

Morphological and molecular evidence clarifies the taxonomic position of *Indosasa solearis* and reveals the hybrid origin of *Sinobambusa tootsik*

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Abstract

Three-branched bamboo is a taxonomically difficult group due to recent rapid radiation and frequent hybridization, with generic and species delimitation of many taxa problematic. *Indosasa solearis*, described from North Vietnam based on flowering materials, was later transferred to *Sinobambusa*. But its taxonomic position remains arguable due to limited vegetative data. After a detailed morphological study of this bamboo at its type locality, we found that the overall morphology of this species is surprisingly similar to *I. parvifolia* and *I. jinpingensis*. Thus, we conducted morphological and phylogenomic analyses to ascertain the taxonomic position of *I. solearis* and its relationship with those two species. Morphological examination confirmed *I. solearis* exhibits diagnostic characters of *Indosasa*, like leptomorph rhizome, diffuse culms, strongly and asymmetrically raised branch supra-nodal ridges, 4–9 foliage leaves per ultimate branch, pseudospikelet, and each floret with six stamens and three stigmas. No essential difference was found among the three *Indosasa* species both on macro- and micromorphology. Phylogenies based on single-copy orthologous nuclear gene datasets and single nucleotide polymorphism data strongly support *I. solearis* as an *Indosasa* member, closely related to *I. parvifolia* and *I. jinpingensis*. Population genetic analyses revealed identical genetic component across all the three species. Combined with morphological and molecular evidence, we confirmed that *I. solearis* belongs to *Indosasa*, and is conspecific with *I. parvifolia* and *I. jinpingensis*. We therefore reinstate *I. solearis* and synonymize *I. parvifolia* and *I. jinpingensis* with it. Furthermore, our analyses also revealed the hybrid origin of *Sinobambusa tootsik*, with genomic signatures suggesting an ancient cross between *Indosasa* and *Pleioblastus*. This finding highlights the reticulate evolutionary history in the three-branched bamboo.

Introduction

Three-branched bamboo refers to a group of bamboos characterized by leptomorph rhizomes and branch complement with three branches per mid-culm node, mainly including six genera: *Indosasa* McClure, *Acidosasa* B. M. Yang, *Oligostachyum* Z. P. Wang, *Sinobambusa* Makino ex Nakai, *Pleioblastus* Nakai and *Pseudosasa* Makino ex Nakai [1–4]. Due to recent radiate evolution and frequent hybridization, generic and species delimitation within this group has been proven challenging [5, 6]. While previous studies mostly focused on solving the relationships among the groups within Arundinarieae at subtribal or generic level [1–3, 5–12], taxonomic revisions at specific rank have received less attention.

The genus *Indosasa*, a member of the three-branched bamboos, includes about 17 species mainly distributed in southern to eastern China, northern Vietnam and Laos. It is characterized by leptomorph rhizome, diffuse culms, strongly raised culm and branch supra-nodal ridges, pseudospikelets, and each floret with six stamens and three stigmas. [13–22]. Previous studies mainly based on morphology suggested that *Indosasa* has a close relationship with *Sinobambusa*, another three-branched bamboo genus [14, 23–25]. Since these two genera share highly similar vegetative traits, it is always difficult to distinguish them based on sterile materials. The key difference is the stamen number in each floret—*Indosasa* has 6 stamens per floret, whereas *Sinobambusa* has 3, rarely 2 or 4. Other less remarkable

differences include the branch angle (nearly horizontal in *Indosasa* vs. with an acute angle in *Sinobambusa*), the morphology of supranodal ridges (strongly raised and wider than sheath scar in *Indosasa* vs. not strongly raised or as wide as sheath scar in *Sinobambusa*), the shape of culm leaf blade (ovate-lanceolate in *Indosasa* vs. narrowly lanceolate or linear in *Sinobambusa*), etc.

Indosasa solearis was described by McClure [26] based on flowering materials (Fig. 1A) from Tam Dao, Vietnam, of which some taxonomically important vegetative characters, such as culm leaf, are still unknown. McClure stated that this species is morphologically similar to *I. crassiflora* McClure, but differs in having narrower pseudospikelet, lemmas with a thinner texture and more prominent veins, and sandal-shaped (obtuse) apex of palea. Nguyen [27] transferred it to *Sinobambusa*, and made a combination *Sinobambusa solearis* (McClure) T. Q. Nguyen without providing any reason. Nguyen's treatment was followed by some important bamboo works or databases, such as Vorontsova et al. [28] and "Plants of the World Online" (<https://powo.science.kew.org/>). However, this species has six stamens per floret according to the description in the protologue [26], which matches with the diagnostic character of *Indosasa*, rather *Sinobambusa*. Thus, Nguyen's taxonomic treatment seems questionable, and as the information of some key vegetative characters, such as rhizome and culm leaf, are still unknown, the taxonomic position of this species needs a further study.

During a field trip to Tam Dao, Vietnam—the type locality of *Indosasa solearis* in May 2024, we encountered a large bamboo grove mainly composed of one species. This bamboo bore a lot of new shoots at that time, thus we collected complete specimens including rhizomes and culm leaves. After careful observations in the wild and examination of the newly collected specimens, we found that it shares the same key characters with *I. solearis*, such as leptomorph rhizomes, 2–3 m high culm, striated internode, sheath scar with conspicuous remnants, strongly raised culm and branch supra-nodal ridges, prominent groove on the branching side of culm, 4–7 foliage leaves per ultimate branch, lanceolate to narrowly lanceolate foliage leaf blades with developed auricles and oral setae. We also unexpectedly found that the overall morphology of this species, especially the culm leaf, was very similar to two other *Indosasa* species distributed on the border of China and Vietnam, namely *I. parvifolia* C. S. Chao & Q. H. Dai, from Pingxiang City, Guangxi Zhuang Autonomous Region [14], and *I. jinpingensis* T. P. Yi from Jinping County, Yunnan Province (some works accept *I. jinpingensis* as a synonym of *I. parvifolia*, e.g. Vorontsova et al. [28]). Thus, we conducted further morphological and phylogenetic studies to ascertain the taxonomic position of *I. solearis* and its relationship with *I. parvifolia* and *I. jinpingensis*.

Materials and Methods

Morphological study

Most samples used in this study were collected from type locality (Table S1 & Table S2) to minimize identification error, as the long (sometimes 100–150 years) and typically semelparous life cycle of woody bamboos renders their identification using vegetative characters only [7, 9, 12]. Voucher specimens were deposited in IBSC. Other related specimens or specimen photos kept in the following

herbaria were also examined: GXFI, IBSC, KUN, PE, US and ZJFI. Herbarium acronyms follow Thiers [29]. Reproductive material was dissected under a stereo microscope (MZ101, Mshot, Guangzhou Micro-shot Technology Co., Ltd, Guangzhou, China) and photos were taken by the attached camera.

Micromorphology of foliage leaf epidermis of *Indosasa solearis*, *I. jinpingensis*, and *I. parvifolia* was studied by scanning electron microscope (SEM). Dried foliage leaf samples were collected from the type locality. The middle portion of foliage leaves (5×5 mm) were treated by ultrasonication in 0.1% fatty alcohol polyoxyethylene ether (n = 25) for 2 hours, followed by heating in a constant temperature for 12 hours, then retreated by ultrasonication for 2 hours. After the pretreatment, samples were cleared with 70% ethanol and dried at room temperature before mounting on stubs and sputtered by platinum. Observations and image acquisition were carried out using JSM-IT210 scanning electron microscope. Terminology for the epidermis appendages follows Ellis [30] and Chen et al. [31].

Taxon sampling for molecular analyses, DNA extraction and sequencing

Our taxon sampling was based on previous phylogenetic framework of the three-branched bamboos by Guo et al. [6] and Niu et al. [4]. A total of 30 samples represent 27 species from 11 genera were chosen for nuclear genes inference. The ingroup includes four samples of *Acidosasa*, six samples of *Indosasa*, five samples of *Pleioblastus*, two samples of *Pseudosasa*, six samples of *Sinobambusa*, and six samples from other representative genera in subtribe Arundinariinae. *Dendrocalamus latiflorus* Munro from the tribe Bambuseae was chosen as the outgroup (Table S1).

