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A taxonomical revision of *Guadua weberbaueri* Pilg. and *Guadua sarcocarpa* Londoño & P. M. Peterson (Poaceae)

Jean Olivier & Odile Poncy

Abstract

OLIVIER, J. & O. PONCY (2009). A taxonomical revision of *Guadua weberbaueri* Pilg. and *Guadua sarcocarpa* Londoño & P. M. Peterson (Poaceae). *Candollea* 64: 171-178. In English, English and French abstracts.

The taxonomical revision of *Guadua weberbaueri* Pilg. and *Guadua sarcocarpa* Londoño & P. M. Peterson (Poaceae) is proposed here from field observations in SW Amazonia (Peru) and examination of herbarium specimens from other Amazonian countries: *Guadua sarcocarpa* subsp. *purpuracea* Londoño & P. M. Peterson is synonymised with *Guadua weberbaueri* and *Guadua sarcocarpa* s.s. is considered. Descriptions and an identification key for these two species of bamboo are given, including the first description of fruits of *Guadua weberbaueri*.

Key-words

POACEAE – *Guadua* – SW Amazonia – Taxonomy

Résumé

OLIVIER, J. & O. PONCY (2009). Révision taxonomique de *Guadua weberbaueri* Pilg. et *Guadua sarcocarpa* Londoño & P. M. Peterson (Poaceae). *Candollea* 64: 171-178. En anglais, résumés anglais et français.

La révision taxonomique de *Guadua weberbaueri* Pilg. et *Guadua sarcocarpa* Londoño & P. M. Peterson (Poaceae) est proposée suite à des observations de terrain au SO de l'Amazonie (Pérou) et l'examen de spécimens d'herbiers d'autres pays amazoniens: *Guadua sarcocarpa* subsp. *purpuracea* Londoño & P. M. Peterson est mis en synonymie avec *Guadua weberbaueri* et *Guadua sarcocarpa* s.s. est établi. Une description et une clé d'identification de ces deux espèces de bambou sont données, comme la première description des fruits de *Guadua weberbaueri*.

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Introduction

Guadua Kunth (*Poaceae*: *Bambusoideae*: *Bambuseae*: *Guaduinae*) is a neotropical genus, widespread throughout Central and South America, from 23°N in Mexico to 35°S in Argentina, as well as from sea level to 2000 m elevation in the Andes. *Guadua* includes approximately 25 species. The main center of diversity of the genus is the Amazon basin, where nearly half of the species have been recorded (JUDZIEWICZ & al., 1999: 46). Several species constitute the bamboo-dominated forests in South-western Amazonia that occupy vast areas (ca. 200 000 km² in total) within the lowland tropical rain forest (NELSON, 1994; JUDZIEWICZ & al., 1999: 64; NELSON & al., 2006).

Guadua is thus ecologically very important in structuring these ecosystems and the biodiversity of this region. Various plant and animal species are associated with *Guadua*, such as understory plants (GRISCOM & al., 2007), ants (DAVIDSON & al., 2006a, b), aquatic macrofauna (LOUTON & al., 1996), poison frogs (VON MAY & al., 2008), birds (PARKER, 1982; KRATTER, 1997), rodents (EMMONS, 1981, 1997) and primates (EMMONS, 1997). It is also, in places, culturally as important as *Bambusa* Schreb. is in Asia, in providing materials for construction and other human uses (JUDZIEWICZ & al., 1999: 87-103). However, the history, dynamics and future of the low diversity bamboo forests are still not well understood.

While investigating the reasons for the enigmatic spatial distribution of the *Guadua*-dominated forests in South-eastern Peru, some taxonomic problems became evident when we fortuitously encountered a mass flowering event. During field work aiming to locate bamboo patches in the Rio de Los Amigos basin (Madre de Dios, Peru), the first author visited a site (12.06°S 70.29°W) with two *Guadua* species living locally “side by side” (within less than 20 m of distance, respectively on each side of a brook delimiting two distinct geomorphologic terrains, dissected hills vs floodplain). The two species were flowering at the same time (December, 2003) and were both bearing fleshy fruits. This was a great opportunity given that these bamboo species are generally thought to flower only every 30-40 years (JUDZIEWICZ & al., 1999: 74), and that fruits were even more rarely observed.

