



A revision of *Pholidostachys* (Arecaceae)

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Abstract

A taxonomic revision of the neotropical palm genus *Pholidostachys* based on morphological data and morphometric methods was carried out. Two hundred and eighty-eight herbarium specimens were scored for five qualitative variables and 25 quantitative variables. Qualitative variables were divided into four characters and one trait. Using the Phylogenetic Species Concept, characters were used to recognize seven species. These are widely distributed in Central and northwestern South America from Nicaragua to Colombia, Ecuador, Peru, and Brazil. Analysis of each species for geographic distribution and quantitative variables led to recognition, in one species, of two subspecies, giving a total of eight taxa. Four new species (*P. amazonensis*, *P. occidentalis*, *P. panamensis*, *P. sanluisensis*) are described. Two new combinations are made. Nomenclature, descriptions, and distribution maps are provided for each species and subspecies. Images of the type specimens of all new taxa are also provided.

Key words: Palmae, morphometrics, Neotropics, geonomoid palms

Introduction

Pholidostachys Wendl. ex Hooker (1883: 915) is a member of the geonomoid group of palms, formally named the tribe Geonomateae Luer (1882: 342, Dransfield *et al.* 2008). The geonomoids are characterized by their flowers sunken in pits along the rachillae, with each pit covered before anthesis by a proximal lip. Although there have been disagreements over generic boundaries within the group (e.g., Moore 1966; Wessels Boer 1968), these are now mostly resolved (Dransfield *et al.* 2008). The group comprises six genera and 103 species: *Asterogyne* Wendl. ex Hooker (1883: 914)(5 species, Stauffer *et al.* 2003), *Calyptrogyne* Wendl. (1859: 72)(18 species, Henderson 2005a), *Calyptronoma* Griseb. (1864: 518)(3 species, Zona 1995), *Geonoma* Willdenow (1805: 174)(68 species, Henderson 2011), *Pholidostachys* (7 species, this revision), and *Welfia* Wendl. (1869: 242)(2 species, Henderson unpublished). *Pholidostachys* has been recovered as sister genus to *Welfia* and these two as sister to the remaining genera in successive phylogenetic studies (Asmussen *et al.* 2006, Baker *et al.* 2009, 2011, Roncal *et al.* 2005, 2010, 2011).

Pholidostachys has always been considered a small and uncomplicated genus (or subgenus), comprising just three (e.g., Wessels Boer 1968) or four (e.g., de Nevers 1995) species. One reason for this simplistic view was lack of specimens. The most recent monographer (Wessels Boer 1968) used 16 specimens on which to base his revision, this number perhaps reflecting the few specimens available at that time. In the present revision, 288 specimens have been examined. It is not only this eighteen-fold increase in the number of available specimens that has led to a better understanding of the genus. More importantly, it is the application of an explicit species concept, and analysis of qualitative and quantitative morphological data and distribution patterns. *Pholidostachys*, as revised here, comprises seven species, one of them divided into two subspecies, giving a total of eight taxa.

Materials and Methods

Species concept

In this study the Phylogenetic Species Concept (PSC) is used. Under this concept, species are defined as: "the smallest aggregation of populations.... diagnosable by a unique combination of character states in comparable individuals" (Nixon & Wheeler 1990). Individual specimens are considered comparable because all are fertile. The terms character and trait are used in the sense of the PSC. Characters are qualitative variables the same states of which are found in all comparable individuals within a terminal lineage (i.e., species); traits are qualitative variables with more than one state found within species (although some species may have only one state of a given trait). The PSC is chosen here because it has an explicit definition, theoretical background, and discovery operation, as described below. This is discussed in more detail in Henderson (2005b; see also Henderson 2004, 2005a, 2011).

Two operational modifications are necessary in order to apply the PSC. According to Davis & Nixon (1992), phylogenetic species are delimited by successive rounds of aggregation of local populations, based on analysis of characters and traits. Because palm specimens are seldom collected on a population basis, and because there is no *a priori* method of placing specimens in populations and consequently distinguishing *a priori* between characters and traits, all specimens (i.e., treating specimens as populations) and all qualitative variables (i.e., traits and characters) were used in the analysis (see below).

A second modification of the PSC involves subspecific variation. Some groups of specimens with unique combinations of qualitative character states (i.e., species) may vary internally in quantitative variables and may occur in disjunct geographic areas. Based on these criteria, subgroups may be recognizable. Luckow (1995), in her discussion of the PSC, stated that "groups of populations that differ not by fixed characters, but by differences in mean values would be recognized as subspecies or varieties [under the PSC]." A slightly modified version of this is followed here. If subgroups can be delimited by geographic disjunctions and these subgroups are supported by analysis of quantitative variables (see below), then a phylogenetic subspecies concept is applied.

In summary, the PSC is applied to groups of specimens with unique combinations of qualitative character states, and a PSC subspecies concept is applied to subgroups that can be delimited by analysis of geography and quantitative variables.

Species delimited under the PSC function as hypotheses and these can be tested (Wheeler & Platnick 2000). This test depends on distinguishing characters from traits, i.e., the test is that characters are not traits, and traits are not characters. In the former case, a supposed character may turn out to be distributed as a trait. Such a misinterpretation would give an overestimation of the number of species. In the latter case, a supposed trait may be distributed as a character, giving an underestimation of the number of species.

Data matrix construction

Two hundred and eighty-eight specimens from the following herbaria were examined and scored: AAU, BH, BM, COL, COAH, CR, F, GH, K, MO, and NY (herbarium abbreviations from Holmgren *et al.* 1990). Fragmentary type specimens from some herbaria were examined but not necessarily scored. An image of a single specimen (*Hammel 16890*) from CR was examined; the original specimen was not seen. Sometimes, more than one duplicate of a collection was used in scoring. All sterile specimens, including types, were excluded from this study because of the difficulty of identifying them.

Morphological attributes that could be scored or measured from specimens were divided into qualitative (binary or multistate) or quantitative (continuous, meristic) variables. A search was made for qualitative variables in which two or more states of the variable were present among the specimens and could be scored unequivocally. This search was based on a survey of specimens. A dissecting microscope was used to survey floral variables. Six qualitative variables were found and scored (Appendix I).

A search was made for quantitative variables that could be taken from specimen labels (where, in case of ranges, median values were used) or measured from specimens. Variables were counted or measured with a

ruler, digital calipers, or protractor. Twenty-five quantitative variables were found and scored (Appendix II). Three are from stems, ten from leaves, and 12 from reproductive structures. Twenty-one are continuous and four are meristic.

A data matrix was constructed with specimens as rows and variables as columns (<http://sciweb.nybg.org/Science2/res/Henderson/Pholidostachys.xls.zip>). Additional columns recorded a specimen identification number, collector, collector's number, herbarium, country, latitude, longitude, and elevation. Latitude and longitude were taken from the specimen label, when available. On specimens lacking coordinates, these were estimated from the collection locality using either maps or electronic gazetteers.

For each of the 288 specimens in the matrix, three spatial variables and 31 morphological variables were recorded, giving a potential total of 9,792 data points. However, approximately 52% of these potential data is missing in the matrix. Specimens are often fragmentary or incomplete, and various organs are often missing. However, this level of missing data does not adversely affect the results presented here because so few statistical tests are carried out.

Data analyses

Some inferential statistics were used in this study. Although random samples are required for statistical inference, the samples of herbarium specimens are not random. However, there is no reason to believe that collectors favored any particular kind of specimen over others. Therefore inferential statistics were used, but the results should be considered accordingly. Statistical analyses were carried out using the programs NTSYS (Rohlf 2000) and Systat (Wilkinson 1997). Specimens with missing values were excluded. Analyses are thus based on subsets of the data. Because some quantitative variables were not normally distributed, data were \log_{10} -transformed before analysis.

Species delimitation

All specimens were assigned a preliminary species identification, either based on a previous determination or on the keys in local floras (e.g., Henderson 1995; Hammel *et al.* 2003; Galeano & Bernal 2010). Cluster analysis (CA) was used to divide qualitative variables into either characters or traits. The SIMQUAL module of NTSYS with the simple matching coefficient (for binary and multistate variables) was used to produce a similarity matrix. The SAHN module of NTSYS was used to subject the similarity matrix to the unweighted pair group method, arithmetic average (UPGMA) clustering algorithm. Successive analyses were used, with all variables used in the first analysis. Suspected traits (i.e., those variables both states of which occur in adjacent and otherwise homogeneous groupings) were removed, and the analysis run again until groups were found with unique combinations of states. These groups were recognized as species. Specimens that had not been included in these analyses because of missing data were then assigned to their respective species based on their morphology and geography.

Subspecies delimitation

Variation within each species was examined, based on analysis of geographic distributions and quantitative variables. The purpose of these analyses was to look for evidence of presence of discrete subgroups (i.e., subspecies). Traits were not used in subspecies delimitation because only one trait was found and this had many missing data.

Geographic distribution of species was analyzed by examining distribution maps produced by Arcview GIS 3.2 (Environmental Systems Research Institute, Inc.) using latitude and longitude data for each specimen. Each dot on the maps represents at least one specimen. Geographic subgroups were recognized if specimens clustered in discrete groups separated from other such groups.

Quantitative variation was analyzed. A *t*-test (two-sample, separate variance test on \log_{10} -transformed variables) or, with more than two variables, an one-way ANOVA (on \log_{10} -transformed variables) was used to test for geographic subgroup differences for each quantitative variable. The Bonferroni pair wise procedure

was used to see which pairs of means differed significantly ($P < 0.05$). If there were too few specimens, usually less than 10, then tests were not carried out.

If subgroups delimited by geographic disjunctions were supported by analysis of quantitative variables, then they were recognized as subspecies.

Environmental variation

Linear regression was used to analyze relationships within species and subspecies between \log_{10} -transformed quantitative variables and latitude, longitude, and elevation. The first two of these were taken as proxies for correlated variation in environmental variables. If there was a significant ($P < 0.05$) correlation between variables, squared multiple R is reported. This shows the amount of variance in the dependent variable explained by the independent variable.

Taxonomic treatment

A genus description of *Pholidostachys* is given (based on characters, traits, and quantitative variables) (see also section on Morphology for an illustrated discussion of morphology). This is followed by a key to all species, based on all attributes (characters, traits, quantitative variables) and geography.

For each species, arranged in alphabetical order, complete synonymy is given. Most types of names of *Pholidostachys* have been examined for this study and these are followed by a “!”. Those which have not been examined are followed by “*n.v.*”. Excluded names are listed in Appendix III. Plates of type images of all new taxa are given in Appendix IV, and images of types of new taxa deposited at NY are available at the website http://www.nybg.org/bsci/herbarium_imaging/. A numerical list of taxa and a list of specimens examined, ordered by collector, are given in Appendix V, and an Index to Names in Appendix VI.

Results

Analysis of the six qualitative variables divided them into five characters and one trait (Appendix I). Analysis of the five characters divided the 288 specimens into seven species, four of them undescribed. Analysis of quantitative variables and distribution of these species divided one of them into two subspecies, giving a total of eight taxa. A discussion of distribution and habitat, and morphology of these taxa precedes the Taxonomic Treatment section.

Distribution and Habitat

Pholidostachys species are distributed from 11°22'N (Nicaragua) to 13°31'S (Peru) and 68°46'W (Nicaragua) to 84°24'W (Brazil). The country with the highest number of species is Colombia with six. Species of *Pholidostachys* occur from sea level to 1750 m elevation (*P. synanthera* subsp. *synanthera* in Colombia). However, most specimens are from lower elevations. Of the 244 specimens with elevation data, 210 (86%) occur at ≤ 1000 m. Nevertheless, several species of *Pholidostachys* have unusually wide elevation ranges. For example, *P. dactyloides* occurs from 5–1440 m, *P. occidentalis* from 300–1600 m, and *P. synanthera* subsp. *synanthera* from 400–1750 m.

Species of *Pholidostachys* are found in similar habitats. Most commonly they occur in lowland or montane rainforest, in non-flooded (rarely flooded) areas.

Morphology

The genus description given below in the Taxonomic Treatment section is based on the list of characters, traits, and quantitative variables used in this study (Appendix I). In the following discussion, morphology is treated in more detail, and the morphology of several attributes of *Pholidostachys* not used in delimiting species is discussed. A detailed generic description can also be found in Dransfield *et al.* (2008).

Stems are mostly solitary. Of the 110 specimens with relevant data, only seven are reported to have clustered stems, all belonging to *Pholidostachys pulchra*. Stems of all but one species are erect and range from 1–11 m long and 3–22 cm diameter. The exceptional species, *P. panamensis* has shorter stems which are described on some labels as procumbent.

