

Morphological Variation of the Genus *Uraria* and Its Related Genera in China Postprint

Authors: He Aoxiang, Duan Weiwei, Xueli Zhao

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Abstract

The inter- and intra-generic classification of *Uraria* Desv. and its allied genera *Christia* Moench and *Urariopsis* Schindl. has long been controversial. To explore the patterns of morphological variation in *Uraria* and its allied genera and provide morphological data for their classification, this study, based on 296 specimens from 43 populations of 15 species across 3 genera, observed and statistically analyzed 24 morphological characters of leaves, inflorescences, flowers, fruits, and seeds at the population level, and conducted mean analysis, principal component analysis, and cluster analysis. The results showed that: (1) The generic boundaries between *Uraria* and *Christia* (except for *Christia campanulata*) are clear, with leaf length, length and width of terminal leaflets, and whether the calyx swells after flowering being important diagnostic characters at the generic level; whereas the generic boundaries between *Uraria* and *Urariopsis* are unclear. (2) Inter-specific variation in *Uraria* is substantial, with leaf length, lateral leaflet length, standard petal length, inflorescence type, and hair type on the inflorescence axis serving as key diagnostic characters at the species level; in *Christia*, leaf length, stipule length, terminal leaflet length, and lateral leaflet length have important taxonomic value; in *Urariopsis*, inflorescence length is a key diagnostic character at the species level. (3) At a Euclidean distance of 16.5, the 15 species clustered into four groups, with *Uraria picta* and *Uraria crinita* each forming separate groups, *Christia* (except for *Christia campanulata*) forming one group, and *Uraria*, *Urariopsis*, and *Christia campanulata* forming another group, supporting the merger of *Christia campanulata* and *Urariopsis* into *Uraria*. This study provides morphological evidence for taxonomic and evolutionary research on *Uraria* and its allied genera.

Full Text

Preamble

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Morphological Variation of *Uraria* Desv. (Fabaceae) and Its Related Genera in China

HE Aoxiang, DUAN Weiwei, ZHAO Xueli* (College of Forestry, Southwest Forestry University, Kunming 650224, China)

Abstract: The taxonomic boundaries both between and within *Uraria* Desv. and its related genera *Christia* Moench and *Urariopsis* Schindl. have long been controversial. To explore patterns of morphological variation in these taxa and provide morphological data for their classification, we examined 24 morphological characters of leaves, inflorescences, flowers, fruits, and seeds based on 296 specimens representing 43 populations from 15 species across three genera. Population-level statistical analyses included mean analysis, principal component analysis, and cluster analysis. The results revealed: (1) Clear intergeneric boundaries exist between *Uraria* and *Christia* (excluding *C. campanulata*), with leaf length, terminal leaflet length and width, and post-floral calyx enlargement serving as important diagnostic characters; however, boundaries between *Uraria* and *Urariopsis* remain ambiguous. (2) Interspecific variation within *Uraria* is substantial, with leaf length, lateral leaflet length, standard petal length, inflorescence type, and rachis pubescence type representing key taxonomic characters. Within *Christia*, leaf length, stipule length, and terminal and lateral leaflet lengths hold significant taxonomic value. Within *Urariopsis*, inflorescence length is the critical character for species delimitation. (3) At a Euclidean distance of 16.5, the 15 species clustered into four clades: *Uraria picta* and *U. crinita* each formed separate monophyletic clades; *Christia* (excluding *C. campanulata*) formed a monophyletic clade; and the remaining nine species of *Uraria*, *Urariopsis*, and *C. campanulata* clustered together. These results support the merger of both *C. campanulata* and *Urariopsis* into *Uraria*. This study provides comprehensive morphological evidence for the taxonomy and evolutionary studies of *Uraria* and its allied genera.

Keywords: Fabaceae, Desmodieae, cluster analysis, principal component analysis, taxonomic significance

Introduction

Uraria Desv., along with its related genera *Christia* Moench and *Urariopsis* Schindl., belongs to the tribe Desmodieae within Fabaceae. This group comprises approximately 35 species distributed primarily in tropical Asia, with 15 species occurring in China, mainly south of 25°N latitude (Yang et al., 1981). Species such as *Uraria lagopodioides*, *U. picta*, and *Christia vespertilionis* contain triterpenoids, flavonoids, and isoflavanones with medicinal applications for treating asthma, dysentery, ulcers, and malarial fever (Sivakumar et al., 2012; Lee, 2020; Thien et al., 2021, 2022).