Fresh leaves were collected from field and dried in silica gel, then were used to extract genomic DNAs by the TIANGEN Genomic DNA Extraction kit (TIANGEN, Beijing, China). After sample quality controlling, a total amount of 0.2 µg DNA per sample was used as input material for the DNA library preparations and the genomic DNA sample was fragmented by Covaris LE220R-plus (Covaris, USA) to a size of 350 bp. The DNA fragments were amplified by PCR and a paired-end library was prepared for sequencing by DNBSEQ-T7 platform. The original data were filtered by Fastp software v.0.23.2 [32] to get clean data and at least 40 Gb deep genome skimming data (DGS) of each taxon were acquired.

Phylogenetic inference based on orthologous nuclear genes

To elucidate the phylogenetic position of *Indosasa solearis* and ensure robust phylogenetic inference, two nuclear datasets were constructed in this study. The first dataset included 737 common single-copy nuclear orthologous genes (SOGs), which were identified from protein-coding sequences of six published bamboo genomes-*Dendrocalamus latiflorus* Murno [33], *Bonia amplexicaulis* (L. C. Chia, H. L. Fung & Y. L. Yang) N. H. Xia, *Guadua angustifolia* Kunth, *Olyra latifolia* L., *Raddia guianensis* (Brongn.) Hitchc. [34] and *Phyllostachys edulis* (Carriere) J. Houz. [35] by Orthofinder v.2.5.4 [36] followed Niu et al. [4]. The putative SOGs were assembled by Hybpiper v.2.0.1 [37] and the filtered data were mapped to

each SOGs by BWA mapper function in Hybpiper. To confirm the mapping quality, gene mapping rate of each sample was calculated by Hybpiper and the sample was preserved if the rate passes 80%. Then 737 SOGs for each sample were recovered by a python script 'retrive_sequences.py'.

Since the samples in our study are allotetraploid bamboos (except *Dendrocalamus latiflorus*), SOGs detected by orthofinder may have more than two copies [4, 34]. Thus, protein-coding sequences of three temperate bamboos—*Hsuehochloa calcarea* (C. D. Chu & C. S. Chao) D. Z. Li & Y. X. Zhang, *Ampelocalamus luodianensis* T. P. Yi & R. S. Wang and *Phyllostachys edulis* (Carriere) J. Houz [38] were chosen to identify another SOGs dataset. Each sequence was firstly mapped to four BUSCO lineage datasets: eukaryota_odb10, embryophyta_odb10, poales_odb10 and viridiplantae_odb10 by BUSCO [39]. Then, orthologs of three reference sequences from each dataset were identified and combined together. The orthologue genes from three reference were combined and inputted to Orthofinder with 940 common SOGs identified. Sample data were mapped to each SOGs and recovered by Hybpiper. To further confirm the gene number of each sample, paralog_retriever by Hybpiper was conducted. Four genes with more than two copies were removed. Finally, a total number of 936 SOGs was detected.

Each single-copy orthologous gene matrix based on two different datasets was aligned by MAFFT [40] and trimmed by trim Al v.1.4 [41] with default settings. Phylogenetic tree of each SOG dataset was constructed by IQ-TREE v.1.6.12 [42] with Maximum Likelihood (ML) analysis. Branch support was estimated with 1000 bootstrap. Then all ML trees were combined to infer the species tree by ASTRAL [43] with default settings.

SNP calling and phylogenetic inference based on SNP data

Distantly related species might affect the phylogenetic result base on single nucleotide polymorphism site (SNP), especially for those taxa under rapid radiation [44–46]. The progress of SNP calling also consumes massive computer resources and time [47, 48]. Hence, we reduced our taxon sampling to only include 23 samples representing 20 species of subtribe Arundinariinae for SNP analysis (Table S2). *Indocalamus sinicus* Nakai was chosen as the outgroup in this analysis.

A total of 24 chromosome-level scaffolds were filtered from the high-quality genome of the moso bamboo—*Phyllostachys edulis* [35] and chosen as the reference for SNP calling. An index was built based on the reference by software BWA-MEM v.0.7.17 [49] and Picard v.1.16.1 (<https://broadinstitute.github.io/picard/>). The duplicated reads generated in PCR enrichment were removed using Fastuniq v.1.1 [50]. The filtered reads were then aligned to the reference by BWA-MEM with default setting and sorted by SAMtools to BAM files. SNP calling was performed by GATK v.4.3.0.0 [51] and the SNP data were filtered by PLINK v.1.9 [52] with user-recommended settings. For the subsequent analyses, linkage disequilibrium (LD) filtering was conducted by PLINK setting as '--indep-pairwise 50 10 0.5'.

For the phylogenetic analyses, filtered SNP data in GVCF format was transformed into PHYLIP format by a python script 'vcf2phylic.py' [53] and was used to estimate a species tree by CASTER [54]. Branch support was estimated by a bootstrap analysis with 1000 replicates and bootstrap value of at least 95% was considered to be strongly supported.

Population structure analysis

SNP data after LD filtration was converted from GVCF file to a bed file by PLINK and then was used as an input file to ADMIXTURE v.1.3.0 [55] to see the genetic background of different species, with the number of genetic clusters (K) set as 2–10. The values of cross-validation error were obtained from log files and compared, which determine the best genetic cluster (K). The plotting results for K in 3–9 were drawn by pophelper [56] and ggplot2 package [57] in R v.4.4.1. Principal component analyses (PCA) based on SNP data were conducted by PLINK and then plotted by ggplot2 package.

Detection and quantification of interspecific gene flow

Dsuite v0.5 [58] was employed for the allele frequency-based tests to further investigate interspecific gene flow. The f_4 -ratio was firstly calculated on the basis of the SNP coalescent species tree for all populations using the Dtrios program. The significant D-statistic and f_4 -ratio were visualized by scripts plot_d.rb and plot_f4ratio.rb. Then, f -branch statistic values for each phylogenetic branch were estimated by the Fbranch program. Finally, the result of f -branch statistic was plotted by a script dtools.py.

To quantify historical gene flow in *Sinobambusa tootsik*. PhyloNet v3.8.2 [59] was conducted for the phylogenetic network inference. Based on the result of Dsuite, six samples were chosen: *Indosasa crassiflora*, *Indosasa jinpingensis*, *Sinobambusa tootsik* (HB-14), *Pleioblastus maculatus*, *Pleioblastus gramineus* and *Sinosasa longiligulata* (outgroup). Input gene trees were inferred for 936-nuclear SOGs using IQ-TREE. InferNetwork_ML was executed to search for optimal networks containing 1 to 3 reticulations. The inheritance probability (γ) for each hybridization event was estimated to represent the genomic contribution of each parental lineage during the hybrid speciation event. The phylogenetic networks were visualized using Dendroscope v3.5.7 [60].

Results

Morphological comparison

Examination of the type specimen of *Indosasa solearis* revealed that this species owns six stamens per floret (Fig. 1E), supporting its placement within the genus *Indosasa* rather than *Sinobambusa*. The complete specimens with culm leaf and rhizome collected from its type locality exhibit additional morphological characters consistent with those diagnostic characters of *Indosasa*, including leptomorph rhizome, branch complement with 3 branches at each node from mid-culm to the top, branches nearly

horizontal, strongly raised culm and branch supra-nodal ridges, abaxial surface of culm leaf sheath scattered with tufts of setae and triangular to ovate-lanceolate culm leaf blade.

Detailed morphological comparison revealed that *Indosasa solearis* shares the same key characters with *I. jinpingensis* and *I. parvifolia*, such as internodes with ribs (particularly on old culms), prominent groove on the branching side of culm, infranodal region with a white powdery ring, culm leaf sheath with white powder adaxially, culm leaf blade with developed auricles and relatively small foliage leaf blades (Fig. 1B–C) with oral setae. Some small differences among them like indumentum or shape of some organs are unstable, as we found that the population from Vietnam show certain degree of variations (Fig. 2B–C). For example, the culm internodes are usually glabrous, but white-hispidulous ones also exist; the cluster of setae on abaxial surface of culm leaf sheath can be dense or sparse, sometimes even nearly absent (Fig. 3A–D); the shape of culm leaf auricles varies from elliptic, semicircular to falcate (Fig. 3E–G); the base of culm leaf blade is constricted or not (Table 1). Thus, these differences should be recognized as population variation.

