • Leaves are used as fodder for cattle and goat, house roofing and as partition wall in huts. Leaves are also used to produce smoke as insect repellent in the cattle farms.

Table 9. Other uses of edible bamboo species in northeast India *(cont'd)*

Species	Uses of branch, leaf, culm, rhizome and seeds	
Dendrocalamus hamiltonii	• House roofing and partition wall • Physical support for climbers and tawnier agricultural crops. • Firewood • Kitchen and cookware components like spoon, spatula, etc. • Fish traps • Rodent traps • Fish rod • Flower pots • Stray • Cassette stand • Hat • Wall hangings • Pen stands • Bags • Rice carrying baskets • Storing baskets • Hen coop and chicken baskets • Rain shield • Chick baskets and feeder • Piglet carry baskets • Duckling carry baskets	• Cattle trough • Bridge • Used for making pegs for hanging crabs to trap gundhibug *(Leptocorisa oratorius)* of rice crop. • For making *Nal* to feed aqueous feed/solutions to livestock. • Bait station for keeping poison in rodent management. • Levelling stocks. • For making drip irrigation. • For making *Machan* used as shelter to protect crops in jhum fields. • For making coat. • Branches are used to provide physical support to climbers and twiners and also as firewood. • Leaves are used as fodder for cattle and goat, house roofing and as partition wall in huts. Leaves are also used to produce smoke as insect repellent in the cattle farms.

fixed for mass multiplication and production of edible bamboo species not only for domestic consumption but also to earn revenue for economically poor tribal communities of the region. On the basis of the survey conducted, it has been recorded that bamboo shoots may provide the employment opportunities to rural educated youths, school drop outs and females, who are backbone of agricultural development in the region. From the present data, it has been estimated that selling of bamboo shoots alone can provide employment to 131, 88 and 55 persons/yr, respectively, in Meghalaya, Mizoram and Sikkim. Similarly through pickle processing, about 67 persons can get employment on per year basis. Therefore, emphasis should also be given to establish bamboo based small-scale pickle industries in rural sectors of Meghalaya, Mizoram and Sikkim as it has a reasonable high return in local markets as a delicacy.

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Ambiguity and an American Bamboo:
The *Chusquea culeou* Species Complex

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The *Chusquea culeou* species complex is a group of closely related tropical woody bamboos native to the Andes of Chile and Argentina, including entities named *C. culeou, C. andina, C. argentina, C. breviglumis,* and *C. gigantea.* Species in this group are recognized primarily by differences in culm size and branch dimorphism. In these and other vegetative and reproductive characteristics, however, the group appears to exhibit a range of variation in association with factors such as altitude, latitude, and sun versus shade habitat. When these factors are considered, it suggests the current classification is confounded by ecological and geographical variables. This project is a preliminary investigation of morphological variation among these forms in an attempt to find additional criteria for clarifying relationships within the group. Using principal components analysis, composite morphological traits based on vegetative and reproductive characters are compared among putative species and against ecological and geographical gradients. The analyses reveal a range of morphological variation with little or no clustering by species: variation in examined vegetative and floral characters is continuous and cannot be used to demarcate species into morphologically distinct groups. Moreover, strong correlations were not found between the observed characters and eco-geographic factors (altitude and latitude). This investigation emphasizes the fact that additional studies are necessary to resolve the classification of this group.

The bamboo subfamily, Bambusoideae, is a diverse and economically important group of approximately 115 genera that includes the herbaceous bamboos (Tribe Olyreae, ca. 110 spp.) and the woody bamboos (Tribe Bambuseae, ca. 1300 spp.). Systematics of tribe Bambuseae is incomplete in comparison with other major groups of grasses owing to unusual flowering cycles and difficulties associated with obtaining adequate bamboo specimens, along with taxonomic uncertainty relating to the application of different species concepts. Much work remains to clarify the relationships among woody bamboos, to adequately describe species-level diversity, and to produce a classification based on a robust phylogeny of the tribe.

Nine subtribes are currently recognized within the Bambuseae (Dransfield and Widjaja, 1995); subtribe Chusqueinae, including two Neotropical genera and 155 described species, is one of these. Chusqueinae encompasses *Chusquea* Kunth and *Neurolepis* Meissner, and is strongly supported as monophyletic based on a combination of morphological and molecular data (Clark, 1997; Clark *et al.*, unpublished). Shared, uniquely derived features include spikelets with four glumes subtending a single fertile floret with no rachilla extension, and the presence of papillae on the subsidiary cells of the stomatal apparatus.

Chusquea, with an estimated 200 species, is the most diverse genus of bamboo in the world. The genus is defined by solid culms, multiple, dimorphic buds per node, and a base chromosome number of $x = 10$ (Clark, 1997). *Chusquea* is further subdivided into three major groups (Clark, 1997): subgenus *Chusquea* (erect to scandent, mid-altitude bamboos), subgenus Rettbergia Raddi (clambering, low- to mid-altitude bamboos), and subgenus *Swallenochloa* McClure (shrubby, high altitude bamboos). Plants in subgenus *Swallenochloa* are characterized by an erect, shrubby habit, short, waxy internodes, dense growth in clumps, foliage leaves that are often stiff and erect, paniculate inflorescences that are usually narrow and dense, and mostly intravaginal branching. They are primarily restricted to high altitudes in *subpáramos* and *páramos* of the

Andes and Central America, and *campos de altitude* in Eastern Brazil. Subgenus *Swallenochloa* includes section *Swallenochloa* (27 species) and three informal groups (species complexes): the *Chusquea heterophylla* group, the *C. nudiramea* group, and the *C. culeou* group.

The *Chusquea culeou* species complex is a group of closely related tropical woody bamboos native to *Nothofagus* forests of the Andes of Chile and Argentina (Fig. 1), including *C. gigantea* Demoly, *C. culeou* E. Desvaux, *C. breviglumis* R. A. Philippi, *C. argentina* L. Parodi, and *C. andina* R. A. Philippi. The plants occur across a range of habitats, in pure stands in the open as well as beneath the dense canopy of *Nothofagus*, from sea level to altitudes of over 2000 m (Widmer, 1997). The group is well known throughout the region, to the extent that it is recognized by common names (e.g., *colihue*) and used in the daily life and folk arts of some local communities. Worldwide, *C. culeou* is the most widely cultivated species within the genus (Judziewicz *et al.*, 1999).

Collectively, the *C. culeou* species complex appears to exhibit a morphological gradation in association with eco-geographic variables such
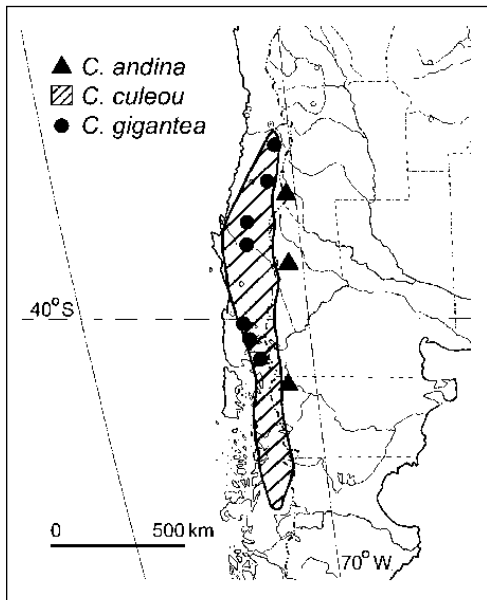
Figure 1. Map showing distribution of species in the *Chusquea culeou* species complex *(C. andina, C. culeou,* and *C. gigantea)* in Chile and Argentina.

as altitude, latitude, and sun versus shade habitat. At least three variants have been identified in natural populations: a low-altitudinal (400-1300 m) form that is relatively tall (4 m) with dimorphic subsidiary branches; a low- to mid-altitudinal (0-1600 m) form that is medium in size (2.5 m) with uniform branches; and a high altitudinal (>1600 m) form that is short (1.5 m) with uniform branches. At low and medium altitudes, distinctions can also be made between a compact, shrubby form in the sun versus a taller form with longer branches in the shade. Variation in cold tolerance has also been observed: the large form is apparently less hardy in cultivation than the medium sized form, while the high altitude, smaller form is the most hardy (Judziewicz *et al.*, 1999).

The taxonomy of the group is complicated by a number of factors, not the least of which is an apparent lack of the usual distinctions associated with species in *Chusquea* (especially discrete characters of the culm leaf, foliage leaf, and spikelet; Fig. 2; Clark, 1989). Current taxonomy in the *C. culeou* group is based largely upon distinctions in overall plant size and branch classes. A tall form with dimorphic subsidiary branches was recently named *Chusquea gigantea* based on material grown in cultivation in France (Demoly, 1999). The more widespread form, both in the Andes and in cultivation worldwide, are the medium-sized plants recognized as *Chusquea culeou*. The high altitude, shorter form is recognized as *Chusquea* andina. *Chusquea breviglumis* and *Chusquea argentina* are considered to be synonyms for *C. culeou* (Judziewicz *et al.*, 1999). To further complicate matters, the name *C. breviglumis* has been incorrectly applied in horticultural circles to the large form (*C. gigantea*), and a dwarf form of *C. culeou* from Chile is widespread in cultivation in the United States under the incorrect name *C. nigricans* (this name is a synonym for plants of the species *C. montana* R. A. Philippi). Also, at least some plants identified in horticulture as *C. macrostachya* R. A. Philippi are actually *C. culeou*.

This paper presents our preliminary work to investigate factors that underlie patterns of morphological variation in the *Chusquea culeou*
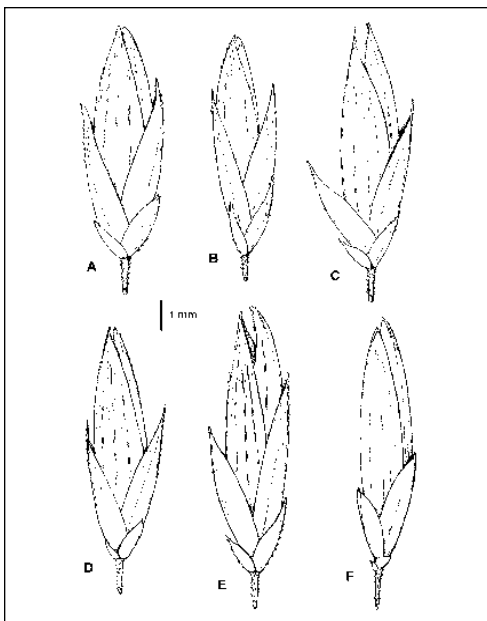
Figure 2. Comparison of spikelets among members of the *Chusquea culeou* species complex (A-E) and a close relative (F). A. *C. gigantea.* B. *C. culeou.* C. *C. breviglumis.* D. *C. argentina.* E. *C. andina.* F. *C. juergensii.* Drawings, A based on Pearson 1095 (ISC), B based on Gay 293 = 126 (P), C based on Philippi 985 (P), D based on Cabrera & Job 253 (BAA), E based on Philippi 521 (P), F based on Jürgens 322 (W). Illustration by J. K. Triplett; (F) after L. G. Clark (1992), Brittonia 44(2).

complex, and a discussion of the potential difficulties with the current taxonomy. Our long range goal is to help clarify relationships and nomenclature within the *C. culeou* species complex.

MATERIALS AND METHODS

Specimens were obtained by Clark during field trips to Chile in 1992. Cultivated material of *C. gigantea* was obtained in 2002 from the Conservatoire Botantique National de Brest, France. Additional field collections were provided by A.K. Pearson from material collected in Argentina in 1989-1990. Herbarium specimens were obtained on loan from the Arnold Arboretum Herbarium and Gray Herbarium, both of Harvard, and the herbarium of the University of Concepción, Chile.

Characters

Specimens were measured for a variety of morphological characters, including foliage leaf length and width, inner ligule length, inflorescence length, spikelet length, and lengths of spikelet bracts (glumes I-IV, lemma and palea). Foliage leaves were measured intact on herbarium specimen. Leaf measurements were standardized to the extent possible (e.g., leaf 3 or 4 from branch terminal), but this was made difficult due to the variable nature of bamboo specimens. Branch dimorphism was noted (i.e., two sizes of branches), as was the occurrence of a large central branch. Culm leaves, when available, were also measured, but this character set was not used in the analysis because of the small number of specimens with culm leaves. Spikelets were removed from specimens and softened using a modified Pohl's solution (Pohl, 1965; 750 ml distilled water, 250 ml 1-propanol, 2 ml liquid dish soap), dissected, examined, and measured for floral characters using a dissecting microscope equipped with a micrometer. Multiple observations of a given character were averaged for each individual, and the averages were used to construct a raw data matrix. A variety of proportions were calculated in order to capture additional qualitative and quantitative differences (e.g., the ratio of glume I:spikelet; ratio of leaf length:width). A total of 21 characters was used for phenetic analyses: 7 vegetative characters and 14 floral characters (Table 1).

For the purposes of the analysis, plants identified as *C. andina* and *C. gigantea* in herbarium specimens were used as such; plants labelled as *C. culeou* or *C.* aff. *culeou* were assigned to *C. culeou* and *C. gigantea* based on characteristics of the branch complement. The raw data matrix consisted of 6 specimens of *C. andina,* 80 specimens of *C. culeou,* and 11 specimens of *C. gigantea.*

Analyses

Vegetative and floral data subsets were analyzed together and separately, with and without the inclusion of branch data. The data were analyzed to compute principal components based on a correlations matrix. Principal com-

Table 1. Morphological characters included in the study of the *Chusquea culeou* species complex.

Vegetative characters
1. Foliage leaf length (cm)
2. Foliage leaf width (cm)
3. Foliage leaf inner ligule length (mm)
4. Leaf L:W
5. Leaf pubescence (presence/absence)
6. Branch dimorphism (presence/absence)
7. Large central branch (presence/absence)
Floral characters
8. Inflorescence length (cm)
9. Spikelet length (mm)
10. Glume I length (mm)
11. Glume II length (mm)
12. Glume III length (mm)
13. Glume IV length (mm)
14. Lemma length (mm)
15. Palea length (mm)
16. Glume I:spikelet
17. Glume II:spikelet
18. Glume III:spikelet
19. Glume IV:spikelet
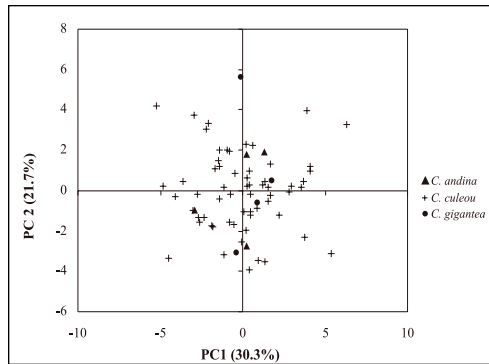20. Lemma:spikelet
21. Palea:spikelet

Figure 3. First two principal components from PCA analysis of combined vegetative and floral data, plotted for individual plants. Symbols indicate putative species. Note substantial overlap among species.

ponents analysis (PCA) is a statistical technique that reduces a dataset of many characters to one or a few new characters, each of which captures distinct (uncorrelated) portions of the variation in the original data. When plotted against one another, the components give a visual indication of the similarity among the predefined units (putative species) based on trends in morphological variation. PCA was conducted using JMP 5 (SAS Institute, Inc. 2002), and principal components were plotted using Microsoft Excel (Microsoft, 2000).

Regression analyses were conducted to examine the relationship between morphology and geographic variables (altitude and latitude). Separate analyses were conducted for each character and for the first principal component from each of the analyses described above.

RESULTS

Principal components analyses
Combined data. PCA of the combined morphology dataset (vegetative and floral data subsets, excluding branch data) reveals a single morphological continuum with no discrete breaks or clusters by species (Fig. 3). The first two principal components account for 52% of the variation (PC1: 30.3%; PC2: 21.7%). Glume III, glume IV, lemma, and palea measurements contribute most heavily to PC1, while the ratio of glume I:spikelet and the ratio of glume II:spikelet contribute most heavily to PC2. However, none of these characters can be used to discriminate among the putative species. The combined data analysis includes 4 specimens of C. andina, 61 of C. culeou, and 4 of C. gigantea.

