Chapter 1
The Pineapple Success Story: From Domestication to Pantropical Diffusion

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The "Old World" discovered the impressive pineapple fruit when Columbus' crew landed in the island of Guadeloupe (French West Indies) during his second voyage to tropical America in 1493. This was the very first stage of its rapid expansion to all African and Asian tropical coasts, which was nearly accomplished in less than one century. Scientific descriptions came later, following the pre-Linnaean work of Plumier (1703) who created the genus *Ananas*, named after the most common Amerindian name, *nanas* or *ananas*. After him, most botanical descriptions of pineapple diversity concerned cultivars that had been adopted for greenhouse cultivation in Europe and circulated among European horticulturist circles before the mid-eighteenth century. They were differentiated on leaf traits (smooth to spiny, erect or undulate) and fruit traits (shape, external and internal color), and designated accordingly, using Latin polynomials, later reduced to binomials, which generated a long-lasting confusion between horticultural and botanical nomenclature for the species (Coppens d'Eeckenbrugge 2014).

The pineapple was already a major pantropical fruit crop when Father Gumilla (1741) reported the existence of wild pineapple in the Orinoco basin. In the same region, Jacinto de Carvajal had already observed in 1647 the existence of "small wild pineapples, white and very green, with black stones or seeds"; however its observation was only published in 1892. Gumilla's report was largely ignored, and Rumphius (1747) even contended that the pineapple was native to Asia, being cultivated in all the regions of India and growing wild in the Celebes (Indonesia), against

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the lack of an original Asian name and all mentions of its introduction by the Portuguese. Thus, in his *Origine des Plantes Cultivées*, De Candolle (1886) could only mention wild pineapples from Mexico (with doubts), the drainage basin of the Upper Orinoco (based on Von Humboldt's report), Guiana, and the Brazilian state of Bahia. And, in fact, the first botanical description of a wild pineapple was written by Baker (1889), who named it *Acanthostachys ananassoides*. Its relation with the cultivated pineapple was duly recognized when Lindman (1891) classified it as a neighbor species, under *Ananas microstachys* Lindman, while Mez (1892) classified it as a botanical variety of the same species, under *Ananas sativus* Schult. and Schult.f. var. *microstachys* Mez. However, the identification of a wild relative of the pineapple did not simplify the problems of its origins and domestication, as exploration of South America continued and other wild and domesticated pineapples were described in the nineteenth and twentieth centuries. Among these were a domesticated fiber crop plant, another small-fruited wild form in northern Amazonia, another domesticated fiber crop plant, and a wild crownless pineapple in southeastern Brazil. As a result of these discoveries, pineapple taxonomy and nomenclature entered a phase of high instability (Leal et al. 1998), which ended in 2003, after a systematic exploration of pineapple germplasm in most of tropical South America and the concomitant accumulation of morphological and genetic data. We shall now present the last classification (Coppens d'Eeckenbrugge and Leal 2003; Coppens d'Eeckenbrugge and Govaerts 2015), relating its divisions to pineapple genetic diversity and its evolution under different domestication processes.

Morphological and Genetic Diversity of Wild and Domesticated Pineapples

Domestication is a form of coevolution in which humans and their crops and animals become dependent upon each other. The domestication syndrome is a set of morphological, phenological, and physiological traits that are modified by conscious or unconscious human selection, which causes this dependence. In particular cases, reproductive modifications induced by domestication may result in partial or complete reproductive isolation, i.e., the domesticated form becomes a new species. This has not been the case for the pineapple, whose domestication has not produced any clear, qualitative, morphological, or physiological differentiation or reproductive isolation.

Among Bromeliaceae, the genus *Ananas* is unique in presenting a syncarpic inflorescence resulting from the fusion of individual flowers. It includes only two species, the pineapple, *A. comosus* (L.) Merrill, and the *gravatá de rede* (*crauatá de rede*) or *yvira* (*ihvíra*), *A. macrodontes* Morren (Coppens d'Eeckenbrugge and Leal 2003). The former is a normally diploid species ($2n = 50$) that includes five botanical varieties, three of which are domesticates. Its sexual propagation is controlled by a self-incompatibility system, whose expression is variable. However, it mainly propagates vegetatively from stem suckers, slips emerging from the fruit peduncle or the fruit base, and from the leafy crown(s) that top the fruit. *Ananas comosus*' natural distribution includes all of tropical South America east of the Andes. *Ananas* *macrodontes* is a self-fertile tetraploid ($2n = 4x = 100$), whose inflorescence lacks a crown and vegetative propagation is ensured by stolons (Fig. 1.1a, b). It grows wild in the humid forests of southeastern South America. Although exploited by natives for the production of fibers (Corrêa 1952), it shows no sign of domestication.

The ploidy difference between *A. comosus* and *A. macrodontes* constitutes a clear reproductive barrier, completed by their ecological divergence. Both species exhibit a wide diversity and a limited but clear differentiation in the nuclear DNA

Fig. 1.1 Pineapples in the wild. (**a** and **b**) *Ananas macrodontes* with flower (**a**, left) and fruit (**b**); note the emission of a stolon (arrow, **a** right); leaves (normally reaching more than 2 m) were severely cut for plant management, so that mostly basal retrorse spines are visible. (**c**) *Ananas comosus* var. *parguazensis*. (**d**) *Ananas comosus* var. *microstachys*, from a northern Mato Grosso population in open forest; (**e**) same population: tangential-longitudinal section showing numerous seeds in the fruit locules (the picture was darkened and saturated to allow a better distinction of the yellowish white immature seeds from the greenish white immature fruit pulp). (**f** and **g**) *A. comosus* var. *microstachys*, on inselbergs in French Guiana. (**h**) Larger wild fruits collected from a monoclonal population of *A. comosus* var. *microstachys* on the edges of a "rock savannah" in French Guiana (the blue pen, used for pictures **f** and **h**, allows comparing fruit size). Photographs Marie-France Duval (**c**) and Geo Coppens d'Eeckenbrugge (**a**, **b**, **d**–**h**)

Table 1.1 Correspondence between the current pineapple classification (Coppens d'Eeckenbrugge and Leal 2003; Coppens d'Eeckenbrugge and Govaerts 2015) and the previous one in use in the late twentieth century (Smith and Downs 1979)

Current classification	Previous classification
Ananas macrodontes Morren	*Pseudananas sagenarius* (Arruda da Câmara) Camargo
Ananas comosus (L.) Merrill	Genus *Ananas* Miller
– *A. comosus* var. *microstachys* (Mez) L.B. Smith	– *Ananas ananassoides* (Baker) L.B. Smith, *Ananas nanus* (L.B. Smith) L.B. Smith
– *A. comosus* var. *parguazensis* (Camargo and L.B. Smith) Coppens and Leal	– *Ananas parguazensis* Camargo and L.B. Smith
– *A. comosus* var. *comosus*	– *Ananas comosus* (L.) Merrill, *Ananas monstrosus* (Carrière) L.B. Smith (invalid)
– *A. comosus* var. *erectifolius* (L.B. Smith) Coppens and Leal	– *Ananas lucidus* Miller
– *A. comosus* var. *bracteatus* (Lindley) Coppens and Leal	– *Ananas bracteatus* (Lindley) Schultes f., *Ananas fritzmuelleri* Camargo

RFLP study of Duval et al. (2001). A similar study on chloroplastic DNA (Duval et al. 2003) showed a wide diversity in *A. comosus*, contrasting with the unique haplotype for *A. macrodontes*, and led its authors to suggest that the latter would have diverged recently through autopolyploidization.