Table 1
Comparison of *Indosasa solearis*, *I. jinpingensis* and *I. parvifolia*.

	<i>I. solearis</i>	<i>I. jinpingensis</i>	<i>I. parvifolia</i>
Vegetative characters			
Culm internode	glabrous, sometimes white-hispidulous, with a white-powder ring below culm node	glabrous, with a white-powder ring below culm node	densely white-hispidulous, with a white-powder ring below culm node
Branch number at each node of mid-culm	3, rare 1 or 2	3, rare 1	3, sometimes 1 or 2
Abaxial surface of culm leaf sheath	with sparse or dense cluster of setae, sometimes subglabrous	with sparse cluster of brown setae	with dense cluster of brown setae, glabrescent
Culm leaf auricle	shape varying, elliptic, semicircular, or falcate, with dense and curly oral setae	elliptic, with dense and curly oral setae	semicircular, with curly and radiated oral setae
Culm leaf blade	triangular to ovate-lanceolate, glabrous, sometime with striga, base constricted or not	triangular, glabrous, base not constricted	triangular to triangular-lanceolate, densely hispidulous both sides, base constricted
Ultimate foliage leaves	4–7	(1)2–4(5)	4–7
Foliage leaf blade size (cm)	9.5–15 × 1–1.8	7.5–13.5 × 1–1.5	6–14 × 1–1.5
Foliage leaf auricle	ovate, with erect or radiated oral setae	oblong, with erect oral setae	small, with erect oral setae
Table 1 continued			
	<i>I. solearis</i>	<i>I. jinpingensis</i>	<i>I. parvifolia</i>
Reproductive characters			unavailable
Type of spikelet	pseudospikelet	pseudospikelet	
Number of florets each spikelet	5–13	5–11	
Gemmiferous bracts	9	4–6	
Note: The data of <i>I. jinpingensis</i> and <i>I. parvifolia</i> were obtained from protologues, while those of <i>I. solearis</i> were from the protologue and the newly collected specimens from Vietnam listed in the text.			

	<i>I. solearis</i>	<i>I. jinpingensis</i>	<i>I. parvifolia</i>
Vegetative characters			
Rachilla segments	glabrous except the ciliate apex, hollow	glabrous, hollow	
Lemma	1.2 cm long, apiculate, glabrous, with many veins	1–1.2 cm long, apiculate, glabrous, with many veins	
Pale	shorter than lemma, apex obtuse	shorter than lemma, apex obtuse	
Stamens	6	6	
Type locality	Tam Dao, Vietnam	Jinping County, Yunnan Province, China	Pingxiang City, Guangxi Zhuang Region, China
Note: The data of <i>I. jinpingensis</i> and <i>I. parvifolia</i> were obtained from protologues, while those of <i>I. solearis</i> were from the protologue and the newly collected specimens from Vietnam listed in the text.			

Comparison of reproductive materials further shows that *I. solearis* and *I. jinpingensis* share nearly the same floral morphology (Fig. 1A & C). Both species having pseudospikelet with 5–13 florets, gemmiferous bracts gradually becoming larger upwards, glabrous and hollow rachilla segments, pointed lemma and blunt apex of palea (Fig. 1D & F). In conclusion, there is no essential macro-morphological difference among *I. solearis*, *I. jinpingensis* and *I. parvifolia*.

The micromorphological analyses also reveal that *I. solearis*, *I. jinpingensis* and *I. parvifolia* (Fig. 4) have identical morphology of foliage leaf epidermis. Specifically, they share the same kind of silica cells, microhairs, prickles (Fig. 4D–F) and stomatal apparatus, which is covered with four to eight elongated papillae (Fig. 4G–I).

Phylogenetic inference

The ASTRAL species trees inferred from 737-nuclear SOG and 936-nuclear SOG gene trees showed that *Indosasa solearis* and other sampled *Indosasa* species as well as the type species of *Indosasa*, i.e., *I. crassiflora*, are clustered into a clade with strong support. *Indosasa solearis* is distantly related to *Sinobambusa* species, but together with *I. jinpingensis* forms a sister clade with *I. parvifolia*, which indicates that these three species have a close relationship (Fig. 5). However, the genus *Sinobambusa* was resolved as a sister group to *Pleioblastus* and *Pseudosasa* (PP = 0.64) in the species tree inferred from 737-nuclear SOG gene trees (Fig. 5A), while it is sister to *Indosasa* (PP = 0.52) based on 936-nuclear SOG gene trees (Fig. 5B).

The coalescent species tree inferred from concatenated SNP matrix also strongly supported *Indosasa solearis*, *I. jinpingensis* and *I. parvifolia* form a clade (Fig. 6A). The species tree inferred from the SNP

matrix is nearly identical to the species tree based on the 936-nuclear SOG gene trees (Fig. 5B), except that *Sinobambusa* was resolved as paraphyletic.

Population genetics analyses

In our population structure analysis (Fig. 6B), the cross-validation (CV) error decreased as the number of ancestral population (K-value) was reduced (Table S3). Hence, we present the population structure for K-values ranging from 3 to 9, which correspond with our morphological observations. When K = 3, all the *Indosasa* samples, including *I. solearis*, were assigned by a dominant genetic component (represented by the red cluster). Across all tested K-values, samples of *I. solearis*, *I. jinpingensis* and *I. parvifolia* consistently shared identical ancestral subpopulation. Besides, both *Sinobambusa sat* and *S. tootsik* have two different subpopulation components with one from *Indosasa* and the other from *Pleioblastus* under the K cluster of 3 or 4.

Principal component analysis (PCA) showed that *Indosasa solearis*, *I. jinpingensis* and *I. parvifolia* are closely clustered and almost overlapped together in the principal component space (PC1: -0.1443 to -0.1432, PC2: 0.3108 to 0.3171), indicating a highly similar genetic background (Fig. 6C).

Gene flow analyses

Given the distinct subpopulation structures observed in *Sinobambusa sat* and *S. tootsik*, we further investigated the underlying patterns of interspecific gene flow. Patterson's D-statistics and the f_4 -ratio tests across all possible species trios revealed widespread and significant signals of introgression in the three-branched bamboo (Fig. S1).

Consistent with the ADMIXTURE analysis, the D-statistic analyses detected specific gene flow events involving both *Sinobambusa* species. Notably, we found significant evidence of gene flow from *Acidosasa glauca* into both *S. sat* and *S. tootsik* (NZY171), also from *Indosasa sinica* into *S. tootsik* (NZY171). The other sample of *S. tootsik* (HB-14) showed introgression signals from both the *Indosasa* and *Pleioblastus* clades (Fig. 7A). This differential pattern of ancestry aligns closely with the multicomponent structure observed in the ADMIXTURE analysis.

Further inference of the phylogenetic network by Phylonet supported hybrid speciation in *Sinobambusa tootsik* (HB-14). The model fit, assessed by total log probability, improved as more hybridization events were allowed (Table S4). The inferred network containing one and two reticulation events suggested an asymmetrical hybrid origin of *S. tootsik* (HB-14), with 44.02–48.24% of the ancestral genome derived from *Indosasa jinpingensis* and 55.98–51.76% from *Pleioblastus maculatus* (Fig. 7B-C).

Discussion

Taxonomic position of *Indosasa solearis* and its relationship with *I. jinpingensis* and *I. parvifolia*

Recent studies suggested that *Indosasa* sensu lato is non-monophyletic [6, 20]. The *Indosasa* sensu stricto (s.s.) is newly defined by the possession of leptomorph rhizomes, diffuse culms, strongly and asymmetrically raised branch supra-nodal ridges, usually 4–9 foliage leaves per ultimate branch, pseudospikelet, and each floret with six stamens and three stigmas [20, 21]. *Indosasa solearis* exhibits all these key diagnostic characteristics of *Indosasa* s.s.. Combined with the phylogenetic evidence (Figs. 5 and 6A), we confirm that this bamboo belongs to *Indosasa*. We therefore reinstate the name *Indosasa solearis* McClure.