These three genera exhibit both distinct morphological differences and overlapping characters. All share the characteristic of pods with repeatedly folded articles, but differ in the position of the connecting points between articles: in

Urariopsis, the connection point is centrally located within adjacent articles, whereas in *Christia* and *Uraria* it is positioned at the margins. Additionally, *Christia* species exhibit post-floral calyx enlargement that completely encloses the fruit, while *Uraria* and *Urariopsis* species do not show this enlargement (Yang et al., 1981, 1995).

Based on these morphological features, the generic boundaries between *Uraria*, *Urariopsis*, and *Christia*, as well as the taxonomic placement of certain species, have remained controversial. Schindler (1916) established *Urariopsis* as a distinct genus based on the central connection point of pod articles, a revision supported by some researchers (Gagnepain et al., 1938; Meeuwen et al., 1961; Yang et al., 1981, 1995). However, others have argued that separation based on such few characters is unwarranted (Hutchinson, 1964; De et al., 1980; Kenicer, 2005; Ohashi et al., 2006).

Christia campanulata (Taiwanese *Christia*) exhibits intermediate morphology between *Uraria* and *Christia*, possessing the characteristic post-floral calyx enlargement typical of *Christia* while sharing vegetative traits such as habit and leaf shape with *Uraria*, leading to persistent taxonomic uncertainty (Yang et al., 1981, 1995; Ohashi et al., 2007). Furthermore, some species within *Uraria* and related genera show substantial intraspecific variation, blurring interspecific boundaries, notably between *Uraria crinita* and *U. picta*, and between *Christia vespertilionis* and *C. hainanensis*. While previous studies have contributed important insights into the systematics of this group (Yang et al., 1981, 1995; Huang et al., 2010; Ohashi et al., 2018), questions remain regarding the validity of *Urariopsis*, the appropriate generic placement of *C. campanulata*, patterns of intra- and interspecific variation among closely related species, and the key diagnostic characters for intergeneric and intrageneric delimitation.

Morphological studies represent a fundamental approach in taxonomy, elucidating patterns of variation that form the basis for accurate species circumscription. Population-level morphological analysis enables comparison of variation patterns under different environmental conditions, establishing variation norms and providing evidence for delimiting closely related species (Yang, 1991; Zhao et al., 2020). Many taxonomic revisions have historically relied on descriptions based on one or a few type specimens to establish species concepts, with subsequent species identification depending on predetermined characters. However, as specimen collections expand and molecular studies advance, such conceptual boundaries often become ambiguous or require revision, potentially rendering species circumscriptions inaccurate (Rakic et al., 2012; Barley et al., 2013; Jacobs et al., 2019; Wieclaw et al., 2021; Ma et al., 2022). For example, morphological variation studies based on extensive specimens in *Castilleja* (Orobanchaceae) and *Carex* (Cyperaceae) have demonstrated that characters derived from type specimens inadequately delimit species within these genera. Therefore, comprehensive morphological variation analysis is essential for accurate species description and delimitation, and contributes to understanding speciation processes and biodiversity conservation.

In this study, we investigated Chinese species of *Uraria* and its allied genera through population-level statistical analysis of morphological characters to address three questions: (1) What are the patterns of morphological variation among and within genera and species? (2) Which characters have taxonomic value for intergeneric and intraspecific delimitation? (3) How should intergeneric boundaries be drawn, and what is the systematic position of controversial taxa? Our goal is to provide more comprehensive and accurate morphological evidence for the taxonomy and evolution of *Uraria* and related genera.

Materials and Methods

1.1 Material Collection

This study examined 296 specimens representing 43 populations from 15 species across three genera (*Uraria*, *Christia*, and *Urariopsis*) in China. Of these, 262 specimens were collected during fieldwork by our research team and deposited in the Southwest Forestry University Herbarium (SWFC), while the remaining 34 specimens were obtained from the following herbaria: South China Botanical Garden, Chinese Academy of Sciences (IBSC); Institute of Botany, Chinese Academy of Sciences (PE); Chengdu Institute of Biology, Chinese Academy of Sciences (CDBI); Kunming Institute of Botany, Chinese Academy of Sciences (KUN); Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (HITBC); Fujian Institute of Subtropical Botany (FJSI); Guangxi Institute of Botany (IBK); Guangxi Medicinal Botanical Garden (GXMG); and Nanjing Institute of Botany, Jiangsu Province and Chinese Academy of Sciences (NAS). Due to differences in species distribution ranges and population sizes in the wild, particularly for narrowly distributed species with small populations, the number of specimens per population ranged from 2 to 21. Detailed collection information is provided in Table 1 .

