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A revision of *Desmoncus* (Arecaceae)

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Abstract

A taxonomic revision of the Neotropical palm genus *Desmoncus* based on morphological data and morphometric methods was carried out. Eight hundred and fifty-one herbarium specimens were scored for 16 qualitative variables and 16 quantitative variables. Qualitative variables were divided into 15 characters and one trait. Using the Phylogenetic Species Concept, characters were applied to recognize 24 species. These are widely distributed in Central and South America from southern Mexico to Bolivia and Paraguay, and to Trinidad, Tobago, and the Lesser Antilles. Analysis of each species for geographic distribution and quantitative variables led to recognition of 9 subspecies in two of the species, giving a total of 31 taxa. Seven new species (*D. kunarius, D. interjectus, D. loretanus, D. madrensis, D. moorei, D. obovoideus, D. osensis*) and two new subspecies (*D. horridus* subsp. *occidentalis, D. mitis* subsp. *ecirratus*) are described. Five new combinations are made. One of the most variable species is considered to be a species complex and is divided into morphotypes: groups of similar specimens without formal taxonomic status. Nomenclature, descriptions, and distribution maps are provided for each species and subspecies. Images of type specimens of all new taxa are also given.

Key words: climbing palm, morphometrics, Neotropics, Palmae

Introduction

Desmoncus is distinctive among Neotropical palms in its climbing habit. The name is derived from the Greek words *desmos*, meaning a band, and *ogkos*, meaning a hook, in reference to the climbing hooks, or acanthophylls on the leaves. However, not all *Desmoncus* species are climbers, and not all Neotropical climbers are *Desmoncus*. One other genus, *Chamaedorea* Willdenow (1806: 638) contains a single species with climbing stems, *C. elatior* Mart. In fact, so similar are the acanthophylls of both genera that specimens of *C. elatior* are commonly misidentified as *Desmoncus*. The climbing organs of *Desmoncus* are also remarkably similar to those of some Old World rattans, although the two are not closely related.

Desmoncus was established by Martius (1824). This original brief description was expanded by the same author (Martius 1823–1837), who also increased the number of species to seven in the description of his Amazon collections. Drude (1881), in the treatment of the palms for *Flora Brasiliensis*, recognized 17 species, and Barbosa Rodrigues (1903), also working only on Brazilian palms, recognized 28 species.

The first revision of the entire genus was that of Burret (1934), a German botanist who worked in the Berlin herbarium. In this revision, 41 species were recognized, nine of them new. In a series of papers, Bailey (1943, 1947, 1948, 1949) described 14 new species, only two of which are recognized here. Bailey, as well as Barbosa Rodrigues and Burret, have been criticized for employing an extremely narrow species concept (Wessels Boer 1965, Henderson 1999). Wessels Boer (1965) gave a detailed discussion of variation in *Desmoncus*. In particular he considered that plants of the same species growing in different but adjacent habitats, for example open areas or forest understory, could exhibit very different leaf morphology, and that leaves of young and old plants could also appear quite different.

Apart from this environmental and ontogenetic variation, there are other sources of taxonomic problems in *Desmoncus*. Because of their spiny nature, plants tend to be shunned by collectors and so there are relatively few specimens in herbaria. Apparently *Desmoncus* plants seldom flower (Henderson 1995) and this means that there are few fertile (and many sterile) specimens in herbaria. Fertile specimens that do exist are often poorly collected and pressed, making it difficult to measure and score them. There are also many areas from which there are few if any specimens, particularly in the Amazon region, making taxonomic decisions difficult. Conversely, some small areas are particularly well collected and specimens from these areas have a tendency to be over-emphasized. Another problem in *Desmoncus* is the apparent presence of numerous hybrids, discussed below in the Morphology section.

Because of these issues, *Desmoncus* has been regarded as a taxonomically difficult genus, and this has led to great variation in the number of species recognized over time. Burret (1934) recognized 41 species, whereas Henderson *et al.* (1995), following Wessels Boer (1965, 1988), recognized only seven. *Desmoncus* thus presents a common problem in taxonomy—how to reconcile the splitting of one botanist with the lumping of others. In the present study, explicit, repeatable, quantitative methods, leading to testable hypotheses, are employed in an attempt to understand variation within the genus.

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 (2005a; see also Henderson 2004, 2005b, 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

Eight hundred and fifty-one specimens from the following herbaria were examined and scored: A, AAU, BH, BM, CEN, COAH, COL, CR, F, GH, HEPH, IBGE, INB, INPA, K, M, MG, MICH, MO, NY, P, PMA, R, S, SPF, UB, and US (herbarium abbreviations from Holmgren *et al.* 1990). Fragmentary type specimens from some herbaria (e.g., M, P) were examined but not necessarily scored. 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. There are two exceptions. Specimens of *Desmoncus cirrhifer* and *D. stans* can be unequivocally identified even when sterile, and all specimens of these species were included.

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. Sixteen 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. Sixteen quantitative variables were found and scored (Appendix II). Two are from stems, six from leaves, and eight from reproductive structures. Thirteen are continuous and three are meristic.

A data matrix was constructed with specimens as rows and variables as columns (http://sciweb.nybg.org/Science2/res/Henderson/Desmoncus.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 851 specimens in the matrix, three spatial variables and 32 morphological variables were recorded, giving a potential total of 29,785 data points. However, approximately 46% of these potential data is missing in the matrix. Specimens are often fragmentary or incomplete, and various organs are often missing (especially staminate flowers). Data on plant height and stem branching are often missing from labels.

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 by using 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.

Three variables with many missing data (stem branching, rachillae tomentum, stamen number) were excluded from this analysis. Subsequently, stem branching was treated as a trait because its states varied within some species, and rachillae tomentum and stamen number were treated as characters. 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, stem branching, 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, a 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.

Morphotypes

Subspecies delimitation in one species was problematic, and this was considered to be a species complex or polymorphic species. Species complexes are widespread, variable species in which numerous local variants occur (see Henderson 2011).

Some groups of specimens within species complexes can be recognized as subspecies. This is based, as discussed above, on geographic separation and this recognition is usually supported by quantitative data. However, this leaves a residual group of specimens which are often widespread and differ slightly from site to site. These patterns of variation make taxonomic treatment of species complexes problematic. Recognition of some subspecies within a species complex means that by default residual specimens must also be treated as subspecies, although the patterns of variation suggest that these would be artificial taxa. Alternatively, no subspecies may be recognized within species complexes, but rather they may be divided into morphotypes—informal groups of similar specimens with no formal taxonomic status. Of the two options for treating species complexes—division into subspecies some of which may be artificial, or division into morphotypes some of which may be subspecies—neither is satisfactory. Here, the species complex is divided into morphotypes. If type specimen(s) are present in morphotype groups, then the name of the earliest type is given to the morphotype.

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

For each species, arranged in alphabetical order, complete synonymy is given. Most types (or images of types) of names of *Desmoncus* have been examined for this study and these are followed by a "!". Those which have not been examined are followed by "*n.v.*". Although most sterile types are treated as excluded names, in a few cases a sterile type is maintained and an epitype is designated. 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. An index to all names is given in Appendix VI.

Results

Analysis of the 16 qualitative variables divided them into 15 characters and one trait (Appendix I). Analysis of the 15 characters divided the 851 specimens into 24 species, seven of them undescribed. Analysis of quantitative variables and geography of these species divided two of them into 9 subspecies, giving a total of 31 taxa. A discussion of distribution and habitat, morphology, and morphological variation of these taxa precedes the taxonomic treatment.

Distribution and Habitat

Desmoncus species are distributed from 18°35'N (Mexico) to 23°20'S (Paraguay) and 96°24'W (Mexico) to 35°06'W (Brazil). The country with the highest number of species is Colombia, with 12 species, followed by Brazil with ten species. Species of *Desmoncus* occur from sea level to 1000 m elevation (*D. polyacanthos* in Ecuador). However, most specimens are from low elevations. Of the 406 specimens with elevation data, 386 (95%) occur at ≤500 m and 309 (76%) occur at ≤250 m.

Species of *Desmoncus* are found in a variety of habitats. Most commonly they occur in lowland rainforest, in both flooded and non–flooded areas. Some taxa have more specialized habitats. For example, *D. horridus* subsp. *palustris* grows along the margins of blackwater streams and rivers where the lower parts of its stems are under water for much of the year, and subsp. *horridus* grows along river margins in coastal areas. *Desmoncus orthacanthos* grows near the sea in restinga or scrub forest, and *D. pumilus* occurs in open campina or campinarana vegetation.

Morphology

The genus description given below in the Taxonomic Treatment section is based on the list of characters and traits used in this study (Appendix I). In the following discussion, morphology is treated in more detail, and the morphology of several attributes of *Desmoncus* not used in delimiting species is discussed. Sources of morphological variation are also discussed.

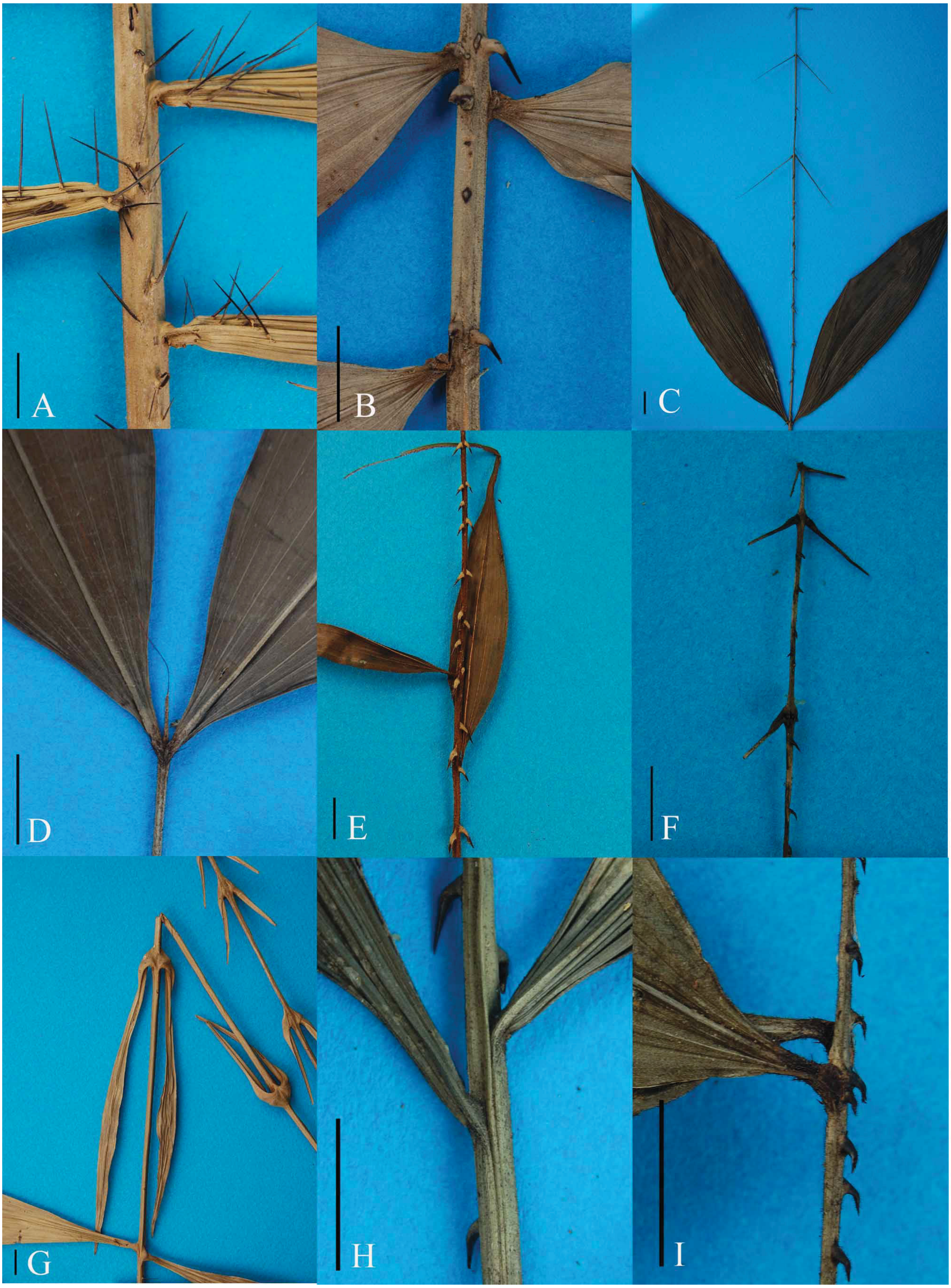
Stems are mostly clustered. Only one species, *Desmoncus giganteus* has solitary stems, although this is recorded from only two specimens. Stems in all but one species, *D. stans*, are not free-standing, and climb by means of acanthophylls. However, one subspecies of *D. mitis*, subsp. *ecirratus* is recorded on several specimen labels as being non-climbing. Despite the climbing habit of most species, stems of *Desmoncus* seldom reach great heights. The mean plant height of all climbers is only 6.2 m. Isnard *et al.* (2005) have discussed the biomechanics and development of the climbing habit of two species of *Desmoncus, D. horridus* subsp. *horridus* (as *D. orthacanthos*) and *D. polyacanthos.*

Leaves of *Desmoncus* are spiny. These spines occur on sheaths, petioles, rachises, cirri, and pinnae and provide several useful taxonomic characters. However, there is considerable variation in spininess of leaf parts both amongst and within species. Spininess also appears to vary according to age of the stem and habitat (Wessels Boer 1965).

Leaves are arranged all along the stems, and are recorded on labels as being distichously arranged. The leaf consists of sheath, petiole, rachis, pinnae, and cirrus. The elongate, basal sheaths tightly enclose the stem and persist even after the leaf has died. Sheaths have well-developed ocreas, extending for several centimeters above the insertion of the petiole. Petioles are usually rather short, and only in *D. cirrhifer* (7.0–16.5 cm long), *D. costaricensis* (8–15 cm long), and *D. giganteus* (15–30 cm long) are they well-developed. Rachises are well-developed in all species, and range from 8–190 cm long. Rachis spines are useful taxonomically and species can be divided into two groups based on these spines. In one group, rachis spines are straight with briefly swollen bases, usually more than 1 cm long, and mostly adaxially or laterally placed on the rachis (Fig. 1A). In the second group, rachis spines are recurved with markedly swollen bases, usually less than 1 cm long, and mostly abaxially placed on the rachis (Fig. 1B).

The rachis is extended into a cirrus. This climbing organ can be defined as a distal section of the rachis which does not bear pinnae but rather acanthophylls. These are pinnae which are modified into reflexed hooks. Cirri can take various forms. They may be well-developed with acanthophylls (Fig. 1C); poorly-developed with the rachis terminating in a short cirrus with or without acanthophylls; virtually absent with the rachis terminating beyond the distal most pair of pinnae in a short 'stub' (Fig. 1D); or poorly-developed with the rachis terminating in a short cirrus with some small, acanthophyll-like pinnae present (Fig. 1E). Arrangement of spines on the cirri differs somewhat, and is useful in identification. In one group of species, the cirri have few spines abaxially, mostly on proximal part of the cirri only (Fig. 1C); in a second group the cirri have spines abaxially throughout (Fig. 1F); in a third group cirri have many, usually paired spines (Fig. 1E); and in a fourth group the cirri are without spines abaxially (Fig. 1G).

FIGURE 1. A. Rachis spines usually >1 cm long, mostly adaxial or lateral, straight with briefly swollen bases; pinnae with an adaxial beard of spines at the bases (*D. chinantlensis; Steyermark 44526*). **B**. Rachis spines <1 cm long, abaxial, recurved with markedly swollen bases (*D. polyacanthos; Coêlho 36032*). **C**. Cirri with no intermediate acanthophylls present, with a wide gap between pinnae and acanthophylls (i.e., gap wider than that between adjacent acanthophylls); cirri with few spines abaxially, mostly on proximal part only (*D. polyacanthos; Henderson 660*). **D**. Cirri absent, the rachis terminating beyond the distalmost pair of pinnae in a short 'stub' (*D. stans; de Nevers 7760*). **E**. Cirri poorly-developed , the rachis terminating in a short cirrus, acanthophylls absent but some small, acanthophyll-like pinnae present; rachis spines <1 cm long, abaxial, recurved with markedly swollen bases (*D. cirrhifer; Barfod 60073*). **F**. Cirri with few spines abaxially throughout (*D. parvulus; Liesner 25728*). **G**. Cirri with intermediate acanthophylls present (i.e., distalmost pair of pinnae reflexed as acanthophylls and with swollen bases and/or proximalmost pair of acanthophylls like vestigial pinnae), without a wide gap between pinnae and acanthophylls; cirri without spines abaxially (*D. chinantlensis; Contreras 2581*). **H**. Pinnae bases with smooth surfaces adaxially, without spinules or dense tomentum; pinnae without a beard of spines at the bases adaxially (*D. polyacanthos; Coêlho 36032*). **I**. Pinnae bases with uneven surfaces at the bases adaxially, covered with spinules and dense tomentum; rachis spines <1 cm long, abaxial, recurved with markedly swollen bases (*D. parvulus; Liesner 25728*). Scale bar = 1 cm.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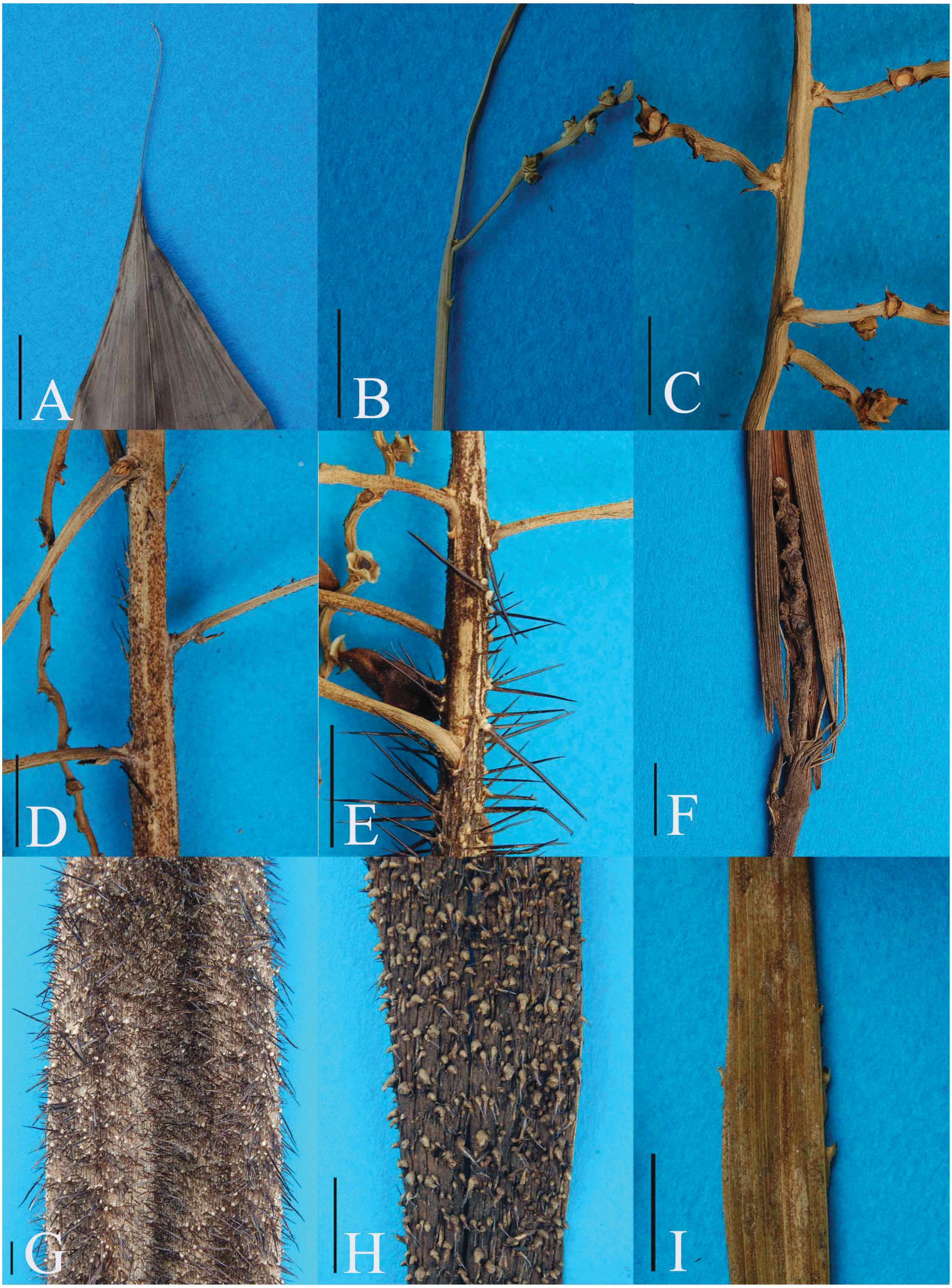
All leaves are pinnate, with pinnae number ranging from 2–28 per side of the rachis. Pinnae are variously arranged; in some species they are irregularly arranged and in others they appear almost regularly arranged. In *D. chinantlensis*, and probably other species, younger leaves have strongly clustered pinnae while in larger plants they are almost regularly arranged. However, pinnae arrangement is difficult to record from most specimens, either because only a short section of the rachis is present, or because folding and pressing of the specimen has obscured the arrangement. Pinnae shape ranges from almost linear to broadly ovate, and again may depend on age of the leaf. Pinnae of younger plants of some species often appear to more ovate leaves; on the other hand, other species have young leaves with narrower pinnae.

Pinnae apices and bases provide several characters. In two species (*D. cirrhifer, D. stans*), pinnae have long, filiform apices (Fig. 2A). In some species there is an adaxial 'beard' of spines at the bases of the pinnae (Fig. 1A). In other species there are spinules at the bases of the pinnae (Fig. 1I), and in one species, *D. moorei*, there are both beards and spinules at the pinnae bases. Other species have the bases of the pinnae with smooth surfaces adaxially (Fig. 1H).

Inflorescences of *Desmoncus* range from densely spiny to almost spineless. They are usually solitary at a node, but in one taxon, *D. mitis* subsp. *leptospadix*, there are often 2–3 inflorescences per node. Inflorescences are always interfoliar and emerge from the apex of the subtending leaf sheath. They have elongate, flattened peduncles which are covered by the subtending sheath, and peduncles are seldom present on specimens in their entirety. Inflorescences are spicate or usually branched to one order; very rarely a proximal rachilla on an inflorescence is bifid. Rachillae number ranges from 1–43. Rachillae are variously arranged on the rachis, and the form of the rachises, rachillae, subtending bracteoles, and pulvini are useful taxonomically.

Inflorescences may have a smooth rachis which is narrower than the few, distantly spaced and alternate rachillae, and each rachilla is usually briefly adnate proximally to the rachis with an irregular bracteole displaced onto the rachis, and a pulvinus may be absent (Fig. 2B); inflorescences may have an angular, slightly twisted rachis which is thicker than the few to numerous, closely spaced and spirally arranged rachillae, and each rachilla is not (or very rarely) adnate to the rachis and is subtended by an acute bracteole and has a well-developed axillary pulvinus (Fig. 2C); inflorescences may have an angular, slightly twisted rachis thicker than the closely spaced and spirally arranged rachillae, and each rachilla is not adnate to the rachis but has an irregular bracteole adnate to the rachilla and appearing displaced distally onto the rachilla (Fig. 2D), with a poorly-developed axillary pulvinus; inflorescences may have a ridged, not twisted rachis which is much thicker than the numerous, closely spaced and spirally or irregularly arranged rachillae, and each rachilla is not or only briefly adnate to the rachis and is subtended by an acute bracteole and with a well-developed axillary pulvinus (Fig. 2E); or the inflorescence may lack a rachis and be spicate (Fig. 2F). Rachillae are mostly glabrous but are tomentose in a few species (Fig. 2E).

FIGURE 2. A. Pinna with long, filiform apex (*D. stans; de Nevers 7760*). **B**. Inflorescence with the rachis smooth, not twisted, narrower than the few, distantly spaced and alternate rachillae, each rachilla briefly adnate proximally to the rachis and with an irregular bracteole displaced onto the rachis, with an axillary pulvinus (*D. mitis; Balslev 4775*). **C**. Inflorescence with the rachis angular, slightly twisted, thicker than the few to numerous, closely spaced and spirally arranged rachillae, each rachilla not adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus (*D. polyacanthos; Wessels Boer 1647*). **D**. Inflorescence with the rachis angular, slightly twisted, thicker than the closely spaced and spirally arranged rachillae, each rachilla not adnate to the rachis and with an irregular bracteole adnate to the rachilla and appearing displaced distally onto the rachilla, with a poorly-developed axillary pulvinus (*D. orthacanthos; Costa 680068*). **E**. Inflorescence with the rachis ridged, not twisted, much thicker than the numerous, closely spaced and spirally or irregularly arranged rachillae, each rachilla not adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; rachillae brown tomentose initially (*D. horridus; Davidse 17831*). **F**. Inflorescence rachis absent (inflorescence spicate) (*D. stans; de Nevers 7760*). **G**. Peduncular bract broad, the surfaces ribbed, brown tomentose, densely covered with long, straight or sinuous, briefly swollen-based, diagonally or vertically oriented spines, these flattened or triangular in cross-section, whitish-brown proximally, black or brown distally, with tomentose margins (*D. chinantlensis; Balick 1715*). **H**. Peduncular bract broad, the surfaces ridged, brown tomentose, densely covered with short, recurved, markedly swollen-based, diagonally oriented spines, these triangular in cross-section, whitish-brown proximally, brown distally, with tomentose margins (*D. polyacanthos; Prance 29626*). **I**. Peduncular bract narrow, elongate, ribbed, scarcely brown tomentose, without spines (*D. mitis; Nee 34905*). Scale bar = 1 cm.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Prophylls are elongate and are inserted near the base of the peduncle. Most of the length of the prophyll, like the peduncle, is covered by the sheath. There is a single peduncular bract, and this is inserted high up on the peduncle usually beyond the apex of the prophyll. The exterior surface of the peduncular bract is useful taxonomically and ten different states are recognized here ranging from spiny (Fig. 2G, 2H, 3A, 3C, 3F, 3G) to lacking spines (Fig. 2I, 3B, 3D, 3E).

Flowers are arranged in triads, at least on the proximalmost parts of the rachillae. Commonly distal most parts of the rachillae bear staminate flowers only, and this part of the rachilla is often deciduous. Triads are surrounded by variously shaped bracteoles. Staminate flowers have a short, three-lobed calyx and much longer, free, lanceolate petals. The apices of the petals are caudate. Stamen number ranges from 5–12, although most species have six stamens. However, this is seldom recorded because staminate flowers are early deciduous and are seldom present on specimens. Filaments are partly and irregularly adnate to the petals. Pistillate flowers have a very short, lobed, cupular calyx and much longer, tubular, lobed corolla. There are approximately six, very small staminodes. The gynoecium is trilocular and triovulate. Where known, inflorescences are protogynous (see Listabarth 1994 for pollination in *Desmoncus*).

Fruits are variously colored and shaped. Most are described on specimen labels as being red or bright red, but yellow is also recorded. Mesocarp fibers are an useful identification character in *Desmoncus*. These fibers, or their lack, give fruit surfaces a characteristic appearance ranging from uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers (Fig. 3H); smooth without any apparent subepidermal fibers (Fig. 3I); uneven with numerous, subepidermal, long, branching fibers (Fig. 4A); to bumpy from the numerous, subepidermal, short, oblique fibers (Fig. 4B). Fruiting corollas in one species, *D. giganteus*, are almost half as long as fruits (Fig. 4C). In most species, fruiting corollas split irregularly into 3 lobes and the lobes often split again (Fig. 4E) but in a few species fruiting corollas do not or scarcely split and tend to remain cupular (Fig. 4D). Endocarp shape varies from globose to obovoid with rounded or slightly peaked apices; narrowly ellipsoid with rounded apices; broadly obovoid with flattened apices; to ovoid to obovoid with prominent, peaked apices (Fig. 4F).

Eophylls have one pair of pinnae. However, only four specimens have been seen with eophylls (representing *D. chinantlensis*, *D. leptoclonos, D. myriacanthos,* and *D. polyacanthos*). Galeano & Bernal (2010) illustrated the eophylls of *D. cirrhifer* and *D. myriacanthos* (as *D. orthacanthos*) as bifid. According to Dransfield *et al.* (2008), the eophyll of *D. costaricensis* has two pairs of pinnae.