Data subsets. Similarly, the separate analyses of vegetative and floral data subsets provide little information about clear distinctions between the putative species. The vegetative morphology analysis reveals a morphological continuum (Fig. 4). Along the axis for PC1, there are two clusters of *C. gigantea:* one within the main cluster, and one towards the positive extreme. This suggests that plants recognized as *C. gigantea* are those at the upper end of the morphological spectrum represented by PC1. The first two principal components account for 74.3% of the variation (PC1: 47.2%; PC2: 27.1%). Leaf length and the ratio of foliage leaf L:W contribute most heavily to PC1, while ligule length and leaf pubescence contribute most heavily to PC2. The vegetative data analysis includes 6 specimens of *C. andina,* 79 of *C. culeou,* and 11 of *C. gigantea.*

The floral morphology subset PCA presents a continuum without discrete clusters (Fig. 5).
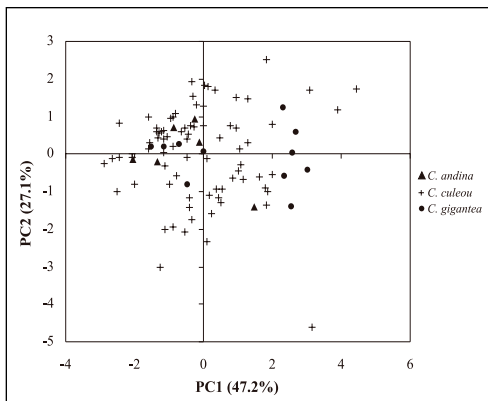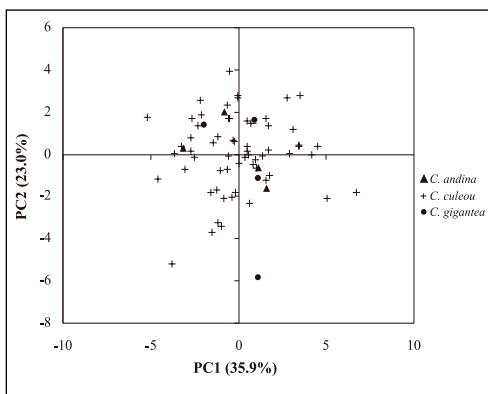
Figure 4. First two principal components from PCA analysis of vegetative data, plotted for individual plants. Symbols indicate putative species. Note substantial overlap among species, with some clustering of *C. gigantea* along PC1.
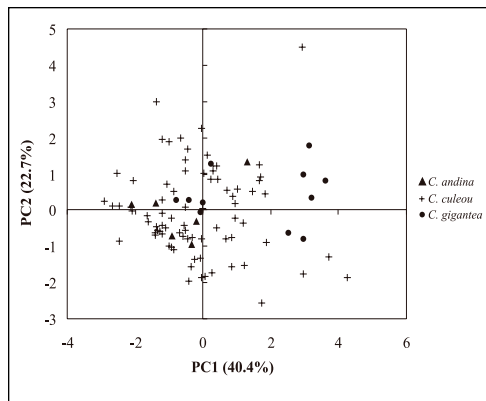

Figure 6. First two principal components from PCA analysis of vegetative data, with the inclusion of branch morphology data. Symbols indicate putative species.

The first two principal components account for 58.9% of the variation (PC1: 35.9%; PC2: 23.0%). Glume measurements contribute most heavily to PC1, while spikelet length, palea, and lemma contribute most heavily to PC2. The floral data analysis includes 4 specimens of *C. andina,* 61 of *C. culeou,* and 4 of *C. gigantea.*

It is important to note that when the branch dimorphism data are included, clusters by species are found only in the analysis of the vegetative data subset (Fig. 6). Two clusters occur along the axis for PC1: one with specimens defined as *C. gigantea,* and another with those defined as *C. andina* and *C. culeou.*

Figure 5. First two principal components from PCA analysis of floral data, plotted for individual plants. Symbols indicate putative species.

Regression analyses

Altitude: None of the vegetative characters exhibit a correlation with altitude. Among the reproductive characters, three show a weak but statistically significant positive correlation with altitude (i.e., longer or larger with increasing altitude): inflorescence length (r-square = 0.085, p = 0.015), palea length (r-square = 0.064, p = 0.035), and the ratio of palea:spikelet (r-square = 0.068, p = 0.029). None of the analyses of the first principal component (PC1) against altitude reveal a strong relationship (combined data analysis: r-square value = 0.029, p = 0.158; vegetative data: r-square = 0.052, p = 0.026; floral data: r-square = 0.012, p = 0.354; see Fig. 7).

Latitude: Foliage leaf length is weakly correlated with latitude (r-square = 0.044, p = 0.039), as is foliage leaf outer ligule length (r-square = 0.137, p = 0.0002). None of the reproductive characters exhibit a clear relationship with latitude, nor do the analyses of the first principal component (PC1) against latitude (combined data analysis: r-square = 0, p = 0.896; vegetative data: r-square = 0.056, p = 0.020; floral data: r-square = 0.005, p = 0.546).

DISCUSSION

Several studies have documented the range of phenotypic variability within *C. culeou* (Pearson *et. al.,* 1994; Haverbeck, 1983; Veblen, 1982). In a 13-year study of *C. culeou* in
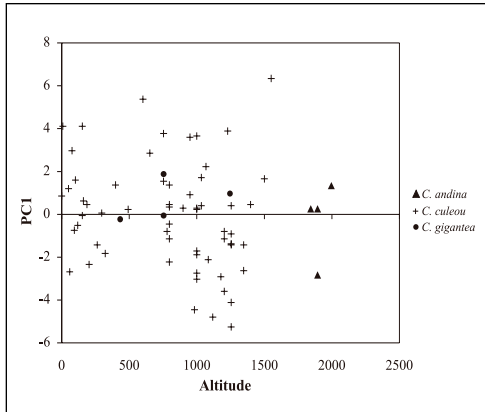
Figure 7. Regression of the first principal component (PC1) from the vegetative data analysis versus altitude. Symbols indicate putative species. Note that putative species overlap along PC1.

Argentina, Pearson observed a range in culm diameter from 5.7 mm to 21.5 mm among study sites, and height from 1.7 m to over 5 m. Pearson also observed clear differences in branch complements in the production of secondary branches: at some sites, branch buds were small and numerous; at others sites, plants produced from 1 to 3 larger buds, with numerous subsidiary buds. Variation in leaf production was also observed among the sites. Sheltered sites with low exposure indices produced leaves that were more "lax, soft to the touch," and exhibited variation in micromorphology, including the occurrence of hairs on the abaxial surface of the leaves. Comparisons of measurements suggest that the plants in Chile tend to be larger than those on the Argentinian side. Plant characteristics were notably variable, and could be correlated with factors such as the age of the plant, position, age and length of branches, as well as light intensity and other eco-geographic factors. The presence of this phenotypic variation within the *C. culeou* group suggests that attempts to recognize species should proceed with caution.

In the present study, phenetic analyses reveal a morphological continuum with little or no clustering by species when a defining character (branch dimorphism) is excluded from the analyses (Figs. 3-5). In other words, our study suggests that the putatively discrete variation in branch morphology is not accompanied by discrete variation in other morphological characters; variation in floral and vegetative characters is continuous, rather than demarcating the species into morphologically discontinuous groups. Similarly, the linear regressions of principal components (combined morphological characters) versus geographical variables do not indicate a clear correlation between the measured morphological characters and altitude or latitude, showing instead continuous variation across the geographical range (Fig. 7).

Species in the genus *Chusquea* are typically differentiated based on a combination of discrete characteristics of the floret and spikelet, leaf morphology, and branch complement (Clark, 1989). Species in the *C. culeou* group are currently recognized based on differences in culm size and branch dimorphism. The present study reinforces the observation that putative species in the *C. culeou* group overlap in morphology and lack distinctions comparable to those used in the taxonomy of other members of the genus *Chusquea*. It appears that the current taxonomy of this group is based upon pockets of apparent discrete variation without a thorough investigation of the implications of continuous variation within and among species in the complex.

A speculative explanation for the pattern of gradation observed in this group may be a relatively recent history of divergence. This speculation is consistent with the biogeographical history of Central and South America and the relatively recent uplift of the Andes, where colonizing populations may still be actively speciating. Such an evolutionary history is postulated for members of *Chusquea* sect. *Longifoliae* L. G. Clark in Central America, where difficulties arise in distinguishing among *C. foliosa* L. G. Clark, *C. subtilis* Widmer & L. G. Clark, and *C. tomentosa* Widmer & L. G. Clark (Clark, 1997).

The question remains as to whether the named entities of the C. culeou group are variants within a species or independent lineages that should be considered distinct species. This investigation, because of the small sample size and limitations as an herbarium

study, can provide only tentative conclusions. A more thorough examination of a variety of traits across a range of the taxa may provide a better overview of the structure of variation.

Three names are currently applied for species within the *C. culeou* complex, based on a few apparent morphological differences:

C. gigantea – large form with dimorphic subsidiary branches; elevation 400-1300 m.

C. culeou – medium form with uniform branches; elevation 0-1600 m.

C. andina – compact form with uniform branches; elevation 1800-2000 m (above the tree line).

Further work is necessary to clarify the taxonomic relationships of species in the *C. culeou* complex. Potential lines of research include:

• Investigation of additional characters using leaf anatomical and micro-morphological techniques.
• Search for molecular markers (AFLPs).
• Examination of the role of eco-geographical factors, using a common garden experiment.

ACKNOWLEDGEMENTS

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Culm Anatomy of Native Woody Bamboos in Argentina and Neighboring Areas: Cross Section.

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The culm cross section was analyzed for fifteen species belonging to six genera of native woody bambuseae of South America. Our objective is to allow the identification of the taxa from the culm anatomy, especially for archaeological work. In the present work, the anatomy is described for mature culms of the genera: *Aulonemia, Colanthelia, Chusquea, Guadua, Merostachys and Rhipidocladum.* These taxa belong to three subtribes: Arthrostylidiinae, Chusqueinae and Guaduinae. The culm cross section is described and illustrated and cross sectional distribution of the vascular bundles was analyzed for peripheral, transitional and central vascular bundles. An identification key to the taxa is given. The relationship between culm anatomy and the subtribes is discussed.

Se realizó el análisis del transcorte caulinar de quince especies pertenecientes a seis géneros de bambúes leñosos nativos de Sud América. Ambos tuvieron como objetivo permitir la identificación de los taxones a partir de la anatomía del tallo y contribuir a la determinación de algunas especies arqueológicas. En este trabajo los estudios anatómicos fueron realizados sobre cañas desarrolladas de los géneros actuales: *Aulonemia, Colanthelia, Chusquea, Guadua, Merostachys y Rhipidocladum.* Estos taxones pertenecen a 3 subtribus: Arthrostylidiinae, Chusqueinae y Guaduinae. Se describió e ilustró el transcorte caulinar y se realizó un análisis comparativo de los haces vasculares según su distribución en el transcorte: haces vasculares periféricos, de transición y centrales. Se incluye también una clave identificatoria de los taxones estudiados y algunas consideraciones sobre los caracteres anatómicos caulinares en relación con las subtribus.

In this study the analysis of culm cross section of fifteen species belonging to six genera of native woody bamboos of South America, corresponding to the Bambuseae tribe (Judziewicz *et al.* 1999) was carried out. In a previous work (Rúgolo de Agrasar & Rodríguez 2002), which is supplemented with the present study, the anatomical characteristics of the culm epidermis were described. Both studies had as objectives 1) the description of stem anatomy and elaboration of anatomical patterns that facilitated the identification of the present day taxa, and 2) its application in the recognition of archaeological material. The identification of woody bamboos is based on vegetative characters because most of them have sporadic flowering, after long vegetative periods (Judziewicz *et al.* 1999; Rúgolo de Agrasar & Clark 2000).

Species of the genera *Chusquea* Kunth and *Rhipidocladum* McClure dated among archaeological material from 8600-4700 years BP have been identified. In two archaeological sites located in Argentina (Antofagasta de la Sierra, Province of Catamarca), several artifacts were recovered, including handles made with Chusquea lorentziana Griseb., two culm fragments of *Rhipidocladum neumannii* Sulekic, Rúgolo & L. G. Clark with signs of use, and a handle fragment elaborated with *Chusquea lorentziana.* The material was found in very good condition without evidence of biodegradation, so that comparative anatomical study with present day material was possible (Rodríguez 1997, 1999a, 1999b; Rúgolo de Agrasar & Rodríguez 2002).

There are few studies dealing with the culm anatomy of woody bamboos. Metcalfe (1960) briefly described the structure of the culm, pointing out the diagnostic characters and the variations, summarizing the characteristics of the cross section of *Guadua angustifolia* Kunth. Sekar and Balasubramanian (1994) discuss the anatomical characters of this species and its systematic position in relation to *Bambusa* Schreber, recognizing the genus *Guadua* Kunth. Londoño *et al.* (2002) also extensively characterized the culm anatomy of *Guadua angustifolia.*

Liese (1980) began culm anatomical studies of Asian woody bamboos stressing the characteristics of vascular bundles in relation to the sclerenchyma sheaths, describing four basic types. Liese (1998) enlarged these studies emphasizing the importance of the stem structures in bamboo taxonomy. Liese and Grosser (2000) described two new subtypes for the vascular bundle basic type.

In this work, the anatomical studies were carried out on mature culms of different extant genera (Figs. 1-23; Tables 1-2). The following genera were studied: *Aulonemia* Goudot,

Colanthelia McClure & E. W. Sm., *Chusquea* Kunth, *Guadua* Kunth, *Merostachys* Spreng. and *Rhipidocladum* McClure (Nicora & Rúgolo de Agrasar 1987; Judziewicz *et al.* 1999; Rúgolo de Agrasar & Clark 2000). *Aulonemia, Chusquea, Guadua* and *Rhipidocladum* are distributed in North and South Andes, *Colanthelia* in Atlantic forest from Brazil and Misiones (Argentina) and *Merostachys* from Central America, Mexico, Venezuela, Guyanas to montane forests in Brazil and east of Argentina (Clark 1995, 2001).

Culm cross sections are here described and illustrated and comparative analysis of the vascular bundles according to their distribution is carried out. On this basis an identification key was produced.

MATERIALS AND METHODS

To analyze the anatomical structure of woody bamboos, herbarium material deposited at (SI) and material cultivated in the Botanical Garden of the Facultad de Agronomía (UBA) were used. The middle portion of the internodes of mature vegetative culms was selected and cut.

Table 1. Variability in the shape of peripheral, transitional and central vascular bundles. Subtribe Arthrostylidiinae.

Table 2. Variability in the shape of peripheral, transitional and central vascular bundles.
Subtribes Chusqueinae and Guaduinae.

The material was boiled in water with commercial use detergent for several hours before making the cuts. The applied methods included complete cross sections obtained with a sliding microtome. The histological sections were stained with safranin and fast-green or dilute safranin and mounted in Canada balsam or glycerine-gelatine respectively (D'Ambrogio de Argüeso 1986). Sections were observed and photographed with light microscope (NIKON FX-TO) (Figs. 1-20, 22). Some observations of cross sections with the scanning electron microscope (SEM) (ZEISS DSM 940 A) of the Instituto de Botánica Darwinion (Figs. 21, 23) are also included.

For the description of the culm cross sections, the following characters were considered: epidermis, hypodermis, cortical parenchyma, sclerenchyma, vascular bundles (peripheral, transitional and central) and interfascicular parenchyma. The transitional vascular bundles are situated towards the middle of the culm walls. The number of vascular bundle cycles, their position and the size and form of central vascular bundles were considered (Tables 1, 2).

