Gerald F. Guala II*: Cyanogenesis in the Bamboos: a Phylogenetic Perspective

Abstract

Cyanogenesis, the production and liberation of cyanogenic compounds, in the shoots of 42 species of bamboos was assessed, and the results were compared to those of previous studies. The tribes of herbaceous bamboos and subtribes of woody bamboos recognized by Soderstrom and Ellis (1987) were found, in general, to be internally consistent for presence or absence of cyanogenesis. The two notable exceptions were in the Guaduinae and Schizostachydinae, in which both cyanogenic and acyanogenic genera occurred. The distribution of cyanogenesis is discussed from a phylogenetic perspective.

Introduction

The real key to a stable, useful classification of the bamboos is the discovery of their phylogeny. Modern classifications are based on phylogeny. Unless rigorous reproducible methods are used to generate and maintain classifications, the classifications will continue to be subjective and become obsolete concurrently with their creators. In a modern phylogenetic system, as the knowledge of phylogeny in a group becomes better known, the classification becomes more predictive and, hence, more stable. In order to be maximally informative, characters must be discussed in a phylogenetic context. This is our purpose in this brief preliminary report on cyanogenesis in the bamboos. Cyanogenesis has been used to elicit phylogenetic relationships in the grasses and other families (Spencer and Seigler 1985, Tjon Sie Fat 1979) although it has never been discussed in a cladistic framework, or used in bamboo systematics. Good discussions of the cladistic method, the one now most commonly used to clarify phylogenetic relationships and the one used in this paper, are given by Wiley (1981) and Wiley et al. (1991). Briefly, groups are delimited on the basis of shared, derived (apomorphic) character states referred to as synapomorphies. Phylogenetic hypotheses in the form of branching diagrams called cladograms are generated and those requiring the fewest character changes or evolutionary events are preferred due to their greater simplicity or parsimony. The groups (clades) recognized in the classification (genera, species, etc.) resulting from the cladogram must be monophyletic, that is, they must include all of the progeny of their most recent common ancestor. Groups that do not include all of these progeny are called **paraphyletic**. A brief introduction to cladistic theory along with an application to bamboos is given by Guala (1992).

Cyanogenesis, as used here, is the production and liberation of cyanogenic compounds and, although it is not widely reported in the bamboos, it is quite common in some groups of both herbaceous and woody bamboos as well as many other grasses.

Although the purpose of this paper is to discuss cyanogenesis from a phylogenetic perspective, the empirical testing for this study was originally instigated by the need for suitable forage in captive breeding programs for cyanogenic bamboo-eating lemurs from Madagascar at the Duke Primate Center (see Glander *et al.* 1989). More generally, cyanogenesis is thought of as detrimental when it occurs in both native and exotic bamboos that are widely found in tropical pastures and used as forage elsewhere (McClure 1958 and references therein, Guala 1992, Filgueiras and Pereira 1984).

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Materials and Methods

In addition to a review of the literature, a preliminary empirical study was undertaken to determine the distribution of cyanogenesis in the bamboos. The presence of cyanogenesis was determined by a positive (blue) reaction in the Feigl Anger test (Feigl and Anger 1966) consisting of a strip of filter paper impregnated with Feigl Anger solution suspended over the fresh crushed plant tissue in a small sealed test tube. Leaves were punched with a 5 mm paper punch to give 5, 5 mm disks from the mid-lamina. Shoot cross sections were taken approximately ½ of the way up young shoots. These were 0.5 cm thick and approximately 1 cm in diameter, or the equivalent, when smaller shoots were used. When shoots were more than 1 cm in diameter, the outer layers were removed until the desired diameter was achieved. Two drops of toluene were also added to macerate the tissue and aid in the liberation of HCN compounds. At least 2 tests for each species were performed, most species were tested at least 4 times.

The results were then compared to current hypotheses about the phylogeny of the bamboos and discussed in this context. The system of classification presented by Soderstrom and Ellis (1987) is employed here as a basis for discussion. All of the plants tested by us and cited in Table I are vouchered at the Vascular Plant Herbarium of the University of Florida (FLAS) unless otherwise noted.

Results

The foliage leaf laminas of 87 species of bamboos were sampled and none showed a positive reaction. This is what one would expect (McClure 1958) and the leaf material is not further discussed here. The young shoots of 41 of these were also sampled and the results are given in Table I. Records from Glander *et al.* (1989) and the records from McClure (1958) using the chlorides of iron test are also included. The leaves and shoots of *Flagellaria indica* L. (Flagellariaceae), a close relative of the grasses, and *Oryza sativa* L., a member of the grass subfamily Oryzoideae, which is often included in the Bambusoideae, were also sampled. *Flagellaria* gave a positive reaction in both its leaves and shoots while *Oryza* was negative in both cases.

The names in Table I are those recognized by the author as valid. In a cladistically consistent classification, only those genera that are themselves monophyletic and do not force the paraphyly of any other genus are recognized. At the present time, we can find no characters to support the monophyly of *Arundinaria* if *Ampelocalamus*, *Pseudosasa*, and *Drepanostachyum* are recognized. The same argument applies to *Thamnocalamus* with respect to *Himalayacalamus*. Equivalent binomials in common use are given in the footnotes.

Discussion

The data in Table I show a striking consistency within the Arundinariinae¹, Bambusinae, Chusqueinae, Olyreae, and Shibataeinae, and appear to follow generic lines elsewhere. They imply that this character may eventually be useful in the elucidation of phylogenetic relationships among genera. There is no correlation with herbaceousness vs. woodiness, Old World vs. New World endemics, or sympodial vs. monopodial rhizomes. This supports the independence of the character and may further support its utility for phylogenetic analysis.

Campbell and Kellogg (1987), using morphological and anatomical data, found

¹ Seigler (1979) found cyanogenesis in the "leaf-culm" of *Sasa variegata*. However, he employed the Guignard test and added emulsion and/or linamarase if a test was initially negative. The results are, therefore, not comparable to ours.

Table 1.

Species of Bamboo tested for the presence of cyanogenesis using either the Feigl Anger test or a Chorides of Iron test. In addition to our data designated with (1), the records of McClure (1958) and Glander *et al.* (1989) are also included and designated with (2) and (3) respectively. Higher level groups are those of Soderstrom and Ellis (1987). Species names and generic circumscriptions are those of the author.

