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An overview of the taxonomy of *Attalea* (Arecaceae)

Una visión general de la taxonomía de *Attalea* (Arecaceae)

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Abstract

The genus *Attalea* (Arecaceae) is distributed in continental habitats of the Neotropical region and in some Caribbean islands. Life forms of *Attalea* species vary from small acaulescent palms to tall and massive palms, always solitary. The ecological range of the genus encompasses most of the Neotropical ecosystems, from coastal sand dunes to sub-Andean forests up to 1600 m in elevation, lowland wet to dry forests, savannas, swamps, etc. The taxonomy of the genus has been poorly understood due to conflicting genus and species concepts that exist since the last decades. Taxonomical problems have been caused by the lack of adequate material, especially species of large size, loss of many types and difficulties in interpreting hybrids. In this article, I review the most recent taxonomic literature on *Attalea*. The number of species in *Attalea* varies from 29 to 67 depending on different authors, with a maximum estimate of 73 species when combining the revised publications. There is a consensus for the validity of 20 species among modern palm taxonomists. The most conflicting species or group of species are discussed in detail as well as the taxonomic significance of some characters such as the pattern of insertion of staminate flowers on rachillae, insertion of pinnae on rachis, and arrangement of fibrous strands in the endocarp.

Keywords: *Attalea*, Arecaceae, taxonomy, palms, Neotropics.

Resumen

Attalea (Arecaceae) es un género distribuido en toda la región Neotropical continental y en algunas islas Caribeñas. Las formas de vida de las especies de *Attalea* incluyen tanto pequeñas palmeras como plantas de gran tamaño, siempre con tallo solitario. El rango ecológico del género abarca prácticamente todos los ecosistemas neotropicales desde las dunas de arena costeras hasta el bosque sub-Andino (algunas especies llegan a 1600 m de altitud), pasando por todo tipo de bosque tropical, seco o húmedo, pantanos, sabanas, etc. La taxonomía del género ha sido poco entendida y conceptos conflictivos sobre géneros y especies existen desde hace décadas. Las dificultades taxonómicas resultan de la falta en los herbarios de material adecuado, en particular para las grandes especies, de la pérdida o destrucción de numerosos tipos y de la frecuente hibridación entre especies. En este artículo se analizan los trabajos taxonómicos más recientes sobre *Attalea*. El número de especies varía entre 29 y 67 según los autores, y un máximo estimado de 73 especies al combinar los diferentes trabajos; siendo 20 las especies en consenso entre autores. Las especies y grupos de especies más problemáticos se tratan detalladamente y se enfatiza el significado taxonómico de algunos caracteres como la inserción de las flores estaminadas en la raquilla, inserción de las pinas en el raquis, distribución de las fibras en el endocarpio, entre otros.

Palabras claves: *Attalea*, Arecaceae, taxonomía, palmeras, neotrópico.

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Introduction

Attalea is one of the most conspicuous palm genera in the Neotropics. Ranging from Mexico to Bolivia, Paraguay, Southern Brazil and the Caribbean, it is found in most tropical lowland ecosystems and in the Andes up to 1200-1600 m elevation. Numerous species are massive palms forming dense stands and they are therefore remarkable elements of the landscape, but there are also smaller acaulescent species in both forests and savannas.

Identification of *Attalea* species has however been difficult for several reasons. The first problem is the paucity of good herbarium collections. Most species have very large leaves, inflorescences and fruits, and also exhibit biological characteristics like very seasonal phenology and functional dioecy which make it difficult to gather complete material. Moreover, many valuable collections, including type specimens were lost or destroyed (Henderson, 1995). Consequently, several large and extremely abundant *Attalea* species remained undescribed until recently or are still very poorly known or of doubtful status.

The second problem is the use of different genus concepts among taxonomists. In the Field Guide to the Palms of the Americas (Henderson et al., 1995), all species of subtribe Attaleinae *sensu* Uhl and Dransfield (1987) are included in a broad genus *Attalea*, while in the Taxonomic Treatment of Palm

