



Synonymies in *Ananas* (Bromeliaceae)

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Abstract

To clarify the last pineapple classification, which only recognizes the tetraploid crownless *A. macrodontes* and the diploid *A. comosus*, with three cultivated and two wild botanical varieties, we re-establish *A. comosus* var. *microstachys* and revise ancient synonymies, underlining misinterpretations and distinguishing horticultural names from botanical names whenever possible.

In 2003 Coppens d'Eeckenbrugge and Leal published a new classification of pineapples, regrouping all of them into the genus *Ananas* Miller, with two species, *A. comosus* (L.) Merrill, including five botanical varieties, and *A. macrodontes* Morren (1878). The latter can be readily distinguished because its inflorescences and fruits generally lack the crown of leaves that typically tops the cultivated pineapples and their wild relatives, and it reproduces vegetatively by stolons instead of stem suckers. Furthermore, it is tetraploid and appears to lack the gametophytic incompatibility system of its diploid relative.

The new classification came after an unprecedented effort of collecting pineapples in their continent of origin, with particular emphasis in Brazil (states of Amapá, Amazonas, Acre, Distrito Federal, Espírito Santo, Goiás, Maranhão, Northern and Southern Mato Grosso, Pará, Paraná, Piauí, Rio Grande do Sul, Roraima), Paraguay, Venezuela, French Guiana, Perú, and Colombia (Leal *et al.* 1986, Bello & Julca 1993, Ferreira *et al.* 1992, Ferreira & Cabral 1993, López *et al.* 1992, Duval *et al.* 1997), followed by studies and reviews on reproductive biology as well as morphological, biochemical and genetic diversity (García 1988, Duval & Coppens d'Eeckenbrugge 1993, Coppens d'Eeckenbrugge *et al.* 1993, 1997, Aradhya *et al.* 1994, Duval *et al.* 2001, 2003). The classification intended to use all the generated information to put an end to a long and chaotic history of pineapple taxonomy (Leal *et al.* 1998), often related to (i) an incomplete knowledge of pineapple diversity and systematics; (ii) the predominance of horticultural concepts; and (iii) the effects of dominant clonal reproduction leading to an overemphasis on seemingly stable differences.

A decade later, although the new classification has been well received in the pineapple scientific community, this has not always been the case among botanists, as it has only been accepted in the USDA Genetic Resources Information Network (2013) and in the New Bromeliad Taxon List (Butcher and Gouda (2013; cited in Butcher and Gouda 2014). Indeed, despite the historical revision of pineapple taxonomy that preceded the 2003 classification, the reasons to assign ancient names as synonyms of the new species and botanical varieties were not understood. Furthermore, Coppens d'Eeckenbrugge and Leal (2003) made a formal error in using the epithet “*ananassoides*”, instead of “*microstachys*”, a varietal name used by Mez (1892). In the present note, we are correcting formal errors, and restating the reasons for synonymies as given in the 2003 treatment of the pineapples. We shall mostly use the World Checklist of Selected Plant Families (WCSP 2013) as a source of reference for pineapple synonyms, and focus on those that are older than the names considered in 2003. Readers interested in further synonymy may consult the WCSP website (<http://apps.kew.org/wcsp/>).

Ananas macrodontes Morren (1878: 140)

Synonyms:

- *Ananas microcephalus* Bertoni (1919: 250).
- *Ananas microcephalus* var. *major* Bertoni (1919: 252).
- *Ananas microcephalus* var. *minor* Bertoni (1919: 252).

- *Ananas microcephalus* var. *missionensis* Bertoni (1919: 252).
- *Ananas microcephalus* var. *mondyanus* Bertoni (1919: 252).
- *Ananas microcephalus* var. *robustus* Bertoni (1919: 252).
- *Pseudananas macrodontes* (Morren) Harms (1930: 153).
- *Pseudananas sagenarius* (Arruda da Câmara) Camargo (1939: 19).
- *Pseudananas sagenarius* var. *macrodontes* (Morren) Camargo (1943: 21).

Refuted synonyms:

- *Bromelia sagenaria* Arruda (1810: 13).