Morphological analyses reveal that *Indosasa solearis*, *I. jinpingensis* and *I. parvifolia* share the same morphology of culm internode, culm leaves, foliage leaves and pseudospikelets, and there is no essential difference among them. Comparison of the micromorphology of leaf epidermis also shows a consistent pattern among these three species (Fig. 4), which is type Ⅱ according to Zhang et al. [61]. Additionally, population genetic analyses indicate that they share distinct genetic composition compared to other *Indosasa* species and mix together with a very close genetic distance (Fig. 6B–C).

In a word, the evidence from morphology and phylogenetics both confirms that *Indosasa solearis*, *I. jinpingensis* and *I. parvifolia* are conspecific. According to the Art. 11.4 of *International Code of Nomenclature for algae, fungi, and plants (Madrid Code)* [62], as the name *I. solearis* McClure (1942) predates *I. parvifolia* C. S. Chao & Q. H. Dai (1983) and *I. jinpingensis* T. P. Yi (2001), we treat the latter two as synonyms of *I. solearis*.

Potential hybrid speciation/introgression in other three-branched bamboos

Gene flow is fundamental for evolution, which will enhance variability within population and facilitates novel trait combinations [63–65]. Temperate woody bamboos (tribe Arundinarieae) are allopolyploids, derived from an ancient hybridization event between two ancestral diploid species [4, 34, 66–69]. Hence, our study also identified additional homoploid speciation, allopolyploidy or introgression events, which are responsible for some phylogenetic conflicts (Figs. 5 and 6A). For instance, two samples of *Sinobambusa tootsik* (NZY171 and HB-14) were close to the *Pleioblastus* and *Pseudosasa* clade in the 737 SOG-based phylogeny but grouped with *Indosasa* in the 936 SOG-based tree and SNP-based tree. Population genetics analysis and gene flow tests further revealed that these individuals possess mixed genetic components from both *Pleioblastus* and *Indosasa* (Fig. 6B, Fig. 7).

Morphologically, *Sinobambusa tootsik* is similar with *Pleioblastus* species in having 3–5 branches per culm node, prominent setose sheath scar usually with a corky ring, and striga at the base of culm leaf sheath, radiated culm leaf oral setae, each spikelet with more than 10 florets, and white powdery lemma, and also shares some traits with *Indosasa* species in protruded culm and branch node, ultimate branchlet with more than 5 foliage leaves, and pseudospikelets [14–16, 23–25, 70–72], which implies its hybrid origin of *Pleioblastus* and *Indosasa*. However, due to limited sampling, the evolutionary

relationships among *Sinobambusa*, *Indosasa* and *Pleiblastus* remain unclear and warrant further investigation.

Taxonomic Treatment

Indosasa solearis McClure, J. Arnold Arbor. 23(1): 94. 1942. $\equiv$ *Sinobambusa solearis* (McClure) T.Q.Nguyen, Bot. Zhurn. (Moscow & Leningrad) 76(6): 879. 1991. (Fig. 8) **Type.** Vietnam, Tonkin: Tam Dao massif, elev. 1000m, December 1930, *Pételot* 4287 (Holotype: US1610012, image!; Isotype: US1610013, image!, US2434123, image!).

= *Indosasa parvifolia* C.S.Chao & Q.H.Dai, Acta Phytotax. Sin. 21(1): 67, pl. 3. 1983. *syn. nov.* **Type.** China, Guangxi Zhuang Autonomous Region, Pingxiang City, Daqingshan, 5 May 1978, Z. D. Zhu & Q. S. Zhao 78008 (holotype: NF!; isotype: PE 01512514–01512517, images!).

= *Indosasa jinpingensis* T.P.Yi, J. Bamboo Res. 20(4): 1. 2001. *syn. nov.* **Type.** China, Yunnan Province, Jinping County, Adebo, Shangzhai, elev. 1500m, 20 April 2001, T. P. Yi 200101 (holotype: SIFS!).

Diagnosis. *Indosasa solearis* is notably distinctive from other *Indosasa* species in its small size of foliage leaf blades, usually $6\text{--}15 \times 1\text{--}1.8$ cm.

Description. Rhizome leptomorph. Culm erect, diffuse, 5–10 m tall; internode with ribs, slightly white powdery, glabrous or with white-hispidulous; supra-nodal ridge prominent, wider than sheath scar, with a white powdery ring below node; branches 3 at each node of mid and upper culm, sometimes 1 or 2, branching side with a prominent groove; secondary branch node conspicuous and asymmetrically raised. Culm leaf sheath orange-yellow, $12\text{--}22 \times 5\text{--}15$ cm, leathery, deciduous, farinose, densely or sparsely with cluster of brown setae or subglabrous; ligule very short, slightly serrulate, sometimes ciliate; auricles prominent, from elliptic to semicircular, or falcate with dense and curly oral setae; blade triangular to ovate-lanceolate, green with brown margin, slightly farinose, glabrous sometimes with striga, base constricted or not, sometimes joint with auricles. Foliage leaves 4–7 per ultimate leafy branchlet; sheath glabrous; auricles ovate to oblong, with oral setae erect or radiated; ligule truncate, ca. 0.5 mm high; blades lanceolate to narrowly lanceolate, $6\text{--}15 \times 1\text{--}1.8$ cm, adaxially glabrous, abaxially pubescent, apex acuminate, serrulate marginally. Pseudospikelet up to 8 cm long, sub-fusiform, base narrow, apex blunt; prophyll membranous, ca. 5 mm long, keels pubescent; bracts ca. 9, papery, glabrous, 3–16 mm long, ovate, apex sometimes with small blades or apiculate, with veins abaxially; florets 5–13 with 1–3 sterile florets at the top; glume 1 or absent, similar to lemma, but shorter; rachilla segments thick, with pith, hollow when dry, twisted, with one side notably concave in the middle, the other side convex with cilia toward apex; lemma ca. 1.2 cm long, apex obtuse or subacute, apiculate, glabrous abaxially, with many conspicuous veins, apex strigose adaxially; palea shorter than lemma, papery, keels 2, ciliate, apex obtuse; lodicules 3, sub-equal, veins prominent, lanceolate or oblong, apex acuminate or acute, ciliate at the margin; stamens 6, anthers ca. 5 mm long, linear, apex emarginate; ovary narrow, glabrous; style short, glabrous; stigmas 3, close to each other. Mature caryopsis unknown.

Distribution and habitat. This species is distributed in China (Guangxi, Yunnan) and Vietnam (Lao Cai, Vinh Phuc). It usually grows under evergreen broad-leaf forests at elevations of 800–1500 m.

Phenology. New shoots from April to May; flowering in December.

Vernacular names. Chinese name “小夜大节竹” [“xiǎo yè dà jié zhú”] or “哈竹” [“hā zhú”]. The reason for the latter name is that this bamboo is widely distributed near the houses of Hani people in Yunnan.

Additional specimens examined. CHINA. Guangxi Zhuang Autonomous Region: Pingxiang City, Daqing Mountain, elev. 830 m, 24 May 2021, Z. Y. Niu, NZY055 (IBSC); *ibid.*, 9 June 2023, Z. Y. Niu NZY247 (IBSC). **Yunnan Province:** Jinping County, Adebo, 15 March 1982, W. W. Zhou JP82315 (ZJFI, image); *ibid.*, elev. 1540 m, 15 May 2021, Z. Y. Niu NZY038 (IBSC); ManHao, elev. 932 m, 29 July 2010, Z. M. Cai *et al.* CZM050 (KUN, barcodes: 1232103–1232107; 1232276), CZM052 (KUN, barcode: 1232108); ShaYiPo, elev. 1400 m, 25 May 2024, Yu L. Huang *et al.* HB-55 (IBSC). **VIETNAM. Vinh Phuc Province:** Tam Dao, elev. 1100 m, 19 May 2024, Y. H. Tong *et al.* BH-330 (IBSC). **Lao Cai Province:** Sa Pa, elev. 1126 m, 23 May 2024, Y. H. Tong *et al.* BH-345 (IBSC).