According to the available descriptions (LONDOÑO & PETERSON, 1991), the fruits we have observed should be attributed to each of the two subspecies of *G. sarcocarpa* Londoño & P. M. Peterson: *G. sarcocarpa* subsp. *sarcocarpa*, and *G. sarcocarpa* subsp. *purpuracea* Londoño & P. M. Peterson. However, the fruits that fitted with the latter were present on bamboos that showed all the vegetative characters of *G. weberbaueri* Pilg. (PILGER, 1905; LONDOÑO & PETERSON, 1991). We thus undertook a thorough investigation into the taxonomic status of the two close relatives *G. sarcocarpa* and *G. weberbaueri*.

The geographical distributions of the two species *G. sarcocarpa* and *G. weberbaueri* greatly overlap; in particular, both are present with high abundance in South-western Amazonia (JUDZIEWICZ & al., 1999: 64). To date, the ecological requirements of each species are not well established and could explain difficulties in understanding their spatial distributions, as well as the distribution of bamboo-dominated forests in general: GRISCOM & ASHTON (2006) reported, for instance, that studies have shown the dominance by *G. sarcocarpa* and *G. weberbaueri* on very different soil types including very well-drained sandy soils and loams with perched water tables, thus suggesting that these two species are soil generalists. But in these studies, the two species are generally treated as a single taxonomic entity.

The taxonomic clarification we here propose should thus help gain a better understanding of the ecological preferences of each species, and then their spatial distribution within the bamboo dominated forests of South-western Amazonia.

Material and methods

Field observations

Field observations were made by the first author within the *Guadua* thickets surrounding the Rio de Los Amigos biological station (CICRA-12.56°S 70.10°W) and within the concession for conservation of the Los Amigos river basin (about 145 000 ha managed by the ACA-Amazon Conservation Association / ACCA-Asociación para la Conservación de la Cuenca Amazónica NGO). Flowering culms were tagged and observed through time from October 2002 to December 2005, to study flowers and fruits. Inflorescence structures and stamen colours were surveyed. Developing fruits (caryopses) were collected from one selected and tagged branch, day after day, at different stages of their maturation.

Nursery experimentation

We also conducted at the biological station a growth experiment with germinated fleshy fruits characteristic of those of *G. sarcocarpa* subsp. *purpuracea*, but which were collected on culms showing all the vegetative characteristics attributed to *G. weberbaueri* (LONDOÑO & PETERSON, 1991).

Herbarium data

Herbarium specimens were examined from the following institutions: CUZ, MOL, USM, LPB, CAR, P.

Additional specimens and information were obtained online from K, US, MO, NY, F, BRIT. A total of more than 250 *Guadua* specimens was examined, including 88 specimens of the two studied species.

Results

Field morphological observations

The relevance of three flower and fruit characters (Fig. 1) that usually help to distinguish *Guadua* taxa was first analyzed in populations that presented all the vegetative characteristics of *G. weberbaueri*.

a. Inflorescence structure

Within a thicket, we observed notable variations in flowering structures. They are found either on leafy culms or on leafless culms with all of the branches flowering. The inflorescences are “complex iterant, bracteate synflorescences” bearing the so-called pseudospikelets (see JUDZIEWICZ & al., 1999: 40). Along a single culm, the pseudospikelets may occur

directly at culm nodes as well as on lateral branchlets, or as isolated primary pseudospikelets at the apex of a foliage leaf complement (leafy branchlet) (Fig. 1A). The synflorescence structure and the position of the pseudospikelets on the culms thus do not seem to be traits useful for clear taxonomic distinctions.

b. Stamen color

In the studied populations the stamens were usually purple, but yellow stamens, or yellow stamens with purple spots, were sometimes observed (Fig. 1B). Moreover this variation appeared during the season of flowering: all yellow in September, all purple in December. This character also should not be considered as accurate for distinguishing taxa.