To determine the position of vascular bundles, the phloem location in relation to the stem cortex was taken into consideration. In solid culms the transitional vascular bundles only were considered, while in the hollow ones all the vascular bundles were used. In all cases, the central and transitional vascular bundles were included. The form of the central vascular bundles was recorded based on Stearn´s (1983) terminology, taking in consideration the most extreme points in their contour. The descriptions were based on Metcalfe (1960). Specimens marked by asterisks correspond to the archaeological material (Rodríguez 1997, 1999a, 1999b).
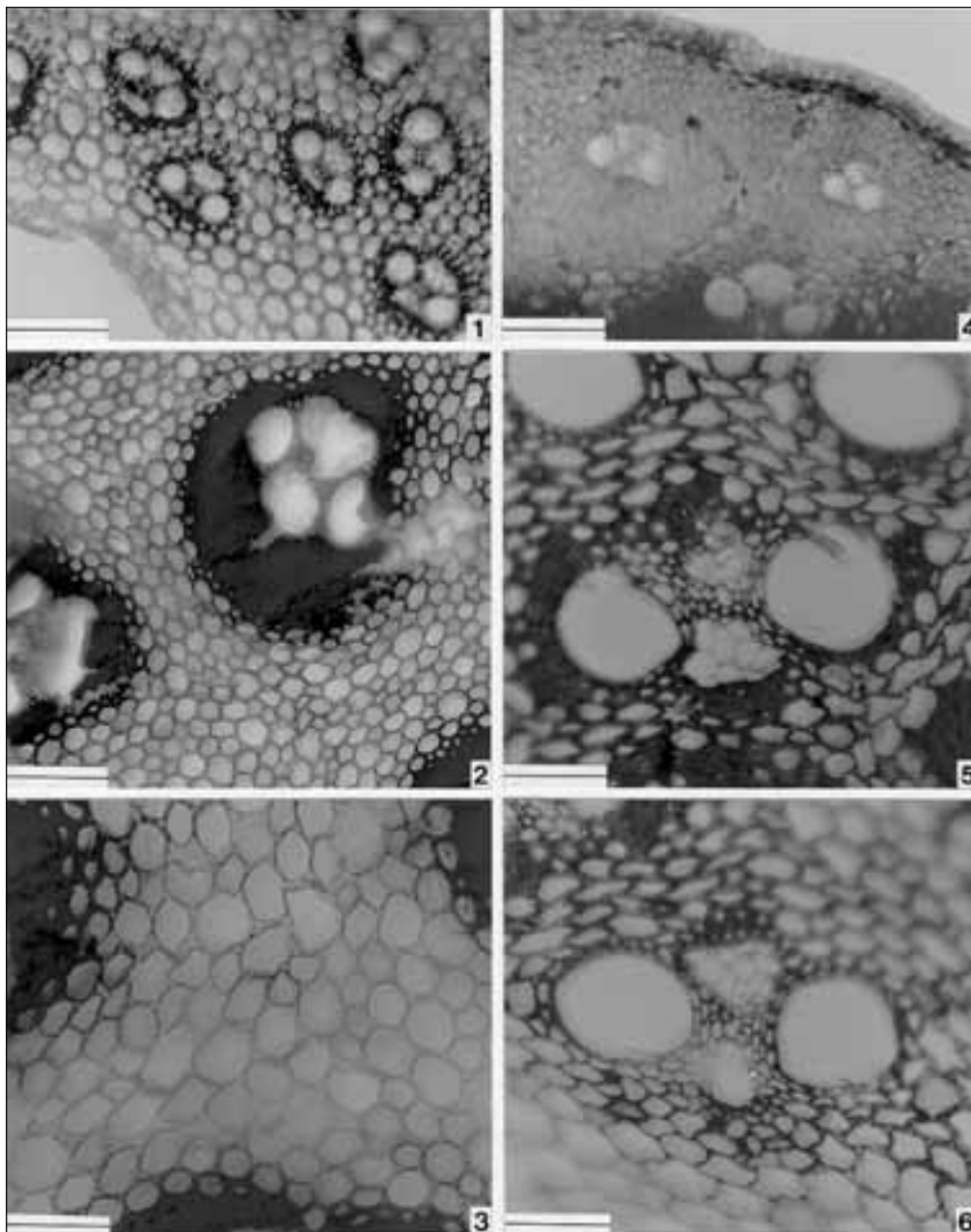
RESULTS

Descriptions of culm anatomy for each species.

*Aulonemia queko* Goudot (Figs. 1, 2, 3; Table 1)

Culm hollow with wide lacuna. Epidermis formed by a single layer of papillate epidermal cells with the external wall thickest. Subepidermal parenchyma of 2-3 cell layers with thick walls. Sclerenchyma continuous with

Figures 1-6. Culm cross sections light microscope micrographs. Figs. 1-3. *Aulonemia queko. (Solomon & Moraes 11436)*. Fig. 1. Flowering culm; transitional and central vascular bundles. Scale bar = 400 μm. Fig. 2. Mature culm; transitional vascular bundles. Scale bar = 400 μm. Fig. 3. Detail of interfascicular parenchyma. Scale bar = 200 μm. Figs. 4-6. *Colanthelia rhizantha (Zuloaga et al. 5137)*, scale bar = 200 μm. Fig. 4. Epidermis and peripheral vascular bundles. Fig. 5. Transitional vascular bundles. Fig. 6. Central vascular bundle.
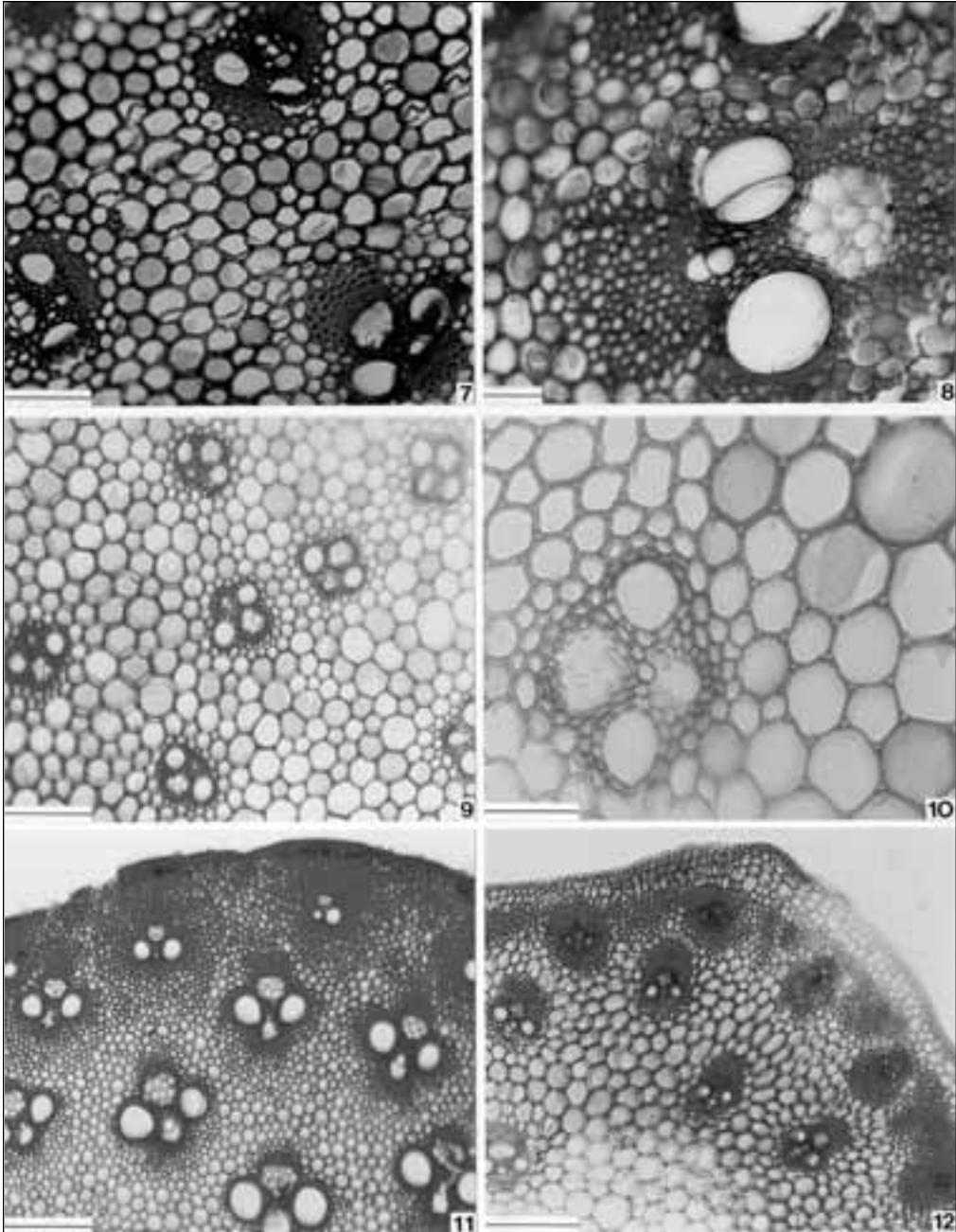
Figures 7-12. Culm cross sections light microscope micrographs. Fig. 7. *Chusquea culeou.
(Rúgolo 1085)*. Central vascular bundles. Scale bar = 200 μm. Fig. 8. *C. lorentziana.
(Krapovickas & Cristóbal 20452)*. Central vascular bundle. Scale bar = 50 μm. Figs. 9-10.
C. montana. (Bernasconi 14780). Fig. 9. Transitional and central vascular bundles.
Scale bar = 200 μm. Fig. 10. Detail of a central vascular bundle. Scale bar = 50 μm.
Fig. 11. *C. ramosissima. (Hunziker 787)*. Epidermis, peripheral and transitional vascular
bundles. Scale bar = 200 μm. Fig. 12. *C. tenella. (Porta 208)*. Epidermis, peripheral,
transitional and central vascular bundles. Scale bar = 200 μm.

the first cycle of vascular bundles, interrupted partly by the interfascicular parenchyma. Vascular bundles in 6-7 cycles with developed protoxylem and metaxylem; phloem oriented toward the external face of the culm. Peripheral vascular bundles surrounded by sclerenchyma, more developed in connection with the protoxylem and the metaxylem; transitional and central vascular bundles similar, broadlly ovate, surrounded by a continuous sclerenchymatic sheath that increases at phloem and protoxylem levels; central vascular bundles 136-408 µm wide and 204-544 µm deep. Parenchyma scarce; vascular bundles separated by 2-3 parenchymatic cells.

Material examined: Bolivia. Dpto. La Paz, Prov. Nor Yungas, Cota Pata, ca. 11 km NE of Unduavi, 16°18' S – 67°51' W, 3100 m, 22 Dec 1983 (fl.), Solomon & Moraes 11436 (SI).

Chusquea culeou Desv. (Fig. 7; Table 2)

Culm solid. Epidermis formed by a layer of sclerified cells with thick external wall. Subepidermal parenchyma formed by 6-7 layers of thick walled cells. Sclerenchyma surrounding the first cycle of peripheral vascular bundles; not interrupted by interfascicular parenchyma. Vascular bundles generally in 8 alternating cycles; developed protoxylem not observed in the most external cycle; phloem oriented toward the external face. Peripheral vascular bundles completely surrounded by sclerenchyma; transitional vascular bundles more or less surrounded by a continuous sclerenchymatic sheath with caps in connection with phloem, protoxylem and metaxylem more developed in relation to the phloem; central vascular bundles with sclerenchymatic caps more reduced. Transitional vascular bundles 402 µm wide and 536 µm deep; the central ones, 335 µm wide and 335 µm deep, ovate or broadly ovate. Parenchyma abundant among the transitional vascular bundles.

Material examined: Argentina. Neuquén, Dpto. Los Lagos, Villa La Angostura, Cerro Belvedere, ca. 1200 m, 18 Febr 1985 (fl.), *Rúgolo 1085* (SI).

The following archaeological material was identified as Chusquea culeou:
*Argentina. Neuquén, Dpto. Collón Cura, 40 km al SW de Piedra del Aguila, 40°23'21" S –

70°11'40" W. Sitio arqueológico Epullán Grande. Muestra 125.

Chusquea lorentziana Griseb. (Fig. 8; Table 2)

Culm solid. Epidermis formed by a layer of sclerified cells with thick external wall. Subepidermal parenchyma formed by 1-3 layers of thin-walled cells. Sclerenchyma surrounding the first cycle of peripheral vascular bundles. Vascular bundles in 5 alternating cycles; the most external without developed protoxylem; phloem always oriented toward the external face of the culm. Peripheral vascular bundles completely surrounded by sclerenchyma, more developed in connection with the protoxylem and the metaxylem; transitional vascular bundles surrounded by a continuous sclerenchymatic sheath that increases at protoxylem level forming a crescent-shaped cap of fibers; elliptic central vascular bundles, 340 µm wide and 374 µm deep, with a perivascular sheath of fibers and two remarkable crescent-shaped caps of similar development formed by 10-12 cells, thickest on phloem and protoxylem sides. Parenchyma abundant with starch grains among the transitional vascular bundles.

Material examined: Argentina. Tucumán, Dpto. Chicligasta, Cuesta del Clamillo, 1200-1800 m, Jan 1942 (fl.), Schreiter 11508 (SI); Dpto. Monteros, Quebrada de los Sosa, Casa de Piedra, 800 m, 26 Dec 1971 (fl.), *Krapovickas & Cristóbal 20452* (BAA).

The following archaeological material was identified as Chusquea lorentziana:
*Argentina. Catamarca, Dpto. Antofagasta de la Sierra, Antofagasta de la Sierra, 26°05' S – 67°25' W, 4100 m. Sitio arqueológico: Quebrada Seca 3, capa 2b, N° 39, 54, 422, 484 y 776; Antofagasta de la Sierra, 3500 m. Sitio arqueológico: Cueva Salamanca 1, capa 3, N° 33 J2D.

*Chusquea montana Phil.* (Figs. 9, 10; Table 2)

Culm solid. Epidermis formed by a layer of sclerified cells with thick external wall, continued by 3-4 layers of sclerified parenchymatic cells. Cortical sclerenchyma continuous and peripheral vascular bundles in formation. Vascular bundles in 9-10 alternating cycles; phloem always oriented toward the external face of the culm. Peripheral vascular bundles included in the
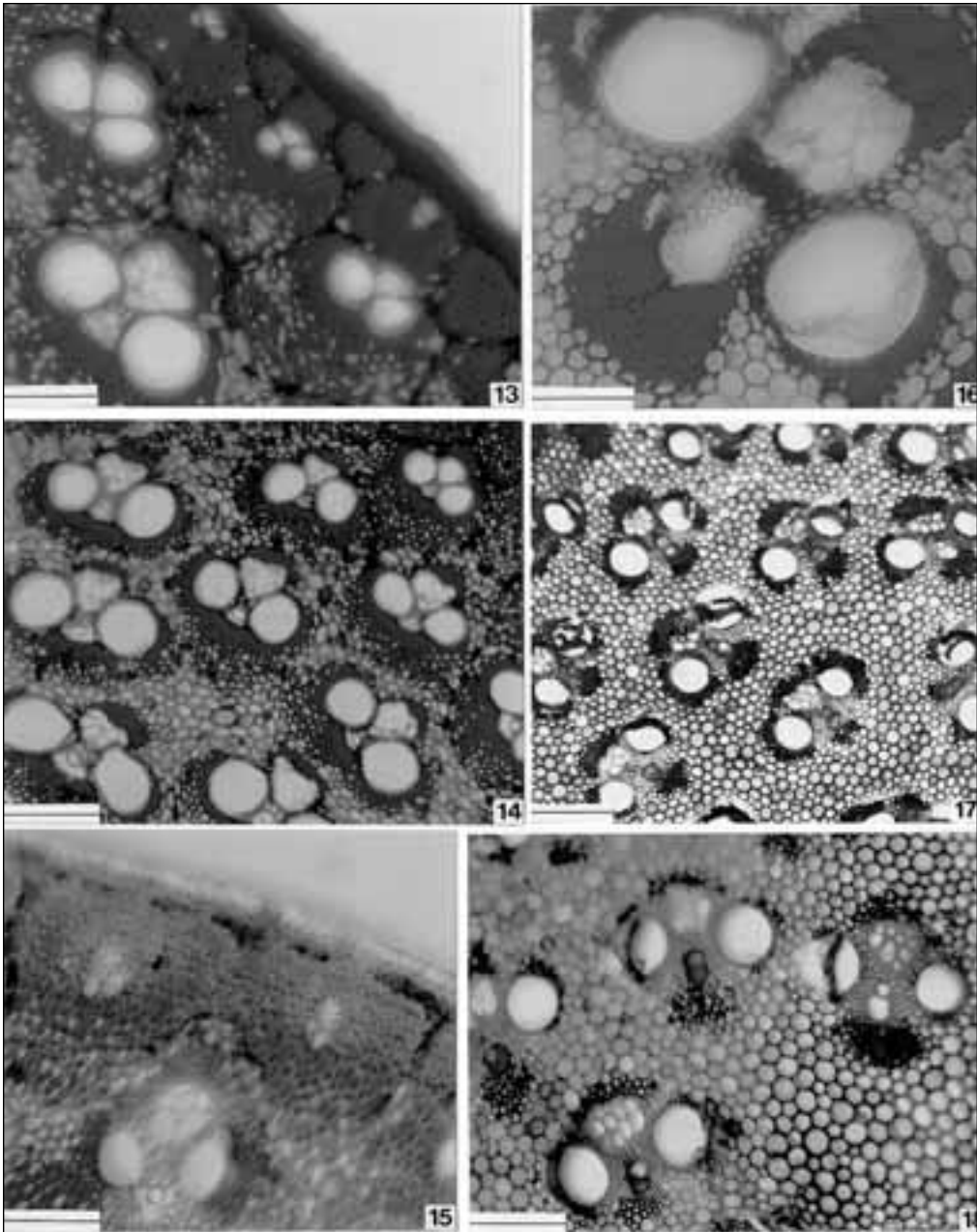
Figures 13-18. Culm cross sections light microscope micrographs. Figs. 13-14. *Merostachys clausenii (Porta 33),* scale bar = 400 μm. Fig. 13. Epidermis, peripheral and transitional vascular bundles. Fig. 14. Peripheral, transitional and central vascular bundles. Figs. 15-16. *Rhipidocladum harmonicum (Vargas 3260),* scale bar = 200 μm. Fig. 15. Epidermis and peripheral vascular bundles. Fig. 16. Central vascular bundle. Fig. 17. *Guadua chacoensis. (Rodríguez, M. F. s. n.., FAATECA FCEN 653).* Central vascular bundles. Sacale bar = 100 μm. Fig 18. *G. Trinii. (Rodríguez, M. F. s.n., FAATECA FCEN 654).* Central vascular bundles. Scale bar = 400 μm.
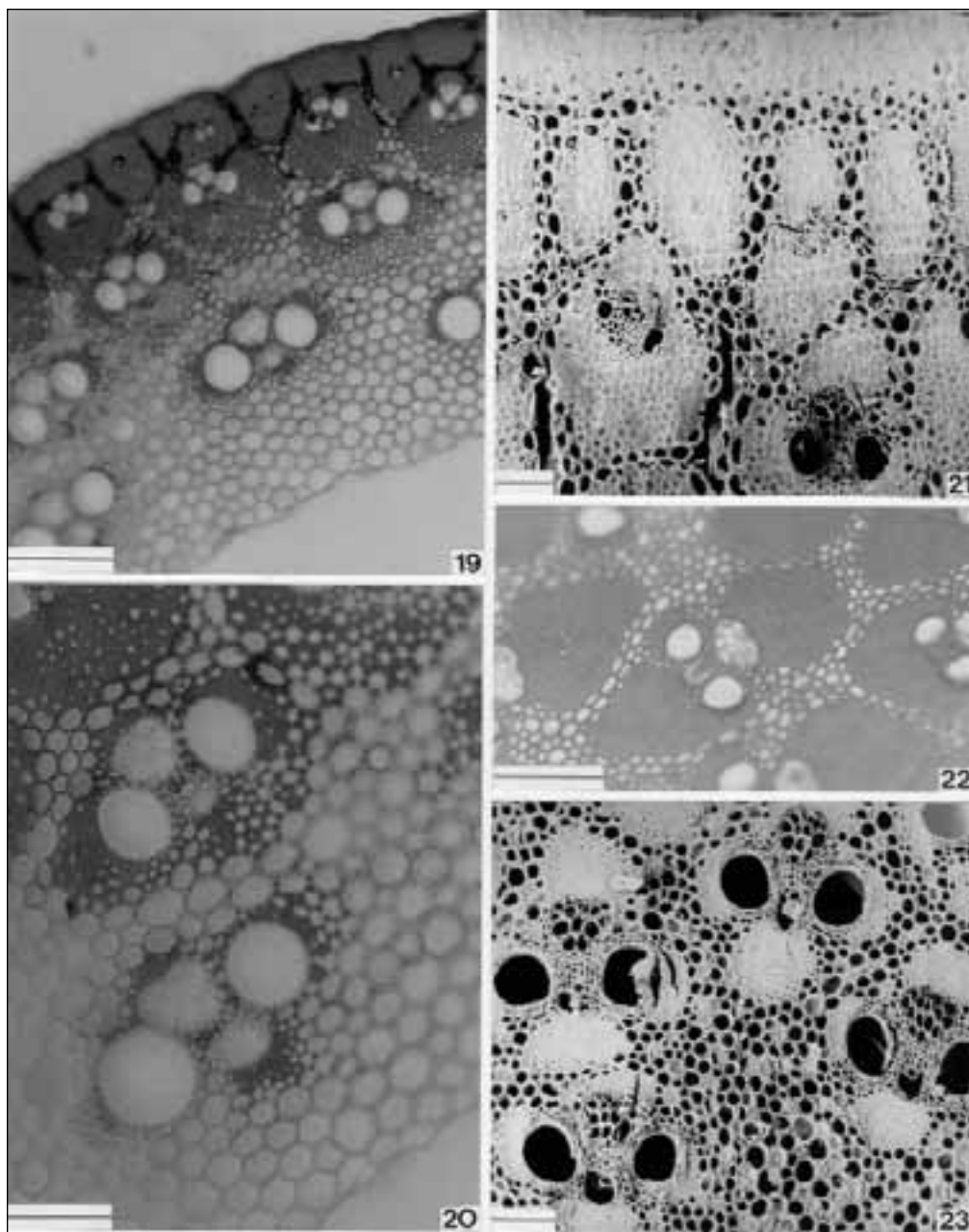
Figures 19-23. Culm cross sections. Figs. 19-20. *Rhipidocladum racemiflorum. (Hilgert & Gil 2367).* Light microscope micrographs. Fig. 19. General view. Scale bar = 400 μm. Fig. 20. Detail of transitional and central vascular bundles depressed. Scale bar = 200 μm. Figs. 21-23. *R. neumannii. (Sulekic & Cano 2053).* Fig. 21. Scanning electron micrograph. Epidermis and peripheral vascular bundles. Scale bar = 50 μm. Fig. 22. Light microscope micrograph. Detail of transitional vascular bundles. Scale bar = 400 μm. Fig. 23. Scanning electron micrograph. Central vascular bundles. Scale bar = 100 μm.