Within *A. comosus*, five botanical varieties are recognized. Two are wild: *A. comosus* var. *microstachys* (Mez) L.B. Smith (formerly *A. comosus* var. *ananassoides* (Baker) Coppens and F. Leal) and *A. comosus* var. *parguazensis* (Camargo and L.B. Smith) Coppens and Leal. Three are domesticates: *A. comosus* var. *comosus* (the edible pineapple), *A. comosus* var. *erectifolius* (L.B. Smith) Coppens and Leal (the curagua, a fiber crop), and *A. comosus* var. *bracteatus* (Lindley) Coppens and Leal, now an ornamental pineapple (Coppens d'Eeckenbrugge and Leal 2003; Coppens d'Eeckenbrugge and Govaerts 2015). Table 1.1 gives the synonyms that were used for these pineapple taxa in diversity studies of the second half of the twentieth century.

Wild Pineapples

Within *A. comosus*, the two wild botanical varieties display the highest genetic diversity, which is a common situation in crop gene pools. The most common and diverse is *A. comosus* var. *microstachys*, which has long and narrow leaves, up to 2 m long and less than 4 cm wide, subdensely serrate with wholly antrorse spines. The fruit peduncle is elongate (most often over 40 cm) and slender (usually less than 15 mm wide). It is also the common ancestor of the three domesticated botanical varieties (Duval et al. 2001, 2003). Its natural distribution covers that of the whole species, and it is generally found in savannahs or clear open forests (Brazilian *cerrados*), growing on soils with limited water-holding capacity (sand dunes or "campinas," inselbergs, and "rock savannahs," common on and around the Guiana shield) and forming populations of variable densities. In the Guianas, it can also be found, although rarely, in secondary rain forest. In contrast, it is absent from the seasonally flooded lands along the Amazon and its main southern tributaries, which seem to act as a barrier dividing its distribution into two main areas where, according to the chloroplast haplotype map presented by Duval et al. (2003), the populations are genetically differentiated. They consist of a northern one corresponding to the Guiana shield, Orinoco basin, and northern drainage of Rio Negro (i.e., from the northern Brazilian state of Amapá to eastern Colombia) and a southern one roughly corresponding to the Brazilian shield, northeastern Brazil, and the basins of the upper Paraná and Paraguay rivers (from the Brazilian states of Acre and Mato Grosso over to Pernambuco and down to Paraguay and northern Argentina). In the southern part of its distribution, the inflorescence is very generally small (less than 10 cm), globose to cylindrical, and it shows little growth after anthesis, so the fruit has little flesh. The pulp is white or cream, very firm and fibrous, with high sugar content and acidity and numerous seeds (Fig. 1.1d, e).

The southern habitat of *A. comosus* var. *microstachys* appears mostly restricted to areas that are open and markedly dry (poor grass savannahs and low open forests). In contrast, in the northern area, the habitats of *A. comosus* var. *microstachys* appear more variable (Leal and Medina 1995), and a higher morphological diversity is observed, with clones producing larger, fleshy fruits (up to 12–15 cm long) due to significant growth of the syncarp after anthesis (Fig. 1.1f–h), which, however, are still smaller than the cultivated forms. Their fruits were consumed in the Orinoco (Patiño 2002) and are still occasionally consumed in the Guianas. Similar types, morphologically intermediate between the wild and cultivated forms, are sometimes found in patches in secondary forest and savannahs in French Guiana, indicating an ancient settlement, or cultivated in gardens (Fig. 1.2a). Such clones constitute the most plausible basis for initial domestication in the Guianas. Indeed, in the cpDNA study of Duval et al. (2003), these intermediate phenotypes display four haplotypes, sharing three of them with *A. comosus* var. *comosus* and all four with typical representatives of *A. comosus* var. *microstachys*, which is consistent with the hypotheses of semidomestication and/or introgression between the two botanical varieties.

The contribution of *A. comosus* var. *parguazensis* to the evolution of the cultivated *A. comosus* var. *comosus* is less likely, on geographic, morphological, and genetic grounds. Its geographical distribution appears more centered on the drainage basins of the Orinoco, its area of greatest diversity, and upper Rio Negro, with few observations in eastern Colombia and in the Guianas (Coppens d'Eeckenbrugge et al. 1997; Duval et al. 2001, 2003). It grows in lowland forests, under canopies of variable densities, from clearings or riverbanks to dense forest. As compared to specimens of *A. comosus* var. *microstachys* growing in close proximity, it seems restricted to shadier environments, because of lower water use efficiency (Leal and Medina 1995).

Morphologically, *A. comosus* var. *parguazensis* differs from variety *microstachys* by having wider leaves, slightly constricted at their base, and larger spines, some of them retrorse (Fig. 1.1c). Some Orinoco/Rio Negro specimens appear to be intermediate between varieties *parguazensis* and *microstachys*, indicating natural hybrid-

Fig. 1.2 Cultivated pineapples. (**a**) A form of pineapple intermediate between *A. comosus* var. *microstachys* and *A. comosus* var. *comosus*, cultivated in a home garden in French Guiana; similar plants are also found in subspontaneous populations, among secondary vegetation. (**b**) A West Amazonian young boy presenting a legacy from his ancestors. (**c**) *Ananas comosus* var. *erectifolius*, a domesticated form exploited for its fibers. (**d**) The rare form of *A. comosus* var. *bracteatus*, previously named *A. fritzmuelleri* (Camargo). (**e** and **f**) Two clones of the common form of *A. comosus* var. *bracteatus*, the original one cultivated for fiber or for fences, and a variegated chlorophyll mutant commonly used as a garden ornamental in tropical countries. (**g** to **i**) The four most important pre-Columbian cultivars of the edible pineapple that reached an intercontinental distribution: 'Singapore Canning' (**g**), 'Pérola' (**h**), 'Queen' (**i**), and 'Smooth Cayenne' (**j**)

ization. However, retrorse spines and the basal leaf constriction have not been observed in the domesticated *A. comosus* var. *comosus* (M.-F. Duval and G. Coppens d'Eeckenbrugge, personal observations on field germplasm collections).

The genetic studies of Duval et al. (2001, 2003) confirm some gene flow between varieties *parguazensis* and *microstachys* in the Orinoco/Rio Negro region, while the few *A. comosus* var. *parguazensis* clones found in the Brazilian state of Pará (eastern Guianas) appear to originate from a distinct genetic background, shared with sympatric representatives of other botanical varieties, suggesting that they represent cases of morphological convergence. In any case, four of the seven *parguazensis* chloroplast haplotypes, including the most common ones, are not shared with other botanical varieties (Duval et al. 2003). In conclusion, a contribution of *A. comosus* var. *parguazensis* to the genomes of the cultivated pineapples cannot be ruled out, but it would be marginal, and necessarily indirect, through occasional hybridization with *A. comosus* var. *microstachys* as the wild ancestor of *A. comosus* var. *comosus* and *A. comosus* var. *erectifolius*.