separate genera (*Attalea sensu stricto*, *Orbignya*, *Scheelea*, *Maximiliana* and *Ynesa*). It is to be noted that the subtribe Attaleinae has been subsequently extended (Dransfield et al., 2005) to genera previously included in Beccariophoenicinae and Butiinae by Uhl and Dransfield (1987). Zona (2002) established the still needed corresponding names in the *Attalea sensu lato* concept for the species treated by Glassman in other genera, so that the two concepts are now fully compatible. However, in order to do these transfers of genera, it was needed to disentangle particularly complex nomenclatural problems. This is exemplified by the case of the *babaçu*, one of the best known and economically most important species (Anderson et al., 1991). The first name apparently applied to this species is *Attalea speciosa* Mart., described from Brazil in 1826, but although there is an indication of type locality in the original description, no specimen was cited as type for this name, so it is a *nomen confusum* (Glassman, 1999). Martius described again this palm in 1844, based on d'Orbigny's collections from Bolivia as *Orbignya phalerata* Mart. In the five genera concept, this should be the correct name of the *babaçu*, although Barbosa Rodrigues made the combination *Orbignya speciosa* based on the older *nomen confusum*. When considering a single, broad genus *Attalea*, it is not possible to make a new combination, *Attalea phalerata*, for the *babaçu*, because it would be homonymous with an older name for another palm, *Attalea phalerata* Mart. ex Spreng. described in 1825, which was latter

for the *babaçu* if one considers that *A. speciosa* is not valid. Zona (2002) proposed *Attalea glassmanii*, but Govaerts and Dransfield (2005), following Henderson et al. (1995) and other authors, chose to conserve the old name *Attalea speciosa* under which this important palm has been known since a long time.

Recognizing a single genus is biologically sound since there are many fertile hybrids between *Attalea sensu stricto*, *Orbignya*, *Scheelea* and *Maximiliana*, which indicate a very close affinity of these taxa (Balick et al., 1987 a, b). At the seedling stage, *Attalea sensu lato* species are recognizable by the lanceolate eophylls with dentate upper margins and latter by the asymmetrical pinna apex with a lateral projection, brownish on the abaxial side (Fig. 3). These characters make *Attalea s.l.* instantly recognizable at any developmental stage, while any further identification generally requires flowers and fruits. Wessels Boer (1965) gave a lengthy argumentation in favor of a single genus *Attalea*. Henderson and Balick (1991) provided additional arguments upon examining a poorly known species, *Attalea crassispatha*. However, within a broad genus *Attalea*, there most probably exist monophyletic entities corresponding closely to taxa previously considered at the generic level. As a matter of fact, when attempting to identify a species of this group of palms, the distinction of four entities corresponding to the genera *Attalea*, *Scheelea*, *Orbignya* and *Maximiliana*, as it was adopted in Genera Palmarum (Uhl and Dransfield, 1987), remains the easiest way to proceed. These taxa differ markedly in staminate flower structure, although they are often undistinguishable vegetatively. Palms referred to as *Orbignya* are characterized by stamens with coiled anthers, and staminate flowers often densely packed on rachillae (Fig. 8). All the other staminate flower types have straight anthers. *Maximiliana* has staminate flowers with petals much shorter than the stamens. There is a single species of this type, *A. maripa*, which is widespread in the Amazon region. *Attalea sensu stricto* and *Scheelea* have staminate flowers with petals longer than stamens. *Attalea s.s.* has flattened petals which enclose the stamens (Fig. 7) while *Scheelea* has linear-cylindrical fleshy petals which do not enclose the stamens (Fig. 5-6). Assigning an *Attalea sensu lato* species to its staminate flower type narrows considerably the search for the species name at any particular location. In some places, there are species of *Attalea*, *Scheelea* and *Orbignya* types which are vegetatively almost identical but which can be readily recognized when staminate flowers are available.

Excluding unambiguous hybrids, there are in fact only five species which do not fit well within the four genera scheme, and constitute an argument to consider a single genus *Attalea* (Wessels Boer, 1965; Henderson and Balick, 1991). One species from the upper Rio Negro region, *A. luetzelburgii*, has mixed characters of *Orbignya* and *Scheelea* and some unique characteristics which led at one time to place it in a separate genus, *Parascheelea* (Dugand, 1940). Another species from north-eastern Amazonia, *Attalea dahlgreniana* has mixed characters of *Orbignya* and *Maximiliana* and had been considered either as a distinct genus, *Markleya* (Bondar, 1957) or an intergeneric hybrid, \times *Maximibignya* (Glassman, 1999). *Attalea attaleoides*, from central and eastern Amazonia has characters of *Scheelea* and *Maximiliana*. *Attalea colenda*, a species endemic to the Pacific coast of northern South America (Fig. 1), has been placed in its own genus as well, *Ynesa*. Balslev and Henderson (1987) interpreted it as a typical *Attalea sensu stricto*, while Glassman (1999) considered it as a

putative hybrid between *Orbignya* and *Attalea* or *Maximiliana*. The outlying *Attalea crassispatha*, the only species of the Greater Antilles (Haiti), has also unusual characteristics, especially in staminate flower structure and pollen morphology (Henderson and Balick, 1991). It somewhat resembles *Orbignya*, however, especially for the curled anthers at anthesis, and Glassman (1999) transferred it to this genus.