sclerenchyma; transitional vascular bundles surrounded by a continuous sclenchymatic sheath with caps in relation to the phloem, protoxylem and metaxylem; central vascular bundles depressed, 293 μm wide and 225 μm deep, perivascular sheath formed by 1-2 layers of fibers forming two crescent-shaped caps of 3 cells of thickness, with similar development in phloem and protoxylem levels. Parenchyma abundant.

Material examined: Argentina. Río Negro, Laguna de Frías, Refugio del Rigi, Nahuel Huapi, 19 Mar 1944, *I. Bernasconi 14780 (SI).*

Chusquea ramosissima Lindm. (Fig. 11; Table 2)

Culm solid. Epidermis formed by a single layer of papillate epidermal cells with thick external wall. Subepidermal parenchyma formed by 2-3 layers of thick-walled cells. Sclerenchyma surrounding the first cycle of peripheral vascular bundles. Vascular bundles in 5 alternating cycles. Peripheral vascular bundles surrounded by sclerenchyma, more developed in connection with phloem and metaxylem; transitional vascular bundles surrounded by a continuous sclerenchymatic sheath with caps in connection with phloem, protoxylem and metaxylem with more size in relation to the phloem; central vascular bundles subcircular, 100 μm wide and 124 μm deep, with a perivascular sheath formed by 2-4 layers of fibers, which form two crescent-shaped caps with 4-5 cells of thickness, in phloem and protoxylem sides, larger in connection with the protoxylem. Parenchyma abundant.

Material examined: Argentina. Misiones, Dpto. Cainguás, Puerto Rico, orilla del Arroyo Garuhapé, 12 Jul 1945 (fl.), *J. Hunziker 787* (SI).

Chusquea tenella Nees (Fig. 12; Table 2)

Culm hollow. Epidermis formed by a layer of papillate epidermal cells with thickness external wall. Parenchyma formed by 2-3 layers of sclerified cells. Sclerenchyma formed by packages of fibers alternating with peripheral vascular bundles in formation, surrounded by abundant sclerenchyma. Vascular bundles in 3 alternating cycles; phloem oriented towards the external face. Peripheral vascular bundles

surrounded by sclerenchyma, more developed in connection with phloem and protoxylem; transitional vascular bundles surrounded by a continuous sclerenchymatic sheath with caps in relation to the phloem, metaxylem and protoxylem; the last one larger than the others. Central vascular bundles depressed, 169 μm wide and 203 μm deep, perivascular sheath formed by 2-3 layers of fibers with two crescent-shaped caps in phloem and protoxylem sides, more developed around the phloem, with 5-6 layers of cells. Abundant parenchyma with cells of wide lacuna; vascular bundles separated by 3-8 parenchymatic cells.

Material examined: Argentina. Misiones, Dpto. San Pedro, San Pedro, 5 Apr 1944 (veg.), *Porta 208* (SI).

Colanthelia rhizantha (Hack.) Mc Clure (Figs. 4, 5, 6; Table 1)

Culm hollow. Epidermis formed by a single layer of sclerified cells with a thick external wall. Hypodermis represented by 2 layers of cells. Subepidermal parenchyma interrupted by the most external vascular bundle cycle; parenchyma scarcely developed. Sclerenchyma generally forming packages of fibers alternating with subepidermal vascular bundles. Vascular bundles in 5 cycles alternating with protoxylem and developed metaxylem; phloem oriented toward the external face. Peripheral vascular bundles completely surrounded by sclerenchyma, more developed in relation to the protoxylem and metaxylem; transitional vascular bundles surrounded by a continuous sclerenchymatic sheath that increases in the phloem side, protoxylem and metaxylem with 3 layers of cells; central vascular bundles depressed, 340 μm wide and 204 μm deep, with a perivascular sclerenchymatic sheath, one or two fiber layers on phloem and protoxylem sides. Parenchyma abundant among the transitional and central vascular bundles.

Material examined: Argentina. Misiones, Dpto. General Belgrano, Ruta 101, de Bernardo de Yrigoyen a San Antonio, Salto Andrecito. 26°12' S – 53°40' W. 570 m, 1 Mar 1995 (fl.), *Zuloaga et al. 5137* (SI).

Guadua chacoensis (Rojas Acosta) Londoño & P. M. Peterson (Fig. 17; Table 2)

Culm hollow. Epidermis formed by a single layer of papillate epidermal cells with thick external walls. Prickle hairs absent. Subepidermal parenchyma formed by 4-5 layers of thick-walled cells. Sclerenchyma continuous, surrounding the first cycle of peripheral vascular bundles. Vascular bundles in 7 alternating cycles; phloem oriented toward the external face in the peripheral vascular bundles, alternating one and another position in the inner ones. Peripheral vascular bundles surrounded by sclerenchyma, more developed in connection with the protoxylem and metaxylem; transitional and central vascular bundles surrounded by a discontinuous sclerenchymatic sheath, with 4 caps of similar size in relation to the phloem, protoxylem and metaxylem; central vascular bundles depressed, 578 μm wide and 476 μm deep. Parenchyma abundant among the vascular bundles.

Material examined: Argentina. Corrientes, Dpto. Capital, Riachuelo, ruta 12, 21 Dec 1974 (fl.), *Maruñak 635* (SI). Distrito Federal, Facultad de Agronomía, UBA, Cultivada en el Jardín Botánico, Sep 1997 (veg.), *M. F. Rodríguez s.n.* (Preparado: FAATECA 653, FCEN).

*Guadua paraguayan*a Döll (Table 2)

Culm solid. Epidermis with a layer of sclerified cells with thick external wall. Prickle hairs absent. Subpidermal parenchyma formed by 3-4 layers of sclerified cells. Sclerenchyma continuous, surrounding the first cycle of peripheral vascular bundles. Vascular bundles in 7 or more alternating cycles; phloem oriented toward the external face in the peripheral cycles, their position varied in the inner ones. Peripheral vascular bundles surrounded by sclerenchyma, more developed in connection with the protoxylem and phloem; transitional and central vascular bundles surrounded by sclerenchymatic sheath with 4 caps to level of phloem, protoxylem and metaxylem; sometimes more developed in connection with protoxylem and phloem in the transitional vascular bundles; sheath discontinuous in the last ones. Central vascular bundles subcircular,

204-221 μm wide and deep. Parenchyma more or less abundant among the vascular bundles, separated by 1-4 parenchymatic cells.

Material examined: Argentina. Corrientes, Isla del Paraná, frente a la isla Curuzú Chalí, 10 Apr 1968 (fl.), *Burkart et al. 26828* (SI).

Guadua trinii (Nees) Nees ex Rupr. (Fig. 18; Table 2)

Culm hollow. Epidermis formed by a layer of papillate epidermal cells with thick external walls; prickle hairs evident. Subepidermal parenchyma formed by 4-5 layers of thick walled cells. Sclerenchyma continuous, surrounding the first cycle of peripheral vascular bundles. Vascular bundles in 9-10 alternating cycles; phloem oriented toward the external face in the peripheral vascular bundles, in the inners alternating position. Peripheral vascular bundles surrounded by sclerenchyma, more developed in connection with protoxylem and metaxylem; transitional and central vascular bundles surrounded by a discontinuous sclerenchymatic sheath, with 4 caps of similar size in relation to phloem, protoxylem and metaxylem; central vascular bundles depressed, 374-391 μm wide and 272-340 μm deep. Parenchyma abundant among the vascular bundles.

Material examined: Argentina. Misiones, Dpto. Iguazú, Salto Iguazú, 12 Sep 1910 (veg.), *Rodríguez 481* (SI). Distrito Federal, Facultad de Agronomía, UBA, Cultivada en el Jardín Botánico, Sep 1997 (veg.), *M. F. Rodríguez s.n.* (Preparado: FAATECA 654, FCEN).

Merostachys clausenii Munro (Figs. 13, 14; Table 1)

Culm hollow. Epidermis formed by a layer of papillate epidermal cells with thick external walls; prickle hairs evident. Subepidermal sclerenchyma formed by packages of fibers surrounded by parenchyma and peripheral vascular bundles in formation with abundant sclerenchyma. Vascular bundles generally in 9 alternating cycles completely surrounded by sclerenchyma, more developed in connection with protoxylem and metaxylem; the transitional vascular bundles surrounded by a continuous

sclerenchymatic sheath, the central ones with a narrow perixylematic sheath and two caps of fibers, one linked with the protoxylem of 6-9 layers of cells and another with the phloem formed by 2-3 layers of cells. Central vascular bundles depressed, 374 μm wide and 272 μm deep. Scarce parenchyma among the vascular bundles, sometimes more abundant surrounding the medullar cavity, some cells with crystals.

Material examined: Argentina. Misiones, Dpto. Gral Belgrano, Ruta 101 de Bernardo de Yrigoyen a San Antonio, Salto Andrecito, 26°12' S 53°40', W 570 m, 1 Mar 1995 (veg.), *Zuloaga et al. 5139;* Dpto. Montecarlo, Colonia Montecarlo, 2 May 1943 (fl.), *Porta 33* (SI).

Merostachys multiramea Hack. (Table 1)

Culm hollow. Epidermis formed by a layer of papillate epidermal cells with thick external walls; prickle hairs evident. Subepidermal parenchyma with two layers of thick wall cells. Interfascicular parenchyma abundant among the peripheral vascular bundles. Vascular bundles generally in 7 alternating cycles. Similar peripheral and transitional vascular bundles; central vascular bundles depressed. Vascular bundle, 612 μm wide and 476 μm deep, with two caps of sclerenchymatic fibers linked with the protoxylem, metaxylem and phloem, more developed in the peripheral and transitional ones. Parenchyma abundant.

Material examined: Argentina. Misiones, Dpto. Iguazú, Reserva Forestal Parque Nacional Iguazú, 3 km al sur del cruce con ruta 101, próximo a la casa del guardaparque, 25°44' S 54°26'W, 1 Feb 1976 (fl.), *Romanczuk et al. 644* (SI). Brasil. Paraná, Río Itararé, Guaratuba, 23 Feb 1973 (fl.), *Kummrow 154* (SI).

Rhipidocladum harmonicum (Parodi) McClure (Figs. 15, 16; Table 1)

Culm hollow. Epidermis formed by a layer of papillate epidermal cells with thick external wall. Subepidermal parenchyma of 1-2 layers of cells. Sclerenchyma formed by packages of fibers. Parenchyma scarce, 1-2 layers of cells among the peripheral vascular bundles, cells with thick walls and pits. Vascular bundles in 4-5 alternating cycles; new peripheral vascular bundles surrounded by a thick sclerenchymatic

sheath with incipient conduction tissues; transitional vascular bundles with a continuous sclerenchymatic sheath, more developed in connection with protoxylem and metaxylem; central vascular bundles with a continuous sclerenchymatic sheath with 1-3 cells, small cap linked with the protoxylem and the phloem; transitional vascular bundles 340 μm wide and 374 μm deep, the central ones subcircular, 510 μm wide and 340 μm deep. Parenchyma scarce among the peripheral and transitional vascular bundles.

Material examined: Bolivia. Utilizado para fabricación de instrumentos, Oct.1999 (veg.), *Sampedro del Río s.n.* (SI 28462). Perú. Dpto. Cuzco, Prov. Convención, Pintobamba, 2700 m, 3-4 Mar 1943 (fl.), *Vargas 3260* (SI).

Rhipidocladum neumannii Suleckic, Rúgolo & L. G. Clark (Figs. 21, 22, 23; Table 1)

Culm hollow. Epidermis formed by a layer of papillate epidermal cells with thick external walls. Subepidermal sclerenchyma with 3-4 layers of fibers with thick walls and pits. Interfascicular parenchyma scarce, with 1-2 layers of cells among the peripheral vascular bundles. Vascular bundles in 9-10 alternating cycles; peripheral vascular bundles in development surrounded by a thick sclerenchymatic sheath, with incipient conduction tissues; transitional vascular bundles with 4 caps of sclerenchymatic fibers, two crescent-shaped link with the metaxylem; in relation to the protoxylem and the phloem two subtriangular caps with 3-4 layers of cells; central vascular bundles with caps in connection with protoxylem and phloem; the transitional vascular bundles 340 μm wide and 680 μm deep and the central ones 476 μm wide and 476 μm deep. Parenchyma scarce among the peripheral and transitional vascular bundles.