FIGURE 3. A. Peduncular bract broad, ridged, densely covered with short, straight, swollen-based, vertically oriented spines, these terete, whitish-brown proximally, brown distally, without tomentum (*D. parvulus; Mori 8063*). **B**. Peduncular bract broad, ribbed, densely brown tomentose, without spines (*D. vacivus; Vásquez 2646*). **C**. Peduncular bract broad, ribbed or ridged, densely covered with felty, reddish-brown tomentum, sparsely covered with short, scarcely swollen-based, diagonally oriented, flattened spines, whitish-brown proximally, brown distally, with tomentose margins (*D. cirrhifer; Moore 9471*) **D**. Peduncular bract broad, ribbed with several more prominent, lighter colored ribs, brown, scarcely or not tomentose, without spines (*D. loretanus; Gentry 25785*). **E**. Peduncular bract narrow, ribbed, densely whitish-brown tomentose, not spiny (*D. stans; Grayum 8115*). **F**. Peduncular bract broad, the surface ribbed or ridged, brown tomentose or glabrous, sparsely to moderately covered with short, straight or sinuous, briefly swollen-based, diagonally or vertically oriented spines, these flattened or triangular in cross-section, whitish-brown proximally, black or brown distally, with tomentose margins (*D. leptoclonos; Irwin 7194*). **G**. Peduncular bract broad, the surface deeply ridged, dark brown tomentose, sparsely covered with long, straight or sinuous spines, the bases scarcely swollen but running directly into the ridges of the bract and lying flat against the bract surface, flattened in cross-section, brown proximally and distally, with tomentose margins (*D. interjectus; Schultes 16233*). **H**. Fruit surface uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers (*D. orthacanthos; Carvalho 627*). **I**. Fruit surfaces smooth, without any apparent subepidermal fibers; fruiting corolla splitting irregularly into 3 lobes, the lobes splitting again (*D. polyacanthos; Nascimento 723*). Scale bar = 1 cm.


A
B
C
D
E
F
G
H
I

FIGURE 4. A. Fruit surface uneven with numerous, subepidermal, long, branching fibers (*D. obovoideus; Morales 6333*). **B**. Fruit surface bumpy from numerous, subepidermal, short, oblique fibers (*D. kunarius; de Nevers 4415*). **C**. Fruiting corollas to half as long as fruits (*D. giganteus; Henderson 1688*). **D**. Fruiting corollas not or scarcely splitting, tending to remain cupular; fruiting corollas less than one quarter as long as fruits (*D. myriacanthos; Cuadros 1855*). **E**. Fruiting corollas splitting irregularly into 3 lobes, the lobes often splitting again (*D. polyacanthos; Smith 3791*). **F**. Endocarps. Top right—endocarp broadly obovoid with flattened apices, the pores lateral on or near flattened apices; (*D. obovoideus; Aguilar 11417*). Middle left—endocarp globose to obovoid with rounded or slightly peaked apices, the pores lateral (*D. chinantlensis; Bangham 368*). Middle right—endocarp narrowly ellipsoid with rounded apices, the pores lateral (*D. myriacanthos; Croat 9314*). Bottom left—endocarp ovoid to obovoid with prominent, peaked apices, the pores lateral (*D. giganteus; Huashikat 1099*). Scale bar = 1 cm.

Morphological variation

There are several sources of infraspecific variation in morphology and these make the taxonomy of *Desmoncus* problematic. There appears to be no evidence that this variation is due to any cytological or breeding system abnormality (e.g., polyploidy, apomixis). The genus has a chromosome number of 2n = 30 (although only 3 species have been counted) and there is no evidence of polyploidy (Dransfield *et al.* 2008).

Plants of *Desmoncus* are monoecious and, where known, they are outcrossing and pollinated by beetles (Listabarth 1994). Observed variation may be due to only a few factors—environment, ontogeny, clines, and hybridization.

Environmental variation has been mentioned in the introduction. Wessels Boer (1965) gave a detailed discussion and illustration of this. He showed that plants of the same species growing in different but adjacent habitats could exhibit very different leaf morphology and spininess. Plants of *D. polyacanthos* exposed to full sunlight had sheaths with numerous, rather straight, swollen-based spines; plants growing in dense shade had almost spineless sheaths; and plants growing in a riparian habitat in full sun were larger than normal and were densely spiny. Exactly this type of variation is observed amongst the specimens of *D. polyacanthos*, and it has misled earlier botanists (e.g., Bailey 1943, 1947, 1948, 1949).

Ontogenetic variation in *Desmoncus* is also apparent. For example, in *D. chinantlensis*, leaves of young plants have rachises which often lack spines and pinnae which are shorter, ovate, strongly clustered, and lack spines at the bases. Adult plants have spiny rachises and longer, more linear, irregularly arranged pinnae with beards of spines at the bases. It was this kind of variation that led to confusion over the types of *D. chinantlensis* (Bailey 1933). On the other hand, juvenile plants of one outlying population of *D. moorei* have numerous, linear, regularly arranged pinnae and appear quite different from adult plants with fewer, ovate, irregularly arranged pinnae.

There is only one known case of clinal variation in *Desmoncus*. In *D. orthacanthos*, which has a linear distribution along the Atlantic coast of Brazil, regression shows petiole length, rachis length, basal pinna length, basal pinna width, peduncular bract length, and rachilla length decrease from north to south whereas fruit length increases from north to south. Clinal variation seems a minor source of variation within *Desmoncus*, particularly compared with *Geonoma* (Henderson 2011). However, *Geonoma* species usually have much wider elevation ranges than *Desmoncus* and many *Geonoma* species exhibit variation with change in elevation.

A fourth source of variation is hybridization. Interspecific hybrids in palms have been reported in only a few genera, and most of these are cocosoid palms (especially *Attalea, Bactris, Butia, Allagoptera, Syagrus*). *Desmoncus* is also a cocosoid palm, so perhaps it is not surprising to find frequent hybrids. Although it is difficult to recognize hybrids from herbarium specimens, they are identified here based on two criteria. First, that specimens exhibit intermediate morphology, and second that they occur sympatrically with both putative parent species. Eighteen specimens (2% of all specimens) are here postulated to be of hybrid origin. All these involve *D. polyacanthos*, the most widespread and variable species, and either *D. pumilus, D. mitis* or *D. horridus.* These last two, *D. mitis* and *D. horridus,* are also widespread and variable. All postulated hybrids come from the central and western Amazon region and none occur in other regions.

A fifth problem causing taxonomic problems has to do with species complexes. One species, *Desmoncus polyacanthos*, the most variable in the genus, is here regarded as a species complex. Such complexes were defined by Henderson (2011) as widespread, variable species in which numerous local variants occur. *Desmoncus polyacanthos* is extremely variable and defies subspecific division. It is of interest to note that the greatest variation in this species occurs in the same area as that of several species complexes in *Geonoma*—the western Amazon basin and sub-andean foothills. Here, *D. polyacanthos* exhibits a myriad of local forms, often with more than one form occurring sympatrically. Henderson (2011) considered that the high levels of variability in species complexes may be based on resource (habitat) polymorphisms, and these may represent an intermediate step in sympatric speciation.

These factors—environment, ontogeny, clines, hybridization, and species complexes—make a revision of *Desmoncus* difficult. The characters used here in the delimitation of species (Appendix I) are sometimes difficult to define and score, particularly those to do with spininess in both leaves and peduncular bracts. The difficulties of definition and scoring of characters also lead to problems in using these characters in phylogenetic reconstruction. There are also other problems with phylogeny in *Desmoncus*. One character in particular illustrates this very well. The genus has traditionally been split into two sections depending on whether the leaf rachis spines are straight or recurved (e.g. Burret 1934), and this character is also used here.

However, there is evidence that in at least one species, *D. interjectus*, recurved spines appear to have been secondarily derived from straight spines. Such reversals complicate phylogenetic reconstruction.

A second problem in phylogenetic reconstruction is found in choice of outgroups. If more evidence of the potential of morphology to mislead is needed, it is found in generic relationships. *Desmoncus* is placed in the subfamily Arecoideae, tribe Cocoseae, subtribe Bactridinae (Dransfield *et al.* 2008). The Bactridinae contains five genera (*Acrocomia, Aiphanes, Astrocaryum, Bactris*, and *Desmoncus*). Recently Eiserhardt *et al.* (2011) have proposed that *Desmoncus* and *Acrocomia* are sister genera. Such a relationship would never be postulated based on morphology; in fact *Desmoncus* appears most dissimilar to *Acrocomia* and most similar to *Bactris*. The final point in considering phylogeny based on morphology is that the leaf structure of *Desmoncus* is so different from potential outgroups (e.g., *Acrocomia*) that it is not possible to polarize character states. For these reasons, phylogenetic reconstruction based on morphological data is not attempted here.

Taxonomic Treatment

Desmoncus Martius (1824: 20)

Type:—*Desmoncus polyacanthos* Martius.
Atitara Barrère ex Kuntze (1891: 726). Type:—*Atitara polyacantha* (Martius) Kuntze.

Stems solitary, or clustered. **Leaf** rachis spines usually >1 cm long, mostly adaxial or lateral, straight with briefly swollen bases, or rachis spines usually <1 cm long, mostly abaxial, recurved with markedly swollen bases; cirri well-developed, with acanthophylls, or cirri poorly-developed, the rachis terminating in a short cirrus, acanthophylls present or absent, or cirri absent, the rachis terminating beyond the distalmost pair of pinnae in a short ‘stub’, or cirri poorly-developed , the rachis terminating in a short cirrus, acanthophylls absent but some small, acanthophyll-like pinnae present; cirri with few spines abaxially, mostly on proximal part only (rarely, when cirri poorly-developed, without spines), or cirri without spines abaxially, or cirri with few spines abaxially, throughout, or cirri with many, usually paired spines; cirri, when well-developed, with intermediate acanthophylls present (i.e., distalmost pair of pinnae reflexed as acanthophylls and with swollen bases and/or proximalmost pair of acanthophylls like vestigial pinnae), without a wide gap between pinnae and acanthophylls, or cirri with no intermediate acanthophylls present, usually with a wide gap between pinnae and acanthophylls (i.e., gap wider than that between adjacent acanthophylls); pinnae with long, filiform apices, or pinnae without long, filiform apices; pinnae without a beard of spines at the bases adaxially, or pinnae with an adaxial beard of spines at the bases; pinnae bases with smooth surfaces adaxially, without spinules or dense tomentum, or pinnae bases with uneven surfaces at the bases adaxially, usually covered with spinules and/or dense tomentum. **Inflorescences** with the rachis smooth, not twisted, narrower than the few, distantly spaced and alternate rachillae, each rachilla usually briefly adnate proximally to the rachis and with an irregular bracteole displaced onto the rachis, with or without an axillary pulvinus, or inflorescences with the rachis angular, slightly twisted, thicker than the few to numerous, closely spaced and spirally arranged rachillae, each rachilla not (or very rarely) adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus, or inflorescences with the rachis angular, slightly twisted, thicker than the closely spaced and spirally arranged rachillae, each rachilla not adnate to the rachis and with an irregular bracteole adnate to the rachilla and appearing displaced distally onto the rachilla, with a poorly- to well-developed axillary pulvinus, or inflorescences with the rachis ridged, not twisted, much thicker than the numerous, closely spaced and spirally or irregularly arranged rachillae, each rachilla not or only briefly adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus, or inflorescences with the rachis ridged, not twisted, much thicker than the numerous, closely spaced and spirally arranged rachillae, each rachilla not adnate to the rachis, subtended by an acute bracteole and without an axillary pulvinus, or inflorescence rachis absent (inflorescence spicate); peduncular bracts broad, the surfaces ribbed, brown tomentose, sparsely to densely covered with long, straight or sinuous, briefly swollen-based, diagonally or vertically oriented spines, these flattened or triangular in cross-section, whitish-brown proximally, black or brown distally, with tomentose margins (rarely without spines), or peduncular bracts broad, the surfaces ridged, brown tomentose, sparsely to densely covered with short, recurved, markedly swollen-based, diagonally oriented spines, these triangular in cross-section, whitish-brown proximally, brown distally, with tomentose margins (rarely without spines), or peduncular bracts narrow, elongate, ribbed, scarcely brown tomentose, without spines (rarely with few spines), or peduncular bracts broad, ridged, densely covered with short, straight, swollen-based, vertically oriented spines, these terete, whitish-brown proximally, brown distally, without tomentum, or peduncular bracts broad, ribbed, densely brown tomentose, without spines (very rarely with a few spines), or; peduncular bracts broad, ribbed or ridged, densely covered with felty, reddish-brown tomentum, sparsely covered with short, scarcely swollen-based, diagonally oriented, flattened spines, whitish-brown proximally, brown distally, with tomentose margins, or peduncular bracts broad, ribbed with several more prominent, lighter colored ribs, brown, scarcely or not tomentose, without spines (rarely with a few spines), or peduncular bracts narrow, ribbed, densely whitish-brown tomentose, not spiny, or peduncular bracts broad, the surfaces ribbed or ridged, brown tomentose or glabrous, sparsely to moderately covered with short, straight or sinuous, briefly swollen-based, diagonally or vertically oriented spines, these flattened or triangular in cross-section, whitish-brown proximally, black or brown distally, with tomentose margins, or peduncular bracts broad, the surfaces deeply ridged, dark brown tomentose, sparsely covered with long, straight or sinuous spines, the bases scarcely swollen but running directly into the ridges of the bract and lying flat against the bract surface, flattened in cross-section, brown proximally and distally, with tomentose margins; rachillae brown tomentose initially, or rachillae glabrous or scarcely tomentose initially; stamens five to seven, or stamens eight to 12; **fruit** surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers, or fruit surfaces smooth, without any apparent subepidermal fibers, or fruit surfaces uneven with numerous, subepidermal, long, branching fibers, or fruit surfaces bumpy from numerous, subepidermal, short, oblique fibers; fruiting corollas less than one quarter as long as fruits, or fruiting corollas to half as long as fruits; fruiting corollas splitting irregularly into 3 lobes, the lobes often splitting again, or fruiting corollas not or scarcely splitting, tending to remain cupular; endocarps globose to obovoid with rounded or slightly peaked apices, the pores lateral, or endocarps narrowly ellipsoid with rounded apices, the pores lateral, or endocarps broadly obovoid with flattened apices, the pores lateral on or near flattened apices, or endocarps ovoid to obovoid with prominent, peaked apices, the pores lateral.

Key to the species of *Desmoncus*

1 Mexico and Central America 2
- South America, Trinidad and Tobago, and the Lesser Antilles 10
2 Pinnae with long, filiform apices; cirri absent, the rachis terminating beyond the distalmost, opposite pair of pinnae in a <1 cm long 'stub', this with an easily broken, longer, smooth, brown extension, or cirri poorly-developed, the rachis terminating in a short cirrus with spines abaxially, acanthophylls absent but some small, acanthophyll-like pinnae present 3
- Pinnae without long, filiform apices; cirri well-developed, with acanthophylls 4
3 Cirri poorly-developed, the rachis terminating in a short cirrus with spines abaxially, acanthophylls absent but some small, acanthophyll-like pinnae present; rachillae 24(19–30); central and eastern Panama .... *D. cirrhifer*
- Cirri absent, the rachis terminating beyond the distal most, opposite pair of pinnae in a <1 cm long 'stub', this with an easily broken, longer, smooth, brown extension; rachilla 1; Osa Peninsula and adjacent areas in Costa Rica .... *D. stans*
4 Fruits 25.1(23.9–27.4) mm long, 22.7(20.1–24.1) mm wide, the surfaces bumpy from numerous, subepidermal, short, oblique fibers; proximal rachillae 18.5(17.5–19.5) cm long, 2.5(2.1–2.9) mm wide; central Panama .... *D. kunarius*
- Fruits 14.7(11.1–21.0) mm long, 11.4(7.0–16.3) mm wide, the surfaces uneven with numerous, subepidermal, short,

often branching (Y-shaped) fibers, or fruit surfaces with numerous, subepidermal, long, branching fibers; proximal rachillae 12.1(5.5–19.0) cm long, 1.2(0.6–2.2) mm wide; widespread 5

5 Rachillae brown tomentose initially; pinnae with spinules at the bases; Caribbean coast of Nicaragua and Costa Rica and Nicoya Peninsula, Costa Rica .... *D. moorei*

\- Rachillae glabrous or scarcely tomentose initially; pinnae with smooth surfaces at the bases adaxially, without spinules or dense tomentum; widespread 6

6 Fruiting corollas cupular, not or scarcely splitting; endocarps narrowly ellipsoid with rounded apices; central and eastern Panama .... *D. myriacanthos*

\- Fruiting corollas splitting irregularly into 3 lobes, the lobes often splitting again; endocarps globose to obovoid with rounded apices and lateral pores, or endocarps broadly obovoid with flattened apices, the pores lateral on or near flattened apices; widespread 7

7 Fruit surfaces with numerous, subepidermal, long, branching fibers 8

\- Fruit surfaces with numerous, subepidermal, short, often branching (Y-shaped) fibers 9

8 Basal pinna 14.0 cm long, 4.9(4.2–5.5) cm wide; central Panama with outliers in western and eastern Panama .... *D. obovoideus*

\- Basal pinna 23.2(18.0–26.0) cm long, 3.7(2.4–5.0) cm wide); Osa Peninsula and adjacent areas in Costa Rica .... *D. osensis*

9 Petioles 10.5(8.0–15.5) cm long; pinnae without a beard of spines at the bases adaxially Caribbean coast of Costa Rica .... *D. costaricensis*

\- Petioles 2.2(0.5–4.7) cm long; pinnae with an adaxial beard of spines at the bases; southern Mexico, Belize, Guatemala, Honduras, and Nicaragua .... *D. chinantlensis*

10 Pinnae with long, filiform apices; cirri poorly-developed, the rachis terminating in a short cirrus with spines abaxially, acanthophylls absent but some small, acanthophyll-like pinnae present; western Colombia and western Ecuador .... *D. cirrhifer*

\- Pinnae without long, filiform apices; cirri well-developed, with acanthophylls, or poorly-developed, the rachis terminating in a short cirrus, acanthophylls present or absent, or absent, the rachis terminating beyond the distalmost pair of pinnae in a short ‘stub’; widespread 11

11 Leaf spines, especially on the rachis (where usually >1 cm long and mostly adaxial or lateral), straight with briefly swollen bases; cirri without spines abaxially 12

\- Leaf spines, especially on the rachis (where usually <1 cm long and mostly abaxial), recurved with markedly swollen bases; cirri with spines abaxially (rarely, when cirri poorly-developed, without spines) 15

12 Fruits 36.2(21.5–42.6) mm long, 16.6(12.7–18.3) mm wide, the surfaces smooth, without any apparent subepidermal fibers; fruiting corollas to half as long as fruits .... *D. giganteus*

\- Fruits 14.5(8.2–23.9) mm long, 9.9(5.0–17.9) mm wide, the surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers; fruiting corollas less than one quarter as long as fruits 13

13 Inflorescences with the rachis angular, slightly twisted, thicker than the closely spaced and spirally arranged rachillae, each rachilla not adnate to the rachis and with an irregular bracteole adnate to the rachilla and appearing displaced distally onto the rachilla; Atlantic Coastal Forest of Brazil .... *D. orthacanthos*

\- Inflorescences with the rachis ridged, not twisted, much thicker than the numerous, closely spaced and spirally or irregularly arranged rachillae, each rachilla not or only briefly adnate to the rachis, subtended by an acute bracteole; northern South America 14

14 Pinnae without a beard of spines at the bases; fruiting corollas splitting irregularly into 3 lobes, the lobes often splitting again; Amazon and adjacent regions, including Trinidad and Tobago .... *D. horridus*

\- Pinnae with a beard of adaxial spines at the bases; fruiting corollas cupular, not or scarcely splitting; northwestern Colombia, and just reaching Venezuela (Zulia) .... *D. myriacanthos*

15 Cirri with spines abaxially throughout .... *D. parvulus*

\- Cirri with spines abaxially mostly on proximal part only (rarely, when cirri poorly-developed, without spines) … 16

16 Inflorescences with the rachis smooth, not twisted, narrower than the few, distantly spaced and alternate rachillae, each rachilla usually briefly adnate proximally to the rachis and with an irregular bracteole displaced onto the rachis 17

\- Inflorescences with the rachis angular, slightly twisted, thicker than the few to numerous, closely spaced and spirally arranged rachillae, each rachilla not (or very rarely) adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus 18

17 Pinnae bases with smooth surfaces adaxially, without spinules or dense tomentum (sometimes with short spines)..... .... *D. pumilus*

\- Pinnae bases with uneven surfaces at the bases adaxially, usually covered with spinules and/or dense tomentum .... *D. mitis*

18 Fruit surfaces uneven with numerous, subepidermal, long, branching fibers 19

\- Fruit surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers, or smooth, without any apparent subepidermal fibers 20

19 Peduncular bract surfaces ridged, brown tomentose, densely covered with short, recurved, markedly swollen-based, diagonally oriented spines; fruits 11.9(11.2–12.8) mm long; central Amazon region of Brazil and Colombia .... *D. setosus*

\- Peduncular bract surfaces ribbed, densely brown tomentose, without spines (very rarely with a few spines); fruits 20.9(18.4–23.9) mm long; western Amazon region in Colombia, Peru, and Brazil .... *D. vacivus*

20 Fruit surfaces smooth, without any apparent subepidermal fibers .... *D. polyacanthos*

\- Fruit surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers 21

21 Peduncular bract surfaces deeply ridged, dark brown tomentose, sparsely covered with long, straight or sinuous spines, the bases scarcely swollen but running directly into the ridges of the bract and lying flat against the bract surface; Colombia (Amazonas, Vaupés) .... *D. interjectus*

\- Peduncular bracts ribbed with several more prominent, lighter colored ribs, brown, scarcely or not tomentose, without spines (rarely with a few spines), or peduncular bract surfaces ridged, brown tomentose, sparsely to densely covered with spines; widespread, excluding Colombia 22

22 Peduncular bracts ribbed with several more prominent, lighter colored ribs, brown, scarcely or not tomentose, without spines (rarely with a few spines); Peru (Loreto) .... *D. loretanus*

\- Peduncular bract surfaces ridged, brown tomentose, sparsely to densely covered with spines; Peru (Madre de Dios, Ucayali), eastern Bolivia, Brazil (Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Rondônia), and Paraguay (San Pedro) 23

23 Pinnae bases with uneven surfaces at the bases adaxially, usually covered with spinules and/or dense tomentum; Peru (Madre de Dios, Ucayali) .... *D. madrensis*

\- Pinnae bases with smooth surfaces adaxially, without spinules or dense tomentum 24

24 Endocarps globose to obovoid with rounded or slightly peaked apices; eastern Bolivia .... *D. latisectus*

\- Endocarps narrowly ellipsoid with rounded apices; Brazil (Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Rondônia) and Paraguay (San Pedro) .... *D. leptoclonos*

1. ***Desmoncus chinantlensis*** Liebm. ex Martius (1837–1837: 321).

Atitara chinantlensis (Liebm. ex Martius) Kuntze (1891: 727).

Lectotype (designated by Bailey 1933):—MEXICO. Oaxaca: Lacoba, Chinantla, no date, *F. Liebmann 6595* (C, *n.v.*, lectotype image!).

Desmoncus anomalus Bartlett (1935: 84). Type:—GUATEMALA. Alta Vera Paz: Secanquím, 29 April 1904, *O. Cook & C. Doyle 97* (holotype US!). ***Synon. nov.***

Desmoncus lundellii Bartlett (1935: 84). Type:—GUATEMALA. Petén: near El Paso de Petén, 26 April 1932, *C. Lundell 1555* (holotype MICH!).

Desmoncus quasillarius Bartlett (1935: 85). Type:—BELIZE. Corozal: San Andres, July 1933, *P. Gentle 348* (holotype MICH!).

Desmoncus uaxactunensis Bartlett (1935: 86). Type:—GUATEMALA. Petén: Uaxactún, 18 April 1931, *H. Bartlett 12576* (holotype MICH!).

Desmoncus ferox Bartlett (1935: 87). Type:—GUATEMALA. Petén: Tikal, 12–15 April 1931, *H. Bartlett 12584* (holotype MICH!).

Plants 8.1(2.5–20.0) m tall; stems 2.5(1.4–3.8) cm diameter, solitary or clustered. **Leaf** petioles 2.2(0.5–4.7) cm long; rachises 108.0(96.0–128.0) cm long, 10.5(5.7–15.0) mm wide, the spines usually >1 cm long, mostly adaxial or lateral, straight with briefly swollen bases; pinnae 23(18–35) per side of rachis, without long, filiform apices, with an adaxial beard of spines at the bases, without spinules or dense tomentum at the bases adaxially; basal pinna 21.6(7.5–31.0) cm long, 1.9(1.0–2.5) cm wide; cirri well-developed, with acanthophylls, without spines abaxially, with intermediate acanthophylls present, without a wide gap between pinnae and acanthophylls. **Inflorescences** with the rachis ridged, not twisted, much thicker than the numerous, closely spaced and spirally or irregularly arranged rachillae, each rachilla not or only briefly adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 7.2(5.0–13.1) mm wide; peduncular bracts 37.3(26.5–69.0) cm long, broad, the surfaces ribbed, brown tomentose, sparsely to densely covered with long, straight or sinuous, briefly swollen-based, diagonally or vertically oriented spines, these flattened or triangular in cross-section, whitish-brown proximally, black or brown distally, with tomentose margins; rachillae 38(28–43), glabrous or scarcely tomentose initially; proximal rachillae 13.0(9.0–19.0) cm long, 1.2(0.9–1.7) mm wide; stamens 9(8–11); **fruits** 15.2(12.1–18.6) mm long, 12.7(10.3–16.2) mm wide, the surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers; fruiting corollas less than one quarter as long as fruits, splitting irregularly into 3 lobes, the lobes often splitting again; endocarps globose to obovoid with rounded or slightly peaked apices, the pores lateral.

Distribution and habitat:—From 13°03'–18°35'N and 84°58'–96°24'W in southern Mexico (Campeche, Chiapas, Oaxaca, Quintana Roo, Tabasco, and Veracruz), Belize, Guatemala, Honduras, and Nicaragua at 187(10–550) m elevation in lowland rainforest, often in limestone areas (Fig. 5).

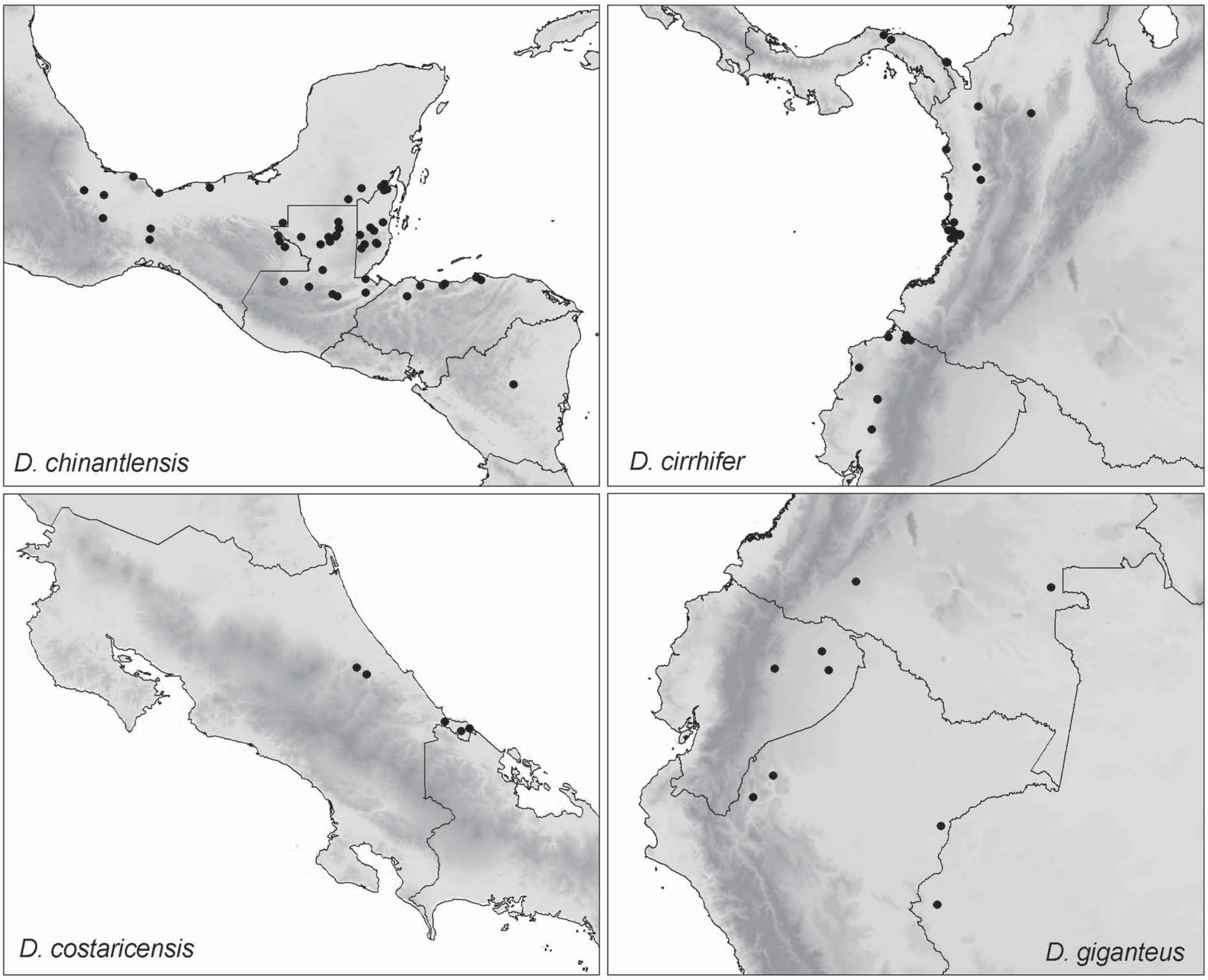

FIGURE 5. Distribution maps of *Desmoncus chinantlensis*, *D. cirrhifer, D. costaricensis*, and *D. giganteus*.