Leaf number ranges from 4–17 per stem, with a mean of 14. Sheaths are open and do not form crownshafts, and are usually rather fibrous along the margins. Petioles are well-developed, and mean length per species ranges from 51.7–102.1 cm long. Rachises are well-developed in all species, and mean length per species ranges from 42.0–192.40 cm long. Leaves are pinnate and never undivided. There are 3–18 pinnae per side of the rachis, and these are equally to unequally wide and appear almost regularly arranged (Fig. 1A). Pinna shape is usually lanceolate to slightly sigmoid. Pinnae are often somewhat plicate with a contracted base and elongate, acuminate apex.

Inflorescences of *Pholidostachys* take several forms. They can be branched to one order with an elongate peduncle, short rachis, and several rachillae that are pendulous at anthesis (e.g., *P. occidentalis*, Fig. 1B); branched one to two orders with a well-developed peduncle and rachis, and several rachillae that are spreading at anthesis (e.g., *P. synanthera*); branched to one or rarely two orders with a well-developed peduncle, short rachis, and several rachillae that are erect at anthesis (e.g., *P. dactyloides*, Fig. 1C); spicate with a well-developed peduncle, absent rachis, and one rachilla that is arching or erect at anthesis (e.g., *P. pulchra*); or spicate, with a short peduncle, absent rachis, and one rachilla that is erect at anthesis (e.g., *P. panamensis*, Fig. 1D).

These different inflorescence forms have different prophylls and peduncular bracts. For example, in *P. dactyloides* the rachillae are completely covered at anthesis by the fibrous bracts (Fig. 2A). In most other species the bracts are woody and do not cover the rachillae before or during anthesis (Fig. 2B). Henderson (2002) has given a discussion of inflorescences in *Pholidostachys*.

Flower pits are covered by proximal lips, and the form of these is taxonomically useful. Proximal lips may be irregularly shaped, often acute or acuminate, and completely covering the pits before anthesis, as in *P. dactyloides* (Fig. 3A) and *P. sanluisensis*; regularly shaped, rounded, and completely covering the pits before anthesis and not recurved, as in *P. panamensis* (Fig. 3B) and *P. pulchra* (Fig. 3C); or they may be regularly shaped, rounded, and not covering the pits before anthesis and recurved, as in *P. amazonensis*, *P. occidentalis* (Fig. 3D), and *P. synanthera* (Fig. 3D).

Flowers are arranged in triads, at least on the proximalmost parts of the rachillae. Commonly distalmost parts of the rachillae bear staminate flowers only. Staminate flowers have three, free, narrow sepals; three, valvate petals that are slightly connate at the bases; and six stamens. The filaments are connate for most of their length into a tube, but are free at the apices. This free part is usually short and triangular, but in two species the free part is linear and inflexed (*Pholidostachys occidentalis*, *P. synanthera*). Pistillate flowers have similar sepals and petals to those of staminate flowers. There is a staminodial tube with lobed apices, and these lobes are exerted at anthesis and spread in a star-shaped fashion. There is an elongate style with three, spreading stigmas. Inflorescences of all species appear to be protandrous, judged from specimens. Nothing is known of pollination in *Pholidostachys*, although based on inflorescence structure the genus could have diverse pollinators.

Fruits are variously shaped but always have basal stigmatic residues. They can be compressed, obovoid in lateral view with an asymmetric base, ellipsoid in frontal view, and with a pronounced longitudinal ridge on one side and several lesser ridges on the opposite side, as in *P. occidentalis* (Fig. 4B) and *P. pulchra* (Fig. 4D); compressed, obovoid in lateral view with an asymmetric base, ellipsoid in frontal view, with a pronounced meridional ridge, as in *P. sanluisensis* (Fig. 4E); scarcely compressed, obovoid, with an obscure longitudinal ridges, as in *P. dactyloides* (Fig. 4A); widely obovoid, without a pronounced longitudinal ridges, as in *P. panamensis* (Fig. 4C); or scarcely compressed, ellipsoid, with an obscure longitudinal ridges, as in *P. synanthera* (Fig. 4F). Eophylls are bifid.



FIGURE 1. A. Leaf blade of *Pholidostachys occidentalis* (Henderson 138). B. Inflorescence of *P. occidentalis* (Henderson 138). C. Inflorescence of *P. dactyloides* (Balslev 60677). D. Infructescence of *P. panamensis* (Henderson 3037).



FIGURE 2. **A.** Fibrous inflorescence bracts of *Pholidostachys dactyloides* (Balslev 60677). **B.** Rachillae of *P. occidentalis*, free from inflorescence bracts at staminate anthesis (Henderson 138).

FIGURE 3. **A.** Proximal lips of flower pits irregularly shaped, often acute or acuminate, completely covering pits before anthesis (*Pholidostachys dactyloides*; left *de Nevers* 8402, right *Arguëlo* 477). **B.** Proximal lips of flower pits regularly shaped, rounded, completely covering pits before anthesis and not recurved (*P. panamensis*; *de Nevers* 6767). **C.** Proximal lips of flower pits regularly shaped, rounded, completely covering pits before anthesis and not recurved (*P. pulchra*; left *Henderson* 712, right *Henderson* 59). **D.** Proximal lips of flower pits regularly shaped, rounded, not covering pits before anthesis, recurved (left *P. occidentalis*, *Henderson* 138; right *P. synanthera* subsp. *synanthera*, *Henderson* 161). Scale bar = 1 cm.

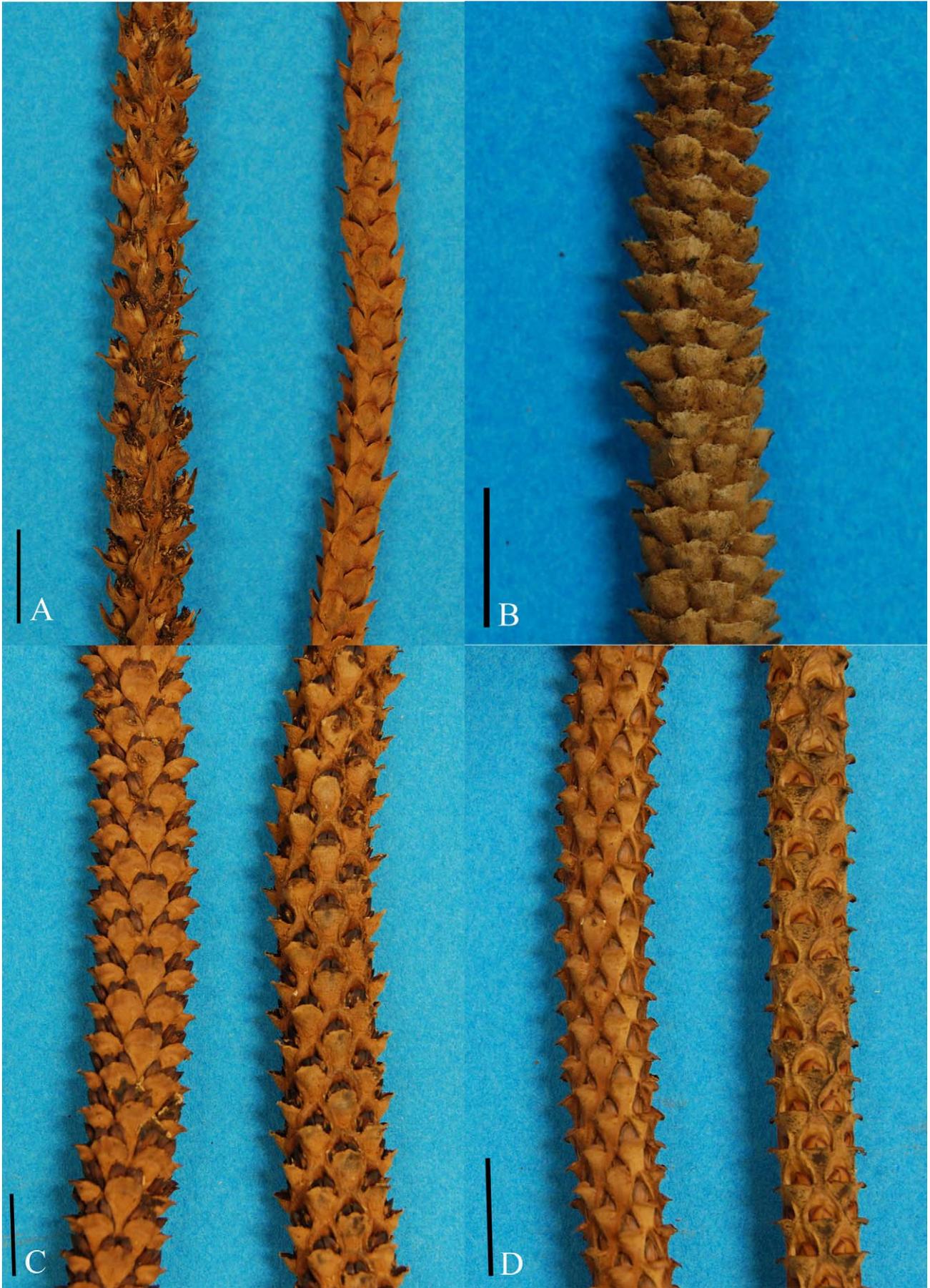




FIGURE 4. **A.** Fruits of *Pholidostachys dactyloides* (Dodson 14491). **B.** Fruits of *P. occidentalis* (Balslev 60678). **C.** Fruits of *P. panamensis* (Liesner 1255). **D.** Fruits of *P. pulchra* (de Nevers 4285). **E.** Fruits of *P. sanluisensis* (Juncosa 726). **F.** Fruits of *P. synanthera* subsp. *synanthera* (Couvreur 119). Scale bar = 1 cm.

Taxonomic Treatment

Pholidostachys Wendl. ex Hooker 1883

Pholidostachys Wendl. ex Hooker 1883: 915. Type: *Pholidostachys pulchra* Wendl. ex Burret
Calyptrogyne subgen. *Pholidostachys* (Wendl. ex Hooker) Wessels Boer 1968: 73.

Stems solitary, more rarely clustered, 3.8(0.1–11.0) m long, 6.6(3.0–22.0) cm diameter. **Leaves** 14(4–27); sheaths 34.7(14.0–110.0) cm long; petioles 73.5(20.0–150.0) cm long; rachises 106.9(32.0–234.0) cm long, 9.6(3.3–24.4) cm wide; pinnae 9(3–18) per side of rachis; basal pinna 50.7(26.5–92.0) cm long, 2.1(0.2–10.0) cm wide, forming an angle of 54(27–93)° with the rachis; apical pinna 42.7(23.0–65.0) cm long, 13.2(2.5–27.0) cm wide, forming an angle of 16(7–29)° with the rachis. **Inflorescences** branched 1 order, with an elongate peduncle, short rachis, and several rachillae, these pendulous at anthesis, or inflorescences branched 1–2 orders, with a well-developed peduncle and rachis, and several rachillae, these spreading at anthesis, or inflorescences branched 1 order (rarely 2 orders), with a well-developed peduncle, short rachis, and several rachillae, these erect at anthesis, or inflorescences spicate, with a well-developed peduncle, absent rachis, and 1 rachilla, this arching or erect at anthesis, or inflorescences spicate, with a short peduncle, absent rachis, and 1 rachilla, this erect at anthesis; prophylls 23.9(5.0–62.0) cm long; peduncular bracts 33.9(12.5–65.0) cm long, the bracts inserted 5.1(1.1–12.5) cm apart; prophylls and peduncular bracts fibrous, covering all or part of the rachilla(e) at anthesis, or prophylls and peduncular bracts woody, not covering rachilla(e) at anthesis;

peduncles 25.5(3.5–171.0) cm long, 9.0(3.2–19.1) cm wide; rachillae 5(1–25), 33.3(7.5–85.0) cm long, 7.4(3.7–16.2) mm wide; proximal lips of flower pits regularly shaped, rounded, completely covering pits before anthesis and not or seldom recurved, or proximal lips of flower pits irregularly shaped, often acute or acuminate, completely covering pits before anthesis, or proximal lips of flower pits regularly shaped, rounded, not covering pits before anthesis, recurved; **fruits** compressed, obovoid in lateral view with an asymmetric base, ellipsoid in frontal view, with a pronounced longitudinal ridge on one side and several lesser ridges on opposite side, or fruits compressed, obovoid in lateral view with an asymmetric base, ellipsoid in frontal view, with a pronounced meridional ridge, or fruits scarcely compressed, obovoid, with obscure longitudinal ridges, or fruits widely obovoid, without pronounced longitudinal ridges, or fruits scarcely compressed, ellipsoid, with obscure longitudinal ridges.