1.2 Morphological Trait Selection and Measurement

Based on descriptions and identification keys for *Uraria* and related genera in *Flora Reipublicae Popularis Sinicae* and *Flora of China* (Yang et al., 1981, 1995; Huang et al., 2010), we selected 24 important taxonomic characters, including 21 quantitative traits and 3 qualitative traits (Table 2). Quantitative traits were measured using digital calipers with 0.1 mm precision; to reduce measurement error, each trait was measured three times. Qualitative traits were numerically coded according to their different states (Table 2).

1.3 Data Analysis

Data were compiled in Microsoft Excel 2019. Statistical analyses including mean analysis, non-parametric testing, and principal component analysis were performed using SPSS 27.0 (IBM Corp., Armonk, NY, USA). Coefficients of variation ($CV = \text{standard deviation}/\text{mean}$) were calculated for interspecific and intraspecific variation across genera. For interspecific CV calculations, median

values for each species were used to exclude the influence of intraspecific variation. After removing extreme values and outliers from the mean analysis, violin dot plots were generated using Origin 2021 (OriginLab Corporation, Northampton, MA, USA) for visualization. To clarify phylogenetic relationships among *Uraria* and related genera, initial data were standardized by standard deviation, followed by correlation analysis. Characters with high correlation ($r > 0.7$) were excluded prior to cluster analysis.

Results

2.1 Mean Analysis

Mean analysis of 21 quantitative traits (Table 3 , Table 4) revealed that traits with interspecific $CV > 0.7$ were petiole length, lateral leaflet width, and terminal leaflet length-width ratio in *Uraria*; leaf length, stipule length, terminal leaflet length, and lateral leaflet length in *Christia*; and inflorescence length in *Urariopsis*. Within *Uraria*, *U. picta* showed substantially greater median values and ranges for petiole length, lateral leaflet width, and terminal leaflet length-width ratio compared to other species, resulting in higher interspecific CV values. Analysis indicated that traits with $CV > 0.45$ could effectively differentiate species within *Uraria*: leaf length, terminal leaflet length, pedicel length, standard petal length, and pod length. Intraspecific $CV > 0.5$ was observed for stipule length in *U. neglecta*, terminal leaflet length-width ratio in *C. vespertilionis* and *U. picta*, inflorescence length in *U. crinita* and *U. sinensis*, and pedicel length in *C. constricta*.

Both *U. crinita* and *U. picta* had maximum and minimum leaflet numbers of five or more, while all other species had three or fewer leaflets. *Uraria oblonga*, *U. rufescens*, *Urariopsis cordifolia*, and *U. brevissima* showed consistent leaflet numbers within species.

Nine traits with average intraspecific $CV > 0.2$ were selected for visualization using violin dot plots (Figure 1 [Figure 1: see original paper]): petiole length, stipule length, terminal leaflet length, terminal leaflet width, lateral leaflet length, terminal leaflet length-width ratio, inflorescence length, pedicel length, and pod length. Figure 1 shows that when sample distributions fall within the 25th–75th percentiles, some species exhibit distinct morphological differences: terminal leaflet length, lateral leaflet length, and terminal leaflet length-width ratio in *C. vespertilionis*, *C. hainanensis*, *C. constricta*, and *C. obcordata* are smaller than in other species; stipule length in these four *Christia* species plus *U. cordifolia* and *U. brevissima* is significantly shorter than in other taxa; terminal leaflet length-width ratio in *U. picta* is notably larger, consistent with its linear-oblong or narrowly lanceolate leaf shape; inflorescence length in *U. lagopodioides* and *U. brevissima* is markedly shorter than in other species; petiole length and terminal leaflet length-width ratio in *U. picta* exceed those of other species; stipule length in *U. lacei*, *U. neglecta*, and *C. campanulata* is greater than in other taxa; and pod length in *U. lacei* and *U. oblonga* is significantly longer. Among these

nine traits, only terminal leaflet length-width ratio, inflorescence length, and pod length could individually distinguish *U. picta*, *U. brevissima*, and *U. oblonga* from the other 15 species, respectively; remaining traits could not reliably separate individual species.

A. Uraria lacei; *B. U. neglecta*; *C. U. rufescens*; *D. U. lagopodioides*; *E. U. crinita*; *F. U. picta*; *G. U. oblonga*; *H. U. sinensis*; *I. Christia vespertilionis*; *J. C. hainanensis*; *K. C. obcordata*; *L. C. campanulata*; *M. C. constricta*; *N. Urariopsis brevissima*; *O. U. cordifolia*.

Figure 1 Violin dot plots of nine quantitative traits.

