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TAXONOMY OF THE GENERA *ANANAS* AND *PSEUDANANAS*—AN HISTORICAL REVIEW

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ABSTRACT. From the first observations of the pineapple by European explorers to the classification into *Pseudananas sagenarius* and the seven *Ananas* species prevailing at present, the evolution of pineapple taxonomy has shown considerable variation. Most early botanists named or renamed species from previous dubious descriptions or from particular horticultural types. More recently, the genus *Pseudananas* was created, while horticultural types disappeared from the *Ananas* species. Subsequently, the total number of species increased again as botanical varieties and forms with minor variation were elevated to species rank. The resulting classification is questionable, as neither discontinuous morphological variation nor reproductive barriers exist in the genus *Ananas*.

Ananas and *Pseudananas* are the only genera in the Bromeliaceae whose fused flowers develop into a sorose-type fruit formed by the coalescence of up to 200 berries. The most recent classification (Smith & Downs 1979) established *Pseudananas* as a monotypic genus, *Pseudananas sagenarius* (Arruda) Camargo, and divided *Ananas* divided into eight species, one of which has been invalidated (Leal 1990). The species considered valid now are presented in TABLE 1.

The best known species of *Ananas* is the cultivated *A. comosus* (L.) Merr., thanks to its impressive and delicious fruit, which is considered an important taxonomic character (more than 15 cm long according to the key in Smith & Downs 1979). This large fruit is borne on a wide, short-to-long peduncle. In the spiny genotypes, spines are antrorse and generally smaller and denser than in other species. Partially spiny genotypes also exist as well as completely smooth genotypes, characterized by a folding of the lower epidermis over the leaf edge ("piping" character as named by Collins & Kerns 1946).

Ananas lucidus Mill., the curagua, is cultivated by the peoples of the Orinoco basin and to the North of the Amazon River. They use its strong and long fibers to make breechcloths, hammocks, fishing nets and rods (Leal & Amaya 1991). This species is mainly characterized by long, smooth, and erect leaves and a small, fibrous, inedible fruit borne on a medium-to-long peduncle. The dry fibers constitute 6% of plant weight (Camargo 1943). The absence of spines facilitates manual fiber extraction, although some spiny or partially spiny mutants have been observed. *Ananas lucidus* has never been found in the wild.

Ananas bracteatus (Lindl.) Schult. f. comes from southern South America (southern Brazil, Paraguay, and northern Argentina), where it is always found cultivated as a living hedge or for fruit juice, or abandoned in ancient settlements. Its variegated form has been widely diffused as a garden ornamental. The plant is vigorous with wide and long leaves, large spines, and suckers abundantly. The inflorescence is characterized by its bright pink to red color and long bracts. The fruit and peduncle are medium-sized (according to the key presented in Smith and Downs (1979), the syncarp is more than 15 cm long; however it is often less). *Ananas bracteatus,* well adapted to cool conditions and altitude, has been observed at 1,000 m in the subtropics. The variability of this species is very limited. *Ananas fritzmuelleri* Camargo is almost identical to *A. bracteatus* with some retrorse spines (Camargo 1943). Formerly included in *A. bracteatus* (Smith 1939), *A. fritzmuelleri* has floral bracts that turn a pale green color at fruit maturity.

Ananas ananassoides (Baker) L.B. Sm., *A. parguazensis* Camargo and L.B. Sm., and *A. nanus* (L.B. Sm.) L.B. Sm. are wild species. *Ananas ananassoides* is the most widespread species, from southern Brazil to Venezuela and Co-

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TABLE 1. Current composition of the genera *Pseudananas* and *Ananas*. Based on Smith and Downs (1979) and Leal (1990).

Scientific name	Common name
Pseudananas sagenarius (Arruda) Camargo	Gravatá de cerca, gravatá de rede, yvira, nana caçaba, nana brava
Ananas ananassoides (Baker) L.B. Sm.	Ananas de ramosa, curibijul, maya piñón, nanaí, piñuela
Ananas nanus (L.B. Sm.) L.B. Sm.	Ananaí
Ananas parguazensis Camargo and L.B. Sm.	Gravatá, piña montañera
Ananas lucidus Mill.	Curagua, curaná, curauá, kulaiwat
Ananas bracteatus (Lindl.) Schult. f.	Ananas bravo, ananas do mato
Ananas fritzmuelleri Camargo	Ananas silvestre, gravatá de cerca
Ananas comosus (L.) Merr.	Abacaxí, ananas, piña, matzatli

lombia. Although a few genotypes thrive in dense rainforest (in the Guianas), it is generally observed in savannas or in low-shade forest, growing well on soils with limited water-holding capacity (such as sand or rocks), and forming populations of variable densities. Most of these populations are monoclonal, but some are polyclonal, with variation of recent sexual origin (Duval *et al.* 1997). The plant has long and generally narrow spiny leaves and bears a small, globular-to-cylindrical syncarp on a long and thin peduncle. The fruit is often seedy, and its pulp is white, firm and fibrous, with a high sugar and acidity content, good flavor and aroma, and a narrow heart. According to the key, *A. ananassoides* is distinguished from *A. comosus* by the size of the fruit (shorter than 15 cm).