Declarations

Ethics approval and consent to participate

All plant materials used in this study were collected from the field with permissions from local authorities. Voucher specimens have been deposited in the herbarium (IBSC), South China Botanical Garden, Chinese Academy of Sciences. Specimens were identified by Yu-Ling Huang, Zheng-Yang Niu and Yi-Hua Tong.

Consent for publication

Not applicable.

Availability of data and materials

Data supporting the findings of this study are available within the article and its supplementary materials.

Competing interests

The authors declare no competing interests.

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Authors' contributions

Yu-Ling Huang: manuscript drafting, data analysis; Zheng-Yang Niu: manuscript review; Jing-Bo Ni, Tien Chinh Vu and Jian-Quan Chen: field investigations; Yi-Hua Tong: resources, field investigations, manuscript review; Nian-He Xia: field investigations, manuscript review. All authors read and approved the final version of the manuscript.

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Figures



Figure 1

Comparison of reproductive material of *Indosasa solearis* and *I. jinpingensis*. **(A)** Holotype of *I. solearis* (Petelot 4287). **(B)** Isotype of *I. solearis* (Petelot 4287). **(C)** Flowering specimen of *I. jinpingensis* (W. W. Zhou JP82315). **(D)** Dissection of spikelet from Petelot 4287. **(E)** Stamens. **(F)** Dissection of spikelet of *I. jinpingensis*, from left to right: pseudospikelet, bract, rachilla segment, two lemmas, abaxial view of palea, adaxial view of palea, based on W. W. Zhou JP82315.

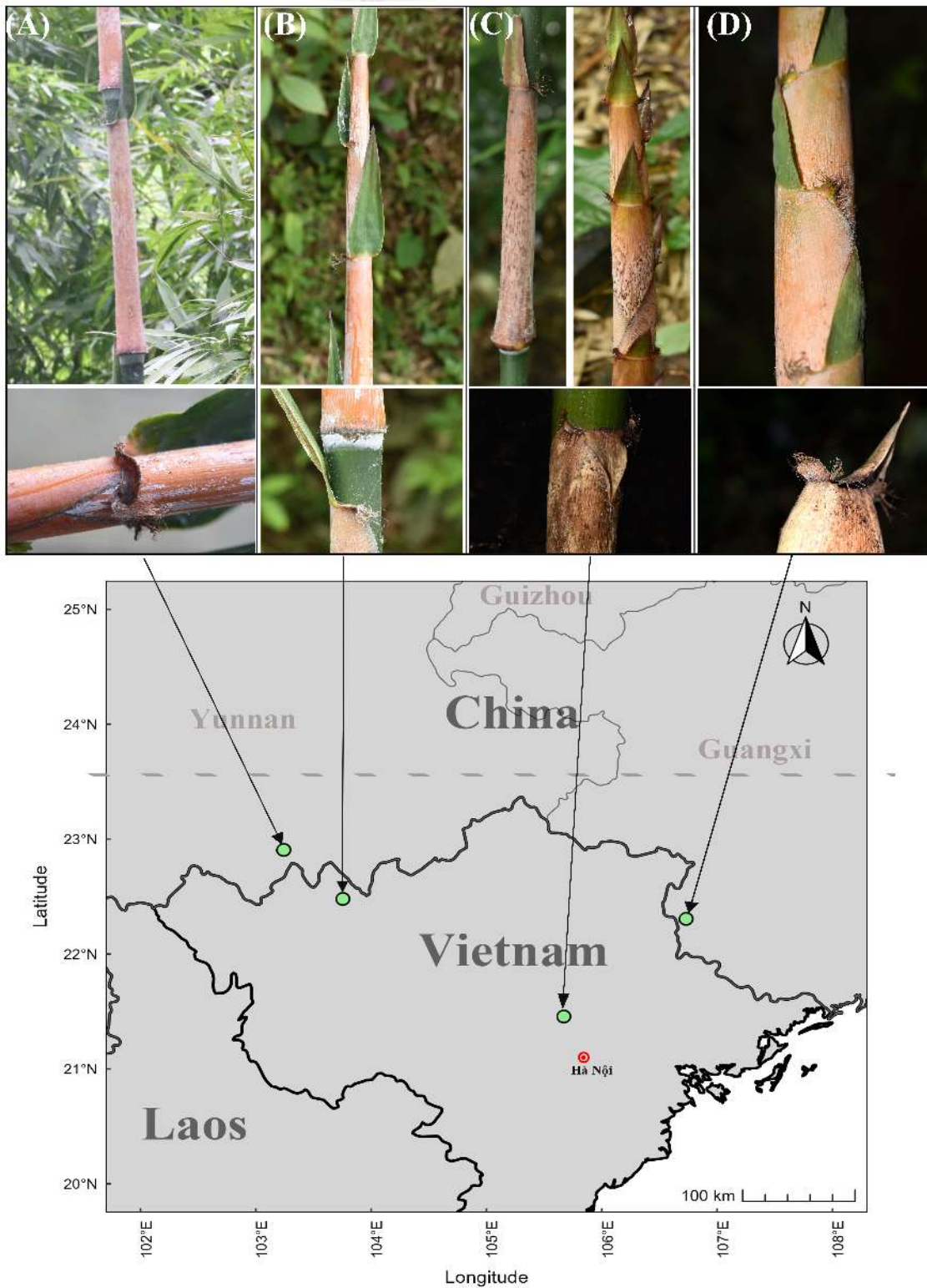


Figure 2

Culm leaf morphology of different populations of *Indosasa solearis*. **(A)** Jinping County, Yunnan Province, China (type locality of *I. jinpinensis*). **(B)** Lao Cai, Vietnam. **(C)** Tam Dao, Vietnam (type locality of *I. solearis*). **(D)** Pingxiang City, Guangxi Zhuang Autonomous Region, China (type locality of *I. parvifolia*).