Key to the species of *Pholidostachys*

- 1 Prophylls and peduncular bracts fibrous, covering all or part of the rachilla(e) at anthesis 2
- Prophylls and peduncular bracts woody, not covering rachilla(e) at anthesis 4
- 2 Inflorescences spicate, with a short peduncle, absent rachis, and one rachilla, this erect at anthesis; central Panama .
..... *P. panamensis*
- Inflorescences branched 1 order, with a well-developed peduncle, short rachis, and several rachillae, these erect at anthesis; eastern Panama, western Colombia, and western Ecuador 3
- 3 Fruits 19.8(19.6–19.9) mm long, compressed in lateral view with an asymmetric base, ellipsoid in frontal view, with a pronounced meridional ridge; Colombia (Cordillera Central).....*P. sanluisensis*
- Fruits 12.2(8.8–16.3) mm long, scarcely compressed, obovoid, with obscure longitudinal ridges; western Colombia (Cordillera Occidental and Chocó) and western Ecuador.....*P. dactyloides*
- 4 Inflorescences branched 1 order, with an elongate peduncle, short rachis, and several rachillae, these pendulous at anthesis; western Colombia and western Ecuador*P. occidentalis*
- Inflorescences branched 1–2 orders, with a well-developed peduncle and rachis, and several rachillae, these spreading at anthesis, or inflorescences spicate, with a well-developed peduncle, absent rachis, and one rachilla, this arching or erect at anthesis 5
- 5 Inflorescences branched 1–2 orders, with a well-developed peduncle and rachis, and several rachillae, these spreading at anthesis *P. synanthera*
- Inflorescences spicate, with a well-developed peduncle, absent rachis, and one rachilla, this arching or erect at anthesis 6
- 6 Proximal lips of flower pits completely covering pits before anthesis and not recurved; Nicaragua, Costa Rica, Panama, and Colombia *P. pulchra*
- Proximal lips of flower pits not covering pits before anthesis, recurved; Peru*P. amazonensis*

1. *Pholidostachys amazonensis* Henderson, *sp. nov.* (Appendix IV, Plate 1)

It differs from other species in its spicate inflorescence and proximal lips of flower pits regularly shaped, rounded, not covering pits before anthesis, recurved.

Type:—PERU. Amazonas: Bagua Province, along roadside from Chiriaco to Puente Venezuela, 43 km (by road) NE of Chiriaco, ca. 1050–2400 ft., 5 November 1978, *P. Barbour 4471* (holotype USM *n.v.*, isotype MO!).

Stems no data. **Leaves** number per stem no data; sheaths and petioles no data; rachises 42.0 cm long, 3.7 mm diameter; pinnae 6 per side of rachis; basal pinna no data; apical pinna length no data, 3.5 cm wide, forming an angle of 15° with the rachis. **Inflorescences** spicate, with a well-developed peduncle, absent rachis, and 1 rachilla, this arching at anthesis; prophylls and peduncular bracts woody, not covering rachilla at anthesis; prophylls and peduncular bracts no data; peduncles length no data, 3.2 mm diameter; rachilla 1, 18.7 cm long, 5.9 mm diameter; proximal lips of flower pits regularly shaped, rounded, not covering pits before anthesis, recurved; **fruits** no data.

Distribution and habitat. At 4°56'N and 78°10'W in Peru (Amazonas) at medium elevations in lowland rainforest (Fig. 5).

Taxonomic notes. For inflorescence bracts and proximal flower pit shape, *Pholidostachys amazonensis* shares the same character states as *P. synanthera*. Fruits are lacking on the single specimen available. However, inflorescences of the two are quite different. *Pholidostachys amazonensis* has spicate inflorescences with a well-developed peduncle, absent rachis, and 1 rachilla, this arching at anthesis. *Pholidostachys synanthera* has inflorescences branched 1–2 orders with a well-developed peduncle and rachis, and several rachillae, these spreading at anthesis.

2. *Pholidostachys dactyloides* Moore (1967: 148). *Calyptrogyne dactyloides* (Moore) Wessels Boer, 1968: 74. Type:—COLOMBIA. El Valle: Costa del Pacifico, río Yurumanguí, El Papayo, 10–20 m, 5 February 1944, J. Cuatrecasas 15982 (holotype BH!, isotypes COL!, F!, US!).

Stems 5.4(2.0–10.0) m long, 7.7(4.0–12.0) cm diameter, solitary. **Leaves** 15(6–25) per stem; sheaths 45.4(14.0–110.0) cm long; petioles 56.8(20.0–122.0) cm long; rachises 135.4(68.0–231.0) cm long, 13.3(7.9–20.1) mm diameter; pinnae 10(6–17) per side of rachis; basal pinna 57.9(34.0–92.0) cm long, 2.4(0.7–7.5) cm wide, forming an angle of 53(30–74)° with the rachis; apical pinna 45.0(36.0–58.0) cm long, 15.3(4.5–22.5) cm wide, forming an angle of 13(7–20)° with the rachis. **Inflorescences** branched 1 order (rarely 2 orders), with a well-developed peduncle, short rachis, and several rachillae, these erect at anthesis; prophylls and peduncular bracts fibrous, covering all or part of the rachillae at anthesis; prophylls 46.0(30.0–59.0) cm long; peduncular bracts 56.7(50.0–65.0) cm long, inserted 6.2(2.5–11.0) cm above the prophyll; peduncles 16.3(8.5–25.5) cm long, 10.4(4.7–19.0) mm diameter; rachillae 9(2–16), 35.5(15.5–75.0) cm long, 6.3(4.5–9.7) mm diameter; proximal lips of flower pits irregularly shaped, often acute or acuminate, completely covering pits before anthesis; **fruits** scarcely compressed, obovoid, with obscure longitudinal ridges, 12.2(8.8–16.3) mm long, 7.9(5.8–11.5) mm diameter.

Distribution and habitat. From 8°50'N–3°11'S and 76°03'–79°14'W in eastern Panama, western Colombia, and western Ecuador at 444(5–1440) m elevation in lowland or montane rainforest (Fig. 5).

Taxonomic notes. *Pholidostachys dactyloides* is a widespread and variable species with an unusually wide elevation range.

Subspecific variation. Specimens occur in several different populations. The northernmost specimens, from two localities in eastern Panama, are distinct in their short rachillae and acuminate proximal lips (Fig. 3A, left).

These Panamanian specimens strongly resemble others from the northern part of the Chocó region of Colombia, where they occur at both high and low elevations. However, some of these have rachillae of the more usual length.

Further south, in the Valle region of Colombia, specimens are similar to those from southwestern Colombia and northwestern Ecuador, and both populations have less acuminate proximal lips (Fig. 3A, right).

There is a large population in southwestern Colombia and northwestern Ecuador. One specimen from there (*Vargas 6108*) has inflorescences branched to 2 orders. Regression shows there are significant associations between elevation and four leaf and five inflorescence variables in this population. Squared multiple *R* for the regression of leaf number on elevation is 0.29, rachis width 0.40, number of pinnae 0.27, basal pinna angle 0.40, peduncle width 0.37, rachilla length 0.30, rachilla width 0.42, fruit length 0.62, fruit diameter 0.51. Values for these variables increase with elevation except for basal pinna angle. Notably, rachillae are thicker at higher elevations.

The southernmost specimens, in southwestern Ecuador, differ slightly from those in southwestern Colombia and northwestern Ecuador. Although there are too few specimens to test for differences, they have shorter and narrower apical pinnae.

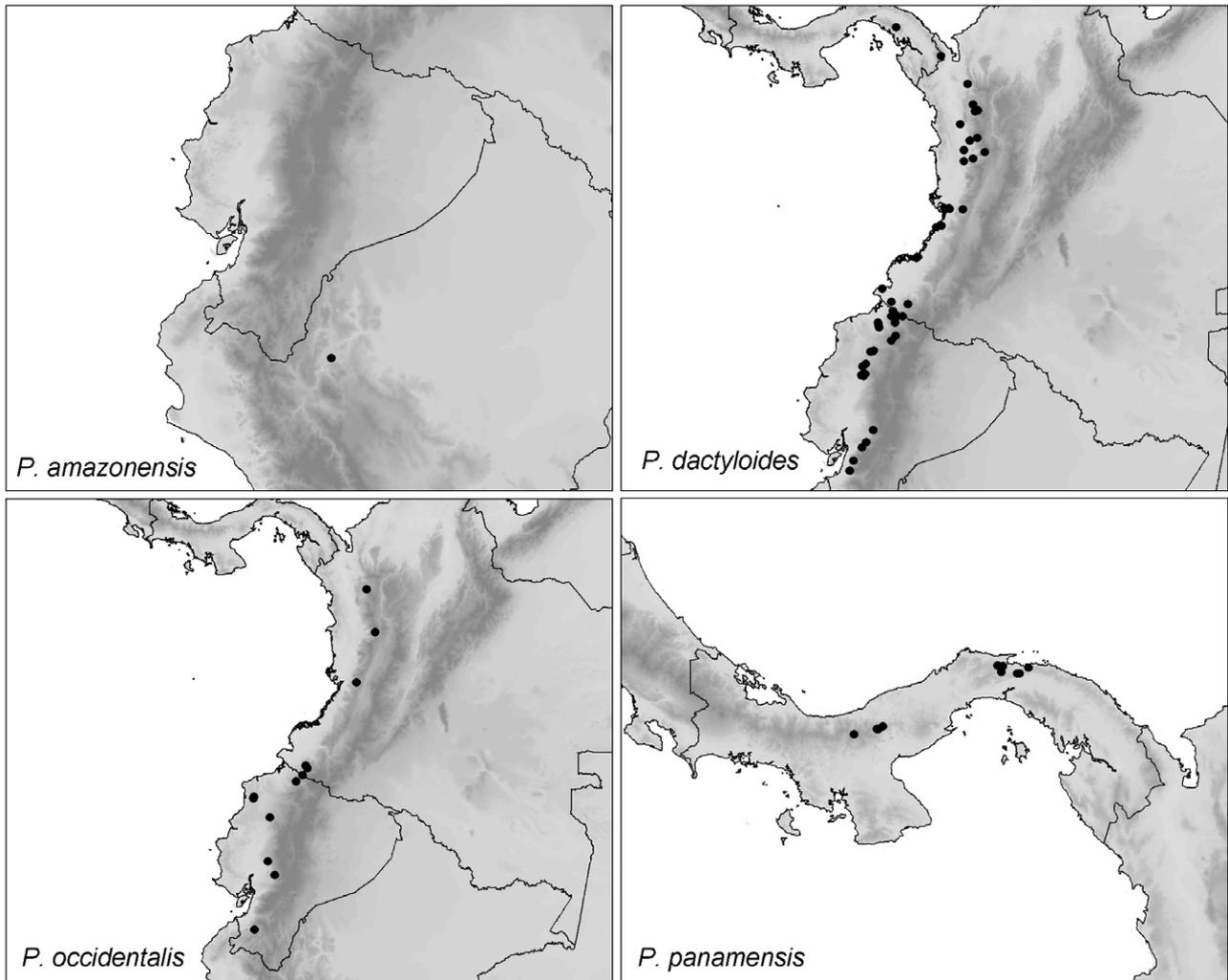


FIGURE 5. Distribution maps of *Pholidostachys amazonensis*, *P. dactyloides*, *P. occidentalis*, and *P. panamensis*.

3. *Pholidostachys occidentalis* Henderson, *sp. nov.* (Appendix IV, Plates 2–8)

It differs from other species in its branched inflorescences and compressed, obovoid fruits with a pronounced longitudinal ridge on one side.

Type:—ECUADOR. Pichincha: Road from Santo Domingo to Quevedo, 12 km S of Santo Domingo, 0°17'S 79°15'W, 300 m, 24 July 1985, *H. Balslev, A. Henderson & F. Skov* 60678 (holotype QCA *n.v.*, isotypes AAU!, K!, NY!).

Stems 5.4(2.5–11.0) m long, 10.4(7.0–15.0) cm diameter, solitary. **Leaves** 15(12–20) per stem; sheaths 25.3(16.0–40.0) cm long; petioles 51.7(45.0–60.0) cm long; rachises 192.0(150.0–234.0) cm long, 16.3(7.8–24.4) mm diameter; pinnae 12(8–13) per side of rachis; basal pinna 47.4(34.0–83.0) cm, long, 3.9(1.4–10.0) cm wide, forming an angle of 54(34–67)° with the rachis; apical pinna 42.9(34.0–54.0) cm long, 18.5(10.0–25.5) cm wide, forming an angle of 25(18–29)° with the rachis. **Inflorescences** branched 1 order, with an elongate peduncle, short rachis, and several rachillae, these pendulous at anthesis; prophylls and peduncular bracts woody, not covering rachillae at anthesis; prophylls 62.0 cm long; peduncular bracts 59.0 cm long, inserted 7.8(4.0–11.5) cm above the prophyll; peduncles 114.1(72.0–171.0) cm long, 10.1(6.3–12.5) mm diameter; rachilla 8(6–11), 50.8(33.0–64.0) cm long, 7.4(6.3–8.6) mm diameter; proximal lips of flower pits regularly shaped, rounded, not covering pits before anthesis, recurved; **fruits** compressed, obovoid in lateral

view with an asymmetric base, ellipsoid in frontal view, with a pronounced longitudinal ridge on one side and several lesser ridges on opposite side, 17.0(16.2–18.0) mm long, 9.3(8.5–9.8) mm diameter.

