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Genetic Diversity in Eastern Polynesian Eumusa Bananas[1]

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ABSTRACT: Genetic variation within and between the Polynesian Eumusa bananas from Hawai'i, the Marquesas, and the Society Islands is described. Morphological, isozymic, ethnographic, and linguistic assessments of accessions are used to identify base clones and somatic mutants. A historical review of relevant studies is summarized.

MANY KINDS OF BANANAS are cultivated on the high islands of Eastern Polynesia. Most of these varieties are known to have been introduced after the islands were first contacted by European explorers. However, well before the arrival of Europeans, bananas were brought into Eastern Polynesia and cultivated by Polynesians. In this paper, we describe the extent of genetic variation within and between the Polynesian Eumusa bananas from Hawai'i, the Marquesas, and the Society Islands.

HISTORICAL REVIEW

Interest in cataloging the Polynesian bananas began in the late nineteenth century (Thrum 1890), but the most useful work dates to the first half of the twentieth century. Pope (1926), referring to a manuscript written in 1870, reported that the Hawaiians of Kona (Hawai'i Island) knew and named no fewer than 70 different bananas at that time. Notwithstanding, after systematic collecting and assessment, Pope (1926) recognized only 18 distinct cultivars: the undifferentiated '*Mai'a 'oa*' clone and 17 morphotypes belonging to the three principal Polynesian base clones, *iholena*, *maoli*, and *pōpō'ulu* (see *Materials and Methods* section for explanation of taxonomic terminology). Four additional morphotypes of the base clones and a fifth undifferentiated cultivar, '*Hāpai*', were later recognized (Pope 1927) from fragmentary accounts of earlier writers, such as Thrum (1890), Higgins (1904), and MacCaughey (1918).

Elsewhere in Polynesia, Brown (1931) claimed that "not less than 75 varieties seem to have been cultivated by the ancient Marquesans," though he cited only 50 names, some of which clearly refer to recent introductions and others to *Musa fehi* Bert. ex Vieill. bananas of the Australimusa series. Dordillon (1931–1932) cited 40 banana names; as in Brown, several references were recent arrivals (e.g., *kina* undoubtedly refers to Chinese or Cavendish clones) and at least one, *huetu*, refers to *M. fehi*.

The geographic origin of these bananas has been a longstanding subject of speculation and debate among banana taxonomists. MacDaniels (1947) suggested that the Hawaiian bananas were brought by the Polynesians from the Marquesas or the Society Islands. Simmonds (1954) initially concluded that the Hawaiian cultivars originated in Malaya or Indo-Malaya, from whence they were spread

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to Polynesia and Hawai'i in cultivation; later, Simmonds (Stover & Simmonds 1987) reversed himself, stating that "these bananas are clearly not of Indo-Malaysian origin ... nor can they have come from Papua New Guinea." Despite this last assertion, recent work demonstrates that the Polynesian Eumusa bananas are not limited in their distribution to Eastern Polynesia and that Papua New Guinea is the most likely region of their domestication (Horry 1989, Daniells 1990, Tezenas du Montcel 1990, Lebot et al. 1993). Sterility in these bananas ensures that they could only have come into and through Polynesia via human agency. Thus, their characterization as "native" in Hawai'i by MacCaughey (1918) and others is inappropriate.

Several of the Polynesian cultivars have been incorporated into international germplasm collections and their agronomic performance evaluated. We have observed that they are highly susceptible to Panama disease, a wilt caused by *Fusarium oxysporum* (Schlecht.) f.sp. *cubense* (E. F. Smith) Snyd. & Hans.; to nematodes; and to corm borers (*Cosmopolites* sp.). Polynesian bananas have also suffered in competition with aggressive exotic plants and from development of a commercial banana industry based on non-Polynesian cultivars. Although Polynesian bananas show some resistance to black leaf streak, a widespread banana disease caused by *Mycosphaerella fijiensis* Morelet, the combined effects of these pests, other diseases, and economic changes are undoubtedly responsible for their drastic reduction and extirpation on many Eastern Polynesian islands. Nevertheless, they are still occasionally found for sale in local markets. With the exception of '*Hāpai*', which is a sweet-fleshed dessert banana, and '*Mai'a 'oa*', which is seedy and inedible, all of the Polynesian Eumusa cultivars are "cooking bananas," with the starchy flesh typical of plantains. Several continue to be used sporadically in Eastern Polynesian medicine (Gutmanis 1976).

It has been suggested that cultivars of the *maoli* and *pōpō'ulu* base clones—still poorly known internationally—be collected more extensively and evaluated as crop genetic resources (Persley and De Langhe 1987). It is our purpose here, in part, to respond to this suggestion.

SCOPE OF THE PROBLEM

Tremendous morphological variation exists within the cultivated bananas. Worldwide, there may be as many as 500 cultivars (Simmonds 1976, Purseglove 1988), most of which are sterile and parthenocarpic, and therefore vegetatively propagated.

Most edible bananas have been domesticated from *Musa acuminata* Colla and from hybrids of this species with *M. balbisiana* Colla. Traditionally, classification of domesticated bananas and plantains has been accomplished by scoring clones for 15 morphological characters that differ between the parent species (Simmonds & Shepherd 1955). This method, coupled with chromosome counts, has permitted descriptions of clones in terms of ploidy levels and the genomic contributions of the two parental species. Recent analyses of isozyme variation in banana clones have generally confirmed the relationships proposed on the basis of morphological data (Jarret and Litz 1986*a*, *b*, Horry 1989, Lebot et al. 1993). Those investigations demonstrated the existence of species-specific allozymes in *M. acuminata* and *M. balbisiana*, and multivariate analysis of isozyme data has produced clusters of clones that correspond neatly with genomic groupings (AA, AAA, AAB, ABB, etc.) determined by morphological analysis.

Both of the above approaches have identified the Hawaiian base clones, *maoli*, *pōpō'ulu*, and *iholena*, as belonging to the AAB genomic group (although Stover and Simmonds [1987], using only morphological data, misclassified *iholena* as a member of the AAA genomic group). These three base clones of the Pacific Plantain subgroup have also been shown to have different and diagnostic zymotypes (Lebot et al. 1993). However, neither of the above methods of classification can resolve the subtle distinctions between morphotypes of the same base clone; that is, differences arising by mutation that have been noted and named by both ancient and modern farmers.