However, even when the staminate flower type has been identified, the conflicts between taxonomic treatments and generic concepts make it difficult to choose the appropriate name for a particular palm. For example, around Iquitos in Peru, there are three acaulescent species with pinnae regularly arranged and spreading in one plane, which key out as *Attalea racemosa*, *Attalea microcarpa* and *Attalea butyracea* in Henderson's Palms of the Amazon (1995), and as *Attalea ferruginea*, *Orbignya polysticha* and *Scheelea plowmanii*, respectively, in Glassman's (1999) monograph.

It is therefore very difficult to determine how many species of *Attalea sensu lato* should be recognized. Wessels Boer (1965) gave an estimate of around 100 species. The treatment of Glassman (1999), with 65 species, recognizes fine-scale variation at the species level (Zona 2002). Many of the species accepted or described as new by Glassman (1999) are based on one or very few and generally incomplete herbarium collections, preventing an adequate evaluation of the natural variability of populations. Nevertheless Glassman's treatment provides names for very distinctive species previously undescribed like *A. plowmanii* (Galeano and Bernal, 2002) or *Attalea moorei* (Fig. 5). Henderson et al. (1995) used generally a broad species concept, which in some instances, like in the complex of *Attalea butyracea*, has not been supported by subsequent detailed field studies (Stauffer and Fariñas, 2006). The two treatments nevertheless agree on the definition of 20 species (Table 1).

The World Checklist of Palms (Govaerts and Dransfield, 2005), mostly based on Glassman's treatment, includes 67 accepted species in the genus *Attalea*. These authors tentatively accept *Attalea blepharopus* from Bolivia, *A. hoehnei* from Brazil and *A. rhynchocarpa* from Colombia, all considered as uncertain names by Glassman (1999) and Henderson et al. (1995). Henderson (1995) listed *A. blepharopus* as a synonym of *A. phalerata* while Moraes (2004) included it as a synonym of *A. butyracea*. Govaerts and Dransfield (2005) and Henderson et al. (1995) also accept *Attalea dahlgreniana*, *A. spectabilis* and *A. attaleoides* while Glassman (1999) considers the first a hybrid and the latter two doubtful names. Henderson (1995) discussed various hypotheses about the uncertain nature of *A. spectabilis*. Four species, *Attalea burretiana*, *A. liebmanni*, *A. lundellii* and *A. sagotii* are accepted by Glassman (1999) but not by Govaerts and Dransfield (2005) nor by Henderson et al. (1995). Both Glassman (1999) and Govaerts and Dransfield (2005), listing 65 and 67 species, respectively, are far from the 29 species estimate of Henderson et al. (1995). Correspondences of species names (when possible) are given in Table 1. The first column of the table includes all taxa accepted in at least one of four most recent partial or complete treatments of the genus (Glassman 1999; Govaerts and Dransfield, 2005; Henderson et al., 1995; Noblick, 2007). This results in the highest possible estimate of 73 species in *Attalea*, among which only 20 species have been

Table 1. Comparative listing of accepted names in *Attalea*. Names accepted in all recent treatments, or corresponding to the same species concept are in bold. The combined taxon list is based on the narrowest species concept, or unambiguous type specimen, in the case of controversial taxa.