Ananas nanus is characterized by an even smaller fruit (shorter than 4 cm). In fact, Smith (1939) formerly classified it as a dwarf variety of *A. ananassoides*. *Ananas nanus* has sometimes been used as an ornamental.

Ananas parguazensis is also very similar to *A. ananassoides* but differs in the retrorse orientation of some spines and a wider leaf slightly constricted at its base. *Ananas parguazensis* seems less adapted to drought, but an anatomical and physiological comparison showed no other differences (Leal & Medina 1995). Its distribution is also limited to the northern Amazon (Rio Negro basin) and Río Orinoco, with a wider variability in the Orinoco region (Duval *et al.* 1996). It grows in the lowland forests, under canopies of variable densities, from clearings or riverbanks to dense forest.

As commonly found in Bromeliaceae, the genus *Ananas* is diploid, characterized by having 50 minute and almost spherical chromosomes in both root tips and pollen mother cells (Collins & Kerns 1931, Canpinpin & Rotor 1937, Marchant 1967, Sharma & Ghosh 1971, Lin *et al.* 1987, Brown & Gilmartin 1989, Dujardin 1991). Giant unreduced gametes may appear and produce natural triploids and tetraploids (Collins 1933, 1960). Most genotypes display reduced fertility and a self-incompatibility system with considerable variation in its expression (Coppens d'Eeckenbrugge *et al.* 1993). Vegetative reproduction is largely dominant over sexuality in *Ananas*. This is particularly true in domesticated types. Pineapples multiply by suckers (terrestrial and aerial), slips (suckers from the peduncle), and crown.

Pseudananas sagenarius has been cultivated as a source of fibers, which explains the origin of its common name, yvira, meaning fiber, as well as of its Latin epithet, which refers to a fishing net (*sagena*). The fibers constitute 7.6% of the leaf dry weight and reach a length of 1.60 m (Corrêa 1952). In contrast to *Ananas*, *P. sagenarius* is a tetraploid ($2n = 100$), characterized by a complete lack of crown and asexual reproduction by stolons. Its leaf margins bear strong spines, which are retrorse at the leaf base. Floral bracts are longer than in *Ananas comosus*. The fruits are low in acid. The habitat of *P. sagenarius*, limited to forest areas, is under semidense shade and subjected to a rainy season during most of the year, or even to periods of flooding. This species may be found in southern South America (southern Brazil, Paraguay, Bolivia and northern Argentina), and along the eastern Brazilian coast, up to Pernambuco. Populations of *P. sagenarius* are rare now because of severely reduced habitat. The few populations recently observed, however, showed significant variation (Ferreira & Cabral 1993, Ferreira 1996, Duval *et al.* 1997, Coppens d'Eeckenbrugge *et al.* 1997).

HISTORY OF PINEAPPLE TAXONOMY

The main steps in the evolution of pineapple taxonomy are presented in FIGURE 1.

The Amerindians had domesticated pineapples and the curagua for fruit and fiber and had dispersed the former all over Latin America and the Caribbean and the latter from the North bank of the Amazon to the Caribbean well before the arrival of Columbus (Leal & Coppens d'Eeckenbrugge 1996). They also had domesticated the yvira, as observed by Thévet (1557) around Rio de Janeiro. Native Americans were the first pineapple taxonomists. On the island of Hispaniola,