Anomochloea Anomochloa marantoidea Brongn ²	+
Arthrostylidiinae Rhipidocladum racemiflorum (Steud.) McClure (1)	-
Arundinariinae Arundinaria actinotricha Merr. & Chun³ (1)	-
Arundinariinae Arundinaria falcata Nees ⁴ (1)	-
Arundinariinae Arundinaria fastuosa (Marc. ex Mitf.) Houz. (1)	-
Arundinariinae Arundinaria gigantea (Walt.) Chapm. (1)	-
Arundinariinae Arundinaria hindsii Munro ⁵ (2)	-
Arundinariinae Arundinaria japonica Sieb. & Zucc. ⁶ (1,2)	-
Arundinariinae Arundinaria khasiana Munro ⁷ (1)	-
Arundinariinae <i>Thamnocalamus falconeri</i> Hook f.8 (1)	-
Bambusinae <i>Bambusa bambos (L.)</i> Voss. ex Vilm. (1,2)	+
Bambusinae Bambusa beecheyana Munro (1)	+
Bambusinae Bambusa cf. dissimulator McClure ⁹ (1)	+
Bambusinae Bambusa flexuosa Munro (1)	+
Bambusinae Bambusa lineata Munro (2)	+
Bambusinae Bambusa cf. longispiculata Gamble ex Brandis (1)	+
Bambusinae Bambusa malingensis McClure (1)	+
Bambusinae Bambusa multiplex (Lour.) Raeusch. ex Schult. (1,2)	+
Bambusinae Bambusa polymorpha Munro (2)	+
Bambusinae Bambusa textilis McClure (1)	+
Bambusinae Bambusa ventricosa McClure (1)	+
Bambusinae Bambusa vulgaris Schrad. ex Wendl. (1,2)	+
Bambusinae Dendrocalamus asper (Schultz) Backer (1,2)	+
Bambusinae Dendrocalamus balcooa (Roxb.) Voigt. (2)	+
Bambusinae Dendrocalamus hamiltonii Nees & Arn. ex Munro (1)	+
Bambusinae Dendrocalamus strictus (Roxb.) Nees (2)	+
Bambusinae Dinochloa scandens (Blume) Kuntze (1)	+
Bambusinae Gigantochloa apus (Bl. ex Schult. f.) Kurz (2)	+
Bambusinae Gigantochloa atroviolacea Widjaja (1)	+
Bambusinae Gigantochloa atter (Hassk.) Kurz ex Munro (2)	+

² Not vouchered. Our material is from living collections originally at U.S., and believed to be from the locality of *Calderón 2381*.

³ Ampelocalamus scandens Hsueh & Li.

⁴ Drepanostachyum falcatum (Nees) Keng.

⁵ Although McClure obtained no reaction with the iron chloride test, he saw an "apparently weak" reaction using the Guignard test.

⁶Pseudosasa japonica (Sieb. & Zucc.) Makino.

⁷ Drepanostachyum khasianum (Munro) Keng.

^{*} Himalayacalamus falconeria (Hook. f. ex Munro) P. C. Keng.

⁹ cf. = confer: compare. This is often employed when the identification of the specimen at hand is uncertain.

Table 1, continued

Bambusinae Gigantochloa hasskarliana (Kurz) Backer (2)	+
Chusqueinae Chusquea cf. circinata Soderstrom & Calderón (1)	_
Chusqueinae Chusquea coronalis Soderstrom & Calderón (1)	-
Chusqueinae Chusquea liebmanii Fourn. (1)	-
Chusqueinae Chusquea pittieri Hack. (1)	-
Chusqueinae Chusquea simpliciflora Munro (1)	-
Guaduinae Guadua angustifolia Kunth (1)	+
Guaduinae Guadua chacoensis (Rojas) Londoño and Peterson (1)	+
Guaduinae Otatea acuminata (Munro) Calderón & Soderstrom (1)	_
Guaduinae Otatea fimbriata Soderstrom (1)	-
Nastinae Cephalostachyum perrieri A. Camus (3)	+
Nastinae Cephalostachyum perrieri cf. viguieri A. Camus (3)	+
Olyreae Pariana sp. (1)	-
Olyreae Raddia brasiliensis Bertol. (1)	-
Olyreae Raddia distichophylla (Schrad.) Chase (1)	-
Phareae <i>Pharus lappulaceus</i> Fusée-Aubl. (1)	+
Schizostachydinae Schizostachyum blumii Nees (2)	-
Schizostachydinae Melocanna zollingeri Kurz ex Munro (2)	+
Schizostachydinae Melocanna brachyclada Kurz (2)	+
Shibataeinae <i>Phyllostachys aurea</i> Rivière (1,2)	<u>.</u>
Shibataeinae <i>Phyllostachys bambusoides</i> Sieb. & Zucc. (1,2)	_
Shibataeinae <i>Phyllostachys meyeri</i> McClure (1)	_
Shibataeinae <i>Phyllostachys nigra</i> (Lodd.) Munro (1)	-
Shibataeinae Shibataea kumasaca (Zoll.) Makino (1,2)	-
Streptochaetae Streptochaeta angustifolia Soderstrom (1)	-

that the Joinvilleaceae and Flagellariaceae are the likely sistergroups (most closely related clades) to the grasses, with the Flagellariaceae being the probable sistergroup to the Poaceae+Joinvilleaceae clade and other studies have supported this.

Our data shows that *Flagerallaria*, a representative of the Flagellariaceae, does produce cyanogenic glycosides. By the method of outgroup comparison (Maddison *et al.* 1984) we can infer that the common ancestor of the grasses was cyanogenic. That is, the basal state in the grasses is positive for cyanogenesis. We must keep in mind, however, that the basal character state in the grasses would be equivocal if the Joinvilleaceae were found to be negative (see Maddison *et al.* 1984). Cyanogenesis is also known, apparently sporadically, from all six subfamilies (Stebbins and Crampton 1961) of grasses (See Petrie 1913, McClure 1933, Seigler 1976, 1979, Leemann 1935). This implies that the character shows homoplasy (phylogenetic inconsistency) and may not be useful at the subfamilial level.

Positive readings are often thought to be the only logically useful ones because they are "more indicative of the plant[']s genetic potential" (Seigler 1979) or because one can never assume total absence because a given biochemical may only be present at levels lower than that detectable using the current apparatus. This is probably the situation with *Arundinaria hindsii* which McClure reported as giving a negative reaction with iron chloride and a weakly positive one using the Guignard test. Unfortunately, because the basal state for cyanogenesis in the grasses is positive, the <u>lack</u> of cyanogenesis is the most important state in a phylogenetic sense because it is the derived and hence defining (synapomorphic) state for phylogenetic groups within the grasses.

It is quite a bit more difficult to give the basal state for all of the subfamily Bambusoideae. This is primarily because there has been a great divergence of opinions on the actual constitution of the Bambusoideae. Clayton and Renvoize (1986) and Watson and Dallwitz (1992) included the Oryzeae in their Bambusoideae, while Prat (1960), Stebbins and Crampton (1961), Tsvelev (1983) and Gould and Shaw (1983) did not. The Centotheceae, Ehrharteae, Diarrheneae, and Brachylytreae are also variously placed, in or out of the Bambusoideae, among the systems mentioned above.

In a cladistic analysis, Kellogg and Campbell (1987) found the woody bamboos (Bambusodae) to be monophyletic; this has been confirmed by Kellogg and Watson (1993) and Davis and Soreng (1993) using independent data sets. However, none of these studies was able to satisfactorily discern what the relationships of the various groups of herbaceous bamboos (Olyrodae) are to the Oryzeae or to each other. It is clear from both studies, however, that the Olyrodae cannot be both basal in the grasses and monophyletic. If the Olyrodae is basal and paraphyletic then our preliminary data suggests that the possession or lack of cyanogenesis will be a useful character in defining the subgroups because it is variant between, but not within, the tribes that make up the Olyrodae. Our data confirms the monophyly of the Olyreae which is consistently negative for cyanogenesis. Within the Bambusodae, the absence of cyanogenesis confirms the monophyly of the Arundinariinae, Chusqueinae and Shibataeinae. The presence of both cyanogenic and acyanogenic genera in the Guaduinae and Schizostachydinae suggests that both are paraphyletic. Soderstrom and Ellis (1987) expressed limited reservations about the monophyly of the Guaduinae but were quite confident in the naturalness of the Schizostachydinae. Clayton and Renvoize (1986) widely separate Guadua and Otatea, putting the Guadua into Bambusa of the Bambusinae and Otatea into Sinarundinaria in the Arundinariinae. Although their generic and tribal assignments are supported by our data, and we feel that their tribal assignments are more parsimonious, we believe that the anatomical and morphological data would indicate paraphyly at the generic level with their expanded generic circumscriptions of Bambusa and Sinarundinaria.