In Polynesia, as elsewhere in the Pacific, banana names consist either of a generic head term meaning "banana" (e.g., *mai'a* in Hawai'i and Tahiti [syn. *mei'a* in Tahiti] and *meika* or *mei'a* in the Marquesas) followed by a secondary epithet that generally designates the clone (as in the Hawaiian '*Mai'a hāpai*', or '*Mai'a maoli*'), or the epithet stands alone (as in '*Hāpai*', or becomes the head term for a modifier denoting minor morphological variants or morphotypes (such as '*Maoli hai*' or '*Iholena lele*', etc.). Common qualifiers for morphotypes reflect variation noted in aerial parts of the plant, which are often related to distinctive pigmentation or size. For example, *'ele'ele* means "black," and designates a morphotype of the Hawaiian *maoli* cultivar exhibiting intense black pigmentation on the pseudostem and petiole bases. Farmers may refer to this cultivar as '*Mai'a maoli 'ele'ele*', although '*Maoli 'ele'ele*' or sometimes just '*'Ele'ele*' are more common.

Accurate identification, description, and naming of Polynesian bananas has been difficult because the phenotypic appearance of cultivars is influenced by environmental factors as well as by genetic differences. Cultivars may exhibit a range of variation under different physical circumstances, and even when specific banana plants are considered, there may still be substantial disagreement among local farmers on names and taxonomic relationships. Taxonomic and nomenclatural uniformity among farmers is even less likely over wider geographical areas of the Pacific. Morphological classifications of clones typically are valid only in areas of environmental and cultural homogeneity.

It is likely that some banana germplasm has been lost in Hawai'i and French Polynesia since Pope (1926), Brown (1931), and Dordillon (1931–1932) studied bananas in the Pacific. Names may persist for clones that no longer exist, just as clones may exist that have lost their names through acculturation. In many cases, cultivars introduced since European contact have received local names, obscuring their origins.

MATERIALS AND METHODS

Taxonomical Terminology

We follow the taxonomical terminology of Stover and Simmonds (1987) and use the term "series" to refer to the major edible banana categories having basic chromosome numbers of 10 (Australimusa series) and 11 (Eumusa series). "Group" is used to refer to major subdivisions within series. These are designated by letters that indicate both ploidy level and the genomic composition (e.g., AAB group of the Eumusa series) with regard to their parent species *M. acuminata* (A genome) and/or *M. balbisiana* (B genome). "Subgroup" refers to distinctive sets of clones within groups, such as the Pacific Plantain subgroup of the AAB group. Because of the high degree of selection in some Polynesian Eumusa bananas, we modify Stover and Simmonds somewhat and use the term "clone" to distinguish bananas within subgroups that differ in both morphological and isozymic characters, and "base clone" to describe those clones that were further differentiated through selection of somatic mutations (e.g., *maoli* base clone of the Pacific Plantain subgroup of the AAB group). The term "morphotype" is applied to mutants of base clones that are distinguishable by analyses of morphological and ethnographical-linguistic data, but not by isozyme analysis (e.g., morphotype '*Maoli hai*' of the *maoli* base clone; Stover and Simmonds [1987] usually referred to these as "subclones" or "forms"). "Cultivar" is used to refer to cultivated banana populations at the lowest level of distinguishability by Polynesian farmers, whether these are clones or morphotypes. *Maoli* was thus once a cultivar, but now, after several thousand years of selection by humans, is a base clone from which numerous morphotypes or cultivars have arisen. The original *maoli* clone is presumably now one of the extant *maoli* morphotypes.

Linguistics

Polynesian names are used throughout the paper and are italicized. Hawaiian names are written in accordance with conventions described in Pukui and Elbert (1986). For the Marquesan and Tahitian, where no single convention has been adopted, we gratefully acknowledge the assistance of J. H. Ward of the Indo-Pacific Languages Department of the University of Hawai'i at Mānoa. Cultivar names are capitalized and in single quotes.

Banana and Plantain Collections

Because quarantine regulations restrict interisland and international movement of banana propagules, it was not possible to create a common garden for bananas and plantains in Hawai'i. Morphological variation was assessed primarily through observation of accessions in established collections and in the wild. Most of the Hawaiian collections consisted of bananas collected from remote areas of Hawai'i in the 1950s and 1960s (A. Brash, pers. comm.). Brash's collection, identified by him from Pope (1926), constituted the bulk of what was known about Hawaiian bananas before our work began. Bananas were also observed under cultivation in French Polynesia. Isozyme investigations were conducted on leaves collected fresh (in Hawai'i) or cryogenically preserved (in French Polynesia) from plants in the wild, under cultivation, and in the following established collections:

Hawai'i: University of Hawai'i, College of Tropical Agriculture and Human Resources, Kaua'i Branch Station; Waimea Arboretum and Botanical Garden; Hawaiian Studies Institute Ethnobotanical Garden; Amy B.H. Greenwell Ethnobotanical Garden, B. P. Bishop Museum; and the personal collection of A. Brash, Honolulu, Hawai'i.

French Polynesia: Service de l'Economie Rurale, Station de Recherche Agronomique de Papara, Tahiti. In French Polynesia, 11 islands were surveyed in June and July 1991, six in the Marquesas Islands (Fatu Hiva, Hiva Oa, Nuku Hiva, Tahuata, Ua Huka, Ua Pou) and five in the Society Islands (Huahine, Mo'orea, Ra'iatea, Taha'a, Tahiti). Banana suckers were collected on each island and transferred to the germplasm collection at Papara. Bananas were also studied on Tahiti during 1 day in December 1991.

Isozyme Analysis

Overall, 72 accessions, known under different local names and originating from 14 islands in Eastern Polynesia, were studied for isozyme variation (Table 1). Four enzyme systems, aconitase (ACO), malate dehydrogenase (MDH), phosphoglucose isomerase (PGI), and phosphoglucomutase (PGM), were successfully resolved, and zymograms were scored for each accession. In Hawai'i, freshly collected tissue from the youngest fully extended leaf was ground in modified Bousquet's extraction buffer (Lebot et al. 1991) and subjected to electrophoresis. In French Polynesia, portions of young leaves were rolled and sealed in 1.5-ml microcentrifuge tubes, immersed in liquid nitrogen in the field, and transported in a cryogenic shipping container to the University of Hawai'i at Mānoa, where electrophoretic studies were undertaken. Samples were electrophoresed at 4°C for 7 hr at a constant 15 V/cm. After electrophoresis, the gels were sliced horizontally into four slabs and stained for ACO, MDH, PGI, and PGM (Lebot et al. 1991). Each accession was electrophoresed at least twice to confirm its zymogram.

Chromosome counts were conducted on root tips of Hawaiian cultivars to determine ploidy levels following the technique employed by Lebot et al. (1991).