Distribution and habitat. From 3°43'S–6°45'N and 76°02'–79°46'W in western Colombia and western Ecuador at 854(300–1600) m elevation in lowland or montane rainforest (Fig. 5).

Taxonomic notes. Borchsenius *et al.* (1998) were the first to point out the differences between populations of *Pholidostachys synanthera* from west and east of the Andes. The western population, here recognized at the specific level as *P. occidentalis*, has inflorescences that are branched to 1 order and have elongate peduncles, short rachises, and several rachillae that are pendulous at anthesis (Fig. 1B) (versus *P. synanthera* with inflorescences that are branched 1–2 orders and have well-developed peduncles and rachises, and several rachillae that are spreading at anthesis). The fruits of the two species also differ. *Pholidostachys occidentalis* has compressed fruits, obovoid in lateral view with an asymmetric base, ellipsoid in frontal view, with a pronounced longitudinal ridge on one side and several lesser ridges on the opposite side (Fig. 4B). *Pholidostachys synanthera* has scarcely compressed fruits that are ellipsoid with obscure longitudinal ridges (Fig. 4F).

Subspecific variation. *Pholidostachys occidentalis* occurs in scattered localities from southwestern Ecuador to northwestern Colombia, but there are too few specimens to test for differences amongst these populations. Like *P. dactyloides*, this species has an unusually wide range in elevation.

4. *Pholidostachys panamensis* Henderson, *sp. nov.* (Appendix IV, Plates 9–14)

It differs from other species in its spicate inflorescences and widely obovoid fruits without pronounced longitudinal ridges.

Type:—PANAMA. Coclé: Continental Divide above El Copé, 8°38'N, 80°39'W, 650–750 m, 27 November 1985, G. de Nevers, A. Henderson, H. Herrera, G. McPherson & L. Brako 6371 (holotype NY!, isotype MO!).

Stems 1.1(0.1–3.0) m long, 7.4(4.0–11.0) cm diameter, solitary. **Leaves** 12(8–19) per stem; sheaths 21.5(15.0–27.0) cm long; petioles 102.1(36.0–150.0) cm long; rachises 126.1(72.0–155.0) cm long, 8.8(6.1–11.1) mm diameter; pinnae 6(5–8) per side of rachis; basal pinna 52.8(28.5–78.0) cm, long, 5.2(0.7–10.0) cm wide, angle with the rachis no data; apical pinna 42.4(32.5–49.5) cm long, 18.0(10.0–27.0) cm wide, forming an angle of 17(10–28)° with the rachis. **Inflorescences** spicate, with a short peduncle, absent rachis, and 1 rachilla, this erect at anthesis; prophylls and peduncular bracts fibrous, covering all or part of the rachilla at anthesis; prophylls 15.2(11.5–18.5) cm long; peduncular bracts 20.2(19.0–22.5) cm long, inserted 3.3(2.0–5.0) cm above the prophyll; peduncles 4.6(3.5–6.2) cm long, 10.0(8.2–13.5) mm diameter; rachilla 1, 13.6(11.5–15.5) cm long, 10.0(8.2–12.1) mm diameter; proximal lips of flower pits regularly shaped, rounded, completely covering pits before anthesis and not recurved; **fruits** widely obovoid, without pronounced longitudinal ridges, 28.6(22.5–32.1) mm long, 20.8(18.1–24.5) mm diameter.

Distribution and habitat. From 8°34'–9°25'N and 78°48'–80°56'W in Panama at 483(60–768) m elevation in lowland rainforest (Fig. 5).

Taxonomic notes. *Pholidostachys panamensis* differs from other species in its spicate inflorescences and widely obovoid fruits (Fig. 4C). See notes on *Pholidostachys kalbreyeri* under Excluded Names.

Subspecific variation. There are two separate populations of *Pholidostachys panamensis*, occurring 170 km apart in Panama. Although sample size is small, the western population, on the eastern end of the Central Cordillera, has shorter stems, shorter petioles, and shorter and thinner basal pinnae than the eastern population, on the western end of the Serranía de San Blas. The western population also occurs at a higher mean elevation—722(695–768) m versus 303(60–450) m.

de Nevers (1995) reported that some specimens have bifid inflorescences, but no such specimens have been seen in the present study.

5. *Pholidostachys pulchra* Wendl. ex Burret (1930: 130). *Calypstrogyne pulchra* (Wendl. ex Burret) Wessels

Boer, 1968: 74. Type: COSTA RICA. Heredia: “flum. Sarapiquí”, 1857, *H. Wendland s. n.* (holotype GOET *n.v.*, isotype K!).

Stems 3.7(1.5–6.6) m long, 4.6(3.0–8.0) cm diameter, solitary or rarely clustered. **Leaves** 12(7–23) per stem; sheaths 32.1(20.0–48.0) cm long; petioles 85.3(49.0–150.0) cm long; rachises 70.5(32.0–130.0) cm long, 6.8(3.3–13.1) mm diameter; pinnae 6(3–9) per side of rachis; basal pinna 48.1(35.5–61.0) cm long, 1.2(0.4–3.0) cm wide, forming an angle of 62(42–93)° with the rachis; apical pinna 40.3(30.0–54.0) cm long, 11.3(4.0–20.0) cm wide, forming an angle of 16(11–27)° with the rachis. **Inflorescences** spicate, with a well-developed peduncle, absent rachis, and 1 rachilla, this arching or erect at anthesis; prophylls 14.8(5.0–29.0) cm long; peduncular bracts 31.4(12.5–59.0) cm long, inserted 3.4(1.1–10.0) cm above the prophyll; peduncles 13.1(4.5–33.0) cm long, 5.7(3.6–11.8) mm diameter; rachilla 1, 37.2(7.5–85.0) cm long, 9.4(6.2–16.2) mm diameter; proximal lips of flower pits regularly shaped, rounded, completely covering pits before anthesis and not recurved; **fruits** compressed, obovoid in lateral view with an asymmetric base, ellipsoid in frontal view, with a pronounced longitudinal ridge on one side and several lesser ridges on opposite side, 22.3(11.5–29.2) mm long, 11.1(6.6–14.6) mm diameter.

Distribution and habitat. From 11°22'–3°10'N and 76°13'–84°24'W in Nicaragua, Costa Rica, Panama, and western Colombia at 331(12–1000) m elevation in lowland rainforest (Fig. 6).

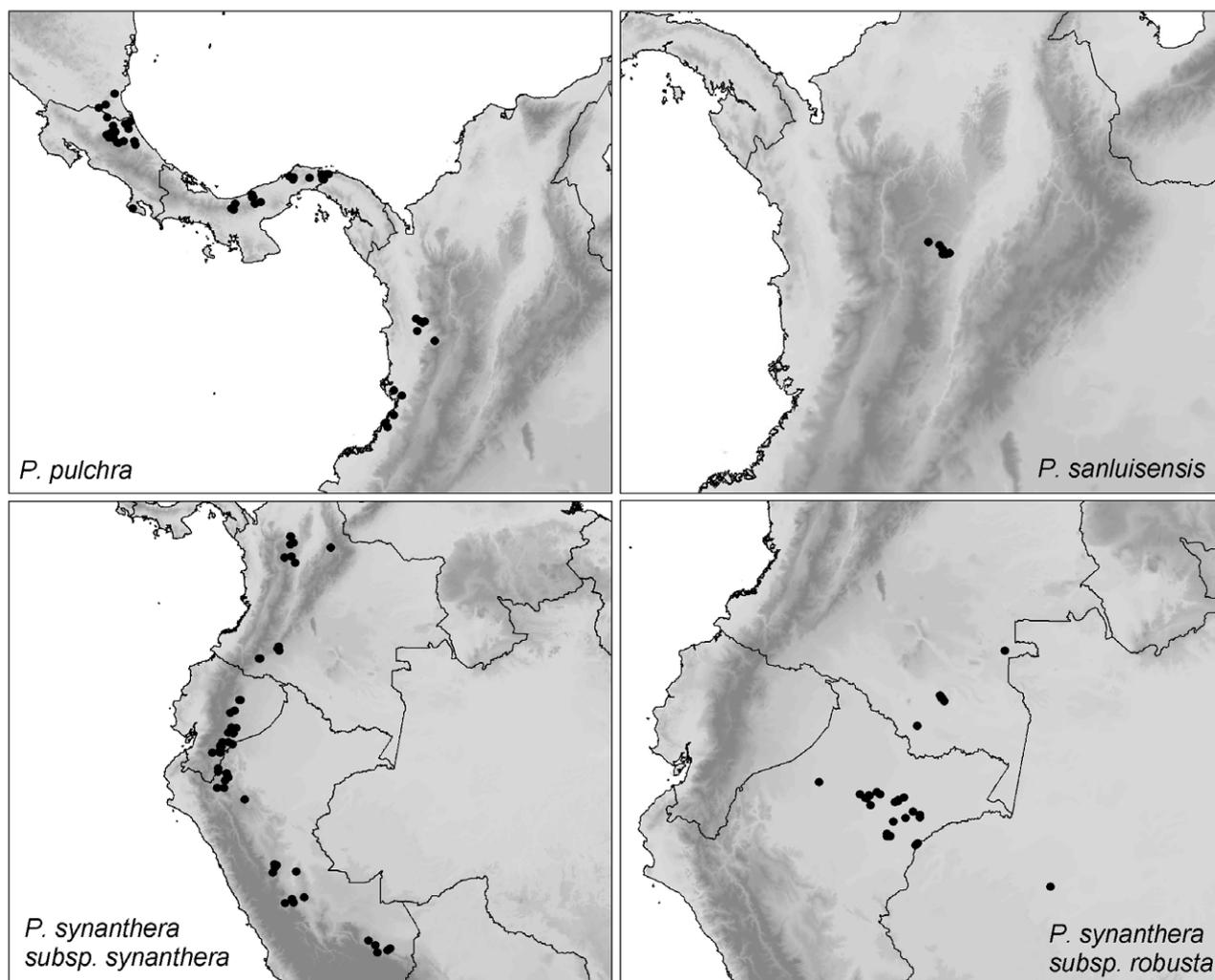


FIGURE 6. Distribution maps of *Pholidostachys pulchra*, *P. sanluisensis*, *P. synanthera* subsp. *synanthera*, and *P. synanthera* subsp. *robusta*.

Taxonomic notes. *Pholidostachys pulchra* shares with *P. panamensis* a spicate inflorescence and unequal

prophyll and peduncular bract. It is a widespread and variable species.

Subspecific variation. *Pholidostachys pulchra* occurs in at least six geographically separate populations. However, no subspecific division is made here for two reasons. It is not clear if the gaps between some of the populations are artifacts of insufficient collecting, and in most cases there are too few specimens to test for differences amongst populations.

From the north, at low elevations of 245(15–750) m in Nicaragua and Costa Rica there is a large and apparently uniform population. This population has proximal lips that are slightly different from other populations; they are wider than long and the apex of each lip slightly overlaps the bases of the next two, distal lips (Fig. 3C, left). One specimen from near Puerto Viejo in Costa Rica is reported to have clustered stems; all others are solitary. There is a single outlier in Costa Rica, from the Osa Peninsula.

The gap between the Nicaraguan and Costa Rican population and the next, in Veraguas, Panama appears real since there are collections of many other palms from the intervening region. The Veraguas population occurs at higher elevations of 712(400–1000) m and has shorter stems, smaller leaves, smaller inflorescences, and larger fruits than the Nicaragua/Costa Rica population.

The next population, in Coclé, Panama, occurs at slightly lower elevations at 519(100–775) m. It has shorter and narrower apical pinnae with a narrower angle and longer peduncular bracts and interbract distances than other populations. One specimen from here is reported to have clustered stems.

The next population occurs east of the Canal Zone, in three areas, the Santa Rita Ridge, Cerro Brewster, and the western end of the Serranía de San Blas. These are likely to represent collecting localities rather than populations, and all are treated together. This population occurs also occurs at slightly lower elevations at 426(200–850) m. It has longer stems, longer and wider rachises, longer and wider peduncles, and longer and wider rachillae than other Central American populations. One specimen (*de Nevers 5206*) has an unusually short inflorescence. In this population, several specimens are reported to have clustered stems. This and other Panamanian populations (Veraguas, Coclé) have different proximal lips from the Costa Rican/Nicaraguan population; they are usually longer than wide and do not overlap the two distal lips (Fig. 3C, right). However, a few specimens from San Blas have proximal lips more like the Costa Rican/Nicaraguan population.