Finally, it can not be emphasized enough that this is a preliminary study and that the results should be interpreted as such. When a positive reaction is obtained using the Feigl Anger test it means only that some cyanogenic glycoside is being produced along with its complimentary liberating enzyme. It is possible that different cyanogenic glycoside/enzyme pairs with different phylogenetic histories and, thus, different homologies, are present among the groups showing a positive reaction here. It is also possible that either the enzyme or the cyanogenic glycoside has been lost, thus giving another level of complexity to the problem. Cyanogenesis can also vary widely with respect to season, temperature and age of tissue (Leemann 1935). The Feigl Anger test has also been known to give false positives in rare instances. Although our data appears to be very promising, only further, more extensive tests will demonstrate the complete usefulness of this character in elucidating bamboo phylogeny.

Acknowledgements

The author is grateful to Charlie Welch and Ken Glander of the Duke Primate Center for instigating the data collection associated with this work and providing a vehicle with which to do it. He also wishes to express his gratitude to Thia Hunter for contributing her exceptional organizational skills and much needed assistance with the processing of material, Kim Higbie and Paul Smith for providing the majority of the material used here from their excellent bamboo collection as well as advice and literature, Karen and Jim Taylor for their major contributions of leaf material, Elizabeth Haverfield and Tony Chapman for some important additions to the shoot material and for lodging on the high seas, Lynn Clark for important contributions of material and advice, Don Goodman at the Kanapaha Botanical Garden for much of the temperate bamboo material, Robert Knight and Raymond Schnell at the USDA Chapman Field for bamboo material, David Jones and Scott Zona for providing the Feigl Anger test strips and other equipment as well as exceptionally clear and useful advice, and Walter Judd for insightful comments on the manuscript.

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University of Kansas Museum of Natural History Special Publication No. 19.

Chi-Ju Hsueh (Xue Ji-ru)* and De-Zhu Li[†]: Five Genera of Bambusoideae (Gramineae) Recently Discovered in Yunnan, China

The province of Yunnan is located in the southwest of China. Geographically, it lies between 21° 8′ 32" and 29° 15′ 18" north latitude and 97° 31′ 39" and 106° 11′ 27" east longitude with a total area of 383,000 square kilometers. The Tropic of Cancer passes through the south of the province. Topographically, it is higher in the north and lower in the south. The range between the highest elevation (6740 m) and the lowest (70 m) is over 6500 meters. It not only belongs to the North Tropics and subtropics latitudinally but has a vertical climatic range from the subtropics of the valleys to the alpine freezing zone. As a result of the complicated geomorphology and the broad three-dimensional differentiation of climate, diverse vegetation types can be found here. From south to north there are tropical rain forests, monsoon forests, leurilignosa, aestilignosa and aciculignosa. Vertically, the vegetation includes four to five layers, from the subtropical laurilignosa, mixed evergreen-deciduous, broad-leaved forest to the subalpine aciculignosa, alpine shrubs and alpine meadows and ice-boundary vegetation. Bamboo is an important element in the natural vegetation of Yunnan. The Abies-Sinarundinaria community, a subalpine vegetation type, is a good example of this. Sinarundinaria is the main food for the giant panda, which has its centre of distribution in Southwest China, especially in Yunnan Province.

From the point of view of phytogeography, the Yunnan bamboos belong to a series of floristic elements. *Dendrocalamus*, *Cephalostachyum*, and *Thyrsostachys* are of Southeast Asian (Indo-Malayan) elements, which have their natural distribution in southern Yunnan, especially in Xishuangbanna and Dehong Autonomous Prefectures. *Indosasa* and *Lingnania* (*Bambusa* subgenus *Lingnania*) have their center of distribution in Southeast Yunnan. The two genera are also distributed in the neighboring Guangdong and Guangxi Provinces and North Vietnam. The bamboo elements of Northeast Yunnan are the same as those of the Sino-Japanese floristic region, especially that of Central China. The *Phyllostachys* are an example. The subalpine area of Northwest Yunnan has a concentration of *Thamnocalamus* and *Sinarundinaria*, which are of Sino-Himalayan areal type. Nearly two hundred species can be found in the province. This paper introduces some of the genera discovered in the past twelve years by Chinese botanists.

1. Chimonocalamus Hsueh et Yi (1979)

The genus, with thirteen species and one variety, has its centre of distribution in South Yunnan. It can be classified as belonging to the Sino-Himalayan areal type. There are nine species in Yunnan, some four species in adjacent Northeast India and Burma, and another species in Southeast Tibet (see Table 1). *Chimonocalamus* are very important bamboos in the mountainous areas of Yunnan, especially in the altitude between 1500 and 2300 meters. They are usually dominant plants under the evergreen broad-leaved forests.

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Table 1. A list of *Chimonocalamus* species and Their Distribution

Scientific Name	Locality	Elevation
C. delicatus Hsueh et Yi	SE Yunnan	1400-2000 m
C. pallens Huseh et Yi*	SE Yunnan	
C. fimbriatus Huseh et Yi	SW Yunnan	
C. longiligulatus Hsueh et Yi	S Yunnan	
C. montanus Hsueh et Yi	SW Yunnan	1740 m
C. makuanensis Hsueh et Yi	SE Yunnan	1700-1900 m
C. longiusculus Hsueh et Yi	SE Yunnan	1650 m
C. dumosus Hsueh et Yi		
var. dumosus	SE Yunnan	1500 m
var. pygmaeus Hsueh et Yi	SW Yunnan	
C. tortuosus Hsueh et Yi	SW Yunnan, SE Tibet	
C. gallatyi (Gamble) Hsueh et Yi	Amherst, Burma	1650 m
C. griffithianus (Munro) Hsueh et Yi	NE India; Thaton, Burma	1200-1500 m
C. burmaensis (C.S. Chao et Renoize)		
Hsueh et D.Z. Li, comb. nov.	Burma	
C. longispiculatus (C.S. Chao		
et Renoize)		
Hsueh et D.Z.Li, comb. nov.	Burma	

^{*}Karyotype of the species: 2n=4x=48=15m(SAT)+8sm(SAT)+1st

The vegetative features, except the rhizome system, and the distributional habitats of the genus are similar to those of *Chimonobambusa*. A Japanese botanist (Nakai, 1925) dealt with *Chimonocalamus griffithianus* as *Chimonobambusa griffithiana*. But the inflorescence type and the structure of the spikelets and florets follow the *Sinarundinaria* type. Rhizomes of *Chimonocalamus* are sympodial with no elongated neck. *Chimonocalamus* is also characterized by fragrant essential oils in the culms. The main constituents of these oils are sesquiterpenoids, e.g. caryophyllane, humulane, and nerolidol (N. Feng and Hsueh, in press). These have provided a solid chemotaxonomic basis for the establishment of the genus. Because of their fragrant essential oils, young shoots of *Chimonocalamus* species are all delicious vegetables. The internodes *Chimonocalamus fimbriatus* are used as containers for a special tea, which is now exported abroad.