Taxonomic notes:—There are three original collections from Oaxaca of *Desmoncus chinantlensis*—*Liebmann 6594, 6595,* and *6596*, none of which was cited by Martius. Bailey (1933; see also Schultes 1940) designated *Liebmann 6595* from C as lectotype, and this specimen is illustrated by Dahlgren (1959, plate 180). Bailey noted that this specimen was somewhat different from the other two specimens, both at US. This is probably because the leaf represented by the lectotype is from a young plant. Leaves of young plants, which are frequently collected, have rachises which often lack spines and pinnae which are shorter, ovate, strongly clustered, and lack spines at the bases.

Bartlett (1935) described five species from Belize and Guatemala, none of which are recognized here. One of these, *D. anomalus* has narrow pinnae and pistillate flowers with unusual staminodes. Another specimen (*Cook 53*) from the same locality has normal pinnae and staminodes. Both *Desmoncus quasillarius* and *D. uaxactunensis* were said to have peduncular bracts ‘entirely or nearly unarmed’ or ‘almost unarmed’, but both are spiny as in other specimens.

Subspecific variation:—There is no geographic disjunction except for an outlying specimen from Nicaragua, but this is likely to be an artifact of insufficient collecting. Two specimens from Honduras (*Evans 1702, Saunders 553*) have somewhat tomentose rachillae, more like those of *Desmoncus moorei*. Other specimens from Honduras have less pronounced beards of spines at the pinnae bases, although this may be because they represent young leaves.

2. *Desmoncus cirrhifer* Gentry & Zardini in Gentry (1988: 1436), as “*cirrhifera*”.

Type:—COLOMBIA. Valle: Bahía Malaga, 0 m, 4°02'N, 76°15'W, 16 December 1985, *A. Gentry, M. Monsalve, C. Restrepo & J. Gamboa 53392* (holotype CUVC *n.v.*, isotypes MO!, COL *n.v.*, K!).

Plants 11.0(3.0–20.0) m tall; stems 2.0(1.2–3.0) cm diameter, clustered. **Leaf** petioles 10.8(7.0–16.5) cm long; rachises 105.3(91.0–117.0) cm long, 6.0(4.0–8.1) mm wide, the spines usually <1 cm long, mostly abaxial, recurved with markedly swollen bases; pinnae 9(7–15) per side of rachis, with long, filiform apices, without a beard of spines at the bases, without spinules or dense tomentum at the bases adaxially; basal pinna 19.4(17.0–21.0) cm long, 4.2(2.5–6.0) cm wide; cirri poorly-developed, the rachis terminating in a short cirrus, acanthophylls absent but some small, acanthophyll-like pinnae present, with many, usually paired spines. **Inflorescences** with the rachis angular, slightly twisted, thicker than the few to numerous, closely spaced and spirally arranged rachillae, each rachilla not (or very rarely) adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 5.4(3.3–7.1) mm wide; peduncular bracts 22.5 cm long, broad, ribbed or ridged, densely covered with felty, reddish–brown tomentum, sparsely covered with short, scarcely swollen-based, diagonally oriented, flattened spines, whitish-brown proximally, brown distally, with tomentose margins; rachillae 24(19–33), tomentose initially; proximal rachillae 6.0(4.0–8.0) cm long, 1.7(1.4–2.0) mm wide; stamens 6; **fruits** 18.2(14.3–20.9) mm long, 13.4(9.8–15.7) mm wide, the surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers; fruiting corollas less than one quarter as long as fruits, splitting irregularly into 3 lobes, the lobes often splitting again; endocarps globose to obovoid with rounded or slightly peaked apices, the pores lateral.

Distribution and habitat:—From 9°24’N–1°27’S and 75°05’–79°84’W in central and eastern Panama, western Colombia, and western Ecuador at 180(1–700) m elevation in wet, lowland rainforest, sometimes in disturbed areas (Fig.5).

Subspecific variation:—There is a gap in the distribution of this species, in southern Colombia. Although this may be an artifact of insufficient collecting, specimens from Ecuador appear larger than those from Colombia and Panama. However, there are too few data to test for differences.

3. *Desmoncus costaricensis* (Kuntze) Burret (1934: 202).

Atitara costaricensis Kuntze (1891: 726). Type:—COSTA RICA. Province unknown: “sudlich von San José im Gebirge”, June 1874, *O. Kuntze s. n.* (holotype NY!). Epitype (Grayum 1998):—COSTA RICA. Limón: ridge separating Quebrada Cañabral from Río Barbilla, and slope leading down to the latter, Cordillera de Talamanca, 10°02’N, 83°26’W, 200–400 m, 4 September 1998, *M. Grayum, G. Herrera & R. Robles 8746* (epitype MO *n.v.*, isoepitype INB!).

Plants 5.3(4.0–6.0) m tall; stems 1.9(1.3–2.3) cm diameter, clustered. **Leaf** petioles 10.5(8.0–15.5) cm long; rachises 74.8(67.0–80.0) cm long, 7.3(5.7–9.3) mm wide, the spines usually >1 cm long, mostly adaxial or lateral, straight with briefly swollen bases; pinnae 9(8–10) per side of rachis, without long, filiform apices, without a beard of spines at the bases adaxially, without spinules or dense tomentum at the bases adaxially; basal pinna 24.5(14.5–32.0) cm long, 5.7(3.0–9.0) cm wide; cirri well-developed, with acanthophylls, without spines abaxially, with intermediate acanthophylls present, without a wide gap between pinnae and acanthophylls. **Inflorescences** with the rachis ridged, not twisted, much thicker than the numerous, closely spaced and spirally or irregularly arranged rachillae, each rachilla not or only briefly adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 6.4(4.6–8.2) mm wide; peduncular bracts 20.5(15.0–28.5) cm long, broad, the surfaces ribbed, brown tomentose, sparsely to densely covered with long, straight or sinuous, briefly swollen-based, diagonally or vertically oriented spines, these flattened or triangular in cross-section, whitish-brown proximally, black or brown distally, with tomentose margins; rachillae 33, glabrous or scarcely tomentose initially; proximal rachillae 8.5 cm long, 1.0(0.7–1.2) mm wide; stamens 6; **fruits** 13.8(12.7–14.5) mm long, 11.3(9.1–13.8) mm wide, the surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers; fruiting corollas less than one quarter as long as fruits, splitting irregularly into 3 lobes, the lobes often splitting again; endocarps globose to obovoid with rounded or slightly peaked apices, the pores lateral.

Distribution and habitat:—From 9°34'–10°02'N and 82°36'–83°26'W on the Caribbean coast of Costa Rica at 128(1–400) m elevation in lowland rainforest (Fig. 5).

Taxonomic notes:—*Desmoncus costaricensis* is characterized by its leaves with few spines and large pinnae. See Grayum (1998) for a discussion of the nomenclature of this species.

Subspecific variation:—One specimen (*Mora 580*) is tentatively included here. It is from the same locality as other specimens of *Desmoncus costaricensis* but the leaf, possibly from a juvenile plant, is considerably smaller.

4. *Desmoncus giganteus* Henderson (1995: 225).

Type:—BRAZIL. Acre: Rio Moa near mouth of Rio Azul, 7°25'S, 73°15'W, 14 February 1992, *A. Henderson, F. Chávez & J. Guedes 1688* (holotype INPA!, isotypes K!, NY!).

Plants 22.3(4.5–50.0) m tall; stems 4.4(4.0–4.8) cm diameter, solitary. **Leaf** petioles 20.5(15.0–30.0) cm long; rachises 157.5(125.0–190.0) cm long, 12.2(10.1–14.2) mm wide, the spines usually >1 cm long, mostly adaxial or lateral, straight with briefly swollen bases; pinnae 10 per side of rachis, without long, filiform apices, with an adaxial beard of spines at the bases, without spinules or dense tomentum at the bases adaxially; basal pinna 39.2(32.0–46.5) cm long, 6.5(5.7–7.3) cm wide; cirri well-developed, with acanthophylls, without spines abaxially, with intermediate acanthophylls present, without a wide gap between pinnae and acanthophylls. **Inflorescences** with the rachis ridged, not twisted, much thicker than the numerous, closely spaced and spirally or irregularly arranged rachillae, each rachilla not or only briefly adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 8.5(6.5–11.7) mm wide; peduncular bracts length no data, broad, the surfaces ribbed, brown tomentose, densely covered with long, straight or sinuous, briefly swollen-based, diagonally or vertically oriented spines, these flattened or triangular in cross-section, whitish-brown proximally, black or brown distally, with tomentose margins; rachillae number no data, glabrous or scarcely tomentose initially; proximal rachillae 16.0 cm long, 1.7 mm wide; stamens number no data; **fruits** 36.2(21.5–42.6) mm long, 16.6(12.7–18.3) mm wide, the surfaces smooth, without any apparent subepidermal fibers; fruiting corollas to half as long as fruits, splitting irregularly into 3 lobes, the lobes often splitting again; endocarps ovoid to obovoid with prominent, peaked apices, the pores lateral.

Distribution and habitat:—From 0°32'–7°25'S and 70°10'–78°15'W in the western Amazon region in Colombia, Ecuador, Peru, and Brazil at 266(150–440) m elevation in lowland rainforest or secondary forest (Fig. 5).

Taxonomic notes:—*Desmoncus giganteus* is characterized by its large size and unusually large fruits with long fruiting corollas. It is the only species of *Desmoncus* always reported to have solitary stems; all other species have clustered or rarely solitary stems. It is probably more common than the few specimens suggest.

Moreno Suárez and Moreno Suárez (2006) consider that this species occurs in Bolivia. However, the description and illustrations they give of the fruits do not match those of *D. giganteus*, and appear more like those of the *large* morphotype of *D. polyacanthos*.

5. *Desmoncus horridus* Splitg. ex Martius (1844: 51).

Atitara horrida (Splitg. ex Martius) Kuntze (1891: 727). Type:—SURINAME. Paramaribo, no date, *F. Splitgerber 61* (holotype BR, *n.v.,* holotype image!).

Plants 6.7(2.0–15.0) m tall; stems 2.4(1.2–4.8) cm diameter, clustered. **Leaf** petioles 4.6(2.0–11.5) cm long; rachises 123.8(32.0–220.0) cm long, 9.5(3.4–20.5) mm wide, the spines usually >1 cm long, mostly adaxial or lateral, straight with briefly swollen bases; pinnae 19(7–28) per side of rachis, without a beard of spines at the bases, without spinules or dense tomentum at the bases adaxially; basal pinna 21.6(12.0–34.0) cm long, 1.9(1.3–3.7) cm wide; cirri well-developed, with acanthophylls, without spines abaxially, with intermediate acanthophylls present, without a wide gap between pinnae and acanthophylls. **Inflorescences** with the rachis ridged, not twisted, much thicker than the numerous, closely spaced and spirally or irregularly arranged rachillae, each rachilla not or only briefly adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 6.4(2.3–13.1) mm wide; peduncular bracts 28.3(10.5–47.0) cm long, broad, the surfaces ribbed, brown tomentose, sparsely to densely covered with long, straight or sinuous, briefly swollen-based, diagonally or vertically oriented spines, these flattened or triangular in cross-section, whitish-brown proximally, black or brown distally, with tomentose margins (rarely without spines); rachillae 19(7–33), brown tomentose initially; proximal rachillae 10.8(5.0–17.5) cm long, 1.3(0.7–1.9) mm wide; stamens 6–7; **fruits** 15.4(10.6–21.1) mm long, 9.5(7.4–12.4) mm wide, the surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers; fruiting corollas less than one quarter as long as fruits, not or scarcely splitting, tending to remain cupular; endocarps narrowly ellipsoid with rounded apices, the pores lateral.

Taxonomic notes:—Specimens included in this species were placed by both Wessels Boer (1965) and Henderson (1995) within a widespread *Desmoncus orthacanthos* Martius. This is a mistake, and the two species are quite distinct, especially in their fruits. The specimen from W illustrated in Dahlgren (1959, plate 186) is not the type of *D. horridus*, and is anyway now destroyed.

Subspecific variation:—There is geographic disjunction and specimens occur in five regions—a coastal region stretching from Tobago and Trinidad southeast through the Guianas to Brazil (Maranhão, Pará, Tocantins); an Orinoco region comprising the Orinoco river and its tributaries north and west of the Guayana Highland in Venezuela and reaching adjacent Colombia; an upper Rio Negro region, along the river and its main tributaries in Brazil and adjacent Venezuela and Colombia; a Pantanal region in Brazil and adjacent Bolivia; and a western Amazon region in Ecuador and Brazil (Acre). For most variables there are too few data to test for differences amongst these different regions. However, ANOVA shows that for pair wise comparison probabilities, seven variables (rachis length, basal pinna width, peduncular bract length, peduncle width, rachilla length, number of rachillae, fruit length) differ significantly (P <0.05) between at least one pair of regions, although no variable differs amongst all five regions. Based on these results, specimens from the five regions are recognized as subspecies (subspp. *apureanus, horridus, occidentalis, palustris, prostratus*).

Key to the subspecies of *Desmoncus horridus*

1 Fruits 17.7(15.5–21.1) mm long; upper Rio Negro region of Brazil, Colombia, and Venezuela and western Amazon region of Ecuador and Brazil (Acre).. 2
- Fruits 15.0(13.7–19.0) mm long; all other areas 3
2 Peduncles 3.2(2.3–4.8) mm wide; rachillae 11(7–17); upper Rio Negro region of Brazil, Colombia, and Venezuela.. .... subsp. *palustris*
- Peduncles 9.8(6.1–12.0) mm wide; rachillae 23(18–27); western Amazon region of Ecuador and Brazil (Acre) .... subsp. *occidentalis*
3 Rachillae 14(11–16); Pantanal region in Brazil and adjacent Bolivia .... subsp. *prostratus*
- Rachillae 21(10–33); all other areas 4
4 Peduncular bracts 19.5(10.5–27.0) cm long; Río Orinoco and its tributaries north and west of the Guayana Highland in Colombia and Venezuela .... subsp. *apureanus*
- Peduncular bracts 32.2(20.5–47.0) cm long; coastal regions from Tobago and Trinidad southeast through the Guianas to Brazil (Maranhão, Pará, Tocantins) .... subsp. *horridus*

5.1. ***Desmoncus horridus* subsp. *horridus***

Desmoncus hartii Bailey (1947: 369). Type:—TRINIDAD. Mayaro, March 1922, *L. Bailey 619a* (holotype BH!).
Desmoncus brittonii Bailey (1947: 371). Type:—TRINIDAD. Arena Road, 7 March 1946, *L. Bailey 172* (holotype BH!).
Desmoncus tobagonis Bailey (1947: 371). Type:—TOBAGO. Mile End, 22 February 1911, *W. Broadway 4077* (holotype NY!, isotypes BH!, K!).
Desmoncus demeraranus Bailey (1949: 181). Type:—GUYANA. River Demerara, near Craig village, between Georgetown and Atkinson Field, 20 February 1948, *L. Bailey 418* (holotype BH!).

Inflorescences peduncular bracts 32.2(20.5–47.0) cm long; rachillae 24(15–33); **fruits** 14.2(10.6–17.9) mm long.

Distribution and habitat:—From 11°15'N–3°48'S and 44°15'–62°22'W in Trinidad and Tobago, Venezuela (Delta Amacuro), Guyana, Surinam, French Guiana, and Brazil (Maranhão, Pará, Tocantins) at 23(0–50) m elevation, mostly in coastal areas in open places, often along river margins (Fig. 6).

5.2. ***Desmoncus horridus* subsp. *apureanus* (Bailey) Henderson, *comb. & stat. nov*.**

Basionym: *Desmoncus apureanus* Bailey (1949: 183). Type:—VENEZUELA. Apure: road to Churruscao, west of San Fernando de Apure, 15 April 1939, *C. Chardon s.n.* (holotype BH!).
Desmoncus velezii Bailey (1949: 186). Type:—VENEZUELA. Apure: Puerto Paez, 5 April 1946, *I. Velez 2308* (holotype US!, isotype BH!).
Desmoncus multijugus Steyermark (1951: 85). Type:—VENEZUELA. Bolívar: Tumeremo, 18 December 1944, *J. Steyermark 60968* (holotype F!).

Inflorescences peduncular bracts 19.5(10.5–27.0) cm long; rachillae 18(10–29); **fruits** 16.0(13.7–19.0) mm long.

Distribution and habitat:—From 5°24'–7°53'N and 61°00'–71°39'W in Venezuela (Apure, Barinas, Bolívar) and Colombia (Casanare, Vichada) at 107(30–305) m elevation, usually in riparian habitats especially gallery forest along the Río Orinoco and its tributaries or in shrubby savannas (Fig. 6).

5.3. ***Desmoncus horridus* subsp. *occidentalis* Henderson, *subsp. nov*.** (Appendix IV Plates 1–4)

A subspeciebus aliis fructibus maioribus, pedunculis longioribus atque rachillis magis numerosis differt.

Type:—ECUADOR. Napo: Lago Garza–Yagu on opposite side of Río Napo from Añangu, 0°32'S, 76°26'W, 300 m, 9 August 1985, *H. Balslev, A. Barfod, A. Henderson, F. Skov & A. Argüello 60752* (holotype NY!, isotypes AAU!, QCA *n.v.*).

Inflorescences peduncular bracts 30.5(22.0–38.0) cm long; rachillae 23(18–27); **fruits** 17.3(15.6–19.3) mm long.

Distribution and habitat:—From 0°02'N–7°45'S and 72°45'–76°26'W in the western Amazon region in Colombia, Ecuador, and Brazil (Acre) at 267(200–300) m elevation along river or lake margins in black or white water areas (Fig. 6).

Taxonomic notes:—A specimen (*Bernal 2033*) from Colombia (Putumayo), not included in the above description, has narrow, lanceolate pinnae and a densely spiny peduncular bract (like *D. polyacanthos*), and fruits with Y-shaped fibers. It is sympatric with subsp. *occidentalis* and *D. polyacanthos*, and may be a hybrid.

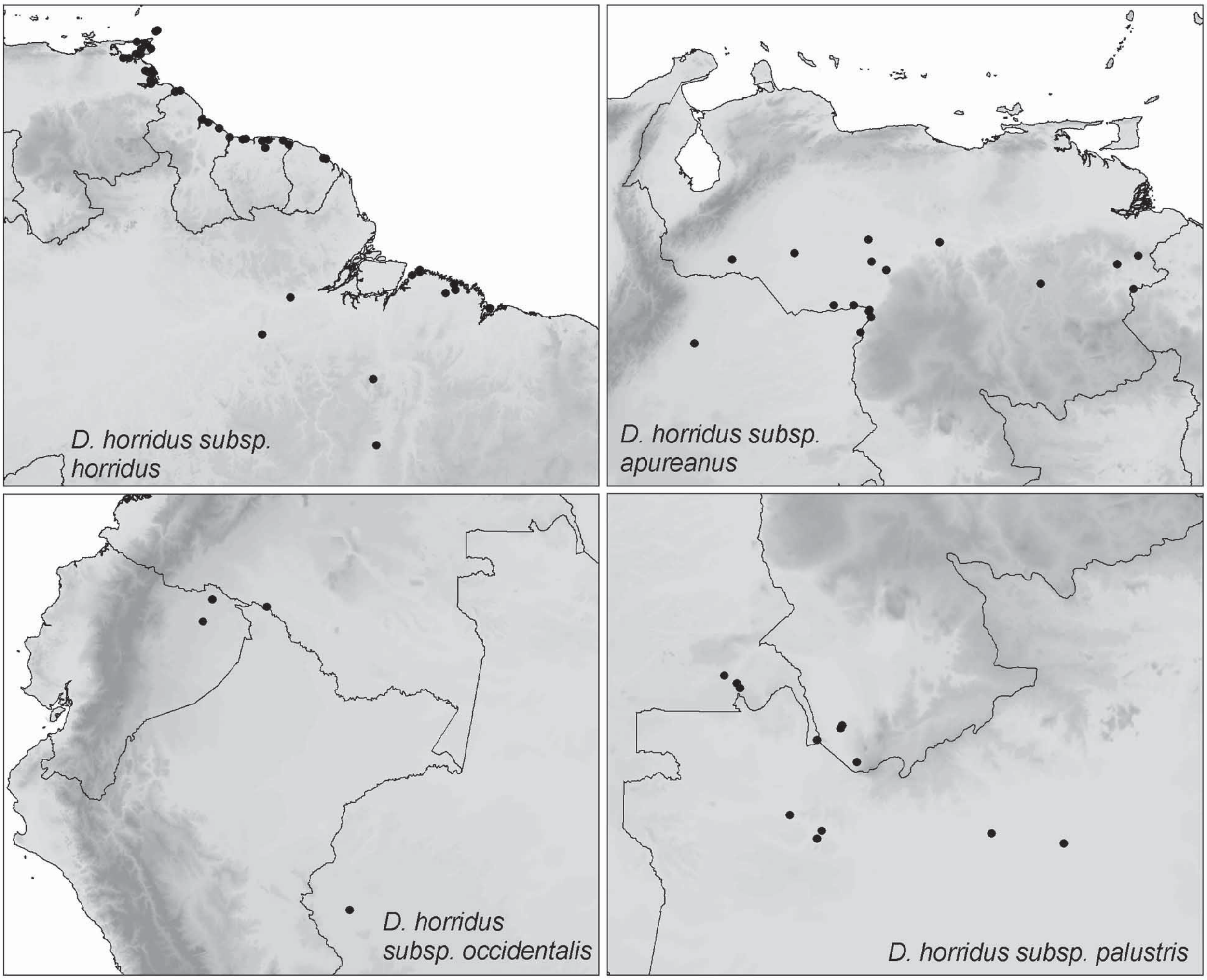

FIGURE 6. Distribution maps of *Desmoncus horridus* subsp. *horridus*, *D. horridus* subsp. *apureanus, D. horridus* subsp. *occidentalis*, and *D. horridus* subsp. *palustris*.

5.4. *Desmoncus horridus* subsp. *palustris* (Trail) Henderson, *comb. & stat. nov.*

Basionym: *Desmoncus palustris* Trail (1876: 353). *Atitara palustris* (Trail) Kuntze (1891: 727). Type:—BRAZIL. Amazonas: Rio Padauiri, 28 June 1874, *J. Trail 1087/LXXXI* (holotype K!, isotype BM!).

Inflorescences peduncular bracts 24.1(14.5–32.5) cm long; rachillae 11(7–17); **fruits** 18.1(15.7–21.1) mm long.

Distribution and habitat:—From 2°19'N–0°25'S and 62°55'–68°25'W in Colombia (Guainía), Brazil (Amazonas), and Venezuela (Amazonas) at 107(80–140) m elevation, along margins of the upper Rio Negro and its blackwater tributaries, growing in water at least part of the year (Fig. 6).

Subspecific variation:—Rachis spines are less developed in subsp. *palustris* than in other subspecies, and in some cases are abaxial and appear short and recurved, almost like those of *Desmoncus polyacanthos*. See also notes under *D. interjectus*.

Although *Desmoncus riparius* is an older name than *Desmoncus palustris*, its type specimen ((*Desmoncus riparius* Spruce (1869: 156). *Atitara riparia* (Spruce) Kuntz (1891: 727). Type:—VENEZUELA. Amazonas: Río Negro, San Carlos de Río Negro, October 1854, *R. Spruce 46* (holotype K!)) may be of hybrid origin. A group of specimens (*Clark 7982, Liesner 8940, Spruce 46*, type of *D. riparius*) from Venezuela (Amazonas), not included in the above description, appear intermediate between subsp. *palustris* and *D. polyacanthos*, both of which occur in this area. These intermediates resemble *D. polyacanthos* but have scarcely spiny peduncular bracts and fruit surfaces with Y-shaped fibers. Another specimen (*Liesner 6274*) is from the same locality but much smaller and with a non-spiny sheath.

5.5. *Desmoncus horridus* subsp. *prostratus* (Lindman) Henderson, *comb. & stat. nov.*

Basionym: *Desmoncus prostratus* Lindman (1900: 8). *Atitara prostrata* (Lindman) Barbosa Rodrigues 1902: 75. Type:—BRAZIL. Mato Grosso: Santa Cruz da Barra, June 1894, *C. Lindman 2827* (holotype S!).

Inflorescences peduncular bracts no data; rachillae 14(11–16); **fruits** 14.7(14.6–14.7) mm long.

Distribution and habitat:—From 14°45’–15°20’S and 57°11’–62°20’W in Bolivia (Santa Cruz) and Brazil (Mato Grosso) at 178(150–250) m elevation, mostly in the Pantanal region in gallery forest, forest patches in savanna, shrubby forest, or semideciduous forest, often in flooded areas (Fig. 7).

Two specimens, not included in the above description, are unusual and may be hybrids. One (*Krapovickas 31940*) appears intermediate between subsp. *prostratus* and possibly *D. polyacanthos*. The second (*Cid 4636*) is from the north of the main range of subsp. *prostratus* and is reported to come from “campo natural cerrado”.

6. *Desmoncus interjectus* Henderson, *sp. nov.* (Appendix IV Plate 5)

A speciebus aliis spinis secus costis bracteae peduncularis praedita differt.

Type:—COLOMBIA. Amazonas: Río Yarí, cerca a la desembocadura de la quebrada El Mochilero, 120–200 m, 21 April 1986, *G. Galeano, J. Torres, J. Huitoto & B. Plazas 1092* (holotype COL!, isotype NY!).

Plants 6 m tall; stems 2.1(1.7–2.8) cm diameter. **Leaf** petioles 2.9(1.0–10.5) cm long; rachises 125.0 cm long, 8.2(6.2–11.0) mm wide, the spines usually <1 cm long, mostly abaxial, recurved with markedly swollen bases; pinnae 10(9–11) per side of rachis, without a beard of spines at the bases, without spinules or dense tomentum at the bases adaxially; basal pinna 23.3(17.0–28.5) cm long, 2.1(1.0–3.0) cm wide; cirri well-developed, with acanthophylls, with few spines abaxially, mostly on proximal part only, with no intermediate acanthophylls present, usually with a wide gap between pinnae and acanthophylls. **Inflorescences** with the rachis angular, slightly twisted, thicker than the few to numerous, closely spaced and spirally arranged rachillae, each rachilla not (or very rarely) adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 4.1(2.6–4.8) mm wide; peduncular bracts 28.7(19.0–46.0) cm long, broad, the surfaces deeply ridged, dark brown tomentose, sparsely covered with long, straight or sinuous spines, the bases scarcely swollen but running directly into the ridges of the bract and lying flat against the bract surface, flattened in cross-section, brown proximally and distally, with tomentose margins; rachillae 16(13–18); proximal rachillae 8.5(7.0–11.5) cm long, 1.8(1.2–2.2) mm wide; stamens 8; **fruits** 14.2(13.5–15.1) mm long, 10.7(9.8–12.3) mm wide, the surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers; fruiting corollas less than one quarter as long as fruits, not or scarcely splitting, tending to remain cupular; endocarps narrowly ellipsoid with rounded apices, the pores lateral.

Distribution and habitat:—From 0°00’–0°37’S and 70°11–72°26’W in Colombia (Amazonas, Vaupés) at 194(160–250) m elevation along margins of blackwater streams (Fig. 7).

Taxonomic notes:—Except for its short, recurved, swollen-based rachis spines and peduncular bracts, *D. interjectus* strongly resembles *D. horridus* subsp. *palustris*. This subspecies, as noted above, has rachis spines which are less developed than in other subspecies, and in some cases are abaxial and appear short and recurved, almost like those of *D. polyacanthos*. In fact, *D. interjectus* appears more similar to *D. horridus* than to other species with recurved rachis spines, and its recurved rachis spines may be secondarily derived from straight spines.