Ethnographic Inquiry

Observation of live material in both Hawai'i and French Polynesia also involved ethnographic inquiry of Polynesian farmers, garden personnel, and/or other parties thought to possess traditional or modern horticultural knowledge relevant to the bananas in question. Assessment was most complete in Hawai'i, resulting from more than 1 yr of periodic field observation in conjunction with published written descriptions and from a series of interviews with elderly Native Hawaiians and several local banana experts.

TABLE 1

ZYMOTYPES OF MORPHOTYPES STUDIED (INCLUDING SEVERAL RECENT INTRODUCTIONS)

ACCESSION NAME		ORIGIN[a]	MDH	PGM	PGI	ACO	ZYMOTYPE
Prehistoric Polynesian introductions							
Maoli	*a'ea'e*	HSIEG, O'ahu	A	A	A	A	1
	'eka	A. Brash, O'ahu	A	A	A	A	1
	'ele'ele	A. Brash, O'ahu	A	A	A	A	1
	hai	UHBS, Kaua'i	A	A	A	A	1
	iho'ū	UHBS, Kaua'i	A	A	A	A	1
	ka'ualau	UHBS, Kaua'i	A	A	A	A	1
	māhoe	AGEG, Hawai'i	A	A	A	A	1
	mānai'ula	UHBS, Kaua'i	A	A	A	A	1
	maoli	UHBS, Kaua'i	A	A	A	A	1
Mā'ohi	*'ere'ere*	Mo'orea	A	A	A	A	1
	hai	Tahiti	A	A	A	A	1
	hai	Ra'iatea	A	A	A	A	1
	hai	Mo'orea	A	A	A	A	1
	hai	Huahine	A	A	A	A	1
	huapoto	Tahiti	A	A	A	A	1
	matie pa'o	Tahiti	A	A	A	A	1
	pa'arūtia	Ra'iatea	A	A	A	A	1
	pa'arūtia	Tahiti	A	A	A	A	1
	pa'o	Huahine	A	A	A	A	1
	pa'o	Ra'iatea	A	A	A	A	1
	pa'o	Tahiti	A	A	A	A	1
	papa'i	Mo'orea	A	A	A	A	1
	porapora	Taha'a	A	A	A	A	1
	tā'iri	Tahiti	A	A	A	A	1
	teatea	Mo'orea	A	A	A	A	1
	'uo'uo	Taha'a	A	A	A	A	1
Mao'i	*hai*	Nuku Hiva	A	A	A	A	1
	hai	Hiva Oa	A	A	A	A	1
	ko'otea	Nuku Hiva	A	A	A	A	1
	maita	Fatu Hiva	A	A	A	A	1
	moepu'a	Nuku Hiva	A	A	A	A	1
	pe'ehatu	Nuku Hiva	A	A	A	A	1
	tekiteki	Fatu Hiva	A	A	A	A	1
	'umi'umi	Nuku Hiva	A	A	A	A	1
Pōpō'ulu	*ka'io*	AGEG, Hawai'i	A	A	B	A	2
	lahilahi	AGEG, Hawai'i	A	A	B	A	2
	mālei	HSIEG, O'ahu	A	A	B	A	2
	moa	AGEG, Hawai'i	A	A	B	A	2
	no'u	UHBS, Kaua'i	A	A	B	A	2
	'ula'ula	HSIEG, O'ahu	A	A	B	A	2
Po'u	*hu'amene*	Tahiti	A	A	B	A	2
Po'upo'u		Nuku Hiva	A	A	B	A	2
Iholena	*ha'a*	AGEG, Hawai'i	A	B	A	C	3
	kāpua	A. Brash, O'ahu	A	B	A	C	3
	lele	HSIEG, O'ahu	A	B	A	C	3
	'ula'ula	HSIEG, O'ahu	A	B	A	C	3
	iholena	A. Brash, O'ahu	A	B	A	C	3
'Ōre'a	*'ute'ute*	Tahiti	A	B	A	C	3
		Tahiti	A	B	A	C	3
Hāpai		A. Brash, O'ahu	C	D	C	C	4
Mai'a hapū		Tahiti	C	D	C	C	4

TABLE 1 (continued)

ACCESSION NAME		ORIGIN[a]	MDH	PGM	PGI	ACO	ZYMOTYPE
Era of introduction uncertain							
Mai'a 'oa		A. Brash, O'ahu	B	C	D	C	5
Poro'ini	*hinuhinu*	Tahiti	E	E	E	A	6
	pa'a	Ra'iatea	E	E	E	A	6
	papa'i	Ra'iatea	E	E	E	A	6
	rehu	Tahiti	E	E	E	A	6
	rehu	Ra'iatea	E	E	E	A	6
	'uo'uo	Tahiti	E	E	E	A	6
	'uo'uo	Ra'iatea	E	E	E	A	6
Poro'ini		Nuku Hiva	E	E	E	A	6
Poro'ini		Hiva Oa	E	E	E	A	6
	pime	Fatu Hiva	E	E	E	A	6
	pivai	Nuku Hiva	E	E	E	A	6
Poro'ini	*fe'i*	Hiva Oa	D	F	F	A	7
Poro'ini	*fe'i*	Fatu Hiva	D	F	F	A	7
Poro'ini	*fe'i*	Ra'iatea	D	F	F	A	7
Poro'ini	*fe'i*	Tahiti	D	F	F	A	7
'Ōre'a	*nīnamu*	Tahiti	C	G	C	B	8
	'uo'uo	Tahiti	C	G	C	B	8
	'uo'uo	Huahine	C	G	C	B	8
	'uo'uo	Ra'iatea	C	G	C	B	8

[a] HSIEG: Hawaiian Studies Institute Ethnobotanical Garden; AGEG: Amy Greenwell Ethnobotanical Garden; UHBS: University of Hawaii Branch Station.

RESULTS

Morphotypes of the Hawaiian base clones *maoli* (Figure 1) and *pōpō'ulu* (Figure 2) were found on all islands visited. In French Polynesia, *maoli* is known as *mā'ohi* (Society Islands) and *mao'i* (Marquesas Islands), and *pōpō'ulu* as *po'u* (Society Islands) and *po'upo'u* (Marquesas). Both are recognized as Polynesian introductions, but in Tahiti *po'u* is often considered to be a *mā'ohi* morphotype and not a distinct base clone.

