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R. M. Baldini^{ab} & O. O. Ortiz^c

^a Department of Biology, CSET (Centro Studi Erbario Tropicale), University of Firenze, Firenze, Italy

^b Smithsonian Tropical Research Institute Fellowship,, Balboa, Panama City, Republic of Panama

^c Herbario PMA, Estafeta Universitaria, Universidad de Panama, Panama City, Republic of Panama

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Panama as a crucial centre of differentiation for the herbaceous bamboos (Poaceae: Bambusoideae: Olyreae): a study in progress

R. M. BALDINI^{1,2} & O. O. ORTIZ³

¹Department of Biology, CSET (Centro Studi Erbario Tropicale), University of Firenze, Firenze, Italy; ²Smithsonian Tropical Research Institute Fellowship, Balboa, Panama City, Republic of Panama and ³Herbario PMA, Estafeta Universitaria, Universidad de Panama, Panama City, Republic of Panama

Abstract

This contribution introduces the ongoing research on herbaceous bamboos started by the University of Florence (FT herbarium), the Universidad de Panama (PMA herbarium) and the Smithsonian Tropical Research Institute in 2011. The main goal of this project consists in collecting field data, in order to provide updated material to be used in a phylogenetic analysis to improve the knowledge of the complex tribe *Olyreae*.

Keywords: Bambusoideae, *Cryptochloa*, *Flora of Panama*, *herbaceous bamboos*, *Olyreae*, *Poaceae*

Introduction

Within the huge differentiation in the *Poaceae* family, the herbaceous bamboos (Poaceae: Bambusoideae: Olyreae) stand as one of the most interesting and unusual groups, due to their intriguing evolutionary history in the tropical forest understory, and their specific adaptations to those habitats (Judziewicz et al. 1999). Herbaceous bamboos (*Olyreae*) belong to the subfamily *Bambusoideae* in the BEP clade of the *Poaceae* family (Figure 1) and consist of three subtribes: *Buergersiochloinae* (*Buergersiochloa* Pilg., with 2 species), *Parianinae* (*Pariana* Aubl. with ca. 35 species and *Eremitis* Döll with 1 species) and *Olyrinae* with 19 genera and ca. 78 species (Bamboo Phylogeny Group 2006, 2012; Judziewicz & Clark 2007; Kelchner and Bamboo Phylogeny Group 2013). Recent molecular studies support this taxonomic arrangement (Zhang & Clark 2000; Davis & Soreng 2007), but problems still exist, as in the genus *Olyra* L., where polyphyletic taxa are as yet unsolved (Zhang & Clark 2000). Kelchner and Bamboo Phylogeny Group (2013) have recently stated the paraphyly of the woody bamboos with respect to the *Olyreae*, but not rejecting their monophyly.

Herbaceous bamboos are perennial herbs with unisexual flowers, i.e. monoecious species. The

phenology in herbaceous bamboos is completely distinct from that of the woody bamboos and most *Olyreae* flower annually (with few exceptions such as *Olyra standleyi* Swallen which is monocarpic), in contrast to the long cycles of the woody bamboos, most of which are monocarpic.

The diversity of herbaceous bamboos is mostly concentrated in the Neotropics, especially in the Brazilian Atlantic Forest, Amazonian areas and Central America, while woody bamboos are broadly distributed either in neotropical or paleotropical areas of the world (Judziewicz et al. 1999; Judziewicz & Clark 2007; Kelchner & Bamboo Phylogeny Group 2013) (Figure 2).

Reproductive biology of herbaceous bamboos is also interesting and not well known. Hybridization and polyploidization are important evolutionary forces (Soltis & Soltis 1995, 1999, 2000; Soltis et al. 2009) in flowering plants, including the grass family (Hilu 2004). In herbaceous bamboos polyploidization seems to be the rule, with different base chromosome numbers: $x = 7, 9, 10, 11, 12$ (Hunziker et al. 1982; Hilu 2004, 2006). *Olyreae* are also very specialized in insect pollination and ant-mediated fruit dispersal, as reported in *Olyra*, *Pariana*, *Cryptochloa* and so on by the presence of showy stamens and elaiosomes (Davidse 1986; Lengyel et al.