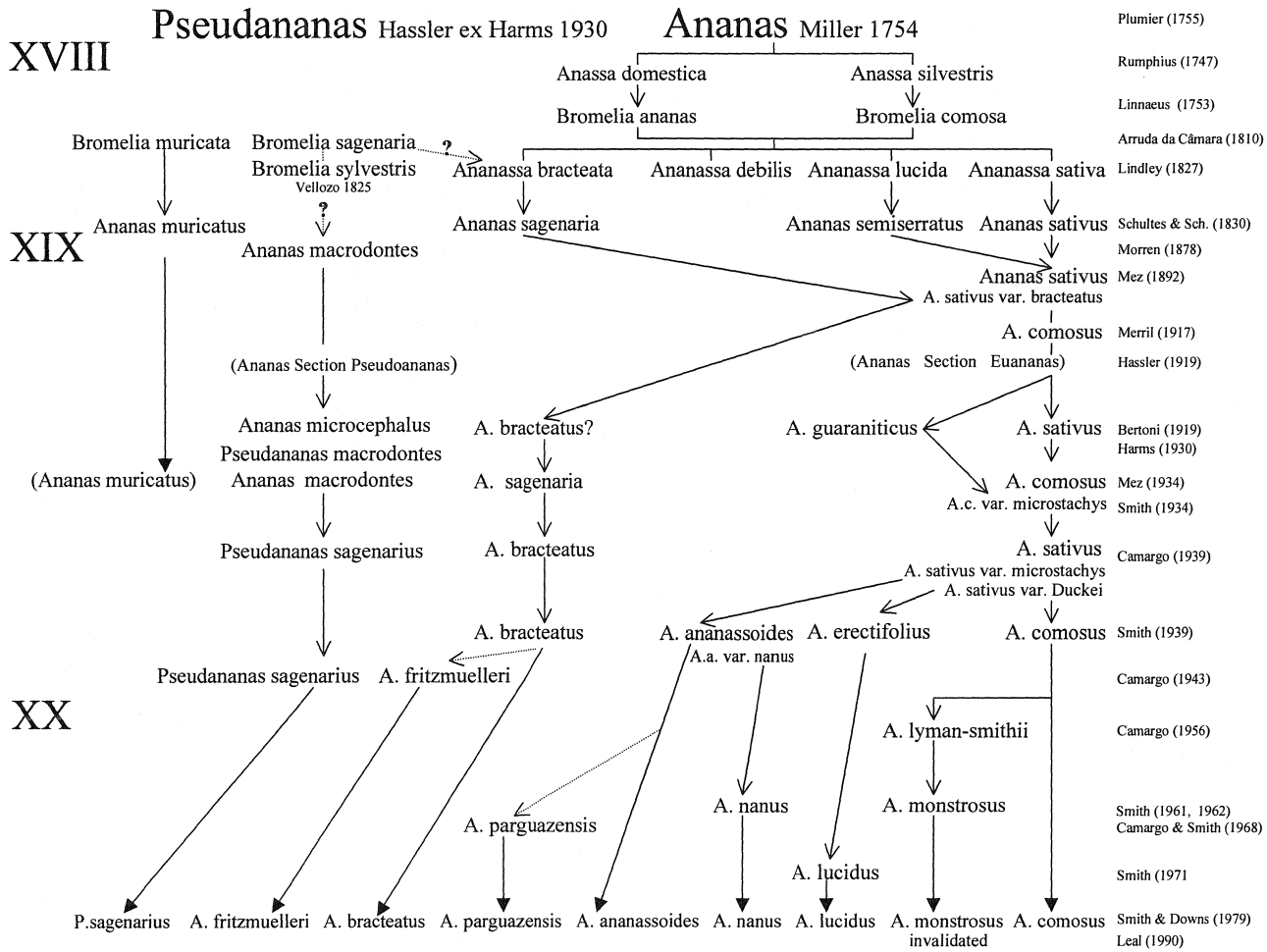

FIGURE 1. A diagrammatic representation of the main changes in pineapple taxonomy during the 18th, 19th, and 20th centuries.

they distinguished different bromeliads, such as "karatas" and "ananas" (Plumier 1755). The vernacular "karatas" and related names as "karagwata" or the Brazilian "gravatá" are still used by local people throughout South America to name terrestrial bromeliads—in addition to "nana" and "anana" which are used commonly for pineapple throughout the Amazon and Orinoco basins, as well as in southern South America. Wild pineapples are often called "nanaí" or "ananaí" (Leal & Coppens d'Eeckenbrugge 1996). The word "anana" from the Carib "nana" is also present in the Galibi and Chaima dialects, as well as in the Arawak and Tupi. In the latter, the form "anana" already exists. In Tupi, "nana" is the plant and "anana" is the fruit (Alvarado 1939). The name *Nanas* is first mentioned by Thévet (1557) and *Ananas* by de Léry (1580, cited by Beer 1856). The Spanish "piña" and the English "pineapple" came from the comparison with the exotic pinecone. The Brazilian name "abacaxi," originally designating particular cultivars, is derived from the Guarani word for the maize ear (Bertoni 1919). Amerindians had a thorough knowledge of the plant and its cultivation, differentiating cultivars and wild types (Thévet 1557, Carvajal 1647, Gumilla 1741). Based on their common knowledge, Fernández de Oviedo (1535) described three cultivars from La Hispaniola: 'Yayama,' 'Yayagua,' and 'Boniama.'

When Charles Plumier initiated the taxonomic work on the Bromeliaceae at the end of the 17th century (Leal 1989), he followed the native classification. He created the genus *Bromelia* for the *karatas,* in honor to the Swedish physician Olaf Bromel, and described the *Ananas,* using polynomials such as *Ananas aculeatus fructu ovato carne albida* for a pineapple cultivar or *Ananas non aculeatus pitta dictus* for the curagua (Plumier 1755). In 1747, Rumphius published his Herbarium Amboinense, where he classified the pineapple in three botanical forms: *mas, femina,* and *alba.* He then considered *femina* as *Anassa domestica* and *alba* as *Anassa silvestris.* His view was likely biased, for he thought the pineapple originated in the Moluccas islands and described cultivated forms, probably brought by the Portuguese when they first settled there. Rumphius thus compared cultivars instead of species and, in addition, observed them at different phenological stages. In his Species Plantarum, Linnaeus (1753) redesignated *Anassa domestica* and *Anassa silvestris* as *Bromelia ananas* and *Bromelia comosa.* Quite at the same time, Miller (1754) published a list of six *Ananas* species in the fourth edition of the Gardener's Dictionary, maintaining Plumier's genus *Ananas* in his polynomials (TABLE 2). The fourth

TABLE 2. The genus *Ananas* according to P. Miller's *The Gardener's Dictionary,* 4th ed., 1754, and 8th ed., 1768. London.