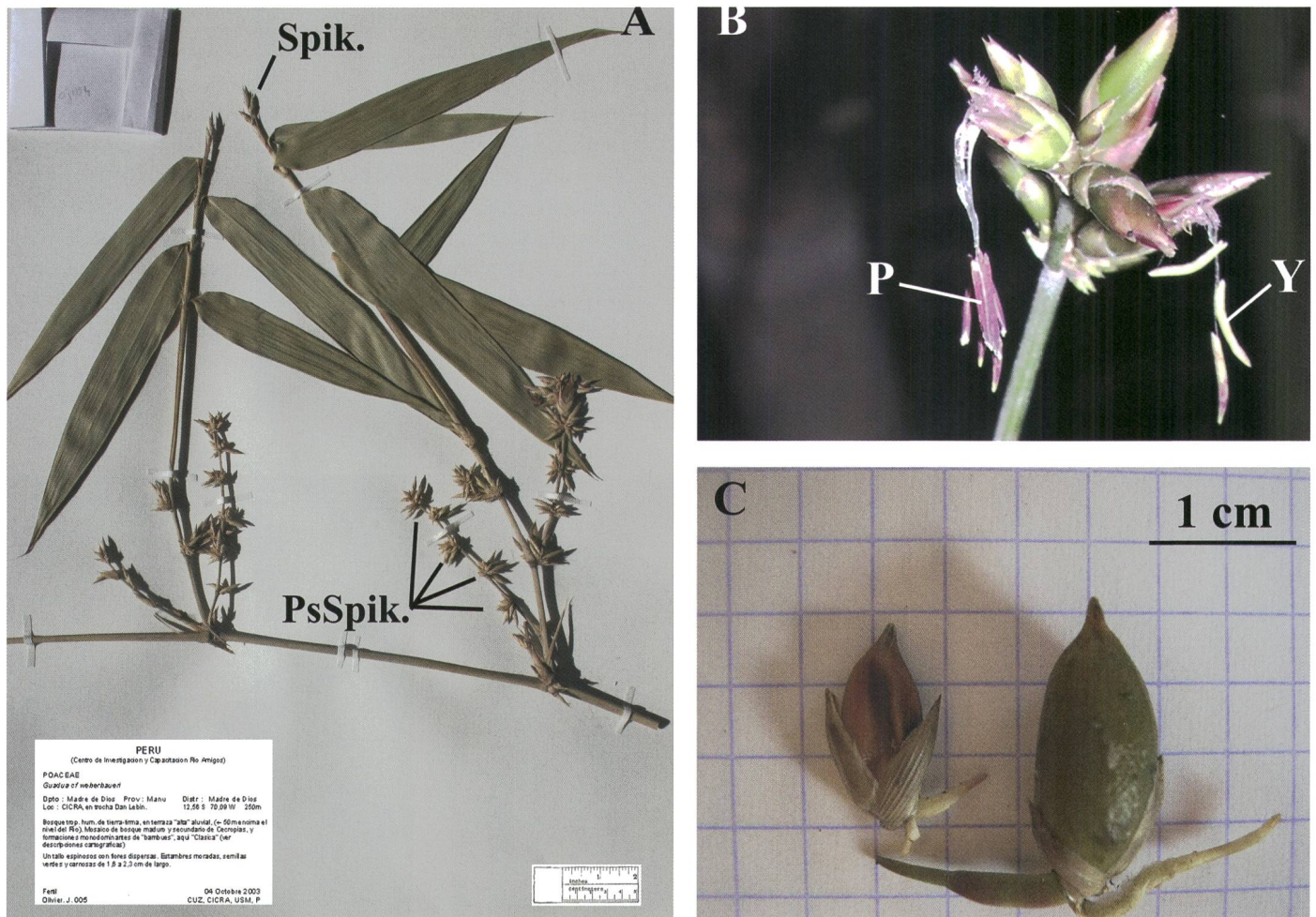


Fig. 1. – Variability in three characters. **A.** Isolated primary pseudospikelet (**Spik.**) and pseudospikelets (**PsSpik.**), respectively at the apex of the leaf complement and on flowering branchlets beared by the stem node; **B.** Example of both purple (**P**) and yellow (**Y**) stamens on the same *Guadua* Kunth branchlet; **C.** Fruits from the same branchlet, both germinated, respectively 13 days and 18 days after the same flowering event.