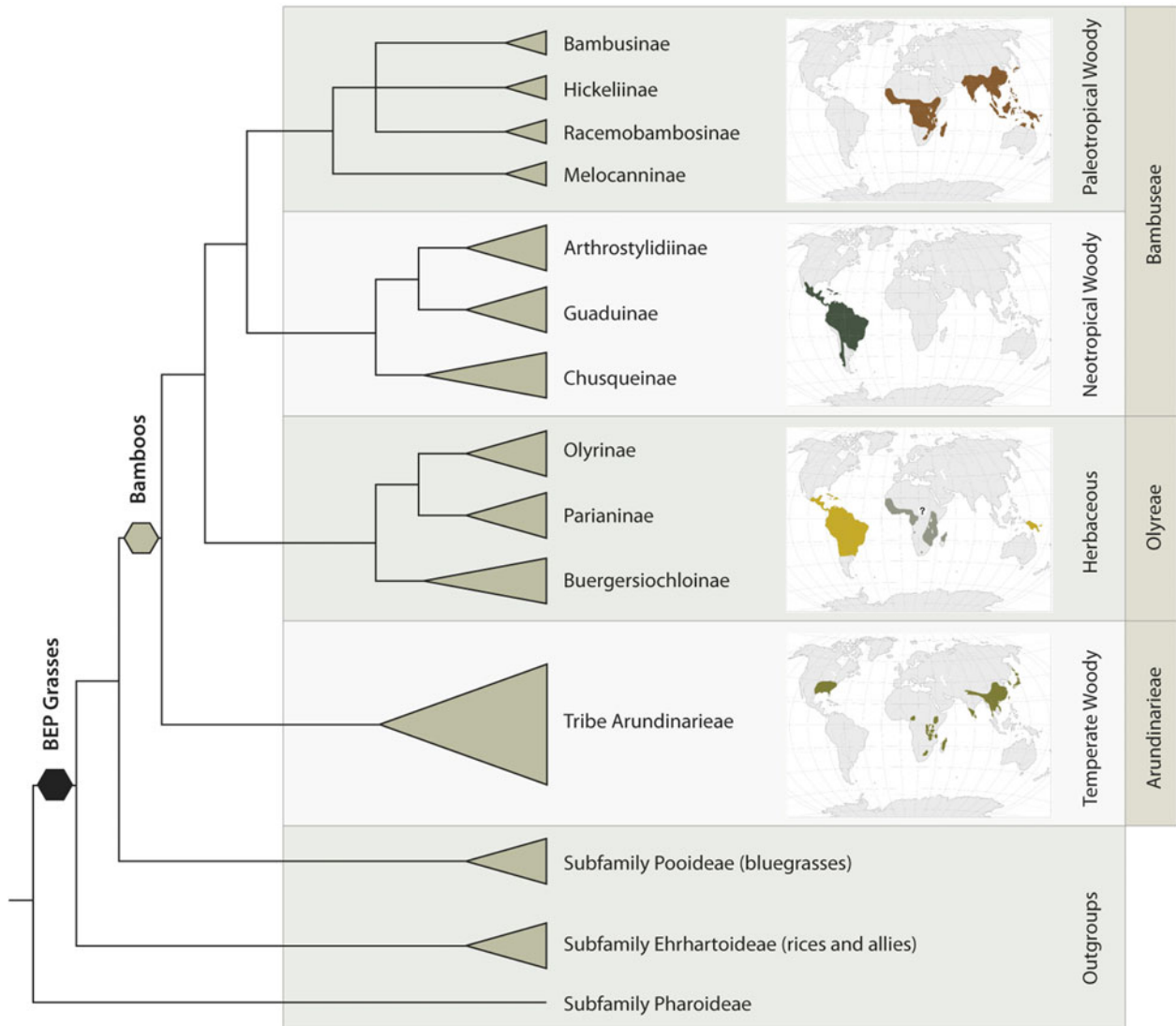


Figure 1. The BEP clade with emphasis on the subtribe relationships and geographic distributions of the major lineages. *Source:* Modified from Kelchner & Bamboo Phylogeny Group 2013.