Domesticated Pineapples

The three domesticated botanical varieties are *A. comosus* var. *comosus*, the pantropical pineapple cultivated for its spectacular and exquisite large fruit; *A. comosus* var. *erectifolius*, a small-fruited pineapple cultivated for its fiber; and *A. comosus* var. *bracteatus*, a robust pineapple with multiple uses, involving its medium-sized fruit for juice and its armed leaves for fences. The two latter varieties are now increasingly cultivated as ornamentals.

In *A. comosus* var. *comosus*, the syncarp grows very significantly after anthesis, so the fruit is generally very large and fleshy (up to several kilograms in certain cultivars; Fig. 1.2b), with many fruitlets (“eyes”); they are borne on a wide and strong, relatively short, peduncle. Seeds are rare in the fruits, because of reduced fertility, conjugated with stronger self-incompatibility and monoclonal cultivation (Coppens d’Eeckenbrugge et al. 1993). Vegetative reproduction, through shoots, slips, suckers, and crowns in the vernacular language of pineapple, is often initiated at the time of or after floral induction. In altitudinal or latitudinal “subtropical” environments, stem storage reserves provide the extra resources needed to support sucker and slip growth during fruit development; while under tropical conditions, suckers resume growth after fruit maturity. The plant has numerous wide leaves (40–80), with antrorse spines; these marginal spines are generally smaller and denser than in wild varieties and can be partially or completely suppressed by dominant mutations.

The genetic relationship between *A. comosus* var. *comosus* and *A. comosus* var. *microstachys* clearly appears from the chloroplast DNA study of Duval et al. (2003). The three var. *comosus* haplotypes (3–1, 3–2, 3–6) found in the Guianas are shared with the Guianese clones that are morphologically intermediate between these two botanical varieties. These haplotypes, as well as the fourth haplotype found in the intermediate group (3–4), are found in Guianese representatives of var. *microstachys*. Among them, only haplotypes 3–1 and, to a lesser extent, 3–2 are common in the other regions of *A. comosus* natural range. Similarly, RFLP markers show clear genetic affinities between clones of *A. comosus* var. *comosus*, *A. comosus* var. *microstachys*, and intermediate forms of Guianese origin. However, despite their wide morphological variation and the high number of accessions involved in the study, all *A. comosus* var. *comosus* cultivars appear relatively well clustered in the RFLP study, which suggests that the diversity of chloroplast haplotypes can be attributed to sexual recombination involving Guianese clones of *A. comosus* var. *microstachys* during the early domestication phases.

At the time of the conquest, *A. comosus* var. *comosus* was planted throughout tropical America (Fig. 1.3) and included cultivars having wide variation in fruit size, shape, color, and flavor. Considerable morphological and genetic diversity was found in the eastern Guianas and in the western Amazon, where wild forms are rare or absent (Duval et al. 1997, 2001, 2003). Variation in adaptation to different environments, including Andean hillsides was also evident. The fruit was widely consumed and appreciated in the form of fermented drinks. Other traditional uses were based on its properties as digestive, vermifuge, antiamoebic, abortifacient, and emmenagogue, most of which are related to the presence of a proteolytic enzyme complex in pineapples as well as in many other bromeliads (Leal and Coppens d'Eeckenbrugge 1996; Patiño 2002).

Plants of *A. comosus* var. *erectifolius* are much less massive, with abundant and early shoots, frequent crownlets at the base of the main crown, numerous erect, fibrous leaves, and a small, very fibrous, inedible fruit borne on a long and slender peduncle (Fig. 1.2c). In some clones, the fruit appears to be rare. *A. comosus* var. *erectifolius* is quite similar to the wild *A. comosus* var. *microstachys*, except for its smooth leaves, a trait which is under dominant monogenic control (Collins 1960) and its erect habit, which is much less common in the latter.

Fig. 1.3 Pre-Columbian distribution of the edible pineapple according to archaeological and palaeolinguistic data (oblique fonts), as well as sixteenth century historical records (upright fonts). Mesoamerican date according to the Cascajal block datation and palaeobiolinguistics, both South American dates from archaeobotanical remains (see main text). Historical dates as in Coppens d'Eeckenbrugge et al. (1997) and Collins (1960), except for the 1500 date for Porto Seguro (eastern Brazil), inferred from the early diffusion of cultivars Singapore Canning and Selangor Green by the Portuguese (see main text)

A. comosus var. *erectifolius* (curagua) does not occur in the wild. It is still cultivated by the natives in the north of the Amazon basin, the Orinoco basin, and the Guianas, for the strong, smooth, shiny, and long fibers associated with its typical erect habit. Indeed, the dry fibers constitute around 6% of the plant weight. They are used to make hammocks and fishing nets (Leal and Amaya 1991) but now suffer competition from synthetic fibers such as nylon. The curagua has found a new economic use in the production of cut flowers and more recently in the biocomposite industry. Thus, it is cultivated near Santarem (Pará) for the automotive industry, for the excellent characteristics of its fibers for the reinforcement of polymer composites (Zah et al. 2007; Monteiro Neves et al. 2013). As summed up by Ferreira and Bustamante (2001), "the curauá therefore can be seen as an example of a domestication process carried out by indigenous peoples, followed by complete neglect of the species, almost to the point of extinction. After a long period, knowledge of the species has been salvaged in conjunction with the traditional populations, which has enabled it to be used once more, now with the status of a commercial plant."

Vernacular names include *curagua*, *curauá or kurawa*, *curaná*, *kulaiwat*, and *pita*. The latter is a vernacular name applied to several other Bromeliaceae and Agavaceae used for their fiber, which has produced confusion on its possible pre-Columbian cultivation in the Antilles. Indeed, the first botanical description of the curagua was believed to be a polynomial from Plumier (1703) "*Ananas non aculeatus, Pitta dictus*," described there. However, the unpublished drawing of Plumier, deposited in the Paris herbarium, represents an edible smooth-leaved pineapple. Furthermore, 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). Thus, the "Ananas pitte" described by Plumier (1703) was not a curagua, whose small inedible fruits are very fibrous, which questions the pre-Columbian introduction of this plant in the Antilles. As a matter of fact, and in contrast with reports from northern South America, to the best of our knowledge, the curagua has not been reported by ethnobotanists in this region.

In the genetic study of Duval et al. (2001), *A. comosus* var. *erectifolius* exhibits a high polymorphism, and it is represented in three different clusters including clones of *A. comosus* var. *microstachys*, among them two clones that, despite their spiny leaves, were found under cultivation. These data clearly indicate multiple convergent domestications based on a few traits. Indeed, the typical absence of spines along the curagua leaf margin, as well as its erect habit, is the likely result of artificial selection among strains of *A. comosus* var. *microstachys* for high yield of easily extractable fibers. The suppression of spines appears central in the domestication syndrome, which constitutes a particular case where domestication can be essentially related to a single dominant mutation. Further selection for clones with more profuse vegetative growth may have altered the balance between the vegetative and generative phases, which would explain why particular curagua clones appear to produce less fruits than leaf rosettes. In contrast, other clones, as the ornamental red-leafed cultivar Chocolate, exhibit a very high sexual fertility (Coppens d'Eeckenbrugge et al. 1993). Such differences in sexual reproductive potential can be explained by domestication processes of very different time depth, sexual fertility being more affected in ancient domesticated lineages than in more recent ones.