The full title of Arruda da Câmara's treaty, in ancient Portuguese, can be translated as follows "dissertation on plants from Brazil that can provide fibres for many uses of society and compensate for the lack of hemp." And Arruda da Câmara's focus is clearly more on particular properties and economic uses of Brazilian vegetal fibres, than on botanical aspects. His interest in fibres can explain why it has been considered as the first description of this species, sometimes named by the Amerindian word "yvira" (meaning "fiber"), or the creole expression "Crauatá de rede" (meaning "net bromeliad"). However, all pineapples can be used for their fibres, as mentioned by Arruda da Câmara.

For *Bromelia sagenaria*, the description given by Arruda da Câmara includes: "flowers united from their receptacle, or berries united in one ... leaves ciliate-serrate, berries united into one pyramidal fruit; the bracts very long, imbricate, covering the fruit." This description is repeated a bit further. Even more clearly in his "Observations", Arruda mentions the traits that are common with the "ananas manso" (meek pineapple, the edible kind with small spines or no spines, as opposed to the feral pineapple or "ananas bravo", a name given to *A. comosus* var. *bracteatus*): "This species of *Ananas* (*Bromelia*) is new; its fruit is similar to that of the meek ananas, although smaller; its berries are less succulent, unpalatable; bracts are long, three inches long, high, one over the other as tiles, so that they cover the fruit." Later, he praises the species to be tolerant to poorly fertile soils and mentions cultivation close to sugar cane plantations, i.e., in an ecology that is very distinct from the organic soils of the rain forests where *A. macrodontes* thrives. After *Bromelia sagenaria*, Arruda da Câmara describes the edible pineapple, *Bromelia ananas* or ananas manso (p. 18), and *Bromelia muricata*, a pineapple similar to *B. sagenaria*, except for the bracts that are replaced by 3.5in-spines [sic]. Strangely, this improbable species unseen by others, was placed in the genus *Aechmea* based only on geographic distribution). Considering the three species, the most extensive chapter concerns *B. sagenaria*, with a two redundant descriptions of floral morphology, but in no case does the author mention the absence of the leaf crown on the fruit or the vegetative reproduction by long stolons. Thus we consider *B. sagenaria* a synonym for our *A. comosus* var. *bracteatus*, not for *A. macrodontes*. This position logically leads us to discard two other synonyms listed by Camargo (1943): *Ananas sagenaria* (Arruda) Schultes & Schultes (1830: 1286) and *Bromelia silvestris* Vellozo (1829: 129).

- Indeed, the description of *Ananas sagenaria* (Arruda) Schultes & Schultes (1830) was entirely based on that of *Bromelia sagenaria* Arruda. Schultes and Schultes themselves questioned the differentiation between *A. sagenaria* and *A. bracteatus* Lindley (1827) (syn. of *A. bracteatus* var. *bracteatus*): "ab. *A. Sagenaria satis diversa*?" Later, Mez (1892) answered their question by recognizing the synonymy between *B. sagenaria* Arruda da Câmara. and *A. sativus* var. *bracteatus* Lindley.

- *Bromelia silvestris* Vellozo (1829: 129). This synonymy was proposed by Camargo (1943). Vellozo's description clearly mentions the crown: "*spica comosa ... folia comae ciliata, spinosa, lanceolata*". The mention of hooked spines and the presence of a crown on the fruit attests that the description refers to a spiny form of *A. comosus*, may be *A. comosus* var. *bracteatus*. According to Camargo (1939, 1943), this plant is also the same that was represented by Thevet in 1557, however Thevet's drawing and text clearly refer to a large yellow pineapple (compared to a medium-sized pumpkin) ["moyenne citrouille"], with sweet flesh and one or several crowns, i.e. *A. comosus* var. *comosus*.

- *Ananas silvestris* (Vellozo) Müller (1896: 4). Fritz Müller gave the first precise description of *A. fritzmuelleri* Camargo (1943), a diploid form with a crown, now considered under *A. comosus* var. *bracteatus*.