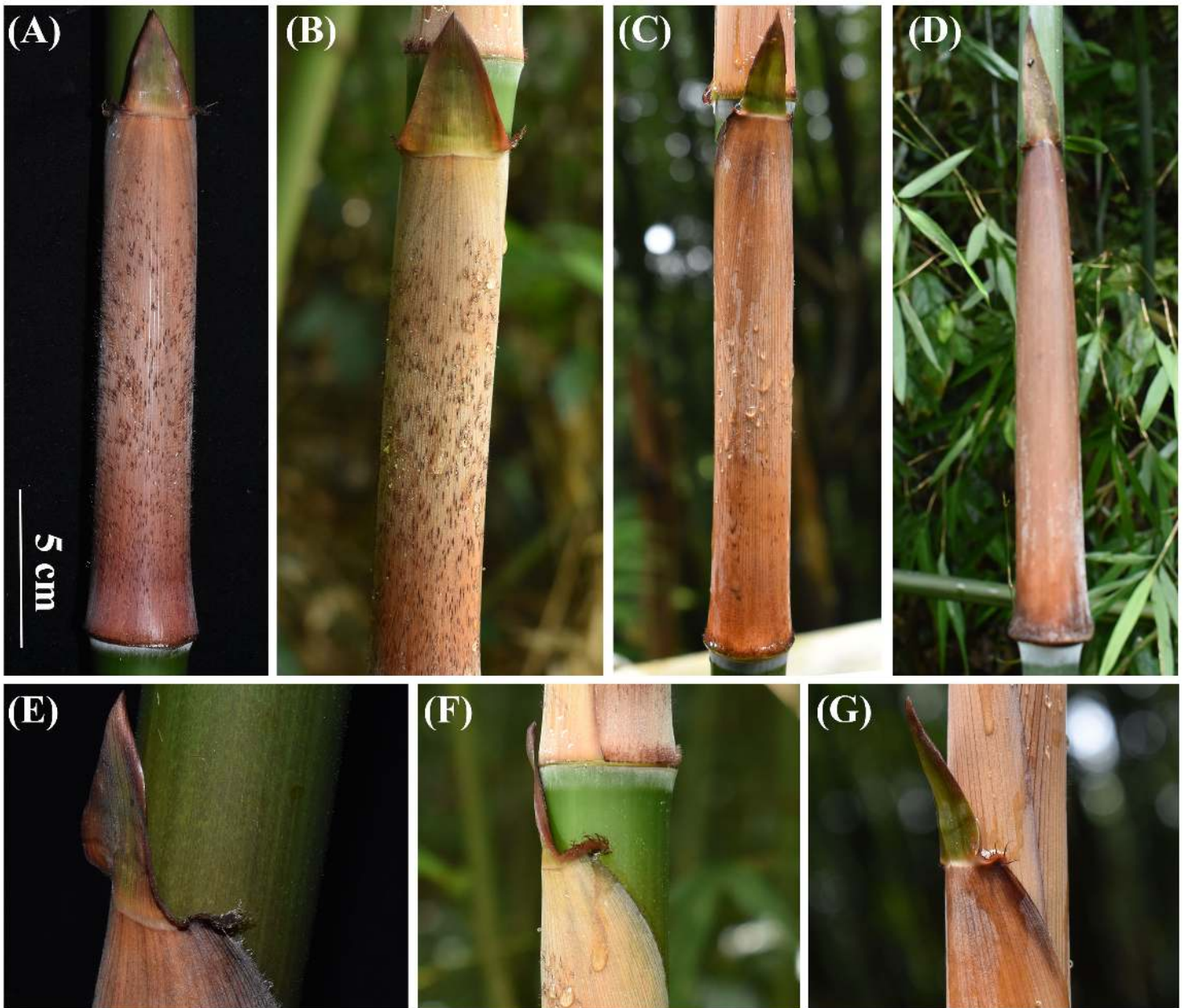


Figure 3

Morphological variations in the population of *Indosasa solearis* in Tam Dao, Vietnam. **(A)-(D)** Culm leaves, showing variations on blade shape and indumentum of abaxial surface of sheath. **(E)-(G)** Variations of culm leaf auricles.

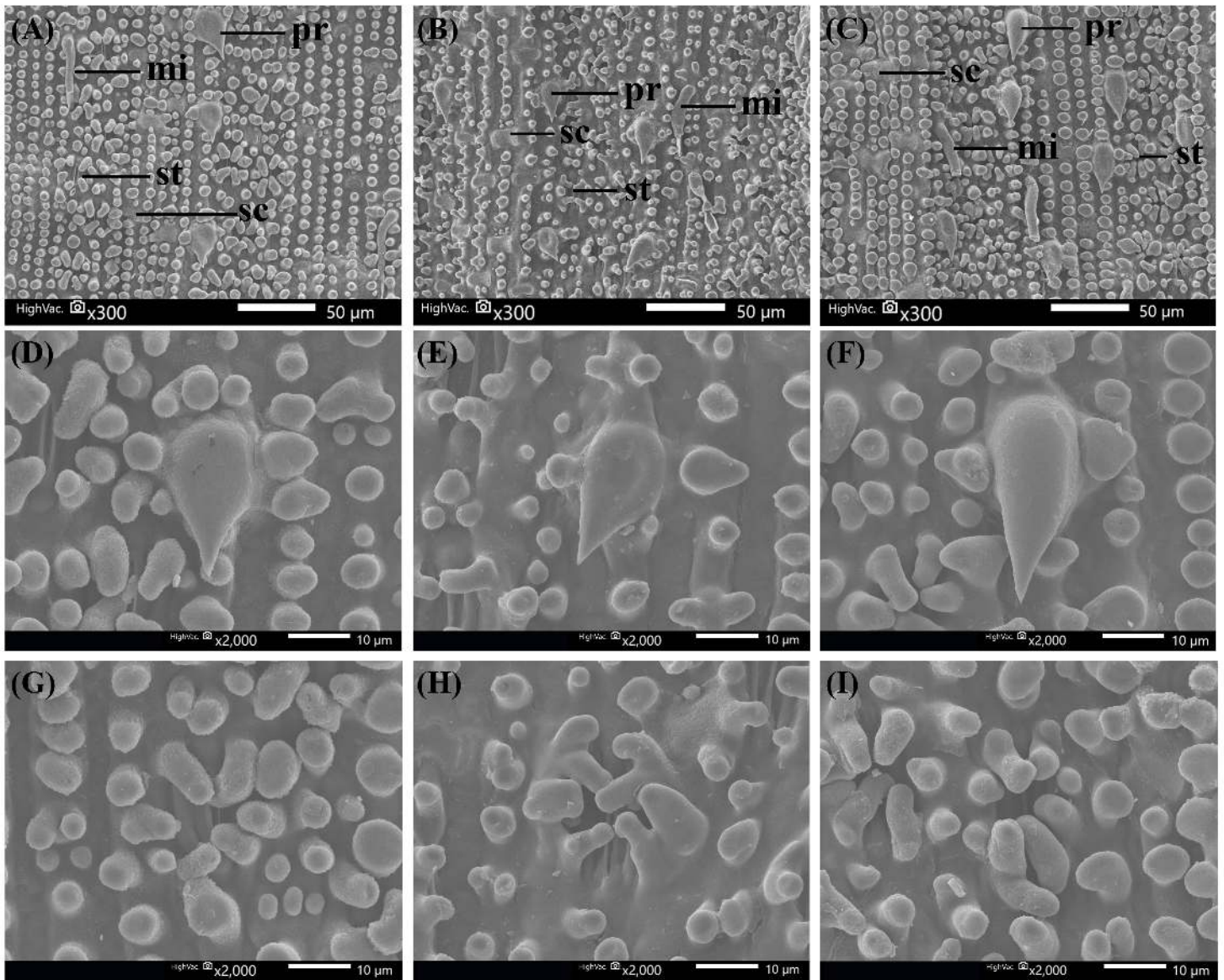


Figure 4

Micromorphology of the abaxial leaf epidermis of *Indosasa solearis*, *I. jinpingensis* and *I. parvifolia*. **(A)**, **(D)**, **(G)** *I. solearis* (Y. H. Tong et al., BH-330). **(B)**, **(E)**, **(H)** *I. jinpingensis* (Z. Y. Niu, NZY038). **(C)**, **(F)**, **(I)** *I. parvifolia* (Z. Y. Niu, NZY247). **(A)–(C)** microhairs (mi), prickles (pr), silica cells (sc) and stomatal apparatus (st) at 300× magnification. **(D)–(F)** prickles. **(G)–(I)** stomatal apparatus, covered with several elongated papillae.