Ananas comosus var. *bracteatus* is an assemblage of two cultivated forms that show the same geographic distribution as *A. macrodontes* in southeastern Brazil and that are morphologically and genetically intermediate between *A. comosus* and *A. macrodontes* (Fig. 1.2d–f). The syncarp of *A. comosus* var. *bracteatus* is of intermediate size (0.5 to 1.0 kg), borne by a strong peduncle, and covered by long and imbricate floral bracts, as in *A. macrodontes*. These bracts are pink to red at anthesis, producing a spectacular inflorescence. Morphological and genetic variations are very limited in the first form, being comparable to within-cultivar variations (Duval et al. 2001, 2003) and suggesting very narrow origins, probably a single genotype. The second form is extremely rare, so its variation is not known.

The most common form, with antrorse spines and bright red bracts, corresponds to *A. bracteatus* sensu Smith and Downs, which was first cultivated for fiber. It was first described by Arruda da Câmara (1810) as a plant from Pernambuco, under the binomial *Bromelia sagenaria* (from the Latin *sagena* for net). He mentions the vernacular names of *crauatá/caroatá de rede* (net bromeliad) or *ananás bravo* (fierce pineapple), as opposed to the *ananás manso* (meek pineapple) for *A. comosus* var. *comosus*. Its fiber, rougher than that of the curagua and inferior in quality to that of the *ananás manso*, was also used to make ropes for the sugarcane industry. Similarly Bertoni (1919) mentions that *A. comosus* var. *bracteatus* was used as a living hedge and harvested for fiber and fruit juice, or for traditional medicine, in southern Brazil and Paraguay. Obviously, its use in living hedges necessarily followed the introduction of cattle and the development of private property with the European colonization. The dense, large leaves of the *ananás bravo* are strongly armed by large antrorse spines and form impenetrable barriers. It is very robust and still thrives today in abandoned farms, but it seems unable to naturalize and colonize new habitats. Several variegated somatic mutations have been selected, giving it a completely new career, as a pantropical garden ornamental (Fig. 1.2f). A private flower producer selected a smooth-leaved mutant in Ivory Coast for the European cut flower market.

The second form, corresponding to *A. fritzmuelleri* Camargo, shares an additional trait with *A. macrodontes*, as it exhibits retrorse spines on the leaf base. According to Camargo (1943) and Smith and Downs (1979), it was also used in living fences. Presently, one clone is conserved in the Brazilian germplasm collection and at the botanical garden of Rio de Janeiro (Fig. 1.2d). The chromosome number is $2n = 2x = 50$ (Camargo 1943).

In the genetic studies of Duval et al. (2001, 2003), the first, common, form of *A. comosus* var. *bracteatus* presents a very common chloroplast haplotype, which it shares with all other botanical varieties of *A. comosus*, and a small part of its nuclear genome with *A. macrodontes*, indicating a hybrid origin. The nuclear genome of the second, rare, form presents an even closer affinity with that of *A. macrodontes*, while their chloroplast haplotypes are only differentiated by one mutation. This closer genetic affinity is consistent with their closer morphological similarity. The rare form may come directly from an exceptional hybridization of *A. macrodontes*, or an extinct diploid ancestor, with *A. comosus*. The common form may originate from an introgressive cross onto an *A. comosus* female genitor, which would explain its *comosus* chloroplast haplotype and the lesser affinity of its nuclear genome with that of *A. macrodontes*.

Domestication Syndrome in the Cultivated Botanical Varieties of *Ananas comosus*

A rapid comparison of the edible pineapple and its wild relative shows the direct effects of human selection and the associated evolution for phenological and reproductive traits. Greater fruit size resulted from selection for larger individual fruitlets (pineapple-eyes) and an increase in their number, which also modified their phyllotaxy. A larger number of wider, and generally shorter, leaves provide more energy, and a stouter and longer stem allows greater starch storage capacity during the vegetative phase. The latter has been extended by reduced susceptibility to natural flowering induction. As a result, the cultivation cycle of edible pineapples is longer than the natural season cycles, which is also a condition for the production of a much larger fruit. Seed production has been reduced through the combination of lower sexual fertility and stronger self-incompatibility (Leal and Coppens d'Eeckenbrugge 1996). For a few cultivars that have maintained some level of sexual fertility, the higher number of flowers per fruit may partly compensate for the lower number of seeds per flower, provided other fertile cultivars are grown in the vicinity.

Strictly speaking, the domestication syndrome relates to those modified traits that hamper spontaneous propagation of the cultivated plants. On one hand, the partial loss of sexuality in *A. comosus* var. *comosus* is an obstacle for sexual recombination, hampering any regressive evolution to wild forms, and thence its long-term propagation and conservation in the absence of man. On the other hand, as vegetative reproduction is largely dominant in *Ananas*, this reduced sexual potential affects plant survival in the wild less than the changes in the vegetative organs and the plant vegetative cycle. Thus, the domestication syndrome in *A. comosus* var. *comosus* essentially lies in its lack of adaptation to the natural conditions prevailing where its wild progenitors are found. Pineapple plants from rustic cultivars can survive when their cultivation is abandoned, resisting competition in sufficiently open vegetation and even in dry edaphic or climatic conditions. However, they do not propagate efficiently to form subspontaneous feral populations. This is the likely cost of an excessive harvest index (i.e., the production of a relatively large fruit) and/or the loss of dispersal capacity, as only man can transport large fruits and their crown over medium to long distances (assuming that no animal has an interest/capacity for the dispersal of other vegetative propagules). Indeed, wild pineapple populations are distributed discontinuously in the Guianese forests. They are most often found in relatively elevated areas (inselbergs, "rock savannahs," sand dunes) where there is no risk of water stagnation. Such sites are often isolated in the forest, which implies long-distance vectors for seed dispersal, very probably large birds and/or monkeys. Indeed, sexual propagation might play an important role in the initial foundation of scattered wild populations, as only one or two clones were observed at most sites, while clones appeared distinct among sites (G. Coppens d'Eeckenbrugge, M.-F. Duval, J.R.S. Cabral, and F.R. Ferreira field observations).