***Ananas comosus* (L.) Merrill (1917: 133)**

- *Ananas comosus* var. *comosus* (the edible pineapple)

Most ancient synonyms of this botanical variety come from horticultural treatises, printed at a time when the fruit was a luxury good grown in European glasshouses, with no direct knowledge about the plant relatives and their habitat (pineapple being sometimes considered native to Africa or Asia, or pre-Columbian Mexican cultivars cited as Brazilian

varieties (Schultes & Schultes 1830). The confusion between botanical forms (species and varieties) and horticultural forms, i.e. cultivars) is the most frequent problem in determining synonymies.

A first series of cultivars is found in the successive editions of Miller's *Gardeners Dictionary* (1754, 1768). In 1754, Miller describes six "varieties", indicating the presence of spines, the shape and color (internal and external) of the fruit, using Latin polynomials and their English translation. The first two are taken directly from Plumier (1703). In 1768, Miller adds a Latin name for each of the six cultivars *Ovatus*, *Pyramidalis*, *Glabra*, *Lucidus*, *Serotinus*, and *Viridis*, and the list is not exhaustive, as Miller (1754, 1768) states that "there are several other varieties of this fruit, some of which may have been obtained from seeds." This perception was probably common in the late 18th century. For example, in his *Encyclopédie*, De Felice (1770) presents four polynomials from Plumier, stating that "when the white-fleshed pineapple is propagated from seeds, it is highly variable: and it is probably from there ... that come the varieties we have indicated." As Miller did not intend to describe distinct species, *A. glaber* Miller, *A. lucidus* Miller, *A. ovatus* Miller, *A. pyramidalis* Miller, *A. serotinus* Miller, and *A. viridis* Miller were derived from a misinterpretation, and should not be considered valid names. Thus, we shall only consider those that were treated as species or botanical varieties/forms by later authors.

Synonyms

- *Ananas sativus* Schultes & Schultes (1830: 1283) (spiny cultivars).

In this synonym, Schultes & Schultes include a list of seven spiny cultivars ("*In hortis ... An. sativi varietates*"), including the 'Ovata', 'Pyramidalis', 'Serotina' and 'Viridis' of Miller (1754, 1768), 'Sugar Loaf', and 'Pomme de ReINETTE,' with synonyms (polynomial names and English or French cultivar names), followed by common or Latin names of tens of other cultivars reported in the literature at that time.

- *Bromelia semiserrata* Willdenow (1809: 345). *Ananas semiserratus* (Willd.) Schultes & Schultes (1830: 1286). (Cultivars with spines at leaf apex).

- *Ananas lucidus* (Aiton) Schultes & Schultes (1830: 1286) (smooth-leaved cultivars).

- *Ananas debilis* (Lindley) Schultes & Schultes (1830: 1287) (a wave-leaved cultivar).

- *Bromelia ananas* subvar. *variegata* Noisette (1825: 289) as "*ananas variegata*". *Ananassa sativa* var. *variegata* (Noisette) Lowe (1868: 43). *Ananas comosus* var. *variegatus* (Noisette) Moldenke (1938: 38).

- *Ananas porteanus* Veitch ex Koch (1871: 130). Ornamental variegated cultivar with fasciated crown, introduced in European glasshouses from the Philippines (see also Morren, 1872: 193).

- *Ananassa mordilona* Linden (1869). *Ananas mordilona* (Linden) VanGeert (1873). *Ananas sativus* f. *mordilona* (Linden) Bertoni (1919: 271).

Smooth-leaved cultivar from the Colombian Andes, very probably cv. *Manzana*.

- *Ananassa bracamorensis* Linden (1869: 2). *Ananas bracamorensis* (Linden) Van Geert (1878). Large-fruited cultivar from Maranhão.

- *Ananas sativus* var. *viridis* Bertoni (1919: 272). Bertoni mentions an inconsistent list of very diverse cultivars that he relates to this name.

- *Ananas comosus* f. *sativus* (Schult. & Schult.f.) Mez (1934: 102). Spiny cultivars.

- *Ananas comosus* f. *lucidus* Mez (1934: 103). Smooth-leaved cultivars "preferred in the European *Ananas*-houses".