[Olivier 005, TLM] [[© Muséum d'Histoire Naturelle de Toulouse. Reproduced with permission]

c. Fruit size

Except for very small and obviously immature ones, all caryopses collected at different stages of maturation germinated spontaneously within 24 hours. We found that caryopses 13 days old (1.4 cm long) can germinate as well as 18 day-old ones (2.1 cm long) from the same branch and from pseudospikelets of the same size (2.5×0.3 cm) (Fig. 1C). This indicates that any species identification based only on fruit size requires extreme caution, even when the maturity of a fruit is tested by the aptitude to germinate. The size of the fertile pseudospikelets is thus more important to take into account.

Growth experiment

The juveniles grown from fleshy fruits (Fig. 2A) collected on culms showing all the vegetative characteristics attributed to *G. weberbaueri* also show all the characteristics of *G. weberbaueri*, particularly auricles and well developed fimbriae at the margins of the culm leaf ligules (Fig. 2B, 2C). These vegetative characters then appeared to be constant within this taxon with fleshy fruits.

Herbarium data

According to the original description and type specimen (Fig. 3A), *Guadua sarcocarpa* subsp. *sarcocarpa* has oblong, date-like fruits of $4-6 \times 1-2$ cm, with an acute apex, on $3-7 \times 0.4-1$ cm pseudospikelets (see LONDOÑO & PETERSON, 1991, for details). Most herbarium specimens identified

as *Guadua sarcocarpa* subsp. *sarcocarpa* that we examined presented reproductive characteristics conforming to the type. Their vegetative characters also corresponded to those described for this species, which are clearly distinct from those of *G. weberbaueri*.

By contrast, we could not observe any clear difference between *G. sarcocarpa* subsp. *purpuracea* (Fig. 3B) and *G. weberbaueri* (Fig. 3C). The description of *G. sarcocarpa* subsp. *purpuracea* mentions ovoid fruits ($1.5-2.5 \times 0.6-1.2$ cm), with an apiculate apex, on $1-3 \times 0.15-0.4$ cm pseudospikelets; this latter character, together with others (including vegetative characters) are very similar to those observable on the type specimen of *G. weberbaueri* (flowering specimen without fruit; Fig. 3C).

Twenty specimens (other than the type) were determined as *G. weberbaueri*: one bears fruit and eight also present pseudospikelets very similar in size and morphology to those of *G. sarcocarpa* subsp. *purpuracea* sensu LONDOÑO & PETERSON (1991).

Three specimens were attributed to *G. sarcocarpa* subsp. *purpuracea* and three others were identified as *G. sarcocarpa* without annotation of subspecies but showing pseudospikelets similar of those described for the subsp. *purpuracea*. Two specimens from these latter present fruits: the type specimen of the subspecies (Fig. 3B) and another one (Vargas 16 285, CUZ). The type specimen does not show indument on the pseudopetioles, but the latter does, which is considered by LONDOÑO & PETERSON (1991) and by LONDOÑO & ZURITA (2008) to be a distinctive vegetative character of *G. weberbaueri*.