4th Edition	8th Edition
Ananas aculeatus, fructu ovato, carne albida. Plum.	*Ananas* (*Ovatus*). Oval shaped pineapple, with a whitish flesh
Ananas aculeatus, fructu pyramidato, carne aurea. Plum.	*Ananas* (*Pyramidalis*). Pyramidal pineapple, with a yellowish flesh, (called the sugar loaf pine)
Ananas folio vix serrato. Boerh.	*Ananas* (*Glabra*). Pineapple with smooth leaves
Ananas lucide virens, folio vix serrato.	*Ananas* (*Lucidus*). Pineapple with shining green leaves and scarcely any spines on their edges
Ananas fructu pyramidato olivae colore, intus aureo.	*Ananas* (*Serotinus*). Pyramidal olive-colored pineapple, with a yellow flesh
Ananas aculeatus, fructu pyramidato eax viridi flavescente.	*Ananas* (*Viridis*). The green pineapple

of these species is a pineapple with "scarce any spines" on the leaf edges. In the eighth edition, Miller (1768) disputed Linnaeus' inclusion of the pineapple in the genus *Bromelia* and reduced his former six species to varieties of a single one.

In 1805, Saint-Hilaire created the Bromeliaceae family, using the terminology established by Plumier (1755). In 1827, Lindley renamed the genus as *Ananassa* and the pineapple as *A. sativa.* He also recognized the species *A. lucida,* from Miller's *Ananas lucidus,* and created the species *A. bracteata.* According to Smith and Downs (1979), *A. lucida* corresponds to the curagua, and *A. bracteata* to the form presently named *A. bracteatus.* The description of *A. lucida,* however, indicates that this species corresponds to smooth-leafed cultivars of pineapple (see also Beer 1856). In the same way, the species *A. debilis* described by Lindley (1827) and then used by Beer (1856) only corresponds to a particular pineapple cultivar with undulated leaves.

Schultes and Schultes (1830) returned to the original name *Ananas,* as given by Plumier and by Miller, recognizing the cultivated fruit species as (i) *Ananas sativus,* (ii) *Ananas semiserratus* (instead of *Ananassa lucida*), and (iii) *Ananas sagenaria* (instead of *Ananassa bracteata*). According to Camargo (1943) and Smith and Downs (1979), this last species also included the "yvira," first described with dubious character-

istics as *Bromelia sagenaria* in 1810, by Arruda da Câmara, and as *Ananas sylvestris* in 1825 by Vellozo. Another incomplete and dubious description by Arruda da Câmara is that of *Bromelia muricata,* possibly a particular form of yvira, which was renamed *Ananas muricatus* by Schultes and Schultes (1830). The first clear description of yvira, with an excellent drawing, was published by Morren (1878) who named it *Ananas macrodontes* because of its large and strong spines.

Two new species from Colombia, *Ananas mordilona* and *Ananas pancheanus* were proposed respectively by Linden (1879) and by André (1889). *Ananas mordilona,* with completely smooth leaves, is strikingly similar to the present day cultivars 'Perolera' and 'Manzana,' still widely cultivated in what was the territory of the Motilones Indians (*mordilona* is probably a corruption of "Motilona"). *Ananas pancheanus* is a wild pineapple, with long leaves, minute spines, antrorse and retrorse, and a long scape bearing a small cylindrical fruit. Smith and Downs (1979) stated that it is possibly *A. parguazensis.* The exsiccata observed in Kew by F. Leal is too poor on which to offer an opinion. Neither *A. mordilona* nor *A. pancheanus* have been validated later. André (1889) collected another wild pineapple at Panché, which he classified as *A. sativus.*

Until the end of the nineteenth century, no distinct species was recognized for the wild pineapples. Beer (1856) had described an exsiccata of a wild type with an erect habit, a limited number of thin leaves, spines, and a small fruit, corresponding to the present description of *Ananas ananassoides* (Baker) L.B. Sm. He stated that the differences with the cultivated pineapple were only the result of domestication (hypertrophy of the syncarp) and found no reasons not to include it in *A. sativus.* On the other hand, in classifications proposed by early taxonomists for the cultivated types, confusion persisted regarding the levels of genus, species, botanical varieties, and cultivars; for this reason, the present review does not consider subdivisions of the cultivated pineapple.

Baker (1889) was the first to give species rank to a wild pineapple, using the binomial *Acanthostachys ananassoides*; and in 1891, Lindman included it in the genus *Ananas,* as *A. microstachys,* a *nomen illegitimum*—as stated by Smith and Downs (1979) in their list of the synonyms of *A. ananassoides.*

Mez (1892) proposed a first simplification in Flora Brasiliensis, with *Ananas* a monotypic genus. He considered *A. sagenaria* together with *A. macrodontes* E. Morren as a variety of *A. sativus,* naming it (i) *A. sativus* var. *bracteatus,* because he supposed that the absence of a crown in *A. macrodontes* was only the result of observing a juvenile inflorescence. The other varieties were: (ii) *A. sativus* var. *lucidus,* for smooth-leafed pineapples, a synonym for *A. lucidus* Mill., *A. semiserratus* Schult. & Schult. f., *A. mordilona* Linden, and the curagua described by Plumier; (iii) *A. sativus* var. *debilis* ("only from European glasshouses"); (iv) *A. sativus* var. *muricatus,* with doubts on its classification within *Ananas*; and (v) *A. sativus* var. *microstachys* for the wild pineapple.