- *Ananas comosus* f. *debilis* Mez (1934: 104). Cultivar with undulated leaves, "mihi dubia".

Refuted synonyms

- *Ananas monstrosus* (Carrière) Smith (1961: 12). This name was derived from *Ananassa monstrosa*, a name that Carrière (1870) associated with crownless pineapples. Leal (1990) underlined that Smith misunderstood Carrière's paper. In fact, Carrière openly mocked botanists who would make it a distinct species, and concluded: "We do not ignore that the Pineapple, considered as a type and provided with a crown, sometimes produces, by a kind of low dimorphism, crownless individuals (democratized pineapples in a way), which is, according to us a reason more to consider this fact as fully natural."

- *Ananas penangensis* Baker (1889: 143). Ornamental variegated form, listed by Baker among many cultivars. Baker only recognized three species in *Ananas* (*A. sativus*, *A. bracteatus*, and *A. macrodontes*).

- *Ananas proliferus* Baker (1889: 23). This is a fruit malformation, caused by a dominant mutation (Collins 1960) and known as "knobs" by pineapple growers. In any case, it is listed as a horticultural variant by Baker.

- *Ananas comosus* var. *microstachys* (Mez) Smith (1934: 72) (wild pineapple)

Synonyms

- *Acanthostachys ananassoides* Baker (1889: 25). *Ananas microstachys* Lindman (1891: 39), nom. superfl. *Ananas sativus* Schult. & Schult.f. var. *microstachys* Mez (1892: 294). *Ananas ananassoides* (Baker) Smith (1939: 79). *Ananas comosus* var. *ananassoides* (Baker) Coppens & F.Leal (2003: 25), nom. superfl.

- *Ananas guaraniticus* Bertoni (1919: 274).

- *Ananas ananassoides* Baker var. *nanus* Smith (1939: 79). *Ananas microstachys* var. *nanus* (L.B.Sm.) Camargo (1942: 189). *Ananas nanus* (L.B.Sm.) Smith (1962: 54).

- *Ananas genesio-linsii* Reitz (1968: 109). The “Ananas do Indio” population still exists in Aguas Emendadas. Its general morphology relates it clearly to *Ananas comosus* var. *microstachys*, except for the size of the fruit, which is intermediate between that of wild and domesticated pineapples. This unusual fruit size must be related to its triploid nature (Lin *et al.* 1987, Dujardin 1991). Similar clones are found in the wild and in home gardens, in the Guianas (personal observations).

- *Ananas comosus* var. *parguazensis* (Camargo & L.B.Sm.) Coppens & Leal (2003) (wild pineapple)

Wild pineapple, mostly found in the basins of Rio Orinoco (south-eastern Colombia and southern Venezuela) and Rio Negro (north-western Brazil), and more rarely in the Guianas, together with *Ananas comosus* var. *microstachys* and forms that appear intermediate between the two wild botanical varieties.

Synonyms

- *Ananas parguazensis* Camargo & Smith (1968: 464).

- *Ananas pancheanus* André (1889: 5). A wild pineapple, with spaced small spines and a small subglobose syncarp on a long peduncle. Long leaves and regularly spaced spines are reminiscent of *A. comosus* var. *microstachys*, however wide (6 cm) and convoluted leaves, as well as the combination of antrorse and retrorse spines point more clearly to *Ananas comosus* var. *parguazensis*. Such intermediate forms are relatively common in the Orinoco and Rio Negro basins (personal observations) as well as in the Guianas (Gouda 1999).

- *Ananas comosus* var. *erectifolius* (L.B.Smith) Coppens & Leal (2003)

This is the Curagua, a small-fruited pineapple cultivated only for fibre (Leal & Amaya 1991), north of the Amazon River (Guianas and Venezuela). This cultigen evolved from *Ananas comosus* var. *microstachys* through multiple domestication events (Duval *et al.* 2003), which determined its most characteristic features: erect leaves, related to selection for a high fibre content, and absence of marginal spines, related to a dominant mutation (Collins 1960).