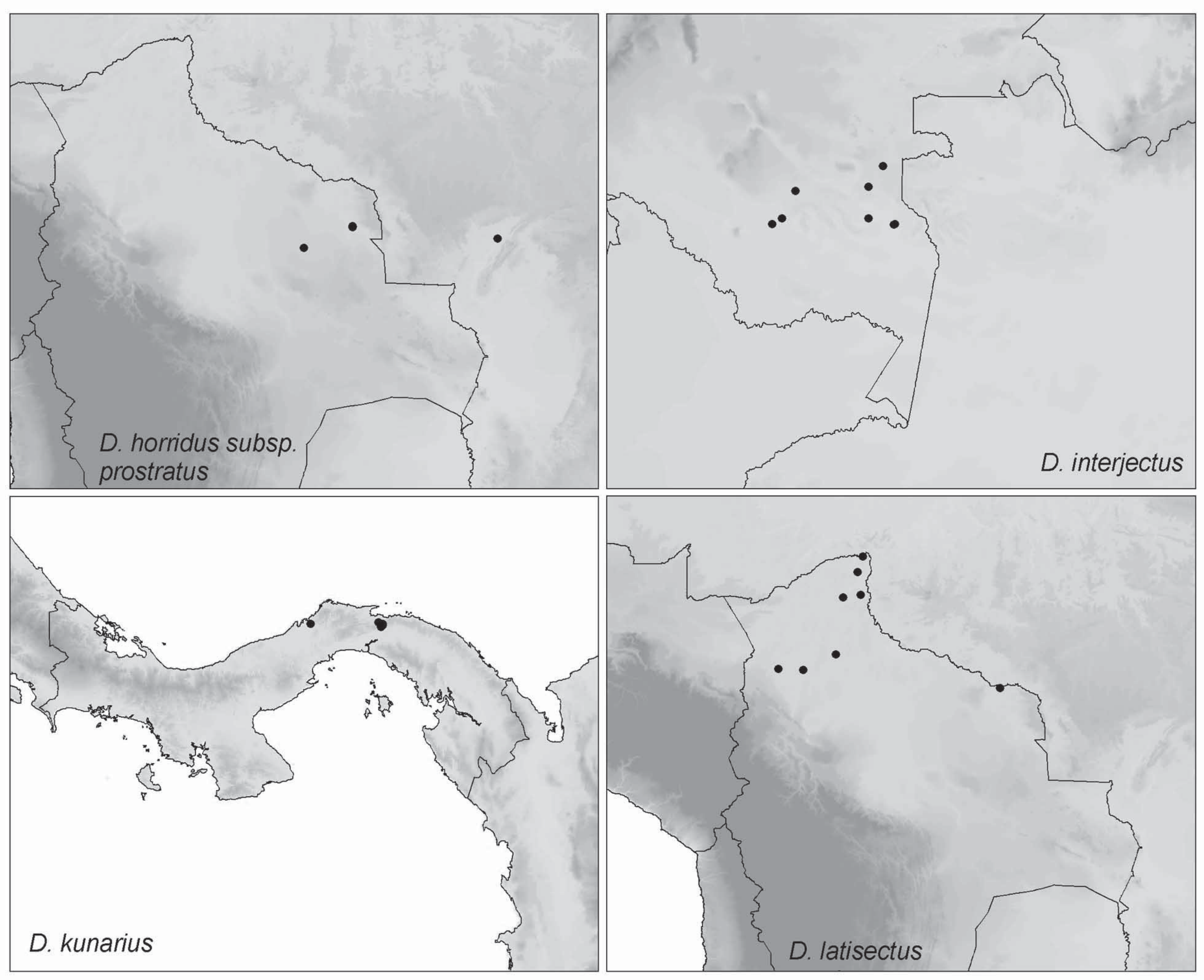

FIGURE 7. Distribution maps of *Desmoncus horridus subsp. prostratus*, *D. interjectus, D. kunarius*, and *D. latisectus*

7. *Desmoncus kunarius* de Nevers ex Henderson, *sp. nov.* (Appendix IV Plates 6–12)

A speciebus aliis crusta fructuum fibris subepidemalibus numerosis, brevibus atque obliquis tuberculata differt.
Type:—PANAMA. Panama: El Llano–Cartí road, 16–18½ km by road N of Pan. Am. Hwy. at El Llano, 400–450 m, 28 March 1974, *M. Nee & E. Tyson 10982* (holotype PMA!, isotype MO!).

Plants height no data; stems 3.3(3.1–3.6) cm diameter. **Leaf** petioles 4.5(3.0–5.5) cm long; rachises 100.0 cm long, 14.2(11.6–18.5) mm wide, the spines usually >1 cm long, mostly adaxial or lateral, straight with briefly swollen bases; pinnae 19 per side of rachis, without long, filiform apices, with an adaxial beard of spines at the bases, without spinules or dense tomentum at the bases adaxially; basal pinna 29.5 cm long, 4 cm wide;

cirri well-developed, with acanthophylls, without spines abaxially, with intermediate acanthophylls present (i.e., distalmost pair of pinnae reflexed as acanthophylls and with swollen bases and/or proximalmost acanthophylls like vestigial pinnae), without a wide gap between pinnae and acanthophylls. **Inflorescences** with the rachis ridged, not twisted, much thicker than the numerous, closely spaced and spirally or irregularly arranged rachillae, each rachilla not or only briefly adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 8.8(7.8–10.6) mm wide; peduncular bracts 48.5 cm long, broad, the surfaces ribbed, brown tomentose, densely covered with long, straight or sinuous, briefly swollen-based, diagonally or vertically oriented spines, these flattened or triangular in cross-section, whitish-brown proximally, black or brown distally, with tomentose margins; rachillae 21(20–22), glabrous or scarcely tomentose initially; proximal rachillae 18.5(17.5–19.5) cm long, 2.5(2.1–2.9) mm wide; stamens 12; **fruits** 25.1(23.9–27.4) mm long, 21.7(20.1–24.1) mm wide, the surfaces bumpy from numerous, subepidermal, short, oblique fibers; fruiting corollas less than one quarter as long as fruits, splitting irregularly into 3 lobes, the lobes often splitting again; endocarps obovoid with rounded apices, the pores lateral.

Distribution and habitat:—From 9°17'–9°21'N and 78°55'–79°47'W in central Panama at 270(150–425) m elevation in lowland rainforest (Fig. 7).

Taxonomic notes:—*Desmoncus kunarius* is characterized by its large size and unusually large fruits.

8. *Desmoncus latisectus* Burret (1934: 215).

Lectotype (here designated):—BOLIVIA. Beni: Trinidad, Missiones Guarayos, 300 m, September 1926, *E. Werdermann 2508* (S!, isolectotype MO!; the holotype in B was destroyed).

Desmoncus kuhlmannii Burret (1938: 267). Lectotype (here designated):—BOLIVIA. Beni: Riberalta, 28 November 1923, *J. Kuhlmann 522* (R!; the holotype of B was destroyed).

Plants 2.8(2.0–4.0) m tall; stems 0.9(0.5–1.4) cm diameter. **Leaf** petioles 2.0(1.0–3.0) cm long; rachises 34.1(29.0–40.0) cm long, 3.1(2.2–3.8) mm wide, the spines usually <1 cm long, mostly abaxial, recurved with markedly swollen bases; pinnae 6(5–8) per side of rachis, without long, filiform apices, without a beard of spines at the bases, without spinules or dense tomentum at the bases adaxially; basal pinna 11.2(7.9–14.5) cm long, 1.6(1.2–2.0) cm wide; cirri well-developed, with acanthophylls, with spines abaxially mostly on proximal part only, with no intermediate acanthophylls present, with a wide gap between pinnae and acanthophylls (i.e., gap wider than that between adjacent acanthophylls). **Inflorescences** with the rachis angular, slightly twisted, thicker than the few, closely spaced and spirally arranged rachillae, each rachilla not adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 2.4(1.1–3.2) mm wide; peduncular bracts 23.9(21.7–26.0) cm long, peduncular bracts broad, the surfaces ribbed or ridged, brown tomentose or glabrous, sparsely to moderately covered with short, straight or sinuous, briefly swollen-based, diagonally or vertically oriented spines, these flattened or triangular in cross-section, whitish-brown proximally, black or brown distally, with tomentose margins; rachillae 9(5–11), glabrous or scarcely tomentose initially; proximal rachillae 5.3(3.7–6.1) cm long, 0.8(0.7–1.0) mm wide; stamens no data; **fruits** 11.3 mm long, 9.0 mm wide, the surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers; fruiting corollas less than one quarter as long as fruits, splitting irregularly into 3 lobes, the lobes often splitting again; endocarps globose to obovoid with rounded or slightly peaked apices, the pores lateral.

Distribution and habitat:—From 9°48'–13°36'S and 61°33'–67°58'W in eastern Bolivia at 173(150–200) m elevation in forest margins, forest patches in savannas, or near rocky river margins (Fig. 7).

Taxonomic notes:—Only one specimen of *Desmoncus latisectus* has fruits (*Moreno 19*). These are scored as having uneven surfaces with numerous, subepidermal, short, often branching (Y-shaped) fibers, although these are obscure and not easily seen. *Desmoncus latisectus* is very similar to *D. leptoclonos*, and without fruits the two are difficult to distinguish. There are several quantitative differences between them (*D.*

latisectus has narrower stems, shorter petioles, narrower rachises, fewer divisions, narrower basal pinnae), and their habitat also appears different. *Desmoncus latisectus* grows mostly at lower elevations in northeastern Bolivia in savanna-forest margins, whereas *D. leptoclonos* grows at higher elevations in gallery forest in the Cerrado in Brazil and Paraguay.

9. *Desmoncus leptoclonos* Drude (1881: 315).

Atitara leptoclona (Drude) Barbosa Rodrigues, 1902: 76. Type:—BRAZIL. Goiás: between Goiás and Cuiabá, November–December 1844, *H. Weddell 2900* (holotype P!).

Plants 4.6(1.0–10.0) m tall; stems 1.3(0.9–1.9) cm diameter, clustered. **Leaf** petioles 3.4(1.0–6.0) cm long; rachises 47.9(17.0–77.0) cm long, 5.7(4.2–7.5) mm wide, the spines usually <1 cm long, mostly abaxial, recurved with markedly swollen bases; pinnae 9(7–13) per side of rachis, without long, filiform apices, without a beard of spines at the bases, without spinules or dense tomentum at the bases adaxially; basal pinna 14.0(5.5–24.0) cm long, 2.3(1.4–3.0) cm wide; cirri well-developed, with acanthophylls, with few spines abaxially, mostly on proximal part only, with no intermediate acanthophylls present, usually with a wide gap between pinnae and acanthophylls (i.e., gap wider than that between adjacent acanthophylls). **Inflorescences** with the rachis angular, slightly twisted, thicker than the few, closely spaced and spirally arranged rachillae, each rachilla not or rarely adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 2.4(1.0–5.4) mm wide; peduncular bracts 26.3(20.5–33.0) cm long, broad, the surfaces ribbed or ridged, brown tomentose or glabrous, sparsely to moderately covered with short, straight or sinuous, briefly swollen-based, diagonally or vertically oriented spines, these flattened or triangular in cross-section, whitish-brown proximally, black or brown distally, with tomentose margins; rachillae 11(10–16), glabrous or scarcely tomentose initially; proximal rachillae 6.0(3.5–10.5) cm long, 0.9(0.6–1.2) mm wide; stamens 6; **fruits** 12.3(10.9–13.9) mm long, 8.0(7.0–9.4) mm wide, the surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers; fruiting corollas less than one quarter as long as fruits, splitting irregularly into 3 lobes, the lobes often splitting again; endocarps narrowly ellipsoid with rounded apices, the pores lateral.

Distribution and habitat:—From 12°49'–23°20'S and 48°03'–58°27'W in the Cerrado region of Brazil (Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Rondônia) and just reaching Paraguay (San Pedro) at 516(310–900) m elevation in wet areas in gallery forest, cerrado steeps, or brejo vegetation (Fig. 8).

Taxonomic notes:—A rather variable and heterogeneous species. Peduncular bracts are particularly difficult to score in this species, and subepidermal fibers are difficult to see in fruiting specimens.

Subspecific variation:—Some specimens (e.g., *Coradin 7331, Lindman 3273, Macedo 705, Pereira-Silva 4766, 4648*) have slender inflorescences in which there is some adnation of the rachillae, and they occur at lower elevations. However, these specimens do not have a discrete range and are mixed with others. Other specimens (*Archer 75, Ferreira 518, Hassler 11293, Mendes 251, Schinini 29368*) have larger leaves and inflorescences. They come from the western margins of the range, near the Pantanal, where *D. horridus* subsp. *prostratus* occurs. There seems a possibility that there are either two different taxa here, or hybrids with other species, or both, but many more specimens are needed to decide the matter.

10. *Desmoncus loretanus* Henderson, *sp. nov.* (Appendix IV Plates 13–14)

A speciebus aliis bractea pedunculari lata, brunnea, costas prominentibus coloris levioris pluribus praedita, parum tomentosa vel haud tomentosa, spinis carens (vel rarior spinis paucis) differt.

Type:—PERU. Loreto: Maynas Province, near mouth of Río Tamshiyacu, E of Tamshiyacu, 130 m, 18 March 1979, *A. Gentry, C. Diaz, J. Aronson & N. Jaramillo 25785* (holotype NY!, isotype MO!).

Plants height no data; stems 1.2(0.7–1.6) cm diameter. **Leaf** petioles 1.5(0.7–2.2) cm long; rachises 39.7(33.5–46.5) cm long, 4.2(3.3–5.7) mm wide, the spines usually <1 cm long, mostly abaxial, recurved with markedly swollen bases; pinnae 6(6–7) per side of rachis, without long, filiform apices, without a beard of spines at the bases, without spinules or dense tomentum at the bases adaxially; basal pinna 11.4(3.0–15.5) cm long, 2.6(1.0–3.5) cm wide; cirri well-developed, with acanthophylls, with spines abaxially mostly on proximal part only, with no intermediate acanthophylls present, with a wide gap between pinnae and acanthophylls(i.e., gap wider than that between adjacent acanthophylls). **Inflorescences** with the rachis angular, slightly twisted, thicker than the few to numerous, closely spaced and spirally arranged rachillae, each rachilla not (or very rarely) adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 2.1(1.0–2.6) mm wide; peduncular bracts 15.8(12.0–24.5) cm long, broad, ribbed with several more prominent, lighter colored ribs, brown, scarcely or not tomentose, without spines (rarely with a few spines); rachillae 9(6–12), glabrous or scarcely tomentose initially; proximal rachillae 4.5(2.5–6.5) cm long, 0.9(0.8–1.2) mm wide; stamens 7; **fruits** 13.0(10.5–15.9) mm long, 8.0(7.0–9.6) mm wide, the surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers; fruiting corollas less than one quarter as long as fruits, splitting irregularly into 3 lobes, the lobes often splitting again; endocarps narrowly ellipsoid with rounded apices, the pores lateral.

Distribution and habitat:—From 3°27'–5°12'S and 72°50'–73°58'W in Amazonian Peru (Loreto) at 112(90–130) m elevation in seasonally flooded tahuampa forest (Fig. 8).

Taxonomic notes:—It differs from *Desmoncus madrensis* in its ribbed, scarcely tomentose, non-spiny peduncular bracts and from *D. polyacanthos* in its fruit surfaces with Y-shaped fibers.

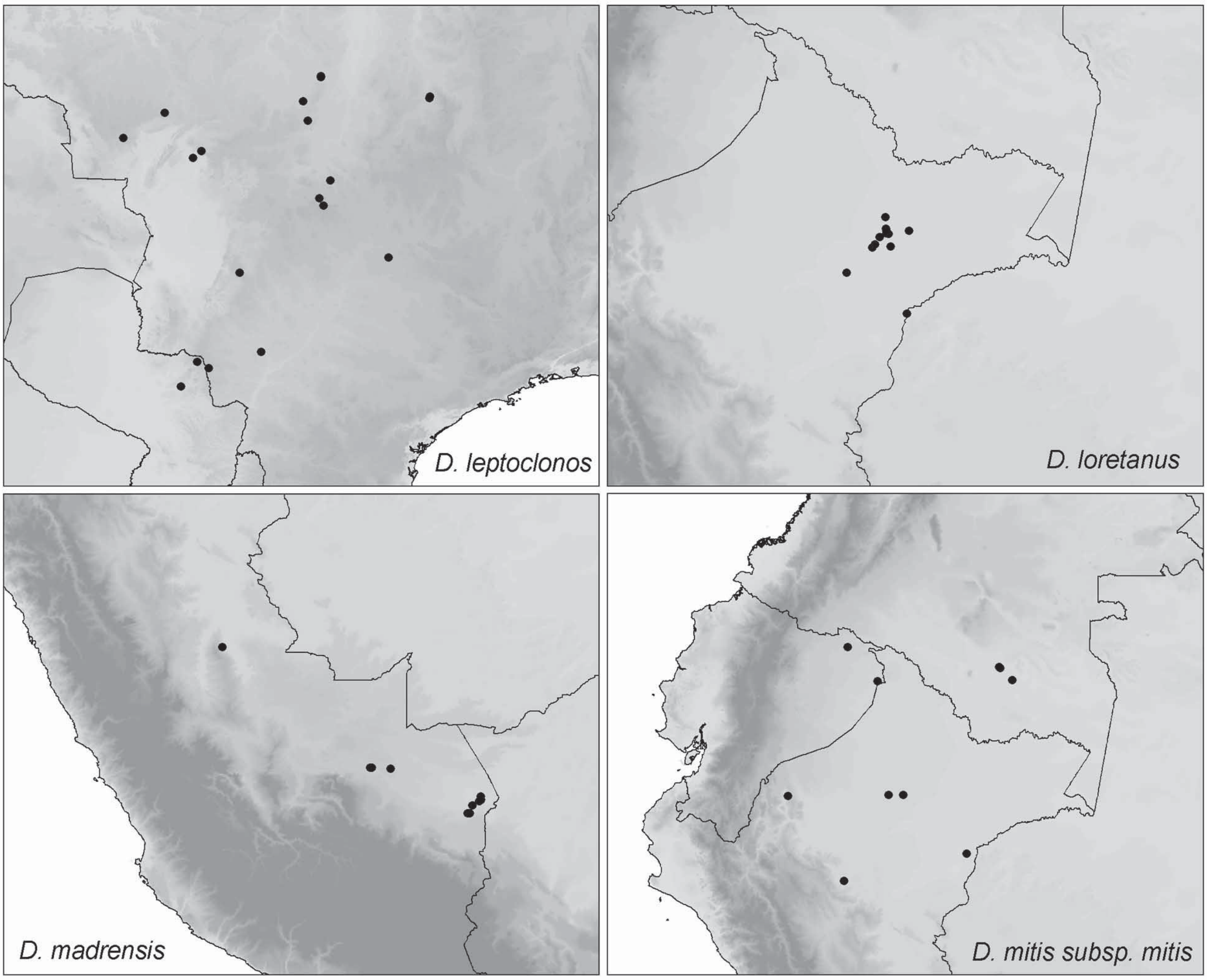

FIGURE 8. Distribution maps of *Desmoncus leptoclonos*, *D. loretanus, D. madrensis*, and *D. mitis* subsp. *mitis*.

11. *Desmoncus madrensis* Henderson, *sp. nov.* (Appendix IV Plate 15)

A Desmonco loretano bractea pedunculari spinescenti differt; a D. polyacanthos fructuum crusta fibris Y-formis differt.
Type:—PERU. Madre de Dios: Manu, Pakitza, Parque Nacional de Manu, trocha Pacal, 11˚53'S, 70˚58'W, 400 m, 24 February 1990, *F. Chávez 626* (holotype NY!, isotypes CUZ *n.v.,* USM *n.v.*).

Plants 4.0(2.5–6.5) m tall; stems 0.7(0.5–0.9) cm diameter. **Leaf** petioles 5.9(2.5–9.0) cm long; rachises 28.7(19.5–35.0) cm long, 2.1(1.5–2.8) mm wide, the spines usually <1 cm long, mostly abaxial, recurved with markedly swollen bases; pinnae 5(4–6) per side of rachis, without long, filiform apices, without a beard of spines at the bases, with uneven surfaces at the bases adaxially, usually covered with spinules and/or dense tomentum; basal pinna 12.0(8.8–21.0) cm long, 2.5(1.6–4.5) cm wide; cirri well-developed, with acanthophylls, with few spines abaxially, mostly on proximal part only, with no intermediate acanthophylls present, usually with a wide gap between pinnae(i.e., gap wider than that between adjacent acanthophylls). **Inflorescences** with the rachis angular, slightly twisted, thicker than the few to numerous, closely spaced and spirally arranged rachillae, each rachilla not (or very rarely) adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 2.2(1.6–2.9) mm wide; peduncular bracts 22.3(18.0–26.5) cm long, broad, the surfaces ridged, brown tomentose, sparsely to densely covered with short, recurved, markedly swollen-based, diagonally oriented spines, these triangular in cross-section, whitish-brown proximally, brown distally, with tomentose margins; rachillae 14(10–17), glabrous or scarcely tomentose initially; proximal rachillae 5.6(2.3–15.0) cm long, 1.1(1.0–1.2) mm wide; stamens no data; **fruits** 10.4(9.3–11.4) mm long, 6.8(6.1–7.2) mm wide, the surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers; fruiting corollas less than one quarter as long as fruits, splitting irregularly into 3 lobes, the lobes often splitting again; endocarps narrowly ellipsoid with rounded apices, the pores lateral.

Distribution and habitat:—From 9°18'–12°50'S and 69°03'–74°32'W in the western Amazon region in Peru (Madre de Dios, with an outlying specimen in Ucayali) at 273(184–400) m elevation in lowland rainforest (Fig. 8).

Taxonomic notes:—*Desmoncus madrensis* differs from *D. loretanus* in its spiny peduncular bracts and from *D. polyacanthos* in its fruit surfaces with Y-shaped fibers.

Subspecific variation:—The outlying specimen in Ucayali may be an artifact of insufficient collecting.

12. *Desmoncus mitis* Martius (1823–1837: 90).

Atitara mitis (Martius) Kuntze (1891: 727). Lectotype (here designated):—BRAZIL. Amazonas: Rio Negro, no date, *C. Martius s. n.* (M!).

Plants 2.7(0.7–8.5) m tall; stems 0.6(0.3–1.1) cm diameter. **Leaf** petioles 3.9(0.5–10.5) cm long; rachises 30.4(8.0–76.0) cm long, 2.3(1.1–3.8) mm wide, the spines usually <1 cm long, mostly abaxial, recurved with markedly swollen bases; pinnae 8(2–25) per side of rachis, without a beard of spines at the bases, with uneven surfaces at the bases adaxially, usually covered with spinules and/or dense tomentum; basal pinna 12.3(3.5–27.5) cm long, 2.5(0.2–6.5) cm wide; cirri well-developed, with acanthophylls, or cirri poorly-developed, the rachis terminating in a short cirrus, acanthophylls present or absent, or cirri absent, the rachis terminating beyond the distalmost pair of pinnae in a short 'stub', with few spines abaxially, mostly on proximal part only (rarely, when cirri poorly-developed, without spines), with no intermediate acanthophylls present, usually with a wide gap between pinnae and acanthophylls (i.e., gap wider than that between adjacent acanthophylls). **Inflorescences** with the rachis smooth, not twisted, narrower than the few, distantly spaced and alternate rachillae, each rachilla usually briefly adnate proximally to the rachis and with an irregular bracteole displaced onto the rachis, with or without an axillary pulvinus; peduncles 1.2(0.6–3.1) mm wide; peduncular bracts 24.2(14.6–37.0) cm long, narrow, elongate, ribbed, scarcely brown tomentose, without spines (rarely with few spines); rachillae 5(3–7), glabrous or scarcely tomentose initially; proximal rachillae 5.3(2.0–9.0) cm long, 0.8(0.5–1.5) mm wide; stamens 6; **fruits** 10.9(8.9–15.7) mm long, 7.1(5.5–10.9) mm wide, fruit surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers; fruiting corollas splitting irregularly into 3 lobes, the lobes often splitting again; endocarps narrowly ellipsoid with rounded apices, the pores lateral.

Subspecific variation:—Specimens occur in the western and central Amazon region in Colombia, Ecuador, Peru, Bolivia, and Brazil. Based on geography, as well as sheaths, number of pinnae, and cirri development, it is possible to recognize four subgroups—one from subAndean regions of southern Peru and Bolivia having finely and densely spiny sheaths, numerous, linear or lanceolate pinnae, and well-developed cirri; the second from the western Amazon region, mostly from the southwestern Amazon region of Brazil but also in adjacent Peru and Bolivia having non- or scarcely spiny sheaths, few, ovate pinnae, and poorly-developed cirri; the third from the western Amazon region of Peru and in adjacent Colombia and Brazil having non-spiny sheaths, few, ovate pinnae, and usually well-developed cirri; and the fourth from the western Amazon region in Colombia, Ecuador, and Peru, having non-spiny sheaths, numerous, lanceolate pinnae, and well-developed cirri. ANOVA shows that for pair wise comparison probabilities, six variables (plant height, petiole length, rachis length, rachis width, basal pinna length, basal pinna width) differ significantly (P <0.05) between at least one pair of subgroups, and one variable (number of pinnae) differs amongst all four subgroups. Based on these results, specimens from the four subgroups are recognized as subspecies (subspp. *ecirratus, leptospadix, mitis, rurrenabaquensis*).

Key to the subspecies of *D. mitis*

1 Pinnae linear or lanceolate, 17(12–25) per side of rachis 2
- Pinnae ovate, 5(2–11) per side of rachis 3
2 Sheaths densely and finely spiny; subAndean areas of southwestern Amazon region of Peru (Cuzco, Madre de Dios, Puno) and Bolivia (Beni, Cochabamba, La Paz, Santa Cruz) .... subsp. *rurrenabaquensis*
- Sheaths non-spiny, rarely sparsely spiny; western Amazon region in Colombia (Amazonas, Caquetá), Ecuador (Napo), and Peru (Amazonas, Loreto) .... subsp. *mitis*
3 Rachises 34.9(17.2–76.0) cm long; pinnae 6(3–11) per side of rachis; cirri usually well-developed; western Amazon region in Colombia (Amazonas), Peru (Amazonas, Cuzco, Huánuco, Loreto, Ucayali), and Brazil (Acre, Amazonas) .... subsp. *leptospadix*
- Rachises 20.9(8.0–41.0) cm long; pinnae 3(2–5) per side of rachis; cirri usually absent, the rachis terminating beyond the distalmost pair of pinnae in a short 'stub'; south–central Amazon region of Peru (Ucayali), Brazil (Acre, Amazonas, Mato Grosso, Rondônia) and Bolivia (Beni, Pando) with an outlier in Peru (Loreto) subsp. *ecirratus*

12.1. *Desmoncus mitis* subsp. *mitis*

Leaf sheaths non-spiny, rarely sparsely spiny; rachises 38.0(30.0–50.0) cm long; pinnae linear or lanceolate, 15(12–25) per side of rachis; cirri well-developed.

Distribution and habitat:—From 0°05'–5°59'S and 72°00'–77°40'W in the western Amazon region in Colombia (Amazonas, Caquetá), Ecuador (Napo), Peru (Amazonas, Loreto) at 204(145–300) m elevation in lowland rainforest in non-flooded areas (Fig. 8). It also probably occurs in the western Amazon region of Brazil (Amazonas)(see below).

Taxonomic notes:—Henderson (1995) recognized this taxon as *Desmoncus mitis* Martius var. *mitis*, and included *D. pumilus* Trail and *D. setosus* var. *mitescens* Drude as synonyms. *Desmoncus pumilus* Trail is here treated as a distinct species, and *D. setosus* var. *mitescens* Drude as an Excluded Name. The type of *D. mitis* was given by Henderson (1995) as *Martius s. n.*, and this specimen is extant at M and is here lectotypified. However, there is some doubt concerning the type locality. It is given on the label as "Provinciae flum. Nigri" and in Martius (1823–1837) as "fluvii Solimoës", presumably in Brazil (Amazonas). All the specimens cited here come from further west than the most westward point of Martius' journey in modern-day Colombia, with the exception of *Aguirre-Galviz 1152* from Colombia (Amazonas).

12.2. *Desmoncus mitis* subsp. *ecirratus* Henderson, *subsp. nov.* (Appendix IV Plate 16)

A subspeciebus aliis pinnis paucis ovatis atque cirro normaliter absenti differt.

Type:—BRAZIL. Rondônia: road to casserite mine, north bank of Rio Madeira in Serra dos Tres Irmãos 8 km above Mutumparaná, 5 July 1968, *G. Prance, E. Forero, L. Coêlho, J. Ramos & L. Farias 5636* (holotype INPA!, isotype NY!).

Leaf sheaths non-spiny, rarely sparsely spiny; rachises 20.9(8.0–41.0) cm long; pinnae ovate, 3(2–5) per side of rachis; cirri usually absent, the rachis terminating beyond the distalmost pair of pinnae in a short 'stub'.

Distribution and habitat:—From 3°30'–10°58'S and 56°00'–73°14'W in the south–central Amazon region of Peru (Ucayali), Brazil (Acre, Amazonas, Mato Grosso, Rondônia) and Bolivia (Beni, Pando) with an outlier in Peru (Loreto) at 177(120–300) m elevation in lowland rainforest (Fig. 9).

Taxonomic notes:—This taxon was mistakenly referred to by Henderson (1995) as *Desmoncus mitis* var. *leptoclonos*, based on *D. leptoclonos* Dammer. However, this name is pre-occupied by *D. leptoclonos* Drude.

Subspecific variation:—The outlying specimen (*Asplund 14687*) from Loreto, Peru, has much wider pinnae than other specimens. Some specimens are described on labels as being non–climbers. On some specimens (e.g., *Moreno 163, Schunke 15033, Nee 34990, Forero 6384*) there are some leaves with weakly developed cirri as well as leaves with the more usual poorly-developed cirri; on a few other specimens there are weakly developed cirri. Specimens from the eastern part of the range, from eastern Acre, Rondônia, Mato Grosso, and adjacent Bolivia usually have 2 pinnae per side of the shorter rachis, and these have very few spinules at the bases. Specimens from the western part of the range, from western Acre and adjacent Peru tend to have 3 pinnae per side of the longer rachis, and usually have spinulose pinnae bases. These specimens overlap with those of *D. mitis* subsp. *leptospadix*.