In 1917, Merrill established the binomial *Ananas comosus* based on Linnaeus' *Bromelia comosa,* considered synonymous with *Bromelia ananas.* In 1919, Hassler divided the genus *Ananas* in two sections: *Euananas* and *Pseudoananas.*

Another division was proposed simultaneously by Bertoni (1919), who worked on his collection of Paraguayan material, now unfortunately lost. He divided the genus into five species: *Ananas microcephalus, A. bracteatus, A. muricatus, A. sativus,* and *A. guaraniticus,* with many botanical varieties for each species. This classification is not only confusing but also erroneous. *Ananas microcephalus* is clearly the yvira, as it lacks a crown. In addition to *A. sativus* var. *bracteatus* (Lindl.) Mez, Bertoni's *A. bracteatus* includes botanical varieties as diverse as those corresponding to *Bromelia sagenaria* Arruda; *Ananas macrodontes* E. Morren, a wild pineapple of Honduras described by Hume and Miller (1904); and a Paraguayan cultivar. Bertoni maintained *A. muricatus* Arruda, although no one had observed it after Arruda da Câmara. He included in *A. sativus* the most common world cultivars, botanical varieties corresponding to wild pineapples, already mentioned invalid species (as *A. debilis*), and *A. sativus* var. *bracteatus. Ananas guaraniticus* clearly corresponds to *A. ananassoides* (Baker) L.B. Sm. Despite all these mistakes, Bertoni's work and ethnobotanical arguments on the origin of the genus had a long-lasting influence on subsequent studies. Thus, the first systematic collecting of *Ananas* and *Pseudananas* germplasm by Baker and Collins (1939) was based on Bertoni's hypothesis of a southern origin of pineapple. Baker and Collins were convinced that pineapple distribution and variability was concentrated under the natural barrier constituted by the Amazonian forest, and, impressed indeed by the diversity found in the area, they ignored the possibility of a wide diversity in the North of the continent.

In 1930, Harms raised Hassler's section *Pseudoananas* to the genus rank, with *Pseudananas macrodontes* (E. Morren) Harms. Mez (1934) did not recognize this new genus, and proposed

a new classification into three species: (i) *Ananas comosus,* including the cultivated forms (previously considered botanical varieties) *sativus, lucidus* and *debilis*; (ii) *A. sagenaria,* corresponding to *A. bracteatus*; and (iii) *A. macrodontes* E. Morren. Mez (1934) reiterated doubts about the form *debilis,* as well about *A. muricatus,* an improbable species.

From 1934 on, the evolution of pineapple taxonomy has been dominated by the views of L.B. Smith in the context of his monumental work on Bromeliaceae. The Brazilian horticulturist Felisberto Camargo also made significant contributions to these studies. Smith (1934) first proposed to reintegrate the wild pineapple, *Ananas microstachys* Lindm., into *A. comosus* as *A. comosus* var. *microstachys.*

In 1939, Camargo created a new botanical variety, *Ananas sativus* var. *duckei,* for the curagua. He also introduced a new combination, changing *Pseudananas macrodontes* (E. Morren) Harms to *P. sagenarius* (Arruda) Camargo based on the partial descriptions of Arruda da Câmara (1810) and Corrêa (1910, cited in Camargo 1939). This proposal is not supported because, as stated by Camargo himself, the description by Arruda da Câmara does not clearly mention the absence of a crown on the fruit, or the presence of stolons, which are specific to *Pseudananas.* Indeed this description may correspond to either *Ananas bracteatus* or *Pseudananas macrodontes* and provides no reason to abandon Morren's basionym.

Smith (1939), working in part with the material collected by Baker and Collins, revised *Ananas* taxonomy and divided the genus into four species: *A. comosus, A. ananassoides, A. bracteatus,* and *A. erectifolius.* Of these, *Ananas ananassoides,* with two varieties, *typicus* and *nanus,* corresponds to Smith's previous *A. comosus* var. *microstachys,* and *A. erectifolius* corresponds to Camargo's *A. sativus* var. *duckei,* the curagua.

In 1943, Camargo added a new species, *Ananas fritzmuelleri,* based on specimens collected from southeastern Brazil. The botanical features presented by Camargo were petals bearing vertical folds, identical to those of *Pseudananas;* long bracts; multiple crown; axillary suckers; antrorse or retrorse spines; and pink floral bracts getting green at syncarp maturity. This species differs from *Ananas bracteatus* only by the orientation of some spines, the petal folds, and the change in bract color with maturation. Indeed, Smith (1939) previously classified it as *A. bracteatus* var. *albus.* Camargo also mentioned synonymy with Fritz Müller's *A. sylvestris.* Camargo considered *A. fritzmuelleri* an intermediate form between *Pseudananas* and *Ananas.* The distinction is disputable because of the paucity of Camargo's arguments. Curiously, he underlined in his paper that Fritz Müller himself negated taxonomic value to petal scales in the bromeliads.