Material examined: Argentina. Río Negro, Dpto. Los Lagos, Lago Nahuel Huapi, Laguna de Frías, Feb 1948 (fl.), *Parodi 15682* (SI). Salta, Dpto. Orán, Finca Arrazayal, aprox. 20 km al NW de Agua Blanca, 600-700 m, 23 Apr 1998 (fl.), *Sulekic & Cano 2053* (SI). The following archaeological material was identified as *Rhipidocladum neumannii:* *Argentina. Catamarca, Dpto. Antofagasta de

la Sierra, Antofagasta de la Sierra, 26°05' S 67°25' W, 4100 m. Sitio arqueológico: Quebrada Seca 3, capa 2b, N° 1020 y 1038.

Rhipidocladum racemiflorum (Steud.) McClure (Figs. 19, 20; Table 2)

Culm hollow. Epidermis formed by a layer of papillate epidermal cells with thick external wall. Subepidermal sclerenchyma with packages of fibers surrounded by parenchymatic and peripheral vascular bundles in formation surrounded by abundant sclerenchyma. Interfascicular parenchyma scarce, reduced to 1-2 layers of cells among the peripheral vascular bundles, cells with thick walls and pits. Vascular bundles generally in 4 alternating cycles; peripheral vascular bundles in development surrounded by a thick scleremnchymatic sheath, with incipient conduction tissues; transitional vascular bundles surrounded by a continuous crescent-shaped sclerenchymatic cap less developed on the phloem side and broadly developed in connection with protoxylem and metaxylem; central vascular bundles surrounded by a continuous sclerenchymatic sheath, 1-3 cell thick, small cap linked with the protoxylem; transitional vascular bundles 204-238 µm wide and 170-204 µm deep; central vascular bundles depressed, 238 µm wide and 153-170 µm deep. Parenchyma scarce among the peripheral and transitional vascular bundles.

Material examined: Argentina. Salta, Dpto. Santa Victoria, Parque Nacional Baritú, camino hacia termas, 22 Jun 1999 (veg.), *Hilgert & Hill 2367* (SI); Dpto. Santa Victoria, El Lipeo, 11 Feb 2001 (fl.), *Sulekic, Cano & Villagrán 3199* (SI). Bolivia. Dpto. La Paz, Prov. Sur Yungas, cerranía de Marimonos, 15°30' S 67°10' W, 25 Jul 1987 (fl.), *Killeen 2628* (SI).

Key based on culm characters in cross section
1. Culm hollow; subepidermal parenchyma present or absent. – (2)
1. Culm solid; subepidermal parenchyma present. – (12)
2 (1). Subepidermal parenchyma present; cortical sclerenchyma not linked with the epidermis or absent. – (3)
2. Subepidermal parenchyma absent; cortical sclerenchyma linked with the epidermis or the hypodermis. – (7)
3 (2). Central and transitional vascular bundles with the phloem oriented in different directions; central vascular bundles depressed. – (4)
3. Central and transitional vascular bundles with the phloem always oriented toward the external face; central vascular bundles depressed, broadly ovate, subcircular, elliptic or ovate. – (5)
4 (3). Vascular bundles in 7 alternating cycles. – *Guadua chacoensis*
4. Vascular bundles in 9-10 alternating cycles. – *Guadua trinii*
5 (3). Cortical sclerenchyma absent; vascular bundles with two caps of sclerenchymatic fibers, one linked with the protoxylem and the metaxylem and another with the phloem; central vascular bundles depressed. – *Merostachys multiramea*
5. Cortical sclerenchyma present; central vascular bundles broadly ovate, depressed, elliptic or subcircular. – (6)
6 (5). Vascular bundles generally in 3 alternating cycles; central vascular bundles depressed with perivascular sclerenchymatic sheath more developed near the phloem (5-6 layers of cells), smaller near the protoxylem. – *Chusquea tenella*
6. Vascular bundles in 4-10 cycles; central vascular bundles with perivascular sheath more or less even in thickness. – (7)
7 (6). Hypodermis present; fundamental parenchyma abundant among the transitional and central vascular bundles; central vascular bundles depressed. – *Colanthelia rhizantha*
7. Hypodermis absent; fundamental parenchyma scarce among the transitional and central vascular bundles; central vascular bundles broadly ovate, depressed, elliptic or subcircular. – (8)
8 (7). Vascular bundles in 4-7 alternating cycles. – (9)
8. Vascular bundles in 9-10 alternating cycles. – (11)

9 (8). Transitional and central vascular bundles similar, broadly ovate, surrounded by a continuous sclerenchymatic sheath with more than 5 layers of cells, thicker near the phloem and protoxylem. – *Aulonemia queko*

9.   Transitional vascular bundles with a continuous sclerenchymatic sheath more developed nera the protoxylem and metaxylem; central vascular bundles surrounded by a continuous sclerenchymatic sheath, 1-3 cells thick, more developed near the protoxylem and the phloem. – (10)

10 (9). Culm of 1 cm in diam. or bigger; vascular bundles subcircular, approximately 500 μm wide and 350 μm deep. – *Rhipidocladum harmonicum*

10.   Culm smaller than 1 cm in diam., generally 0.7 cm; central vascular bundles depressed, approximately 240 μm wide and 150-170 μm deep. – *Rhipidocladum racemiflorum*

11 (8). Central vascular bundles depressed with a narrow perixylematic sheath and two caps of fibers, one linked with the protoxylem with 6-9 layers of cells and the other with the phloem with 2-3 layers of cells. – *Merostachys clausenii*

11.   Central vascular bundles ovate with four caps of fibers, two crescent-shaped linked with the metaxylem and two subtriangular in connection with the protoxylem and the phloem. – *Rhipidocladum neumannii*

12 (2). Subepidermal parenchyma formed by 1-3 layers of thick-walled cells; central vascular bundles elliptic; transitional vascular bundles with the phloem always oriented toward the external face. – *Chusquea lorentziana*

12.   Subepidermal parenchyma formed by 2-7 layers of thick-walled cells, in some cases sclerified; central and transitional vascular bundles depressed or subcircular. – (13)

13 (12). Subepidermal parenchyma formed by 6-7 layers of thick-walled cells; central and transitional vascular bundles ovate with the phloem oriented in different directions, primarily in the transitional ones. – *Chusquea culeou*

13.   Subepidermal parenchyma formed by 2-4 layers of cells; central and transitional vascular bundles depressed or subcircular. – (14)

14 (13). Subepidermal parenchymatic cells sclerified; central and transitional vascular bundles with the phloem oriented toward the external face or in different directions. – (15)

14.   Subepidermal parenchymatic cells non – sclerified; central and transitional vascular bundles with the phloem oriented toward the external face; central vascular bundles subcircular. – *Chusquea ramosissima*

15 (14). Central vascular bundles depressed, approximately 290 μm wide and 220 μm deep surrounded by a sclerenchymatic sheath of 1-2 layers of cells. – *Chusquea montana*

15.   Central vascular bundles subcircular, approximately 200-220 μm wide and deep surrounded by a sclerenchymatic sheath which forms two caps of 4-5 layers of cells at level of the phloem and the protoxylem. – *Guadua paraguayana*

DISCUSSION

The distribution of the vascular and sclerenchymatic tisuues in the vascular bundles (Tables 1, 2) that we encountered correspond to the type I (subtype Ib and Ic) proposed by Liese & Grosser (2000). The epidermis is represented by a single layer of sclerified cells. In cross section it is not easy to distinguish the different elements described previously for each one of the taxa (Rúgolo de Agrasar & Rodríguez 2002). Prickle hairs and papillae are visualized in cross section. Hypodermis was observed in *Colanthelia rhizantha* (Fig. 4). Cortical parenchyma is scarce and sclerified or

it is absent in several species (Figs. 13, 15, 19, 21). In many species with solid culms (*Chusquea spp.* and *Guadua paraguayana*) or hollow (*Aulonemia queko, Merostachys multirramea* and *Rhipidocladum harmonicum*) the cortical parenchyma is present. The amount of the cortical sclerenchyma varies in the different genera, but it generally represents a third of the radius of the culm. The sclerenchyma can be cortical or it can be developed linking with the vascular bundles; it is represented by fibers with thick walls, in many cases with a small lacuna and evident pits (Figs. 4, 13, 15, 19, 21). The sclerenchyma associated with the vascular bundles forms bands or girders with varied form and distribution (Tables 1, 2).

The vascular bundles have more or less developed phloem, two metaxylem vessels, protoxylem, xylem parenchyma and sclerenchyma sheaths associated with the phloem and the xylem, surrounding the vascular bundles and defining their contour. The size and form of the vascular bundles vary from the periphery toward the center of the culm (Figs. 11, 19). In relation to these characteristics, types of such vascular bundles could differ as peripheral, transitional and central (Tables 1, 2). It is interesting to highlight that, in the studied material of *Merostachys multiramea,* peripheral and transitional vascular bundles are similar (Table 1), while in other species such as *Rhipidocladum neumannii,* the transitional vascular bundles differ from the remaining ones because of the abundance of sclerenchymatic tissue (Fig. 22; Table 1).

The peripheral vascular bundles generally are embedded in the cortical sclerenchyma, the transitional and the central ones in the parenchyma. The protoxylem lacuna is visualized in all the vascular bundles, but it is not evident in the peripheral vascular bundles of *Chusquea culeou* and *Guadua chacoensis* (Table 2). The phloem tissue is incipient or has little development in the peripheral vascular bundles and increases toward the central ones (Tables 1, 2). The sclerenchyma however is more abundant in the peripheral vascular bundles, with observable differences at generic and specific levels in connection with the distribution of fibers in relation to these vascular bundles

(Tables 1, 2). In some cases the sclerenchymatic sheath is continuous and more or less uniform as in *Aulonemia queko, Chusquea culeou* and *C. tenella* (Figs. 1, 2, 7, 12); in other cases greater development of the sclerenchyma is observed in relation to the protoxylem and the metaxylem, as in *Colanthelia rhizantha, Chusquea lorentziana* and *Guadua trinii* (Figs. 5, 6, 8, 18). Less frequently, the sclerenchyma is more developed in connection with the phloem as in *Chusquea ramosissima* (Fig. 11). Conversely, in most of the species analyzed the phloem is located toward the external face; and in some species, e.g., *Guadua chacoensis, G. paraguayana* and *G. trinii,* the position of this tissue is variable (Figs. 17, 18).

The metaxylem vessels are visualized clearly in the peripheral, transitional and central vascular bundles (Tables 1, 2). In some cases, like in *Guadua chacoensis,* the size generally increases towards the center (Fig. 17, Table 2).

The outline of the peripheral and transitional vascular bundles register variations inside certain ranges in each one of the studied taxa. The central vascular bundles show a defined and more constant form that allows a more consistent evaluation of their characteristics. For example, *Colanthelia rhizantha, Chusquea tenella, Guadua chacoensis, G. trinii, Merostachys multiramea* and *Rhipidocladum racemiflorum* among others, have depressed vascular bundles (Figs. 6, 12, 17, 18, 19, 20); ovate vascular bundles were observed in *Aulonemia queko, Chusquea culeou* and *Rhipdocladum neumannii* (Figs. 2, 7, 23); subcircular vascular bundles in *C. ramosissima* and *R. harmonicum* (Figs, 11, 16); elliptic vascular bundles in *C. lorentziana* (Fig. 8) and isodiametric vascular bundles in *Guadua paraguayana* (Tables 1, 2).

The parenchyma is distributed among the vascular bundles; its cells have more or less thick walls and occasionally grains of starch are observed, as in *Chusquea lorentziana.* The species with solid culms have a medullar parenchyma. The species with hollow culms occasionally present the most internal layers cells with crystals surrounding the central cavity *(Merostachys clausenii).*

The included taxa in this study have been classified into three subtribes (Judziewicz *et al.* 1999): Arthrostylidiinae *(Aulonemia, Colanthelia, Merostachys* and *Rhipidocladum*), Chusqueinae *(Chusquea)* and Guaduinae *(Guadua)* (Tables 1, 2). The analyzed species of the subtribe Chusqueinae have solid culms, except *Chusquea tenella,* with develops subepidermal parenchyma. Those of the tribes Arthrostylidiinae and Guaduinae have hollow culms (except *Guadua paraguayana* which is solid) and may or may not have cortical parenchyma; however in the subtribe Guaduinae the transitional and central vascular bundles exhibit the phloem oriented in different directions, a character not observed in species of the subtribe Arthrostylidiinae. These brief considerations allow us to suggest that a significant correlation does not exist among the culm anatomical characters of the three subtribes taken into consideration, which have been defined on the basis of other morphological and reproductive characters.

The genus *Guadua* comprises 26 species (Clark 2001) of which *G. angustifolia* has been studied from the point of view of the caulinar anatomy (Metcalfe 1960; Sekar & Balasubramanian 1994, Londoño *et al.* 2002). In the present study, all three species of *Guadua* studied were similar in relation to the presence of sclerified cortical parenchyma and the form of the vascular bundles (Figs. 17, 18; Table 2).

ACKNOWLEDGMENTS

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Morphology and taxonomy of the Top End Bamboo
Bambusa arnhemica F. Muell.,
a little-known bamboo from northern Australia

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The first comprehensive morphological description of *Bambusa arnhemica,* a little-known species from the monsoonal tropics of northern Australia, is provided. *Bambusa arnhemica* is a medium-sized, pachymorph, unicaespitose and thorny bamboo. Its affinities remain unclear, although its inclusion in *Bambusa* is confirmed on the basis of a range of traits including the pseudospikelet, floret, caryopsis and thorny basal branches. Features of the species include: culm sheaths that lack auricle lobes; trimerous, thorny basal branches that contrast with the thornless, unrestricted branch complements of the upper culm; slender, rigid thorns that rarely give rise to leafy shoots; the formation of caducous leaf-like inflorescence bracts immediately prior to flowering, and culm shoots of highly variable colour. No synonymous Australian or Asian species could be identified, and it is concluded that *B. arnhemica* is endemic to Australia.

Since being named late in the 19th century (Mueller 1886), the northern Australian bamboo *Bambusa arnhemica* F. Muell. has received remarkably little scientific attention. Its has not been described adequately, its affinities are unknown, and Soderstrom and Calderon (1979) queried its placement in Bambusa. The suggestion that more than one species of bamboo may occur within the area occupied by *B. arnhemica* was made as a footnote to the original description (Mueller 1886) and has never been formally addressed or resolved (but see Muller 1997). Although Mueller described it as an endemic species, and this is the official position (e.g. Liddle et al. 1994, Cowie *et al.* 2000), the notion has never been formally examined. Indeed, it is popularly held by some to be a recent introduction to northern Australia from Asia, perhaps transported by Macassan trepangers, though Macknight (1976) refuted the latter suggestion, pointing out that *B. arnhemica* is not associated with Macassan camp sites along the northern Australian coast.

Mueller's description was of less than 200 words and the species was not illustrated. However, fertile as well as vegetative material was described, contrary to suggestions by Soderstrom and Calderon (1979), Spencer (1986) and Ohrnberger (1999). Cowie *et al.* (2000) illustrated leaves, the flowering branch, spikelets, lemma, palea and seed, and Muller (1997) illustrated culm sheaths. However, the rhizome, branch bud, branching pattern and culm shoot, structures fundamental to bamboo taxonomy, remain to be described.

Bambusa arnhemica is thought to be endemic to the sparsely-populated, monsoonal tropical "Top End" of the Northern Territory, Australia. It is largely confined to watercourses (Fig. 1a) embedded in the wooded savanna environment of the high rainfall (1,200 – 1,800 mm mean annual rainfall) north-western portion of the region (Fig. 2), where it commonly occurs as a mono-dominant or co-dominant in riparian forest or vine-thicket. Much less frequently, it occurs in non-riparian vine-thicket on rocky hillsides (Fig. 1b) and coastal headlands. It has a very limited and recent history in cultivation (Hearne 1975, Cusack 1999, Wood 2001). In this paper, I provide a morphological description of the taxon thanks to recent partial mass-flowering rendering both vegetative and flowering material available. This information is then applied to a consideration of its generic placement and endemicity. These notes and data are intended to provide context for further studies into the ecology, management and biogeographic history of the taxon.

MATERIALS AND METHODS

This description is based on an examination of leafy and flowering clumps throughout the range of the taxon, combined with more detailed, site-specific observations. Vegetative material and data were mostly obtained from Mary River Park (12°55'S, 131°39'E). Inflorescence and flower structure is described from fresh collections from Mt Bundy Station (13°14'S, 131°08'E) on the Adelaide River, as well as observations elsewhere in the Adelaide River catchment. Clump heights were measured with a clinometer and tape measure at the 22 of 38 sites selected for study of environmental attributes (to be reported elsewhere) at which there had been no recent mass-flowering. The 38 sites were widely dispersed throughout the range of the species, but the strong spatial aggregation of flowering has unavoidably structured the spatial availability of vegetatively-mature sites.