Nor is the base clone *iholena* (Figure 3) as coherent in the Society and Marquesas islands as it is in Hawai'i. Farmers were unfamiliar with the Hawaiian term, and only two probable *iholena* plants were sighted in French Polynesia (V.L., pers. obs.), the authenticity of which was later confirmed by isozyme analysis. One of these was called *'ōre'a* by a farmer on Presqu'ile, Tahiti, and the second, growing in the germplasm collection at Papara, Tahiti, was labeled *'ōre'a 'ute'ute*. In Tahiti, the folk category *'ōre'a* is poorly known and ill-defined, and farmers judge it to be unimportant in French Polynesia. Two of the several bananas that were classed in the *'ōre'a* category proved to have zymotypes identical to triploid *M. acuminata* (AAA) cultivars, and were thus unrelated to *iholena*. One of these appears to be the cultivar 'Leyte', probably originating in the Philippines (Tezenas du Montcel, pers. comm.). Because 'Leyte' has not been found elsewhere in the Pacific (Lebot et al. 1993), it is unlikely to be a Polynesian introduction in Tahiti.

Another ambiguous clone that is very popular today among French Polynesian farmers is *poro'ini* (ABB). A robust plantain, it is tolerant of drought and salt and is possibly the same as 'Bluggoe' in Hawai'i and *pata* in Samoa. Farmers, however, claim that *poro'ini* is a Polynesian introduction, and its differentiation into seven morphotypes seems to support this.

Poro'ini fe'i has been demonstrated to be an entirely different cultivar. It is robust and high yielding, with an enormous male bud and drooping leaves, and it appears to be highly resistant to black leaf streak. Fruits are angular with thick, dark green skin, and the flesh

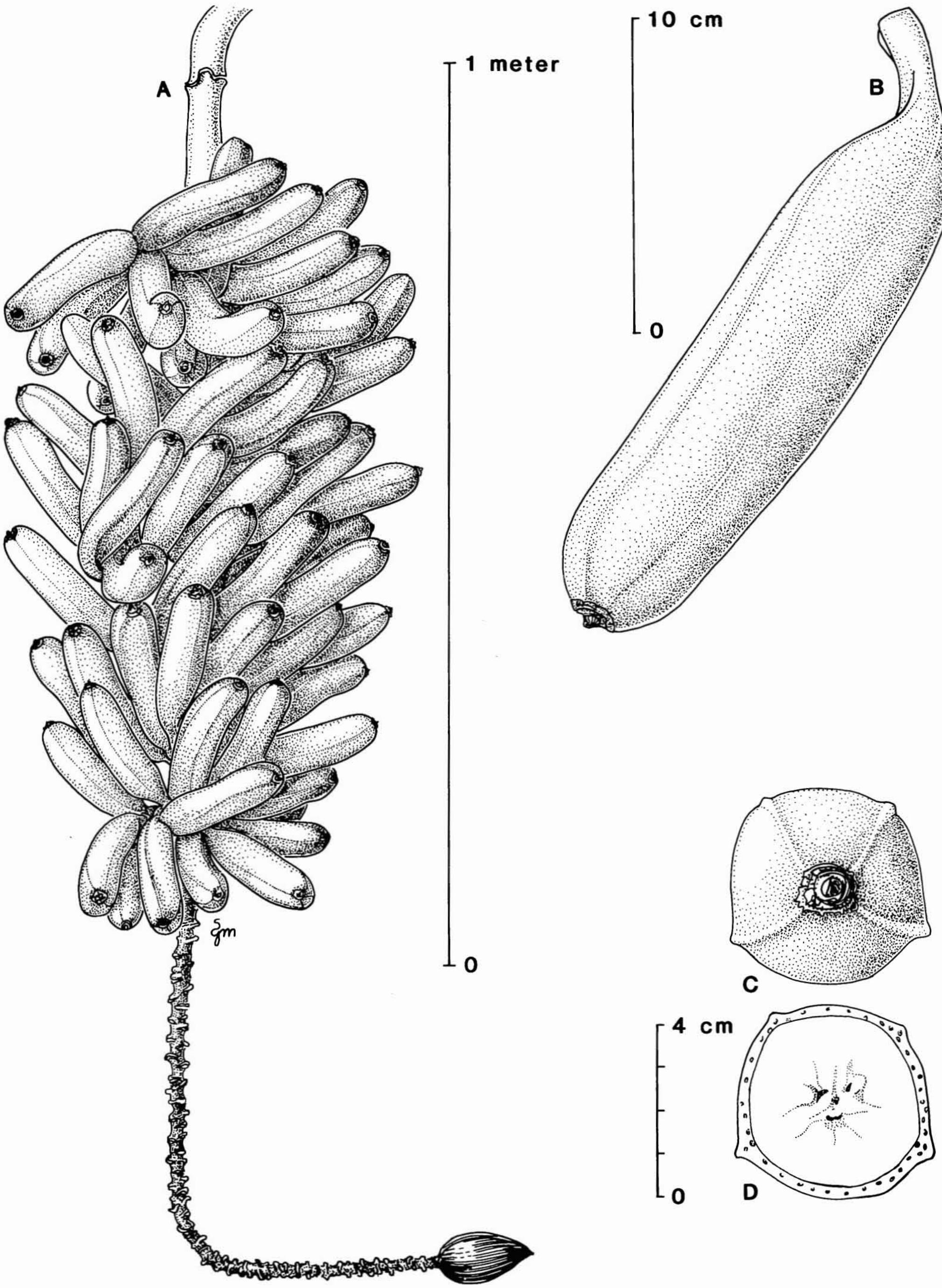


FIGURE 1. *Maoli. A*, fruit bunch. *B*, individual fruit. *C*, fruit, stylar end view. *D*, fruit, cross section.