None of *A. comosus* var. *comosus*, *A. comosus* var. *bracteatus*, and *A. comosus* var. *erectifolius* show any capacity for spontaneous colonization in the wild. The large size of var. *bracteatus* must be equally as limiting to its natural dispersal as it is the fruit of var. *comosus*. For the more gracile, small-fruited, var. *erectifolius*, the main component of the domestication syndrome appears to be the loss of leaf spines, as it increases its susceptibility to herbivory. For those clones of var. *erectifolius* that rarely produce a fruit, there is an additional restriction on sexual recombination, and thence on the plant adaptive potential, strengthening the dependence on man. On the other hand, we must keep in mind that the absence of spines is also the main characteristic that distinguishes var. *erectifolius* from var. *microstachys*. Thus, when smooth-leaved clones of var. *erectifolius* mutate back to the spiny condition, as has been observed in germplasm collections as well as under cultivation, these reverse mutants should be formally classified in var. *microstachys*. In this case, the domesticate status and the domestication syndrome may look as fragile as the morphological difference between both these cultivated and wild varieties.

Pineapple Domestications in Space and Time

Bertoni (1919) proposed that the pineapple was domesticated in southern South America by the Tupi-Guarani Indians who would have diffused the crop in their northward migrations. Later, most reviewers of pineapple domestication (Collins 1960; Purseglove 1972; Pickersgill 1976; Sauer 1993) accepted this southern origin. Only Brücher (1971), whose paper was written in German and subsequently ignored, underlined the presence of wild forms and primitive cultivars in the north of South America and proposed a Guianese origin. In any case, both hypotheses were based on very incomplete knowledge of pineapple diversity and distribution. Leal and Antoni (1981) called attention to the greater morphological diversity to be found north of the Amazon. Since then, the extensive exploration of pineapple diversity has given much substance to the hypothesis of a northern origin of *A. comosus* varieties *comosus* and *erectifolius* (Leal and Coppens d'Eeckenbrugge 1996; Coppens d'Eeckenbrugge et al. 1997; Coppens d'Eeckenbrugge and Leal 2003; Duval et al. 2003), resulting in the general domestication scenario proposed by Coppens d'Eeckenbrugge and Duval (2009). As the three pineapple domesticates have different domestication histories, in relation to their different utilizations by man and their regions of origin, we shall consider them successively.

Ananas comosus *var.* comosus

The combination of morphological and genetic data (Duval et al. 1997, 2001, 2003) clearly point to an East-Guianese origin of *A. comosus* var. *comosus*. This area is home to its wild ancestor, *A. comosus* var. *microstachys* and the greatest phenotypic and genetic diversity. The diversity that can be found in this region includes primitive cultivars and intermediate wild phenotypes that could be used as a basis for domestication or that could enrich the primitive cultivated gene pool through introgression. A very plausible hypothesis is that such materials were collected on "rock savannahs," sand dunes, and similar places where they thrive and planted in home gardens and fields. Nowadays, inhabitants of the Guianese forests, and even creolized newcomers, still collect materials from the wild to incorporate into their cultivated plots and gardens. This explains why some clones are found both under cultivation and in patches of secondary vegetation in the wild, marking likely sites of ancient cultivation. Such practices constitute a basis for a process involving "domestication cycles." In these cycles, pineapples are sampled in the wild, put in cultivation, semi-abandoned, re-sampled for cultivation, etc., with possible selection at each step. Indeed, fields and home gardens are never completely abandoned and forgotten, as they are located near pathways and remain useful, for example, for picking tree fruits that come well after first crops or hunting animals attracted by the fruits (Vélez 1998). They also serve as stocks of useful planting materials. The most interesting genotypes are thus progressively concentrated, in a process that has been described for Amazonian fruits (Gnecco 2003; Miller and Nair 2006).

In the long term, sexual reproduction can contribute to the exploitable diversity by the creation of new clones, some of which can be more attractive for man. On the other hand, wild types may be more highly fertile than semi-domesticated materials (Coppens d'Eeckenbrugge et al. 1993), so wild genes are probably transmitted more efficiently by sexual reproduction, reducing the effects of selection. Their robustness may also be an advantage for a safer harvest, so growers may want to maintain them among the diversity of their clones in a context of subsistence production. The result is the multiclonal production system still observed in the Guianas, which maintains a balance between genotypes at very different stages of domestication. This is not a problem for a grower more interested in diversity and safety than in productivity, but it slows down further genetic improvement and full domestication. The relatively slow pace of domestication in other species has also been attributed to the coexistence of genotypes at different stages of domestication (e.g., Otero-Arnaíz et al. 2005). Wild relatives of domesticates can even behave as weeds in the crop, as is the case of teosinte in Mexican maize plots (Wilkes 1972) or wild sorghum (Dogget and Majisu 1968) in African fields, contaminating seed materials through pollen-mediated gene flow and diversifying the cultivated genepool while delaying the evolution to more highly selected forms of the crop. Such limitations to genetic improvement obviously disappear when the crop is grown in the absence of its wild relatives (Galinat 1974).

In the case of pineapple, this second phase of evolution probably occurred in the western Amazon (along the upper Amazon, close to the triple frontier between Colombia, Peru, and Brazil, and along the lower Rio Negro), where we can observe a high diversity of cultivars, while wild forms are very rare or absent (Bello and Julca 1993; Duval et al. 1997). There the prevalence of large seasonally flooded areas and the rarity of elevated sites with good drainage seem to constitute a natural barrier against the extension of *A. comosus* var. *microstachys*. Once established in this area, the cultivated pineapple could evolve and diversify in completely artificial conditions, in a dynamic process combining sexual recombination restricted to domesticated germplasm, somatic mutations, and clonal selection. Human societies peopling western Amazonia may have reinforced the domestication process through particular horticultural skills. Indeed, this area is also an important center of domestication and diversification for many other fruits (Clement 1989, 1999). Peoples like the Tikunas and the Huitotos still value and maintain a wide diversity of pineapple cultivars and other fruits. In the course of their collecting trips, Duval et al. (1997) observed as many as 12 cultivars in a small plot maintained by a single Tikuna family. Schultes (1991) gives similar numbers for the pineapple cultivars named by the Huitotos. The species is culturally very important for peoples of the area. For example, the Yukunas celebrate nine fruit festivals yearly; five of them being pineapple festivals (Jacopin 1988). Cristancho (2001; cited in Cristancho and Vining 2004) ranked pineapple among the three primary Culturally Defined Keystone Species (CKS) of the Letuama people (CKS are "species whose existence and symbolic value are essential to the stability of a cultural group over time"), along with tobacco and coca.

The existence of two centers for the diversification of *A. comosus* var. *comosus*, a primary one in the Guianas, with diversification involving clones at different stages of domestication, and a secondary one in the western Amazon/Andean foothills, with sexual recombination between large-fruited cultivars, is also suggested by the distribution of particular leaf margin types (Duval et al. 1997). Thus, genotypes that present a partial suppression of spines are particularly frequent in the Guianas. The most famous of such cultivars is 'Smooth Cayenne', the most widely distributed pineapple cultivar, which commonly presents a few spines at the leaf tip. This trait is under the control of the S gene, and the allele for the partial suppression of spines is dominant. In the western Amazon and in the Andes (from Peru to Colombia), leaf smoothness is determined by another gene, named P by Collins (1960). The dominant allele determines the "piping" trait, where the lower epidermis is folded over the leaf edge, and all spines, except for the terminal one, are suppressed (Coppens d'Eeckenbrugge and Sanewski 2011). The existence of homozygotes for the "piping" gene (Cabral et al. 1997) indicates sexual recombination among cultivars within this western pool. Another indication of sexual reproduction in the cultivar diversification process is the advent of triploid pineapples, as the Ecuadorian landrace investigated by Heilborn (1921); the cultivar Gigante de Tarauacá, selected for its huge fruit, reaching up to 15 kg (Scherer et al. 2015); and other Brazilian landraces (Lin et al. 1987). Indeed, such triploids, resulting from the fertilization of unreduced ovules, are sometimes found in hybrid progenies (Collins 1960).