2. Qiongzhuea Hsueh et Yi (1980)

Belonging to the tribe Shibataeae, *Qiongzhuea* is similar to *Chimonobambusa* in the inflorescences and the spikelet structure. The main differences in the reproductive organs are that *Qiongzhuea* has primary branching of the pseudospikelets, bracts and nutlike fruits, while *Chimonobambusa* does not. Otherwise, the shoot growth is often initiated in spring, and the shoots are never blackened by the reaction of enzymes. The culm nodes are usually prominent and have no spinelike root primordia.

The genus *Qiongzhuea* comprises eight species and one form (D.Z. Li and Hsueh, 1988; see Table 2). It has its natural distribution in the Central China floristic regions (C.Y. Wu, 1979): Sichuan, Hubei, and Guizhou Provinces and NE Yunnan. The natural elevation of the genus ranges from 860 to 2600 meters, mostly 1500-2100 meters, which is also the upper part of the area in which *Chimonobambusa* grow. The habitats of *Qiongzhuea* are mostly to be found in the understory of evergreen broad-leaved forests.

The currently known distribution shows that the genus is endemic to China, falling

Scientific Name	Locality	Elevation
Q. tumidinoda Hsueh et Yi	Sichuan, Yunnan	1600-2000 m
Q. macrophylla Hsueh et Yi		
f. macrophylla	Sichuan	1430 m.
f. leiboensis Hsueh et D.Z. Li	Sichuan	1430 m.
Q. intermedia Hsueh et D.Z. Li	Sichuan	1250-1800 m
Q. communis Hsueh et Yi	Sichuan, Guizhou	
Q. puberula Hsueh et Yi	Guizhou	
Q. luzhiensis Hsueh et Yi	Guizhou	
Q. rigidula Hsueh et Yi	Sichuan	1300-1700 m
Q. opienensis Hsueh et Yi	Sichuan	

Table 2. Qiongzhuea Species and their Distribution

into the Central China endemic group according to C.Y. Wu's (1965, 1983) scheme, while *Chimonobambusa* is of the Sino-Himalayan areal type. Recent study of the cytology (F. Du and Hsueh, in press) shows the karyotype of *Qiongzhuea tumidinoda* to be 2n=4x=48=14m+8sm(SAT)+2st, which may be classified in the 2C type, while *Chimonobambusa microflora* may be recognized as belonging to the 2B type. We have reason to propose here that *Qiongzhuea* is a sister group (W. Hennig, 1965) to *Chimonobambusa*, and that it forms a monophyletic and more advanced group, adapted to colder environments.

Young shoots of *Qiongzhuea* are traditional vegetables in the distributional area. Those of *Q. tumidinoda* are the best for this purpose. Shoots of the species are currently exported to Japan and other foreign countries. The species has been famous for its sticks since the Han Dynasty, i.e. 1775 years ago. These sticks also reached Persia via India in ancient times. We guess that there was once a "south silk way" from Southwestern China to Persia. In this manner commodities like Qiong Zhu sticks and Sichuan clothes were introduced into India, Central Asia, and even Africa. *Qiongzhuea tumidinoda* is also one of the two species of *Bambusoideae* in the List of Chinese Preserved Plants, which was adopted by the China Natural Conservation Administration.

3. Ferrocalamus Hsueh et Keng F. (1982)

Both Ferrocalamus and Indocalamus have terminal panicles, multi-floreted and pedicelled spikelets, florets with three stamens and three lodicules, large leaves and unibranchlets. The two genera fall systematically into the tribe Arundinariae. A major difference is that the rhizomes are monopodial in Ferrocalamus versus amphipodial in Indocalamus. Ferrocalamus is also distinguished by apical pubescence of the lemma and a pubescent, non-bifid palea, single style, and berry-like fruit. Further, Indocalamus is a small, shrub-like bamboo while Ferrocalamus is arborescent, growing 5-7 (-9) meters high.

A monotypic genus, Ferrocalamus is only known in Yunnan Province's southern area, at an elevation of 900-1200 meters. The accompanying species include Pandanus tetorius, Callicarpa macrophylla, Begonia spp., Microstegium spp. and Angiopteris evecta. A genus endemic to China, it is of tropical distribution. Cytological studies on Yunnan bamboos (F. Du and Hsueh) show that Ferrocalamus has a karyotype of 2n=4x=48=1M + 13m(SAT) + 4sm + 5st + 1T, falling into the 2B type. This suggests that it has a close relationship with Indocalamus. The symmetry of the karyotype in Ferrocalamus is greater than that of Indocalamus. Evidence from cytology may support the argument that the genus is more primitive than Indocalamus, its sister group, which has an areal type of East

Asia.

The culms of *Ferrocalamus* are hard, and the local residents, the Kuchong (an ethnic group of Yunnan), call the bamboo, "iron bamboo." The Kuchong people have a long history of hunting, and they use this bamboo for arrows. Nowadays, the culms also provide a good material for making chopsticks and weaving-sticks.

4. Leptocanna Chia et H.L. Fung (1981)

Only one species has been found up to now in this genus. The species, *Leptocanna chinensis*, is a middle-size bamboo with pendant upper culms which can be up to 20 m long and 4-5 cm in diameter. Sometimes this bamboo is climbing in habit. Originally, *L. chinensis* was treated as a species of *Schizostachyum*. After careful study of the type material (flowering branchlets with leaves, A. Henry 10420, K) and field investigation of the type locality, Mengzi of Yunnan, Chia and H.L. Fung (1981) created a new generic name, *Leptocanna*, for the species. *Leptocanna* is a genus intermediate between *Melocanna* and *Schizostachyum* in the phylogenetic process. It is distinguished from the former by its sympodial, caespitose culms, spikelets with one fertile floret and one sterile floret (lemma), and bicarinate palea apex, and from the latter by its three lodicules and erect vaginablade.

Growing in the mountainous evergreen, broad-leaved forest, *Leptocanna* is endemic to Yunnan, China, at elevations of 1500-2500 meters. The chromosome numbers of *L. chinensis* are 2n=6x=72, the same as those of *Melocanna baccifera* (F. Du and Hsueh, in press). It seems that *Leptocanna* is more primitive than *Schizostachyum*. Both genera have a tropical floristic origin.

The name, *Leptocanna*, Lepto-(from the Greek), thin and -canna (also from the Greek), cane, refers to the thin walls of the culms, as little as 2-3 mm thick. These culms are a very good material for weaving. The native residents of Southeast Yunnan also use them for making "Gao-Sheng," a kind of native rocket used in festivals.

5. Gaoligongshania D.Z. Li, Hsueh et N.H. Xia (in ed.)

A recent expedition to the Gaoligong Shan Mountains Natural Preserve by the Southwest Forestry College and the Forests Department of the Yunnan Provincial Government in 1990 collected a very peculiar specimen of bamboo. It is a shrub-like, sometimes epiphytic on trees, large leaved, slender-culmed and single branchleted bamboo. The vegetative parts resemble those of *Indocalamus*. However, this bamboo has sympodial rhizomes while *Indocalamus* always has monopodial or amphipodial ones.

Chia et al. (1988) published Monocladus, which is similar to Indocalamus in the vegetative parts. The main differences between them are that Monocladus has sympodial rhizomes and iterauctant inflorescences, while Indocalamus has monopodial or amphipodial rhizomes and semelauctant inflorescences. Without flowering material, we immedialtely considered that the bamboo in the Gaoligong Shan Mountains was a member of Monocladus. Therefore, a new species, Monocladus macrophyllus Hsueh et Hue (H. Li, in press), was proposed.