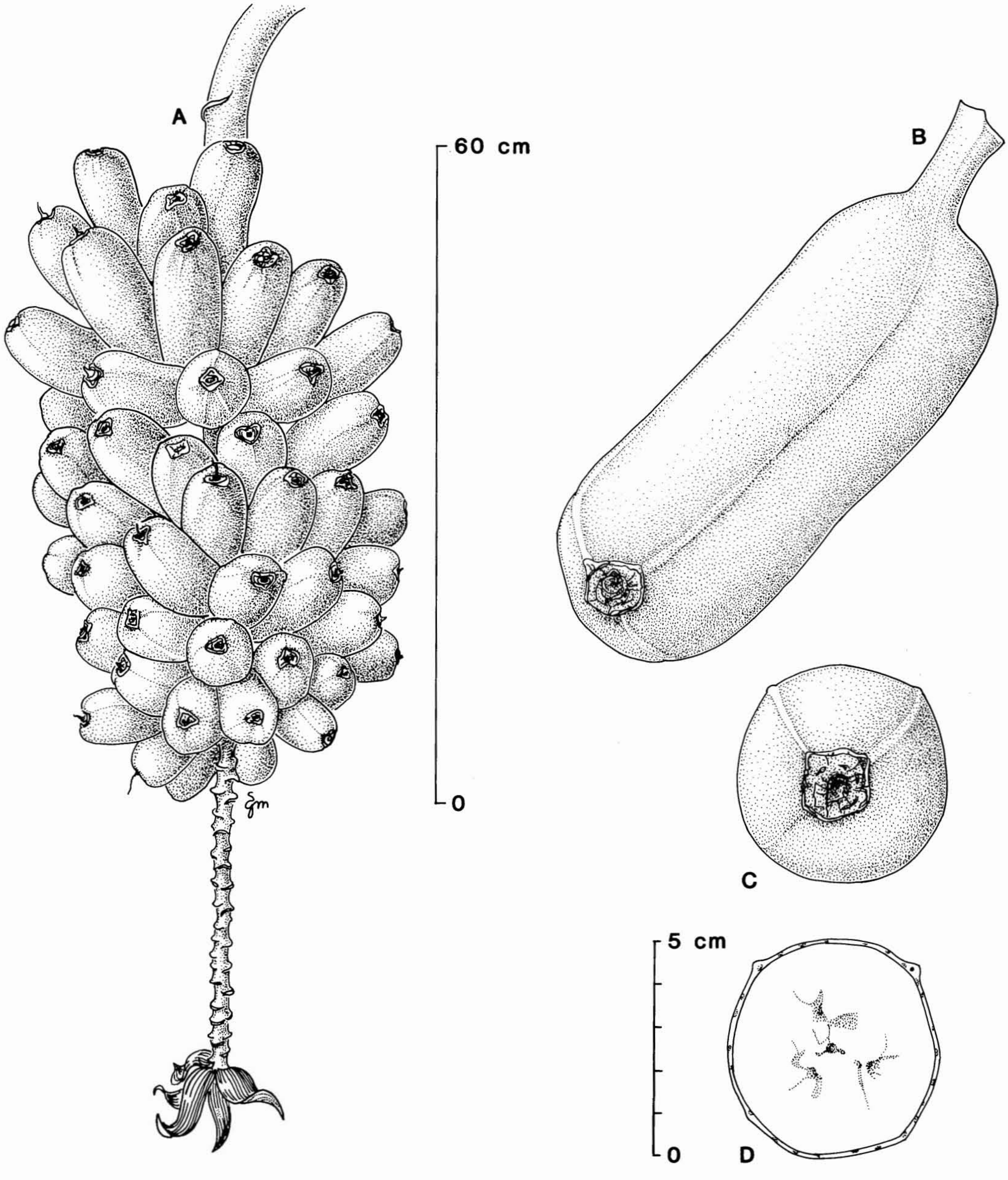


FIGURE 2. *Pōpō'ulu*. *A*, fruit bunch. *B*, individual fruit. *C*, fruit, stylar end view. *D*, fruit, cross section.

turns deep yellow-orange when baked. It is possibly the same as *fa'i pata tonga* recorded by Daniells (1990) in Western Samoa. Its zymotype (Table 1) corresponds to 'Giant Kalapua' of Papua New Guinea (Lebot et al. 1993), which has been described as a possible ABBB tetraploid (cover photo, INIBAP 1990).

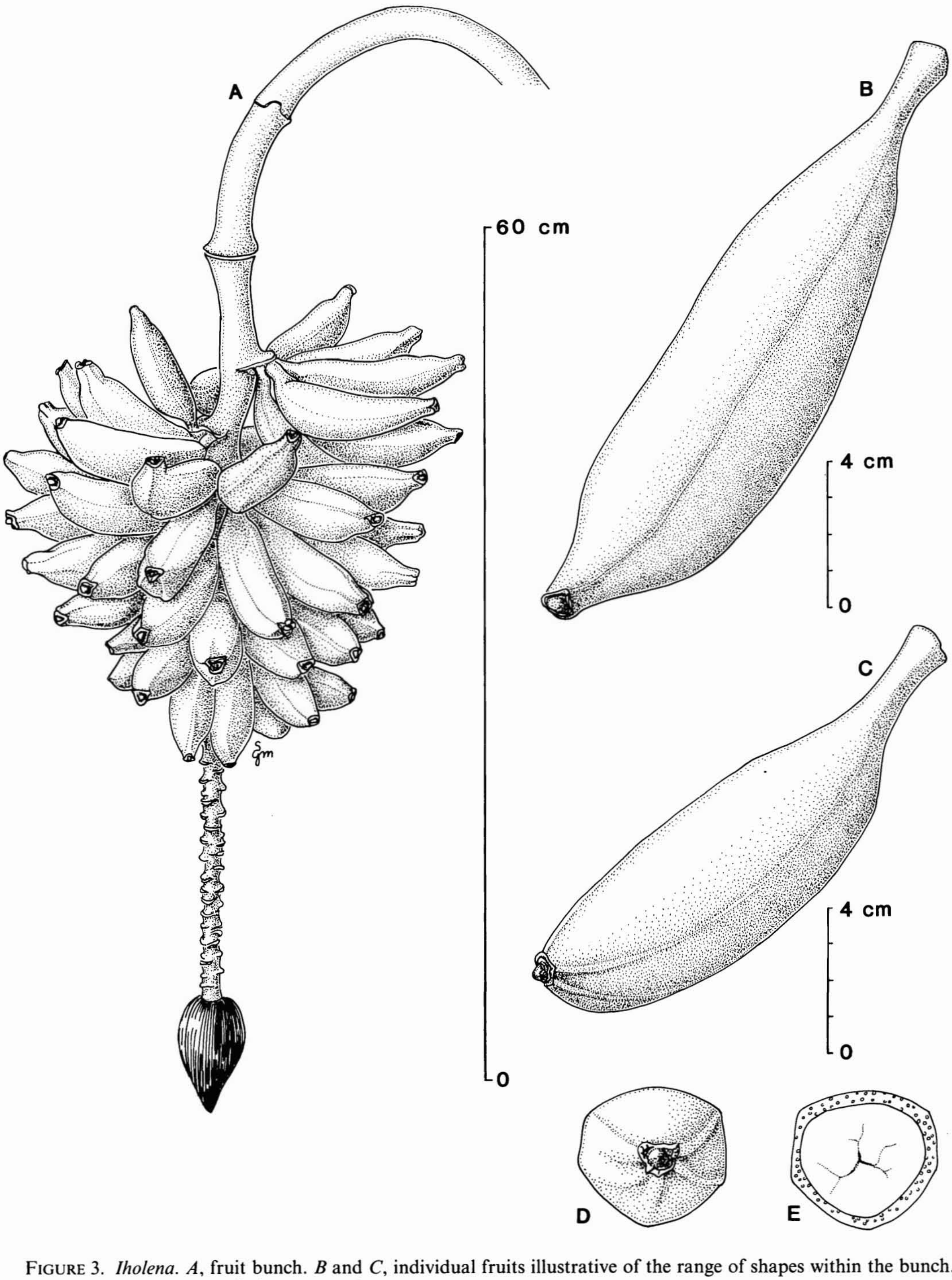


FIGURE 3. *Iholena*. *A*, fruit bunch. *B* and *C*, individual fruits illustrative of the range of shapes within the bunch. *D*, fruit, stylar end view. *E*, fruit, cross section.