Because of very poor conservation conditions in the rain forest and/or the lack of archaeobotanical research in Amazonia, no ancient pineapple remains had been observed in the two putative centers of diversification/domestication. This has changed recently, with the identification of pineapple phytoliths in relatively deep levels (0.80 m) of anthropic soils, indicating cultivation of the species around 3000BP in western Amazonia (Morcote-Rios et al. 2013). Larger pineapple remains have only been conserved under arid conditions, and identified in archaeological layers dated from 3200 to 2800 BP on the Peruvian Coast (Pearsall 1992), while seeds and bracts were found in coprolites from the Tehuacán Valley caves (Mexico) dated between 2200 and 1300 BP (Callen 1967). Another indication of the early presence and the importance of pineapple in Ancient Mesoamerica is the stone block known as the Cascajal Block, which is the oldest written document known in the Americas. It was discovered near the archaeological site of San Lorenzo, in the Mexican state of Veracruz, associated with the Olmec civilization, and dated 2800–3000 years BP. The pineapple is represented four times on the block, among several natural organisms or products (Coppens d'Eeckenbrugge et al. 2011). The application of historical linguistics to the names of the pineapple in Ancient Mesoamerica (glottochronology) also gives us a minimal estimation of the antiquity of pineapple domestication. Consistently, glottochronological data indicate that the crop was highly significant to Mesoamerican people more than 2500 years BP (Brown 2010). Thus, domesticated pineapple was traded and adopted as an important fruit crop at the continental scale more than 3000 years BP. Such an early extension of its cultivation area implies the preliminary development of cultivars specifically adapted to the high latitudes and/or altitudes of Peru and Mexico. Indeed, highland cultivars from Andean countries show specific adaptations and tend to perform poorly in lowland conditions, presenting lower sugar, acidity, and firmness, as well as frequent fruit lodging and deformation. Given the rarity of reproduction through seeds in *A. comosus* var. *comosus*, the development of environmentally specialized cultivars was necessarily a long and slow process, taking place in situ, after the arrival of the domesticated pineapple in these particular environments. In conclusion, a likely time frame for pineapple domestication lies between 6000 and 10,000 years BP, which is consistent with current hypotheses for other major American crops. For example, cassava, another crop combining sexual and vegetative reproductions, was domesticated in southwestern Amazonia (Clement et al. 2010), probably before 10,000 BP, as it arrived in northern Peru before 8500 BP (Dillehay et al. 2007) and in Mexico around 5800 BP (Pope et al. 2001).

Ananas comosus *var.* erectifolius

The high genetic diversity of the curagua, its scattering in the phenetic and phylogenetic trees, and its proximity to various var. *microstachys* genotypes, generally from the same origins, indicate several independent domestication events in the Guianas. If we take the reduction in sexual reproduction capacity as an indicator of the antiquity of evolution under clonal cultivation for leaf production, the highly variable fertility in var. *erectifolius* appears consistent with multiple domestication and introgression events (Coppens d'Eeckenbrugge et al. 1997; Duval et al. 2003). However, the difference in the final outcome must not hide several similarities between the domestications of varieties *erectifolius* and *comosus*. First, the *A. comosus* var. *microstachys* genetic contribution was relatively similar for both domesticates, as they share two of their four chloroplast haplotypes (Duval et al. 2003; counting clones with intermediate and large fruits in the var. *comosus* lineages). Second, in their early stages, both domestication processes involved different lineages and introgression events. Finally, the main difference may be that the curagua did not diffuse out of the range of its wild relative.

Ananas comosus *var.* bracteatus

The case of this botanical variety is much simpler, as it very probably corresponds to two particular hybrid clones from southern South America. The remaining question concerns the genitors involved, particularly on the *A. comosus* side. Was it a domesticated (*A. comosus* var. *comosus*) or a wild (*A. comosus* var. *microstachys*) pineapple? In any case, the resulting hybrids had to be maintained by man, which situates these hybridizations in the context of pre-existing agriculture. Since then, the two clones have been exploited for multiple purposes. However, as was also the case for their wild relative *A. macrodontes*, they were more important for fiber than for their poor-quality fruits.

Diffusion of the most Common Pre-Columbian Pineapple Cultivars

The great majority of pineapple cultivars have been confined to a particular region within a country and have never crossed provincial or national borders, remaining largely ignored by pineapple experts. 'Manzana', common in the Andean regions of Colombia and Venezuela (where it is known as 'Capachera') is a relative exception. Paradoxically, the insignificant exploitation of pineapple diversity is related to the very wide and rapid diffusion of the crop and its adoption by farmers and consumers of all cultures.

In the last century, five ancient cultivars have largely dominated the pineapple world production landscape: 'Smooth Cayenne' was present in all major production regions, progressively displacing regional cultivars, until it was partly displaced by hybrids from the former Pineapple Research Institute of Hawaii (PRI); in the Old World, 'Queen' and 'Singapore Canning' were present in the Indo-Pacific basin, whereas 'Española Roja' ('Red Spanish') and 'Pérola' presented better circumscribed distributions in the New World, the former in the Caribbean basin and the latter in Brazil and Paraguay.

Early South-South Diffusion of Cultivars from the Brazilian Coast

'Singapore Canning' is a common cultivar in Southeast Asia, where it has maintained relatively strong positions in the processed fruit market, particularly in Malaysia, where it is also known as 'Singapore Spanish', 'Ruby', 'Red Pine', 'Nanas Merah', 'Nangka', 'Gandol', 'Betek', and 'Masmerah'. An anthocyanless cultivar was derived by mutation, and its strains are designated as 'Green Pine', 'Selangor Green', 'Nanas Hijau', 'Green Spanish', and 'Selassie' (Wee 1972).

In the common red cultivar, the peduncle and inflorescence bracts are deep bright red. The fruit is of moderate size, cylindrical, and dark purple, turning reddish-orange from the base when ripening, with a profuse crown. The plant is vigorous with regular production of slips and suckers. Spininess is variable, from complete in some clones to a few spines in others (Fig. 1.2g). The green cultivar, 'Selangor Green' presents light green leaves and heart and produces green fruits that turn yellow at maturity.

No direct historical records are available concerning the geographic origin of 'Singapore Canning' and 'Selangor Green'. However, a very likely hypothesis can be deduced from the early diffusion of the crop by the Portuguese, as several early reports explicitly mention a Brazilian origin of the pineapples introduced in India (e.g., Cristovão da Costa 1578, cited in Dalgado 1919, Van Linschoten 1610). Linguistics provide another significant indication of the importance of the Portuguese explorations in the intertropical diffusion of the pineapple and many other crops, as many African and Asian languages have incorporated and maintained Portuguese names for American plants (Dalgado 1913, 1919; Blench 1998).