2.2 Non-parametric Test

As variance analysis revealed heteroscedasticity, we employed the Kruskal-Wallis non-parametric test. Results showed that asymptotic significance values for all 21 quantitative traits (Table 5) were far less than 0.01, allowing us to reject the null hypothesis that these traits derive from populations with identical distributions. Additionally, the three qualitative traits showed intergeneric and interspecific differences. Thus, all 24 characters exhibited statistically significant differences among the 15 species of *Uraria* and related genera.

2.3 Principal Component Analysis

Principal component analysis was performed separately for *Uraria*, *Christia*, *Urariopsis*, and the combined dataset. Figure 2 [Figure 2: see original paper] shows that the first principal component explained 37.796%, 37.912%, 51.091%, and 37.208% of variation, respectively, while the second component explained 26.799%, 26.223%, 23.826%, and 13.869%. In *Uraria*, characters with absolute loadings > 0.8 included leaf length, leaflet number, terminal leaflet length and width, lateral leaflet length and width, standard petal length, inflorescence type, and rachis pubescence type. In *Christia*, leaf length, stipule length, terminal leaflet length and width, and lateral leaflet length and width exceeded this threshold. In *Urariopsis*, leaf length, terminal leaflet length and width, and inflorescence length showed loadings > 0.8 . Comparison of trait contributions across three hierarchical levels (overall, intergeneric, and intrageneric) revealed that characters with intergeneric contributions > 0.8 remained significant within genera. Leaf length and terminal leaflet length were significant in all analyses, with contributions of 0.896, 0.913, 0.886, and 0.886 for leaf length, and 0.966, 0.911, 0.968, and 0.935 for terminal leaflet length in the overall, *Uraria*, *Christia*, and *Urariopsis* analyses, respectively. Terminal and lateral leaflet lengths and widths were significant in both overall and intrageneric analyses for *Uraria* and *Christia*, with loadings of 0.911, 0.912, 0.922, 0.908 and 0.968, 0.863, 0.947, 0.935, respectively. Petiole length showed notable contributions in both overall and *Uraria*-specific analyses (-0.865 and -0.723, respectively).

2.4 Cluster Analysis

Based on correlation analysis of 24 characters, seven highly correlated traits ($r > 0.7$) were excluded: leaf length, lateral leaflet length, lateral leaflet width, lateral leaflet length-width ratio, pedicel length, petiole length, and seed length. Cluster analysis of the remaining characters (Figure 3 [Figure 3: see original paper]) revealed that at a Euclidean distance of approximately 22.5, the 15 species formed two major clades: one containing *U. picta* and *U. crinita*, and the other comprising the remaining 13 species. At a Euclidean distance of 16.5, four clades were resolved: *U. picta* and *U. crinita* as separate monophyletic clades; *C. hainanensis*, *C. obcordata*, *C. constricta*, and *C. vespertilionis* as a clade; and a fourth clade containing *U. lagopodioides*, *U. neglecta*, *U. oblonga*, *U. rufescens*, *U. brevissima*, *U. cordifolia*, *U. lacei*, *U. sinensis*, and *C. campanulata*.

Discussion

3.1 Morphological Variation in *Uraria* and Related Genera

Phenotypic diversity in plants results from the interaction between genetic adaptation and environmental heterogeneity, reflecting adaptive responses to different environments. The coefficient of variation serves as a crucial metric for assessing phenotypic variation (Yang, 1991; Pigliucci et al., 2006; Verbeeck et al., 2014; Saenger et al., 2018; Ai et al., 2020). Our statistical analysis of morphological traits across different populations revealed that leaf-related characters such as leaf length, petiole length, and stipule length show high variation in *Uraria* (mean CV = 0.54) and *Christia* (mean CV = 0.68), whereas reproductive characters show lower variation (mean CV = 0.34 and 0.21, respectively). This indicates that reproductive organs are more stable and less environmentally influenced than vegetative organs, conferring higher taxonomic value (Lan et al., 2019; Tong et al., 2019).

The taxonomic treatments and morphological descriptions in *Flora Reipublicae Popularis Sinicae* and *Flora of China* provide essential baseline data for botanical research. However, limitations in historical specimen availability and information technology at the time of compilation resulted in incomplete or insufficiently accurate descriptions for some taxa (Huang, 2017; Shao et al., 2021; Yang et al., 2023). Through population-level analysis of extensive specimens, we have supplemented and refined morphological characterizations of *Uraria* and related genera.