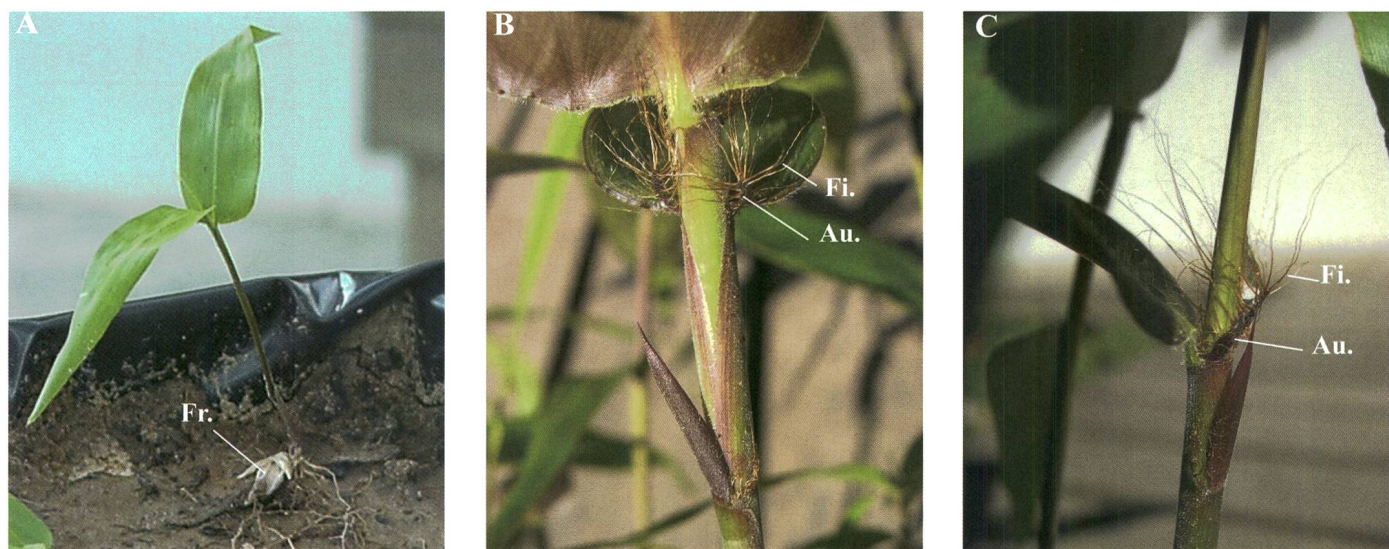


Fig. 2. – Nursery experimentation result. A. Fleshy fruit (Fr.) at the base of the juvenile; B-C. Auricles (Au.) and fimbriae (Fi.) well developed at the summit of the culm leaf sheath of the same juvenile two months later.

Discussion

LONDOÑO & PETERSON (1991) segregated the bamboo species *G. sarcocarpa* from its closest relative among the 25 species of the genus, *G. weberbaueri*. According to these authors, these species share particular characters unique within the genus *Guadua* and have very similar vegetative morphologies, although *G. sarcocarpa* is less hairy. The key character given for *G. sarcocarpa* was its fleshy fruit, a very rare feature among bamboos, and unknown in the neotropical genus *Guadua* until it was first described by LONDOÑO & PETERSON (1991).

Although *G. weberbaueri* is recognized as the “most widespread Amazonian species” in the genus (JUDZIEWICZ & al., 1999: 246), considerable confusion remains regarding the morphology of its fruit. The protologue of PILGER (1905) does not include any mention of the fruit, and the statement made by LONDOÑO & PETERSON (1991) that *G. sarcocarpa* subsp. *purpuracea* differs from *G. weberbaueri* by its fruit does not appear to be based on any of the specimens they examined. More recently, LONDOÑO & ZURITA (2008) lectotypified *G. weberbaueri* and mentioned that the fruit is a “dry caryopsis”, but again no specimen is cited. Consequently the comparison between the two taxa based on characters of their fruit does not appear to be reliable. Given the other similarities between *G. sarcocarpa* subsp. *purpuracea* and *G. weberbaueri* (vegetative as well as reproductive ones), our interpretation is

that the fruit described in reference to the former taxon in fact corresponds to the previously undescribed fruit of *G. weberbaueri*, and that *G. sarcocarpa* subsp. *purpuracea* must therefore be treated as a synonym of *G. weberbaueri*.

Consequently, the two close species *G. weberbaueri* and *G. sarcocarpa* have fleshy fruits (Fig. 3A, 3B). There is little information about the fruits of the other species of *Guadua* (see JUDZIEWICZ & al., 1999). However, fleshy fruits are perhaps more frequent in the genus than previously thought. In our observations, *G. weberbaueri* has fleshy fruits noticeably smaller than *G. sarcocarpa* as shown in Fig. 4 comparing the most common characteristics of *G. weberbaueri* and *G. sarcocarpa*. Besides, *G. weberbaueri* has fimbriate auricles at the summit of the culm leaf sheaths while *G. sarcocarpa* does not present such characteristics (PILGER, 1905; LONDOÑO & PETERSON, 1991). However LONDOÑO & ZURITA (2008) give a contrary information, but no other material than the type of *G. weberbaueri* (a poor and damaged specimen) is cited in this recent paper. We have examined several herbarium specimens that clearly show such fimbriate auricles and that were identified as *G. weberbaueri* by various taxonomists (e.g. Bell & Wiser 88-219 (P), det. E. Judziewicz, conf. X. Londoño in 2004).