12.3. *Desmoncus mitis* subsp. *leptospadix* (Martius) Henderson, *comb. & stat. nov.*

Basionym: *Desmoncus leptospadix* Martius (1844: 52). *Atitara leptospadix* (Martius) Kuntze (1891: 727). *Desmoncus mitis* var. *leptospadix* (Martius) Henderson (1995: 228). Type:—PERU. Loreto: Maynas, Yurimaguas, no date, *E. Poeppig 2207* (holotype G *n.v.*, holotype image!). Epitype (here designated):—PERU. Loreto: Santa Rosa, lower Río Huallaga below Yurimaguas, ca. 125 m, 1–5 September 1929, *E. Killip & A. Smith 28807* (epitype NY!, isoepitype US!).

Leaf sheaths non-spiny, rarely sparsely spiny; rachises 35.0(17.2–76.0) cm long; pinnae ovate, 6(3–11) per side of rachis; cirri usually well-developed.

Distribution and habitat:—From 0°52'–11°46'S and 59°00'–77°40'W in the western Amazon region in Colombia (Amazonas), Peru (Amazonas, Cuzco, Huánuco, Loreto, Ucayali), and Brazil (Acre, Amazonas) at 166(100–400) m elevation in lowland rainforest (Fig. 9).

Taxonomic notes:—Henderson (1995) referred to this taxon as *Desmoncus mitis* var. *leptospadix* (Martius) Henderson, based on *D. leptospadix* Martius. The type of this is sterile and an epitype is therefore designated.

Subspecific variation:—Most specimens from Maynas, Loreto, Peru have multiple (2–3) inflorescences at a node. Two specimens (*Prance 12310, 12490*), both from the same locality in western Acre, Brazil have larger fruits than usual; others from the same area have normal fruits. Most specimens from western Acre have smaller leaves than usual. A few specimens from the western part of the range have spiny peduncular bracts (e.g., *Schunke 15629*) or spiny sheaths (e.g., *Huashikat 2309*). Three specimens from Loreto, Peru (*Tessmann 5236, Vásquez 8325, 8329*) have poorly-developed cirri.

One unusual specimen (*Simpson 698*) from Loreto, possibly a mixed collection, has leaves like those of subsp. *mitis* and infructescences like those of *D. polyacanthos*. Another specimen from Loreto (*Kvist 1156*) appears intermediate between subsp. *leptospadix* and *D. polyacanthos* and may be a hybrid. A specimen from Huánuco (*Listabarth 1110589*) may also be a hybrid. The easternmost specimen (*Rabelo 79*), from from the Rio Urubu near Manaus, is outside the main range of subsp. *leptospadix* and has completely smooth peduncular bracts and slender rachillae with some adnation. It may belong here; it is not included in the above description but is mapped.

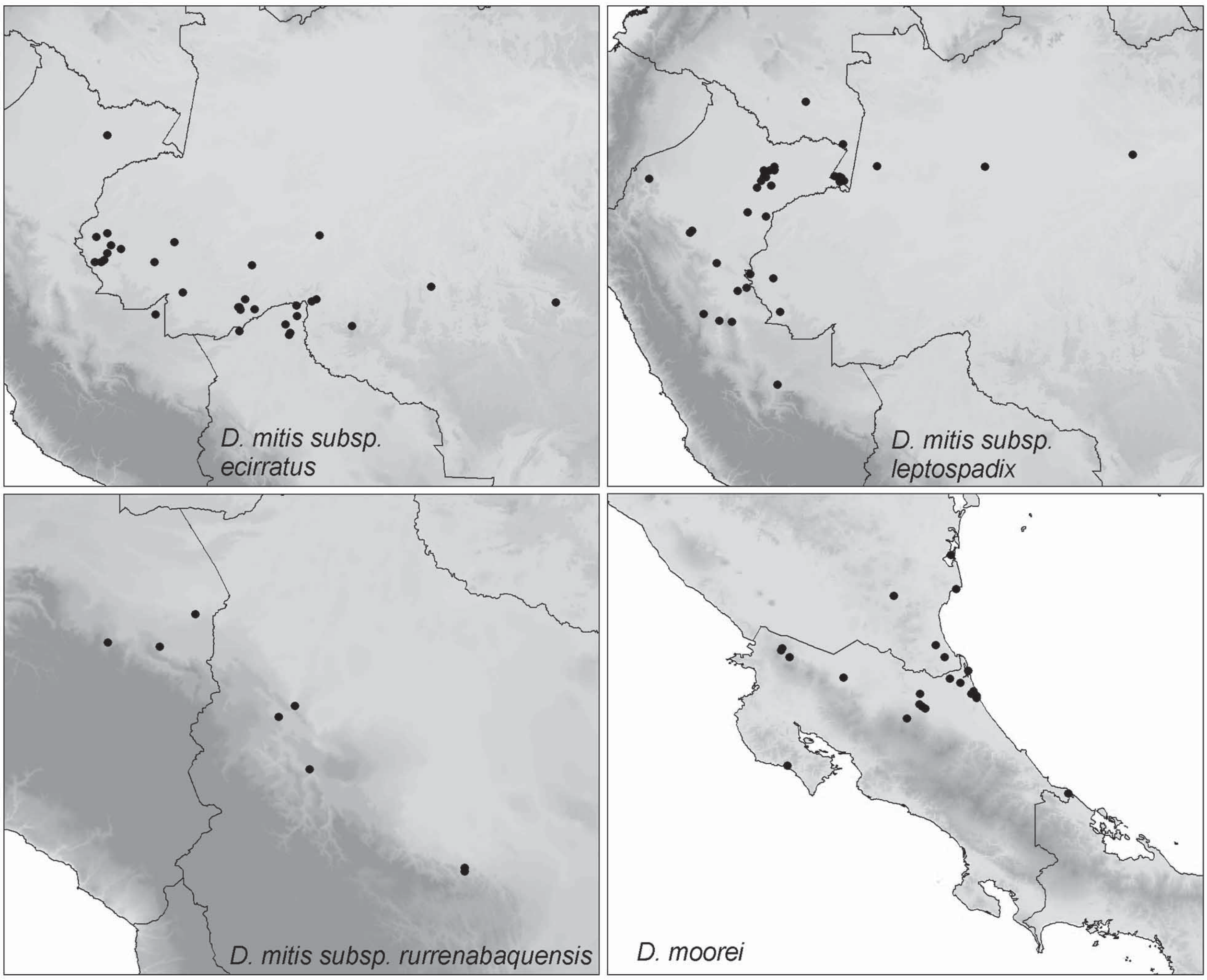

FIGURE 9. Distribution maps of *Desmoncus mitis* subsp. *ecirratus*, *D. mitis* subsp. *letpospadix, D. mitis* subsp. *rurrenabaquensis*, and *D. moorei*.

12.4. *Desmoncus mitis* subsp. *rurrenabaquensis* (Henderson) Henderson, *comb. & stat. nov.*

Basionym: *Desmoncus mitis* var. *rurrenabaquensis* Henderson (1995: 228). Type:—PERU. Madre De Dios: Explorer's Inn on Río Tambopata, 12°50'S, 69°17'W, ca. 250 m, 6 November 1991, *A. Henderson & F. Chávez 1640* (holotype USM!, isotypes, CUZ!, NY!). Epitype (here designated):—BOLIVIA. La Paz: Franz Tamayo, Parque Nacional Madidi, río Hondo, arroyo Negro, pica hacia la serranía de Toregua, 14°39'S 67°48'W, 340 m, 25 March 2002, *A. Fuentes, M. Villanueva & B. Guili 4081* (epitype NY!, isoepitypes LPB *n.v.*, MO!).

Leaf sheaths densely and finely spiny; rachises 45.1(25.0–69.0) cm long; pinnae linear or lanceolate, 19(16–22) per side of rachis; cirri well-developed.

Distribution and habitat:—From 12°50'–17°24'S and 64°30'–70°50'W in subAndean areas of the southwestern Amazon region of Peru (Cuzco, Madre de Dios, Puno) and Bolivia (Beni, Cochabamba, La Paz, Santa Cruz) at 421(250–920) m elevation in lowland rainforest (Fig. 9).

Taxonomic notes:—This taxon was referred to by Henderson (1995) as *Desmoncus mitis* var. *rurrenabaquensis*. The type of this is sterile and an epitype is therefore designated.

13. *Desmoncus moorei* Henderson, *sp. nov.* (Appendix IV Plate 17)

A Desmonco chinantlensi, quod similis, rachillis tomentosis atque staminibus paucioribus differt.

Type:—COSTA RICA. Limón: P. N. Tortuguero, Pococi, Llanura de Tortuguero, Estación Cuatro Esquinas, 10˚32'N, 83˚30'W, 2 m, 18 October 1989, *J. Solano 21* (holotype INB!, isotype MO!).

Plants 9.4(1.0–32.5) m tall; stems 2.4(1.6–3.4) cm diameter. **Leaf** petioles 2.1(1.0–4.0) cm long; rachises 96.1(70.0–113.0) cm long, 9.6(6.7–12.0) mm wide, the spines usually >1 cm long, mostly adaxial or lateral, straight with briefly swollen bases; pinnae 18(15–20) per side of rachis, without long, filiform apices, with an adaxial beard of spines at the bases, with uneven surfaces at the bases adaxially, covered with spinules; basal pinna 18.4(16.0–20.0) cm long, 1.5(1.2–1.8) cm wide; cirri well-developed, with acanthophylls, without spines abaxially, with intermediate acanthophylls present (i.e., distalmost pair of pinnae reflexed as acanthophylls and with swollen bases and/or proximalmost acanthophylls like vestigial pinnae), without a wide gap between pinnae and acanthophylls. **Inflorescences** with the rachis ridged, not twisted, much thicker than the numerous, closely spaced and spirally or irregularly arranged rachillae, each rachilla not or only briefly adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 5.8(3.2–7.7) mm wide; peduncular bracts 37.8(25.5–54.5) cm long, broad, the surfaces ribbed, brown tomentose, sparsely to densely covered with long, straight or sinuous, briefly swollen-based, diagonally or vertically oriented spines, these flattened or triangular in cross-section, whitish-brown proximally, black or brown distally, with tomentose margins; rachillae 30(19–38), brown tomentose initially; proximal rachillae 14.2(11.5–18.0) cm long, 1.2(0.8–1.4) mm wide; stamens 6; **fruits** 12.6(11.1–14.3) mm long, 11.4(10.2–13.8) mm wide, the surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers; fruiting corollas less than one quarter as long as fruits, splitting irregularly into 3 lobes, the lobes often splitting again; endocarps globose to obovoid with rounded or slightly peaked apices, the pores lateral.

Distribution and habitat:—From 9°35'–11°55'N and 82°36'–85°25'W on the Caribbean slope of Nicaragua and Costa Rica, with an outlier in the Nicoya Peninsula in Costa Rica at 138(1–700) m elevation in lowland rainforest and forest margins along rivers (Fig. 9).

Taxonomic notes:—This species is named for Harold E. Moore (1917–1980) of Cornell University, preeminent student of palms. Hammel *et al.* (2003) identified the specimens included here as *Desmoncus schippii* Burret. The type of this is no longer extant and it is therefore treated here as an Excluded Name. *Desmoncus moorei* is similar to *D. chinantlensis* but differs in its spinulose pinnae bases, tomentose rachillae, and fewer stamens (6 versus 8–11). Specimens dry a distinctive dark brown color compared to *D. chinantlensis*.

Subspecific variation:—Intermediate acanthophylls and adaxial beards of spines at the pinnae bases are much less well-developed than in similar species. The specimen from the Nicoya Peninsula in Costa Rica is tentatively included here. It has narrower pinnae than other specimens. Sterile, juvenile plants from the same locality have numerous, linear pinnae and appear quite distinct. However, there is only one fertile specimen from Nicoya.

14. *Desmoncus myriacanthos* Dugand (1943: 75).

Type:—COLOMBIA. Bolívar: Norosí–Tiquísio trail, lands of Loba, 150–600 m, 24 April 1916, *H. Curran 174* (holotype US!).

Desmoncus isthmius Bailey (1943: 211). Type:—PANAMA. Darién: Marraganti and vicinity, 5 April 1908, *R. Williams 691* (holotype NY!, isotype US!). ***Synon. nov.***

Plants 5.8(3.0–9.0) m tall; stems 2.5(1.4–3.7) cm diameter, clustered. **Leaf** petioles 2.6(2.0–3.5) cm long; rachises 99.0(67.0–131.0) cm long, 8.2(4.8–11.0) mm wide, the spines usually >1 cm long, mostly adaxial or lateral, straight with briefly swollen bases; pinnae 23(18–29) per side of rachis, without long, filiform apices, with an adaxial beard of spines at the bases, without spinules or dense tomentum at the bases adaxially; basal pinna 22.0(18.0–27.0) cm long, 2.2(1.2–4.2) cm wide; cirri well-developed, with acanthophylls, without spines abaxially, with intermediate acanthophylls present (i.e., distalmost pair of pinnae reflexed as acanthophylls and with swollen bases and/or proximalmost acanthophylls like vestigial pinnae), without a wide gap between pinnae and acanthophylls. **Inflorescences** with the rachis ridged, not twisted, much thicker than the numerous, closely spaced and spirally or irregularly arranged rachillae, each rachilla not or only briefly adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 5.6(3.2–8.6) mm wide; peduncular bracts 26.7(20.0–34.0) cm long, broad, the surfaces ribbed, brown tomentose, sparsely to densely covered with long, straight or sinuous, briefly swollen-based, diagonally or vertically oriented spines, these flattened or triangular in cross-section, whitish-brown proximally, black or brown distally, with tomentose margins; rachillae 23(16–32), glabrous or scarcely tomentose initially; proximal rachillae 10.7(5.5–15.8) cm long, 1.3(0.8–2.2) mm wide; stamens 8–9; **fruits** 15.1(12.6–21.0) mm long, 8.2(7.0–10.3) mm wide, the surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers; fruiting corollas less than one quarter as long as fruits, not or scarcely splitting, tending to remain cupular; endocarps narrowly ellipsoid with rounded apices, the pores lateral.

Distribution and habitat:—From 6°13’–11°18’N and 72°00’–80°18’W in central and eastern Panama, northwestern Colombia, and just reaching Venezuela (Zulia) at 73(10–125) m elevation in lowland rainforest (Fig. 10).

Taxonomic notes:—Although published in the same year, 1943, *Desmoncus myriacanthos* predates *D. isthmius* by several months.

Subspecific variation:—Specimens are from scattered areas but this is likely to be an artifact of insufficient collecting. The southernmost specimen (*Forero 9080*) from the Chocó region comes from one of the wettest areas in Colombia, in contrast to the much dryer habitat of the other specimens from northwestern Colombia.

15. *Desmoncus obovoideus* Henderson, sp. nov. (Appendix IV Plates 18–19)

A speciebus affinibus crusta fructuum aspera fibris subepidemalibus numerosis, longis atque brachiatis differt.

Type:—PANAMA. Colón: Santa Rita ridge east of Transisthmian Highway, 300–500 m, 20 September 1972, *A. Gentry 6115* (holotype PMA!, isotype MO!).

Plants 4.9(3.5–7.0) m tall; stems 1.7(1.4–2.0) cm diameter, branching no data. **Leaf** petioles 3.1(2.0–4.5) cm long; rachises length no data, 6.3(6.0–6.6) mm wide, the spines usually >1 cm long, mostly adaxial or lateral, straight with briefly swollen bases; pinnae number no data, without long, filiform apices, with an adaxial beard of spines at the bases, without spinules or dense tomentum at the bases adaxially; basal pinna 14.0 cm long, 4.9(4.2–5.5) cm wide; cirri well-developed, with acanthophylls, without spines abaxially, with intermediate acanthophylls present, without a wide gap between pinnae and acanthophylls. **Inflorescences** with the rachis ridged, not twisted, much thicker than the numerous, closely spaced and spirally or irregularly arranged rachillae, each rachilla not or only briefly adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 4.3(2.8–5.7) mm wide; peduncular bracts length no data, broad, the surfaces ribbed, brown tomentose, sparsely to densely covered with long, straight or sinuous, briefly swollen-based, diagonally or vertically oriented spines, these flattened or triangular in cross-section, whitish-brown proximally, black or brown distally, with tomentose margins (rarely without spines); rachillae 21(20–21), glabrous or scarcely tomentose initially; proximal rachillae 8.5 cm long, 1.0 mm wide; stamens no data; **fruits** 15.8(14.0–17.9) mm long, 14.2(12.8–16.3) mm wide, the surfaces uneven with numerous, subepidermal, long, branching fibers; fruiting corollas less than one quarter as long as fruits, splitting irregularly into 3 lobes, the lobes often splitting again; endocarps broadly obovoid with flattened apices, the pores lateral on or near flattened apices.

Distribution and habitat:—From 8°40'–9°30'N and 77°25'–80°29'W in central Panama, with outliers to the west and east, at 173(25–400) m elevation in lowland rainforest (Fig. 10).

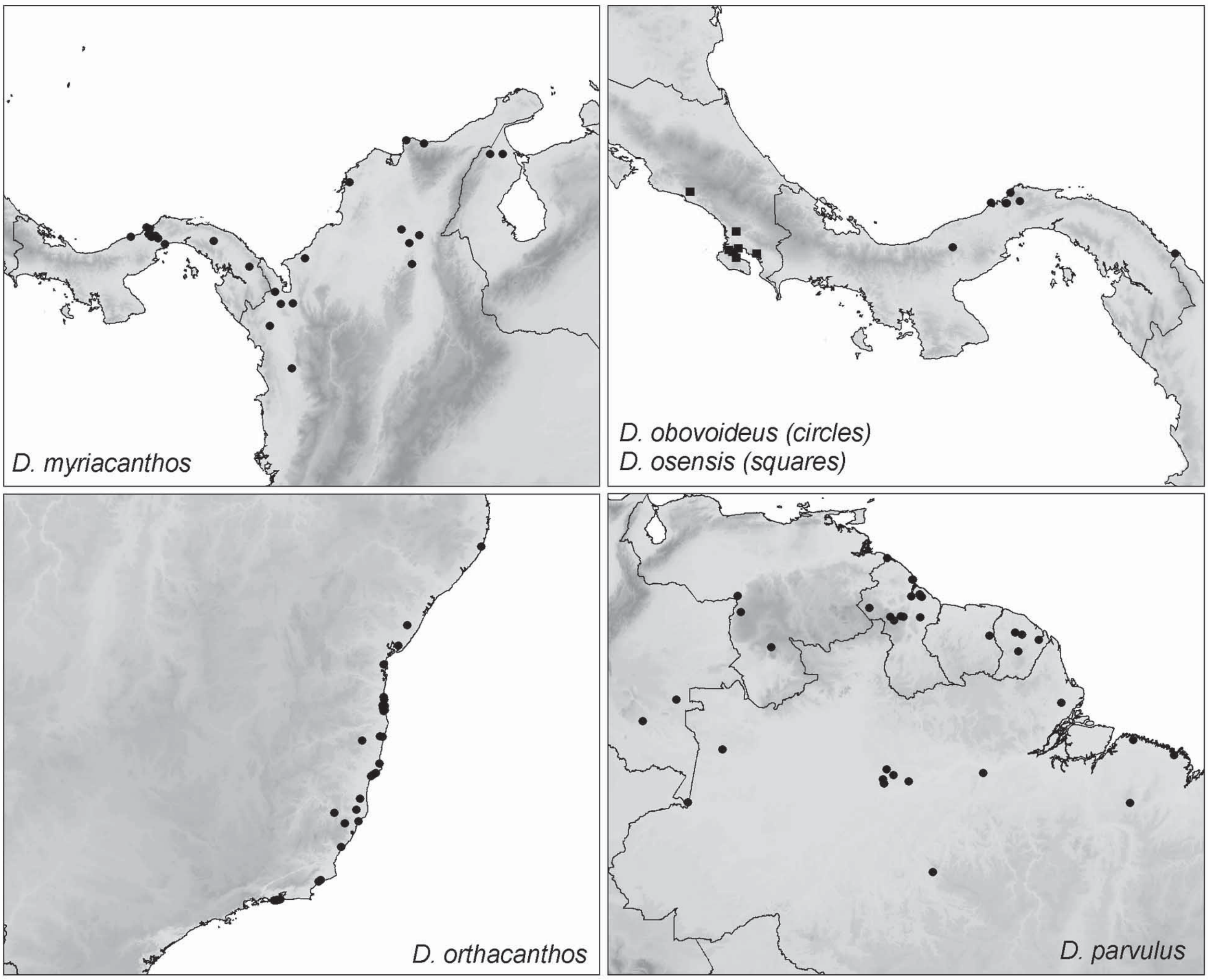

FIGURE 10. Distribution maps of *Desmoncus myriacanthos*, *D. obovoideus, D. osensis, D. orthacanthos*, and *D. parvulus*.

Taxonomic notes:—*Desmoncus obovoideus* is similar to *D. osensis* and shares all character states except that *D. obovoideus* lacks data for stamen number. *Desmoncus obovoideus* also has shorter and wider basal pinna compared to *D. osensis* (mean of 14.0 cm long and 4.9 cm wide versus 23.2 cm long and 3.7 cm wide). Based on this, and geographic separation, the two are recognized as separate species.

A few specimens have abaxial rachis spines which appear almost recurved, more like those of *D. polyacanthos*. There are two outliers, both of which are tentatively included here. The one from eastern

Panama (*McPherson 6961*) is without fruits. The other (*Hammel 1863*), from central Panama, also has abaxial rachis spines which appear almost recurved.

Subspecific variation:—In most specimens the adaxial beard of spines at the bases of the pinnae is poorly-developed. One specimen (*Garwood 2178*) is smaller than the others.

17. *Desmoncus orthacanthos* Martius (1823–1837: 87).

Atitara orthacantha (Martius) Barbosa Rodrigues (1902: 76). Type:—BRAZIL. Bahia: Rio Mucuri, no date, *M. Neuwied s. n.* (holotype M!).

Desmoncus lophacanthos Martius (1844: 50). *Atitara lophacantha* (Martius) Barbosa Rodrigues (1902: 76). Type:—BRAZIL. Bahia: Ilhéus, 20 March 1837, *B. Luschnath s.n.* (holotype M!).

Plants 2.6(1.2–4.0) m tall; stems 1.3(0.7–2.2) cm diameter, clustered. **Leaf** petioles 6.4(2.0–15.0) cm long; rachises 59.6(30.5–85.0) cm long, 4.6(2.9–6.8) mm wide, the spines usually >1 cm long, mostly adaxial or lateral, straight with briefly swollen bases; pinnae 9(6–14) per side of rachis, without long, filiform apices, without a beard of spines at the bases, without spinules or dense tomentum at the bases adaxially; basal pinna 14.3(7.6–25.0) cm long, 2.6(1.0–4.8) cm wide; cirri well-developed, with acanthophylls, without spines abaxially, with intermediate acanthophylls present (i.e., distalmost pair of pinnae reflexed as acanthophylls and with swollen bases and/or proximalmost acanthophylls like vestigial pinnae), without a wide gap between pinnae and acanthophylls. **Inflorescences** with the rachis angular, slightly twisted, thicker than the closely spaced and spirally arranged rachillae, each rachilla not adnate to the rachis and with an irregular bracteole adnate to the rachilla and appearing displaced distally onto the rachilla, with a poorly- to well-developed axillary pulvinus; peduncles 3.9(2.0–7.2) mm wide; peduncular bracts 26.4(19.0–39.0) cm long, broad, the surfaces ribbed, brown tomentose, rarely with long, straight or sinuous, briefly swollen-based, diagonally or vertically oriented spines, these flattened or triangular in cross-section, whitish-brown proximally, black or brown distally, with tomentose margins; rachillae 14(8–22), glabrous or scarcely tomentose initially; proximal rachillae 10.4(5.0–20.5) cm long, 0.8(0.3–1.2) mm wide; stamens 5–7; **fruits** 14.4(11.4–18.4) mm long, 10.9(8.4–15.2) mm wide, the surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers; fruiting corollas less than one quarter as long as fruits, splitting irregularly into 3 lobes, the lobes often splitting again; endocarps globose to obovoid with rounded or slightly peaked apices, the pores lateral.

Distribution and habitat:—From 8°45'–23°01'S and 35°06'–43°28'W in the Atlantic Coastal Forest of Brazil at 105(0–700) m elevation, usually near the sea in restinga or scrub forest (Fig. 10).

Taxonomic notes:—Both Wessels Boer (1965) and Henderson *et al.* (1995) considered *Desmoncus orthacanthos* to be much more widespread. This was based on a misinterpretation, and it is here considered to be confined to the Atlantic Coastal Forest of Brazil (see notes under *Desmoncus horridus*). *Desmoncus orthacanthos* has an unique inflorescence structure with each rachilla with an irregular, adnate bracteole that appears displaced distally onto the rachilla (Fig. 2D). Pinnae spines are also distinctive. All specimens have at least some pinnae with one or rarely two large spines right at the very base of the pinnae on the abaxial surface.

Subspecific variation:—There is no geographic disjunction, except for two outlying specimens from Pernambuco. There is geographical variation in this species. Regression shows there are significant ($P<0.05$) associations between latitude and four leaf and three inflorescence variables. Squared multiple R for the regression of petiole length on latitude is 0.19, rachis length 0.27, basal pinna length 0.29, basal pinna width 0.16, peduncular bract length 0.29, rachilla length 0.17, and fruit length 0.41. These variables decrease from north to south except for fruit length which increases from north to south.

16. *Desmoncus osensis* Henderson, *sp. nov.* (Appendix IV Plates 20–21)

A Desmonco obovoideo pinnis basalibus longioribus atque angustioribus diifert.

Type:—COSTA RICA. Puntarenas: Golfito, Distrito Golfito, Refugio de Vida Silvestre Golfito, camino a La Gamba, 8°40'N 83°11'W, 94 m, 9 October 2008, *R. Aguilar 11417* (holotype NY!, isotypes CR *n.v.*, USJ *n.v.*).

Plants height no data; stems 1.6(1.2–2.6) cm diameter, branching no data. **Leaf** petioles 2.7(2.0–3.5) cm long; rachises 85 cm long, 7.1(6.4–7.8) mm wide, the spines usually >1 cm long, mostly adaxial or lateral, straight with briefly swollen bases; pinnae 13 per side of rachis, without long, filiform apices, with an adaxial beard of spines at the bases, without spinules or dense tomentum at the bases adaxially; basal pinna 23.2(18.0–26.0) cm long, 3.7(2.4–5.0) cm wide; cirri well-developed, with acanthophylls, without spines abaxially, with intermediate acanthophylls present, without a wide gap between pinnae and acanthophylls. **Inflorescences** with the rachis ridged, not twisted, much thicker than the numerous, closely spaced and spirally or irregularly arranged rachillae, each rachilla not or only briefly adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 4.5(4.1–4.8) mm wide; peduncular bracts length no data, broad, the surfaces ribbed, brown tomentose, sparsely to densely covered with long, straight or sinuous, briefly swollen-based, diagonally or vertically oriented spines, these flattened or triangular in cross-section, whitish-brown proximally, black or brown distally, with tomentose margins (rarely without spines); rachillae 19(18–19), glabrous or scarcely tomentose initially; proximal rachillae length no data, 1.6 mm wide; stamens 9; **fruits** 15.1(13.9–17.3) mm long, 13.6(11.0–15.9) mm wide, the surfaces uneven with numerous, subepidermal, long, branching fibers; fruiting corollas less than one quarter as long as fruits, splitting irregularly into 3 lobes, the lobes often splitting again; endocarps broadly obovoid with flattened apices, the pores lateral on or near flattened apices.

Distribution and habitat:—From 8°36'–9°31'N and 83°11'–84°06'W in the Osa Peninsula and adjacent areas in Costa Rica at 145(50–350) m elevation in lowland rainforest (Fig. 10).

Taxonomic notes:—*Desmoncus osensis* is similar to *D. obovoideus* and shares all character states except that *D. obovoideus* lacks data for stamen number. *Desmoncus osensis* also has longer and narrower basal pinna compared to *D. obovoideus* (mean of 23.2 cm long and 3.7 cm wide versus 14.0 cm long and 4.9 cm wide). Based on this, and geographic separation, the two are recognized as separate species.

Subspecific variation:—Hammel *et al.* (2003) had only two specimens (*Aguilar 290, Morales 6333*) available from the Osa Peninsula, and identified them as *Desmoncus* sp. *A.* They considered that these two specimens were different from one another and possibly not conspecific. In the present study, seven specimens have been examined. They are indeed variable, and in some the adaxial beard of spines at the bases of the pinnae are poorly-developed. Some of this variation may be due to the age of the leaves represented by the specimens. There is also variation in fruit size. Without more specimens it is not possible to resolve this problem.

18. *Desmoncus parvulus* Bailey (1948: 115).

Type:—GUYANA. Potaro–Siparuni: Tumatumari, 18 June–8 July 1921, *H. Gleason 164* (holotype NY! isotype US!).