Combined taxon list	Govaerts & Dransfield (2005)	Glassman (1999)	Henderson et al. (1995)
<i>Attalea allenii</i>	Accepted	Accepted	Accepted
<i>Attalea amygdalina</i>	Accepted	Accepted	Accepted
<i>Attalea amylycea</i>	Accepted	Accepted	Syn. of <i>A. phalerata</i>
<i>Attalea anisitsiana</i>	Accepted	Accepted	Syn. of <i>A. phalerata</i>
<i>Attalea apoda</i>	Accepted	Accepted	Erroneous syn. of <i>A. speciosa</i>
<i>Attalea attaleoides</i>	Accepted	Doubtful	Accepted
<i>Attalea barreirensis</i>	Accepted	Described as new	Incl. in <i>A. exigua</i>
<i>Attalea bassleriana</i>	Accepted	Accepted	Syn. of <i>A. butyracea</i>
<i>Attalea blepharopus</i>	Accepted	Doubtful	Doubtful
<i>Attalea brasiliensis</i>	Accepted	Described as new	?
<i>Attalea brejinhoensis</i>	Accepted	Described as new	Incl. in <i>A. speciosa</i>
<i>Attalea buretiana</i>	Syn. of <i>A. oleifera</i>	Accepted	Syn. of <i>A. oleifera</i>
<i>Attalea butyracea</i>	Accepted	Accepted	<i>A. butyracea pro parte</i>
<i>Attalea camopiensis</i>	Accepted	Described as new	Tentatively included in <i>A. attaleoides</i>
<i>Attalea cephalotus</i>	Accepted	Accepted	Syn. of <i>A. butyracea</i>
<i>Attalea cohune</i>	Accepted	Accepted	<i>A. cohune pro parte</i>
<i>Attalea colenda</i>	Accepted	Accepted	Accepted
<i>Attalea compta</i>	Accepted	Accepted	Syn. of <i>A. oleifera</i>
<i>Attalea crassispatha</i>	Accepted	Accepted	Accepted
<i>Attalea cuatrecasana</i>	Accepted	Accepted	Accepted
<i>Attalea dahlgreniana</i>	Accepted	Considered hybrid	Accepted
<i>Attalea degranvillei</i>	Accepted	Described as new	Tentatively included in <i>A. attaleoides</i>
<i>Attalea dubia</i>	Accepted	Accepted	Accepted
<i>Attalea eichleri</i>	Accepted	Accepted	Accepted
<i>Attalea exigua</i>	Accepted	Accepted	Accepted
<i>Attalea fairchildensis</i>	Accepted	Described as new	?
<i>Attalea ferruginea</i>	Accepted as <i>A. racemosa</i>	Accepted	Accepted as <i>A. racemosa</i>
<i>Attalea funifera</i>	Accepted	Accepted	Accepted
<i>Attalea geraensis</i>	Accepted	Accepted	Accepted
<i>Attalea guacuyule</i>	Accepted	Accepted	Syn. of <i>A. cohune</i>
<i>Attalea guianensis</i>	Accepted	Accepted	Incl. in <i>A. attaleoides</i>
<i>Attalea guaranitica</i>	Syn. of <i>A. geraensis</i>	Syn. <i>A. geraensis</i>	Syn. of <i>A. geraensis</i>
<i>Attalea hoehnei</i>	Accepted	Doubtful	Doubtful
<i>Attalea huebneri</i>	Accepted	Accepted	Syn. of <i>A. butyracea</i>
<i>Attalea humboldtiana</i>	Syn. of <i>A. butyracea</i>	Tentatively included in <i>A. butyracea</i>	Syn. of <i>A. butyracea</i>
<i>Attalea humilis</i>	Accepted	Accepted	Accepted
<i>Attalea iguadummat</i>	Accepted	Accepted	Accepted
<i>Attalea insignis</i>	Accepted	Accepted	Accepted
<i>Attalea kewensis</i>	Accepted	Accepted	Tentative synonym of <i>A. butyracea</i>
<i>Attalea lauromuelleriana</i>	Accepted	Accepted	Syn. of <i>A. phalerata</i>
<i>Attalea leandroana</i>	Accepted	Accepted	Syn. of <i>A. phalerata</i>
<i>Attalea liebmannii</i>	Syn. of <i>A. rostrata</i>	Accepted	Syn. of <i>A. butyracea</i>
<i>Attalea luetzelburgii</i>	Accepted	Accepted	Accepted
<i>Attalea lundellii</i>	Syn. of <i>A. rostrata</i>	Accepted	Syn. of <i>A. butyracea</i>
<i>Attalea macrocarpa</i>	Accepted	Accepted	Tentative synonym of <i>A. butyracea</i>
<i>Attalea macrolepis</i>	Accepted	Accepted	Syn. of <i>A. butyracea</i>

Table 1. continue.