Due to a more recent expedition to the Dulongjiang area (upper reaches of the Irrawaddy River) by the Kunming Institute of Botany, Academia Sinica in 1991 made a comprehensive collection of the same bamboo. The junior author (DZL) visited the Vienna herbaria bearing in mind the above-mentioned collections, and found the obviously conspecific status of *Arundinaria megathyrsa* Hand.-Mzt. and *Monocladus macrophyllus* Hsueh et Hue, for its conspicuous auricles, large leaves, single branchlets, as well as for

its type locality. The type of *A. megathyrsa* was collected in the Dulongjiang area. Meanwhile, Yi Tongpei (1993) had the same idea but he ignored the fact that *A. megathyrsa* has a semelauctant inflorescence. Thus, Yi's new combination, *Monocladus megathyrsus*, is incorrect.

In due course a new genus, *Gaoligongshania* D.Z. Li, Hsueh et N.H. Xia (in press), should be erected to accommodate *Arundinaria megathyrsa* Hand.-Mzt. The new genus differs from *Indocalamus* by its sympodial rhizomes, clustering clumps, larger inflorescences, linear spikelets and three stigmas. In that case, the combination, *Indocalamus megathyrsus* (Hand.-Mzt.) C.D. Chu et C.S. Chao (1981), is not correct. Although there are some vegetative similarities with *Monocladus*, there is indeed little affinity with the latter due to the different types of inflorescences.

If the genus *Yushania* is recognized, there are some relationships between them. Further, the new genus is somewhat close to the *Arundinaria hirsuta* and *Yushania uniramosa* group (Campbell, 1991), whereas the culm-necks are always elongated in the latter. Besides, *Yushania* have much shorter inflorescences and spikelets, with 2 stigmas in the florets (see Table 3).

Table 3. Main Points of Similarities and Differences among Gaoligongshania and Related Genera (Group)

	Character										
Group	Rhizome	Culm	Branchlet(s)	Leaves	Inflorescence	Stigmas					
Gaoligong- shania	Sympodial with no elongated necks	Clustering	1, equal to the culm	Large	Very large, up to 45 cm long; semelauctant; spikelets linear	3					
Monocladus	Sympodial with no elongated necks	Clustering	l, equal to the culm	Large	Iterauctant	3					
Indo- calamus	Monopodial or amphipodial	Scattering	l, equal to the culm	Large	Semelauctant 6 stamens	2					
Yushania hirsuta group	Sympodial with elongated necks	Scattering	1-3 (-several)	Small to medium	Semelauctant 3 stamens	(2)					
Arundi- naria	Monopodial or amphipodial	Scattering	3 - several	Small to medium	Semelauctant 3 stamens	3					

A phytogeographical survey shows *Gaoligongshania* is endemic to the Irrawaddy Salween watershed, at the elevation of 1300-2200 meters of the Gaoligong Shan Mountains, while *Monocladus* are distributed in South China's Hainan Island, Guangdong and Guangxi Provinces. In addition, *Indocalamus* are usually distributed in the Sino-Japanese floristic region, at mostly below 1000 meters. *Arundinaria* have a distribution pattern of East Asia and North America.

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Punya P. Poudyal*: Fodder Value of Some Bamboo Species of the Kathmandu Valley of Nepal

Abstract

The fodder value of Tama Bans (*Dendrocalamus* spp.), Taru Bans (*Bambusa tulda*) and Dhanu Bans (*B. balcooa*) are analyzed. The crude protein content was found to be between 12 and 15 per cent.

Introduction

Nepal is an agricultural country. Farming is done by traditional methods. Bulls and male water buffaloes help in ploughing the fields. Cows and female buffaloes provide milk. Cattle are the source of manure as well. Milk, yogurt and butter can be sold fairly easily and at a good price too. Hence, farmers prefer to rear a few milking cows for economic reasons, and a pair or two of the working animals for supplying the "manpower." These animals are fed with tree fodder, straw, etc. There is little shortage of fodder during the spring, rainy and autumn seasons (April to November). The animals are fed with dry matter like paddy straw, lentil husk and vine, corn husk, etc. and some tree fodder. Since the dry fodder can be stored for a long time, the farmers prefer to save it for unforeseen emergency periods and switch over to alternative fodder during the late winter season of February and March.

Out of the 170 plus fodder species in Nepal, over 30 species are used extensively. Bamboo fodder plays a significant role during the late winter by being one of the main sources of fodder. Cattle are allowed to graze in the natural forest on Tite Nigalo (*Drepanostachyum intermedia*), Ghode Nigalo (*Thamnocalamus* spp.), and Malinge Nigalo (*Arundinaria racemosa*) in the higher elevations.

Importance of Bamboo Fodder

Bamboo is the first priority fodder during the winter season in southern Terai (plains) whereas it is third or fourth priority fodder in northern Terai. Some 77 percent of the farmers of Bariyarpur village of Bara district put bamboo as their most favored species for planting (Upadhyay, 1991). The farmers of Baglung and Parbat districts pay up to Rs500.00 per clump per year for leaf fodder of *Dendrocalamus* and *Bambusa* species (Shrestha and Tiwari, 1992). *Dendrocalamus* of western Nepal contained 14 to 18 percent crude protein, and this species seems to be one of the best fodder species in terms of nutritional value because it contains no tannins (Shrestha and Tiwari, 1992). Bamboo ranks as third to fourth priority fodder in most of the mountainous districts of Nepal except the far west where there is not enough bamboo for fodder (Upadhyay, 1991).

Specimen Collection

Since bamboo fodder is used in the driest season of the late winter, it was decided to collect the driest specimens. A culm facing the south was selected, pulled down, and leaves collected from the top, middle and bottom parts. The weight of each specimen was 200 g or more. The sun-scorched parts of the leaves were removed, but the petiole was left intact because cattle chew the petiole as well when feeding on bamboo fodder. In the case of Dhanu Bans, about 33 percent of each leaf was badly scorched by heat, but, of course, that part was removed. The specimens were air dried in a carpeted room for 6 days and 7 nights (about 156 to 160 hours). Then, out of the dried leaves of each specimen

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100g was weighed and packed in labeled polyethylene bags and brought to a laboratory for analysis. There, each specimen was pounded to acquire 30 grams of granules/powder to undergo various tests. The specimens of Tama Bans (*Dendrocalamus* spp.), Taru Bans (*Bambusa tulda*) and Dhanu Bans (*B. balcooa*) were collected from Dholahiti section of Khumaltar Village, Lalitpur District. This district lies in the southern part of the Kathmandu Valley.

Results

The laboratory report showed that the percentage of ash content was slightly high in four out of nine specimens. According to Mr. Shree Krishna Khanal, who did the tests, most of the newly flushed leaves of tree fodder showed 6 to 7 percent of ash, but mature leaves contained 11 to 16 percent. The mature leaves of bamboo fodder would show about 15% of ash-content. The higher percentage could have been because of the petiole which is normally not used while analyzing the tree fodder, or the leaves were too dry. This author could not avail the services of a moisture meter suitable for the leaves. The specimens collected from the base of Dhanu Bans culm showed 14.97%, the highest percentage of crude protein. The lowest of 12.22% was acquired from the base of the Taru Bans culm. In Taru and Tama Bans the highest crude protein content was found in the mid-culm specimens, with 14.4% and 14.05% respectively. The people of Khumaltar Village, however, didn't feed bamboo fodder to the milking cows because, people from all 11 houses surveyed believed that bamboo fodder would decrease the amount of milk.