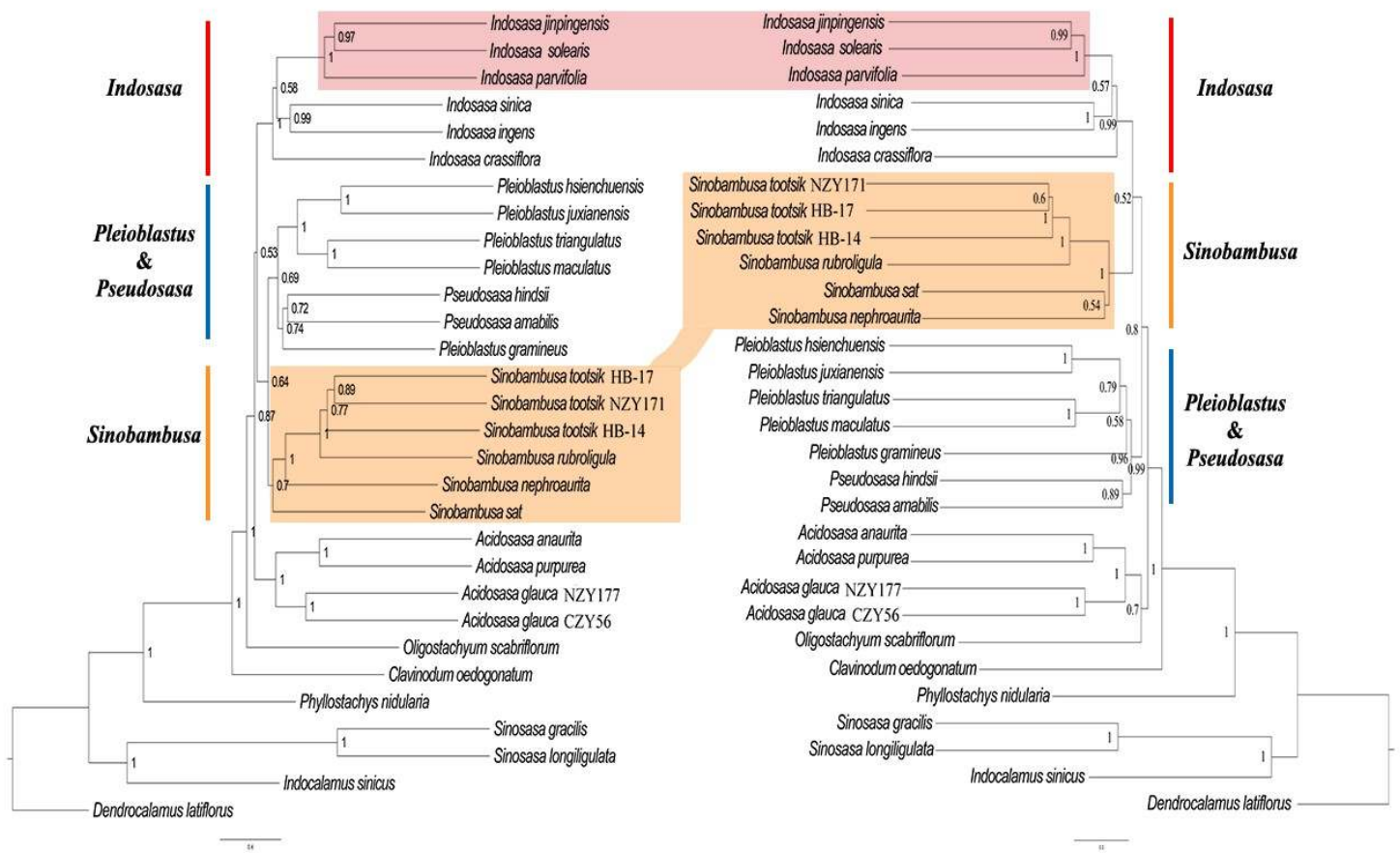


Figure 5

Phylogenetic relationships of 29 samples representing 26 species in 10 genera belonging to tribe Arundinarieae based on single-copy orthologous nuclear gene (SOG). Posterior probabilities are shown around nodes. ASTRAL species tree inferred from 737 SOGs trees (left). ASTRAL species tree inferred from 936 SOGs trees (right).

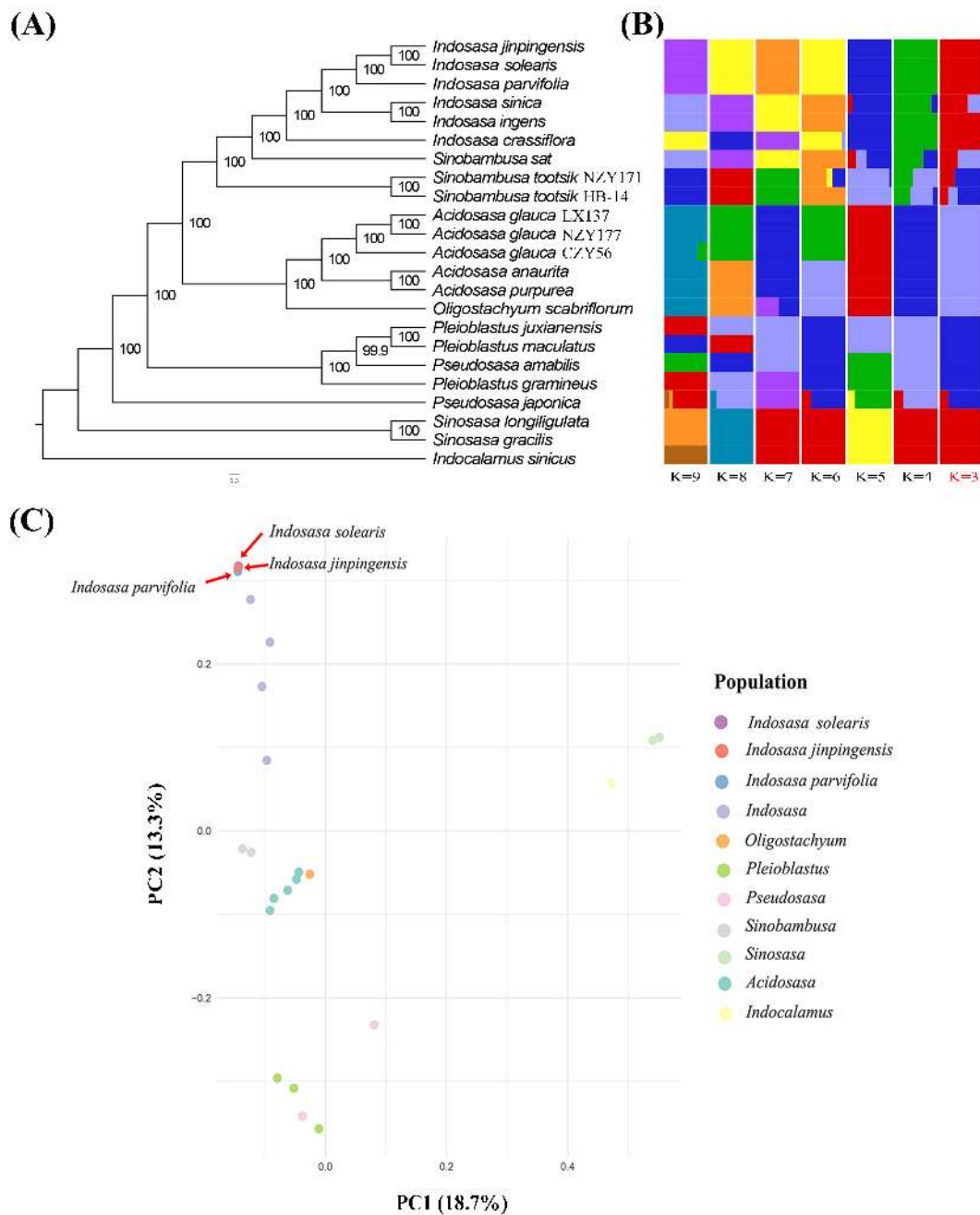
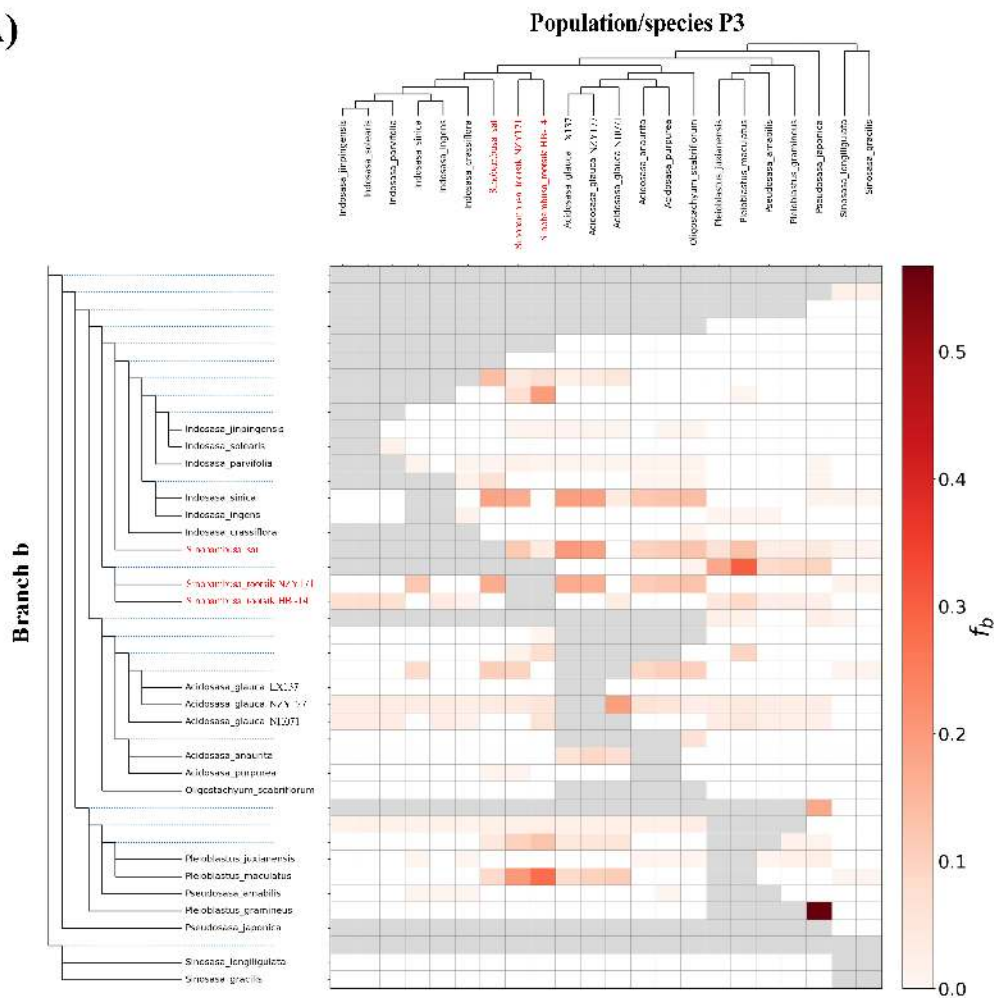
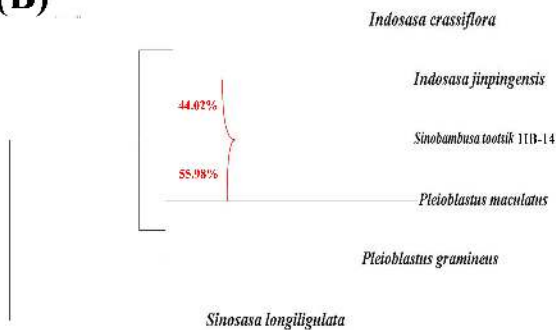
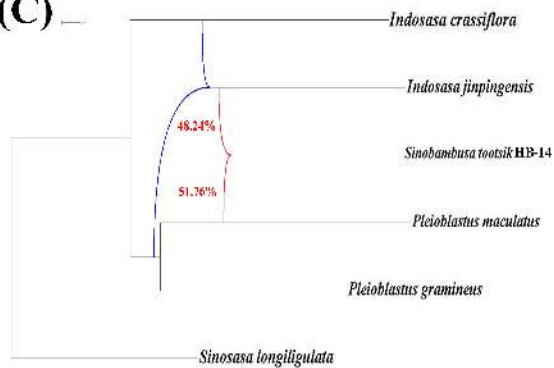