Combined taxon list	Govaerts & Dransfield (2005)	Glassman (1999)	Henderson et al. (1995)
<i>Attalea magdalena</i>	Accepted	Accepted	Syn. of <i>A. butyracea</i>
<i>Attalea maracaibensis</i>	Accepted	Accepted	Syn. of <i>A. butyracea</i>
<i>Attalea maripa</i>	Accepted	Accepted	Accepted
<i>Attalea maripensis</i>	Accepted	Described as new	Incl. in <i>A. attaleoides</i>
<i>Attalea moorei</i>	Accepted	Described as new	Incl. in <i>A. phalerata</i>
<i>Attalea nucifera</i>	Accepted	Accepted	Accepted
<i>Attalea oleifera</i>	Accepted	Accepted	Accepted
<i>Attalea osmantha</i>	Accepted	Accepted	Syn. of <i>A. butyracea</i>
<i>Attalea peruviana</i>	Accepted	Accepted as <i>Scheelea tessmannii</i>	Syn. of <i>A. butyracea</i>
<i>Attalea phalerata</i>	Accepted	Accepted	<i>A. phalerata pro parte</i>
<i>Attalea pindobassu</i>	Accepted	Accepted	Accepted
<i>Attalea plowmanii</i>	Accepted	Described as new	Tentatively included in <i>A. butyracea</i>
<i>Attalea polysticha</i>	<i>A. microcarpa pro parte</i>	Accepted	<i>A. microcarpa pro parte</i>
<i>Attalea princeps</i>	Accepted	Accepted	Syn. of <i>A. phalerata</i>
<i>Attalea rhynchocarpa</i>	Accepted	Doubtful	Doubtful
<i>Attalea rostrata</i>	Accepted	Accepted	Syn. of <i>A. butyracea</i>
<i>Attalea sagotii</i>	<i>A. microcarpa pro parte</i>	Accepted	<i>A. microcarpa pro parte</i>
<i>Attalea salazarii</i>	Accepted	Described as new	Incl. in <i>A. butyracea</i>
<i>Attalea salvadorensis</i>	Accepted	Described as new	Incl. in <i>A. oleifera</i>
<i>Attalea seabrensis</i>	Accepted	Described as new	Incl. in <i>A. pindobassu</i>
<i>Attalea septuagenata</i>	Accepted	Accepted	Accepted
<i>Attalea speciosa</i>	Accepted	Accepted as <i>Orbignya phalerata</i>	<i>A. speciosa pro parte</i>
<i>Attalea spectabilis</i>	Accepted	Doubtful	Accepted
<i>Attalea tessmannii</i>	Accepted	Accepted	Accepted
<i>Attalea vitrivir</i>	Accepted	Accepted as <i>Orbignya oleifera</i>	<i>A. speciosa pro parte</i>
<i>Attalea weberbaueri</i>	Accepted	Accepted	Syn. of <i>A. phalerata</i>
<i>Attalea wesselsboerii</i>	Accepted	Described as new	Material not studied but would fall into <i>A. butyracea sensu lato</i>

Uncontroversial species of *Attalea*

These 20 species include *Attalea maripa*, which has leaves arranged in five vertical ranks or orthostichies, corresponding to a 2/5 phyllotactic fraction, while most other species of *Attalea sensu lato* and Coccoseae in general have a 3/8 fraction. This species has a unique staminate flower structure and has been placed in its own genus, *Maximiliana*. Other very distinctive species include *A. luetzelburgii*, also formerly placed in a separate genus, *Parascheelea*, *A. colenda*, formerly placed in *Ynesa* (Fig. 1), and the morphologically and geographically isolated *A. crassispata*. Within *Attalea sensu stricto*, *A. tessmannii* is highly distinctive vegetatively with its rigid leaflets dark glaucous-green above and whitish beneath (Fig. 2 and 4); within the *Orbignya* group, *A. cuatrecasana* is remarkable for its very large fruits to 15 cm long and 10 cm in diameter, only surpassed in size by the coconut within Arecoideae. The most problematic group remains that of *Scheelea*, in which a single species, *A. insignis*, has been uncontroversial among authors.