Conclusion

Bamboo is said to be available in 73 of the 75 districts of Nepal. The remaining two districts need to be studied. Except in exceptional cases, bamboo fodder is fed to the cattle, and is a very appropriate fodder plant during seasons of food shortage. Since the fodder value varies from month to month, species to species, and place to place, Nepal needs to have the specimens of some common bamboo species from various places collected at different seasons, their fodder value analyzed and this information disseminated to the farmers.

Acknowledgment

I would like to express my sincerest thanks to Dr. Ian J. McCracken of the Community Forestry Development Project for his support in one way or another, to Mr. Shree Krishna Khanal of the Central Animal Nutrition Division for doing the laboratory tests of the specimens, and to Mrs. Mary Rolle for typewriting this text.

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Table 1. Bamboo Fodder Value Analysis

Name	Date of Collection	Part	DM %	OM %	CP %	NDF %	ADF %	Lignin %	Total Ash %	CSC %	С %	НС %
Taru		Тор	87.25	89.86	12.46	73.72	50.64	12.75	10.14	26.28	37.89	23.08
(Bambusa tulda)	3 Mar 92	Middle	93.58	89.68	14.40	74.08	54.50	13.24	10.21	25.92	41.26	19.58
		Bottom	82.58	89.68	12.22	73.86	51.24	12.92	10.32	26.14	38.32	22.62
Tama		Тор	91.7	80.17	13.49	70.22	52.18	20.02	19.83	29.78	32.16	18.04
(Dendro- calamus spp.)	7 Mar 92	Middle	90.87	79.32	14.05	71.70	55.57	21.95	20.68	28.30	33.62	16.13
		Bottom	87.39	81.18	13.23	73.19	49.34	16.65	18.82	26.81	32.69	23.85
Dhanu		Тор	93.38	84.12	13.06	67.88	46.83	16.97	15.88	32.12	29.86	21.05
(Bambusa balcooa)	5 Apr 92	Middle	92.81	84.47	12.93	73.01	48.82	18.00	15.53	26.99	30.82	24.19
		Bottom	93.36	82.52	14.97	70.36	47.71	18.20	17.48	29.64	29.51	22.64

DM = Dry Matter, OM = Organic Matter, CP = Crude Protein, NDF = Neutral Detergent Fiber, ADF = Acid Detergent Fiber, CSC = Cell Soluble Contents, C = Cellulose, HC = Hemi Cellulose.

Table 2. Khumaltar Village, Lalitpur District, Kathmandu Valley, Nepal

Elevation: 1350 m. Latitude: 27 40' North. Longitude: 85 20' East. Rainfall in millimeters.

	1	2	3	4	5	6	7	8	9	10	11	12	Annual	Monsoon
1987	19.4	52	28.8	36.7	35.8	108.4	503.2	210.2	149.1	288.6	0	17	1449.2	970.9
1988	2	33.5	73.5	53.5	133.2	266.6	350	328.5	120	9	21	106	1496.8	1065.1
1989	58.5	10	4	0	217	61.5	357	136	149.5	2.8	0	0	996.3	704
1990	0	40.6	61.3	60.8	81.1	103.5	396.9	246.5	111	48.8	0	5.4	1173.9	875.9
1991	18.2	8.6	39.6	60.6	90.1	153.3	137.4	231.9	107.4	0.6	0	22.3	870	630
1992	6	17	0	44	70	-	-	-	-	-	-	-	-	-

Source: Department of Meteorology, Kathmandu. This study concluded in May of 1992.

Table 3.

Khumaltar. Elevation: 1350 m Latitude: 27° 40′ North, Longitude: 85° 20′ East.

Temperature in Degrees Celsius

	19	87	19	88	1989 1990 1991 1992 (Air		1991		Airport)			
	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min
January	17.8	0.3	18.2	1.4	15.8	1.8	19.7	2.5	-	-	-	8.0
February	19.4	4.7	20.9	5.0	19.1	1.6	18.6	4.8	-	-	19.0	3.0
March	21.9	7.0	22.3	7.1	24.2	6.0	20.2	6.8	-	-	28.0	8.0
April		10.3	27.2	10.6	28.8	9.9	25.2	9.9	-	-	30.0	11.0
May	28.0	13.3	27.4	15.5	28.4	14.9	26.3	-	-	-	27.0	14.0
June	28.0	18.8	27.9	18.7	28.3	18.9	28.6	19.8	-	_	-	-
July	26.8	19.9	27.2	19.9	26.3	19.4	26.6	20.4	-	_	-	-
August	26.3	19.4	26.8	19.6	27.2	19.2	27.4	20.1	-	-	-	-
September	26.4	18.8	27.2	17.6	26.4	18.2	26.9	18.8	-	-	-	-
October	24.8	12.4	26.0	13.5	26.5	15.1	24.8	13.2	-	-	-	_
November	22.5	6.5	23.2	5.8	21.8	6.0	23.5	6.9	-	-	-	-
December	20.0	2.9	20.5	3.7	18.9	1.8	19.8	2.5	-	-	-	-

Source: Department of Meteorology, Kathmandu. 1991 and 1992 records were not available for Khumaltar. 1992 records are for the Tribhuvan International Airport; Elevation: 1,464 m; 5 km from Khumaltar. This study concluded in May of 1992. Hence, latest data available up to May 1992 is included.

Margaret J. Stern*: Bamboo parasites - The occurrence of gall midges (Diptera: Cecidomyiidae) on Guadua and Fargesia

Abstract

Gall-forming midges and a hymenopteran parasitoid were found in herbarium collections of *Guadua paniculata* from Brazil and *Fargesia nitida* from China. It is unusual to find evidence of ecological associations in herbaria specimens as most plant collections are made of healthy typical-looking individuals. The gall-makers had entered the living bamboo and induced a branch node and its surrounding leaves to swell. The bamboo galls resembled large grass spikelets and were similar in form to other known grass stem galls, suggesting phylogenetic constraint on gall architecture. The gall midges from Brazil are in the generalist plant-feeding genus *Contarinia*. The Chinese specimens are part of the nominal species complex, closely related to the Asian rice gall midge, *Orseolia oryzae*. Apparently, no bamboo of any species has been previously described as a host plant for cecidomyiids. These host associations are of significance to insect and plant ecologists and systematists for implicating potential host shifts and for chemical and biological control efforts against gall midges.

Introduction

Bamboos are hosts to a wide variety of insect taxa. Fly larvae, ants, termites, and some beetles are known to feed on culms of *Bambusa* spp. in Bangladesh (Boa and Rahman, 1987) and beetles have also been seen feeding on young internodes of *Chusquea* spp. in the tropical Andes (pers. observ.). Bamboos have a distinctive aphid fauna (Homoptera: Aphididae) with cultivated bamboos being particularly prone to infestation (Eastop, 1986). For example, the aphid *Pseudoregma bambucicola* develops large, dense colonies on the culms of an introduced ornamental species, *Bambusa multiplex* (Loureiro) Raeuschel, in Japan (Sunose *et al.*, 1991). In Taiwan, five species of aphids are known to attack the makino bamboo, *Phyllostachys makinoi* Hayata, and one of them, *Phyllaphoides bambusicola*, is a major pest (Chang, 1980). The hemipteran, *Barreratalpa bambusi*, was found eating leaves of *Otatea acuminata* (Munro) Calderón & Soderstrom in the Mexican highlands (Brailovsky, 1988), and, caterpillars of pronophiline butterflies (Lepidoptera: Satyridae) feed on the leaves of *Chusquea* spp. throughout their overlapping ranges in the highlands of Central and South America. They do not, however, appear to cause much defoliation (Stern, unpublished).