Culm dimensions were measured at Mary River Park. The large sample of diameters were measured with a diameter tape at the middle of the internode nearest 1.3 m above the ground. Every culm of 39 clumps in a 90 m long by 15-25 m wide riparian stand on the fringe of a billabong (stranded meander) of the Mary River selected for a detailed demographic study (to be reported elsewhere) was measured except that six waterside clumps were excluded for safety reasons, the billabong being inhabited by Saltwater Crocodiles *Crocodylus porosus.* Three culms from separate clumps, selected for intactness and accessibility, were felled. For each internode, the culm diameter and internode length were measured to 0.1 cm. Every fifth internode was then cut, the wall thickness measured to 0.1 mm using Bergeon vernier callipers at three points, and the results averaged. In the description of branching orders, the culm is considered to be order zero.

Seed was collected at six sites in the upper tributaries of the Adelaide and Daly River systems in November 2000, the samples mixed thoroughly and then sub-sampled. After removal of the lemma, palea and rachilla, seeds were weighed air-dry to 0.1 mg on Sartorius scales, and measured to 0.1 mm using Bergeon vernier callipers, oven-dried for 24 hours at 70°C and weighed again.

RESULTS

Amended description based on living material

Bambusa arnhemica F. Mueller in Australasian Journal of Pharmacy 1: 447; Type: Australia, On the Daly-River, M. Holtze *s.n.*

Terrestrial, clumping, rarely epiphytic (Franklin 2003), (10-) 12-18 (-21) m tall (Fig. 3a), with fewer than 10 to more than 100 live culms per clump, the clump often compact and unicaespitose (Fig. 4) but sometimes open and/or not always distinguishable, facultatively deciduous. Rhizomes: short-necked pachymorph; to 30 (-40) cm long by 10 cm in diameter, sub-fusiform, slightly dorso-ventrally compressed, broadest a short distance below the culm base (Fig. 5*h*), the primary roots to 4 mm diameter. Culm shoots variously shiny mid-green, dull pale green, dull pale green tinged maroon, or violet-grey (Fig. 5*i*). Culm, erect and straight when young except for the somewhat arching slender tip, or somewhat zig-zag on young clumps, arching progressively with age sometimes to the ground, (3-) 6-8 (-13) cm diameter at (DBH) 1.3 m, or less when damaged or stressed, highly variable within (e.g. Fig. 6) and between sites, tapering progressively from ground level (Fig. 3*c*), hollow; walls to 3 cm thick (Fig. 3*d*); nodes to more than 80 per culm (Fig. 3), sheath scar prominent and slightly expanded above the internode to form a collar around the derived internode, depressed below the branch buds, a supra-nodal ridge generally absent but may be present on smaller branches, lower nodes often bearing root primordia which may develop into a mat of aerial roots to 5 cm long. Branch buds solitary, present at all nodes, broadly triangular to obcordate, to 37 mm long by 54 mm wide; prophylla united, with lateral wings sometimes fringed with hairs on each side (Fig. 5*d*). Internodes glabrous, or with scattered silky hairs when young, cylindrical, almost circular in cross-section, smooth, uniformly darkish glossy green or sometimes glaucous on young culms and becoming olive-green with age, to 30 (-43) cm long (Fig 3*b*), longest just below the mid-culm. Culm leaves with their sheaths to 30 (-38) cm long by 30 cm across the base, arched-convex at apex,

with minute pale hairs when young becoming glabrous to glabrate when mature, striate with fine venation, drying to a thick, papery texture smooth on the inside and corrugate on the outside, varying little in form along the length of culm, mostly shed shortly after culm elongation but lower ones persisting for up to several years; ligule scarcely developed to 5 mm long, forming a low curved or sometimes a higher and pointed arch, stiff, sometimes with stiff bristles to 1 mm long in the middle; blade erect, narrowly triangular, to 15 cm tall by 5.5 (-9) cm wide at base, with its base often with a slight and corrugate neck, roughly striate with fine venation on both surfaces, glabrous or almost so on the outer surface, the inner surface with an abundance of appressed, bristle-like opaque hairs along the veins and a sparse cover of minute, dark brown, erect hairs between the veins, obscurely toothed on the lower margins, auricles rudimentary and grading into a narrow tapered blade shoulder which is often corrugate; the lower margin of the blade, its shoulder and sometimes also the upper margin of the sheath with bristles to 10 mm long (Fig. 5*b,c*). Culm branches absent from the lowest culm nodes to c. 0.5 m and usually from a 2-8 m section about and below the mid-culm, lower branches may be scattered or altogether lacking, or so regularly and sufficiently developed as to form a thicket around the clump base, lower and upper branches morphologically well-differentiated but with some intergradation, upper branch complements of 2-4 (-5) orders, of unrestricted monoclade form (sensu McClure 1973 per Wong 1995) (Fig. 5*e*) or trimerous around the mid-culm, not spinose, primary branches somewhat ascending or almost perpendicular to the culm, to 4 m in length, basal branches of 2-3 (-5) orders, usually three per node, the central branch dominant, to 4 m in length, more or less perpendicular to the culm, the lateral branches equal and almost perpendicular to it (Fig. 5*f*), but often reduced at the culm nodes and sometimes increased near the tips, the inner part of the branch system rigid with the smaller branches forming thorns, the outer part flexuose and sparingly leafy with small foliage leaves, the thorns slender, rigid,

straight or slightly recurved, to 10 cm long, often multi-nodal and then bearing secondary thorns but rarely leafy shoots at the nodes (Fig. 5*g*). Foliage leaves with their sheath striate, yellow to yellow-green, finely fringed, finely pubescent when young with scattered hairs persisting mainly along the central vein, a cupule prominent, with a raised rim, the ligule often covered by chaffy scales dorsally to 1 mm or exceptionally to 3 mm long, with long cilia, at times reduced to a short fringe or ragged edge, the auricles on new growth comprising *ca.* 5 filiform lobes, each to 2 mm, usually caduceus; pseudopetiole 2-4 by 1-2 mm, flattened dorso-ventrally, yellow, pubescent above and below, blade linear-lanceolate to lanceolate or narrowly elliptical when larger, with a rounded base and acuminate tip (Fig. 5*a*), 5-20 by 0.8-3.0 cm, green, somewhat pubescent when young, the pubescence persisting sparsely on the undersurface, the central vein depressed above and raised below, central and secondary veins yellow or brown, secondary veins scarcely distinguishable from the tertiary above but quite distinct below, tertiary veins green, transverse veins not apparent. Fertile branches to 2.5 m long and with up to 30 nodes, simple or sparingly branched at the lower nodes, sometimes complexly branched (Fig. 7*b*), arising by rapid unbranched apical extension of leafy branchlets and terminating in a pseudospikelet, but subsequently incorporating the original branchlet and often branching from the original growth (the *flowering long-shoots of Wong* 1995), onset of flowering accompanied by leaf loss, new growth of flowering branches support caducous leaf-like bracts (the inflorescence sheath blades of Wong 1995) to 8 by 1 cm but mostly less than 4.5 by 0.6 cm prior to development of the inflorescence (Fig. 5*j*). Inflorescence (synflorescence) an irregular iterauctant cluster of 1-25 pseudospikelets. Pseudospikelets linear, slightly laterally compressed, to 45 (-70) mm long, comprising 2-4 glumes and up to 16 florets (Fig. 5*f*), the florets variously bisexual, male or sterile; fertile and especially bisexual florets mostly in the lower section of the spikelet, bisexual florets commonly more than

one per spikelet, prophylls to 3 mm, lacking obvious keels or sometimes with a single, central keel, often oblique, the lateral wings fringed with cilia, glumes boat-shaped, acute, glabrous or somewhat ciliate and with scattered pale hairs, unequal, the longest 4.5-8 mm in length and with *ca.* 15 raised veins on the abaxial surface, the central vein (keel) slightly more prominent, rachilla pubescent to densely hairy, flattened, jointed below the lemma; internodes 2-3 mm long, inflated below the joint. Florets bisexual or male or sterile: male and sterile florets similar externally, somewhat reduced above; bisexual florets widely expanded at anthesis, exposing the stigmas and anthers at the same time, lemmas 7-9 mm long, acute to acuminate, similar in venation and texture to the empty glumes (Fig. 5*g*), palea of similar length or slightly exceeding the lemma, acute to acuminate, two-keeled and with strongly incurved margins, strongly ciliate on the upper portion of the keels, the inner surface glabrous (Fig. 5*h,i*), the entire pistil and its subtending lodicules translucent white, the ovary obovoid with scattered short cilia, *c.* 2 x 1 mm, the stigmas 3, plumose, marginally exerted at maturity (Fig. 5*l*), the stamens 6, with free exerted slender filaments to c. 10 mm long, anthers 5-6 mm long, two-celled and emarginate with the distal 15% of each cell opening at anthesis, lemon-yellow at anthesis, drying straw-coloured (Fig. 5*k*), the lodicules usually 3, to 3 mm long, long-ciliate (Fig. 5*m*). Caryopses shed individually with a section of rachilla attached, or as loosely-connected sections of the spikelet disarticulating above the glumes, 6.2-9.1 by 1.7-2.4 mm and 7.4-26.9 mg oven-dry (Table 1), ellipsoid, broader laterally than dorso-ventrally and broadest a little below the middle, grooved prominently on the ventral surface and finely dorsally, with a short stout and blunt beak (Fig. 5*c,d,e*). Seedlings observed with an initial culms 10-25 cm tall and 0.6-1.0 mm in diameter at the base, unbranched, with 6-10 leaves to 60 by 10 mm and 0-2 leafless nodes below. Flowering gregariously, anecdotal records (unpubl. data) suggesting a flowering cycle of 41-51 years, strictly semelparous (mono-carpic), reproducing freely from seed.

Table 1: Weight and dimensions of seed of the bamboo Bambusa arnhemica.
Mean weights are for a pooled sample of 100 seeds and weight ranges from 20 individual seeds. Length and widths are for 20 air-dried seeds.

Parameter	Mean	Range
Weight, air-dry	19.3 mg	11.4 – 31.0 mg
Weight, oven-dry	17.5 mg	7.4 – 26.9 mg
Length	7.6 mm	6.2 – 9.1 mm
Width, dorso-ventral	1.7 mm	1.3 – 2.0 mm
Width, lateral	2.1 mm	1.7 – 2.4 mm

DISCUSSION

This description concords with and substantially extends those provided by Mueller (1886), Muller (1997) and Cowie *et al.* (2000). Features of the species include rudimentary (unlobed) culm sheath auricles, caducous leaf-like inflorescence sheaths, and the presence and arrangement of the thorns including their restriction to the basal branches. None of these features have previously been reported in the scientific literature (but see popular works by

Figure 1. Natural occurrences of *Bambusa arnhemica* in northern Australia: *a.* mono-dominant riparian stand, Mary River; *b.* deciduous vine-thicket stand on rocky hillside, Mt. Paqualin.
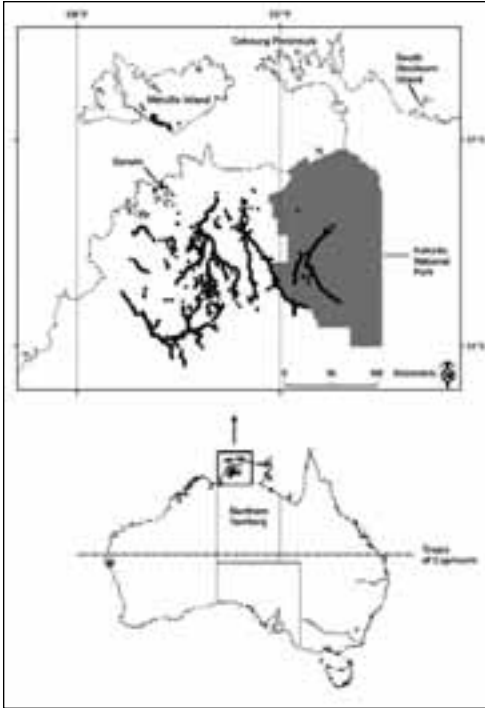
Figure 2. Distribution of *Bambusa arnhemica* (black dots), based on 1601 locations identified by the author during ground, boat and air surveys. Note the predominance of linear stands, which are associated with watercourses. Map prepared by Daniel McIntyre.

Brock 1993 and Muller 1997), herbarium material being confined to leaves and inflorescences. Mueller was apparently unfamiliar with the species in the field, his description being based on material sent by Holtze, a local collector.

I can find no evidence to support suggestions (Mueller 1886, Bindon 1991, Spencer 1986, various current observers pers. comm.) that *B. arnhemica* comprises more than one taxon, or that a second species is present in the area, an opinion in concordance with that of Muller (1997). Morphological variation, particularly in the development of the basal branches and colour of the culm shoot, is considerable but gradational. One basis given for these suggestions is ecological: that whilst most *B. arnhemica* is riparian in occurrence, a small number of stands occur on rocky hillsides and coastal headlands. However, no absolute morphological variation is evident, though non-riparian *B. arnhemica* is shorter with smaller culm diameters, presumably

reflecting harsher growing conditions. Furthermore, preliminary AFLP analysis of 27 polymorphic bands (Isagi, Tsukagoshi and Franklin unpubl. data) reveals no genetic dichotomy between riparian and non-riparian stands.

Approximately 140 species are attributed to *Bambusa* Schreb. (Ohrnberger 1999). Recent publications concerning its circumscription and relationships (Wong 1993a, Stapleton 1994, Widjaja 1997, Bedell 1997, Zhu Shilin *et al.* undated) emphasize a wide range of vegetative and floral traits with little agreement as to the definitive characters. Amongst Asian bamboos, thorny basal branches are unique to *Bambusa* (McClure 1966). Genetic analyses suggest that *Bambusa* is close to *Gigantochloa* and *Dendrocalamus* (Watanabe *et al.* 1994, Loh *et al.* 2000). It may be distinguished from *Dendrocalamus* by its three stigmas, three lodicules, clustered inflorescence, linear many-flowered pseudospikelets, presence of basal branching, and small leaves lacking obvious transverse venation, from *Gigantochloa* by the free filaments, clustered inflorescence, pale glume hairs, ovoid caryopsis, presence of basal branching and small leaves (Bedell 1997, Zhu Shilin *et al.* undated), and from both by its long rachilla internodes disartulating below the lemma (Wong 1993*a*, Widjaja 1997). Wong (1993*b*) and Widjaja (1997) described new genera allied to *Bambusa* but distinguished primarily on floret, pseudospikelet and branch structures. Stapleton (1994) proposed, on the basis of Himalayan species, that *Bambusa* characteristically has two-keeled bud prophylla, a feature used to separate it from *Dendrocalamus*. *Bambusa arnhemica* does not have two-keeled bud prophylla, and use of the trait has not been taken up by subsequent workers.

By almost all criteria, *B. arnhemica* is correctly placed in *Bambusa*. Furthermore, the development of the flowering branch as described here is identical to the detailed analysis provided for *Bambusa* by Wong (1995, pp. 120-127), including the presence of inflorescence sheath blades as illustrated by Wong for *B. farinacea*. However, *B. arnhemica* lacks the lobed culm sheath auricles that are generally a feature of the genus, a character reduction it shares with *B. balcooa* Roxburgh (Stapleton 1994).
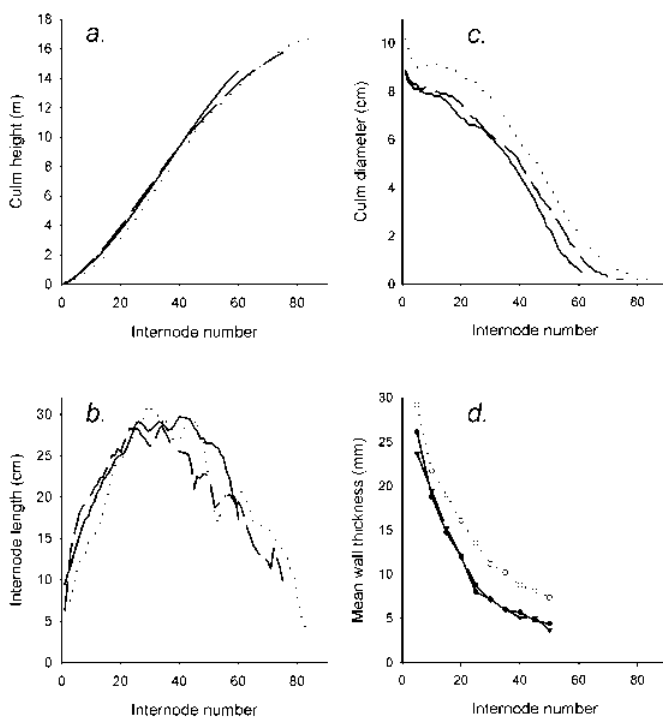
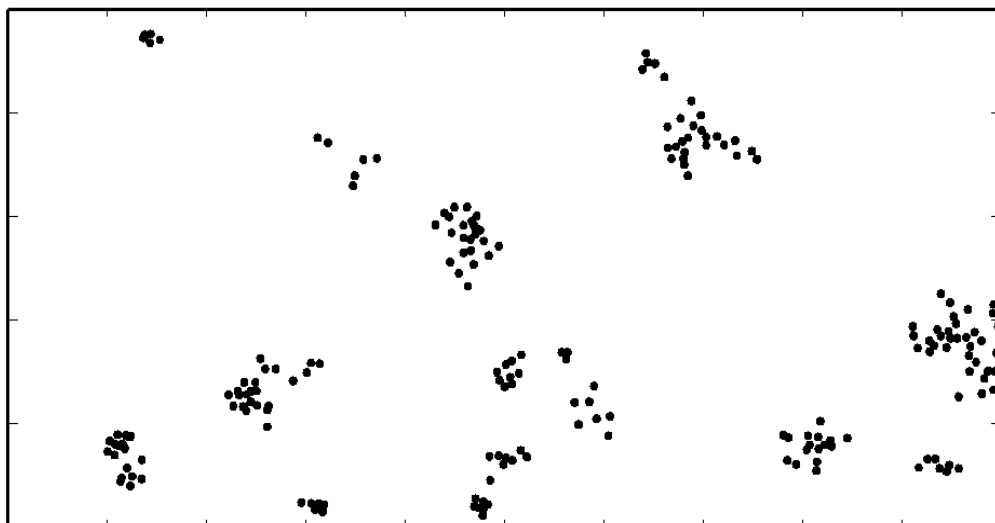Figure 3. Dimensions of three Bambusa arnhemica culms at Mary River Park.