Based on fertile material only, the distribution range of *G. weberbaueri* confirms that it is a widely distributed species in South-western Amazonia (Bolivia, Peru, Brazil) while *G. sarcocarpa* appears more restricted (found to date only in

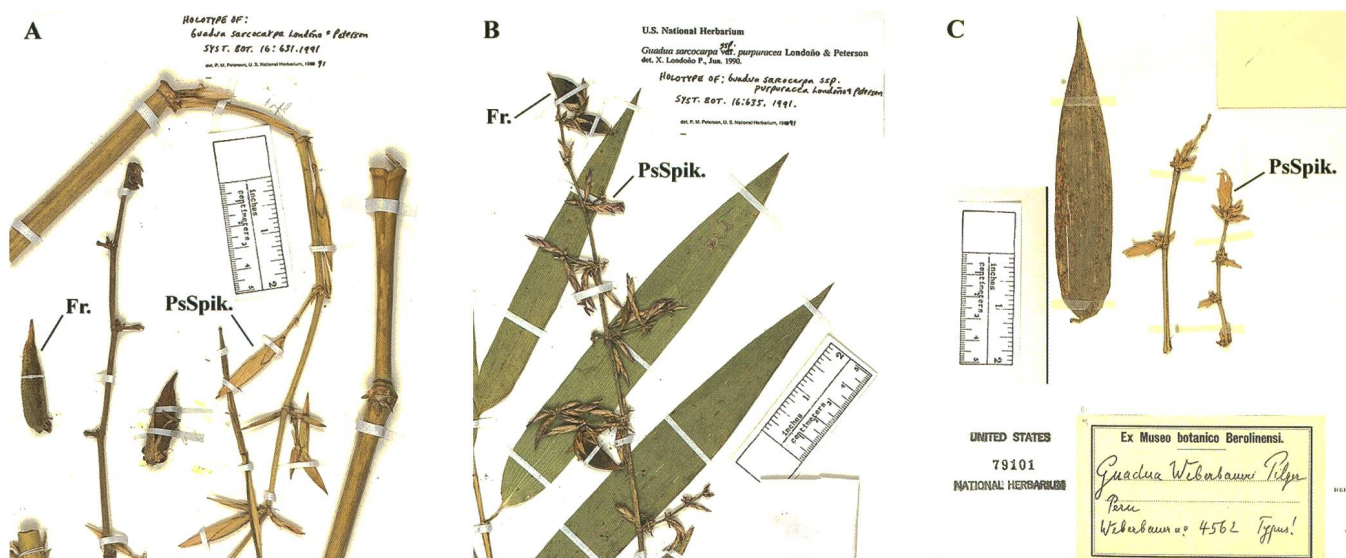


Fig. 3. – Types of: **A.** *Guadua sarcocarpa* Londoño & P. M. Peterson subsp. *sarcocarpa*; **B.** *G. sarcocarpa* subsp. *purpuracea* Londoño & P. M. Peterson; **C.** *G. weberbaueri* Pilg. [PsSpik.: pseudospikelets; Fr.: fleshy fruits]

[A: Reategui, F. s.n., US; B: Wasshausen, D. C. & F. Encarnacion 760, US; C: Weberbauer, A. 4562, US]

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Peru, but expected also from Acre-Brazil in 2004, B. Nelson, *pers. comm.*). There is to date, to our knowledge, no fertile specimen evidence to support the range of *G. sarcocarpa* given by LONDOÑO & ZURITA (2008).

Based on field observations, that need to be tested more systematically in the field for definitive acceptance, *G. weberbaueri* appears to be found on floodplains and *terra-firme* terraces with poorly-drained soils (unpublished data), and *G. sarcocarpa* appears to be found on well drained dissected hills. They are sometimes found growing (and flowering) “side by side” in some sites where the two different geomorphologic terrains are neighboring.

Finally, the taxonomic clarification proposed here (recognizing two distinct species and not subspecies) could agree with the biological species concept (see MAYR, 1992; LEE, 2003; RIESEBERG & al., 2006), that if growing side by side and flowering simultaneously, two distinct taxa should be two distinct biological species (reproductively isolated). This revised taxonomic status should also make clearer the puzzling existence and distribution of the multi-taxa bamboo forests of South-western Amazonia: one species, *G. weberbaueri*, might be associated with poorly-drained soils, while another one, *G. sarcocarpa*, would prefer well-drained substrates.