Desmoncus kaieteurensis Bailey (1948: 115). Type:—GUYANA. Potaro-Siparuni: trail from Tukeit to Kaiatuk Plateau, 29 April 1944, *B. Maguire & D. Fanshawe 23093* (holotype BH!, isotypes K!, NY!).

Plants 4.4(1.5–10.0) m tall; stems 0.8(0.4–1.8) cm diameter, clustered. **Leaf** petioles 6.0(0.7–13.8) cm long; rachises 31.7(22.5–47.0) cm long, 2.7(1.7–3.8) mm wide, the spines usually <1 cm long, mostly abaxial, recurved with markedly swollen bases; pinnae 6(4–9) per side of rachis, without long, filiform apices, without a beard of spines at the bases, with uneven surfaces at the bases adaxially, usually covered with spinules and/or dense tomentum; basal pinna 10.8(4.2–22.0) cm long, 3.0(1.0–5.8) cm wide; cirri well-developed, with acanthophylls, with few spines abaxially throughout, with no intermediate acanthophylls present, usually with a wide gap between pinnae and acanthophylls (i.e., gap wider than that between adjacent acanthophylls). **Inflorescences** with the rachis angular, slightly twisted, thicker than the few to numerous, closely spaced and spirally arranged rachillae, each rachilla not (or very rarely) adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 1.6(1.0–3.1) mm wide; peduncular bracts 12.5(8.5–17.0) cm long, broad, ridged, densely covered with short, straight, swollen-based, vertically oriented spines, these terete, whitish-brown proximally, brown distally, without tomentum; rachillae 9(7–14), glabrous or scarcely tomentose initially; proximal rachillae 4.6(3.0–6.2) cm long, 0.7(0.5–0.9) mm wide; stamens 6; **fruits** 11.1(8.9–14.3) mm long, 9.4(7.1–11.2) mm wide, the surfaces uneven with numerous, subepidermal, long, branching fibers; fruiting corollas less than one quarter as long as fruits, splitting irregularly into 3 lobes, the lobes often splitting again; endocarps globose to obovoid with rounded or slightly peaked apices, the pores lateral.

Distribution and habitat:—From 4°05'S–8°20'N and 45°19'–72°12'W in the eastern and central Amazon region in Brazil, the Guianas, Venezuela, and Colombia at 209(5–650) m elevation in lowland rainforest (Fig. 10).

Taxonomic notes:—The name *Desmoncus macroacanthos* Martius was used by Wessels Boer (1965) for specimens included here. This name is here treated under Excluded Names; the sterile type has spiny leaf sheaths and non–spiny cirri and does not appear to represent this species. The name *Desmoncus phoenicocarpus* Barbosa Rodrigues was used for this species by Henderson (1995). The type is an illustration, also having spiny leaf sheaths and non–spiny cirri, and is also here treated under Excluded Names.

Subspecific variation:—Specimens come from widely scattered localities but this may be an artifact of insufficient collecting. Two specimens from the Rio Tapajos in Brazil are unusual. One (*Maciel 167*) has very short petiole, numerous, small pinnae, and cirrus without spines abaxially throughout; the second (*Anderson 10577*) has very large pinnae. These may be of hybrid origin.

19. *Desmoncus polyacanthos* Martius (1823–1837: 85).

Atitara polyacantha (Martius) Kuntze (1891: 726). Lectotype (here designated):—BRAZIL. Bahia: without locality, no date, *C. Martius s.n.* (M!).

Desmoncus oxyacanthos Martius (1823–1837: 88). *Desmoncus polyacanthos* var. *oxyacanthos* (Martius) Drude (1881: 314). *Atitara oxyacantha* (Martius) Kuntze (1891: 727). Type:—BRAZIL. Rio de Janeiro: Sebastianopolis, no date, *M. Neuwied s.n.* (holotype M!).

Desmoncus ulei Dammer (1907: 129). Lectotype (here designated):—BRAZIL. Amazonas: Manaus, Rio Negro, February 1901, *E. Ule 5388* (MG!).

Desmoncus campylacanthus Burret (1934: 210). Lectotype (here designated):—BRAZIL. Rio de Janeiro: Serra de Bica, Cascadura, 10 December 1882, *A. Glaziou 14366* (P!, holotype B, isolectotypes C *n.v.,* K!; the holotype at B was destroyed).

Desmoncus prestoei Bailey (1943: 215). Type:—TRINIDAD. "Hort. Trin.", no date, *W. Broadway 5568* (holotype BH!).

Desmoncus peraltus Bailey (1947: 373). Type:—TRINIDAD. Arena, 17 January 1946, *L. Bailey 101* (holotype BH!).

Desmoncus maguirei Bailey (1948: 108). Type:—SURINAME. Kwakoegron, 19 October 1947, *B. Maguire & G. Stahel 25011* (holotype NY!, isotypes BH!, U!).

Desmoncus mirandanus Bailey (1949: 183). Type:—VENEZUELA. Miranda: Cárdenas (Guinand Estate), Siquire Valley, 400–800 m, 6 April 1917, *H. Pittier 7078* (holotype BH!, isotype US!).

Plants 7.2(1.0–37.0) m tall; stems 1.4(0.5–2.9) cm diameter, clustered. **Leaf** petioles 3.2(0.5–13.5) cm long; rachises 63.8(25.0–173.0) cm long, 5.2(1.8–12.9) mm wide, the spines usually <1 cm long, mostly abaxial, recurved with markedly swollen bases; pinnae 8(4–15) per side of rachis, without long, filiform apices, without a beard of spines at the bases, without spinules or dense tomentum at the bases adaxially; basal pinna 15.8(3.3–40.0) cm long, 2.7(0.3–5.8) cm wide; cirri well-developed, with acanthophylls, cirri with spines abaxially mostly on proximal part only, without intermediate acanthophylls present, with a wide gap between pinnae and acanthophylls. **Inflorescences** with the rachis thicker than the few, closely spaced and spirally arranged rachillae, each rachilla subtended by an acute bracteole and with an axillary pulvinus; peduncles 3.5(1.6–12.4) mm wide; peduncular bracts 26.3(16.5–34.0) cm long, broad, sparsely to densely covered with short, markedly swollen-based, diagonally oriented spines, these triangular in cross-section, whitish-brown proximally, brown distally, with tomentose margins, rarely spines few or absent; rachillae 15(5–37), glabrous or scarcely tomentose initially; proximal rachillae 7.4(3.3–13.0) cm long, 1.1(0.6–2.0) mm wide; stamens 5–6; **fruits** 16.4(11.2–23.5) mm long, 11.9(7.9–17.9) mm wide, the surfaces smooth, without any apparent subepidermal fibers; fruiting corollas less than one quarter as long as fruits, splitting irregularly into 3 lobes, the lobes often splitting again; endocarps globose to obovoid with rounded apices, the pores lateral, not equidistant, the sterile pores closer latitudinally.

Distribution and habitat:—From 10°37'N–21°31'S and 35°09'–78°38'W in Trinidad, Venezuela, the Guianas, Brazil (including the Atlantic Coastal Forest), Colombia, Ecuador, Peru, and Bolivia at 205(0–1000) m elevation in a variety of habitats including lowland rainforest on terra firme, flooded forest, campina, restinga, or scrub forest near the sea (Fig. 11). Read (1979) also included the Lesser Antillean island of St. Vincent in the distribution of this species, but only one, sterile specimen from there has been seen. There is another specimen at P labelled "Martinique" but without more precise locality.

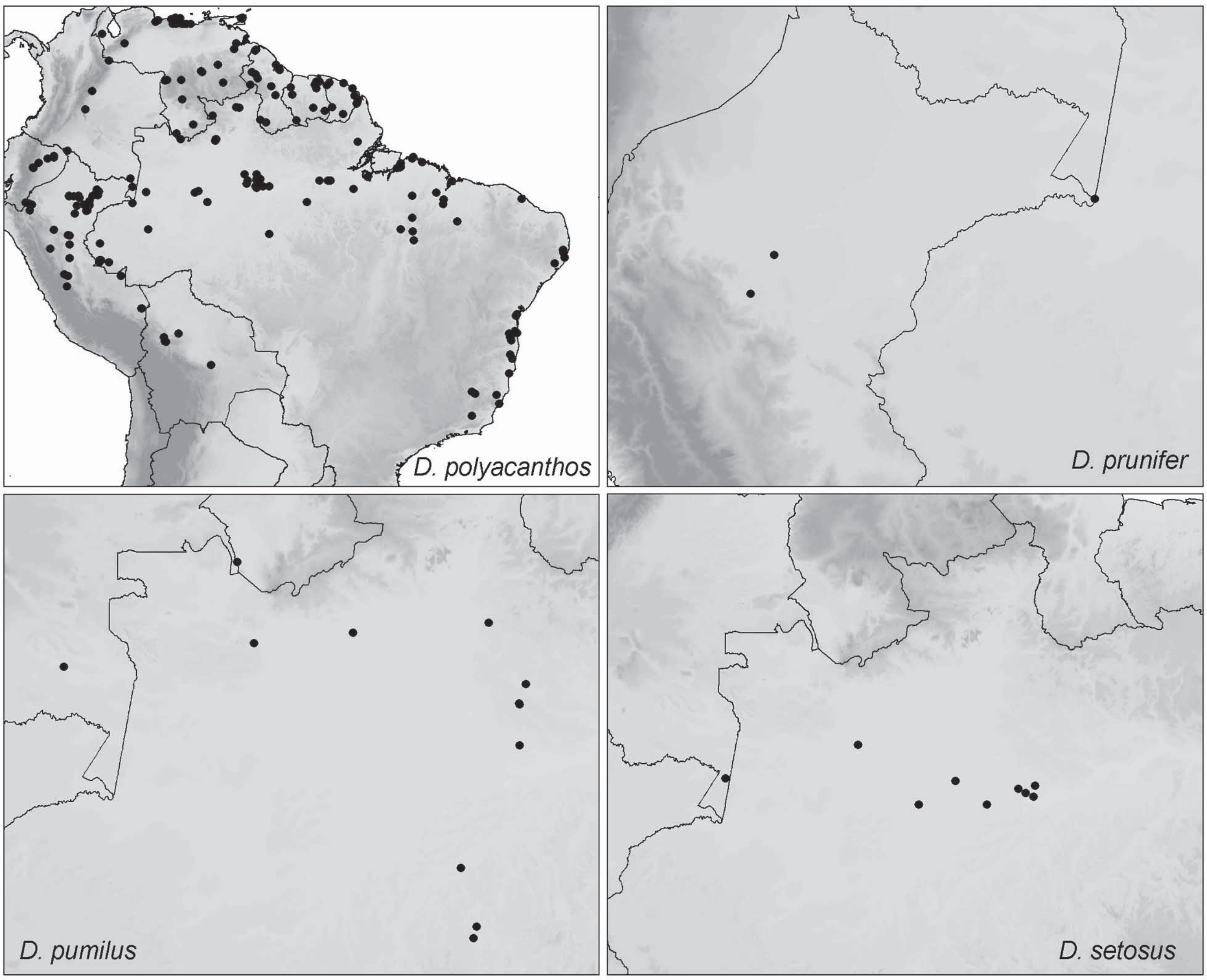

FIGURE 11. Distribution maps of *Desmoncus polyacanthos*, *D. prunifer, D. pumilus*, and *D. setosus*.

Taxonomic notes:—*Desmoncus polyacanthos* Martius was emended by Drude (1881) and excluded by Burret (1934). However there seems no reason for these designations. Martius's (1823–1837) description and illustration, based on an extant type collected by Martius himself, perfectly represent this widespread species.

Subspecific variation:—There is geographic disjunction and specimens occur in two regions—the Atlantic Coastal Forest of Brazil, and all other areas. Specimens from the Atlantic Coastal Forest differ significantly from others from Brazil in only three variables (rachis length, number of pinnae, rachilla width)(t-test, P <0.05). Only one species is therefore recognized, without any subspecific division. Nevertheless, *Desmoncus polyacanthos* is, after *D. mitis*, the second most variable species in the genus, and is by far the most widespread.

Starting from the north, specimens from the Coastal Range in Venezuela (*mirandanus* morphotype) have larger inflorescences with more rachillae (mean of 19 versus 12) than other specimens from Venezuela. Specimens from western (Apure, Barinas, Zulia) and southern parts of Venezuela (Amazonas, Bolívar, Delta Amacuro) are rather uniform (*ulei* morphotype).

Specimens from Trinidad and the Guianas are also rather uniform, apart from the usual variation in size and spininess, and are considered part of the *ulei* morphotype. Along the coast of the Guianas, *D. polyacanthos* occurs slightly more inland than the sympatric, coastal *D. horridus* subsp. *horridus*.

Specimens from Brazil (Amazonas, Maranhão, Pará, Roraima) are rather uniform (*ulei* morphotype), with some exceptions. Two specimens (*Balick 951, Cavalcante 1611)* from near the Rio Tapajós, Pará, have exceptionally wide pinnae. A few specimens from Amazonas are unusual. The type of *D. ulei* (*Ule 5388*), from the Rio Negro near Manaus, is atypical in having straight spines on the pinnae veins. A few other specimens have these kind of spines, and others have short, recurved spines on the pinnae veins. In western Amazonas two specimens (*Mori 9128, Pardini 39)* are much larger than the others and are referred to the *large* morphotype (see below).

Some specimens from Amazonas and Pará may be hybrids and are from campinas near areas where both *D. polyacanthos* and *D. pumilus* occur. One (*Loureiro s.n.*) from north of Presidente Figueiredo has narrow pinnae and fruits with Y-shaped fibers. A second (*Scariot 621*), from the same general area, has more usual pinnae but also has fruits with Y-shaped fibers. A third (*Henderson 300*) from near Manicoré has narrow pinnae and an elongate inflorescence. A group of specimens from near Tucurui in Pará may also be hybrids. They are reported to occur in low forest on white sand and are from a highly disturbed area near the Tucurui Dam. Two (*Plowman 9742, 9577*) have very slender stems, narrow pinnae, and fruits with Y-shaped fibers. Other specimens from nearby (*Miranda 470, Plowman 9881*) are somewhat larger and have smooth fruit surfaces without any apparent subepidermal fibers.

There is extreme variation amongst specimens from the western Amazon region and subAndean foothills in Colombia, Ecuador, Peru, and Brazil. Much of this appears to be regional, i.e., specimens from the same region are similar and differ from those of other regions. These regions are separate from one another, but the gaps between them are likely to be artifacts of insufficient collecting. In most cases there are too few specimens to test for differences amongst regions. In general, western Amazon specimens are larger than the *ulei* morphotype, sometimes markedly so. Most are referred to as the *large* morphotype, although there is great variation amongst them.

There is a curious absence of specimens from the Colombian Amazon, especially the central part. Specimens from Meta and Cudinamarca in the northwestern part are included in the *ulei* morphotype, and another (*Rudas 2297*) from the southeastern part (Amazonas) in the *large* morphotype.

In Ecuador specimens are variable and two (*Balslev 62438, Croat 88912*) come from unusually high elevations (1000–1121 m). Other specimens from lower elevations are smaller. The two easternmost specimens in Ecuador have the widest pinnae, similar to another specimen (*Gentry 22007*) from adjacent Peru on the border with Ecuador which has unusually wide, ovate pinnae. All these are referred to as the *large* morphotype.

In central and eastern Loreto, Peru, especially in the Iquitos region, most specimens are large with mostly ovate, rarely lanceolate pinnae, sparsely and coarsely spiny peduncular bracts, and large fruits. They are referred to as the *large* morphotype. However, there are a few specimens that are smaller and are referred to the *ulei* morphotype. One specimen (*Vásquez 2300*) has spinulose pinnae bases and may be a hybrid with *Desmoncus mitis*. In southern Loreto, the few specimens have ovate pinnae and densely spiny peduncular bracts and are referred to the *ulei* morphotype.

In northwestern Peru (Amazonas) and just reaching extreme southern Ecuador (Zamora-Chinchipe), specimens are large with ovate pinnae, densely spiny peduncular bracts, and large fruits. They are referred to as the *amazonas* morphotype.

In central Peru (San Martín) specimens are extremely variable. A single specimen from southern San Martín (*Schunke 6927*) is larger, with densely spiny sheaths and long, almost linear pinnae (*sanmartin* morphotype). A second specimen from the northern part of the department (*Williams 6661*) is completely different, with smaller, ovate pinnae and a finely spiny peduncular bract (*ulei* morphotype).

In south-central Peru (Pasco) there are two specimens (*Henderson 3009, Smith 3791*) which are considerably larger than others and have large stems, long, lanceolate pinnae, and large inflorescences with densely spiny peduncular bracts (*pasco* morphotype). A specimen from Ucayali (*Gentry 25466*) is similar, but another from adjacent Junín (*Macbride 5470*) has more ovate pinnae and is referred to the *large* morphotype.

In western Acre, Brazil, and adjacent Peru (Ucayali) specimens are of the *large* morphotype. One specimen (*Henderson 1675*) from western Acre on the border with Amazonas is of the *ulei* morphotype. Five specimens from eastern Acre (*Coêlho 28, Daly 9387, 11986, Figueiredo 342, 615*) resemble those of the *ulei* morphotype except for their pinnae with spinulose bases. They may represent hybrids with the sympatric *D. mitis* subsp. *ecirratus*.

In Madre de Dios, Peru and western Bolivia specimens are all of *ulei* morphotype, although there is much variation in fruit size.

Specimens from the Atlantic Coastal Forest of Brazil (*polyacanthos* morphotype) occur in two areas, with northern outliers in Ceará, Alagoas, and Pernambuco. There are too few specimens from there to test for differences between these areas. Along the Atlantic coast, *D. polyacanthos* occurs slightly more inland than the sympatric *D. orthacanthos*.

20. *Desmoncus prunifer* Poepp. ex Martius (1823-1837: 148).

Atitara prunifera (Poepp. ex Martius) Kuntze (1891: 727). *Desmoncus polyacanthos* var. *prunifer* (Martius) Henderson, 1995: 233. Type:—PERU. Loreto: Maynas, Yurimaguas, December 1830, *E. Poeppig 2148* (holotype G *n.v.*, holotype image!, isotypes GOET *n.v.*, P!). Epitype (here designated):—PERU. Loreto: Yurimaguas, lower Río Huallaga, ca. 135 m, 22 August–9 September 1929, *E. Killip & A. Smith 28045* (epitype US!).

Plants height no data; stems 0.8(0.7–0.8) cm diameter, branching no data. **Leaf** petioles 3.8(2.2–5.4) cm long; rachises 46.5 cm long, 3.2(2.8–3.6) mm wide, the spines usually <1 cm long, mostly abaxial, recurved with markedly swollen bases; pinnae 8 per side of rachis, without long, filiform apices, without a beard of spines at the bases, with uneven surfaces at the bases adaxially, usually covered with spinules and/or dense tomentum; basal pinna 11.3(10.0–12.5) cm long, 2.4(2.3–2.4) cm wide; cirri well-developed, with acanthophylls, with few spines abaxially, mostly on proximal part only, with no intermediate acanthophylls present, usually with a wide gap between pinnae and acanthophylls (i.e., gap wider than that between adjacent acanthophylls). **Inflorescences** with the rachis angular, slightly twisted, thicker than the few to numerous, closely spaced and spirally arranged rachillae, each rachilla not (or very rarely) adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 2.6(2.3–2.9) mm wide; peduncular bracts 18.0 cm long, broad, the surfaces ridged, brown tomentose, densely covered with short, recurved, markedly swollen-based, diagonally oriented spines, these triangular in cross-section, whitish-brown proximally, brown distally, with tomentose margins; rachillae 10(7–13), glabrous or scarcely tomentose initially; proximal rachillae 5.4(5.2–5.5) cm long, 1.7(1.5–1.9) mm wide; stamens no data; **fruits** no data.

Distribution and habitat:—From 5°13'–5°54'S and 75°40'–76°05'W in Peru (Loreto) at 135 m elevation in lowland rainforest (Fig. 11).

Taxonomic notes:—This name, as *Desmoncus polyacanthos* var. *prunifer* (Poeppig ex Martius) Henderson, based on *D. prunifer* Poeppig ex Martius, was mistakenly used by Henderson (1995) for specimens here identified as *Desmoncus vacivus*. The type of *D. prunifer* was given by Henderson as *Poeppig 2148*, although this specimen was not cited by Martius. Three sheets of *Poeppig 2148* are extant at G but comprise leaves only. Two other specimens were at W but are both now destroyed, although images are extant. Neither is labeled as *Poeppig 2148*, although both appear to have been collected by Poeppig at the type locality. One is illustrated by Dahlgren (1959, plate 194, negative 31323) and appears to be the same species as *Poeppig 2148*. The second specimen at W, an image of which is present at NY (negative 31325), also appears to be the same species, and has a densely spiny peduncular bract.

The images of these five specimens strongly resemble one another and three recently-collected specimens (*Croat 18115, Killip 28045, Williams 785*) from the same general locality, including one from Yurimaguas itself. Based on this, they are all regarded as conspecific, and the Yurimaguas specimen (*Killip 28045*) is designated as epitype of *D. prunifer* (because the type is sterile). Unfortunately these specimens still lack fruits (described by Martius as "magnitudine juglandum" but apparently lost). *Desmoncus prunifer* shares all character states with *Desmoncus polyacanthos*, but differs it its much more densely spiny peduncular bract and spinulose pinnae bases. A fourth specimen (*Galeano 2113*) from some distance away in Colombia (Amazonas) may also belong here. This specimen has a single fruit, but this is not unusually large and appears similar to those of *D. polyacanthos*. This specimen is not included in the above description but is mapped.

21. *Desmoncus pumilus* Trail (1876: 353).

Atitara pumila (Trail) Kuntze, 1891: 727. Type:—BRAZIL. Amazonas: Rio Padauiri, 26 June 1874, *J. Trail 1086/LXXV* (holotype K!, isotypes BM!, GH!, P!).

Plants height 4.0(3.0–5.0) m; stems 0.5(0.3–0.7) cm diameter. **Leaf** petioles 1.7(0.5–8.0) cm long; rachises 23.1(10.0–42.5) cm long, 2.6(1.9–4.4) mm wide, the spines usually <1 cm long, mostly abaxial, recurved with markedly swollen bases; pinnae 7(2–15) per side of rachis, without long, filiform apices, without a beard of spines at the bases, without spinules or dense tomentum at the bases adaxially; basal pinna 9.1(4.3–18.7) cm long, 0.9(0.3–2.2) cm wide; cirri well-developed, with acanthophylls, with few spines abaxially mostly on proximal part only, with or without intermediate acanthophylls present. **Inflorescences** with the rachis smooth, not twisted, narrower than the few, distantly spaced and alternate rachillae, each rachilla usually briefly adnate proximally to the rachis and with an irregular bracteole displaced onto the rachis, with or without an axillary pulvinus; peduncles 1.1(0.8–1.6) mm wide; peduncular bracts 16.3(14.0–22.5) cm long, narrow, elongate, ribbed, scarcely brown tomentose, without spines (rarely with few spines); rachillae 4(2–5), glabrous or scarcely tomentose initially; proximal rachillae 3.5(2.5–6.0) cm long, 0.8(0.5–1.1) mm wide; stamens 7; **fruits** 10.0(8.2–11.6) mm long, 6.7(5.0–8.5) mm wide, the surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers; fruiting corollas less than one quarter as long as fruits, splitting irregularly into 3 lobes, the lobes often splitting again; endocarps narrowly ellipsoid with rounded apices, the pores lateral.

Distribution and habitat:—From 1°29'N–7°44'S and 59°50'–71°10'W in the Brazilian Amazon (Amazonas, Roraima) and just reaching Colombia (Amazonas) at 75(57–92) m elevation in campina or campinarana vegetation (Fig. 11).

Taxonomic notes:—This species appears most similar to *D. mitis*, with which it shares slender inflorescences and uneven fruit surfaces Y-shaped fibers.

Subspecific variation:—There is geographic disjunction but there are too few specimens (only 12) to test for differences. The species occurs in widely scattered areas in the central and western Amazon in campina or campinarana vegetation. It comprises small palms with short, slender stems. The specimens from different areas are quite different from one another and there seems a possibility that there is more than one taxon here, but many more specimens are needed to decide the matter.

Two specimens (*dos Santos 75, Rabelo 87)* have pinnae bases with small spines but these appear different from the pinnae bases of *D. mitis* (pinnae bases with uneven surfaces at the bases adaxially, usually covered with spinules and/or dense tomentum). Some specimens (*Calderon 2709, Carvalho 2149, Cid 10996, dos Santos 757*) have distal pinnae intermediate between acanthophylls and more usual pinnae, almost like those of *D. chinantlensis* and similar species.

22. *Desmoncus setosus* Martius (1823–1837: 89).

Atitara setosa (Martius) Kuntze (1891: 727). Lectotype (here designated):—BRAZIL. Amazonas: Rio Japurá, near Tefé, no date, *C. Martius s. n.* (M!). Epitype (here designated):—BRAZIL. Amazonas: Mun. Tefé, near mouth of Rio Tefé, 19 January 1991, *A. Henderson & J. Guedes 1588* (epitype INPA!, isoepitype NY!).

Plants 7.0(2.0–15.0) m tall; stems 0.7(0.5–1.1) cm diameter. **Leaf** petioles 2.0(1.0–4.0) cm long; rachises 41.7(14.0–67.0) cm long, 2.9(2.2–4.1) mm wide, the spines usually <1 cm long, mostly abaxial, recurved with markedly swollen bases; pinnae 8(6–11) per side of rachis, without a beard of spines at the bases, without spinules or dense tomentum at the bases adaxially; basal pinna 12.7(5.5–19.5) cm long, 0.7(0.3–1.3) cm wide; cirri well-developed, with acanthophylls, acanthophylls present, with few spines abaxially, mostly on proximal part only, with no intermediate acanthophylls present, usually with a wide gap between pinnae and acanthophylls (i.e., gap wider than that between adjacent acanthophylls). **Inflorescences** with the rachis angular, slightly twisted, thicker than the few to numerous, closely spaced and spirally arranged rachillae, each rachilla not (or very rarely) adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 1.5(0.9–1.9) mm wide; peduncular bracts 19.1(14.5–23.0) cm long, broad, the surfaces ridged, brown tomentose, sparsely to densely covered with short, recurved, markedly swollen-based, diagonally oriented spines, these triangular in cross-section, whitish-brown proximally, brown distally, with tomentose margins; rachillae 9(4–15), glabrous or scarcely tomentose initially; proximal rachillae 5.3(2.8–7.0) cm long, 0.9(0.5–1.7) mm wide; stamens no data; **fruits** 11.9(11.2–12.8) mm long, 7.5(6.1–8.5) mm wide, the surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers; fruiting corollas splitting irregularly into 3 lobes, the lobes often splitting again; endocarps globose to obovoid with rounded or slightly peaked apices, the pores lateral.

Distribution and habitat:—From 1°51’–3°45’S and 59°58’–69°50’W in the central Amazon region of Brazil (Amazonas) and Colombia (Amazonas) at low elevations in várzea forest or disturbed forest near rivers (Fig. 11).

Taxonomic notes:—Specimens included here were placed by Henderson (1995) in *Desmoncus polyacanthos*. They differ from that species in their uneven fruit surfaces with numerous, subepidermal, short, often branching (Y-shaped) fibers. However, they are a heterogeneous group of specimens and there seems a possibility that there is more than one taxon here (or hybrids), but many more specimens are needed to decide the matter. An epitype is designated because the type is sterile.

Subspecific variation:—One specimen (*Coêlho 2078*), tentatively included here, from Ilha do Marapata has inflorescences with the rachilla bracteoles displaced distally onto the rachilla, similar to those of *D. orthacanthos*. Several specimens have pinnae bases with small spines but these appear different from the pinnae bases of some other taxa (pinnae bases with uneven surfaces at the bases adaxially, usually covered with spinules and/or dense tomentum).

23. *Desmoncus stans* Grayum & de Nevers (1988: 106).

Type:—COSTA RICA. Puntarenas: 7 km W of Rincón de Osa, ridge between Río Riyito and Quebrada Banegas, 8°41'N, 83°32'W, 200–300 m, 26 May 1986, *G. de Nevers, B. Hammel & M. Grayum 7760* (holotype MO *n.v.*, isotypes CAS *n.v.*, CR!, K!, NY!).

Plants 1.3(0.5–2.3) m tall; stems 0.7(0.5–1.0) cm diameter, clustered. **Leaf** petioles 8.7(5.5–12.5) cm long; rachises 21.7(15.0–28.0) cm long, 2.4(1.7–3.3) mm wide, the spines usually >1 cm long, mostly adaxial or lateral, straight with briefly swollen bases; pinnae 5(4–6) per side of rachis, with long, filiform apices, without a beard of spines at the bases, with uneven surfaces at the bases adaxially, usually covered with spinules and/or dense tomentum; basal pinna 14.2(10.7–19.0) cm long, 3.7(2.4–4.3) cm wide; cirri absent, the rachis terminating beyond the distalmost, opposite pair of pinnae in a <1 cm long 'stub', this with an easily broken, longer, smooth, brown extension. **Inflorescences** rachis absent (inflorescence spicate); peduncles 2.3(1.8–2.7) mm wide; peduncular bracts 14.4(12.3–18.0) cm long, narrow, ribbed, densely whitish-brown tomentose, not spiny; rachillae 1, brown tomentose initially, 2.5(1.8–3.0) cm long, 1.6(1.4–2.0) mm wide; stamens 6; **fruits** 13.3(12.8–13.7) mm long, 10.5(9.5–11.1) mm wide, the surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers; fruiting corollas less than one quarter as long as fruits, splitting irregularly into 3 lobes, the lobes often splitting again; endocarps globose to obovoid with rounded or slightly peaked apices, the pores lateral.