The first objective of the Portuguese explorations, well before their interest in inland colonies, was the control of the spice trade with Asia. Culminating their systematic exploration of West African coasts, they reached the Cape of Good Hope in 1488, opening the road to India, effectively followed in 1497–1498 by Vasco da Gama. On his way, he explored the coasts of Mozambique and Kenya. Immediately after his return in 1499, a new expedition was prepared, which set sails in 1500 under the command of Cabral. Avoiding the windless Gulf of Guinea, the fleet went southwest and reached the eastern coast of Brazil, landing in Porto Seguro. One boat returned to Portugal to report the discovery, while the rest of the fleet continued to India. This Brazilian route, improved by the discovery of Saint Helena Island in 1502, was repeatedly used by large fleets (seven fleets in the first 5 years of the sixteenth century) and the Portuguese soon established a network of stopovers and fortified trading posts between Brazil and India (Saint Helena, Madagascar, Island of Mozambique, Malindi in Kenya, and Kochi in India). They soon extended their explorations and commercial network to Southeast Asia, with the conquest of Malacca and the establishment of trading relations with Thailand in 1511, landing in Java in 1512, southern China in 1513, and Luzon (Philippines) between 1513 and 1516. They were authorized to settle in Macao (continental China) in 1557.

In their early explorations of the West African coasts, the Portuguese used to carry plant seeds and propagules and test them in the newly discovered lands for the survival of the colonies and garrisons that could allow further southward navigation. Thus, in 1505–1508, Valentim Fernandes (cited by Ferrão et al. 2008) mentioned the presence of "all the fruits of Portugal" in the Island of Santiago (Azores), including figs, vine, melons, and sugar cane. After the discovery of Brazil, they continued this strategy, introducing systematically American crops in tropical Africa and Asia, so that Lopes and Pigafetta (1591; cited by Ferrão et al. 2008), referring to Saint Helena Island, could write that "every ship brings some plant, fruit or garden grass."

Among these plants was the pineapple, which diffused very soon along the Portuguese routes to the Indian Ocean and South-East Asia. In the gardens of Mozambique, where he arrived in 1586, Frei João dos Santos (1891) observed "many pineapples," both on the coast (province of Sofala) and far inland (province of Tete, more than 400 km from the coast). Similarly Van Linschoten (1610), who worked in India between 1583 and 1592, noted: "The pineapple is not native there, instead it was brought from Brazil by the Portuguese. They were much prized at the beginning, …, but now they are of little value as a result of their abundance… they are the size of a melon, the shape of a distaff or a pine-apple, easy to cut, of a red color admixed with green, and grow to the height of a cubit." Additional comments confirm Porto Seguro as the original source of these Indian pineapples. Certainly, the same planting materials diffused to Southeast Asia when the Portuguese extended their activities eastward. The pineapple may even have preceded them in some countries, as sea trade was very ancient and active across the Indian Ocean and insular Southeast Asia. Indeed, the Portuguese had to compete and/or collaborate with Arabs, Indian, Indonesian, Chinese, and other Asian peoples, and, to some extent, they mostly connected this pre-existing trade network to Europe through eastern Brazil. Figure 1.4 presents a temporal synthesis of the Portuguese progression in the region and reports of the pineapple in the sixteenth century while pointing to countries where 'Singapore Canning' and 'Selangor Green' have been reported in modern times. The coincidence clearly suggests that these closely related cultivars originated in the region around Porto Seguro (southern Bahia state).

To our knowledge, 'Singapore Canning' and 'Selangor Green' have not been reported along the West African coasts. Instead, 'Pérola', the most common Brazilian cultivar, is found in this region. This rustic cultivar presents very spiny erect leaves, medium-sized conical fruits, mostly green at maturity, with a high number of slips (Fig. 1.2h). Its main interest lies in its highly perfumed white flesh and its rusticity. A few countries, including mainly Benin and secondarily Togo and Côte d'Ivoire, export it at high prices to feed a niche market in Europe. This difference of ancient cultivars in West Africa, as compared to East Africa, may be chronological in origin. Indeed, as noted by Ferrão (2013), direct relations between America and West Africa developed with the slave trade associated with the direct exploitation of the Brazilian agricultural potential, after the establishment of Portuguese India. Then, the Portuguese had explored and colonized other Brazilian regions, so this trade was also oriented to the South of the country, where another major pineapple cultivar was appreciated.

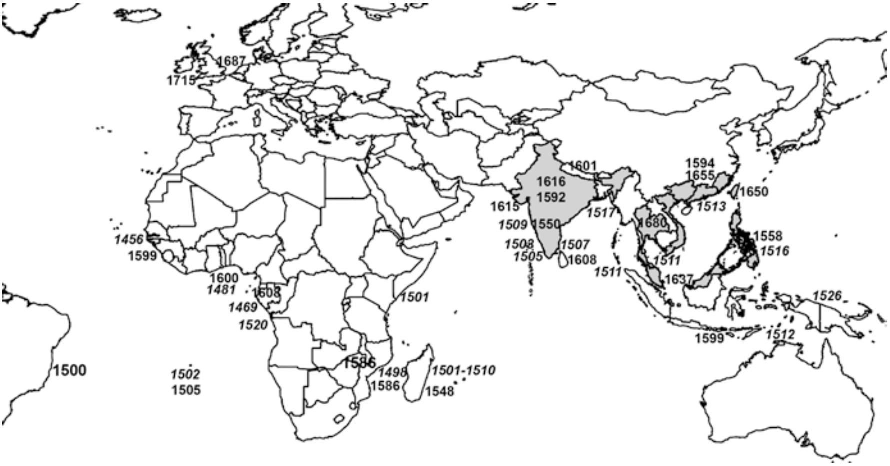

Fig. 1.4 Early intertropical diffusion of the pineapple following Portuguese explorations and expansion in the sixteenth and early seventeenth centuries. Dates in oblique fonts refer to early Portuguese explorations, commercial missions, and settlements of trading posts and fortresses. Dates in upright fonts refer to observations of pineapple "naturalization" or cultivation by travelers (see Dalgado 1919, Laufer 1929, Collins 1960, Vansina 1979, Morton 1987, Coppens d'Eeckenbrugge et al. 1997, Alpern 2008, and main text). Shaded areas correspond to the documented distribution of cultivars Singapore Canning and Selangor Green. Earliest successful glasshouse cultivation in Europe mentioned for the Netherlands and England

Origin and Diffusion of 'Queen'

The cultivar Queen is present in all tropical Indo-Pacific regions, being more extended than that of 'Singapore Canning', as it is also present in South Africa and Australia, as well as in far islands, like Mauritius and La Réunion, and in French Polynesia. To realize this distribution, 'Queen' necessarily diffused from Europe and/or the Antilles. Surprisingly, for a cultivar of such importance, 'Queen' presents many negative traits: the plant is small, with short and very spiny leaves; its yellow fruit is particularly small (0.5–1 kg), with prominent eyes (Fig. 1.2i), which makes it unsuitable for canning. Its predominant quality is its deep golden yellow and crispy flesh, with a medium to high sugar content and low acidity. Another trait that could have contributed to its early reputation is its relatively long shelf life (Coppens d'Eeckenbrugge et al. 1997), at a time when pineapples had to suffer long sea travels, attached to the whole plant, before they could be appreciated on royal tables. Indeed, Evelyn (1661, cited in Collins 1960) mentioned the "famous Queen Pine" brought from Barbados and presented to King Charles II. This cultivar long remained present on the lists of cultivars grown in European glasshouses. According to Griffin (1806) and Munro (1835), it was one of the best varieties for general cultivation in England: "it grows freely, fruits early, and although not so high flavoured as some of the larger kinds is still the most valuable for a small family" (Munro 1835).