In 1956, Camargo presented a new species, *Ananas lyman-smithii,* to designate crownless pineapples. This species was placed in the synonymy of *A. monstrosus* by Smith in 1961. Then in 1962, Smith further increased the number of species, with *A. nanus* (L.B. Sm.) L.B. Sm., created from *A. ananassoides* var. *nanus.* His argument was that this last change resulted from conservation of the original dwarf type through prolonged cultivation. Such conservation, however, is only normal if plants were propagated vegetatively.

In 1966, Camargo (Camargo & Smith 1968) visited the area of the Parguaza River, an Orinoco affluent, where Velez and Badillo (1946) had collected wild pineapples. Similar material had been collected before and classified as *Ananas ananassoides* based on the Smith (1939) key. On the basis of these two collections, however, Camargo and Smith (1968) described a new species, *A. parguazensis.* Therefore, the herbarium collections from this region had to be reclassified and divided between *A. ananassoides* and *A. parguazensis.* Part of this material, showing intermediate characteristics, could not be attributed to either species and was left aside.

The ideas of Camargo have been published separately by Reyes-Zumeta (1967). Apparently, Camargo still considered *Ananas nanus* as a variety of *A. ananassoides.* He classified *Pseudananas sagenarius* into three botanical varieties: *thevetii* (corresponding to *Ananas macrodontes* E. Morren), *bertonii* (corresponding to the southern types described by Bertoni), and *dardanensis* (a form from northeastern Brazil).

In 1968, Reitz proposed a new species, *Ananas genesio-linsii,* from Aguas Emendadas (Central Brazil), where it is named Ananas dos Indios. The original population, which still exists, is a typical wild pineapple, with erect leaves and a fruit of intermediate size borne on a long peduncle, similar to many wild or partially domesticated clones from the Guianas to western Venezuela. Determined to be a triploid (Lin et al. 1987, Dujardin 1991), it appears to be a vigorous *A. ananassoides* with larger fruits. No particular trait justifies the species rank.

In 1971, in the *Flora de Venezuela, Ananas erectifolius* became a synonym of *A. lucidus* (Smith 1971). The most recent revision was by Smith and Downs (1979), who retained the eight species mentioned. Since then, Leal (1990) invalidated *A. monstrosus,* a *nomen nudum* synonym of *A. comosus,* because the absence of a

crown is not a permanent character. Indeed, the epithet *monstrosus* given by Smith was based on Carrière's description of *Ananassa monstrosa.* This was "a simple form of *Ananas sativa* of which it has all characters, except the terminal bud" (Carrière 1870). It is amusing that Carrière insisted his sample could not be considered a new species but just an exception to the common rule for *Ananas sativa.* Carrière knew that "the Ananas, considered as a type and provided with a crown, sometimes produces, by a kind of slow dimorphism, individuals without crown (democratized *Ananas,* we could say)."

Pineapple taxonomy is not satisfactory yet, and the seven remaining species reported in TABLE 1 could yet be reduced. Loison-Cabot (1992), underlining the similarity among *Ananas ananassoides, A. nanus,* and *A. parguazensis* and between *A. bracteatus* and *A. fritzmuelleri,* has proposed a reduction in the number of species. Such a reduction would lead back to the first classification of Smith (1939).

Indeed the Smith and Downs key (1979) is not tenable. Mostly based on quantitative traits (e.g., fruit size), it does not consider genetic and strong environmental variations. The best example of the key's problems is the importance assigned to fruit size, which separates *Ananas comosus* and *A. bracteatus/A. fritzmuelleri* from the other species and *A. ananassoides* from *A. nanus.* The few discriminate qualitative traits, such as presence or absence of spines, only depend on one or two genes (Collins & Kerns 1946). Most of the intraspecific variation has been neglected. The presence of some retrorse spines, generally at the leaf base, in certain species, is not constant. Morphological traits such as petal appendages do not justify the division into species, as they show variation within species as well as between species, for instance between cultivars of *A. comosus.* The same could be said for fragility of the fruit on the peduncle, which contributes to separating *A. nanus* from *A. ananassoides* or for bract color at maturity that contributes to separating *A. fritzmuelleri* from *A. bracteatus.* In recent works, pineapple specialists using the Smith and Downs key could not identify intermediate material that combines traits specifically attributed by Smith and Downs to distinct species (e.g., Duval *et al.* 1997). Some hybrids between *A. comosus* cultivars produce a small fruit borne on a long and thin peduncle, resembling *A. ananassoides* more than *A. comosus.* The genus organization requires simplification.