Distribution and habitat:—From 8°31'–8°46'N and 83°15'–83°36'W in the Osa Peninsula and adjacent areas in Costa Rica at 301(100–700) m elevation in lowland rainforest (Fig. 12).

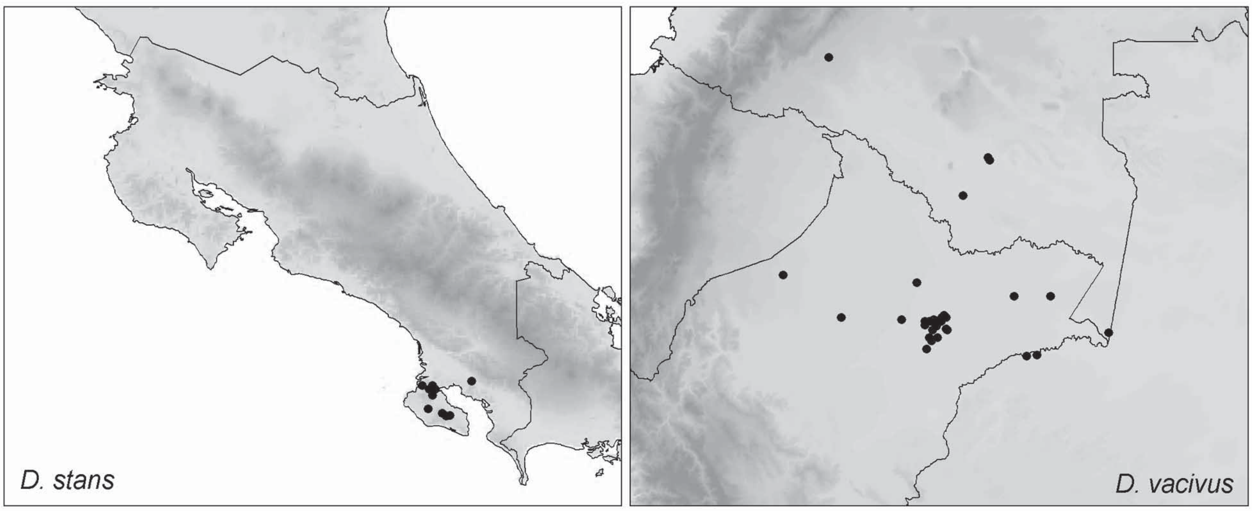

FIGURE 12. Distribution maps of *Desmoncus stans* and *D. vacivus*.

Taxonomic notes:—Unusual in its non-climbing habit, pinnae with long, filiform apices, and spicate inflorescences.

Subspecific variation:—There is no geographic disjunction. The length of the rachilla is given above as 2.5(1.8–3.0) cm long. However, one cultivated specimen (*Grayum 8115* at CR), not included here, has a rachilla 11 cm long with a distal, 7 cm section with only staminate flowers. It appears that this distal staminate section is always present but soon separates and falls from the inflorescence, and so the rachilla seems shorter.

24. *Desmoncus vacivus* Bailey (1949: 186).

Type:—COLOMBIA. Amazonas: Río Igaraparaná, near La Chorrera, ca. 180 m, 4–10 June 1942, *R. Schultes 3941* (holotype BH!).

Plants 5.3(1.5–10.0) m tall; stems 0.7(0.4–0.9) cm diameter, clustered. **Leaf** petioles 4.8(1.5–11.5) cm long; rachises 31.1(22.5–46.5) cm long, 2.9(1.8–5.0) mm wide, the spines usually <1 cm long, mostly abaxial, recurved with markedly swollen bases; pinnae 5(3–7) per side of rachis, without long, filiform apices, without a beard of spines at the bases, with uneven surfaces at the bases adaxially, usually covered with spinules and/

or dense tomentum; basal pinna 13.1(7.0–17.7) cm long, 3.1(1.6–4.7) cm wide; cirri well-developed, with acanthophylls, with few spines abaxially, mostly on proximal part only, with no intermediate acanthophylls present, usually with a wide gap between pinnae and acanthophylls (i.e., gap wider than that between adjacent acanthophylls). **Inflorescences** with the rachis angular, slightly twisted, thicker than the few, closely spaced and spirally arranged rachillae, each rachilla not (or very rarely) adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus; peduncles 2.0(1.0–3.0) mm wide; peduncular bracts 18.8(16.0–24.5) cm long, broad, ribbed, densely brown tomentose, without spines (very rarely with a few spines); rachillae 5(4–9), glabrous or scarcely tomentose initially; basal rachilla 5.1(3.5–6.8) cm long, 1.5(1.0–2.3) mm wide; stamens 6; **fruits** 20.9(18.4–23.9) mm long, 13.3(11.1–15.3) mm wide, the surfaces uneven with numerous, subepidermal, long, branching fibers; fruiting corollas less than one quarter as long as fruits, splitting irregularly into 3 lobes, the lobes often splitting again; endocarps globose to obovoid with rounded or slightly peaked apices, the pores lateral.

Distribution and habitat:—From 1°20'–4°31'S and 69°56'–76°25'W in the western Amazon region in Colombia, Peru, and Brazil at 174(112–550) m elevation in lowland rainforest, often on sandy soils (Fig. 12).

Taxonomic notes:—This distinctive species, with its small leaves and large fruits, was referred to by Henderson (1995) as *Desmoncus polyacanthos* var. *prunifer* (Poeppig ex Martius) Henderson, based on *D. prunifer* Poeppig ex Martius. This is a mistake, as explained under *D. prunifer*.

Undescribed species

Four specimens from the same locality on eastern Andean slopes in Ecuador are unusual in their straight leaf spines, narrow pinnae with long, filiform apices and with an adaxial beard of spines at the bases, and high elevation habitat (700–1350 m). They are all sterile but appear to represent an undescribed species.

ECUADOR. Napo: Hollin-Loreto road to Coca 11 km from take-off from Baeza-Tena road, 1350 m, 0°42'S 77°43'W, 1 Oct 1995, *Balslev et al. 6424* (AAU); Santa Rita west of Archidona, 800–1130 m, 0°55'S 77°52'W, 12 Aug 1996, *Balslev et al. 6447* (AAU); Llanganates, ca. 700 m, 23 Nov 2010, *Cornejo et al. 8398* (NY); km 2, carretera nueva Cotundo-Coca, 1130 m, 5 Aug 1984, *Dodson et al. 15042* (MO).

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Appendix I. Qualitative Variables—Characters and Traits

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/Desmoncus.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. Rachis spines usually >1 cm long, mostly adaxial or lateral, straight with briefly swollen bases (1); rachis spines usually <1 cm long, mostly abaxial, recurved with markedly swollen bases (2). (rachis**)**

2. Cirri well-developed, with acanthophylls, or cirri poorly-developed, the rachis terminating in a short cirrus, acanthophylls present or absent, or cirri absent, the rachis terminating beyond the distalmost pair of pinnae in a short 'stub' (1); cirri poorly-developed , the rachis terminating in a short cirrus, acanthophylls absent but some small, acanthophyll-like pinnae present (2). (cirrus)

3. Cirri with few spines abaxially, mostly on proximal part only (rarely, when cirri poorly-developed, without spines) (1); cirri without spines abaxially (2); cirri with few spines abaxially throughout (3); cirri with many, usually paired spines (4). (cirrusabax)

4. Cirri, when well-developed, with intermediate acanthophylls present (i.e., distalmost pair of pinnae reflexed as acanthophylls and with swollen bases and/or proximalmost pair of acanthophylls like vestigial pinnae), without a wide gap between pinnae and acanthophylls (1); cirri with no intermediate acanthophylls present, usually with a wide gap between pinnae and acanthophylls (i.e., gap wider than that between adjacent acanthophylls). (2). (inters)

5. Pinnae with long, filiform apices (1); pinnae without long, filiform apices (2) (filiform)

6. Pinnae without a beard of spines at the bases adaxially (1); pinnae with an adaxial beard of spines at the bases (2). Pinnae of leaves from young plants often lack these spines. (pinnabase)

7. Pinnae bases with smooth surfaces adaxially, without spinules or dense tomentum (1); pinnae bases with uneven surfaces at the bases adaxially, usually covered with spinules and/or dense tomentum (2). (spinules)

8. Inflorescences with the rachis smooth, not twisted, narrower than the few, distantly spaced and alternate rachillae, each rachilla usually briefly adnate proximally to the rachis and with an irregular bracteole displaced onto the rachis, with or without an axillary pulvinus (1); inflorescences with the rachis angular, slightly twisted, thicker than the few to numerous, closely spaced and spirally arranged rachillae, each rachilla not (or very rarely) adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus (2); inflorescences with the rachis angular, slightly twisted, thicker than the closely spaced and spirally arranged rachillae, each rachilla not adnate to the rachis and with an irregular bracteole adnate to the rachilla and appearing displaced distally onto the rachilla, with a poorly- to well-developed axillary pulvinus (3); inflorescences with the rachis ridged, not twisted, much thicker than the numerous, closely spaced and spirally or irregularly arranged rachillae, each rachilla not or only briefly adnate to the rachis, subtended by an acute bracteole and with a well-developed axillary pulvinus (4); inflorescence rachis absent (inflorescence spicate) (5). (inflos)

9. Peduncular bracts broad, the surfaces ribbed, brown tomentose, sparsely to densely covered with long, straight or sinuous, briefly swollen-based, diagonally or vertically oriented spines, these flattened or triangular in cross-section, whitish-brown proximally, black or brown distally, with tomentose margins (rarely without spines) (1); peduncular bracts broad, the surfaces ridged, brown tomentose, sparsely to densely covered with short, recurved, markedly swollen-based, diagonally oriented spines, these triangular in cross-section, whitish-brown proximally, brown distally, with

tomentose margins (rarely without spines) (2); peduncular bracts narrow, elongate, ribbed, scarcely brown tomentose, without spines (rarely with few spines) (3); peduncular bracts broad, ridged, densely covered with short, straight, swollen-based, vertically oriented spines, these terete, whitish-brown proximally, brown distally, without tomentum (4); peduncular bracts broad, ribbed, densely brown tomentose, without spines (very rarely with a few spines) (5); peduncular bracts broad, ribbed or ridged, densely covered with felty, reddish-brown tomentum, sparsely covered with short, scarcely swollen-based, diagonally oriented, flattened spines, whitish-brown proximally, brown distally, with tomentose margins (6); peduncular bracts broad, ribbed with several more prominent, lighter colored ribs, brown, scarcely or not tomentose, without spines (rarely with a few spines) (7); peduncular bracts narrow, ribbed, densely whitish-brown tomentose, not spiny (8); peduncular bracts broad, the surfaces ribbed or ridged, brown tomentose or glabrous, sparsely to moderately covered with short, straight or sinuous, briefly swollen-based, diagonally or vertically oriented spines, these flattened or triangular in cross-section, whitish-brown proximally, black or brown distally, with tomentose margins (9); peduncular bracts broad, the surfaces deeply ridged, dark brown tomentose, sparsely covered with long, straight or sinuous spines, the bases scarcely swollen but running directly into the ridges of the bract and lying flat against the bract surface, flattened in cross-section, brown proximally and distally, with tomentose margins (10). (peduncbract)

10. Rachillae brown tomentose initially (1); rachillae glabrous or scarcely tomentose initially (2). Recorded only from inflorescences with flowers because tomentum is early deciduous. (tomentum)

11. Stamens five to seven (1); stamens eight to 12 (2). (stamenno)

12. Fruit surfaces uneven with numerous, subepidermal, short, often branching (Y-shaped) fibers (1); fruit surfaces smooth, without any apparent subepidermal fibers (2); fruit surfaces uneven with numerous, subepidermal, long, branching fibers (3); fruit surfaces bumpy from numerous, subepidermal, short, oblique fibers (4). (fruitsurf)

13. Fruiting corollas less than one quarter as long as fruits (1); fruiting corollas to half as long as fruits (2). (frcorolla)

14. Fruiting corollas splitting irregularly into 3 lobes, the lobes often splitting again (1); fruiting corollas not or scarcely splitting, tending to remain cupular (2). (splitting)

15. Endocarps globose to obovoid with rounded or slightly peaked apices, the pores lateral (1); endocarps narrowly ellipsoid with rounded apices, the pores lateral (2); endocarps broadly obovoid with flattened apices, the pores lateral on or near flattened apices (3); endocarps ovoid to obovoid with prominent, peaked apices, the pores lateral (4). (endocarps)

Traits

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

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

Appendix II. Quantitative variables

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

1. Plant height (m); data taken from specimen labels. (plheight)
2. Stem diameter (cm); data taken from specimens only, not from labels, measured just above petiole insertion, and including sheaths. (stemdiameter)
3. Petiole length (cm); measured from leaf sheath to first pinna. (petiole)
4. Rachis length (cm); measured from proximal to distal pinna, excluding cirri. (rachislen)
5. Rachis width (mm); measured at base of leaf blade. (rachiswid)
6. Number of pinnae per side of rachis, excluding acanthophylls. (nodivisions)
7. Basal pinna length (cm). (baspinlen)
8. Basal pinna width (cm); measured at the widest part. (baspinwid)
9. Peduncular bract length (cm). (pedbract)
10. Peduncle width (mm); measured just below the peduncular bract scar. (pedunclewid)
11. Proximal rachillae length (cm). (rachillen)
12. Proximal rachilla width (mm); measured at middle of rachilla, between triad scars. (rachillwid)
13. Number of rachillae. (norachillae)
14. Number of stamens. (stamen)
15. Fruit length (mm). (fruitlen)
16. Fruit diameter (mm). (fruitdiam)

Appendix III. Excluded Names

This list of names comprises published names that have been included in *Desmoncus* but for which no type specimens are available, or the type specimens are insufficient for identification (i.e., the specimen lacks reproductive structures), or the type host institution is unknown, or the name has been transferred to another genus, or the specimen is an illustration. In particular, no type specimens of Barbosa Rodrigues have survived and all his types are drawings. These have not proved possible to identify with any certainty and all Barbosa Rodrigues' names are treated here as Excluded Names. Note that both Glassman (1972) and Wessels Boer (1965) designated lectotypes for many of Barbosa Rodrigues' (1875, 1888, 1902) species; however, these should have been neotypes because they were not designated from the original material.

Atitara drudiana Kuntze (1891: 727). Type not designated.

Atitara paraensis Barbosa Rodrigues (1902: 76). *Desmoncus paraensis* (Barbosa Rodrigues) Barbosa Rodrigues (1903: 57). Type not designated. Neotype (designated by Wessels Boer 1965):—Barbosa Rodrigues 1903: t. 57.

Bactris tenerrima Drude (1881: 328). *Desmoncus tenerrimus* (Drude) Drude ex Burret (1934: 236). *Desmoncus mitis* var. *tenerrimus* (Drude) Henderson (1995: 228). Type:—COLOMBIA. Amazonas: Río Caquetá, Araracuara, no date, *C. Martius s. n.* (holotype M!).

Desmoncus aculeatus Wendland (1854: 20). *Atitara aculeata* (Wendland) Kuntze (1891: 727). Type not designated.

Desmoncus aereus Drude (1881: 307). *Atitara aerea* (Drude) Barbosa Rodrigues (1902: 75). Type:—BRAZIL. Amazonas: Rio Negro, Ayrão, 4 July 1874, *J. Trail 1088/LXXXVIII* (holotype K!).

Desmoncus americanus Lodd. ex Loudon (1830: 382). *Atitara americana* (Lodd. ex Loudon) Kuntze (1891: 727). Type not designated.

Desmoncus andicola Pasquale (1867: 36). Type not designated.

Desmoncus angustisectus Burret (1930: 1025). Type:—BRAZIL. Amazonas: Rio Negro, Trinidade, 12 September 1928, *P. Luetzelburg 22171* (holotype B, destroyed, isotype M!).

Desmoncus ataxacanthus Barbosa Rodrigues (1875: 25). *Atitara ataxacantha* (Barbosa Rodrigues) Kuntze (1891: 727). Type not designated. Neotype (designated by Wessels Boer 1965):—Barbosa Rodrigues, 1903: t. 55.

Desmoncus brevisectus Burret (1934: 215). Type:—BRAZIL. Pará: without locality, 15 November 1932, *W. Hopp 35* (holotype B, destroyed).

Desmoncus caespitosus Barbosa Rodrigues (1888: 37). *Atitara caespitosa* (Barbosa Rodrigues) Barbosa Rodrigues (1902: 76). Type:—BRAZIL. Rio de Janeiro: Serra do Rodeio, no date, *J. Barbosa Rodrigues s. n.* (holotype destroyed). Neotype (designated by Glassman 1972):—Barbosa Rodrigues 1903: t. 63.

Desmoncus cuyabaensis Barbosa Rodrigues (1898: 30). *Atitara cuyabaensis* (Barbosa Rodrigues) Barbosa Rodrigues (1902: 75). Type:—BRAZIL. Mato Grosso: Rio Cuiabá, no date, *J. Barbosa Rodrigues s. n.* (holotype destroyed). Neotype (designated by Wessels Boer 1965):—Barbosa Rodrigues 1903: t. 54A.

Desmoncus dasyacanthus Burret (1934: 213). Type:—VENEZUELA. Carabobo: Puerto Cabello, no date, *P. Preuss 1567* (holotype W, destroyed).

Desmoncus duidensis Steyermark (1951: 85). Type:—VENEZUELA. Amazonas: Caño Negro, SE of Cerro Duida, 23 August 1944, *J. Steyermark 57944* (holotype F!).

Desmoncus dubius Lodd. ex Loudon (1830: 382). *Atitara dubia* (Lodd. ex Loudon) Kuntze (1891: 727). Type not designated.

Desmoncus granatensis Bull (1875: 5). *Atitara granatensis* (Bull) Kuntze (1891: 727). Type not designated.

Desmoncus grandifolius Linden (1881: 16). Type not designated.

Desmoncus huebneri Burret (1934: 200). Type:—BRAZIL. Roraima: Serra do Frechal, Rio Branco, no date, *G. Huebner 80* (holotype B, destroyed).

Desmoncus inermis Barbosa Rodrigues (1901: 17). *Atitara inermis* (Barbosa Rodrigues) Barbosa Rodrigues (1902: 76). Type:—BRAZIL. Rio de Janeiro: Serra do Mar, no date, *J. Barbosa Rodrigues s. n.* (holotype not known). Neotype (designated by Glassman 1972):—Barbosa Rodrigues 1903: t. 60.

Desmoncus intermedius Martius ex Wendland in Kerchove de Dentergarten (1878: 243). Type not designated.

Desmoncus latifrons Bull. *Atitara latifrons* (Bull) Kuntze (1891: 727). Place of original publication not known.

Desmoncus leiorhachis Burret (1934: 203). Type:— BELIZE. Toledo: Rio Grande, 29 March 1933, *W. Schipp S.517a* (holotype B, destroyed).

Desmoncus leptochaete Burret (1934: 204). Type:—COSTA RICA. Puntarenas: Río Abrojo, 12 January 1898, *H. Pittier 11969* (holotype B, destroyed).

Desmoncus leptoclonos Dammer (1907: 129). *Desmoncus mitis* var. *leptoclonos* Henderson (1995: 227). Superfluous names.

Desmoncus longifolius Martius (1844: 52). Type:—PERU. Pasco: Pozuzo, 1784, *J. Pavón s. n.* (holotype MA *n.v.*, isotypes F!, G *n.v.*, K!).

Desmoncus longisectus Burret (1934: 212). Type:—BRAZIL. Alagoas: Serra do Porco, 300 m, March 1932, *E. Werdermann 2984* (holotype B, destroyed).

Desmoncus luetzelburgii Burret (1930: 1025). Type:—BRAZIL. Amazonas: Rio Papuri, Rio Uaupés, Trinidade, 13 December 1928, *P. Luetzelburg 23833* (holotype B, destroyed, isotypes, M! R!).

Desmoncus macroacanthos Martius (1823-1837: 86). *Atitara macroacantha* (Martius) Kuntze (1891: 727). Type:—BRAZIL. Pará: without locality, no date, *C. Martius s.n.* (holotype M!).

Desmoncus macrocarpus Barbosa Rodrigues (1888: 34). *Atitara macrocarpa* (Barbosa Rodrigues) Barbosa Rodrigues (1902: 75). Type not designated. Neotype (designated by Wessels Boer 1965):—Barbosa Rodrigues 1903: t. 53.

Desmoncus macrodon Barbosa Rodrigues (1888: 39). *Atitara macrodon* (Barbosa Rodrigues) Barbosa Rodrigues (1902: 75). Type not designated. Neotype (designated by Glassman 1972):—Barbosa Rodrigues 1903: t. 59.

Desmoncus major Crueg. ex Grisebach (1864: 519). *Atitara major* (Crueg. ex Grisebach) Kuntze, 1891: 727. Type:—TRINIDAD. Caroni, no date, *H. Crueger s.n.* (holotype not known).

Desmoncus melanacanthos Drude (1881: 306). Type not designated.

Desmoncus nemorosus Barbosa Rodrigues (1888: 36). *Atitara nemorosa* (Barbosa Rodrigues) Barbosa Rodrigues (1902: 75). Type not designated. Neotype (designated by Glassman 1972):—Barbosa Rodrigues 1903: t. 56.

Desmoncus oligacanthus Barbosa Rodrigues (1875: 24). *Atitara oligacantha* (Barbosa Rodrigues) Kuntze (1891: 727). Type not designated. Neotype (designated by Glassman 1972) :—Barbosa Rodrigues 1903, t. 58.

Desmoncus orthacanthos var. *trailiana* Drude (1881: 311). Type:—BRAZIL. Amazonas: Rio Purus, Jauaria, 10 September 1874, *J. Trail 1079/CXXVI* (holotype K!).

Desmoncus orthacanthos var. *mitis* Drude (1881: 311). Type:—BRAZIL. "Sertão Amaroleité", September–October 1844, *H. Weddell 2493* (holotype P!).

Desmoncus panamensis Linden (1881: 16). Type not designated.

Desmoncus phengophyllus Drude (1881: 314). *Atitara phengophylla* (Drude) Kuntze (1891: 727). Type:—BRAZIL. Amazonas: Rio Jutahi, 27 January 1875, *J. Trail 1075/CCV* (holotype K!).

Desmoncus philippianus Barbosa Rodrigues (1888: 38). *Atitara philippiana* (Barbosa Rodrigues) Barbosa Rodrigues (1902: 76). Type not designated. Neotype (designated by Glassman 1972):—Barbosa Rodrigues 1903: t. 61.

Desmoncus phoenicocarpus Barbosa Rodrigues (1875: 24). *Atitara phoenicocarpa* (Barbosa Rodrigues) Kuntze (1891: 727). Type not designated. Neotype (designated by Glassman 1972):—Barbosa Rodrigues 1875 t. 1, f. 3–4a–d.

Desmoncus polyacanthos var. *cuspidata* Drude (1881: 314). Type not designated.

Desmoncus polyacanthos var. *angustifolia* Drude. This name appears in Glassman (1972) and the citation of Drude (1881: 313) is given. The type specimen is said to be *Spruce 627* at M. This specimen still exists, with this name written on the label. However, this name is not found on page 313 of Drude (1881), nor on any other page.

Desmoncus polyphyllus Poit. ex Desfontaines (1829: 30). *Atitara polyphylla* (Poit. ex Desfontaines) Kuntze (1891: 727). Type not designated.

Desmoncus pycnacanthos Martius (1823-1837: 89). *Atitara pycnacantha* (Martius) Kuntze (1891: 727). Type:—BRAZIL. Goias: Villa de Palma, Rio Pillões, no date, *J. Pohl 2488* (holotype W, destroyed).

Desmoncus pycnacanthos var. *sarmentosus* Drude (1881: 313). Type:—BRAZIL. Rio de Janeiro, no date, *A. Glaziou 8068* (holotype C *n.v.*, holotype image!, isotype P!).

Desmoncus rudentum Martius (1844: 48). *Atitara rudenta* (Martius) Barbosa Rodrigues (1902: 75). Type:—BOLIVIA. Santa Cruz: Río Piray, near Palometa, no date, *A. d'Orbigny 26* (holotype P!).

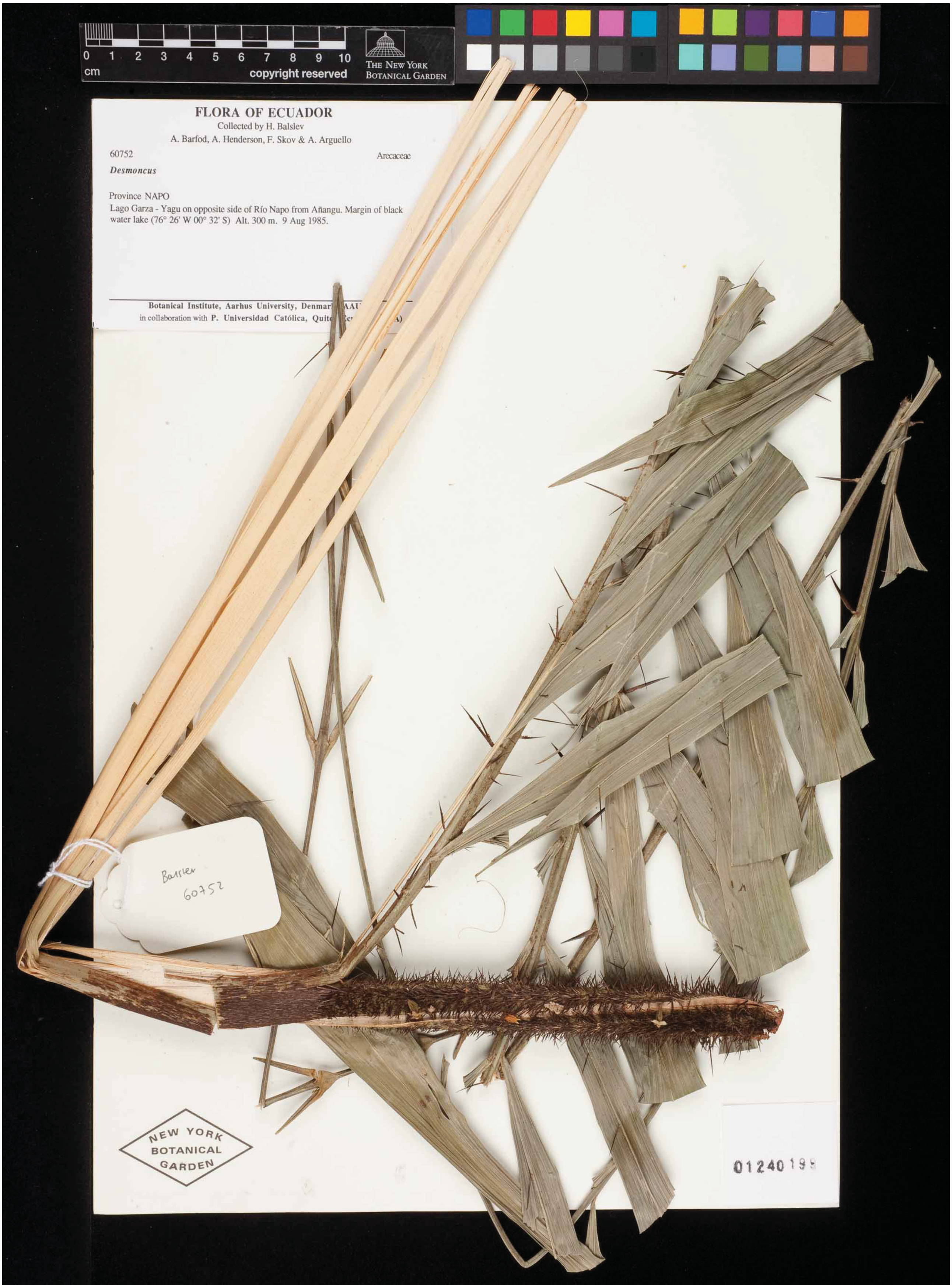
Desmoncus schippii Burret (1934: 202). Type:—BELIZE. Toledo: Rio Grande, 29 March 1933, *W. Schipp S.517* (holotype B, destroyed).

Desmoncus setosus var. *mitescens* Drude (1881: 316). Type not designated.

Desmoncus wallisii Linden (1881:16). Type not designated.

Desmoncus werdermannii Burret (1933: 114). Type:—BRAZIL. Bahia: Feira Santa Ana, ca. 100 m, April 1932, *E. Werdermann 3201* (holotype B, destroyed).

Appendix IV. Plates of Type Images



Appendix IV, Plates 1–4. Isotype of *Desmoncus horridus* subsp. *occidentalis* (*H. Balslev, A. Barfod, A. Henderson, F. Skov & A. Argüello 60752*, NY). Plates 2–3 on next 3 pages.