Almost 500 km further south, there are two populations in western Colombia. One of these, from near Quibdó at 356(200–450) m elevation, comprises several specimens that have unusually short inflorescences and smaller fruits. These tend to have the inflorescence bracts surrounding, although not covering, the rachilla at anthesis.

Furthest south, from Valle at 129(12–600) m elevation, there are several specimens that also have unusually small fruits, like those of the population from near Quibdó. However, unlike that population, the Valle specimens have the longest rachillae of any population of *Pholidostachys pulchra*.

6. *Pholidostachys sanluisensis* Henderson, *sp. nov.* (Appendix IV, Plates 15–23)

It differs from other species in its compressed fruits, obovoid in lateral view with an asymmetric base, ellipsoid in frontal view, with a pronounced meridional ridge.

Type:—COLOMBIA. Antioquia: Municipio San Luis, Vereda Manizales, 12 km de San Luis en la via San Luis-San Carlos, a lo largo del río Dormilón, 1440 m, 26 June 1987, R. Callejas, H. Correa, J. Betancur & A. Arbelaez 4274 (holotype HUA *n.v.*, isotype NY!).

Stems 3.1(2.0–5.0) m long, 4 cm diameter, solitary. **Leaves** 11(9–15) per stem; sheaths 50 cm long; petioles 93.5(87.0–100.0) cm long; rachises 92 cm long, 9.5(7.6–11.9) mm diameter; pinnae 9(7–12) per side of rachis; basal pinna 39 cm long, 1.4(1.0–2.0) cm wide, forming an angle of 74(57–85)° with the rachis; apical pinna 30.5 cm long, 12.8(6.0–19.3) cm wide, forming an angle of 13(9–20)° with the rachis. **Inflorescences** branched 1 order, with a welldeveloped peduncle, short rachis, and several rachillae, these erect at anthesis; prophylls and peduncular bracts fibrous, covering all or part of the rachillae at anthesis; prophylls length no data; peduncular bracts 41.4 cm long, inserted 7.0(4.5–11.5) cm above the prophyll; peduncles 18.0(13.5–

26.0) cm long, 8.3(7.6–9.2) mm diameter; rachillae 4, 36.4(26.0–43.5) cm long, 7.9(6.7–8.8) mm diameter; proximal lips of flower pits irregularly shaped, often acute or acuminate, completely covering pits before anthesis; **fruits** compressed, obovoid in lateral view with an asymmetric base, ellipsoid in frontal view, with a pronounced meridional ridge, 19.8(19.6–19.9) mm long, 10.3(9.8–10.7) mm diameter.

Distribution and habitat. From 5°57'–6°08'N and 74°51'–75°10'W in Colombia (Antioquia) on the Cordillera Central at 1004(700–1440) m elevation in lowland or montane rainforest (Fig. 6).

Taxonomic notes. Specimens of *Pholidostachys sanluisensis* have been determined as *P. dactyloides*. They differ from that species in their fruits that are compressed, obovoid in lateral view with an asymmetric base, ellipsoid in frontal view, with a pronounced meridional ridge (Fig. 4E) (versus fruits that are scarcely compressed, obovoid, with an obscure longitudinal ridge in *P. dactyloides*, Fig. 4A). Fruits of *P. sanluisensis* are also larger—19.8(19.6–19.9) mm long and 10.3(9.8–10.7) mm diameter versus 9.0(6.0–16.5) mm long and 6.8(5.1–12.9) mm diameter in *P. dactyloides*.

Subspecific variation. There is no geographic discontinuity and only a few specimens are known.

7. *Pholidostachys synanthera* (Mart.) Moore (1969: 231). *Geonoma synanthera* Martius, 1823–1837: 13. *Calypstrogyne synanthera* (Mart.) Burret, 1930: 137. *Calyptronoma synanthera* (Mart.) Bailey, 1938: 166. Type:—PERU. Huánuco: Chicoplaya, no date, H. Ruíz & J. Pavón s. n. (holotype M n.v., isotype F!).

Stems 3.3(1.0–6.0) m long, 5.6(3.0–22.0) cm diameter, solitary. **Leaves** 15(4–27) per stem; sheaths 32.8(15.0–74.0) cm long; petioles 70.1(24.0–136.0) cm long; rachises 84.0(48.0–124.0) cm long, 8.1(3.6–12.6) mm diameter; pinnae 10(4–18) per side of rachis; basal pinna 49.6(26.5–67.5) cm, long, 1.7(0.2–7.6) cm wide, forming an angle of 50(27–72)° with the rachis; apical pinna 45.0(23.0–65.0) cm long, 10.5(2.5–22.5) cm wide, forming an angle of 15(9–24)° with the rachis. **Inflorescences** branched 1–2 orders, with a well-developed peduncle and rachis, and several rachillae, these spreading at anthesis; prophylls and peduncular bracts woody, not covering rachillae at anthesis; prophylls 38.0(25.5–55.0) cm long; peduncular bracts 32.1(19.0–41.0) cm long, inserted 8.6(5.0–12.5) cm above the prophyll; peduncles 44.8(20.0–70.0) cm long, 11.4(5.3–19.1) mm diameter; rachilla 12(4–25), 28.5(14.0–56.0) cm long, 6.1(3.7–10.3) mm diameter; proximal lips of flower pits regularly shaped, rounded, not covering pits before anthesis, recurved **fruits** scarcely compressed, ellipsoid, with obscure longitudinal ridges, 14.3(10.2–17.7) mm long, 8.4(6.1–10.5) mm diameter.

Taxonomic notes. *Pholidostachys synanthera* is the most widespread species in the genus.

Subspecific variation. There are three geographically separate populations of *Pholidostachys synanthera*. One occurs at 146(90–250) m elevation in the western Amazon region; the second on eastern Andean slopes at 1040(400–1620) m elevation; and the third on the Cordilleras Central and Oriental in Colombia at 1206(550–1750) m elevation. Only three variables (rachis length, number of divisions, apical pinna angle) are significantly different between the two Andean populations (*t*-test, *P* < 0.05), and they are here treated as one. Between this expanded Andean population and the Amazon population, 11 variables (stem height, stem diameter, leaf number, rachis length, rachis width, number of divisions, basal pinna length, basal pinna angle, apical pinna length, apical pinna width, rachillae width) are significantly different (*t*-test, *P* < 0.05). Most of these variables are from stems and leaves, and only one from inflorescences. Based on these results, Amazon and Andean populations are recognized as subspecies (subsp. *robusta*, *synanthera*).

Key to the subspecies of *P. synanthera*

- 1 Stems 2.6(1.0–6.0) m long; rachises 74.1(48.0–91.0) cm long; pinnae 7(4–12) per side of rachis; western Amazon region in Colombia, Peru, and Brazil at 146(90–250) m elevation subsp. *robusta*
- Stems 3.9(1.8–6.0) m long; rachises 92.2(55.0–124.0) cm long; pinnae 12(7–18) per side of rachis; Cordilleras Central and Oriental in Colombia and eastern Andean slopes in Colombia, Ecuador, and Peru at 1064(400–1750) m elevation subsp. *synanthera*

7.1 *Pholidostachys synanthera* subsp. *synanthera*

Stems 3.9(1.8–6.0) m long. **Leaf** rachises 92.2(55.0–124.0) cm long; pinnae 12(7–18) per side of rachis.

Distribution and habitat. From 7°19'N–13°31'S and 70°07'–78°57'W in the Cordilleras Central and Oriental in Colombia and eastern Andean slopes in Colombia, Ecuador, and Peru at 1064(400–1750) m elevation in lowland or montane rainforest (Fig. 6).

Subspecific variation. Regression shows there are significant associations between elevation and one stem, four leaf, and one inflorescence variables. Squared multiple *R* for the regression of stem height on elevation is 0.30, sheath length 0.88, number of pinnae 0.42, basal pinna width 0.37, apical pinna length 0.69, and rachilla width 0.13. Values for these variables decrease with elevation, except for number of pinnae and rachillae width which increase.

The northernmost population of subsp. *synanthera* occurs in the Cordilleras Central and Oriental in Colombia and has 13–17 rachillae per inflorescence. The northernmost specimen (*Soejarto 2743*) is tentatively included here; it is unusual in having only 4 rachillae. One specimen (*Callejas 4221*) appears to be a mixed collection, with the fruits (excluded from this study) belonging to *P. sanluisensis*.

Along eastern Andean slopes in Colombia, Ecuador, and Peru, subsp. *synanthera* occurs in scattered localities. There do not appear to be any differences between these populations although sample size in small in some of them. The gaps between them may anyway be collecting artifacts. In Amazonas and Cajamarca, Peru, there is extreme variation. Two specimens (*Díaz 8093*, *Rodríguez 1013*) are the smallest seen with narrow pinnae and slender inflorescences with the rachillae 19.0–22.5 cm long and 4.0–4.3 mm diameter. Another specimen (*Campos 4243*), from less than 40 km away, has the some of the largest rachillae seen in the subspecies, 34.0 cm long and 9.6 mm diameter. Other specimens from this region are more usual in size. This kind of variation is reminiscent of that seen in *Geonoma poeppigiana* from the same region (Henderson 2011). It is also of interest that *Pholidostachys amazonensis* occurs in this same region, and only differs from subsp. *synanthera* in its spicate inflorescence.

7.2 *Pholidostachys synanthera* subsp. *robusta* (Trail) Henderson, *comb. & stat. nov.*

Basionym:—*Calyptronoma robusta* Trail (1876: 330). *Calyptrogyne robusta* (Trail) Burret, (1930: 137). Type:—BRAZIL. Amazonas: Camana, Rio Javari, 5 December 1874, *J. Trail 961/CLXXXVI* (holotype K!, isotypes BM!, NY!, P n.v.).

Stems 2.6(1.0–6.0) m long. **Leaf** rachises 74.1(48.0–91.0) cm long; pinnae 7(4–12) per side of rachis.

Distribution and habitat. From 0°34'N–6°28'S and 68°46'–75°50'W in the western Amazon region of Colombia, Peru, and Brazil at 146(90–200) m elevation in lowland rainforest (Fig. 6).

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Appendix I. Qualitative Variables

Characters

Abbreviations in parentheses at the end of each character are the column labels in the Data Matrix (<http://sciweb.nybg.org/Science2/res/Henderson/Pholidostachys.xls.zip>). The states of the characters here are scored as '(1)' or '(2)' etc., and these correspond with the states in the Data Matrix.

1. Inflorescences branched 1 order, with an elongate peduncle, short rachis, and several rachillae, these pendulous at anthesis (1); inflorescences branched 1–2 orders, with a well-developed peduncle and rachis, and several rachillae, these spreading at anthesis (2); inflorescences branched 1 order (rarely 2 orders), with a well-developed peduncle, short rachis, and several rachillae, these erect at anthesis (3); inflorescences spicate, with a well-developed peduncle, absent rachis, and 1 rachilla, this arching or erect at anthesis (4); inflorescences spicate, with a short peduncle, absent rachis, and 1 rachilla, this erect at anthesis (5) (inflobran)
2. Prophylls and peduncular bracts fibrous, covering all or part of the rachilla(e) at anthesis (1); prophylls and peduncular bracts woody, not covering rachilla(e) at anthesis (2). (bracts)
3. Proximal lips of flower pits regularly shaped, rounded, completely covering pits before anthesis and not or seldom recurved (1); proximal lips of flower pits irregularly shaped, often acute or acuminate, completely covering pits before anthesis (2); proximal lips of flower pits regularly shaped, rounded, not covering pits before anthesis, recurved (3). (proxshape)
4. Fruits compressed, obovoid in lateral view with an asymmetric base, ellipsoid in frontal view, with a pronounced longitudinal ridge on one side and several lesser ridges on opposite side (1); fruits compressed, obovoid in lateral view with an asymmetric base, ellipsoid in frontal view, with a pronounced meridional ridge (2); fruits scarcely compressed, obovoid, with obscure longitudinal ridges (3); fruits widely obovoid, without pronounced longitudinal ridges (4); fruits scarcely compressed, ellipsoid, with obscure longitudinal ridges (5). (fruits)

Traits

Abbreviation in parentheses at the end of the variable is the column label in the Data Matrix.

1. Stems solitary (1); stems clustered (2). (stembranch)

Appendix II. Quantitative variables

Abbreviations in parentheses at the end of each variable are the column labels in the Data Matrix.