2010). These evolutionary adaptations may be due to the specific ecology of this group of grasses related to the tropical forest understory, where the initial differentiation of the family *Poaceae* began (Clayton 1981) between 55 and 30 mya (Eocene), firstly in forests and then in open habitats (see also Bouchenak-Khelladi et al. 2010). In other words: dinosaurs did not eat grasses (Kellogg 2001).

Why study the herbaceous bamboos of Panama?

The first data on *Poaceae* family for the Panamanian Flora are reported by Jason R. Swallen in 1943 (Woodson et al. 1943–1980) with 276 taxa. Later D’Arcy (1987) reports 359 taxa, and in the most recent check list of the Panamanian Flora, Correa et al. (2004) list 417 taxa. As for herbaceous bamboos from the 6

taxa listed by Swallen in Woodson et al. (1943–1980), now the number reaches 23 taxa (Correa et al. 2004). Herbaceous bamboos are a very important group of grasses in Panama, being represented by nine genera, with several endemic species such as *Arberella dressleri* Soderstr. & CE Calderón, *A. lancifolia* Soderstr. & Zuloaga, *Cryptochloa decumbens* Soderstr. & Zuloaga, *C. dressleri* Soderstr. and *C. soderstromii* Davidse, *Machurolyra tecta* CE Calderón & Soderstr. (a monotypic genus), *Pariana argentea* Davidse & Hollowell, *P. strigosa* Swallen and taxa with a restricted distribution but present also in nearby Costa Rica and Colombia, such as *Cryptochloa concinna* (Hook. f.) Swallen, *C. variana* Swallen, *C. unispiculata* Soderstr., *C. strictiflora* (E. Fourn.) Swallen, and *Olyra standleyi* Swallen, *O. holttumiana* Soderstr. & Zuloaga.

Panama, with its peculiar geographical position, represents a connection between taxa mainly



Figure 2. Geographic distribution of Bambusoideae. *Source:* Modified from Kelchner & Bamboo Phylogeny Group 2013.

distributed in South America and those strictly distributed in Central America (Davidse 1985). According to Soderstrom and Calderón (1974), the main centre of differentiation of basal grasses (*Anomochloideae* and *Streptochaeteae*) and of herbaceous bamboos (*Olyreae*) may be considered the Tropical Atlantic Forest in Brazil, from where the migration started towards the remaining neotropical areas (Figure 3) during the Tertiary Era, not excluding a further area of differentiation, such as Panama and its neighbouring areas (Figure 3). Genera present in Panama such as *Arberella*, *Cryptochloa*, *Machurolyra* and *Raddiella* might support this hypothesis which needs to be confirmed by phylogenetic data, with the aim to obtain a phylogeographic synthesis of the genus in a comparative context within the tribe *Olyreae*.

Herbaceous bamboos in Panama: *Cryptochloa* as a case of study

Since 2011, we have been carrying out a study on the herbaceous bamboos in Panama, due to a collaboration between the Centro Studi Erbario Tropicale (CSET) of the University of Florence, the herbarium PMA of the Universidad Nacional de Panama and the

Smithsonian Tropical Research Institute (STRI) in Panama. Our study is mainly focused on the updating of the floristic and taxonomic data, in order to conduct a detailed phylogenetical and biogeographical study. First, the available floristic documentation is very scanty, as results from the herbarium data kept in the most important institution visited by one of us (RMB) such as K, MO, NY, P, PMA, US and W herbaria. Between 2012 and 2013, several field trips have been carried out with encouraging outcomes supported by some young Panamanian botanists involved in this research. Many areas of Panama are well known, such as Canal Zone, Province of Chiriquí, Panamá, Coclé, Herrera, Los Santos and Veraguas (see Dwyer 1964, 1968, 1985), while other regions have not yet been much visited, such as the Comarca de San Blas (Guna Yala), Darién and small areas along the Cordillera Mesoamericana on the Caribbean slope, which connects North and Tropical South America. Therefore, this kind of research is relatively complicated from logistical point of view, but definitely worth doing.