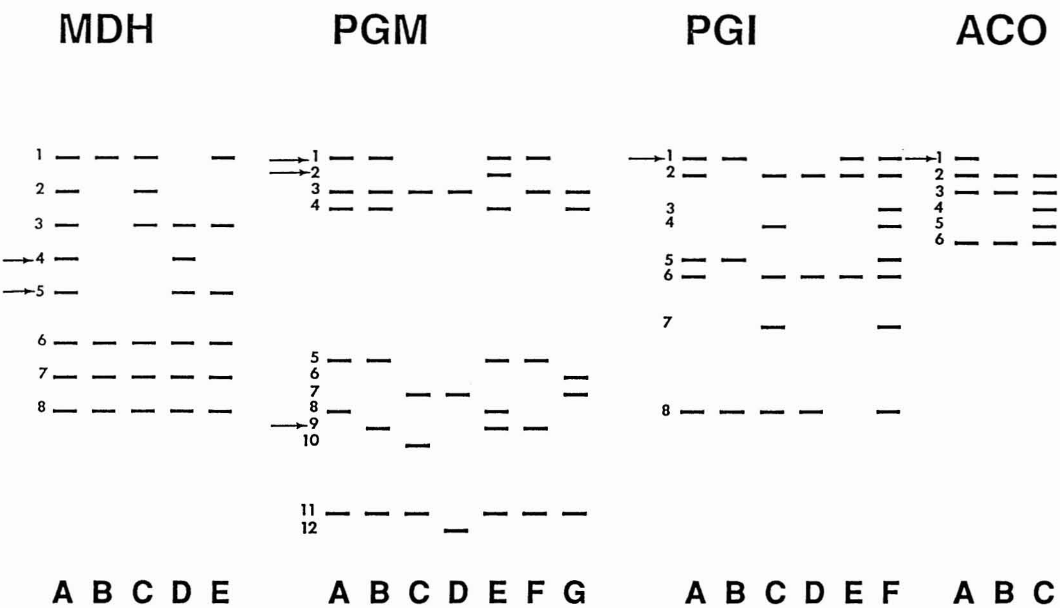


FIGURE 4. Zymograms of MDH, PGM, PGI, and ACO in Eastern Polynesian bananas. Individual bands (electromorphs) within enzyme systems are numbered from most anodic (+) to most cathodic (−) (bands with the same number in different enzyme systems do not necessarily share the same electrophoretic mobility). Arrows indicate bands specific to *M. balbisiana*.

Isozyme Fingerprinting

The different zymograms obtained for each enzyme system are presented in Figure 4. The complete zymotypes of all accessions are presented in coded form in Table 1.

A total of eight zymotypes were identified in the Eastern Polynesian materials suspected of being prehistoric in origin: *maoli* / *mā'ohi* / *mao'i* (1), *pōpō'ulu* / *po'u* / *po'upo'u* (2), *iholena* / *'ōre'a* (AAB) (3), '*Hāpai*' / *hapū* (4), '*Mai'a 'oa*' (5), *poro'ini* (6), *poro'ini fe'i* (7), and *'ōre'a* (AAA) (8). With the exception of the heterogeneous *'ōre'a* category, morphotypes within base clones proved to have identical zymograms for the four enzyme systems studied (Table 1). Morphotypes of *maoli*, *pōpō'ulu*, *iholena*, and *poro'ini*, and the apparent 'Giant Kalapua' or *poro'ini fe'i*, display species-specific electromorphs of both *M. acuminata* and *M. balbisiana*, and thus are species hybrids (Table 1 and Figure 4). '*Mai'a 'oa*' and '*Hāpai*' bananas have only *M. acuminata* electromorphs. Chromosome counts conducted on root tips have shown that *maoli*, *pōpō'ulu*, and *iholena* are triploids with 2n = 3x = 33 chromosomes, and '*Hāpai*' is a parthenocarpic diploid with 2n = 2x = 22 chromosomes. '*Mai'a 'oa*', identified as *M. acuminata* ssp. *zebrina*, produced quantities of germinable seed and is therefore presumed to be diploid.

Morphological Variation

Base clones and morphotypes that we believe to be Polynesian introductions into Eastern Polynesia are presented in a simple morphological classification (Table 2). Sixteen morphotypes of the base clone *maoli*, eight of *pōpō'ulu*, and five of *iholena*, as well as '*Hāpai*' are recognized. Descriptions are limited to the most distinctive morphological features, involving mostly pseudostem, bunch, and fruit characters. Names are provided in Hawaiian (H), Marquesan (M), and Tahitian (T). Several bananas described above ('*Mai'a 'oa*',

TABLE 2

DESCRIPTIVE CLASSIFICATION OF EASTERN POLYNESIAN EUMUSA BANANAS

1. *maoli* (H), *mao'i* (M), *ma'ohi* (T)
Long fruits with rounded tips, not uniformly aligned within the hands, asymmetrical and disorganized bunch arrangement, long pedicels, large bunches, thick heavy skin, yellow flesh (Figure 1).

1.1. '*Maoli a'ea'e*'; syn.: *koa'e*, *manini* (H)
Variegated plant, leaves, and fruit (chloroplast chimera) (Plate I*A*).

1.2. '*Maoli 'eka*' (H)
Brownish red immature fruits, reddish tinge to the ovaries, soft fibers in outer sheaths of pseudostem.

1.3. '*Maoli 'ele'ele*'; syn.: *poni*, *hinupua'a* (H), *'ere'ere*, *iri mo'o* (T)
Pseudostem, petioles, midribs, and young fruits mostly black (Plate I*B*).

1.4. '*Maoli hai*'; syn.: *haikea* (H), *ko'otea*[a], *maita* (M), *'uo'uo*, *teatea* (T)
Silvery, waxy bloom over green parts of the plant (Plate I*C*).

1.5. '*Maoli iho'ū*' (H)
Small bunch, early degenerating male axis, blunt-tipped fruits.

1.6. '*Maoli ka'ualau*' (H)
Dark green immature fruits speckled with light green spots.

1.7. '*Maoli māhoe*'; syn.: *pālua* (H)
Double-bunch, rachis divides into two (or more) stems, small fruits (Plate I*D* and Figure 5*B*, *C*).