1. Stem length (m); data taken from specimen labels. (stemheight)
2. Stem diameter (cm); data taken from specimen labels. (stemdiameter)
3. Number of leaves per stem; data taken from specimen labels. (leafnumber)
4. Sheath length (cm); data taken from specimen labels. The distinction between sheath and petiole is not clear. (sheath)
5. Petiole length (cm); data taken from specimen labels. Petioles in *Pholidostachys* appear to continue lengthening after the blade had unfolded. (petiole)
6. Rachis length (cm); measured from first pinna to apex of rachis, or data taken from specimen labels. (rachislen)
6. Rachis diameter (mm); data taken from specimens, measured at base of leaf blade. (rachiswid)
8. Number of pinnae per side of rachis; data taken from specimen labels (nodivisions)
9. Basal pinna length (cm); data taken from specimens, measured from the base to apex of the pinna. This is very difficult to measure because of the long, deciduous pinnae apices which are sometimes present and sometimes not. (baspinlen)
10. Basal pinna width (cm); data taken from specimens, measured at the base of the pinna. (baspinwid)
11. Basal angle of pinna divergence ($^{\circ}$); data taken from specimens, measured at 7.5 cm distance, between the axis of the rachis and proximal margin of basal pinna. (baspinang)
12. Apical pinnae length (cm); data taken from specimens, measured from the base to apex of the pinna. This is very difficult to measure because of the long, deciduous pinnae apices which are sometimes present and sometimes not. (apinlen)
13. Apical pinna width (cm); data taken from specimens, measured at the base of the pinna. (apinwid)
14. Apical angle of pinna divergence ($^{\circ}$); data taken from specimens, measured at 7.5 cm distance, between the axis of the rachis and distal margin of apical pinna. (apinang)
15. Orders of inflorescence branching; data taken from specimens. (orders)
16. Prophyll length (cm); data taken from specimens or specimen labels. (prophyll)
17. Peduncular bract length (cm) data taken from specimens or specimen labels. (pedbract)
18. Distance between peduncular bract and prophyll insertion (cm); data taken from specimens or specimen labels. (distance)
19. Peduncle length (cm); data taken from specimens or specimen labels, measured from base of inflorescence to first branch. (pedunclelen)
20. Peduncle diameter (mm); data taken from specimens, measured just below the proximalmost rachilla. (pedunclewid)
21. Number of rachillae; data taken from specimens or specimen labels. (norachillae)
22. Rachilla length (cm); data taken from specimens. (rachilllen)
23. Rachilla diameter (mm); data taken from specimens, measured at middle of rachilla. (rachillwid)
24. Fruit length (mm); data taken from specimens. (fruitlen)
25. Fruit diameter (mm); data taken from specimens, in flattened fruits, narrowest side measured. (fruitdiam)

Appendix III. Excluded Names

This list of names comprises published names that have been included in *Pholidostachys* but for which no type specimens are available.

Geonoma amabilis Wendl. ex Dahlgren, 1936: 158. Nomen nudum.

Calyptrognye kalbreyeri Burret, 1930: 137. *Calyptronoma kalbreyeri* (Burret) Bailey, 1938: 166. Type: COLOMBIA. Antioquia: Uranao, no date, *W. Kalbreyer 1967* (holotype B, destroyed).

Calyptrognye weberbaueri Burret, 1930: 139. *Calyptronoma weberbaueri* (Burret) Bailey, 1938: 166. Type: PERU. Puno: Chunchusmayo, no date, *A. Weberbauer 1234* (holotype B, destroyed).

Pholidostachys kalbreyeri Wendl. ex Burret (1930: 131). Type: COLOMBIA. Antioquia: Ciñegetas [Cieneguetas], 23 July 1880, *W. Kalbreyer 1881* (holotype B, destroyed).

Pholidostachys kalbreyeri was described (but not illustrated) by Burret based on a collection made by Kalbreyer in Antioquia, Colombia. The type was destroyed in Berlin and no isotypes are known. Despite intensive collecting in the region (Bernal *et al.* 1989), no palm resembling the description of *P. kalbreyeri* has been found. de Nevers (1995) designated a Panamanian specimen as neotype (*G. de Nevers & H. Herrera 4467*) for *P. kalbreyeri*, thereby applying a name to, and extending the range of, a species otherwise known only from central Panama. However, the Panamanian species (newly described here as *P. panamensis*) is certainly distinct from *P. kalbreyeri* as understood from Burret's description. *Pholidostachys panamensis* has stems 4.4–11.0 cm diameter, peduncles 8.2–13.5 mm wide, and the proximal lips of flower pits are broad and rounded. *Pholidostachys kalbreyeri* is described as having a stem “daumendick” (thick as a thumb), a peduncle 3 mm wide, and proximal lips “ovato-acutatum, sequentia ovata, dein semiorbicularia”. This neotypification is therefore superseded, according to Article 16 (<http://ibot.sav.sk/icbn/main.htm>), and *P. kalbreyeri* is treated as an Excluded Name.

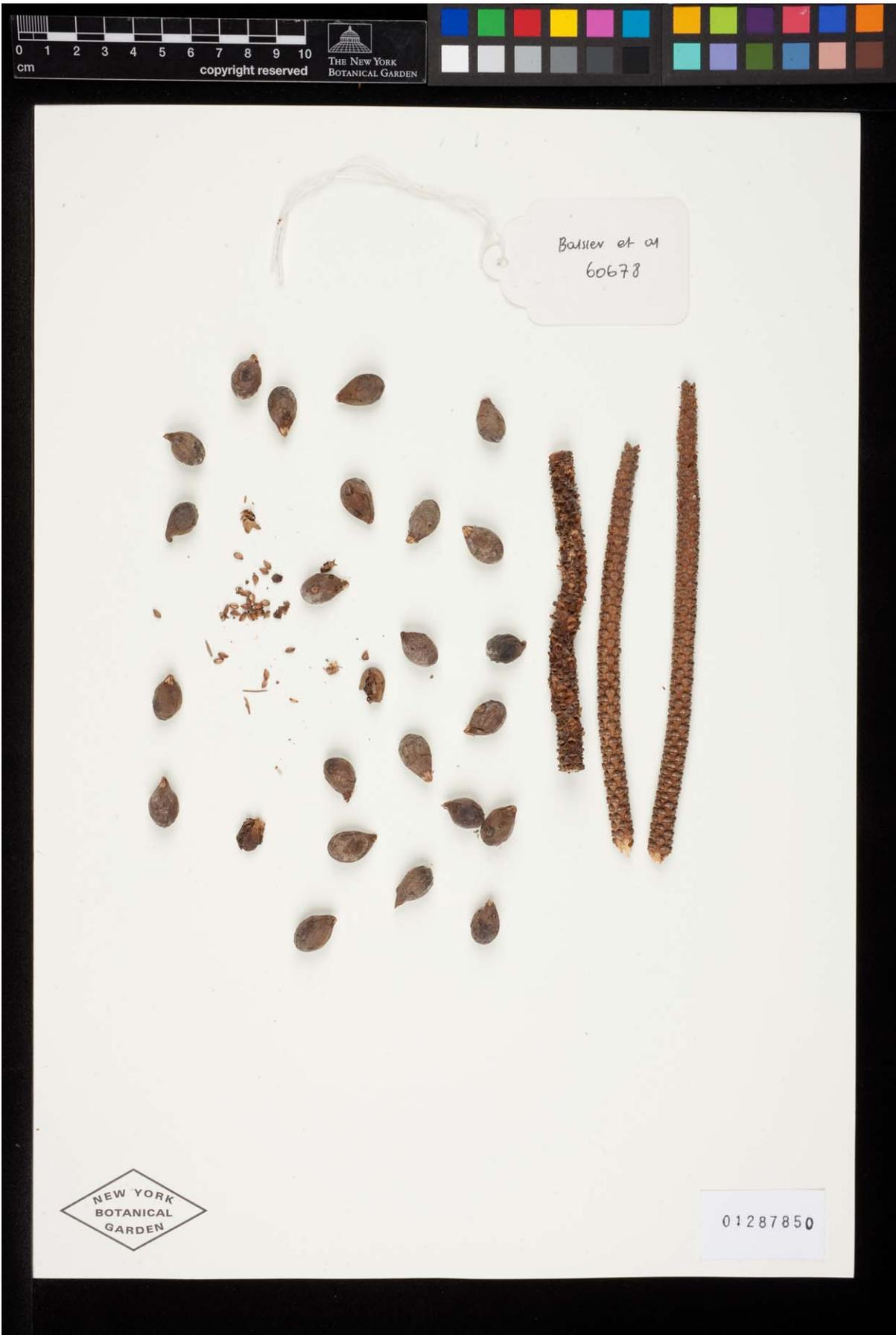
Appendix IV. Plates of Type Images



Appendix IV, Plate 1. Isotype of *Pholidostachys amazonensis* (P. Barbour 4471, MO).



Appendix IV, Plates 2–8. Isotype of *Pholidostachys occidentalis* (H. Balslev, A. Henderson & F. Skov 60678, NY).



Appendix IV, Plates 3



Appendix IV, Plates 4



Appendix IV, Plates 5



Appendix IV, Plates 6



Appendix IV, Plates 7



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cm
copyright reserved

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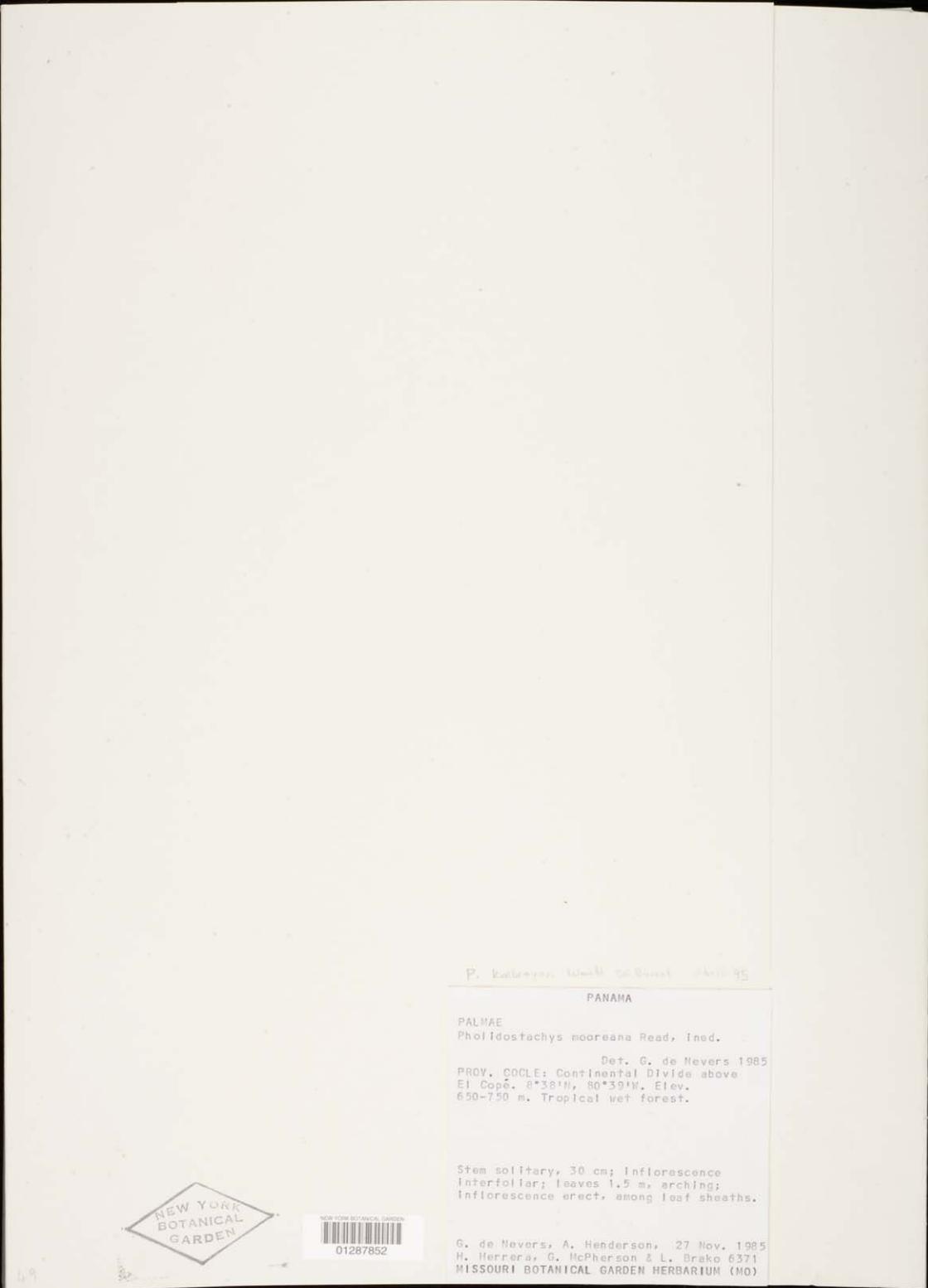


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60678

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Appendix IV, Plates 8



P. kabayan, World 26, 2001, 2/10/95

PANAMA

PALMAE
Pholidostachys mooreana Read, Ined.