The first mention of the curagua was believed to be a polynomial from Plumier (1703) *Ananas non aculeatus*, *Pitta dictus*, described in the Antilles. This seemed logical, as *pita* is a name used for several bromeliads and Agavaceae exploited for their fibres. However, Labat (cited by De Felice 1770), who worked with Plumier, credited the Pitte edible pineapple as the best one. The excellent fruit quality of this cultivar is corroborated by Krünitz (1773) and Lemery (1755), who notes that this edible pineapple is sometimes confused with the caraguata (a South American generic name for terrestrial bromeliads). This implies that the “Ananas pitte” described by Plumier (1703) was not a curagua, whose small inedible fruits are very fibrous, and questions the pre-Columbian introduction of this plant in the Antilles. As a matter of fact, the curagua has not been reported by ethnobotanists in this region, in contrast with reports from South America.

Krünitz (1773) mentions the curagua later in his text, under the polynomial *Ananasa sylvestris non aculeata*, *Pita dicta* “or the wild pineapple without spines Pita”, whose “fibres are used in America for the production of socks, surpassing silk in fineness, whiteness and durability.” This sock industry was already reported by the comment of an Americanist (Denis 1864) on the mention of pita fibre by Yves d’Evreux (1615). Caulin (1779) and Gilij (1782, cited by Leal & Amaya 1991) mention its importance and fibre quality in Venezuela. In any case, the first botanical description of the curagua is that of Smith (1939), under the name: *Ananas erectifolius* Smith (1939: 78).

Smith later changed his mind (Smith & Downs 1979: 2056), and inexplicably relegated his *A. erectifolius* to a

synonym of *A. lucidus* Miller. We have seen that the latter was not described as a species, but as an edible pineapple cultivar.

- *Ananas comosus* var. *bracteatus* (Lindley) Coppens & Leal (2003: 28)

This botanical variety is particular in resulting from the introgression of *A. macrodontes* genes into *A. comosus*). It includes two introgressed forms that have been propagated through vegetative reproduction, which explains their very low genetic diversity. The very rare form, corresponding to *A. fritzmulleri* Camargo, shares nuclear and cytoplasmic genes with *A. macrodontes*, as well as more morphological traits (longer bracts, retrorse spines). The second form, by far the most common one, has been mostly given the epithet or variety name *bracteatus*. It appears to share a lesser proportion of nuclear genes and no cytoplasmic genes with *A. macrodontes* (Duval *et al.* 2001, 2003).

Synonyms

- *Bromelia sagenaria* Arruda da Câmara (1810: 13). *Ananas sagenaria* (Arruda da Câmara) Schultes & Schultes (1830: 1286). *Ananassa sagenaria* (Arruda da Câmara) D. Dietrich (1840: 1088).
- *Bromelia silvestris* Vellozo (1829: 129). *Ananas silvestris* Müller (1896: 4). *Ananas fritzmulleri* Camargo (1943: 16).
- *Ananassa bracteata* Lindley (1827: t. 1081). *Ananas bracteatus* (Lindley) Schultes & Schultes (1830: 1286). *Ananas bracteatus* (Lindley) Baker (1889: 23). *Ananas sativus* var. *bracteatus* (Lindley) Mez (1892: 293), *Ananas bracteatus* var. *typicus* Smith (1939: 76), nom. inval.
- *Ananas bracteatus* var. *albus* Smith (1939: 76).
- *Ananas bracteatus* var. *hondurensis* Bertoni (1919: 258). With many doubts.
- *Ananas bracteatus* var. *macrodontes* Bertoni (1919: 256). With many doubts.
- *Ananas bracteatus* var. *paraguariensis* Bertoni (1919: 259). With many doubts.
- *Ananas bracteatus* var. *rudis* Bertoni (1919: 256). With many doubts.
- *Ananas bracteatus* var. *rudis* subvar. *tricolor* Bertoni (1919: 258); *Ananas bracteatus* var. *tricolor* (Bertoni) Smith (1939: 76); and *Ananas comosus* var. *tricolor* (Bertoni) Camargo (1942: 187).
- *Ananas bracteatus* var. *striatus* Foster (1958: 97).

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