Within *Uraria*, we support the use of leaflet number, inflorescence type, and inflorescence length as interspecific diagnostic characters. Legume morphology holds significant taxonomic value in Fabaceae, such as trichome types in *Desmodium* (e.g., hooked, unicellular, and conical hairs) and pod shape in *Indigofera* (e.g., erect, curved, or falcate) (Leite et al., 2009; Freitas et al., 2014; Shi, 2016). While *Flora Reipublicae Popularis Sinicae* and *Flora of China* emphasized pod pubescence type for intrageneric classification (Yang et al., 1995; Huang et al., 2010), our results indicate that pod length also has high taxonomic value in

Uraria. For the closely related species pair *U. crinita* and *U. picta*, previous works used leaflet number, width, and shape as diagnostic characters. We found these characters to be highly variable and overlapping between the two species, whereas terminal leaflet length-width ratio, petiole length, and pedicel length serve as more reliable diagnostic traits.

In Christia, *Flora Reipublicae Popularis Sinicae* and *Flora of China* identified terminal leaflet length and article number as primary characters distinguishing *C. hainanensis* from *C. obcordata*. Our analysis based on extensive specimens shows substantial overlap in these traits, and we instead recommend stipule length and inflorescence length as important diagnostic characters for these closely related species. For the controversial taxon *C. campanulata*, in addition to previously noted characters such as terminal leaflet length-width ratio, vein number, and degree of fusion of the two upper calyx lobes (Yang et al., 1995; Huang et al., 2010), we found that terminal and lateral leaflet lengths and width also clearly differentiate it from other species.

In Urariopsis, *U. cordifolia* and *U. brevissima* were previously distinguished based on leaf shape, inflorescence length, and pedicel curvature at fruiting (Yang et al., 1995; Huang et al., 2010). Our results support inflorescence length as a reliable character for species delimitation in this genus.

3.2 Numerical Taxonomy of Uraria and Related Genera

Principal component analysis and cluster analysis are widely used in numerical taxonomy to reflect differences and relationships among taxa (Chen et al., 2014; Xue et al., 2022; He et al., 2023). Our PCA results indicate that leaf length, terminal leaflet length and width, and post-floral calyx enlargement are important intergeneric diagnostic characters between Uraria and Christia. Within Uraria, leaf length, lateral leaflet length, standard petal length, inflorescence type, and rachis pubescence type show substantial intrageneric variation and serve as primary morphological criteria for species delimitation. Within Christia, leaf length, stipule length, and terminal and lateral leaflet lengths are most valuable, while inflorescence length is the key character in Urariopsis.

Current research on the classification and evolution of Uraria and allied genera remains limited. Numerical taxonomic studies based on extensive morphological data can provide crucial evidence for taxonomic boundaries and evolutionary relationships. Our cluster analysis demonstrates clear intergeneric boundaries between Uraria (excluding *C. campanulata*) and Christia, but ambiguous boundaries between Uraria and Urariopsis. Our results also provide morphological evidence for taxonomic revision of controversial taxa. Although Urariopsis was established as a separate genus based on the central connection point of pod articles (Gagnepain et al., 1938; Van et al., 1961; Huang et al., 2010), our findings show extensive overlap in multiple morphological characters between Urariopsis and Uraria, with cluster analysis supporting the merger of Urariopsis into Uraria (Kenicer, 2005; Ohashi et al., 2006). Yang et al. (1981, 1985) placed *C. cam-*

panulata in *Christia* based on its post-floral calyx enlargement, but our results indicate that its vegetative morphology, including leaf length, stipule length, and lateral leaflet length, is more similar to *Uraria*. Cluster analysis places *C. campanulata* within the *Uraria* clade, indicating closer affinity and supporting its transfer to *Uraria*—a conclusion consistent with leaf venation studies (Duan et al., 2023). Additionally, the clustering of *U. oblonga* with other *Uraria* species aligns with SSR-based studies (Liu et al., 2023) and supports Ohashi et al.'s (2018) merger of *U. oblonga* into *Uraria*.

Morphological variation studies provide objective, statistics-based analyses that yield additional taxonomic information. When combined with geographic and ecological data from collection sites, these analyses can reveal patterns of variation across environmental gradients. Our population-level investigation of Chinese *Uraria* and related genera has uncovered patterns of morphological variation among and within genera and species, establishing a foundation for future analyses of geographic variation. However, some critical characters were missing from our specimens, such as incomplete floral and fruit data for *C. hainanensis*, *C. obcordata*, and *C. constricta*, limiting data completeness. Therefore, more comprehensive morphological data, integrated with chemotaxonomic and molecular systematic evidence, are needed for robust classification of *Uraria* and its allies.

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