Nomenclatural and taxonomic problems in *Attalea*

The *Attalea attaleoides* complex

Attalea attaleoides, *A. camopiensis*, *A. degranvillei*, *A. guian-*

Attalea attaleoides is based on *Maximiliana attaleoides* Barb. Rodr. (not to be confused with *Scheelea attaleoides* H. Karst. which is a synonym of *A. insignis*). Glassman (1999) considered *Maximiliana attaleoides* as a *species confusa* belonging in fact to the *Scheelea* group. Henderson (1995) considered that *A. attaleoides* is part of the *Maximiliana* group, in accordance with its original assignment. Glassman (1999) described four new species from French Guyana in the genus *Scheelea*, latter transferred to *Attalea* by Zona (2002), on the basis of material previously assigned (at least tentatively) to *Attalea attaleoides* by Henderson (1995). However Glassman (1999) did not provide any statement on the material from Suriname and Brazil also included in *A. attaleoides* by Henderson (1995). Govaerts and Dransfield (2005), in accepting all four French Guyanan species (*A. camopiensis*, *A. degranvillei*, *A. guianensis*, *A. maripensis*) and *A. attaleoides*, implicitly consider that some material from outside French Guiana do correspond to the latter species. In fact, the material of *A. guianensis*, *A. maripensis* from French Guyana and *A. attaleoides* from Suriname and Brazil is very similar and it is likely that all these taxa represent the same species, which would be *A. attaleoides* if this name is accepted. On the other hand Henderson (1995) noted that the two specimens now known as *A. camopiensis* and *A. degranvillei* did depart from the



Figure 1. *Attalea colenda*, habit (south-western Ecuador)

Attalea dahlgreniana

This species, known from Suriname and eastern Brazil is accepted by Henderson (1995) and Govaerts and Dransfield (2005). They followed Wessels Boer (1965) who argued about the distinctiveness of this species and the fact that it was probably not of hybrid origin since it is fully fertile, very abundant and morphologically homogeneous from Suriname to Brazil. It was originally described as a new genus, *Markleya* by Bondar (1957), who regarded it as a possible hybrid between *A. maripa* and *A. speciosa*. These two species grow sympatrically with *A. dahlgreniana* near the mouth of the Amazon river but allopatric populations of the latter exist in Suriname. Glassman noted that the staminate flowers of *A. dahlgreniana* do not match in any way those of the putative parent species *A. maripa* and *A. speciosa*, but nevertheless accepted *A. dahlgreniana* as an intergeneric hybrid called \times *Maximbignya*.

The *Orbignya* group

The *Attalea speciosa* complex

Attalea brejinhoensis, *A. speciosa*, *A. spectabilis*, *A. vitrivir*

This widespread peri-Amazonian group, the “babaçu” has been intensively studied due to the usefulness and extension of its populations. Nevertheless, its taxonomy remains controversial. Nomenclatural problems associated with the name *A. speciosa* have been described in the introduction of this paper. Henderson (1995) considered *A. speciosa* (= *O. phalerata*) to

populations restricted to Minas Gerais and Bahia. Balick et al. (1987), Anderson and Balick (1988) and Glassman (1999) nevertheless provide convincing elements to maintain this geographically and morphologically distinct population as a separate species. Glassman (1999) described a third species in the complex, *A. brejinhoensis*, from Bahia. Henderson (1995) considered also the acaulescent *A. spectabilis* as part of the complex, being either an acaulescent form of *A. speciosa* or a hybrid with *A. microcarpa*. Glassman (1999) considered both *A. spectabilis* and *A. microcarpa* as doubtful species, since description of staminate flowers is ambiguous or lacking, and no material, type or otherwise mentioned in the literature, if it ever existed, is presently available for study.

The *Attalea microcarpa* complex

Attalea polysticha, *A. sagotii*

This species is accepted by Henderson (1995) and also by Govaerts and Dransfield (2005). As mentioned above, Glassman (1999) considered *A. microcarpa* doubtful and instead recognized two species, *A. polysticha* and *A. sagotii*. These species differ in the arrangement of staminate flowers on the rachillae. In *A. polysticha*, staminate flowers are inserted all around the rachillae (fig. 8) while in *A. sagotii*, they are clearly unilateral. This distinction is known to be significant in many other groups of *Attalea* (Fig. 5-7) and has been widely used by Glassman (1999) to distinguish species and groups of species. The recent discovery of *A. polysticha* and *A. sagotii* growing almost sympatrically in French Guyana (de Granville, pers. com. and specimens at CAY) can be interpreted in two ways: 1) the two species are clearly distinct,





Figure 3. Leaf patterns. Left: toothed margin of eophyll (*Attalea ferruginea*); right: abaxial view of the asymmetrical pinnae apex with brownish lateral projection (*Attalea maripa*).

and maintain their differences in sympatry due to reproductive isolation, or 2) it is the same species which locally presents a polymorphism in the insertion of the staminate flowers. It is to be noted that while the *A. polysticha* morph is widespread, the *A. sagotii* morph is restricted to northeastern Amazonia.