Det. G. de Nevers 1985

PROV. COCLE; Continental Divide above
El Copé. 8°38'N, 80°39'W. Elev.
650-750 m. Tropical wet forest.

Stem solitary, 30 cm; Inflorescence
interfoliar; leaves 1.5 m, arching;
inflorescence erect, among leaf sheaths.

G. de Nevers, A. Henderson, 27 Nov. 1985
H. Herrera, G. McPherson & L. Brako 6371
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)



Appendix IV, Plates 9–14. Isotype of *Pholidostachys panamensis* (G. de Nevers, A. Henderson, H. Herrera, G. McPherson & L. Brako 6371, NY).



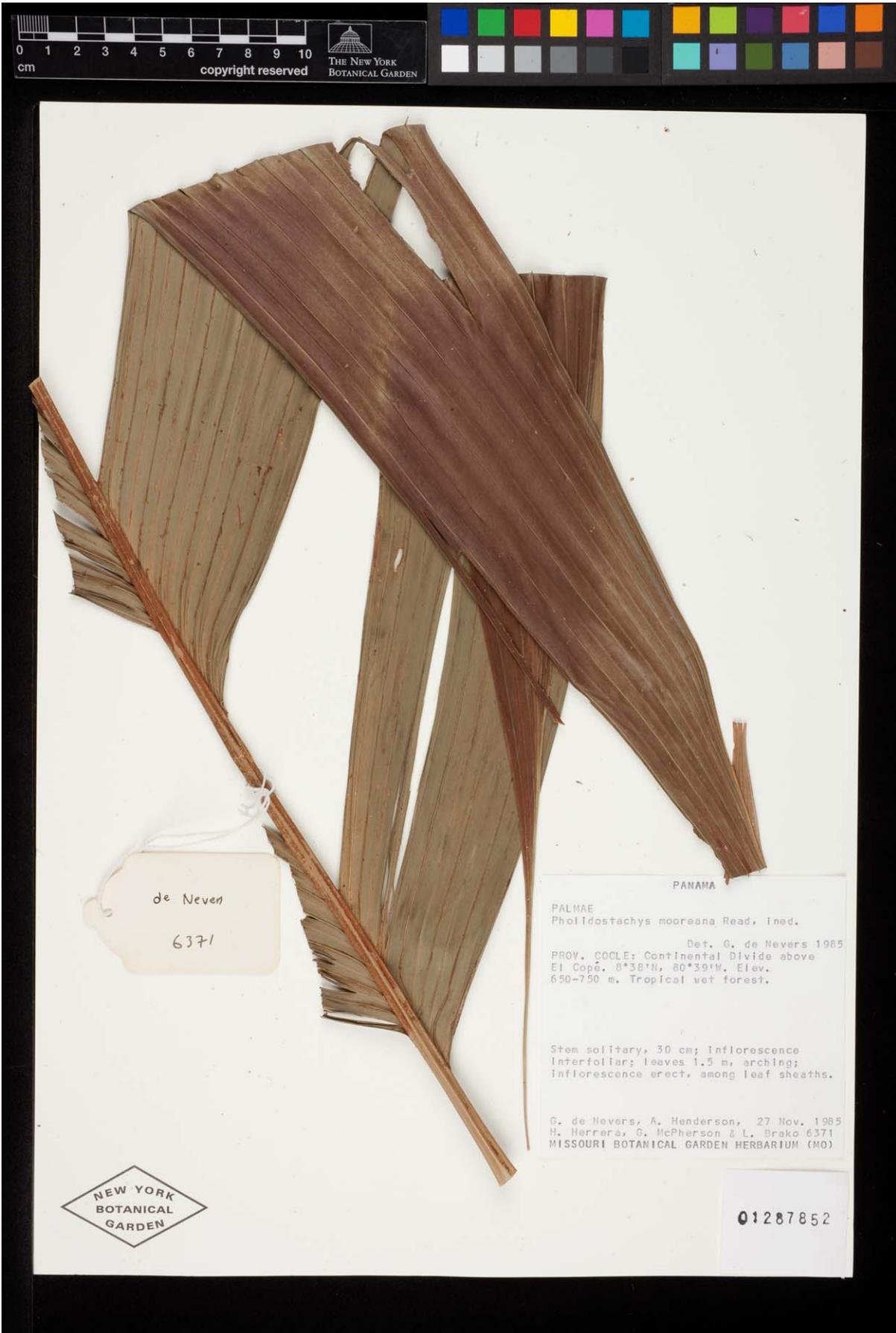
Appendix IV, Plates 10



Appendix IV, Plates 11



Appendix IV, Plates 12



de Neven

6371

PANAMA

PALMAE
Pholidostachys mooreana Read, ined.

Det. G. de Nevers 1985

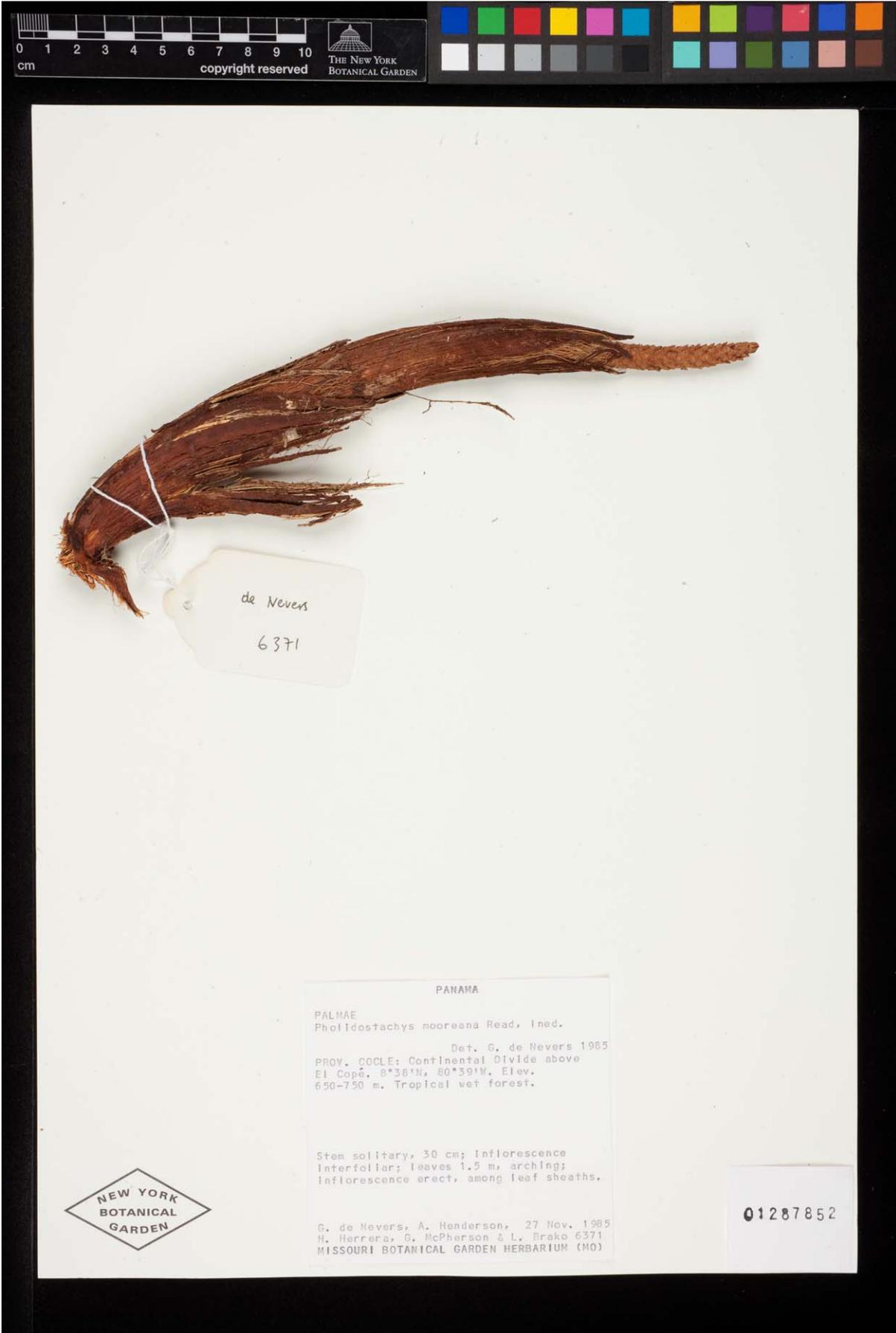
PROV. COCLE: Continental Divide above
El Copé. 8°38'N, 80°39'W. Elev.
650-750 m. Tropical wet forest.

Stem solitary, 30 cm; inflorescence
interfoliar; leaves 1.5 m, arching;
inflorescence erect, among leaf sheaths.

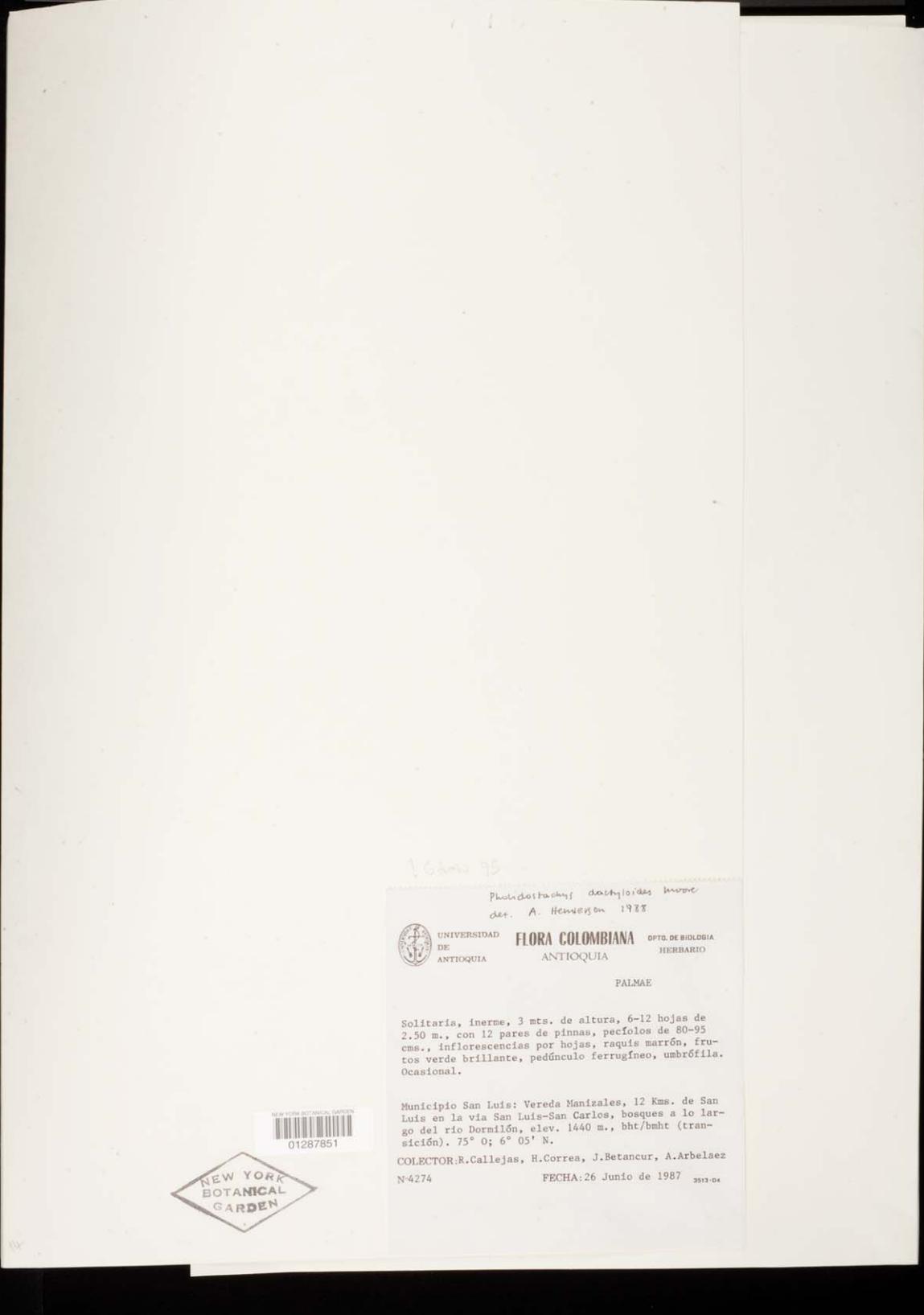
G. de Nevers, A. Henderson, 27 Nov. 1985
H. Herrera, G. McPherson & L. Brako 6371
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01287852



Appendix IV, Plates 14



1640 95

Pholidostachys dactyloides Moore
det. A. Henderson 1988

UNIVERSIDAD DE ANTIOQUIA **FLORA COLOMBIANA** OPTO. DE BIOLOGIA HERBARIO ANTIOQUIA

PALMAE

Solitaria, inerme, 3 mts. de altura, 6-12 hojas de 2.50 m., con 12 pares de pinnas, pecíolos de 80-95 cms., inflorescencias por hojas, raquis marrón, frutos verde brillante, pedúnculo ferrugíneo, umbrófila. Ocasional.