Figure 4. Position of bases of the 201 live *Bambusa arnhemica* culms present in a 20 x 10 m plot positioned in a dense, mono-dominant stand of small clumps on level ground in the vicinity of Finniss River (12°50'S, 130°38'E). Hash marks are at 2m intervals.
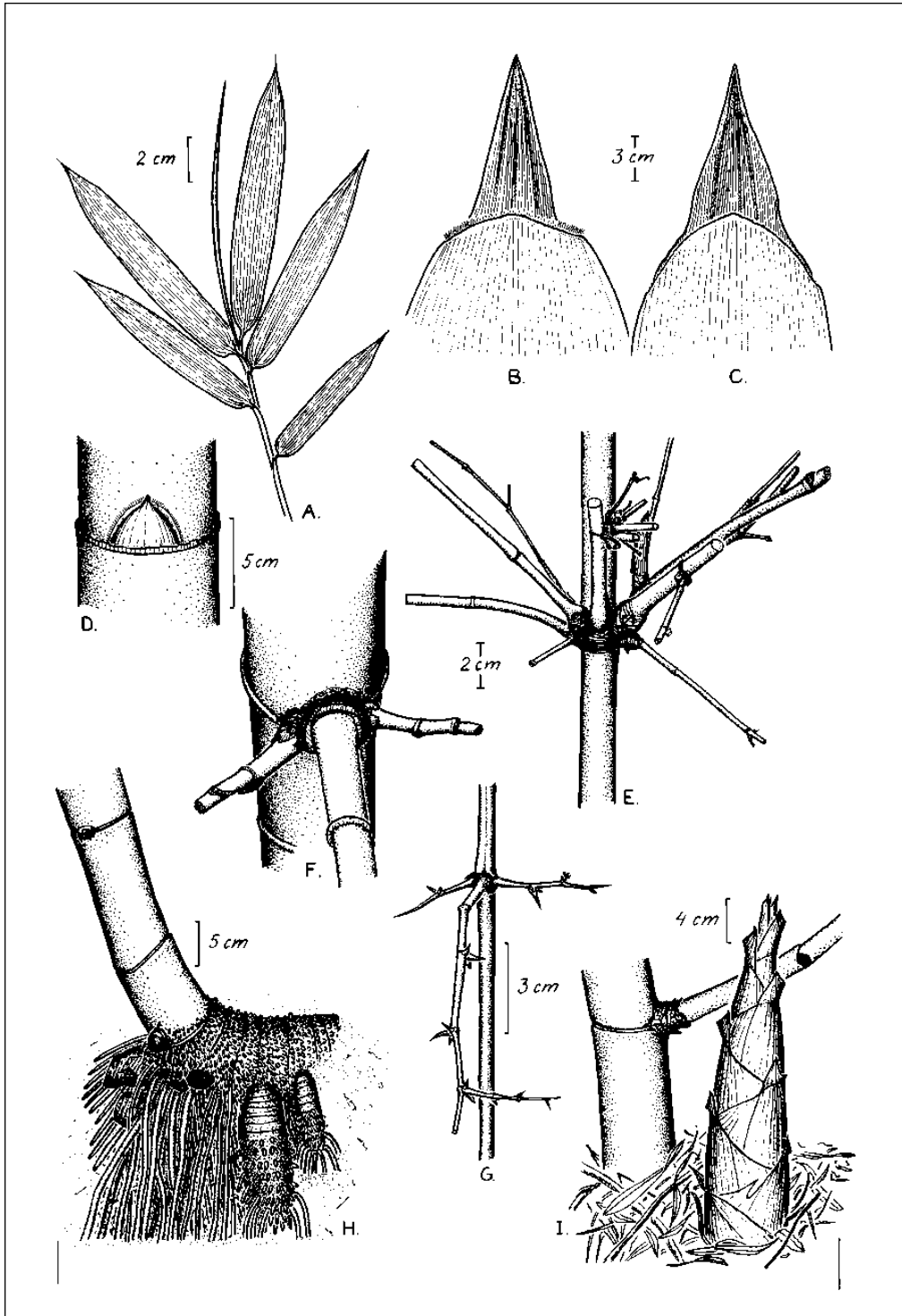
Figure 5. *Bambusa arnhemica:* *a.* leafy shoot; *b., c.* culm sheath and blade variants; *d.* branch bud; *e.* upper branch complement; *f.* lower branch complement; *g.* section of lower branch with thorns; *h.* rhizome and lower culm; *i.* culm shoot. Illustrations prepared by Monika Osterkamp Madsen.
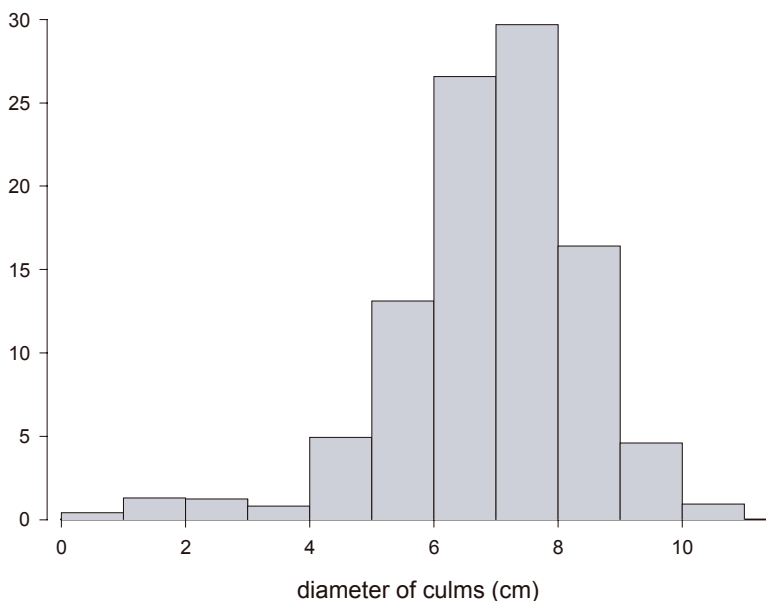
Figure 6. Culm diameters of *Bambusa arnhemica* at Mary River Park.
N = 1219 culms from 39 clumps; culms measured at the internode nearest 1.3 m above the ground.
Figure 7. *Bambusa arnhemica*: a. leafy clump; b. flowering branch; c., d., e. seed; f. pseudospikelet; g. lemma; h., i. palea; j. developing flowering branch showing leaf-like inflorescence sheath blades; k. set of stamens; l. ovary and stigmas; m. lodicule. Illustration prepared by Monika Osterkamp Madsen. Some material has been reproduced or modified from Cowie et al. (2000) with permission.

At least 15 species of *Bambusa* are thorny (But *et al.* 1985, Benton and Weatherhead 1996, Ohrnberger 1999, this study). Whether thorniness has phylogenetic significance or is a labile and convergent trait with multiple origins within *Bambusa* is unknown. The origins of *B. arnhemica* are also unknown, and I have been unable to identify any potentially synonymous or closely related species. Muller (1997) suggested that *B. arnhemica* has affinities with the widespread and thorny *B. bambos* (L.) A. Voss (syn. *B. arundinacea*) and *B. blumeana* J. H. Schultes.

Bambusa arnhemica differs from these species in its lack of lobed culm sheath auricles, in its culm leaf, and in several other characteristics (*cf* Dransfield and Widjaja 1995), and also in that the thorns of *B. arnhemica* are less robust, confined to the basal branches, and do not often give rise to leafy shoots (pers. obs.). Basal branches, and thus thorniness, are more prominent in clumps whose lower culms are

exposed to light (pers. obs.), and may even be quite absent. Hearne (1975) suggested that the thorniness of *B. arnhemica* could be minimised in cultivation by watering and application of fertiliser. There are three native species of "woody" bamboo in mainland Australia (Spencer 1986, Muller 1997, Mallett and Orchard 2002), of which only *B. arnhemica* is thorny. Although all have been placed in *Bambusa* (but see Widjaja 1997), they are quite dissimilar (Muller 1997). This could suggest that bamboo may have colonised Australia from the north on at least three occasions.

Liddle *et al.* (1994) and Mallett and Orchard (2002) reported outlying occurrences of *B. arnhemica* at Cobourg Peninsula (11°22'S, 132°09'E) and South Goulbourn Island (11°40'S, 133°23'E) (Fig. 1). Examination of leaf material from both locations, and of a photograph of a culm shoot from Cobourg Peninsula, clearly identifies these records as erroneous and possibly
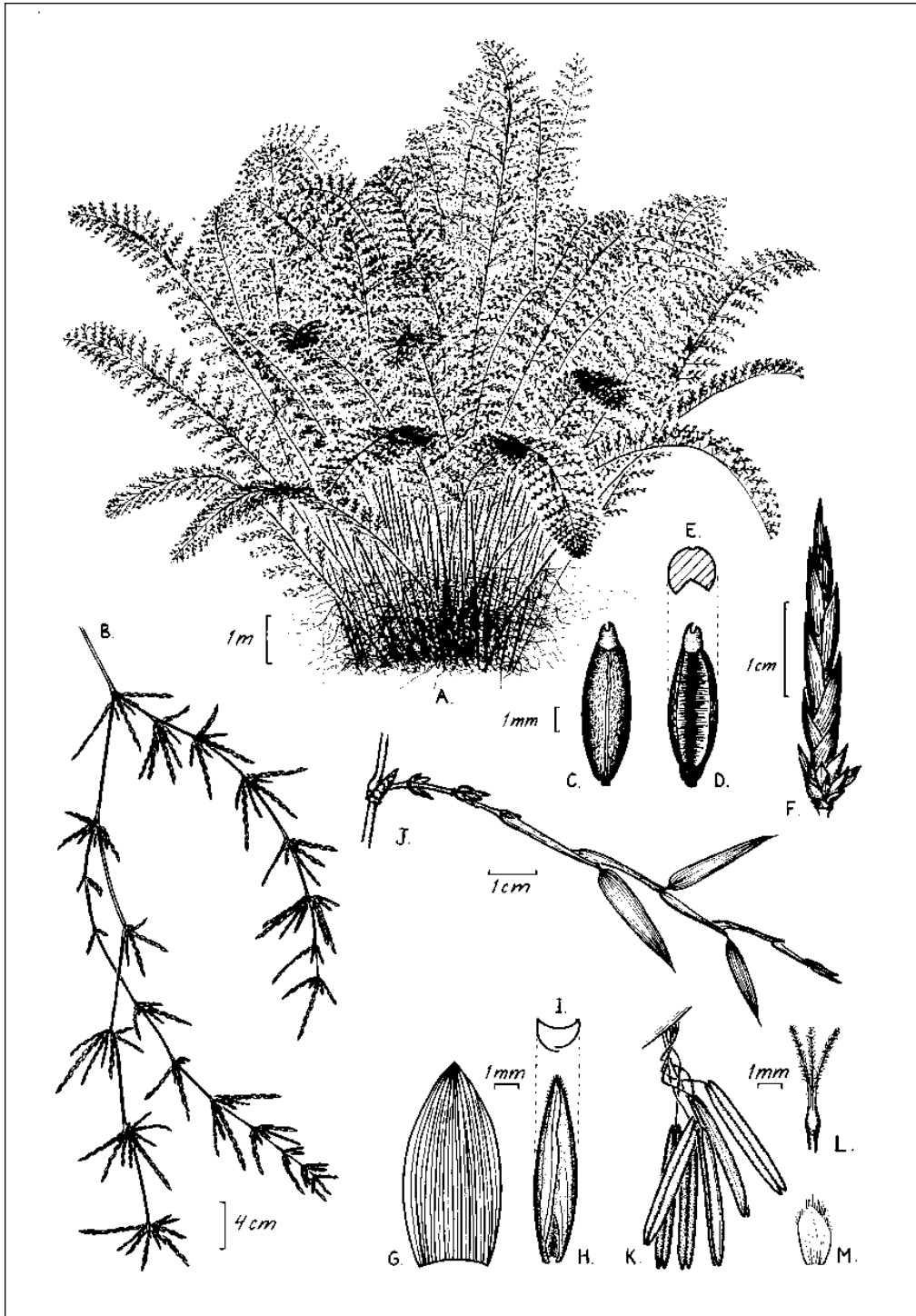
Figure 7. *Bambusa arnhemica: a.* leafy clump; *b.* flowering branch; *c., d., e.* seed; *f.* pseudospikelet;
g. lemma; *h., i.* palea; *j.* developing flowering branch showing leaf-like inflorescence sheath blades;
k. set of stamens; *l.* ovary and stigmas; *m.* lodicule. Illustration prepared by Monika Osterkamp Madsen.
Some material has been reproduced or modified from Cowie et al. (2000) with permission.

referrable to a green form of B. vulgaris Schrader ex Wendland. Leaf material differs from *B. arnhemica* in having (on smaller branches, at least) a raised, 1 mm wide sheath scar forming a distinct lip perpendicular to the culm surface, a prominent supra-nodal ridge, and robust and apparently non-deciduous leaf auricles. The Cobourg Peninsula occurrence is restricted to the immediate vicinity of an historic garden (Alan Withers, pers. comm.) to which plants were introduced from the Sydney Botanic Gardens and Timor (Spillett 1979). It seems likely that both occurrences are the result of deliberate introductions, and it is unclear whether they can even be regarded as naturalised. Material from Melville Island (11°50'S, 130°50'E, Fig. 1), where extensive wild stands of bamboo are to be found near the south coast, is confirmed as *B. arnhemica*.

Other than "bamboo", there is no well-established vernacular for *B. arnhemica*. It has been termed "Native Bamboo" and "Arnhemland Bamboo" (Spencer 1986, Clarke and Traynor 1987). The former is unhelpful nationally or internationally, and on current definitions of Arnhemland, the latter is inappropriate. "Top End Bamboo" is recommended as distinctive and appropriate.

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A New Species of *Chusquea* Sect. *Swallenochloa* (Poaceae: Bambusoideae) from Bolivia

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Chusquea renvoizei is described as new, and selected diagnostic features are illustrated. This species is classified within *Chusquea* section *Swallenochloa*, and is compared and contrasted with *C. depauperata, C. neurophylla, C. smithii, C. spicata,* and *C. tessellata,* five other members of this section that occur (or may occur) in Peru and Bolivia. *Chusquea renvoizei* is endemic to Bolivia, and is distinguished based on its long foliage leaf blades tapering to a ridged, navicular apex and obtuse anterior lodicules, among other characters.

Se describe Chusquea renvoizei como una especie nueva, y se ilustra ciertos característicos diagnósticos. Esta especie está clasificada dentro de *Chusquea* sección *Swallenochloa*, y se la compara con *C. depauperata, C. neurophylla, C. smithii, C. spicata* y *C. tessellata,* las cinco otras especies de esta sección que ocurren (o que puedan ocurrir) en Perú y Bolivia. Se distingue *C. renvoizei* basado en sus láminas de las hojas de follaje largas y atenuadas en un apice longitudinalmente corrugado y navicular, y las lodículas anteriores obtusas, entre otros caracteres.

During a visit in 2002 to the herbarium at the Royal Botanic Gardens, Kew, I discovered a new species of *Chusquea* while examining collections of bamboo from Bolivia. The short internodes and intravaginal branching of this species clearly placed it within *Chusquea* sect. *Swallenochloa* (Clark 1989) but a combination of flowering and vegetative features distinguished it from other described members of the section in Bolivia and Peru. The description of *C. renvoizei* brings the total number of species in *Chusquea* sect. *Swallenochloa* to 29. The species is named for Steven A. Renvoize, Head of the Grass Section at the Kew Herbarium, in recognition of his work on the grasses of Bolivia and his forthcoming retirement.