The *Attalea cobune* complex

Attalea cobune, *A. guacuyule*

The question about this group is to determine whether *A. guacuyule* from Mexico is distinct or not from *A. cobune* from Guatemala, Belize, Honduras and Nicaragua. Galeano and Bernal (2002) confirmed the presence of typical *A. cobune* in the Magdalena valley of Colombia, separated by about 1300 km from the previously known Central American populations.

The *Scheelea* group

Scheelea is the most complex and controversial entity within *Attalea s.l.* Excluding the *Attalea attaleoides* complex, previously treated, which has been assigned either to the *Maximiliana* or the *Scheelea* group, the other species could tentatively be organized as follows.

Attalea phalerata complex

Attalea amyloacea, *A. anisitsiana*, *A. moorei*, *A. phalerata*, *A. weberbaueri*

This group is defined by the unilateral staminate flowers on staminate rachillae and conspicuous fiber clusters organized in one circle in the thick endocarp (Fig. 5). Within this group, *A. moorei* is distinguished by its leaves with regularly arranged pin-

anisitsiana by a comparatively thin peduncular bract, all other species of this group having a very thick peduncular bract. *A. weberbaueri* has been described as acaulescent, but recent observations of this species in Junín and Pasco (Peru) showed that although it actually begins to flower at an acaulescent stage, it eventually develops a short aerial trunk, obscured by persistent leaf bases. This group is well characterized and composed of evidently related species. Although Henderson et al. (1995) put all of them in synonymy of *A. phalerata*, there are evidences to maintain them separated (Noblick, 2007 and pers. obs.). The newly described *A. moorei* is particularly noteworthy for the very regular arrangement of pinnae, spreading in one plane, a feature not shared with the other members of the group. This species grows sympatrically with *A. phalerata* in Madre de Dios, Peru, without evidence of hybridization, and allopatrically all along the Huallaga valley.

Attalea butyracea complex

Attalea butyracea, *A. kewensis*, *A. macrocarpa*, *A. magdalenica*

This group is defined by petiolate leaves with very regularly arranged pinnae, these with a prominent spine-shaped auricle basally (Fig. 4), peduncular bract thin, staminate flowers spirally arranged on staminate rachillae and dispersed fibers within a thin endocarp (Fig. 6). All species of this group are tall-stemmed. Typical *A. butyracea* has small (4-5 cm long) fruits, turning yellow at maturity, with inconspicuous endocarp fibers, and with two seeds (Fig. 6), leaf segments are stiff, glossy green adaxially and waxy-glaucous abaxially (Fig. 4). *A. macrocarpa* is distinguished by larger fruits (8-9 cm long) and *A. kewensis* has very short staminate petals. Characters of *A. butyracea* and *A. magdalenica*



Figure 4. Leaf patterns. Left: whitish abaxial indument of *Attalea tessmannii*; right: waxy-glaucous abaxial indument and spine-shaped



Figure 5. *Attalea moorei*. Left: transverse section of fruit showing the thick endocarp with a ring of conspicuous fiber clusters, and four seeds. Right: unilateral arrangement of staminate flowers on rachillae (Photos by Gloria Galeano).

merge when a large number of specimens are examined, so that the latter is better considered as a synonym. *Attalea kewensis* has been described in cultivation but some specimens from Peru match relatively well the type (Glassman, 1999).

Attalea macrolepis complex

Attalea bassleriana, *A. cephalotes*, *A. fairchildensis*, *A. huebneri*, *A. lauromuelleriana*, *A. leandroana*, *A. macrolepis*, *A. maracai-bensis*, *A. peruviana*, *A. princeps*, *A. wesselsboerii*

These species share many characters with the *A. phalerata* complex but have spirally arranged staminate flowers on staminate rachillae similar to those of the *A. butyracea* complex. They all have grouped pinnae (*A. peruviana* = *Scheelea tessmannii* only known from the type lacking leaves is tentatively included here). Henderson et al. (1995) put *A. princeps*, *A. lauromuelleriana* and *A. leandroana* in synonymy of *A. phalerata* but included the other ones in *A. butyracea*. Stauffer and Fariñas (2006) showed that *A. macrolepis* is a distinct species with a unique combination of characters. Since several species included here are very poorly known, it is not possible to determine to which extent this group is natural.