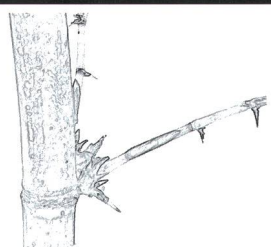

	<i>G. weberbaueri</i>	<i>G. sarcocarpa</i>
Fruit		
Pseudospikelet		
Thorny node		
Culm diameter [cm]	3.5–6	6–8

Fig. 4. – Schematic information about culm diameter, thorns, pseudospikelets and fruits from *Guadua weberbaueri* Pilg. and *G. sarcocarpa* Londoño & P. M. Peterson (the size proportions are the same between the two species for each character but not between the different characters).

Key to the two species of *Guadua* with fleshy fruits

1. Pseudospikelets large and elongated ($3-7 \times 0.4-1$ cm) frequently with two fertile florets. Fruits (caryopses) oblong, the apex obtuse to acute ($3-6 \times 1-2$ cm) **1. *G. sarcocarpa***
- 1a. Pseudospikelets short and relatively wide ($1-3 \times 0.15-0.6$ cm), only with a single terminal fertile floret. Fruits (caryopses) ovate, the apex abruptly apiculate ($1.5-2.5 \times 0.6-1.2$ cm) **2. *G. weberbaueri***

1. *Guadua sarcocarpa* Londoño & P. M. Peterson in Syst. Bot. 16: 631. 1991 (Fig. 3A).

Typus: PERU: Cuzco, $12^{\circ}30'S$ $72^{\circ}58'W$, growing in recent alluvial soils, hills up to 400 m, 13.VIII.1982 (fl, fr), *Reategui s.n.* (holo-: US!).

Culms and leaves slightly pilose to glabrescent. Culm diameter in mature thickets 6-8 cm. *Thorns* generally few and simple (only one on each culm node). *Pseudospikelets* $3-7 \times 0.4-1$ cm, frequently with two fertile florets, a terminal one, and a lateral one. *Fruits* fleshy, $3-6 \times 1-2$ cm, oblong, the apex obtuse to acute.

Vernacular name. – “Paca negra” sometimes used in SE Peru seems to refer to the relatively dark color of leaves.

Distribution and ecology. – Species mainly found on the “Fitzcarrald Arch” corresponding to the Camisea and Manu areas in Peru, and not recorded from fertile material in the public herbaria visited but expected to occur in the state of Acre in Brazil. Based on field observations, *G. sarcocarpa* appears to be found mainly on hills known to have very well-drained soils.

Material examined. – **PERU. Cuzco:** La Convention, Echarati, San Martin 3 Wellsite, $11^{\circ}47'S$ $72^{\circ}42'W$, 15.II.1997 (fl, fr), *Núñez & al.* 18942 (USM); La Convencion, Echarati, Cashiriari-3 well site, 5 km south of Camisea river, 700 m, $11^{\circ}52'S$ $72^{\circ}39'W$, 2.IX.1998 (fl), *Núñez* 23733 (CUZ); La Convencion, Echarati, Cashiriari-3 well site, 5 km south of Camisea river, 700 m, $11^{\circ}52'S$ $72^{\circ}39'W$, 2.IX.1998 (fl, fr), *Núñez & al.* 23861 (CUZ, USM); Cusco, Camisea, Campamento San Martin-C, Camisea Production Unit, 467 m, $11^{\circ}47'S$ $72^{\circ}41'W$, 11.I.1997 (fl, fr), *Acevedo-RDGZ & al.* 8609 (CUZ, USM). **Madre de Dios:** Manu, Concesion para la Conservación del Río los Amigos, Río el Amiguillo “Punto 13”, 350 m, $12.06^{\circ}S$ $70.29^{\circ}W$, 9.XII.2003 (fr), *Olivier, J.* 010 (TLM).

2. *Guadua weberbaueri* Pilger in Repert. Spec. Nov. Regni Veg. 1: 152. 1905 (Fig. 3B, C).