CONCLUSIONS

A new classification and resulting key will need to take into account reproduction biology and heredity of traits. No differences are apparent between the *Ananas* species either in floral structure and cytology or in chromosome number or breeding system. Fertility and self-fertility are often lower in *A. comosus* than in the other species. This, however, seems to be the result of artificial selection for reduced fertility and stronger self-incompatibility in the course of domestication. Self-incompatibility is present in all species (Coppens d'Eeckenbrugge *et al.* 1993). No interspecific incompatibility has been observed in the genus *Ananas,* neither at the level of pollen-pistil interaction or in embryogenesis and seed development. Interspecific crosses involving *A. comosus* are at least as fertile as intercultivar crosses, and the hybrids are fertile (Collins 1960, pers. obs.). When *A. comosus* is crossed with *Pseudananas sagenarius,* a few fertile seeds are produced. Hybrids are tetraploid, vigorous, highly fertile, and self-fertile. Similarly, crossing *P. sagenarius* with other *Ananas* species produces a majority of tetraploids and some smaller and self-sterile triploids (Collins 1960). The isozyme study by Aradhya *et al.* (1994) indicated that 86% of variation was found within species, underlining a moderate interspecific divergence. Despite the geographical differentiation observed in the genus, either at the molecular level (see Leal and Coppens d'Eeckenbrugge 1996 for a review) or at the morphological level (Duval *et al.* 1997), it seems that no definitive speciation has yet taken place. If the species concept is to be narrowly applied, taxonomists will need to recognize only one from the present *Ananas* species.

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LITERATURE CITED

ALVARADO L. 1939. Glosario de voces indígenas. Obras completas, Vol I. Fundación la Casa de Bello, Caracas.

ANDRÉ E. 1889. Description et histoire des Broméliacées récoltées dans La Colombie, L'Equateur et Le Venezuela. G. Masson, Paris, 118 pp.

ARADHYA M., F. ZEE, AND R.M. MANSHARDT. 1994. Isozyme variation in cultivated and wild pineapple. Euphytica 78: 87–99.

ARRUDA DA CÂMARA M. 1810. Dissertação sobre as plantas do Brasil, pp.1–49.

BAKER J.G. 1889. Handbook of the Bromeliaceae. London.

BAKER K. AND J.L. COLLINS. 1939. Notes on the distribution and ecology of *Ananas* and *Pseudananas* in South America. Am. J. Bot. 26: 697–702.

BEER J.G. 1856 [1857]. Die Familie der Bromeliaceen. Vienna (Tendler & Co.).

BERTONI M.S. 1919. Contributions à l'étude botanique des plantes cultivées. I. Essai d'une monographie du genre *Ananas.* An. Cient. Paraguay (Ser. II) 4: 250–322.

BROWN G.K. AND A. J. GILMARTIN. 1989. Chromosome numbers in Bromeliaceae. Am. J. Bot. 76: 657–665.

CAMARGO F. 1939. Ananás e abacaxí. Rev. Agr. Piracicaba 14: 321–338.

———. 1943. Vida e utilidade das Bromeliáceas. Brasil Min. Agr. Nac. Ens. Pesq Agr. Nac. Pesq. Inst. Agron. Norte, Belem, Pará, Boletin Técnico 1: 31 pp.

———. 1956. Nota previa. *Ananas lyman-smithii* n. sp. Arquiv. Jard. Bot. Rio de Janeiro 14: 281–289.

CAMARGO F. AND L.B. SMITH. 1968. A new species of *Ananas* from Venezuela. Phytologia 16: 464–465.

CANPINPIN J.H. AND G.B. ROTOR. 1937. A cytological and morphogenetic study of some pineapple varieties and their mutant and hybrid derivatives. Philippines Agr. 26: 139–158.

CARRIÈRE E.A. 1870. *Ananassa monstrosa.* Revue Hort. 42: 228–229.

CARVAJAL G. DE. 1647. Relación del nuevo descubrimiento del famoso Rio Grande de las Amazonas. Fondo de Cultura Económica, México.

COLLINS J.L. 1933. Morphological and cytological characteristics of triploid pineapples. Cytologia 4: 248–256.

———. 1960. The pineapple, botany, utilization, cultivation. Leonard Hill, London.

COLLINS J.L. AND K.R. KERNS. 1931. Genetic studies of the pineapple. I. A preliminary report upon the chromosome number and meiosis in seven pineapple varieties (*Ananas sativus* Lindl.) and in *Bromelia pinguin* L. J. Hered. 22: 139–142.

———. 1946. Inheritance of three leaf types in the pineapple. J. Hered. 37: 123–128.

COPPENS D'EECKENBRUGGE G., M.-F. DUVAL AND F. VAN MIEGROET. 1993. Fertility and self-incompatibility in the genus *Ananas.* Acta Hort. 334: 45–51.

COPPENS D'EECKENBRUGGE G., F. LEAL AND M.-F. DUVAL. 1997. Germplasm resources of pineapple. Hort. Rev. 21: 133–175.

CORRÊA P. 1952. Dicionario das plantas úteis do Brasil, Vol. III. Imprenta Nacional. Rio de Janeiro.

DUJARDIN M. 1991. Cytogénétique de l'ananas. Fruits 46: 376–379.

DUVAL M.-F., G. COPPENS D'EECKENBRUGGE, F.R. FERREIRA, J.R.S. CABRAL, AND L. DE B. BIANCHETTI. 1997. First results from joint EMBRAPA-CIRAD *Ananas* germplasm collecting in Brazil and French Guyana. Acta Hort. 425: 137–144.

FERNÁNDEZ DE OVIEDO G. 1535. Historia general y natural de las Indias. Atlas, Madrid.

FERREIRA F.R. 1996. Expediçao para coleta de germoplasma de abacaxi no Sul do Estado da Bahia. XIV Congresso Brasileiro de Fruticultura. (in press).