Municipio San Luis: Vereda Manizales, 12 Kms. de San Luis en la vía San Luis-San Carlos, bosques a lo largo del río Dormilón, elev. 1440 m., bht/bmht (transición). 75° 0; 6° 05' N.

COLECTOR: R. Callejas, H. Correa, J. Betancur, A. Arbelaez
N-4274 FECHA: 26 Junio de 1987 2913-04



Appendix IV, Plates 15–23. Isotype of *Pholidostachys sanluisensis* (R. Callejas, H. Correa, J. Betancur & A. Arbelaez 4274, NY).



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FLORA COLOMBIANA
ANTIOQUIA

DPTO. DE BIOLOGIA
HERBARIO

PALMAE

Solitaria, inerme, 3 mts. de altura, 6-12 hojas de 2.50 m., con 12 pares de pinnas, pecíolos de 80-95 /cms., inflorescencias por hojas, raquis marrón, frutos verde brillante, pedúnculo ferrugíneo, umbrófila. Ocasional.

Municipio San Luis: Vereda Manizales, 12 Kms. de San Luis en la vía San Luis-San Carlos, bosques a lo largo del río Dormilón, elev. 1440 m., bht/bmht (transición). 75° 0'; 6° 05' N.

COLECTOR: R. Callejas, H. Correa, J. Betancur, A. Arbelaez
N°4274 FECHA: 26 Junio de 1987 3513-84



01287851



Appendix IV, Plates 17



Appendix IV, Plates 18



Appendix IV, Plates 19



Appendix IV, Plates 20



Appendix IV, Plates 21



Appendix IV, Plates 22



Appendix IV, Plates 23

Appendix V. Numerical List of Taxa and Specimens Examined

Numerical List of Taxa

1. *Pholidostachys amazonensis*
2. *Pholidostachys dactyloides*
3. *Pholidostachys occidentalis*
4. *Pholidostachys panamensis*
5. *Pholidostachys pulchra*
6. *Pholidostachys sanluisensis*
- 7.1. *Pholidostachys synanthera* subsp. *robusta*
- 7.2. *Pholidostachys synanthera* subsp. *synanthera*

Specimens Examined

Specimens are arranged by collector (with first initial) in alphabetical order, followed by collector's number in increasing order (s. n. = without number), followed by species number in parentheses.

Alverson, W. 92 (7.2)
Ancuash, E. 587 (7.2)
Anderson, A. 12 (2), 13 (5)
Argüello, A. 424 (2), 477 (2), 526 (2)
Bacon, C. 65 (5)
Balslev, H. 4423 (7.2), 6451 (7.2), 6891 (7.1), 6941 (7.1), 7012 (7.1), 7028 (7.1), 7295 (7.1), 7296 (7.1), 7316 (7.1), 7320 (7.1), 7452 (7.1), 7491 (7.1), 60677 (2), 60678 (3), 62023 (2), 62096 (3), 62097 (2), 62408 (7.2), 62520 (2)
Barbour, P. 4471 (1), 4474 (7.2)
Barfod, A. 60109 (2)
Bennett, B. 3683 (7.2), 4120 (7.2)
Bergmann, B. 62180 (2)
Bernal, R. 74 (2), 302 (2), 351 (2), 424 (2), 680 (2), 876 (2), 906 (3), 1035 (2), 1076 (5), 1384 (7.2), 1519 (2), 1536 (3), 1759 (5), 2495 (2), 2579 (7.1), 2588 (7.1), 2589 (7.1), 2890 (7.2), 2948 (7.1), 4228 (2), 4343 (6)
Betancur, J. 2972 (5), 3191 (3), 5389 (7.2)
Borchsenius, F. 204 (7.2), 636 (7.2)
Boyle, B. 1427 (5), 2048 (3), 2862 (5)
Bunting, G. 772 (5)
Busey, P. 883 (5)
Callejas, R. 4021 (6), 4221 (7.2), 4274 (6)
Campos, J. 4243 (7.2)
Cannarella, R. 8812 (5)
Castaño, N. 562 (7.1)
Cerón, C. 466 (7.2), 10131 (2)
Clark, J. 3976 (3)
Cogollo, A. 3473 (2), 5056 (2)
Cook, O. 165 (2)
Cornejo, X. 2766 (7.2), 3804 (2), 4253 (3), 4713 (2), 6593 (2)
Correa, M. 677 (5)
Couvreur, T. 119 (7.2)
Croat, T. 23014 (5), 26038 (5), 33765 (5), 61463 (2)
Cuatrecasas, J. 9111 (7.2), 14012 (5), 15982 (2), 17257 (2), 17377 (5)
Davidse, G. 31013 (5)
Del Carpio, C. 2171 (7.1)
de Nevers, G. 4285 (5), 4465 (5), 4467(4), 5206 (5), 5364 (5), 5432 (5), 6160 (5), 6246 (5), 6294 (5), 6371(4), 6654 (5), 6713 (5), 6767 (4), 6964(4), 7031 (4), 7310 (4), 7644 (4), 7972 (5), 8043 (4), 8402 (2), 8551 (5), 8552 (4), 10598 (5), 10653 (5)

Díaz, C. 8093 (7.2)
Dodson, C. 5604 (2), 8630 (2), 8706 (2), 9093 (3), 10323 (2), 14491 (2)
Dransfield, J. 4906 (5)
Fleck, D. 818 (7.1)
Folsom, J. 1488 (5), 5250 (5), 6639 (2)
Foster, R. 7327 (7.2)
Frankie, G. 430 (5)
Freire, E. 525 (7.2)
Galeano, G. 406 (5), 445 (2), 451 (2), 1148 (7.1), 1968 (7.2), 7987 (5), 8006 (5), 8129 (5)
Garwood, N. 1045 (5)
Gentry, A. 21363 (7.1), 23777 (5), 30155 (5), 35374 (2), 36843 (2), 36970 (2), 37269 (7.2), 56140 (7.1), 56337 (7.1),
56886 (2), 76539 (7.1)
Gómez, L. 21158 (5)
Grayum, M. 6757 (5), 8988 (5)
Hammel, M. 2396 (5), 8647 (5), 12712 (5), 13661 (4), 14141 (5), 16890 (5), 17148 (3)
Harling, G. 3498 (7.2)
Henderson, A. 52 (5), 59 (5), 138 (3), 161 (7.2), 709 (5), 712 (5), 3037 (4), 3049 (5)
Hernández, J. 442 (6)
Holm-Nielsen, L. 4365 (7.2)
Janovec, J. 1284 (2)
Jiménez, Q. 1757 (5)
Juncosa, A. 726 (6), 735 (6), 1316 (2)
Kahn, F. 1890 (7.1), 1969 (7.1)
Killip, E. 15314 (7.2)
Klug, G. 1495 (7.1)
Knapp, S. 3470 (5)
Knudsen, J. 451 (3), 613 (5), 9605 (3), 9606 (3)
Langlois, A. 4 (5), 16 (5)
Lent, R. 319 (5), 2130 (5)
Lewis, W. 10073 (7.1)
Liesner, R. 818 (5), 1255 (4)
Lleras, E. 16971 (7.1)
Løjtnant, B. 15866 (2)
Londoño, C. 378 (7.1)
Macbride, J. 5674 (7.2)
Malagón, W. 17 (7.2)
McDonagh, J. 275 (5)
McPherson, G. 20789 (5)
Merello, M. 3098 (5), 3163 (5)
Monsalve, M. 971 (2)
Moore, H. 5119 (5), 6586 (5), 8343 (7.2), 8383 (7.2), 9410 (5), 10211 (2)
Morales, C. 1509 (7.2)
Morales, J. 1858 (5)
Mori, S. 2640 (5), 3183 (5), 7626 (5)
Nee, M. 10515 (5), 10961 (5)
Neill, D. 14073 (7.2)
Orozco, C. 2233 (2)
Ortiz, A. 124 (2)
Palacios, P. 485 (7.1), 11314 (2), 13689 (3), 15661 (7.2)
Pardini, R. 16 (7.1)
Quelal, C. 690 (2)
Quizhpe, W. 1222 (7.2)
Rainer, H. 1922188 (7.2), 2126888 (7.2)
Ramírez, J. 4879 (7.2), 15907 (7.2)

Revilla, J. 3757 (7.1)
Rodríguez, A. 1013 (7.2), 5397 (5)
Roncal, J. 319 (4), 326 (5), 334 (4), 337 (5)
Rubio, D. 1137 (2), 1473 (2)
Rueda, R. 1398 (5), 4038 (5), 5773 (5), 10221 (5)
Ruíz, J. s. n. (7.2)
Ruokolainen, K. 4548 (7.1)
Sánchez, D. 1080 (3), 1957 (7.2)
Schultes, R. 3879 (7.1)
Schunke, J. 10125 (7.2), 10449 (7.2), 10460 (7.2)
Siefke, R. 4 (2)
Skov, F. 64707 (2), 64718 (7.2)
Smith, D. 2124 (7.2), 4834 (7.2), 5146 (7.2), 8434 (7.2)
Soejarto, D. 2743 (7.2)
Soto, A. 1597 (5)
Stevens, W. 23971 (5), 24529 (5)
Timaná, M. 907 (7.2)
Tipaz, G. 1369 (2)
Toasa, G. 8676 (7.2)
Tomlinson, P. s. n. (5)
Trail, J. 961 (7.1)
Van den Eynd, V. 581 (7.2)
van der Werf, H. 10117 (7.1), 13092 (7.2)
Vargas, C. 7748 (7.2), 17582 (7.2)
Vargas, H. 5591 (2), 6108 (2)
Vásquez, R. 481 (7.1), 1051 (7.1), 2164 (7.1), 4628 (7.1), 6745 (7.1), 7580 (7.1), 10794 (7.1), 12017 (7.1), 22490 (7.2),
23220 (7.1), 39359 (7.1),
Zamora, N. 441 (5)

Appendix VI. Index of Names

Accepted taxa are bold face.

Calyptrogyne kalbreyeri Burret
Calyptrogyne dactyloides (Moore) Wessels Boer
Calyptrogyne pulchra (Wendland ex Burret) Wessels Boer
Calyptrogyne robusta (Trail) Burret
Calyptrogyne subgen. *Pholidostachys* (Wendland ex Hooker) Wessels Boer
Calyptrogyne synanthera (Martius) Burret
Calyptrogyne weberbaueri Burret
Calyptronoma kalbreyeri (Burret) Bailey
Calyptronoma robusta Trail
Calyptronoma synanthera (Martius) Bailey
Calyptronoma weberbaueri (Burret) Bailey
Geonoma amabilis Wendl. ex Dahlgren
Geonoma synanthera Martius
Pholidostachys amazonensis Henderson
Pholidostachys dactyloides Moore
Pholidostachys kalbreyeri Wendl. ex Burret
Pholidostachys occidentalis Henderson
Pholidostachys panamensis Henderson
Pholidostachys pulchra Wendland ex Burret
Pholidostachys sanluisensis Henderson
Pholidostachys synanthera (Martius) Moore
Pholidostachys synanthera subsp. ***robusta*** (Trail) Henderson
Pholidostachys synanthera subsp. ***synanthera***
Pholidostachys Wendl. ex Hooker

Acknowledgements

I thank the many people who have helped with this work. The staff of the herbarium of the New York Botanical Garden processed the many loans I requested, particularly Dr. Tom Zanoni, Lucy Klebieko, and Wilson Ramos. The curators of the following herbaria sent these loans, or allowed me to study specimens in their care: AAU, BH, BM, COL, COAH, CR, F, GH, K, MO, and NY. Michael Bevans of the Herbarium Digitization Laboratory provided the type images. I especially thank Drs. Gloria Galeano and Rodrigo Bernal of the Universidad Nacional de Colombia for their help. Two anonymous reviewers greatly improved the manuscript.