Our interest has focused on the genus *Cryptochloa* Swallen, with nine known species, seven of which are present in Panama: *C. concinna* (Hook. f.) Swallen, *C. decumbens* Soderstr. & Zuloaga, *C. dressleri* Soderstr.,



Figure 3. Eastern Brazil Atlantic forest (Bahian refugium) as an area of differentiation from which migration of bambusoid taxa proceeded towards the Amazonian Area. Panama provided bambusoid elements as yet unsolved. Source: adapted from Soderstrom & Calderón (1974).

C. soderstromii Davidse, *C. strictiflora* (E. Fourn.) Swallen, *C. unispiculata* Soderstr. and *C. variana* Swallen (the taxonomic value of *C. granulifera* Swallen is not well defined), which leads us to consider Panama as the centre of differentiation of this genus. A widespread species, *C. capillata* (Trin.) Soderstr., previously described in *Olyra* L. by Trinius (1835), is present from Northern South America through Tropical Atlantic Forest until Southern Brazil.

During the last 2 years of field collecting trips, we have obtained several important results. One of these

was the rediscovery after 35 years of the rare endemic species *Cryptochloa soderstromii* Davidse in Guna Yala, known only on the holotype specimen, and incompletely described (Davidse in Davidse & Pohl 1992) (Figure 4).

According to Davidse and Pohl (1992), *C. soderstromii* is considered an allied species of *C. capillata* (Trin.) Soderstrom (Soderstrom 1982). After a first comparison between the re-collected *C. soderstromii* Davidse and *C. capillata* (Trin.) Soderstr. and their types, kept, respectively, in MO, USA (*C. soderstromii*



Figure 4. *Cryptochloa soderstromii* Davidse (above) in Guna Yala (01.19.2013) and particular of the female and male florets (below). Source: photos O.O. Ortiz ©.

Davidse) and LE [*C. capillata* (Trin.) Soderstr. (bas.: *Olyra capillata* Trin.)], we are quite convinced that *C. capillata* Trin. might be a different taxon when compared with the species of *Cryptochloa* Swallen known until now, especially on the morphology and arrangement of the male and female florets (Figure 5).

The assignment of *Olyra capillata* Trin. to *Cryptochloa* Swallen must be basically verified by detailed morpho-anatomical and phylogenetic analysis, with possible reassessment of the distribution of the genus *Cryptochloa* Swallen (Figure 6).

Other interesting and encouraging results concern the floristic data of the endemic *C. dresslerii*, more common than it was considered in the past, the localized *C. decumbens*, and the high variation between *C. varians* Swallen and *C. concinna* (Hook. f.) Swallen, especially in Veraguas, where intermediate morphotypes between them have been found. Furthermore, we confirm the presence of *C. strictiflora* (E. Fourn.) Swallen and *C. unispiculata* Soderstr., the latter known only for Colombia and Peru.

Comments and perspectives

Data presented here represent only the preliminary results of the research in progress conducted in collaboration between the University of Florence, the Universidad Nacional de Panama and the STRI. Our