1.8. '*Maoli mānai'ula*'; syn.: *mālei'ula*, *mālai'ula* (H)
Reddish bronze immature fruits, red ovaries, strong fibers in outer sheaths of pseudostem.

1.9. '*Maoli puhi*' (H)
Long, flattened, sometimes serpentine young fruits, twisted leaf tips.

1.10. '*Maoli*'[b] (H), *hai* (T)
Red blush on the pseudostem.

1.11. '*Mā'ohi pa'arūtia*' (T)[c]
Small bunch, early degenerating male axis, blunt-tipped and black-spotted fruits.

1.12. '*Mā'ohi pa'o*'; syn.: *matie pa'o* (T)
Black patches on the pseudostem and base of petioles.

1.13. '*Mao'i moepu'a*' (M)
Fruits produce very slimy, foamy sap.

1.14. '*Mao'i papa'i*' (M); syn.: *porapora* (T)
Fruits with striped, necrotic skin.

1.15. '*Mao'i pe'ehatu*' (M); syn.: *'umi'umi*, *tā'iri* (T)
Fully developed fruits need to be squeezed in hands to ripen.

1.16. '*Mao'i tekiteki*' (M); syn.: *hu'apoto* (T)
Short, very thick, dark green fruits.

2. *pōpō'ulu* (H), *po'upo'u* (M), *po'u* (T)
Short, blunt, thick fruits, round in cross section, fruits set at right angles to the rachis, thick skin, male axis degenerating early, light salmon-colored flesh (Figure 2).

2.1. '*Pōpō'ulu ka'io*' (H)
Usually at least six hands (though often fewer) of up to 12 fruits, arched, at right angles to the rachis, prominent floral scar on fruit (Figure 5*D*).

2.2. '*Pōpō'ulu lahilahi*' (H)
Thin-skinned fruits.

2.3. '*Pōpō'ulu mālei*' (H)[d]
Reddish black pigmentation on upper surface of midrib base.

2.4. '*Pōpō'ulu moa*'; syn.: *huamoa* (H)
Usually no more than one hand of three to six short, thick fruits, skin splits at maturity (Plate I*E* and Figure 5*E*).

2.5. '*Pōpō'ulu no'u*' (H)
Short, heavy, thick pseudostem.

2.6. '*Pōpō'ulu 'ula'ula*' (H)[e]
Reddish pseudostem, midribs, and petioles (Plate I*F*).

2.7. '*Po'upo'u*' (M)
Small bunches, small fruits with dark green skin.

2.8. '*Po'u huamene*'; syn.: *tāmene* (T)
Medium bunches loosely arranged, large fruits, light green pseudostem and fruit skin.

3. *iholena* (H), *'ōre'a* [AAB] (T)
Angular fruits, tapering toward the tip, fruits set at right angles to the reddish rachis and bunched in the middle of it; thick skin, salmon-colored flesh (Figure 3).

TABLE 2 (continued)

3.1. '*Iholena ha'a*'; syn.: *ha'aha'a* (H)
Dwarf plant, mature leaves lose their copper color on the underside of the lamina (Plate I*G*).
3.2. '*Iholena kāpua*'; syn.: *puapuanui* (H)
Cylindrical fruits, variably filled to the tip, uniformly thick pseudostem (Figure 5*F*).
3.3. '*Iholena lele*' (H)
Very long rachis, three to six hands of angled fruits tapering toward the tip, compactly arranged on the bunch, tall, slender pseudostem.
3.4. '*Iholena 'ula'ula*' (H)[e]; syn.: *'ōre'a* [AAB], *'ōre'a 'ute'ute* (T)
Reddish pseudostem, midribs, and petioles (Plate I*H*).
3.5. '*Iholena*'[b]; syn.: *hilahila* (H)
Fruits tapering toward the tip, with prominent nipple.
4. '*Hāpai*' (H); syn.: *hapū* (T)
Medium to small bunch size, four to six hands, fruits tapering toward the tip, uniformly aligned within the hands, bunch often emerges through the side of the pseudostem (Figure 5*A*).

[a] Of the Marquesan banana terms we present here, *ko'otea, mao'i, pe'ehatu*, and *po'upo'u* are found in both Dordillon (1931–1932) and Brown (1931); *tekiteki* is found in Dordillon, but not in Brown, though *uekiteki* is found in Brown and may be a misprint; *maita* and *papa'i* are not found in either as referential terms for bananas.

[b] In Hawai'i, the *maoli* and *iholena* base clones each contain one morphotype polysemously named '*Maoli*' (Table 2, 1.10) and '*Iholena*' (Table 2, 3.5), respectively. Although these lack the usual descriptive modifying term, they are valid morphotypes, distinct from others of their respective base clones. The absence of modifying terms here might imply priority of introduction in Hawai'i, but this could not be independently verified.

[c] *Rūtia*, meaning "Russian," is a loan word of recent introduction into Tahitian (J. H. Ward, pers. comm.). Nevertheless, the banana labeled by this term presented a *mā'ohi / maoli* zymotype.

[d] '*Pōpō'ulu mālei*', which we retain here with considerable reservation, is an ambiguous morphotype. Late nineteenth- and early twentieth-century Hawaiian banana researchers did not cite or describe it, and possible naming confusion with '*Maoli mānai'ula*', *mālai'ula*, or *mālei'ula* has not been addressed. No adequate written description currently exists. Nevertheless, several contemporary Hawaiian banana experts insist on this cultivar's legitimacy, and morphological features of plants in current collections seem to fit the cursory description of Handy (1940) and Pukui and Elbert (1986).

[e] The names for cultivars '*Pōpō'ulu 'ula'ula*' and '*Iholena 'ula'ula*' could not be found in the older published literature, even though the morphotypes they label do not appear to be recent introductions to Hawai'i. The two terms are now in common usage among Hawaiian banana experts. A. Brash claims that the term '*Iholena 'ula'ula*', clumps of which he found growing wild in several locations over 30 yr ago, was spontaneously coined in his presence by Marie Neal, a well-known Bishop Museum researcher. Origin of the term '*Pōpō'ulu 'ula'ula*' is unknown. Detailed morphological description or finer laboratory fingerprinting techniques may show that '*Pōpō'ulu 'ula'ula*' is the same as *hopa* red, a *pōpō'ulu* morphotype believed to have been introduced in recent historic times around La'ie, O'ahu, by Tongan Mormans.

'ōre'a [AAA], *poro'ini*, and *poro'ini fe'i*) are not included because of our uncertainty about their status as Polynesian introductions.