Typus: PERU. **San Martin:** Loreto, Moyobamba, VIII.1904 (fl), *Weberbauer, A.* 4562 (holo-: B [destroyed]; lecto-: MOL!; iso-: US!) (lectotypified by LONDOÑO & ZURITA, 2008).

= *Guadua sarcocarpa* subsp. *purpuracea* Londoño & P. M. Peterson in Syst. Bot. 16: 635. 1991, **syn. nov.**
Typus: PERU: Cuzco, $13^{\circ}30'S$ $71^{\circ}35'W$, ca. 1100 m, along trail directly south of Quincemil, 11.X.1976 (fl, fr), *Wasshausen & Encarnacion* 760 (holo-: US!; iso-: K!, MO!, NY!, USM).

Auricles with fimbriae present at the summit of the culm leaf sheaths and surfaces of the leaf blades pilose, particularly on juveniles. *Culm* diameter in mature thickets 3.5-6 cm. *Culm nodes* generally with ramified thorns (like reiterated “cow horns”) and numerous ramified spiny branches (like “barbed wire”). *Pseudospikelets* $1-3 \times 0.15-0.6$ cm only with a single terminal fertile floret. *Fruits* fleshy, $1.5-2.5 \times 0.6-1.2$ cm, ovate, the apex abruptly apiculate.

Vernacular name. – “Paca blanca” sometimes used in SE Peru seems to refer to the relatively light color of leaves.

Distribution and ecology. – Species widely distributed throughout South-western Amazonia, from Brazil to Bolivia and Peru. Based on field observations, *G. weberbaueri* appears to be found mainly on ancient terraces and on river banks with poorly-drained soils.

Material examined. – **BOLIVIA. Beni:** Ballivian, Forest island at Espirituviejo, 4.IV.1987 (fl), *Renvoize* 4671 (LPB).

BRAZIL. Acre: s.l., 15.VII.1933 (fl), *Krukoff, B. A.* 5235 (MO, F); Villa Assis (localité 23), 181 m, $10^{\circ}56'S$ $69^{\circ}34'W$, 20.VII.1995 (fl), *Núñez & al.* 16988 (CUZ, USM).

PERU. Cuzco: Paucartambo, entre Mistiana y Kesos, 660 m, 27-29.VII.1948 (fl), *Vargas* 7375 (CUZ); Paucartambo, Pilcopata, borde río Yunguyo, 620 m, 1.V.1965 (fl, fr), *Vargas* 16285 (CUZ); La Convention, Río Camisea, Ernesto’s old garden, 11.II.1996 (fl), *GHS* 1773 (USM). **Madre de Dios:** Manu, CC up recruit terra Cocha Cashu, 380 m, 27.X.2001 (fl), *Núñez* 30828 (CUZ); Manu, Río Alto MdD, Erika - junction of río Carbon y R Alto MdD, 650 m, 8.VII.1994 (fl), *Núñez & al.* 15543 (CUZ); Manu, Los Amigos Biological Station, Madre de Dios River, ca. 7 km upriver from mouth of Río Los Amigos, collections starting at 1220 m along Trail 4, 8.V.2001 (fl), *Janovec & al.* 1929 (BRIT); Tambopata, Explorer’s Inn Tourist Lodge, Río Tambopata, 270 m, $12^{\circ}50'S$ $69^{\circ}17'W$, 27.VIII.1994 (fl), *Núñez & al.* 15680 (CUZ); Tambopata, à 15 km de Maldonado, 200 m, 20.XI.1973 (fl), *Vargas* 22460 (CUZ); Tambopata, Río Tambopata - Tambopata Jungle Lodge Forest, Galbunca, 300 m, 28.VII.1992 (fl), *Núñez & al.* 14755 (CUZ); Tambopata Reserved Zone, Bamboo trail, $12^{\circ}50'S$ $69^{\circ}17'W$, 17.III.1988 (fl), *Bell, D. & S. Wiser* 88-219 (USM, P); Manu, Los Amigos Biological Station, 250 m, $12^{\circ}56'S$ $70^{\circ}09'W$, 4.X.2003 (fl, fr), *Olivier, J.* 005 (CUZ, USM, MOL, P, TLM).

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