FERREIRA F.R. AND J.R.S. CABRAL. 1993. Pineapple germplasm in Brazil. Acta Hort. 334: 23–26.

GUMILLA J. 1741. El Orinoco ilustrado y defendido. Biblioteca de la Academia Nacional de la Historia, Caracas.

HARMS H. 1930. Bromeliaceae. In: Engler and Prantl. Die natürlichen Pflanzenfamilien. 15a: 65–159

HASSLER E. 1919. Bromeliacearum paraguariensium conspectus. Annuaire Conserv. J. Bot. Genève. 268–341.

HUME H.H., AND H.K. MILLER. 1904. Pineapple culture. II. Varieties. Florida Agr. Expl. Sta. Bul. 70: 37–62.

LEAL F. 1989. On the history, origin and taxonomy of the pineapple. Interciencia 14: 235–241.

———. 1990. On the validity of *Ananas monstruosus.* J. Bromeliad Soc. 40: 246–249.

LEAL F. AND L. AMAYA. 1991. The curagua (*Ananas lucidus*: Bromeliaceae) crop in Venezuela. Econ. Bot. 45: 216–224.

LEAL F. AND G. COPPENS D'EECKENBRUGGE. 1996. Pineapple. Pp. 565–606 *in* J. JANICK AND J. N. MOORE, ed., Fruit breeding. Wiley, New York.

LEAL F. AND E. MEDINA. 1995. Some wild pineapples in Venezuela. J. Bromeliad Soc. 45: 152–158.

LIN B.Y, P.S. RITSCHEL, AND F. R. FERREIRA. 1987. Número cromossômico de exemplares da familia Bromeliaceae. Rev. Bras. Frutic. 9: 49–55.

LINDEN J.J. 1879. *Ananas mordilona* Linden. Belgique Hort. 29: 302–303.

LINDMAN C.A.M. 1891. Kongl. Svenska Vetenskapsakad. Handl. 24(8): 39.

LINDLEY J. 1827. *Billbergia.* Bot. Reg. 13: 1068.

LINNAEUS C. 1753. Species plantarum, Stockholm.

LOISON-CABOT C. 1992. Origin, phylogeny and evolution of pineapple species. Fruits 47: 25–32.

MARCHANT C. J. 1967. Chromosome evolution in the Bromeliaceae. Kew Bull. 21: 161–168.

MERRILL E.D. 1917. An interpretation of Rumphius' Herbarium Amboinense. Bureau of Science, Manila.

MEZ C. 1892. Bromeliaceae; *Ananas.* In: Martius, Fl. Bras. 3: 172–634.

———. 1934. Das Pflanzenreich. Bromeliaceae. Engler & Prantl.

MILLER P. 1754. Gard. Dict., 4th ed. London.

———. 1768. Gard. Dict., 8th ed. London.

MORREN E. 1878. Description de l'*Ananas macrodontes.* sp. nov. *Ananas* à fortes épines. Belgique Hort. 28: 140–144.

PLUMIER C. 1755. Plantarum Americanarum. Amstelaedami.

REITZ P.R. 1968. A new species of pineapple from central Brazil. Bromeliad Soc. Bull. 18(5): 109–111.

REYES-ZUMETA H. 1967. Breve nota taxonómica sobre piñas cultivadas *Ananas comosus* (L.) Merr. con mención de dos nuevas variedades silvestres. Rev. Fac. Agron. L.U.Z. (Maracaibo) 39: 131–142.

RUMPHIUS G.E. 1747. Anassa, Nanas. Herbarium Amboinense. 5: 227–231.

SAINT-HILAIRE J. 1805. Expos Family I. 122–125, t. 19.

SCHULTES J.A. AND J.H. SCHULTES. 1830. *Ananas sativus.* Syst. Veg. 7: 1283–1285.

SHARMA A.K. AND I. GHOSH. 1971. Cytotaxonomy of the family Bromeliaceae. Cytologia 36: 237–247.
SMITH L.B. 1934. Studies in the Bromeliaceae—V. Contr. Gray Herb. 104: 71–83.
———. 1939. Notes on the taxonomy of *Ananas* and *Pseudananas*. Bot. Mus. Leafl. 7(5): 73–81.
———. 1961. Notes on Bromeliaceae. Phytologia 8: 12.
———. 1962. A new look at the species of pineapple. Bromeliad Soc. Bull. 12(3): 54–55.
———. 1971. Bromeliaceae. Flora de Venezuela. Min. Agric. & Cría, Caracas. 12(1): 1–361.
SMITH L.B. AND R.J. DOWNS. 1979. Bromelioideae (Bromeliaceae). Fl. Neotr. Monogr. 14(3): 1493–2142.
THÉVET A. 1557. Les singularités de la France Antarctique. Maspero, Paris.
VELEZ I. AND V.M. BADILLO. 1946. Comentarios sobre los piñales silvestres y cultivados de la región del Parguaza, Guayana Venezolana. Rev. Agric. Puerto Rico 37: 127–130.
VELLOZO J.M. C. 1825. Florae fluminensis. Arch. Mus. Nac. 5: 122.