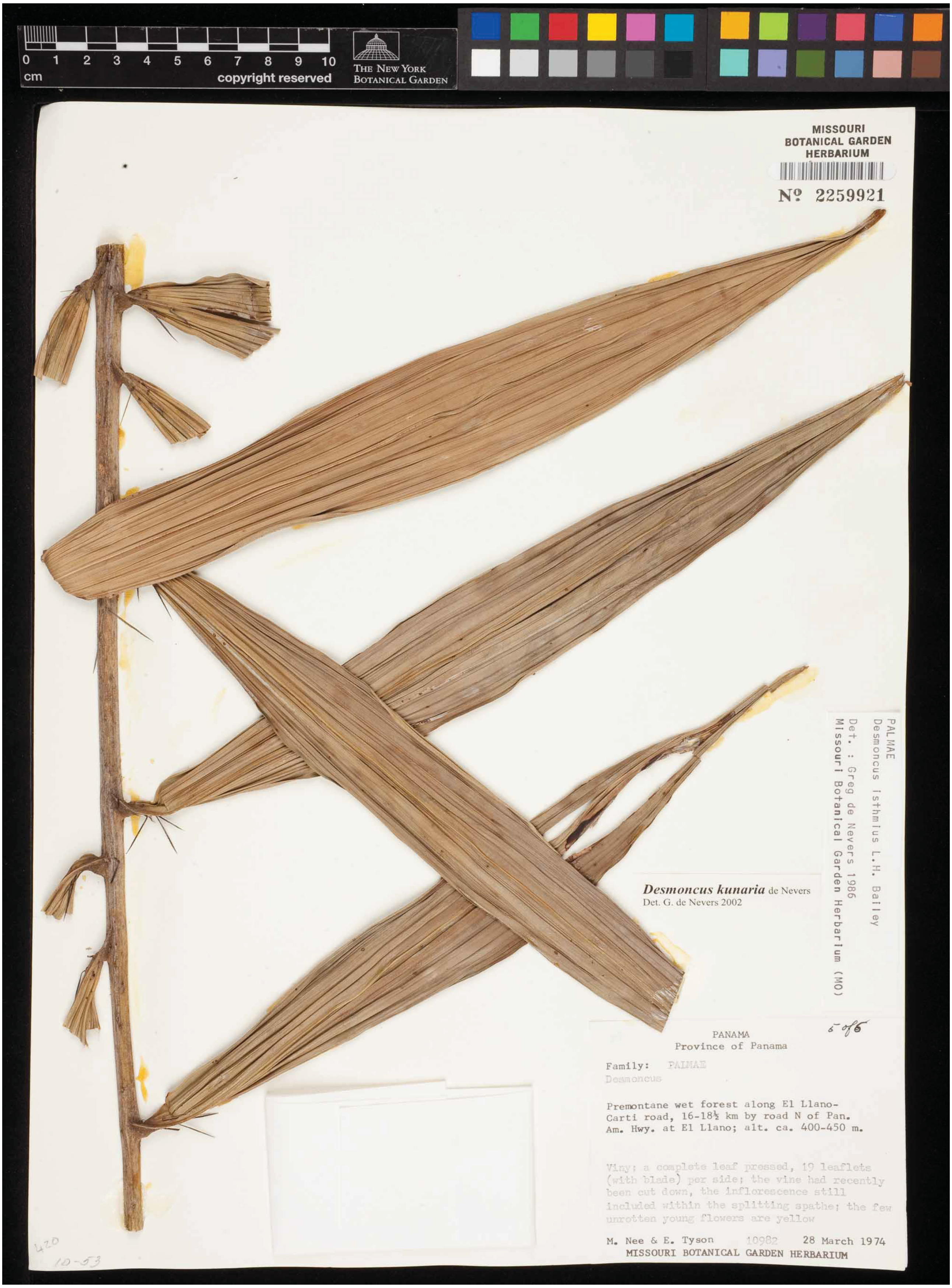
Appendix IV, Plate 2.

Appendix IV, Plate 3.

Appendix IV, Plate 4.

Appendix IV, Plate 5. Isotype of *Desmoncus interjectus* (*G. Galeano, J. Torres, J. Huitoto & B. Plazas 1092,* NY).

Appendix IV, Plates 6–12. Isotype of *Desmoncus kunarius* (*M. Nee & E. Tyson 10982,* MO). Plates 7–12 on the following 6 pages.



Appendix IV, Plate 7.

Appendix IV, Plate 8.

Appendix IV, Plate 9.

Appendix IV, Plate 10.

Appendix IV, Plate 11.

Appendix IV, Plate 12.

Appendix IV, Plates 13–14. Holotype of *Desmoncus loretanus* (*A. Gentry, C. Diaz, J. Aronson & N. Jaramillo 25785,* NY). Plate 14 on the next page.

Appendix IV, Plate 14.

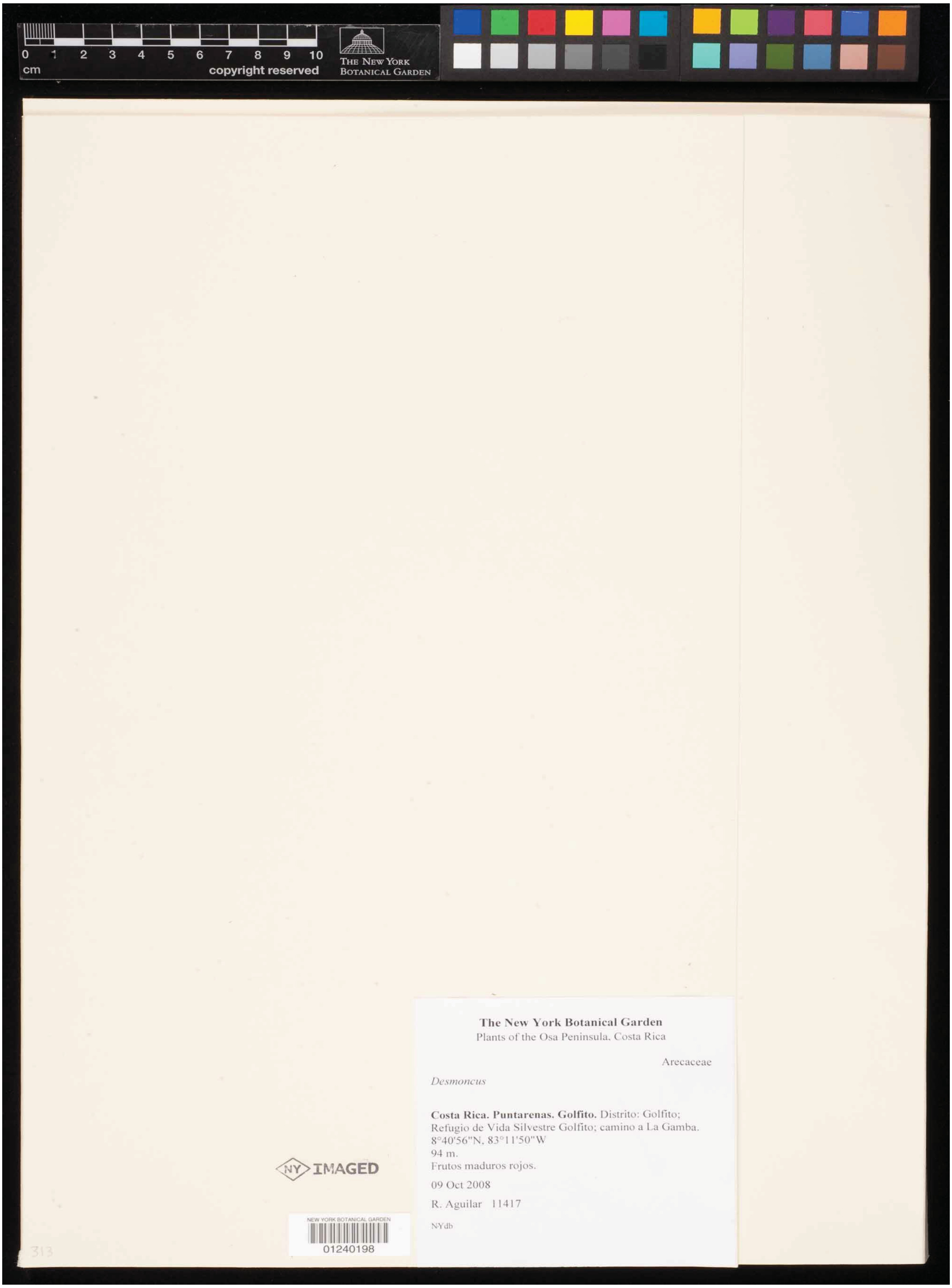
Appendix IV, Plate 15. Isotype of *Desmoncus madrensis* (*F. Chávez 626,* NY).

Appendix IV, Plate 16. Isotype of *Desmoncus mitis* subsp. *ecirratus* (*G. Prance, E. Forero, L. Coêlho, J. Ramos & L. Farias 5636,* NY).

Appendix IV, Plate 17. Isotype of *Desmoncus moorei* (*J. Solano 21,* MO).

Appendix IV, Plates 18–19. Isotype of *Desmoncus obovoideus* (*A. Gentry 6115,* MO). Plate 19 on the next page.

Appendix IV, Plate 19.



Appendix IV, Plates 20–21. Isotype of *Desmoncus osensis* (*R. Aguilar 11417,* NY). Plate 21 on the next page.

Appendix IV, Plate 20.

Appendix V. Numerical List of Taxa and Specimens Examined

Numerical List of Taxa

1. *Desmoncus chinantlensis*
2. *Desmoncus cirrhifer*
3. *Desmoncus costaricensis*
4. *Desmoncus giganteus*
5. *Desmoncus horridus*
5.1. *Desmoncus horridus* subsp. *horridus*
5.2. *Desmoncus horridus* subsp. *apureanus*
5.3. *Desmoncus horridus* subsp. *occidentalis*
5.4. *Desmoncus horridus* subsp. *palustris*
5.5. *Desmoncus horridus* subsp. *prostratus*
6. *Desmoncus interjectus*
7. *Desmoncus kunarius*
8. *Desmoncus latisectus*
9. *Desmoncus leptoclonos*
10. *Desmoncus loretanus*
11. *Desmoncus madrensis*
12. *Desmoncus mitis*
12.1. *Desmoncus mitis* subsp. *mitis*
12.2. *Desmoncus mitis* subsp. *ecirratus*
12.3. *Desmoncus mitis* subsp. *leptospadix*
12.4. *Desmoncus mitis* subsp. *rurrenabaquensis*
13. *Desmoncus moorei*
14. *Desmoncus myriacanthos*
15. *Desmoncus obovoideus*
16. *Desmoncus osensis*
17. *Desmoncus orthacanthos*
18. *Desmoncus parvulus*
19. *Desmoncus polyacanthos*
20. *Desmoncus prunifer*
21. *Desmoncus pumilus*
22. *Desmoncus setosus*
23. *Desmoncus stans*
24. *Desmoncus vacivus*

Specimens Examined

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

Acevedo, P. 6667 (19); 8070 ((5.4)); 14585 (19); 14657 (18)
Agostini, G. 2663 (19)
Aguilar, R. 286 (23); 290 (16); 2672 (23); 4676 (3); 5655 (13); 5656 (3); 5711 (16); 6606 (16); 11417 (16); 11975 (16)
Aguilar, G. 703 (1)
Aguirre-Galviz, L. 1152 (12.1)
Aizprua, R. 1443 (14)
Allen, P. 5117 (14); 5787 (16)

Altamirano, S. 3294 (8)
Amaral, I. 368 (22); 706 (19)
Anderson, A. 296 (12 .2); 1175 (19); 2041 (19); 2205 (5.1)
Anderson, W. 9625 (9); 10577 (18)
Antonio, T. 1785 (15)
Arango, J. 4579 (14)
Araújo, A. 386 (5.1)
Arbeláez, M. 652 (21)
Archer, W. 75 (9); 8353 (5.1)
Arias, J. 1187 (24); 1373 (18); 1552 (12.3)
Asplund, E. 14047 (24); 14247 (24); 14687 (12.2)
Aulestia, M. 3553 (4)
Baca, V. 190 (19)
Bailey, L. 101 (19); 172 (5.1); 418 (5.1); 619 (5.1)
Balée, W. 2301 (18)
Balick, M. 951 (19); 1493 (19) , 1715 (1); 2201 (1); 3275 (1)
Balslev, H. 4775 (12.1); 6265 (19); 6599 (19); 6620 (19); 6630 (19); 6640 (19); 6649 (12.1); 6650 (12.1); 6656.1 (19); 6657 (12.1); 6681 (12.1); 6684 (12.1); 6688 (19); 6689 (19); 6690 (19); 6843 (24); 6859 (12.3); 6925 (24); 7122 (10); 7328 (19); 7342 (19); 7388 (19); 7404 (19); 7408 (19); 7430 (12.1); 7441 (19); 7462 (10); 7463 (19); 7950 (19); 8085 (19); 8097 (19); 8200 (1); 60752 (5.3); 62042 (4); 62050 (19); 62057 (5.3); 62438 (19)
Bangham, N. 368 (1)
Barbour, P. 5067 (19)
Barfod, A. 60073 (2)
Bartlett, H. 12576 (1); 12584(1); 16728 (14)
Bastos, M. 1905 (19); 2238 (19)
Beck, H. 2272 (2); 10191 (8)
Berlin, B. 743 (4)
Bernal, R. 507 (14); 523 (14); 2033 (*); 2083 (5.3); 2538 (12.3); 4408 (5.4)
Bernardi, A. 6522 (19)
Betancur, J. 13982 (6)
Blum, K. 2105 (14)
Bond, F. 63 (5.1)
Borchsenius, F. 285 (2)
Britton, N. 1035 (5.1); 1559 (19)
Broadway, W. 309 (5.1); 3498 (5.1); 4077 (5.1)
Bunting, G. 10219 (14)
Byg, A. 47 (19)
Byron 1066 (18)
Cabrera, R. 3054 (12.3)
Calderón, C. 2709 (21); 2851 (12.2)
Calonje, M. 7004 (7)
Campo, J. 450 (5.2)
Cárdenas, D. 4534 (6); 4642 (22); 6801 (6); 22353 (6); 23658 (6); 24503 (5.4)
Carvalho, F. 627 (17); 2149 (21); 4522 (17); 6849 (19)
Cascante, A. 988 (13)
Castillo, A. 2084 (18)
Castro, E. 150 (3)
Cavalcante, P. 1611 (19)
Chagas, F. 132 (9)
Chagas, J. 1103 (18); 3853 (21)

Chardon, C. s.n (5.2)
Chávez, F. 626 (11); 683 (11)
Churchill, H. 5662 (7)
Cid, C. 37 (19); 2892 (12.2); 2929 (12.2); 3299 (12.3); 4636 (*); 10996 (21)
Clark, J. 4223 (2)
Clark, H. 7982 (*)
Clarke, H. 12189 (19)
Coêlho, D. 688 (22)
Coêlho, L. s.n. (19); 28 (*); 28 (18); 1523 (19); 2078 (22); 36032 (19)
Colque, O. 572 (12.4); 594 (12.4)
Contreras, E. 868 (1); 976 (1); 2581 (1)
Cook, O. 11 (1); 42 (14); 53 (1); 97 (1); 142 (2)
Coradin, L. 7331 (9)
Cordeiro, I. 199 (19)
Cornejo, F. 2946 (12.4)
Costa, J. 680066 (19); 680068 (17); 680069 (17); 680083 (19)
Couvreur, T. 291 (8)
Cowan, C. 3378 (1)
Cremers, G. 11838 (18); 12139 (19); 14340 (19)
Croat, T. 7759 (14); 9314 (14); 10047 (14); 14561 (14); 16806 (2); 18115 (20); 18439 (24); 18767 (24); 18793 (10); 19176 (24); 19584 (24); 20039 (24); 21619 (19); 23338 (1); 24746 (1); 40249 (1); 62352 (12.2); 88912 (19)
Cuadros, H. 1855 (14)
Cuatrecasas, J. 3977 (5.2)
Curran, H. 174 (14); 533 (19)
Dahlgren, B. 437 (19); 523 (19)
Daly, D. 535 (19); 6494 (12.4); 9387 (*); 10779 (19); 10894 (12.3); 11467 (12.2); 11627 (12.3); 11734 (12.2); 11800 (12.2); 11986 (*)
Davidse, G. 12721 (5.2); 13822 (5.2); 14755 (5.2); 15872 (5.2); 17831 (5.1); 17988 (19); 21852 (19); 27672 (19); 27712 (5.4); 30963 (13)
De La Cruz, J. 3360 (18)
Delascio, F. 7964 (5.2)
Díaz, C. 252 (10)
Diaz, W. 319 (19)
Dodson, C. 7190 (2)
Dorr, L. 7779 (19)
Dransfield, J. 4861 (2)
Duke, J. 9806 (14)
Duque, J. 7391 (12.3)
Dwyer, J. 10958 (1); 11352 (1)
da Vinha, S. 76 (19)
de Bruijn, J. 1235 (19)
de Castro, A. 573 (19)
de Granville, J.-J. 2259 (19); 11232 (18); 13678 (18)
de Nevers, G. 4415 (7); 4716 (2); 4784 (7); 7760 (23)
de Paula, J. 1213 (19)
dos Santos, J. 757 (21)
Eiten, G. 9209 (9); 10208 (19)
Ek, R. 835 (18)
Espinelli, F. 406 (21)
Estupiñán, C. 464 (14)

Evans, R. 1702 (1); 2742 (19)
Fendler, A. 732 (19); 2468 (19)
Fernandes, H. 90 (19); 2090 17
Fernández, A. 2410 (19); 3942 (19); 11383 (19)
Ferreira, E. 145 (19); 321 (12.2); 518 (9)
Fiaschi, P. 244 (17); 256 (17); 723 (17)
Figueiredo, C. 342 (*); 615 (*)
Fleck, D. 508 (12.3); 795 (4); 815 (12.1)
Fleury, M. 1435 (19)
Folli, D. 673 (17); 1696 (17)
Fonnegra, R. 272 (2)
Fonsêca, S. 163 (19)
Forero, E. 6384 (12.2); 9080 (14)
Forest Dept. 3579 (19); 5212 (5.1)
Foster, R. 8814 (12.3)
França, G. 303 (19)
Freitas, J. 216 (12.2)
Fróes, R. 2001 (5.1); 11765 (19); 31198 (19)
Fuchs, H. 21833 (2)
Fuentes, A. 4081 (12.4)
Furtado, P. 76 (9)
Galeano, G.1092 (6); 2113 (20)
Garwood, N. 2178 (15)
Gentle, P. 348 (1); 528 (1); 2453 (1); 4750 (1)
Gentry, A. 4999 (14); 6115 (15); 8035 (1); 13351 (18); 14819 (19); 16560 (12.3); 19108 (10); 20734 (24) , 22007 (19); 25466 (19); 25785 (10); 27084 (11); 27743 (12.3); 29230 (12.3); 30363 (2); 31736 (24); 35355 (2); 38752 (19); 39709 (12.3); 41015 (2); 42260 (12.3); 43657 (11); 43738 (19); 46310 (5.2); 47293 (5.4); 47988 (2); 49428 (17); 49499 (17); 50223 (5.1); 50347 (19); 53319 (2); 53392 (2); 53795 (2); 54546 (19); 54608 (12.3); 56146 (19); 58515 (12.3); 60885 (12.3); 61654 (19); 61699 (19); 61978 (12.1); 68598 (11); 74275 (19); 76380 (19); 78307 (11); 78784 (23)
Gillespie, L. 812 (19); 1050 (18); 1226 (5.1)
Gines, H. 5248 (5.1)
Gleason, H. 164 (18); 269 (18)
Goldenberg, R. 1347 (19)
González, A. 813 (19)
Gottsberger, I. 111482 (5.1)
Graham, J. 4699 (12.3)
Grández, C. 434 (19); 1069 (24); 1782 (10); 2336 (24)
Grayum, M. 4463 (3); 8746 (3); 11117 (13)
Guánchez, F. 1731 (19)
Gudiño, E. 397 (19)
Guillén, R. 1517 (5.5); 1559 (5.5); 3169 (5.5); 3841 (8)
Hage, J. 400 (19); 858 (17)
Hahn, W. 5134 (18)
Hammel, B. 1863 (15); 19136 (23); 21197 (13); 21940 (3)
Harley, R. 11230 (9); 17904 (19); 17969 (17); 18151 (17)
Harmon, W. 2543 (1)
Hassler, E. 11293 (9)
Hatschbach, G. 47732 (17); 57017 (17)
Hayes, S. 359 (14)
Hemmendorff, E. 349 (17)

Henderson, A. 36 (19); 62 (13); 178 (22); 300 (*); 336 (19); 875 (24); 977 (19); 1077 (18); 1101 (12.2); 1588 (22); 1607 (19); 1609 (18); 1610 (19); 1617 (17); 1640 (12.4); 1642 (19); 1675 (19); 1688 (4); 1693 (12.2); 1696 (5.3); 1811 (23); 3009 (19)
Heringer, E. 15163 (19)
Hernández, H. 373 (1); 629 (1)
Herrera, G. 1107 (13); 4596 (23)
Hoffman, B. 799 (19); 6380 (19)
Hoffman, D. 141 (5.4)
Holdridge, L. 5126 (13)
Hollowell, T. 412 (5.1)
Holm, R. 931 (13)
Howard, R. 10405 (5.1)
Huashikat, V. 979 (4); 1098 (4); 1099 (4); 2309 (12.3)
Idrobo, J. 506 (19) , 4707 (12.3)
Irwin, H. 7194 (9)
Jangoux, J. 85007 (12.2)
Jansen-Jacobs, M. 2539 (19)
Jaramillo, J. 4344 (12.1); 4607 (12.1)
Jaramillo, N 1290 (19)
Jardim, J. 89 (17); 1538 (19)
Jativa, C. 644 (2)
Jenman, G. 7726 (5.1)
Juncosa, A. 1570 (2)
Kahn, F. 504 (19); 540 (*); 563 (19); 3503 (19); 3506 (19)
Kelloff, C. 631 (19); 917 (18)
Kennedy, H. 2800 (15)
Killip, E. 27071 (12.3); 28045 (20); 28807 (12.3); 30573 (19)
Kinupp, V. 1410 (22); 2334 (9)
Knab-Vispo, C. 368 (19)
Kohn, E. 1163 (4)
Kramer, K. 2472 (19); 2708 (5.1); 3146 (19)
Krapovickas, A. 23228 (17); 31940 (*)
Krieger, L. 18905 (19)
Krukoff, B. 4996 (12.2)
Kuhlmann, J. 522 (8)
Kvist, L. 1156 (*); 1196 (19); 1545 (19)
La Rotta, C. 137 (24)
Lanna, J. 973 (17)
Leal, E. 140 (5.1)
Lemos, R. 6321 (19)
Lewis, M. 813 (17); 1059 (19); 37933 (19)
Liebmann, F. 6596 (1); 6956 (1)
Liesner, R. 5694 (19); 6274 (*); 8940 (*) , 9216 (19); 13632 (19); 25728 (18)
Lima, J. 796 (19)
Lindman, C. 2827 (5.5); 3273 (9)
Listabarth, C. 1110589 (*)
Little, D. 16639 (5.1)
Lleras, E. 17184 (10)
Lobato, L. 34 (5.1)
Loomis, H. 54 (19); 63 (5.1)

López, R. 10994 (19)
Loureiro, A. s. n. (*)
Luetzelburg, P. 20026 (17)
Lundell, C. 1555 (1); 2646 (1); 3421 (1); 4750 (1); 16237 (1)
Maas, P. 3559 (18); 12879 (12.2); 13130 (12.2)
Macbride, J. 5470 (19)
Macedo, A. 705 (9)
Maciel, U. 167 (18)
Madison, P. 31 (19); 361 (21)
Madriñán, S. 931 (5.4)
Maguire, B. 23093 (18); 25011 (19)
Malagón, W. 85 (4)
Malave, I. 23 (5.1)
Manriquez, G. 2535 (1); 3482 (1)
Marín, J. 194 (23); 1983 (24)
Martínez, E. 6344 (1); 27903 (1)
Martius, C. s. n. (12.1)
Mata 4 (19); 18 (19)
Matos, F. 244 (19)
Matuda, E. 3196 (1)
Mauro, J. 50 (19)
Maxon, W. 6573 (14)
Mayfield, M. s. n.. (23)
McDaniel, S. 14208 (19); 21624 (24); 32182 (10)
McDowell, T. 3109 (18); 3730 (19); 4104 (18)
McPherson, G. 6961 (15)
Mendes, V. 251 (9)
Mendoza, A. 2733 (1)
Miraña, J. 8 (24)
Miranda, F. 470 (*)
Molina, A. 1808 (13)
Monteiro, O. 1317 (19)
Moore, H. 6361 (1); 8273 (1); 8432 (24); 8449 (24); 8591 (12.4); 9471 (2); 10121 (13); 10349 (5.1); 10360 (19); 10377 (5.1); 10380 (5.1); 10510 (14)
Mora, E. 580 (3); 626 (23)
Moraes, M. 845 (12.4)
Moraga, C. 975 (13)
Morales, J. 6333 (16); 9284 (13)
Moreno, L. 162 (8); 163 (12.2); 175 (12.4); 185 (12.2); 192 (8)
Moreno, P. 12428 (13); 24093 (1)
Mori, S. 5184 (15); 7737 (2); 8063 (18); 8100 (18); 8455 (18); 9128 (19); 15604 (18); 17735 (19); 22378 (22)
Morillo, G. 8873 (19)
Mowbray, T. 1441 (13)
Murillo, J. 1940 (19)
Murray, N.1550 (24)
Mutchnick, P. 829 (19)
Nascimento, J. 723 (19)
Nee, M. 10982 (7); 14003 (14); 17811 (19); 34905 (12.2); 34990 (12.2); 39611 (19); 42329 (18)
Noblick, L. 1796 (17); 4695 (17); 4721 (17); 4724 (19); 4771 (19); 4791 (17); 4804 (19)
Nogueira, P. 688 (5.1)

Núñez, P. 10015 (11); 10483 (11); 19077 (12.3)
Oldeman, R. 1269 (19)
Oliveira, J. 732 (19)
Ortega, F. 3290 (5.2)
Pabon, M. 329 (5.4)
Palacios, W. 932 (19)
Pardini, R. 39 (19); 72 (19)
Peixoto, A. 3010 (17); 3402 (17); 3491 (17)
Pereira-Silva, G. 4648 (9); 4766 (9); 9567 (19)
Persaud, A. 77 (18)
Pessôa, C. 254 (12.2); 319 (12.2)
Pinto, E. 1278 (5.2)
Pipoly, J. 7442 (18); 7451 (19); 9236 (18); 9956 (18); 15001 (24); 16068 (12.3)
Pirani, J. 2330 (19); 2418 (19); 2485 (17); 2961 (17); 3062 (17)
Pires, O. 222 (22)
Pires, M. 484 (19); 2602 (19); 47538 (19)
Pittier, H. 416 (2); 2606 (14); 7078 (19); 7795 (19)
Plowman, T. 3720 (14); 9547 (18); 9577 (*); 9742 (*); 9881 (*); 12572 (19)
Poncy, O. 249 (19)
Poole, J. 2005 (5.4)
Posada, A. 2244 (12.3)
Prance, G. 5636 (12.2); 10067 (19); 12310 (12.3); 12490 (12.3); 13946 (12.2); 23993 (24); 29511 (19); 29626 (19)
Prévost, M. 1852 (5.1); 2729 (19)
Quesada, F. 801 (23)
Quinet, A. 1343 (12.2)
Rabelo, A. 79 (12.3); 87 (21); 88 (19)
Rabelo, B. 2533 (18)
Ratter, J. 5735 (19)
Read, R. 3564 (19); 3570 (17)
Redden, K. 5943 (19)
Renteria, E. 3554 (14); 4812 (14)
Revilla, J. 341 (10); 957 (24); 1078 (19); 1166 (10); 1568 (24)
Rimachi, M. 10809 (10); 11783 (12.3)
Robles, R. 1381 (13)
Rocha, A. 258 (18); 688 (19); 725 (19); 991 (5.1)
Rodrigues, W. 9790 (21)
Rodriguez, A. 364 (13)
Rosa, N. 665 (19)
Rosero, L. 2007 (18)
Rubio, D. 1422 (2)
Rudas, A. 2297 (19); 2868 (12.3); 3103 (12.3)
Rueda, R. 1726 (13); 3544 (13); 4097 (13); 4718 (13)
Rusby, H. 98 (19)
Sacco, J. 43 (11)
Saldias, M. 2624 (5.5)
Santos, N. 5162 (17)
Sasaki, D. 14 (12.2)
Saunders, J. 553 (1)
Scariot, A. 617 (19); 621 (*)
Schinini, A. 29368 (9)

Schultes, R. 3941 (24); 15158 (6); 16233 (6)
Schunke, J. 2644 (11); 6927 (19); 14877 (19); 15033 (12.2); 15269 (12.3); 15726 (12.3)
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