Figure 6

Population genetic analyses based on SNP data. **(A)** Phylogenetic relationship of 23 samples representing 20 species in 8 genera belonging to tribe Arundinarieae based on SNP dataset by using the moso bamboo genome as reference, bootstrap support values are shown near nodes. **(B)** Population genetic analyses by ADMIXTURE with k from 3 to 9. **(C)** Two principal component analyses based on SNP data.

(A)**(B)****(C)****Figure 7**

Inference of interspecific gene flow and phylogenetic networks. **(A)** Heatmap of the f_b -branch statistic calculated by Dsuite, identifying possible gene flow from the branch of the tree on the y axis to the species or population on the x axis. *Sinobambusa* species are highlighted in red text. **(B)-(C)** Phylogenetic network inferred by PhyloNet under models allowing for **(B)** one and **(C)** two hybridization

events. The numbers on the hybrid edges represent the inheritance probability, indicating the proportion of the genome derived from each parental lineage for *Sinobambusa tootsik* (HB-14).

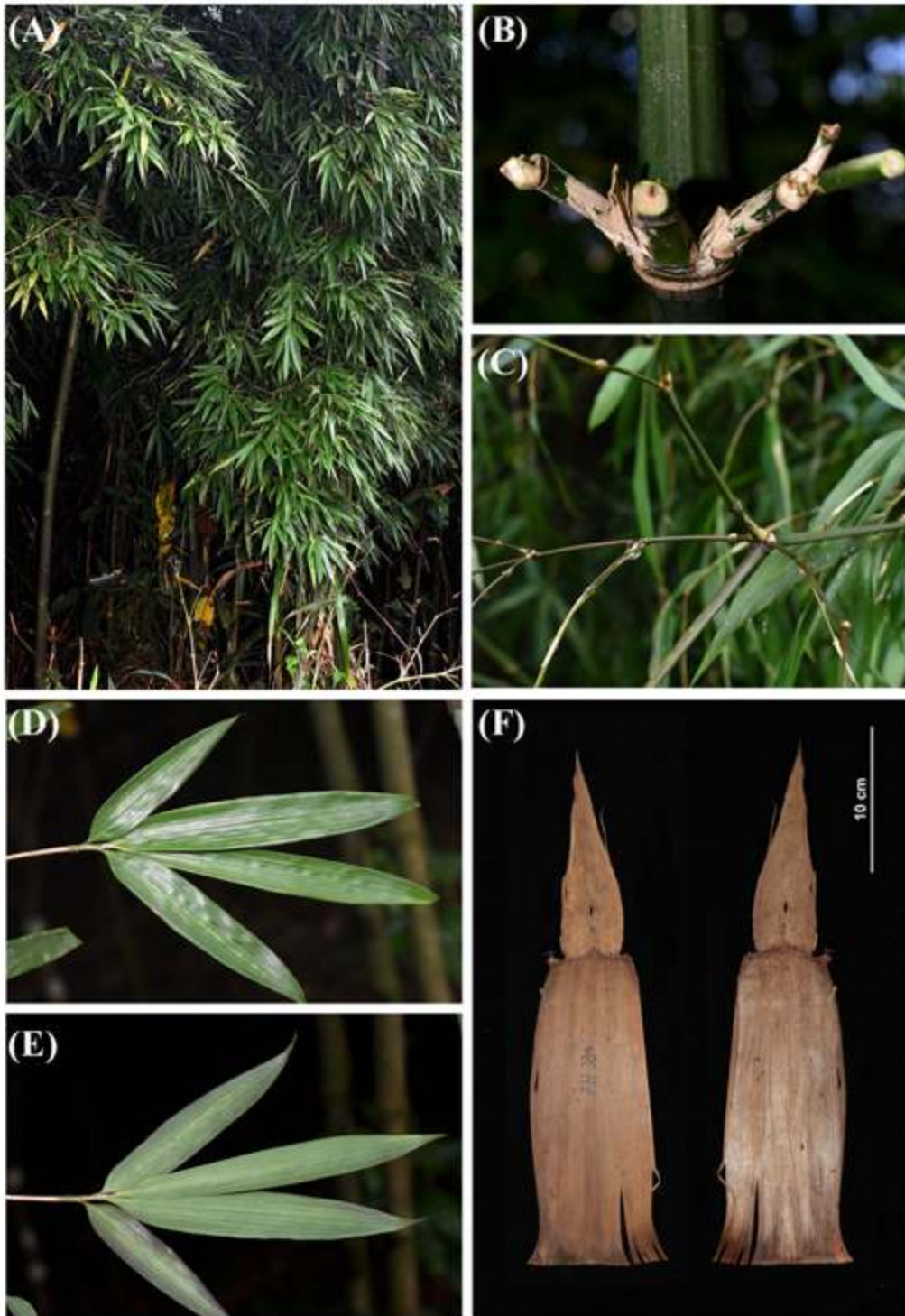


Figure 8

Indosasa solearis McClure. (A) Habit. (B) Culm internode and branch complement with 3 branches at each node. (C) Branches with prominent and asymmetrically raised nodes. (D) Ultimate foliage leaf branch, adaxial view. (E) Ultimate foliage leaf branch, abaxial view. (F) Culm leaves, abaxial view (left) and culm sheath (right), with a 10 cm scale bar.

adaxial view (right). **(A)**, **(B)**, **(D)** & **(E)** based on *Z. Y. Niu, NZY247*; **(C)** & **(F)** based on *Y. H. Tong et al. BH-330*.

Supplementary Files

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- [Supplementaryfigure1.jpg](#)
- [SupplementaryTableS1S4.xlsx](#)