Many insect herbivores and parasites on bamboos around the world remain undescribed. The present study is a step towards identifying and learning the natural history of some of these insects. The objectives of this study were to (1) report the occurrence of morphologically similar stem galls on two geographically and taxonomically disparate bamboo species, *Guadua paniculata* Munro and *Fargesia nitida* (Mitford) Keng f., (2) describe the gall architecture, (3) determine the causal agent of those stem galls, and (4) discuss the ecological implications of their presence on a bamboo host.

Materials and Methods

Bamboo specimens

Guadua paniculata is a widespread and morphologically variable species extending from Bolivia north into Mexico, at elevations between 50 and 700 m (Soderstrom et al., 1988). Various species of Fargesia, including F. nitida, are widespread in the forested hills of central China. They are often the dominant bamboo in evergreen and deciduous broad-leafed forests between 1600 to 2000 m elevation and in mixed coniferous and broad-leafed forests between 2000 to 2600 m elevation (Schaller et al., 1985). Both these species are represented in the

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United States National Herbarium (US) at the Smithsonian Institution in Washington, DC. Although these specimens do not constitute a random survey, they do provide interesting initial information on galls associated with bamboo. The woody bamboos with stem galls were brought to my attention by the late T. R. Soderstrom, curator of botany and bamboo expert. What had momentarily appeared to him to be a new bamboo species in flower, upon close inspection, turned out instead to be bamboos infested with gall-forming insects.

The external morphology of galled bamboo collections of *Guadua paniculata* (four collections) and *Fargesia nitida* (three collections) was described. Galls from the following two collections (three sheets each) were then removed from herbarium sheets, rehydrated, and dissected for detailed study:

- (1) Guadua paniculata, Brazil, State of Maranhão, Município de Loreto: "Ilha de Balsas" in the region between the Balsas and the Parnaíba Rivers "3 km E of main house of Fazenda Morros, 100 m E of house at 'Sambaíba,' in gallery scrub of brook gully," (7° 23′ S, 45° 3′ W), 300 m, February 1970, G. Eiten and L.T. Eiten 10595. Species determination was made by Soderstrom when the specimens were accessioned in 1980. The sheets were annotated (perhaps at a later date) by Soderstrom as follows: "Dissection of the spikelet-like processes reveals that they are distorted leaves enclosing developing insect larvae."
- (2) Fargesia nitida, China, Shensi Province, Taipaishan, 2000 to 2200 m, 2 m in height and occurring in a dense "pure association." September 1932, K.-S. Hao 4459. Ta-Pa Shan [pinyin: Taibaishan] was located and identified as a mountain range that reaches an elevation of 4107 m in Shenshi Province [pinyin: Shaanxi] of central China (108° E, 34° N) (Soderstrom, 1979; and annotated herbarium sheet).

The following nomenclatural changes pertain to the bamboo species and specific collections reported on here. *Guadua paniculata* was originally accessioned as *Bambusa paniculata* (Munro) Hack. McClure's generic revision (1973) recognized the New World *Guadua* as a subgenus of Old World *Bambusa*, but *Guadua* is now considered a separate and valid genus (Soderstrom and Ellis, 1987; Soderstrom and Londoño, 1987). The 1932 Hao collection of *Fargesia nitida* also underwent nomenclatural revision; it was originally accessioned in US as *Arundinaria nitida*.

Galls and gall makers

Individual galls from dried herbarium specimens were measured with calipers from the basal end of the enlargement to the approximate distal point where the swelling ceased. Eight galls were then removed from the mount and rehydrated at room temperature in 1% Aerosol-OT for 48 hours. When the galls reached a slightly supple state, they were slit open lengthwise with a scalpel blade. The positions of all life stages of parasites (larvae, pupae) and parasitoids (adults) within the galls were noted. They were later dissected out of the gall, identified by experts R. Gagné and E. Grisell at the US National Museum (ent.), and fixed in F.A.A. (formalin-glacial acetic acid-70% ethanol [5:5:90, vol.]) for later examination. Light microscope observations of the galls and the gall makers were made and photographs were taken with a SLR 35 mm camera. Voucher specimens of all insects removed from the bamboo galls are housed in USNM (ent.).

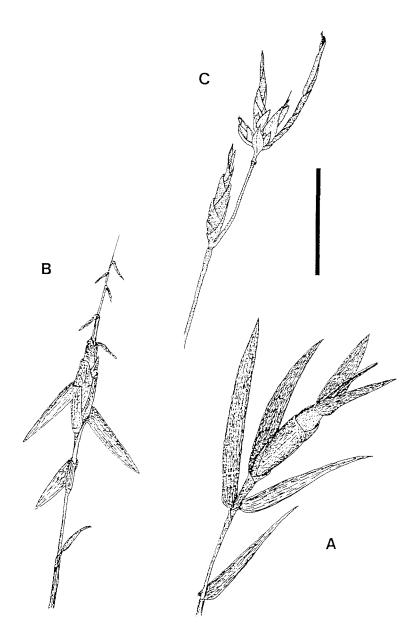


Fig. 1. Cecidomyiid galls on sterile bamboo specimens of (A) Guadua paniculata and (B) Fargesia nitida, and (C) normal florets (no parasitism) of a pseudospikelet of G. paniculata. Note the gross morphological similarities among the three bamboo specimens. Scale bar = 50 mm.

Results and Discussion

Gall position and morphology

Galls on the parasitized bamboo were located on branches, not the main stem (culm). They were located at a node within the woody secondary stem and were covered by foliage

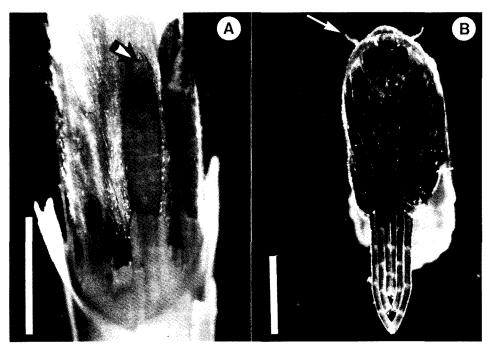


Fig. 2. (A) Internal view of dissected cecidomyiid gall on *Guadua paniculata*; three pupal cases are visible. The arrow points to the opening at the distal end of a pupal case. Scale bar = 5 mm. (B) Ventral view of a gall midge (Cecidomyiidae) pupa, *Orseolia* near *oryzae*. The arrow indicates sclerotized, pointed structures at the anterior end of the body that are used to cut an exit hole through the gall prior to emergence. Scale bar = 1 mm.

leaves. It appeared as though the internode of the affected stem was severely shortened so that a number of leaves arose abnormally close to one another on the stem. The external appearance of all the galls on both species of bamboo was morphologically similar (Fig. 1A, B). The leaf sheaths were enlarged, the blades were smaller than average, and the associated branch was lignified and fused to them to form the wall of the gall. Bambusoid inflorescences are of different types and much generic and specific-level specialization takes place in the structure of spikelets and their arrangement in the inflorescence (Soderstrom, 1981). Tissue modification resulting from insect damage at the terminal end of a branch could therefore be mistaken for a spikelet of a species not previously observed in flower (Fig. 1C).