TAXONOMIC TREATMENT

Chusquea renvoizei L. G. Clark, sp. nov. TYPE: BOLIVIA. Depto. La Paz, Prov. Nor Yungas, cerca de Cotapata, ceja de monte, 16°17'S, 67°53'W, 3,500 m, 12 Oct 1997 (fl), S. G. Beck 24406 (holotype: LPB (n.v.); isotype: K!, 2 sheets). Fig. 1.

Culmi plus minusve 0.2 cm diam., 1.5 m alti, erecti. Folia culmorum ignota. Ramificatio intravaginalis; ramus subsidiarius cujusquisque nodi singularis. Folia ramorum 4-5 in cujusquisque complementi; vaginae striatae, glabrae; laminae 20.4-25.8 cm longae, 0.5-0.6 cm latae, longitudo versus latitudo = 34-50, glabrae, virides, adaxialiter non tessellatae, abaxialiter non tessellatae vel leviter tessellatae, basi attenuata, apice attenuato, naviculari, mucronato; ligulae interiorae 0.3-0.4 mm longae, truncatae. Synflorescentiae 12.5-15 cm longae, 0.5-0.8 cm latae, paniculatae, contractae, ad basim interruptae. Spiculae 6.5-7.2 mm longae; glumae I et II glabrae; gluma I 0.6-1.3 mm longa, obtusa; gluma II 1-2 mm longa, late acuta; glumae III et IV naviculares, aristatae, abaxialiter scabro-pubescentae in dimidio superiore; gluma III 4.8-6.1 mm longa aristis inclusis, arista 1.7-2.4 mm longa; gluma IV 5.3-6.8 mm longa aristis inclusis, arista 1.5-2.7 mm longa; lemma 6.3-7 mm longum, naviculare, aristatum, scabro-pubescentum in dimidio superiore, arista 1-1.6 mm longa; palea 4.8-5 mm longa, biapiculata, abaxialiter scabro-pubescente. Lodiculae 3, hyalinae, par anticum 1.7-2 mm longum, ca. 1 mm latum, obtusum, lodicula postica 1.4-1.5 mm longa, obtusa vel acuta.

Culms ca. 0.2 cm in diameter, ca. 1.5 m tall, erect. Internodes 6-8.5 cm long, terete to

Table 1. Morphological comparison of the species of *Chusquea* sect. Swallenochloa in Bolivia and Peru.

Character	C. renvoizei	C. depauperata	C. neurophylla	C. smithii	C. spicata	C. tessellata
Culm diameter (cm)	ca. 0.2	ca. 0.5	ca. 0.2	ca. 0.2	ca. 0.3	0.5-1
Foliage leaf blade length (cm)	20.4-25.8	3.4-5.5	3-8	5.7-7	5.9-6.2	5.8-23
Foliage leaf blade width (cm)	0.5-0.6	0.2-0.5	0.2-0.25	0.7-0.9	ca. 0.5	0.6-2.6
Foliage leaf blade L:W	34-50	9-17	15-32	7.6-8.2	ca. 12	(5-) 7-21.5
Foliage leaf apex	long tapering, navicular, ridged, mucronate	acuminate, subulate	navicular, ridged, apiculate	shortly tapering, navicular, ridged, mucronate	tapering, subulate	acuminate, subulate
Foliage leaf sheath summit	extension 1-1.5 mm long, juncture with the inner ligule pubescent	extension 0.5-2 mm long, juncture with the inner ligule glabrous	extension 0.3-0.4 mm long, juncture with the inner ligule ciliolate	extension absent, juncture with the inner ligule sparsely pubescent	extension absent, juncture with the inner ligule pubescent	extension absent, juncture with the inner ligule pubescent
Spikelet length (mm)	6.5-7.2	4-6	5.7-6.4	7.7-9.5	4-5	3.9-9
Glumes I and II relative to the lemma	ca. 1/10	< 1/10, often much less	up to 1/6	< 1/10	ca. 1/6	1/5-1/3
Apex of glumes III and IV	awned	acute or mucronate	apiculate, obtuse	acute	awned	subulate
Glume IV relative to the lemma	4/5-9/10	2/3	2/3	± equal	2/3-3/4	3/4-7/8
Geographic distribution	Bolivia	Bolivia, Peru	Ecuador, Peru	Peru	Bolivia, Peru	Ecuador to Venezuela, possibly Peru

slightly flattened, glabrous. Culm leaves not seen. Branching intravaginal; apparently one branch per node developing and not rebranching. Foliage leaves 4-5 per complement; sheaths striate, glabrous, rounded on the back, margins glabrous, summit extension 1-1.5 mm long, pubescent along juncture with the inner ligule; blades 20.4-25.8 cm long, 0.5-0.6 cm wide, L:W = 34-50, glabrous, green, adaxially not tessellate, abaxially not tessellate or weakly so, the base attenuate, the apex tapering at length to a narrow, adaxially ridged, navicular, mucronate tip, the margins serrulate; pseudopetioles 1-1.5 mm long, glabrous; outer ligules to 0.5 mm long, often shallowly bilobed, glabrous; inner ligules 0.3-0.4 mm long, truncate. Synflorescences 12.5-15 cm long, 0.5-0.8 cm wide, paniculate, contracted, interrupted at the base; rachis with one side broader and slightly rounded in cross-section, the other side ridged, becoming angular toward the apex, pubescent, branches emerging from the ridged side, appressed; branches and pedicels angular, appressed, pubescent, the lowermost branches 1.2-1.5 cm long, pedicels 0.5-2 mm long. Spikelets 6.5-7.2 mm long,
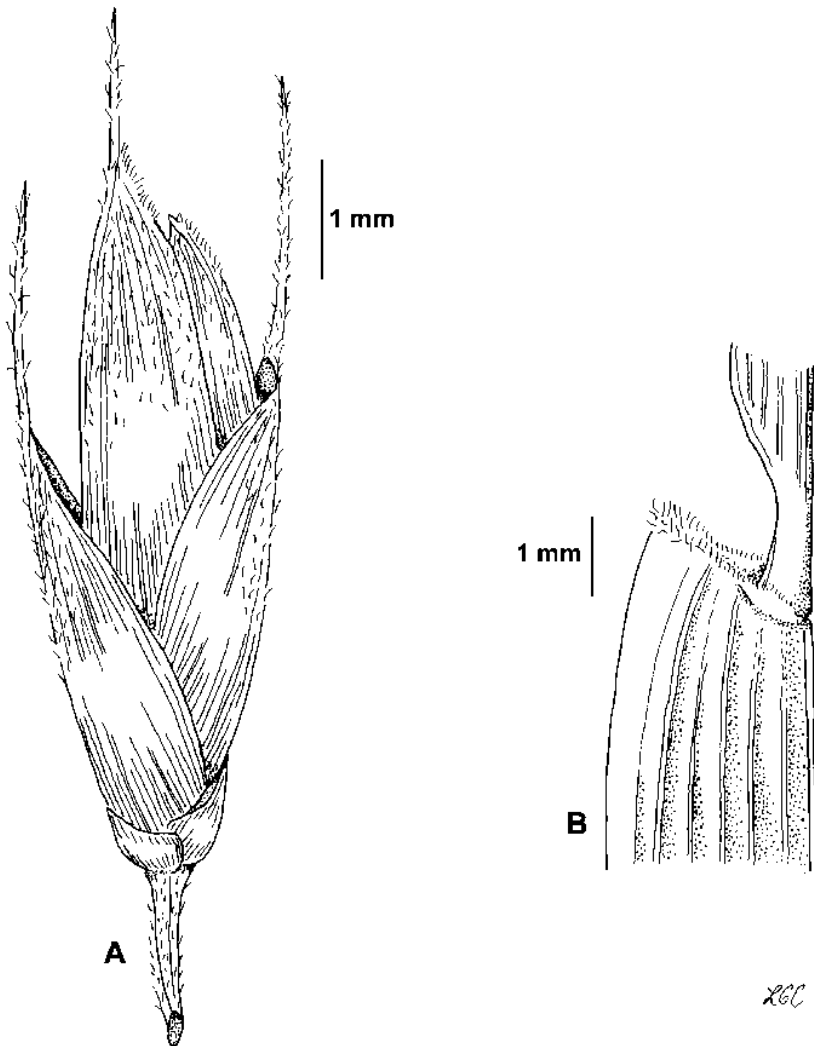
Figure 1. *Chusquea renvoizei.* A. Spikelet. B. Ligular area of foliage leaf showing the sheath summit extension and pubescence pattern.

slightly laterally compressed; glumes I and II glabrous; glume I 0.6-1.3 mm long, ca. 1/10 the spikelet length, obtuse, nerveless; glume II 1-2 mm long, ca. 1/5 the spikelet length, broadly acute, 0-1-nerved; glumes III and IV navicular, awned, abaxially scabrous-pubescent on the upper half, 5-nerved, the awns scabrous; glume III 4.8-6.1 mm including the awn, ca. 3/4 the spikelet length, the body 3.1-3.7 mm long, the awn 1.7-2.4 mm long; glume IV 5.3-6.8 mm long including the awn, 4/5-9/10 the spikelet length, the body 3.8-4.1 mm long, the awn 1.5-2.7 mm long; lemmas 6.3-7 mm long including the awn, navicular, awned, abaxially scabrous-pubescent on the upper half, 7-nerved, the body 5.3-5.4 mm long, the awn 1-1.6 mm long; paleas 4.8-5 mm long, biapiculate, abaxially scabrous-pubescent, 4-nerved, sulcate only toward the apex, the sulcus scabrous toward the apex. Lodicules 3, hyaline, apically ciliate; the anterior pair 1.7-2 mm long, ca. 1 mm wide, obtuse, the posterior one 1.4-1.5 mm long, obtuse or acute. Stamens 3; anthers 3.3-3.6 mm long. Ovary apex tapering, stigmas apparently two. Fruit not seen.

This species is known only from the type collection, and thus is considered endemic to Bolivia. *Chusquea renvoizei* is easily distinguished from the other species of this section in Bolivia and Peru (*C. depauperata* Pilger, *C. neurophylla* L. G. Clark, *C. smithii* L. G. Clark, *C. spicata* Munro and *C. tessellata* Munro) by its long, green foliage leaf blades (20.4-25.8 cm long) with long tapering, ridged, navicular apices; sheath summit extensions with pubescence along the juncture with the inner ligule; and spikelets 6.5-7.2 mm long with glumes III and IV and the lemma awned (Table 1). The obtuse anterior lodicules appear to be unique for this species, at least within the section, although lodicules for some species of sect. Swallenochloa have not been observed.

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Lectotypification of Three Bamboo Species

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Three species of woody bamboo, *Chusquea fendleri, C. spadicea,* and *Neurolepis acuminatissima,* are lectotypified based on observations of specimens from several herbaria, principally the Kew Herbarium (K) and the U. S. National Herbarium (US).

Se propone lectotipos para tres espécies de bambues leñosos, *Chusquea fendleri, C. spadicea* y *Neurolepis acuminatissima*, basado en observaciones hechas de muestras depositadas principalmente en el herbario de Kew (K) y el herbario nacional de los Estados Unidos (US).

The rules of botanical nomenclature (Greuter et al., 2000) require that a single specimen be permanently connected to the name of a species. This specimen is known as the type. Many older bamboo names do not conform to the rules for one reason or another, and so lectotypes (or neotypes) must be designated retroactively. In this paper, I lectotypify three bamboo species of *Chusquea* and *Neurolepis*.

Chusquea fendleri Munro, Trans. Linn. Soc. London 26: 61-62. 1868. Type: VENEZUELA. In Colonia Tovar, 6000-7900 ft., *Fendler 1627* (lectotype, here designated: K! 2 sheets; isolectotypes: K!, G!, P!).
    Munro (1868) originally described this species based on two specimens (syntypes), *Fendler 1627* from Venezuela and *Jameson 9* from Ecuador. He noted that the species was distinguished "by its extremely small, almost invisible glumes" among other features. Munro also quoted Fendler as saying that "this grass spreads in many places of the primeval forest so as to exclude all other plants, and even deadens shrubs and trees, forming cane-brakes or 'carizals.'" A note on one of the sheets of *Fendler 1627* at Kew says "on the young shoots of this cane a large coleoptera feeds."
    A number of workers, including the author, have collected this species at or near the Colonia Tovar locality, and elsewhere in the Andes of Venezuela. Both vegetative and flowering features of these various collections match the *Fendler 1627* specimen. *Jameson 9* indeed represents a species with extremely reduced glumes I and II, but although it is probably related to *C. fendleri,* it is not the same species. I have also collected extensively in Ecuador and have not found *C. fendleri*

there. Therefore, I am designating *Fendler 1627* as the lectotype for the name *C. fendleri.* This is also consistent with Munro's clear intention to name the species for Fendler, recognizing his work in Venezuela.
    An emended description of this species will be published in the future, but at present, it is sufficient to say that *Chusquea fendleri* is characterized by possession of: amphimorph rhizomes; culm leaves with the girdle pilose and the hairs appressed downward; extravaginal branching; triangular central buds; foliage leaves with an inner ligule ca. 1 mm long and blades that are attenuate at the base and linear-lanceolate above; paniculate, narrow synflorescences 8-12 cm long; and slightly falcate spikelets 7-8 mm long, with glumes I and II extremely reduced, glume III ca. 1/2 the spikelet length, and glume IV ca. 2/3 the spikelet length. The large beetle that feeds on the shoots of C. fendleri is illustrated in Judziewicz et al. (1999; Fig. 38) and Steyermark and Huber (1987; Plate 139A).

Chusquea spadicea Pilger, Bot. Jarhb. Syst. 27: 35. 1899. Type: COLOMBIA. Antioquia: Westabhange des Ruiz, 2800 m, Oct 1883 (fl), *Lehmann 3171* (Holotype: B, destroyed; lectotype, here designated: US 821330!; isotypes: G! 2 sheets, K!, US 1646309! frag.).
    The holotype of this species was deposited at the Berlin Botanical Garden, and, like many other grass and apparently all neotropical bamboo holotypes, is presumed destroyed. Fortunately, several extant, relatively complete isotypes of this collection exist at other herbaria. I have chosen one of these at the U.S. National Herbarium to serve as the lectotype. The second US sheet is a fragment (flowering

branch) taken from the specimen at Kew.

This species grows from approximately 2,800 to 3,600 m in at least the departments of Caldas and Risaralda in the Parque de los Nevados in Colombia, including the type locality on the west slope of the Nevado del Ruiz. *Chusquea spadicea* is characterized by culm leaves with very small blades, relatively narrow foliage leaves, and spikelets with glumes III and IV mucronate with all four glumes spreading.

Neurolepis acuminatissima (Munro) Pilger in Engler & Prantl, Naturl. Pflanzenfam. Erganz. heft 2 (Nachtr. III zu Teil II, Abt. 2): 21. 1906. *Planotia acuminatissima* Munro, Trans. Linn. Soc. London 26: 72-73. 1868. Type: COLOMBIA. Tolima, *Goudot s.n.* (Lectotype, here designated: K!; isolectotype: US! frag.).

This species was described by Munro (1868) based on two specimens (syntypes) from Colombia, *Goudot s.n.* from Tolima, and *Triana* (on some labels as *Triana and Linden* or *Linden and Triana*) 50 without a locality given. Both are flowering specimens that represent this species, but only one specimen can serve as the type. I have chosen the *Goudot s.n.* specimen as the lectotype because it has a definite locality. The *Triana 50* specimen is represented by fragments at US, a full inflorescence with subtending leaves at Kew, and another comparable specimen at Paris (P). The flowering piece of the Paris specimen of *Triana 50* is definitely *N. acuminatissima,* but the vegetative piece may represent another species of *Neurolepis*.

McClure (1973), based on the fragmentary material available to him, considered this species to be synonymous with *Neurolepis aristata* (Munro) Pilger. Upon examination of the syntypes at Kew during a visit there in 1995, however, and based on detailed study of *N. aristata,* I determined that *N. acuminatissima* was probably a distinct species, but no recent collections, and certainly none with good vegetative material, were available. Therefore, Ximena Londoño and I went looking for it in 1997 in Colombia. Because we knew that 1) the species had been collected in Tolima, and 2) species of *Neurolepis* generally grow at very high altitudes, we began our search on the east slope of the Nevado del Ruiz (in the department of Tolima), where neither of us had collected previously. On our very first day of collecting, we found the plant growing at 4,000 m in a remnant *Polylepis* forest, and

confirmed that, based on the reddish sheaths, lack of a pseudopetiole, relatively long, sword-like blades, and slightly excentric midribs, as well as the very long-awned glumes I and II, this was indeed a good species. We also located a second population of this species in the Páramo de Chili in the department of Quindio, growing in an elfin forest adjacent to an Espeletia *páramo* at 3660 m.

ACKNOWLEDMENTS

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