Figure 5 shows the distinctive features of the minor cultivar '*Hāpai*' (*A*) and remarkable morphotypes of the three principal base clones (*B–F*). Plate I (*A–H*) illustrates several morphotypes that are striking examples of somatic mutations, including dwarf habit, pigmentation, waxy cuticle, and fruit bunch variants.

DISCUSSION AND CONCLUSIONS

The great amount of genetic variation in domesticated bananas has arisen from three sources: (1) sexual recombination within and between the original parent species, (2) ploidy level differences, and (3) somatic mutations. Major differentiation into groups, subgroups, and clones occurred early in the history of banana domestication through intra- and interspecific hybridization. These sexual processes established the type and number of genomes present in different bananas, before sterility had become an effective barrier to gene flow. As fertility declined, because of human selection for seedless fruit among triploids and partially sterile hybrids, further genetic change was limited to minor variations caused by somatic mutations. Mutations affecting traits of economic or horticultural interest, such as pigmentation, dwarfing, or fruit/bunch size, were selected from base clones by farmers and multiplied by vegetative propagation, constituting morphotypes.

The Eastern Polynesian bananas illustrate

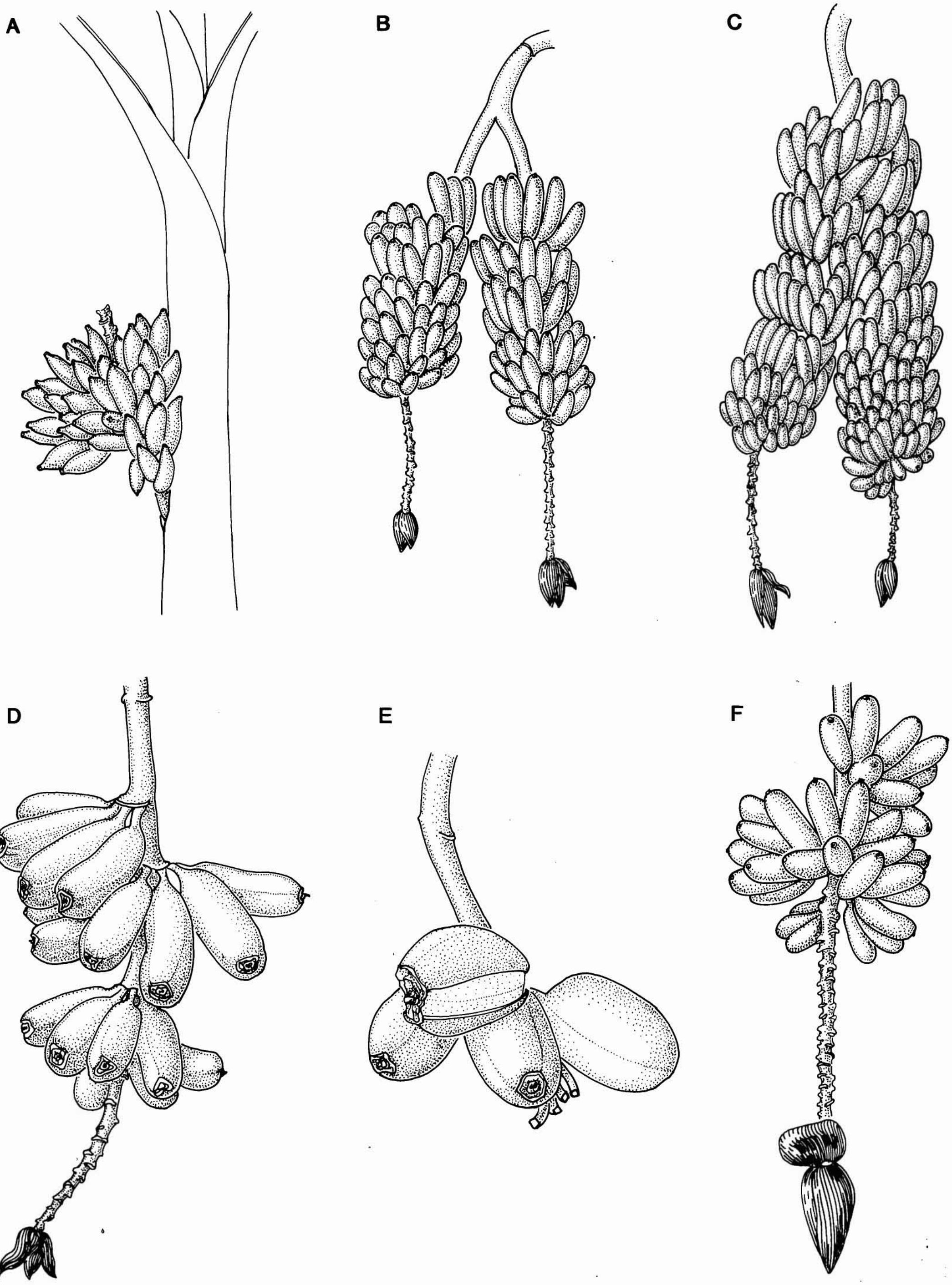


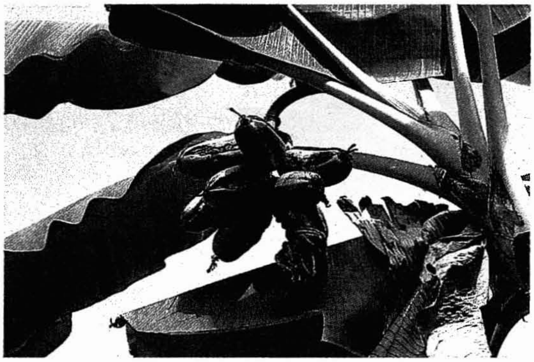
FIGURE 5. Fruit bunch variants of the Eastern Polynesian bananas. *A*, '*Hāpai*'. *B*, '*Maoli māhoe*' *pālua*. *C*, '*Maoli māhoe*'. *D*, '*Pōpō'ulu ka'io*'. *E*, '*Pōpō'ulu moa*'. *F*, '*Iholena kāpua*'.

A

B

C

D



E

F

G

H

PLATE I. *A*, *'Maoli a'ea'e'*. *B*, *'Maoli 'ele'ele'*. *C*, *'Maoli hai'*. *D*, *'Maoli māhoe'*. *E*, *'Pōpō'ulu moa'*. *F*, *'Pōpō'ulu 'ula'ula'*. *G*, *'Iholena ha'a'*. *H*, *'Iholena 'ula'ula'*.

of Eastern Polynesia. Good germplasm collections now exist in Hawai'i and Tahiti, in part as a result of this work, and these should be protected and maintained.

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