Attalea rostrata complex

Attalea osmantha, *A. rostrata*

This Caribbean-Central American group seems distinct from the western South-American *A. butyracea* complex, especially in having petiolate leaves. The two species differ in petiole length, fruit shape and flower arrangement.

Attalea liebmannii complex

Attalea liebmannii, *A. lundellii*

This group is the northern-most one (Mexico and Guatemala). These two species were included in synonymy of *A. rostrata* by Govaerts and Dransfield (2005), but this seems unjustified since *A. rostrata* has regularly pinnate leaves while the other two have clustered pinnae. In other instances (e.g. *A. moorei* vs *A. phalerata*, *A. butyracea* vs *A. macrolepis*), leaf arrangement proved to be very consistent within species. Little differentiation was found between *A. liebmannii* and *A. lundellii* in a chemotaxonomic survey of flavonoids (Williams et al., 1983).

Attalea plowmanii and *A. salazarii*

These are two species recently described from the Peruvian Amazon (Glassman, 1999). *Attalea plowmanii* is very distinctive by its acaulescent habit, and has been later found in Colombia (Galeano and Bernal, 2002). Henderson (1995) tentatively included it in *A. butyracea*, but suggested that it may be a new species. *A. salazarii* is known from very few collections around Iquitos and is still in need of further studies to confirm its identity and relationships.

The *Attalea sensu stricto* group

This group is mostly diversified in southeastern Brazil (especially Bahia), and to a lesser extent in Central Brazil, with only three, not problematic species in the Amazon forest (*A. ferruginea* = *A. racemosa*, *A. septuagenata* and *A. tessmannii*). Contrary to the *Scheelea* and *Orbignya* groups which reach southern Mexico and the Caribbean, the *Attalea sensu stricto* group is almost exclusively



Figure 6. *Attalea butyracea*. Left: pistillate flowers, fruits and transverse section of fruit showing the thin endocarp with few, dispersed fibers, and two seed cavities. Right: spirally arranged staminate flowers on rachillae.



Figure 7. *Attalea ferruginea*. Staminate inflorescence showing unilateral arrangement of rachillae on rachis and of staminate flowers on rachillae.

South American, just reaching Panama (de Nevers, 1987) with two species, *A. allenii* and *A. iguadummat*. Two more species, *A. amygdalina* and *A. nucifera* grow in inter-Andean valleys of Colombia and *A. colenda* grows on the Pacific coast of southern Colombia and Ecuador.

Taxonomic problems in *Attalea sensu stricto* are restricted to southeast and central Brazil.

The *Attalea apoda* complex

Attalea apoda, *A. brasiliensis*

Attalea apoda is clearly a species of the *Attalea sensu stricto* group, but a confusion arose because Henderson et al. (1995) put it in synonymy of *A. speciosa*, which is a totally unrelated species of the *Orbignya* group. Glassman (1999) described a new species allied to *A. apoda*: *A. brasiliensis*.

The *Attalea oleifera* complex

A. burretiana, *A. compta*, *A. oleifera*, *A. pindobassu*, *A. salvadorensis*, *A. seabrensis*

Henderson et al. (1995) had a broad concept of this complex, recognizing two species: *A. oleifera* (including *A. burretiana* and *A. compta* in synonymy) and *A. pindobassu*. Glassman (1999) considered these two species but also *A. burretiana* and *A. compta* as distinct species, and described two new species, *A.*

burretiana, and *A. seabrensis* most closely related to each other. The status of *A. salvadorensis* remains doubtful, it may be a mere synonym of *A. burretiana* (Noblick, pers. com.), or it may be a hybrid (Glassman, 1999).

Conclusion

Despite the publication of several recent accounts on the genus, the taxonomy of *Attalea* is still confusing. However, most problems are restricted to particular complexes of species, which have suffered excessive lumping (*Attalea butyracea* group), or possibly excessive splitting (*Attalea attaleoides* group) obscuring species delimitation. The identity and variability of many species still need to be checked in the field. New and ongoing studies, including DNA analyses, should disentangle most of the remaining problems.

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Figure 8. *Attalea polysticha*. Staminate inflorescence showing spirally arranged rachillae and staminate flowers (Photo by Rommel

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