The pre-Columbian presence of 'Queen' in the Antilles is likely to result from their colonization by South American Amerindian groups. Indeed, landraces with very similar morphologies have been observed under traditional shifting cultivation systems in the Orinoco basin (under the local name 'Panare') and far inland in the Guianas (French Guiana and the Brazilian state of Amapá). The Guianese clones were included in the RFLP study of Duval et al. (2001), where they appear identical to other 'Queen' clones. Thus, 'Queen' may be one of the earliest clones having reached a relatively wide regional distribution in pre-Columbian times.

Origin and Diffusion of 'Smooth Cayenne'

In the twentieth century, 'Smooth Cayenne' was by far the leading pineapple cultivar out of the Americas, which was clearly due to its high yielding potential and good characteristics as fresh fruit as for canning. Recently, it has been displaced on the international fresh fruit market by the PRI hybrid 'MD-2'. The plant is medium-sized with dark green leaves whose margins bear only a few spines at their base or near the tip. The fruit is medium-sized, ovoid, and green with a yellow base at maturity (Fig. 1.2j). Its pale yellow flesh is juicy, with medium to high sugar content and higher acidity than most other cultivars. But it is fragile and the plant is sensitive to most pests and diseases; also, in tropical environments the main clones are poor producers of planting stock.

'Smooth Cayenne' was collected in 1819 by Perrottet in French Guiana, under the name 'Maipuri' (Collins 1960). This name, which means tapir, is still used for many large-fruited cultivars in the Amazon and Orinoco basins, where it is the biggest native animal. 'Smooth Cayenne' can still be observed in French Guiana, quite far from the city of Cayenne, in traditional shifting cultivation systems (Coppens d'Eeckenbrugge personal observations, 1993). The five plants collected by Perrottet were multiplied and sent to England, Belgium, Holland, and the Azores and, then, from England to Florida, Jamaica, Sri Lanka, and Australia. In the late nineteenth century, they arrived in Hawaii, from where they were distributed to the Greater Antilles, Mexico, the Philippines, Taiwan, and Kenya in the first half of the twentieth century (Collins 1960). At the end of the twentieth century, 'Smooth Cayenne' had achieved an impressive domination over other cultivars, both economically and geographically, and the international pineapple industry had become extremely vulnerable to any severe phytopathological threat affecting this cultivar (e.g., an extension of the Brazilian fusariosis to other continents). This situation also distorted the views of most technical and scientific experts, and 'Smooth Cayenne' characteristics largely dictated all technical and commercial parameters of pineapple production, processing, and international trade, making any varietal change more difficult. Only in South America, the continent of origin, regional cultivars were still resisting, particularly 'Manzana' and 'Española Roja' in the northeast and 'Pérola' in the south. Remarkably, 'Smooth Cayenne' never gained any economic importance in the Amazonian cradle of the crop.

Conclusions

Recent explorations in South America, followed by extensive morphological and genetic diversity studies have allowed significant progress in our understanding of the evolution of pineapple under cultivation and its diversity (Leal et al. 1986; López et al. 1992; Ferreira et al. 1992; Ferreira and Cabral 1993; Bello and Julca 1993; Ferreira 1996; Duval et al. 1997; Duval et al. 2001, 2003; Coppens d'Eeckenbrugge and Leal 2003). As compared to the RFLP techniques used by Duval et al. (2001), currently available genetic tools, including next-generation sequencing, have an enormous potential for further progress on these questions (Zhang et al. 2014). However, the expected success depends on the availability of well-defined and well-identified samples representing the diversity of wild and domesticated materials, at least that of varieties *comosus* and *microstachys*. This has not been the case so far, as modern tools have been mostly applied on the few widely distributed cultivars whose diffusion has been presented here. These cultivars were often exchanged among germplasm collections in the Indo-Pacific area, and they were not always accompanied by the proper documentation, because of labeling errors, as mentioned by Zhou et al. (2015). Indeed, the results of the latter study give an example of the difficulties related to a poor-quality sample and common mistakes on the domestication status of the different pineapple taxa. A first problem comes from the fact that the *A. comosus* var. *comosus* sample is mostly represented by four cultivars and their somaclonal variants ('Smooth Cayenne', 'Queen', 'Singapore Canning'/'Selangor Green', and 'Pérola') originating from eastern South America. Western South America, where the presumed secondary diversification center is located, is even more poorly represented. Furthermore, many inconsistencies appear between the groups detected by the genetic analysis on one hand and the groups expected when considering well-known synonymies in the names of these widely distributed cultivars. Several genetic groups gather different cultivars, whereas several cultivars are split among several genetic groups, indicating frequent labeling errors. Some classification errors reach a taxonomic level. Thus, the F1 hybrid between 'Smooth Cayenne' and *A. comosus* var. *microstachys* (see Collins 1960) is considered a cultivated pineapple and classified under *A. comosus* var. *comosus*, while its backcross onto 'Smooth Cayenne' is simply classified as a hybrid. The domesticated status of *A. comosus* var. *bracteatus* and its particular relationship with *A. macrodontes* are not recognized either (although the results of the cluster analysis point to their relative proximity).

To overcome such problems, there is an urgent need of practical field expertise on morphological characterization. People managing collections and organizing germplasm exchanges must be able to recognize common cultivars, use correct cultivar nomenclature, and must have access to basic information on less common cultivars (Bartholomew 2016), so they can detect likely label errors and discard affected materials. To promote international collaboration and ensure access to wider study samples, efforts should be made to alleviate the legal burden so often associated with germplasm exchanges, while ensuring due recognition to the field expertise of collection curators. Only after taking this direction will we be in a better position to address general and particular questions on pineapple evolution under domestication, such as:

- Comparative genetics of the eastern and western South American pools, evolution after domestication, during pre-Columbian migrations, origins of Andean cultivars, origins of Mesoamerican cultivars (we miss practically all information on the latter as the Mesoamerican traditional cultivars have not been explored).
- Deepening the comparison between the genetic basis of domestication of varieties *comosus* and *erectifolius.*
- About var. *bracteatus*, (1) can we confirm that the two very uniform types are basically two clones? (2) Do they correspond to two different stages of the same interspecific introgression process? (3) Which was (were) their *A. comosus* var. *comosus* genitor(s), a wild or a domesticated form? To answer these questions, diverse samples of *A. macrodontes* are needed, as well as representatives of varieties *comosus* and *microstachys*.

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