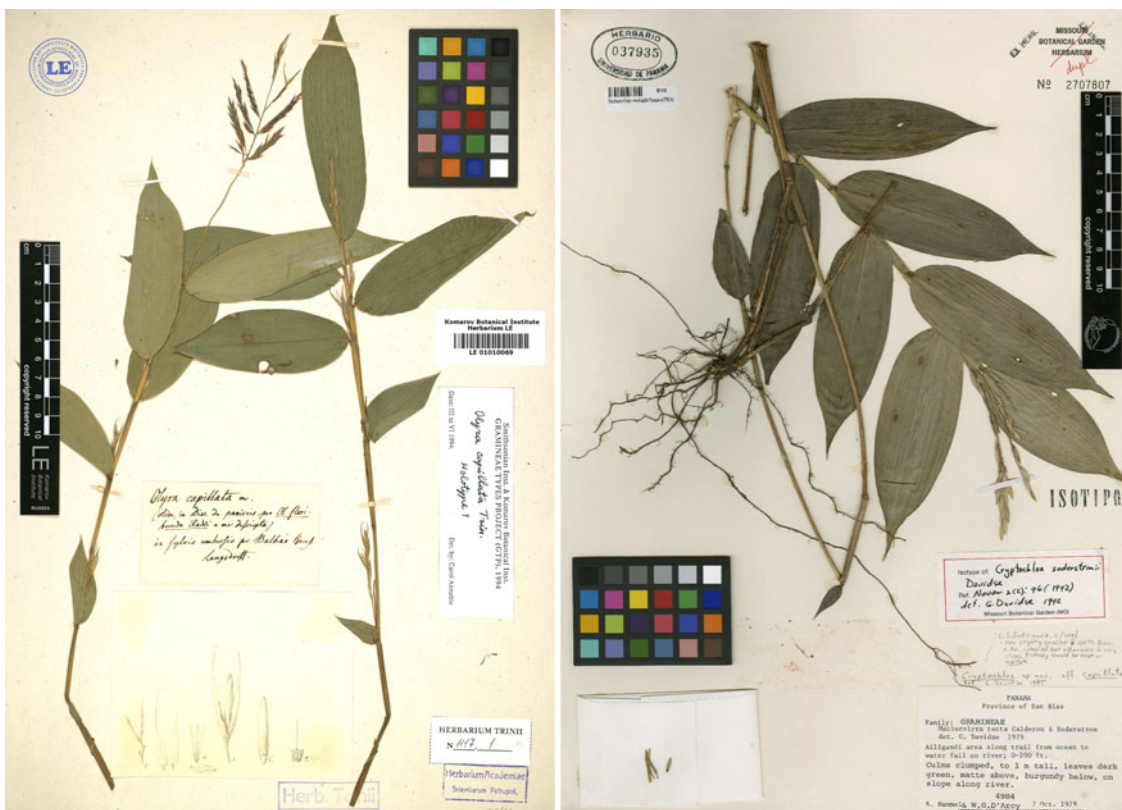


Figure 5. Comparison between *Cryptochloa capillata* (Trin.) Soderstr. (= *Olyra capillata* Trin., holotype in LE herbarium) and *Cryptochloa soderstromii* Davidse (isotype in US herbarium). (© LE & © US herbarium).



Figure 6. Distribution of the genus *Cryptochloa* Swallen (modified from Judziewicz et al. 1999) – *C. capillata* (Trin.) Soderstr. is shown in red and is deliberately distinct from the major area of distribution in numbers of species (black).

efforts are mainly focused on collecting data with the purpose of using them for a phylogenetic analysis of the *Olyreae* tribe. The importance of herbaceous bamboos is strictly related to the conservation of the habitats where they live, often under stress and threatened by the deforestation and urbanization, especially in a small, but definitely important country like Panama.

The destiny of the *Olyreae* is linked to that of the tropical forest, and this is particularly true in Panama, where a high level of endemism is present, also amongst herbaceous bamboos (Lewis 1971). In a different occasion, we confirmed the presence of rare herbaceous bamboos in Panama in critical conservation status, such as for *Arberella lancifolia*

Sodestr. & Zuloaga, *Cryptochloa* sp.pl., *Lithachne pauciflora* (O. Swartz) Poir., *Maclurolyra tecta* C.E. Calderón & Soderstr., *Olyra holttumiana* Soderstr. & Zuloaga *O. standleyi* Hitchc., *Pariana argentea* Hollowell & Davidse and *Raddiella esenbeckii* (Steud.) C.E. Calderón & Soderstr., and many others.

The state of the art in the study of herbaceous bamboos in Panama, especially in *Cryptochloa*, may be considered encouraging for further research, considering the strategic biogeographical meaning of Panama in relation to the *Olyreae* tribe. Further specific contributions will be issued about the *Poaceae* of the Panamanian Flora.

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