The galls were elongated, rounded swellings of similar size (29-42 mm) in both bamboo species and there were fewer galls per stem on *G. paniculata* collections (one gall/stem) than on *F. nitida* collections (average 2.1 galls/stem). None of the galls examined showed evidence of exit holes that would indicate emergence of an adult insect. The stem galls on bamboo were comparable with those found on domesticated rice, known as "silver shoots." Gagné (1989) described this gall morphology as "imbricated [overlapping, like shingles] stem galls." The gall produced by the North American gall midge *Chilophaga gyrantis* on the perennial "three-awn" *Aristida gyrans* Chapm. (Gagné 1989, p. 252, Fig. 364) appears virtually identical to those found on the bamboos. The occurrence of morphologically similar galls on different host species, when many possible gall morphs are known to exist, suggest that there are some physical characteristics about grass stems that may constrain growth and determine gall architecture.

Gall inhabitants

Gall midges (Diptera: Cecidomyiidae) of two genera were the causative agents of the bamboo stem galls. Cecidomyiid eggs may be laid singly or in groups on leaves and, once hatched, the larvae crawl along the inside of a leaf sheath to feed on growing points by sucking plant juices, provoking an extensive reorganization of plant tissue. The larvae removed from galls on *Guadua paniculata* were identified as a species of *Contarinia* Rondani *sensu lato*. Gagné (pers. comm.) commented that "it is a strange *Contarinia* for the fact that its terminal abdominal segment is slightly recurved dorsally, possibly to give the larva purchase against the side of the gall." The galls contained four to nine discrete cylindrical cells where remnants of pupal cases (one per cell) were found buried in the lignified base of the gall at the base of the leaf sheath. Their empty pupal cases were elongated with an opening at the anterior end (Fig. 2A). *Contarinia* is a cosmopolitan gall midge genus that afflicts a wide variety of hosts. These hosts include economically important cereal, vegetable, fodder, and fruit species such as wheat (*Triticum* spp.), sorghum (*Sorghum bicolor* (L.) Moench), mustards (Brassicaceae), alfalfa (*Medicago sativa* L.), tomato (*Lycopersicum* spp.), and pear (*Pyrus communis* L.) (Skuhravá *et al.*, 1984; Gagné, 1989).

Late larval instar and pupal life stages of a cecidomyiid were found in stem galls on Fargesia nitida. Only a single midge was extracted from each of these galls, in contrast to those containing multiple inhabitants on G. paniculata. The gall-forming midge was identified as Orseolia sp. in the oryzae complex (R. Gagné, pers. comm.). The specimens of Orseolia were anatomically similar to the Asian rice gall midge, Orseolia oryzae (Wood-Mason), (see Gagné, 1985 for taxonomic revision of the genus), but a conclusive species determination was not possible due to the lack of adult forms. The rice gall midge has been recorded from India and southern China (PRC) to Indonesia within the latitudinal belt of 10° to 24° N (Hidaka, 1974). Given the extratropical and northerly location of Hao's bamboo collection (F. nitida, this study), at 10° north of the known distributional limit for the Asian rice gall midge, it is possible that this was not O. oryzae but rather a distinct species. All Orseolia species make similar fleshy type stem galls and it is impossible to distinguish the species strictly on gall morphology (Gagné, 1985). The pupae of Orseolia had well-developed anterior horn-like projections (Fig. 2B), probably used to cut a channel through the plant tissue to the exterior prior to emergence as an adult.

An adult form of a hymenopteran parasitoid was also found within a single gall on Fargesia nitida and identified as a member of the family Platygastridae (E. Grissell, pers. comm.), known to be natural enemies of gall midges in general. Species of Platygaster have been isolated from Orseolia oryzae and proved very effective in suppressing populations of its rice gall midge host (Hidaka et al., 1974). This finding could be important in biological control and pest management.

Ecological implications of the bamboo-gall midge association.

This study provided an example of unusual ecological information gleaned from herbarium sheets of plant collections made long ago; the presence of galls, parasites, and parasitoids implicating associations with previously unrecorded hosts. The possible off-season host shift between rice and bamboo is not surprising due to their taxonomic affinities and the ecological setting. Many non-bambusoid grasses have been previously recorded as off-season or primary hosts to *O. oryzae* in areas where rice is seasonal (e.g., in temperate regions of China) or not cultivated (Hidaka, 1974; Hidaka *et al.*, 1974; Gagné, 1985; Litsinger *et al.*, 1987). Within the Poaceae, the hypothesis of a close phylogenetic relationship between the oryzoids and the bamboos is likely, based on anatomical and morphological characters, and further supported by recent results from molecular research (Davis and Soreng, 1993; L. Clark,

pers. comm.). Furthermore, gall midges are more numerous in plant taxa with woody representatives than in those that are herbaceous (Gagné, 1989). Woody plants tend to live longer and be a more reliable resource to herbivores, parasites, and other plant symbionts, than ephemeral herbaceous plants.

There is no evidence for coevolution (*sensu stricto*) of plants and their gall midges, meaning that there can be a long evolutionary history without coevolution. The atypical growth and yield reduction resulting from *Orseolia oryzae* infestations on many cultivars of domestic rice, some specifically bred for gall midge resistance, is well documented (Hidaka *et al.*, 1974; Rajamani and Chatterji, 1986), and it is possible that a single rice cultivar or other plant species is host to more than one closely-related species of gall midge (Gagné, 1985). Gall midges are adapted to their hosts in specific ecological settings, and their distribution areas are strictly limited by the distribution of those hosts, particularly as they are not free-living insects. In such cases, the proximity or accessibility of appropriate hosts plays an important role in host transfer, equally or more important than close host relatedness (Mitter and Brooks, 1983; Gagné, 1985). This is the case both for access to off-season hosts and the acquisition of novel primary hosts that may lead to new ecological associations.

Extensive stands of Guadua paniculata typically occur in areas where the forest has been disturbed (e.g., river meander zones and areas of human colonization), and therefore are commonly found as "edge" vegetation near commercial and subsistence crops (pers. observ.). In central China, Fargesia nitida is often surrounded by upland rice and mixed crops of low-land and upland rice (Matsuo, 1975). Many other bamboos grow in association with crops since they thrive in forest openings created by humans during the conversion of forest to cultivated land. If gall midges are pests on commercial or subsistence crops, it is conceivable that nearby bamboos could be alternate hosts, facilitating pest access to the crops. This possibility deserves attention by agricultural entomologists as the management of gall midges is more difficult when wide ranges of hosts exist.

Acknowledgments

This paper is dedicated to the memory of the late Dr. Thomas R. Soderstrom who offered me the opportunity to learn about bamboos under his expertise and enthusiasm. I thank M. Sangrey for assistance in the grass collection at US and B. Lindsay for the drawing of galls and florets. For insect identification, I am very grateful to R. Gagné and E. Grissell. My thanks are extended to L. Clark, G. Romero, A. Shapiro, P. Ward, G. Webster, and anonymous reviewers for helpful comments on the manuscript. This project was funded by a Smithsonian Institution predoctoral fellowship and a S. I. visiting scientist grant.

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